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# *CYCLOGRAPSUS INTEGER* H. MILNE EDWARDS, 1837 (BRACHYURA, GRAPSIDAE): THE COMPLETE LARVAL DEVELOPMENT IN THE LABORATORY, WITH NOTES ON LARVAE OF THE GENUS *CYCLOGRAPSUS*

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## ABSTRACT

The complete larval development of *Cyclograpsus integer*, a small sesarmine grapsid crab, is described and illustrated from larvae reared in the laboratory. *Cyclograpsus integer* attains five, and often six, zoeal stages plus one megalopal stage. Temperature affects both duration of larval development and number of larval stages. At 25°C, the megalopal stage was attained in 26-27 days from fifth stage zoeae and 31-32 days from sixth stage zoeae, while metamorphosis at 20°C occurred in 53-55 days from sixth stage zoeae. The zoeal and megalopal stages of *C. integer* are compared to all known cultured species of the genus and morphological differences are noted. *Cyclograpsus integer* zoeae may be distinguished from both other species in the genus and other species in the family by its antennal morphology, being the only species with the type A antenna (i.e., the exopodite about equal in length to the protopodite). Megalopae of this species may be distinguished from other species in the genus by the formation of the frontal region and the terminal setation of the telson. Other potentially useful zoeal morphological characters are discussed regarding both the taxonomic and phylogenetic position of *C. integer*.

The sesarmine genus *Cyclograpsus* is cosmopolitan, containing at least 16 species, 13 of which occur in the Indo-West Pacific region (Griffin 1968). *Cyclograpsus integer*, one of four species in the genus occurring in the New World and the only one known from the western Atlantic, is quite widespread with records from western and eastern Africa, and localities in the Indo-West, eastern central, and northern west Pacific Ocean (Monod 1956; Griffin 1968; Manning and Holthuis 1981). Although Rathbun (1918) listed the Peruvian and South American species *Cyclograpsus cinereus* Dana, 1851 as being the eastern Pacific analog to *C. integer*, Griffin (1968) noted that *Cyclograpsus escondidensis* Rathbun, 1933, an eastern Pacific species known only from Central America, was closer to *C. integer* than to any other member of the genus. In the same study, Griffin described *Cyclograpsus sanctaecrucis*, a new species from Santa Cruz Island in the southwestern Pacific Ocean, stating that "Except in the presence of a lateral notch on the carapace, [this] species most closely resembles *C. integer*." Thus, *Cyclograpsus integer* appears similar to at least two other species in the genus from the Pacific Ocean.

The larvae of members of the genus are not well known, and the complete larval development has been determined for only two New World species at present. Costlow and Fagetti (1967) described and illustrated the complete development of *C. cinereus* from Chile, and in a subsequent paper Fagetti and Campodonico (1971) recorded the development of a species from Juan Fernandez Islands which they identified as *Cyclograpsus punctatus* H. Milne Edwards, 1837. Griffin, however (1968), suggested that specimens of *Cyclograpsus* from those islands are actually referable to *Cyclograpsus lavauxi* H. Milne Edwards, 1837, stating that *C. punctatus* is restricted to South Africa. To add to this confusion, Wear (1970) described and illustrated the first zoeal stages of two New Zealand species, *Cyclograpsus insularum* Campbell and Griffin, 1966, and *C. lavauxi*. But a comparison of his illustrations of the latter species with the first zoeal stage figured by Fagetti and Campodonico shows substantial differences in the number and position of chromatophores, appendage processes, and segmentation of the maxillule, suggesting that notable variation occurs between eastern and western Pacific populations of *C.*

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*lavauxi*, if Fagetti and Campodonico's species was misidentified. These differences raise the possibility that the New Zealand (Wear 1970) and Chilean (Fagetti and Campodonico 1971) forms of *C. lavauxi* are subspecies, assuming that Griffin is correct in restricting *C. punctatus* to South Africa. On the other hand, the Chilean specimens may indeed have been correctly identified as *C. punctatus*, thus accounting for the observed differences in the larvae, as well as reinstating the Juan Fernandez Islands as the westernmost zoogeographical boundary for the species. Until further data are available, we will consider Fagetti and Campodonico's species to be correctly identified as *C. punctatus*, so that we may compare the morphological features of this species with others in the genus.

The aforementioned confusion, and the widespread occurrence of *C. integer*, as well as its close morphological relationship to *C. escondidensis*, its Central American analog, all illustrate the importance of determining the larval development of these species. Accomplishing this would facilitate identification of their respective larvae in the plankton and also allow comparisons of morphological features in zoeal and megalopal stages. The latter stages provide a means of elucidating phylogenetic relationships both intra- and intergenerically among the Grapsidae. Accordingly, in this paper we describe and illustrate the complete larval development of *Cyclograpsus integer* and compare salient characters shared by the zoeae and megalopae in *C. punctatus*, *C. cinereus* from the New World, and *C. lavauxi* and *C. insularum* first zoeae from the Indo-West Pacific.

## MATERIALS AND METHODS

Three ovigerous females (carapace width 7.0, 9.3, 10.4 mm) were collected among medium-sized cobbles in the high intertidal zone at Bodden Town, Grand Cayman Island, on 15 July 1980. Following previous methodology (Gore 1968), the crabs were maintained in 19 cm diameter glass bowls filled with seawater (34‰) and fed *Artemia* spp. nauplii daily until hatching occurred on 25, 28, and 29 July 1980 (largest to smallest female, respectively). A total of 192 larvae were cultured in eight 24-compartmented polystyrene trays, one larva per compartment. The eight trays were maintained in controlled temperature units in a diel fluorescent light cycle of 12 h light, 12 h dark. A total of 144 larvae (72 at each temperature) were cultured at 20° and 25°C (±0.5°C). Another 48 larvae were maintained at 15°C (±0.5°C). Seawater (34-36‰) was changed and the larvae were fed *Artemia* nauplii daily. All dead larvae, molts, and representative live specimens were preserved in 70% ethanol. Descriptions and illustrations were made with the aid of dissecting stereomicroscope and compound microscope with camera lucida attachments, using specimens from all three hatches. Measurements are the arithmetic mean of all specimens examined in a given stage. Carapace length was measured from the base of the rostrum to the posterior margin of the carapace, lateral view in zoeae and dorsal view in megalopae. Carapace width in the latter was measured dorsally across the widest part of the carapace. In all descriptions, setal formulae progress distally.

The first 4 zoeal stages are denoted as ZI to ZIV. One series of fifth zoeal stages (ZVu; ultimate) molted directly to megalopa stage; another (ZVp; penultimate) molted to a sixth (ZVI) stage. The morphological differences in these two forms are noted in the text.

A complete larval series and/or their molts is deposited in the National Museum of Natural History, Washington, D.C. (USNM 184669); the Allan Hancock Foundation, University of Southern California, Los Angeles (AHF 2328-1); the British Museum (Natural History), London (1981-447); the Rijksmuseum van Natuurlijke Historie, Leiden (D-34220); the Museum National d'Histoire Naturelle, Paris (M.N.H.N.-B7294, 7295); and the Indian River Coastal Zone Museum, Fort Pierce, Fla. (IRCZM 89:5096). The adult females are divided among the National Museum of Natural History, the Indian River Coastal Zone Museum, and the Paris Museum.

## RESULTS OF THE REARING EXPERIMENT

Temperature not only influences the duration of larval development within stages, but also affects the number of zoeal stages attained (Table 1, Fig. 1). At the warmer temperature (25°C) either 5, or occasionally 6, zoeal stages occurred. However, the single first crab stage was reached after 37 d in the laboratory by a megalopa which molted from a stage V zoea. Of 3 other stage V zoeae that molted to stage VI, only 2 eventually reached megalopa and none sur-

TABLE 1.—Duration in days of larval and postlarval stages in *Cyclograpsus integer* at two laboratory-culture temperatures. (Mean based only on larvae attaining next stage.)

| Temperature (°C) | Stage | Minimum | Mean | Mode | Maximum | Number molting to next stage (or dying in molt) |
|---|---|---|---|---|---|---|
| 25 | Zoea I | 5 | 6.6 | 6 | 11 | 44 |
| | II | 4 | 4.3 | 4 | 6 | 22 (+2) |
| | III | 4 | 4.2 | 4 | 6 | 18 |
| | IV | 4 | 4.2 | 4 | 5 | 14 |
| | Zoea V-Megalopa | 4 | 5.2 | 6 | 6 | 5 (+2) |
| | Zoea V-VI | 4 | 4.0 | 4 | 4 | 3 |
| | Zoea VI-Megalopa | 6 | 6.0 | 6 | 6 | 2 |
| | Megalopa (V) | 11 | — | — | — | 1 |
| | Megalopa (VI) | All died in stage after 1 day | | | | 0 |
| 20 | Zoea I | 9 | 10.9 | 10 (13)[1] | 14 (21)[1] | 21 (+1) |
| | II | 7 | 9.2 | 8 | 17 | 14 |
| | III | 6 | 7.3 | 8 | 9 | 13 |
| | IV | 7 | 7.9 | 8 | 9 | 10 |
| | Zoea V-Megalopa | No fifth stage zoeae molted to megalopa | | | | |
| | Zoea V-VI | 6 | 7.7 | 7-8 | 12 | 9 |
| | Zoea VI-Megalopa | 11 | 11.7 | 12 | 12 | 6 (+1) |
| | Megalopa | 18 | 21.7 | — | 25 | 3 |

[1]Died in stage.

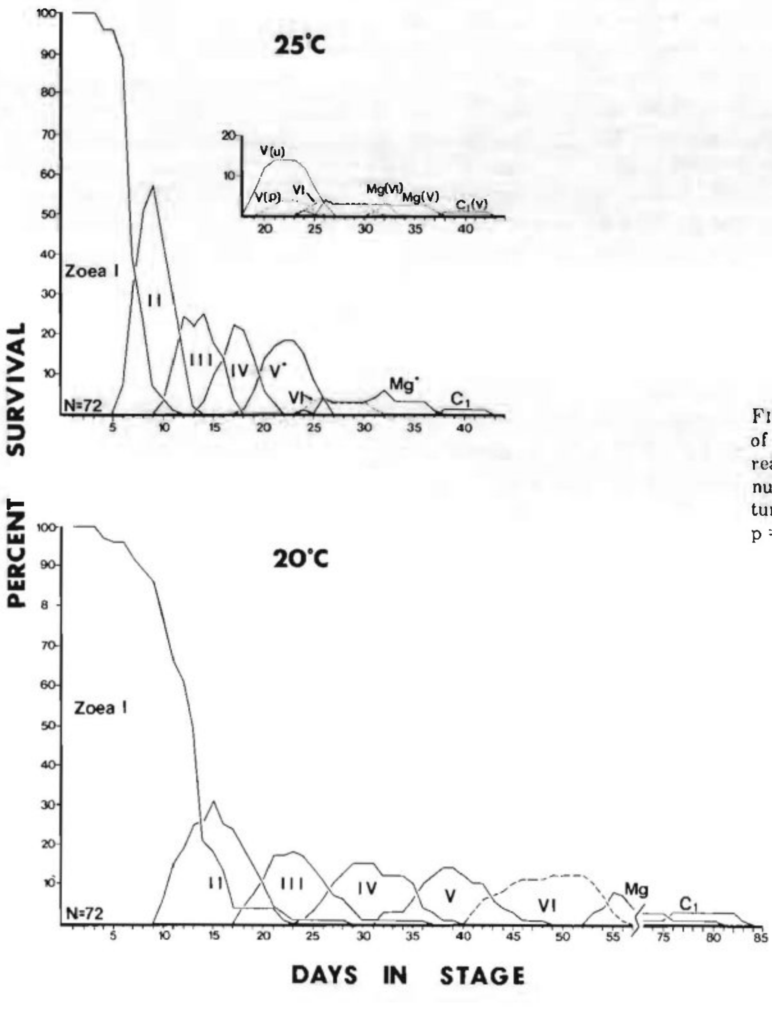


FIGURE 1.—Percent survival and duration of larval stages in *Cyclograpsus integer* reared under laboratory conditions. N = number of larvae cultured at each temperature; * = combined stages; u = ultimate stage; p = penultimate stage. [See text.]

vived to first crab stage. The time period of 37 d may well be a reasonable reflection of what takes place in the plankton, because at 25°C in the laboratory a hypothetical zoea passing through the minimum duration for each stage could conceivably attain first crab stage in as few as 32 d (5 stages) or 38 d (6 stages) after hatching.

The variation in duration of each zoeal stage at 25°C (except for the first zoea) was rather low, comprising no more than 2 d. Stage I, however, could last from 5 to 11 d, although most individuals molted to stage II between 6 and 7 d after hatching. A single zoea that remained in stage I for 11 d also molted to stage II, but died the following day. A comparison of the values in Table 1 with the survival graph (Fig. 1) shows that mortality was quite high on the days just prior to, and during, the ecdysial period in stage I, but as development progressed the mortality subsequently fell. These results are similar to others obtained in our laboratory with brachyuran and anomuran larvae, and indicate that the more mature zoeal stages have a greater survival potential. This might be a result of one or a combination of factors, including the type, quality, and amount of food consumed, the genetic makeup of the parents, or a response by the larvae to unfavorable physical conditions in the laboratory (see Bookhout and Costlow 1970; Knowlton 1974; Gore et al. 1981, for summaries of the various hypotheses).

At 20°C, both within-stage and overall developmental duration were more variable. Extended zoeal durations and the production of a sixth zoeal stage were both noted at the cooler temperature. Larvae remained in stage I 9-14 d before proceeding with further development. Most larvae molting to stage II did so 10 d after hatching. However, a larger component of zoeae died than survived during this ecdysis, most dying at day 14, with 3 zoeae lasting until day 21. It would seem that whatever general effect the lower temperature has on zoeal stages cannot be overridden after about 12-13 d in the first stage, so that the larvae eventually die if they have not molted by this time. Once stage II was reached, most zoeae were capable of continuing their development with relatively little mortality compared to that seen in stage I (Fig. 1). Modal values of within-stage developmental time were generally twice that seen at 25°C. The rearing data also show that the megalopal stage was attained following 6, rather than 5, zoeal stages, approximately 53-55 d after eclosion. Another 18-25 d were required before the first crab stage was reached. Thus, a minimum of 73 d was required after hatching to complete development, even though an extrapolation from the minima in Table 1 suggests that a hypothetical zoea might possibly reach first crab stage in as few as 64 d after hatching at 20°C. Extended developmental times such as these are not necessarily detrimental if the larvae can avoid predation and find sufficient and suitable food. Such longer periods of development could aid in the dispersal of the larvae, thereby accounting, at least in part, for the wide distribution of the adults of this species. However, at the lower temperature of 15°C, all of the 48 larvae remained in stage I up to 12 d before dying. This high mortality suggests very unfavorable conditions for the survival of this species.

*Cyclograpsus integer*, along with some species of *Sesarma*, is among the few Sesarminae, and among still fewer Varuninae and Plagusiinae (Wilson 1980; Wilson and Gore 1980) known to have extra larval stages. The species presently stands alone in the genus in having this feature, but joins an increasingly large group of brachyuran (and anomuran) crustaceans in which an additional larval stage occurs either at lower, or perhaps suboptimum, temperatures (Sandifer 1973; Knowlton 1974; Scotto 1979; Gore et al. 1981). The studies just cited follow classic investigations by Costlow et al. (1960), Bookhout (1972), and Bookhout and Costlow (1974) in which temperature and salinity were manipulated and the effects on survival, duration, and number of larval stages were observed. The data in all these studies add to a large body of circumstantial evidence from the plankton (e.g., alleged substages, morphological variants, oversized larvae, etc.) which suggests that additional larval stages may be an integral part of a decapod crustacean's larval potentiality in nature, and not just an artifact observed during laboratory culture of the species. Whether extra stages occur commonly, or only rarely, they are still classifiable as a response to change in conditions, and as such constitute an evolutionary adaptation toward survival.

## Description of the Larvae

### First Zoea

Carapace length: 0.38 mm; 5 specimens examined.

*Carapace* (Fig. 2A, a).—Smooth, globose, dorsal spine short, slightly curving posteriorly, rostral spine stout, bluntly rounded, ventrally directed; no lateral spines present in this stage. A mediodorsal knob (Fig. 2a) midway between bases of dorsal and rostral spines with 5 integumental sensilla arranged as illustrated, these present in all stages. Posterolateral margin of carapace indistinctly and irregularly dentate; ventrolateral margin produced into a blunt V-shaped process. Paired setae posterolaterally to base of dorsal spine in all stages. Eyes unstalked.

*Abdomen and Telson* (Fig. 2B).—Five somites; first naked, second, third, and fourth with paired lateral knobs (fourth smallest) directed anteriorly, ventrally, and laterally respectively, these also with bluntly rounded posterolateral process; fifth somite with bluntly rounded posterolateral process. Pair of posterodorsal setae on somites 2-5 in all stages. Telson rectangular with pair of short, minutely hairy, furcae, 6 spines in between, each armed with rows of spinules. Shallow median notch present.

*Antennule* (Fig. 2C).—Conical rod directed anteriorly, flanking rostral spine, with 4 aesthetascs of varying size.

*Antenna* (Fig. 2D).—Biramous; protopodite and exopodite spinelike processes approximately equal in length, both armed with 2 rows of spinules; exopodite with a simple seta one-third distance from base.

*Mandibles* (Fig. 2E).—Asymmetrically scoop-shaped process; incisor process with 1 large tooth anteriorly as well as posteriorly, 3 bluntly rounded denticles in between, plus 3 similarly on posterior edge of right mandible, 2 on left; molar process irregularly dentate, a large rounded tooth on the posterior angle.

*Maxillule* (Fig. 2F).—Endopodite 2-segmented, setal formula progressing distally 1,5 (4 terminal plus 1 subterminal); basal endite with 5 stout setae, coxal endite with 4 stout, 1 thinner seta. Additional pubescence as illustrated.

*Maxilla* (Fig. 2G).—Endopodite irregularly bilobed, each with 2 setae; basal and coxal endite bilobed, setal formula proximally to distally 5,4 and 4,3, respectively. Scaphognathite with 4 plumose setae on outer margin, distal portion tapering to setose apical process. Other pubescence as illustrated.

*Maxilliped 1* (Fig. 2H).—Coxopodite naked; basipodite with 9 ventral setae, progressing distally 2,2,3,2; endopodite 5-segmented, setal formula 2,2,1,2,4+I (Roman numeral = dorsal setae), third segment with several minute hairs on dorsal surface; exopodite indistinctly 2-segmented, 4 terminal natatory setae.

*Maxilliped 2* (Fig. 2I).—Coxopodite naked; basipodite with 4 ventral setae, progressing distally 1,1,1,1; endopodite 3-segmented, setal formula 0,1,5+I; exopodite indistinctly 2-segmented, 4 natatory setae.

*Color.*—Overall golden-brown under refracted light, abdomen colored more intensely than cephalothorax. Cornea black under refracted, iridescent blue under reflected light. Grouped brown and orange chromatophores appear as follows: carapace, 4 interocular, 1 at base of dorsal spine, 1 at position of posterodorsal knob, 2 at future position of lateral spines, 4 along posterior margin, 3 at posteroventral angle; appendages, 1 on mandibles, 1 each on antennular and antennal protopodites, 2 on each maxillipedal basipodite; abdomen, 1 pair ventromedially on first somite, second through fifth somites with 1 pair anteroventrally and 1 pair posteroventrally; telson with 1 pair anteriorly and 1 pair posteriorly at base of each set of 3 spines.

### Second Zoea

Carapace length: 0.50 mm; 5 specimens examined.

*Carapace* (Fig. 3A).—Enlarged, pair of ventrally curved lateral spines now present. Dorsal and rostral spines both elongated, thinner, ends more tapered than first stage. Pair of interocular and 1 posterolateral seta now present. Posterodorsal knob midway between base of dorsal spine and posterior edge of carapace more prominent. Eyes stalked.

*Abdomen and Telson* (Fig. 3B).—Similar in shape and armature to first stage with addition of single long dorsal seta on posteromedial edge of first somite.

*Antennule* (Fig. 3C).—As in first stage but with 6 unequal aesthetascs.

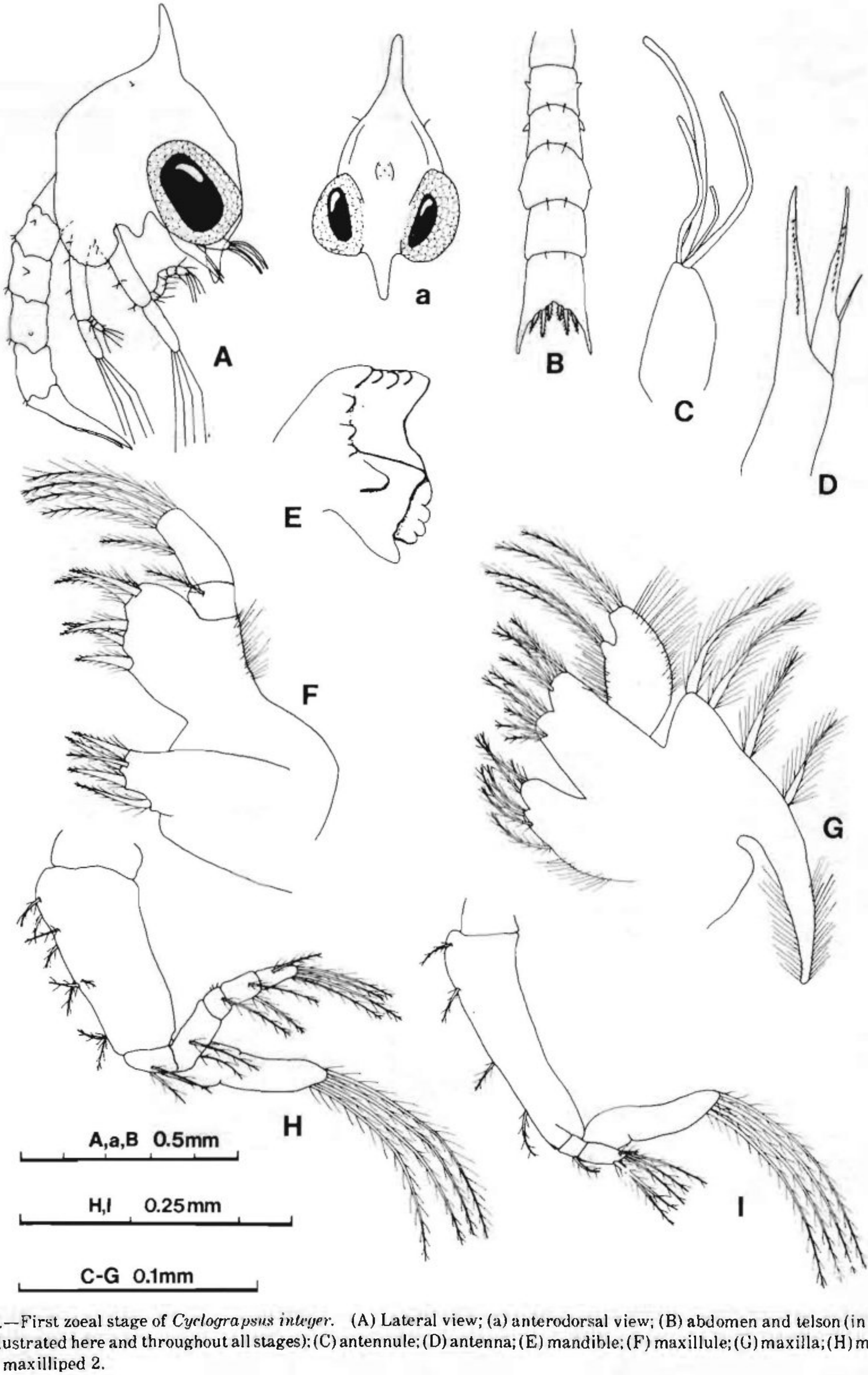


FIGURE 2.—First zoeal stage of *Cyclograpsus integer*. (A) Lateral view; (a) anterodorsal view; (B) abdomen and telson (in dorsal view as illustrated here and throughout all stages); (C) antennule; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2.

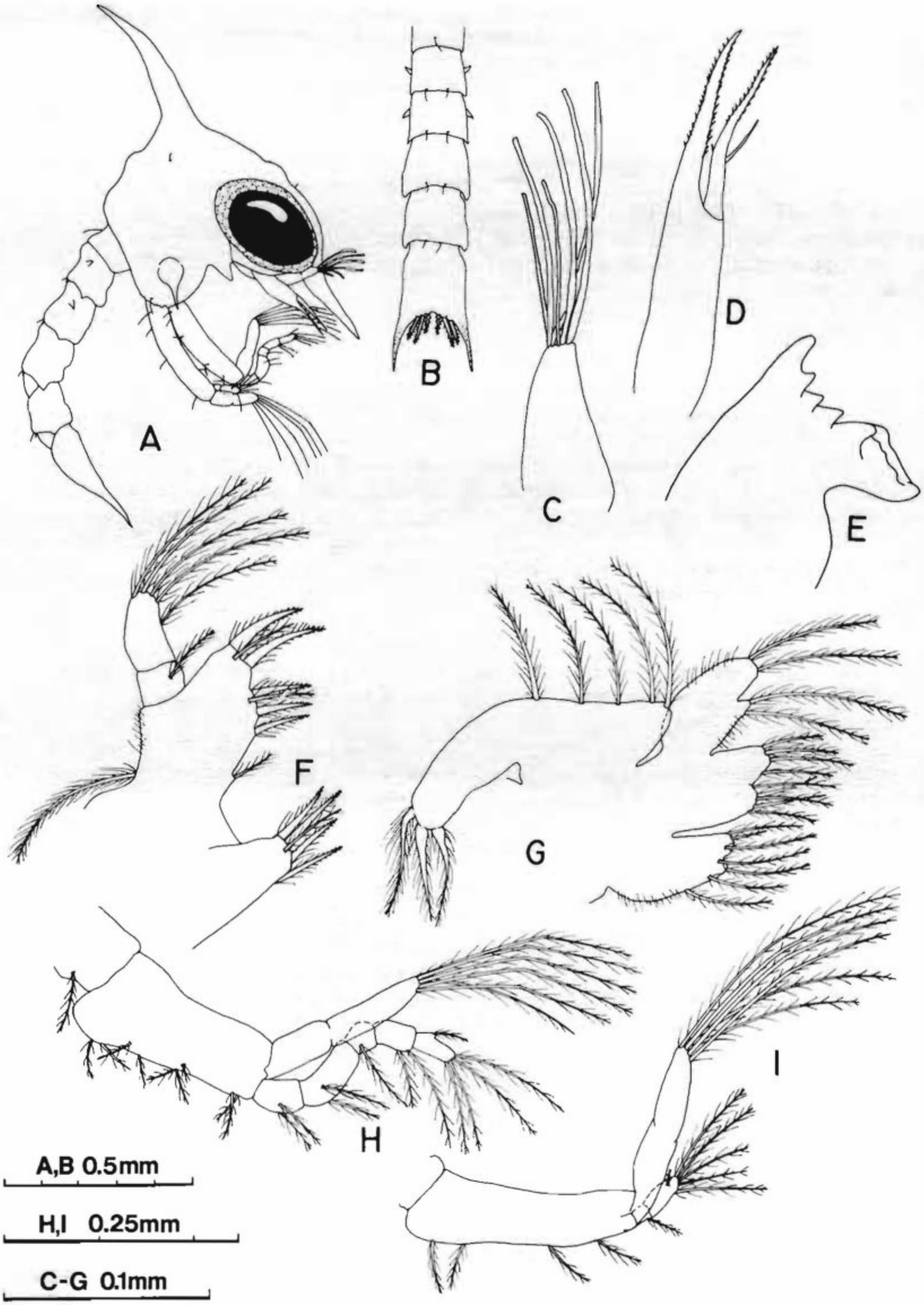


FIGURE 3.—Second zoeal stage of *Cyclograpsus integer*. (A) Lateral view; (B) abdomen and telson; (C) antennule; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2.

*Antenna* (Fig. 3D).—Similar in form and armature to first stage, with addition of minute hair on exopodite opposite of simple seta one-third from base.

*Mandible* (Fig. 3E).—Increased in size, shape and armature similar to first stage.

*Maxillule* (Fig. 3F).—Endopodite and coxal endite setation unchanged. Basal endite now with 5 stout, 3 thinner setae plus 1 long plumose seta on basal margin.

*Maxilla* (Fig. 3G).—Endopodite, basal, and coxal endite setation unchanged. Scaphognathite with 5 long, thin, plumose setae proximally, 3 stout plumose setae on distal margin.

*Maxilliped 1* (Fig. 3H).—Coxopodite with 1 ventral seta. Basi- and endopodite setation unchanged. Exopodite with 6 natatory setae.

*Maxilliped 2* (Fig. 3I).—Coxo-, basi-, and endopodite setation unchanged. Exopodite now with 6 natatory setae.

*Color.*—Overall darker golden brown than first stage. Color much more intense at dorsal spine, fifth somite, and telson. Lateral spines, rostrum, maxillipedal endo- and exopodites transparent. Deep golden hue around base of dorsal spine. Other chromatophore color and position as in first stage.

### Third Zoea

Carapace length: 0.70 mm; 5 specimens examined.

*Carapace* (Fig. 4A).—Zoea much enlarged, dorsal, rostral, and lateral spines elongate, 2 pair of interocular setae, posterodorsal knob more prominent, posterolateral margin now with 4 or 5 setae placed as illustrated, irregular denticulation ventral to setae present here and in all stages. Posterodorsal margin of carapace with 3 setae.

*Abdomen and Telson* (Fig. 4B).—Sixth abdominal somite now present, with small bluntly rounded posterolateral process. First somite with 3 dorsomedial setae, middle the longest. Paired lateral knobs on second and third somites enlarged, posterolateral processes on somites 2-5. Telson with interfurcal setal formula now 4+4, innermost pair the shortest.

*Antennule* (Fig. 4C).—Unchanged in form from second stage, with 4 unequal aesthetascs.

*Antenna* (Fig. 4D).—Similar to second stage, exopodite now slightly shorter than protopodite.

*Mandible* (Fig. 4E).—Similar in form and armature to second stage.

*Maxillule* (Fig. 4F).—Endopodite and basal endite armature unchanged, 1,5 and 8+1 processes basally, respectively. Coxal endite with 5 setae plus 1 long plumose seta on basal margin.

*Maxilla* (Fig. 4G).—Endopodite 2,2, as before, basal endites 5,4, coxal endites now 5,3. Scaphognathite setae increased to 10 thinner plus 6 stout distal setae, separated by sparse hairs as illustrated.

*Maxilliped 1* (Fig. 4H).—Coxo- and basipodite setation unchanged. Endopodite setal formula now 2,2,1 plus spine replacing dorsal setae, 2, 4+I. Exopodal natatory setae 8.

*Maxilliped 2* (Fig. 4I).—Coxo-, basi-, and endopodite setation unchanged. Exopodite with 8 natatory setae.

*Color.*—Now appearing ocherous orange. Dorsal spine, abdomen, and telson darkest. Lateral spine with orange coloration on ventral surface. Orange chromatophores: at base of rostral spine, another midway to tip; on 2 or 3 basipodite of maxillipeds. Sixth somite and telson each with pair of orange-brown chromatophores medioventrally. Other chromatophore pattern remains as in first stage.

### Fourth Zoea

Carapace length: 0.80 mm; 5 specimens examined.

*Carapace* (Fig. 5A).—Similar in form to third stage, elongate dorsal spine now with 5 setae on anterior margin as illustrated. Posterodorsal border now with 4 setae, posterolateral margin with 6. V-shaped process on ventrolateral margin less blunt than previous stages.

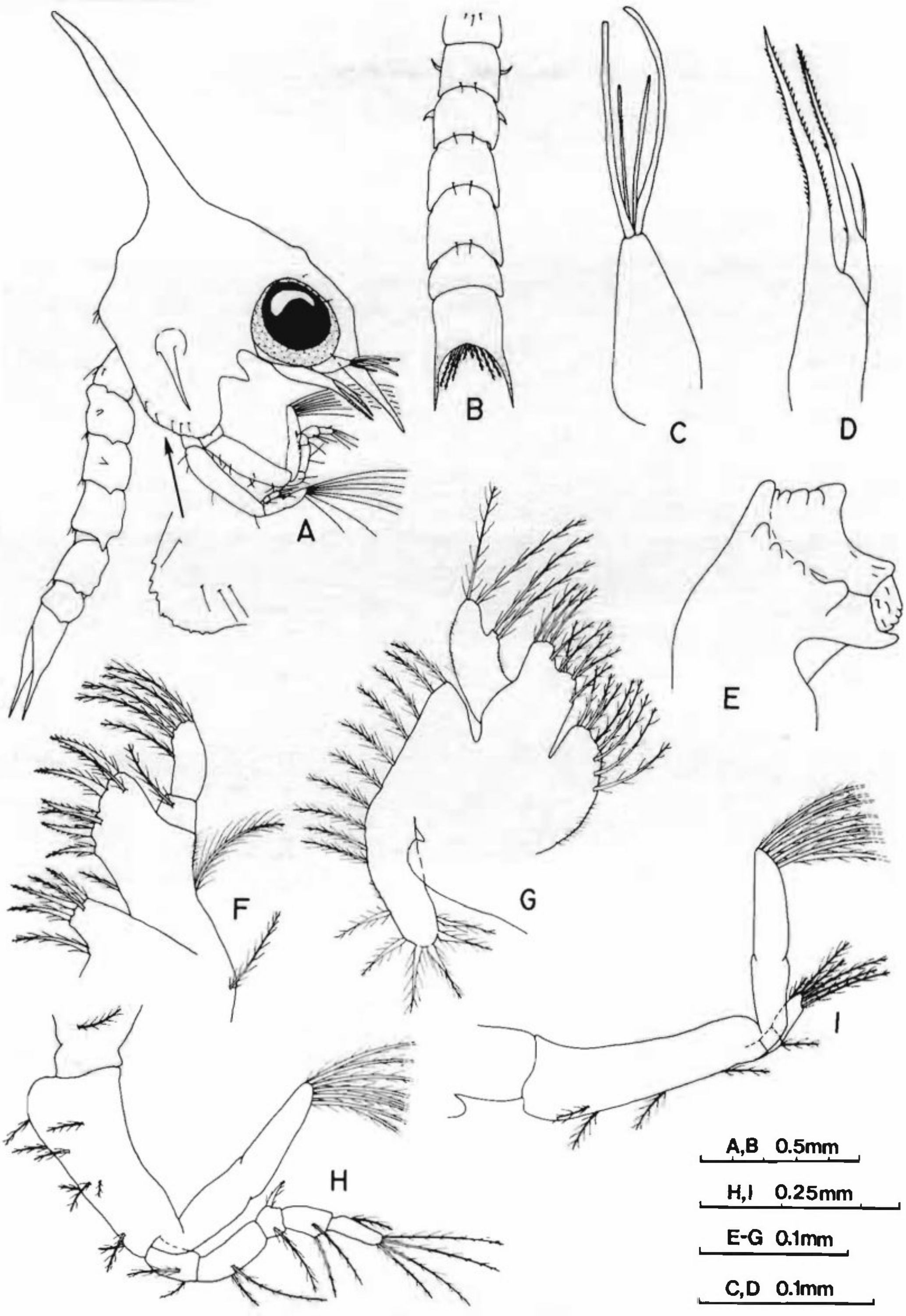


FIGURE 4.—Third zoeal stage of *Cyclograpsus integer*. (A) Lateral view; (B) abdomen and telson; (C) antennule; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2.

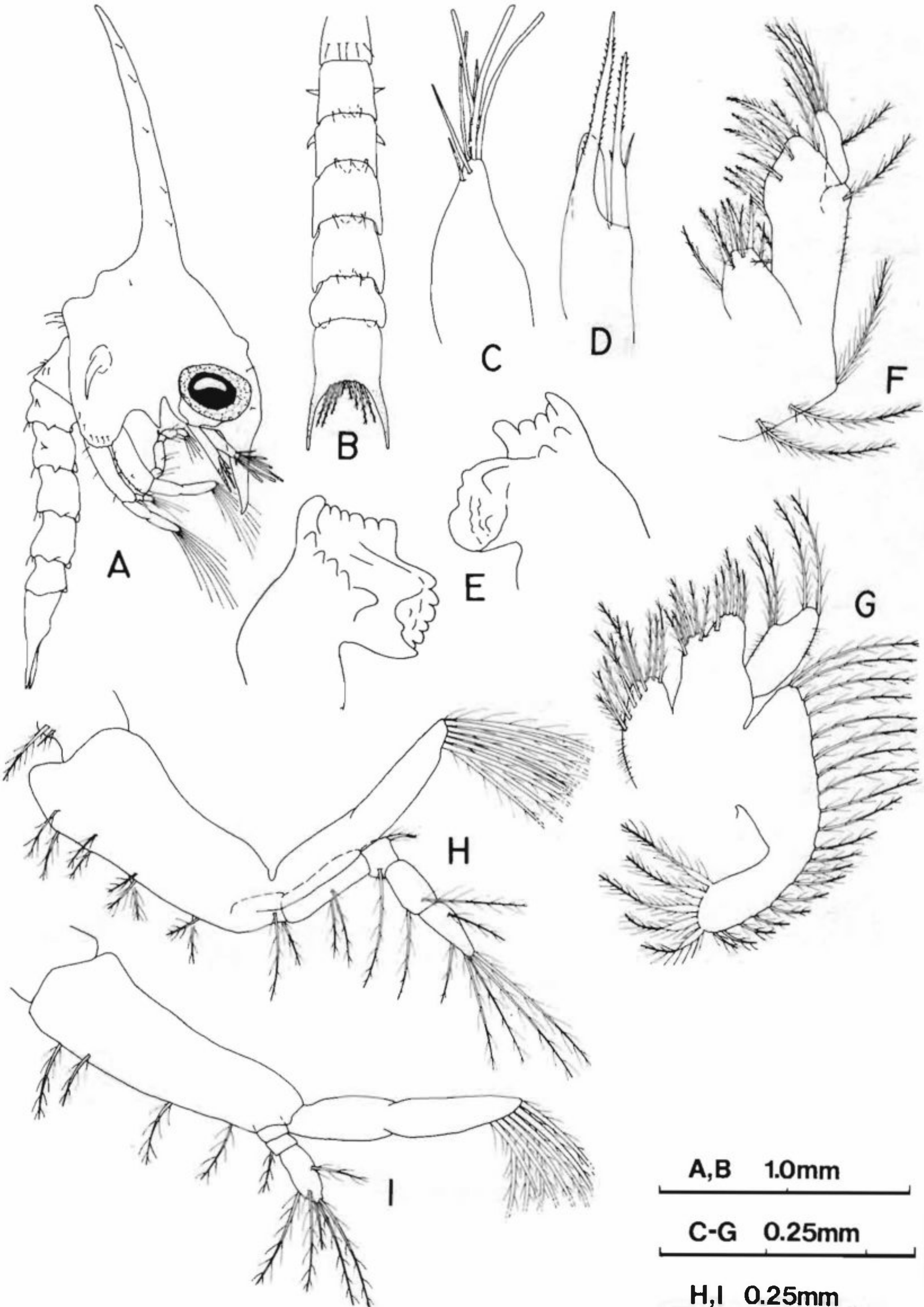


FIGURE 5.—Fourth zoeal stage of *Cyclograpsus integer*. (A) Lateral view; (B) abdomen and telson; (C) antennule; (D) antenna; (E) mandibles; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2.

*Abdomen and Telson* (Fig. 5B).—Pleopod and uropod buds now present on somites 2-5 and 6, respectively. First somite now with 5 middorsal setae.

*Antennule* (Fig. 5C).—Conical rod with 5 terminal plus 2 subterminal aesthetascs.

*Antenna* (Fig. 5D).—Armature and form similar to previous stage. Endopodal bud now present, less than one-half length of protopodal process.

*Mandible* (Fig. 5E).—Similar to third stage with addition of 1 bluntly rounded tooth on posterior edge of incisor process.

*Maxillule* (Fig. 5F).—Endopodite setation unchanged, basal endite now with 11 or 12 setae, coxal endite with 8 setae, 3-5 plumose setae on basal margin, placed as illustrated.

*Maxilla* (Fig. 5G).—Setal formulae on endopodite 2,2; basal endites 6,5; coxal endites 7,3. Scaphognathite with 17-21 thinner setae, plus 5 or 6 stouter distal setae.

*Maxilliped 1* (Fig. 5H).—Coxopodite now with 2 ventral setae. Basipodite setation unchanged. Endopodite now with 2,2,1 plus 1 spine, 2,5+I. Exopodal natatory setae 9.

*Maxilliped 2* (Fig. 5I).—Coxo-, basi-, and endopodal setation unchanged. Exopodite now with 9 natatory setae.

*Color.*—Ocherous orange; additional orange and brown chromatophores appear together as follows: 1 each posterior to eyestalks, 1 anteromedially on somites 2-4, a pair anteroventrally on somites 5 and 6, 1 anteroventral plus another medioventral pair on telson, and 1 each at base of lateral spine.

### Fifth Zoea (Ultimate)

Carapace length: 1.2 mm; 3 specimens examined.

*Carapace* (Fig. 6A).—Similar to previous stage, dorsal spine elongate, posterodorsal border with 4 setae, posterolateral margin with 8 setae.

*Abdomen and Telson* (Fig. 6B).—First somite with 6 or 7 middorsal setae, all other morphological features similar to fourth stage. Pleopod buds elongate, all now with endopodites.

*Antennule* (Fig. 6E).—Endopodal bud present laterally below 2 tiers of aesthetascs, 5 unequal terminal aesthetascs plus 1 seta, and 6 subterminal aesthetascs. Basal region swollen, unsegmented.

*Antenna* (Fig. 6F).—Endopodal bud now three-fourths length of protopodal process. Exopodal spine remains shorter than protopodite.

*Mandible* (Fig. 6I).—Palp bud present on anterior surface. Incisor and molar form and armature as in fourth stage.

*Maxillule* (Fig. 6J).—Endopodal setation unchanged. Basal endite with 15 or 16 setae, coxal endite with 10-13 setae, 3 additionally on basal margin.

*Maxilla* (Fig. 6K).—Endopodite unchanged. Setae of basal endites 8,8, coxal endites 11,4. Scaphognathite with 31-33 marginal setae.

*Maxilliped 1* (Fig. 6L).—Coxopodite now with 3 ventral setae. Basi- and endopodite setation unchanged. Exopodite now with 11 natatory setae.

*Maxilliped 2* (Fig. 6M).—Coxo-, basi-, and endopodal setation unchanged. Exopodite now with 12 natatory setae.

*Maxilliped 3* (Fig. 6N).—Rudimentary trilobed, unsegmented naked process.

*Color.*—Similar to previous stage. Numerous additional brown and orange chromatophores appear especially on anterior region of cephalothorax and sixth abdominal somite and telson. Tips of maxillipedal exopodites now with orange hue. On day before metamorphosis to megalopa, ultimate fifth stage zoea has very dark brown cephalothorax with innumerable spidery brown and orange chromatophores interspersed. Dorsal spine and abdomen vermilion. Coalesced orange and brown chromatophore occur posteriorly on the eyestalk.

### Fifth Zoea (Penultimate)

Carapace length: 1.1 mm; 3 specimens examined.

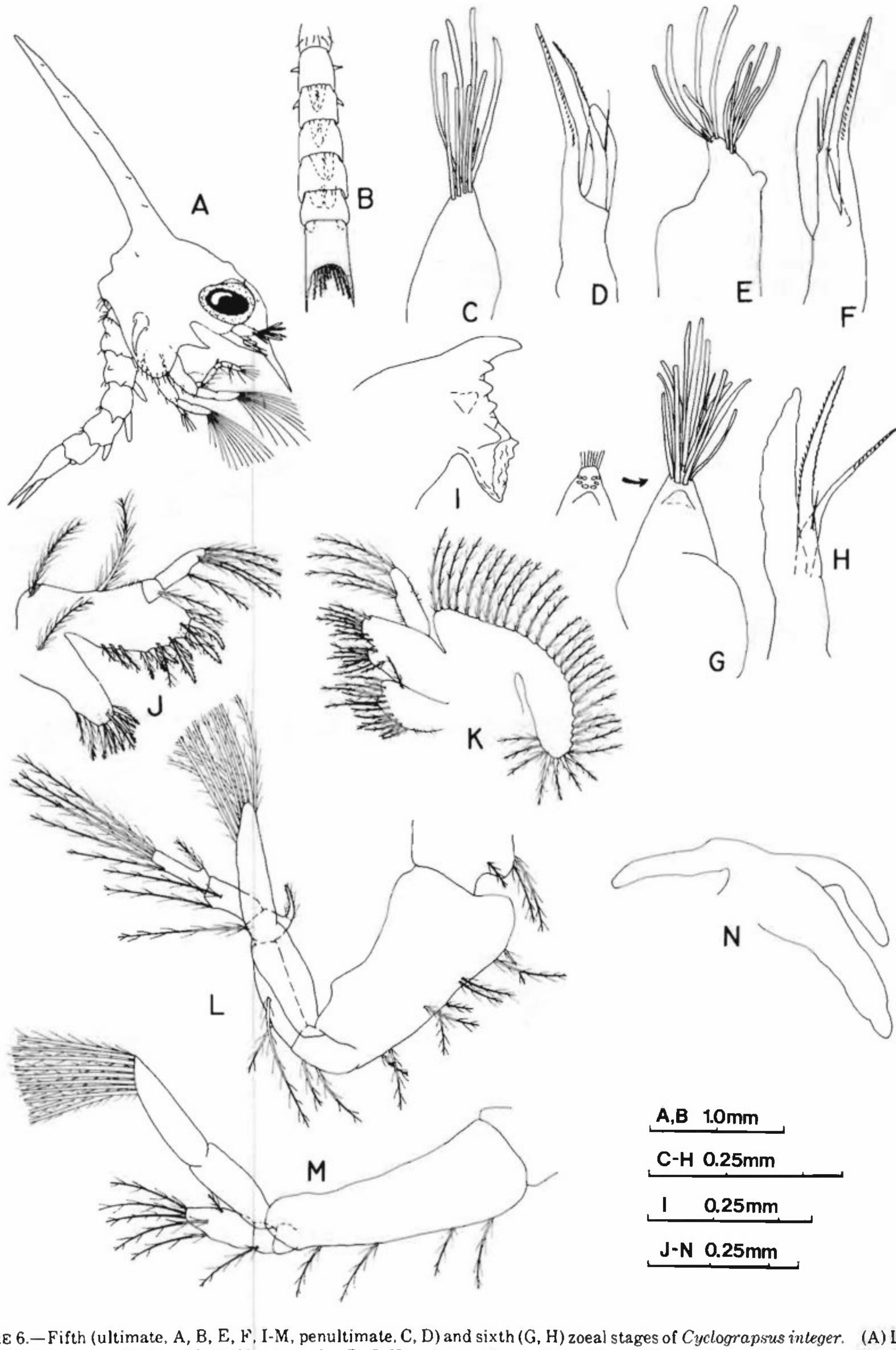


FIGURE 6.—Fifth (ultimate, A, B, E, F, I-M, penultimate, C, D) and sixth (G, H) zoeal stages of *Cyclograpsus integer*. (A) Lateral view; (B) abdomen and telson; (C, E, G) antennule; (D, F, H) antenna; (I) mandible; (J) maxillule; (K) maxilla; (L) maxilliped 1; (M) maxilliped 2; (N) maxilliped 3.

*Remarks.*—The penultimate fifth stage zoea molted to a sixth stage before metamorphosing to megalopa. Only morphological features differing significantly from the ultimate fifth stage, which molts directly to megalopa, are discussed below.

*Antennule* (Fig. 6C).—No endopodal bud present, 5 terminal plus 4 subterminal unequal aesthetascs present.

*Antenna* (Fig. 6D).—Endopodal bud only one-half length of protopodal process, other armature and processes similar.

*Mandible.*—No palp present, other armature similar.

*Abdomen.*—Pleopod buds without endopodites, less elongate and developed.

### Sixth Zoea

Carapace length: 1.3 mm; 3 specimens examined.

*Remarks.*—The sixth stage zoea appear similar in form and armature to the ultimate fifth stage. Only morphological characters which may be used to distinguish between the two stages are discussed below.

*Carapace.*—Little inflated, posterodorsal border with 6 setae.

*Abdomen and Telson.*—First somite with 8 or 9 middorsal setae, pleopod buds more elongate.

*Antennule* (Fig. 6G).—Aesthetascs arranged in tiers as illustrated, progressing distally 2,2,4,4.

*Antenna* (Fig. 6H).—Endopodal bud obscurely segmented, five-sixth length of protopodal process.

*Mandible.*—Palp more elongate.

*Maxillule.*—Basal endite with 18 setae, coxal endite with 12 setae, basal margin with 3 or 4 plumose setae.

*Maxilla.*—Basal endites with 9,8, coxal with 12,4 setal formulae. Scaphognathite with 34-37 marginal setae.

*Maxilliped 1.*—Coxopodite with 4 or 5 ventral setae. Basipodite setal formulae variable from 9 to 11 ventral setae, exopodite with 12 or 13 natatory setae.

*Maxilliped 2.*—Coxopodite naked or with 1 seta ventrally, endopodite setation variable either 0,1,5+I or 1,1,5+I. Exopodite with 13 or 14 natatory setae.

*Maxilliped 3.*—Trilobed as in fifth stage, may have 1 seta on each lobe.

*Color.*—Similar to fifth stage, innumerable spidery brown and orange chromatophores, entire maxillipeds now orange brown.

### Megalopa

Carapace length × width: 1.45 × 1.25 mm; 7 specimens examined.

*Remarks.*—Megalopae molting from both fifth and sixth zoeal stages are similar in form and armature. Morphological characters distinguishing megalopae, which molted from ZVI, are placed in brackets under the appropriate headings.

*Carapace* (Fig. 7A, B).—Cephalothorax subquadrate, laterally inflated. Smooth surface covered with hairs as illustrated, plus innumerable setae on posterior and posterolateral borders. Frontal region developed into ventrally deflexed, bluntly rounded rostrum with distinct median cleft, appearing as U-shaped sinus viewed dorsally. Anterolateral margins of carapace produced into 2 indistinctly rounded lobes. Eyes large, projecting laterally.

*Abdomen and Telson* (Fig. 7A, a, E-I).—Somites 1-5 with bluntly rounded posterolateral processes, somite 6 much broader than long; all with setae as illustrated; telson semicircular, no posterior marginal setae, 2 pairs medially, others as illustrated. Pleopods well developed, with variable setation 16-19, 20 or 21, 19-22, 22 [19-21, 21, 22, 22], all endopods with 3 hooked setae terminally. Uropods with 10 or 11 exopodal plus 1 protopodal seta [11 or 12 plus 1].

*Pereopods* (Fig. 7A, C, D).—Chelipeds well developed, somewhat inflated, unarmed, equal, shorter than walking legs, gape of chelae irregularly serrated, setae on remaining articles as

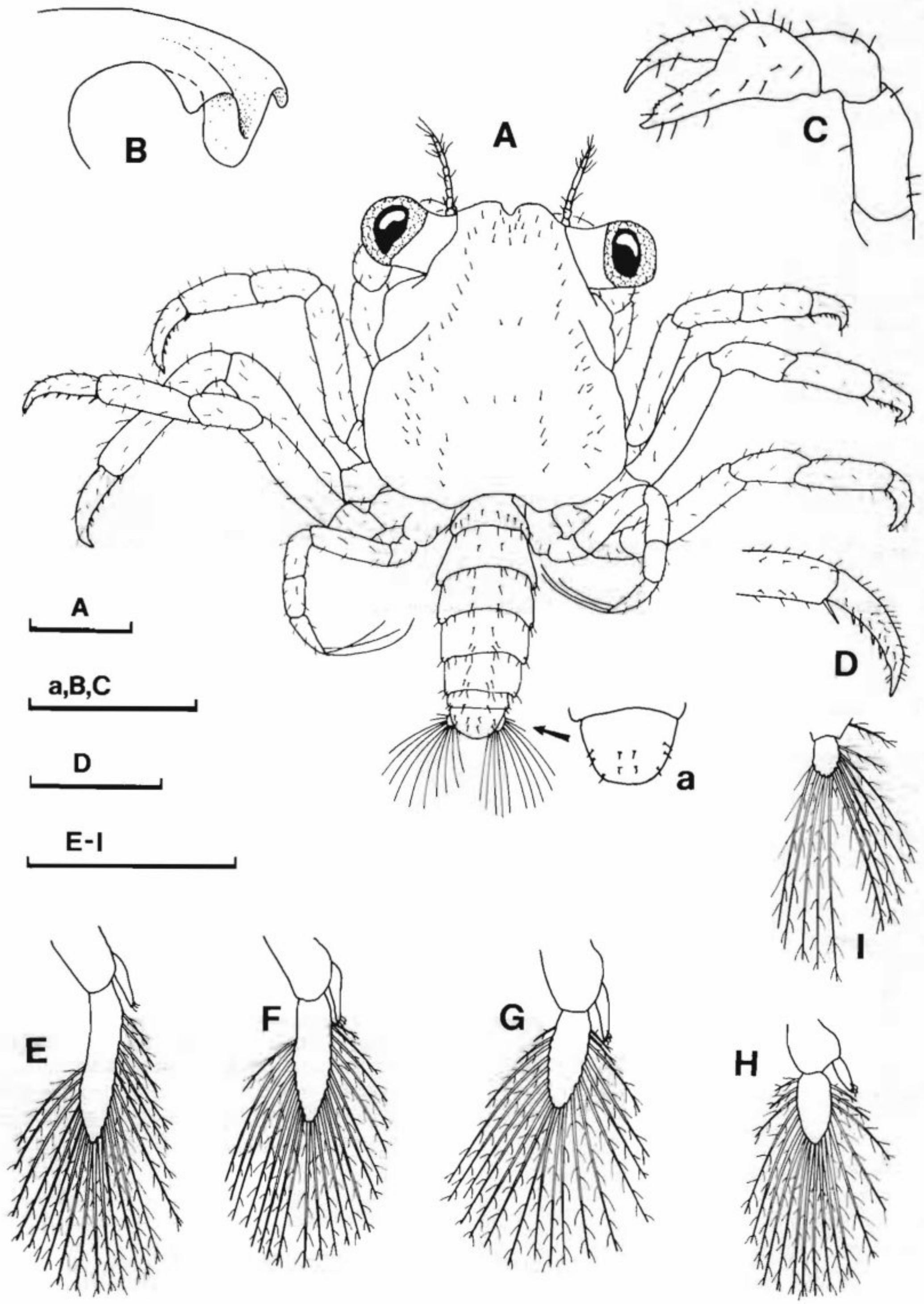


FIGURE 7.—Megalopa stage of *Cyclograpsus integer*. (A) Dorsal view; (a) telson; (B) rostrum (anterolateral view); (C) left cheliped; (D) second pereopod dactyl; (E) first pleopod; (F) second pleopod; (G) third pleopod; (H) fourth pleopod; (I) uropod. Scale lines = 0.5 mm.

illustrated. Second to fourth pereopods elongate, similar, each with distoventral tooth on propodus and 4 ventral teeth on dactyl. Fifth pereopod dactyl with 3 [3 or 4] long pectinate setae (= brachyuran feelers).

*Antennule* (Fig. 8A).—Biramous, peduncle 3-segmented, extremely enlarged, bulbous basal segment with 2 or 3 [3-5] setae, middle segment much smaller ovoid, with 2 or 3 [3 or 4] setae, distal segment larger than middle, expanded distally, naked. Flagellar lower ramus 1-segmented, 3 terminal, 1 subterminal setae; upper ramus 4-segmented, tiered aesthetascs usually arranged (0)(6), (6, plus 1 lateral seta), (5, plus 1 terminal seta).

*Antenna* (Fig. 8B).—Peduncle with 2-4 distal setae; flagella with setation 1,2,0,0,2-3, 0,5,3,3, [1,2,0,0,4,0,4-5,3,3-4].

*Mandible* (Fig. 8C).—Incisor process smooth, spatulate; molar process elongate, tubular; palp 2-segmented with 0,9 setae.

*Maxillule* (Fig. 8D).—Endopodite irregularly shaped, with 4 distal, 2 or 3 lateral setae; basal endite with 12 spines, 12-14 setae [25-29], coxal endite with 8 spines plus 2 rows of about 9 or 10 processes each [32] arranged in tiers as illustrated. Basal margin with 4 [3-5] long setae.

*Maxilla* (Fig. 8E).—Endopodite unsegmented, 2 [3] setae on lower lateral margin. Basal endites with 9-11, 12-14, [10-12, 13-16] processes, coxal endites with 7, 18-20 [8 or 9, 20-22] processes. Scaphognathite with 61-62 marginal setae plus 5 laterally on the blade as shown [70-72 plus 5].

*Maxilliped 1* (Fig. 8F).—Exopodite 2-segmented, with 2 distal, 4 terminal setae. Endopodite irregularly shaped, unsegmented, 4-8 setae scattered over length. Basal endite with 13-17 [15-17], coxal endite with 17-20, setae. Epipodite with 9 or 10 [13-18] long, aesthetascoid processes.

*Maxilliped 2* (Fig. 8G).—Exopodite 2-segmented, 2 lateral, 4 terminal setae. Endopodite 5-segmented setation progressing distally 3-7, 1, 1, 3 or 4, 6 or 7. Epipodite with 4-7 distal, 1 proximal, aesthetascoid processes, [9-11, plus 1]. Protopodite setae not determined.

*Maxilliped 3* (Fig. 8H).—Exopodite 2-segmented with 5 or 6 proximal, 4 or 5 terminal setae; endopodite 5-segmented setae progressing distally 16-18, 12 or 13, 8-10, 10 or 11, 6 or 7 [18-20, 13, 8-12, 9-12, 8], protopodite with 21 or 22 [22-26] setae, epipodite with 21-26 aesthetascoid processes distally plus 8 or 9 setae proximally [30-32, plus 8-11].

*Color.*—Innumerable spidery orange and brown chromatophores completely covering cephalothorax, abdomen, pereopods, eyestalks, and all feeding appendages.

## DISCUSSION

### Zoeal Stages

The complete larval development of <20% of the known species of *Cyclograpsus* has been studied, and zoeal stages within the genus will be difficult to identify in the plankton. Larvae of the genus are unusual in several respects; therefore, some morphological and developmental characters may yet prove to be of aid in identification. For example, in at least two species (*C. integer* and *C. cinereus*) lateral carapace spines are lacking in the first stage, but appear in all later stages (Costlow and Fagetti 1967). Within the genus, some form of armature occurs on the ventrolateral carapace margin, either as spines, small teeth, setae, or a combination of these. In general, teeth or spines occur in the early stages and are replaced by setae as development proceeds. The number and time of appearance of these processes seems to be species specific (Table 2; and summary in Fagetti and Campodonico 1971). In addition to the ventrolateral processes, later larval stages of all species of *Cyclograpsus* studied to date bear some form of setation of spination on the posterior middorsal margin of the carapace above the insertion of the abdomen. In *C. cinereus*, this takes the form of paired spines in the second and subsequent zoeal stages (Costlow and Fagetti 1967); in *C. punctatus*, a similar situation appears in the third and later stages (Fagetti and Campodonico 1971), whereas in *C. integer*, 3 setae appear in the third and subsequent stages.

Unfortunately, the characters noted above are not restricted to *Cyclograpsus* but are shared, at least in part, among zoeae of several other genera in the four grapsid subfamilies. For instance, several genera in the Grapsinae, Varuninae, and Sesarminae have zoeal stages which lack lateral


FIGURE 8.—Megalopa stage of *Cyclograpsus integer*. (A) Antennule; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3.

TABLE 2.—Comparison of selected zoeal characters in five species of *Cyclograpsus*.

| Species | Carapace spines: Dorsal | Carapace spines: Lateral | Ventro-lateral | Appendages antennule | Antennae (exopod) | Maxilliped 1: Basipod | Maxilliped 1: Endopod | Maxilliped 2: Basipod | Maxilliped 2: Endopod | Abdomen/ (telson) armeture |
|---|---|---|---|---|---|---|---|---|---|---|
| *C. cinereus* (Costlow and Fagetti 1967) | | | | | | | | | | |
| Zoea I | Gibbose | Absent | 8 spines | 2 aesth., 2 setae | Protopod 1.3× exopod (1 lat. spine) | [1]1,2,3,3 | 2,1,1,2,4+I | 1,1,1,1 | 0,1,1+3+I | Somite 2 spined; (t+3) |
| Zoea II | Curved | Present | 6 spines, 6 setae | 4 aesth. | Protopod 1.5× exopod | [1]1,2,3,3 | 2,2,1,2,4+I | 1,1,1,1 | 0,1,1+3+I | Somite 2 spined: (t+3) |
| Zoea III | Curved | Present | 5 spines, 10 setae | 4 aesth. | Protopod 1.5× exopod | [1]2,1,3,3 | 2,2,1+t,2,4+I | 1,1,1,1 | [1]0,1,2+3+I | Somite 2 spined: (I+4) |
| Zoea IV | Nearly straight | Present | 4 spines, 14 setae | 5+1 aesth. | Protopod 1.6× exopod (1.4× endopod) | [1]1,1,3,3 | 2,2,2,2,1+4+I | 1,1,1,1 | [1]0,1,2+3+I | Somite 1 with 5 dorsal spines |
| Zoea V | Straight | Present | 10 spinules, 18 setae | 5+4 aesth., 2 lateral setae | Protopod 1.8× exopod (0.7× endopod) | [1]4,2,3,2? | 2,1+II,1+I, 1+I,1+4+I | 1,1,1,1 | 0,1,1+3+It | Somite 1 with 5 dorsel spines |
| *C. punctetus* (Fagetti and Campodonico 1971) | | | | | | | | | | |
| Zoea I | Curved | Present | 12 spines | 2 aesth., 2 setae | Protopod 1.25× exopod (2 lat. spines) | 2,2,3,3 | 2,2,1,2,4+I | 1,1,1,1 | 0,1,2+3+I | Somites 2,3 spined; (I+3) |
| Zoea II | Nearly straight | Present | 2 setae | 4 aesth. | Protopod 1.5× exopod | 2,2,3,3 | 2,2,1,2,4+I | 1,1,1,1 | 0,2,2+3+I | Somites 2,3 spined; (I+3) |
| Zoea III | Nearly straight | Present | 11 setae | 5 aesth. | Protopod 1.4× exopod | 2,2,3,3 | 2,2,1+I,2, 1+4+I | 1,1,1,1 | 0,1,2+3+I | Somite 1 with 3 setae; (I+4) |
| Zoea IV | Nearly straight | Present | 12 setae | 6+1 aesth. | Protopod 1.1× exopod (2.9× endopod) | 2,2,3,3 | 2,2,1+I,2, 1+4+I | 1,1,1,1 | 0,1,2+3+I | Somite 1 with 3 setae; (I+4) |
| Zoea V | Nearly straight | Present | 15 setae | 4+4 aesth., 1 lateral | Protopod 1.23× exopod (1.4× endopod) | 2,2,3,4 | 2,2,1+I,2, 1+4+I | 1,1,1,1 | 0,1,2+3+I | Somite 1 with 3 setae; (I+5) |
| *C. integer* | | | | | | | | | | |
| Zoea I | Slightly curved | Absent | Irregularly dentate | 4 aesth. | Protopod ≅ exopod (1 lat. seta) | 2,2,3,2 | 2,2,1,2,4+I | 1,1,1,1 | 0,1,2+3+I | Somites 2-4 with knobs (I+3) |
| Zoea II | Slightly curved | Present | 1 seta | 6 aesth. | Protopod ≅ exopod (1 lat. seta) | 2,2,3,2 | 2,2,1,2,4+I | 1,1,1,1 | 0,1,2+3+I | Somites 2,3 with knobs |
| Zoea III | Nearly straight | Present | 5 setae | 4 aesth. | Protopod ⪷ exopod | 2,2,3,2 | 2,2,1+I,2,4+I | 1,1,1,1 | 0,1,2+3+I | Somites 2,3 with knobs (I+4) |
| Zoea IV | Sparsely setose | Present | 6 setae | 5+2 aesth. | Protopod 1.2× exopod (1.9× endopod) | 2,2,3,2 | 2,2,1+I,2, 1+4+I | 1,1,1,1 | 0,1,2+3+I | Somites 2,3 with knobs (I+4) |
| Zoea V (U) | Sparsely setose | Present | 8 setae | 5+6 aesth., 1 lateral seta | Protopod 1.07× exopod (1.18× endopod) | 2,2,3,2 | 2,2,1+I,2, 1+4+I | 1,1,1,1 | 0,1,2+3+I | Somites 2,3 with knobs (I+4) |
| Zoea V (P) | Sparsely setose | Present | 8 setae | 5+6 aesth. | Protopod 1.05× exopod (1.75× endopod) | 2,2,3,2 | 2,2,1+I,2, 1+4+I | 1,1,1,1 | 0,1,2+3+I | Somites 2,3 with knobs (I+4) |
| Zoee VI | Sparsely setose | Present | 8 setae | 2,2,4,4 aesth. | Protopod 1.18× exopod (= endopod) | 9-11 setae (variable) | 2,2,1+I,2, 1+4+I | 1,1,1,1 | 0,1,2+3+I or 1,1,2+3+I | Somites 2,3 with knobs (I+4) |
| *C. levauxi* (Wear 1970) | | | | | | | | | | |
| Zoea I | Slightly sigmoid | Present | ca. 7 setae | 3 aesth. | Protopod 1.3× exopod (3 lat. setae) | [1]2+1,1,1,1 | 1,2,1,2,4+I | 1,1,1,1 | 0,1,2+3+I | Somites 2,3 with knobs (I+3) |
| *C. insularum* (Weer 1970) | | | | | | | | | | |
| Zoea I | Slightly curved | Present | ca. 20 small teeth | 4 aesth. | Protopod 1.5× exopod (3 lat. setae) | 3,3,3,3 | 2,2,1,2,4+I | 1,1,1,1 | 0,2,2+3+I | Somites 2-4 spined; (I+3) |

[1]Data interpolated from illustrations.

carapace spines. No first stage grapsine zoeae, no *Sesarma* (Sesarminae), nor *Acmaeopleura* (or possible *Gaetice*) larvae in the Varuninae have these spines (see summary in Wilson 1980). Moreover, *Pachygrapsus* zoeae (Grapsinae), like some larvae in *Cyclograpsus*, apparently lack lateral spines in the first, but possess these in subsequent, zoeal stages (Schlotterbeck 1976; Bourdillon-Casanova 1960). On the other hand, all known plagusiine larvae have lateral spines from the first stage onward (Wilson 1980).

Setation or spination on the ventrolateral carapace margin is another widely shared feature among grapsid genera. Examples include *Brachynotus* (Bourdillon-Casanova 1960), *Hemigrapsus* (Kurata 1968), and *Cyrtograpsus* (Scelzo and Lichtschein de Bastida 1979) in the Varuninae, *Sesarma* (Baba and Miyata 1971) in the Sesarminae, *Leptograpsus* (Wear 1970) in the Grapsinae, and *Plagusia* (Wilson and Gore 1980) in the Plagusiinae. In many instances, however, carapace and telson spine formulae differ substantially from that seen in larvae of *Cyclograpsus*, thereby allowing at least provisional separation among these zoeae.

Regarding middorsal carapace setation, many descriptions of brachyuran larvae either fail to note its occurrence or do not allow judgment to be made because of undetailed illustrations. A general perusal of the literature available on grapsid larvae (Wilson 1980) shows that, in addition to *Cyclograpsus*, only a few sesarmine genera had this feature indicated, including *Chasmagnathus* (Boschi et al. 1967), *Helice* (Baba and Moriyama 1972), and in the Varuninae *Hemigrapsus* (Hart 1935) and *Cyrtograpsus* (Scelzo and Lichtschein de Bastida 1979). Several other studies provide suitably detailed illustrations which suggest that this character may be more or less widespread among the zoeae of these subfamilies. However, these setae are apparently absent in plagusiine and grapsine larvae, as far as can be ascertained from the literature. Because these setae usually do not appear until later zoeal stages (ZIII and beyond) their usefulness as an identifying character is somewhat limited.

One other carapace feature that seems noteworthy, at least for the genus *Cyclograpsus*, is the pterygostomian region of *C. integer*; this region is produced into a triangular, toothlike prominence in the first stage, which becomes more sharply pronounced as development proceeds. In *C. cinereus*, this prominence is always bluntly rounded until the last stage, when it becomes more acute. In *C. punctatus* the prominence develops very slowly and apparently never becomes acute. Only the first zoeal stages are known in *C. lavauxi* and *C. insularum* (Wear 1970) and the prominence is not well developed in either, being similar to that seen in *C. punctatus*. Although the toothlike prominence is seen to some extent in other grapsid zoeae, it does not appear to be quite as prominent, based on the illustrations provided in several studies.

The type of antenna has always been considered an important classification feature in brachyuran larvae (Aikawa 1929). Most brachyuran larvae have a type B antenna (i.e., exopod about 0.5-0.75× the length of the protopodal spine). This type is widely present throughout the Grapsidae, being found predominantly in the Sesarminae and Varuninae, but seen in only isolated instances in either the Grapsinae or Plagusiinae. Nearly all Grapsinae have a type C antenna (exopod substantially reduced in size to the protopodal spine), an advanced character also shared for the most part among the known larvae of plagusiine genera (see summary in Wilson 1980).

All *Cyclograpsus* larvae possess a type B antenna, with the exception of *C. integer*, which has a type A antenna (exopod and protopod about equal). The type A antenna is considered to be primitive (Aikawa 1929). The larvae of *C. integer* are even more remarkable in having the antennal protopodal spine and exopod both armed along their respective lengths with rows of teeth, in a manner similar to that seen in *Eriocheir* zoeae (Varuninae; Aikawa 1929), and reminiscent of some antennae exhibited by larvae in several xanthid genera (e.g., Scotto 1979). In other *Cyclograpsus* zoeae, the exopod is entire, and only the protopodal spine is so armed. *Cyclograpsus integer* is thus noteworthy for two exceptions: 1) an antenna of a form (i.e., doubly armed) rarely noted within the Grapsidae, and 2) an antenna type (A) found in no other zoeae of any genus in the Grapsidae.

Rice (1980) summarized the available knowledge on the Grapsidae in a major paper dealing with brachyuran zoeal classification. In attempting to delineate useful features among the four subfamilies of grapsid crabs, he suggested that the known zoeae of the Varuninae and Sesarminae might be distinguished from the Grapsinae and Plagusiinae by always having a well-developed antennal exopod at least half as long as the spinous (protopodal) process (i.e., type B) and bearing at least 10 medial setae on the basis of the first maxilliped. Wilson (1980) subsequently demonstrated that *Euchirograpsus* larvae (Varuninae) have extremely shortened antennal exopods (type C) plus only 8 basipodal setae, and therefore are more allied to Grapsinae and Plagusiinae larvae than to those of the Sesarminae or other Varuninae. As noted above, *C. integer* also refute Rice's suggestion in regard to the Sesarminae, by having a type A antenna and by bearing 9 (instead of 10) basipodal setae. Larvae of *C. cinereus* also have 9 basipodal setae on maxilliped 1, but these occur in a grouping different from that seen in *C. integer*; *C. lavauxi* larvae have 6 and *C. insularum* have 12 setae (Table 2).

As to other features for distinguishing among the larvae of *Cyclograpsus*, setation and armature of abdominal somites can be useful. Beginning with the second (*C. integer*), third (*C. cinereus*), or fourth zoeal stage (*C. punctatus*), nonpaired, usually elongate or spinelike setae are found on the posterodorsal margin of the first abdominal somite. As development proceeds these setae either increase in number (1, 3, 5, in *C. integer* stages), or remain unchanged (3, *C. punctatus*; 5, *C. cinereus*). Somite armature shows similar diversity, with a hooklike spine or knob on the second (*C. cinereus*), second and third (*C. punctatus*, *C. lavauxi*), or second through fourth somites (*C. integer*, *C. insularum* first zoea). Regrettably, neither of these characters are specific for *Cyclograpsus* larvae because they occur in other brachyuran zoeae and are seen, for example, in the Goneplacidae (*Carcinoplax*, Lee and Hong 1970; *Tritodynamia*, Boucquet 1965), as well as several other families less closely related to the Grapsidae (Lebour 1928, fig. 5, p. 483).

The telsons in *Cyclograpsus* zoeae all seem referrable to Aikawa's (1929) type B (i.e., without supernumerary lateral spines, and typically brachyuran in shape). The telson formula of I+3 (= furcal spine, plus movable spiny seta; Gore 1979) changes in stage III to I+4 in *C. integer*, *C. cinereus*, and *C. punctatus*; the latter species, however, adds an additional medial pair of setae in stage V, becoming I+5. Table 2 provides a summary of all of these features.

## Megalopal Stage

The megalopae of the three *Cyclograpsus* species in which complete development is known differ substantially from one another and should prove more easily separable than their respective larvae. The frontal region bears a strongly deflexed rostral spine in *C. punctatus* (Fagetti and Campodonico 1971), has a ventrally deflexed, bluntly rounded rostrum with a median cleft in *C. integer*, and is only slightly produced and without a rostral spine in *C. cinereus* (Costlow and Fagetti 1967). Other easily observed characters not requiring dissection include terminal setation on the telson, aesthetascs on the antennule, exopodal setae of the third maxillipeds, pleopods, and uropods. These, plus characters requiring some dissection to observe, are summarized in Table 3.

None of the megalopal stages in any of the three species considered resembles the juvenile or adult crabs. Moreover, they do not exhibit easily noticeable differences from many other brachyuran megalopae, let alone grapsid megalopae. In general, lack of rostral spines, or with the rostrum only poorly developed, usually deflexed, and unarmed, is seen in many grapsid postlarvae. Many of the species have the lower ramus of the antennule appearing as a 1-segmented, simple, palplike process (as in *Chasmagnathus*, *Helice*, *Cyrtograpsus*, and others, Costlow and Fagetti 1967), or even reduced to a simple seta (*Sesarma*; Costlow and Bookhout 1962). But because of the paucity of descriptions there is little use in attempting further classification at this time.

In the discussion above we have demonstrated that several suggestions proposed by Rice (1980) for classifying grapsid larvae can no longer be considered useful. Although the distinctions among the larvae of the subfamilies Grapsinae and Varuninae, and Varuninae and Sesarminae have become blurred, we nonetheless reiterate the value of Rice's classification attempt, and draw special attention to his key to the brachyuran families based on zoeal characters. By using the characters he proposed, one may still arrive within the Grapsidae using the key, provided that the subfamilial headings are disregarded. Rice's couplet 26 may then be modified to read as follows:

26. Carapace without lateral spines in *all zoeal stages* .......................... 27
    Carapace *usually* with lateral spines *in all zoeal stages or without only* in first zoeal stage .......................... 28

TABLE 3.—Comparison of selected megalopal characters in three species of *Cyclograpsus*.

| | *C. integer* | *C. cinereus* | *C. punctatus* |
|---|---|---|---|
| Cephalothorax | Numerous hairs dorsally | Dorsally naked[1] | Dorsally naked[1] |
| Front | Bluntly rounded, ventrally deflexed medially cleft rostrum | Slightly produced, without rostral spine | Strongly deflexed rostral spine |
| Telson processes | 0 terminal, 3 lateral, 2 pairs dorsally | 3 terminal, 3 lateral, 2 pairs dorsally | 9 terminal, 8 dorsal (6 transversely) |
| Antennular aesthetascs | (0)(6)(6,+1 seta) (5,+1 seta) | (0)(3)(4,+1 seta)(5) | (0)(4)(4,+2 setae) (4,+3 setae) |
| Antennal flagella | 9 articles | 11 articles | 9 articles |
| Mandibular palp | 0,9 setae | 0,9 setae | 0,7 setae |
| Maxillule | | | |
| Basipod | 24-26 processes [25-29] | 21 processes | ca. 24 processes |
| Coxopod | 28-30 processes [32] | 11 processes | 16 processes |
| Basal margin | 4 setae [3-5] | No data | 2 setae |
| Maxilla | | | |
| Endopod | 0, +2 lateral setae | 2, +1 lateral setae | 1, 1+4 lateral setae |
| Scaphognathite | 61-62 marginal setae [70-72] | ca. 70 marginal setae | ca. 65 marginal setae |
| Maxilliped 3 | | | |
| Exopod | 5-6 proximal, 4-5 distal setae | 3 proximal, 5 distal setae[1] | 2 proximal, 5 distal setae[1] |
| Pleopods | | | |
| Exopod setae | 16-22 [19-22] | 17-20 | 15-16 |
| Uropod setae | 1 protopodal, 10-11 exopodal [11-12] | 1 protopodal, 10 exopodal | 1 protopodal, 8 exopodal |

[1]Data interpolated from illustrations; no specific description given [ ] = megalopal stage obtained from zoeal stage VI.

We look to future studies that will provide descriptions of several common genera in the Grapsinae (e.g., *Geograpsus*, *Goniopsis*), Sesarminae (*Metapograpsus*), as well as to additional studies on larvae of previously known genera in the Plagusiinae (*Plagusia*, *Percnon*), and Varuninae (*Euchirograpsus*, *Cyrtograpsus*, and the as yet unknown zoeae of *Glyptograpsus*). All have the potential for providing further clarification of relationships among the Grapsidae.

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