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**ABSTRACT**
The larval development of the spider crab *Rochinia gracilipes* Milne-Edwards, 1875 (Crustacea: Decapoda: Brachyura: Majoidea: Epialtidae: Pisinae) is described and illustrated from laboratory-reared larvae. Development consisted of two zoeal stages and one megalopa, following the typical pattern in Majoidea. Zoea I of *R. gracilipes, R. debilis* and *R. carpenteri* differed in lengths of the rostral spine of the carapace, in the number of setae and aesthetascs of several head appendages (exopods of antennules, endopods of maxillules, and endopods and scaphognathites of maxillae) and in the length of posterolateral processes of abdominal somites; lateral carapace spines were present only in *R. carpenteri* and pleopod buds only in *R. debilis*. Megalopae of *Rochinia gracilipes* and *R. carpenteri* differed in several notable characters: a dorsal spine and long rostrum of the carapace, as well as spines in coxa and ischium of pereiopods, appeared only in *R. carpenteri*, and podobranchiae of the 3rd maxilliped appeared only in *R. gracilipes*; they also differed in setation of abdomen and pleopods. The comparison of the available information on Pisinae larval development suggested that larval morphology would not help to accurately understand the phylogenetic relationships of this subfamily of spider crabs.

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Spider crab; larval morphology; Decapoda; Brachyura; Argentina



## Introduction

The brachyuran superfamily Majoidea Samouelle, 1819 (Decapoda: Pleocyemata: Brachyura) is considered to be a diverse, though monophyletic, group of spider crabs that share two morphological synapomorphies: the terminal moult, and a highly abbreviated larval development (Tsang et al. 2014). It includes aproximately 800 extant species (Tsang et al. 2014) grouped in five families: Epialtidae MacLeay, 1838; Inachidae MacLeay, 1838; Inachoididae Dana, 1851; Majidae Samouelle, 1819; and Oregoniidae Garth, 1958. However, the monophyly of some majoid families has been questioned

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Supplemental data for this article can be accessed here.

(Hultgren and Stachowicz 2008; Hultgren et al. 2009). Previous checklists also included Hymenosomatidae MacLeay, 1838 in Majoidea (Ng et al. 2008; De Grave et al. 2009; Ahyong et al. 2011), but Guinot (2011) argued that these small crabs are not part of it and recognised a separate superfamily. The most diversified family of Majoidea is Epialtidae with four subfamilies: Epialtinae MacLeay, 1838; Pisinae Dana, 1851; Pliosomatinae Števcic, 1994 and Tychinae Dana, 1851 (Ng et al. 2008).

The most speciose genus of Pisinae is *Rochinia* Milne-Edwards, 1875. The systematics of *Rochinia* has suffered many changes in the last 30 years (e.g. Griffin and Tranter 1986; Tavares 1991; Ng et al. 2008). At present, 38 species are included: 22 live in the south-western Pacific and eastern Indian Ocean, four in Japan, three in the Galápagos Islands, two near South Africa, four in the northwestern Atlantic (including the Caribbean Sea and northern Brazil) and one in the northeastern Atlantic, and two are endemic to the southwestern Atlantic (Komatsu and Takeda 2003; Ng et al. 2008; Richer De Forges and Ng 2009; Richer De Forges and Poore 2008; De Grave et al. 2009; McLay 2009; Takeda 2009; Pettan 2013; Pettan and Tavares 2014). In addition, a Miocene fossil species, *R. boschii*, has been described from Patagonia (Casadio et al. 2005). The type species of *Rochinia* is *R. gracilipes* A. Milne-Edwards, 1875 from Cabo Corrientes, Argentina; it is the only shallow-water species of this genus and inhabits a range from Cabo Frio (Brasil) to Cabo de Hornos (Argentina) (Rathbun 1925; Boschi et al. 1992; Pettan and Tavares 2014).

Detailed descriptions of the larval stages of crabs, as well as other decapod crustaceans, reared in the laboratory, have been increasing in both quantity and quality (e.g. Clark et al. 1998a; Anger 2001). The aims of such larval descriptions are twofold: to identify species within plankton samples and to examine phylogenies on the basis of a different set of characters, and to compare the results with those obtained from adult data (e.g. Pohle and Marques 2000; Santana et al. 2004, 2006; Clark 2009; Hultgren et al. 2009). The larval morphology of Pisinae has been reviewed by Santana et al. (2006); among 256 valid species corresponding to 53 genera (De Grave et al. 2009; McLay 2009; Takeda 2009), there are descriptions for larvae of only 29 species belonging to 15 genera (Table 1). Larvae of *Rochinia* spp. have been scarcely studied: only a description of the complete larval development of *R. carpenteri* (Thomson 1873) from the Northeastern Atlantic (Ingle 1979) and a description of the first zoea of *R. debilis* Rathbun 1932 from Japan (Komatsu and Takeda 2003) were available prior to the present work. The specific purpose of this study is to describe and illustrate the complete larval development of *R. gracilipes* and to compare its larval morphology with *R. carpenteri* and *R. debilis*, and with other Pisinae species, in order to contribute to the taxonomy of Pisinae and, especially, of *Rochinia*.

## Material and methods

Ovigerous crabs of *Rochinia gracilipes* were collected from the macrofouling community adhering to marinas in Mar del Plata Harbour, Argentina (38°02´S, 57°31´30″W). The material was extracted with spatulas, and crabs were separated *in situ*, transported alive to the laboratory and maintained in an aquarium containing natural sea water until hatching. Immediately after hatching, only actively swimming larvae were transferred with wide-bore pipettes to individual cultivation vials (25 mL) and cultured at 20°C, 33–35 psu, and an artificial light regime of 8/16 h (light/dark). From zoea I to megalopa, *Artemia* sp. nauplii were offered as food *ad libitum*. Water and food were changed daily, and larvae were checked for mortality

**Table 1.** Species of Pisinae with known larval descriptions taken into account. Developmental stages are abbreviated 1, 2 (zoeas 1 and 2), M (megalopa) and C (first crab).

| | Source | Stage described |
|---|---|---|
| *Anamathia rissoana* (Roux 1828) | Guerao and Abelló (1996) | 1 |
| *Apiomithrax violaceus* (A. Milne-Edwards 1868) | Santana et al. (2004) | 1–2-M-C |
| *Doclea muricata* (Herbst 1788) | Krishnan and Kannupandi (1987), Ghory and Siddiqui (2009) | 1–2-M |
| *Doclea rissoni* Leach 1815, as *D. gracilipes* | Krishnan and Kannupandi (1988) | 1–2-M-C |
| *Goniopugettia sagamiensis* (Gordon 1930) | Taishaku and Konishi (2001) | 1–2-M-C |
| *Herbstia condyliata* (Fabricius 1787) | Guerao et al. (2008) | 1–2-M |
| *Hyastenus elongatus* Ortmann 1893 | Ko (1997) | 1–2-M |
| *Libidoclaea granaria* H. Milne Edwards & Lucas 1843 | Fagetti (1969a) | 1–2-M |
| *Libinia dubia* H. Milne-Edwards 1834 | Sandifer and Van Engel (1971) | 1–2-M |
| *Libinia emarginata* Leach 1815 | Johns and Lang (1977) | 1–2-M |
| *Libinia ferreirae* Brito Capello 1871 | De Bakker et al. (1990) | 1–2-M |
| *Libinia spinosa* H. Milne-Edwards 1834 | Boschi and Scelzo (1968), Clark et al. (1998b) | 1–2-M-C |
| *Lissa chiragra* (Fabricius 1775) | Guerao et al. (2003) | 1–2-M-C |
| *Notolopas brasiliensis Miers 1886* | Santana et al. (2006) | 1–2-M |
| *Pisa armata* (Latreille 1803) | Ingle and Clark (1980) | 1–2-M-C |
| *Pisa tetraodon* (Pennant 1777) | Rodríguez (1997) | 1–2-M-C |
| *Pisoides bidentatus* (A. Milne-Edwards 1873) | Kornienko and Korn (2007) | 1–2 M |
| *Pisoides edwardsii* (Bell 1835) | Fagetti (1969b) | 1–2-M |
| *Rochinia carpenteri* (Thomson 1873) | Ingle (1979) | 1–2-M |
| *Rochinia debilis* Rathbun 1932 | Komatsu and Takeda (2003) | 1 |
| *Scyra acutifrons* Dana 1852 | Oh and Ko (2010) | 1–2-M |
| *Scyra compressipes* Stimpson 1857 | Kim and Hong (1999) | 1–2-M |

and molts during each water change. Five females were used to obtain individuals of each stage for morphological studies, which were preserved in 4% formaldehyde.

Specimens were dissected under an Olympus SZ40 stereomicroscope. Measurements and drawings were made using an Olympus CH30 compound microscope equipped with a *camera lucida*. The following measurements were made with a micrometre eyepiece (40X): in zoea larvae, carapace length (CL) from the base of the rostrum to the posterior margin, rostrodorsal length (RDL) from the tip of the rostral spine to the tip of the dorsal spine; in the megalopa stage, carapace length (CL) from the base of the rostrum to the posterior margin, and carapace width (CW) as the maximum width. Drawings and measurements were based at least on five larvae per stage. Descriptions were arranged according to the standard proposed by Pohle and Telford (1981) and Clark et al. (1998a). Long setae of the 1st maxilliped of zoea I (Figure 2A) and of the 1st and 2nd maxillipedes of zoea II (Figure 4A and B) were drawn truncated, as well as pereiopods of megalopa (whole animal) (Figure 5A), aesthetascs of antennula and long setae of all pleopods of megalopae (Figure 5D and 7E–I), respectively.

Samples of larvae and the adult females were deposited together in the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' under the catalog number MACN-In 40,304.

## Results

### *Larval development and description*

The larval development included two zoeas and a megalopa phase. Only larvae that were very active after hatching were selected for further rearing in the laboratory. From

80 larvae cultured in February 2008, 16 (20%) reached the megalopa stage after 27.5 ± 2.22 days and one reached the first crab after passing 21 days as megalopa. Body measurements of zoeal and megalopal stages are summarised in Table 2.

Infraorder **BRACHYURA** Linnaeus, 1758
Superfamily **MAJOIDEA** Samouelle, 1819
Family **EPIALTIDAE** MacLeay, 1838
Subfamily **PISINAE** Dana, 1851
Genus ***Rochinia*** A. Milne Edwards 1875
***Rochinia gracilipes*** A. Milne Edwards 1875
First zoea (Figures 1A–G, 2A–F)

***Carapace (Figure 1A, B).*** Globose, smooth, without tubercles. Dorsal spine well developed, not spinulated. Rostral spine minute. Without lateral spines. One pair of anterodorsal simple setae, one pair of posterodorsal simple setae. Eyes sessile. Ventral margin with densely plumose 'anterior seta' (Clark et al. 1998b) followed by three posterior smaller plumose setae.

***Antennule (Figure 1C).*** Uniramous. Endopod absent. Exopod unsegmented, with four aesthetascs (two long and two shorter) and two setae.

***Antenna (Figure 1D).*** Protopod well developed, spinous process armed with strong spines arranged in two lines. Endopod bud aproximately 1/3 of protopod length. Exopod longer than protopod, spinous process armed with strong spines arranged in two lines, one spinulated seta, one simple seta.

***Mandible (Figure 1E).*** Palp absent.

***Maxillule (Figure 1F).*** Coxal endite with three sparsely plumose subterminal setae and four sparsely plumose terminal setae. Basial endite with three (one sparsely plumose, two plumose) subterminal setae and four plumodenticulate cuspidate terminal setae. Endopod two-segmented, one sparsely plumose seta in proximal segment, four terminal sparsely plumose setae on distal segment. Exopod and epipod setae absent.

***Maxilla (Figure 1G).*** Coxal endite bilobed with 4 + 4 plumose setae. Basial endite bilobed with five (two subterminal, three terminal sparsely plumose) and four (two subterminal, two terminal sparsely plumose). Endopod with four setae (two subterminal, two terminal sparsely plumose) setae. Microtrichia on lateral margin of endopod. Scaphognathite with 10 marginal plumose setae and posterior process.

**Table 2.** *Rochinia gracilipes* A. Milne-Edwards, 1875. Body dimensions of each larval stage.

| Stage | Rostrodorsal length | Carapace length | Carapace width | Number of larvae measured |
|---|---|---|---|---|
| | mean ± standard deviation (mm) | | | |
| Zoea I | 1.10 ± 0.02 | 0.70 ± 0.02 | – | 10 |
| Zoea II | 1.26 ± 0.04 | 0.92 ± 0.02 | – | 10 |
| Megalopa | – | 1.24 ± 0.01 | 0.99 ± 0.01 | 5 |

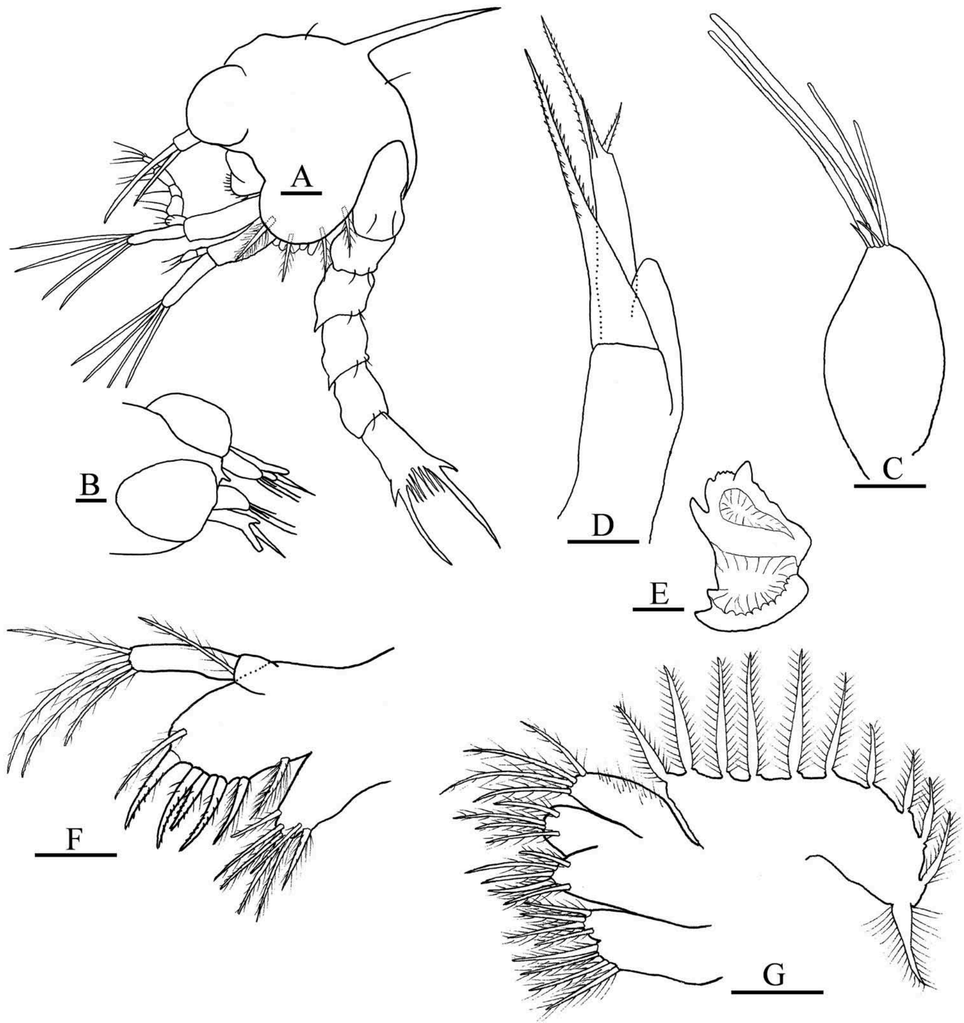


**Figure 1.** First zoea of *Rochinia gracilipes* A. Milne Edwards, 1875. (A) lateral view; (B) magnified latero-dorsal view showing the short rostrum; (C) antennule; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla. Scale bars = 0.1 mm.

***First maxilliped (Figure 2A).*** Coxa without setae. Basis with 10 plumose setae arranged two, two, three, three. Endopod five-segmented with three, two, one, two and five (one subterminal, four terminal) sparsely plumose, plumodenticulate setae. Exopod two-segmented; distal segment with four long plumose natatory setae with one conspicuous annuli.

***Second maxilliped (Figure 2B).*** Coxa without setae. Basis with three sparsely plumose setae arranged one, one, one. Endopod three-segmented with zero, one (sparsely plumose) and four (one plumodenticulate subterminal, two simple subterminal, one

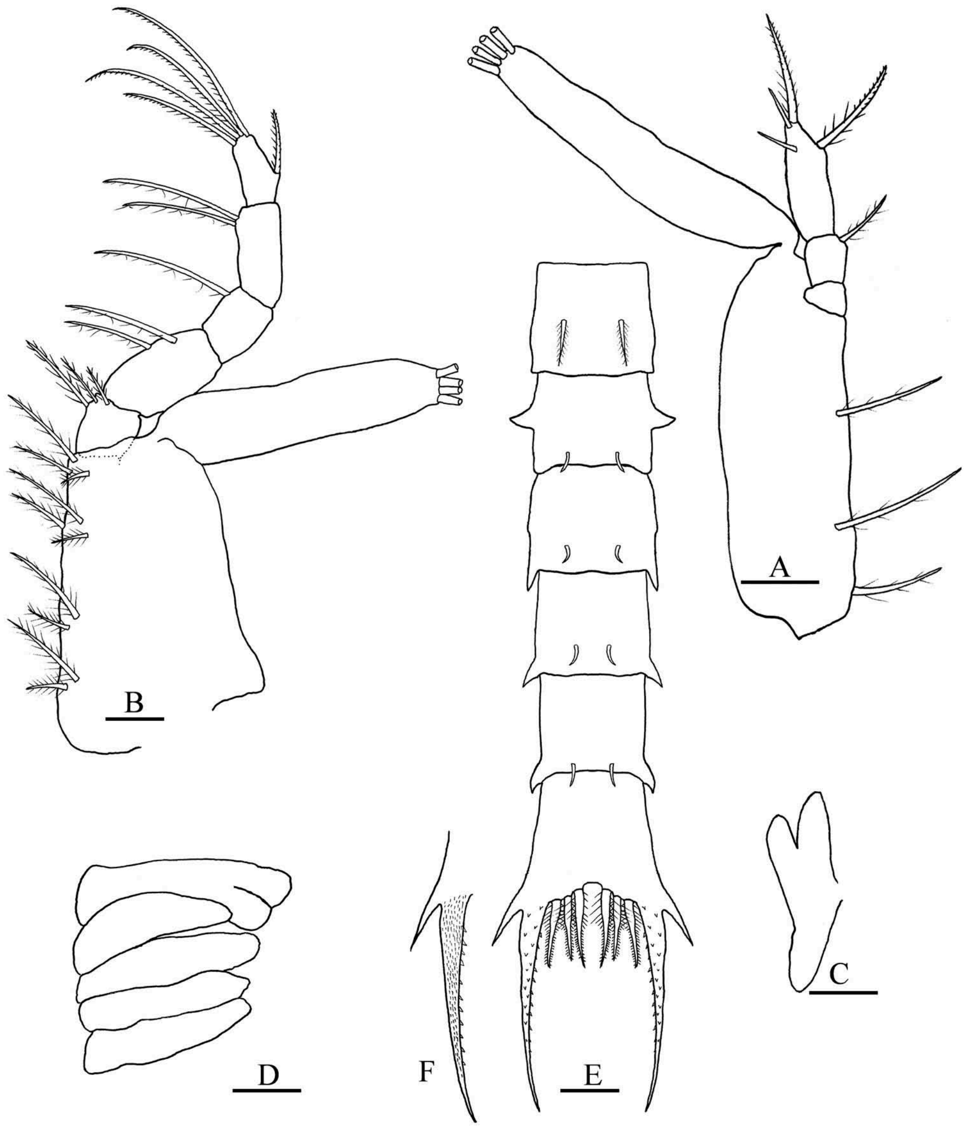


**Figure 2.** First zoea of *Rochinia gracilipes* A. Milne Edwards, 1875. (A) maxilliped I; (B) maxilliped II; (C) maxilliped III buds; (D) pereiopod buds; (E) dorsal view of abdomen and telson; (F) magnified view of left furca. Long setae of the maxilliped I (A) were drawn truncated. Scale bars = 0.1 mm.

plumodenticulate terminal) setae. Exopod two-segmented; distal segment with four long plumose natatory setae with one conspicuous annulus.

***Third maxilliped (Figure 2C).*** Triramous bud.

***Pereiopods (Figure 2D).*** Buds present, chela bilobed.

***Abdomen (Figure 2E).*** Five somites. Somite 2 with a pair of dorsolateral processes. Two dorsal plumose setae on somite 1. Pair of posterodorsal setae on somites 2–5. Somites 3–5 with pair of short posterolateral processes. Pleopods absent.

***Telson (Figure 2E, F).*** Bifurcated. Each fork with two lateral spines. Dorsal surfaces of furcae covered by small, disperse spinules; ventral surfaces densely spinulated. Inner margin with two groups of three spinulated setae separated by medial sinus.

## Second zoea (Figures 3A–G, 4A–F)

***Carapace (Figure 3A, B).*** Three pairs of anterodorsal simple setae, one pair of posterodorsal simple setae, one pair of simple setae near the base of dorsal spine. Ventral margin with 'anterior seta' followed by five posterior smaller plumose setae. Eyes stalked. Otherwise as in zoea I.

***Antennule (Figure 3C).*** Exopod with two long, four medium and two shorter aesthetascs, endopod absent.

***Antenna (Figure 3D).*** Endopod bud aproximately 1/2 of protopod length. Otherwise unchanged.

***Mandible (Figure 3E).*** Palp bud absent.

***Maxillule (Figure 3F).*** Coxal endite with seven (four subterminal, three terminal) sparsely plumose setae. Basial endite with four (two plumose, one sparsely plumose, one plumodenticulate) subterminal setae and six (three plumodenticulate, three plumodenticulate cuspidate) terminal setae. Exopod present as a pappose marginal seta. Endopod two-segmented, with one sparsely plumose seta in proximal segment and five (one subterminal, four terminal) sparsely plumose setae on distal segment.

***Maxilla (Figure 3G).*** Coxal endite bilobed with five (one subterminal, four terminal) and four (one subterminal, three terminal) plumose setae. Basial endite bilobed with five (one subterminal, four terminal sparsely plumose) + five (two subterminal, three terminal sparsely plumose) setae. Endopod with four terminal sparsely plumose setae. Microtrichia on lateral margin of endopod. Scaphognathite with 20 marginal plumose setae.

***First maxilliped (Figure 4A).*** Exopod two-segmented with six long plumose natatory setae with two conspicuous annuli. Epipod bud present. Otherwise as in zoea I.

***Second maxilliped (Figure 4B).*** Exopod two-segmented with six terminal longer plumose natatory setae with two conspicuous annuli. Otherwise as in zoea I.

***Third maxilliped (Figure 4C).*** As in zoea I.

***Pereiopods (Figure 4D).*** As in zoea I.

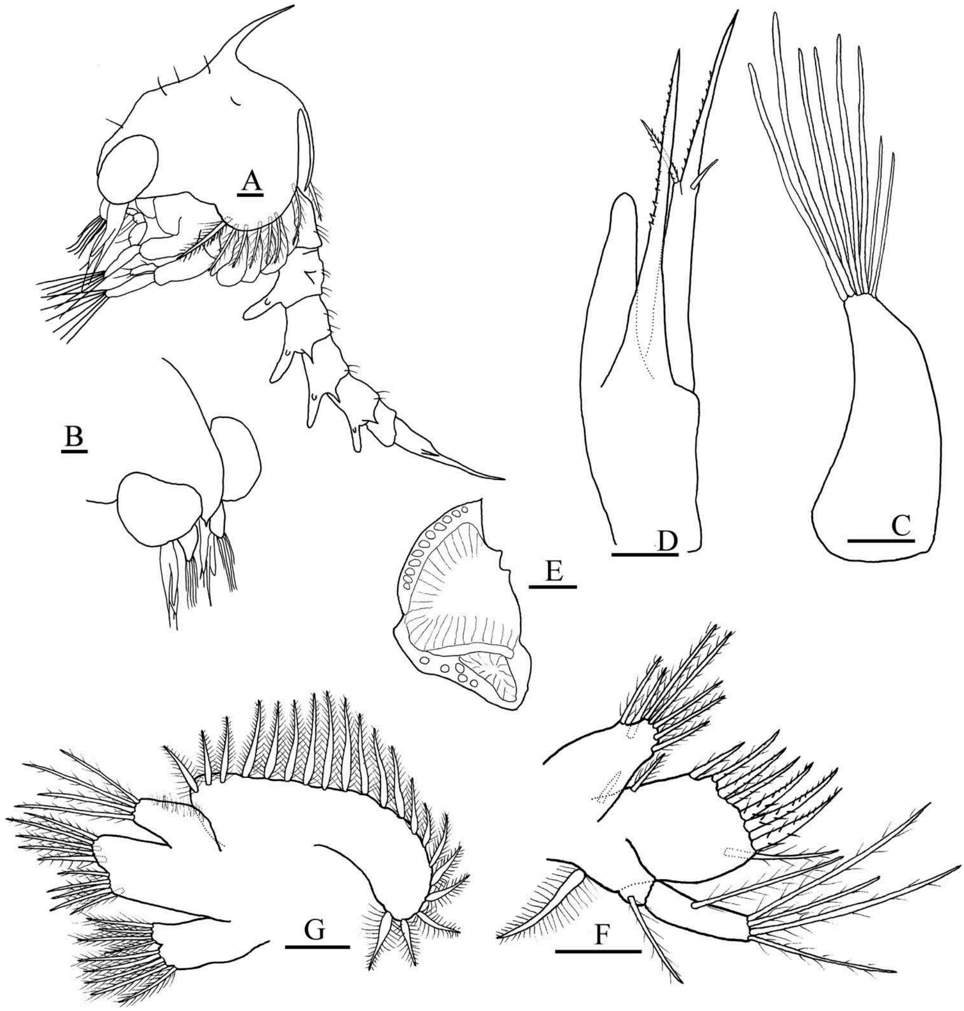


**Figure 3.** Second zoea of *Rochinia gracilipes* A. Milne Edwards, 1875. (A) lateral view; (B) magnified latero-dorsal view showing the short rostrum; (C) antennule; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla. Scale bars = 0.1 mm.

***Abdomen (Figure 4E).*** Six somites. Somite 2 with pair of dorsolateral processes. Somite 1 with three dorsal plumose setae. Somites 2–3 with two pairs of dorsal and anterodorsal setae. Somites 4–5 with one pair of anterodorsal setae. Somites 2–6 with one pair of short or medium posterolateral processes. Pleopod buds present.

***Telson (Figure 4E, F).*** As in zoea I.

## Megalopa (Figures 5A–G, 6A–M, 7A–I)

***Carapace (Figure 5A–B).*** Longer than broad, posteromedial tubercle present, dorsal spine absent. Rostrum ventrally deflected, extending approximately to distal end of

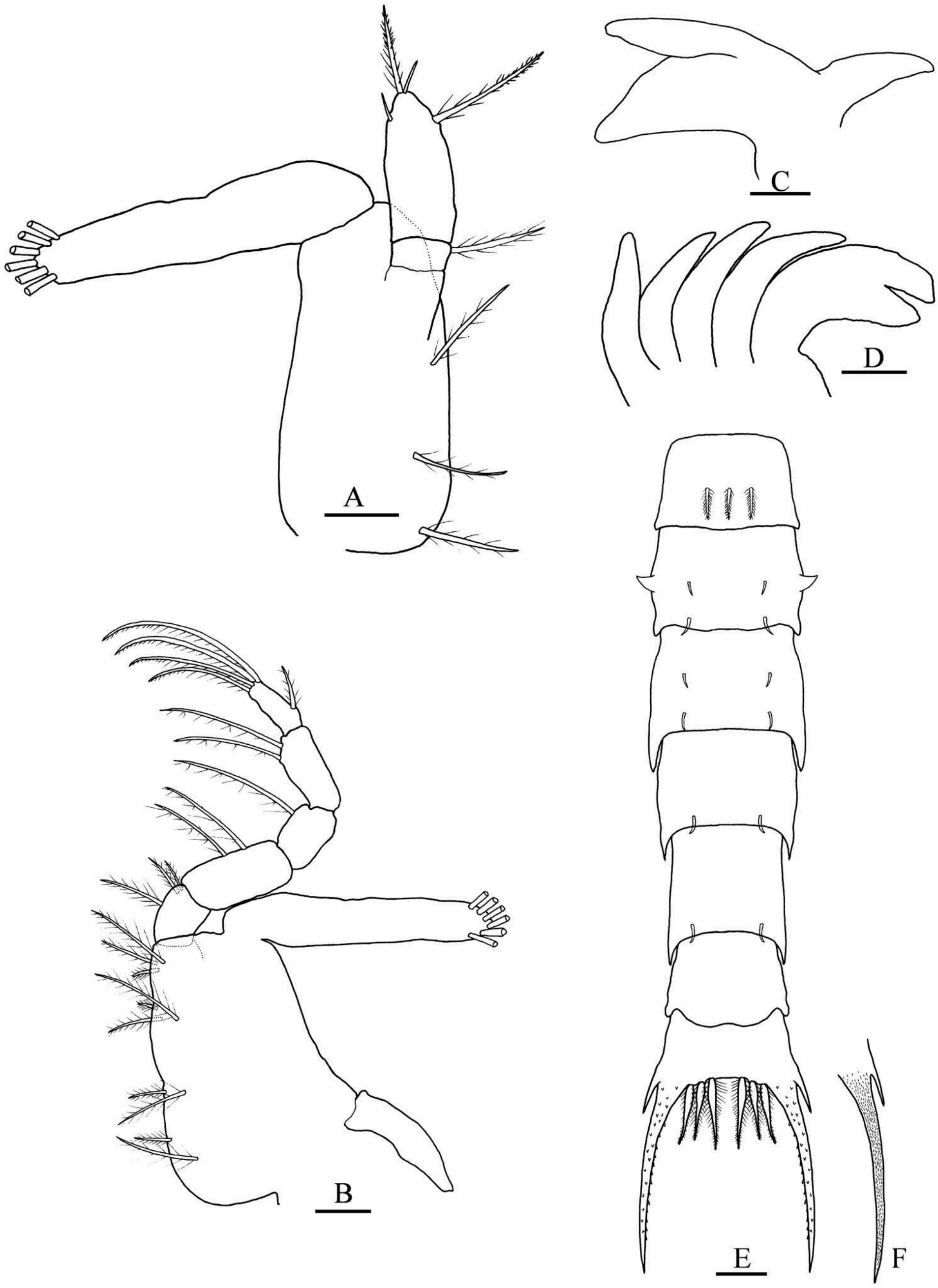


**Figure 4.** Second zoea of *Rochinia gracilipes* A. Milne Edwards, 1875. (A) maxilliped I; (B) maxilliped II; (C) maxilliped III buds; (D) pereiopod buds; (E) dorsal view of abdomen and telson; (F) magnified view of right furca. Long setae maxillipeds I and II (A and B) were drawn truncated. Scale bars = 0.1 mm.

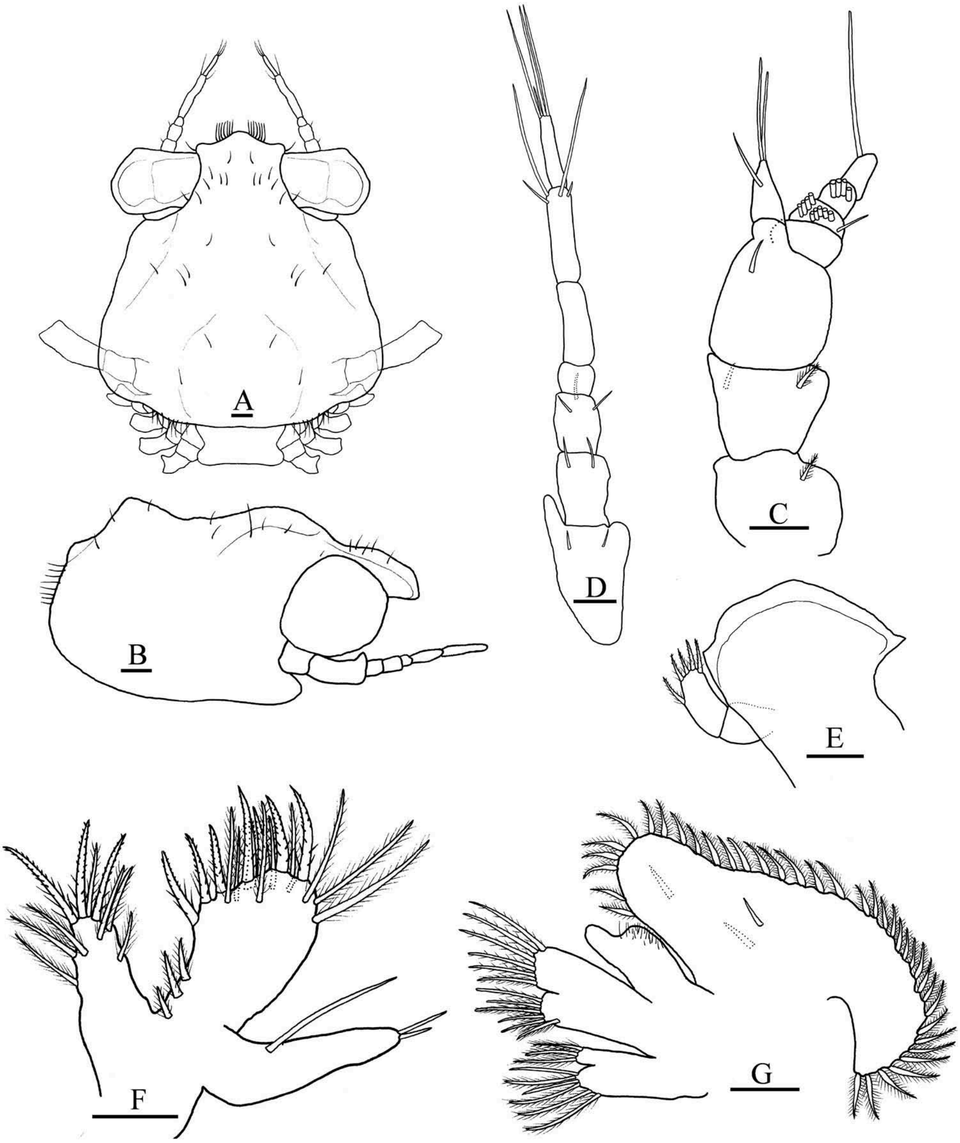


**Figure 5.** Megalopa of *Rochinia gracilipes* A. Milne Edwards, 1875. (A) dorsal view, pereiopods drawn trunctated; (B) lateral view; (C) antennules, aesthetascs drawn truncated; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla. Scale bars = 0.1 mm.

segment 3 of antenna. Dorsal surface setose, posterior margin with two groups of plumose setae, other setal arrangement as figured.

***Antennule (Figure 5C).*** Peduncle three-segmented with one, two, and one plumose setae. Endopod unsegmented with one subterminal, two terminal simple setae. Exopod four-segmented with zero, nine (arranged in two tiers), four, one aesthetascs, and zero, one, zero, zero simple setae.

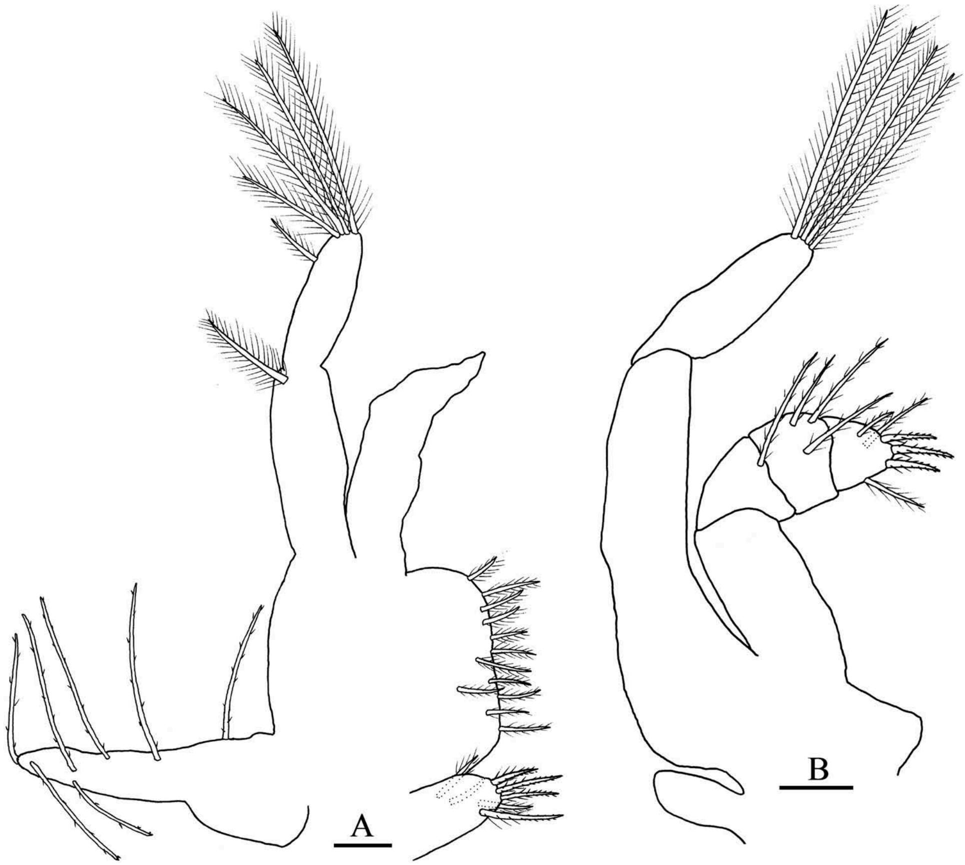


**Figure 6.** Megalopa of *Rochinia gracilipes* A. Milne Edwards, 1875. (A). maxilliped I; (B) maxilliped II. Scale bars = 0.1 mm.

***Antenna (Figure 5D).*** Peduncle three-segmented, with two, two, and three simple setae. Flagellum four-segmented with zero, zero, four and four simple setae.

***Mandible (Figure 5E).*** Palp two-segmented, distal segment with five plumodenticulate setae.

***Maxillule (Figure 5F).*** Coxal endite with five subterminal and five terminal plumose and plumodenticulate setae. Basial endite with 11 subterminal plumose and plumodenticulate and six terminal plumodenticulate cuspidate setae. Endopod unsegmented, one subterminal sparsely plumose, two terminal simple setae. Exopod seta absent.

***Maxilla (Figure 5G).*** Coxal endite bilobed, 6 + 3 plumose setae. Basial endite bilobed with two subterminal plumose and four terminal sparsely plumose setae on proximal lobe, six sparsely plumose setae on distal lobe. Endopod unsegmented without setae; marginal microtrichia present. Scaphognathite with 37 plumose marginal setae and three inner sparsely plumose setae.

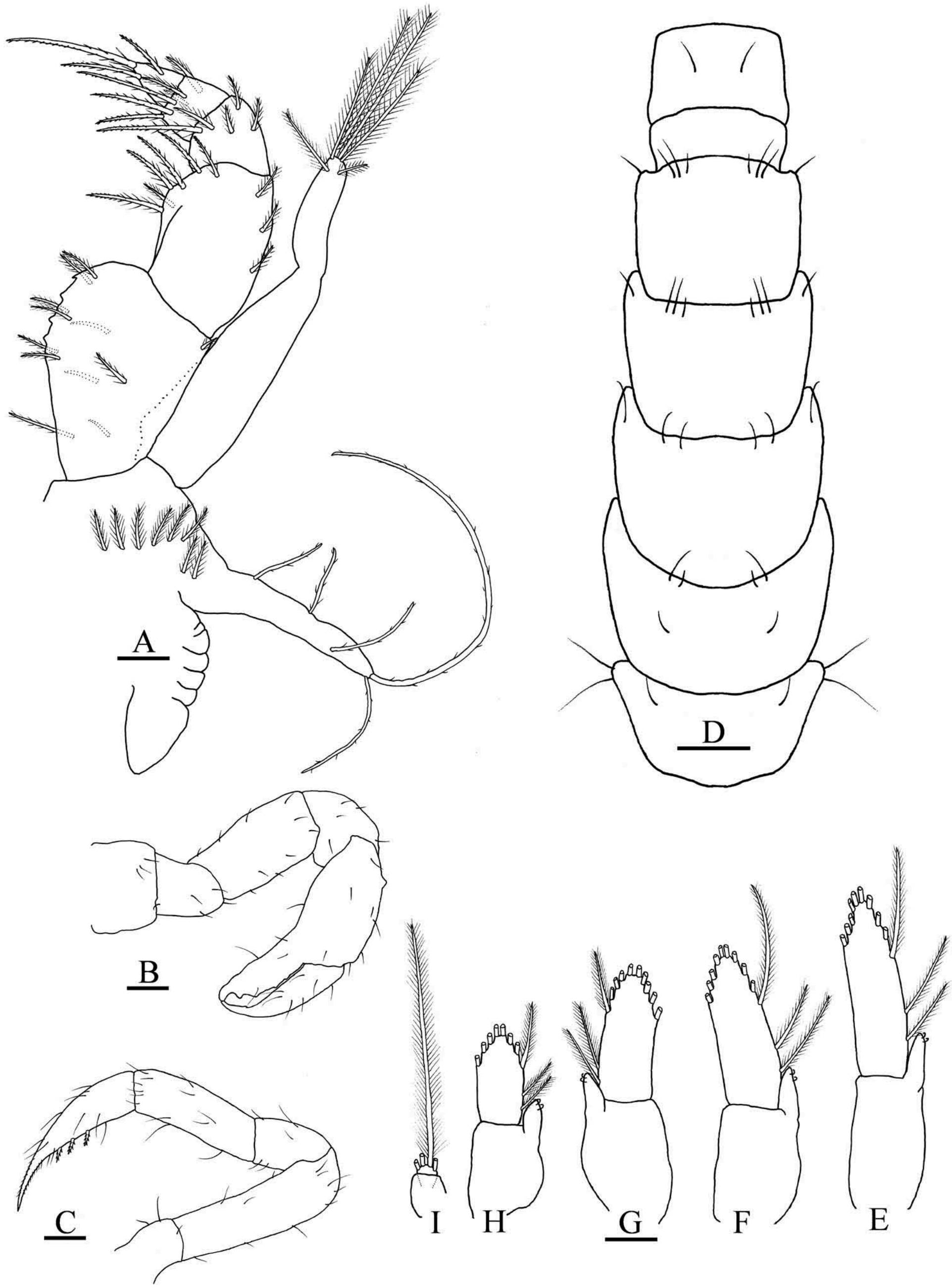


**Figure 7.** Megalopa of *Rochinia gracilipes* A. Milne Edwards, 1875. (A) maxilliped III; (B) pereiopod I; (C) pereiopod II; (D) dorsal view of abdomen; (E) pleopod I; (F) pleopod II; (G) pleopod III; (H) pleopod IV; (I) uropod. Long setae of all pleopods and uropods (E–I) were drawn truncated. Scale bars = 0.1 mm.

***First maxilliped (Figure 6A).*** Epipod with seven long sparsely denticulate setae. Coxal endite with two subterminal plumose, and three subterminal and two terminal plumodenticulate setae. Basial endite with 13 subterminal and terminal plumodenticulate setae. Endopod unsegmented, without setae. Exopod two-segmented, proximal segment with one distal papose seta, distal segment with four long terminal plumose setae.

***Second maxilliped (Figure 6B).*** Epipod bud present. Coxa and basis undifferentiated, one single plumose seta. Endopod four-segmented (ischium and merus undifferentiated), with zero, one, three and six sparsely plumose, plumodenticulate and plumodenticulate cuspidate setae. Exopod two-segmented, distal segment with four terminal plumose feeding setae.

***Third maxilliped (Figure 7A).*** Coxa-epipod joint indistinct. Epipod elongated, six sparsely denticulate setae. Lamellate podobranch well developed. Coxa and basis undifferentiated, nine sparsely plumose and plumose setae. Endopod five-segmented: ischium, merus, carpus, propodus and dactylus with 12, nine, five, six and three sparsely plumose or plumodenticulate setae. Ischium inner margin four-toothed. Exopod two-segmented, distal segment with two subterminal and four terminal plumose feeding setae.

***Cheliped (Figure 7B), pereiopods (Figure 7C).*** Cheliped setae as illustrated. All pereiopod segments well differentiated; dactyli of pereiopods 2–5 with three serrulate ventral spine; coxae and ischii without spines.

***Sternum (not illustrated).*** Maxilliped and cheliped sternites fused with six (arranged 2 + 2 + 2) setae; all sternal sutures are medially interrupted.

***Abdomen (Figure 7D).*** Six somites. Somite 1 with two anterodorsal simple setae and two pairs of lateral setae. Somites 2–6, proximally to distally with six, six, eight, eight and zero simple setae.

***Pleopods (Figure 7E–H).*** Endopods 1–4 unsegmented, two coupling hooks on inner margin. Exopods 1–4 with nine, nine, nine and seven long marginal plumose natatory setae, respectively, on distal segments.

***Uropods (Figure 7I).*** Exopod with four natatory setae on distal segment; endopod absent.

***Telson (Figure 7D).*** With two dorsal simple setae.

## Discussion

Majoid larval development includes only two zoeal stages and *Rochinia gracilipes* follows this pattern. The larval morphology of species in Epialtidae, Inachidae, Inachoididae, Majidae and Oregoniidae has been used to propose relationships among families and subfamilies and to construct phylogenies. A recent molecular phylogeny supports several relationships predicted from larval, but not from adult, morphology, suggesting that the adult morphological characters traditionally used may be subject to convergence (Hultgren and Stachowicz 2008, and references therein). In fact, zoeal morphology may reflect phylogenetic relationships more accurately than adult morphology since the former live in a uniform planktonic environment subjected to relatively constant selection pressures, although it has been recognised that homoplasy is widespread in brachyuran zoeal lineages and many derived characters evolved many times in different clades (Clark 2009).

### *Comparison among known* Rochinia *larvae*

The larval morphology of three *Rochinia* species have been described: *R. carpenteri, R. debilis* and *R. gracilipes* (Ingle 1979; Komatsu and Takeda 2003; this paper) and compared (Supplementary material 1, 2, 3). The zoeae I of *R. gracilipes* differs from the other two species in having: (1) a minute rostral spine (whereas *R. carpenteri* and *R. debilis* have long and short rostral spines, respectively); (2) four setae and two aesthetascs in the antennular protopod (whereas *R. carpenteri* and *R. debilis* have two, one and four, one, respectively); (3) antennal exopod longer than protopod (whereas they have similar size in *R. carpenteri* and *R. debilis*); (4) four setae in the distal segment of the endopod of the maxillule (whereas *R. carpenteri* and *R. debilis* have six and two setae, respectively); (5) four setae in the endopod of the maxilla (whereas *R. carpenteri* and *R. debilis* have six and three setae, respectively); and (6) 10 marginal setae in the scaphognathite of the maxilla (whereas *R. carpenteri* and *R. debilis* have 11 and 17–18 marginal setae, respectively). *Rochinia gracilipes* shares with *R. debilis* the absence of the lateral spine (present in *R. carpenteri*), short posterolateral abdominal processes (abdominal process long in *R. carpenteri*) and the presence of eight setae in the coxal endite of the maxilla and four setae in the distal segment of the endopod of the 2$^{nd}$ maxilliped (nine and five, respectively, in *R. carpenteri*). *R. gracilipes* share with *R. debilis* the presence of carapace ventral anterior setae ('majid setae') (present in *R. carpenteri*) and with *R. carpenteri* the absence of pleopod buds (present in *R.debilis*).

The zoea II of *R. gracilipes* and *R. carpenteri* differ from each other in having in *R. gracilipes* (1) eight aesthetascs and no setae in the protopod of the antennules (whereas *R. carpenteri* has five aesthetascs and one seta); (2) nine setae in the basial endite of the maxillule (whereas *R. carpenteri* has 10 setae); (3) 10 setae in the basial endite, four setae in the endopod and 20 setae in the scaphognathite of maxilla (whereas *R. carpenteri* has 13, four and 20, respectively); (4) short posterolateral processes in abdominal somites 2 to 6 (whereas they are longer, but are present only in somites 3 to 5 in *R. carpenteri*); (5) three, four, four, two and two setae in abdominal somites 1 to 5 (whereas *R. carpenteri* has two, two, four, four and two setae). In addition, *R. gracilipes* has no setae near the base of the dorsal spine (whereas *R. carpenteri* has five) and the palp bud of the mandible is absent (present in *R. carpenteri*). The zoea II of *R. debilis* is presently unknown.

The megalopae of *R. gracilipes* and *R. carpenteri* differ from each other in having in *R. gracilipes* (1) short rostrum and carapace without dorsal spine (long rostrum and carapace dorsal surface provided with spine in *R. carpenteri*); (2) one and one setae in the peduncle of antennule; zero, nine, four and one aesthetascs; and zero, one, zero and zero setae in the exopod of the antennule (whereas *R. carpenteri* has no setae in the peduncle and zero, 10, three and one aesthetascs and zero, zero, zero and one setae in the exopod, respectively); (3) three setae in segment 3 of the peduncle of the antenna, four setae each in segments 3 and 4 of the flagellum of the antenna (whereas *R. carpenteri* has two setae in the peduncle and three and three setae in the flagellum, respectively); (4) 17 setae in the basial endite of the maxillule and three setae in the distal segment of the endopod of maxillule (whereas *R. carpenteri* has 10 and four setae, respectively); (5) nine setae in the coxal endite of the maxilla, 37 marginal and three lateral setae in the scaphognathite (whereas *R. carpenteri* has 12–13, 40 and no setae, respectively); (6) seven, seven and 13 setae, respectively in the epipod, the coxal endite and the basial endite of the 1st maxilliped (whereas *R. carpenteri* has six, six and 10 setae, respectively); (7) three, six and one setae in the propodus and dactylus of the endopod and in the distal segment of the exopod of 2nd maxilliped (whereas *R. carpenteri* has four, seven and no setae, respectively); (8) six setae in the epipod of the 3rd maxilliped (whereas *R. carpenteri* has five setae); 12, nine, six and three setae in the ischium, merus, propodus and dactylus of the 3rd maxilliped, four teeth in the ischium of the 3rd maxilliped (whereas *R. carpenteri* has 11–15, 6–7, five and four setae, and seven teeth, respectively); podobranchiae on the 3rd maxilliped (podobranchiae putatively lacking in *R. carpenteri*); (9) coxae and ischii of pereipods inermis in *R. gracilipes* (whereas provided with 2–4 spines in *R. carpenteri*); (10) six, six, six, eight, eight and zero setae in the abdominal somites 1–6 (whereas there are four, three, two, two, three and one setae, respectively, in *R. carpenteri*); (11) nine, nine, nine and seven setae, respectively, in the exopods of pleopods 2–5 (whereas there are 14–16 setae in *R. carpenteri*); four setae in the exopod of the uropods (whereas *R. carpenteri* has five setae) and (12) two setae in the telson (whereas *R. carpenteri* has four setae). The megalopa of *R. debilis* is presently unknown.

The results of this study pose interesting further questions that should be answered in the context of evolutionary developmental biology. For example, does *R. gracilipes* have the developmental potential to originate lateral spines or a long rostral spine, as observed in the (alleged) congeneric *R. carpenteri* (Ingle 1979)? In addition, ecological information could help to understand morphological differences between megalopae, a transitional stage that, unlike zoeae, may be subjected to selective pressures related to the change of habitat, from planktonic to benthic (e.g. Martin 1988). For example, are coxal and ischial spines in pereiopods 2–4 involved in grasping filamentous substrata, and could the presence of such spines in *R. carpenteri*, but not in *R. gracilipes*, be explained by textural differences of megalopal habitats and settlement behaviour between them?

### *Comparison among* Rochinia *and* Pugettia *spp. larval development*

The classification of *Rochinia* in Pisinae was challenged in the description of *R. carpenteri* larvae by Ingle (1979), who detected affinities with, for example, Oregoniidae (e.g. prominent lateral spines) among other majoid subfamilies. In addition, the genera *Rochinia* and *Pugettia* Dana, 1851 were historically considered closely related on the basis of adult morphology although they are currently classified as Pisinae and Epialtinae, respectively (Colavite et al. 2014). Three species of *Pugettia* have had their larvae described so far (*P. quadridens, P. marisinica* and *P. intermedia*) (Ko 1998; Kornienko and Korn 2004) whose larval morphologies are herein compared with *R. gracilipes* (Supplementary material 4).

The zoea I of *R. gracilipes* differs of the zoea of the above-mentioned *Pugettia* in having (1) a minute rostral spine (versus short rostrum in *Pugettia*); (2) the number of aesthetascs and setae in the protopod of antennula (although *R. gracilipes* shares the number with *P. intermedia*); (3) a longer exopod of antenna relative to protopod; (4) the size of the exopod relative to endopod of the antenna (although *R. gracilipes* shares this character with *P. quadridens*); (5) 10 setae in the basis of the 1$^{st}$ maxilliped (versus nine setae in *Pugettia* spp.); (6) the absence of pleopod buds (present in all *Pugettia* spp.). *Rochinia gracilipes* shares with *Pugettia* spp. the absence of lateral carapace spine, the same number of antero and posterolateral carapace setae, the same setation on the antenna exopod; the absence of palp bud on the mandible; the same setation on the maxillule, maxilla, endopod of the 1$^{st}$ maxilliped, 2$^{nd}$ maxilliped, abdominal somites and telson; the presence of 3$^{rd}$ maxilliped and pereiopod buds; the same size of the dorsolateral and posterolateral processes on the abdomen; and the same size and spinulation of the lateral spines of the telson fork.

The zoeae II of *R. gracilipes* differs from the zoea of *Pugettia*, in addition to setation on the protopod of antennula and on the basis of the 1$^{st}$ maxilliped, in having (1) the absence of the endopod bud of antennula and of palp bud of mandible (both present in all *Pugettia* spp.); (2) nine setae in the basial endite of maxillule (whereas *Pugettia* spp. have 10); (3) nine setae in the coxal endite of maxilla (whereas *Pugettia* spp. have 10); (4) the pattern of posterolateral processes of the abdomen; (5) three setae in the proximal somite of abdomen (whereas *Pugettia* spp. have two). *Rochinia gracilipes* share with *Pugettia* spp. the total number of carapace setae; the size of endopod of antenna (relative to exopod); the setation of coxal endite and exopod of maxillule, basial endite, endopod and scaphognathite of maxilla, exopod of 1$^{st}$ and 2$^{nd}$ maxilliped, 2$^{nd}$ to 5$^{th}$ somites of abdomen; and the presence of pleopod buds.

The megalopa of *R. gracilipes* differs from that of *P. quadridens* in having (1) one and two setae in segments 1 and 2 of the antennular peduncle, and nine, four and one setae in segments 2, 3 and 4 of the exopod of the antennules (whereas *P. quadridens* has zero and one setae and eight, zero and zero setae, respectively); (2) two setae in segment 1 of the antennal peduncle (whereas *P. quadridens* has 1); (3) 10 setae in the coxal endite of the maxillule (whereas *P. quadridens* has 9); (4) 9 and 12 setae in the coxal and basial endites of the maxilla (whereas *P. quadridens* has 13–15 and 9–10 respectively); (5) 13 setae in the basial endite of the 1$^{st}$ maxilliped (whereas *P. quadridens* has 10–11); (6) six setae in the epipod of the 3$^{rd}$ maxilliped (whereas *P. quadridens* has 10); the presence of podobranchiae on the 3rd maxilliped (podobranchiae putatively lacking in *P. quadridens*); four teeth in the ischium of the endopod of the 3$^{rd}$ maxilliped (whereas *P. quadridens* has 15–16); nine and three setae in the merus and dactylus of the endopod of the 3$^{rd}$ maxilliped (whereas *P. quadridens* has 7–8 and four, respectively); (7) absence of the ischial spine of the pereiopods (whereas *P. quadridens* has two); (8) six, six, six, eight, eight and zero setae in the abdominal somites (whereas *P. quadridens* has eight, five, five, four, four, and two); (9) nine, nine, nine and seven natatory setae in the pleopods (whereas *P. quadridens* has 12, 11, 10 and nine); (10) four setae in the exopod of the uropod (whereas *P. quadridens* has five). *Rochinia gracilipes* shares with *Pugettia quadridens* the absence of dorsal spine and of spines in the coxa and ischium of pereiopods; the presence of an epipod bud of the 2$^{nd}$ maxilliped; three spines in the inner margin of dactylus of the pereiopods; and the setation of segment 3 of peduncle, endopod and segment 1 of exopod of the antennules; segments

2 and 3 of peduncle and segment 1, 2, 3 and 4 of flagellum of the antenna; distal segment of palp of the mandible; basial endite and exopod of the maxillule; scaphognathite; epipod, coxal endite, endopod and exopod of the 1st maxilliped; endopod and exopod of the 2nd maxilliped; ischium, carpus and propodus of endopod and both segments of exopod of the 3rd maxilliped; and telson. The megalopae of *P. marisinica* and *P. intermedia* are presently unknown.

## *Comparison among known Pisinae larval developments*

Phylogenetic reconstructions based on majoid larval characters supported a monophyletic Oregoniidae, a monophyletic Majidae, an Inachidae–Inachoididae clade, and close associations among Epialtinae (Epialtidae), Pisinae (Epialtidae), and Mithracinae (Majidae) (Clark and Webber 1991; Marques and Pohle 1998, 2003; Pohle and Marques 2000). At present, the family Epialtidae includes four recognised subfamilies, and one of them is the previously separated Pisinae (Ng et al. 2008). Colavite et al. (2014, p. 2283) considered that Epialtidae is 'probably the most heterogeneous among Majoidea' families, that the separation among its subfamilies is sometimes unclear, and that a revision based on adult morphology is needed. Could larval morphology help to understand the relationships within Epialtidae or, at least, within Pisinae?

An actualised compilation of the larval morphology of Pisinae species with partial or complete descriptions (Table 1), that would help future researchers to compare zoeae I, zoeae II and megalopae is presented here (Supplementary online material 1, 2, 3, respectively). Previous comparisons of Pisinae larvae (Santana et al. 2004, 2006) included species that are now considered to be within Majidae: *Eurynolambrus australis* Webber and Wear, 1981, *Eurynome aspera* Kinahan, 1858; *E. spinosa* Salman, 1982 and *Naxioides serpulifera* Rathbun, 1914 = *Paranaxia serpulifera*. This new comparison of larval morphologies corroborates the previous assertion that larvae of Pisinae are morphologically heterogeneous and that this subfamily cannot be defined on the basis of larval characters (Santana et al. 2004, 2006), and suggests that larval morphology would not help to accurately understand the phylogenetic relationships of this subfamily of spider crabs.



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