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First zoeal stages of *Epigrapsus politus* Heller, *E. notatus* (Heller) and *Gecarcoidea lalandii* H. Milne-Edwards, with remarks on zoeal morphology of the Gecarcinidae Macleay (Crustacea: Brachyura)

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The crab family Gecarcinidae Macleay, 1838 currently consists of 18 species that are grouped in four genera. Larval data for the Gecarcinidae were only known for species of the genera *Cardisoma* Latreille, 1825 and *Gecarcinus* Leach, 1814. In the present paper, the first zoeal stage of *Gecarcoidea lalandii* H. Milne-Edwards, 1837, *Epigrapsus politus* Heller, 1862 and *E. notatus* Heller, 1865 are described and illustrated. Zoeal morphology of the Gecarcinidae is reviewed, taking into account all previous descriptions and analysing the relationships between the different genera of Gecarcinidae based on zoeal morphological characters. A series of typical morphological features is proposed for the zoea larvae of this family differentiating them from the rest of the Grapsoidea.

KEYWORDS: Larval morphology, Gecarcinidae, *Gecarcoidea*, *Epigrapsus*, zoea.

Introduction

The grapsoid family Gecarcinidae has a circumtropical distribution, with many species known only from oceanic islands. The family presently consists of 18 species that are distributed among four genera: *Cardisoma* Latreille, 1825, *Gecarcinus* Leach, 1814, *Gecarcoidea* H. Milne Edwards, 1837 and *Epigrapsus* Heller, 1862 (Türkay, 1970, 1973, 1974; Tavares, 1991). At this point, we follow Tavares (1991) in considering *Discoplax* A. Milne Edwards, 1873 and *Johngarthia* Türkay, 1970 subgenera of *Cardisoma* and *Gecarcinus*, respectively.

Crabs included in the Gecarcinidae are often large in size and commonly referred to as 'land crabs', based on the terrestrial habits shown by adults of most of the

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species of this family. Some species can be found several kilometres away from the coast (Gilchrist, 1988). However, no gecarcinid species is a true land crab, since all of them have to return to the sea for larval release. All zoea larvae so far known are marine planktonic, and larval development consists of five to six zoeal stages and one megalopal stage.

Currently, larval data are available for only two genera and six species of Gecarcinidae. Complete larval development is known for *Cardisoma (C.) guanhumi* Latreille, 1825 (Costlow and Bookhout, 1968), *Cardisoma (C.) carnifex* (Herbst, 1794) (Kannupandi *et al.*, 1980), *Gecarcinus (G.) lateralis* (Freminville, 1835) (Willems, 1982) and *Cardisoma (Discoplax) hirtipes* Dana, 1851 (Shokita and Shikatani, 1990). The prezoea of *Cardisoma (C.) armatum* Herklots, 1852 has been described by Cannon (1923) and the prezoea and first zoeal stage of *Gecarcinus (Johngarthia) planatus* Stimpson, 1860 has been described by Erhardt and Niaussat (1968). Previous incomplete descriptions of the first zoeal stages of *Cardisoma guanhumi* by Moreira (1913) and *Gecarcinus lateralis* by Cabrera (1965) have not been considered in the present study due to the availability of newer and more complete descriptions.

This paper provides a detailed morphological description of the first zoeal stages of *Gecarcoidea lalandii* H. Milne Edwards, 1837, *Epigrapsus politus* Heller, 1862 and *E. notatus* (Heller, 1865) based on laboratory-hatched material. For both of these genera, there were no previous zoeal descriptions. The comparison with descriptions of other gecarcinid genera gives new insights into possible phylogenetic relationships within this family.

Materials and methods

First stage zoea larvae were obtained from two hatches of *Gecarcoidea lalandii*, nine hatches of *Epigrapsus politus* and two hatches of *E. notatus*. Ovigerous crabs of *Gecarcoidea lalandii* were collected in Hsiang-Chiao-Wan, Pingtung Province, Taiwan (30 May 1997 and 3 August 1999 by H.-C.L.). One ovigerous *Epigrapsus politus* was from Pingtung, Taiwan (28 August 1999 by H.-C.L.), another one from Hsiang-Chiao-Wan, Taiwan (2 September 1999 by H.-C.L.), and seven were collected from Malalayang Beach, Sulawesi, Indonesia (23 January 2000 by C.D.S.). Two ovigerous crabs of *E. notatus* were collected from Hengchun and Hualien, Taiwan (2 and 30 September 1999 by H.-C.L.). Ovigerous crabs were maintained in containers with natural sea water until hatching. Freshly hatched larvae with an active natatory behaviour were fixed in 70% ethanol. Appendages were dissected under a Wild MZ8 binocular microscope, and drawings were made using an Olympus BH-2 microscope equipped with Nomarski interference contrast and attached camera lucida. All measurements were made by an ocular micrometer. Drawings were based on 10 larvae, and measurements on 20–30 larvae. One hatch of *G. lalandii*, three hatches of *E. politus* (one from Taiwan, and two from Indonesia) and two hatches of *E. notatus* were measured. No significant differences in morphology and morphometry were found between hatches of the same species. In the case of *E. politus*, all drawings are based on larvae from one hatch (female 4) from Sulawesi. The following measurements were made: rostro-dorsal length (rdl) was measured 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; carapace width (cw) as the distance between the tips of the lateral spines. The long natatory setae on the distal exopod segments of the first and second maxillipeds are truncated in figures 2 and 5. Descriptions

and figures are arranged according to the standard proposed by Clark *et al.* (1998). Maternal crabs of *Gecarcoidea lalandii*, *Epigrapsus politus*, and *E. notatus* were deposited at the National Taiwan Museum, Taipei (TMCD 3276–3278). Samples of larvae of the three species were deposited at the United States National Museum of Natural History, Washington, DC under the accession number USNM 310337, 310336 and 310335 respectively.

Results

Descriptions

Gecarcoidea lalandii H. Milne-Edwards, 1837
Zoea I
(figures 1A–C, 2A–D, 3A–C)

Dimensions. rdl: 0.54±0.02 mm; cl: 0.33±0.01 mm; cw: 0.37±0.01 mm.

Cephalothorax (figure 1A). Globose, smooth and without tubercles, with an anterodorsal protuberance as a carina. Dorsal spine short and slightly curved. Rostral and lateral spines short and straight. One pair of posterodorsal setae. Anterodorsal region, posterior and ventral margin without setae. Eyes sessile.

Antennule (figure 1B). Uniramous. Endopod absent. Exopod unsegmented with three aesthetascs (two long and one thin and short) and two setae.

Antenna (figure 1C). Well-developed protopod almost reaching the tip of rostral spine and bearing two rows of well-developed spines. Exopod elongated, reaching the middle of the protopod and bearing a group of three minute subterminal spinules, one long and one short terminal setae, and five short terminal spines.

Mandible. Endopod palp absent.

Maxillule (figure 2A). Coxal endite with six plumodenticulate setae. Basial endite with five setae (two cuspidate and three plumodenticulate). Endopod two-segmented with one plumodenticulate seta on the proximal segment and one medial, two subterminal and two terminal plumodenticulate setae on the distal segment. Exopod absent.

Maxilla (figure 2B). Coxal and basial endites bilobed with 5+ 4 plumodenticulate setae. Endopod unsegmented, bilobed with one long plumodenticulate and one short simple seta on inner lobe and two long plumodenticulate setae on outer lobe. Scaphognathite with four plumose marginal setae and one long setose posterior process.

First maxilliped (figure 2C). Coxa with one seta. Basis with 10 medial setae arranged 2, 2, 3, 3. Endopod five-segmented with 2, 2, 1, 2, 5 (one subterminal+ four terminal) setae. Exopod two-segmented, with four long terminal plumose natatory setae on the distal segment. Dorsal part of basis and exopod covered with minute spinules.

Second maxilliped (figure 2D). Coxa without setae. Basis with four medial setae arranged 1, 1, 1, 1. Endopod three-segmented with 1, 1, 6 (three subterminal+ three terminal) setae. Exopod two-segmented, with four long terminal plumose natatory setae on distal segment. Dorsal part of basis and exopod covered with minute spinules.

Third maxilliped. Absent.

Pereiopods. Absent.

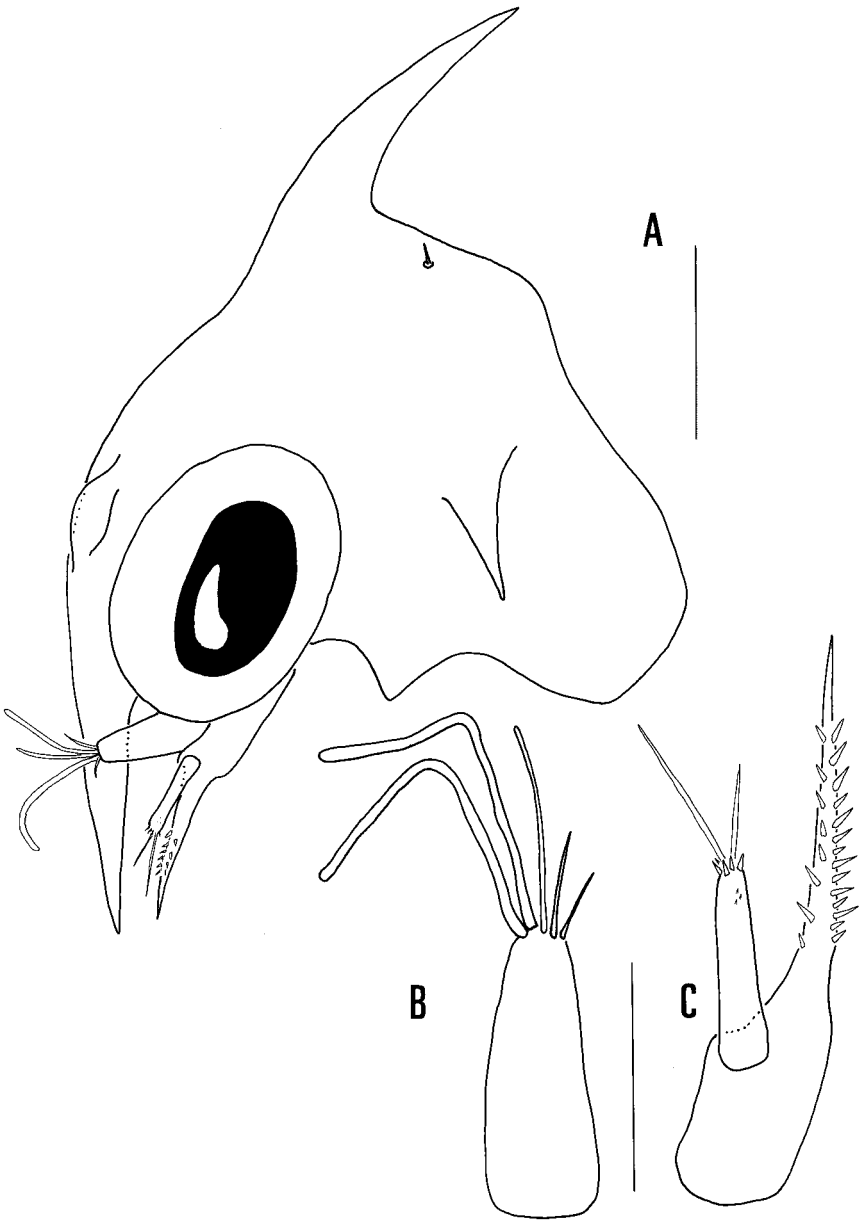

FIG. 1. *Gecarcoidea lalandii* H. Milne Edwards, 1837, Zoea I. (A) Cephalothorax, lateral view; (B) antennule; (C) antenna. Scale bars: (A) 0.1 mm, (B, C) 0.05 mm.

Abdomen (figure 3A, B). Five abdominal somites. Somites 2–3 with one pair of dorsolateral processes. Somites 3–5 with conspicuous posterolateral processes. Somites 2–5 with one pair of posterodorsal setae. Pleopods absent.

Telson (figure 3A–C). Bifurcated with three pairs of stout spinulate setae on posterior margin. Along the distal part of each furcal arm two rows of minute spines. Two lateral spines on outer margin of each furcal arm.

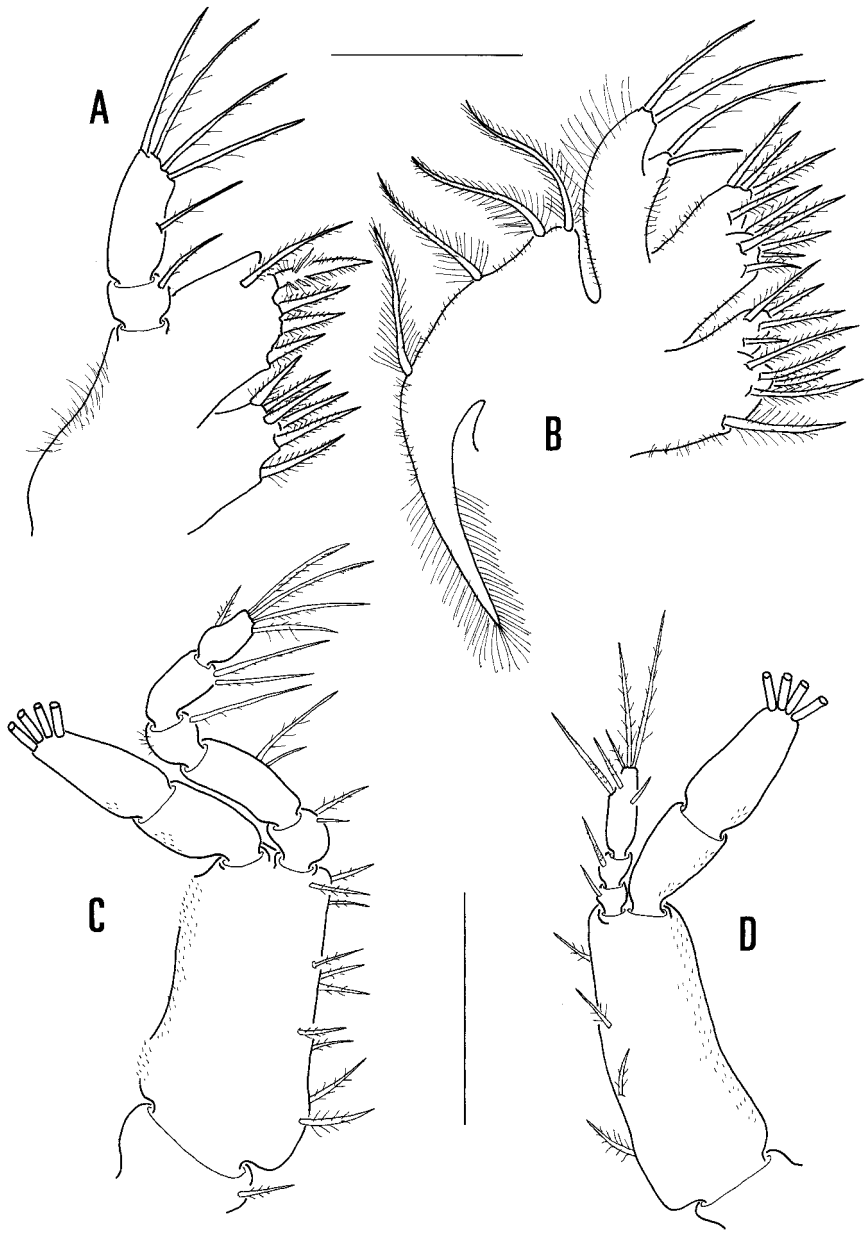

FIG. 2. *Gecarcoidea lalandii* H. Milne Edwards, 1837, Zoea I. (A) Maxillule; (B) maxilla; (C) first maxilliped; (D) second maxilliped. Scale bars: (A, B) 0.05 mm, (C, D) 0.1 mm.

Epigrapsus politus Heller, 1862
Zoea I
(figures 4A–C, 5A–D, 6A–C)

Dimensions. rdl: 0.42±0.02 mm; cl: 0.24±0.01 mm; cw: 0.33±0.01 mm.

Cephalothorax (figure 4A). Globose, smooth and without tubercles, with an anterodorsal protuberance as a carina. Dorsal spine short and slightly curved.

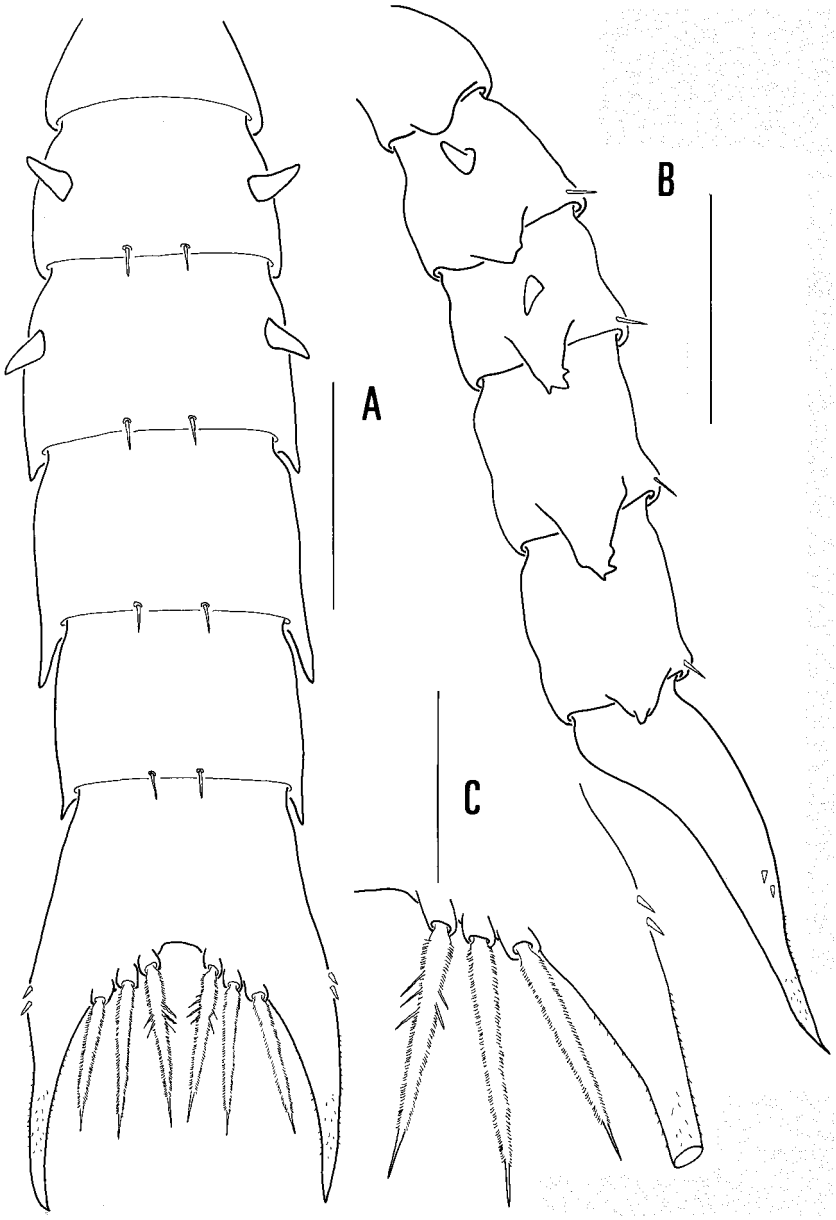

FIG. 3. *Gecarcoidea lalandii* H. Milne Edwards, 1837, Zoea I. (A) Abdomen, dorsal view; (B) abdomen lateral view; (C) telson detail. Scale bars: (A, B) 0.1 mm, (C) 0.05 mm.

Rostral and lateral spines short and straight. One pair of posterodorsal setae. Anterodorsal region, posterior and ventral margin without setae. Eyes sessile.

Antennule (figure 4B). Uniramous. Endopod absent. Exopod unsegmented with three aesthetascs (two long and one short), and two setae.

Antenna (figure 4C). Well-developed protopod reaching the tip of rostral spine and bearing two unequal rows of well-developed spines. Exopod elongated, bearing

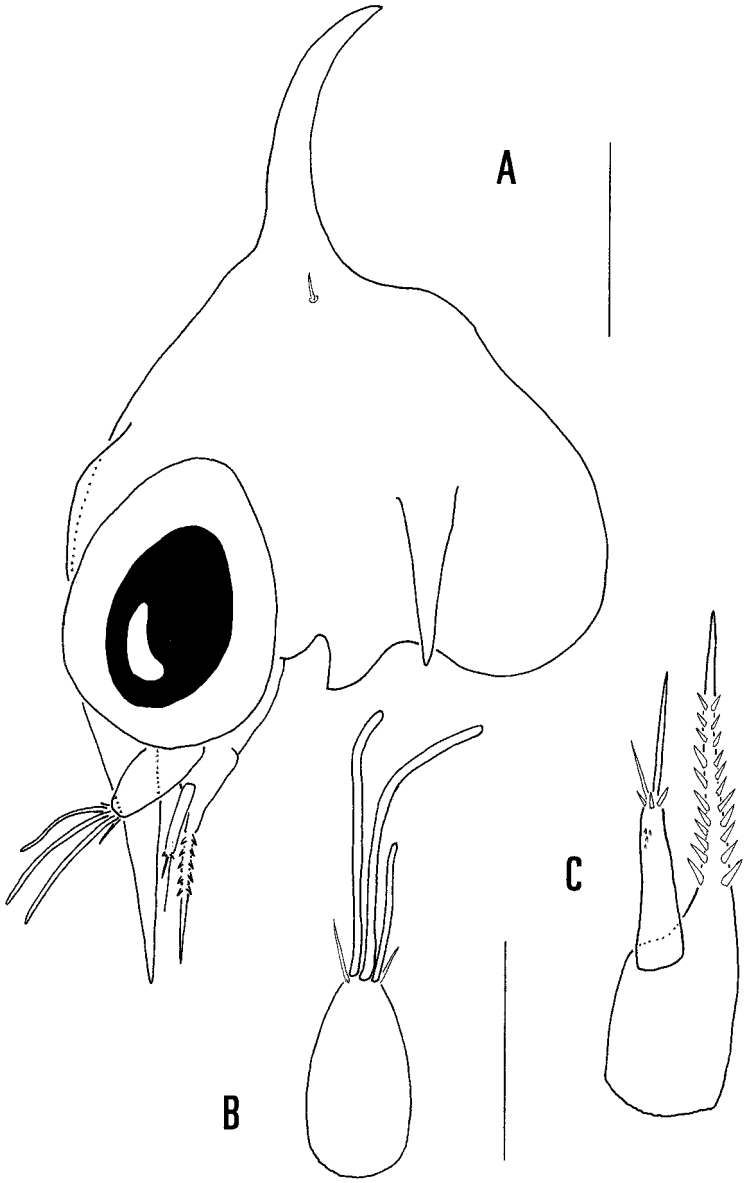

FIG. 4. *Epigrapsus politus* Heller, 1862, Zoea I from Sulawesi, Indonesia. (A) Cephalothorax, lateral view; (B) antennule; (C) antenna. Scale bars: (A) 0.1 mm, (B, C) 0.05 mm.

a group of four minute subterminal spinules, one long and one short terminal setae, and three short terminal spines.

Mandible. Endopod palp absent.

Maxillule (figure 5A). Coxal endite with six plumodenticulate setae. Basial endite with five setae (two cuspidate and three plumodenticulate). Endopod two-segmented with one plumodenticulate seta on the proximal segment and one medial, two subterminal and two terminal plumodenticulate setae on the distal segment. Exopod absent.

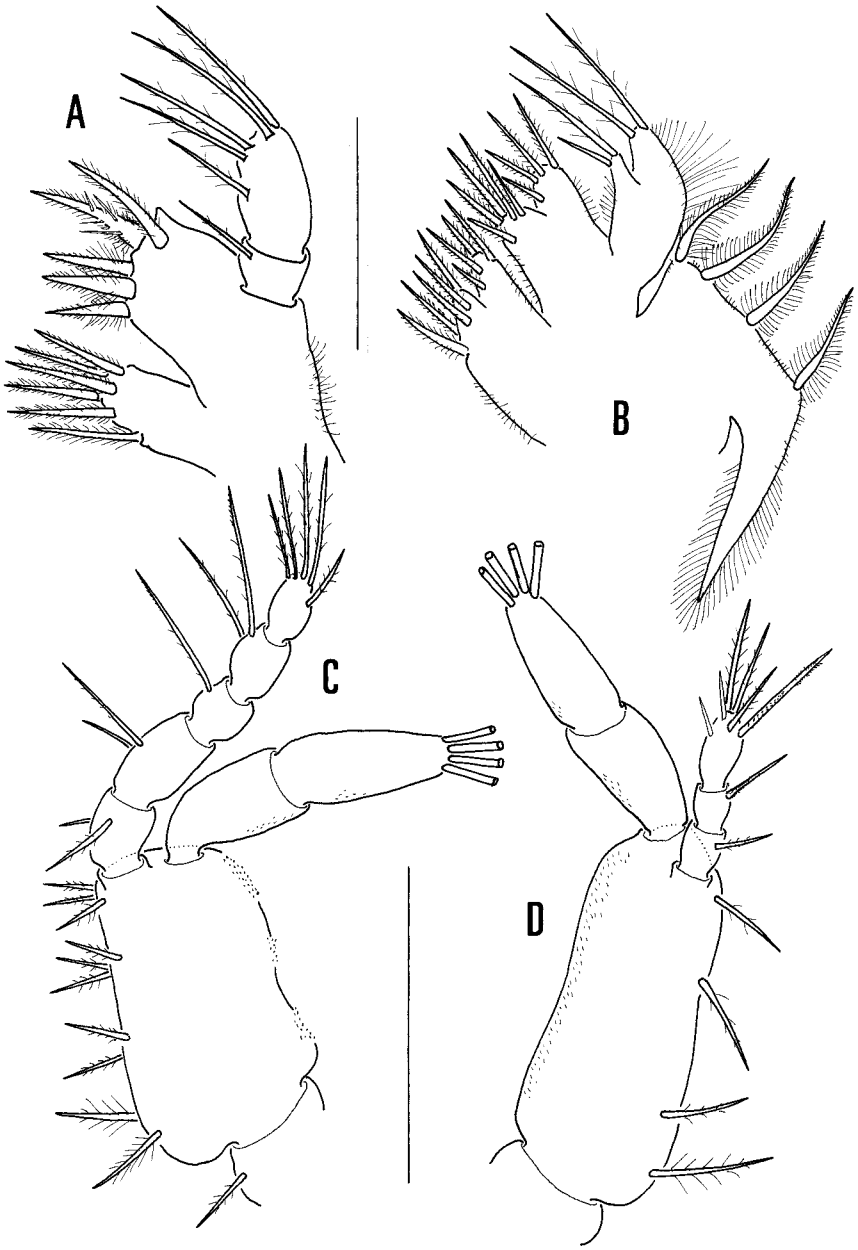

FIG. 5. *Epigrapsus politus* Heller, 1862, Zoea I from Sulawesi, Indonesia. (A) Maxillule; (B) maxilla; (C) first maxilliped; (D) second maxilliped. Scale bars: (A, B) 0.05 mm, (C, D) 0.1 mm.

Maxilla (figure 5B). Coxal and basial endites bilobed with 5+ 4 plumodenticulate setae. Endopod unsegmented, bilobed, with one long plumodenticulate and one short simple seta on inner lobe and two long plumodenticulate setae on outer lobe. Scaphognathite with four plumose marginal setae and one long setose posterior process.

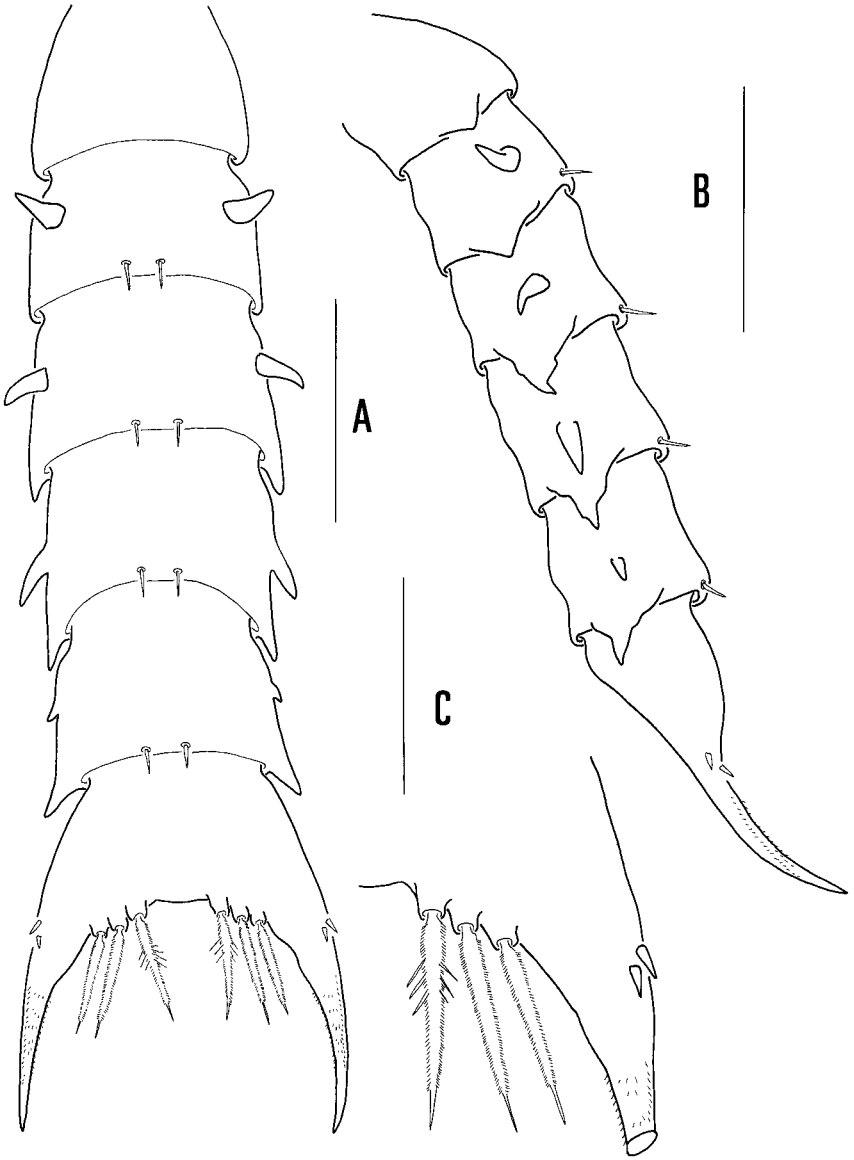

FIG. 6. *Epigrapsus politus* Heller, 1862, Zoea I from Sulawesi, Indonesia. (A) Abdomen, dorsal view; (B) abdomen lateral view; (C) telson detail. Scale bars: (A, B) 0.1 mm, (C) 0.05 mm.

First maxilliped (figure 5C). Coxa with one seta. Basis with 10 medial setae arranged 2, 2, 3, 3. Endopod five-segmented with 2, 2, 1, 2, 5 (one subterminal + four terminal) setae. Exopod two-segmented, with four long terminal plumose natatory setae on the distal segment. Dorsal part of basis and exopod covered with minute spinules.

Second maxilliped (figure 5D). Coxa without setae. Basis with four medial setae arranged 1, 1, 1, 1. Endopod three-segmented with 1, 1, 6 (three subterminal + three terminal) setae. Exopod two-segmented, with four long terminal plumose natatory

setae on the distal segment. Dorsal part of basis and exopod covered with minute spinules.

Third maxilliped. Absent.

Pereiopods. Absent.

Abdomen (figure 6A, B). Five abdominal somites. Somites 2–5 with one pair of dorsolateral processes and one pair of posterodorsal setae. Somites 3–5 with long posterolateral processes. Pleopods absent.

Telson (figure 6A–C). Bifurcated with three pairs of stout spinulate setae on posterior margin. Along the distal part of each furcal arm two rows of minute spines. One dorsal and one lateral spine on outer margin of each furcal arm.

Epigrapsus notatus (Heller, 1865)
Zoea I
(figure 7A, B)

Dimensions. rdl: 0.49±0.03 mm; cl: 0.26±0.02 mm; cw: 0.38±0.01 mm.

The first zoeal stage of *E. notatus* is very similar to that of *E. politus*; differences were only found in the size and abdominal morphology. We therefore do not repeat here the complete description, and the appendages are not illustrated, except for the abdominal characters.

Abdomen (figure 7A, B). Five abdominal somites. Somites 2–5 with one pair of dorsolateral processes and one pair of posterodorsal setae. Somites 3–5 with long posterolateral processes, those of somites 4–5 longer and more acute than in *E. politus*. Pleopods absent.

Discussion

The genera *Gecarcoidea* and *Epigrapsus* are both restricted to the Indo-West Pacific region. The distribution of *Gecarcoidea lalandii* includes the Red Sea (Holthuis, 1977), South-East Asia (de Man, 1929) and the western Pacific (Dai and Yang, 1991) (see Ng, 1998). The distributions of *Epigrapsus politus* and *E. notatus* have recently been revised by Ng *et al.* (1998, 2000). However, *E. politus* had not been previously reported from Taiwan (Liu and Schubart, unpublished) and Sulawesi, localities from where ovigerous females were collected for the present study. Previously, *E. politus* was only known from Tahiti, Tuamotu, Caroline Islands, Japan, Bertrand Island (Papua New Guinea), Christmas Islands and northern Sumatra (see Ng *et al.*, 2000).

The larval morphology of the Gecarcinidae is poorly documented. For only six species and two genera was there knowledge of larval data (see Introduction). Furthermore, some of the larval descriptions present incorrect setal counts or lack detail, as shown by a recent comparison of zoea larvae of *Cardisoma carnifex* from Taiwan with the ones described by Kannupandi *et al.* (1980) from India (table 1) and further exemplified by the study of Erhardt and Niaussat (1968) on larvae of *Gecarcinus planatus*. With the present description of the first zoeal stage of *Gecarcoidea lalandii*, *Epigrapsus politus* and *E. notatus*, larval data become available for all four genera of the Gecarcinidae and allow first intergeneric comparisons. Morphological characters of all Gecarcinidae zoea I that have been described are compiled in table 1. The following observations can be made: all first zoeae show the same setation pattern on the basis of first maxilliped (2, 2, 3, 3) and second maxilliped endopod (1, 1, 6), and also the same type of antennal and telson

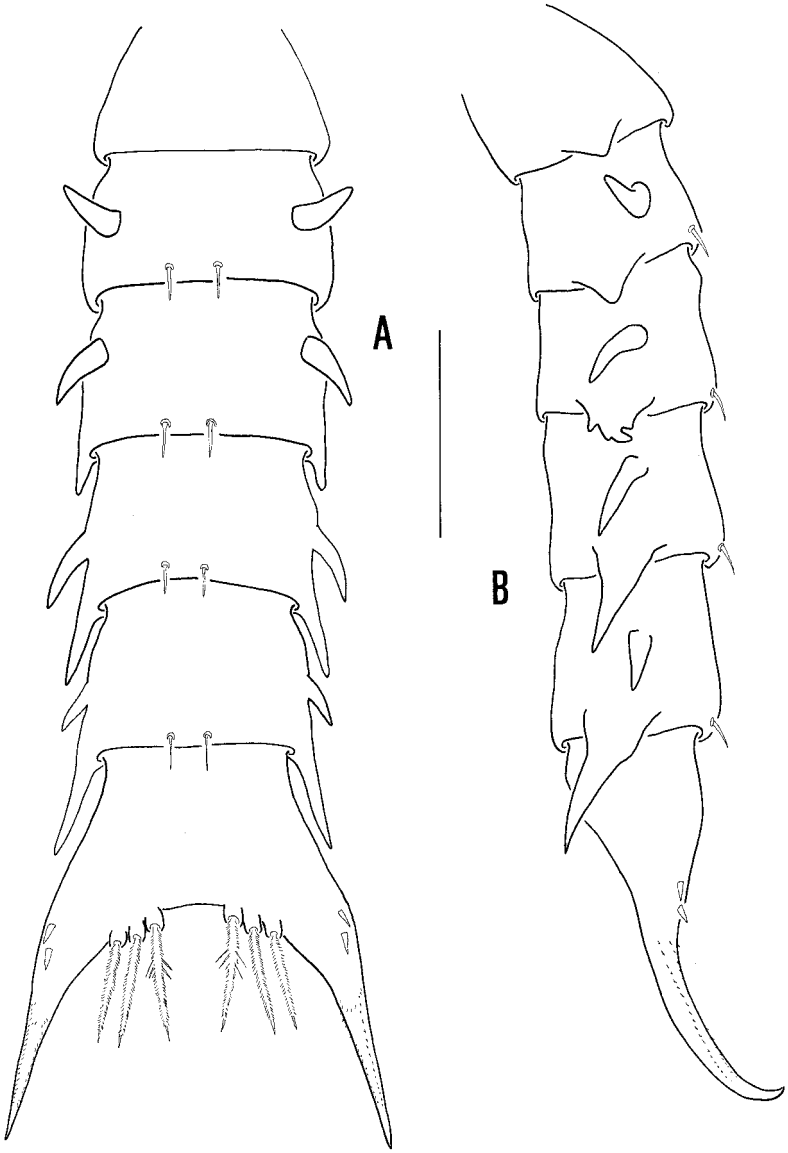

FIG. 7. *Epigrapsus notatus* (Heller, 1865), Zoea I. (A) Abdomen, dorsal view; (B) abdomen, lateral view. Scale bar = 0.1 mm.

morphology (telson with the current exception of *G. lateralis*). The setation pattern of the endopod of the maxillule (1, 1+4) and basis of second maxilliped (1, 1, 1, 1) are not shown in the table 1 because they are shared within the Gecarcinidae as well as with all other Grapsoidea. Zoea larvae of the family Gecarcinidae display a combination of characters that unifies them and allows them to be distinguished from the rest of the grapsoid families (Grapsidae, Plagusiidae, Sesarmidae, Varunidae, *sensu* Schubart *et al.*, 2000a). The combination of antennal and telson morphology, and setation of the second maxilliped endopod (1, 1, 6) is not present in any other family of grapsoids. This seems to reflect a possible monophyletic origin

Morphological features of known first zoeal stages of species included in the family Gecarcinidae.

Species	Zoeal stages	Telson type	Antenna type	Mxl Endp	Mxp 1 basis	Mxp 2 Endp	Abd Dlp	Reference
Cardisoma (C.) armatum Herklots, 1851	5–6	A	A	2, 3	2, 2, 3, 3	1, 1, 6	2–3	Cuesta and Anger, in preparation
Cardisoma (C.) carnifex (Herbst, 1794)	5	A	A	2, 3[†]	2, 2, 3, 3	1, 1, 6[‡]	2–3	Cuesta *et al.*, in preparation
Cardisoma (C.) guanhumi Latreille, 1825	5	A	A	2, 3	2, 2, 3, 3[§]	1, 1, 6	2–3	Costlow and Bookhout, 1968
Cardisoma (Discoplax) hirtipes Dana, 1852	5	A	A	2, 3	2, 2, 3, 3	1, 1, 6	2–3	Shokita and Shikatani, 1990
Epigrapsus politus Heller, 1862	?	A	A	2, 2	2, 2, 3, 3	1, 1, 6	2–5	Present study
Epigrapsus notatus (Heller, 1865)	?	A	A	2, 2	2, 2, 3, 3	1, 1, 6	2–5	Present study
Gecarcinus (G.) lateralis Fréminville, 1835	6	B	A	2, 2	2, 2, 3, 3	1, 1, 6	2–3	Willems, 1982
Gecarcoidea lalandii H. Milne Edwards, 1837	?	A	A	2, 2	2, 2, 3, 3	1, 1, 6	2–3	Present study

Abbreviations: Mxl, maxilla; Mxp, maxilliped; Abd, abdomen; Endp, endopod; Dlp, dorsolateral processes; ?, no data. Telson type A refers to furca with outer spines, and type B refers to furca without outer spines. Antenna type A refers to exopod equal to two-thirds of protopod length, with two unequal-sized simple terminal setae and two to five terminal short spines.

[†]3, 4 in Kannupandi *et al.* (1980).

[‡]1, 3, 3 in Kannupandi *et al.* (1980).

[§]Cuesta *et al.*, in preparation.

of the Gecarcinidae, which was also suggested for the genera *Cardisoma* and *Gecarcinus* based on mtDNA sequence data (Schubart *et al*., 2000a, 2000b).

Within the Gecarcinidae, the only important difference is the setation of the maxillar endopod. According to this, two major groups can be distinguished within the Gecarcinidae: *Epigrapsus*, *Gecarcinus* and *Gecarcoidea* on one hand (with a 2, 2 setation), and the genus *Cardisoma* on the other hand (with 2, 3). The setation of the maxillar endopod has already been noted by Rice (1980) as of important taxonomic value, and recently it has been used to distinguish between grapsoid families (Cuesta, 1999). This character would thus support the recognition of two distinct taxa by separating *Cardisoma* with both of its subgenera (*Cardisoma* and *Discoplax*) from the rest of the Gecarcinidae. The assumption that the Gecarcinidae is a heterogeneous group was already mentioned by Willems (1982), but new data on adult and megalopal morphology, as well as molecular evidence will be necessary to establish the taxonomic status of these two groups of genera within the Grapsoidea.

Within the genera *Gecarcoidea*, *Gecarcinus* and *Epigrapsus* the only differences are in abdominal morphology. The two species of *Epigrapsus* have dorsolateral processes on somites 2–5, whereas *Gecarcoidea* and *Gecarcinus* only on somites 2–3. *Gecarcoidea lalandii* possesses conspicuous posterolateral processes on somites 3–5, similar to those of the Grapsidae s. str. (see Cuesta *et al*., 1998; Cuesta and Schubart, 1999) and characterized by the lobulate shape of the tip versus the triangular shape of the tip of these processes in *Epigrapsus politus*, *E. notatus* and *Gecarcinus lateralis*. Despite the fact that larvae of *Gecarcinus (Johngarthia) planatus* have been mentioned and illustrated in the literature (Erhardt and Niaussat, 1968), larval characters of this species could not be included in our comparison because a proper description of the larvae is lacking, and the drawings and photographs are poor and do not allow distinction of morphological characters.

Within the Grapsoidea, the gecarcinid group comprising *Epigrapsus*, *Gecarcinus* and *Gecarcoidea* shows great similarity with the Varunidae based on zoeal morphology. The features shared between these two groups are the setation pattern of endopod of maxilla (2, 2) and the presence of lateral cephalothoracic spines. On the other hand, these groups can be clearly differentiated by telson and antennal morphology and the setation of the endopod of second maxilliped (1, 1, 6 versus 0, 1, 6). The genus *Cardisoma* shares antennal and telson morphology, the number of abdominal dorsolateral processes and the setation pattern of the endopod of the maxilla (2, 3) with Sesarmidae. However, the presence of lateral spines on the cephalothorax, and the setation of the endopod of the second maxilliped (1, 1, 6 versus 0, 1, 6) are clearly distinguishing characters. The setation of the basis of the first maxilliped (2, 2, 3, 3) is shared by all Gecarcinidae, Sesarmidae and Varunidae (see table 1; Schubart and Cuesta, 1998; Cuesta *et al*., 2000) and distinguishes them from the Plagusiidae and Grapsidae s. str. (2, 2, 2, 2). The description and comparison of the larvae of Gecarcinidae show that these larvae carry a mosaic of characters that are also present in other grapsoid families (especially Sesarmidae and Varunidae) and confirms the conclusion of Schubart *et al*. (2000a) that this family should be included within the Grapsoidea, at the same taxonomic level as the other grapsoid families.

Acknowledgements

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