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EARLY LARVAL STAGES OF THE INDO-PACIFIC CORAL GALL-FORMING CRAB *HAPALOCARCINUS MARSUPIALIS* STIMPSON, 1859 (BRACHYURA, HAPALOCARCINIDAE) CULTURED IN THE LABORATORY

BY

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INTRODUCTION

Hapalocarcinus marsupialis, the type-species in the family Hapalocarcinidae, is one of at least 27 species in 8 genera of these remarkable little crabs that settle on living scleractinian corals and eventually become partially or completely imprisoned in the resultant gall produced by the host coral. *Hapalocarcinus marsupialis* is widely distributed and has been recorded from the eastern tropical Pacific (Garth & Hopkins, 1968) and throughout the Indo-west Pacific (Edmondson, 1933; Fize & Serène, 1957; Takeda & Tamura, 1979; among others). Although much is known about the general biology of the species (see e.g., Potts, 1915), only the first stage larvae have been described. Potts (1915), Edmondson (1933), Fize (1956) and Al-Kholy (1963) all provided brief descriptions or illustrations of first zoeal stages, most of which are inadequate to allow meaningful comparisons with larvae from other hapalocarcinids. Coupled with the inadequacies just noted is the fact that hapalocarcinid larvae are among the more difficult of brachyurans to culture in the laboratory, apparently requiring extended lengths of time in several zoeal stages in order to complete their development (see Fize, 1956; Scotto & Gore, 1981). In order to further clarify the systematic position of the adult members, an attempt was made to rear larvae of *H. marsupialis* through as many developmental stages as possible. Regrettably, only the first 2 zoeal stages of *H. marsupialis* were obtained. Accordingly, we provide herein complete descriptions of these stages and compare the larvae with those of *Troglocarcinus corallicola* Verrill, noting several morphological characters which may be important at both the generic and specific levels.

METHODS AND MATERIALS

Seventeen ovigerous female *Hapalocarcinus marsupialis* were collected from the same number of inhabited intact galls on two 15 cm coral colonies of *Pocillopora damicornis* (L.) which were interspersed within a patch reef of corals at 1 to 2 m depth dominated by *Porites compressa* Dana, from Kaneohe Bay, Oahu, Hawaii, on 4 June 1981. The galls and contained crabs were sealed in plastic bags with oxygenated ambient seawater, and flown to the Ft. Pierce, Florida laboratory. Crabs were placed one each, in four 9.0 cm diameter glass bowls containing aerated seawater (35‰). These were replaced on hatching with additional individuals from crabs maintained in a community aquarium under similar conditions. All crabs were held at room temperature of approximately 25°C, maintained by reverse-cycle air conditioning, and fed daily with newly hatched *Artemia* nauplii. In each of 7 separate hatches, occurring between June 7 and July 18, the larvae were transferred to 24-compartmented polystyrene trays with 1 zoea per compartment, following methodology described by Gore (1968). Larvae were cultured in controlled temperature units on 12 h light-dark diel cycles under fluorescent light, 104 zoeae at 22.5 (± 0.5°)C and another 120 at 25 (± 0.5°)C. Seawater (35‰) was changed and larvae were fed an excess of *Artemia* nauplii daily. All molts, dead zoeae and adults were preserved in 70% ethanol. Illustrations and measurements were made using methodology of Wilson et al. (1979).

First larval stage and adult specimens were deposited in the National Museum of Natural History, Washington, D.C. (USNM 189212), the Allan Hancock Foundation, University of Southern California, Los Angeles (AHF 238701), the British Museum (Natural History), London (1981-452), and the Rijksmuseum van Natuurlijke Historie, Leiden (D-34674). First and second larval stages and/or their molts and adult specimens were deposited in the Indian River Coastal Zone Museum, Fort Pierce, Florida (IRCZM 89:5129).

REARING RESULTS

Of the 224 larvae that were reared none hatched as prezoea, and only 3 attained stage II, with 3 more dying while molting to this stage. The 2.5°C temperature difference between the 2 series had pronounced effects on survivorship. Maximum stage I duration, without molting, was 29 days at 22.5°C and 16 days at 25°C, with 50% survivorship recorded on days 19-20 and day 11, respectively (fig. 1). Larvae cultured at 22.5°C (solid line; fig. 1) that either molted, or died while molting, to stage II, spent an average of 19.8 days in stage I (range: 17-22 days). Maximum stage II survival at 22.5°C was 12 days. None of the larvae reared at 25°C (dashed line; fig. 1) survived stage I, the last zoea dying on day 16. Fize (1956) also noted an extended developmental time in stage I, not molting after 20 days, a consequence she attributed to incorrect nourishment of the larvae.

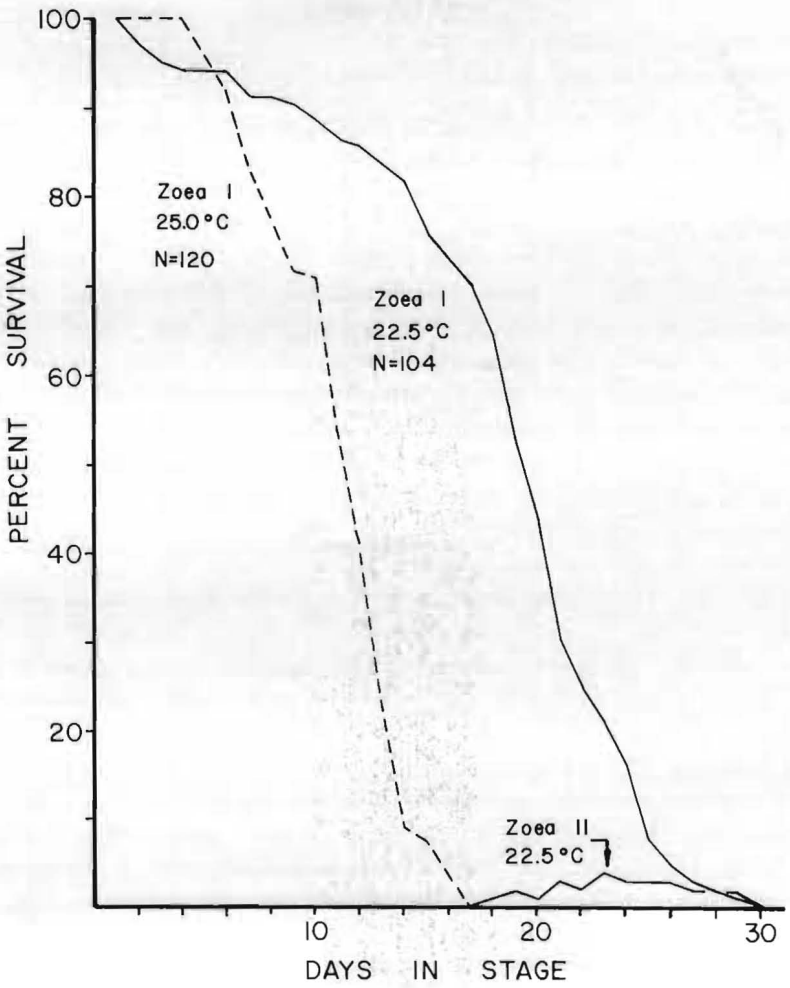

Fig. 1. Percentage survival and duration of stages in *Hapalocarcinus marsupialis* Stimpson larvae reared under 2 temperature regimes. N = number of larvae cultured at each temperature. Solid line = 22.5°C, dashed line = 25°C.

In the Atlantic *Troglocarcinus corallicola*, the only other hapalocarcinid in which larvae are well known, survivorship at 25°C was enhanced and the duration of stage I averaged only 12.8 days (Scotto & Gore, 1981). Thus, the Pacific *H. marsupialis* probably has a much longer planktonic period, possibly lasting 120 days, extrapolated from the average duration of stage I, and an estimated 6 zoeal stages. This might account in part for the wide distribution of *H. marsupialis* throughout the Indo-Pacific. It is possible, however, that our larvae, cultured under artificial conditions using Atlantic Ocean seawater, may have lacked a chemical cue or other feed-back that would stimulate ecdysis, thereby shortening larval time.

LARVAL DESCRIPTIONS

First zoea. — Carapace length 0.59 mm; 7 specimens examined.

Carapace (fig. 2A, B, b) inflated, subglobose; ventrolateral margin with blunt tooth; dorsal and rostral spines straight, naked, longer than ventrally curved lateral spines; the latter armed with tubercles; small antero- and posterodorsal knobs each bearing integumental sensillae; a lateral seta at base of dorsal spine; eyes unstalked.

Abdomen (fig. 2A, C, D, E). Somite 1 naked, 2-5 with pair of median postero-dorsal setae; 2 and 3 with lateral knobs and bluntly rounded posterolateral processes forming caplike structures; 4 with broad posterolateral aliform extensions; 5 with bluntly rounded posterolateral processes and a median tubercle-like extension anteroventrally.

Telson (fig. 2C, F). Prongs of the furca each with 2 lateral hairs, bases of prongs with pubescence; six interfurcal spines armed with spinules, medial pair ventral to others; formulae i + ii + III + 4-6.

Antennule (fig. 2G). 3 aesthetascs, 1 hair.

Antenna (fig. 2H). Spinous exopod 1.2 × longer than spinous protopodal process.

Mandible (fig. 2I) large, asymmetrically dentate; incisor process cutting edge with single tooth on anterior and posterior edges; molar process indistinctly dentate.

Maxillule (fig. 2J). Endopod 2-segmented, 0,4 setae; basal endite 5, coxal endite 6, setae of variable stoutness.

Maxilla (fig. 2K). Endopod unilobate, 1 + 2 setae; basal endite 8, coxal endite 5 setae, fine hairs as illustrated; scaphognathite with 4 marginal setae proximally plus a thickened plumose terminal process.

Maxilliped 1 (fig. 2L). Coxopod naked; basipod with 1,1,1,2 medial setae; endopod segments with 1,2,0,2,4 + I setae (Roman numeral = dorsal setae); exopod with 4 natatory setae.

Maxilliped 2 (fig. 2M). Coxopod naked; basipod with 1,1,1 medial setae; endopod segments with 0,0,1 + 3 + I setae; exopod with 4 natatory setae.

Second zoea. — Carapace length 0.68 mm; 1 specimen examined.

Carapace (fig. 3A, B, b) more angular, ventrolateral tooth more acute; additional pairs of setae anterior to base of dorsal spine and intraocularly anteriorly to dorsal knob; rostral spine with 3 rows of long hairs; eyes stalked.

Abdomen (fig. 3A, C, D, E). Posterolateral processes on somites 2 and 3 elongate; aliform extensions of 4 indistinctly tuberculate on posterodistal border; medioventral extension of somite 5 elongate.

Telson (fig. 3C, F) similar in form, armature and article ratios to first stage.

Antennule (fig. 3G). 4 aesthetascs, 1 hair.

Antenna (fig. 3H) similar in form, armature and article ratios to first stage.

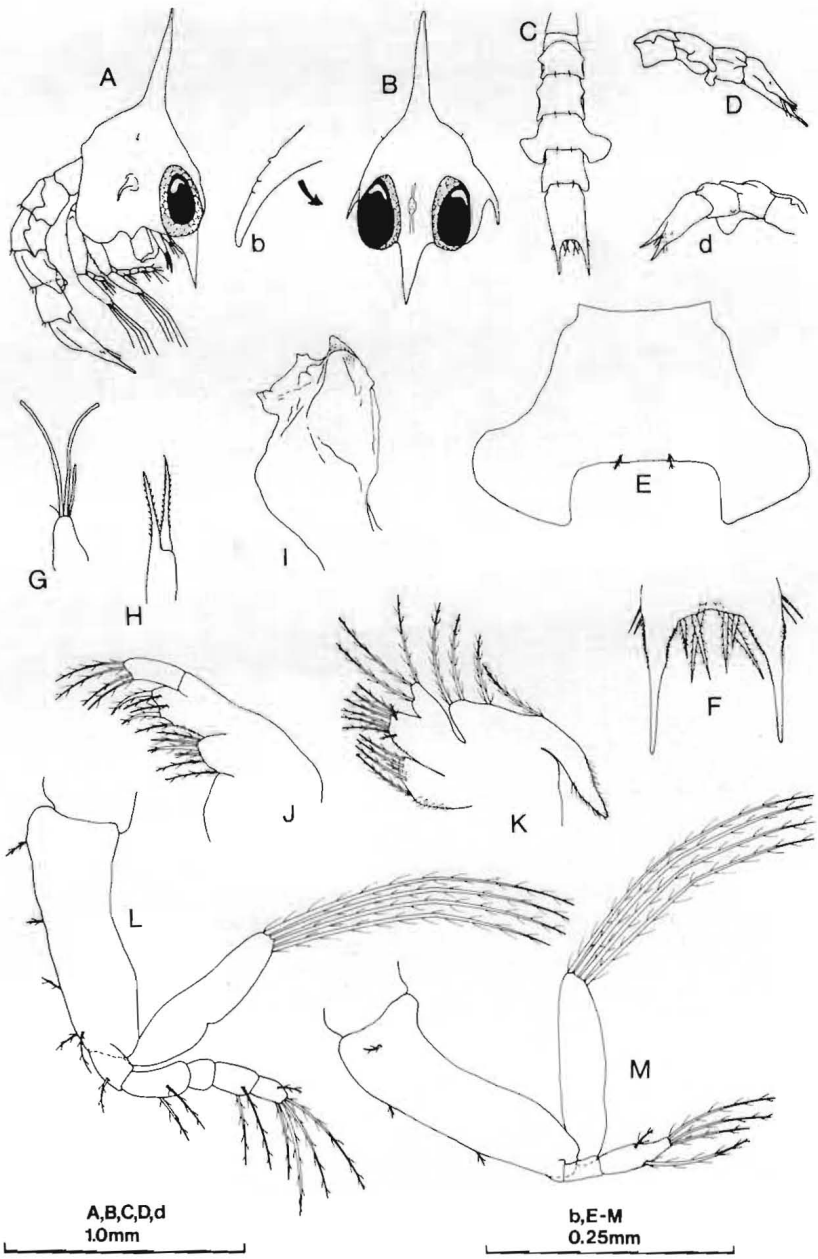

Fig. 2. First zoeal stage of *Hapalocarcinus marsupialis* Stimpson. A, lateral view; B, anterodorsal view; b, detail, lateral spine; C, abdomen and telson, dorsal view; D, abdomen and telson, lateral view; d, same, first zoeal stage of *Troglocarcinus corallicola* Verrill (see text); E, detail, fourth abdominal somite; F, detail, telsonal furca and spines; G, antennule; H, antenna; I, mandible; J, maxillule; K, maxilla; L, maxilliped 1; M, maxilliped 2.

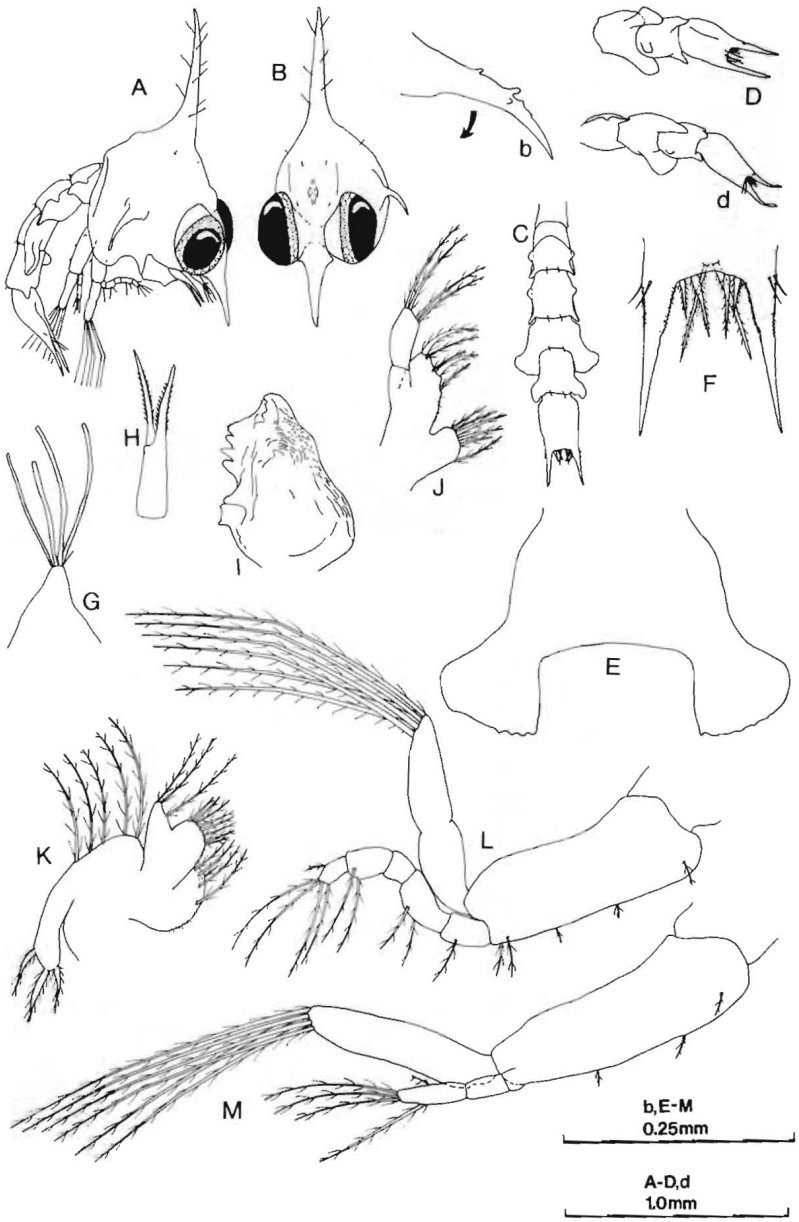

Fig. 3. Second zoeal stage of *Hapalocarcinus marsupialis* Stimpson. A, lateral view; B, anterodorsal view; b, detail, lateral spine; C, abdomen and telson, dorsal view; D, abdomen and telson, lateral view; d, same, second zoeal stage of *Troglocarcinus corallicola* Verrill (see text); E, detail, fourth abdominal somite; F, detail, telsonal furca and spines; G, antennule; H, antenna; I, mandible; J, maxillule; K, maxilla; L, maxilliped 1; M, maxilliped 2.

Mandible (fig. 3I). Incisor process with 4 teeth each on anterior and posterior edges; molar process irregularly dentate.

Maxillule (fig. 3J). Setation and form as in first stage.

Maxilla (fig. 3K). Scaphognathite with 5 setae proximolaterally plus 3 stout plumose setae on distal margin.

Maxillipeds 1 and 2 (fig. 3L, M). Endopods unchanged from stage I: exopods with 6 natatory setae.

DISCUSSION

The zoeae of *Hapalocarcinus marsupialis* exhibit many morphological similarities to those of *Troglocarcinus corallicola*. Among the shared features in the first 2 zoeal stages are (1) well-developed dorsal, rostral and lateral carapace spines; (2) distal flattened tubercles on the lateral spines; (3) noticeable hairs along the dorsal spine in stage II; (4) identical form and setation on all the cephalothoracic sensory and masticatory appendages; (5) unilobate maxillary endites and an endopodal setal formula of 1 + 2; (6) pronounced caplike dorsal structures, distinct dorsolateral knobs and bluntly rounded posterolateral processes on abdominal somites 2 and 3; (7) paired aliform expansions on abdominal somite 4; (8) paired dorsomedial setae on the posterior margins of somites 2 to 5; (9) an elongate rectangular telson bearing 2 lateral setae proximal to each setose furcal prong; (10) a telsonal formula of i + ii + III + 4-6. These characters, now known to exist within the early stage larvae of 2 of the 8 known genera, may therefore represent familial features by which hapalocarcinid larvae can be recognized in the plankton (see Fize, 1956). Indeed, the general similarity between *H. marsupialis* and *T. corallicola* larvae is so great that it was difficult to find any differences that would allow separation of the 2 species. However, early zoeal stages of *H. marsupialis* we cultured can be distinguished from those of *T. corallicola* by 3 easily observable features; the greater length of the antennal exopod to the protopod (both are equal in *T. corallicola* and in Fize's *H. marsupialis*), the endopodal setal formula on maxilliped 2 of 0, 0, 1 + 3 + I (0, 1, 1 + 3 + I in *T. corallicola*), and a distinct, well-developed medioventral tubercle on abdominal somite 5 (this tubercle is present in Fize's *H. marsupialis* as a hook, but is not nearly as pronounced in *T. corallicola*; compare figs. 2 and 3D, d). Inasmuch as only a single species is known at present in the genus *Hapalocarcinus* (but see below), these differences may provisionally be recognized as generic in nature, until further evidence from other hapalocarcinid larvae is presented. Another feature of possible diagnostic value may be the duration of larval stages which, as noted above, was noticeably longer at similar temperatures in *Hapalocarcinus* than in *Troglocarcinus*. It will also be remembered that the genus (and consequently the larvae) of *Hapalocarcinus* are as yet unknown in the Atlantic Ocean, although *Troglocarcinus*, on the other hand, is represented by at least 1 species in the

Atlantic and several in the Pacific Ocean (Fize & Serène, 1957), so that elimination on zoogeographic grounds remains relatively uncertain at present.

Additional features in *H. marsupialis* which will require examination of zoeal stages later than Z-II before they can be properly evaluated include whether: 1) 5 or 6 abdominal somites occur, 2) the development of the antennule remains retarded, 3) the reduction of maxilliped 2 endopod from 3 to 2 articles takes place, 4) the number of natatory exopodal setae on the maxillipeds increases in a regular manner (see Scotto & Gore, 1981, for complete discussion).

We have not been able to consider in much detail the work of other authors on hapalocarcinid larvae. The larva described by Fize (1956) and attributed to *H. marsupialis* differs from those we cultured in the structure and setation of the antennule, antenna, maxillule, maxilla and telsonal morphologies. On the other hand, Edmondson's (1933) sketchy illustrations of *Cryptochirus minutus* Edmondson, and *H. marsupialis* allow little to be concluded except that they show some hapalocarcinid morphological characters. A similar conclusion is reached with the brief description and incomplete illustrations of Al Kholy (1963). More important, however, is Edmondson's fig. 6d (1933: 17) and Fize's figs. 6, 7, and 8. The former allegedly illustrate the abdomen and telson, the latter the antennules, antenna and mouthparts, of *H. marsupialis*. As can be seen, all these characters differ markedly from those observed in our larvae. For example, in Edmondson's larvae the telson has only a single seta proximal to each furcal prong (the latter are also apparently non-setose), and possesses only 4 (instead of 6) interfurcal setae, thereby giving a telson formula of i + II + 3-4, instead of i + ii + III + 4-6 as noted in our material. We do not think that Edmondson's figures were transposed, because the abdomen and telson assigned to *C. minutus* (1933: fig. 6c) are sufficiently distinct from that indicated as *H. marsupialis* (fig. 6d), and from our material. Similarly, the anatomical configuration and setal formulae of sensory and feeding/locomotory appendages in Fize's zoea, especially the maxillule and maxilla, show little relationship to that observed in our larvae. In Fize's larva the maxillule, for example, has 3 endopodal setae and 4 processes on the coxal and basal endites, instead of 4, 5, and 6 processes, respectively, as seen in ours. The maxilla is most remarkable, bearing no relationship whatever with that of our larvae.

This raises 3 possibilities: 1) Both authors overlooked extra setation (which we consider unlikely given both Edmondson's and Fize's reputation for careful research); 2) substantial variation occurs in larval characters over the geographic range of *H. marsupialis* (which we do not dismiss); 3) there may exist other, as yet unrecognized species in the genus *Hapalocarcinus* in the Pacific. The latter 2 options are not without evidence.

Variation in brachyuran larval anatomical characters, especially telsons is not unknown. The best example is a recent paper by Ingle (1981) which demonstrated that both bifid and uniramous telsonal furcae may occur in

zoeae of *Cancer pagurus* from the North Sea. Ingle was unable to state whether the aberrant bifid furcae which were found in only a small percentage of zoeae were phenotypic or genotypic in origin. Variation in setation on other appendages also occur within species of Brachyura (see Gurney, 1942), but usually is not as extensive as that seen between larvae Fize and we cultured. Such variation might argue for subspecific differentiation, at least, among the adults from the Indo-West, and Central Pacific regions.

The alternative possibility, the occurrence of a possible second species in the genus *Hapalocarcinus* is intriguing. In an admirable review of the Hapalocarcinidae, Fize & Serène (1957: 19) cited studies by Verrill in 1860 and 1868, in which that author thought a second species of *Hapalocarcinus* might exist, based on alleged differences in form between specimens inhabiting 2 different coral hosts. The 17 ovigerous females available to us all agreed very well with Fize & Serène's expanded description of *H. marsupialis*. But we noted that the basal articles of the antennular peduncle, contrary to descriptions by Rathbun (1937) and Fize & Serène (1957), never carried a small, sharp or blunt tooth, but were instead rather rounded. These, however, are admittedly small differences to consider establishing a second species in the genus *Hapalocarcinus*. Inasmuch as the larvae described by Fize, Edmondson, and us were produced from adults presumably belonging to the same morphological species, and specimens collected in the latter 2 studies both came from Hawaiian waters, we can for the moment merely draw attention to these discrepancies and hope that other workers may find the opportunity to confirm or deny our suppositions.

Finally, we stated in an earlier paper (Scotto & Gore, 1981) that the phylogenetic relationships of the Hapalocarcinidae, based on similarities in larval features, lay closest to the Pinnotheridae, Leucosiidae, and Hymenosomatidae, basing our conclusions on data available to us at that time. We have recently obtained a complete copy of Fize's (1956) paper, which clearly shows that she arrived earlier at these same conclusions. Thus zoeal stages of *H. marsupialis* in this study provide additional evidence confirming the aforementioned relationships, while at the same time raising questions concerning variation and conservatism in larval characters within the genus.

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ZUSAMMENFASSUNG

Die beiden ersten Larvenstadien der gallbildenden Art *Hapalocarcinus marsupialis* Stimpson aus dem Pazifik wurden unter laborbedingungen aufgezogen. Die Larven werden abgebildet und beschrieben und mit den Larven von *Troglocarcinus corallicola* Verrill aus dem Atlantik verglichen.

Die Larven beider Arten haben wenigstens 10 Merkmale gemein und unterscheiden sich nur in den drei folgenden: Verhältnis der Antennaldornen, Borstenformel der Endopodite, relative Grösse der medioventralen Tuberkel am 5. Abdominalsegment. Aufgrund der Larvalmerkmale ist die Gattung *Hapalocarcinus* in der Nähe der Familien Pinnotheridae, Hymenosomatidae und Leucosiidae zu stellen.

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