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*

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The complete larval development of the sesarmid crab Perisesarma fasciatum (Lanchester, 1900) from Singapore was obtained from laboratory culture. All four zoeal stages, the megalopa and the first crab stage are described and illustrated. The morphological characteristics of the larvae of P. fasciatum are compared with those of other known larvae of the genera Perisesarma and Parasesarma. The larval morphology of P. fasciatum clearly presents the typical combination of features that characterize sesarmid larvae. Overall, larval stages are very similar in Perisesarma and Parasesarma and it is impossible to distinguish these two genera by larval morphology.

INTRODUCTION

Sesarmid crabs are among the most diverse and important faunal components of mangrove forest communities worldwide. Their importance for ecological processes related to leaf turnover is only recently being revealed (Macintosh, 1988; Lee, 1989, 1998; Emmerson and McGwynne, 1992; Micheli, 1993a, b; Schrijvers *et al.*, 1996). Otherwise, very little is known about the biology of most of these tropical crabs, and even the systematic classification is far from being resolved. For a long time, most of the sesarmids were included in the genus *Sesarma* Say, 1817. In 1895, de Man (de Man, 1895) introduced three subgenera (i.e. *Episesarma*, *Parasesarma* and *Perisesarma*) based on the presence or absence of an anterolateral tooth and the type of tuberculation on the chelar carpus. Serène and Soh (Serène and Soh, 1970) elevated these subgenera to full genus level and created a large number of new genera, thereby establishing a taxonomic system which even today is not fully accepted, only slowly adopted and still being revised (Davie, 1992, 1994; Ng and Schubart, 2003).

According to the new taxonomy of Serène and Soh (Serène and Soh, 1970), the genus *Sesarma* is now restricted to the American continent, which has an impoverished sesarmid fauna compared to the Indo-WestPacific (<30 species in America as compared with >200 species in the Indo-WestPacific). There are no sesarmid crabs in Europe. Many larval stages of *Sesarma* and its sister genera *Aratus* H. Milne Edwards, 1853 and *Armases* Abele, 1992 have been described over the past 50 years from American waters (Costlow and Bookhout, 1960, 1962; Díaz and Ewald, 1968; Warner, 1968; Fransozo and Hebling, 1986; Schubart and Cuesta, 1998; Cuesta and Anger, 2001). In contrast, there are only very few larval descriptions of sesarmid crabs from Africa, Asia and Oceania (Fukuda and Baba, 1976; Terada, 1976; Krishnan and Kannupandi, 1987; Pasupathi and Kannupandi, 1987; Pereyra Lago, 1987, 1993; Greenwood and Fielder,

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1988; Selvakumar, 1999; Flores *et al.*, 2003; Schubart *et al.*, 2003), especially considering the large number of species that are present in the mangroves of these continents.

Two of the more conspicuous and species-rich genera of African, Asian and Australian mangroves are *Parasesarma* (26 species) and *Perisesarma* (23 species). They are often colourful crabs, similar in their overall squarish appearance and even sharing the defining morphological characteristic of two transverse pectinated crests on the upper border of the male chelar carpus. The only distinguishing characteristic between the two genera is the absence (*Parasesarma*) or presence (*Perisesarma*) of an anterolateral tooth. In American sesarmid crabs, it has been shown that the anterolateral tooth is not a very consistent characteristic and it is often weakly pronounced or absent in some of the species (von Hagen, 1978; Abele, 1992). Also in one Asian species of *Perisesarma*, *Perisesarma fasciatum* (Lanchester, 1900), the anterolateral tooth is not always clearly defined. Therefore, Lanchester (1900) originally placed this species in the subgenus *Parasesarma*, however, noticing that one of the females has 'indications of a tooth behind the orbital angle'. Also Tweedie (1936) states that the 'epibranchial tooth is always low and obtuse, often obscure, and in one adult male, scarcely indicated'.

Perisesarma fasciatum is a relatively small and rounded representative of its genus. It lives in the upper, often dry, fringes of mangroves on relatively hard and sandy substratum and was repeatedly observed scurrying on mounds of the burrowing decapod *Thalassina* (C. D. Schubart, personal observation). The known distribution of this species ranges from Thailand [Rathbun, 1909 as *Sesarma* (*Chiromantes*) *siamense*], Malaysia (Sasekumar, 1972), Singapore (Tweedie, 1936) and Indonesia (Serène and Moosa, 1971) to Hong Kong (Soh, 1978). Otherwise, there is no published information on the biology of this crab species.

In this study, we newly describe the complete larval and early juvenile development of *P. fasciatum* from Singapore and compare it with other published larval descriptions of species of *Parasesarma* and *Perisesarma* to test whether there are consistent larval differences between these two genera (Fukuda and Baba, 1976; Terada, 1976; Pasupathi and Kannupandi, 1987; Pereyra Lago, 1987, 1993; Greenwood and Fielder, 1988; Selvakumar, 1999; Flores *et al.*, 2003). This is only the fourth species of the genus *Perisesarma* for which zoeal stages are described, the third megalopal description, and the second which includes the first juvenile.

METHOD

Several adult specimens of *P. fasciatum* were collected in the Lim Chu Kang mangroves in Singapore in January 2002. They were transported alive to Regensburg (Germany) where they were slowly acclimated to fresh water. Two females and two males were transported to the Biologische Anstalt Helgoland (Germany) in July 2002, where they were maintained at a salinity of 5 (24°C) and in an artificial 12:12 h light:dark cycle. The extrusion and incubation of eggs took place at the same conditions. Larval rearing of one hatch was carried out at identical conditions of temperature and light, but at a salinity of 25. The larvae were fed freshly hatched nauplii of *Artemia* sp. (Great Salt Lake). Water and food were changed daily. Exuviae and specimens of each developmental stage were preserved in 70% alcohol. First zoeal stages from three additional females were obtained in Regensburg and Barcelona (Spain) for comparative purposes.

A Wild 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 microscope was used for the determination of the setal formula and measurements of the appendages. The following measurements were taken: total length (TL) 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; and basal telson length (BT), from a line across the anterior margin to the posterior margin of the telson (base of the outer seta). The proportions of the zoeal measurements EL, PL, FL and BT were shown to be useful for separating species and genera of the Sesarmidae (Cuesta, 1999). For the megalopa, 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 a camera lucida and microscope photography. The number of individuals of each larval stage examined 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 not fully illustrated and are drawn truncated, instead. 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 (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, under the catalogue numbers ICMD 52-56/2004.

RESULTS

The larval development of *P. fasciatum* was found to consist of four zoeal stages and one megalopa. The development through the zoea I stage lasted on average 4.6 ± 1.2 d, the zoea II stage took 3.7 ± 0.7 d, the zoea III 3.4 ± 0.5 d, the zoea IV 4.7 ± 0.5 and the megalopa 8.0 ± 0.7 d (values are mean ± SD; initial $n = 100$). Total larval development from hatching to metamorphosis lasted 23.9 ± 1.2 d. The comparison of zoeae I from four different hatches allowed to determine morphological and morphometric homogeneity (i.e. no significant differences). The first zoeal stage is described in detail, while in subsequent stages only differences and changes are described.

Zoea 1

Size
TL, 0.62–0.67 mm; CL, 0.38–0.42 mm.

Carapace (Fig. 1a)
Globose, smooth and without tubercles. Dorsal spine present, well developed and strongly curved posteriorly with sparsely minute protuberances. Rostral spine present, straight and similar in length to spinous process of the antenna. Lateral spines absent. Pair of setae on the posterodorsal and anterodorsal regions. Posterior and ventral margin without setae. Eyes sessile.

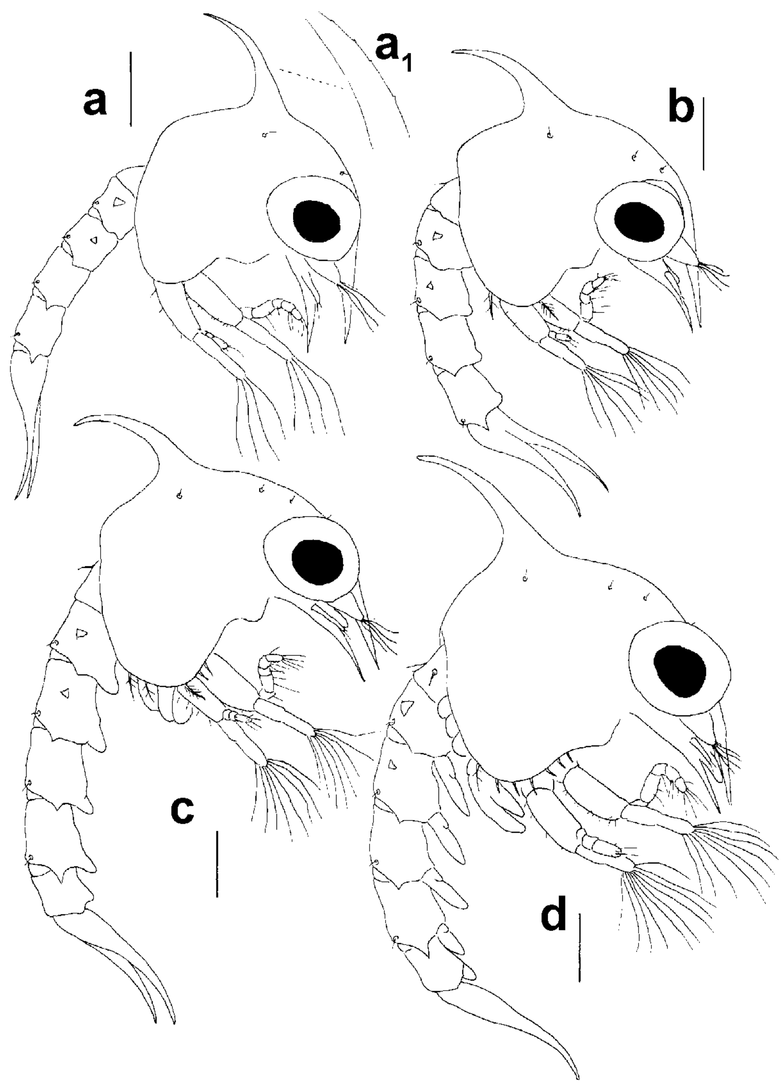

Fig. 1. *Perisesarma fasciatum* (Lanchester, 1900). Total animal, lateral view. (**a**) zoea I; (**b**) zoea II; (**c**) zoea III; (**d**) zoea IV. (**a₁**) detail of the dorsal spine. Scale bars = 0.15 mm.

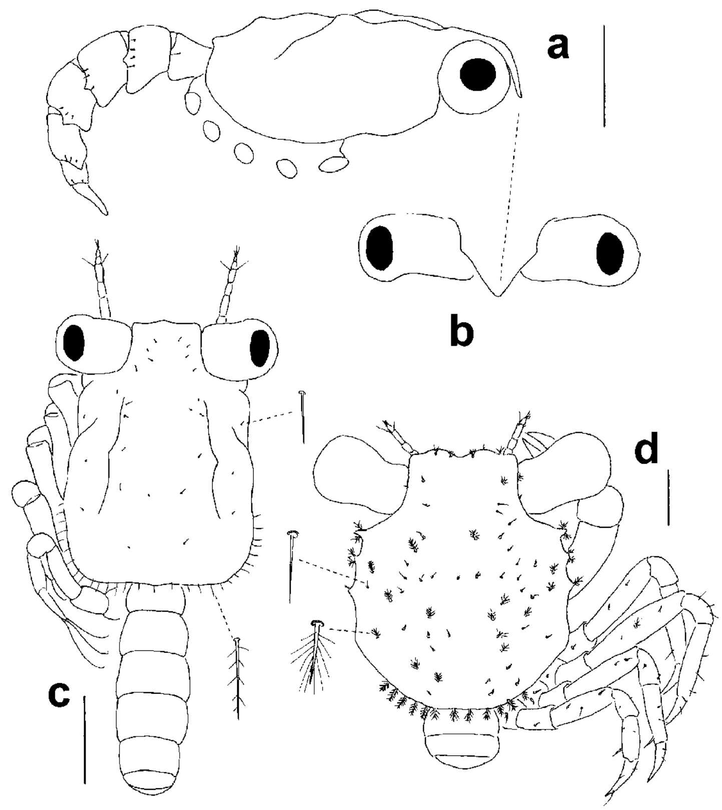

Fig. 2. *Perisesarma fasciatum* (Lanchester, 1900). (**a**) megalopa, lateral view; (**b**) megalopa, detail of frontal view of the rostrum; (**c**) megalopa, dorsal view; (**d**) first crab, dorsal view. Scale bars = 0.2 mm.

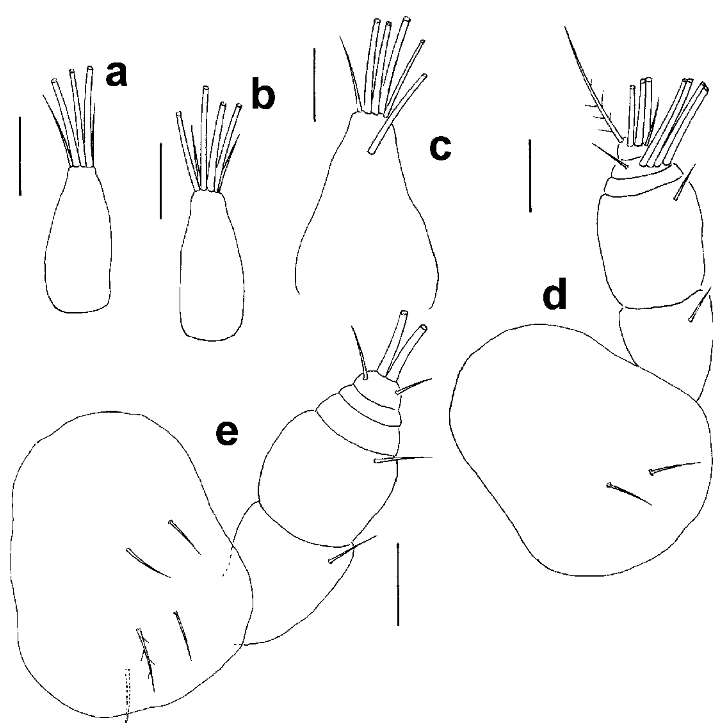

Fig. 3. *Perisesarma fasciatum* (Lanchester, 1900). Antennule. (**a**) zoea I; (**b**) zoea II; (**c**) zoea IV; (**d**) megalopa; (**e**) first crab. Scale bars = 0.05 mm.

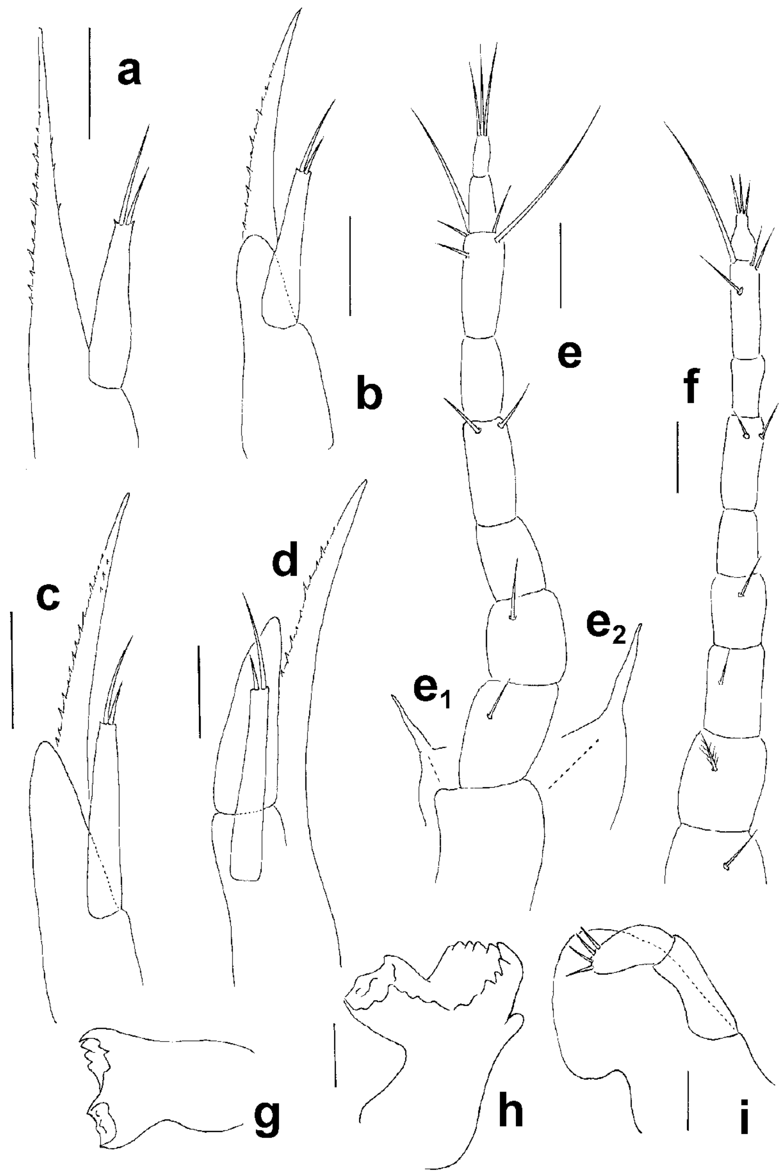

Fig. 4. *Perisesarma fasciatum* (Lanchester, 1900). Antenna. (**a**) zoea I; (**b**) zoea II; (**c**) zoea III; (**d**) zoea IV; (**e**) megalopa; (**f**) first crab. (**e₁**) modified basal segment; (**e₂**) modified basal segment. Mandible. (**g**) zoea I; (**h**) zoea IV; (**i**) megalopa. Scale bars = 0.05 mm.

Antennule (Fig. 3a)
Uniramous. Endopod absent. Exopod unsegmented with three terminal aesthetascs and two terminal seta.

Antenna (Fig. 4a)
Similar in size to rostral spine. Protopodal process with one row of 12–15 spines of different size. Exopod elongated, with two terminal simple setae (one long and one medium-sized) and two minute spines. PL/EL = 2.35–2.40.

Mandible (Fig. 4g)
Incisor and molar processes differentiated. Endopod palp absent.

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

Maxilla (Fig. 7a)
Coxal endite bilobed, with 5 + 3 setae, distal lobe terminates in a spine. Basial endite bilobed with 5 + 4 setae. Endopod unsegmented, bilobed, with 2 + 3 long setae on the proximal and distal lobe respectively.

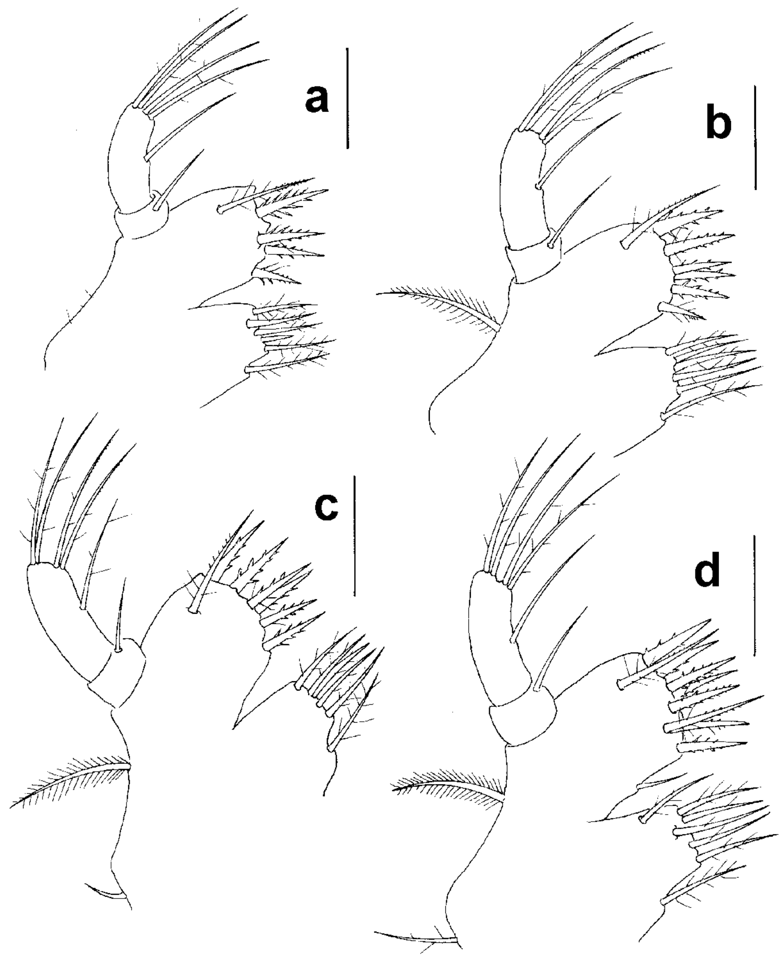

Fig. 5. *Perisesarma fasciatum* (Lanchester, 1900). Maxillule. (**a**) zoea I; (**b**) zoea II; (**c**) zoea III; (**d**) zoea IV. Scale bars = 0.05 mm.

Scaphognathite (exopod) with four plumose marginal setae and long setose posterior process.

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

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

Abdomen (Figs 14a and 15a)
Five somites. Somites 2 and 3 with pairs of dorsolateral processes. Somites 3–5 with posterolateral processes. Somites 2–5 with pairs of posterodorsal setae.

Pleopods
Absent.

Telson (Fig. 14a)
Lateral and dorsal medial spines absent. Furca large, slightly divergent with three pairs of serrate setae on the posterior margin. Two rows of arrow-shaped small spines on the margins of furcal arms. FL/BT $\leq$ 2 (1.8–2.0).

Zoea 2

Size
TL, 0.85–0.87 mm; CL, 0.50–0.51 mm.

Carapace (Fig. 1b)
Two pairs of anterodorsal setae. Each lateroventral margin with two setae. Eyes stalked.

Antennule (Fig. 3b)
Exopod with four aesthetascs and two setae.

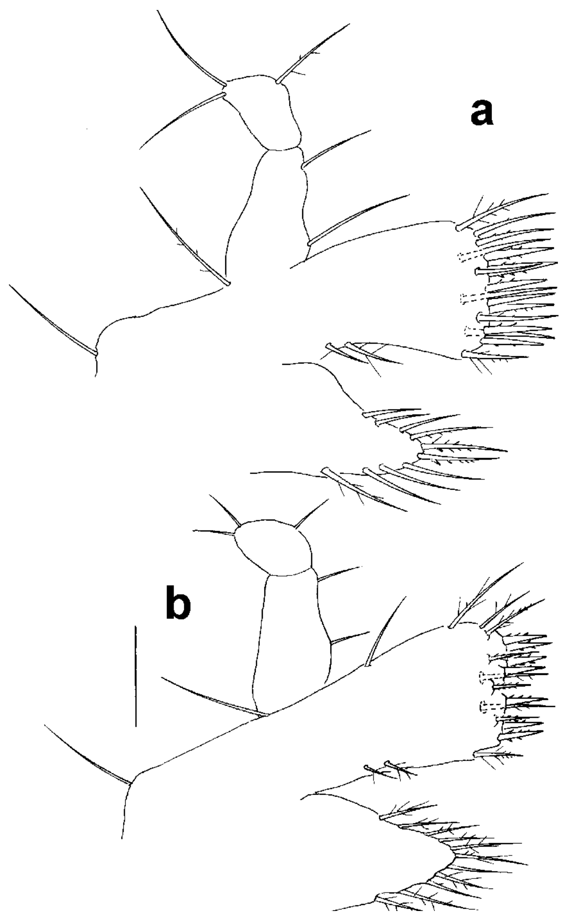

Fig. 6. *Perisesarma fasciatum* (Lanchester, 1900). Maxillule. (**a**) megalopa; (**b**) first crab. Scale bars = 0.05 mm.

Antenna (Fig. 4b)
Endopod bud present. PL/EL = 2.1–2.3.

Mandible
Unchanged.

Maxillule (Fig. 5b)
Basial endite with seven setae. Exopod plumose seta present.

Maxilla (Fig. 7b)
Scaphognathite with eight (3 + 5) plumose marginal setae, without long setose posterior process present in zoea 1.

First maxilliped
Basis without a mat of long dorsobasal microtrichiae. Exopod distal segment with six long plumose natatory setae.

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

Third maxilliped and pereiopods
Present as undifferentiated buds.

Abdomen (Figs 14b and 15b)
First somite with one long mid-dorsal seta.

Pleopods
Absent.

Telson (Fig. 14b)
Unchanged.

Zoea 3

Size
TL, 0.90–0.92 mm; CL, 0.60–0.62 mm.

Carapace (Fig. 1c)
Three pairs of anterodorsal setae. Each lateroventral margin with five setae.

Antennule
Unchanged.

Antenna (Fig. 4c)
Endopod bud elongated, not as long as exopod.

Mandible
Unchanged.

Maxillule (Fig. 5c)
Epipod seta present.

Maxilla (Fig. 7c)
Scaphognathite with 12–14 plumose marginal setae.

First maxilliped (Fig. 9b)
Segments 2 and 3 of endopod with additional setae (2, 2 + 1, 2, 2, 1 + 4). Exopod distal segment with eight long plumose natatory setae.

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

Third maxilliped
Biramous unsegmented.

Pereiopods (Fig. 12a)
Unsegmented. Chelipeds bilobed.

Abdomen (Figs 14c and 15c)
Somite 6 now present without setae.

Pleopods (Fig. 15c)
Presents as buds on somites 2–5, endopods absent.

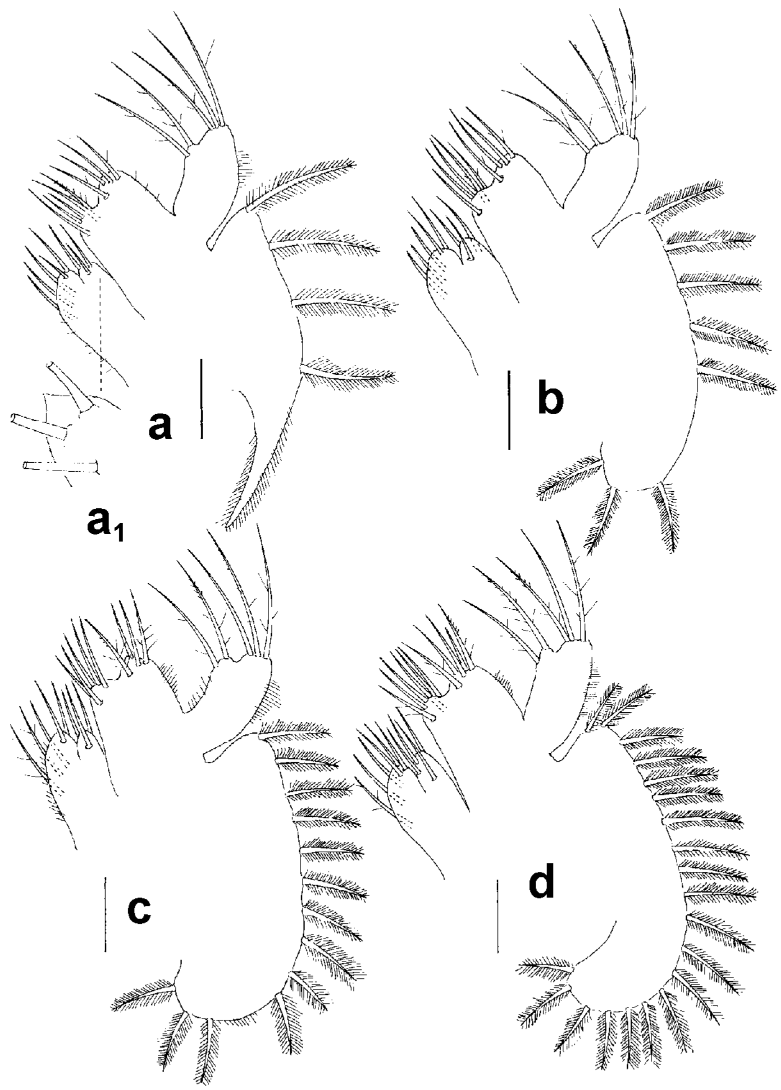

Fig. 7. *Perisesarma fasciatum* (Lanchester, 1900). Maxilla. (**a**) zoea I; (**b**) zoea II; (**c**) zoea III; (**d**) zoea IV. (**a_1**) detail of the distal lobe of the coxal endite. Scale bars = 0.05 mm.

Telson (Fig. 14c)
FL/BT > 2 (2.2–2.4).

Zoea 4

Size
TL, 1.2–1.25 mm; CL, 0.67–0.72 mm.

Carapace (Fig. 1d)
Each lateroventral margin with seven setae. Otherwise unchanged.

Antennule (Fig. 3c)
With one subterminal and four terminal aesthetascs, and one terminal seta.

Antenna (Fig. 4d)
Protopodal process with one row of 15–19 spines of different size. Exopod with two terminal setae (one long and one medium-sized). Endopod segmented, slightly more than half the length of spinous process. PL/EL = 2.0–2.1.

Mandible (Fig. 4h)
Palp bud present.

Maxillule (Fig. 5d)
Coxal endite with seven setae. Basial endite with 10–11 setae.

Maxilla (Fig. 7d)
Coxal endite bilobed, with 6 + 4 setae. Basial endite bilobed with 6 + 5 setae. Scaphognathite with 20 plumose marginal setae.

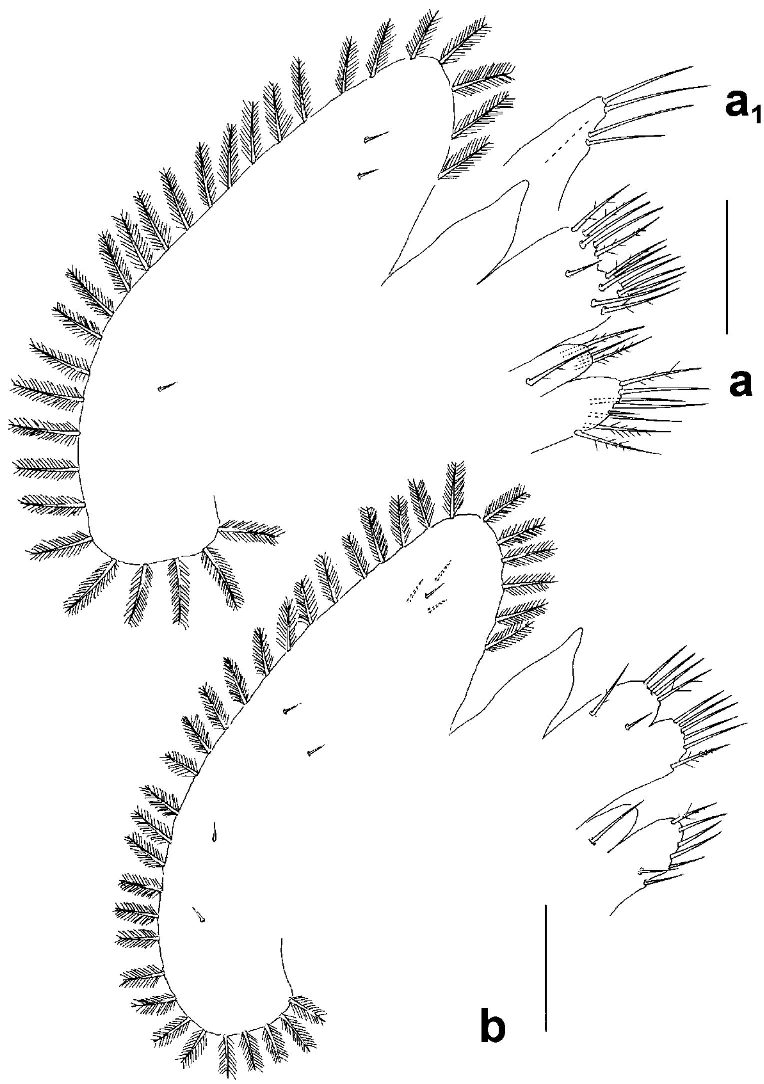

Fig. 8. *Perisesarma fasciatum* (Lanchester, 1900). Maxilla. (**a**) megalopa; (**b**) first crab. (**a₁**) modified endopod. Scale bars = 0.1 mm.

First maxilliped (Fig. 9c)
Fifth segment of endopod with an additional subterminal seta (2 + 4). Exopod distal segment with nine long plumose natatory setae.

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

Third maxilliped (Fig. 11a)
Epipod rudiment now present.

Pereiopods (Fig. 12b)
Chelipeds and pereiopods 2–5 slightly segmented.

Abdomen (Figs 14d and 15d)
First somite with three long mid-dorsal setae.

Pleopods (Fig. 15d)
Pleopod buds elongated, endopod buds present.

Telson (Fig. 14d)
Unchanged. FL/BT > 2 (2.3–2.5).

Megalopa

Size
CL, 0.82 mm; CW, 0.55 mm.

Carapace (Fig. 2a–c)
Longer than broad. With two lateral and longitudinal carinae. Rostrum ventrally deflected with median cleft. Setal arrangement as figured.

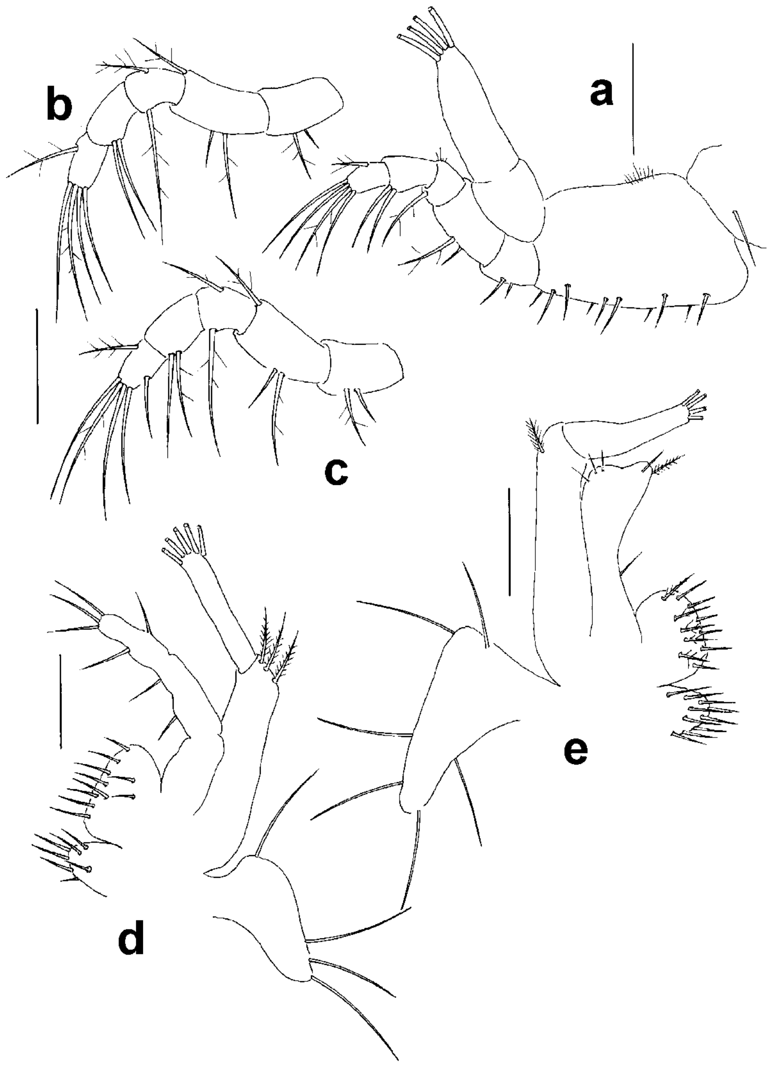

Fig. 9. *Perisesarma fasciatum* (Lanchester, 1900). First maxilliped. (**a**) zoea I; (**b**) zoea III, endopod; (**c**) zoea IV, endopod; (**d**) megalopa; (**e**) first crab. Scale bars = 0.1 mm.

Antennule (Fig. 3d)
Peduncle three-segmented, with 2,1,1 setae respectively. Endopod absent. Exopod three-segmented, with 0, 4 and 3 aesthetascs, respectively, and 0, 1, 2 setae.

Antenna (Fig. 4e)
Peduncle three-segmented, with 0,1,1 setae respectively. In several cases, exopod and spinous process present in different degrees of development. Flagellum six-segmented, with 0,2,0,5,0,3 setae respectively.

Mandible (Fig. 4i)
Palp two-segmented, with four setae on the distal segment.

Maxillule (Fig. 6a)
Coxal endite with 10 setae. Basial endite with 17(15 + 2) −18(16 + 2) setae. Endopod two-segmented, proximal segment with two setae, distal segment with three setae. Two setae on the outer propodal margin.

Maxilla (Fig. 8a)
Coxal endite bilobed, with always 8 + 4 setae. Basial endite bilobed with 8–9 + 6–7 setae. Endopod unsegmented, with variable setation (2 + 3, 1 + 3, 2 + 2, 0 + 0 setae). Scaphognathite with 29–33 plumose marginal setae and two anterior setae and one posterolateral seta.

First maxilliped (Fig. 9d)
Epipod with four long setae. Coxal endite with seven to eight setae. Basial endite with 10–11 setae. Endopod very variable and different degrees of reduction with zero to nine setae (0, 3, 4, 9 setae). Exopod

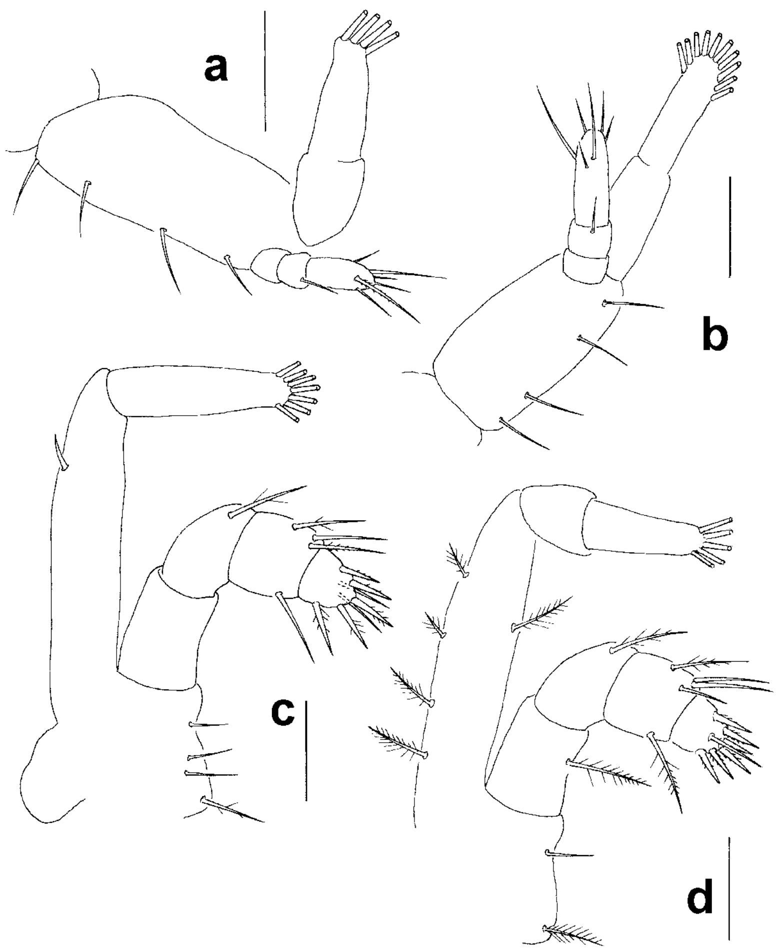

Fig. 10. *Perisesarma fasciatum* (Lanchester, 1900). Second maxilliped. (**a**) zoea I; (**b**) zoea IV; (**c**) megalopa; (**d**) first crab. Scale bars = 0.1 mm.

two-segmented, proximal segment with three distal setae, distal segment with five long terminal plumose setae.

Second maxilliped (Fig. 10c)
Epipod rudimentary. Coxa and basis not differentiated, with three to four setae. Endopod four-segmented, with 0,1,4,7 setae respectively. Exopod two-segmented, proximal segment with one medial seta, distal segment with seven terminal plumose setae.

Third maxilliped (Fig. 11b)
Epipod elongated with 12 long setae. Coxa and basis not differentiated with nine setae. Endopod five-segmented, ischium, merus, carpus, propodus and dactylus with 8–9,7,3,3–4,4 setae respectively. Exopod two-segmented, proximal segment without seta and distal segment with three long terminal plumose setae and one simple seta.

Pereiopods (Fig. 13a–e)
All segments well differentiated, chelipeds and pereiopods 2–4 without spines. Dactylus of fifth pereiopod with three long terminal setae and one short terminal spine. Setal arrangement as figured.

Abdomen (Fig. 14e)
Six somites present, setation on somites as figured.

Pleopods (Fig. 16a and b)
Somites 2–5 each with pairs of biramous pleopods, endopod unsegmented, with two terminal hooks; exopod unsegmented with 13,13,13,10 long marginal plumose natatory setae respectively.

Uropods (Fig. 16c)
Uropods two-segmented on somite 6, proximal segment with one and distal segment with five long plumose setae respectively.

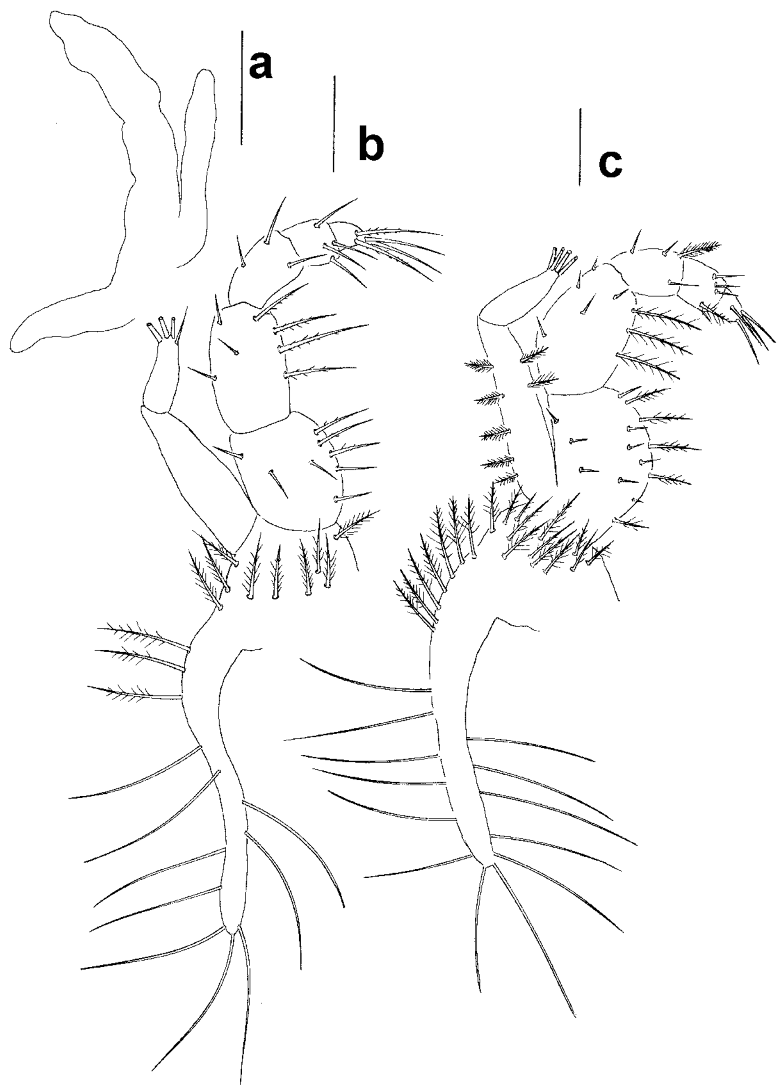

Fig. 11. *Perisesarma fasciatum* (Lanchester, 1900). Third maxilliped. (**a**) zoea IV; (**b**) megalopa; (**c**) first crab. Scale bars = 0.1 mm.

Fig. 12. *Perisesarma fasciatum* (Lanchester, 1900). Pereiopods 1–5. (**a**) zoea III; (**b**) zoea IV. Scale bars = 0.1 mm.

Telson (Fig. 14e)
Square-shaped, setation as figured. In two examined individuals, telson with two to three pairs of long setae and furcal branches present in two different degrees of development (Fig. 14e$_1$ and e$_2$).

First juvenile

Size
CL, 1.02–1.05 mm; CW, 0.85 mm.

Carapace (Fig. 2d)
Longer than broad. Frontal region broad, measuring one half of carapace width. Anterolateral margins with

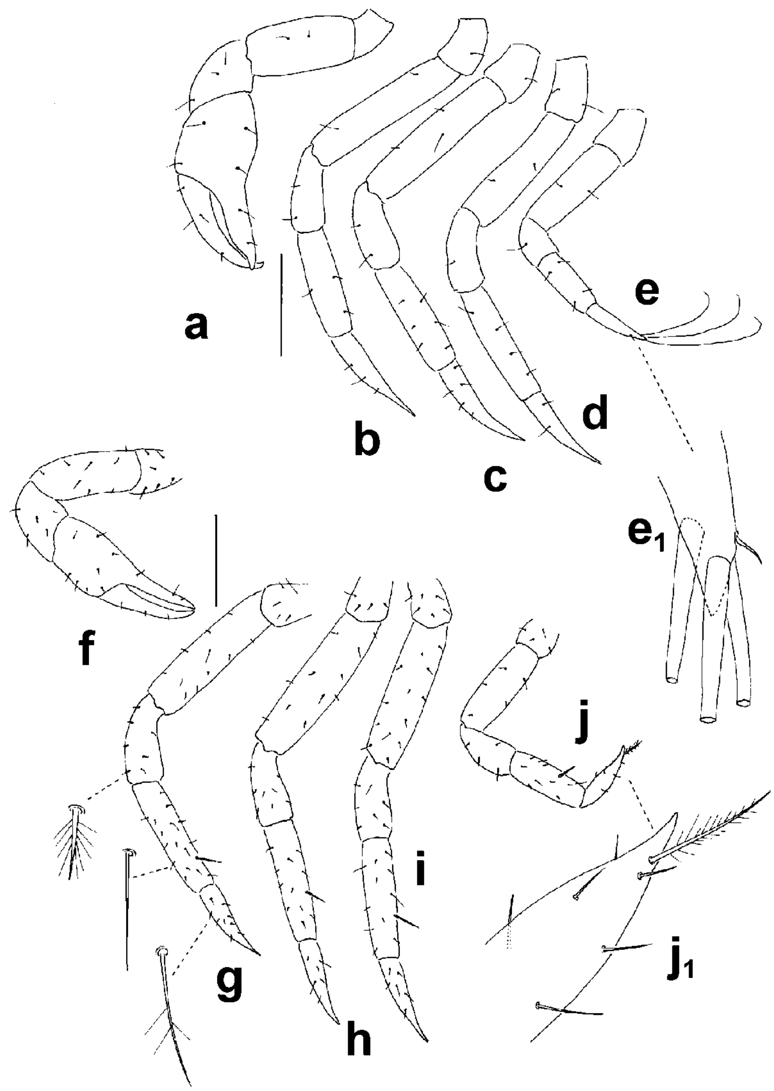

Fig. 13. *Perisesarma fasciatum* (Lanchester, 1900). Pereiopods 1–5. (**a**–**e**) megalopa; (**f**–**j**) first crab. (**e$_1$**) detail of the distal part of dactyl of the fifth pereiopod; (**j$_1$**) detail of the distal part of dactyl of the fifth pereiopod. Scale bars = 0.1 mm.

three teeth, first largest and third smallest. Setal arrangement as figured.

Antennule (Fig. 3e)
Peduncle three-segmented, with 5,1,1 setae respectively. Endopod absent. Exopod three-segmented, with 0, 0 and 2 aesthetascs, respectively, and 0,0,2 setae.

Antenna (Fig. 4f)
Peduncle four-segmented, with 1–2,1,1,1 setae respectively. Flagellum five-segmented, with 0,2,0,4–5,3 setae respectively.

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

Maxillule (Fig. 6b)
Coxal endite with 11 setae. Basial endite with 19 setae. Endopod two-segmented, proximal segment with two setae, distal segment with three setae.

Maxilla (Fig. 8b)
Coxal endite bilobed with 7 + 1 seta. Basial endite bilobed with 6–7 + 6 setae. Endopod unsegmented, without setae. Scaphognathite with 34–36 plumose marginal setae and eight lateral setae.

First maxilliped (Fig. 9e)
Epipod with 6–7 long setae. Coxal endite with 10 setae. Basial endite with 11–12 setae. Endopod with six setae. Exopod two-segmented, proximal segment

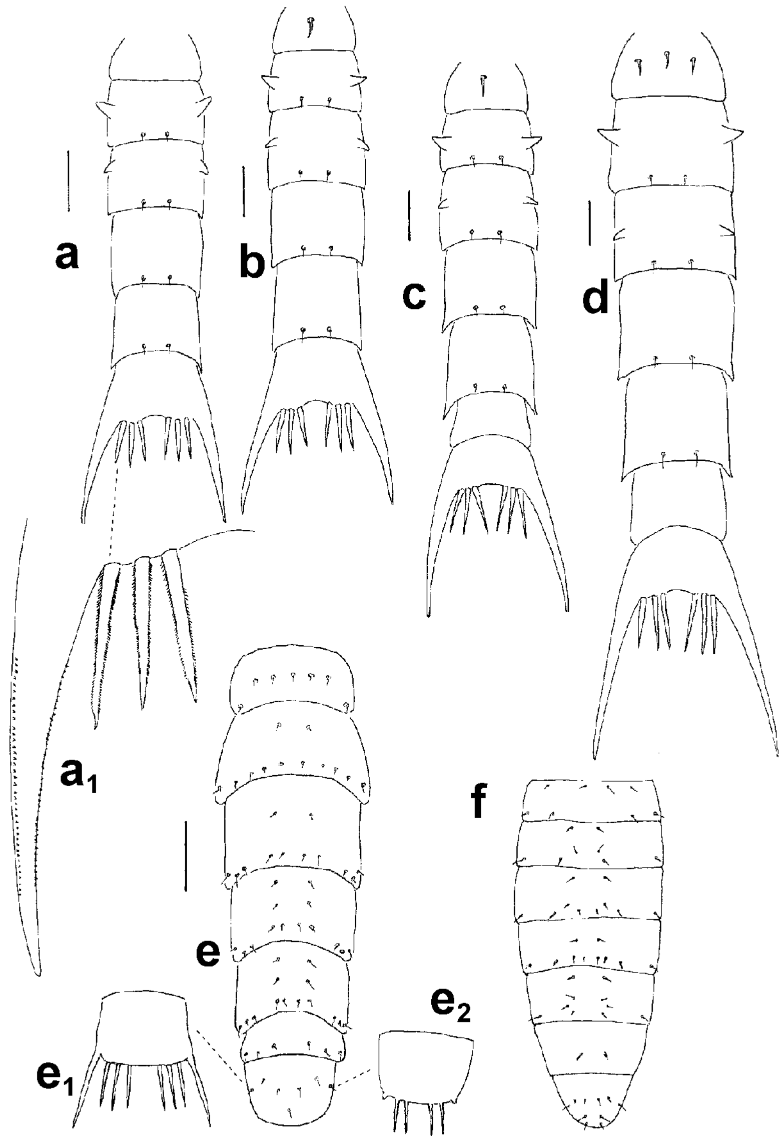

Fig. 14. *Perisesarma fasciatum* (Lanchester, 1900). Abdomen, dorsal view. (**a**) zoea I; (**b**) zoea II; (**c**) zoea III; (**d**) zoea IV; (**e**) megalopa; (**f**) first crab. (**a₁**) detail of the furca; (**e₁**) modified telson; (**e₂**) modified telson. Scale bars = 0.1 mm.

with one distal seta, distal segment with four long terminal plumose setae.

Second maxilliped (Fig. 10d)
Coxa and basis undifferentiated, with 1–2 setae. Endopod four-segmented with 0–2,1,4–5,7 setae respectively. Exopod three-segmented, proximal segment with five setae, second segment without setae and distal segment with five terminal plumose setae.

Third maxilliped (Fig. 11c)
Epipod elongated with 20 long setae. Coxa and basis undifferentiated with 14 setae. Endopod five-segmented with 14,8,4,4–5,4 setae respectively. Exopod two-segmented, proximal segment with seven setae and distal segment with four long terminal plumose setae.

Pereiopods (Fig. 13f–j)
Setation as figured. Propodus of pereiopods 2–5 with one long seta. Dactylus of fifth pereiopod with one long terminal plumose seta.

Abdomen (Fig. 14f)
Six somites present. Setation on somites as figured.

Pleopods
Pleopods reduced.

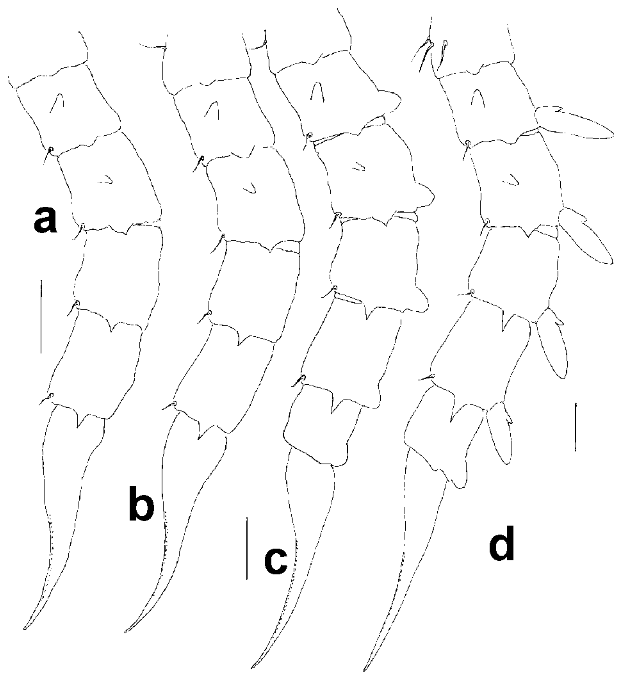

Fig. 15. *Perisesarma fasciatum* (Lanchester, 1900). Abdomen, lateral view. (**a**) zoea I; (**b**) zoea II; (**c**) zoea III; (**d**) zoea IV. Scale bars = 0.1 mm.

Second to fourth crab stages

Second to fourth crab stages are similar in morphology to the first stage, differing only in size (Fig. 16d) and in most of the setal counts.

DISCUSSION

Overall, the zoeal morphology of *P. fasciatum* is similar to that known of other sesarmid species. It conforms very closely to the characteristic listed by Rice (Rice, 1980) and Cuesta (Cuesta, 1999) for sesarmid larvae: (1) carapace without lateral spines; (2) a 2,3 setation of the maxillar endopod; (3) a 2,2,3,3 setation of the first maxilliped basis; (4) a 0,1,6 setation of the second maxilliped endopod; and (5) an abdomen with dorsolateral processes in somites 2 and 3.

Likewise, the morphology of the megalopal stage is similar to that known from the other species of the family Sesarmidae (Cuesta, 1999): (1) antennule without endopod; (2) an antennular flagellum with 5–6 segments; (3) a 0,4 mandibular palp setation; (4) scaphognathite with 25–50 marginal plumose setae; (5) endopod of the pleopods with two terminal hooks and exopod with seven and 14 plumose setae; (6) propodus of the uropod with one seta and exopod with ≤7 setae.

It has already been observed that the conserved morphological characteristics of the larvae of Sesarmidae make differentiation at generic levels difficult in this family (Cuesta, 1999). Likewise, differentiation at species level are only possible, if at all, using a combination of several morphological features (Schubart and Cuesta, 1998; Cuesta and Anger, 2001). Tables I and II summarize the morphological differences of all described zoeal stages and the megalopa stage among species of *Perisesarma* and *Parasesarma*. We here included the larvae of the genus *Parasesarma* because *P. fasciatum* was originally described as a member of *Parasesarma* and because of the morphological similarity of the two genera (see *Introduction*). Preliminary molecular comparisons also suggest a close phylogenetic relationship of these genera (Fratini *et al.*, 2004). In the present study, we provide evidence that larval stages of *Perisesarma* and *Parasesarma* are very similar, to the point that it is impossible to distinguish the larvae consistently at the generic level. The first zoeal stage of *Parasesarma* species bears five setae on the coxal endite of the maxillule (Table I), while *P. fasciatum* and *Perisesarma*

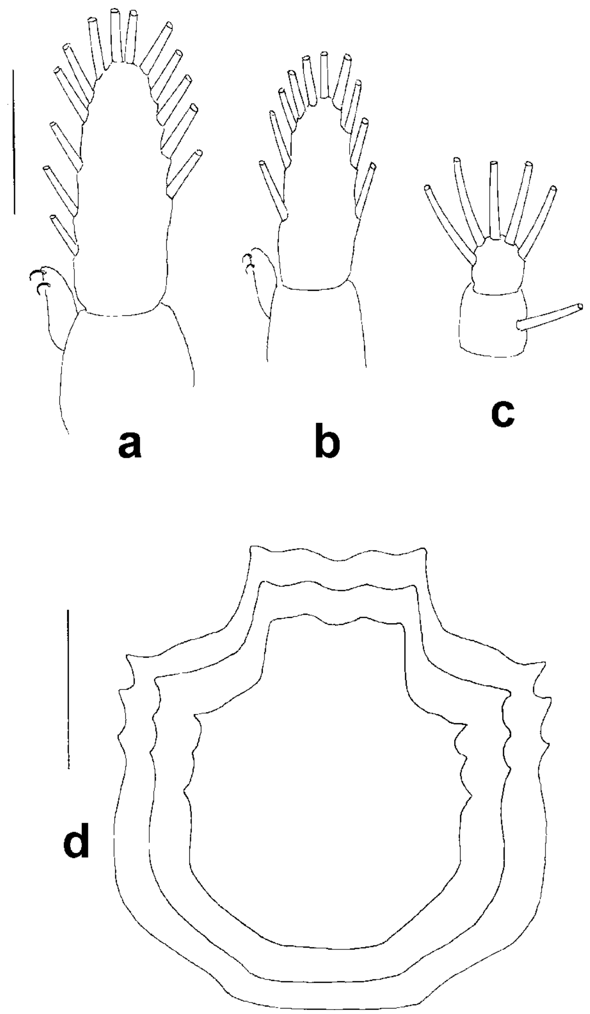

Fig. 16. *Perisesarma fasciatum* (Lanchester, 1900). (**a**) megalopa, pleopod 1; (**b**) megalopa, pleopod 4; (**c**) megalopa, uropod; (**d**) carapace of crabs 1–3. Scale bars of a and b, 0.1 mm; scale bar of D, 0.5 mm.

Table I: Morphological differences among described zoeal stages of the genera Perisesarma and Parasesarma [Perisesarma fasciatum, this study; Perisesarma guttatum (Pereyra Lago, 1993; Flores et al., 2003); Perisesarma bidens (Fukuda and Baba, 1976); Perisesarma messa (Greenwood and Fielder, 1988); Parasesarma leptosoma (Flores et al., 2003); Parasesarma acis (Terada, 1976); Parasesarma catenata (Pereyra Lago, 1987; Flores et al., 2003)*; Parasesarma pictum (Pasupathi and Kannupandi, 1987); Parasesarma erythrodactyla (Greenwood and Fielder, 1988); Parasesarma plicatum (Fukuda and Baba, 1976; Selvakumar, 1999)*]*

	P. fasciatum	*P. guttatum*	*P. bidens*	*P. messa*	*P. leptosoma*	*P. acis*	*P. catenata*	*P. pictum*	*P. erythrodactyla*	*P. plicatum*
Number of stages	4	5	4	Not described	Not described	4	4	4	5	5
Zoea I										
TL (mm)	0.62–0.65	0.7	0.67	0.58	0.63	0.6	0.44	0.86	0.59	0.63 (0.65)*
Antennule (aesthetascs, setae)	3,2	3,2	3,1	5,0	3,3	3,1	(3)*4,1	3,1	4,1	3,1
Maxillule										
Setae on coxal end	6	6 (5)*	5	5	6	5	5 (6)*	5	5	5
Maxilla										
Setae on coxal end	8	8	7	7	8	8	8	6	9	8
Setae on basial end	9	8 (9)*	9	9	9	9	8 (9)*	9	9	9
Maxilliped 1										
Setae on basis	2,2,3,3	2,2,3,3	2,2,3,3	2,2,3,3	2,2,3,2	2,2,3,3	2,2,3,3	2,2,3,3	2,2,3,3	2,2,3,3
Zoea II										
TL (mm)	0.85–0.87	0.97	0.95	Not described	Not described	0.86	0.98	1.01	0.66	0.71(0.82)*
Carapace										
Setae on ventral margin	2	1	1	Not described	Not described	Not described	2	3	Not described	Not described
Antennule (aesthetascs, setae)	4,2	3,2	4,2	Not described	Not described	4,1	4,1	4,1	5,1	3,1
Maxillule										
Setae on coxal end	6	6	5	Not described	Not described	6	5	5	5	6
Setae on basial end	7	7	7	Not described	Not described	7	7	5	7	7
Maxilla										
Setae on coxal end	8	8	7	Not described	Not described	8	8	6	9	9
Setae on basial end	9	9	9	Not described	Not described	9	9	9	9	10
Setae on scaphognathite	8	8	8	Not described	Not described	8	8	9	8	8
Zoea III										
Carapace										
Setae on ventral margin	5	3	2	Not described	Not described	Not described	4	6	Not described	Not described
TL (mm)	0.9	1.09	1.13	Not described	Not described	0.77	1.09	1.16	0.83	0.86 (1.10)*
Antennule (aesthetascs, setae)	4,2	3,1	3,2	Not described	Not described	2,1	4,2	5,1	5,1	3,2
Maxillule										
Setae on coxal end	6	6	5	Not described	Not described	6	5	6	5–6	6
Setae on basial end	7	7	7	Not described	Not described	7	7	6	7	7

Maxilla										
Setae on coxal end	8	8	7	Not described	Not described	8	8	6	9	9
Setae on basial end	9	9	9	Not described	Not described	10	9	10	9	10
Setae on scaphognathite	12–14	11	11	Not described	Not described	12	11	10	11	11
Maxilliped 1										
Setae on endopod	2,3,2,2,5	2,2,2,2,5	2,2,2,2,5	Not described	Not described	2,2,2,2,6	2,2,2,2,6	2,3,2,2,5	2,2,2,2,5	(2,3,2,2,5)* 2,2,2,2,5
Zoea IV										
Carapace										
Setae on ventral margin	7	5	5	Not described	Not described	Not described	8	7	Not described	Not described
TL (mm)	1.20–1.25	1.31	1.21	Not described	Not described	1.13	1.5	1.44	0.92	1.02 (1.2)*
Antennule (aesthetascs, setae)	5,1	3,3	5,2	Not described	Not described	6,1	4,3	6,1	5,1	4,2
Maxillule										
Setae on coxal end	7	7	7	Not described	Not described	7	6	6	6	6
Setae on basial end	10–11	11	11	Not described	Not described	11	11	7	11	10
Maxilla										
Setae on coxal end	10	11	11 (10)*	Not described	Not described	9	10	9	9	9
Setae on basial end	11	11	10 (11)*	Not described	Not described	13	12	11	10	10
Setae on scaphognathite	20–21	17	18 (18–19)*	Not described	Not described	21	20	20	15	16
Maxilliped 1										
Setae on endopod	2,3,2,2,6	2,2,2,2,5	2,3,2,2,6	Not described	Not described	2,2,2,2,6	2,2,2,2,6	2,3,2,2,6	2,2,2,2,6	2,3,2,2,6
Setae on exopod	9	9	9*	Not described	Not described	9	9	9	9–10	9
Maxilliped 2										
Setae on exopod	9–10	10	10*	Not described	Not described	10	10	10	10	9
Zoea V	Not present		Not present	Not described	Not described	Not present	Not present	Not present		
Carapace										
Setae on ventral margin				Not described	Not described					
TL (mm)		1.4		Not described	Not described				1.19	1.3
Antennule (aesthetascs, setae)		6,4		Not described	Not described				7,1	5,2
Maxillule										
Setae on coxal end		6		Not described	Not described				6–7	7
Setae on basial end		11		Not described	Not described				11	12
Maxilla										
Setae on coxal end		12		Not described	Not described				10	10
Setae on basial end		12		Not described	Not described				10	13
Setae on scaphognathite		24		Not described	Not described				20	24
Maxilliped 1										
Setae on endopod		2,2,2,2,6		Not described	Not described				2,2,2,2,6	2,3,2,2,6

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Table II: Morphological differences among described megalopae of the genera Perisesarma and Parasesarma

	Perisesarma fasciatum	*Perisesarma guttatum*	*Perisesarma bidens*	*Parasesarma acis*	*Parasesarma catenata*	*Parasesarma pictum*	*Parasesarma erythrodactyla*	*Parasesarma plicatum*
Carapace length (mm)	0.825	0.80	0.96	0.83	0.95	0.75	0.50	0.89
Carapace width (mm)	0.55	0.78	0.67	0.65	0.82	0.58	0.34	0.79
Antennule								
Setae on peduncle	2,1,1	3,1,1	3,0,0	2,1,1	1,0,0	2,1,1	5,2,1	3,1,1
Aesthetascs + setae on exopod	0,4,3 + 0,1,2	0,7,4 + 0,2,1	0,5,3 + 0,2,2	0,6,3 + 0,0,1	0,4,2 + 1,1,2	0,5,7 + 0,0,1	0,8,3 + 0,2,2	0,5,4 + 0,1,1
Antenna								
Setae on peduncle	0,1,1	0,1,1	0,1,1	0,0,1	1,1,1	0,1,2	1,1,1	1,1,1
Setae on flagellum	0,2,0,5,0,3	0,2,2,5,2	0,2,1,3,0,2	0,1,0,3,2	0,2,0,5,2	0,0,1,1,2,3	0,2,0,5,2	0,2,1,4,2
Maxillule								
Setae on coxal end	10	11	11	11	12	10	10–11	11
Setae on basial end	17–18	18	15	19	16	14	18	13
Maxilla								
Setae on coxal end	12	15	13	14	11	14	13	13
Setae on basial end	14–16	15	12	14	12	12	12–15	11
Setae on scaphognathite	29–33 + 3	36 + 2	32 + 2	31	37 + 4	25	32–35 + 3	28
Maxilliped 1								
Setae on coxal end	7–8	8	6	7	9	6	9	8
Setae on basial end	10–11	11	10	9	9	8	11	8
Setae on endopod	0–9	3	1	7	1	3	4–6	3
Setae on exopod	3,5	3,3	3,5	3,4	3,3	3,4	4,4–7	3,5
Setae on epipod	4	5	5	4	5	4	6	4
Maxilliped 2								
Setae on endopod	0,1,4,7	0,1,4,7	0,1,3,6	0,1,5,9	0,1,3,6	0,0,3,5	0,1,3,6	0,1,4,8
Setae on exopod	1,7	1,7	1,5	1,7	1,5	0,5	1,5–11	1,5
Maxilliped 3								
Setae on endopod	8–9,7,3,3–4,4	8,6,2,5,7	6,6,4,4,5	8,5,3,4,6	7,7,3,4,4	6,6,3,4,5	8–9,8,3,4,7	9,7,2,4,7
Setae on exopod	0,4	1,5	1,3	1,5	1,4	0,4	1,4	0,5
Setae on epipod	12	15	9	13	16	10	12–14	17
Pleopod								
Setae on exopod	13,13,13,10	13,13,13,11	10–13	11–13	13,12,12,12	11,11,12,10	11–13	13,14,13,11
Uropod								
Setae on exopod	5	6	6	6	6	6	6	6

guttatum bear six setae on the coxal endite (cf. Pereyra Lago, 1993). However, the first zoeal stages of *Perisesarma messa* and *Perisesarma bidens* bear five setae, as the species of *Parasesarma* (Fukuda and Baba, 1976; Greenwood and Fielder, 1988). It needs to be taken into account that the number of larval stages is variable (4–5 zoeal stages) in both genera, and part of the variability in the setation of appendages could be due to this variability. For example, the number of scaphognathite setae on the maxilla of the zoea IV is reduced in species with five zoeal stages as compared with species with four zoeal stages (Table I). The zoea IV of *P. guttatum* is the only fourth stage with five setae on the distal segment of the endopod of the first maxilliped; the sixth seta does not appear before the last zoeal stage (zoea V). In contrast, *Parasesarma erythrodactyla* and *Parasesarma plicatum*, both species with five zoeal stages, show the sixth seta on the distal segment of the endopod of the first maxilliped already in stage IV. Overall, the larval data (zoea and megalopa) support previous morphological and molecular indications and confirm a very close relationship between the genera *Perisesarma* and *Parasesarma*.

For a species–specific identification, there is one very useful characteristic by which megalopae of *P. fasciatum* can be distinguished from those of all other so-far described sesarmid megalopae: the presence of only five setae on the exopod of the uropod (Table II). This is a useful characteristic, since these setae can be observed and counted easily with a microscope and since the uropod setation normally is characterized by low intraspecific variability (Cuesta, 1999).

Some megalopal features described in the present study for *P. fasciatum* appear to represent remnants of zoeal morphology: (1) the first segment of the antennular peduncle with a rudimentary exopod and/or spinous process in different stages of reduction; (2) the bilobed endopod of the maxilla with a similar setation as in the zoeal stages (2 + 3, 1 + 3, 1 + 2); (3) the telson with a rudimentary furca and/or with three pairs of serrulate setae on the posterior margin in different stages of reduction. These features have been observed in only some of the studied individuals. Similar traits were also found in the megalopae of other grapsoid species: *Aratus pisonii* (Warner, 1968), *Sesarma reticulatum* (Costlow and Bookhout, 1962), *P. plicatum* (Selvakumar, 1999), *P. erythrodactyla* (Greenwood and Fielder, 1988) and *Armases angustipes* (Cuesta and Anger, 2001). Cuesta and Anger (2001) suggested that retainment of zoeal characteristics in the megalopa could be due to unfavourable conditions during larval culturing. However, this still remains to be tested.

Knowledge of the first juvenile of sesarmid crabs is very limited. The first crab stage was previously only described for *P. bidens* (Fukuda and Baba, 1976). The overall morphology of *P. fasciatum* and *P. bidens* is very similar, and some morphometric and meristic features are summarized in Table III.

Table III: Morphological differences between the first juvenile stages of Perisesarma fasciatum and Perisesarma bidens (~, described from the figure)

Feature	*P. fasciatum* (present study)	*P. bidens* (Fukuda and Baba, 1976)
Carapace length (mm)	1.02–1.05	1.00
Carapace width (mm)	0.85	0.86
Antenna		
Setae on peduncle	1–2,1,1,1	~0,1,1,1
Setae on flagellum	0,2,0,4–5,3	~0,0,2,1,5,2
Maxillule		
Setae on coxal end	11	~11
Setae on basial end	19	~16
Maxilla		
Setae on scaphognathite	34–36	~33
Maxilliped 1		
Setae on endopod	6	~4
Setae on exopod	1,4	~0,4
Setae on epipod	6–7	~8
Maxilliped 2		
Setae on endopod	0–2,1,4–5,7	1,1,6,9
Maxilliped 3		
Setae on endopod	14,8,4,4–5,4	8,8,3,4,7
Setae on exopod	6,4	~6
Setae on epipod	20	~19

This study confirms that there is a useful set of morphological characteristics that allows to distinguish larvae of the crab family Sesarmidae *sensu* (Schubart *et al.*, 2002) from all other decapod larvae, and these characteristics are shared by the Asian mangrove crab *P. fasciatum*, as described here. However, for the identification of larval stages from the plankton at a genus and species level, descriptions of many more larvae of sesarmid crabs will be necessary and taxonomic revisions of the genera currently comprised within this family will need to be continued.

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