

ATERGATIS SUBDENTATUS (DE HAAN, 1835), ATERGATOPSIS GERMAINI A. MILNE EDWARDS, 1865 AND PLATYPODIA EYDOUXI (A. MILNE EDWARDS, 1865) (CRUSTACEA: DECAPODA: XANTHOIDEA: XANTHIDAE: ZOSIMINAE) – FIRST STAGE ZOEAL DESCRIPTIONS WITH IMPLICATIONS FOR THE SUBFAMILY

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ABSTRACT. – The first stage zoeas of *Atergatis subdentatus* (de Haan, 1835), *Atergatopsis germaini* A. Milne-Edwards, 1865, and *Platypodia eydouxi* (A. Milne-Edwards, 1865) are described for the first time, *Actaeodes tomentosus* (H. Milne Edwards, 1834) are fully illustrated, *Atergatis floridus* (Linnaeus, 1767) are redescribed, and those of *Platypodiella spectabilis* (Herbst, 1794) are re-examined. A list of characters is tabulated for all known zosimine first stage zoeas. The zoeal evidence appears to support adult taxonomy by highlighting the difficulties in clarifying the systematics within the xanthoidean taxa, Zosiminae Alcock, 1898 and Actaeinae Alcock, 1898.

KEY WORDS. – Crustacea, Decapoda, Xanthoidea, Xanthidae, Zosiminae, first stage zoeal description, taxonomy, systematics.

INTRODUCTION

Nine genera with 67 species are currently assigned to the xanthoidean subfamily Zosiminae Alcock, 1898. Serène (1984) listed *Atergatis* de Haan, 1833, *Atergatopsis* A. Milne Edwards, 1862, *Lophozozymus* A. Milne Edwards, 1863, *Paratergatis* Sakai, 1965, *Platypodia* Bell, 1835, *Zosimus* Leach in Desmarest, 1823 and *Zozymodes* Heller, 1861, from the Red Sea and western Indian Ocean. Guinot (1967: 562) established *Platypodiella* to accommodate four xanthid species distributed around the Pacific and Atlantic coasts of America coast namely, *Platypodia spectabilis* (Herbst, 1794), *P. picta* (A. Milne Edwards, 1869), *P. rotundata* (Stimpson, 1860) and *P. gemmata* (Rathbun, 1902). She considered that this genus had affinities with the Indo-Pacific genera *Atergatis* and *Atergatopsis*. Ng & Huang (1997) subsequently described a new genus, *Pulcratis*, from Taiwan and assigned it to the Zosiminae (see also Ng & Chen, 2004).

For these taxa, larval descriptions are known only for *Atergatis floridus* (Linnaeus, 1767) by Tanaka & Konishi

(2001) [ZI-IV, Meg.]; *Atergatis reticulatus* de Haan, 1835, by Terada (1980) [ZI-IV]; *Lophozozymus pictor* (Fabricius, 1798) by Clark & Ng (1998) [ZI-IV, Meg.]; *Platypodiella spectabilis* (Herbst, 1794) by Fransozo et al. (2001) [ZI]; *Zosimus aeneus* (Linnaeus, 1758) by Tanaka (1999) [ZI-IV] and *Zozymodes xanthoides* (Krauss, 1843) by Clark & Paula (2003) [ZI].

Four ovigerous zosimine crabs were collected and their first stage zoeas hatched out in the laboratory, *Atergatis floridus* (Linnaeus, 1767), *A. subdentatus* (de Haan, 1835), *Atergatopsis germaini* A. Milne Edwards, 1865 and *Platypodia eydouxi* (A. Milne Edwards, 1865). Zoeal descriptions for *Atergatopsis* and *Platypodia* species are currently unknown. *Platypodia spectabilis* (Herbst, 1794) first stage zoeas, reported on by Fransozo et al. (2001), were made available for re-examination. The first stage zoeas of the actaeine, *Actaeodes tomentosus* (H. Milne Edwards, 1834), were partially illustrated and described by Clark & Al-Aidaros (1994) to show only the differences between the larvae of this species and *A. hirsutissimus* (Rüppell, 1830).

Actaeodes tomentosus first stage zoeas are therefore described in full.

The subfamilial classification of the Xanthidae MacLeay, 1838, sensu Guinot, 1978, based on adult taxonomy is still unsatisfactory, particularly in the case of genera assigned to the Actaeinae Alcock, 1898, and Zosiminae Alcock, 1898. For example the status of the *Atergatopsis* remains uncertain within these two subfamilies (Serène, 1984). Similarly the subfamilial position of *Paratergatis* and *Pulcratis* has also been questioned (Ng & Chen, 2004). The purpose of this study is to compare the known first stage zoeas of the xanthoidean taxa, Zosiminae and Actaeinae in order to clarify the systematic position of *Atergatopsis*.

Abbreviations used: coll. = collected, LACM = Natural History Museum of Los Angeles, Los Angeles, United States, NHM = The Natural History Museum, London, NTOU = National Taiwan Ocean University, Keelung, Taiwan and ZRC = Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore, ZI, ZII etc. = first stage zoea, second stage zoea etc., Meg. = megalop, coll. = collected, reg. = registration number.

MATERIAL EXAMINED

Actaeodes tomentosus, coll. 23 Jul.1990, Obhor Creek, 21°40'N, 39°12'E, Red Sea, ca. 20km north of Jeddah, Saudi Arabia, hatched 4 Aug.1990, NHM reg. 1994.3230, five zoeas examined.

Atergatis floridus, coll. P. K. L. Ng, Apr.1982, Siloso Beach, Sentosa Island Singapore, hatched 13 Apr.1982, ZRC reg. 1984.608-4007, six zoeas examined.

Atergatis subdentatus, coll. P.-H. Ho, 5 May1993, Heping Island, Keelung, Taiwan, hatched 17 Ma.1993, NTOU reg. CX9304-2, five zoeas examined.

Atergatopsis germainii, coll. P.-H. Ho, 15 Apr.1993, Heping Island, Keelung, Taiwan, hatched 17 May1993, NTOU reg. CX930415-2, five zoeas examined.

Platypodia eydouxi, coll. R. De Felice 4 Jan.2002, hatched 7 Jan.2000 by P. K. L. Ng, Heeia Kea, Kaneohe Bay, Oahu, Hawaii, NHM reg. 2004.243, five zoeas examined.

Platypodiella spectabilis, coll. Zimmerman & Martin, 14 Jul.2000, hatched 14 Jul.2000, North Beach, Guana Island, British Virgin Islands, LACM CR 2000006, five zoeas examined.

METHODS

The zoeas were dissected on glass slides in polyvinyl lactophenol using a Wild M5 binocular and the appendages were 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 Nomarski interference contrast and a *camera lucida*. Setal ambiguities were resolved using a Zeiss Axioskop differential interference contrast microscope. The sequence of the zoeal descriptions is based on the malacostracan somite plan and described from anterior to posterior. Setal armature of appendages was described from proximal to distal segments and in order of endopod to exopod (see Clark et al., 1998). The first stage zoeas were described and fully illustrated except for the mandible because the only significant character of this appendage is the appearance of the palp in the zoeal phase and it is not present in the stage examined in the present study. The long antennular aesthetascs and the long plumose natatory setae of the first and second maxillipeds were drawn truncated. The approximate measurement of the antennal exopod (for its ratio with the protopod) was taken from the base to the tip excluding the terminal setae.

TAXONOMY

XANTHIDAE MACLEAY, 1838

ZOSIMINAE ALCOCK, 1898

Atergatis floridus (Linnaeus, 1767)
(Figs. 1-4)

Atergatis floridus: Tanaka & Konishi, 2001: 21-42, Tabs. 1-2, Figs. 1-11, ZI-IV, Meg.

Description. – Carapace (Figs. 1a, b): dorsal spine long, curved distally and approximately twice the length of rostral spine; rostral spine shorter in length than the antennal protopod and distally spinulate; lateral spines present and straight; 1 pair of posterodorsal setae; ventral margin without setae; eyes sessile.

Antennule (Fig. 1c): uniramous, endopod absent; exopod unsegmented with 2 broad, long and 2 slender, shorter, terminal aesthetascs plus 1 terminal seta.

Antenna (Fig. 1d): protopodal process distally multispinulate, just longer in length than rostral spine; endopod reduced to small spine; exopod ca. 15% length of protopod, possessing 3 (1 long subterminal, 2 unequal terminal) setae.

Mandible: palp absent.

Maxillule (Fig. 2a): epipod seta absent; coxal endite with 7 setae; basal endite with 5 setal processes and 2 small teeth; endopod 2-segmented, proximal segment with 1 seta; distal segment with 6 (2 subterminal, 4 terminal) setae; exopod seta absent.

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

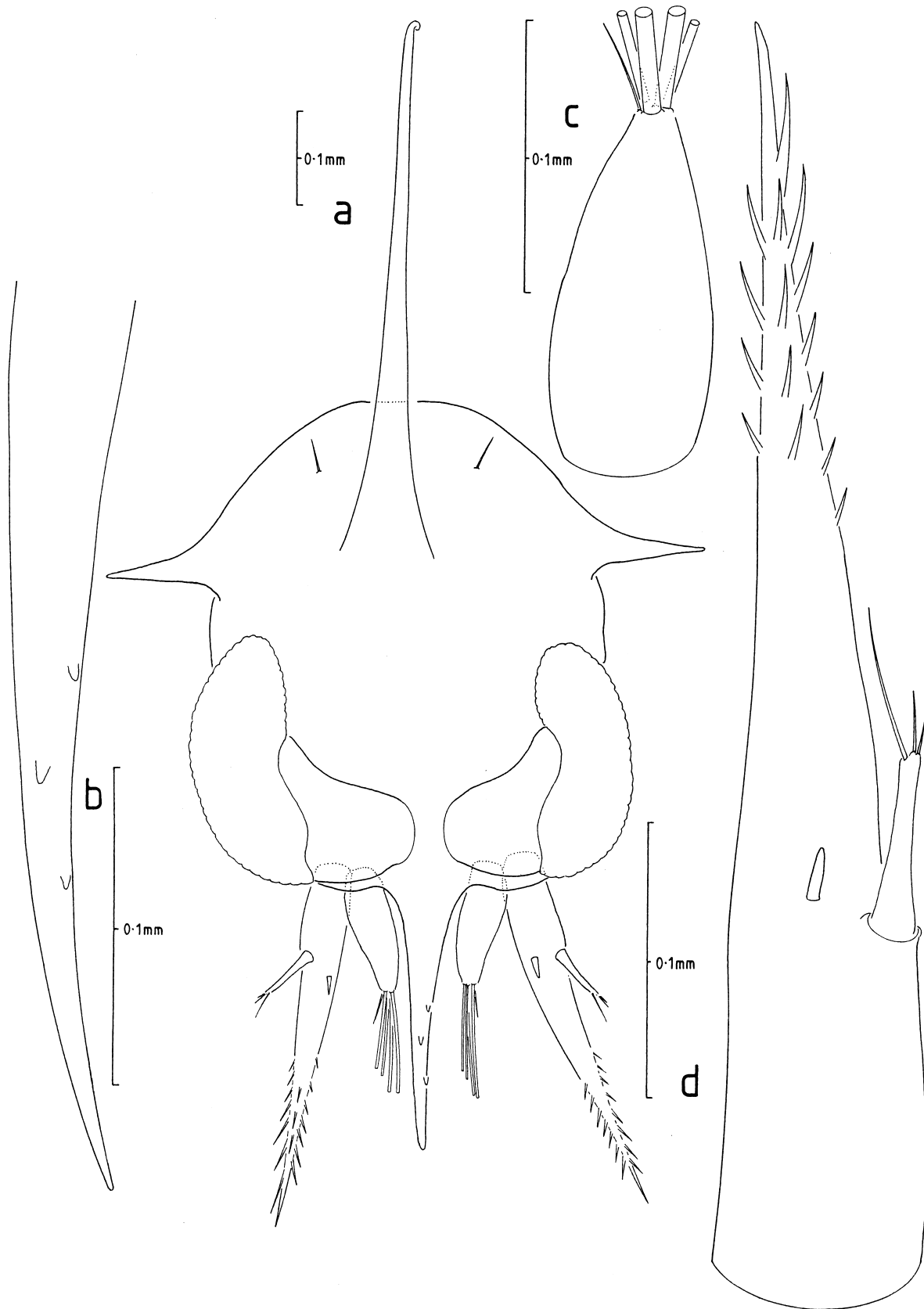


Fig. 1. *Atergatis floridus* (Linnaeus, 1767) first stage zoea; a) anterior view of carapace; b) rostral spine; c) antennule; d) antenna.

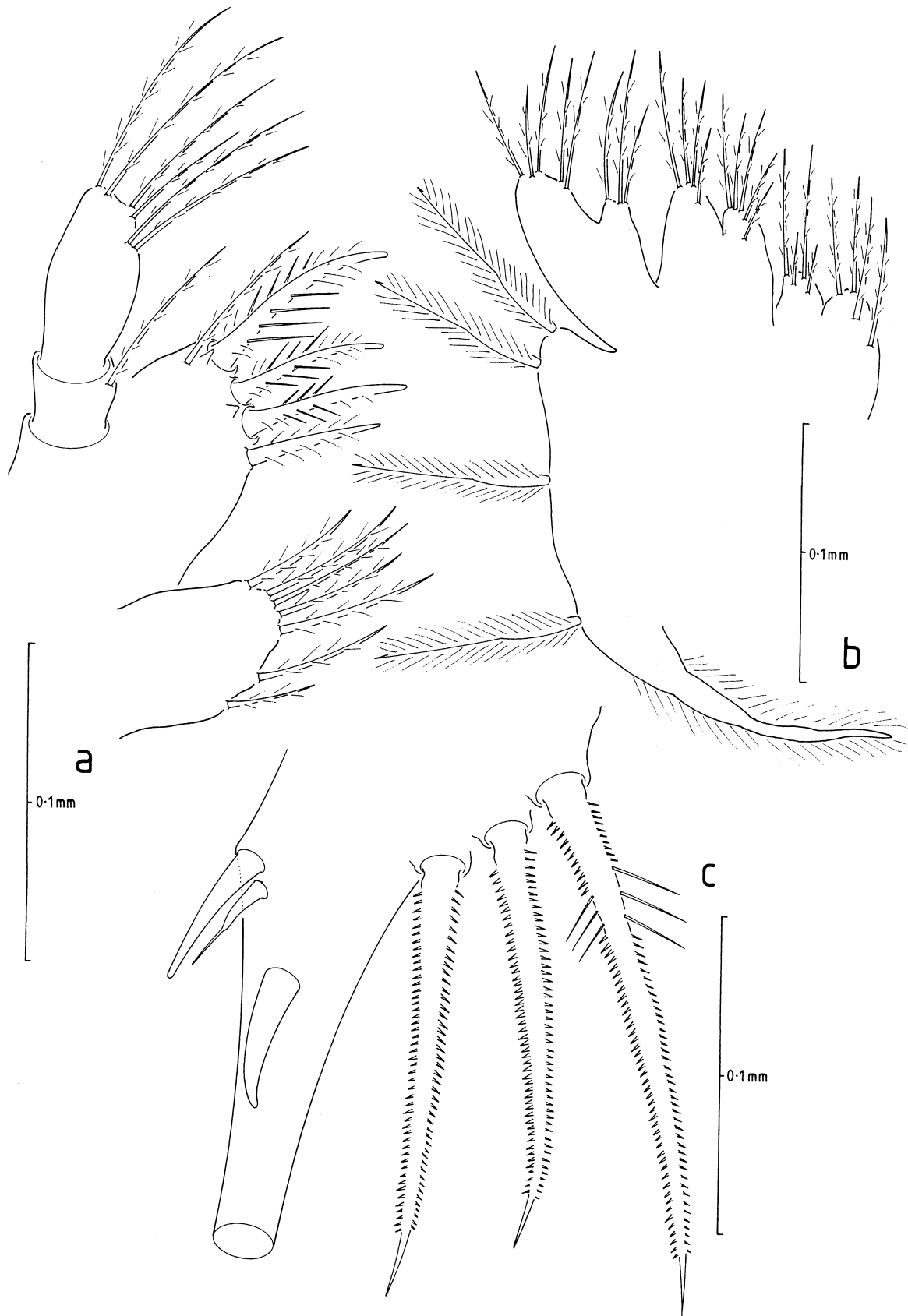


Fig. 2. *Atergatis floridus* (Linnaeus, 1767) first stage zoea; a) maxillule; b) maxilla; c) telson.

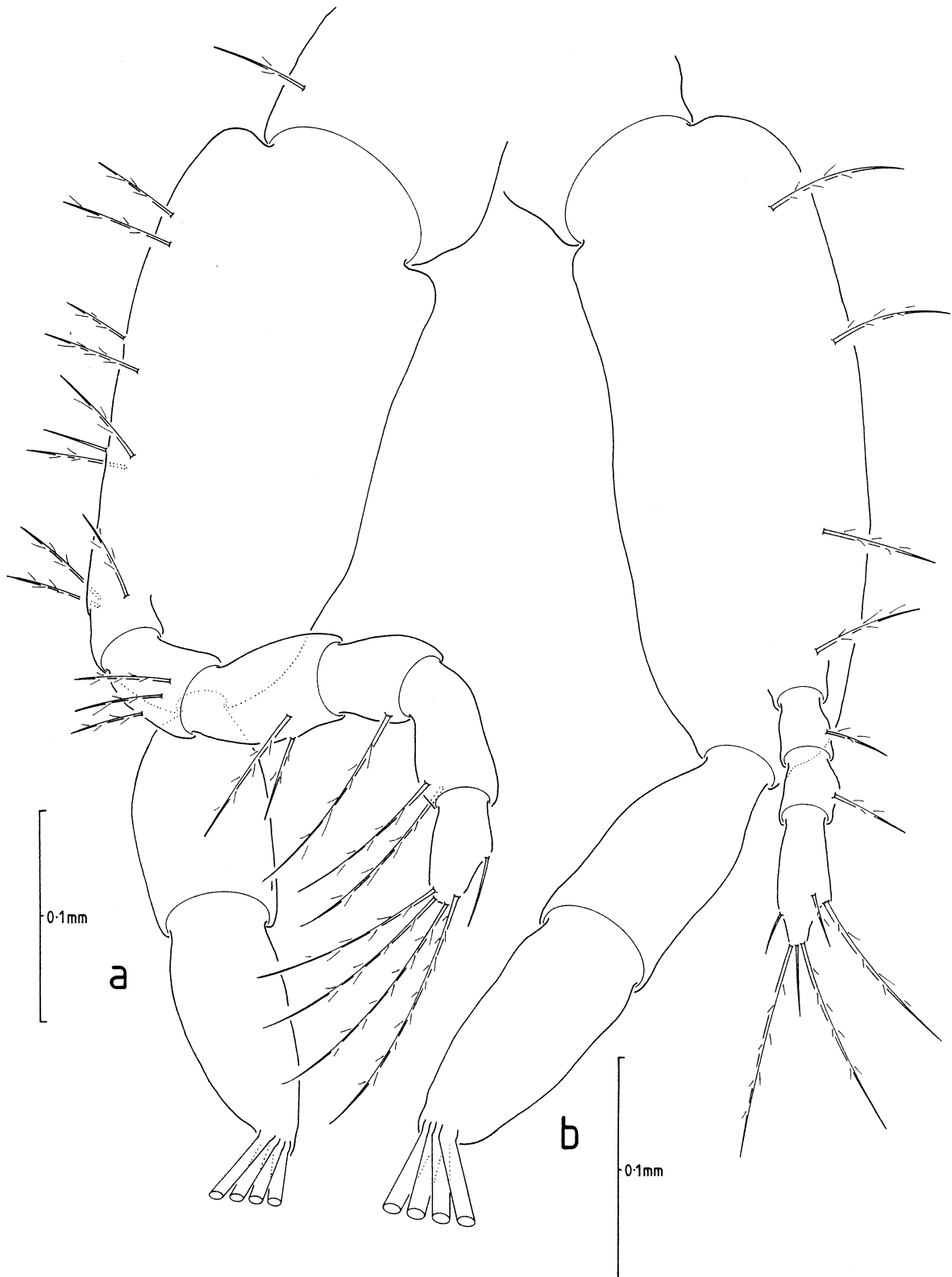


Fig. 3. *Atergatis floridus* (Linnaeus, 1767) first stage zoea; a) first maxilliped; b) second maxilliped.

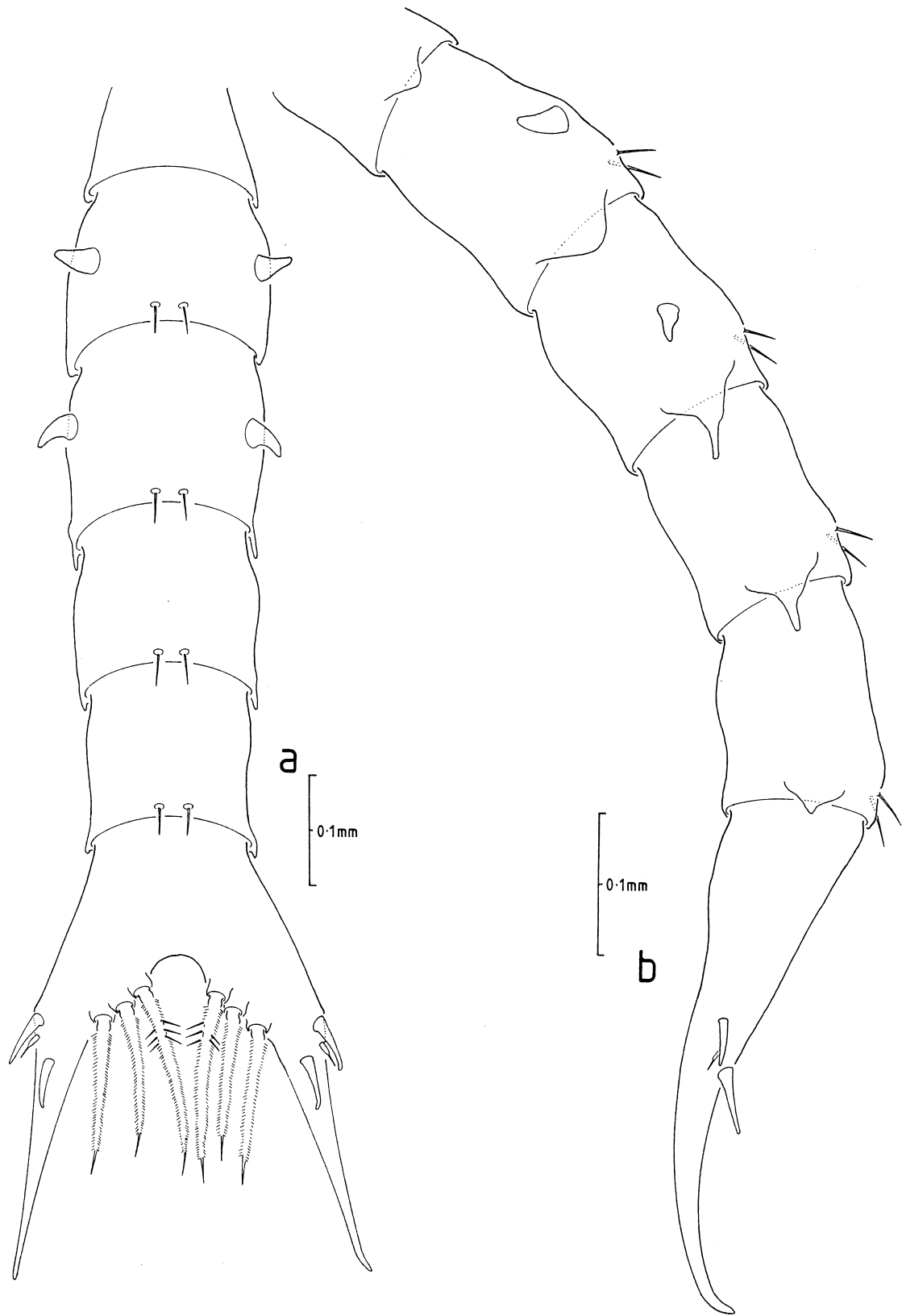


Fig. 4. *Atergatis floridus* (Linnaeus, 1767) first stage zoea; a) dorsal view of abdomen; b) lateral view of abdomen.

First maxilliped (Fig. 3a): coxa with 1 seta; basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 3,2,1,2,5 (1 subterminal, 4 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 3b): coxa without setae; basis with 4 setae arranged 1,1,1,1; endopod 3-segmented, with 1,1,6 (3 subterminal, 3 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

Abdomen (Figs. 4a, b): 5 somites; somite 2 with 1 pair of dorsolateral processes directed anteriorly; somite 3 with 1 pair of dorsolateral processes directed ventrally; somites 1-2 with rounded posterolateral processes and 3-5 with short posterolateral spinous processes; somite 1 without setae; somites 2-5 with 1 pair of posterodorsal setae; pleopod buds absent.

Telson (Figs. 2c, 4a, b): each fork long, gradually curved distally; 1 large and 1 smaller lateral spine; 1 large dorsal medial spine; posterior margin with 3 pairs of stout spinulate setae.

***Atergatis subdentatus* (de Haan, 1835)**

(Figs. 5-8)

Description. – Carapace (Figs. 5a, b): dorsal spine long, curved distally and approximately twice the length of the rostral spine; rostral spine just shorter in length than the antennal protopod and distally spinulate; lateral spines present and straight; 1 pair of posterodorsal setae; ventral margin without setae; eyes sessile.

Antennule (Fig. 5c): uniramous, endopod absent; exopod unsegmented with 2 broad, long and 2 slender, shorter, terminal aesthetascs plus 1 terminal seta.

Antenna (Fig. 5d): protopodal process distally multispinulate, just longer in length than rostral spine; endopod reduced to small spine; exopod *ca.* 16% length of protopod, possessing 3 (1 long subterminal, 2 unequal terminal) setae.

Mandible: palp absent.

Maxillule (Fig. 6a): epipod seta absent; coxal endite with 7 setae; basal endite with 5 setal processes and 2 small teeth; endopod 2-segmented, proximal segment with 1 seta; distal segment with 6 (2 subterminal, 4 terminal) setae; exopod seta absent.

Maxilla (Fig. 6b): coxal endite bilobed with 4+4 setae; basal endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal, 3 terminal) setae; exopod (scaphognathite) margin with 4 setae and 1 long stout distal process.

First maxilliped (Fig. 7a): coxa with 1 seta; basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 3,2,1,2,5 (1 subterminal, 4 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 7b): coxa without setae; basis with 4 setae arranged 1,1,1,1; endopod 3-segmented, with 1,1,6 (3 subterminal, 3 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

Abdomen (Figs. 8a, b): 5 somites; somite 2 with 1 pair of dorsolateral processes directed anteriorly; somite 3 with 1 pair of dorsolateral processes directed ventrally; somites 1-2 with rounded posterolateral processes and 3-5 with short posterolateral spinous processes; somite 1 without setae; somites 2-5 with 1 pair of posterodorsal setae; pleopod buds absent.

Telson (Figs. 6c, 8a, b): each fork long, gradually curved distally; 1 large and 1 finer lateral spine; 1 large dorsal medial spine; posterior margin with 3 pairs of stout spinulate setae.

***Atergatopsis germaini* A. Milne Edwards, 1865**

(Figs. 9-12)

Description. – Carapace (Figs. 9a, b): dorsal spine long, curved distally and approximately twice the length of the rostral spine; rostral spine shorter in length than the antennal protopod and distally spinulate; lateral spines present and straight; 1 pair of posterodorsal setae; ventral margin without setae; eyes sessile.

Antennule (Fig. 9c): uniramous, endopod absent; exopod unsegmented with 2 broad, long and 2 slender, shorter, terminal aesthetascs plus 1 terminal seta.

Antenna (Fig. 9d): protopodal process distally multispinulate, longer than the length of the rostral spine; endopod reduced to small spine; exopod rudimentary *ca.* 16% length of protopod, possessing 3 (1 long subterminal, 2 unequal terminal) setae.

Mandible: palp absent.

Maxillule (Fig. 10a): epipod seta absent; coxal endite with 7 setae; basal endite with 5 setal processes and 2 small teeth; endopod 2-segmented, proximal segment with 1 seta; distal segment with 6 (2 subterminal, 4 terminal) setae; exopod seta absent.

Maxilla (Fig. 10b): coxal endite bilobed with 4+4 setae; basal endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal, 3 terminal) setae; exopod (scaphognathite) margin with 4 setae and 1 long stout distal process.

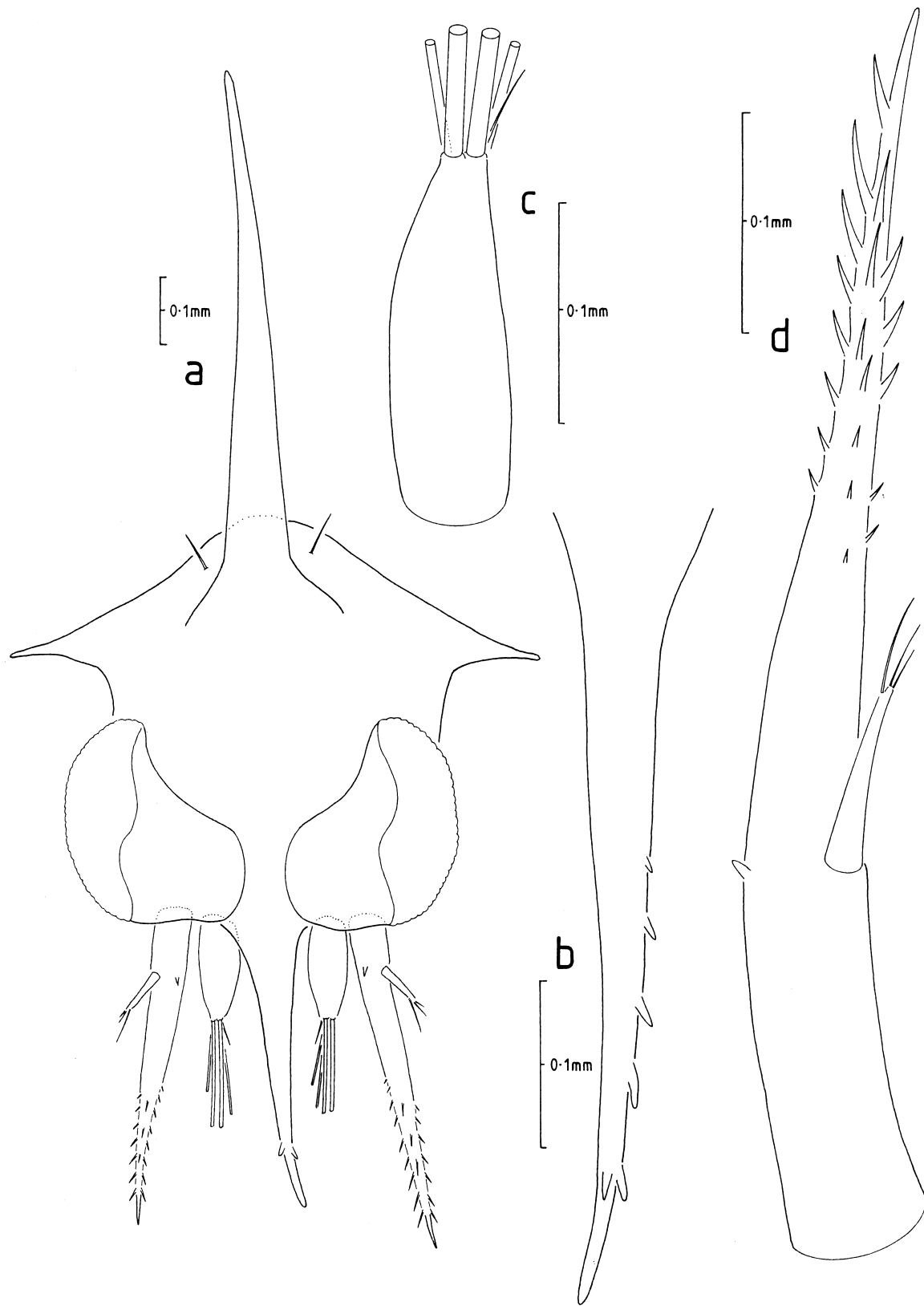


Fig. 5. *Atergatis subdentatus* (de Haan, 1835) first stage zoea; a) anterior view of carapace; b) antennule; c) antenna; d) rostral spine.

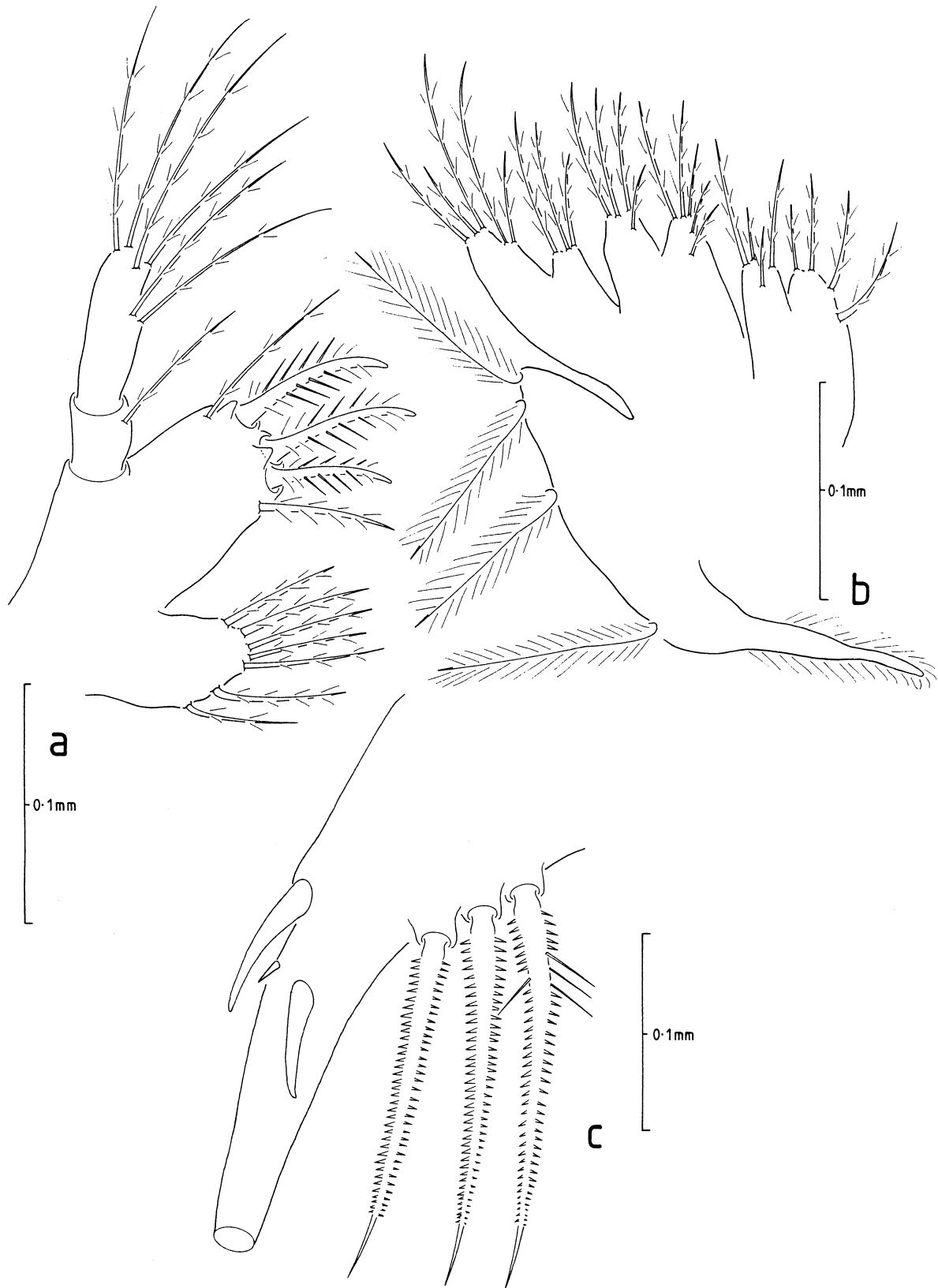


Fig. 6. *Atergatis subdentatus* (de Haan, 1835) first stage zoea; a) maxillule; b) maxilla; c) telson.

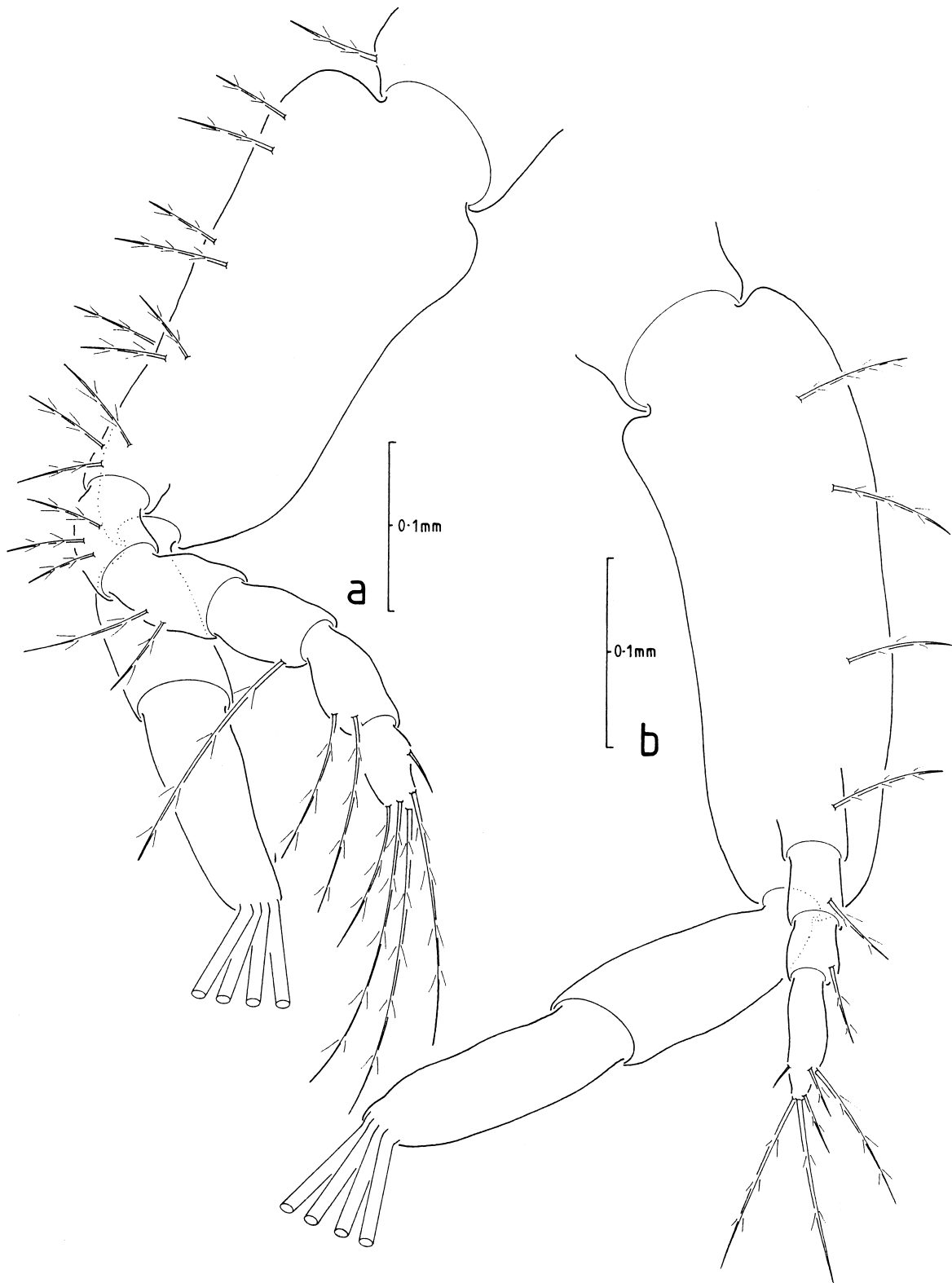


Fig. 7. *Atergatis subdentatus* (de Haan, 1835) first stage zoea; a) first maxilliped; b) second maxilliped.

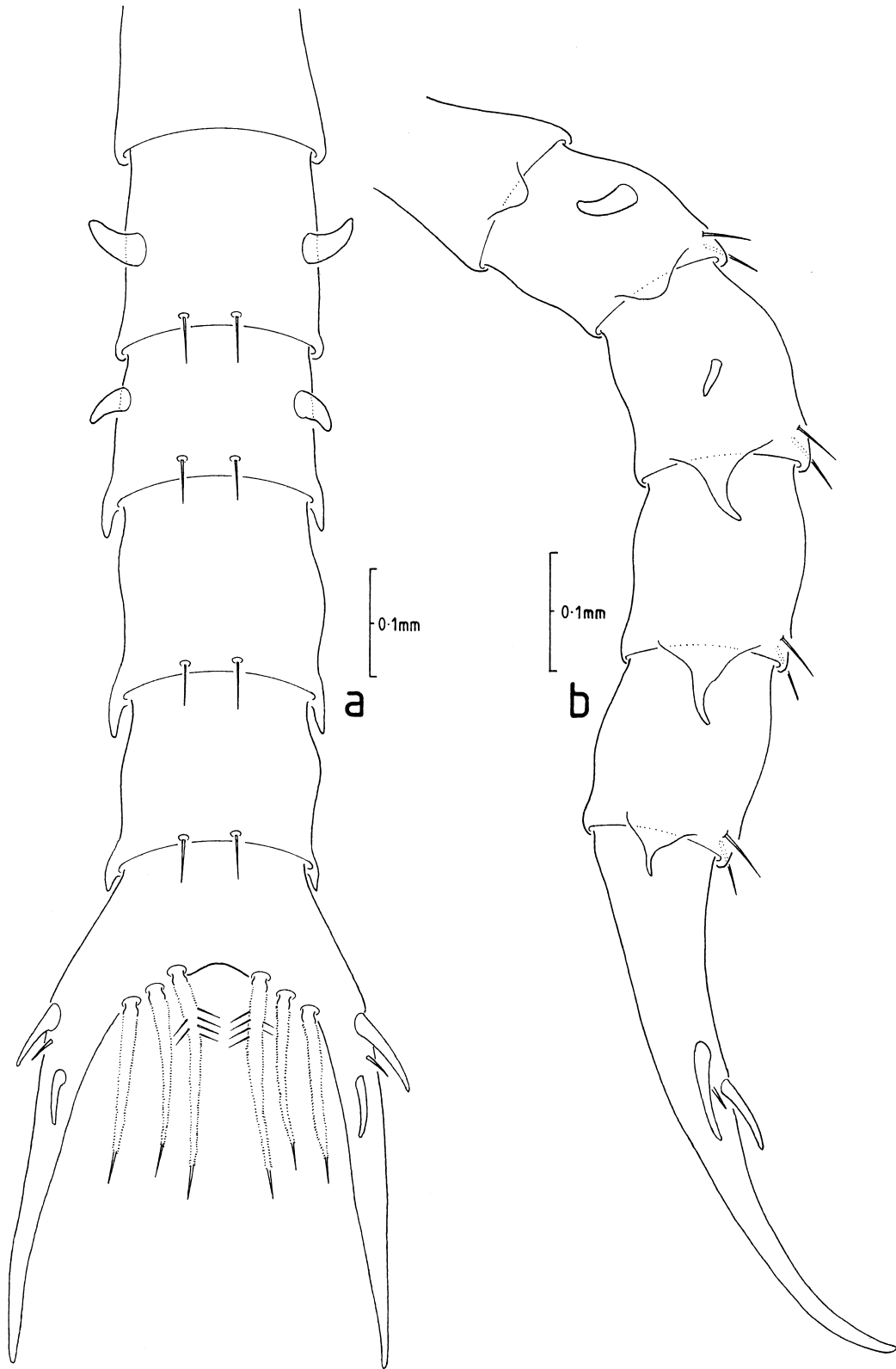


Fig. 8. *Atergatis subdentatus* (de Haan, 1835) first stage zoea; a) dorsal view of abdomen; b) lateral view of abdomen.

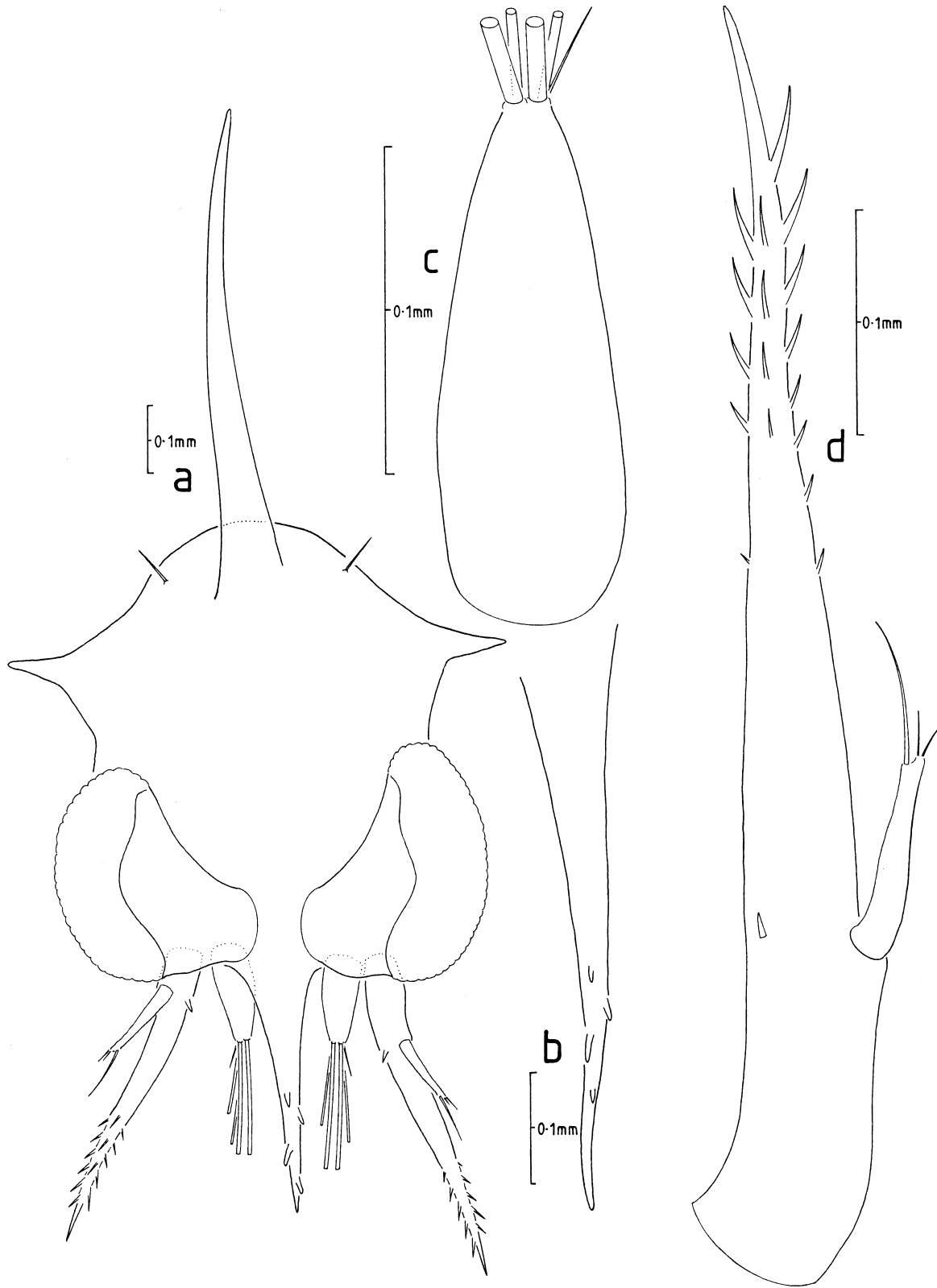


Fig. 9. *Atergatopsis germaini* A. Milne Edwards, 1865 first stage zoea; a) anterior view of carapace; b) rostral spine; c) antennule; d) antenna.

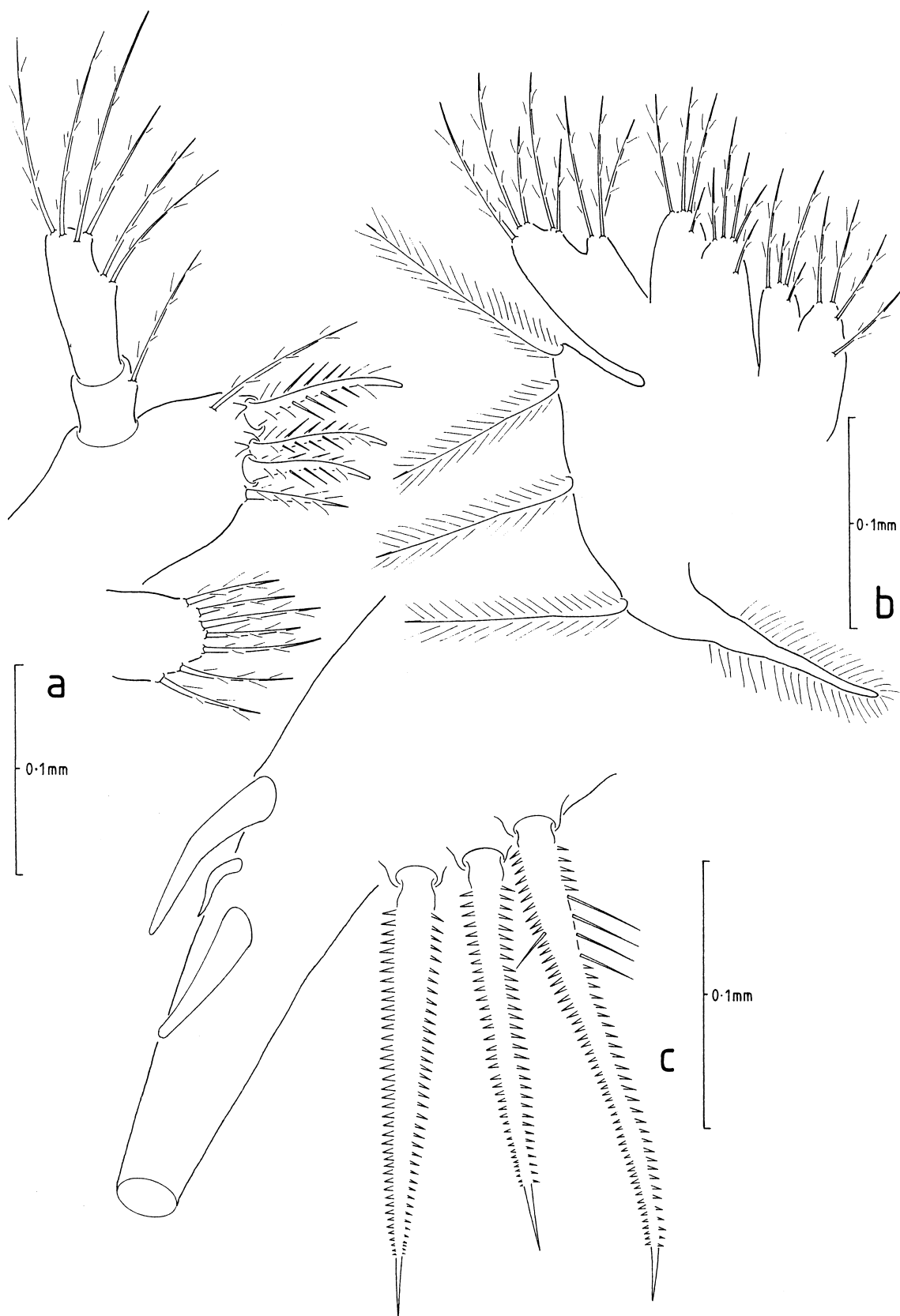


Fig. 10. *Atergatopsis germaini* A. Milne Edwards, 1865 first stage zoea; a) maxillule; b) maxilla; c) telson.

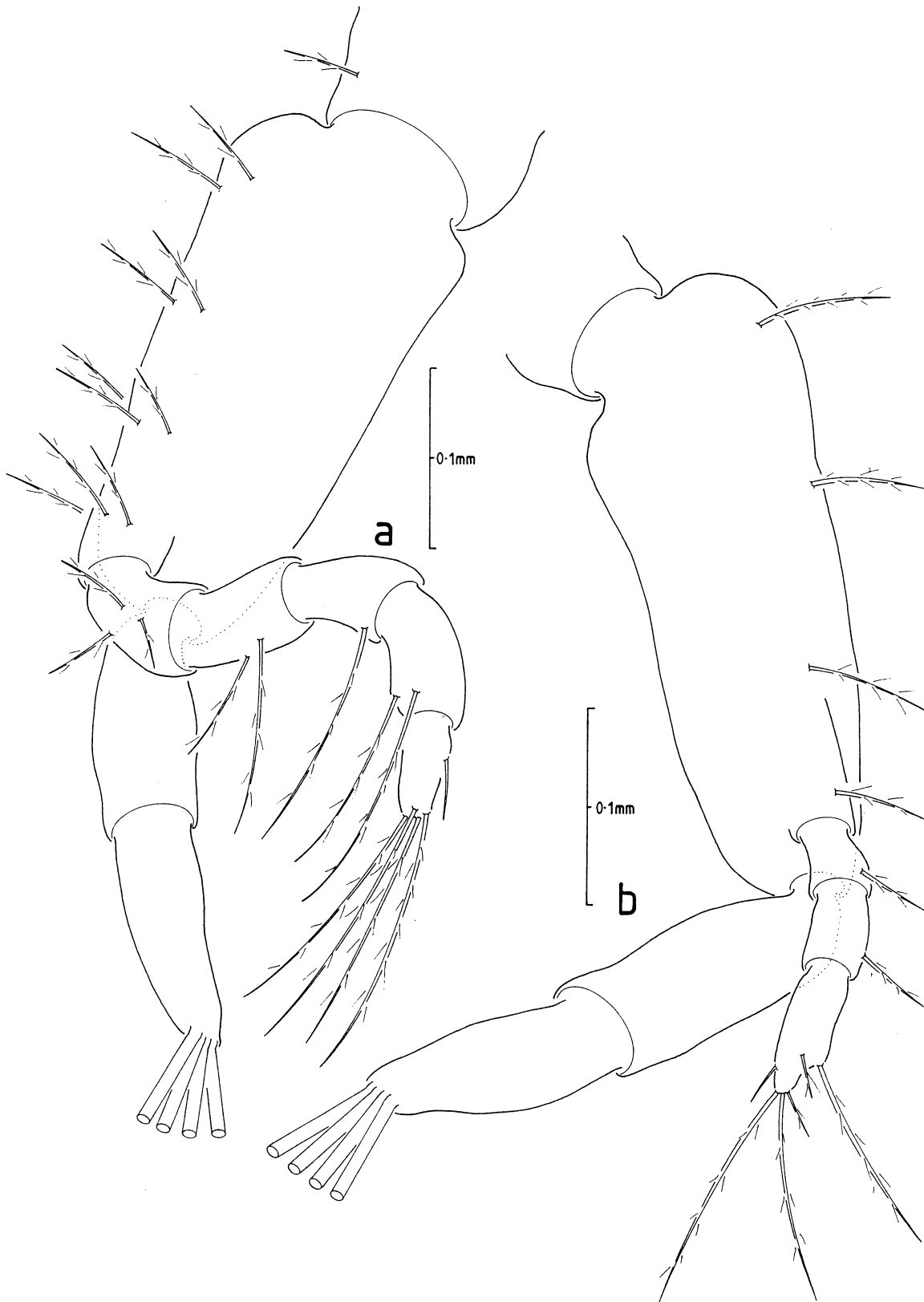


Fig. 11. *Atergatopsis germaini* A. Milne Edwards, 1865 first stage zoea; a) first maxilliped; b) second maxilliped.

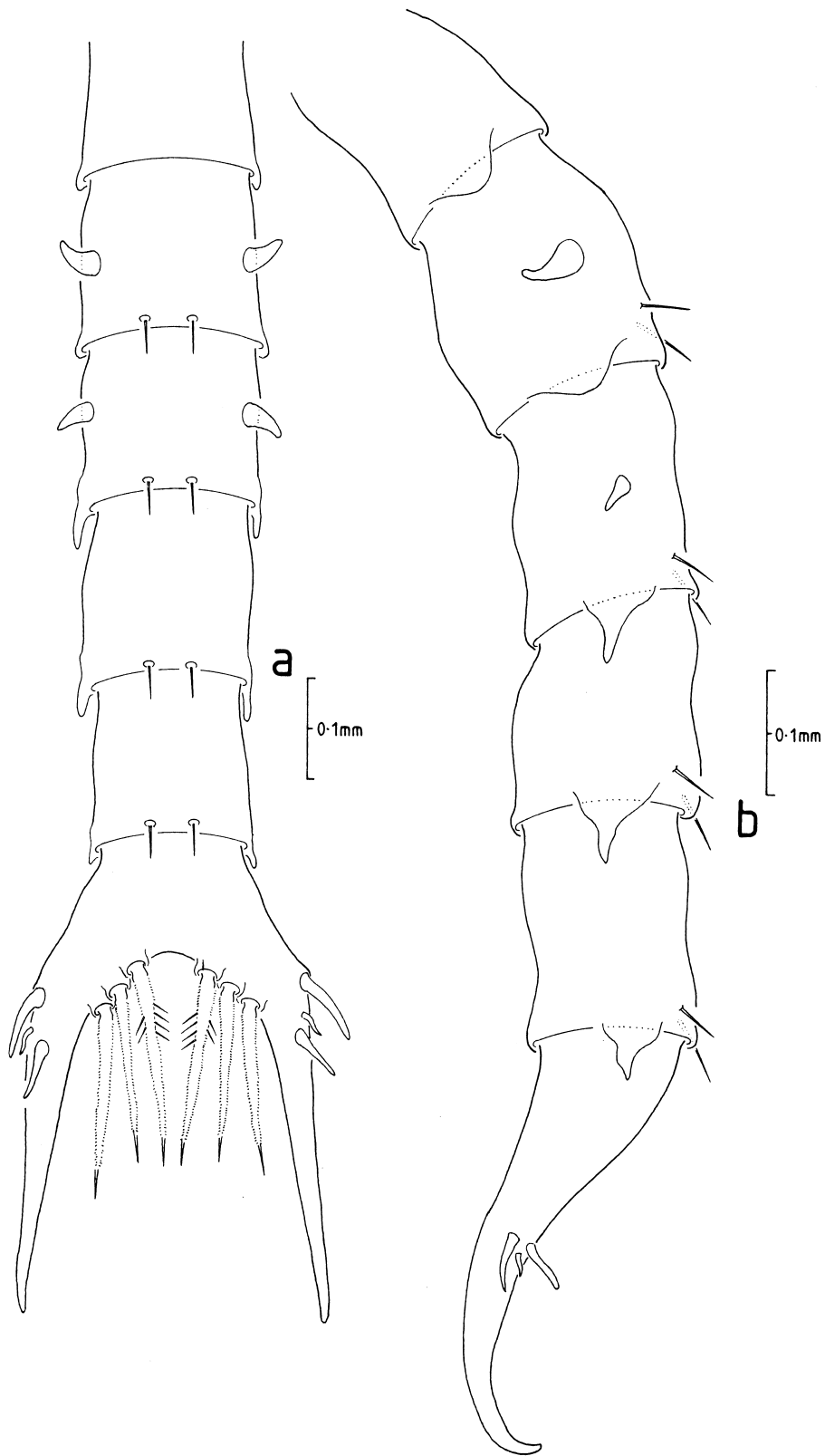


Fig. 12. *Atergatopsis germaini* A. Milne Edwards, 1865 first stage zoea; a) dorsal view of abdomen; b) lateral view of abdomen.

First maxilliped (Fig. 11a): coxa with 1 seta; basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 3,2,1,2,5 (1 subterminal, 4 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 11b): coxa without setae; basis with 4 setae arranged 1,1,1,1; endopod 3-segmented, with 1,1,6 (3 subterminal, 3 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

Abdomen (Figs. 12a, b): 5 somites; somite 2 with 1 pair of dorsolateral processes directed anteriorly; somite 3 with 1 pair of dorsolateral processes directed ventrally; somites 1-2 with rounded posterolateral processes and 3-5 with short posterolateral spinous processes; somite 1 without setae; somites 2-5 with 1 pair of posterodorsal setae; pleopod buds absent.

Telson (Figs. 10c, 12a, b): each fork long, gradually curved distally; 1 large and 1 smaller lateral spine; 1 large dorsal medial spine; posterior margin with 3 pairs of stout spinulate setae.

***Platypodia eydouxi* (A. Milne Edwards, 1865)**

(Figs. 13-16)

Description. – Carapace (Figs. 13a, b): dorsal spine long, curved distally and approximately twice the length of the rostral spine; rostral spine shorter in length than the antennal protopod and distally spinulate; lateral spines short; 1 pair of posterodorsal setae; ventral margin without setae; eyes sessile. Antennule (Fig. 13c): uniramous, endopod absent; exopod unsegmented with 2 broad, long and 2 slender, shorter, terminal aesthetascs plus 1 terminal seta.

Antenna (Fig. 13d): protopodal process distally multispinulate, longer than rostral spine; endopod reduced to small spine; exopod *ca.* 16% length of protopod, possessing 3 (1 long subterminal, 2 unequal terminal) setae.

Mandible: palp absent.

Maxillule (Fig. 14a): epipod seta absent; coxal endite with 7 setae; basal endite with 5 setal processes and 2 small teeth; endopod 2-segmented, proximal segment with 1 seta; distal segment with 6 (2 subterminal, 4 terminal) setae; exopod seta absent.

Maxilla (Fig. 14b): coxal endite bilobed with 4+4 setae; basal endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal, 3 terminal) setae; exopod (scaphognathite) margin with 4 setae and 1 long stout distal process.

First maxilliped (Fig. 15a): coxa with 1 seta; basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 3,2,1,2,5 (1 subterminal, 4 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 15b): coxa without setae; basis with 4 setae arranged 1,1,1,1; endopod 3-segmented, with 1,1,6 (3 subterminal, 3 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

Abdomen (Figs. 16a, b): 5 somites; somite 2 with 1 pair of dorsolateral processes directed anteriorly; somite 3 with 1 pair of dorsolateral processes directed ventrally; somites 1-2 with rounded posterolateral processes [spinulated on somite 2] and 3-5 with short posterolateral spinous processes; somite 1 without setae; somites 2-5 with 1 pair of posterodorsal setae; pleopod buds absent.

Telson (Figs. 14c, 16a, b): each fork long, gradually curved distally; 1 large and 1 smaller lateral spine; 1 large dorsal medial spine; posterior margin with 3 pairs of stout spinulate setae.

ACTAEINAE ALCOCK, 1898

***Actaeodes tomentosus* (H. Milne Edwards, 1834)**

(Figs. 17-20)

Actaeodes tomentosus: Clark & Al-Aidaros, 1996: 208, Figs. 1f,g, 3a, ZI (not complete).

Description. – Carapace (Figs. 17a, b): dorsal spine long, curved distally and approximately twice the length of the rostral spine; rostral spine shorter in length than the antennal protopod and distally spinulate; lateral spines present; 1 pair of posterodorsal setae; ventral margin without setae; eyes sessile.

Antennule (Fig. 17c): uniramous, endopod absent; exopod unsegmented with 2 broad, long and 2 slender, shorter, terminal aesthetascs plus 1 terminal seta.

Antenna (Fig. 17d): protopodal process distally multispinulate, longer than rostral spine; endopod reduced to small spine; exopod *ca.* 16% length of protopod, possessing 3 (1 long subterminal, 2 unequal terminal) setae.

Mandible: palp absent.

Maxillule (Fig. 18a): epipod seta absent; coxal endite with 7 setae; basal endite with 5 setal processes and 2 small teeth; endopod 2-segmented, proximal segment with 1 seta; distal segment with 6 (2 subterminal, 4 terminal) setae; exopod seta absent.

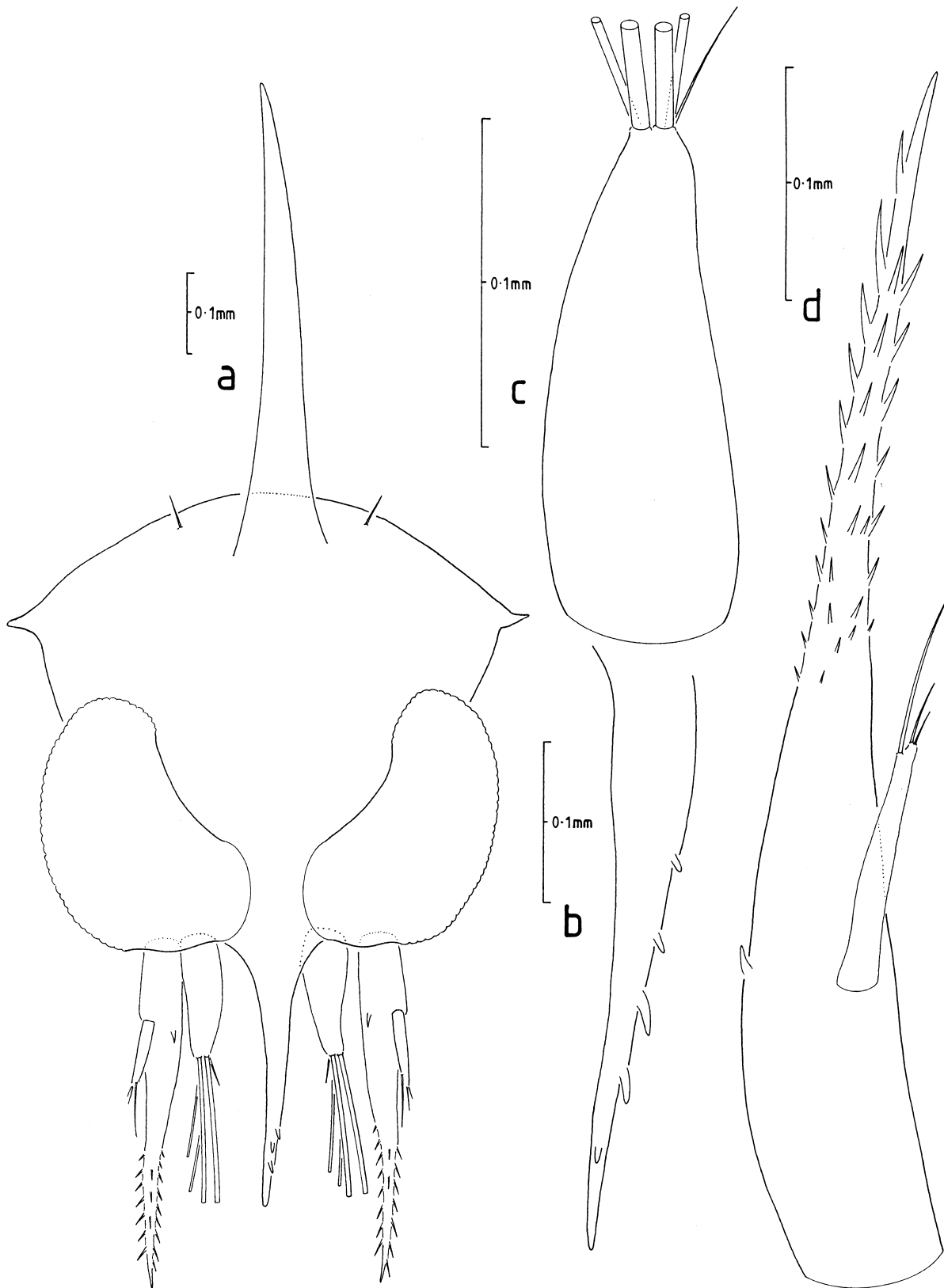


Fig. 13. *Platypodia eydouxi* (A. Milne Edwards, 1865) first stage zoea; a) anterior view of carapace; b) antennule; c) antenna; d) rostral spine.

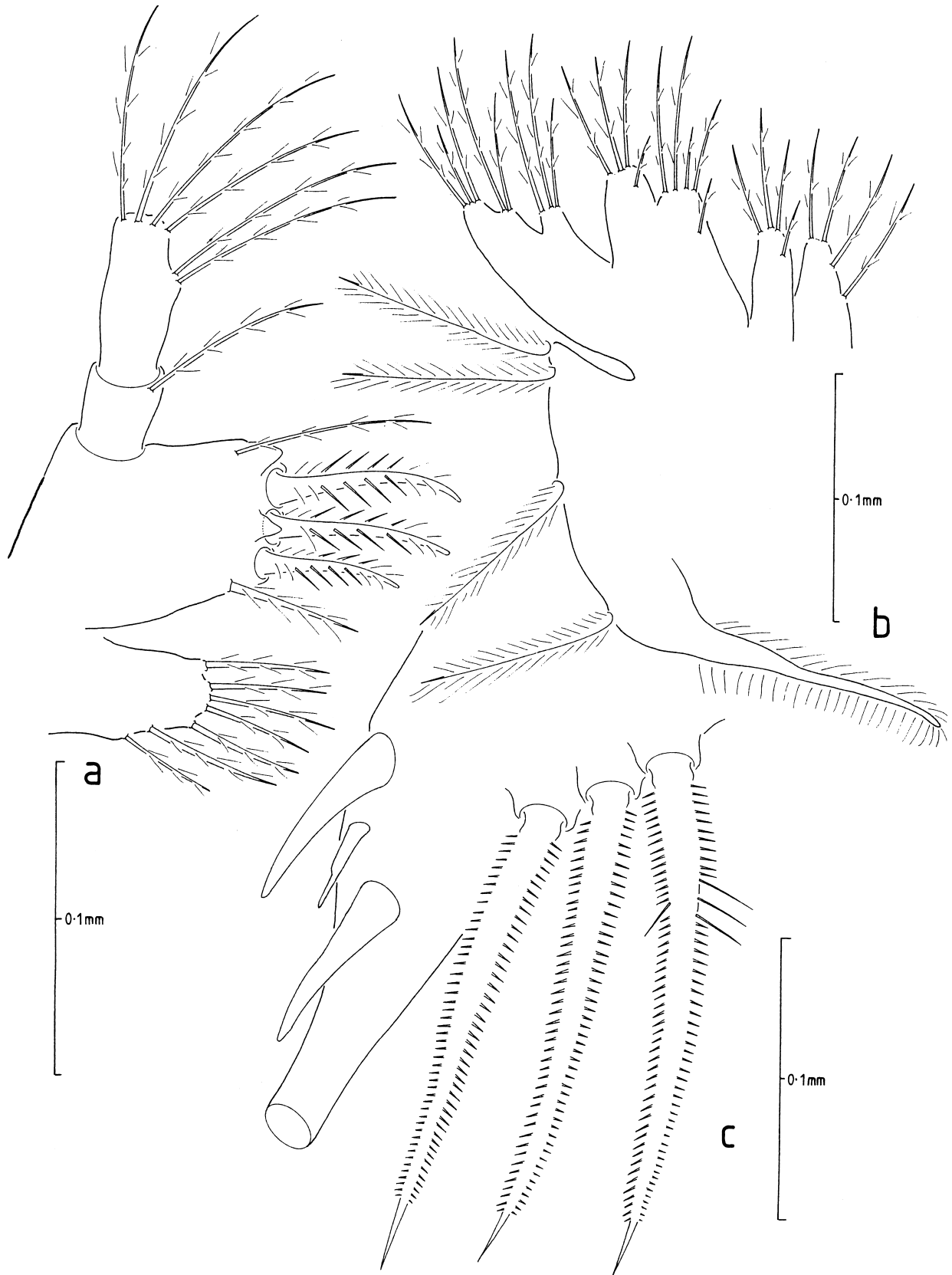


Fig. 14. *Platypodia eydouxi* (A. Milne Edwards, 1865) first stage zoea; a) maxillule; b) maxilla; c) telson.

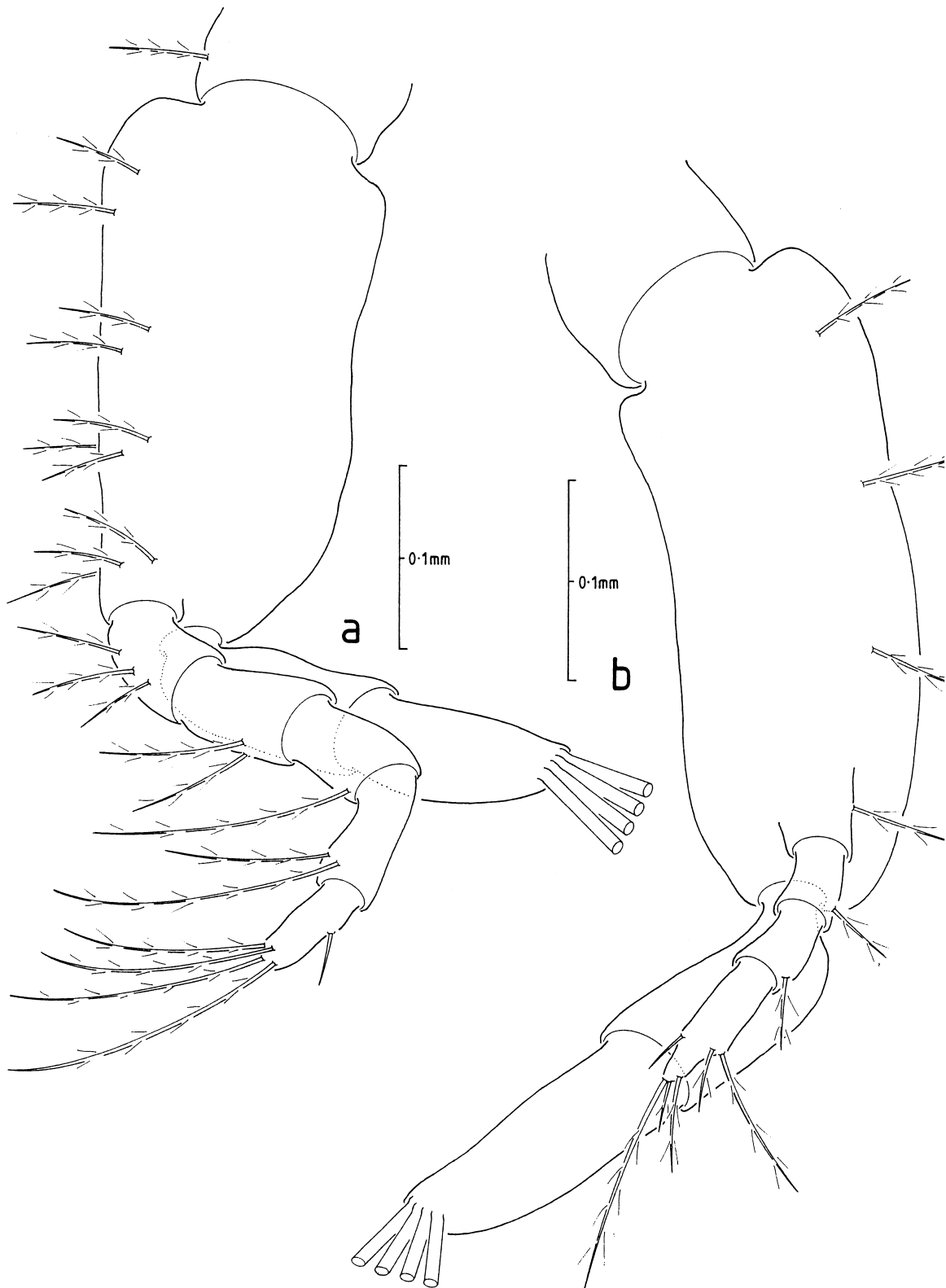


Fig. 15. *Platypodia eydouxi* (A. Milne Edwards, 1865) first stage zoea; a) first maxilliped; b) second maxilliped.

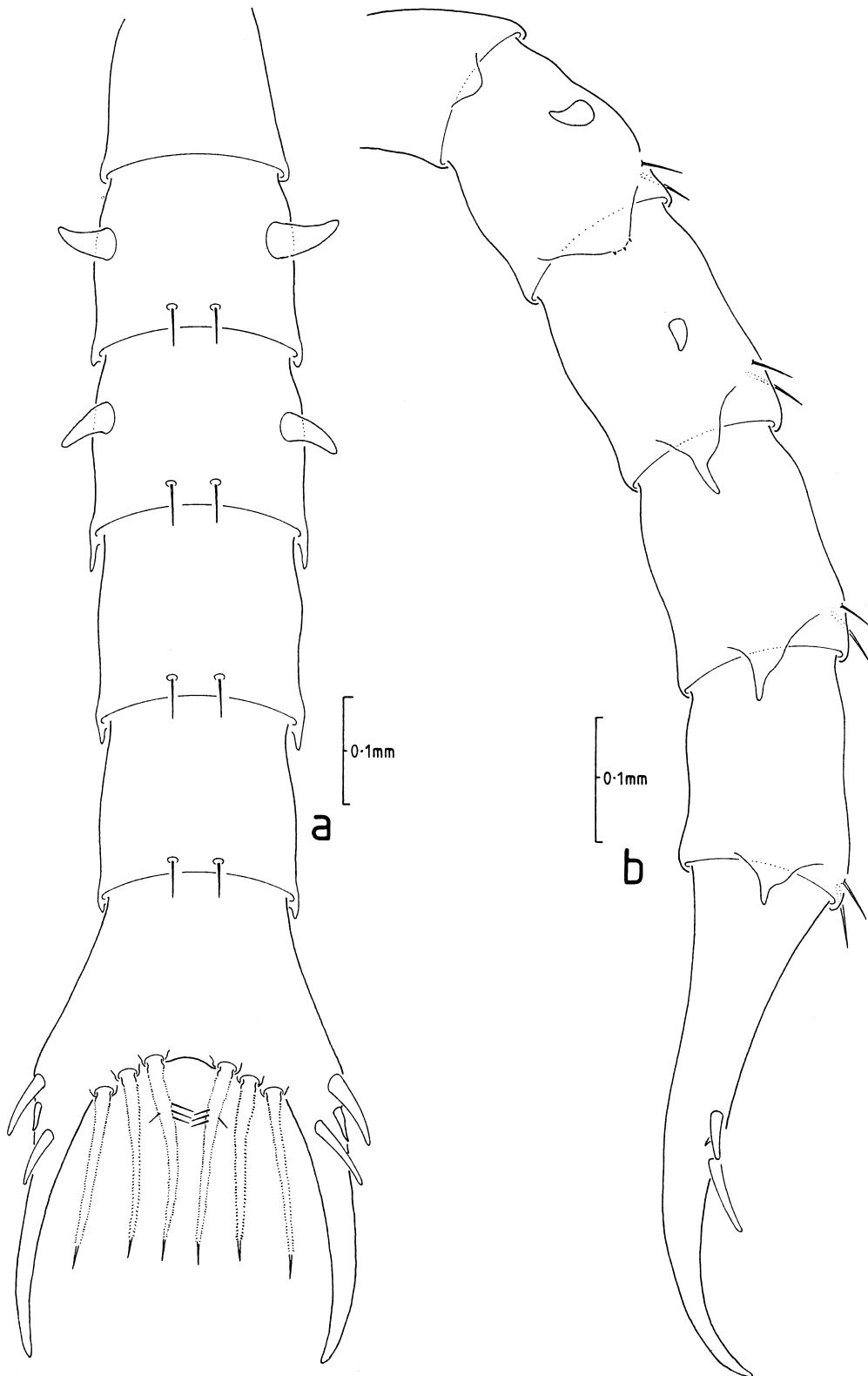


Fig. 16. *Platypodia eydouxi* (A. Milne Edwards, 1865) first stage zoea; a) dorsal view of abdomen; b) lateral view of abdomen.

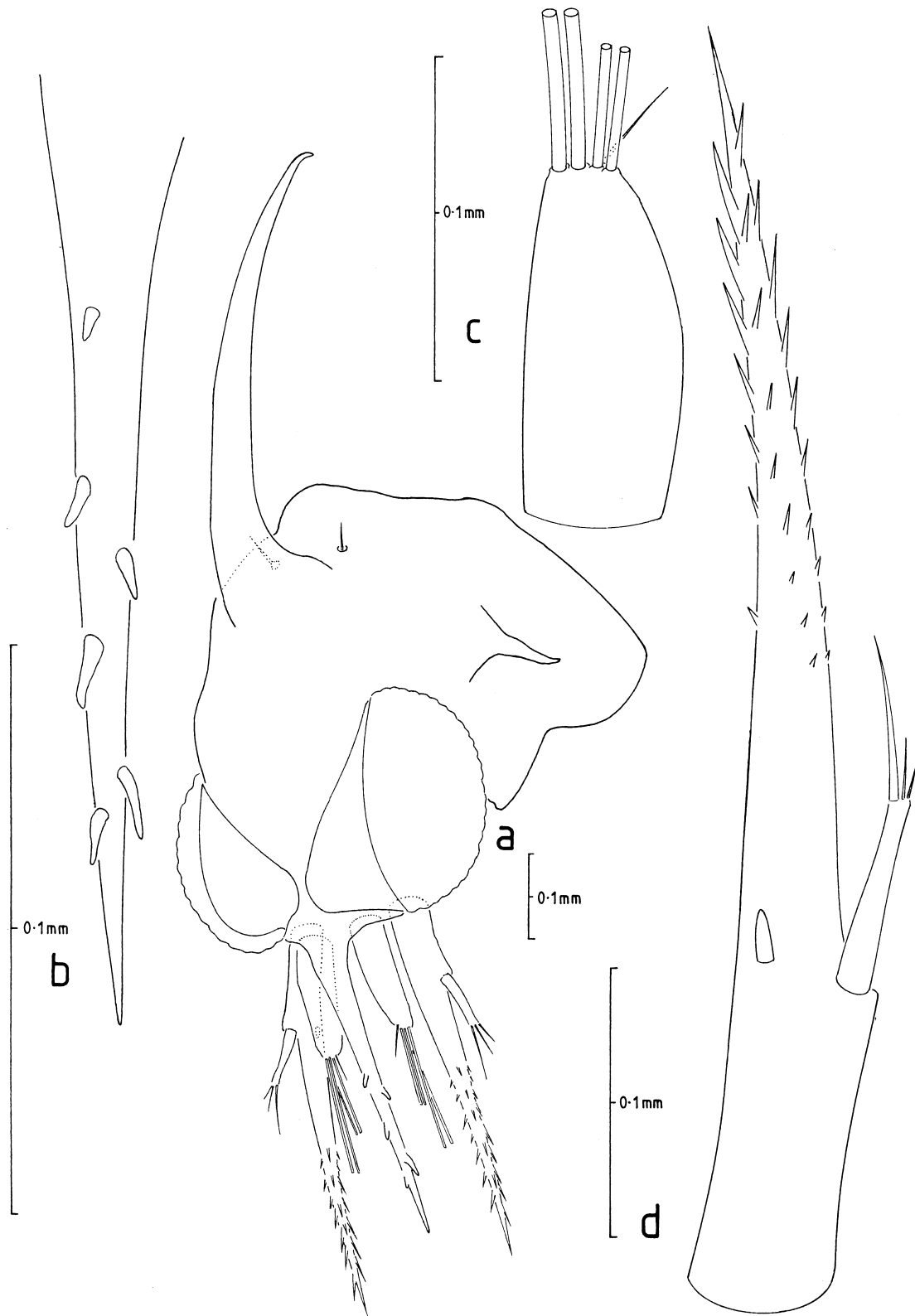


Fig.17. *Actaeodes tomentosus* (H. Milne Edwards, 1834) first stage zoea; a) lateral view of carapace; b) antennule; c) antenna; d) rostral spine.

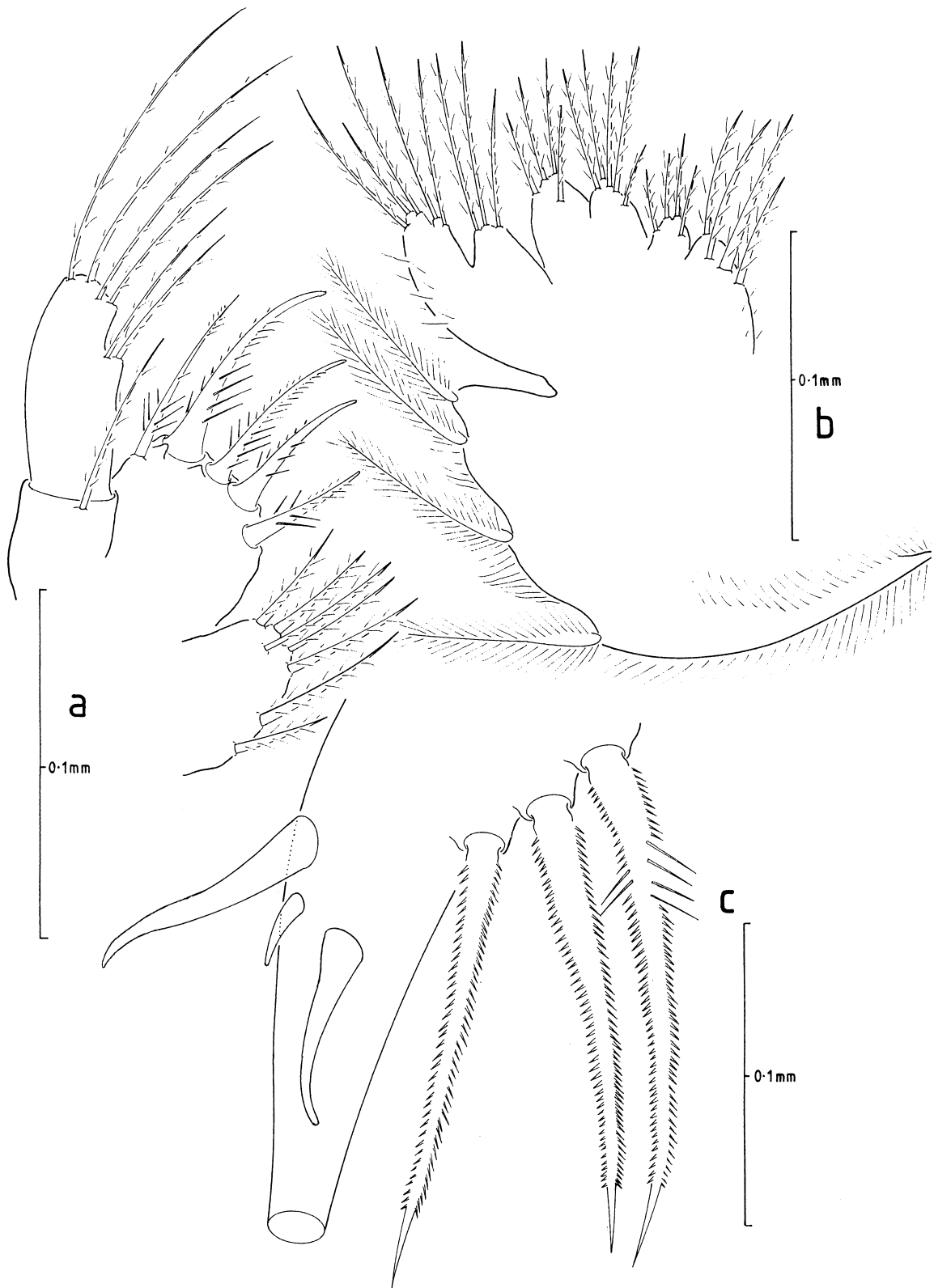


Fig. 18. *Actaeodes tomentosus* (H. Milne Edwards, 1834) first stage zoea; a) maxillule; b) maxilla; c) telson.

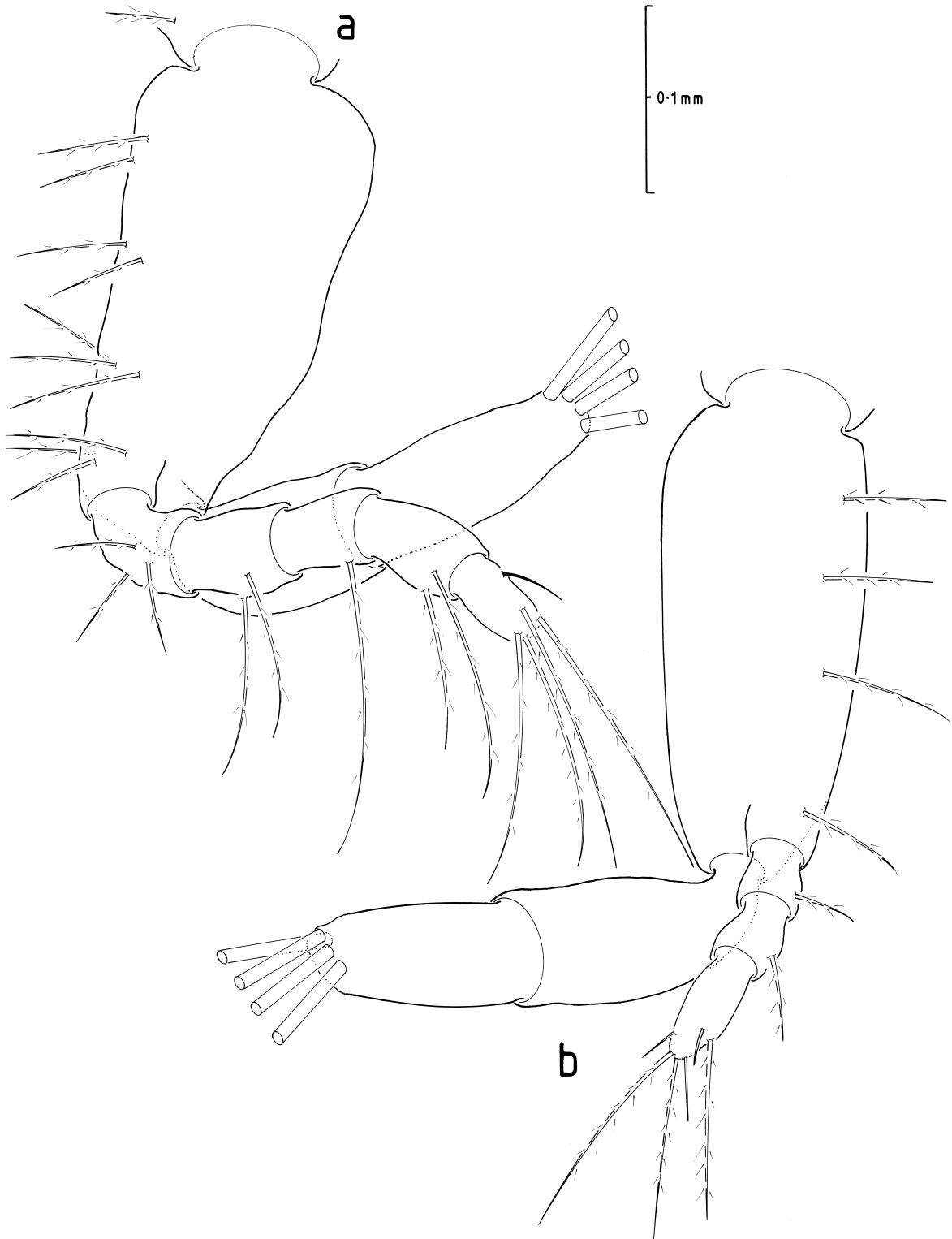


Fig. 19. *Actaeodes tomentosus* (H. Milne Edwards, 1834) first stage zoea; a) first maxilliped; b) second maxilliped.

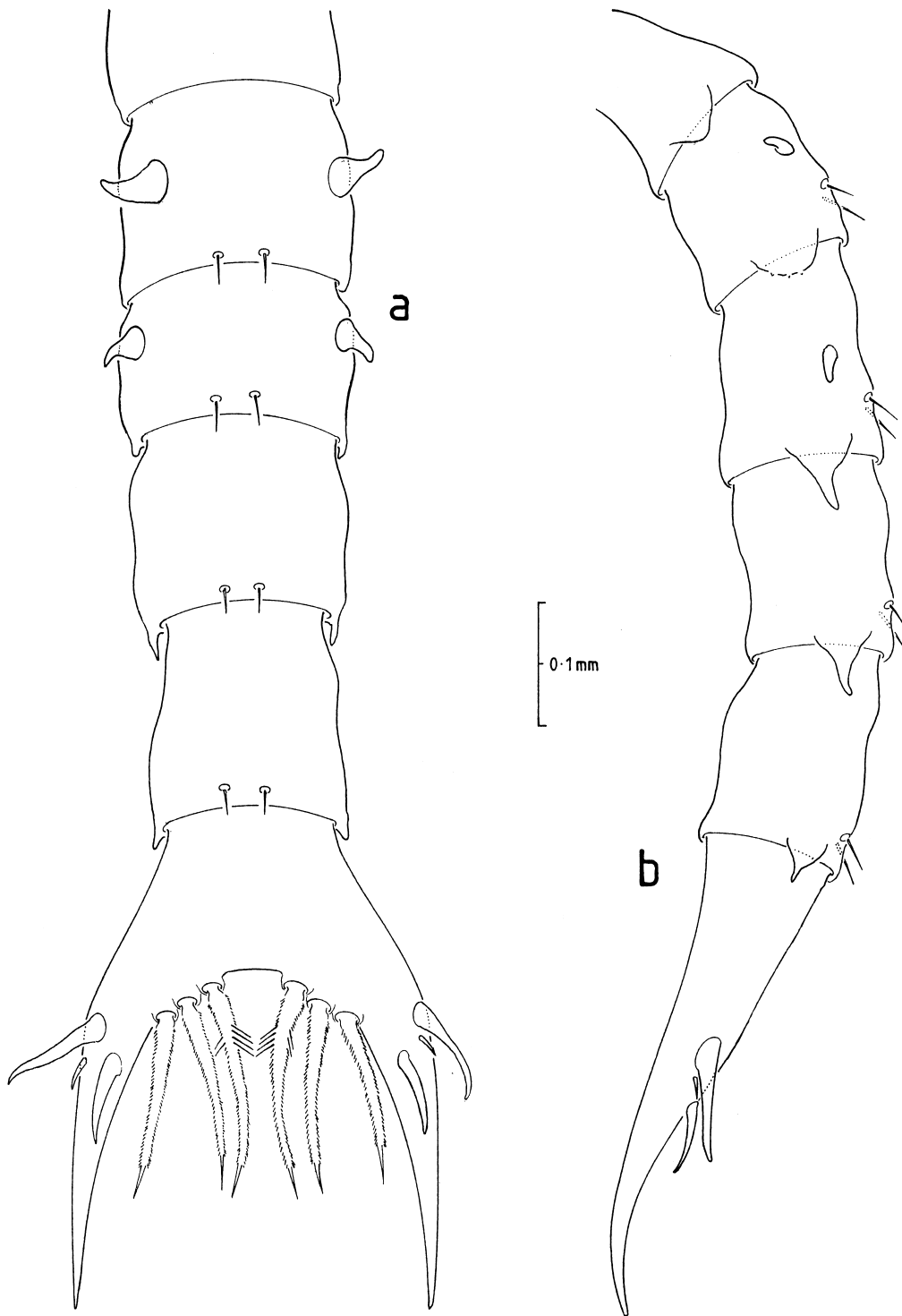


Fig. 20. *Actaeodes tomentosus* (H. Milne Edwards, 1834) first stage zoea; a) dorsal view of abdomen; b) lateral view of abdomen.

Table 1. A comparison between the zozimine first stage zoeal descriptions of *Atergatis floridus* by Tanaka & Konishi (2001) and the specimens described from Singapore for the present study.

Character	<i>Atergatis floridus</i> (see Tanaka & Konishi, 2001)	<i>Atergatis floridus</i> (present study)
CARAPACE	Fig. 2A	Fig. 1b
rostral spine distally spinulate	absent	present
ANTENNULE	Fig. 3A	Fig. 1c
terminal setation	3 aesthetascs, 1 seta	4 aesthetascs, 1 seta
ANTENNA	Fig. 3F, F'	Fig. 1d
endopod spine	absent	present
exopod terminal setation	2	3

Table 2. A comparison between known *Atergatis* first stage zoeal descriptions; *A. reticulatus* by Terada (1980) plus *A. floridus* and *A. subdentatus* both examined for the present study.

Character	<i>Atergatis reticulatus</i> (see Terada 1980)	<i>Atergatis floridus</i> (present study)	<i>Atergatis subdentatus</i> (present study)
CARAPACE	Fig. 1.D1	Fig. 1a, b	Fig. 5a, b
pair of posterodorsal setae	absent	present	present
rostral spine distally spinulate	absent	present	present
ANTENNA	Fig. 2 D'1	Fig. 1d	Fig. 5d
endopod spine	absent	present	present
protopod - exopod %	6%	15%	16%
TELSON	Fig. 3 D1	Figs. 2a, 4a, b	Figs. 6a, 8a, b
lateral spines	2 fine spines	1 large + 1 smaller spine	1 large + 1 smaller

Maxilla (Fig. 18b): coxal endite bilobed with 4+4 setae; basal endite bilobed with 5+4 setae; endopod bilobed, with 3+5 (2 subterminal, 3 terminal) setae; exopod (scaphognathite) margin with 4 setae and 1 long stout distal process.

First maxilliped (Fig. 19a): coxa with 1 seta; basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 3,2,1,2,5 (1 subterminal, 4 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 19b): coxa without setae; basis with 4 setae arranged 1,1,1,1; endopod 3-segmented, with 1,1,6 (3 subterminal, 3 terminal) setae respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

Abdomen (Figs. 20a, b): 5 somites; somite 2 with 1 pair of dorsolateral processes directed anteriorly; somite 3 with 1 pair of dorsolateral processes directed ventrally; somites 1-2 with rounded posterolateral processes [spinulated on somite 2] and 3-5 with short posterolateral spinous processes; somite 1 without setae; somites 2-5 with 1 pair of posterodorsal setae; pleopod buds absent.

Telson (Figs. 18c, 20a, b): each fork long, gradually curved distally; 1 large and 1 smaller lateral spine; 1 large dorsal medial spine; posterior margin with 3 pairs of stout spinulate setae.

COMPARATIVE ZOEAL MORPHOLOGY

The first stage zoeas of *Atergatis floridus* described from Japan by Tanaka & Konishi (2001) were compared with material collected and hatched in Singapore. The two accounts differ with respect to the spinulation on the rostral spine, the terminal setation of the antennule, the antennal endopod spine and the number of terminal seta on the antennal exopod (see Table 1). These characters were most likely overlooked by Tanaka & Konishi (2001). *Atergatis subdentatus* first stage zoeas are described in the present study for the first time and together with *A. floridus* are compared with the description of *A. reticulatus* by Terada (1980). The *Atergatis* zoeal descriptions from this study differ from those of Terada (1980) in the following characters: a pair of posterodorsal setae on the carapace; the distal spinulation on the rostral spine; the endopod spine on the antennal protopod and the size of the lateral spines on the telson (see Table 2). These differences were probably overlooked by Terada (1980). From Table 2, antennal protopod/exopod ratios of 6% for *Atergatis reticulatus* versus 15% and 16% for *A. floridus* and *A. subdentatus* respectively, suggest that it may not be a significant taxonomic character within the Zosiminae.

The zoeal stages of *Zosimus aeneus*, the type species of the type genus of the Zosiminae, were described by Tanaka (1999) and his first zoeal stage description is compared here with those of *A. floridus* and *A. subdentatus*. These descriptions differ with respect to the recording of the following characters: a pair of posterodorsal setae on the carapace; the distal spinulation of the rostral spine; the terminal setation of the antennule, the endopod spine on the antennal protopod, the antennal protopod/exopod ratio and

Table 3. A comparison between the first zoeal stage descriptions of *Zosimus aeneus* by Tanaka (1999) with *Atergatis floridus* and *A. subdentatus* examined for the present study.

Character	<i>Zosimus aeneus</i> (see Tanaka, 1999)	<i>Atergatis floridus</i> (present study)	<i>Atergatis subdentatus</i> (present study)
CARAPACE	Fig. 1A	Fig. 1a, b	Fig. 5a, b
pair of posterodorsal setae	absent	present	present
rostral spine distally spinulate	absent	present	present
ANTENNULE	Fig. 2A	Fig. 1c	Fig. 5c
terminal setation	2 aesthetascs, 1 seta	4 aesthetascs, 1 seta	4 aesthetascs, 1 seta
ANTENNA	Fig. 2E	Fig. 1d	Fig. 5d
endopod spine	absent	present	present
protopod - exopod %	21%	15%	16%
MAXILLULE	Fig. 3A	Fig. 1a	Fig. 6a
coxal setation	6	7	7

Table 4. A comparison between the first stage zoeal description of *Platypodiella spectabilis* by Fransozo et al. (2001) and re-examined by the present study.

Character	<i>Platypodiella spectabilis</i> (Fransozo et al., 2001)	<i>Platypodiella spectabilis</i> (present study)
CARAPACE	Figs. 1a, 3a	
pair of posterodorsal setae	absent	present
ANTENNULE	Fig. 1c	
terminal setation	3 aesthetascs, 2 setae ¹	4 aesthetascs, 1 seta
ANTENNA	Fig. 1d	
exopod terminal setation	2	3
protopod - exopod %	7%	13%
MAXILLULE	Fig. 2b	
coxal setation	6	7
MAXILLA	Fig. 2c	
basal endite setation	4+4	5+4
SECOND MAXILLIPED	Fig. 2e	
setation of distal endopod segment	5 setae (2 subterminal, 3 terminal)	6 setae (3 subterminal, 3 terminal)

¹Antennules of *Platypodiella spectabilis* from British Virgin Islands scored 2 aesthetascs and 2 setae (see Fransozo et al., 2001, Fig. 3c).

Table 5. A comparison between the first stage zoeal description of *Actaeodes hirsutissimus* and *A. tomentosus* by Clark & Al-Aidaros (1994), and *Atergatopsis germaini* by the present study.

Character	<i>Actaeodes hirsutissimus</i> (Clark & Al-Aidaros, 1994)	<i>Actaeodes tomentosus</i> (Clark & Al-Aidaros, 1994 and figures from this present study)	<i>Atergatopsis germaini</i> (present study)
ANTENNA	Fig. 1e, h	Fig. 17d	Fig. 9d
exopod terminal setation	1	3	3
protopod - exopod %	8%	16%	16%
TELSON	Fig. 3d	Fig. 18c	Fig. 10c
lateral spines	1 large + 1 minute spine	1 large + 1 smaller spine	1 large + 1 smaller spine

the coxal setation of the maxillule (see Table 3). Unfortunately, the larval stages described by Tanaka (1999) were not available for study (Tanaka, pers. comm.) as detailed by Rice (1979) and Clark et al. (1998). There is no explanation for the discrepancies listed in Table 3, especially the coxal setation score of 6 for the maxillule by Tanaka (1999) when all xanthids examined by the authors of the present study score 7 setae for this character.

The only Atlantic zosimine first stage zoea to be described is that of *Platypodiella spectabilis* by Fransozo et al. (2001). The first stage zoeas of *Platypodiella spectabilis* from the British Virgin Islands were re-examined by this study and were compared with the description of Fransozo et al. (2001). There are a number of significant zoeal differences between the two studies (see Table 4).

Table 6. A comparison between known Zosiminae first stage zoeal descriptions; *Atergatis reticulatus* by Terada (1980), *Platypodiella spectabilis* by the present study, *Zosimus aeneus* by Tanaka (1999), *Lophozozymus pictor* by Clark & Ng (1998), *Zozymodes xanthoides* by Clark & Paula (2003) plus *Atergatis floridus*, *A. subdentatus*, *Atergatis germaini* and *Platypodia eydouxi* examined for the present study, and two Actaeinae, *Actaeodes hirsutissimus* and *A. tomentosus* both by Clark & Al-Aidaros (1996) with supplementary figures for the latter species provided by the present study.

Character	<i>Actaeodes hirsutissimus</i> (see Clark & Al-Aidaros, 1996)	<i>Actaeodes tomentosus</i> (present study)	<i>Atergatis floridus</i> (present study)	<i>Atergatis reticulatus</i> (see Terada 1980)	<i>Atergatis subdentatus</i> (present study)	<i>Atergatis germaini</i> (present study)	<i>Lophozozymus pictor</i> (see Clark & Ng, 1998)	<i>Platypodia eydouxi</i> (present study)	<i>Platypodiella spectabilis</i> (present study)	<i>Zosimus aeneus</i> (see Tanaka, 1999)	<i>Zozymodes xanthoides</i> (Clark & Paula, 2003)
CARAPACE	Figs. 1a, b present	Figs. 17a, b present	Figs. 1a, b present	Fig. 1.D1 absent	Figs. 5a, b present	Figs. 9a, b present	Fig. 1A present	Fig. 13a, b present	present	Fig. 1A absent	Fig. 25a, d present
pair of posterodorsal setae	present	present	present	absent	present	present	absent	present	present	absent	present
distal spinulation on rostral spine	present	present	present	absent	present	present	absent	present	present	absent	present
spinulation on lateral spines	absent	absent	absent	absent	absent	absent	present	absent	absent	absent	absent
ANTENNULE	Fig. 1d 4 aesthetascs, 1 seta	Fig. 17c 4 aesthetascs, 1 seta	Fig. 1c 4 aesthetascs, 1 seta	Fig. 1.D1 4 aesthetascs, 1 seta	Fig. 5c 4 aesthetascs, 1 seta	Fig. 9c 4 aesthetascs, 1 seta	Fig. 2A 4 aesthetascs, 1 seta	Fig. 13c 4 aesthetascs, 1 seta	4 aesthetascs, 1 seta	Fig. 2A 2 aesthetascs, 1 seta	Fig. 25b 4 aesthetascs, 1 seta
terminal setation	Fig. 1e, h present	Fig. 17d present	Fig. 1d present	Fig. 2.D'1 present	Fig. 5d present	Fig. 9d present	Fig. 8A, B absent	Fig. 13d present	present	Fig. 2E present	Fig. 25c present
ANTENNA	present	present	present	absent	present	present	present ¹	present	present	present	present
protopod spinulation	present	present	absent	present	present	present	present	present	present	present	present
endopod spine	present	present	absent	present	present	present	present	present	present	present	present
exopod terminal setation	1	3	3	3	3	3	3	3	3	3	3
protopod - exopod %	8%	16%	15%	6%	16%	16%	10%	16%	13%	21%	13%
MAXILLAE	Fig. 2a 7	Fig. 18a 7	Fig. 2a 7	Fig. D'1 7	Fig. 6a 7	Fig. 10a 7	Fig. 9A 7	Fig. 14a 7	13%	Fig. 3A, Tab. 1 6	Fig. 26a 7
coxal endite	Fig. 2b 5+4	Fig. 18b 5+4	Fig. 2b 5+4	Fig. D'1 5+4	Fig. 6b 5+4	Fig. 10b 5+4	Fig. 10A 5+4	Fig. 15a 5+4	5+4	Fig. 3E 5+4	Fig. 26b 5+4
basial endite	Fig. 2d	Fig. 19b	Fig. 3b	Fig. D'2	Fig. 7b	Fig. 11c	Fig. 12A	Fig. 16b	5+4	Fig. 4E	Fig. 27b
SECOND MAXILLIPED	6 setae (3 subterminal, 3 terminal)	6 setae (3 subterminal, 3 terminal)	6 setae (3 subterminal, 3 terminal)	6 setae (3 subterminal, 3 terminal)	6 setae (3 subterminal, 3 terminal)	6 setae (3 subterminal, 3 terminal)	6 setae (3 subterminal, 3 terminal)	6 setae (3 subterminal, 3 terminal)	6 setae (3 subterminal, 3 terminal)	6 setae (3 subterminal, 3 terminal)	6 setae (3 subterminal, 3 terminal)
setation of distal endopod segment	Figs. 3a-d 1 large + 1 minute spine	Figs. 17c, 20a, b 1 large + 1 minute spine	Fig. 2c, 4a, b 1 large + 1 smaller spine	Fig. 3.D1 2 fine spines	Fig. 6a, 8a, b 1 large + 1 smaller spine	Fig. 10a, 11a, b 1 large + 1 smaller spine	Fig. 15A 2 fine spines	Fig. 14c 1 large + 1 smaller spine	1 large + 1 smaller spine	Fig. 1E 1 large + 1 smaller spine	Fig. 26c 1 large + 1 smaller spine

¹See Clark & Paula, 2003, Table 7.

DISCUSSION

The adult subfamilial classification of the Xanthidae MacLeay, 1838, sensu Guinot, 1978, is still unsatisfactory. Of the 10 recognized subfamilies, the characters defining two in particular, Actaeinae Alcock, 1898 and Zosiminae Alcock, 1898, are dubious (Serène, 1984: 138). According to Serène (1984), the zosimines are recognized mainly by their pereopods (especially the dorsal margins of the carpus and propodus) being crested. In xanthines, the walking legs are never obviously crested while in actaeines, the legs are subcylindrical and not crested. These are not good characters and Ng & Chen (2004) commented that it would probably not work when all the species are considered. Within what is now the Zosiminae (sensu Serène, 1984), the status of the genus *Atergatopsis* is uncertain. *Atergatopsis* does not have distinctly crested legs but nevertheless bears a marked external resemblance to some species of *Atergatis* [e.g. *Atergatopsis signatus* (Adams & White, 1848); see Serène, 1984: 142]. The similarities between *Atergatopsis* and actaeines are also marked, and some of the species now in *Atergatopsis* used to be classified in *Actaea* de Haan, 1833 (see Odhner, 1925).

The larval evidence also highlights the difficulties in clarifying the systematics of *Atergatopsis* - is this genus a member of the Zosiminae or Actaeinae? Clark & Al-Aidarous (1996) described the first stages zoeas of *Actaeodes hirsutissimus* (Rüppell, 1830) and *A. tomentosus* (H. Milne Edwards, 1834). They noted that the setation of the antennal exopods (see Figs. 1e-h) and the lateral spinuation of the telson (Figs. 3d, e) differ between these two actaeines. Table 5 compares the two *Actaeodes* with *Atergatopsis germaini* described in this study. *Atergatopsis germaini* appears to be closer to *Actaeodes tomentosus* in possessing three distal setae on the antennal exopod and similar lateral spines on the telson forks. *Actaeodes hirsutissimus* differs from the other two species by having only one terminal seta on the antennal exopod, and one large and one minute lateral spine on the on the telson. The zoeal characters of *Actaeodes hirsutissimus* are atypical for actaeines and zosimines, and the taxonomy of the species and its generic assignment should re-assessed. The genus *Actaeodes* now contains six recognised species and revision may well show it to be heterogeneous. In any case, on larval characters alone, *Atergatopsis germaini* and *Actaeodes tomentosus* seem to be better placed within the Zosiminae rather than Actaeinae (see Table 6) based on the presence of three setae (1 subterminal, 2 terminal) on the antennal exopod. This is not in agreement with their current classification based on adult morphology, i.e. Actaeinae (see Serène, 1984).

Lophozozymus is also problematic. The larval stages of *L. pictor* (Fabricius, 1798) were described by Clark & Ng (1998), and Clark & Paula (2003) corrected the description of the antenna because the presence of the endopod spine on the protopod was originally overlooked. As already discussed by Clark & Ng (1998) and Clark & Paula (2003), the zoeas of *L. pictor* are rather aberrant from what is known for other zosimines: the rostral spine is without distal spinulation, the lateral carapace spines are lightly spinulate, the antennal

protopod is smooth and not armed with spinules, and the telson fork has two fine lateral spines (not strong spines). However the adult characters of *Lophozozymus* are very similar to those of species of *Zosimus* and *Platypodia*, and some of the species in these genera need to be rearranged (P. K. L. Ng & P. Davie, unpublished data). On the basis of the adult morphology at least, there is nothing to suggest the three genera are not related. Some of the larger species of *Lophozozymus* (*L. pictor* inclusive) also bear a marked resemblance to species of *Xantho* Leach, 1814, and in fact, they have been described under that genus (see Ng & Chia, 1997). The strongly crested anterolateral margins, walking legs and chelipeds of these *Lophozozymus* species, however, clearly distinguish the two genera. Certainly from the adult characters, there is no basis for recognizing a distinct subfamily or even tribe for *Lophozozymus* that is separate from *Platypodia* and *Zosimus*. As such, it would appear that the unusual larval characters of *L. pictor* observed here (loss of spinules on the antennal protopod and rostrum, as well as the reduction of furcal lateral spines) are possibly autapomorphs.

The present study suggests that the current taxonomy of the two subfamilies (Actaeinae and Zosiminae) based on adult and first stage zoeal morphological characters is dubious. Guinot (1967: 563) too highlighted this problem by stating that *Platypodiella* and *Platyactaea* had affinities with the Indo-Pacific genera *Atergatis* and *Atergatopsis*, as did *Platypodia* and *Actaea*. A more concerted effort will be needed to consolidate adult and zoeal characters before any clarification is possible.

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