LARVAL DEVELOPMENT OF *HYPOCONCHA SABULOSA* (DECAPODA: DROMIIDAE)[1]

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ABSTRACT

Larval development of the dromiid crab, *Hypoconcha sabulosa*, consists of three zoeal stages and one megalopa. The zoea exhibit numerous characteristics normally associated with anomuran larvae.

Hypoconcha sabulosa (Herbst) is a relatively uncommon inhabitant of coastal waters from North Carolina to the coast of Texas. Another member of the genus, *H. arcuata* Stimpson, coexists throughout much of the range (Williams 1965). These crabs are frequently overlooked owing to their habit of carrying an empty clam shell on their back. Kircher (1970) described the laboratory-reared larval stages of *H. arcuata* the larval stages of *H. sabulosa* are undescribed.

The family Dromiidae is an enigmatic group which has remained a point of contention in the phylogeny of the Decapoda. It has often been suggested that the brachyurans are a monophyletic group and that the dromiids represent a primitive true crab (Balss and Gruner 1961; Glaessner 1969; Stevcic 1974; Warner 1977). However, it is also strongly argued that the brachyurans are polyphyletic and that the dromiids are more closely related to anomuran or thalassinid groups (Gurney 1942; Williamson 1974).

METHODS

On 14 June 1976, a single gravid *H. sabulosa* female was collected by dredging in the North Inlet estuary, near Georgetown, S.C. Water temperature at the time of collection was 24° C; salinity was 27‰. The female was returned to the Baruch Laboratory, Columbia, S.C., and placed in a 9 cm Carolina culture dish containing filtered natural seawater of 25‰ salinity and maintained at 25° C under a 14L:10D light schedule. On 21 June, the brood began hatching and 22 active larvae were placed individually in 6 cm dishes containing 15 ml filtered seawater (25‰) and maintained as described for the adult. Water was changed daily and freshly hatched brine shrimp nauplii (San Francisco Bay Brand[4]) were added as food following each water change. Additional larvae hatching during the following day were reared in a 1 l shallow glass dish under similar conditions. These larvae were sacrificed during development to provide replicate material for descriptions.

Records were kept for each of the 22 larvae individually cultured to determine the number and duration of larval stages. Exuviae and larvae were preserved in 70% ethyl alcohol. Drawings were made from preserved larvae using a Zeiss drawing tube. Measurements of preserved larvae were made with an ocular micrometer; total length and carapace length are as defined by Pike and Williamson (1960a). Abbreviations and setal types mentioned are as in Johns and Lang (1977). Descriptions and sizes are based on at least five apparently healthy larvae sacrificed at each stage.

RESULTS

Development

Three zoeal stages and a megalopa were obtained through laboratory rearing; no variability in the number of larval molts was observed. Larvae were easily reared in both mass culture and individual chambers. Of larvae not sacrificed, 72% survived to megalopa and 75% of the megalopae successfully molted to first crab (Table 1).

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[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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TABLE 1.—Survival, development time, and duration of the larval stages of *Hypoconcha sabulosa* reared in the laboratory.

Item	Zoea I	Zoea II	Zoea III	Magalopa	1st crab
Percent survival from first zoeal stage to successive stages (% based on original 22 minus those sacrificed for figures)		86	76	72	53
Percent survival within each stage (% of stage not sacrificed to reach subsequent stage)	86	89	93	75	
Days from hatching to reach each stage mean (range)		3.6 (3-6)	7.2 (6-9)	10.5 (9-13)	20.9 (17-25)
Duration of each stage in days mean (range)	3.6 (3-6)	3.9 (3-4)	3.4 (3-4)	10.6 (8-14)	

At 25° C, 25‰ salinity, development to first crab averaged 21 days (Table 1). Mean duration of each zoeal stage was 3 or 4 days while the megalopa lasted approximately 10 or 11 days. Mean sizes and ranges for five larvae at each stage are given in Table 2.

TABLE 2.—Size of *Hypoconcha subulosa* larvae stages, based on five larvae at each stage.

	Carapace length (mm)		Carapace width (mm)		Total length (mm)	
Stage	Mean	Range	Mean	Range	Mean	Range
Zoea I	1.30	1.20-1.37	0.72	0.66-0.74	2.39	2.21-2.50
Zoea II	1.49	1.40-1.55	0.81	0.73-0.88	2.51	2.33-2.70
Zoea III	1.62	1.51-1.70	0.90	0.85-0.93	2.90	2.81-2.92
Megalopa	1.60	1.54-1.64	1.20	1.11-1.24	—	—

Larval Description

Live *H. sabulosa* zoeae are strong, active swimmers which readily capture *Artemia salina* nauplii. At first sight they generally look like large, proportionally short and bulky pagurid zoeae. The zoeae have a generally reddish-brown color and are most noted by the distinctive line of chromatophores along the ventral and posterior carapace margin (Figure 1).

Figures of the larval stages show the most common arrangement of setal numbers observed. For the most part, the figures should be self-explanatory; the descriptive text is intended to note significant morphological features and outline setal numbers with observed variations.

Zoea I

Carapace (Figure 1A, a) without dorsal and lateral spines, rostrum directed anteriorly, ventrolateral carapace margin smooth. Carapace striated with crisscrossing fine ridges giving a textured "skinlike" appearance. At least one pair of transverse grooves evident, eyes sessile.

Abdomen (Figure 1A, a) without spines or distinct projections, somite six and telson fused, small pleopod buds may be present.

Telson (Figure 2A) triangular with distinct median notch; setation 7 + 7 with outer fixed spine, hairlike plumose seta, and five large plumose setae.

AN1 (Figure 3A) — Single segment; terminal setation of three aesthetascs and two simple setae; subterminal setation of two plumose setae.

AN2 (Figure 3E) — With 10 plumose setae on scale and 4 plumose setae on endopodite.

MN (Figure 4A, a) — With concave median surface and lateral serrate rim. Ventroposterior region with asymmetric group of teeth.

MAX1 (Figure 5A) — With two-segmented endopodite, distal segment with six setae, proximal segment with two setae; basal endite with three cuspidate and two plumodenticulate setae; coxal endite with four stout multidenticulate setae, three plumodenticulate setae, and one simple seta.

MAX2 (Figure 6A) — With indistinctly segmented endopodite, 2 or 3 setae; bilobed basal endite, distal lobe with 5 setae, proximal lobe with 5 setae, bilobed coxal endite, distal lobe with 5 setae, proximal lobe with 9 setae, scaphognathite with 17 or 18 marginal plumose setae. All setae plumose, plumodenticulate, or simple.

MXP1 (Figure 7A) — Exopodite with four plumose setae; endopodite five-segmented with numerous median margin setae and one lateral margin seta on distal segment.

MXP2 (Figure 7E) — Exopodite with four plumose setae; endopodite four-segmented with indicated pattern of median margin setae and one lateral margin seta on distal segment.

MXP3 — Limited to undeveloped bud.

P1 (Figure 7L) — Unsegmented biramous appendage with up to two plumose setae.

Zoea II

Carapace (Figure 1B, b) with same basic features as stage I but with two distinct pairs of transverse grooves; eyes stalked.

Abdominal somites (Figure 1B) with pleopod buds; somite six and telson partially fused.

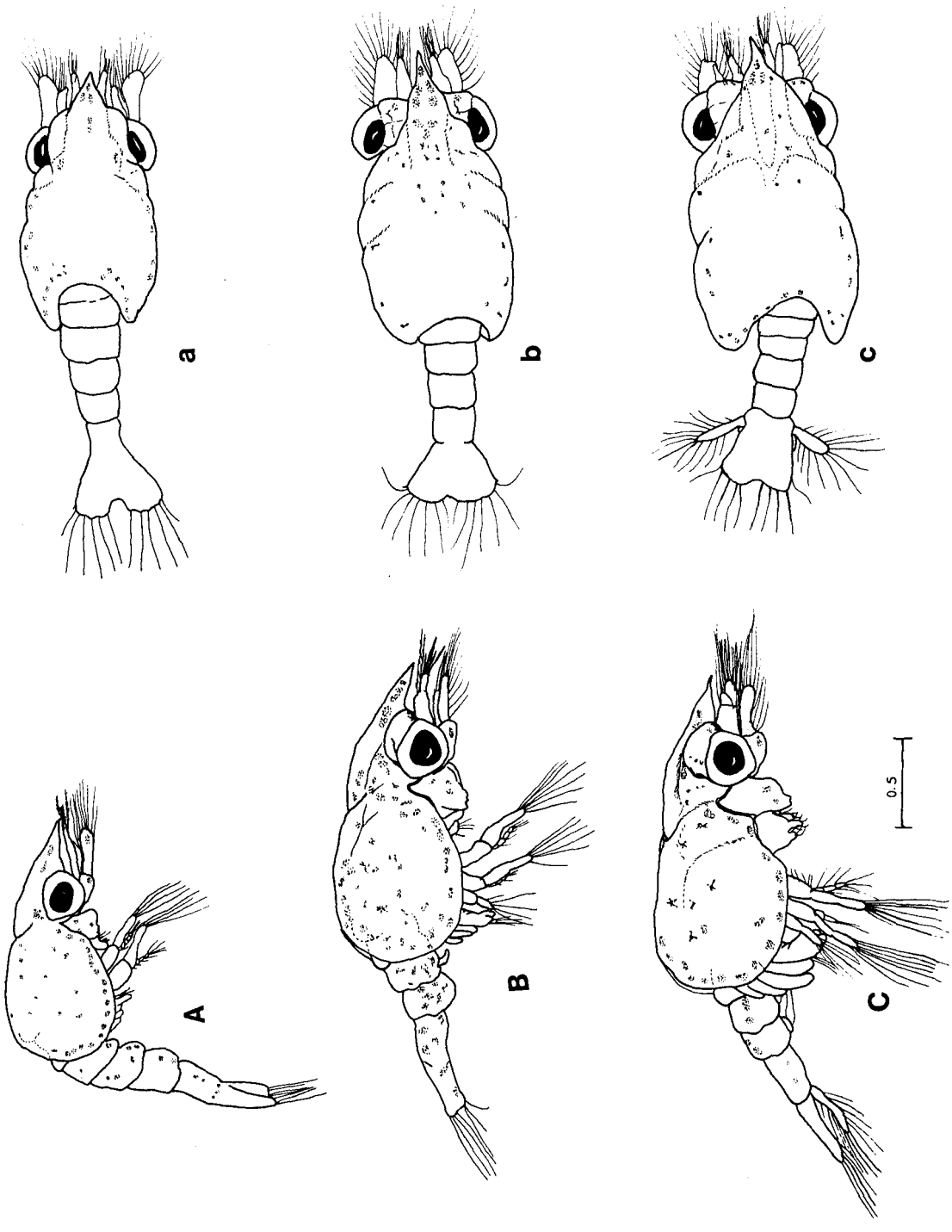

FIGURE 1.—*Hypoconcha sabulosa*: Lateral and dorsal view of zoeal stages I (A, a), II(B, b), and III (C, c).

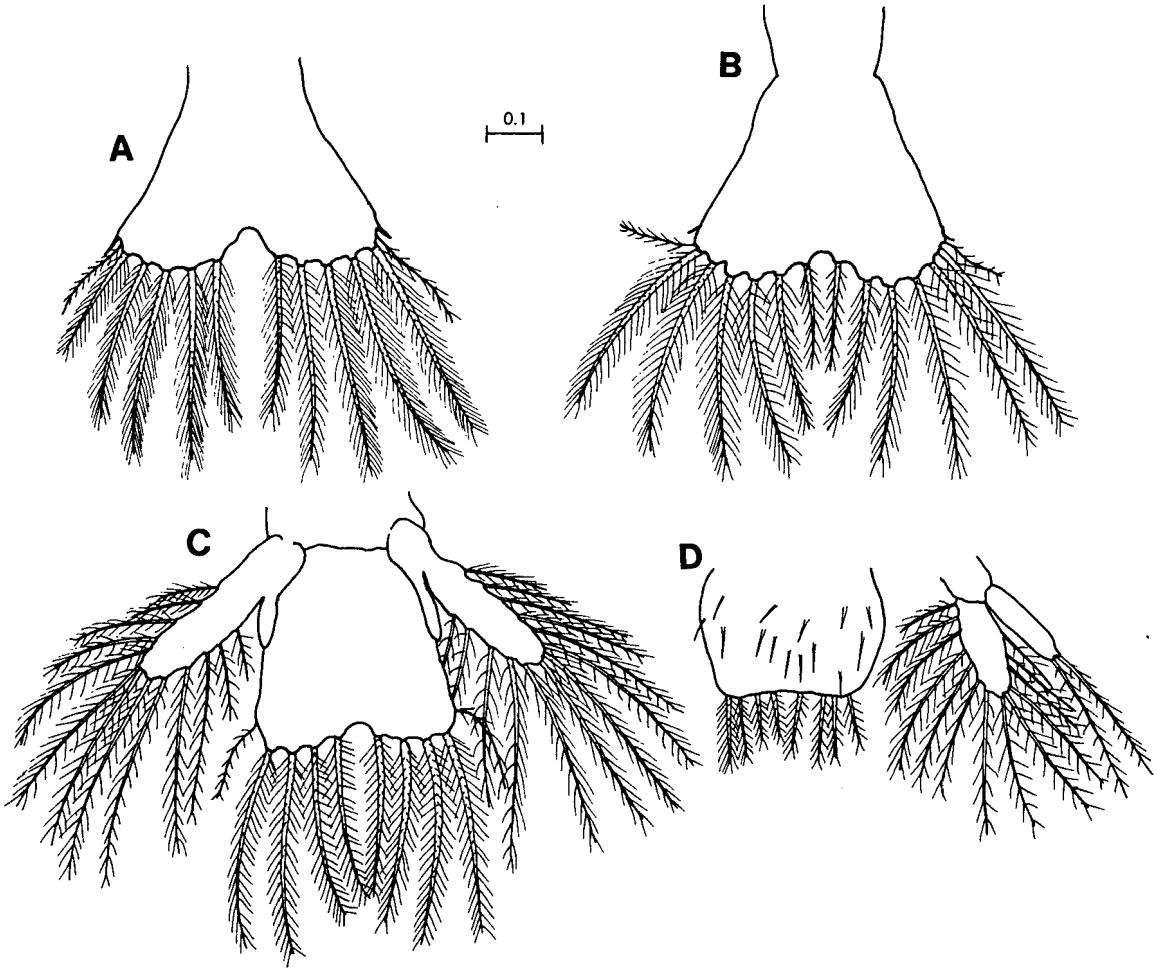

FIGURE 2.—*Hypoconcha sabulosa*: telson of zoeal stages I (A), II (B), and III (C), and megalopa (D). Only one disarticulated uropod is shown for megalopa.

Telson (Figure 2B) with reduced median notch; setation 8 + 8 with small outer fixed spine, hair-like plumose seta, and six large plumose setae.

AN1 (Figure 3B) — Indistinctly segmented; terminal setation of five aesthetascs and three fine simple processes; subterminal setation of two large plumose setae and two or three short plumose setae; additional one or two short setae may be present along basal margin.

AN2 (Figure 3F) — Similar to stage I with 19 plumose setae on scale and 3 plumose setae on endopodite.

MN — Similar to stage I; no palp.

MAXI (Figure 5B) — With major features as in stage I, basal endite (7 setae) and coxal endite (10 or 11 setae) with additional fine setae as indicated.

MAX2 (Figure 6B) — With two-segmented endopodite, 5 setae distal, 3 setae proximal; bilobed basal endite with 5 or 6 setae distal, 6 setae proximal; bilobed coxal endite with 4 setae distal, 11 setae proximal; and scaphognathite with 21-23 plumose setae. Setal types a mixture of simple, plumose, and plumodenticulate.

MXP1 (Figure 7B) — Exopodite with six plumose setae; endopodite as in stage I but with two additional plumose setae on lateral margin.

MXP2 (Figure 7F) — Exopodite with five plumose setae, endopodite as in stage I but with two additional plumose setae on lateral margin.

MXP3 (Figure 7I) — Exopodite with five plumose setae; endopodite indistinctly segmented with two to three plumose setae.

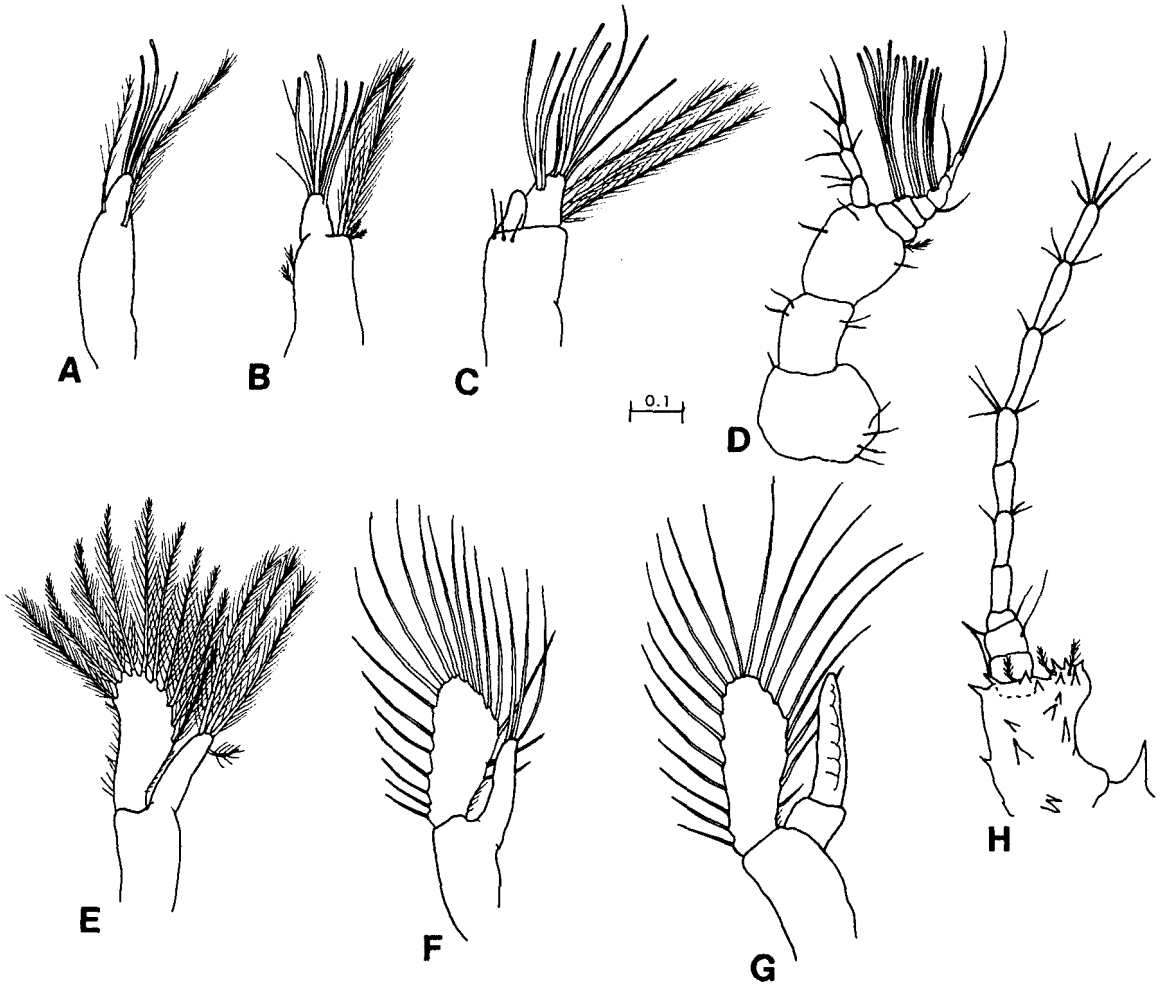

FIGURE 3:—*Hypoconcha sabulosa*: antennule of zoeal stages I (A), II (B), III (C), and megalopa (D); antenna of zoeal stages I(E), II (F), and II (G), and megalopa (H).

P1 to P5 (Figure 1B) — Conspicuous buds, first pereiopod distinctly biramous, four plumose setae on rudimentary exopodite (Figure 7M).

Zoea III

Carapace (Figure 1C, c) similar to stage II, a small blunt lateral spine near ventral carapace margin and posterior to second transverse groove present in some individuals; eyestalk with anterodorsal papilla.

Abdominal somites (Figure 1c) with elongated pleopod buds; sixth somite and telson distinctly segmented.

Telson (Figure 2C) normally 6 + 6 with very small outer spine, hairlike plumose seta, and 4 plumose setae; 2 zoeae 7 + 7 with 5 plumose setae, uropods with simple endopodite lobe and 13 or 14 setae on exopodite.

AN1 (Figure 3C) — Two-segmented; inner ramus a simple lobe; outer ramus with three terminal stout aesthetascs, three or four terminal fine processes (either simple setae or aesthetascs), three or four subterminal aesthetascs; basal segment with three stout plumose setae and three or four short plumose setae, also two short plumose setae (not figured) or proximal margin.

AN2 (Figure 3G) — With simple two-segmented endopodite and 18-21 plumose setae on scale.

MN (Figure 4B) — With simple palp.

MAX1 (Figure 5C) — With two-segmented endopodite, distal segment with two or three termi-

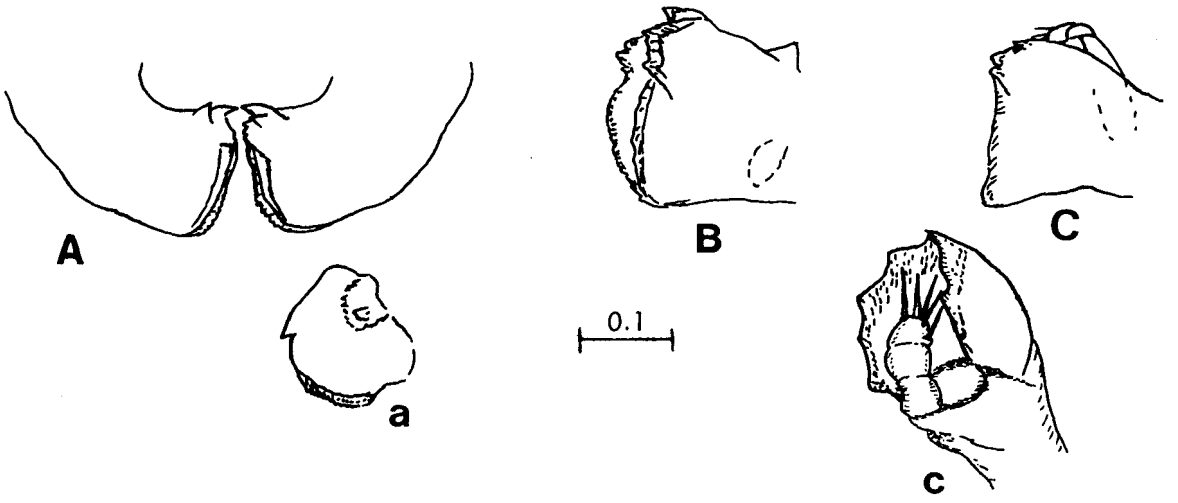

FIGURE 4.—*Hypoconcha sabulosa*: ventral view (A) and outline of biting survace (a) of stage zoeal I mandible: ventral view of zoeal stage III mandible (B); ventral view (C) and dorsal view (c) of megalopa mandible.

nal setae and two pairs of subterminal setae, proximal segment with two setae; basal endite with four or five stout cuspidate setae and five to seven finer plumose or plumodenticulate setae; coxal endite with six or seven stout multidenticulate setae and seven to nine finer setae.

MAX2 (Figure 6C) — With two-segmented endopodite, 5 setae on terminal segment, 3 or 4 setae on proximal segment; bilobed basal endite with 6 setae each lobe; bilobed coxal endite with 4 or 5 setae distal lobe, 14-17 setae in three rows proximal lobe (3 subterminal setae on opposite surface not figured); scaphognathite with 25-28 plumose setae.

MXP1 (Figure 7C) — Same as stage II but with one additional seta on endopodite lateral margin.

MXP2 (Figure 7G) — Exopodite with six or seven plumose setae; endopodite as in stage II but with additional seta on lateral margin.

MXP3 (Figure 7J) — Exopodite with six or seven plumose setae; endopodite with two distinct segments, four setae on terminal segment, one or two setae on proximal segment.

P1 to P5 (Figure 1C) — With pronounced extension beyond carapace; first pereiopod (Figure 7N) biramus, exopodite with six terminal setae; remaining pereiopods uniramus with segmentation evident and some simple setae or hairs.

Megalopa

Carapace (Figure 8A) dorsoventrally flattened with circular anterior margin and concave posterior margin; hepatic carapace margin with seven to nine distinct spines on each side, median anterior region depressed leading to short tapered rostrum; ventroposterior margins with short plumose setae; surface generally covered with numerous hairs, spinules, and plumose setae; eyestalk with distinct anterodorsal spine.

Abdominal segments with distinct lateral spines on segments two to six; dorsal surface with numerous hairs and spinules.

Telson (Figure 2D) nearly square, covered with hairs; anterior margin straight to slightly concave with 8 plumose setae; articulated uropods, endopodite with 2 plumose setae, exopodite with 13 or 14 plumose setae.

AN1 (Figure 3D) — With three basal segments; outer ramus with five segments, setation from tip to base, three simple setae, three or four aesthetascs, four aesthetascs, no setae; inner ramus with three segments with 2-3-2 setae.

AN2 (Figure 3H) — Basipodite with palp, numerous spines and three or four plumose setae; endopodite with 10 segments.

MN (Figure 4C, c) — With outer cutting edge and depressed center; palp three-segmented with five processes on distal segment.

MAX1 (Figure 5D) — With three-segmented endopodite, setation reduced to 6 setae as shown; basal endite with 7 cuspidate setae, 8 or 9 plumodenticulate setae, and 3 plumose setae on

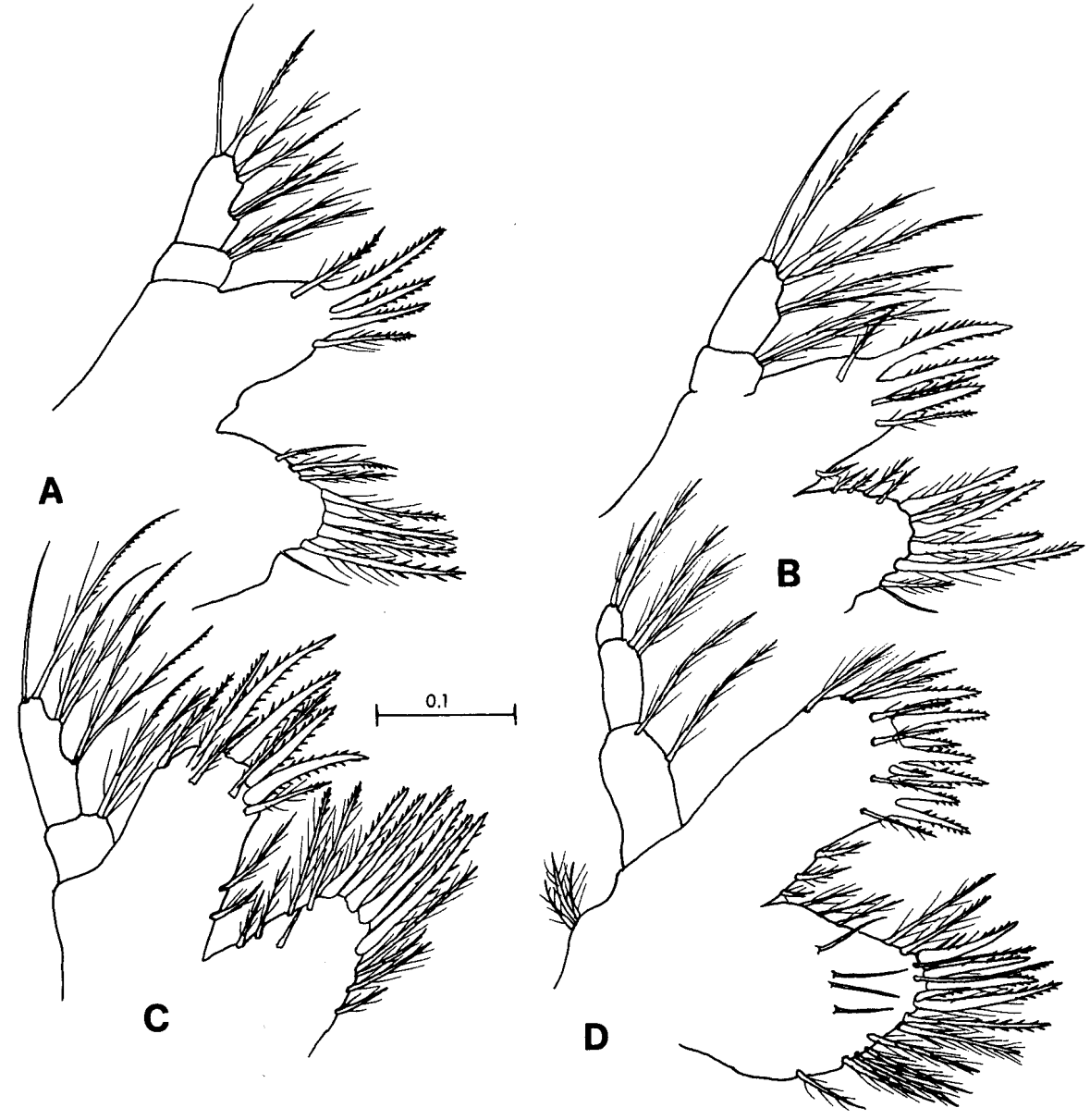

FIGURE 5.—*Hypoconcha sabulosa*: maxillule of zoeal stages I (A), II (B), and III (C), and megalopa (D).

proximal margin; coxal endite with 5 or 6 stout multidenticulate setae and 18-20 finer setae.

MAX2 (Figure 6D) — With two-segmented endopodite, 5 setae on terminal segment, 1 or 2 setae on proximal segment; bilobed basal endite with 9 setae distal lobe, 8-10 setae proximal lobe, bilobed coxal endite with 7-9 setae distal lobe, 20-22 setae proximal lobe; scaphognathite with 37-40 plumose setae.

MXP1 (Figure 7D) — Exopodite with 2 or 3 terminal and 2 or 3 subterminal plumose setae; endopodite indistinctly segmented with 8 setae; basipodite with 24-28 setae; coxapodite with about 15 setae.

MXP2 (Figure 7H) — Exopodite with 5-7 terminal and 2 subterminal plumose setae; endopodite five-segmented, 5 or 6 terminal setae and 8-10 setae subterminal.

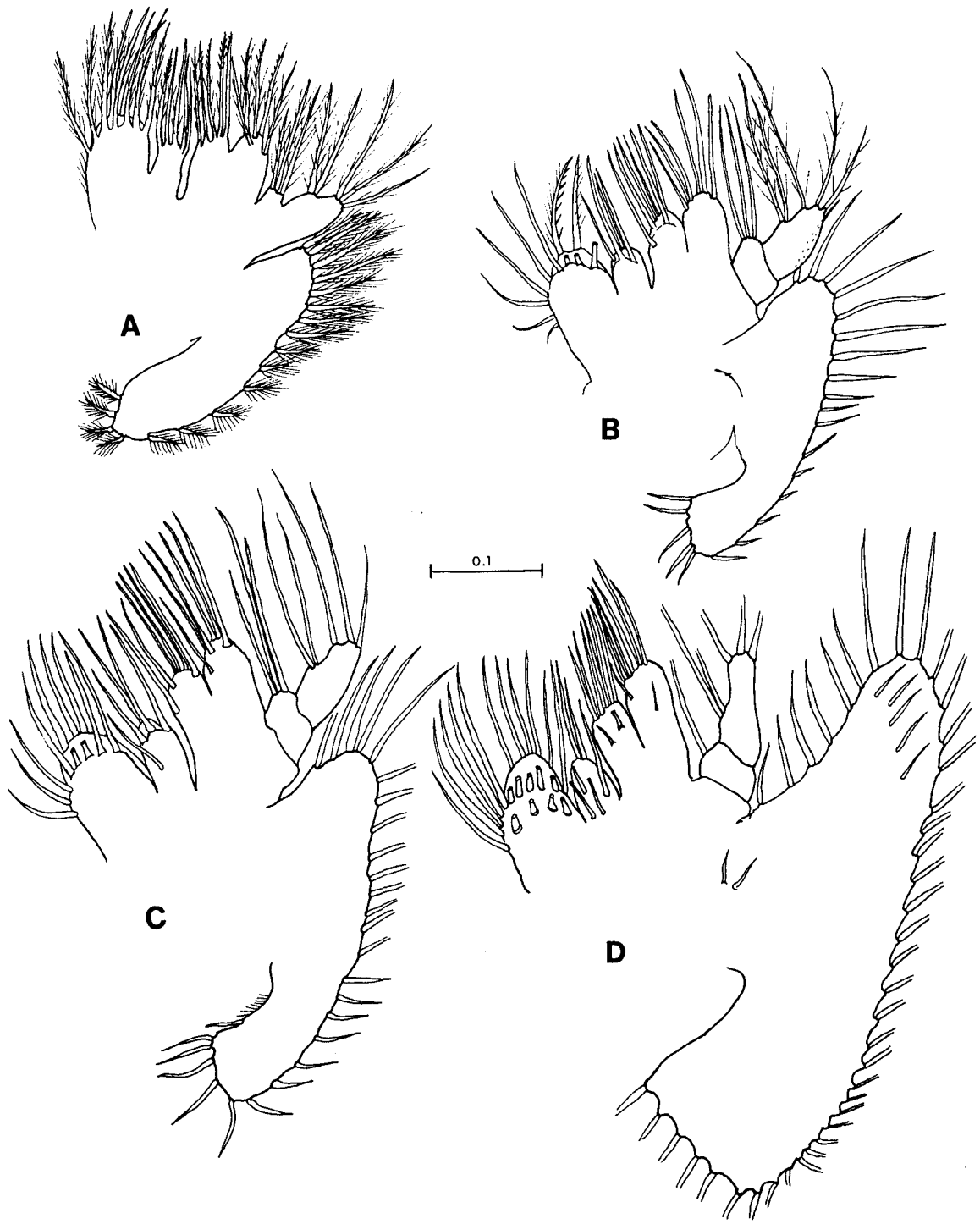

FIGURE 6.—*Hypoconcha sabulosa*: maxilla of zoeal stages I (A), II (B), and III (C), and megalopa (D). Setules have been omitted from B-D for graphic clarity.

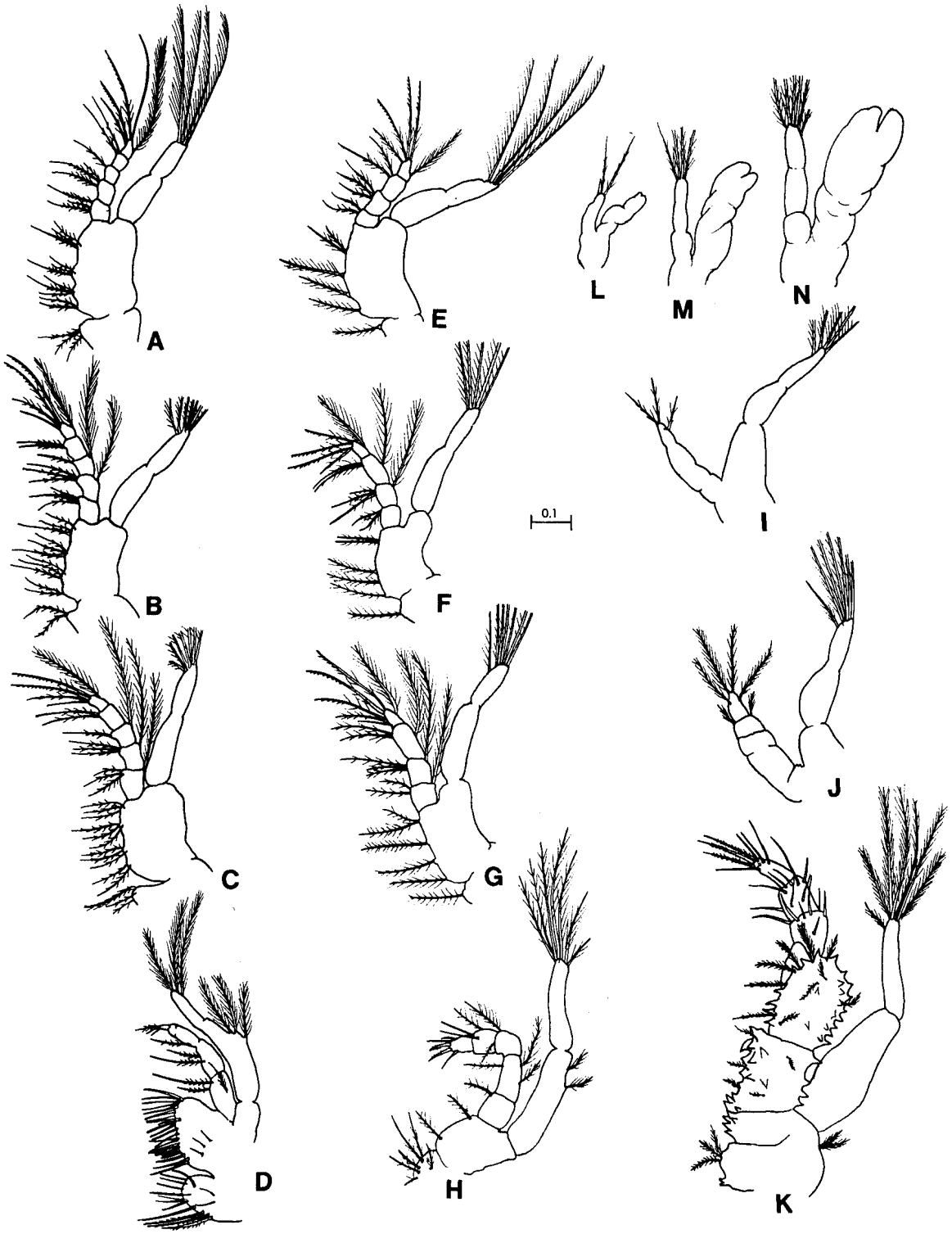

FIGURE 7.—*Hypoconcha sabulosa*: first maxilliped of zoeal stage I-megalopa (A-D); second maxilliped of zoeal stage I-megalopa (E-H); third maxilliped of zoeal stage II-megalopa (I-K); and first pereiopod of zoeal stage I-III (L-N).

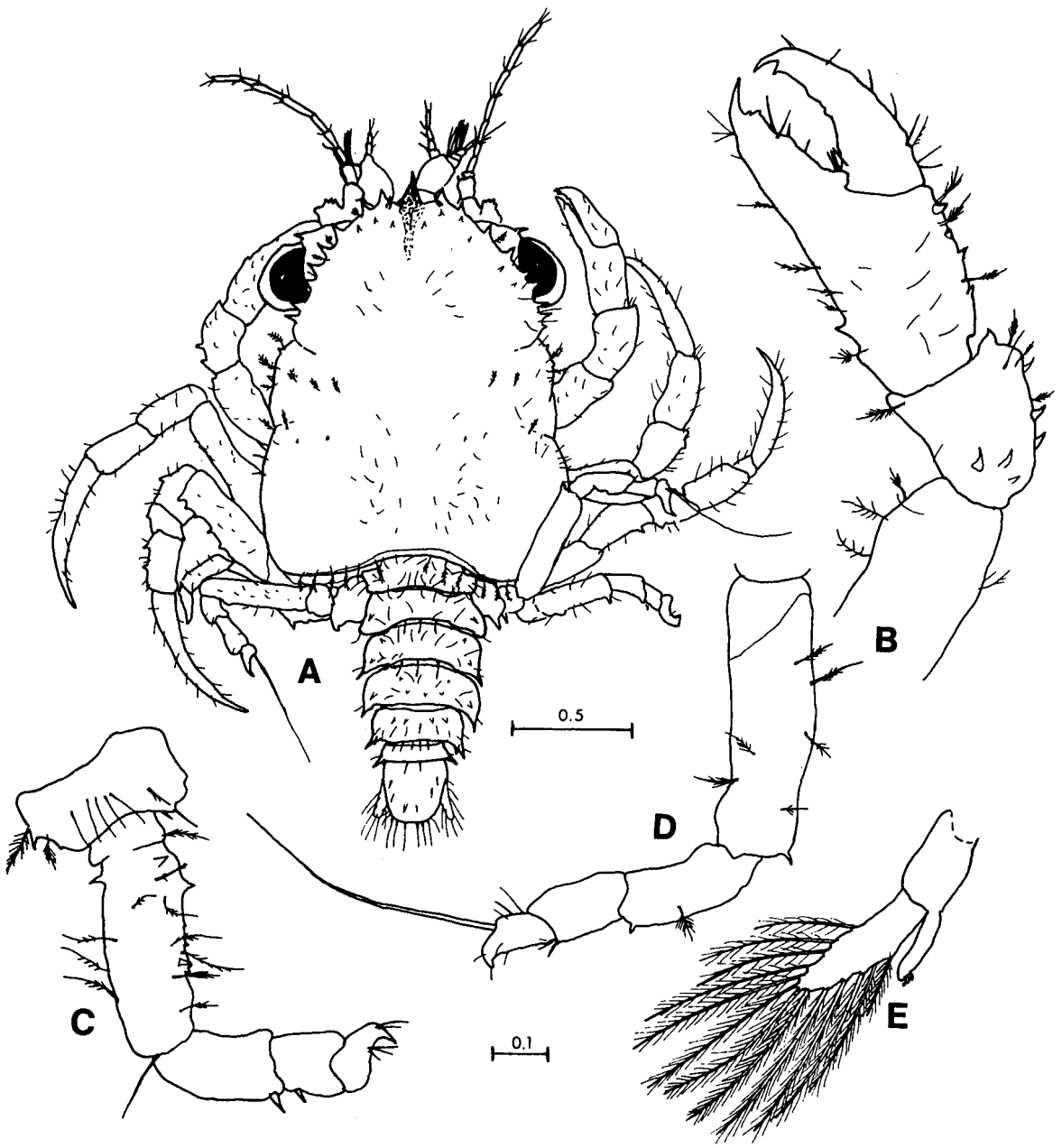

FIGURE 8.—*Hypoconcha sabulosa*: dorsal view of megalopa (A) and details of appendages; cheliped (B), fourth pereiopod (C), fifth pereiopod (D), and second pleopod (E).

MXP3 (Figure 7K) — Exopodite with 6 or 7 plumose setae; endopodite five-segmented, setation tip to base, 6 or 7, 6-8, 6, 10-12, 5-8, numerous spines on two lower segments.

P1 to P5 (Figure 8A-D) — Uniramous with numerous hairs and short plumose setae. First pereiopod (Figure 8B) with equal-sized claws; second and third pereiopod similar, dactylpods with simple tapered tip; fourth pereiopod (Figure 8C) shorter, dactylpod hooked; fifth pereiopod (Figure 8D) carried high and over carapace, dactylpod hooked with long stiff simple process.

DISCUSSION

Hypoconcha Species Distinction

Both *H. arcuata* and *H. sabulosa* have similar ranges and habitats along the southeastern United States coast (Hay and Shore 1918; Williams 1965) and adult morphology is quite similar (Rathbun 1937; Williams 1965). The source of larvae for this study was a small (carapace 17 × 17 mm) female with characteristics dorsal carapace, color, and marginal spines (Williams 1965). However, the ventral carapace ridges were weakly developed and the three characteristic tubercles (Rathbun 1937) were not evident (one small tubercle was present). This may be characteristic of young specimens or it may indicate hybridization of the two species. The distinction of species for these two forms should perhaps be reinvestigated.

Not surprisingly, the differences between the larval morphology of *H. arcuata* given by Kircher (1970) and *H. sabulosa* are slight. The differences we observed overlap the ranges of variation reported for setation or represent fine points open to interpretation. Based on present published information, a reliable means to distinguish corresponding zoeal stages between the two species is absent. *Hypochoncha sabulosa* megalopae have spines on the eyestalk and abdominal segments, features not noted for *H. arcuata*. However, these may be points of omission by Kircher (1970) and represent only tentative differences. A detailed direct comparison of larvae is needed to determine if these species can be identified during ontogeny.

Characteristics of Dromiidae Larvae

Knowledge of dromiid larvae is limited to five genera within the family Dromiidae (Table 3). The larvae of *H. sabulosa* demonstrate most general features of dromiid larval development; some features, however, such as carapace armature are surprisingly diverse. Larval development ranges from six zoeal stages in *Dromidia antillensis* to two zoeal stages in *Conchoecetes artifiosus*. Four of ten documented species have abbreviated development (Table 3).

The dromiid zoeal carapace is elongated with a large, anteriorly directed rostrum, transverse grooves, and, in most cases, a textured surface of fine ridges. The carapace may lack armature (*Hypoconcha, Conchoecetes*), have posterolateral spines (*Dromia*), have supraorbital spines (*Dromidia*), or have a dorsal spine and lateral "wings" (*Petalomera*). Carapace margins are either smooth or denticulate. All zoeae are richly pigmented with a general orange-red color.

The antennal morphology is unique to the group. The endopodite has 3 or 4 plumose setae in stage I larvae. The exopodite is a flat scale and after stage I has setae on its outer margin.

The mandibular palp generally does not develop until the terminal zoeal stage while the maxilla endopodite is well developed and often distinctly segmented. The endopodites of the first and second maxillipeds are five- and four-segmented respectively. The third maxilliped is usually biramous and rudimentary in stage I but well developed with a basally situated endopodite by stage II.

TABLE 3.—Principal studies on the postembryonic development in taxa of the family Dromiidae.

Taxon	Author	Material
Dromiidae	Gurney (1924) Gurney (1942)	Plankton sample with unknown parents
Conchoecetes artifiosus	Sankolli and Shenoy (1968)	Laboratory—all stages
Cryptodromia octodentata	Hale (1925)	Abbreviated development
Dromia personata	Cano[1](1893)	Plankton—I, IV, megalopa
	Williamson[1] (1915)	Plankton—I, IV, megalopa
	Lebour[1] (1934)	Plankton—I,II,IV, megalopa
	Pike and Williamson[2](1960b)	Plankton—I,II,III
	Rice et al. (1970)	Laboratory—all stages
Dromidia antillensis	Rice and Provenzano (1966)	Laboratory—all stages
Dromidia australis	Hale (1927)	Abbreviated development
Epipedodromia thomsoni	Hale (1925)	Abbreviated development
Hypoconcha arcuata	Kircher (1970)	Laboratory—all stages
Hypoconcha sabulosa	Present paper	Laboratory—all stages
Petalomera lateralis	Montgomery (1922) Hale (1925)	Abbreviated development
Petalomera wilsoni	Wear (1970) Wear (1977)	Plankton—I, II Plankton—magalopa

[1]Described as *Dromia vulgaris*,
[2]Described as *Dromia personatus*.

The pereiopods may be uniramous (*Conchoecetes, Petalomera*) or biramous (*Dromidia*). Only the first pereiopod is biramous in *Dromidia* and *Hypoconcha*. Uropods are well developed in late zoeae of *Dromia, Dromidia,* and *Hypoconcha* but are reduced in *Conchoectes* and *Petalomera*.

Systematic Position of the Dromiidae

The classification and phylogeny of the Dromiidae and other decapod groups rests princi-

pally on three lines of evidence: comparative morphology, fossil records, and larval development (Stevcic 1971). Based primarily on comparative morphology of adult crabs and sparse fossil records, the family Dromiidae has usually been considered primative but true brachyurans (Balss and Grunner 1961; Burkenroad 1963; Glaessner 1969; Hartnoll 1975; Warner 1977).

In contrast to these findings, the larval development of dromiids is, in many aspects, typically anomuran. Gurney (1924) found all larvae of *Dromia* to be "definitely Anomuran." Brachyuran and anomuran larvae have since been well characterized in several comprehensive studies (Gurney 1942; Pike and Williamson 1960a; Williamson 1974); the findings of Gurney (1924) have been consistently substantiated. The megalopa is not so easily characterized and appears to more closely resemble its parents than both postlarval anomurans and nondromiid brachyurans (Wear 1977). A detailed account of the classification of the Brachyura and a proposed new system has recently been published by Guinot (1978).

The Brachyura are characterized not only by the advanced organizational level of adults but also by a consistant larval form. The evolutionary path should include "brachyurization" to both a crab body (Stevcic 1971) and a "brachygnath zoea" (Williamson 1974). A key to better understanding the dromiids is to find larval types which appear to lead toward a brachygnath form. If, like the Dromiidae, the Dynomenidae and Homolodromidae are found to have larvae showing no tendency to develop brachygnath features, the Dromiacea (Guinot 1978) may have progressed toward a crablike form independent of lines leading toward the true brachyurans.

The combination of adult and larval characteristics exhibited by the Dromiidae has not been satisfactorily explained. In view of obvious contradictions and the relative importance of adult morphology in decapod classification, removal of the Dromiidae from the Brachyura based solely on known larval features (Gurney 1924, 1942; Kircher 1970; Williamson 1974) is not warranted. Placement of the Dromiidae within the Brachyura, is by no means "of little doubt" as claimed by Warner (1977) but represents more a matter of convenience (Guinot 1978); their position is tenuous at best. Hopefully additional material (larval, morphological, or fossil) will lead to a comprehensive account of the Dromiidae and related families.

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