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First zoeal stages of grapsoid crabs (Crustacea: Brachyura) from the East African coast

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In this study, the larvae of 14 grapsoid species from the East African coast are examined. Original descriptions of the first zoeal stage are provided for the grapsids *Grapsus fourmanoiri*, *G. tenuicrustatus*, *Pachygrapsus minutus* and *P. plicatus*, and the sesarmids *Sarmatium crassum* and *Sesarma leptosoma*. The first zoea of *Ilyograpsus paludicola* is illustrated for the first time. Redescriptions are presented for the grapsid *Metopograpsus messor* and the gecarcinid *Cardisoma carnifex*, while the appendage setation of the varunid *Helice leachii*, and the sesarmids *Chiromantes eulimene*, *Neosarmatium meinerti*, *Parasesarma catenata* and *Perisesarma guttatum* are also given and compared with previous work. The first zoeal stages of all these species can be identified, either by comparing their overall morphology or their appendage setation. The validity of combining setation features of the maxilla and maxillipeds to separate grapsoid families is further supported, but special attention is called to the sesarmid *Sesarma leptosoma*, which presents an unexpected setal arrangement on the basis of the first maxilliped. A more troublesome situation is that of the grapsid *Ilyograpsus paludicola*. The present descriptions provide evidence of a surprising combination of characters, suggesting that this species should be removed from the Grapsoidea as already indicated by other authors.

ADDITIONAL KEYWORDS: First zoeal stages – Grapsoidea – Indo-Pacific – mangroves – rocky shores – tidal flats

INTRODUCTION

Recent proposals for the classification of brachyuran crustaceans are still largely based on the early work of former systematists, which was almost restricted to the examination of adult morphology. However, it is believed that similar adult characteristics may have resulted from convergent adaptation to a specific benthic environment; a problem thought to be minimal in planktonic zoeal stages, which inhabit a more uniform environment (Rice, 1980).

Some morphological characters of zoeal stages, for instance the setation patterns of appendages, are known to be rather conservative and thus particularly useful for systematic analyses. However, early larval descriptions often lack information on appendage setation and many recent accounts do not provide enough detail on such features (Clark *et al.*, 1998). In addition, information on larval morphology is only available for the minority of known species; less than 30% in the case of grapsoids (Felder *et al.*, 1985; Cuesta, 1999). Most descriptive work has been carried out on Atlantic species, whereas larvae of the more diverse Indo-Pacific brachyuran fauna have seldom been examined.

Studies based on larval morphology (Cuesta *et al.*, 1997; Cuesta & Schubart, 1997; Schubart & Cuesta, 1998; Cuesta & Schubart, 1999; Cuesta, Diesel & Schubart, 2001) and mtDNA sequences (Schubart *et al*., 2000) have contributed to clarify phylogenetic relationships within the Grapsoidea. The main alteration proposed from the Bowman & Abele's (1982) classification is the placement of the Gecarcinidae and the grapsid subfamilies at the same taxonomic rank by raising the latter to the familial level. Martin & Davis (2001) have adopted such suggestions, and also recognized the recently established grapsoid family Glyptograpsidae for the former varunid genera *Glyptograpsus* and *Platychirograpsus* (Schubart, Cuesta &

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Felder, 2002). Other modifications include the transfer of the genera *Cyclograpsus*, *Chasmagnathus*, *Metaplax*, *Paragrapsus* and *Helice* s.l. from the Sesarmidae to the Varunidae, the transfer of *Euchirograpsus* from the Varunidae to the Plagusiidae and the exclusion of *Percnon* from the latter; a genus whose taxonomic status is still to be defined.

In this study, original descriptions are provided for the first zoeal stages of the grapsids *Grapsus fourmanoiri* Crosnier, *G. tenuicrustatus* (Herbst), *Pachygrapsus minutus* A. Milne Edwards and *P. plicatus* (H. Milne Edwards), and the sesarmids *Sarmatium crassum* Dana and *Sesarma leptosoma* Hilgendorf. The first zoea of *Ilyograpsus paludicola* (Rathbun) is illustrated for the first time. Early descriptions by Chhapgar (1956), Rajabai (1961), Hashmi (1971) and Al-Khayat & Jones (1996) for the grapsoid *Metopograpsus messor* (Forskål), as well as that of the gecarcinid *Cardisoma carnifex* (Herbst) by Kannupandi *et al*. (1980) are fully revised; while the appendage setation of the varunid *Helice leachii* Hess, and the sesarmids *Chiromantes eulimene* (de Man), *Neosarmatium meinerti* de Man, *Parasesarma catenata* Ortman and *Perisesarma guttatum* (A. Milne Edwards) are given and compared with previous descriptions (see Baba *et al.*, 1984; Pereyra Lago, 1987, 1989, 1993a, 1993b; Mia & Shokita, 1996, respectively). These are in some cases dominant species, forming large populations in the intertidal zone of rocky shores, mangrove swamps or tidal flats along the eastern African coast. First zoeal stages of these species are therefore likely to be common in the near-shore plankton community, and the present descriptions will make possible their identification in samples. Because a relatively large number of species was examined, the use of key morphological characters of zoeae in defining phylogenetic relationships within the Grapsoidea is further evaluated.

MATERIALS AND METHODS

Ovigerous crabs were collected by hand at a number of sites along the eastern coast of Africa and identified according to Barnard (1950) and Crosnier (1965). The list of valid grapsoid species in Cuesta (1999) was consulted to confirm synonymies. The locality and date of collection as well as date of hatching for each female caught for this study are listed in Table 1.

Table 1. Local of collection and date of hatching of the species examined

Species	Local of collection	Date of hatching
Grapsidae		
[1]*Grapsus fourmanoiri* Crosnier, 1965	Praia da Estação, Inhaca Island, Mozambique	December 1997
[1]*Grapsus tenuicrustatus* (Herbst, 1783)	Praia do Farol, Inhaca Island, Mozambique	February 2002
[2]*Ilyograpsus paludicola* (Rathbun, 1909)	Mangal da Ponta Rasa, Inhaca Island, Mozambique	November 1999
[2]*Metopograpsus messor* (Forskål, 1775)	Mangal do Saco, Inhaca Island, Mozambique	October 1995
[1]*Pachygrapsus minutus* A. Milne Edwards, 1873	Praia da Estação, Inhaca Island, Mozambique	December 1997
[1]*Pachygrapsus plicatus* (H. Milne Edwards, 1837)	Praia do Farol, Inhaca Island, Mozambique	November 1999
Sesarmidae		
[3]*Chiromantes eulimene* (de Man, 1897)	Mgazana estuary, Transkei, South Africa	November 1997
[3]*Neosarmatium meinerti* de Man, 1887	Mangal do Saco, Inhaca Island, Mozambique	January 1998
[3]*Parasesarma catenata* Ortman, 1897	Mgazana estuary, Transkei, South Africa	November 1997
[3]*Perisesarma guttatum* (A. Milne Edwards, 1869)	Mangal do Saco, Inhaca Island, Mozambique	October 1995
[1]*Sarmatium crassum* Dana, 1851	Mangal da Ponta Rasa, Inhaca Island, Mozambique	November 1999
[1]*Sesarma leptosoma* Hilgendorf, 1869	Mida Creek, Kenya	December 1997
Varunidae		
[3]*Helice leachii* Hess, 1865	Mgazana estuary, Transkei, South Africa	November 1997
Gecarcinidae		
[2]*Cardisoma carnifex* (Herbst, 1796)	Praia da Estação, Inhaca Island, Mozambique	November 1999

[1]First descriptions in this study; [2]redescriptions; [3]accounts of appendage setation.

Captive females were kept unfed in aerated brackish or salt water until hatching. Every day the water was changed and the presence of swimming zoeae was checked. After hatching, spent females and larvae were separately fixed and preserved in buffered 5% formaldehyde.

Five specimens were measured and dissected using a Wild stereomicroscope provided with a micrometric ocular. Morphometric dimensions included the distance between the tips of rostral and dorsal spines (TT), the carapace width (CW) and the carapace length (CL), measured laterally from the posterior to the anterior margin. In the case of *Cardisoma carnifex*, carapace width measurements included lateral spines. After measured, the specimens were dissected and mounted in permanent slides using polyvinyl lactophenol. In addition, a number of entire specimens were mounted in different positions in excavated slides to check for the presence of setae on the carapace and to prepare the illustrations of the whole zoea. Slides were examined using an Olympus BH-2 microscope in order to record the morphological features of appendages. Drawings were made with the aid of a *camera lucida*. Aesthetascs and long natatory setae of the maxillipeds were drawn truncated. When clearly visible, particular setal features were described as in Pohle & Telford (1981). Other terminology followed the standards proposed by Clark *et al*. (1998). When describing species of the same genus, a full account is only given for the first one. In the following species, only the differences are described.

Apart from larvae first described in this study, full accounts are also given in cases where significant improvements could be provided. For species for which adequate larval accounts are already available, differences regarding the setation pattern of appendages are pointed out.

Spent females and respective larvae were deposited in the Decapod Larval Collection at the NEBECC (Núcleo de Estudos em Biologia, Ecologia e Cultivo de Crustáceos), Department of Zoology – IB, Universidade Estadual Paulista, Botucatu, São Paulo, Brazil.

RESULTS

Table 2 shows the setation patterns of zoeal stages already described in previous studies. For the remaining species a full account is given below.

GRAPSIDAE

GRAPSUS FOURMANOIRI CROSNIER, 1965 (FIGS 1,2)

Dimensions: TT 0.90 mm ± 0.02, CW 0.52 mm ± 0.07, CL 0.50 mm ± 0.01.

Carapace (Fig. 1a): dorsal spine short and straight; rostral spine anteriorly directed; lateral spines absent; a pair of postero-dorsal setae present; setae absent from ventral carapace margin; eyes sessile.

Antennule (Fig. 1b): uniramous, endopod absent; exopod unsegmented bearing 3 unequal terminal aesthetascs and 2 unequal terminal setae.

Antenna (Figs 1a,c): shorter than rostral spine; protopodal process with 2 rows of spines of increasing size

Table 2. Present account of setation patterns of antennule, antenna, maxillule and maxilla of the first stage zoea for species formally described elsewhere. Abbreviations: a = aesthetascs; ce = coxal endite; be = basial endite; en = endopod; ex = exopod; sc = scaphognathite. Numbers in bold indicate discrepant counts in original descriptions

	Chiromantes eulimene	*Perisesarma guttatum*	*Neosarmatium meinerti*	*Parasesarma catenata*	*Helice leachi*
Antennule	4a + 1	4a + 1	4a + 1 **3**	3a + 1 **4**	2a + 2
Antenna[1]	3 + 1 **2**	1 + 1	2 + 1 3	1 + 1	2 + 1
Maxillule (ce; be; en)	5; 5[2]; 1, 5 **6**	5; 5[2]; 1, 5 **6**	5; 5[2]; 1, 5	6; 5[2]; 1, 5 **5**	5; 5; 1, 5 **4**
Maxilla (ce; be; en; sc)	5, 3[3]; 5, 4; 2, 3; 4 **6 4**	5, 3[3]; 5, 4; 2, 3; 4 **3**	5, 3[3]; 5, 4; 2, 3; 4	5, 3; 5, 4; 2, 3; 4 **4**	4, 2; 5, 4; 2, 2; 4 **2, 3; 4, 3**

[1]Setation of the exopod (number of simple setae + number of large terminal setae); [2]with two teeth; [3]with an additional seta-like protuberance.

References of original descriptions: Pereyra Lago (1993b) (*Chiromantes eulimene*); Pereyra Lago (1993a) (*Perisesarma guttatum*); Pereyra Lago (1989) (*Neosarmatium meinerti*); Pereyra Lago (1987) (*Parasesarma catenata*); Baba *et al*. (1984) and Mia & Shokita (1996) (*Helice leachi*).

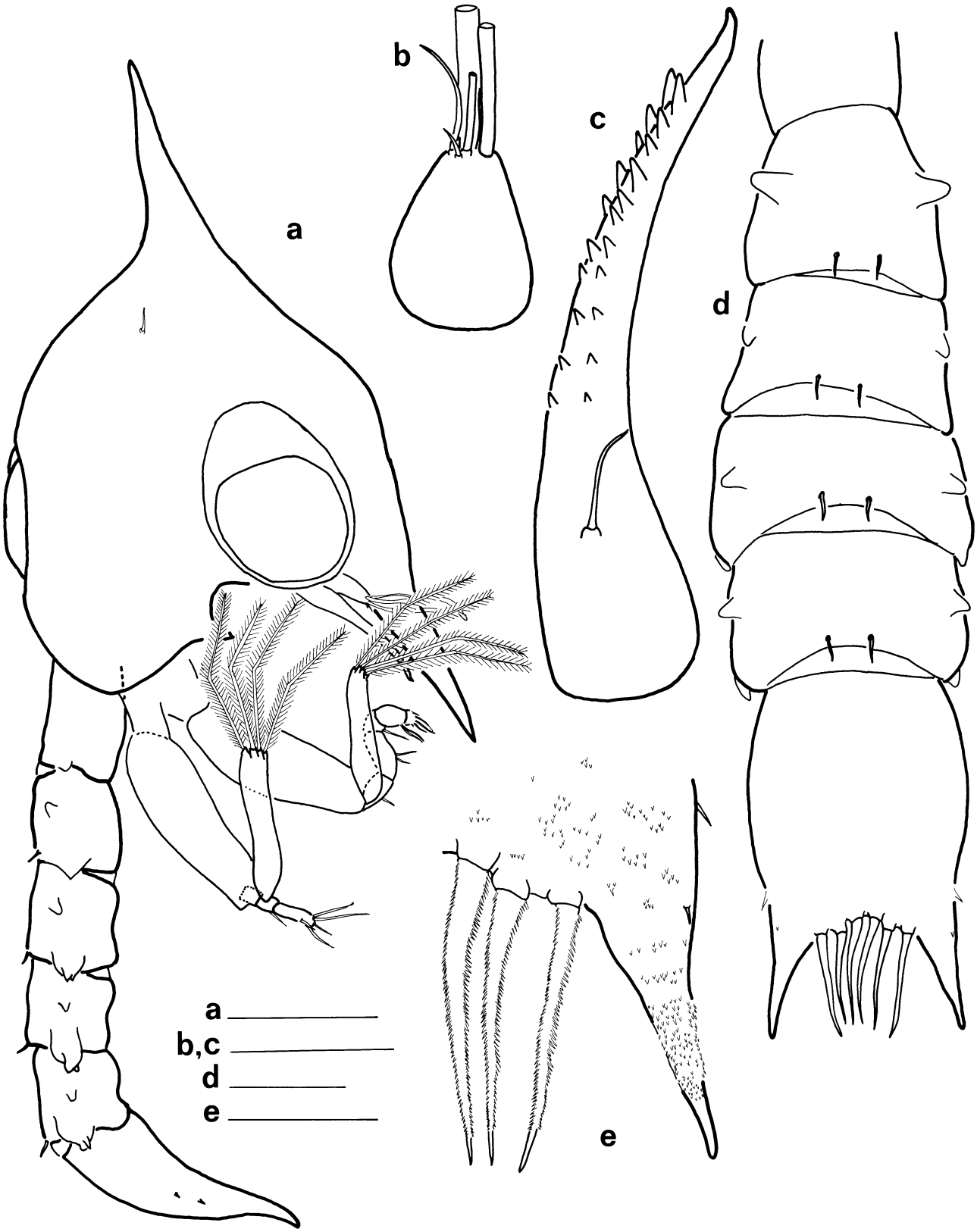

Figure 1. *Grapsus fourmanoiri* Crosnier. First zoeal stage: (a) lateral view; (b) antennule; (c) antenna; (d) dorsal view of abdomen; (e) detail of telson. Scale bars represent 0.2 (a), 0.05 (b, c and e) and 0.1 mm (d).

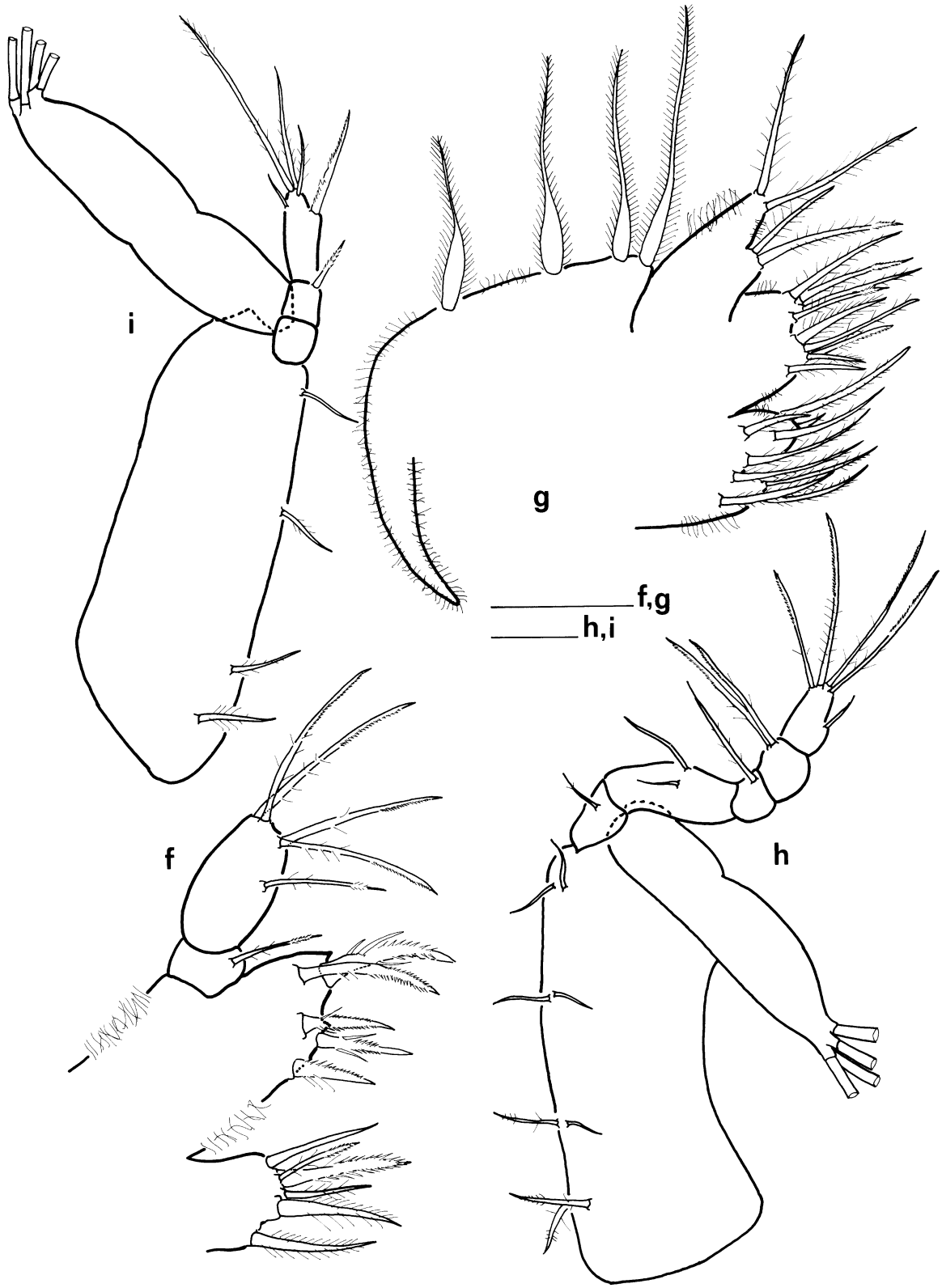

Figure 2. *Grapsus fourmanoiri* Crosnier. First zoeal stage: (f) maxillule; (g) maxilla; (h) first maxilliped; (i) second maxilliped. Scale bars represent 0.05 mm.

towards the tip; endopod absent; exopod reduced to a small bud with a terminal simple seta.

Maxillule (Fig. 2f): epipod seta absent; coxal endite with 6 (3 sparsely plumose, 2 plumodenticulate and 1 simple) setae; basial endite with 5 (1 subterminal, plumodenticulate; 4 stout, terminal plumodenticulate) setae and 2 acute teeth present; endopod 2-segmented, proximal segment with 1 (plumodenticulate) seta; distal segment with 5 (1 subterminal, plumodenticulate + 4 distal, plumodenticulate) setae; exopod seta absent.

Maxilla (Fig. 2g): coxal endite bilobed bearing 4 (sparsely plumose) + 5 (sparsely plumose) setae, basial endite bilobed with 5 (4 sparsely plumose, 1 plumodenticulate) setae + 4 (2 sparsely plumose, 2 plumodenticulate) setae; endopod bilobed with 2 (1 plumodenticulate, 1 sparsely plumose) setae + 2 (sparsely plumose) setae; scaphognathite (exopod) margin with 4 plumose setae and 1 long distal stout process.

First maxilliped (Fig. 2h): basis with 8 setae (arranged 2 sparsely plumose; 1 sparsely plumose, 1 simple; 2 simple; 2 simple); endopod 5-segmented with 1 (sparsely plumose), 2 (simple), 1 (sparsely plumose), 2 (plumodenticulate), 5 (1 subterminal simple + 4 terminal plumodenticulate) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Second maxilliped (Fig. 2i): basis with 4 setae (arranged 1 sparsely plumose, 1 sparsely plumose, 1 sparsely plumose, 1 simple); endopod 3-segmented with 0, 1 (denticulate), 5 (1 subterminal denticulate + 1 terminal simple, 3 terminal sparsely plumose) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Third maxilliped: absent

Pereiopods: absent

Abdomen (Figs 1a,d): 5 somites; somite 2 with a pair of dorsolateral processes directed anteriorly; somites 3–5 with 1 pair of dorsolateral processes directed ventrally; postero-lateral processes in all somites, small in somite 1, acute in somite 2, and more developed, bearing distinct lobes in somites 3–5; a pair of median postero-dorsal setae in somites 2–5; maximum abdomen width at somite 4.

Telson (Figs 1d,e): with 2 postero-lateral pairs of spines, the posterior one smaller; dorsal median spine absent; small denticles distributed in scattered patches, but completely covering intermediate regions of forks; forks small, slightly divergent; posterior margin with 3 pairs of stout setae spinulated as shown in Fig. 1(e).

GRAPSUS TENUICRUSTATUS (HERBST, 1783) (FIGS 3,4)

Dimensions: TT 0.92 mm ± 0.01, CW 0.50 mm ± 0.01, CL 0.38 mm ± 0.01.

Carapace (Fig. 3a): rostral spine straight.

Antenna (Figs 3a,c): as long as rostral spine; protopodal process with 2 rows of a few large spines of increasing size towards the tip.

Maxillule (Fig. 4f): coxal endite with 6 (sparsely plumose) setae.

Maxilla (Fig. 4g): basial endite bilobed with 5 (3 sparsely plumose, 2 plumodenticulate) setae + 4 (3 sparsely plumose, 1 plumodenticulate) setae; endopod bilobed with 2 (sparsely plumose) + 2 (sparsely plumose) setae.

First maxilliped (Fig. 4h): basis with 8 setae (arranged 1 sparsely plumose, 1 simple; 2 simple; 2 simple; 2 simple); endopod five-segmented with 1 (simple), 2 (simple), 1 (simple), 2 (plumodenticulate), 5 (1 subterminal simple + 4 terminal plumodenticulate) setae.

Second maxilliped (Fig. 4i): basis with 4 setae (arranged 1 sparsely plumose, 1 sparsely plumose, 1 simple, 1simple); endopod 3-segmented with 0, 1 (denticulate), 5 (1 subterminal denticulate + 2 terminal simple, 2 terminal sparsely plumose) setae.

Abdomen (Figs 3a,d): postero-lateral processes in all somites, small in somite 1, larger but still blunt in somite 2, and especially well-developed in somite 3.

Telson (Figs 3d,e): with 2 postero-lateral pairs of spines, the posterior one larger; forks small, divergent.

ILYOGRAPSUS PALUDICOLA (RATHBUN, 1909) (FIGS 5,6)

Ilyograpsus paludicola; Fukuda, 1978: 15.

Dimensions: CW 0.23 mm ± 0.01, CL 0.35 mm ± 0.01.

Carapace (Fig. 5a): with large lateral expansions, bearing a distinct spine on posterior edge; dorsal spine absent; rostral spine short; lateral spines absent; 1 pair of dorsal setae present; eyes sessile.

Antennule (Fig. 5b): uniramous, endopod absent; exopod unsegmented bearing 2 terminal aesthetascs and 1 terminal seta.

Antenna (Figs 5a,c): of similar size to rostral spine; protopodal process with 2 rows of spines of different size; endopod absent; exopod well developed, slightly longer than protopodal process, with spines aligned, smaller towards the tip.

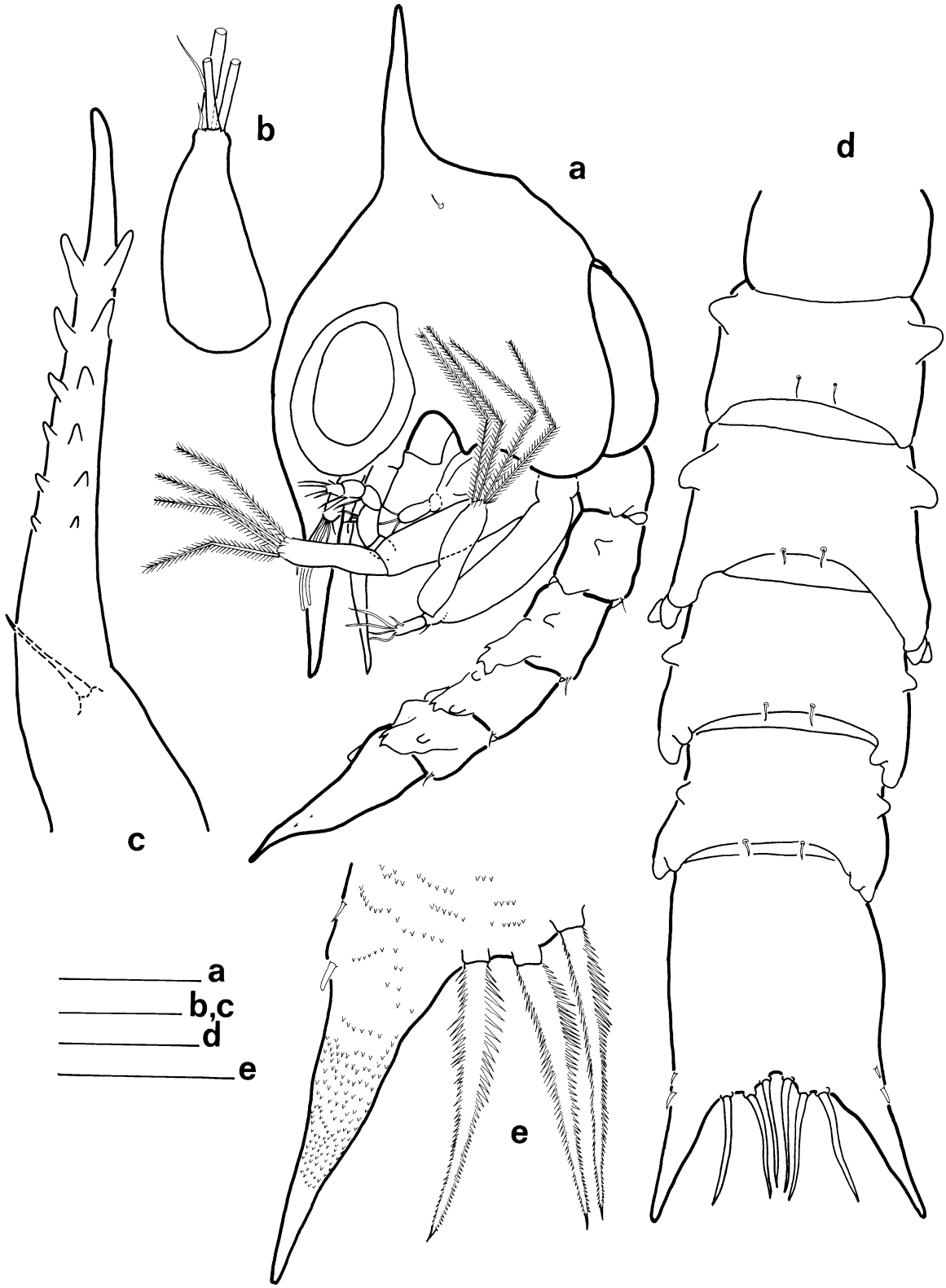

Figure 3. *Grapsus tenuicrustatus* (Herbst). First zoeal stage: (a) lateral view; (b) antennule; (c) antenna; (d) dorsal view of abdomen; (e) detail of telson. Scale bars as in Figure 1.

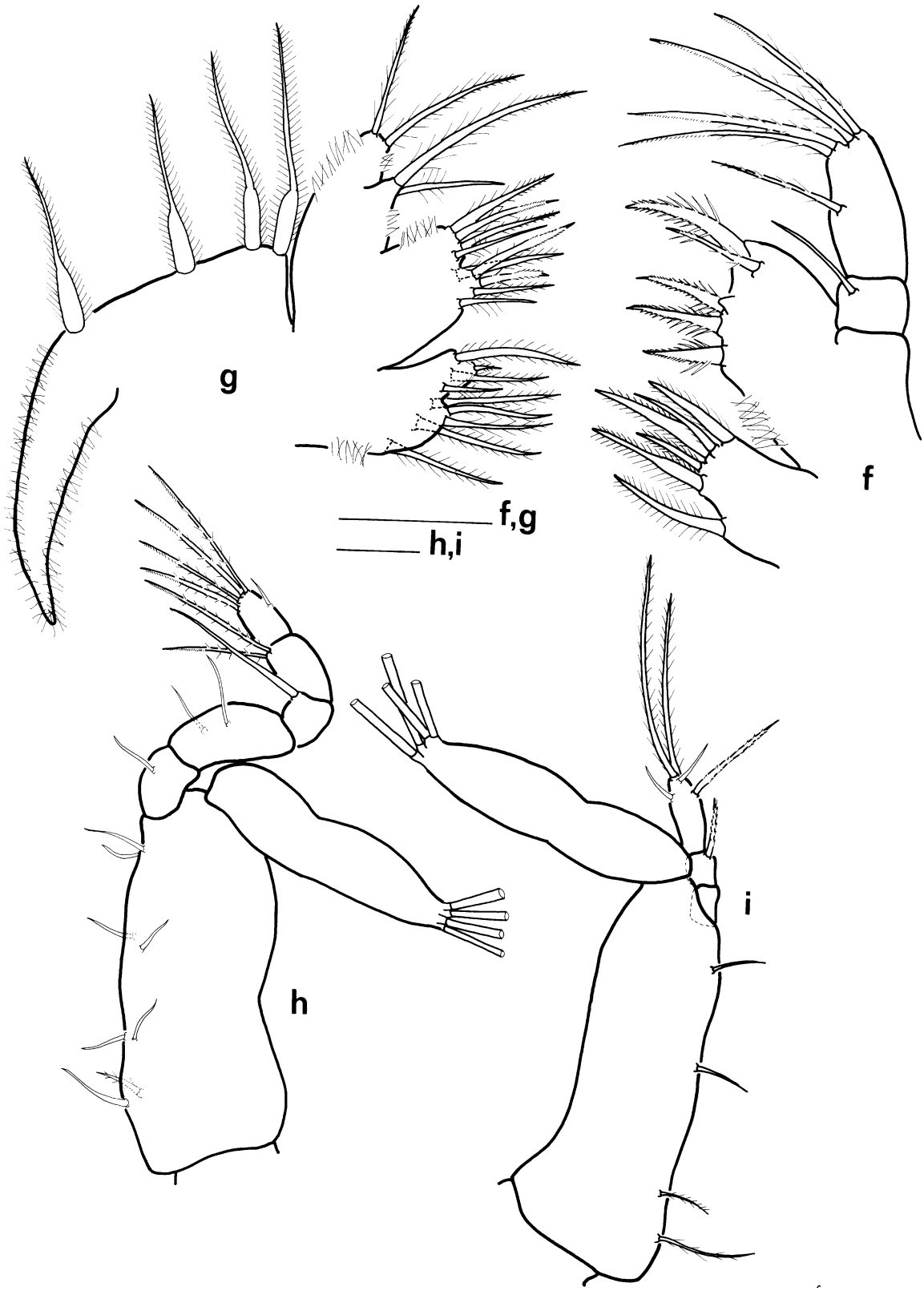

Figure 4. *Grapsus tenuicrustatus* (Herbst). First zoeal stage: (f) maxillule; (g) maxilla; (h) first maxilliped; (i) second maxilliped. Scale bars as in Figure 2.

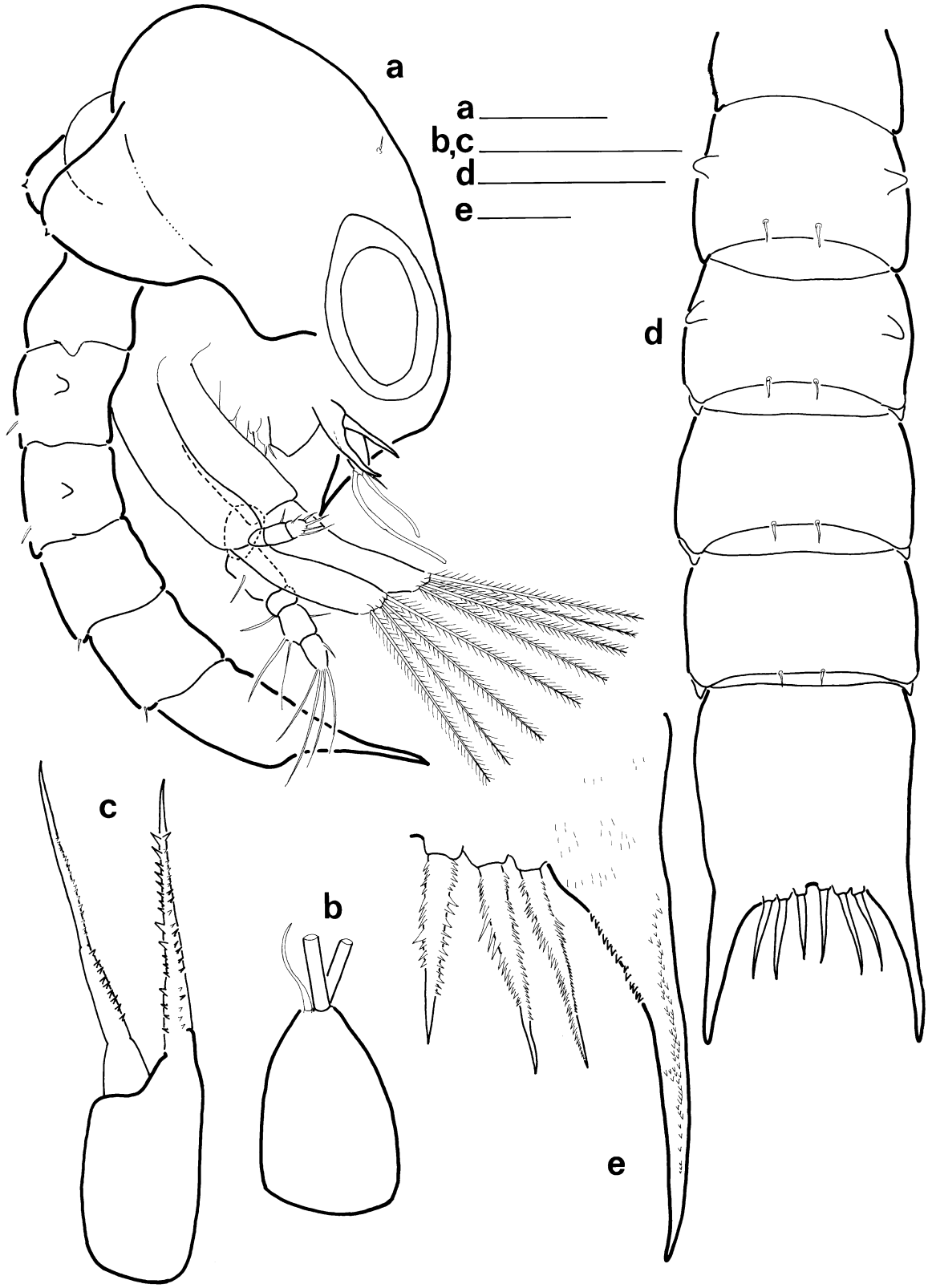

Figure 5. *Ilyograpsus paludicola* (Rathbun). First zoeal stage: (a) lateral view; (b) antennule; (c) antenna; (d) dorsal view of abdomen; (e) detail of telson. Scale bars represent 0.1 (a), 0.05 (b, c and e) and 0.1 mm (d).

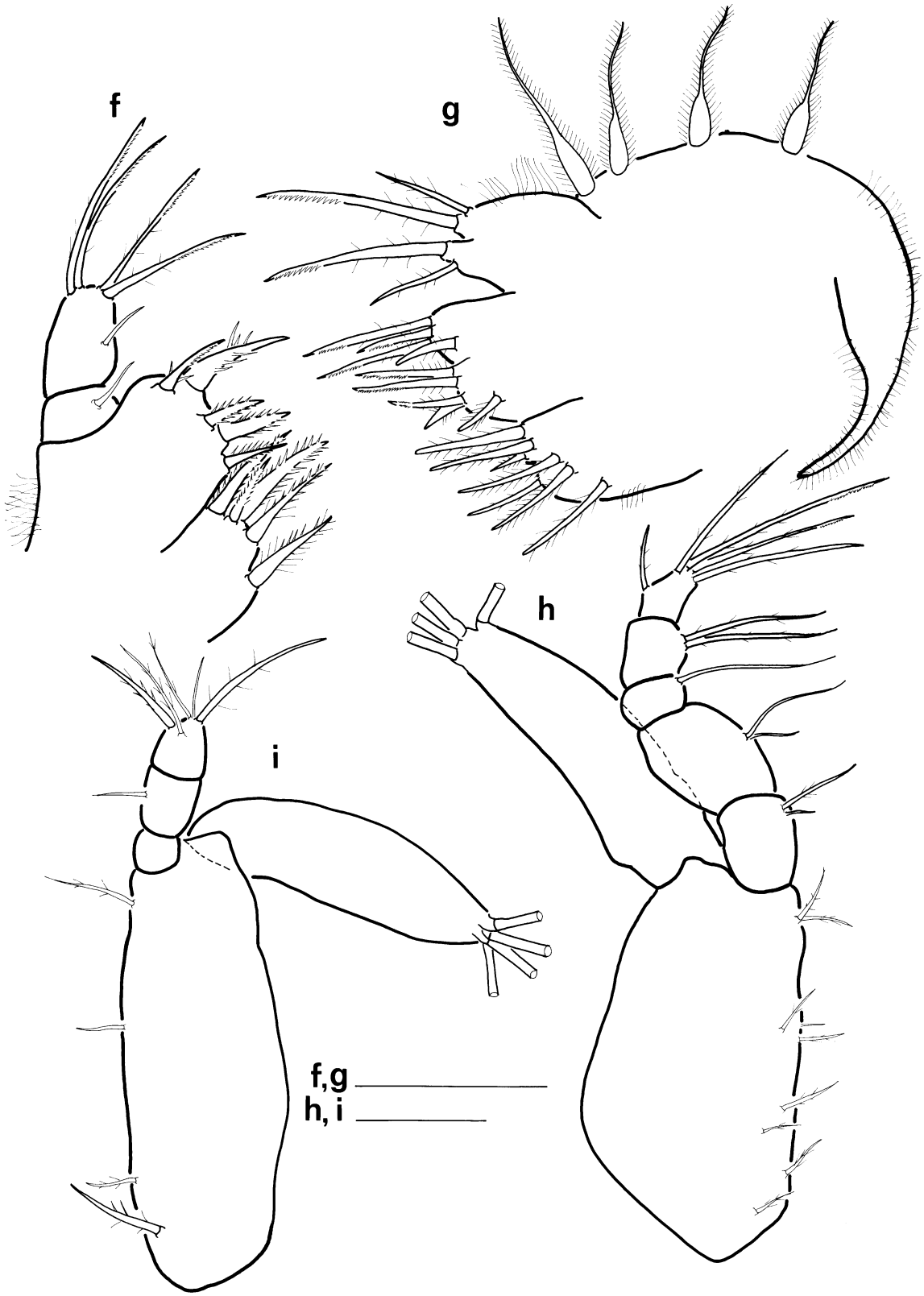

Figure 6. *Ilyograpsus paludicola* (Rathbun). First zoeal stage: (f) maxillule; (g) maxilla; (h) first maxilliped; (i) second maxilliped. Scale bars as in Figure 2.

Maxillule (Fig. 6f): epipod seta absent; coxal endite with 5 (2 sparsely plumose, 3 denticulate) setae; basial endite with 5 (1 subterminal, plumodenticulate, 4 stout, terminal denticulate) setae; endopod 2-segmented with 1 (simple) seta on proximal segment and 5 (1 simple, subterminal + 4 distal, plumodenticulate) setae in distal segment; exopod seta absent.

Maxilla (Fig. 6g): coxal endite bilobed bearing 4 (sparsely plumose) + 3 (sparsely plumose) setae, basial endite bilobed with 5 (2 sparsely plumose, 3 plumodenticulate) setae + 4 (1 sparsely plumose, 3 plumodenticulate) setae; endopod bilobed with 2 (1 longer plumodenticulate, 1 shorter sparsely plumose) setae + 2 (1 longer plumodenticulate, 1 shorter sparsely plumose) setae; scaphognathite (exopod) margin with 4 plumose setae and 1 long distal stout process.

First maxilliped (Fig. 6h): basis with 9 setae (arranged 2 sparsely plumose; 2 sparsely plumose; 2 sparsely plumose, 1 simple; 2 sparsely plumose); endopod 5-segmented with 2 (1 sparsely plumose, 1 simple), 2 (simple), 1 (simple), 2 (sparsely plumose), 5 (1 subterminal sparsely plumose + 2 terminal plumodenticulate, 2 terminal sparsely plumose) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Second maxilliped (Fig. 6i): basis with 4 setae (arranged 1 sparsely plumose, 1 sparsely plumose, 1 simple, 1 sparsely plumose); endopod 3-segmented with 0, 1 (simple), 5 (1 terminal simple, 4 terminal sparsely plumose) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Third maxilliped: absent

Pereiopods: absent

Abdomen (Figs 5a, d): 5 somites; somites 2–3 with a pair of lateral processes, posteriorly directed in somite 3; postero-lateral process only conspicuous in somite 1; a pair of median postero-dorsal setae in somites 2–5.

Telson (Figs 5d,e): small spinules distributed in scattered patches, lateral and dorsal medial spines absent; acute denticles bordering the proximal inner margin of forks and a row of small denticles aligned close to the outer margin; forks slightly divergent; posterior margin with 3 pairs of stout setae margined by spinulae of different size.

METOPOGRAPSUS MESSOR (FORSKÅL, 1775) (FIGS 7,8)

Metopograpsus messor; Chhapgar, 1956 [publication not seen]; Rajabai (1961): 156–158, Text-fig. I; Hashmi, 1971: 105–107, figs 1,2; Al-Khayat & Jones, 1996: 803,806, fig. 4.

Dimensions: TT 1.13 mm ± 0.04, CW 0.37 mm ± 0.01, CL 0.53 mm ± 0.04.

Carapace (Fig. 7a): with a slight postero-dorsal protuberance; dorsal spine straight; rostral spine relatively long, anteriorly directed; lateral spines absent; a pair of dorsal setae present; eyes sessile.

Antennule (Fig. 7b): uniramous, endopod absent; exopod unsegmented bearing 2 terminal aesthetascs and 2 unequal terminal setae.

Antenna (Figs 7a,c): much shorter than rostral spine; protopodal process anteriorly covered with numerous spines of similar size; endopod absent; exopod absent.

Maxillule (Fig. 8f): epipod seta absent; coxal endite with 6 (3 sparsely plumose, 3 plumodenticulate) setae; basial endite with 5 (1 subterminal, sparsely plumose; 4 stout, terminal plumodenticulate) setae, 1 acute tooth in distal margin; endopod 2-segmented, proximal segment with 1 (simple) seta, distal segment with 5 (1 subterminal, plumodenticulate + 4 distal, plumodenticulate) setae; exopod seta absent.

Maxilla (Fig. 8g): coxal endite bilobed bearing 5 (sparsely plumose) + 4 (sparsely plumose) setae, basial endite bilobed with 5 (1 sparsely plumose, 4 plumodenticulate) setae + 4 (plumodenticulate) setae; endopod bilobed with 2 (1 longer plumodenticulate, 1 shorter sparsely plumose) setae + 2 (sparsely plumose) setae; scaphognathite (exopod) margin with 4 plumose setae and 1 long distal stout process.

First maxilliped (Fig. 8h): basis with 8 setae (arranged 2 sparsely plumose; 1 sparsely plumose, 1 simple; 1 sparsely plumose, 1 simple; 1 sparsely plumose, 1 simple); endopod 5-segmented with 1 (sparsely plumose), 2 (sparsely plumose), 1 (plumodenticulate), 2 (plumodenticulate), 5 (1 subterminal simple + 4 terminal plumodenticulate) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Second maxilliped (Fig. 8i): basis with 4 setae (arranged 1 sparsely plumose, 1 sparsely plumose, 1 sparsely plumose, 1 sparsely plumose); endopod 3-segmented with 0, 1 (denticulate), 5 (1 subterminal denticulate + 1 subterminal simple, 3 terminal sparsely plumose) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Third maxilliped: absent

Pereiopods: absent

Abdomen (Figs 7a,d): 5 somites; somite 2 and 3 with 1 pair of dorsolateral processes ventrally; postero-lateral processes reduced in somite 1, short and nearly blunt in somites 2 and 3, forming large lateral expansions in somites 4 and 5, much larger in the latter; a pair of median postero-dorsal setae in somites 2–5; maximum abdomen width at somite 5.

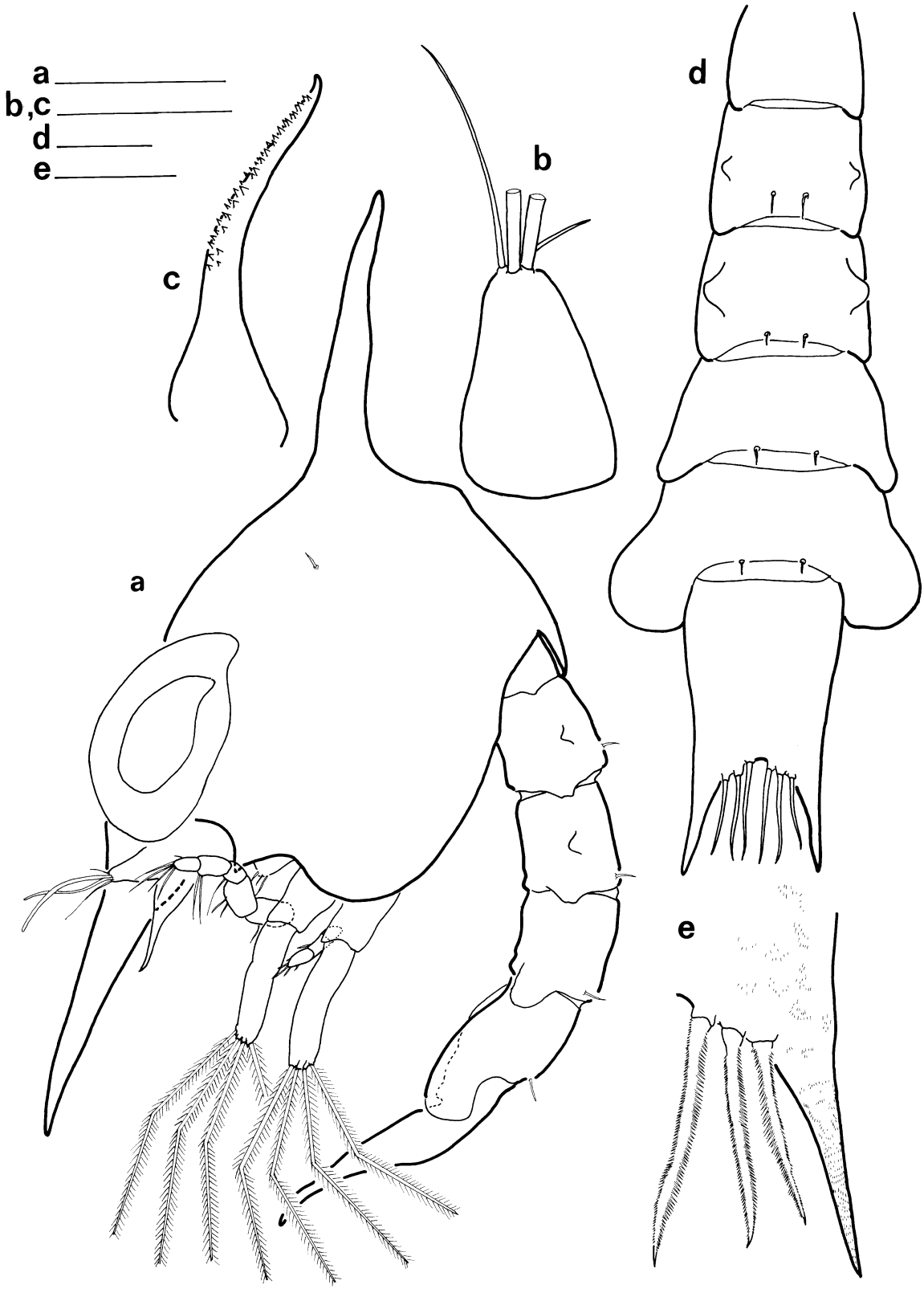

Figure 7. *Metopograpsus messor* (Forskål). First zoeal stage: (a) lateral view; (b) antennule; (c) antenna; (d) dorsal view of abdomen; (e) detail of telson. Scale bars as in Figure 1.

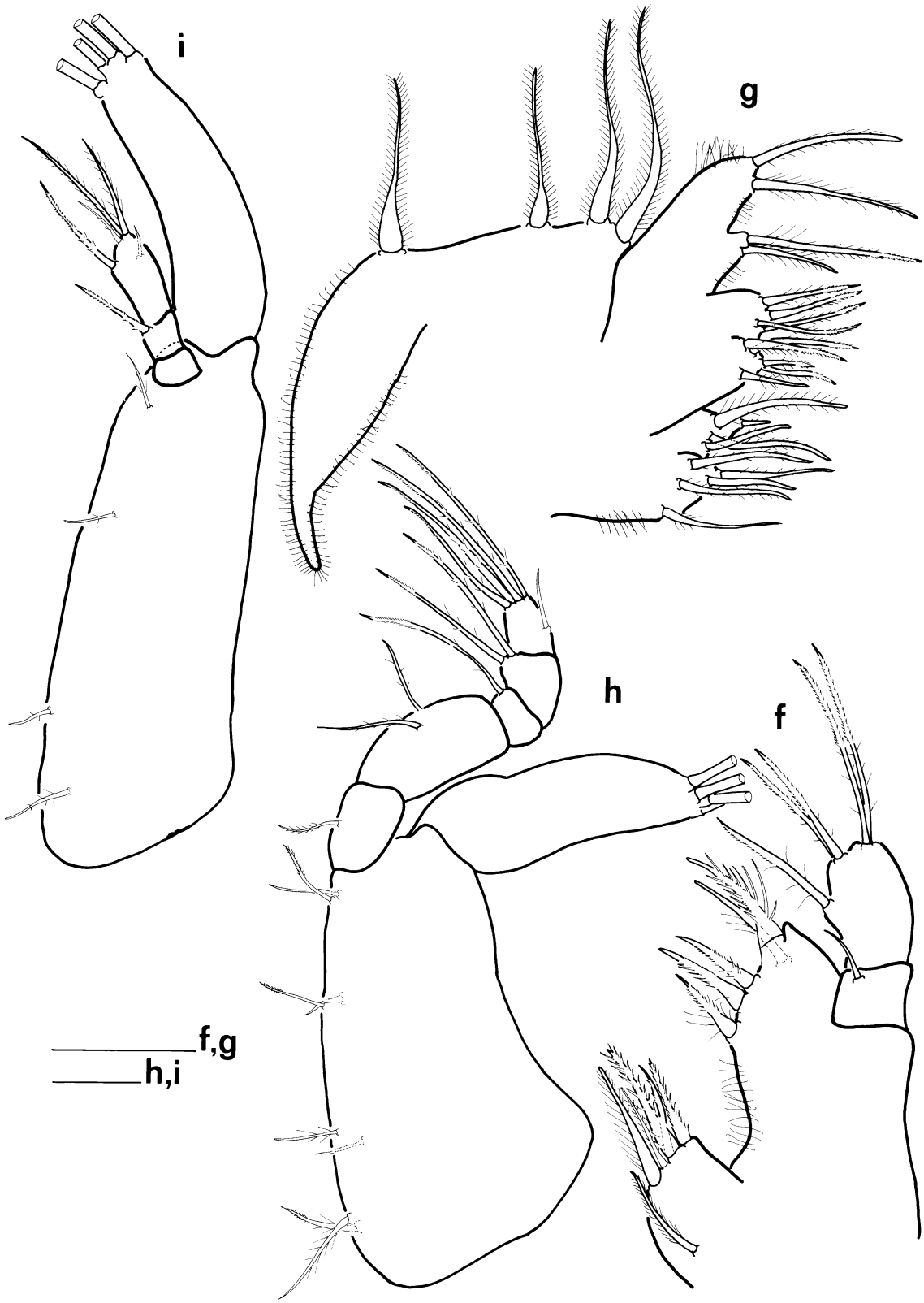

Figure 8. *Metopograpsus messor* (Forskål). First zoeal stage: (f) maxillule; (g) maxilla; (h) first maxilliped; (i) second maxilliped. Scale bars as in Figure 2.

Telson (Figs 7d,e): small setae distributed in scattered patches, nearly covering the forks; lateral and dorsal medial spines absent; forks small, slightly divergent; posterior margin with 3 pairs of stout setae regularly spinulated as shown in Fig. 7(e).

PACHYGRAPSUS MINUTUS A. MILNE EDWARDS, 1837 (FIGS 9,10)

Dimensions: TT 0.62 mm ± 0.01, CW 0.29 mm ± 0.02, CL 0.43 mm ± 0.01.

Carapace (Fig. 9a): with a distinct postero-dorsal protuberance; dorsal spine short and straight; rostral spine straight and larger than dorsal spine; lateral spines absent; a pair of dorsal setae present; eyes sessile.

Antennule (Fig. 9b): uniramous, endopod absent; exopod unsegmented bearing 3 unequal terminal aesthetascs and 1 terminal seta.

Antenna (Figs 9a,c): slightly shorter than rostral spine; protopodal process with scattered spines of increasing size towards the tip; endopod absent; exopod very reduced bearing a terminal simple seta.

Maxillule (Fig. 10f): epipod seta absent; coxal endite with 6 (sparsely plumose) setae; basial endite with 5 (1 subterminal, plumodenticulate; 3 stout, terminal plumodenticulate; 1 stout, terminal denticulate) seta; 1 acute tooth present in distal margin; endopod 2-segmented, proximal segment with 1 (sparsely plumose) seta, distal segment with 5 (1 subterminal, sparsely plumose + 4 terminal plumodenticulate) setae; exopod seta absent.

Maxilla (Fig. 10g): coxal endite bilobed bearing 5 (sparsely plumose) + 4 (sparsely plumose) setae, basial endite bilobed with 5 (sparsely plumose) + 4 (sparsely plumose) setae; endopod bilobed with 2 (sparsely plumose) + 2 (sparsely plumose) setae; scaphognathite (exopod) margin with 4 plumose setae and 1 long distal stout process.

First maxilliped (Fig. 10h): basis with 8 setae (arranged 2 simple; 2 simple; 2 simple; 2 simple); endopod 5-segmented with 1 (simple), 2 (simple), 1 (simple), 2 (1 simple, 1 plumodenticulate), 5 (1 subterminal simple + 4 terminal plumodenticulate) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Second maxilliped (Fig. 10i): basis with 4 setae (arranged 1 sparsely plumose, 1 sparsely plumose, 1 simple, 1 simple); endopod 3-segmented with 0, 1 (simple), 5 (1 subterminal denticulate + 1 subterminal simple, 1 terminal simple, 2 terminal sparsely plumose) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Third maxilliped: absent

Pereiopods: absent

Abdomen (Figs 9a,d): 5 somites; somite 2 with 1 pair of dorsolateral processes directed anteriorly, somites 3–4 with 1 pair of dorsolateral processes directed ventrally; postero-lateral processes in all somites, small in somite 1, and increasingly conspicuous, bearing distinct lobes in somites 2–5; a pair of median postero-dorsal setae in somites 2–5; maximum abdomen width at somite 4.

Telson (Figs 9d,e): with 2 postero-lateral pairs of spines, the posterior one larger; dorsal median spine absent; small setae distributed in scattered patches, almost covering forks except the tips; forks small, slightly divergent; posterior margin with 3 pairs of stout setae spinulated as shown in Fig. 9(e).

PACHYGRAPSUS PLICATUS (H. MILNE EDWARDS, 1837) (FIGS 11,12)

Dimensions: TT 0.80 mm ± 0.02, CW 0.37 mm ± 0.02, CL 0.46 mm ± 0.02.

Carapace (Fig. 11a): without a distinct postero-dorsal protuberance as found in P. minutus.

Antennule (Fig. 11b): with 2 terminal setae.

Antenna (Figs 11a,c): protopodal process with 2 rows of spines of increasing size towards the tip.

Maxillule (Fig. 12f): coxal endite with 6 (4 sparsely plumose, 1 simple, 1 plumodenticulate) setae; basial endite with 5 (1 subterminal, plumodenticulate; 1 stout, terminal sparsely plumose; 2 stout, terminal plumodenticulate; 1 stout, terminal denticulate) setae.

First maxilliped (Fig. 12h): basis with 8 setae (arranged 2 sparsely plumose; 2 sparsely plumose; 2 sparsely plumose; 2 sparsely plumose); endopod 5-segmented with 1 (sparsely plumose), 2 (sparsely plumose), 1 (plumodenticulate), 2 (plumodenticulate), 5 (1 subterminal simple + 4 terminal plumodenticulate) setae.

Second maxilliped (Fig. 12i): basis with 4 setae (arranged 1 sparsely plumose, 1 sparsely plumose, 1 sparsely plumose, 1 sparsely plumose); endopod 3-segmented with 0, 1 (denticulate), 5 (1 subterminal simple + 1 subterminal denticulate, 2 terminal sparsely plumose, 1 terminal simple) setae.

Abdomen (Figs 11a, d): somite 2 with 1 pair of dorsolateral processes directed anteriorly, somite 3 with 1 pair of dorsolateral processes directed ventrally;

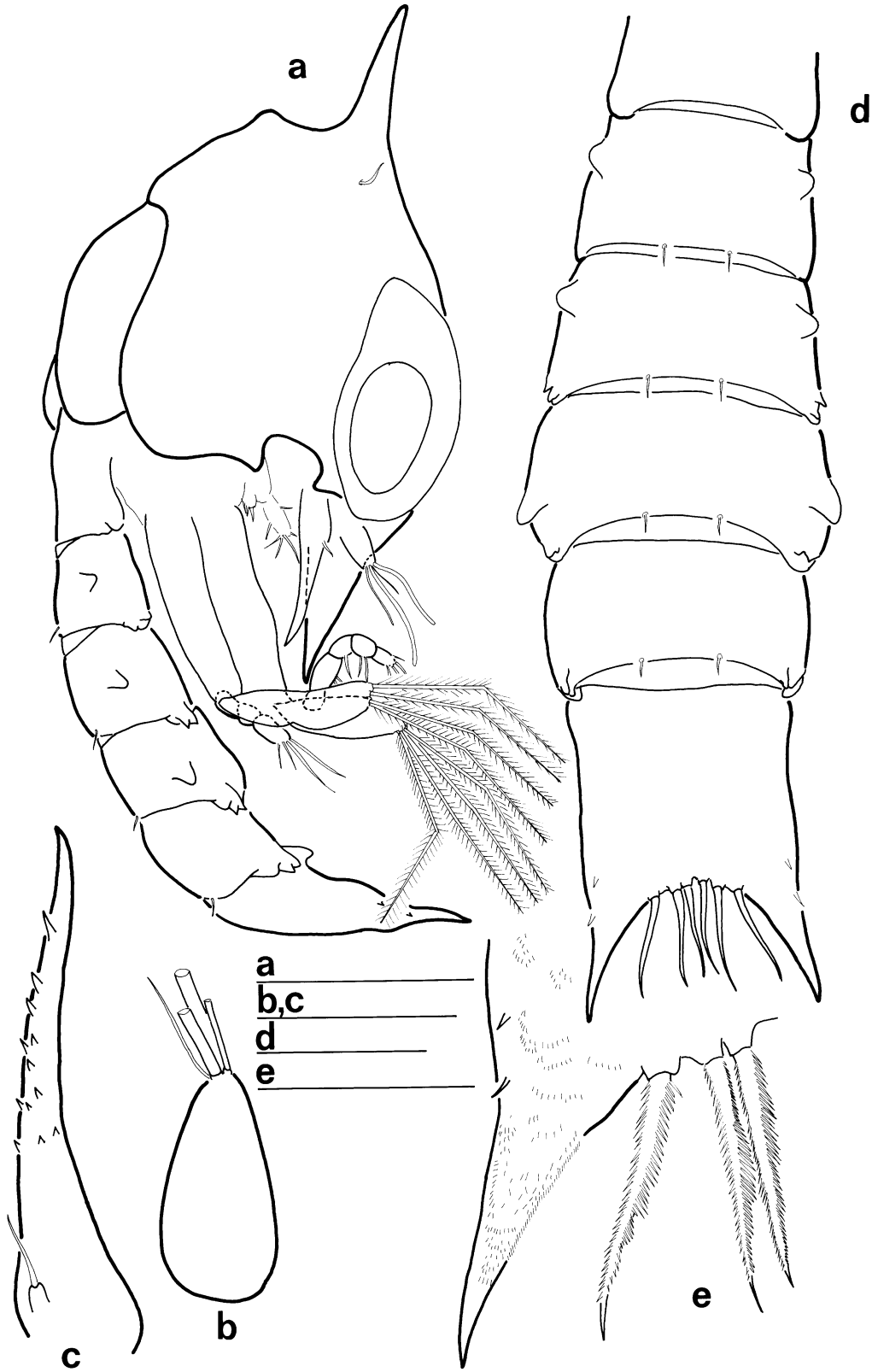

Figure 9. *Pachygrapsus minutus* Crosnier. First zoeal stage: (a) lateral view; (b) antennule; (c) antenna; (d) dorsal view of abdomen; (e) detail of telson. Scale bars as in Figure 1.

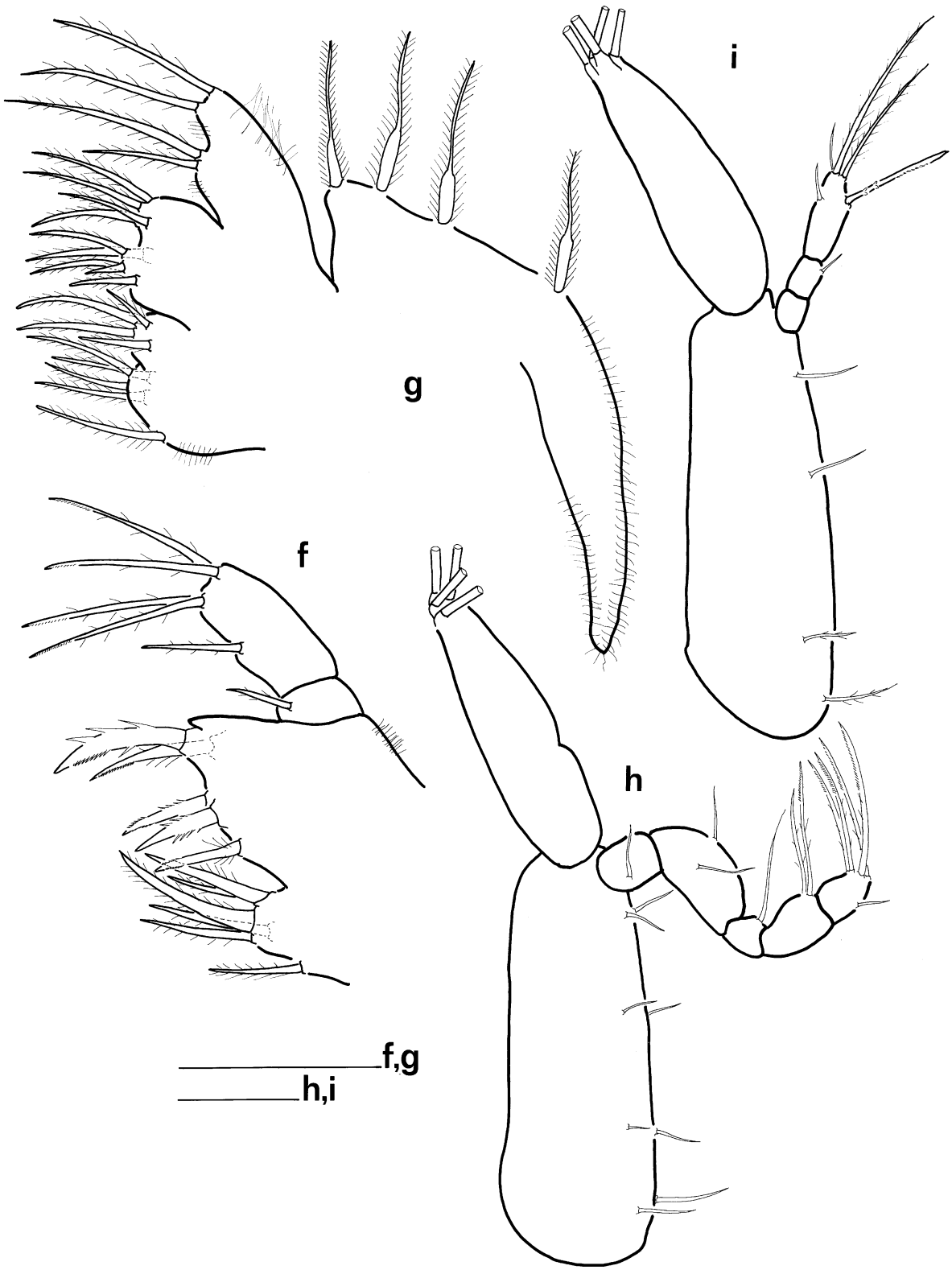

Figure 10. *Pachygrapsus minutus* Crosnier. First zoeal stage: (f) maxillule; (g) maxilla; (h) first maxilliped; (i) second maxilliped. Scale bars as in Figure 2.

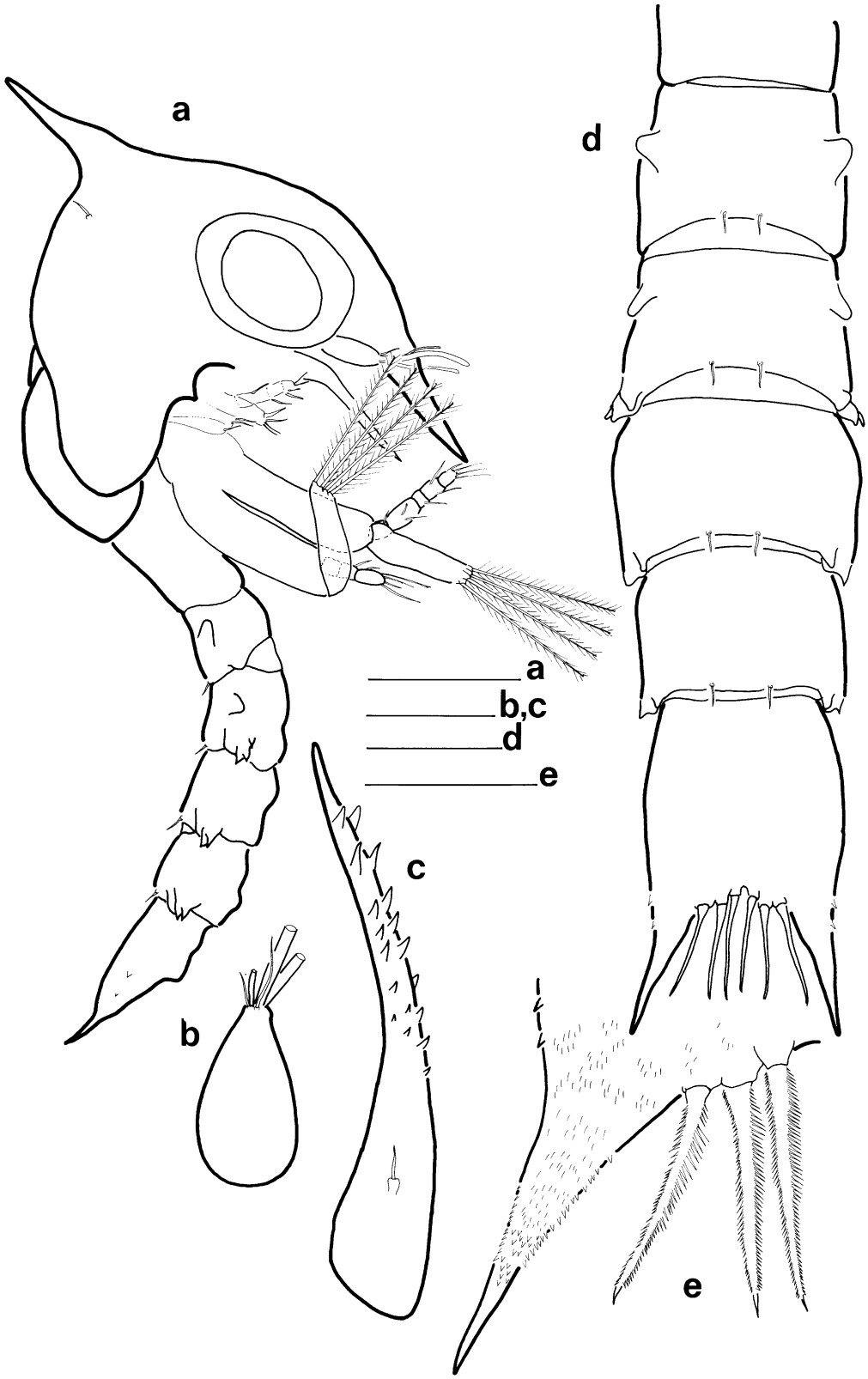

Figure 11. *Pachygrapsus plicatus* (H. Milne Edwards). First zoeal stage: (a) lateral view; (b) antennule; (c) antenna; (d) dorsal view of abdomen; (e) detail of telson. Scale bars as in Figure 1.

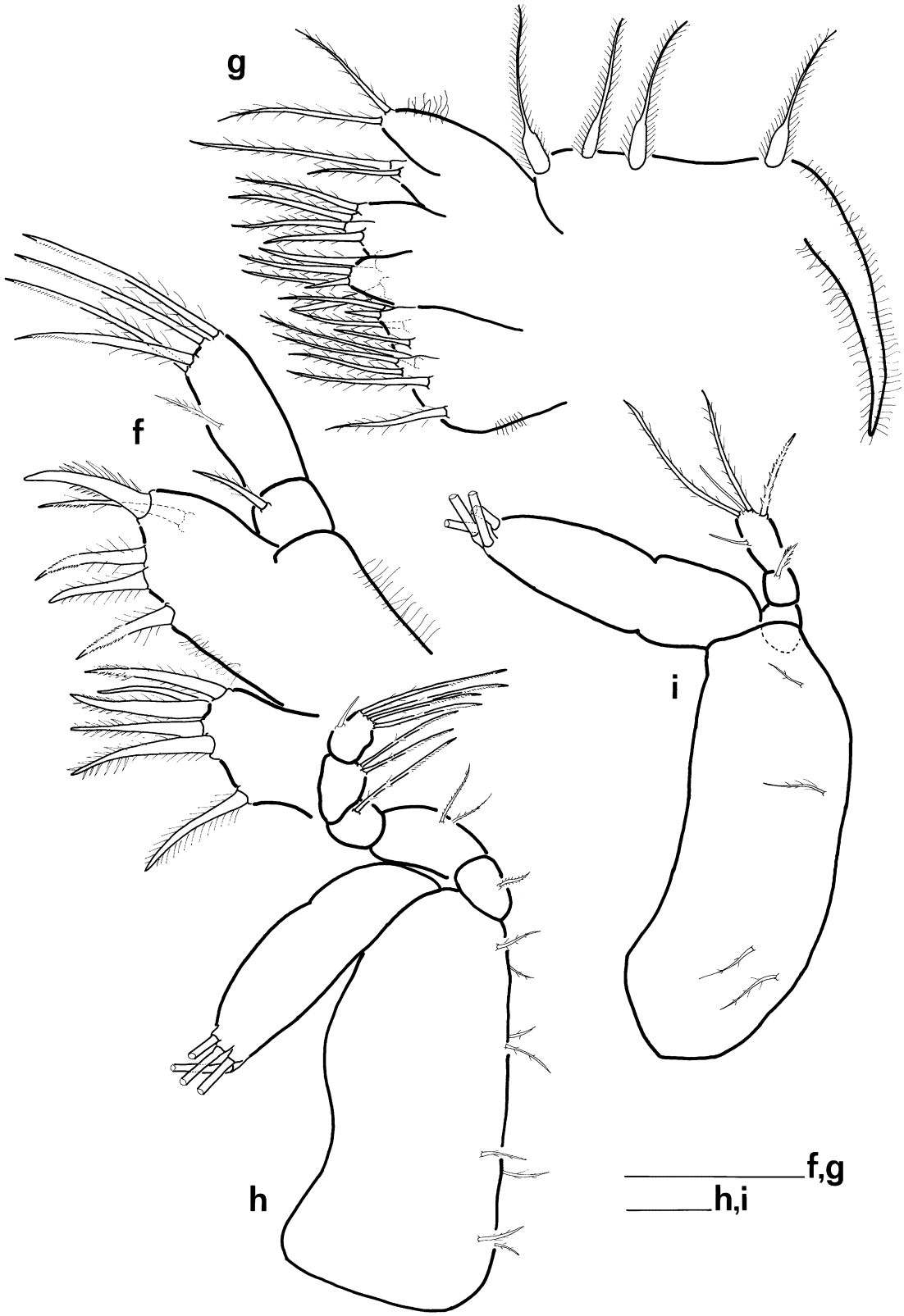

Figure 12. *Pachygrapsus plicatus* (H. Milne Edwards). First zoeal stage: (f) maxillule; (g) maxilla; (h) first maxilliped; (i) second maxilliped. Scale bars as in Figure 2.

lateral processes absent in somite 4; postero-lateral processes in somites 2–5, small in somite 2, and conspicuous, bearing distinct lobes in somites 3–5.

Telson (Figs 11d,e): with 2 postero-lateral pairs of spines of similar size; spinules distributed over margins and distal half of forks, except the tips; forks small, divergent.

Family Sesarmidae

Sarmatium crassum Dana, 1851 (Figs 13,14)

Dimensions: TT 0.92 mm ± 0.04, CW 0.43 mm ± 0.04, CL 0.58 mm ± 0.02.

Carapace (Fig. 13a): dorsal spine slightly curved posteriorly; rostral spine straight, of similar size of dorsal spine; lateral spines absent; a pair of postero-dorsal and a pair of antero-dorsal setae present; eyes sessile.

Antennule (Fig. 13b): uniramous, endopod absent; exopod unsegmented bearing 3 unequal terminal aesthetascs and 1 terminal seta.

Antenna (Figs 13a,c): of similar size than rostral spine; protopodal process with aligned spines of different size; endopod absent; exopod developed but considerably shorter than protopodal process, with 2 very reduced, 1 small and 1 stout, long-terminal setae.

Maxillule (Fig. 14f): epipod seta absent; coxal endite with 5 (denticulate) setae; basial endite with 5 (1 subterminal, denticulate; 4 stout, terminal denticulate) setae, 2 acute teeth also present; endopod 2-segmented, proximal segment with 1 (simple) seta, distal segment with 5 (1 subterminal, sparsely plumose + 4 distal, plumodenticulate) setae; exopod seta absent.

Maxilla (Fig. 14g): coxal endite bilobed bearing 5 (sparsely plumose) + 3 (sparsely plumose) setae, basial endite bilobed with 5 (plumodenticulate) + 4 (plumodenticulate) setae; endopod bilobed with 2 (unequal, plumodenticulate) + 3 (plumodenticulate) setae; scaphognathite (exopod) margin with 4 plumose setae and 1 long distal stout process.

First maxilliped (Fig. 14h): basis with 10 setae (arranged 2 simple; 2 simple; 3 simple; 3 simple); endopod 5-segmented with 2 (sparsely plumose), 2 (sparsely plumose), 1 (sparsely plumose), 2 (1 sparsely plumose, 1 plumodenticulate), 5 (1 subterminal sparsely plumose + 4 terminal plumodenticulate) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Second maxilliped (Fig. 14i): basis with 4 setae arranged (1 simple, 1 simple, 1 simple, 1 simple); endopod 3-segmented with 0, 1 (plumodenticulate), 6 (1 subterminal, sparsely plumose + 1 subterminal, simple; 4 terminal simple) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Third maxilliped: absent

Pereiopods: absent

Abdomen (Figs 13a,d): 5 somites; somite 2 with 1 pair of dorsolateral processes directed anteriorly, somite 3 with 1 pair of dorsolateral processes directed ventrally; postero-lateral processes in somites 2–5, round in somite 2, and increasingly acute in somites 3–5; a pair of median postero-dorsal setae in somites 2–5.

Telson (Figs 13a,d,e): lateral and dorsal medial spines absent; small setae arranged in a few patches in proximal fourth of forks, small spines bordering margins of forks, except for the proximal fourth and tip; forks large, curved dorsally and divergent; posterior margin with 3 pairs of stout setae spinulated.

Sesarma leptosoma Hilgendorf, 1869 (Figs 15,16)

Dimensions: TT 0.63 mm ± 0.02, CW 0.44 mm ± 0.04, CL 0.42 mm ± 0.02.

Carapace (Fig. 15a): small spinules bordering ventral margins; dorsal spine strongly curved posteriorly; rostral spine straight, slightly shorter than dorsal spine; lateral spines absent; a pair of postero-dorsal and a pair of antero-dorsal setae present; eyes sessile.

Antennule (Fig. 15b): uniramous, endopod absent; exopod unsegmented bearing 3 terminal aesthetascs and 3 terminal setae of unequal size.

Antenna (Figs 15a,c): similar in size to rostral spine; protopodal process with 2 rows of spines of different size, smaller ones aligned in distal third of process, except the tips; endopod absent; exopod developed but shorter than protopodal process, with 3 very reduced, 1 small and 1 stout, long-terminal setae.

Maxillule (Fig. 16f): epipod seta absent; coxal endite with 6 (3 sparsely plumose, 3 plumodenticulate) setae; basial endite with 5 (1 subterminal, plumodenticulate; 4 stout, terminal plumodenticulate) setae, 2 acute teeth also present; endopod 2-segmented, proximal segment with 1 (simple) seta, distal segment with 5 (1 subterminal, simple + 4 distal, plumodenticulate) setae; exopod seta absent.

Maxilla (Fig. 16g): coxal endite bilobed bearing 5 (sparsely plumose) + 3 (sparsely plumose) setae, basial endite bilobed with 5 (2 sparsely plumose, 3 plumodenticulate) setae + 4 (3 sparsely plumose, 1 plumodenticulate) setae; endopod bilobed with 2 (unequal,

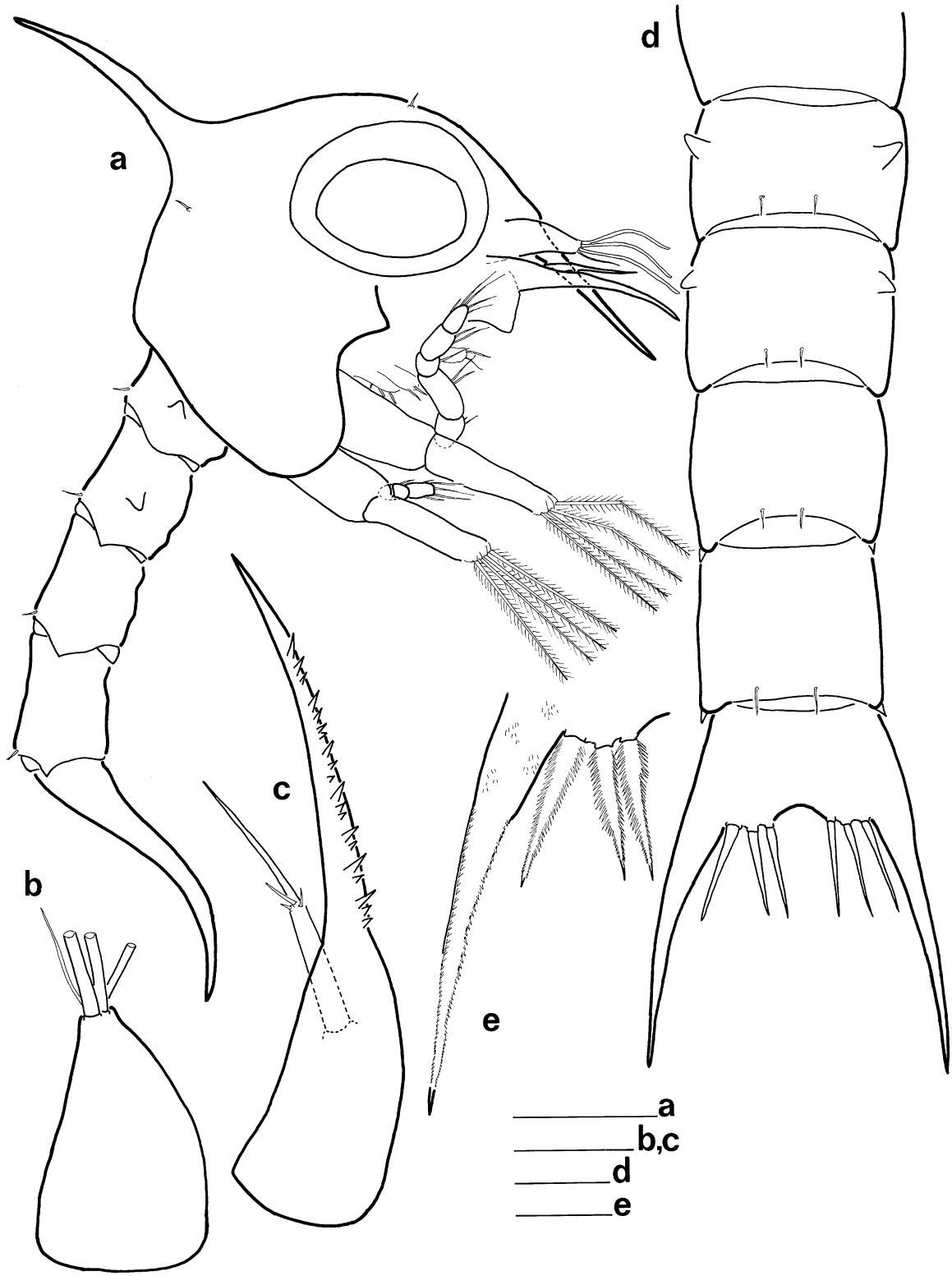

Figure 13. *Sarmatium crassum* Dana. First zoeal stage: (a) lateral view; (b) antennule; (c) antenna; (d) dorsal view of abdomen; (e) detail of telson. Scale bars as in Figure 1.

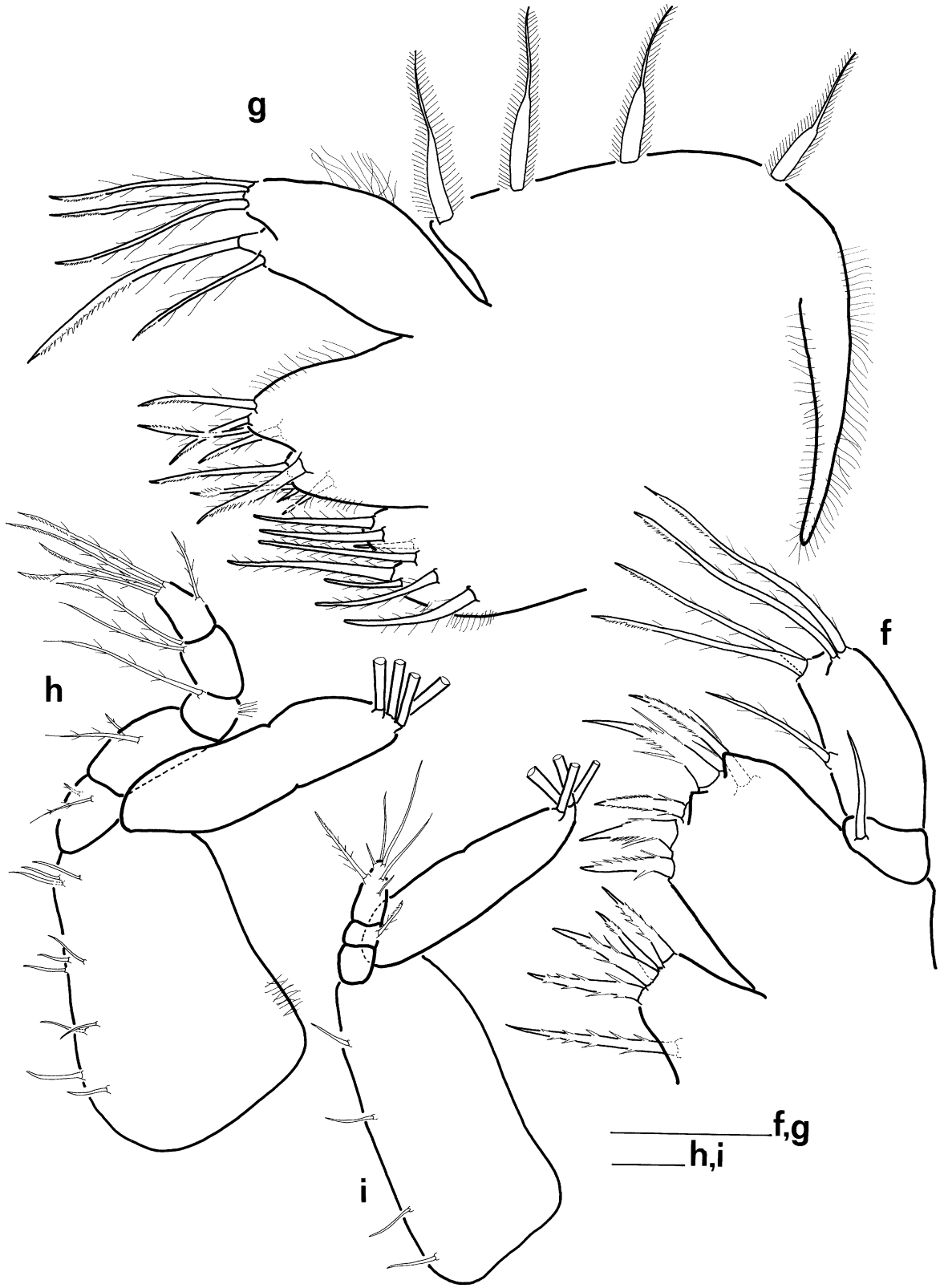

Figure 14. *Sarmatium crassum* Dana. First zoeal stage: (f) maxillule; (g) maxilla; (h) first maxilliped; (i) second maxilliped. Scale bars as in Figure 2.

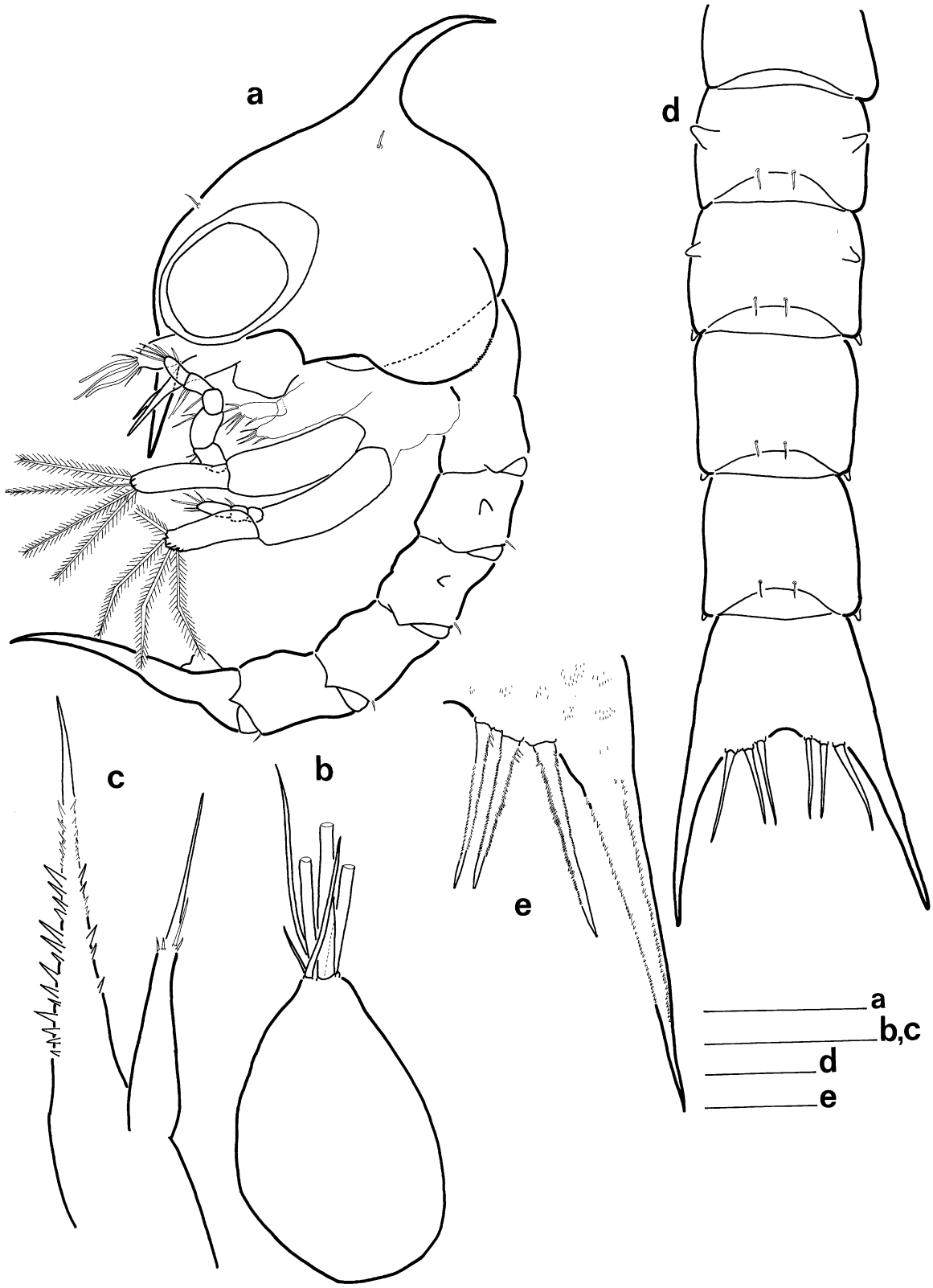

Figure 15. *Sesarma leptosoma* Hilgendorf. First zoeal stage: (a) lateral view; (b) antennule; (c) antenna; (d) dorsal view of abdomen; (e) detail of telson. Scale bars as in Figure 1.

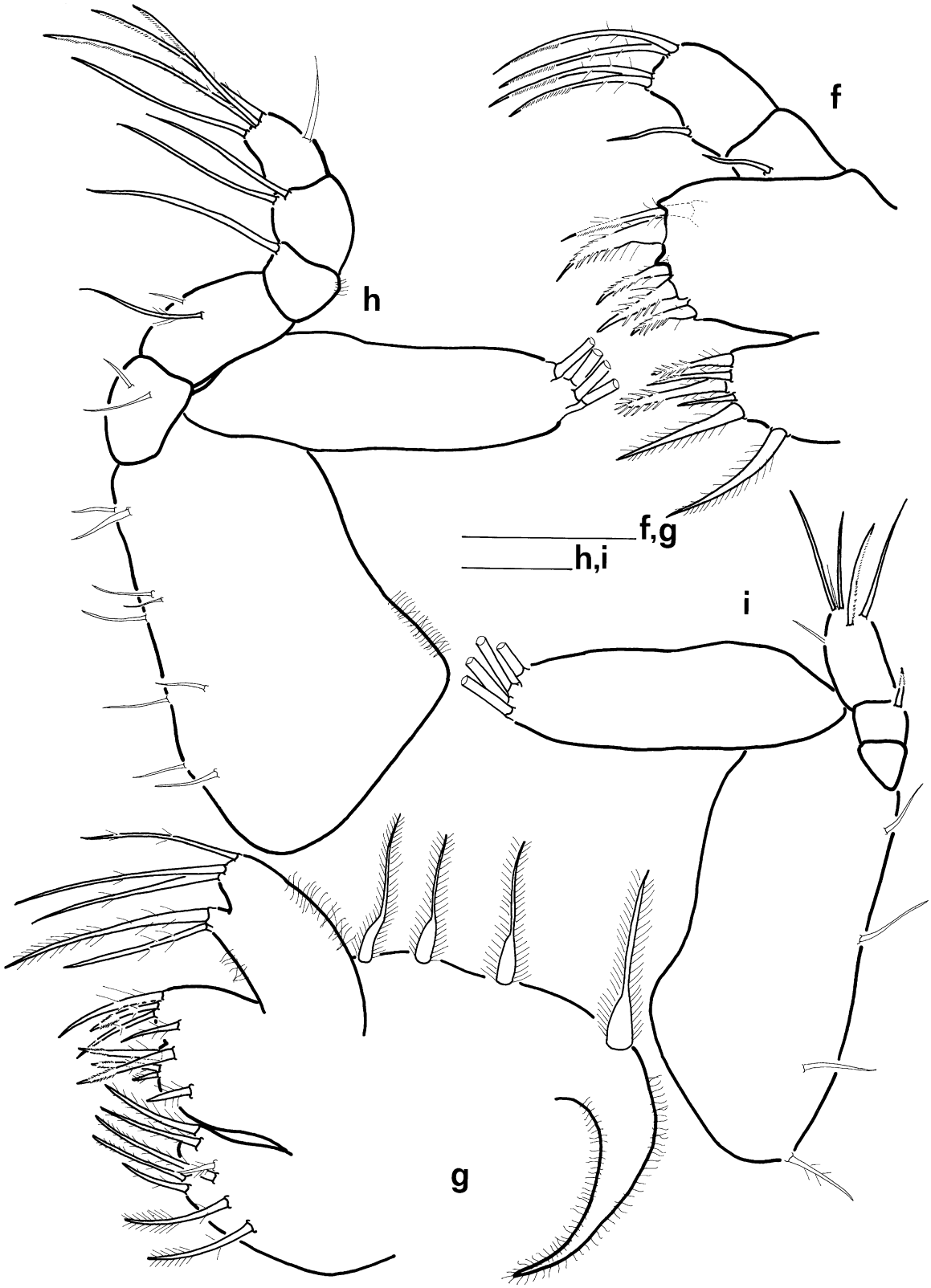

Figure 16. *Sesarma leptosoma* Hilgendorf. First zoeal stage: (f) maxillule; (g) maxilla; (h) first maxilliped; (i) second maxilliped. Scale bars as in Figure 2.

sparsely plumose) + 3 (sparsely plumose) setae; scaphognathite (exopod) margin with 4 plumose setae and 1 long distal stout process.

First maxilliped (Fig. 16h): basis with 9 setae (arranged 2 simple; 2 simple; 3 simple; 2 simple); endopod 5-segmented with 2 (simple), 2 (1 simple, 1 sparsely plumose), 1 (simple), 2 (simple), 5 (1 subterminal simple + 1 terminal simple, 3 terminal plumodenticulate) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Second maxilliped (Fig. 16i): basis with 4 setae (arranged 1 sparsely plumose, 1 simple, 1 simple, 1 simple) setae; endopod 3-segmented with 0, 1 (plumodenticulate), 6 (1 subterminal simple + 4 terminal simple, 1 terminal plumodenticulate) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Third maxilliped: absent

Pereiopods: absent

Abdomen (Figs 15a,d): 5 somites; somite 2 with 1 pair of dorsolateral processes directed anteriorly, somite 3 with 1 pair of dorsolateral processes directed ventrally; postero-lateral processes from round to acute in somites 1–5; a pair of median postero-dorsal setae in somites 2–5.

Telson (Figs 15d,e): lateral and dorsal medial spines absent; small setae distributed in scattered patches, small spines in fork margins, except for the tips; forks large, slightly divergent; posterior margin with 3 pairs of stout setae, the median ones with proximal larger spinulae on external margin.

FAMILY GECARCINIDAE

CARDISOMA CARNIFEX (HERBST, 1796) (FIGS 17,18)

Cardisoma carnifex; Kannupandi *et al*., 1980: 274, figs 1–9.

Dimensions: TT 0.90 mm ± 0.04, CW 0.48 mm ± 0.03, CL 0.50 mm ± 0.04.

Carapace (Fig. 17a): carapace globose; dorsal spine posteriorly directed; rostral spine straight, anteriorly directed, slightly shorter than dorsal spine; small lateral spines present; a pair of dorsal setae present; eyes sessile.

Antennule (Fig. 17b): uniramous, endopod absent; exopod unsegmented bearing 3 terminal aesthetascs of unequal size and 1 terminal seta.

Antenna (Figs 17a,c): similar in size to rostral spine; protopodal process with 2 rows of spines, larger in the inner margin; endopod absent; exopod developed but shorter than protopodal process, with 2 very reduced, 1 small and 1 stout, long-terminal setae.

Maxillule (Fig. 18f): epipod seta absent; coxal endite with 6 (5 sparsely plumose, 1 plumodenticulate) setae; basial endite with 5 (1 subterminal, plumodenticulate; 2 stout, terminal sparsely plumose; 2 stout, terminal plumodenticulate) setae, 2 acute teeth also present; endopod 2-segmented, proximal segment with 1 (simple) seta, distal segment with 5 (1 subterminal, simple + 4 distal, plumodenticulate) setae; exopod seta absent.

Maxilla (Fig. 18g): coxal endite bilobed bearing 5 (1 simple, 2 sparsely plumose, 2 plumodenticulate) setae + 4 (3 sparsely plumose, 1 simple) setae, basial endite bilobed with 5 (2 sparsely plumose, 3 plumodenticulate) + 5 (plumodenticulate) setae; endopod bilobed with 2 (unequal, sparsely plumose) + 3 (unequal, sparsely plumose) setae; scaphognathite (exopod) margin with 4 plumose setae and 1 long distal stout process.

First maxilliped (Fig. 18h): basis with 10 setae (arranged 2 sparsely plumose; 2 simple; 1 sparsely plumose, 2 simple; 1 sparsely plumose, 2 simple); endopod 5-segmented with 2 (simple), 2 (sparsely plumose), 1 (sparsely plumose), 2 (1 simple, 1 sparsely plumose), 5 (1 subterminal simple + 1 terminal simple, 3 terminal plumodenticulate) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Second maxilliped (Fig. 18i): basis with 4 setae (arranged 1 sparsely plumose, 1 sparsely plumose, 1 sparsely plumose, 1 sparsely plumose); endopod 3-segmented with 1 (simple), 1 (plumodenticulate), 6 (1 subterminal denticulate + 3 subterminal simple, 2 terminal sparsely plumose) setae; exopod unsegmented with 4 terminal plumose natatory setae.

Third maxilliped: absent

Pereiopods: absent

Abdomen (Figs 17a,d): 5 somites; somite 2 with 1 pair of dorsolateral processes directed anteriorly, somite 3 with 1 pair of dorsolateral processes directed ventrally; postero-lateral processes from round to acute in somites 1–5, indented in somites 3–5; a pair of median postero-dorsal setae in somites 2–5.

Telson (Figs 17d,e): a pair of minute lateral spines present; small setae distributed in scattered patches, small spines in fork margins, except for the tips; forks large, divergent; posterior margin with 3 pairs of stout setae, the median one with proximal larger spinulae on external margin.

DISCUSSION

All species examined in this study can be distinguished either by verifying the setation patterns of

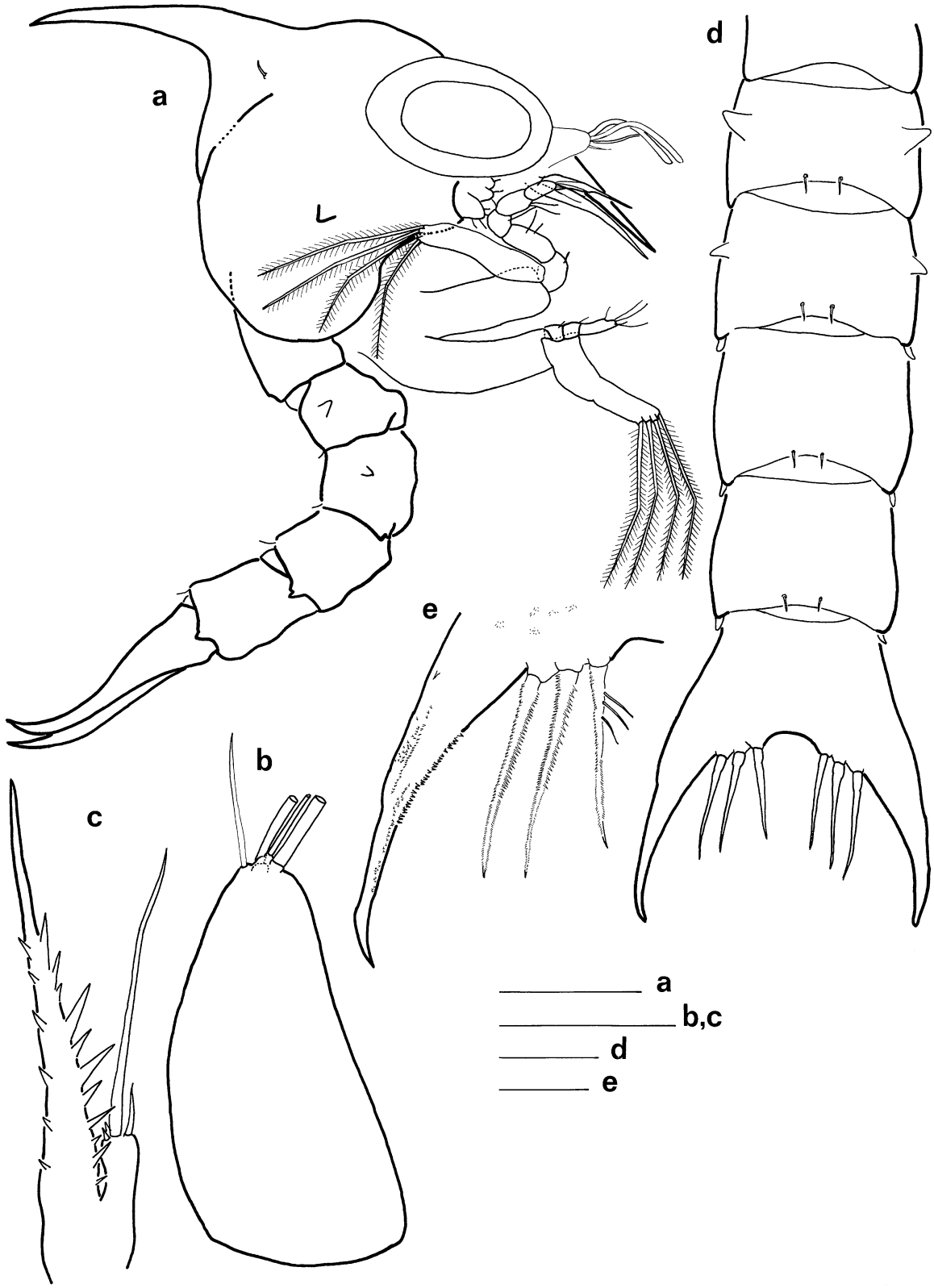

Figure 17. *Cardisoma carnifex* (Herbst). First zoeal stage: (a) lateral view; (b) antennule; (c) antenna; (d) dorsal view of abdomen; (e) detail of telson. Scale bars as in Figure 1.

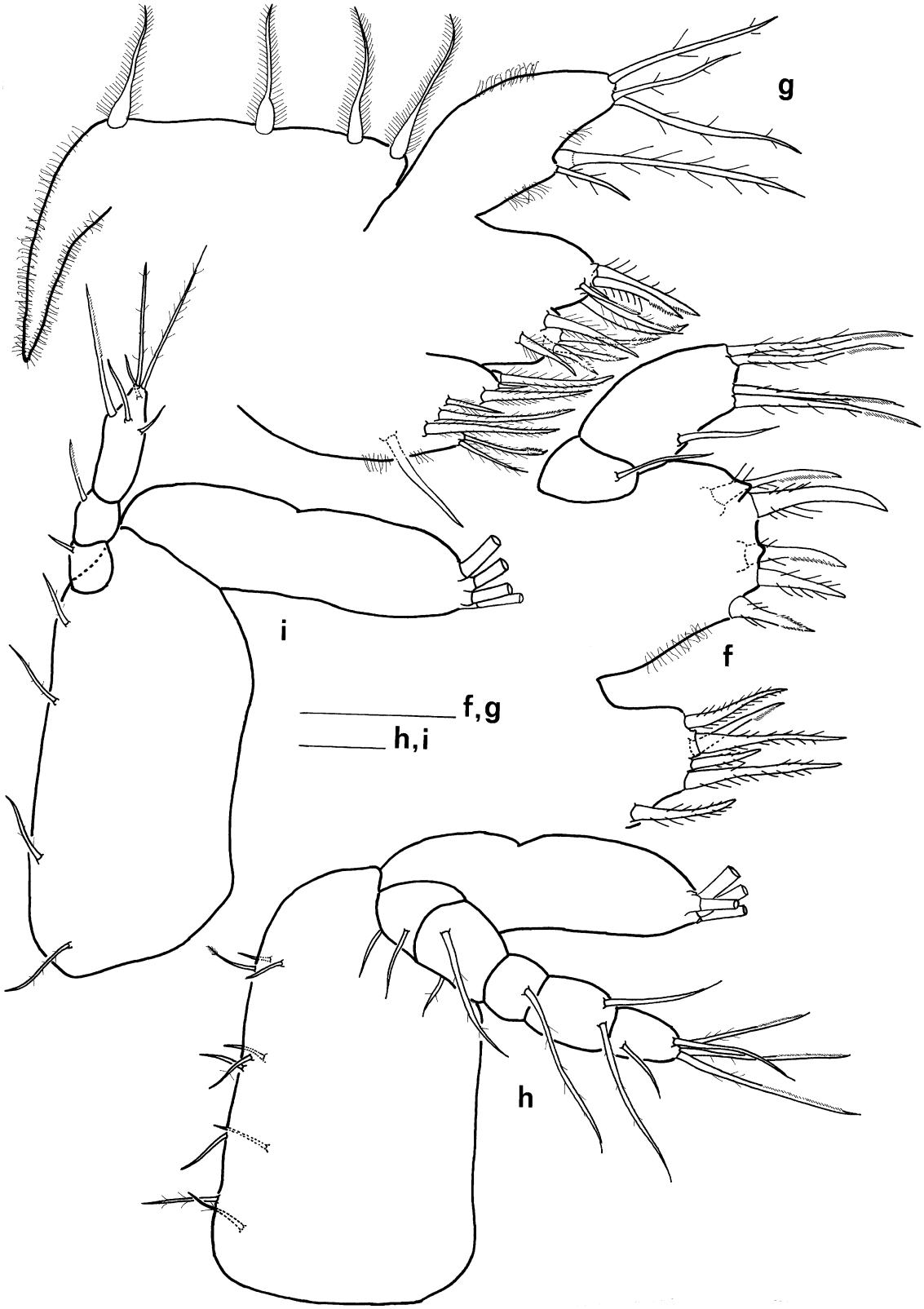

Figure 18. *Cardisoma carnifex* (Herbst). First zoeal stage: (f) maxillule; (g) maxilla; (h) first maxilliped; (i) second maxilliped. Scale bars as in Figure 2.

appendages, or by comparing the morphology of carapace and abdominal somites. In general, grapsid species can be identified more easily than sesarmids. Compared to *Pachygrapsus*, the first stage zoea of *Grapsus* is considerably larger and bears lateral processes in the 5th abdominal somite. Within *Grapsus*, *G. tenuicrustatus* can be readily distinguished from *G. fourmanoiri* in that the antenna is longer, reaching the tip of the rostral spine, and the abdominal lateral processes are more developed in the former. For *Pachygrapsus*, *P. minutus* differs from *P. plicatus* in that the abdomen is relatively wider in the first, with a distinctly broad 4th somite bearing a pair of lateral processes. Other differences between these pair of species are described above and, although requiring the dissection of appendages, may be of most importance for systematic and phylogenetic studies. *Metopograpus messor and Ilyograpsus paludicola* are strikingly different from the *Grapsus – Pachygrapus* group; *M. messor* presents considerably longer carapacial spines, an antenna lacking the exopod, and a much more developed 5th abdominal somite, while the small first zoea of *I. paludicola* shows a type-B antenna (*sensu* Aikawa, 1929) and has no dorsal spine. In all these grapsids, the small knob-like lateral spine usually described in the first zoeal stage of members of this family (see Cuesta, 1999) was not found. This is a minute structure, which precedes the fully developed spine in more advanced stages. Because larvae were fixed soon after full natatory activity was observed, it is possible that such minute structures might not have expanded completely as to be detected under light microscopy.

For the Sesarmidae, *Sarmatium crassum* can easily be distinguished because it bears a nearly straight dorsal spine. Slight differences regarding the shape of carapace and fork may enable the identification of the remaining sesarmids, as noted by Pereyra Lago (1993b). Setation patterns may also be used to separate them, namely in the case of the antennule, antenna exopod and the coxal endite of the maxillule, but these differences may not be consistent, as there is some disagreement between the present account and the descriptions provided by Pereyra Lago (1993b; see Table 2). Apart from the maxillipeds, this study suggests that the chaetotaxy of the maxilla is also conservative, despite the results obtained in previous work showing alternative setation of coxal and basial endites (Pereyra Lago, 1987, 1993a, 1993b). As in these sesarmids, discrepancies concerning the setation of the maxillule and maxilla in the varunid *Helice leachi* were also found. All these differences may reflect intraspecific variability, but more conclusive results would be gathered if larval samples were taken along their latitudinal range, and concurrent molecular analyses were carried out in order to verify the occurrence of genetic divergence. As Baba *et al*. (1984), Mia & Shokita (1996) did not illustrate posterodorsal pairs of setae on abdominal somites in *H. leachi*. The latter authors (Mia & Shokita, 1997) used this characteristic to distinguish the first stage zoeae of *H. leachi* from that of *H. formosensis*. However, those setae were located in this study indicating that their absence in the decriptions provided by Mia & Shokita (1996) should not be used as a diagnostic feature.

The present descriptions for *Metopograpsus messor* and *Cardisoma carnifex* add some detail to the work published by Chhapgar (1956), Rajabai (1961), Hashmi (1971), Kannupandi *et al*. (1980) and Al-Khayat & Jones (1996). In spite of the characteristic overall morphology of the first stage zoea of *M. messor*, it is shown that more conservative features of appendages are typical of a grapsid. Among other dubious characteristics, Hashmi (1971) showed 10 setae on the first maxilliped basis, Rajabai (1961) figured a very particular setation of the endopods of first and second maxillipeds and Al-Khayat & Jones illustrated unexpected setation of both mouthparts and maxillipeds. However, a closer examination of these structures suggests that such information is inaccurate. The setation of the first maxilliped basis (2, 2, 2, 2), and the endopods of the first and second maxillipeds (1, 2, 1, 2, 5 and 0, 1, 5, respectively) follows the grapsid formula as expected. Similar inconsistencies were found regarding an early description of the first zoea of *Cardisoma carnifex* carried out by Kannupandi *et al*. (1980). The authors have, for instance, found seven setae on the endopod of the maxilla, two setae on the third segment of the first maxilliped endopod, and three setae on both the second and the third segment of the second maxilliped endopod. In this present study, the setation patterns of the endopod of the first and second maxilliped were found to be 2, 2, 1, 2, 5 and 1, 1, 6, respectively, which seem to be shared among representatives of this family because they were reported in previously described gecarcinid zoeae (see Costlow & Bookhout, 1968; Willems, 1982; Shokita & Shikatani, 1990). In contrast, the setation formula of the endopod of the maxilla is more variable, i.e. 2, 3 in *Cardisoma* (see Costlow & Bookhout, 1968; Shokita & Shikatani; this study) and 2, 2 in *Gecarcinus* (see Cabrera, 1966; Willems, 1982), allowing the separation of these genera.

Cuesta (1999) revised and compared the morphology of grapsoid zoeae and indicated the validity of certain characters to separate all families. Apart from the obvious differences with respect to the type of telson and antenna, grapsoid families can be identified unambiguously by a combination of conservative fea-

tures, namely the setation of the endopod of the maxilla, the basis of the first maxilliped and the endopod of the second maxilliped. In general, the present study further supports these trends, but special attention should be paid to the sesarmid *Sesarma leptosoma*; a species with a first maxilliped basis bearing a 2, 2, 3, 2 setal arrangement, instead of the 2, 2, 3, 3 expected. Otherwise, it closely resembles other Sesarmidae. Adults of this mangrove crab present a number of morphological adaptations for a highly specialized tree-dwelling life style, and perhaps a more detailed examination of adults and other larval stages, mainly the megalopa, would eventually reveal additional differences from its congenerics and therefore help to reappraise its taxomic status.

More divergent characteristics were found for the grapsid *Ilyograpsus paludicola*. Although showing a 2, 2 setation formula on the endopod of the maxilla and a 0, 1, 5 setation pattern on the second maxilliped, this larva does not present other key characters of grapsid zoeae, such as the 1,2,1,2,5 setal formula of the first maxilliped endopod. This quite surprising combination of characters is not found in any other grapsoid and therefore its inclusion in this superfamily seems inappropriate. By running the identification key proposed by Rice (1980), it was found that *I. paludicola* could belong to the Ocypodidae, as already suggested by Fukuda (1978), more precisely the subfamily Macrophthalminae, as indicated by Cuesta (1999). On the other hand, tentative larval analysis suggested that the Ocypoidea may be paraphyletic in that the Macrophthalminae could be assigned to the Grapsoidea (P. F. Clark, pers. comm.). Therefore, apart from more detailed studies on this particular species, the clarification of phylogenetic relationships among higher taxa are also pending for a correct identification of the systematic position of *Ilyograpsus*.

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