Abbreviated Larval Development in the Australian Terrestrial Hermit Crab Coenobita variabilis McCulloch (Anomura: Coenobitidae)

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Alan Harvey
Georgia Southern University

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ABBREVIATED LARVAL DEVELOPMENT IN THE AUSTRALIAN TERRESTRIAL HERMIT CRAB *COENOBITA VARIABILIS* McCULLOCH (ANOMURA: COENOBITIDAE)

Alan W. Harvey

ABSTRACT

The complete larval development of the Australian terrestrial hermit crab *Coenobita variabilis* McCulloch is described from laboratory-reared specimens. Development consists of two brief, nonfeeding zoeal stages and one megalopal stage. The megalopal stage does feed, but will metamorphose only on land. This is the first case of abbreviated development known in the Coenobitidae. Both zoeal stages exhibit character development typical of all stages of other coenobitids, allowing for easy identification of the species but preventing a clear determination of which stages were eliminated during the evolution of the abbreviated developmental mode. Compared to known megalopae of other coenobitids, the megalopa shows no evidence of advanced development.

Terrestrial hermit crabs (family Coenobitidae) are found in tropical and subtropical coastal regions throughout the world, particularly on islands. Adults are committed to terrestrial environments, but the larvae maintain a typical planktonic existence. Published descriptions of laboratory-reared larvae exist for six of the approximately 16 known species: *Coenobita clypeatus* (Herbst), by Provenzano (1962); *C. rugosus* H. Milne Edwards, by Shokita and Yamashiro (1986); *C. cavipes* Stimpson, by Shokita and Yamashiro (1986) and Nakasone (1988); *C. purpureus* Stimpson, by Nakasone (1988); *C. scaevola* (Forskål), by Al-Aidaroos and Williamson (1989); and the coconut crab *Birgus latro* (L.), by Reese and Kinzie (1968).

Only one species is known to occur on the Australian mainland (McCulloch, 1909; Morgan, 1987), traditionally assigned to *Coenobita spinosus* H. Milne Edwards. McCulloch (1909) described two varieties from Australia, which he designated *C. s. spinosus* and *C. s. variabilis.* I compared most of the material McCulloch used to describe these forms (courtesy of the Australian Museum) with a specimen determined by Prof. J. Forest of the Muséum National d'Histoire Naturelle as conspecific with the type of *C. spinosus* H. Milne Edwards. The Australian material clearly is not referable to *C. spinosus* sensu stricto. It is likely that McCulloch's taxa are extremes in an intraspecific grade, with *C.* "*s. variabilis*" representing smaller specimens, *C.* "*s. spinosus*" representing larger specimens. I therefore elevate the Australian forms to full species status as *C. variabilis* McCulloch, 1909.

In this paper I describe the complete larval development of *Coenobita variabilis* under laboratory conditions. *Coenobita variabilis* is the first member of the Coenobitidae reported to undergo abbreviated development, reaching the megalopal stage in only six days at 30°C after two nonfeeding zoeal stages.

MATERIALS AND METHODS

I collected several ovigerous female *C. variabilis* from the shore at Darwin, Northern Territory, Australia, from 22–24 February 1990. These were transported by air to James Cook University, Townsville, Queensland, Australia, where I conducted all rearing studies. Adults were kept at 30°C in large cardboard boxes with several inches of leaf litter and a bowl of sea water. By about 0200 on 26 February, several females had already released hundreds of larvae into the sea water. One hundred and two larvae were reared in compartmented plastic trays; each compartment held one larva and 20 ml filtered sea water. The remainder of the larvae were mass-reared in a 20-l aquarium that was provided clean water continually by a 20,000-l recirculating sea water system. Temperature was a constant 30°C; salinity was uncontrolled. The light cycle was a constant 14L:10D.

Larval Culture.—Larvae were provided newly hatched nauplii of *Artemia*, but did not appear to feed. Another female provided a hatch on 1 March 1990; these larvae were used in a small experiment to determine whether

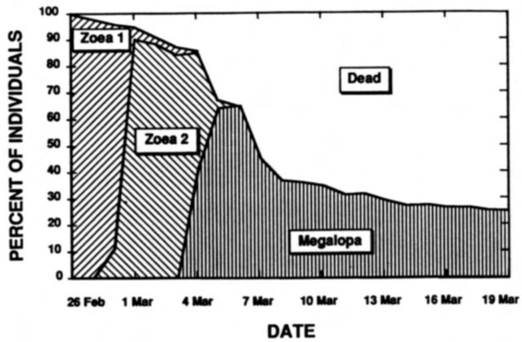

Fig. 1. Larval development in *Coenobita variabilis* under laboratory conditions. This is an area chart, in which percentage values are stacked on top of each other. For example, on 28 February 1990, 90% of the individuals were second stage zoeae, 5% were first stage zoeae and 5% were dead. On 19 March 1990, surviving megalopae were used in shell-and-land experiments (see text). $N = 102$.

food was required for successful growth in this species. Twenty-one larvae were reared as above, with newly hatched nauplii of *Artemia*; 21 larvae were starved. To see whether temperature influenced larval development rates, survival, or feeding, 7 larvae from each feeding treatment were maintained at 20°, 25° and 30°C. These data were analyzed in a factorial design that evaluated the effects of temperature, food, and the interaction between the two.

When the zoeae metamorphosed into megalopae, it became clear that these fed, since they were heavily cannibalistic upon the remaining zoeae in the mass-rearing tank. However, megalopae did not seem to feed on nauplii of *Artemia* in the individual compartments, and were given flake fish food. On 8 March 1990, about a week after megalopae appeared, I provided half of the surviving megalopae (including those from the feeding/temperature experiments described above) with tiny empty gastropod shells. By 19 March, no megalopae had molted to first crab. I then moved half of the survivors (with their shells, if offered) to covered plastic boxes (16 × 10 × 5 cm) each containing a layer of moist ultrafine sand and a bivalve shell, which held approximately 10 ml sea water. The bivalve shell was partly buried in the sand, so that the megalopa could climb out of the water if it so desired. Megalopae in these boxes received the same daily maintenance as those remaining in the compartmented trays.

Larval Descriptions.—Descriptions are based on molts and preserved and living stages. Dissections were made in glycerin under a Wild M-5 stereomicroscope. The abbreviation CL refers to carapace length, measured from the tip of the rostrum to the posterior midpoint of the carapace, TL refers to the total length of the animal, measured from the tip of the rostrum to the midpoint of the telson (excluding telsonal processes), n refers to the number of specimens measured and/or dissected, and N refers to the number of individuals reared at 30°C that survived and molted to the next stage. Length measurements were made with an ocular micrometer. All setal formulae are proximal to distal. All drawings were made using a computerized illustration system of my own design. Illustrations were printed on a high resolution laser printer.

Results

Coenobita variabilis passed through two zoeal stages and a megalopal stage (Figs, 1, 2). The megalopal stage was reached after six or seven days at 30°C and eight to ten days at 25°C. The larvae kept at 20°C died without successfully completing the molt to the second zoeal stage. However, upon examination these larvae were found to be fully developed second stage zoeae, still partially swathed in a filmy, ragged first stage cuticle that appeared to be in the process of gradually sloughing off. Feeding had no effect on survival or stage duration ($P = 0.35$). None of the 30 megalopae that were confined to water molted to first crab, whether or not shells were provided. Megalopae that were kept in the sand-filled plastic boxes quickly left the water, whether or not they had access to a shell. Once out of the water, megalopae typically wandered on the sand for a few days before burying themselves just under the surface of the sand to molt, emerging as a first stage crab the next day. There were no significant differences between shelled and shell-less megalopae either in probability of survival to first crab (89% versus 75%; $n = 17$, $P = 0.49$) or in number of days spent on land before metamorphosing (8.75 ± 3.11 days versus 12.0 ± 6.45 days, $P = 0.23$).

Description of the Larvae

First Zoea

Size.—CL = 2.18 ± 0.05 mm; TL = 5.18 ± 0.09 mm; $n = 15$. Duration: 2–4 days, mean 2.77 ± 0.46, mode 3; $N = 102$.

Carapace (Fig. 2A, D).—Rostrum long, pointed, tapering, extending beyond tip of antennules; carinate, especially posteriorly. Posterolateral margins of carapace rounded. Eyes sessile.

Antennule (Fig. 3A).—Uniramous; terminally with 3 or 4 large aesthetascs, 1 long and often 1 short plumose seta, and often 1 short simple seta; 1 long subterminal plumose seta.

Antenna (Fig. 3B).—Endopod unsegmented, fused to protopod, with 2 long and 1 short plumose terminal setae; exopod with 10 plumose setae on distal margin, row of

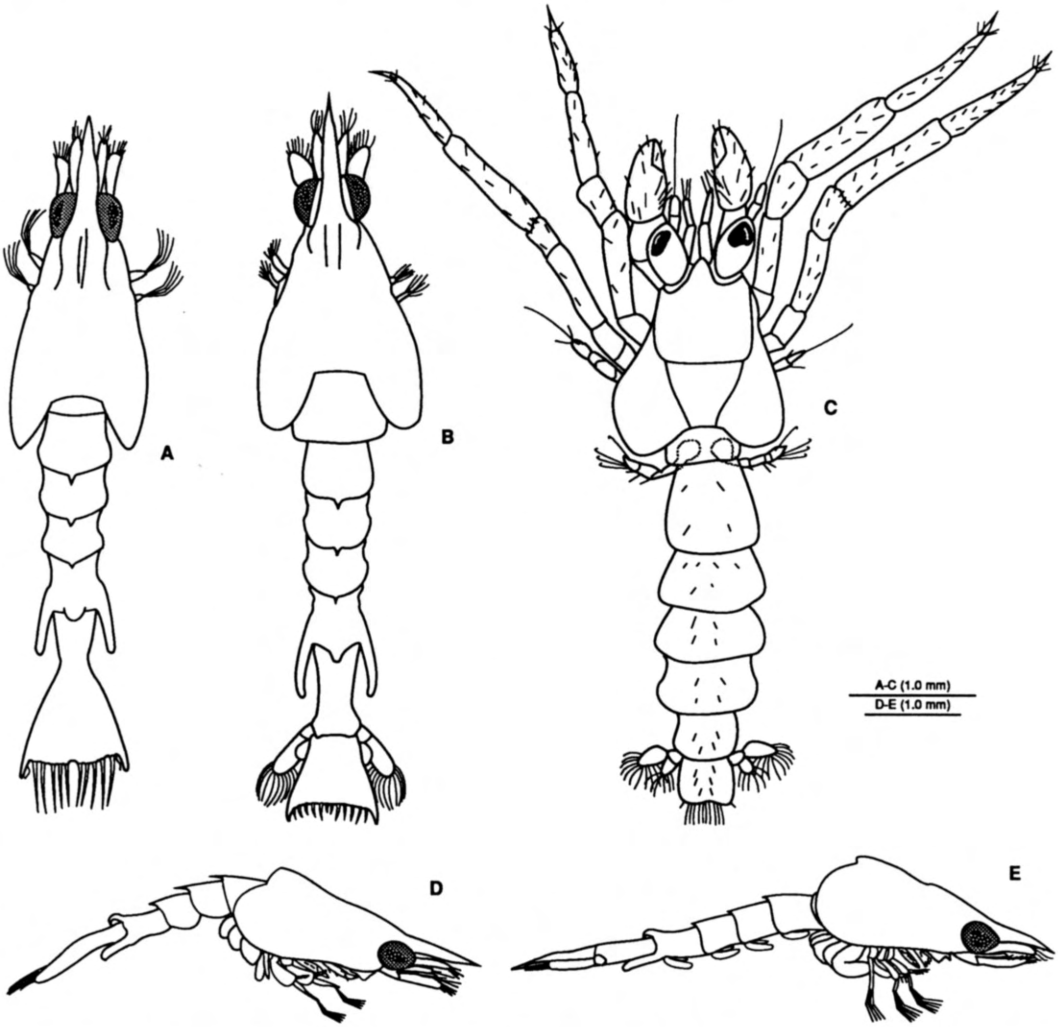

Fig. 2. *Coenobita variabilis,* whole animals; A–C, dorsal views; D, E, lateral views. A, zoea I; B, zoea II; C, megalopa; D, zoea I; E, zoea II.

fine setae on mesial margin, no spine on outer distal margin; strong serrated distal spine on protopod at base of exopod.

Mandible (Fig. 3C, D).—Cutting edge with large incisor and molar processes, interspersed with smaller spines; palp bud present.

Maxillule (Fig. 3E).—Coxal endite with 5 terminal plumose setae and 2 subterminal simple setae. Basal endite with 2 strong spines, each with several denticles, and 2 subterminal simple setae. Endopod 3-segmented, third segment with 3 simple setae, first with simple seta.

Maxilla (Fig. 3F).—Proximal lobe of coxal endite with 5 subterminal and 2 terminal setae (not visible in figure), distal lobe with 3 terminal setae; proximal lobe of basal endite with 4 (rarely 5) setae, distal lobe with 3 setae. Proximal lobe of endopod with 3 setae, distal lobe with 3 (rarely 2) setae, single seta between proximal and distal lobes, distal margin of endopod with row of fine setules; scaphognathite with 10 (rarely 9) plumose setae, proximal margin with row of fine setules.

Maxilliped 1 (Fig. 3G).—Basis with hooked process at proximal end of inner face, process with fine seta basally and distally; inner face of basis with 2, 3, 3 (rarely 2) setae distally. Endopod 5-segmented; setal formula 2 (rarely 3), 2, 1, 2, 4+I (Roman numeral denoting dorsolateral seta), mostly

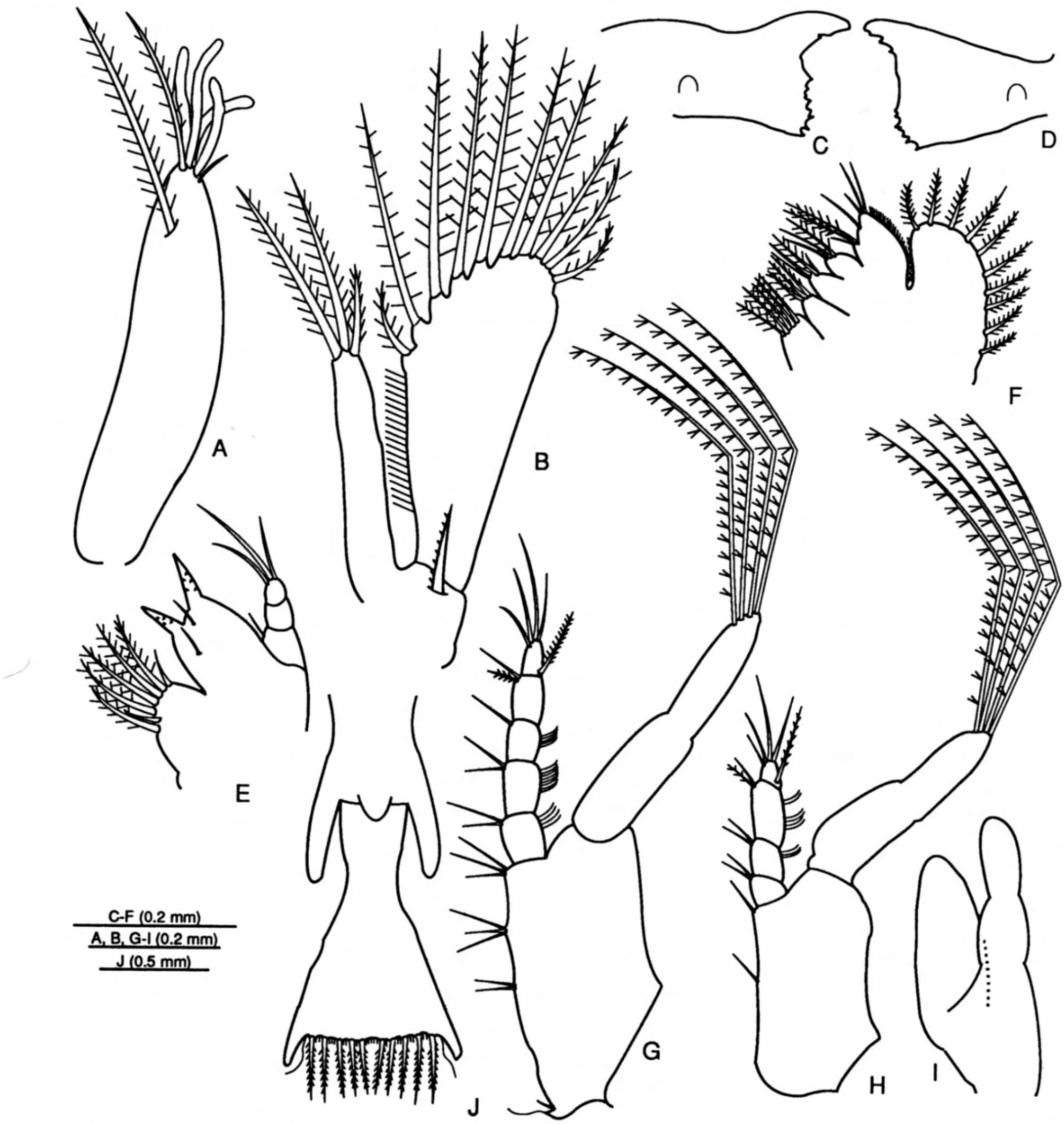

Fig. 3. *Coenobita variabilis,* zoea I. A, antennule; B, antenna; C, D, mandibles; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, telson.

simple except for 1 plumose seta on penultimate segment and dorsolateral seta on ultimate segment; also fine hairs on first 3 segments; exopod incompletely 2-segmented, with 4 natatory plumose setae.

Maxilliped 2 (Fig. 3H).—Basis with 1 medial and 1 distal seta on inner face. Endopod 4-segmented, setal formula 2, 2, 2, 4+I setae, mostly simple except for 1 plumose seta on penultimate segment and dorsolateral plumose seta on ultimate segment; also fine hairs on segments 2 and 3; exopod incompletely 2-segmented with 4 natatory plumose setae.

Maxilliped 3 (Fig. 3I).—Endopodal bud as long as exopod, broader at base; exopod incompletely 2-segmented.

Pereiopods (Fig.6A–E).—Buds of all limbs present and relatively well developed, but unsegmented.

Abdomen (Fig. 2A, D).—Five free somites, with sixth somite fused to telson; second somite with prominent, slightly curved mediodorsal spine; third and fourth somites with much smaller mediodorsal spines; fifth somite with large, blunt, deeply recurved mediodorsal spine and huge, blunt, dorsoventrally compressed posterolateral spines.

Telson (Fig. 3J).—Posterior margin straight, median gap straight to slightly notched; 7+7 marginal processes (I, ii, 3–7), outermost fixed spine (I), second fine simple hair (ii), third through seventh articulated plumose setae, spinules present basally on both margins of fifth, along full length of both margins of sixth and along full length of lateral margin of seventh (spinules not illustrated).

Color.—Zoea transparent overall, although carapace and lateral margins of abdomen with numerous white chromatophores that are often dense enough to give animal whitish cast. Corneas black with heavy silver iridescence. Bases of antennae, antennules, and mandibles with red chromatophores; abdomen with few red chromatophores on first somite, becoming more abundant distally, especially on fifth and sixth somites, telson and lateral spines on fifth somite. Antennae and antennules with large yellow chromatophores distal to red chromatophores.

Second Zoea

Size.—CL = 2.32 ± 0.21; TL = 5.30 ± 0.21; n = 8. Duration: 2–5 days, mean 3.61 ± 0.61, mode 3–4; N = 76.

Carapace (Fig. 2B, E).—Rostrum and carapace essentially unchanged. Eyes stalked.

Antennule (Fig. 4A).—Exopod with 3 or 4 large terminal aesthetascs, 3 terminal plumose setae and 1 subterminal simple seta; protopod with 1 or 2 short terminal setae and often large plumose seta at base of distal segment; endopodal bud vestigial to well developed, with 1 or 2 plumose setae.

Antenna (Fig. 4B).—Endopod exceeding exopod, with short simple seta and blunt tubercle terminally, incompletely 4-segmented, ultimate segment equal to length of first 3 segments; exopod with 17 (rarely 15–18) plumose setae on inner and distal margin; strong serrated spine on protopod at base of exopod.

Mandible (Fig. 4C, D).—Well developed, unsegmented palp.

Maxillule (Fig. 4E).—Coxal endite with 7 or 8 setae, few usually simple. Basal endite with 4 strong spines, each with several denticles; often with 1 or 2 very small submarginal spinules. Endopod 3-segmented, distal segment with 3 simple setae.

Maxilla (Fig. 4F).—Proximal lobe of coxal endite with 6 or 7 submarginal plumose and 1 or 2 marginal setae, distal lobe with 2 or 3 setae; proximal lobe of basal endite with 5 plumose and 1 short simple setae, distal lobe with 4 plumose and 1 or 2 short setae. Proximal lobe of endopod with 2 setae, distal lobe with 2 or 3 setae, 1 seta between proximal and distal lobes; scaphognathite with 14–16 plumose setae, well-developed posterior lobe (usually naked, but occasionally with 1 or 2 setae).

Maxilliped 1 (Fig. 4G).—Basis with hooked process and 2 short simple setae at proximal end of inner face, and 2, 3, 3 setae more distally on this face. Endopod 5-segmented with setal formula 2+I, 2+I, 1+I, 2, 4+I; exopod incompletely 2-segmented, with 6 natatory plumose setae.

Maxilliped 2 (Fig. 4H).—Basis with 1 or 2, 2 distal setae on inner face. Endopod 4-segmented (penultimate segment deeply indented), with setal formula 2, 2+I, 2+I, 4+I setae; exopod incompletely 2-segmented, with 6 natatory plumose setae.

Maxilliped 3 (Fig. 4I).—Endopod same length as endopods of maxillipeds 2 and 3, but unsegmented; exopod incompletely 2-segmented, with 6 natatory plumose setae.

Pereiopods (Fig. 6A–E).—Limb buds incompletely segmented; most specimens unarmed, occasionally dactyl of each pereiopod with clear corneous claw and single seta ventral to claw, propodus of pereiopod 2 with dorsodistal spine, pereiopod 4 dactyl with 4 additional distal setae.

Abdomen (Fig. 2B, E).—Six somites; armature of second to fifth somites unchanged, sixth somite unarmed. Biramous, paired pleopods (Fig. 4J) present on abdominal somites 2–5.

Uropods (Fig. 4K).—Exopod and endopod separated from protopod; endopod with short row of fine setules on lateral margin, mesial margin crenulate; exopod with 10 or

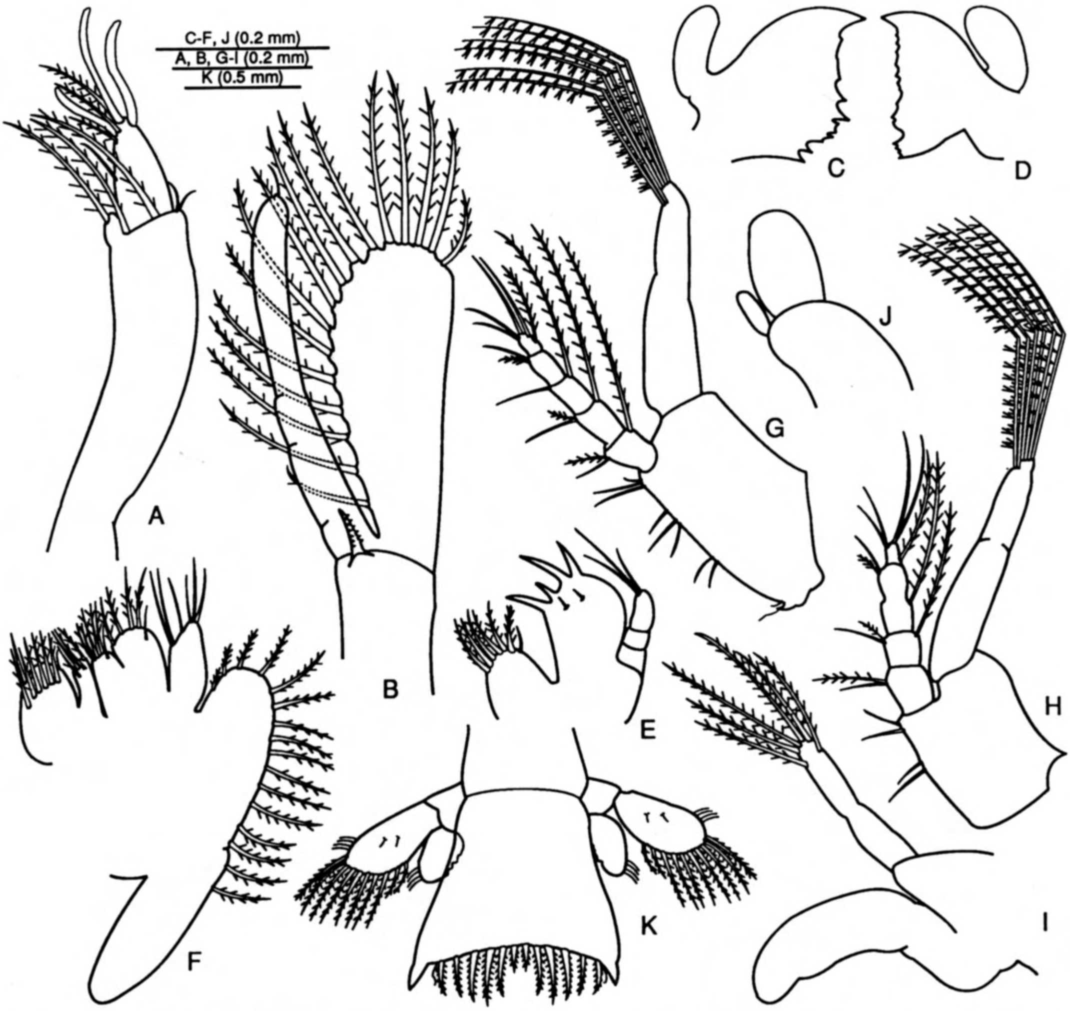

Fig. 4. *Coenobita variabilis,* zoea II. A, antennule; B, antenna; C, D, mandibles; E, maxillule, F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, pleopod; K, telson.

11 plumose setae along posterior and mesial margins, short row of fine setules on lateral margin, 1 or 2 simple setae on ventral surface.

Telson (Fig. 4K).—Posterior margin slightly concave, median notch absent, 8 + 8 marginal processes (I, ii, 3–8), including additional medial pair of short plumose setae; third and fourth processes reduced in size compared to first stage; spinules present along margins of fifth through seventh processes (sometimes absent from mesial margins).

Color.—No changes noted in chromatophore distribution. The day prior to the megalopal molt, the previously transparent limb buds take on an opaque olive color that strongly contrasts with the transparent-whitish body color.

Megalopa

Size.—CL = 1.64 ± 0.09 mm; TL = 4.38 ± 0.16 mm; $n = 6$. Duration variable, depending on conditions (see above); megalopae kept in water survived for 33 days without metamorphosing; metamorphosis occurred 5–24 days after the megalopae left the water (mean 10.14 ± 4.90, mode 8–9; $N = 13$).

Carapace (Fig. 2C).—Shield slightly more than half total carapace length, slightly wider than long; rostrum prominent, rounded.

Ocular peduncles reaching to base of ultimate segment of antennular peduncle, length less than twice width; corneas not inflated.

Antennule (Fig. 5A).—Biramous, peduncle 3-segmented; basal segment with up to 3 dorsal marginal setae; penultimate segment with 1–3 dorsal setae and single ventroproximal seta; ultimate segment with 3 dorsodistal and 1 ventrodistal setae; upper ramus unsegmented, with 8–10 aesthetascs and 3 or 4 short simple setae terminally, single seta along mediodorsal margin; lower ramus unsegmented, with 2 terminal setae and 1 medioventral seta.

Antenna (Fig. 5B).—Peduncle 5-segmented, with clearly differentiated supernumerary segment and articulated acicle. First, second, and third segments with scattered setae; fourth segment with 1 dorsal seta and 1 ventral seta; fifth segment with 2–5 distal setae and 1 dorsomedial seta. Acicle rounded knob with 1 or 2 setae. Flagellum usually with 5 articles, occasionally additional article inserted after basal article; setal formula of 5-articled flagellum 0, 0–1, 5, 0–1, 5–7; setal formula of 6-articled flagellum 0, 2, 0–1, 5, 0–1, 5–7; all setae less than 1 article long except 1 terminal seta (approximately 4 articles long).

Mandible (Fig. 5C).—Palp 3-segmented, ultimate segment with 8 or 9 plumose setae.

Maxillule (Fig. 5D).—Coxal endite with 10–15 marginal and submarginal plumose setae, usually 1 simple submarginal seta; basal endite with 5 or 6 marginal plumose setae, 10–12 stout spines, and 3 or 4 submarginal simple setae, also 2 plumose setae along inner margin; endopod unsegmented, with well developed, recurved external lobe, internal lobe with 1 simple seta, inner margin with short basal seta.

Maxilla (Fig. 5E).—Proximal lobe of coxal endites with 15 or 16 submarginal plumose setae and 10–12 marginal simple setae (not all illustrated), distal lobe with 5 plumose setae; proximal lobe of basal endites with 7 or 8 plumose and 1 simple setae, distal lobe with 10–12 setae, some plumose; endopod lacking setae; scaphognathite with 48–55 plumose setae.

Maxilliped 1 (Fig. 5F).—Coxal endite with 6 or 7 plumose setae, basal endite with 12–14 plumose and 4 or 5 simple setae. Endopod unsegmented, with 1 or 2 terminal setae; exopod basally inflated, with 8 marginal plumose setae.

Maxilliped 2 (Fig. 5G).—Endopod 4-segmented, basal segment with 1 mesial and 3 dorsodistal setae, second segment with 2 distal submarginal setae, penultimate and ultimate segments each with 6–8 marginal and submarginal setae; exopod 2-segmented, with 1–3 short simple setae along inner margin of basal segment, ultimate segment with 6 terminal plumose setae.

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

Pereiopods (Fig. 6A–E).—Chelipeds similar, dactyl subequal to palm in length, both dactyl and fixed finger terminating in corneous claw surrounded by short setae; all segments with scattered setae, mesial surfaces of palm and carpus with tufts of longer setae. Ambulatory legs with dactyl terminating in corneous claw; all segments with scattered setae. Fourth pereiopods with scattered short setae on coxa, basis, and merus; carpus with longer setae on dorsal margin; propodus with numerous short and long setae, 4 or 5 marginal and 2–5 submarginal corneous scales; dactyl terminating in corneous claw, with scattered short setae and single long seta. Fifth pereiopods with scattered short setae on proximal segments; propodus with several long curved setae, scattered short setae and 6–8 corneous scales; dactyl with few long curved setae and short setae.

Gills.—Third pereiopod with 1 pair of arthrobranchs; fourth pereiopod with 1 pair of arthrobranchs and 1 pleurobranch.

Abdomen (Fig. 2C).—Six unarmed somites, with scattered, paired dorsal setae; biramous pleopods on somites 2–5, exopod well developed, with 9 plumose setae; endopod simple lobe, with 2 (rarely 3) small coiled subterminal setae.

Tail Fan (Figs. 2C, 5J).—Telson slightly wider than long, with scattered, paired setae on dorsal surface; posterior margin with 8–10 plumose setae, 1–3 short simple setae laterally. Uropods biramous, symmetrical; exopods with 1 or 2 short proximal setae

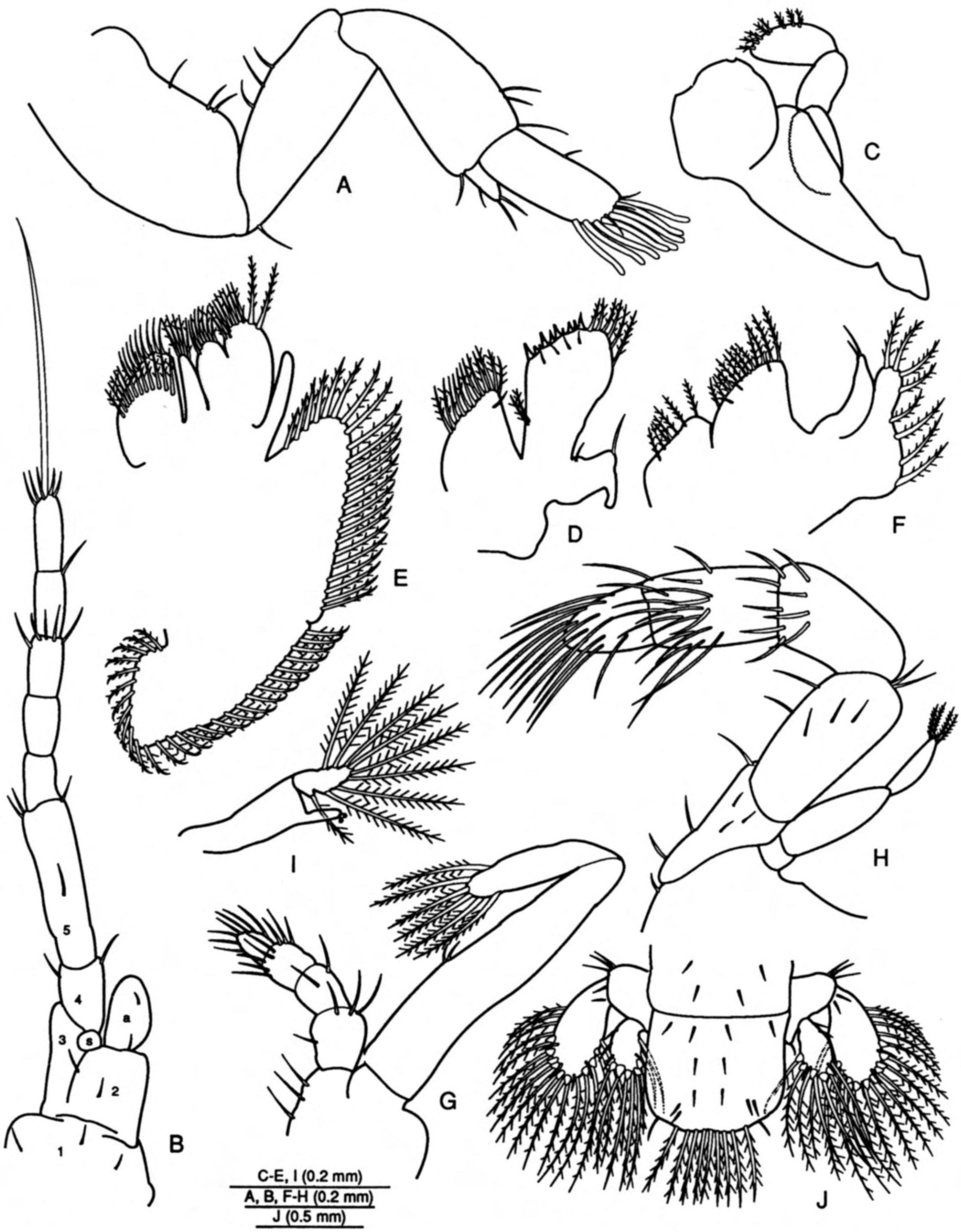

Fig. 5. *Coenobita variabilis,* megalopa. A, antennule; B, antenna (1–5 = peduncular segments, s = supernumerary segment, a = acicle); C, mandible; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, third maxilliped, I, pleopod; J, telson.

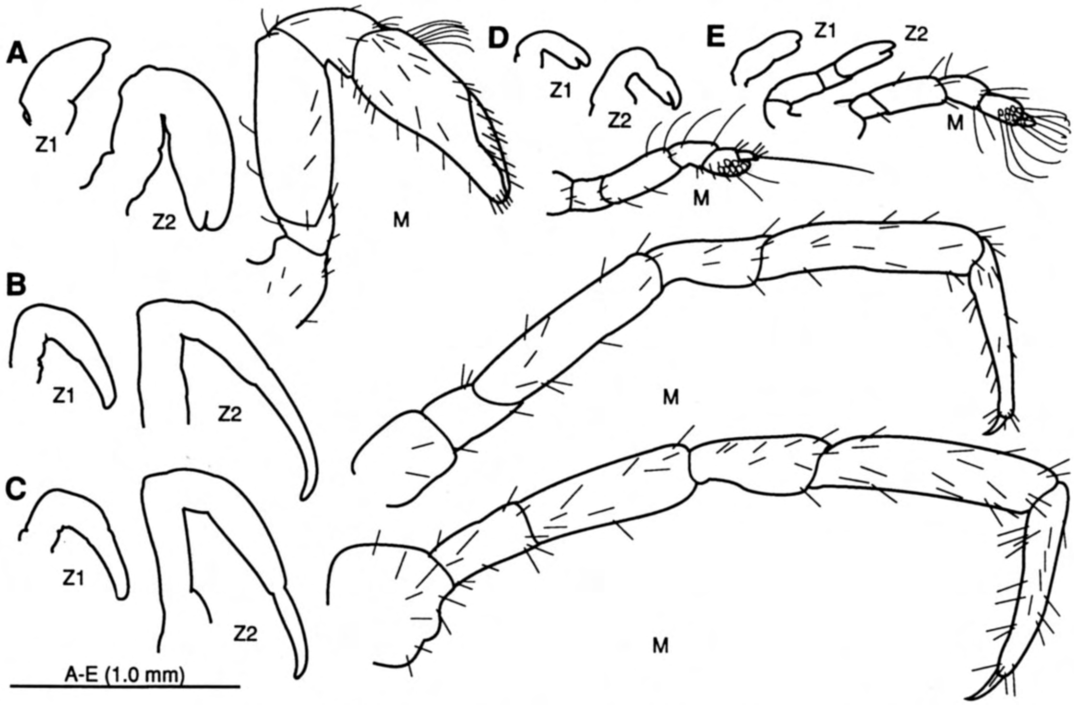

Fig. 6. *Coenobita variabilis,* pereiopods. A, first pereiopod; B, second pereiopod; C, third pereiopod; D, fourth pereiopod; E, fifth pereiopod. Z = zoea, M = megalopa.

on dorsal surface, 15–20 long plumose setae and 6–10 corneous scales marginally, plus 2–4 submarginal short simple setae; endopodal margins with 7–9 long plumose setae, 2–6 simple setae, and 5–10 corneous scales; protopod with 2 or 3 setae at anterodistal angle, and 1 or 2 short setae on knoblike posterior protuberance.

Color.—Uniformly transparent, pale olive with dense whitish (sometimes yellow) chromatophores remaining on fifth and sixth abdominal somites and telson. Older megalopae, whether on land or in water, tend to develop pronounced pinkish-magenta tint on propodus, carpus, and sometimes dactyl of pereiopods 1–3.

Discussion

Coenobita variabilis is the first species in the Coenobitidae known to have an abbreviated larval development. All other members of the family whose larvae have been reared exhibit a more typical larval development, with several feeding zoeal stages that require three to seven weeks to reach the megalopal stage (Provenzano, 1962; Reese and Kinzie, 1968; Shokita and Yamashiro, 1986; Nakasone, 1988; Al-Aidaroos and Williamson, 1989).

Both zoeal stages of *C. variabilis* are easily identified by their numerous developmental "anachronisms," i.e., character states typical of different stages of other coenobitid species (Table 1; hereafter, the two stages of *C. variabilis* will be referred to as first and second stage zoeae, whereas references to the "typical" stages of other coenobitids will use Roman numerals, e.g., typical stage IV). For example, the first stage zoea retains several typical stage I character states (e.g., sessile eyes, sixth abdominal somite fused to telson, no uropod development). These features are quite peculiar in such a large zoea (nearly twice as long as any other known stage I coenobitid), especially in combination with some of the advanced morphological features, such as the well-developed leg buds, third maxillipeds and maxilla scaphognathite, and the presence of a mandibular palp bud.

Similarly, the second stage zoea is larger than all but the final zoeal stage of other

Table 1. Development of zoeal characters in *Coenobita variabilis* compared to typical coenobitid development.

Character	Stage of *C. variabilis*	
	First[1]	Second
Maxillule: coxal endite setation	I	II
Maxilla: basal endite distal setation	I	II
Second maxilliped: exopod setation	I	II
Telson: paired terminal processes	I	II
Telson: fourth process development	I	II
Eyes: mobility	I	II–V
Antennule: terminal aesthetascs	I	II–V
Antennule: lateral setae	I	II–V
Maxillule: basal endite spines	I	II–V
First maxilliped: exopod setation	I	II–V
First maxilliped: endopod setation	I	II–V
Second maxilliped: endopod setation	I	II–V
Third maxilliped: exopod setation	I	III
Antennule: segmentation	I–II	III–IV
Antennule: endopod development	I–II	III–IV
Antenna: basis terminal spine	I–II	III–IV
Antenna: endopod setation	I–II	III–IV
Maxilla: coxal endite proximal setation	I–II	III–IV
Sixth abdominal somite: distinct from fifth	I–II	III–IV
Uropods: presence	I–II	III–IV
Third maxilliped: endopod development	II	III
Telson: posterior median notch/seta	II	III
Rostrum: carina	II	III–V
Antenna: endopod fusion to protopod	II	III–V
Third maxilliped: exopod segmentation	II	III–V
Uropods: anterodistal spine	—	III
Uropods: endopod setation	—	III
Uropods: articulation	—	IV–V
Antenna: scale setation	I–II	V
Antenna: endopod development	I–IV	V
Maxilla: scaphognathite, posterior lobe development	I–IV	V
Pleopod: development	I–IV	V
Maxilla: scaphognathite, anterior lobe setation	III	V
Leg bud: development	III	V
Uropods: exopod setation	—	V
Body size	V	V
Mandibular palp: development	IV–V	>V

[1] Roman numerals refer to stage in "typical" (as determined from published descriptions of other species) coenobitid development; e.g., mandibular palp development in first stage *C. variabilis* is comparable to that of stage IV or V zoeae in other coenobitid species; whereas development of this character in second stage *C. variabilis* is even more advanced than stage V zoeae in other species.

coenobitids, and can be easily identified by the combination of fully articulated uropods (not present in other species before stage IV), uropodal exopods that lack an anterodistal spine (present in other species after stage III), and a telson that lacks an enlarged fused fourth process (present in other species after stage II). Other appendages, or sets of appendages, exhibit similarly distinctive combinations of character development. For example, the antenna consists of an advanced endopod and scale, but lacks the small subterminal spine that appears on the basis in typical stage II or III. The third maxillipeds most closely resemble typical stage IV, whereas the first and second maxillipeds are typical stage II.

Most zoeal characters in *C. variabilis* show within-stage variation on a level comparable to other coenobitids. In second stage zoeae, however, I observed two exceptions that were apparently uncorrelated with zoeal viability. The development of the antennular endopod can range from completely absent (typical stage II) to a well-developed bud more typical of stage III. The number of teeth on the basal endite of the maxillule varies from four, the stage II norm, to six, the stage IV norm. It is unclear why these particular characters should show so much intrastage variability. Variation that may be correlated with zoeal viability occurs in the development of the uropods of second stage zoeae. One specimen reached stage II without any uropods at all, but died the same day it molted. A few of the specimens that died during stage II seemed to possess incompletely articulated uropods, but all of the stage II exuviae (i.e., specimens that successfully molted to megalopae) examined have fully articulated uropods.

Certain characters, whose expression is not obviously related to abbreviated development, are apparently unique to *C. variabilis*. For example, both stages are most easily recognized by the enormous, paddle-shaped lateral projections and the strongly decurved dorsal spine on the fifth abdominal somite. Most other species in the genus *Coenobita* possess both a dorsal spine and paired lateral spines on this somite, but these are never strongly decurved, flattened, or enlarged. The lack of a distolateral spine on the antennal scale and the presence of a medial seta on the maxilla endopod are unique also to *C. variabilis* among known coenobitids at any stage of development. A feature that distinguishes the second stage of *C. variabilis* from other described coenobitids at stage II or older is the lack of a mediodorsal spine on the sixth abdominal somite.

The fact that the zoeal stages of *C. variabilis* show several different patterns of developmental acceleration (compared to typical coenobitids) allows for easy identification of zoeae of *C. variabilis*, but makes it impossible to determine which stages were eliminated during the evolution of the abbreviated developmental mode (Table 2). Typical stage I expression is unambiguously retained for more characters than any other stage, and unambiguously lost in relatively few characters. Typical stage II expression is lost in the fewest characters, and retained in many characters, but half of these are expressed in first stage *C. variabilis*, half in second stage, which argues against stage II being retained as a single functional unit. Stage V expression has been lost in the most characters, but has been retained in as many characters as typical stage II. Stage IV seems a good candidate for deletion, as no characters have unambiguous stage IV expression, and many have unambiguously lost it. However, typical stage IV has few if any stage-specific characteristics, as evidenced by the large number of ambiguous stage IV characters (Table 2).

This mixing of typical stages is not unusual in species with abbreviated development (Rabalais and Gore, 1985). Furthermore, suites of characters that are advanced (e.g., development of third maxillipeds, leg buds, pleopods, and uropods) or not (e.g., eye mobility and maxilliped setation) in *C. variabilis* are generally similar to those in other abbreviated species (Benzie and de Silva, 1983; Rabalais and Gore, 1985).

Table 2. Character state expression in *Coenobita variabilis*.

Typical stage	States lost[1]	States present in *Coenobita variabilis*: First stage	Second stage	Ambiguous[2]
I	8	14	0	15
II	6	4	5	22
III	10	2	5	20
IV	15	0	0	22
V	17	1	8	11

[1] Number of characters (from Table 1) whose expression in a given typical coenobitid zoeal stage is not found in either stage of *C. variabilis*. For example, the first four characters in Table 1 do not progress beyond typical stage II; therefore, typical stage III, IV, and V expression has been lost for these characters.
[2] States whose expression is unchanged from preceding or following stage; therefore, there is no way to determine which stages were lost.

Compared to other decapods with nonfeeding zoeae, *C. variabilis* is unusual in that the zoeal feeding appendages are fully developed and fully setose. Typically, appendages of advanced, nonfeeding larvae are reduced (Benzie and de Silva, 1983; Rabalais and Cameron, 1983; Rabalais and Gore, 1985; Shokita *et al.*, 1991); alternatively, some species with fully developed larval appendages are facultative feeders; that is, they do not need to eat in order to develop, but will do so given the opportunity (Rice, 1968; Rabalais and Gore, 1985). Neither observational nor experimental data provide any indication that zoeae of *C. variabilis* fed on nauplii of *Artemia*. In contrast, megalopae feed (as is often the case in decapods with nonfeeding zoeae; Rabalais and Gore, 1985), and are, in fact, highly cannibalistic. In other coenobitids both zoeal and megalopal stages feed.

Unlike the zoeal stages, the megalopa shows little indication of abbreviated development compared to other coenobitids, nor does it possess obviously unique characteristics. Thus, a combination of characters is required to unambiguously separate the megalopa of *C. variabilis* from other coenobitids (Table 3). The most distinctive characteristics of megalopae of *C. variabilis*

Table 3. A comparison of coenobitid hermit crab megalopae.

Character	*C. variabilis*	*C. clypeatus*	*C. rugosus*	*C. cavipes*	*C. purpureus*	*C. scaevola*	*B. latro*
Size (TL, mm)	4.38	4.3	3.74–4.0[1]	4.33	4.28	3.95	4
Antennule							
Upper ramus segmentation	1	1	1	1	1	1	4
aesthetascs	8–10	7+	6	8	8	7	Numerous
Lower ramus segmentation	1	1	1	1	1	1	2
Antennal flagellar segmentation	5 (6)	7	6	6	6	5	11
Mandible							
Palp segmentation	3	3	0–2[1]	3	3	3	3
setae	8 or 9	~9	5–8[1]	8–11	6–9	?	6
Maxillule							
Coxal endite plumose setae	10–15	~15	12	16	15	9	18–20
Basal endite spines	10–12	7+	6	12	15	Many	~15
submarginal setae	3 or 4	~5?	6	9	8	5	5
inner margin setae	2	0	0	2	0	0	0
Endopod external lobe setae	0	2	0	0	0	NA	2
Maxilla							
Coxal endite proximal lobe setae	25–28	~25	19–21[1]	29	27	23	~25
distal lobe setae	5	4	5–7[1]	6	7	7	9
Basal endite proximal lobe setae	7 or 8	6	4 or 5[1]	7	7	7	10
Endopod setae	0	2	1	1	2	0	4
Scaphognathite setae	48–55	49–56	50	75	51	49	~45
First maxilliped							
Coxal lobe setae	6 or 7	Numerous	9–11[1]	7	10	Numerous	Numerous
Endopod setae	1 or 2	2	0–2[1]	2	0	2	2 + 3
Second maxilliped							
Endopod segmentation	4	4	4	4	4	3?	4
Exopod terminal setae	6	7+	7 (4?[1])	7	6	7	7
Third maxilliped							
Endopod segmentation	3	Indistinct	2	3	3	3	Indistinct
Exopod terminal setae	4	1	0	1	0	2 (simple)	3
Pleopods, exopod setae	9	10 or 11	9	9	9	9	7 or 8
Uropods, endopod marginal setae	7–9	~12	10–13[1]	8	11	13	9–11

[1] First value from Nakasone (1988), second from Shokita and Yamashiro (1986).

involve the segmentation of the antenna and the setation of the inner margin of the basal endite of the maxillule, the endopod and the distal coxal lobe of the maxilla, the exopod of the second and third maxillipeds, and the endopod of the uropods.

The antenna of the megalopa deserves special comment. In adult hermit crabs (and perhaps many other crustaceans; see Martin and Abele, 1986), the antenna consists of five segments plus a sixth "supernumerary" segment between and connected to the second and third or fourth segments, an acicle or scale, and an articulated flagellum (McLaughlin, 1974, 1983). In adult coenobitids, with the exception of *C. brevimanus,* the acicle is fused to the second segment. Previous descriptions of coenobitid megalopae have illustrated only the flagellum, acicle, and three antennal segments. Reese and Kinzie (1968) explicitly reported three segments in *Birgus latro,* whereas other written descriptions discuss the flagellum and acicle only. In *C. variabilis,* five segments and the supernumerary segment are clearly distinguishable; these are labeled in Fig. 5B. However, both the second and supernumerary segments sit directly atop the third segment (in the normally illustrated orientation, which places the acicle and flagellum next to each other), and easily could be overlooked. The peculiar acicle of *C. clypeatus* described by Provenzano (1962) as a "double knob (?)" may in fact represent a reduced acicle and adjacent supernumerary segment. The acicle is clearly not fused to the second segment in megalopae of *C. variabilis,* but this generally cannot be determined for other species. The presence of only five articles in the antennal flagellum of *C. variabilis* is unusual, but apparently not unique; although Al-Aidaroos and Williamson (1989) reported seven articles in *C. scaevola,* their fig. 10C clearly shows only five, and suggests that they mistakenly considered the fourth and fifth peduncular segments as articles.

Although abbreviated development has not been previously reported in the Coenobitidae, known or suspected examples can be found in other families of hermit crabs. In the Diogenidae, which is generally considered to be the sister taxon of the Coenobitidae (MacDonald *et al.*, 1957; McLaughlin, 1983; Martin and Abele, 1986), abbreviated development is common in the genus *Paguristes* (e.g., Dechancé, 1963; Provenzano, 1978; Hebling and Negreiros-Fransozo, 1983; Morgan, 1987), and has been reported in the genus *Cancellus* (see Mayo, 1973, and references therein). Forest (1987) suggested that abbreviated development may occur in the Pylochelidae, especially in the genus *Pomatocheles*. The monotypic genus *Lithopagurus* is the only documented example of abbreviated development in the Paguridae, although this mode is suspected in other pagurid genera and species with large eggs (Provenzano, 1968).

Temperature exerts a strong effect on the survival and duration of zoeal stages in *C. variabilis*. Larvae reared at 25°C took almost 50% longer to reach the megalopal stage and suffered higher mortality than siblings reared at 30°C, whereas larvae reared at 20°C failed to reach stage II. Adults are also very sensitive to temperatures much below 25°C (personal observation), and it is very probable that temperature is a primary factor that prevents this species from occurring south of the subtropical regions of northern Australia.

This study is the first to successfully obtain first stage crabs of the genus *Coenobita* in the laboratory, although Reese (1968) and Reese and Kinzie (1968) successfully induced metamorphosis in *Birgus latro* by allowing megalopae to crawl out of the water, as in the present study. From the available data (including unpublished work on *C. brevimanus* and *C. pseudorugosus*, for which I have also obtained crab stages), it appears that coenobitids will not metamorphose in water. Adult coenobitids are adapted to terrestrial respiration and will in fact drown if kept underwater (Bliss, 1968; de Wilde, 1973). If early crab stages also cannot respire when submerged, then metamorphosis before the megalopa has been able to leave the water would obviously be a fatal development.

It is also interesting to note that although megalopae of *C. variabilis* will use shells when available, these are neither necessary nor sufficient to induce metamorphosis. Shells probably enhance the survival of coenobitid megalopae through protection from desiccation and predation; only megalopae with shells were able to successfully molt in *B. latro* (see Reese, 1968), which do not use shells as adults. In *C. variabilis*, the possession of a shell did not significantly affect megalopal duration or survival, but this difference could as easily be a laboratory artifact as a valid interspecific difference (for example, my terraria might have maintained a much higher humidity than those used by Reese, thus eliminating the effects of desiccation). Perhaps a more significant difference between *B. latro* and *C. variabilis* is the length of time megalopae remain buried during the molt to first crab. *Coenobita variabilis* typically emerged as a first crab after only a day or two, whereas *B. latro* remained buried for three or four weeks (Reese and Kinzie, 1968).

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Address: Shannon Point Marine Center, 1900 Shannon Point Road, Anacortes, Washington 98221; (present address) California Academy of Sciences, Department of Invertebrate Zoology and Geology, Golden Gate Park, San Francisco, California 94118.