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COMPLETE LARVAL DEVELOPMENT OF TWO SPECIES OF THE ASIAN CRAB GENUS *PSEUDOSESARMA* (BRACHYURA: THORACOTREMATA: SESARMIDAE)

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A B S T R A C T

The complete larval development of the sesarmid crabs *Pseudosesarma bocourti* (A. Milne-Edwards, 1869) and *P. moeschii* (de Man, 1892) was obtained through laboratory culture. The previously unknown larval stages of both species, consisting of four zoeal stages and a megalopa, are morphologically almost identical and thus described and illustrated as one.The morphology of the zoeae and megalopae is similar to that known from other species of Sesarmidae, but zoeal stages of three species of *Pseudosesarma* can be differentiated from other known larvae of sesarmids by the presence of the very long curved posterolateral processes on pleomere 5. While zoeal stages of *P. bocourti* and *P. moeschi* are morphologically very similar, the megalopae of both species can be easily distinguished by the setation on the uropod (1,5 in *P. moeschii versus* 1,6 in *P. bocourti*).

Introduction

In spite of a great number of larval descriptions of the family Sesarmidae Dana, 1851 (see Cuesta et al., 2006b), only the ones from the last decade fit modern standards for systematic comparisons and phylogenetic conclusions based on larval morphology (Schubart and Cuesta, 1998; Cuesta, 1999; Cuesta and Anger, 2001; Islam et al., 2002; Guerao et al., 2004; Cuesta et al., 2006a). In addition, there are still a number of genera whose complete larval development is unknown (Cuesta et al., 2006b). This was the case of the genus *Pseudosesarma* Serène and Soh, 1970, for which until now only a description of the first zoea of *P. crassimanum* (de Man, 1888) was available (Cuesta et al., 2006b).

Both species for which the larval development is described here are common in the aquarium trade and originate from Southeast Asia. They are semiterrestrial, living in or near lowland streams or swamps, in close vicinity to the ocean (Tweedie, 1940; Ng, 1995). *Pseudosesarma bocourti* (A. Milne-Edwards, 1869) is widely distributed throughout Southeast Asia and has so far been recorded from Thailand (type locality Bangkok), Borneo (de Man, 1880, 1895; Zehntner, 1894; Ng, 1995), Sumatra (Nobili, 1899; Tesch, 1917; Roux, 1933), Peninsular Malaysia (Tweedie, 1940; Ng, 1995; Yeo et al., 1999) and Pulo Condore (today Con Son) in Vietnam (de Man, 1895). The description of *Sesarma cheiragona* Targioni-Tozzetti, 1877 from Yokohama (Japan), a species that was later synonymized with *P. bocourti* by de Man (1887), is attributed to erroneous locality assignment according to Tweedie (1940). Ecologically, *P. bocourti* has been associated with mangroves (Tan & Ng, 1994), peat swamps (Ng, 1995), freshwater swamps (Tweedie, 1940), "tidal freshwaters beyond the limits of the mangrove" (Yeo et al., 1999: 203), and with terrestrial habitats, being encountered "several hundred metres from the nearest water source" (Ng, 1995: 202). The last author adds that representatives of this species "dig burrows in the peat substrate, often among roots and debris, and emerge only late at night to feed on dead leaves and other vegetable matter" (Ng, 1995: 202).

The distribution of the "Thai red crab," *Pseudosesarma moeschii* (de Man, 1892), currently includes Sumatra (type locality Deli), the Mergui Archipelago in the Andaman Sea (de Man, 1888; Alcock, 1900), Sulawesi (Tesch, 1917), Peninsular Malaysia (Tweedie, 1940), and the Gulf of Thailand (Naiyanetr, personal communication in McLaughlin et al., 1996). De Man (1888) reports this species (as *Sesarma intermedia* de Haan, 1833 = *Sesarmops intermedium*) from mangrove swamps of Zediwon, de Man (1892) recorded the type material from a river of the lower Batak country in Sumatra. Tweedie (1940) found his specimen occurring among nipah palms (*Nypa fruticans*) beside the river Sedili in Johor. Also, Naiyanetr (in McLaughlin et al., 1996) reports them from burrows in nipah forests adjoining mangrove areas in the lower reaches of estuaries, with water salinities averaging 20-28 PSU. McLauglin et al. (1996) document strong osmotic abilities (hypo- and hyperregulation) of *P. moeschii* over a wide range of external salinities. This type of osmotic behaviour is typical for semiterrestrial crabs of the family Sesarmidae (see Schubart & Diesel, 1998).

The present study describes the morphology of all larval stages of *Pseudosesarma bocourti* and *P. moeschii* and compares their larval features with those known from other species of the family Sesarmidae. Thereby, we provide the first description of complete larval developments for the genus *Pseudosesarma*. To our knowledge there are no published records of larvae of these two species from the plankton, with which our material could be compared.

Materials and Methods

Pseudosesarma bocourti and *P. moeschii* were purchased from an aquarium supply store in Barcelona, Spain, and kept in an aquarium with brackish

Table 1. Meristic and morphological differences between *Pseudosesarma bocourti* and *P. moeschii*. Abbreviations: s, setae; a, aesthetascs.

Feature	*Pseudosesarma bocourti*	*Pseudosesarma moeschii*
Zoea I		
rdl (mm)	0.70 ± 0.02	0.68 ± 0.01
cl (mm)	0.41 ± 0.01	0.37 ± 0.01
Zoea II		
rdl (mm)	0.97 ± 0.01	0.93 ± 0.02
cl (mm)	0.55 ± 0.01	0.50 ± 0.01
Antennule (a+s)	4 + 1	4
Zoea III		
rdl (mm)	1.20 ± 0.02	1.17 ± 0.02
cl (mm)	0.70 ± 0.01	0.66 ± 0.01
Zoea IV		
rdl (mm)	1.40 ± 0.02	1.30 ± 0.02
cl (mm)	0.80 ± 0.01	0.77 ± 0.01
Antennule (a)	2-3, 5	2,4-5
Megalopa		
cl (mm)	0.94 ± 0.03	0.87 ± 0.02
cw (mm)	0.64 ± 0.02	0.60 ± 0.02
Antennule		
Exopod (a)	0,6,3	0,5,3
Maxillule		
Coxal end. (s)	9	10
Maxilla		
Coxal end. (s)	8 + 4	7 + 4
Scaphog. (s)	29-32	26-27
Maxilliped 1		
Epipod (s)	4-5	4
Maxilliped 3		
Epipod (s)	12-13	9-11
Endopod (s)	8,9,4,3,5	8,7-9,4,3,5-6
Exopod (s)	1,4	0,4
Pleon		
Pleopods (s)	13,13,13,11	13,13,12,10
Uropods (s)	1,6	1,5

water (3-5 PSU salinity). Taxonomic identities were later confirmed by morphological and genetic analyses (Schubart, unpublished data). After females extruded eggs, they were maintained in brackish water (15 PSU salinity). Larvae of both species hatched in June 2006. They were mass-reared in gently aerated 2-l beakers with about 100 larvae per beaker, kept at constant 26-27°C, 30 salinity PSU, and an artificial 12:12 h light:dark cycle. Water and food (freshly hatched *Artemia* sp. nauplii) were changed daily, and the larvae were checked for moulting and mortality. Exuviae and specimens of each developmental stage were preserved in 70% ethanol.

A Wild binocular microscope equipped with an ocular micrometer was used for the dissection and morphometrics of individuals (5-10 individuals of each hatch and larval stage were measured). An Olympus BH-2 microscope was used for the determination of setal formulae 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, 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.

The number of examined individuals of each larval stage to describe the morphology varied between 5 and 10. The long aesthetascs of the antennules and the long plumose setae on the distal exopod of the maxillipeds and pleopods are drawn truncated instead. Larval descriptions followed the basic malacostracan body pattern from anterior to posterior and setal armature on appendages is described from proximal to distal segments and from endopod to exopod (see Clark et al., 1998).

Samples of all larval stages were deposited in the Biological Collections of Reference of the Institut de Ciències del Mar (CSIC) in Barcelona (Codes: ICMD 1-5/2007 and ICMD 6-10/2007 for the larval stages of *Pseudosesarma bocourti* and *P. moeschii*, respectively).

Results

The larval developments of *Pseudosesarma bocourti* and *P. moeschii* consist of four zoeal stages and one megalopa each. The first megalopae of *P. bocourti* and *P. moeschii* appeared 17 and 16 days after hatching, respectively. The comparison of zoeae I from three different hatches of *P. bocourti* and two hatches of *P. moeschii* revealed that these are very similar morphologically and morphometrically, with no appreciable differences in size and shape. The following description is based upon *P. bocourti* but applies equally to *P.moeschii*. The morphological and meristic differences with *P. bocourti* are presented in Table 1. The first zoeal stage is described in detail, while in subsequent stages only differences and changes are described.

Pseudosesarma bocourti (A. Milne-Edwards, 1869) (Figs. 1-15)

Zoea I

Size.—rdl: 0.70 ± 0.02 mm; cl: 0.41 ± 0.01 mm.

Morphology.—Carapace (Fig. 1a). Globose, smooth, without tubercles. Dorsal spine well developed, strongly curved posteriorly. Rostral spine, straight, similar in length to protopod of antenna. Lateral spines absent. Pair of setae on posterodorsal and anterodorsal regions. Posterior and ventral margin without setae. Eyes sessile.

Antennule (Fig. 3a) uniramous, endopod absent, exopod unsegmented with 3 terminal aesthetascs and 1 terminal seta.

Antenna protopod (Fig. 4a) almost reaching tip of rostral spine and bearing two unequal rows of 6-7 and 4-5 long spines, respectively, increasing in size distally, and a terminal unpaired well-developed spine; exopod elongated, more than 1/2 of the protopod length, with 2 terminal setae (1 long, 1 shorter) and 2 small terminal spines; pl/el = 2.4-2.5.

Mandible palp absent; molar and incisor processes well developed.

Maxillule (Fig. 5a) with exopod and epipodal setae absent. Coxal endite with 6 setae. Basial endite with 5 setae and with 2 teeth. Endopod 2-segmented, with 1 seta on proximal segment and 1 subterminal and 4 terminal setae on distal segment.

Maxilla (Fig. 6a) with coxal endite bilobed, with 5 + 3 setae, distal lobe terminates in a spine (see Fig. 6b, c and Fig. 7a). Basial endite bilobed with 5 + 4 setae. Endopod unsegmented, bilobed, with 2 + 3 long setae on inner and outer lobe, respectively and microtrichiae on lateral margin. Scaphognathite with 4 plumose marginal setae and long setose posterior process.

First Maxilliped (Fig. 8a) coxa with 1 seta. Basis with 10 medial setae arranged 2 + 2 + 3 + 3, and a mat of long

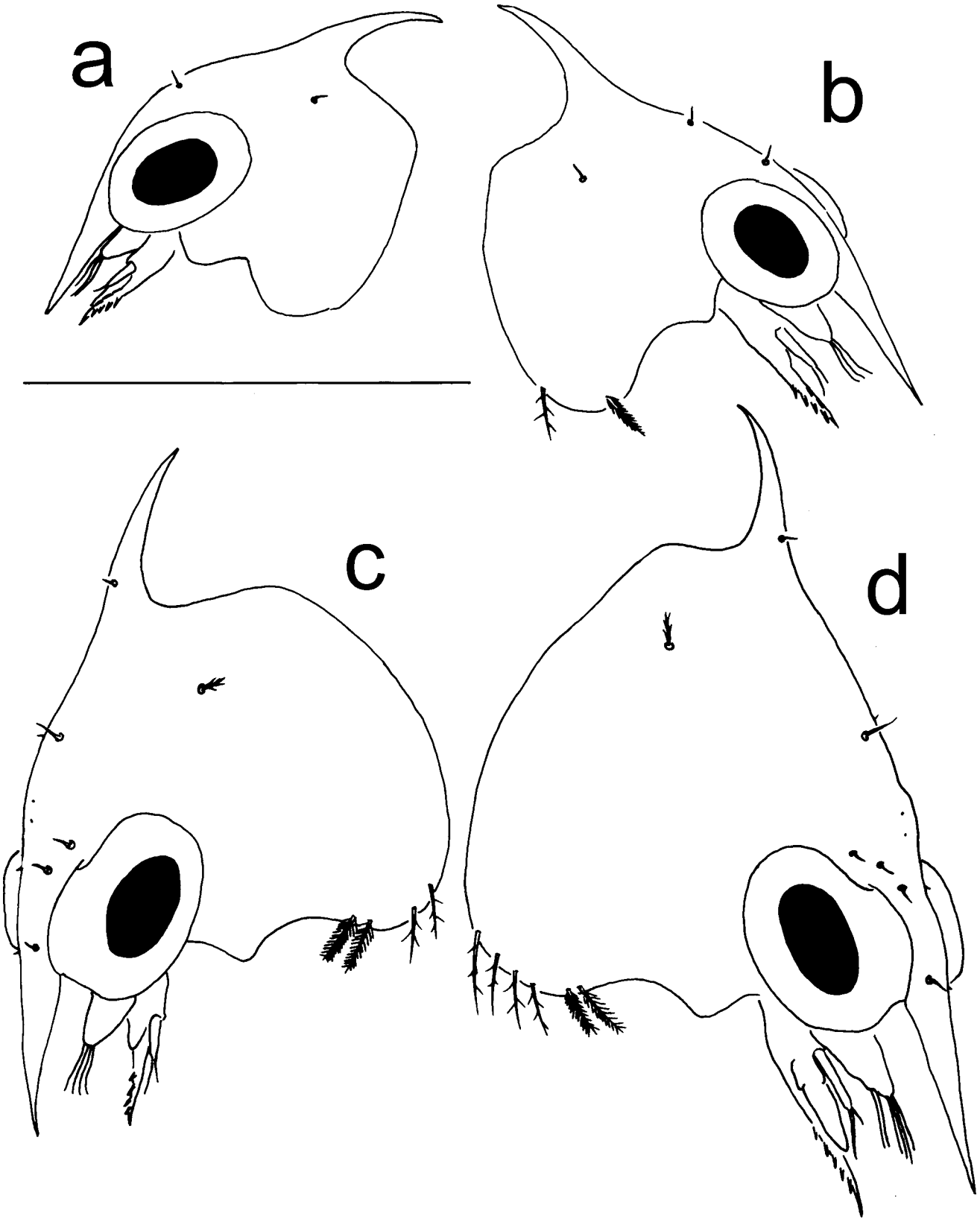

Fig. 1. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Carapace, lateral view: a, zoea I; b, zoea II; c, zoea III; d, zoea IV. Scale bar = 0.6 mm.

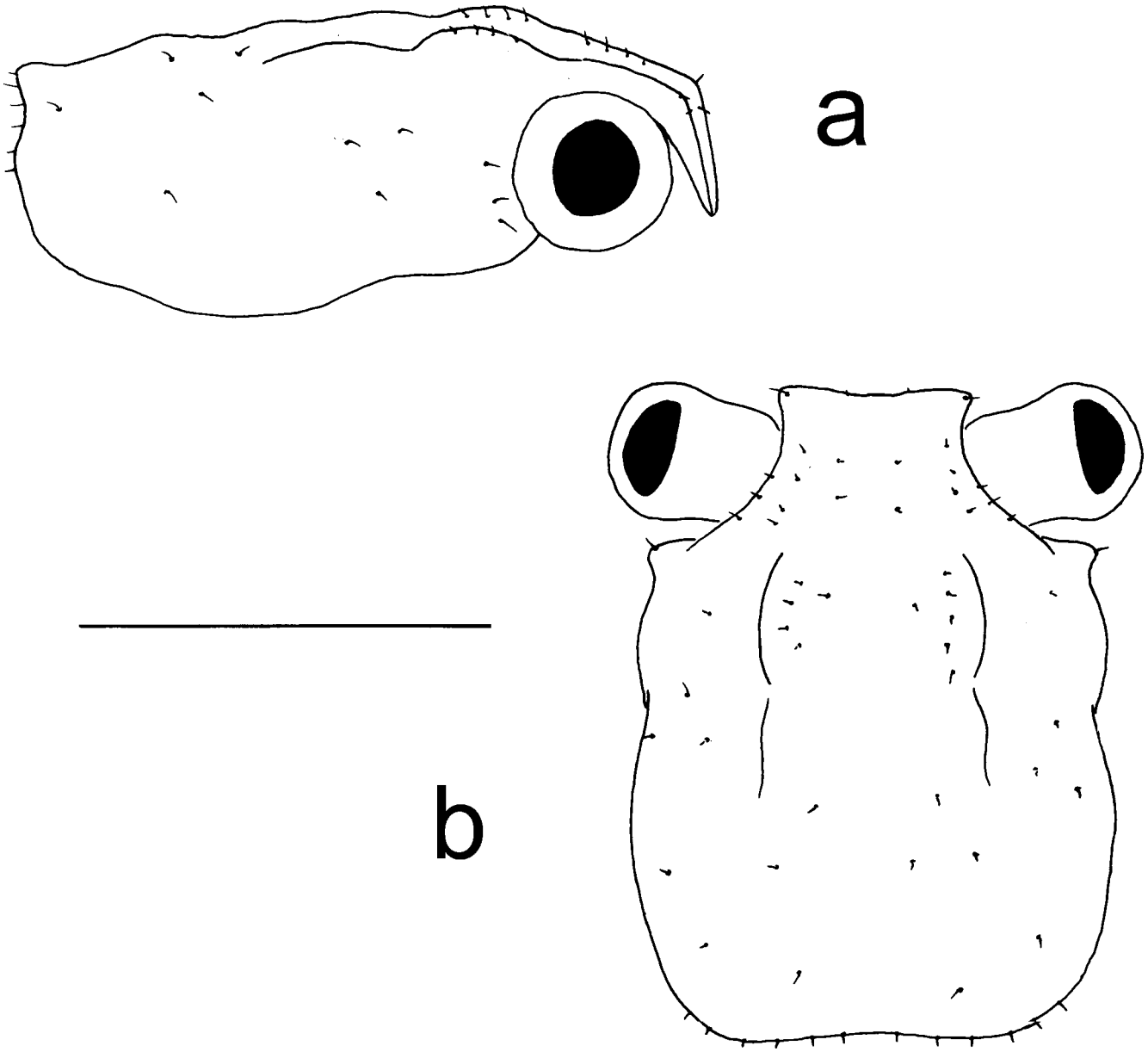

Fig. 2. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Carpace: a, megalopa, lateral view; b, megalopa, dorsal view. Scale bar = 0.6 mm.

dorsobasal microtrichiae. Endopod 5-segmented, with 2, 2, 1, 2, 5 (1 subterminal + 4 terminal); third segment with a mat of dorsal microtrichiae. Exopod incompletely bi-segmented; distal segment with 4 long plumose natatory setae.

Second maxilliped (Fig. 9a) coxa without seta. Basis with 4 medial setae arranged 1 + 1 + 1 + 1. Endopod 3-segmented, with 0, 1, 6 setae. Exopod incompletely bi-segmented; distal segment with 4 long plumose natatory setae.

Third maxilliped absent.

Pereiopods absent.

Pleon (Figs. 13a, 14a). Somites 2 and 3 with pair of dorsolateral processes; somites 3-4 with posterolateral processes of subtriangular shape, and posterolateral processes on somite 5 very long curved and acute distally; somites 2-5 with a pair of posterodorsal simple setae.

Telson (Figs. 13a, b, 14a). Bifurcated, distinct median notch, 3 pairs of serrulate setae on inner margin; medial side of inner pair sparsely spinulate; furcal arms long, with two rows of spines and outer part without spines, only scattered minute spinules; fl/bt = 1.6-1.7.

Zoea II

Size.—rdl: 0.97 ± 0.02 mm; cl: 0.55 ± 0.01 mm.

Morphology.—Carapace (Fig. 1b) with two pairs of anterodorsal setae. Each ventral margin with two setae. Eyes stalked.

Antennule (Fig. 3b) with exopod with 4 terminal aesthetascs and 1 seta.

Antenna (Fig. 4b) with endopod present as minute bud. Minute terminal spines on exopod absent.

Maxillule (Fig. 5b) basial endite with 7 setae. Exopodal plumose seta present.

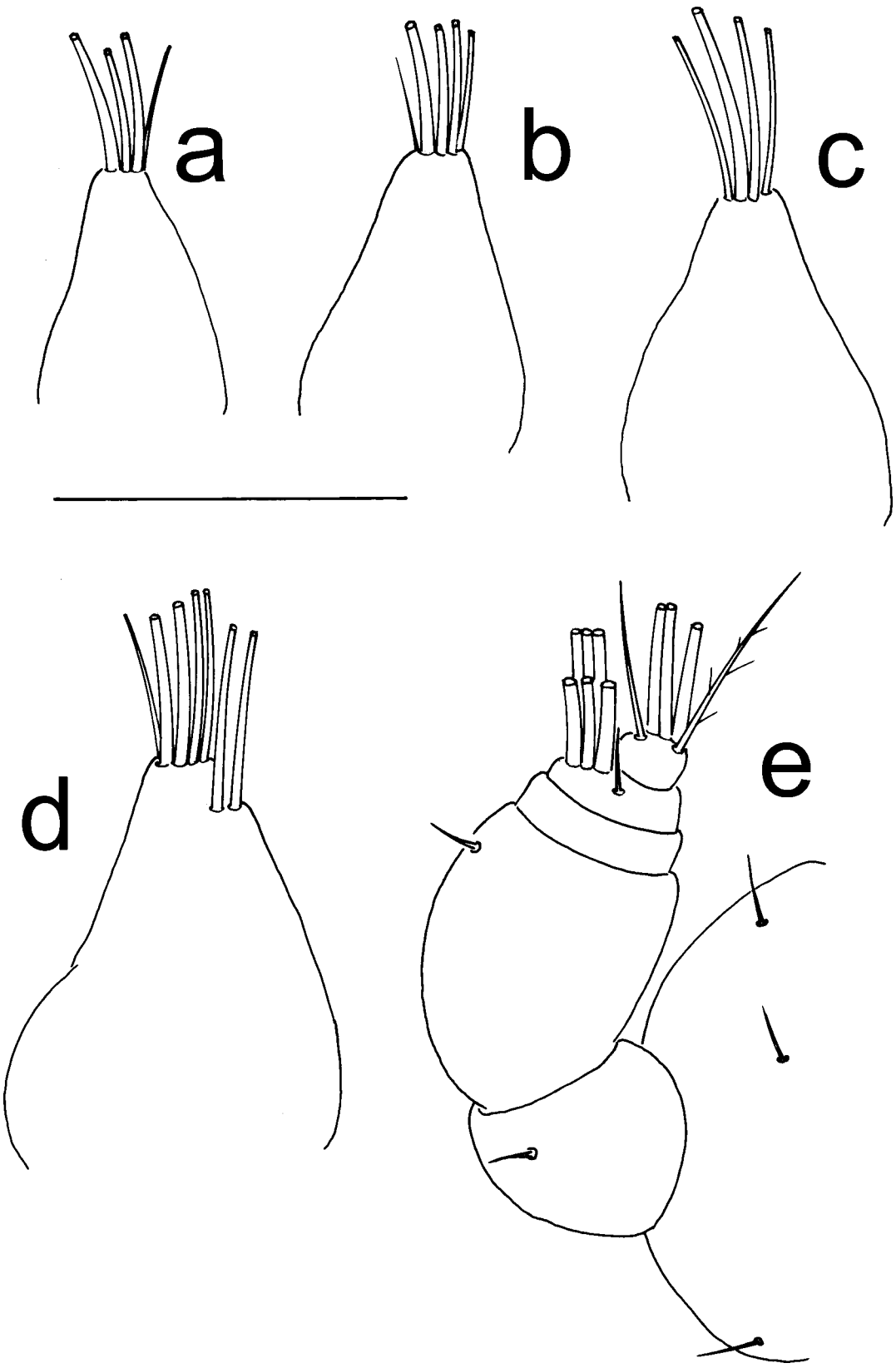

Fig. 3. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Antennule: a, zoea I; b, zoea II; c, zoea III; d, zoea IV; e, megalopa. Scale bar = 0.15 mm.

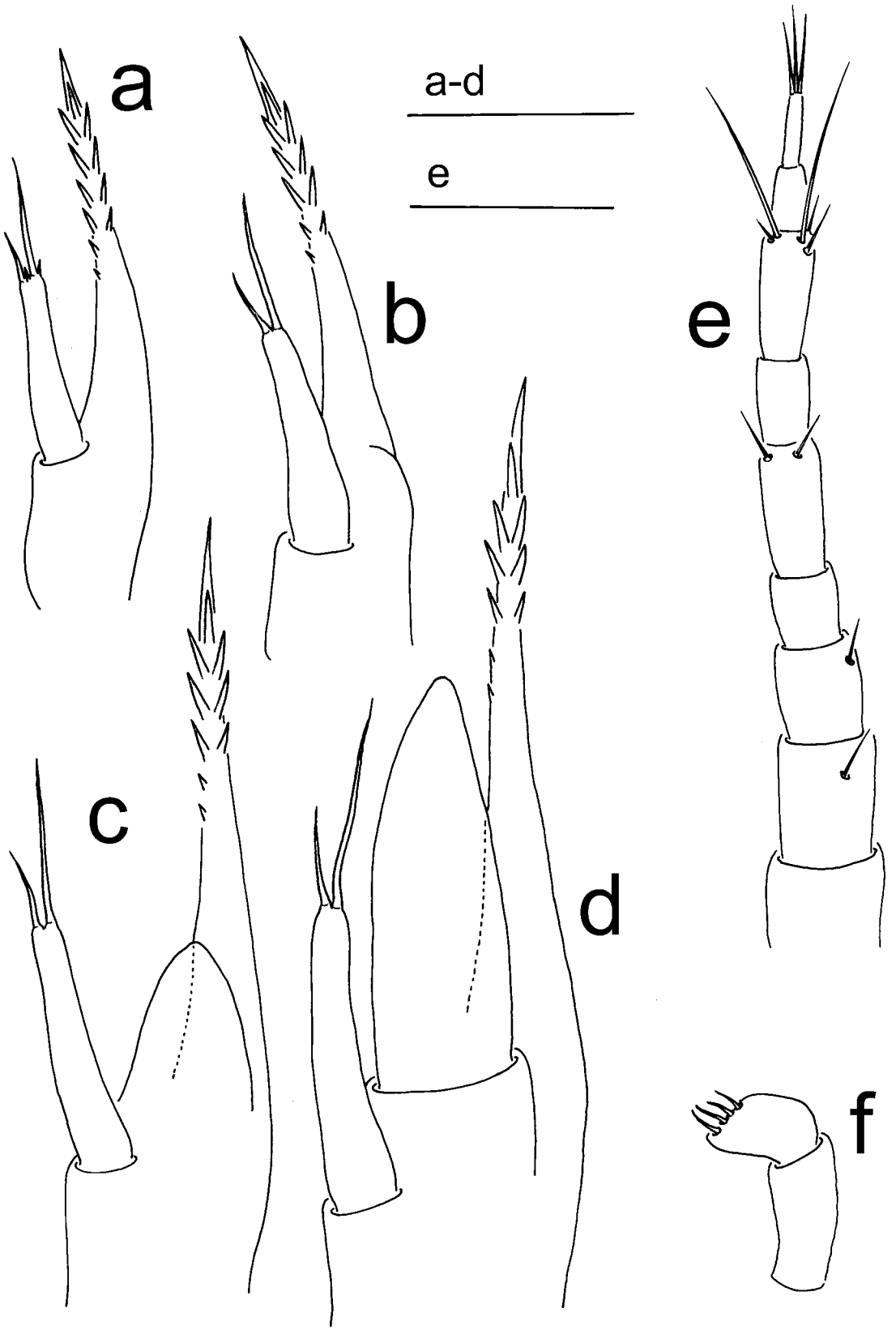

Fig. 4. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Antenna: a, zoea I; b, zoea II; c, zoea III; d, zoea IV; e, megalopa; f, megalopa, mandibular palp. Scale bars = 0.1 mm.

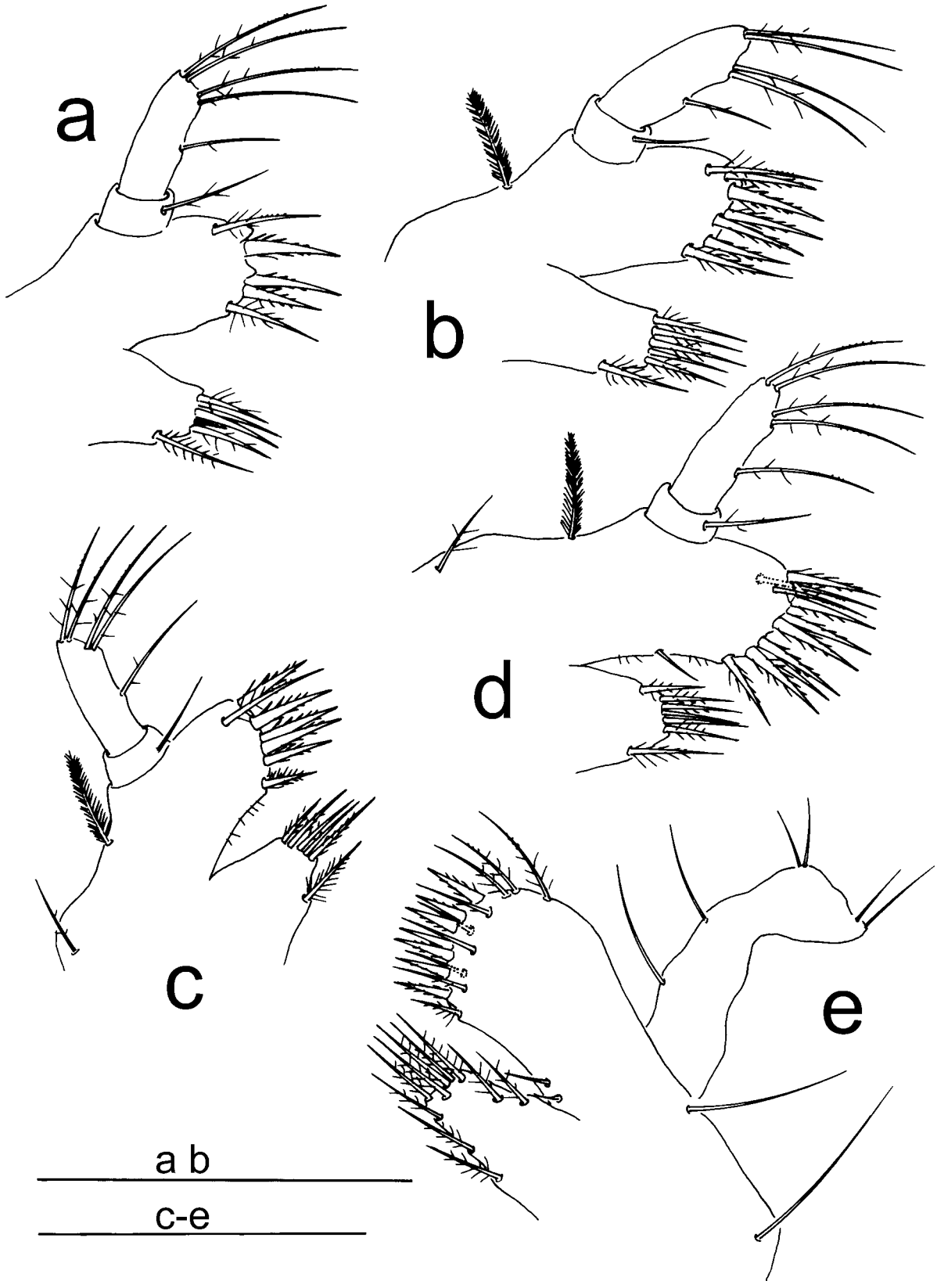

Fig. 5. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Maxillule: a, zoea I; b, zoea II; c, zoea III; d, zoea IV; e, megalopa. Scale bars = 0.15 mm.

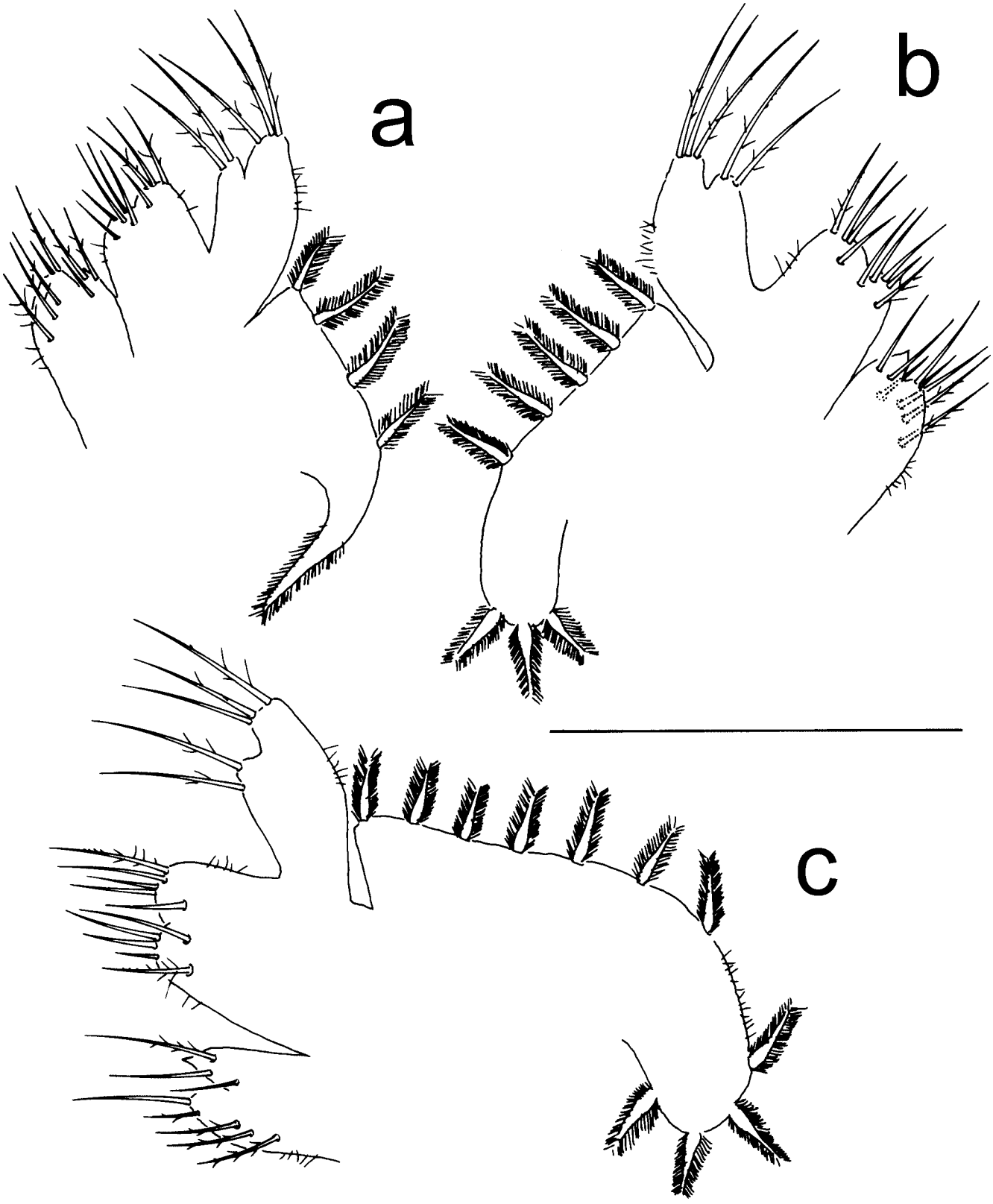

Fig. 6. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Maxilla: a, zoea I; b, zoea II; c, zoea III. Scale bar = 0.15 mm.

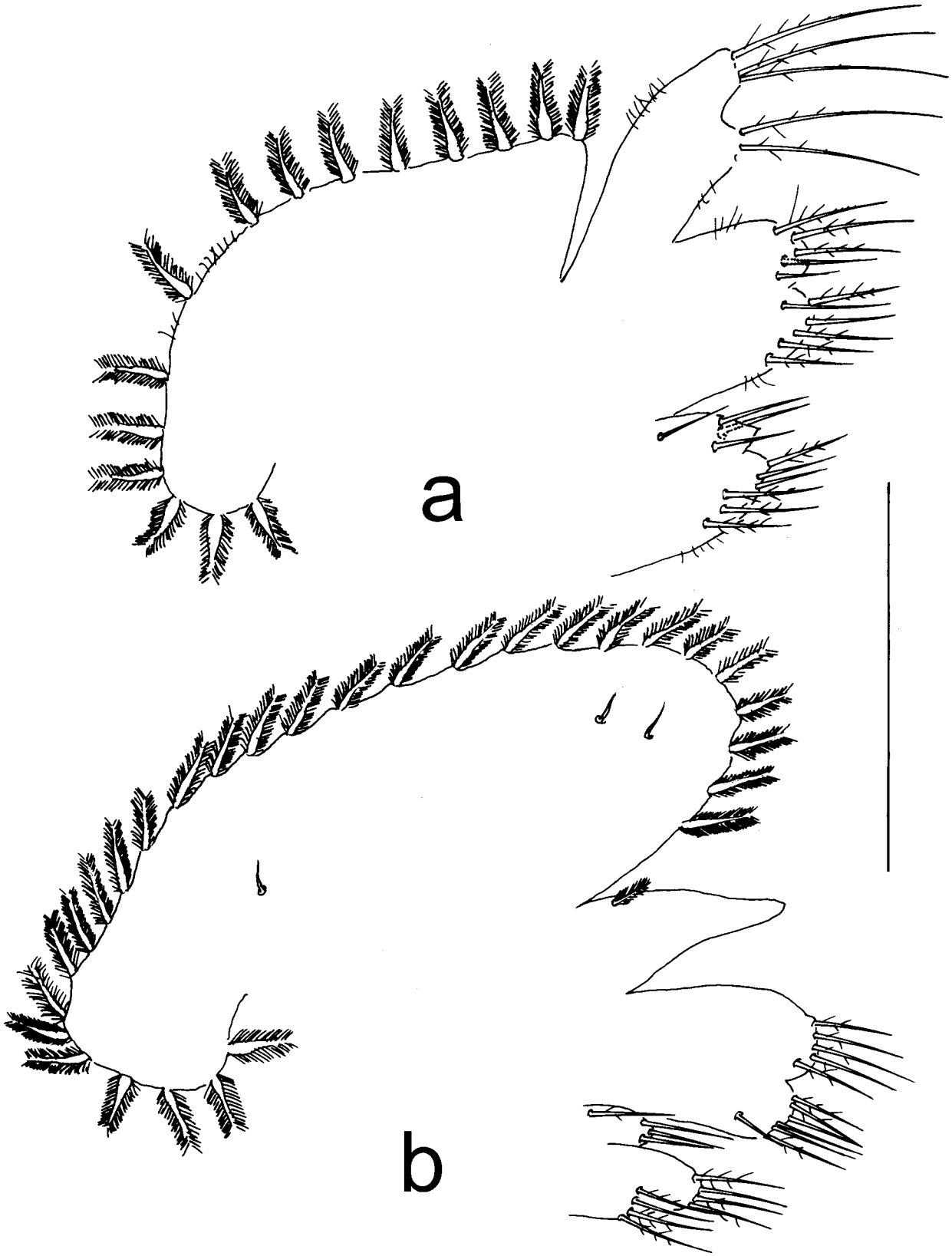

Fig. 7. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Maxilla: a, zoea IV; b, megalopa. Scale bar = 0.15 mm.

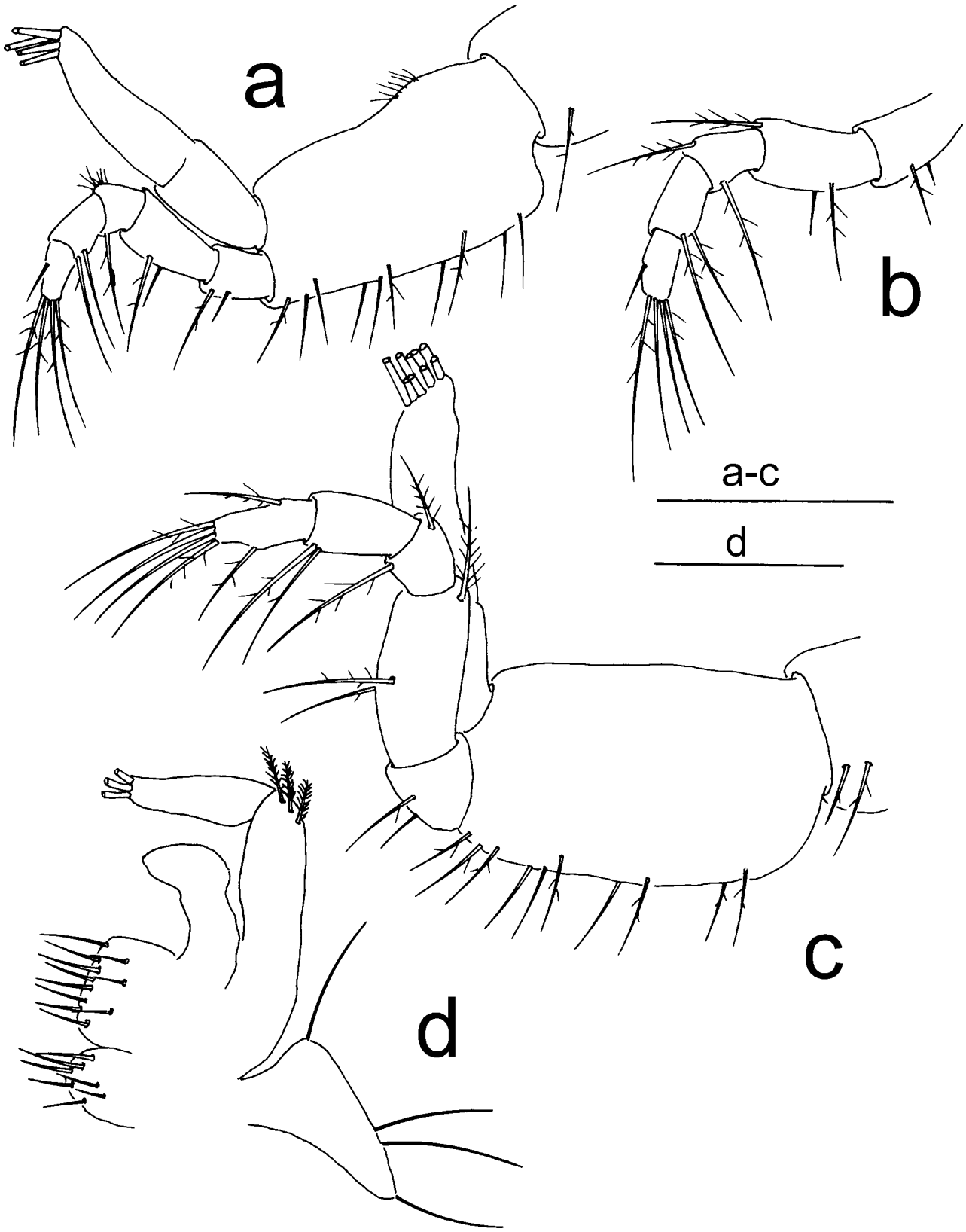

Fig. 8. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). First maxilliped: a, zoea I; b, zoea III, endopod; c, zoea IV; d, megalopa. Scale bars = 0.15 mm.

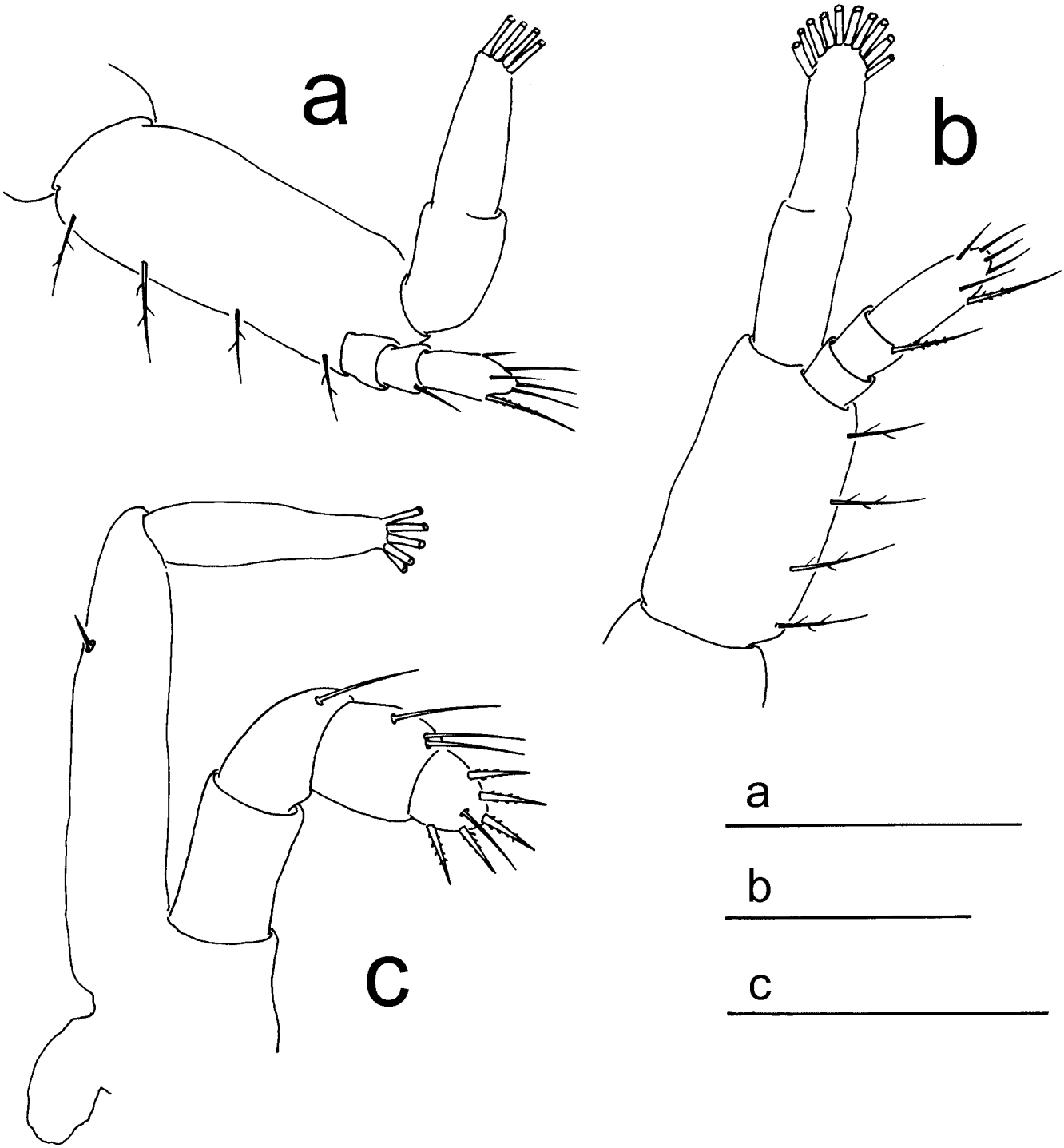

Fig. 9. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Second maxilliped: a, zoea I; b, zoea IV; c, megalopa. Scale bars = 0.15 mm.

Maxilla (Fig. 6b) scaphognathite with 8 (5 + 3) plumose marginal setae.

First maxilliped exopod distal segment with 6 long plumose natatory setae.

Second maxilliped exopod distal segment with 6 long plumose natatory setae.

Third maxilliped as undifferentiated bud.

Pereiopods as undifferentiated buds.

Pleon (Figs. 13c, 14b) first somite with 1 mid-dorsal seta. Telson (Figs. 13c, 14b). Unchanged.

Zoea III

Size.—rdl: 1.20 ± 0.03 mm; cl: 0.70 ± 0.01 mm.

Morphology.—Carapace (Fig. 1c) with four pairs of antero-dorsal setae. A pair of minute setae near base of dorsal spine. Each ventral margin with four setae.

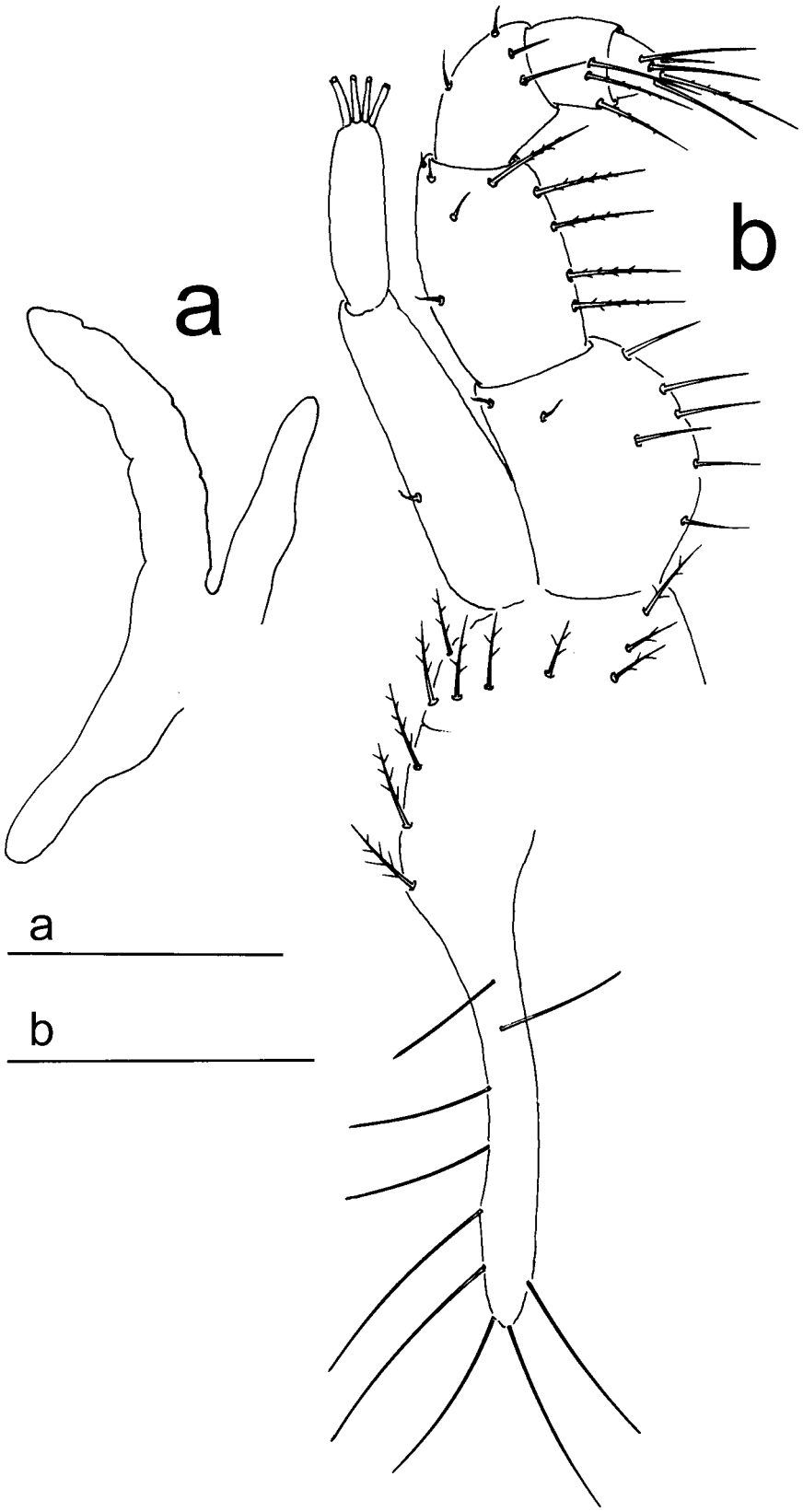

Fig. 10. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Third maxilliped: a, zoea IV; b, megalopa. Scale bars = 0.15 mm.

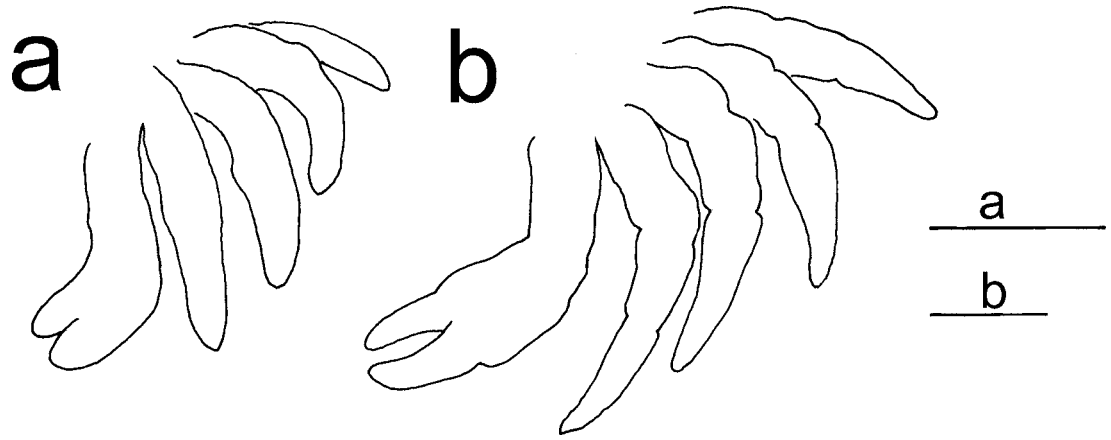

Fig. 11. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Pereiopods 1-5: a, zoea III; b, zoea IV. Scale bars = 0.1 mm.

Antennule (Fig. 3c). Exopod with 4 terminal aesthetascs.

Antenna (Fig. 4c) endopod bud elongated, shorter than exopod and without setae. pl/el = 2.6.

Maxillule (Fig. 5c) with epipodal seta present.

Maxilla (Fig. 6c) basial endite with 5 + 5 setae. Scaphognathite with 10-11 plumose marginal setae.

First maxilliped (Fig. 8b) endopod segments 2 and 3 with 1 additional dorsal seta each. Exopod with 8 long plumose natatory setae.

Second maxilliped exopod with 8 long plumose natatory setae.

Third maxilliped biramous and unsegmented.

Pereiopods (Fig. 11a) unsegmented. Chelipeds bilobed.

Pleon (Figs. 13d, 14c) somite six now present, without setae. Tip of posterolateral processes of somite 5 reaching posterior margin of somite 6. Pleopods buds present on somites 2-5, endopods absent.

Telson (Figs. 13d, 14c) outer part of the furca with two minute scale-like spines. fl/bt = 2.9.

Zoea IV

Size.—rdl: 1.40 ± 0.02 mm; cl: 0.80 ± 0.01 mm.

Morphology.—Carapace (Fig. 1d) with five pairs of anterodorsal setae. Each ventral margin with 6 setae.

Antennule exopod (Fig. 3d) with 2-3 subterminal and 5 terminal aesthetascs.

Antenna protopod (Fig. 4d) bearing two unequal rows of 5-3 spines. Endopod 2-segmented, longer, reaching middle of spinous process. pl/el = 2.3-2.4.

Mandible with a palp bud present.

Maxillule (Fig. 5d) coxal endite with 7 setae. Basial endite with 11 setae.

Maxilla (Fig. 7a) coxal endite with 6 + 4-5 setae. Basial endite with 6 + 5 setae. Scaphognathithe with 15-17 marginal plumose setae.

First maxilliped (Fig. 8c) with coxa with two setae. Fifth segment of endopod with additional subterminal seta. Exopod distal segment with 9 long plumose natatory setae.

Second maxilliped (Fig. 9b) with exopod distal segment with 10 long plumose natatory setae.

Third maxilliped (Fig. 10a) with epipod rudimentary present.

Pereiopods (Fig. 11b) slightly segmented.

Pleon (Figs. 13e, 14d) with first somite with 3 long middorsal setae. Pleopod buds elongated, endopod buds present.

Telson (Figs. 13e, 14d) unchanged.

Megalopa

Size.—cl: 0.94 ± 0.03 mm; cw: 0.64 ± 0.02 mm.

Morphology.—Carapace (Figs. 2a, b) longer than broad. Rostrum ventrally deflected, with median cleft. With lateral prominent carina. Setae as shown.

Antennule peduncle (Fig. 3e) 3-segmented, with 3, 1, 1 setae, respectively. Endopod absent. Exopod 3-segmented, with 0, 6, 3 aesthetascs and 0, 1, 2 setae, respectively.

Antenna peduncle (Fig. 4e) 3-segmented, with 0, 1, 1 setae, respectively. Flagellum 6-segmented, with 0, 2, 0, 5, 0, 3 setae, respectively.

Mandible palp (Fig. 4f) 2-segmented, with 4 terminal setae on distal segment.

Maxillule (Fig. 5e) coxal endite with 9-10 setae. Basial endite with 17-18 setae. Endopod unsegmented, proximal segment with 2 setae, distal segment with 4 setae.

Maxilla (Fig. 7b) coxal endite bilobed, with 8 + 4 setae. Basial endite bilobed with 7 + 5 setae. Endopod unsegmented, with 0-2 setae. Scaphognathite with 29-32 plumose marginal setae, 2 anterior setae and 1 posterior lateral setae.

First maxilliped (Fig. 8d) epipod with 4-5 long setae. Coxal endite with 7 setae. Basial endite with 8-11 setae. Endopod unsegmented and without setae. Exopod 2-segmented, proximal segment with 3 distal plumose setae, distal segment with 3 long terminal plumose setae.

Second maxilliped (Fig. 9c) with epipod rudimentary. Coxa and basis not differentieted, without setae. Endopod 4-segmented with 0, 1, 3, 6 setae, respectively. Exopod 2-segmented, proximal segment with 1 seta, distal segment with 5 terminal plumose setae.

Third maxilliped (Fig. 10b) epipod elongated, with 12-13 setae. Coxa and basis not differentiated, with 5-8 setae. Endopod 5-segmented, ischium, merus, carpus, propodus and dactylus with 8, 9, 4, 3, 5 setae, respectively. Exopod

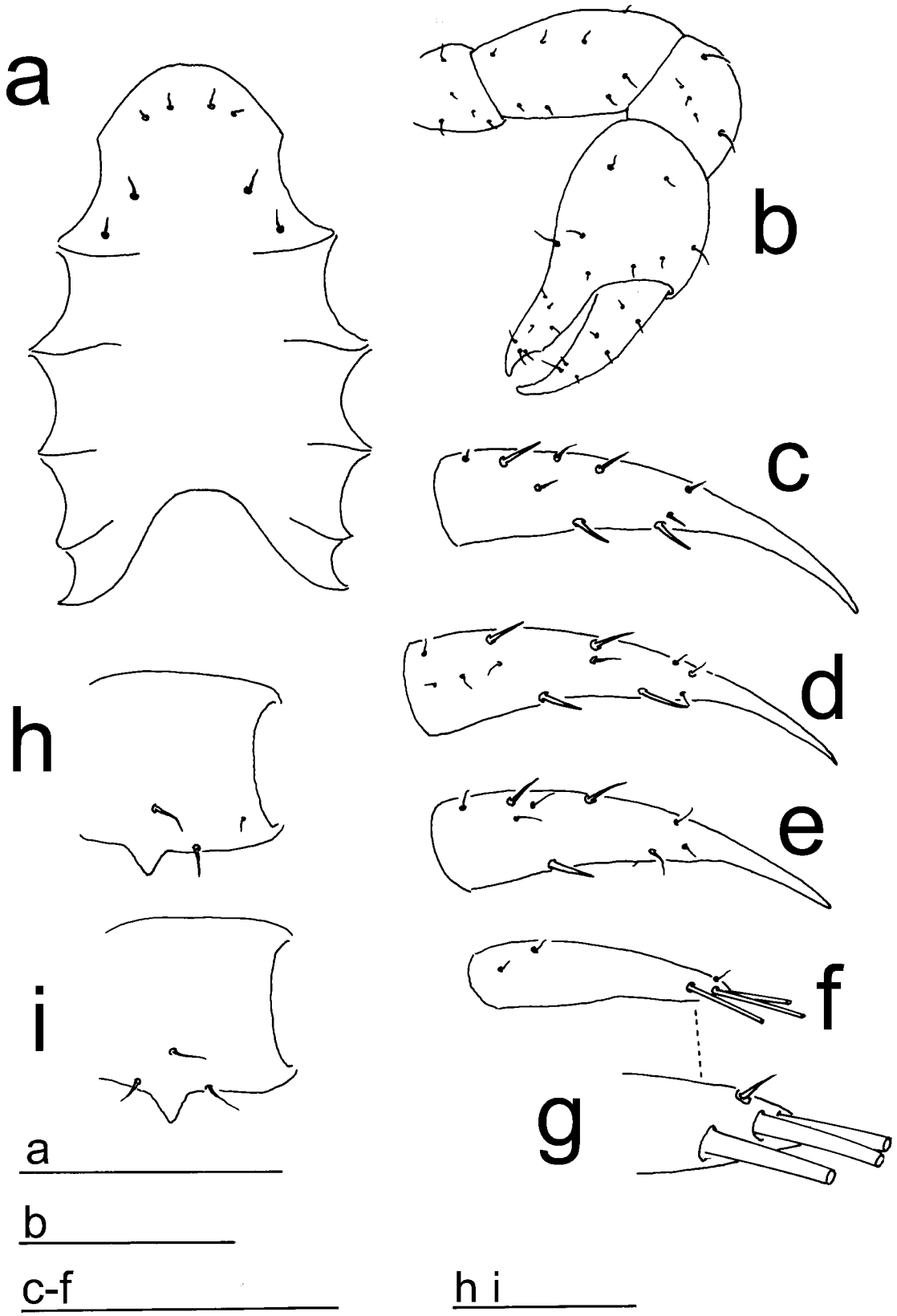

Fig. 12. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Megalopa: a, sternum; b, pereiopod 1; c-g, dactyl, pereiopods 2-5; h, coxa, pereiopod 3; i, coxa, pereiopod 4. Scale bar of a = 0.3 mm, b-f = 0.07 mm, h and i = 0.02 mm.

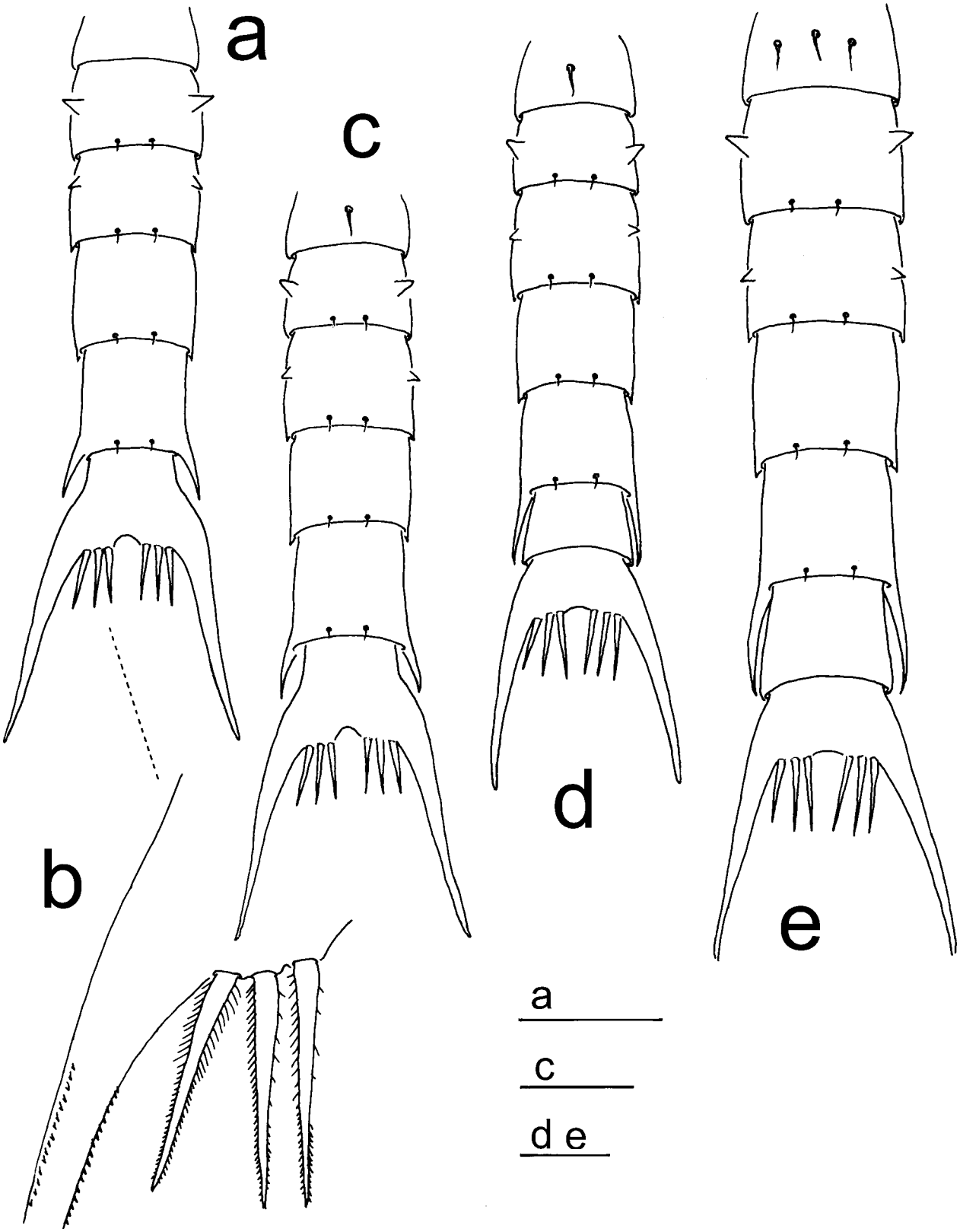

Fig. 13. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Pleon, dorsal view: a, zoea I; b, zoea I, detail of the furca and serrulate setae; c, zoea II; d, zoea III; e, zoea IV. Scale bars = 0.15 mm.

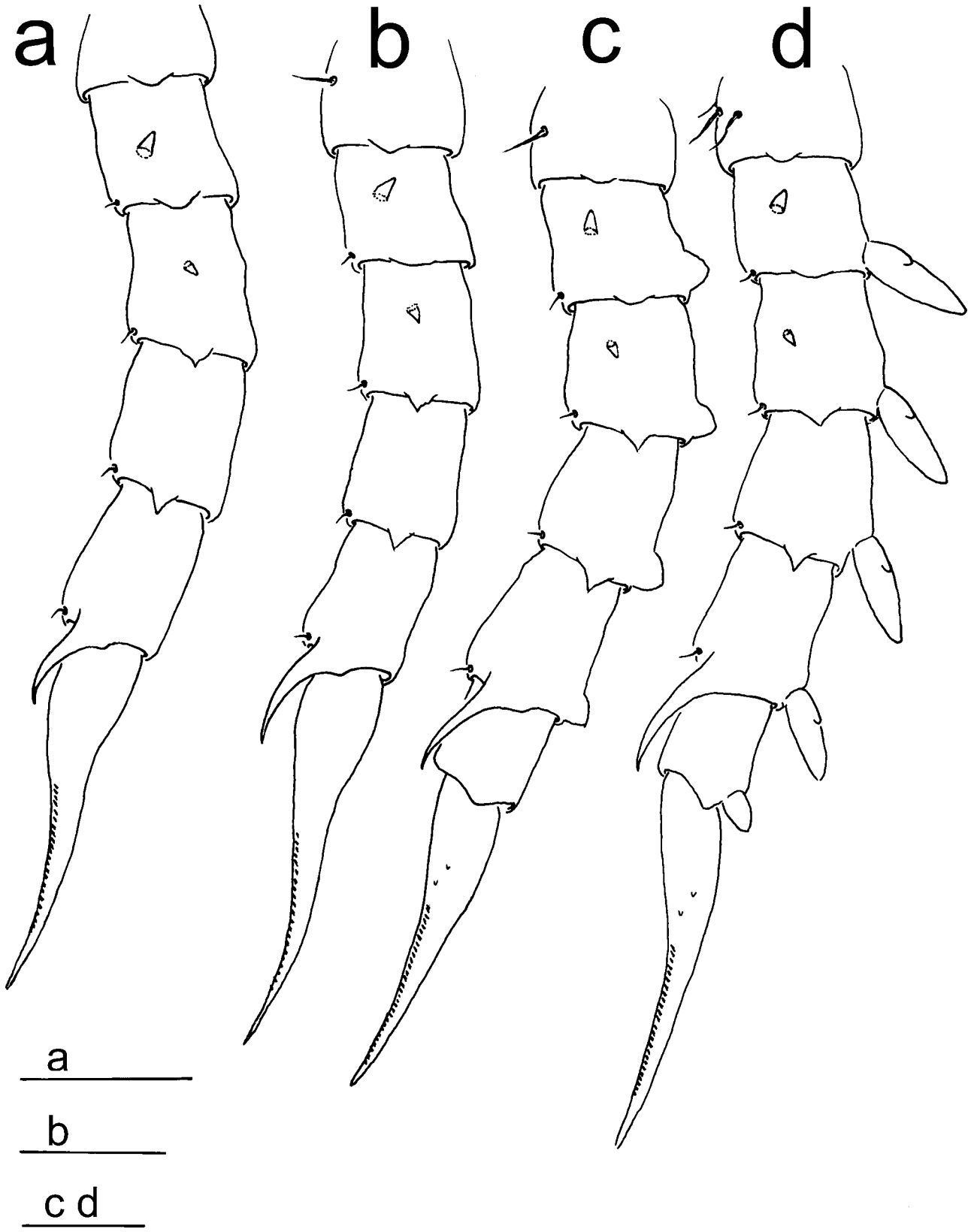

Fig. 14. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Pleon, lateral view: a, zoea I; b, zoea II; c, zoea III; d, zoea IV. Scale bars = 0.15 mm.

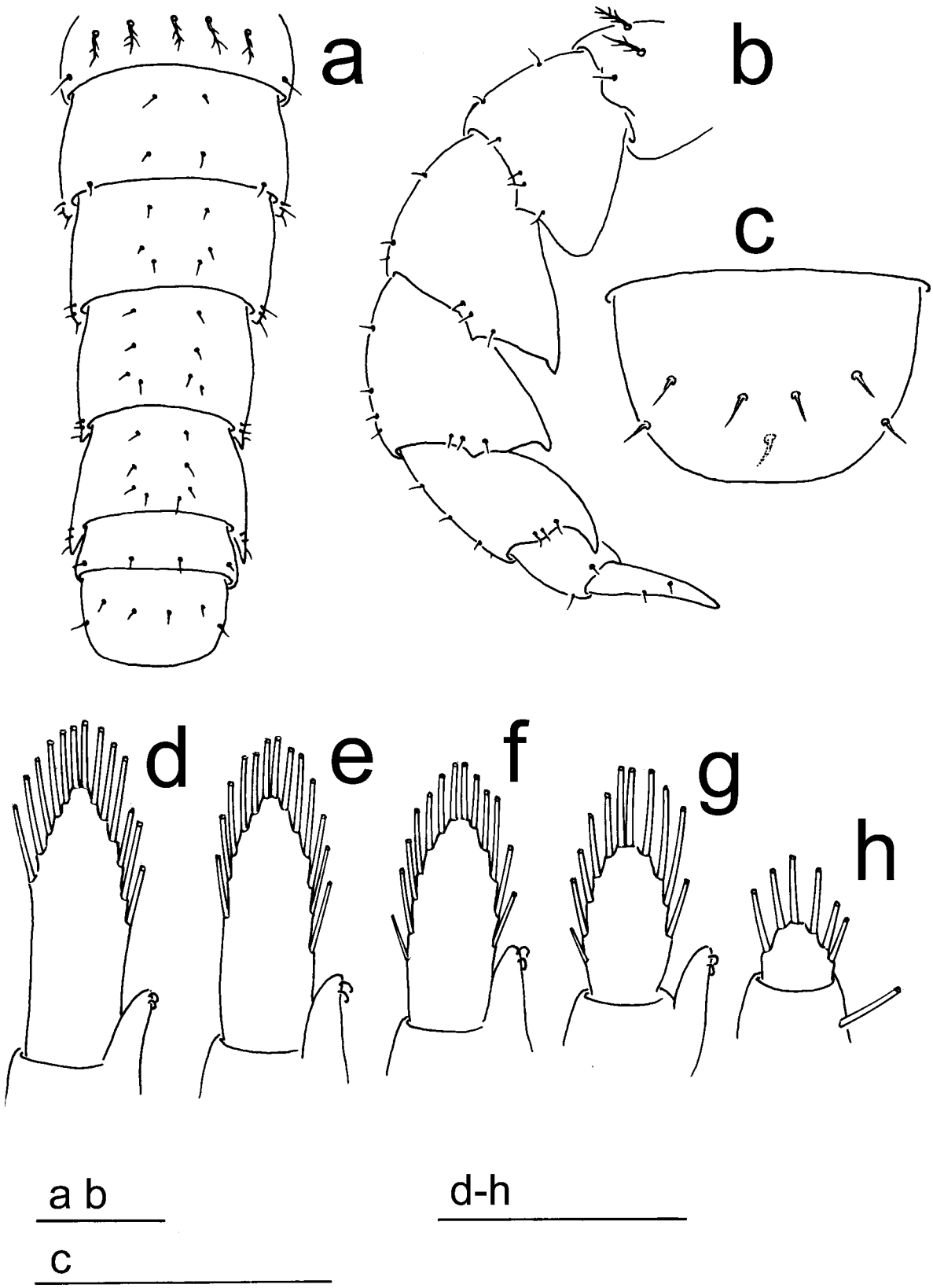

Fig. 15. *Pseudosesarma bocourti* (A. Milne-Edwards, 1869). Megalopa: a, pleon, dorsal view; b, pleon, lateral view; c, telson; d-g, pleopods 1-4; h, uropod. Scale bars = 0.15 mm.

2-segmented, proximal segment without seta and distal segment with 4 long terminal plumose natatory setae.

Pereiopods (Fig. 12 b-i) with all articles well differentiated. Pereiopods 3 and 4 with coxal process. Dactylus of fifth pereiopod with three long apical setae and 1 short seta.

Sternum (Fig. 12a) with maxillipeds and cheliped sternites fused with 8 (4 + 2 + 2) setae. All sternal sutures are interrupted medially.

Pleon (Figs. 15a, b) with six somites. Somites 1-6 with 7, 12, 12, 14, 14, 4 setae. Somite 3-5 with posterolateral processes. Somites 2-5 each with pair of well developed biramous pleopods.

Pleopods (Figs. 15 d-g) with endopod unsegmented, with 2 terminal cincinuli, exopod unsegmented with 13, 13, 13, 11 long marginal plumose natatory setae, respectively.

Uropods (Fig. 15h) 2-segmented, proximal segment with 1, and distal segment with 6 long plumose setae, respectively.

Telson (Fig. 15c) sub-square shaped; dorsal surface with six setae and ventral surface with 1 seta.

Discussion

Overall, the zoeal morphology of *Pseudosesarma bocourti* and *P. moeschii* is very similar (Table 1). They conform very closely to the characteristics listed by Cuesta et al. (2006b) for sesarmid larvae: 1) carapace without lateral spines; 2) zoea I with a pair of anterodorsal setae; 3) antennal exopod of zoea I with terminal small spines and setae of different size, exopod half length of the protopod and protopod with well developed spines distributed in two rows, normally with unequal number of spines; 4) maxillar endopod bilobed with 2 + 3 setae; 5) first maxilliped basis with 2 + 2 + 3 + 3 setae, endopod setation 2, 2, 1, 2, 5 in the first zoea, through development segments 2 and 5 acquire one seta each and possibly another one in segment 3, the last zoeal stages present a setation of 2, 3, 2, 2, 6; 6) second maxilliped basis with 1 + 1 + 1 + 1 setae; endopod setation 0, 1, 6; 7) pleon of first zoeal stage with 5 somites and last zoeal stage with 6 somites, dorsolateral processes only on somites 2 and 3, in last stage somite 1 presents 3 middorsal setae; 8) telson with 3 serrulate setae on posterior margin through zoeal development, furcal arms with two dorsal rows of spinules of varying size.

The first zoeal stages of *Pseudosesarma moeschii* and *P. bocourti* are indistinguishable from the recently described one of *P. crassimanum* (de Man, 1888) (Cuesta et al., 2006b).

The conservative morphological characteristics of the larvae of Sesarmidae make differentiation at generic levels also difficult in this family (Cuesta, 1999; Guerao et al., 2004). However, the presence of very long and curved posterolateral processes of abdominal somite 5, compared to more anterior ones, has so far only been described for *Pseudosesarma* (see Cuesta et al., 2006b; present study). The presence of these distinct processes may constitute a synapomorphy at generic level, if this feature is confirmed in currently undescribed zoeae of *Pseudosesarma*. Serène & Soh (1970) established the genus *Pseudosesarma* based on adult morphological characters, like the presence of an anterolateral tooth and the absence of pectinated crests on the male chela. These authors placed in their new genus six species, i.e., *P. edwardsi* (de Man, 1888) as type species, *P. bocourti*, *P. crassimanum*, *P. modestum* (de Man, 1902), *P. moeschii*, *P. johorense* (Tweedie, 1940) and the subspecies *P. edwardsi laevimanum* (Zehntner, 1894). Not too much later, Soh (1978) added one new species from Hong Kong to the genus, *P. patshuni*. Consequently, for most representatives of the genus, it remains to be seen if the lateral processes of the zoeal fifth pleomere are similarly distinc in these other species.

Minute scale-like spines on the outer margin of the telson furcal arms have recently been described for zoeal stages of Sesarmidae (Cuesta et al., 2006a; Cuesta et al., 2006b). This feature has been omitted in many larval descriptions of sesarmid species, due to the very small size of the spines. These spines are only present in the late zoeal stages (III and IV) of *Pseudosesarma moeschii* and *P. bocourti*; and were not observed in zoea I of *P. crassimanum*, and zoeae I-II of *P. moeschii* and *P. bocourti*.

The presence of one and two setae on the coxa of the first maxilliped of zoea stage I-III and zoea IV, respectively, has not been described previously, but is also present in *Perisesarma fasciatum* (Lanchester, 1900) (Guerao, personal observation, but not mentioned in Guerao et al., 2004). This pattern of setation may be common in other sesarmid species, although Cuesta et al. (2006a) reported one seta in all zoeal stages of *Aratus pisonii* H. Milne Edwards, 1853.

The morphology of the megalopal stage is similar to that known from other species of the family Sesarmidae (Cuesta et al., 2006b; see Table 1): 1) carapace longer than broad, rostrum ventrally deflected with a medial cleft; 2) antennule endopod absent; 3) antennal peduncle 3-segmented and flagellum with 6 segments; 4) mandibular palp 2-segmented with 4 setae on distal one; 5) maxillary scaphognathite with less than 40 marginal plumose setae (27-32) and with 2 anterior and 1 posterior lateral setae; 6) first maxilliped epipod with 4-5, but always less than 7 setae; 7) second maxilliped without fully developed epipod; 8) pleopod endopods with two cincinuli; (9) uropods with setation 1, 5-6.

Contrary to zoeal stages, it is possible to easily distinguish the megalopae of *Pseudosesarma moeschii* and *P. bocourti*. The most important character to differentiate the two species is the number of setae on the uropods (Table 1). To date it has not been demonstrated that in sesarmids this character may present intraspecific variability. However, it can be variable among species of the same genus (Guerao et al., 2004). Setation of the sternum has only very recently been included in the description of sesarmid species (Cuesta et al., 2006a) and no differences exist in the sternal setation pattern between *P. moeschii* and *P. bocourti*. Also, *Perisesarma fasciatum* presents the same pattern as *Pseudosesarma* (Guerao, personal observation). The processes of the coxa of pereiopods 2 and 3 are reported here for the first time in sesarmid megalopae.

The setation of the carapace of zoeal stages and the setation of pleon of the megalopa are important conservative characters, which are frequently omitted from larval descriptions or are not described with enough accuracy. For both these features *P. moeschii* and *P. bocourti* do not present differences.

This study confirms that there is a useful set of morphological characteristics that allows one to distinguish larvae of the family Sesarmidae (sensu Schubart et al., 2002) from all other decapod larvae, and that these characteristics are also shared by the Asian crabs *P. bocourti* and *P. moeschii*, as described here. The identification of larval stages from the plankton at a generic level (and in some case to specific level) should be possible for at least three species of the genus *Pseudosesarma*.

References

Alcock, A. 1900. The Brachyura Catometopa or Grapsoidea: Material for a carcinological fauna of India, No. 6. Journal of the Asiatic Society of Bengal 69(II: 3): 279-456.

Clark, P. F., D. K. Calazans, and G. W. Pohle. 1998. Accuracy and standardization of brachyuran larval descriptions. Invertebrate Reproduction and Development 33: 127-144.

Cuesta, J. A. 1999. *Morfología larval de la familia Grapsidae* (*Crustacea*, *Decapoda*, *Brachyura*). Ph.D. thesis. Universidad de Sevilla, 291 pp.

———, and K. Anger. 2001. Larval morphology of the sesarmid crab *Armases angustipes* Dana, 1852 (Decapoda, Brachyura, Grapsoidea). Journal of Crustacean Biology 21: 821-838.

———, M. U. García-Guerrero, A. Rodríguez, and M.E. Hendrickx. 2006a. Larval morphology of the sesarmid crab, *Aratus pisonii* (H. Milne Edwards, 1837) (Decapoda, Barchyura, Grapsoidea) from laboratory-reared material. Crustaceana 79: 175-196.

———, G. Guerao, H-C. Liu, and C. D. Schubart. 2006b. Morphology of the first zoeal stages of eleven Sesarmidae (Crustacea, Brachyura, Thoracotremata) from the Indo-West Pacific, with a summary of familial larval characters. Invertebrate Reproduction and Development 49: 151-173.

Guerao, G., K. Anger, U. Nettelmann, and C. D. Schubart. 2004. Complete larval and early juvenile development of the mangrove crab *Perisesarma fasciatum* (Crustacea: Brachyura: Sesarmidae) from Singapore, with a larval comparison of *Parasesarma* and *Perisesarma*. Journal of Plankton Research 26: 1389-1408.

Islam, M. S., S. Shokita, and N. Shikatani. 2002. Larval development of the mangrove sesarmid crab *Neosarmatium indicum* (Brachyura: Grapsoidea) described from laboratory-reared material. Journal of Crustacean Biology 22: 916-937.

Man, J. G., de. 1880. On some species of the genus *Sesarma* Say and *Cardisoma* Latr. Notes of the Leyden Museum 2(5): 21-36.

———. 1887. Uebersicht der Indo-Pacifischen Arten der Gattung Sesarma Say nebst einer Kritik der von W. Hess und E. Nauck in den Jahren 1865 und 1880 beschriebenen Decapoden. Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 2: 639-722, pl. 17.

———. 1888. Report on the podophthalmous Crustacea of the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr. John Anderson, F.R.S., Superintendent of the Museum. Journal of the Linnean Society 22: 1-312, pl. 1-19.

———. 1892. Decapoden des Indischen Archipels. In: Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien (M. Weber, ed.; Leiden) 2: 265-527, pl. 15-29.

———. 1895. Bericht über die von Herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. Zweiter Theil. Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 9: 75-218, pl. 13.

McLaughlin, R., N. Firooznia, and C.W. Holliday. 1996. Branchial Na, K-ATPase Activity and Osmotic and Chloride Ion Regulation in the Thai Crab, *Pseudosesarma moeschi*. Journal of the Pennsylvania Academy of Science 70: 45-52.

Milne-Edwards, A. 1869. Note sur quelques nouvelles espèces du genre *Sesarma* (Say). Nouvelles Archives du Muséum d'Histoire Naturelle, Paris 5(4): 25-31.

Ng, P. K. L. 1995. The freshwater crabs and prawns (Crustacea: Decapoda) of Bako National Park, Sarawak, Malaysia. with descriptions of one new genus and three new species. The Raffles Bulletin of Zoology 43: 181-205.

Nobili, G. 1899. Contribuzioni alla conoscienza della fauna carcinologica della Papuasia, delle Molucche e dell' Australia. Annali di Museo Civico di Storia Naturale di Genova 2: 230-282.

Roux, J. 1933. Résultats scientifiques du voyage aux Indes Néerlandaises de LL. AA. RR. le Prince et de la Princesse Léopold de Belgique. Crustacés Décapodes d'eau douce. Mémoires du Musée Royal d'Histoire Naturelle de Belgique, Hors Série 3(14): 1-18.

Schubart, C. D., and J. A. Cuesta. 1998. First zoeal stages of four *Sesarma* species from Panama, with identification keys and remarks on the American Sesarminae (Crustacea: Brachyura: Grapsidae). Journal of Plankton Research 20: 61-84.

———, and R. Diesel. 1998. Osmoregulatory capacities and penetration into terrestrial habitats: a comparative study of Jamaican crabs of the genus *Armases* Abele, 1992 (Brachyura: Grapsidae: Sesarminae). Bulletin of Marine Science 62: 743-752.

———, J. A. Cuesta, and D. L. Felder. 2002. Glyptograpsidae, a new brachyuran family from Central America: larval and adult morphology, and a molecular phylogeny of the Grapsoidea. Journal of Crustacean Biology 22: 28-44.

Serène, R., and C. L. Soh. 1970. New Indo-Pacific genera allied to *Sesarma* Say 1817 (Brachyura, Decapoda, Crustacea). Treubia 27: 387-416.

Soh, C. L. 1978. On a collection of sesarmine crabs (Decapoda, Brachyura, Grapsidae) from Hong Kong. Memoirs of the Hong Kong Natural History Society 13: 9-22.

Tan, C. G. S, and P. K. L. Ng. 1994. An annotated checklist of mangrove brachyuran crabs from Malaysia and Singapore. In, A. Sasekumar, N. Marshall, and D. J. Macintosh (eds.), Ecology and conservation of Southeast Asian marine and freshwater envionments including wetlands. Hydrobiologia 285: 75-84.

Targioni-Tozzetti, A. 1877. Crostacei Brachiuri e Anomuri. In: Zoologie del viaggio intormo al globo della R. pirocorvetta "Magenta". Firenze, 257 pp.

Tesch, J. J. 1917. Synopsis of the genera *Sesarma*, *Metasesarma*, *Sarmatium* and *Clistocoeloma*, with a key to the determination of the Indo-Pacific species. Zoologische Mededelingen, Leiden 3: 127-260, pls. 15-17.

Tweedie, M. W. F. 1940. New and interesting Malaysian species of *Sesarma* and *Utica* (Crustacea, Brachyura). Bulletin of the Raffles Museum 16: 88-113.

Yeo, D. C. J., Y. Cai, and P. K. L. Ng. 1999. The freshwater and terrestrial decapod Crustacea of Pulau Tioman, Peninsular Malaysia. The Raffles Bulletin of Zoology Suppl. 6: 197-244.

Zehntner, L. 1894. Crustacés de l'Archipel Malais. Revue Suisse de Zoologie 2: 135-214.

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