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Morphology of the first zoeal stages of eleven Sesarmidae (Crustacea, Brachyura, Thoracotremata) from the Indo-West Pacific, with a summary of familial larval characters

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Summary

The first zoeal stages of eleven species of Sesarmidae from the Indo-West Pacific were obtained from ovigerous females. Those of *Labuanium scandens*, *L. rotundatum*, *L. trapezoideum*, *L. politum*, *Metasesarma aubryi*, *Pseudosesarma crassimanum*, *Stelgistra stormi*, and *Sesarmops impressum*, are described for the first time, while the first zoeal stages of *Clistocoeloma merguiense*, *Metasesarma obesum* and *Sesarmops intermedium* are re-described. Larval characters of all these species are compared with previously described ones for the family and morphological features are re-evaluated. Minute spines on the telson of the zoeae are described as a new larval character in Sesarmidae and their presence or absence in other grapsoid groups is discussed. The results demonstrate that a recurrent combination of reliable larval characters distinguishes zoeae and megalopae of the examined sesarmids from the rest of the Grapsoidea. This appears to be consistent with recent studies that redefine the Sesarmidae.

Key words: Sesarmidae, Thoracotremata, larval morphology, zoea, megalopa, taxonomy, Indo-West Pacific

Introduction

The larval descriptions of 54 species of Sesarmidae are known from 53 publications. About 230 species are assigned to this grapsoid family and these are mostly intertidal to semi-terrestrial, which allows relatively easy collecting. Furthermore, sesarmid larvae can be effortlessly reared in laboratory due to the large size of early zoeal stages. In contrast, Grapsidae have small first stage zoeae that do not feed on *Artemia* nauplii and this makes their rearing difficult. Consequently the complete larval development is only known for *Metopograpsus*.

Larval morphology has become an increasingly useful tool for grapsoid systematics. For example, Wear (1970), Green and Anderson (1973), Terada (1976), Fielder and Greenwood (1983), and Krishnan and Kannupandi (1989) suggested that the assignment of *Chasmagnathus*, *Cyclograpsus*, *Helice*, *Helograpsus*, *Metaplax* and *Paragrapsus* to the then Sesarminae was

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anomalous. However no formal changes to the classification were proposed. Recently, all grapsoid families, including the Sesarmidae, were redefined using molecular and adult data as well as larval morphology (Schubart et al., 2000; Cuesta et al., 2001; Schubart et al., 2002) and the above six genera have been excluded from among the taxa now assigned to the Sesarmidae.

The first zoeal stages of eight sesarmid species from the Indo-West Pacific including *Labuanium scandens* Ng and Liu, 2003; *L. rotundatum* (Hess, 1865); *L. trapezoideum* (H. Milne Edwards, 1837); *L. politum* (de Man, 1888); *Metasesarma aubryi* A. Milne-Edwards, 1869; *Pseudosesarma crassimanum* (de Man, 1887); *Stelgistra stormi* (de Man, 1895); and *Sesarmops impressum* (H. Milne-Edwards, 1837) are described and illustrated for the first time. Previous accounts for the first zoeae of *Clistocoeloma merguiense* de Man, 1888; *Metasesarma obesum* (Dana, 1851) and *Sesarmops intermedium* (de Haan, 1835) have been reported, but they are here re-described to include new characters previously overlooked.

The aim of this study is to review the known sesarmid larval descriptions and incorporate the above new data in order to summarise the distinctive characters that now define this family.

Materials and Methods

The first zoeal stages of *Laubuanium scandens*, *L. trapezoi-deum*, *L. rotundatum*, *L. politum*, *Metasesarma aubryi*, *M. obesum* (previously known as *M. rousseauxi*, see Ng and Schubart, 2003), *Pseudosesarma crassimanum*, *Stelgistra stormi*, *Clistocoeloma merguiense*, *Sesarmops impressum*, and *Sesarmops intermedium* were obtained from ovigerous crabs collected from the Indo-West Pacific (for details see Table 1).

All zoeae with active natatory behaviour were fixed in 4% formaldehyde–seawater. Dissections were carried out under a Wild MZ6 stereo microscope and drawings and measurements were made using a Zeiss Axioskop compound microscope equipped with a *camera lucida*. All measurements were made with a calibrated ocular micrometer. Drawings were based on 5 larvae and morphometrics on 10 larvae per stage. Measurements were made of the following: rostro-dorsal length (rdl) from the tip of the rostral spine to the tip of the dorsal spine; carapace length (cl) from the base of the rostrum to the posterior margin; 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

Table 1. List of the first zoeal stages described in the present study, indicating localities and date of collection, collectors, and accession numbers. Zoological Reference Collection, National University of Singapore, Singapore: ZRC; Colecciones Biológicas de Referencia, Instituto de Ciencias del Mar de Barcelona, Spain: ICM; Institute of Zoology, Academia Sinica, Nankang, Taiwan: ASIZ

Species	Locality	Data	Collector	Accession number
Labuanium scandens	Pingtung, Taiwan	10 August 1998	H-C Liu	ZRC 2005.0127
Labuanium trapezoideum	Taitung, Taiwan	14 November 2001	H-C Liu	ZRC 2005.0128
Labuanium rotundatum	Pago Bay, Guam	4 August 2001	H-C Liu and P.K.L. Ng	ZRC 2005.0129
Labuanium politum	Loboc River, Philippines	5 March 2003	H-C Liu and P.K.L. Ng	ASIZ 72932
Metasesarma aubryi	Pingtung, Taiwan	18 October 1998	H-C Liu	ZRC 2005.0130 / ICMD 2/2006
Metasesarma obesum	Malotoy, Sulawesi, Indonesia	17 January 2000	Schubart et al.	ZRC 2005.0131 / ICMD 10/2006
Metasesarma obesum	Pingtung, Taiwan	26 August 1999	H-C Liu	ZRC 2005.0132 / ICMD 11/2006
Stelgistra stormi	Hengchun, Taiwan	12 July 1999	H-C Liu	ZRC 2005.0133 / ICMD 7/2006
Pseudosesarma crasssimanum	Sungei Benut, Malaysia	30 September 1999	Schubart et al.	ZRC 2005.0134 / ICMD 3/2006
Clistocoeloma merguiense	Mandai, Singapore	10 September 1999	Schubart and Sivasothi	ZRC 2005.0135 / ICMD 6/2006
Sesarmops impressum	Pingtung, Taiwan	22 September 1998	H-C Liu and C-H Wang	ZRC 2005.0136 / ICMD 8/2006
Sesarmops intermedium	Harbor Bay, Taiwan	3 September 1999	H-C Liu	ZRC 2005.0137 / ICMD 9/2006

of the outer seta on the posterior margin of the telson to the furcal tip; and basal telson length (bt), from a line across the anterior margin to the posterior margin of the telson (base of the outer seta). Plumose natatory setae of the maxillipeds' exopods are drawn truncated in Fig. 3. Descriptions and figures are arranged according to the standard proposed by Clark et al. (1998).

The morphology and setation of the mouthparts of all described sesarmid species is similar and does not show any variation between species. Therefore, these appendages are described and illustrated only for *Labuanium scandens*.

Maternal females and samples of the first zoeal stage of all species were deposited at the Zoological Reference Collection (ZRC), National University of Singapore, Singapore, while another set of the first zoeae was deposited at the Colecciones Biológicas de Referencia, Instituto de Ciencias del Mar de Barcelona (ICM), Spain (for catalog numbers see Table 1).

Results — Zoea I descriptions

Labuanium scandens Ng and Liu, 2003 (Figs. 1A–3B)

Dimensions: rdl: 0.77 ± 0.014 mm; cl: 0.52 ± 0.01 mm.

Carapace (Fig. 1A). Globose, smooth and without tubercles; dorsal spine present, short and curved; rostral spine present, straight and similar in length to dorsal spine; lateral spines absent; pair of setae on anterodorsal and posterodorsal regions; posterior and ventral margin without setae; eyes sessile.

Antennule (Fig. 1B). Uniramous; endopod absent; exopod unsegmented with 4 terminal aesthetascs (3 long, 1 shorter and thin) and 1 terminal seta.

Antenna (Fig. 1C). Well developed protopod almost reaching the tip of the rostral spine and bearing two unequal rows of 11–12, and 15–16 spines of different size, respectively; endopod absent; exopod elongated,

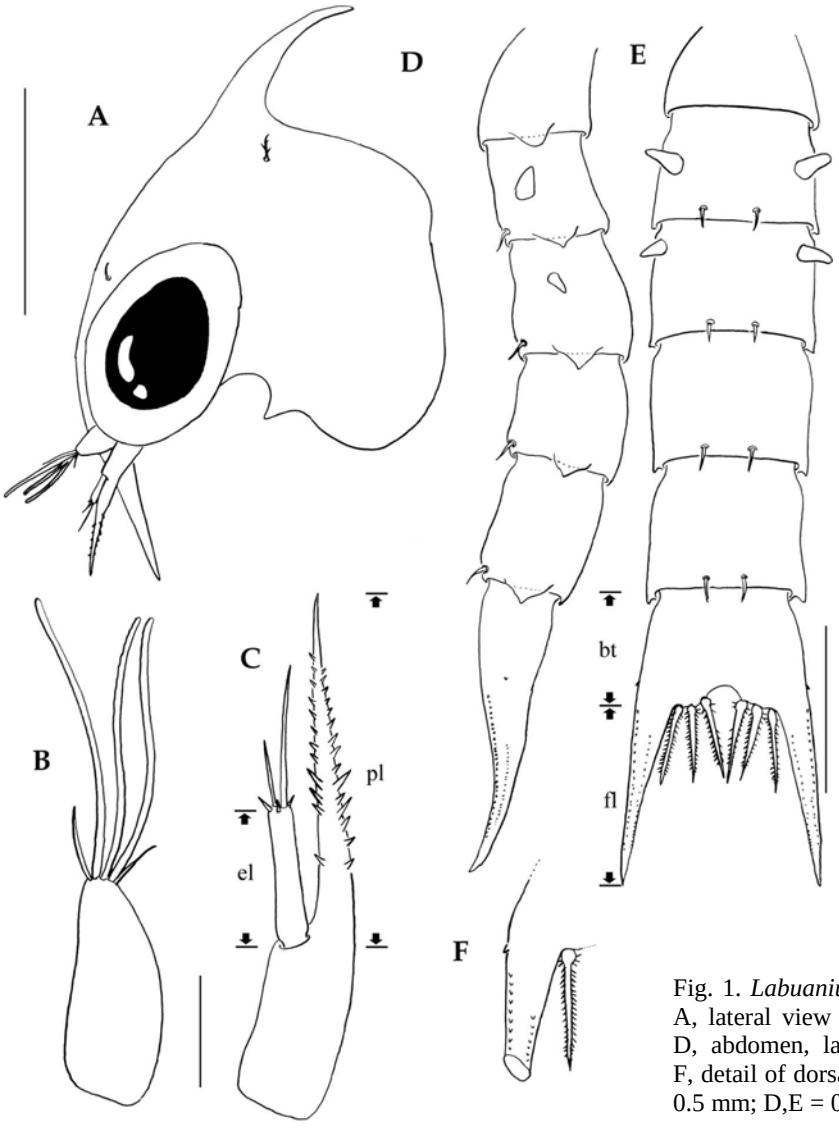

Fig. 1. *Labuanium scandens* Ng and Liu, 2003, zoea I. A, lateral view of carapace; B, antennule; C, antenna; D, abdomen, lateral view; E, abdomen, dorsal view; F, detail of dorsal area of furcal arm. Scale bars, A–C = 0.5 mm; D,E = 0.1 mm.

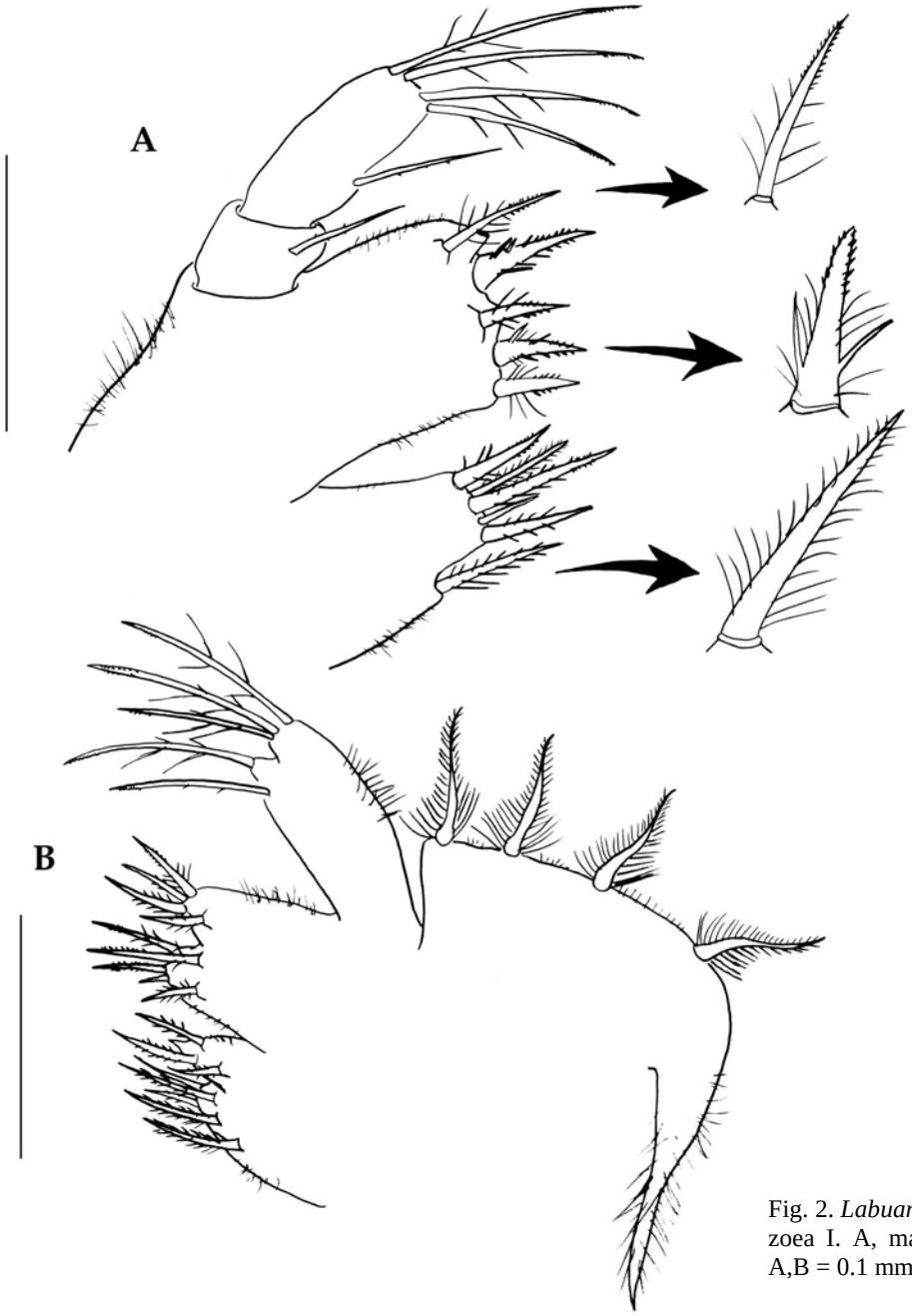

Fig. 2. *Labuanium scandens* Ng and Liu, 2003, zoea I. A, maxillule; B, maxilla. Scale bars: A,B = 0.1 mm.

more than 2/3 of the protopod length, with 2 terminal setae (1 long but not reaching the tip of protopod, 1 shorter) and 3 small terminal spines; pl/el = 2.2–2.3.

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

Maxillule (Fig. 2A). Coxal endite with 6 plumose setae; basial endite with 5 setae (2 cuspidate and 3 plumodenticulate) and 2 teeth (setal buds); endopod 2-segmented with 1 simple seta on the proximal segment and 5 (1 subterminal and 4 terminal) plumodenticulate setae on the distal segment; exopod seta absent; epipod seta absent.

Maxilla (Fig. 2B). Coxal endite bilobed with 5+3 (plus a marginal spine) plumodenticulate setae; basial endite bilobed with 5+4 plumodenticulate setae; endopod unsegmented, bilobed with 2+3 long plumodenticulate setae on the inner and outer lobe respectively; scaphognathite (exopod) with 4 plumose marginal setae and a long setose posterior process.

First Maxilliped (Fig. 3A). Coxa with 1 sparsely plumose seta; basis with 10 inner setae arranged 2 sparsely plumose + 2 sparsely plumose + 3 simple + 3 simple, and a mat of long dorsobasal microtrichiae on the outer side; endopod 5-segmented with 2 (1 simple, 1

Fig. 3. *Labuanium scandens* Ng and Liu, 2003, zoea I. A, first maxilliped; B, second maxilliped. Scale bar: A,B = 0.1 mm.

plumodenticulate), 2 (1 simple, 1 plumodenticulate), 1 plumodenticulate, 2 plumodenticulate, and 5 (1 plumose subterminal + 4 plumodenticulate terminal) setae; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Second Maxilliped (Fig. 3B). Coxa without setae; basis with 4 medial setae arranged 1 plumodenticulate + 1 simple + 1 simple + 1 simple; endopod 3-segmented with 0, 1 denticulate, 6 [3 (1 denticulate, 1 sparsely plumose, 1 simple) subterminal + 3 (2 sparsely plumose, 2 simple) terminal] setae; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Third Maxilliped. Absent.

Pereiopods. Absent.

Abdomen (Fig. 1D, E). Five abdominal somites; somites 2 and 3 with a pair of dorsolateral processes; somites 3-5 with small posterolateral processes of subtriangular shape; somites 2–5 with a pair of posterodorsal simple setae; pleopods absent.

Telson (Fig. 1F). Bifurcated with 3 pairs of serrulate setae on posterior margin; mid-internal side of inner pair without spines; dorsal part of each furcal arm with two rows of spines and outer part with shorter row of minute spines and a minute scale-like spine; fl/bt = 1.5–1.6.

Labuanium rotundatum (Hess, 1865) (Figs. 4A–E)

Dimensions: rdl: 0.80 ± 0.02 mm; cl: 0.46 ± 0.03 mm.

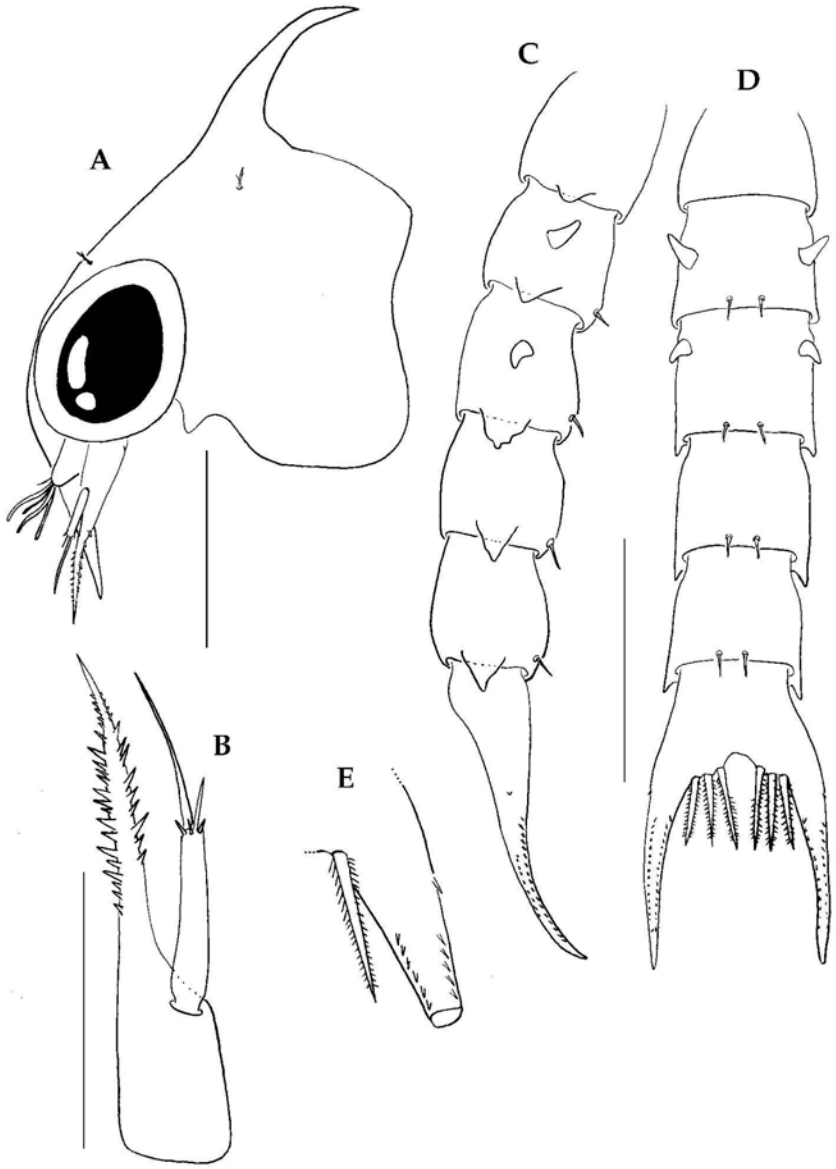

Fig. 4. *Labuanium rotundatum* (Hess, 1865), zoea I. A, lateral view of carapace; B, antenna; C, abdomen, lateral view; D, abdomen, dorsal view; E, detail of dorsal area of furcal arm. Scale bars: A,C,D = 0.25 mm; B = 0.125 mm.

Carapace (Fig. 4A). Smooth and without tubercles; dorsal spine present, short and curved; rostral spine present, straight and similar in length to dorsal spine.

Antenna (Fig. 4B). Protopod longer than rostral spine and bearing two unequal rows of 13-14 and 20-21 spines of different size, respectively; exopod elongated, more than 2/3 of the protopod length, with 2 terminal setae (1 long, 1 shorter) and 3 small terminal spines; pl/el = 2.0–2.1.

Abdomen (Fig. 4C,D). Somites 2 and 3 with a pair of dorsolateral processes; somites 3–5 with small posterolateral processes of subtriangular shape, more developed than those of *L. scandens*; somites 2–5 with a pair of posterodorsal simple setae.

Telson (Fig. 4E). Mid-internal side of inner pair without spines; dorsal part of each furcal arm with two rows of spines and outer part with a shorter row of minute spines and a minute scale-like spine; fl/bt = 1.6–1.7.

Labuanium trapezoideum (H. Milne Edwards, 1837) (Figs. 5A–E)

Dimensions: rdl: 0.81 ± 0.03 mm; cl: 0.49 ± 0.02 mm.

Carapace (Fig. 5A). Smooth and without tubercles; dorsal spine present, short and strongly curved; rostral spine present, straight and similar in length to dorsal spine.

Antenna (Fig. 5B). Protopod slightly longer than rostral spine and bearing two unequal rows of 11 and 14 spines of different size, respectively; exopod elongated, more than 2/3 of the protopod length, with 2 terminal

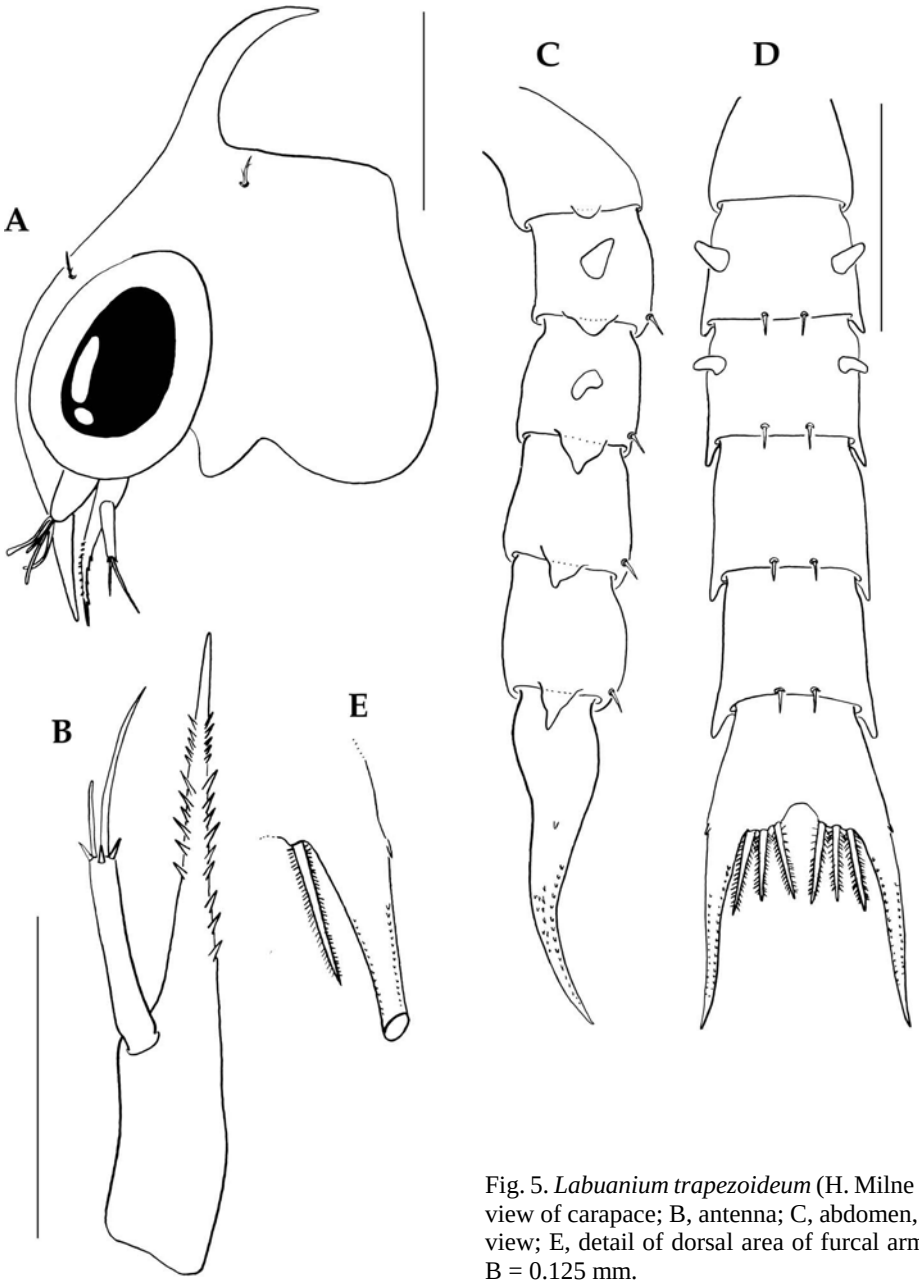

Fig. 5. *Labuanium trapezoideum* (H. Milne Edwards, 1837), zoea I. A, lateral view of carapace; B, antenna; C, abdomen, lateral view; D, abdomen, dorsal view; E, detail of dorsal area of furcal arm. Scale bars, A,C,D = 0.25 mm; B = 0.125 mm.

setae (1 long almost reaching the tip of protopod, 1 shorter) and 3 small terminal spines; pl/el = 2.0-2.1.

Abdomen (Fig. 5C, D). Somites 2 and 3 with pair of dorsolateral processes; somites 3–5 with small posterolateral processes of subtriangular shape, more developed than those of *L. scandens*; somites 2–5 with a pair of posterodorsal simple setae.

Telson (Fig. 5E). Mid-internal side of inner pair sparsely spinulate; dorsal part of each furcal arm with two rows of spines and outer part with a shorter row of minute spines and a minute scale-like spine; fl/bt = 1.4–1.5.

Labuanium politum (de Man, 1888) (Figs. 6A-E)

Dimensions: rdl: 0.85 ± 0.03 mm; cl: 0.49 ± 0.04 mm.

Carapace (Fig. 6A). Smooth and without tubercles; dorsal spine present, straight; rostral spine present, straight and similar in length to dorsal spine.

Antenna (Fig. 6B). Protopod almost reaching to the tip of the rostral spine and bearing two unequal rows of 6–7, and 12–13 spines of different size, respectively; exopod elongated, more than 2/3 of the protopod length, with 2 terminal setae (1 long, 1 shorter) and 3 small terminal spines; pl/el = 2.05–2.10.

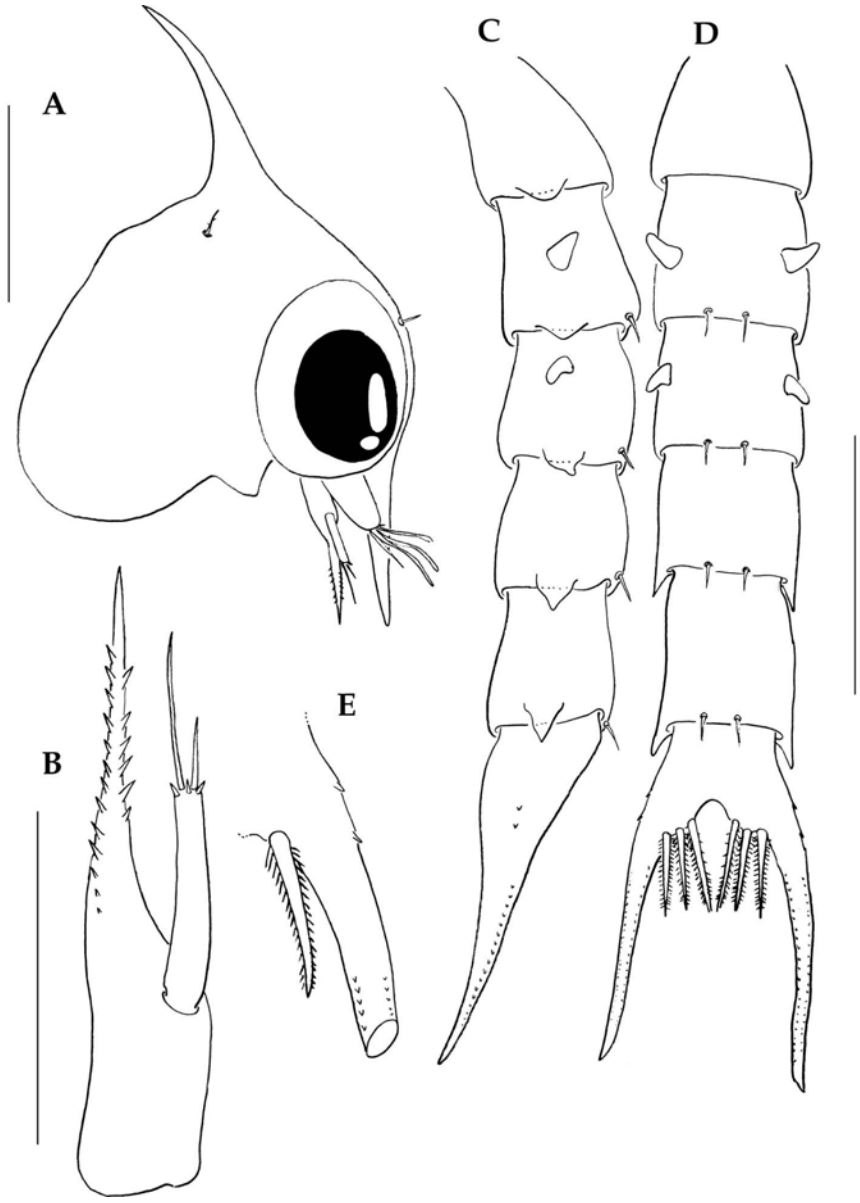

Fig. 6. *Labuanium politum* (de Man, 1888), zoea I. A, lateral view of carapace; B, antenna; C, abdomen, lateral view; D, abdomen, dorsal view; E, detail of dorsal area of furcal arm. Scale bars: A,C,D = 0.25 mm; B = 0.125 mm.

Abdomen (Fig. 6C, D). Somites 2 and 3 with pair of dorsolateral processes; somites 3–5 with small posterolateral processes with subtriangular shape; somites 2–5 with a pair of posterodorsal simple setae.

Telson (Fig. 6E). Mid-internal side of inner pair sparsely spinulate; dorsal part of each furcal arm with two rows of minute spines and outer part with two minute scale-like spine; fl/bt = 2.50–2.65.

Metasesarma aubryi A. Milne Edwards, 1869 (Figs. 7A–E)

Dimensions: rdl: 0.87 ± 0.04 mm; cl: 0.60 ± 0.01 mm.

Carapace (Fig. 7A). Smooth and without tubercles; dorsal spine present, short and curved; rostral spine present, straight and similar in length to dorsal spine.

Antenna (Fig. 7B). Protopod almost reaching to the tip of the rostral spine and bearing two unequal rows of 15–16, and 24–26 spines of different size, respectively; exopod elongated, more than 2/3 of the protopod length, with 2 terminal setae (1 long, 1 shorter) and 3 terminal spines; pl/el = 2.1–2.2.

Abdomen (Fig. 7C, D). Somites 2 and 3 with a pair of dorsolateral processes; somites 3–5 with small posterolateral processes of subtriangular shape; somites 2–5 with a pair of posterodorsal simple setae.

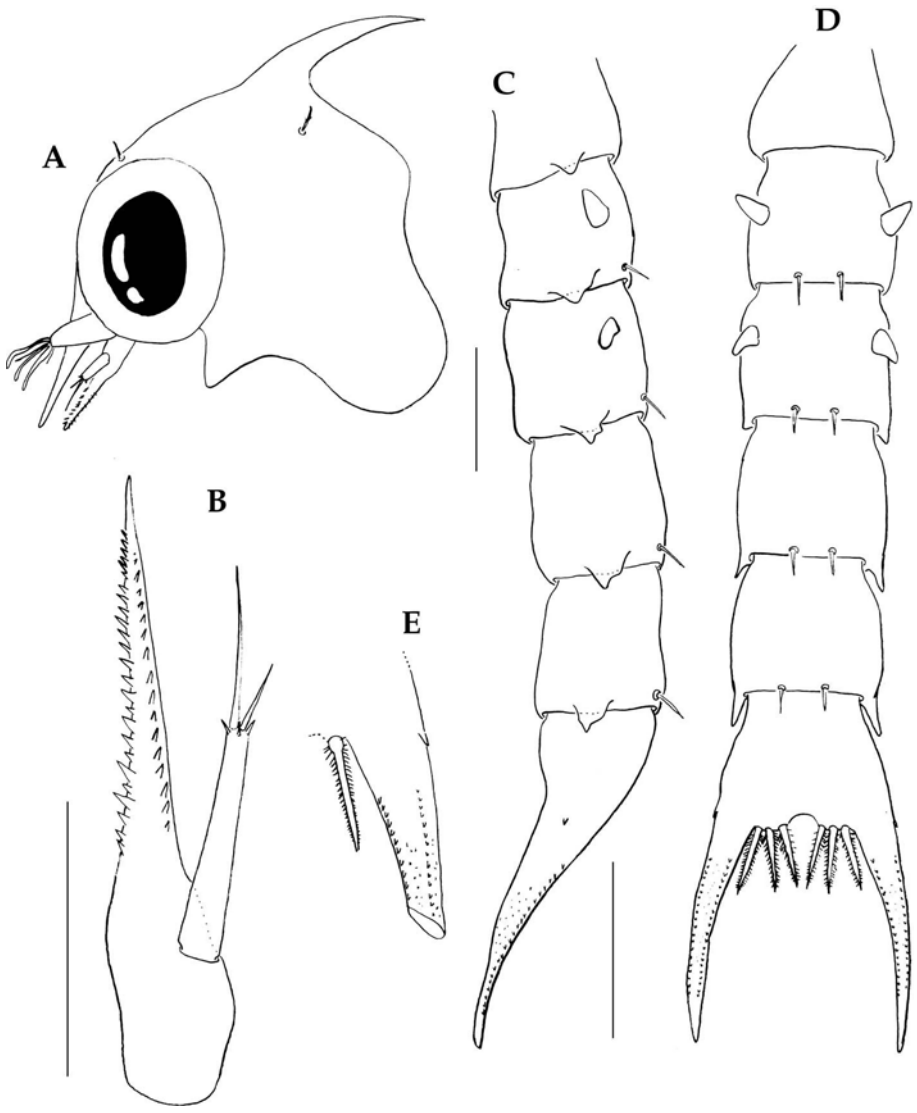

Fig. 7. *Metasesarma aubryi* A. Milne-Edwards, 1869, zoea I. A, lateral view of carapace; B, antenna; C, abdomen, lateral view; D, abdomen, dorsal view; E, detail of dorsal area of furcal arm. Scale bars: A,C,D = 0.2 mm; B = 0.1 mm.

Telson (Fig. 7E). Mid-internal side of inner pair without spines; dorsal part of each furcal arm with two rows of spines and outer part covered with minute spinules and a minute scale-like spine; fl/bt = 2.0–2.1.

Metasesarma obesum (Dana, 1851) (Figs. 8A–E)

Rajabai (1961: 160–162, Fig. III, 1–12), prezoea, zoea I (as *M. rousseauxii*).

Dimensions: rdl: 0.69 ± 0.02 mm; cl: 0.44 ± 0.02 mm (Taiwan).

Dimensions: rdl: 0.63 ± 0.02 mm; cl: 0.42 ± 0.02 mm (Sulawesi).

Carapace (Fig. 8A). Smooth and without tubercles; dorsal spine present, strongly curved (almost 90° angle); rostral spine present, straight shorter than dorsal spine.

Antenna (Fig. 8B). Protopod almost reaching to the tip of the rostral spine and bearing two unequal rows of 10–12, and 13–16 spines of different size, respectively; exopod elongated, more than 2/3 of the protopod length, with 2 terminal setae (1 long almost reaching to the tip of protopod, 1 shorter) and 2 terminal spines; pl/el = 2.10–2.26.

Abdomen (Fig. 8C, D). Somites 2 and 3 with pair of dorsolateral processes; somites 3–5 with small posterolateral processes of subtriangular shape; somites 2–5 with a pair of posterodorsal simple setae.

Telson (Fig. 8E). Mid-internal side of inner pair sparsely spinulate; dorsal part of each furcal arm with two rows of spines and covered with spinules, and outer part with 2 minute scale-like spines; fl/bt = 1.3–1.5.

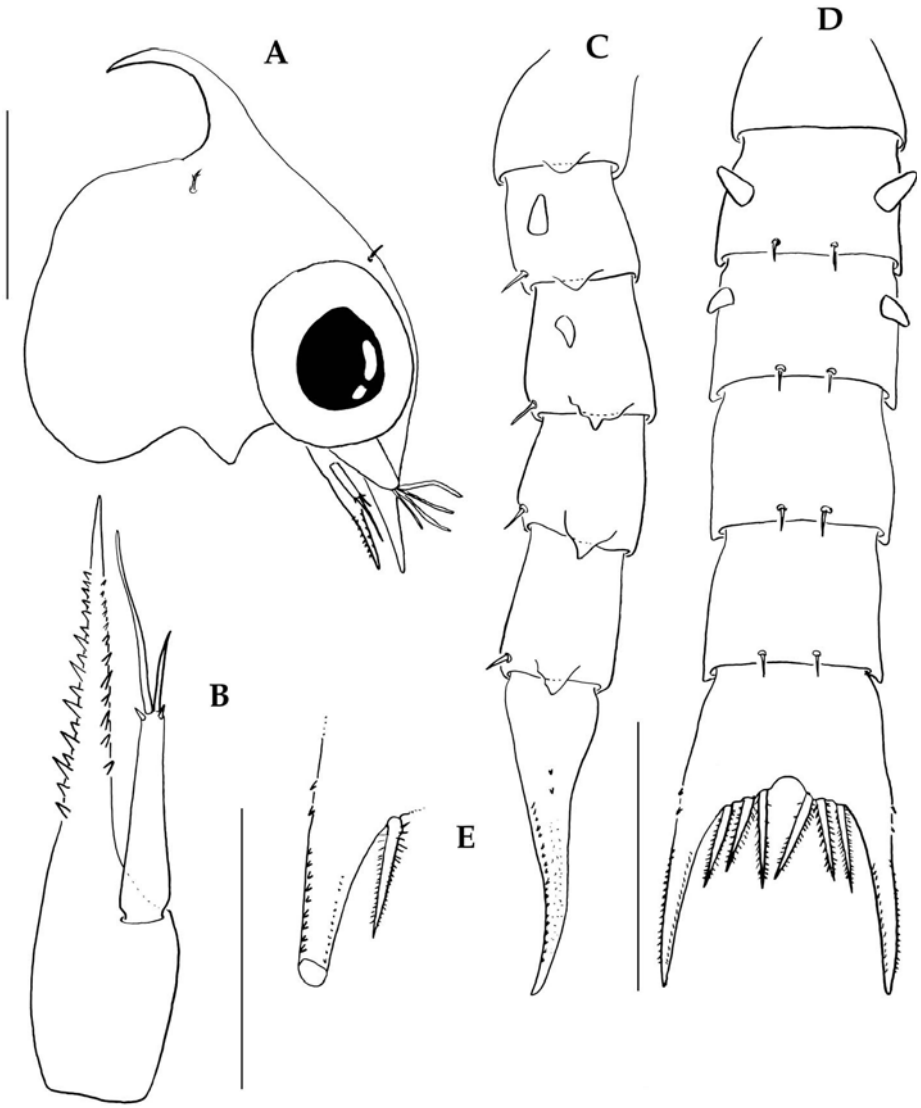

Fig. 8. *Metasesarma obesum* (Dana, 1851), zoea I. A, lateral view of carapace; B, antenna; C, abdomen, lateral view; D, abdomen, dorsal view; E, detail of dorsal area of furcal arm. Scale bars: A = 0.2 mm; C,D = 0.25 mm; B = 0.1 mm.

Pseudosesarma crassimanum (de Man, 1887) (Figs. 9A–E)

Dimensions: rdl: 0.72 ± 0.03 mm; cl: 0.43 ± 0.02 mm.

Carapace (Fig. 9A). Smooth and without tubercles; dorsal spine present, almost strait; rostral spine present, straight and similar in length to dorsal spine.

Antenna (Fig. 9B). Protopod almost reaching to the tip of the rostral spine and bearing two unequal rows of 4-5, and 6 spines of different size, respectively; exopod elongated, more than 2/3 of the protopod length, with 2 terminal setae (1 long, 1 shorter) and 3 small terminal spines; pl/el = 2.18–2.42.

Abdomen (Fig. 9C, D). Somites 2 and 3 with pair of dorsolateral processes; somites 3–4 with posterolateral processes of subtriangular shape, and posterolateral processes on somite 5 long and acute distally; somites 2–5 with a pair of posterodorsal simple setae.

Telson (Fig. 9E). Mid-internal side of inner pair sparsely spinulate; dorsal part of each furcal arm with two rows of spines and outer part without spines, only scattered minute spinules; fl/bt = 1.7–1.8.

Stelgistra stormi (de Man, 1895) (Figs. 10A–E)

Dimensions: rdl: 0.89 ± 0.01 mm; cl: 0.63 ± 0.03 mm.

Carapace (Fig. 10A). Smooth and without tubercles; dorsal spine present, short and curved; rostral spine present, straight and longer than dorsal spine.

Antenna (Fig. 10B). Protopod almost reaching to the tip of the rostral spine and bearing two unequal rows of 13–14, and 23–24 spines of different size, respectively;

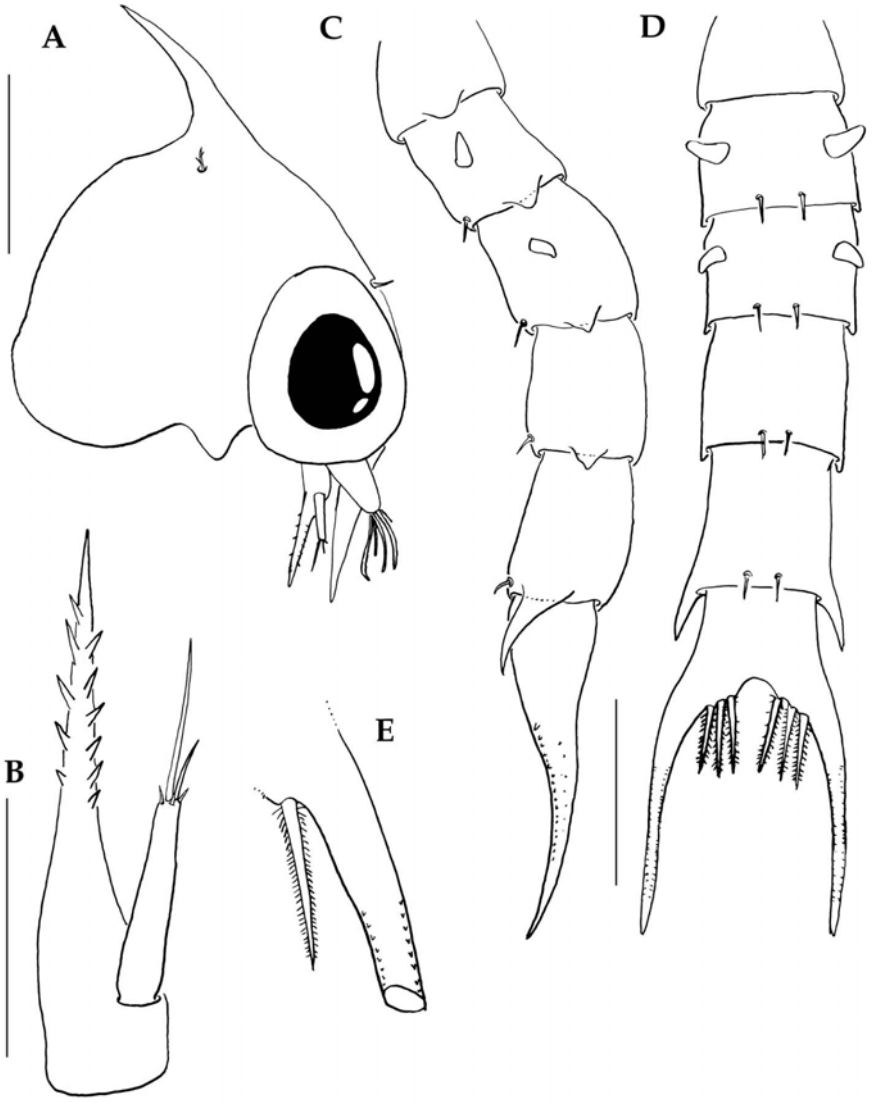

Fig. 9. *Pseudosesarma crassimanum* (de Man, 1887), zoea I. A, lateral view of carapace; B, antenna; C, abdomen, lateral view; D, abdomen, dorsal view; E, detail of dorsal area of furcal arm. Scale bars: A,C,D = 0.2 mm; B = 0.125 mm.

exopod elongated, more than 2/3 of the protopod length, with 2 terminal setae (1 long, 1 shorter) and 3 small terminal spines; pl/el = 2.0–2.2.

Abdomen (Fig. 10C, D). Somites 2 and 3 with pair of dorsolateral processes; somites 3–5 with small rounded posterolateral processes; somites 2–5 with a pair of posterodorsal simple setae.

Telson (Fig. 10E). Mid-internal side of inner pair sparsely spinulate; dorsal part of each furcal arm with two rows of minute spines and outer part without spines; fl/bt = 1.2–1.3.

Clistocoeloma merguiense de Man, 1888 (Figs. 11A-E)

Saba (1972: 25, Figs. 1, 2a, 3a, 4a).

Dimensions: rdl: 0.61 ± 0.01 mm; cl: 0.39 ± 0.04 mm.

Carapace (Fig. 11A). Smooth and without tubercles; dorsal spine present, short and curved; rostral spine present, straight and shorter in length to dorsal spine.

Antenna (Fig. 11B). Protopod longer than the rostral spine and bearing two unequal rows of 6, and 11-12 spines of different size, respectively; exopod elongated, more than 2/3 of the protopod length, with 2 terminal setae (1 long almost reaching to the tip of protopod, 1 shorter) and 3 small terminal spines; pl/el = 2.0–2.1.

Abdomen (Fig. 11C, D). Somites 2 and 3 with pair of dorsolateral processes; somites 3–5 with small posterolateral processes of subtriangular shape; somites 2–5 with a pair of posterodorsal simple setae; pleopods absent.

Telson (Fig. 11E). Mid-internal side of inner pair

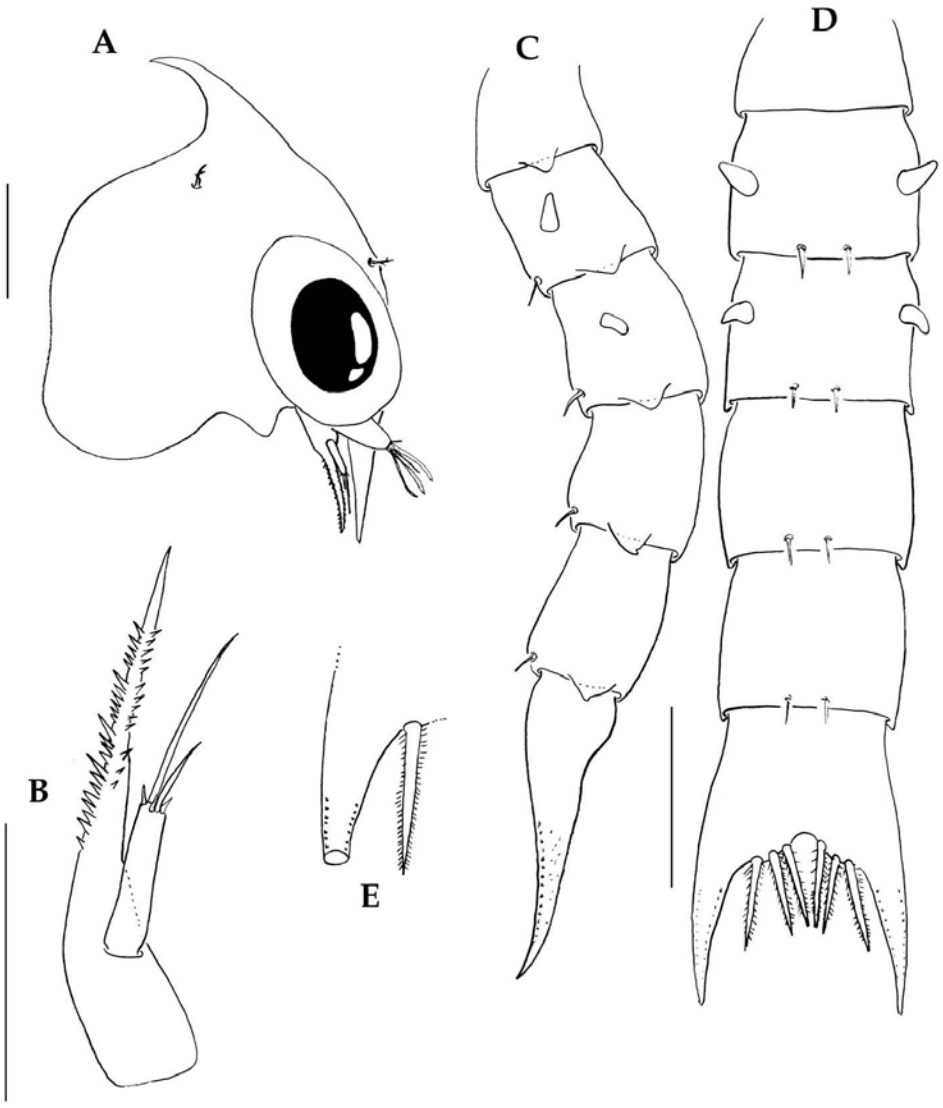

Fig. 10. *Stelgistra stormi* (de Man, 1895), zoea I. A, lateral view of carapace; B, antenna; C, abdomen, lateral view; D, abdomen, dorsal view; E, detail of dorsal area of furcal arm. Scale bars: A,C,D = 0.2 mm, B = 0.125 mm.

without spines; dorsal part of each furcal arm with two rows of spines and outer part with a shorter row of minute spines and a minute scale-like spine; fl/bt = 1.5–1.6.

Sesarmops impressum (H. Milne Edwards, 1837) (Figs. 12A–E)

Dimensions: rdl: 0.80 ± 0.01 mm; cl: 0.45 ± 0.01 mm.

Carapace (Fig. 12A). Smooth and without tubercles; dorsal spine present, straight; rostral spine present, straight and similar in length to dorsal spine.

Antenna (Fig. 12B). Protopod, slightly longer than rostral spine and bearing two unequal rows of 5–6, and 7–8 spines of different size, respectively; exopod elongated, more than 2/3 of the protopod length, with 2 terminal setae (1 long reaching the tip of protopod, 1 shorter) and 3 small terminal spines; pl/el = 2.8–2.9.

Abdomen (Fig. 12C, D). Somites 2 and 3 with pair of dorsolateral processes; somites 3–5 with small posterolateral processes of subtriangular shape; somites 2–5 with a pair of posterodorsal simple setae.

Telson (Fig. 12E). Mid-internal side of inner pair without spines; dorsal part of each furcal arm with two rows of spines and outer part with a shorter row of minute spines and a minute scale-like spine; fl/bt = 1.5–1.7.

Sesarmops intermedium (de Haan, 1835) (Figs. 13A–E)

Baba and Fukuda (1975: 63–64, Fig. 1) (as *Sesarma*

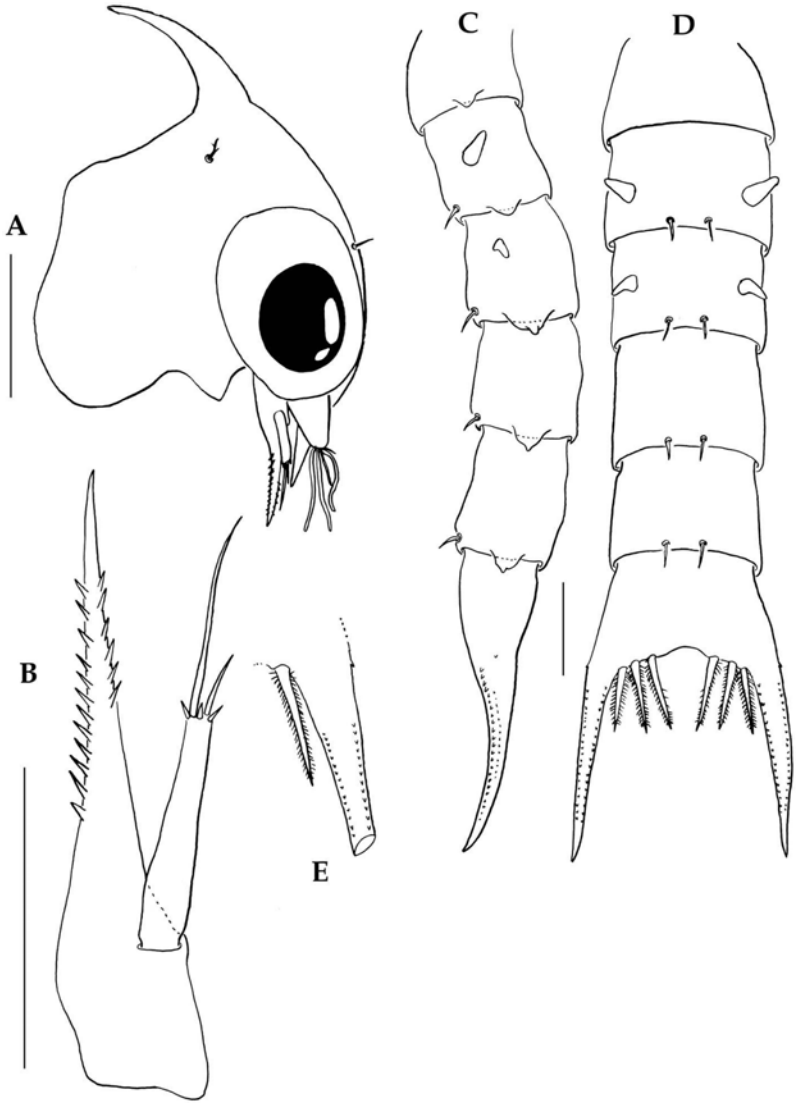

Fig. 11. *Clistocoeloma merguiense* de Man, 1888, zoea I. A, lateral view of carapace; B, antenna; C, abdomen, lateral view; D, abdomen, dorsal view; E, detail of dorsal area of furcal arm. Scale bars: A = 0.2 mm; C,D = 0.1 mm; B = 0.125 mm.

intermedium); Fukuda and Baba (1976: 63, Fig 5f) (as *Sesarmops intermedius*); Terada (1976: 143–148, Figs. 5A1, B1, C1, D1, 6E1, F1, G1, H1) (as *Sesarmops intermedia*).

Dimensions: rdl: 0.75 ± 0.05 mm; cl: 0.42 ± 0.02 mm.

Carapace (Fig. 13A). Smooth and without tubercles; dorsal spine present, slightly curved; rostral spine present, straight and similar in length to dorsal spine.

Antenna (Fig. 13B). Protopod almost reaching to the tip of the rostral spine and bearing two unequal rows of 4–5, and 7–8 spines of different size, respectively; exopod elongated, less than 1/4 of the protopod length, with 2 terminal setae (1 long reaching the tip of protopod, 1 shorter) and 2 small terminal spines; pl/el = 4.9–5.0.

Abdomen (Fig. 13C, D). Somites 2 and 3 with a pair of dorsolateral processes; somites 3–5 with postero-lateral processes of subtriangular shape, those of somites 4 and 5 more developed; somites 2–5 with a pair of postero-dorsal simple setae.

Telson (Fig. 13E). Mid-internal side of inner pair without spines; dorsal part of each furcal arm with two rows of spines and outer part with scattered minute spines and a minute scale-like spine; fl/bt = 1.6–1.7.

Discussion

The first zoeal stage morphology of the eleven species from the present study and the previously described sesarmids is similar. Larval morphology of

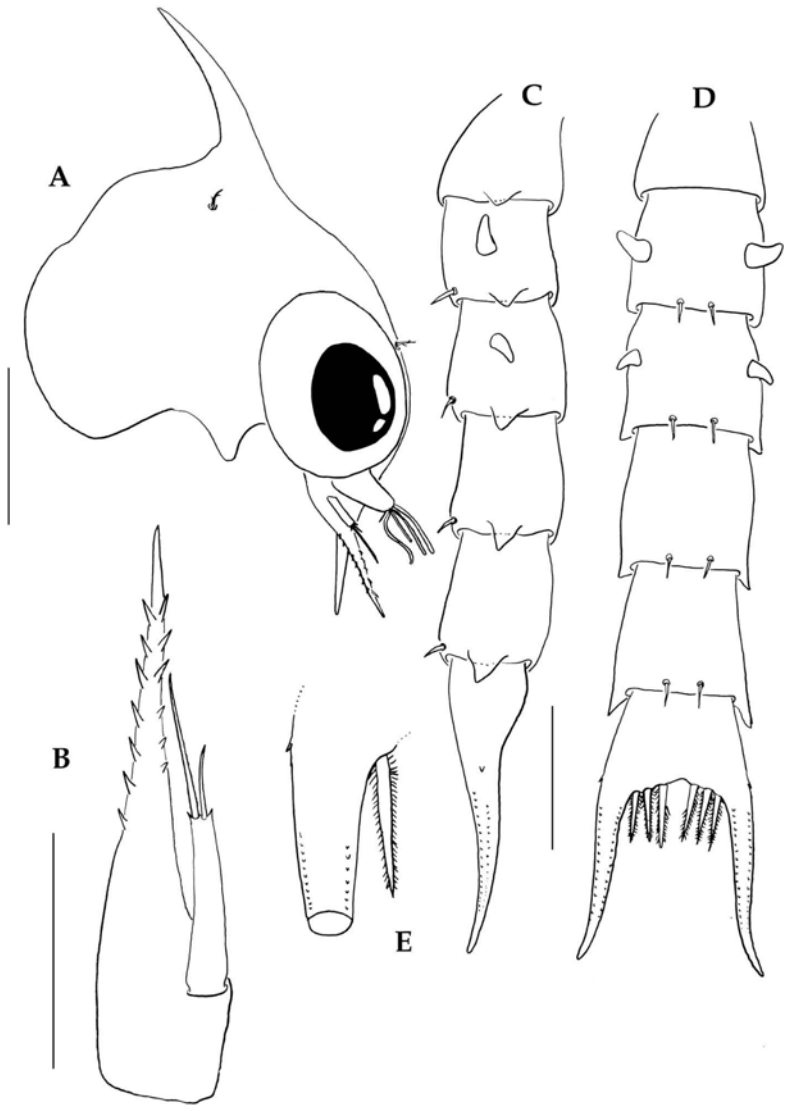

Fig. 12. *Sesarmops impressum* (H. Milne Edwards, 1837), zoea I. A, lateral view of carapace; B, antenna; C, abdomen, lateral view; D, abdomen, dorsal view; E, detail of dorsal area of furcal arm. Scale bars: A,C,D = 0.2 mm; B = 0.125 mm.

the Sesarmidae in general presents little variation between species and genera; the carapace, antennule, mouthparts, and abdomen do not vary in number of setae. The main differences were only found in carapace spinulation, antennal type, abdomen and telson morphology and armature (see Schubart and Cuesta, 1998; Cuesta et al., 1999; Figs. 1, 4–13 of present study). These differences allow, in some cases, identification of first zoeal stages to species, but the homogeneity of larvae often renders it difficult to characterise them to genus level.

In this study, the first zoeal stage of species belonging to *Labuanium*, *Stelgistra*, and *Pseudosesarma* are described for the first time. They do not present any diagnostic characters that would facilitate their identification to genus level. In this study, the first zoeae of *Clistocoeloma merguiense*, *Metasesarma obesum* and *Sesarmops intermedium* are re-described and new characters are presented. A comparison with previous descriptions are summarised in Table 2. In Table 3, a comparison among the eleven first zoeal stages described in this study time is presented. Differences are mostly found in the antennal spinulation and exopod length (ratio pl/el), dorsal carapace spine morphology (from strongly curved to almost strait), and telson armature and furcal length (measured as ratio fl/bt). Among the observed differences is the size of the antennal exopod of *Sesarmops intermedium*, which is highly reduced when compared to that of *S. impressum* (pl/el 4.9–5 vs. 2.8–2.9). This difference surpasses the

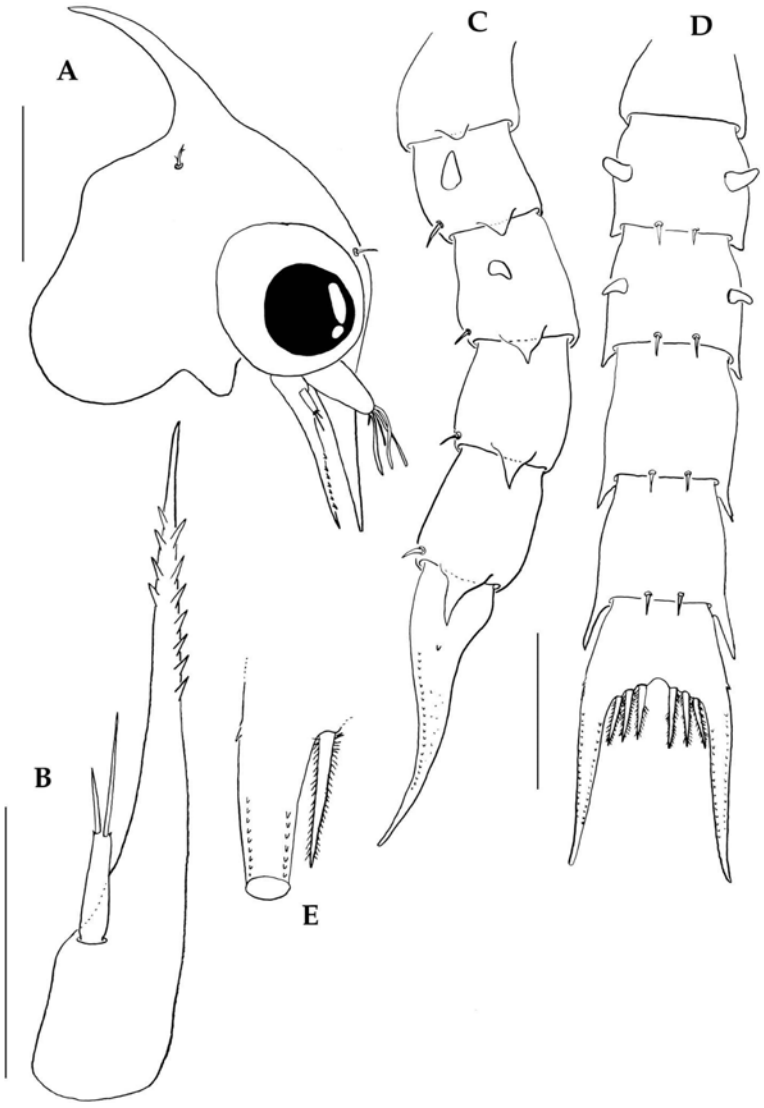

Fig. 13. *Sesarmops intermedium* (de Haan, 1835), zoea I. A, lateral view of carapace; B, antenna; C, abdomen, lateral view; D, abdomen, dorsal view; E, detail of dorsal area of furcal arm. Scale bars: A,C,D = 0.2 mm; B = 0.125 mm.

expected variation for congeneric species and questions the placement of these two species within the same genus. This confirms the unpublished findings of Schubart and Cuesta based on larval morphology and mitochondrial DNA, which suggested that *S. intermedium* was closer to *Chiromantes* than to *Sesarmops impressum* (type species of the genus).

This study discloses a character never previously described for sesarmid zoea: the presence of one or two scale-like outer minute spines on the telson furcae. These minute spines have been observed in all studied species with the exception of *Pseudosesarma crassimanum* and *Stelgistra stormi*. Careful re-examination of previously described sesarmids also revealed the presence of these spines in all zoeal stages of *Aratus pisonii* (Cuesta et al., 2006), *Perisesarma fasciatum*, *Armases angustipes*, and *A. miersii*, and in zoeal stages of *Armases ricordi* (Z I–III), *A. cinereum* (Z I), *A. rubripes* (Z I), *Sesarma rectum*, *S. reticulatum*, *S. rhizophorae*. These spines were not present in *Sesarma curacaoense*, a species with abbreviated development. In zoea I of *Sesarma rubinofforum* and *Scandarma lintou*, the spines could not be observed clearly, so we cannot confirm their presence or absence. Due to the minute size of these spines, new studies with scanning electron microscopy will be needed to clarify the detailed morphology of these structures and to confirm their presence in other species.

Table 2. Comparison of morphological and meristic features between previous and present descriptions of the first zoeal stage of re-described species, *Clistocoeloma merguiense* (CLMER), *Metasesarma obesum* (MEOBE), and *Sesarmops intermedium* (SEINT). Abbreviations: ps, present study; a, aesthetascs; s., setation, s, seta/e; sp, spine/s; pp, posterior process, (-) equal to present description

	CLMER (Saba, 1972)	CLMER (ps)	MEOBE (Rajabai, 1961)	MEOBE (ps)	SEINT (Baba and Fukuda, 1975)	SEINT (Fukuda, and Baba, 1976)	SEINT (Terada, 1976)	SEINT (ps)
Carapace								
Anterodorsal s.	No data	1 pair	No data	1 pair	No data	No data	No data	1 pair
Dorsolateral s.	No data	1 pair	No data	1 pair	No data	No data	No data	1 pair
Antennule								
Protopod	3a	4a. 1s	3a	4a, 1s	4a	4a	-	4a, 1s
Antenna								
Exopod	2s	2s, 3 sp	2s	2s, 3 sp	1s	2s	2s	2s, 2 sp
Maxillule								
Coxal endite s.	No data	6	3	6	-	5	5	6
Basial endite s.	No data	5	2	5	-	-	-	-
Endopod	No data	1, 1+4	-	-	-	-	-	-
Maxilla								
Coxal endite s.	No data	5 + 3	2 + 2	5 + 3	5	4 + 3	-	5 + 3
Basial endite s.	No data	5 + 4	4 + 4	5 + 4	-	-	-	-
Endopod s.	No data	2 + 3	2 + 2	2 + 3	-	-	-	-
Scaphognathite	No data	4 s + pp	-	-	-	-	-	-
First maxilliped								
Basis s.	No data	2+2+3+3	1+1+2+2	2+2+3+3	No data	-	-	2+2+3+3
Endopod	No data	2,2,1,2,5	0,1,1,2,4	2,2,1,2,5	-	-	-	-
Second maxilliped								
Basis s.	No data	1+1+1+1	-	-	No data	1+1+1+1	-	1+1+1+1
Endopod	1, 0, 5	0, 1, 6	0, 1, 4	0, 1, 6	-	-	-	-
Abdomen								
Dorsolateral processes	somite 2	somites 2–3	-	-	-	-	-	-
Telson								
Outer minute spines	No data	1 pair	No data	2 pairs	No data	No data	No data	1 pairs

Table 3. Comparison of morphological and meristic features of the first zoeal stages described in the present study. Abbreviations: Plp, posterolateral process; fl, furcal length; bt, base of telson length. In brackets the variation in the number of spines for each row on antennal protopod

Species			Telson	
	Antennal protopod # spines	Abdomen Plp 5th somite	# scale-like spines	fl/bt
Labuanium scandens	(11–12) (15–16)	Not elongated	1	1.5–1.6
Labuanium rotundatum	(13–14) (20–21)	Elongated	1	1.6–1.7
Labuanium trapezoideum	(11) (14)	Elongated	1	1.4–1.5
Labuanium politum	(6–7) (12–13)	Not elongated	2	2.5–2.65
Metasesarma aubryi	(15–16) (24–26)	Not elongated	1	2–2.1
Metasesarma obesum	(10–12) (13–16)	Not elongated	2	1.3–1.5
Pseudosesarma crassimanum	(4–5) (6)	Elongated	0	1.7–1.8
Stelgistra stormi	(13–14) (23–24)	Not elongated	0	1.2–1.3
Clistocoeloma merguiense	(6) (11–12)	Not elongated	1	1.5–1.6
Sesarmops impressum	(5–6) (7–8)	Not elongated	1	1.5–1.7
Sesarmops intermedium	(4–5) (7–8)	Not elongated	1	1.6–1.7

Table 4. Sesarmidae species for which larvae have been described, including the number of described larval stages and authors. Abbreviations: *, papers not examined; (-),data not accessible

Species	Larval stages described	Authors
Aratus pisonii	Prezoea–Zoea I	Hartnoll, 1965
	Zoea I–IV–megalopa	Warner, 1968
	Zoea I	Fransozo et al., 1998
	Zoea I–IV–megalopa	Cuesta et al., 2006
Armases angustipes	Zoea I–IV–megalopa	Kowalczuk, 1994
	Zoea I–IV–megalopa	Cuesta and Anger, 2001
Armases cinereum	Zoea I	Hyman, 1924
	Zoea I–IV–megalopa	Costlow and Bookhout, 1960
Armases magdalenense	Megalopa	Rathbun, 1923
Armases miersii	Zoea I–III–megalopa	Cuesta et al., 1999
Armases ricordi	Zoea I–IV–megalopa	Díaz and Ewald, 1968
	Zoea I	Schubart and Cuesta, 1998
Armases rubripes	Zoea I–IV–megalopa	Díaz and Ewald, 1968
	Zoea V	Montú et al., 1990
	Zoea I	Schubart and Cuesta, 1998
Beanium andersoni	Zoea I–IV	Vijayakumar and Kannupandi, 1986
Bresedium brevipes	Zoea I–IV–megalopa	Fielder and Greenwood, 1983
Chiromantes dehaani	Zoea I–IV[(1)]–megalopa	Yatsuzuka, 1957*
	(–)	Terada, 1974*
	Zoea I–IV–megalopa	Baba and Miyata, 1971
	Zoea I	Muraoka, 1979a*
Chiromantes eulimene	Zoea I–V	Pereyra Lago, 1993a
	Zoea I	Flores et al., 2003
Chiromantes haematocheir	Zoea I–V–megalopa	Terada, 1974
	Zoea I–V[(2)]–megalopa	Fukuda and Baba, 1976
	Zoea I	Muraoka, 1979a*
	Megalopa	Muraoka, 1980*
Clistocoeloma lanatum	Zoea I–IV–megalopa	Kakati and Sankolli, 1975
Clistocoeloma merguiense	Zoea I–III	Saba, 1972
	Zoea I	present study
Episesarma lafondi	Zoea I–IV–megalopa	Islam et al., unpublished data
Episesarma mederi	(–)	Selvakumar, 1988*
Geosesarma notophorum	Direct development	Ng and Tan, 1995
Geosesarma peraccae	Zoea I–II–"megalopa"	Soh, 1969
Labuanium politum	Zoea I	Present study
Labuanium rotundatum	Zoea I	Present study
Labuanium scandens	Zoea I	Present study
Labuanium trapeZoideum	Zoea I	Present study
Metasesarma aubryi	Zoea I	Present study
Metasesarma obesum	Prezoea–zoea I	Rajabai, 1961
	Zoea I	Present study
Metopaulias depressus	Zoea I–II–megalopa	Hartnoll, 1964
Muradium tetragonum	Prezoea–zoea I	Rajabai, 1961
	(–)	Sundaramoorthy, 1987*
Nanosesarma gordoni	Zoea I–V	Fukuda, 1978
	Zoea I	Muraoka, 1979b*
	Zoea I–V	Terada, 1982
Nanosesarma minutum	Zoea I	Fukuda, 1978
Neosarmatium indicum	Zoea I–V–megalopa	Islam et al., 2002
Neosarmatium meinerti	Zoea I–V–megalopa	Pereyra Lago, 1989
	Zoea I	Flores et al., 2003
Neosarmatium trispinosum	Zoea I	Greenwood and Fielder, 1988
	Zoea I–V–megalopa	Islam et al., 2004
Parasesarma acis	Zoea I	Baba and Fukuda, 1975

Table 4, continued

Species	Larval stages described	Authors
Parasesarma acis	Zoea I–IV–megalopa	Terada, 1976
	Megalopa	Muraoka, 1980*
Parasesarma batavicum	(–)	Selvakumar, 1988*
Parasesarma catenatum	Zoea I–IV–megalopa	Pereyra Lago, 1987
	Zoea I	Flores et al., 2003
Parasesarma erythrodactylum	Zoea I	Green and Anderson, 1973
	Zoea I–V–megalopa	Greenwood and Fielder, 1988
Parasesarma leptosoma	Zoea I	Flores et al., 2003
Parasesarma pictum	(–)	Terada, 1974*
	Zoea I–IV–megalopa	Pasupathi and Kannupandi, 1987
	Zoea I	Muraoka, 1979a*
	Megalopa	Muraoka, 1980
Parasesarma plicatum	Zoea I	Baba and Fukuda, 1975
	Zoea I–IV–megalopa	Fukuda and Baba, 1976
	Zoea I–V–megalopa	Selvakumar, 1999
Perisesarma bidens	Zoea I–IV–megalopa	Terada, 1976
	Zoea I–IV–megalopa	Fukuda and Baba, 1976
	Zoea I–IV–megalopa	Krishnan and Kannupandi, 1987
	Zoea I–IV–megalopa	Islam and Shokita, 2000
Perisesarma fasciatum	Zoea I–IV–megalopa	Guerao et al., 2004
Perisesarma guttatum	Zoea I–V[(3)]–megalopa	Pereyra Lago, 1993b
	Zoea I	Flores et al., 2003
Perisesarma messa	Zoea I	Greenwood and Fielder, 1988
Pseudosesarma crassimanum	Zoea I	Present study
Sarmatium crassum	Zoea I	Flores et al., 2003
Scandarma lintou	Zoea I	Schubart et al., 2003
Selatium brockii	Zoea I–IV–megalopa	Vijayakumaran and Kannupandi, 1987
Sesarma aequatoriale	Zoea I	Schubart and Cuesta, 1998
Sesarma bidentatum	Prezoea–Zoea I	Hartnoll, 1964
Sesarma curacaoense	Zoea I–II–megalopa	Anger et al., 1995
	Zoea I	Schubart and Cuesta, 1998
Sesarma rectum	Zoea I–III–megalopa	Fransozo and Hebling, 1986
Sesarma reticulatum	Zoea I	Hyman, 1924
	Zoea I–III–megalopa	Costlow and Bookhout, 1962
Sesarma rhizophorae	Zoea I	Schubart and Cuesta, 1998
Sesarma rubinofforum	Zoea I	Schubart and Cuesta, 1998
Sesarma sp.	Zoea I	Aikawa, 1929
Sesarmops impressum	Zoea I	Present study
Sesarmops intermedium	Zoea I	Baba and Fukuda, 1975
	Zoea I–V–megalopa	Terada, 1976
	Zoea I–V–megalopa	Fukuda and Baba, 1976
	Zoea I	Present study
	Zoea I	Muraoka, 1979a*
Stelgistra stormi	Zoea I	Present study

Notes: (1) sometimes presents a zoeal V stage; (2) zoea IV and zoea V can moult to megalopa; (3) sometimes presents a zoeal VI stage, but do not moult to megalopa.

This type of telson spinulation has also been observed in other Grapsoidea, viz. Glyptograpsidae (*Glyptograpsus impressus* and *Platychirograpsus spectabilis*) (see Schubart et al., 2002) and in two genera of the Gecarcinidae (*Cardisoma armatum*, *C. carnifex*, *C. guanhumi* and *Discoplax hirtipes*) (see Cuesta et al., 2002; Flores et al., 2003; Cuesta and Anger, 2005). A possible relationship of Sesarmidae with *Cardisoma* and *Discoplax* has been suggested previously by Cuesta et al. (2002) based on the following shared larval features: antennal and telson morphology, and maxillar setation (2 + 3), but differing in second maxilliped endopod

Table 5. Zoeal morphological and meristic characters of the families Sesarmidae, Varunidae, Grapsidae, Plagusiidae, Glyptograpsidae and Gecarcinidae. Abbreviations: (–), absent; (+), present; Antenna type A refers to exopod equal to 1/4-2/3 of protopod length, with 2 unequal-sized simple terminal setae and 2–5 terminal short spines; B refers to exopod less than 1/2 of protopod length, with 2 simple terminal setae; C refers to exopod well developed, more than 1/2 protopod length with 0–2 medial setae; and D refers to exopod absent or reduced to a small protuberance with one terminal simple seta. Telson type A refers to a furca with or without minute outer spines, but always with 3 pairs of posterior processes throughout development; B refers to furca with or without minute outer spines, but with the number of pairs of posterior processes increasing throughout development

	Carapace lateral spines	Antenna type	Maxilla endopod	First maxilliped		Second maxilliped endopod	Telson type
				Basis	Endopod 1st seg. s.		
Gecarcinidae Macleay, 1838	(+)	A	2, 2/ 2, 3	2, 2, 3, 3	2	1, 1, 6	B
Glyptograpsidae Schubart, Cuesta and Felder, 2002	(+)	A	1, 2	2, 2, 3, 3	2	0, 1, 6 / 1, 1, 6	B
Grapsidae Macleay, 1838	(–)/(+)	D	2, 2	2, 2, 2, 2	1	0, 1, 5	B
Plagusiidae Dana, 1851	(+)	B	2, 3	2, 2, 2, 2	2	1, 1, 6	B
Sesarmidae Dana, 1851	(–)	A	2, 3	2, 2, 3, 3	2	0, 1, 6	A
Varunidae H. Milne Edwards, 1853	(–)/(+)	C	2, 2	2, 2, 3, 3	2	0, 1, 6	B

Table 6. Megalopal morphological and meristic characters of the families Gecarcinidae, Grapsidae, Plagusiidae, Sesarmidae, and Varunidae. Abbreviations: (–), absent; (+), present; m, marginal setae; l, lateral setae (presented as anterior-posterior)

	Antennule endopod	Antenna no. of segments	Mandible palp setation	Maxilla scaphognatite setation	Second maxilliped epipodite	Pleopod cincinuli	Uropod setation
Gecarcinidae	(+)	9–10	0–2, 7–11	(60–85) m, (3/4–0/1/2) l	(–)	3–4	0–5, 12–17
Grapsidae	(+)	11	0, 7–15	(58–86) m, (3–1) l	(+)	3–6	0–3, 13–23
Plagusiidae	(+)	11	0, 1–4, 15–30	(73–134) m, (5–6) l	(+)	8–17	5–9, 27–33
Sesarmidae	(-)	8–9	0, 4	(25–50) m, (2–0/1) l	(–)	2	1, 5–7
Varunidae	(+)	10	0, 5–13	(39–90) m, (3–2) l	(+)	3	1, 8–13

setation (0, 1, 6 vs 1, 1, 6) and lateral carapace spines (absent vs present). Close phylogenetic relationship of these taxa has not been confirmed to date by molecular systematics, though a possible sister group relationship between Glyptograpsidae and Sesarmidae was weakly supported in the phylogeny of Schubart et al. (2000), but not in Schubart et al. (2002).

The Varunidae do not present outer spines on the telson (Cuesta et al., 2000), but in Plagusiidae, Grapsidae, and *Gecarcoidea lalandii*, *Epigrapsus notatus*, *E. politus* (Gecarcinidae) they are well developed.

Complete or partial larval development is now known for only 23 Sesarmidae genera (ca. 75% of the sesarmid genera) and 54 species (ca. 25% of the species) (see Table 4). This is the case for zoeal stages, but megalopae are known from only 12 genera (*ca*. 40% of sesarmid genera). However, although no larval descriptions are available for *Episesarma*, *Haberma*, *Metagrapsus*, *Namlacium*, *Neosesarma*, *Sesarmoides*, and *Tiomanum* it is possible to propose a suite of characters that define sesarmid larvae similar to the general larval characters established for other grapsoid families (Cuesta et al., 1997, Cuesta and Schubart, 1997, 1999, Cuesta et al., 2000, Schubart et al., 2002, Cuesta et al., 2002; Cuesta and Anger, 2005).

These sesarmid zoeal characters are:

(1) Carapace without lateral spines. Zoea I with a pair of anterodorsal setae.

(2) Antennal exopod with terminal small spines and setae of different size. Exopod with variable length, commonly between 1/4 and 2/3 of the protopod length. Protopod with well developed spines distributed in two rows, normally with unequal number of spines.

(3) Maxillar endopod bilobed with 2+3 setae.

(4) First maxilliped basis with 2+2+3+3 setae. Endopod setation 2, 2, 1, 2, 5 in the first zoea. Through development the segments 2 and 5 acquire one seta each, and likewise another one in segment 3. The last zoeal stages present a setation 2, 2, 2, 2, 6 or more frequently 2, 3, 2, 2, 6.

(5) Second maxilliped basis with 1+1+1+1 setae. Endopod setation 0, 1, 6.

(6) Abdomen 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.

(7) Telson with 3 serrulate setae on posterior margin throughout development. Furcal arms with two dorsal rows of spinules of varying size.

Sesarmid megalopal characters:

(1) Carapace longer than broad. Rostrum ventrally deflected (approximately 70º) with a medial cleft.

(2) Antennule endopod absent.

(3) Antennal peduncle 3-segmented and flagellum with 5 or 6 segments.

(4) Mandibular palp 2-segmented with 4 setae on distal segment.

(5) Maxillar scaphognathite with less than 40 marginal plumose setae, and with 2 anterior and 1 posterior lateral setae.

(6) First maxilliped epipod with a maximum of 7 setae.

(7) Second maxilliped epipod absent or in a few cases rudimentary and without setae.

(8) Pleopod exopods with 7-14 plumose setae and two cincinuli on endopod.

(9) Uropods with setation 1,5, 1,6 or 1,7.

The number of zoeal stages in sesarmid species varies from 5 as in *Neosarmatium trispinosum* and *Perisesarma guttatum*, to 4 (typical) as in *Aratus pisonii*, *Armases angustipes* and *Parasesarma catenatum*, 3 as in *Sesarma reticulatum* and Armases miersii, 2 as in *Metopaulias depressus* and *Sesarma curacaoense*, and direct development as in *Geosesarma notophorum* (see Table 4). A similar case of variability in the number of zoeal stages has been described by Clark (2005) for the Pilumninae.

All grapsoid larval stages can be identified to family level by the combination of the zoeal and megalopal features listed in Tables 5 and 6 with the exception of Glyptograpsidae for which the megalopae are unknown. Although sesarmid zoeae tend to be larger than those of other families, their megalopae are the smallest ones among the Grapsoidea. Decrease in megalopa size goes along with the reduction in the appendage setation and the reduction and loss of structures such as antennular endopod or the second maxilliped epipodite (see Table 6), but not the reduction of segmentation (i.e. antennal flagellum).

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