STUDIES ON DECAPOD CRUSTACEA FROM THE INDIAN RIVER REGION OF FLORIDA. XXIII. THE LABORATORY CULTURED ZOEAL STAGES OF THE CORAL GALL-FORMING CRAB *TROGLOCARCINUS CORALLICOLA* VERRILL, 1908 (BRACHYURA: HAPALOCARCINIDAE) AND ITS FAMILIAL POSITION
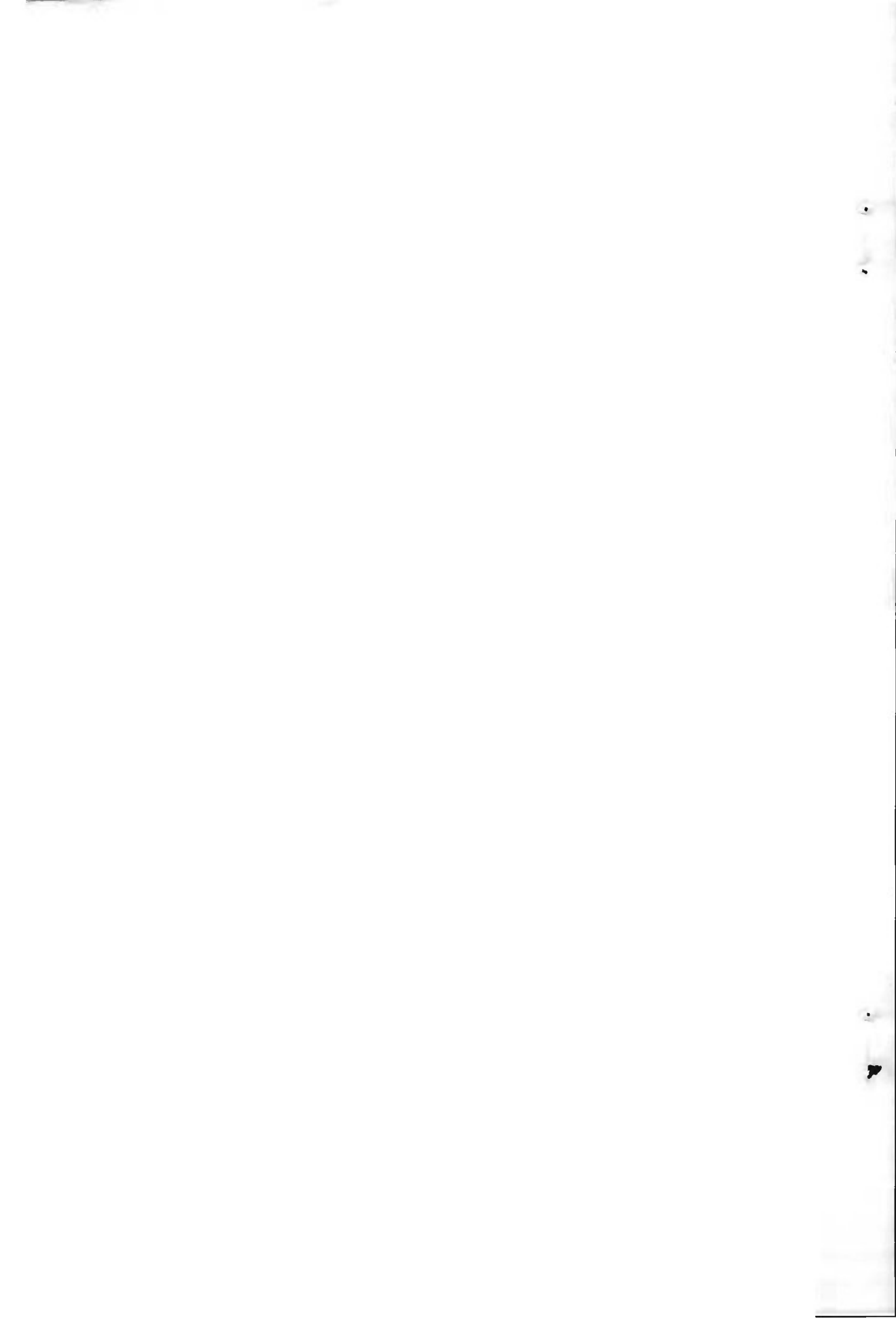
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ABSTRACT

The first 5 zoeal stages of the brachyuran, coral-inhabiting, gall-forming crab *Troglocarcinus corallicola* Verrill, 1908, are described and illustrated. Based on the sequential appearance of morphological characters, this species passes through at least 5, and perhaps 6 or 7 larval stages before metamorphosing to megalopa. The zoeae can be easily recognized in the plankton by a combination of lateral aliform expansions on the fourth, and a distinct dorsal caplike process on the second abdominal somite. The number of abdominal somites (5) remains constant throughout the first 5 (and probably subsequent) zoeal stages. Evidence from larval morphology supports the contention based on adult characters, that the Hapalocarcinidae are closely related to the Pinnotheridae, as well as having close affinities to the Hymenosomatidae and Leucosiidae.

The family Hapalocarcinidae is a widespread group of approximately 27 species in at least 8 genera (Fizé and Serène, 1957; Takeda and Tamura, 1979). The major distribution is throughout the Pacific and Indian Oceans, with only 3 species presently recorded from the Atlantic Ocean (2 from the western Atlantic and one from the eastern Atlantic). The family is unique in that the members symbiotically associate with scleractinian corals by forming galls, dens, or depressions within the substratum of the living corallum. Previous studies have been primarily taxonomic in nature, but the group is so taxonomically confusing that its phylogenetic position within the brachyuran Decapoda has not been established with certainty. Within the family, first zoeal larvae have been briefly described and inadequately illustrated for only 3 species (Potts, 1915; Edmondson, 1933; Fizé, 1956; Al-Kholy, 1963; as reviewed in Castro, 1976), so that the larval development within the family can be considered practically unknown.

Of the 2 species known from the western Atlantic Ocean, *Troglocarcinus corallicola* is the most widespread, being recorded from Bermuda (the type-locality of Verrill, 1908), Straits of Florida, northeastern Gulf of Mexico, and Dominica, British West Indies (Rathbun, 1937; Shaw and Hopkins, 1977). The species is a known symbiont of madreporarian hermatypic corals, in which it forms lunate galls or dens. However, our collections made off the central eastern Florida coast showed the species to be an associate of the Ivory Tree Coral *Oculina varicosa* Lesueur, 1820, as well. Among specimens obtained were several ovigerous females. These offered an opportunity to study the larval development of the species, and perhaps clarify systematic relationships within the family. Accordingly, this paper reports on the first 5 larval stages of *Troglocarcinus corallicola,* and (as far as previously published data allow) compares morphological characters of the zoeae with those noted for the Pacific species *Hapalocarcinus marsupialis* Stimpson, 1859 (Potts, 1915; Al-Kholy, 1963) and *Cryptochirus minutus* Edmondson, 1933 [=*C. coralliodytes* Heller, 1861, *fide* Utinomi, 1944].

MATERIALS AND METHODS

An ovigerous female 3.0 mm in carapace width was removed from a den in a branch of *Oculina varicosa* which had been collected from a depth of 6 m, south of Pepper State Park, St. Lucie County, Florida (27°29.6′N, 80°17.3′W) on 25 May 1979. The crab was maintained in a glass bowl 18 cm in diameter filled with seawater (35‰) and fed nauplii of the brine shrimp *Artemia* sp. daily, until hatching occurred on 14 June. Larvae were transferred to 24-compartmented polystyrene trays, 1 zoea per compartment. Seventy-one larvae were cultured at 2 temperature regimes, 47 larvae in 2 trays at 25°C (±0.5°C) and 24 in a third tray at 30°C (±0.5°C). All 3 trays were held in controlled temperature units in a diel fluorescent light cycle of 12 h light–12 h dark. Seawater (35‰) in the trays was changed and larvae were fed an excess of brine shrimp daily. All larval molts and dead zoeae, plus a small series of representative living zoeae were preserved in 70% ethanol. Descriptions and illustrations of zoeal stages were made with the aid of binocular dissecting stereo- and compound microscopes. Carapace length was measured in lateral view from the base of the rostrum to the posterior edge of the carapace, and the measurement provided is the arithmetic mean of all specimens examined in that stage. For further details on methodology see Gore (1968).

First stage larvae were deposited in the National Museum of Natural History, Washington, D.C. (USNM 181980), the Allan Hancock Foundation, University of Southern California, Los Angeles (AHF 2249-01), the British Museum (Natural History), London (1980-510), and the Rijksmuseum van Natuurlijke Historie, Leiden (D-33131). First through fourth zoeal stages and/or their molts were deposited in the Indian River Coastal Zone Museum, Ft. Pierce, FL (IRCZM 89: 4807).

REARING RESULTS

In general, brachyuran larval development follows a sequential pattern in appearance of morphological characters (e.g., Lebour, 1928). First stage zoeae are distinguished by having unstalked eyes and 4 natatory setae on maxillipeds 1 and 2. In stage II (and later) the eyes become stalked, and the natatory setae usually increase to 6, 8, 10, and 12 depending on the species in question and how many subsequent stages are required to complete development. Pleopod buds usually appear in the penultimate larval stage, and these become partially or fully segmented in the ultimate zoeal stage. The antennular endopodal bud and mandibular palp also develop in the ultimate zoeal stage. Thus, by using this combination of morphological characters on planktonic or laboratory reared zoeae it is possible to either estimate the sequential number of the existing stage, or to project the probable number of larval stages remaining.

A maximum of five zoeal stages was observed in our laboratory culture of *Troglocarcinus corallicola*. However, we believe that at least 1 and possibly 2 more stages would follow before attainment of the megalopal stage. We base our contention on the fact that the fifth larval stage in this species exhibited undivided pleopod buds, and that neither an antennular endopodal bud nor a mandibular palp were evident. We suspect that segmentation in the former, and development in the latter 2 appendages, would occur in subsequent stages if *T. corallicola* follows the general pattern of brachyuran development. Whether the number of abdominal somites would increase from 5 to 6 by division of the telsonal somite in later stages is not known, but because it had not yet occurred in stage V we think it unlikely.

Of the 47 larvae of *Troglocarcinus corallicola* cultured at 25°C, 5 reached stage II, 4 stage III, and 3 stage IV, but only 1 attained the fifth zoeal stage. The 24 larvae at 30°C remained almost entirely in stage I, with only 1 zoea molting to stage II before dying. Mortality was high at both temperatures (Table 1; Fig. 1). Although duration and number of zoeal stages in brachyurans has often been shown to be temperature-dependent (e.g., Scotto, 1979), the unequal number of larvae reared at the two temperatures yielded inconclusive results. However, based on a mean number of days in stage for zoea I at 25°C and 30°C (12.8 and 10.8, respectively, Table I) temperature can be conjectured to influence devel-

Table 1. Duration of larval stages of *Troglocarcinus corallicola* at two temperatures. (* Died in stage.)

Tempera-ture (°C)	Stage	Duration in days				Died in molt	Total molting to next stage
		Min.	Mean	Mode	Max.		
25°	Zoea I	2*	12.8	11	21*	6	5
	II	5*	13.2	—	18	—	4
	III	11	11.5	12	12	—	3
	IV	13	14.3	—	17*	1	1
	V	8	8.0	8	8	—	0
30°	Zoea I	2*	10.8	11	16	—	1
	II	4*	4.0	4	4	—	0

opmental duration. The lower temperature also seemed more favorable for general survival; on day 11, the day before any larvae molted to second stage, survival was 64% at 25°C, and only 17% at 30°C.

The sole fifth zoeal stage was attained in 49 days at 25°C, with an average of 12.9 days spent in the first 4 stages. If we are correct in assuming that the total number of larval stages is either 6 or 7, and laboratory duration is similar to that seen in nature, we suspect that *Troglocarcinus corallicola* zoeae would remain in the plankton from 75 to 90 days before metamorphosing to megalopa.
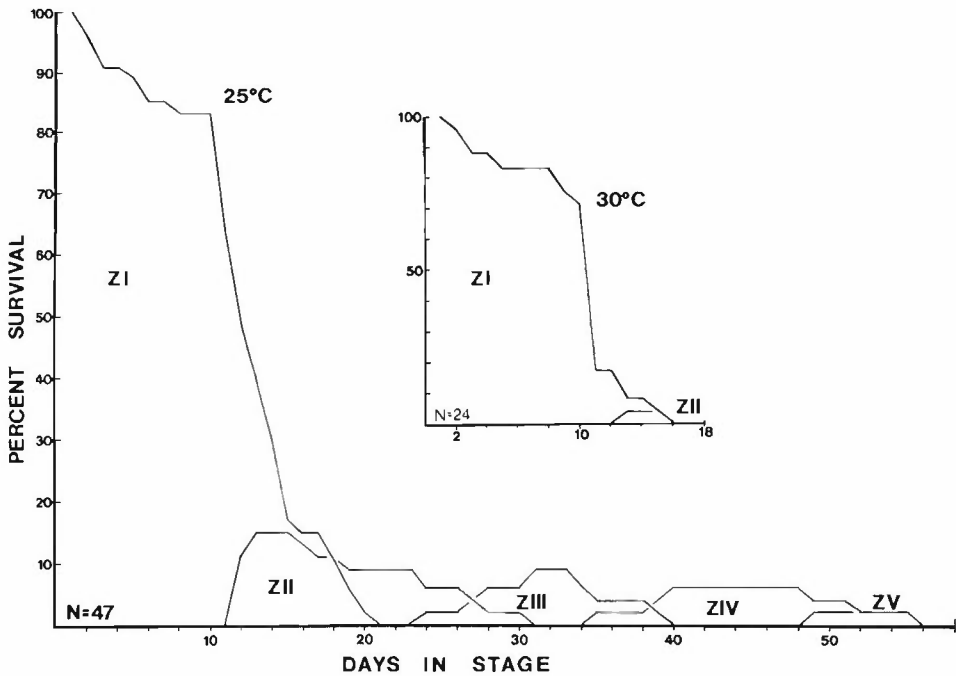

Fig. 1. *Troglocarcinus corallicola* Verrill: Percentage survival and duration in stage of larvae cultured under laboratory conditions. N = number of larvae cultured at each temperature.
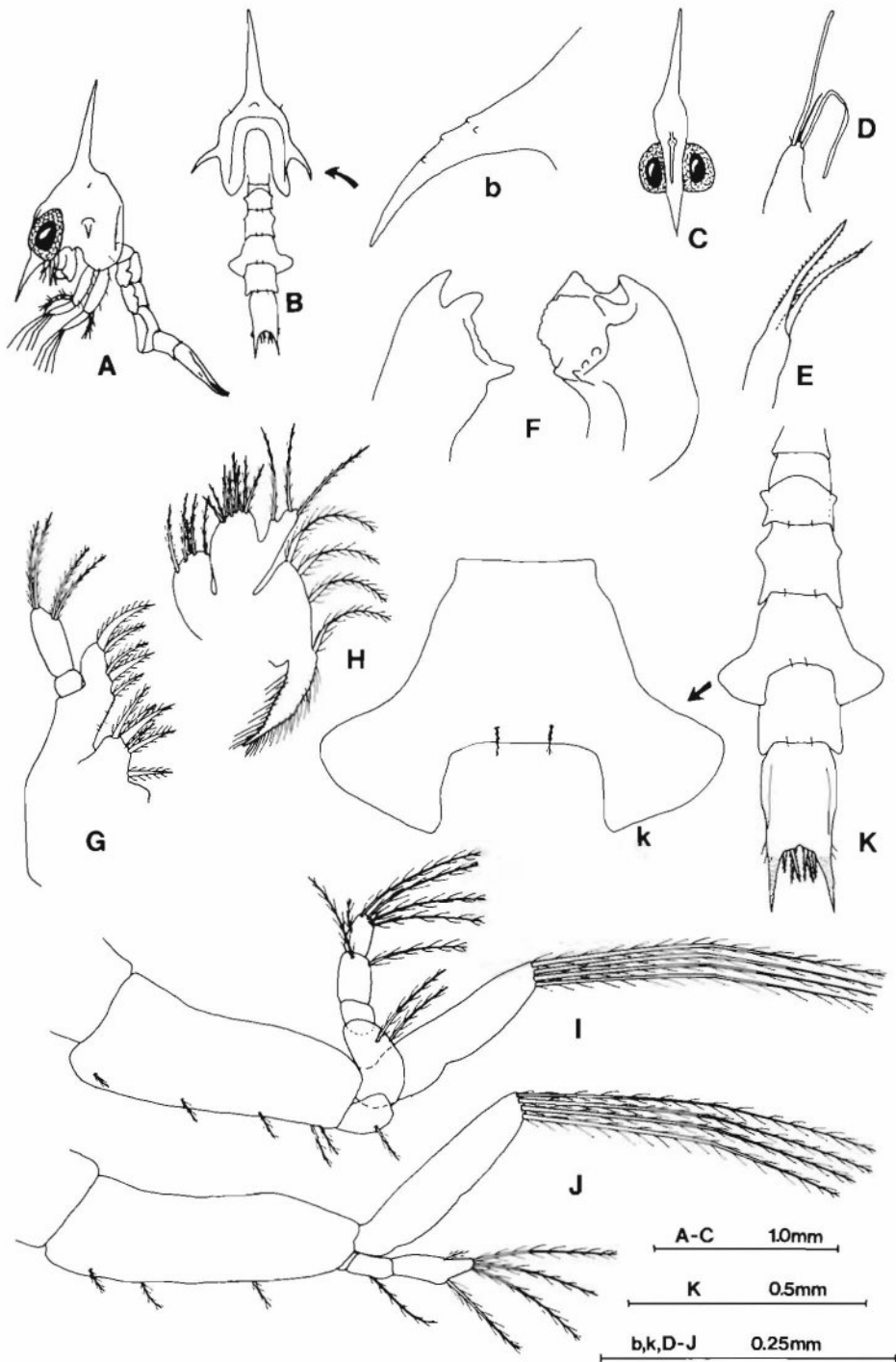
Fig. 2. *Troglocarcinus corallicola* Verrill: First zoeal stage. (A) Lateral view; (B) posterodorsal view; (b) detail, lateral spine; (C) dorsal and rostral spines, anterodorsal view; (D) antennule; (E) antenna; (F) mandibles, posterior and posteromedial views; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2; (K) abdomen and telson, dorsal view; (k) detail, fourth abdominal somite.

DESCRIPTION OF THE LARVAE

First Zoea

Carapace length 0.44 mm; 6 specimens examined.

Carapace (Fig. 2A, B, b, C).—Cephalothorax globose, with straight rostral and dorsal spines, 2 ventrally curved lateral spines, latter armed with several minute tubercles (Fig. 2b); lateral spines shortest, rostral spine longer, dorsal spine longest. A mediodorsal knob (Fig. 2C) with blunt anterior and posterior ridge between bases of dorsal and rostral spines; a posterodorsal knob midway between base of dorsal spine and posterodorsal edge of carapace; both knobs with integumental sensilla present in all stages. A minute seta, present in all stages, positioned laterally to base of dorsal spine. A ridge located around posterior edge of carapace in all stages; ventrolateral margin of carapace posterior to eye produced into blunt V-shaped tooth. Eyes unstalked.

Antennule (Fig. 2D).—Short, bluntly conical rod with 2 long stout, 1 thin short aesthetasc, 1 fine hair.

Antenna (Fig. 2E).—Biramous, short, less than half length of rostral spine; protopodite and exopodite approximately equal in length, slender, both processes armed along length with 2 rows of small teeth.

Mandible (Fig. 2F).—Unusually large, asymmetrically dentate, shallow, scoop-shaped. Cutting edge of incisor process with 1 large tooth each, anteriorly and posteriorly; molar process oval, blunt, with irregular denticles along ventral margin.

Maxillule (Fig. 2G).—Endopodite 2-segmented; proximal short naked, distal longer, 2 terminal, 2 subterminal setae. Coxal endite with 6, basal endite with 4 terminal plus 1 subterminal, processes; of these, 2 stouter on basal, 1 stouter on coxal endite, these stout spinelike processes remaining quite noticeable in subsequent zoeal stages. Lateral pubescence on endites as shown.

Maxilla (Fig. 2H).—Endopodite unilobate; 2 terminal, 1 subterminal seta. Coxal endite with 5, basal endite with 8, setae, both endites unilobate. Lateral pubescence on all endites. Scaphognathite with 4 plumose setae along outer margin, distal portion tapering to setose apical process.

Maxilliped 1 (Fig. 2I).—Coxopodite in first 4 zoeal stages naked. Basipodite with 5 setae progressing distally as 1, 1, 1, 2. Endopodite 5-segmented, setal formula progressing distally 1, 2, 0, 2, 4 + 1 (Roman numeral denoting dorsal seta). Exopodite obscurely 2-segmented, 4 terminal natatory setae.

Maxilliped 2 (Fig. 2J).—Coxopodite naked for 5 zoeal stages. Basipodite with 3 ventral setae, positioned more or less medially. Endopodite 3-segmented, setal formula progressing distally 0, 1, 1 + 3 + I. Exopodite obscurely 2-segmented, 4 terminal natatory setae.

Abdomen (Fig. 2K, k).—Five somites, first naked, second and third with paired lateral knobs and bluntly rounded posterolateral processes, borders of which forming caplike structure visible in lateral and dorsal view; fourth with broad posterolateral aliform extension; fifth with pair of bluntly rounded posterolateral processes; somites 2–5 with pair of middorsal setae in 5 zoeal stages.

Telson (Fig. 2K).—Rectangular, with shallow median notch; twin furcae relatively short, approximately ⅓ length of telson proper, covered with minute hairs visible

only under high (200×) magnification; 2 long hairs on distolateral margin adjacent to bases of furcae. Posterior margin with 6 spines, each armed with 3 rows of spinules, innermost pair of spines situated below plane of other 2 pairs.

Color.—Zoea transparent, with rose-red chromatophores placed as follows. Cephalothorax, 1 interocular, 1 proximally at base of rostrum, 1 at base of lateral spine, 1 at posteroventral angle, 5 arranged in semicircular pattern following posterior ridge dorsally to dorsolaterally. Mandibles, 1 on peduncle. Abdomen, first somite clear; second and third each with 2 lateral pairs at base of paired lateral knobs and just posterior thereto; fourth with 4 pairs, first 2 pairs dorso-laterally, third dorsomedially, fourth on aliform extensions proximal to lateral margin of somite; fifth somite with 1 pair posterodorsally. Telson, 1 pair dorso-laterally about midlength. Corneas of eyes black in refracted light, rose-red with iridescent lime-green highlights under reflected light. Paired pale yellow chro-matophores, very difficult to discern, at anterodorsal base of dorsal spine, an-terodorsally on mediodorsal knob, and ventral to eyes on cephalothorax; laterally near posterior margin of abdominal somites 2–5; these best seen under reflected light.

Second Zoea

Carapace length 0.52 mm; 3 specimens examined.

Carapace (Fig. 3A, B, C).—Similar in shape to first stage; additional setae placed as follows: 1 pair at anterior base of dorsal spine, 1 pair anterior to dorsal knob, dorsal spine now with 3 rows of long hairs as illustrated. No setae on postero-lateral border. Posterodorsal knob and posterior ridge more prominent than pre-vious stage; base of rostral spine produced laterally to form V-shaped protuber-ance. Eyes stalked.

Antennule (Fig. 3D).—Short, shaped similarly to that of first stage, but wider at base; 1 long stout, 1 short thin aesthetasc, 1–3 fine hairs.

Antenna (Fig. 3E).—Similar in form and armature to first stage; appendage show-ing no substantial change in morphology in this or following 2 stages.

Mandible (Fig. 3F).—Except for increase in size in this and subsequent stages, showing no noteworthy modifications in armature of either process.

Maxillule (Fig. 3G).—Unchanged from previous stage.

Maxilla (Fig. 3H).—Endopodal and basal endite setation essentially unchanged. Coxal endite now with 1 additional subterminal seta; scaphognathite bearing 5 long thin plumose setae proximally, 3 additional stout plumose setae on distal margin; apical process, previously tapering, now bluntly rounded. Neither coxal nor basal endites divided into anterior-posterior lobes.

Maxilliped 1 (Fig. 3I).—In this and following stage similar in form and setation to first zoea, except for natatory setae on exopodite (now 6).

Maxilliped 2 (Fig. 3H).—Exopodite now bearing 6 natatory setae; endopodite and basipodite otherwise unchanged from stage 1.

Abdomen (Fig. 3K).—Somites 1–4 essentially unchanged, except posterolateral processes more elongate; fifth somite with posterolateral extensions now broader; somites unchanged in subsequent stages (except for addition of minor setae).

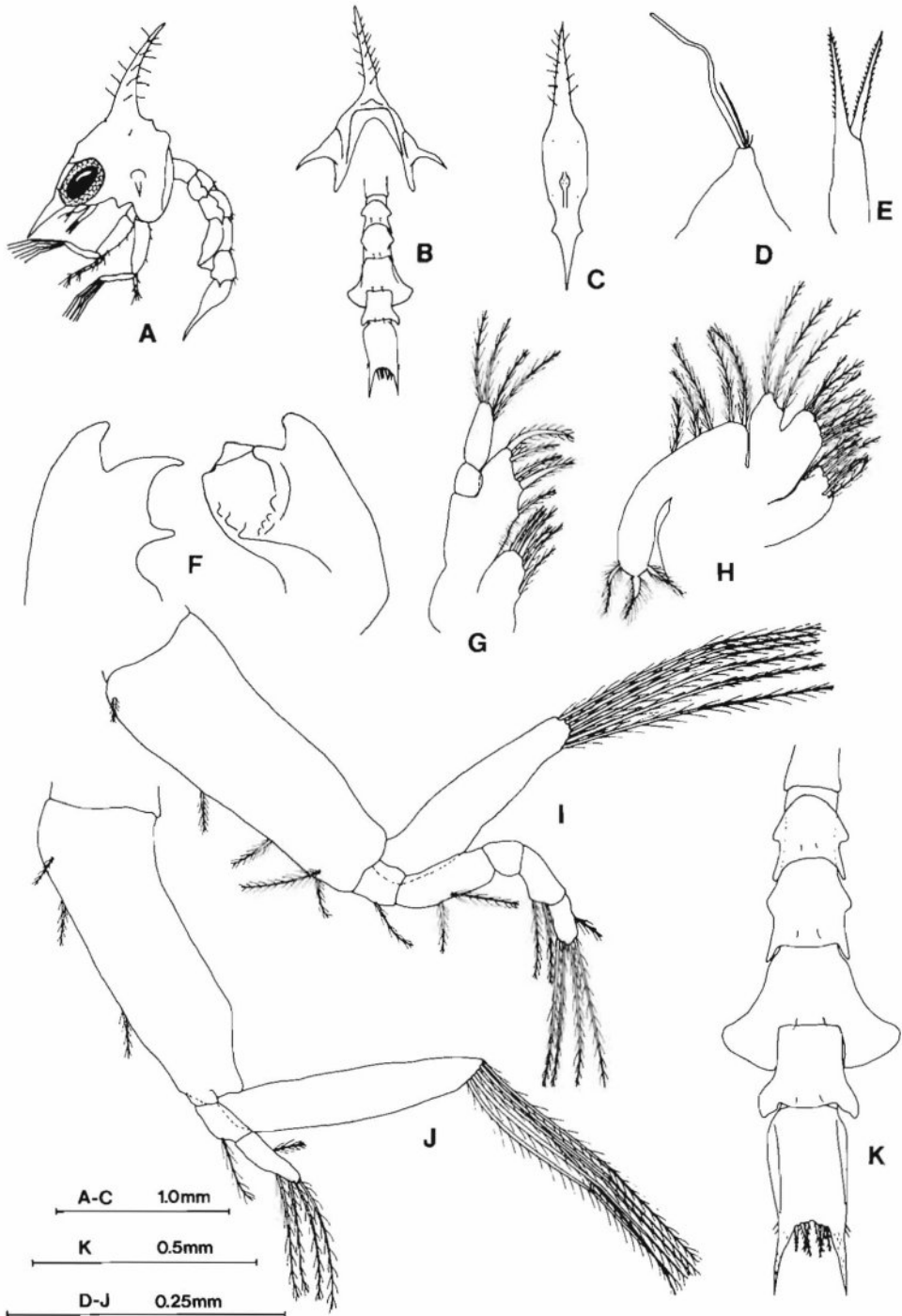*Telson* (Fig. 3K).—Similar in this and following stages to first zoea; length and

Fig. 3. *Troglocarcinus corallicola* Verrill: Second zoeal stage. (A) Lateral view; (B) posterodorsal view; (C) dorsal and rostral spines, anterodorsal view; (D) antennule; (E) antenna; (F) mandibles, posterior and posteromedial views; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2; (K) abdomen and telson, dorsal view.
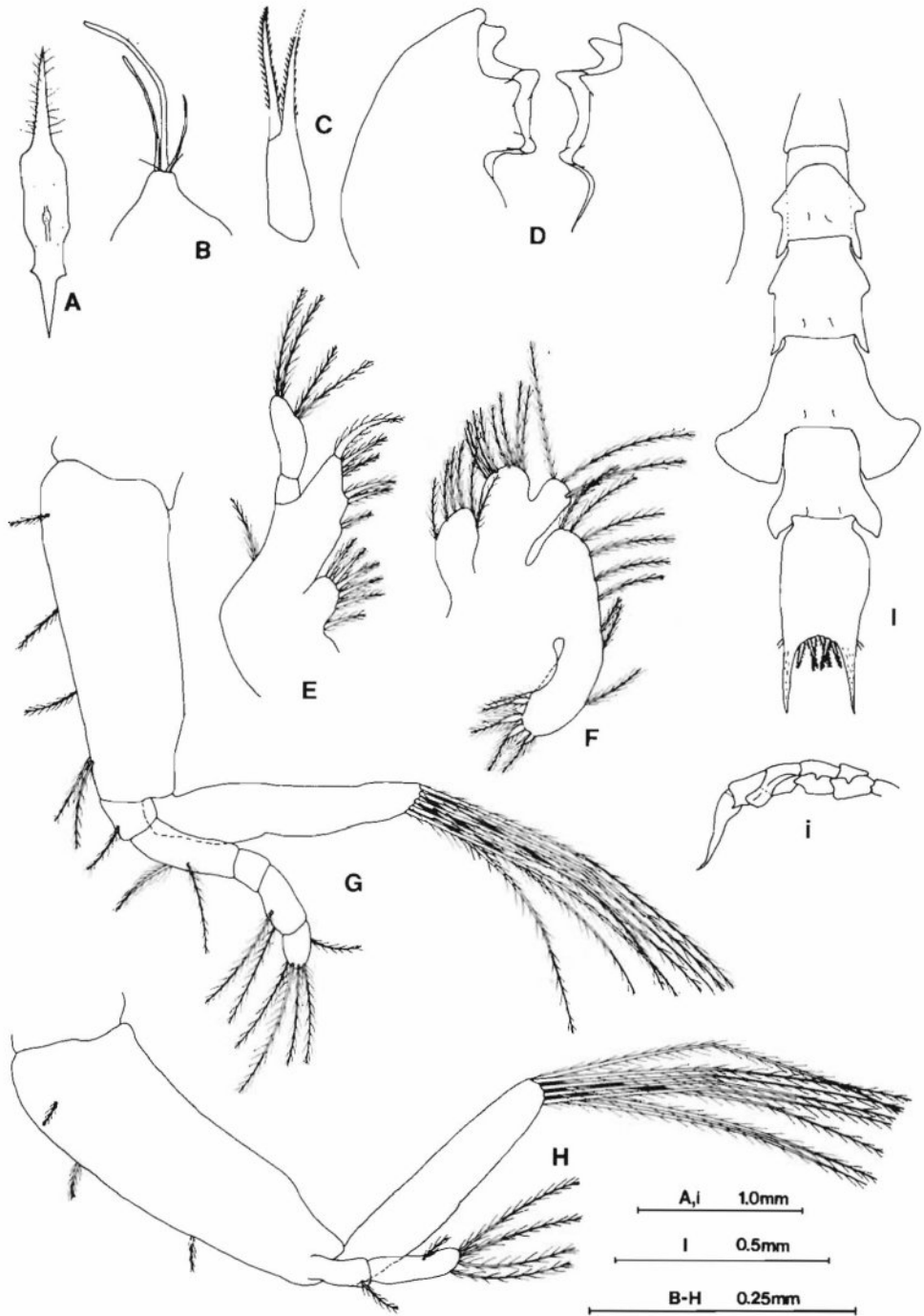
Fig. 4. *Troglocarcinus corallicola* Verrill: Third zoeal stage. (A) Dorsal and rostral spines, antero-dorsal view; (B) antennule; (C) antenna; (D) mandibles; (E) maxillule; (F) maxilla; (G) maxilliped 1; (H) maxilliped 2; (I) abdomen and telson, dorsal view; (i) abdomen and telson, lateral view.

width increasing proportionately to abdominal somites in next 3 stages, armature unchanging.

Color.—Rose-orange chromatophores present, placed as in first stage, with following additions: 1 dorsal to each lateral spine, 1 pair anterior to base of dorsal spine, 1 each at base of antennal and antennular protopodite; distal tip of dorsal spine diffused with rose-orange.

Third Zoea

Carapace length undeterminable; 1 molt examined.

Carapace (Fig. 4A).—Description not available owing to condition of exuvia; 1 additional pair interocular setae noted.

Antennule (Fig. 4B).—Extremely short, reduced, very broad at base, 3 aesthetascs, 1 long stout, 1 medium, 1 thin, plus 1–3 fine hairs.

Antenna (Fig. 4C).—As illustrated.

Mandible (Fig. 4D).—As illustrated.

Maxillule (Fig. 4E).—Endopodite and coxal endite not much changed; basal endite bearing 5 terminal, 1 subterminal processes plus 1 long feathery seta on basal margin.

Maxilla (Fig. 4F).—Endopodal, coxal, and basal endite setation and morphology remaining unchanged in this and next 2 stages; major differences confined to setation on margin of scaphognathite, now appearing as interrupted series 8, 1, 4, proximally to distally.

Maxilliped 1 (Fig. 4G).—Exopodite with 8 natatory setae.

Maxilliped 2 (Fig. 4H).—Most notable change seen in endopodite, now only 2-segmented (instead of 3 as in previous stages); proximal segment with 1 distal seta, distal segment with 5 setae (essentially 4 + I); exopodite with 8 natatory setae.

Abdomen and Telson (Fig. 4I, i).—As illustrated; no sixth somite present.

Color.—Zoea generally dark orange overall owing to greatly expanded chromatophores; position and number of these as in previous stage; posterior pair on third abdominal somite not seen, but may have been too constricted to determine.

Fourth Zoea

Carapace length 1.04 mm; 1 specimen examined.

Carapace (Fig. 5A, B).—Cephalothorax quite globose, enlarged; posterodorsal knob and posterior ridge prominent; setation as in previous stages, plus 1 additional seta midway between bases of rostral and dorsal spines each side of midline.

Antennule (Fig. 5C).—Shape unchanged; 2 stout, 2 thinner aesthetascs, plus usual fine hairs.

Antenna (Fig. 5D).—Exopodite approximately 0.1–0.2 times longer than protopodal process; armature unchanged.
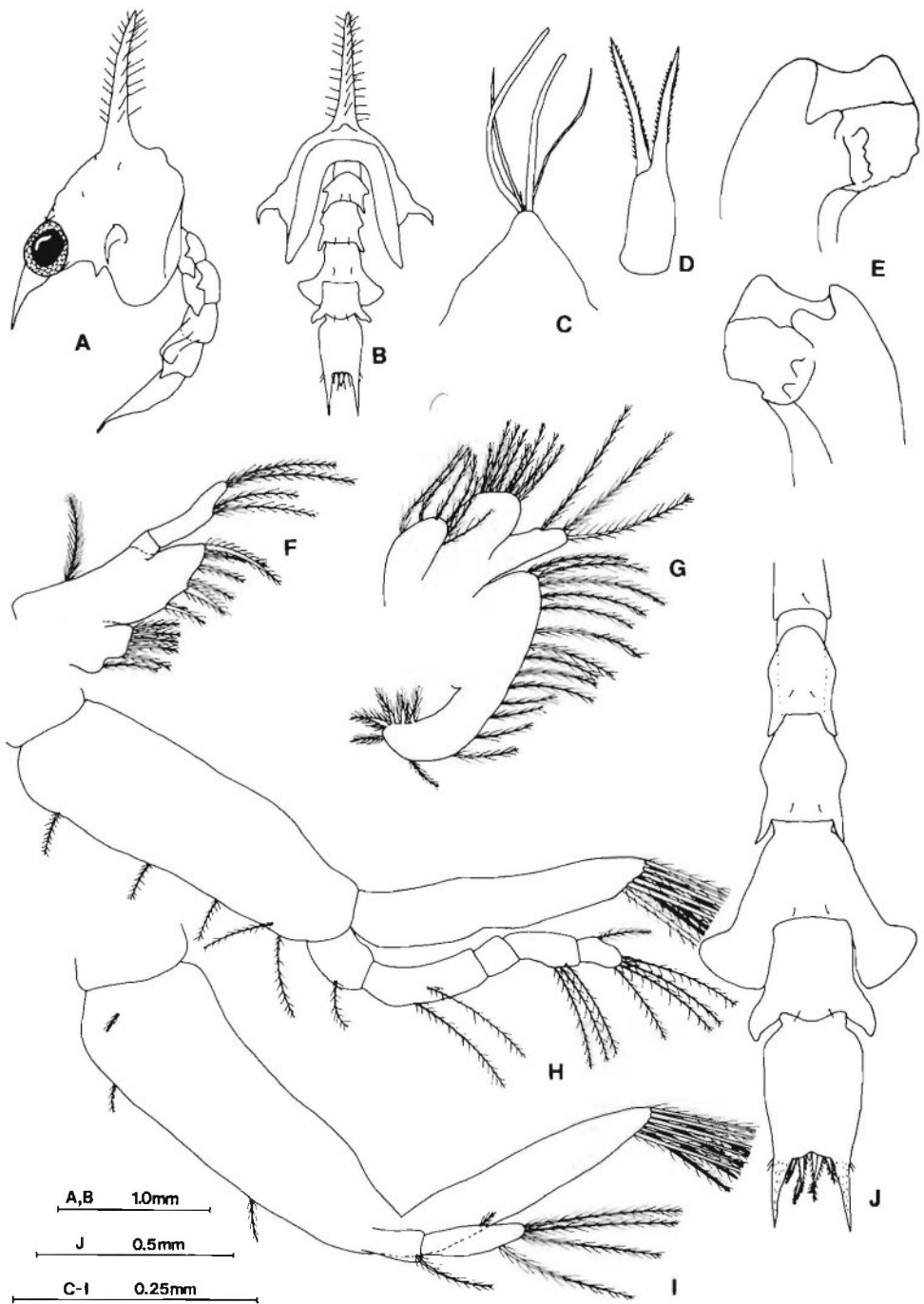
Mandible (Fig. 5E).—As illustrated.

Fig. 5. *Troglocarcinus corallicola* Verrill: Fourth zoeal stage. (A) Lateral view; (B) posterodorsal view; (C) antennule; (D) antenna; (E) mandibles; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2; (J) abdomen and telson, dorsal view.

Maxillule (Fig. 5F).—As illustrated.

Maxilla (Fig. 5G).—Scaphognathite interrupted setal series now 14, 1, 5.

Maxilliped 1 (Fig. 5H).—Endopodal setal formula 1, 2, 0, 3, 4–5 + I (adding 1 seta on fourth and fifth segments); exopodite with 10 natatory setae.

Maxilliped 2 (Fig. 5I).—Exopodite with 10 natatory setae.

Abdomen and Telson (Fig. 5J).—A middorsal seta on first somite; 5 somites only.

Color.—Essentially as in previous stage; a faint lime-green line on margins of aliform extensions of fourth somite; eyes under reflected light with distal ⅔ of cornea black, proximal ⅓ rose-orange.

Fifth Zoea

Carapace length 1.54 mm; 1 specimen examined.

Carapace (Fig. 6A, a, B).—Noticeably larger than preceding stage; preorbital protuberances at base of rostral spine more prominent, angular, deflexed in lateral view; setation as in previous stage but with addition of 1 interocular pair.

Antennule (Fig. 6C).—As illustrated.

Antenna (Fig. 6D).—Endopodal bud present, approximately ⅓ length of exopodal or protopodal process.

Mandible (Fig. 6E).—As illustrated.

Maxillule (Fig. 6F).—Endopodal and coxal endite setation unchanged; basal endite bearing 5 terminal, 2 subterminal processes, plus 2 long feathery setae basally.

Maxilla (Fig. 6G).—Scaphognathite setal series not interrupted except at distal lobe, 21 + 7 marginally.

Maxilliped 1 (Fig. 6H).—Coxopodite bearing 2 short setae; exopodite with 11 natatory setae.

Maxilliped 2 (Fig. 6I).—Exopodite with 11 natatory setae.

Abdomen and Telson (Fig. 6J).—First somite with 2 dorsal setae; pleopod buds present on somites 2–5, although much reduced on fifth somite (see discussion); no evidence of sixth somite forming.

Color.—More intense than preceding stages; ventral margin of carapace, margins of aliform extensions of fourth somite, anterolateral margin of telson, and tips of pleopod buds vinous-purple; rose-orange or rose-red chromatophores on cephalothorax as in preceding stages; mandibles rose-pink with dark red chromatophores on outer lateral surface; lime-green highlights at junction of somites 2–3, 3–4, 4–5, 5-telson; aliform extensions lime-green interiorly; first somite with 1 rose-orange chromatophore middorsally; eyes under refracted light with black corneas, rose-orange facets surrounding latter; under reflected light appearing burgundy-red.

Discussion

The zoeal stages of *Troglocarcinus corallicola* may be distinguished in the plankton from all other known decapod zoeae by a combination of easily notice-
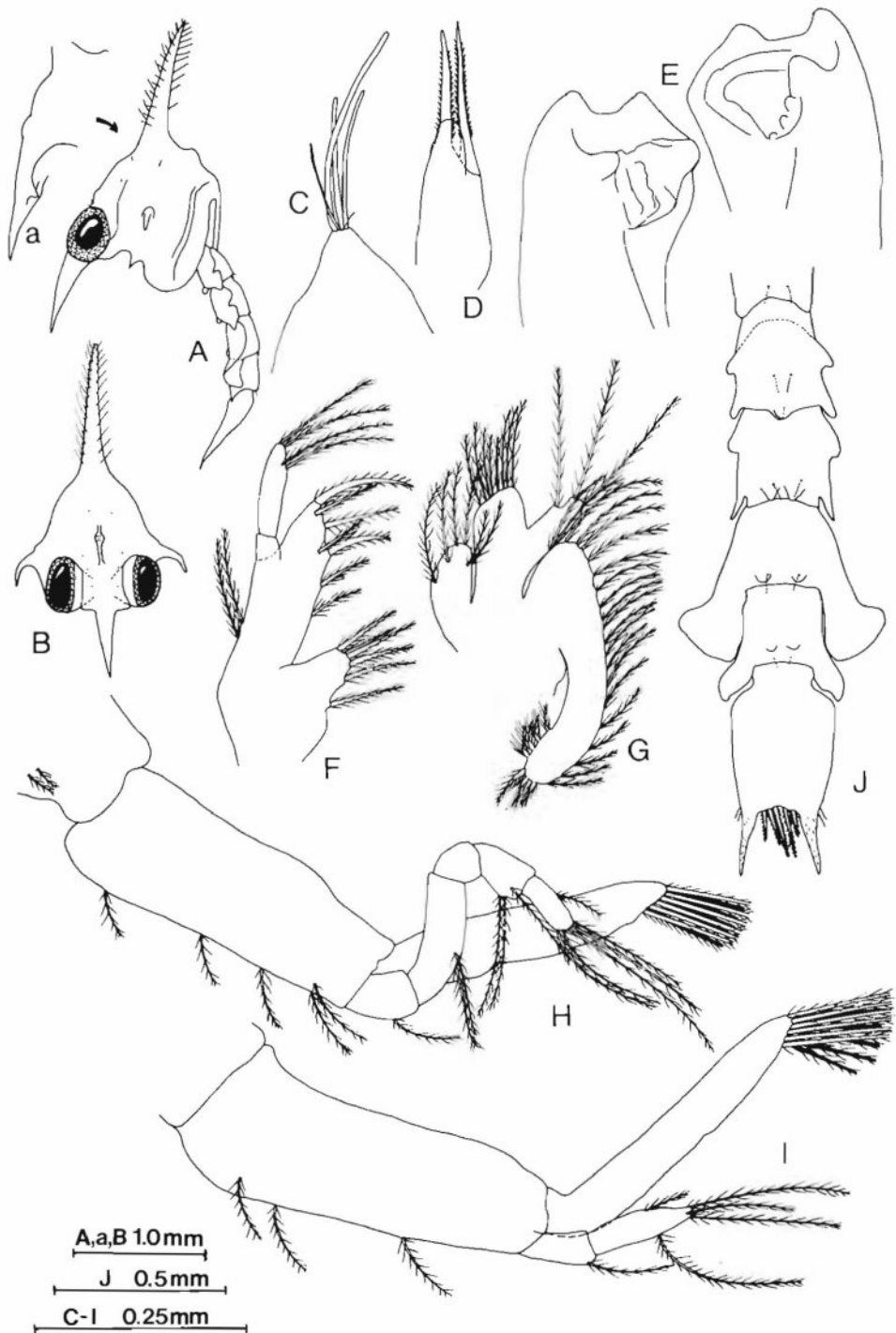
Fig. 6.   *Troglocarcinus corallicola* Verrill: Fifth zoeal stage. (A) Lateral view; (a) detail, rostral spine and pre-orbital protuberance, lateral view; (B) frontal view; (C) antennule; (D) antenna; (E) mandibles; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2; (J) abdomen and telson, ventral view.

able features. These include the distinct caplike process dorsally on the second, and the lateral aliform expansions on the fourth abdominal somites; the elongate telson narrowing distally with foreshortened furcae; the presence of dorsal, lateral, and rostral carapace spines; the lack of hairs on the posterolateral carapace margin; the short truncated antennule, broadly expanded at the base; and the antennal exopodal process of equal length to the protopodal spine (Type A antenna of Aikawa, 1937). Other features easily seen as development proceeds are the change from 3 to 2 segments in the endopod of maxilliped 2 at stage III and thereafter, and the retention of only 5 abdominal somites, the presence of paired knobs or protuberances on abdominal somites 2 and 3, and a maxillipedal exopod natatory setal formula of 4, 6, 8, 10, 11 in the respective first to fifth stages. In addition, with dissection it will be seen that the coxal and basal endites of the maxilla are fused (unilobate), and the endopod has a setal formula of 2 + 1 in the 5 stages that were obtained. Another quite remarkable character is the extremely large size of the mandibles, disproportionate to the whole zoea, so that the observer's attention is immediately drawn to the greatly oversized mouthparts.

The Taxonomic Position of the Hapalocarcinidae

Rice (1980b) recently hypothesized that a comparison of larval maxillular and maxillary morphologies and setal formulae could be used to elucidate relationships among the various brachyuran crab families. Based on previous studies in our laboratory, and considering additional data provided through comparisons of antennal and telsonal morphologies as well, we had arrived at the same conclusion. In the discussion that follows the evidence derived from these comparisons allies the family Hapalocarcinidae with the Pinnotheridae and the Hymenosomatidae, both families containing highly specialized members. Hapalocarcinid larvae also exhibit morphological similarities with larvae of the Leucosiidae, but whether this similarity is indicative of close phylogenetic relationship seems unclear at present (see Rice, in press). All of these families are presently thought to be highly advanced Decapoda (Rice, 1980b).

In comparing zoeal morphologies between *Troglocarcinus* and other brachyuran genera we considered the following characters to be most useful: the foreshortened antennule, the fused unilobate maxillary endites, the 2 + 1 setal formula on the maxillary endopod, the reduction from 3 to 2 articles in the endopod of maxilliped 2, the presence of only 5 abdominal somites in all stages, the unique caplike process on abdominal somite 2 and the tapering aliform expansions on somite 4, and the rectangular distally-tapering telson with a process formula of i + ii (=hairs) + III (=fixed spine) + 4–6 (=movable spines) (see Gore, 1979, for explanation).

On the other hand, characters of uncertain value in *Troglocarcinus* zoeae, because of limitations of our present knowledge of decapod larvae, include the presence of rostral, dorsal, and lateral carapace spines, the lack of posterolateral setae on the carapace, the Type A antenna, the absence of pleopod buds until stage 5, and the total number of zoeal stages required to complete development in the Hapalocarcinidae. These characters will not be used in the comparison that follows.

Antennular Morphology

Troglocarcinus corallicola exhibits a close resemblance to some zoeae in the families Leucosiidae and Pinnotheridae. In *Ebalia nux* (Rice, 1980a) and *Pinnotheres pisum* (Atkins, 1954; Rice, 1975) or *P. gracilis* (Kakati and Sankolli,

1975), for example, the antennule is similarly as foreshortened, and bears a reduced number of aesthetascs and setae as that seen in *T. corallicola*. Such reduction or simplification of cephalic appendages is considered an indication of advanced evolutionary condition in brachyuran larvae (see Rice, 1980b).

Unilobate Maxillary Endites

Larvae in several families have fused, reduced, or unilobate endites, including those in the Hymenosomatidae (e.g., *Halicarcinus australis*; see Lucas, 1971), Leucosiidae (e.g., *Philyra corallicola*; see Hashmi, 1970), Pinnotheridae (e.g., *Pinnotheres taylori*; see Hart, 1935), and to some extent in species of Dorippidae (e.g., *Dorippe granulata*; see Kurata, 1964), and in the subfamily Pilumninae (e.g., *Pilumnus dasypodus*; see Sandifer, 1974) of the Xanthidae. Except for the Xanthidae, which are cyclometopes, the remaining families are either catametopes or catametopous-like, indicating that they are advanced decapods. The reduction of the endites in these families, and in the Hapalocarcinidae if *Troglocarcinus* be indicative, is considered an advanced character. Beyond this, both the Xanthidae (which are more primitive) and the Dorippidae (which, in Rice's view, have evolved independently from other brachyurans) show little relationship to the hapalocarcinid zoeae, except perhaps in exhibiting some relative similarity in antennal exopod:protopodal spine lengths, or in possession of carapace spines. Both of these features tend to be more primitive, but, more important, do not seem to carry much weight because of their widespread occurrence in other decapod larvae.

Maxillary Endopodal Setal Formula

The endopodal formula of 2 + 1 is similar to that noted in leucosiid and some pinnotherid zoeal stages (e.g., *Pinnotheres maculatus*; see Costlow and Bookhout, 1966), and in some ocypodine Ocypodidae (e.g., *Ocypode quadrata*; see Diaz and Costlow, 1972). The endopodal setal formula appears to be the only important character in which the Ocypodidae show affinity to the Hapalocarcinidae. This formula is substantially different, however, in the Hymenosomatidae, even though the coxal endites are quite reduced, thus suggesting that the latter family may also be less closely related to hapalocarcinids than the leucosiids, pinnotherids, and ocypodids. The presence of lateral expansions on the fourth abdominal somite of some ocypodine zoeae seems less relevant, in that they are of a different form from that seen in either hapalocarcinid or in some pinnotherid zoea (see below).

Reduction in Maxillipedal Endopodal Articles

The reduction in later zoeal stages of the number of endopodal articles in the second maxilliped from 3 to 2 is shared with larvae of the Leucosiidae, Pinnotheridae, and even by some majid zoeae. Larvae in the Majidae almost invariably possess but 2 zoeal stages, and although the sequential reduction in the appendage is similar, the durational development over which it occurs is not. Rice (1980b) has provided an extensive discussion and comparison with Williamson's (1976) hypothesis as to the relative phylogenetic position of the Majidae. Suffice it to say here that the Majidae show no close relationships to the Hapalocarcinidae in any other of the important characters under consideration.

Number of Abdominal Somites Throughout Development

In the majority of brachyuran larvae 5 abdominal somites are present in the

first one or two stages, with a sixth somite usually dividing from the telson in either stage II, III, or rarely IV. Rice (1980a) considers the suppression of the sixth abdominal somite to be an advanced character. Hymenosomatid, leucosiid, many pinnotherid (those with less than 4 zoeal stages), and some majid zoeae never have more than 5 somites, thus sharing this trait with *Troglocarcinus* larvae, as far as the latter are known. The failure to subdivide the pretelsonal somite prevents concomitant development of uropodal buds in the ultimate zoeal and subsequent megalopal stage. In the Hymenosomatidae this is no problem because this family has dispensed with the megalopal stage entirely. In at least some pinnotherid, and in *Philyra corallicola* (Leucosiidae) larvae, uropodal development in the megalopa is suppressed. We suspect that this is true also of *Troglocarcinus*.

Abdominal Somite Ornamentation

The most remarkable combination of features possessed by *Troglocarcinus* zoeae, the caplike process on somite 2, and the aliform expansions on somite 4, are shared in these exact positions by no other decapod larvae. However, lateral expansions of one form or another, but not exactly similar to those seen in *Troglocarcinus,* occur on either the fourth somite of *Pachygrapsus crassipes* (Schlotterbeck, 1976), or on the fifth somite in larvae of some Hymenosomatidae (*Elamena mathaei*; see Gurney, 1942), Pinnotheridae (*Pinnixa* sp.; see Faxon, 1879 [=*P. sayana*? *fide* Smith, 1880]), *Fabia* (see Irvine and Coffin, 1960), Grapsidae (*Metopograpsus messor*; see Rajabai, 1961), and Ocypodidae (*Dotilla sulcata*; see Gohar and Al-Kholy, 1957). It appears that the possession of these lateral expansions in the zoeae of the several families (especially because the character occurs on different somites) is an evolutionary response to some ecological or environmental factor which the larvae experience while in the plankton. It is also interesting that this feature occurs primarily in those species having known or imputed commensal or symbiotic relationships. Thus, *Troglocarcinus corallicola* is a known commensal of stony corals, the pinnotherids are well-known symbionts of a number of invertebrates, and *Metopograpsus* inhabits tubes made by wood-boring molluscs (see Rajabai, 1961).

Except for zoeae of *Pinnotheres pisum* (Atkins, 1954) and in Aikawa's (1933, 1942) "Pinnozoea," the caplike process on somite 2 is not known to occur in any other brachyuran zoeae, and if it is found in other hapalocarcinids, it would provide another easily utilizable character for identifying members of this family in the plankton.

Telson Shape and Process Formulae

In the shape of the telson, *Troglocarcinus* larvae are most similar to larvae of the Hymenosomatidae. However, at least some larvae in the latter family may lack the lateral setae found in *Troglocarcinus* zoeae. Larvae in other brachyuran families usually have telsons with either longer furcae, more truncated or more widely expanded (often spatulate) telsonal segments, or (as seen especially in the Pinnotheridae) with varying degrees of modification of the medial posterior margin into flattened spines, bladelike protrusions, or horns (e.g., Sandoz and Hopkins, 1947). Leucosiid zoeae have expanded spatulate telsons (see e.g., Miyake, 1935; Rajabai, 1961; Williamson, 1967; Hashmi, 1970), or (in prezoeal larvae of *Ixa*) a rather ornately rounded telson with a pronounced medial gap (Rajabai, 1961). Interestingly, first zoeae of *Metopograpsus messor* (Grapsidae; see Rajabai, 1961) possess a telson morphologically similar to that seen in *Troglocarcinus*

and some hymenosomatids, but beyond this, and in the expanded fifth (instead of the fourth) abdominal somite noted earlier, show little other affinity.

Although similarity with hymenosomatid larvae is seen in general telson shape, the posterior spine formula in *Troglocarcinus corallicola* of i + ii + III + 4–6 is not shared with any other genus or species. In the family Hymenosomatidae, the formulae may be I + 2–4, i + II + 3–5, or i + ii + iii + IV + 5–7, with several forms of zoeae occurring in some genera (see Boschi *et al.,* 1969; Lucas, 1971). Chief differences among the hymenosomatid larvae and those of *T. corallicola* are in the absence, or supernumerary presence, of fine lateral hairs (processes i, ii, or iii) proximad to the large lateral spine (either process II or IV) in the hymenosomatids, whereas in *T. corallicola* the lateral spine is always process III. Until other hapalocarcinid larvae become known we are forced to speculate with the admittedly scanty data, but the general telson shape shared by both families seems worthy of note, even if the posterior marginal process formula differs.

Phylogenetic Relationships of the Hapalocarcinidae

The data just presented suggest that, if *Troglocarcinus corallicola* larvae can be considered as typifying the family Hapalocarcinidae, then the closest morphological relationships should be sought among the families Pinnotheridae, Leucosiidae, and Hymenosomatidae, because larvae from these families share many features with *Troglocarcinus* zoeae. In fact, using the characters discussed above and applying them to a key to zoeal larvae provided by Rice (1980b) one arrives at a similar conclusion, with *Troglocarcinus* falling among these 3 families in the couplets. The Hymenosomatidae, however, are somewhat apart in this same key and differ from pinnotherid, leucosiid, and (now) hapalocarcinid larvae by possessing 3 medial setae on the endopod of maxilliped 1, rather than 1 or 2 as seen in the former 3 families. This offers the alternative possibility that medial setation on the maxilliped 1 endopod has either been derived separately, or is perhaps not as important a character as others.

How does this derivation fit into the classification scheme proposed by Rice (1980b)? In his Figure 47 he considered only primitive Brachyrhyncha in reconstructing evolutionary lines (not as a phylogenetic tree), so that none of the families considered here are applicable. However, in Table XI of the same work the Pinnotheridae and Leucosiidae, as well as the ocypodine Ocypodidae, are considered the most advanced brachyrhynchous families, whereas the Hymenosomatidae are relegated to a more primitive level, primarily based on a maxillary setal formula of 2 + 3, close to the menippine Xanthidae. Although Rice noted in his study (1980b: 315) that hymenosomatid larvae possessed very advanced features, allying them with the most advanced catometopous families, viz., Pinnotheridae and Leucosiidae, the positioning based on maxillary endopodal setae placed the relatively advanced Hymenosomatidae zoeae among the more primitive brachyuran families. For as noted by Scotto (1979), if the family Menippidae (as suggested for re-establishment by Guinot, 1979b) be accepted, it would include genera having some of the most primitive brachyuran zoeae yet recognized, based on antennular, antennal, abdominal, telsonal, and developmental duration features. Moreover, the data, using larval characters, suggest that the Hapalocarcinidae are also relatively advanced crabs, although the zoeal stages (as do those in other advanced families) apparently retain some primitive features.

We believe this classification, based on larval features, continues to support

that proposed for the adults of these families. Even though Balss, *et al.*, (1940–1961) was one of several authors who considered the hapalocarcinids to be so aberrant as to require their own superfamily, Števčić (1971) pointed out that such aberrancies may be secondarily derived, thus obviating the unnecessary establishment of a higher, and separate, taxon. As long ago as 1859, Stimpson considered *Hapalocarcinus marsupialis* (the first genus and species of hapalocarcinid described) to be close to both the Pinnotheridae and Hymenosomatidae. The latter family had already a long history of uncertainty as to its relationships with other brachyurans, and both MacCleay (1838) and Dana (1852), for example, had allied it with the pinnotherids as a subtaxon. Rice's (1980b) synopsis of larvae clearly showed that the pinnotherids and hymenosomatids were relatively closely related, with the leucosiids thought to be even closer to the pinnotherids (see also Lebour, 1928). In further support, Fizé and Serène (1957) provided an excellent review of the long and tangled history of the family Hapalocarcinidae, and in summarizing, considered these crabs to have closest affinities with the Pinnotheridae.

Rice, however (in press), after examining a new classification of brachyurans proposed by Guinot (1979a) and further developed by Saint-Laurent (1980a, b), in which the position and structure of the adult genital opening was given new importance, became more skeptical of relying on larval features to support established adult phylogenetic relationships. Guinot's horizontal (cladistic) scheme postulated an evolutionary migration of the genital opening from the most primitive (coxal) position, found in her taxon Podotremata, to the intermediate position (female sternal, male sternal or coxal; Heterotremata), and finally to the advanced condition (sternal in male and female) seen in her taxon Thoracotremata. In Guinot's classification (e.g., 1979a: 195–196) the leucosiids were considered advanced heterotremes (almost thoracotrematous), whereas hymenosomatids, pinnotherids, ocypodids (and now hapalocarcinids, based on our examinations of adults in the genus *Troglocarcinus*), exhibit the advanced thoracotrematous state.

Although Saint-Laurent (1980a, b) agreed with Guinot's general taxonomic classification, she proposed a phylogenetic (vertical) scheme in which the Podotremata evolved separately from both the Heterotremata and Thoracotremata, and the latter two groups, which Saint-Laurent placed in her new taxon Eubrachyura, then diverged from each other and from the Podotremata at an early stage. Her divisions, although considering the positioning of the genital openings, were primarily based on the structure of the openings, and whether fertilization was external (podotrematous) or internal (hetero- and thoracotrematous).

Rice (in press), agreed with Saint-Laurent's (1980a, b) classification and, with a re-examination of larval features, postulated that the leucosiids, hymenosomatids, and pinnotherids represented end points of different phylogenetic lines owing to their advanced larval characters. He proposed that these apomorphic characters, shared by the three families, have been acquired independently. If this be true, the same condition could exist for the hapalocarcinids. Therefore, whether based on larval or adult characters, a close relationship, be it phylogenetic or cladistic (i.e., sharing of apomorphic characters) is indicated between the hapalocarcinids and the pinnotherids, hymenosomatids, and leucosiids. This concept supports Guinot's (1979b) establishment of superfamilies Pinnoteroidea [*sic*], Hymenosomatidoidea, and Leucosioidea. All that would remain is to acknowledge Balss' suggestion (reviewed in Števčić, 1971) that the hapalocarcinids be placed in their own superfamily Hapalocarcinoidea. This scheme thus accepts Guinot's original establishment of superfamilial relationships based on adult char-

acters, while at the same time it could incorporate Saint-Laurent's (1980b: 1320) views that ". . . il est en effet possible qu'un ou plusieurs rameaux . . ." [e.g., Line A—Leucosiodea?] separated from the eubrachyuran stem before the thoracotrematous condition became established.

We can in retrospect only concur heartily with Utinomi's earlier statement (1944) on the Hapalocarcinidae, which has proved to be prophetic, when he thought it ". . . wise to reserve any final decision of the systematic position of this group to the time when its development will be thoroughly worked out." Our data, which consider the relationships of pinnotherid, leucosiid, hymenosomatid, and hapalocarcinid larvae to be at least morphologically close, are a first contribution to this effort.

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