RAFFLES BULLETIN OF ZOOLOGY Supplement No. **37**: 1–365
Date of publication: 6 February 2023
DOI: 10.26107/RBZ-2023-0006
http://zoobank.org/urn:lsid:zoobank.org:pub:B7C2B81F-A624-409D-9B01-8E34227E927C

A zoeal atlas of selected xanthoid crabs and allied superfamilies, with reference to Heterotremata (Crustacea: Brachyura: Eubrachyura) larval characters

Paul F. **Clark**

Abstract. For the present study, 60 first-stage zoeas of representative Heterotremata (Crustacea: Brachyura: Eubrachyura) species from the Xanthoidea MacLeay, 1838, and related superfamilies such as Aethroidea Dana, 1851, Bellioidea Dana, 1852, Dairoidea Serène, 1965, Eriphioidea MacLeay, 1838, Pilumnoidea Samouelle, 1819, Portunoidea Rafinesque, 1815, and Pseudocarcinoidea P.K.L. Ng & Davie, 2020, were dissected, illustrated, described, and where appropriate, comments were made on previous zoeal descriptions with character differences being tabulated. The majority of zoeas were collected in the field and hatched in the laboratory from ovigerous specimens, while the remainder were made available by various colleagues and scientific institutions. Twenty-eight zoeas are described for the first time and thirty-two are redescribed to include a comparative table from previous accounts. This is followed by a discussion on zoeal character states and their possible phylogenetic relationships with respect to heterochrony.

Key words. Decapoda, first stage zoea, descriptions, illustrations, zoeal character states, heterochrony

CONTENTS

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ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

INTRODUCTION

All brachyuran zoeal stages are adapted to the same habitat, a planktonic existence, and setal patterns are consequently subject to the same selection pressures. Differences between larvae may therefore reflect the phylogeny-based genotypic relationships. Consequently, producing an accurate and authoritative account of zoeal larval stages is essential. Many institutions have invested in laboratory facilities for rearing decapod larvae and success in rearing all developmental stages is now commonplace. This is a significant advance for descriptive studies that lay the foundation for many aspects of research from correct identification of planktonic samples to reconstructing phylogenetic relationships. Advantages of rearing, other than positive identification of the species, include collection of all life cycle stages in a relatively short period of time and the provision of sufficient specimens for detailed morphological studies. Reliable data is everything and setotaxy must be founded on high quality observations and interpretation. A good high-powered microscope is fundamental in these studies if setal ambiguities are to be resolved. Brachyuran first stage zoea of congeneric species appear to have virtually identical setotaxy (Christiansen, 1973; Clark, 1983, 1984; Ng & Clark, 2000). This similarity appears to provide a degree of predictability within a taxon, however, setal differences (incongruence) within a group is not indicative of systematic compatibility and, instead, they suggest incorrect assignment of taxa.

Sixty first stage zoeas of selected Heterotremata (Crustacea: Brachyura: Eubrachyura) species were collected in the field and hatched in the laboratory from ovigerous specimens or made available by various colleagues and scientific institutions for this atlas. These larvae were dissected, illustrated and described, with comments on morphology where appropriate, for the present study. Twenty-seven first zoeas are described for the first time and a further 33 are redescribed. For these species, a comparative table from previous accounts is included. This is followed by a discussion on zoeal characters. These are either descriptive and lack phylogenetic information or represent the linear evolutionary steps towards gradual loss of characters as postulated by heterochrony, an evolutionary change in character development as shown between an ancestor and its descendant (McKinney & McNamara, 1991).

MATERIAL AND METHODS

The systematics of this study follows P.K.L. Ng et al. (2008) and Mendoza et al. (2022). Abbreviations used: Institut de Recherche pour le Developpement = IRD, Instituto de Investigaço das Pescas e do Mar in Lisbon, Portugal = IPIMAR, Natural History Museum of Los Angeles, Los Angeles, United States = LACM, Museo Nacional de Ciencias Naturales de Madrid, Spain = MNCN, National Museum of Natural History, Washington = USNM, National Museum of New Zealand = NMNZ, The Natural History Museum, London = NHM, National Taiwan Ocean University, Keelung, Taiwan = NTOU, Rijksmuseum van Natuurlijke Historie = RMNH, Ryukyu University Museum, Fujukan, Okinawa = RUMF, Senckenberg Museum, Frankfurt-am-Main = SMF, Silla University, Korea = SUZ, Zoological Reference Collection of the Raffles Museum, National University of Singapore (now the Lee Kong Chian Natural History Museum) = ZRC, collected = coll., prezoea = PZ, first stage zoea, second stage zoea, etc. = ZI, ZII, etc., megalop = Meg., crab = Cr., number = no., registration = reg., Self Contained Underwater Breathing Apparatus = SCUBA.

Material examined. *Acantholobulus bermudensis* (Benedict & Rathbun, 1891): coll. P.F. Clark, 06 May 1997, south side of Fort Pierce Inlet, west end of Causeway Island, St. Lucie County, Fort Pierce, Florida, United States, hatched 10 May 1997. [not registered]

Acantholobulus schmitti (Rathbun, 1930): coll. February 1988, from mussel bank located between Pontal do Poço and the Baguaçu River in the Paranaguá Estuary, Paraná, Brasil, pres. Monica Montú. [not registered]

Actaea areolata (Dana, 1852): coll. P.F. Clark & P.K.L. Ng, 27 July 2003, Balicasag Island, Philippines, hatched 09 August 2003. [not registered]

Actaeodes mutatus Guinot, 1976: coll. P.F. Clark, 30 July 2003, Buyong, Maribago, Mactan Island, Cebu Island, Philippines, hatched 06 August 2003, reg. no. ZRC 2003.0278.

Actumnus elegans De Man, 1887: coll. P.K.L. Ng by dredge ca. 15 m, 21 November 1986, Pulau Ayer Chawan, Singpore, hatched 22 November 1986, reg. no. ZRC 1998.70.

Aethra scruposa (Linnaeus, 1764): coll. S.H. Wu, June 2002, Longtong, NE Taiwan, hatched 14–15 July 2002, reg. no. ZRC 2003.0295.

Banareia subglobosa (Stimpson, 1858): coll. D.G.B. Chia, T.M. Sin, R. Teo & A. Wang, 12 September 1994, Johore Shoal, 01°19′02″N, 104°03′13″E, Singapore, hatched 19 September 1994, reg. no. ZRC 1995.353.

Chaceon quinquedens (Smith, 1879): coll. H. Perkins, February 1971, 300 fms (548.64 m), Baltimore Canyon area of the continental shelf, 37°56′N, 73°55′W, off Delaware Bay, Delaware, United States, hatched 10 May 1971. [not registered]

Cryptopilumnus changensis (Rathbun, 1909): coll. P.K.L. Ng, 30 December 1986, Pulau Tekukor, Singapore, reg. no. ZRC 1998.72.

Cymo lanatopodus Galil & Vannini, 1990: coll. P.F. Clark & B.S. Galil by SCUBA, 4 m, 09 May 1995, Trou aux Biches, Mauritius, hatched 24 May 1995. [not registered]

Cymo melanodactylus Dana, 1853: coll. P.F. Clark & B.S. Galil by SCUBA, 4 m, 09 May 1995, Trou aux Biches, Mauritius, hatched 24 May 1995. [not registered]

Dacryopilumnus rathbunae Balss, 1932: coll. P.K.L. Ng, 30 May 1998, Okinawa, Japan. [not registered]

Daira perlata (Herbst, 1790): coll. H. Ping-Ho & L. Hung-Chang, 09 January 2000, Kenting, Pingtung, Taiwan, hatched 24 January 2000. [not registered]

Dyspanopeus sayi (Smith, 1869): coll. P.F. Clark, R.B. Manning, K. Reed & J. Clark, 13 May 1997, night collection with hand net through “grass” north side of Harbor Branch, off Indian River Lagoon, St. Lucie

County, Florida, United States, hatched 21 May 1997. [not registered]

Epiactaea nodulosa (White, 1848): coll. D. Lane, Southern Islands, Singapore, reg. no. ZRC 1995.331.

Eriphia smithii MacLeay, 1838: coll. S.S. Hashmi, Buleji Rocks, Native Jetty, Manora Island, Karachi, Pakistan, reg. no. NHM 1986:908.

Etisus anaglyptus H. Milne Edwards, 1834: coll. P.K.L. Ng, Sentosa reefs, Singapore, reg. no. ZRC 1985.1855.

Etisus frontalis (Dana, 1852): coll. P.K.L. Ng, July 2001, Guam. [not registered]

Etisus utilis H. Jacquinot in H. Jacquinot & Lucas, 1854: coll. P.F. Clark by SCUBA, 07 December 1998, Chenal des 5 miles, au sud du récif Niagi, 22°23′S, 166°45.37′E, Nouvelle-Calédonie, hatched 17 December 1998. [not registered]

Eurycarcinus integrifrons De Man, 1879: coll. 09 February 1993, North of Jubail Saudi Arabia, hatched 10 February 1993, reg. no. SMF 23481.

Eurypanopeus depressus (Smith, 1869): coll. P.F. Clark & S. Reed, 21 April 1997, Jack Island, Indian River Lagoon, St. Lucie County, Florida, United States, hatched 28 April 1997. [not registered]

Eurytium limosum (Say, 1818): coll. P.F. Clark, 03 July 1997, Macau, Brasil, hatched 08 July 1997, reg. no. NHM 2001.119.

Garthiope barbadensis (Rathbun, 1921): coll. J.K. Reed by SCUBA, lockout diving, 19 May 1977, R/V *Sea Diver*, 80 m, Jeff's Reef, 27°32.8′N, 79°58.8′W, 27 km north east of Fort Peirce, St. Lucie County, Florida, United States, hatched 01 June 1977, reg. no. Harbor Branch Museum ID 89:4614.

Geryon longipes A. Milne-Edwards, 1882: coll. by trawling, 1208–1210 m, R/S García del Cid, 18 March 1994, 41°01′N, 2°16′E, western Mediterranean, off Barcelona, Spain. The adult female and the larvae are deposited in the Biological Collections of Reference of the Institut de Ciències de Mar (CSIC) in Barcelona.

Glabropilumnus edamensis (De Man, 1888): coll. P.K.L. Ng, 1981, Sentosa Reef, Singapore, reg. no. ZRC 1983.1128.19–68.

Harrovia albolineata Adams & White, 1849: coll. D. Vandenspiegel, May 1992, Singapore, reg. no. ZRC 2000.91.

Heteropanope glabra Stimpson, 1858: coll. P.K.L. Ng, 23 March 2000, Lim Chu Kang mangrove, Singapore, hatched 25 March 2000. [not registered]

Heteropilumnus holthuisi P.K.L. Ng & L.W.H. Tan, 1988: coll. P.K.L. Ng, intertidal area, East Coast, Singapore, under rocks, hatched 27 May 1982. [not registered]

Heterozius rotundifrons A. Milne-Edwards, 1867: coll. R.G. Wear, Whangaroa Harbour, Mangonui Estuary North, Auckland, New Zealand, November 1965, reg. no. NMNZ CR 3087.

Hexapanopeus paulensis Rathbun, 1930: coll. by otter trawl, 6–8 m on sandy bottom, near Ubatuba, 23°26′S, 45°05′W, São Paulo, Brasil, July 1989. [not registered]

Hypothalassia armata (De Haan, 1835): coll. A. Gerbault, Nouvelle-Calédonie. [not registered]

Lachnopodus subacutus (Stimpson, 1858): coll. P.F. Clark & P.K.L. Ng, 27 July 2003, Balicasag Island, Philippines, hatched 08 July 2003, reg. no. ZRC 2003.0282.

Leptodius sanguineus (H. Milne Edwards, 1834): Aldabra Island, hatched March 1968, no further details. [not registered]

Liomera bella (Dana, 1852): coll. P.K.L. Ng, January 2003, intertidal area, Maipalaoa Beach, near Maili Point, Maili, Waianae Coast, Hawaii, United States. [not registered]

Liomera cinctimana (White, 1847): coll. P.K.L. Ng, July 2001, Guam. [not registered]

Liomera loevis (A. Milne-Edwards, 1873): coll. P.F. Clark & P.K.L. Ng, 05 May 2000, beach reef, Ao Tang Khaen, Phuket, hatched 17 May 2000. [not registered]

Macromedaeus crassimanus (A. Milne-Edwards, 1867): coll. P.F. Clark, 27 July 2003, Balicasag, Philippines, hatched 09 August 2003. [not registered]

Medaeops granulosus (Haswell, 1882): coll. P.K.L. Ng, 22 May 1982, Singapore, reg. no. ZRC 1985.1861.

Menippe mercenaria (Say, 1818): coll. P.F. Clark by potting, 21 April 1997, off Link Port, Smithsonian Marine Station, Harbor Branch Oceanographic Institute, Off Indian River Lagoon, St. Lucie County, Florida, United States, hatched 26–27 April 1997. [not registered]

Menippe nodifrons Stimpson, 1859: coll. L. Scotto, 05 June 1977, from a sabellarid worm reef at Seminole Shores, Martin County, Florida, United States, hatched 26 June 1977, reg. no. Harbor Branch Museum I.D. 89:4156.

Menippe rumphii (J.C. Fabricius, 1798): coll. K.L. Yeo, 08 May 2000, East Coast Park, Singapore, hatched 21 May 2000. [not registered]

Myomenippe hardwickii (Gray, 1831): coll. P.F. Clark, S. Sothi, & G. Lee et al., 13 May 2000, Sungei Mandai Kechil mangrove, off Western Johor Straits, Singapore, hatched 19 May 2000. [not registered]

Novactaea bella Guinot, 1976: coll. P.F. Clark & P.K.L. Ng, 27 July 2003, Balicasag Island, Philippines. [not registered]

Ozius truncatus H. Milne Edwards, 1834: North Island, New Zealand, 1964, reg. no. NMNZ Cr. 2494, 3071.

Panopeus americanus de Saussure, 1857: coll. P.F. Clark, 03 May 1997, south side, Fort Pierce Inlet, Fort Pierce, St. Lucie County, Florida, United States, hatched 09 May 1997. [not registered]

Panopeus harttii Smith, 1869: coll. P.F. Clark, 30 April 1997, by dredging, 30 m, R/V *Sunburst*, off Bethel Shoals, 27°40′N, 80°06′W, Florida, United States, hatched 03 May 1997. [not registered]

Panopeus occidentalis de Saussure, 1857: coll. P.F. Clark, 03 May 1997, south side, Fort Pierce Inlet, Fort Pierce, St. Lucie County, Florida, United States, hatched 06 May 1997. [not registered]

Panopeus simpsoni Rathbun, 1930: coll. P.F. Clark, 04 May 1997, Jack Island, Indian River Lagoon, St. Lucie County, Florida, United States, hatched 16 May 1997. [not registered]

Parapanope euagora De Man, 1895: coll. P.K.L. Ng, 1985, shallow water in fishermen nets, East Coast of Singapore. [not registered]

Pilumnus kempi Deb, 1987: shore at Buleji, Karachi, Pakistan, 15 November 1986, hatched 29 November 1986; reg. no. ZRC 1991.305–313.

Pilumnus ohshimai Takeda & Miyake, 1970: coll. P.K.L. Ng, January 1982, Sentosa reefs, Siloso Beach, Singapore, hatched 15 January 1982. [not registered]

Pilumnus spinifrons P.K.L. Ng & L.W.H. Tan, 1984: coll. P.F. Clark, P.K.L. Ng, C. McLay & P. Castro, 12 May 2000, dredging, southern islands, Singapore, hatched 19 May 2000. [not registered]

Platypodiella spectabilis (Herbst, 1794): coll. T.L. Zimmerman & J.W. Martin, 14 July 2000, North Beach, Guana Island, British Virgin Islands, hatched 14 July 2000, reg. no. LACM CR 2000006.

Psaumis cavipes (Dana, 1852): coll. P.F. Clark & P.K.L. Ng, 29 July 2003, west of Alona Beach, Panglao Island, Philippines, hatched 06 August 2003, reg. no. ZRC 2003.0287.

Pseudactea corallina (Alcock, 1898): coll. P.F. Clark & P.K.L. Ng, 27 July 2003, Balicasag Island, Philippines, hatched 28 July 2003, reg. no. ZRC 2003.0276.

Pseudocarcinus gigas (Lamarck, 1818): coll. C. Gardener, 300–380 m, off the east coast of Tasmania, 41°17′S, 148°40′E, June 1995, reg. no. NHM 1999.1195.

Rhithropanopeus harrisii (Gould, 1841): coll. J. Paula, August 1998, Beaufort, North Carolina, United States. [not registered]

Xantho hydrophilus (Herbst, 1790): coll. R.W. Ingle & J. Paula, 08 June 1988, Mira Estuary, Portugal, reg. no. NHM 2000.1907.

Xantho pilipes A. Milne-Edwards, 1867: coll. J. Paula, July 1989, by SCUBA, 10 m, crater of Guia Mount, Faial Island, Azores, reg. no. IPIMAR AdS10/1991.

Xantho poressa (Olivi, 1792): coll. A. Rodríquez, 14 June 1995, El Chato Beach, Cádiz, Gulf of Cádiz, Spain, hatched 16 June 1995, reg. no. MNCN 20.04/3627.

Collection of samples. For the majority of the species listed above, ovigerous crabs were collected and just held in seawater (artificial seawater was not used) until the first stage zoea had hatched. The zoea were then preserved in alcohol. Large species like *Etisus utilis* were aerated with a diffuser stone. Air was gently bubbled through the water so that the aeration would not deposit the hatching zoea around the rim of the container, killing them before they could be preserved. Females were collected by SCUBA diving, from the intertidal zone by hand, and trawling at various depths. Some females were transported long distances to Singapore by air, but this did not appear to affect their hatching in the laboratory. Females were not fed while in captivity because remaining food fragments tended to decay in the containers and could cause fungal or bacterial infections of the eggs which may halt development and cause them to be dropped from the pleopods. If the crabs were held over a long period of time (over a week) the water was changed. If the water is not changed, the eggs can become contaminated by excretion from the female and they then fail to develop and hatch.

Preparation of larvae. The zoea were dissected using tungsten needles (0.2 mm or 0.36 mm gauge) sharpened by electrolysis in potassium hydroxide inserted into an aluminum alloy needle holder. A brass chuck grips the tungsten needle.

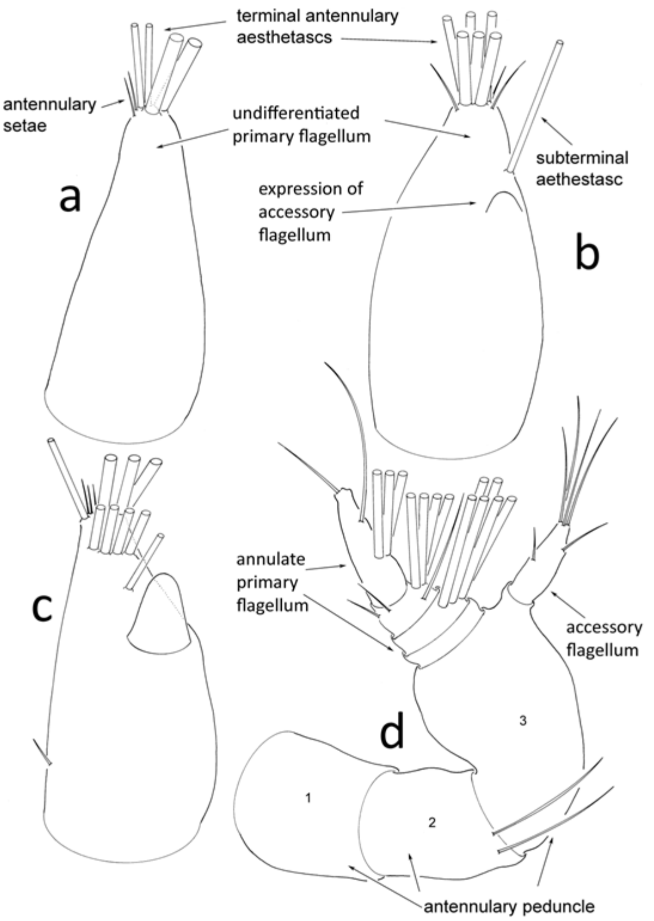

Fig. 1. Antennulary morphology; a, ZI; b, ZII; c, ZIII; d, megalopa.

Dissections of larvae were carried out in polyvinyl lactophenol dropped onto a glass slide under a Leica MZ16 and the appendages allowed to clear for 24 h before examination. Cover-slips were sealed with clear nail varnish. Appendages were drawn using an Olympus BH-2 microscope equipped with differential interference contrast (DIC) and a camera lucida. Any setal ambiguities such as the number of setae and aesthetascs on the antennule were resolved using a Zeiss Axioskop or a Leica DMR HC microscope each with DIC.

Description of appendages. Boxshall (2004) has challenged the traditional description of the malacostracan antennule developing from a uniramous appendage to a biramous structure with endopod and exopod. Instead, he proposes two basic arthropod limb types, uniramous antennules and biramous postantennulary limbs. According to Boxshall, the malacostracan antennule is uniramous, possesses intrinsic muscles, but lacks differentiation into protopod and endopod (or telopod as preferred by Boxshall). The traditionally termed antennulary endopod and exopod are devoid of intrinsic musculature and have undergone annulation, not segmentation. Consequently, the biramous antennule is in fact biflagellate. The terminology biramous is considered inappropriate for the antennule, and instead of exopod and endopod, the terms primary and accessory flagella should be used (Boxshall et al., 2010; Boxshall & Jaume, 2013). The primary flagellum bears the sensory setae called aesthetascs (Fig. 1). The terms primary and accessory flagellum are followed here.

In contrast, the postantennulary appendages, which include the antenna, mandible, maxillule, maxilla, maxillipeds, pereiopods, and the pleopods, were regarded by Boxshall as fundamentally derived from a biramous limb possessing a distinct protopod with an endopod and exopod distally. The endopod and exopod have intrinsic musculature and were consequently considered to be articulated and not annulations.

The sequence of the zoeal descriptions was based on the malacostracan somite plan and described from anterior to posterior (Fig. 2). Appendage/pereiopod segments are referred to as "articles" (a term first proposed by H. Milne Edwards, 1834 and recently used by Clark & Cuesta, 2015). Setal armature of appendages was described from proximal to distal articles and endopod first, then exopod (Clark et al., 1998a; Clark & Cuesta, 2015). The long antennular aesthetascs, the antennal protopod, the long plumose natatory setae of the first and second maxillipeds, and the tips of the enlarged telsonal fork were drawn truncated. The mandible is not fully described or illustrated because the only significant character of this appendage is considered to be the appearance of the palp in the zoeal phase. The approximate measurement of the antennal endopod (for its ratio with the protopod) was made from its base to the tip. Arrangements of setae on the same article are separated by a plus sign, e.g., basis with 10 setae arranged 2+2+3+3, compared with those on different articles by a comma, e.g., endopod comprising 5 articles with 3,2,1,2,5 setae (Clark & Cuesta, 2015).

CEPHALOTHORAX	CEPHALON	eye	Acron		BODY SOMITES
		antennule	1	1	
		antenna	2	2	
		mandible	3	3	
		maxillule	4	4	
		maxilla	5	5	
	PEREION	1st maxilliped	1	6	
		2nd maxilliped	2	7	
		3rd maxilliped	3	8	
		1st pereiopod (cheliped)	4	9	
		2nd pereiopod	5	10	
		3rd pereiopod	6	11	
		4th pereiopod	7	12	
		5th pereiopod	8	13	
	PLEON	1st pleopod*	1	14	
		2nd pleopod	2	15	
		3rd pleopod	3	16	
		4th pleopod	4	17	
		5th pleopod	5	18	
		6th pleopod (uropod)	6	19	
	telson with anal orifice				
	*1st pleopod not expressed (absent) in zoeal and megalop phases described in the present study.				

Fig. 2. A schematic diagram of the body somites and appendages of a brachyuran larva. Note the 1st pleopod is not expressed in brachyuran larvae until the metamorphosis to 1st crab stage.

Illustrations. With respect to illustrating larval appendages, the figures presented here were first drawn in pencil via a camera lucida attached to the microscope. Consideration was given to the final size of the published figures because in some cases these can appear so small that setae cannot be easily checked. The purpose of the figures is to illustrate the text and they remain universally informative regardless of language. Layout for illustrations is also important and drawings should be as large as possible to fit on a page; the less space between figures on the same page the better and this improves final image size of the appendages. A scale bar was inserted close to the figure of the original appendage pencil drawing, so that both can be later enlarged to an appropriate size for the plate using a photocopier. The enlarged photocopy was then used to produce the final illustration and the scale bar remained in proportion. The enlarged photocopies were "inked in" by copying them onto Canson® A3 size tracing paper of 110/115 g in weight. This weight of tracing page allowed errors to be erased using a sharp flat blade. Later, however, the whole plate was scanned into a bitmap format at 400 dpi and edited using Adobe Photoshop. In this format, scale bars could be re-drawn at right angles to the page and figure letters inserted. Long setae were drawn truncated to enable some appendages to be enlarged still further. When 'inking in' appendages, the setae were arranged in their natural orientation and care was taken to avoid crossing setae because this could lead to "blacking out" in the final reproduction. Further, drawing many setules on a seta can also lead to "blacking out" and consequently, fewer were drawn. Different pen sizes were used to ink in the figures, setules were 0.18 mm; setae = 0.2 mm; and the main outline of the appendage was 0.3–0.4 mm. To help create the 3D effect of the drawing, small gaps were made where lines crossed, the upper line being continuous. The drawing of long lines was assisted by a ruler if straight or by flexi/French curve if not.

In order to facilitate comparison between larvae, all the different development stages of an appendage were drawn from the same aspect. If drawing several zoeal stages, consideration should be given to arranging all the same developing appendages on one page, i.e., all the maxillules together and so on. This is sometimes difficult for the appendages of the megalop because these are usually much larger than those of the last zoeal stage and as such could be separated onto a page of their own. The sequence and arrangement of illustrations attempted to follow the text descriptions, starting with drawings of the carapace followed by appendages progressing from anterior to posterior, although the telson was figured with the maxillule and the maxilla for convenience because this illustration was difficult to add to those of the dorsal and lateral views of the pleon.

The drawing process, from microscope to achieving the final product after editing in Photoshop, is extremely time consuming. “Inking in” one page of figures took between 2–3 h, if not more, depending on the appendages concerned. In future, the use of a drawing tablet could considerably reduce the time factor and the frustration of having to maintain inking pens!

TAXONOMIC ACCOUNT

Section Eubrachyura Saint Laurent, 1980

Subsection Heterotremata Guinot, 1977

Superfamily Aethroidea Dana, 1851

Family Aethridae Dana, 1851

Aethra scruposa (Linnaeus, 1764)

(Figs. 3–6)

Description of Zoea I.

CARAPACE (Fig. 3a): dorsal spine slightly curved distally, relatively long, nearly twice that of rostral spine length; rostral spine longer than antennal protopod length, without distal spinulation; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 3a): sessile.
Antennule (Fig. 3b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length + 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 3c): uniramous; protopodal process distally bilaterally spinulate, shorter than rostral spine length; endopod spine absent; exopod ca. 36.5% length of protopod, possessing 2 (1 long subterminal+1 terminal) setae plus elongated spine.
Mandible: palp absent.
Maxillule (Fig. 4a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 2 subterminal + 4 terminal setae; exopod seta absent.
Maxilla (Fig. 4b): biramous; coxal endite bilobed with 5+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 5a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 5b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 6a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 4c, 6a, b): each fork long, gradually curved distally, not spinulate, 1 long lateral spine, 1 smaller lateral spine, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate spines.

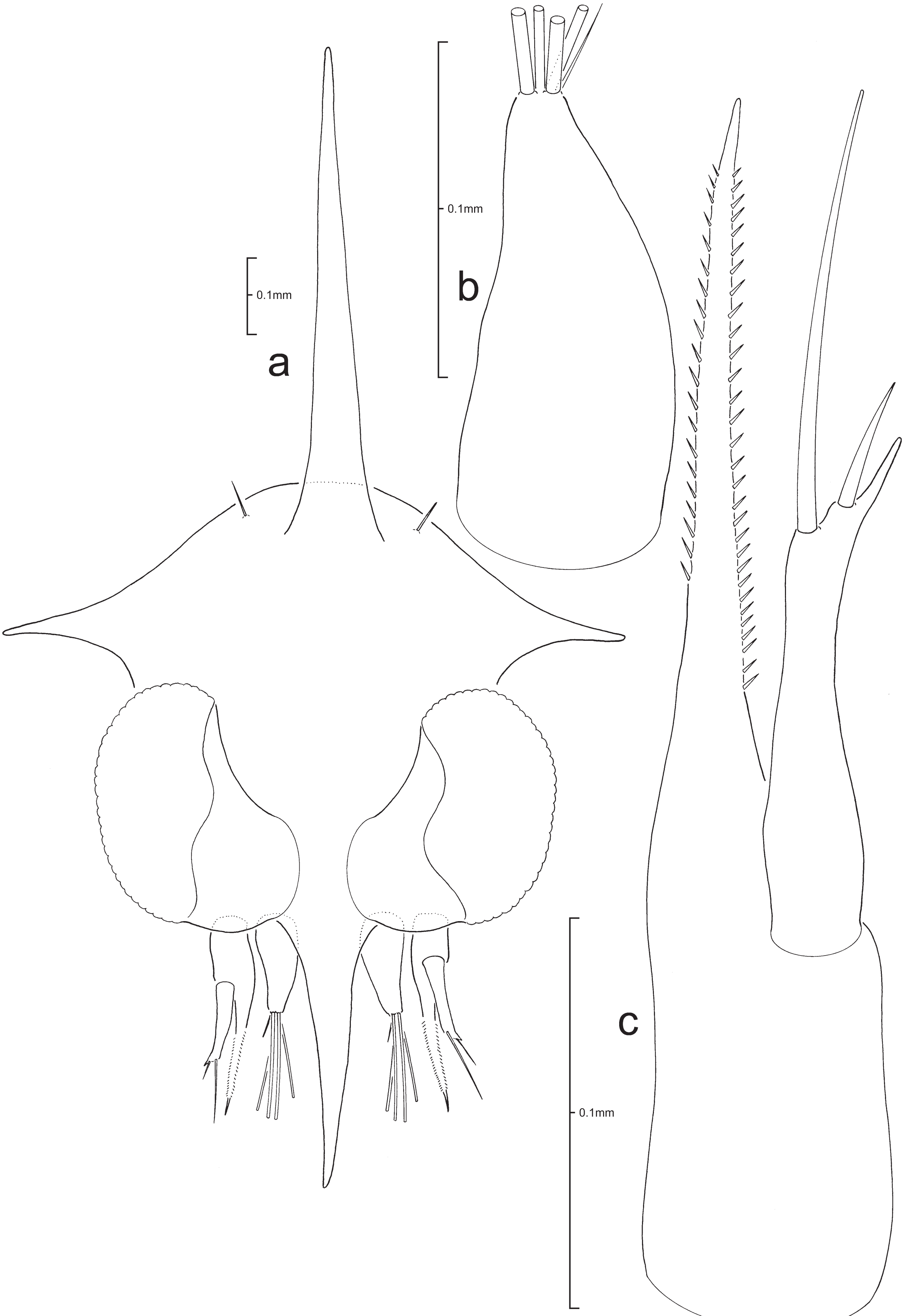

Fig. 3. *Aethra scruposa* (Linnaeus, 1764), ZI: a, anterior view of carapace; b, antennule; c, antenna.

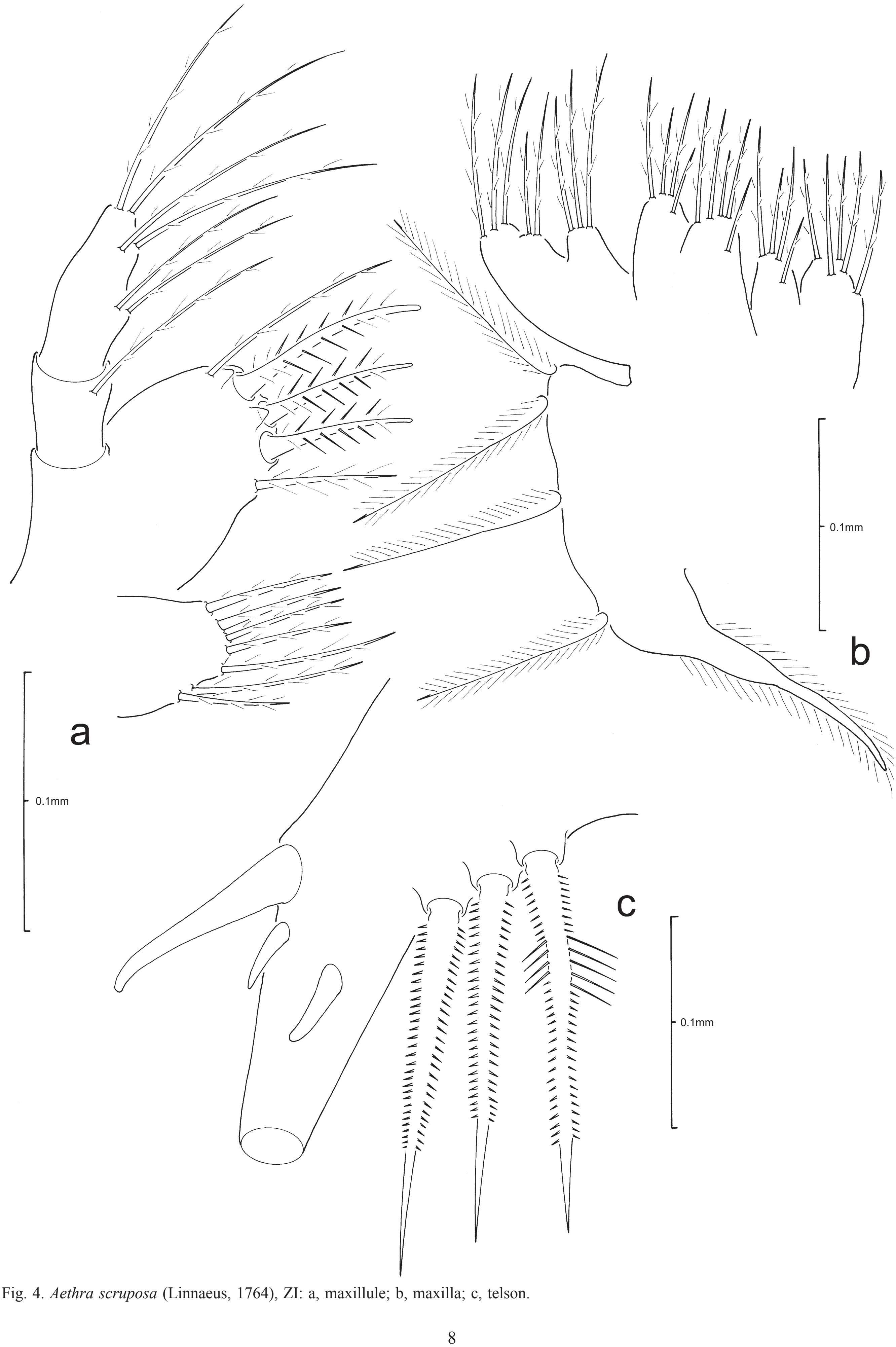

Fig. 4. *Aethra scruposa* (Linnaeus, 1764), ZI: a, maxillule; b, maxilla; c, telson.

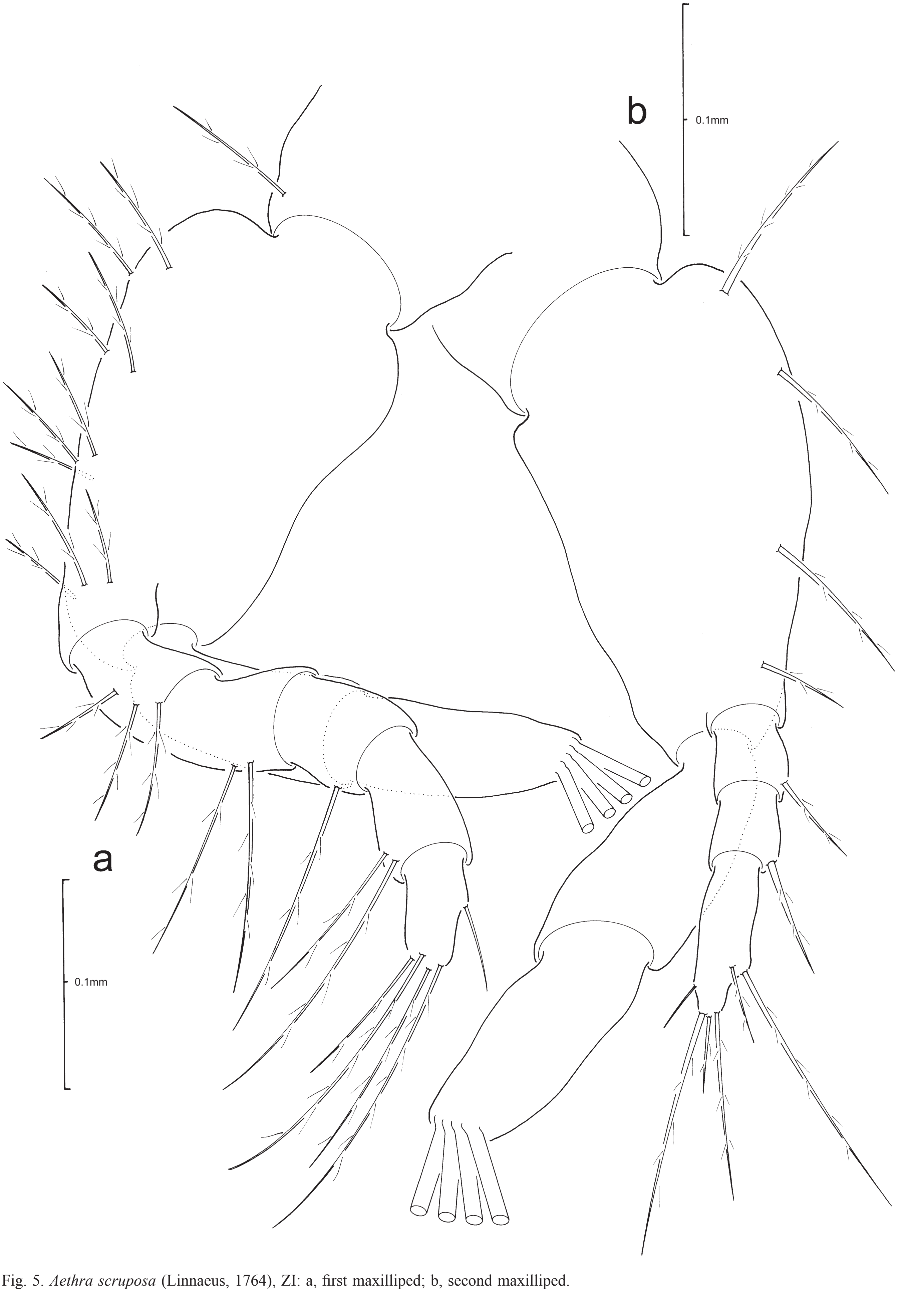

Fig. 5. *Aethra scruposa* (Linnaeus, 1764), ZI: a, first maxilliped; b, second maxilliped.

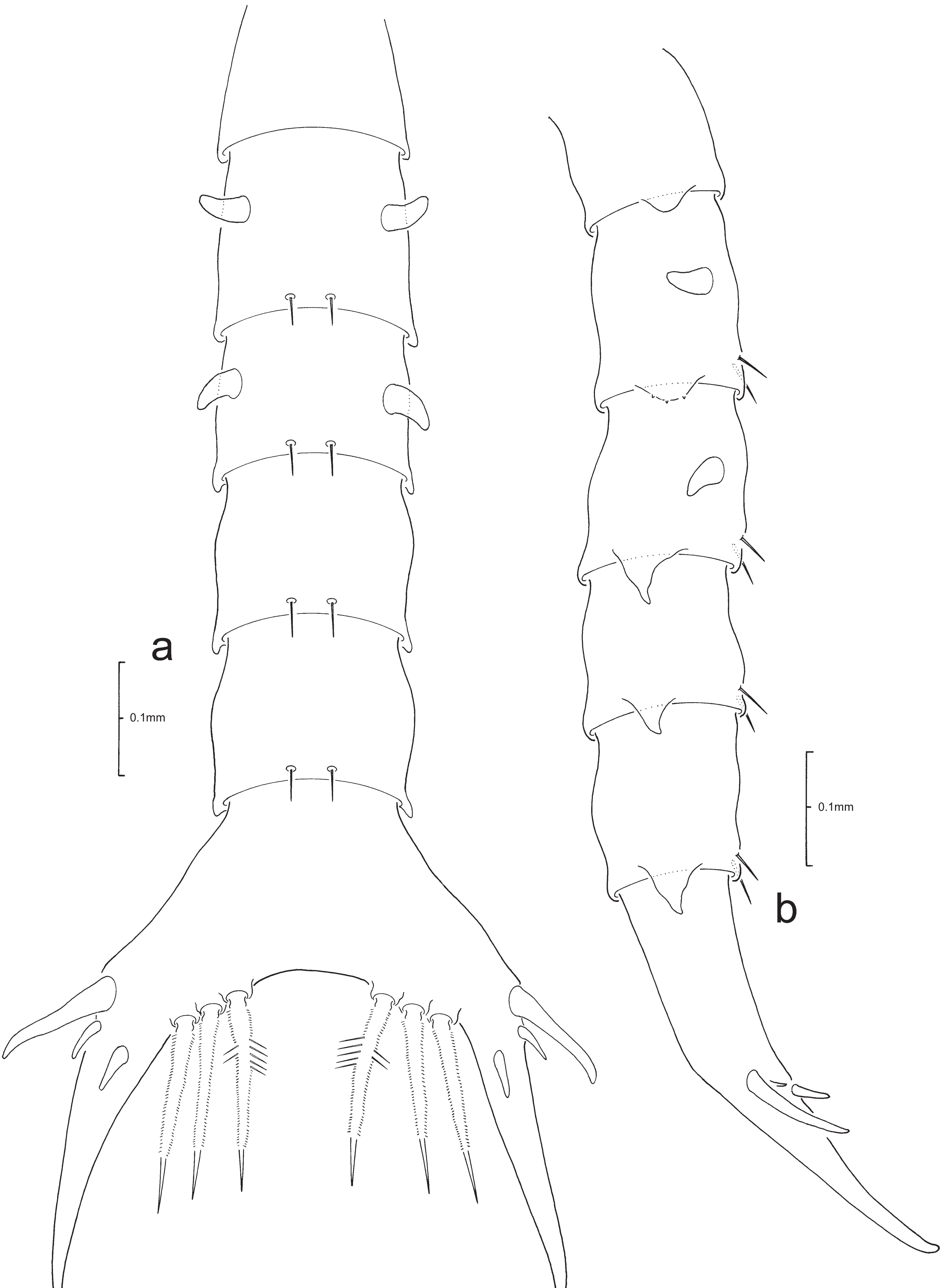

Fig. 6. *Aethra scruposa* (Linnaeus, 1764), ZI: pleon and telson; a, dorsal view; b, lateral view.

Superfamily Bellioidea Dana, 1852

Family Belliidae Dana, 1852

Heterozius rotundifrons A. Milne-Edwards, 1867
(Figs. 7–10)

Heterozius rotundifrons. Wear, 1965: text-fig. 6H (ZI); 1968: 294, figs. 1–25 (ZI–II, Meg.); Wear & Fielder, 1985: 56–58, figs. 146–149 (ZI, Meg.).

Description of Zoea I.
CARAPACE (Fig. 7a): dorsal spine long, curved distally, longer than rostral spine length; rostral spine much shorter than antennal protopod length, without distal spinulation; lateral spines curved ventrally and without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 7a): sessile.
Antennule (Fig. 7b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 2 terminal setae; accessory flagellum absent.
Antenna (Fig. 7c): biramous; protopodal process distally laterally spinulate, much longer than rostral spine length; endopod present; exopod ca. 14.8% length of protopod.
Mandible: palp absent.
Maxillule (Fig. 8a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 8b): biramous; coxal endite bilobed with 3+4 setae; basial endite bilobed with 7+7 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 9a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 9b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,2,7 (3 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped (Fig. 10c): present; biramous with epipod.
Pereiopods (Fig. 8d): present; uniramous; cheliped bilobed.

PLEON (Fig. 10a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 with 1 seta; pleomeres 2–5 each with 1 pair of posterodorsal setae; posterior margin of pleomeres 2–5 spinulate; pleopod buds present, uniramous, without endopods.

TELSON (Figs. 8c, 10a, b): each fork long, spinulate, gradually curved distally, lateral spines absent, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Remarks. According to Wear (1968) the larval development of *H. rotundifrons* comprises two zoeal stages and a megalop. The first stage zoea has hatched at an advanced state of development and includes the expression of the following characters, the antennal endopod, a biramous third maxilliped with epipod, pereiopods with a bilobed chela and uniramous pleopods. Three other characters may be considered to be in a state of advanced development: the expression of two setae on the primary antennular flagellum, 6+6 setae on the basial endites of the maxilla, and a medial seta of the first pleomere. The presence of two setae on the second endopodal article of the second maxilliped is possibly a unique zoeal character.

Table 1. A comparison between the ZI of *Heterozius rotundifrons* A. Milne-Edwards, 1867 by Wear (1965, 1968), Wear & Fielder (1985), and the present study.

Character	**Wear (1965)**	**Wear (1968)**	**Wear & Fielder (1985)**	**Present study**
CARAPACE	text-fig. 6H	figs. 1, 2	figs. 146, 147	Fig. 7a
posterodorsal setae	absent	1 pair present	1 pair present	1 pair present
ANTENNULE	text-fig. 6H	figs. 1, 3	fig. 146	Fig. 7b
terminal setation	3 long aesthetascs & 1 seta	2 long & 2 shorter aesthetascs	2 long & 2 shorter aesthetascs	4 long (2 broad, 2 slender) terminal aesthetascs of unequal length, 2 terminal setae of unequal length
ANTENNA	text-fig. 6H	fig. 1	fig. 146	Fig. 7c
endopod	absent	absent	absent	present
MAXILLA	not figured or described	fig. 6	not figured or described	Fig. 8b
coxal setation		2+4		3+4
basial setation		8+8		7+7
scaphognathite (exopod)		6 setae		4 setae + 1 long distal stout process
FIRST MAXILLIPED	text-fig. 6H	fig. 7	fig. 146	Fig. 9a
basial setation	absent	8 (2+2+2+2)	6 (2+2+2) ?	10 (2+2+3+3)
endopod setation	1,1,1,2,2 terminal ?	3,2,1,2,5 (1 subterminal+4 terminal)	?,2,1,2,5 (1 subterminal+4 terminal)	3,2,1,2,5 (1 subterminal+4 terminal)
SECOND MAXILLIPED	text-fig. 6H	fig. 7	fig. 146	Fig. 9b
basial setation	absent	4 (1+1+1+1)	3 (1+1+1)?	4 (1+1+1+1)
endopod articulation	4	4	4	3
endopod setation	1,1,1,3	1,2,2,5 (2 subterminal+3 terminal)	1,2,2,5 (2 subterminal+3 terminal)	1,2,7 (3 subterminal+4 terminal)
PLEON	text-fig. 6H	figs. 1, 2	figs. 146, 147	Fig. 10a, b
pleomere 1; setation	absent	fig. 1, pair of posterodorsal; Text p. 301, 2 or 3	1 pair of posterodorsal	1 medial seta
pleomere 2 with dorsolateral processes	absent	1 pair	1 pair	1 pair
pleomeres 2–5; setation	absent	1 pair of posterodorsal setae on pleomeres 2–4; absent from pleomere 5 ?	1 pair of posterodorsal setae on pleomeres 2–4; absent from pleomere 5 ?	1 pair of posterodorsal setae on each pleomere

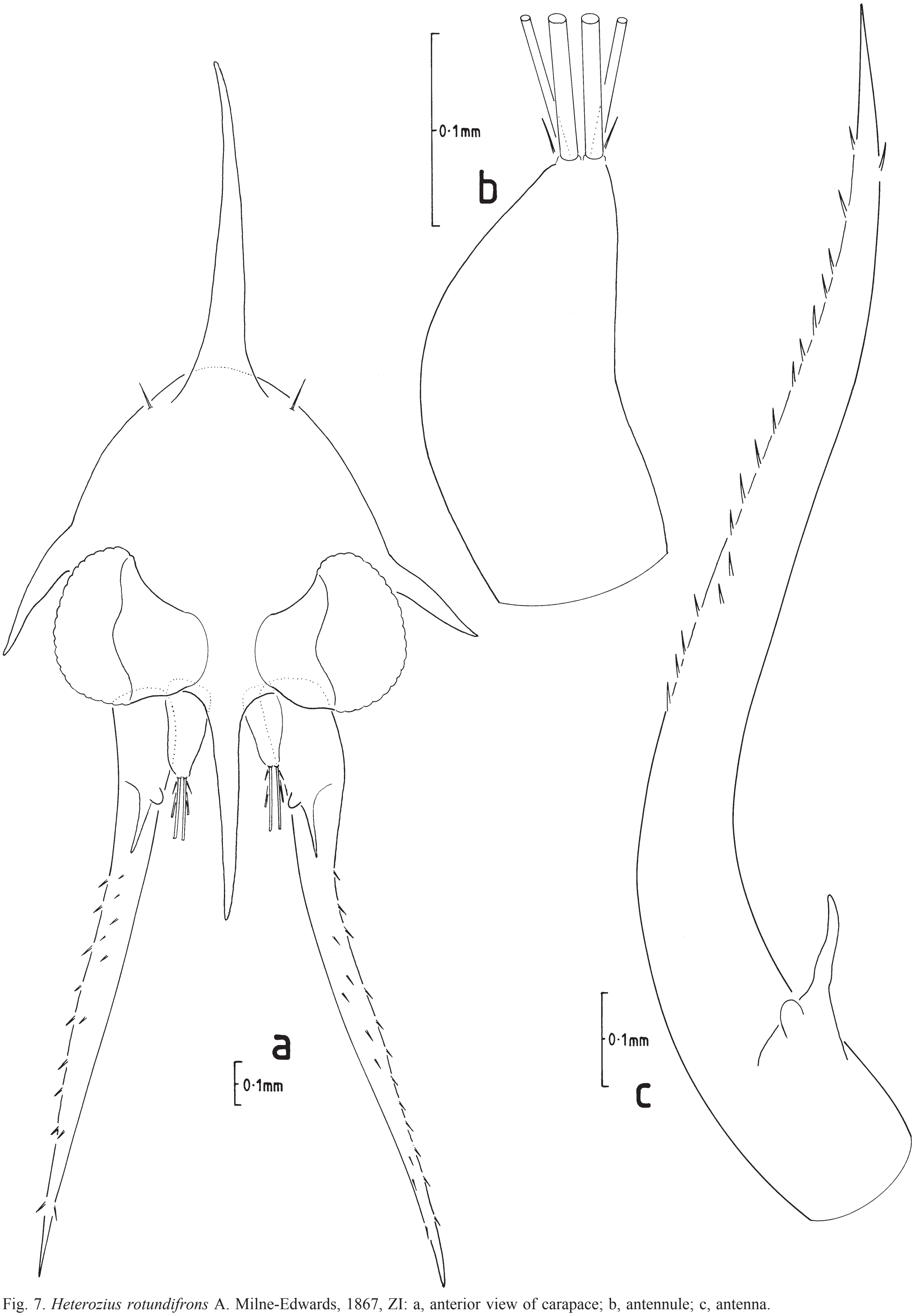

Fig. 7. *Heterozius rotundifrons* A. Milne-Edwards, 1867, ZI: a, anterior view of carapace; b, antennule; c, antenna.

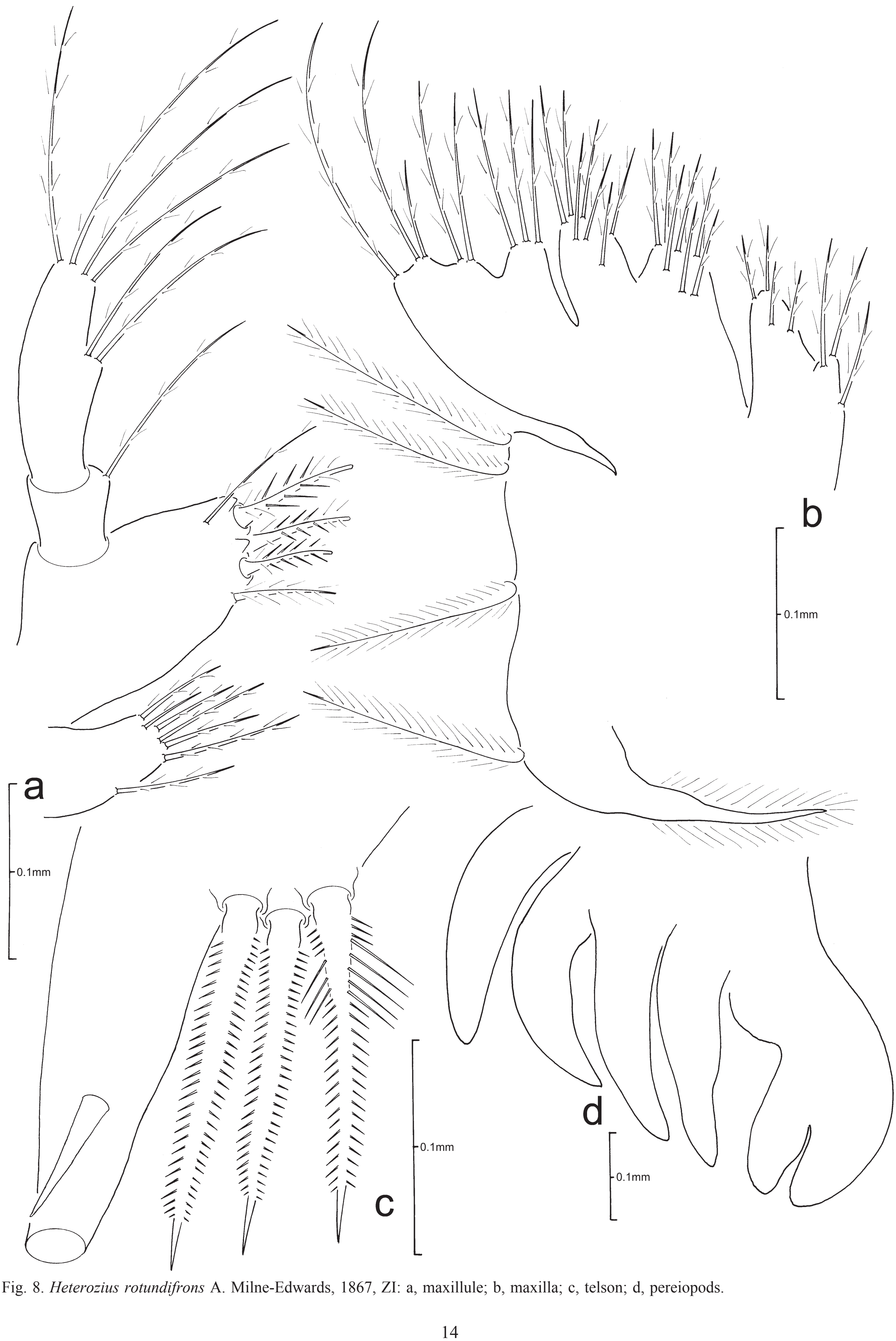

Fig. 8. *Heterozius rotundifrons* A. Milne-Edwards, 1867, ZI: a, maxillule; b, maxilla; c, telson; d, pereiopods.

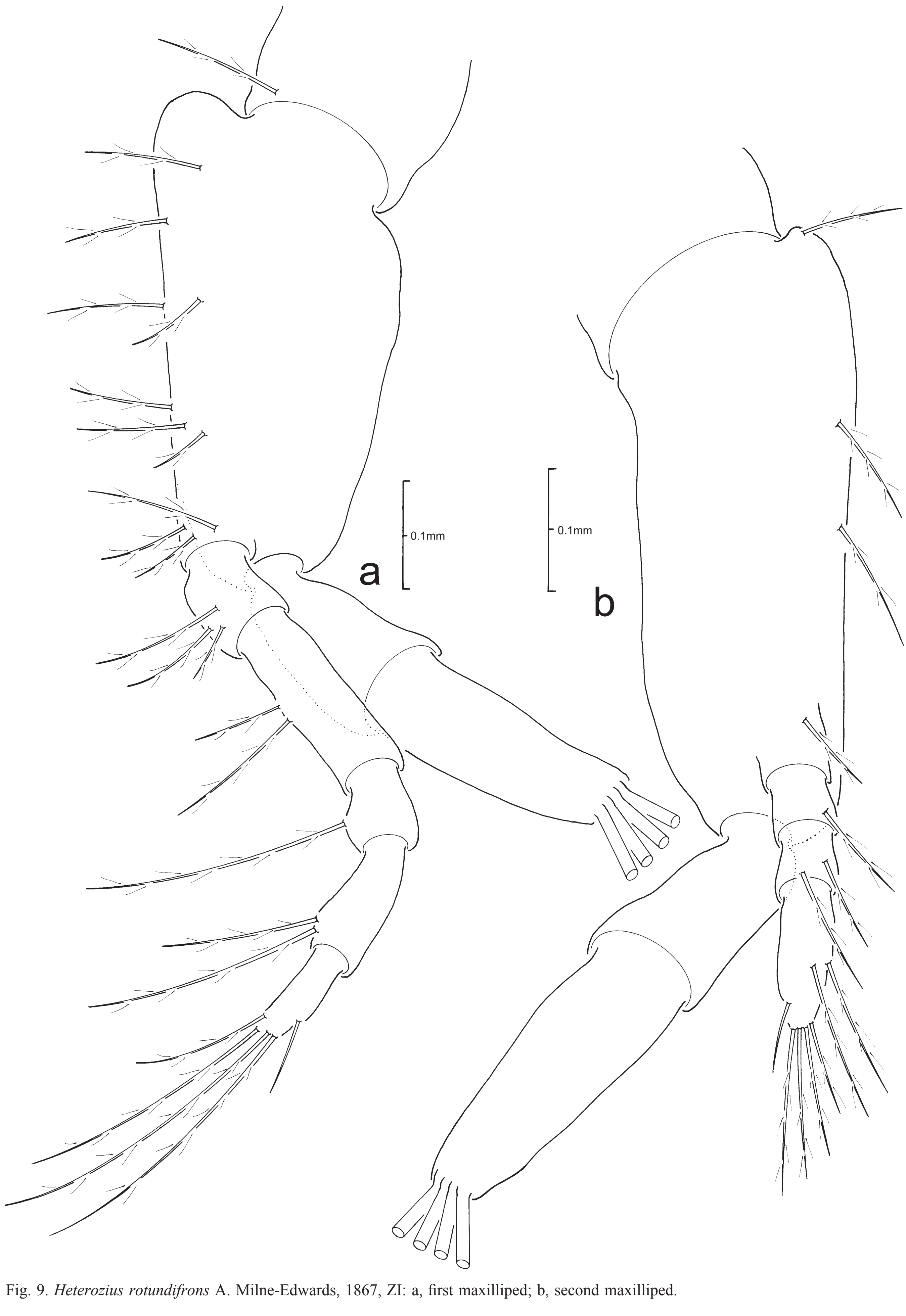

Fig. 9. *Heterozius rotundifrons* A. Milne-Edwards, 1867, ZI: a, first maxilliped; b, second maxilliped.

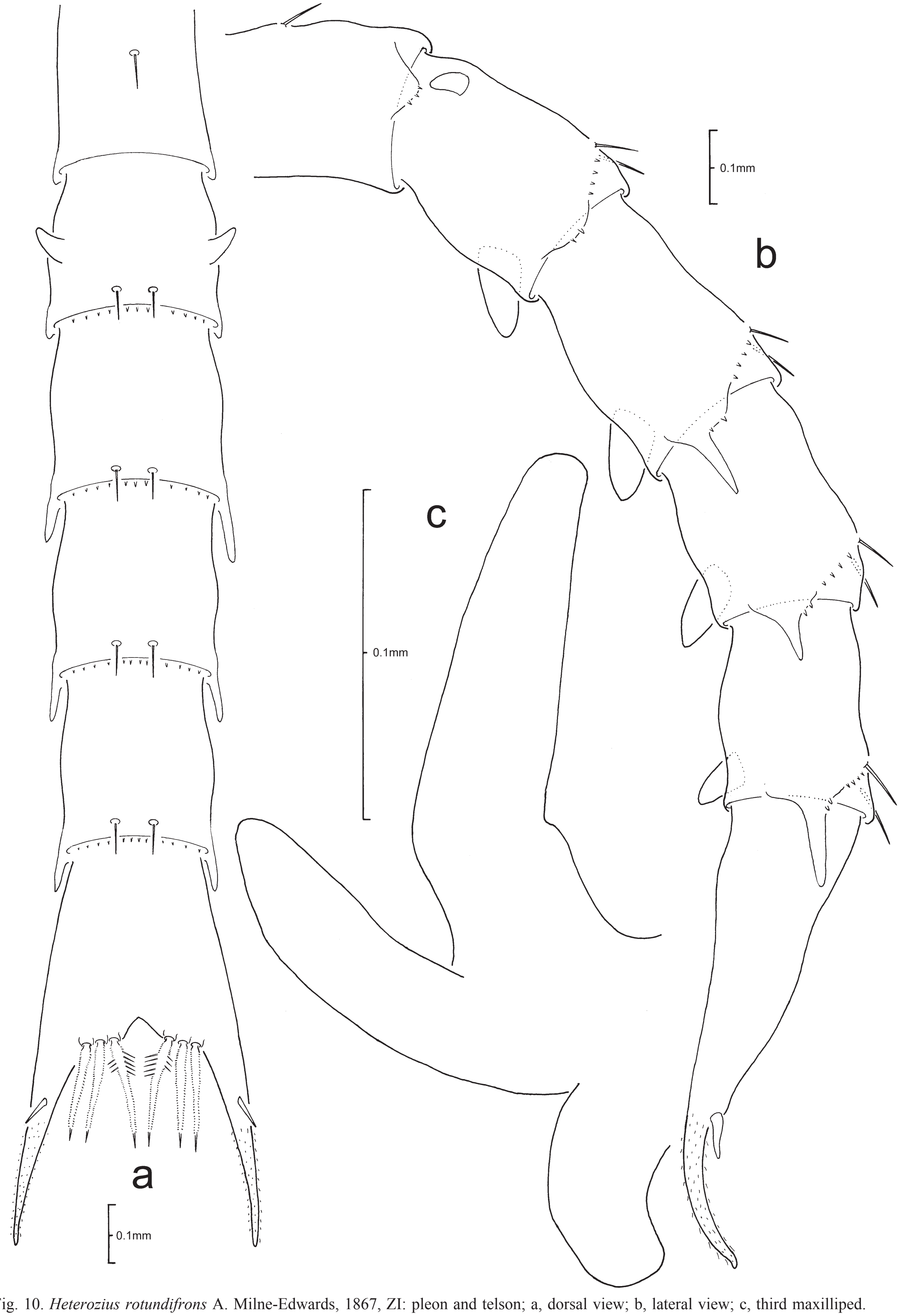

Fig. 10. *Heterozius rotundifrons* A. Milne-Edwards, 1867, ZI: pleon and telson; a, dorsal view; b, lateral view; c, third maxilliped.

Superfamily Dairoidea Serène, 1965

Family Dairidae Serène, 1965

***Daira perlata* (Herbst, 1790)**
(Figs. 11–14)

Description of Zoea I.
CARAPACE (Fig. 11a): dorsal spine relatively short, curved distally, with 2 pairs of setae, longer than rostral spine length; rostral spine ca. equal to antennal protopod length and without distal spinulation; lateral spines straight, without distal spinulation; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 11a): sessile.
Antennule (Fig. 11b): primary flagellum unsegmented with 5 (2 broad, 3 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 11c): biramous; protopodal process distally, bilaterally spinulate, ca. equal to rostral spine length; endopod spine present; exopod ca. 44.9% length of protopod, possessing 2 (1 long subterminal+1 terminal) setae plus process.
Mandible: palp absent.
Maxillule (Fig. 12a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 12b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 13a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 13b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 14a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with a reduced posterolateral process; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 12c, 14a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

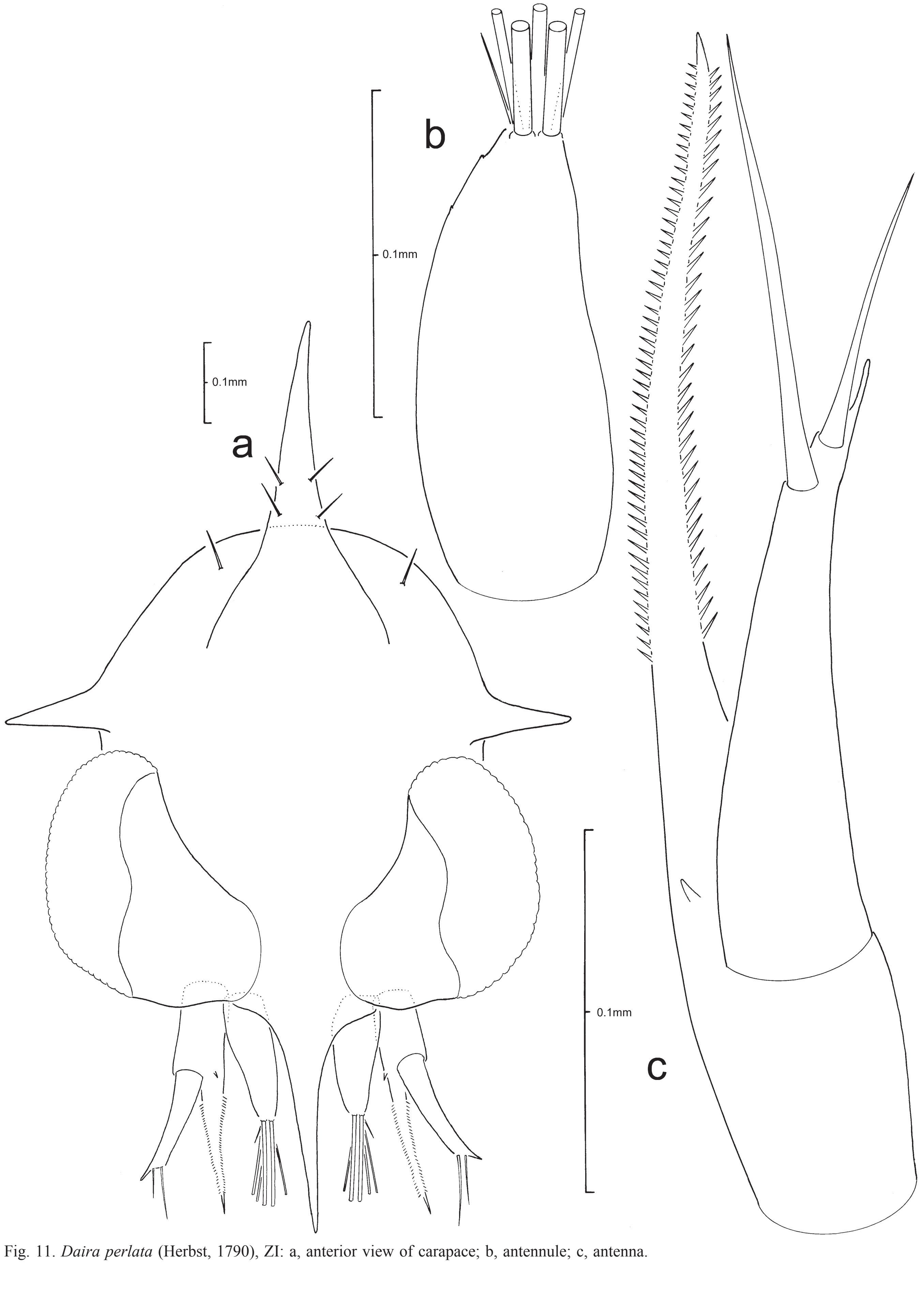

Fig. 11. *Daira perlata* (Herbst, 1790), ZI: a, anterior view of carapace; b, antennule; c, antenna.

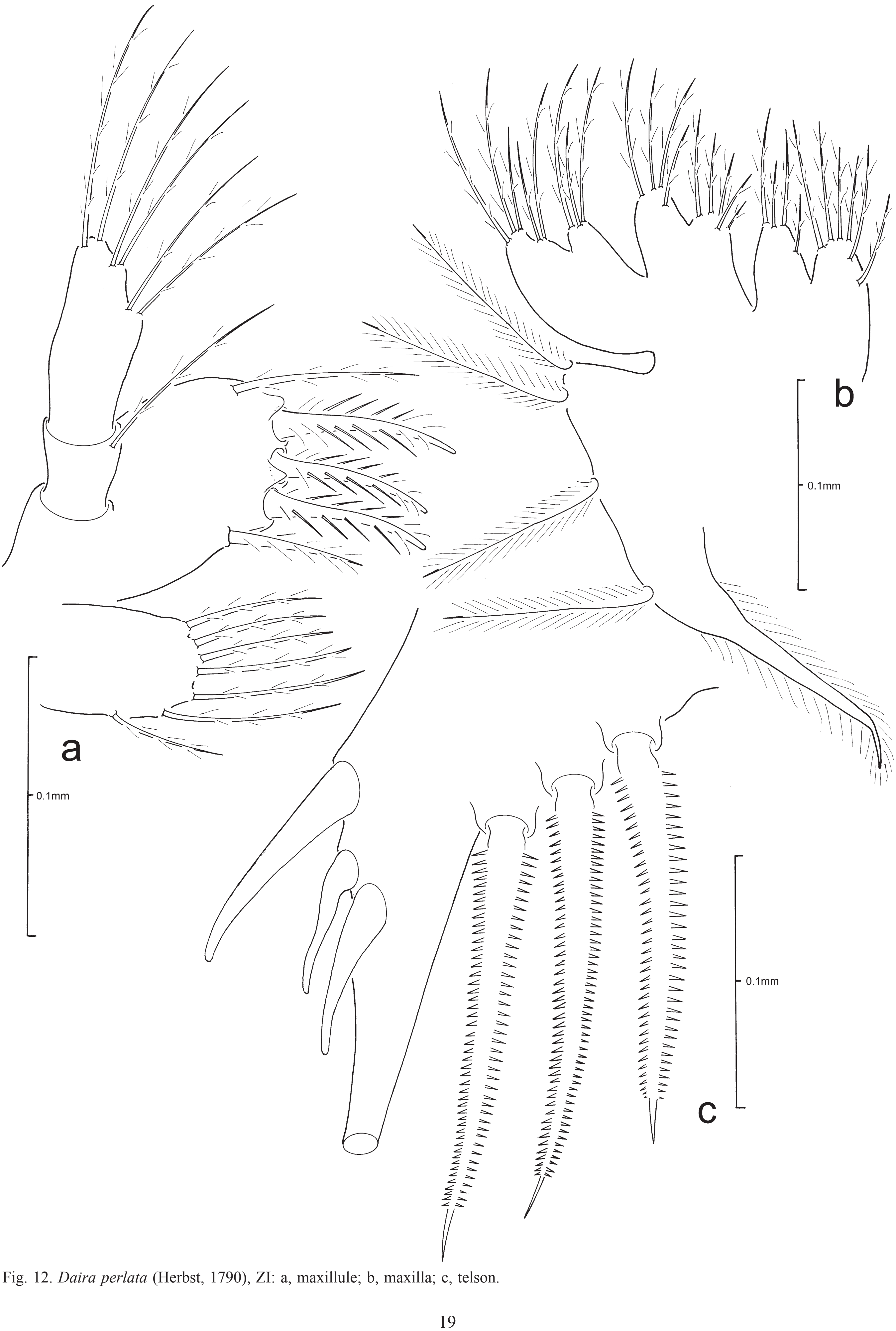

Fig. 12. *Daira perlata* (Herbst, 1790), ZI: a, maxillule; b, maxilla; c, telson.

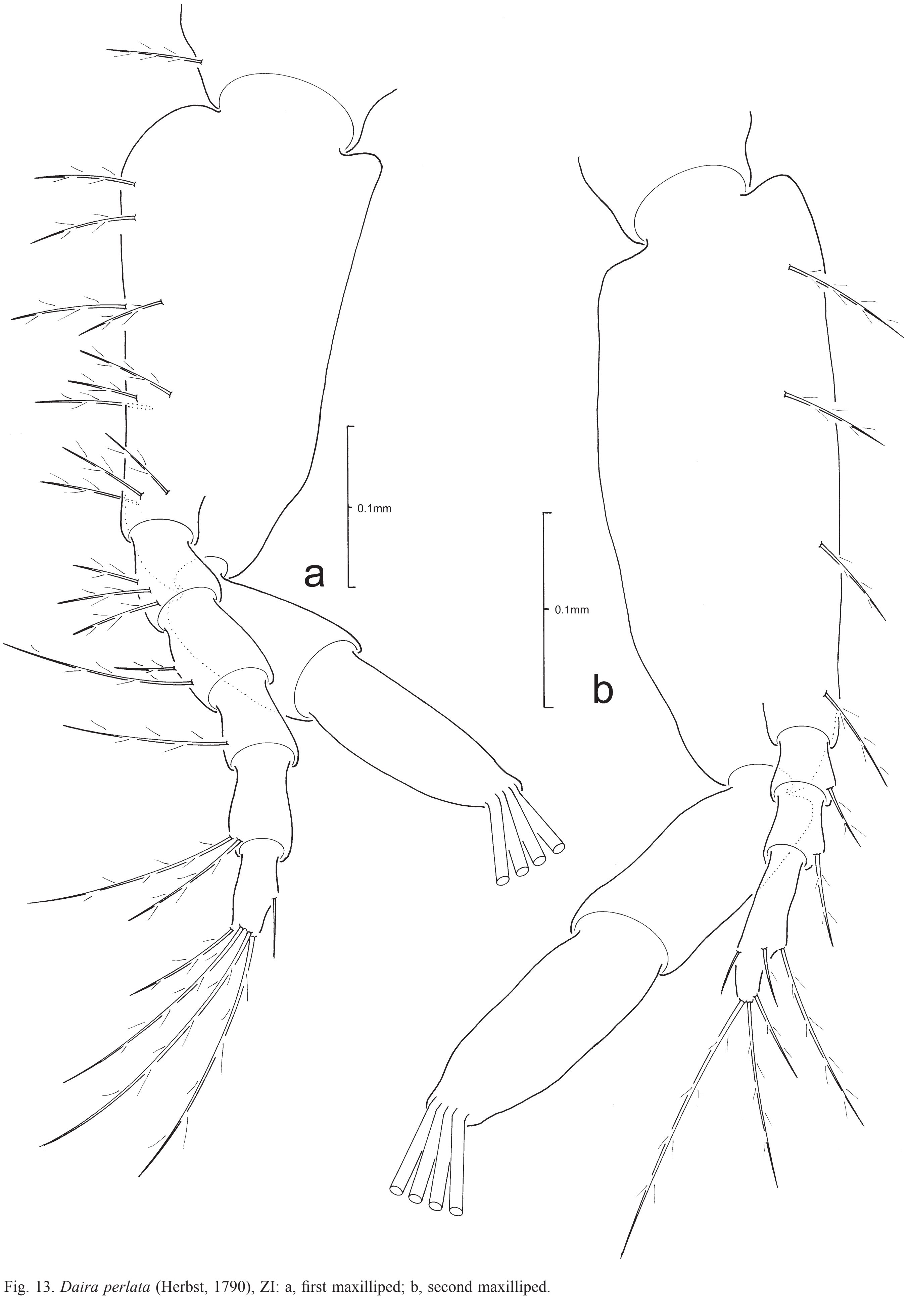

Fig. 13. *Daira perlata* (Herbst, 1790), ZI: a, first maxilliped; b, second maxilliped.

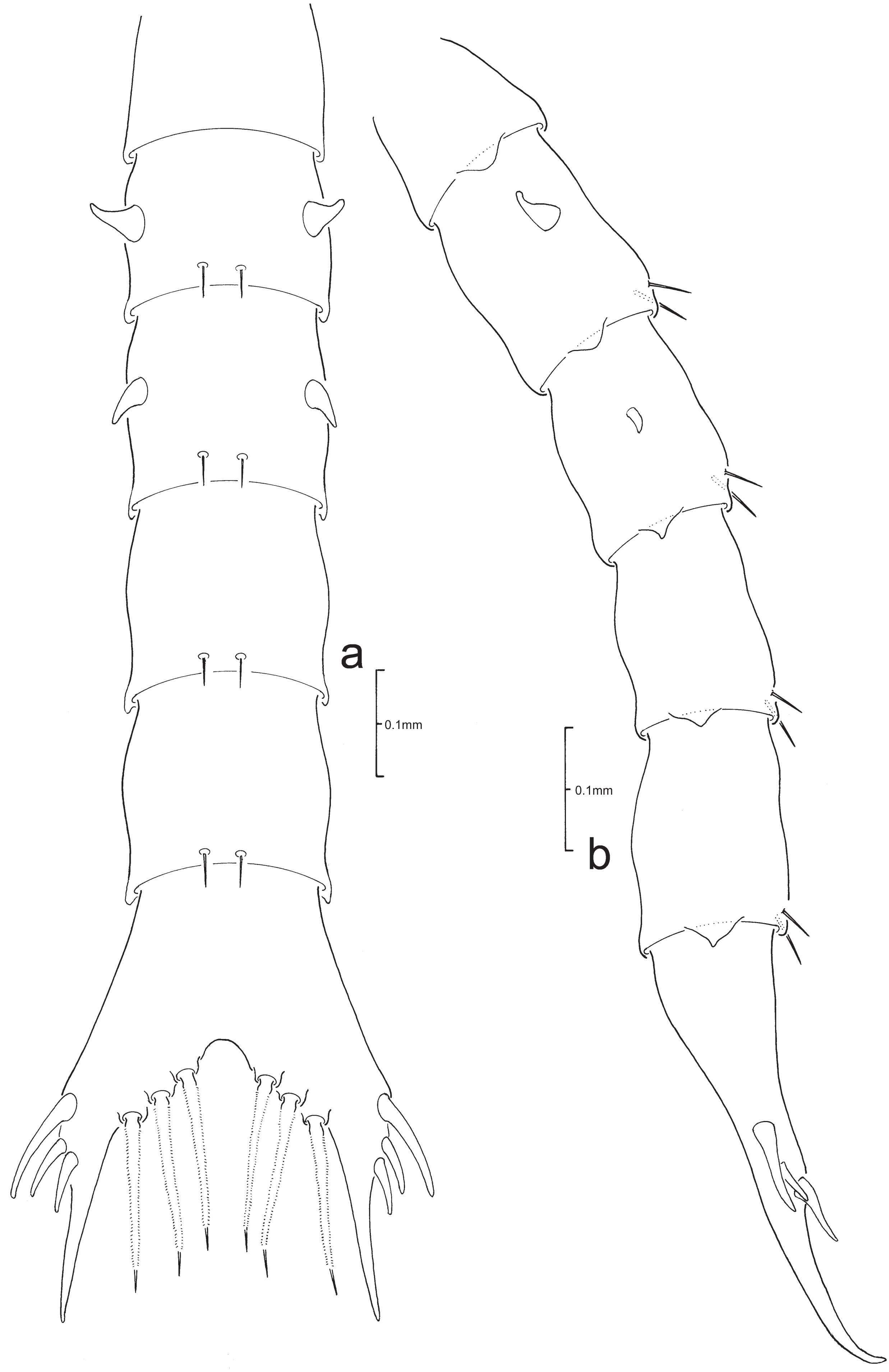

Fig. 14. *Daira perlata* (Herbst, 1790), ZI: pleon and telson; a, dorsal view; b, lateral view.

Superfamily Eriphioidea MacLeay, 1838

Family Dacryopilumnidae Serène, 1984

***Dacryopilumnus rathbunae* Balss, 1932**
(Figs. 15–18)

Description of Zoea I.
CARAPACE (Fig. 15a): dorsal spine relatively short, curved distally, longer than rostral spine length; rostral spine ca. equal to antennal protopod length, without distal spinulation; lateral spines slightly curved ventrally, without dorsal spinulation; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 15a): sessile.
Antennule (Fig. 15b): primary flagellum unsegmented with 5 (2 broad, 3 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 15c): biramous; protopodal process distally bilaterally spinulate, ca. equal to rostral spine length; endopod spine present; exopod ca. 27.6% length of protopod, possessing 3 (1 extremely long subterminal+2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 16a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 16b): biramous; coxal endite bilobed with 5+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 17a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 17b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 18a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 16c, 18a, b): each fork relatively long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine spine; posterior margin with 3 pairs of stout spinulate setae.

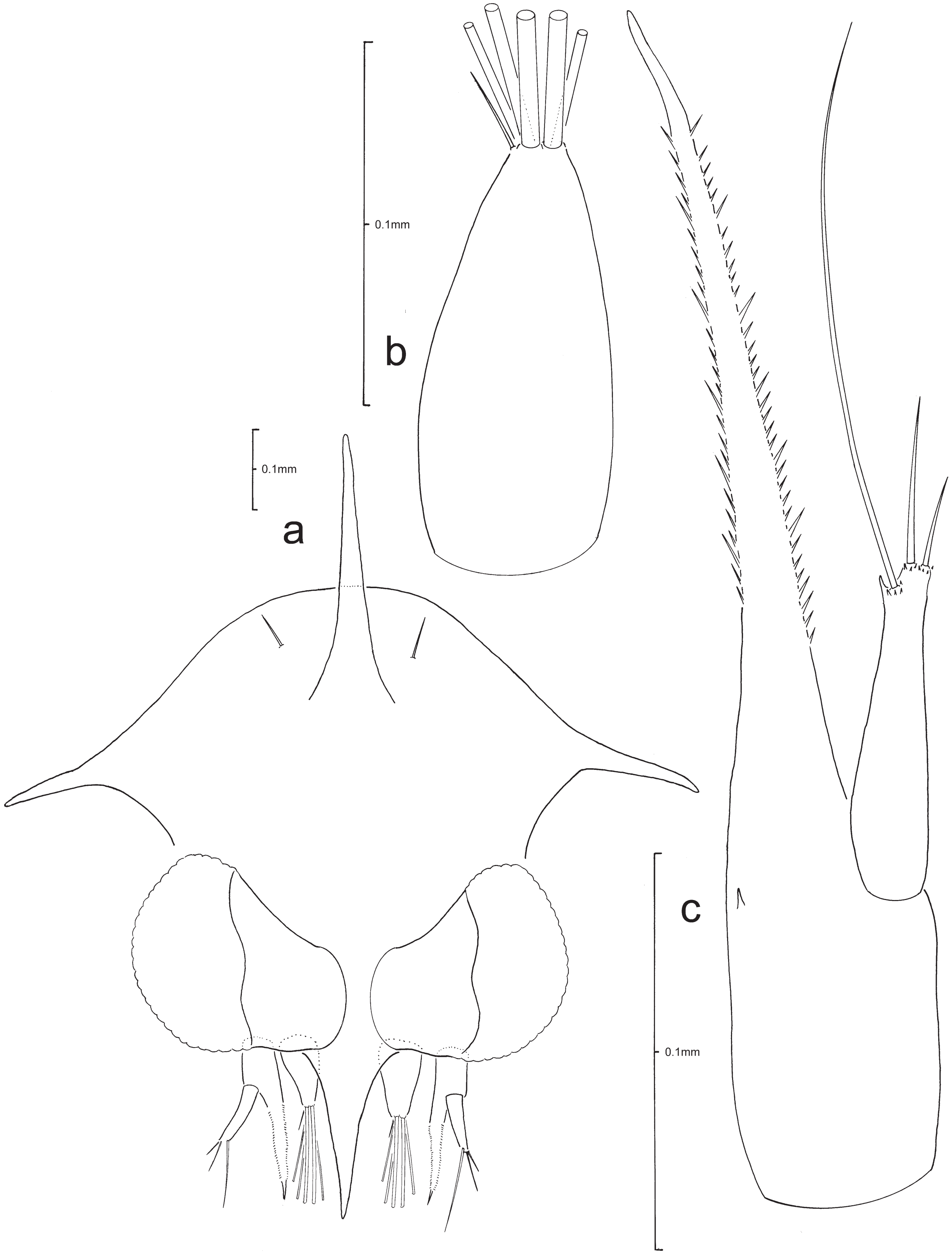

Fig. 15. *Dacryopilumnus rathbunae* Balss, 1932, ZI: a, anterior view of carapace; b, antennule; c, antenna.

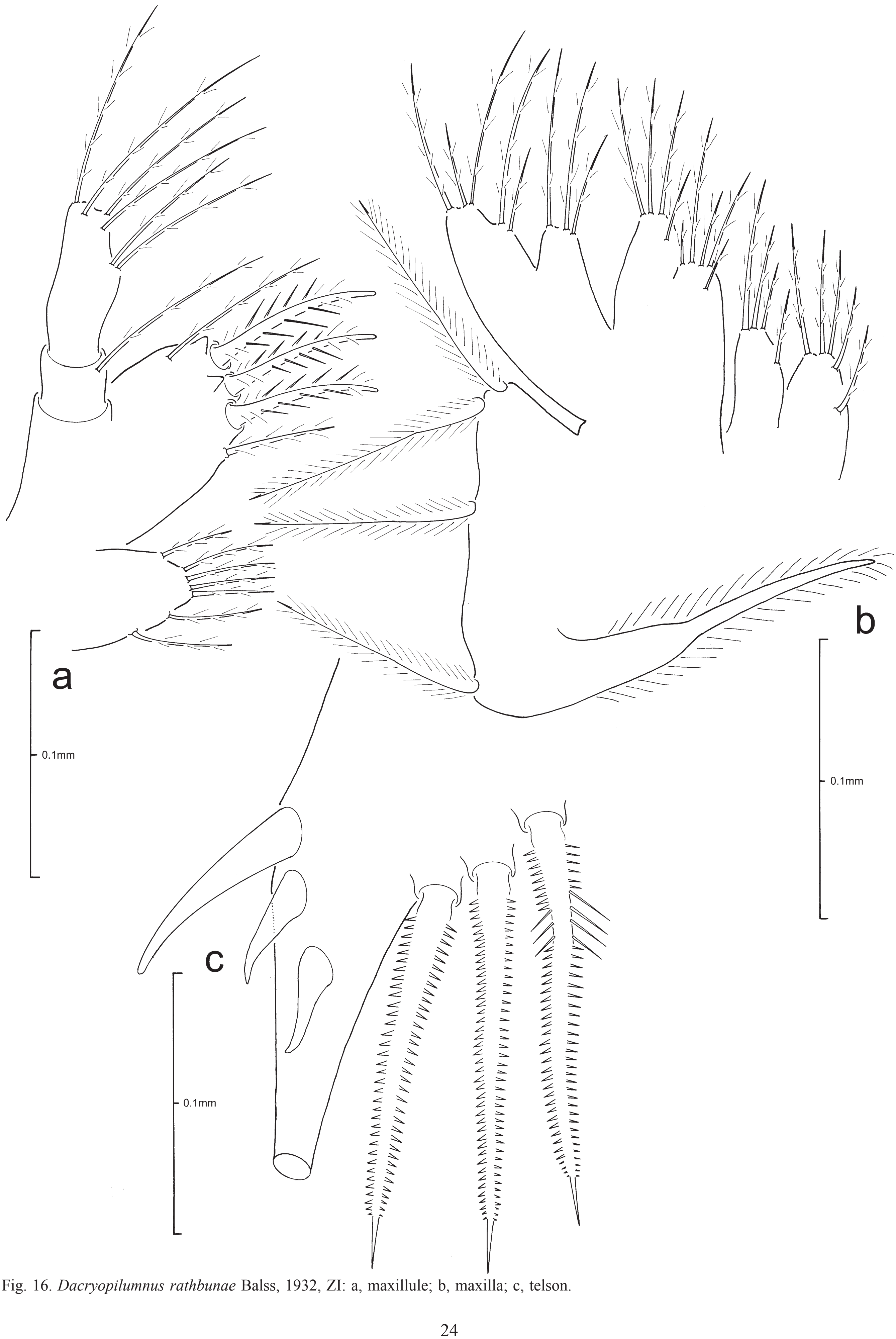

Fig. 16. *Dacryopilumnus rathbunae* Balss, 1932, ZI: a, maxillule; b, maxilla; c, telson.

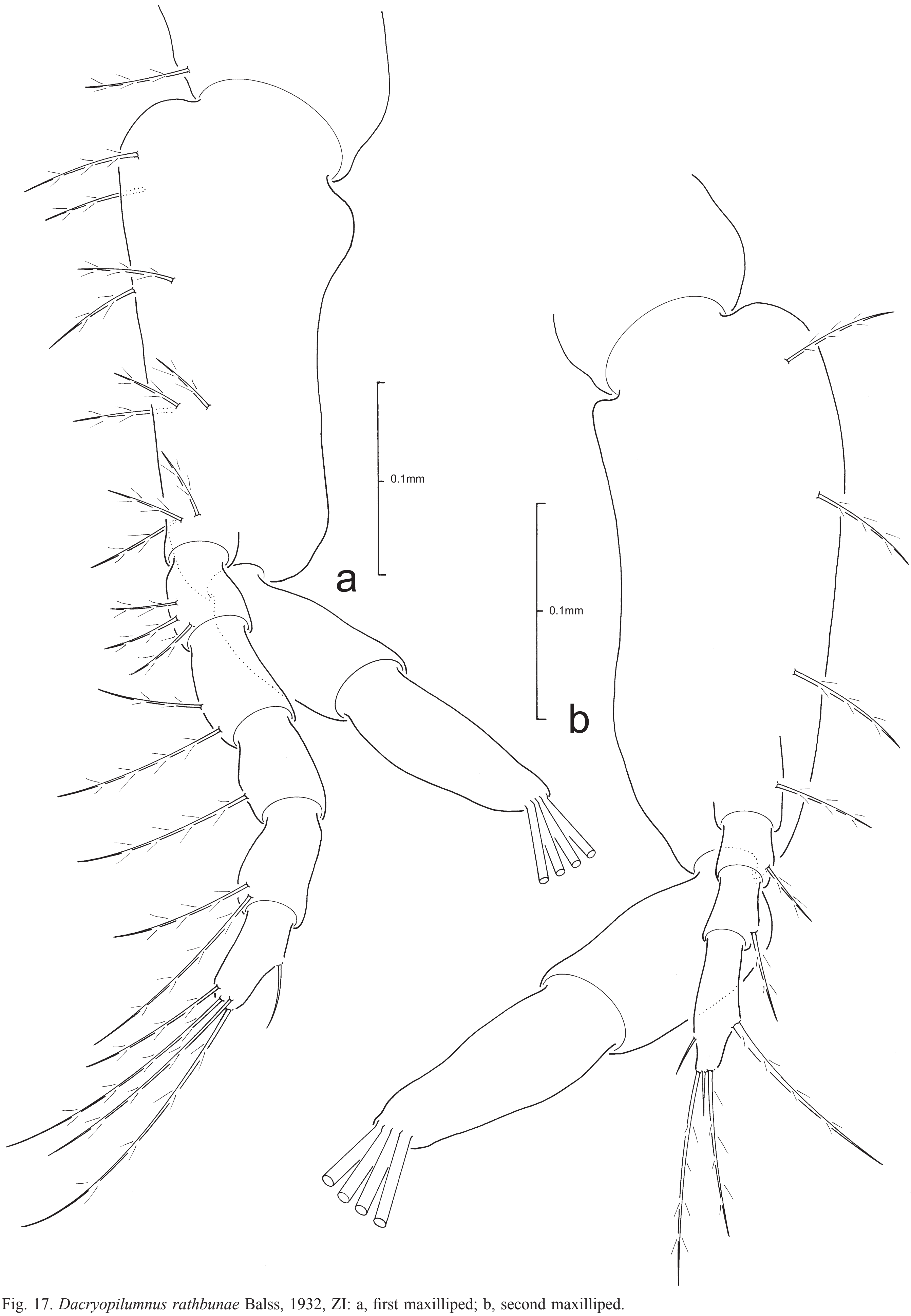

Fig. 17. *Dacryopilumnus rathbunae* Balss, 1932, ZI: a, first maxilliped; b, second maxilliped.

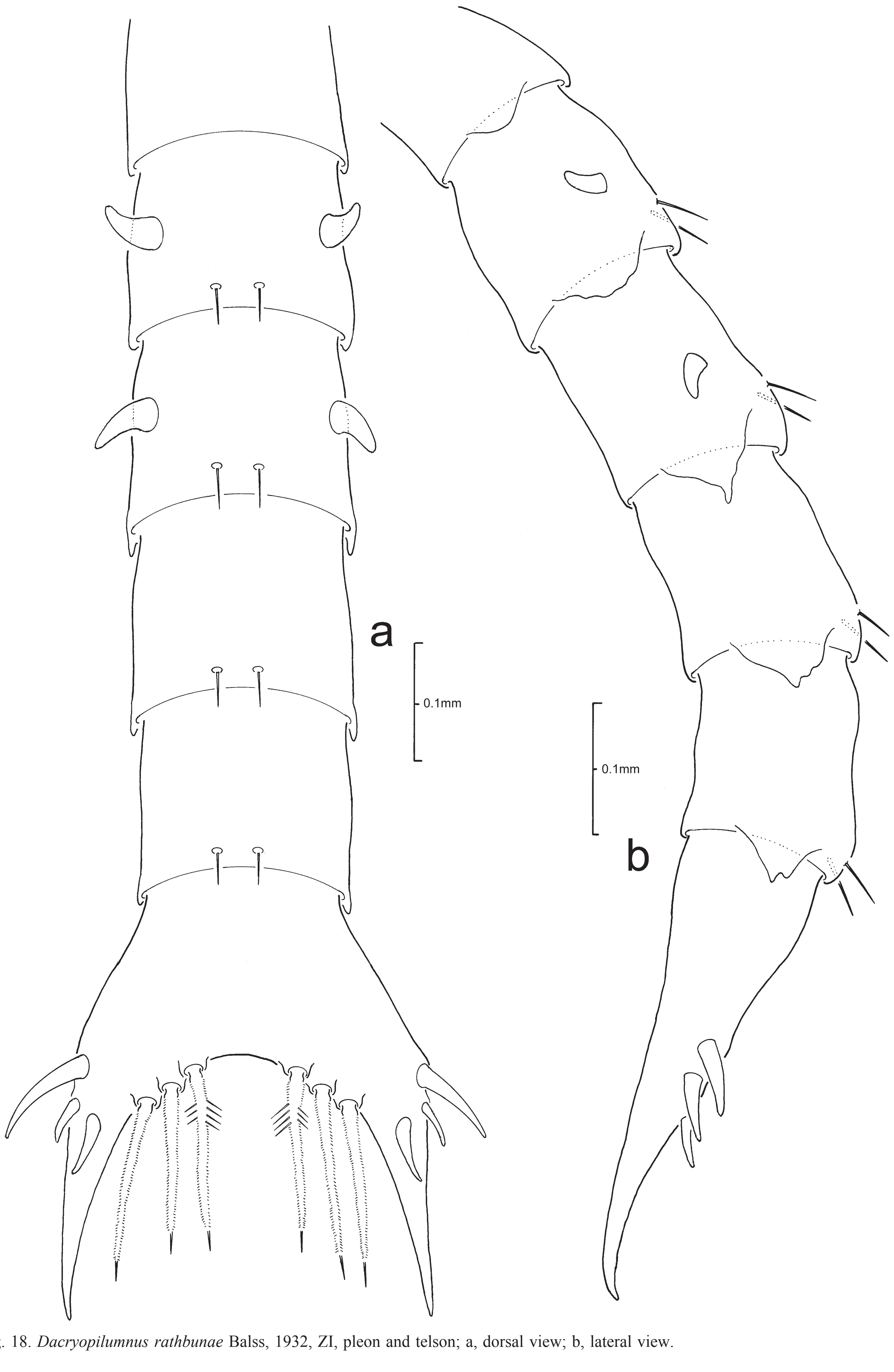

Fig. 18. *Dacryopilumnus rathbunae* Balss, 1932, ZI, pleon and telson; a, dorsal view; b, lateral view.

Family Eriphiidae MacLeay, 1838

***Eriphia smithii* MacLeay, 1838**
(Figs. 19–22)

Eriphia laevimana smithii. Hashmi, 1970: 459–461, figs. 7–10 (PZ, ZI).
Eriphia smithii. Terada, 1982: 256–259, fig. 1 (ZI–IV).

Description of Zoea I.
CARAPACE (Fig. 19a): dorsal spine curved distally, longer than rostral spine length; rostral spine slightly longer than antennal protopod length, without distal spinulation; lateral spines straight, granulated on dorsal surface; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 19a): sessile.
Antennule (Fig. 19b): primary flagellum unsegmented with 5 (2 broad, 3 slender) terminal aesthetascs of unequal length plus 1 short terminal seta; accessory flagellum absent.
Antenna (Fig. 19c): uniramous; protopodal process distally bilaterally spinulate, slightly shorter than rostral spine length, with two small lateral basal spines; endopod absent; exopod ca. 39.7% length of protopod, possessing 3 (1 long subterminal+2 shorter unequal terminal) setae with small spinules at base.
Mandible: palp absent.
Maxillule (Fig. 20a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 20b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 21a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 21b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 22a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomeres 3–5 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–5 each with rounded posterolateral processes; pleomere 1 with 1 pair of medial setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 20c, 22a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Table 2. A comparison between the ZI of *Eriphia smithii* MacLeay, 1838 by Hashmi (1970), Terada (1982), and the present study.

Character	Hashmi (1970)	Terada (1982)	Present study
CARAPACE	fig. 9a	fig. 1AI	Fig. 19a
posterodorsal setae	absent	absent	1 pair present
ANTENNULE	fig. 10a	fig. 1AI	Fig. 19b
terminal setation	2 long terminal aesthetascs, 1 terminal seta	4 aesthetascs ?	5 (2 broad, 3 slender) terminal aesthetascs of unequal length, 1 terminal seta
MAXILLA	fig. 10f	fig. 1EI	Fig. 20b
coxal endite setation	5+4	6+4	6+4
basial endite setation	4+4	5+4	5+4
FIRST MAXILLIPED	fig. 10g	fig. 1FI	Fig. 21a
coxal seta	absent	absent	present
basial setation	8 (2+2+2+2)	10 (2+2+3+3)	10 (2+2+3+3)
endopod setation	2,1,1,2,5 (1 subterminal+4 terminal)	3,2,1,2,5 (1 subterminal+4 terminal)	3,2,1,2,5 (1 subterminal+4 terminal)
PLEON	fig. 9a		Fig. 22a, b
pleomere 1 with medial setae	1 pair	absent	1 pair

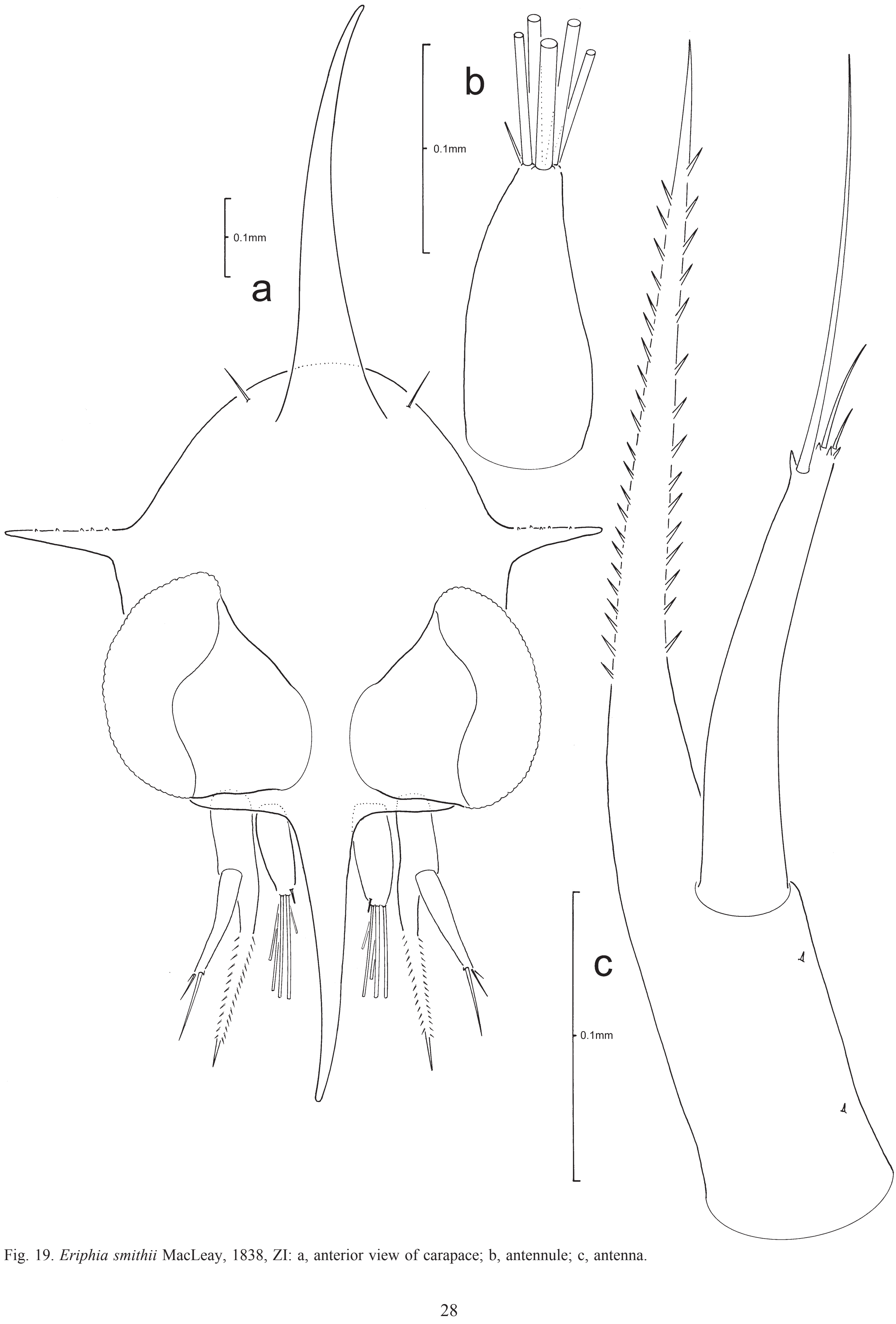

Fig. 19. *Eriphia smithii* MacLeay, 1838, ZI: a, anterior view of carapace; b, antennule; c, antenna.

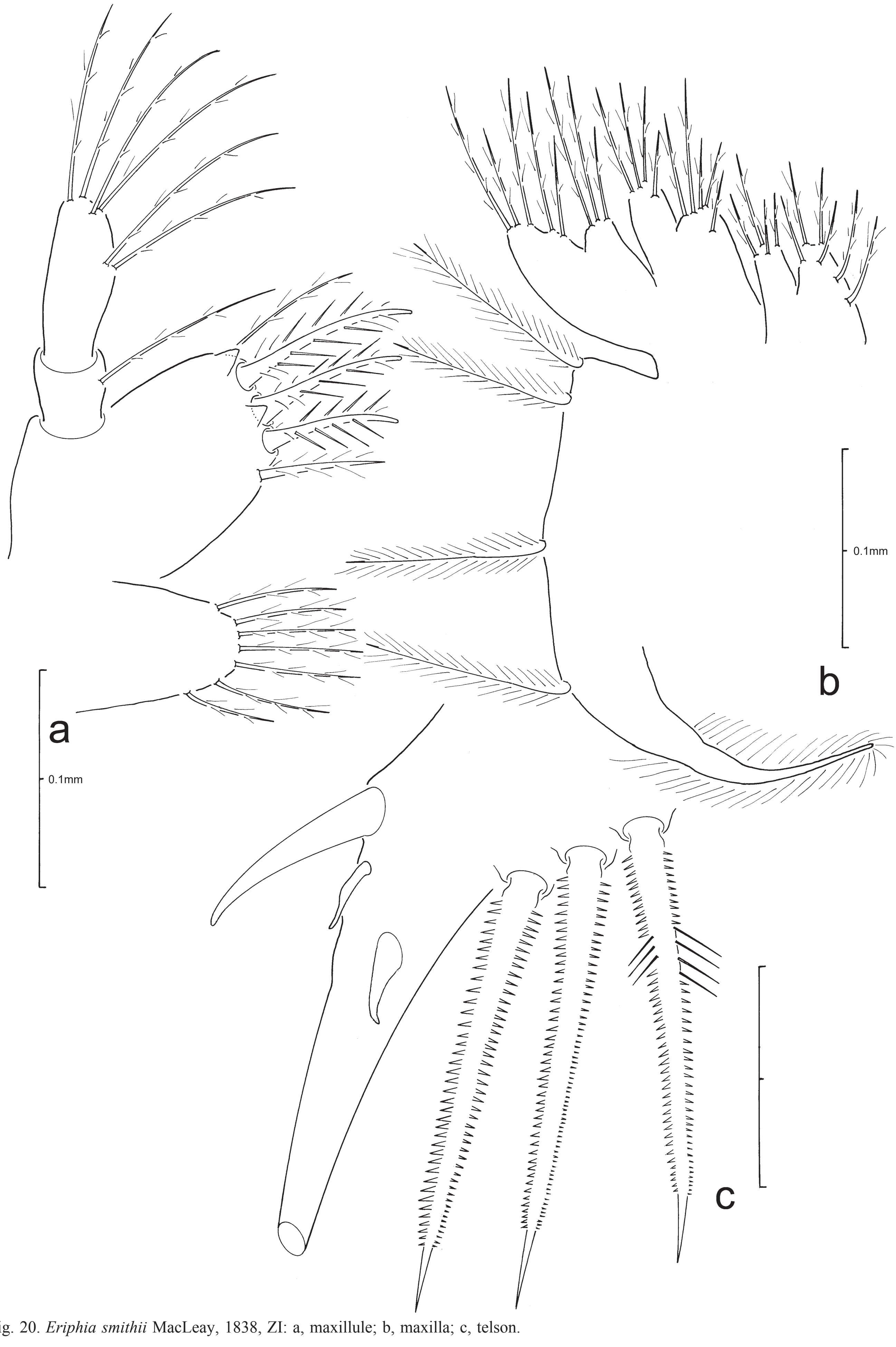

Fig. 20. *Eriphia smithii* MacLeay, 1838, ZI: a, maxillule; b, maxilla; c, telson.

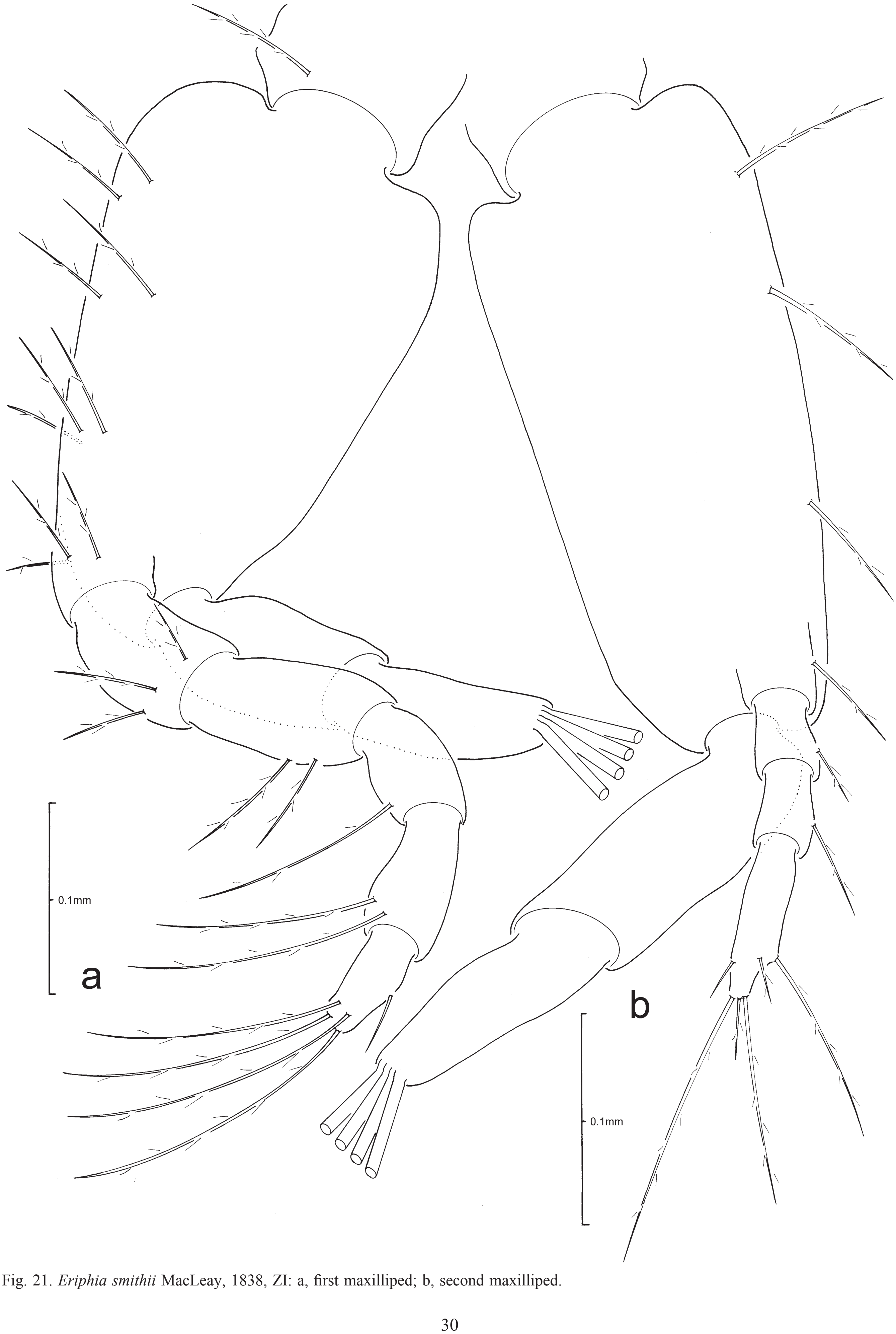

Fig. 21. *Eriphia smithii* MacLeay, 1838, ZI: a, first maxilliped; b, second maxilliped.

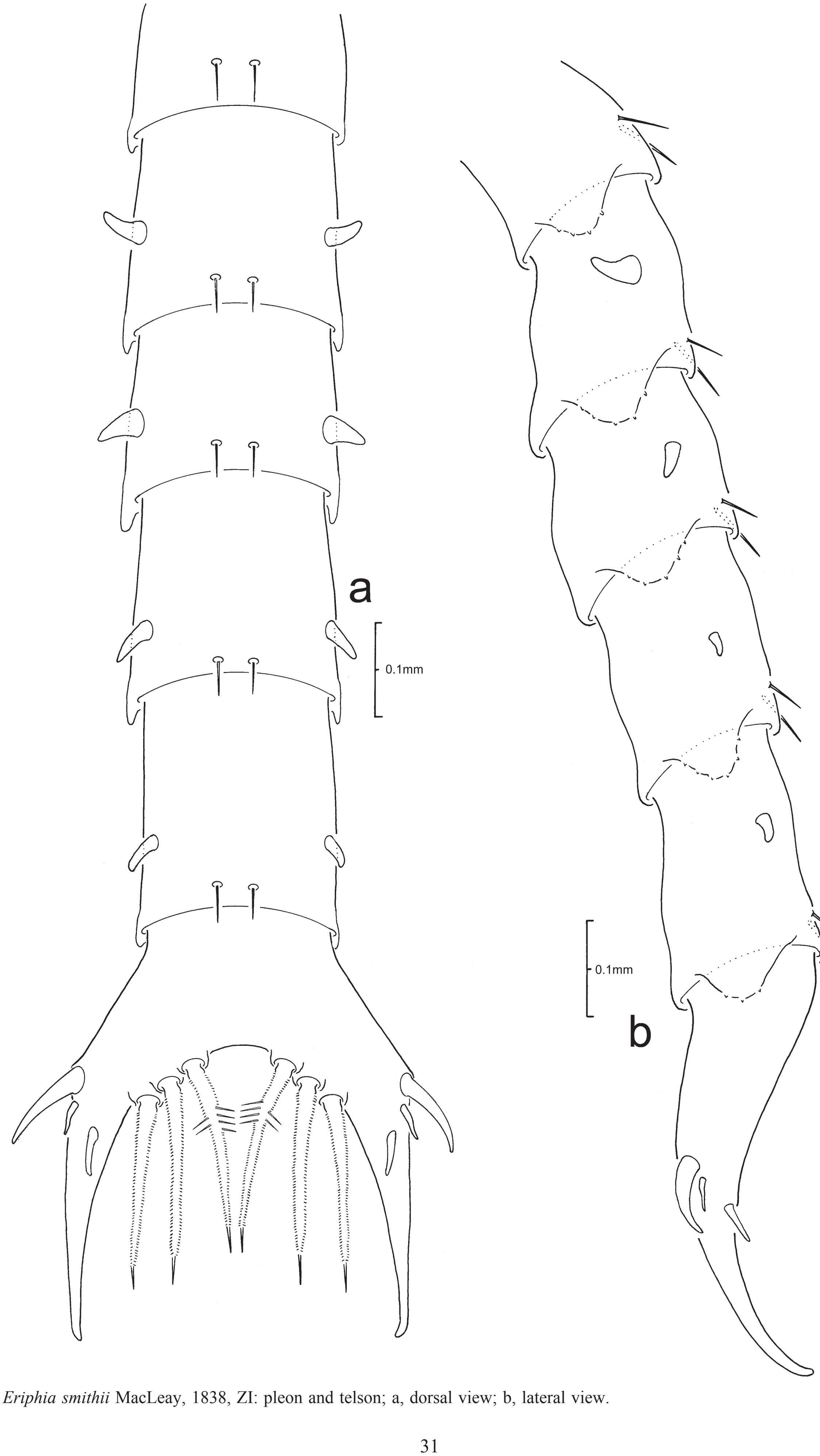

Fig. 22. *Eriphia smithii* MacLeay, 1838, ZI: pleon and telson; a, dorsal view; b, lateral view.

Family Hypothalassiidae Karasawa & Schweitzer, 2006

Hypothalassia armata (De Haan, 1835)
(Figs. 23–26)

Description of Zoea I.
CARAPACE (Fig. 23a): dorsal spine curved distally, longer than rostral spine length; rostral spine slightly longer than antennal protopod length, without distal spinulation; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 23a): sessile.
Antennule (Fig. 23b): primary flagellum unsegmented with 5 (2 broad, 3 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 23c): uniramous; protopodal process distally bilaterally spinulate, slightly shorter than rostral spine length; endopod spine absent; exopod ca. 43.3% length of protopod, possessing 3 (1 long subterminal+2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 24a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 24b): biramous; coxal endite bilobed with 7+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 25a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 25b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 26a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomeres 3–5 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 24c, 26a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

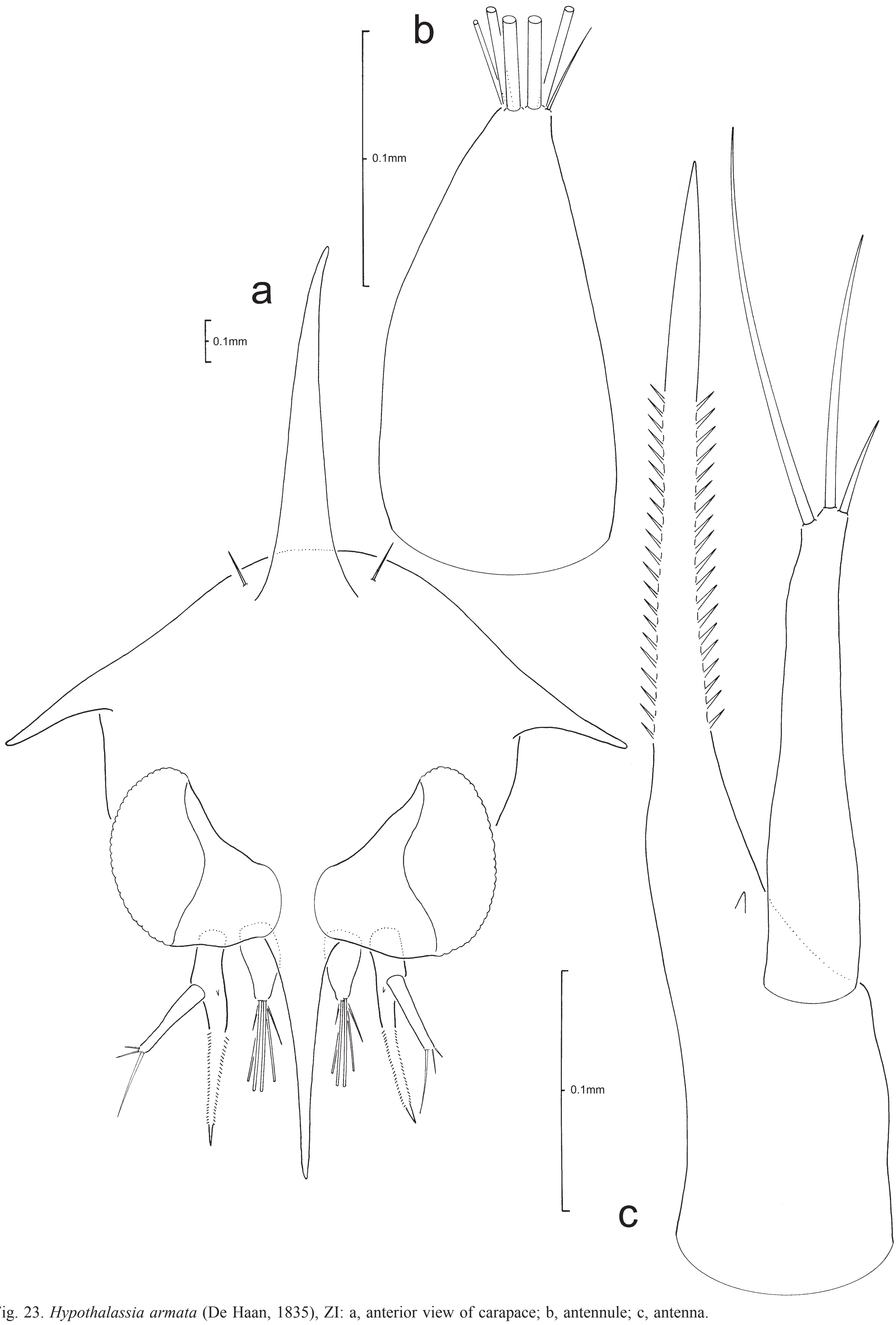

Fig. 23. *Hypothalassia armata* (De Haan, 1835), ZI: a, anterior view of carapace; b, antennule; c, antenna.

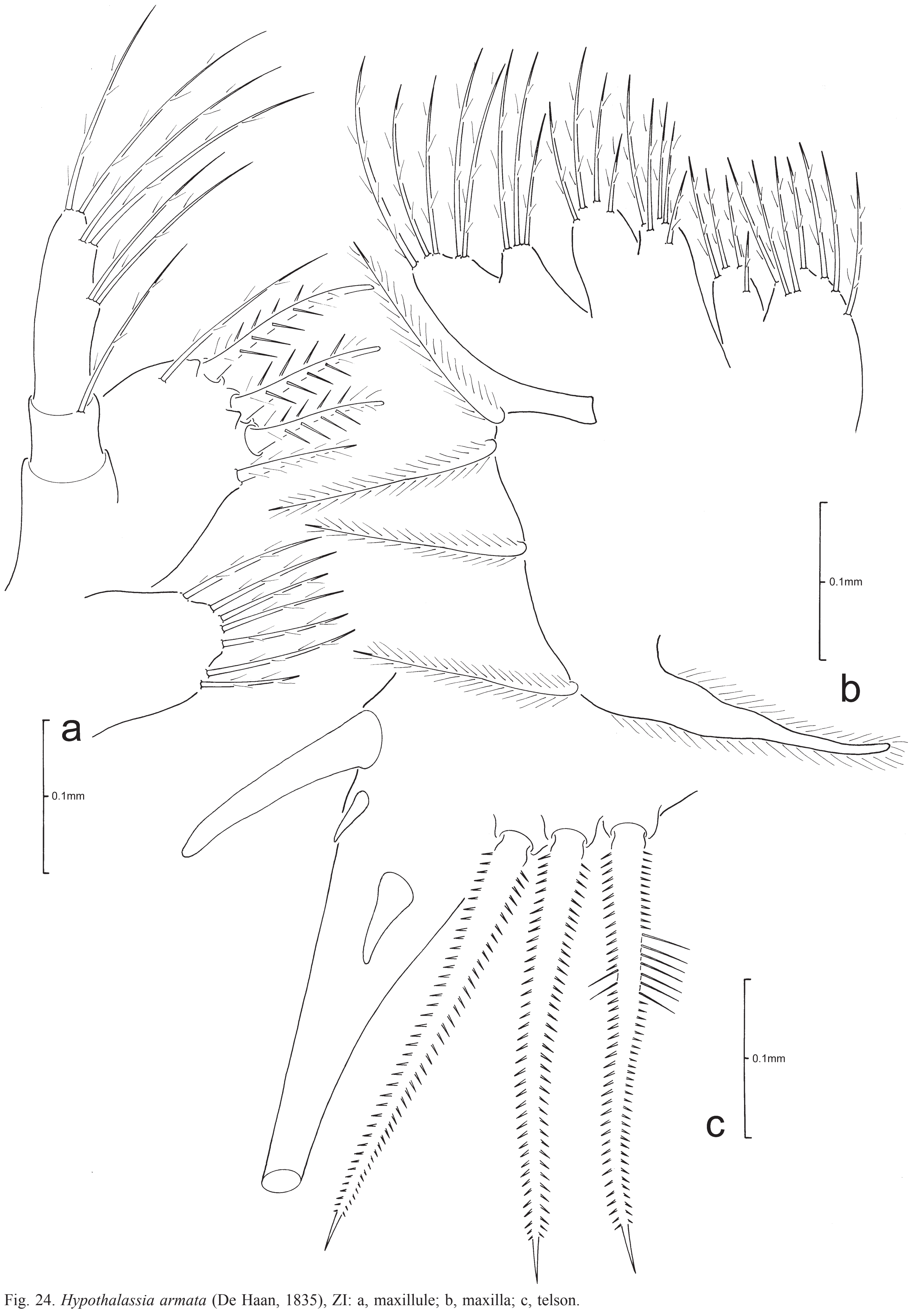

Fig. 24. *Hypothalassia armata* (De Haan, 1835), ZI: a, maxillule; b, maxilla; c, telson.

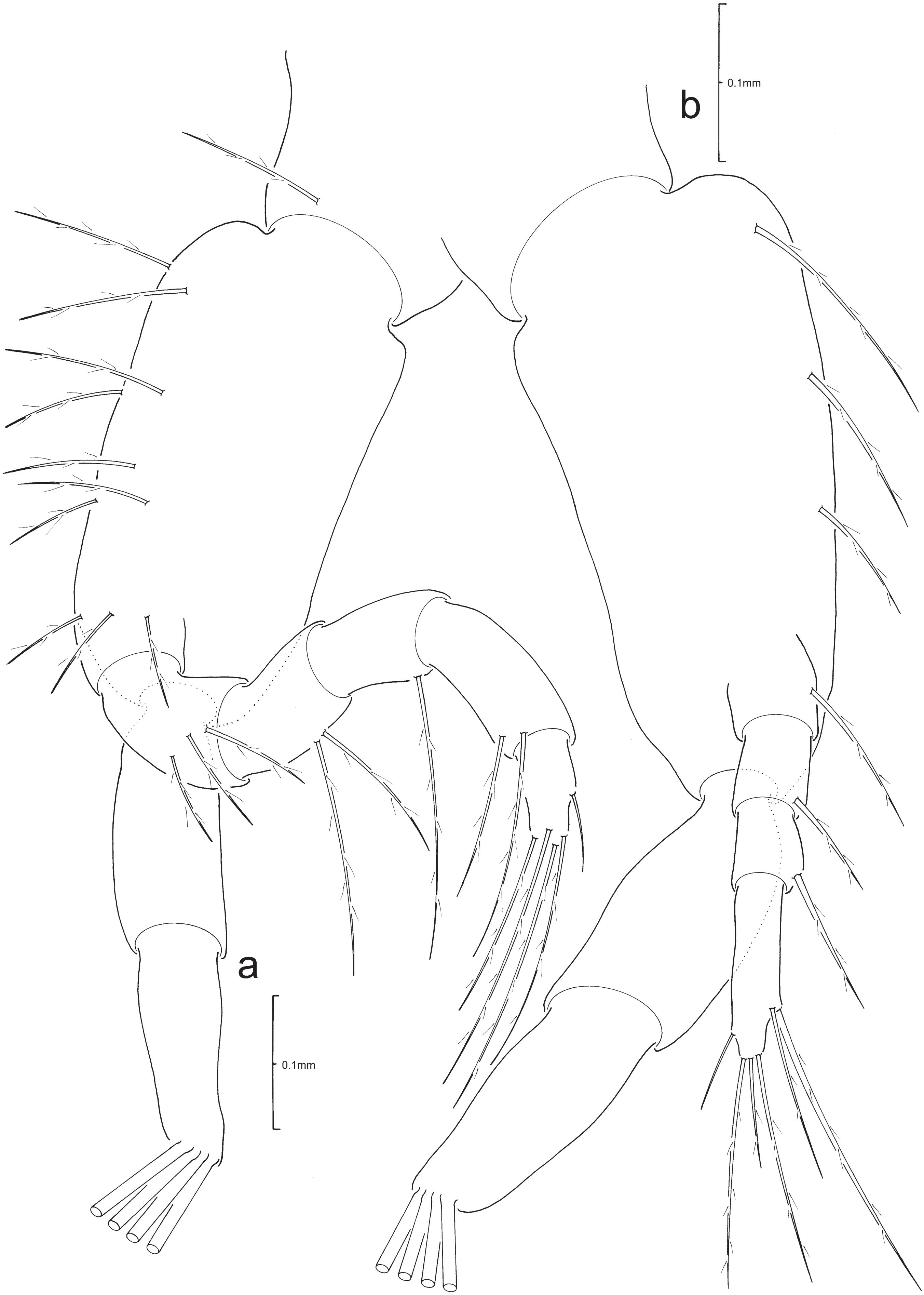

Fig. 25. *Hypothalassia armata* (De Haan, 1835), ZI: a, first maxilliped; b, second maxilliped.

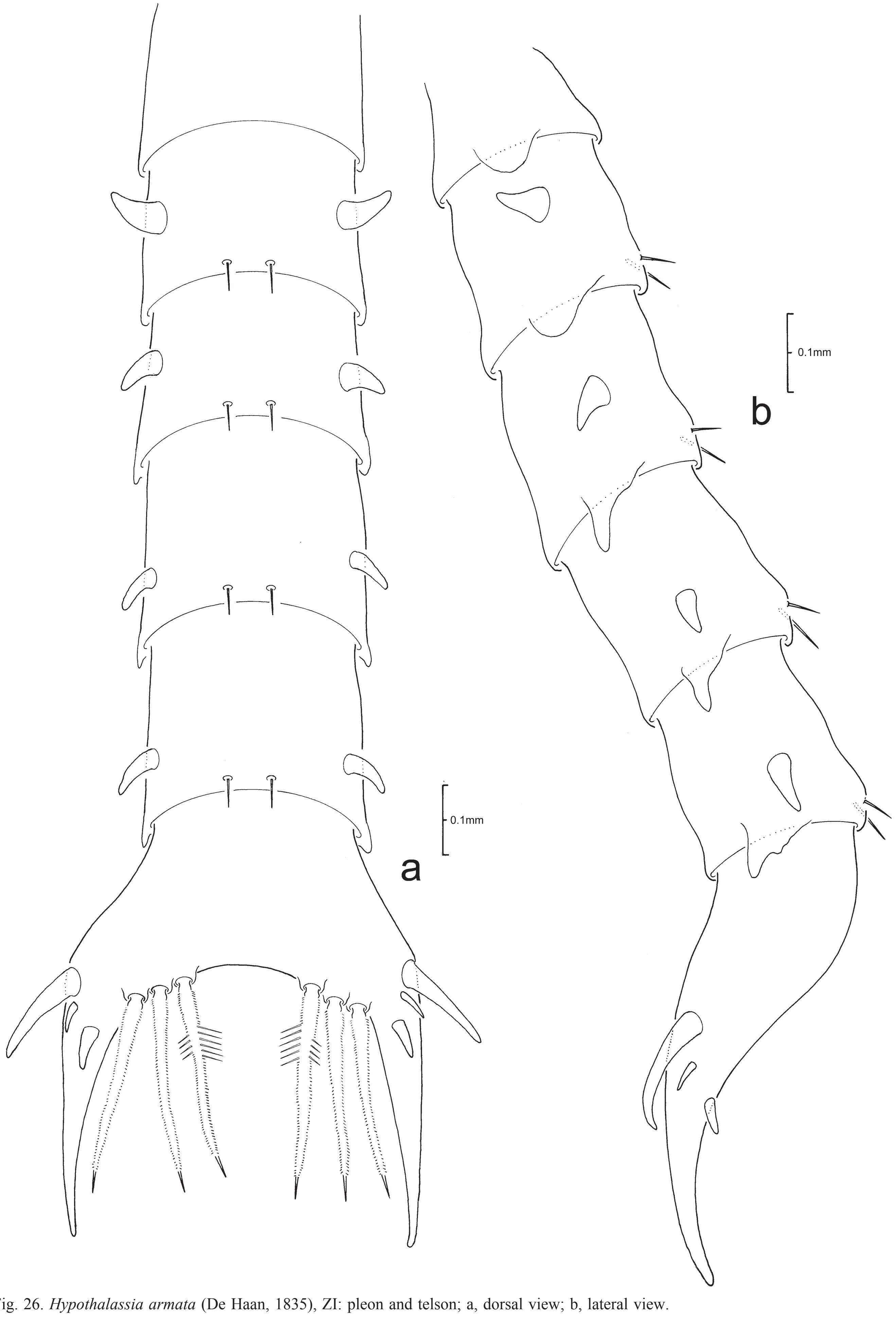

Fig. 26. *Hypothalassia armata* (De Haan, 1835), ZI: pleon and telson; a, dorsal view; b, lateral view.

Family Menippidae Ortmann, 1893

Menippe mercenaria **(Say, 1818)**
(Figs. 27–30)

Menippe mercenaria. Hyman, 1925: 14, 15, pl. 13 (PZ, ZI); Porter, 1960: 169–172, (ZI–VI); Kurata, 1970: 209–215, pls. 73–74 (ZI–V, Meg., Cr. I–II).

Description of Zoea I.
CARAPACE (Fig. 27a): dorsal spine curved distally, slightly longer than rostral spine length; rostral spine much longer than antennal protopod length, without distal spinulation; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 27a): sessile.
Antennule (Fig. 27b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 2 terminal setae of unequal length; accessory flagellum absent.
Antenna (Fig. 27c): biramous; protopodal process distally, bilaterally spinulate, much shorter than rostral spine length; endopod spine present; exopod ca. 50.4% length of protopod, possessing 1 long terminal seta plus elongated spine.
Mandible: palp absent.
Maxillule (Fig. 28a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 4 terminal setae; exopod seta absent.
Maxilla (Fig. 28b): biramous; coxal endite bilobed with 5+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+3 setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 29a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 29b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 0,1,4 (2 subterminal+2 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 30a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 4, 5 with 1 pair of dorsolateral processes directed posteriorly; pleomeres 1–5 each with rounded posterolateral processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 28c, 30a, b): each fork long, gradually curved distally, not spinulate, 1 small lateral spine only, 1 small dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Table 3. A comparison between the ZI of *Menippe mercenaria* (Say, 1818) by Hyman (1925), Porter (1960), Kurata (1970), and the present study.

Character	**Hyman (1925)**	**Porter (1960)**	**Kurata (1970)**	**Present study**
CARAPACE	pl. 13, fig. 167	fig. 1A, C	pl. 73A	Fig. 27a
posterodorsal setae	1 pair present	absent	absent	1 pair present
ANTENNULE	pl. 13, fig. 169	fig. 1E	pl. 73A	Fig. 27b
terminal setation	4 terminal aesthetascs, 1 seta	5 terminal aesthetascs of unequal length, 1 terminal seta	3 aesthetascs of unequal length	5 (2 broad, 3 slender) terminal aesthetascs of unequal length, 1 terminal seta
ANTENNA	pl. 13, fig. 170	fig. 1K	pl. 73H	Fig. 27c
endopod spine	absent	absent	absent	present
MAXILLULE	pl. 13, fig. 172	fig. 1K	pl. 73I	Fig. 28a
coxal endite setation	5	6	not figured	7
MAXILLA	pl. 13, fig. 173	fig. 1M	pl. 73J	Fig. 28b
coxal setation	5+3?	5+4	not figured	5+4
basial setation	3+2?	5+4	not figured	5+4
FIRST MAXILLIPED	pl. 13, fig. 175	fig. 1O	pl. 73A	Fig. 29a
coxal seta	absent	absent	not figured	present
basial setation	6 (1+2+3)	10 (2+2+3+3?)	none	10 (2+2+3+3)
endopod setation, first article	2	2	3	3
endopod setation, second article	1	2	2	2
SECOND MAXILLIPED	pl. 13, fig. 174	fig. 1Q	pl. 73A	Fig. 29b
basial setation	3 (1+1+1)	4 (1+1+1+1)	not figured	4 (1+1+1+1)
endopod setation	0,1,4 (2 subterminal+2 terminal)	0,1,4 (4 terminal?)	1,1,3 (1 subterminal+2 terminal)	0,1,4 (2 subterminal+2 terminal)
TELSON	pl. 13, fig. 176	fig. 1A, C	pl. 73C	Figs. 28c, 30a, b
fork spination	1 small lateral spine + 1 small dorsomedial spine	1 small dorsomedial spine	2 small lateral spines only + 1 small dorsomedial spine	1 small lateral spine only + 1 small dorsomedial spine

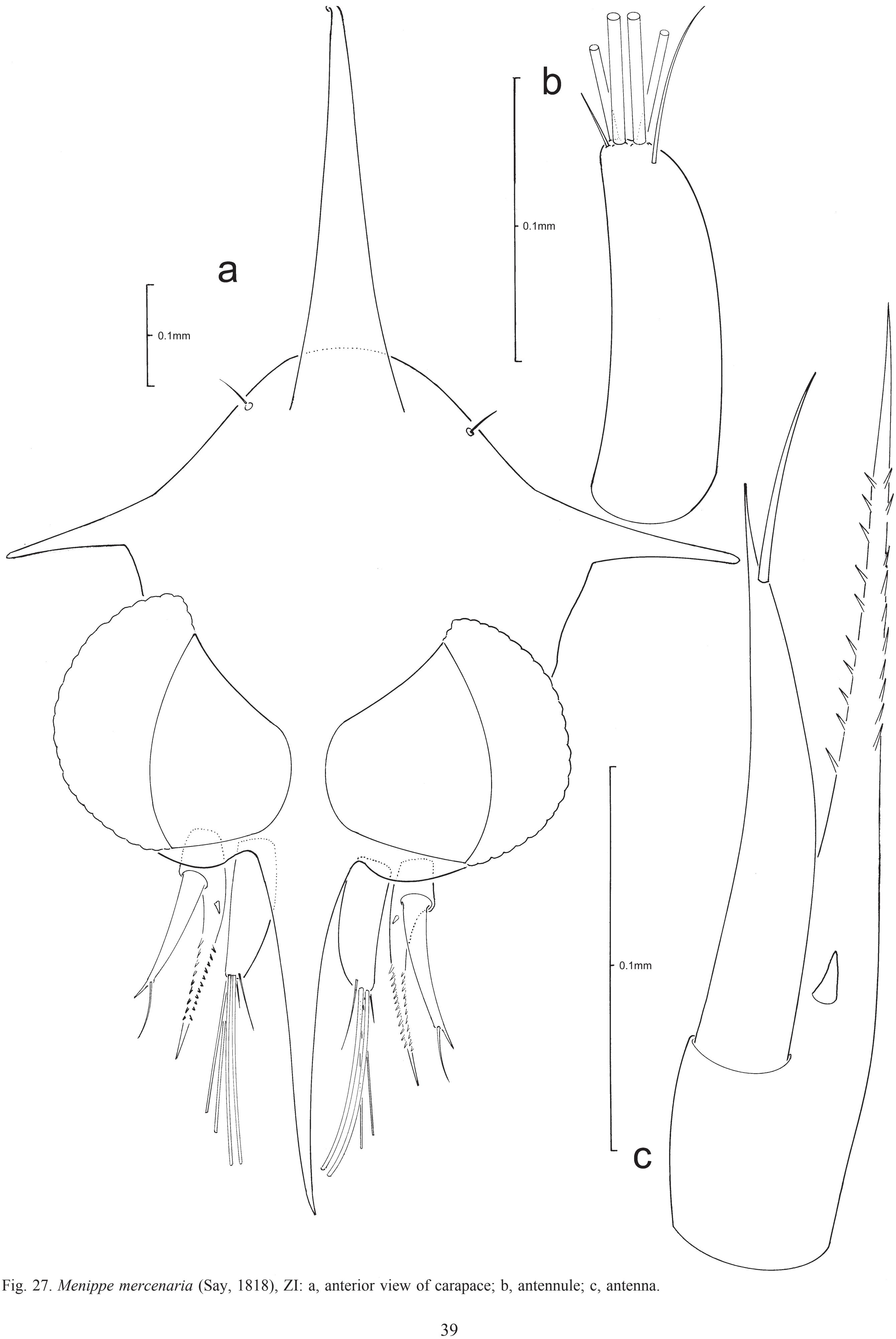

Fig. 27. *Menippe mercenaria* (Say, 1818), ZI: a, anterior view of carapace; b, antennule; c, antenna.

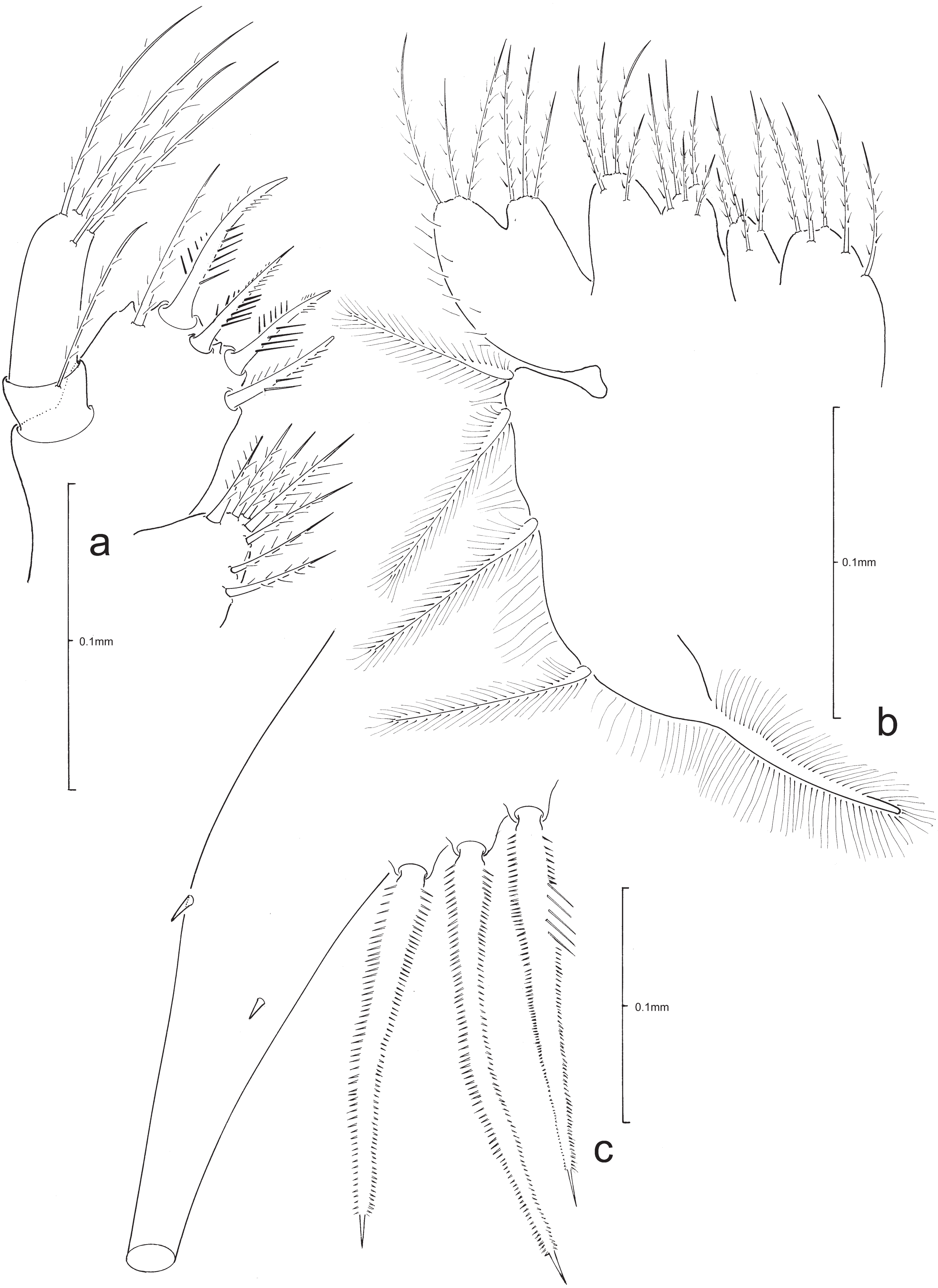

Fig. 28. *Menippe mercenaria* (Say, 1818), ZI: a, maxillule; b, maxilla; c, telson.

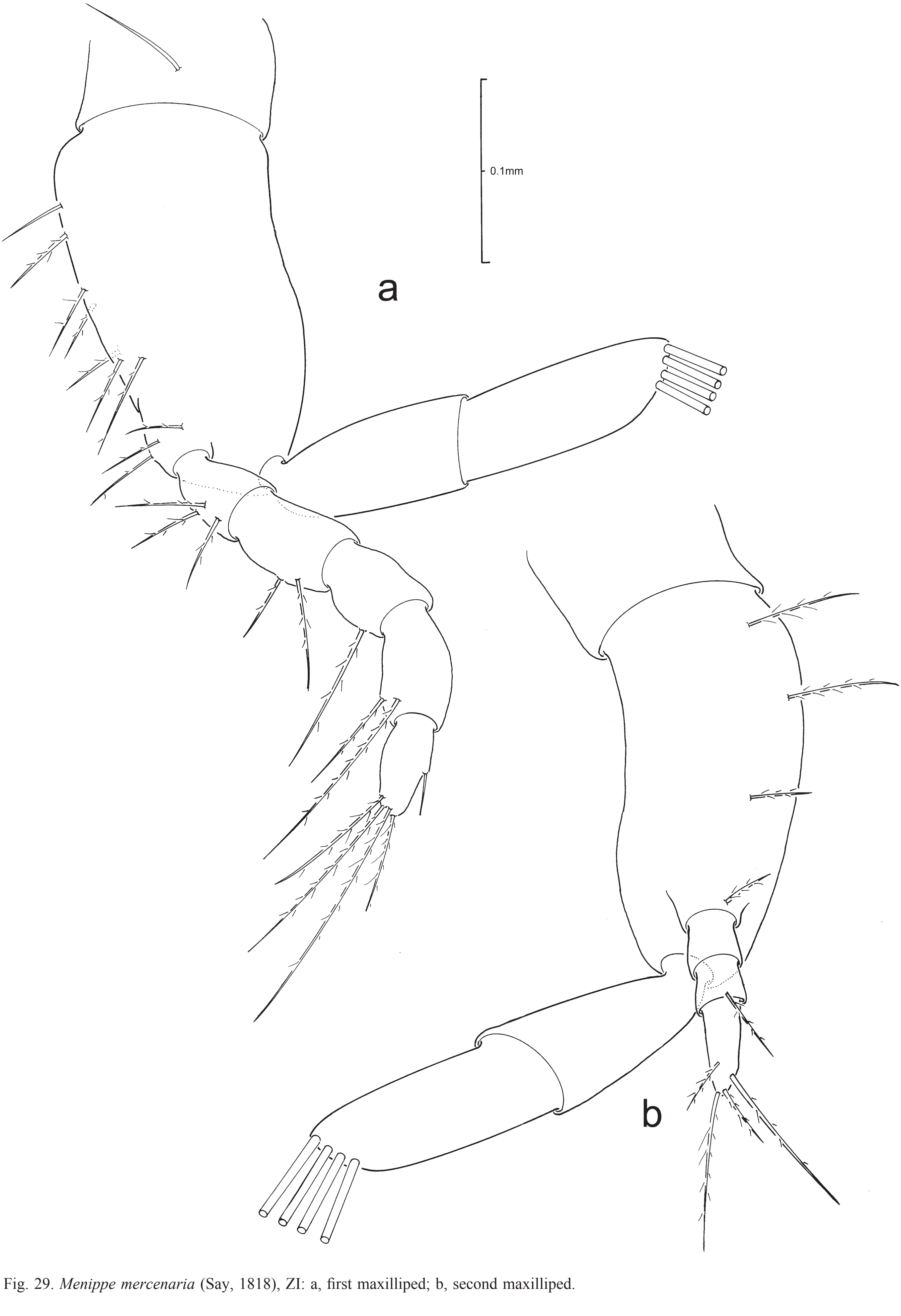

Fig. 29. *Menippe mercenaria* (Say, 1818), ZI: a, first maxilliped; b, second maxilliped.

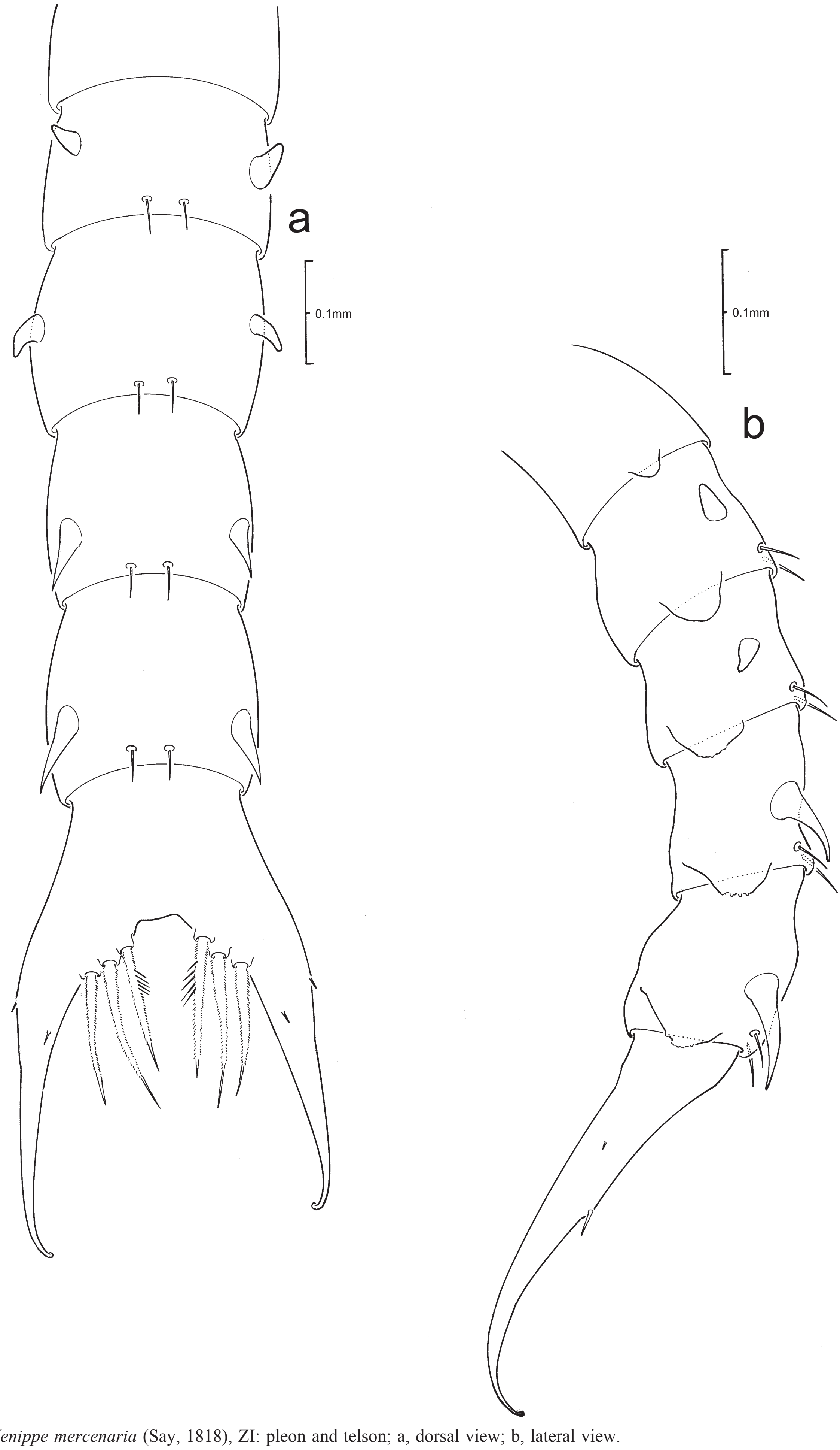

Fig. 30. *Menippe mercenaria* (Say, 1818), ZI: pleon and telson; a, dorsal view; b, lateral view.

Menippe nodifrons **Stimpson, 1859**
(Figs. 31–34)

Menippe nodifrons. Scotto, 1979: 360–374, figs. 1–9 (ZI–VI, Meg.).

Description of Zoea I.

CARAPACE (Fig. 31a): dorsal spine curved distally, relatively short, slightly longer than rostral spine length; rostral spine slightly longer than antennal protopod length, without distal spinulation; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 31a): sessile.
Antennule (Fig. 31b): primary flagellum unsegmented with 5 (2 broad, 3 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 31c): biramous; protopodal process distally bilaterally spinulate, slightly shorter than rostral spine length; endopod spine present; exopod ca. 50.4% length of protopod, possessing 1 long terminal seta plus elongated spine.
Mandible: palp absent.
Maxillule (Fig. 32a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 4 terminal setae; exopod seta absent.
Maxilla (Fig. 32b): biramous; coxal endite bilobed with 5+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+3 setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 33a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 33b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 0,1,4 (2 subterminal+2 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 34a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomere 4 with 1 pair of dorsolateral protuberances; pleomere 5 with long pair of dorsolateral processes directed posteriorly; pleomeres 1–5 each with rounded posterolateral process; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 32c, 34a, b): each fork long, gradually curved distally, not spinulate, 1 small lateral spine only, 1 larger dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Table 4. A comparison between the ZI of *Menippe nodifrons* Stimpson, 1859 by Scotto (1979) and the present study.

Character	Scotto (1979)	Present study
ANTENNULE	fig. 1d	Fig. 31b
terminal setation	4 aesthetascs of unequal length	5 (2 broad, 3 slender) terminal aesthetascs of unequal length, 1 terminal seta
ANTENNA	fig. 1E	Fig. 31c
endopod spine	absent	present
PLEON	fig. 1A, B	Fig. 34a, b
pleomere 4 with 1 pair of dorsolateral protuberances	text: absent fig. 1A present fig. 1B absent	present
TELSON	fig. 1C	Figs. 32c, 34a, b
fork spination	2 small lateral spines + 1 small dorsomedial spine	1 small lateral spine only + 1 small dorsomedial spine

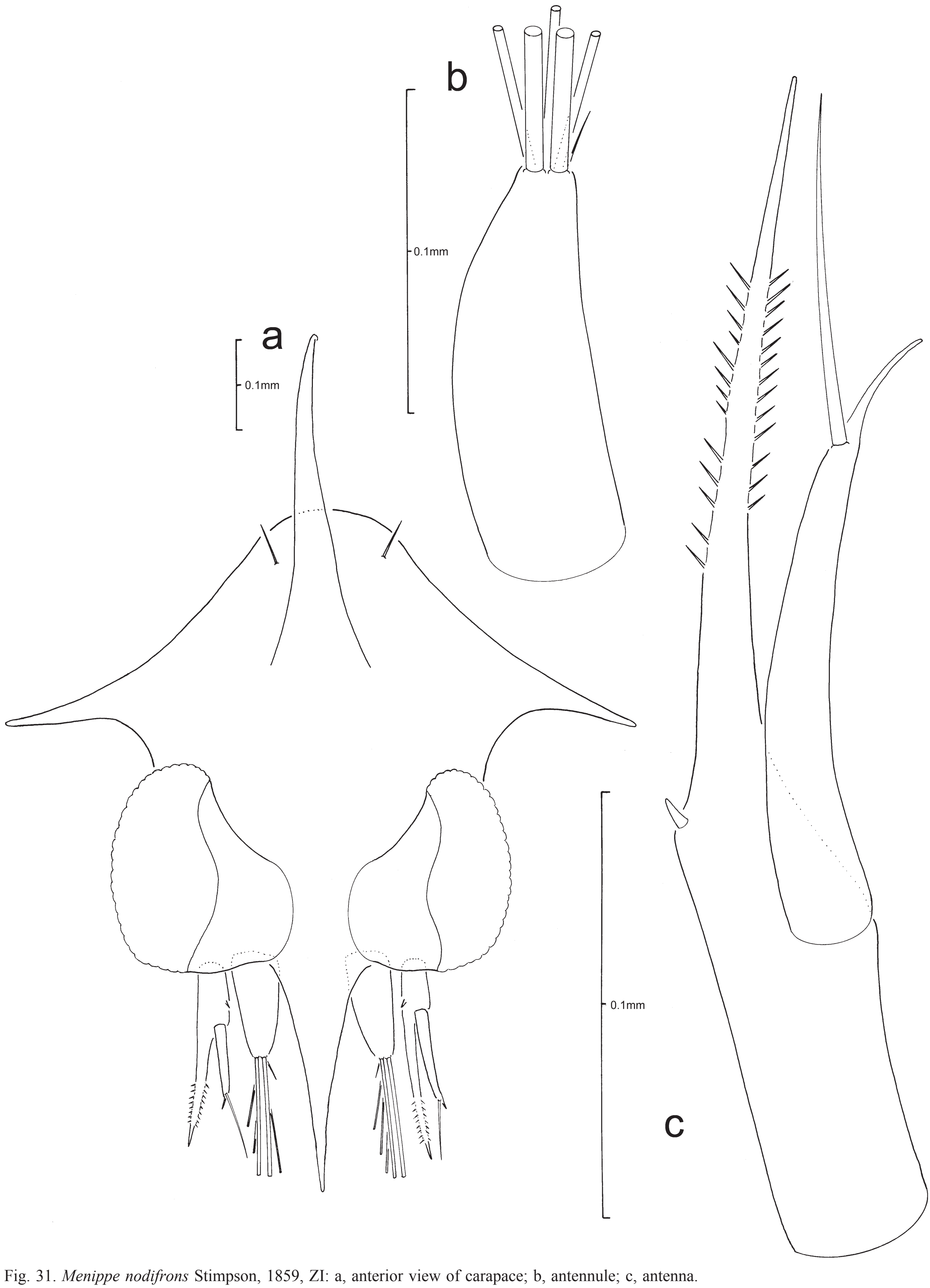

Fig. 31. *Menippe nodifrons* Stimpson, 1859, ZI: a, anterior view of carapace; b, antennule; c, antenna.

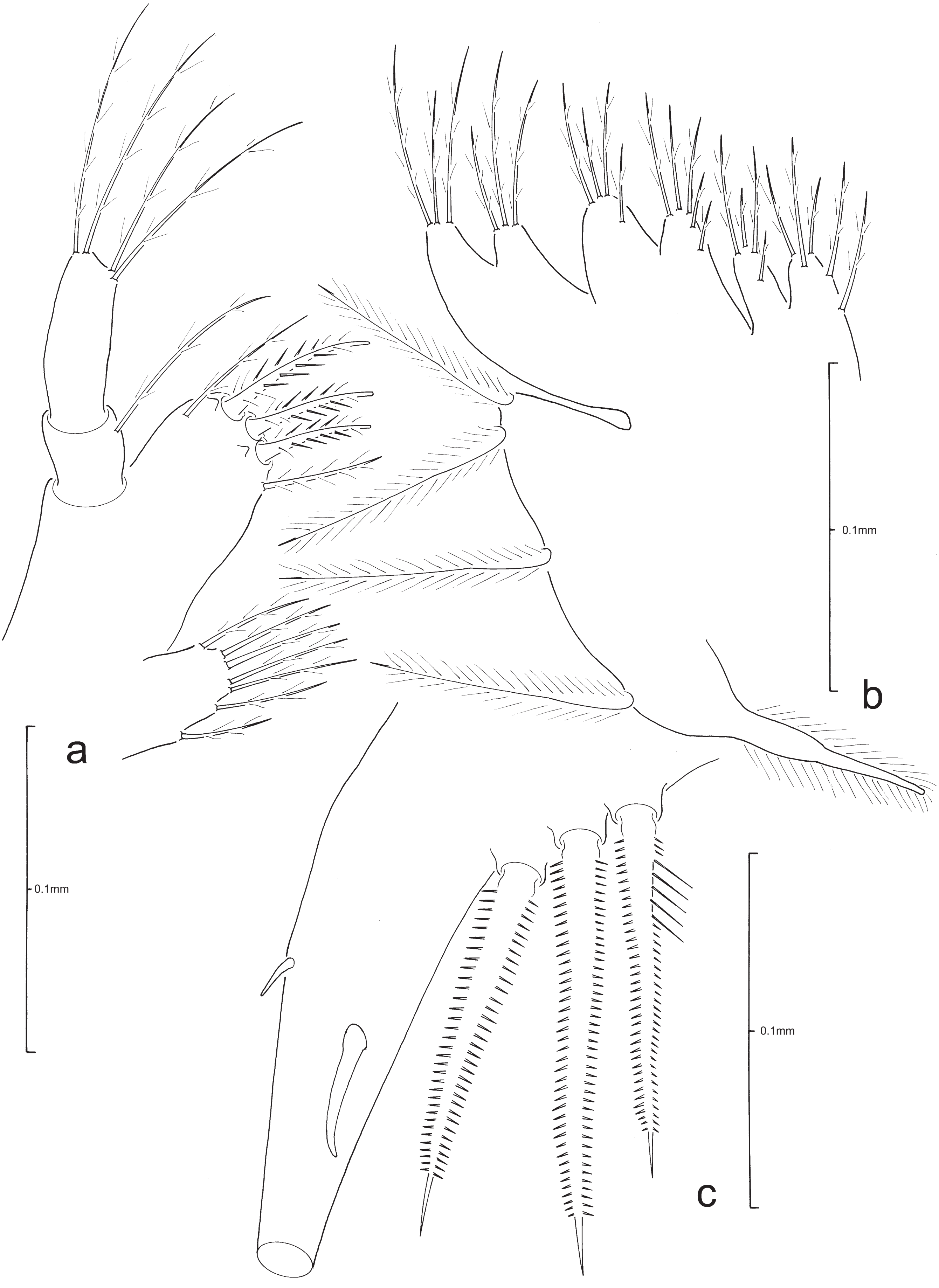

Fig. 32. *Menippe nodifrons* Stimpson, 1859, ZI: a, maxillule; b, maxilla; c, telson.

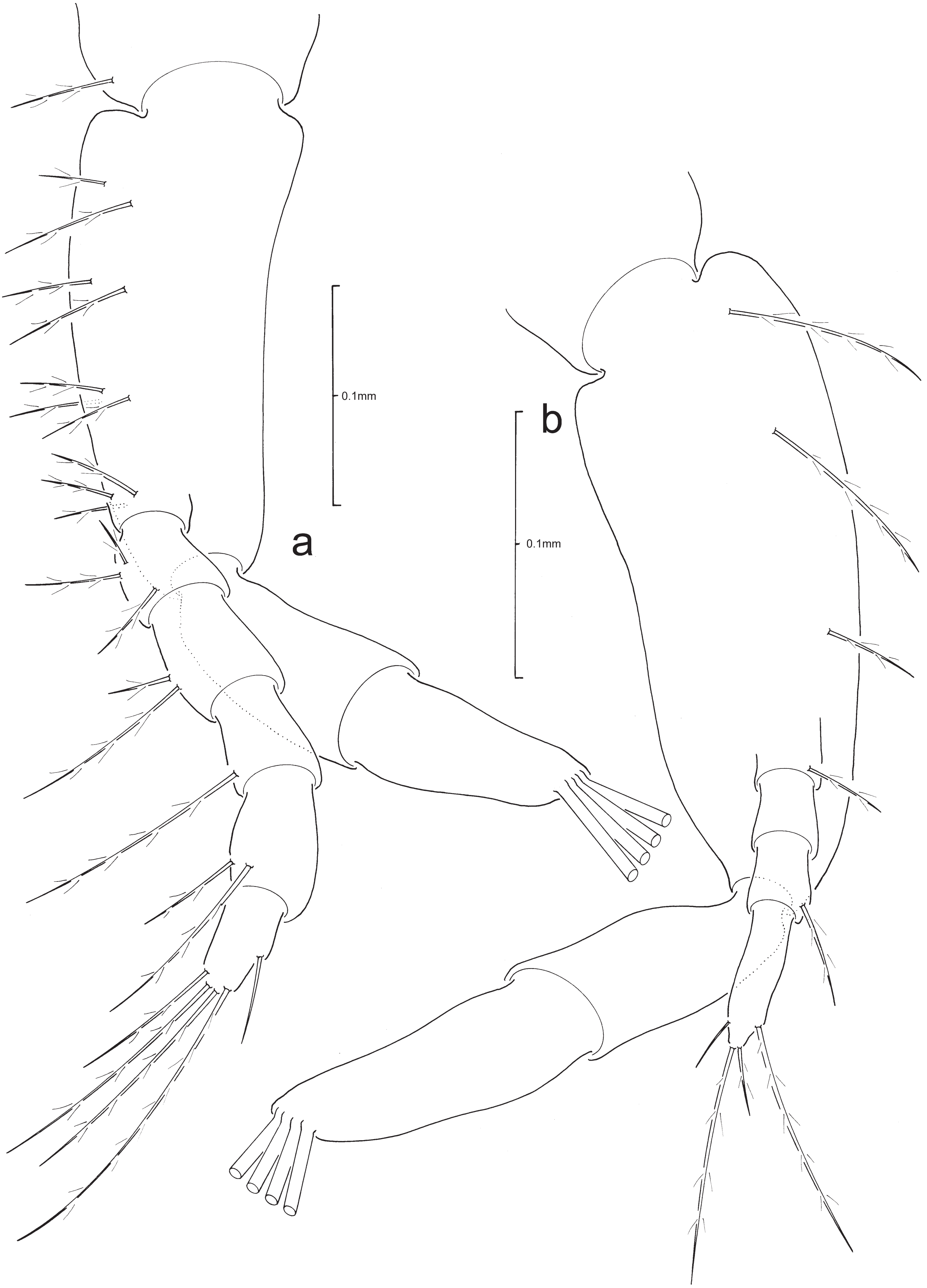

Fig. 33. *Menippe nodifrons* Stimpson, 1859, ZI: a, first maxilliped; b, second maxilliped.

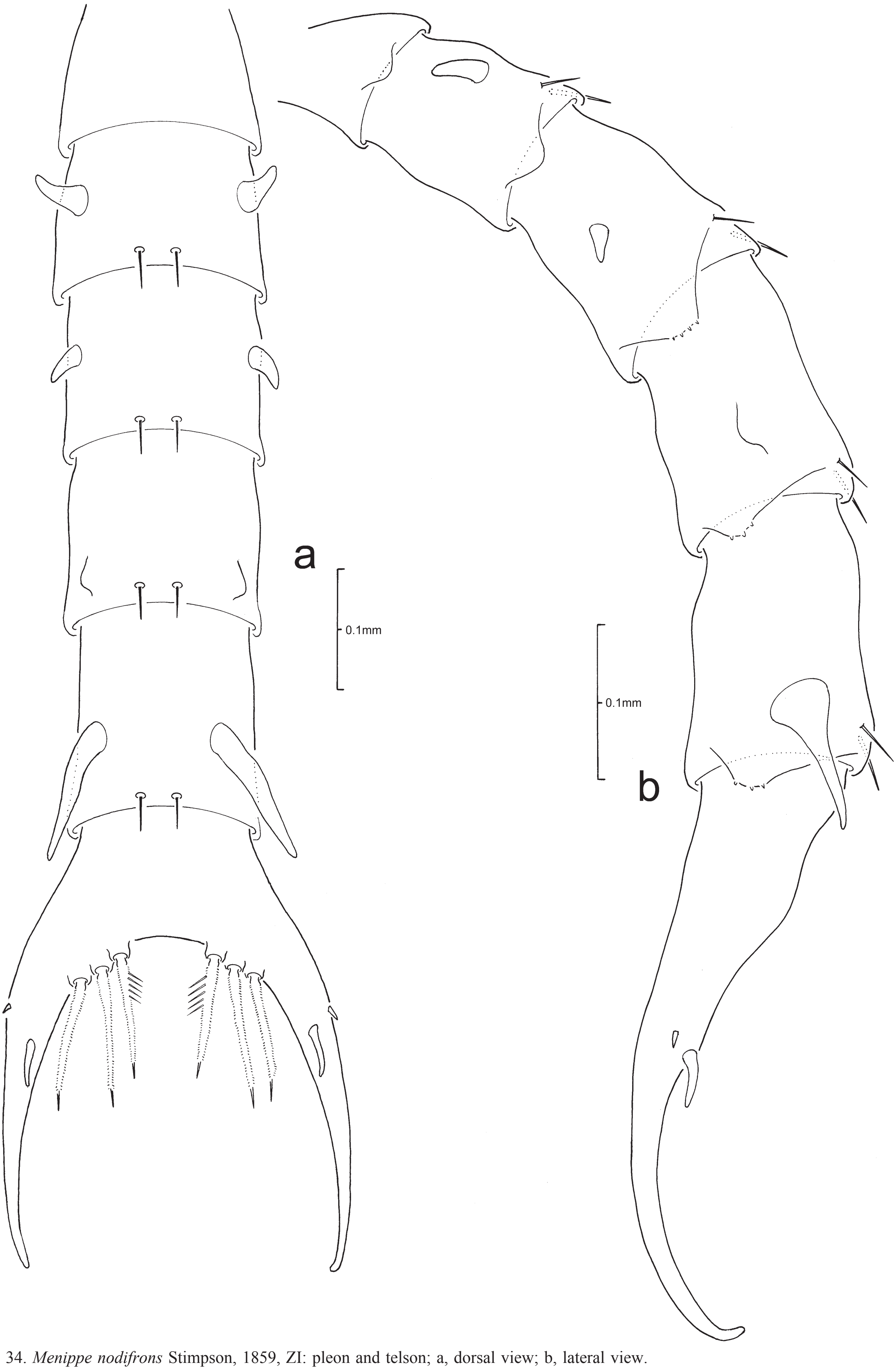

Fig. 34. *Menippe nodifrons* Stimpson, 1859, ZI: pleon and telson; a, dorsal view; b, lateral view.

Menippe rumphii **(J.C. Fabricius, 1798)**
(Figs. 35–38)

Menippe rumphii. Prasad & Tampi, 1957: 25, 26, fig. 2 (ZI); Kakati, 1977: 635–640, figs. 1–2 (ZI–V, Meg.); Ghory, 2009: 77–81, fig. 1 (ZI).

Description of Zoea I.
CARAPACE (Fig. 35a): dorsal spine curved distally, relatively long, slightly longer than rostral spine length; rostral spine longer than antennal protopod length, without distal spinulation; lateral spines straight with swollen at tips, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 35a): sessile.
Antennule (Fig. 35b): primary flagellum unsegmented with 5 (2 broad, 3 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 35c): biramous; protopodal process distally bilaterally spinulate, shorter than rostral spine length; endopod spine present; exopod ca. 42.2% length of protopod, possessing 1 long terminal seta plus elongated process.
Mandible: palp absent.
Maxillule (Fig. 36a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 4 terminal setae; exopod seta absent.
Maxilla (Fig. 36b): biramous; coxal endite bilobed with 5+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+3 setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 37a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 37b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 0,1,4 (2 subterminal+2 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 38a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–4 each with rounded posterolateral processes; pleomere 5 with an exceedingly long posterolateral spinous process; pleomere 1 without setae; pleomeres 2–5 with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 36c, 38a, b): each fork long, gradually curved distally, not spinulate, 1 lateral seta only, 1 dorsomedial seta present; posterior margin with 3 pairs of stout spinulate setae.

Table 5. A comparison between the ZI of *Menippe rumphii* (J.C. Fabricius, 1798) by Prasad & Tampi (1957), Kakati (1977), Ghory (2009) and the present study.

Character	**Prasad & Tampi (1957)**	**Kakati (1977)**	**Ghory (2009)**	**Present study**
CARAPACE	fig. 2a	fig. 1.1	fig. 1A, B	Fig. 35a
posterodorsal setae	absent	1 pair present	1 pair present	1 pair present
ANTENNULE	fig. 2b	fig. 1.2	fig. 1C	Fig. 35b
terminal setation	4 terminal aesthetascs of unequal length	2 terminal aesthetascs of unequal length plus 1 terminal seta	2 terminal aesthetascs	5 (2 broad, 3 slender) terminal aesthetascs of unequal length, 1 terminal seta
ANTENNA	fig. 2c	fig. 1.3	fig. 1D	Fig. 35c
endopod spine	absent	present	present	present
MAXILLULE	fig. 2e	fig. 1.5	fig. 1F	Fig. 36a
coxal endite setation	6	7	6	7
FIRST MAXILLIPED	fig. 2g	fig. 1.7	fig. 1H	Fig. 37a
coxal seta	present	absent	absent	present
basial setation	6 (1+1+2+2?)	10 (2+2+3+3?)	10 (2+2+3+3)	10 (2+2+3+3)
endopod setation	2,2,1,2,4 (terminal?)	2,2,1,2,5 (1 subterminal+4 terminal)	2,2,1,2,5 (1 subterminal+4 terminal)	2,2,1,2,5 (1 subterminal+4 terminal)
SECOND MAXILLIPED	fig. 2h	fig. 1.8	fig. 1I	Fig. 37b
basial setation	5	4	4	4
endopod setation of first article	1	0	0	0
TELSON	fig. 2h	fig. 1.8	fig. 1K	Figs. 36c, 38a, b
fork spination	absent	absent	1 small lateral spine only	1 small lateral spine only + 1 small dorsomedial spine

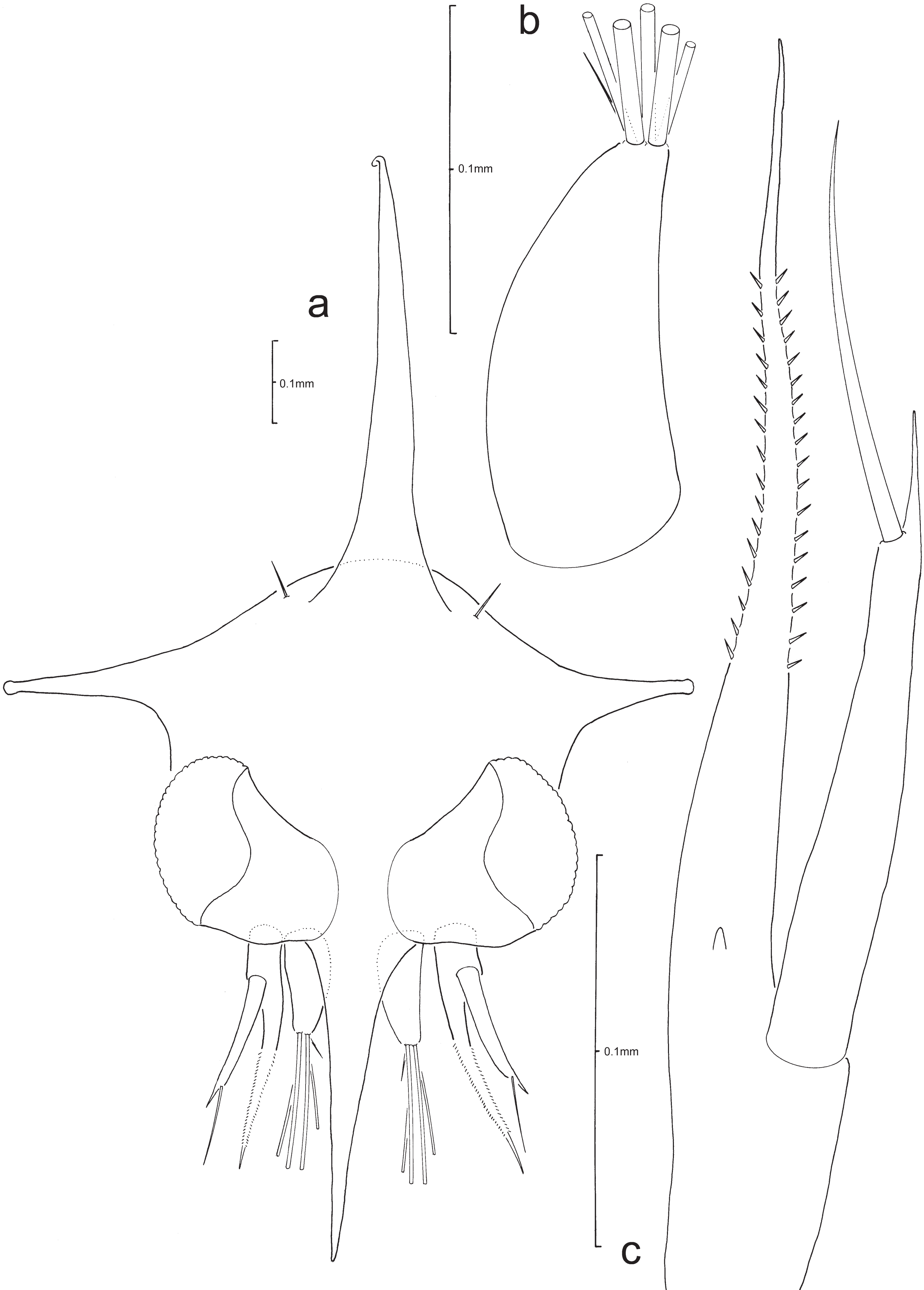

Fig. 35. *Menippe rumphii* (J.C. Fabricius, 1798), ZI: a, anterior view of carapace; b, antennule; c, antenna.

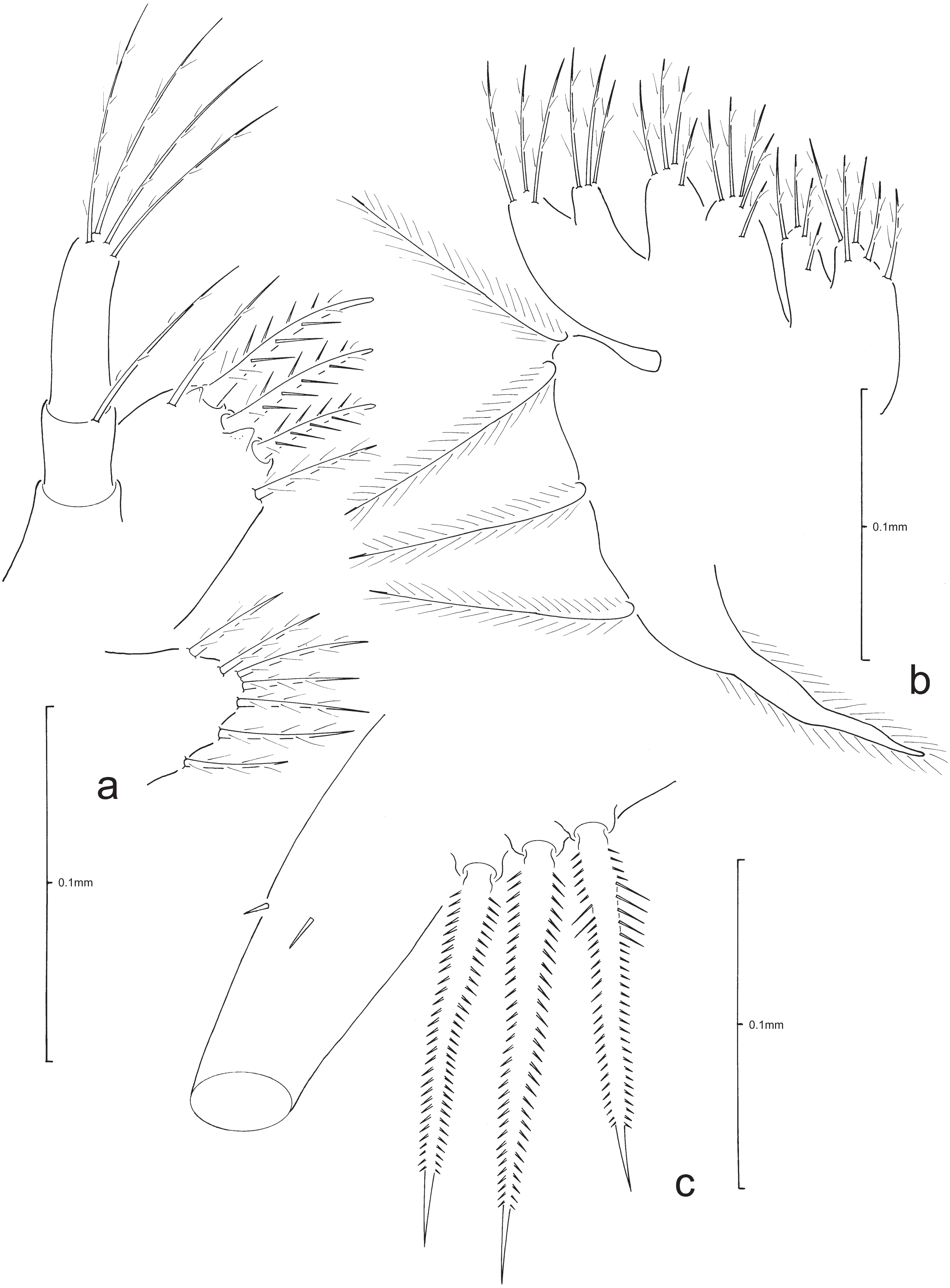

Fig. 36. *Menippe rumphii* (J.C. Fabricius, 1798), ZI: a, maxillule; b, maxilla; c, telson.

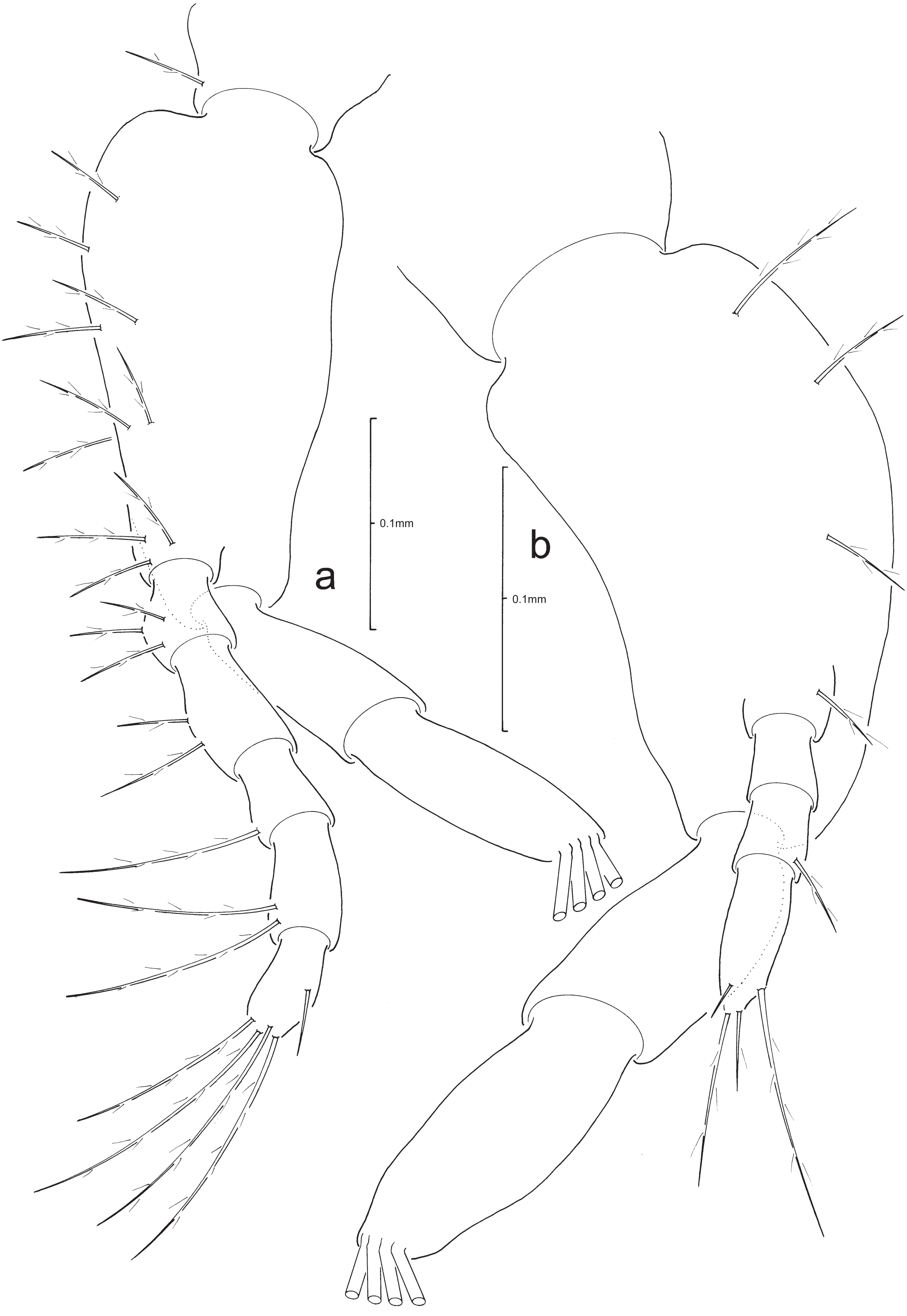

Fig. 37. *Menippe rumphii* (J.C. Fabricius, 1798), ZI: a, first maxilliped; b, second maxilliped.

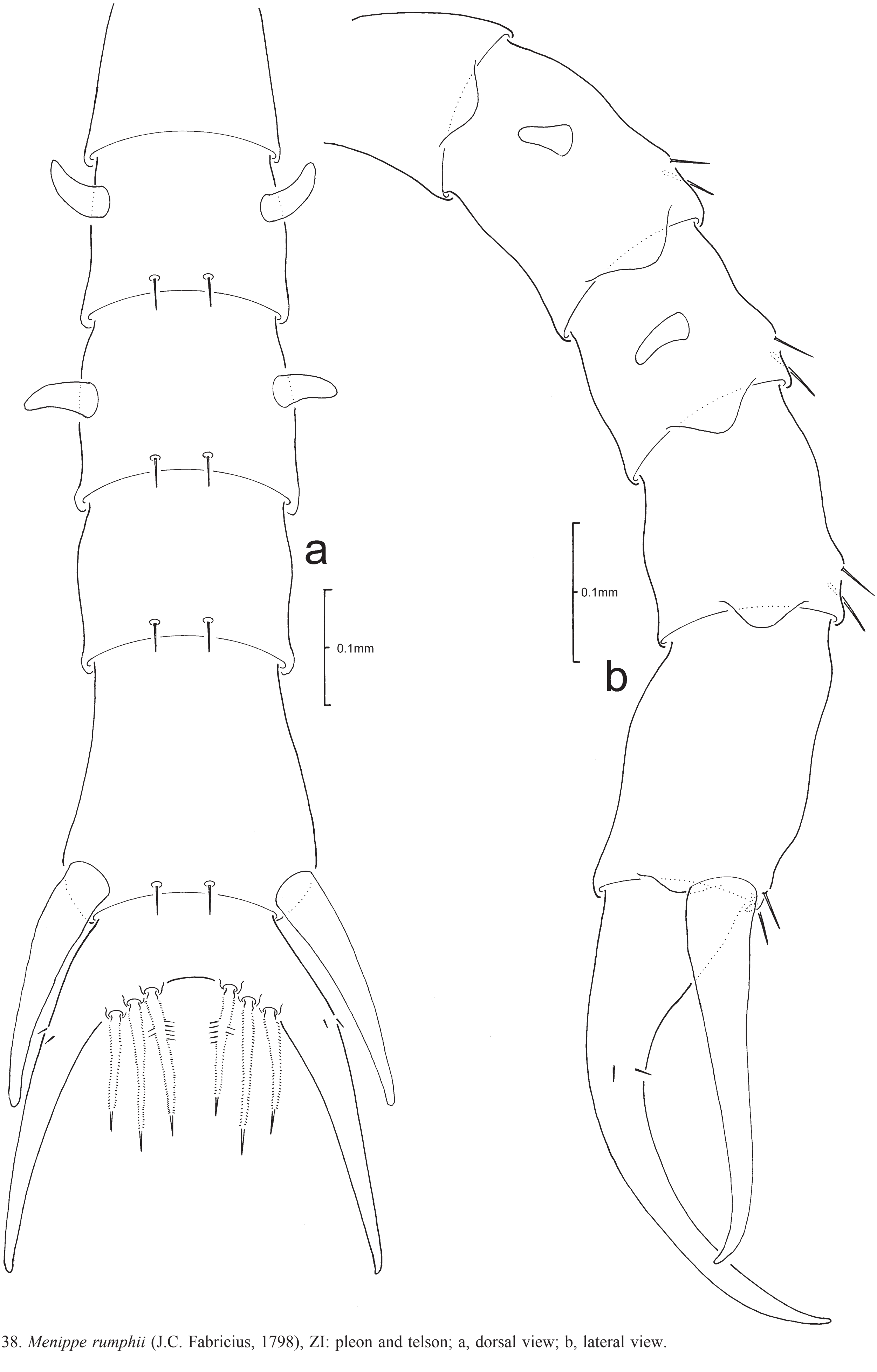

Fig. 38. *Menippe rumphii* (J.C. Fabricius, 1798), ZI: pleon and telson; a, dorsal view; b, lateral view.

Myomenippe hardwickii (Gray, 1831)

(Figs. 39–42)

Description of Zoea I.

CARAPACE (Fig. 39a, b): dorsal spine curved distally, relatively long, slightly longer than rostral spine length; rostral spine much longer than antennal protopod length, granulate; lateral spines relatively long, straight, with tips turned posteriorly, granulate on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin with 4 posterior setae.

CEPHALON

Eyes (Fig. 39a): sessile.

Antennule (Fig. 39c): primary flagellum unsegmented with 5 (2 broad, 3 slender) terminal aesthetascs of unequal length + 1 terminal seta; accessory flagellum absent.

Antenna (Fig. 39d): biramous; protopodal process distally multispinulate, much shorter than rostral spine length; endopod spine present; exopod ca. 65.6% length of protopod, possessing 1 long terminal seta plus elongated spine.

Mandible: palp absent.

Maxillule (Fig. 40a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 4 terminal setae; exopod seta absent.

Maxilla (Fig. 40b): biramous; coxal endite bilobed with 5+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+3 setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION

First maxilliped (Fig. 41a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 41b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,4 (2 subterminal+2 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

PLEON (Fig. 42a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 without dorsolateral processes; pleomere 4 with pair of relatively short lateral processes directed ventrally; pleomere 5 with 1 pair of dorsolateral processes directed ventrally, slightly longer than pleomere; pleomeres 1, 2, 5 each with rounded posterolateral processes; pleomeres 3–4 each with short posterolateral spinous processes; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 40c, 42a, b): each fork extremely long, gradually curved distally, not spinulate, lateral spines absent, 1 dorsomedial seta present; posterior margin with 3 pairs of stout spinulate setae.

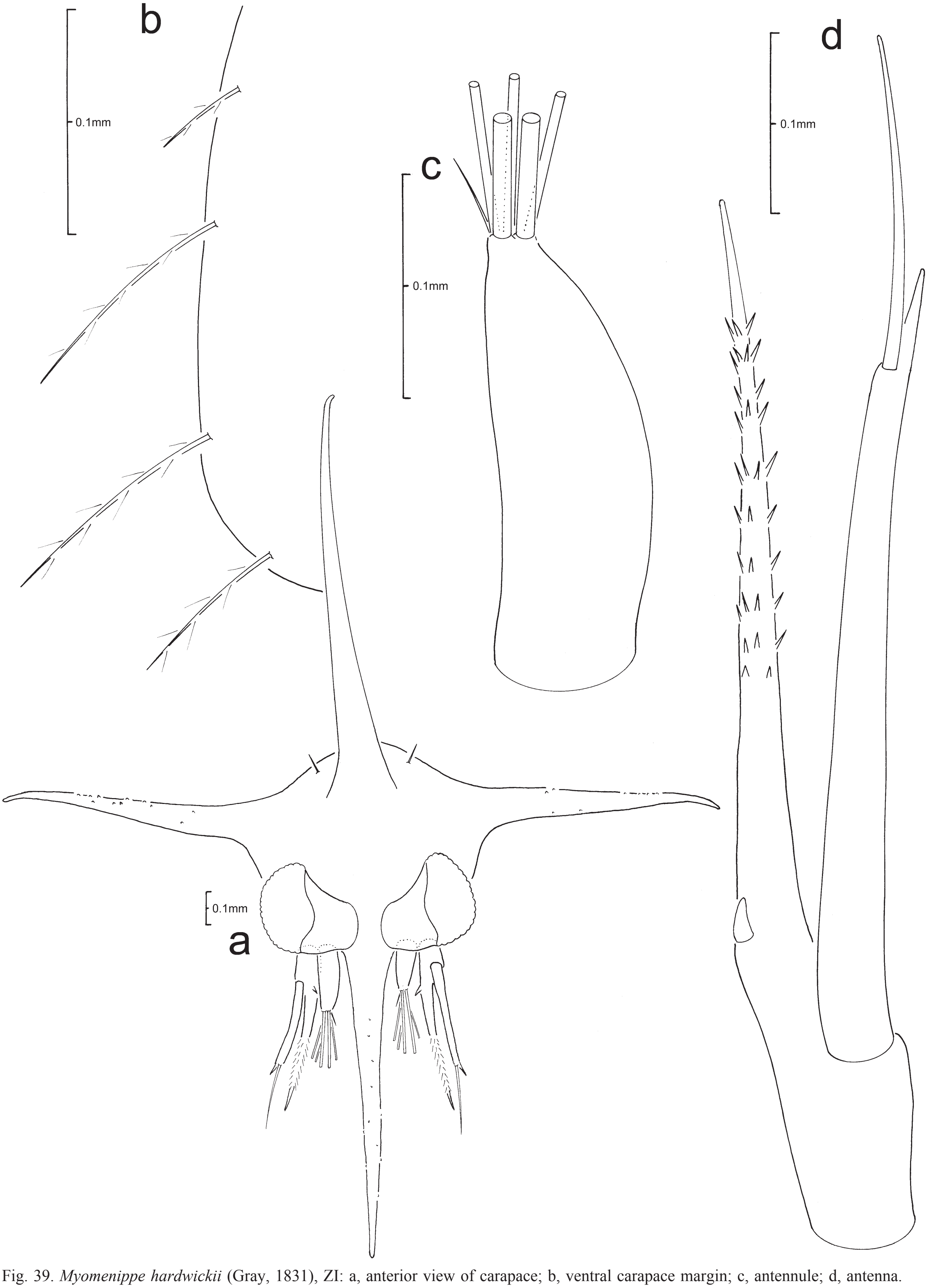

Fig. 39. *Myomenippe hardwickii* (Gray, 1831), ZI: a, anterior view of carapace; b, ventral carapace margin; c, antennule; d, antenna.

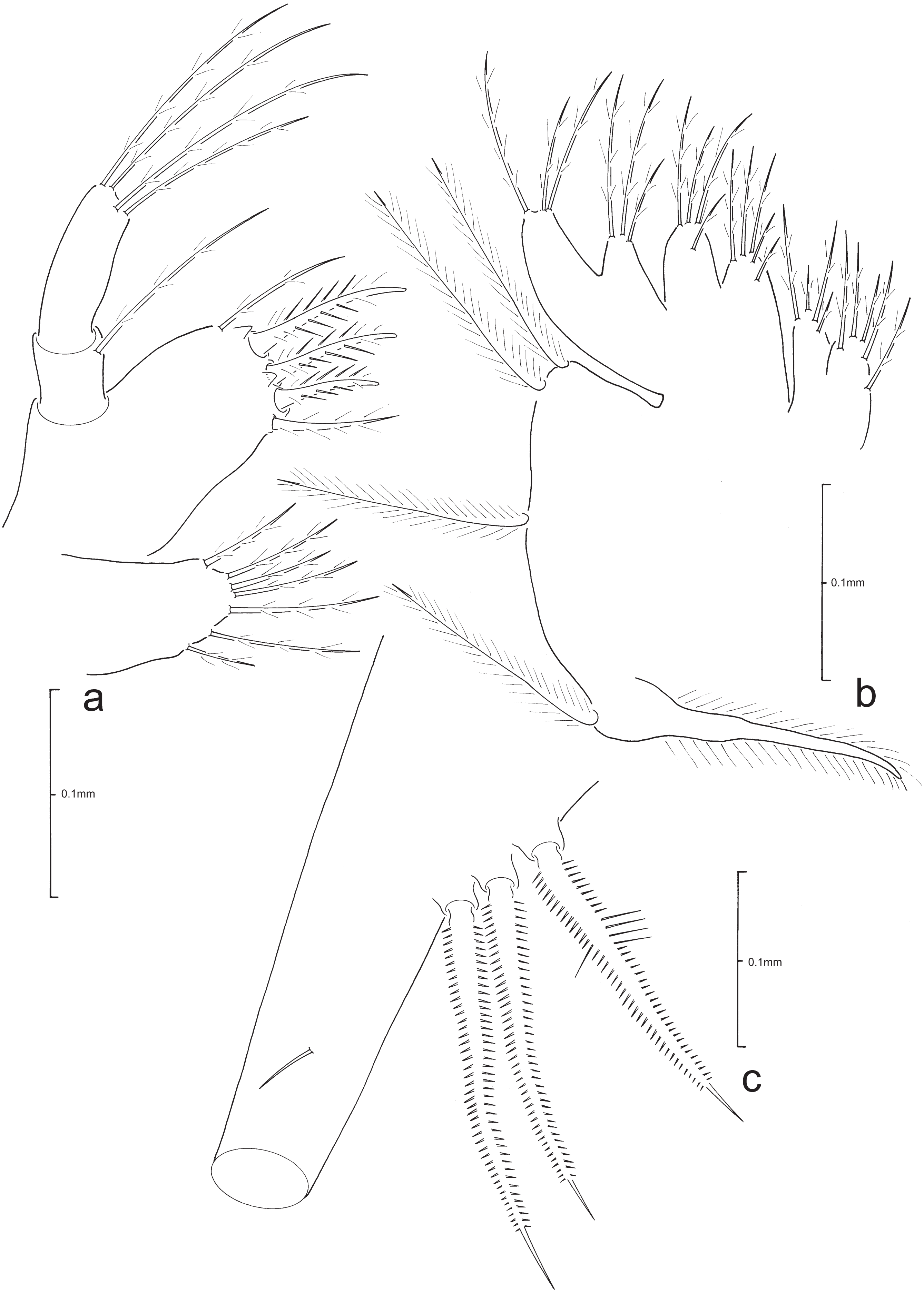

Fig. 40. *Myomenippe hardwickii* (Gray, 1831), ZI: a, maxillule; b, maxilla; c, telson.

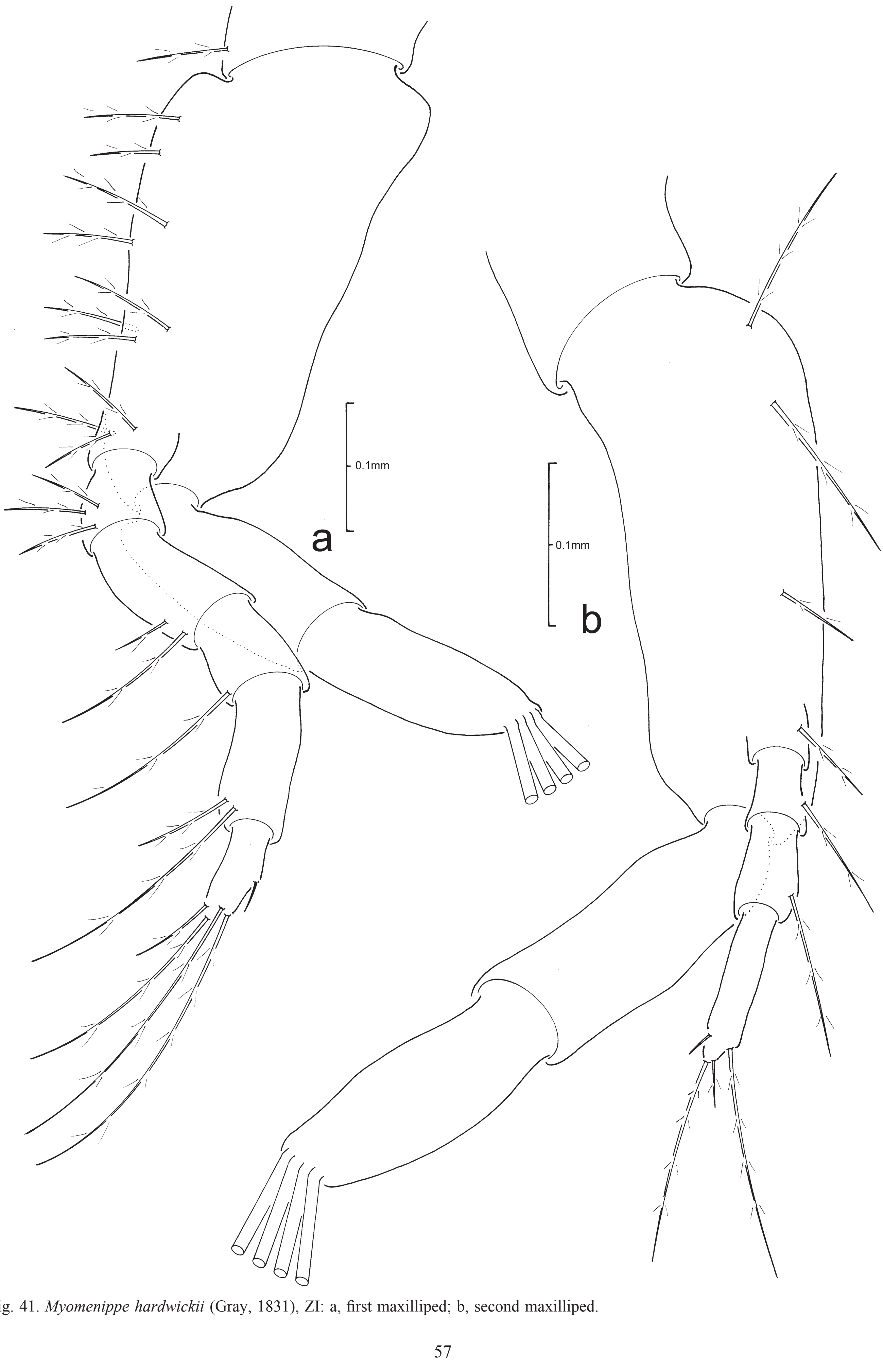

Fig. 41. *Myomenippe hardwickii* (Gray, 1831), ZI: a, first maxilliped; b, second maxilliped.

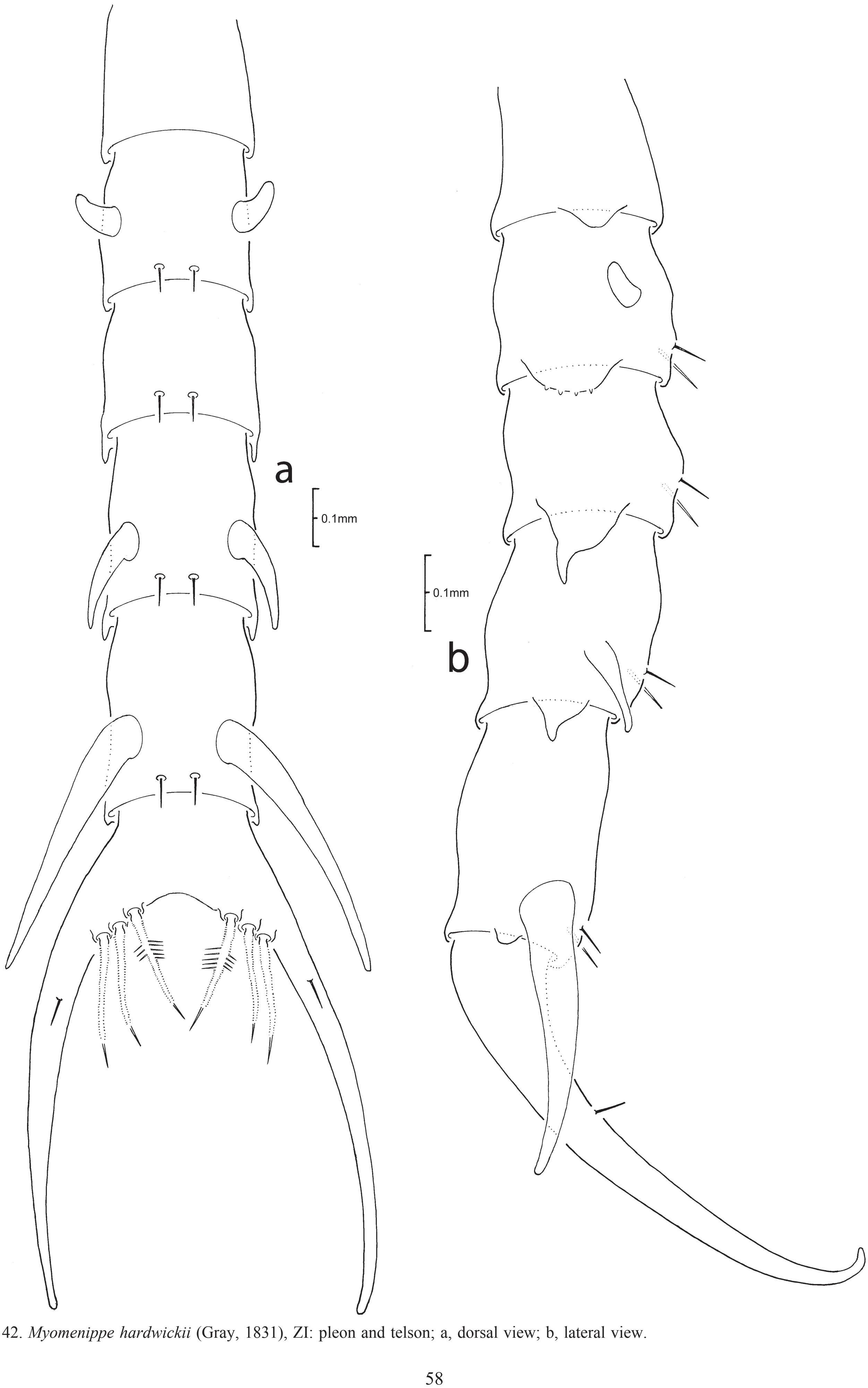

Fig. 42. *Myomenippe hardwickii* (Gray, 1831), ZI: pleon and telson; a, dorsal view; b, lateral view.

Family Oziidae Dana, 1851

Ozius truncatus H. Milne Edwards, 1834
(Figs. 43–46)

Ozius truncatus. Wear, 1968: 307–322, figs. 26–74 (ZI–IV, Meg.); Wear & Fielder, 1985: 60, figs. 154–157 (ZI, Meg.).

Description of Zoea I.
CARAPACE (Fig. 43a): dorsal spine curved distally, longer than rostral spine length; rostral spine much longer than antennal protopod length, without distal spinulation; lateral spines curved ventrally, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 43a): sessile.
Antennule (Fig. 43b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 43c): biramous; protopodal process distally, bilaterally spinulate, much shorter than rostral spine length; endopod spine present; exopod ca. 37% length of protopod, possessing 3 (1 long subterminal+2 terminal of unequal length) setae plus small elongated spine.
Mandible: palp absent.
Maxillule (Fig. 44a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 44b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 45a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 45b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 46a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomere 1 with median dorsal process; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 44c, 46a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine with spinule present, positioned more dorsally, dorsomedial spine absent; posterior margin with 3 pairs of stout spinulate setae.

Table 6. A comparison between the ZI of *Ozius truncatus* H. Milne Edwards, 1834 by Wear (1968) and the present study.

Character	Wear (1968)	Present study
ANTENNULE	fig. 33	Fig. 43b
terminal setation	3 aesthetascs	4 (2 broad, 2 slender) aesthetascs of unequal length, 1 terminal seta
ANTENNA	fig. 34	Fig. 43c
endopod spine	absent	present
MAXILLULE	fig. 36	Fig. 44a
coxal setation	text: 5 or 6 fig.: 5	7
basial setation	text: 5 or 6 fig.: 6	5
MAXILLA	fig. 37	Fig. 44b
coxal endite setation	4+4	6+4
basial endite setation	4+4	5+4
FIRST MAXILLIPED	fig. 38	Fig. 45a
basial setation	text: 10 to 12 fig.: 12	10 (2+2+3+3)
endopod setation	1,1,1,2,4	3,2,1,2,5 (1 subterminal+4 terminal)
SECOND MAXILLIPED	fig. 39	Fig. 45b
endopod setation	1,2,4	1,1,6 (3 subterminal+3 terminal)

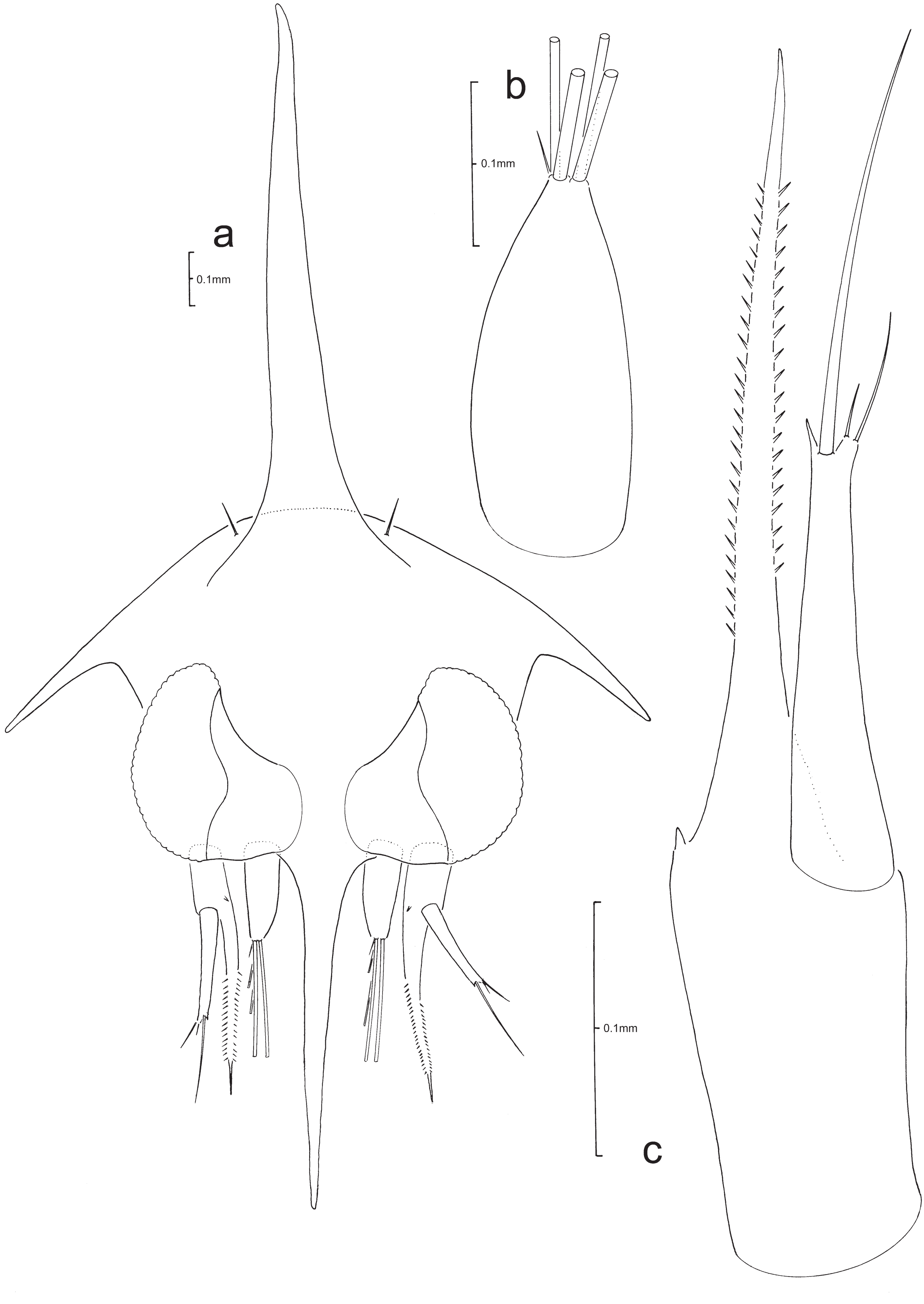

Fig. 43. *Ozius truncatus* H. Milne Edwards, 1834, ZI: a, anterior view of carapace; b, antennule; c, antenna.

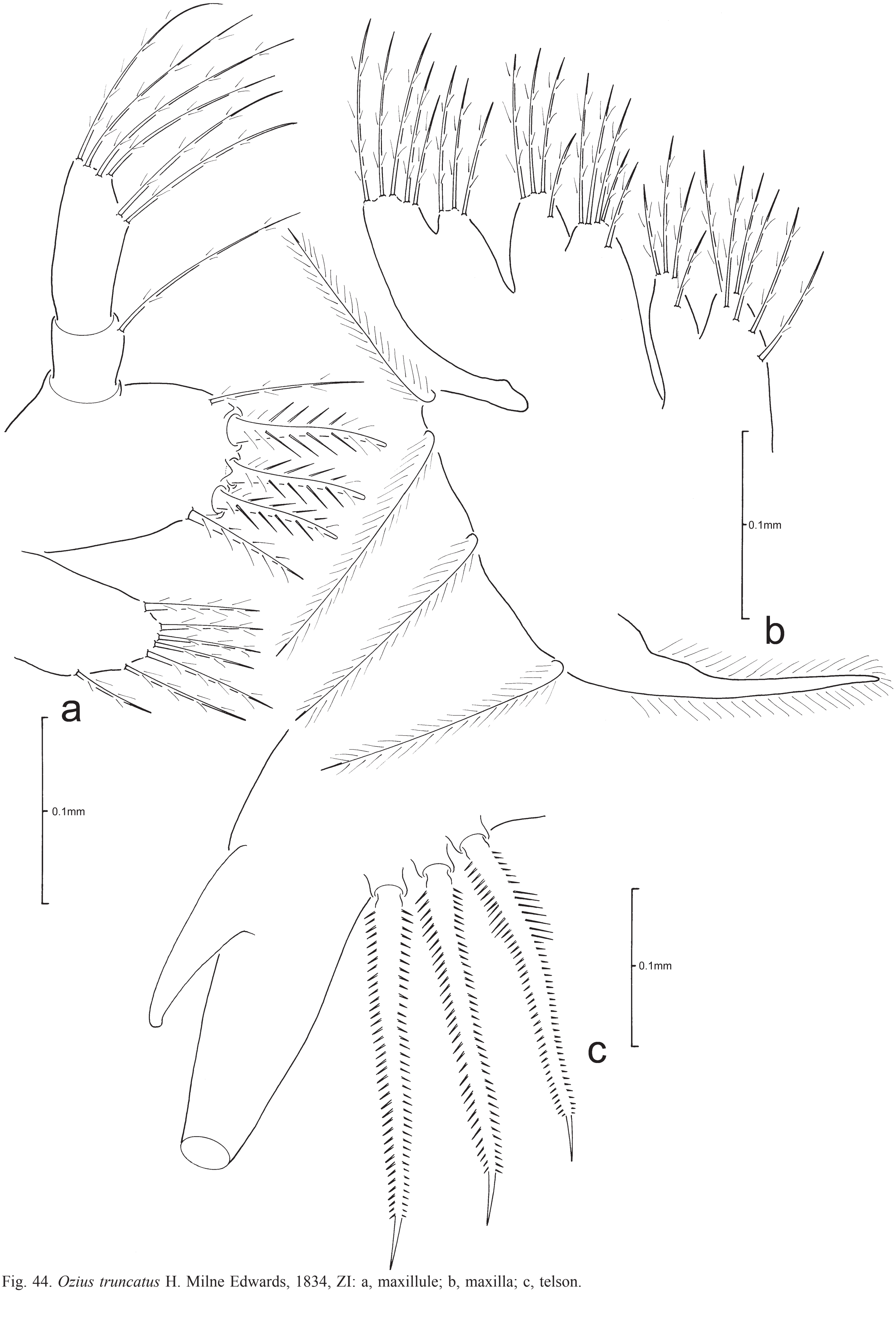

Fig. 44. *Ozius truncatus* H. Milne Edwards, 1834, ZI: a, maxillule; b, maxilla; c, telson.

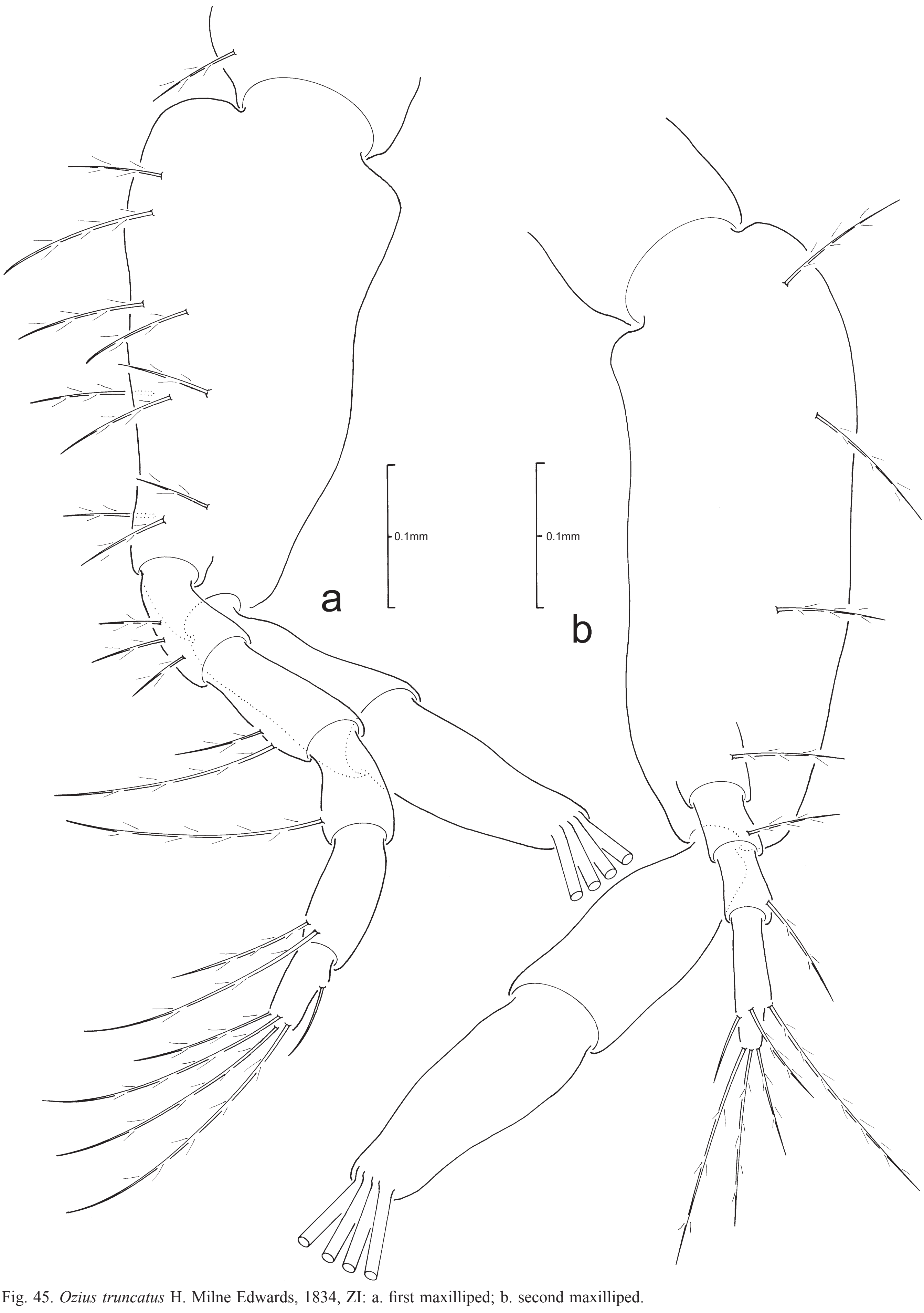

Fig. 45. *Ozius truncatus* H. Milne Edwards, 1834, ZI: a. first maxilliped; b. second maxilliped.

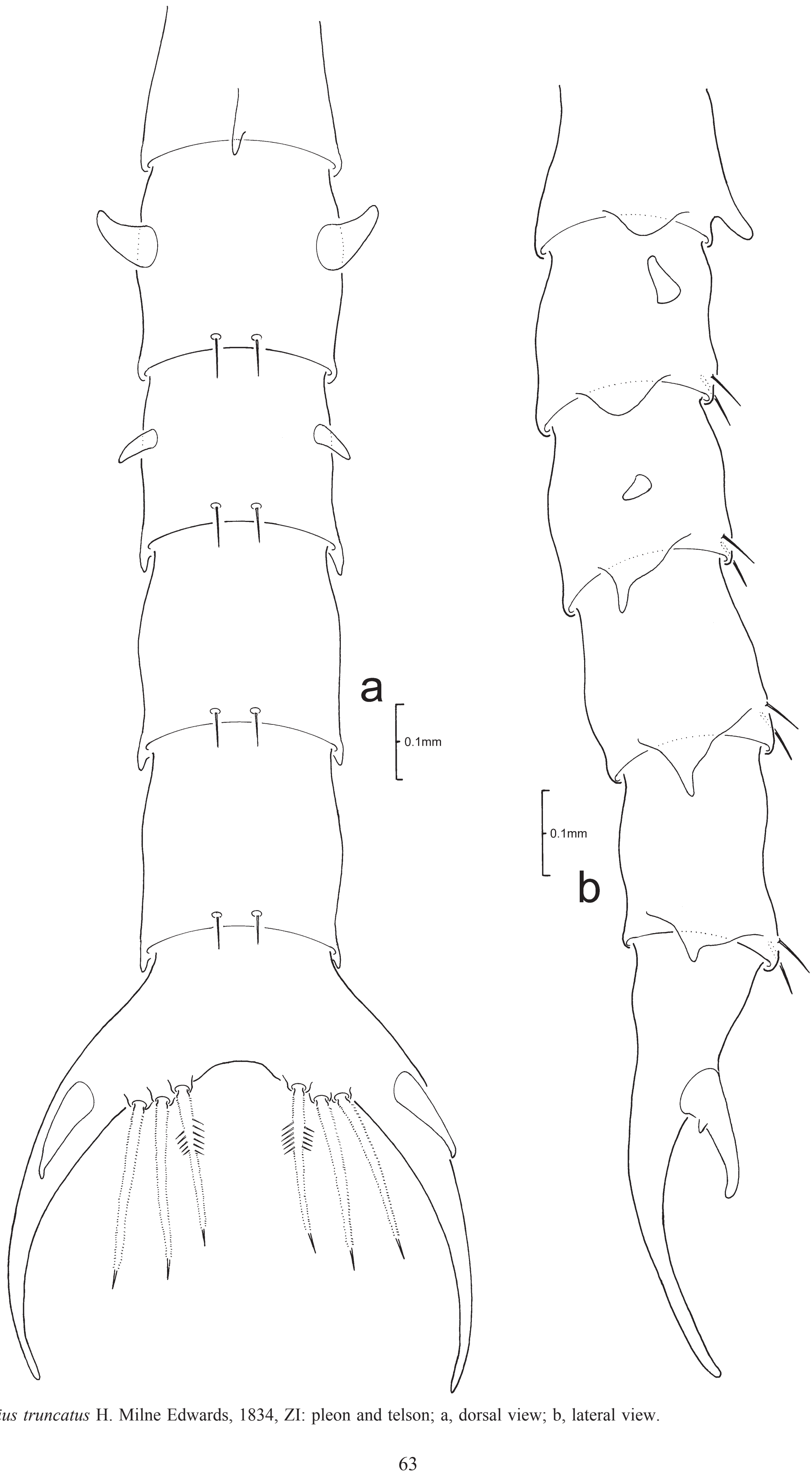

Fig. 46. *Ozius truncatus* H. Milne Edwards, 1834, ZI: pleon and telson; a, dorsal view; b, lateral view.

Superfamily Pilumnoidea Samouelle, 1819

Family Galenidae Alcock, 1898

Subfamily Parapanopinae Števčić, 2005

***Parapanope euagora* De Man, 1895**
(Figs. 47–50)

non *Parapanope eugora*. Lee & Ko, 2016: 135, fig. 1B (ZI) = *P. orientalis* P.K.L. Ng & Guinot, 2021.

Description of Zoea I.
CARAPACE (Fig. 47a): dorsal spine curved distally, longer than rostral spine length; rostral spine much longer than antennal protopod length, without distal spinulation; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 47a): sessile.
Antennule (Fig. 47b): primary flagellum unsegmented with 4 (2 broad, 2 slender) aesthetascs of unequal length plus 2 terminal setae of unequal length; accessory flagellum absent.
Antenna (Fig. 47c): uniramous; protopod distally bilaterally spinulate, much shorter than rostral spine length; endopod bud absent; exopod distally bilaterally spinulate with 2 medial setae of unequal length.
Mandible: palp absent.
Maxillule (Fig. 48a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 terminal setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 48b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal setae); exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 49a): biramous; coxa without setae; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 49b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 50a, b): 5 pleomeres; pleomere 2 with pair of dorsolateral processes directed anteriorly; pleomere 3 with pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without dorsal setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 48c, 50a, b): each fork long, spinulate, gradually curved distally, 2 lateral setae, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

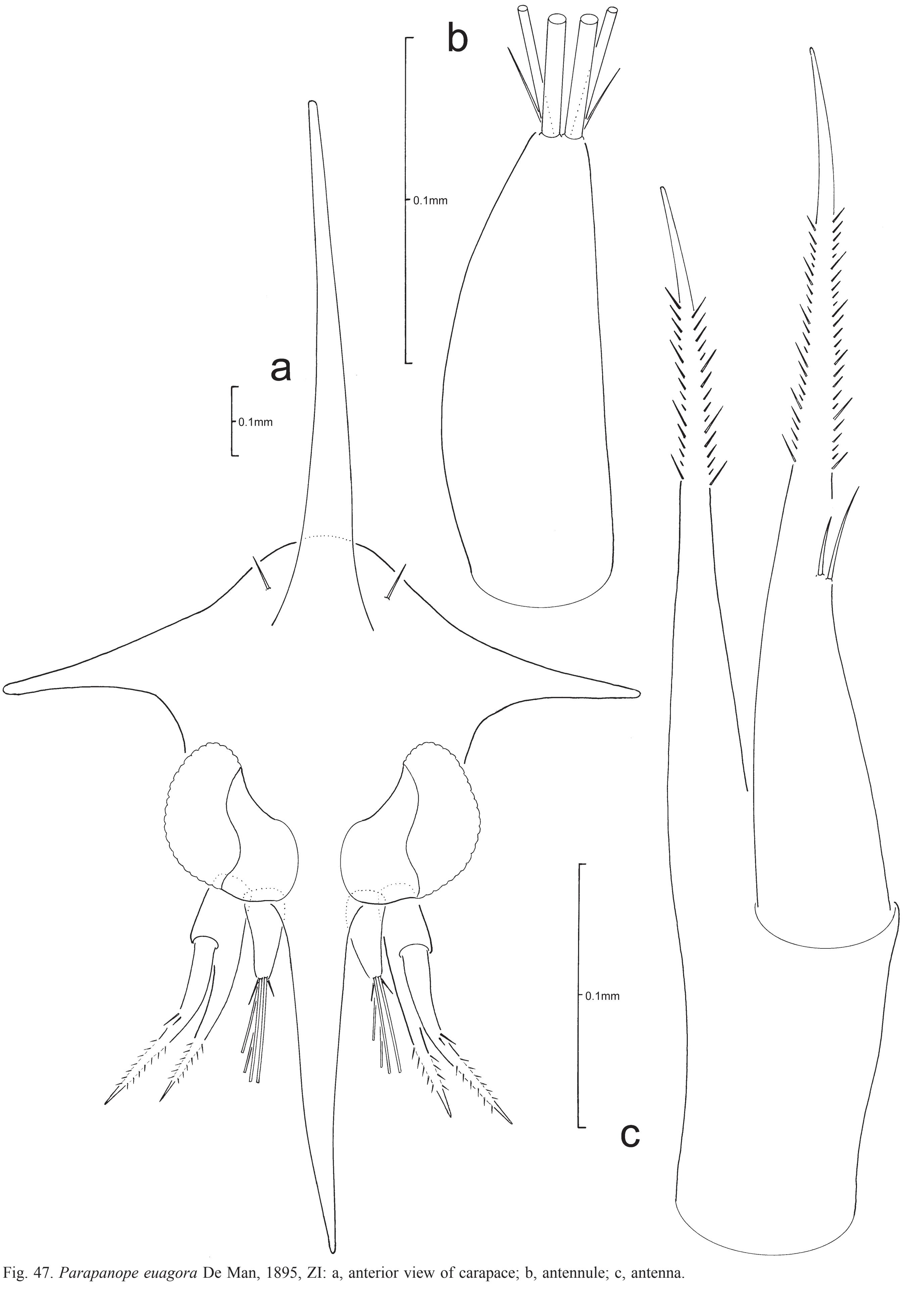

Fig. 47. *Parapanope euagora* De Man, 1895, ZI: a, anterior view of carapace; b, antennule; c, antenna.

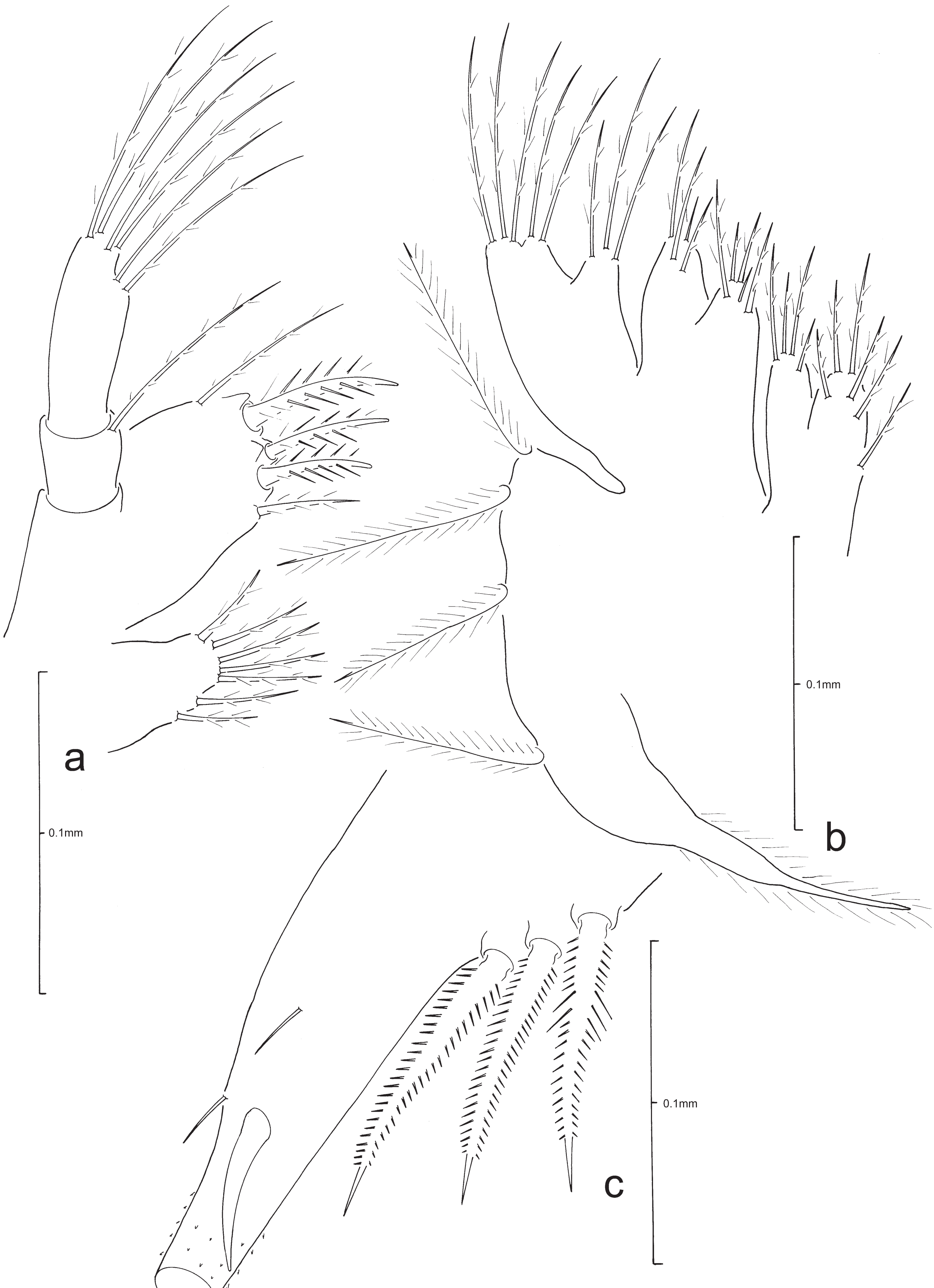

Fig. 48. *Parapanope euagora* De Man, 1895, ZI: a, maxillule; b, maxilla; c, telson.

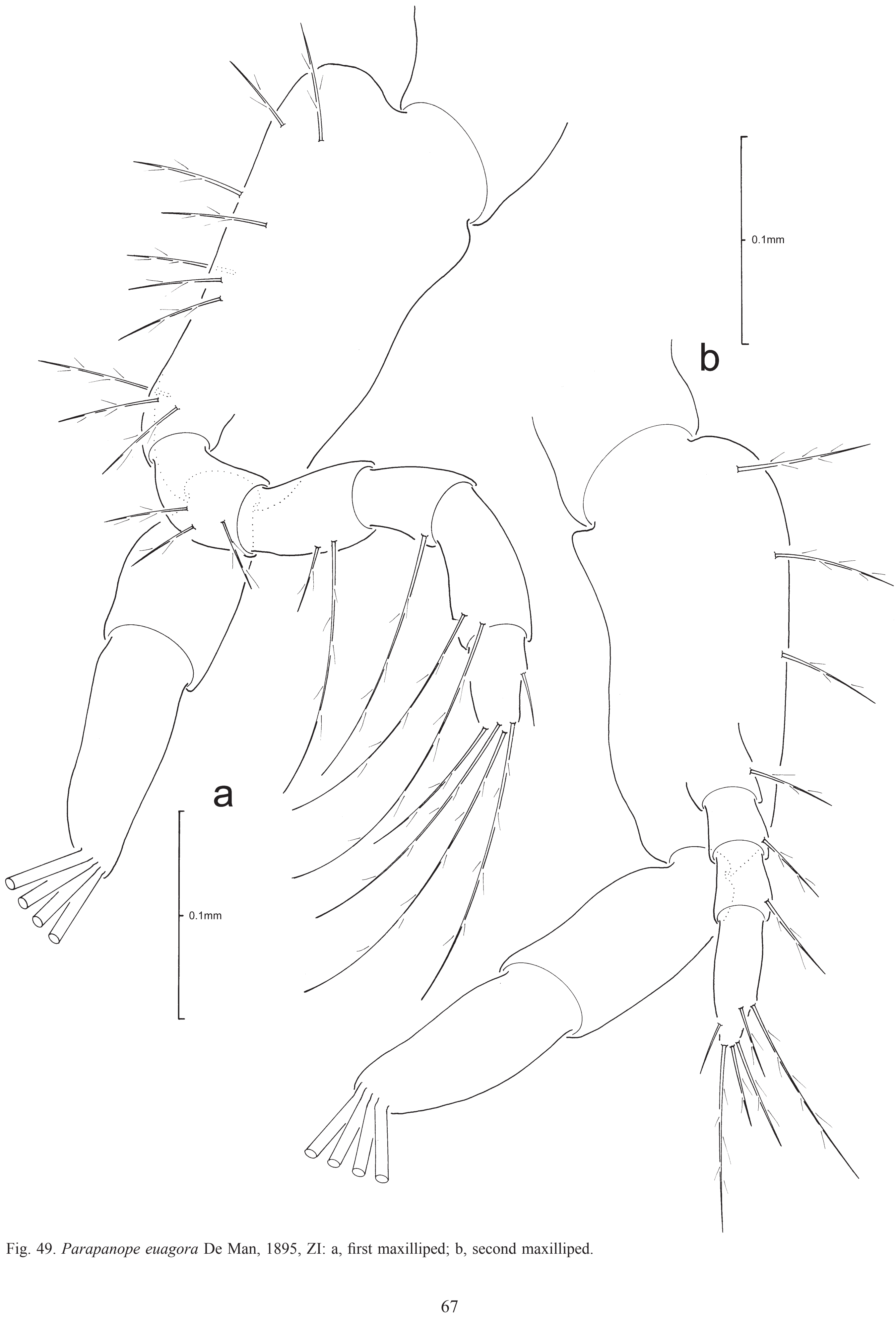

Fig. 49. *Parapanope euagora* De Man, 1895, ZI: a, first maxilliped; b, second maxilliped.

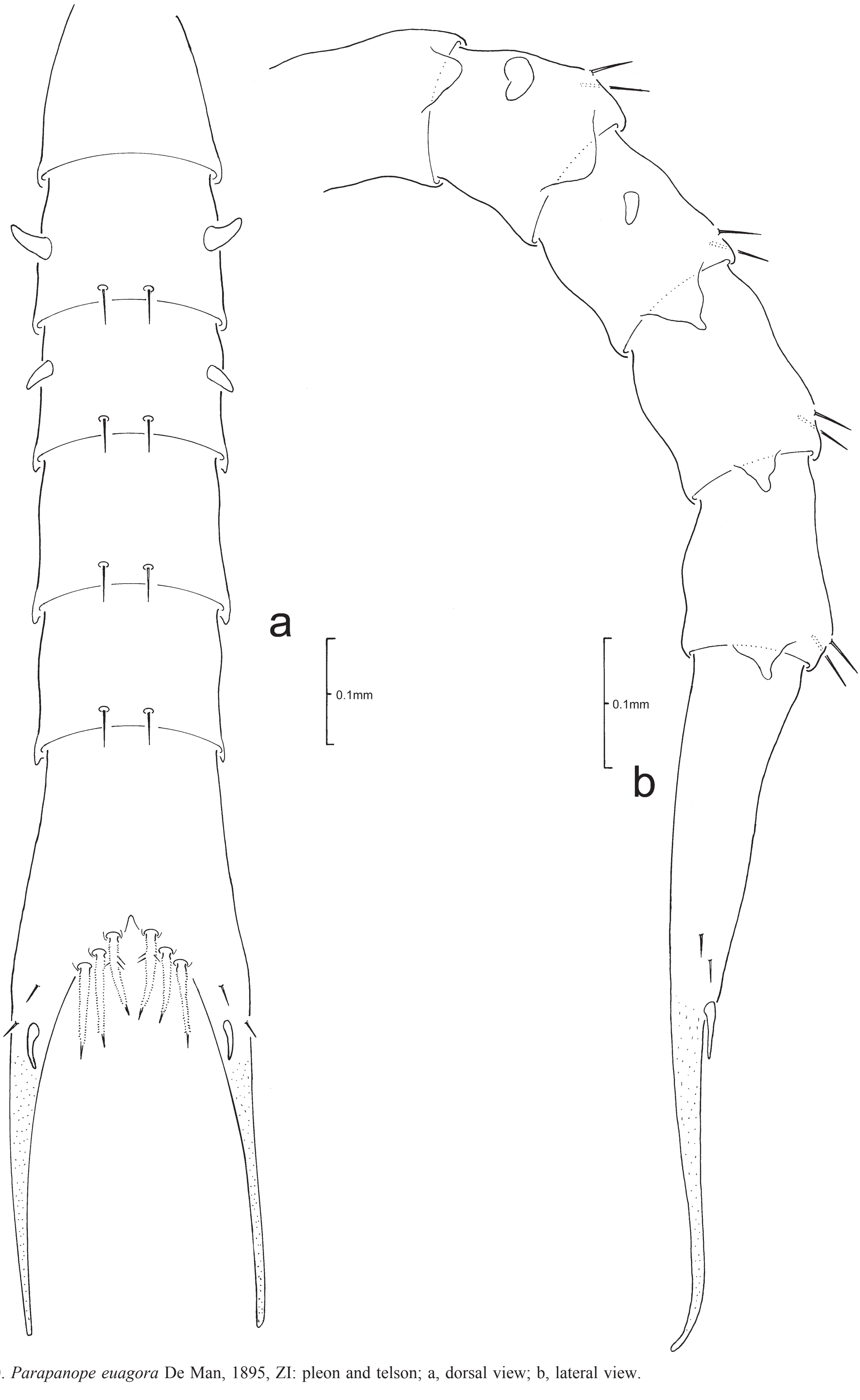

Fig. 50. *Parapanope euagora* De Man, 1895, ZI: pleon and telson; a, dorsal view; b, lateral view.

Family Pilumnidae Samouelle, 1819

Subfamily Eumedoninae Dana, 1853

Harrovia albolineata **Adams & White, 1849**
(Figs. 51–54)

Harrovia albolineata. Chia et al., 1993: 276, fig. 8B–K (ZI).
non *Harrovia albolineata*. G.S.Y. Lim & P.K.L. Ng, 1988: 218, fig. 1 (ZI) = *H. longipes* (see Chia et al., 1993: 275).

Description of Zoea I.
CARAPACE (Fig. 51a, b): carapace spinulate; dorsal spine smooth, curved distally, ca. twice rostral spine length; rostral spine ca. half antennal protopod length, distally spinulate; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 51a): sessile.
Antennule (Fig. 51c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 2 terminal setae of unequal length; accessory flagellum absent.
Antenna (Fig. 51d): biramous; protopod distally spinulate, ca. twice rostral spine length, approximately equal in length to exopod; endopod absent; exopod approximately equal in length to protopod, unsegmented, distally bilaterally spinulate with 2 medial setae of unequal length.
Mandible: palp absent.
Maxillule (Fig. 52a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 terminal setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 52b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 53a): biramous; coxa without setae; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 53b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 54a, b): 5 pleomeres; pleomere 2 with pair of dorsolateral processes directed anteriorly; pleomeres 3–5 with pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without dorsal setae; pleomeres 2–5 each with 1 pair of posterodorsal setae and spinulated dorsal posterior margin; pleomeres 2–5 medially spinulate; pleopod buds absent.

TELSON (Figs. 52c, 54a, b): each fork long, spinulate, gradually curved distally, margin with 2 pairs of minute lateral spines, 1 long lateral spine, 1 small lateral spine, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Table 7. A comparison between the ZI of *Harrovia albolineata* Adams & White, 1849 by Chia et al. (1993) and the present study.

Character	Chia et al. (1993)	Present study
CARAPACE	fig. 8B	Fig. 51a
posterodorsal setae	absent	1 pair present
ANTENNULE	fig. 8D	Fig. 51b
terminal setation	2 stout, long aesthetascs, 2 stout, short aesthetascs	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 2 terminal setae of unequal length
MAXILLULE	fig. 8H	Fig. 52a
coxal endite setation	text: 6 fig. 5?	7
MAXILLA	fig. 8I	Fig. 52b
coxal endite	2+6	6+4
SECOND MAXILLIPED	fig. 8K	Fig. 53b
setation of third endopod article	5 (1 subterminal, 4 terminal)	6 (3 subterminal, 3 terminal)
TELSON	fig. 8C	Figs. 52c, 54a, b
fork spination	1 large lateral spine + 1 small dorsal spine	1 long and 1 small lateral spine + 1 dorsomedial spine

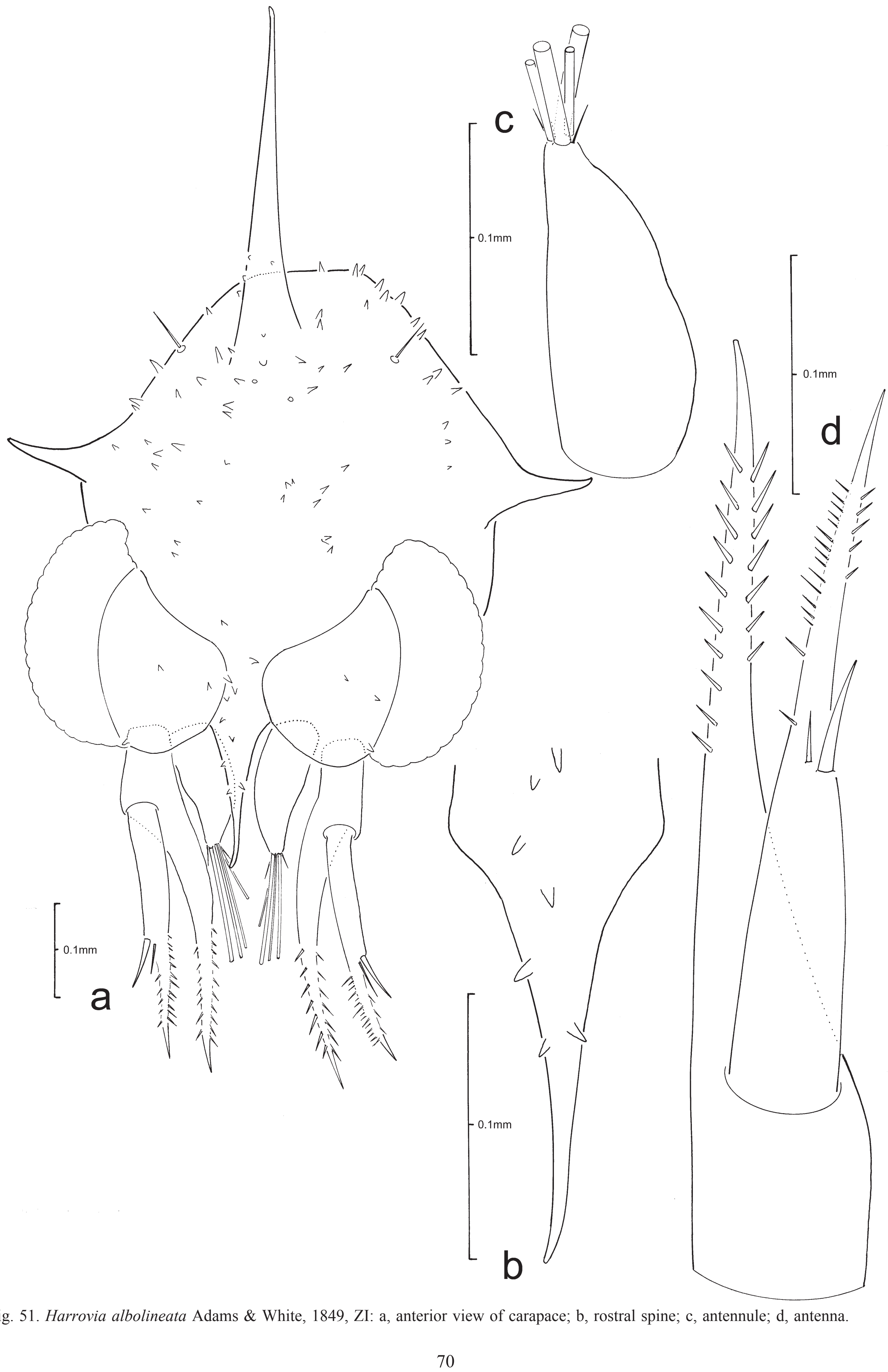

Fig. 51. *Harrovia albolineata* Adams & White, 1849, ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

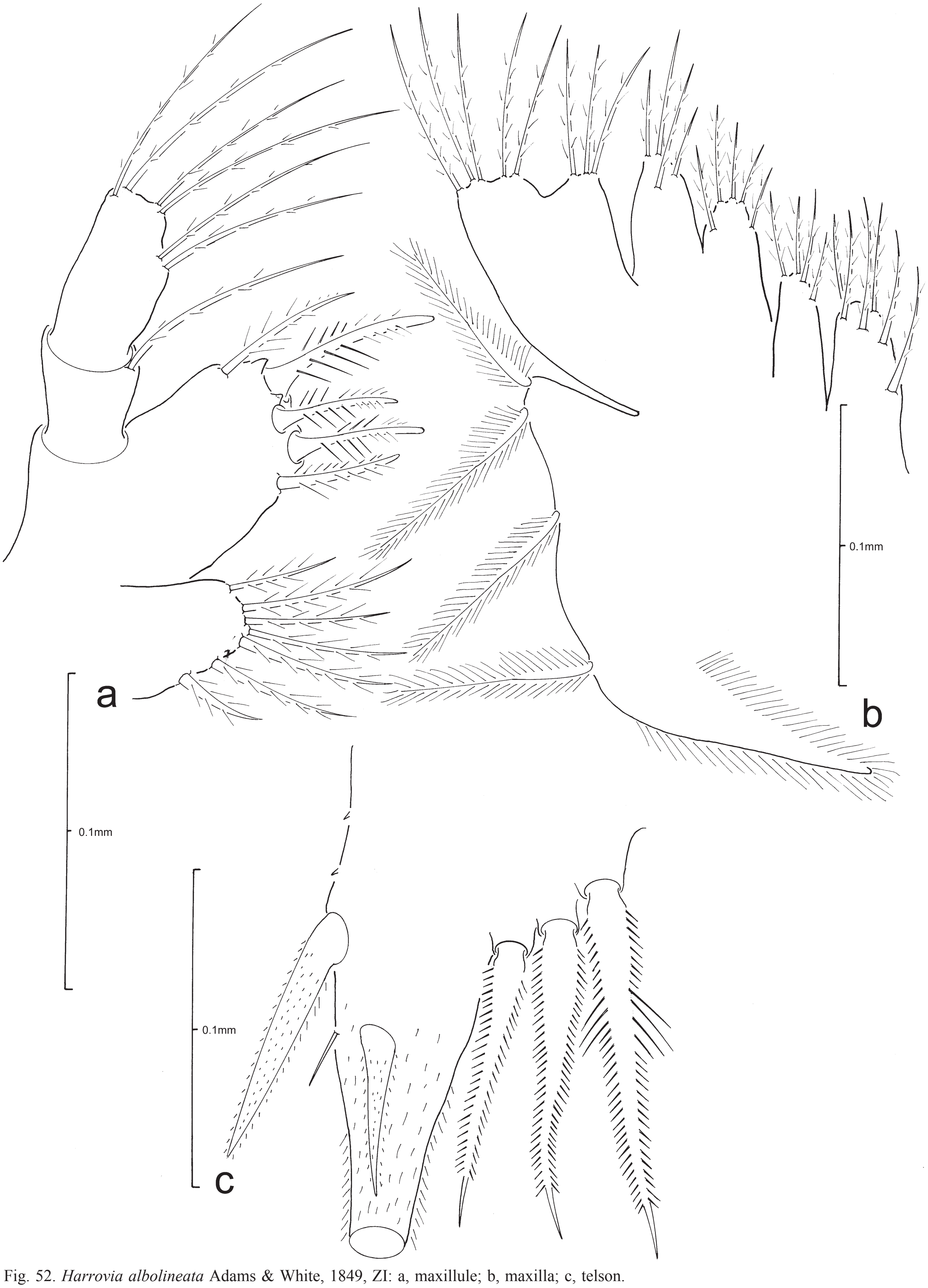

Fig. 52. *Harrovia albolineata* Adams & White, 1849, ZI: a, maxillule; b, maxilla; c, telson.

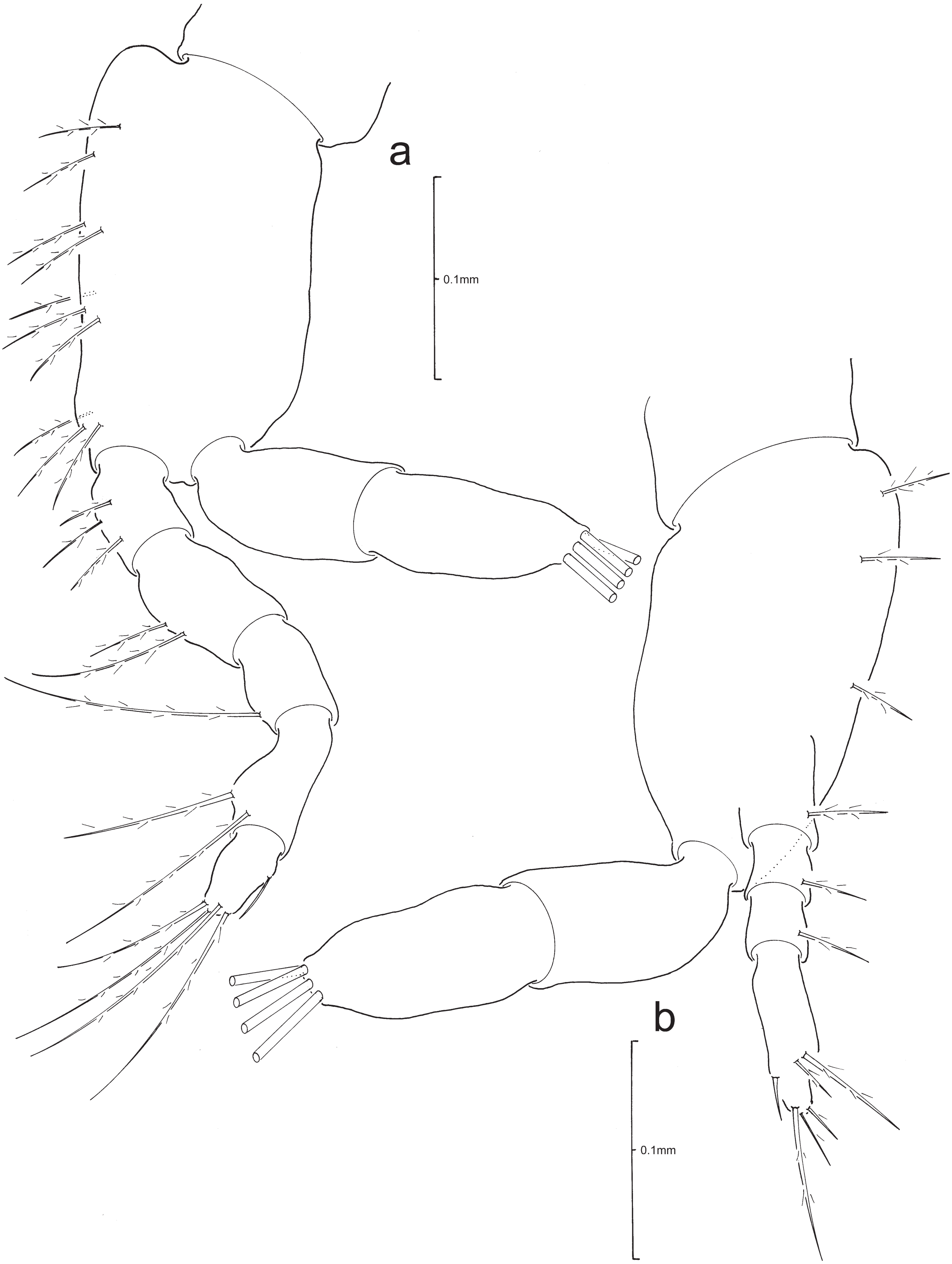

Fig. 53. *Harrovia albolineata* Adams & White, 1849, ZI: a, first maxilliped; b, second maxilliped.

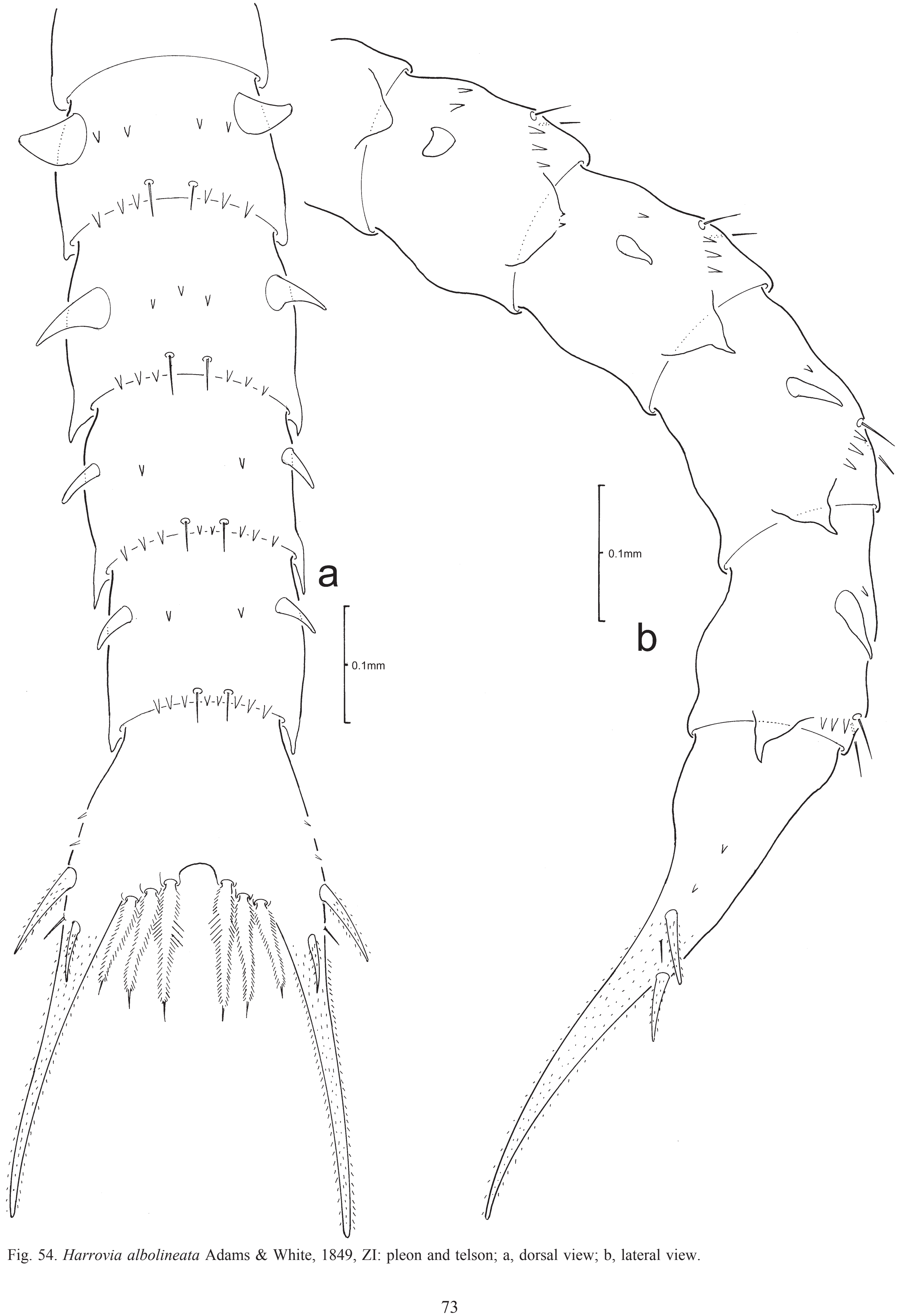

Fig. 54. *Harrovia albolineata* Adams & White, 1849, ZI: pleon and telson; a, dorsal view; b, lateral view.

Subfamily Pilumninae Samouelle, 1819

***Actumnus elegans* De Man, 1887**
(Figs. 55–58)

Description of Zoea I.
CARAPACE (Fig. 55a): dorsal spine smooth, curved distally, relatively short, just longer than rostral spine length; rostral spine shorter than antennal protopod length, without distal spinulation; lateral spines present, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 55a): sessile.
Antennule (Fig. 55b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 2 terminal setae of unequal length; accessory flagellum absent.
Antenna (Fig. 55c): uniramous; protopod distally bilaterally spinulate, longer than rostral spine length; endopod bud absent; exopod unsegmented, distally bilaterally spinulate with 2 medial setae of unequal length.
Mandible: palp absent.
Maxillule (Fig. 56a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 terminal setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 56b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal setae); exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 57a): biramous; coxa without setae; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 57b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 58a, b): 5 pleomeres; pleomere 2 with pair of dorsolateral processes directed anteriorly; pleomere 3 with pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 with short posterolateral spinous processes; pleomere 1 without dorsal setae; pleomeres 2–5 each with 1 pair of posterodorsal setae and spinulated dorsal posterior margin; pleopod buds absent.

TELSON (Figs. 56c, 58a, b): each fork long, spinulate, gradually curved distally, 1 long lateral spine, 1 fine lateral spine, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

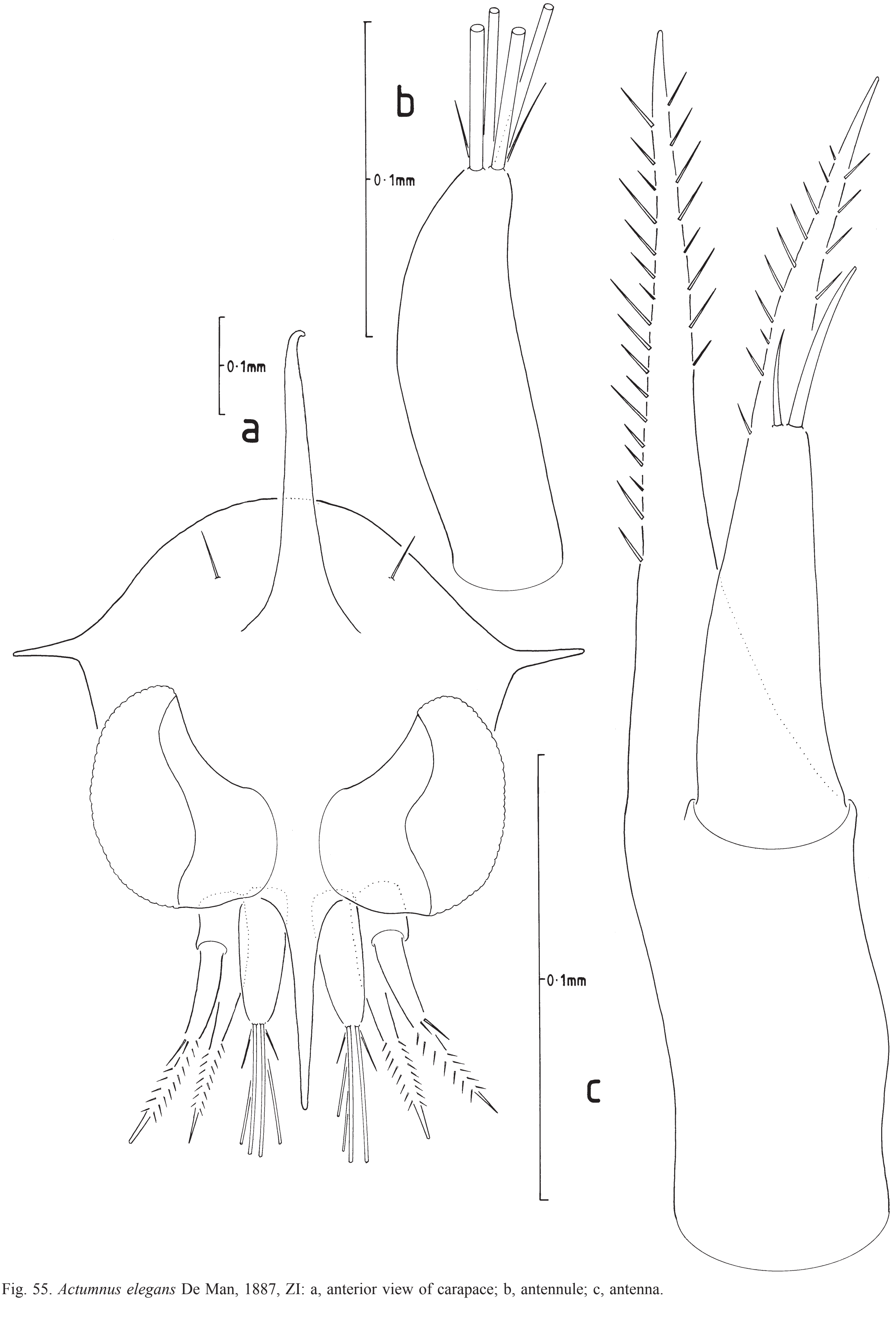

Fig. 55. *Actumnus elegans* De Man, 1887, ZI: a, anterior view of carapace; b, antennule; c, antenna.

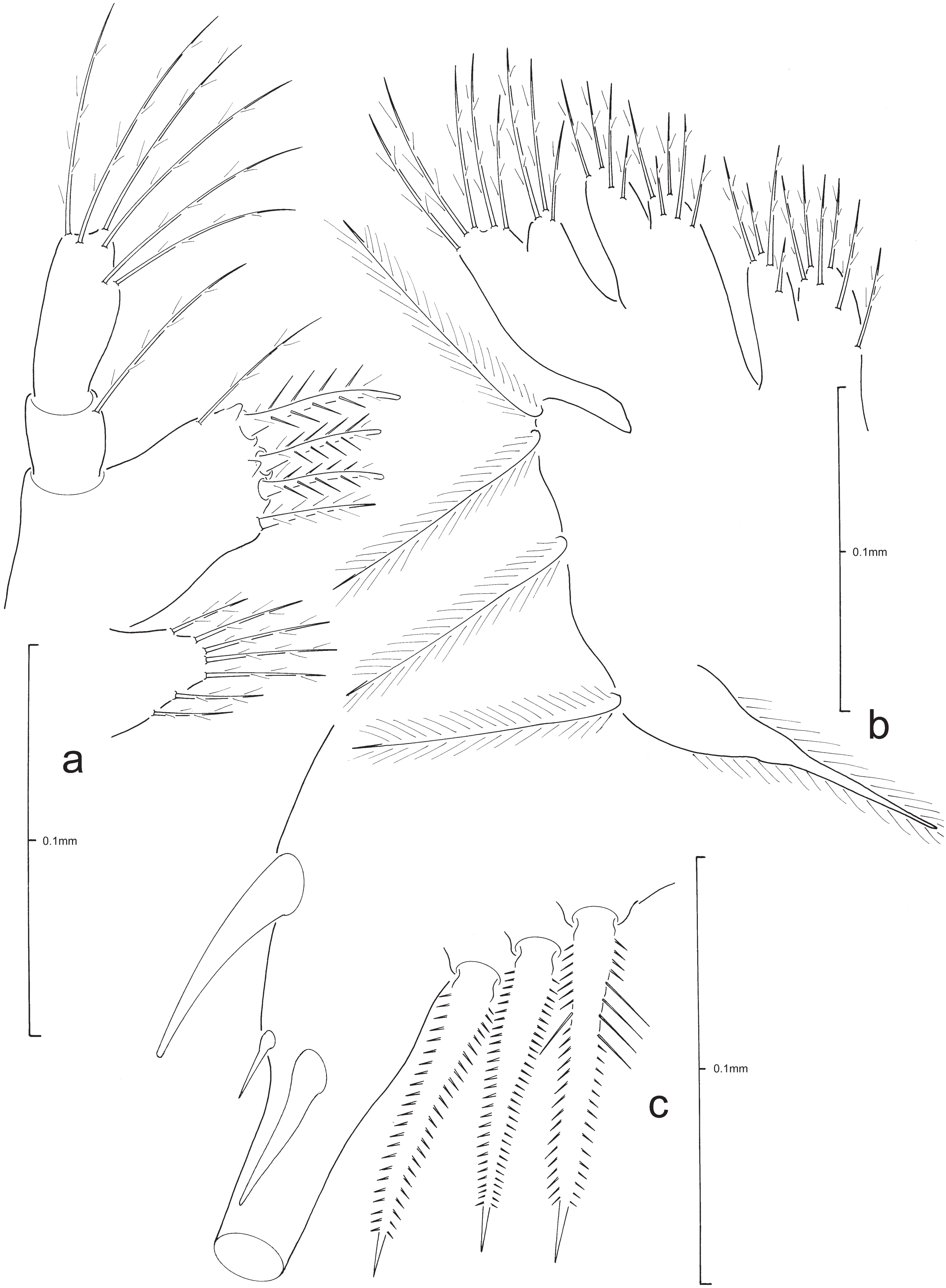

Fig. 56. *Actumnus elegans* De Man, 1887, ZI: a, maxillule; b, maxilla; c, telson.

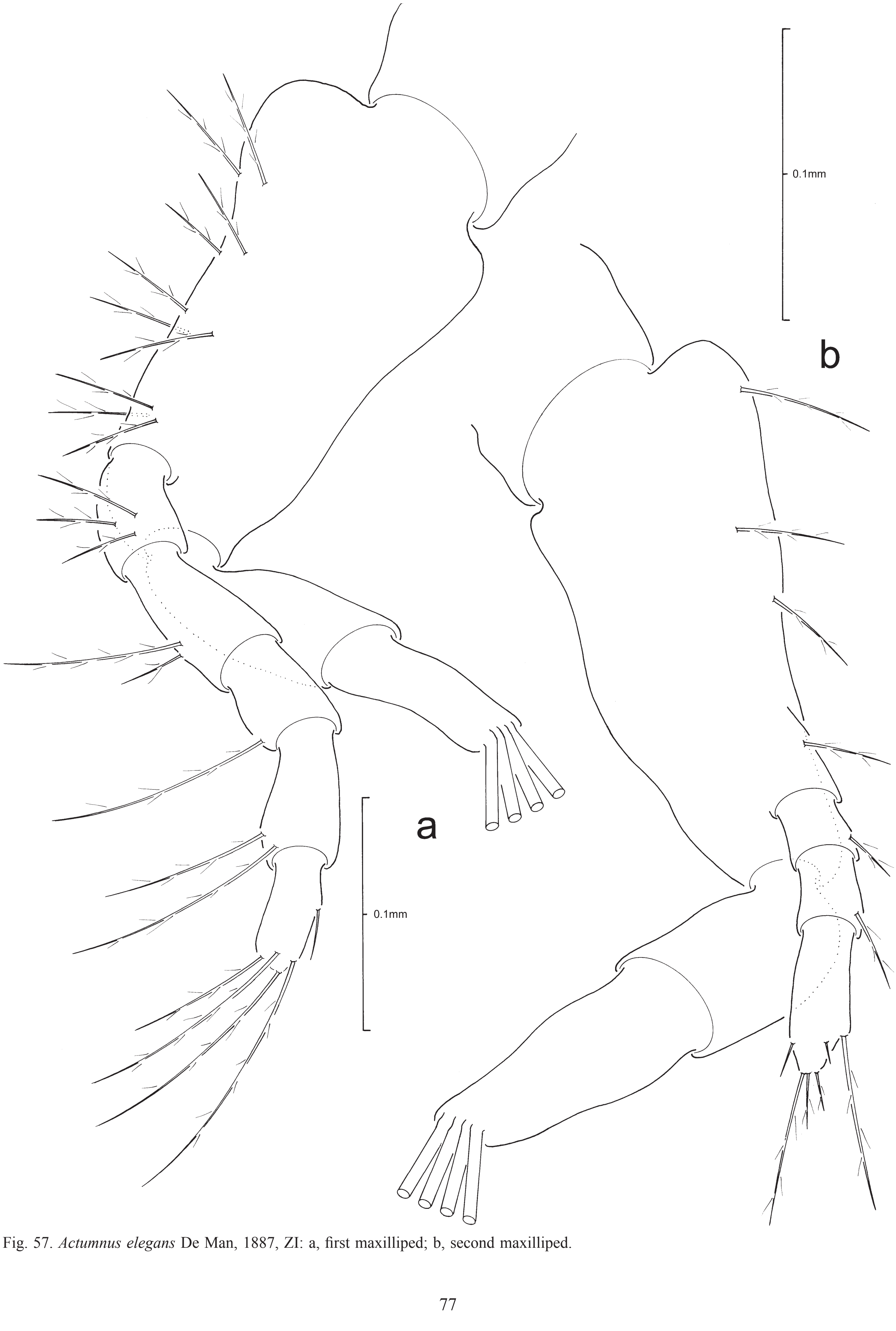

Fig. 57. *Actumnus elegans* De Man, 1887, ZI: a, first maxilliped; b, second maxilliped.

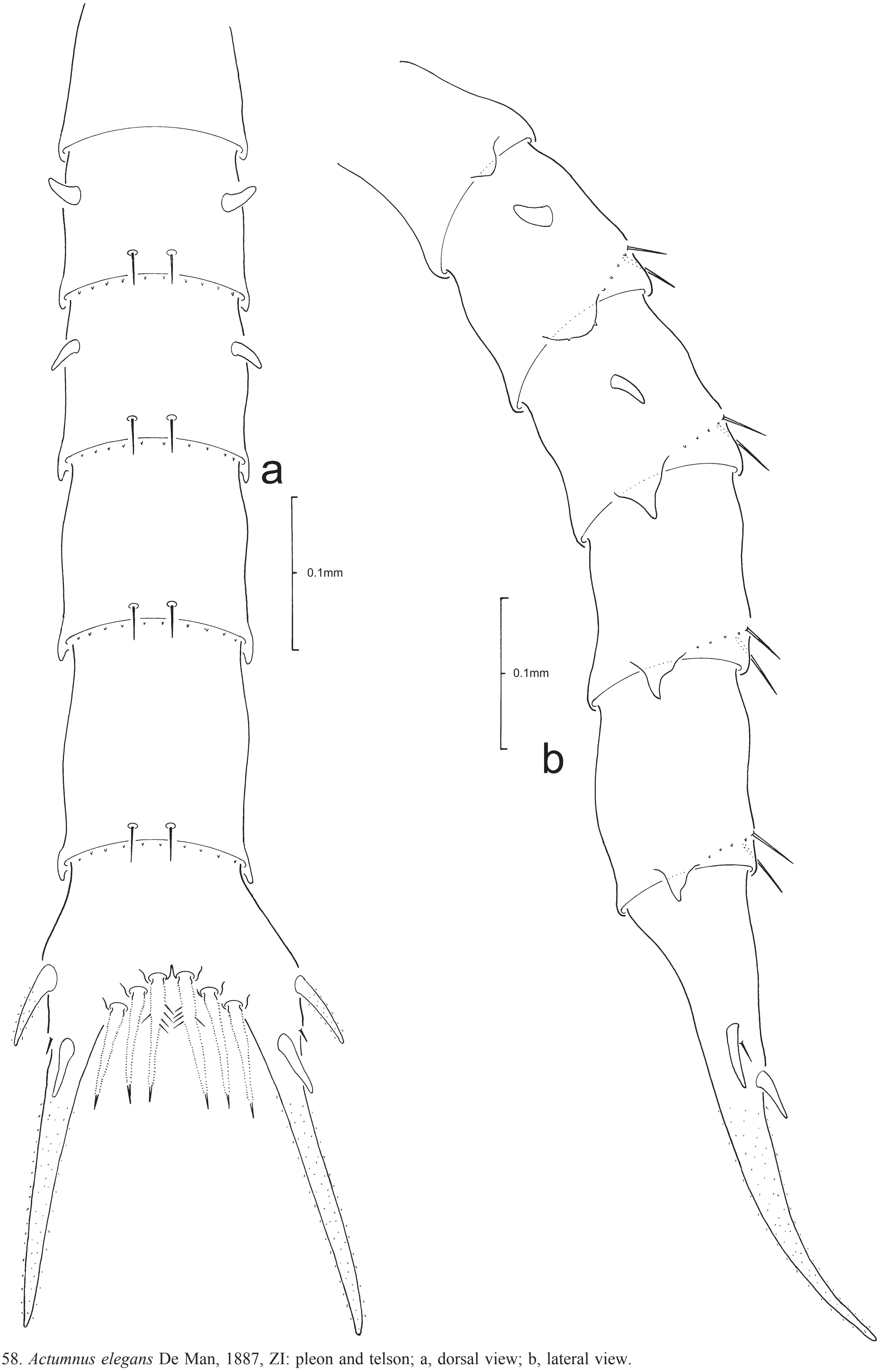

Fig. 58. *Actumnus elegans* De Man, 1887, ZI: pleon and telson; a, dorsal view; b, lateral view.

***Cryptopilumnus changensis* (Rathbun, 1909)**
(Figs. 59–62)

Description of Zoea I.
CARAPACE (Fig. 59a): dorsal spine smooth, curved distally, relatively short, longer than rostral spine length; rostral spine ca. equal to antennal protopod length, without distal spinulation; lateral spines present, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 59a): sessile.
Antennule (Fig. 59b): primary flagellum unsegmented with 4 (2 broad, 2 slender) aesthetascs of unequal length plus 2 terminal setae of unequal length; accessory flagellum absent.
Antenna (Fig. 59c): uniramous; protopod distally bilaterally spinulate, ca. equal to rostral spine length; endopod absent; exopod unsegmented, distally bilaterally spinulate with 2 medial setae of unequal length.
Mandible: palp absent.
Maxillule (Fig. 60a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 terminal setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 60b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal setae); exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 61a): biramous; coxa without setae; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 61b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 62a, b): 5 pleomeres; pleomere 2 with pair of dorsolateral processes directed anteriorly; pleomere 3 with pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with long posterolateral spinous processes; pleomere 1 without dorsal setae; pleomeres 2–5 each with 1 pair of posterodorsal setae and spinulated dorsal posterior margin; pleopod buds absent.

TELSON (Figs. 60c, 62a, b): each fork long, spinulate, gradually curved distally, 1 long lateral spine, 1 more slender lateral spine, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

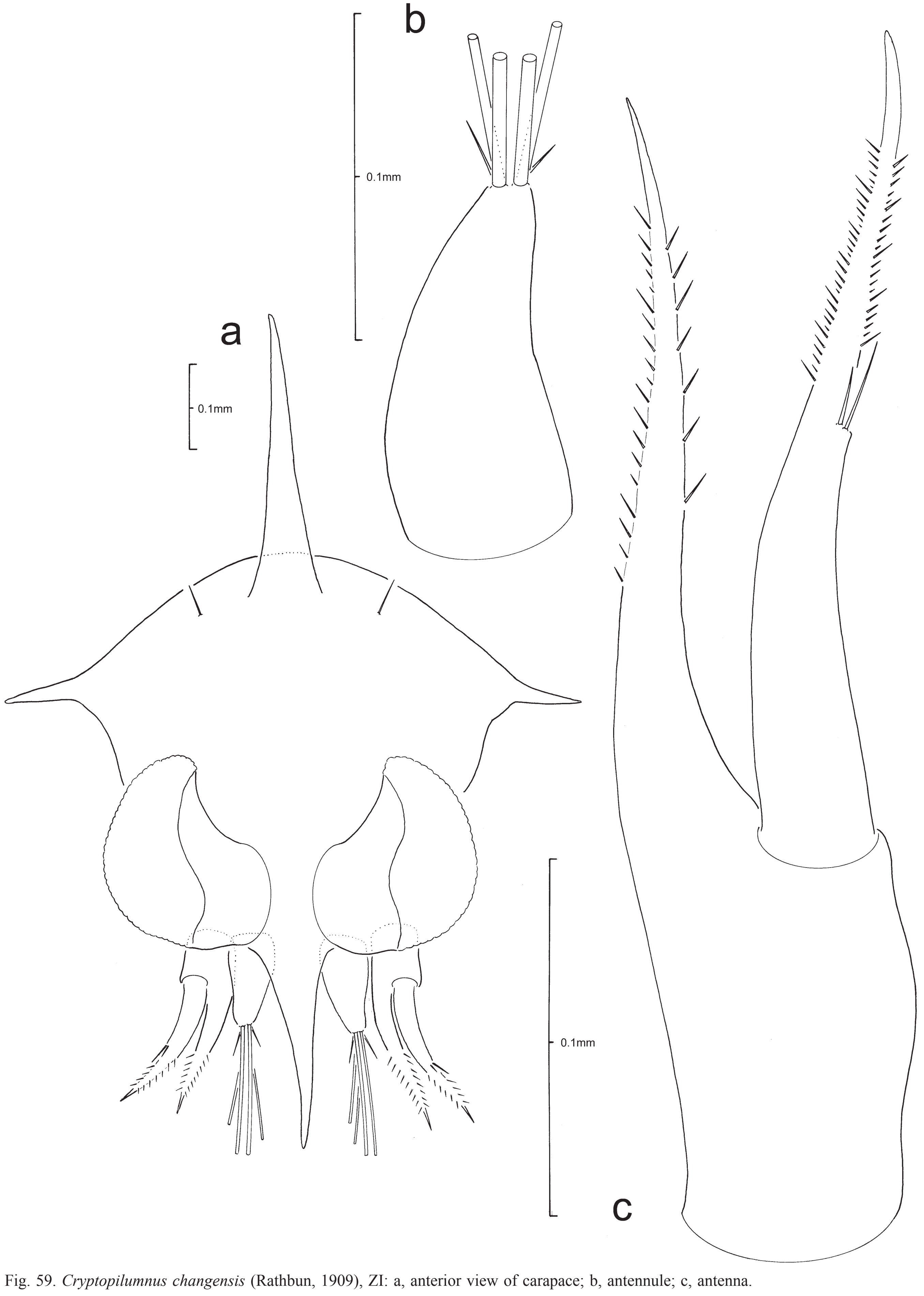

Fig. 59. *Cryptopilumnus changensis* (Rathbun, 1909), ZI: a, anterior view of carapace; b, antennule; c, antenna.

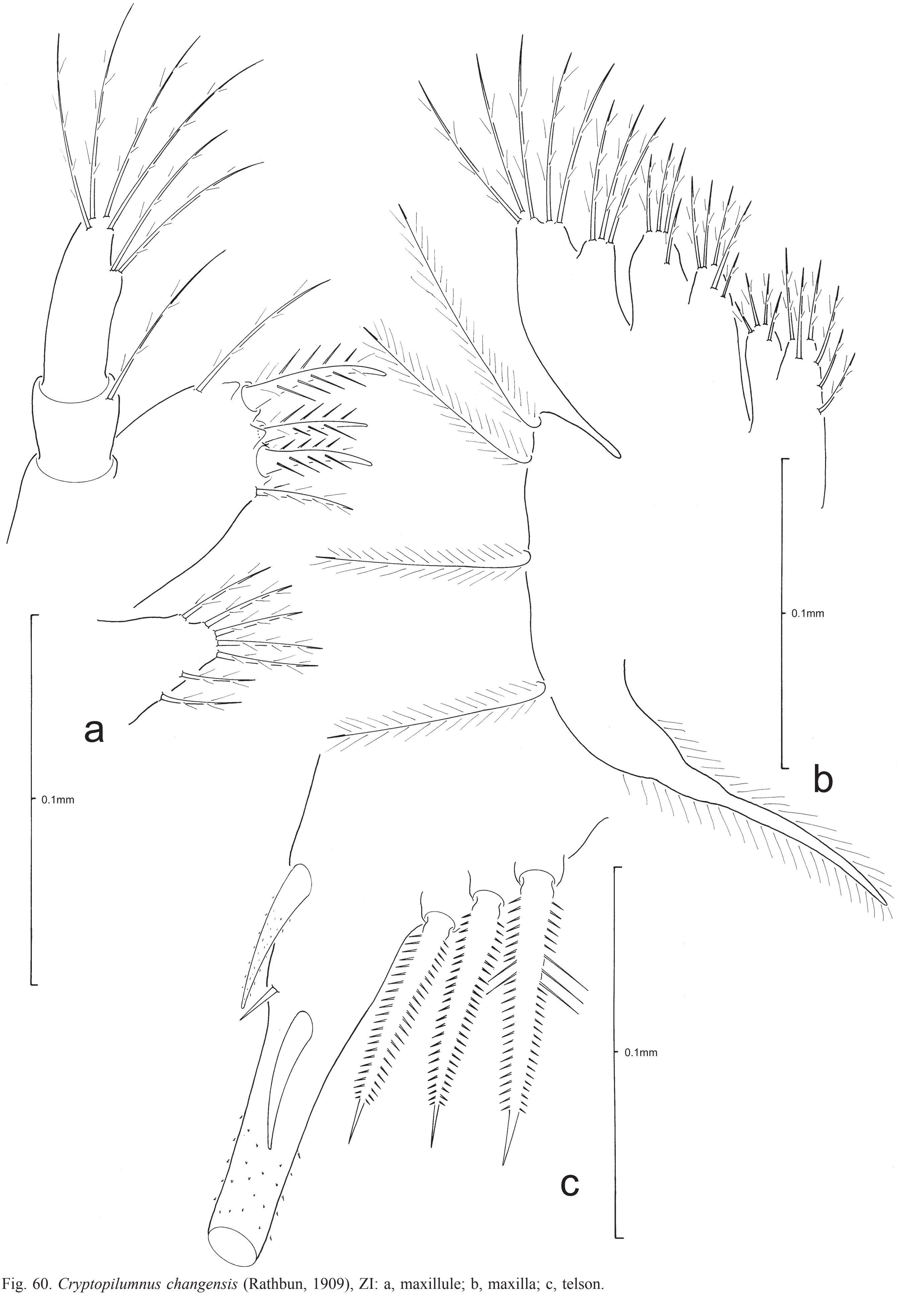

Fig. 60. *Cryptopilumnus changensis* (Rathbun, 1909), ZI: a, maxillule; b, maxilla; c, telson.

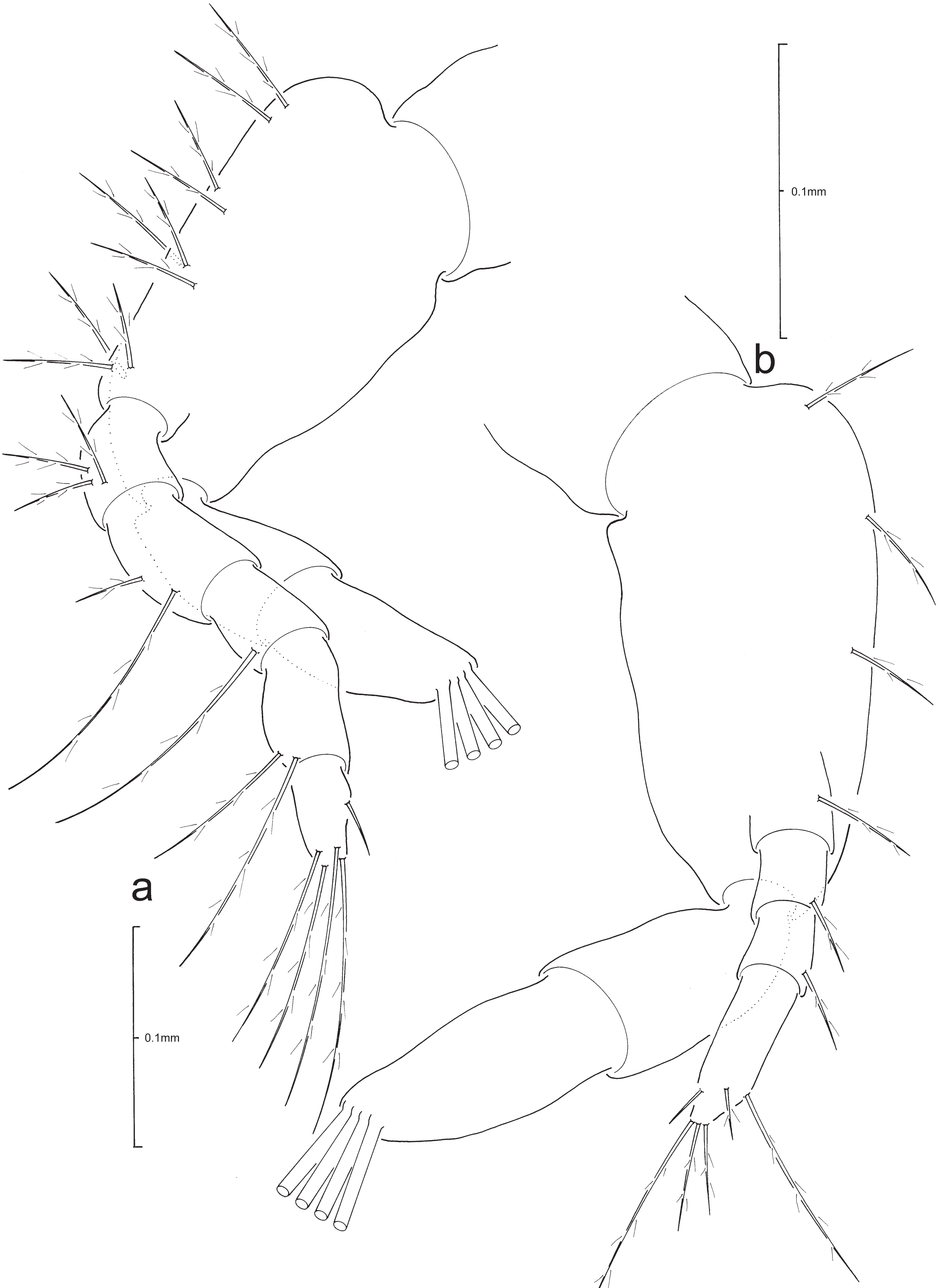

Fig. 61. *Cryptopilumnus changensis* (Rathbun, 1909), ZI: a, first maxilliped; b, second maxilliped.

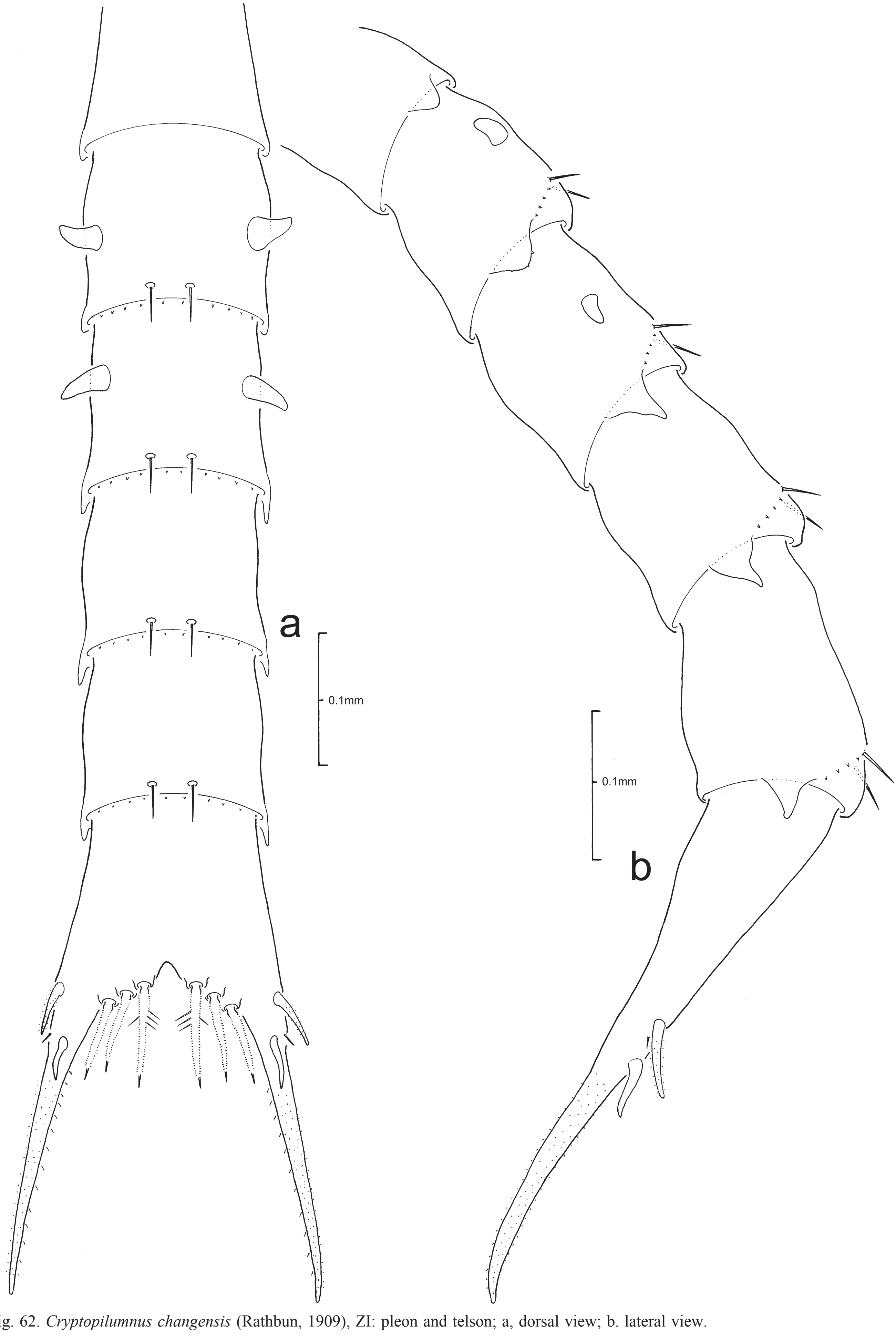

Fig. 62. *Cryptopilumnus changensis* (Rathbun, 1909), ZI: pleon and telson; a, dorsal view; b. lateral view.

Eurycarcinus integrifrons De Man, 1879
(Figs. 63–66)

Description of Zoea I.
CARAPACE (Fig. 63a): dorsal spine long, curved distally, ca. over four times rostral spine length; rostral spine much shorter than antennal protopod length, without distal spinulation; lateral spines short, without spinulation on distal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 63a): sessile.
Antennule (Fig. 63b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 2 terminal setae of unequal length; accessory flagellum absent.
Antenna (Fig. 63c): uniramous; protopod distally bilaterally spinulate, much longer than rostral spine length, equal in length to exopod; endopod bud absent; exopod distally bilaterally spinulate with 2 medial setae of unequal length.
Mandible: palp absent.
Maxillule (Fig. 64a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 terminal setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 64b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 65a): biramous; coxa without setae; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 65b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 66a, b): 5 pleomeres; pleomere 2 with pair of dorsolateral processes directed anteriorly; pleomere 3 with pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without dorsal setae; pleomeres 2–5 each with 1 pair of posterodorsal setae and spinulated dorsal posterior margin; pleopod buds absent.

TELSON (Figs. 64c, 66a, b): each fork long, spinulate, gradually curved distally, 1 long lateral spine, 1 fine lateral spine, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

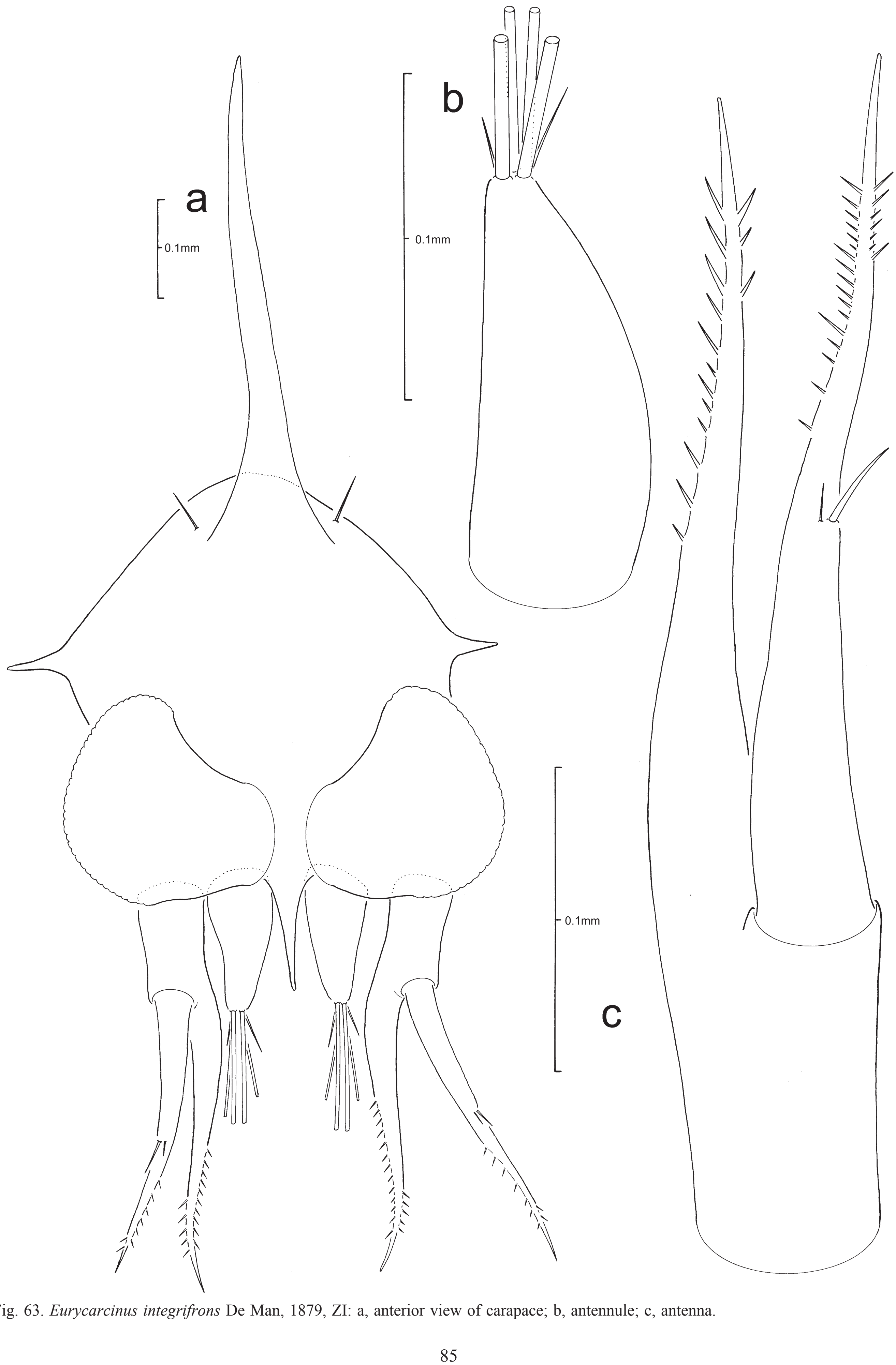

Fig. 63. *Eurycarcinus integrifrons* De Man, 1879, ZI: a, anterior view of carapace; b, antennule; c, antenna.

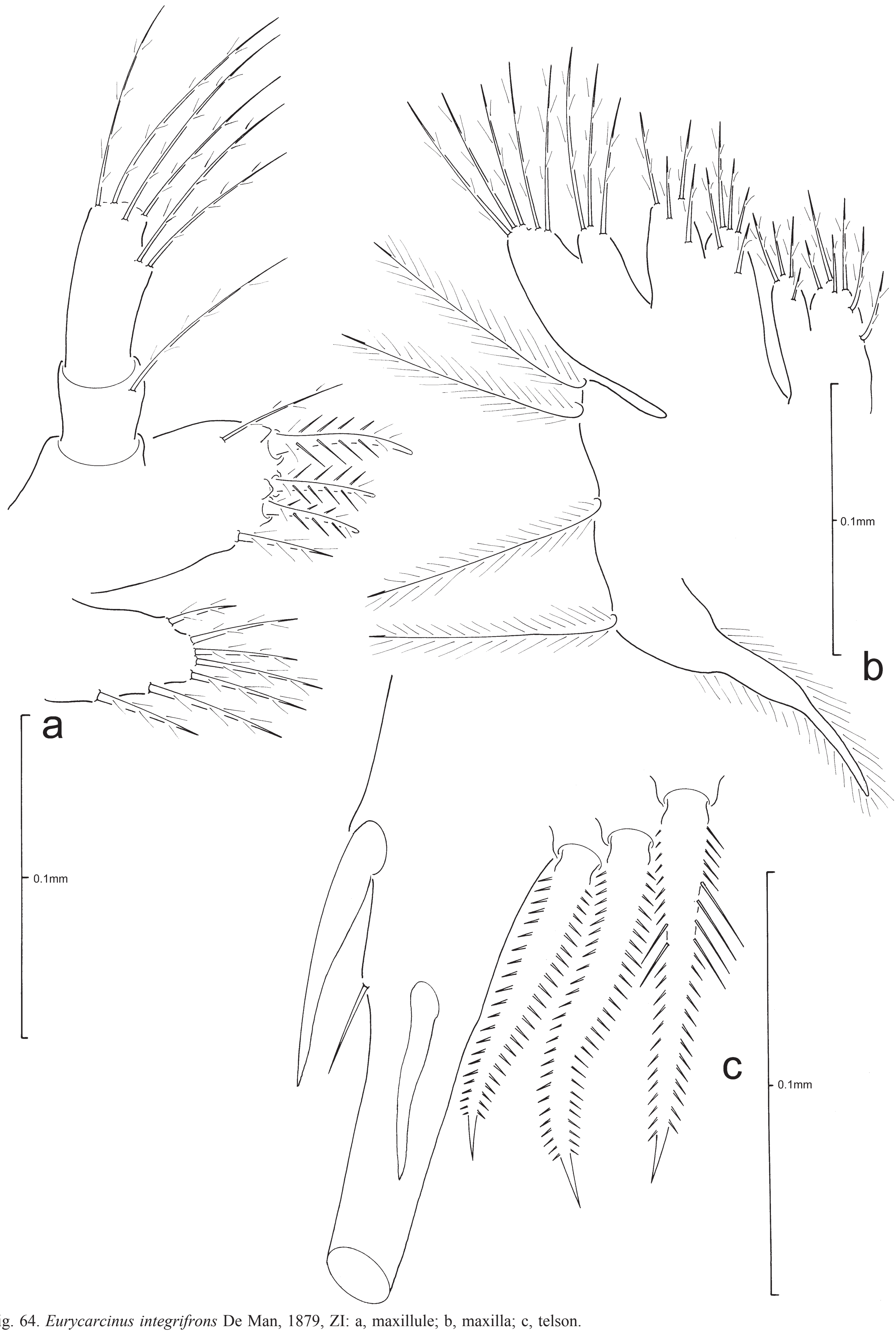

Fig. 64. *Eurycarcinus integrifrons* De Man, 1879, ZI: a, maxillule; b, maxilla; c, telson.

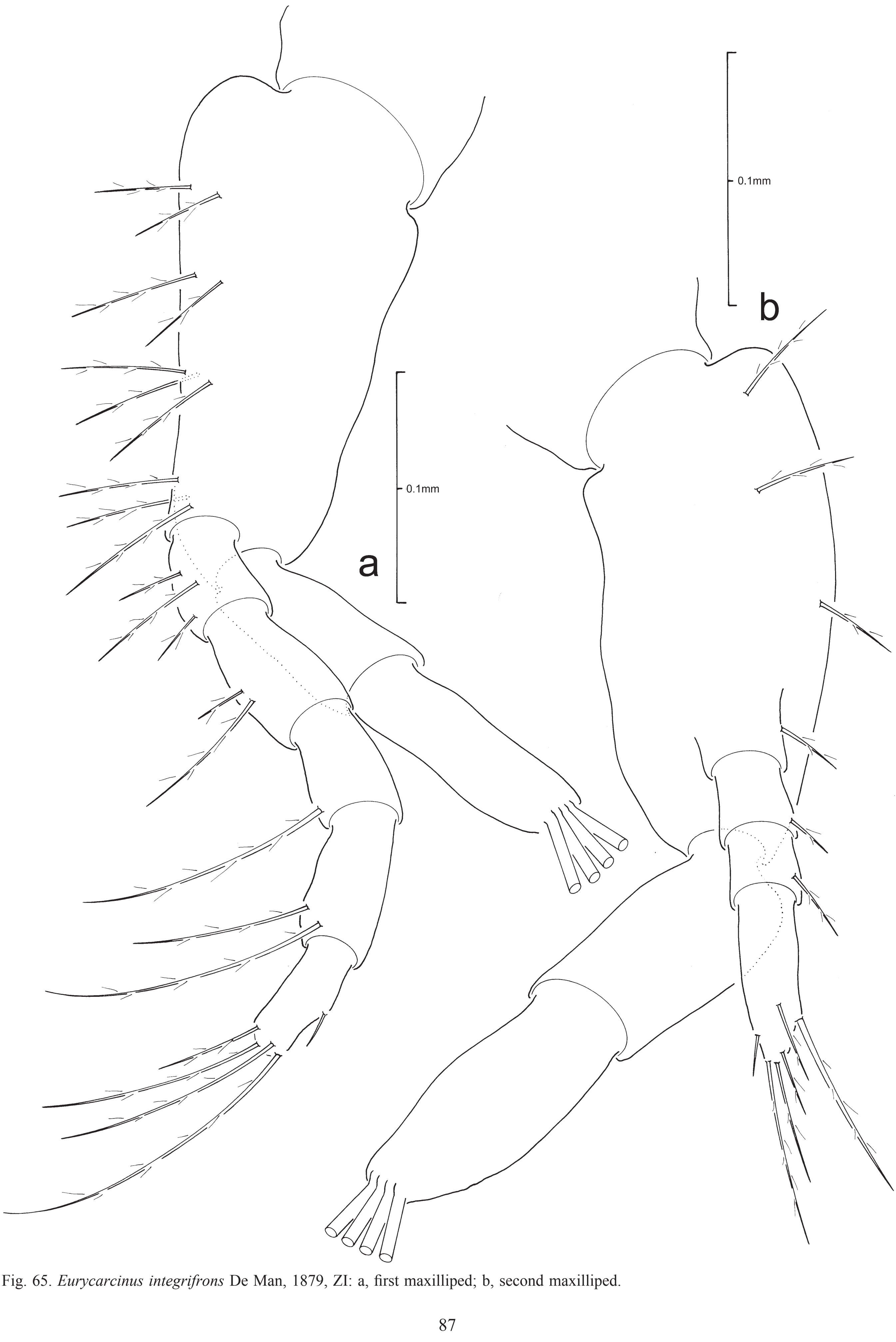

Fig. 65. *Eurycarcinus integrifrons* De Man, 1879, ZI: a, first maxilliped; b, second maxilliped.

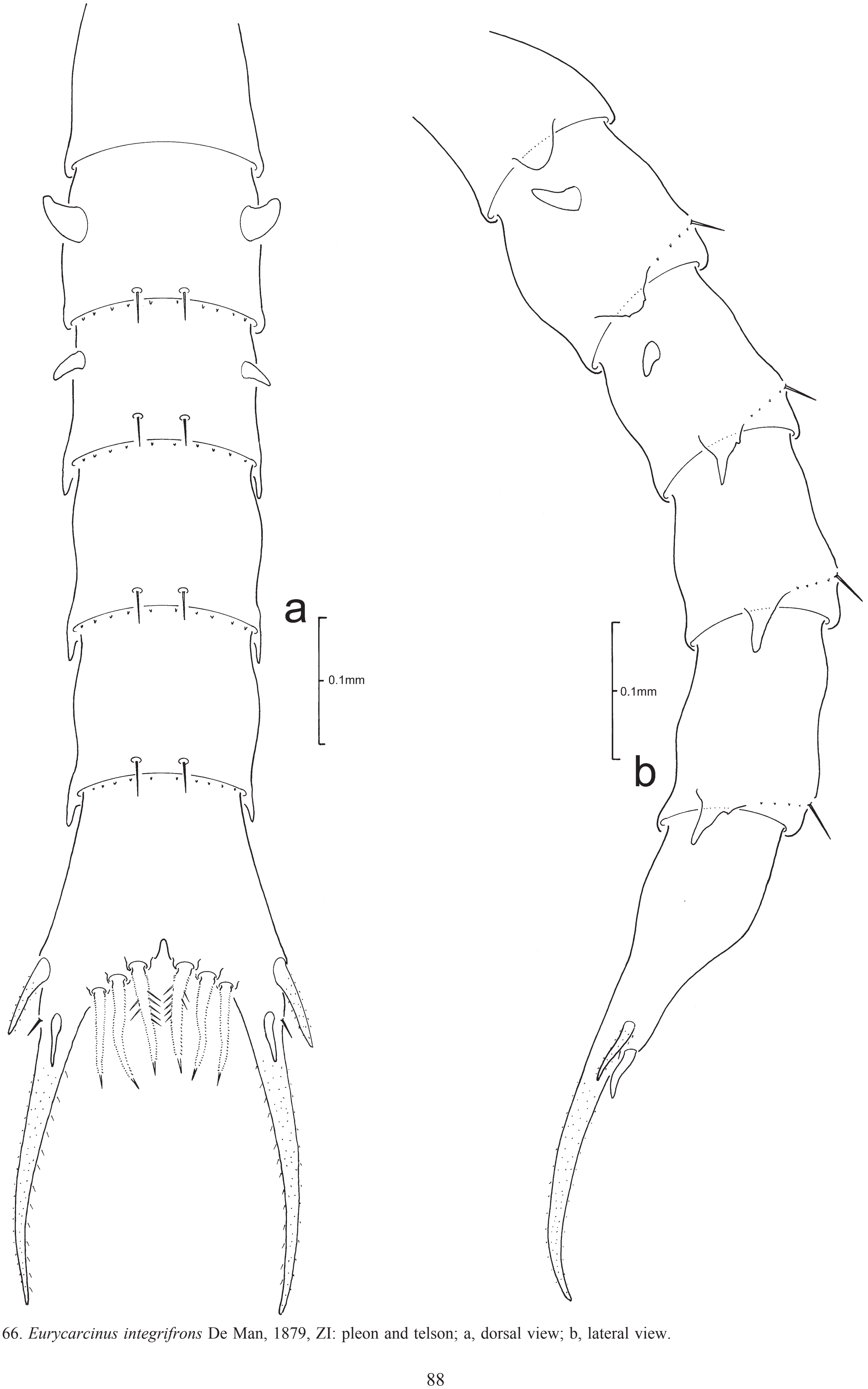

Fig. 66. *Eurycarcinus integrifrons* De Man, 1879, ZI: pleon and telson; a, dorsal view; b, lateral view.

***Glabropilumnus edamensis* (De Man, 1888)**
(Figs. 67–70)

Description of Zoea I.
CARAPACE (Fig. 67a): dorsal spine short, curved distally, ca. five times rostral spine length; rostral spine ca. quarter of antennal protopod length, without distal spinulation; lateral spines present, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 67a): sessile.
Antennule (Fig. 67b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 2 terminal setae of unequal length; accessory flagellum absent.
Antenna (Fig. 67c): biramous; protopod distally spinulate, ca. four times longer than rostral spine length; endopod present; exopod approximately equal in length to protopod, unsegmented, distally bilaterally spinulate with 2 medial setae of unequal length.
Mandible: palp absent.
Maxillule (Fig. 68a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 terminal setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 68b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 69a): biramous; coxa without setae; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 69b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped (Fig. 70c): present, biramous.
Pereiopods (Fig. 68d): present; uniramous; chela bilobed.

PLEON (Fig. 70a, b): 5 pleomeres; pleomere 2 with pair of dorsolateral processes directed anteriorly; pleomeres 3–5 with pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without dorsal setae; pleomeres 2–5 each with 1 pair of posterodorsal setae and spinulated dorsal posterior margin; pleopod buds absent.

TELSON (Figs. 68c, 70a, b): each fork long, spinulate, gradually curved distally, 1 large lateral spine, 1 lateral seta, 1 small dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

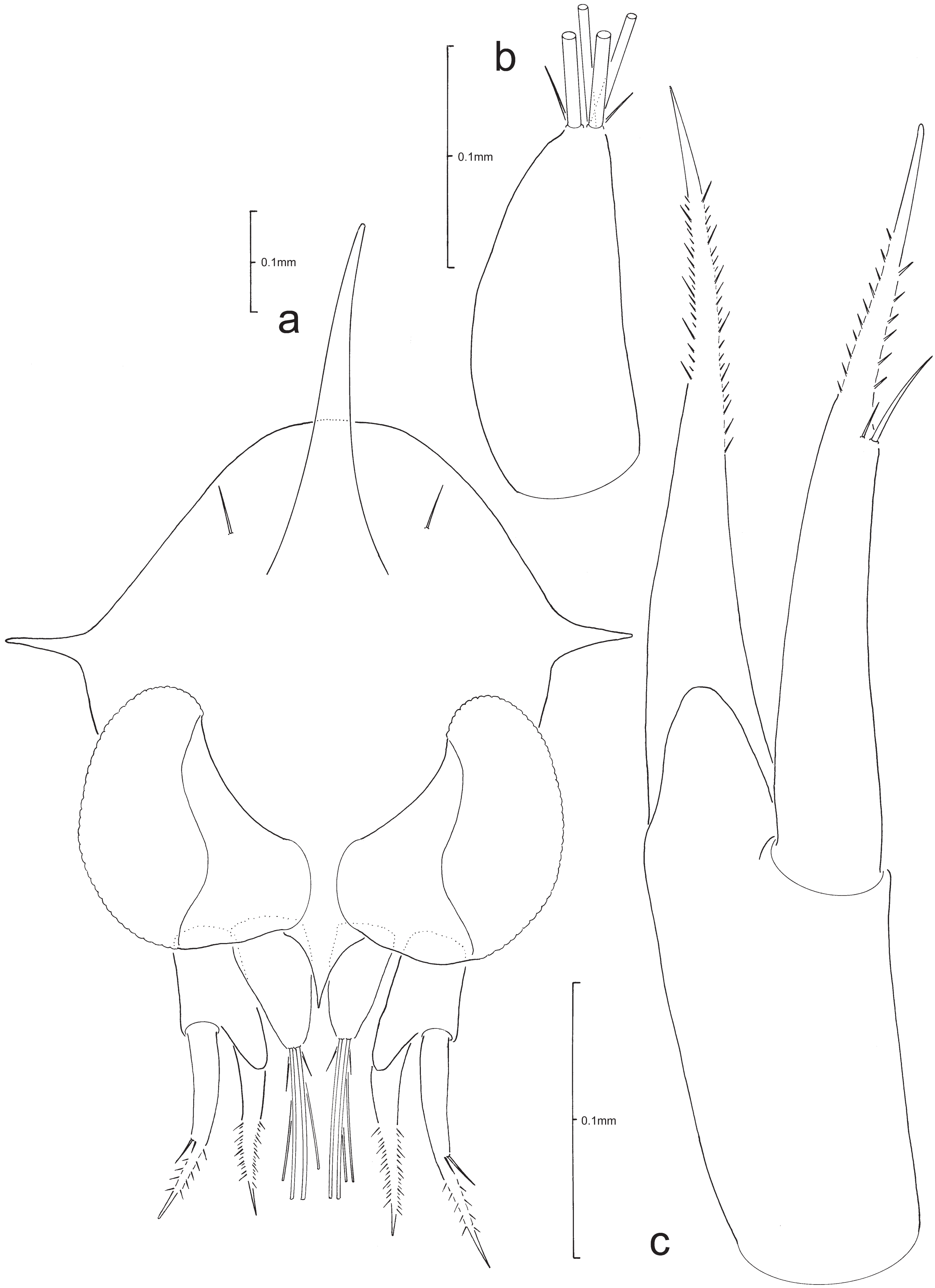

Fig. 67. *Glabropilumnus edamensis* (De Man, 1888), ZI: a, anterior view of carapace; b, antennule; c, antenna.

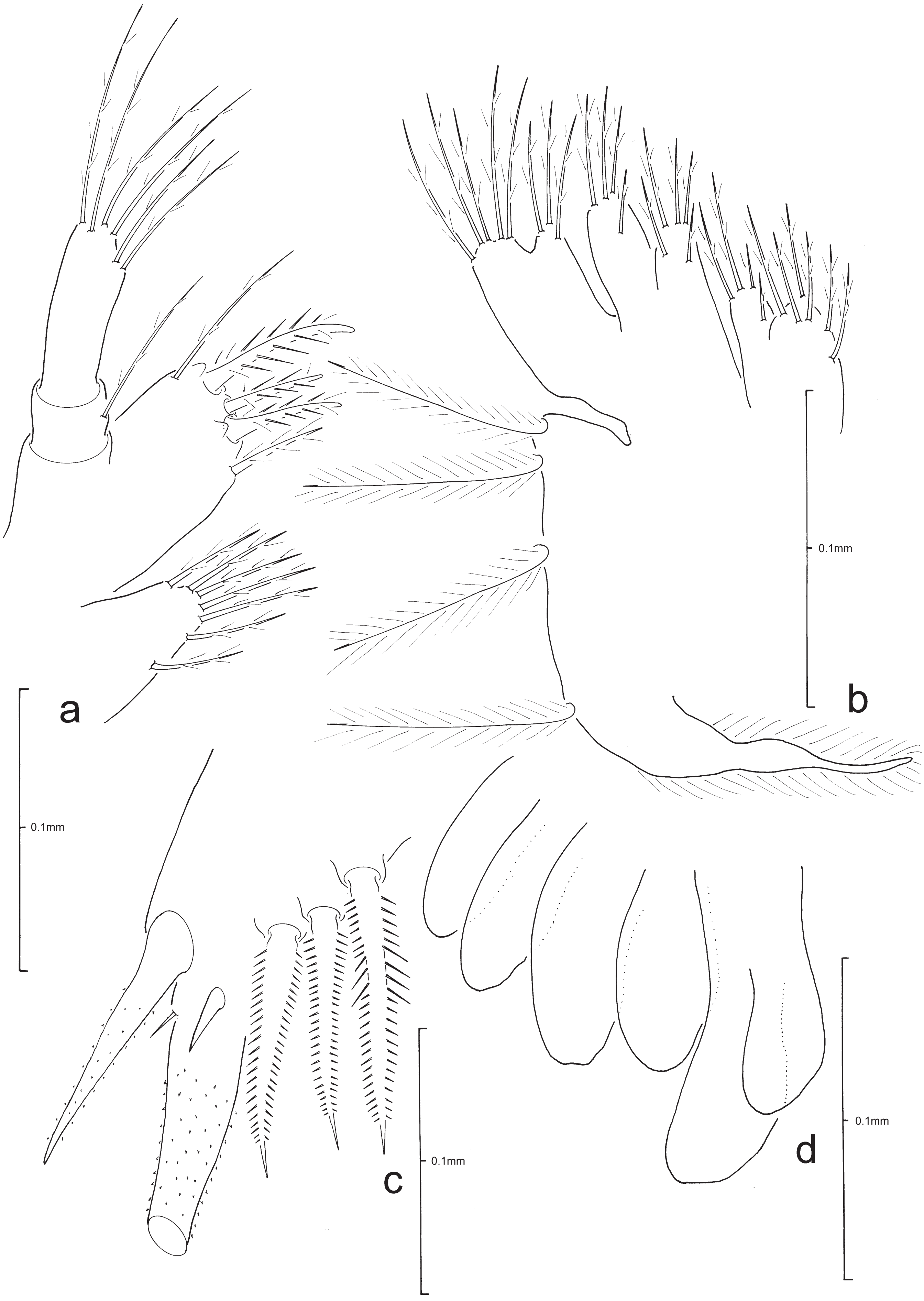

Fig. 68. *Glabropilumnus edamensis* (De Man, 1888), ZI: a, maxillule; b, maxilla; c, telson; d, pereiopods.

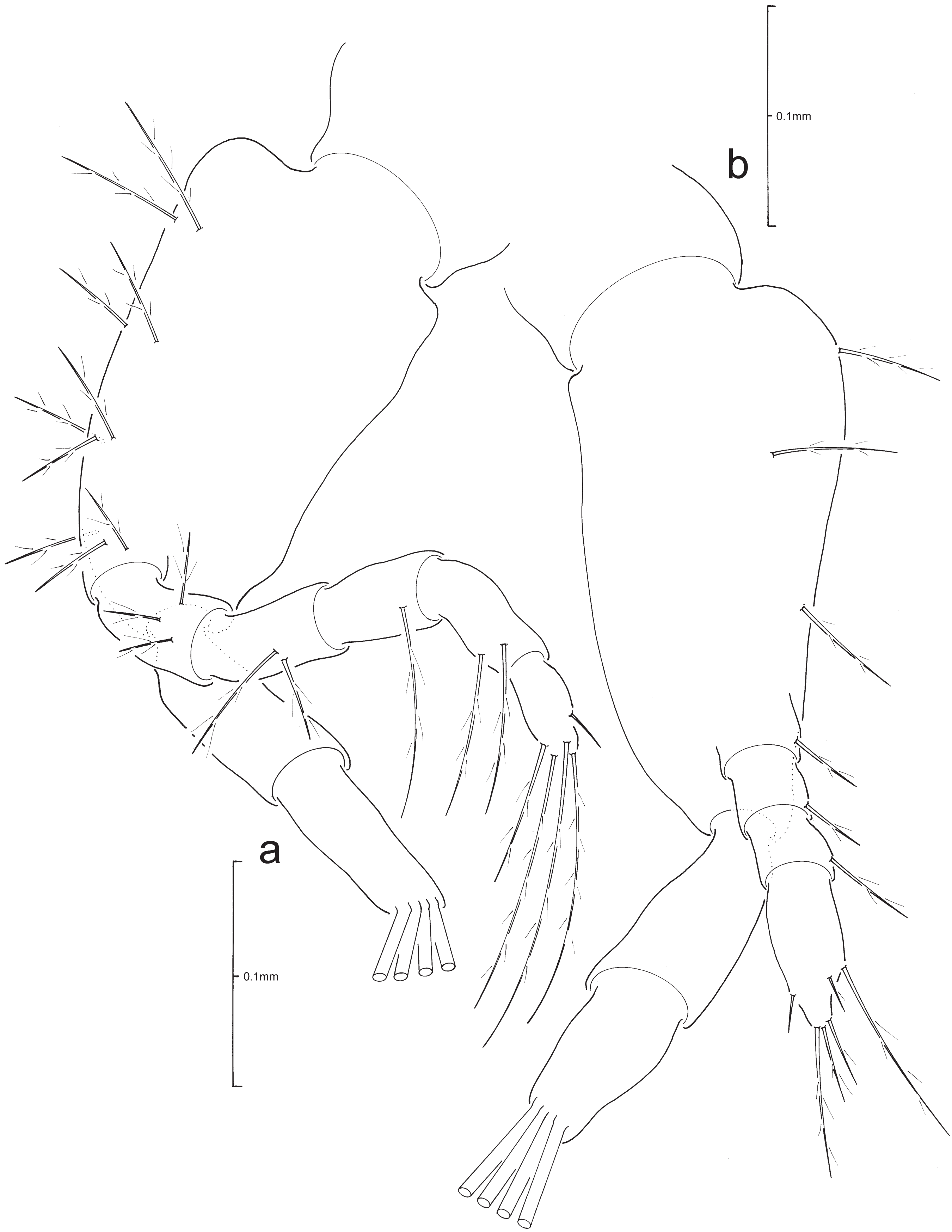

Fig. 69. *Glabropilumnus edamensis* (De Man, 1888), ZI: a, first maxilliped; b, second maxilliped.

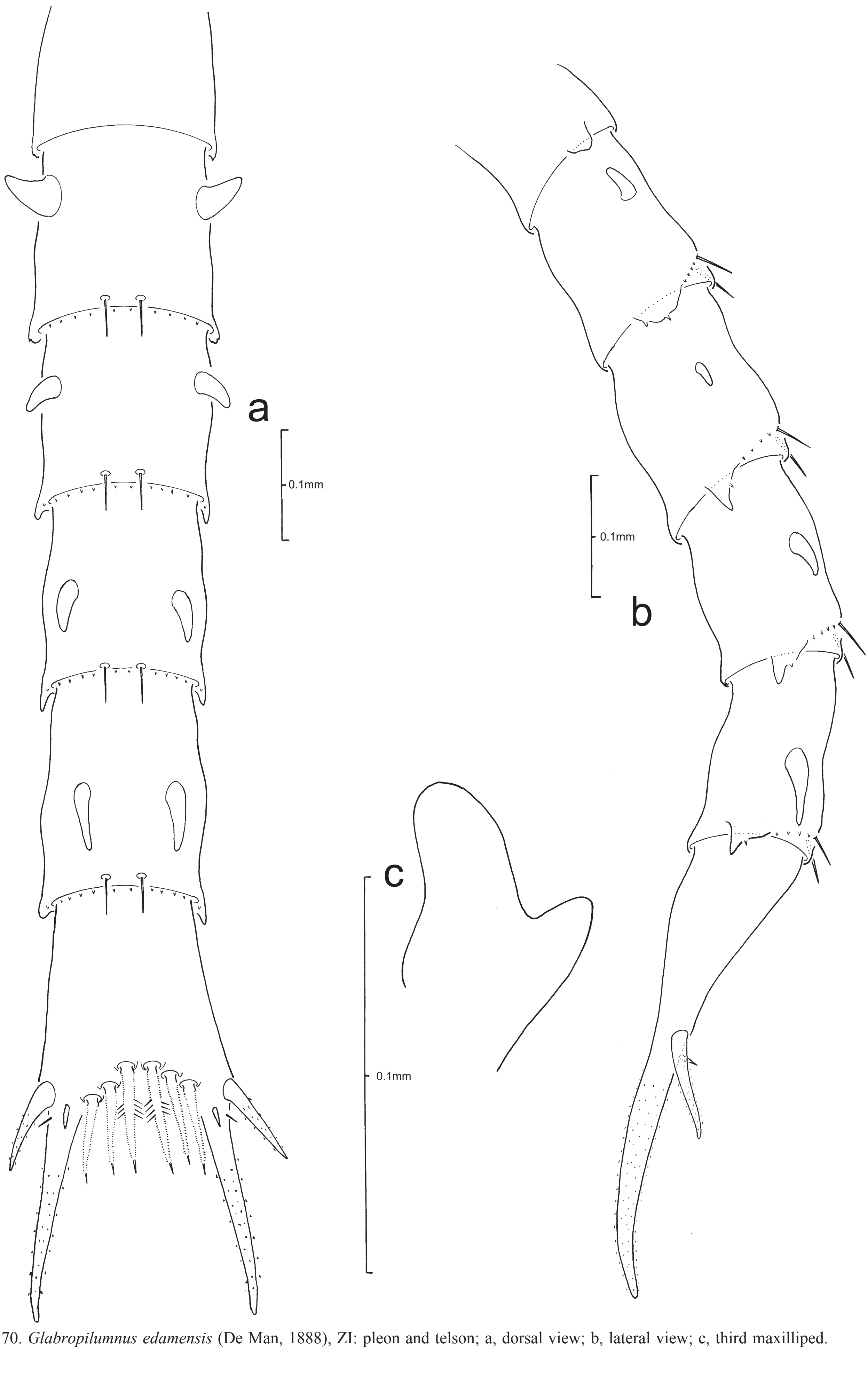

Fig. 70. *Glabropilumnus edamensis* (De Man, 1888), ZI: pleon and telson; a, dorsal view; b, lateral view; c, third maxilliped.

Heteropanope glabra Stimpson, 1858
(Figs. 71–74)

Heteropanope glabra. Aikawa, 1929: 40, 41, pl. III, fig. 13, pl. IV, figs. 29, 47, 48 (ZI); S.S.L. Lim et al., 1984: 2–12, figs. 1–7 (ZI–IV, Meg.); Greenwood & Fielder, 1984: 293–295, figs. 1–6 (ZI–IV, Meg.).

Description of Zoea I.
CARAPACE (Fig. 71a): dorsal spine smooth, curved distally, relatively short, longer than rostral spine length; rostral spine shorter than antennal protopod length, without distal spinulation; lateral spines present, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 71a): sessile.
Antennule (Fig. 71b): primary flagellum unsegmented with 4 (2 broad, 2 slender) aesthetascs of unequal length plus 2 terminal setae of unequal length; accessory flagellum absent.
Antenna (Fig. 71c): uniramous; protopod distally bilaterally spinulate, longer than rostral spine length; endopod bud absent; exopod unsegmented, distally bilaterally spinulate with 2 medial setae of unequal length.
Mandible: palp absent.
Maxillule (Fig. 72a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 terminal setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 72b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal setae); exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 73a): biramous; coxa without setae; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 73b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 74a, b): 5 pleomeres; pleomere 2 with pair of dorsolateral processes directed anteriorly; pleomere 3 with pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without dorsal setae; pleomeres 2–5 each with 1 pair of posterodorsal setae and spinulated dorsal posterior margin; pleopod buds absent.

TELSON (Figs. 72c, 74a, b): each fork long, spinulate, gradually curved distally, 1 long lateral spine, 1 more slender lateral spine, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Remarks. According to S.S.L. Lim et al. (1984: fig. 1A, B), the first pleomere of ZI and ZII bears three medial setae, but Greenwood & Fielder (1984: fig. 1E) did not figure these setae until ZIII. For the present study, the ZI was devoid of three setae on the first pleomere (Fig. 74).

Table 8. A comparison between the ZI of *Heteropanope glabra* Stimpson, 1858 by Aikawa (1929), Lim et al. (1984), Greenwood & Fielder (1984), and the present study.

Character	**Aikawa (1929)**	**Lim et al. (1984)**	**Greenwood & Fielder (1984)**	**Present study**
CARAPACE	pl. III, fig. 13	fig. 1A	fig. 1A, B	Fig. 71a
posterodorsal setae	absent	absent	absent	1 pair present
ANTENNULE	pl. III, fig. 13	fig. 2C	fig. 2A	Fig. 71b
terminal setation	2 terminal aesthetascs	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 2 terminal setae of unequal length	3 aesthetascs of unequal length, 2 terminal setae of unequal length	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 2 terminal setae of unequal length
ANTENNA	pl. IV, fig. 29	fig. 2D	fig. 2B	Fig. 71c
exopod setation	1 medial seta	2 medial setae of unequal length	2 medial setae of unequal length	2 medial setae of unequal length
MAXILLULE	not figured	fig. 2F	fig. 2C	Fig. 72a
coxal endite setation		6	7	7
MAXILLA	not figured	fig. 2G	fig. 2D	Fig. 72b
coxal endite setation		text: 6+5 fig.: 6+4	6+4	6+4
basial endite setation		4+4	5+4	5+4
FIRST MAXILLIPED	pl. IV, fig. 47	fig. 2H	fig. 2E	Fig. 73a
basial setation	Tab. VI: 8 (2+2+2+2) fig. 47: 8 (2+2+3+1)	10 (2+2+3+3)	10 (2+2+3+3)	10 (2+2+3+3)
endopod setation	Tab. VI: 3,2,1,2,6 fig. 47: 3,2,1,1,6	3,2,1,2,5 (1 subterminal+4 terminal setae)	3,2,1,2,5 (1 subterminal+4 terminal setae)	3,2,1,2,5 (1 subterminal+4 terminal setae)
SECOND MAXILLIPED	pl. IV, fig. 48	fig. 2I	fig. 2E	Fig. 73b
basial setation	3 (1+1+1)	4 (1+1+1+1)	4 (1+1+1+1)	4 (1+1+1+1)
endopod setation	1,1,6	1,1,6 (3 subterminal+3 terminal)	1,1,6 (3 subterminal+3 terminal)	1,1,6 (3 subterminal, 3 terminal)
PLEON	pl. III, fig. 13	fig. 2A	fig. 1A, B	Fig. 74a, b
pleomere 1; setation	absent	3	absent	absent

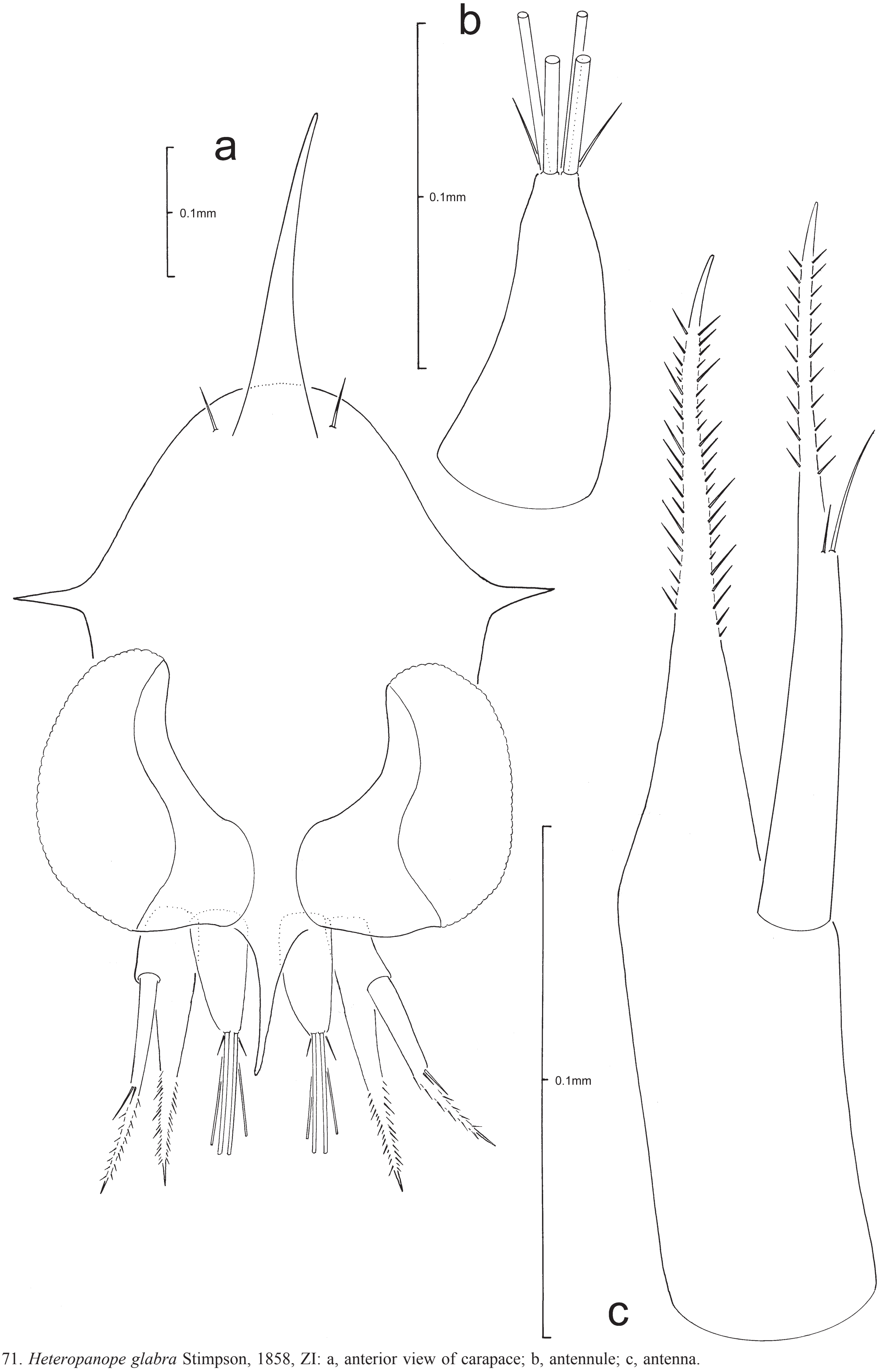

Fig. 71. *Heteropanope glabra* Stimpson, 1858, ZI: a, anterior view of carapace; b, antennule; c, antenna.

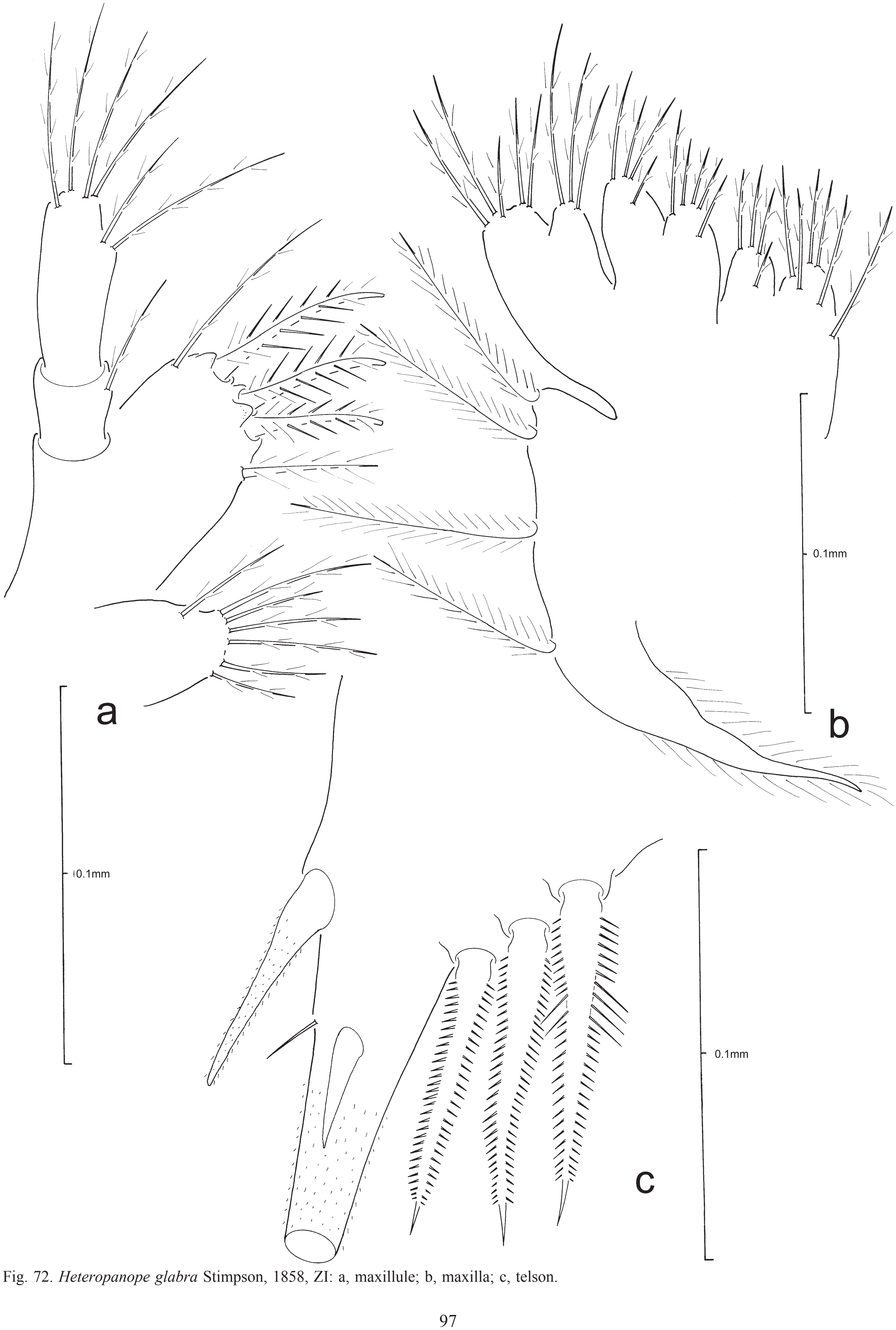

Fig. 72. *Heteropanope glabra* Stimpson, 1858, ZI: a, maxillule; b, maxilla; c, telson.

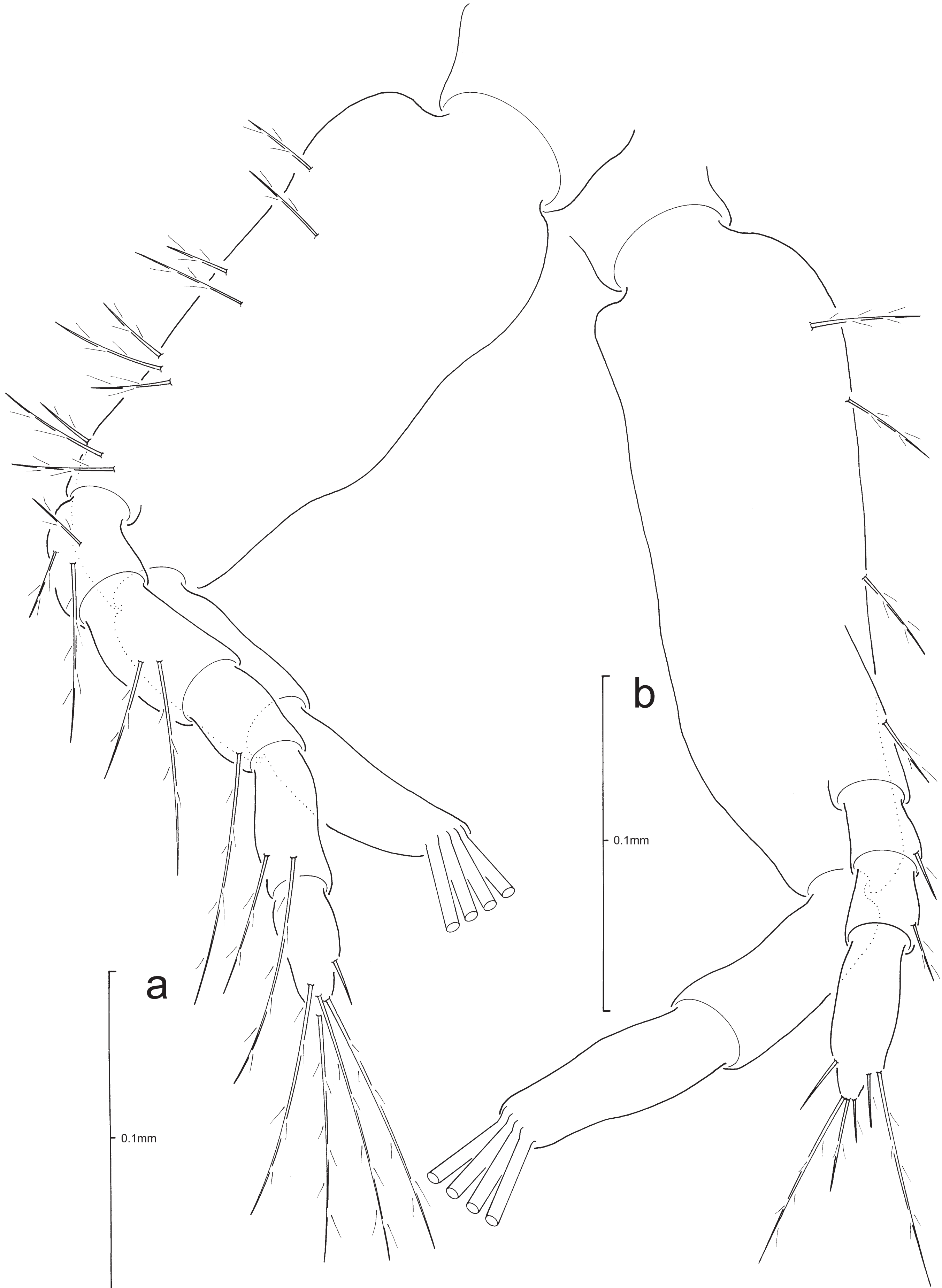

Fig. 73. *Heteropanope glabra* Stimpson, 1858, ZI: a, first maxilliped; b, second maxilliped.

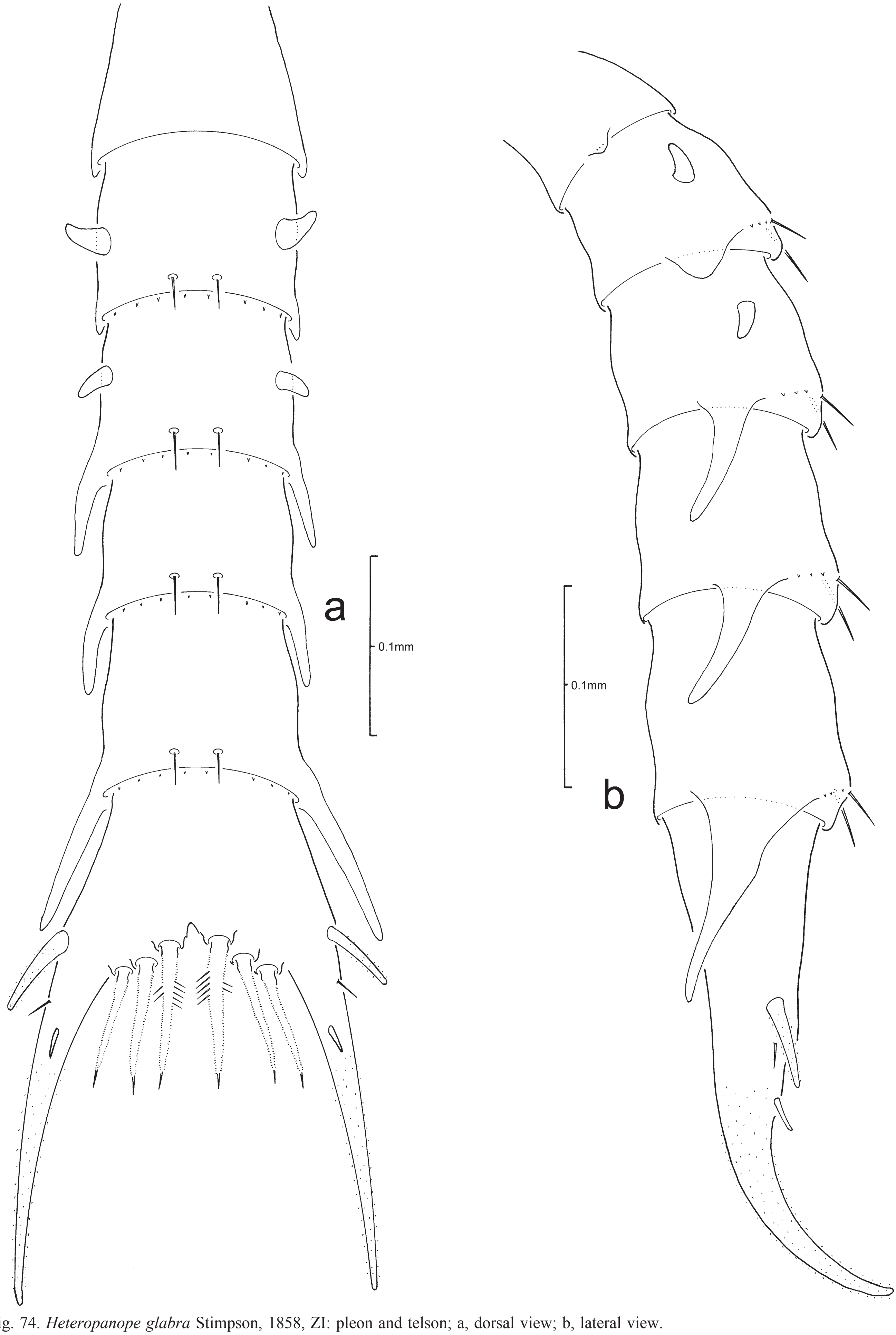

Fig. 74. *Heteropanope glabra* Stimpson, 1858, ZI: pleon and telson; a, dorsal view; b, lateral view.

***Heteropilumnus holthuisi* P.K.L. Ng & L.W.H. Tan, 1988**
(Figs. 75–78)

Description of Zoea I.
CARAPACE (Fig. 75a): dorsal spine smooth, curved distally, relatively short, just longer than rostral spine length; rostral spine just shorter than antennal protopod length, without distal spinulation; lateral spines present, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 75a): sessile.
Antennule (Fig. 75b): primary flagellum unsegmented with 4 (2 broad, 2 slender) aesthetascs of unequal length plus 2 terminal setae of unequal length; accessory flagellum absent.
Antenna (Fig. 75c): uniramous; protopod distally bilaterally spinulate, just longer than rostral spine length; endopod bud absent; exopod unsegmented, distally bilaterally spinulate 2 medial setae of unequal length.
Mandible: palp absent.
Maxillule (Fig. 76a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 terminal setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 76b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal setae); exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 77a): biramous; coxa without setae; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 77b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 78a, b): 5 pleomeres; pleomere 2 with pair of dorsolateral processes directed anteriorly; pleomere 3 with pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without dorsal setae; pleomeres 2–5 each with 1 pair of posterodorsal setae and spinulated dorsal posterior margin; pleopod buds absent.

TELSON (Figs. 76c, 78a, b): each fork long, spinulate, gradually curved distally, 1 long lateral spine, 1 more slender lateral spine, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

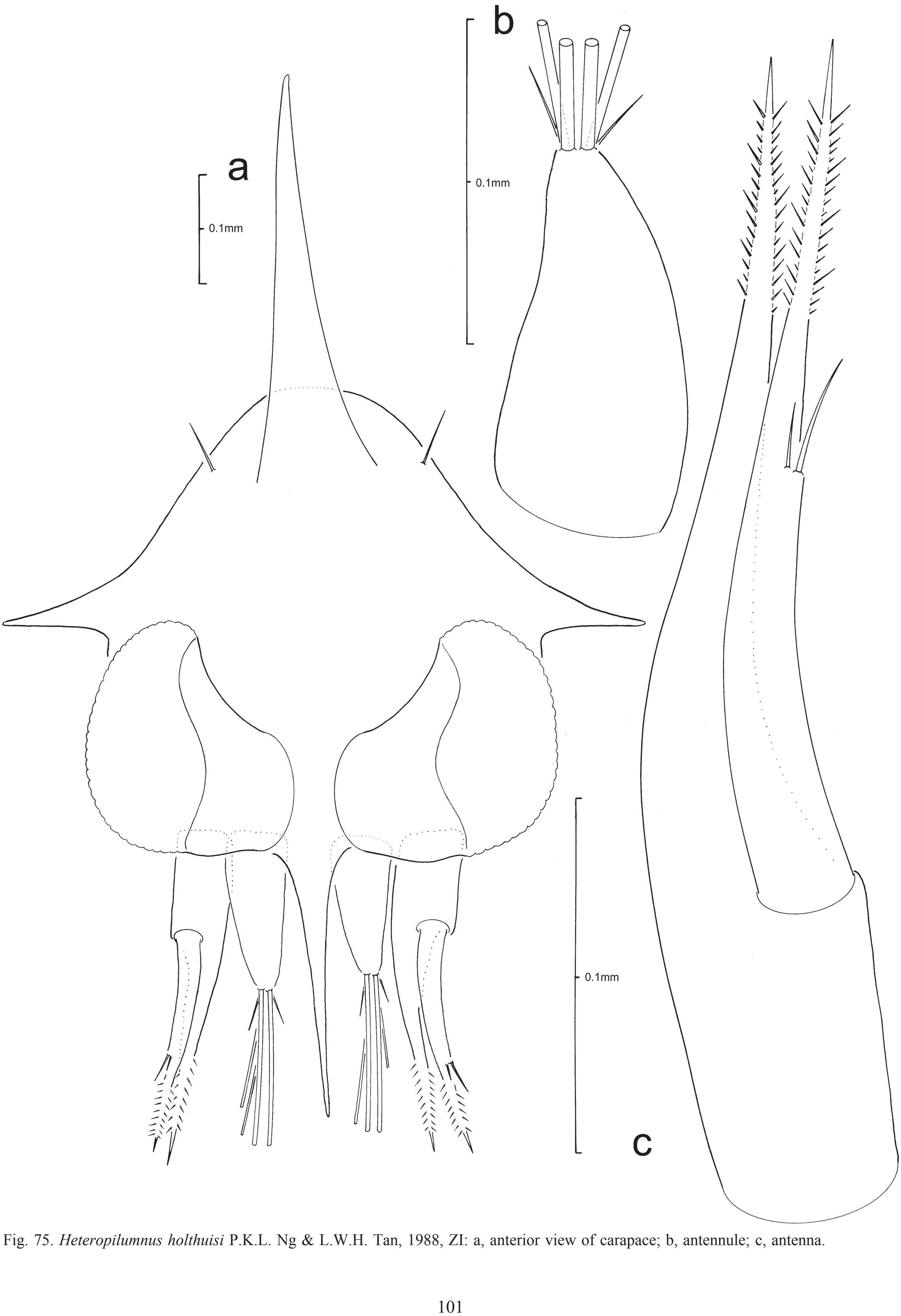

Fig. 75. *Heteropilumnus holthuisi* P.K.L. Ng & L.W.H. Tan, 1988, ZI: a, anterior view of carapace; b, antennule; c, antenna.

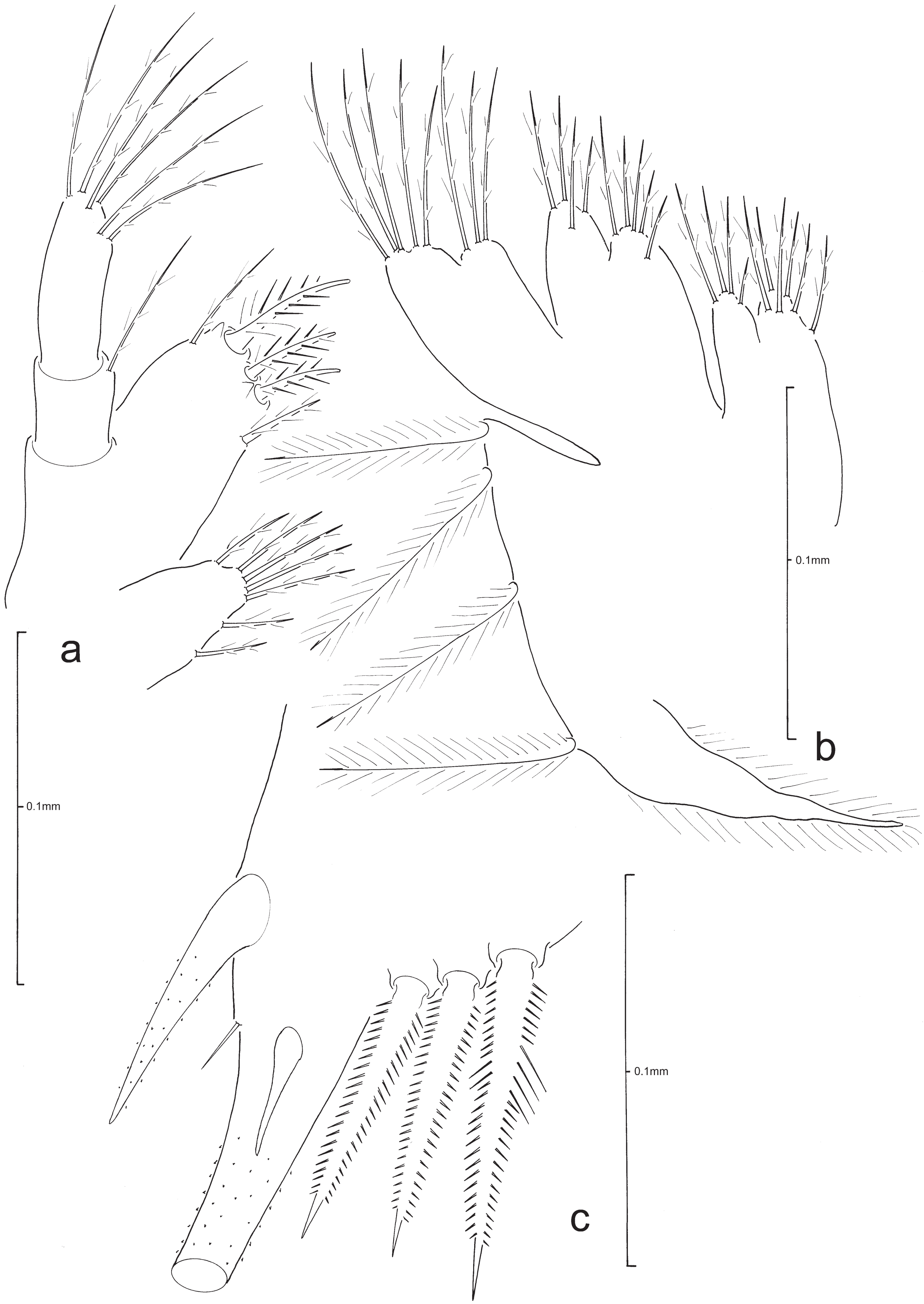

Fig. 76. *Heteropilumnus holthuisi* P.K.L. Ng & L.W.H. Tan, 1988, ZI: a, maxillule; b, maxilla; c, telson.

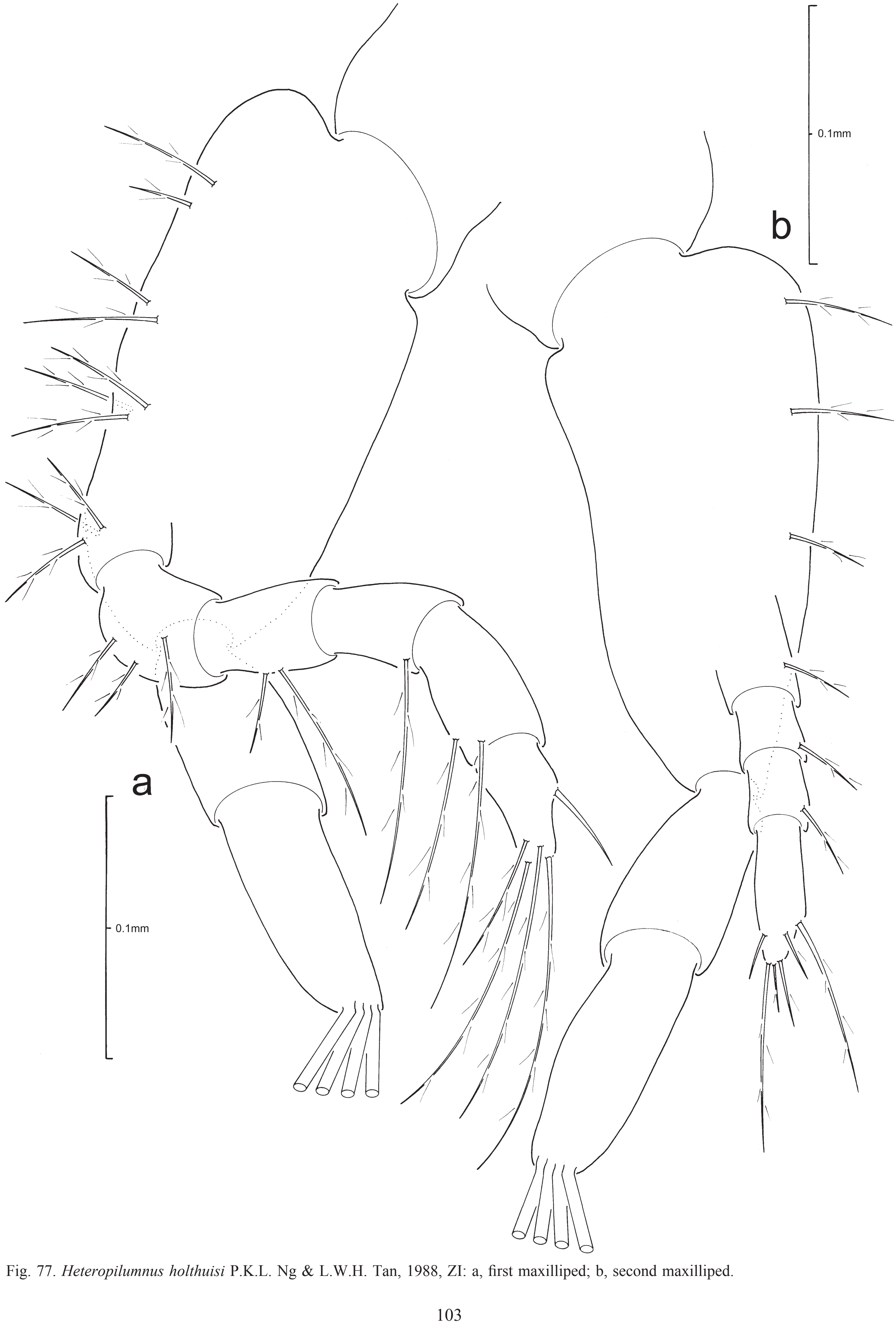

Fig. 77. *Heteropilumnus holthuisi* P.K.L. Ng & L.W.H. Tan, 1988, ZI: a, first maxilliped; b, second maxilliped.

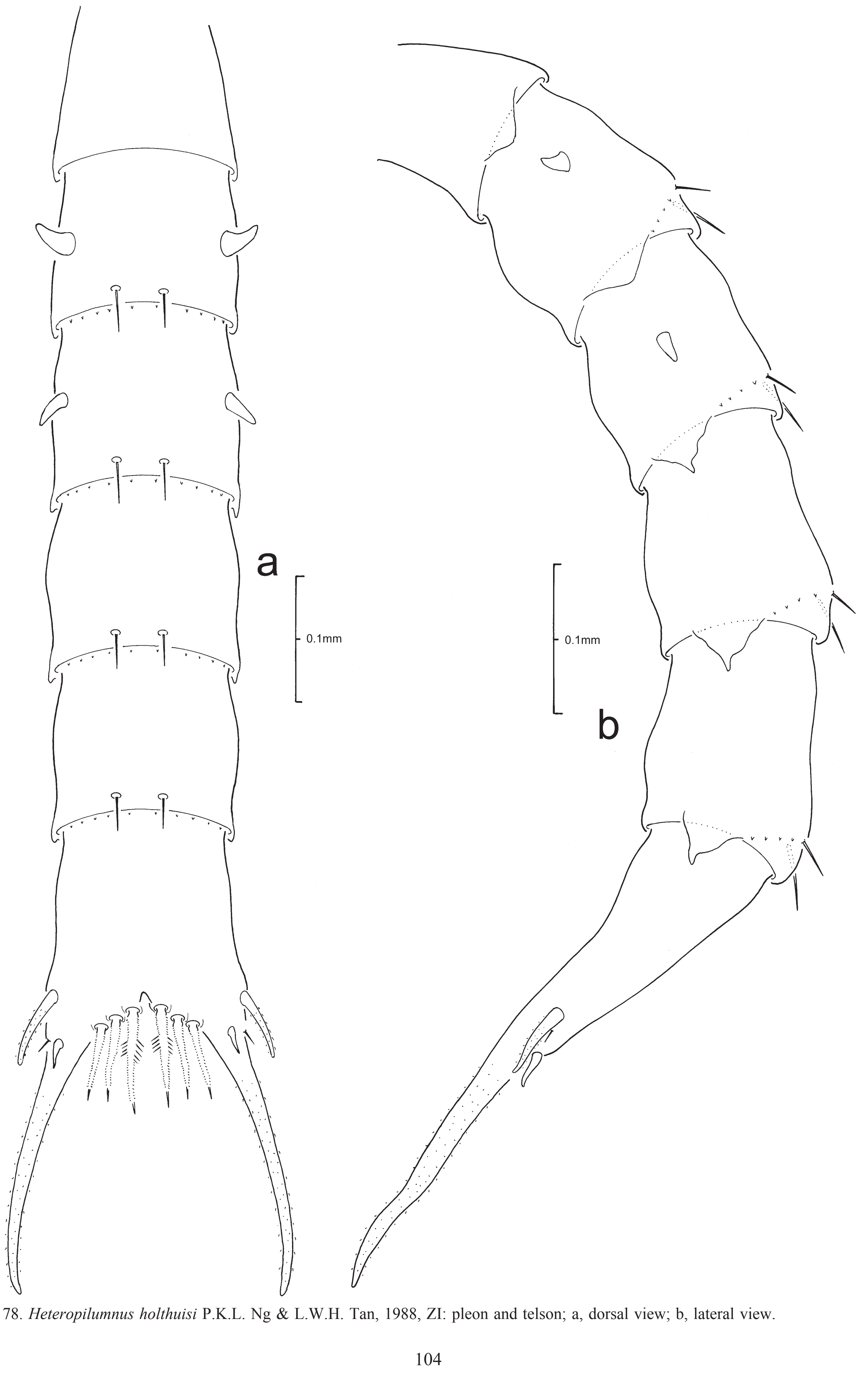

Fig. 78. *Heteropilumnus holthuisi* P.K.L. Ng & L.W.H. Tan, 1988, ZI: pleon and telson; a, dorsal view; b, lateral view.

Pilumnus kempi Deb, 1987
(Figs. 79–88)

Pilumnus kempi. Siddiqui & Tirmizi, 1992: 230–241, figs. 1–7, (ZI–II, Meg., Cr. I); Clark & P.K.L. Ng, 2004a: tabs. 1, 2 (ZI–II).

Description of Zoea I.
CARAPACE (Figs. 79, 81a): dorsal spine smooth, curved distally, relatively short, ca. 5 times longer than rostral spine length; rostral spine significantly shorter than antennal protopod length, without distal spinulation; lateral spines short, without spinulation on dorsal margin; 1 pair of anterodorsal setae present; 1 pair of posterodorsal setae present; ventral margin with 1 anterior seta.

CEPHALON
Eyes (Fig. 79): eyes sessile.
Antennule (Fig. 81c): primary flagellum unsegmented with 1 subterminal, 3 broad and long aesthetascs, 3 slender aesthetascs + 2 setae of unequal length, all terminal; accessory flagellum present as small bud.
Antenna (Fig. 82a): biramous; protopod distally bilaterally spinulate, ca. 7 times longer than rostral spine length; endopod bud present, ca. 58% of protopod; exopod unsegmented, distally bilaterally spinulate with 2 medial setae of unequal length.
Mandible: palp absent.
Maxillule (Fig. 83a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 terminal setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 83c): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal setae); exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 84a): biramous; coxa without setae, epipodal bud present; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 84c): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped (Fig. 85b): biramous with epipod; endopod longer than exopod.
Pereiopods (Fig. 85d): present; uniramous; chela bilobed; some segmentation of appendages developing; first 4 appendages with gills developing.

PLEON (Figs. 86a, 87a): 5 pleomeres; pleomere 2 with pair of dorsolateral processes directed anteriorly; pleomere 3 with pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae and spinulated dorsal posterior margin; pleomeres 2–5 with uniramous pleopod buds present, endopods absent.

TELSON (Figs. 86a, 87a, 88f): each fork long, spinulate, gradually curved distally, 1 long lateral spine, 1 lateral seta, 1 short dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Description of Zoea II.
CARAPACE (Figs. 80, 81b): 3 pairs of anterodorsal setae present; ventral margin with 2 anterior setae plus 10 posterior setae; otherwise unchanged.

CEPHALON
Eyes (Fig. 80): stalked.
Antennule (Fig. 81d): protopod with 1 seta; primary flagellum now with 5 proximal subterminal aesthetascs, 6 distal subterminal aesthetascs; 5 broad aesthetascs, 2 slender aesthetascs + 3 terminal setae of unequal length, accessory flagellum developing.
Antenna (Fig. 82b): endopod now ca. 70% of protopod; otherwise unchanged.
Mandible (Fig. 85a): palp present.
Maxillule (Fig. 83b): biramous; epipod seta present; coxal endite with 9; basial endite with 9 setal processes; exopod seta present; otherwise unchanged.
Maxilla (Fig. 83d): basial endite bilobed with 6+5 setae; exopod (scaphognathite) margin with 20 setae of equal length + distal, stout process no longer prominent; otherwise unchanged.

PEREION
First maxilliped (Fig. 84b): epipod bilobed with podobranch gill developing; exopod distal article with 6 long terminal plumose natatory setae; otherwise unchanged.
Second maxilliped (Fig. 84d): exopod distal article with 6 long terminal plumose natatory setae; otherwise unchanged.
Third maxilliped (Fig. 85c): epipod with developing arthrobranch; endopod developing articles; otherwise unchanged.
Pereiopods (Fig. 85e): developing; otherwise unchanged.

PLEON (Figs. 86b, 87b, 88a–e): now with 6 pleomeres; pleomere 1 with 5 dorsomedial setae plus 1 dorsomarginal seta; pleomeres 2–5 with pleopod buds present; biramous; endopods present; pleomere 6, uropods present, biramous, endopod present; otherwise unchanged.

TELSON (Figs. 86b, 87b, 88g): posterior margin with 3 pairs of stout spinulate setae plus 1 pair of medial setae; otherwise unchanged.

Remarks. Only two *Pilumnus* species to date have been described with two zoeal stages, *P. kempi* by Siddiqui & Tirmizi (1992) and *P. sluiteri* by Clark & P.K.L. Ng (2004a).

Table 9. A comparison between the ZI descriptions of *Pilumnus kempi* Deb, 1987 by Siddiqui & Tirmizi (1992) and the present study.

Character	**Siddiqui & Tirmizi (1992)**	**Present study**
CARAPACE	fig. 1A	Figs. 79, 81a
anterodorsal setae	not described	1 pair
posterodorsal setae	not described	1 pair
posterior marginal setae	not described	1 anterior seta
ANTENNULE	fig. 1B	Fig. 81c
number of terminal aesthetascs and setae	7 aesthetascs	6 aesthetascs + 2 setae of unequal length
endopod	absent	present
MAXILLA	fig. 1F	Fig. 83c
coxal endite	5+4	6+4
basial endite	4+4	5+4
FIRST MAXILLIPED	fig. 1F	Fig. 84a
setation of basis	11 (1+2+2+3+3)	10 (2+2+3+3)
THIRD MAXILLIPED	text page 231	Fig. 85b
epipod	biramous only	biramous with epipod
PLEON	figs. 1A, A’	Figs. 86a, 87a
pleomeres 2–5; setation	not figured	1 pair of posterodorsal setae on each pleomere

Table 10. A comparison between the ZII descriptions of *Pilumnus kempi* by Siddiqui & Tirmizi (1992) and the present study.

Character	**Siddiqui & Tirmizi (1992)**	**Present study**
CARAPACE	fig. 2A	Figs. 80, 81b
anterodorsal setae	not described	2 pairs
posterodorsal setae	not described	1 pair
posterior marginal setae	not described	2 anterior + 10 posterior setae
ANTENNULE	fig. 2B	Fig. 81d
proximal seta	not described	present
number of subterminal aesthetascs	one row of 6 large and 4 small subterminal aesthetascs	two rows of subterminal aesthetascs; proximal row with 5 aesthetascs and distal row with 6 aesthetascs
MANDIBLE	fig. 2D	Fig. 85a
palp articulations	comprising 2 articles	comprising 1 article
MAXILLULE	fig. 2E	Fig. 83b
coxal endite	8 setae	9 setae
FIRST MAXILLIPED	fig. 3A	Fig. 84b
setation of basis	description suggests 11 (1+2+2+3+3) figure shows 10 setae, 2+2+3+3	10 (2+2+3+3)
SECOND MAXILLIPED	fig. 3B	Fig. 84d
setation of basis	5 setae, 2,2,1	4 setae, 1,1,1,1
THIRD MAXILLIPED	fig. 3C	Fig. 85c
epipod	biramous only	biramous with epipod
PLEON	fig. 3C	Figs. 86b, 87b
pleomere 1; setation	not described	5 dorsomedial setae + 1 small dorsal marginal seta
pleomeres 2–5; setation	not described	1 pair on each pleomere
pleomere 6; pleopods	not described	1 pair of posterodorsal setae on each pleomere
TELSON	fig. 2G	Figs. 86b, 87b, 88g
small lateral spine	absent	present
pair of medial setae on posterior margin	absent	present

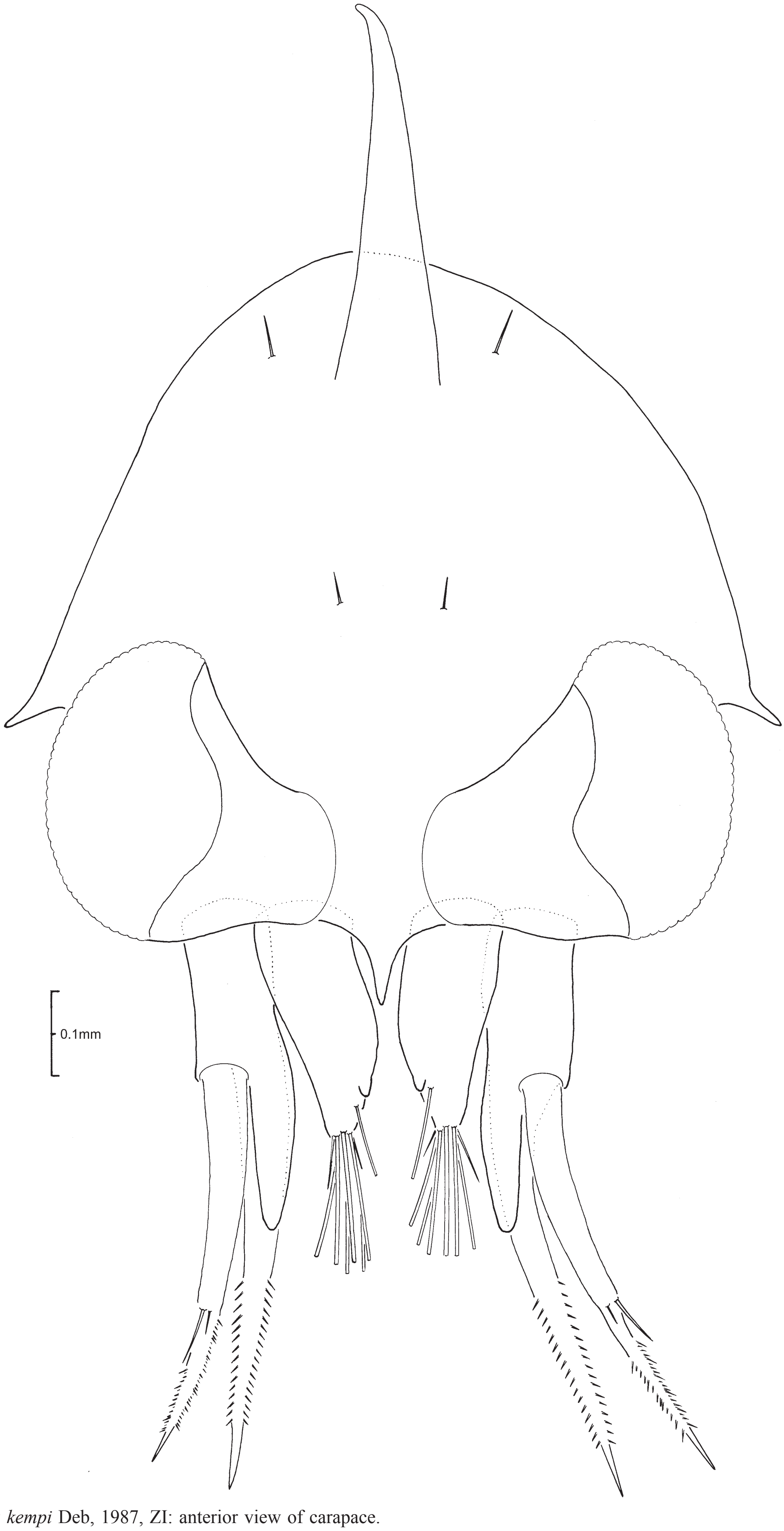

Fig. 79. *Pilumnus kempi* Deb, 1987, ZI: anterior view of carapace.

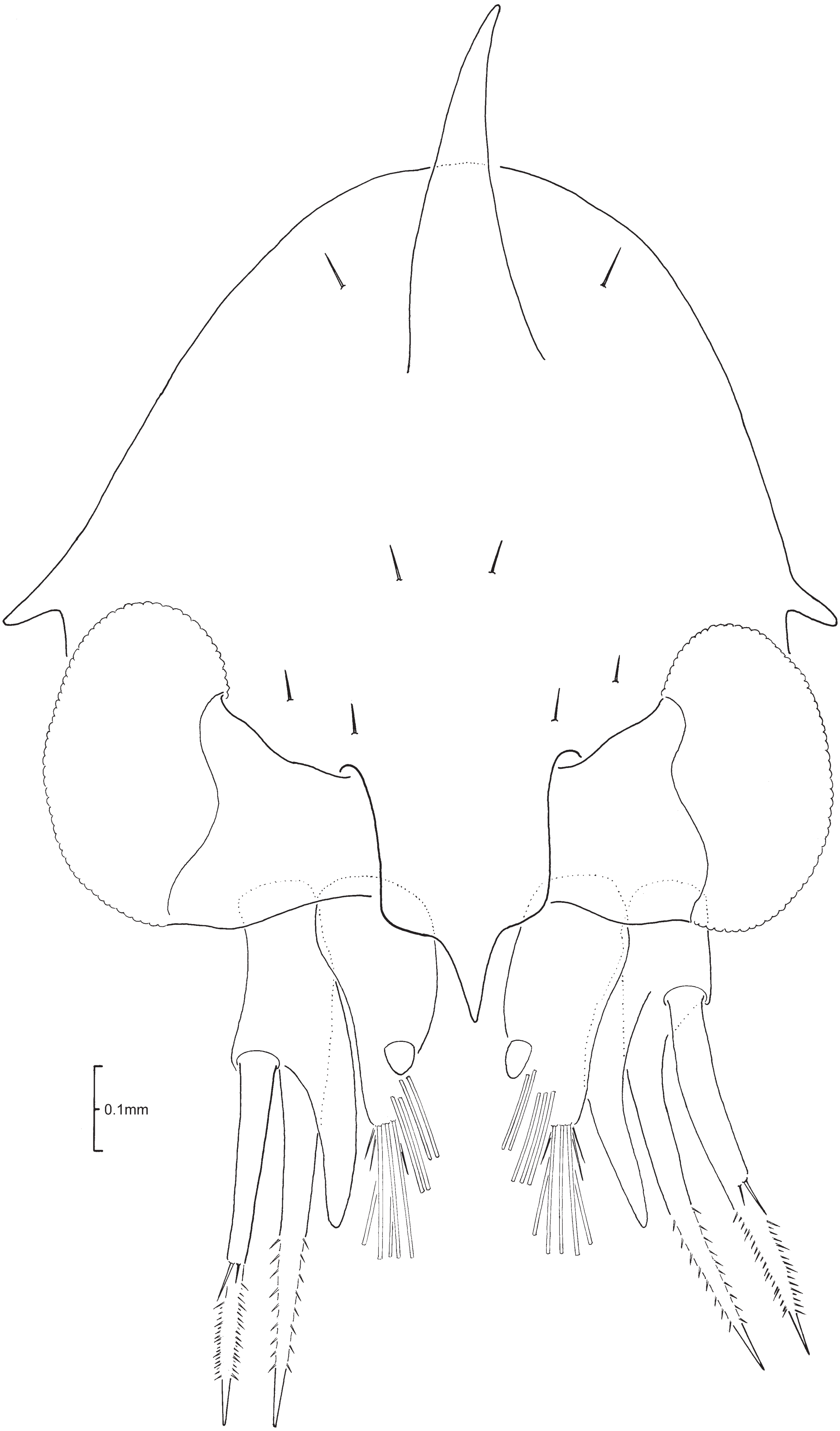

Fig. 80. *Pilumnus kempi* Deb, 1987, ZII: anterior view of carapace

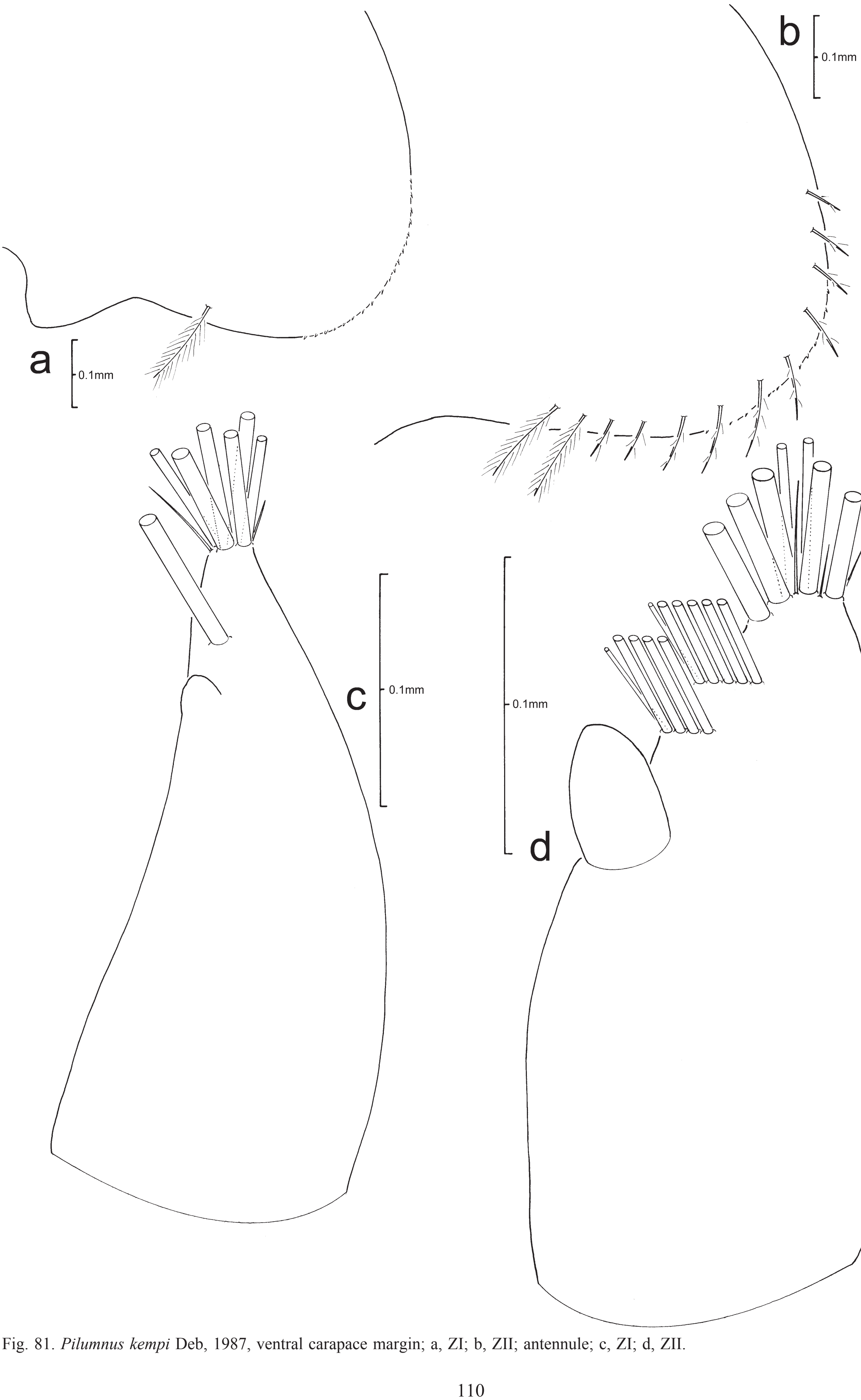

Fig. 81. *Pilumnus kempi* Deb, 1987, ventral carapace margin; a, ZI; b, ZII; antennule; c, ZI; d, ZII.

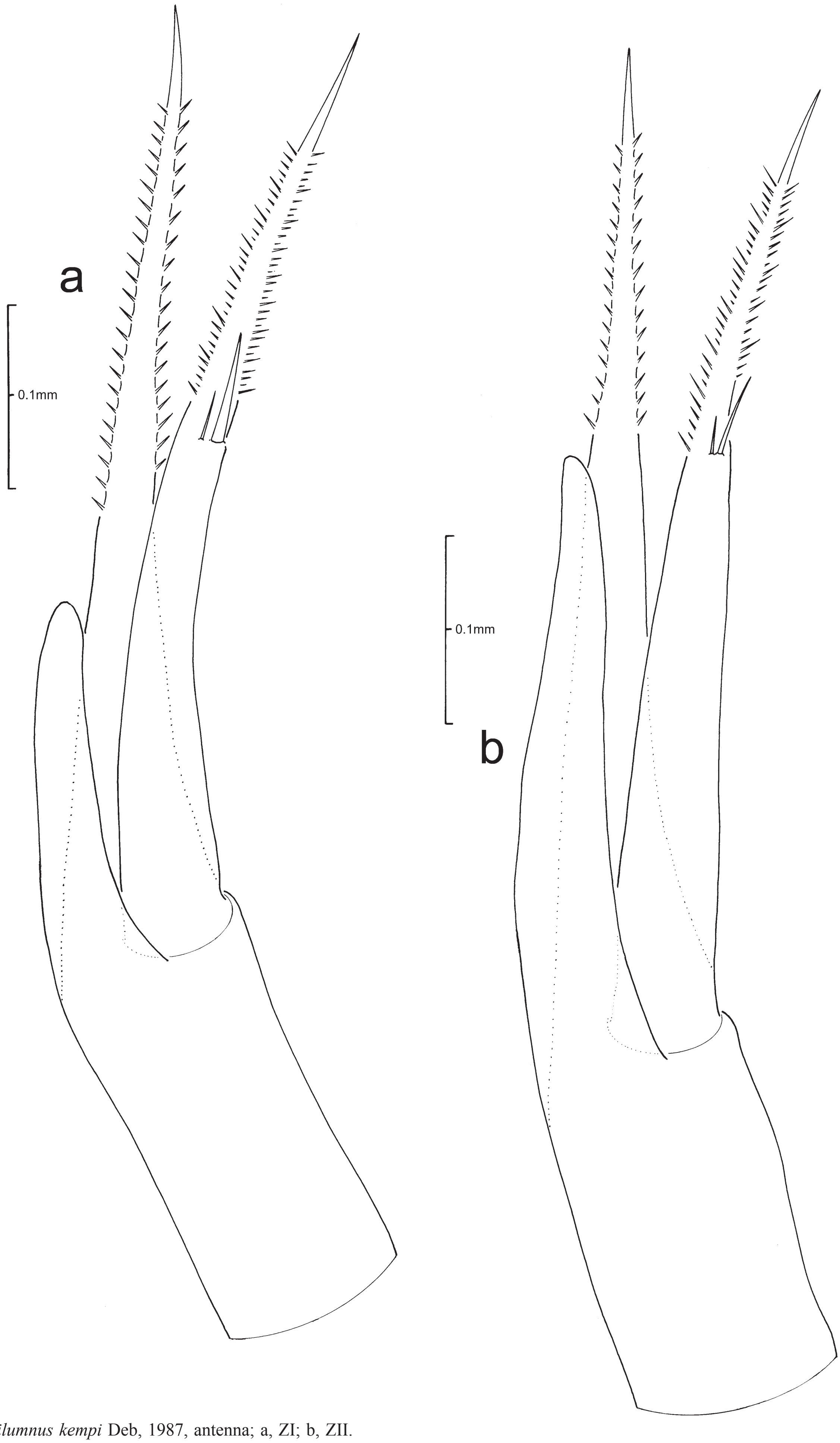

Fig. 82. *Pilumnus kempi* Deb, 1987, antenna; a, ZI; b, ZII.

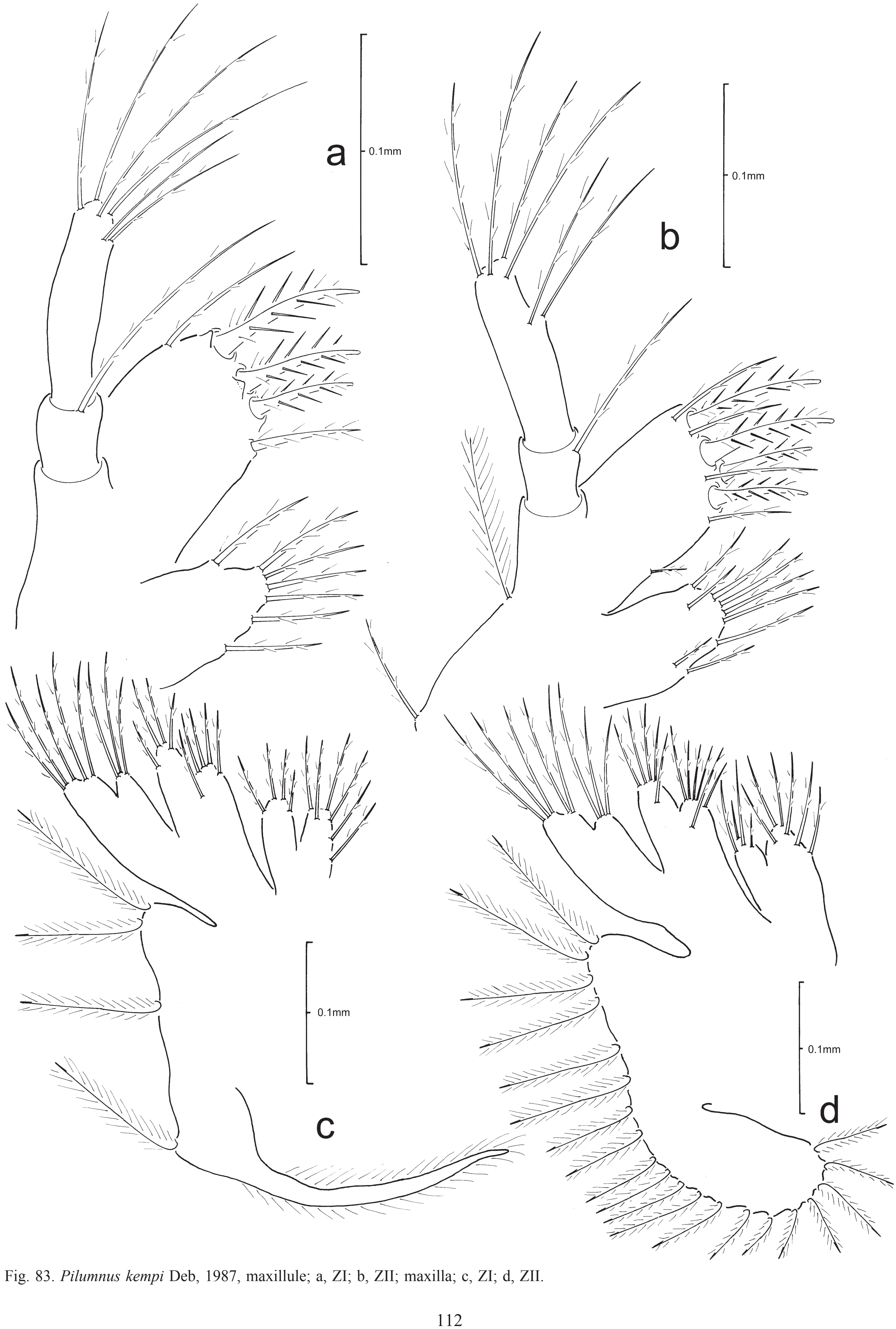

Fig. 83. *Pilumnus kempi* Deb, 1987, maxillule; a, ZI; b, ZII; maxilla; c, ZI; d, ZII.

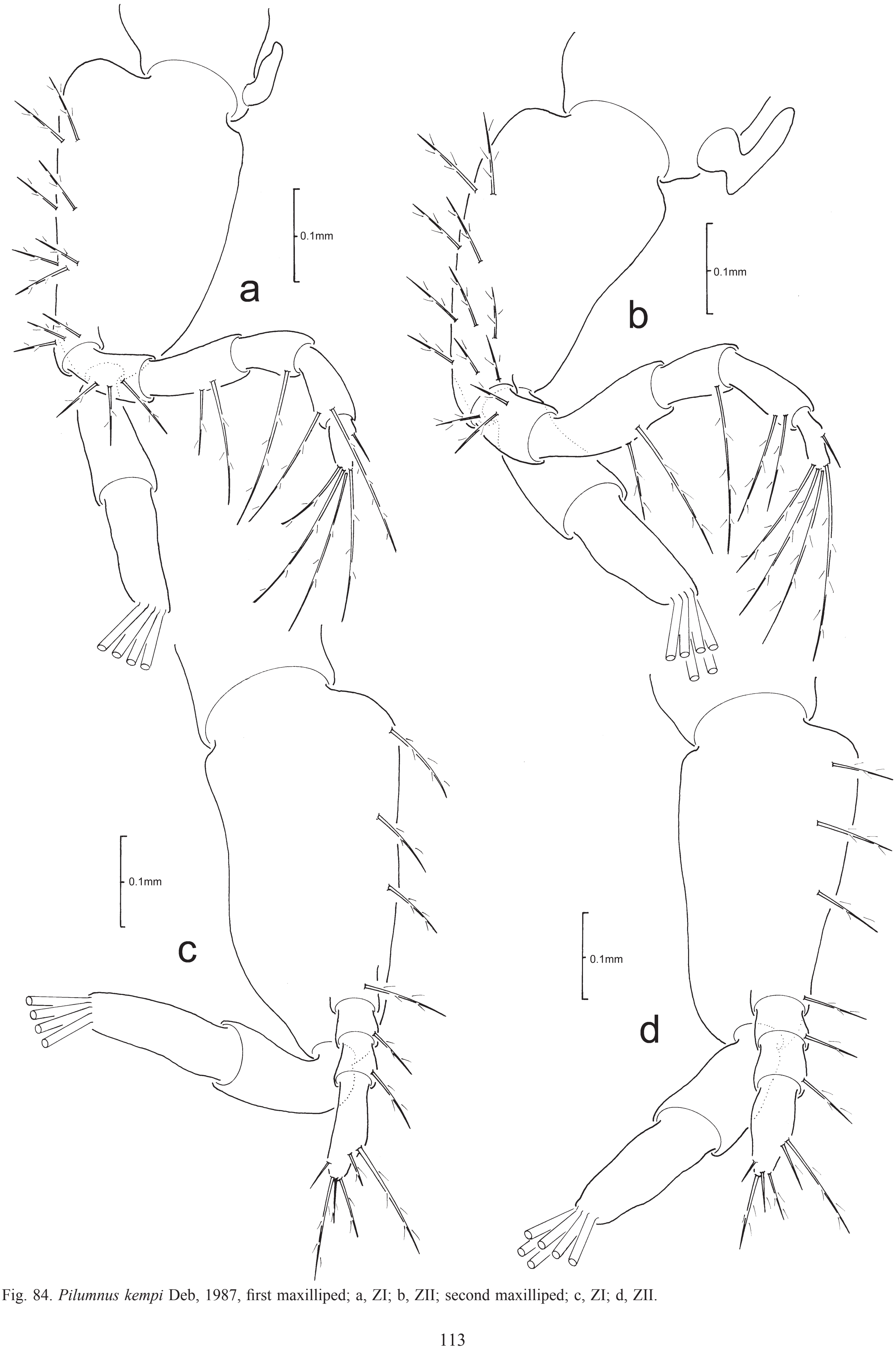

Fig. 84. *Pilumnus kempi* Deb, 1987, first maxilliped; a, ZI; b, ZII; second maxilliped; c, ZI; d, ZII.

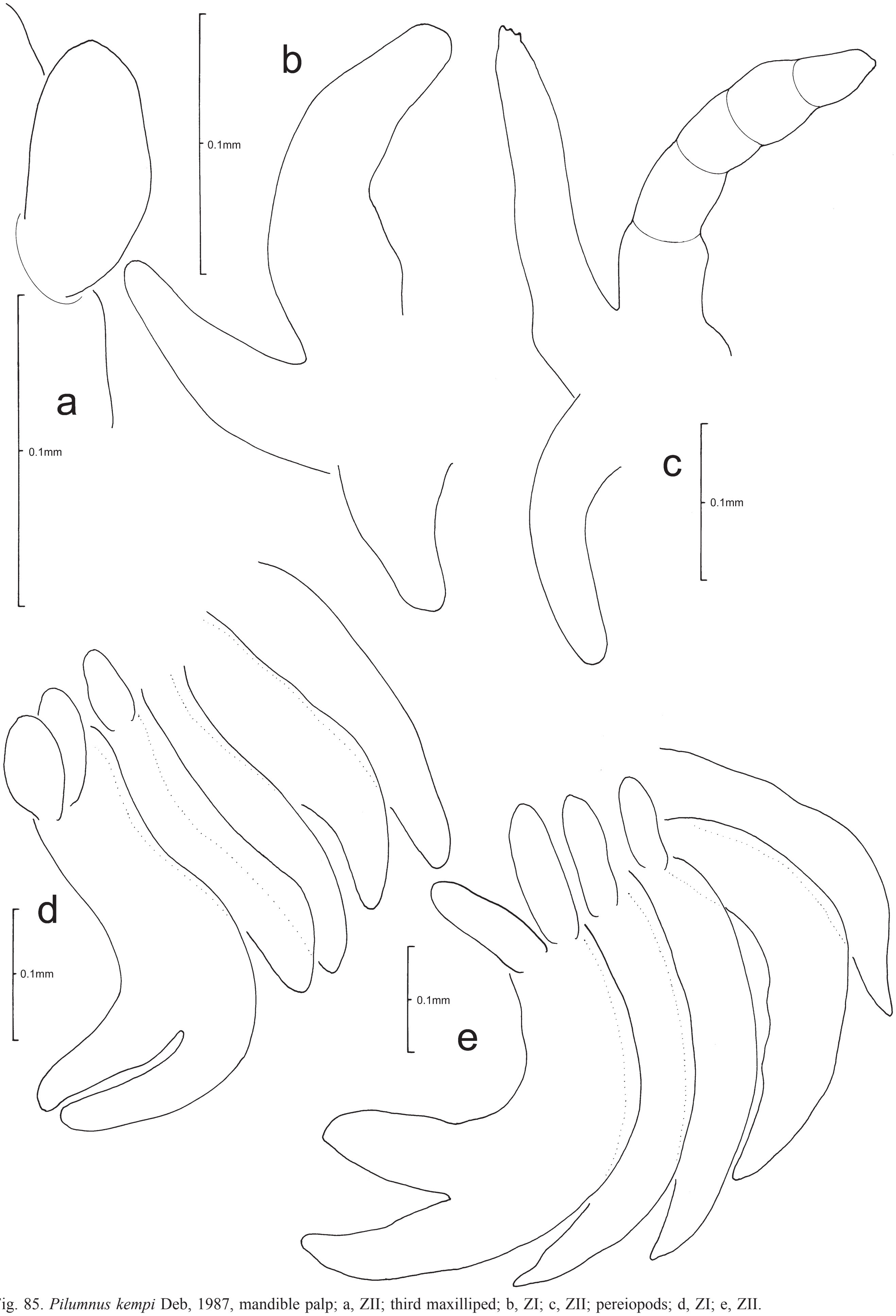

Fig. 85. *Pilumnus kempi* Deb, 1987, mandible palp; a, ZII; third maxilliped; b, ZI; c, ZII; pereiopods; d, ZI; e, ZII.

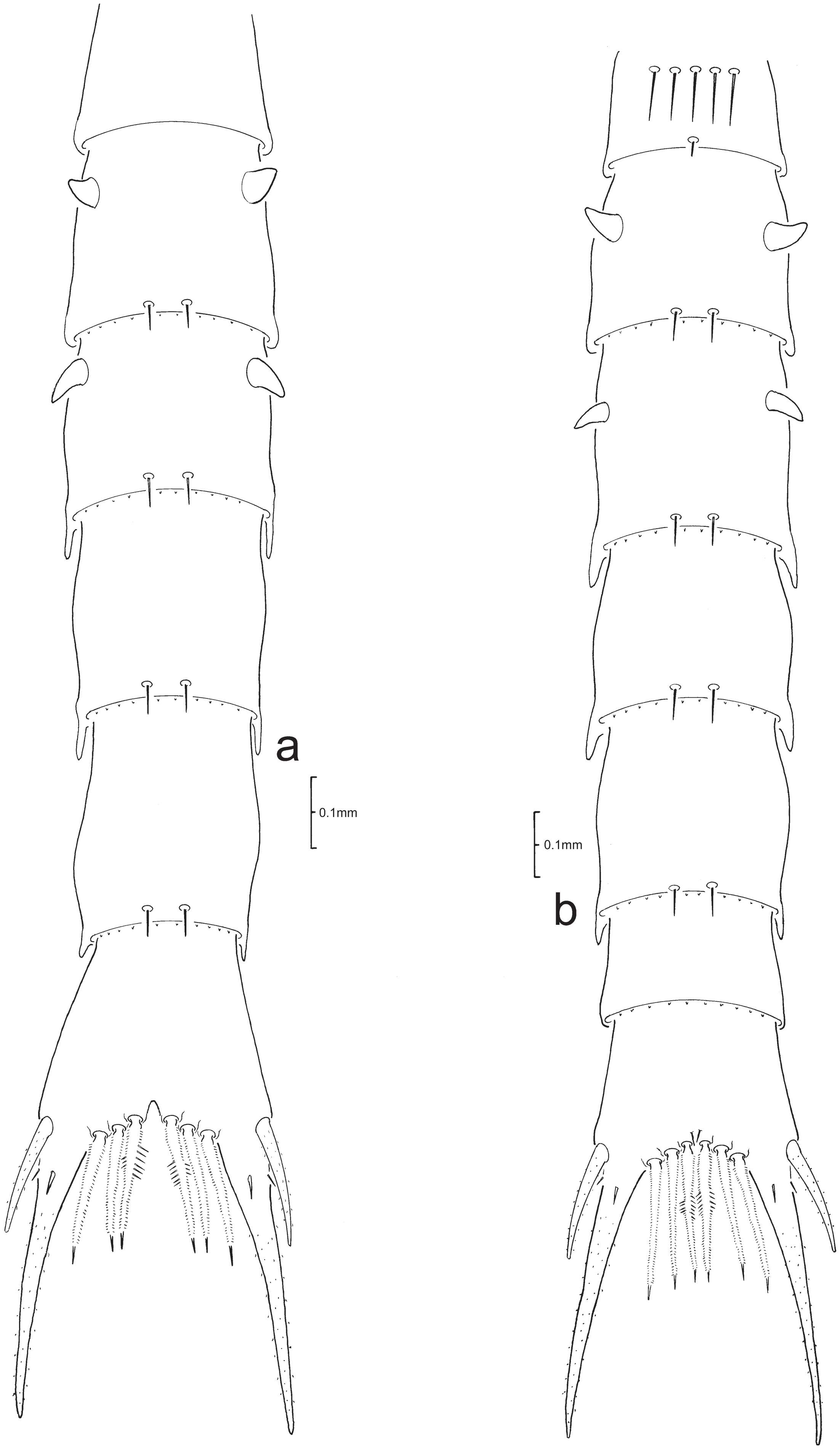

Fig. 86. *Pilumnus kempi* Deb, 1987, dorsal view of pleon and telson; a, ZI; b, ZII.

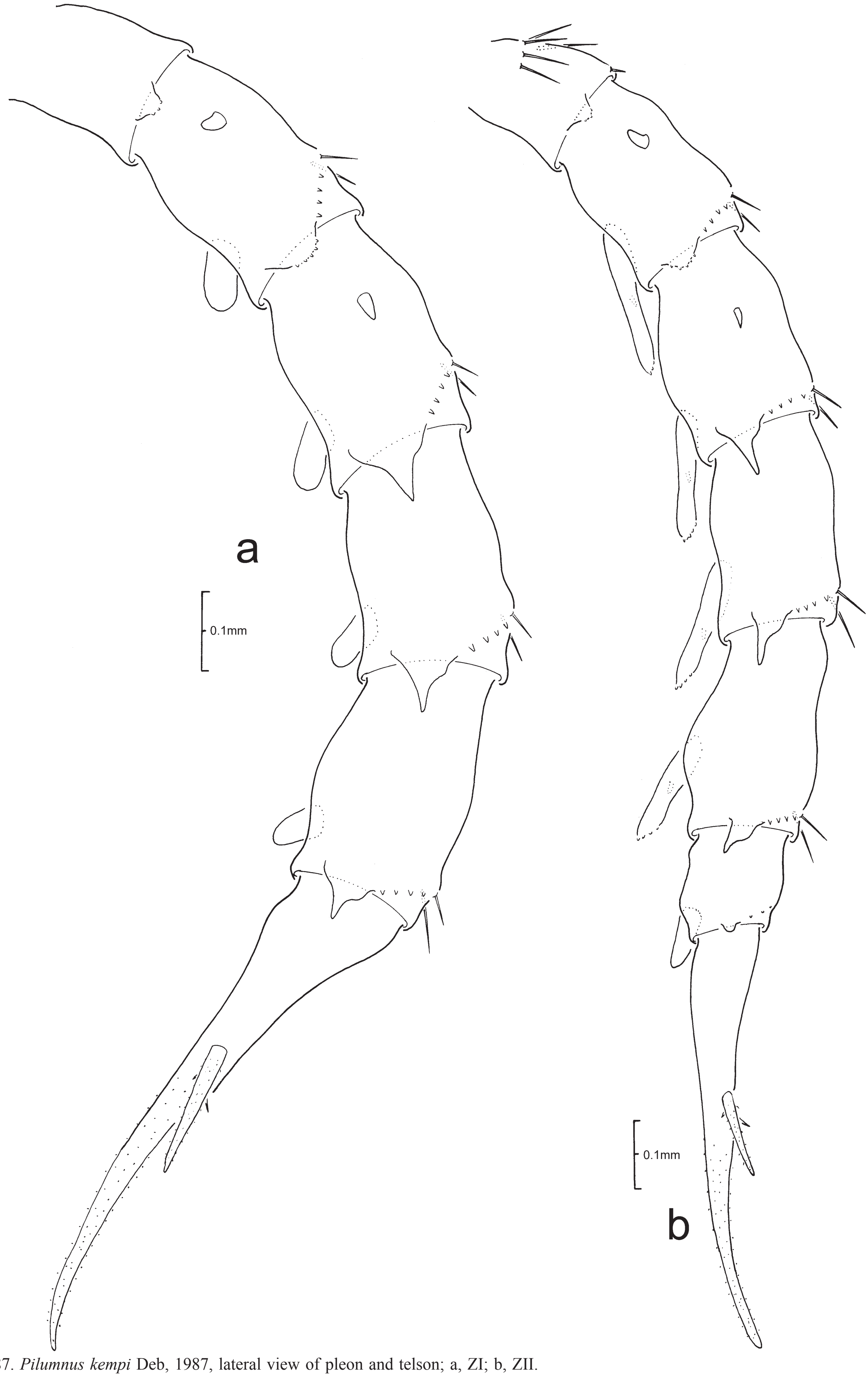

Fig. 87. *Pilumnus kempi* Deb, 1987, lateral view of pleon and telson; a, ZI; b, ZII.

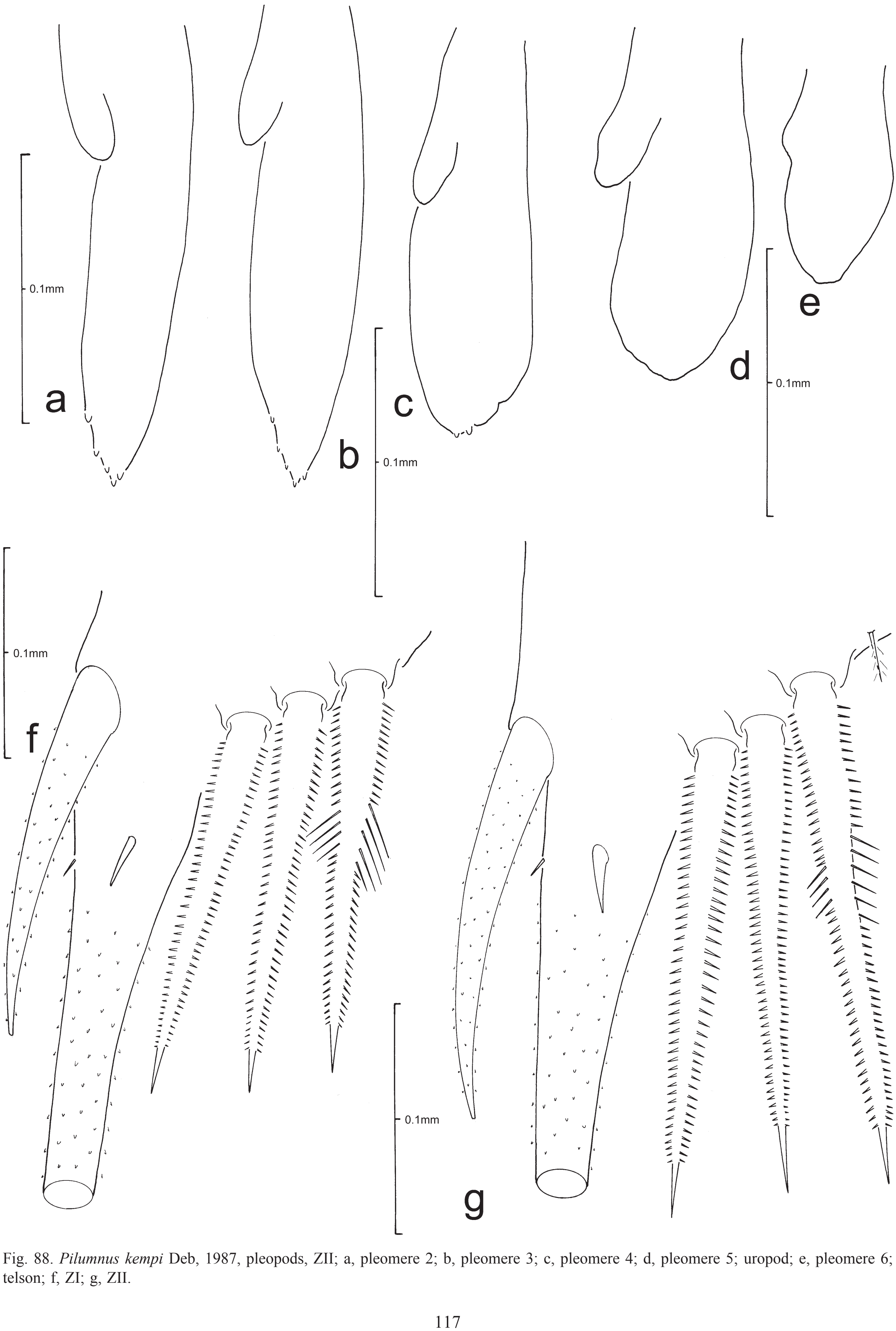

Fig. 88. *Pilumnus kempi* Deb, 1987, pleopods, ZII; a, pleomere 2; b, pleomere 3; c, pleomere 4; d, pleomere 5; uropod; e, pleomere 6; telson; f, ZI; g, ZII.

Pilumnus ohshimai Takeda & Miyake, 1970
(Figs. 89–92)

Description of Zoea I.
CARAPACE (Fig. 89a): dorsal spine smooth, curved distally, relatively short, just longer than rostral spine length; rostral spine shorter than antennal protopod length, without distal spinulation; lateral spines without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 89a): sessile.
Antennule (Fig. 89b): primary flagellum unsegmented with 4 (2 broad, 2 slender) aesthetascs of unequal length plus 2 terminal setae of unequal length; accessory flagellum absent.
Antenna (Fig. 89c): biramous; protopod distally bilaterally spinulate, longer than rostral spine length; endopod bud present; exopod unsegmented, distally bilaterally spinulate with 2 medial setae of unequal length.
Mandible: palp absent.
Maxillule (Fig. 90a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 terminal setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 90b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal setae); exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 91a): biramous; coxa without setae; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 91b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped (Fig. 92c): present; biramous.
Pereiopods (Fig. 90d): present; uniramous; chela bilobed.

PLEON (Fig. 92a, b): 5 pleomeres; pleomere 2 with pair of dorsolateral processes directed anteriorly; pleomere 3 with pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without dorsal setae; pleomeres 2–5 each with 1 pair of posterodorsal setae and spinulated dorsal posterior margin; pleopod buds absent.

TELSON (Figs. 90c, 92a, b): each fork long, spinulate, gradually curved distally, 1 long lateral spine, 1 more slender lateral spine, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Remarks. The ZI of *Pilumnus ohshimai* has hatched in an advanced state of development; characters expressed include an antennal endopod bud, a biramous third maxilliped, and presence of the pereiopods with a bilobed chela. These characters suggest that this pilumnid has three zoeal stages before the metamorphosis to the megalopal phase (Clark & P.K.L. Ng, 2004b for *P. setifer*).

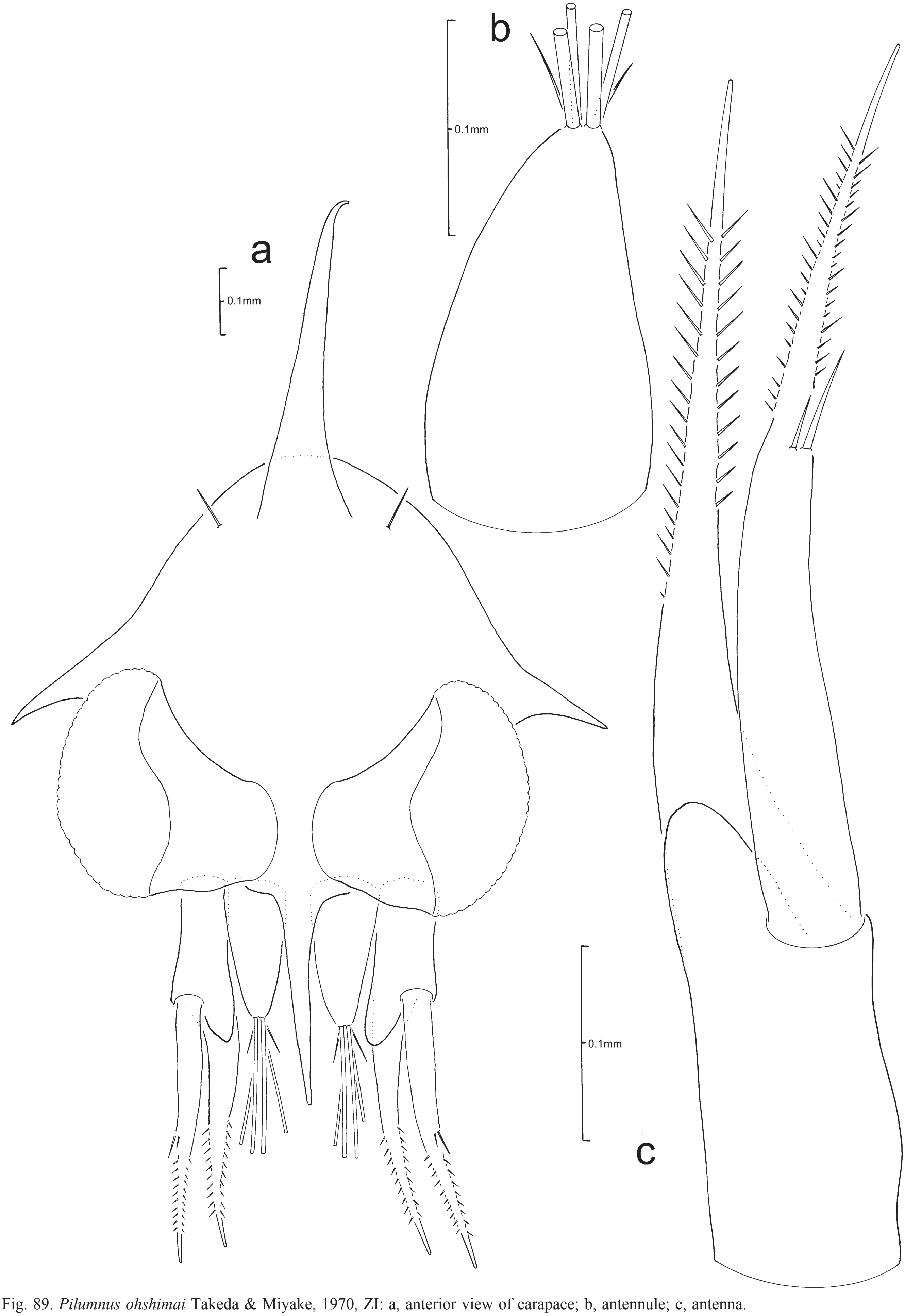

Fig. 89. *Pilumnus ohshimai* Takeda & Miyake, 1970, ZI: a, anterior view of carapace; b, antennule; c, antenna.

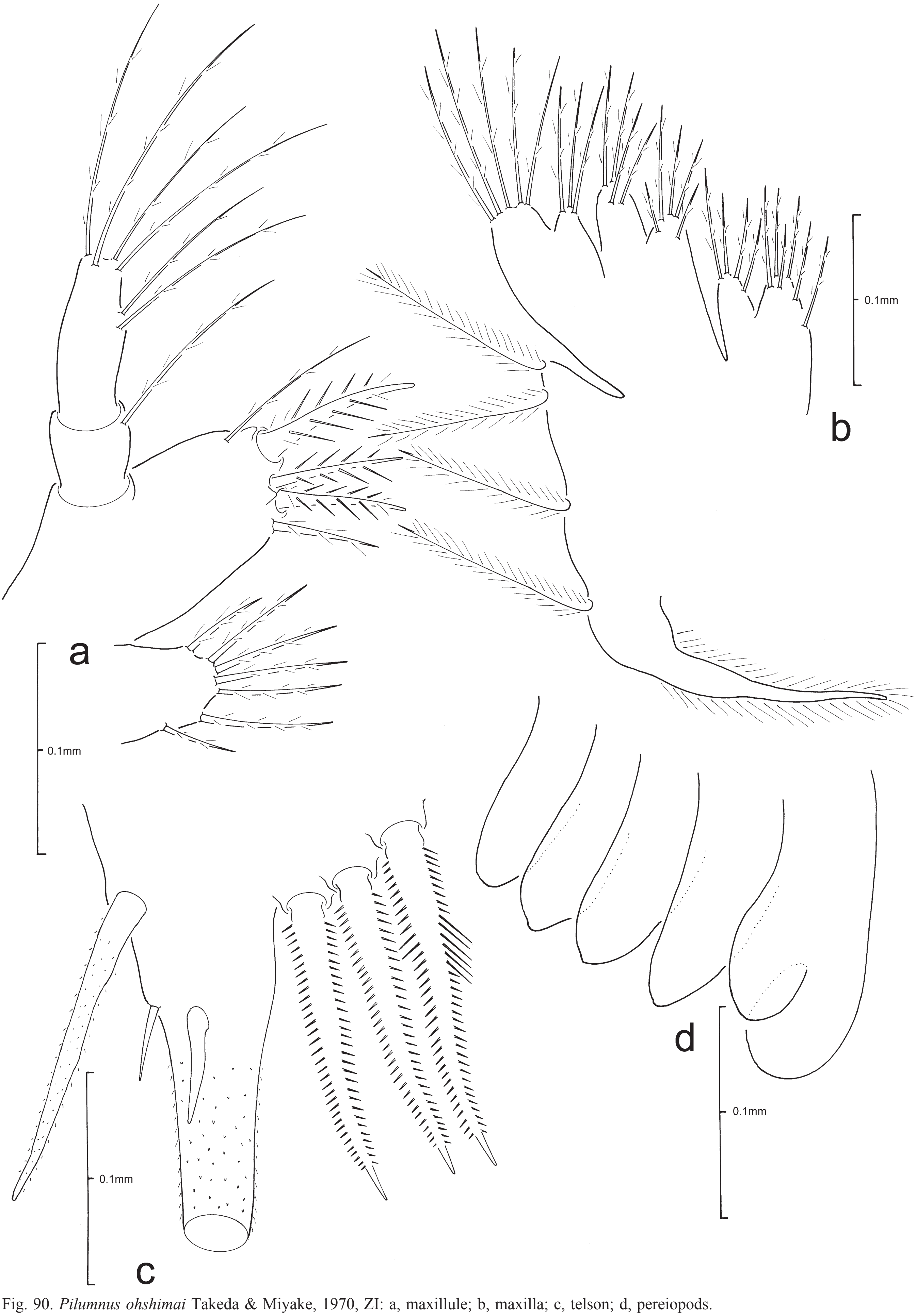

Fig. 90. *Pilumnus ohshimai* Takeda & Miyake, 1970, ZI: a, maxillule; b, maxilla; c, telson; d, pereiopods.

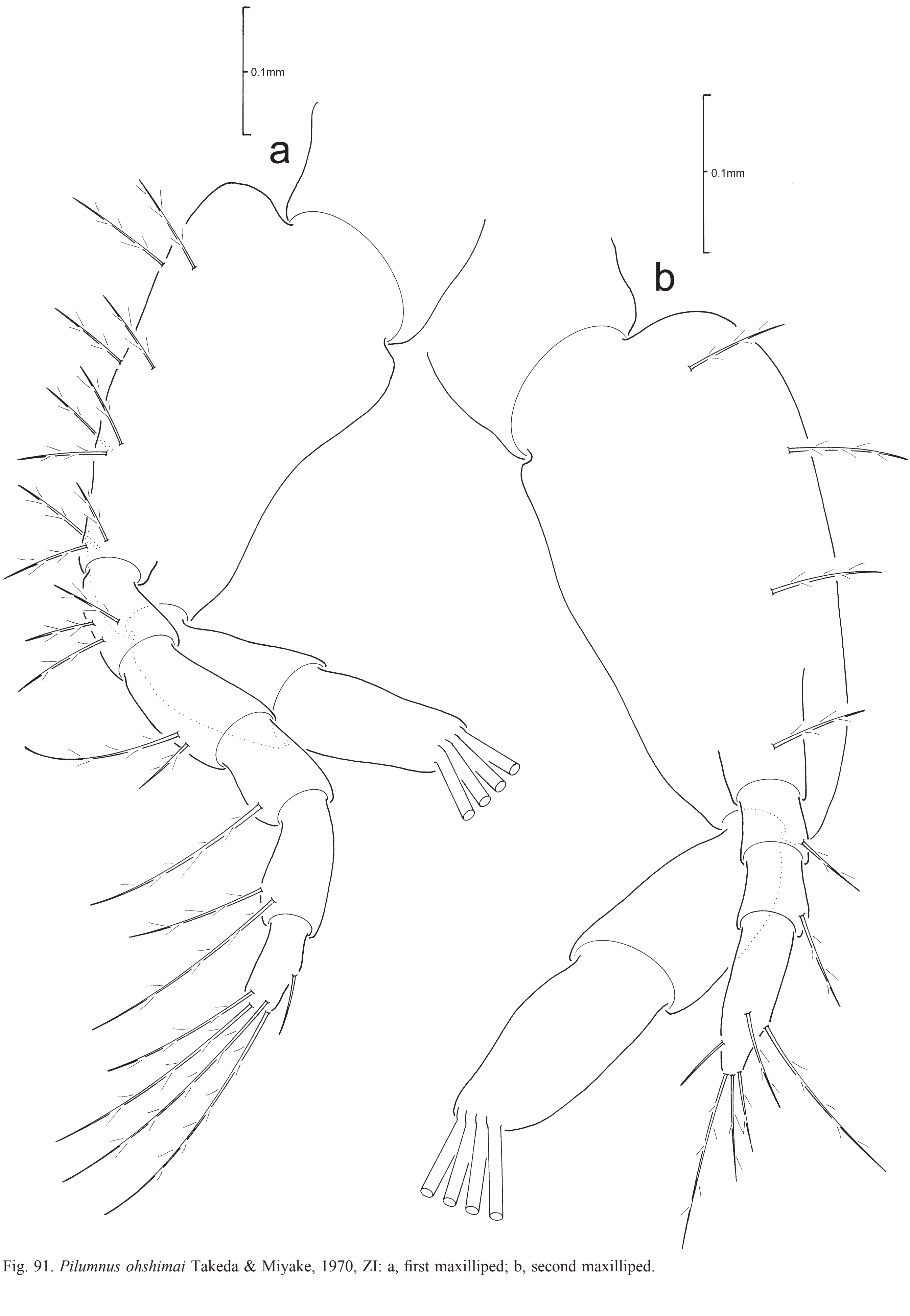

Fig. 91. *Pilumnus ohshimai* Takeda & Miyake, 1970, ZI: a, first maxilliped; b, second maxilliped.

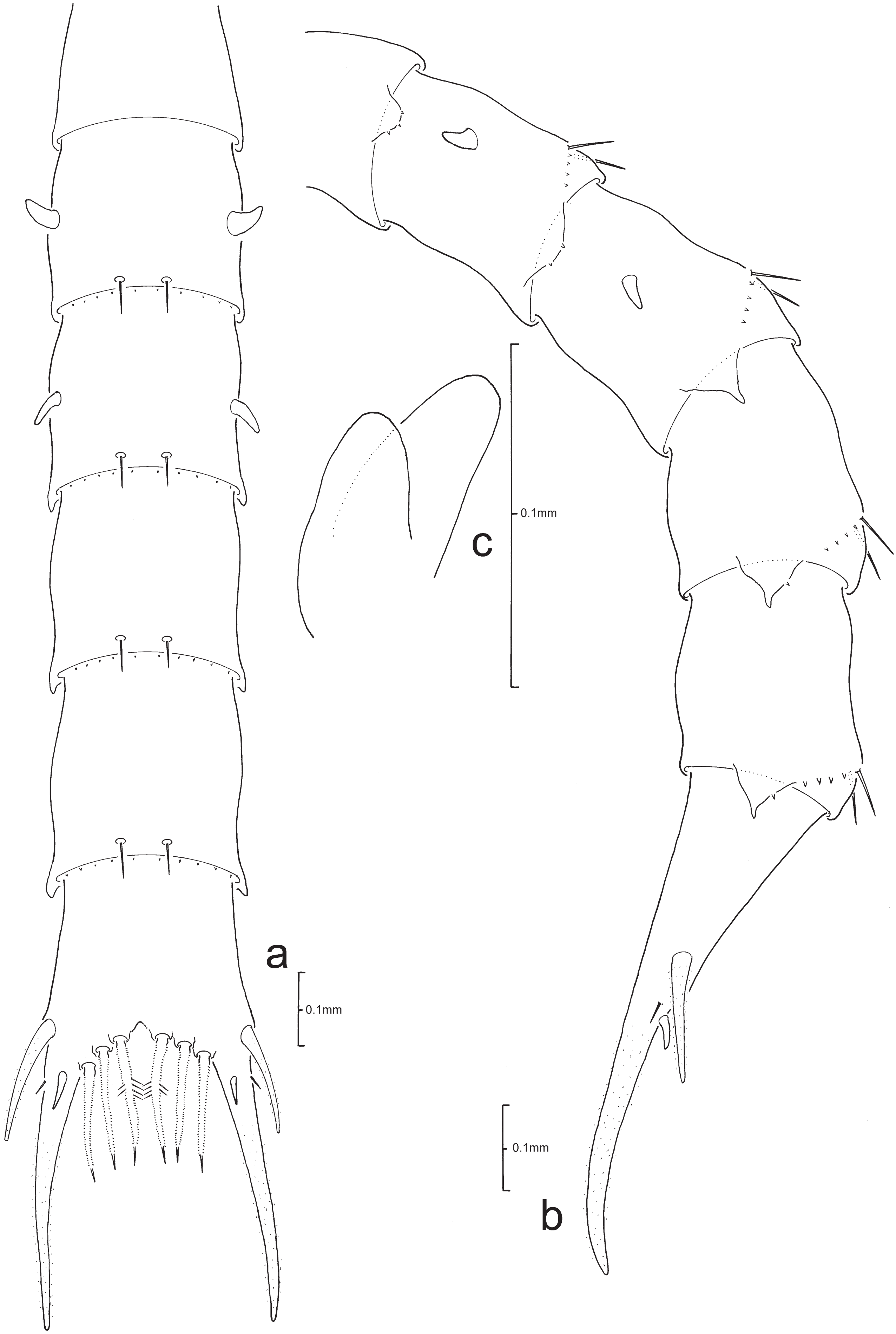

Fig. 92. *Pilumnus ohshimai* Takeda & Miyake, 1970, ZI: pleon and telson; a, dorsal view; b, lateral view; c, third maxilliped.

Pilumnus spinifrons **P.K.L. Ng & L.W.H. Tan, 1984**
(Figs. 93–96)

Description of Zoea I.
CARAPACE (Fig. 93a): dorsal spine relatively short, curved distally, approximately three times longer than rostral spine length; rostral spine distinctively shorter than antennal protopod length, without distal spinulation; lateral spines without spinulation dorsal on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 93a): sessile.
Antennule (Fig. 93b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 2 terminal setae of unequal length; accessory flagellum absent.
Antenna (Fig. 93c): uniramous; protopod distally bilaterally spinulate, much longer than rostral spine length; endopod absent; exopod unsegmented, distally bilaterally spinulate with 2 medial setae of unequal length.
Mandible: palp absent.
Maxillule (Fig. 94a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 terminal setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 94b): biramous; coxal endite bilobed with 6+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 95a): biramous; coxa without setae; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 95b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 96a, b): 5 pleomeres; pleomere 2 with pair of dorsolateral processes directed anteriorly; pleomere 3 with pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without dorsal setae; pleomeres 2–5 each with 1 pair of posterodorsal setae and spinulated dorsal posterior margin; pleopod buds absent.

TELSON (Figs. 94c, 96a, b): each fork long, spinulate, gradually curved distally, 1 long lateral spine, 1 small lateral seta, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Remarks. Pilumnoidea zoeas are remarkable in that they are characterised by possession of an antennal exopod with two medial setae of unequal length (Figs. 51d, 55c, 59c, 63c, 67c, 71c, 75c, 82a, 89c, 93c). Although this character defines the taxon, other characters in combination may also be diagnostic including an antennule with a primary flagellum comprising, in general for pilumnoids with four zoeal stages, four (two broad, two slender) terminal aesthetascs of unequal length plus two terminal setae of unequal length and the coxa of the first maxilliped without a seta.

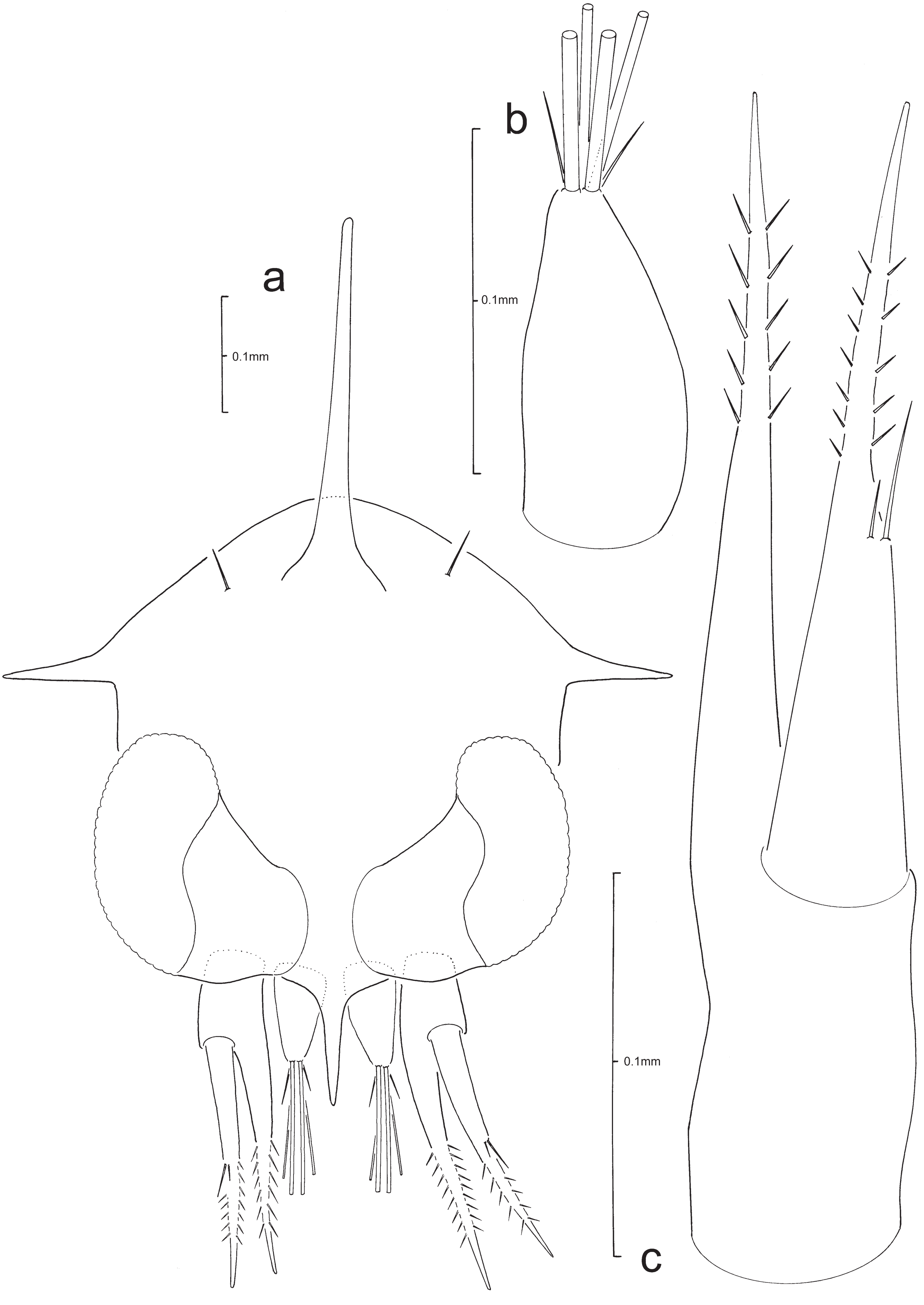

Fig. 93. *Pilumnus spinifrons* P.K.L. Ng & L.W.H. Tan, 1984, ZI: a, anterior view of carapace; b, antennule; c, antenna.

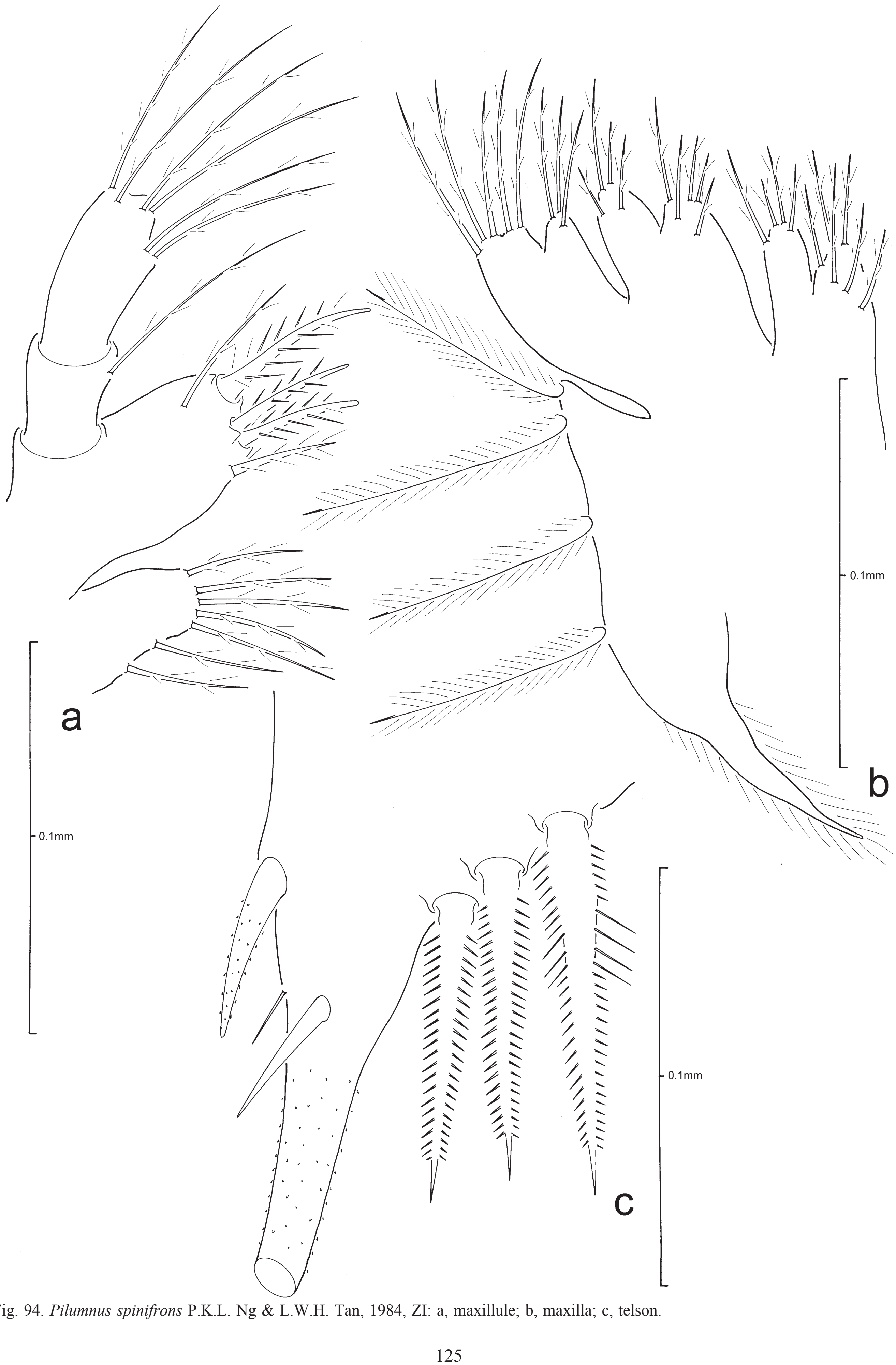

Fig. 94. *Pilumnus spinifrons* P.K.L. Ng & L.W.H. Tan, 1984, ZI: a, maxillule; b, maxilla; c, telson.

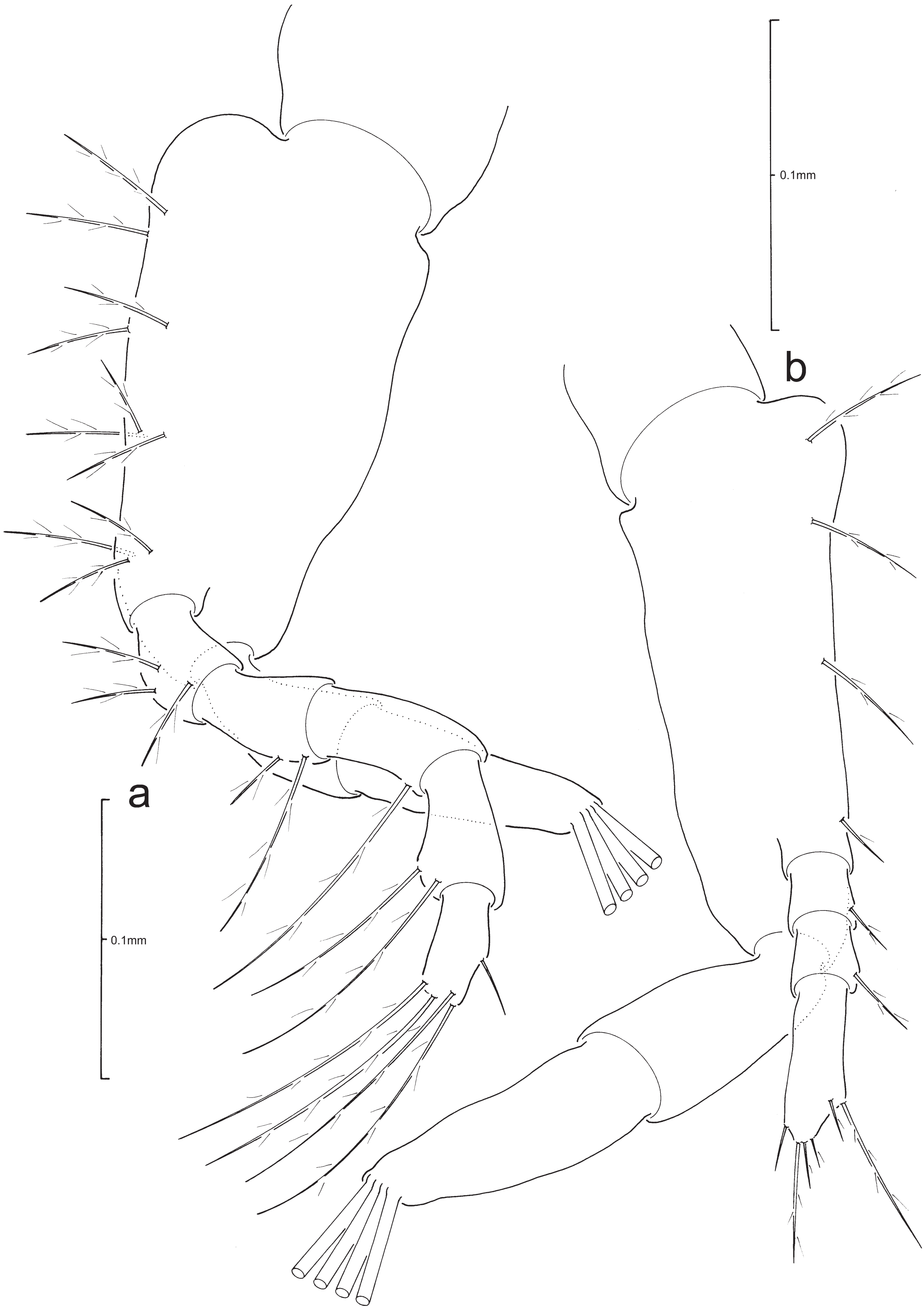

Fig. 95. *Pilumnus spinifrons* P.K.L. Ng & L.W.H. Tan, 1984, ZI: a, first maxilliped; b, second maxilliped.

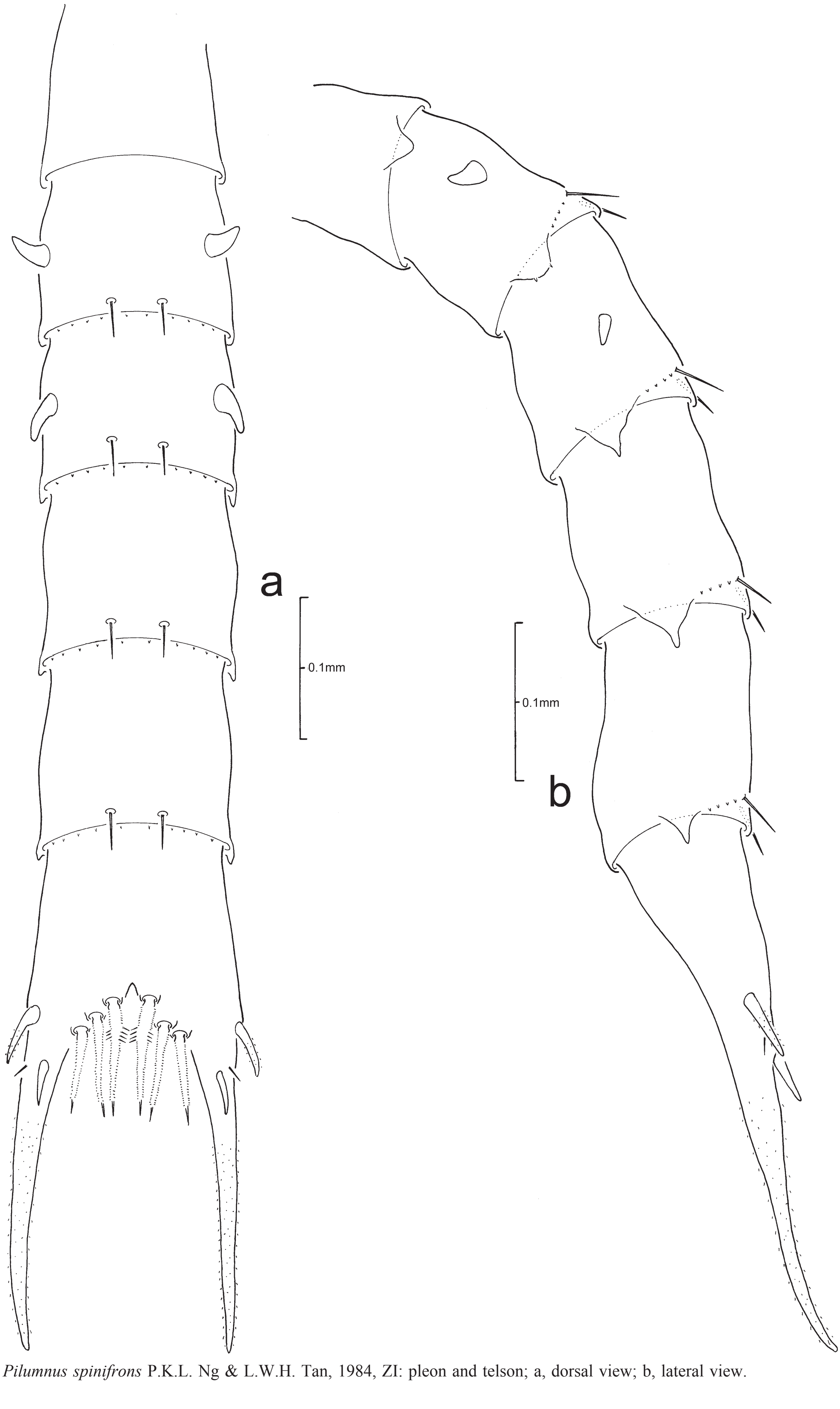

Fig. 96. *Pilumnus spinifrons* P.K.L. Ng & L.W.H. Tan, 1984, ZI: pleon and telson; a, dorsal view; b, lateral view.

Superfamily Portunoidea Rafinesque, 1815

Family Geryonidae Colosi, 1924

Chaceon quinquedens (Smith, 1879)
(Figs. 97–100)

Geryon quinquedens. Perkins, 1973: 70–80, figs. 1–7, (ZI–IV, Meg.); Roff et al., 1984: 26, figs. 76–79 (ZI); 48, figs. 159, 160 (Meg.).

Description of Zoea I.
CARAPACE (Fig. 97a): dorsal spine slightly curved distally, relatively long, twice rostral spine length; rostral spine longer than antennal protopod length, without distal spinulation; lateral spines straight, without spinulation on distal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 97a): sessile.
Antennule (Fig. 97b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 short terminal seta; accessory flagellum absent.
Antenna (Fig. 97c): uniramous; protopodal process distally bilaterally spinulate, shorter than rostral spine length; endopod absent; exopod ca. 35.3% length of protopod, possessing 1 long subterminal seta plus extended process.
Mandible: palp absent.
Maxillule (Fig. 98a): uniramous; epipod seta absent; coxal endite with 9 setae; basial endite with 6 setal processes; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 98b): uniramous; coxal endite bilobed with 3+4 setae; basial endite bilobed with 5+5 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 7 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 99a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 2,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 99b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 100a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomeres 3–5 each with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with posterolateral processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 98c, 100a, b): each fork long, gradually curved distally, not spinulate, 1 long spine, 1 much smaller lateral spine, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate spines.

Table 11. A comparison between the ZI of *Chaceon quinquedens* (Smith, 1879) by Perkins (1973), Roff et al. (1984), and the present study.

Character	Perkins (1973)	Roff et al. (1984)	Present study
MAXILLULE	fig. 2D	not figured	Fig. 98a
coxal endite setation	6		9
MAXILLA	fig. 2E	not figured	Fig. 98b
coxal endite setation	3+3		3+4
FIRST MAXILLIPED	fig. 2F	fig. 79	Fig. 99a
endopod distal article	5 (1 subterminal+4 terminal)	4 (4 terminal)	5 (1 subterminal+4 terminal)
SECOND MAXILLIPED	fig. 2G	not figured	Fig. 99b
endopod distal article setation	5 (2 subterminal+3 terminal)		6 (3 subterminal+3 terminal)

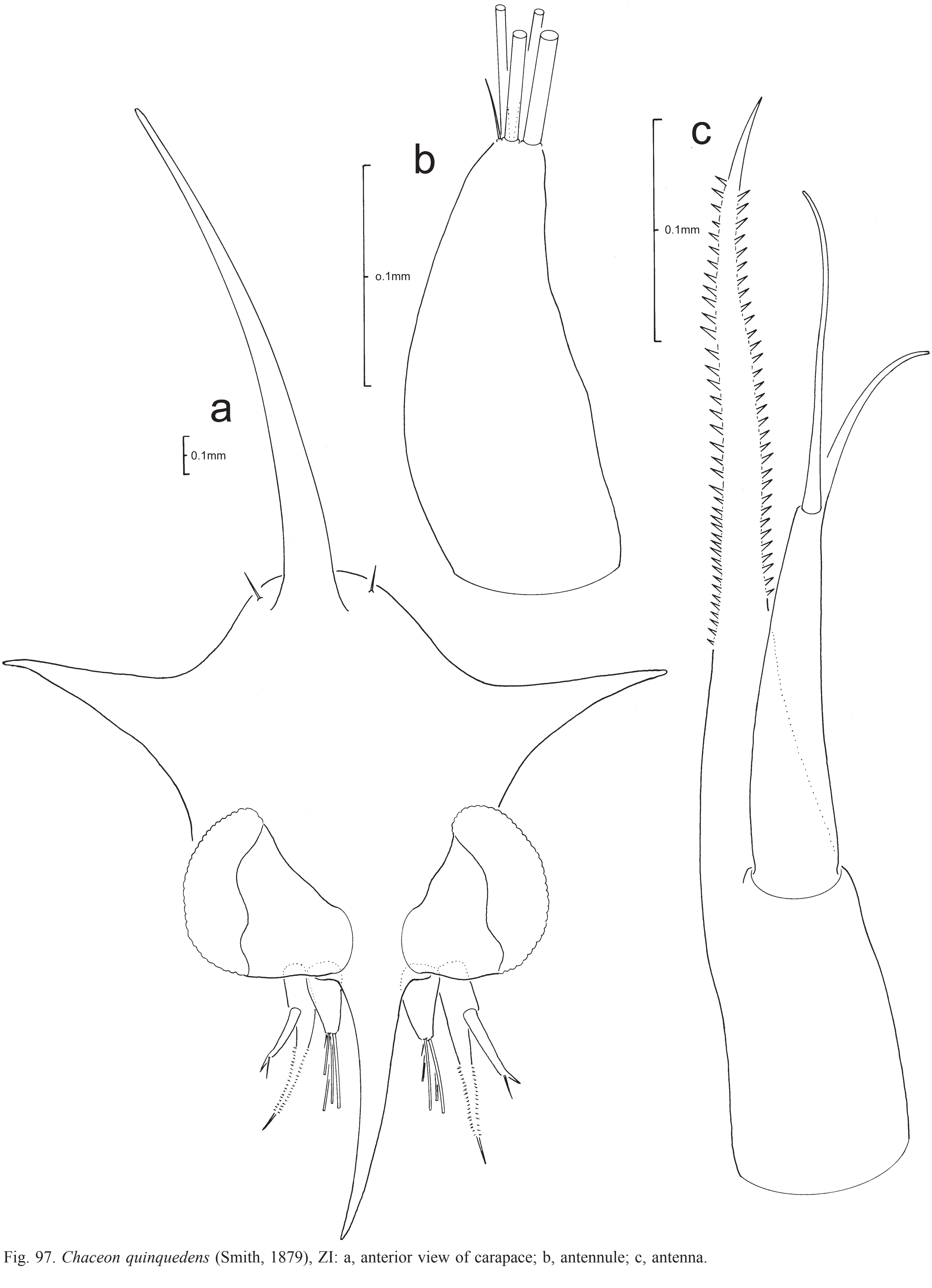

Fig. 97. *Chaceon quinquedens* (Smith, 1879), ZI: a, anterior view of carapace; b, antennule; c, antenna.

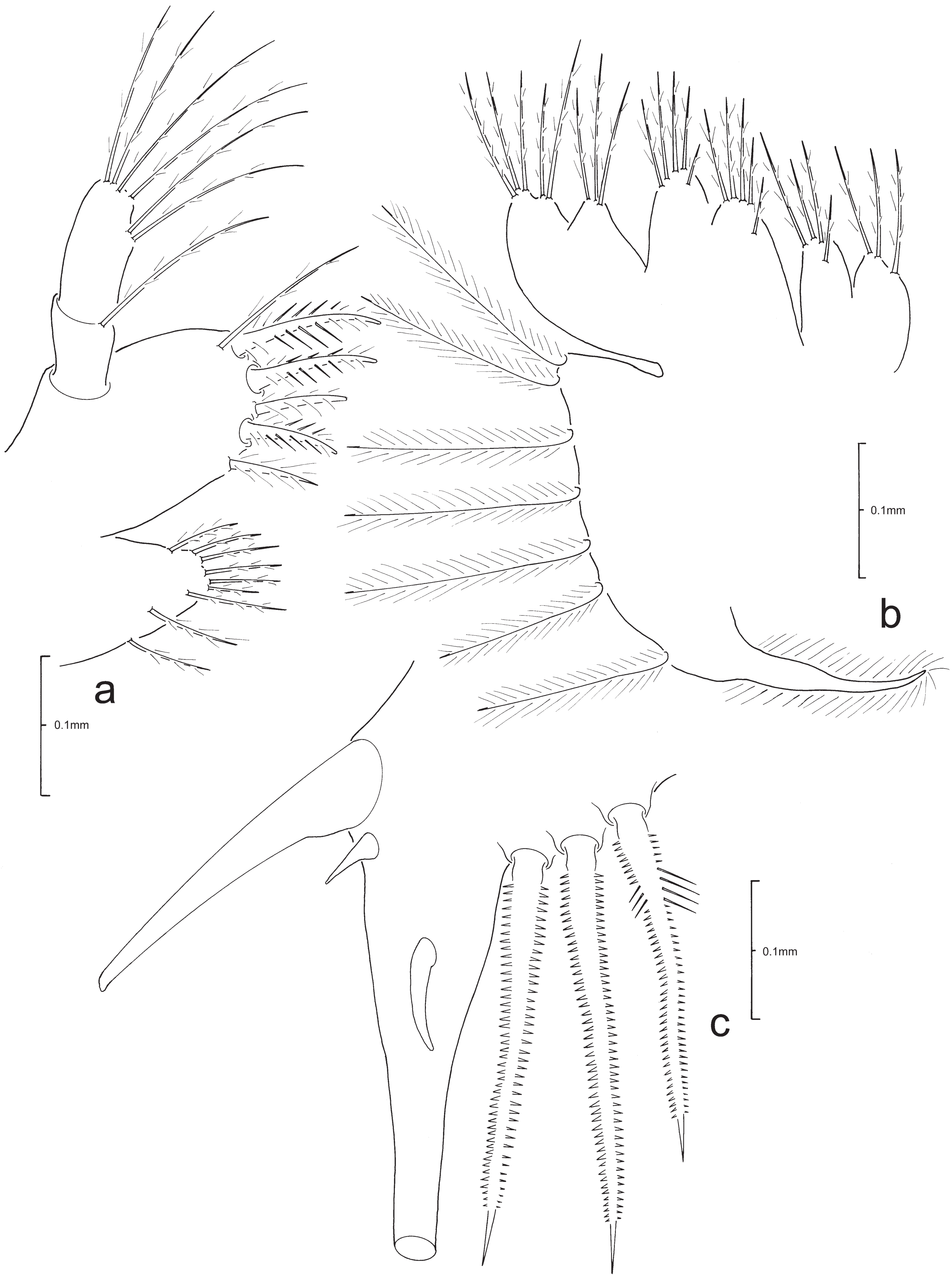

Fig. 98. *Chaceon quinquedens* (Smith, 1879), ZI: a, maxillule; b, maxilla; c, telson.

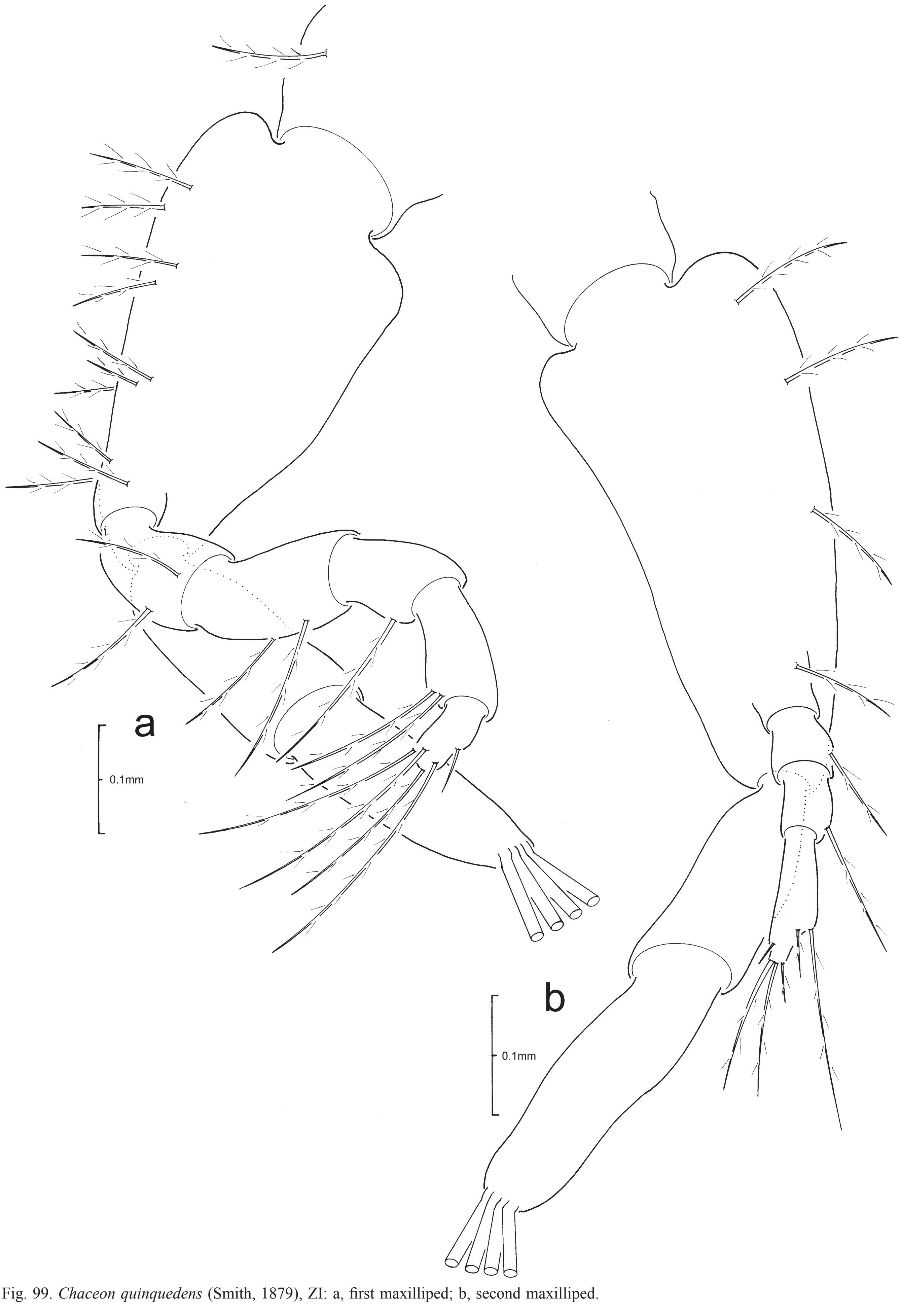

Fig. 99. *Chaceon quinquedens* (Smith, 1879), ZI: a, first maxilliped; b, second maxilliped.

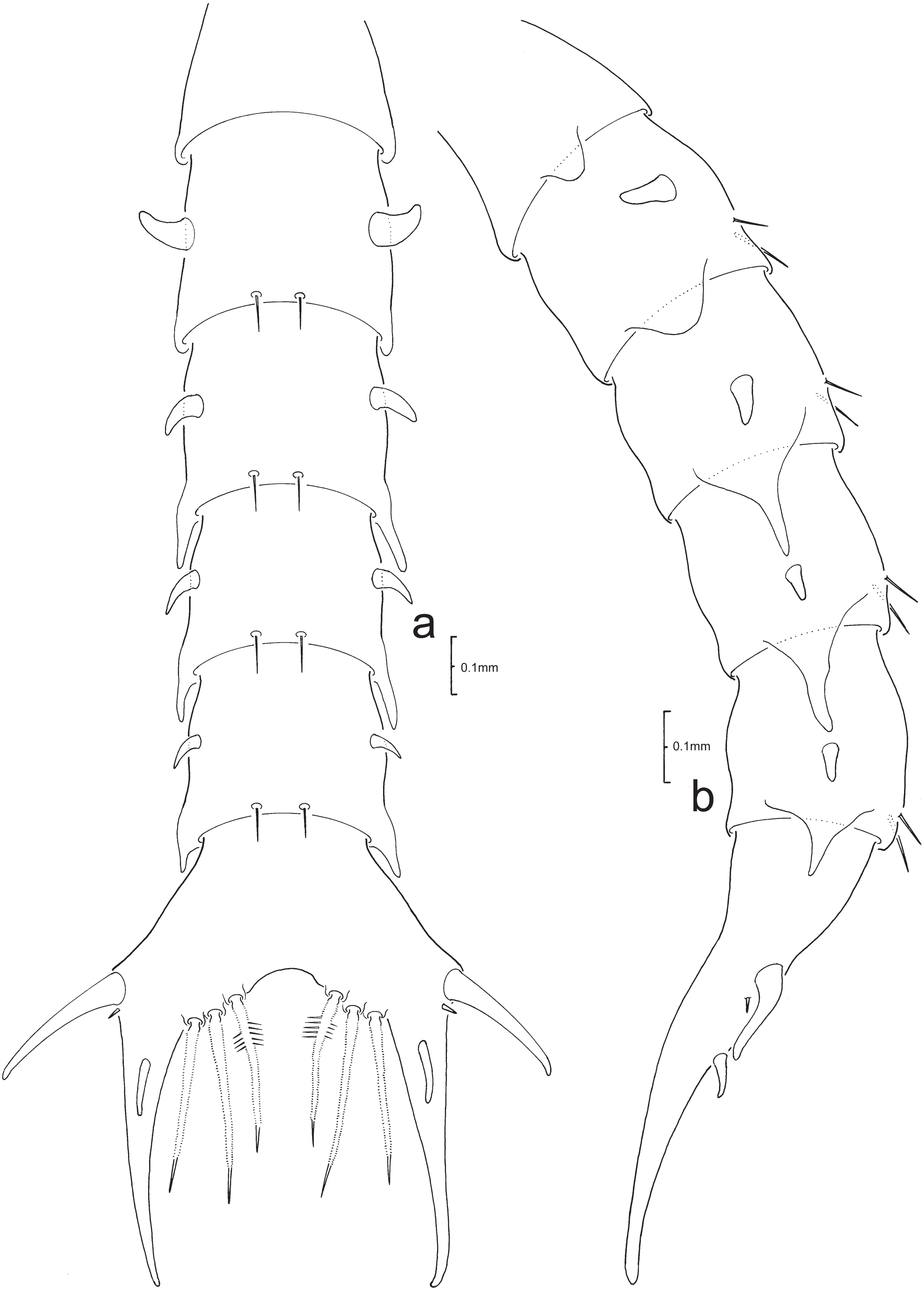

Fig. 100. *Chaceon quinquedens* (Smith, 1879), ZI: pleon; a, dorsal view; b, lateral view.

***Geryon longipes* A. Milne-Edwards, 1882**
(Figs. 101–104)

Geryon longipes. Guerao et al., 1996: 506–516, figs. 1–9 (ZI–IV, Meg.).

Description of Zoea I.
CARAPACE (Fig. 101a): dorsal spine slightly curved distally, longer than rostral spine length; rostral spine much longer than antennal protopod length, without distal spinulation; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 101a): sessile.
Antennule (Fig. 101b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta plus minute spine; accessory flagellum absent.
Antenna (Fig. 101c): biramous; protopodal process distally bilaterally spinulate, much shorter than rostral spine length; endopod spine present; exopod ca. 32.4% length of protopod, possessing 1 long subterminal seta plus elongated spine.
Mandible: palp absent.
Maxillule (Fig. 102a): uniramous; epipod seta absent; coxal endite with 9 setae; basial endite with 7 setal processes; endopod comprising 2 articles, proximal article with 1 seta; distal article with 4 terminal setae; exopod seta absent.
Maxilla (Fig. 102b): biramous; coxal endite bilobed with 3+4 setae; basial endite bilobed with 5+6 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 7 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 103a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles, with 2,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 103b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal (1 is minute) + 3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 104a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomeres 3–5 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with posterolateral processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 102c, 104a, b): each fork long, gradually curved distally, not spinulate, 1 long lateral spine, 1 much smaller lateral spine, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate spines.

Table 12. A comparison between the ZI of *Geryon longipes* A. Milne-Edwards, 1882 by Guerao et al. (1996) and the present study.

Character	**Guerao et al. (1996)**	**Present study**
CARAPACE	fig. 1A	Fig. 101a
posterodorsal setae	absent	1 pair present
ANTENNULE	fig. 3A	Fig. 101b
terminal setation	2 aesthetascs, 2 terminal setae	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal seta
ANTENNA	fig. 3F	Fig. 101c
endopod spine	absent	present
exopod setation	2 terminal setae	1 long subterminal seta plus elongated spine.
FIRST MAXILLIPED	fig. 6A	Fig. 103a
coxal seta	absent	present
SECOND MAXILLIPED	fig. 7A	Fig. 103b
endopod articles	2	3
endopod setation	1,5 (2 subterminal+3 terminal)	1,1,6 (3 subterminal (1 is minute) + 3 terminal)

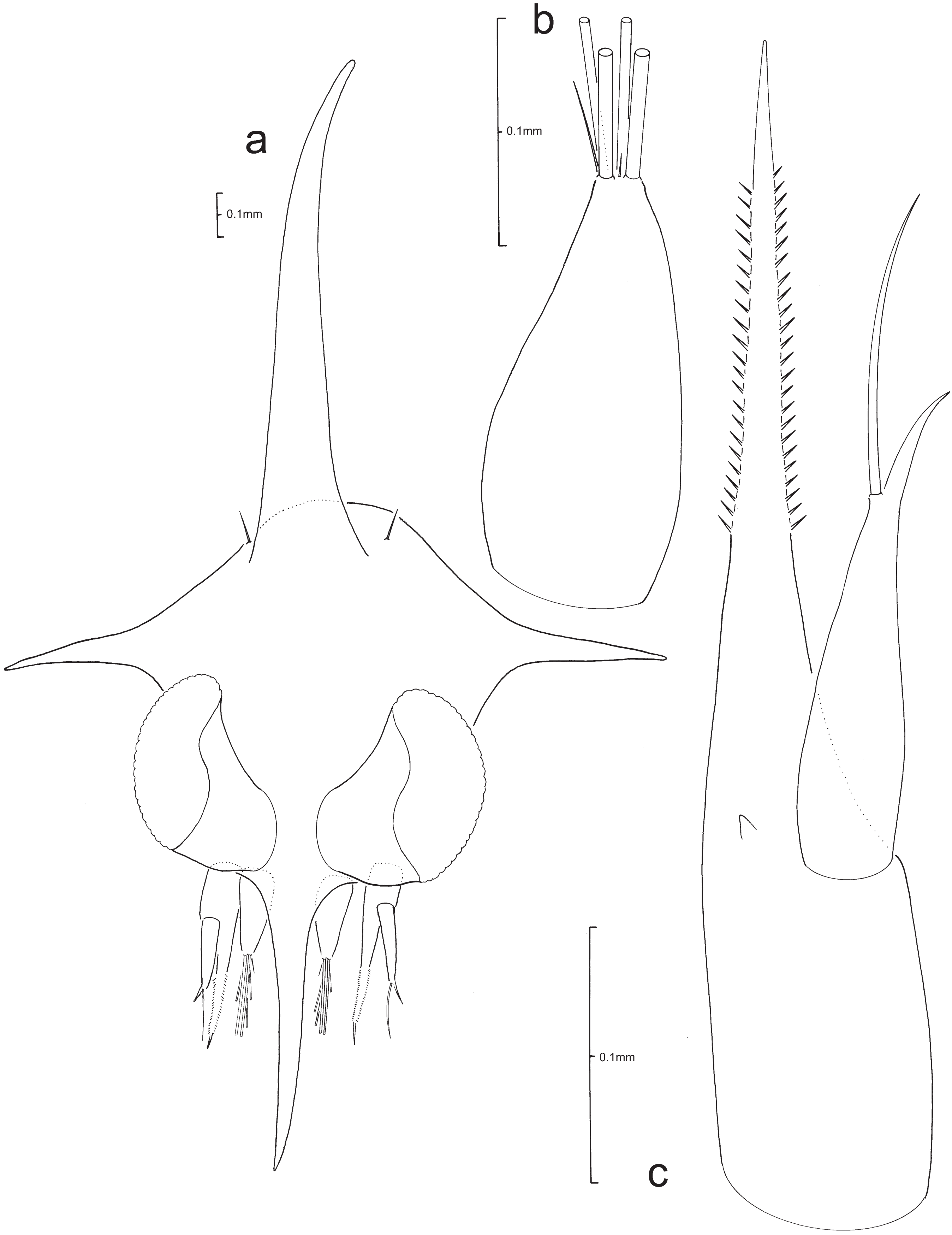

Fig. 101. *Geryon longipes* A. Milne-Edwards, 1882, ZI: a, anterior view of carapace; b, antennule; c, antenna.

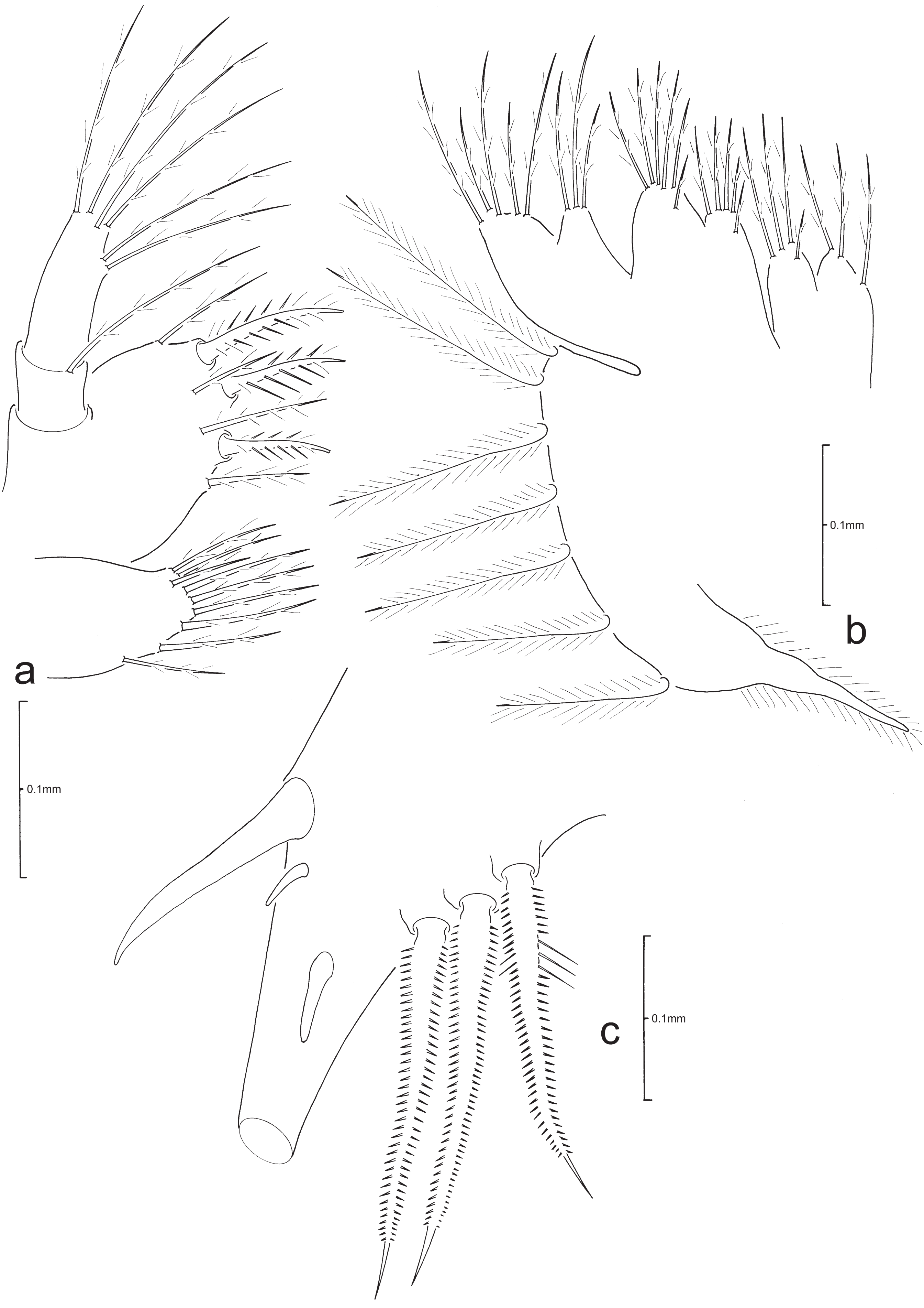

Fig. 102. *Geryon longipes* A. Milne-Edwards, 1882, ZI: a, maxillule; b, maxilla; c, telson.

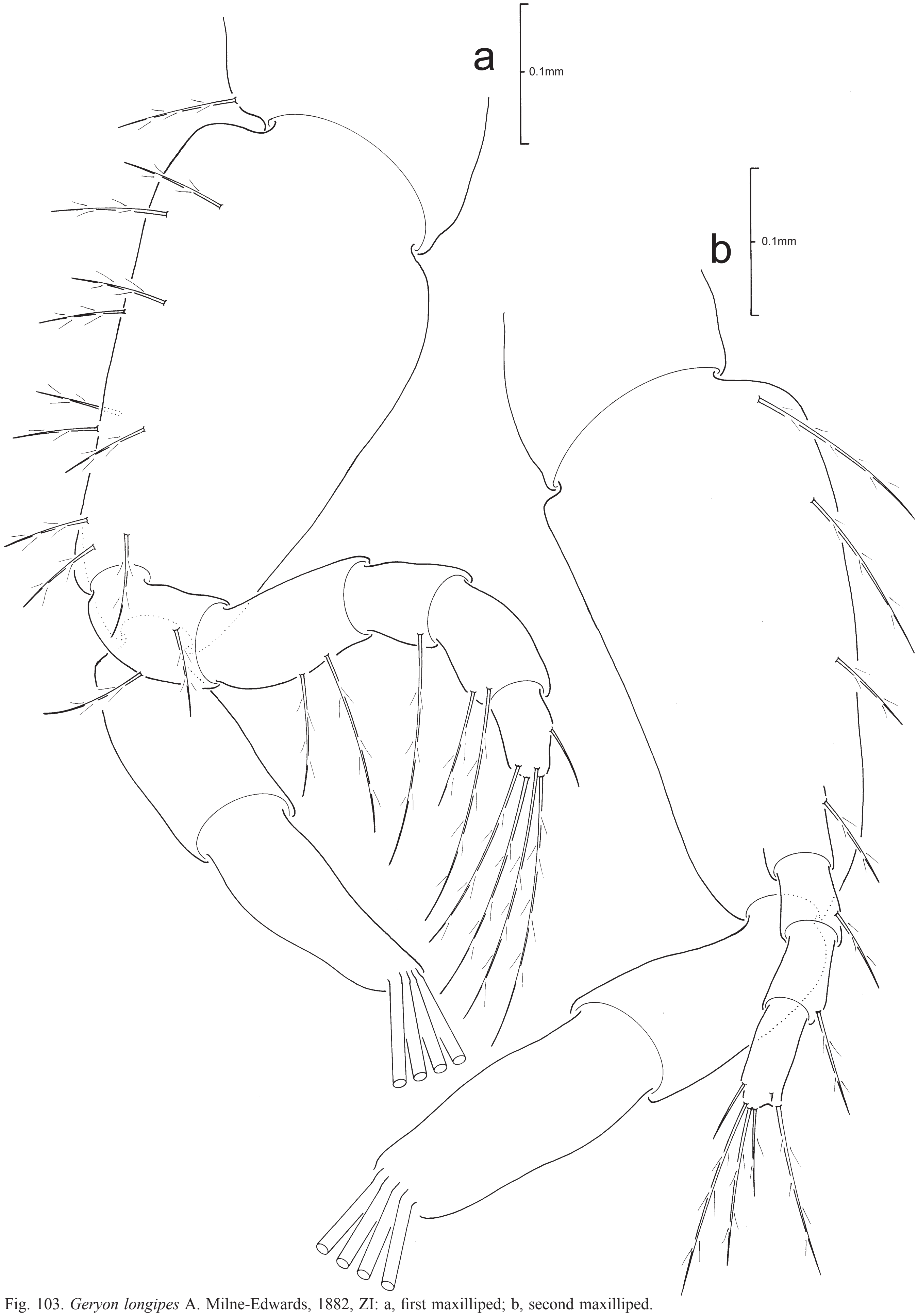

Fig. 103. *Geryon longipes* A. Milne-Edwards, 1882, ZI: a, first maxilliped; b, second maxilliped.

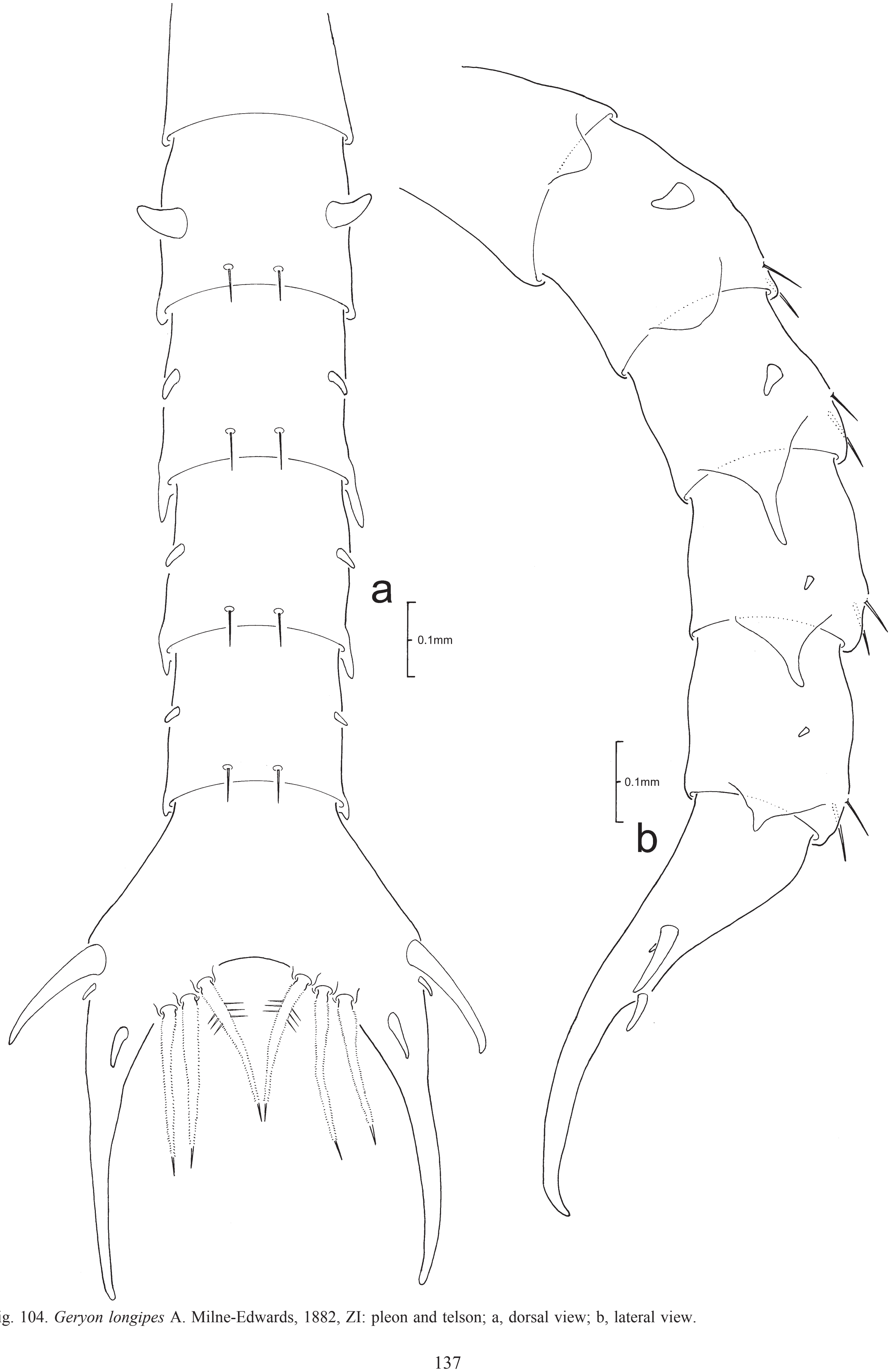

Fig. 104. *Geryon longipes* A. Milne-Edwards, 1882, ZI: pleon and telson; a, dorsal view; b, lateral view.

Superfamily Pseudocarcinoidea P.K.L. Ng & Davie, 2020

Family Pseudocarcinidae P.K.L. Ng & Davie, 2020

Pseudocarcinus gigas (Lamarck, 1818)
(Figs. 105–108)

Pseudocarcinus gigas. Gardner & Quintana, 1998: 1170–1185, figs. 1–11 (ZI–V, Meg.).

Description of Zoea I.
CARAPACE (Fig. 105a): dorsal spine long, straight, curved distally, ca. twice rostral spine length; rostral spine longer than antennal protopod length, without distal spinulation; lateral spines present relatively long, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; each ventral margin without setae; eyes sessile.

CEPHALON
Eyes (Fig. 105a): sessile.
Antennule (Fig. 105b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 105c): uniramous; protopod distally bilaterally spinulate, shorter than rostral spine length; endopod absent; exopod relatively long, ca. 40% of protopod with 3 (1 subterminal+2 terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 106a): uniramous; epipod seta absent; coxal endite with 8 setae; basial endite armed with 5 processes, inner margin with 2 setal buds, single seta absent from outer margin; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 106b): biramous; coxal endite bilobed with 7+4 setae; basial endite bilobed with 5+5 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 distal stout process.

PEREION
First maxilliped (Fig. 107a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles, with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 107b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae; exopod comprising 2 articles, distal article with 4 terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 108a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly, pleomere 3 with 1 pair of dorsolateral processes directed posteriorly; pleomere 1 with medial spine; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with long posterolateral processes that nearly overlap succeeding pleomere; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 106c, 108a, b): each fork long, gradually curved, not spinulate, 1 relatively long spine, 1 smaller lateral spine, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Table 13. A comparison between the ZI of *Pseudocarcinus gigas* (Lamarck, 1818) by Gardner & Quintana (1998) and the present study.

Character	Gardner & Quintana (1998)	Present study
MAXILLA	fig. 3G	Fig. 106b
coxal endite	6+4	7+4
basial endite	6+5	5+5
FIRST MAXILLIPED	fig. 3H	Fig. 107a
coxal seta	absent	present
basial setation	11 (2+3+3+3)	10 (2+2+3+3)
endopod	2,2,1,2,5–6	3,2,1,2,5 (1 subterminal+4 terminal)

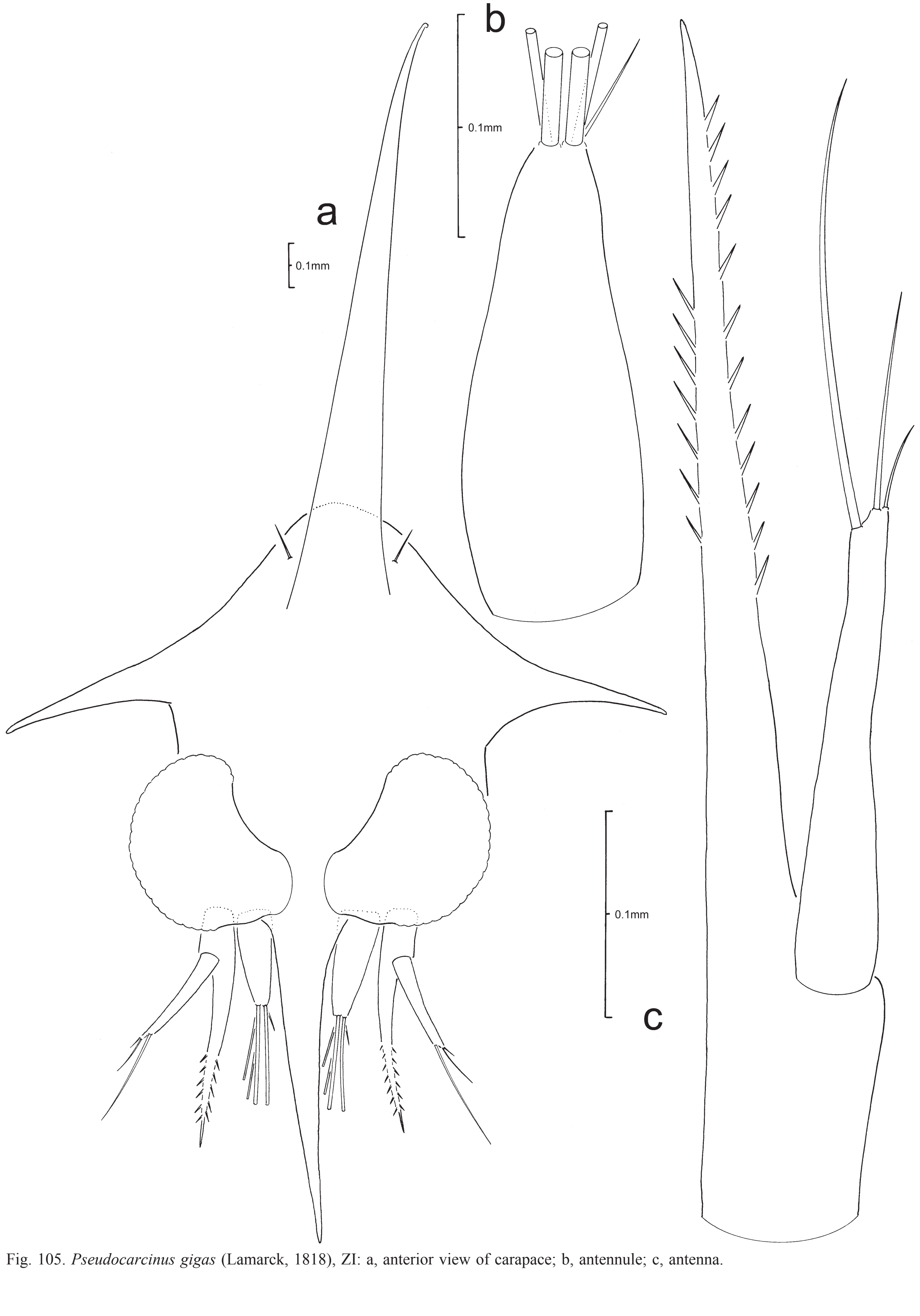

Fig. 105. *Pseudocarcinus gigas* (Lamarck, 1818), ZI: a, anterior view of carapace; b, antennule; c, antenna.

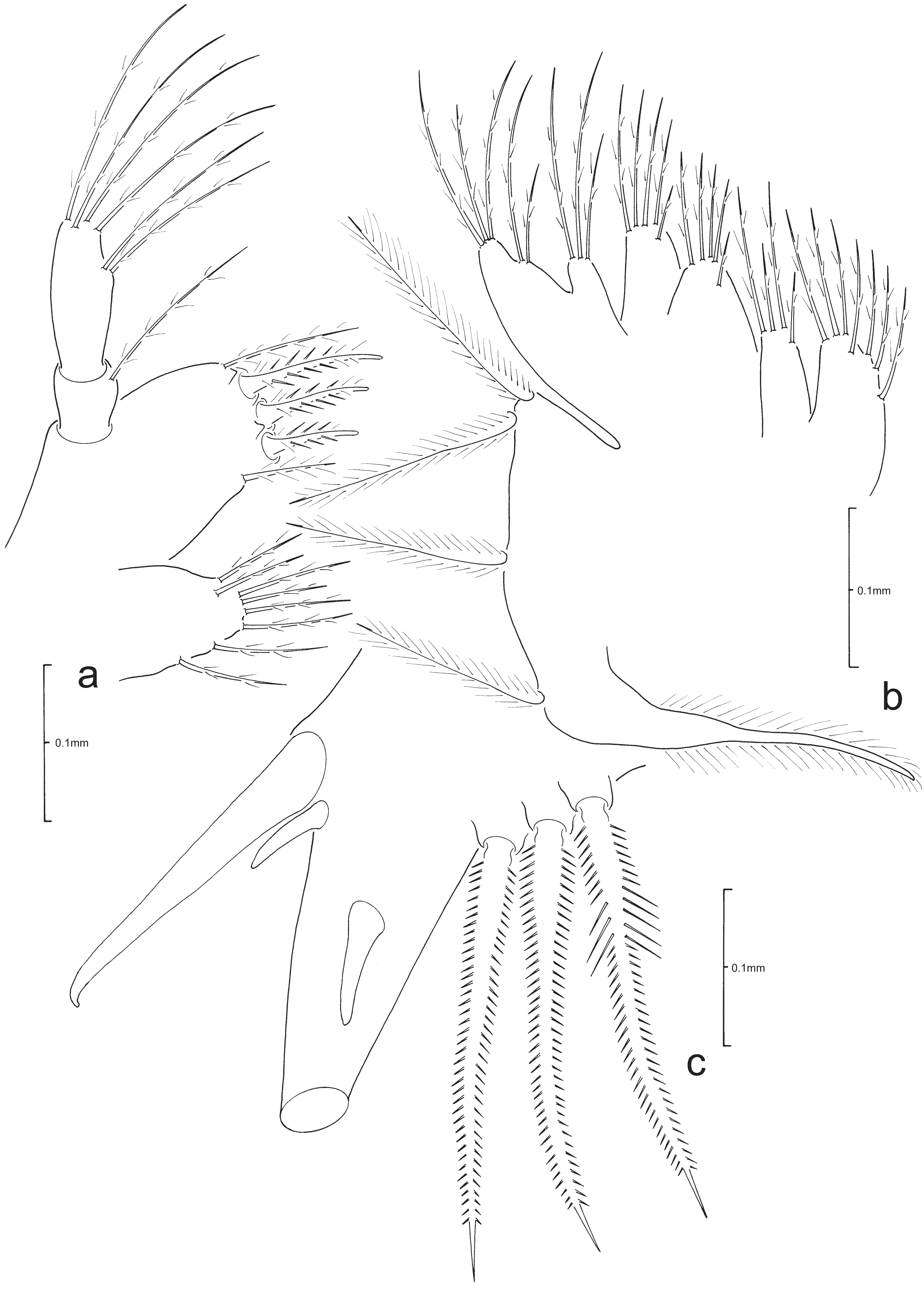

Fig. 106. *Pseudocarcinus gigas* (Lamarck, 1818), ZI: a, maxillule; b, maxilla; c, telson.

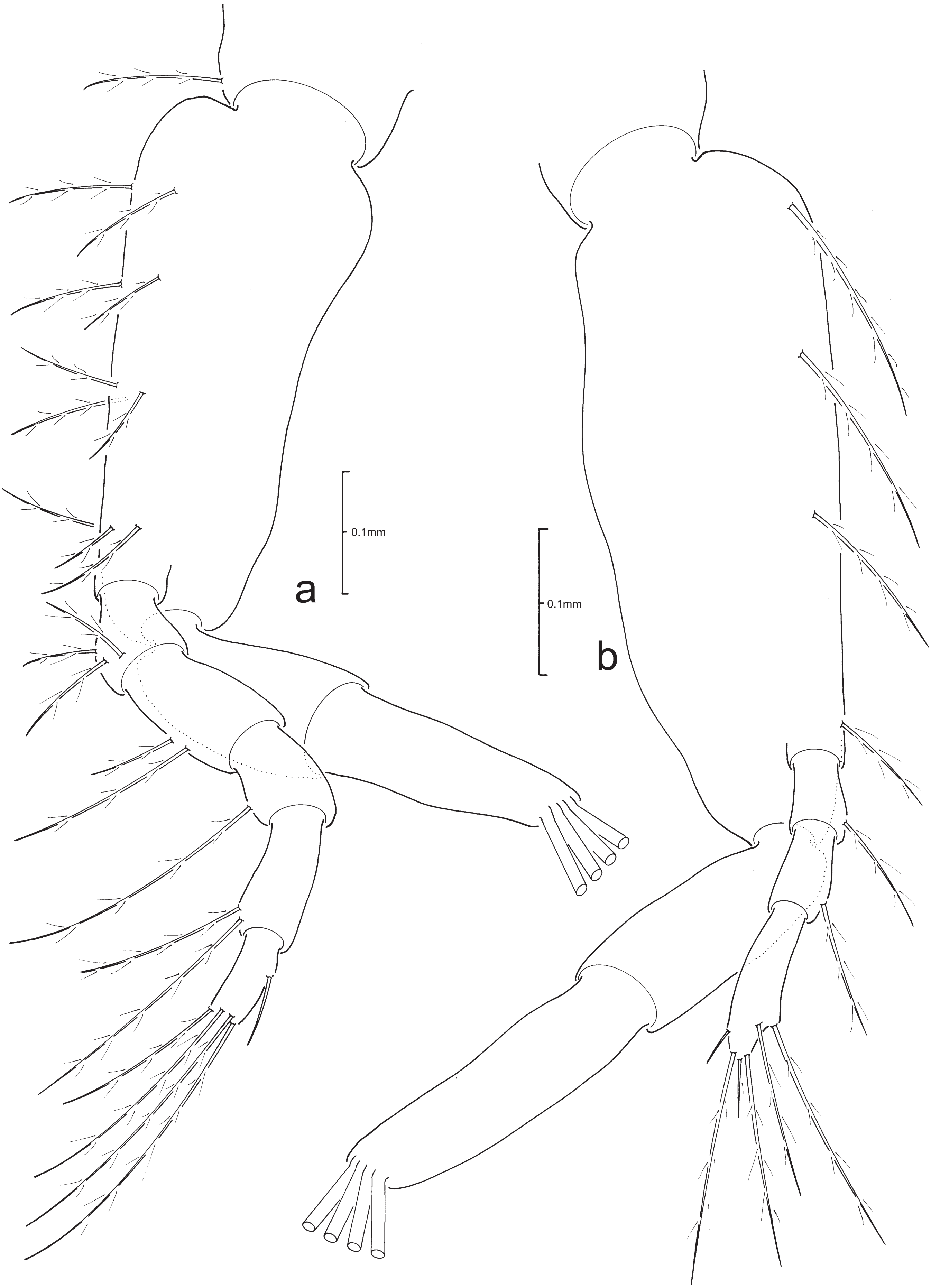

Fig. 107. *Pseudocarcinus gigas* (Lamarck, 1818), ZI: a, first maxilliped; b, second maxilliped.

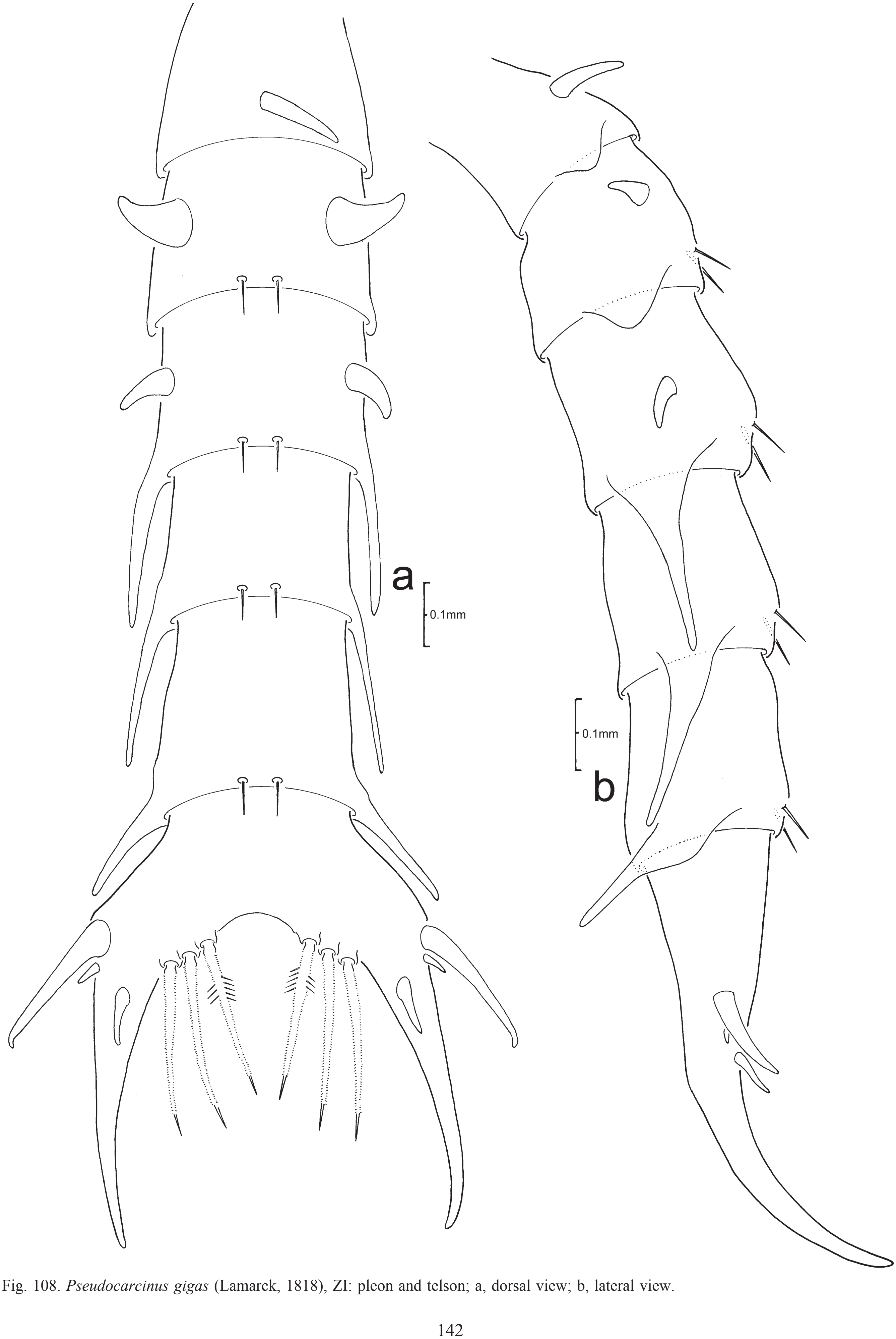

Fig. 108. *Pseudocarcinus gigas* (Lamarck, 1818), ZI: pleon and telson; a, dorsal view; b, lateral view.

Superfamily Xanthoidea MacLeay, 1838

Family Panopeidae Ortmann, 1893

Acantholobulus bermudensis (Benedict & Rathbun, 1891)

(Figs. 109–112)

Panopeus bermudensis. Martin, 1981 (ZI–IV, Meg.; not seen); Martin et al., 1985: 86–92, figs. 1–6 (ZI–IV, Meg.).
Acantholobulus bermudensis. Felder & Martin, 2003: 439, fig. 3a–d (ZI, IV).
non *Panopeus bermudensis*. Lebour, 1944: 119, text-fig. 9a–d = *Pilumnus* sp. (see Rice, 1980).

Description of Zoea I.
CARAPACE (Fig. 109a): dorsal spine long, slightly curved distally, ca. equal to rostral spine length; rostral spine slightly shorter than antennal protopod length, without distal spinulation; lateral spines not developed, reduced to protuberances; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 109a): sessile.
Antennule (Fig. 109b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 109c): uniramous; protopod without distal spinulation, just longer than rostral spine length, with swollen tip; endopod absent; exopod minute, ca. 2% length of protopod, with 1 terminal seta.
Mandible: palp absent.
Maxillule (Fig. 110a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 110b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 111a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 111b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 112a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–5 each with rounded posterolateral processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 110c, 112a, b): each fork long, gradually curved distally, not spinulate, 1 minute lateral spine, 1 filamentous lateral spine (both difficult to see under low power), 1 large dorsomedial spine on inner margin of fork present; posterior margin with 3 pairs of stout spinulate setae.

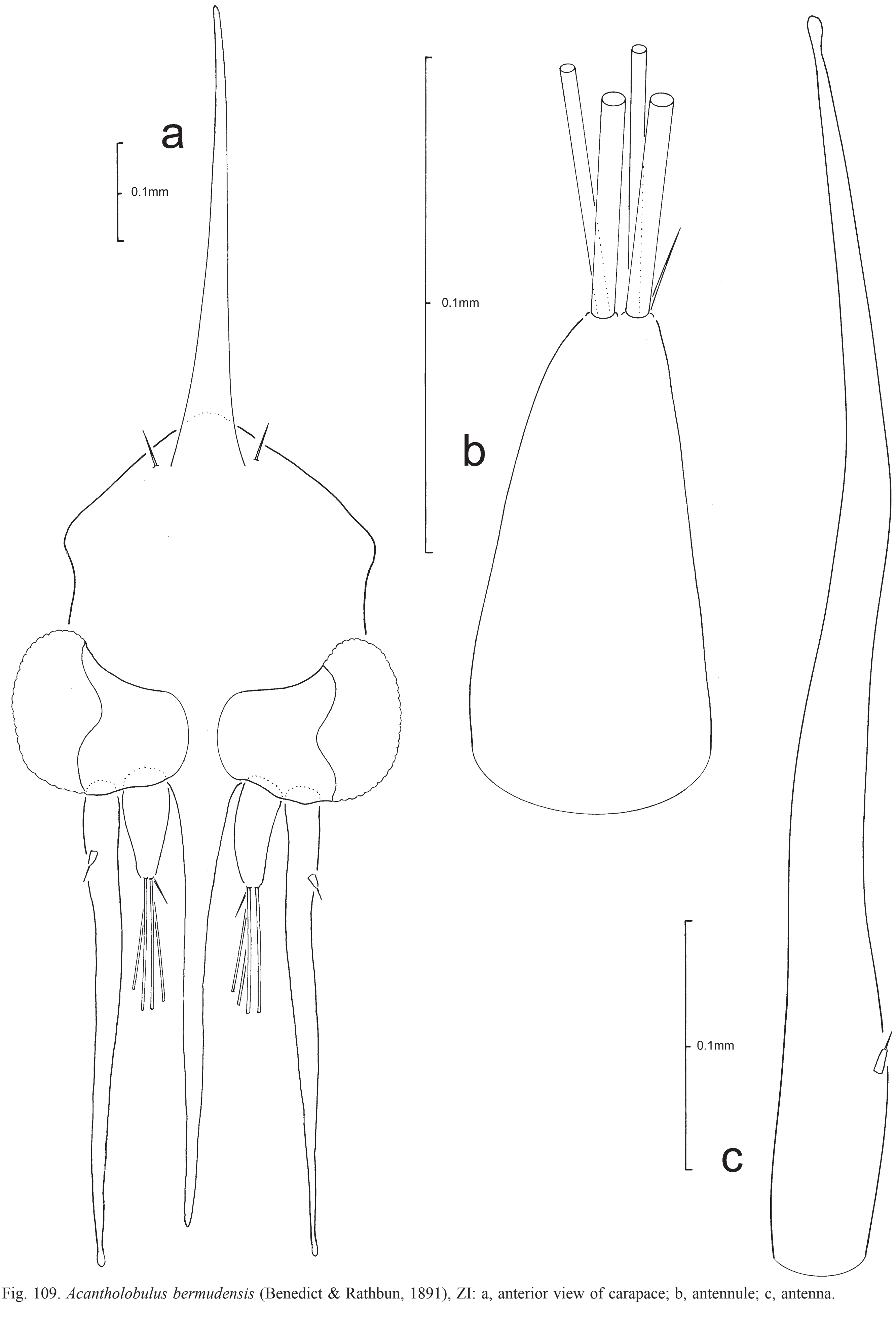

Fig. 109. *Acantholobulus bermudensis* (Benedict & Rathbun, 1891), ZI: a, anterior view of carapace; b, antennule; c, antenna.

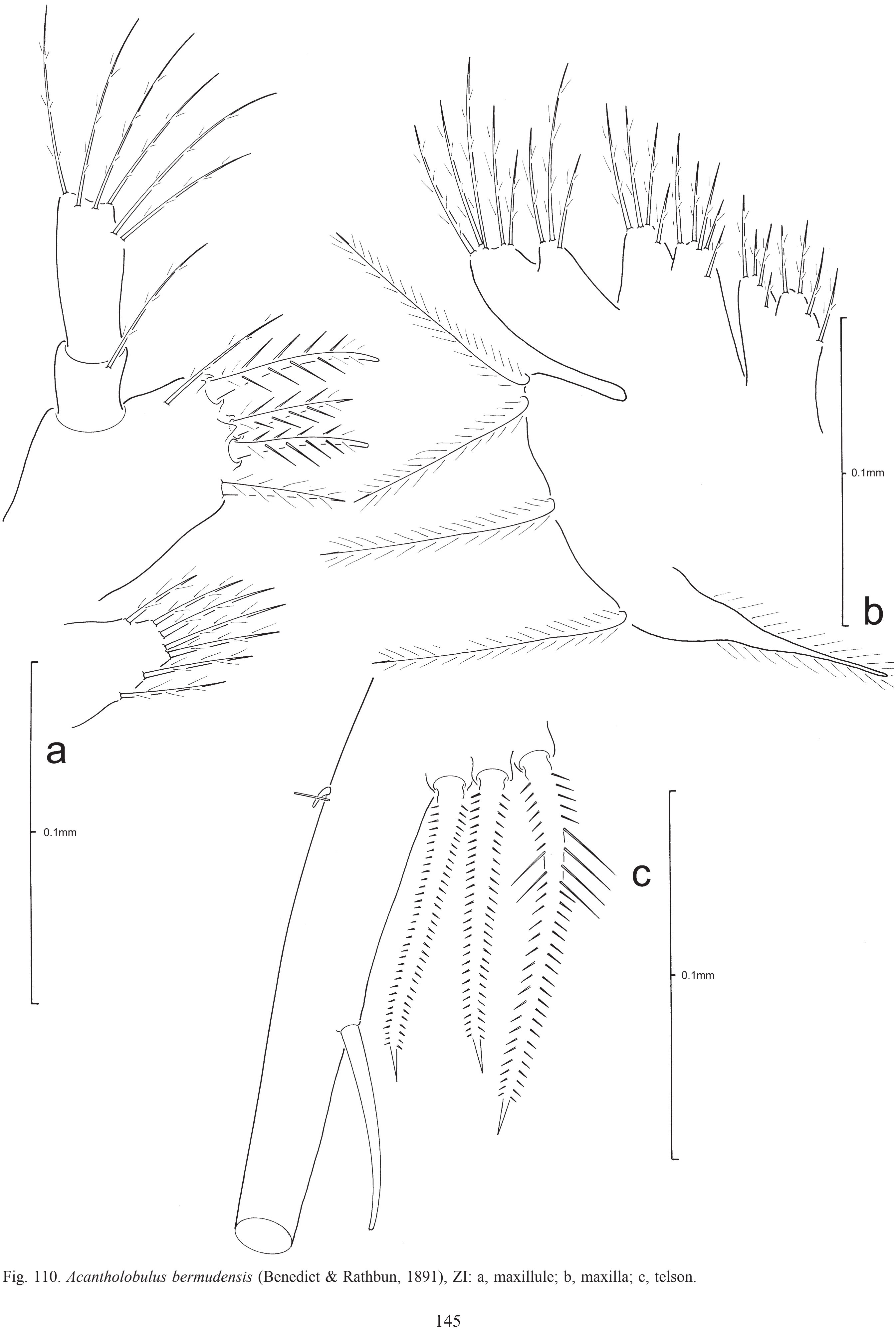

Fig. 110. *Acantholobulus bermudensis* (Benedict & Rathbun, 1891), ZI: a, maxillule; b, maxilla; c, telson.

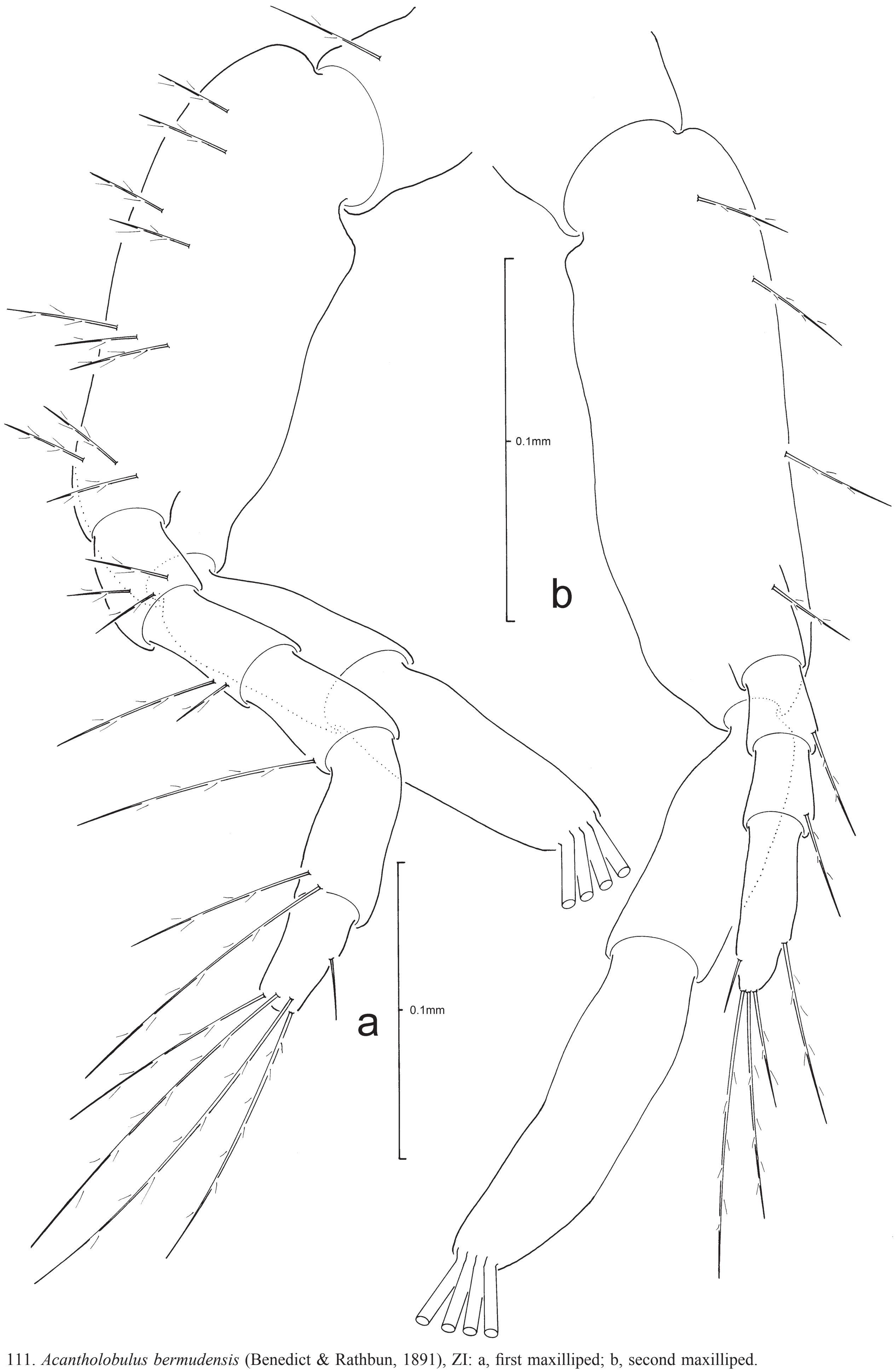

Fig. 111. *Acantholobulus bermudensis* (Benedict & Rathbun, 1891), ZI: a, first maxilliped; b, second maxilliped.

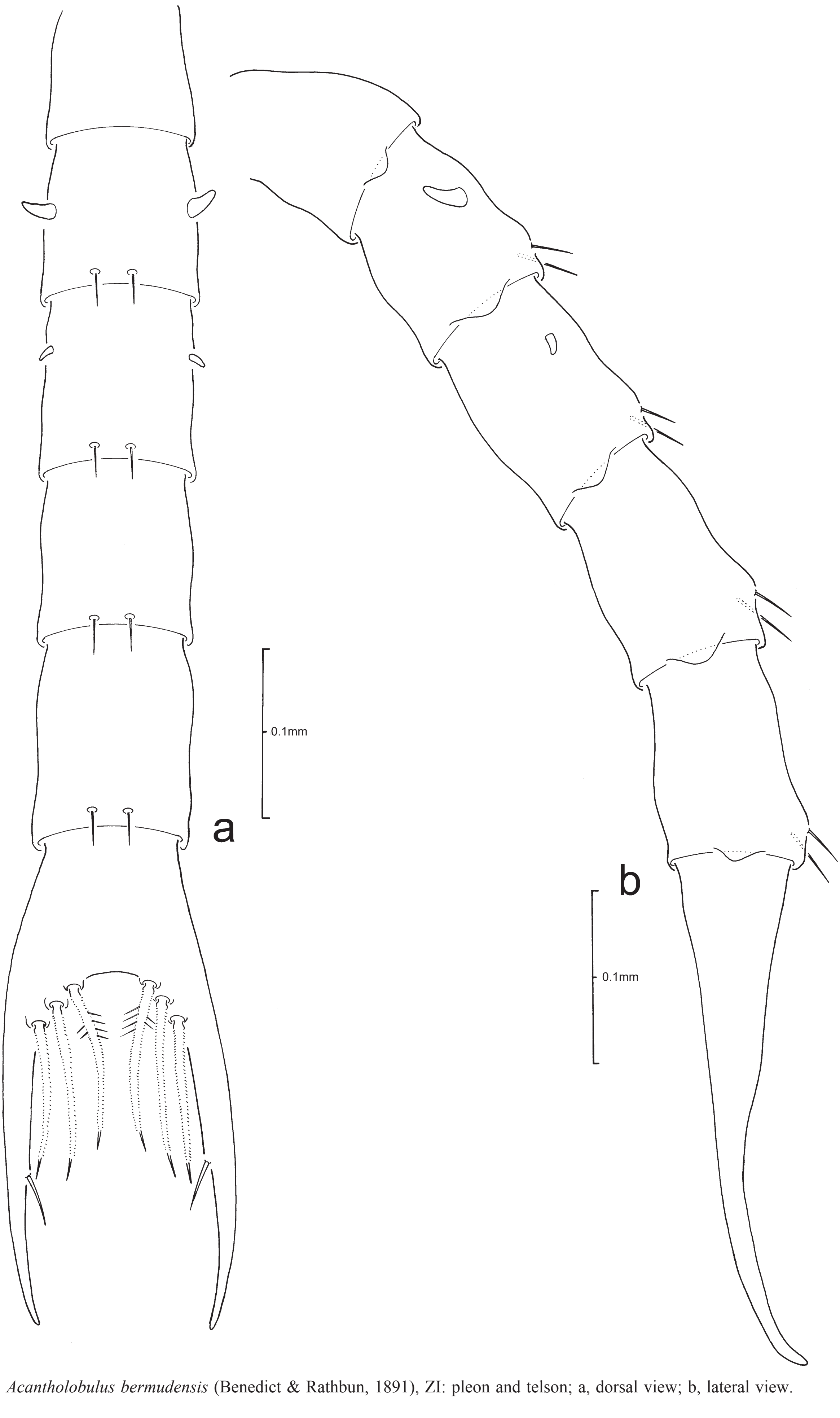

Fig. 112. *Acantholobulus bermudensis* (Benedict & Rathbun, 1891), ZI: pleon and telson; a, dorsal view; b, lateral view.

Acantholobulus schmitti (Rathbun, 1930)

(Figs. 113–116)

Hexapanopeus schmitti. de Bakker et al., 1989: 140–144, figs. 1–10, tabs. 1–2 (ZI–IV, Meg.); Felder & Martin, 2003: fig. 3e–k (ZII–III); Koettker et al., 2012: 3 (key), 12 (list), fig. 3F (ZI).

Description of Zoea I.

CARAPACE (Fig. 113a): dorsal spine long, slightly curved distally, ca. equal to rostral spine length; rostral spine just shorter than antennal protopod, without distal spinulation; lateral spines not developed, reduced to protuberances; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON

Eyes (Fig. 113a): sessile.

Antennule (Fig. 113b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal seta; accessory flagellum absent.

Antenna (Fig. 113c): uniramous; protopod without distal spinulation, just longer than rostral spine length, with swollen tip; endopod absent; exopod minute, ca. 2% length of protopod, with 1 terminal seta.

Mandible: palp absent.

Maxillule (Fig. 114a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.

Maxilla (Fig. 114b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION

First maxilliped (Fig. 115a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 115b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

PLEON (Fig. 116a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 114c, 116a, b): each fork long, gradually curved distally, not spinulate, 2 minute lateral spines, 1 large medial spine on inner margin of fork present; posterior margin with 3 pairs of stout spinulate setae.

Table 14. A comparison between the ZI of *Acantholobulus schmitti* (Rathbun, 1930) by de Bakker et al. (1989) and the present study.

Character	**de Bakker et al. (1989)**	**Present study**
CARAPACE	fig. 1a	Fig. 113a
posterodorsal setae	absent	1 pair present
ANTENNULE	fig. 2a	Fig. 113b
terminal setation	2	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal seta
ANTENNA	fig. 3a	Fig. 113c
exopod	absent	exopod present, minute, ca. 2% length of protopod, with 1 terminal seta
MAXILLULE	fig. 5a	Fig. 114a
coxal endite setation	6 setae	7 setae
endopod, setation of distal article	3 terminal	4 terminal
MAXILLA	fig. 6a	Fig. 114b
coxal endite setation	3+4 setae	4+4 setae
basial endite setation	4+4 setae	5+4 setae
FIRST MAXILLIPED	fig. 7a	Fig. 115a
coxal seta	absent	present
SECOND MAXILLIPED	fig. 8a	Fig. 115b
basial setation	2	4 (1+1+1+1)
endopod setation of second article	0	1
endopod setation of distal article	4 (1 subterminal+3 terminal)	5 (2 subterminal+3 terminal)
TELSON	fig. 9a	Figs. 114c, 116a, b
fork spination	1 large medial spine on inner margin of fork	2 minute lateral spines + 1 large medial spine on inner margin

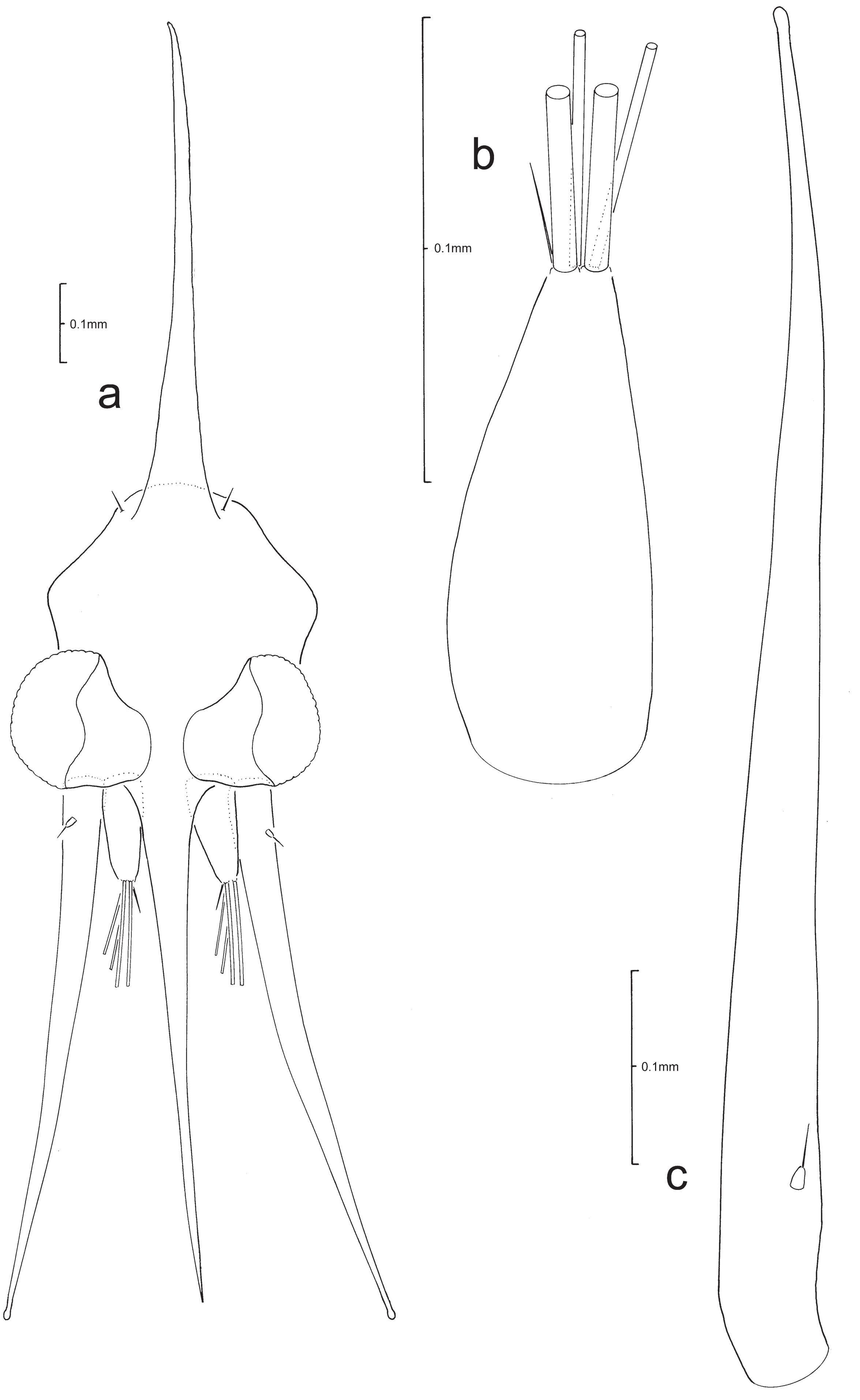

Fig. 113. *Acantholobulus schmitti* (Rathbun, 1930), ZI: a, anterior view of carapace; b, antennule; c, antenna.

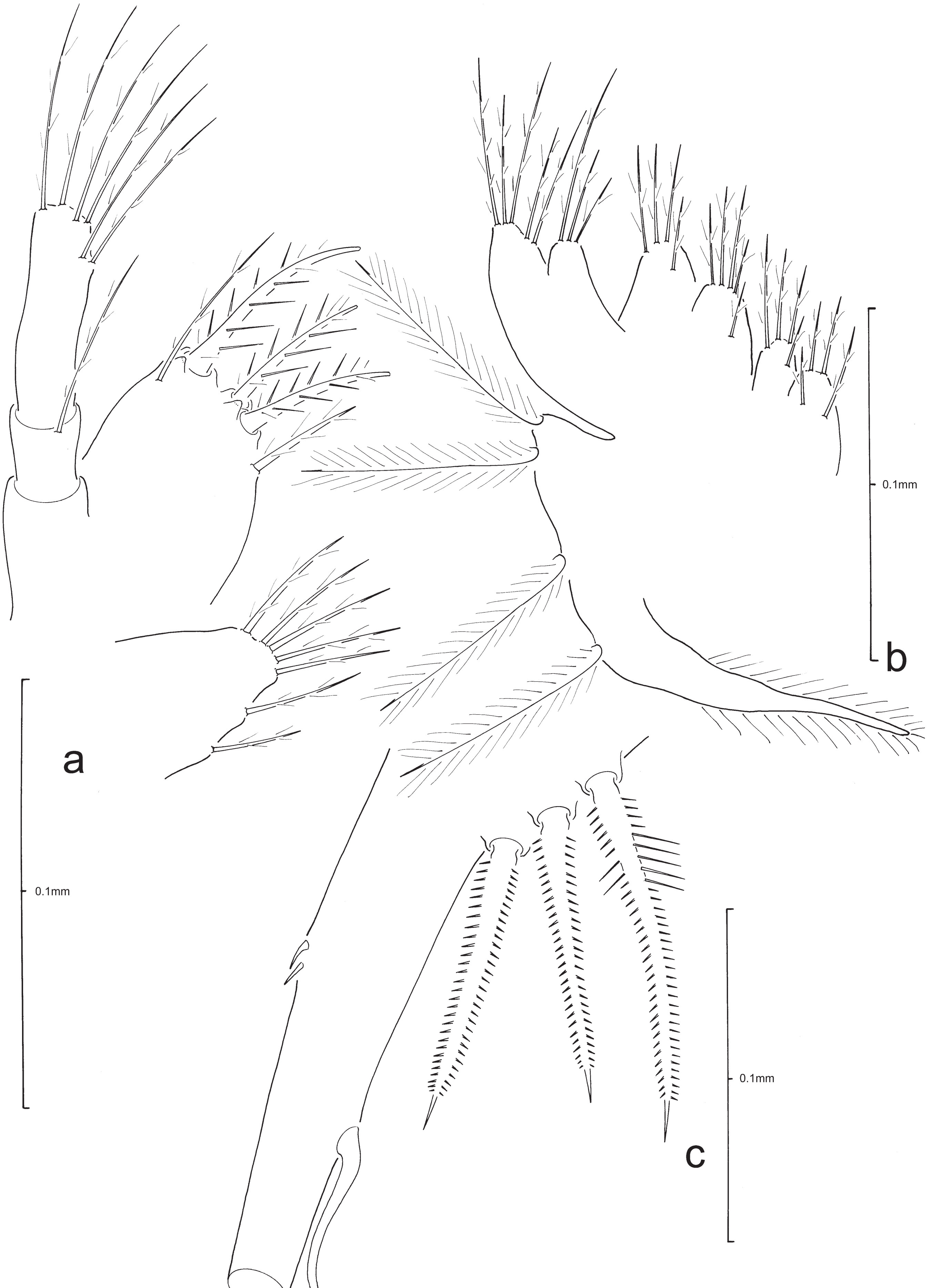

Fig. 114. *Acantholobulus schmitti* (Rathbun, 1930), ZI: a, maxillule; b, maxilla; c, telson.

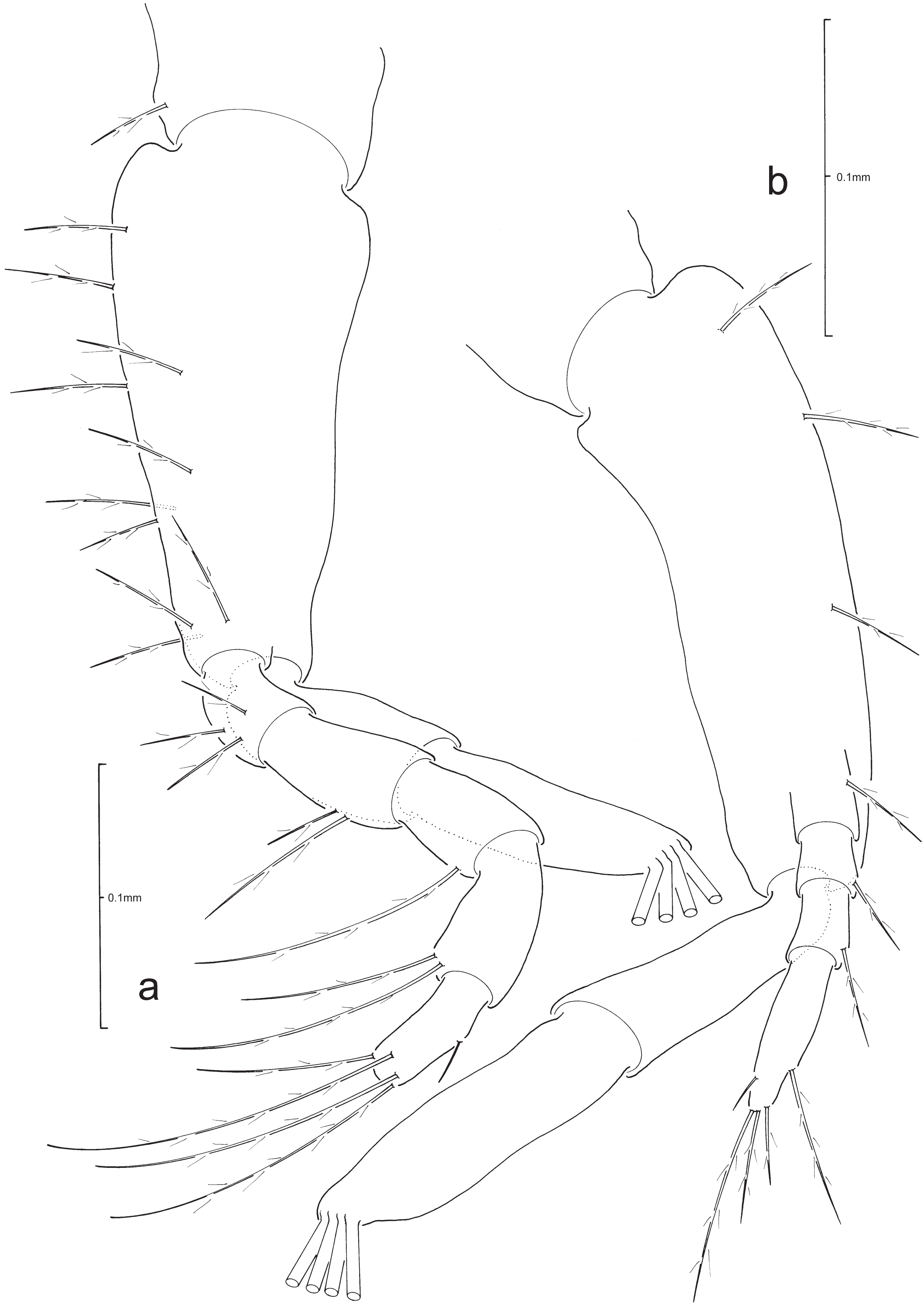

Fig. 115. *Acantholobulus schmitti* (Rathbun, 1930), ZI: a, first maxilliped; b, second maxilliped.

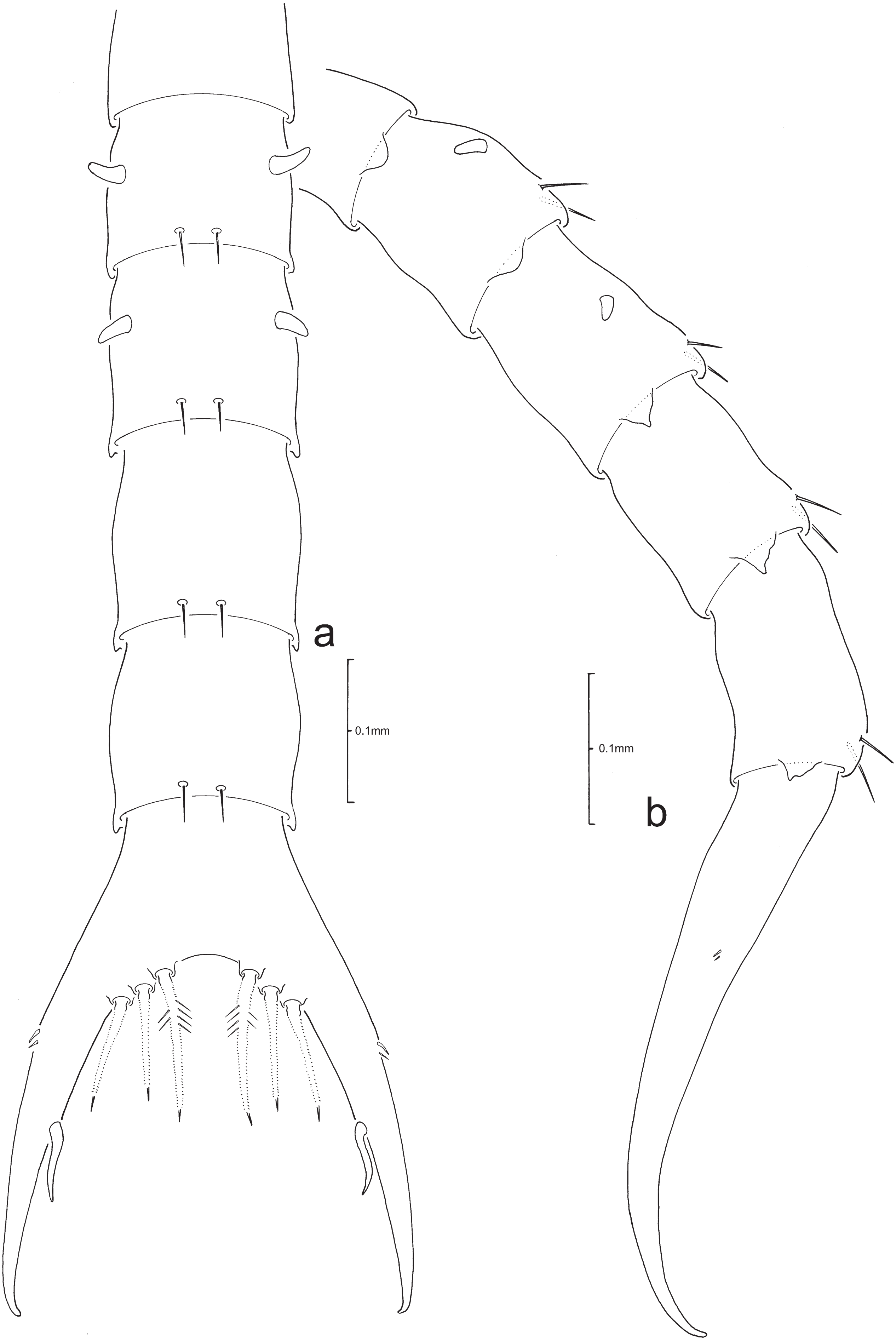

Fig. 116. *Acantholobulus schmitti* (Rathbun, 1930), ZI: pleon and telson; a, dorsal view; b, lateral view.

Dyspanopeus sayi **(Smith, 1869)**
(Figs. 117–120)

Neopanope taxana sayi. Faxon, 1880: 165, fig. pl. II, figs. 4–8 (ZI); Hyman, 1925: 3–8, pl. 1, figs. 1, 3, 7, 11, 13, 17, pl. 2, figs. 23, 27, 31, pls. 3–8 (PZ, ZI–IV, Meg., Cr. I); Chamberlain, 1961: 20–32, pls. 1–16 (ZI–IV, Meg., Cr. I); Kurata, 1970: 215–217, pls. 77–78 (ZI–IV, Meg., Cr. I); Roff et al., 1984: 57, fig. 161 (Meg.).
Panopeus sayi. Birge, 1883: 411–426, pls. 30–33 (ZI–VI, Meg., Cr. I).

Description of Zoea I.
CARAPACE (Fig. 117a): dorsal spine long, ca. equal to rostral spine length; rostral spine shorter than antennal protopod length, without distal spinulation; lateral spines present, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 117a): sessile.
Antennule (Fig. 117b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 117c): uniramous; protopodal process without spinulation, longer than rostral spine length, with slightly swollen end; endopod absent; exopod minute, ca. 1.5% length of protopod, with 1 terminal seta.
Mandible: palp absent.
Maxillule (Fig. 118a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 118b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 119a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 119b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 120a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 118c, 120a, b): each fork long, gradually curved distally, not spinulate, lateral spines absent, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Remarks. The ZI of Birge (1883: pl. XXX, fig. 9, pl. XXXI, fig. 1) is in fact a prezoea while his ZII (pl. XXXI, fig. 2) has four plumose setae on the distal exopod articles of the first two maxillipeds and is therefore the ZI.

Table 15. A comparison between the ZI of *Dyspanopeus sayi* (Smith, 1869) by Faxon (1880), Hyman (1925), Chamberlain (1961), Kurata (1970), and the present study.

Character	**Faxon (1880)**	**Hyman (1925)**	**Chamberlain (1961)**	**Kurata (1970)**	**Present study**
CARAPACE	pl. 2, fig. 4	pl. 3, fig. 35	pl. I		Fig. 117a
posterodorsal setae	absent	1 pair present	absent	not figured	1 pair present
ANTENNULE	pl. 2, fig. 4	pl. 3, fig. 37	pl. II, 2	fig. 77a	Fig. 117b
terminal setation	4 terminal aesthetascs of unequal length	2 terminal aesthetascs of equal length, 1 terminal seta	text: 3–4 terminal setae fig.: 2 terminal aesthetascs, 2 terminal setae	4 terminal aesthetascs of unequal length, 1 terminal seta	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal seta
MAXILLULE	pl. 2, fig. 4	pl. 5, fig. 51	pl. II, 3		Fig. 118a
coxal endite setation	4	5	6	not figured	7
basial endite	2 setal processes	5 setal processes	5 setal processes	not figured	5 setal processes
endopod setation of proximal article	absent	absent	1 seta	not figured	1 seta
endopod setation of distal article	5 (2 subterminal, 3 terminal)	6 (2 subterminal, 4 terminal)	6 (2 subterminal, 4 terminal)	not figured	6 (2 subterminal, 4 terminal)
MAXILLA	pl. 2, fig. 4	pl. 5, fig. 55	pl. II, 4	fig. 77h	Fig. 118b
coxal endite setation	2	0+2	text: 5 to 8 fig.: 4+4	not figured	4+4
basial endite setation	2	3+2	text: 5 to 9 fig.: 5+4	not figured	5+4
endopod setation	2	2+4 (1 subterminal, 3 terminal)	text: 7 to 8 fig.: 3+5 (2 subterminal, 3 terminal)	3+5 (2 subterminal, 3 terminal)	3+5 (2 subterminal, 3 terminal)
FIRST MAXILLIPED	pl. 2, fig. 4	pl. 6, fig. 63	pl. II, 7	fig. 77a	Fig. 119a
coxal seta	absent	absent	present	not figured	present
basial setation	absent	absent	10 (2,2,3,3)	not figured	10 (2,2,3,3)
endopod setation	1,2,0,0,3 (1 subterminal+2 terminal)	0,1,1,2,3	text: 2/3,2,1,1/2,4/5 fig.: 2,2,1,1,5 (2 subterminal+3 terminal)	1,2,1,2,4 (1 subterminal+3 terminal)	3,2,1,2,5 (1 subterminal+4 terminal)
SECOND MAXILLIPED	pl. 2, fig. 4	pl. 7, fig. 67	pl. II, 8	fig. 77a	Fig. 119b
basial setation	absent	absent	4 (1+1+1+1)	not figured	4 (1+1+1+1)
endopod setation	0,0,3 (1 subterminal+2 terminal)	0,0,3 (1 subterminal+2 terminal)	text: 1,4,4/5 fig.: 1,1,5 (2 subterminal+3 terminal)	1,1,3 (2 subterminal+1 terminal)	1,1,5 (2 subterminal+3 terminal)
TELSON	pl. 2, figs. 4, 5	pl. 7, fig. 72	pl. II, 6	fig. 77b	Figs. 118c, 120a, b
fork spination	1 dorsomedial spine present	absent	1 dorsomedial spine present	1 dorsomedial spine present	1 dorsomedial spine present

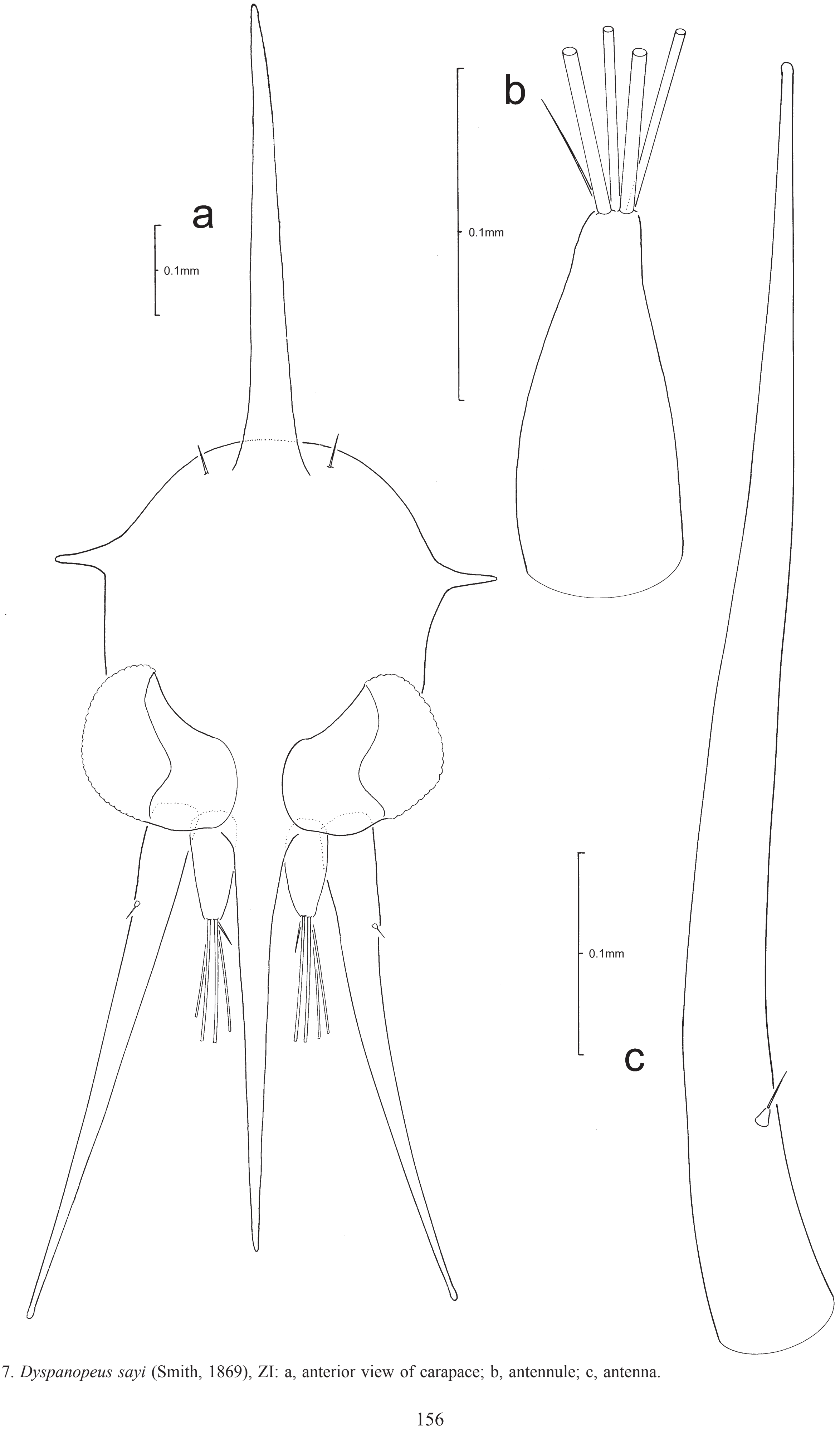

Fig. 117. *Dyspanopeus sayi* (Smith, 1869), ZI: a, anterior view of carapace; b, antennule; c, antenna.

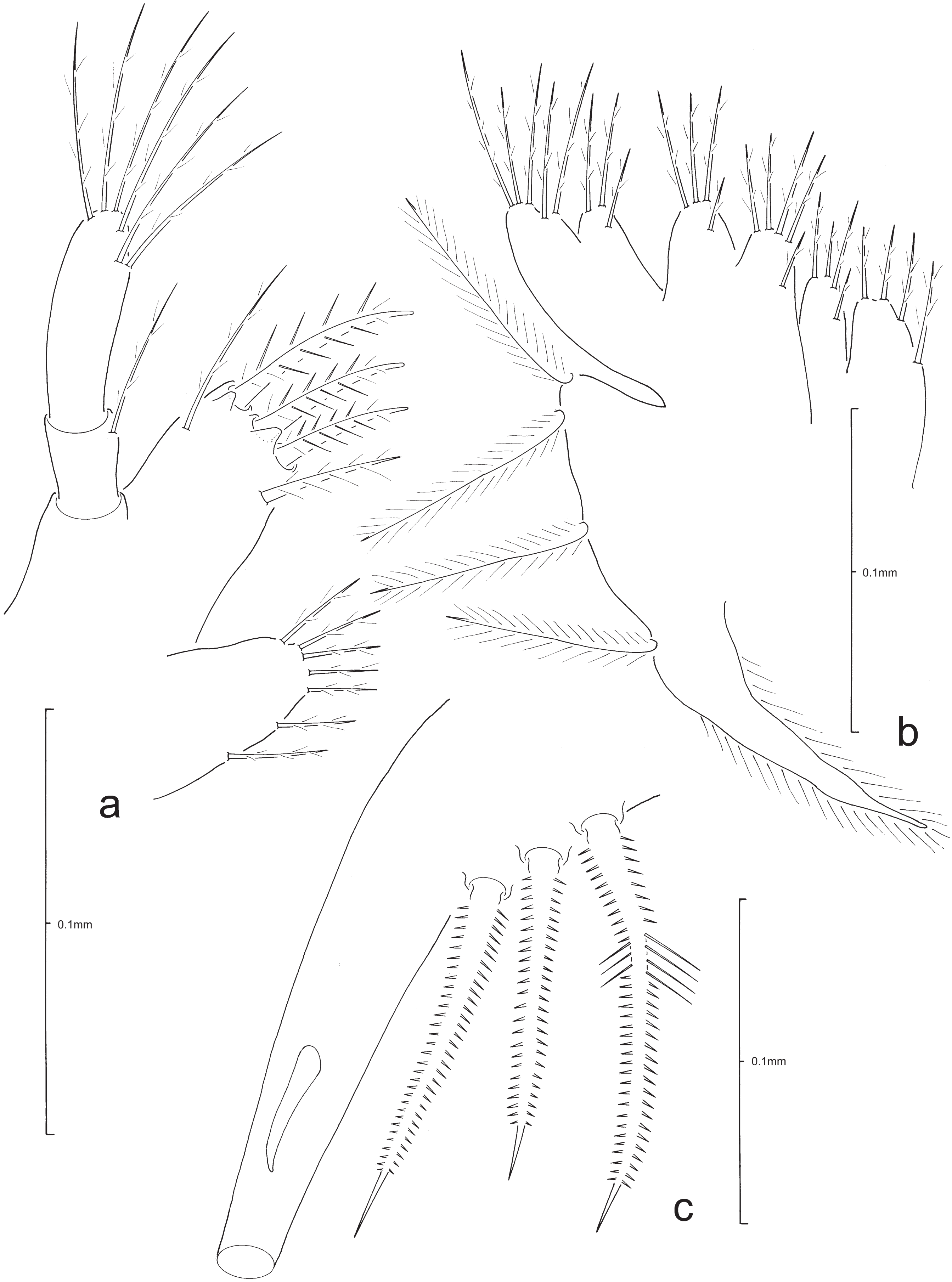

Fig. 118. *Dyspanopeus sayi* (Smith, 1869), ZI: a, maxillule; b, maxilla; c, telson.

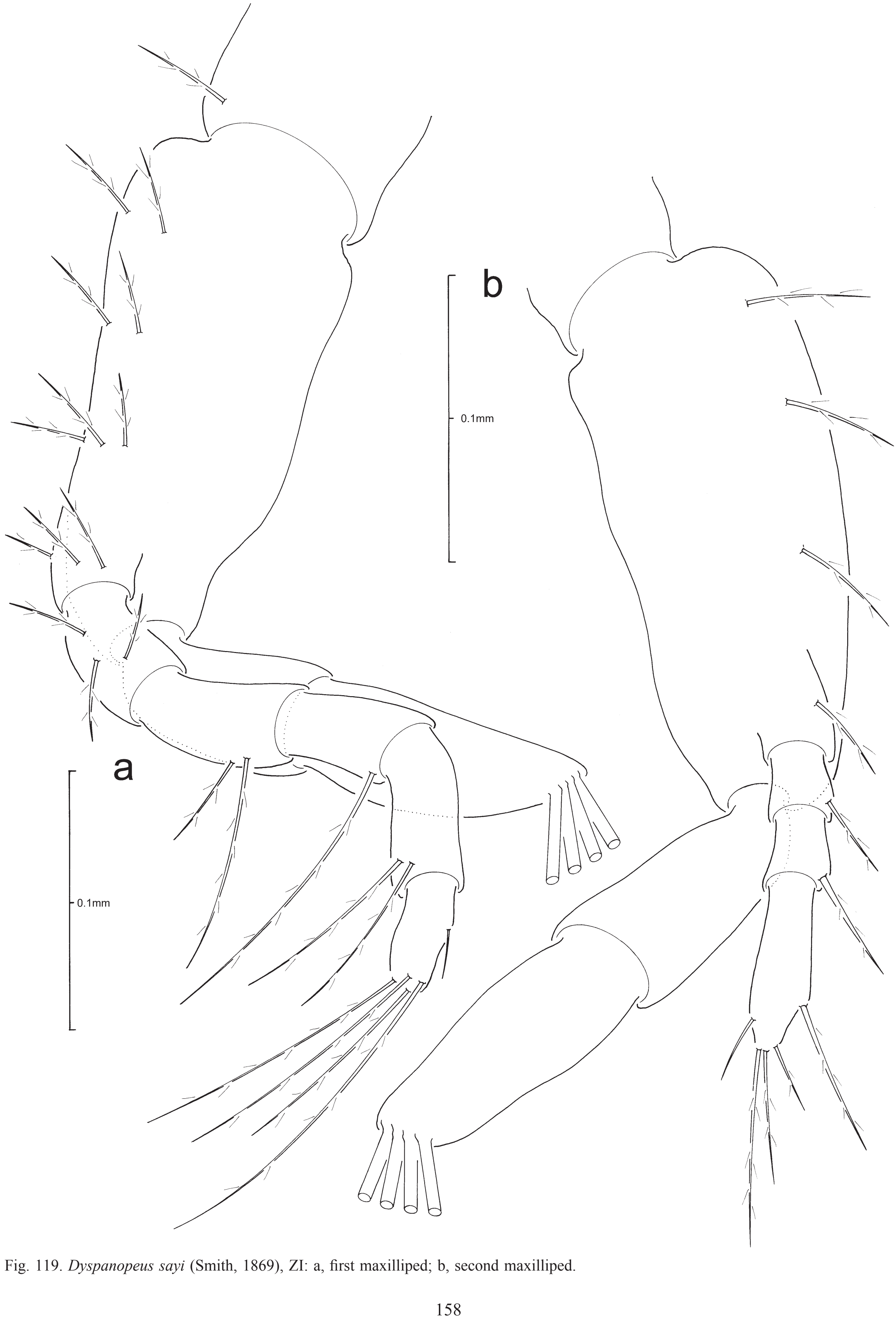

Fig. 119. *Dyspanopeus sayi* (Smith, 1869), ZI: a, first maxilliped; b, second maxilliped.

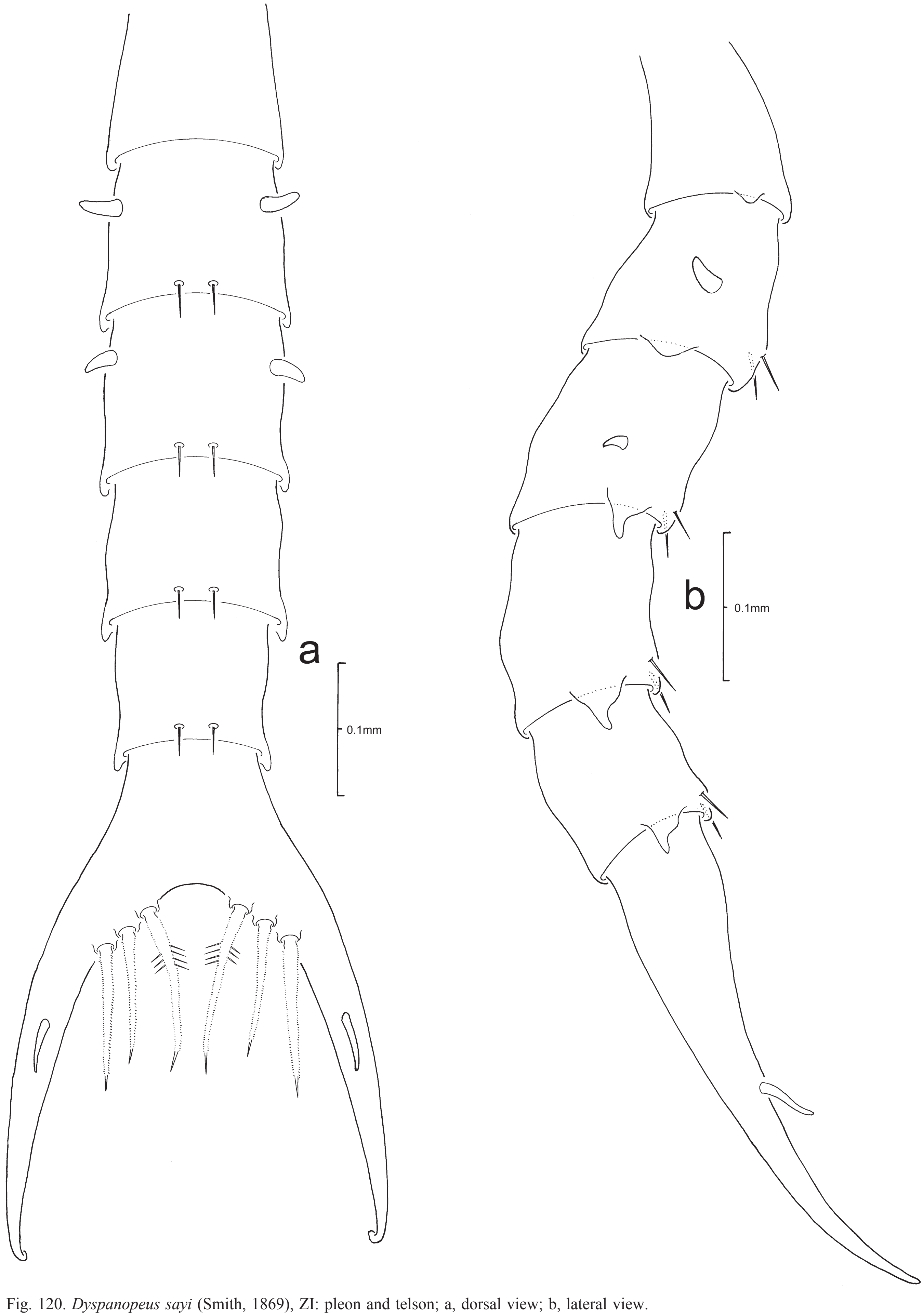

Fig. 120. *Dyspanopeus sayi* (Smith, 1869), ZI: pleon and telson; a, dorsal view; b, lateral view.

Eurypanopeus depressus (Smith, 1869)
(Figs. 121–124)

Eurypanopeus depressus. Hyman, 1925: 8, 9, pl. 1, figs. 2, 4, 8, 14, 18, pl. 2, figs. 24, 28, 32, pl. 9 (PZ, ZI); Costlow & Bookout, 1961: 7–13, figs. 1–41 (ZI–IV, Meg.); Kurata, 1970: 217–219, pls. 79–80 (ZI–IV, Meg.); Koettker et al., 2012: 4 (key), 12 (list), fig. 3F (ZI).

Description of Zoea I.
CARAPACE (Fig. 121a): dorsal spine extremely long, longer than rostral spine length; rostral spine, although long, is shorter than antennal protopod length, without distal spinulation; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 121a): sessile.
Antennule (Fig. 121b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal setae; accessory flagellum absent.
Antenna (Fig. 121c): uniramous; protopodal process distally multispinulate, longer than rostral spine length; endopod absent; exopod minute, ca. 4.6% length of protopod, with 1 terminal seta.
Mandible: palp absent.
Maxillule (Fig. 122a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 122b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 123a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles, with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 123b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 124a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes, pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 122c, 124a, b): each fork long, gradually curved distally, not spinulate, 2 minute lateral spines of equal length, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Remarks. Koettker et al. (2012) only figure the antenna of *Eurypanopeus depressus*.

Table 16. A comparison between the ZI of *Eurypanopeus depressus* (Smith, 1869) by Hyman (1925), Costlow & Bookout (1961), Kurata (1970), and the present study.

Character	**Hyman (1925)**	**Costlow & Bookout (1961)**	**Kurata (1970)**	**Present study**
CARAPACE	pl. 9, fig. 106	figs. 1, 2	fig. 79a	Fig. 121a
posterodorsal setae	absent	absent	absent	1 pair present
ANTENNULE	pl. 9, fig. 108	fig. 3	fig. 77a	Fig. 121b
terminal setation	3 terminal aesthetascs of unequal length, 1 terminal seta	2 terminal aesthetascs of equal length, 1 terminal seta	2 terminal aesthetascs of equal length, 1 terminal seta	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal seta
MAXILLULE	pl. 9, fig. 111	fig. 6		Fig. 122a
coxal endite setation	5	7	not figured	7
basial endite	4 setal processes	5 setal processes	not figured	5 setal processes
MAXILLA	pl. 9, fig. 112	fig. 7		Fig. 122b
coxal endite setation	4+3	4+4	not figured	4+4
basial endite setation	4+3	5+4	not figured	5+4
FIRST MAXILLIPED	pl. 9, fig. 113	fig. 8		Fig. 123a
coxal seta	not figured	not figured	not figured	present
basial setation	3 (1+1+1)	8 (2+3+3)	not figured	10 (2+2+3+3)
endopod setation	2,2,1,2,4 (1 subterminal+3 terminal)	3,2,1,2,5 (1 subterminal+4 terminal)	not figured	3,2,1,2,5 (1 subterminal+4 terminal)
SECOND MAXILLIPED	pl. 9, fig. 114	fig. 9		Fig. 123b
basial setation	absent	4 (1,1,1,1)	not figured	4 (1,1,1,1)
endopod setation	0,0,4 (1 subterminal+3 terminal)	1,1,5 (2 subterminal+3 terminal)	not figured	1,1,5 (2 subterminal+3 terminal)

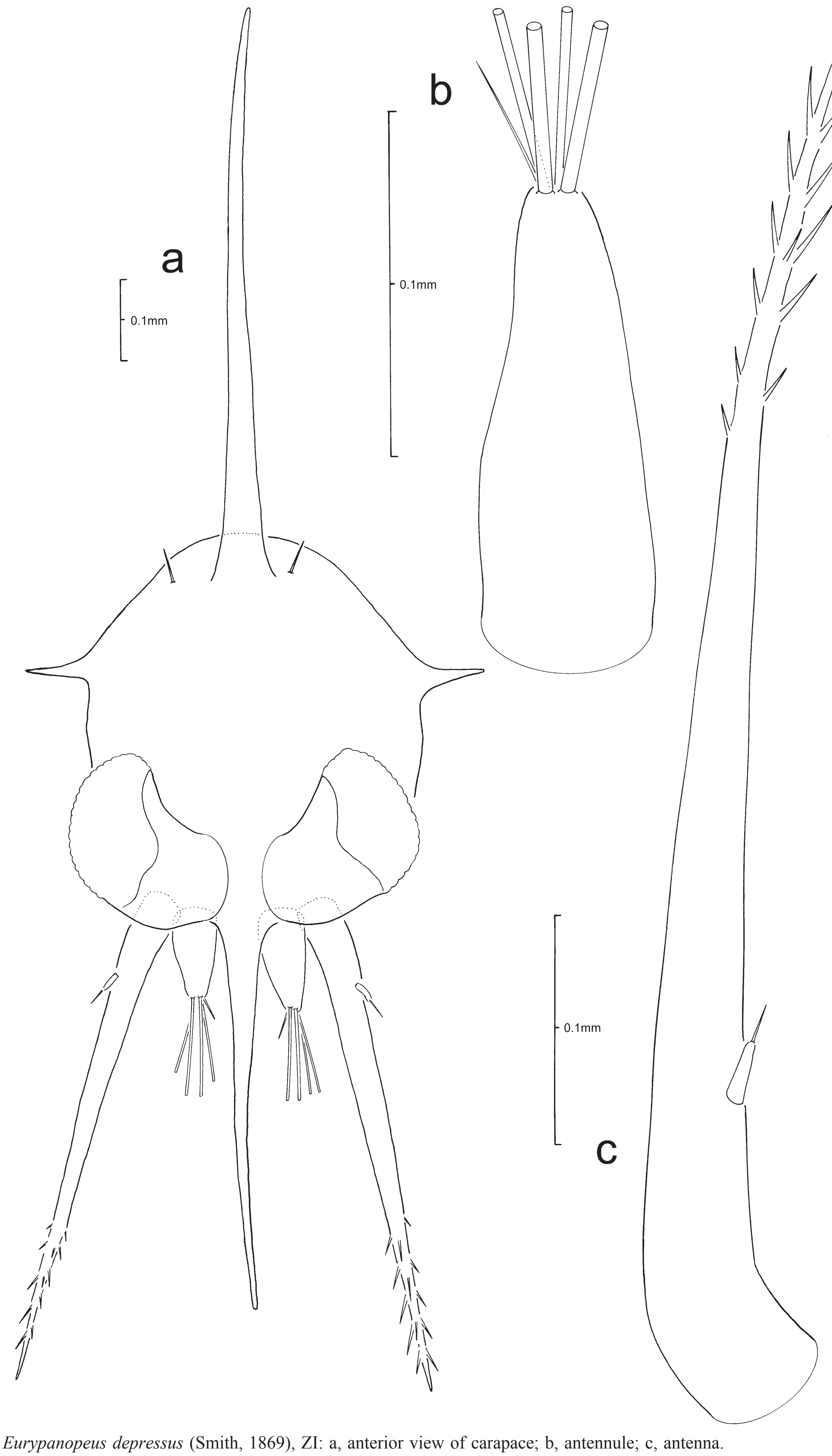

Fig. 121. *Eurypanopeus depressus* (Smith, 1869), ZI: a, anterior view of carapace; b, antennule; c, antenna.

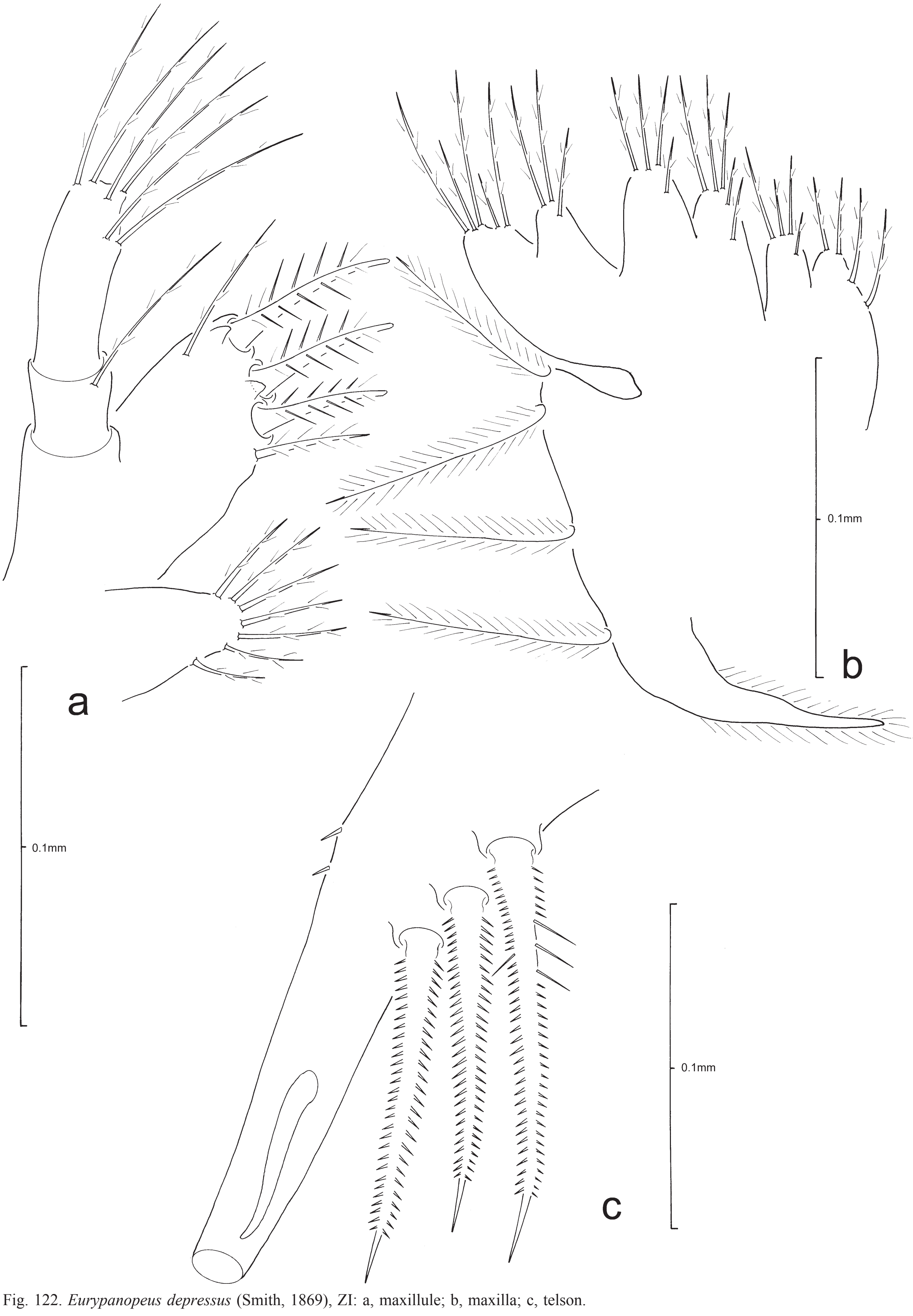

Fig. 122. *Eurypanopeus depressus* (Smith, 1869), ZI: a, maxillule; b, maxilla; c, telson.

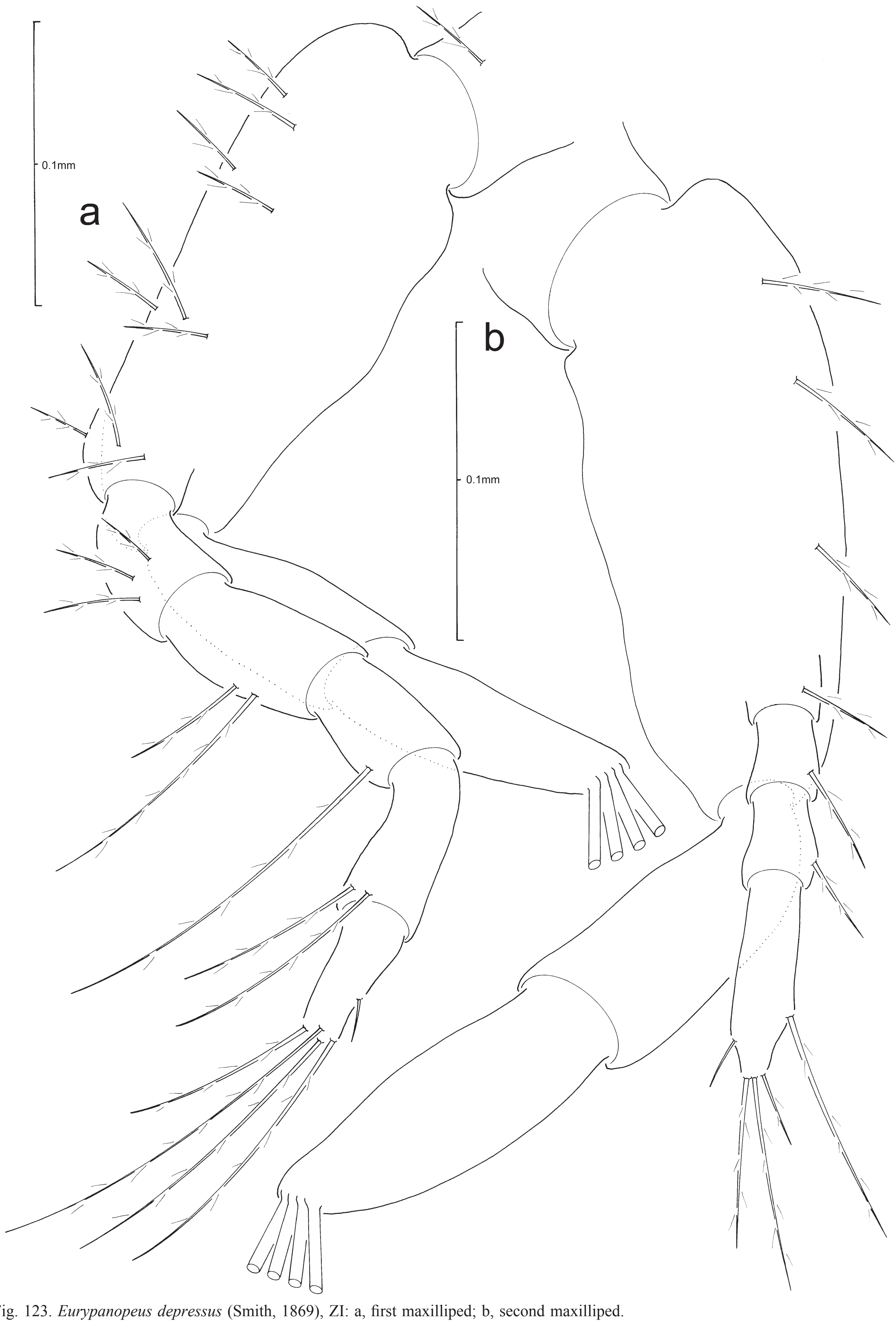

Fig. 123. *Eurypanopeus depressus* (Smith, 1869), ZI: a, first maxilliped; b, second maxilliped.

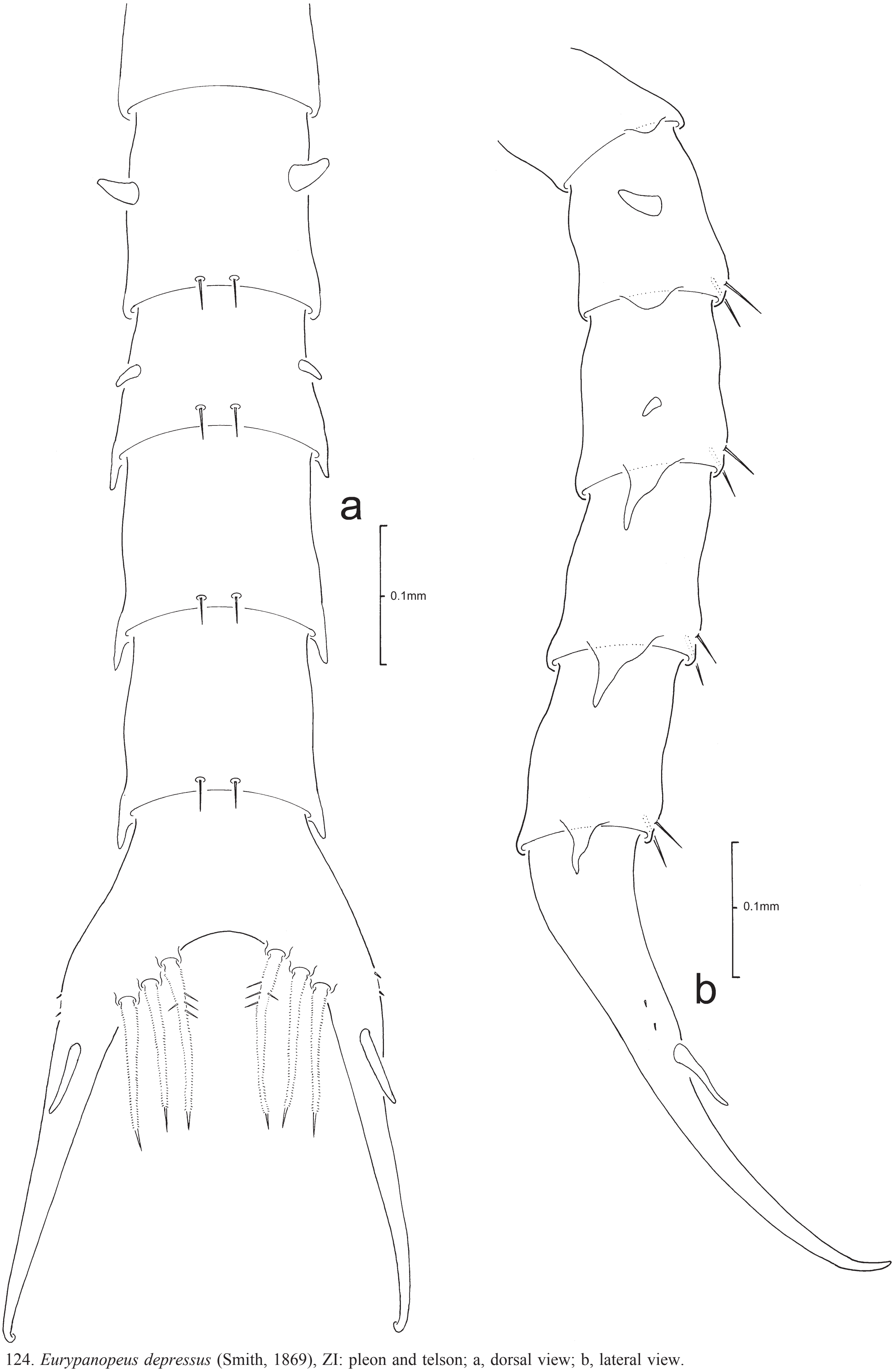

Fig. 124. *Eurypanopeus depressus* (Smith, 1869), ZI: pleon and telson; a, dorsal view; b, lateral view.

***Eurytium limosum* (Say, 1818)**
(Figs. 125–128)

Eurytium limosum. Kurata, 1970: 227–229, pls. 88–89 (ZI–IV, Meg., Cr. I); Kurata et al., 1981: 20–24, figs. 1–4 (ZI–IV, Meg., Cr. I); Messerknecht et al., 1991: 277–293, figs. 1–17 (ZI–IV, Meg., Cr. I–II); Koettker et al., 2012: 5 (key), 12 (list), figs. 2D, 5A (ZI); de Souza et al., 2013: 275, figs. 9–16 (ZI).

Description of Zoea I.
CARAPACE (Fig. 125a): dorsal spine long, distally curved, equal to rostral spine length; rostral spine straight, shorter than antennal protopod length, without distal spinulation; lateral spines present, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 125a): sessile.
Antennule (Fig. 125b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 small terminal seta; accessory flagellum absent.
Antenna (Fig. 125c): uniramous; protopod longer than rostral spine, distally multispinulate; endopod absent; exopod small, ca. 3.6% length of protopod, with 1 terminal seta.
Mandible: palp absent
Maxillule (Fig. 126a): uniramous; epipod seta absent; coxal endite with 7 terminal setae; basial endite with 5 setal processes; endopod comprising 2 articles, proximal article with 1 seta, distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 126b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 plumose setae plus distal stout process.

PEREION
First maxilliped (Fig. 127a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 terminal natatory plumose setae.
Second maxilliped (Fig. 127b): biramous; coxa without seta; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 terminal natatory plumose setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 128a, b): 5 pleomeres; pleomere 2 with pair of lateral processes directed laterally; pleomere 3 with pair of lateral processes directed posteriorly; pleomeres 1–2 with rounded posterolateral processes; pleomeres 3–5 each with posterolateral spinous processes; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopods absent.

TELSON (Figs. 126c, 128a, b): each fork relatively long, not spinulate with 1 large lateral spine, 1 minute lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Remarks. Koettker et al. (2012: fig. 5E) illustrate the appendages of some first stage zoeas of brachyuran larvae including the maxillule of *E. limosum*. This maxillule is not from a ZI because it possesses an exopod seta (normally absent in ZI, see Fig. 126a) and a basis with 10 setal processes (normally five in ZI, see Fig. 126a). Furthermore, key couplet 80a of Koettker et al. (2012) states that the "ventral margin of (ZI, *E. limosum*) carapace fringed with up to 10 hairs" and suggests a later stage. The ventral carapace margin of the ZI examined for the present study was without setae.

Table 17. A comparison between the ZI of *Eurytium limosum* (Say, 1818) by Kurata (1970), Kurata et al. (1981), Messerknecht et al. (1991), Koettker et al. (2012), de Souza et al. (2013), and the present study.

Character	**Kurata (1970)**	**Kurata et al. (1981)**	**Messerknecht et al. (1991)**	**Koettker et al. (2012)**	**de Souza et al. (2013)**	**Present study**
CARAPACE	fig. 88a	fig. 2A	fig. 1A	fig. 2D	fig. 9	Fig. 125a
posterodorsal setae	absent	1 pair present	1 pair present	1 pair present	1 pair present	1 pair present
ANTENNULE	fig. 88a	fig. 2A	fig. 2A	fig. 2D	fig. 10	Fig. 125b
terminal setation	2 terminal aesthetascs of equal length, 1 terminal seta	2 aesthetascs, 1 simple setae	2 aesthetascs, 3 setae of different lengths	2 aesthetascs, 1 simple setae	2 aesthetascs, 2 simple setae	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal seta
MAXILLULE	not figured	not figured	fig. 5A	not figured	fig. 12	Fig. 126a
coxal endite setation			7		6	7
basial endite			5 setal processes		5 setal processes	5 setal processes
MAXILLA	not figured	not figured	fig. 6A	not figured	fig. 13	Fig. 126b
coxal endite setation			4+4		4+4	4+4
basial endite setation			5+4		5+4	5+4
FIRST MAXILLIPED	fig. 88a	fig. 2A	fig. 7A	fig. 2D	fig. 14	Fig. 127a
coxal seta	not figured	not figured	not figured	not figured	not figured	present
basial setation	not figured	not figured	10 (2+2+3+3)	not figured	10 (2+2+3+3)	10 (2+2+3+3)
endopod setation	1,2,1,2,5 (1 subterminal+4 terminal)	3,2,1,2,5 (1 subterminal+4 terminal)	3,2,1,2,5 (1 subterminal+4 terminal)	3,2,1,2,5 (1 subterminal+4 terminal)	2,2,1,2,5 (1 subterminal+4 terminal)	3,2,1,2,5 (1 subterminal+4 terminal)
SECOND MAXILLIPED	fig. 88a	fig. 2A	fig. 8A	fig. 2D	fig. 15	Fig. 127b
basial setation	not figured	not figured	4 (1+1+1+1)	not figured	4 (1+1+1+1)	4 (1+1+1+1)
endopod setation	0,1,3 (1 subterminal+2 terminal)	1,1,4	1,1,5 (2 subterminal+3 terminal)	1,1,4	1,1,5 (2 subterminal+3 terminal)	1,1,5 (2 subterminal+3 terminal)
TELSON	fig. 88b	fig. 2A	fig. 9A	fig. 2D	fig. 16	Figs. 126c, 128a, b
fork spination	1 large and 1 minute lateral spines + 1 large dorsomedial spine	1 large lateral spine + 1 large dorsomedial spine	1 large and 1 minute lateral spine + 1 large dorsomedial spine	1 large lateral spine + 1 large dorsomedial spine	1 large and 1 minute lateral spine + 1 large dorsomedial spine	1 large and 1 minute lateral spine + 1 large dorsomedial spine

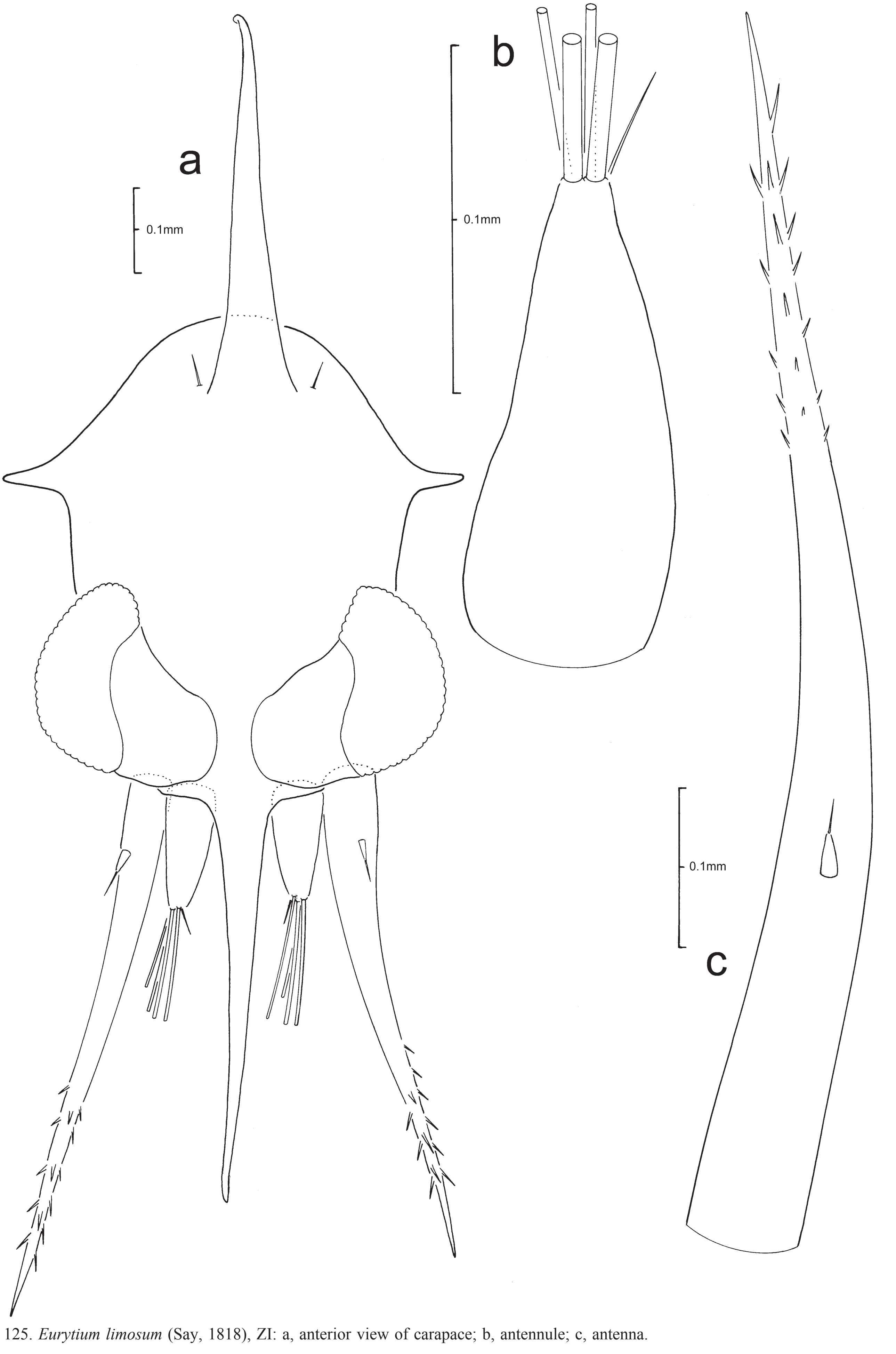

Fig. 125. *Eurytium limosum* (Say, 1818), ZI: a, anterior view of carapace; b, antennule; c, antenna.

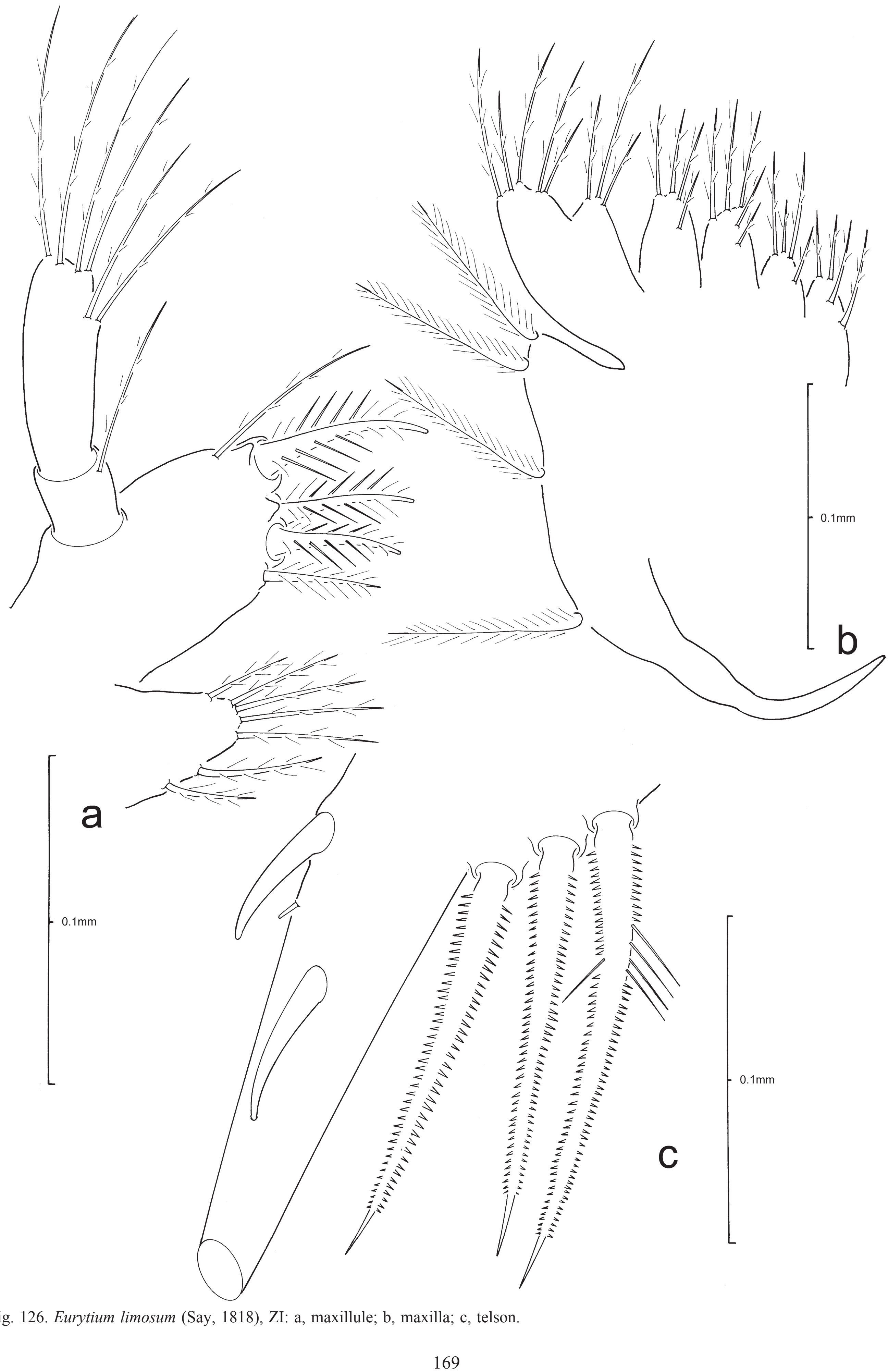

Fig. 126. *Eurytium limosum* (Say, 1818), ZI: a, maxillule; b, maxilla; c, telson.

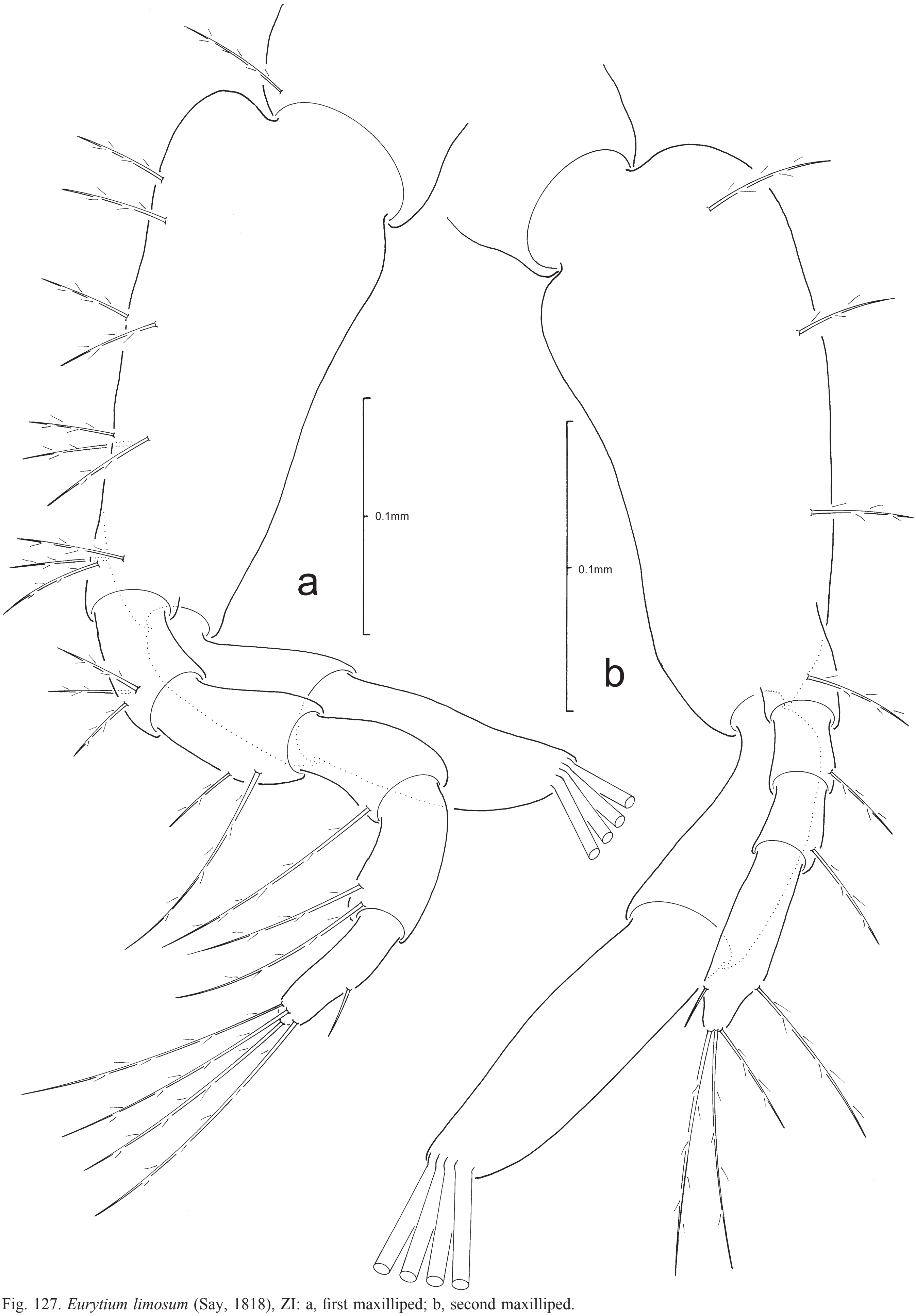

Fig. 127. *Eurytium limosum* (Say, 1818), ZI: a, first maxilliped; b, second maxilliped.

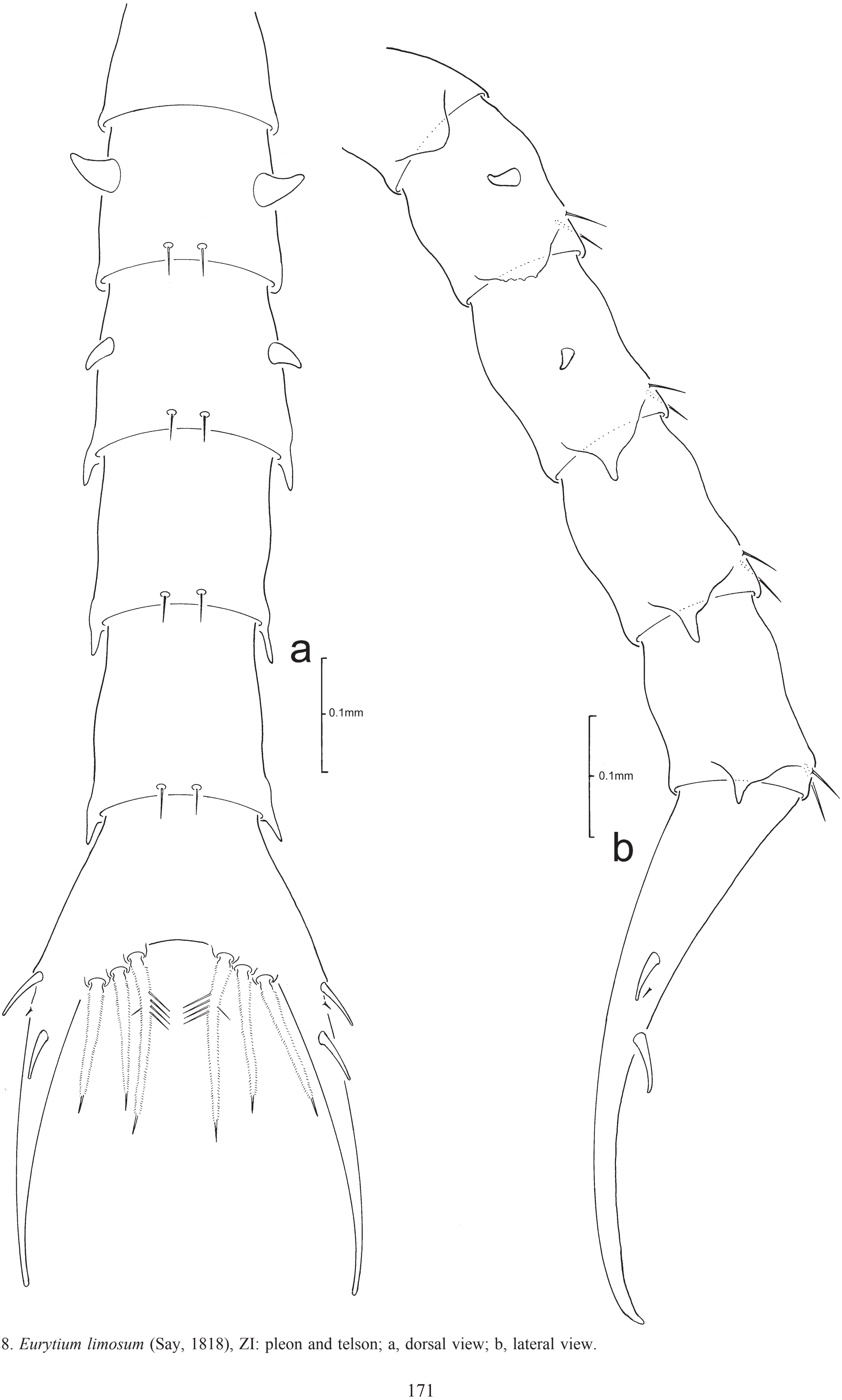

Fig. 128. *Eurytium limosum* (Say, 1818), ZI: pleon and telson; a, dorsal view; b, lateral view.

Hexapanopeus paulensis **Rathbun, 1930**
(Figs. 129–132)

Hexapanopeus paulensis. Fransozo et al., 1991: 32–43, figs. 2–7 (ZI–IV, Meg.).

Description of Zoea I.
CARAPACE (Fig. 129a): dorsal spine extremely long, longer than rostral spine length; rostral spine extremely long, shorter than antennal protopod length, without distal spinulation; lateral spines present, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 129a): sessile.
Antennule (Fig. 129b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal setae; accessory flagellum absent.
Antenna (Fig. 129c): uniramous; protopodal process without spinulation, longer than rostral spine length, tip blunt; endopod absent; exopod minute, ca. 2.6% length of protopod, with 1 terminal seta.
Mandible: palp absent.
Maxillule (Fig. 130a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 130b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 131a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 131b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 132a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 with rounded posterolateral processes; pleomeres 3–5 with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 130c, 132a, b): each fork long, gradually curved distally, not spinulated, lateral and dorsomedial spines absent; posterior margin with 3 pairs of stout spinulate setae.

Table 18. A comparison between the ZI of *Hexapanopeus paulensis* Rathbun, 1930 by Fransozo et al. (1991) and the present study.

Character	**Fransozo et al. (1991)**	**Present study**
CARAPACE	fig. 2a	Fig. 129a
posterodorsal setae	absent	1 pair present
ANTENNULE	fig. 2c	Fig. 129b
terminal setation	3 terminal aesthetascs, 1 terminal setae	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal setae
MAXILLA	fig. 2g	Fig. 130b
coxal endite setation	4+3	4+4
basial endite setation	4+4	5+4
FIRST MAXILLIPED	fig. 2h	Fig. 131a
coxal seta	absent	present
PLEON	fig. 2b	Fig. 132a, b
pleomeres 2–5; setation	absent	1 pair of posterodorsal setae on each pleomere

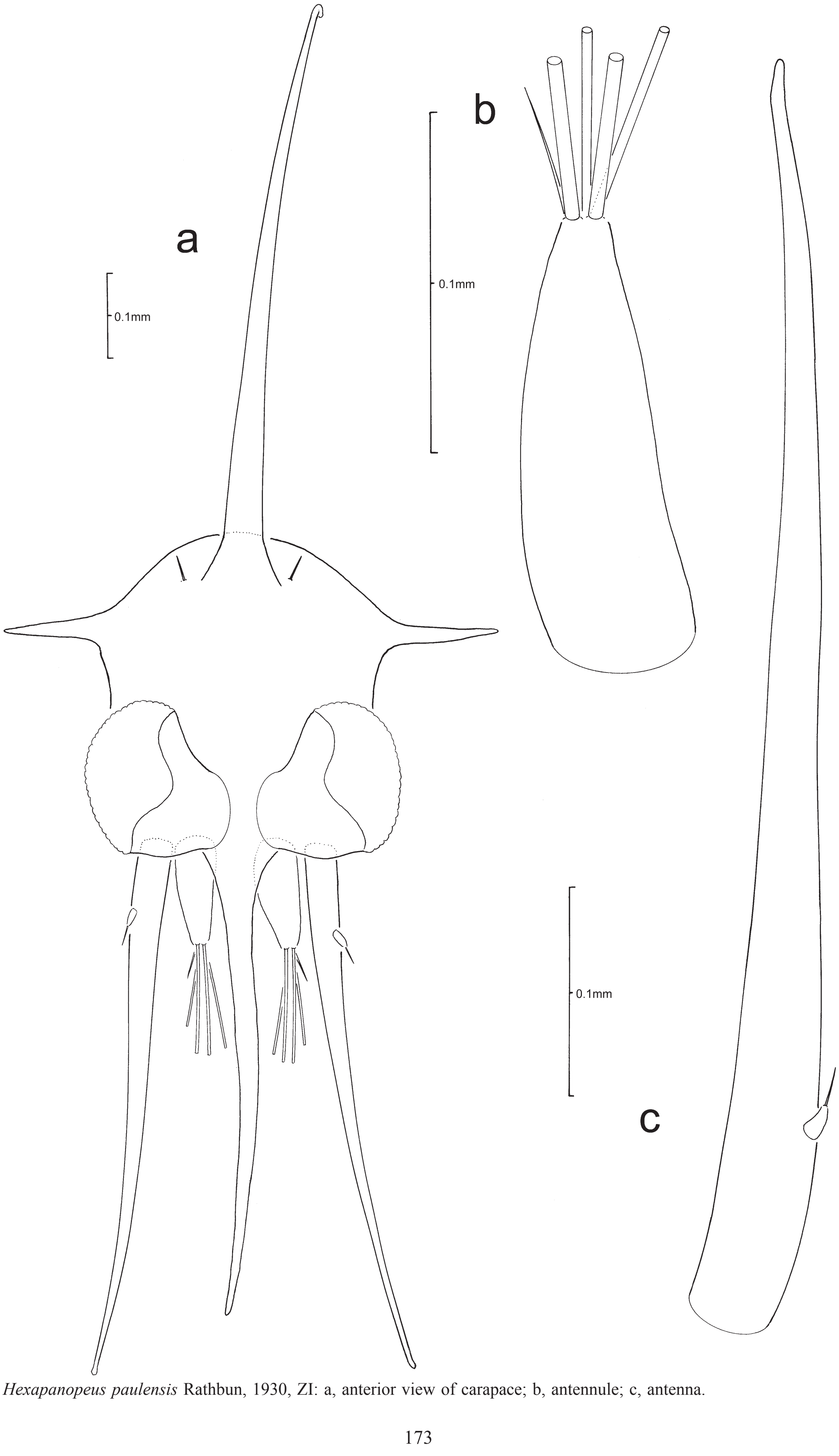

Fig. 129. *Hexapanopeus paulensis* Rathbun, 1930, ZI: a, anterior view of carapace; b, antennule; c, antenna.

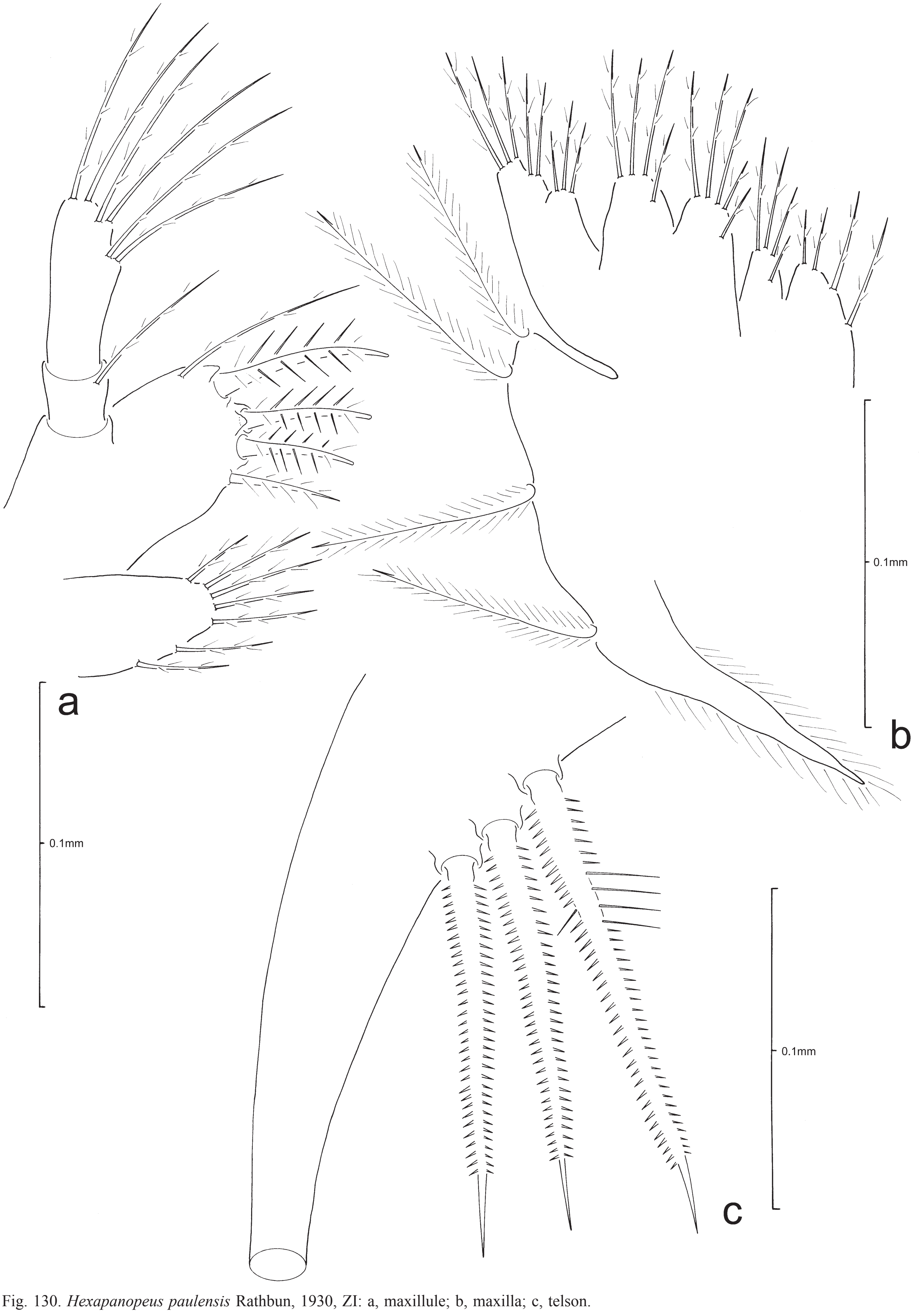

Fig. 130. *Hexapanopeus paulensis* Rathbun, 1930, ZI: a, maxillule; b, maxilla; c, telson.

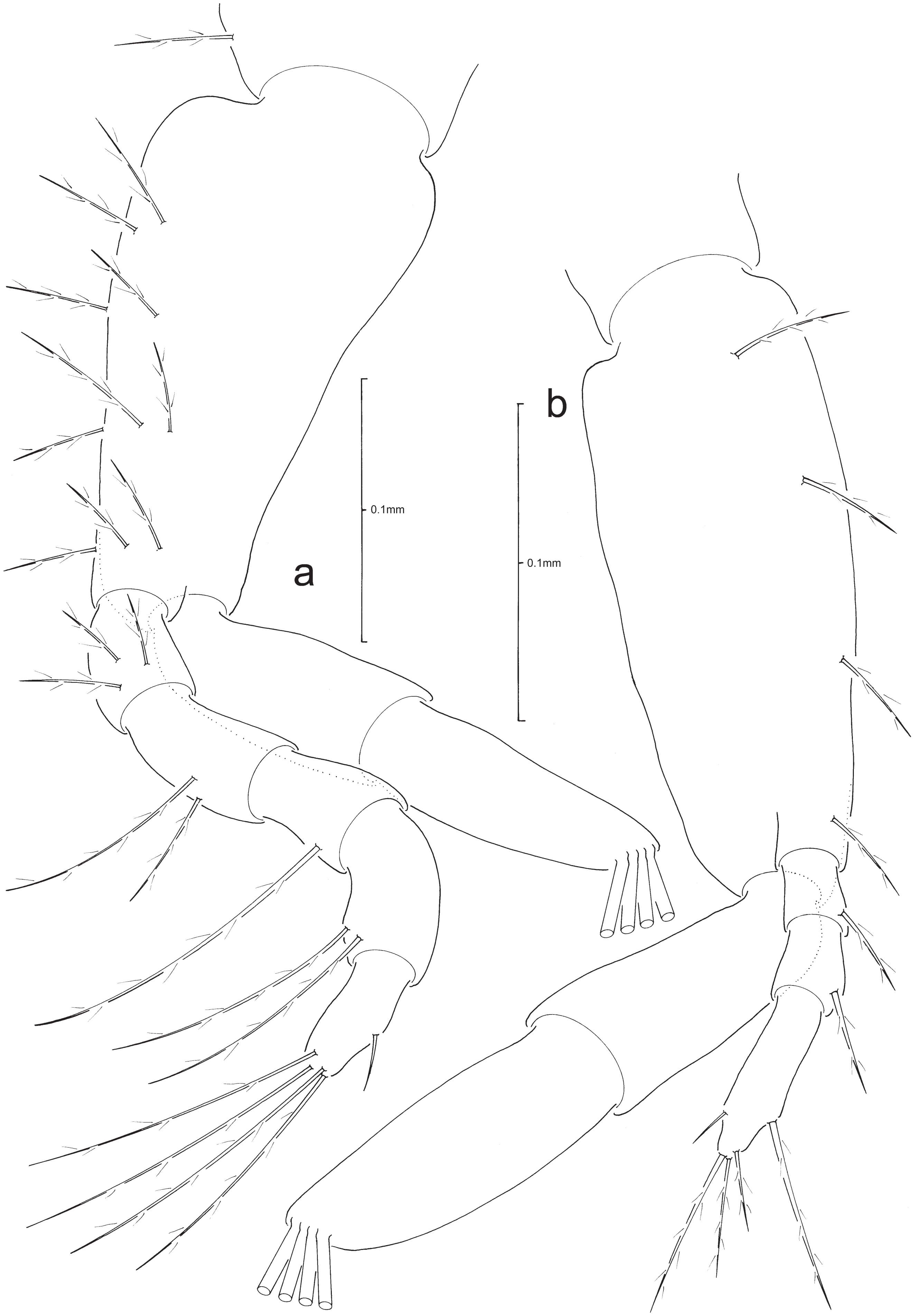

Fig. 131. *Hexapanopeus paulensis* Rathbun, 1930, ZI: a, first maxilliped; b, second maxilliped.

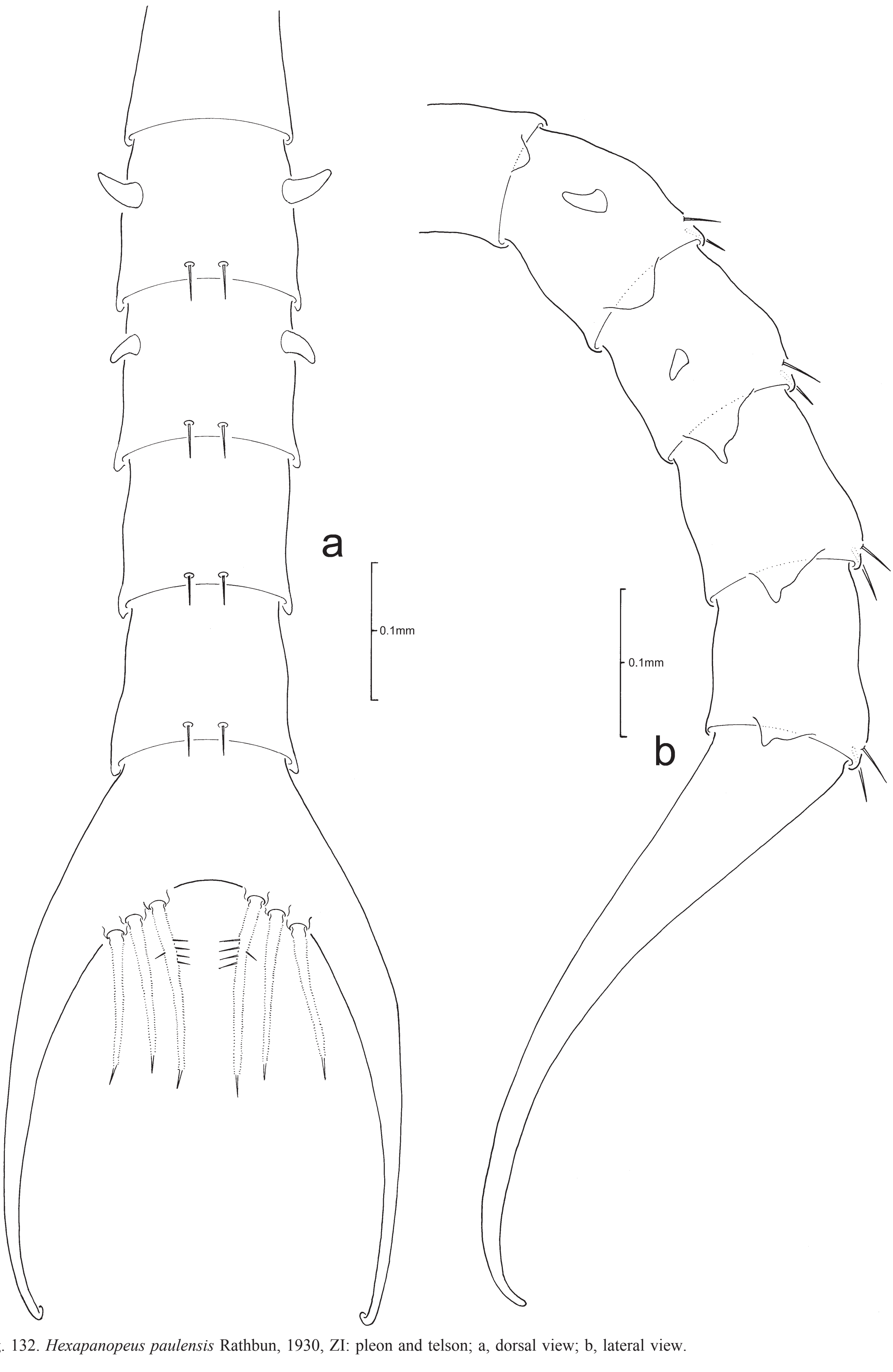

Fig. 132. *Hexapanopeus paulensis* Rathbun, 1930, ZI: pleon and telson; a, dorsal view; b, lateral view.

Panopeus americanus **de Saussure, 1857**
(Figs. 133–136)

Panopeus americanus. Negreiros-Fransozo, 1986: 174–184, figs. 1–9 (ZI–IV, Meg.).

Description of Zoea I.
CARAPACE (Fig. 133a): dorsal spine relatively long, curved distally, longer than rostral spine length; rostral spine just shorter than antennal protopod length, without distal spinulation; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 133a): sessile.
Antennule (Fig. 133b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 133c): uniramous; protopodal process distally multispinulate, just longer than rostral spine length; endopod absent; exopod ca. 12% length of protopod, with 1 terminal seta.
Mandible: palp absent.
Maxillule (Fig. 134a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 134b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 135a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 135b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 136a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 134c, 136a, b): each fork long, gradually curved distally, not spinulate, 1 small spine, 1 finer lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Table 19. A comparison between the ZI of *Panopeus americanus* de Saussure, 1857 by Negreiros-Fransozo (1986) and the present study.

Character	Negreiros-Fransozo (1986)	Present study
CARAPACE	fig. 1I	Fig. 133a
posterodorsal setae	absent	1 pair present
ANTENNULE	fig. 3AI	Fig. 133b
terminal setation	3 aesthetascs, 1 seta	4 (2 broad, 2 slender) aesthetascs of unequal length, 1 seta
MAXILLULE	fig. 4BI	Fig. 134a
coxal setation	6	7
MAXILLA	fig. 5AI	Fig. 134b
coxal endite setation	3+2	4+4
basial endite setation	3+3	5+4
FIRST MAXILLIPED	fig. 5BI	Fig. 135a
coxal seta	absent	present
PLEON	fig. 2I	Fig. 136a, b
pleomeres 2–5; setation	absent	each with 1 pair of posterodorsal setae
TELSON	fig. 2I	Figs. 134c, 136a, b
fork spination	1 fine spine	1 small and 1 finer lateral spine

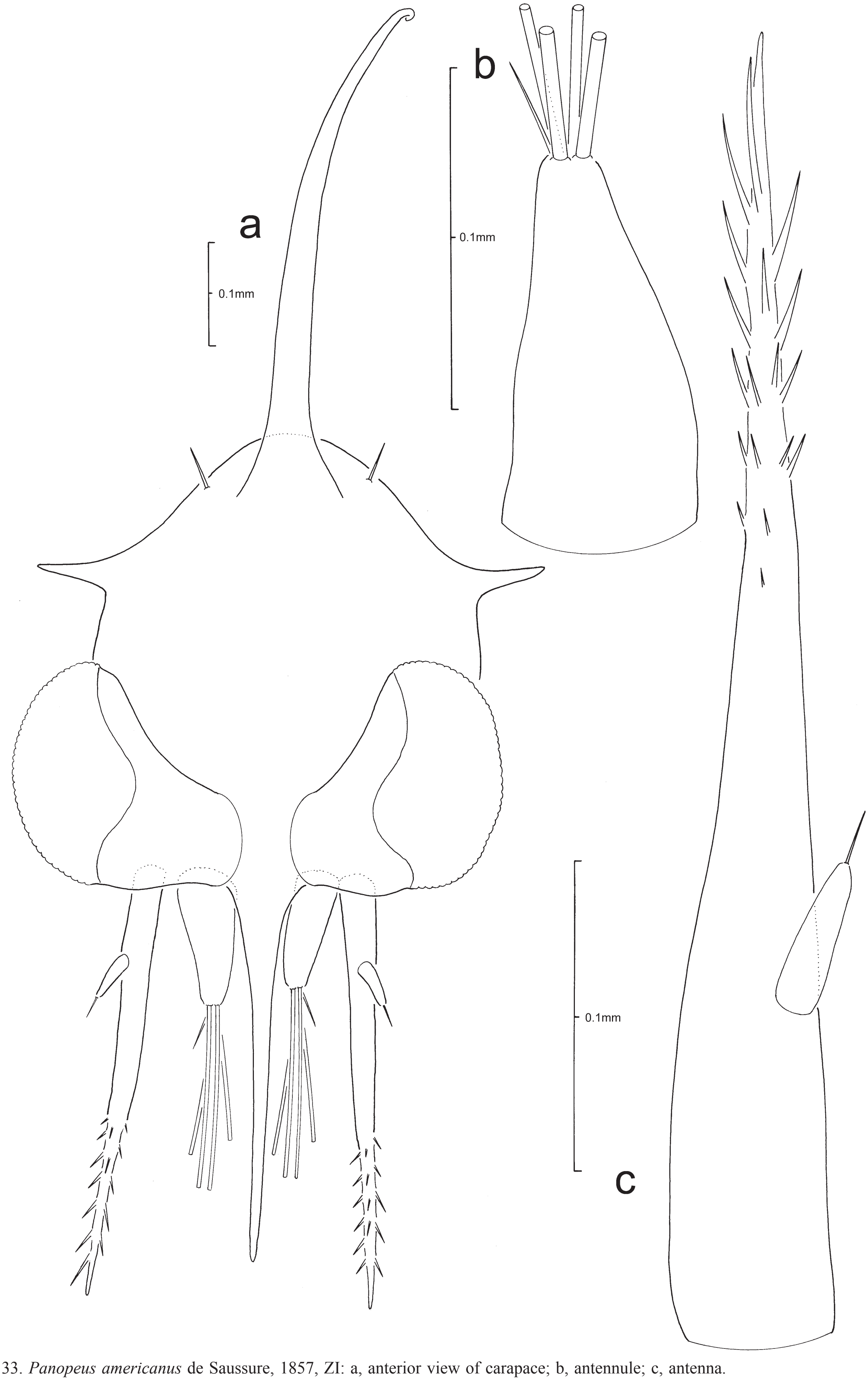

Fig. 133. *Panopeus americanus* de Saussure, 1857, ZI: a, anterior view of carapace; b, antennule; c, antenna.

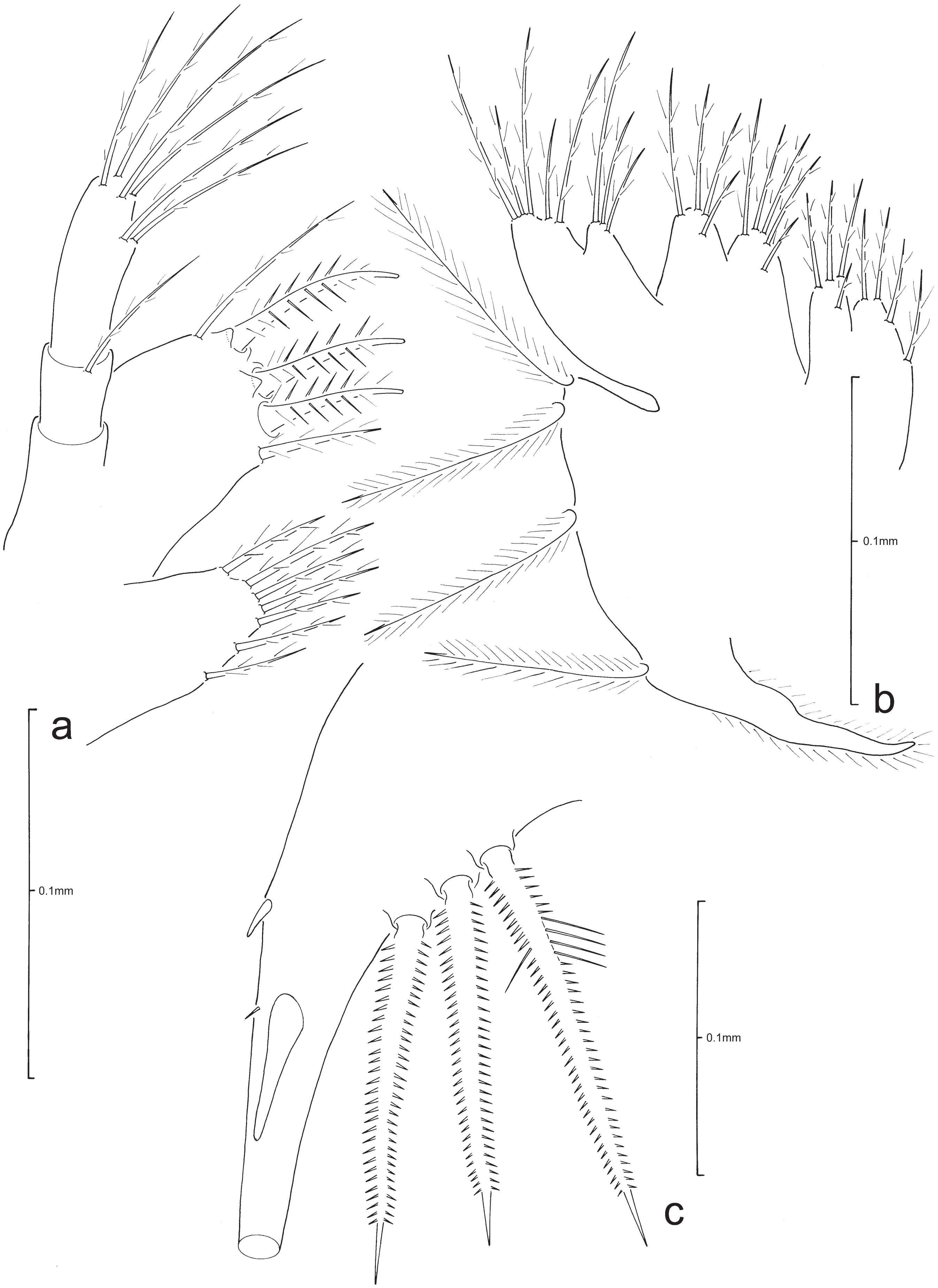

Fig. 134. *Panopeus americanus* de Saussure, 1857, ZI: a, maxillule; b, maxilla; c, telson.

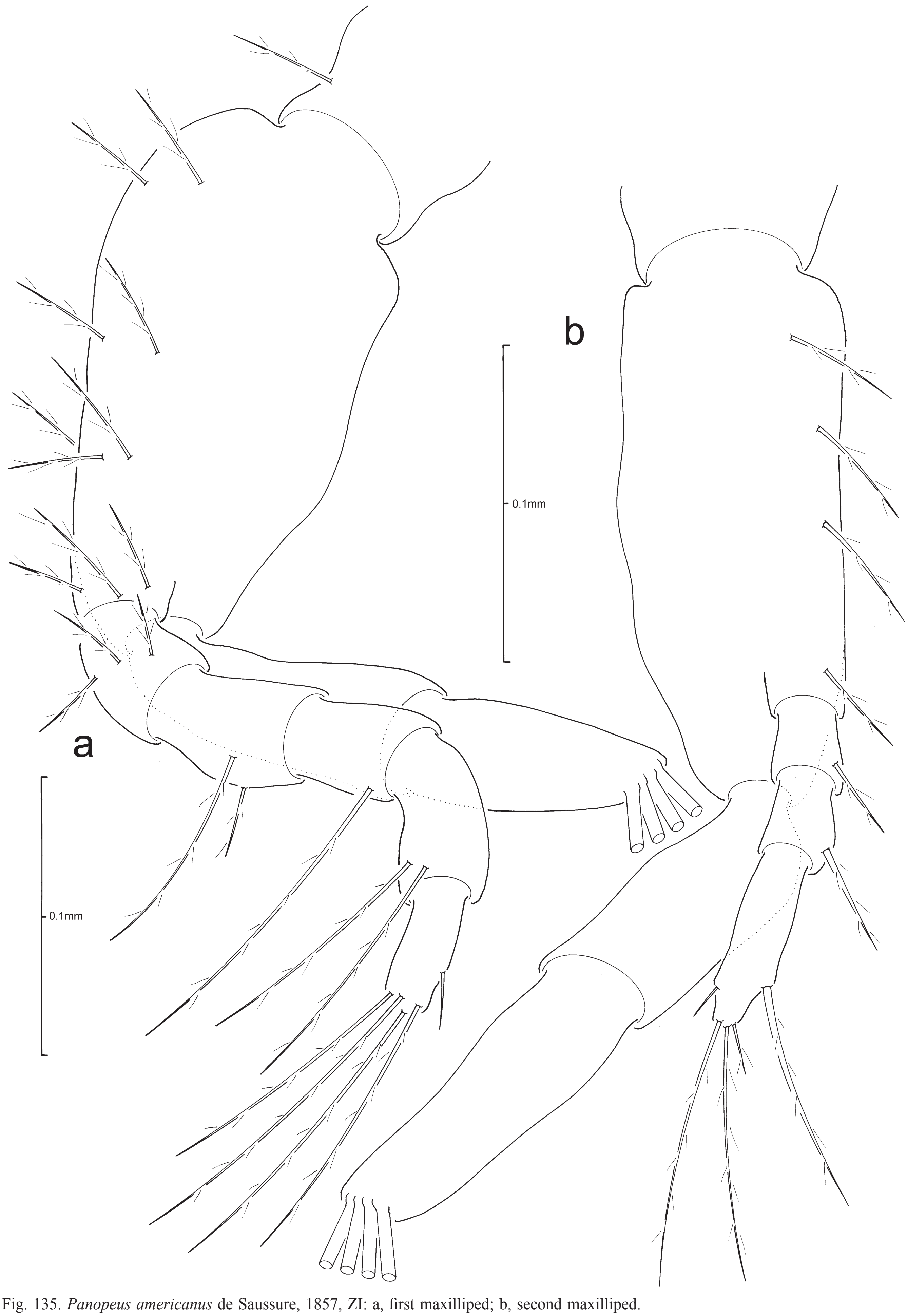

Fig. 135. *Panopeus americanus* de Saussure, 1857, ZI: a, first maxilliped; b, second maxilliped.

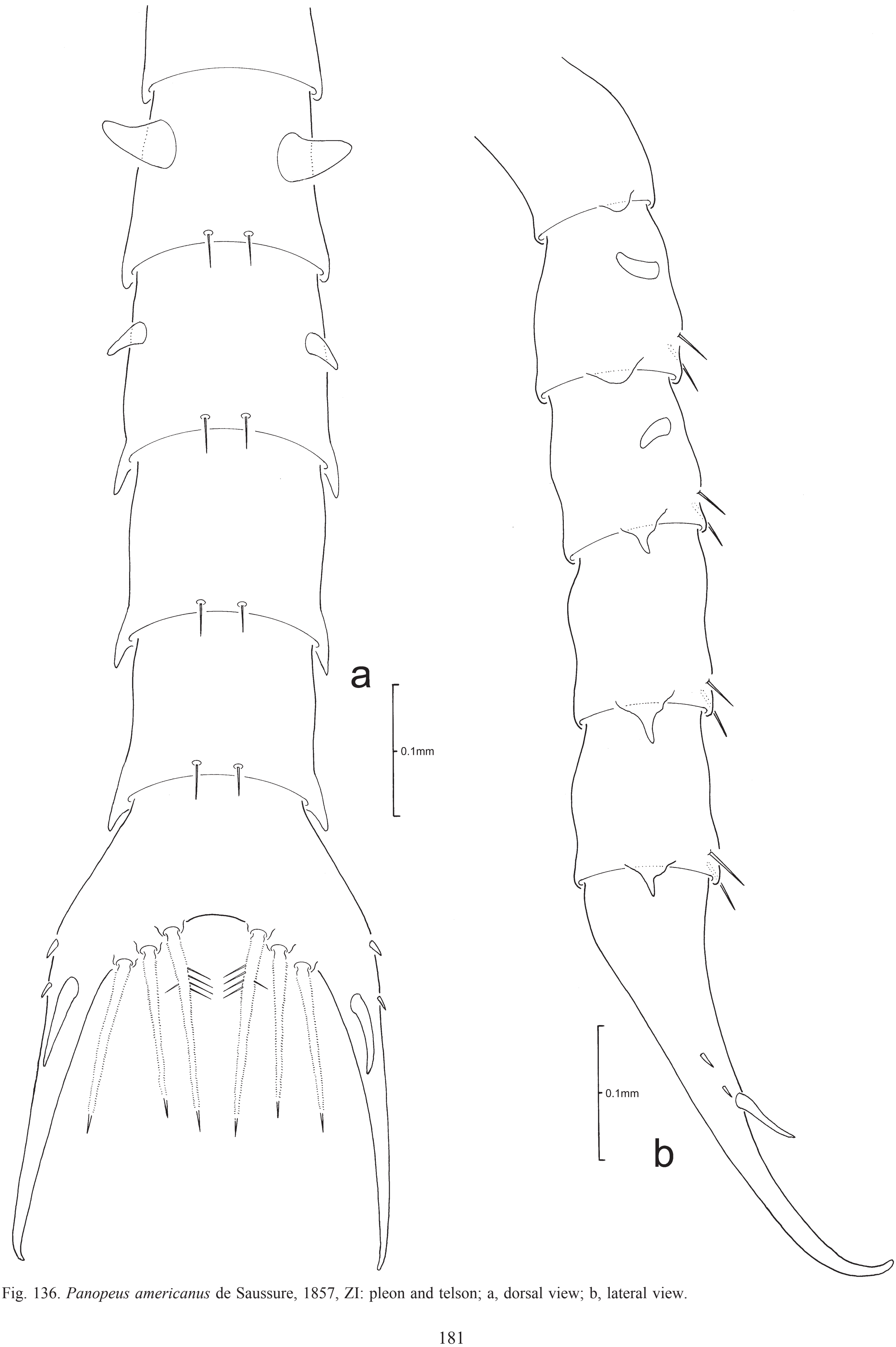

Fig. 136. *Panopeus americanus* de Saussure, 1857, ZI: pleon and telson; a, dorsal view; b, lateral view.

***Panopeus harttii* Smith, 1869**
(Figs. 137–140)

Description of Zoea I.
CARAPACE (Fig. 137a): dorsal spine long, curved distally, just longer than rostral spine length; rostral spine just shorter than antennal protopod length, without distal spinulation; lateral spines without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 137a): sessile.
Antennule (Fig. 137b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 137c): uniramous; protopodal process without distal spinulation, just longer than rostral spine length, tip blunt; endopod absent; exopod ca. 4% length of protopod, with 1 terminal seta.
Mandible: palp absent.
Maxillule (Fig. 138a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 138b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 139a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 139b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 140a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 138c, 140a, b): each fork long, gradually curved distally, not spinulate, 1 minute lateral spine only, 1 small dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

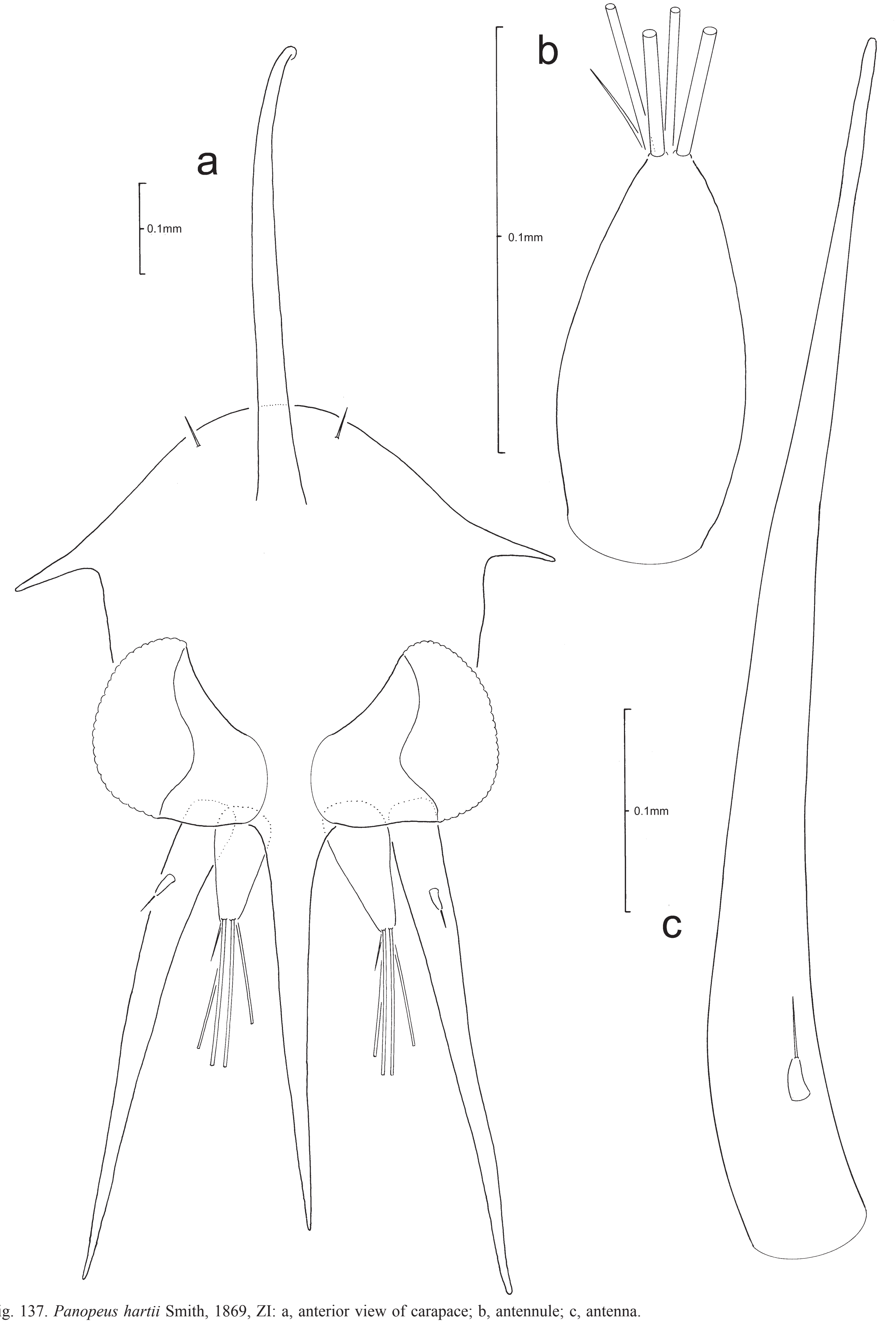

Fig. 137. *Panopeus hartii* Smith, 1869, ZI: a, anterior view of carapace; b, antennule; c, antenna.

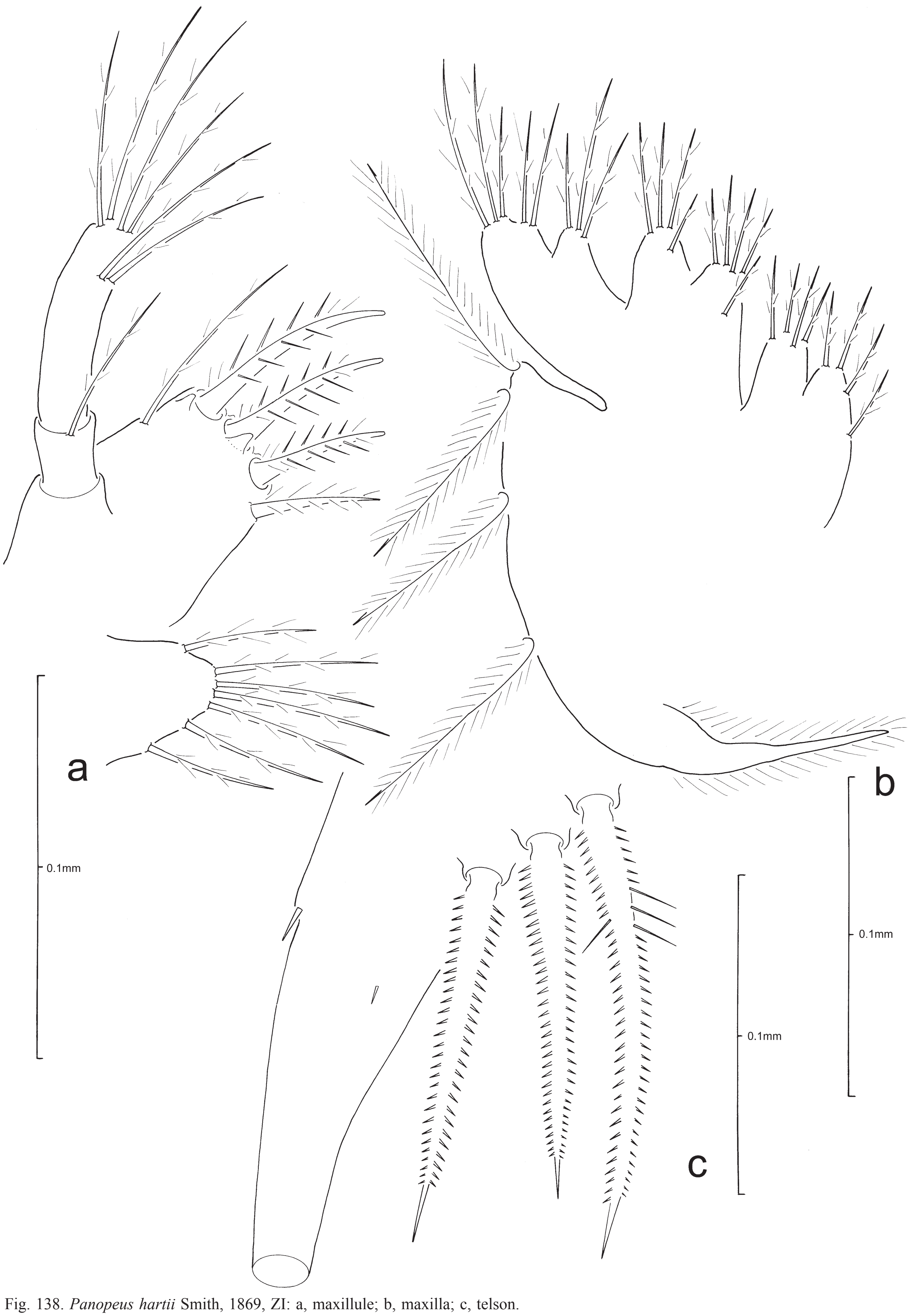

Fig. 138. *Panopeus hartii* Smith, 1869, ZI: a, maxillule; b, maxilla; c, telson.

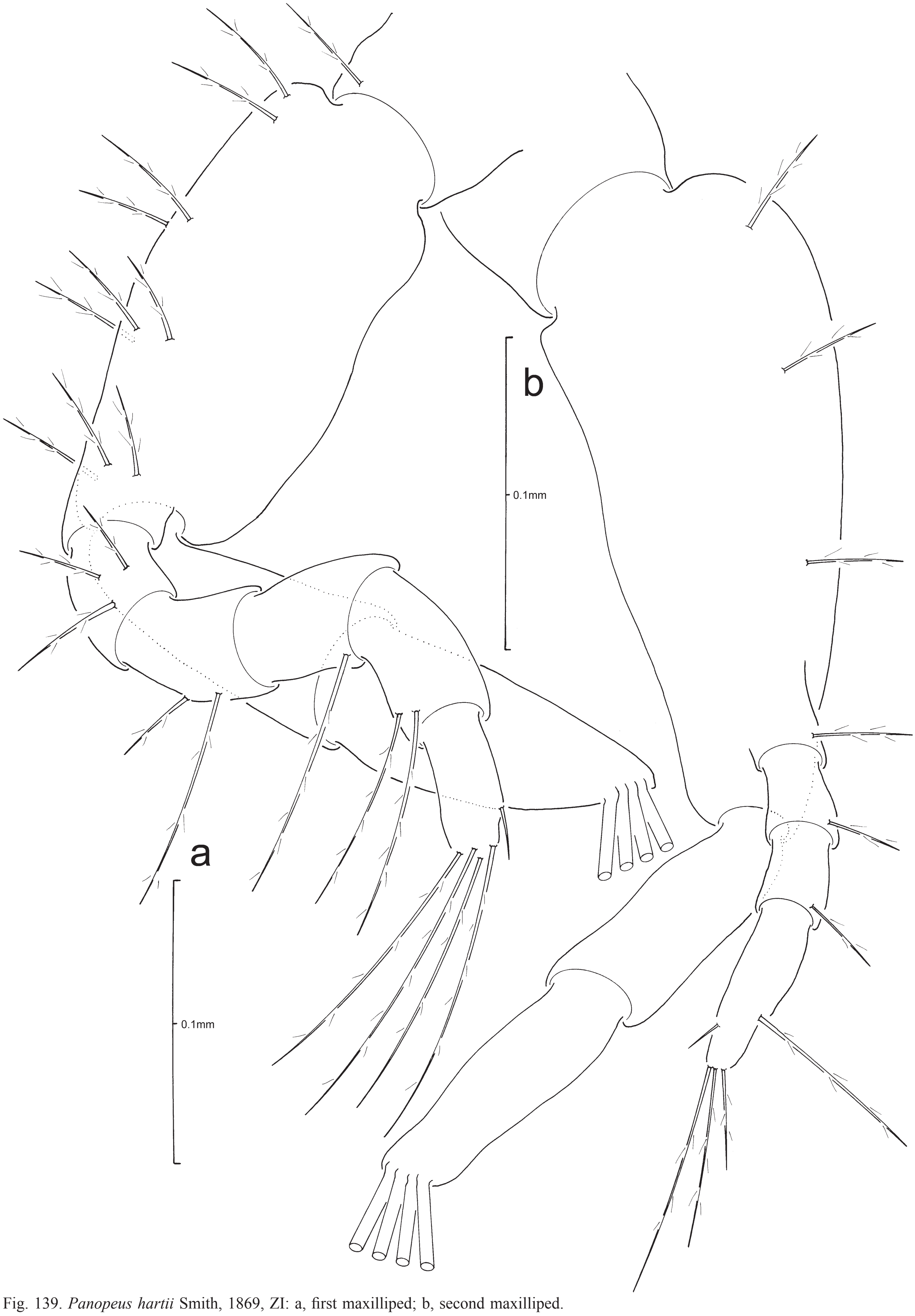

Fig. 139. *Panopeus hartii* Smith, 1869, ZI: a, first maxilliped; b, second maxilliped.

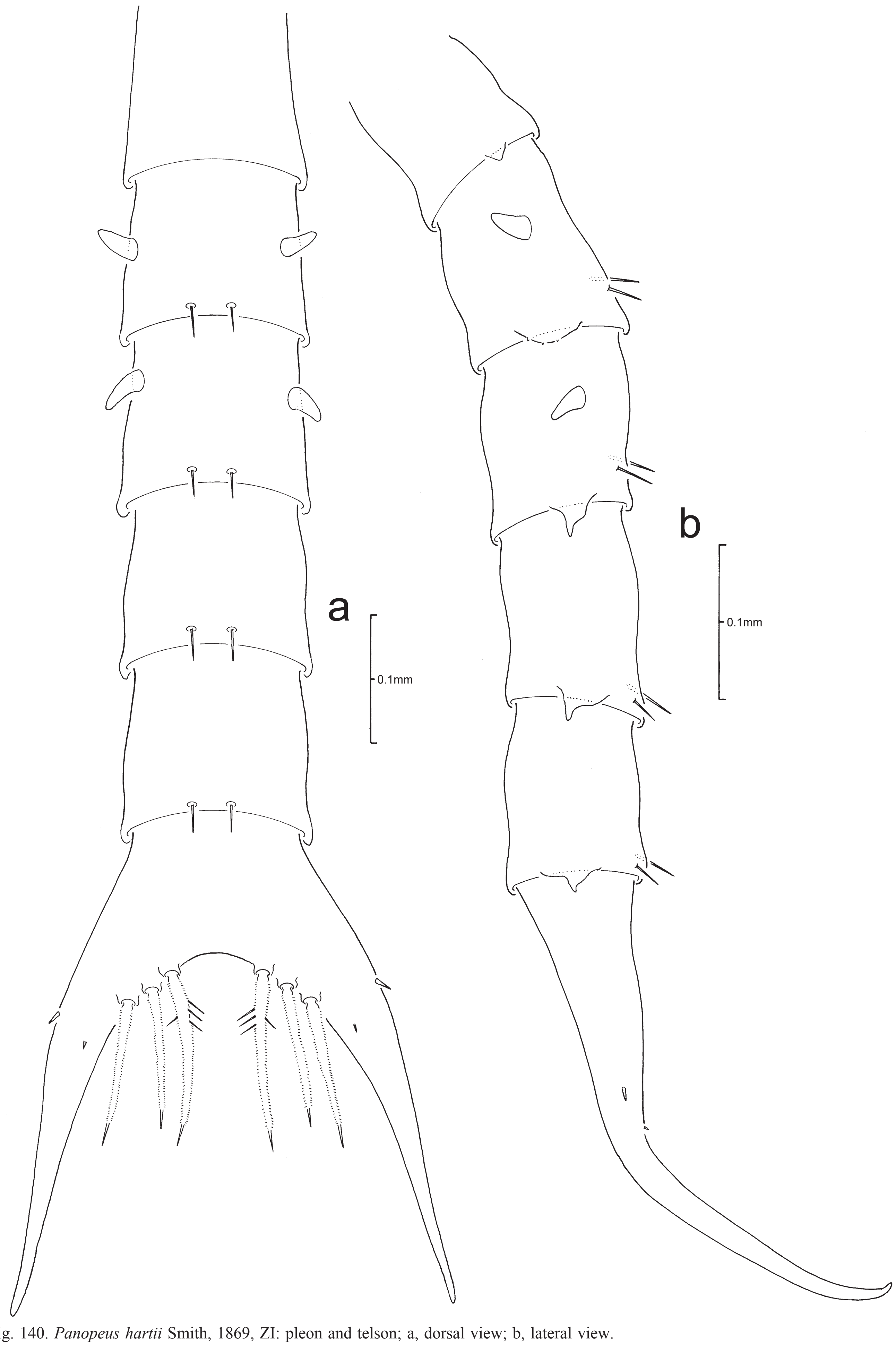

Fig. 140. *Panopeus hartii* Smith, 1869, ZI: pleon and telson; a, dorsal view; b, lateral view.

Panopeus occidentalis de Saussure, 1857
(Figs. 141–144)

Panopeus occidentalis. Kurata, 1970: 222–225, pls. 84–85 (ZI–IV, Meg., Cr. I); Ingle, 1985: 234–243, figs. 1–7, tabs. 1–2 (ZI–IV, Meg.).

Description of Zoea I.
CARAPACE (Fig. 141a): dorsal spine long, distally curved, longer than rostral spine length; rostral spine straight, slightly shorter than antennal protopod length, without distal spinulation; lateral spines without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 141a): sessile.
Antennule (Fig. 141b): primary flagellum unsegmented with 4 (2 broad, 2 slender) aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 141c): uniramous; protopod distally multispinulate, slightly longer than rostral spine length; endopod absent; exopod ca. 7% length of protopod with 1 terminal seta.
Mandible: palp absent
Maxillule (Fig. 142a): uniramous; epipod seta absent; coxal endite with 7 terminal setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta, distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 142b): uniramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 plumose setae + distal stout process.

PEREION
First maxilliped (Fig. 143a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 terminal natatory plumose setae.
Second maxilliped (Fig. 143b): biramous; coxa without seta; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 terminal natatory plumose setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 144a, b): 5 pleomeres; pleomere 2 with pair of lateral processes directed laterally; pleomere 3 with pair of lateral processes directed posteriorly; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 with posterolateral spinous processes; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopods absent.

TELSON (Figs. 142c, 144a, b): each fork long, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Table 20. A comparison between the ZI of *Panopeus occidentalis* de Saussure, 1857 by Kurata (1970), Ingle (1985), and the present study.

Character	**Kurata (1970)**	**Ingle (1985)**	**Present study**
CARAPACE	pl. 84A	fig. 1a	Fig. 141a
posterodorsal setae	absent	1 pair present	1 pair present
ANTENNULE	pl. 84A	fig. 1e	Fig. 141b
terminal setation	2 aesthetascs, 1 seta?	4 aesthetascs of equal length, 1 seta	4 (2 broad, 3 slender) aesthetascs of unequal length, 1 seta
ANTENNA	pl. 84G	fig. 4f	Fig. 141c
exopod setation	1	2	1
FIRST MAXILLIPED	pl. 84A	fig. 1.7	Fig. 143a
coxal seta	not figured	not figured	present
endopod setation	2,2,1,2,5 (1 subterminal+4 terminal)	5,2,1,2,5 (1 subterminal+4 terminal)	2,2,1,2,5 (1 subterminal+4 terminal)
SECOND MAXILLIPED	pl. 84A	fig. 1.8	Fig. 143b
endopod setation	0,1,3	1,1,5 (2 subterminal+3 terminal)	1,1,5 (2 subterminal+3 terminal)
TELSON	pl. 84B	figs. 2a, 3a	Figs. 142c, 144a, b
fork spination	absent	1 large and 1 smaller lateral spine + 1 large dorsomedial spine	1 large and 1 smaller lateral spine + 1 large dorsomedial spine

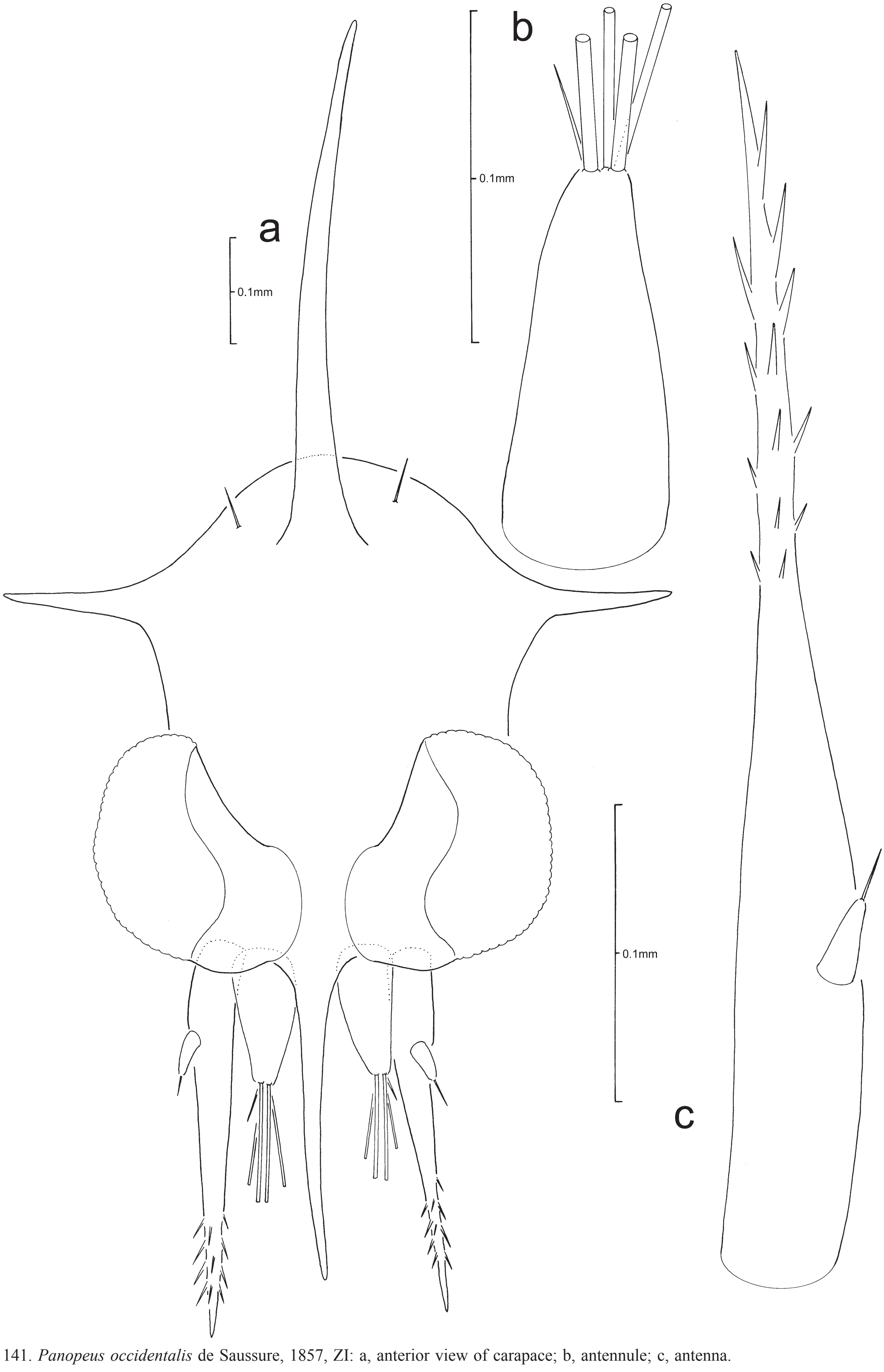

Fig. 141. *Panopeus occidentalis* de Saussure, 1857, ZI: a, anterior view of carapace; b, antennule; c, antenna.

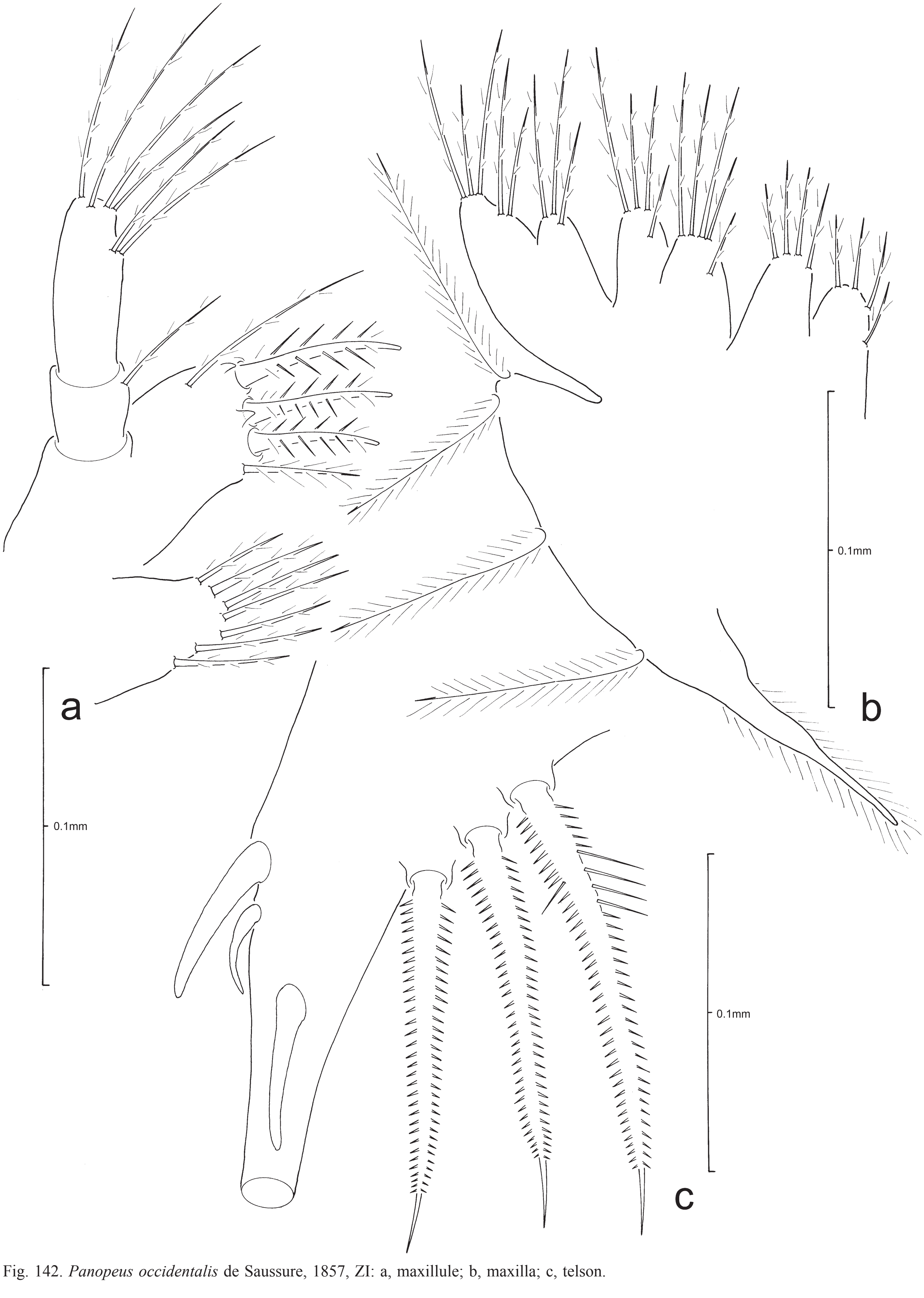

Fig. 142. *Panopeus occidentalis* de Saussure, 1857, ZI: a, maxillule; b, maxilla; c, telson.

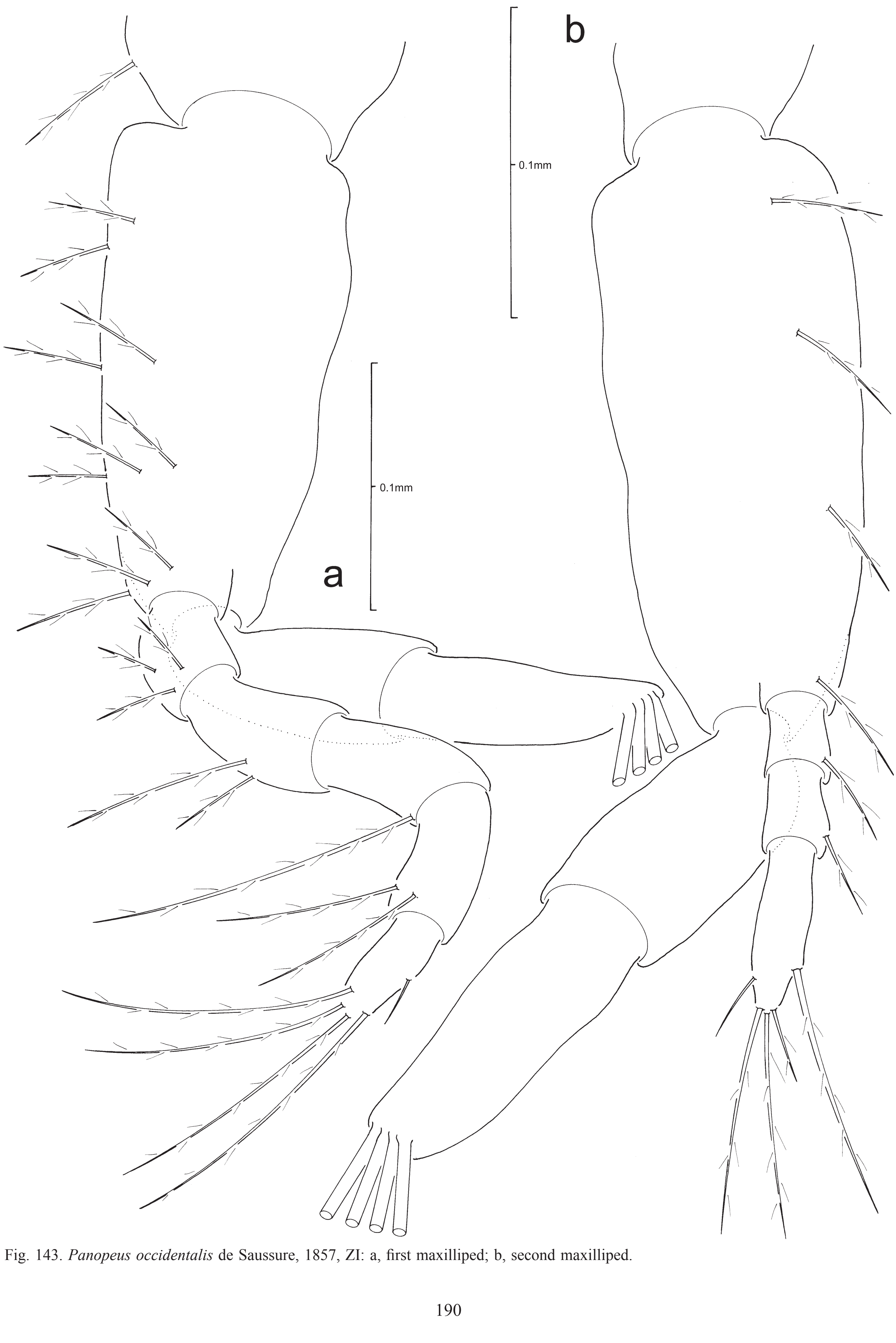

Fig. 143. *Panopeus occidentalis* de Saussure, 1857, ZI: a, first maxilliped; b, second maxilliped.

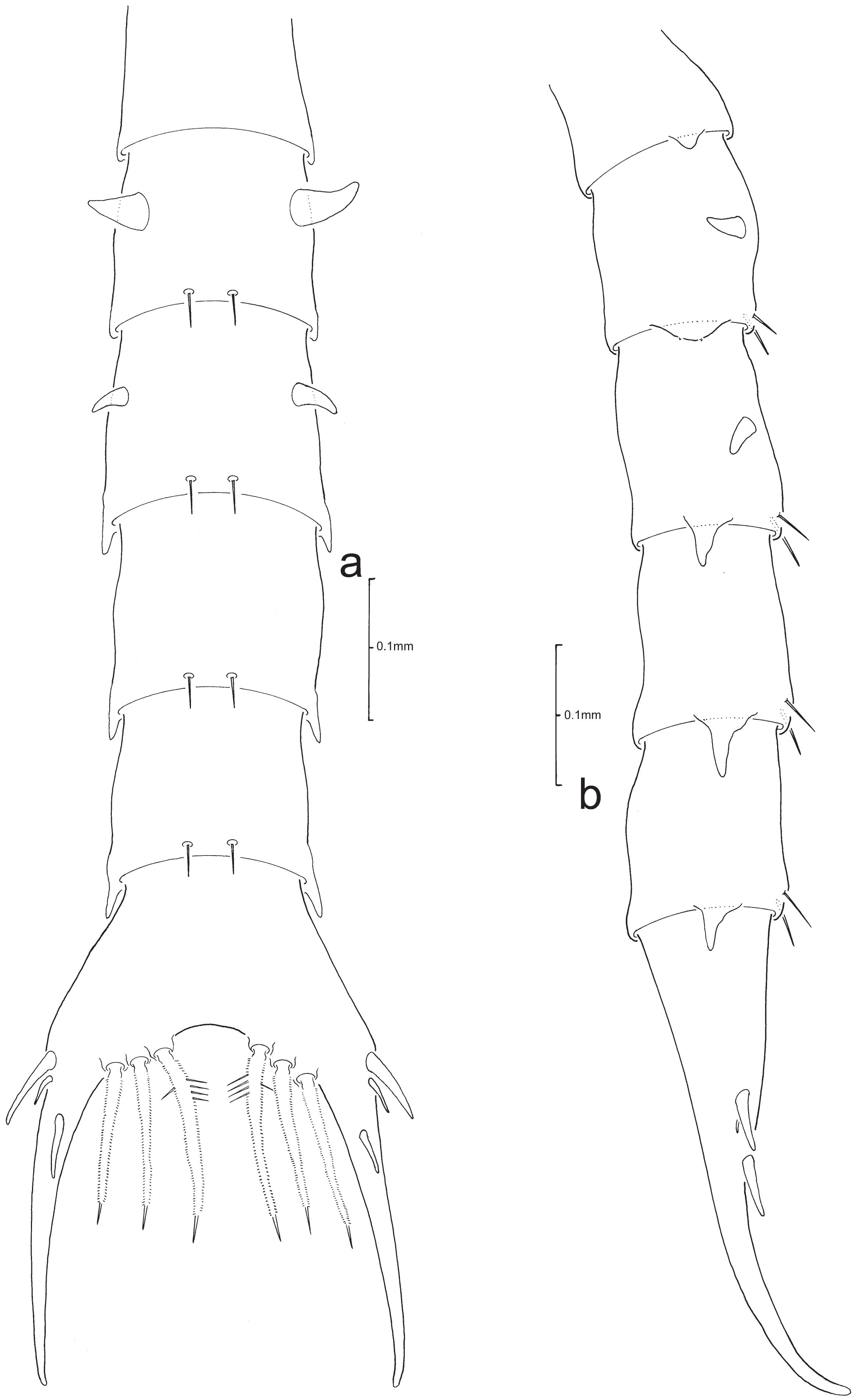

Fig. 144. *Panopeus occidentalis* de Saussure, 1857, ZI: pleon and telson; a, dorsal view; b, lateral view.

Panopeus simpsoni **Rathbun, 1930**
(Figs. 145–148)

Description of Zoea I.
CARAPACE (Fig. 145a): dorsal spine long, curved distally, longer than rostral spine length; rostral spine shorter than antennal protopod length, without distal spinulation; lateral spines without spinulation on distal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 145a): sessile.
Antennule (Fig. 145b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta accessory flagellum absent.
Antenna (Fig. 145c): uniramous; protopodal process distally multispinulate, longer than rostral spine; endopod absent; exopod ca. 6% length of protopod, with 1 terminal seta.
Mandible: palp absent.
Maxillule (Fig. 146a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 146b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 147a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 147b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 148a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 146c, 148a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 slightly smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

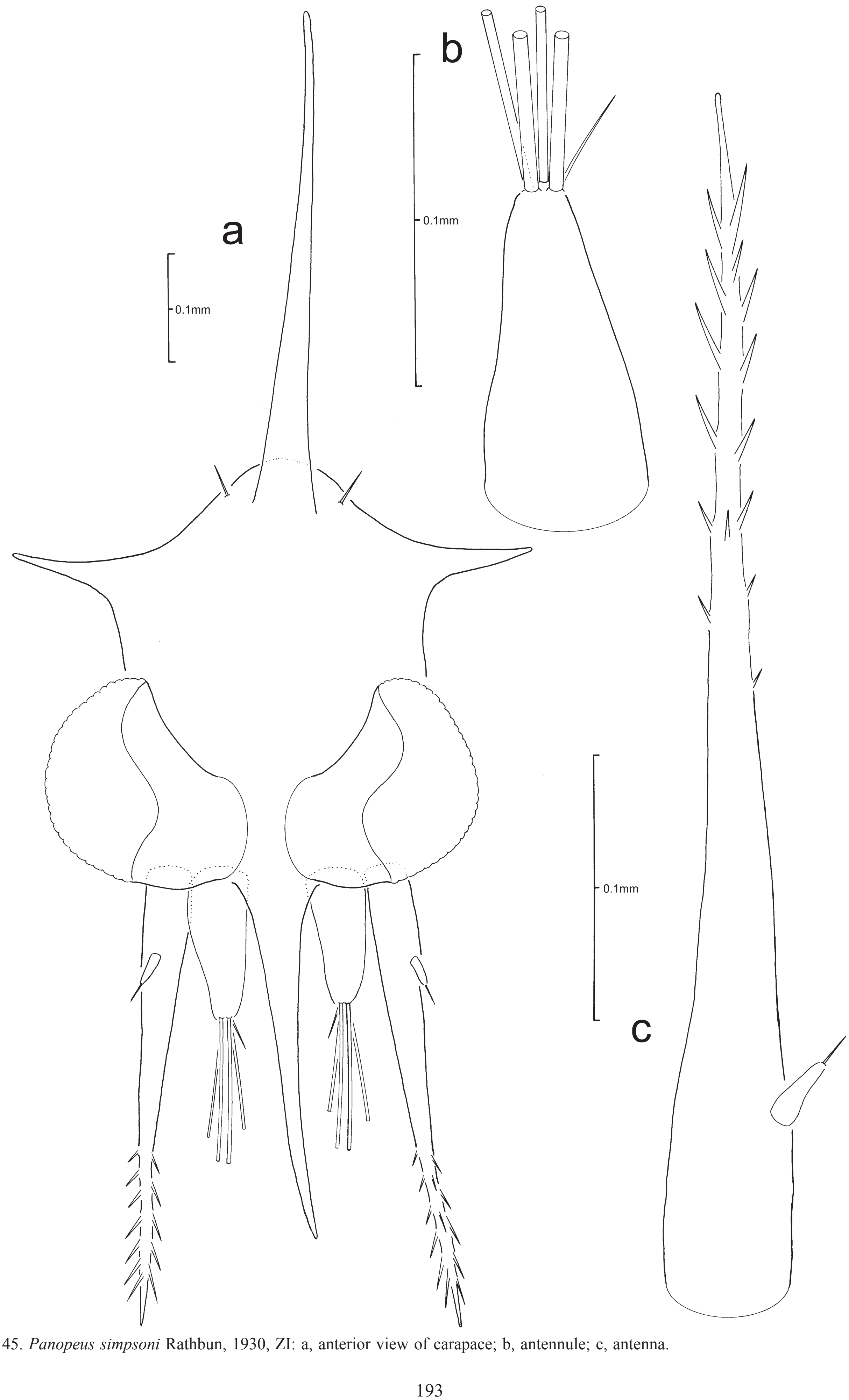

Fig. 145. *Panopeus simpsoni* Rathbun, 1930, ZI: a, anterior view of carapace; b, antennule; c, antenna.

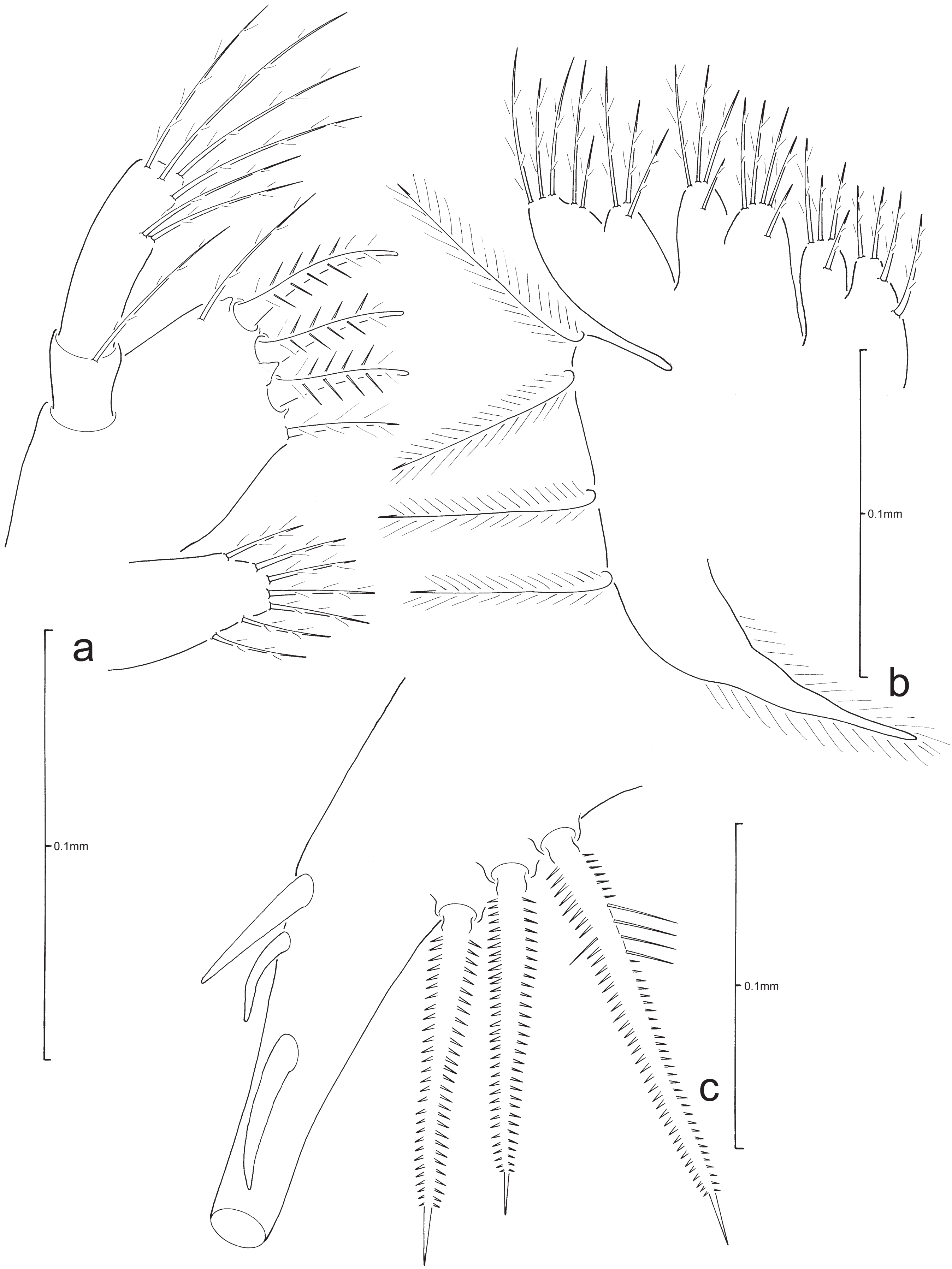

Fig. 146. *Panopeus simpsoni* Rathbun, 1930, ZI: a, maxillule; b, maxilla; c, telson.

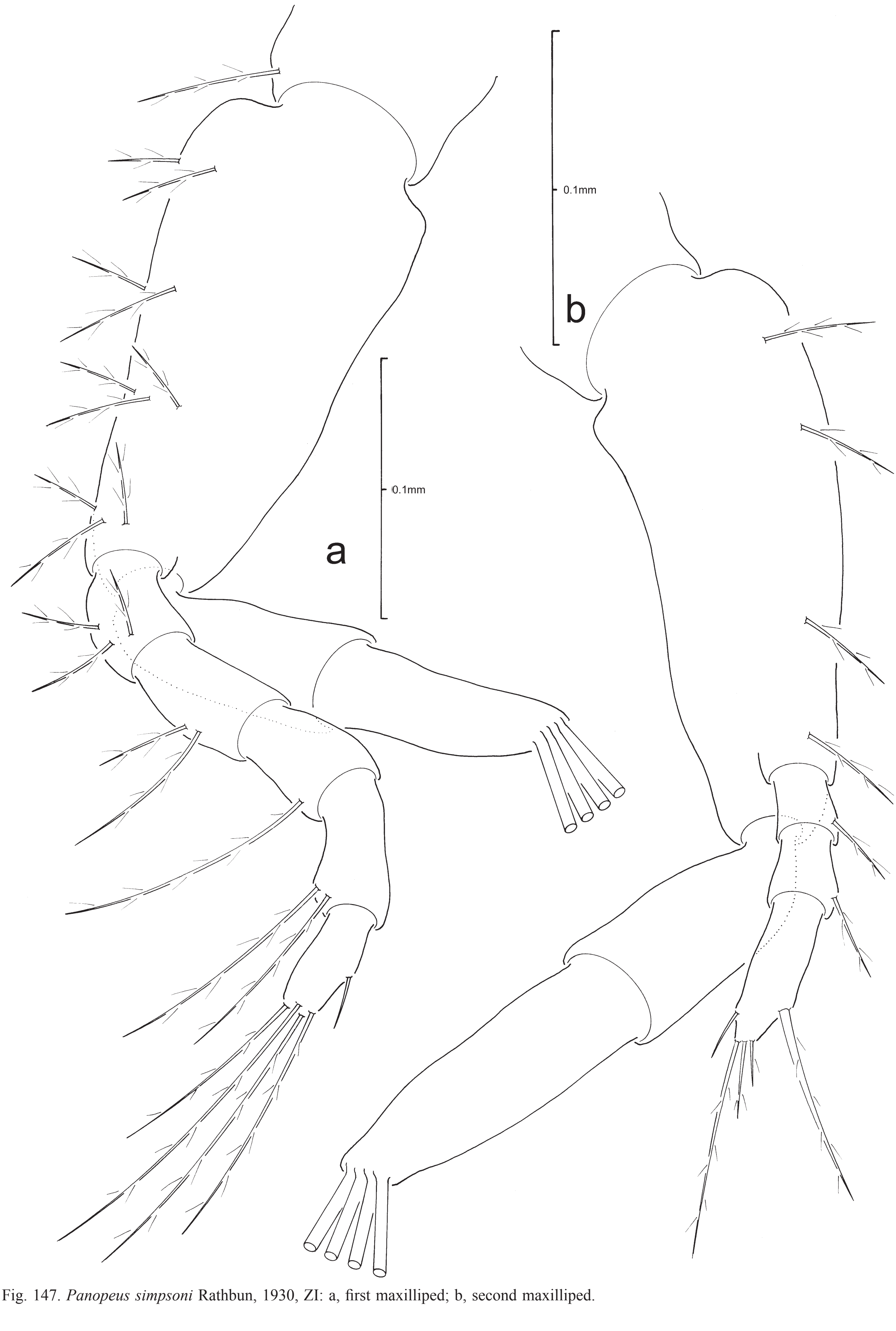

Fig. 147. *Panopeus simpsoni* Rathbun, 1930, ZI: a, first maxilliped; b, second maxilliped.

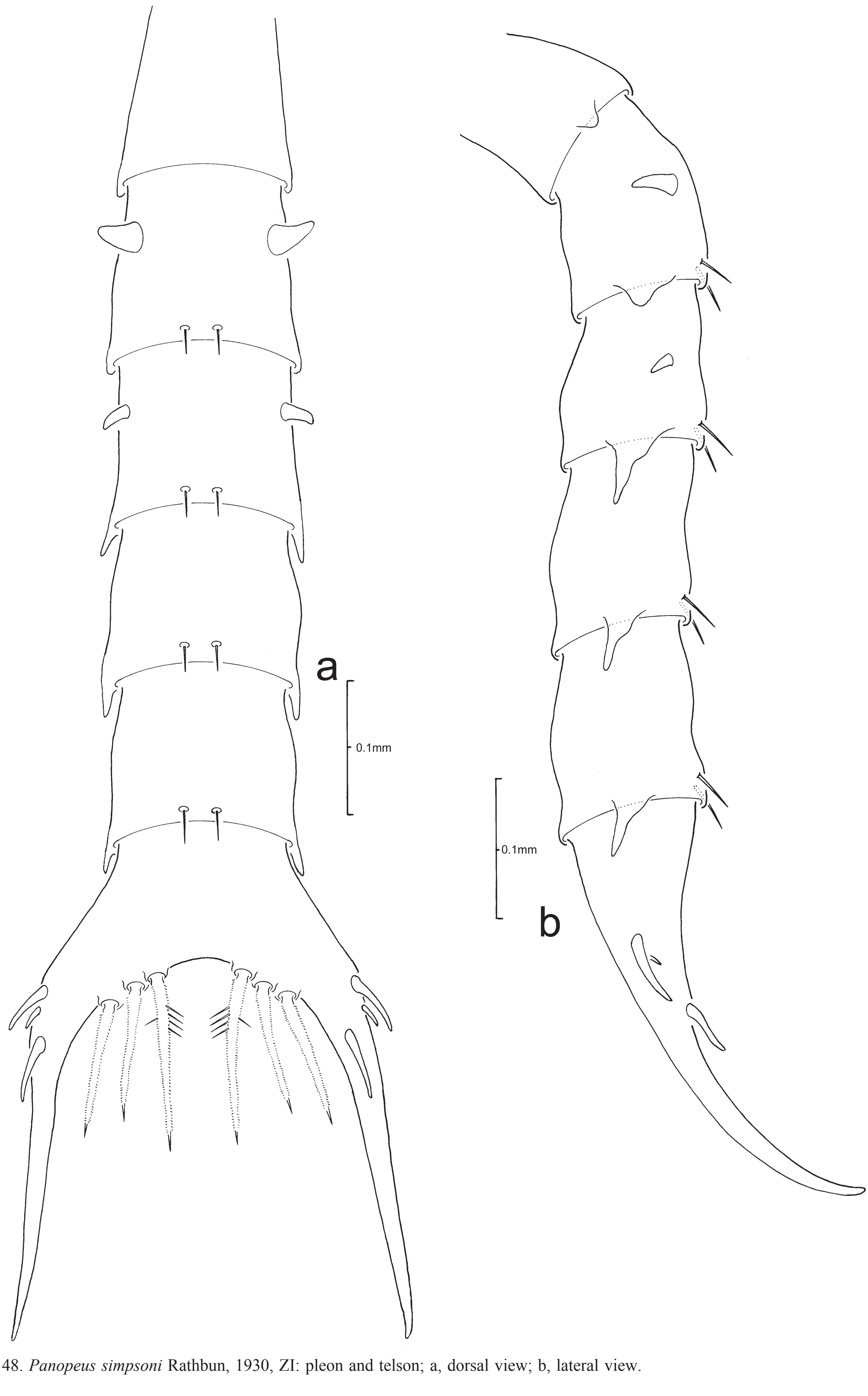

Fig. 148. *Panopeus simpsoni* Rathbun, 1930, ZI: pleon and telson; a, dorsal view; b, lateral view.

***Rhithropanopeus harrisii* (Gould, 1841)**
(Figs. 149–152)

Heteropanope tridentata. Tesch, 1922: 348–362, figs. 1–19 (PZ, ZI–IV, Meg., Cr. I).
Rhithropanopeus harrisi. Connolly, 1925: 4–6, pls. 1–3 (ZI–IV, Meg.).
Rhithropanopeus harrisii. Chamberlain, 1962: 4–11, fig. 1 (ZI–IV, Meg.); Hood, 1962: 126–129, pls. 1–3 (ZI–IV, Meg.); Kurata, 1970: 212–214, pls. 75–76 (ZI–IV, Meg.); Roff et al., 1984: 20, 39, figs. 51, 52, 128 (ZIII–IV, Meg.); Ingle, 1991: 239–241, fig. 2.33 (ZI–IV, Meg.).
Rhithropanopeus harrisi tridentatus. Ławiński & Pautsch, 1969: 495–504, pls. I–IV (ZI–IV, Meg., Cr. I); Phan, 1972: 39, fig. 1 (ZI–IV).
Rhithropanopeus harrisii tridentatus. Băcescu, 1952: 573, fig. 4 (ZI).

Description of Zoea I.
CARAPACE (Fig. 149a): dorsal spine long, curved distally, ca. half rostral spine length; rostral spine extremely long, equal in length to antennal protopod length, without distal spinulation; lateral spines present, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 149a): sessile.
Antennule (Fig. 149b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 149c): uniramous; protopodal process extremely long, without distal spinulation, equal in length to rostral spine, tip blunt; endopod absent; exopod minute, ca. 0.7% length of protopod, with 1 terminal seta.
Mandible: palp absent.
Maxillule (Fig. 150a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 150b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 151a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 151b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 152a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomeres 1–4 each with rounded posterolateral processes; pleomere 5 with an elongated posterolateral process; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 150c, 152a, b): each fork long, gradually curved distally, not spinulate, lateral spines absent, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Table 21. A comparison between the ZI of *Rhithropanopeus harrisii* (Gould, 1841) by Tesch (1922), Connolly (1925), Băcescu (1952), Chamberlain (1962), Hood (1962), Kurata (1970), Phan (1972), Ingle (1991), and the present study.

Character	Tesch (1922)	Connolly (1925)	Băcescu (1952)	Chamberlain (1962)	Hood (1962)	Kurata (1970)	Phan (1972)	Ingle (1991)	Present study
CARAPACE	fig. 9	pl. 1, fig. 1	fig. 4A, B	text p. 4	pl. I, fig. 1	pl. 75A	fig. 1A	fig. 2.33a	Fig. 149a
posterodorsal setae	absent	absent	absent	not described	absent	absent	absent	absent	1 pair present
ANTENNULE	fig. 9	pl. 1, fig. 1	fig. 4A, B	text p. 4	text p. 126	pl. 75a	fig. 1A	fig. 2.33a	Fig. 149b
terminal setation	4 (2 broad, 2 slender) terminal aesthetascs of unequal lengths	text: 2 aesthetascs, 3 small hairs fig.: 2 aesthetascs	2 aesthetascs	4 or 5 setae	3–4 long hairs	2 long, aesthetascs, 1 shorter aesthetasc ?	2 aesthetascs ?	text: 5 aesthetascs fig.: 2 aesthetascs	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal seta
ANTENNA	fig. 9	not figured, text p. 4	fig. 4A, B	not figured, text p. 4	not figured	not figured, text p. 213	fig. 1A	not figured, text p. 239	Fig. 149c
exopod	not figured	small needle-like spine	absent	small dorsal seta	not described or figured	rudimentary exopod with terminal hair	absent	minute and spinous	exopod minute ca. 0.7% length of protopod, with 1 terminal seta
MAXILLULE	fig. 10	not figured	not figured	not figured, text p. 4	not figured	not figured	not figured	not figured, text p. 239	Fig. 150a
coxal endite setation	7	not described		5 or 6	not described	not described		7	7
basial endite	5 setal processes	not described		5 setae	not described	not described		5 setae	5 setal processes
endopod, setation of proximal article	absent	not described		1	not described	not described		absent?	1
MAXILLA	fig. 10	not figured	not figured	not figured, text p. 6	not figured	not figured	fig. Mx II	not figured, text p. 240	Fig. 150b
coxal endite setation	text: 2+3 fig.: 4+3	not described		6–8	not described	not described	2+4?	3+2	4+4
basial endite setation	text: 3–4+4 fig.: 4+3	not described		7 or 8	not described	not described	2+4?	3+3–4	5+4

Character	Tesch (1922)	Connolly (1925)	Băcescu (1952)	Chamberlain (1962)	Hood (1962)	Kurata (1970)	Phan (1972)	Ingle (1991)	Present study
endopod setation	3+5 (2 subterminal, 3 terminal)	not described		7	not described	not described	0+5	3+5	3+5 (2 subterminal, 3 terminal)
exopod setation	3 setae and 1 long thin process	not described		5 setae	not described	not described	2 setae and 1 long distal stout process	3 setae and 1 long thin posterior process	4 setae and 1 long distal stout process
FIRST MAXILLIPED	fig. 9	not figured	fig. 4B	not figured, text p. 6	pl. II, fig. 1	pl. 75A	fig. 1 Mxp I	text p. 240	Fig. 151a
coxal seta	not figure	not described	not figured	not described	absent	not figured	not figured	not described	1
basial setation	3	not described	absent	9 or 10	4	0	3	not described	10 (2+2+3+3)
endopod setation	1,2,1,2,3/4 (?)	not described	not figured	2/3,2,1,2,4	1,1,2,2,3	2,2,1,2,5 (1 subterminal+4 terminal)	4 terminal setae	?2,2,1,2,?3–4+1	3,2,1,2,5 (1 subterminal+4 terminal)
SECOND MAXILLIPED	fig. 9	not figured	fig. 4B	not figured, text p. 6	pl. II, 2	pl. 75A	fig. 1 Mxp II	not figured, text p. 240	Fig. 151b
basial setation	1	not described	absent	4	4	0	3	?4	4 (1+1+1+1)
endopod setation	1,1,4 (2 subterminal+2 terminal)	not described	?,?,3	1,1,5	2,1,3	1,1,3	0,1,4?	1,1,?3+1	1,1,5 (2 subterminal+3 terminal)
PLEON	fig. 9	not figured	fig. 4B	not figured	pl. I, fig. 1	pl. 75A, B	fig. 1A	not figured	Fig. 152a, b
pleomeres 2–5; setation	absent	not described	absent	not described	absent	1 pair of posterodorsal setae on each pleomere	not figured	not described	1 pair of posterodorsal setae on each pleomere
TELSON	fig. 9	pl., figs. 1, 2	fig. 4A, B, C	not figured, text p. 6	pl. I, fig. 1	pl. 75A, B	fig. 1A, Б	fig. 2.33b	Figs. 150c, 152a, b
fork with 1 large dorsomedial spine	present	present	absent	present	present	present	absent	present	present

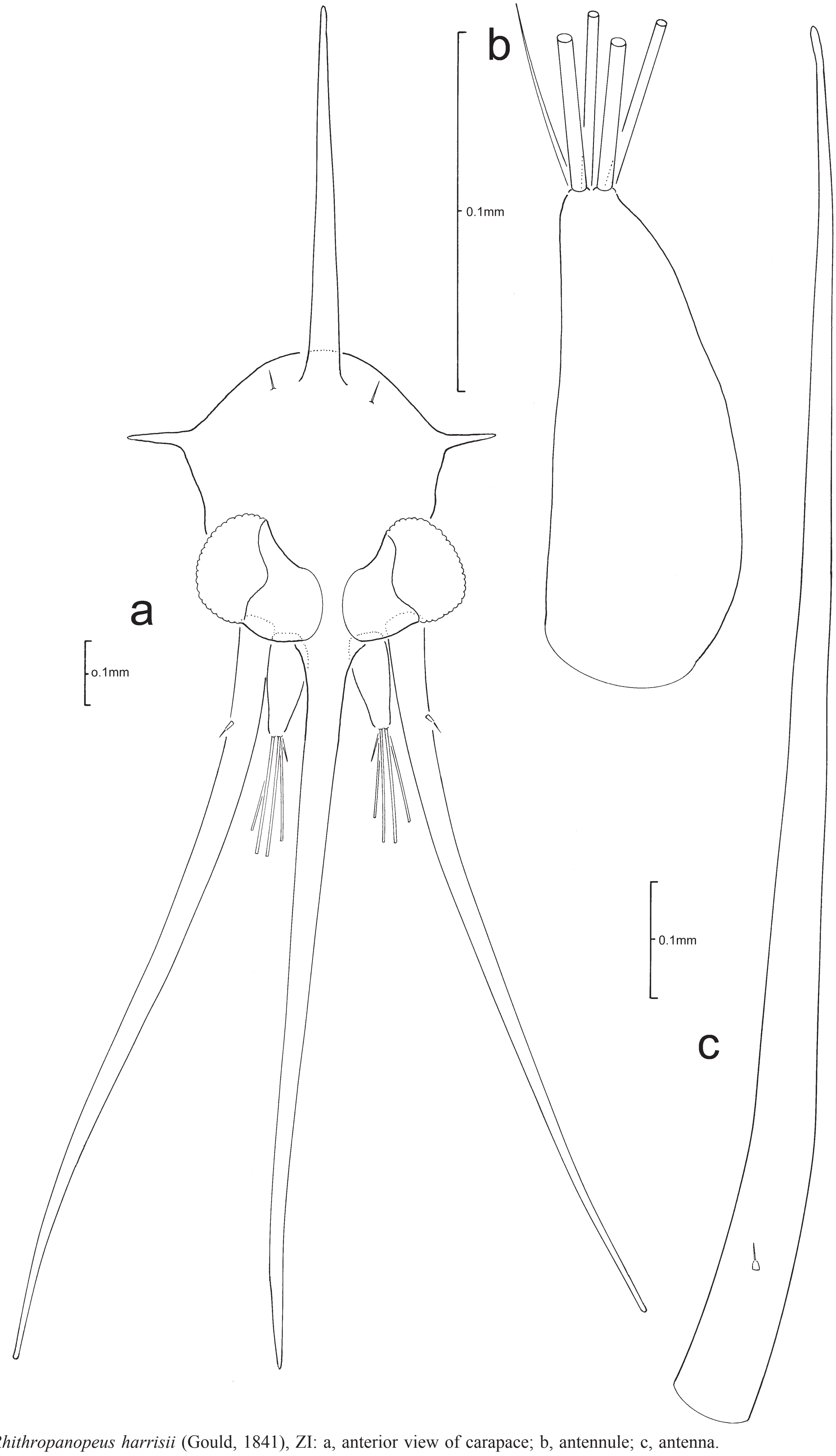

Fig. 149. *Rhithropanopeus harrisii* (Gould, 1841), ZI: a, anterior view of carapace; b, antennule; c, antenna.

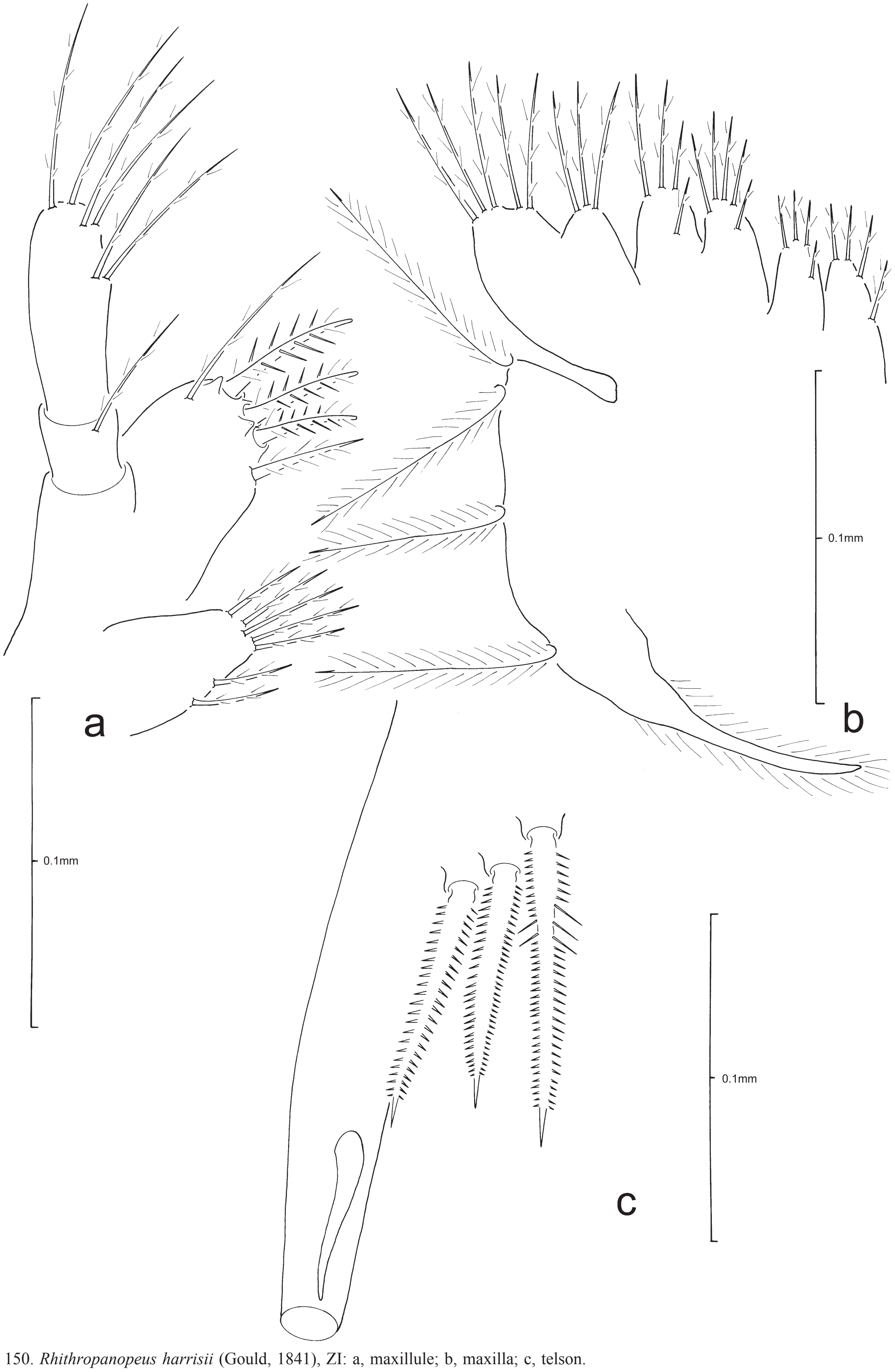

Fig. 150. *Rhithropanopeus harrisii* (Gould, 1841), ZI: a, maxillule; b, maxilla; c, telson.

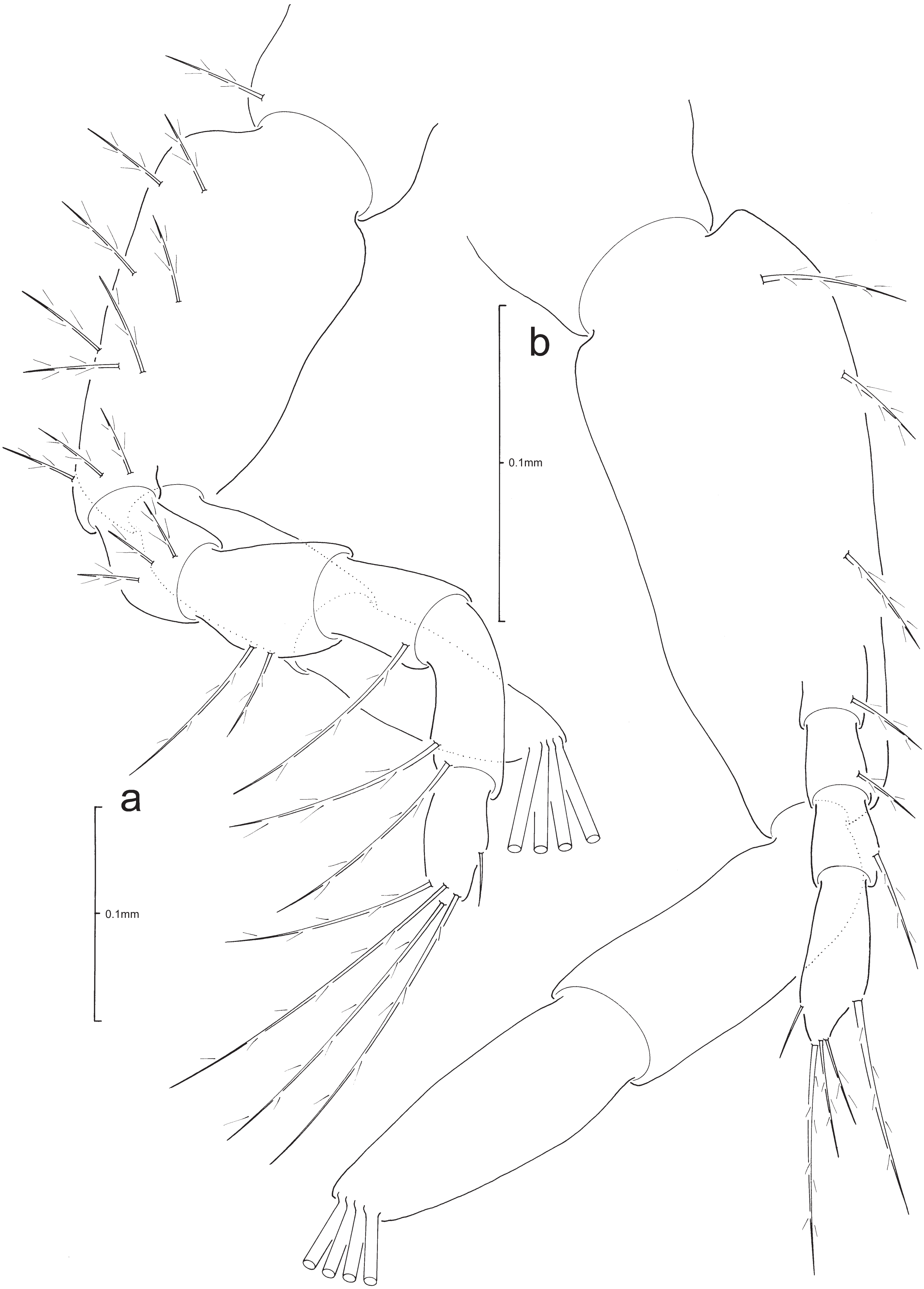

Fig. 151. *Rhithropanopeus harrisii* (Gould, 1841), ZI: a, first maxilliped; b, second maxilliped.

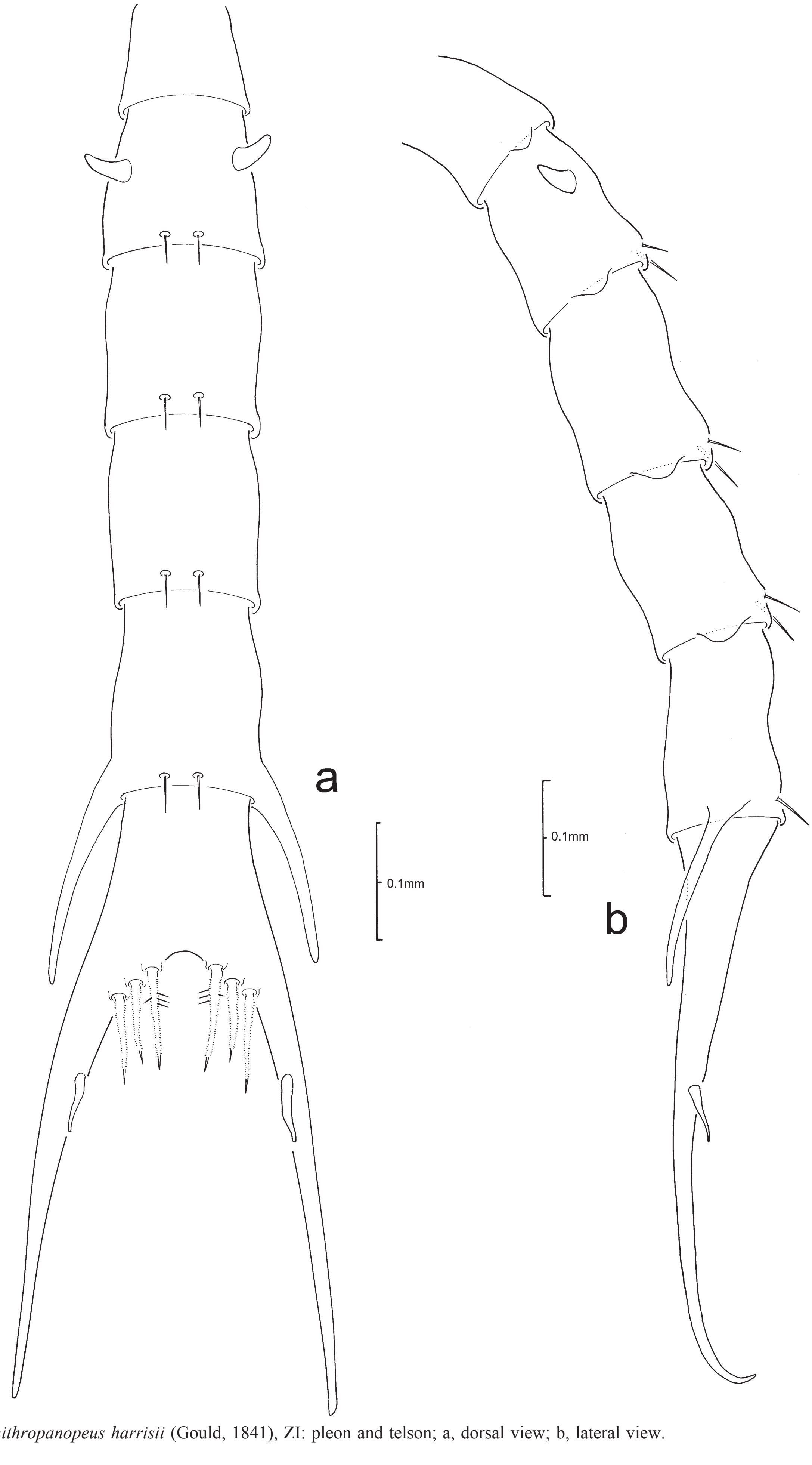

Fig. 152. *Rhithropanopeus harrisii* (Gould, 1841), ZI: pleon and telson; a, dorsal view; b, lateral view.

Family Pseudorhombilidae Alcock, 1900

Garthiope barbadensis (Rathbun, 1921)
(Figs. 153–156)

Micropanope barbadensis. Gore et al., 1981: 33–45, figs. 2–9 (ZI–IV, Meg.); Koettker et al., 2012: 5 (key), 12 (list), figs. 2Q, 3N, 5B (ZI).

Description of Zoea I.

CARAPACE (Fig. 153a, b): dorsal spine long, straight, curved distally, longer than rostral spine length; rostral spine straight, shorter than antennal protopod length, with distal spinulation; lateral spines present, straight, spinulate on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON

Eyes (Fig. 153a): sessile.

Antennule (Fig. 153c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.

Antenna (Fig. 153d): biramous; protopod distally spinulate, longer than rostral spine length; endopod spine minute; exopod ca. 18% of protopod, with 3 (1 subterminal+2 terminal) setae.

Mandible: palp absent.

Maxillule (Fig. 154a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite armed with 5 processes, inner margin with 2 setal buds, single seta absent from outer margin; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.

Maxilla (Fig. 154b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed with 3+5 (2 subterminal, 3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 distal stout process.

PEREION

First maxilliped (Fig. 155a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 terminal plumose natatory setae.

Second maxilliped (Fig. 155b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae; exopod comprising 2 articles, distal article with 4 terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

PLEON (Fig. 156a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly, pleomere 3 with 1 pair of dorsolateral processes directed posteriorly; pleomeres 2–3 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 154c, 156a, b): each fork long, gradually curved, not spinulate, 1 long lateral spine, 1 minute lateral spine, 1 dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Table 22. A comparison between the ZI of *Garthiope barbadensis* (Rathbun, 1921) by Gore et al. (1981) and the present study.

Character	Gore et al. (1981)	Present study
ANTENNULE	fig. 2B	Fig. 153b
terminal setation	2–3 aesthetascs, 0–2 terminal setae	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal seta
ANTENNA	fig. 2B	Fig. 153c
endopod spine	absent	present
exopod setation	2–3	3 (1 subterminal, 2 terminal)
MAXILLA	fig. 2F	Fig. 154b
coxal endite setation	text: 2–3 terminal, 1–2 subterminal+2–3 terminal, 1–2 subterminal fig.: 4+5	4+4
basial endite setation	3 terminal, 1 subterminal+3 terminal, 1 subterminal	5+4
FIRST MAXILLIPED	fig. 2G	Fig. 155a
coxal seta	1–2	present
endopod setation	2,2,1,2,5 (1 subterminal+4 terminal)	3,2,1,2,5 (1 subterminal+4 terminal)
SECOND MAXILLIPED	fig. 2H	Fig. 155b
coxal setation	text: 0–1 fig.: 1	0

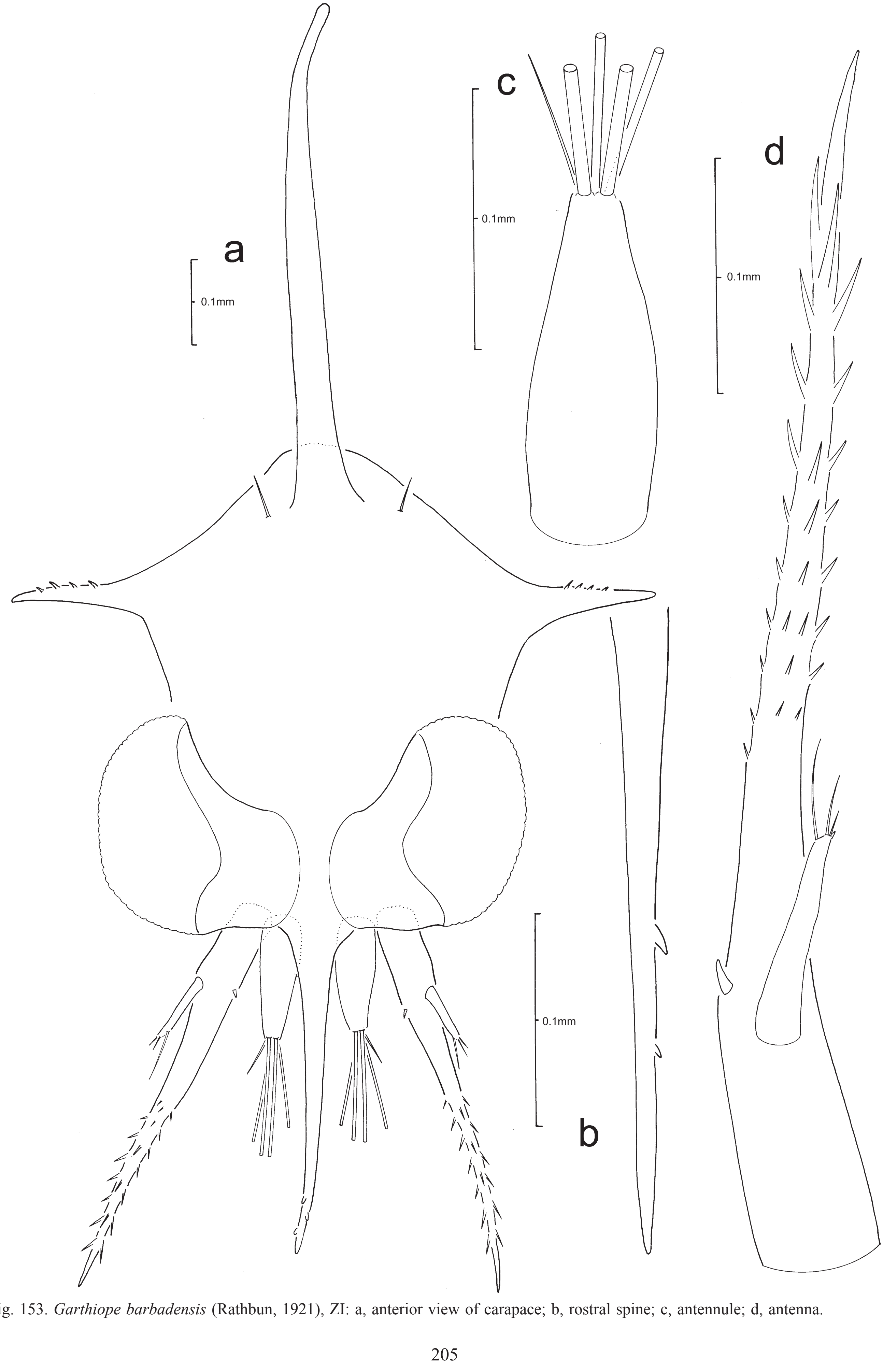

Fig. 153. *Garthiope barbadensis* (Rathbun, 1921), ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

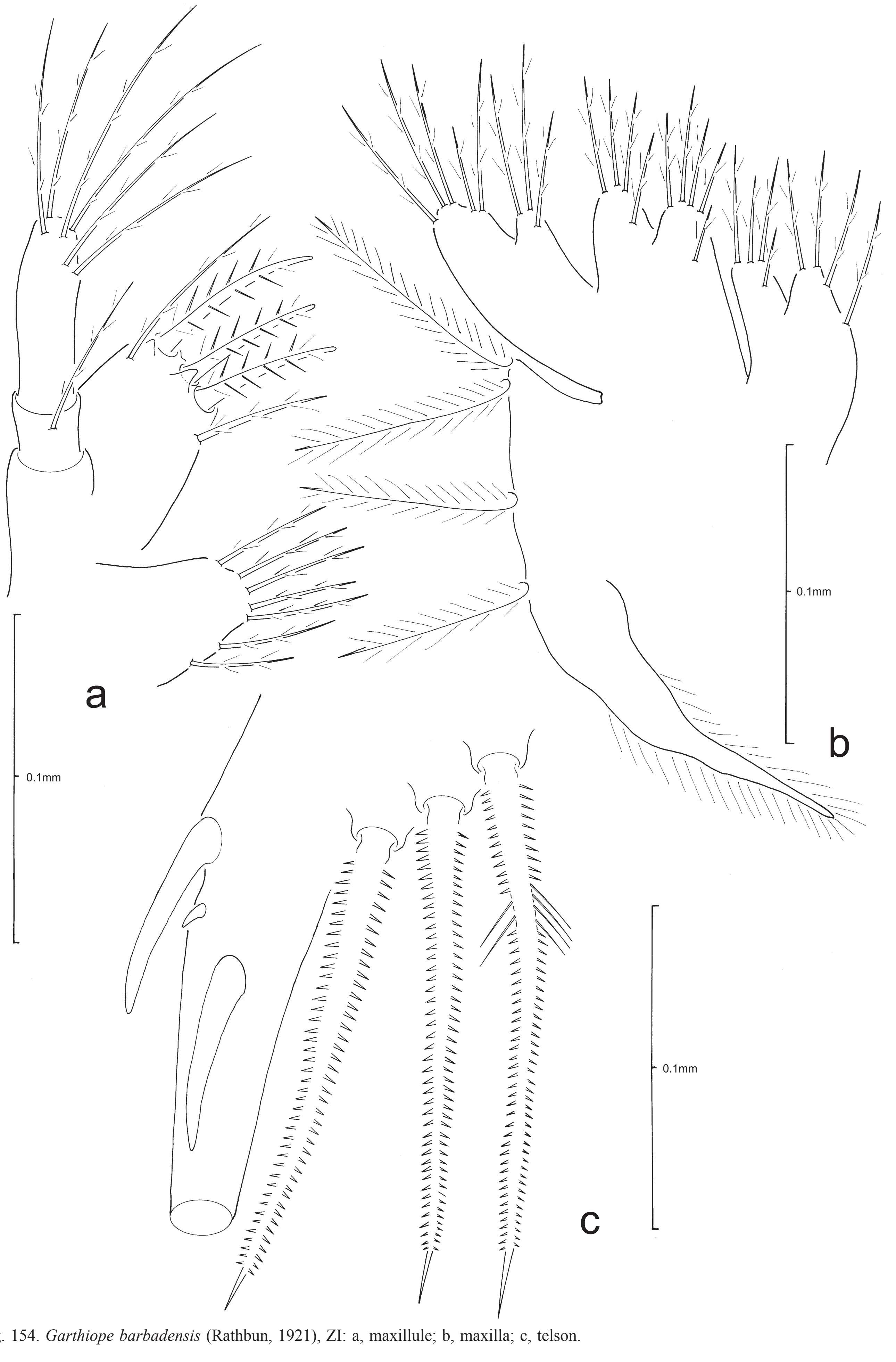

Fig. 154. *Garthiope barbadensis* (Rathbun, 1921), ZI: a, maxillule; b, maxilla; c, telson.

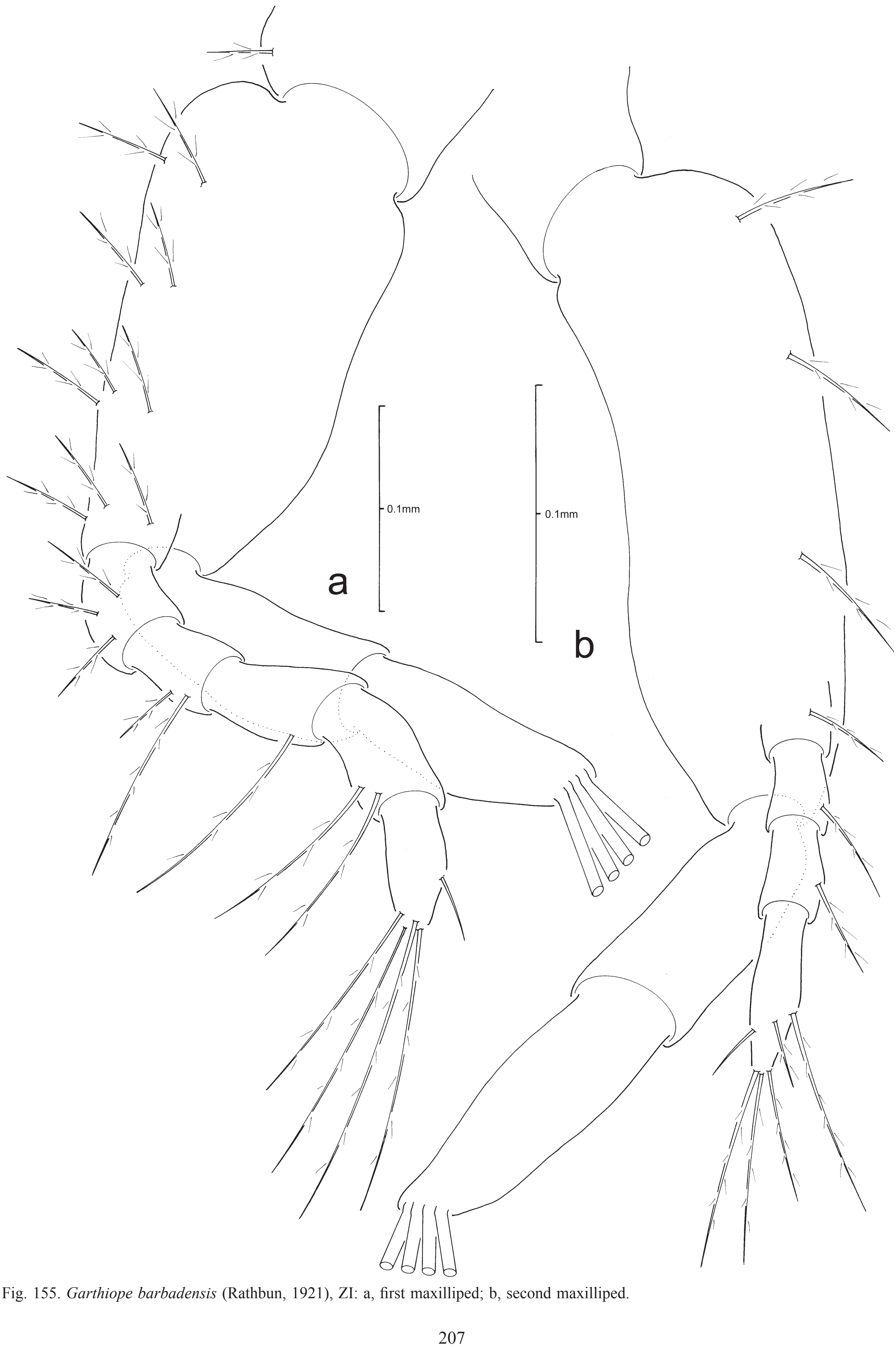

Fig. 155. *Garthiope barbadensis* (Rathbun, 1921), ZI: a, first maxilliped; b, second maxilliped.

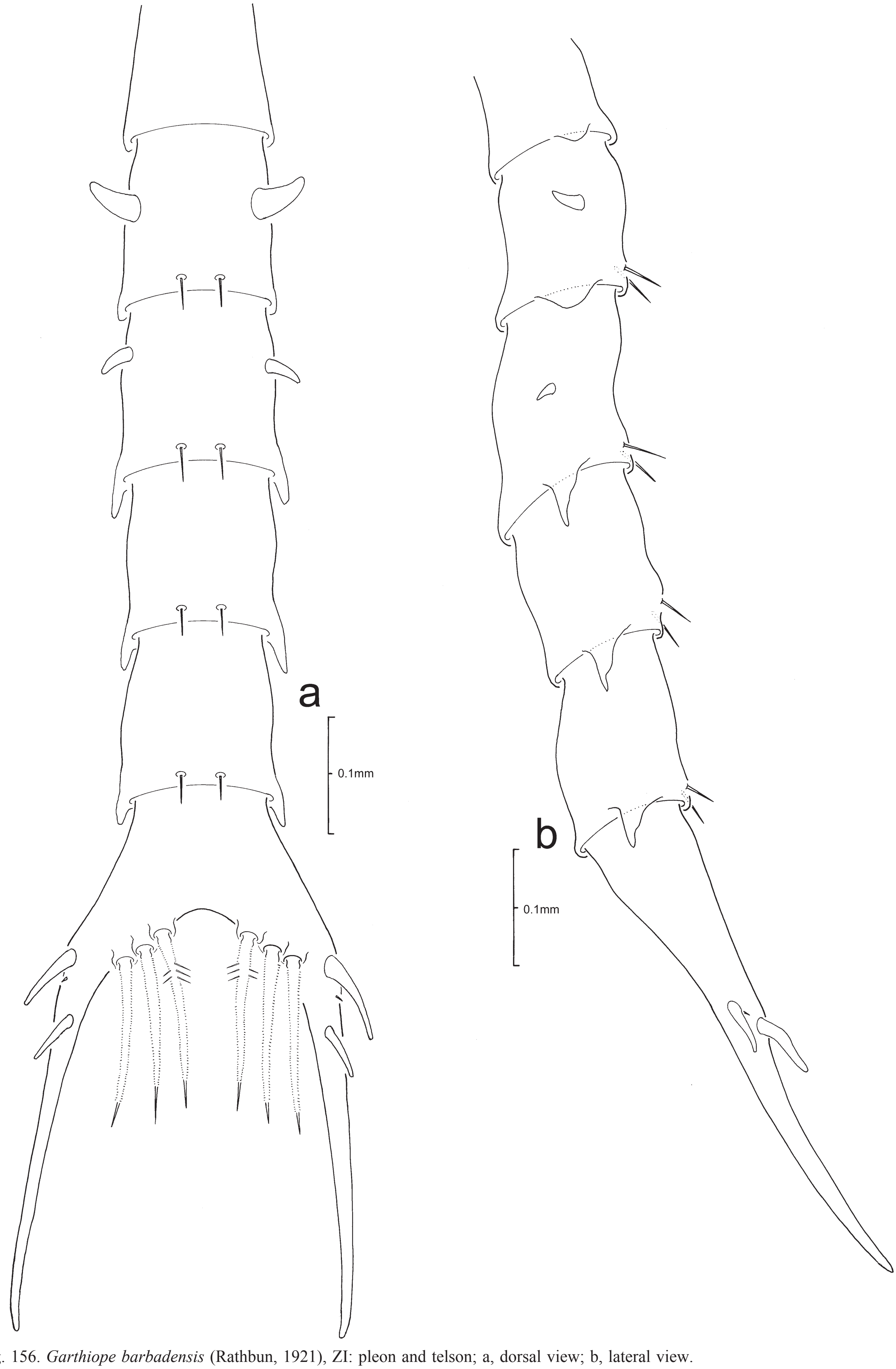

Fig. 156. *Garthiope barbadensis* (Rathbun, 1921), ZI: pleon and telson; a, dorsal view; b, lateral view.

Family Xanthidae MacLeay, 1838

Subfamily Actaeinae Alcock, 1898

***Actaea areolata* (Dana, 1852)**
(Figs. 157–160)

Description of Zoea I.
CARAPACE (Fig. 157a): dorsal spine long, curved distally, ca. twice rostral spine length; rostral spine ca. equal to antennal protopod length, not distally spinulate; lateral spines present, straight, without spinulation on dorsal margin; anterodorsal margin absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 157a): sessile.
Antennule (Fig. 157b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 157c): biramous; protopodal process distally multispinulate, ca. equal to rostral spine length; endopod spine present; exopod ca. 13% length of protopod, possessing 3 (1 long subterminal+2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 158a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 158b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 159a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 159b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 160a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 158c, 160a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

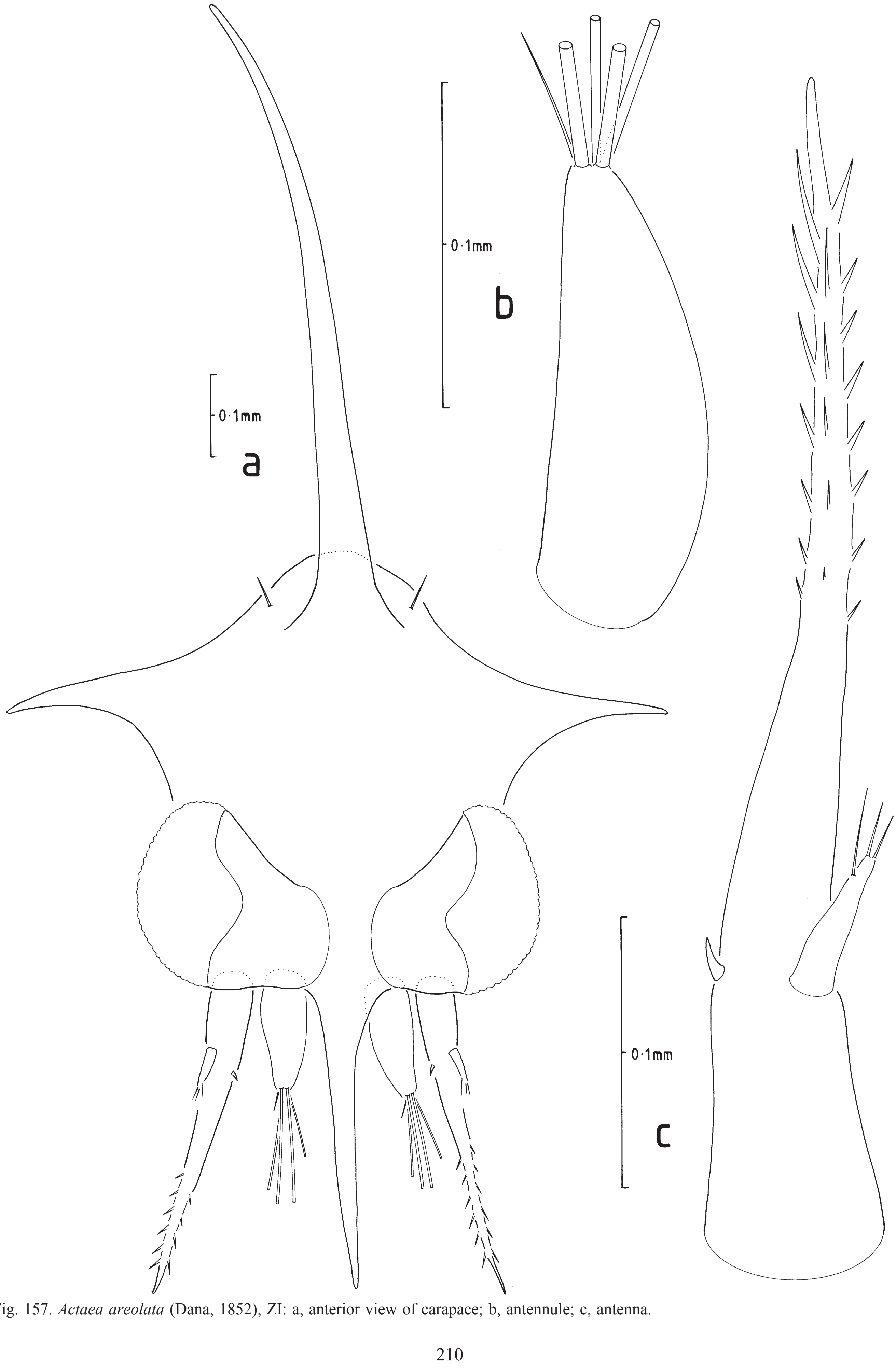

Fig. 157. *Actaea areolata* (Dana, 1852), ZI: a, anterior view of carapace; b, antennule; c, antenna.

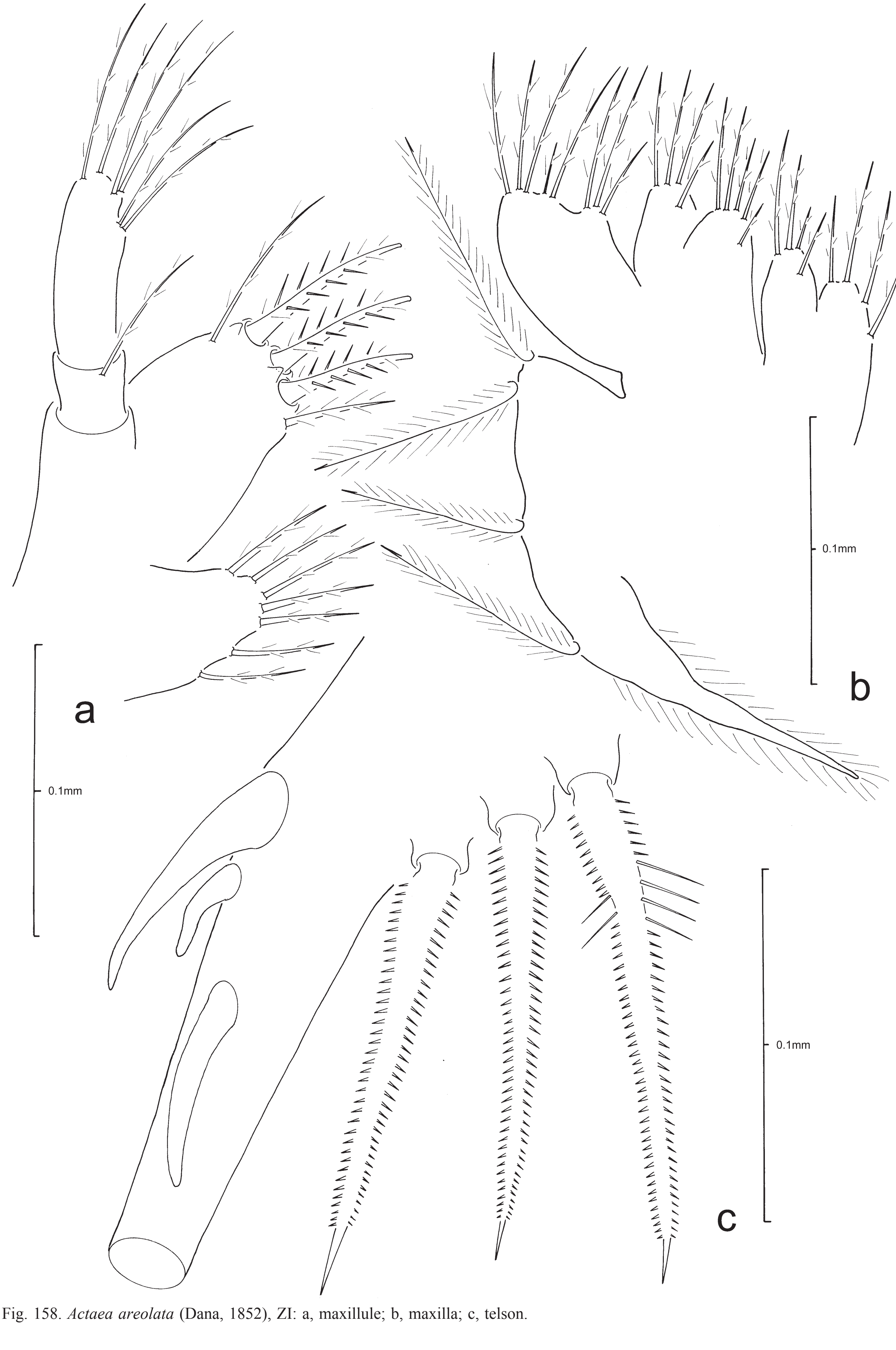

Fig. 158. *Actaea areolata* (Dana, 1852), ZI: a, maxillule; b, maxilla; c, telson.

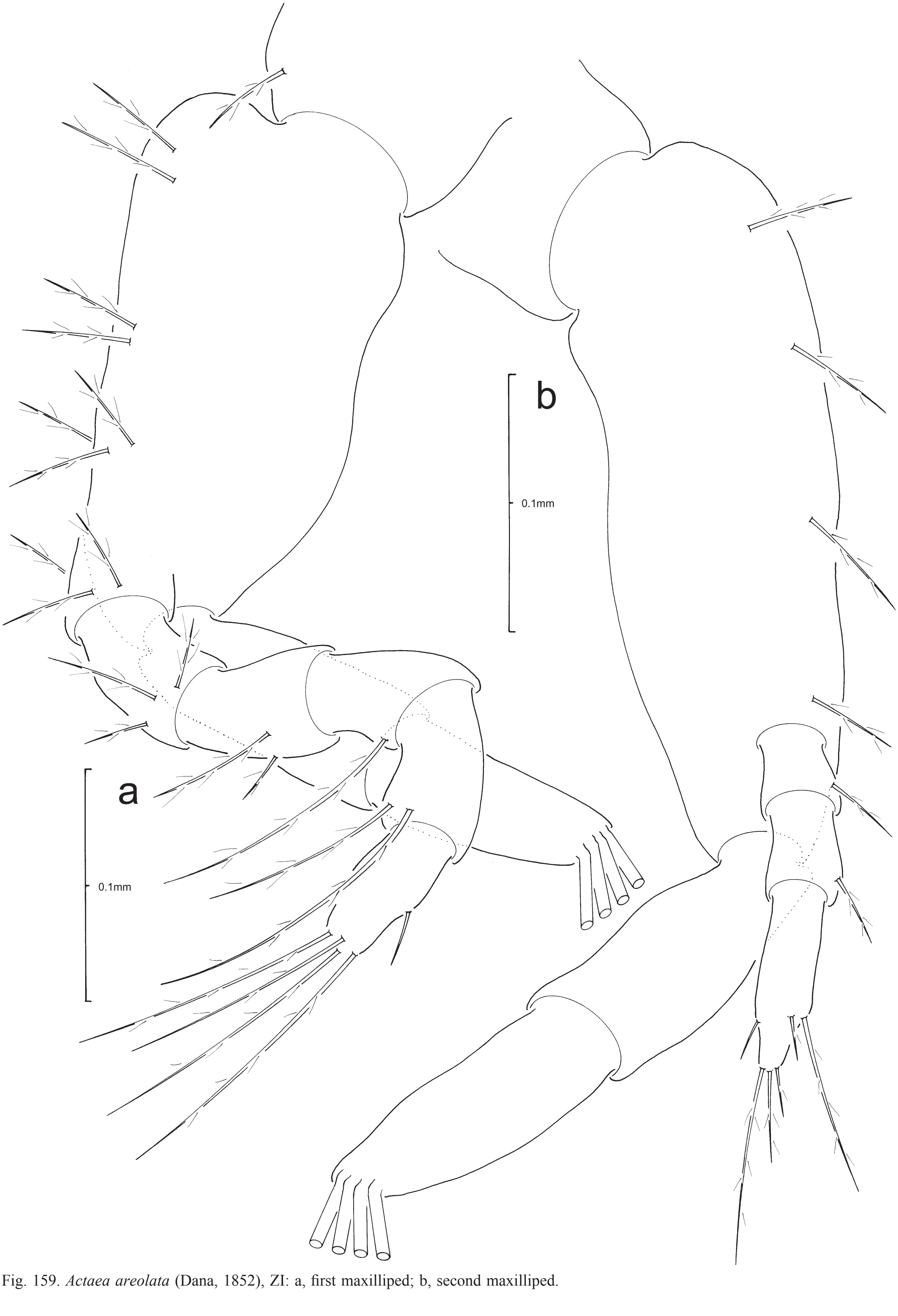

Fig. 159. *Actaea areolata* (Dana, 1852), ZI: a, first maxilliped; b, second maxilliped.

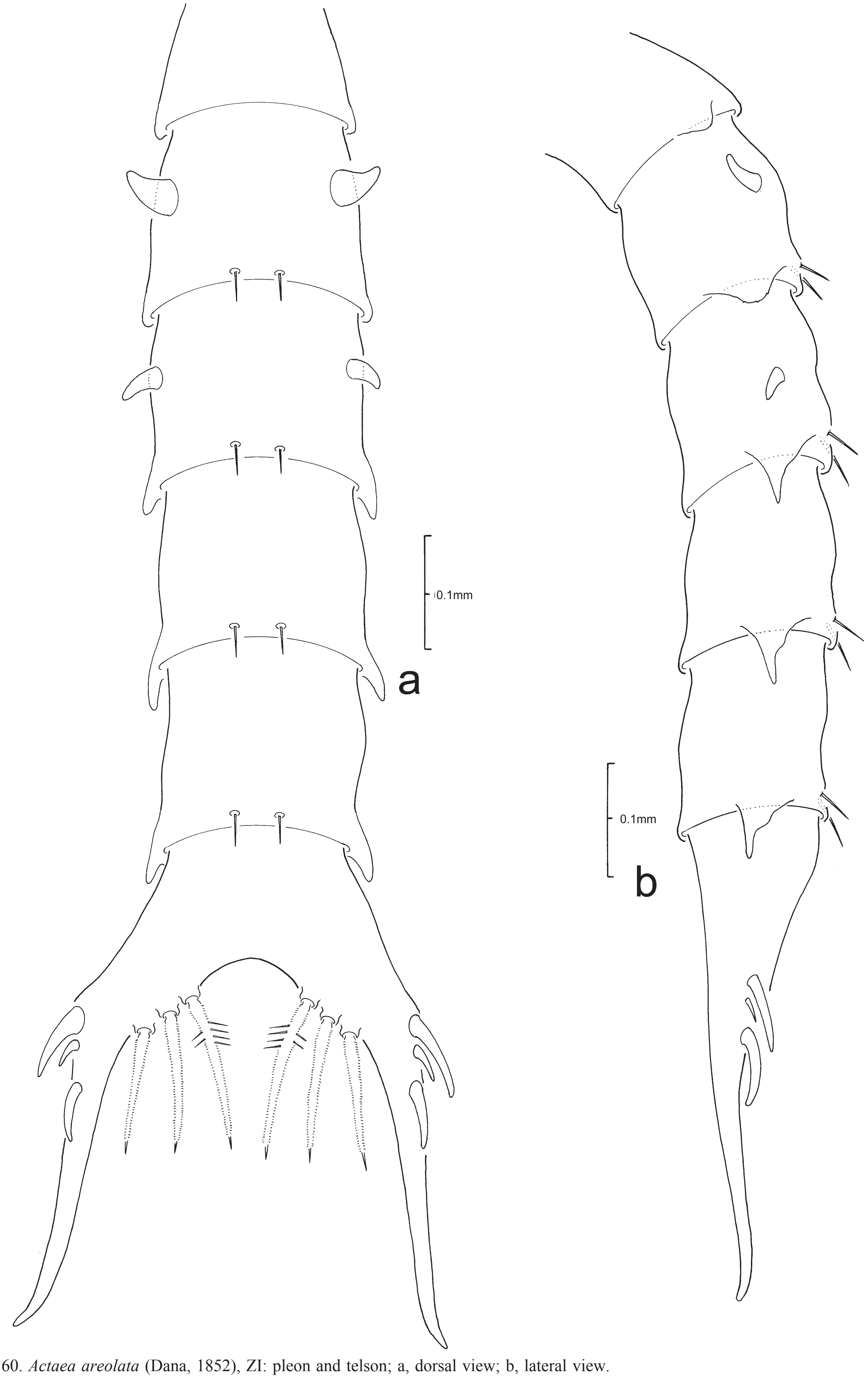

Fig. 160. *Actaea areolata* (Dana, 1852), ZI: pleon and telson; a, dorsal view; b, lateral view.

Actaeodes mutatus Guinot, 1976
(Figs. 161–164)

Description of Zoea I.
CARAPACE (Fig. 161a, b): dorsal spine long, curved distally, ca. twice rostral spine length; rostral spine just shorter than antennal protopod length, distally spinulate; lateral spines present, straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 161a): sessile.
Antennule (Fig. 161c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 161d): biramous; protopodal process distally multispinulate, just longer than rostral spine length; endopod spine present; exopod ca. 18% length of protopod, possessing 3 (1 long subterminal+2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 162a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 162b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 163a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 163b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 164a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 162c, 164a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

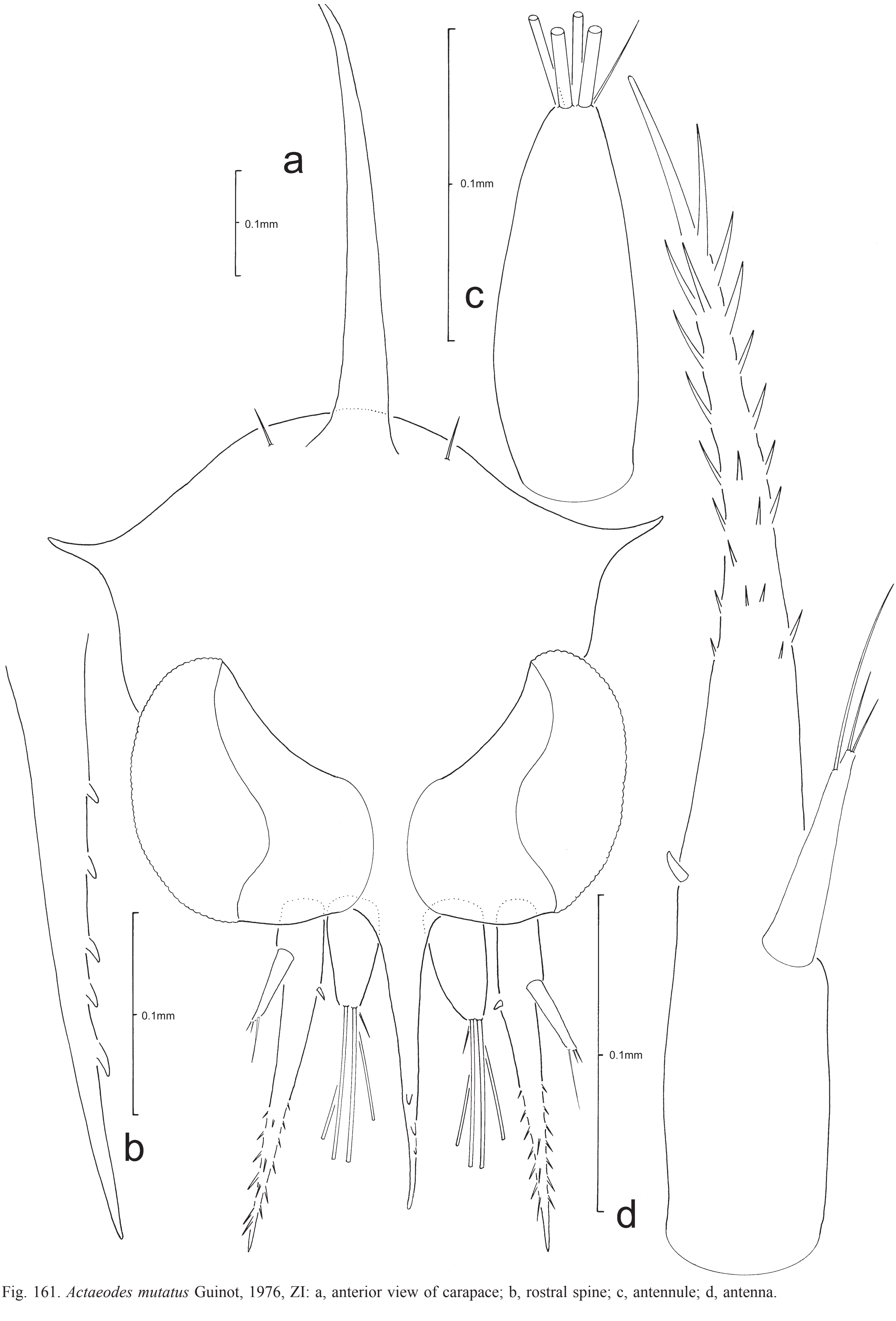

Fig. 161. *Actaeodes mutatus* Guinot, 1976, ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

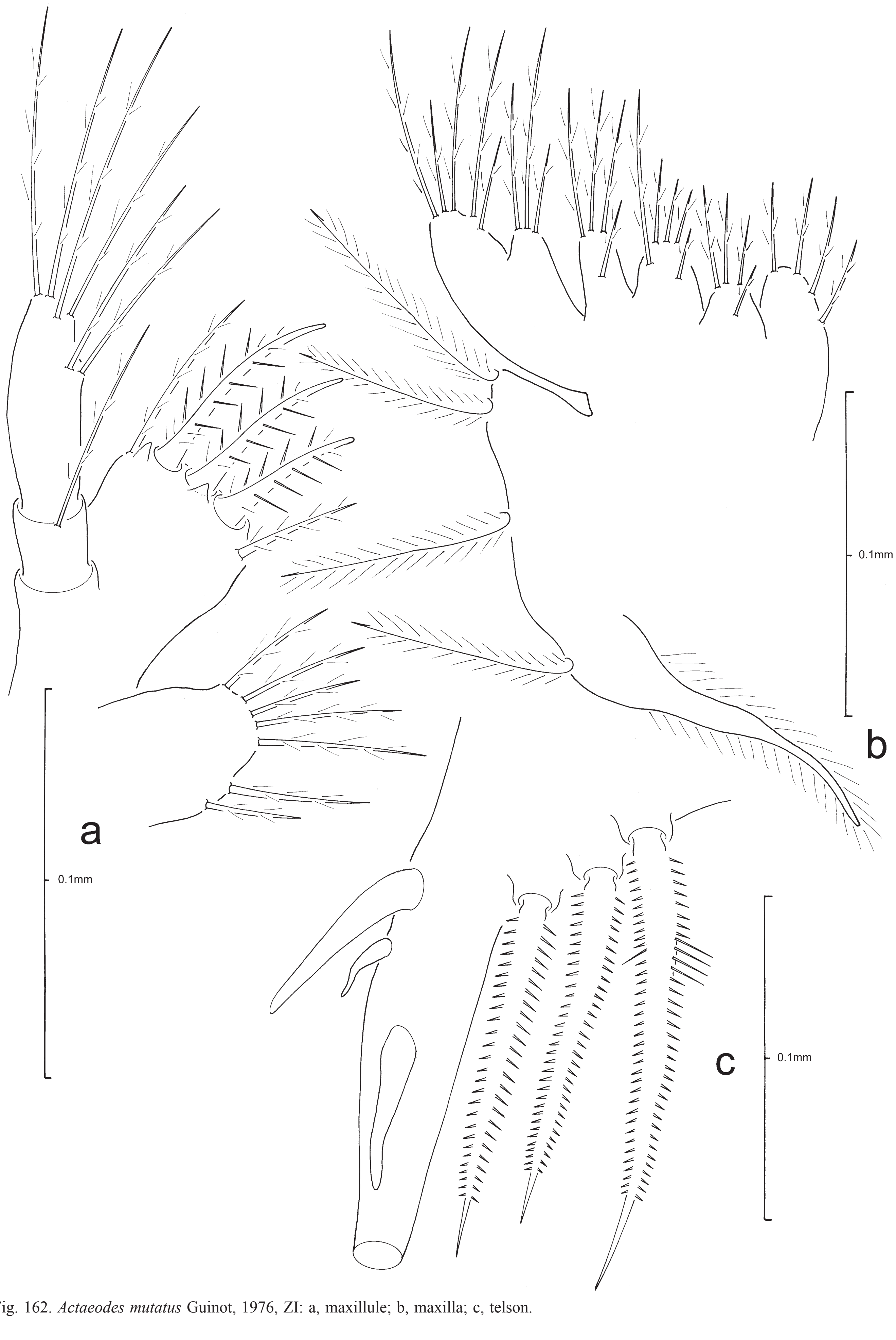

Fig. 162. *Actaeodes mutatus* Guinot, 1976, ZI: a, maxillule; b, maxilla; c, telson.

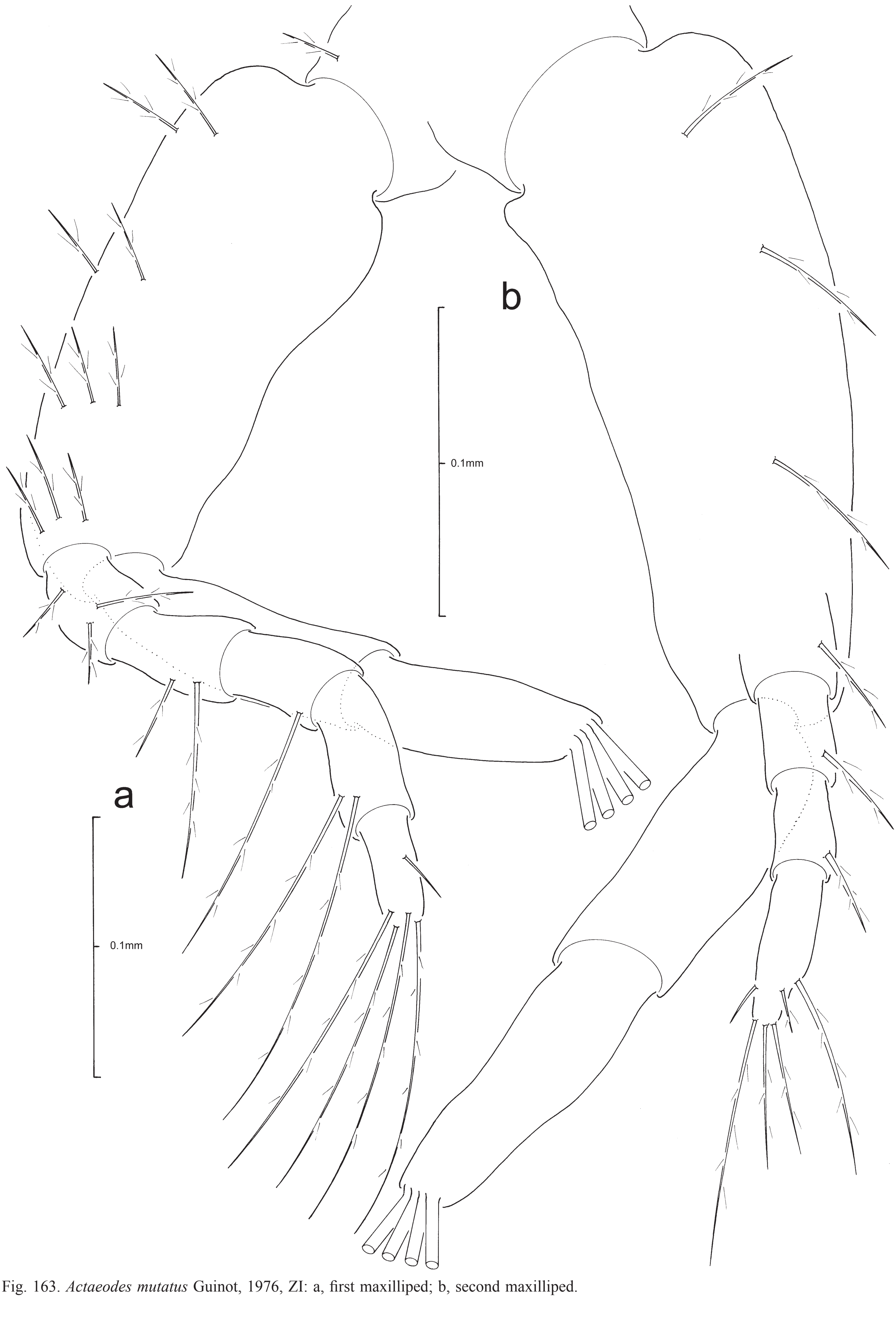

Fig. 163. *Actaeodes mutatus* Guinot, 1976, ZI: a, first maxilliped; b, second maxilliped.

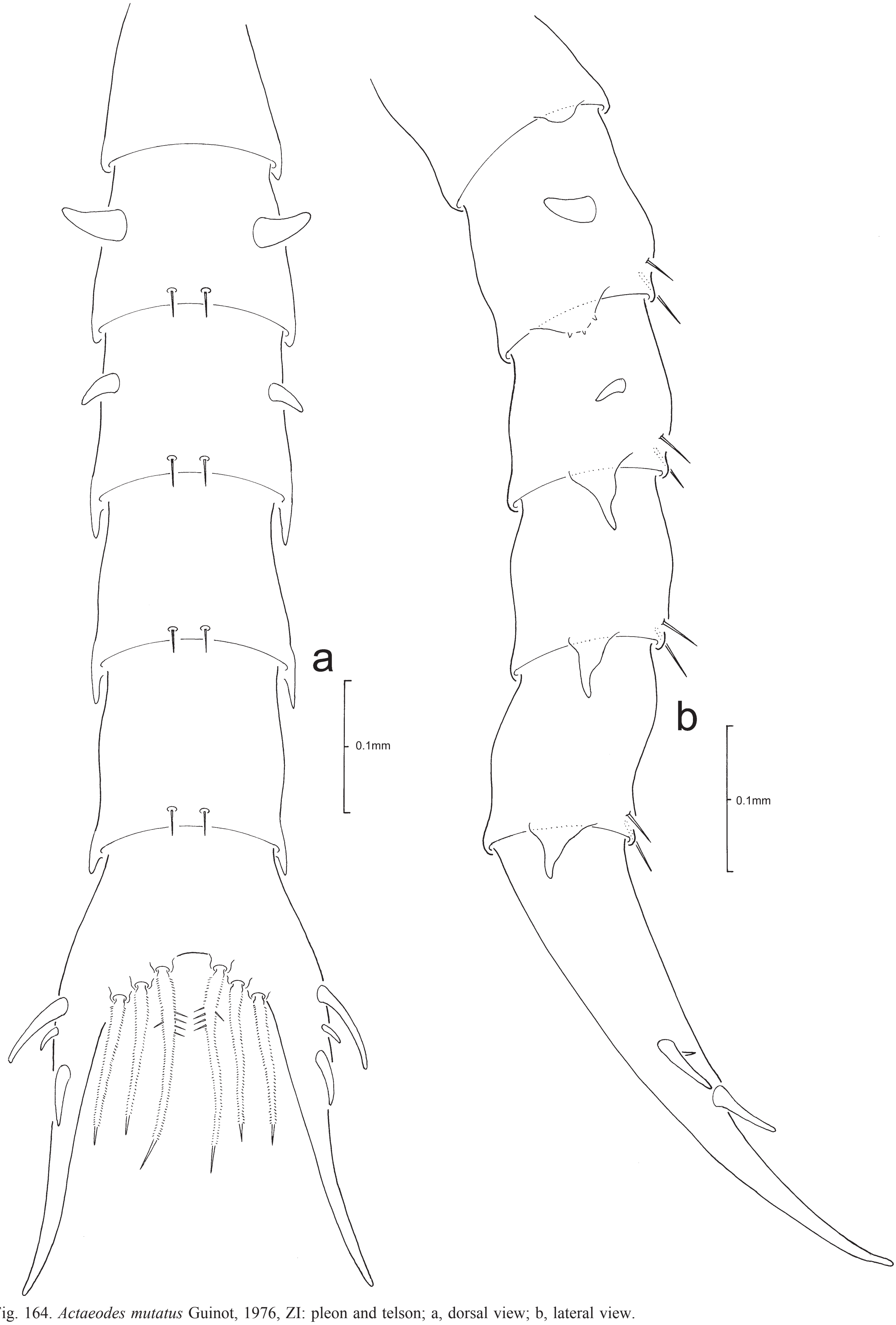

Fig. 164. *Actaeodes mutatus* Guinot, 1976, ZI: pleon and telson; a, dorsal view; b, lateral view.

***Epiactaea nodulosa* (White, 1848)**
(Figs. 165–169)

Description of Zoea I.
CARAPACE (Figs. 165, 166a): dorsal spine slightly curved distally with swollen tip, extremely long, just longer than rostral spine; rostral spine equal to antennal protopod length, without distal spinulation; lateral spines present, straight, with swollen tips, without spinulation on dorsal margin; 1 pair of anterodorsal setae present; 1 pair of posterodorsal setae present; ventral margin with 1 anterior + 5 posterior setae.

CEPHALON
Eyes (Fig. 165): sessile.
Antennule (Fig. 166b): primary flagellum unsegmented with 1 slender subterminal aesthetasc, 6 (4 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal seta; accessory flagellum present.
Antenna (Fig. 166c): biramous; protopodal process without distal spinulation, equal to rostral spine length, with swollen tip; endopod bud present; exopod ca. 13.7% length of protopod, possessing 3 (1 subterminal, 2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 167a): uniramous; epipod seta absent; coxal endite with 8 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 167b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 7 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 168a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,6 (2 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 168b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped (Fig. 166d): present; biramous.
Pereiopods (Fig. 166e): present; uniramous; bilobed chela.

PLEON (Fig. 169a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 with rounded posterolateral processes; pleomeres 3–5 with short posterolateral spinous processes; pleomere 1 with medial seta; pleomeres 2–5 with 1 pair of posterodorsal setae, uniramous pleopod buds, endopods absent.

TELSON (Figs. 167c, 169a, b): each fork extremely long, gradually curved distally, not spinulated, 2 minute lateral spines, 1 slightly larger dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Remarks. The ZI of *E. nodulosa* have hatched in an extremely advanced state of development including the expression of one pair of anterodorsal carapace setae, six setae on the ventral carapace margin, presence of the accessory flagellum on the antennule, presence of the antennal endopod bud, presence of a biramous third maxilliped, presence of the pereiopods with a bilobed chela, and presence of uniramous pleopods. The expression of all these characters suggests that this xanthid will only have two zoeal stages before the moult to megalop.

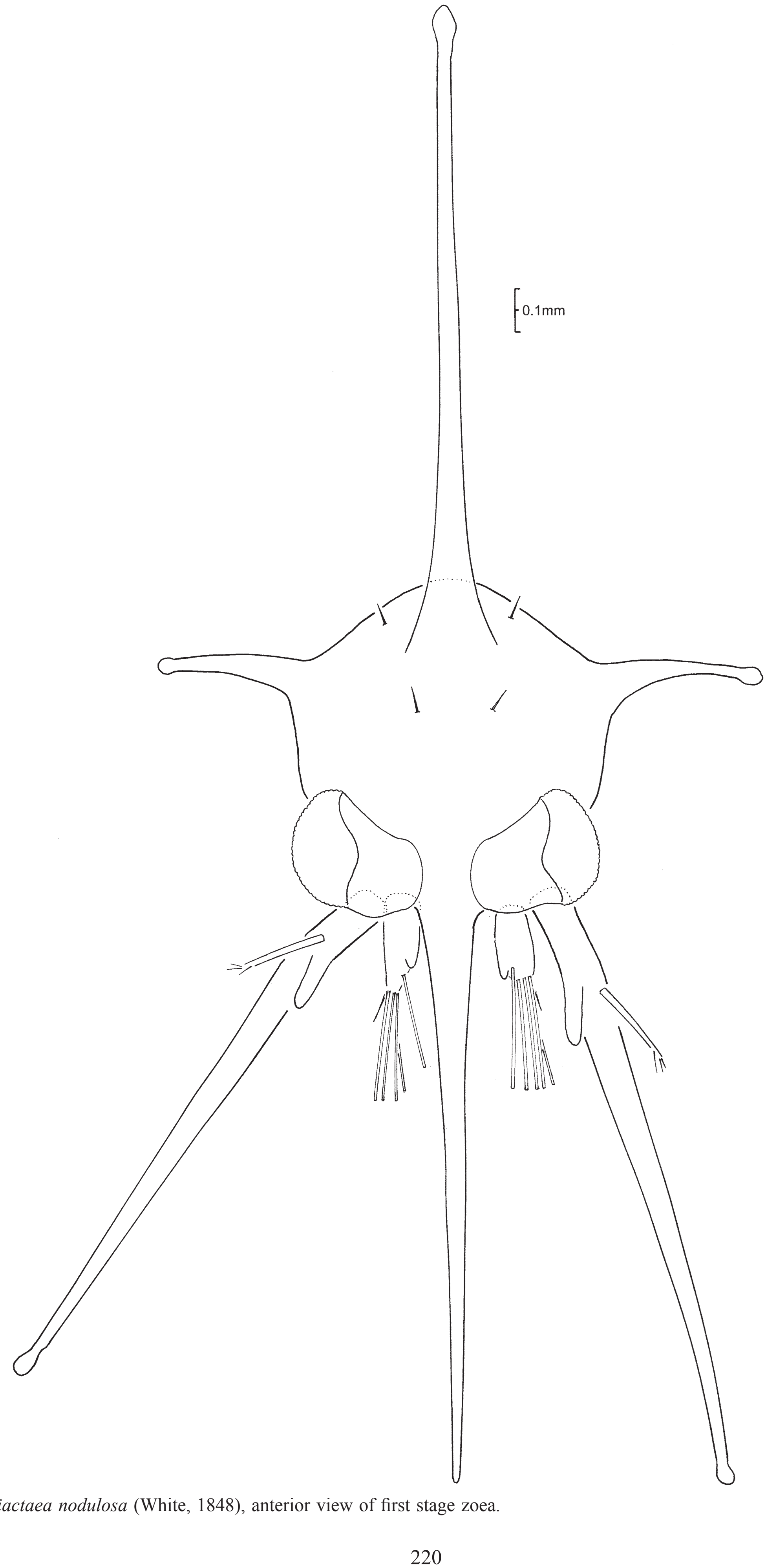

Fig. 165. *Epiactaea nodulosa* (White, 1848), anterior view of first stage zoea.

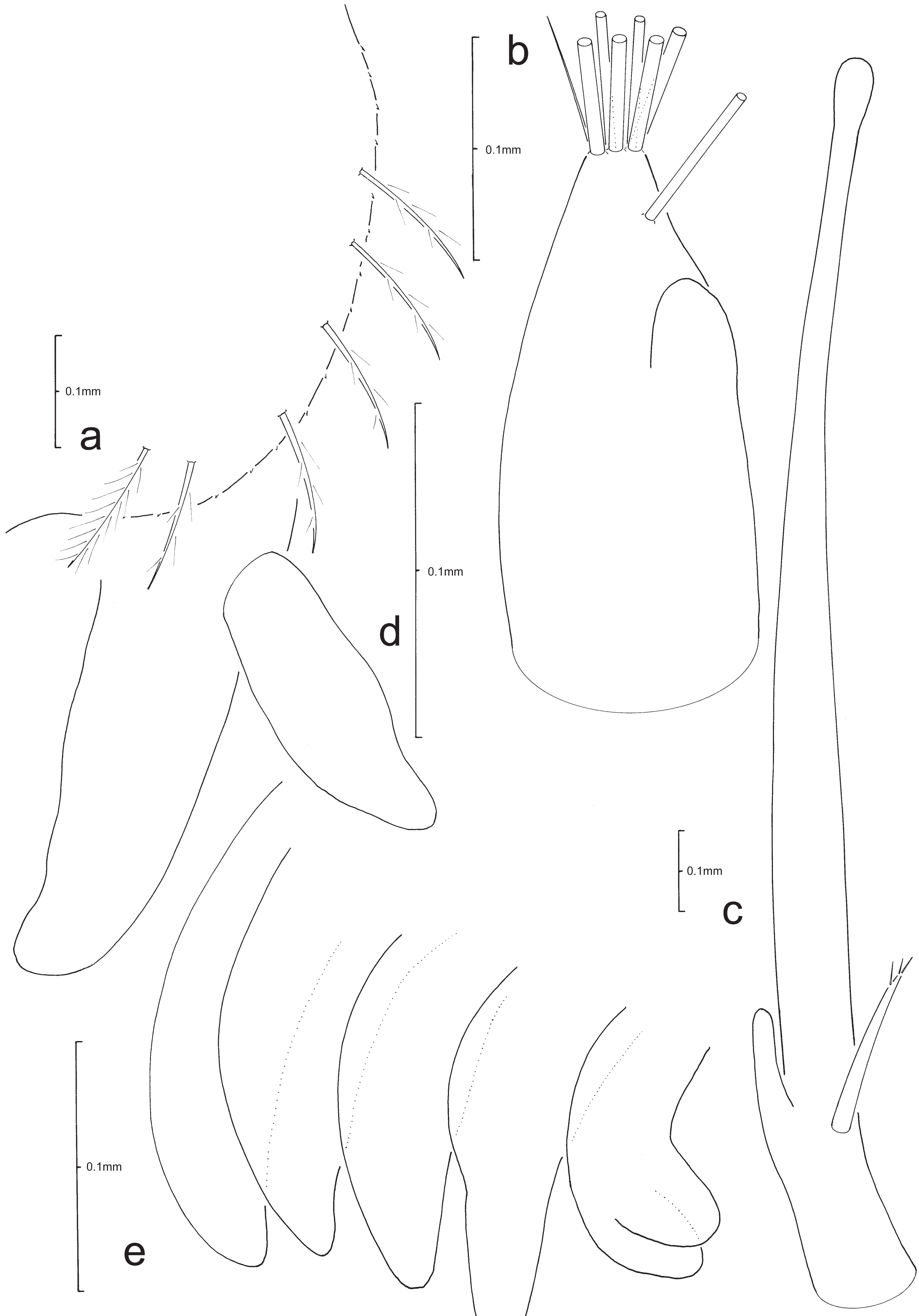

Fig. 166. *Epiactaea nodulosa* (White, 1848), ZI: a, posterior carapace margin, b, antennule; c, antenna; d, third maxilliped; e, pereiopods.

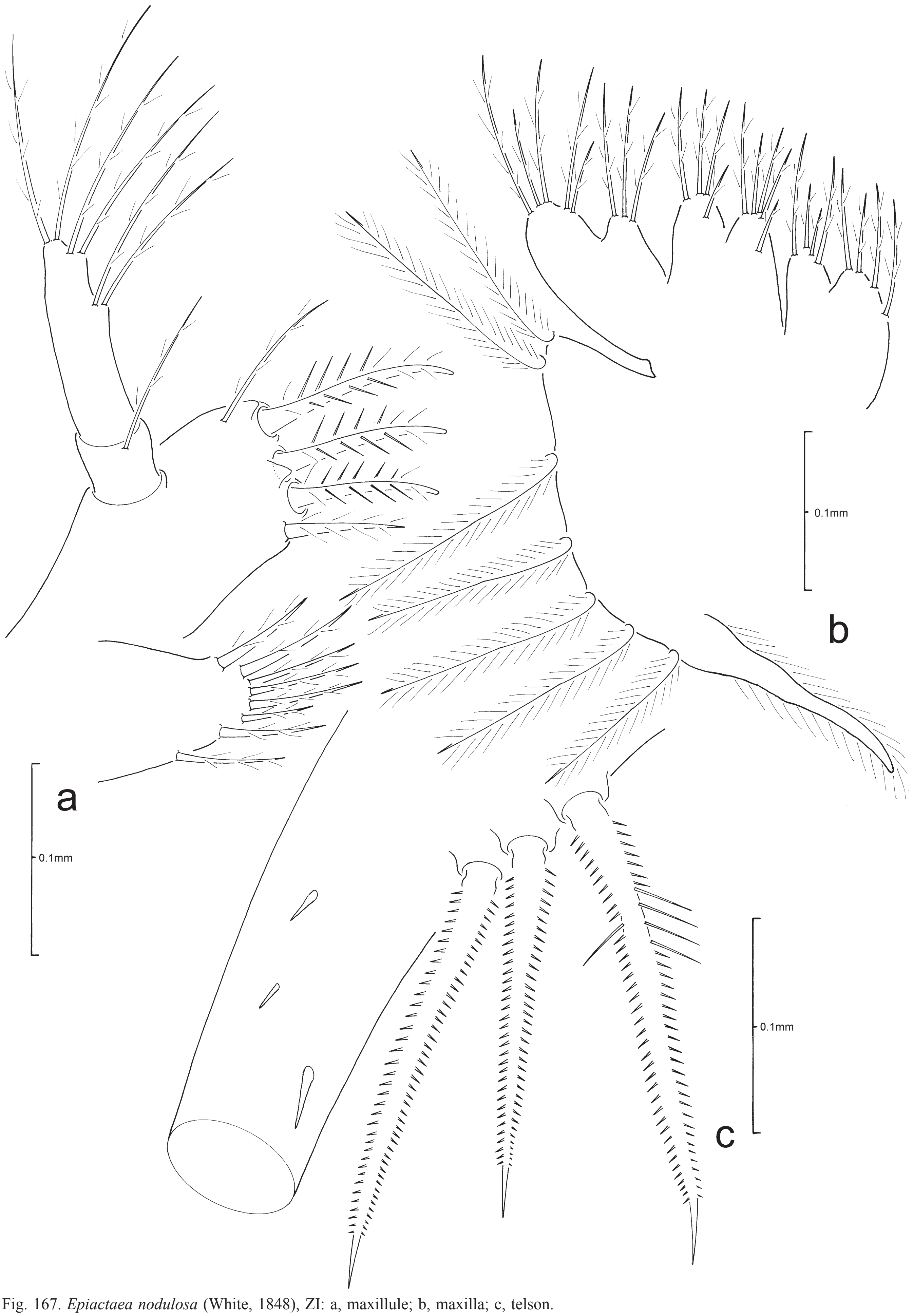

Fig. 167. *Epiactaea nodulosa* (White, 1848), ZI: a, maxillule; b, maxilla; c, telson.

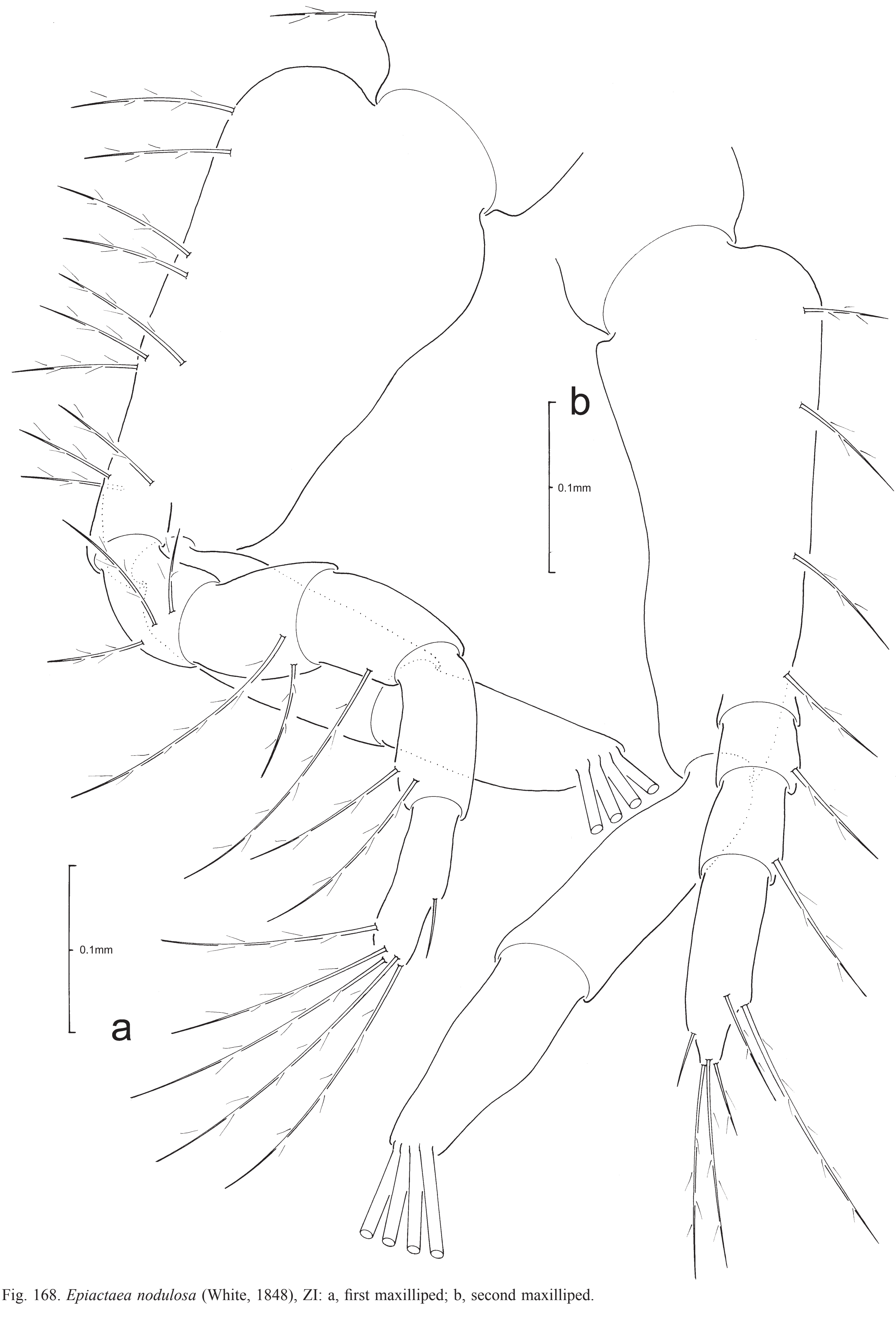

Fig. 168. *Epiactaea nodulosa* (White, 1848), ZI: a, first maxilliped; b, second maxilliped.

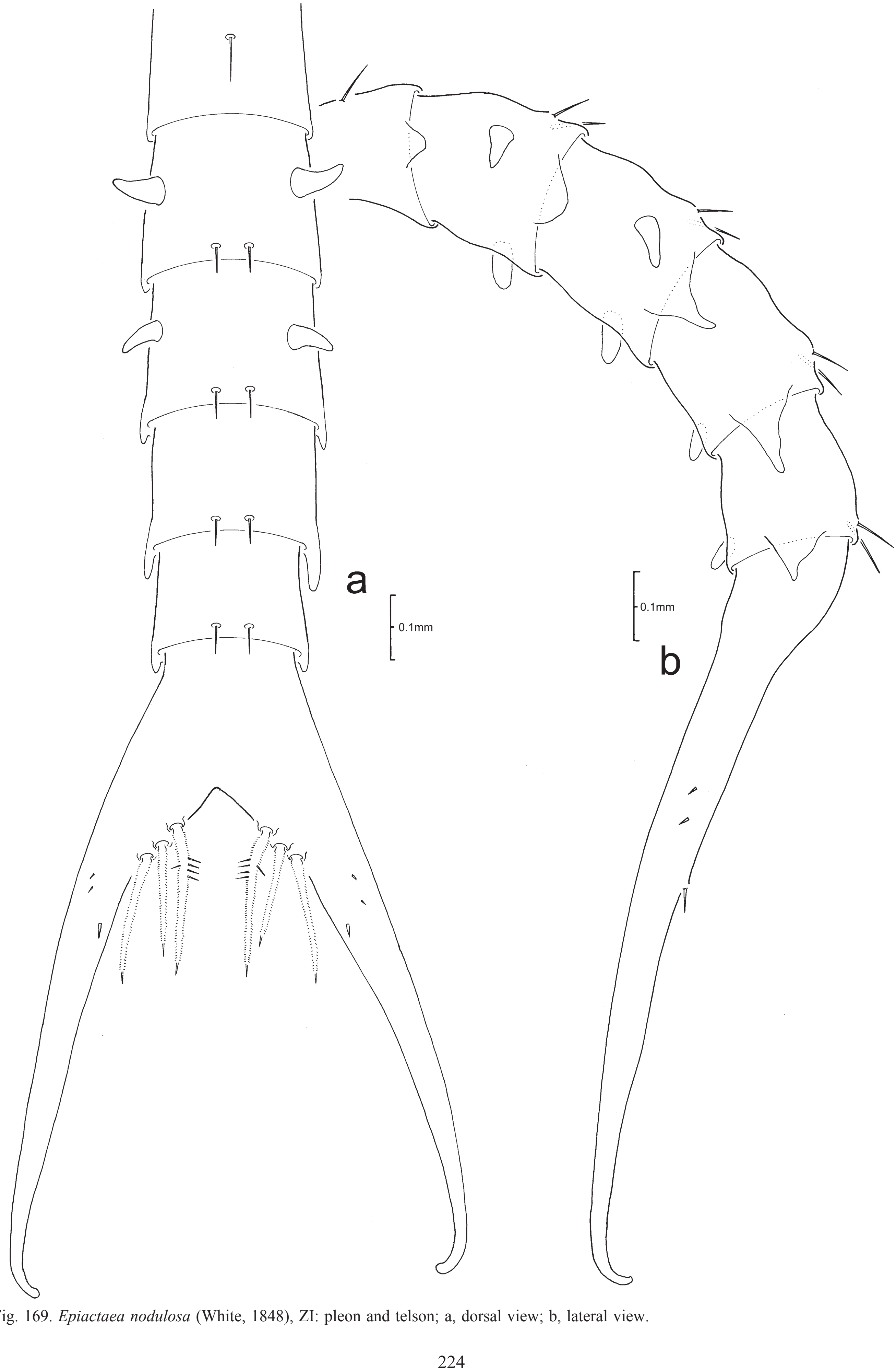

Fig. 169. *Epiactaea nodulosa* (White, 1848), ZI: pleon and telson; a, dorsal view; b, lateral view.

Novactaea bella Guinot, 1976
(Figs. 170–173)

Novactaea bella. S.S.L. Lim & P.K.L. Ng, 1997: 76–79, figs. 1–4 (ZI–II).

Description of Zoea I.
CARAPACE (Fig. 170a, b): dorsal spine extremely long, curved distally, just longer than rostral spine length; rostral spine equal to antennal protopod length, without distal spinulation; lateral spines straight, relatively short, without spinulation on dorsal margin; 1 pair of anterodorsal setae present; 1 pair of posterodorsal setae present; ventral margin with 1 anterior plus 6 posterior setae.

CEPHALON
Eyes (Fig. 170a): sessile.
Antennule (Fig. 170c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 170d): biramous; protopodal process without distal spinulation, equal to rostral spine length, terminally swollen; endopod bud present; exopod ca. 8.7% length of protopod, possessing 3 (1 subterminal, 2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 171a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 171b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 172a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 172b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped (Fig. 173c): biramous with epipod, developing arthrobranch.
Pereiopods (Fig. 171d): present; uniramous; bilobed chela.

PLEON (Fig. 173a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 with 1 seta; pleomeres 2–5 each with 1 pair of posterodorsal setae, uniramous pleopod buds present, endopods absent.

TELSON (Figs. 171c, 173a, b): each fork long, gradually curved distally, not spinulate, lateral and dorsomedial spines absent; posterior margin with 3 pairs of stout spinulate setae.

Remarks. The ZI of *N. bella* has hatched in an extremely advanced state of development. Characters expressed include one pair of anterodorsal carapace setae, ventral carapace margin with one anterior plus six posterior setae, antennal endopod present, biramous third maxilliped with epipod and arthrobranch, pereiopods including bilobed chela and uniramous pleopods. Zoeal development of xanthids normally comprises four stages but, according to Lim & P.K.L. Ng (1997), *N. bella* only has two zoeal stages before the metamorphosis to megalop.

Table 23. A comparison between the ZI of *Novactaea bella* Guinot, 1976 by S.S.L. Lim & P.K.L. Ng (1997) and the present study.

Character	**Lim & Ng (1997)**	**Present study**
CARAPACE	fig. 1A	Fig. 170a
1 pair of anterodorsal setae	absent	present
1 pair of posterodorsal setae	absent	present
		Fig. 170b
ventral margin setation	absent	1 anterior plus 6 posterior setae
ANTENNA	fig. 2B	Fig. 170d
exopod setation	absent	3 (1 subterminal, 2 unequal terminal) minute setae
FIRST MAXILLIPED	fig. 1D	Fig. 172a
coxal seta	not figured	present
THIRD MAXILLIPED	not figured	Fig. 173c
	text: absent	biramous with epipod and gill bud
PEREIOPODS	not figured	Fig. 171d
	text: absent	present with bilobed chela
PLEON	fig. 1A, B, C	Fig. 173a, b
pleomere 1; setation	absent	1 medial posterodorsal seta
pleomeres 2–5; setation	text: without posterodorsal setae fig. absent	1 pair of posterodorsal setae on each pleomere

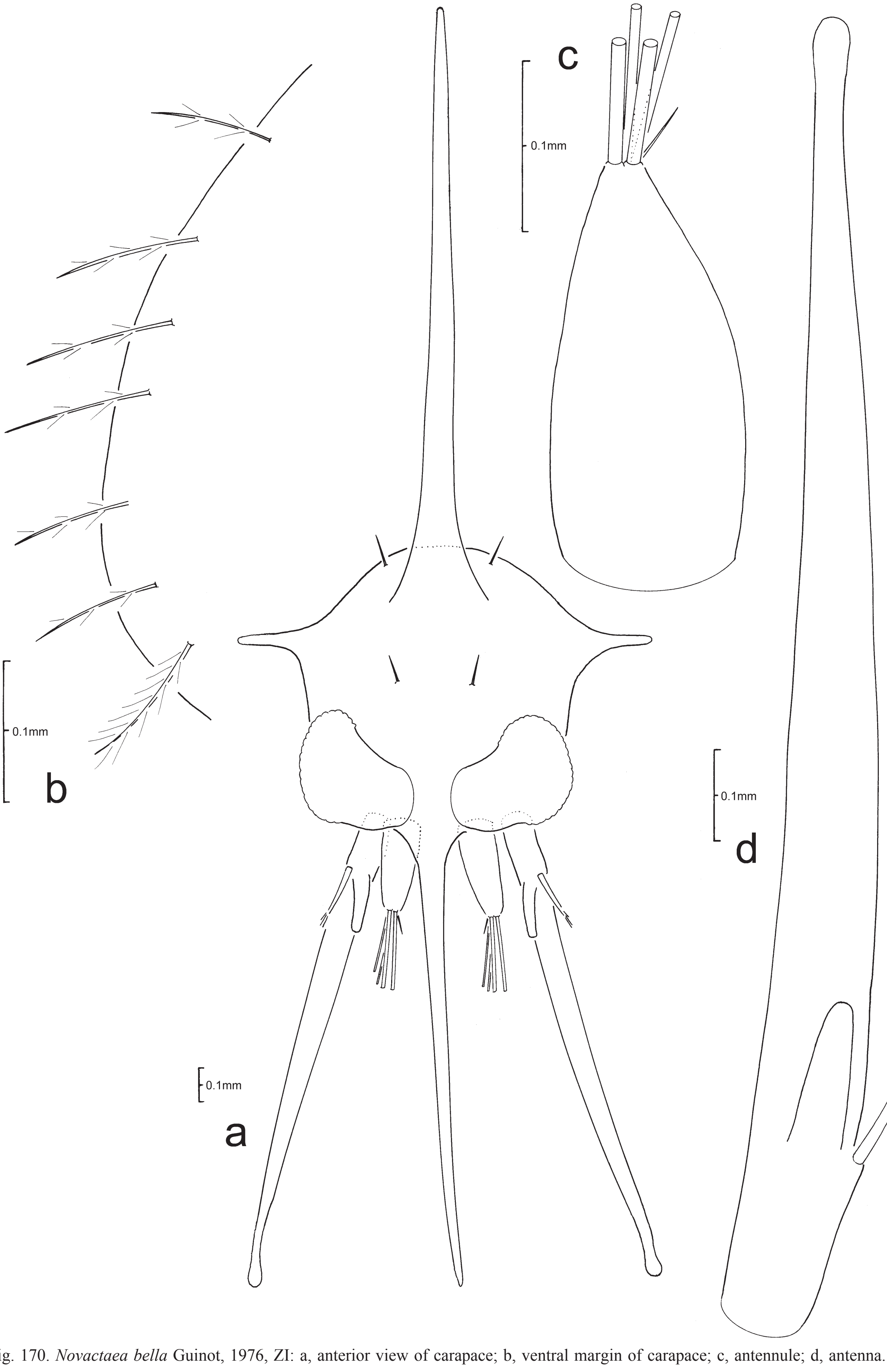

Fig. 170. *Novactaea bella* Guinot, 1976, ZI: a, anterior view of carapace; b, ventral margin of carapace; c, antennule; d, antenna.

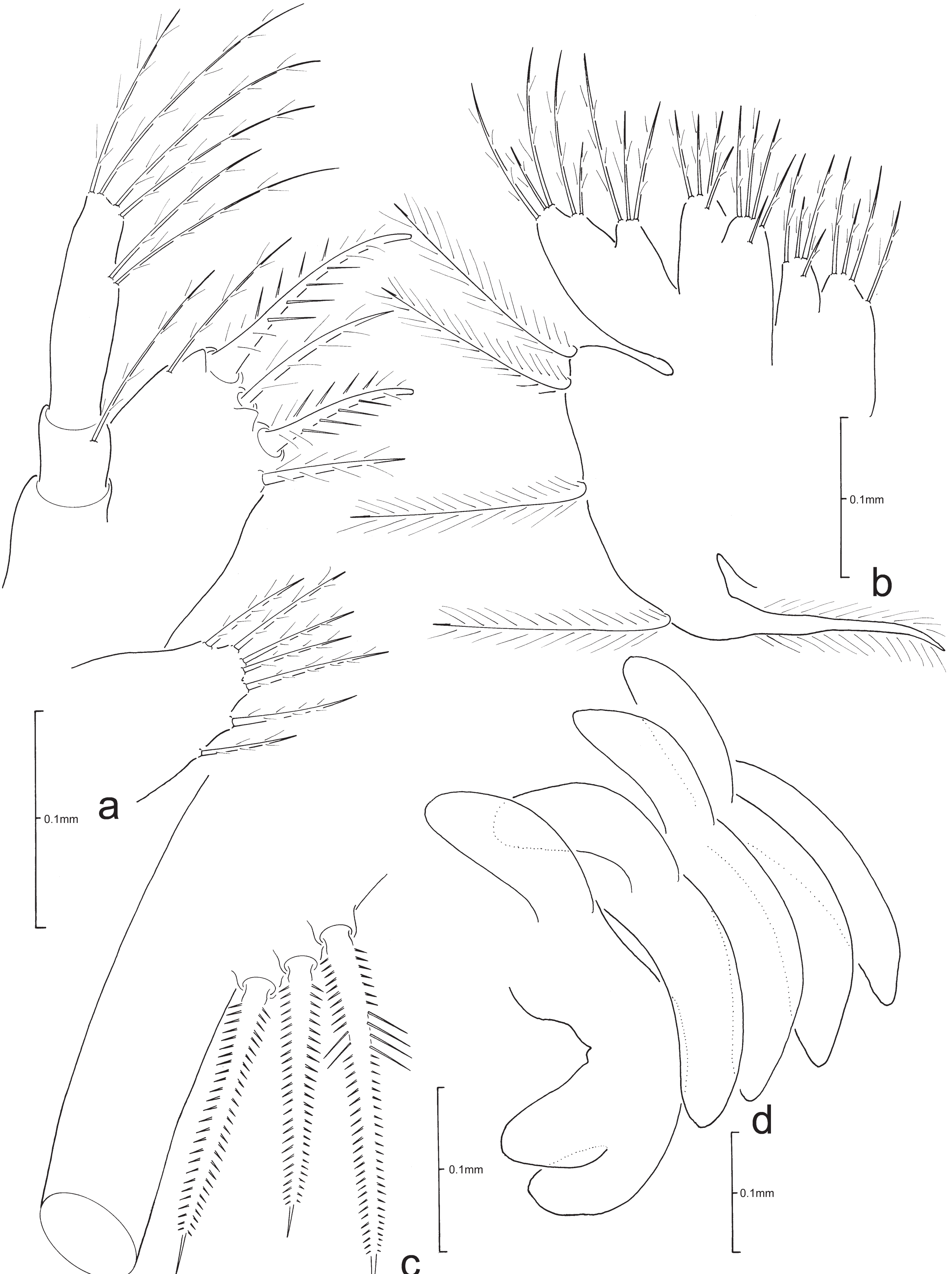

Fig. 171. *Novactaea bella* Guinot, 1976, ZI: a, maxillule; b, maxilla; c, telson; d, pereiopods.

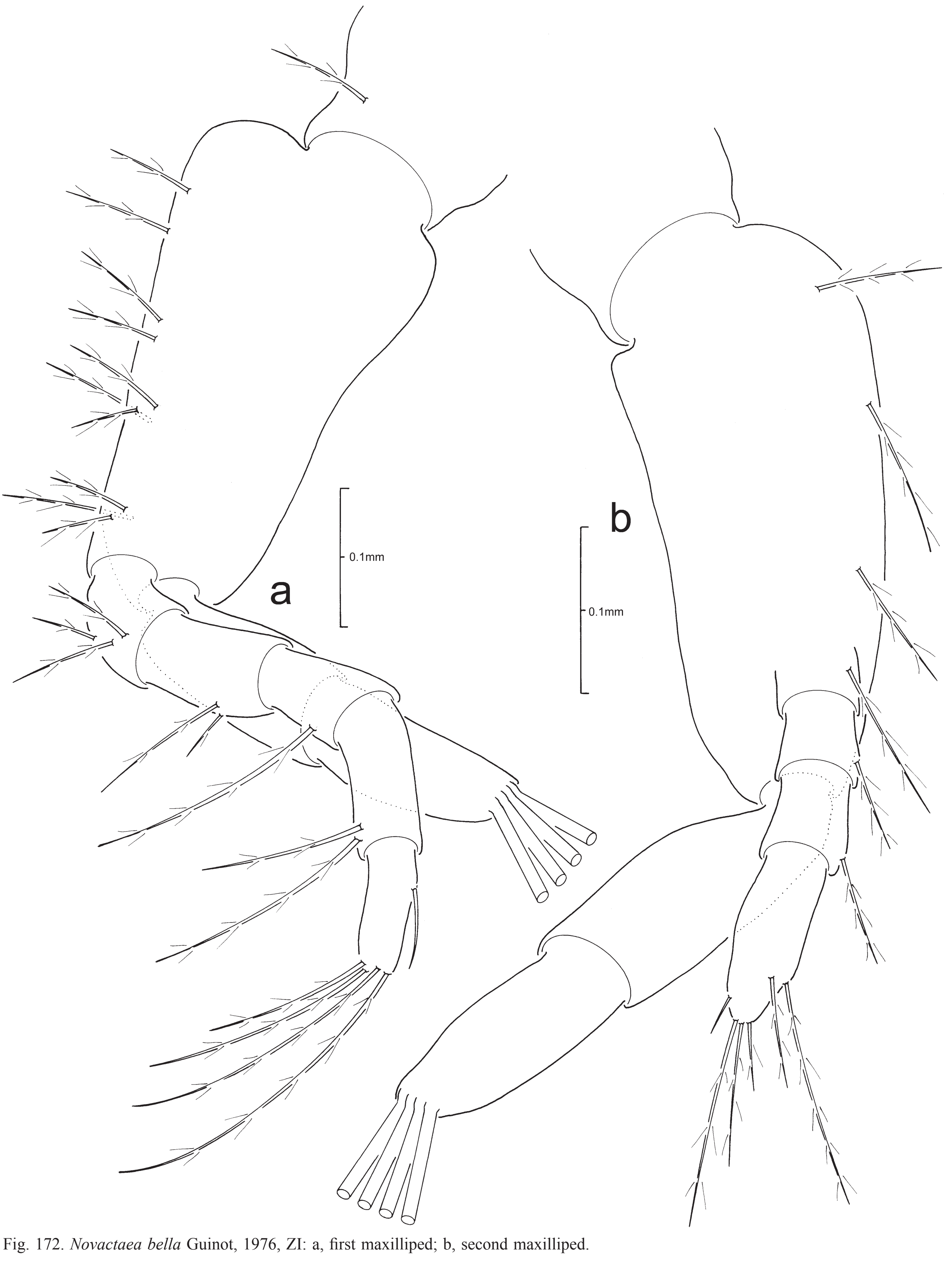

Fig. 172. *Novactaea bella* Guinot, 1976, ZI: a, first maxilliped; b, second maxilliped.

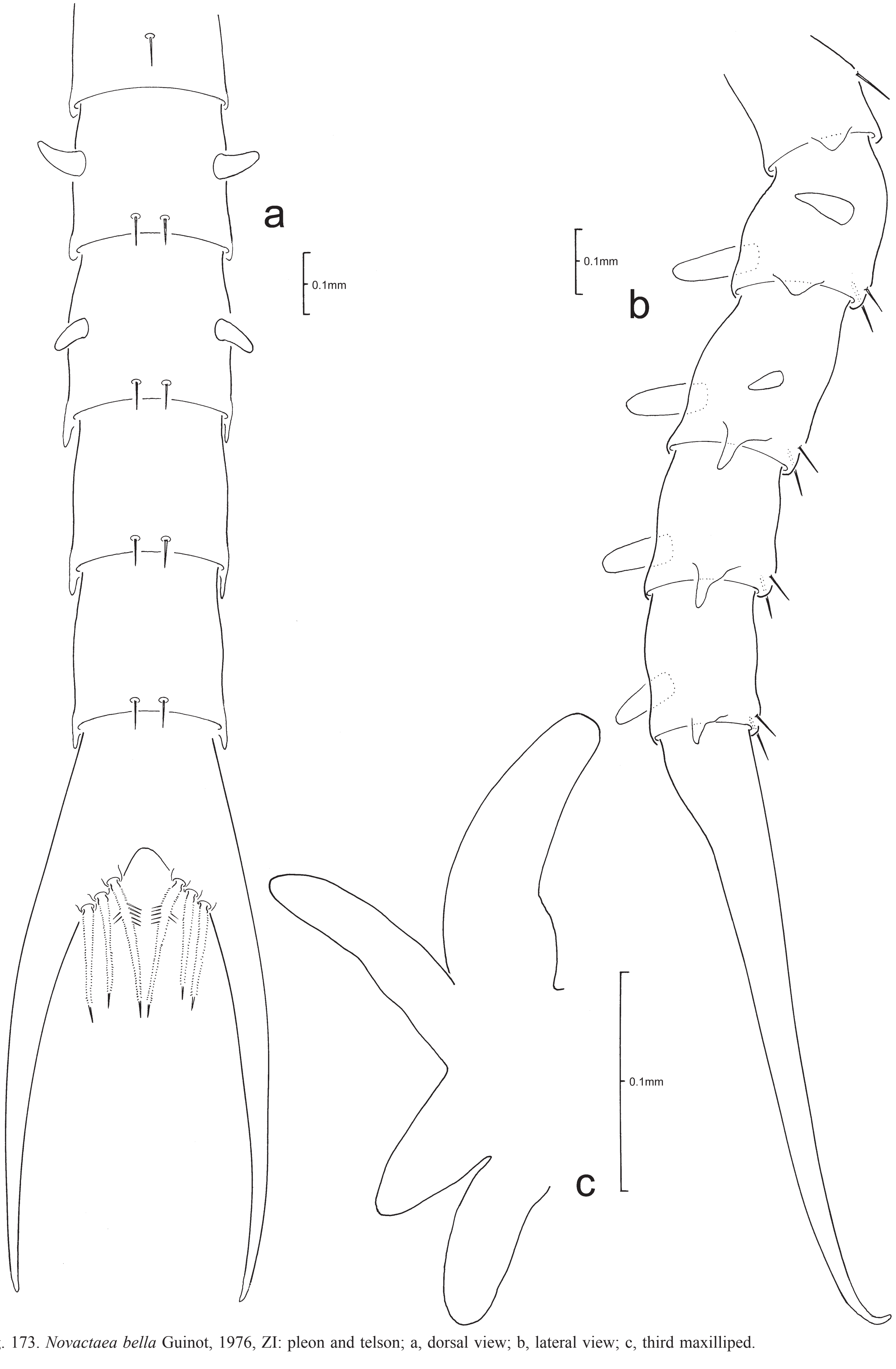

Fig. 173. *Novactaea bella* Guinot, 1976, ZI: pleon and telson; a, dorsal view; b, lateral view; c, third maxilliped.

***Psaumis cavipes* (Dana, 1852)**
(Figs. 174–177)

Description of Zoea I.
CARAPACE (Fig. 174a, b): dorsal spine long, curved distally, ca. twice rostral spine length; rostral spine much shorter than antennal protopod length, distally spinulate; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 174a): sessile.
Antennule (Fig. 174c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 174d): biramous; protopodal process distally multispinulate, much longer than rostral spine length; endopod small spine present; exopod ca. 15% length of protopod, possessing 3 (1 long subterminal, 2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 175a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 175b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 176a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 176b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 177a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 175c, 177a, b): each fork relatively long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

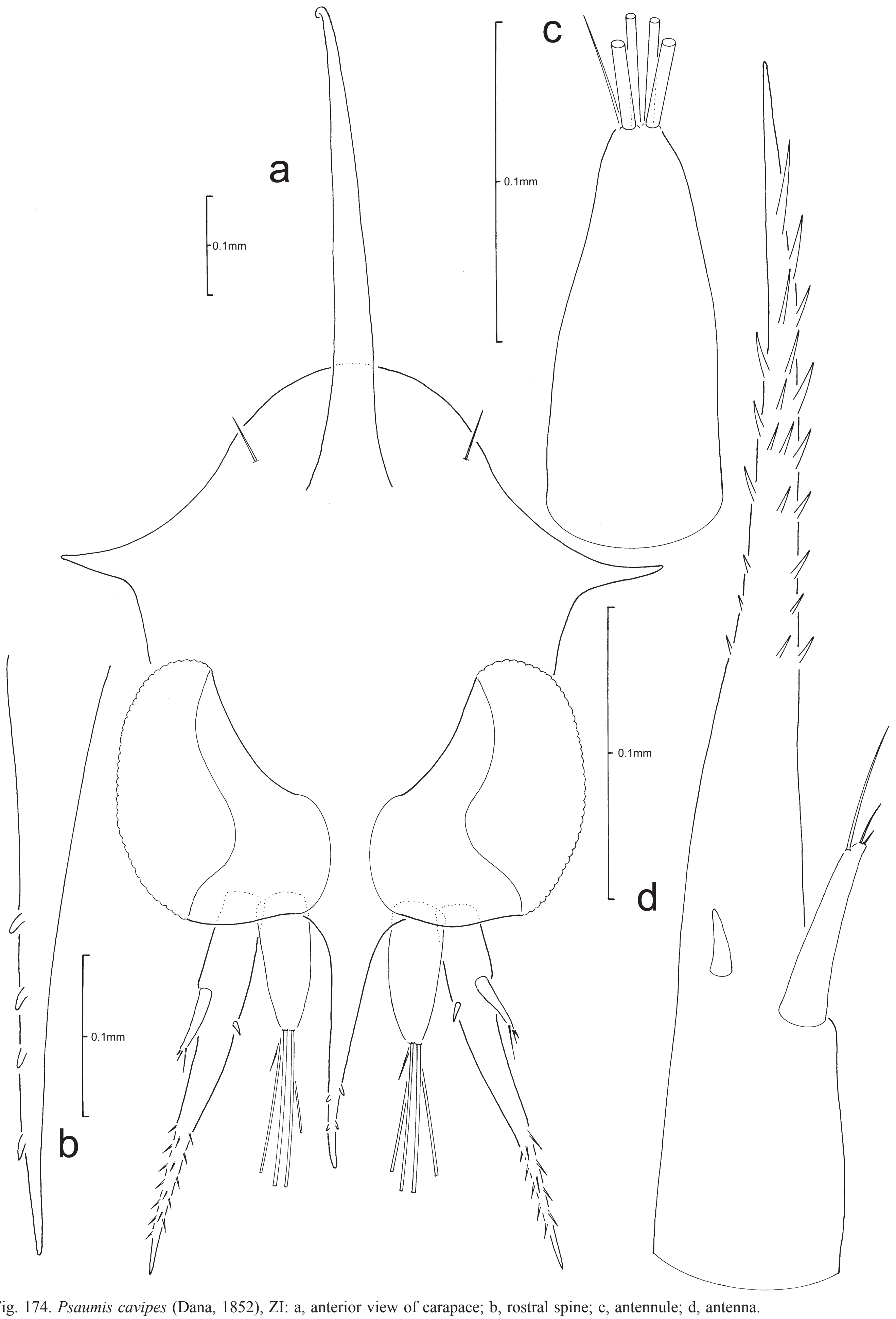

Fig. 174. *Psaumis cavipes* (Dana, 1852), ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

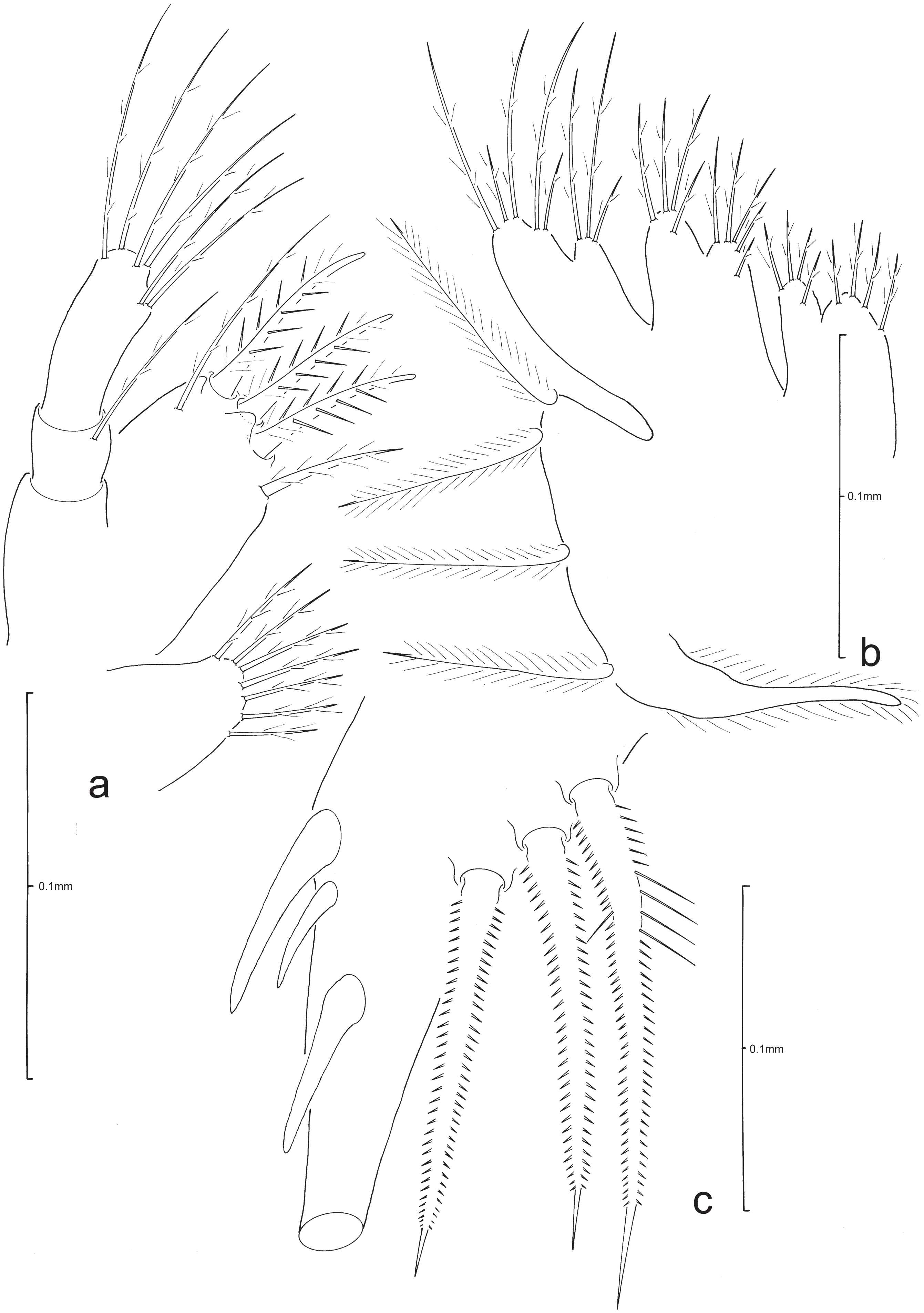

Fig. 175. *Psaumis cavipes* (Dana, 1852), ZI: a, maxillule; b, maxilla; c, telson.

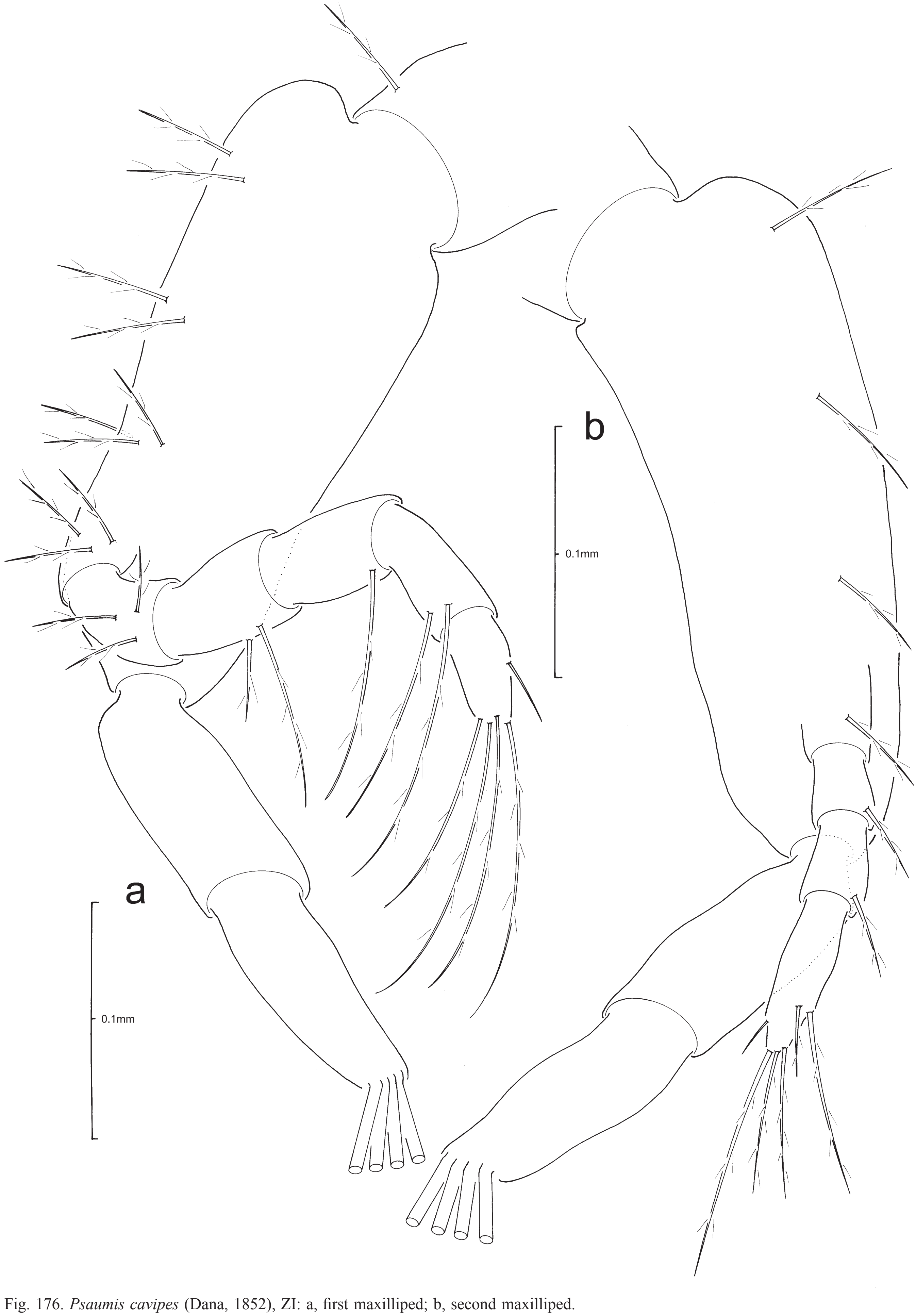

Fig. 176. *Psaumis cavipes* (Dana, 1852), ZI: a, first maxilliped; b, second maxilliped.

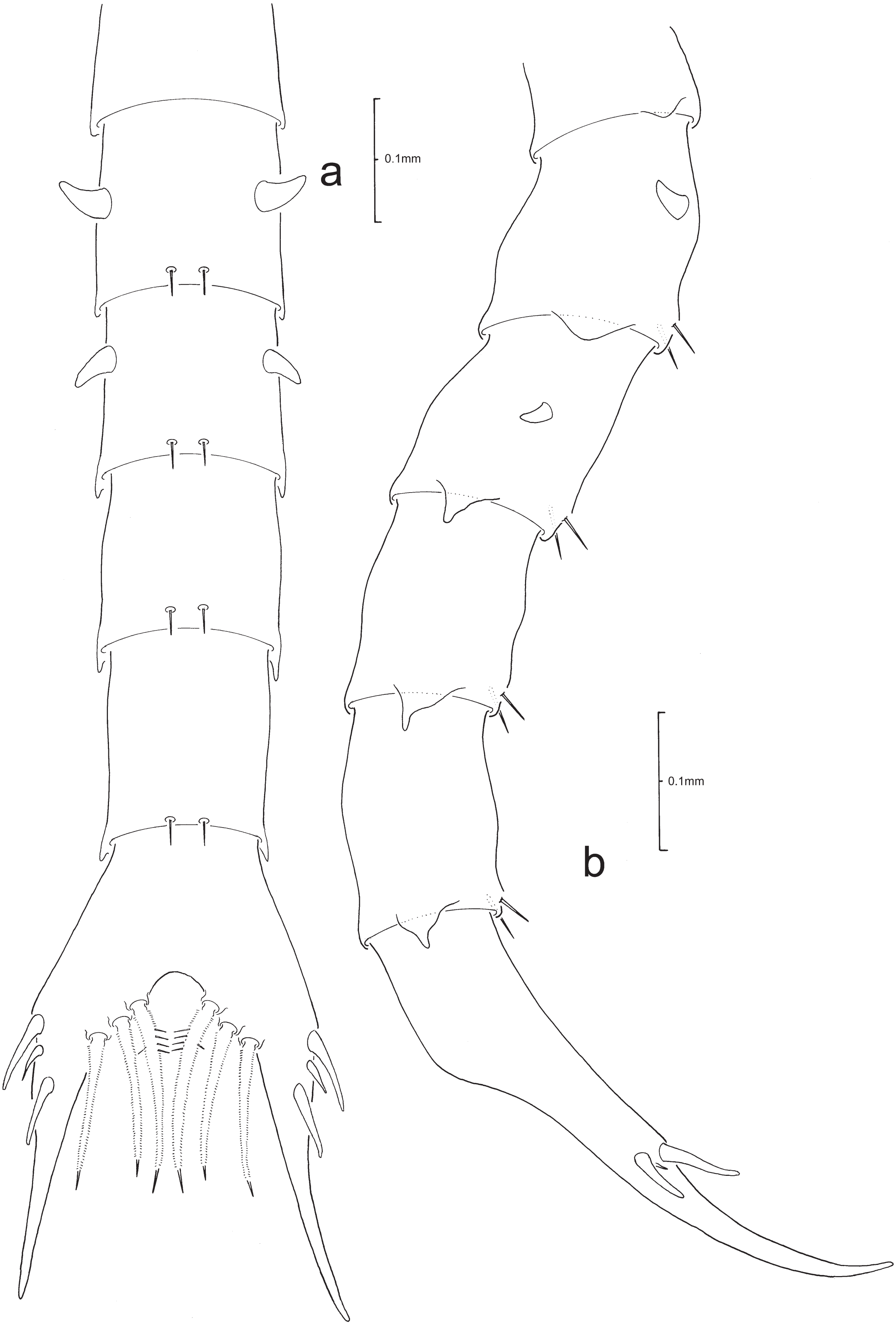

Fig. 177. *Psaumis cavipes* (Dana, 1852), ZI: pleon and telson; a, dorsal view; b, lateral view.

***Pseudactea corallina* (Alcock, 1898)**
(Figs. 178–181)

Description of Zoea I.
CARAPACE (Fig. 178a, b): dorsal spine long, curved distally, longer than rostral spine length; rostral spine ca. equal to antennal protopod length, distally spinulate; lateral spines straight, spinulated on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 176a): sessile.
Antennule (Fig. 178c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 178d): biramous; protopodal process distally multispinulate, ca. equal to rostral spine length; endopod spine present; exopod ca. 9.3% length of protopod, possessing 3 (1 subterminal+2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 179a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 179b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 180a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 180b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 181a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; somite 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 179c, 181a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

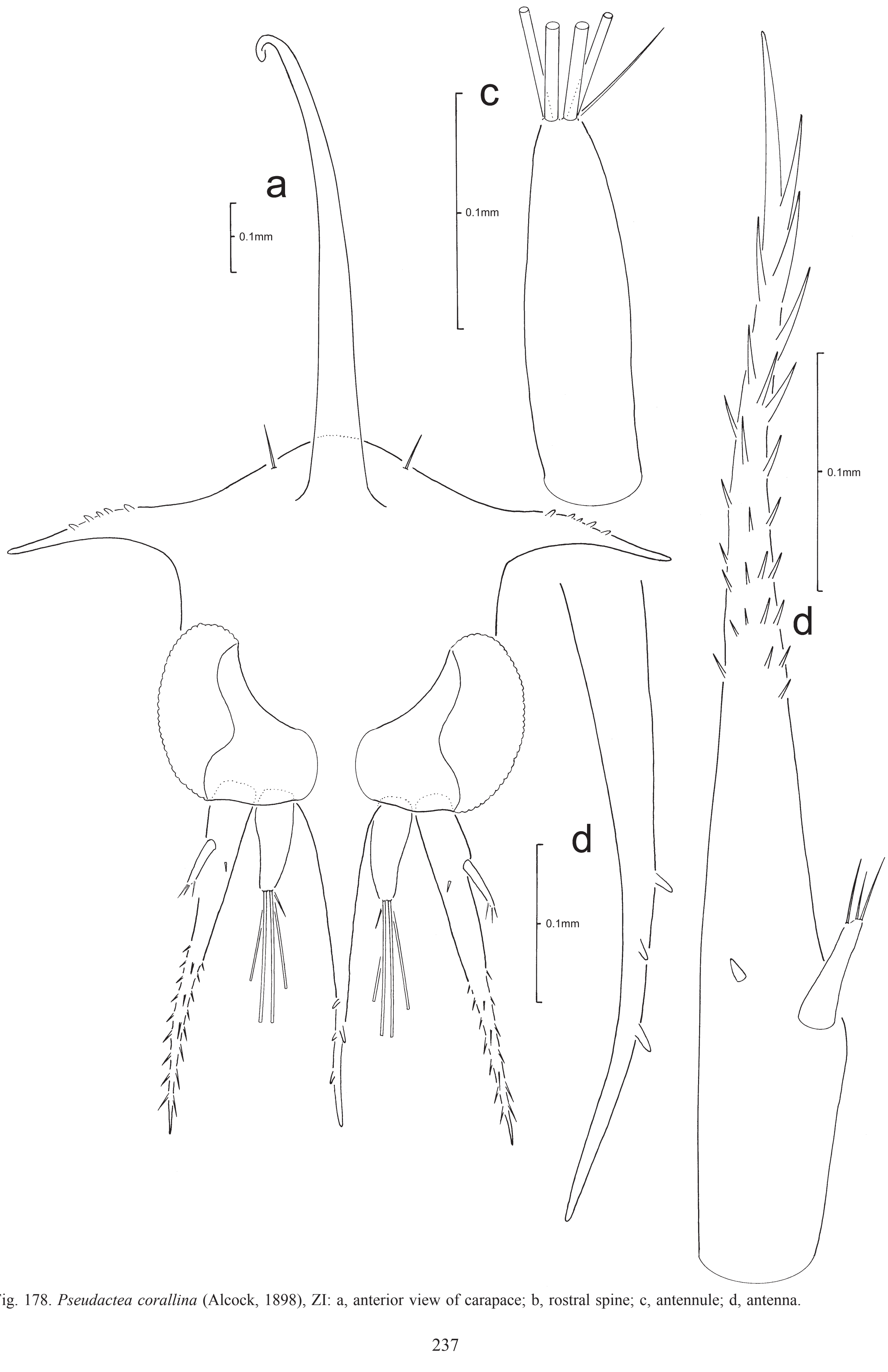

Fig. 178. *Pseudactea corallina* (Alcock, 1898), ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

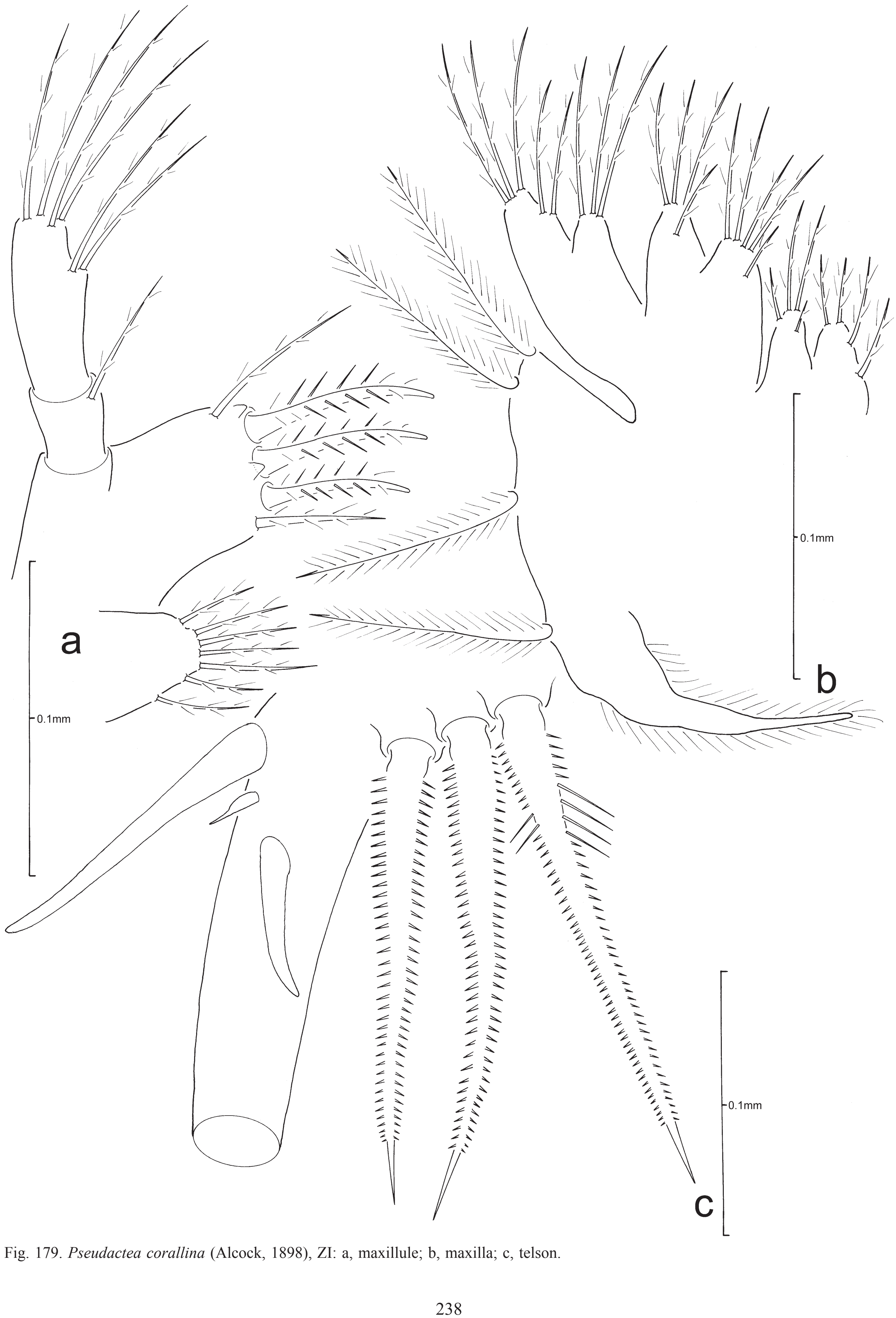

Fig. 179. *Pseudactea corallina* (Alcock, 1898), ZI: a, maxillule; b, maxilla; c, telson.

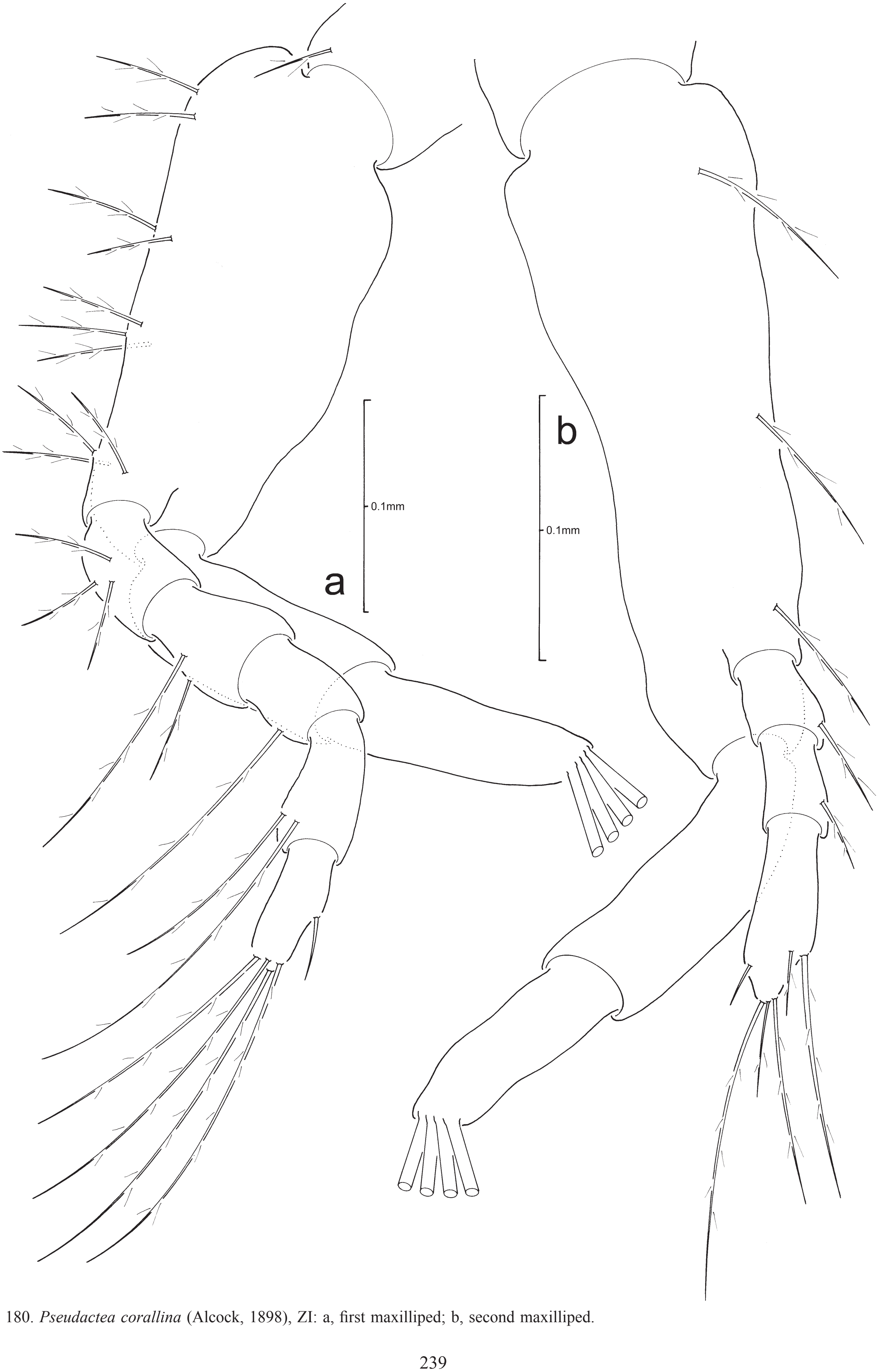

Fig. 180. *Pseudactea corallina* (Alcock, 1898), ZI: a, first maxilliped; b, second maxilliped.

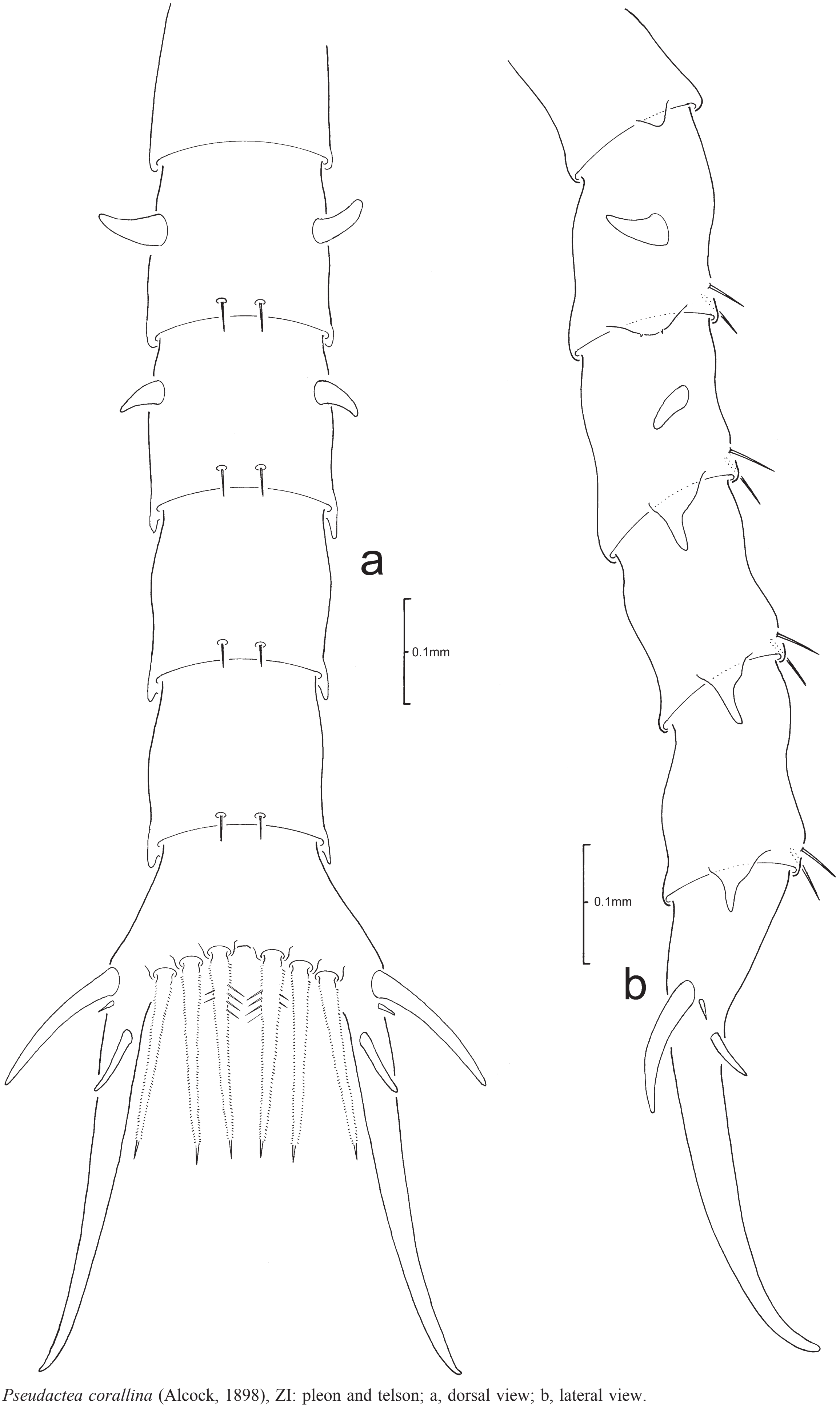

Fig. 181. *Pseudactea corallina* (Alcock, 1898), ZI: pleon and telson; a, dorsal view; b, lateral view.

Subfamily Banareiinae Števčić, 2005

***Banareia subglobosa* (Stimpson, 1858)**
(Figs. 182–185)

Description of Zoea I.
CARAPACE (Fig. 182a): dorsal spine relatively long, curved distally, longer than rostral spine length; rostral spine ca. equal to antennal protopod length, distally without spinulation; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 182a): sessile.
Antennule (Fig. 182b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 182c): biramous; protopodal process distally multispinulate, ca. equal to rostral spine length; endopod spine present; exopod ca. 10.6% length of protopod, possessing 3 (1 long subterminal+2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 183a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 183b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 2+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 184a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 184b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 185a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 183c, 185a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 lateral seta, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

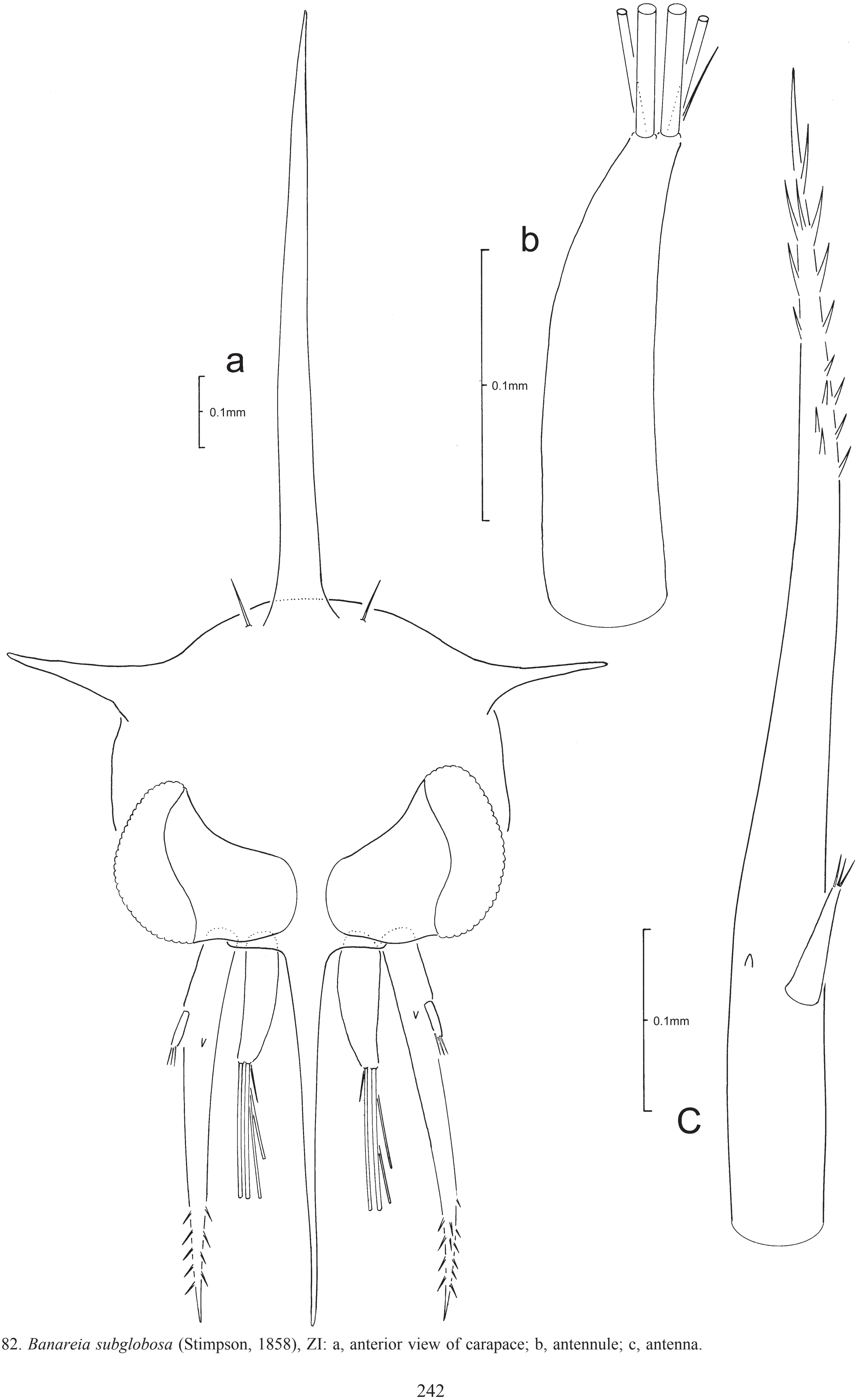

Fig. 182. *Banareia subglobosa* (Stimpson, 1858), ZI: a, anterior view of carapace; b, antennule; c, antenna.

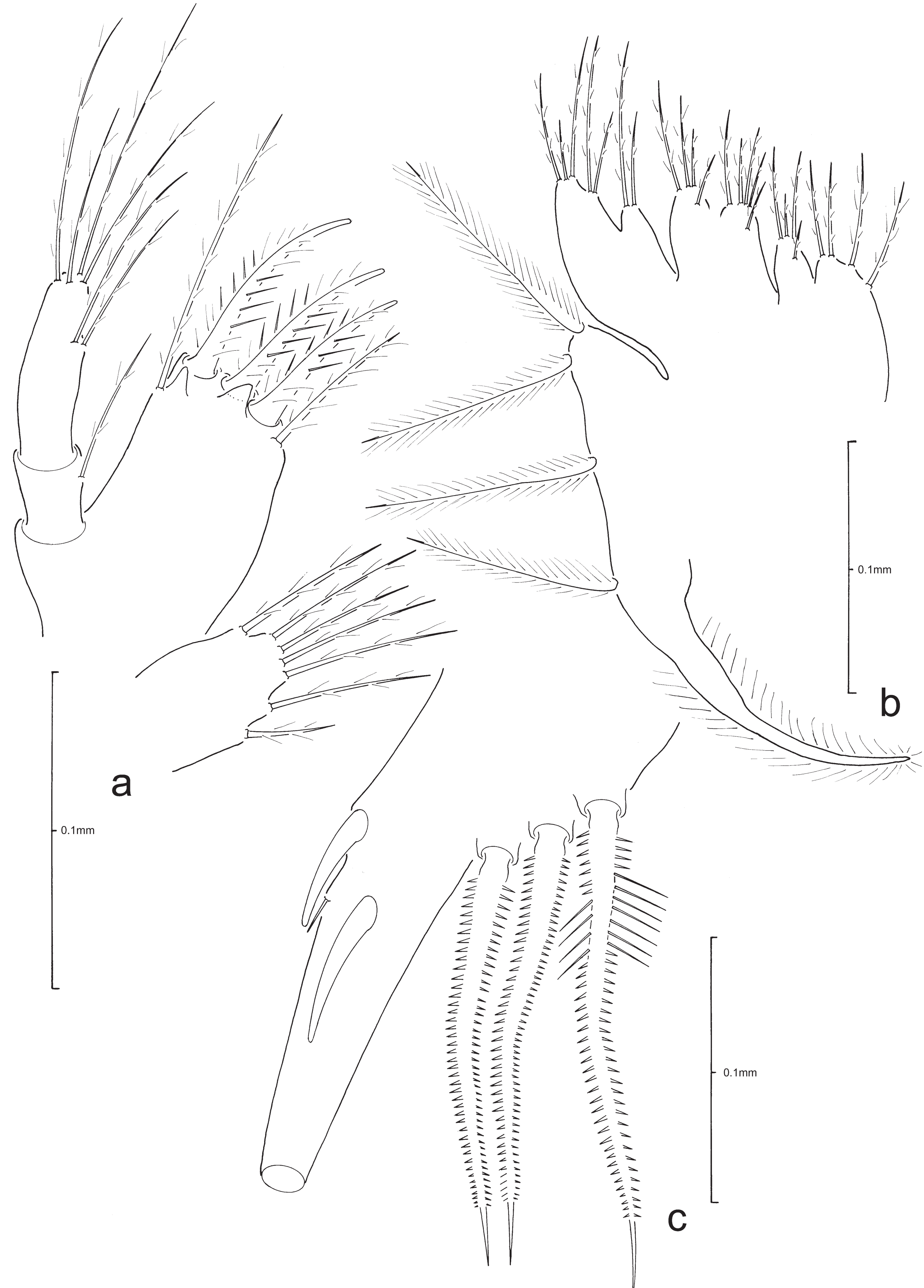

Fig. 183. *Banareia subglobosa* (Stimpson, 1858), ZI: a, maxillule; b, maxilla; c, telson.

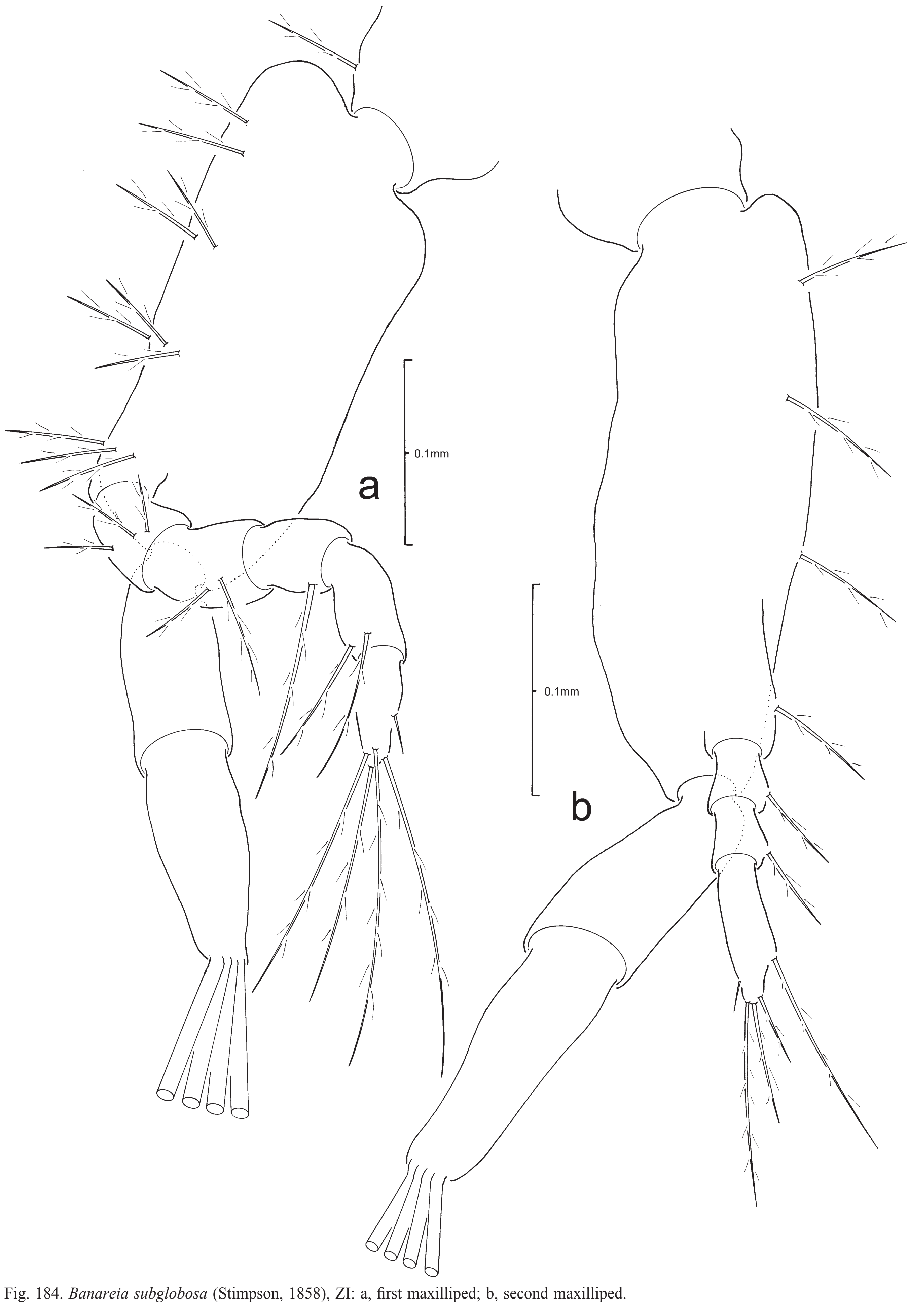

Fig. 184. *Banareia subglobosa* (Stimpson, 1858), ZI: a, first maxilliped; b, second maxilliped.

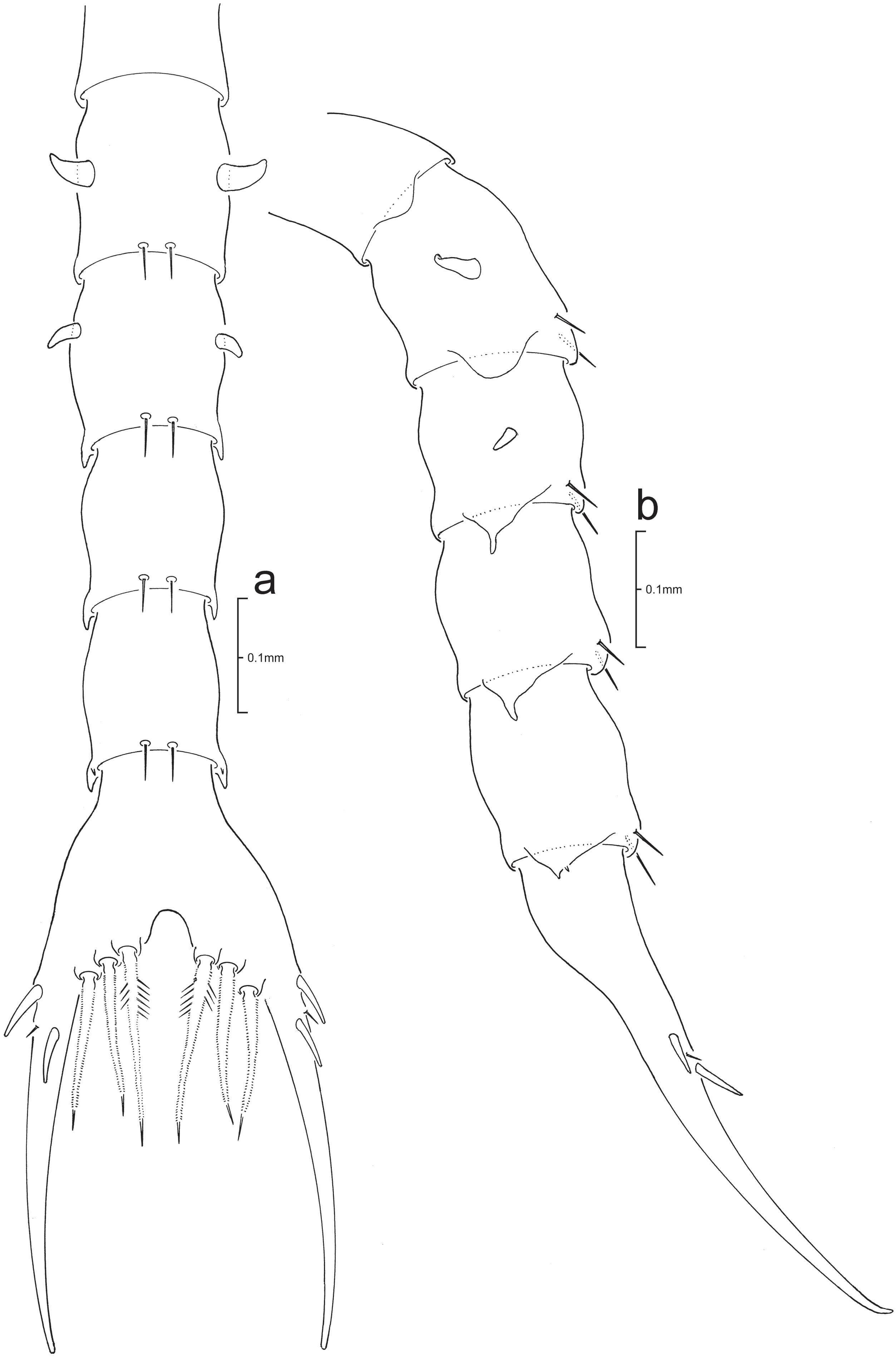

Fig. 185. *Banareia subglobosa* (Stimpson, 1858), ZI: pleon and telson; a, dorsal view; b, lateral view.

Subfamily Cymoinae Alcock, 1898

Cymo lanatopodus Galil & Vannini, 1990
(Figs. 186–189)

Description of Zoea I.
CARAPACE (Fig. 186a, b): dorsal spine long, curved distally, longer than rostral spine length; rostral spine shorter than antennal protopod length, distally spinulate; lateral spines straight, without distal spinulation; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 186a): sessile.
Antennule (Fig. 186c): uniramous; primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 186d): biramous; protopodal process distally multispinulate, longer than rostral spine length; endopod spine present; exopod ca. 16.3% length of protopod, possessing 3 (1 long subterminal+2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 187a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 187b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 188a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 188b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 189a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomere 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 187c, 189a, b): each fork relatively long, gradually curved distally, not spinulate, 1 large lateral spine, 1 shorter lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

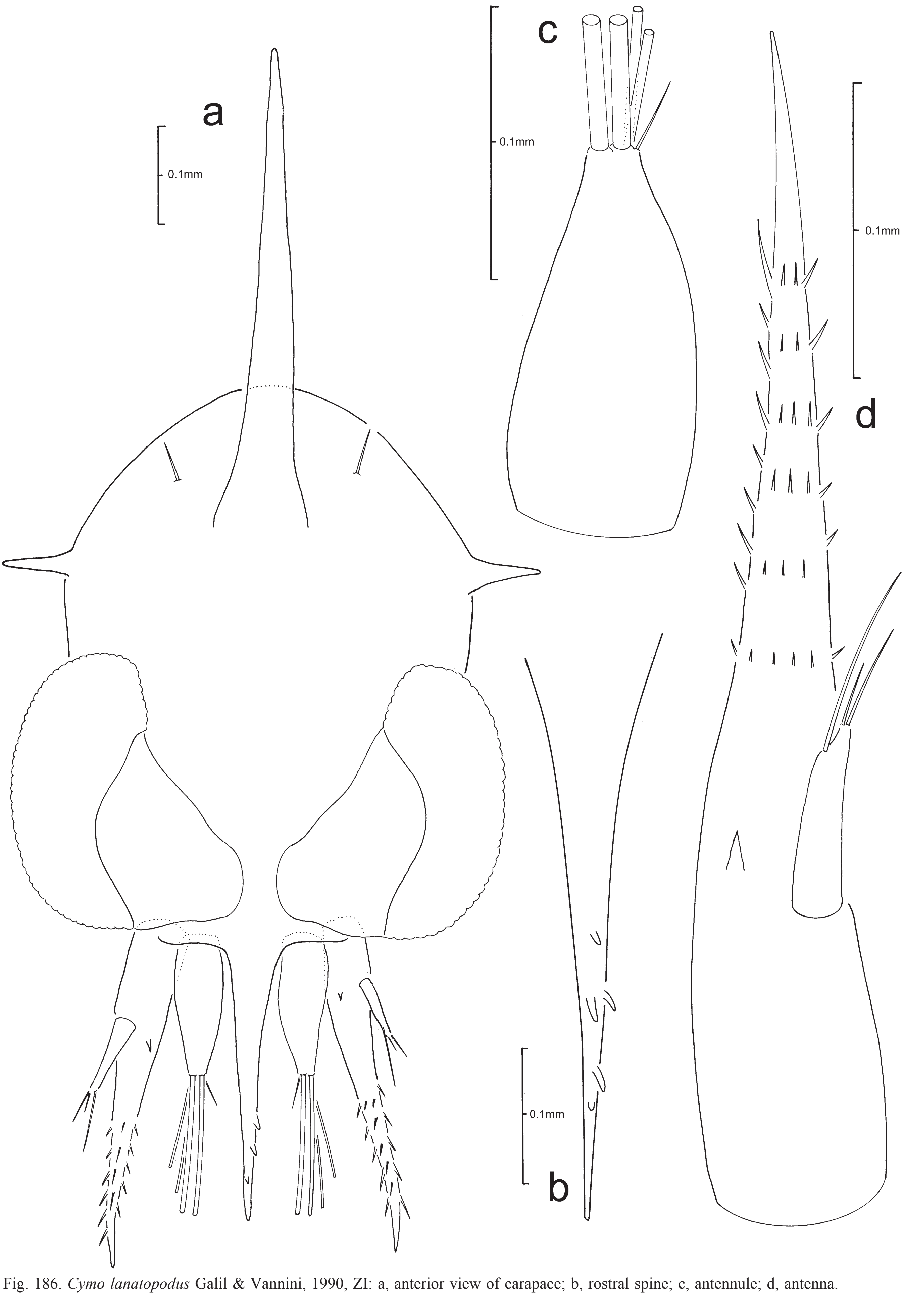

Fig. 186. *Cymo lanatopodus* Galil & Vannini, 1990, ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

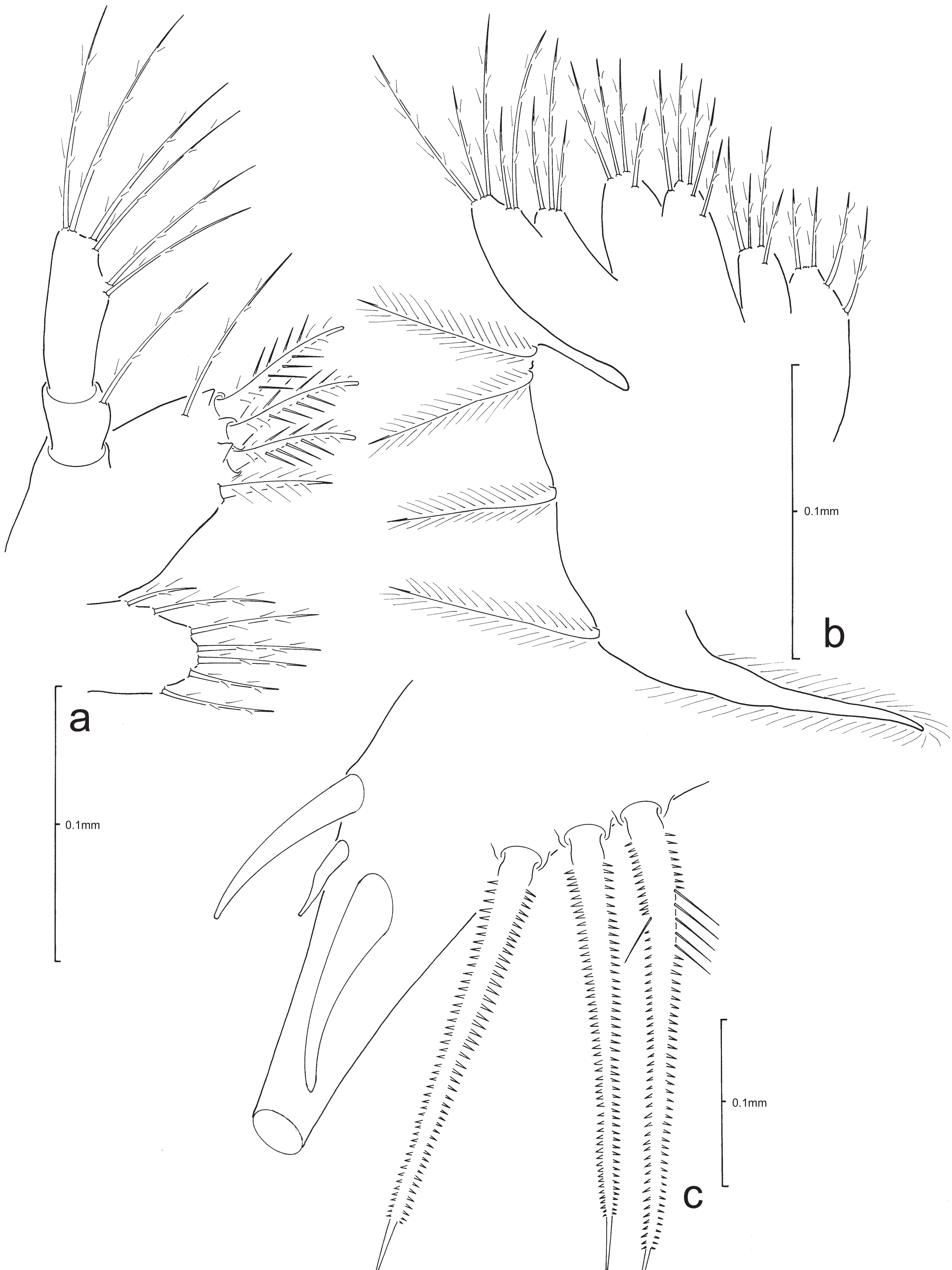

Fig. 187. *Cymo lanatopodus* Galil & Vannini, 1990, ZI: a, maxillule; b, maxilla; c, telson.

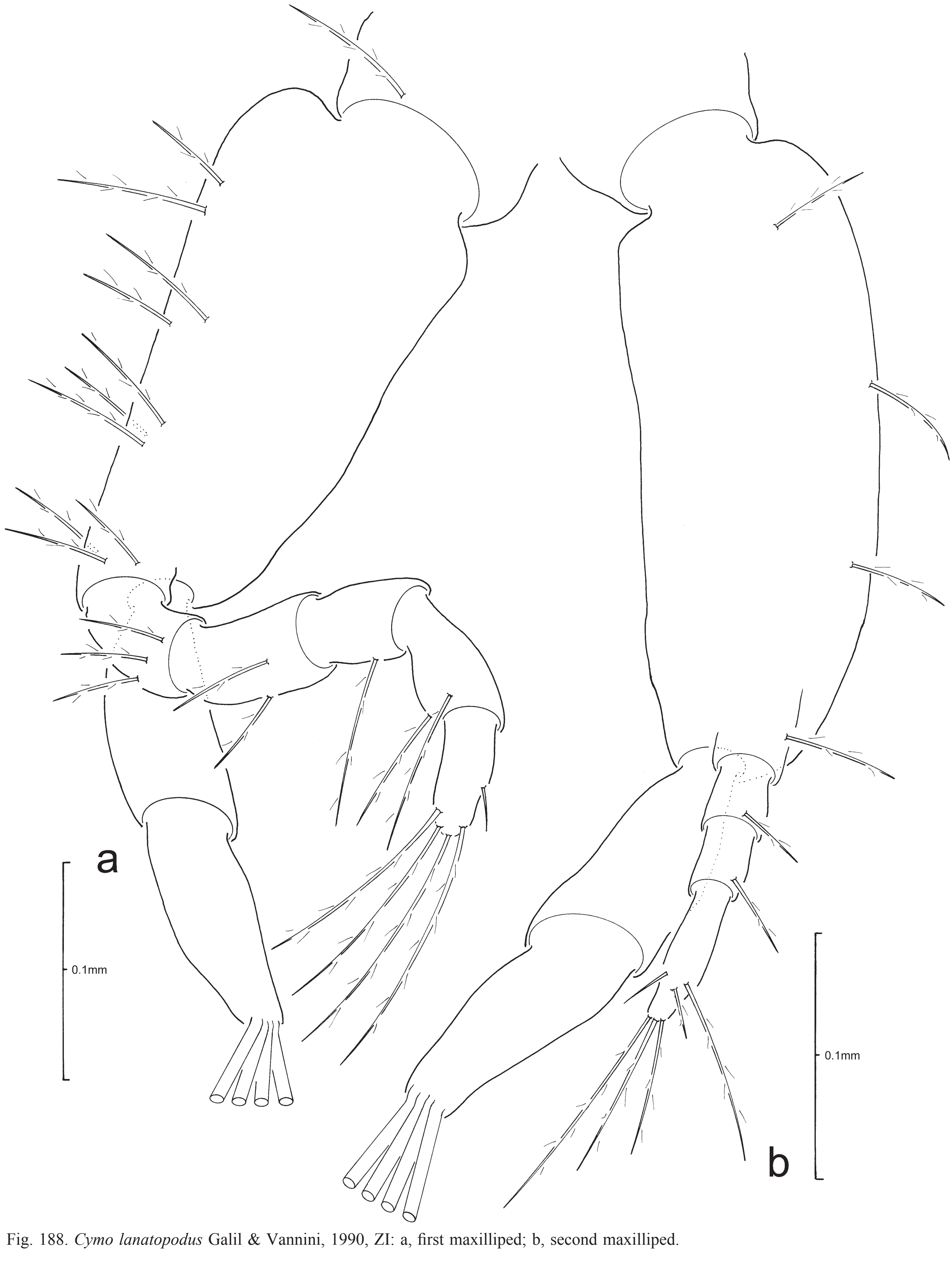

Fig. 188. *Cymo lanatopodus* Galil & Vannini, 1990, ZI: a, first maxilliped; b, second maxilliped.

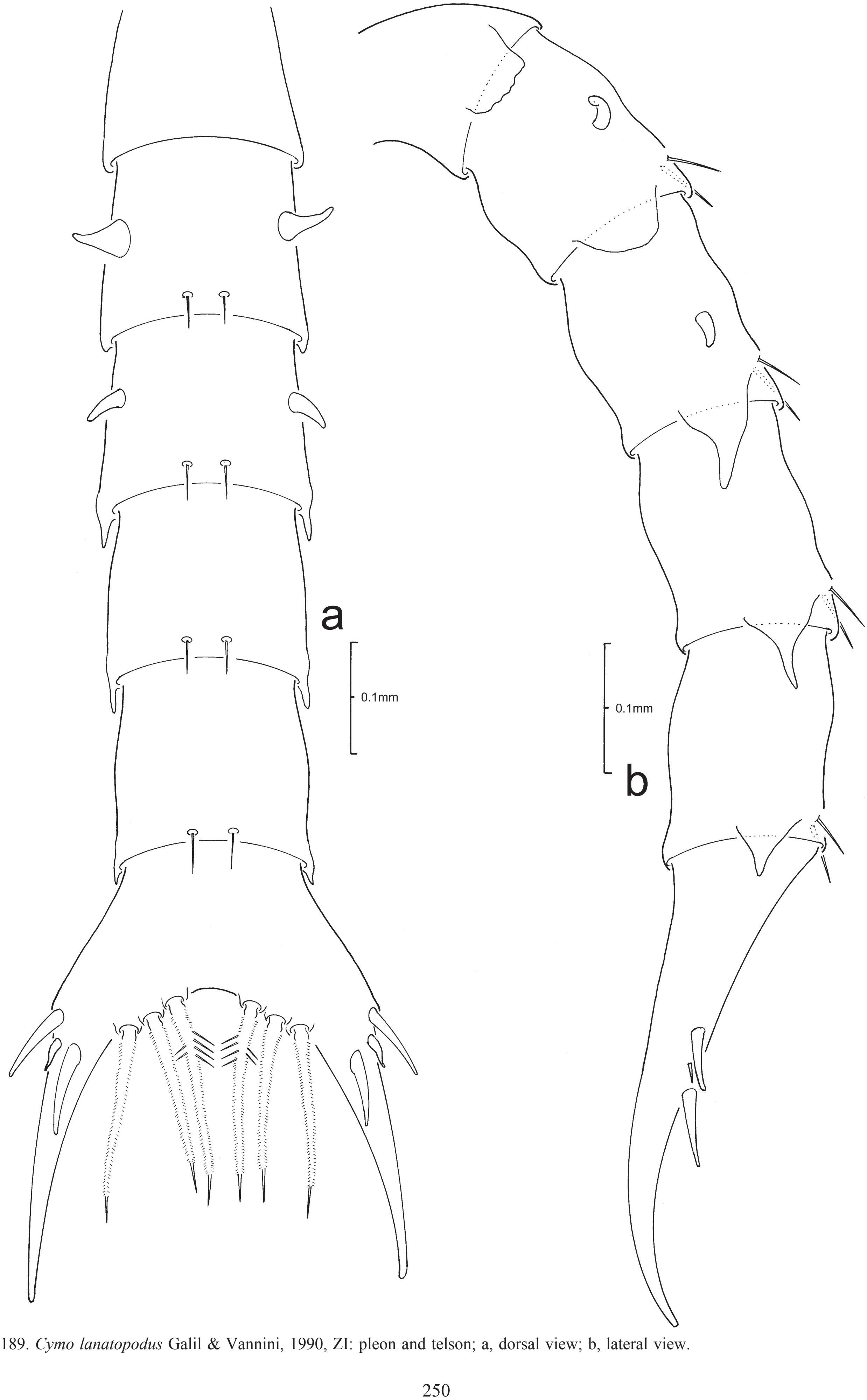

Fig. 189. *Cymo lanatopodus* Galil & Vannini, 1990, ZI: pleon and telson; a, dorsal view; b, lateral view.

***Cymo melanodactylus* Dana, 1853**
(Figs. 190–193)

Cymo andreossyi var. *melanodactylus*. Gurney, 1938: 76, pl. I, figs. 11–13, pl. II, figs. 14–18 (PZ, ZI).

Description of Zoea I.
CARAPACE (Fig. 190a, b): dorsal spine long, curved distally, longer than rostral spine length; rostral spine shorter than antennal protopod length, distally spinulate; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 190a): sessile.
Antennule (Fig. 190c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 190d): biramous; protopodal process distally multispinulate, longer than rostral spine length; endopod spine present; exopod ca. 14% length of protopod, possessing 3 (1 long subterminal+2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 191a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 191b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 192a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 192b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 193a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 191c, 193a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 finer lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Remarks. There are some minor problems with R. Gurney (1938: 76) because in his text he states that the prezoea is illustrated on his pl. I, figs. 11–13, while the caption indicates that these refer to *Chlorodopsis spinipes*. Furthermore, in his text R. Gurney describes the distal endopod article of the second maxilliped with six setae in comparison to his figure (R. Gurney, 1938: fig. 18) which illustrates only five. Robert Gurney does not describe all the zoeal appendages for *C. melanodactylus*.

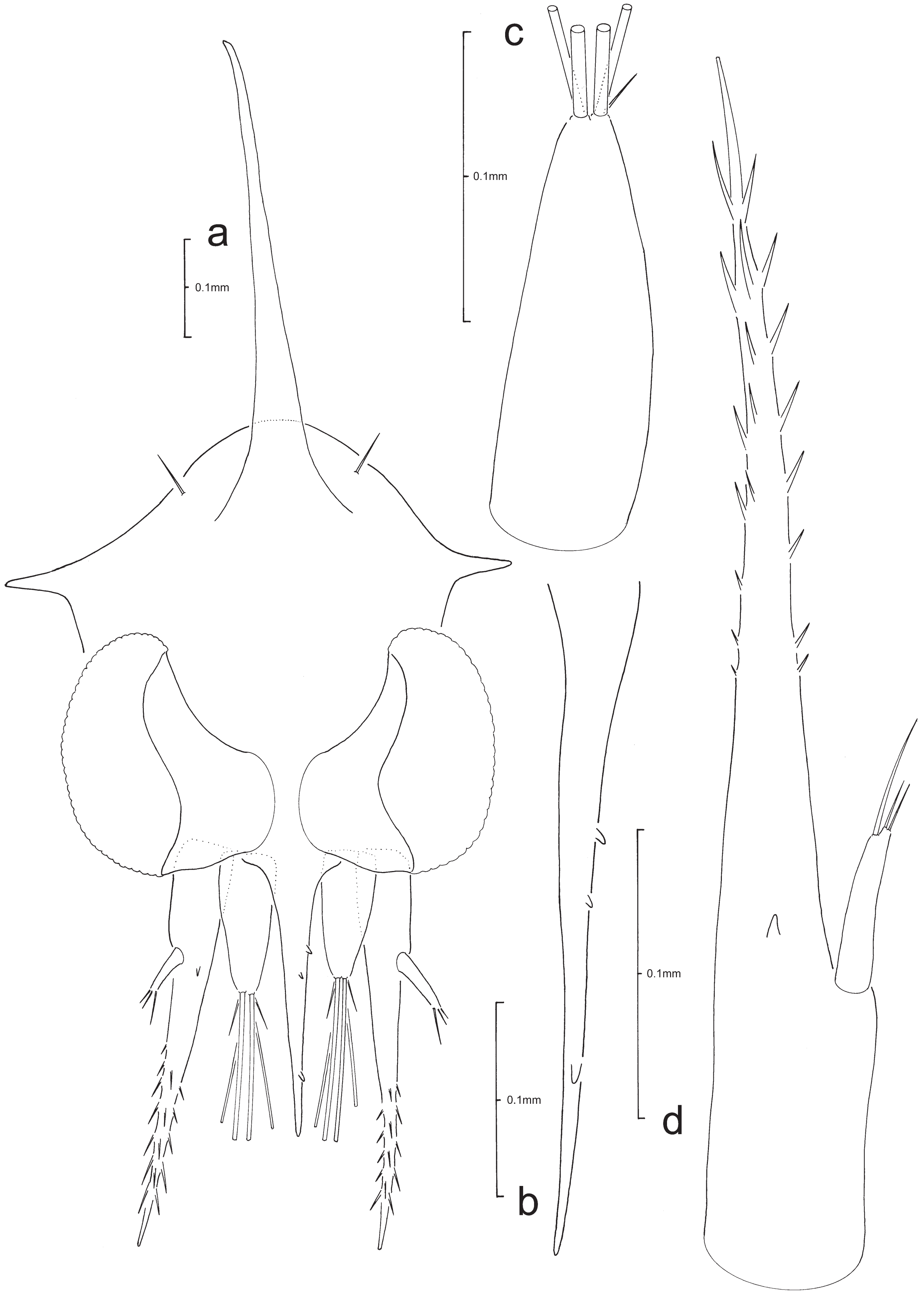

Fig. 190. *Cymo melanodactylus* Dana, 1853, ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

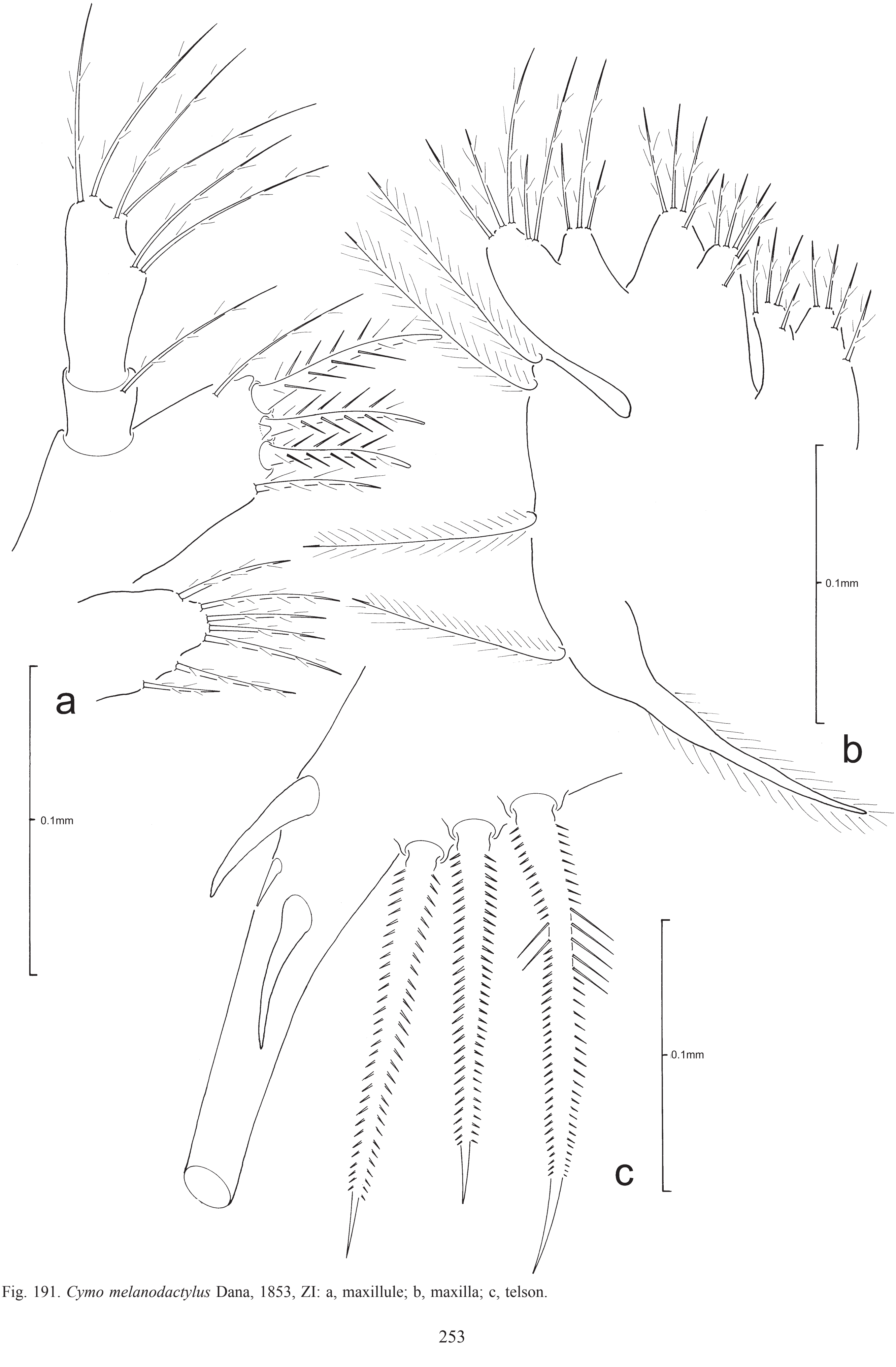

Fig. 191. *Cymo melanodactylus* Dana, 1853, ZI: a, maxillule; b, maxilla; c, telson.

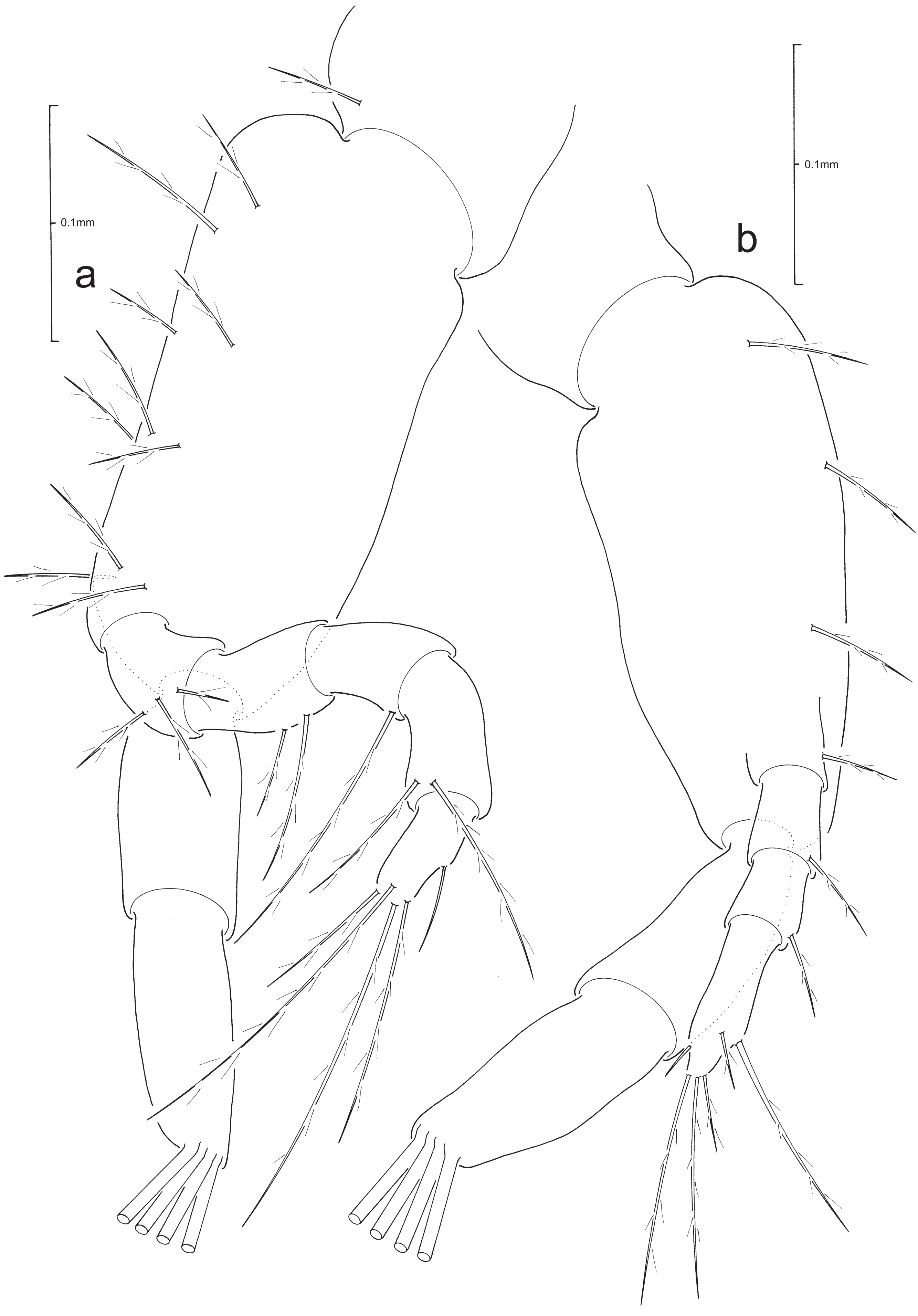

Fig. 192. *Cymo melanodactylus* Dana, 1853, ZI: a, first maxilliped; b, second maxilliped.

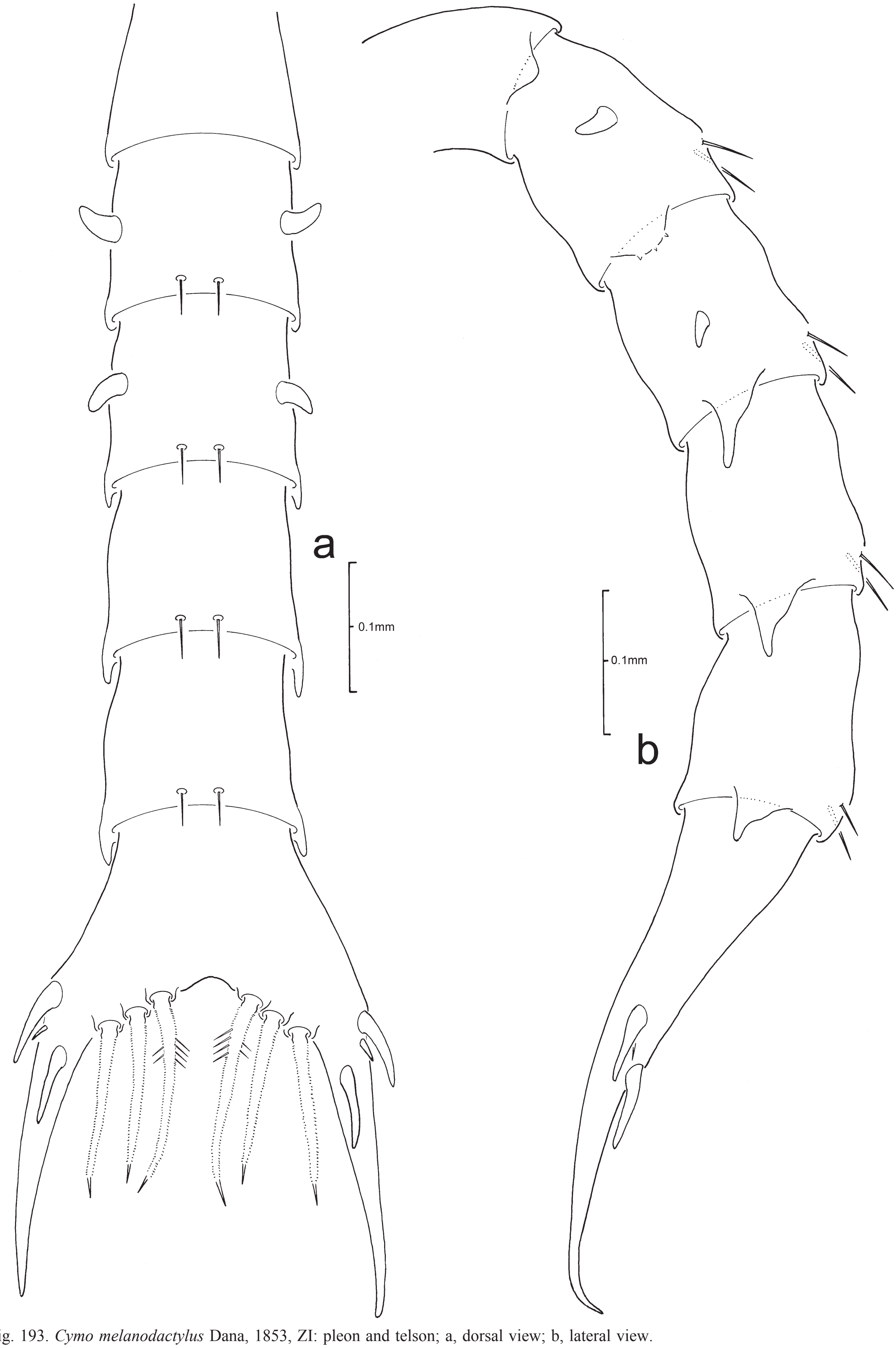

Fig. 193. *Cymo melanodactylus* Dana, 1853, ZI: pleon and telson; a, dorsal view; b, lateral view.

Subfamily Etisinae Ortmann, 1893

Etisus anaglyptus H. Milne Edwards, 1834
(Figs. 194–197)

Description of Zoea I.
CARAPACE (Fig. 194a, b): dorsal spine long, curved distally, longer than rostral spine length; rostral spine shorter than antennal protopod length, distally spinulate; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 194a): sessile.
Antennule (Fig. 194c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 194d): biramous; protopodal process distally multispinulate, longer than rostral spine length; endopod spine present; exopod ca. 9.2% length of protopod, possessing 2 terminal setae of unequal lengths.
Mandible: palp absent.
Maxillule (Fig. 195a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 195b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 196a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 196b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal, 1 of which is minute+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 197a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 195c, 197a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

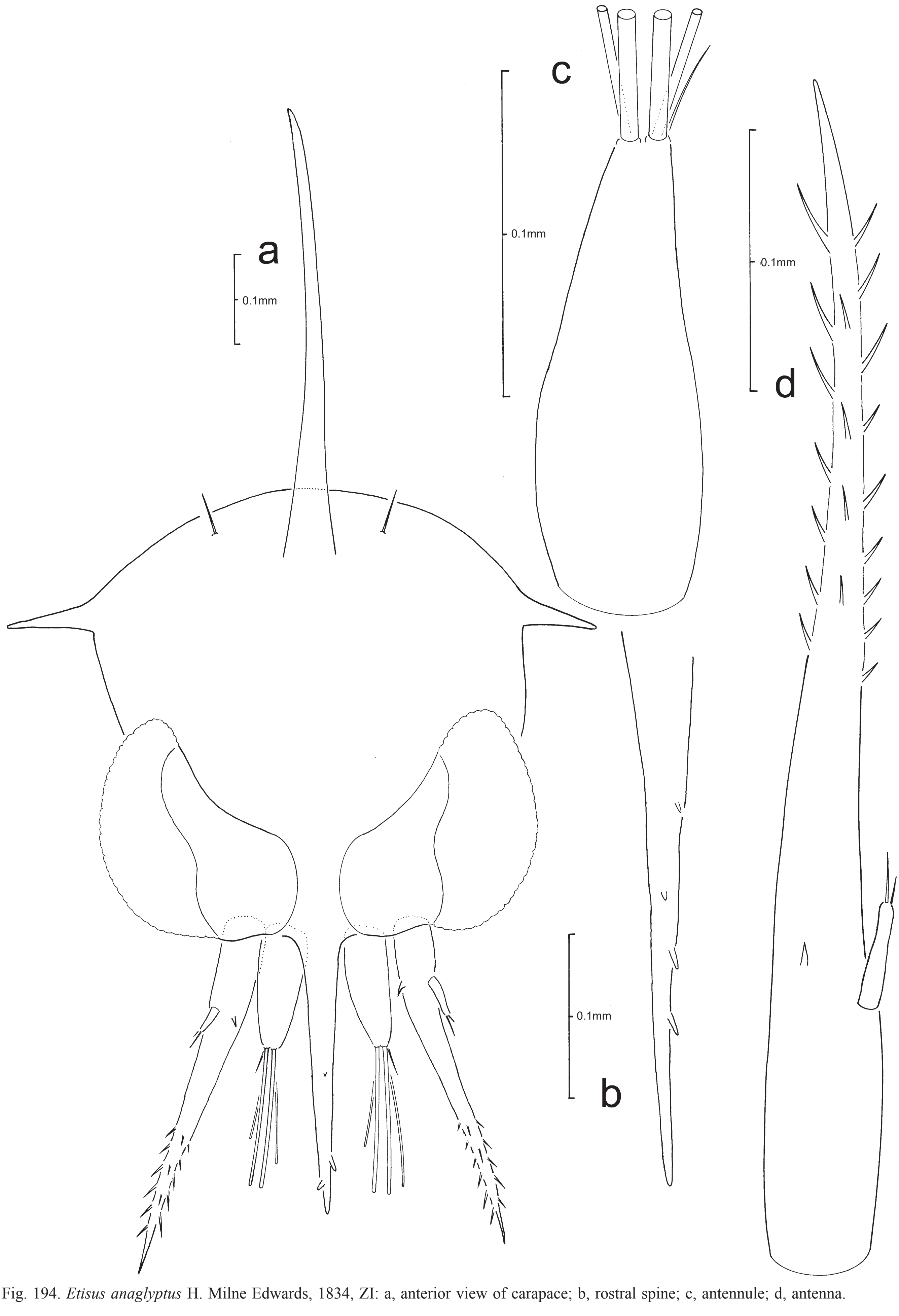

Fig. 194. *Etisus anaglyptus* H. Milne Edwards, 1834, ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

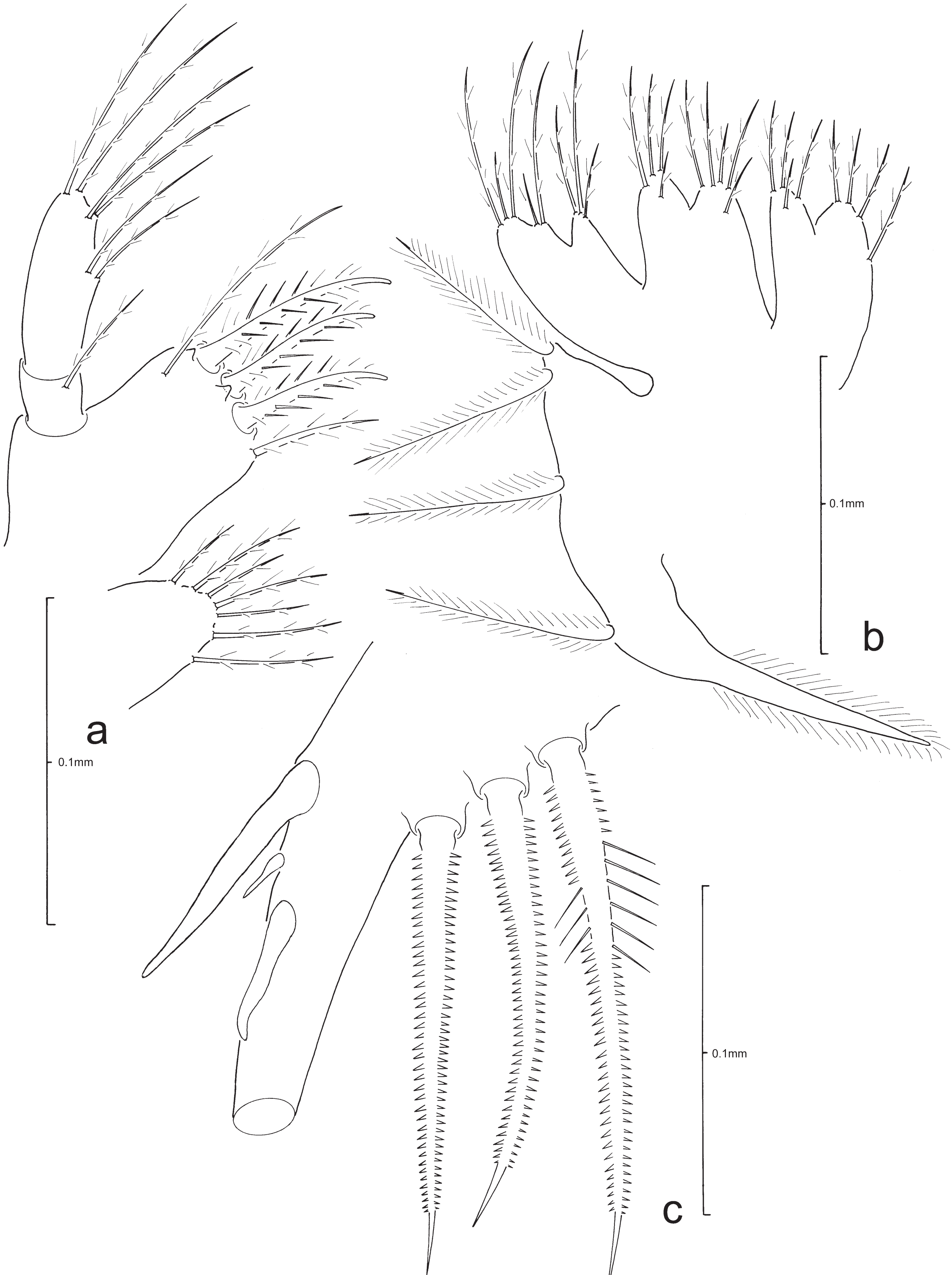

Fig. 195. *Etisus anaglyptus* H. Milne Edwards, 1834, ZI: a, maxillule; b, maxilla; c, telson.

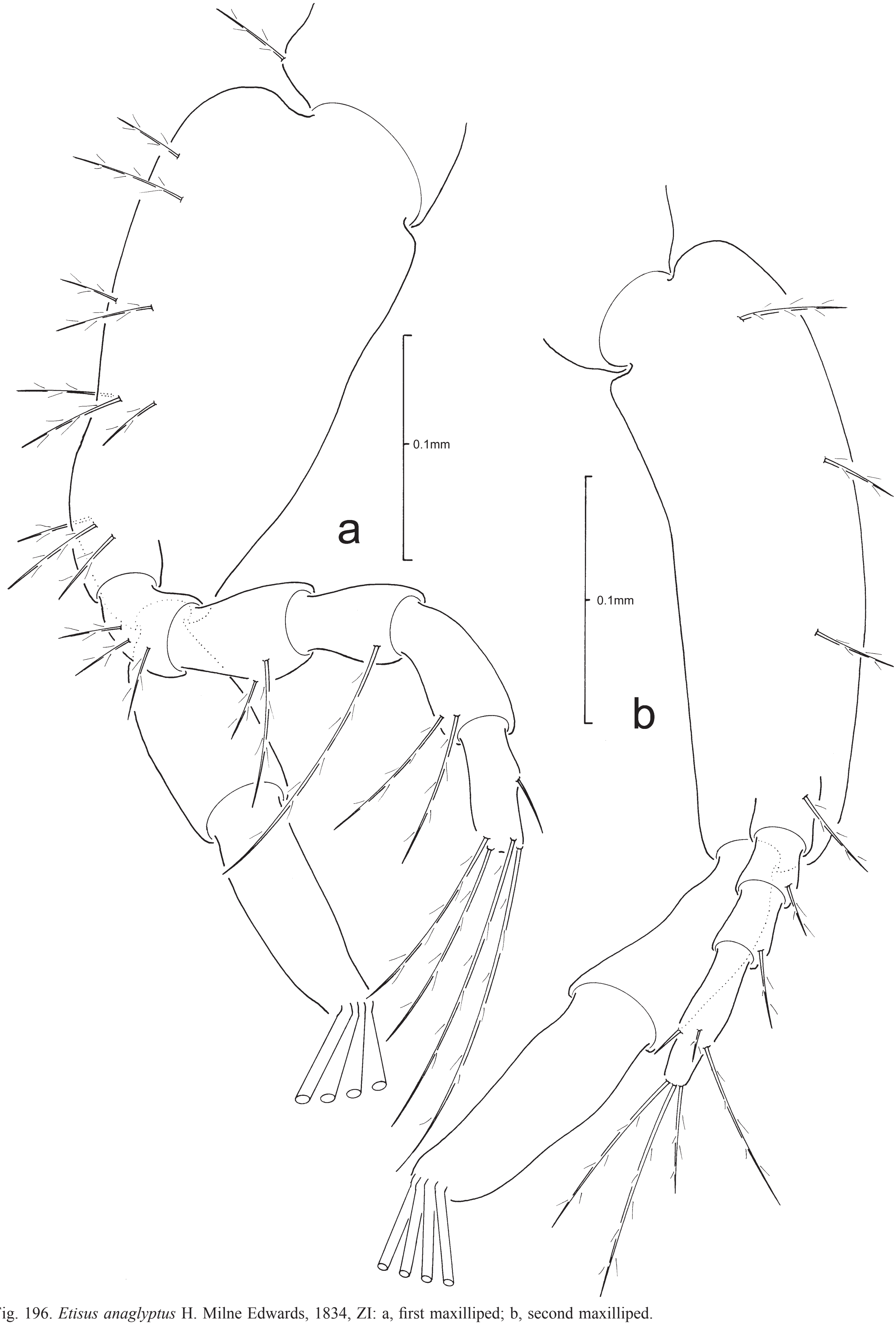

Fig. 196. *Etisus anaglyptus* H. Milne Edwards, 1834, ZI: a, first maxilliped; b, second maxilliped.

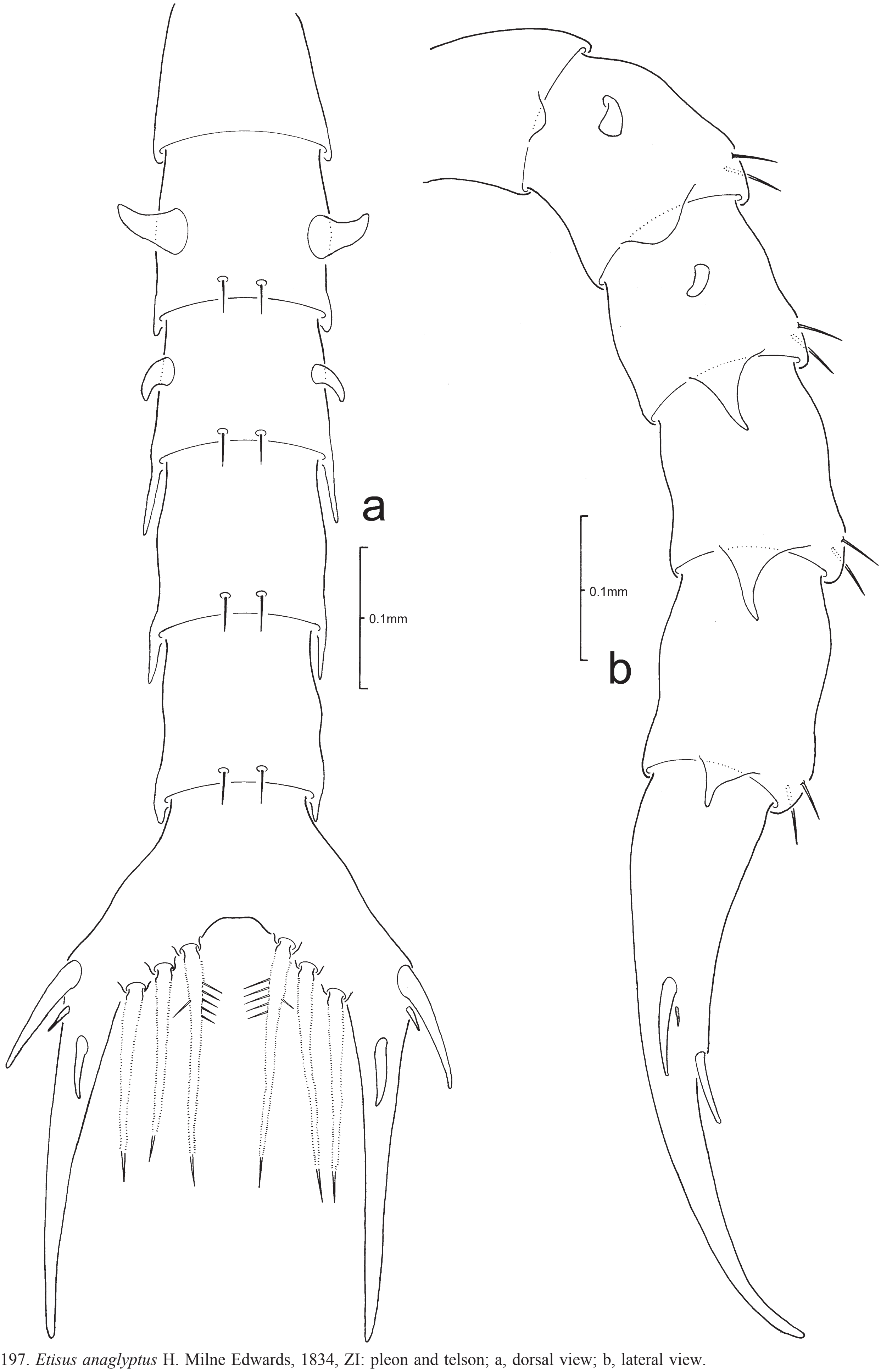

Fig. 197. *Etisus anaglyptus* H. Milne Edwards, 1834, ZI: pleon and telson; a, dorsal view; b, lateral view.

***Etisus frontalis* (Dana, 1852)**
(Figs. 198–201)

Etisus frontalis. Al-Haj & Al-Aidaroos, 2017: 1187, fig. 2 (ZI).

Description of Zoea I.
CARAPACE (Fig. 198a, b): dorsal spine long, curved distally, longer than rostral spine length; rostral spine shorter than antennal protopod length, distally spinulate; lateral spines straight, without spinulation on distal margin; anterodorsal setae absent, 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 198a): sessile.
Antennule (Fig. 198c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 198d): biramous; protopodal process distally multispinulate, longer than rostral spine length; endopod spine present; exopod ca. 9.8% length of protopod, possessing 2 terminal setae of unequal lengths.
Mandible: palp absent.
Maxillule (Fig. 199a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 199b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 200a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 200b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal, 1 of which is minute+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 201a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 199c, 201a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

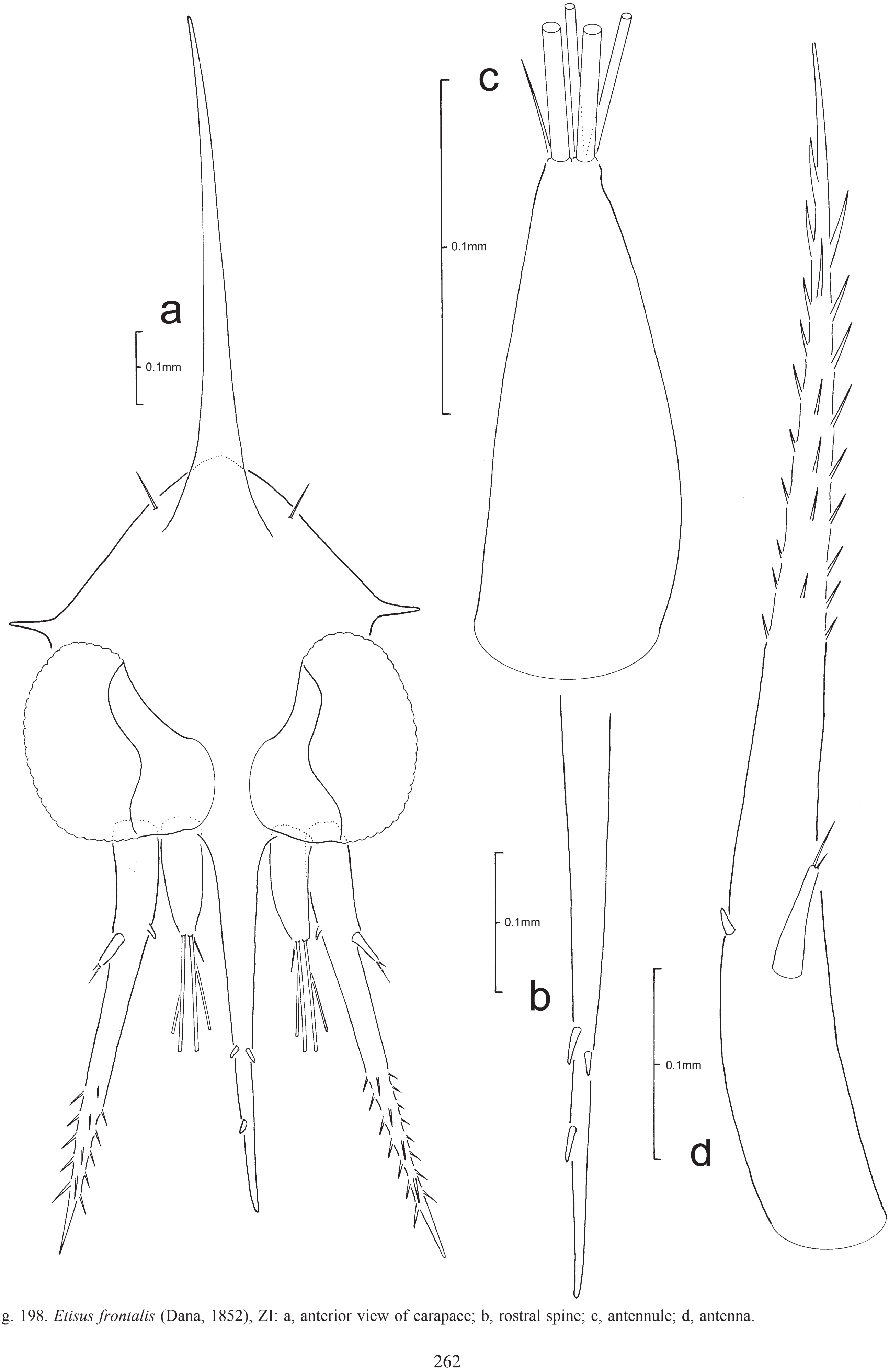

Fig. 198. *Etisus frontalis* (Dana, 1852), ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

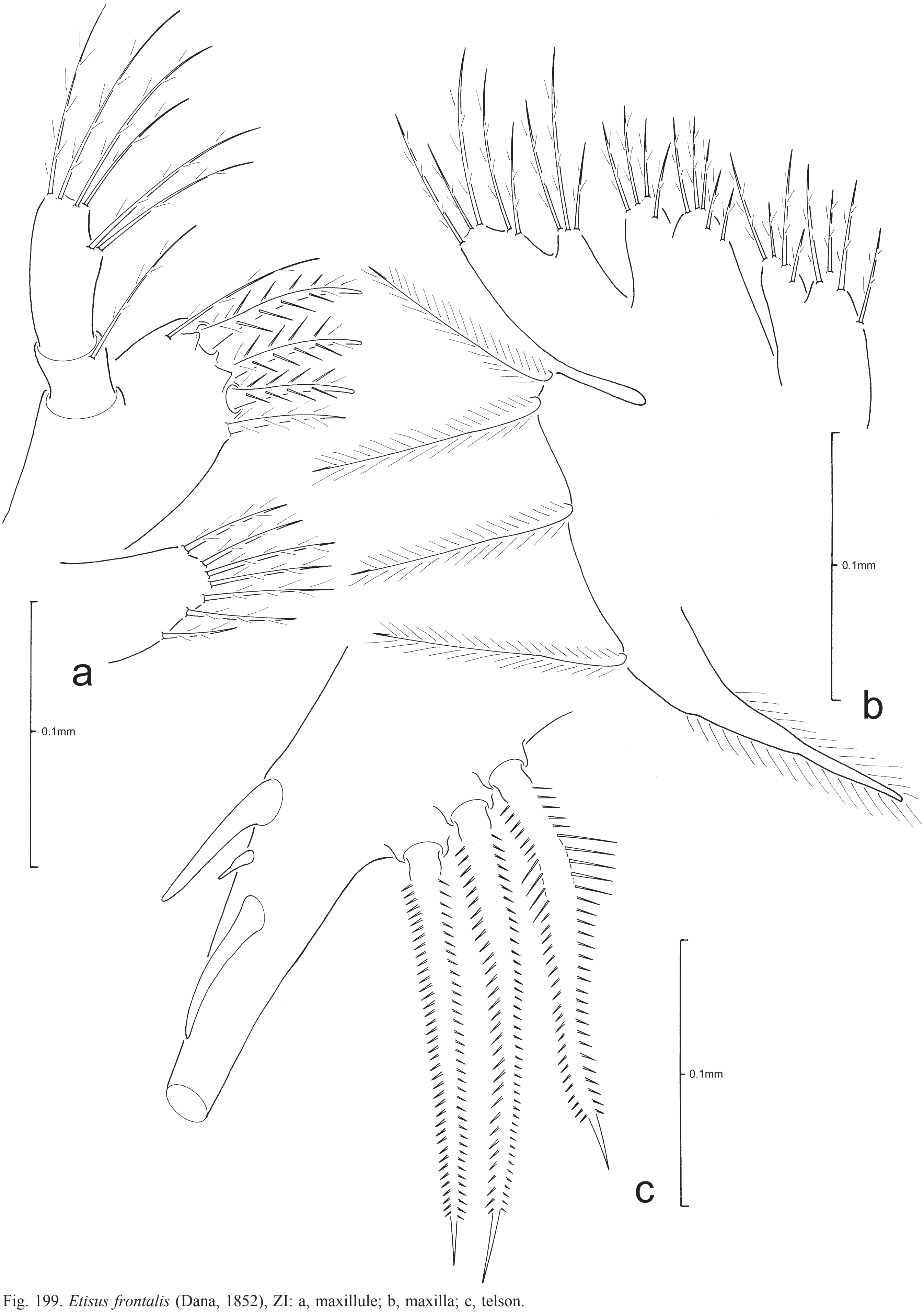

Fig. 199. *Etisus frontalis* (Dana, 1852), ZI: a, maxillule; b, maxilla; c, telson.

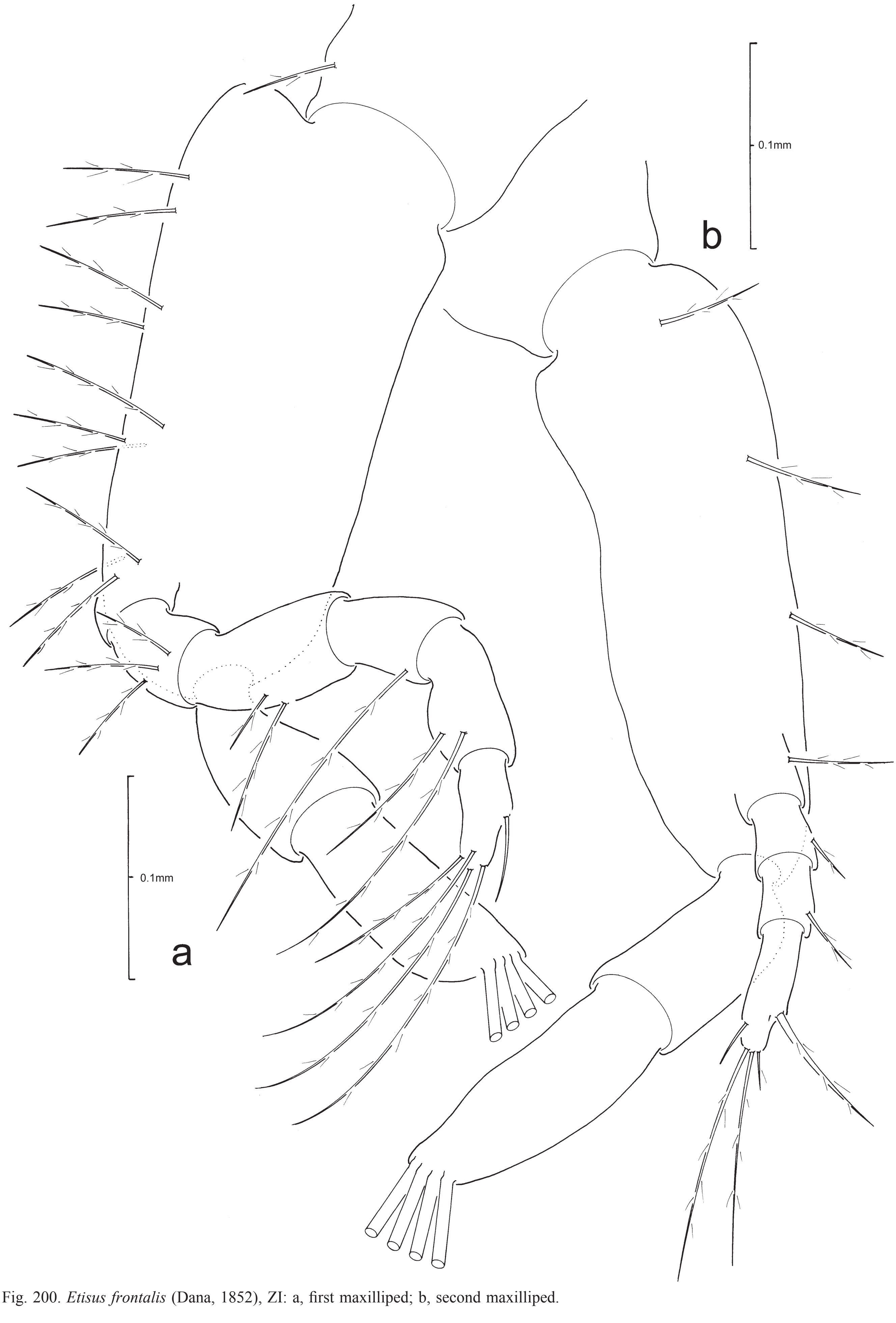

Fig. 200. *Etisus frontalis* (Dana, 1852), ZI: a, first maxilliped; b, second maxilliped.

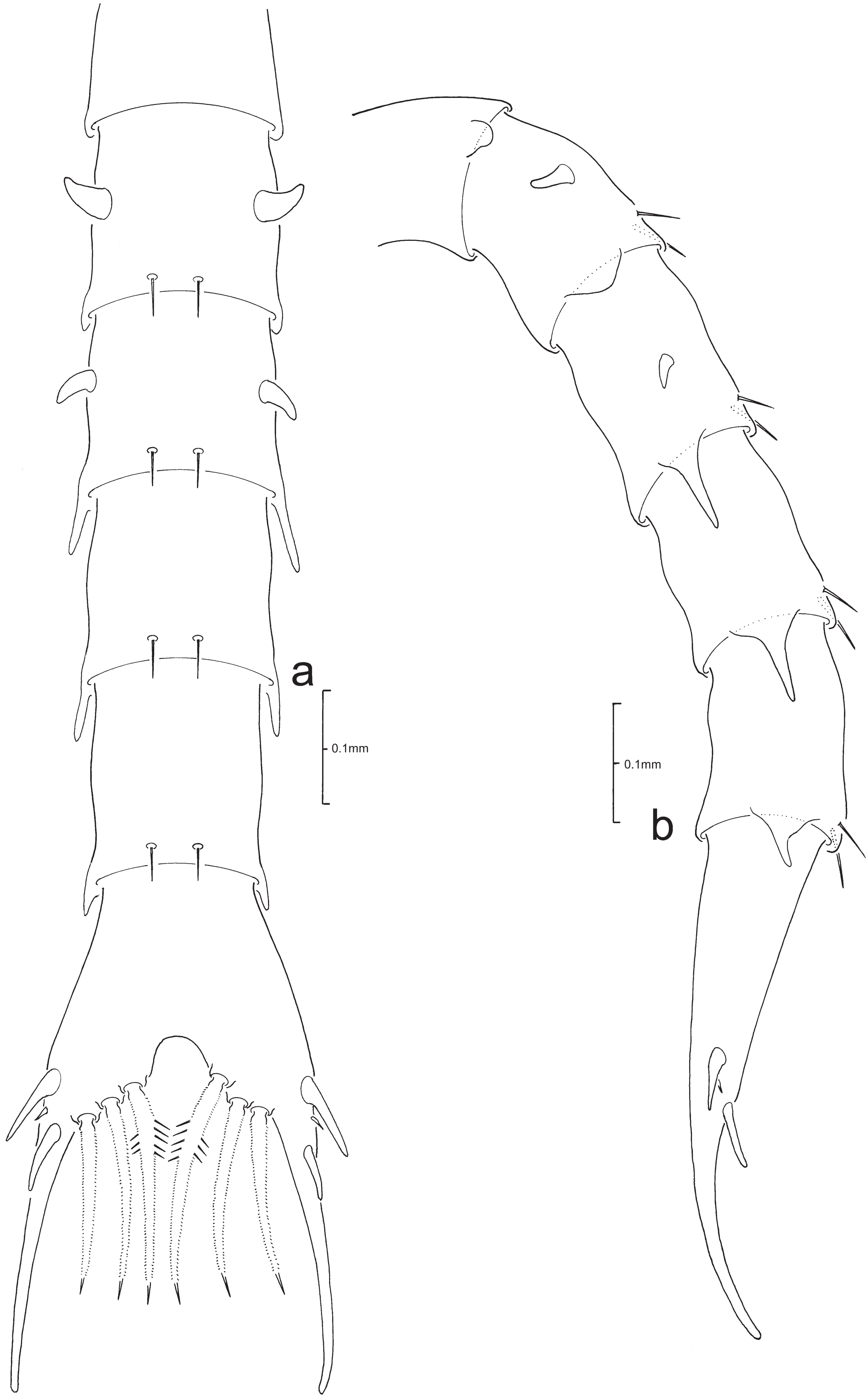

Fig. 201. *Etisus frontalis* (Dana, 1852), ZI: a, dorsal view pleon and telson; b, lateral view.

Etisus utilis H. Jacquinot in H. Jacquinot & Lucas, 1854

(Figs. 202–205)

Description of Zoea I.

CARAPACE (Fig. 202a, b): dorsal spine long, curved distally, longer than rostral spine length; rostral spine shorter than antennal protopod length, distally spinulate; lateral spines straight, without spinulation on distal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON

Eyes (Fig. 202a): sessile.

Antennule (Fig. 202c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.

Antenna (Fig. 202d): biramous; protopodal process distally multispinulate, longer than rostral spine length; endopod spine present; exopod ca. 9.2% length of protopod, possessing 2 terminal setae of unequal lengths.

Mandible: palp absent.

Maxillule (Fig. 203a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.

Maxilla (Fig. 203b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION

First maxilliped (Fig. 204a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 204b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

PLEON (Fig. 205a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 203c, 205a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

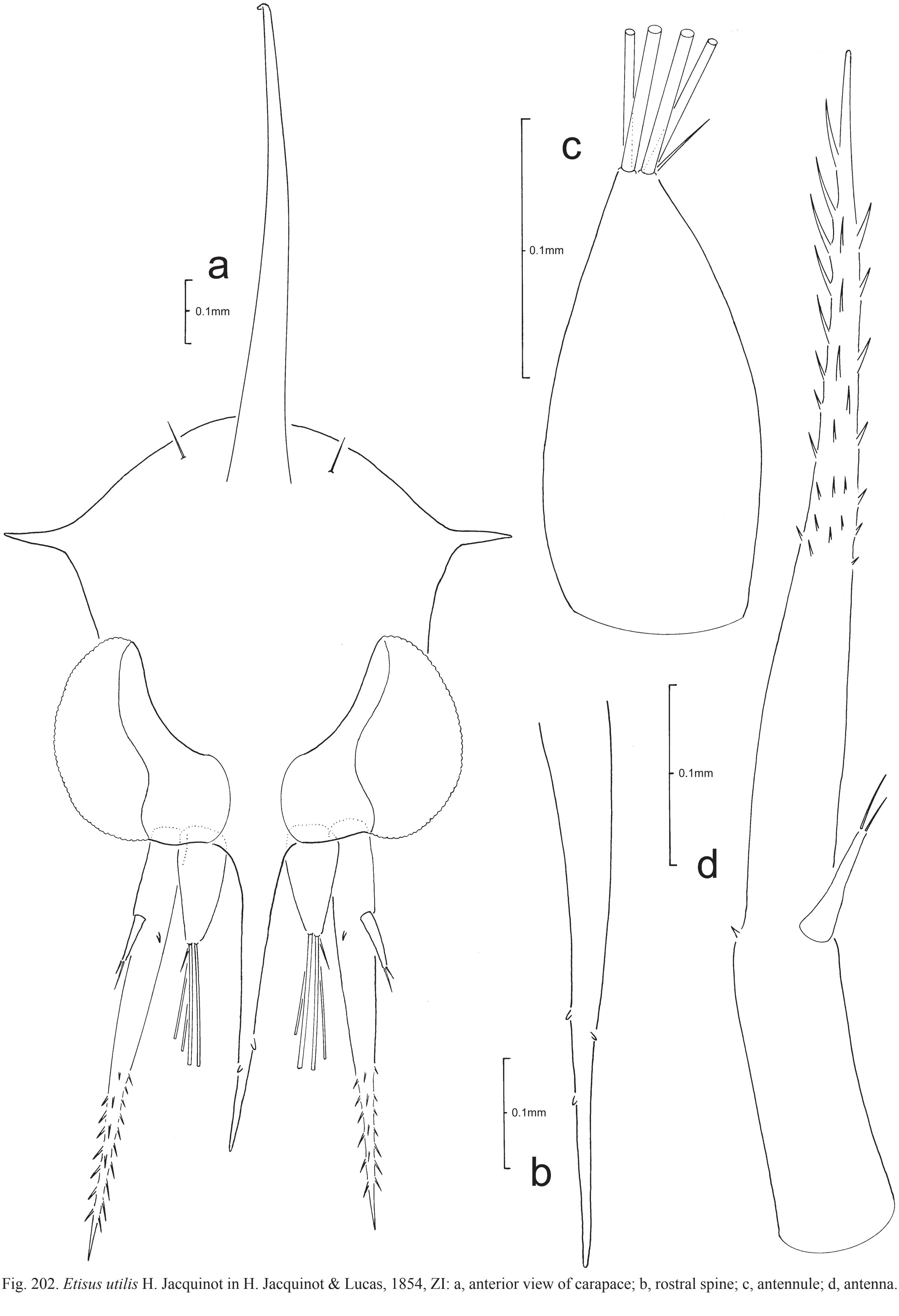

Fig. 202. *Etisus utilis* H. Jacquinot in H. Jacquinot & Lucas, 1854, ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

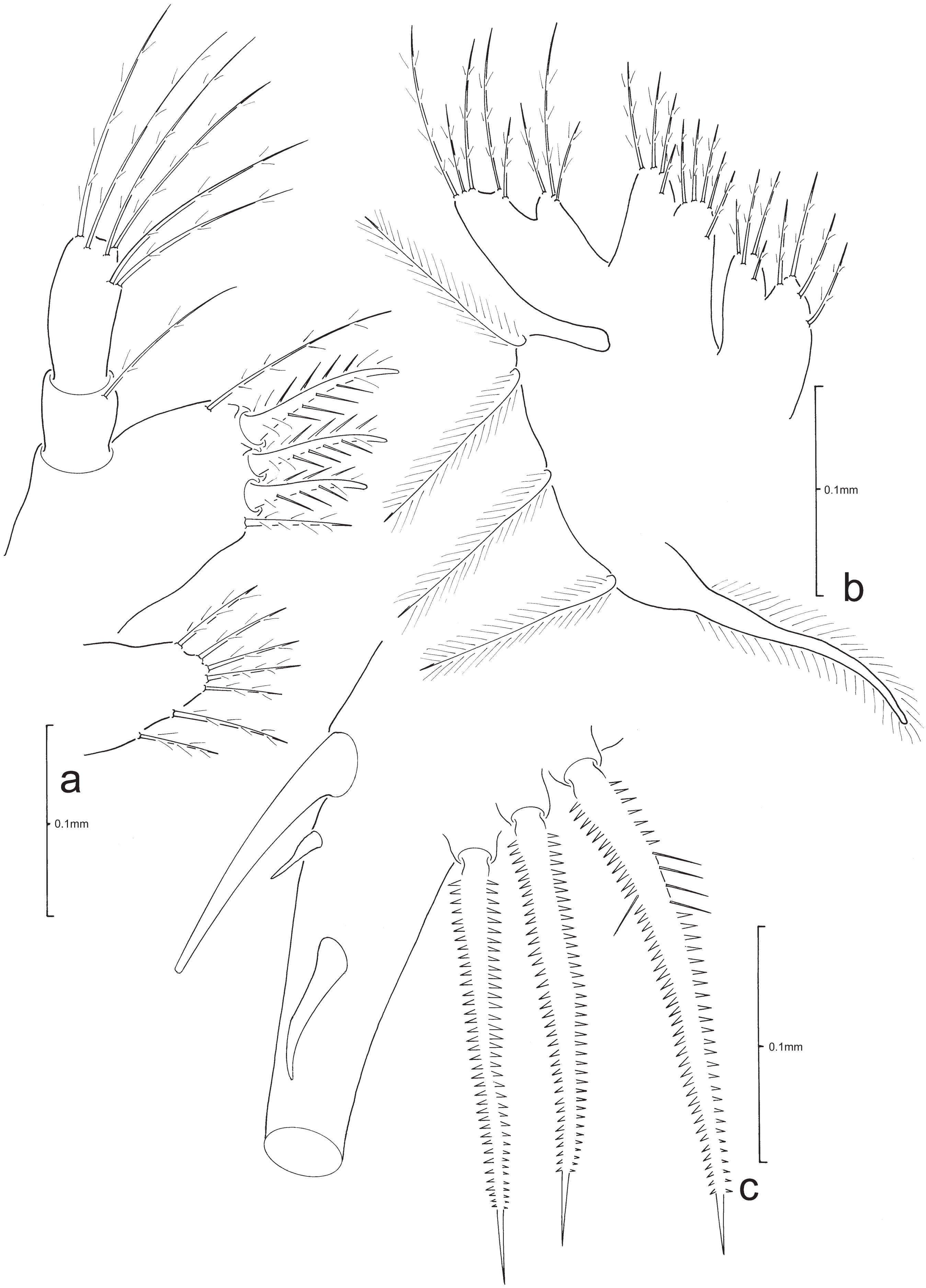

Fig. 203. *Etisus utilis* H. Jacquinot in H. Jacquinot & Lucas, 1854, ZI: a, maxillule; b, maxilla; c, telson.

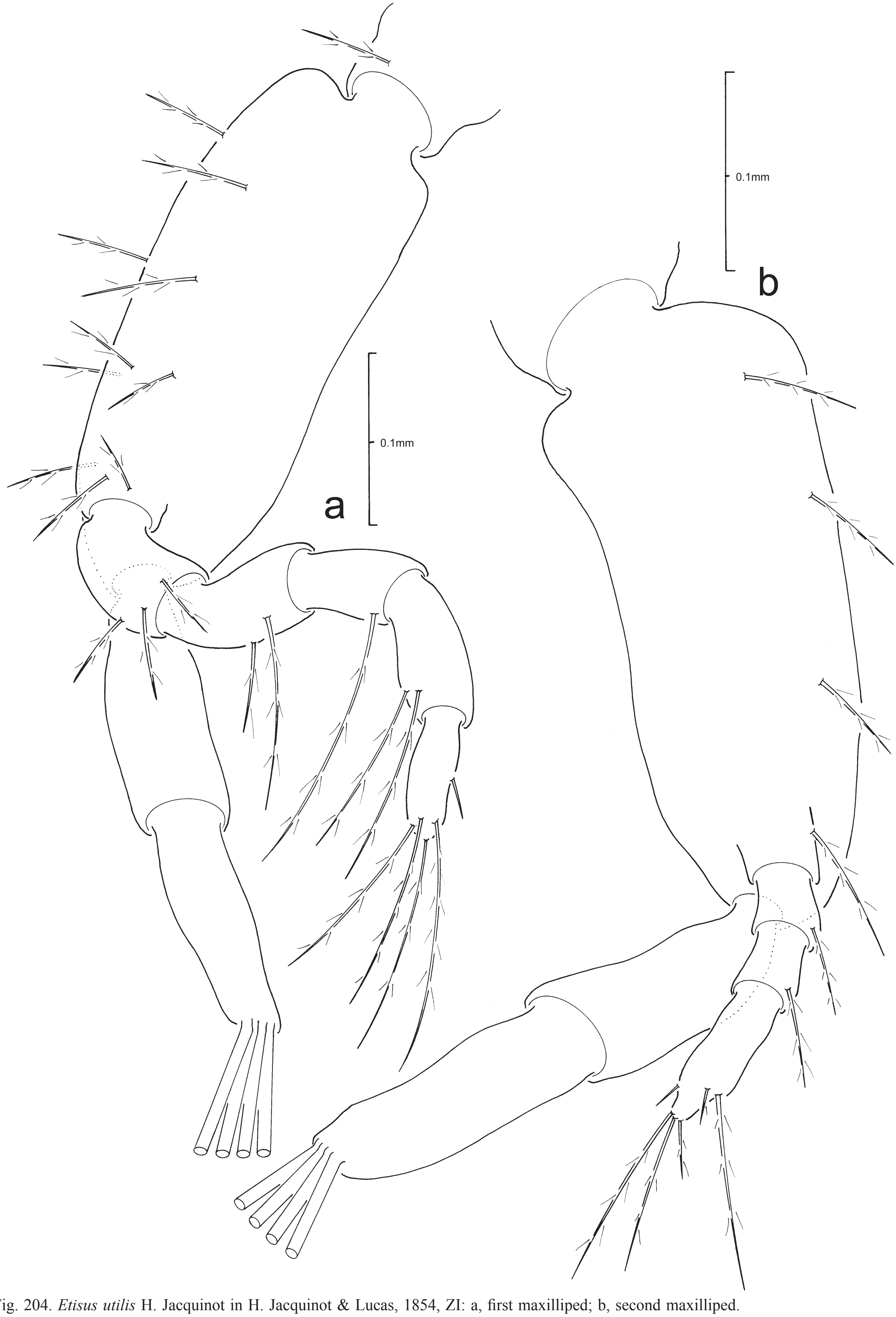

Fig. 204. *Etisus utilis* H. Jacquinot in H. Jacquinot & Lucas, 1854, ZI: a, first maxilliped; b, second maxilliped.

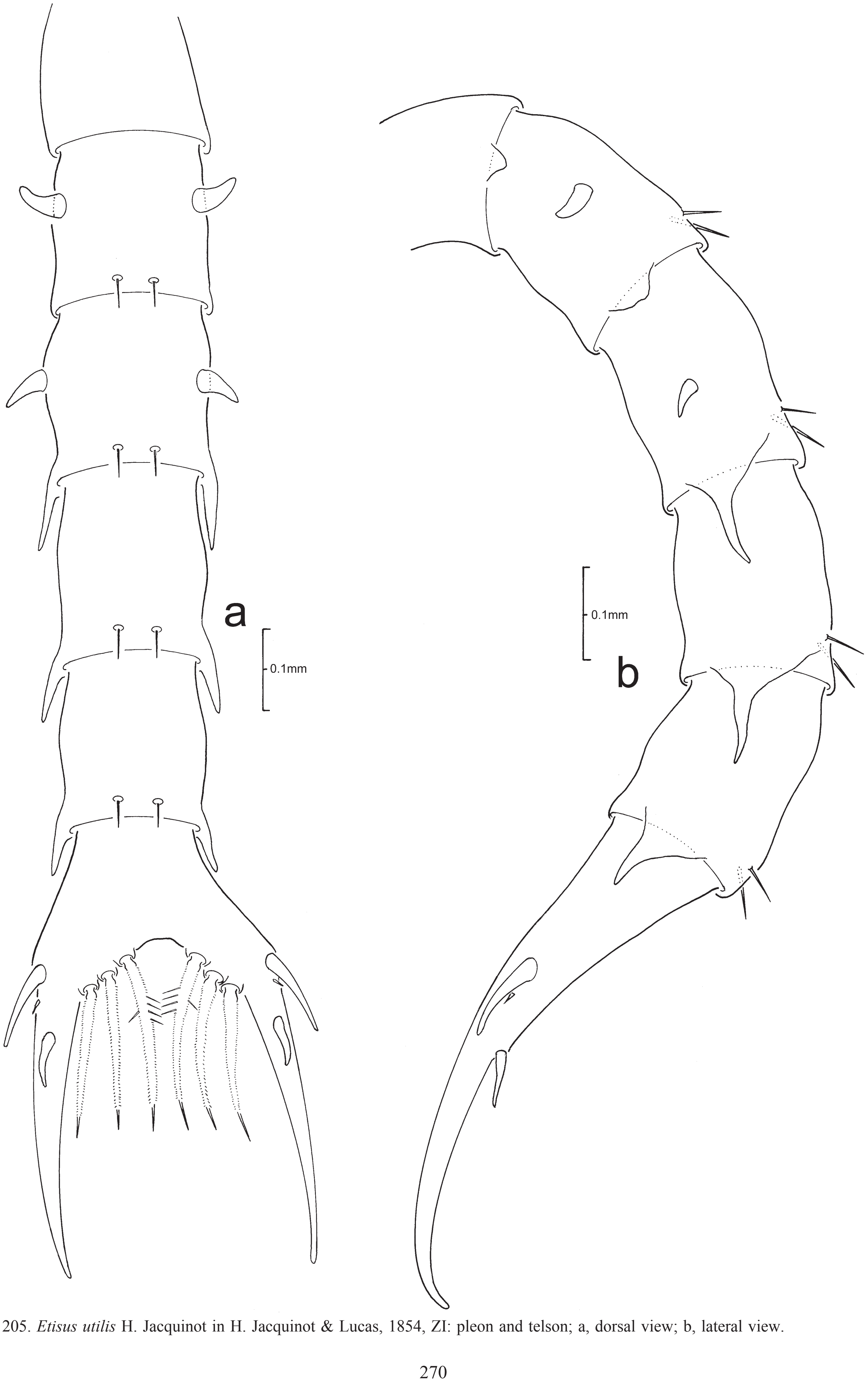

Fig. 205. *Etisus utilis* H. Jacquinot in H. Jacquinot & Lucas, 1854, ZI: pleon and telson; a, dorsal view; b, lateral view.

Subfamily Euxanthinae Alcock, 1898

***Medaeops granulosus* (Haswell, 1882)**
(Figs. 206–209)

Medaeops granulosus. Terada, 1990: 26, 29, figs. 1–2 (ZI–IV).

Description of Zoea I.
CARAPACE (Fig. 206a): dorsal spine curved distally with slightly swollen tip, just longer than rostral spine length; rostral spine much longer than antennal protopod length, without distal spinulation; lateral spines straight with swollen tips, without spinulation on distal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 206a): sessile.
Antennule (Fig. 206b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 206c): biramous; protopodal process distally multispinulate, much shorter than rostral spine length; endopod spine present; exopod ca. 30% length of protopod, possessing 3 (1 long subterminal+2 unequal terminal) setae with small spinules at base.
Mandible: palp absent.
Maxillule (Fig. 207a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 207b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 208a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 208b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 209a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–4 each with short posterolateral processes; pleomere 5 with lateral process almost twice length of pleomere, end swollen; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 207c, 209a, b): each fork long, gradually curved distally, not spinulate, 2 small lateral spines, 1 larger dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Table 24. A comparison between the ZI of *Medaeops granulosus* (Haswell, 1882) by Terada (1990) and the present study.

Character	Terada (1990)	Present study
CARAPACE	fig. 1AI	Fig. 206a
carapace setation	absent	1 pair of posterodorsal setae
dorsal spine tip	pointed	swollen
lateral spine tips	pointed	swollen
ANTENNULE	fig. 1BI	Fig. 206b
terminal setation	2 terminal aesthetascs, 1 terminal setae	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal setae
ANTENNA	fig. 1CI	Fig. 206c
endopod spine	absent	present
MAXILLULE	fig. 1DI	Fig. 207a
coxal setation	6	7
FIRST MAXILLIPED	fig. 1FI	Fig. 208a
coxal seta	absent	1 seta
TELSON	fig. 1HI	Figs. 207c, 209a, b
lateral spines	1 small spine	2 small spines

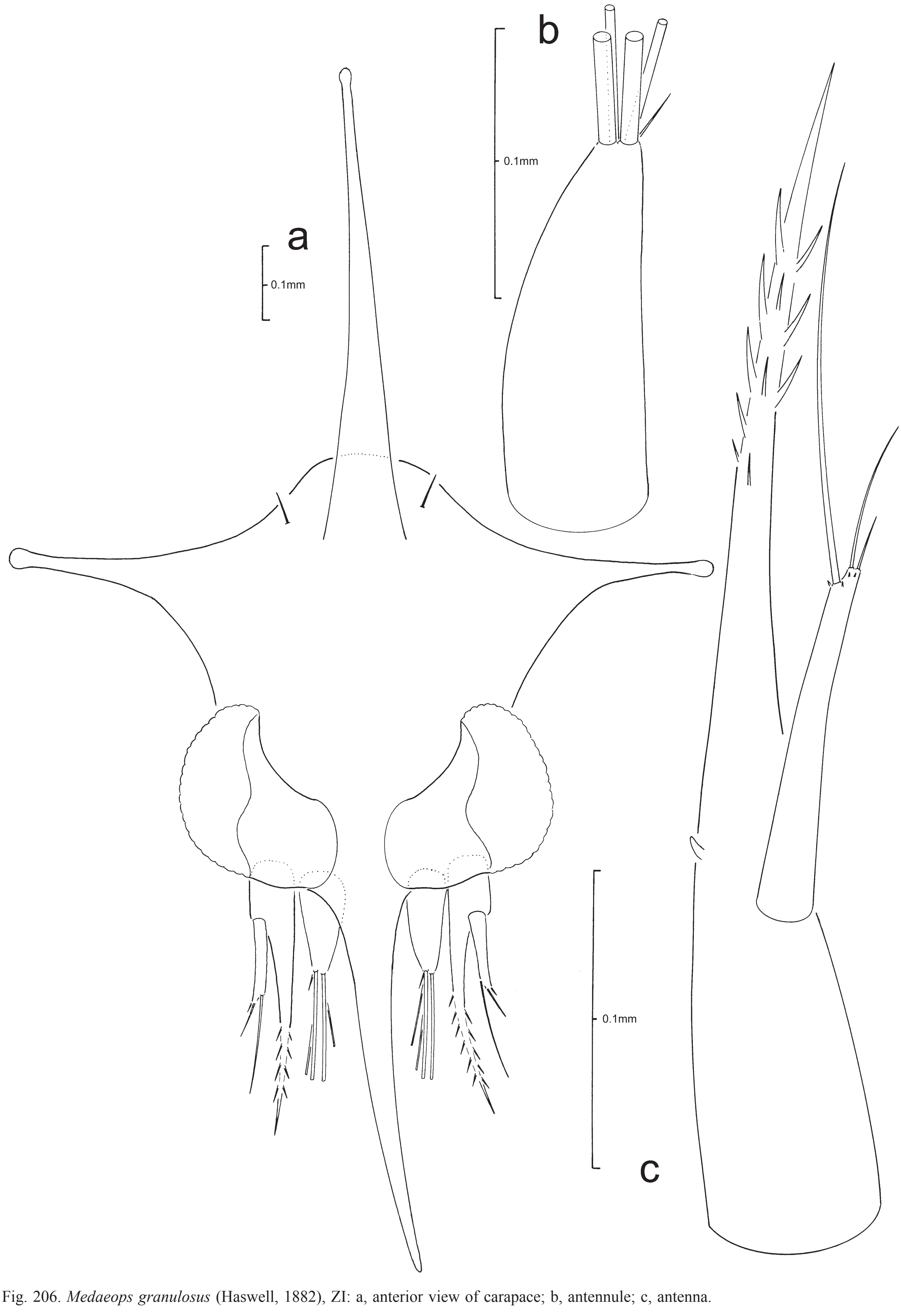

Fig. 206. *Medaeops granulosus* (Haswell, 1882), ZI: a, anterior view of carapace; b, antennule; c, antenna.

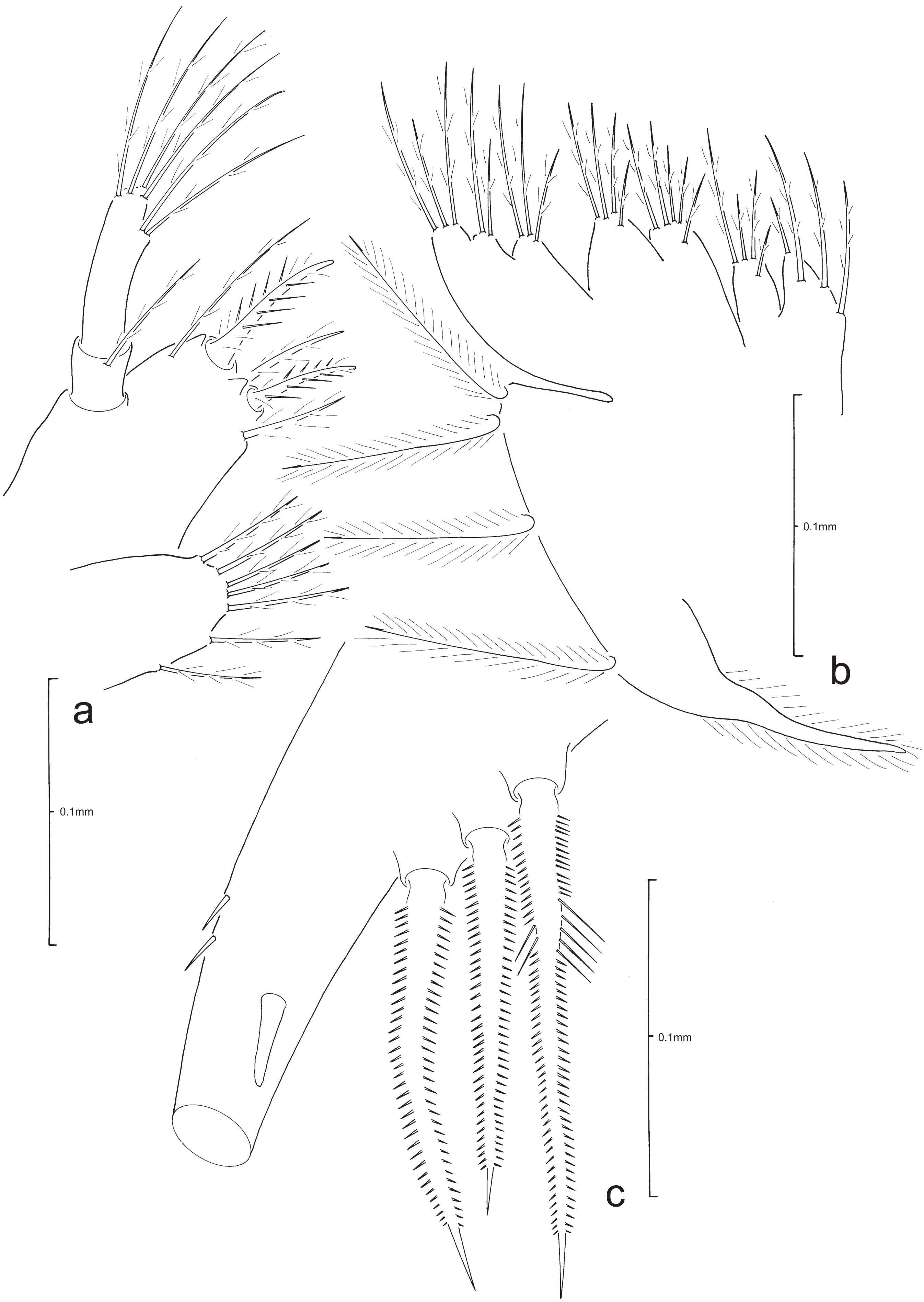

Fig. 207. *Medaeops granulosus* (Haswell, 1882), ZI: a, maxillule; b, maxilla; c, telson.

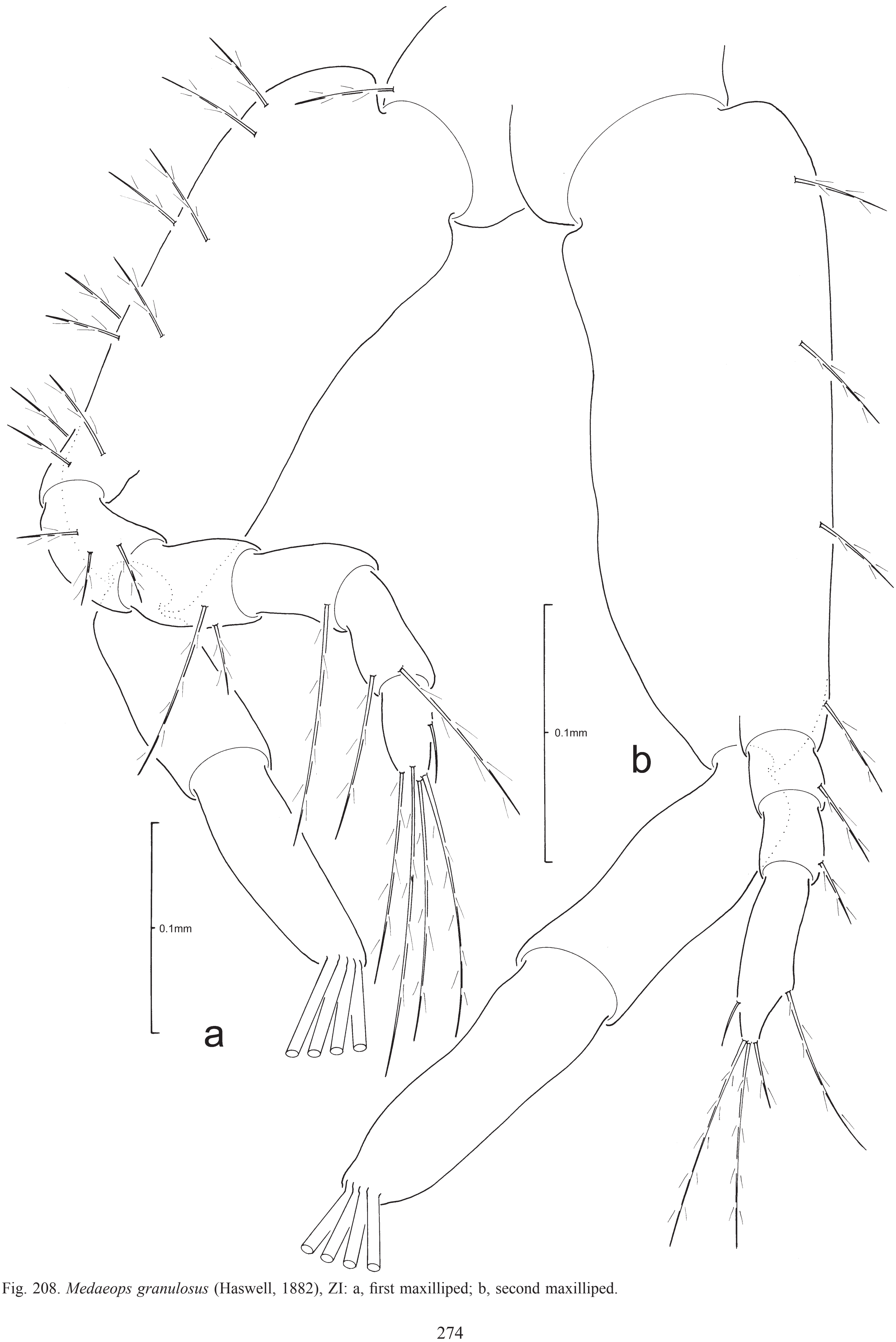

Fig. 208. *Medaeops granulosus* (Haswell, 1882), ZI: a, first maxilliped; b, second maxilliped.

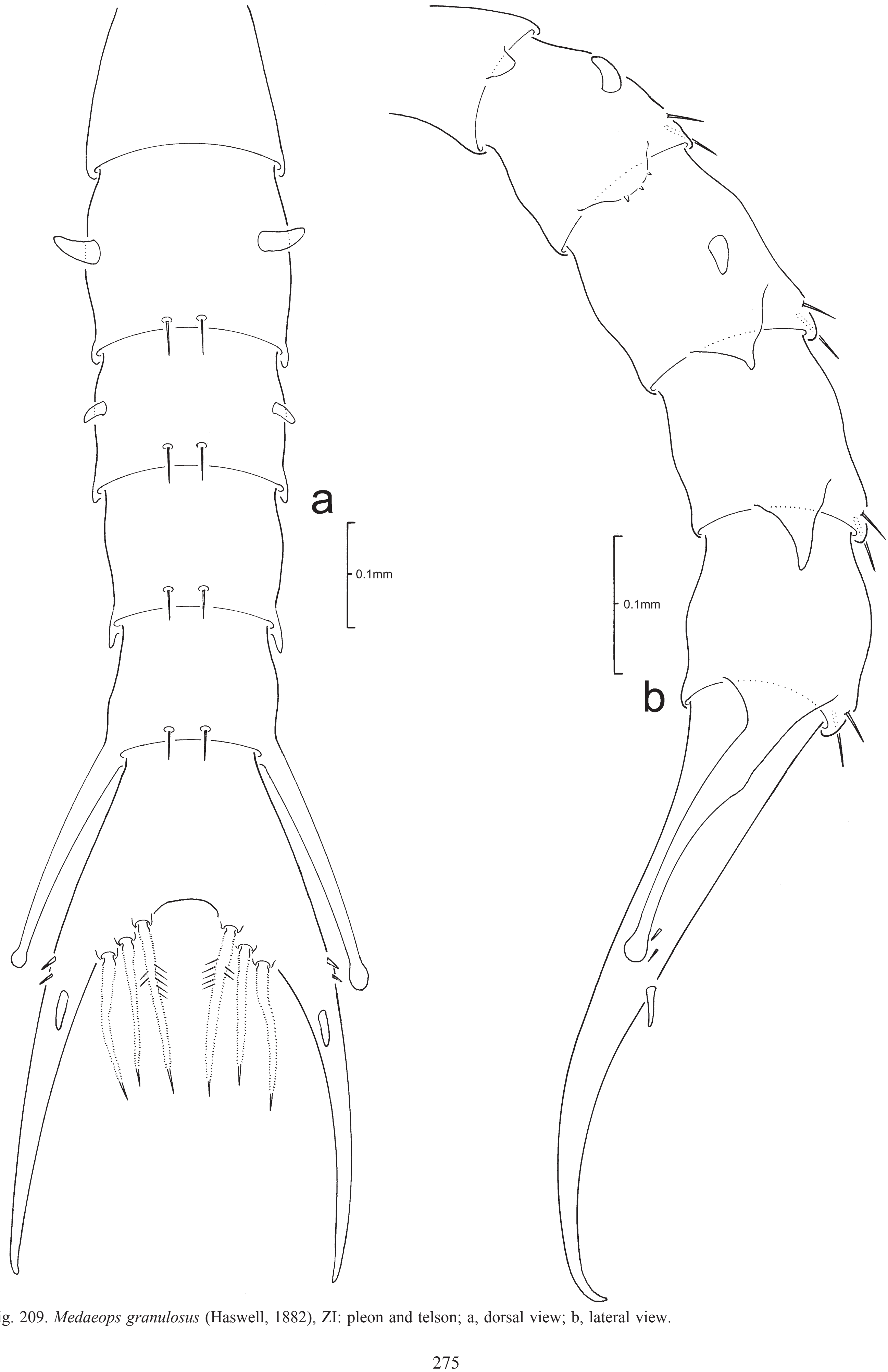

Fig. 209. *Medaeops granulosus* (Haswell, 1882), ZI: pleon and telson; a, dorsal view; b, lateral view.

Subfamily Liomerinae T. Sakai, 1976

***Liomera bella* (Dana, 1852)**
(Figs. 210–213)

Liomera bella. Yang & Ko, 2005: 193–199, fig. 1 (ZI).

Description of Zoea I.
CARAPACE (Fig. 210a, b): dorsal spine granulate, longer than rostral spine length; rostral spine shorter than antennal protopod length, distally spinulate; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 210a): sessile.
Antennule (Fig. 210c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 210d): biramous; protopodal process distally multispinulate, longer than rostral spine length; endopod spine present; exopod relatively small, ca. 12.1% length of protopod, possessing 3 (1 subterminal, 2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 211a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 211b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 212a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 212b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 213a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 211c, 213a, b): each fork long, gradually curved distally, not spinulate, 1 long lateral spine, 1 shorter lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

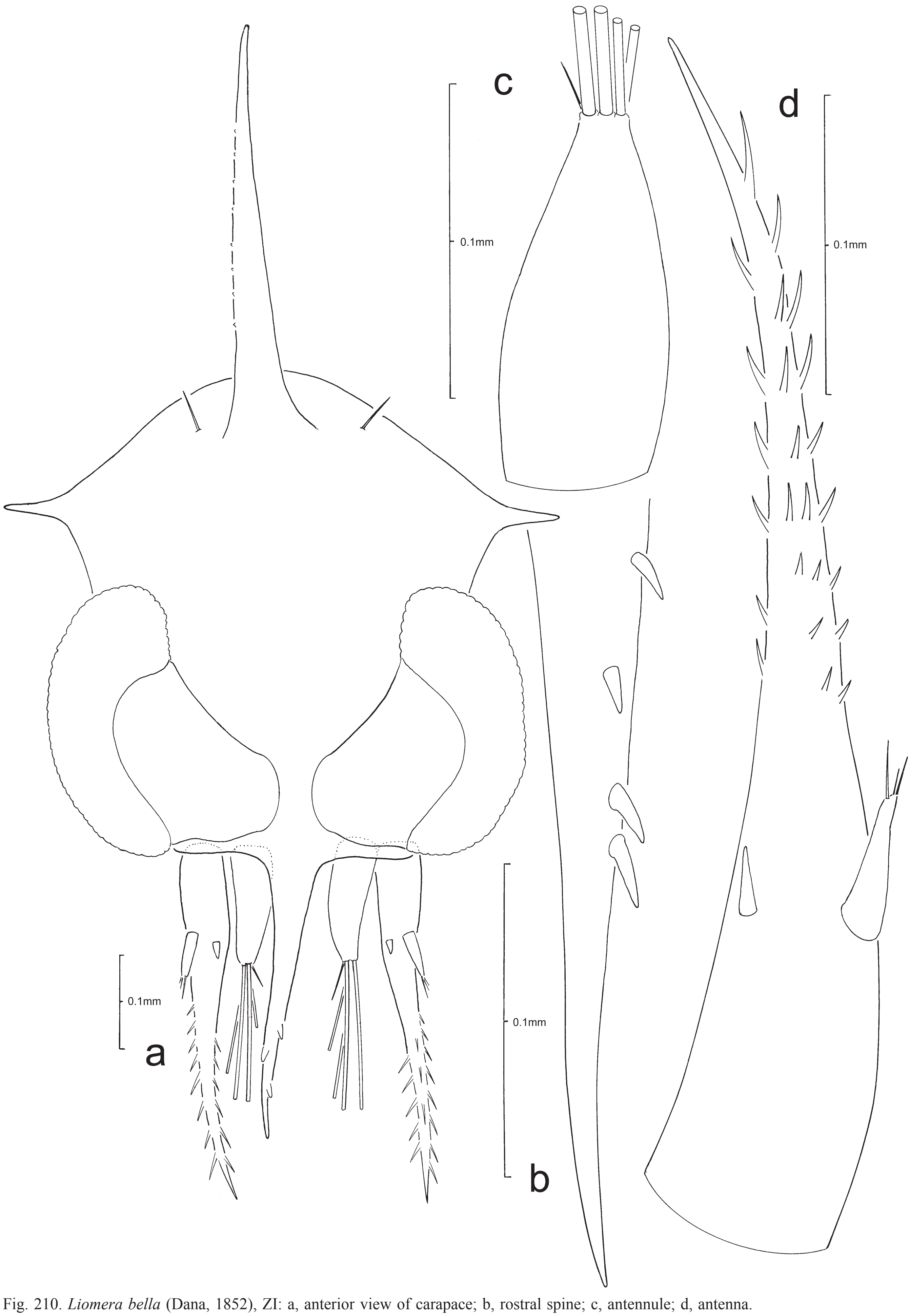

Fig. 210. *Liomera bella* (Dana, 1852), ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

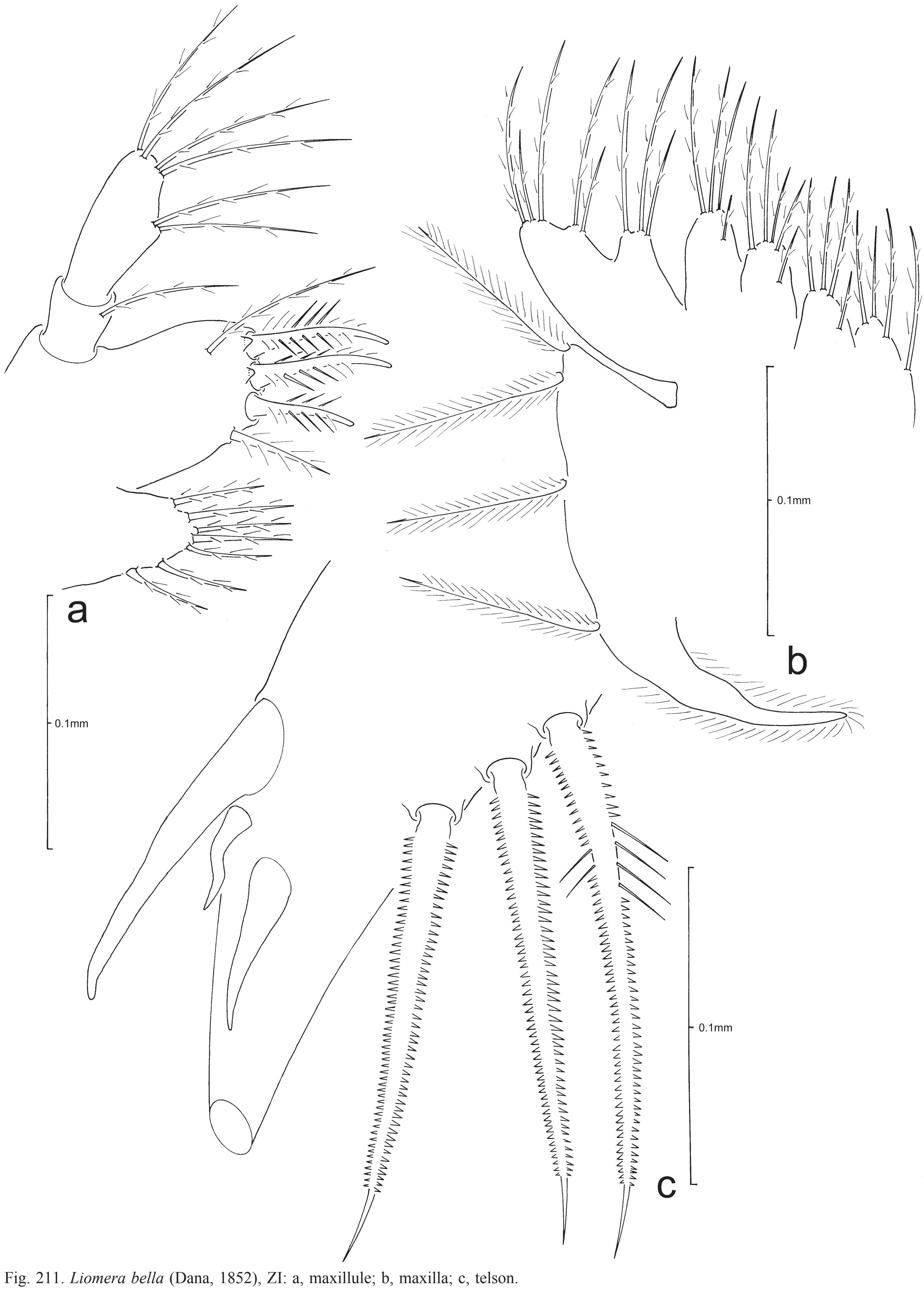

Fig. 211. *Liomera bella* (Dana, 1852), ZI: a, maxillule; b, maxilla; c, telson.

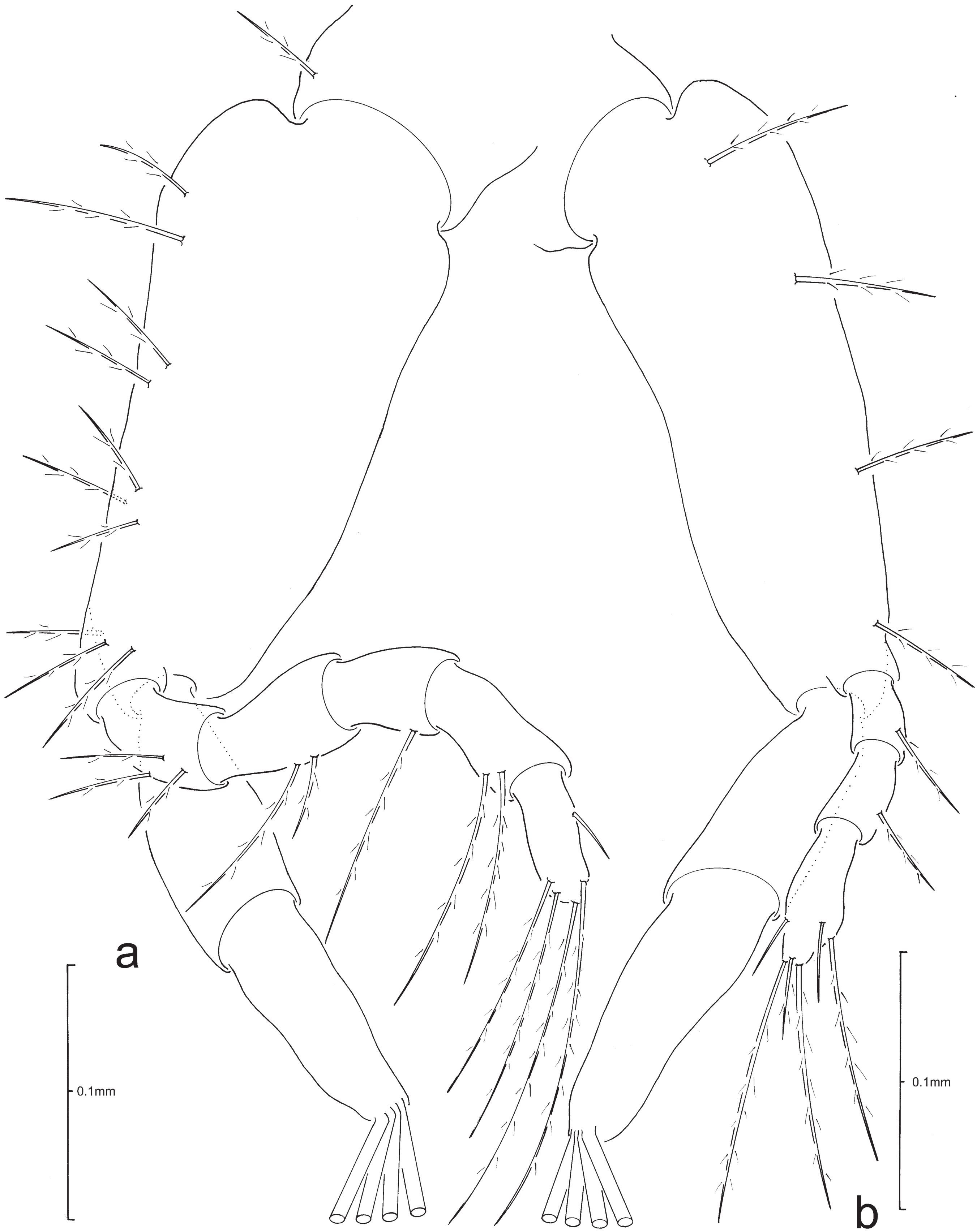

Fig. 212. *Liomera bella* (Dana, 1852), ZI: a, first maxilliped; b, second maxilliped.

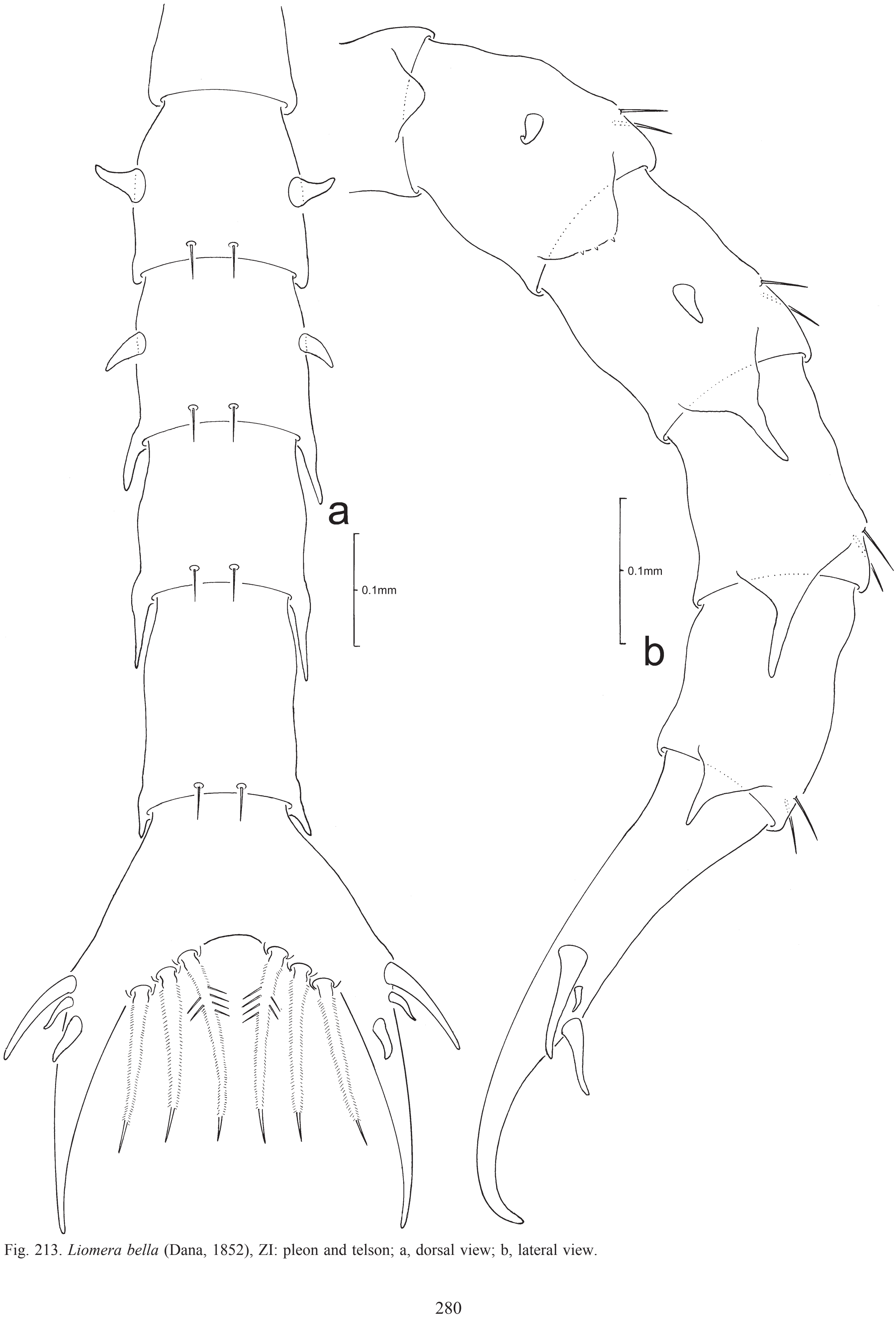

Fig. 213. *Liomera bella* (Dana, 1852), ZI: pleon and telson; a, dorsal view; b, lateral view.

Liomera cinctimana (White, 1847)

(Figs. 214–217)

Description of Zoea I.

CARAPACE (Fig. 214a, b): dorsal spine longer than rostral spine length; rostral spine ca. equal to antennal protopod length, distally spinulate; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON

Eyes (Fig. 214a): sessile.

Antennule (Fig. 214c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.

Antenna (Fig. 214d): biramous; protopodal process distally multispinulate, ca. equal to rostral spine length; endopod spine present; exopod relatively small, ca. 11.2% length of protopod, possessing 3 (1 subterminal+2 unequal terminal) setae.

Mandible: palp absent.

Maxillule (Fig. 215a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.

Maxilla (Fig. 215b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal, 3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION

First maxilliped (Fig. 216a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 216b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

PLEON (Fig. 217a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 215c, 217a, b): each fork long, gradually curved distally, not spinulate, 1 long lateral spine, 1 shorter lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

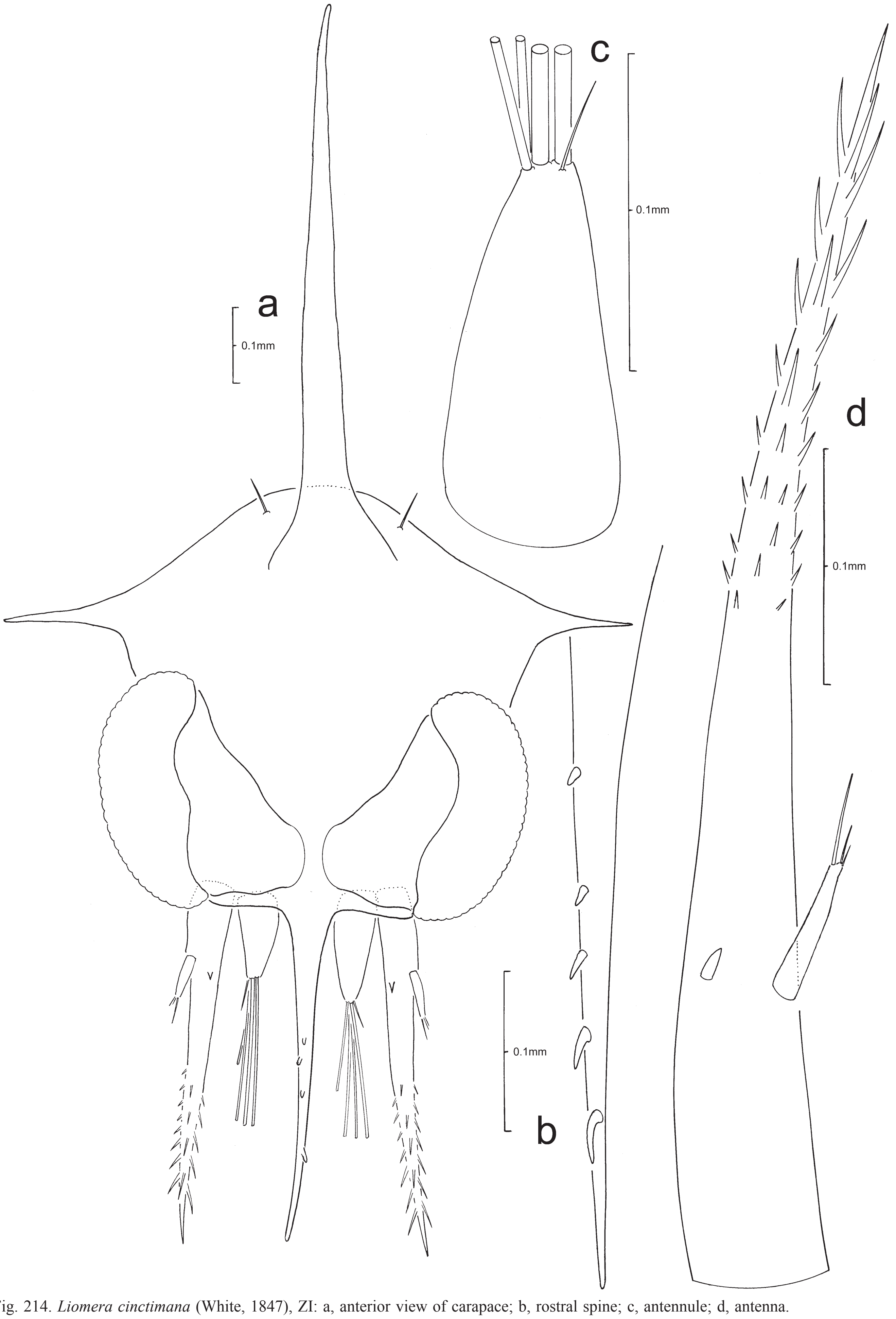

Fig. 214. *Liomera cinctimana* (White, 1847), ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

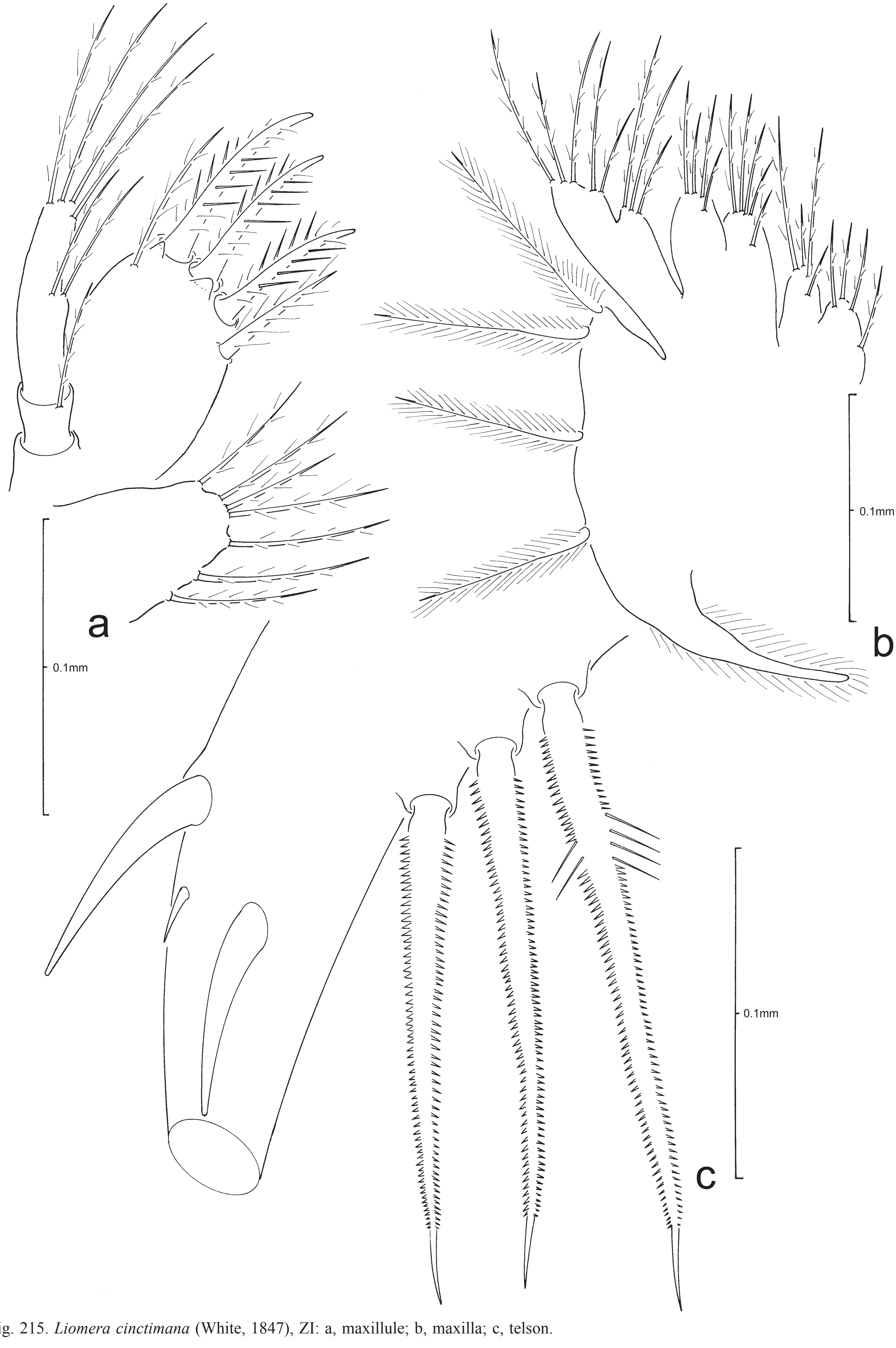

Fig. 215. *Liomera cinctimana* (White, 1847), ZI: a, maxillule; b, maxilla; c, telson.

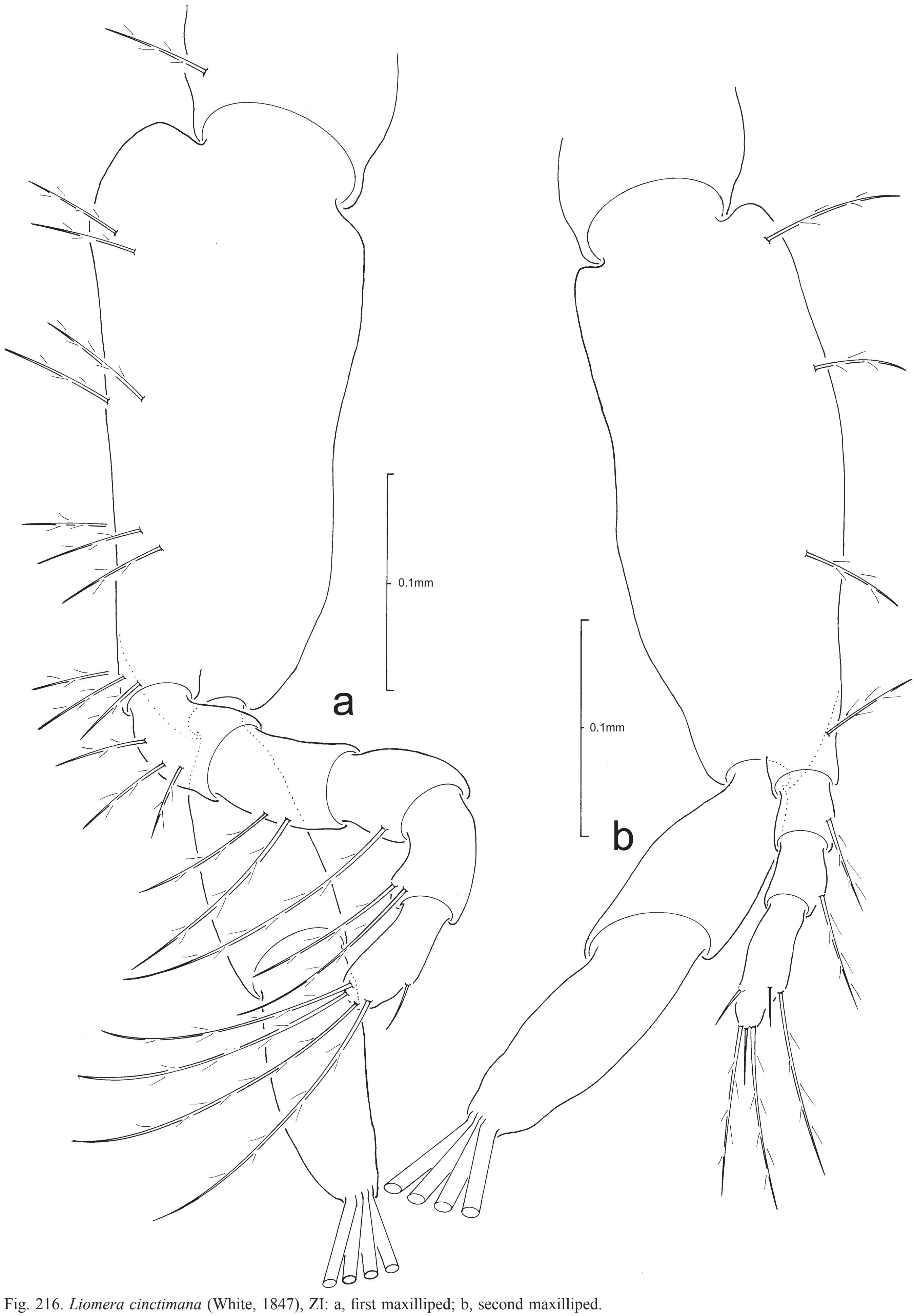

Fig. 216. *Liomera cinctimana* (White, 1847), ZI: a, first maxilliped; b, second maxilliped.

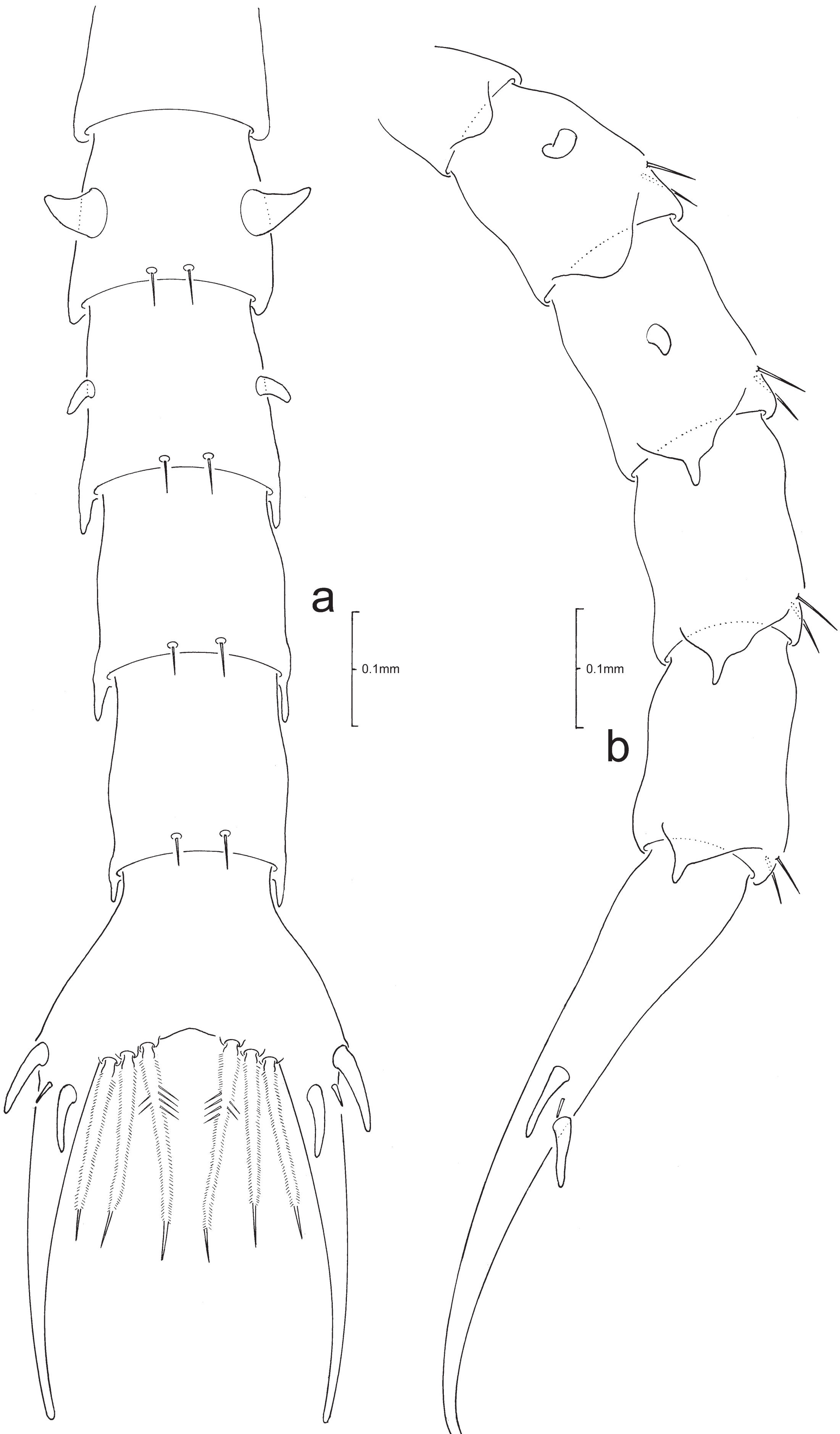

Fig. 217. *Liomera cinctimana* (White, 1847), ZI: pleon and telson; a, dorsal view; b, lateral view.

***Liomera loevis* (A. Milne-Edwards, 1873)**
(Figs. 218–221)

Description of Zoea I.
CARAPACE (Fig. 218a–c): dorsal spine spinulate, extremely long, nearly five times rostral spine length; rostral spine significantly shorter than antennal protopod length, distally spinulate; lateral spines straight, without spinulation on dorsal margin; anterior region of carapace spinulate; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin with 1 plumose anterior seta plus 3 posterior setae.

CEPHALON
Eyes (Fig. 218a): sessile.
Antennule (Fig. 218d): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal lengths plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 218e): biramous; protopodal process medially spinulate, distally multispinulate, extremely long, ca. five times rostral spine length; endopod spine present; exopod relatively small, ca. 8.8% length of protopod, possessing 3 (1 subterminal, 2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 219a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 219b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 220a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 220b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 221a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomeres 3–5 each with 1 pair of dorsolateral processes directed posteriorly; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–3 with small pair of dorsomedial spines; pleomeres 2–5 with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 219c, 221a, b): each fork long, gradually curved distally, not spinulate, 1 long lateral spine, 1 shorter lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

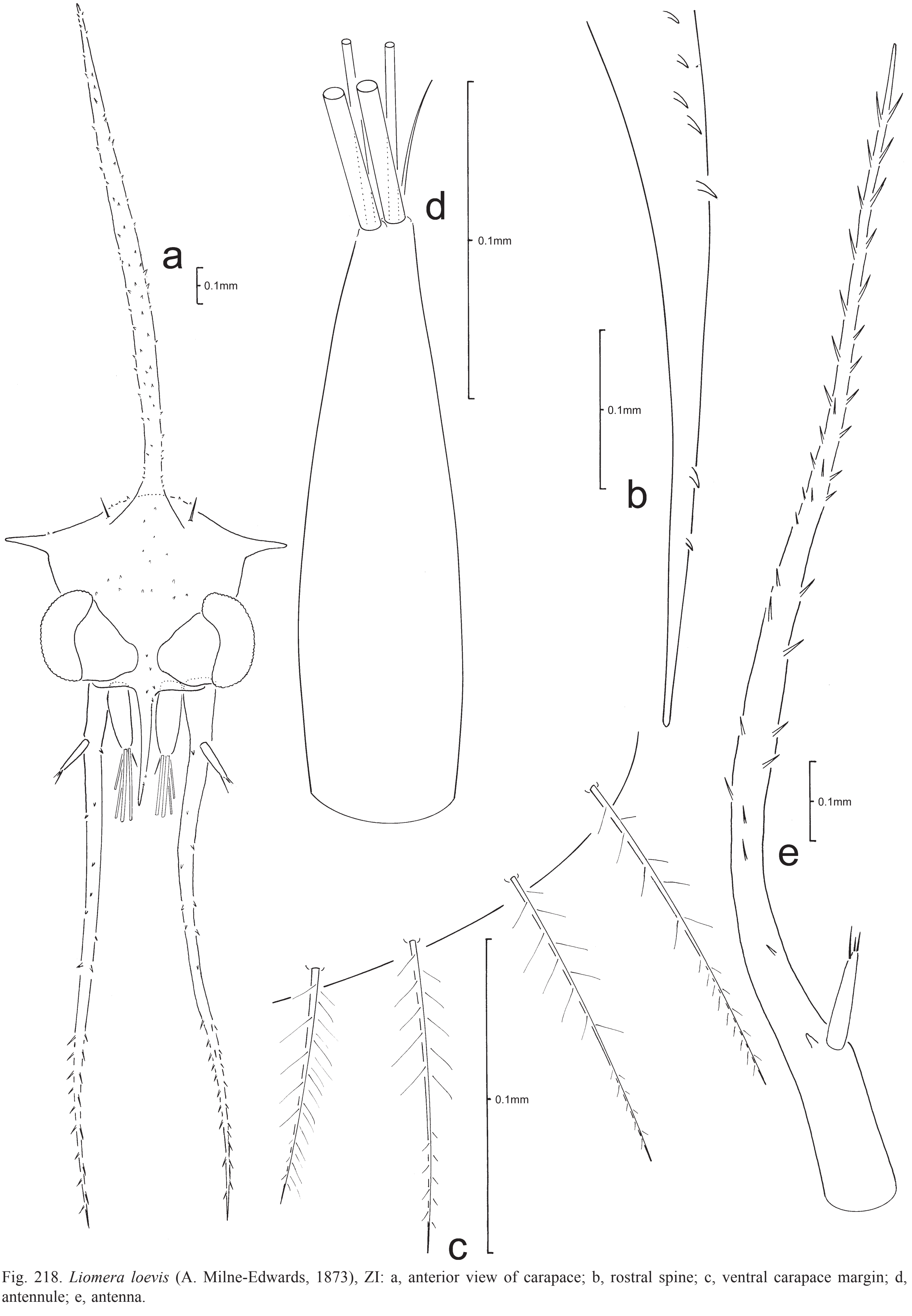

Fig. 218. *Liomera loevis* (A. Milne-Edwards, 1873), ZI: a, anterior view of carapace; b, rostral spine; c, ventral carapace margin; d, antennule; e, antenna.

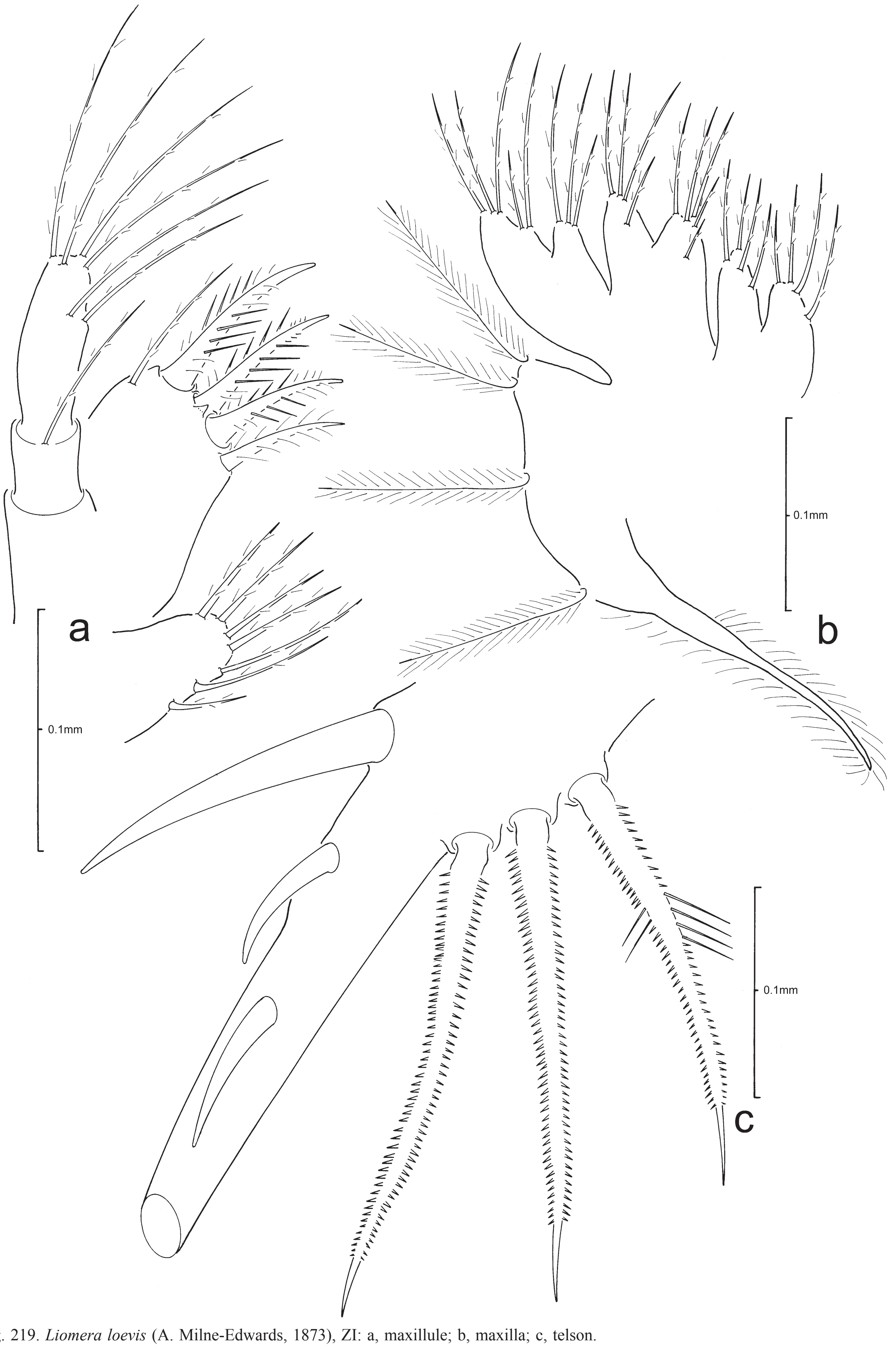

Fig. 219. *Liomera loevis* (A. Milne-Edwards, 1873), ZI: a, maxillule; b, maxilla; c, telson.

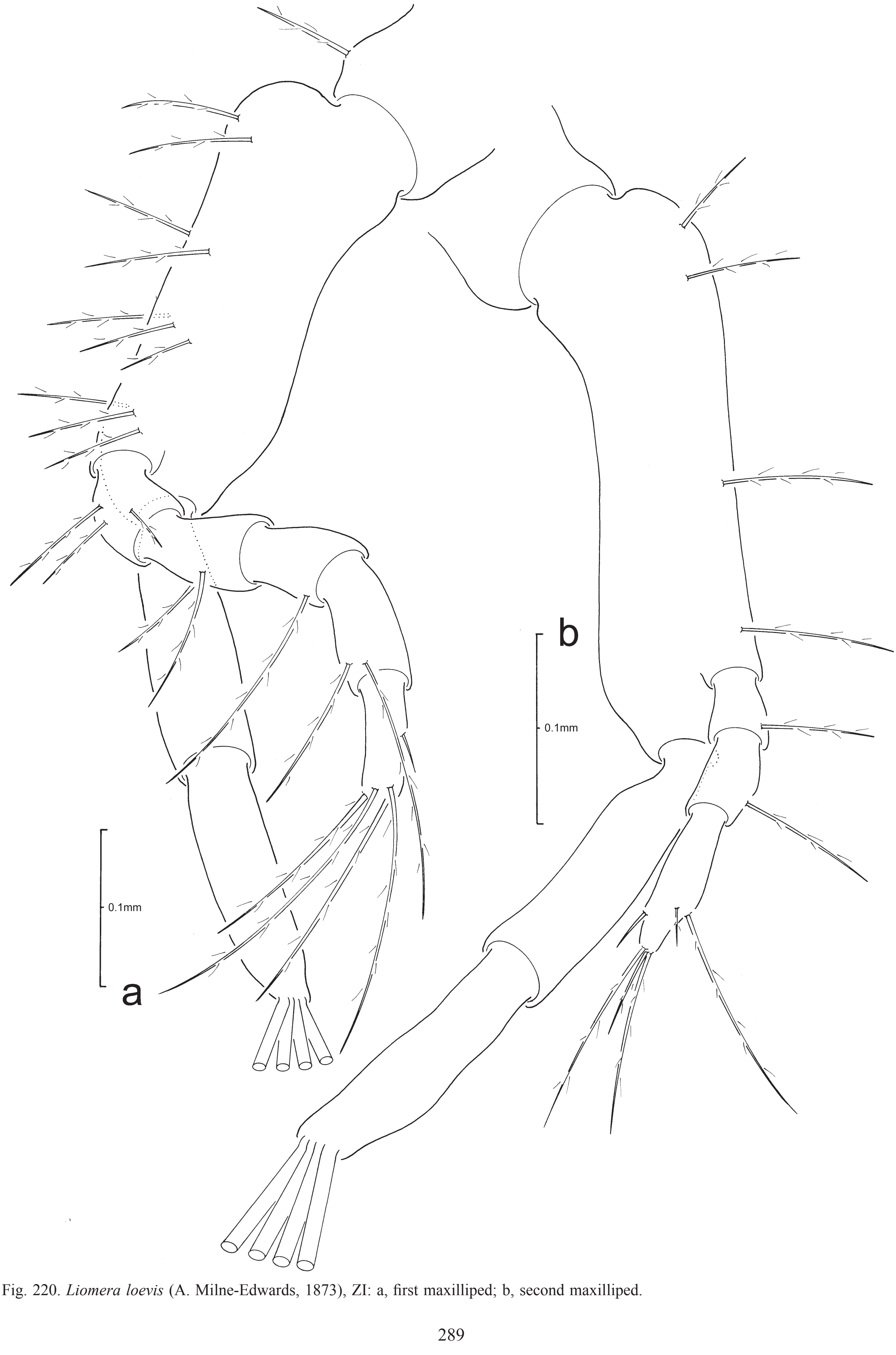

Fig. 220. *Liomera loevis* (A. Milne-Edwards, 1873), ZI: a, first maxilliped; b, second maxilliped.

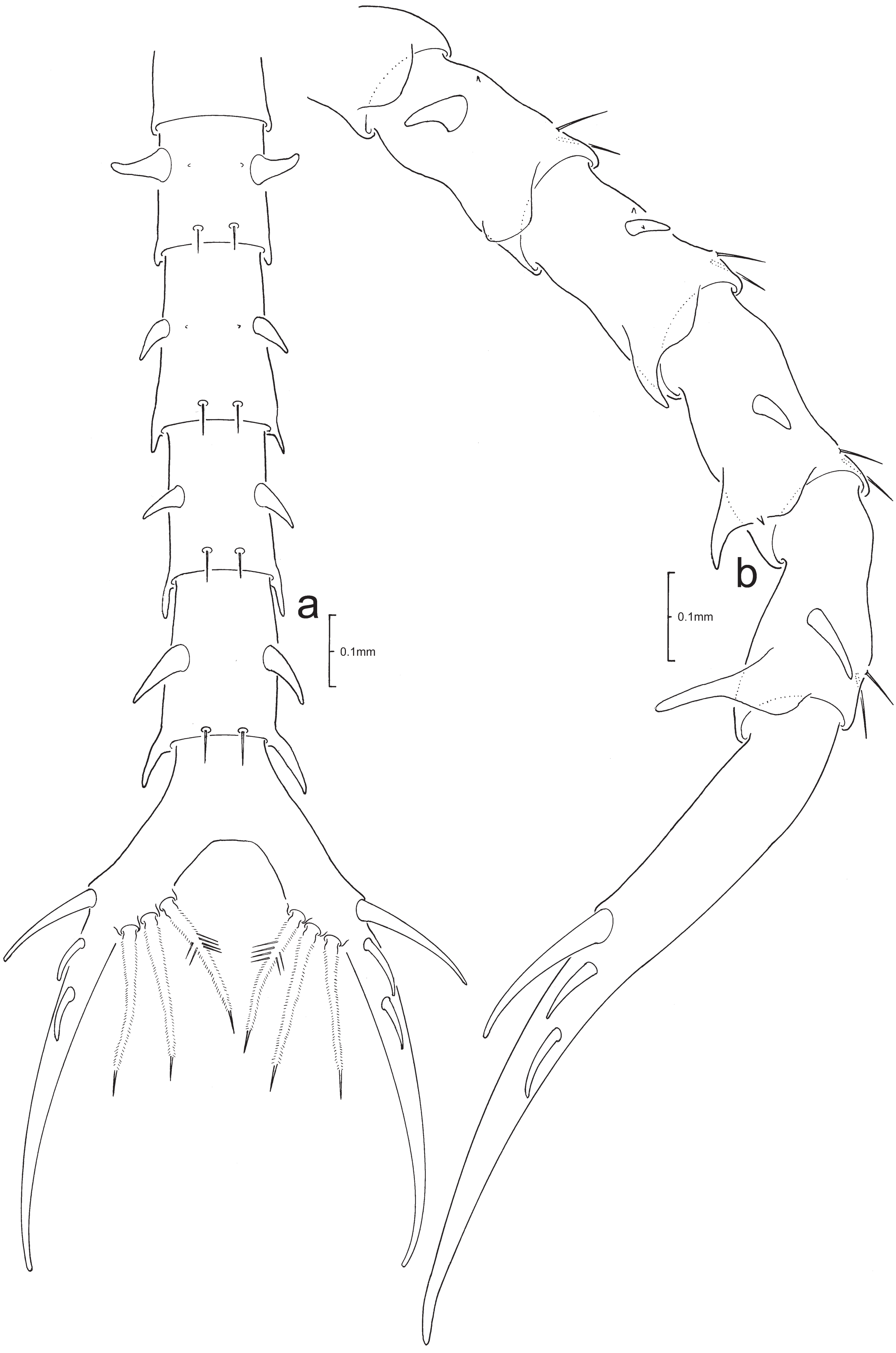

Fig. 221. *Liomera loevis* (A. Milne-Edwards, 1873), ZI: pleon and telson; a, dorsal view; b, lateral view.

Subfamily Xanthinae MacLeay, 1838

Lachnopodus subacutus (Stimpson, 1858)

(Figs. 222–225)

Lachnopodus subacutus. Al-Haj et al., 2019: 332, figs. 25–27.

Description of Zoea I.

CARAPACE (Fig. 222a): dorsal spine long, curved distally, longer than rostral spine length; rostral spine just shorter than antennal protopod length, without distal spinulation; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON

Eyes (Fig. 222a): sessile.

Antennule (Fig. 222b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.

Antenna (Fig. 222c): biramous; protopodal process distally multispinulate, just longer than rostral spine length; endopod spine present; exopod ca. 30.4% length of protopod, possessing 3 (1 long subterminal, 2 unequal terminal) setae.

Mandible: palp absent.

Maxillule (Fig. 223a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.

Maxilla (Fig. 223b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 2+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION

First maxilliped (Fig. 224a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 224b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

PLEON (Fig. 225a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 with rounded posterolateral processes; pleomeres 3–5 with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 223c, 225a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Remarks. Endopod of maxilla with seven setae is unusual.

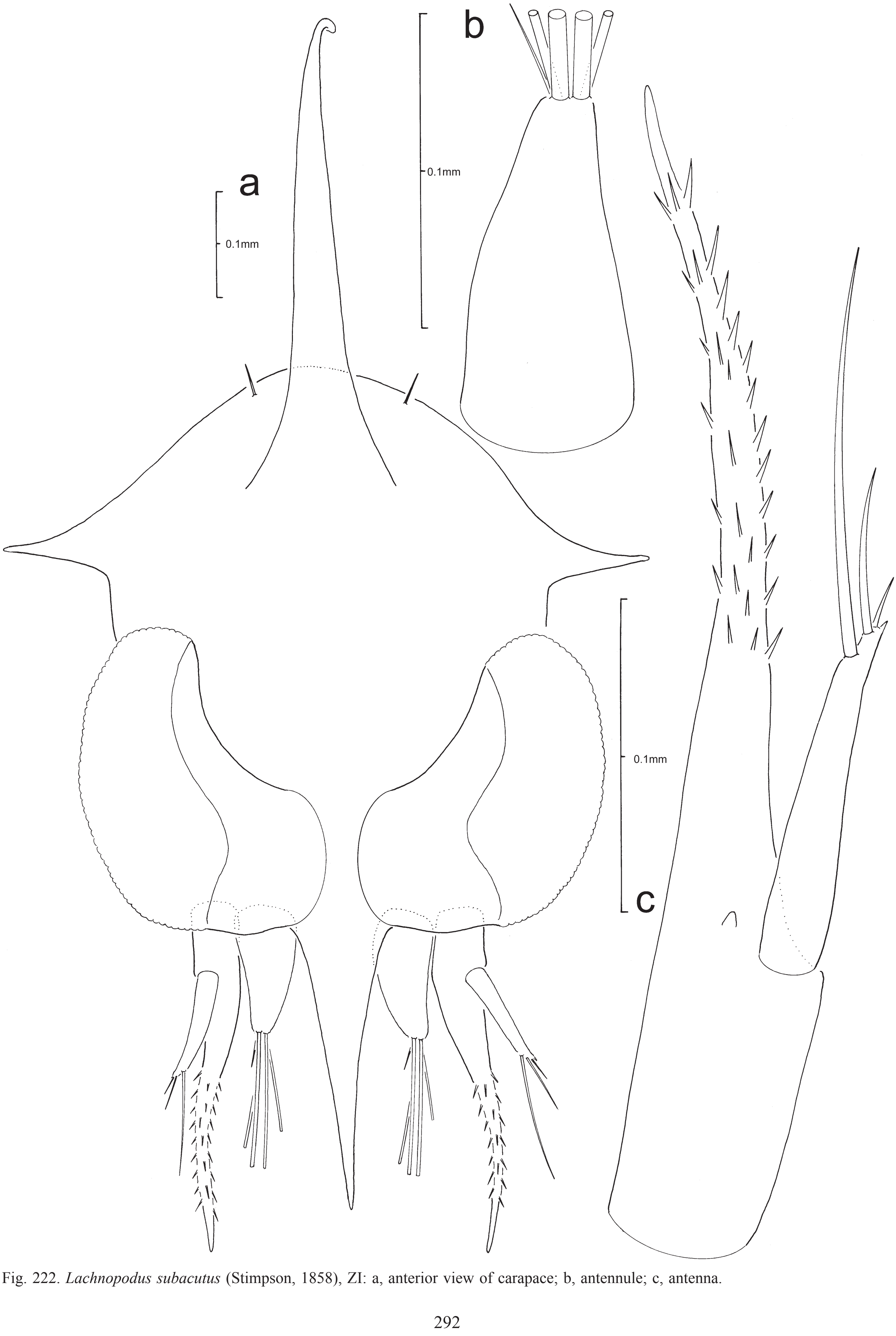

Fig. 222. *Lachnopodus subacutus* (Stimpson, 1858), ZI: a, anterior view of carapace; b, antennule; c, antenna.

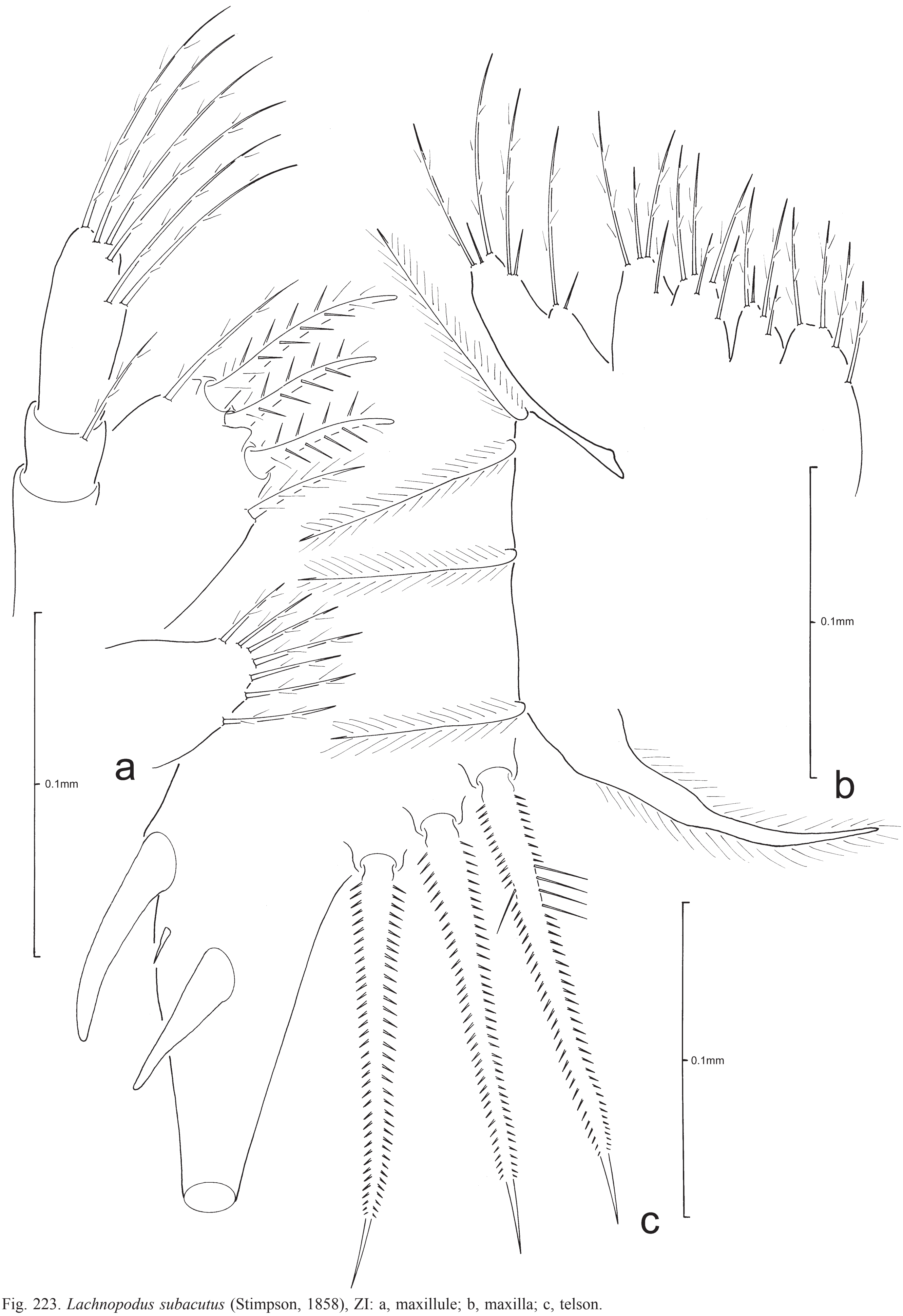

Fig. 223. *Lachnopodus subacutus* (Stimpson, 1858), ZI: a, maxillule; b, maxilla; c, telson.

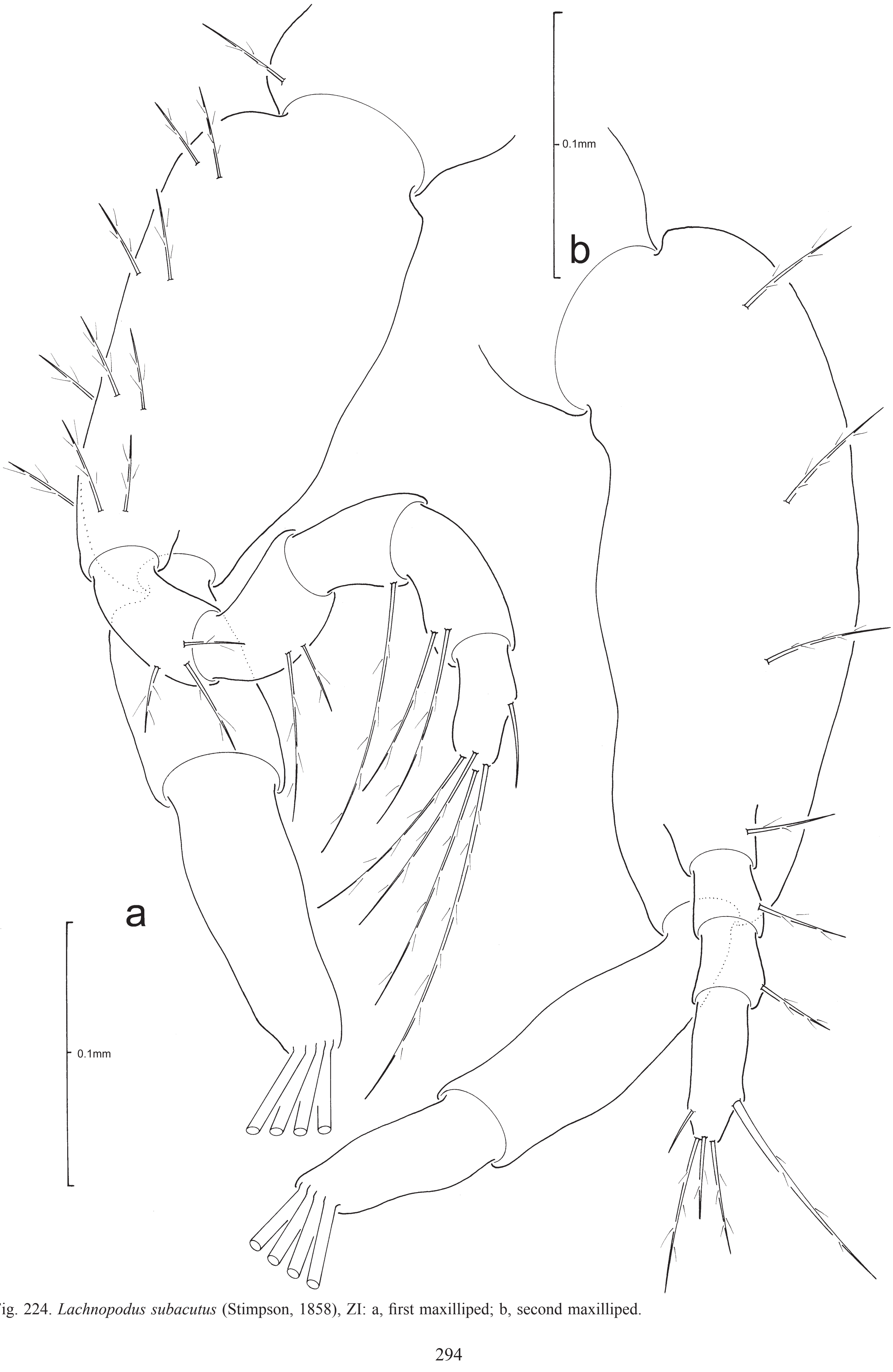

Fig. 224. *Lachnopodus subacutus* (Stimpson, 1858), ZI: a, first maxilliped; b, second maxilliped.

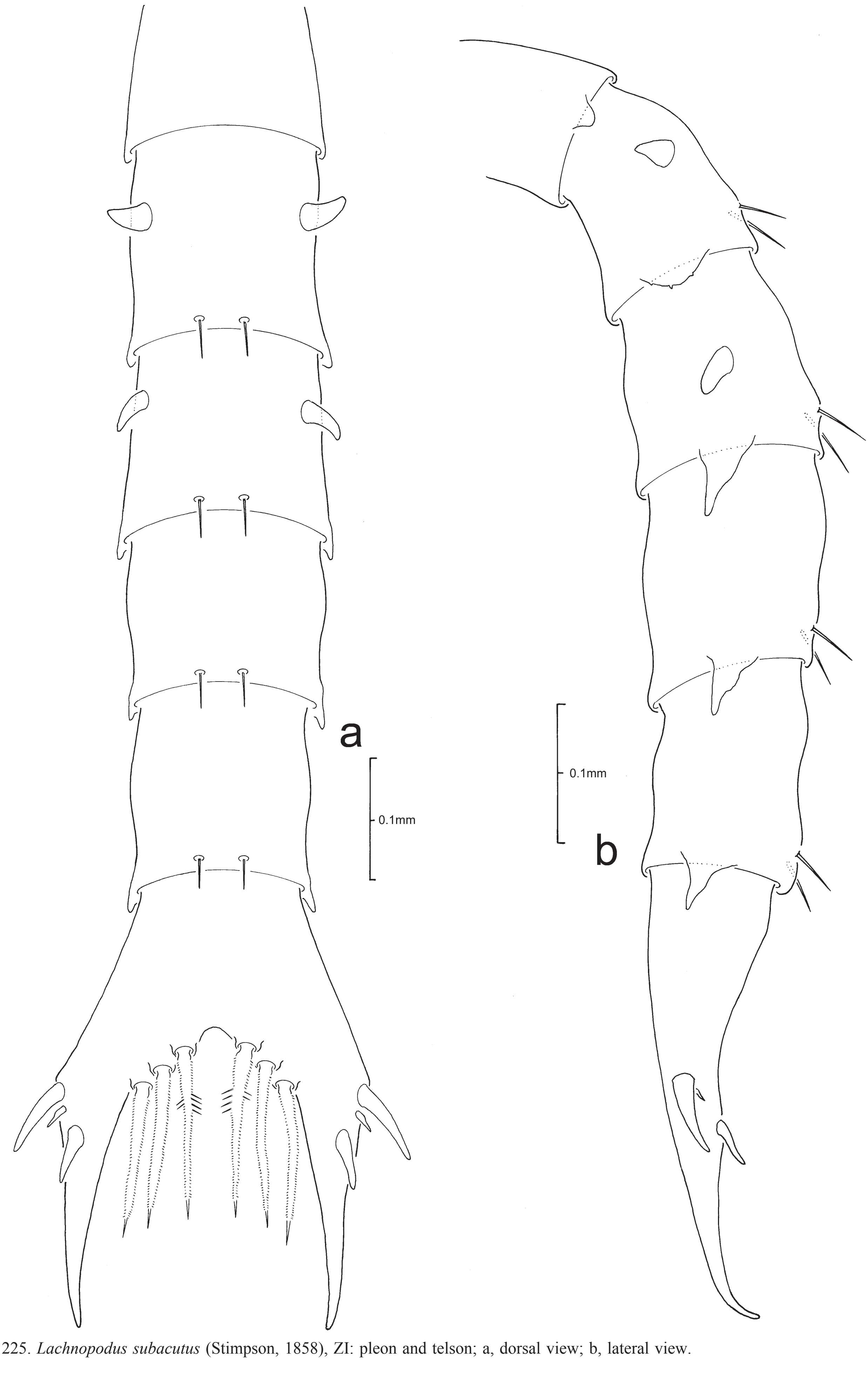

Fig. 225. *Lachnopodus subacutus* (Stimpson, 1858), ZI: pleon and telson; a, dorsal view; b, lateral view.

Leptodius sanguineus **(H. Milne Edwards, 1834)**
(Figs. 226–229)

Leptodius sanguineus. Al-Haj et al., 2019: 332, 335, 336, figs. 28–30.

Description of Zoea I.
CARAPACE (Fig. 226a, b): dorsal spine curved distally, longer than rostral spine length; rostral spine shorter than antennal protopod length, distally spinulate; lateral spines straight, without spinulation on distal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 226a): sessile.
Antennule (Fig. 226c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 226d): biramous; protopodal process distally multispinulate, longer than rostral spine length; endopod spine present; exopod ca. 14% length of protopod with 1 terminal seta.
Mandible: palp absent.
Maxillule (Fig. 227a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 227b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 228a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 228b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 229a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with long posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 227c, 229a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 much smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

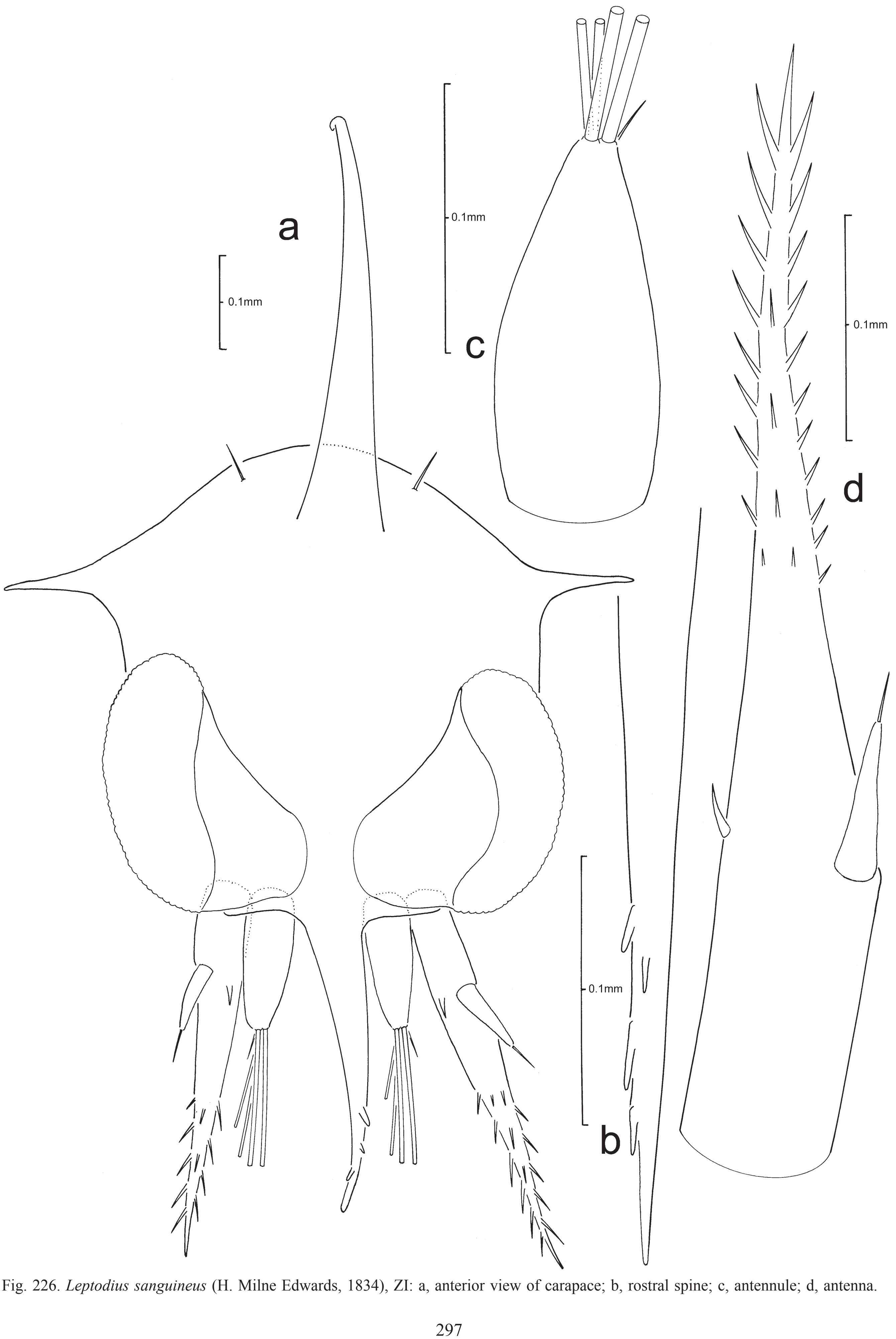

Fig. 226. *Leptodius sanguineus* (H. Milne Edwards, 1834), ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

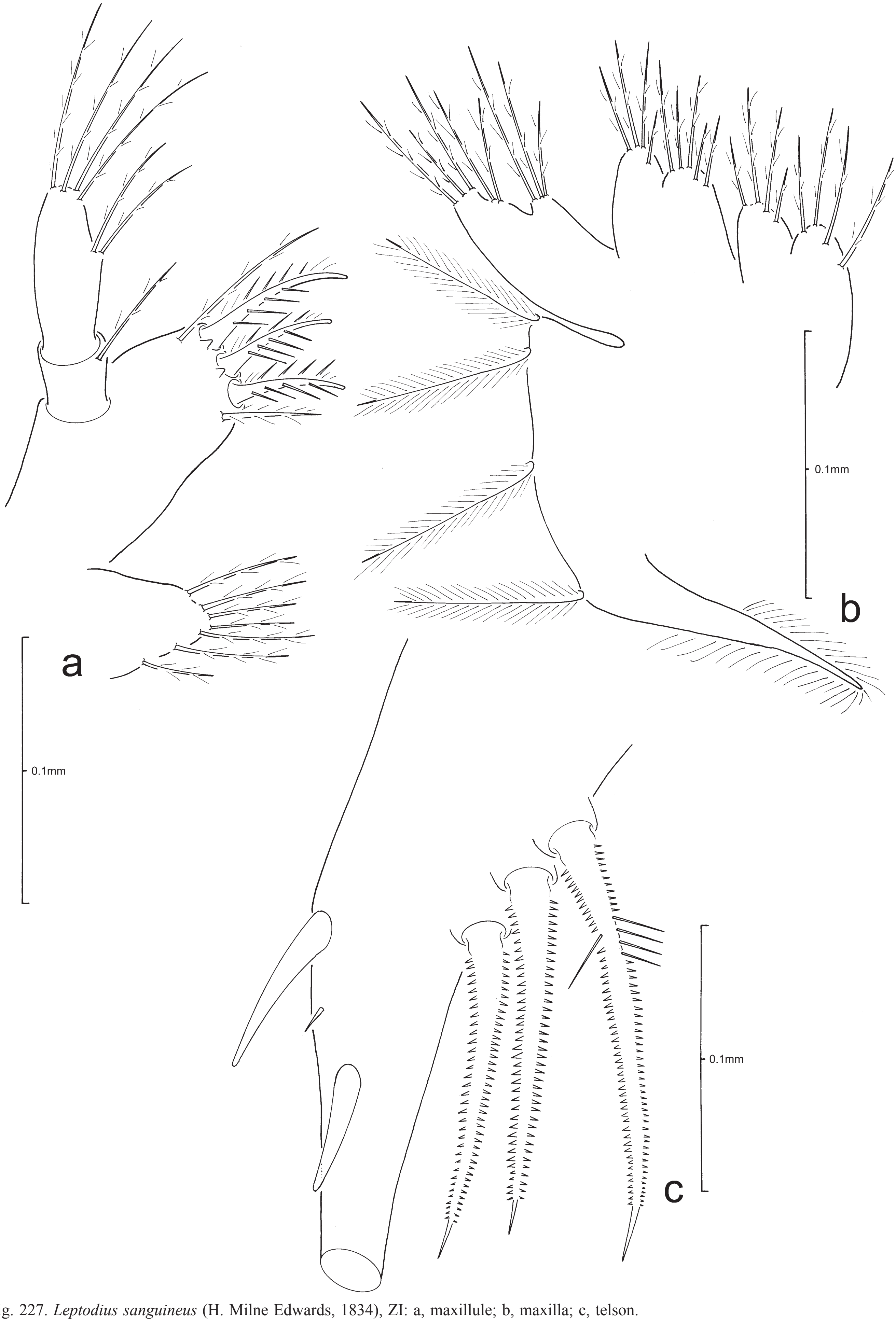

Fig. 227. *Leptodius sanguineus* (H. Milne Edwards, 1834), ZI: a, maxillule; b, maxilla; c, telson.

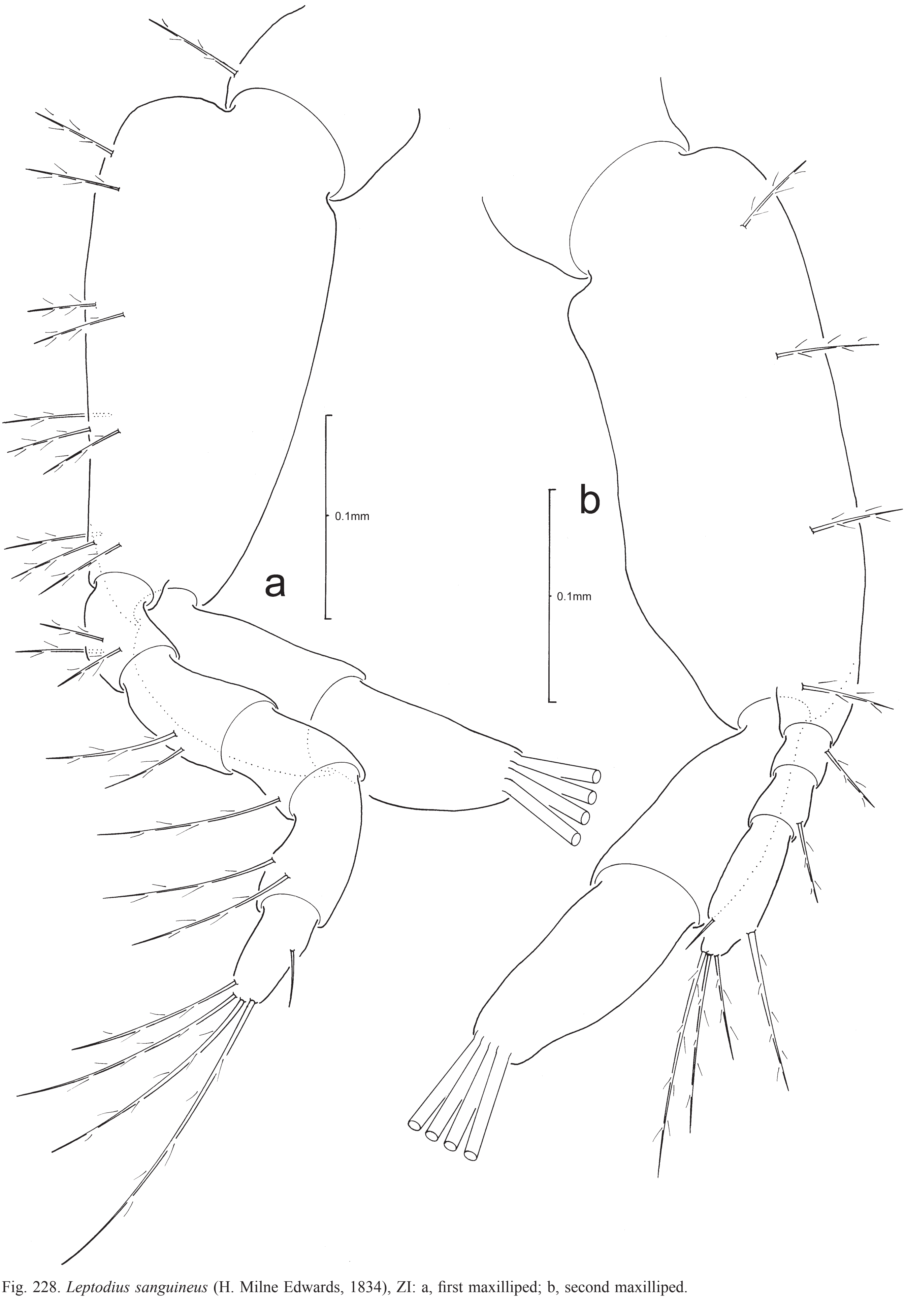

Fig. 228. *Leptodius sanguineus* (H. Milne Edwards, 1834), ZI: a, first maxilliped; b, second maxilliped.

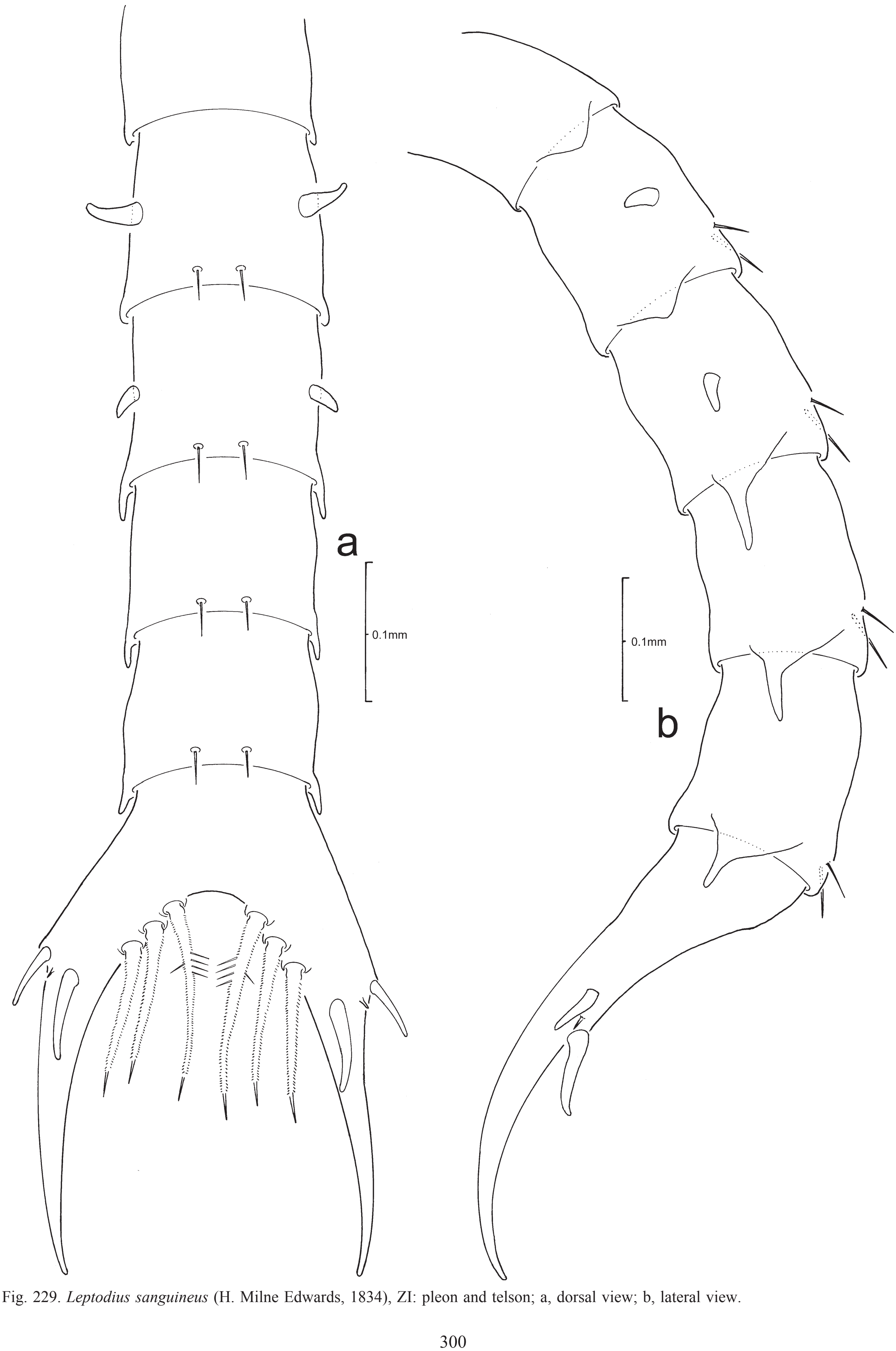

Fig. 229. *Leptodius sanguineus* (H. Milne Edwards, 1834), ZI: pleon and telson; a, dorsal view; b, lateral view.

Macromedaeus crassimanus **(A. Milne-Edwards, 1867)**
(Figs. 230–233)

Description of Zoea I.
CARAPACE (Fig. 230a, b): dorsal spine long, curved distally, just longer than rostral spine length; rostral spine just shorter than antennal protopod length, distally spinulate; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 230a): sessile.
Antennule (Fig. 230c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 230d): biramous; protopodal process distally spinulate, just longer than rostral spine length; endopod spine present; exopod ca. 12.5% of protopod, unsegmented with 1 terminal seta.
Mandible: palp absent.
Maxillule (Fig. 231a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 231b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 232a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 232b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,5 (2 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 233a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 231c, 233a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 small lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

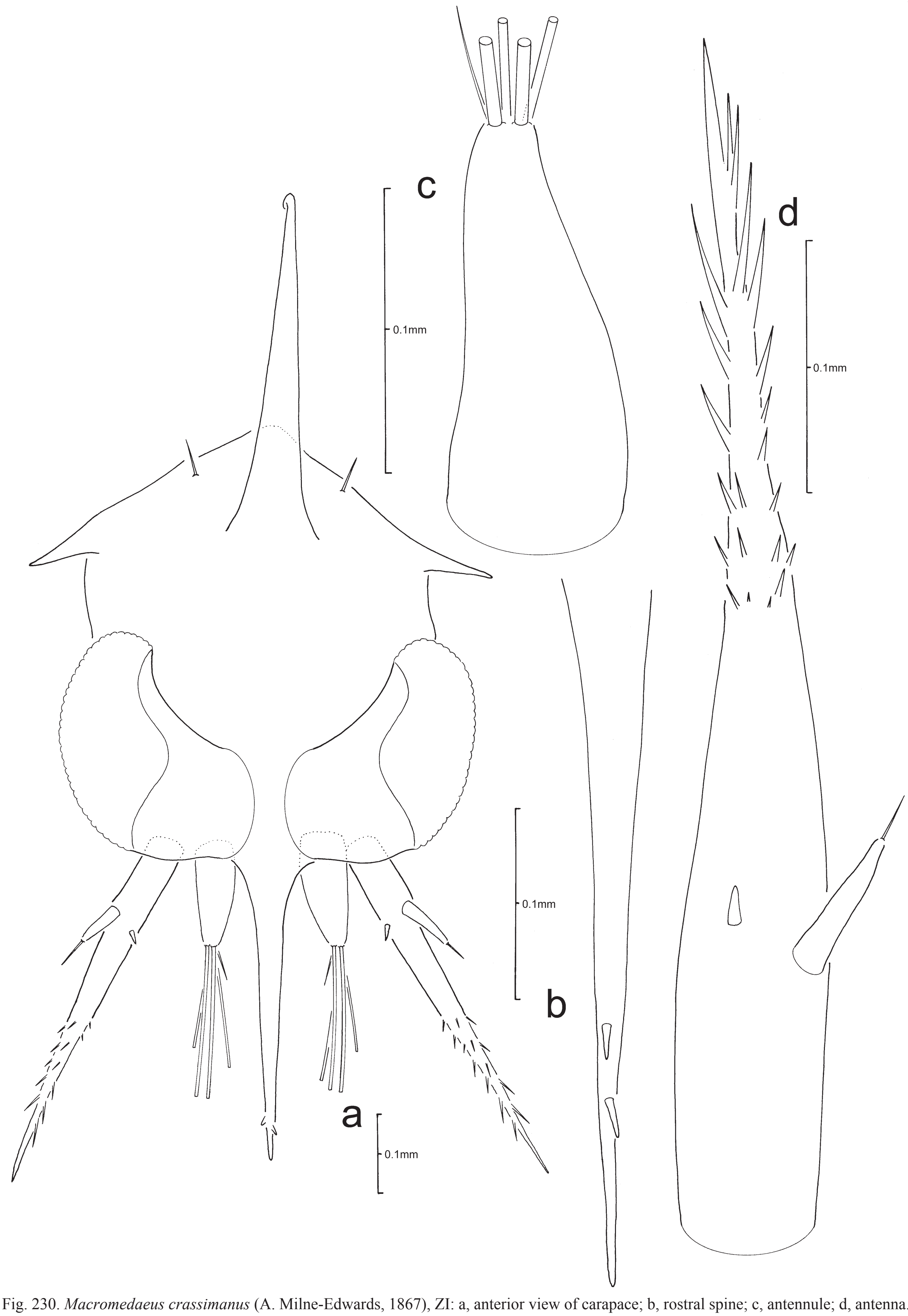

Fig. 230. *Macromedaeus crassimanus* (A. Milne-Edwards, 1867), ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

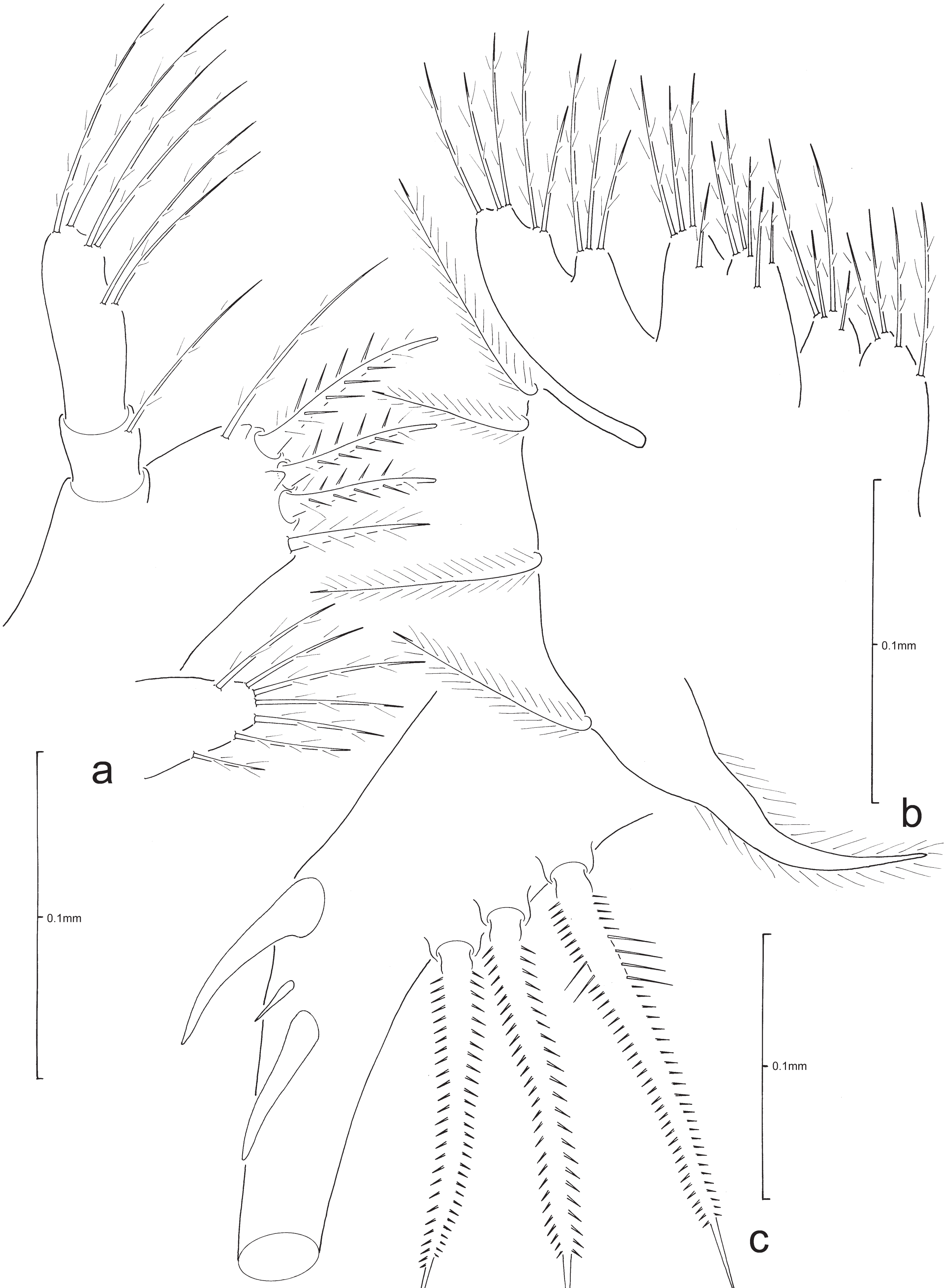

Fig. 231. *Macromedaeus crassimanus* (A. Milne-Edwards, 1867), ZI: a, maxillule; b, maxilla; c, telson.

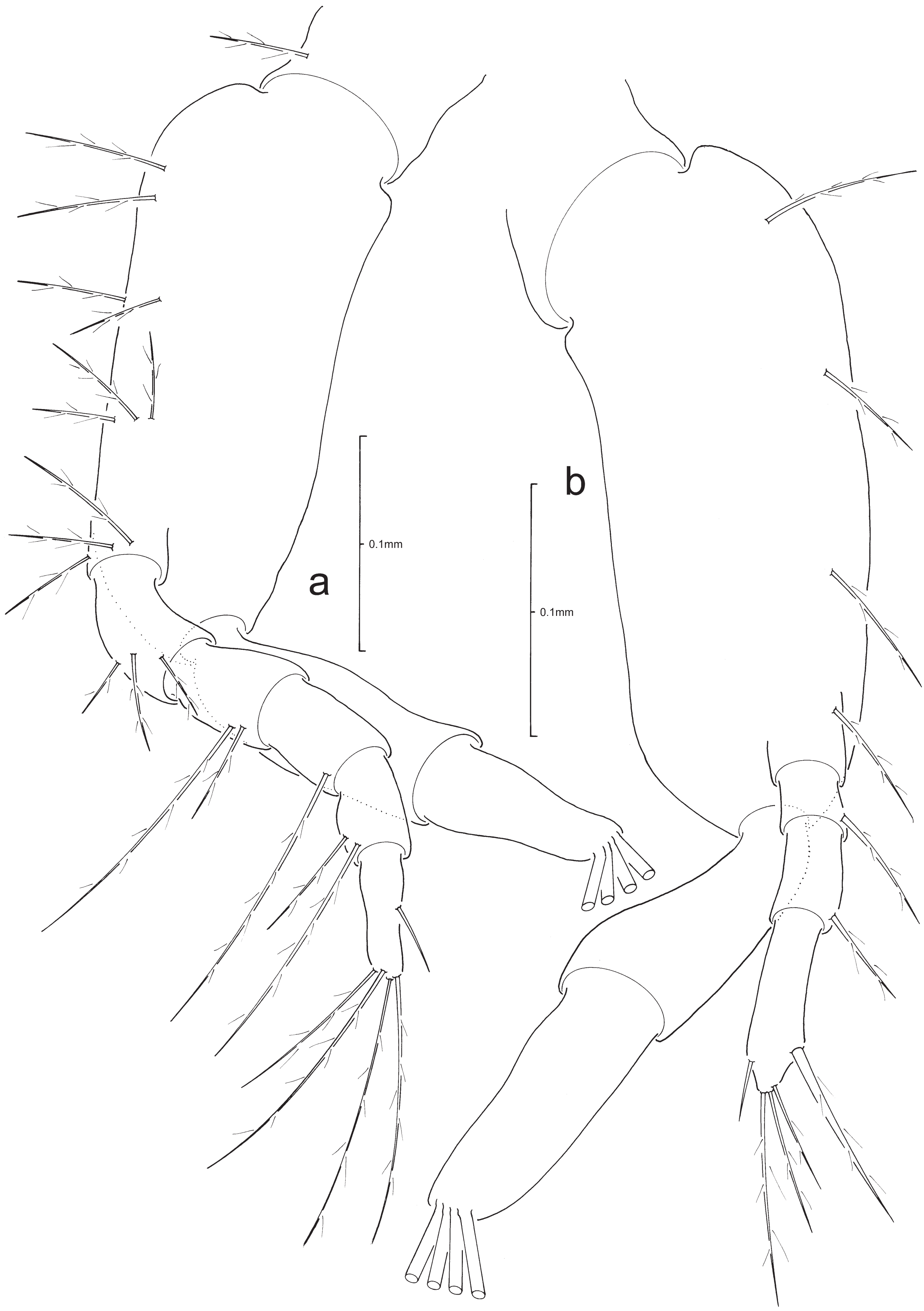

Fig. 232. *Macromedaeus crassimanus* (A. Milne-Edwards, 1867), ZI: a, first maxilliped; b, second maxilliped.

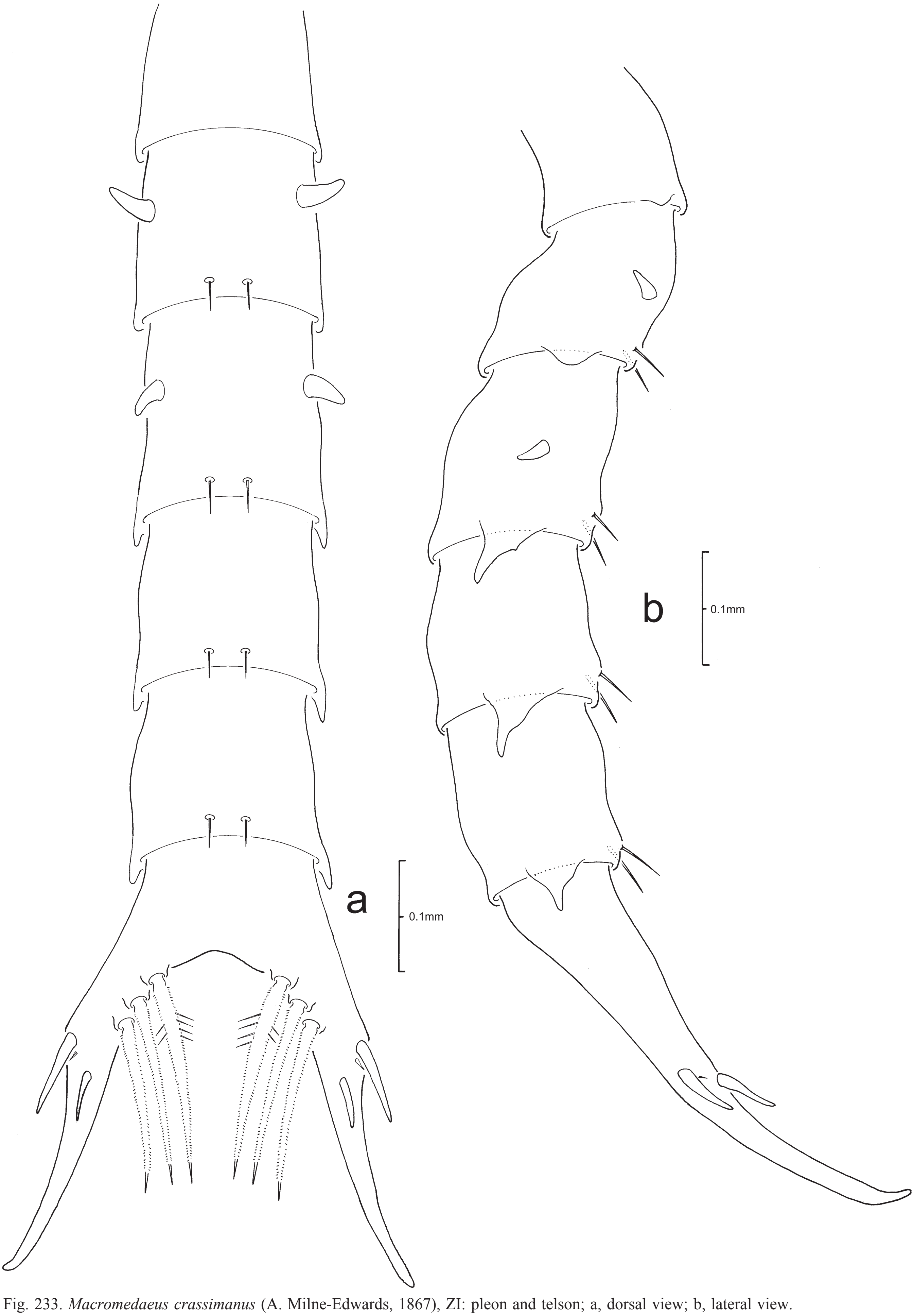

Fig. 233. *Macromedaeus crassimanus* (A. Milne-Edwards, 1867), ZI: pleon and telson; a, dorsal view; b, lateral view.

***Xantho hydrophilus* (Herbst, 1790)**
(Figs. 234–237)

Xantho incisus. Lebour, 1928: 530, 531, pl. II, fig. 3, pl. XI, figs. 5–9 (PZ, ZI–IV, Meg., Cr. I); Ingle, 1983: 970–973, figs. 7–12 (ZI–IV, Meg.); 1991: 237, 238, figs. 1.3d, 1.13p, 1.23d, 1.29d, 1.32e, 1.35a, 1.36j; 1.38f, 2.32, pl. 6g (ZI–IV).
Xantho hydrophilus. Lebour, 1928: 531, 532, pl. II, fig. 4 (PZ, ZI).

Description of Zoea I.
CARAPACE (Fig. 234a): dorsal spine long, curved distally, longer than rostral spine length; rostral spine just shorter than antennal protopod length, without distal spinulation; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 234a): sessile.
Antennule (Fig. 234b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 234c): biramous; protopodal process distally multispinulate, just longer than rostral spine length; endopod spine present; exopod ca. 4% length of protopod with 2 unequal terminal setae.
Mandible: palp absent.
Maxillule (Fig. 235a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 235b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 236a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 236b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 237a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 235c, 237a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae, outer most with prominent distal denticles.

Table 25. A comparison between the ZI of *Xantho hydrophilus* (Herbst, 1790) by Lebour (1928), Ingle (1983, 1991) as *X. incisus* Leach 1814, and the present study.

Character	**Lebour (1928)**	**Ingle (1983)**	**Ingle (1991)**	**Present study**
CARAPACE	pl. II, fig. 3; fig. 4	fig. 7a	fig. 2.32, a	Fig. 234a
1 pair of posterodorsal setae	absent	present	present	present
ANTENNULE	pl. II, fig. 3; fig. 4	fig. 7e	text p. 237	Fig. 234b
terminal setation	2 aesthetascs ?	text: 2–3 terminal aesthetascs, 2 setae fig.: 2 terminal aesthetascs, 2 setae	4 aesthetascs	4 (2 broad, 2 slender) terminal aesthetascs of unequal length, 1 terminal seta
ANTENNA	not figured or described	fig. 7f	text p. 235	Fig. 234c
endopod spine	not figured or described	absent	undeveloped	present
MAXILLULE	not figured or described	fig. 7g	text p. 237	Fig. 235a
coxal setation	not figured or described	6	6	7
MAXILLA	not figured or described	fig. 7h	text p. 237	Fig. 235b
basial setation	not figured or described	4+4	4,5	4+5
FIRST MAXILLIPED	pl. II, fig. 3; fig. 4	fig. 7i	text p. 237	Fig. 236a
coxal seta	not figured or described	not figured or described	not described	present
endopod setation	0,0,1,0,2*	3,2,1,2,5 (1 subterminal+4 terminal)	3,2,1,2,5 (1 subterminal+4 terminal)	3,2,1,2,5 (1 subterminal+4 terminal)
SECOND MAXILLIPED	pl. II, fig. 3; fig. 4	fig. 7j	text p. 237	Fig. 236b
endopod setation	not figured**	1,1,5 (2 subterminal+3 terminal	1,1,5+1	1,1,6 (3 subterminal+3 terminal)

*For *X. incisus* Lebour (1928) illustrates first maxilliped endopod setation as 0,2,1,0,3; 0,2,2,0,3; 0,3,2,0,3 (pl. XI, figs. 5, 6, 7 for ZII, ZIII, ZIV, respectively).

** For *X. incisus* Lebour (1928) illustrates second maxilliped endopod setation as 0,0,3 (pl. XI, figs. 5, 6, 7 for ZII, ZIII, ZIV respectively)

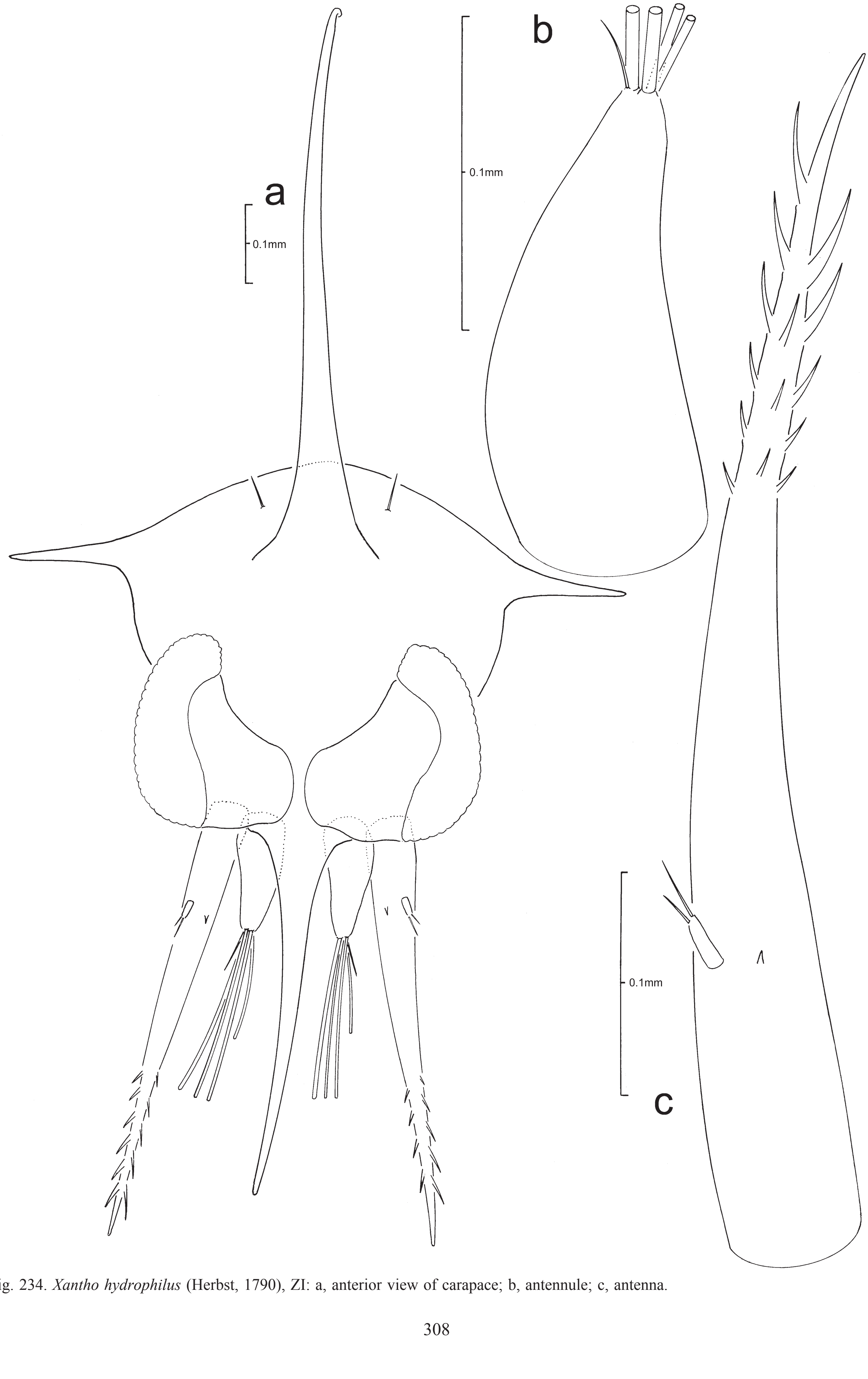

Fig. 234. *Xantho hydrophilus* (Herbst, 1790), ZI: a, anterior view of carapace; b, antennule; c, antenna.

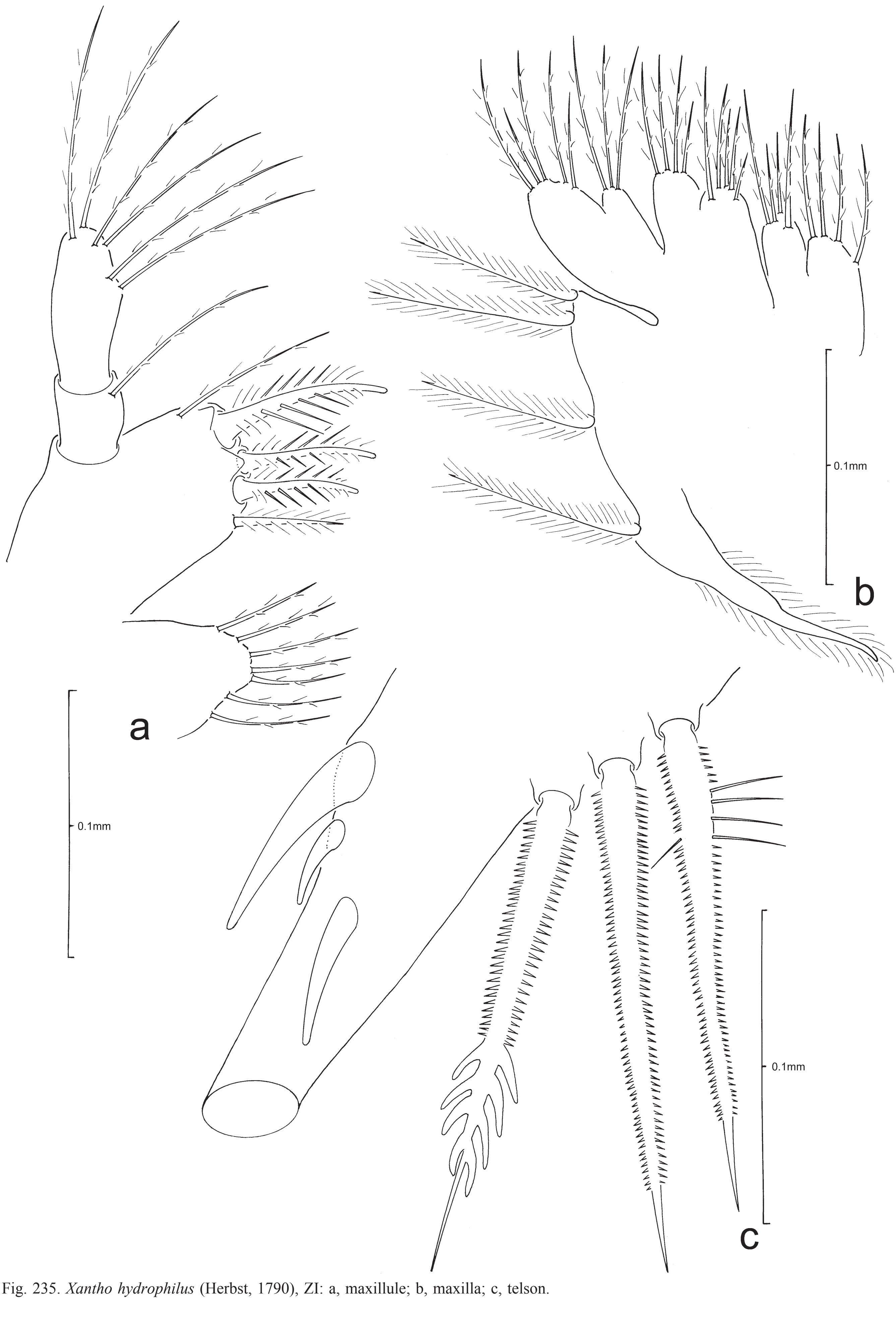

Fig. 235. *Xantho hydrophilus* (Herbst, 1790), ZI: a, maxillule; b, maxilla; c, telson.

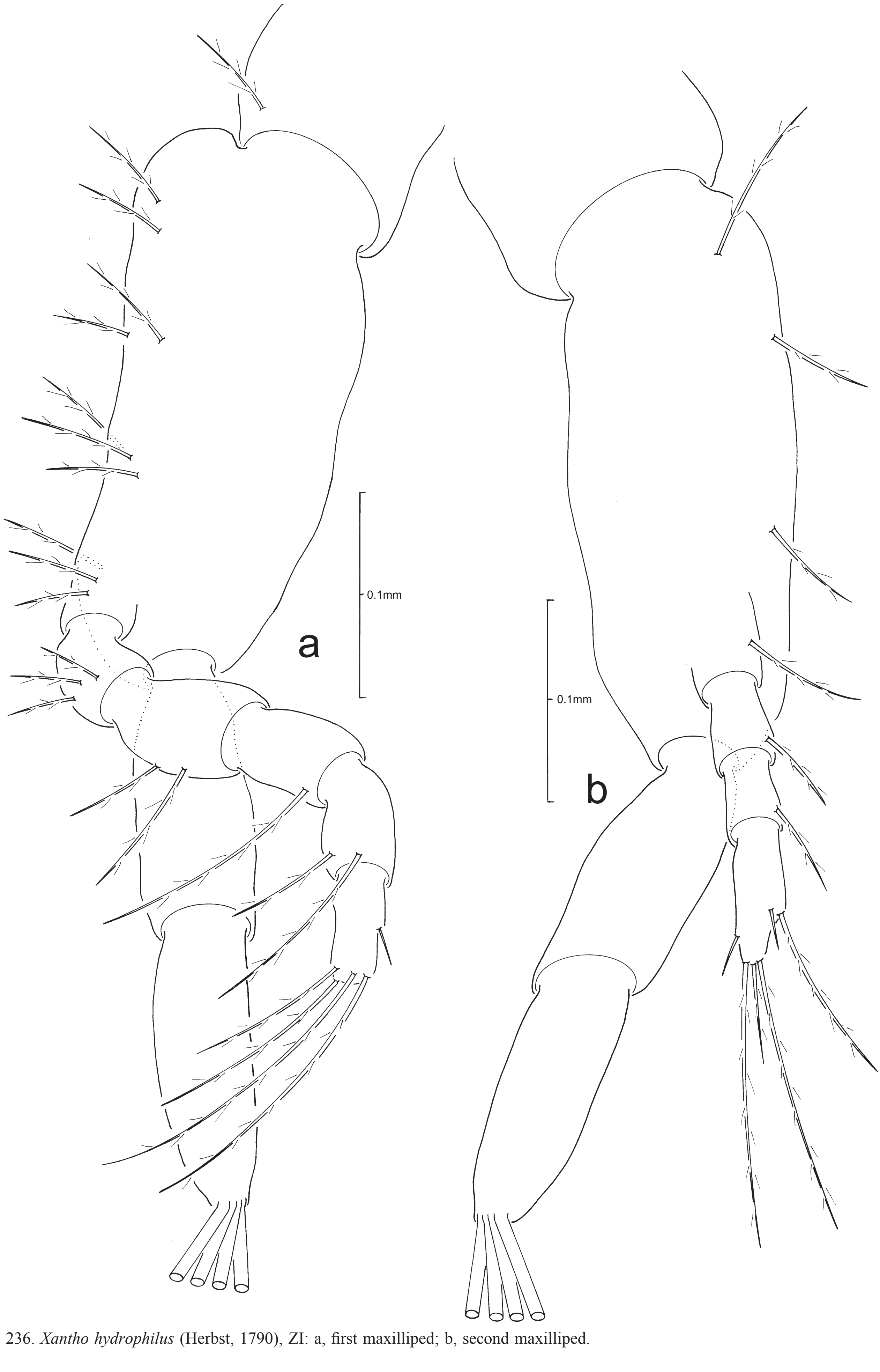

Fig. 236. *Xantho hydrophilus* (Herbst, 1790), ZI: a, first maxilliped; b, second maxilliped.

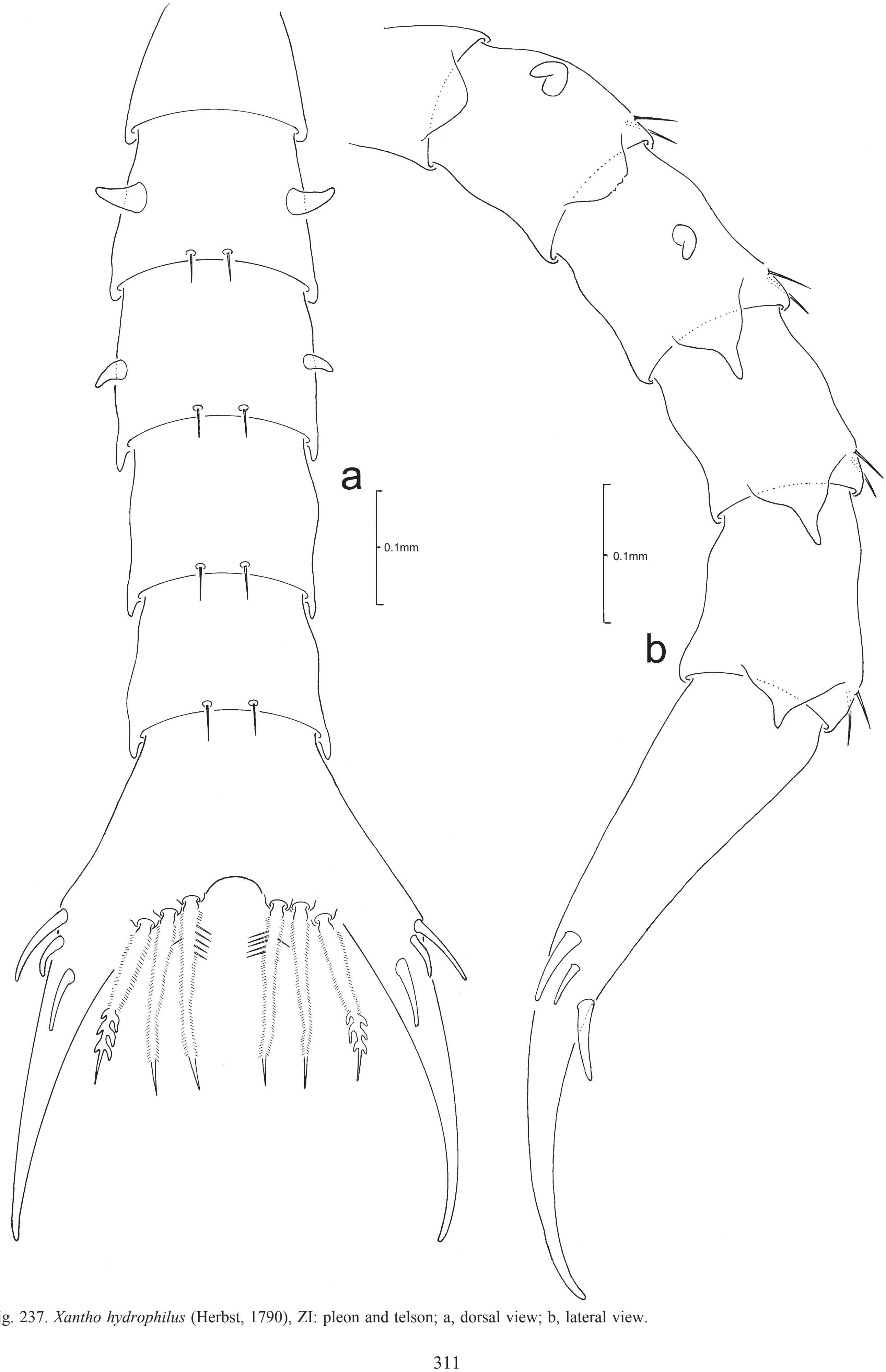

Fig. 237. *Xantho hydrophilus* (Herbst, 1790), ZI: pleon and telson; a, dorsal view; b, lateral view.

Xantho pilipes A. Milne-Edwards, 1867
(Figs. 238–241)

Xantho pilipes. Paula & dos Santos, 2001: 254–263, figs. 1–6 (ZI–IV, Meg.); Ingle, 1991: 141, 229, 236, 238.
Xantho hydrophilus. Lebour, 1928: 531, 532, pl. II, fig. 4 (PZ, ZI).

Description of Zoea I.
CARAPACE (Fig. 238a, b): dorsal spine long, curved distally, longer than rostral spine length; rostral spine ca. equal in length to antennal protopod, distally spinulate; lateral spines slightly curved ventrally, with spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 238a): sessile.
Antennule (Fig. 238c): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 238d): biramous; protopodal process distally multispinulate, ca. equal to rostral spine length; endopod spine present; exopod ca. 17% length of protopod with 2 unequal terminal setae.
Mandible: palp absent.
Maxillule (Fig. 239a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 239b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 4+5 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION
First maxilliped (Fig. 240a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 240b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 241a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 239c, 241a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Table 26. A comparison between the ZI of *Xantho pilipes* A. Milne-Edwards, 1867 by Paula & dos Santos (2001) and the present study.

Character	Paula & dos Santos (2001)	Present study
ANTENNA	fig. 1D	Fig. 238c
endopod spine	absent	present
MAXILLA	text p. 254, fig. 1G	Fig. 239b
basial setation	text: 5+4 fig.: 6+4	4+5
FIRST MAXILLIPED	fig. 1H	Fig. 240a
coxal seta	not figured	present
SECOND MAXILLIPED	fig. 1I	Fig. 240b
endopod setation	1,1,5 (2 subterminal+3 terminal)	1,1,6 (3 subterminal+3 terminal)

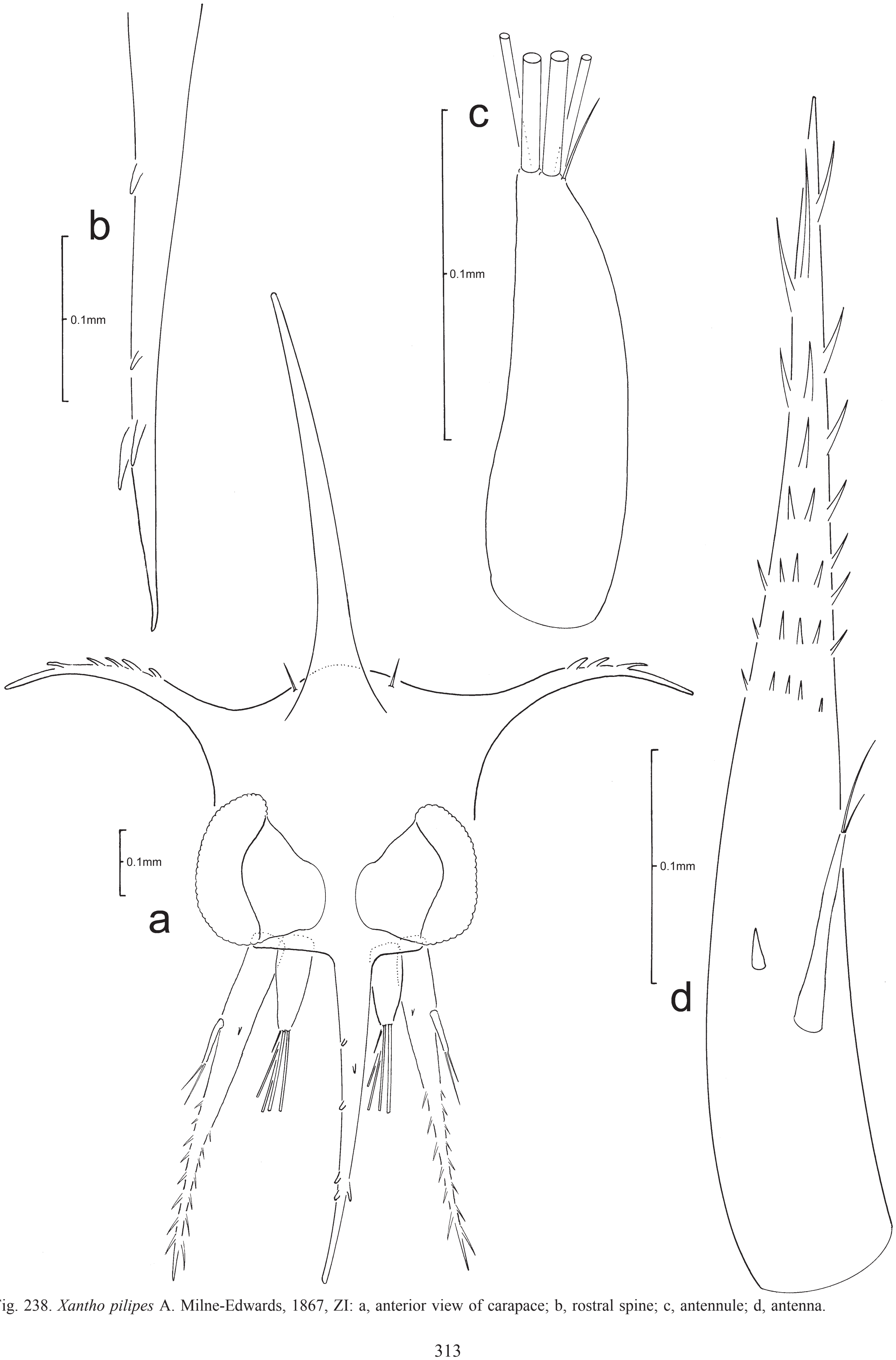

Fig. 238. *Xantho pilipes* A. Milne-Edwards, 1867, ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

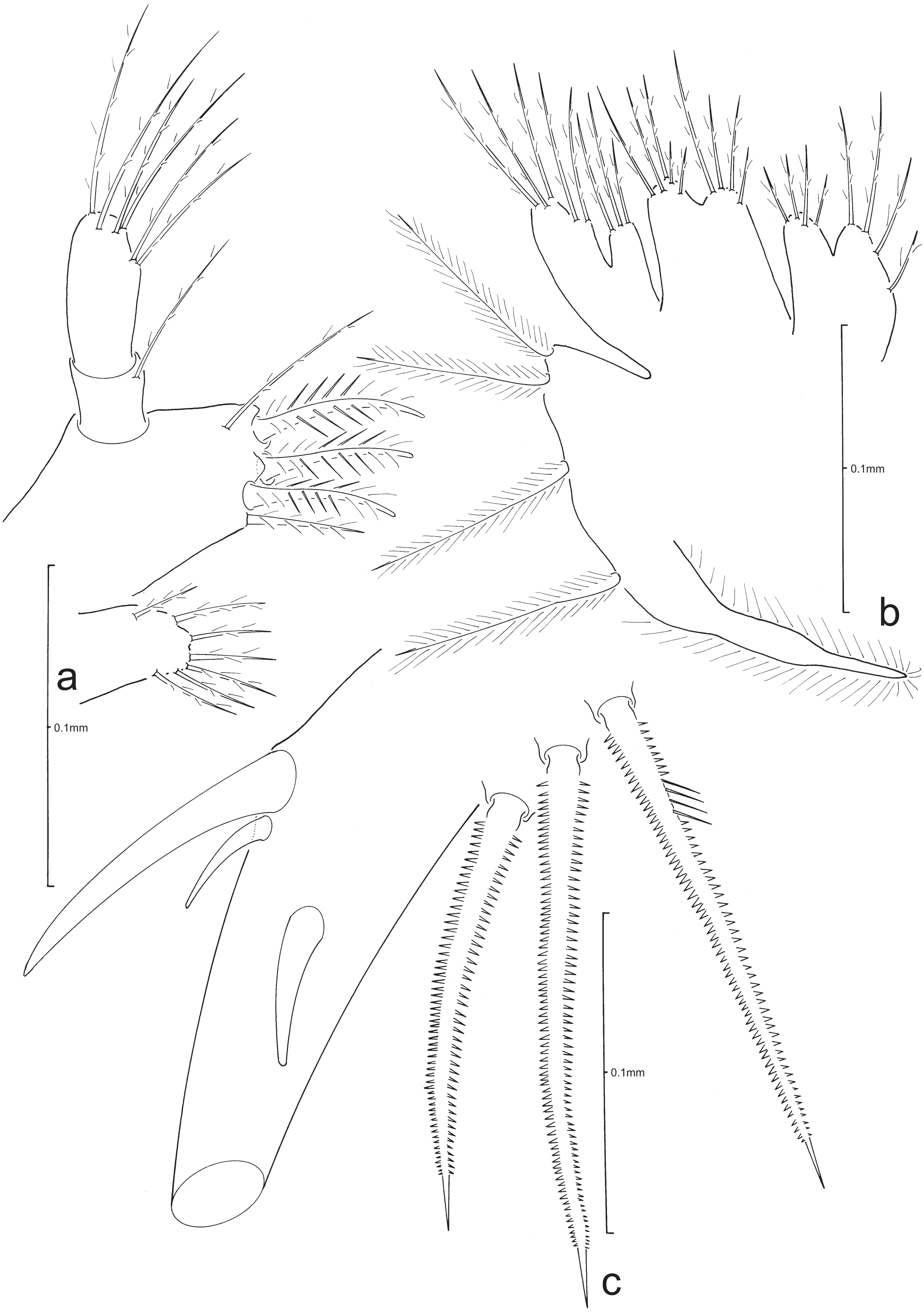

Fig. 239. *Xantho pilipes* A. Milne-Edwards, 1867, ZI: a, maxillule; b, maxilla; c, telson.

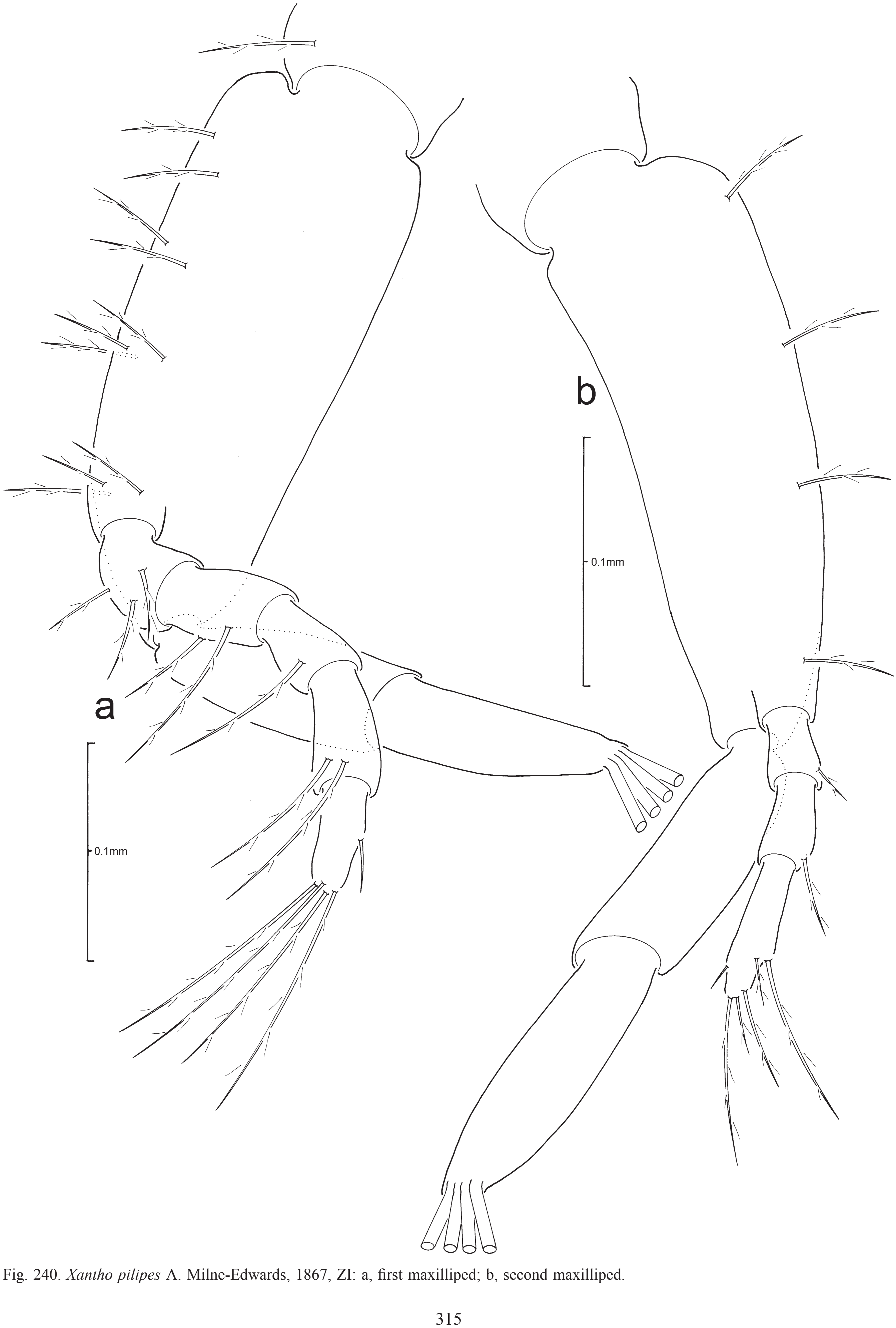

Fig. 240. *Xantho pilipes* A. Milne-Edwards, 1867, ZI: a, first maxilliped; b, second maxilliped.

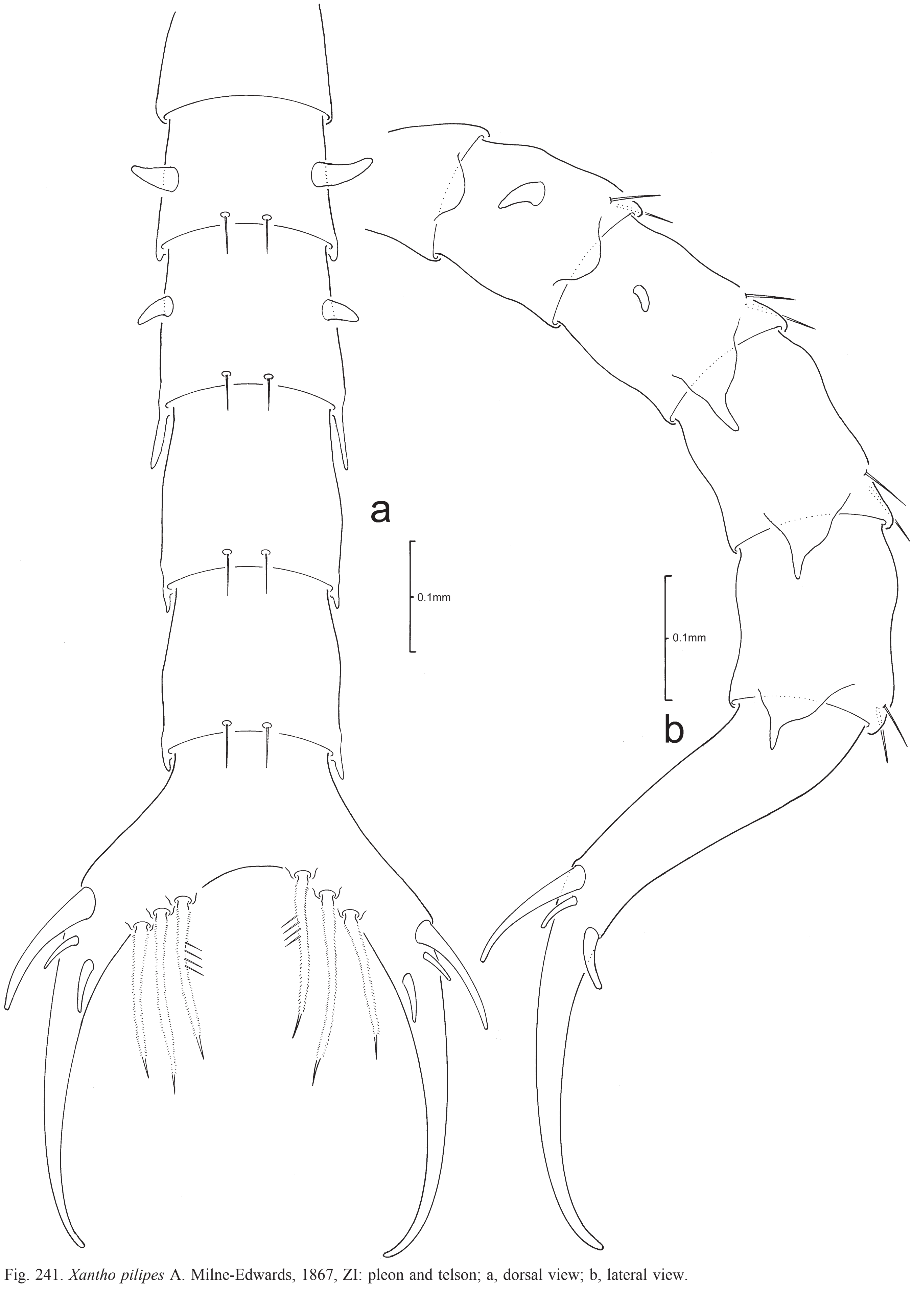

Fig. 241. *Xantho pilipes* A. Milne-Edwards, 1867, ZI: pleon and telson; a, dorsal view; b, lateral view.

Xantho poressa (Olivi, 1792)

(Figs. 242–245)

Xantho poressa. Gourret, 1884: pl. 1, fig. 7 (Z1)? (see Ingle, 1991: 238); Rodríguez & Martin, 1997: 99–108, figs. 1–8 (ZI–IV, Meg., Cr. I).

non *Xantho poressa*. Bourdillon-Casanova, 1960: 170, fig. 3 (ZI)? (see Ingle, 1991: 238; Rodríguez & Martin, 1997: 108, 109).

Description of Zoea I.

CARAPACE (Fig. 242a): dorsal spine long, curved distally, longer than rostral spine length; rostral spine just shorter than antennal protopod length, without distal spinulation; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON

Eyes (Fig. 242a): sessile.

Antennule (Fig. 242b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.

Antenna (Fig. 242c): biramous; protopodal process distally multispinulate, just longer than rostral spine length; endopod spine present; exopod ca. 3% length of protopod with 2 unequal terminal setae.

Mandible: palp absent.

Maxillule (Fig. 243a): uniramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.

Maxilla (Fig. 243b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal+3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long distal stout process.

PEREION

First maxilliped (Fig. 244a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 244b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

PLEON (Fig. 245a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 243c, 245a, b): each fork long, gradually curved distally, not spinulated, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae.

Table 27. A comparison between the ZI of *Xantho poressa* (Olivi, 1792) by Rodríguez & Martin (1997) and the present study.

Character	Rodríguez & Martin (1997)	Present study
ANTENNA	fig. 2F	Fig. 242c
endopod spine	absent	present
FIRST MAXILLIPED	fig. 5A	Fig. 244a
coxal seta	not figured	present

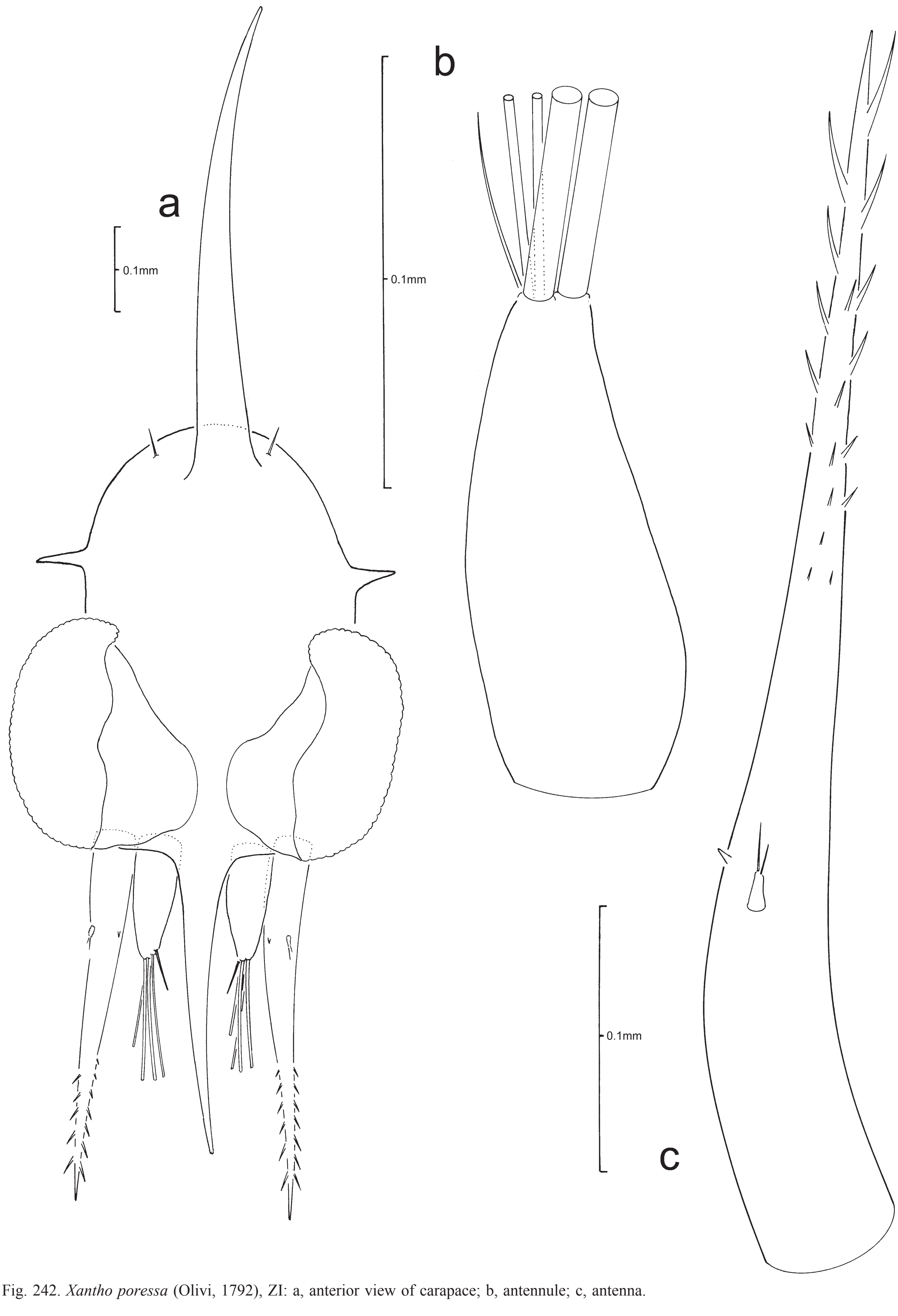

Fig. 242. *Xantho poressa* (Olivi, 1792), ZI: a, anterior view of carapace; b, antennule; c, antenna.

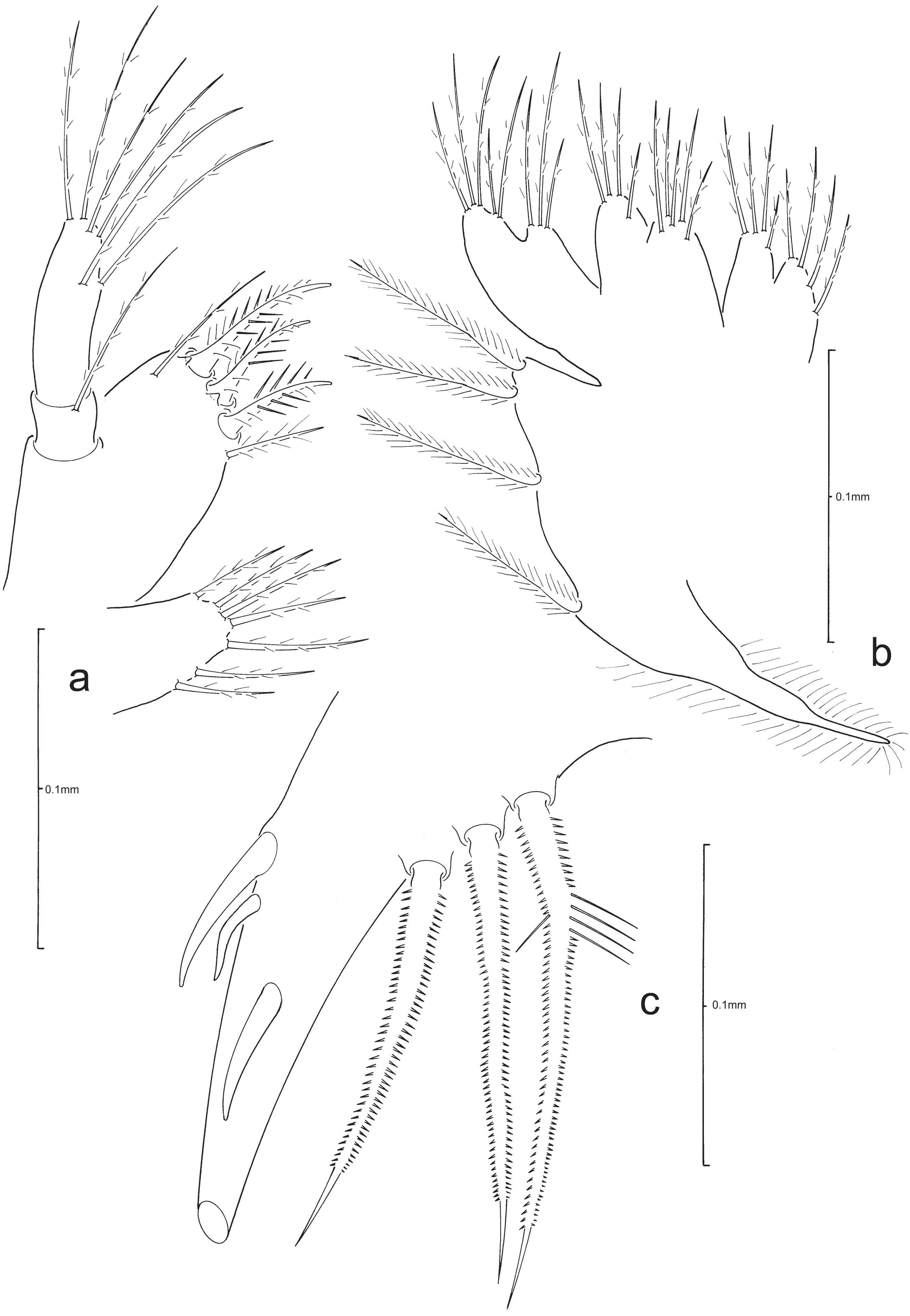

Fig. 243. *Xantho poressa* (Olivi, 1792), ZI: a, maxillule; b, maxilla; c, telson.

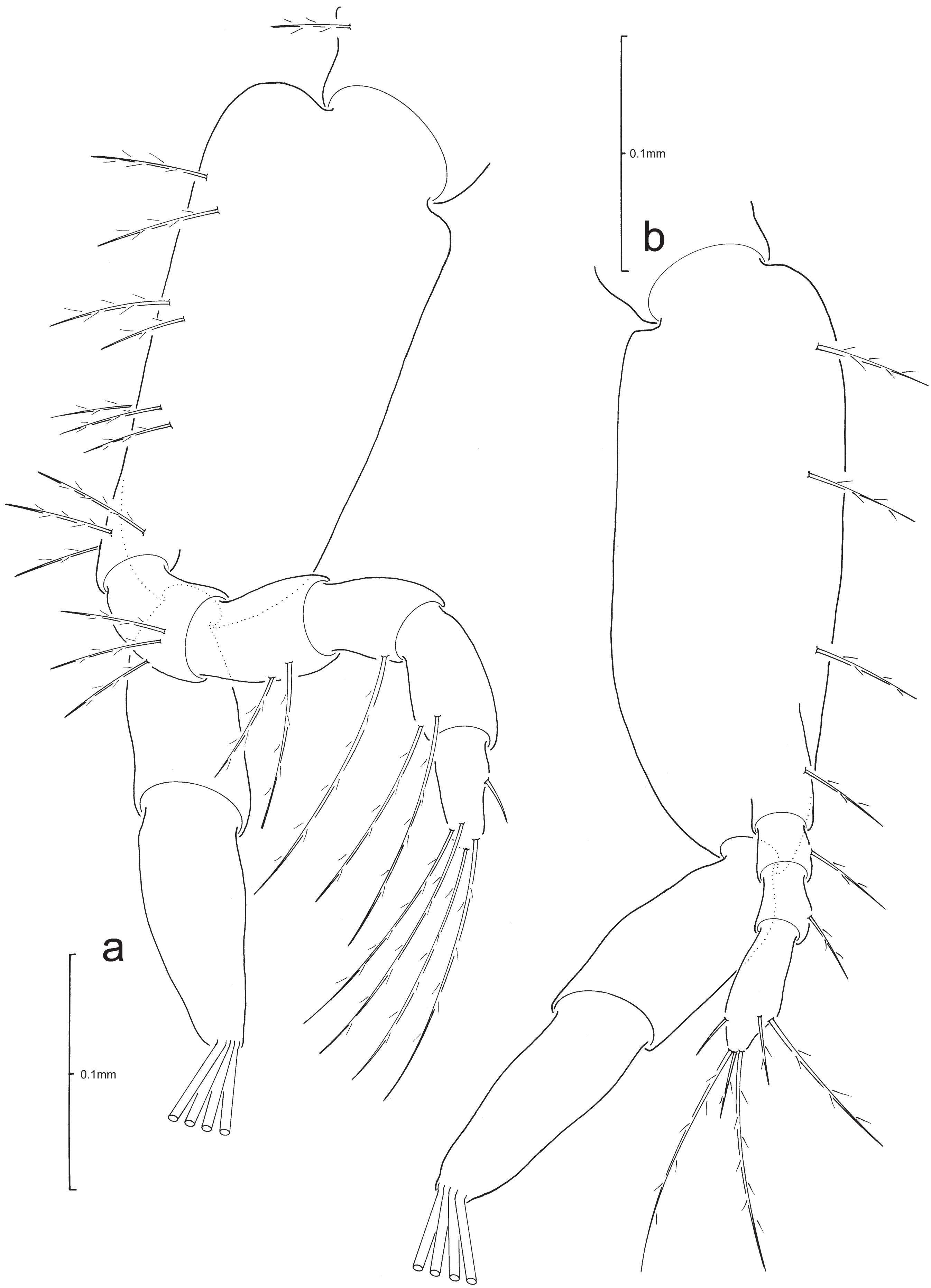

Fig. 244. *Xantho poressa* (Olivi, 1792), ZI: a, first maxilliped; b, second maxilliped.

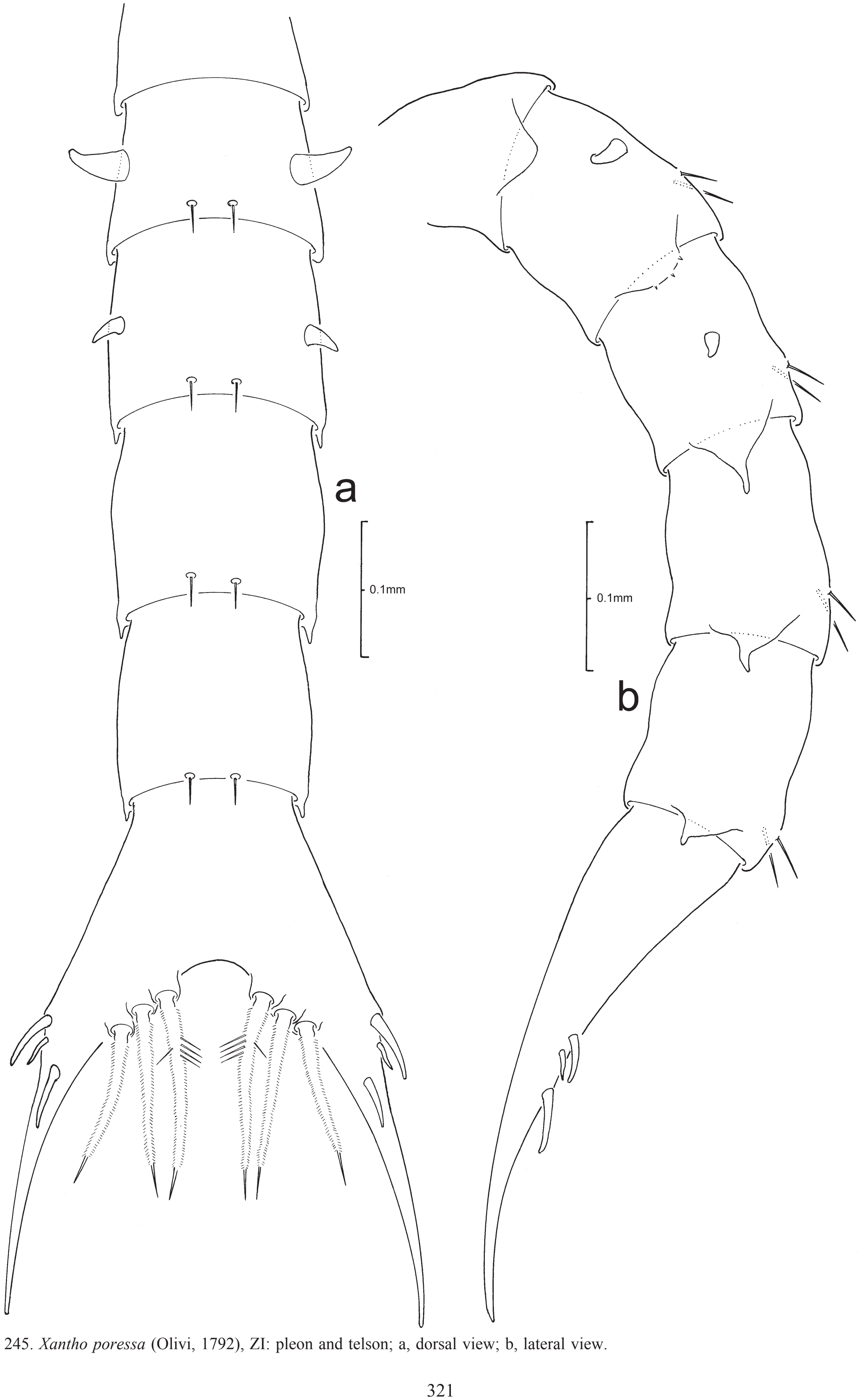

Fig. 245. *Xantho poressa* (Olivi, 1792), ZI: pleon and telson; a, dorsal view; b, lateral view.

Subfamily Zosiminae Alcock, 1898

***Platypodiella spectabilis* (Herbst, 1794)**
(Figs. 246–249)

Platypodiella spectabilis. Fransozo et al., 2001: 80, 81, figs. 1–3 (ZI).

Description of Zoea I.
CARAPACE (Fig. 246a, b): dorsal spine long, curved distally, ca. twice rostral spine length; rostral spine ca. equal to antennal protopod length, distally spinulate; lateral spines straight, without spinulation on dorsal margin; anterodorsal setae absent; 1 pair of posterodorsal setae present; ventral margin without setae.

CEPHALON
Eyes (Fig. 246a): sessile.
Antennule (Fig. 246b): primary flagellum unsegmented with 4 (2 broad, 2 slender) terminal aesthetascs of unequal length plus 1 terminal seta; accessory flagellum absent.
Antenna (Fig. 246c): biramous; protopodal process distally multispinulate, ca. equal to rostral spine length; endopod spine present; exopod ca. 14% length of protopod, possessing 3 (1 long subterminal+2 unequal terminal) setae.
Mandible: palp absent.
Maxillule (Fig. 247a): biramous; epipod seta absent; coxal endite with 7 setae; basial endite with 5 setal processes + 2 small setal buds; endopod comprising 2 articles, proximal article with 1 seta; distal article with 6 (2 subterminal+4 terminal) setae; exopod seta absent.
Maxilla (Fig. 247b): biramous; coxal endite bilobed with 4+4 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal, 3 terminal) setae; exopod (scaphognathite) margin with 4 setae + 1 long stout distal process.

PEREION
First maxilliped (Fig. 248a): biramous; coxa with 1 seta; basis with 10 (2+2+3+3) setae; endopod comprising 5 articles with 3,2,1,2,5 (1 subterminal+4 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Second maxilliped (Fig. 248b): biramous; coxa without setae; basis with 4 (1+1+1+1) setae; endopod comprising 3 articles, with 1,1,6 (3 subterminal+3 terminal) setae respectively; exopod comprising 2 articles, distal article with 4 long terminal plumose natatory setae.
Third maxilliped: absent.
Pereiopods: absent.

PLEON (Fig. 249a, b): 5 pleomeres; pleomere 2 with 1 pair of dorsolateral processes directed anteriorly; pleomere 3 with 1 pair of dorsolateral processes directed ventrally; pleomeres 1–2 each with rounded posterolateral processes; pleomeres 3–5 each with short posterolateral spinous processes; pleomere 1 without setae; pleomeres 2–5 each with 1 pair of posterodorsal setae; pleopod buds absent.

TELSON (Figs. 247c, 249a, b): each fork long, gradually curved distally, not spinulate, 1 large lateral spine, 1 smaller lateral spine, 1 large dorsomedial spine present; posterior margin with 3 pairs of stout spinulate setae

Table 28. A comparison between the ZI of *Platypodiella spectabilis* (Herbst, 1794) by Fransozo et al. (2001) and the present study.

Character	Fransozo et al. (2001)	Present study
ANTENNULE	figs. 1c, 3c	Fig. 246c
terminal setation	text & fig. 1c: 3 aesthetascs, 2 simple setae fig. 2c: 2 aesthetascs, 2 simple setae?	4 (2 broad, 2 slender) aesthetascs of unequal length, 1 seta
ANTENNA	figs. 1d, 3c	Fig. 246d
exopod setation	2 terminal setae	3 (1 long subterminal, 2 unequal terminal) setae
MAXILLULE	fig. 2b	Fig. 247a
coxal setation	6	7
MAXILLA	fig. 2c	Fig. 247b
basial setation	4+4	5+4
SECOND MAXILLIPED	fig. 2e	Fig. 248b
endopod setation	1,1,5 (2 subterminal+3 terminal) setae	1,1,6 (3 subterminal+3 terminal) setae

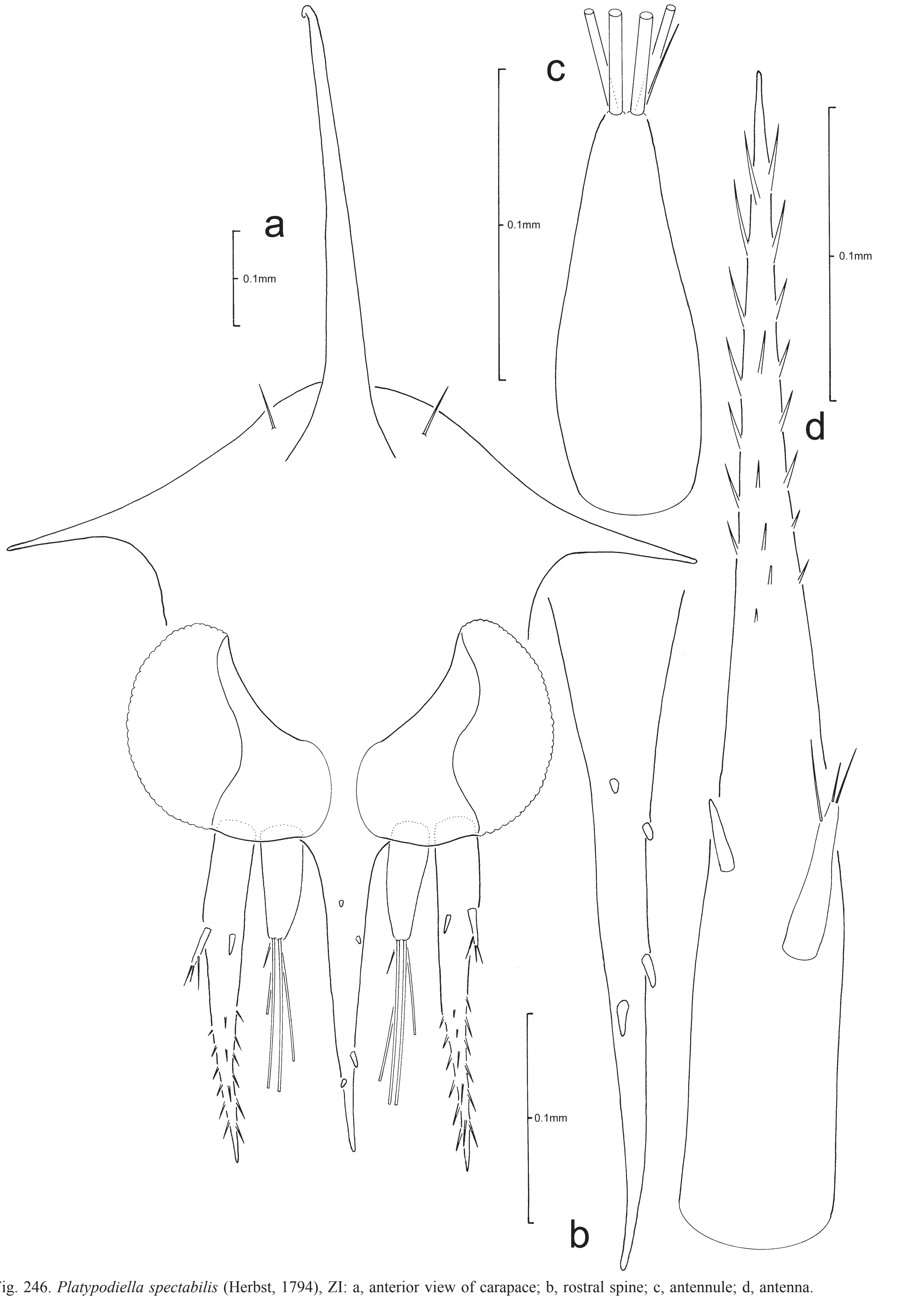

Fig. 246. *Platypodiella spectabilis* (Herbst, 1794), ZI: a, anterior view of carapace; b, rostral spine; c, antennule; d, antenna.

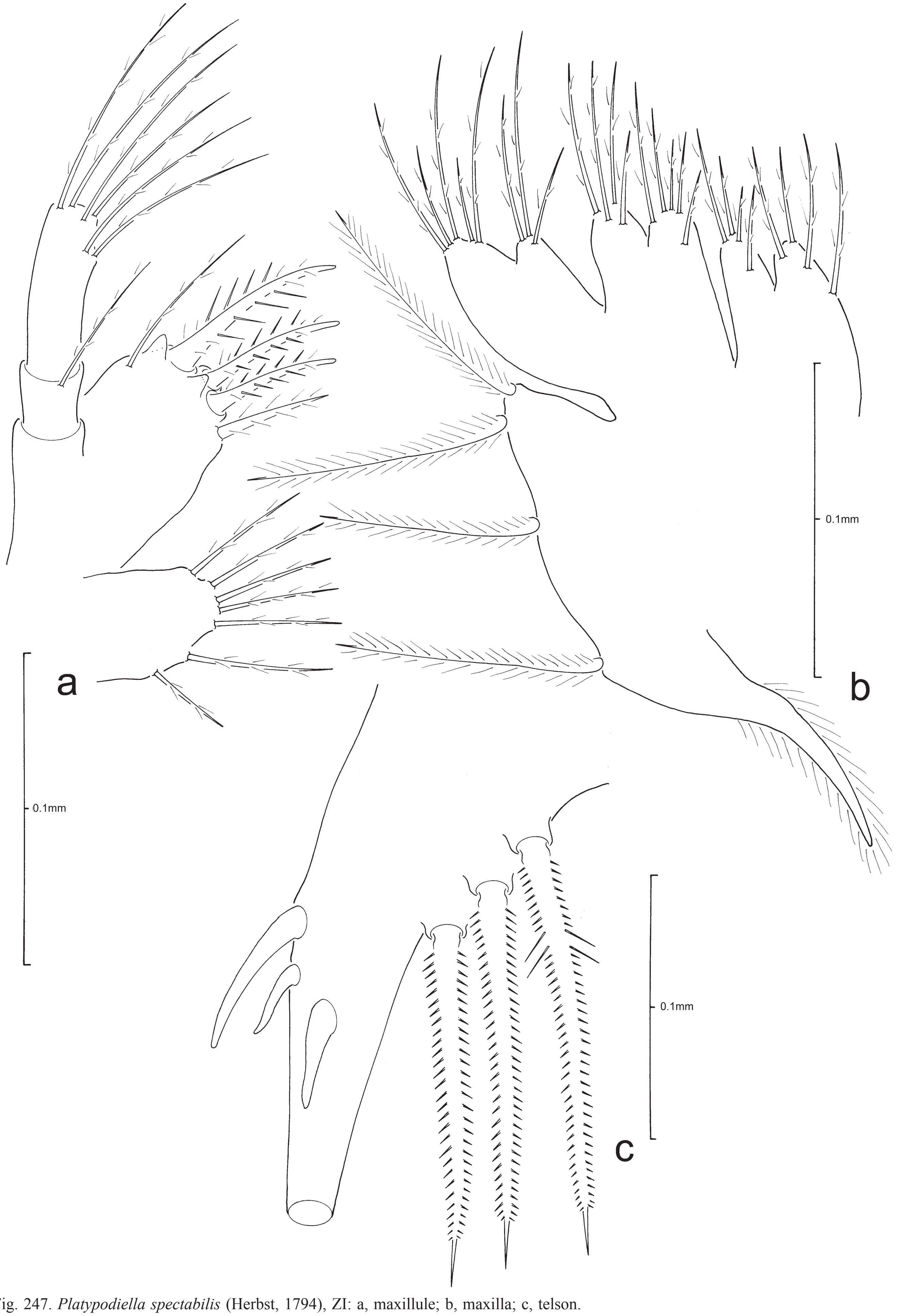

Fig. 247. *Platypodiella spectabilis* (Herbst, 1794), ZI: a, maxillule; b, maxilla; c, telson.

Fig. 248. *Platypodiella spectabilis* (Herbst, 1794), ZI: a, first maxilliped; b, second maxilliped.

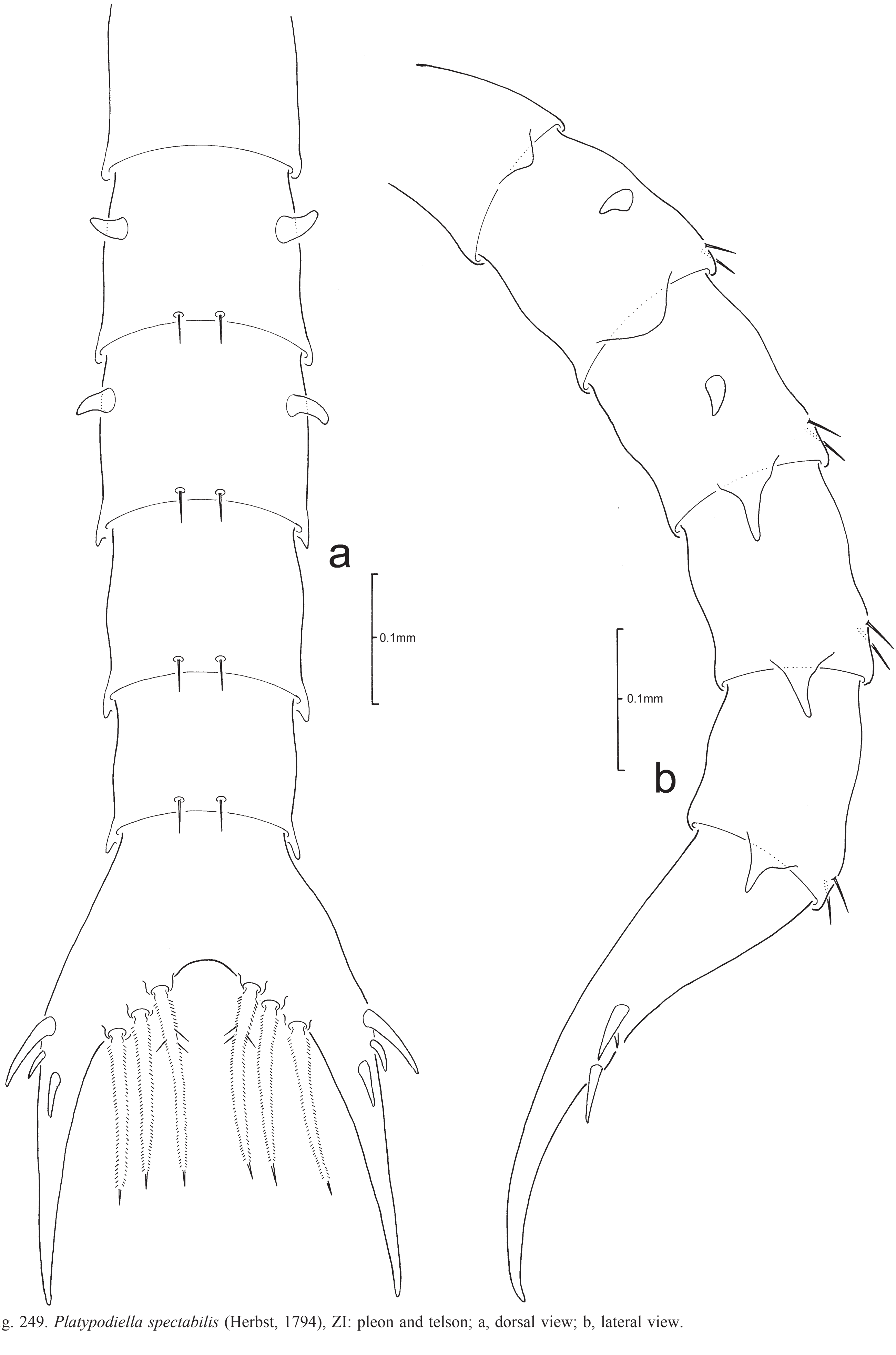

Fig. 249. *Platypodiella spectabilis* (Herbst, 1794), ZI: pleon and telson; a, dorsal view; b, lateral view.

ZOEAL CHARACTERS AND STATES

Zoeas display an array of characters including chromatophore colouration, spinulation, spinature, division of pleuron somites, setation, and development of appendages. The information such characters provide can be solely descriptive (diagnostic, comparative, identification) without evolutionary or phylogenetic information (homologous, ancestral or derived characters) providing evidence of relationships within and between taxa. Some characters are developmental, being transient and non-functional in the zoeal phase, and become functional after the moult to megalop and crab phase. Two further types of characters can be identified, conservative and accumulative. Conservative characters do not change during stage moults; they remain constant throughout development and are considered to either be expressed (present) or absent (lost) when comparing zoeas from different taxa. Loss of such characters may be considered to be of phylogenetic importance. For example, Rice (1980: 299–301) recorded a series of characters that he considered present in ancestral zoeas of higher Brachyura. This was followed by a list of advanced (derived) features found in majoid zoeas comprising characters that were either reduced (in number) or lost. In contrast, accumulative characters increase in number on body somites and appendage articles at successive stage moults. Polarising these characters can prove difficult especially in zoeas with abbreviated development as they can be expressed early during stage moults or delayed even to the point of being lost entirely. When comparing zoeal stages, Clark (2001) concluded that development of different characters occurred at different times and/or rates, suggesting that evolutionary history of brachyuran zoeae provided robust examples of heterochrony. Clark (2001), however, made no attempt to relate this zoeal theory to the heterochronic process as discussed by McKinney & McNamara (1991). According to them, heterochrony can be defined as an evolutionary change in the appearance/rate of character development shown between an ancestor and its descendants. McKinney & McNamara (1991) considered three basic heterochronic changes: changes in onset (presence/expression) time, changes in offset (absence/delayed/termination/loss) time, and changes in rate (acceleration/retardation).

In the present study zoeal characters, including developmental and setal, were identified, and their expression was correlated to an outgroup species with a long zoeal development phase. Furthermore, the onset/offset of these characters or their rate of development was associated with abbreviated zoeal development. Cuesta et al. (2011) investigated the larval development of *Geograpsus lividus* (H. Milne Edwards, 1837), reared under laboratory conditions. It comprised 8 zoeal stages and, according to the authors, represented the longest recorded developmental pathway for any brachyuran. For this present study, 8 zoeal stages is considered to be the ancestral condition and, in comparison, descendants show abbreviated development, e.g., *Charybdis helleri* (A. Milne-Edwards, 1867) by Dineen et al. (2001) with 6 zoeal stages; *Liocarcinus navigator* (Herbst, 1794) (as *L. arcuatus* (Leach, 1814) by Clark, 1984) with 5 zoeal stages; *Nanocassiope granulipes* (T. Sakai, 1939) by Ko & Clark (2002) with 4 zoeal stages; *Actumnus setifer* (De Haan, 1835) by Clark & P.K.L. Ng (2004b) with 3 zoeal stages; and *Maja brachydactyla* Balss, 1922 (as *M. squinado* (Herbst, 1788) by Clark, 1986). Here, possessing 2 zoeal stages was considered to be the most derived condition. Each zoeal stage can be unequivocally defined and directly compared for heterochronic development by the number of terminal plumose natatory setae on the distal exopod article of the first and second maxillipeds, e.g., 4 in ZI, 6 in ZII, 8 in ZIII, and 10 in ZIV, etc.

CARAPACE

Dorsal, rostral, lateral spines (Figs. 250–252): A number of characters relate to carapace spines, including presence or absence, terminal ending, relative length, and presence of spinature and setae. The information provided is mainly descriptive, but Rice (1980) considered the reduction of carapace spines especially within the majoids and their loss to be advanced (derived) characters. Presence or absence of carapace spines was generally conservative with phylogenetic significance between taxa. Lateral spines within the Grapsidae, however, can be accumulative characters, being minute in ZI, but their length increases to become fully expressed in ZII, e.g., *Metopograpsus frontalis* Miers, 1880 by Fielder & Greenwood (1983); *Pachygrapsus marmoratus* (Fabricius, 1787), *P. maunus* (Lucas, 1846) and *P. transversus* (Gibbes, 1850) all by Cuesta & Rodriquez (1994), and *Geograpsus lividus* by Cuesta et al. (2011).

Quantifying the relative length of carapace spines is, however, problematic. For example, the dorsal carapace spine of *Carpilius convexus* (Forskål, 1775) is short (Fig. 250b) compared to that of *Liomera loevis* (A. Milne-Edwards, 1873) (Fig. 250f) which is extremely long and ancestral according to Rice (1980). The problem with spine length is defining what to measure. The tip is well defined, but the base as a reference point for measurement is arbitrary and possibly inconsistent. In addition, length is a continuous variable, merging from long to short through various intermediates. Furthermore, how is polarity assigned to such a suite of characters? Lateral spines provide two additional descriptive features; normally they are straight but may be curved dorsally or ventrally and may possess a pair of smaller secondary lateral spines as in *Tetralia cavimana* Heller, 1861 and *Quadrella maculosa* Alcock, 1898 (Fig. 252e, f, respectively).

The presence of setae on ZI carapace spines is not common, especially with reference to the laterals. Some ZI do have setae present on the dorsal spine, e.g., *Rhabdonotus pictus* A. Milne-Edwards, 1879 (Fig. 250j) has 1 seta and *Daira perlata* (Herbst, 1790) (Fig. 250c) has 2 pairs. The same is apparent for ZI rostral setae, and a pair is present on *Rhabdonotus pictus* (Fig. 251g). With respect to the dorsal spines, setae may be present in later stages as an accumulative character. Within the Pilumninae, e.g., *Pilumnus hirtellus* (Linnaeus, 1761) (Clark, 2005: figs. 1, 2; 2007: figs. 437, 438) has 0 dorsal spine setae in ZI, 0 in ZII, 1 pair in ZIII, 1 pair in ZIV; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 1), 0 in ZI, 0 in ZII, 1 pair in ZIII; *P. sluiteri* De Man, 1892 (Clark & P.K.L. Ng, 2004a: figs. 1, 2), 0 in ZI, 0 in ZII;

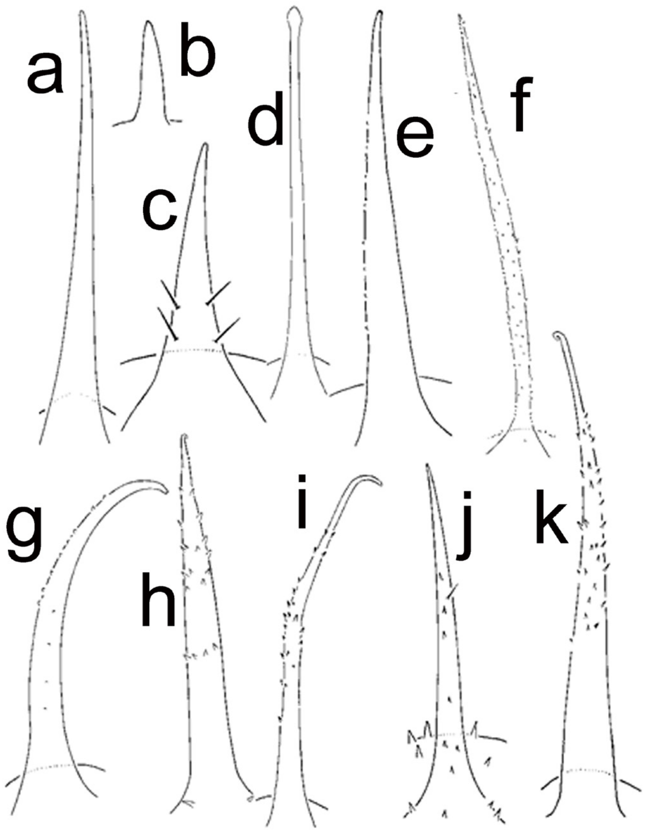

Fig. 250. Carapace: ZI; dorsal spine: a, *Acantholobulus bermudensis* (Benedict & Rathbun, 1891); b, *Carpilius convexus* (Forskål, 1775); c, *Daira perlata* (Herbst, 1790); d, *Epiactaea nodulosa* (White, 1848); e, *Liomera bella* (Dana, 1852); f, *Liomera loevis* (A. Milne-Edwards, 1873); g, *Microcassiope minor* (Dana, 1852); h, *Pseudoliomera speciosa* (Dana, 1852); i, *Quadrella maculosa* Alcock, 1898; j, *Rhabdonotus pictus* A. Milne-Edwards, 1879; k, *Tetralia cavimana* Heller, 1861.

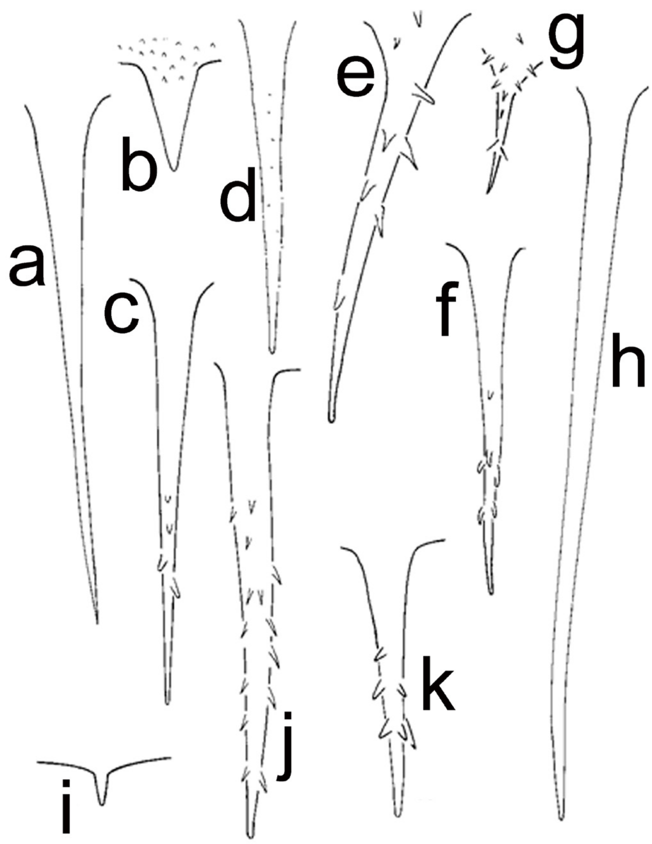

Fig. 251. Carapace: ZI; rostral spine: a, *Acantholobulus schmitti* (Rathbun, 1930); b, *Carpilius maculatus* (Linnaeus, 1758); c, *Chlorodiella nigra* (Forskål, 1775); d, *Myomenippe hardwickii* (Gray, 1831); e, *Pseudoliomera speciosa* (Dana, 1852); f, *Quadrella serenei* Galil, 1986; g, *Rhabdonotus pictus* A. Milne-Edwards, 1879; h, *Rhithropanopeus harrisii* (Gould, 1841); i, *Tanaocheles bidentata* (Nobili, 1901); j, *Tetralia rubridactyla* Garth, 1971; k, *Trapezia richtersi* Galil & Lewinsohn, 1983.

and *P. kempi* Deb, 1987 (Figs. 79, 80), 0 in ZI, 0 in ZII. In *P. hirtellus* and *A. setifer*, the onset of a pair of setae on the dorsal spine was offset, and terminally delayed in *P. sluiteri* and *P. kempi*.

Spinulation/granulation on carapace spines, when present, appears to be a descriptive character only and difficult to polarise. Tips of carapace spines are commonly pointed, but, in some instances, the termination can be swollen as in *Epiactaea nodulosa* (White, 1848) (Fig. 250d). As such, they may be autapomorphies and only useful as descriptive/identification characters.

Ornamentation (Fig. 253): Unique types of carapace ornamentation are found in some ZI zoeae, e.g., *Carpilius convexus*, *Harrovia albolineata* Adams & White, 1849, *Liomera loevis*, *Pseudoliomera speciosa* (Dana, 1852), and *Rhabdonotus pictus*. Attributing any phylogenetic significance to such characters proved difficult, consequently they were considered here to be helpful only for descriptions and identification purposes.

Posterodorsal setation (Fig. 254a): In general, the presence of a pair of posterodorsal setae in ZI is common, and to date there is no example of them increasing in number during zoeal development. Consequently, this is considered to be a descriptive character with little phylogenetic significance.

Anterodorsal setation (Fig. 254b, c): Anterodorsal setae are normally absent in ZI, and increase (accumulative) in number during subsequent zoeal moults as seen in *Charybdis helleri* (Dineen et al., 2001) to 12 pairs in zoea VI. Anterodorsal setae are, however, typically expressed in first-stage zoeas of majoids, and the onset of this character is accelerated when compared to *C. helleri*; e.g., *Macrocheira kaempferi* (Temminck, 1836) (Clark & Webber, 1991: fig. 1a); *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 1A); *Libinia spinosa* H. Milne Edwards, 1834 (Clark et al., 1998b: fig. 1a), and *Pisa armata* (Latreille, 1803) (Ingle & Clark, 1980: fig. 1a); all with 2 zoeal stages. But anterodorsal setae are expressed in the first-stage zoeas of some other taxa, i.e., *Carpilius maculatus* (Linnaeus, 1758) (Fig. 254c) possessing 4 pairs, *C. convexus* (Clark et al., 2005: fig. 1) with 9 pairs present, and *Pilumnus sluiteri* (Fig. 254b) with 1 pair. Their early expression (acceleration) can be associated with abbreviated zoeal development as in the Pilumninae: e.g., *P. hirtellus* (Clark, 2005: figs. 1, 2; 2007: figs. 437, 438), 0 anterodorsal setae in ZI, 2 pairs ZII, 5 pairs in ZIII, 6 pairs in ZIV; *Actumnus setifer* (Clark & P.K.L. Ng, 2004b: fig. 1), 0 in ZI, 2 pairs in ZII, 6 pairs in ZIII; *P. sluiteri*

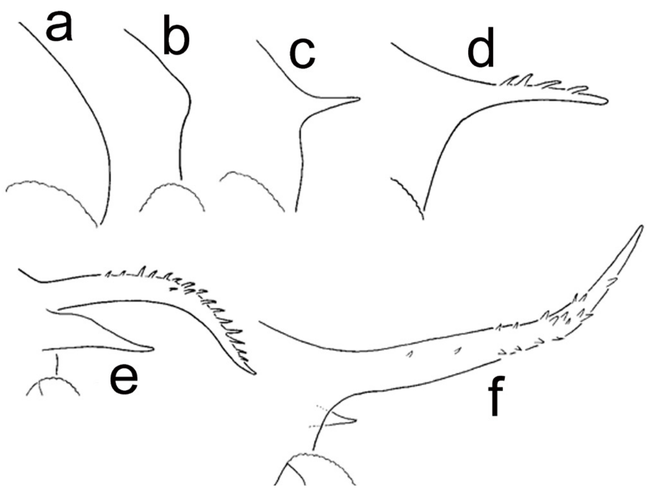

Fig. 252. Carapace: ZI; lateral spine: a, *Benthopanope indica* (De Man, 1887); b, *Acantholobulus bermudensis* (Benedict & Rathbun, 1891); c, *Eurypanopeus depressus* (Smith, 1869); d, *Microcassiope minor* (Dana, 1852); e, *Tetralia cavimana* Heller, 1861; f, *Quadrella serenei* Galil, 1986.

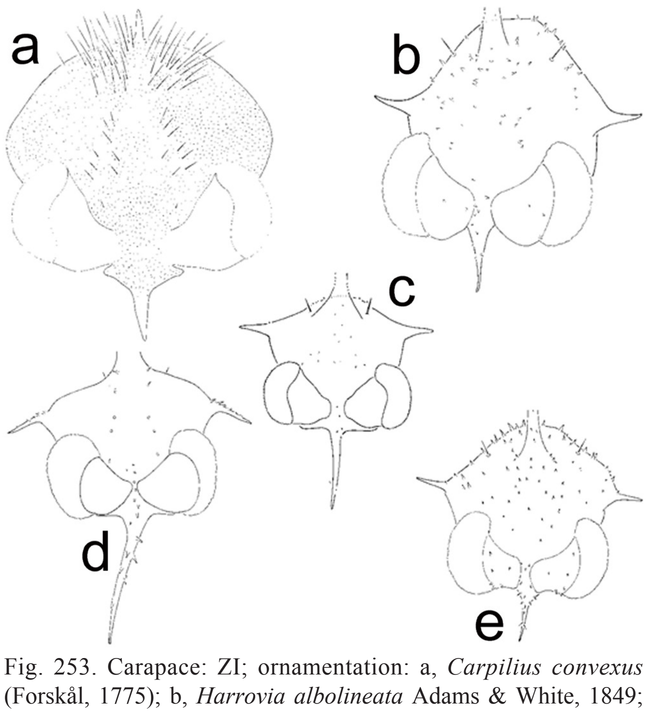

Fig. 253. Carapace: ZI; ornamentation: a, *Carpilius convexus* (Forskål, 1775); b, *Harrovia albolineata* Adams & White, 1849; c, *Liomera loevis* (A. Milne-Edwards, 1873); d, *Pseudoliomera speciosa* (Dana, 1852); e, *Rhabdonotus pictus* A. Milne-Edwards, 1879. The dorsal carapace spine has been drawn truncated in b–e.

(Clark & P.K.L. Ng, 2004a: figs. 1, 2), 1 pair in ZI, 3 pairs in ZII; and *P. kempi* (Figs. 79; 80), 1 pair in ZI, 3 pairs in ZII. In *P. sluiteri* and *P. kempi* the onset of the first pair of anterodorsal setae was accelerated to appear in ZI, compared to ZII in *P. hirtellus* and *A. setifer*. Furthermore, an extra 3 pairs of anterodorsal setae that were onset in *P. hirtellus* in ZIV and *A. setifer* in ZIII, were offset and terminally delayed in *P. sluiteri* and *P. kempi*.

Ventral margin setae (Fig. 255): These are submarginal, originate on the inner surface of the carapace, extend into the branchial cavity (gill chamber), and comprise two types,

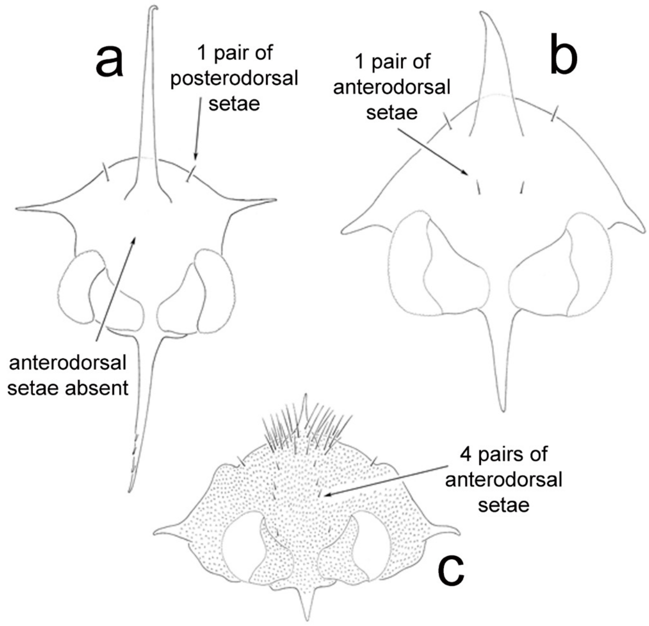

Fig. 254. Carapace: ZI; anterodorsal setae: a, *Leptodius exaratus* (H. Milne Edwards, 1834); b, *Pilumnus sluiteri* De Man, 1892; c, *Carpilius maculatus* (Linnaeus, 1758).

anterior plumose and posterior setose setae. Both setae are accumulative, increasing in number during subsequent zoeal moults, i.e., *Geograpsus lividus* (Cuesta et al., 2011: figs. 14, 15), 0 in ZI, 1 ant. ZII, 2 ant. ZIII, 3 ant. ZIV, 4 ant. ZV, 5 ant., 1 post. ZVI, 6 ant., 2 post. ZVII, and 7 ant., 12 post. ZVIII; *Charybdis helleri* (Dineen et al., 2001: fig. 6), 0 in ZI, 1 ant. ZII, 2 ant., 3 post. ZIII, 2 post., 5 ant., ZIV, 2 ant., 10 post. ZV, and 3 ant., 14 post. ZVI; *P. hirtellus* (Clark, 2005: fig. 3; 2007: fig. 439), 0 in ZI, 1 ant., 2 post., ZII, 2 ant., 3 post. ZIII, and 2 ant., 6 post. in ZIV; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 3), 0 in ZI, 1 ant., 3 post. ZII, and 2 ant., 4 post. ZIII. Typically, in taxa with more than three zoeal stages, the ZI is devoid of setae on the ventral margin of the carapace with their onset being delayed until later development.

The ventral margin setae of majids were recorded and first illustrated by Bocquet (1954) for the zoea of *Achaeus cranchii* Leach, 1817 (Majoidea: Inachidae). From this work and her own studies, Bourdillon-Casanova (1960) noted that the first seta on the ventral margin was different from the posterior setae. She referred to this seta as the "soie antérieure" (Bourdillon-Casanova, 1960: 136) and considered it a character of the Oxyrhyncha (majoids). Heegaard (1963: 487) referred to this seta as the "maiid spine". Clark & P.K.L. Ng (1998) described the zoeae of the xanthid *Lophozozymus pictor* (Fabricius, 1798) and noted that marginal carapace setae were absent in the first zoea but appeared in increasing numbers in the remaining three zoeal stages. The anterior seta on the ventral margin is plumose and quite distinctive, differing from the remaining posterior marginal setae. The anterior seta appeared similar in ornamentation and position for both *Lophozozymus pictor* and the epialtid majoid *Libinia spinosa* H. Milne Edwards, 1834 (Clark et al., 1998b: fig. 2), and was interpreted as homologous. Further, this plumose seta is present in the first zoea of *P. kempi* (Fig. 81a) and

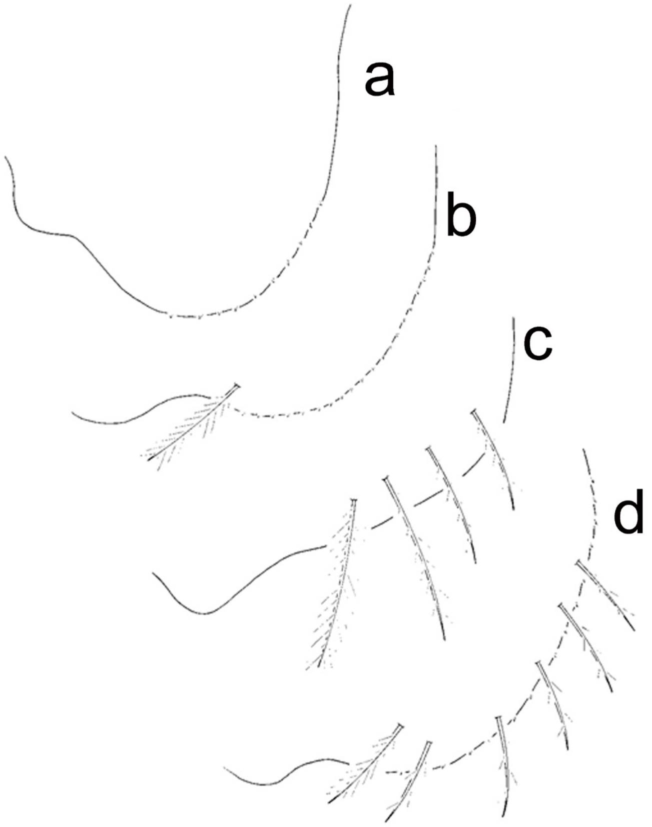

Fig. 255. Carapace: ZI; ventral marginal setae: a, *Leptodius exaratus* (H. Milne Edwards, 1834); b, *Pilumnus sluiteri* De Man, 1892; c, *Carpilius maculatus* (Linnaeus, 1758); d, *Epiactaea nodulosa* (White, 1848).

P. sluiteri (Clark & P.K.L. Ng, 2004a: fig. 4; Fig. 255b), both with 2 zoeal stages. Carapace ventral margin setae are also present in the first stage zoea of *Carpilius maculatus* (Clark et al., 2005: fig. 7a; Fig. 255c), *C. convexus* (Clark et al., 2005: fig. 2a), and *E. nodulosa* (Fig. 255d). Therefore, the interpretation by Heegaard (1963) of this "spine" as "majid" should be reconsidered and that character will now be referred to as the anterior seta (soie antérieure) after Bourdillon-Casanova (1960).

Within the majoids with 2 zoeal stages, the anterior seta is expressed together with numerous posterior setae, and the onset of the latter has been accelerated; see *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 1a), *Maja brachydactylus* (as *M. squinado* by Clark, 1986: fig. 1A), *L. spinosa* (Clark et al., 1998b: fig. 2a), and *Pisa armata* (Ingle & Clark, 1980: fig. 1a), compared with *G. lividus* (Cuesta et al., 2011: figs. 14, 15), *Charybdis helleri* (Dineen et al., 2001: fig. 6), *Pilumnus hirtellus* (Clark, 2005: fig. 3; 2007: fig. 439), and *Actumnus setifer* (Clark & P.K.L. Ng, 2004b: fig. 3).

In *P. kempi* (Fig. 81a, b), 1 ant. in ZI, and 2 ant., 6 post. in ZII and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 4a, b), 1 ant. in ZI, and 2 ant., 10 post. in ZII, these ventral margin setae, when compared with *P. hirtellus* (Clark, 2005: fig. 3; 2007: fig. 439) and *A. setifer* (Clark & P.K.L. Ng, 2004b, fig. 3), were onset early (accelerated) in association with abbreviated zoeal development.

Dorsoposterior marginal setae (not figured): These setae were described for *Cyrtograpsus affinis* Dana, 1851 (Spivak & Cuesta, 2000: fig. 1E, F), 4 in ZIV, 5 in ZV and *Eriocheir sinensis* (H. Milne Edwards, 1853) (Kim & Hwang, 1995: figs. 3A, 4A, 5A, tab. III), 0 in ZI–ZII, 2 in ZIII, 4 in ZIV–ZV. These carapace marginal setae have been described to date for two Varunidae species and may have been overlooked in other taxa; consequently, this character requires further clarification.

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Proximal setation (Fig. 1c): An accumulative character increasing in number during zoeal development, e.g., *G. lividus* (Cuesta et al., 2011: fig. 9A–E), 0 in ZI, 0 in ZII, 0 in ZIII, 0 in ZIV, 0 in ZV, 2 in ZVI, 3 in ZVII, 4 in ZVIII; *Charybdis helleri* (Dineen et al., 2001: fig. 7), 0 in ZI, 0 in ZII, 0 in ZIII, 0 in ZIV, 1 in ZV, 4 in ZVI; *P. hirtellus* (Clark, 2005: fig. 4; 2007: fig. 440), 0 in ZI, 0 in ZII, 1 in ZIII, 2 rows of 1+5 in ZIV; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 4), 0 in ZI, 0 in ZII, 1 in ZIII and *P. kempi* (Fig. 81c, d), 0 in ZI, 1 in ZII and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 4c, d), 0 in ZI, 1 in ZII. In comparison, this proximal setation is offset and terminally delayed in the majoids, all with 2 zoeal stages, *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 2a, c); *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 2A, B); *Pisa armata* (Ingle & Clark, 1980: fig. 2a, e); *L. spinosa* (Clark et al., 1998b: fig. 6a, b), and *Inachus dorsettensis* (Pennant, 1777), *I. leptochirus* Leach, 1817 and *I. phalangium* (Fabricius, 1775) (Clark, 1980: fig. 11).

The expression of the antennule proximal setation can be shown to accelerate with abbreviated development from 8 to 2 zoeal stages with ultimate terminal delay of this character in the majoids.

Accessory flagellum (Fig. 1b, c): The accessory flagellum is a developmental character, non-functional in the zoeal phase, initially expressed as a small bud and followed, in some cases, by an increase in size during subsequent moults, e.g., *G. lividus* (Cuesta et al., 2011: fig. 9A–E), - in ZI, - in ZII, - in ZIII, - in ZIV, - in ZV, - in ZVI, + in ZVII, ++ in ZVIII; *Charybdis helleri* (Dineen et al., 2001: fig. 7), - in ZI, - in ZII, - in ZIII, - in ZIV, - (?) in ZV, ++ in ZVI; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 2A–E), - in ZI, - in ZII, - in ZIII, + in ZIV, ++ in ZV; *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 2), - in ZI, - in ZII, + in ZIII, ++ in ZIV; *Pilumnus hirtellus* (Clark, 2005: fig. 4; 2007: fig. 440), - in ZI, - in ZII, + in ZIII, ++ in ZIV; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 4a–c), - in ZI, + in ZII, ++ in ZIII; *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 4c, d); and *P. kempi* (Fig. 81c, d), both + in ZI, ++ in ZII. In majoids, all with 2 zoeal stages, *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 2a, c), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 2A, B), and *Pisa armata* (Ingle & Clark, 1980: fig. 2a, e) all score - in ZI, + in ZII; while in *Libinia spinosa* (Clark et al., 1998b: fig. 6a, b), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9a, b), the accessory flagellum is offset and terminally delayed. Incidentally, the accessory flagellum is onset in the ZI of both *Carpilius* species, *C. convexus* and *C. maculatus* (Clark et al., 2005: figs. 2c, 7c, respectively) and the xanthoidean, *E. nodulosa* (Fig. 166b).

The onset of the accessory flagellum can be shown to accelerate with abbreviated development from 8 to 2 zoeal stages with ultimate terminal delay of this character in the majoids, *Libinia spinosa*, *I. dorsettensis*, *I. leptochirus*, and *I. phalangium*.

Primary flagellum. Subterminal aesthetascs (Fig. 256a, b): An accumulative character which may be difficult to assess in later zoeal stages as numbers increase and because of the fragile structure of aesthetascs. In later zoeal stages, two subterminal rows may be present and consequently this character is divided into proximal and distal subterminal aesthetascs.

Proximal subterminal aesthetascs (Fig. 81d): In *G. lividus* (Cuesta et al., 2011: fig. 9E), with 8 zoeal stages, 5 in ZVIII; *Charybdis helleri* (Dineen et al., 2001: fig. 7), with 6 zoeal stages, 6 in ZVI; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 2E), with 5 zoeal stages, 1 in ZV; *Pilumnus hirtellus* (Clark, 2005: fig. 4; 2007: fig. 440), with 4 zoeal stages, 1 in ZIV; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 4), with 3 zoeal stages, 1 in ZIII; with 2 zoeal stages, *P. kempi* (Fig. 81d), 5 in ZII and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 4d), 1 in ZII.

In the majoids with 2 zoeal stages, there were no proximal row of aesthetascs recorded for *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 2c), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 2B), *Pisa armata* (Ingle & Clark, 1980: fig. 2e), *Libinia spinosa* (Clark et al., 1998b: fig. 6a), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9d).

The onset of proximal subterminal aesthetascs can be shown to accelerate with abbreviated development from 8 to 2 zoeal stages with ultimate offset of this character and terminal delay as in the majoids. Furthermore, there is an offset (delay) in the number of proximal subterminal aesthetascs expressed, from 6 to 1 associated with abbreviated development.

Distal subterminal aesthetascs (Fig. 256b): In *G. lividus* (Cuesta et al., 2011: fig. 9A–E), with 8 zoeal stages, 1 in ZVI, 5 in ZVII, 7 in ZVIII; *Charybdis helleri* (Dineen et al., 2001: fig. 7), with 6 zoeal stages, 2 in ZIV, 5 in ZV, 5 in ZVI; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 2A–E), with 5 zoeal stages, 2 in ZIV, 6 in ZV; *Pilumnus hirtellus* (Clark, 2005: fig. 4; 2007: fig. 440), with 4 zoeal stages, 1 in ZIII, 5 in ZIV; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 4), with 3 zoeal stages, 1 in ZII, 4 in ZIII; with 2 zoeal stages, *P. kempi* (Figs. 81c, d, 256b), 1 in ZI, 6 in ZII and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 4c, d), 5 in ZII. In the majoids with 2 zoeal stages, *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 2a, c) has 5 in ZII, and the following are devoid of subterminal aesthetascs: *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 2A, B); *Pisa armata* (Ingle & Clark, 1980: fig. 2a, e); *Libinia spinosa* (Clark et al., 1998b: fig. 6a, b); and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9d).

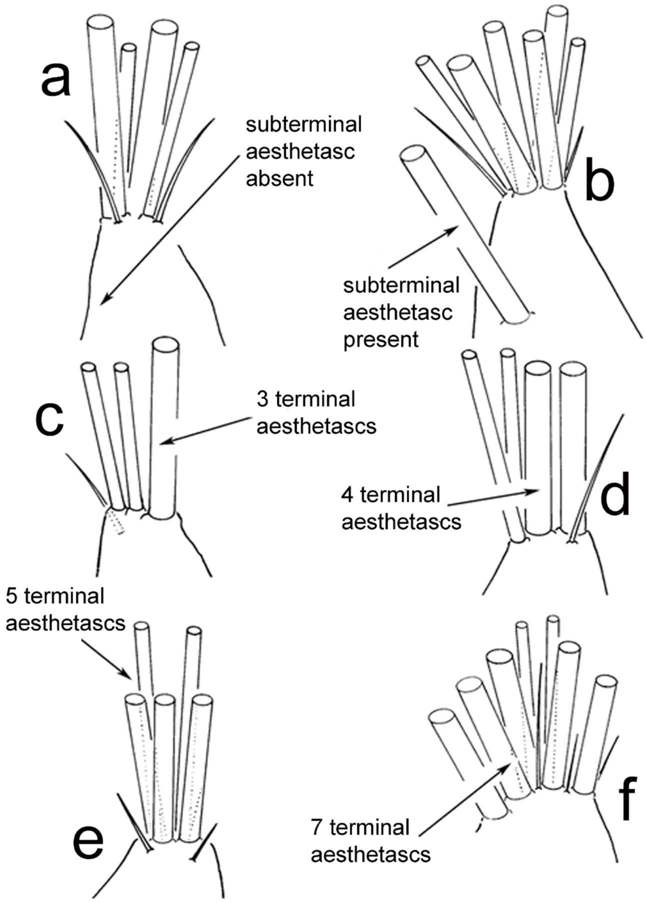

Fig. 256. Antennule: ZI; aesthetascs: a, *Pilumnus longicornis* Hilgendorf, 1878; b, *Pilumnus kempi* Deb, 1987; terminal aesthetascs: c, *Charybdis helleri* (A. Milne-Edwards, 1867); d, *Liomera cinctimana* (White, 1847); e, *P. sluiteri* De Man, 1892; ZII: f, *P. kempi* Deb, 1987.

The onset of distal subterminal aesthetascs can be shown to accelerate with abbreviated development from 8 to 2 zoeal stages with ultimate offset of this character and terminal delay as in the majoids, *M. brachydactyla*, *P. armata*, *L. spinosa*, and *Inachus*. Furthermore, there may be an offset (delay) in the number of proximal subterminal aesthetascs expressed when associated with abbreviated development, but this may require further clarification.

Terminal aesthetascs (Figs. 1a–c, 256): Normally an accumulative character increasing in numbers during development, but extremely difficult to assess in later zoea stages due to fragility of aesthetascs and their close proximity to one another. Onset of aesthetascs can be shown to accelerate with abbreviated zoeal development, e.g., *G. lividus* (Cuesta et al., 2011: fig. 9A–E), 3 in ZI, 4 in ZII, 4 in ZIII, 4 in ZIV, 5 in ZV, 6 in ZVI, 6 in ZVII, 6 in ZVIII; *Charybdis helleri* (Dineen et al., 2001: fig. 7), 3 in ZI, 5 in ZII, 5 in ZIII, 5 in ZIV, 5(6?) in ZV, 5(6?) in ZVI; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 2A–E), 4 in ZI, 5 in ZII, 6(5?) in ZIII, 6(5?) in ZIV, 5(6?) in ZV; *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 2), 4 in ZI, 5 in ZII, 5 in ZIII, 5 in ZIV; *Pilumnus* *hirtellus* (Clark, 2005: fig. 4; 2007: fig. 440), 4 in ZI, 5 in ZII, 5 in ZIII, 5 in ZIV; *Nanocassiope granulipes* (Ko & Clark, 2002: fig. 4), 4 in ZI, 6 in ZII, 6 in ZIII, 6 in ZIV; *N. melanodactylus* (A. Milne-Edwards, 1867) (Dornelas et al., 2004: fig. 4), 4 in ZI, 5 in ZII, 6 in ZIII, 5(6?) in ZIV; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 4), 4 in ZI, 6(4?) in ZII, 4 in ZIII; *P. kempi* (Figs. 81c, d, 256b, f), 6 in ZI, 7 in ZII and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 4c, d; Fig. 256e), 5 in ZI, 8 in ZII; and the majoids, *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 2a, c), 5 in ZI, 9 in ZII, *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 2A, B), 4 in ZI, 9 in ZII, *Pisa armata* (Ingle & Clark, 1980: fig. 2a, e), 4 in ZI, 6 in ZII, *Libinia spinosa* (Clark et al., 1998b: fig. 6a, b), 4 in ZI, 6 in ZII, and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9a, b), 4 in ZI, 7(6?) in ZII.

Numbers of terminal aesthetascs vary in ZI ranging from 3 as in *G. lividus* (Cuesta et al., 2011: fig. 9A) with 8 zoeal stages; 3 in *C. helleri* (Fig. 256c) with 6 zoeal stages; 4 in *Liomera cinctimana* (White, 1847) (Fig. 256d) with 4 zoeal stages; 4 in *Pilumnus setifer* (Clark & P.K.L. Ng, 2004b: fig. 4) with 3 zoeal stages; 5 in *P. sluiteri* (Fig. 256e) with 2 zoeal stages; to 6 in *P. kempi* (Fig. 256b) with 2 zoeal stages. The onset of aesthetasc expression was accelerated in association with abbreviated development. This was more pronounced in majoids with the expression of an additional 5 to 2 (ancestral to derived; offset and terminal delay) aesthetascs after the moult to ZII.

Setation (Figs. 1a, 256a–d): This was a difficult character to assess because the increasing numbers of aesthetascs with successive moults obscure these setae and, as a result, their development may not have been recorded accurately. Only 1 seta is recorded on the zoeal development of *G. lividus* (Cuesta et al., 2011: fig. 9A–E) with 8 zoeal stages; *Charybdis helleri* (Dineen et al., 2001: fig. 7) with 6 zoeal stages, only 1 seta (?); with 4 zoeal stages, *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 2) with only 1 seta (?), *N. granulipes* (Ko & Clark, 2002: fig. 4) with only 1 seta (?), and *N. melanodactylus* (Dornelas et al., 2004: fig. 4) with 2 setae in ZIV. In *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 2A–E) with 5 zoeal stages, 3 (?) in ZI, 2 in ZII, 2 in ZIII, 2 in ZIV, 2 in ZV, and may require clarification.

The presence of two terminal setae in pilumnid ZI appears to be a diagnostic character for the taxon. In *P. hirtellus* (Clark, 2005: fig. 4; 2007: fig. 440) with 4 zoeal stages, 2 in ZI, 2 in ZII, 3 in ZIII, 3 in ZIV; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 4) with 3 zoeal stages, 2 in ZI, 3 in ZII, 3 in ZIII; and *P. kempi* (Figs. 81c, d, 248b, f), 2 in ZI, 3 in ZII and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 4c, d; Fig. 256e), 2 in ZI, 3 in ZII, both with 2 zoeal stages. The onset of the 3rd seta is accelerated with abbreviated development from ZIII to ZII.

For the ZI of both *Carpilius* species (*C. convexus* & *C. maculatus*; Clark et al., 2005: figs. 2b, 7b, respectively), 2 terminal setae are recorded.

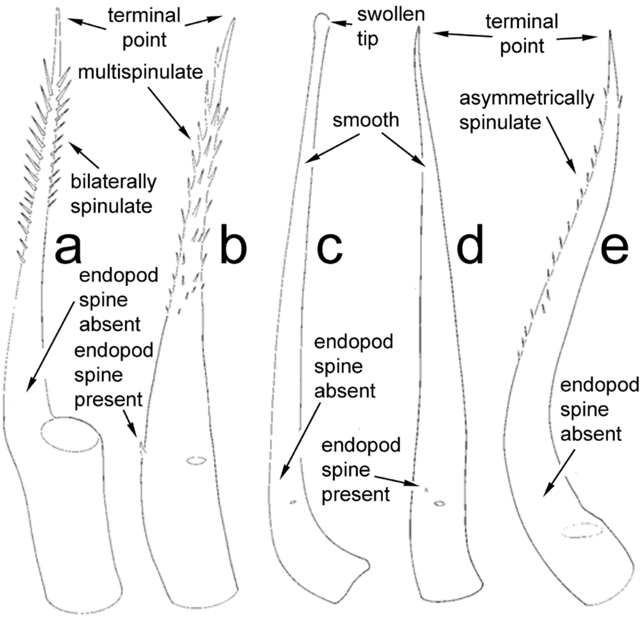

Fig. 257. Antenna: ZI; protopod: a, *Pilumnus longicornis* Hilgendorf, 1878; b, *Platypodia eydouxi* (A. Milne-Edwards, 1865); c, *Gaillardiellus orientalis* (Odhner, 1925); d, *Acantholobulus schmitti* (Rathbun, 1930); e, *Heterozius rotundifrons* A. Milne-Edwards, 1867.

Within the majoids analysed for the present study, the setation requires clarification: *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 2a, c) with 0 (?) in ZI, 0 (?) in ZII; *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 2A, B) with 2 in ZI, 3 in ZII; *Pisa armata* (Ingle & Clark, 1980: fig. 2a, e) with 2 in ZI, 2 in ZII; *Libinia spinosa* (Clark et al., 1998b: fig. 6a, b) with 2 in ZI, 2 in ZII; and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9a, b) with 2 in ZI, 3 in ZII, all with 2 zoeal stages.

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Protopod termination (Fig. 257): The protopod of most zoeas terminated in a point, as in *Pilumnus longicornis* Hilgendorf, 1878 (Fig. 257a). In a few species the termination was a swelling, e.g., *Gaillardiellus orientalis* (Odhner, 1925) (Fig. 257c). The protopod termination appeared to be conservative throughout zoeal development, with unknown phylogenetic significance. It may be diagnostic of certain taxa and was regarded as a descriptive character, but appeared to have little phylogenetic relevance. Polarising this character was difficult.

Protopod spinulation (Fig. 257): Spinulation was a conservative character. Various types of protopod spinulation were described for the present study: i.e., bilaterally spinulate, *P. longicornis* (Fig. 257a); multispinulate, *Platypodia eydouxi* (A. Milne-Edwards, 1865) (Fig. 257b); spinulation absent (smooth), *Acantholobulus schmitti* (Rathbun, 1930) (Fig. 257d); and asymmetrical spinulation, *Heterozius rotundifrons* A. Milne-Edwards, 1867 (Fig. 257e). Rice (1980) regarded the reduction in size of the spinous process (protopod) as an advanced character. While there are no issues with this statement, e.g., compare the protopods of *H. rotundifrons* (Fig. 7c) with *Dacryopilumnus rathbunae* Balss, 1932

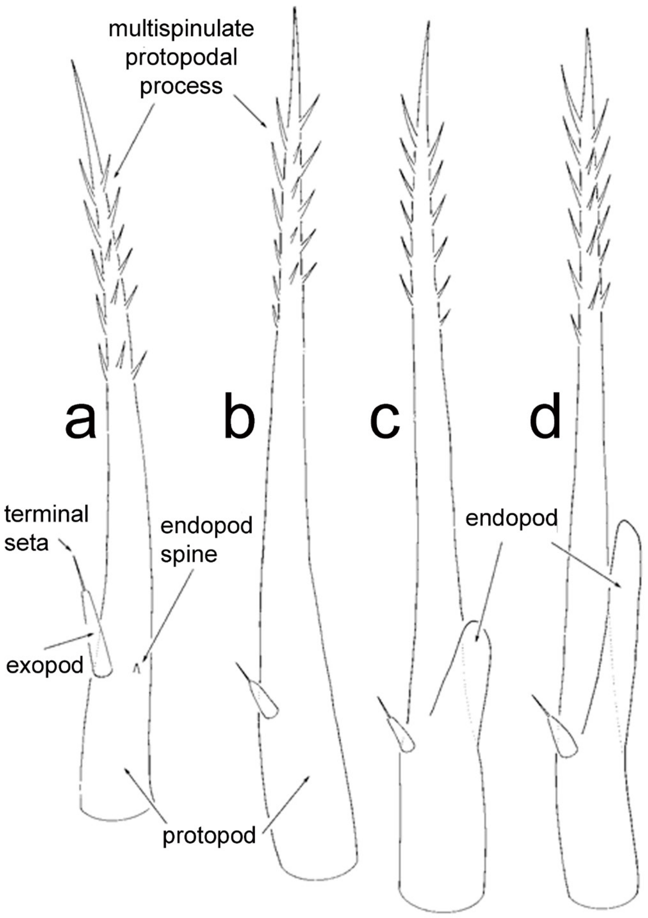

Fig. 258. *Nanocassiope granulipes* (T. Sakai, 1939); antenna showing endopod spine and development: a, ZI; b, ZII; c, ZIII; d, ZIV. Note that the endopod spine appears to be absent in ZII, but probably requires clarification. (From Ko & Clark, 2002).

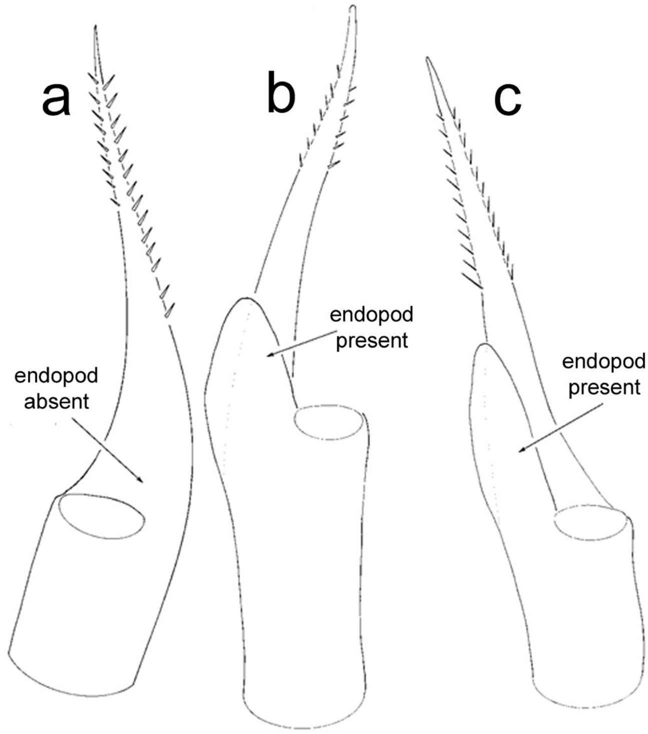

Fig. 259. Antenna: ZI; endopod: a, *Pilumnus hirtellus* (Linnaeus, 1761); b, *Actumnus setifer* (de Haan, 1835); c, *P. sluiteri* De Man, 1892.

(Fig. 15c), quantifying and polarising this character proved difficult. For the present study, the protopod was regarded as a descriptive character, and diagnostic of taxa.

Endopod (Figs. 257b, d, 258, 259): The antennary endopod was a developmental character being expressed at some time during the zoeal sequence, increasing in length relative to the protopod, being non-functional during the zoeal phase, but becoming segmented and functional after the metamorphosis to megalop. Ko & Clark (2002: 19–20) discussed the significance of the antennary endopod spine in xanthoid larval descriptions. They commented that the development of this antennal (endopod) spine was unclear in stages after ZI and not observed in second stage zoeae of *N. granulipes* (Fig. 258a–d). In the study of *N. melanodactylus* (Dornelas et al., 2004), however, the protopodal (endopod) spine was observed in ZII, again raising questions regarding its relationship to the development of the antennal endopod in some xanthoidean species. This spine appeared to be situated in the position from where the bud developed and was therefore regarded as a rudimentary endopod (Figs. 257b, d, 258a–d). Rice (1980) regarded the presence of the antennal endopod as a short bud armed with a single terminal seta in ZI, as an ancestral character of the higher Brachyura. The endopod development reported here does not include a terminal seta, which suggests that its absence is a derived character.

In *Geograpsus lividus* (Cuesta et al., 2011: fig. 10A–E), the antennal endopod was offset in ZI–ZV, but onset thereafter, + ZVI, ++ ZVII, +++ ZVIII; in *Charybdis helleri* (Dineen et al., 2001: figs. 8, 9), offset in ZI–ZIII, onset in + ZIV, + ZV, +++ ZVI; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 2F–J), offset in ZI, onset in ZII–ZV; *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 8A, C, E, G), offset in ZI, onset in + ZII, ++ ZIII, +++ ZIV; *Pilumnus hirtellus* (Clark, 2005: fig. 5; 2007: fig. 441), offset in ZI, onset in + ZII, ++ ZIII, +++ ZIV; *Actumnus setifer* (Clark & P.K.L. Ng, 2004b: fig. 5a–c), onset in + ZI, ++ in ZII, +++ in ZIII; *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 5a, b) and *P. kempi* (Fig. 82), both onset ++ in ZI, +++ in ZII. Note that in the pilumnoids *A. setifer* (Fig. 259b) and *P. sluiteri* (Fig. 259c), the endopod was proportionately more advanced in ZI with regard to abbreviated development. This is also the case with majoids, all with 2 zoeal stages, *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 2b, d) and *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 2D, E), but slightly less so in *Pisa armata* (Ingle & Clark, 1980: fig. 2b, f), *Libinia spinosa* (Clark et al., 1998b: fig. 7a, c), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9c, d).

The onset of the antennary endopod can be shown to accelerate with abbreviated development from 8 to 2 zoeal stages.

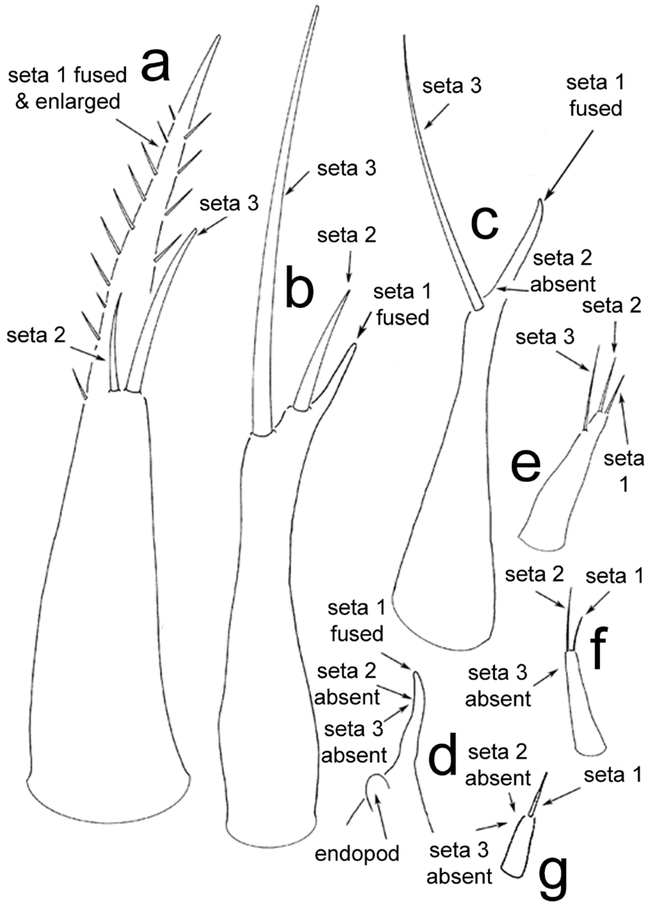

Fig. 260. Antenna: ZI; exopod: a, *Actumnus elegans* De Man, 1887; b, *Aethra scruposa* (Linnaeus, 1764); c, *Chaceon fenneri* (Manning & Holthuis, 1984); d, *Heterozius rotundifrons* A. Milne-Edwards, 1867; e, *Actaea areolatus* (Dana, 1852); f, *Cataleptodius floridanus* (Gibbes, 1850); g, *Acantholobulus bermudensis* (Benedict & Rathbun, 1891).

Exopod: Antennary exopod characters examined for the present study were conservative. While the exopod is functional during the zoeal phase, it may become reduced or lost after the metamorphosis to megalop. Rice (1980) regarded a reduction in the armature of the antennal exopod as an advanced character, but polarising these characters between taxa and with respect to heterochronic development is difficult. There may, however, be some phylogenetic information available if the armature/setation of exopod is divided into a number of individual characters states. Within the present study, the antennal exopod was divided into two types; extension/seta 1 "fused" or all setae free.

Exopod extension/seta 1 fused (Fig. 260a–d): Seta 1 may be treated as fused with setae 2 and 3 being free. A pair of medial setae of unequal length on the antennary exopod appears to be diagnostic and appears to be autapomorphy for Pilumnoidea zoeae. "Seta 1" is extended beyond that of seta 3 and is bilaterally spinulate (Fig. 260a). This compares with *Aethra scruposa* (Linnaeus, 1764) where the extension is more reduced, devoid of bilateral spinulation, and seta 3 is greatly extended (Fig. 260b) and subterminal. The exopod of *A. scruposa* may be regarded as similar in *Chaceon fenneri* (Manning & Holthuis, 1984), but seta 2 is offset (absent; Fig. 260c). In *H. rotundifrons* (Fig. 260d), the exopod is much reduced with both setae 2 and 3 offset.

There appears to be a series from the ancestral condition of a bilaterally spinulate extended "seta 1" with two medial setae (2 and 3), to a reduction in length of the extension without bilateral spinulation to include the offset of setae 2 and 3 (subterminal), and to the derived condition which is greatly reduced as in *H. rotundifrons* with both setae (2 and 3) offset.

Exopod all setae free (Fig. 260e–g): This appears to form a transformation series from the ancestral condition with subterminal seta 3 and two terminal setae (1 and 2; Fig. 260e; *Actaea areolatus*), an overall size reduction to include the loss (offset) of the subterminal seta 3 and two terminal setae 1 and 2 (Fig. 260f; *Cataleptodius floridanus* (Gibbes, 1850)), and another size reduction with a loss of seta 2 and only the onset of terminal seta 1 (Fig. 260g; *Acantholobulus bermudensis* (Benedict & Rathbun, 1891) and *N. granulipes* by Ko & Clark, 2002: fig. 5).

MANDIBLE

Mandible palp (Fig. 85a): The only character of significance in zoea is the onset of the palp. According to Boxshall (2004: 287) the mandible gnathobase is formed from the proximal article and is therefore coxal in origin. Distal to the coxa is the basis and the endopodal and exopodal rami originate from this article. In brachyuran larval development the exopod is not expressed. The palp is a developmental character, normally expressed in last zoeal stage prior to the metamorphosis to megalop. During zoeal development the palp may be expressed. It is non-functional and undifferentiated during the zoeal phase. Following the metamorphosis to megalop, the palp becomes articulated, armed and functional with the endopod expressed, but with a reduced number of articles.

In *G. lividus* (Cuesta et al., 2011: 232) with 8 zoeal stages, the palp is onset in ZVIII; *Charybdis helleri* (Dineen et al., 2001: fig. 17a) with 6 zoeal stages, in ZVI; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: 279) with 5 zoeal stages, in ZV; *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 16A) with 4 zoeal stages, in ZIV; *Actumnus setifer* (Clark & P.K.L. Ng, 2004b: fig. 11b) with 3 zoeal stages, in ZIII; with 2 zoeal stages, *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 11a) and *P. kempi* (Fig. 85a) both in ZII. In majoids, all with 2 zoeal stages, the onset of the palp is observed in ZII for *Macrocheira kaempferi* (Clark & Webber, 1991: 1266), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: 829); *Libinia spinosa* (Clark et al., 1998b: fig. 19a) and *Pisa armata* (Ingle & Clark, 1980: 725, fig. 2g) in ZII. Within the Inachidae, e.g., *I. dorsettensis*, *I. leptochirus*, *I. phalangium*, *Macropodia tenuirostris* (Leach, 1814) and *M. rostrata* (Linnaeus, 1761) (Clark, 1983: fig. 6), however, the mandibular palp is offset and terminally delayed on the zoeal phase.

The onset of the mandibular palp appears to be expressed normally in the last zoeal stage prior to the moult to megalop.

Early (accelerated) onset of the palp is in association with abbreviated zoeal development, including terminal delay in *Inachus* and *Macropodia*. Of interest is the abbreviated zoeal development of the sesarmid *Geosesarma peraccae* (Nobili, 1903) described by Soh (1969) as *Sesarma* (*Geosesarma*) *perracae* sic., with 2 zoeal stages. According to Soh (1969: 359, fig. 5) the mandibular palp is onset in ZI, extremely early when compared with zoeal stages cited here. With the moult to ZII (Soh, 1969: 363, fig. 15), however, the palp comprises 3 articles, proximally the basis and distally a 2-articled endopod.

MAXILLULE

Coxal endite (Fig. 261a–c): The ZI setation of the coxa ranged from 7 to 9 setae with the majority of ZI possessing 7. These are accumulative setae and were numbered individually from 1 to 9 (Fig. 261a).

Coxal seta 1 (Fig. 261a): In *Geograpsus lividus* (Cuesta et al., 2011: 231) with 8 zoeal stages, coxal seta 1 was expressed after ZV; *Charybdis helleri* (Dineen et al., 2001: fig. 10) with 6 zoeal stages, expressed in ZIII, but in *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 3) with 5 zoeal stages, after ZIII. For species with 4 zoeal stages, in *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 9) coxal seta expressed in ZII; *N. granulipes* (Ko & Clark, 2002: fig. 6c) and *N. melanodactylus* (Dornelas et al., 2004: fig. 6C), expressed in ZIII. In the pilumnoids *Pilumnus hirtellus* (Clark, 2005: fig. 6; 2007: fig. 442) with 4 zoeal stages, coxal seta 1 was expressed in ZIV; *A. setifer* (Clark & Ng, 2004b: fig. 6c) with 3 zoeal stages, delayed until ZIII; *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 6b) and *P. kempi* (Fig. 83b) both with 2 zoeal stages, expressed in ZII. In majoids, all with 2 zoeal stages, coxal seta 1 was expressed in ZI of *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3a) and expressed in ZII of *Libinia spinosa* (Clark et al., 1998b: fig. 8a, b), but terminally delayed in *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 3A, B); *Pisa armata* (Ingle & Clark, 1980: fig. 2d, h), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9f, i).

Early expression of coxal seta 1 was generally associated with abbreviated zoeal development from 8 to 2 zoeal stages with the onset of this character being terminally delayed in some majoids. In contrast, however, the onset of coxal seta 1 is accelerated and present in the ZI of the following geryonids all with 4 zoeal stages, *Chaceon fenneri* (Clark, 2007: fig. 95a), *C. quinquedens* (Smith, 1879) (Fig. 98a), and *Geryon longipes* A. Milne-Edwards, 1882 (Fig. 102a).

Coxal seta 9 (Fig. 261a): This seta was expressed during the zoeal phase. In *Geograpsus lividus* (Cuesta et al., 2011: 231) with 8 zoeal stages, coxal seta 9 was expressed sometime after ZV; *Charybdis helleri* (Dineen et al., 2001: fig. 10) with 6 zoeal stages, expressed after ZIII, but in *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 3) with 5 zoeal stages, is expressed in ZV. For species with 4 zoeal stages, e.g., *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 9), expressed in ZIII; *N. granulipes* (Ko & Clark, 2002: fig. 6) and *N. melanodactylus* (Dornelas et al., 2004: fig. 6C), expressed in ZIV. In the pilumnoids *Pilumnus hirtellus* (Clark, 2005: fig. 6; 2007: fig. 442) with 4 zoeal stages and *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 6a–c) with 3 zoeal stages, coxal seta 9 was not expressed (being terminally delayed), but in *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 6b) and *P. kempi* (Fig. 83b) both with 2 zoeal stages, coxal seta 9 was expressed in ZII. In majoids, all with 2 zoeal stages, coxal seta 9 was expressed in ZII of *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3a) but was terminally delayed in *Libinia spinosa* (Clark et al. 1998b: fig. 8a, b), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 3A, B), *Pisa armata* (Ingle & Clark, 1980: fig. 2d, h), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9f, i).

Early expression of coxal seta 9 was generally associated with abbreviated zoeal development from 8 to 2 zoeal stages, with the onset of this character being terminally delayed in some majoids. A really different pattern, however, is being exhibited in geryonids. The onset of coxal seta 9, together with coxal seta 1, is accelerated and onset in the ZI of the following (all with 4 zoeal stages), e.g., *Chaceon fenneri* (Clark, 2007: fig. 95a), and *C. quinquedens* (Fig. 98a) and *Geryon longipes* (Fig. 102a).

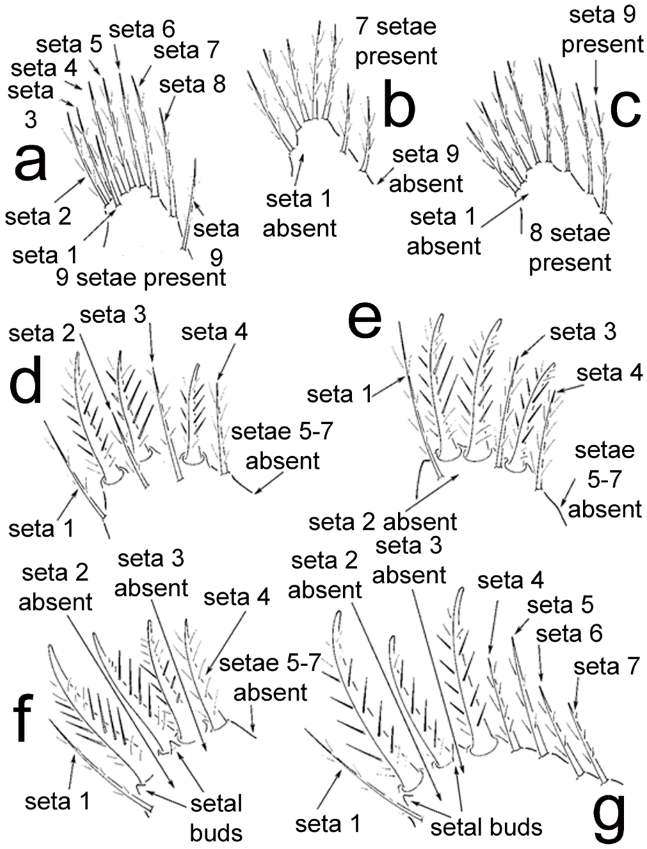

Fig. 261. Maxillule: ZI; coxal endite: a, *Geryon longipes* A. Milne-Edwards, 1882; b, *Heteropanope glabra* Stimpson, 1858; c, *Carpilius convexus* (Forskål, 1775); basial endite: d, *G. longipes* A. Milne-Edwards, 1882; e, *Chaceon fenneri* (Manning & Holthuis, 1984); f, *Liomera loevis* (A. Milne-Edwards, 1873); g, *Carpilius maculatus* (Linnaeus, 1758).

Basial endite setation (Fig. 261d–g): Seven setae can be identified on the basial endite and these were numbered 1–7. The onset of setae 2, 3, and 5–7 were considered to be accumulative characters being expressed sometime during the zoeal phase and were found to be phylogenetically informative.

Basial endite seta 2 (Fig. 261d): This seta was onset in *Geryon longipes* (Fig. 261d) ZI, but typically offset and delayed in most other ZI such as *Liomera loevis* (Fig. 261f). In *Geograpsus lividus* (Cuesta et al., 2011: 231) with 8 zoeal stages, basial seta 2 was onset in ZII; *Charybdis helleri* (Dineen et al., 2001: figs. 10, 11) with 6 zoeal stages, in ZII; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 3) with 5 zoeal stages, in ZIII; with 4 zoeal stages, *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: figs. 9, 17D), *N. granulipes* (Ko & Clark, 2002: fig. 6), and *N. melanodactylus* (Dornelas et al., 2004: fig. 6), all in ZIII; *Cyrtograpsus affinis* (Cuesta, 1999: fig. 44B; Spivak & Cuesta, 2000) with 5 zoeal stages, in ZII. Within the pilumnoids, *Pilumnus hirtellus* (Clark, 2005: fig. 6; 2007: fig. 442b) with 4 zoeal stages, in ZIII; but accelerated in association with abbreviated development in *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 6b) with 3 zoeal stages; and with 2 zoeal stages, *P. kempi* (Fig. 83b) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: figs. 13, 14), onset in all these three species in ZII. For the majoids, all with 2 zoeal stages, *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3b), *Maja brachydactylus* (as *M. squinado* by Clark, 1986: fig. 6A–D), *Libinia spinosa* (Clark et al., 1998b: fig. 8a), *Pisa armata* (Ingle & Clark, 1980: fig. 2d), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980:, fig. 11), seta 2 is onset in all ZI.

Seta 2 was onset in the ZI of *Geryon longipes* (Fig. 102a) but offset in ZI of *Chaceon fenneri* and delayed until ZII (Stuck et al., 1992: fig. 2D). For the grapsoids *Geograpsus lividus* and *C. affinis* and the portunoid *Charybdis helleri*, seta 2 was onset in ZII but in comparison offset until ZIII in the xanthoids, *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 3), *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: figs. 9, 17D), *N. granulipes* (Ko & Clark, 2002: fig. 6), and *N. melanodactylus* (Dornelas et al., 2004: fig. 6). In comparison with the grapsoids, xanthoids, and pilumnoids, the onset of seta 2 was accelerated in ZI majoid development.

Basial endite seta 3 (Fig. 261d, e): This seta was onset in *Geryon longipes* (Fig. 261d) and *Chaceon fenneri* (Fig. 261e) ZI, but typically offset and delayed in most other ZI, such as *Liomera loevis* (Fig. 261f). Consequently, for *G. longipes* and *C. fenneri*, the onset of seta 3 is considered to be early (accelerated). In *Geograpsus lividus* (Cuesta et al., 2011: 230) with 8 zoeal stages, seta 3 was onset in ZIV (?); *Charybdis helleri* (Dineen et al., 2001: fig. 10c) with 6 zoeal stages, in ZIII; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 3) with 5 zoeal stages, in ZIV; with 4 zoeal stages, *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 9C), *N. granulipes* (Ko & Clark, 2002: fig. 6c), and *N. melanodactylus* (Dornelas et al., 2004: fig. 6C), all in ZIII. Within the pilumnoids, *Pilumnus hirtellus* (Clark, 2005: fig. 6; 2007: fig. 442b) with 4 zoeal stages, *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 6b) with 3 zoeal stages, and *P. kempi* (Fig. 83b) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: figs. 13, 14) both with 2 zoeal stages, all in ZII. In the pilumnoids treated for this study, the onset of seta 3 was in ZII and therefore not associated with abbreviated development. For the majoids, all with 2 zoeal stages, seta 3 is onset in ZII in *Libinia spinosa* (Clark et al., 1998b: fig. 8b) but offset and terminally delayed in *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3b), *Maja brachydactylus* (as *M. squinado* by Clark, 1986: fig. 3A, B), *Pisa armata* (Ingle & Clark, 1980: fig. 2d), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 11f, i). This interpretation for the majoids, however, may require further clarification.

Basial endite seta 5 (Fig. 261g): The onset of seta 5 in ZI of *Carpilius convexus* (Clark et al., 2005: fig. 2a) and *C. maculatus* (Fig. 261g) was early (accelerated) when compared with *Geryon longipes*, *Chaceon quinquedens*, *Lophozozymus pictor*, *N. granulipes*, and *N. melanodactylus*, for example. In *Geograpsus lividus* (Cuesta et al., 2011: 228, fig. 2B) with 8 zoeal stages, seta 2 was onset in ZII (?); *Charybdis helleri* (Dineen et al., 2001: fig. 10c) with 6 zoeal stages, in ZII; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 3) with 5 zoeal stages, in ZII; *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 9B), *N. granulipes* (Ko & Clark, 2002: fig. 6c), and *N. melanodactylus* (Dornelas et al., 2004: fig. 6C), all with 4 zoeal stages, all in ZII. For the majoids, all with 2 zoeal stages, *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3b), *Maja brachydactylus* (as *M. squinado* by Clark, 1986: fig. 6A–D), *Pisa armata* (Ingle & Clark, 1980: fig. 2d), and *Libinia spinosa* (Clark et al., 1998b: fig. 8b), seta 5 appears to be onset in ZII. In *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 11f), seta 5 may be present in ZI, but further clarification could be required.

Basial endite seta 6 (Fig. 261g): The early appearance of basial seta 6 in ZI is associated with abbreviated zoeal development as in *Carpilius maculatus* (Fig. 261g) when compared to ZI such as *Geryon longipes*, *Chaceon quinquedens*, *Lophozozymus pictor*, *N. granulipes*, and *N. melanodactylus*, for example.

Basial endite seta 7 (Fig. 261g): The expression of basial seta 7 in ZI was also associated with abbreviated zoeal development such as in *Carpilius maculatus* (Fig. 261g), and it was early compared to most ZI, such as *Geryon longipes*, *Chaceon quinquedens*, *L. pictor*, *N. granulipes*, and *N. melanodactylus*.

Endopod (Fig. 262): The endopod was reduced to only 2 articles, both of which may be setose. These setal characters appear to be conservative, being present or absent and, to date, have not been described as increasing during zoeal development. Rice (1980), however, regarded the loss of setae as the advanced (derived) condition, especially with respect to the majoids.

Endopod, proximal article seta (Fig. 262a, b): A conservative character and, to date, only the presence or

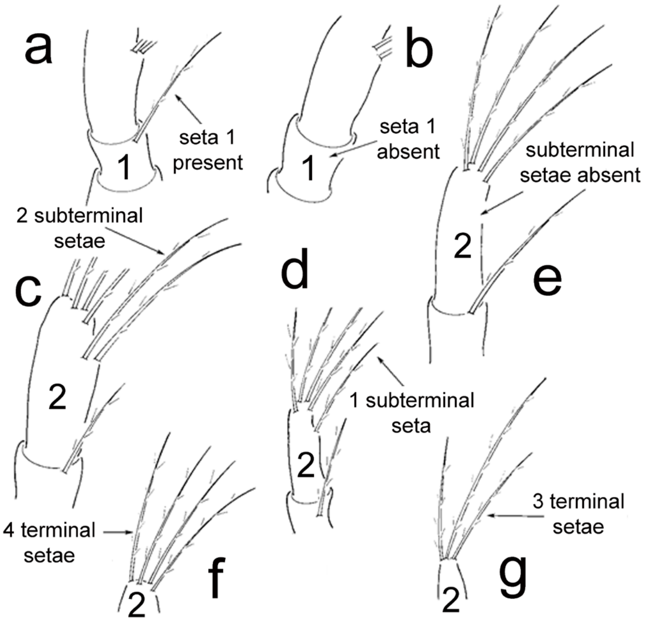

Fig. 262. Maxillule: ZI; endopod; setation of proximal article: a, *Etisus frontalis* (Dana, 1852); b, *Rhinolambrus pelagicus* (Rüppell, 1830); subterminal setation of distal article: c, *Lachnopodus subacutus* (Stimpson, 1858); d, *Carpilius maculatus* (Linnaeus, 1758); e, *Menippe rumphii* (Fabricius, 1798); terminal setation of distal article: f, *Leptodius sanguineus* (H. Milne Edwards, 1834); g, *C. convexus* (Forskål, 1775).

absence, as in *Rhinolambrus pelagicus* (Rüppell, 1830) (Fig. 262b), of a single seta has been described on this article. All the zoea described in this atlas possessed this character. The presence of this seta was considered to be the ancestral condition, while its absence was regarded as derived.

Endopod, distal article, subterminal setae (Fig. 262c–e): A conservative character with three states: 2, 1, and 0 setae (ancestral to derived, respectively). Two subterminal setae are described for *Lachnopodus subacutus* (Stimpson, 1858) (Fig. 262c), 1 subterminal seta in *Carpilius maculatus* (Fig. 262d), and none in *Menippe rumphii* (J.C. Fabricius, 1798) (Figs. 36a, 262e).

Endopod, distal article, terminal setae (Fig. 262f, g): A conservative character with 4 terminal setae being considered typically ZI such as *Leptodius sanguineus* (H. Milne Edwards, 1834) (Fig. 262f) and occasionally 3 as in *Carpilius convexus* (Fig. 262g). Loss of the fourth seta was regarded as the derived condition.

Exopod: This plumose seta was a developmental character. It was onset in ZII for *Geograpsus lividus* (Cuesta et al., 2011: fig. 2B) with 8 zoeal stages; *Charybdis helleri* (Dineen et al., 2001: fig. 10b) with 6 zoeal stages, *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 3B) with 5 zoeal stages; the following species with 4 zoeal stages, *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 9B), *N. granulipes* (Ko & Clark, 2002: fig. 6b), *N. melanodactylus* (Dornelas et al., 2004: fig. 6B), and *Pilumnus hirtellus* (Clark, 2005: fig. 6; 2007: fig. 442b); *Actumnus setifer* (Clark & P.K.L. Ng, 2004b: fig. 6b) with 3 zoeal stages;and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 6b) and *P. kempi* (Fig. 83b) both with 2 zoeal stages; and in majoids, all with 2 zoeal stages, *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3b), *Libinia spinosa* (Clark et al., 1998b: fig. 8b), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 3B), *Pisa armata* (Ingle & Clark, 1980: fig. 2h), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9i).

Rice (1980) regarded the presence of the exopod seta from ZII to be the ancestral condition; however, the expression of this character in *Carpilius convexus* and *C. maculatus* (Clark et al., 2005: figs. 3a, 8a, respectively) was accelerated and onset in ZI. This is considered to be the derived condition.

Epipod: This seta was a developmental character. In *G. lividus* (Cuesta et al., 2011: fig. 2C) with 8 zoeal stages, the epipod was onset in ZV; *Charybdis helleri* (Dineen et al., 2001: fig. 10c) with 6 zoeal stages, in ZIII; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 3) with 5 zoeal stages, overlooked (?); the following species with 4 zoeal stages, *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 9C) in ZIII, *N. granulipes* (Ko & Clark, 2002: fig. 6d) in ZIV, *N. melanodactylus* (Dornelas et al., 2004: fig. 6B) in ZII, *Pilumnus hirtellus* (Clark, 2005: fig. 6; 2007: fig. 442b) in ZII; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 6b) with 3 zoeal stages, in ZII, and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 6b) and *P. kempi* (Fig. 83b) both with 2 zoeal stages, in ZII.

The epipodal seta was not figured in the following majoids, *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3a, b); *Libinia spinosa* (Clark et al., 1998b: fig. 8a, b); *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 3A, B); *Pisa armata* (Ingle & Clark, 1980: fig. 2d, h), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9f, i). This may indicate terminal delay for this character or that the epipodal seta was overlooked as it can be a difficult character to observe, being easily lost during dissection.

In comparison, the onset of the epipodal seta in *Carpilius convexus* and *C. maculatus* (Clark et al., 2005: figs. 3a, 8a, respectively) has been accelerated and it was onset in ZI.

MAXILLA

Setation of proximal coxal endite (Fig. 263a–e): For the present study, the armature of ZI proximal endite ranged from 3 to 7 setae and setae 4 to 7 can be numbered individually (Fig. 263e); in non-majoids, these are accumulative setae and may be expressed at some stage during the zoeal phase or terminally delayed. In majoids, with two zoeal stages, these coxal setae appeared to be conservative.

Coxal seta 4 (Fig. 263): Seta 4 was onset in the ZI of *Aethra scruposa* (Fig. 4b), *Dacryopilumnus rathbunae* (Fig. 16b), *Daira perlata* (Fig. 12b), *Pseudocarcinus gigas* (Lamarck, 1818) (Gardner & Quintana, 1998: fig. 3G), *Carpilius convexus* and *C. maculatus* (Clark et al., 2005: figs. 3b, 8b, respectively) together with the Eriphioidea, Pilumnoidea, and species allied to *Etisus utilis* H. Jacquinot in H. Jacquinot & Lucas (Fig. 263b) described here, and *G. lividus* (Cuesta et al., 2011: fig. 3A). In comparison, the onset of seta 4 in the

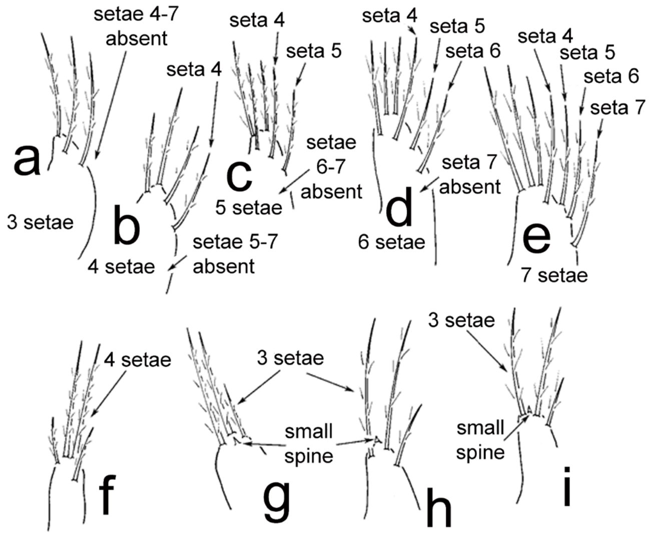

Fig. 263. Maxilla: ZI; setation of proximal coxal endite: a, *Chaceon fenneri* (Manning & Holthuis, 1984); b, *Etisus utilis* H. Jacquinot in H. Jacquinot & Lucas, 1854; c, *Pilumnus hirtellus* (Linnaeus, 1761); d, *P. minutus* de Haan, 1835; e, *Pseudocarcinus gigas* (Lamarck, 1818); setation of distal coxal article: f, *Lydia annulipes* (H. Milne Edwards, 1834); g, *Rhinolambrus pelagicus* (Rüppell, 1830); h, *Tetralia cavimana* Heller, 1861; i, *Trapezia cymodoce* (Herbst, 1801).

ZI of *Chaceon fenneri* (Stuck et al., 1992: fig. 1F; Fig. 263a), *C. quinquedens* (Perkins, 1973: fig. 2E; Fig. 98b), *Geryon longipes* (Guerao et al., 1996: fig. 5A; Fig. 102b), *Charybdis helleri* (Dineen et al., 2001: fig. 12a), and *H. rotundifrons* (Fig. 8b) was delayed. In zoeal development of *C. helleri* (Dineen et al., 2001: fig. 13a), with 6 zoeal stages, seta 4 was onset in ZV; in *Geryon longipes* (Guerao et al., 1996: fig. 5) and *Chaceon fenneri* (Stuck et al., 1992: fig. 2e), both with 4 zoeal stages, seta 4 was expressed in ZII. This was early (accelerated) compared to *C. helleri* (ZV), however, it was offset and delayed when compared with xanthoids also with 4 zoeal stages, in which seta 4 was onset in ZI.

In majoids, seta 4 was onset in ZI of *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3c, d), *Libinia spinosa* (Clark et al., 1998b: fig. 9), *Pisa armata* (Ingle & Clark, 1980: fig. 3a, d), and *I. dorsettensis*, *I. leptochirus*, and *I. phalangium* (Clark, 1980: fig. 9g, j), all with 2 zoeal stages. In *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 4A, B), seta 4 was offset and terminally delayed in the zoeal phase because the proximal coxal endite comprised only 3 setae.

Coxal seta 5 (Fig. 263c): Seta 5 was offset in the ZI of species allied to *E. utilis* (Fig. 263b) and delayed compared to onset in ZI of *Aethra scruposa* (Fig. 4b), *Dacryopilumnus rathbunae* (Fig. 16b), *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 3G), *Carpilius convexus* and *C. maculatus* (Clark et al., 2005: figs. 3b, 8b, respectively), and *Daira perlata* (Fig. 12b) together with the Eriphioidea and Pilumnoidea decribed here, and *Geograpsus lividus* (Cuesta et al., 2011: fig. 3A). In the zoeal development of *C. helleri* (Dineen et al., 2001: fig. 13b) with 6 zoeal stages, seta 5 was onset in ZVI. In comparison, seta 5 was offset and terminally delayed in *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 4) with 5 stages, but shows early onset in *Geryon longipes* (Guerao et al., 1996: fig. 5c) with 4 zoeal stages, being onset in ZIII, and in *Chaceon fenneri* (Stuck et al., 1992, fig. 2e) in ZII. In *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 10C), *N. granulipes* (Ko & Clark, 2002: fig. 7c) and *N. melanodactylus* (Dornelas et al., 2004: fig. 7c) seta 5 was onset (early, accelerated compared to *C. helleri*) in ZIII but was delayed when compared with *C. fenneri*.

In majoids, all with 2 zoeal stages, seta 5 was offset and terminally delayed in the zoeal phase of *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3c, d), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 4A, B), *Libinia spinosa* (Clark et al., 1998b: fig. 9), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9g, j). For *Pisa armata*, Ingle & Clark (1980: fig. 3a, d) illustrate 6 setae in ZI and 5 setae in ZII respectively, while Ingle (1991: 174) describes 5 setae in ZI and ZII. Consequently, seta 5 may be onset in *P. armata*, but requires confirmation.

Coxal seta 6 (Fig. 263d): Seta 6 was onset in ZI of *Daira perlata* (Fig. 12b), *Eriphia smithii* (De Haan, 1835) (Fig. 20b), *Hypothalassia armata* (Fig. 24b), *Ozius truncatus* H. Milne Edwards, 1834 (Fig. 44b), *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 3G), *Carpilius convexus* and *C. maculatus* (Clark et al., 2005: figs. 3b, 8b, respectively), and the pilumnoids described here. In comparison, seta 6 was offset and terminally delayed in the zoeal development of *Geograpsus lividus* (Cuesta et al., 2011: fig. 3A) with 8 zoeal stages, being expressed in ZV or ZVI?; for *C. helleri* (Dineen et al., 2001: fig. 13b) with 6 zoeal stages, in ZVI; *N. granulipes* (Ko & Clark, 2002: fig. 7d) and *N. melanodactylus* (Dornelas et al., 2004: fig. 8A), both with 4 zoeal stages, in ZIV; *Geryon longipes* (Guerao et al., 1996: fig. 5C) with 4 zoeal stages, in ZIII; *Chaceon quinquedens* (Perkins, 1973: fig. 4E) with 4 zoeal stages, in ZIII; and *C. fenneri* (Stuck et al., 1992: fig. 2e) with 4 zoeal stages, in ZII. For *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: figs. 10, 17A) and *Pilumnus hirtellus* (Clark, 2005: fig. 7; 2007: fig. 443), both with 4 zoeal stages, seta 6 was offset and terminally delayed as it did not appear during the zoeal phase.

In majoids, seta 6 was offset and terminally delayed in the zoeal phase of *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3c, d), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 4A, B), *Libinia spinosa* (Clark et al., 1998b: fig. 9), *Pisa armata* (Ingle & Clark, 1980: fig. 3a, d), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9g, j).

Coxal seta 7 (Fig. 263e): This seta is typically offset (Fig. 263a–d) in most ZI, including both species of *Chaceon*, *Charybdis helleri*, *Geryon longipes*, species allied to *Etisus utilis* (Fig. 263b), *Pilumnus hirtellus* (Clark, 2005: fig. 7; Fig. 263c), and *P. minutus* (Fig. 263d). In comparison, exceptions appear to be *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7a) and *H. rotundifrons* (Fig. 8b) where the onset of seta 7 is accelerated and early in ZI. In zoeal development, seta 7 is onset in *Geograpsus lividus* (Cuesta et al., 2011: 231), with 8 zoeal stages, at ZVI; and with 4 zoeal stages, *Chaceon fenneri* (Stuck et al., 1992: fig. 3E) at ZIII and *Geryon longipes* (Guerao et al., 1996: fig. 5) at ZVI. This suggests that the onset of seta 7 was early and accelerated when the geryonids are compared to the grapsoid and in *Chaceon* when compared with *Geryon*. Seta 7 was, however, offset and terminally delayed in the zoeal phase of *Charybdis hellerii* (Dineen et al., 2001: fig. 13b) with 6 stages; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 4) with 5 stages; *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: figs. 10, 17F), *N. granulipes* (Ko & Clark, 2002: fig. 7), and *N. melanodactylus* (Dornelas et al., 2004: figs. 7, 8A), all with 4 stages; *Actumnus setifer* (Clark & P.K.L. Ng, 2004b: fig. 7) with 3 stages; and *P. kempi* (Fig. 83d) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 7) both with 2 stages. Furthermore, seta 7 was offset and terminally delayed in the following majoids: *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3c, d); *Libinia spinosa* (Clark et al., 1998b: fig. 9); *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 4A, B); *Pisa armata* (Ingle & Clark, 1980: fig. 3a, d), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9g, j), all with 2 zoeal stages.

Setation of distal coxal endite (Fig. 263f, g): The setation of the distal endite ranged from 3 to 6 setae. It was normally an accumulative character, but in some species it was conservative as with the majoids *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9g, j), with only 3 setae expressed. A number of species, however, had 3 setae plus a small spine, as in the ZI of *Rhinolambrus pelagicus* (Rüppel, 1830) (Fig. 263g), *Tetralia cavimana* (Fig. 263h), and *Trapezia cymodoce* (Herbst, 1801) (Fig. 263i). This minute "spine" was in fact rudimentary seta 4 which became fully developed later in zoeal development.

Coxal seta 4 (Fig. 263f): The setation of the distal coxal endite for the majority of ZI studied here comprised 4 setae as in *Lydia annulipes* (H. Milne Edwards, 1834) (Clark & Paula, 2003: 329, 338, fig. 10; Fig. 263f). In *Charybdis hellerii* (Dineen et al., 2001: fig. 12a–c) with 6 zoeal stages, the onset of seta 4 was delayed in ZI and ZII, and was expressed in ZIII. In comparison, the onset of setae 4 was expressed in ZI and was a conservative character for the following species: *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 4) with 5 stages; *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: figs. 10, 17F), *N. granulipes* (Ko & Clark, 2002: fig. 7) and *N. melanodactylus* (Dornelas et al., 2004: figs. 7, 8A), all with 4 stages; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 7) with 3 stages; and *P. kempi* (Fig. 83c) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 7), both with 2 stages.

The development of this character in the following majoids, all with 2 zoeal stages, was of interest because the setae did not increase in number with successive moults but remained conservative. In *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3c, d), *Libinia spinosa* (Clark et al., 1998b: fig. 9), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 4A, B), and *Pisa armata* (Ingle & Clark, 1980: fig. 3a, d), the distal endite possesses 4 setae in both zoeal stages. In comparison, seta 4 was terminally delayed within the majoids *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9g, j).

Coxal seta 5 (not figured): This seta was onset in *Geograpsus lividus* (Cuesta et al., 2011: 231), with 8 zoeal stages, at ZVI; *Charybdis hellerii* (Dineen et al., 2001: fig. 12d) with 6 stages, at ZIV; and with 4 zoeal stages, *Chaceon fenneri* (Stuck et al., 1992: fig. 3E) at ZIII and *Geryon longipes* (Guerao et al., 1996: fig. 5D) at ZVI. With respect to *Geograpsus lividus* and *Charybdis hellerii*, the onset of seta 5 in *Chaceon fenneri* was expressed early (accelerated), and, in comparison with *G. lividus*, only the onset of seta 5 in *Geryon longipes* is early. In *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7c) with 4 zoeal stages, seta 5 was expressed in ZIII, its onset being early compared to *Geograpsus lividus* and *Charybdis hellerii*.

Within the majoids, in *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3c, d), *Libinia spinosa* (Clark et al., 1998b: fig. 9), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 4A, B), *Pisa armata* (Ingle & Clark, 1980: fig. 3a, d), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9g, j), the appearance of seta 5 was offset and terminally delayed.

Coxal seta 6 (not figured): Seta 6 was only onset in *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7d). In all zoea examined for the present study, seta 6 was offset and terminally delayed.

Setation of proximal basial endite (Fig. 264a–c): An accumulative character with a range between 4 to 9 setae. For the present study, the armature of the proximal endite ranged from 4 to 6 setae in ZI. In *R. pelagicus* (P.K.L. Ng & Clark, 2001: fig. 2; Fig. 264c), 4 setae and a small spine were described. In this instance the spine represents a rudimentary seta which at the next moult will be fully expressed in the identical position.

Proximal seta 5 (Fig. 264b): Most ZI treated for the present study typically had seta 5 expressed on the proximal basial endite; e.g., *Geograpsus lividus* (Cuesta et al., 2011: fig. 3A), *Chaceon quinquedens* (Perkins, 1973: fig. 2E), *Geryon longipes* (Guerao et al., 1996: fig. 5A), *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 4A), *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 10A), *N. granulipes* (Ko & Clark, 2002: fig. 7a), and *N. melanodactylus* (Dornelas et al., 2004: fig. 7A), *Pilumnus hirtellus* (Clark, 2005: fig. 7; 2007: fig. 443a), *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 7), *P. kempi* (Fig. 83c), *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 7a), and the majoids, *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3c), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 4A), *Pisa armata* (Ingle, 1991: fig. 1.21a), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9g, j). The expression of seta 5 was, however, offset and delayed in the ZI of *Charybdis hellerii* (Dineen et al., 2001: fig. 12), and the majoid *Libinia spinosa* (Clark et al., 1998b: fig. 9) has only 4 setae on the proximal basial endite. Seta 5 was onset in *Charybdis*

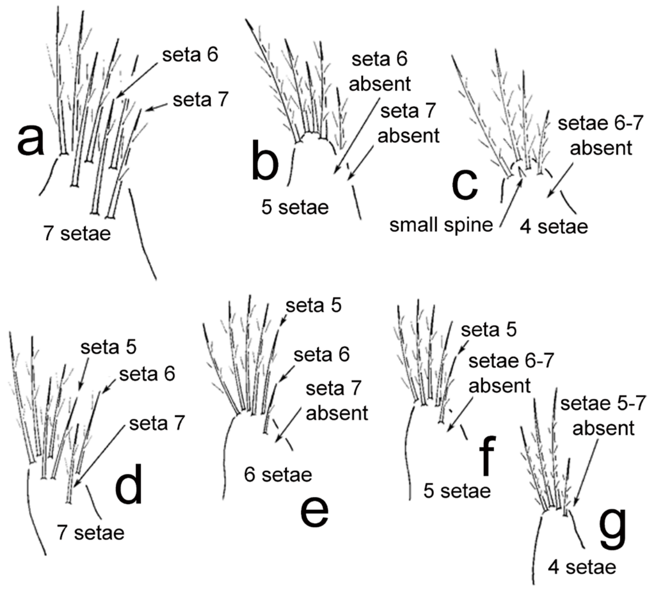

Fig. 264. Maxilla: ZI; setation of proximal basial endite: a, *Heterozius rotundifrons* A. Milne-Edwards, 1867; b, *Zozymodes xanthoides* (Krauss, 1843); c, *Rhinolambrus pelagicus* (Rüppell, 1830); setation of distal basial endite: d, *Heterozius rotundifrons* A. Milne-Edwards, 1867; e, *Geryon longipes* A. Milne-Edwards, 1882; f, *Chaceon fenneri* (Manning & Holthuis, 1984); g, *Eriphia scabricula* Dana, 1852.

hellerii (Dineen et al., 2001: fig. 12c) with 6 zoeal stages, at ZIII, and *L. spinosa* (Clark et al., 1998b: fig. 9b) with 2 zoeal stages, at ZII.

Proximal seta 6 (Fig. 264a): The expression of seta 6 was accelerated with abbreviated development. In *Geograpsus lividus* (Cuesta et al., 2011: 231) with 8 zoeal stages, seta 6 was expressed in ZVI; *Charybdis helleri* (Dineen et al., 2001: fig. 12d) with 6 zoeal stages, in ZIV; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 4D) with 5 zoeal stages, in ZIV; *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7A) with 5 zoeal stages, in ZII; in the following species with 4 zoeal stages; in *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 17F), it was terminally delayed; but onset in *N. granulipes* (Ko & Clark, 2002: fig. 6d) in ZIV, and in *N. melanodactylus* (Dornelas et al., 2004: fig. 8A) in ZIV; *Geryon longipes* (Guerao et al., 1996: fig. 5B) with 4 zoeal stages, in ZII; *Geryon trispinosus* (Herbst, 1803) (Ingle, 1991: 227; as *G. tridens* Krøyer, 1837 by Ingle, 1979: 225, fig. 5d) with 4 zoeal stages, at ZII, and in *H. rotundifrons* (Fig. 8b) with 2 zoeal stages, at ZI. In the following pilumnids, seta 6 was onset in *Pilumnus hirtellus* (Clark, 2005: fig. 6; 2007: fig. 443c) with 4 zoeal stages, at ZIII; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 7c) with 3 zoeal stages, at ZIII; and in ZII for *P. kempi* (Fig. 83d) and *P. sluiteri* (Clark & Ng, 2004a: fig. 7b), both with 2 stages.

Seta 6 was offset and terminally delayed in the majoids, *Macrocheira kaempferi* (Clark & Webber, 1991: 1266, fig. 3d), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: 829, fig. 4A), *Pisa armata* (Ingle & Clark, 1980: 726, fig. 3d; Ingle, 1991: 174), *Libinia spinosa* (Clark et al., 1998b: 154, fig. 9b), *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9g, j).

Proximal seta 7 (Fig. 264a): The expression of seta 7 was accelerated with abbreviated development. In *Geograpsus lividus* (Cuesta et al., 2011: 232) with 8 zoeal stages, seta 7 was onset in ZVII; *Charybdis helleri* (Dineen et al., 2001: fig. 13a) with 6 zoeal stages, in ZV; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 4D) with 5 zoeal stages, in ZIV; *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7B) with 5 zoeal stages, in ZIII; *Geryon longipes* (Guerao et al., 1996: fig. 5B) with 4 zoeal stages, in ZII; *Geryon trispinosus* (Ingle, 1991: 227) with 4 zoeal stages, at ZII; and in *H. rotundifrons* (Fig. 8b) with 2 zoeal stages, at ZI.

Seta 7 was offset and terminally delayed in the following species with 4 zoeal stages, *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998), *N. granulipes* (Ko & Clark, 2002), *N. melanodactylus* (Dornelas et al., 2004); in the following pilumnids, *Pilumnus hirtellus* (Clark, 2005: fig. 7; 2007: fig. 443) with 4 zoeal stages, *A. setifer* (Clark & P.K.L. Ng, 2004b) with 3 zoeal stages, *P. kempi* (Fig. 83d) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a), both with 2 stages; and in the following majoids, *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3c, d), *Maja brachydactyla* (as *M. squinado* by Clark, 1986), *Pisa armata* (Ingle & Clark, 1980; Ingle, 1991: 174), *Libinia spinosa* (Clark et al., 1998b), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980).

Proximal seta 8 (not figured): The expression of seta 8 was accelerated with abbreviated development. In *Geograpsus lividus* (Cuesta et al., 2011: 232) with 8 zoeal stages, seta 8 was onset in ZVIII; *Charybdis helleri* (Dineen et al., 2001: fig. 13b) with 6 zoeal stages, in ZVI; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 4E) with 5 zoeal stages, in ZV; *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7B) with 5 zoeal stages, in ZIII; *Geryon longipes* (Guerao et al., 1996: fig. 5D) with 4 zoeal stages, in ZIII ?, ZIV; *G. trispinosus* (Ingle, 1991: 227) with 4 zoeal stages, in ZIII.

Seta 8 was offset and terminally delayed in the following species with 4 zoeal stages, *Lophozozymus pictor* (Clark & Ng, 1998), *N. granulipes* (Ko & Clark, 2002), and *N. melanodactylus* (Dornelas et al., 2004); in the following pilumnids, *Pilumnus hirtellus* (Clark, 2005: fig. 7; 2007: fig. 443) with 4 zoeal stages, *A. setifer* (Clark & P.K.L. Ng, 2004b) with 3 zoeal stages, and *P. kempi* (Fig. 83d) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a), both with 2 stages; and in the following majoids, *Macrocheira kaempferi* (Clark & Webber, 1991), *Maja brachydactyla* (as *M. squinado* by Clark, 1986), *Pisa armata* (Ingle & Clark, 1980; Ingle, 1991), *Libinia spinosa* (Clark et al., 1998b), *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980).

Proximal seta 9 (not figured): The onset of seta 9 was accelerated with abbreviated development. In *Geograpsus lividus* (Cuesta et al., 2011: 232) with 8 zoeal stages, seta 9 was onset in ZVIII; *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7B) with 5 zoeal stages, in ZIV; *Geryon longipes* (Guerao et al., 1996: fig. 5E) with 4 zoeal stages, in ZIV; *Geryon trispinosus* (Ingle, 1991: 228) with 4 zoeal stages, in ZIV.

Seta 9 was offset and terminally delayed in the following species: *Charybdis helleri* (Dineen et al., 2001) with 6 zoeal stages; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984) with 5 zoeal stages; the following species with 4 zoeal stages, *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998), *N. granulipes* (Ko & Clark, 2002), *N. melanodactylus* (Dornelas et al., 2004); in the following pilumnids, *Pilumnus hirtellus* (Clark, 2005: fig. 7; 2007: fig. 443) with 4 zoeal stages, *A. setifer* (Clark & P.K.L. Ng, 2004b) with 3 zoeal stages, and *P. kempi* (Fig. 83c, d) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a) both with 2 stages; and the following majoids, *Macrocheira kaempferi* (Clark & Webber, 1991), *Maja brachydactyla* (as *M. squinado* by Clark, 1986), *Pisa armata* (Ingle & Clark, 1980; Ingle, 1991), *Libinia spinosa* (Clark et al., 1998b), *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980).

Setation of distal basial endite (Fig. 264d–g): An accumulative character with the armature of ZI ranging from 4 to 10 setae.

Distal endite seta 4 (Fig. 264g): Typically, most ZI treated in the present study possessed 4 setae on the distal endite, as in *Eriphia scabricula* Dana, 1852 (Fig. 260g), with setae 5 to 10 absent.

Distal endite seta 5 (Fig. 264f): The onset of seta 5 was accelerated with abbreviated development. In *Geograpsus lividus* (Cuesta et al., 2011: 231) with 8 zoeal stages, seta 5 was expressed in ZVI; *Charybdis helleri* (Dineen et al., 2001: fig. 12c) with 6 zoeal stages, in ZIII; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 4C) with 5 zoeal stages, in ZIII; in the following with 4 zoeal stages, *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 9C), *N. granulipes* (Ko & Clark, 2002: fig. 6d) and *N. melanodactylus* (Dornelas et al., 2004: fig. 7C), all in ZIII. With respect to the following pilumnids, at ZII for *Pilumnus hirtellus* (Clark, 2005: fig. 7; 2007: fig. 443b) with 4 zoeal stages, *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 7b) with 3 zoeal stages, and *P. kempi* (Fig. 83d) and *P. sluiteri*, both with 2 zoeal stages; and at ZII for the majoids *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3d), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 4B), *Pisa armata* (Ingle, 1991: fig. 3d), *Libinia spinosa* (Clark et al., 1998b: fig. 9b), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9j). Seta 5 was onset at ZI in the following species: *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7A) with 5 zoeal stages, *Geryon longipes* (Guerao et al., 1996: fig. 5B) and *G. trispinosus* (Ingle, 1991: 227), both with 4 zoeal stages, and *Heterozius rotundifrons* (Fig. 8b) with 2 zoeal stages.

Distal endite seta 6 (Fig. 264e): The onset of seta 6 was accelerated with abbreviated development. In *Geograpsus lividus* (Cuesta et al., 2011: 231) with 8 zoeal stages, seta 6 was expressed in ZVI; for *Charybdis helleri* (Dineen et al., 2001: fig. 12d) with 6 zoeal stages, in ZIV; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 4D) with 5 zoeal stages, in ZIV; in the following with 4 zoeal stages, *Geryon longipes* (Figs. 102b, 264e), in ZI; *G. trispinosus* (Ingle, 1991: fig. 1.19a), in ZI; *Chaceon fenneri* (Stuck et al., 1992: fig. 2E), in ZII; *C. quinquedens* (Perkins, 1973: fig. 3E), in ZII; *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 17F), in ZIV; *N. granulipes* (Ko & Clark, 2002: fig. 7d) in ZIV; *N. melanodactylus* (Dornelas et al., 2004: fig. 8A), in ZIV; and in the pilumnoids, *Pilumnus hirtellus* (Clark, 2005: fig. 7; 2007: fig. 443c) with 4 zoeal stages, in ZIII; *Actumnus setifer* (Clark & P.K.L. Ng, 2004b) with 3 zoeal stages, at ZIII; and it was offset and terminally delayed in *P. kempi* (Fig. 83d) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 7b), both with 2 stages. In *Heterozius rotundifrons* (Figs. 8b, 264d), seta 6 was present in ZI.

Seta 6 was offset and terminally delayed in the majoids, *Macrocheira kaempferi* (Clark & Webber, 1991), *Maja brachydactyla* (as *M. squinado* by Clark, 1986), *Pisa armata* (Ingle & Clark, 1980; Ingle, 1991: 174), *Libinia spinosa* (Clark et al., 1998b), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980).

Distal endite seta 7 (Fig. 264d): This seta was typically offset (Fig. 264e–g) in most ZI, including both species of *Chaceon*, *Charybdis helleri*, *Geryon longipes*, species allied to *E. utilis*, and the pilumnoids. *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7a) and *Heterozius rotundifrons* (Fig. 8b) appear to be exceptions, where the onset of seta 7 was accelerated and early, in ZI. The onset of seta 7 was accelerated with abbreviated development. In *Geograpsus lividus* (Cuesta et al., 2011: 232) with 8 zoeal stages, seta 7 was onset in ZVII; *Charybdis helleri* (Dineen et al., 2001: fig. 13a) with 6 zoeal stages, in ZVI; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 4E) with 5 zoeal stages, in ZV; and in the following with 4 zoeal stages, *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 17F), in ZIV; *Nanocassiope granulipes* (Ko & Clark, 2002: fig. 7d), in ZIV; *N. melanodactylus* (Dornelas et al., 2004: fig. 8A), in ZIV.

Seta 7 was offset and terminally delayed in the pilumnoids, *Pilumnus hirtellus* (Clark, 2005: fig. 7; 2007: fig. 443c) with 4 zoeal stages; *A. setifer* (Clark & P.K.L. Ng, 2004b) with 3 zoeal stages; and *P. kempi* (Fig. 83d) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 7b), both with 2 stages; and in the majoids *Macrocheira kaempferi* (Clark & Webber, 1991), *Maja brachydactyla* (as *M. squinado* by Clark, 1986), *Pisa armata* (Ingle & Clark, 1980; Ingle, 1991: 174), *Libinia spinosa* (Clark et al., 1998b), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980).

Distal endite seta 8 (not figured): The onset of seta 8 was accelerated with abbreviated development. In *Geograpsus lividus* (Cuesta et al., 2011: 232) with 8 zoeal stages, seta 8 was onset in ZVII; *Charybdis helleri* (Dineen et al., 2001: fig. 13b) with 6 zoeal stages, in ZVI; with 5 zoeal stages, *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 4E) in ZV, and *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7D) in ZIV; with 4 zoeal stages, *Geryon longipes* (Guerao et al., 1996: fig. 5D) in ZIV, and *G. trispinosus* (Ingle, 1991: 227) in ZIII.

Seta 8 was offset and terminally delayed in the pilumnoids, *Pilumnus hirtellus* (Clark, 2005: fig. 7; 2007: fig. 443d) with 4 zoeal stages, *Actumnus setifer* (Clark & P.K.L. Ng, 2004b) with 3 zoeal stages, and *P. kempi* (Fig. 83d) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a) both with 2 zoeal stages; in *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 17F), *N. granulipes* (Ko & Clark, 2002: fig. 6d), and *N. melanodactylus* (Dornelas et al., 2004: fig. 8A), all with 4 zoeal stages; and the majoids *Macrocheira kaempferi* (Clark & Webber, 1991), *Maja brachydactyla* (as *M. squinado* by Clark, 1986), *Pisa armata* (Ingle & Clark, 1980; Ingle, 1991: 174), *Libinia spinosa* (Clark et al., 1998b), *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980), all with 2 zoeal stages.

Distal endite seta 9 (not figured): The onset of seta 9 was accelerated with abbreviated development. In *Geograpsus lividus* (Cuesta et al., 2011: fig. 3C) with 8 zoeal stages, seta 9 was onset in ZVIII; *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7D) with 5 zoeal stages, in ZIV; with 4 zoeal stages *Geryon longipes* (Guerao et al., 1996: fig. 5D), in ZIV and *G. trispinosus* (Ingle, 1991: 227), in ZIV.

Seta 9 was offset and terminally delayed in *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998), *Nanocassiope granulipes* (Ko & Clark, 2002) in ZIV, and *N. melanodactylus* (Dornelas et al., 2004), all with 4 zoeal stages; the pilumnoids, *Pilumnus hirtellus* (Clark, 2005: fig. 7; 2007: fig. 443) with 4 zoeal stages, *Actumnus setifer* (Clark & P.K.L. Ng, 2004b) with 3 zoeal stages, and *P. kempi* (Fig. 83d) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 7b) both with 2 stages; and the majoids, *Macrocheira kaempferi* (Clark & Webber, 1991), *Maja brachydactyla* (as *M. squinado* by Clark, 1986), *Pisa armata* (Ingle & Clark, 1980; Ingle, 1991: 174), *Libinia spinosa* (Clark et al., 1998b), *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980), all with 2 zoeal stages.

Distal endite seta 10 (not figured): The expression of seta 10 was accelerated with abbreviated development. In *Geograpsus lividus* (Cuesta et al., 2011: fig. 3C) with 8 zoeal stages, seta 10 was onset in ZVIII; for *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7D) with 5 zoeal stages, in ZIV, and for *Geryon trispinosus* (Ingle, 1991: 227) with 4 zoeal stages, in ZIV.

Seta 10 was offset and terminally delayed in *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998), *N. granulipes* (Ko & Clark, 2002) in ZIV, and *N. melanodactylus* (Dornelas et al., 2004), all with 4 zoeal stages; *Pilumnus hirtellus* (Clark, 2005: fig. 7; 2007: fig. 443c) with 4 zoeal stages; *A. setifer* (Clark & Ng, 2004b) with 3 zoeal stages; *P. kempi* (Fig. 83d) and *P. sluiteri* (Clark & Ng, 2004a) both with 2 stages; and the majoids, *Macrocheira kaempferi* (Clark & Webber, 1991), *Maja brachydactyla* (as *M. squinado* by Clark, 1986), *Pisa armata* (Ingle & Clark, 1980; Ingle, 1991: 174), *Libinia spinosa* (Clark et al., 1998b), *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980), all with 2 zoeal stages.

Endopod: The endopod is a conservative character, unsegmented, and according to Rice (1980), comprises

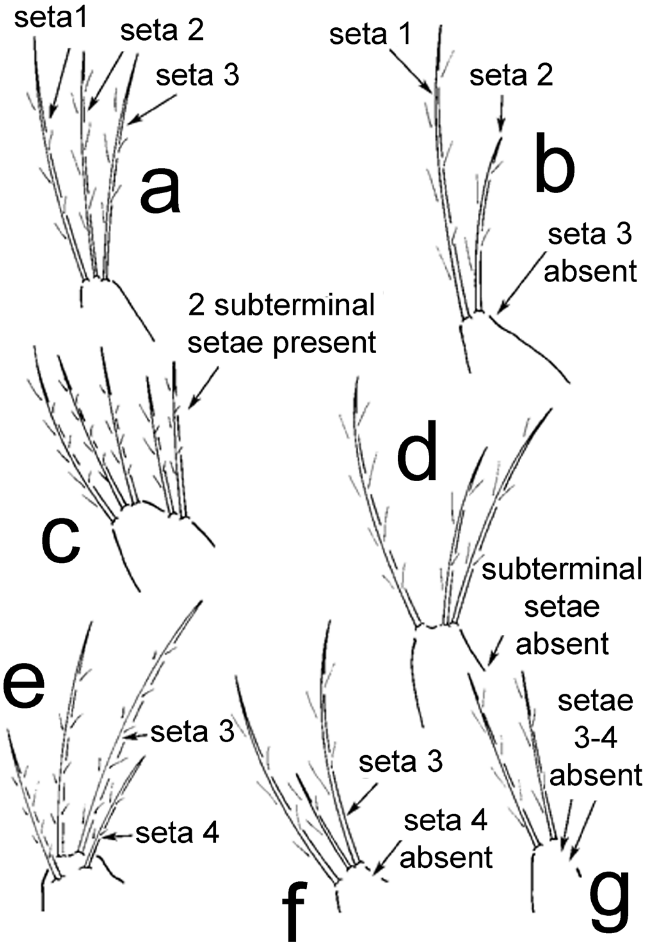

Fig. 265. Maxilla: ZI; setation of proximal endopod lobe: a, *Xantho hydrophilus* (Herbst, 1790); b, *Tetralia cavimana* Heller, 1861; subterminal setae on distal endopod lobe: c, *Nanocassiope melanodactylus* (A. Milne-Edwards, 1867); d, *Myomenippe hardwickii* (Gray, 1831); terminal setae on distal lobe: e, *Charybdis helleri* (A. Milne-Edwards, 1867); f, *Novactaea bella* Guinot, 1976; g, *Trapezia richtersi* Galil & Lewinsohn, 1983.

two types: bilobed, the ancestral condition; and simple (not bilobed), the derived state. Endopod lobes possess terminal setae with the additional possibility of subterminal setae on the distal lobe. Rice (1980) noted that within the majoids the ancestral condition was bilobed as in *Chionoecetes bairdi* Rathbun, 1893 (Haynes, 1973: fig. 2g; 1981: fig. 2G), *C. opilio* (Fabricius, 1788) (Motoh, 1973: figs. 1G, 2F), *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3c, d) and *Hyas araneus* (Linnaeus, 1758) (Ingle, 1991: 161), and that a simple endopod, lacking a lobe, was diagnostic of most spider crab species and was the derived condition. To date, endopod setation appears to be conservative, and according to Rice (1980), the ancestral condition is a total of 8 setae arranged in three more or less distinct groups. Within this present study, however, the endopod of *Lachnopodus subactus* (Stimpson, 1858) is unusual, comprising a total of 7 setae, e.g., 2+5 (2 subterminal+3 terminal) setae (Fig. 223).

Setation of proximal endopod lobe (Fig. 265): The proximal lobe either had the typical 3 terminal setae, as in *Xantho hydrophilus* (Herbst, 1790) (Fig. 265a), or 2 terminal setae as in *Tetralia cavimana* (Fig. 265b). Seta 3 was either present or absent, with the latter being considered as the derived condition.

Subterminal setae of distal endopod lobe (Fig. 265): Two subterminal setae were typically present on the distal endopod lobe, as in *N. melanodactylus* (Fig. 265c), but were absent in *Myomenippe hardwickii* (Gray, 1831) (Fig. 265d). The latter was considered to be the derived condition.

Setation of distal endopod lobe. Seta 3 (Fig. 265e–g): Present in *Charybdis helleri* (Fig. 265e) and *Novactaea bella* Guinot, 1976 (Fig. 265f) and absent in *Trapezia richtersi* Galil & Lewinsohn, 1983 (Fig. 265g). The latter was considered to be the derived state.

Seta 4 (Fig. 265): Present in *Charybdis helleri* (Fig. 265e) but absent in *T. richtersi* (Fig. 265g) and *N. bella* (Fig. 265f). The latter was considered to be the derived condition.

Exopod (scaphognathite) (Fig. 266): Two characters were considered, the long distal stout seta and the marginal setae.

Scaphognathite long distal stout seta (Fig. 266): Typically present in the majority of ZI, e.g., *Chaceon quinquedens* (Fig. 266a) and *Benthopanope indica* (De Man, 1887) (Fig. 262b), this long distal stout seta is reduced to the same size as other marginal setae on the scaphognathite during the subsequent moult to ZII as illustrated by *P. kempi* (Fig. 83d). In comparison, this distal stout seta was found to be reduced in ZI majoids.

Rice (1980) considered that a well-developed setose posterior process in ZI Brachyura, which was indistinguishable from the marginal setae in the later stages, was the ancestral condition.

Scaphognathite marginal setae (Fig. 266): The number of marginal setae is an accumulative character and the majority of ZI studied here have four, e.g., *B. indica* (Fig. 266b). In *Geograpsus lividus* (Cuesta et al., 2011: 228–233, fig. 3), the development of these marginal setae was as follows, 4 in ZI, 8 in ZII, 11 in ZIII, 19 in ZIV, 20 in ZV, ca. 26 in ZVI, ca. 33 in ZVII, ca. 40 in ZVIII; *Charybdis helleri* (Dineen et al., 2001: figs. 12, 13), 4 in ZI, 8 in ZII, 10 in ZIII, ca. 23 in ZIV, ca. 25 in ZV, ca. 31 in ZVI; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 4), 4 in ZI, 9 in ZII, 15 in ZIII, ca. 28 in ZIV, ca. 31 in ZV; *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: figs. 10, 17F), 4 in ZI, 13 in ZII, ca. 23 in ZIII, ca. 32 in ZIV; *Nanocassiope granulipes* (Ko & Clark, 2002: fig. 7), 4 in ZI, 11 in ZII, 19 in ZIII, ca. 29 in ZIV; and *N. melanodactylus* (Dornelas et al., 2004: figs. 7, 8A), 4 in ZI, 11 in ZII, 19 in ZIII, ca. 26 in ZIV. In the pilumnoids, *P. hirtellus* (Clark, 2005: fig. 7; 2007: fig. 443), 4 in ZI, 11 in ZII, 18 in ZIII, ca. 22 in ZIV; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 7), 4 in ZI, 11 in ZII, 21 in ZIII; *P. kempi* (Fig. 83c, d), 4 in ZI, 20 in ZII; and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 7a, b), 4 in ZI, 19 in ZII. These taxa demonstrate a trend towards accelerated development together with terminal delay of some marginal setae associated with abbreviated zoeal development, e.g., *G. lividus* (Cuesta et al., 2011: 228–233, fig. 3), last zoeal stage with 40 setae in ZVIII, compared with *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 7b) with 19 in the last stage, ZII.

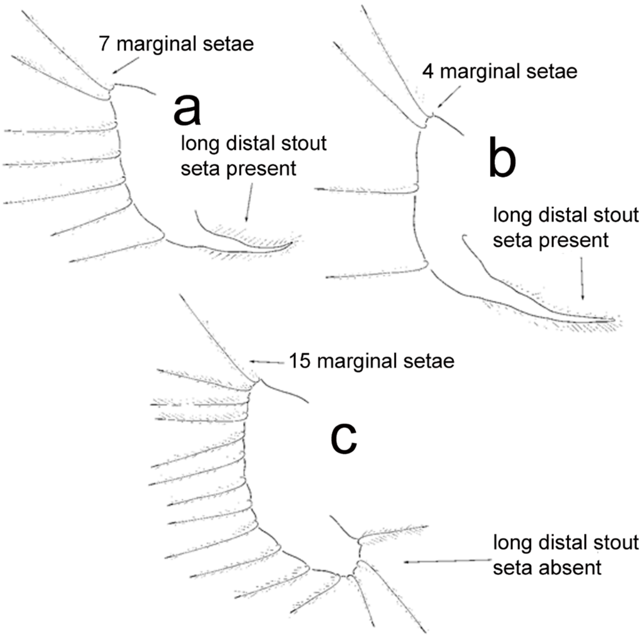

Fig. 266. Maxilla: ZI; scaphognathite (exopod): a, *Chaceon quinquedens* (Smith, 1879); b, *Benthopanope indica* (De Man, 1887); c, *Carpilius convexus* (Forskål, 1775).

In majoids, the development of these marginal setae was as follows: *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 3c, d), 14 in ZI, ca. 29 in ZII; *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 4A, B), 11 in ZI, 21 in ZII; *Pisa armata* (Ingle, 1991: fig. 1.21a), 10 in ZI, 21 in ZII; *Libinia spinosa* (Clark et al., 1998b: fig. 9), 10 in ZI, 20 in ZII; and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 9g, j), 10 in ZI, 19 in ZII. The onset of the marginal setae in ZI appears to have been accelerated to the equivalent of ZII, with respect to many of the above taxa.

Rice (1980) regarded a scaphognathite with four to six marginal setae in ZI to be the ancestral condition for higher Brachyura. Of interest are the ZI marginal setae of *Carpilius*, *Chaceon*, and *Geryon*. In *Carpilius convexus*, there were 15 in ZI (Fig. 266c), and in *C. maculatus*, 17 in ZI (Clark et al., 2005: figs. 3b, 8b, respectively). These setae show early onset with accelerated development of the scaphognathite being considered the equivalent of ZIII in some of the taxa cited above.

For *Chaceon fenneri* (Stuck et al., 1992: figs. 1F, 2E, 3E, 4F), the pattern is ca. 6–8 in ZI, ca. 13–18 in ZII, ca. 26–30 in ZIII, ca. 38–50 in ZIV; *C. quinquedens* (Perkins, 1973: figs. 2E, 3E, 4E, 5E), 4 in ZI, 13 in ZII, ca. 23 in ZIII, ca. 32 in ZIV; and *Geryon longipes* (Guerao et al., 1996: fig. 5A–D), 7 in ZI, ca. 17–20 in ZII, ca. 30–32 in ZIII, ca. 43–45 in ZIV. These setae may show early onset with accelerated development of the scaphognathite and are considered the equivalent of ZII in respect to many of the above taxa with the last zoeal stage being comparable to that of *Geograpsus lividus*.

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Coxal setae (Fig. 267a, b): This was an accumulative character and had been overlooked in many zoeal descriptions; in *Geograpsus lividus* (Cuesta et al., 2011: fig. 4A–C), 1 coxal seta in ZI–ZVI, 2 in ZVII, 5 in ZVIII; *Charybdis helleri* (Dineen et al., 2001: figs. 14, 15a, b), 1 in ZI–ZIII, 2 in ZIV–ZV, 3 in ZVI; *Lophozozymus pictor* (Clark, 2007: figs. 288, 289), *Nanocassiope granulipes* (Ko & Clark, 2002: fig. 8) and *N. melanodactylus* (Dornelas et al., 2004: fig. 9), all with 1 in ZI–ZIII, 2 in ZIV. Although the coxal seta was expressed in *Pilumnus hirtellus* (Clark, 2005: fig. 8; 2007: fig. 444) in ZIV, this seta was terminally delayed in *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 8), with 3 stages, and *P. kempi* (Fig. 84a, b) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 8), both with 2 stages.

The coxal seta may have been overlooked in the majoids *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 4a, b), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 5A, B), *Pisa armata* (Ingle & Clark, 1980: fig. 3b, e), *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 10a, d); however, it was described in the zoeal stages of *Libinia spinosa* (Clark et al., 1998b: fig. 12). This character may require further investigation in majoids.

Coxal epipod and podobranch (Fig. 84a, b): This was a developmental character that was often overlooked in the zoeal phase. In *Lophozozymus pictor* (Clark, 2007: figs. 288, 289), *N. granulipes* (Ko & Clark, 2002: fig. 8) and *N. melanodactylus* (Dornelas et al., 2004: fig. 9), all with 4 zoeal stages, a bud appears in ZIII and becomes more developed in ZIV. In *Charybdis helleri* (Dineen et al., 2001: figs. 14, 15a, b) with 6 zoeal stages, the epipod was not expressed for ZI–ZIV, but was well developed in ZVI; however, the appearance of a bud may have been overlooked in ZV. The coxal epipod was absent in the ZI pilumnoid zoea treated for the present study, in *Pilumnus hirtellus* (Clark, 2005: fig. 8; 2007: fig. 444) with 4 zoeal stages, the epipod and podobranch was onset in ZIV; *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 8) with 3 zoeal stages, in ZII; and in *P. kempi* (Fig. 84a, b) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 8) both with 2 zoeal stages, in ZI–ZII. For the latter three species, the onset of the epipod is accelerated when associated with abbreviated development. This character may have been overlooked in the majoids *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 4a, b), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 5A, B), *Pisa armata* (Ingle & Clark, 1980: fig. 3b, e), *Libinia spinosa* (Clark et al., 1998b: fig. 12), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 10a, d), or it may have been terminally delayed but requires further investigation in majoids.

Basial setation: Rice (1980) considered a basis with a total of nine or ten medial setae arranged in four groups to be the ancestral condition in ZI. He went on to consider that the reduction of basial setation was the advanced condition, e.g., 10 ancestral, 9 advanced etc. ? All zoeas described for the present study possessed 10 (2+2+3+3) setae. This character was constant for all the following species: *Epixanthus frontalis* (H. Milne Edwards, 1834), *Lydia annulipes*,

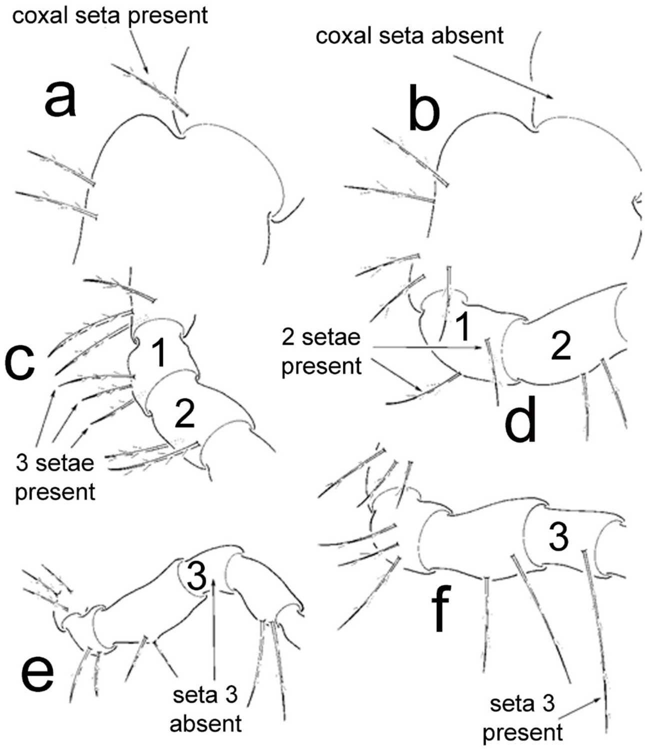

Fig. 267. First maxilliped: ZI; setation of coxa: a, *Eurytium limosum* (Say, 1818); b, *Pilumnus spinifrons* P.K.L. Ng & L.W.H. Tan, 1984; setation of endopod article 1: c, *Lybia plumosa* Barnard, 1947; d, *Geryon longipes* A. Milne-Edwards, 1882; setation of endopod article 3: e, *Charybdis helleri* (A. Milne-Edwards, 1867); f, *Carpilius maculatus* (Linnaeus, 1758).

Eriphia scabricula, *Lybia plumosa* Barnard, 1947, *Pilodius paumotensis* Rathbun, 1907, *Zozymodes xanthoides* (Krauss, 1843), *Eurycarcinus natalensis* (Krauss, 1843), *Leptodius exaratus* (H. Milne Edwards, 1834), *Pilumnus longicornis*, and *P. vespertilio* (Fabricius, 1793) (see Clark & Paula, 2003); the pilumnines examined for the present study; the majoids; and *Charybdis helleri* (Dineen et al., 2001). Initially, the number of setae on the basial article appeared not to be affected by abbreviated zoeal development and Clark (2001, 2005) considered this to be a conservative character. Although this was the commonly accepted rule, there are exceptions to be found within grapsoid taxa; e.g., *Geograpsus lividus* (Cuesta et al., 2011: fig. 4A–C), the basis of ZI–ZVII had 8 (2+2+2+2) setae and in the subsequent stage ZVIII this increased to 10 (2+2+3+3). A similar accumulation was reported for zoeas of *Eriocheir sinensis* (Montú et al., 1996: fig. 10). Although their setal description for the basis of ZI–ZVI varied; ZI with 6 (2+2+2) setae; ZII, 9 (2+2+3+2); ZIII, 6 (2+2+2); ZIV, 8 (2+1+3+2); ZV, 10 (2+2+3+3); and ZVI, 11 (2+2+3+4). *Eriocheir sinensis* zoeas recently examined by Kamanli et al. (2018), however, suggested a slightly different setation for the basis; ZI–ZV (Kamanli et al., 2018: figs. 6C, 13C, 20A, 29A, 39A) were constant with 10 (2+2+3+3) setae and ZVI (Kamanli et al., 2018: fig. 49A) increased with 12 (2+2+4+4). Whether this increase in basis setation for the first maxilliped is a characteristic of some grapsoid taxa only remains uncertain. Furthermore, for the two grapsoids mentioned here, the setation of the basis was an accumulative character which was offset, terminally delayed, and constant for other taxa treated in this study.

The basial setation in majoids is conservative and as follows: *Macrocheira kaempferi* with 10 (2+2+3+3) (Clark & Webber, 1991: fig. 4a, b); *Pisa armata* with 10 (2+2+3+3); (Ingle & Clark, 1980: fig. 3b, e); *Libinia spinosa* with 10 (2+2+3+3) (Clark et al., 1998b: fig. 12); *Maja brachydactyla* with 9 (2+2+2+3) (as *M. squinado* by Clark, 1986: fig. 5A, B); and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* with 9 (2+2+2+3) (Clark, 1980: fig. 10a, d). When compared with *M. kaempferi*, *P. armata*, and *Libinia spinosa*, the third row is reduced from 3 to 2 setae in *Maja* and *Inachus*, with one of the setae being offset, and this is considered to be the derived condition.

Endopod articulation (Fig. 267c–f): The endopod of the first maxilliped comprises 5 articles and, according to Rice (1980), the ancestral condition in ZI higher Brachyura was for these 5 articles to carry 3,2,1,2,5 setae, respectively. For the present study, however, this setal pattern was divided into additional distinct characters.

Ischium (Fig. 267c, d): Endopod article 1 possessed 3, 2, or 1 setae; ancestral to derived, respectively. To date, these setae appear to be conservative throughout zoeal development; in *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: figs. 11, 18), *Nanocassiope granulipes* (Ko & Clark, 2002: fig. 8), *N. melanodactylus* (Dornelas et al., 2004: fig. 9), and *Pilumnus hirtellus* (Clark, 2005: fig. 8; 2007), all with 3 setae (Fig. 267c); *Charybdis helleri* (Dineen et al., 2001: figs. 14, 15a, b), 2 setae (Fig. 267d); and for *Geograpsus lividus* (Cuesta et al., 2011: fig. 4A–C), 1 seta. Perhaps this character should have been scored for the onset/offset of a seta, but out of the 3 setae, it was not possible to establish with confidence exactly which seta was delayed or expressed. These setae are phylogenetically informative between higher taxa and loss was considered to be the derived state.

Merus, medial ventral setae (Fig. 267c, d): Within the present study, the ventral setation of the second endopodal article appeared to remain conservative throughout zoeal development with only 2 setae being recorded, and therefore appeared to provide no phylogenetic information within the taxa studied. This was also the situation in the majoids *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 4a, b), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 5A, B), *Pisa armata* (Ingle & Clark, 1980: fig. 3b, e), *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 10a, d), and *Libinia spinosa* (Clark et al., 1998b: fig. 12).

Merus, distal dorsal seta (Fig. 268a, b): The dorsal setation of the second endopodal article was an accumulative character in some grapsoid species and its onset was accelerated with abbreviated development. In the zoeal development of *Eriocheir sinensis* (Kim & Hwang, 1995: figs. 1H, 2H, 3H, 4H, 5H; Montú et al., 1996: fig. 10), a single dorsal seta was onset in ZV and ZIII, respectively. Although their figures and accounts are inconsistent, Kamanli et al. (2018: figs. 6A, D, 13A, B, 20C) confirmed that the dorsal seta was offset in ZI–ZIII) but expressed in ZIV–ZVI (Kamanli et al., 2018: figs. 29A–C, 39C, D, 49B). In *Cyrtograpsus affinis* (Spivak & Cuesta, 2000: fig. 7D) with 5 zoeal stages, the dorsal seta was expressed in ZIV; *Perisesarma fasciatum* (Lanchester, 1900) (Guerao et al., 2004: fig. 9b) with 4 zoeal stages, in ZIII; and *Armases miersii* (Rathbun, 1897) (Cuesta et al., 1999: fig. 8C) with 2 zoeal stages, in ZII. For the majoid zoeas treated in the present study, e.g., *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 4a, b), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 5A, B), *Pisa armata* (Ingle & Clark, 1980: fig. 3b, e), *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 10a, d), and *Libinia spinosa* (Clark et al., 1998b: fig. 12), this distal dorsal seta was conservative and, being absent (offset and terminally delayed) during development, was considered to be the derived condition.

Carpus, ventral seta (Fig. 267e, f): According to Rice (1980), the ancestral condition in ZI higher Brachyura was for article 3 to possess 1 seta and this was the normal condition with regard to this present study. In *Charybdis helleri* (Dineen et al., 2001: figs. 14, 15a, b), however, with 6 zoeal stages, this seta was an accumulative character, offset in ZI–ZIII (Fig. 267e), onset in ZIV–ZVI. For ZI, the offset of a seta on this article was regarded as ancestral. This is in contrast to the polybine, *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 5) with 5 zoeal stages, in which this seta was onset throughout zoeal development and typically conservative as was the situation. This was also the situation for all the majoid species reported for the present study; *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 4a, b), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 5A, B), *Pisa armata* (Ingle & Clark, 1980: fig. 3b, e), *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 10a, d), and *Libinia spinosa* (Clark et al., 1998b: fig. 12).

Carpus, distal dorsal seta (Fig. 268a, b): An accumulative character on article 3 in some grapsoid species with its onset accelerated when associated with abbreviated development. In *Eriocheir sinensis* (Kim & Hwang, 1995: figs. 1H, 2H, 3H, 4H, 5H; Montú et al., 1996: fig. 10), an additional dorsal seta was expressed from ZIII. Although their accounts of *E. sinensis* zoeal development were not compatible, Kamanli et al. (2018) can confirm that this seta was offset in ZI–ZII (Kamanli et al., 2018: figs. 6D, 13B) and onset in ZIII–ZVI (Kamanli et al., 2018: figs. 20C, 29A–C, 39C, D, 49B); *Cyrtograpsus affinis* (Spivak & Cuesta, 2000: fig. 7C) with 5 zoeal stages, this seta was onset in ZIII; *Perisesarma fasciatum* (Guerao et al., 2004: fig. 9b) with 4 zoeal stages, in ZIII; and *Armases miersii* (Cuesta et al., 1999: fig. 8C) with 2 zoeal stages, in ZII. For the zoeas treated in the present study and the majoids *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 4a, b), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 5A, B), *Pisa armata* (Ingle & Clark, 1980: fig. 3b, e), *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 10a, d), and *Libinia spinosa* (Clark et al., 1998b: fig. 12), this distal dorsal seta on endopodal article 3 was conservative and, being absent (offset and terminally delayed) during development, was considered to be the derived condition.

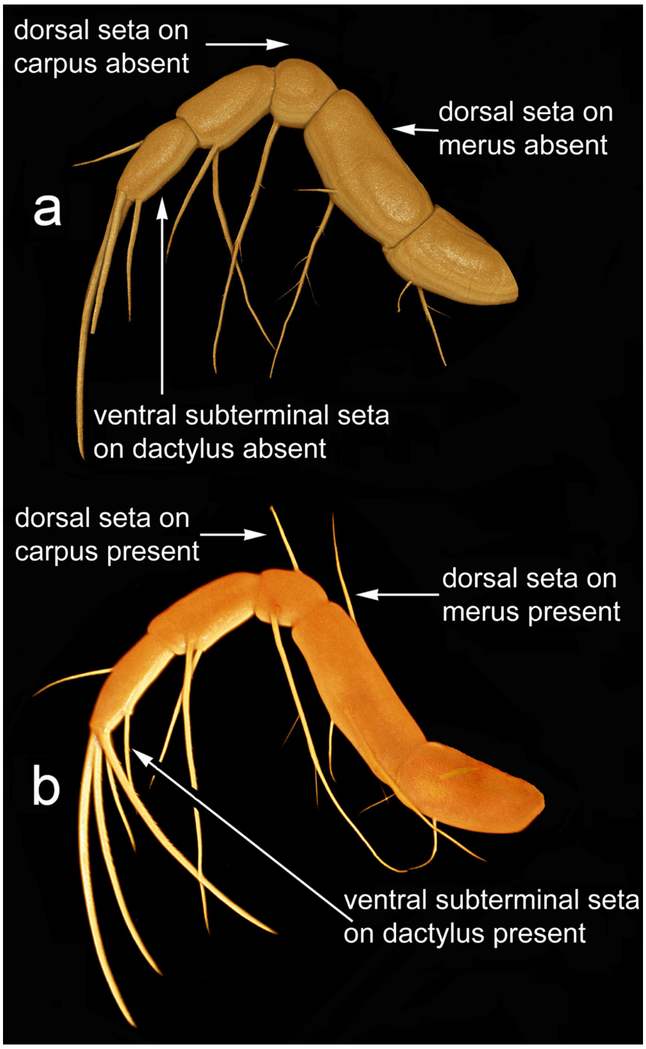

Fig. 268. First maxilliped: *Eriocheir sinensis* H. Milne Edwards, 1853, showing dorsal setation of merus and carpus, and ventral subterminal seta of dactylus: a, ZII; b, ZV. Confocal laser scanning microscopy images courtesy of Seyit A. Kamanli.

Propodus (Fig. 268a, b): Two distal ventral setae on article 4 appeared to be typical for a wide range of taxa, especially those described for the present study, conservative in zoeal development and appear to provide little phylogenetic information.

Dactylus (Fig. 268a, b): Two characters were considered on article 5. For all ZI stages described for the present study and the majoids *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 4a, b), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 5A, B), *P. armata* (Ingle & Clark, 1980: fig. 3b, e), *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 10a, d), and *Libinia spinosa* (Clark et al., 1998b:, fig. 12), this terminal article possessed 1 subterminal dorsal seta and 4 terminal setae. Although this setation pattern remained conservative throughout zoeal development, an additional subterminal ventral setae may be onset in later zoeal stages and these were considered to be accumulative.

Subterminal ventral setae on article 5 (Fig. 268b): In *Geograpsus lividus* (Cuesta et al., 2011: 230–233, fig. 4B, C), accumulative subterminal ventral setae were onset in subsequent moults, 1 in ZIV; 2 in ZV; 3 in ZVI; 4 in ZVII. For *Charybdis helleri* (Dineen et al., 2001: figs. 14d, 15a, b) with 6 zoeal stages, 1 in ZIV; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 5D) with 5 zoeal stages, 1 in ZIV; *Pseudocarcinus gigas* (Gardner & Quintana, 1998: fig. 7a) with 5 zoeal stages, 1 in ZIII; *Goneplax rhomboides* (Linnaeus, 1758) (Ingle & Clark, 1983: fig. 5a, b), *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 18), *N. granulipes* (Ko & Clark, 2002: fig. 8c, d) and *N. melanodactylus* (Dornelas et al., 2004: fig. 9C, D) and *Pilumnus hirtellus* (Clark, 2005: fig. 8; 2007: fig. 444c, d), all with 4 zoeal stages, 1 in ZIII; and *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 8c) with 3 zoeal stages, 1 in ZIII. When compared with *Geograpsus lividus* development, the last 3 subterminal ventral setae were offset and terminally delayed, and the onset of the first subterminal ventral seta was accelerated in association with abbreviated zoeal development.

In the pilumnines *P. kempi* (Fig. 84a, b) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 8), and majoids *Pisa armata* (Ingle & Clark, 1980: fig. 3b, e), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 5A, B), *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 4a, b), *Libinia spinosa* (Clark et al., 1998b: fig. 12), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 10a, d), all with 2 zoeal stages, these subterminal ventral setae were offset and terminally delayed.

Exopod. (Fig. 269): The exopod has been illustrated as incompletely bi-articulated, as in the majoid *Hyas* (Christiansen, 1973: fig. 10A, B; Pohle, 1991: fig. 3K, L; Fig. 269a, b, respectively), or unarticulate, as in the pinnotheroids *Dissodactylus* and *Clypeasterophilus* (Pohle, 1994: fig. 1J, K; Marques & Pohle, 1996: fig. 1J, K; Fig. 269c). It is a character that needs to be carefully checked because during preservation of live zoeae, the larvae can absorb the preservative causing the exopod to swell and open the joint, giving the impression of incomplete articulation or no articulation at all as in Pohle (1994: fig. 1J, K) and Marques & Pohle (1996: fig. 1J, K; Fig. 269). According to Boxshall (2004), it is possible to identify differences between “true segments” (here articles) and annulations combining external morphology and internal anatomic data. “True segments” are characterised by the presence of intrinsic muscles attached to the proximal and distal joint of the article. Annulations, however, are devoid of intrinsic muscature, instead the muscle band passess through the joints and not inserting on them. With respect to the second maxilliped exopod, there appears to be a set of muscle bands in the distal and proximal part of the exopod suggesting two articles (Fig. 269d).

The number of terminal natatory setae on the distal exopod article was an accumulative character but did not provide any phylogenetic information. More importantly, however, the setation of the first and second maxilliped distal exopod article helps define each zoeal stage. For example, the setation of the terminal exopod articulation for the first and second maxilliped is normally 4 in ZI; 6 in ZII; 8 in ZIII; 10 in ZIV; 12 in ZV and 14 in ZIV. In reality, however,

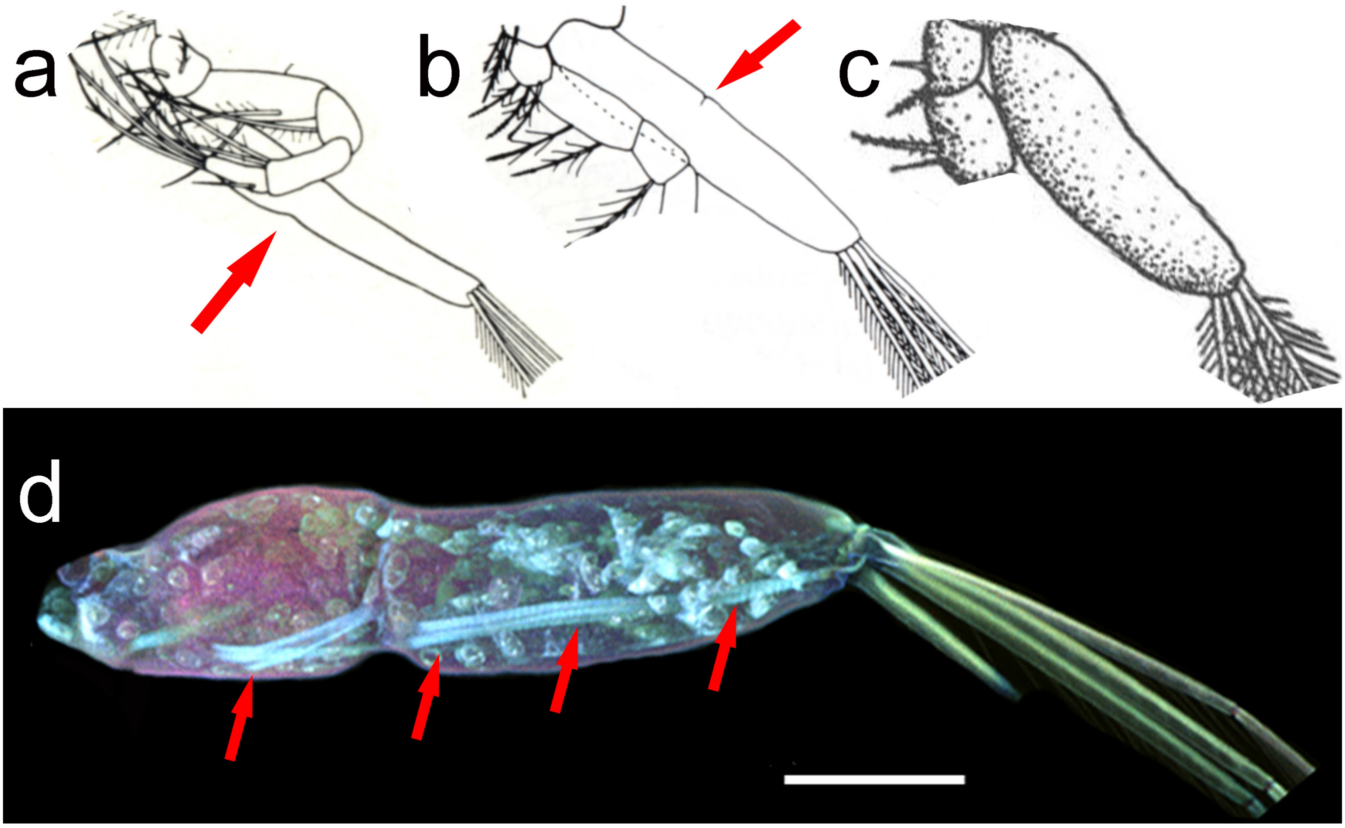

Fig. 269. First maxilliped: ZI; exopods: a, exopod articulation (joint) arrowed, of *Hyas coarctatus* Leach, 1816 by Christiansen (1973: fig. 10b) with 2 articles; b, exopod articulation (joint) arrowed, of *Hyas coarctatus alutaceus* Brandt, 1851 (now *Hyas alutaceus* J.F. Brandt in Middendorf, 1851) by Pohle (1991: fig. 3k) with 2 articles; c, exopod of *Clypeasterophilus stebbingi* (Rathbun, 1918) by Marques & Pohle (1996: fig. 1j) with only 1 article; d, confocal image of muscle bands (arrowed) of *Eriocheir sinensis*; the specimen prepared as undigested and stained with Congo red and acid fuschin. Scale bar = 50 µm. Confocal laser scanning microscopy image courtesy of Seyit Ali Kamanli.

the numbers of these natatory setae can vary in latter zoeal stages, e.g., first maxilliped, 4 in ZI; 6 in ZII; 8 in ZIII and 9 in ZIV in *N. melanodactylus* (Dornelas et al., 2004: 520, 258, 259, fig. 9A–D, respectively). For *Geryon tridens* [now *G. trispinosus* (Herbst, 1803)] first maxilliped, however, the following is recorded: 4 in ZI; 9–10 in ZII; 12–14 in ZIII and 16–17 in ZIV (Ingle, 1979: 220, 221, 223, 225, fig. 6a–d, respectively). A similar situation is reported for *Eriocheir sinensis* first maxilliped natatory setae, 4 in ZI; 6 in ZII; 8 in ZIII; 10 in ZIV; 12–13 in ZV and 14 in ZVI (Kamanli et al., 2018: 6, 9, 12, 15, 15, 20, figs. 6A, E, 13A, D, 20B, 29A, D, 39E, F, 49C, respectively).

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Coxal seta (Fig. 270): None of the zoeae examined during the present study possessed a seta on this article and consequently it was not phylogenetically uninformative. But the expression of this coxal seta may be considered to have been terminally delayed when compared with the development of *Geograpsus lividus* (Cuesta et al., 2011: fig. 5A–C), as a coxal seta was onset in ZVII–ZVIII. Furthermore, this character may have been overlooked in some taxa.

Basial setation (Fig. 270): Current descriptions of the basial setation suggest that this was a conservative character. This setation appeared to be a higher taxon character and the expression of basial setae was shown as an overall loss from 5 to 0 setae (distal to proximal; ancestral to derived) with reference to a number of taxa. Rice (1980) considered a reduction of the basial setation to be the advanced condition.

Basial seta 5 (Fig. 270a): This seta was only described for *Carpilius convexus* and *C. maculatus* (Clark et al., 2005: figs. 4a, 9a, respectively) and its expression was considered to be the ancestral condition. Five (1+1+1+2) setae present.

Basial seta 4 (Fig. 270b): For the taxa described in the present study, seta 5 was offset and seta 4 was present; 4 (1+1+1+1) setae.

Basial seta 3 (Fig. 270c): Basial seta 4 was offset, seta 3 was expressed; 3 (1+1+1) proximal setae as in *Trapezia cymodoce* (Clark & Galil, 1988: fig. 3c), and the majoids, *Pisa armata* (Ingle & Clark, 1980: fig. 4a, b), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 5D, E), *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 4c, d), and *Libinia spinosa* (Clark et al., 1998b: fig. 15).

Basial seta 2 (not figured): The author of the present study was unaware of a brachyuran zoea for which seta 3 was offset with the expression of only 2 proximal setae.

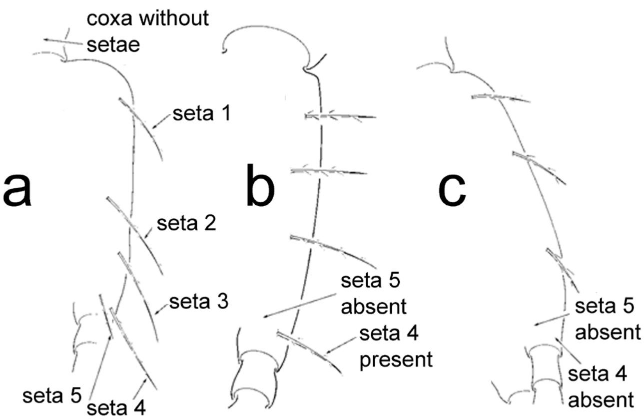

Fig. 270. Second maxilliped: ZI; setation of coxa and basis: a, *Carpilius convexus* (Forskål, 1775); b, *Actaeodes tomentosus* (H. Milne Edwards, 1834); c, *Trapezia cymodoce* (Herbst, 1801).

Basial seta 1 (not figured): Basial seta 2 was offset with the expression of only 1 proximal seta as described for the majoid *I. leptochirus* (Clark, 1980: fig. 10c).

Basial seta 0 (not figured): Basial seta 1 was offset as in the majoids *I. dorsettensis* and *I. phalangium* (Clark, 1980: fig. 10b).

Endopod articulation (Fig. 271): The second maxilliped zoeal endopod is reduced from 5 to 3 articles. It was not possible to determine whether certain articles were lost or fused. Cuesta et al. (2011: fig. 5 unlettered), however, figure details of a "rare" endopod comprising 5 articles. This is considered as an anomaly. According to Rice (1980), the ancestral condition is for these three articles to carry 1, 1, and 4 or 5 setae, respectively, and the reduction of setation to be the advanced condition.

Endopod article 1 (Fig. 271a, b): To date, setation on this article was conservative, with a seta either onset as in *Pilodius pugil* or offset/terminally delayed as in *Menippe nodifrons* and the derived condition.

Endopod article 2 (Fig. 271c, d): To date, setation on this article was conservative with three possible character states; in *H. rotundifrons* (Wear, 1968: figs. 1, 7; Fig. 9a) 2 setae were onset, 2.2 and 2.1. The expression of seta 2.2 (Fig. 271c) was regarded as an autapomorphy but could be the ancestral condition. For the majority of zoeas treated in the present study, seta 2.2 was offset and only seta 2.1 was expressed as in *Atergatis floridus* (Linnaeus, 1767) (Fig. 265d). The author of the present study assumes that seta 2.1 can be offset too and this would be the derived condition; however, he is unaware of an example.

Endopod article 3 (Fig. 271e–i): These setae currently appear to be conservative. From the present, the maximum number of setae expressed on this distal article was 7, numbered 3.1–3.7. Setae 3.1–3.3 were proximal subterminal setae and 3.4–3.7 distal terminal setae. All 7 setae were present in *H. rotundifrons* (Figs. 9b, 271e). Although Rice (1980) regarded the ancestral condition for this article to be 4 or 5 setae, this study reports a reduction from 7 to 4 setae. Rice (1980) considered loss of setae to be the derived condition.

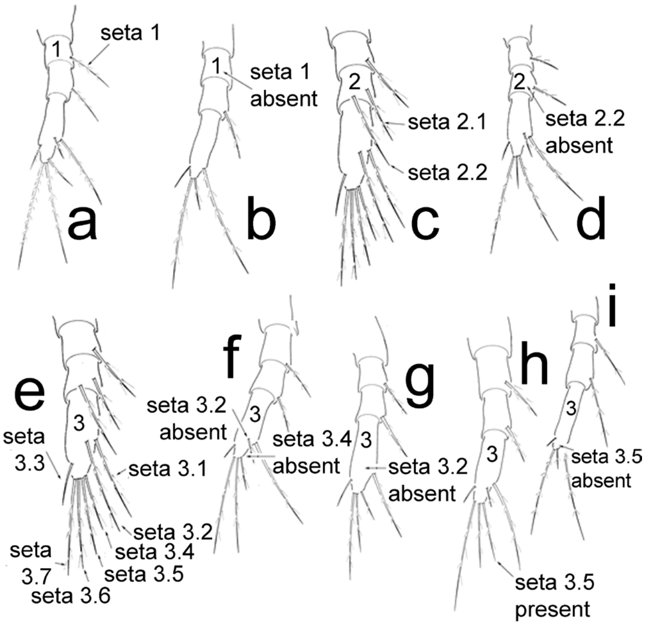

Fig. 271. Second maxilliped: ZI; setation of endopod article 1: a, *Pilodius pugil* Dana, 1852; b, *Menippe nodifrons* Stimpson, 1859; setation of endopod article 2: c, *Heterozius rotundifrons* A. Milne-Edwards, 1867; d, *Atergatis floridus* (Linnaeus, 1767); setation of endopod segment 3: e, *Heterozius rotundifrons* A. Milne-Edwards, 1867; f, *Cymo melanodactylus* Dana, 1853; g, *Dyspanopeus sayi* (Smith, 1869); h, *Actaeodes mutatus* Guinot, 1976; i, *Myomenippe hardwickii* (Gray, 1831).

Subterminal seta 3.2 (Fig. 271e, f): This seta was expressed as in *Cymo melanodactylus* Dana, 1853 (Fig. 271f), or offset as in *Dyspanopeus sayi* (Smith, 1869) (Fig. 271g) and was considered to be derived condition.

Terminal seta 3.4 (Fig. 271e): For the present study, the expression of this seta appeared to be a unique character for *H. rotundifrons* (Figs. 9b, 271e). For all other zoeas examined here, seta 3.4 was offset (Fig. 271e–i), delayed, and considered to be the derived state.

Terminal seta 3.5 (Fig. 271e–h): Seta 3.5 was expressed in *H. rotundifrons* (Fig. 271e), *Cymo melanodactylus* (Fig. 271f), *Dyspanopeus sayi* (Fig. 271g), and *Actaeodes mutatus* Guinot, 1976 (Fig. 271h), but offset in *Myomenippe hardwickii* (Fig. 271i) and was considered to be the derived state.

THIRD MAXILLIPED

Third maxilliped (Fig. 272): During the zoeal phase, the third maxilliped was developmental and non-functional until after the metamorphosis to megalop. It was normally absent in ZI with more than four zoeal stages, i.e., *Pilumnus hirtellus* (Clark, 2005: fig. 10; Fig. 272a–c), and when first expressed in ZII it was simple and biramous (Fig. 272a); ZII was more developed with an epipodal bud present (Fig. 272b) and ZIV was more developed with the presence of an arthrobranch gill (Fig. 272c). In *G. lividus* (Cuesta et al., 2011: fig. 12A) with 8 zoeal stages, the third maxilliped

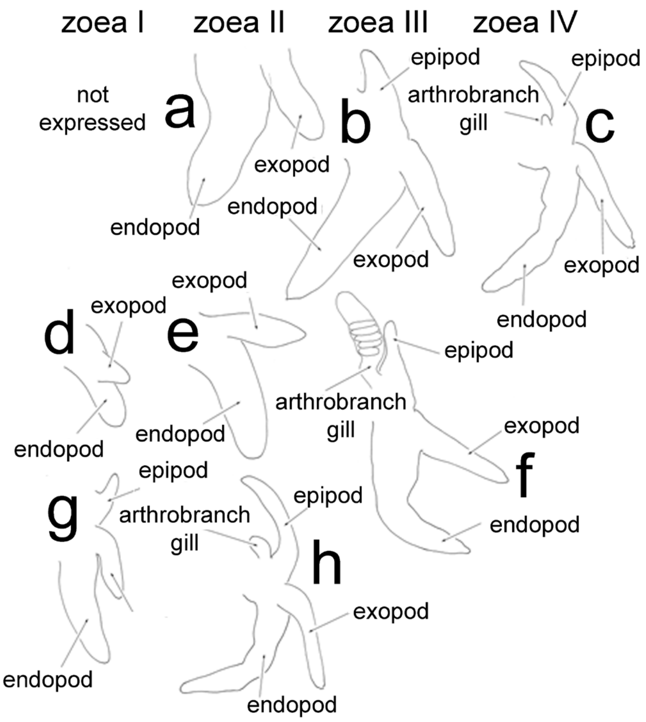

Fig. 272. Third maxilliped: zoeal development; ancestral condition in *Pilumnus hirtellus* (Linnaeus, 1761): a, ZII; b, ZIII; c, ZIV; accelerated development in *Actumnus setifer* (de Haan, 1835): d, ZI; e, ZII; f, ZIII; accelerated development in *P. sluiteri* De Man, 1892: g, ZI; h, ZII; (not drawn to scale).

was expressed in ZVII, and in *Charybdis hellerii* (Dineen et al., 2001: fig. 17b) with 6 zoeal stages, in ZV. The zoeal development of the third maxilliped was compared between *P. hirtellus* (Fig. 272a–c), *Actumnus setifer* (Fig. 270d–f), with 3 zoeal stages, *P. sluiteri* (Fig. 272g, h) and *P. kempi* (Fig. 85b, c), both with 2 zoeal stages. In association with abbreviated development, this appendage exhibited an early (accelerated) onset of growth as a biramous structure including the expression of the epipod and arthrobanch gill. The development of this appendage in majoids may have been overlooked in *Pisa armata* (Ingle & Clark, 1980), *Maja brachydactyla* (as *M. squinado* by Clark, 1986), *Macrocheira kaempferi* (Clark & Webber, 1991), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 10a, d), but was described for *Libinia spinosa* (Clark et al., 1998b: fig. 17a, b). Furthermore, the third maxilliped was expressed in the ZI of *Carpilius convexus*, *C. maculatus* (Clark et al., 2005: figs. 5c, 10c, respectively), *Epiactaea nodulosa* (Fig. 166d), and *Novactaea bella* (Fig. 173c) as a biramous appendage. Rice (1980) refers to the third maxilliped possibly being present as a bud in ZI as the ancestral condition. In comparison, the early onset of the third maxilliped in ZI as a biramous appendage was considered here to be the derived condition.

PEREIOPODS

Pereiopods (not figured): These were developmental appendages being non-functional until the moult to megalop. In brachyuran species with more than 4 zoeal stages, the pereiopods were generally expressed in the last 2 zoeal stages with the cheliped being bilobed. In *Geograpsus lividus* (Cuesta et al., 2011: fig. 13A, B) with 8 zoeal stages, the pereiopods are expressed in ZVII–ZVIII; *Charybdis hellerii* (Dineen et al., 2001: fig. 17d, e) with 6 zoeal stages, in ZV–ZVI; and *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: fig. 16C–H) with 4 zoeal stages, in ZIII–ZIV. In those brachyurans with 3–2 zoeal stages, the pereiopods were expressed early (accelerated) in ZI, i.e., *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 11d–f), *Pilumnus sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 11d, e), *P. kempi* (Fig. 85d, e), and *Libina spinosa* (Clark et al., 1998b: fig. 19d, e). Furthermore, the pereiopods were expressed in the ZI of *Carpilius convexus*, *C. maculatus* (Clark et al., 2005: figs. 3d, 8d, respectively), *E. nodulosa* (Fig. 158d), and *N. bella* (Fig. 167d). A bilobed chela was reported in majoid ZIs including *Macrocheira kaempferi* (Clark & Webber, 1991: 1266), *Maja brachydactyla* (as *M. squinado* by Clark, 1986: 827); *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 10f, g), and *Libinia spinosa* (Clark et al., 1998b: fig. 19d). This was considered to be the derived condition; however, the presence of a bilobed chela in *Pisa armata* ZI (Ingle & Clark, 1980: fig. 3b, e) does require clarification for this species. Rice (1980) refers to the pereiopods possibly being present as a bud in ZI as the ancestral condition. The early onset of the pereiopods in ZI with a bilobed chela was considered here to be the derived condition.

PLEON

Ornamentation of the pleon (Fig. 273a, b): The ornamentation of the pleon was a descriptive character as in *C. convexus* and *C. maculatus* (Clark et al., 2005: figs. 5, 10, respectively; Fig. 273a), and *Rhabdonotus pictus* (Fig. 273b), and probably other brachyuran zoeas. Such ornamentation appears to be a novelty and its phylogenetic significance is unclear.

Pleomere 1. Dorsolateral process: This process has not been described on pleomere 1 of brachyuran zoea.

Dorsomedial setation (Figs. 273a, 274a, b, 276b): Dorsomedial setae were normally accumulative in zoeal development as in *Geograpsus lividus* (Cuesta et al., 2011: figs. 14, 15), 0 setae in ZI, 1 in ZII, 2 in ZIII, 3 in ZIV, 3 in ZV, 5 in ZVI, 7 in ZVII, and 12 in ZVIII; *Charybdis helleri* (Dineen et al., 2001: figs. 18, 19), 0 in ZI, 0 in ZII, 1 in ZIII (expression of an additional seta was delayed when compared with *G. lividus*), 2 in ZIV (expression of an additional seta was delayed when compared with *G. lividus*), 3 in ZV, and 5 in ZVI. Note that when compared to *G. lividus*, there is a subsequent offset and terminal delay of 7 setae in ZVII and 12 in ZVIII in *C. helleri*. *Nanocassiope melanodactylus* (Dornelas et al., 2004: figs. 11, 12), 0 in ZI, 1 in ZII, 2 in ZIII, and 3 in ZIV; *Pilumnus hirtellus* (Clark, 2005: figs. 12–14; 2007: figs. 448–450), 0 in ZI, 0 in ZII, 2 in ZII,I and 4 in ZIV which compares with the pilumnine, *A. setifer* (Clark & P.K.L. Ng, 2004b: figs. 13, 14), 0 in ZI, 3 in ZII, 3 in ZIII in which the onset of 3 setae is early (accelerated). Four medial setae were described for the ZI of *C. convexus* and *C. maculatus* (Clark et al., 2005: figs. 5, 10, respectively) and demonstrated an accelerated onset for this character.

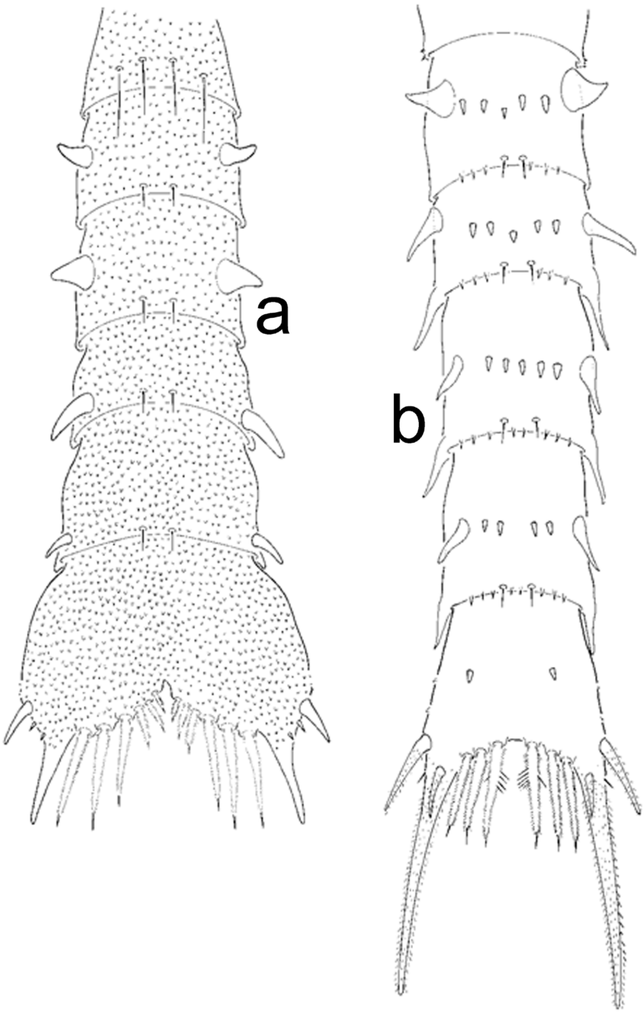

Fig. 273. Pleon and telson: ZI; ornamentation: a, *Carpilius maculatus* (Linnaeus, 1758); b, *Rhabdonotus pictus* A. Milne-Edwards, 1879.

An abbreviated zoeal development of only two stages showed further accelerated development of the medial setae on pleon somite 1. *Pilumnus kempi* 0 in ZI, 5 in ZII (Figs. 86, 87); *P. sluiteri* (Clark & P.K.L. Ng, 2004a: figs. 13, 14) 1 in ZI (early onset) and 3 in ZII (terminal delay of a pair of outer setae). Within the majoids, another developmental pattern was observed for pleomere 1 setation; *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 5) 2 in ZI and 5 in ZII; *Maja brachydactylus* (as *M. squinado* by Clark, 1986: fig. 6A–D) 2 in ZI, 3 in ZII; *Libinia spinosa* (Clark et al., 1998b: figs. 24, 25) 2 in ZI, 3 in ZII; *Pisa armata* (Ingle & Clark, 1980: fig. 5a, b, g, h) 2 in ZI, 2 in ZII; and *I. dorsettensis*, *I. phalangium* and *I. leptochirus* (Clark, 1980: fig. 11) all with 0 in ZI and 0 in ZII, showing the derived condition with offset and terminal delay of medial setae.

<u>Posteromarginal seta</u> (Fig. 274a): This seta on the dorsal margin of pleomere 1 was, to date, only described for pilumnid zoeae and demonstrates accelerated onset associated with abbreviated development. In *Pilumnus hirtellus* (Clark, 2005: figs. 12–14; 2007: figs. 448–450) the single posteromarginal seta was absent in ZI–ZII but expressed in ZIII–ZIV and considered to be the ancestral condition. For *A. setifer* (Clark & P.K.L. Ng, 2004b: figs. 13, 14) its onset was accelerated, 0 in ZI, 1 in ZII–ZIII; in *P. kempi* (Figs.

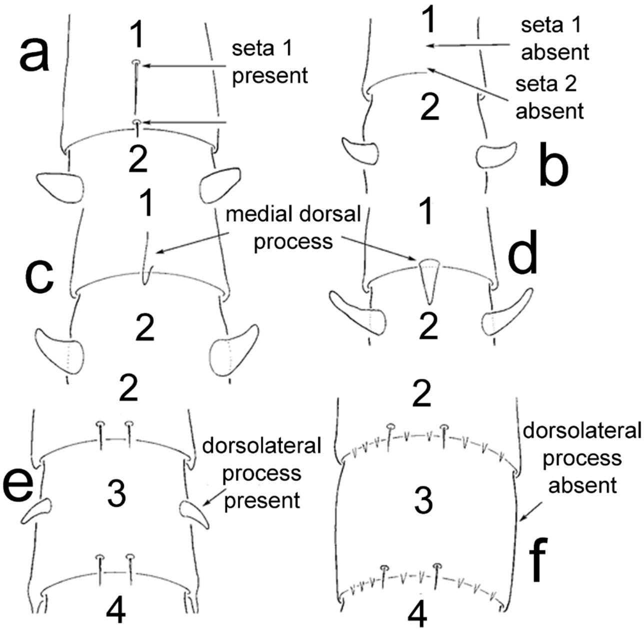

Fig. 274. Pleon: ZI; setation on pleomere 1: a, *Pilumnus sluiteri* De Man, 1892; b, *Banareia subglobosa* (Stimpson, 1858); medial process on pleomere 1: c, *Ozius truncatus* H. Milne Edwards, 1834; d, *Quadrella maculosa* Alcock, 1898; dorsolateral process on pleomere 3: e, *Cymo lanatopodus* Galil & Vannini, 1990; f, *Tanaocheles bidentata* (Nobili, 1901).

86b, 87b) 0 in ZI and 1 in ZII; and in *P. sluiteri* (Clark & P.K.L. Ng, 2004a: figs. 13, 14) 1 in Z1 and 1 in ZII. For the latter, the onset of this seta in ZI was accelerated and regarded as the derived condition.

<u>Dorsomedial process</u> (Fig. 274c, d): A dorsomedial process was only present on somite 1 of ZI in *Ozius truncatus* (Fig. 46) and two species of *Quadrella* (Clark & P.K.L. Ng, 2006: figs. 10, 14). These dorsal medial processes were not regarded as homologous but considered to be an evolutionary novelty in both taxa.

Pleomere 2. <u>Dorsolateral process</u> (Fig. 274a–d): Rice (1980) considered that a reduction in the number of abdominal (pleon) somites (pleomeres) carrying dorso-lateral knobs (dorsolateral process) was an advanced feature. Within the taxa treated for the present study, the dorsolateral process on pleomere 2 was always expressed, it was a conservative character and without phylogenetic information.

<u>Dorsomedial setae</u> (not figured): This was an accumulative character comprising the expression of a pair of setae in later zoeal stages and the onset was accelerated with abbreviated development including terminal delay. A pair of dorsomedial setae was expressed in *Geograpsus lividus* (Cuesta et al., 2011: fig. 15D) with 8 zoeal stages, in ZVIII; *Charybdis helleri* (Dineen et al., 2001: figs. 19a–c, 21a–c) with 6 zoeal stages, in ZIV–ZVI; *Liocarcinus navigator* (as *L. arcuatus*; Clark, 1984: figs. 7E, 8E) with 5 zoeal stages, in ZV; with 4 zoeal stages, *Geryon longipes* (Guerao et al., 1996: fig. 4C, D) in ZIII–ZIV and *G. trispinosus* (Ingle, 1991: 227, fig. 2.28g), in ZIV; and the majoids with 2 zoeal stages, *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig.

6C, D), *Pisa armata* (Ingle & Clark, 1980: fig. 5b) and *Libinia spinosa* (Clark et al., 1998b: figs. 24b, 25b). This pair of dorsomedial setae was offset and terminally delayed in other taxa treated for this study and considered to be the derived condition.

Posterodorsal marginal setae (Figs. 273, 274): This was a conservative character and present in all taxa treated for the present study.

Pleomere 3. Dorsolateral process (Fig. 274e, f): This process was a conservative character being either present or absent. The dorsal lateral process was present on the pleomere 3 for most ZI examined, as in *Cymo lanatopodus* Galil & Vannini, 1990 (Figs. 189, 274e), but was absent in *Tanaocheles bidentatus* (Nobili, 1901) (Fig. 274f). The dorsolateral process on pleomere 3 of *Q. serenei* Galil, 1986 (Fig. 277c) was longer than in other species studied, but the phylogenetic significance of this increased length is unknown. This character was present in *Geograpsus lividus* (Cuesta et al., 2011: figs. 14, 15); *Charybdis helleri* (Dineen et al., 2001: figs. 18, 19); *N. granulipes* (Ko & Clark, 2002: figs. 11, 12); *N. melanodactylus* (Dornelas et al., 2004: figs. 11, 12) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: figs. 13, 14) with 2 zoeal stages. In majoids, with 2 zoeal stages, this process is present in *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 5) and *Maja brachydactylus* (as *M. squinado* by Clark, 1986: fig. 6A–D), but absent in *Libinia spinosa* (Clark et al., 1998b: figs. 24, 25), *Pisa armata* (Ingle & Clark, 1980: fig. 5a, b, g, h), and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 11). The presence of the dorsal lateral process on pleomere 3 was considered ancestral and its absence, derived (Rice, 1980).

Dorsomedial setae (not figured): An accumulative character comprising the expression of a pair of setae in later zoeal stages, the onset of which was accelerated when associated with abbreviated development including their offset (terminal delay). A pair of dorsomedial setae was expressed in *Geograpsus lividus* (Cuesta et al., 2011: fig. 15D) with 8 zoeal stages, in ZVIII; *Charybdis helleri* (Dineen et al., 2001: figs. 19a–c, 21a–c) with 6 zoeal stages, in ZIV–ZVI; with 4 zoeal stages, *Geryon longipes* (Guerao et al., 1996: fig. 2C, D) in ZIII–ZIV and *G. trispinosus* (Ingle, 1991: 227, fig. 2.28g) in ZIV.

This pair of dorsomedial setae was offset and terminally delayed in *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: figs. 7E, 8E) with 5 zoeal stages, in ZV, and in other taxa treated in this study and the majoids with 2 zoeal stages. Terminal delay was considered to be the derived condition.

Posterodorsal marginal setae (Figs. 273, 274e, f, 275a, b): This was a conservative character and present in all taxa treated for the present study.

Pleomere 4. Dorsolateral process (Figs. 275a, b, 276): This process was generally a conservative character present in *Geograpsus lividus* (Cuesta et al., 2011: figs. 14, 15); *Pilumnus minutus* (Ko, 1994a: figs. 1A, I, 2A, F, 3A, G, 4A, F); *P. sluiteri* (Clark & P.K.L. Ng, 2004a: figs. 13, 14); *Carpilius convexus* and *C. maculatus* (Fig. 273a; Clark et al., 2005: figs. 5, 10, respectively); *Trapezia cymodoce* (Fig. 275a) and *Q. serenei* (Fig. 277c). The dorsolateral process on somite 4 of *Q. serenei* (Fig. 277c) was longer than in other species studied but the phylogenetic significance of this increased length is unknown. This process was absent in *A. setifer* (Clark & P.K.L. Ng, 2004b: figs. 13, 14) and the majoids, *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 5); *Maja brachydactylus* (as *M. squinado* by Clark, 1986: fig. 6A–D); *Libinia spinosa* (Clark et al., 1998b: figs. 24, 25); *Pisa armata* (Ingle & Clark, 1980: fig. 5a, b, g, h); and *I. dorsettensis*, *I. leptochirus* and *I. phalangium* (Clark, 1980: fig. 11). The presence of the dorsal lateral process on pleomere 4 was considered ancestral and its absence, derived (Rice, 1980).

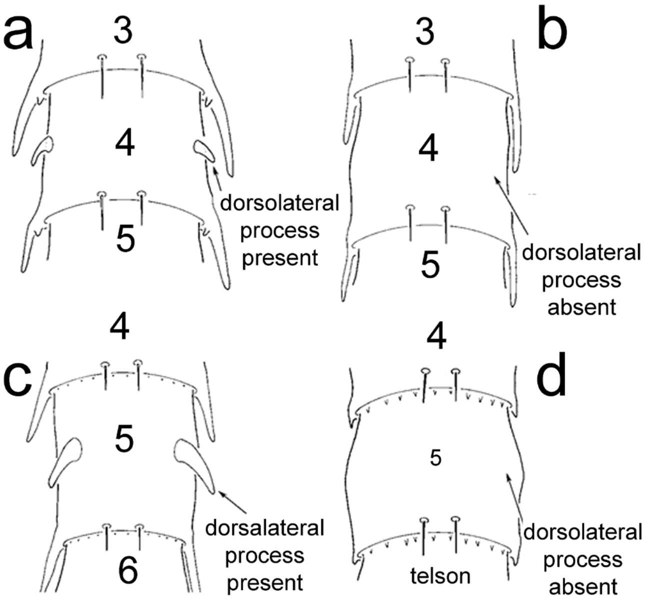

Fig. 275. Pleon: ZI; dorsolateral process on pleomere 4: a, *Trapezia cymodoce* (Herbst, 1801); b, *Monodaeus couchi* (Couch, 1851); dorsolateral process on pleomere 5: c, *Pilumnus sluiteri* De Man, 1892; d, *Actumnus setifer* (De Haan, 1835).

The dorsolateral process on pleomere 4 of *Eriocheir sinensis*, however, was not conservative during zoeal development. According to Kim & Hwang (1995: figs. 1B, 2B, 3B, 4B, 5B), this dorsolateral process was absent in ZII, but these were not the findings of Montú et al. (1996: fig. 14B–F), who figured it as present throughout a 6-stage zoeal development. This character was recently examined by Kamanli et al. (2018: figs. 22A, B, 32A, B, 42A, B, 52A, B) who confirmed that the process was onset from ZII onwards in agreement with Montú et al. (1996: fig. 14B–F).

Dorsomedial setae (not figured): An accumulative character comprising the onset of paired setae. Their expression was onset in later zoeal stages and accelerated in association with abbreviated development including offset and terminal delay. For *G. lividus* (Cuesta et al., 2011: fig. 15D) with 8 zoeal stages, 2 pairs in ZVIII; *Charybdis helleri* (Dineen et al., 2001: figs. 19a–c, 21a–c) with 6 zoeal stages, 1 pair in ZIV–ZVI; with 4 zoeal stages, *Geryon longipes* (Guerao et

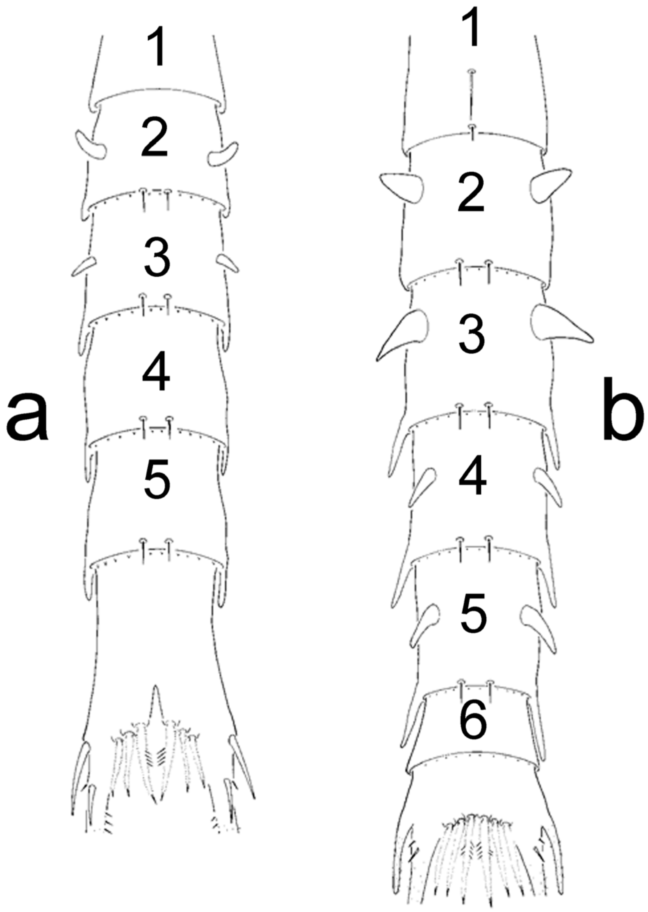

Fig. 276. Pleon: ZI; number of pleomeres: a, *Aniptumnus quadridentatus* (De Man, 1895); b, *Pilumnus sluiteri* De Man, 1892.

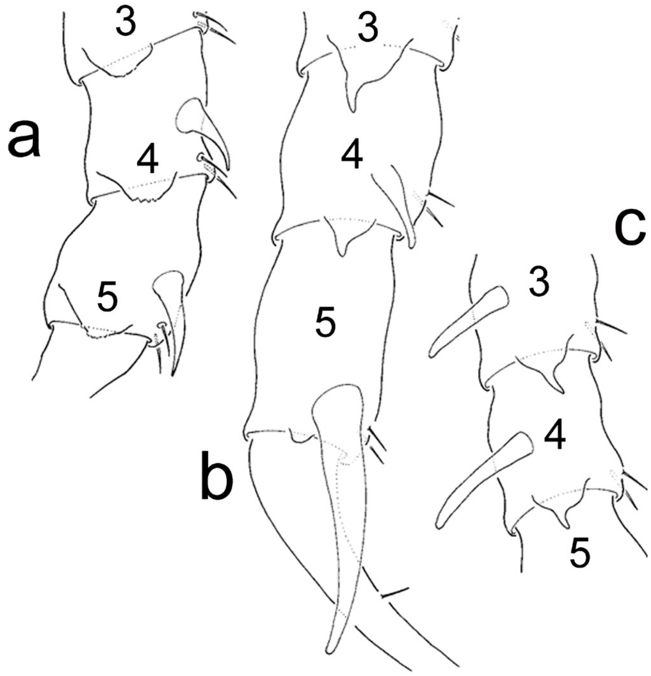

Fig. 277. Pleon: ZI; dorsolateral processes on pleomeres 3–5: a, *Menippe mercenaria* (Say, 1818); b, *Myomenippe hardwickii* (Gray, 1831); c, *Quadrella serenei* Galil, 1986.

al., 1996: fig. 2D) in ZIV and *G. trispinosus* (Ingle, 1991: 227), 1 pair in ZIV.

This pair of dorsomedial setae was offset and terminally delayed in *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: figs. 7E, 8E) and other taxa treated in this study including the majoids.

Posterodorsal marginal setae (Figs. 273, 275, 276): A conservative character, present in all taxa treated for the present study.

Pleomere 5. Dorsolateral process (Fig. 275c, d): A conservative character being either present or absent. It was present in the ZI of *Pilumnus minutus* (Ko, 1994a: figs. 1A, I, 2A, F, 3A, G, 4A, F); *P. sluiteri* (Clark & Ng, 2004a: figs. 13, 14); *Carpilius convexus* and *C. maculatus* (Clark et al., 2005: figs. 5, 10, respectively; Fig. 273a); *Menippe mercenaria* (Say, 1818) (Fig. 277a) and *Myomenippe hardwickii* (Fig. 277b). The dorsolateral process on pleomere 5 of *M. hardwickii* (Figs. 42b, 277b) was longer than in other species studied but the phylogenetic significance of this increase in length was unknown. The presence of the dorsal lateral process was considered ancestral and its absence, derived (Rice, 1980).

With respect to the presence of pleomere dorsolateral processes, the pilumnoids show an interesting transformation series. For the Eumedoninae, *Harrovia albolineata* (Fig. 54), *Zebrida adamsii* White, 1847 (Clark, 2007: fig. 580) and *Permanotus purpureus* (Gordon, 1934) (P.K.L. Ng & Clark, 2001: fig. 8) and the Pilumninae, *Glabropilumnus edamensis* (Fig. 70), *Pilumnus minutus* (Ko, 1994a: figs. 1I, 2F, 3G, 4F), *P. sluiteri* (Clark & P.K.L. Ng, 2004a: figs. 13, 14) and *P. trispinosus* (T. Sakai, 1965) (as *Parapilumnus*; Ko, 1994b: figs. 1I, 2I, 3I, 4I), dorsolateral processes were present on pleomeres 2–5. Dorsolateral processes are present on pleomeres 2–3 for Parapanopinae, *Parapanope euagora* De Man, 1895 (Fig. 50), Eumedoninae, *Echinoecus pentagonus* (A. Milne-Edwards, 1879) (Clark, 2007: fig. 580), and the Pilumninae, *A. elegans* (Fig. 58), *A. setifer* (Clark & P.K.L. Ng, 2004b: figs. 13, 14), *Aniptumnus quadridentatus* (De Man, 1895) (P.K.L. Ng & Clark, 2008: fig. 18), *Eurycarcinus integrifrons* (Fig. 62), *Cryptopilumnus changensis* (Fig. 70), *H. glabra* (Fig. 74), *Heteropilumnus ciliatus* (Stimpson, 1858) (Ko & Yang, 2003: figs. 1A, 2E, 3A, 4F, 5A, 6G), *H. holthuisi* (Fig. 78), *Latopilumnus conicus* P.K.L. Ng & Clark, 2008 (P.K.L. Ng & Clark, 2008: fig. 12), *Pilumnopeus granulata* Balss, 1933 (Ko, 1997: figs. 1I, 2G, 3H, 4G), *Pilumnus hirtellus* (Clark, 2005: figs. 12–14; 2007: figs. 448–450), *P. kempi* (Figs. 86, 87), *P. longicornis* (Clark & Paula, 2003: fig. 36), *P. ohshimai* (Fig. 92), *P. spinifrons* (Fig. 96), and *P. vespertilio* (Clark & Paula, 2003: fig. 40). The derived condition is possessing dorsolateral processes on pleomere 2 only, as described for the Pilumninae, *Benthopanope indica* (Ko, 1995: figs. 1I, 2I, 3I, 4I) and Tanaochelidae, *Tanaocheles bidentata* (P.K.L. Ng & Clark, 2000: fig. 27). Within the pilumnoids, there was a loss of dorsolateral processes from pleomeres distal to proximal with a transformation series 2–5, 2–3 (dorsolateral processes not expressed on pleomeres 5 and 4), to only present on pleomere 2 (dorsolateral processes not expressed on pleomeres 3–5). As of yet, no pilumnoid zoea has been described with dorsolateral processses just on pleomeres 2–4.

Dorsomedial setae (not figured): A developmental character comprising the onset of paired setae. Their expression was onset in latter zoeal stages and accelerated in association with abbreviated development including offset and terminal delay. For *Geograpsus lividus* (Cuesta et al., 2011: fig. 15D) with 8 zoeal stages, 2 pairs of dorsomedial setae expressed in ZVIII; 1 pair is expressed in *Charybdis helleri* (Dineen et al., 2001: figs. 19a–c, 21a–c) with 6 zoeal stages, in ZVI, and *Geryon longipes* (Guerao et al., 1996: fig. 2D) in ZIV and *G. trispinosus* (Ingle, 1991: 227) with 4 zoeal stages, in ZIV.

These paired dorsomedial setae were offset and terminally delayed in *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: figs. 7E, 8E) and other taxa treated in this study including the majoids. Terminal delay was regarded as the derived condition.

Posterodorsal marginal setae (Figs. 273, 275c, d, 276): This was a conservative character and present in all taxa treated for the present study.

Pleomere 6. Differentiation of pleomere 6 (Fig. 274): In species with 4 or more zoeal stages, the differentiation of pleomere 6 occurs in ZIII for *Geograpsus lividus* (Cuesta et al., 2011: fig. 14C), *Charybdis hellerii* (Dineen et al., 2001: fig. 17d, e) and *N. granulipes* (Ko & Clark, 2002: figs. 11c, 12c). The onset of this pleomere division was accelerated in pilumnoid species with less than 4 zoeal stages, i.e., ZII in *A. setifer* (Clark & P.K.L. Ng, 2004b: fig. 13b) with 3 zoeal stages; ZII in *P. kempi* (Figs. 86, 87) and ZI in *P. sluiteri* (Clark & P.K.L. Ng, 2004a: figs. 13a, 14a), both with 2 zoeal stages; and ZII for majoids *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 5b), *Maja brachydactylus* (as *M. squinado* by Clark, 1986: fig. 6C, D), and *Libina spinosa* (Clark et al., 1998b: figs. 24b, 25b). Pleomere 6, however, is not differentiated in the ZII of majoids *I. dorsettensis*, *I. leptochirus* and *I. phalangium*, being offset. The terminal delay of this somite division in *Inachus* was regarded as the derived condition.

The larval development of three Hymenosomatidae species was considered, including *Elamena cimex* Kemp, 1915 (as *Elamena* (*Trigonoplax*) *cimex* by Krishnan & Kannupandi (1988), *Neorhynchoplax kempi* (Chopra & K.N. Das, 1930) (as *Elamenopsis kempi* by Salman & Ali, 1996), and *Hymenosoma orbiculare* Desmarest, 1823 (Dornelas et al., 2003). Their life history is of interest because it is abbreviated with 3 zoeal stages, the last of which metamorphoses directly into the first crab and not a megalop. The megalop phase is absent and offset (Krishnan & Kannupandi, 1988: 219; Salman & Ali, 1996: 414, 412) and is considered to be a derived condition. In addition, the onset/differentiation of pleomere 6 during the zoeal phase is delayed; *Elamena cimex* (as *Elamena* (*T.*) *cimex* by Krishnan & Kannupandi, 1988: 216, 219, figs. 1, 2I, 3I, 3N); *N. kempi* (as *Elamenopsis kempi* by Salman & Ali, 1996: 408, 409, 412, figs. 1a–c, 3a, h, 4a); and *H. orbiculare* (Dornelas et al., 2003: 2581, 2591, figs. 8, 9). This offset of pleomere 6 in the zoeal phase is considered to be a derived condition. There is, however, a little confusion over the demarcation of pleomere 6 in the first crab stage. For *Elamena cimex* (as *Elamena* (*T.*) *cimex*), Krishnan & Kannupandi (1988: 219, fig. 5l, m) describe the abdomen (pleon) with 6 somites (pleomeres). Their figure (Krishnan & Kannupandi, 1988: fig. 5l, m), however, illustrates 5 pleomeres and a telson. Later, Salman & Ali (1996: 415, fig. 6f) described and illustrated the first crab stage of *N. kempi* (as *Elamenopsis kempi*) as "abdomen still with 5 somites". Their figure (Salman & Ali, 1996: fig. 6f) also depicts 5 pleomeres and a telson! According to Guinot (2011: 44), the male and female hymenosomatid pleon never comprises more than 5 pleomeres and always possess a pleotelson, pleomere 6 fused to the telson. Thus, the fusion of additional pleomeres to the pleotelson highlights the pleon sockets of the press-button mechanism which are located at the base of the pleotelson, belonging as usual to pleomere 6. This transfusion of pleomere 6 with the telson to form the pleotelson is unique to the Hymenosomatidae.

Dorsolateral process (not figured): To date, no dorsolateral process has been described on pleomere 6 after its differentiation during zoeal development.

Dorsomedial setae (not figured): To date, dorsomedial setae have not been recorded on pleomere 6.

Posterodorsal marginal setae (not figured): Posterodorsal marginal setae on pleomere 6 were normally conservative, except with respect to *Geograpsus lividus* (Cuesta et al., 2011: figs. 14–17) with 8 zoeal stages, as this character was accumulative. Pleomere 6 was differentiated in ZIII, and the associated paired posterodorsal marginal setae were later onset being expressed in ZVII and ZVIII. In contrast, the onset of these posterodorsal setae was accelerated in *Charybdis helleri* (Dineen et al., 2001: figs. 18c, 19a–c, 20c, 21a–c) with 6 zoeal stages, and expressed in ZIII–ZVI. This character was offset and terminally delayed in the remaining taxa treated in this present study and this was regarded as the derived condition.

Length of dorsolateral processes on pleomeres 3–5 (Fig. 277a–c): The dorsolateral processes on pleomeres 3–5 varied in length. A proportional measurement of the dorsolateral process as a ratio of its pleomere length was considered, but proved too difficult to determine with necessary precision. Length, however, was a good descriptive character, but did not provide useful phylogenetic information.

Posterolateral processes on pleomeres 3–5 (Fig. 278a–f): The posterolateral processes on pleomeres 3–5 varied in length. The typical length of posterolateral processes in *Atergatopsis germaini* A. Milne-Edwards, 1865 (Fig. 278a) was considered to be representative of many first stage zoeae examined. The posterolateral processes of *Cryptopilumnus changensis* (Fig. 278b) and *Pseudocarcinus gigas* (Fig. 278d) were much longer, and those of *Medaeops granulosus* (Fig. 278c) and *Rhithropanopeus harrisii* (Fig.

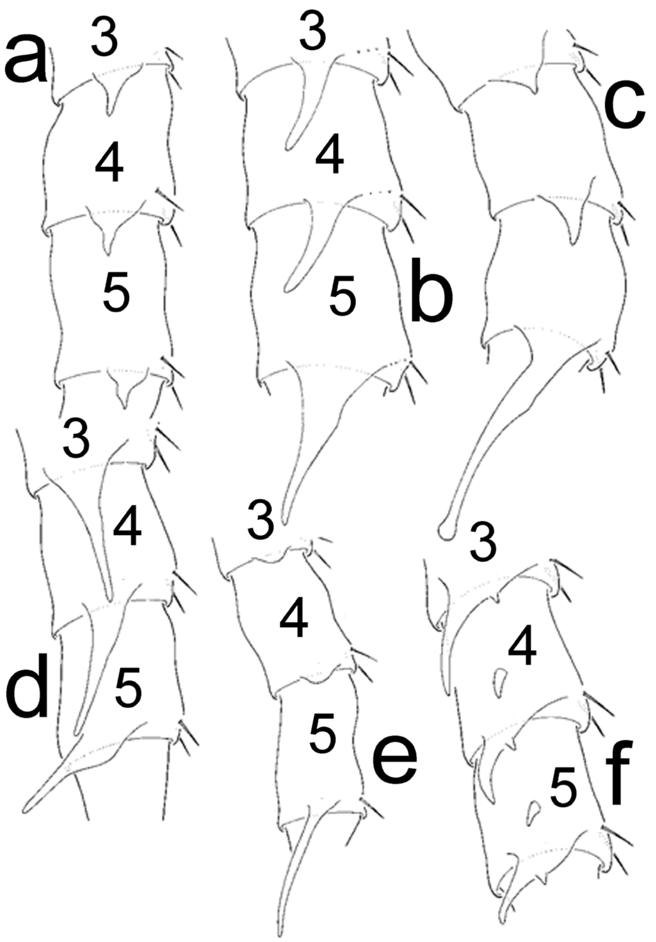

Fig. 278. Pleon: ZI; posterolateral processes on pleomeres 3–5: a, *Atergatopsis germaini* A. Milne-Edwards, 1865; b, *Cryptopilumnus changensis* (Rathbun, 1909); c, *Medaeops granulosus* (Haswell, 1882); d, *Pseudocarcinus gigas* (Lamarck, 1818); e, *Rhithropanopeus harrisii* (Gould, 1841); f, *Trapezia cymodoce* (Herbst, 1801).

278e) were distinctively long on pleomere 5. Although a good descriptive character, length appeared to lack useful phylogenetic information.

Additional characters on posterolateral processes: A diagnostic character of *Trapezia* species appears to be the presence of a tooth (Fig. 278f) on the dorsal margin of the posterolateral processes for pleomeres 3–5. Also diagnostic of *Medaeops granulosus* (Fig. 278c) was a swollen tip on the posterolateral processes of pleomere 5. These two characters were considered to be unique evolutionary novelties and without phylogenetic relevance, but useful descriptive characters.

Pleopods (not figured): A developmental character, being non-functional during the zoeal phase, becoming functional swimming appendages in the megalop phase and, finally, during the crab phase, adapted for reproduction in males and egg attachment in females. During the zoeal phase, their expression is restricted to the last two zoeal stages. Initially they are uniramous, becoming biramous during the moult to the final zoeal stage with the appearance of the endopod. Pleopod onset is accelerated in association with abbreviated development. In *G. lividus* (Cuesta et al., 2011: figs. 16, 17), the pleopods were expressed in ZVII–ZVIII; *Charybdis helleri* (Dineen et al., 2001: figs. 20, 21), in ZV–ZVI; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: fig. 8), in ZIV–ZV; *Pilumnus hirtellus* (Clark, 2005: figs. 12–14; 2007: fig. 450) in ZII–ZIV; *Actumnus setifer* (Clark & P.K.L. Ng, 2004b: fig. 14), in ZII–ZIII; and ZI, ZII in *P. kempi* (Figs. 86, 87) and *P. sluiteri* (Clark & P.K.L. Ng, 2004a: fig. 14). The accelerated expression of pleopods to early stage zoeas (ZVII–ZVIII to ZI–ZII) was regarded as the derived condition. Of interest is the observation that paired pleopods are offset on pleomere 1 during the zoeal (see Fig. 2) and megalop phases but expressed only after the moult to crab phase.

For the majoids with two zoeal stages, rudimentary pleopods are present, but devoid of endopods in ZI and more developed with endopods in ZII.

TELSON

Spinulation of the telson fork (Figs. 273, 279): The naked telson fork of *Xantho incisus* (Fig. 279d) was typical of many first stage zoeae examined, but a spinulated telson fork was characteristic of all pilumnids studied, e.g., *Eurycarcinus natalensis* (Fig. 279b). In contrast, the telson fork of *Q. serenei* (Fig. 279c) was sparsely spinulate; however, in both species of *Carpilius* (Figs. 273a, 279a), the spinulation was restricted to the proximal region and the fork itself was devoid of spines. The homology of these states is equivocal and spinulation was difficult to analyse; these were considered to be only descriptive characters.

Lateral and medial spines. Lateral spine 1 (Figs. 280, 281): The length of the lateral spine 1 varied from minute as in *Acantholobulus schmitti* (Fig. 281a), to long, e.g., *Chaceon fenneri* (Fig. 281e). Precise measurements of lateral spines proved difficult to calculate and spine length was problematic to analyse as a phylogenetic character. Rice (1980), however, regarded the reduction or loss of the outer telson spines as an advanced feature. The shape of lateral spine 1 also varied from being well defined as in *Eurycarcinus integrifrons* (Fig. 281f) to being seta-like as in *Gaillardiellus orientalis* (Fig. 281g). Shape and length were continuously variable between taxa and proved difficult to use phylogenetically, but were suitable as descriptive characters. Consequently, lateral spine 1 can probably only be realistically accessed as present or absent as in *Ozius truncatus* (Fig. 280d) and *Hexapanopeus paulensis* Rathbun, 1930 (Fig. 280e), with loss being considered the derived character.

Lateral spine 2 (Figs. 279, 280, 281): Lateral spine 2 was typically shorter than lateral spine 1, except *Q. maculosa* (Fig. 280a) for example, and it too varied in length and shape, being strong in *Carpilius convexus* (Figs. 279a, 280d) but fine and seta-like in *Gaillardiellus orientalis* (Fig. 281g) and *Parapanope euagora* (Fig. 281h). Phylogenetic interpretation of length and shape characters was difficult and probably not informative, consequently this character could only be recorded as present, vestigial, or absent as in *O. truncatus* (Fig. 280d) and *Hexapanopeus paulensis* (Fig. 280e). Absent was considered to be the derived condition.

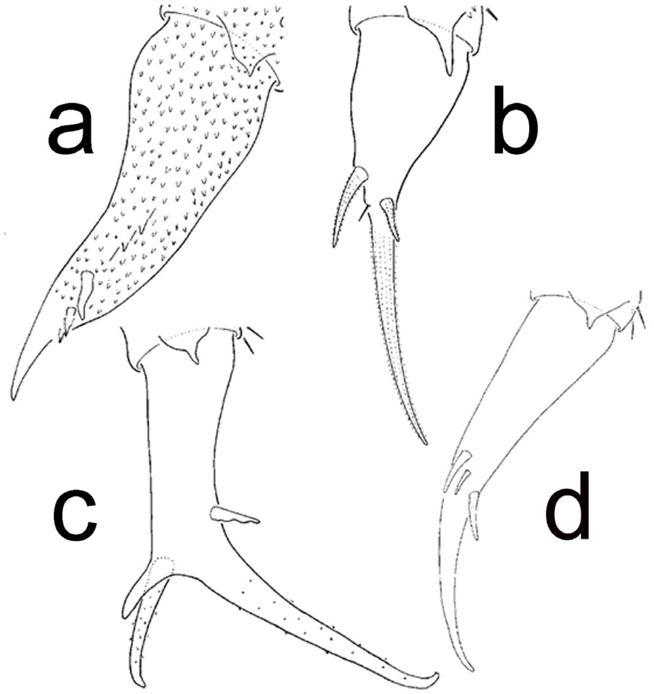

Fig. 279. Telson forks: ZI; a, *Carpilius convexus* (Forskål, 1775); b, *Eurycarcinus natalensis* (Krauss, 1843); c, *Quadrella serenei* Galil, 1986; d, *Xantho incisus* Leach, 1814.

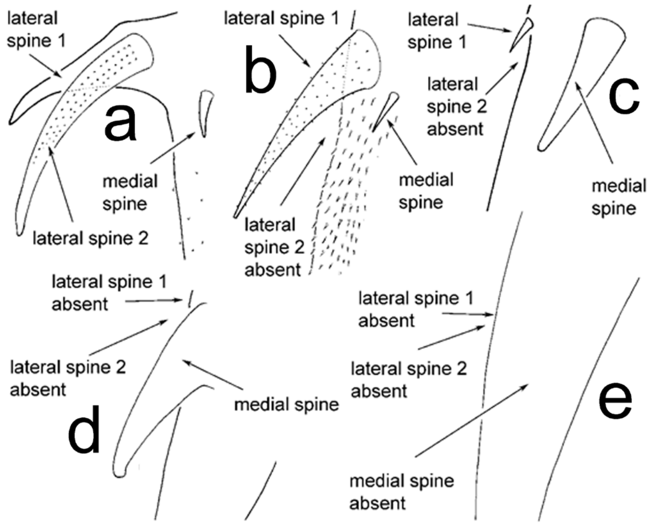

Fig. 280. Telson: ZI; lateral and medial spines: a, *Quadrella maculosa* Alcock, 1898; b, *Tanaocheles bidentata* (Nobili, 1901); c, *Rhinolambrus pelagicus* (Rüppell, 1830); d, *Ozius truncatus* H. Milne Edwards, 1834; e, *Hexapanopeus paulensis* Rathbun, 1930.

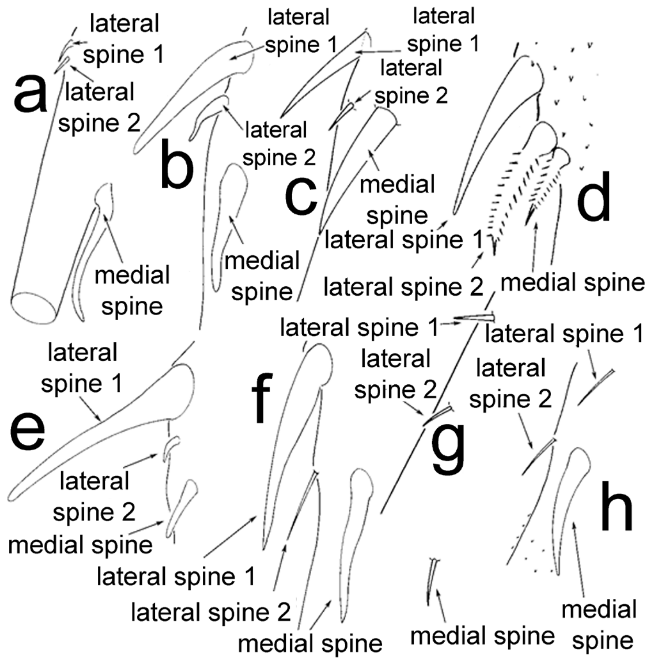

Fig. 281. Telson: ZI; lateral and medial spines: a, *Acantholobulus schmitti* (Rathbun, 1930); b, *Actaeodes mutatus* Guinot, 1976; c, *Actaeodes hirsutissimus* (Rüppell, 1830); d, *Carpilius convexus* (Forskål, 1775); e, *Chaceon fenneri* (Manning & Holthuis, 1984); f, *Eurycarcinus integrifrons* De Man, 1879; g, *Gaillardiellus orientalis* (Odhner, 1925); h, *Parapanope euagora* De Man, 1895.

Dorsomedial spine (Figs. 273, 280, 281): This character varied with regard to length, shape, and position. The medial spines of *Acantholobulus schmitti* (Fig. 281a) and *Eurycarcinus integrifrons* were relatively long while those of *Q. maculosa* (Fig. 280a) and *Carpilius convexus* (Fig. 281d) were comparatively short. The medial spine was well defined in *Ozius truncatus* (Fig. 280d) and *R. pelagicus* (Fig. 280c), but seta-like as in *G. orientalis* (Fig. 281g). The position of the dorsomedial spine appeared variable; typically [as in *Actaeodes mutatus* (Fig. 281b), *A. hirsutissimus* (Fig. 281c), *Chaceon fenneri* (Fig. 281e), *E. integrifrons* (Fig. 281f), *G. orientalis* (Fig. 281g), and *Parapanope euagora* (Fig. 281h)] this spine was located posterior to the lateral spines, in a dorsomedial position on the fork, but in *Acantholobulus schmitti* (Fig. 281a) it was positioned on the inner margin of the telson fork, i.e., lying lateral and not medial. In *Carpilius convexus* (Figs. 279a, 281d) and *C. maculatus* (Fig. 273a), this spine was positioned close to the second lateral spine and appeared to be more lateral than dorsomedial on the fork. This spine in *Tanaocheles bidentata* (Fig. 280b) was close to lateral spine 1, but still medial and dorsal. These characters involving length, shape, and position for the dorsomedial spine were difficult to analyse phylogenetically. Therefore, the character was scored in terms of presence, vestigial state, and absence. The presence of a developed dorsomedial spine was considered ancestral and its absence, derived.

Dorsal medial setae (not figured): This was an accumulative character comprising the onset of a pair of setae. Their expression was normally onset in later zoeal stages and accelerated with abbreviated development including terminal delay. This character was expressed in *Geograpsus lividus* (Cuesta et al., 2011: fig. 15) with 8 zoeal stages, in ZVIII; *Charybdis helleri* (Dineen et al., 2001: figs. 19b, c, 21b, c, 23b, c) with 6 zoeal stages, in ZV, ZVI; *Eriocheir sinensis* (Montú et al., 1996: fig. 14F; Kamanli et al., 2018: fig. 42D) with 6 zoeal stages, in ZVI; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: figs. 7E, 8E, 9E) with 5 zoeal stages, in ZV; in ZIV for *N. granulipes* (Ko & Clark, 2002: figs. 11d, 13d), *N. melanodactylus* (Dornelas et al., 2004: figs. 11D, 12D, 13D), *Pilumnus hirtellus* (Clark, 2005: figs. 12–15; 2007: figs. 449b, 450d, 451d), *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: figs. 17G, 20M), all with 4 zoeal stages; and *Actumnus setifer* (Clark & P.K.L. Ng, 2004b: figs. 13c, 14c, 17c) with 3 zoeal stages, in ZIII.

This pair of dorsal setae was offset and terminally delayed prior to the metamorphosis to megalop in *Pilumnus sluiteri* (Clark & P.K.L. Ng, 2004a: figs. 13b, 14b, 17b), *P. kempi* (Figs. 86b, 88g), and the majoids, *Pisa armata* (Ingle & Clark, 1980: fig. 5b, h, f); *Maja brachydactyla* (as *M. squinado* by Clark, 1986: fig. 6C, D, F); *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 5b); *Libinia spinosa* (Clark et al., 1998b: figs. 24b, 25b, 30b); *I. phalangium* and *I. dorsettensis* (Clark, 1980: fig. 11c, g) and *I. leptochirus* (Clark, 1980: fig. 11d, h); all with 2 zoeal stages.

This pair of dorsomedial setae was expressed on the telson of the following megalops: *G. lividus* (Cuesta et al., 2011: fig. 18C); *E. sinensis* (Montú et al., 1996: fig. 14G); *Nanocassiope granulipes* (Ko & Clark, 2002: figs. 11d, 13d) and *N. melanodactylus* (Dornelas et al., 2004: fig. 17A); *Pilumnus hirtellus* (Salman, 1982: fig. 5a); *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: figs. 17H, 20B, N); *A. setifer* (Clark & P.K.L. Ng, 2004b: figs. 15, 17d); *Pilumnus sluiteri* (Clark & P.K.L. Ng, 2004a: figs. 15, 17c); *Pisa armata* (Ingle & Clark, 1980: fig. 5c, d, l); *M. brachydactyla* (as *M. squinado* by Clark, 1986: fig. 6G, H) and *Libinia spinosa* (Clark et al., 1998b: figs. 26, 30c).

Posterior margin medial setae (not figured): This was an accumulative character and comprised the expression of medial setae between the 3 pairs of stout spinulate setae. Rice (1980) considered that a reduction in the number of posterior processes added to the telson during the zoeal stages was a derived feature. The onset of paired medial setae was accelerated with abbreviated zoeal development including their terminal delay. This character was expressed in *G. lividus* (Cuesta et al., 2011: fig. 15), 1 pair in ZV, 2 pairs in ZVII, 3 pairs in ZVIII; *Charybdis helleri* (Dineen et al., 2001: figs. 18b, c, 21b, c, 22b, c, 23b, c), 1 pair in ZII, ZIII, 3 in ZIV–ZVI; *E. sinensis* (Montú et al., 1996: fig. 14), 1 pair in ZIII, 2 pairs in ZIV–ZVI; *Liocarcinus navigator* (as *L. arcuatus* by Clark, 1984: figs. 7E, 8E, 9E) in ZV; *Lophozozymus pictor* (Clark & P.K.L. Ng, 1998: figs. 13B, C, 15B, C, 17G, 20M), 1 pair in ZII, 2 pairs in ZIII, 4 pairs in ZIV; *N. granulipes* (Ko & Clark, 2002: figs. 11c, d, 13c, d) and *N. melanodactylus* (Dornelas et al., 2004: figs. 11C, D, 13C, D), each with 1 pair in ZIII, 2 pairs in ZIV; *A. setifer* (Clark & P.K.L. Ng, 2004b: figs. 13b, c, 17b, c), 1 pair in ZII, ZIII; *Pilumnus sluiteri* (Clark & P.K.L. Ng, 2004a: figs. 13b, 17b) and *P. kempi* (Figs. 86b, 87g), each with 1 pair in ZII; and *Carpilius convexus* (Clark et al., 2005: figs. 3c, 5a), 2 pairs in ZI and *C. maculatus* (Clark et al., 2005: figs. 8c, 10a), 3 pairs in ZI.

These paired medial setae were offset and terminally delayed in *Pilumnus hirtellus* (Clark, 2005: figs. 12, 13, 15; 2007: figs. 449b, 450d, 451d) with 4 zoeal stages, as well as the majoids, *Pisa armata* (Ingle & Clark, 1980: fig. 5b, h, f), *M. brachydactyla* (as *M. squinado* by Clark, 1986: fig. 6C, D, F), *Macrocheira kaempferi* (Clark & Webber, 1991: fig. 5b), *Libinia spinosa* (Clark et al., 1998b: figs. 24b, 25b, 30b), *I. phalangium* and *I. dorsettensis* (Clark, 1980: fig. 11c, g), and *I. leptochirus* (Clark, 1980: fig. 11d, h), all with 2 zoeal stages.

DISCUSSION

Brachyuran first stage zoeae of congeneric species appear to have virtually identical setotaxy (see Christiansen, 1973; Clark, 1983, 1984; P.K.L. Ng & Clark, 2000). This similarity appears to provide a degree of character predictability within a taxon. Setal differences (incongruence) within a group are not indicative of systematic compatibility; they suggest incorrect assignment of taxa. This would also suggest that congeneric species are extremely difficult to distinguish, but it is sometimes possible, although the characters may be challenging to define. For example, from the present study, *Acantholobulus bermudensis* (Figs. 109–112) and *A. schmittii* (Figs. 113–116) have similar setae patterns, in fact they are identical. Separating these two species is difficult. Two suggested characters are based on relative size and include the lateral process on pleomere 2 which appears to be comparatively smaller in *A. bermudensis* (Fig. 112) than in *A. schmittii* (Fig. 116), as well as the two lateral spines on the telson which are minute in *A. bermudensis* (Fig. 110c) and in fact so small that they cannot be drawn in Fig. 112 (vs. slightly larger in *A. schmittii*, Figs. 114, 116). Another example is the zoeas of *Xantho hydrophilus*, *X. pilipes*, and *X. poressa*. Their setotaxy is also identical, but the three species can be distinguished by the following: the dorsal margin of the carapace lateral spines of *X. pilipes* (Fig. 238a) are spinulate (vs. not spinulate in *X. hydrophilus* and *X. poressa*; Figs. 234a, 242a, respectively); rostral spine is spinulate (Fig. 238a) in *X. pilipes* (vs. not spinulate in *X. hydrophilus* and *X. poressa*; Figs. 234a, 242a, respectively); antennal exopod of *X. pilipes* is ca. 17% length (Fig. 238d) of protopod (vs. exopod ca. 3% length (Fig. 242c) of protopod for *X. poressa* and ca. 4% length (Fig. 234c) of protopod for *X. hydrophilus*); and in *X. hydrophilus*, the outermost pair of stout spinulate setae on posterior margin of telson with prominent distal denticles (Fig. 238d) (vs. spinulate in *X. pilipes* and *X. poressa*; Figs. 239c, 243c, respectively).

Guerao et al. (2001) also discuss the issue of finding marked morphological differences between first stage zoeas of congeneric species and further refer to an example where important morphological differences between zoeas of genera within the same family were not possible (Spivak & Cuesta, 2000). Guerao et al. (2001), however, point out that their study and those of others (Ko & Kim, 1991; Cuesta & Rodriguez, 1994; Schubart & Cuesta, 1998) have shown that there are a number of cases for which zoeas of congeneric species can be separated by their morphology. With reference to *Sesarma curacaoense* De Man, 1892 (Anger et al., 1995; Schubart & Cuesta, 1998), this species shows abbreviated development with only two zoeal stages, compared with other *Sesarma*, i.e., *S. reticulatum* (Say, 1817) by Costlow & Bookout (1986) and *S. rectum* Randall, 1840 by Fransozo & Hebling (1986), both with three zoeal stages. This is similar to *Pilumnus*, i.e., *P. hirtellus* by Clark (2005, 2007) with four zoeal stages, and *P. kempi* by this present study and *P. sluiteri* by Clark & P.K.L. Ng (2004a), both with two zoeal stages.

With respect to similarity providing a degree of predictability within a taxon, this appears not to be the case regarding abbreviated zoeal development and heterochrony. Abbreviated zoeal development can terminally delay the onset time of characters compared to their appearance in the ancestral larval sequence, and also advance the time of onset and/or increase the rate of development (acceleration) of a character relative to its condition in the ancestral larval. This zoeal character study appears to demonstrate that a mosaic of several heterochronic processes provides a dominant evolutionary mechanism influencing oligomerisation within brachyuran zoeae. Further, with reference to ancestral developmental sequences, heterochronic larval characters can provide valuable phylogenetic information.

ACKNOWLEDGEMENTS

I am grateful to Hyun Sook Ko, Jose Cuesta, and an anonymous referee for reviewing this manuscript, their suggestions and comments are acknowledged. I would like to thank Geoff Boxshall for his comment on an earlier draft of this manuscript. I am indebted to Jose Christopher Escano Mendoza and Tashfia Raquib for their meticulous editing of the manuscript. The descriptions present in this study form part of my PhD thesis, therefore I thank Jim Atkinson for providing me with the opportunity to study for this doctorate at the University Marine Biological Station Millport, University of London, and agreeing to be my internal supervisor, and Geoff Boxshall for agreeing to be my external supervisor so that I could undertake this study in the Department of Zoology, The Natural History Museum, London. I also thank the then Keeper of Zoology, Phil Rainbow, for continued support while undertaking this study. I am grateful to Peter Ng for supporting my visits to the National University of Singapore and providing hatching facilities in the Systematics and Ecology Laboratory, Department of Biological Sciences. We collected together in many neighbouring countries to which I would have never gained access without him. I thank Alain Crosnier for providing funds and bench space in the Muséum national d'Histoire naturelle, Paris, and for supporting my visit to New Caledonia. Ray Manning supported my four-week visit to the Smithsonian Marine Laboratory at Link Port, Fort Pierce: collecting around the Indian River Lagoon system was a special period. I will always be grateful to Ray and Lilly for the time they set aside for my visit. I acknowledge the following grants and support; a Smithsonian Short-term Visitors grant to the Smithsonian Marine Station at Link Port, Fort Pierce Florida (Ray Manning). The Albion Fisheries Research Centre, Ministry of Fisheries and Marine Resources, Petite Rivière, Albion, Mauritius, and the Smithsonian Institution for logistical support and providing SCUBA cylinders. Support from European research project, INCO-DC no. IC18-CT96-0127, "Macrobenthos of Eastern African mangroves: life cycles and reproductive biology of exploited species" to work on Inhaca Island, Mozambique and the Estação de Biologia Marítima da Inhaca and for funds to attend the 7th Colloquium Crustacea Decapoda Mediterranea in Lisbon (José Paula). The Swire Marine Laboratory at Cape D'Aguilar, Hong Kong (Brian Morton). A fellowship from the Conservation Fund of the National University of Singapore and Nanyang Technological University, Singapore and the Research Funding from the Raffles Museum, National University of Singapore (Peter Ng). Two Visiting Scientist grants to the Muséum national d'Histoire naturelle, Paris (Alain Crosnier). British Council, Jeddah, for providing finance for travel, the Dean of the Faculty of Marine Sciences, King Abdulaziz University for funding my stay while in Jeddah. British Airways for logistical support. The Zoology Research Fund, Zoology Department and an Enhancement Grant, both from the Natural History Museum, London.

I would like to thank Seyit A. Kamanli, Faculty of Art and Science, Burdur Mehmet Akif Ersoy University, Burdur, Turkey for allowing me to reproduce his figures 268, 269. I also thank the following: Geoff Oliver, Rony Huys, Bertrand Richer de Forges, Jody Martin, Sherry Reed, Sandra Tratwein, Tommy Tan, Ali Al-Aidaroos, Ping-Ho Ho, Heok Hui Tan, Swee Hee Tan, Leo Tan, H. Noho, Joseph Dineen, Tuck Hines, Bella Galil, Karen Reed, Janice Clark, Antonio Rodríquez, Josie Orledge, Guillermo Guerao, José Paula, Rodolfo Quintana, Darryl Felder, Hyun Sook Ko, Monica Montú, Frank Trusdale, Austin Williams, Shane Ahyong, Antonio Rodríguez, Herbert Perkins, and Kenneth Stuck.

LITERATURE CITED

Adams A & White A (1849) Crustacea. In: Adams A (ed.) The Zoology of the voyage of HMS *Samarang* under the command of Captain Sir Edward Belcher during the years 1843–1846. Reeve, Benham, and Reeve, London, (part II) pp. viii + 33–66, pls. 7–13. [For dates of publication, see Sherborn, 1922: cxi].

Aikawa H (1929) On larval forms of some Brachyura. Records of Oceanographic Works in Japan, 2(1): 17–55, pls. 1–5, tabs. 1–6.

Alcock A (1898) Materials for a carcinological fauna of India. No. 3. The Brachyura Cyclometopa. Part I. The Family Xanthidae. Journal of the Asiatic Society of Bengal, Calcutta, 67(2), No. 1: 67–233.

Alcock A (1900) Materials for a carcinological fauna of India. No. 6: The Brachyura Catometopa, or Grapsoidea. Journal on the Asiatic Society of Bengal, 69(2), No. 3: 279–456.

Al-Haj AE & Al-Aidaroos AM (2017) Description of the first stage zoeas of four species of *Etisus* (Brachyura, Xanthoidea, Etisinae) reared from the central Red Sea, Saudi Arabia. Marine Biodiversity, 47: 1185–1191.

Al-Haj AE, Kumar AAJ, El-Sherbiny MM, Al-Sofyani A, Crosby MP & Al-Aidaroos AM (2019) Descriptions of the first zoeas of ten xanthid crabs (Crustacea: Decapoda: Xanthoidea) from the Gulf of Aqaba, Red Sea. Zootaxa, 4686(3): 301–345.

Anger K, Schreiber D & Montú M (1995) Abbreviated larval development of *Sesarma curacaoense* (Rathbun, 1897) (Decapoda: Grapsidae) reared in the laboratory. Nauplius, 3: 127–154.

Băcescu M (1952) *Rhithropanopeus harrisii tridentatus* (Maitland) un crab American pătruns şi aclimatizat de curănd in lagunele sălcii ale razelmului. Buletin Stiintific Secţiunea de Ştiinţe Biologice, Argonomice, Geologice şi Geografice, 4(3): 571–578, figs. 1–4.

de Bakker C, Montú M, Anger K & Loureiro-Fernandes L (1989) Larval development of *Hexapanopeus schmitti*, Rathbun, 1930 (Decapoda, Brachyura Xanthidae) reared in the laboratory. Neritica, 4: 137–164.

Balss H (1922) Crustacea VII: Decapoda Brachyura (Oxyrhyncha bis [und] Brachyrhyncha) und geographische Übersicht über Crustacea Decapoda. In: Michaelsen W (ed.) Beiträge zur Kenntnis der Meeresfauna Westafrikas. L. Friederichsen & Co., Hamburg, 3(3): 71–110.

Balss H (1932) Über einige systematisch interessante Xanthidae (Crustacea Decapoda Brachyura) der Harmsschen Reisen nach dem Sundaarchipel. Zeitscrift für Wissenschaftliche Zoologie, 142(4): 510–519, figs. 1–4.

Balss H (1933) Beiträge zur Kenntnis der Gattungen *Pilumnus* (Crustacea Dekapoda) und verwandter Gattungen. Capita Zoologica, 4(3): 1–47, text-figs. 1–5, pls. 1–7.

Benedict JE & Rathbun MJ (1891) The genus *Panopeus*. Proceedings of the United States National Museum, 14(858): 355–385, pls. 319–324.

Birge EA (1883) Notes on the development of *Panopeus sayi* (Smith). Studies from the Biological Laboratory of the Johns Hopkins University, 2(4): 411–426, pls. 30–33.

Bocquet C (1954) Développement larvaire d'*Achaeus cranchii* Leach (Décapode Oxyrhynque). Bulletin du Société zoologie Français, 79: 50–56.

Bourdillon-Casanova L (1960) Le méroplancton du Golfe de Marseille: les larves de Crustacés Décapodes. Recueil des Travaux de la Station Marine d'Endoume, 30: 1–286.

Boxshall GA (2004) The evolution of arthropod limbs. Biological Reviews of the Cambridge Philosophical Society, 79: 253–300.

Boxshall GA, Danielopol D, Horne D, Smith R & Tabacaru I (2010) A critique of biramous interpretations of the crustacean antennule. Crustaceana, 83: 153–167.

Boxshall GA & Jaume D (2013) Antennules and Antennae in the Crustacea. In: Thiel M & Watling L (eds.) The Natural History of the Crustacea, Volume 1. Functional Morphology and Diversity. Oxford University Press, New York, pp. 191–236.

Chamberlain NA (1961) Studies on the larval development of *Neopanope texana sayi* (Smith) and other crabs of the family Xanthidae (Brachyura). Chesapeake Bay Institute, Johns Hopkins University Technical Report, 22: 1–37.

Chamberlain NA (1962) Ecological studies of the larval development of *Rhithropanopeus harrisii* (Xanthidae, Brachyura). Chesapeake Bay Institute, Johns Hopkins University Technical Report, 28: ii + 47, figs. 1–7, tabs. 1–7.

Chia DGB, Ng PKL & Vandenspiegel D (1993) The identities of two crinoid symbionts, *Harrovia albolineata* Adams & White, 1849, and *H. longipes* Lanchester, 1900 (Decapoda, Brachyura, Eumedonidae). Crustaceana, 64(3): 259–280.

Chopra B & Das KN (1930) Further notes on Crustacea Decapoda in the Indian Museum. I. On two new species of hymenosomatid crabs, with notes on some other species. Records of the Indian Museum, 32(4): 413–429.

Christiansen ME (1973) The complete larval development of *Hyas araneus* (Linnaeus) and *Hyas coarctatus* Leach (Decapoda, Brachyura, Majidae) reared in the laboratory. Norwegian Journal of Zoology, 21(2): 63–89.

Clark PF (1980) British spider crabs of the genus *Inachus*; a morphological study of larval development. Unpublished MSc Thesis. Modern Taxonomy (CNAA). Unpublished MSc. Thesis. Polytechnic of Central London and City of London Polytechnic, 140 pp., figs. 1–29, tabs. 1–15, pls. 1–14.

Clark PF (1983) The larval and first crab stages of three *Inachus* species (Crustacea: Decapoda: Majidae); a morphological and statistical analysis. Bulletin of the British Museum (Natural History), Zoology, 44(2): 179–190.

Clark PF (1984) A comparative study of zoeal morphology in the genus *Liocarcinus* (Crustacea: Brachyura: Portunidae). Zoological Journal of the Linnean Society of London, 82(3): 273–290.

Clark PF (1986) The larval stages of *Maja squinado* (Herbst, 1788) (Crustacea: Brachyura: Majidae) reared in the laboratory. Journal of Natural History, 20: 825–836.

Clark PF (2001) Interpreting patterns in chaetotaxy and segmentation associated with abbreviated brachyuran zoeal development. Invertebrate Reproduction and Development, 38(3) [2000]: 171–181.

Clark PF (2005) The evolutionary significance of heterochrony in the abbreviated zoeal development of pilumnine crabs (Crustacea: Brachyura: Xanthoidea). Zoological Journal of the Linnean Society, 143: 417–446.

Clark PF (2007) Xanthoid crab (Crustacea: Decapoda: Brachyura) classification and phylogeny: an appraisal using the chaetotaxy of first stage zoeae. Thesis. University Marine Station Millport, University of London, pp. 1–473. Appendix I (Larval Descriptions), pp. 1–227; Appendix II (Larval figures *Acantholobulus bermudensis* to *Lophozozymus pictor*), pp. 1–308; Appendix III (Larval figures *Lybia plumosa* to *Zozymodes xanthoides*), pp. 309–590.

Clark PF & Cuesta JA (2015) Chapter 71-17. Larval Systematics of Brachyura. In: Castro P, Davie PJF, Guinot D, Schram FR & von Vaupel Klein JC (eds.) Decapoda: Brachyura, Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea, Volume 9. Part C (2 volumes). Brill, Leiden and Boston, pp. 981–1048. Complementary to the volumes translated from the French of the Traité de Zoologie [founded by P.-P. Grassé (†)]

Clark PF, De Calazans DK & Pohle GW (1998a) Accuracy and standardisation of brachyuran larval descriptions. Invertebrate Reproduction and Development, 33(2–3): 127–144.

Clark PF, De Calazans DK & Rodrigues SS (1998b) *Libinia spinosa* H. Milne Edwards, 1834 (Crustacea: Majidae: Pisinae): a reappraisal of larval characters from laboratory reared material. Invertebrate Reproduction and Development, 33(2–3): 145–157.

Clark PF & Galil BS (1988) Redescriptions of *Tetralia cavimana* Heller, 1861 and *Trapezia cymodoce* (Herbst, 1799) first stage zoeas with implications for classification within the superfamily Xanthoidea (Crustacea: Brachyura). Proceedings of the Biological Society of Washington, 101(4): 853–860.

Clark PF & Harrison K (2021) Malacostraca Podophthalmata Britanniæ 1815–1875 by William Elford Leach and the history of its fragmented publication (Crustacea: Decapoda). Zootaxa, 5075(1): 1–80.

Clark PF, Harrison K & Goodman SL (1990) Brock's Indian Archipelago Decapoda and Stomatopoda by De Man: 1887 or 1888? Archives of Natural History, London, 17(1): 81–82, tab. 1.

Clark PF & Ng PKL (1998) The larval development of the poisonous mosaic crab, *Lophozozymus pictor* (Fabricius, 1798) (Crustacea: Decapoda: Brachyura: Xanthidae: Zosiminae), with comments on familial characters for first stage zoeae. Zoosystema, 20(2): 201–220.

Clark PF & Ng PKL (2004a) Two zoeal stages and the megalopa of *Pilumnus sluiteri* De Man, 1892 [Brachyura: Xanthoidea: Pilumnidae] described from laboratory reared material. Invertebrate Reproduction and Development, 45(3): 205–219.

Clark PF & Ng PKL (2004b) The larval development of *Actumnus setifer* (De Haan, 1835) [Brachyura: Xanthoidea: Pilumnidae] with three zoeal stages and megalopa described from laboratory reared material. Crustacean Research, No. 33: 27–50.

Clark PF & Ng PKL (2006) First stage zoeas of *Quadrella* Dana, 1851 [Crustacea: Decapoda: Brachyura: Xanthoidea: Trapeziidae] and their affinities with those of *Tetralia* Dana, 1851, and *Trapezia* Latreille, 1828. Hydrobiologia, 560(1): 267–294.

Clark PF, Ng PKL, Noho H & Shokita S (2005) The first stage zoeas of *Carpilius convexus* (Forskål, 1775) and *C. maculatus* (Linnaeus, 1758) (Crustacea: Decapoda: Brachyura: Xanthoidea:

Carpiliidae): an example of heterochrony. Journal of Plankton Research, 27(2): 1–9.

Clark PF & Paula J (2003) Descriptions of ten xanthoidean (Crustacea: Decapoda: Brachyura) first stage zoeas from Inhaca Island, Mozambique. Raffles Bulletin of Zoology, 51(2): 323–378.

Clark PF & Webber WR (1991) A redescription of *Macrocheira kaempferi* (Temminck, 1836) zoeas with a discussion of the classification of the Majoidea Samouelle, 1819 (Crustacea: Brachyura). Journal of Natural History, 25: 1259–1279.

Colosi G (1924) Una specie fossile de Gerionide (Decapodi brachiuri). Bolettino della Società dei Naturalisti in Napoli, Serie II, Vol. 15 [1923], 35: 248–255, pls. 1–2, figs. 1–5. [Date of publication on journal wrapper states 10 January 1924]

Connolly CJ (1925) The larval stages and megalopas of *Rhithropanopeus harrisi* (Gould). Contributions to Canadian Biology, new series, 2(No. 15): 327–333 (3–8), pls. 1–3.

Costlow JD & Bookout CG (1961) The larval development of *Eurypanopeus depressus* (Smith) under laboratory conditions. Crustaceana, 2(1): 6–15, figs. 1–41.

Costlow JD & Bookout CG (1986) The larval development of *Sesarma reticulatum* Say reared in the laboratory. Crustaceana, 4(4): 281–294.

Cuesta JA (1999) Morfología larval de la familia Grapsidae (Crustacea, Decapoda, Brachyura). Unpublished PhD Thesis. Universidad de Sevilla, Spain, pp. 1–291.

Cuesta JA, Guerao G, Schubart CD & Anger K (2011) Morphology and growth of the larval stages of *Geograpsus lividus* (Crustacea, Brachyura), with the descriptions of new larval characters for the Grapsidae and an undescribed setation pattern in extended developments. Acta Zoologica, 92(3): 225–240.

Cuesta JA & Rodríguez A (1994) Early zoeal stages of *Pachygrapsus marmoratus* (Fabricius), *P. transversus* (Gibbes) and *P. maurus* (Lucas) (Decapoda, Brachyura, Grapsidae) reared in the laboratory. Scientia Marina, 58: 323–327.

Cuesta JA, Schuh M, Diesel R & Schubart CD (1999) Abbreviated development of *Armases miersii* (Grapsidae: Sesarminae) a crab that breeds in supralittoral rock pools. Journal of Crustacean Biology, 19(1): 26–41.

Dana JD (1851a) On the classification of the Cancroidea. American Journal of Science and Arts, Series 2, XII(34): 121–131. [September 1851]

Dana JD (1851b) Conspectus Crustaceorum quæ in Orbis Terrarum circumnavigatione, Carolo Wilkes e Classe Reipublicæ Fœderatæ Duce, Lexit et descripsit J. D. Dana. Pars VIII. Proceedings of the Academy of Natural Sciences of Philadelphia, V(No. X): 247–254. [Separate: V: 1–8(247–254); December 1851; Fox, 1913].

Dana JD (1852a) 1. On the classification of the Crustacea Corystoidea; Scientific Intelligence, III. Zoology. American Journal of Science and Arts, Series 2, 13(37): 119–121. [see Low & Clark, 2010: 67]. [Issued as a separate with the title: “On the Classification of the Corystoidea, Paguridea, etc.”]

Dana JD (1852b) Conspectus Crustaceorum, &c. Conspectus of the Crustacea of the Exploring Expedition under Capt. Wilkes, U.S.N., including the Crustacea Cancroidea Corystoidea. Proceedings of the Academy of Natural Sciences of Philadelphia, 6: 73–86.

Dana JD (1853) Crustacea, Part 1. In: United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the Command of Charles Wilkes, U.S.N. Volume 13. C. Sherman, Philadelphia, viii + 685 pp. [December 1852; for date of publication, see Haskell, 1942: 1979].

Deb M (1987) Description of seven new species and one new record of Pilumninae: Xanthidae: Crustacea from India. Bulletin of the Zoological Survey of India, 8(1–3): 299–312.

Deiss WA & Manning RB (1981) The fate of the invertebrate collections of the North Pacific Exploring Expedition, 1853–1856. In: Wheeler A & Price JH (eds.) History in the Service of Systematics: Papers from the Conference to celebrate the Centenary of the British Museum (Natural History) 13–16 April, 1981. Society for the Bibliography of Natural History, London, pp. 79–85.

Desmarest AG (1823) Crustacés [Malacostracés, Malacostraca]. In: Levrault FG (ed.) Dictionnaire des sciences naturelles, dans lequel on traite méthodiquement des différens êtres de la nature, considérés soit en eux-mêmes, d´après l´état actuel de nos connoissances, soit relativement à l´utilité qu´en peuvent retirer la médecine, l´agriculture, le commerce et les artes. Suivi d´une biographie des plus célèbres naturalistes. Par Plusieurs Professeurs du Jardens du Roi et des principales Écoles de Paris. Volume 28. Le Normant, Paris, pp. 211–285.

Dineen JF, Clark PF, Hines AH, Reed SA & Walton HP (2001) Life history, larval description and natural history of *Charybdis hellerii* (A. Milne Edwards, 1867) (Crustacea, Decapoda, Brachyura, Portunidae), an invasive crab in the western Atlantic. Journal of Crustacean Biology, 21(3): 774–805.

Dornelas M, Clark PF & Paula J (2004) The larval development of *Nanocassiope melanodactyla* (A. Milne-Edwards, 1867) (Crustacea: Decapoda: Brachyura: Xanthidae). Journal of Natural History, 38: 509–535.

Dornelas M, Paula J & Macia A (2003) The larval development of *Hymenosoma orbiculare* Desmarest, 1825 (Crustacea: Decapoda: Brachyura: Hymenosomatidae). Journal of Natural History, 37(21): 2579–2597.

Duncan FD (1937) On the Dates of Publication of the Society’s ‘Proceedings,’ 1859-1926. With an Appendix containing the dates of Publication of ‘Proceedings,’ 1830-1858, compiled by the late F.H. Waterhouse, and the late Henry Peavot, originally published in P.Z.S. 1893, 1913. Proceedings of the Zoological Society of London, Series A, 1937(1): 71–83.

Dupuis C (1986) Dates de publication de l’Histoire Naturelle Générale et Particulière des Crustacés et des Insectes (1802-1805) par Latreille dans le “Buffon de Sonnini.” Annales de la Société Entomologique de France, Nouvelle Série, 22: 205–210.

Fabricius JC (1775) Systematica Entomologia sistens Insectorum classes, Ordines, Genera, Species, Adjectis Synonymis, Locis, Discriptionibus Observationibus. Flensburgi et Lipsiae, Korte, 32 pp. (unnumbered) + 832 pp.

Fabricius JC (1787) Mantissa Insectorum sistens eorum species nuper detectas adjectis characteribus genericis differentiis specificis, emendationibus, observationibus. Volume 1. Christian Gottlob Proft, Hafniae, xvi + 348 pp.

Fabricius JC (1798) Supplementum Entomologiae systematicae. Proft et Storch, Hafniae, 4 pp. (unnumbered) + 572 pp.

Faxon W (1880) On some points in the structure of the embryonic zoea. Bulletin of the Museum of Comparative Zoology, 6(10): 159–166, pls. I–II.

Felder DL & Martin JW (2003) Establishment of a new genus for *Panopeus bermudensis* Benedict & Rathbun, 1891 and several other xanthid crabs from the Atlantic and Pacific Oceans (Crustacea: Decapoda: Xanthoidea). Proceedings of the Biological Society of Washington, 116(2): 438–452.

Fielder DR & Greenwood JG (1983) The complete larval development of *Metopograpsus frontalis* Miers (Decapoda, Grapsidae), reared in the laboratory. Proceedings of the Royal Society of Queensland, 94: 51–60.

Forskål P (1775) Descriptiones Animalium Avium, Amphibiorum, Piscium, Insectorum, Vermium; quae in Itinere orientali observavit. Petrus Forskål. Post Mortem Auctoris editit Carsten Niebuhr. Adjuncta est materia Medica Kahirina. Atque tubula maris rubri geographica. Hauniæ, 19 + xxxiv + 164 pp., 1 map.

Fox WJ (1913) Dates of Publication. In: Nolan EJ (ed.) An Index to the Scientific Contents of the Journal and Proceedings of the Academy of Natural Sciences of Philadelphia. Published in Commemoration of the Centenary of the Academy, March 21, 1912. The Academy of Natural Sciences, Philadelphia, pp. vi–xiv.

Fransozo A & Hebling HJ (1986) Desenvolvimento larval de *Sesarma* (*Holometopus*) *rectum* Randall, 1840 (Decapoda, Grapsidae) en laboratório. Revista Brasileira de Biologia, 46: 353–364.

Fransozo A, Mantelatto FLM & Negreiros–Fransozo ML (1991) Larval development of *Hexapanopeus paulensis* Rathbun, 1930 (Crustacea, Brachyura, Xanthidae) under laboratory conditions. Revista Brasileira de Zoologia, 7(1–2): 31–45.

Fransozo A, Negreiros-Fransozo ML, Martin JW & Trautwein SE (2001) Morphology of the first zoeal stage of *Platypodiella spectabilis* (Herbst, 1794) (Decapoda, Brachyura, Xanthidae) obtained in the laboratory. Gulf and Caribbean Research, 13: 79–85.

Galil BS (1986) *Quadrella* (Brachyura: Xanthoidea: Trapeziidae): review and revision. Journal of Crustacean Biology, 6(2): 275–293.

Galil BS & Vannini M (1990) Research on the coast of Somalia. Xanthidae, Trapeziidae, Carpiliidae, Menippidae. Tropical Zoology, 3(1): 21–56.

Gardner C & Quintana R (1998) Larval development of the Australian giant crab *Pseudocarcinus gigas* (Lamarck, 1818) (Decapoda: Oziidae) reared in the laboratory. Journal of Plankton Research, 20(6): 1169–1188.

Ghory FS (2009) First zoeal stage of *Menippe rumphii* (Fabricius, 1798) (Decapoda: Brachyura: Menippidae) collected from planktonic samples. Pakistan Journal of Marine Sciences, 18(1–2): 77–81, fig. 1, 1 map.

Gibbes LR (1850) On the carcinological collections of the United States, and an enumeration of species contained in them, with notes on the most remarkable, and descriptions of new species. Proceedings of the American Association for the Advancement of Science, 3: 165–201.

Gordon I (1934) Crustacea Brachyura. In: Résultats scientifiques du Voyage aux Indes Orientales Néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. Mémoires du Musée Royal d'Histoire Naturelle de Belgique, hors série 3: 1–78, figs. 1–37.

Gore RH, Van Dover CL & Wilson KA (1981) Studies on decapod Crustacea from the Indian River region of Florida. XX. *Micropanope barbadensis* (Rathbun, 1921): the complete larval development under laboratory conditions (Brachyura, Xanthidae). Journal of Crustacean Biology, 1(1): 28–50.

Gould AA (1841) Crustacea. In: Report on the Invertebrata of Massachusetts, comprising the Mollusca, Crustacea, Annelida, and Radiata. Published agreeably to an order of the Legislature, by the comissioners on the Zoological and Botanical Survey of the state. Folsom, Wells, and Thurston, Cambridge, Massachusetts, pp. 321–341, 1 text-fig.

Gourret P (1884) Considérations sur la faune pélagique du golfe de Marseille suivies d'une étude anatomique et zoologique de la Spadella marioni, espèce nouvelle de l'ordre des Chaetognathes (Leuckart). Annales du Musée d'Histoire Naturelle de Marseille, Zoologique 2, Mémoire, 2: 1–175, pls. 1–5.

Gray JE (1831) Description of a new genus, and some undescribed species of Crustacea. In: Gray JE (ed.) The Zoological Miscellany. Treuttel, Wurtz and Co., London, pp. 39–40.

Greenwood JG & Fielder DR (1984) The complete larval development, under laboratory conditions, of *Heteropanope glabra* Stimpson, 1858 (Brachyura: Xanthidae), from Australia. Australian Zoologist, 21(3): 291–303.

Guerao G, Abelló P & Castejón MR (1996) Morphology of the larval stages of the deep sea crab *Geryon longipes* (Brachyura: Geryonidae). Journal of Natural History, 30: 505–521.

Guerao G, Anger K, Nettelmann UWE & Schubart CD (2004) Complete larval and early juvenile development of the mangrove crab *Perisesarma fasciatum* (Crustacea: Brachyura: Sesarmidae) from Singapore, with a larval comparison of *Parasesarma* and *Perisesarma*. Journal of Plankton Research, 26(12): 1389–1408.

Guerao G, Schubart CD & Cuesta JA (2001) The first stages of *Grapsus grapsus* (Linnaeus) and *Geograpsus lividus* (H. Milne Edwards) (Decapoda, Brachyura, Grapsidae) from the western Atlantic. Nauplius, 9(2): 11–121.

Guinot D (1976) Constitution de quelques groupes naturels chez les Crustacés Décapodes Brachyoures. I. La superfamille des Bellioidea et trois sous-familles de Xanthidae (Polydectinae Dana, Trichiinae de Haan, Actaeinae Alcock). Mémoires du Muséum national d'Histoire naturelle, Paris, Nouvelle Série, Série A, Zoologie, 97: 1–308, figs. 1–47, pls. 1–19.

Guinot D (2011) The position of the Hymenosomatidae MacLeay, 1838, within the Brachyura (Crustacea, Decapoda). Zootaxa, 2890: 40–52.

Gurney R (1938) Notes on some Decapod Crustacea from the Rea Sea. VI–VIII. Proceedings of the Zoological Society of London, Series B, 1938: 73–84, pls. I–IV.

Haan W De (1835) Crustacea. In: von Siebold PF (ed.) Fauna Japonica, sive Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus et adumbrationibus illustravit P.F. de Siebold. Conjunctis studiis C.J. Temminck et H. Schlegel pro Vertebratis atque W. de Haan pro Invertebratis elaborata Regis aupicus edita. Lugundi–Batavorum, Leiden, Decas II: 25–64, pls. 9–15, 17, C, D. [For dates of publication, see Sherborn & Jentink, 1895; Holthuis, 1953; Holthuis & Sakai, 1970].

Hashmi SS (1970) Study on larvae of the family Xanthidae (*Heteropanope*, *Eurycarcinus* and *Eriphia*) hatched in the laboratory. Brachyura: Decapoda. Agriculture Pakistan, 21(4): 457–472, figs. 1–10.

Haskell DC (1942) The United States Exploring Expedition, 1838-1842 and its publications 1844-1873. With an Introductory Note by Harry Miller Lydenberg. The New York Public Library, New York, xii + 88 pp.

Haswell WA (1882) Catalogue of the Australian stalk - and sessile - eyed Crustacea. The Australian Museum, Sydney, xxiv + 324 pp., figs. 1–8, pls. 1–4.

Haynes E (1973) Description of prozoeae and stage I zoeae of *Chionoecetes bairdi* and *C. opilio* (Oxyrhyncha, Oregoniinae). Fishery Bulletin, 71(3): 769–775.

Haynes E (1981) Description of stage II zoeae of snow crab, *Chionoecetes bairdi*, (Oxyrhyncha, Majidae) from plankton of Lower Cook Inlet, Alaska. Fishery Bulletin, 79(1): 177–182.

Heegaard P (1963) Decapod larvae from the Gulf of Napoli hatched in captivity. Videnskabelige Meddelelser Naturhistorisk Forening i København, 125: 449–493.

Heller C (1861) Beiträge zur Crustaceen-Fauna des rothen Meers. Erster Theil. Sitzungsberichte der mathematisch-naturwissenschaftlichen classe der Kaiserlichen Akademie der Wissenschaften, 43(1): 297–374, pls. 1–4.

Herbst JFW (1788) Versuch einer Naturgeschichte der Krabben und Krebse, nebst einer systematischen Beschreibung ihrer verschiedenen Arten. Bund 1, Heft 7. Joh. Casper Fuessly, Zürich, pp. 207–238, pls. XIV–XVII. [For dates of publication, see Rathbun, 1897: 157].

Herbst JFW (1790) Versuch einer Naturgeschichte der Krabben und Krebse, nebst einer systematischen Beschreibung ihrer verschiedenen Arten. Bund 1, Heft 8. Stralsund, Gottlieb, August und Lange, Berlin, pp. 239–274, pls. XVIII–XXI. [For dates of publication, see Rathbun, 1897: 157].

Herbst JFW (1794) Versuch einer Naturgeschichte der Krabben und Krebse, nebst einer systematischen Beschreibung ihrer verschiedenen Arten. Bund 2, Heft 5. Stralsund, Gottlieb, August und Lange, Berlin, pp. 147–162, pls. XXXVII–XL. [For dates of publication, see Rathbun, 1897: 157].

Herbst JFW (1801) Versuch einer Naturgeschichte der Krabben und Krebse, nebst einer systematischen Beschreibung ihrer verschiedenen Arten. Bund 3, Part 2. Gottlieb, August und Lange, Berlin and Stralsund, pp. 1–46, pls. LI–LIV. [For dates of publication, see Rathbun, 1897: 157].

Herbst JFW (1803) Versuch einer Naturgeschichte der Krabben und Krebse, nebst einer systematischen Beschreibung ihrer verschiedenen Arten. Bund 3, Part 3. Gottlieb, August und Lange, Berlin and Stralsund, pp. 1–54, pls. LV–LVIII. [For dates of publication, see Rathbun, 1897: 157].

Holthuis LB (1953) On the dates of publication of W. De Haan's volume on the Crustacea of P.F. von Siebold's "Fauna Japonica". Journal of the Society for the Bibliography of Natural History, 3(1): 36–47, pl. 31.

Holthuis LB & Sakai T (1970) Ph.F. Von Siebold and Fauna Japonica. A History of Early Japanese Zoology. Academic Press of Japan, Tokyo, pp. i–xviii + part I (English text): pp. 1–137 + part II (Japanese text): pp. 207–323; colour pls. I–XXXII.

Hood MR (1962) Studies on the larval development of *Rhithropanopeus harrisii* (Gould) of the family Xanthidae (Brachyura). Gulf Research Reports, 1(3): 122–130, pls. 1–3.

Hyman OW (1925) Studies on the larvae of crabs of the family Xanthidae. Proceedings of the United States National Museum, 67(3): 1–22, pls. 1–14.

Ingle RW (1979) The larval and post-larval development of the brachyuran crab *Geryon tridens* Kröyer (Family Geryonidae) reared in the laboratory. Bulletin of the British Museum (Natural History), Zoology, 36(4): 217–232.

Ingle RW (1983) A comparative study of the larval development of *Monodaeus couchi* (Couch), *Xantho incisus* (Leach) and *Pilumnus hirtellus* (Linnaeus) (Crustacea: Brachyura: Xanthidae). Journal of Natural History, 17: 951–978.

Ingle RW (1985) Larval development of the Mud Crab *Panopeus occidentalis* de Saussure, from Bermuda (Crustacea: Xanthoidea: Panopeidae). Bulletin of the British Museum (Natural History), Zoology, 48(4): 233–248.

Ingle RW (1991) Larval Stages of Northeastern Atlantic Crabs: An illustrated key. Natural History Museum Publications and Chapman & Hall, London, pp. xii + 1–363. [1992] [Published 28 November 1991].

Ingle RW & Clark PF (1980) The larval and post-larval development of Gibbs' spider crab, *Pisa armata* (Latreille) (Family Majidae: sub-family Pisinae), reared in the laboratory. Journal of Natural History, 14(5): 723–735.

Ingle RW & Clark PF (1983) The larval development of the Angular Crab, *Goneplax rhomboides* (Linnaeus) (Decapoda: Brachyura). Bulletin of the British Museum (Natural History), Zoology, 44(2): 163–177.

Jacquinot H & Lucas MH (1854) Crustacés. In: Hombron JB & Jacquinot H (eds.) Zoologie. Voyage au pole sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée; exécuté par ordre du roi pendant les années 1837–1838–1939–1840, sous le commandent de M.J. Dumont–D'Urville, Capitaine de vaisseau; publié par ordre du gouvernement, sous la direction supérieure de M. Jacquinot, capitaine de Vaisseau, commandant de la Zélée. Volume 3. Gide et J. Baudry, Paris [1853], pp. ii + 1–107.

Kakati VS (1977) Larval development of the crab, *Menippe rumphii* (Fabricius) as observed in the laboratory (Crustacea, Brachyura). In: Proceedings of the Symposium on Warm Water Zooplankton. Special Publication. National Institute of Oceanography, Dona Paula, Goa, India, pp. 634–641, figs. 1–2.

Kamanli SA, Morritt D, Ball AD, Goral T & Clark PF (2018) Re-description of Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards, 1853 (Crustacea: Brachyura: Grapsoidea: Varunidae) zoeal development using Confocal Laser Scanning Microscopy. Zootaxa, 4507(1): 1–67.

Karasawa H & Schweitzer CE (2006) A new classification of the Xanthoidea sensu lato (Crustacea: Decapoda: Brachyura) based on phylogenetic analysis and traditional systematics and evaluation of all fossil Xanthoidea sensu lato. Contributions to Zoology, 75(1–2): 23–73.

Kemp S (1915) Fauna of the Chilka Crustacea Decapoda. Memoirs of the Indian Museum, 5(3): 199–325, pls. 12–13.

Kim CH & Hwang SG (1995) The complete larval development of the mitten crab *Eriocheir sinensis* H. Milne Edwards, 1853 (Decapoda, Brachyura, Grapsidae) reared in the laboratory and a key to the known zoeae of the Varuninae. Crustaceana, 68(7): 793–812.

Ko HS (1994a) The zoeal stages of *Pilumnus minutus* De Haan, 1835 (Decapoda: Brachyura: Pilumnidae) in the laboratory. Korean Journal of Systematic Zoology, 10(2): 145–155.

Ko HS (1994b) Larval development of *Parapilumnus trispinosus* Sakai, 1965 (Crustacea, Brachyura, Xanthidae) reared in the laboratory. Korean Journal of Zoology, 37(3): 331–342.

Ko HS (1995) Larval development of *Benthopanope indica* (De Man, 1887) (Decapoda: Brachyura: Pilumnidae) in the laboratory. Journal of Crustacean Biology, 15(2): 280–290.

Ko HS (1997) Larval development of *Pilumnopeus granulata* Balss, 1933 and *Pilumnus minutus* De Haan, 1835 (Crustacea: Brachyura: Pilumnidae), with a key to the known pilumnid zoeae. Korean Journal of Biological Sciences, 1(1): 31–42.

Ko HS & Clark PF (2002) The zoeal development of *Nanocassiope granulipes* (Sakai, 1939) (Crustacea: Decapoda: Brachyura: Xanthidae) described from laboratory reared material. Journal of Natural History, 36(12): 1463–1488.

Ko HS & Kim CH (1991) The zoeal stages of *Ilyoplax tansuiensis* Sakai, 1939 (Decapoda, Brachyura, Ocypodidae) reared in the laboratory. Crustaceana, 61(1): 81–87.

Ko HS & Yang HJ (2003) Zoeal development of *Heteropilumnus ciliatus* (Decapoda: Pilumnidae) with a key to the known pilumnid zoeas in Korea and adjacent waters. Journal of Crustacean Biology, 23(2): 341–351.

Koettker AG, Sumida PYG, Lopes RM & Freire AS (2012) Illustrated key for the identification of the known zoeal stages of brachyuran crabs (Crustacea: Decapoda) from tropical and subtropical Brazil, southwestern Atlantic. Zootaxa, 3204: 1–19.

Krishnan T & Kannupandi T (1988) Larval development of *Elamena* (*Trigonoplax*) *cimex* Kemp, 1915 in the laboratory: the most unusual larvae known in the Brachyura (Crustacea: Decapoda). Bulletin of Marine Science, 43(2): 215–228.

Krøyer H (1837) Geryon tridens, en ny krabbe. Naturhistorisk Tidsskrift, 1(1): 10–21, pl. I.

Kurata H (1970) Studies on the life histories of decapod Crustacea of Georgia: Part III. Larvae of decapod Crustacea of Georgia. Sapelo Island. Unpublished report. The University of Georgia Marine Institute, Sapelo Island, Georgia, pp. iv + 122–263, pls. 1–105.

Kurata H, Heard RW & Martin JW (1981) Larval development under laboratory conditions of the xanthid mud crab *Eurytium limosum* (Say, 1818) (Brachyura: Xanthidae) from Georgia. Gulf Research Reports, 7(No. 1): 19–25, figs. 1–4.

Lamarck JBPAM, chevalier de (1818) Histoire naturelle des Animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leur classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une Introduction offrant la Détermination des caractères essentials de l'Animal, sa distinction du végétal et des autres corps naturels, enfin, l'Exposition des Principes fondamentaux de la Zoologie. Volume 5. Deterville, Paris, 612 pp.

Latreille PA (1803) Histoire Naturelle, Générale et Particulière, des Crustacés et des Insectes. Ouvrage Faisant Suite aux Oeuvres de Leclerc de Buffon, et Partie du cours Complet d'Histoire Naturelle Rédigé par C. S. Sonnini, membre de plusieurs Sociétés savantes. Volume 6. F. Dufart, Paris, 391 pp., pls. 44–57 [Published 18 April 1803; see Dupuis, 1986]

Ławiński L & Pautsch F (1969) A successful trial to rear larvae of the crab *Rhithropanopeus harrisi* (Gould) subsp. *tridentatus* (Maitland) under laboratory conditions. Zoologica Poloniae, 19(4): 495–504, pls. 1–4.

Leach WE (1814) Crustaceology. In: Brewster D. The Edinburgh Encyclopædia, conducted by David Brewster LL.D. Volume 7(2). William Blackwood & John Waugh, Edinburgh, pp. 385–437, pl. 221. [For dates of publication, see Rathbun, 1897; Sherborn, 1937; pl. 221 was issued with Volume 9(1) in 1815; see Sherborn, 1931: 6433, under *Monotoma terebrans* Leach states Volume 9 was published in 1815].

Leach WE (1817a) Malacostraca Podophthalma Britanniæ; or descriptions of the British species of Crabs, Lobsters, Prawns, and of other Malacostraca with pedunculated eyes, illustrated with colored figures of all species by James Sowerby, F.L.S. G.S. W.S. &c. No. XV. James Sowerby, London, 5 text pp. (unnumbered), 3 pls. (XXII.B, XXXVII.A, XXXVII.B). [Published 1 July 1817; see Clark & Harrison, 2021].

Leach WE (1817b) Malacostraca Podophthalma Britanniæ; or descriptions of the British species of Crabs, Lobsters, Prawns, and of other Malacostraca with pedunculated eyes, illustrated with colored figures of all species by James Sowerby, F.L.S. G.S. W.S. &c. No. XVI. James Sowerby, London. 4 text pp. (unnumbered) + 3 pls. (XXII.C, XXXVIII, XXXIX). [Published 1 December 1817; see Clark & Harrison, 2021].

Lebour MV (1928) The larval stages of Plymouth Brachyura. Proceedings of the Zoological Society of London, 1928: 473–560.

Lebour MV (1944) II. Larval Crabs from Bermuda. Zoologica, 29: 113–128, text-figs. 1–19.

Lee SH & Ko HS (2016) The first zoeal stages of *Parapanope euagora* and *Halimede fragifer* (Decapoda: Pilumnoidea: Galenidae) hatched in the laboratory. Animal Systematics, Evolution and Diversity, 32(2): 133–140.

Lim GSY & Ng PKL (1988) The first zoeal stage of *Harrovia albolineata* Adams and White, 1848 (Crustacea: Brachyura: Pilumnidae), with a note on eumedonine systematics. Journal of Natural History, 22(1): 217–223.

Lim SSL & Ng PKL (1997) The complete zoeal development of the actaeine crab, *Novactaea bella* Guinot, 1976 (Decapoda, Brachyura, Xanthidae) in the laboratory. Crustaceana, 70(1): 75–84.

Lim SSL, Ng PKL & Tan WH (1984) The larval development of *Heteropanope glabra* Stimpson, 1858 (Decapoda, Xanthidae) in the laboratory. Crustaceana, 47(1): 1–16.

Linnaeus C (1758) Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis Synonymis, Locis. Volume 1. Edition 10. Laurentii Salvii, Holmiæ, iii + 824 pp.

Linnaeus C (1761) Fauna Svecica Sistens Animalia Sveciae Regni: Mammlia, Aves, Amphibia, Pisces, Insecta, Vermes. Distributa per Classes & Ordines, Genera & Species, cum Differentiis Specierum, Synonymis Auctorum, Nominibus Incolarum, Locis Natalium, Descriptionibus Insectorum. Laurentii Salvii, Stockholmiæ, 48 pp. (unnumbered) + 578 pp.

Linnaeus C (1764) Museum S:ae R:ae M:tis Ludovicæ Ulricæ Reginæ Svecorum, Gothorum, Vandalorumque &c. &c. &c. In quo animalia rariora, exotica, imprimis insecta & conchilia defcribuntur & determinantur Prodromi inftar editum. Laurentii Salvii, Holmiæ, 8 pp. (unnumbered) + 720 pp. + 2 pp. [Index].

Linnaeus C (1767) Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis Synonymis, Locis. Edition 12. Volume 1, Part 2. Edito Duodecima Reformata. Classis V. Insecta. Laurentii Salvii, Holmiæ, pp. 533–1327.

Low MEY & Clark PF (2010) *Kraussia* Dana, 1852 (Crustacea: Decapoda: Brachyura), the senior homonym of *Kraussia* Davidson, 1852 (Brachiopoda: Terebratulida: Terebratellidina): confirmation and authorship of the replacement name *Kraussina* Suess, 1859. Zootaxa, 2628: 66–68.

Lucas H (1846) Crustacés, arachnides, myriapodes, et hexapodes. Exploration Scientifique de l'Algérie pendant les années 1840, 1841, 1842. Publieé par ordre du Gouvernement et avec le concours d'une commission Académique. Sciences physiques. Zoologie I. Histoire Naturelle des Animaux Articulés. Volume 1. Arthus Bertrand, Paris, 403 pp., 8 pls.

MacLeay WS (1838) On the Brachyurous Decapod Crustacea. Brought from the Cape by Dr. Smith. In: Smith A (ed.) Illustrations of the Zoology of South Africa; consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa, in the years 1834, 1835, and 1836; fitted out by 'The Cape of Good Hope Association for Exploring Central Africa': together with a summary of African Zoology, and an inquiry into the geographical ranges of species in that quarter of the globe, published under the Authority of the Lords Commissioners of Her Majesty's Treasury, Invertebratae. IV [1849]. Smith, Elder & Co., London, pp. 53–71, pls. 2, 3. [For dates of publication, see Waterhouse, 1880: 1489–1491].

Man JG De (1879) On some new or imperfectly known Podophthalmous Crustacea of the Leyden Museum. Notes from the Leyden Museum, 1: 53–73.

Man JG De (1887) Report on the Podophthalmous Crustacea of the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr. John Anderson, F.R.S., Superintendent of the Museum. Volume 22, No. 136, Part I. Journal of the Linnean Society of London, Zoology, pp. 1–64, pls. 1–3. [Published 24 November 1887; date from original wrappers bound into NHM General Library copy and personal copy of EJ Miers presented JG De Man]

Man JG De (1888) Bericht über die im indischen Archipel von Dr. J. Brock gesammelten Decapoden und Stomatopoden. Archiv für Naturgeschichte, Volume 53, Part I, Issue 3. Nicolaische Verlags-Buchhandlung, Berlin, pp. 289–600, pls. XI–XXIIa. [Separate ibid. pp. 77–388, pls. III–XVIa; for dates of publication, see Clark, Harrison & Goodman, 1990].

Man JG De (1892) Decapoden des Indischen Archipels. In: Weber M (ed.) Zoologische Ergebnisse einer reise in Niederländisch Ost–Indien. Volume 2. Brill, Leiden, pp. 265–527, pls. 15–30.

Man JG De (1895) Bericht uber die von Herrn Sciffscaptan Storm zur Atejeh, an den westlichen Kuchen von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. Zoologische Jahrbücher, Systematiks, 8(4): 485–609, pls. 12–14.

Manning RB & Holthuis LB (1984) *Geryon fenneri*, a new deep-water crab from Florida (Crustacea: Decapoda: Geryonidae). Proceedings of the Biological Society of Washington, 97(3): 666–673.

Marques F & Pohle G (1996) Complete larval development of *Clypeasterophilus stebbingi* (Decapoda: Brachyura: Pinnotheridae) and a comparison with other species within the *Dissodactylus* complex. Bulletin of Marine Science, 58(1): 165–185.

Martin JW (1981) A comparative study of morphology and ontogeny in juvenile stages of four Western Atlantic xanthoid crabs (Crustacea: Decapoda: Brachyura). Unpublished MSc Thesis. University of Southwestern Louisiana, Lafayette, 142 pp. (not seen).

Martin JW, Felder DL & Truesdale FM (1985) Larval development of *Panopeus bermudemis* Benedict and Rathbun, 1891 (Brachyura, Xanthidae) with notes on zoeal characters in xanthid crabs. Journal of Crustacean Biology, 5: 84–105.

McKinney ML & McNamara KJ (1991) Heterochrony: the evolution of ontogeny. Plenum Press, New York, xix + 437 pp.

Mendoza JCE, Chan KO, Lai JCY, Thoma BP, Clark PF, Guinot D, Felder DL & Ng PKL (2022) A comprehensive molecular phylogeny of the Xanthoidea (Crustacea: Decapoda: Brachyura) provides novel insights into its systematics and evolutionary history. Molecular Phylogenetics & Evolution, 177: 107627.

Messerknecht I, Montú M & Anger K (1991) Larval development and salinity tolerance of Brazilian *Eurytium limosum* (Say, 1818) (Brachyura: Xanthidae) reared in the laboratory. Meeresforschung, 33(4): 275–296.

Miers EJ (1880) XXX. On a Collection of Crustacea from the Malaysian Region.—Part II. Telphusidea, Catometopa, and Oxystomata. Annals and Magazine of Natural History, Series 5, 5(28): 304–317, pl. XIV.

Milne-Edwards A (1865) Études zoologiques sur les Crustacés récents de la famille des Cancériens. Première Partie. Cancérides, Pirimélides, Carpilides. Nouvelles Archives du Muséum d'Histoire naturelle, Volume 1. Masson et Cie, Paris, pp. 177–308, pls. 11–19.

Milne-Edwards A (1867a) Descriptions de quelques espéces nouvelles de Crustacés Brachyoures, Tribu des Oxyrhinques. Familie des Maiens. Annales de la Societé Entomologique de France, série 4, 7: 263–288.

Milne-Edwards A (1867b) Chapter IX. Descriptions des espèces nouvelles de Crustacés provenant de Saint-Vincent du Cap Vert. In: Folin L de & Périer L (eds.) Les Fonds de la Mer. Étude internationale sur les particularités nouvelles, 1867–1872. Volume 1. Sevy, Paris, pp. 32–44, pls. 21–21bis. [For dates of publication, see Winckworth, 1941; Rehder, 1946].

Milne-Edwards A (1867c) Description de queques espèces nouvelles de Crustacés Brachyures. Annales de la Société Entomologique de France, Série 4, 7: 263–288.

Milne-Edwards A (1873) Recherches sur la faune carcinologique de la Nouvelle-Calédonie, Deuxième. Nouvelles Archives du Muséum d'Histoire naturelle, Volume 9. Masson et Cie, Paris, pp. 155–332, pls. 4–18.

Milne-Edwards A (1879) Description de quelques Crustacés nouveaux. Bulletin de la Société Philomathique de Paris, Série 7, 3: 103–110, pls. 1–2.

Milne-Edwards A (1882) Rapport sur les travaux de la Commission chargée par M. le Ministre de l'Instruction Publique d'étudier la faune sousmarine dans les grandes profondeurs de la Méditerranée et de l'Océan Atlantique. Archives des Missions Scientifiques et Littéraires, Paris, Série 3, 9: 1–59.

Milne Edwards H (1834) Histoire naturelle des Crustacés comprenant l'anatomie, la physiologie et la classification de ces animaux. Volume 1. Librairie de Roret, Paris, xxxv + 468 pp., 3 tabs.

Milne Edwards H (1837) Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. Volume 2. Librairie de Roret, Paris, 532 pp.

Milne Edwards H (1853) Mémoire sur la Famille des Ocypodiens. Annales du Science Naturelles, Zoologie, Série 3, 20: 163–228, pls. 6–11.

Montú M, Anger K & de Bakker C (1996) Larval development of the Chinese mitten crab *Eriocheir sinensis* H. Milne-Edwards (Decapoda: Grapsidae) reared in the laboratory. Helgoländer Meeresuntersuchungen, 50: 223–252.

Motoh H (1973) Laboratory-reared zoeae and megalopae of Zuwai crab from the Sea of Japan. Bulletin of the Japanese Society of Scientific Fisheries, 39(12): 1223–1230.

Negreiros-Fransozo ML (1986) Desenvolvimento pós-embrionário de *Panopeus americanus* Saussure, 1857 (Decapoda, Xanthidae), em laboratório. Revista Brasileira de Zoologia, 46(1): 173–188.

Ng PKL & Clark PF (2000) The Indo-West Pacific Pilumnidae XII. On the familial placement of *Chlorodiella bidentata* (Nobili, 1901) and *Tanaocheles stenochilus* Kropp, 1984, using adult and larval characters with the establishment of a new subfamily, Tanaochelinae (Crustacea: Decapoda: Brachyura). Journal of Natural History, 34(2): 207–245.

Ng PKL & Clark PF (2001) The eumedonid file: a case study of systematic compatibility using larval and adult characters (Crustacea: Decapoda: Brachyura). Invertebrate Reproduction and Development, 38 [2000]: 225–252.

Ng PKL & Clark PF (2008) A revision of *Latopilumnus* Türkay & Schuhmacher, 1985, and *Aniptumnus* Ng, 2002 (Crustacea: Decapoda: Brachyura: Pilumnidae). Journal of Natural History, 42(9): 885–912.

Ng PKL & Davie PJF (2020) A new family and superfamily for the southern giant crab of Australia, *Pseudocarcinus gigas* (Lamarck, 1818) (Decapoda: Brachyura). Journal of Crustacean Biology, 40(5): 607–626.

Ng PKL & Guinot D (2021) *Parapanope* De Man, 1895 (Decapoda: Brachyura: Pilumnoidea: Galenidae): revisited and revised, with descriptions of two new species. Journal of Crustacean Biology, 41(2): 1–22.

Ng PKL, Guinot D & Davie PJF (2008) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. Raffles Bulletin of Zoology, Supplement 17: 1–286.

Ng PKL & Tan LWH (1984) The Indo-Pacific Pilumnidae I. Description of four new species of the genus *Pilumnus* Leach, 1815, and definition of a new genus, *Bathypilumnus*. Journal of the Singapore National Academy of Sciences, 13: 13–19.

Ng PKL & Tan LWH (1988) The identities of *Heteropilumnus subinteger* (Lanchester, 1900) and *Heteropilumnus hirsutior* (Lanchester, 1900) stat. nov., with description of a new species, *Heteropilumnus holthuisi* sp. nov. (Decapoda, Brachyura, Pilumnidae). Crustaceana, 54(1): 13–24.

Nobili G (1901) Decapodi e Stomatopodi Eritrei del Museo Zoologico dell'Università di Napoli. Annuario del Museo Zoologico della Regia Università di Napoli, nuova serie, 1(3): 1–20.

Nobili G (1903) Crostacei di Singapore. Bollettino dei Musei di Zoologia ed Anatomia comparata della Regia, Università di Torino, 18(455): 1–39, pl. 1.

Odhner T (1925) Monographie Gattungen der Krabbenfamillie Xanthidae I. Göteborgs Kungliga Vetenskaps och Vitter Samhälles Handlinger, serie 4, 29(1): 1–92, text-figs. 1–7, pls. 1–5.

Olivi G (1792) Cancer. Ricerche Chimiche intorno la causa della colorazione in ross delle croste de' Granchj, e Gamberi. In: Zoologia Adriatica, ossia Catalogo ragionato degli Animali del Golfo e delle Lagune di Venezia ; preceduto da una Dissertazione sulla Storia fisica e naturale del Golfo ; e accompagnato da Memorie, ed Osservazioni di Fisica Storia naturale ed Economia. Bassano, pp. 41–61, figs. 1–3.

Ortmann A (1893) Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. Abtheilung: Brachyura (Brachyura genuina Boas)

II. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Cyclometopa. Hierzu Tafel 17. Zoologische Jahrbücher (Systematik), 7: 411–495.

Paula J & dos Santos A (2001) Larval and early post-larval stages of the crab *Xantho pilipes* A. Milne-Edwards, 1867 (Crustacea, Decapoda, Xanthidae), reared under laboratory conditions. Invertebrate Reproduction and Development, 38 [2000]: 253–264.

Pennant T (1777) British Zoology. Volume 4. Crustacea. Mollusca. Testacea. London, viii + 11 pp. (unnumbered, Index to illustrations) + 154 pp., pls. 1–93.

Perkins HC (1973) The larval stages of the deep sea red crab *Geryon quinquedens* Smith, reared under laboratory conditions (Decapoda: Brachyrhyncha). Fishery Bulletin, 71(1): 69–82.

Phan CD (1972) МАТЕРИАЛЫ К ИЗУЧЕНИЮ РАЗВИТИЯ (СТАДИИ ЗОЕА) *Rhitropanopeus harrisi* Subsp. *tridentatus* (Maitland) [Material on the study of development in the crayfish *Rhitropanopeus harrisi* subsp. *tridentatus* (zoea stage (Maitland)]. УЧЕНЫЕ ЗАПИСКИ АЗЕРБАИДЖАНСКОГО ГОСУДАРСТВЕННОГО УНИВЕРСИТЕТА (Серцяя бцоаосцчекцХ Наук) [Uchenye Zapiski Azerbaidzhanskogo gosudarstvennogo Universiteta. Baku (Series Biologischeskei Naukl)], 2: 39–42.

Pohle GW (1991) Larval development of Canadian Atlantic oregoniid crabs (Brachyura: Majidae), with emphasis on *Hyas coarctatus alutaceus* Brandt, 1851, and a comparison with Atlantic and Pacific conspecifics. Canadian Journal of Zoology, 69(11): 2717–2737.

Pohle GW (1994) *Dissodactylus xantusi* and *Dissodactylus lockingtoni* (Decapoda: Brachyura: Pinnotheridae): larval development of two sympatric Pacific species. Canadian Journal of Zoology, 72: 575–590.

Porter HJ (1960) Zoeal stages of the stone crab, *Menippe mercenaria* Say. Chesapeake Science, 1(3–4): 168–177.

Prasad RR & Tampi PRS (1957) Notes on some decapod larvae. Journal of the Zoological Society of India, 9: 22–29.

Rafinesque CS (1815) Analyse de la Nature ou Tableau de l'Univers et des Corps organisés. Palerme, pp. 12–24.

Randall JW (1840) Catalogue of the Crustacea brought by Thomas Nuttall and J.K. Townsend, from the West Coast of North America and the Sandwich Islands, with Descriptions of such species as are apparently new, among which are included several species of different Localities existing in the collection of the Academy. Journal of the Academy of Natural Sciences of Philadelphia, 8(1) [1839]: 106–147, pls. 3–7.

Rathbun MJ (1897) A revision of the nomenclature of the Brachyura. Proceedings of the Biological Society of Washington, 11: 153–167.

Rathbun MJ (1909) New crabs from the Gulf of Siam. Proceedings of the Biological Society of Washington, 22: 107–114.

Rathbun MJ (1921) Report on the Brachyura collected by the Barbados-Antigua Expedition from the University of Iowa in 1918. In: University of Iowa Studies. Studies in Natural History. Volume 9, No. 5. Reports on the crinoids, ophiurans, Brachyura, Tanidacea and Isopoda, amphipods & Echinoidea of the Barbados-Antigua Expedition of 1918. University of Iowa, Iowa City, pp. 65–90, pls. I–II.

Rathbun MJ (1930) The cancroid crabs of America. Bulletin of the United States National Museum, 152: i–xvi + 1–609, figs. 1–85, pls. 1–230.

Rehder HA (1946) Additional notes on the Dates of Publication of Les Fonds de la Mer. Proceedings of the Malacological Society of London, 27(2): 74–75.

Rice AL (1980) Crab zoeal morphology and its bearing the classification of the Brachyura. Transactions of the Zoological Society of London, 35: 271–424, figs. 1–47, tabs. I–XI.

Rodríguez A & Martin JW (1997) Larval development of the crab *Xantho poressa* (Decapoda: Xanthidae) reared in the laboratory. Journal of Crustacean Biology, 17(1): 98–110.

Roff RC, Davidson KG, Pohle G & Dadswell MJ (1984) A Guide to the Marine Flora and Fauna of the Bay of Fundy and Scotian Shelf: Larval Decapoda: Brachyura. Canadian Technical Report of Fisheries and Aquatic Sciences, No. 1322. Biological Station, St. Andrews, New Brunswick, Canada, iv + 57 pp., 161 figs.

Rüppell WPES (1830) Beschreibung und Abbildung von 24 Arten Kurzschwänzigen Krabben, als Beitrag zur Naturgeschichte des rothen Meers. HL Brönner, Frankfurt a.M., 28 pp., 6 pls.

Sakai T (1939) Studies on the Crabs of Japan. IV. Brachygnatha, Brachyrhyncha. Yokendo Co., Ltd., Tokyo, pp. 365–741 + 1–23 [Index], figs. 1–129, pls. 42–111.

Sakai T (1965) The crabs of Sagami Bay collected by His Majesty the Emperor of Japan described and illustrated by Tune Sakai, D.Sc. Edited by Biological Laboratory Imperial Household. Maruzen, Tokyo, pp. i–xvi + 1–206 [English Text] + 1–92 [Japanese Text] + 1–32 [Bibliography and Index], figs. 1–27, pls. 1–100.

Sakai T (1976) Crabs of Japan and the adjacent seas. Kodansha, Tokyo. Volume 1 [In English]: xxix + 773 pp.; Volume 2 [In Japanese]: 461 pp.; Volume 3 [plates]: 61 pp., 251 pls.

Salman SD (1982) Larval development of the crab *Pilumnus hirtellus* (L.) reared in the laboratory (Decapoda, Brachyura, Xanthidae). Crustaceana, 42(2): 113–126.

Salman SD & Ali MH (1996) Larval development *Elamenopsis kempi* (Chopra and Das) (Brachyura, Hymenosomatidae). Scientia Marina, 60(2–3): 407–416.

Samouelle G (1819) The Entomologist's Useful Compendium, or an Introduction to the Knowledge of the British Insects comprising the best means of obtaining and preserving them, and a description of the general apparatus used; together with the genera of Linné, and the modern method for arranging the classes Crustacea, Myriapoda, spiders, mites and insects from affinities and structure, according to the views of Dr. Leach. Also an explanation of the terms used in entomology; a calendar of the times of appearance and unusual situations of near 3,000 species of British insects; with instructions for collecting and fitting up objects for the microscope. Illustrated with twelve plates. Thomas Boys, London, 496 pp.

Saussure H de (1857) Diagnoses de quelques Crustacés nouveaux de l'Amérique tropicale. Revue et Magasin de Zoologie, Prue et Appliquée, série 2e, 9: 501–505.

Say T (1817) An Account of the Crustacea of the United States. Journal of the Academy of Natural Sciences of Philadelphia, 1(Part I): 65–80, pl. 4.

Say T (1818) Appendix to the Account of the Crustacea of the United States. Journal of the Academy of Natural Sciences of Philadelphia, 1(Part II): 445–458.

Schubart CD & Cuesta JA (1998) First zoeal stages of *Sesarma* species from Panama, with identification keys and remarks on the American Sesarminae (Crustacea: Brachyura: Grapsidae). Journal of Plankton Research, 20(1): 61–84.

Scotto LA (1979) Larval development of the Cuban stone crab, *Menippe nodifrons* (Brachyura, Xanthidae) under laboratory conditions with notes on the status of the family Menippidae. Fishery Bulletin, 77(2): 359–386.

Serène R (1965) Guide for curators of brachyuran collections in Southeast Asia. Applied Scientific Research Corporation of Thailand, Bangkok, 65 pp.

Serène R (1984) Crustacés Décapodes Brachyoures de l'Océan Indien occidental et de la Mer Rouge, Xanthoidea: Xanthidae et Trapeziidae. Avec un addendum par Crosnier A: Carpiliidae et Menippidae. [Crustacea Decapoda Brachyura of the western Indian Ocean and of the Red Sea. Xanthoidea: Xanthidae and Trapeziidae. With an addendum by Crosnier A]. Faune Tropicale, no. 24: 1–349, figs. A–C + 1–243, pls. 1–48.

Sherborn CD (1922) Index animalium sive index nominum quae ab A. D. MDCCLVIII generibus et speciebus animalium imposita sunt societatibus eruditorum adiuvantibus. Sectio secunda. A Kalendis Ianuariis, MDCCCI usque ad finem Decembris, MDCCCL. Part I. Introduction, Bibliography and Index A–Aff. The Trustees of the British Museum, London, cxxxix + 128 pp.

Sherborn CD (1931) Index animalium sive index nominum quae ab A. D. MDCCLVIII generibus et speciebus animalium imposita sunt societatibus eruditorum adiuvantibus. Sectio secunda. A Kalendis Ianuariis, MDCCCI usque ad finem Decembris, MDCCCL. Part XXVI. Index T–Trichoscelia. The Trustees of the British Museum, London, pp. 6359–6582.

Sherborn CD (1937) Brewster's Edinburgh Encyclopaedia. Issued in 18 vols. from 18— to 1830. Journal of the Society for the Bibliography of Natural History, 1(4): 112.

Sherborn CD & Jentink JA (1895) On the dates of the Parts of Siebold's 'Fauna Japonica' and Giebel's 'Allgemeine Zoologie' (first edition). Proceedings of the Zoological Society of London, 1895: 149–150.

Siddiqui FA & Tirmizi NM (1992) The complete larval development, including the first crab stage of *Pilumnus kempi* Deb, 1987 (Crustacea: Decapoda: Brachyura: Pilumnidae) reared in the laboratory. Raffles Bulletin of Zoology, 40(2): 229–244.

Smith SI (1869) Notes on new or little known species of American cancroid Crustacea. Proceedings of the Boston Society of Natural History, 12: 274–289.

Smith SI (1879) The stalk-eyed crustacea of the Atlantic Coast of North America, north of Cape Cod. Transactions of the Connecticut Academy of Arts and Sciences, 51(1): 27–138, pls. 8–12.

Soh CL (1969) Abbreviated development of a non-marine crab, *Sesarma* (*Geosesarma*) *perracae* (Brachyura; Grapsidae), from Singapore. Journal of Zoology, 158(3): 357–370.

de Souza AS, da Costa RM & Abrunhosa FA (2013) Comparative morphology of the first zoea of twelve brachyuran species (Crustacea: Decapoda) from the Amazon region. Zoologia (Curitiba), 30(3): 273–290.

Spivak ED & Cuesta JA (2000) Larval development of *Cyrtograpsus affinis* (Dana) (Decapoda, Brachyura, Varunidae) from Rio de la Plata estuary, reared in the laboratory. Scientia Marina, 64(1): 29–47.

Stevčić Z (2005) The reclassification of brachyuran crabs (Crustacea: Decapoda: Brachyura). Natura Croatica (Fauna Croatica), 14(1): 1–159.

Stimpson W (1858) Prodromus descriptionis animalium evertebratorum quae in Expeditione ad Oceanum Pacificum Septentrionalem a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit - Part IV, Crustacea Cancroidea et Corystoidea. Proceedings of the Academy of Natural Sciences of Philadelphia, 10: 31–40. [Separate idem. pp. 29–37; for dates of publication, see Deiss & Manning, 1981].

Stimpson W (1859) XI.—Notes on North American Crustacea, No. 1. Annals of the Lyceum of Natural History of New York, 7 [1862]: 49–93, pl. 1. [Separate idem. pp. 1–47].

Stuck KC, Perry HM, Stuck LM & Barett AA (1992) Larval development of the golden crab, *Chaceon fenneri* (Manning & Holthuis, 1984) (Decapoda: Brachyura: Geryonidae), reared in the laboratory. Proceedings of the Biological Society of Washington, 105(3): 521–539.

Takeda M & Miyake S (1970) Pilumnid crabs of the family Xanthidae from the West Pacific. III. Descriptions of two new species of the genus *Pilumnus*. Occasional Papers of Zoological Laboratory, Faculty of Agriculture, Kyushu University, 3(5): 37–44.

Temminck CJ (1836) Coup-d'oeil sur la faune des Iles de la Sonde et de l'Empire du Japon. Discours préliminaire destiné a servir d'introduction a la Faune du Japon. [s.l.], [s.n.], pp. i–xxx.

Terada M (1982) Zoeal development of the menippid crab, *Eriphia smithi* MacLeay. Zoological Magazine, Tokyo Zoological Society, 91(3): 255–262.

Terada M (1990) Zoeal development of five species of xanthid crabs, reared in the laboratory. Researches on Crustacea, 18: 23–47. [Mainly in Japanese]

Tesch JJ (1922) Schizopoden en Decapoden. In: Redeke HC (ed.) Flora en Fauna der Zuiderzee. Monografie van een Brakwatergebied. De Boer, Den Helder, pp. 337–362.

Waterhouse FH (1880) On the dates of publication of the parts of Sir Andrew Smith's 'Illustrations of the Zoology of South Africa'. Proceedings of the Zoological Society of London, 1880: 489–491.

Waterhouse FH (1893) List of the Dates of Delivery of the Sheets of the 'Proceedings' of the Zoological Society of London, from the commencement in 1830 to 1859 inclusive. In: May 2, 1893. Sir W.H. Flower, K.C.B., LL.D., F.R.S., President, in the Chair. Proceedings of the Zoological Society of London, 1893: 435–440. [Reprinted in Duncan, 1937: 1978–1983].

Wear RG (1965) Zooplankton of Wellington Harbour, New Zealand. Zoology Publications from Victoria University of Wellington, No. 38: 1–31.

Wear RG (1968) Life-history studies on New Zealand Brachyura 2. Family Xanthidae. Larvae of *Heterozius rotundifrons* A. Milne Edwards, 1867, *Ozius truncatus* H. Milne Edwards, 1834 and *Heteropanope (Pilumnopeus) serratifrons* (Kinahan, 1856). New Zealand Journal of Marine and Freshwater Research, 2: 293–332.

Wear RG & Fielder DR (1985) The Marine Fauna of New Zealand: Larvae of the Brachyura (Crustacea, Decapoda). New Zealand Oceanographic Institute Memoir, 92: 1–90.

White A (1847a) No. VIII. Descriptions of a new genus and five new species of Crustacea. Appendix. In: Jukes JB (ed.) Narrative of the surveying voyage of H.M.S. Fly, commanded by Captain F.P. Blackwood, R.N. in Torres Strait, New Guinea, and other Islands of the Eastern Archipelago, during the years 1842–1846: together with an excursion into the interior of the eastern part of Java. Volume 2. T. & W. Boone, London, pp. 335–338, figs. 1–3.

White A (1847b) 3. Descriptions of new or little-known Crustacea in the Collection at the British Museum. In: July 27. William Yarrell, Esq., Vice-President, in the chair. Proceedings of the Zoological Society of London, 1847(XV), no. clxxvii: 118–126. [For dates of publication, see Waterhouse, 1893: 1438; Duncan, 1937: 1880].

White A (1848a) Descriptions of new or little-known Crustacea in the Collection at the British Museum. In: Proceedings of Learned Societies. Zoological Society. July 27, 1847.-Wm. Yarrell, Esq., Vice-President, in the Chair. Annals and Magazine of Natural History, Series 2, 1(3): 221–227.

White A (1848b) 2. Short Descriptions of new or little-known Decapod Crustacea. In: November 23, 1847. William Yarrell, Esq., Vice-President, in the Chair. Proceedings of the Zoological Society of London, 1847(XV), no. clxxix: 222–228, 2 text-figs. [For dates of publication, see Waterhouse, 1893: 438; Duncan, 1937: 80].

Winckworth R (1941) Les Fonds de la Mer: dates of publication. Proceedings of the Malacological Society of London, 24(4): 149–151.

Yang H-J & Ko H-S (2005) First zoea of *Liomera bella* (Crustacea: Decapoda: Xanthidae) reared in the laboratory. Korean Society of Systematic Zoology, 21(2): 193–199.