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LARVAL DEVELOPMENT OF THE LAND HERMIT CRAB *COENOBITA COMPRESSUS* H. MILNE EDWARDS REARED IN THE LABORATORY

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ABSTRACT

The complete larval development of the land hermit crab *Coenobita compressus* is described from specimens reared in the laboratory at 26°C. Eighty-eight percent passed through five zoeal stages and 12% passed through four zoeal stages before metamorphosing 21–33 days after hatching. Megalopae left their water dishes as soon as seven days after metamorphosis, buried themselves in damp sand approximately 29 days after metamorphosis, and emerged as young crabs 1–5 days later. *Coenobita compressus* zoeae can be distinguished from the other seven described coenobitids by the setation of the maxillule and antenna, whereas the megalopa can be distinguished by the segmentation of the second and third maxillipeds. Characters are also given to distinguish *C. compressus* zoeae from those of sympatric marine hermit crab zoeae.

Land hermit crabs (family Coenobitidae) occur throughout the tropics, reaching their highest species diversity on the coastlines, islands, and atolls of the Indo-West Pacific (Hartnoll, 1988). Although all adult coenobitids are fully terrestrial, their larvae develop in the plankton. Laboratory-reared coenobitids usually pass through five zoeal stages before metamorphosing into megalopae (e.g., Shokita and Yamashiro, 1986; Nakasone, 1988), but as few as two (Harvey, 1992) and as many as seven (Al-Aidaroos and Williamson, 1989) zoeal stages have been observed. Once the megalopal stage has been attained, coenobitids become more benthically oriented (personal observation in the laboratory for *C. compressus*), show an escalating interest in shells (Brodie, 1999), and finally emerge onto land where they burrow and molt to the first juvenile crab stage (Reese, 1968; Reese and Kinzie, 1968; Harvey, 1992).

Larval development in the laboratory has been described for seven of the approximately 16 known coenobitid species. Five of the seven species are from the Indo-West Pacific: *Coenobita cavipes* Stimpson (Shokita and Yamashiro, 1986; Nakasone, 1988), *C. purpureus* Stimpson (Nakasone, 1988), *C. rugosus* H. Milne-Edwards (Shokita and Yamashiro, 1986), *C. variabilis* McCulloch (Harvey, 1992), and *Birgus latro* (Linneaus) (Reese and Kinzie, 1968). Larval development has also been investigated in *C. clypeatus,* the only western Atlantic coenobitid, and *C. scaevola* (Forskål), the only Red Sea coenobitid (Provenzano, 1962a; Al-Aidaroos and Williamson, 1989). In this paper we describe the development of *C. compressus* in the laboratory. *Coenobita compressus* is the only species of land hermit crab from the eastern Pacific, where its geographical distribution extends from the Gulf of California, Mexico, to Peru (Ball and Haig, 1974).

MATERIALS AND METHODS

Several ovigerous *C. compressus* (generally 3–10 crabs) were intercepted just above the surf zone on Culebra Beach, Naos Island, Panama, shortly before high tide on evenings from March through May, 1997. Each crab was kept inside a round plastic washtub (diameter = 0.5 m) partly filled with damp sand into which was placed a 300-ml Pyrex dish filled with filtered sea water. Tubs were checked every 2 or 3 hours until at least one female had shed zoeae into its water dish.

Larvae from nine females were reared for this study. One batch of larvae each hatched on the evenings of March 7, May 4, and May 6, respectively (three batches total). These zoeae were housed individually in partitioned plastic boxes holding 20 ml of filtered sea water in each of 18 compartments. Three females shed larvae on the evening of April 2 and three more on the evening of April 3; on each occasion the three batches were combined, and larvae were randomly selected for rearing. These larvae were placed five to a compartment in larger plastic boxes holding 75 ml of filtered sea water in each of 24 compartments and were not tracked individually through development. All subsequent rearing took place

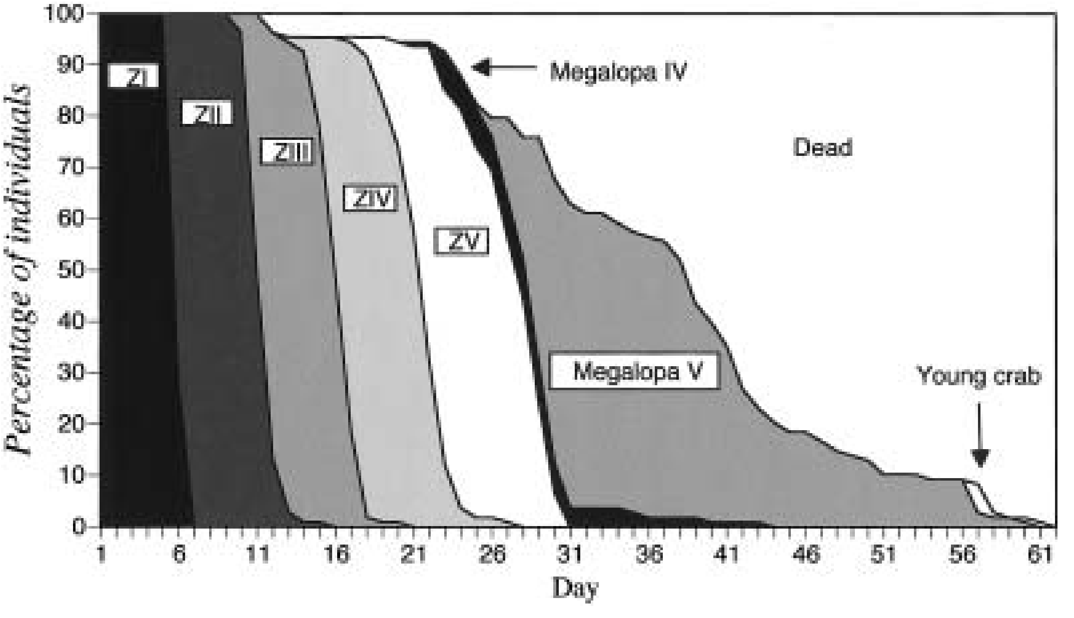

Fig. 1. *Coenobita compressus* H. Milne Edwards, 1837, larval development under laboratory conditions. ZI through ZV denote zoeal stages. Megalopa IVs passed through 4 zoeal stages, while Megalopa Vs passed through 5 zoeal stages.

at the Smithsonian Tropical Research Institute's marine facilities on Naos Island, Panama.

The larvae were reared on a 12:12 L : D light cycle at 26°C, the average local sea-surface temperature for several days before the first batch of larvae was collected. Zoeae were transferred to clean compartments and fed *Artemia* nauplii daily; newly hatched *Artemia* were consumed for the first two weeks of development, after which they fed upon larger 1- or 2-day-old *Artemia.*

When the March 7 batch of individually reared larvae metamorphosed into megalopae they were moved to small plastic containers holding about 4 ml of sea water. Each container was sunk into damp sand in the larger compartmentalized boxes, so that individual megalopae had the opportunity to leave the sea water. Megalopae were fed fish flake food daily and provided small vacant gastropod shells (*Nerita modesta*). On April 24 the 16 surviving megalopae were moved to covered plastic cups (diameter = 9 cm) also containing sea water and sand and placed outside in an open-air, covered arena where they experienced natural daily fluctuations in light and air temperature. All statistics on the timing of larval development were derived from the March 7 batch of larvae.

Larvae and exuviae were preserved in a dilute solution of 70% ethanol and chlorazol black stain. Sacrificed larvae and exuviae were dissected in glycerine and mounted in glycerine jelly. Descriptions were made with the aid of a Nikon microscope with Nomarski optics, and measurements were made using a dissecting microscope with an ocular micrometer. Total length was measured from the tip of the rostrum to the midpoint of the telson and excluded all telson processes. Carapace length was measured from the tip of the rostrum to the posteromedial margin of the carapace. All setal formulae are proximal to distal. Rarely observed variations of setal number are reported in parentheses. Illustrations were created with an approach modified from Harvey (1992): specimen images were first captured on a Macintosh™ computer with a digital camera connected to a Wild M8 dissecting microscope; these images were used as templates from which line drawings were made using the program Adobe Illustrator™.

RESULTS

Coenobita compressus passed through four or five larval stages before attaining the megalopal stage (Fig. 1). Twelve percent of the 88 zoeae that survived to the megalopal stage in the March 7 batch passed through four zoeal stages, whereas the rest passed through five zoeal stages. This variability was seen in all batches of the individually tracked larvae from this study and in three additional batches of *C. compressus* reared for another study. The first four zoeal stages were about five days long, while the fifth lasted about seven days (Table 1). During this period, the zoeae nearly doubled in total length from around 3 mm at hatching to nearly 6 mm at the fifth zoeal stage; the megalopae were slightly over 4 mm long (Table 2).

By the end of April, the surviving megalopae from the March 7 batch were increasingly active on land. Initially, terrestrial megalopae often temporarily abandoned their shells, but this behavior rarely occurred in

Table 1. Duration of the developmental stages of *Coenobita compressus* H. Milne Edwards.

Stage	*n*	Duration (days)	Mean ± SD (days)
Zoea 1	108	5–6	5.3 ± 0.4
Zoea 2	108	4–9	5.3 ± 0.7
Zoea 3	103	1–8	4.9 ± 1.0
Zoea 4	93	3–10	5.1 ± 1.2
Zoea 5	73	6–10	7.4 ± 0.6
Megalopa	9	27–32	29.0 ± 1.7

older megalopae. On April 27 the first megalopa buried into the sand, and by May 6 all megalopae had burrowed underground, emerging as young crabs after one to five days. All nine megalopae that successfully metamorphosed to the young crab stage molted on land.

The length of time spent by megalopae in water before moving to land, and then on land before metamorphosing, was not rigorously measured in this study because the rearing containers and environmental conditions were changed during the course of the experiment. However, in subsequent work, it was found that megalopae could leave the water and successfully metamorphose after as few as 7 days in the water, although megalopae that remained in the water for 9–12 days were more successful (unpublished data). Terrestrial megalopae often returned to their water dishes before burying and metamorphosing.

Description of the Larvae

First Zoea

Specimens Examined.—Five.

Carapace (Figs. 2A, 3A).—Rostrum long, extending beyond tip of antennules, pointed, tapering, faintly carinate. Posterolateral margins of carapace rounded. Eyes sessile.

Antennule (Fig. 4A).—Uniramous; terminus with 3 large aesthetascs, 2 long and often 1 short plumose setae, and 1 long subterminal plumose seta.

Antenna (Fig. 4B).—Endopod unsegmented, fused to protopod, with 2 long and 1 short terminal plumose setae. Exopod with 9 or 10 plumose setae on inner and distal margins, spine on outer distal margin and setules along inner margin. Protopod with 1 strong serrated spine distally at base of exopod.

Mandible (Fig. 4C, D).—Margin asymmetrical, lacking palp.

Maxillule (Fig. 4E).—Coxal endite with 5 terminal plumose setae and 2 or 3 subterminal simple setae. Basal endite with 2 strong spines, each with several denticles, and often 1 subterminal simple seta. Endopod 3-segmented, third segment with 3 simple setae, but sometimes 1 plumose; 1 simple seta sometimes present distally on second segment.

Maxilla (Fig. 4F).—Proximal lobe of coxal endite with 7 (6) plumose setae: 1–3 of these subterminal and 4 or 5 terminal; distal lobe with 3 or 4 setae. Proximal lobe of basal endite with 4 (5) setae, distal lobe with 3 terminal setae and 1 subterminal seta. Proximal lobe of endopod with 2 setae, distal lobe with 3 terminal and 1 (2) subterminal setae, distal margin of endopod with row of fine setules. Scaphognathite with 5 (4) plumose setae, proximal margin with row of fine setules.

Maxilliped 1 (Fig. 4G).—Basis with hooked process at proximal end of inner face, process with fine seta basally (sometimes absent) and distally; 1, 1, 3, 2 or 3 setae on inner face. Endopod 5-segmented, with 2 (3), 2 (1), 1, 2, 5 setae, mostly plumose except on first segment; setules on first 3 segments, sometimes on fourth segment as well; exopod incompletely 2-segmented, with 4 natatory plumose setae.

Table 2. Larval sizes of *Coenobita compressus* H. Milne Edwards.

	Zoea I	Zoea II	Zoea III	Zoea IV	Zoea V	Megalopa
Carapace Length (*n* = 10)						
Mean ± SD (mm)	1.43 ± 0.05	1.79 ± 0.06	2.11 ± 0.1	2.11 ± 0.12	2.49 ± 0.07	1.62 ± 0.1
Maximum	1.5	1.9	2.3	2.3	2.6	1.8
Minimum	1.4	1.7	2.0	1.9	2.4	1.5
Total Length (*n* = 10)						
Mean ± SD (mm)	3.08 ± 0.09	3.92 ± 0.11	4.72 ± 0.15	4.92 ± 0.29	5.72 ± 0.15	4.35 ± 0.16
Maximum	3.2	4.1	5.0	5.2	5.9	4.6
Minimum	3.0	3.7	4.5	4.4	5.5	4.1

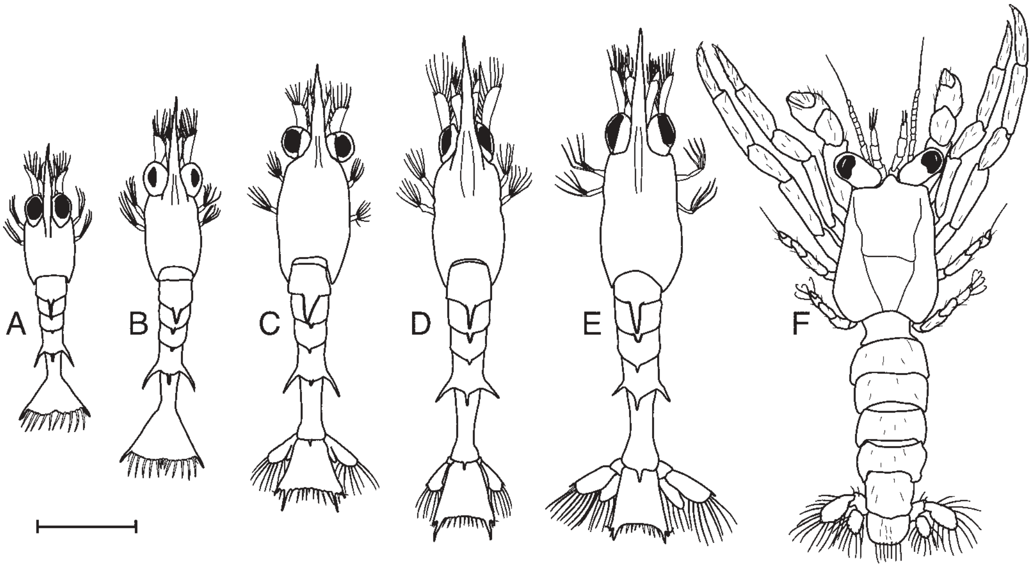

Fig. 2. *Coenobita compressus* H. Milne Edwards, 1837, whole animals, dorsal view. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V; F, megalopa. Scale = 1.0 mm.

Maxilliped 2 (Fig. 4H).—Basis with mediodistal simple seta and 2 distal setae, usually both plumose but sometimes 1 simple. Endopod 4-segmented, with 2, 2 (1), 2, 5 (4) setae, mostly plumose except for 1 seta on second segment and sometimes on ultimate segment; setules on segments 2 and 3; exopod incompletely 2-segmented, with 4 natatory plumose setae.

Maxilliped 3 (Fig. 4I).—2-segmented bud.

Abdomen (Figs. 2A, 3A).—5 somites; second somite with prominent, slightly curved mediodorsal spine; third and fourth somites with much smaller mediodorsal spines; fifth somite with large, blunt, recurved mediodorsal spine and large, blunt, dorsoventrally compressed posterolateral spines, sixth somite fused to telson.

Telson (Fig. 4J).—Posterior margin straight, median gap slightly notched; 7 + 7 marginal processes, outermost (first) fixed spine, second fine plumose hair, third through seventh articulated plumose spines, spinules present on lateral and medial (sometimes only along top half) margins of fifth, along full length of both margins of sixth and along full length of lateral margin and sometimes along top of medial margin of seventh; small spinules between marginal processes and fine setules in median gap.

Second Zoea

Specimens Examined.—Five.

Carapace (Figs. 2B, 3B).—Rostrum and carapace essentially unchanged, except more noticeable rostral carina. Eyes mobile.

Antennule (Fig. 5A).—Uniramous; terminus with 2 large aesthetascs, 2 long setae, both usually plumose but sometimes 1 simple, and 2 short plumose setae; 1 long and usually 1 or 2 short subterminal plumose setae.

Antenna (Fig. 5B).—Endopod fused to protopod. Endopod about half length of exopod, with 2 long and 1 short terminal plumose setae. Exopod with 10 or 11 plumose setae on inner and distal margins, spine on outer distal margin, and setules along inner margin. Strong serrated ventral spine and small tooth on protopod at base of exopod.

Mandibles (Fig. 5C, D).—Margin asymmetrical, palp lacking. Upper process of right mandible with prominent incisor and 3 smaller teeth; lower process with 9 teeth, several denticles, and serrated edges. Left mandible with large dorsal, medial, and ventral teeth with smaller spines and teeth in between.

Maxillule (Fig. 5E).—Coxal endite with 5 terminal plumose setae and 2 simple or plumose subterminal setae. Basal endite with 4 strong spines, each with several denticles, and of-

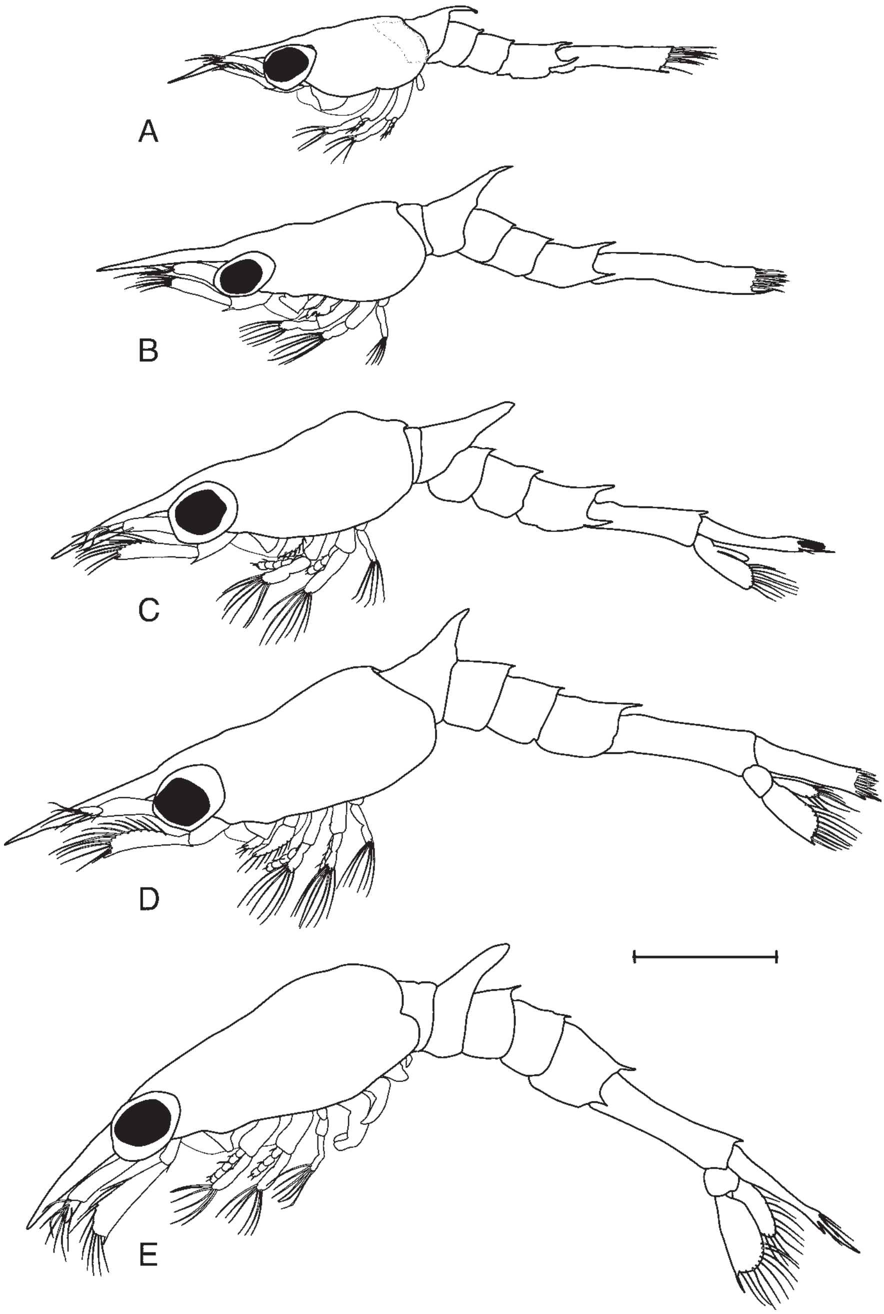

Fig. 3. *Coenobita compressus* H. Milne Edwards, 1837, whole animals, lateral view. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V. Scale = 0.8 mm.

ten 1 subterminal simple seta. Endopod incompletely 3-segmented, third segment with 2 simple and 1 plumose setae; simple seta on second segment.

Maxilla (Fig. 5F).—Proximal lobe of coxal endite with 7 (6) plumose setae: 1–3 of these submarginal and 4 or 5 marginal; distal lobe with 4 plumose setae, 1 submarginal. Proximal lobe of basal endite with 4 (5) plumose setae, 1 submarginal, distal lobe with 3 plumose setae and 1 submarginal simple seta. Proximal lobe of endopod with 2 plumose (sometimes 1 of these simple) setae, distal

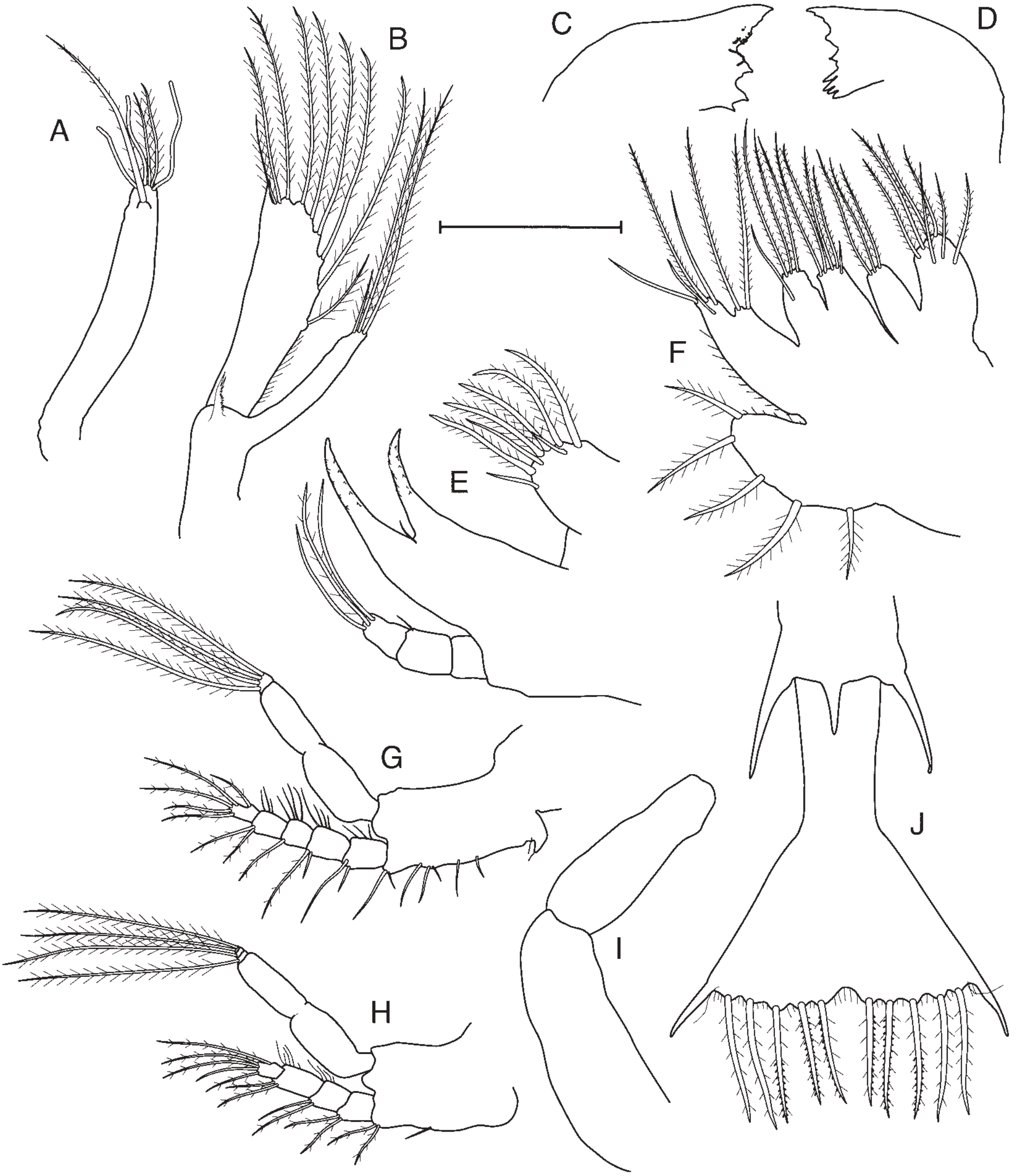

Fig. 4. *Coenobita compressus* H. Milne Edwards, 1837, zoea I. A, antennule; B, antenna; C, right mandible; D, left mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, telson. Scale = 0.1 mm (E, F, I), 0.25 mm (A–D, G, H), and 0.4 mm (J).

lobe with 3 or 4 setae, most plumose. Distal margin of endopod with row of fine setules. Scaphognathite with 7 or 8 plumose setae, proximal margin with row of fine setules.

Maxilliped 1 (Fig. 5G).—Basis with hooked process at proximal end of inner face, process with fine seta basally (sometimes absent) and distally; 1, 1, 3, 1–3 setae (plumosity variable) more distally on this face. Endopod 5-segmented with 3, 2, 1, 2, 4 setae (plumosity variable), single long plumose seta on outer margins of segments 1, 2, 3, and 5 (proximal); exopod incompletely 2-segmented, with 5 or 6 natatory plumose setae.

Maxilliped 2 (Fig. 5H).—Basis with 1 plumose seta and 2 distal plumose setae on

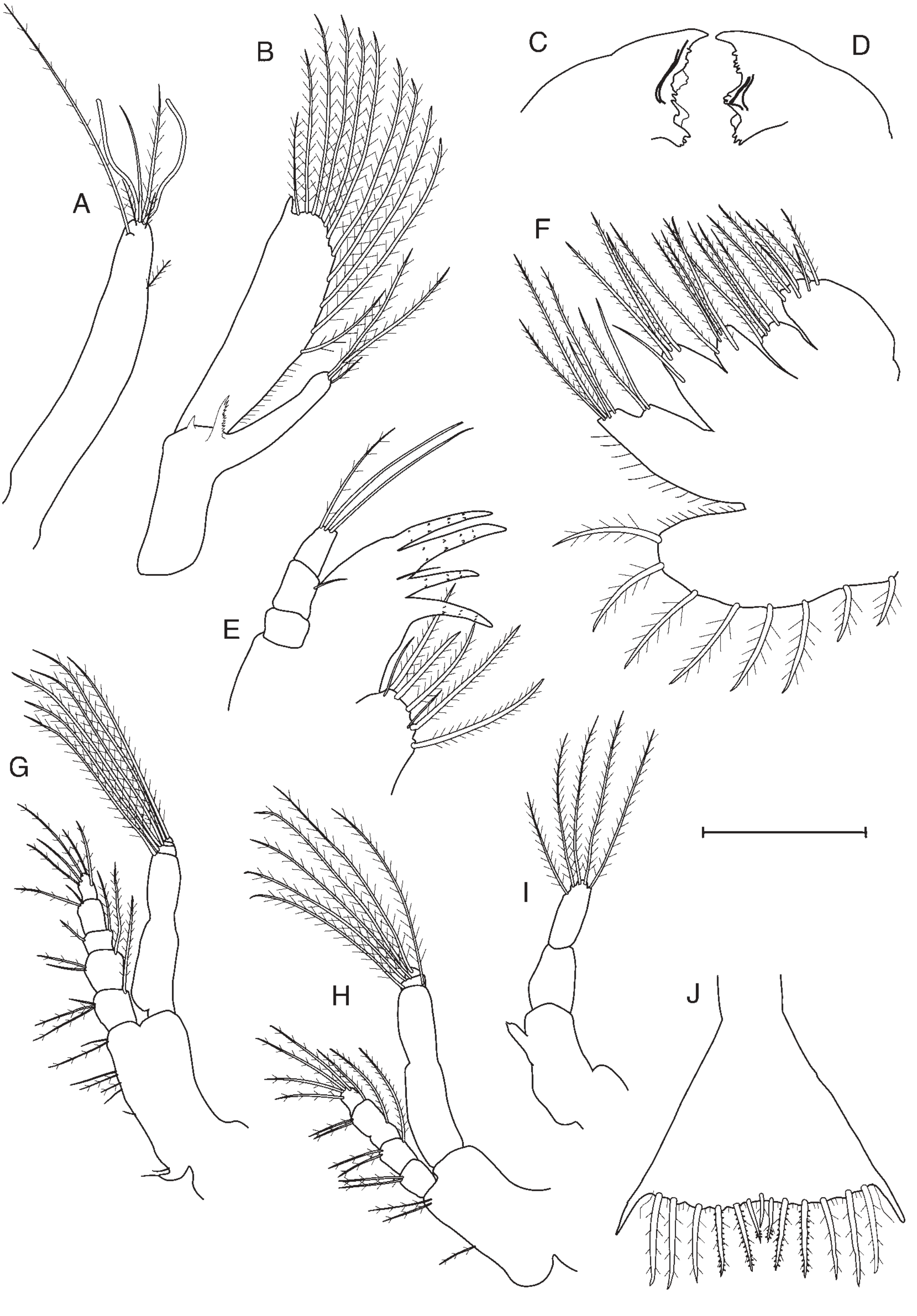

Fig. 5. *Coenobita compressus* H. Milne Edwards, 1837, zoea II. A, antennule; B, antenna; C, right mandible; D, left mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, telson. Scale = 0.1 mm (E, F), 0.25 mm (A–D, G–I), and 0.5 mm (J).

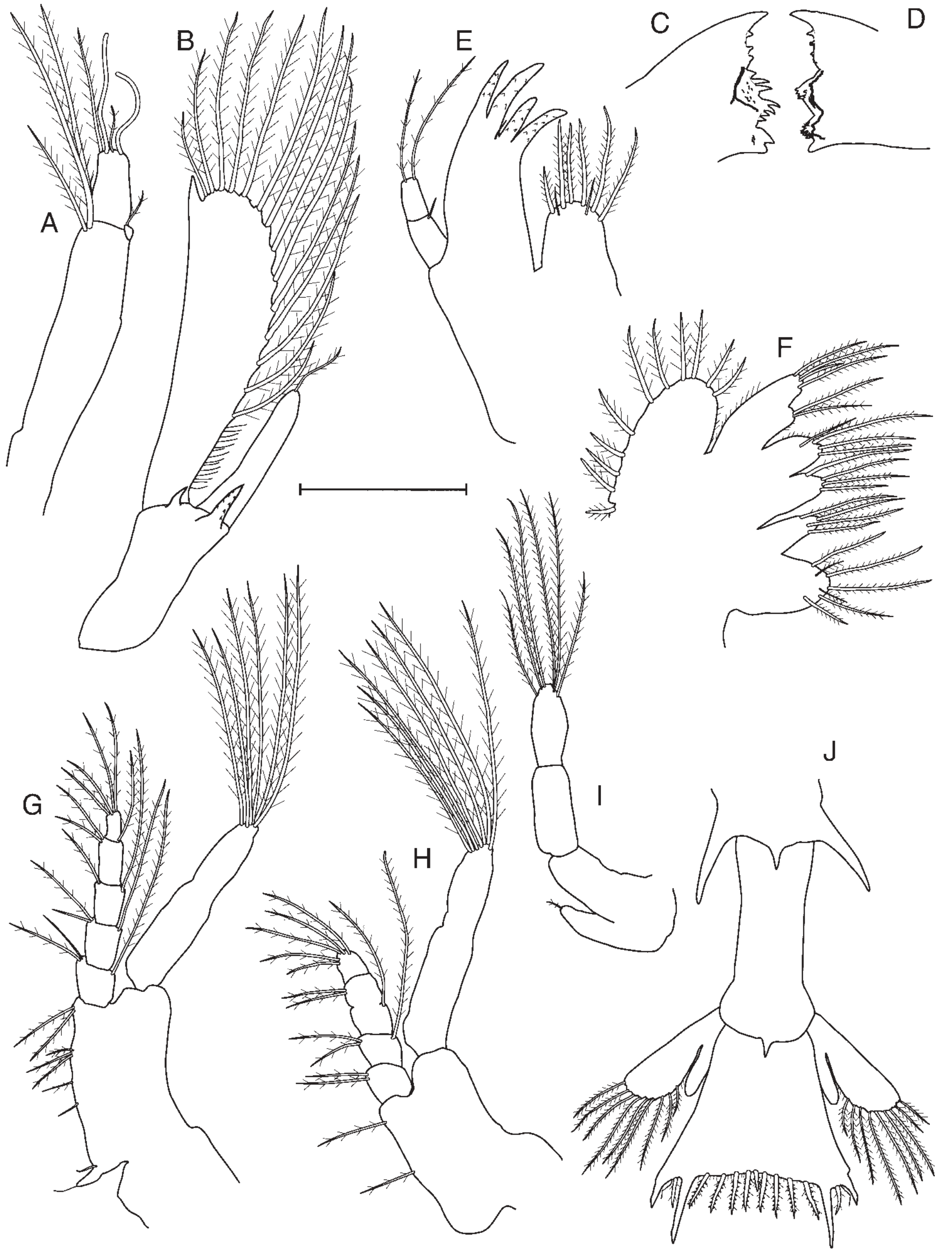

Fig. 6. *Coenobita compressus* H. Milne Edwards, 1837, zoea III. A, antennule; B, antenna; C, right mandible; D, left mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, telson and uropods. Scale = 0.16 mm (E, F), 0.25 mm (A–D, G–I), and 0.6 mm (J).

inner face. Endopod 4-segmented (penultimate segment deeply indented), with 2, 2, 2, 4 plumose setae along inner margin, single long plumose seta on outer margins of segments 2, 3, and 4; exopod incompletely 2-segmented, with 6 natatory plumose setae.

Maxilliped 3 (Fig. 5I).—Exopod 2-segmented, with 5 natatory plumose setae. Endopod bud usually present and terminating in thorn-like seta (not shown in figure).

Pereiopods.—Three pereiopod buds visible.

Abdomen (Figs. 2B, 3B).—Five somites. Second somite with prominent, slightly curved mediodorsal spine; third and fourth somites with much smaller mediodorsal spines; fifth somite with large, blunt, recurved mediodorsal spine and huge, blunt, dorsoventrally compressed posterolateral spines; sixth somite fused to telson.

Telson (Fig. 5J).—Posterior margin slightly concave, slight median notch; 8 + 8 marginal processes and sometimes small medial seta; outermost (first) fixed spine, second fine plumose hair, third through eighth articulated plumose spines, spinules present along medial and lateral margins of both sixth and seventh, along tops of both margins of eighth; small spinules between marginal processes; no fine setules.

Third Zoea

Specimens Examined.—Five.

Carapace (Figs. 2C, 3C).—Essentially unchanged.

Antennule (Fig. 6A).—2-segmented; bud of ventral flagellum vestigial, distal segment with 2 large terminal aesthetascs, 2 terminal plumose setae, 1 long and 1 short, and sometimes 2 terminal simple setae; proximal segment with 2 (1) terminal plumose setae and 3 large plumose setae at base of distal segment.

Antenna (Fig. 6B).—Endopod less than half length of exopod, with 1 short terminal plumose seta. Endopod 1-segmented, not fused to protopod. Exopod with 13 or 14 plumose setae on inner and distal margin, spine on outer distal margin, and setules along inner margin. Protopod with strong serrated spine and acute spine at base of exopod.

Mandible (Fig. 6C, D).—Right mandible with 1 prominent incisor and 3 smaller teeth dorsally, 7 or 8 teeth, prominent tooth and serrated edges more ventrally. Left mandible with prominent incisor and smaller teeth dorsally, large medial incisor with 1 large and several small teeth, ventral incisor with several similarly sized teeth.

Maxillule (Fig. 6E).—Coxal endite with 6 (7) stout terminal plumose setae and 2 (1) simple or plumose subterminal setae. Basal endite with 4–6 strong spines, each with several denticles, and 1 subterminal simple seta. Endopod with 2 or 3 segments, third segment with 2 or 3 setae (plumosity varies); simple seta sometimes on second segment.

Maxilla (Fig. 6F).—Proximal lobe of coxal endite with 7 (6) plumose setae: 3 of these submarginal and 4 marginal; distal lobe with 4 plumose setae, 1 submarginal. Proximal lobe of basal endite with 4 (5) plumose setae, 1 submarginal, distal lobe with 4 plumose setae, 1 submarginal. Proximal lobe of endopod with 2 or 3 plumose (sometimes 1 of these simple) setae, sometimes median margin with 1 simple seta, distal lobe with 3 or 4 setae, most plumose. Distal margin of endopod with row of fine setules. Scaphognathite with 9 or 10 plumose setae, additional seta at base of scaphognathite, proximal margin with row of fine setules.

Maxilliped 1 (Fig. 6G).—Basis with hooked process at proximal end of inner face, process with fine seta basally (sometimes plumose) and usually distally; 1, 1, 3, 1–3 setae (mostly plumose) more distally on this face. Endopod 5-segmented, with 1–3, 2, 1, 2 (1), 4 (3) setae (mostly plumose), a single long plumose seta on outer distal margins of segments 1, 2, and 3, and on outer proximal margin of segment 5; exopod incompletely 2-segmented with 6 natatory plumose setae.

Maxilliped 2 (Fig. 6H).—Basis with 2 plumose setae on inner face. Endopod 4-segmented (penultimate segment deeply indented), with 2, 2 (1), 2, 5 setae along inner margin, single long plumose seta on outer margins of segments 2 and 3; exopod incompletely 2-segmented, with 7 or 8 natatory plumose setae.

Maxilliped 3 (Fig. 6I).—Endopod small and unsegmented, with plumose seta at distal end. Exopod 2-segmented with 6 natatory plumose setae.

Pereiopods.—Four obvious buds.

Abdomen (Figs. 2C, 3C).—Unchanged.

Uropods (Fig. 6K).—Exopod, endopod, and protopod fused. Exopod with 8 or 9 plumose setae along posterior and inner margins, fine setules on mesial margin (not illustrated).

Telson (Fig. 6J).—Posterior margin slightly concave, slight median notch; 8 + 1 + 8 marginal processes: outermost (first) fixed spine, second fine plumose hair, third articulated plumose seta, fourth larger fixed spine, fifth through eighth articulated plumose spines, ninth small articulated plumose spine. Spinules in between all marginal processes and on both margins of fifth through ninth spines.

Fourth Zoea

Specimens Examined.—Seven.

Carapace (Figs. 2D, 3D).—Unchanged.

Antennule (Fig. 7A).—2-segmented; bud of ventral flagellum well developed, distal segment with 2–4 large terminal aesthetascs and sometimes 2 smaller subterminal aesthetascs, 2–4 terminal plumose setae, 1 very long and 1–3 shorter (sometimes 1 of these simple); proximal segment with 2–4 short terminal plumose setae and 4 (3) large plumose setae at base of distal segment.

Antenna (Fig. 7B).—Endopod almost as long as exopod, with 1 short plumose seta and blunt tubercle terminally, incompletely 2-segmented. Exopod with 13–16 plumose setae on inner and distal margins, spine on outer distal margin, and setules along inner margin. Strong serrated ventral spine on protopod at base of endopod and small spine on protopod at base of exopod.

Mandible (Fig. 7C, D).—Right mandible with 1 major incisor and 4 or 5 smaller teeth dorsally, 7 or 8 teeth on medial ridge, and 1 large tooth and several smaller teeth ventrally. Left mandible with 1 major dorsal incisor with several smaller teeth, 1 major incisor and several smaller teeth medially, and several teeth of variable size ventrally.

Maxillule (Fig. 7E).—Coxal endite with 8 (7) stout plumose setae, 1 or 2 of these generally submarginal and 1 sometimes simple. Basal endite with 6 or 7 strong spines, each with several denticles, and 1 subterminal simple (plumose) seta. Endopod incompletely 3-segmented, third segment with 3 setae (1 generally simple); sometimes simple seta on second segment.

Maxilla (Fig. 7F).—Proximal lobe of coxal endite with 8 plumose setae: 3 submarginal and 5 marginal; distal lobe with 5 (4) plumose setae, 1 submarginal. Proximal lobe of basal endite with 5 plumose setae, 1 submarginal, distal lobe with 5 (4) plumose setae, 1 submarginal. Proximal lobe of endopod with 3 plumose setae, distal lobe with 3 (4) plumose setae, 1 submarginal. Distal margin of endopod with row of fine setules. Scaphognathite with 12–15 plumose setae and small ventral lobe; proximal margin with row of fine setules.

Maxilliped 1 (Fig. 7G).—Basis with hooked process at proximal end of inner face, process with fine seta (sometimes plumose) basally and distally; 1, 1, 1–2, 2, 2 (3) setae (plumosity variable) on this face. Endopod 5-segmented, with 3 (2), 2, 1, 2, 4 setae (mostly plumose), single long plumose seta on outer margins of segments 1, 2, 3, and 5 (proximal); exopod incompletely 2-segmented, with 6 natatory plumose setae.

Maxilliped 2 (Fig. 7H).—Basis with 1, 1–2 plumose setae on inner face. Endopod 4-segmented (penultimate segment deeply indented), with 2 (1), 2, 2, 4 plumose setae along inner margin, single long plumose seta on outer margins of segments 2, 3, and 4; exopod incompletely 2-segmented, with 8 (7) natatory plumose setae.

Maxilliped 3 (Fig. 7I).—Endopod same size as protopod and unsegmented, with plumose seta terminally. Exopod 2-segmented, with 7 (8) natatory plumose setae.

Pereiopods (Fig. 7K).—Five buds present.

Abdomen (Figs. 2D, 3D).—Six somites, armature of somites 2–5 unchanged; sixth somite unarmed. Pleopod buds present.

Uropods (Fig. 7J).—Exopod, endopod, and protopod articulated. Endopod with 6 or 7 plumose setae and inner marginal row of fine setules; exopod with 12 (11) plumose setae along posterior and inner margins, fine setules on inner margin.

Telson (Fig. 7J).—Posterior margin slightly concave, slight median notch; 8 + 1 + 8 marginal processes: outermost (first) fixed spine, second fine plumose hair, third articulated plumose seta, fourth larger fixed spine, fifth through eighth articulated plumose spines, ninth small articulated plumose spine. Spinules in between all marginal processes and on both margins of fifth through ninth spines; with or without setules in between some marginal processes.

Fifth Zoea

Specimens Examined.—12.

Carapace (Figs. 2E, 3E).—Unchanged.

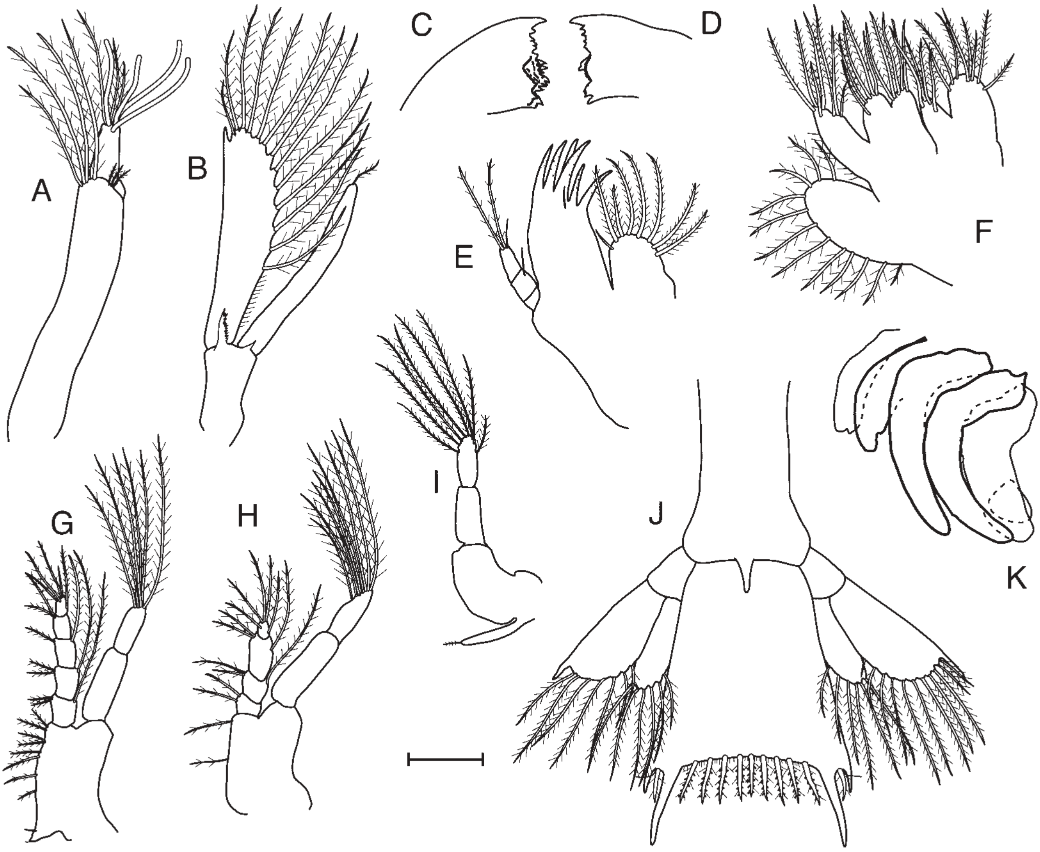

Fig. 7. *Coenobita compressus* H. Milne Edwards, 1837, zoea IV. A, antennule; B, antenna; C, right mandible; D, left mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, telson and uropods; K, pereiopod buds. Scale = 0.125 mm (E, F), 0.2 mm (A, C, D, I, K), and 0.32 mm (B, G, H, J).

Antennule (Fig. 8A).—2-segmented; bud of ventral flagellum well developed, distal segment with 3 large terminal aesthetascs and 2 or 3 smaller subterminal aesthetascs, usually 4 but sometimes as few as 2 terminal plumose setae (1 sometimes simple). Proximal segment with 4 short terminal plumose setae and 4 large plumose setae at base of distal segment; sometimes subterminal plumose seta and 2 plumose setae near base of proximal segment.

Antenna (Fig. 8B).—Endopod as long as exopod, with 1 short plumose seta and blunt tubercle terminally, incompletely 2 or 3-segmented, ultimate segment exceeding length of first 2 segments. Exopod with 16–18 plumose setae on inner and distal margins, spine on outer distal margin, and setules along inner margin. Strong serrated ventral spine on protopod at base of endopod and 1 thorn-like non-serrated spine on protopod at base of exopod.

Mandible (Fig. 8C, D).—Margin asymmetrical. Right mandible with 1 major incisor and 4–6 smaller teeth dorsally, 7 or 8 teeth on medial ridge, and 1 large tooth and several smaller teeth ventrally. Left mandible with 1 major dorsal incisor with several smaller teeth, 1 major incisor and several smaller teeth medially, and several teeth of variable size ventrally. Palp buds present.

Maxillule (Fig. 8E).—Coxal endite with 8 (7) stout plumose setae, 1 or 2 generally submarginal. Basal endite with 6 strong spines, each with several denticles, and 1 submarginal plumose seta. Endopod incompletely 3-segmented, third segment with 3 plumose setae; second segment with simple seta.

Maxilla (Fig. 8F).—Proximal lobe of coxal endite with 10 or 11 plumose seta: 8 (6) submarginal and 3 (4) marginal; distal lobe with 4 plumose setae, 1 terminal and 3 subtermi-

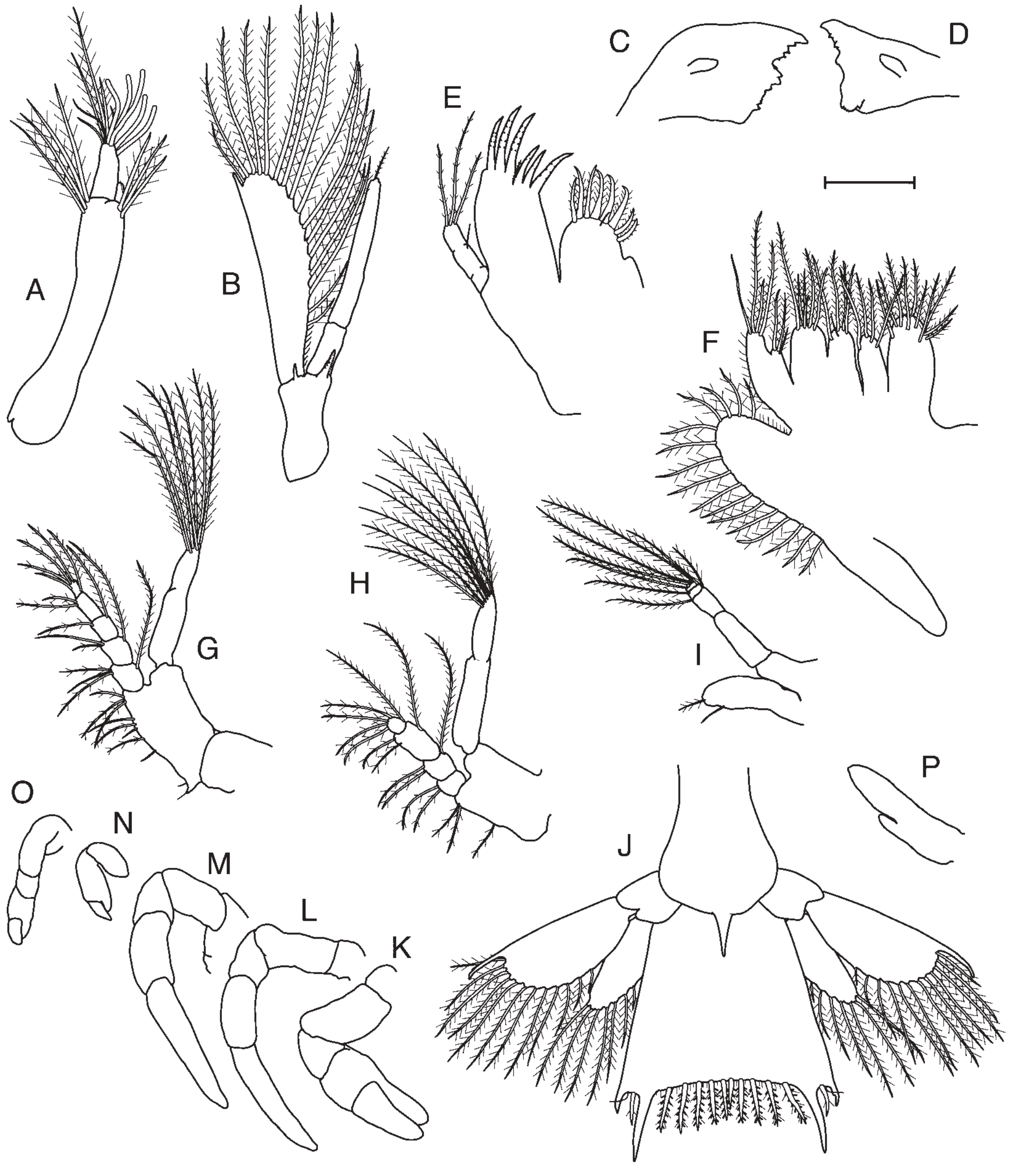

Fig. 8. *Coenobita compressus* H. Milne Edwards, 1837, zoea V. A, antennule; B, antenna; C, right mandible; D, left mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, telson and uropods; K–O, buds of first through fifth pereiopods; P, pleopod bud. Scale = 0.125 mm (E, F, P), 0.25 mm (A–D, G–I), and 0.32 mm (J–O).

nal. Proximal lobe of basal endite with 5 (7) plumose setae, 1 or 2 submarginal and 1 sometimes simple; distal lobe with 6 plumose setae. Proximal lobe of endopod with 2 or 3 plumose setae (1 sometimes simple), distal lobe with 4 setae, usually plumose although 1 sometimes simple. Distal margin of endopod with row of fine setules. Scaphognathite with 16–20 plumose setae, proximal margin with row of fine setules.

Maxilliped 1 (Fig. 8G).—Basis with hooked process at proximal end of inner face, process with fine seta (sometimes plumose) basally and distally; 1, 1, 3, 3 setae (mostly plumose) more distally on this face. Endopod 5-segmented, with 3, 2, 1, 2, 4 setae (mostly plumose), single long plumose seta on outer margins of segments 1, 2, 3, and 5 (proximal); exopod incompletely 2-segmented, with 6 or 7 natatory plumose setae.

Maxilliped 2 (Fig. 8H).—Basis with 1, 2 (3) plumose setae on inner face. Endopod 4-segmented (penultimate segment deeply indented), with 2, 2, 2, 4 plumose setae along inner margin, single long plumose seta on outer margins of segments 1 (sometimes), 2, 3, and 4 (proximal); exopod incompletely 2-segmented, with 8 (7) natatory plumose setae.

Maxilliped 3 (Fig. 8I).—Endopod larger than endopods of maxillipeds 1 and 2, unsegmented, with plumose seta terminally; sometimes with simple seta ventrally. Exopod 2-segmented, with 8 natatory plumose setae.

Pereiopods (Fig. 8K–O).—Limb buds incompletely segmented, most specimens unarmed and without setae. Dactyl of pereiopods 2 and 3 occasionally with clear corneous claw, dactyl of pereiopod 4 with long subterminal and terminal setae, and dactyl of pereiopod 5 with short thorn-like subterminal spine.

Abdomen (Figs. 2E, 3E).—6 somites; armature of somites 2–5 unchanged, sixth somite sometimes armed. Pleopod buds (Fig. 8P) biramous, not articulated.

Uropods (Fig. 8J).—Exopod, endopod, and protopod articulated. Endopod with 9 plumose setae and fine setules in between plumose setae; exopod with 13–15 plumose setae along posterior and inner margins, fine setules on inner margin.

Telson (Fig. 8J).—Posterior margin slightly concave, slight median notch; 8 + 1 + 8 marginal processes; outermost (first) fixed spine, second fine plumose hair, third articulated plumose seta, fourth larger fixed spine, fifth through eighth articulated plumose spines, ninth small articulated plumose spine. Spinules between all marginal processes and on both margins of fifth through ninth spines; setules between fourth and fifth marginal processes.

Megalopa

Specimens Examined.—Five.

Carapace (Fig. 2F).—Shield slightly rounded, more than half total carapace length, slightly wider than long; rostrum prominent, rounded. Ocular peduncles reach to base of ultimate segment of antennular peduncle, width approximately 4/5 length; corneas not inflated.

Antennule (Fig. 9A).—Biramous; peduncle 3-segmented. Basal segment with 3–8 dorsal marginal setae, 1 ventrodistal seta, 1 ventroproximal seta, and 1 lateral seta. Penultimate segment with 4 or 5 dorsal setae and single ventrodistal seta. Distal segment with 2 or 3 dorsal marginal setae, 1 submarginal dorsodistal seta, 2 submarginal ventral setae, and sometimes 3 distal setae. Upper ramus usually unsegmented (occasionally 2-segmented), with 7–9 aesthetascs and 2 or 3 short simple setae terminally, single seta along mediodorsal and medioventral margins; lower ramus unsegmented, with 4 setae, usually terminal but 1 sometimes subterminal, and 1 medioventral seta.

Antenna (Fig. 9B).—5-segmented; supernumerary segment present. Acicle rounded knob with 2 dorsal setae. Flagellum with 6 or 7 articles; setal formula of articles (proximal to distal) 0, 1–3, 4, 1 or 2, 4–6, 2 or 3, 8; all setae less than 1 article long except single terminal seta more than 4 articles long.

Mandible (Fig. 9C).—Palp 3-segmented, ultimate segment with 7 or 8 plumose setae.

Maxillule (Fig. 9D).—Coxal endite 12 marginal and submarginal plumose setae, and usually 3 or 4 simple submarginal setae; basal endite with 6 marginal plumose setae, 7–10 stout marginal teeth, 7–9 thin submarginal teeth, and 3 or 4 simple submarginal setae; 1 or 2 plumose setae along outer margin. Endopod unsegmented, with well-developed, recurved external lobe sometimes bearing simple terminal seta, internal lobe with 1 plumose seta, inner margin with shorter single plumose seta.

Maxilla (Fig. 9E).—Proximal lobe of coxal endites with 14 or 15 submarginal plumose setae and 13 or 14 marginal plumose setae (not all drawn as plumose), distal lobe with 6 plumose setae (2 of these subterminal). Proximal lobe of basal endites with 9 or 10 setae (plumosity variable), distal lobe with 11 or 13 setae (plumosity variable). Endopod with 2–4 setae. Scaphognathite with 56–68 plumose setae.

Maxilliped 1 (Fig. 9F).—Coxal lobe with 9 or 10 plumose setae; basal lobe with 17–19

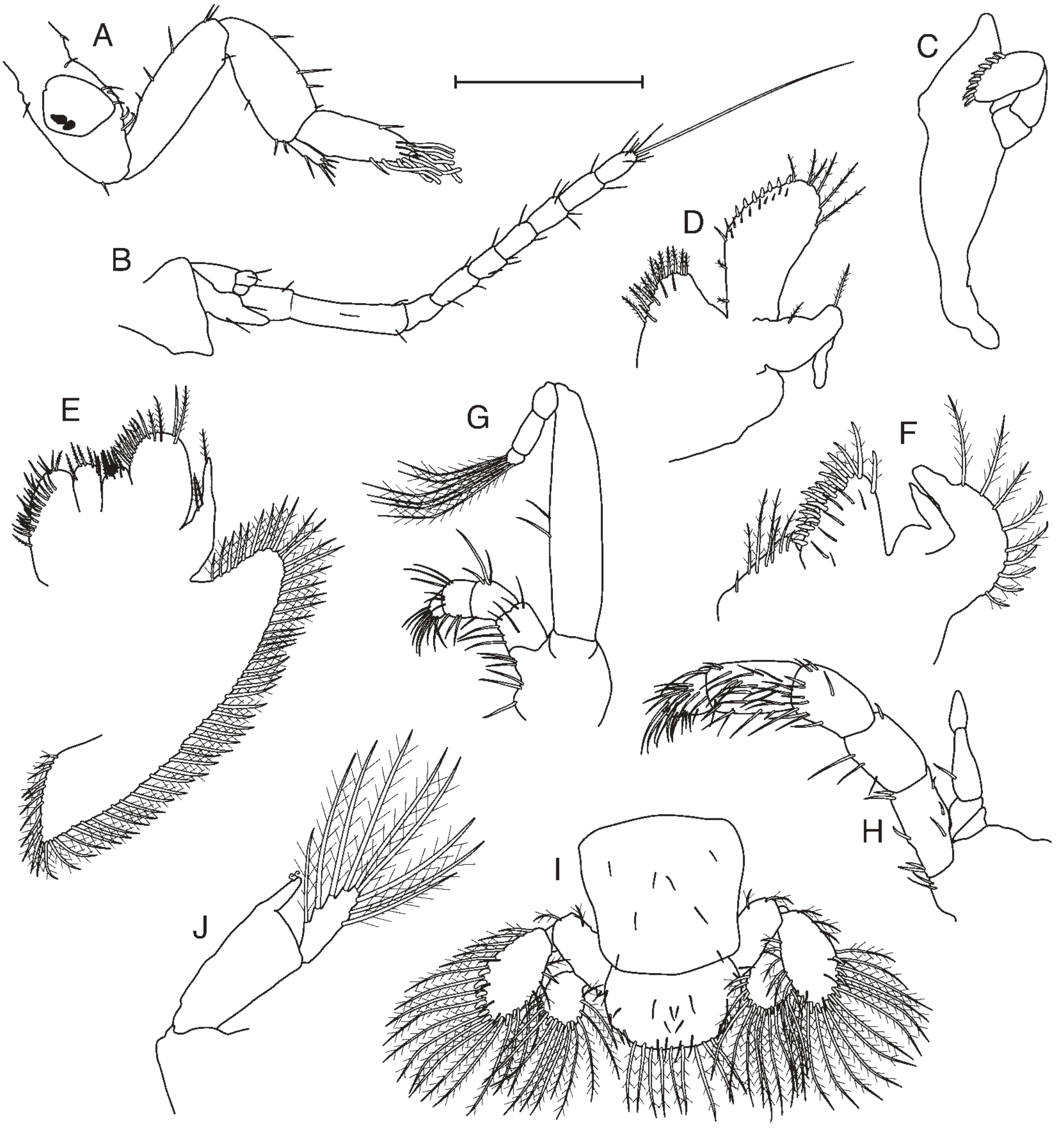

Fig. 9. *Coenobita compressus* H. Milne Edwards, 1837, megalopa. A, antennule; B, antenna; C, mandible; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, third maxilliped; I, telson and uropods; J, pleopod. Scale = 0.25 mm (C–G), 0.4 mm (A, B, H, J), and 1.0 mm (I).

stout, plumose, marginal setae, submarginal row of 4–6 simple setae. Endopod unsegmented, sometimes with 1 terminal plumose seta; exopod with strong lateral constriction, 9–11 marginal and terminal plumose setae.

Maxilliped 2 (Fig. 9G).—Endopod 4-segmented. Basal segment with 2 or 3 ventral, 1 lateral, and 3 dorsodistal setae; second segment with 4 distal submarginal setae; penultimate and ultimate segments each with 7–9 marginal and submarginal setae. Exopod 4-segmented, with 2 or 3 short simple setae along inner margin of basal segment, distal segment with 6 or 7 terminal plumose setae.

Maxilliped 3 (Fig. 9H).—Endopod 5-segmented, ultimate and penultimate segments heavily setose, remaining segments with scattered setae; exopod 4-segmented, rarely with 4 terminal plumose setae.

Pereiopods (Fig. 10A–G).—Chelipeds similar, dactyl subequal to palm in length, both

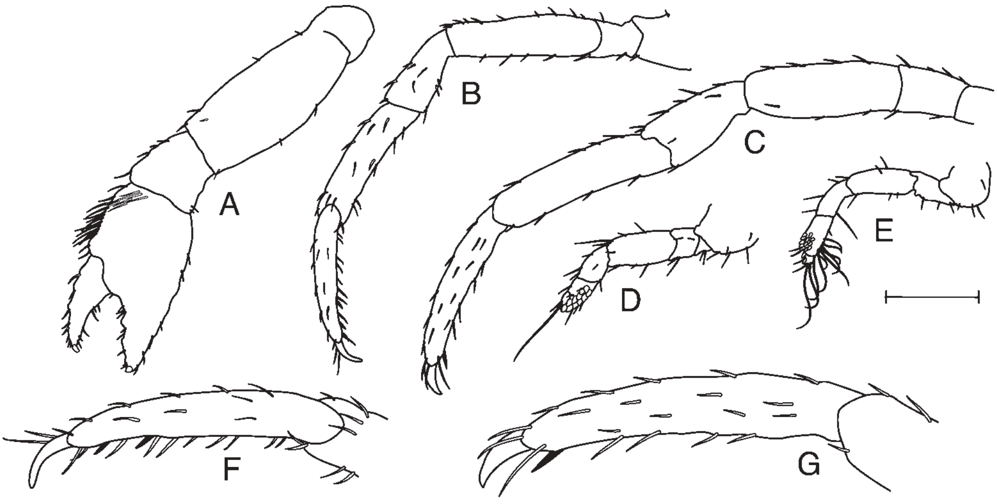

Fig. 10. *Coenobita compressus* H. Milne Edwards, 1837, megalopa. A–E, first through fifth pereiopods; F–G, dactyl of second and third pereiopods. Scale = 0.5 mm (A–E), 0.25 mm (F–G).

dactyl and fixed finger terminating in corneous claw surrounded by short setae; all segments with scattered setae, dorsal surface of chelipeds as well as mesial surface of palm and carpus with tufts of longer setae. Ambulatory legs with dactyl terminating in corneous claw surrounded by long simple setae; all segments with scattered setae. Second pereiopod dactyl with 2 movable teeth along distal half of ventral margin (Fig. 10F). Third pereiopod with 1 movable tooth just proximal to claw ventrally (Fig. 10G). Fourth pereiopod with scattered short setae on coxa, basis, and ischium; merus and carpus with longer setae on dorsal margin; propodus with short and long setae plus 6 marginal and 4 or 5 submarginal corneous scales, dactyl terminating in corneous claw, with scattered short setae and single long seta. Fifth pereiopod with scattered short setae on proximal segments, long dorsal and ventral setae on merus and carpus; propodus and dactyl with several long, curved setae and 12–15 corneous scales plus scattered short setae.

Abdomen (Fig. 2F).—Six unarmed somites with scattered, laterally paired dorsal setae. Biramous pleopods (Fig. 9J) on somites 2 through 5, exopod well developed, with 7 or 9 plumose setae; endopod simple lobe, with 1 or 2 small coiled subterminal setae.

Tail Fan (Fig. 9I).—Telson slightly wider than long (width exaggerated by specimen orientation in figure), with scattered, laterally paired setae on dorsal surface; posterior margin with 9 plumose setae, 1 or 2 short simple setae at posterolateral angle. Uropods biramous, symmetrical. Exopods with 1 or 2 short subproximal setae on dorsal surface, 20–23 long plumose setae and 9–11 corneous scales marginally, plus 4–6 submarginal short simple setae. Endopod margins with 12 or 13 long plumose setae, 2 short marginal plumose setae, 2 simple setae, and 8–10 corneous scales. Protopod with 2 or 3 setae anterior to exopod base and 1 short seta between endopod and telson.

Discussion

Coenobita compressus larvae and postlarvae are morphologically similar to the other described coenobitids but have a few unique morphological traits. In all zoeal stages, *C. compressus* has one seta on the basal endite of the maxillule proximal to the strong distal spines, compared to two setae in others. Starting in the third zoeal stage, the antennal endopod of *C. compressus* has a short, terminal plumose seta, unlike the long simple seta (sometimes called a process) found in most other coenobitids, or the short, terminal simple seta found on the antennal endopod of the last zoeal stage (zoea II) of *C. variabilis*. Also, the antennules of zoea IV *C. compressus* have subterminal aesthetascs, whereas other coenobitids do not acquire subterminal aesthetascs until the fifth stage, if at all.

Coenobita compressus megalopae can be distinguished from other coenobitids by the exopods of the second and third maxillipeds, which each have four segments in *C. compressus* compared to only one or two in other species. Although zoeal and megalopal *C. compressus* appear consistently unique with regards to the characteristics described above, these distinguishing traits should be considered provisional because half of the coenobitids have not yet been described.

The hermit crab family Diogenidae, considered the sister taxon to the Coenobitidae (MacDonald *et al.*, 1957; McLaughlin, 1983; Martin and Abele, 1986), has many representatives throughout the eastern Pacific with larvae that may be morphologically similar to *C. compressus*. From the Diogenidae, 26 species in ten genera (*Dardanus, Clibanarius, Petrochirus, Calcinus, Paguristes, Trizopagurus, Isocheles, Aniculus, Allodardanus*, and *Cancellus*) have been reported from this region (Hendrickx and Harvey, 1999). Unfortunately, published larval descriptions are available for only two of these 26 species: *Trizopagurus magnificus* (Bouvier) in Provenzano (1967) and *Clibanarius albidigitus* Nobili in Siddiqui *et al.* (1993). This limited knowledge on the larval development of the eastern Pacific diogenids makes it difficult to delineate characters that would serve to distinguish them from *C. compressus* in the plankton. Even comparisons based on descriptions of diogenids from outside the eastern Pacific must be considered tentative given the limited knowledge of diogenid larvae worldwide. For example, published larval descriptions are currently available for only 11 of 58 species of *Clibanarius*, two of about 40 species of *Calcinus*, and eight of over 100 species of *Paguristes*.

Within the limitations of such generalizations, the larvae of *C. compressus* can be distinguished from those diogenid genera for which larval data are available by a series of morphological characters that can be observed without dissection. Although it has been suggested that the presence of a median telson spine in third stage and older zoeae distinguishes coenobitids from all other anomurans (e.g., Al-Aidaroos and Williamson, 1989; Seridji, 1992), this character is found in the later zoeal stages of most diogenids, including *Clibanarius, Isocheles, Petrochirus, Trizopagurus,* and often *Calcinus* and *Paguristes.*

Zoeal stages of *Clibanarius* and *Petrochirus* can be easily distinguished from *C. compressus* by their lack of lateral and dorsomedial spines on the abdominal somites and lack of anterolateral spines on the antennal scales (e.g., Provenzano, 1968b; Brossi-Garcia, 1987). *Dardanus* zoeae also lack dorsomedial spines on the abdominal somites and anterolateral spines on the antennal scales (e.g., Kurata, 1968; Hebling and Barros-Mansur, 1995). *Calcinus* zoeae have prominent paired spines on the posterior carapace margin, and only the fifth abdominal somite possesses a dorsomesial spine (Provenzano, 1962b). Zoeae of *Trizopagurus magnificus*, the only eastern Pacific representative of its genus, differ from *C. compressus* in that the carapace, abdomen, and telson are covered with minute spinules, the carapace has small blunt anteroventral spines, and only the fifth abdominal somite has a dorsomesial spine (Provenzano, 1967). In *Paguristes*, the zoeal rostrum is noticeably shorter than the carapace, which has anterolateral (pterygostomian) spines (e.g., Rice and Provenzano, 1965; Provenzano, 1978; Hebling and Negreiros-Fransozo, 1983), whereas *C. compressus* has a long rostrum and no pterygostomian spines. The rostrum is relatively short and broad in the zoeae of *Isocheles*, and apparently lacks a carina; also, the dorsomesial spine on the second abdominal somite is not enlarged as in *C. compressus* (Negreiros-Fransozo and Hebling, 1983).

Unfortunately, we can offer no suggestions for distinguishing the larvae of *C. compressus* from those of *Aniculus, Allodardanus,* or *Cancellus*, because no published data are available on the larval development of members of these genera.

The coenobitid species reared to date reveal considerable intra- and interspecific variation in the number of zoeal stages: *Coenobita clypeatus* passes through 4–6 stages (Provenzano, 1962a), *Birgus latro* 3–5 (Reese and Kinzie, 1968), and *C. compressus* 4 or 5 (this study). Five species showed no variation in the number of zoeal stages. Of these, *C. variabilis* is unique in that it exhibits greatly abbreviated development, which presumably reduces the opportunities for variability in number of stages in this species. We suspect that the reported lack of variability in the number of stages in other species may be artifacts of low survivorship to the megalopal stage and group-rearing. For example, Al-Aidaroos and Williamson (1989) reported that *C. scaevola* requires seven zoeal stages, but this was based on only two megalopae. Likewise, no stage variability was reported for *C. cavipes, C. purpureus*, and *C. rugosus* (Shokita and Yamashiro, 1986; Nakasone, 1988), but these species were mass-reared, a procedure that probably makes it more difficult to detect variation in stage numbers. The risk of overlooking variation in stage numbers is especially great when the variant pathways are rare, as in the present study where only 12% of *C. compressus* larvae required only four zoeal stages prior to metamorphosis. For this reason, we recommend that larvae be reared individually whenever possible.

Shell use by megalopae appears to be an important component of the transition from water to land in coenobitids. Under laboratory conditions, coenobitid megalopae show an escalating interest in shells throughout the megalopal stage, and nearly always leave the water wearing a shell if available (Brodie, 1999). Although coenobitid megalopae will make the transition from water to land without a shell (Reese, 1968; Harvey, 1992; Brodie, 1999), the possession of a shell increases the ability of megalopae to tolerate lower humidity environments (unpublished data).

In *Birgus latro* and *Coenobita compressus*, megalopae wearing shells are more likely to successfully metamorphose than their shell-less siblings (Reese, 1968; Brodie, 1999). In contrast, Harvey (1992) found that the possession of a shell by terrestrial *C. variabilis* megalopae did not significantly increase the probability that megalopae would successfully metamorphose. However, rearing conditions were different in these studies: Harvey (1992) reared his crabs in incubated covered plastic containers where they experienced very high humidities and uniform temperatures. Brodie (1999) kept her more open containers outside in a covered arena where her animals experienced greater fluctuations in temperature and humidity, while Reese's (1968) animals were reared in covered terraria in the laboratory (personal communication). Unfortunately, nothing is known about the microhabitats favored by coenobitid megalopae in the field, and thus what humidity regimes megalopae normally encounter. Nor are there any data concerning the frequency or fate of coenobitid megalopae leaving the sea without shells. In the absence of these essential field data, we cannot draw any conclusions about the biological relevance of these different rearing protocols and their influence on the survival and development of megalopae.

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LITERATURE CITED

Al-Aidaroos, A., and D. I. Williamson. 1989. Larval development of the land hermit crab *Coenobita scaevola* (Forskål, 1775) (Crustacea: Anomura: Coenobitidae) reared in the laboratory.—Journal of Natural History 23: 111–128.

Ball, E. E., and J. Haig. 1974. Hermit crabs from the tropical Eastern Pacific. 1. Distribution, color, and natural history of some common shallow-water species.—Bulletin of the Southern California Academy of Sciences 73: 95–104.

Brodie, R. J. 1999. Ontogeny of shell-related behaviors and transition to land in the terrestrial hermit crab, *Coenobita compressus* H. Milne Edwards.—Journal of Experimental Marine Biology and Ecology 241: 67–80.

Brossi-Garcia, A. L. 1987. Morphology of the larval stages of *Clibanarius sclopetarius* (Herbst, 1796) (Decapoda, Diogenidae) reared in the laboratory.—Crustaceana 52: 251–275.

Hartnoll, R. G. 1988. Evolution, systematics, and geographical distribution. Pp. 6–54 *in* W. W. Burggren and B. R. McMahon, eds. Biology of the Land Crabs. Cambridge University Press, New York.

Harvey, A. W. 1992. Abbreviated larval development in the Australian terrestrial hermit crab *Coenobita variabilis* McCulloch (Anomura: Coenobitidae).—Journal of Crustacean Biology 12: 196–209.

Hebling, N. J., and C. De Barros-Mansur. 1995. Desenvolvimento larval de *Dardanus insignis* (Saussure) (Crustacea, Decapoda, Diogenidae), em laboratorio.—Revista Brasileira de Zoologia São Paulo 12: 471–491.

———, and M. L. Negreiros-Fransozo. 1983. Desenvolvimento pós-embrionario de *Paguristes tortugae* Schmitt, 1933 (Decapoda, Diogenidae), em laboratório.—Boletim de Zoologia, Universidade de São Paulo 6: 157–176.

Hendrickx, M. E., and A. W. Harvey. 1999. Checklist of anomuran crabs (Crustacea: Decapoda) from the Eastern Tropical Pacific.—Belgian Journal of Zoology 129: 363–389.

Kurata, H. 1968. Larvae of Decapoda Anomura of Arasaki, Sagami Bay–II. *Dardanus arrosor* (Herbst) (Diogenidae).—Bulletin of the Tokai Regional Fisheries Research Laboratory 56: 173–180.

MacDonald, J. D., R. B. Pike, and D. I. Williamson. 1957. Larvae of the British species of *Diogenes, Pagurus, Anapagurus,* and *Lithodes* (Crustacea, Decapoda).—Proceedings of the Zoological Society of London 128: 209–257.

Martin, J. W., and L. G. Abele. 1986. Phylogenetic relationships of the genus *Aegla* (Decapoda: Anomura: Aeglidae), with comments on anomuran phylogeny.—Journal of Crustacean Biology 6: 575–616.

McLaughlin, P. A. 1983. Hermit crabs—are they really polyphyletic?—Journal of Crustacean Biology 3: 608–621.

Nakasone, Y. 1988. Larval stages of *Coenobita purpureus* Stimpson and *C. cavipes* Stimpson reared in the laboratory and survival rates and growth factors of three land hermit crab larvae (Crustacea: Anomura).—Zoological Science 5: 1105–1120.

Negreiros-Fransozo, M. L., and N. J. Hebling. 1983. Desenvolvimento pos-embrionario de *Isocheles sawayai* Forest & Saint Laurent, 1967 (Decapoda, Diogenidae), em laboratorio.—Papéis Avulsos de Zoologia, São Paulo 35: 41–53.

Provenzano, A. J., Jr. 1962a. The larval development of the tropical land hermit crab *Coenobita clypeatus* (Herbst) in the laboratory.—Crustaceana 4: 207–228.

———. 1962b. The larval development of *Calcinus tibicen* (Herbst) (Crustacea, Anomura) in the laboratory.—Biological Bulletin 123: 179–202.

———. 1967. The zoeal stages and glaucothoe of the tropical eastern Pacific hermit crab *Trizopagurus magnificus* (Bouvier, 1898) (Decapoda; Diogenidae), reared in the laboratory.—Pacific Science 21: 457–471.

———. 1968. The complete larval development of the West Indian hermit crab *Petrochirus diogenes* (L.) (Decapoda, Diogenidae) reared in the laboratory.—Bulletin of Marine Science 18: 143–181.

———. 1978. Larval development of the hermit crab, *Paguristes spinipes* Milne-Edwards, 1880 (Decapoda, Diogenidae), reared in the laboratory.—Bulletin of Marine Science 28: 512–526.

Reese, E. S. 1968. Shell use: an adaptation for emigration from the sea by the coconut crab.—Science 161: 385, 386.

———, and R. A. Kinzie III. 1968. The larval development of the coconut or robber crab, *Birgus latro* (L.), in the laboratory (Anomura, Paguridea).—Crustaceana 15 (supplement 2): 117–144.

Rice, A. L., and A. J. Provenzano, Jr. 1965. The zoeal stages and the glaucothoe of *Paguristes sericeus* A. Milne-Edwards (Anomura, Diogenidae).—Crustaceana 8: 239–254.

Seridji, R. 1992. On a collection of decapod larvae from the Gulf of Aqaba off the Jordanian coast, I. Thalassinidea and Anomura.—Crustaceana 68: 281–320.

Shokita, S., and A. Yamashiro. 1986. Larval development of the land hermit crabs, *Coenobita rugosus* H. Milne-Edwards and *C. cavipes* Stimpson reared in the laboratory.—Galaxea 5: 267–282.

Siddiqui, F. A., P. A. McLaughlin, and J. A. Crain. 1993. Larval development of the hermit crab *Clibanarius albidigitus* (Crustacea: Anomura: Diogenidae) reared under laboratory conditions.—Marine Biology 116: 603–613.

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