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Larvae and first-stage juveniles of the American genus *Armases* Abele, 1992 (Brachyura: Sesarmidae): a morphological description of two complete developments and one first zoeal stage

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Abstract

Complete larval development and first crab stages of the sesarmid crabs *Armases roberti* (H. Milne Edwards, 1853) and *A. ricordi* (H. Milne Edwards, 1853) from Jamaica were obtained from laboratory culture. All larval stages (four zoeal stages and the megalopa) and the first juvenile crab stage of *A. roberti* are described and illustrated in detail for the first time, and a previous description of the larvae and the first crab of *A. ricordi* is revised and complemented. In addition, the first zoeal stage of *A. americanum* (de Saussure, 1858) is described for the first time. The morphological characters of the larvae of the three sesarmid species are compared with those of other known larvae of the genera *Armases* Abele, 1992 and *Aratus* H. Milne Edwards, 1837. Several characters are described for the first time for zoeal stages of the genus *Armases*, especially minute spines on the telson and the setation of the coxa of the first maxilliped. Minor differences were also observed between the earlier and the present description of *A. ricordi*, and additional characters are included here, in particular the cephalothoracic setation. The zoeal morphologies of *A. roberti* and *A. ricordi* only show minor meristic and morphometric differences, but the megalopae of both species can easily be distinguished by the setation of the sternum.

Keywords: *Armases americanum*, *Armases ricordi*, *Armases roberti*, *Brachyura*, *juvenile*, *larval development*, *megalopa*, *Sesarmidae*, *zoea*

Introduction

Representatives of the semi-terrestrial to terrestrial crab family Sesarmidae (see Schubart et al. 2000) occur along the American east coast from Massachusetts to southern Brazil, including the Gulf of Mexico and the Caribbean, and along the American west coast from

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Baja California (Mexico) to Perú (Abele 1992). Only a few sesarmid species live in the temperate regions [i.e. *Sesarma reticulatum* (Say, 1817) and *Armases cinereum* (Bosc, 1802)], while a high diversity can be found along the subtropical and tropical coasts. Presently, the American species are classified within four genera: *Aratus* H. Milne Edwards, 1837; *Armases* Abele, 1992; the Jamaican endemic *Metopaulias* Rathbun, 1896; and *Sesarma* Say, 1817. The genus *Armases* is closely related to *Aratus* (see Fratini et al. 2005) and consists of 12 known species (Abele 1992; Niem 1996).

Armases roberti (H. Milne Edwards, 1853) is a common semi-terrestrial crab occurring along the banks of freshwater streams and seepage areas (see Diesel and Schuh (1998) and Anger et al. (2006) for detailed description of habitat characteristics). Its known distribution exclusively comprises the Caribbean islands, from Cuba to Trinidad (Chace and Hobbs 1969; Abele 1992). *Armases ricordi* (H. Milne Edwards, 1853) is one of the more terrestrial species in *Armases* and has been reported from dry coastal habitats among rocks and debris in the supralittoral fringe up to several hundred metres inland. This species ranges from Florida, Bermuda, Bahamas, West Indies, the Caribbean coast of Central and South America to Surinam (Abele 1992; Diesel and Schuh 1998). *Armases americanum* (de Saussure, 1858) is common among small freshwater streams, among and under rocks and rubble and among vegetation. The known distribution of this species ranges from Tampico (Gulf of Mexico) across Yucatán, Belize, and Guatemala to the Caribbean coasts of Costa Rica and Panama, but is exclusively continental (Abele 1992; Hernández Aguilera et al. 1996), except for a recent record from Trinidad (C. D. Schubart, unpublished). Aspects of the adult ecology and physiology, breeding patterns, and salinity tolerance of the larval stages of *Armases roberti* and *A. ricordi* have previously been studied (Diesel and Schuh 1998; Schubart and Diesel 1998). Both species show marine and non-abbreviated larval developments with four zoeal stages (Álvarez and Ewald 1990; Diesel and Schuh 1998; Schubart and Diesel 1998; Diesel et al. 2000). Abele (1992, p 38) noted that for *A. americanum* the “eggs are small and numerous, suggesting an estuarine or marine larval development”.

The larval morphology of *Armases* has previously been described for five species: *A. cinereum* by Hyman (1924) and Costlow and Bookhout (1960); *A. ricordi* and *A. rubripes* (Rathbun, 1897) by Díaz and Ewald (1968) and Schubart and Cuesta (1998); *A. angustipes* (Dana, 1852) by Kowalczyk (1994) and Cuesta and Anger (2001); *A. miersii* (Rathbun, 1897) by Zimmermann-Ruf (1997) and Cuesta et al. (1999), and most recently *A. benedicti* (Rathbun, 1897) by Lima and Abrunhosa (2006). The larval stages and the first juvenile of *A. roberti* have recently been documented photographically, with a brief description of the chromatophore patterns (Anger et al. 2006). All these species pass through four zoeal stages, except for *A. miersii*, which shows an abbreviated mode of development with only three zoeal stages (Cuesta et al. 1999), occurring in supratidal rock pools as a peculiar “breeding habitat” (Anger 1995; Schuh and Diesel 1995).

Here, we describe for the first time the complete larval and early juvenile development of *A. roberti* and the first zoeal stage of *A. americanum*, revise the larval and early juvenile morphology of *A. ricordi*, and compare larval and juvenile features with those known from the congeneric species with non-abbreviated development, and from the closely related genus *Aratus*.

Material and methods

Adult specimens of *Armases roberti* were collected in 2003 along the banks of the Rio Bueno (see Anger et al. 2006), those of *Armases ricordi* between the beach and the mangrove zone at Glistening Waters (Trelawny, Jamaica). The crabs were transported alive to the

Helgoland Marine Biological Station (Germany), where they were maintained at salinities of 0.2 and 32 psu, respectively, a constant temperature of 24°C, and an artificial 12 h light–12 h dark cycle. The crabs were fed daily with frozen marine isopods (*Idotea* sp.). The extrusion and incubation of eggs took place under the same conditions. Larvae from three hatches of *A. roberti* and two hatches of *A. ricordi* were mass-reared at 24°C and 25 psu (*A. roberti*) or 32 psu (*A. ricordi*) salinity, and fed daily with freshly hatched nauplii of *Artemia* sp. (Great Salt Lake). Water was changed daily and the larvae were checked for moults and mortality. Exuviae and specimens of each developmental stage were preserved in 70% ethanol.

Ovigerous females of *Armases americanum* were captured near a small stream crossing the narrow beach of Montepío (Veracruz, Mexico) by the third author on 11 February 1999 and were maintained in small containers filled with freshwater during the following days of field work. Larvae of two females hatched on 13 and 14 February 1999, respectively. Some of them were immediately fixed in ethanol, others were kept alive, but died before successful moult to zoea II, due to the lack of appropriate food in the field.

A Wild M7 binocular microscope, equipped with an ocular micrometer, was used for the dissection and measurements of individuals (10 individuals of each hatch and larval stage were measured). An Olympus BH-2 microscope was used for the determination of the setal formula and measurements of the appendages. The following measurements were taken: rostro-dorsal length (rdl) as the distance between the tips of the dorsal and rostral spines; carapace length (cl) from the base of the rostral spine to the posterolateral carapace margin; antennal exopod length (el) from the base of the antennal exopod to the distal margin (without setae); protopodal process length (pl) from the base of the antennal exopod to the tip of the protopodal process; furcal length (fl) from an imaginary line across the base of the outer seta on the posterior margin of the telson to the furcal tip; basal telson length (bt), from a line across the anterior margin to the posterior margin of the telson (base of the outer seta). For the megalopa and first juvenile, carapace length (cl) was measured as the distance from the frontal margin to the posterior margin of the carapace; carapace width (cw) as the greatest distance across the carapace.

All drawings were made with the aid of microscope photography. The number of individuals of each larval stage examined to describe the morphology varied between five and 10, including zoeae from as many hatches as were available. The long aesthetascs of the antennules and the long plumose setae on the distal exopod of the maxillipeds and pleopods are not fully illustrated and are drawn truncated instead. In Figure 7c, d, plumose setae of the scaphognathite are truncate. Larval descriptions followed the basic malacostracan body pattern, and setal armature on appendages is described from proximal to distal segments and from endopod to exopod (see Clark et al. 1998). For setal terminology, we followed Ingle (1992) and Garm (2004).

Parental animals and samples of all larval stages were deposited at the Biological Collections of Reference of the Institut de Ciències del Mar (CSIC) in Barcelona (catalogue numbers ICMD 38–43/2007 and ICMD 44–49/2007 for the larval stages and first juvenile of *Armases roberti* and *A. ricordi*, respectively) and the University of Louisiana Lafayette Zoological Collection (*Armases americanum*; catalogue number ULLZ 4027).

Results

The first zoeal stage of *Armases roberti* is described completely. For the subsequent stages, only the main differences from the first zoea are described in detail. The morphological and

meristic differences with individuals of *A. ricordi* and *A. americanum* are presented in Table I.

Description

Armases roberti

(Figures 1–16)

Zoea I

Size. rdl=0.85 ± 0.02 mm; cl=0.52 ± 0.03 mm.

Carapace (Figure 1a). Globose, smooth, with minute anterolateral protuberance. Dorsal spine present, well developed, strongly curved posteriorly. Rostral spine present, straight, similar in length to antennal protopod. Lateral spines absent. Pair of setae on posterodorsal and anterodorsal regions. Posterior and ventral margin without setae. Eyes sessile.

Antennule (Figure 3a). Uniramous. Endopod absent. Exopod unsegmented with four terminal aesthetascs and one terminal seta.

Antenna (Figure 4a). Similar in size to rostral spine. Protopodal process with two rows of unequal number of spines (8–11) of different sizes. Exopod elongated, with four terminal simple setae (one long, one medium-sized, and two minute). pl/el=2.0–2.2.

Mandible. Palp absent; molar and incisor processes well developed.

Maxillule (Figure 5a). Exopod and epipod setae absent. Coxal endite with six plumose setae. Basial endite with five setae (three cuspidate and two plumodenticulate) and with two teeth. Endopod two-segmented, with one seta on proximal segment, and one subterminal and four terminal plumodenticulate setae on the distal segment.

Maxilla (Figure 7a). Coxal endite bilobed, with 5+3 plumodenticulate setae and with a marginal tooth on distal lobe (detail in Figure 7a). Basial endite bilobed with 5+4 plumodenticulate setae. Endopod unsegmented, bilobed, with 2+3 long plumodenticulate setae on inner and outer lobe, respectively. Scaphognathite (exopod) with four plumose marginal setae and long setose posterior process.

First maxilliped (Figure 9a). Coxa with one sparsely plumose seta. Basis with 10 medial sparsely plumose setae arranged 2+2+3+3 on inner side, and a mat of long microtrichiae on outer proximal side. Endopod five-segmented, with 2, 2, 1, 2, 5 (one subterminal+four terminal) plumodenticulate setae. Exopod two-segmented; distal segment with four long plumose natatory setae.

Second maxilliped (Figure 10a). Coxa without setae. Basis with four medial sparsely plumose setae arranged 1+1+1+1. Endopod three-segmented, with 0, 1, 6 setae. Exopod two-segmented; distal segment with four long plumose natatory setae.

Third maxilliped. Absent.

Table I. Morphological differences among larval stages of the genera *Armases* and *Aratus*, not considering *A. benedicti* (inaccurate description) and *A. miersii* (abbreviated development).

	<i>Aratus pisonii</i> (Cuesta et al. 2006a)	<i>Armases americanum</i> (present paper)	<i>Armases roberti</i> (present paper)	<i>Armases ricordi</i> (present paper)	<i>Armases ricordi</i> (Diaz and Ewald 1968; Schubart and Cuesta 1998)	<i>Armases rubripes</i> (Diaz and Ewald 1968; Schubart and Cuesta 1998)	<i>Armases cinereum</i> (Costlow and Bookhout 1960)	<i>Armases angustipes</i> (Cuesta and Anger 2001)
Zoea 1								
rdl (mm)	0.57±0.04	0.73±0.03	0.85±0.02	0.70±0.03	0.72±0.02	0.63±0.03	nd	0.78±0.04
cl (mm)	0.30±0.02	0.45±0.02	0.52±0.03	0.49±0.02	0.48±0.01	0.37±0.02	nd	0.41±0.02
Carapace ad (s)	4	2	2	2	nd	nd	nd	2
Antennule (a+s)	4	4	5	5	5	4	5	5
Maxillule								
Coxa (s)	5	6	6	6	5	5	5	6
Maxilliped 1								
Coxa (s)	1	1	1	1	nd	nd	nd	nd
Telson								
Furca (mlsp)	2	1	1	1	nd	nd	nd	nd
Zoea 2								
rdl (mm)	0.70±0.03	nd	1.12±0.04	0.95±0.02	nd	nd	nd	0.97±0.03
cl (mm)	0.34±0.02	nd	0.72±0.02	0.58±0.02	nd	nd	nd	0.53±0.02
Carapace vm (s)	2	nd	2	2	nd	nd	nd	1
Carapace ad (s)	4	nd	4	4	nd	nd	nd	6
Abdomen so1 (s)	1	nd	1	1	nd	nd	0	0
Zoea 3								
rdl (mm)	0.79±0.03	nd	1.45±0.04	1.15±0.03	nd	nd	nd	1.21±0.03
cl (mm)	0.41±0.03	nd	0.85±0.03	0.73±0.02	nd	nd	nd	0.66±0.03
Carapace vm (s)	5	nd	5	5	5	5	nd	4
Carapace ad (s)	8	nd	8	8	nd	nd	6	6
Carapace ds (s)	0	nd	2	2	nd	nd	0	0
Maxilliped 1								
Endopod (s)	2, 3, 2, 2, 5	nd	2, 3, 2, 2, 5	2, 3, 2, 2, 5	2, 2, 2, 2, 5	2, 2, 2, 2, 5	2, 2, 1, 2, 5	2, 3, 2, 2, 5
Zoea 4								
rdl (mm)	0.92±0.04	nd	1.50±0.07	1.45±0.04	nd	nd	nd	1.30±0.04
cl (mm)	0.47±0.02	nd	0.97±0.05	0.91±0.03	nd	nd	nd	0.71±0.02
Carapace ad (s)	8	nd	10	10	nd	nd	6	8
Carapace ds (s)	2	nd	2	2	nd	nd	0	0

Table I. (Continued.)

	<i>Aratus pisonii</i> (Cuesta et al. 2006a)	<i>Armases americanum</i> (present paper)	<i>Armases roberti</i> (present paper)	<i>Armases ricordi</i> (present paper)	<i>Armases ricordi</i> (Diaz and Ewald 1968; Schubart and Cuesta 1998)	<i>Armases rubripes</i> (Diaz and Ewald 1968; Schubart and Cuesta 1998)	<i>Armases cinereum</i> (Costlow and Bookhout 1960)	<i>Armases angustipes</i> (Cuesta and Anger 2001)
Maxilla								
Coxal endite (s)	6+4	nd	7+4–5	7+5	11	7+4	7+5	6+4
Basial endite (s)	7+5	nd	7+5–6	6+6	6+6	6+6	6+6	6+5
Scaphognathite (s)	23	nd	18–21	22–24	nd	20	23	20–21
Maxilliped 1								
Coxa (s)	1	nd	2	2	nd	nd	nd	nd
Endopod (s)	2, 3, 2, 2, 6	nd	2, 3, 2, 2, 6	2, 3, 2, 2, 6	2, 3, 2, 2, 6	2, 2, 2, 2, 6	2, 3, 1, 2, 6	2, 3, 2, 2, 6
Exopod (s)	10	nd	9	9	9	9	9	10
Megalopa								
cl (mm)	0.69±0.05	nd	1.18±0.08	1.10±0.06	nd	nd	nd	0.66±0.05
cw (mm)	0.46±0.03	nd	0.85±0.07	0.75±0.04	nd	nd	nd	0.48±0.03
Antennule								
Exopod (a)	0, 6, 3	nd	0, 6, 3	0, 7, 3	nd	nd	0, 6, 5	0, 6, 3
Antenna								
Flagellum (s)	0, 2, 1, 5, 1, 3	nd	0, 2–3, 1, 5, 1, 3	0, 2, 1, 5, 1, 3	0, 2, 1, 5, 1, 3	0, 2, 1, 4, 1, 3	0, 2, 1, 2, 1, 2	0, 2, 1, 5, 1, 3
Maxillule								
Coxal endite (s)	9	nd	11–12	11–12	11	11	9	11
Basial endite (s)	17	nd	16–18	18	18	17	12	15
Maxilla								
Coxal endite (s)	8+4	nd	12+5	10–11+5	11+4	11+3	8+5	11+5
Basial endite (s)	8+5	nd	7+7	7–9+7–8	6+6	6+6	7+7	8+7
Scaphognathite (s)	33	nd	36–39	36–39	45	35	30	39
Maxilliped 1								
Coxa (s)	9	nd	6	7+8	8	6	5	8
Basis (s)	10	nd	11	12+13	11	9	8	11
Exopod (s)	3, 3	nd	3, 3–4	3–4, 8–9	3, 4	3, 4	3, 5	3, 4
Epipod (s)	4	nd	7	6	5	7	5	5
Maxilliped 2								
Coxa+basis (s)	0	nd	0	4	0	0	0	2
Endopod (s)	0, 1, 3, 7	nd	0, 1, 3, 6–7	1, 1, 4–5, 7–8	0, 1, 3, 6	0, 1, 3, 6	0, 1, 6, 6	0, 1, 4, 8
Exopod (s)	1, 5	nd	1, 5	1, 5	1, 5	1, 5	0, 5	1, 6

Table I. (Continued.)

	<i>Aratus pisonii</i> (Cuesta et al. 2006a)	<i>Armases americanum</i> (present paper)	<i>Armases roberti</i> (present paper)	<i>Armases ricordi</i> (present paper)	<i>Armases ricordi</i> (Diaz and Ewald 1968; Schubart and Cuesta 1998)	<i>Armases rubripes</i> (Diaz and Ewald 1968; Schubart and Cuesta 1998)	<i>Armases cinereum</i> (Costlow and Bookhout 1960)	<i>Armases angustipes</i> (Cuesta and Anger 2001)
Maxilliped 3								
Endopod (s)	8, 8, 3, 4, 6	nd	8–9, 8, 3–4, 4, 7	8, 8, 4, 4, 7	8, 9, 4, 3, 6	8, 8–9, 3–4, 6–7	7, 6, 3, 2, 5	10, 8, 3, 4, 6
Sternum (s)	6	nd	8	11–12	nd	nd	nd	nd
Pereiopods 3, 4								
Coxa (pr)	nd	nd	1	1	nd	nd	nd	nd
Abdomen (s)	11, 12, 14, 14, 14, 4	nd	7, 12, 14, 16, 14, 7, 4	12, 14, 14, 14, 4	nd	nd	nd	7, 10, 10, 10, 12, 4
Pleopods (s)	14, 12, 12, 11	nd	14–15, 13–15, 13–14, 11–12	15, 14, 13, 10	13, 13, 13, 11	13, 13, 13, 11	13, 13, 13, 11	13, 16, 17, 15
Uropod (s)	1, 6	nd	1, 7	1, 7	1, 7	1, 6	1, 7	1, 7

a, aesthetascs; ad, anterodorsal; ds, dorsal spine; mlsp, minute lateral spine; nd, no data; pr, processes; s, setae; so, somite; vm, ventral margin.

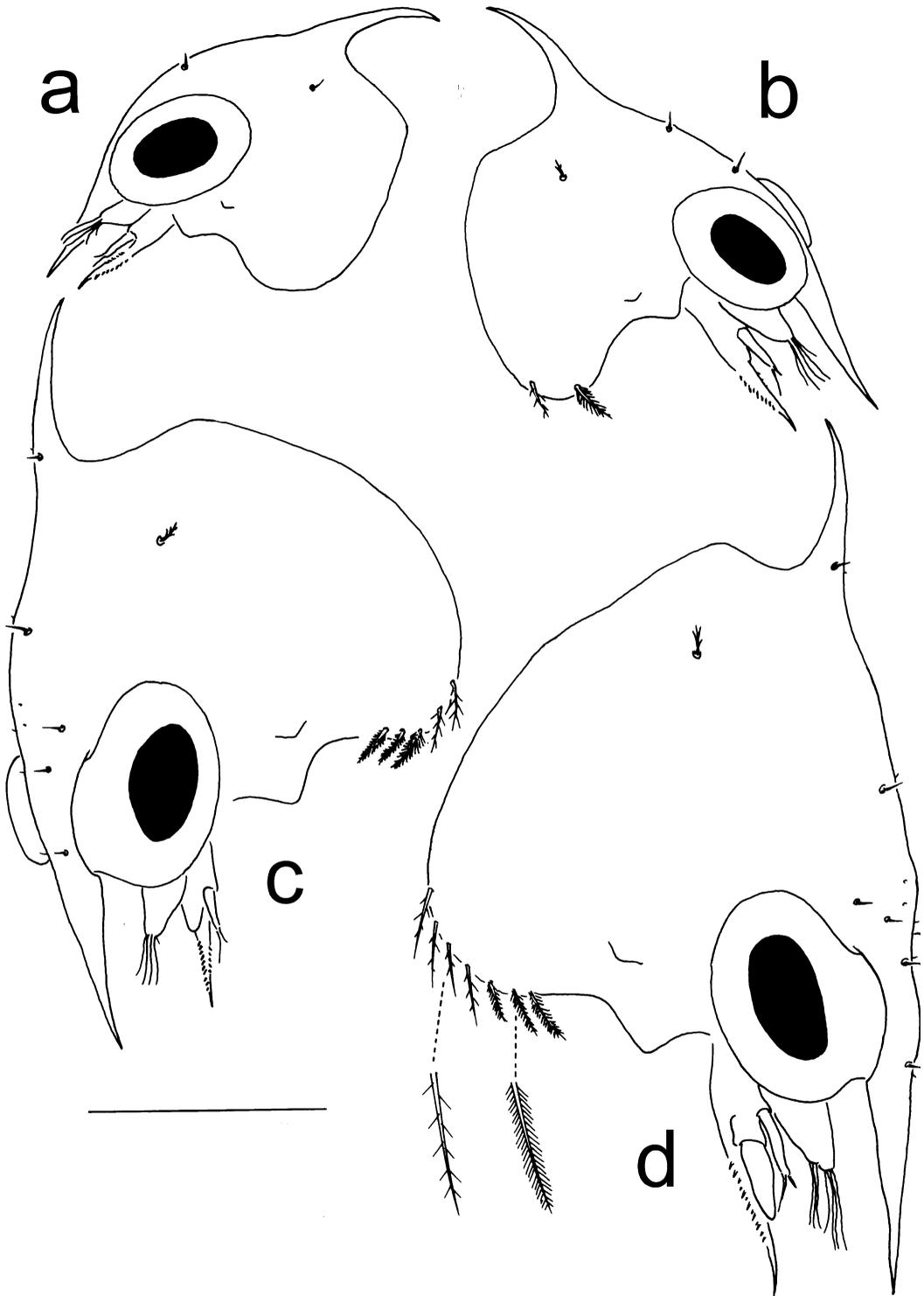


Figure 1. *Armases roberti*, carapace, lateral view. (a) Zoea I; (b) zoea II; (c) zoea III; (d) zoea IV. Scale bar: 0.4 mm.

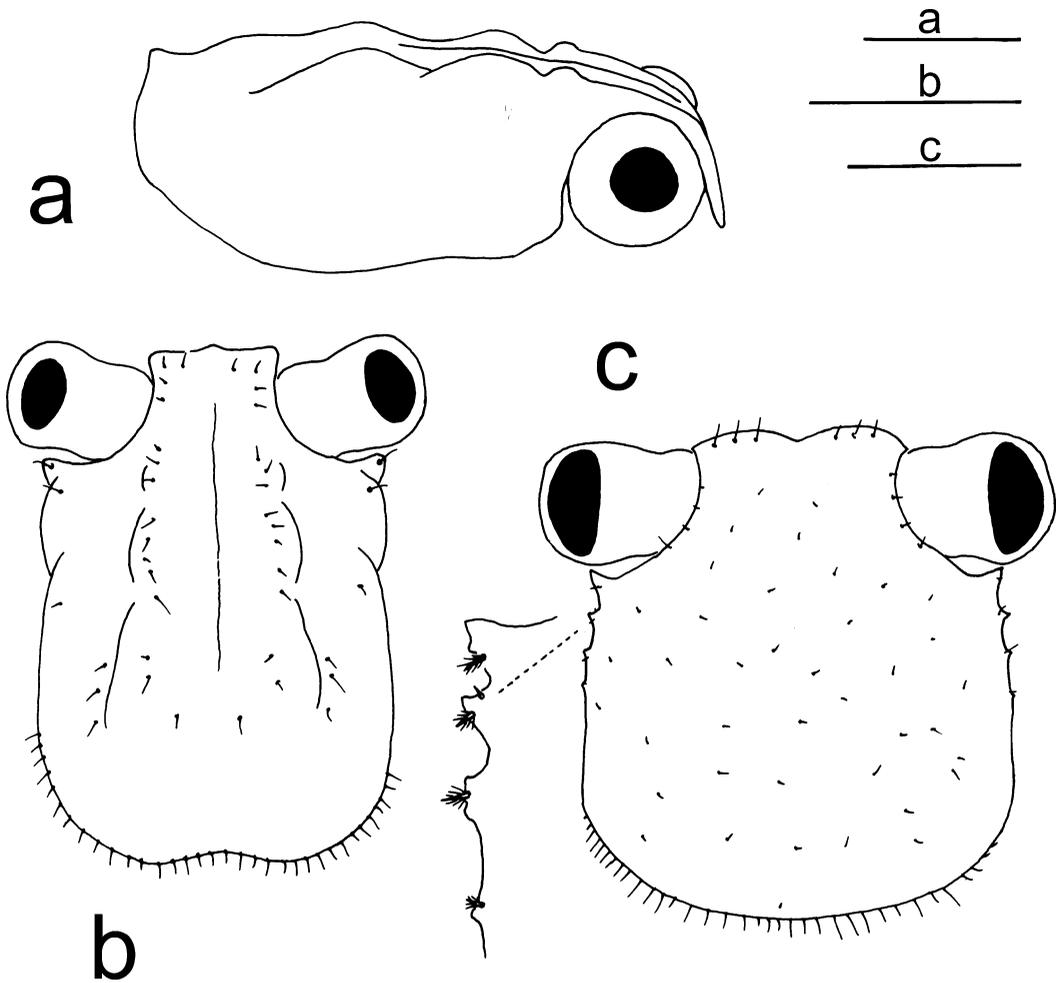


Figure 2. *Armases roberti*, carapace. (a) Megalopa, lateral view; (b) megalopa, dorsal view; (c) first crab, dorsal view, with detail of the anterolateral margin. Scale bars: 0.5 mm.

Pereiopods. Absent.

Abdomen (Figures 14a, 15a). Five somites. Somites 2 and 3 with a pair of dorsolateral processes. Somites 3–5 with posterolateral processes. Somites 2–5 with a pair of posterodorsal simple setae.

Pleopods. Absent.

Telson (Figures 14a, e, 15a, e). Bifurcate, furca large, slightly divergent with three pairs of serrulate setae on posterior margin. A minute scale-like spine on outer margin and two arrow-shaped small spines on dorsal margins of furcal arms. fl/bt=1.5–1.7.

Zoea II

Size. rdl=1.12 ± 0.04 mm; cl=0.72 ± 0.02 mm.

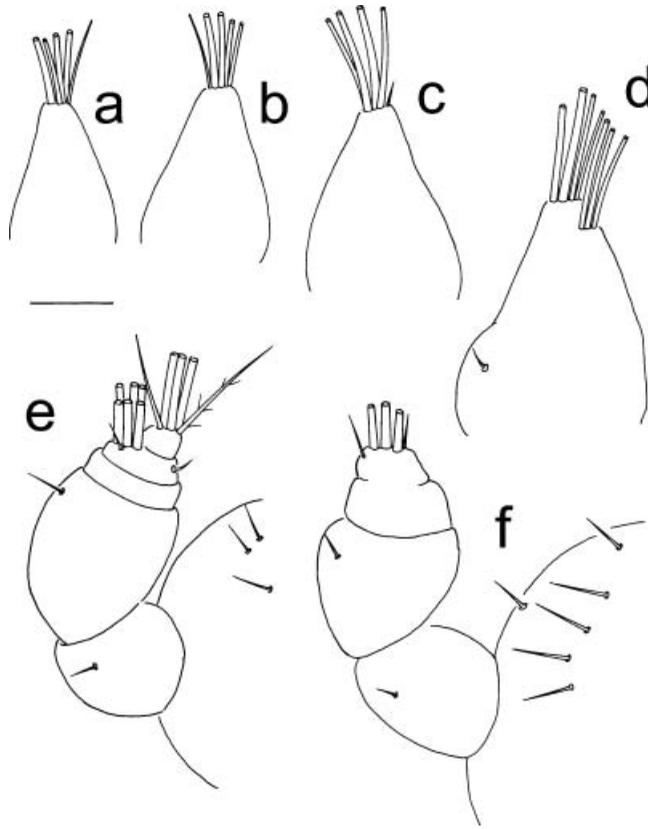


Figure 3. *Armases roberti*, antennule. (a) Zoea I; (b) zoea II; (c) zoea III; (d) zoea IV; (e) megalopa; (f) first crab. Scale bar: 0.05 mm.

Carapace (Figure 1b). Two pairs of anterodorsal setae. Each lateroventral margin with two setae (one sparsely plumose+one pappose). Eyes stalked. Otherwise unchanged.

Antennule (Figure 3b). Unchanged.

Antenna (Figure 4b). Endopod bud present. pl/el=2.2–2.4. Otherwise unchanged.

Mandible. Unchanged.

Maxillule (Figure 5b). Basial endite with seven plumose setae. Exopod plumose seta present. Otherwise unchanged.

Maxilla (Figure 7b). Scaphognathite with eight (3+5) plumose marginal setae. Otherwise unchanged.

First maxilliped. Exopod distal segment with six long plumose natatory setae. Otherwise unchanged.

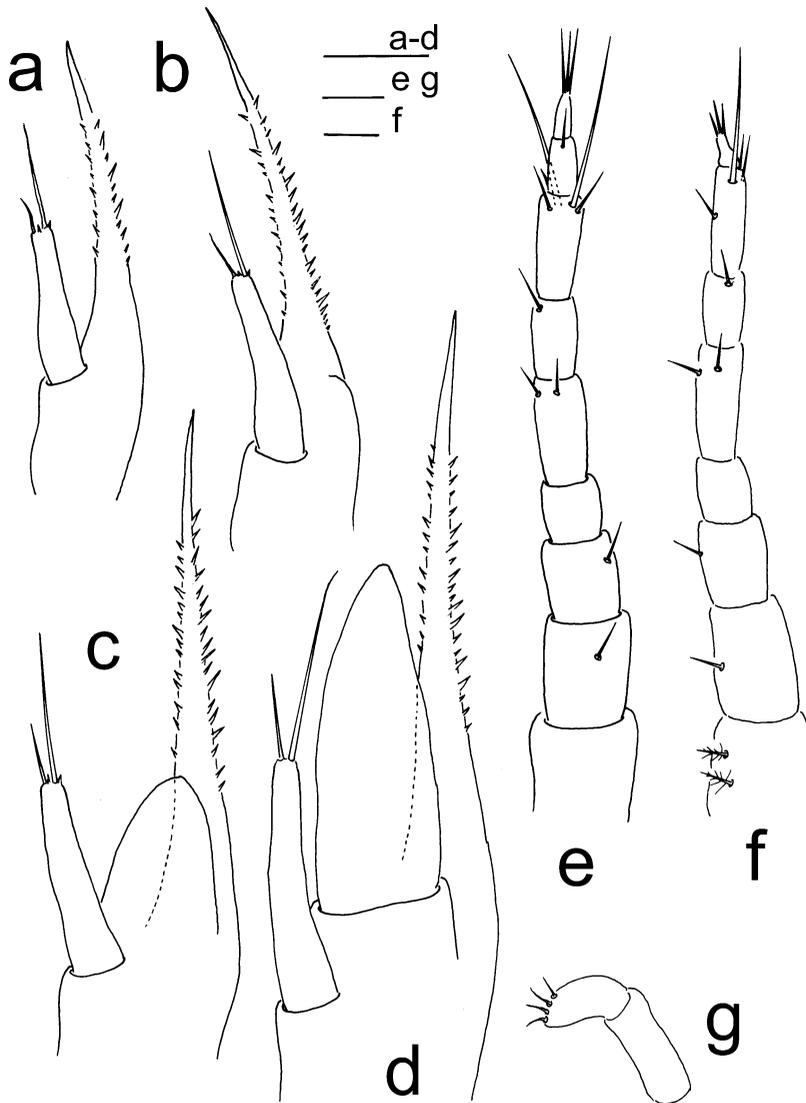


Figure 4. *Armases roberti*. (a–f) Antenna: (a) zoea I; (b) zoea II; (c) zoea III; (d) zoea IV; (e) megalopa; (f) first crab. (g) Mandibular palp, megalopa. Scale bars: 0.05 mm.

Second maxilliped. Exopod distal segment with six long plumose natatory setae. Otherwise unchanged.

Third maxilliped. Present as undifferentiated buds.

Pereiopods. Present as undifferentiated buds.

Abdomen (Figures 14b, 15b). First somite with one mid-dorsal seta. Otherwise unchanged.

Telson (Figure 14b, 15b). fl/bt=1.6–1.7. Otherwise unchanged.

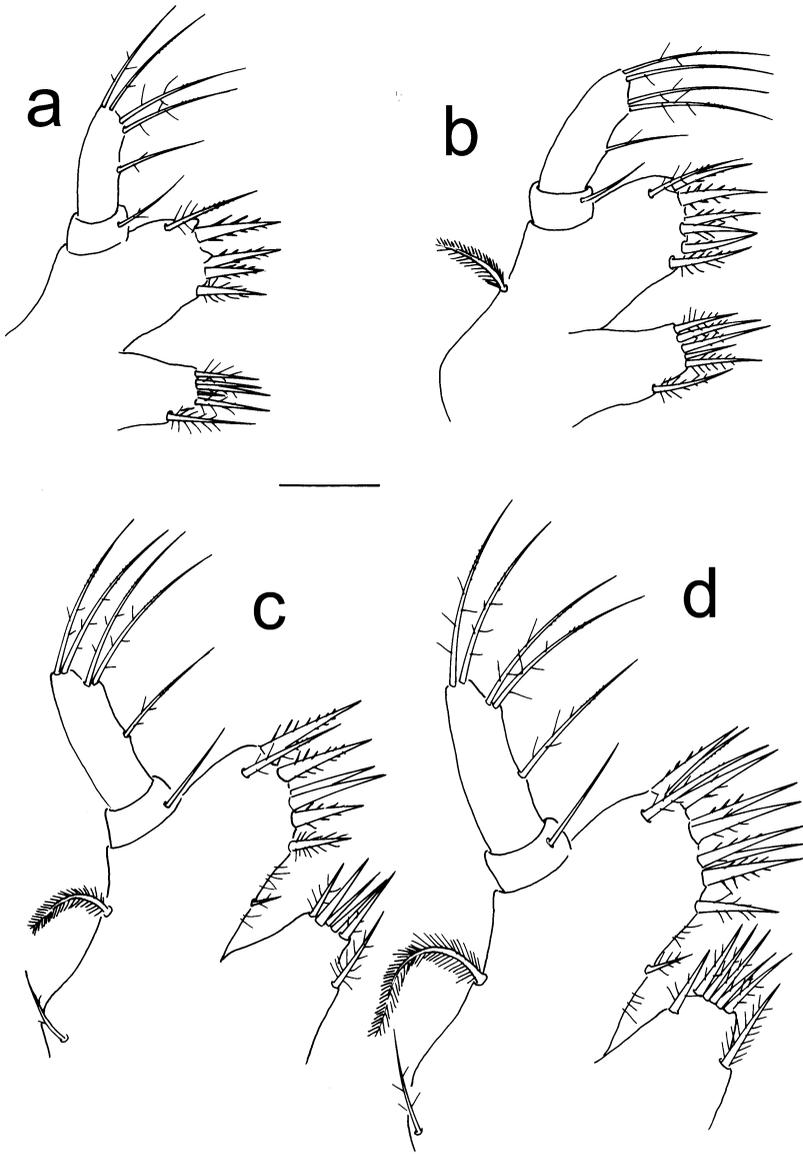


Figure 5. *Armases roberti*, maxillule. (a) Zoea I; (b) zoea II; (c) zoea III; (d) zoea IV. Scale bar: 0.05 mm.

Zoea III

Size. rdl=1.45 ± 0.04 mm; cl=0.85 ± 0.03 mm.

Carapace (Figure 1c). Four pairs of anterodorsal setae. One pair of setae near to the base of the dorsal spine. Each ventral margin with five setae (two sparsely setose+three pappose). Otherwise unchanged.

Antennule (Figure 3c). Exopod with four terminal aesthetascs and one minute terminal seta. Otherwise unchanged.

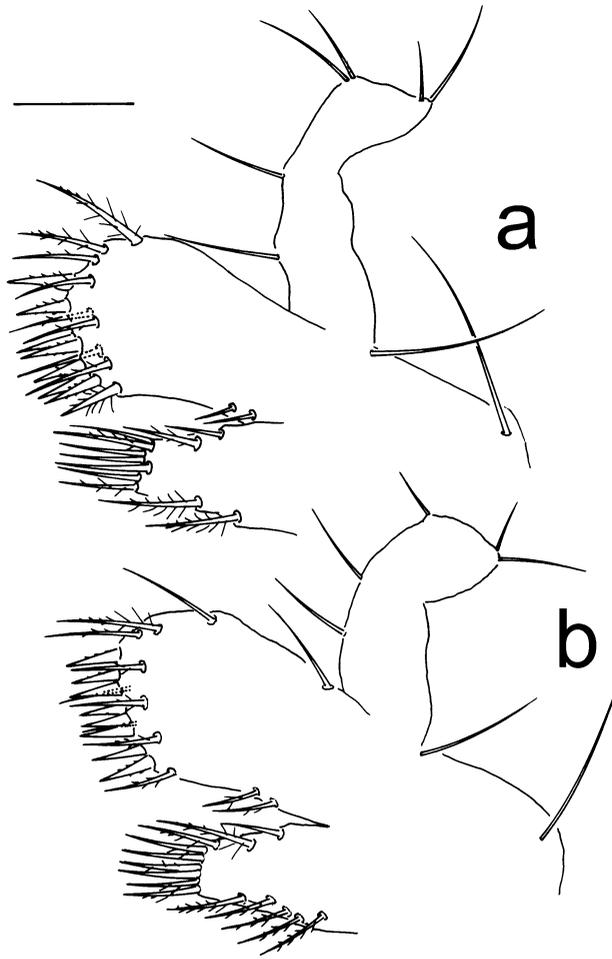


Figure 6. *Armases roberti*, maxillule. (a) Megalopa; (b) first crab. Scale bar: 0.05 mm.

Antenna (Figure 4c). Endopod bud elongated, as long as exopod or slightly longer (without setae). $pl/el=2.6-2.9$. Otherwise unchanged.

Mandible. Unchanged.

Maxillule (Figure 5c). Epipod seta present. Basial endite with eight setae. Otherwise unchanged.

Maxilla (Figure 7c). Basial endite with 5+5 setae. Scaphognathite with 12–13 plumose marginal setae. Otherwise unchanged.

First maxilliped (Figure 9b). Endopod segments 2 and 3 with one additional seta. Exopod distal segment with eight long plumose natatory setae. Otherwise unchanged.

Second maxilliped. Exopod distal segment with eight long plumose natatory setae. Otherwise unchanged.

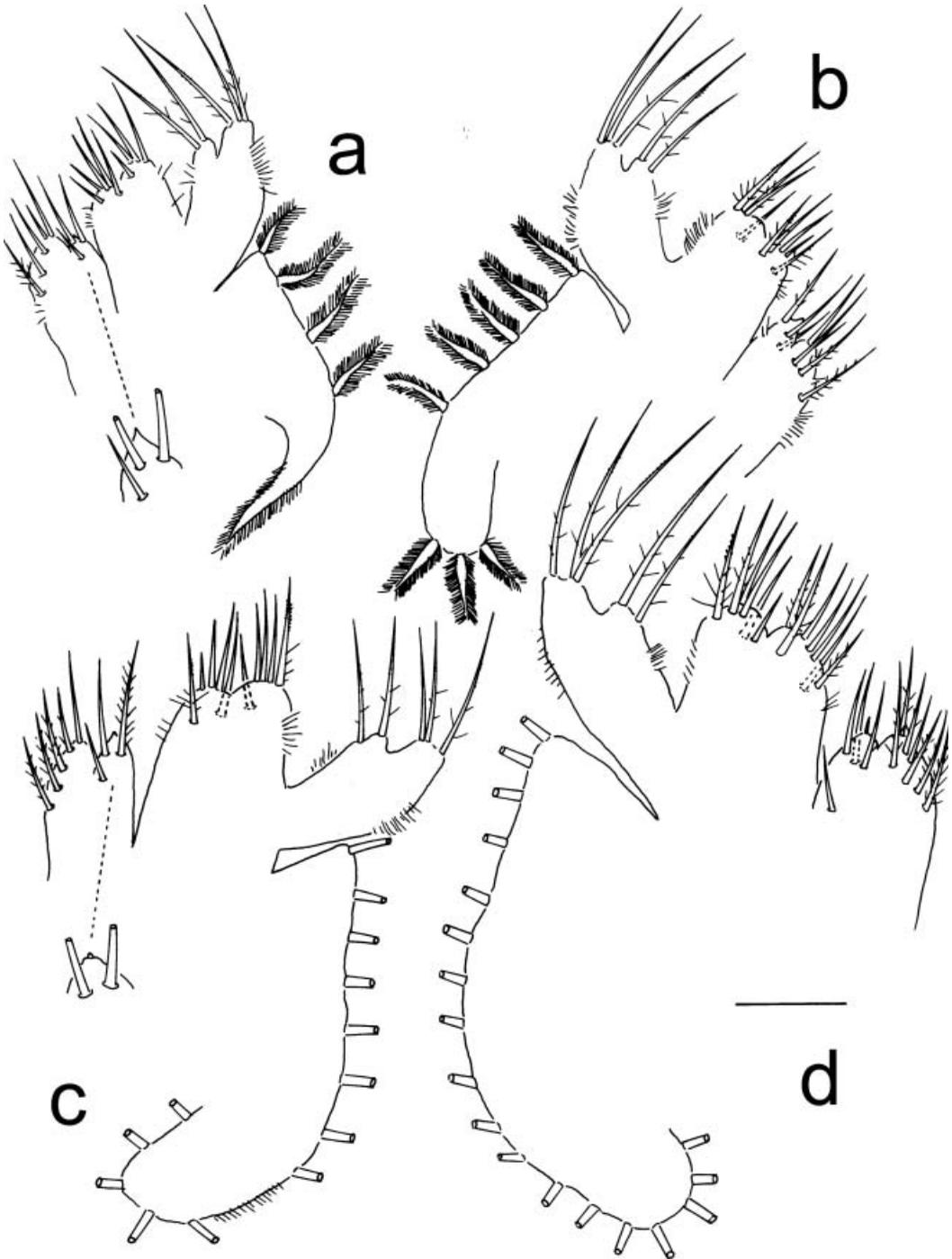


Figure 7. *Armases roberti*, maxilla. (a) Zoea I, with a detail of the distal lobe of the coxal endite; (b) zoea II; (c) zoea III, with a detail of the distal lobe of the coxal endite; (d) zoea IV. Scale bar: 0.05 mm.

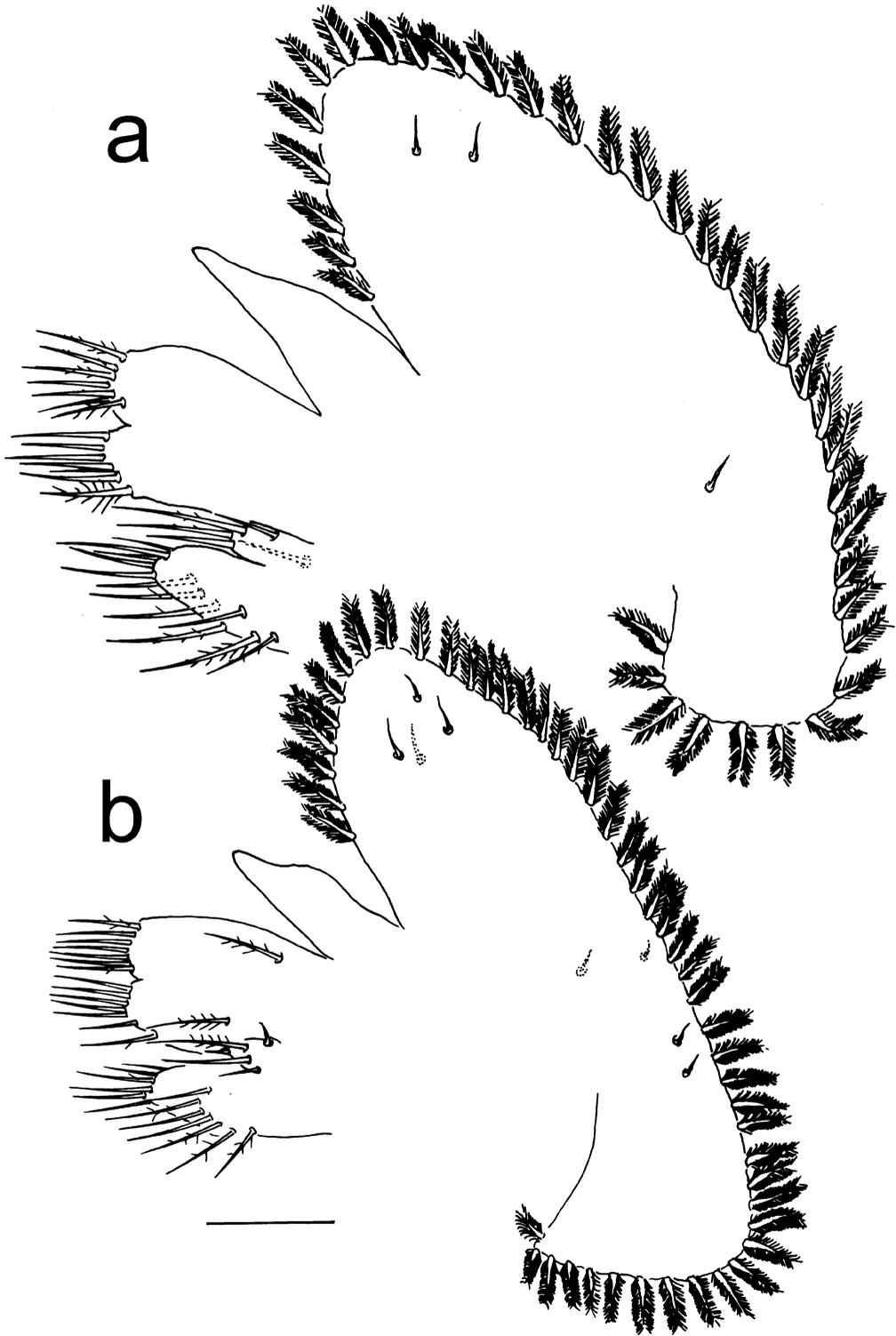


Figure 8. *Armases roberti*, maxilla. (a) Megalopa; (b) first crab. Scale bar: 0.05 mm.

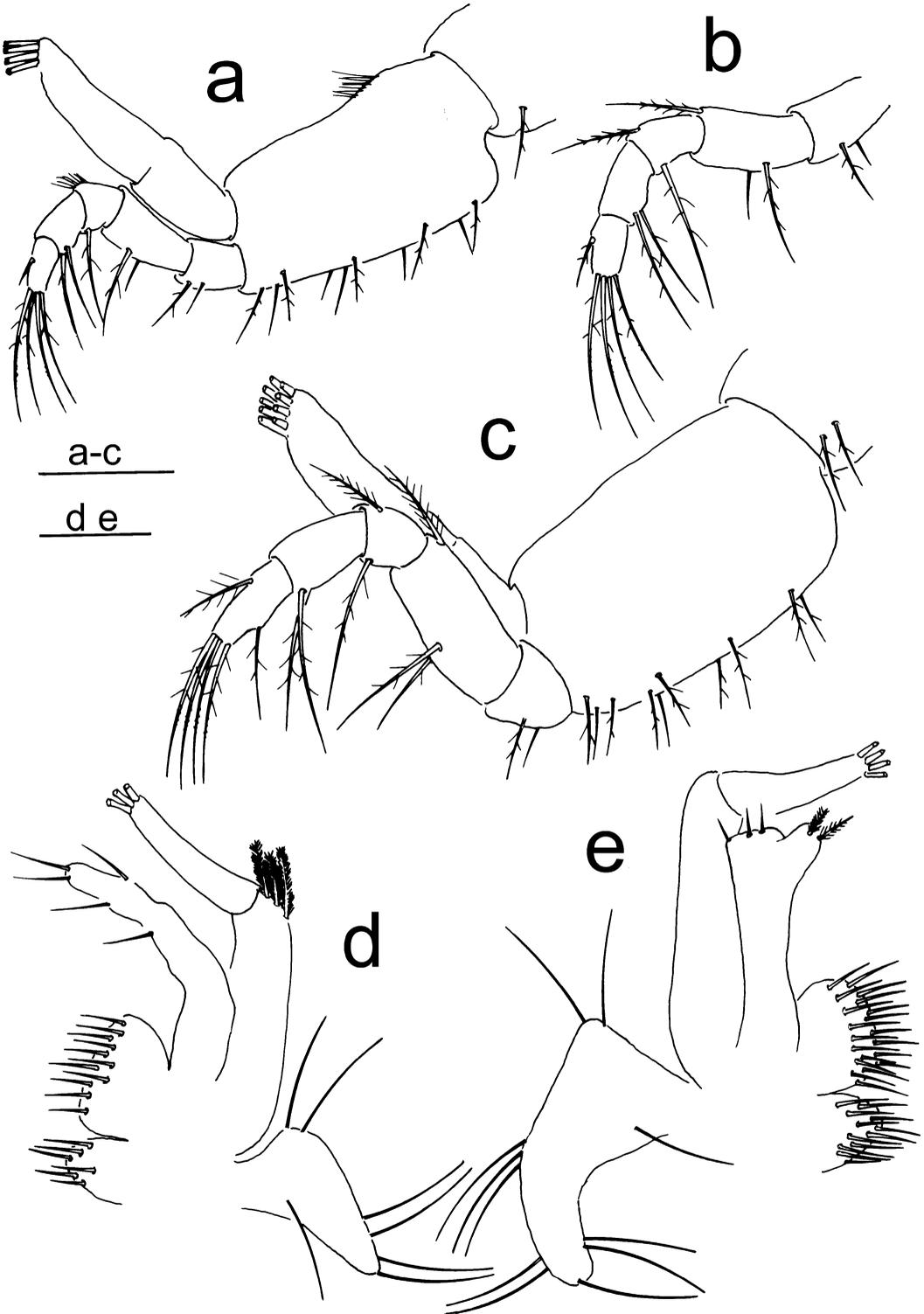


Figure 9. *Armases roberti*, first maxilliped. (a) Zoea I; (b) zoea III, endopod; (c) zoea IV; (d) megalopa; (e) first crab. Scale bars: 0.1 mm.

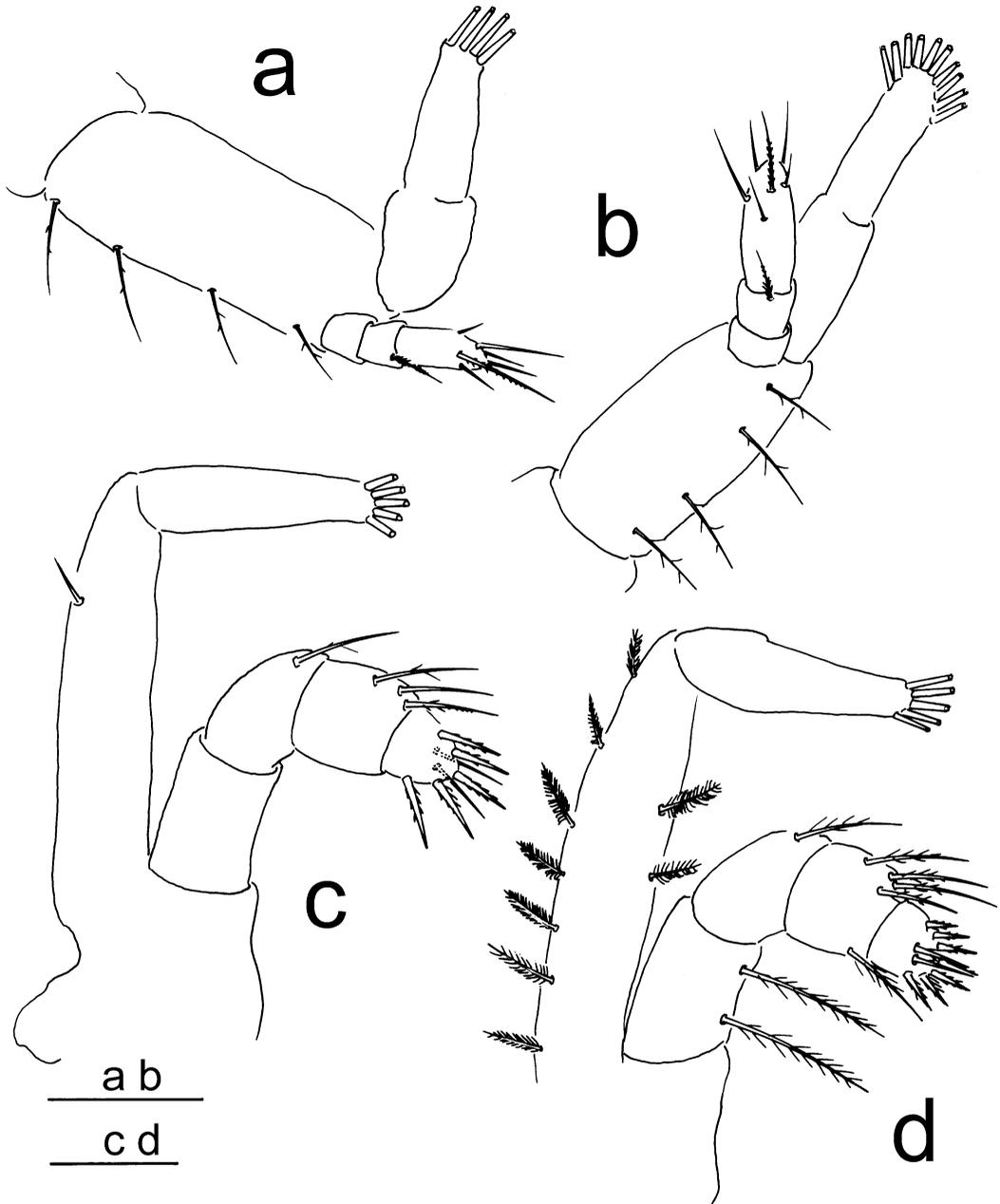


Figure 10. *Armases roberti*, second maxilliped. (a) Zoea I; (b) zoea IV; (c) megalopa; (d) first crab. Scale bars: 0.1 mm.

Third maxilliped. Biramous, unsegmented.

Pereiopods (Figure 12a). Pereiopods unsegmented. Chelipeds bilobed.

Abdomen (Figures 14c, 15c). Somite six present, without setae. Pleopod buds present on somites 2–5, endopods absent. Otherwise unchanged.

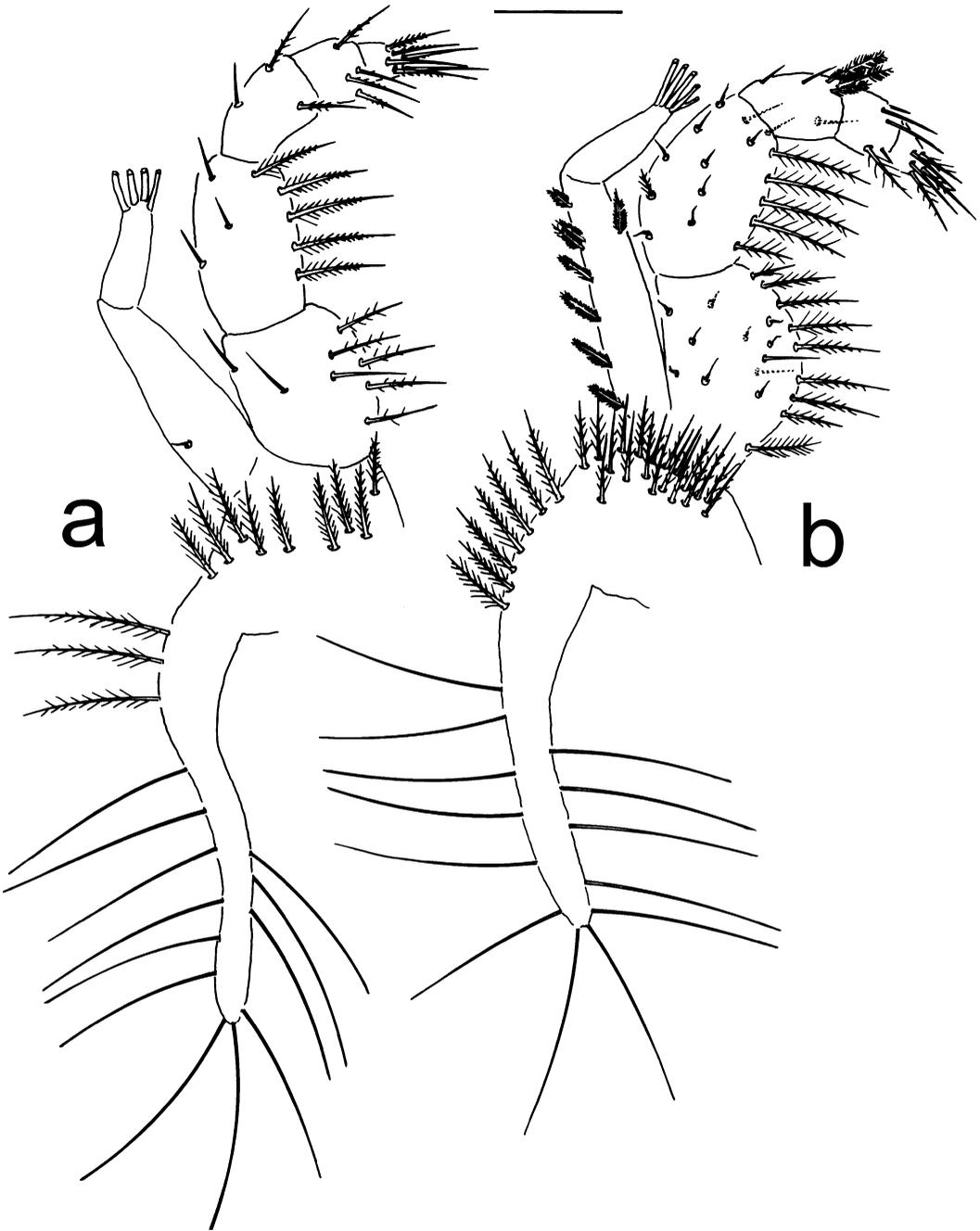


Figure 11. *Armases roberti*, third maxilliped. (a) Megalopa; (b) first crab. Scale bar: 0.1 mm.

Telson (Figures 14c, 15c). fl/bt=2.4–2.6. Otherwise unchanged.

Zoea IV

Size. rdl=1.50 ± 0.07 mm; cl=0.97 ± 0.05 mm.

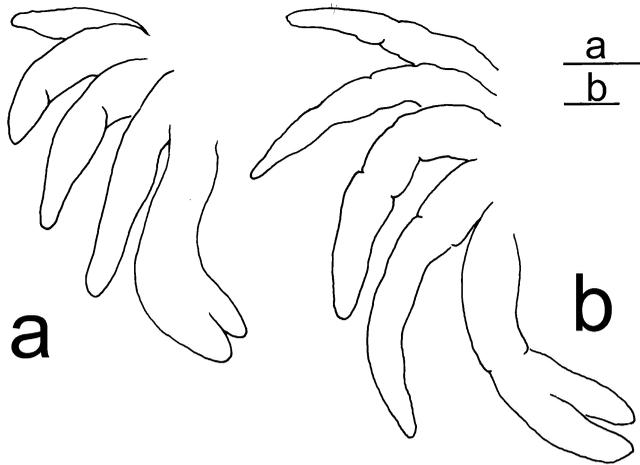


Figure 12. *Armases roberti*, pereopods 1–5. (a) Zoea III; (b) zoea IV. Scale bars: 0.1 mm.

Carapace (Figure 1d). Five pairs of anterodorsal setae. Each ventral margin with seven to eight (four to five sparsely plumose+three pappose) setae. Otherwise unchanged.

Antennule (Figure 3d). Exopod with one basal seta, and three subterminal and four terminal aesthetascs.

Antenna (Figure 4d). Endopod two-segmented, longer, reaching middle of the length of spinous process. Exopod without minute setae. pl/el=2.7–2.9.

Maxillule (Figure 5d). Coxal endite with seven setae. Basial endite with 11 setae. Otherwise unchanged.

Maxilla (Figure 7d). Coxal endite with 7+4–5 setae. Basial endite with 7+5–6 setae. Scaphognathite with 18–21 marginal plumose setae. Otherwise unchanged.

First maxilliped (Figure 9c). Coxa with two setae. Fifth segment of endopod with additional subterminal seta. Exopod distal segment with nine long plumose natatory setae. Otherwise unchanged.

Second maxilliped (Figure 10b). Exopod distal segment with 10 long plumose natatory setae. Otherwise unchanged.

Third maxilliped. Epipod now present, rudimentary.

Pereopods (Figure 12b). Chelipeds and pereopods 2–5 slightly segmented.

Abdomen (Figures 14d, 15d). First somite with three long mid-dorsal setae. Pleopod buds elongated, endopod buds present. Otherwise unchanged.

Telson (Figures 14d, 15d). fl/bt=2.2–2.4. Otherwise unchanged.

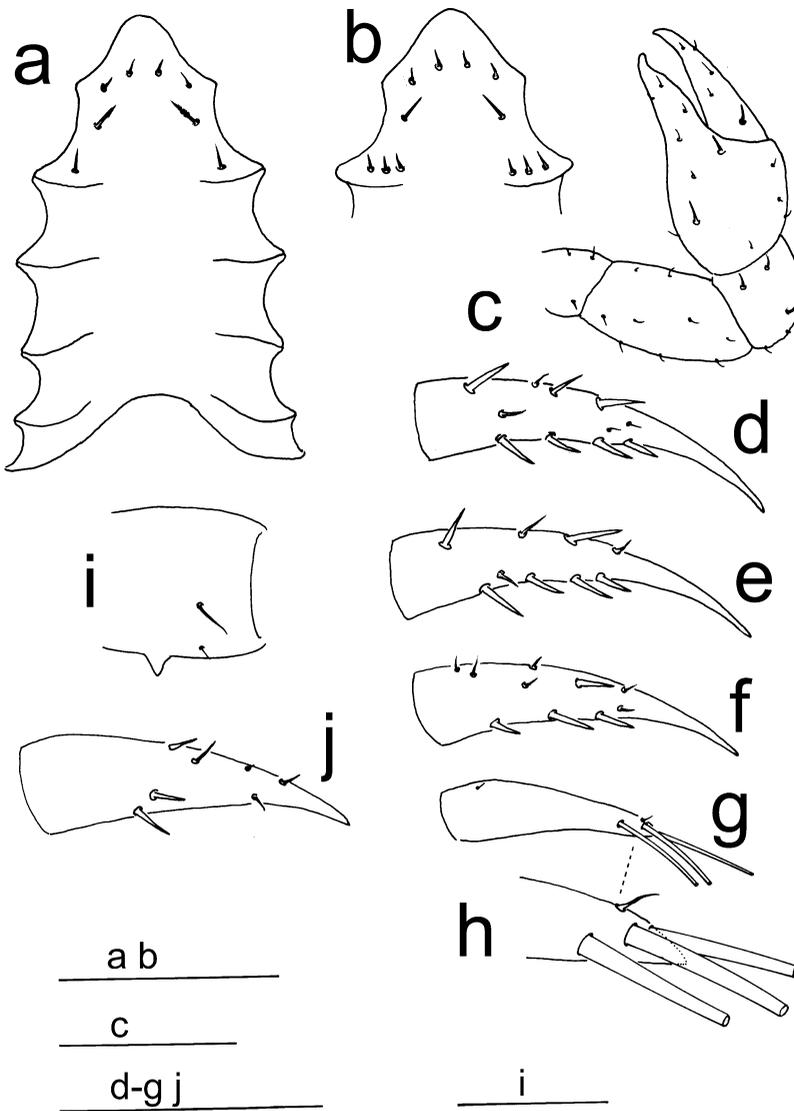


Figure 13. (a, c-i) *Armases roberti*, megalopa: (a) sternum; (c) pereiopod 1; (d-h) dactyl, pereiopods 2-5; (i) coxa, pereiopod 3; (j) *A. roberti*, first crab, dactyl, pereiopod 5. Scale bars: 0.3 mm (a-c); 0.075 mm (d-g, j); 0.02 mm (i).

Megalopa

Size. cl=1.18±0.08 mm; cw=0.85±0.07 mm.

Carapace (Figure 2a, b). Longer than broad. Rostrum ventrally deflected with median cleft, and with longitudinal medial carina and lateral prominent undulations.

Antennule (Figure 3d). Peduncle three-segmented, with 3, 1, 1 setae, respectively. Endopod absent. Exopod three-segmented, with 0, 6, 3 aesthetascs and 0, 2, 2 setae, respectively.

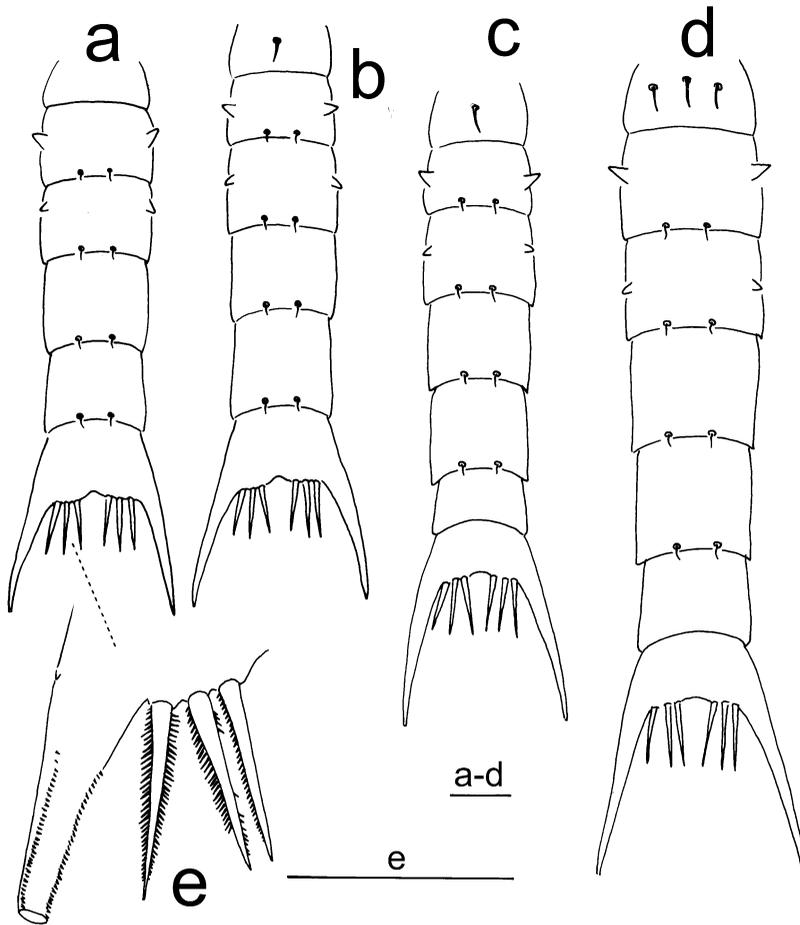


Figure 14. *Armases roberti*, abdomen, dorsal view. (a) Zoea I; (b) zoea II; (c) zoea III; (d) zoea IV; (e) detail of the furca and serrulate setae of zoea I. Scale bars: 0.1 mm.

Antenna (Figure 4d). Peduncle three-segmented, with 0, 1, 1 setae, respectively. Flagellum six-segmented, with 0, 2–3, 1, 5, 1, 3 setae, respectively.

Mandible (Figure 4g). Palp two-segmented, with four setae on distal segment.

Maxillule (Figure 6a). Coxal endite with 11–12 setae. Basal endite with 16(15+1)–18(16+2) setae. Endopod unsegmented, with two proximal and four distal setae.

Maxilla (Figure 8a). Coxal endite bilobed, with 12+5 setae. Basal endite bilobed with 7+7 setae. Endopod unsegmented, with one subterminal seta, or none. Scaphognathite with 36–39 plumose marginal setae and two anterior and one posterior lateral setae.

First maxilliped (Figure 9d). Epipod with seven long setae. Coxal endite with six setae. Basal endite with 11 setae. Endopod with five setae. Exopod two-segmented, proximal segment with three distal plumose setae, distal segment with three to four long terminal plumose setae.

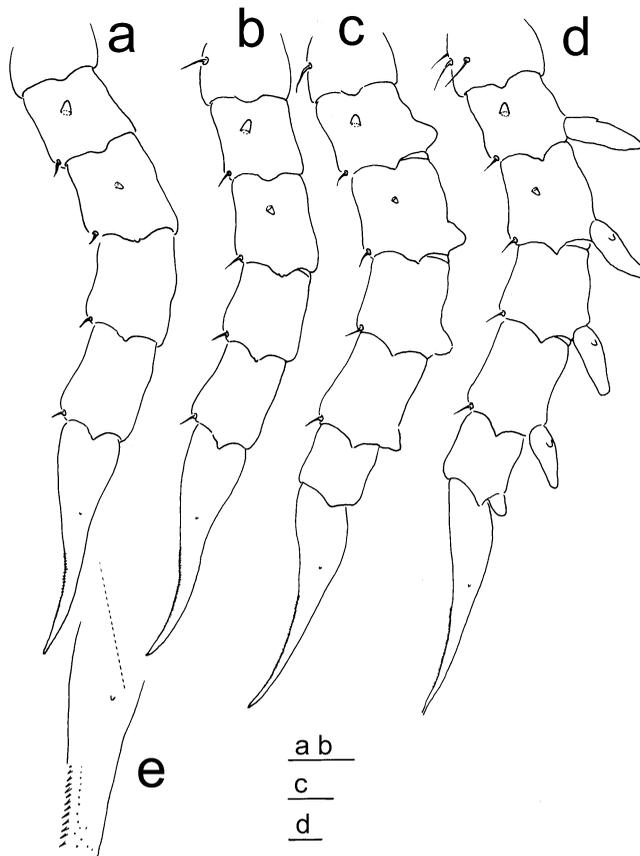


Figure 15. *Armases roberti*, abdomen, lateral view. (a) Zoea I; (b) zoea II; (c) zoea III; (d) zoea IV; (e) detail of the furca of zoea I. Scale bars: 0.1 mm.

Second maxilliped (Figure 10c). Epipod rudimentary. Coxa and basis not differentiated, without seta. Endopod four-segmented with 0, 1, 3, 6–7 setae, respectively. Exopod two-segmented, proximal segment with one seta, distal segment with five terminal plumose setae.

Third maxilliped (Figure 11a). Epipod elongated with 15 long setae. Coxa and basis not differentiated, with nine setae. Endopod five-segmented, with 8–9, 8, 3–4, 4, 7 setae, respectively. Exopod two-segmented, proximal segment with one seta and distal segment with four long terminal plumose natatory setae.

Pereiopods (Figure 13c–i). All articles well differentiated. Pereiopods 3 and 4 with one coxal process each. Dactylus of fifth pereiopod with three long terminal setae and one short terminal spine.

Sternum (Figure 13a). Maxillipeds and cheliped sternites fused with eight setae. All sternal sutures interrupted medially.

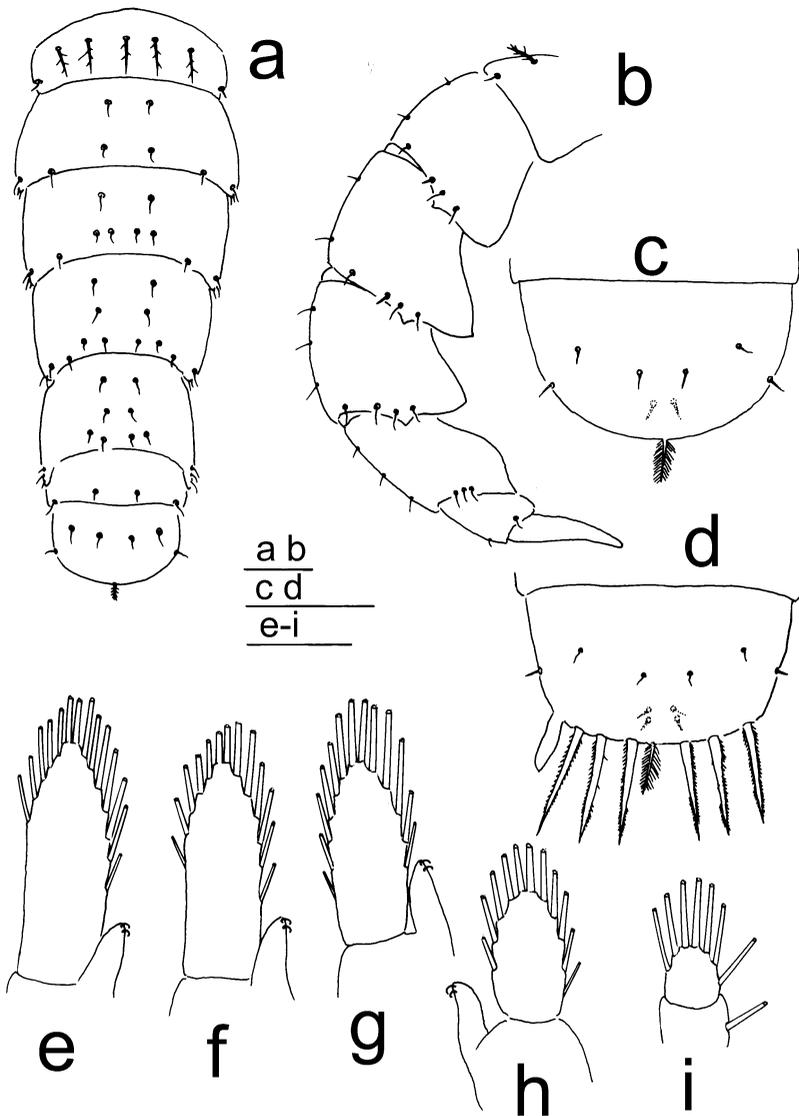


Figure 16. *Armases roberti*, megalopa. (a) Abdomen, dorsal view; (b) abdomen, lateral view; (c) telson; (d) telson with zoeal characters; (e–h) pleopods 1–4; (i) uropod. Scale bars: 0.1 mm.

Abdomen (Figure 16a, b). Six somites present. Somites 1–6 with 7, 12, 14, 16, 14, 4 setae, respectively. Somites 2–5 each with a pair of biramous pleopods.

Pleopods (Figure 16e–h). Endopod unsegmented, with two terminal hooks, exopod unsegmented with 14–15, 13–15, 13–14, 11–12 long marginal plumose natatory setae, respectively.

Uropods (Figure 16i). Two-segmented on somite 6, proximal segment with one, and distal segment with seven long plumose setae, respectively.

Telson (Figure 16a, c, d). Posterior margin rounded, with one or two plumose setae. Dorsal surface with six setae and with two ventral setae.

First juvenile

Size. cl = 1.35 ± 0.02 mm; cw = 1.17 ± 0.02 mm.

Carapace (Figure 2c). Longer than broad, quadrangular. Frontal region broad measuring one half of carapace width. Anterolateral margins with three teeth, first largest and third smallest.

Antennule (Figure 3f). Peduncle three-segmented, with 6, 1, 1 setae, respectively. Endopod absent. Exopod two-segmented, with 0, 3–4 aesthetascs, respectively, and 0, 2–3 setae.

Antenna (Figure 4f). Peduncle three-segmented, with 2, 1, 1 setae, respectively. Usually, flagellum five-segmented, with 0, 2, 1, 4, 3 setae, respectively.

Mandible. Palp two-segmented, with five setae on distal segment.

Maxillule (Figure 6b). Coxal endite with 14 setae. Basial endite with 19–20 setae. Endopod unsegmented, with two proximal and three distal setae.

Maxilla (Figure 8b). Coxal endite bilobed with 13+5 setae. Basial endite bilobed with 9+8 setae. Endopod unsegmented, without setae. Scaphognathite with 48 plumose marginal setae and eight lateral setae.

First maxilliped (Figure 9e). Epipod with 11 long setae. Coxal endite with 12 setae. Basial endite with 20–21 setae. Endopod with five setae. Exopod two-segmented, proximal segment with zero to two setae, distal segment with four long terminal plumose setae.

Second maxilliped (Figure 10d). Coxa and basis undifferentiated, without setae. Endopod four-segmented with 2, 1, 5, 9 setae, respectively. Exopod two-segmented, proximal segment with eight setae and distal segment with five terminal plumose setae.

Third maxilliped (Figure 11b). Epipod elongated with 20 long setae. Coxa and basis undifferentiated with 18–21 setae. Endopod five-segmented with 20, 16, 6–7, 5, 5 setae, respectively. Exopod two-segmented, proximal segment with eight setae and distal segment with five long terminal plumose setae.

Pereiopods (Figure 13c–j). Pereiopods 3 and 4 without coxal processes. Dactylus of fifth pereiopod without long terminal setae.

Abdomen. Six somites present with pleopods reduced, without setae.

Discussion

The zoal morphologies of *A. roberti*, *A. ricordi* and the first stage of *A. americanum* are very similar and agree well with a set of eight characters defined for sesarmid larvae by Cuesta

et al. (2006b). All described species show: (1) a carapace without lateral spines; (2) a zoea I stage with a pair of anterodorsal setae; (3) an antennal exopod with terminal small spines and setae of different sizes, the exopod being half the length of the protopod and the protopod with well-developed spines (usually unequal in number) distributed in two rows; (4) a bilobed maxillar endopod with 2+3 setae; (5) a first maxilliped basis with 2+2+3+3 setae and an endopod setation of 2, 2, 1, 2, 5 in the first zoea, while segments 2 and 5 (and often also segment 3) acquire one seta each through development, so that the last zoeal stages have an endopod setation of 2, 3, 2, 2, 6; (6) a second maxilliped basis with 1+1+1+1 setae and endopod setation of 0, 1, 6; (7) the pleon of the first zoeal stage comprising five somites, that of the last zoeal stage six somites, with dorsolateral processes only found on somites 2 and 3, and with three middorsal setae on somite 1 in the last stage; (8) telson with three serrulate setae on posterior margin throughout zoeal development and furcal arms with two dorsal rows of spinules of varying size.

The meristic and morphometric differences of the described zoeal stages of *Armases* species are shown in Table I. The setation of the coxa of the first maxilliped is described for the first time for all zoeal stages of the genus *Armases* (Table I): *A. roberti* and *A. ricordi* have one seta in zoeal stages I–III and two setae in zoea IV. For comparison, a previous description of the closely related genus *Aratus* reported for all four zoeal stages one seta on the coxa of the first maxilliped (Cuesta et al. 2006a).

Minute scale-like spines on the outer margin of the telson furca have recently been described for the zoeal stages of *Aratus pisonii*, *Armases angustipes*, *A. miersii*, *A. ricordi* (Z I–III), *A. cinereum* (Z I), *A. rubripes* (Z I), and many other species belonging to the Sesarmidae (Cuesta et al. 2006a, 2006b). This feature has been omitted in many larval descriptions of sesarmids due to the very small size of the spines. A spine is also present on the telson furca of all zoeal stages of *A. roberti*, *A. ricordi* and the first zoea of *A. americanum*.

The current description of the zoeal stages of *A. ricordi* differs in some features from previous descriptions (Díaz and Ewald 1968; Schubart and Cuesta 1998). We observed that the coxal endite of the maxillule bears six setae, instead of five. In this species, one of the six setae is very small and not easily visible, because it can be hidden behind larger proximal setae (see Figure 5a). The situation is similar in *A. roberti* and *A. americanum* and seems to be common within the family Sesarmidae (Guerao et al. 2004; Cuesta et al. 2006b). Therefore, it is possible that this seta has been omitted in many descriptions of sesarmid first zoeae. The setation of the carapace of *A. ricordi* was not previously described; it was found to be identical to the pattern of *A. roberti* (see Figure 1; Table I).

The recent larval description of *Armases benedicti* by Lima and Abrunhosa (2006) appears doubtful, due to a number of striking differences, not only to all other species of the genera *Armases* and *Aratus*, but also to the zoeal ground pattern of the Sesarmidae (see above). The differences are: a carapace with lateral carapace spines, an endopod of the maxilla with 2+2 setae, an endopod of the first maxilliped of the first zoea with 2, 2, 2, 1, 5 setae, and a basis of the second maxilliped with three setae. Many other characters have been omitted from the description, for example the setation of the carapace and abdomen. The information on abdominal setation, concluded from the figures, is incomplete and contradictory: abdominal somite 5 of zoea I without setae; somites 4 and 5 of zoea II with only one seta; somite 6 of zoea III and IV with one seta. Lima and Abrunhosa (2006) suggest that the lateral spines of *A. benedicti* zoeae are homologous to the small anterolateral protuberances described for *A. rubripes* and *A. ricordi* by Díaz and Ewald (1968). However, the position of the protuberances, also present in *A. roberti* and *A. americanum*, is more anterior and more ventral than the habitual position of the lateral spines in other

Grapsoidea (Cuesta 1999; Cuesta and Anger 2005). The homology between both characters is thus very doubtful. Due to the presumed inaccuracies in this description of the larval development of *A. benedicti*, we do not include it in Table I and suggest that it should be revised, preferably based on new and accurately identified material.

The morphology of the megalopa of *Armases roberti* and *A. ricordi* is similar to that known for other species of the family Sesarmidae. It corresponds very closely with the characters listed by Cuesta et al. (2006b): (1) a carapace longer than broad, rostrum ventrally deflected with a medial cleft; (2) antennule endopod absent; (3) antennal peduncle three-segmented and flagellum with six segments; (4) mandibular palp two-segmented with four setae on distal one; (5) maxillar scaphognathite with 36–39 marginal plumose setae and with two anterior and one posterior lateral setae; (6) first maxilliped epipod with seven setae; (7) second maxilliped epipod absent; (8) pleopod endopods with two cincinuli; and (9) uropods with setation 1, 7.

The spinulation on the coxal segment of the pereiopods and the setation of the sternum (Table I) has not previously been described for megalopae of the genus *Armases*. *Armases roberti* and *A. ricordi* bear spines on pereiopods 3 and 4 of the megalopa. The megalopae of both species can be easily distinguished by the setation of the sternum and by the fact that the number of setae on the cheliped sternite is larger in *A. ricordi* (see Figure 13a, b). Other differences between *A. ricordi* and *A. roberti*, such as the setation of the second maxilliped, are presented in Table I. The description of the megalopa of *A. benedicti* by Lima and Abrunhosa (2006) is also debatable. The descriptions of the setation of the antenna, maxillule, first maxilliped, third maxilliped, abdominal somites, and uropod are doubtful or incomplete. We have therefore omitted it from Table I, awaiting new material or confirmation of the identification of the mother.

A number of features of the megalopae described herein from some individuals appear to represent remnants of zoeal morphology: (1) first segment of the antennular peduncle with a rudimentary spinous process; (2) bilobed endopod of the maxilla with a similar setation as in the zoeal stages; (3) telson with a rudimentary furca and with three pairs of serrulate setae on the posterior margin. These features have been observed in only some of the individuals studied, and similar traits were also found in the megalopae of other sesarmid species: *Aratus pisonii* (H. Milne Edwards, 1837) (see Warner 1968), *Sesarma reticulatum* (see Costlow and Bookhout 1962), *Parasesarma plicatum* (Latreille, 1806) (see Selvakumar 1999), *Parasesarma erythroductyla* (Hess, 1865) (see Greenwood and Fielder 1988), *Armases angustipes* (see Cuesta and Anger 2001), and *Perisesarma fasciatum* (Lanchester, 1900) (see Guerao et al. 2004). Since these morphological deviations might represent artefacts as a consequence of artificial laboratory-rearing conditions, it remains to be tested whether these zoea-like structures can also be encountered in megalopae collected from the field.

Knowledge of the first crab stage of *Armases*, and other sesarmid crabs is limited. The first juvenile was previously described only for *Armases rubripes* and *A. ricordi* (see Díaz and Ewald 1968). The overall juvenile morphology of *A. roberti*, *A. ricordi*, and *A. rubripes* is similar, and some morphometric and meristic characters are summarized in Table II. The first crab of *A. ricordi* is smaller than that of *A. roberti*, following the tendency of all larval stages (Tables I, II). These results agree with those obtained by Diesel and Schuh (1998): newly deposited eggs are larger in *A. roberti* than in *A. ricordi*; larvae of *A. roberti* hatch with larger body size, show a higher endotrophic potential and have a higher tolerance to fresh water than those of *A. ricordi*. Diesel and Schuh (1998) interpret these differences in accordance with the reproductive behaviour of the adults. Females of *A. ricordi* release their

Table II. Morphological differences among first-stage juveniles of the genus *Armases*.

Feature	<i>Armases roberti</i> (present paper)	<i>Armases ricordi</i> (present paper)	<i>Armases ricordi</i> (Díaz and Ewald 1968)	<i>Armases rubripes</i> (Díaz and Ewald 1968)
cl (mm)	1.35 ± 0.02	1.20 ± 0.03	nd	nd
cw (mm)	1.17 ± 0.02	1.07 ± 0.02	nd	nd
Antennula				
Peduncle (s)	6, 1, 1	12, 1, 1	nd	10, 1, 1
Exopod (a+s)	0, 3-4+0, 2-3	0, 3+0, 2	nd	0, 4+0, 1
Antenna				
Flagellum (s)	0, 2, 1, 4, 3	0, 0, 2, 1, 4, 3	nd	0, 2, 1, 5, 3
Maxillule				
Coxal endite (s)	14	12	nd	11
Basial endite (s)	19-20	20	nd	17
Maxilla				
Coxal endite (s)	13+5	10+4	nd	14
Basial endite (s)	9+8	8+7	nd	13
Scaphognathite (s)	48	41	nd	50
Maxilliped 1				
Coxal endite (s)	12	11	10-11	12
Basial endite (s)	20-21	15	18-20	13
Endopod (s)	5	4	5	5
Exopod (s)	0-2, 4	1, 3	4, 3	1, 4
Maxilliped 2				
Endopod (s)	2, 1, 5, 8-9	1, 1, 6, 10	2, 1, 5, 9	2, 1, 5, 9
Exopod (s)	8-9, 5	6, 5	8, 4	8, 4
Maxilliped 3				
Endopod (s)	20, 16, 6-7, 5, 5	17, 12, 5, 5, 7	18, 14, 4, 6, 5	18, 12, 5, 6, 6

a, aesthetascs; nd, no data; s, setae.

larvae directly into the sea, while those of *A. roberti* release their larvae into freshwater, from where they are transported to the sea by river currents (see also Anger et al. 2006).

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