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DEVELOPMENT OF PELAGIC LARVAE AND POSTLARVA OF *SQUILLA EMPUSA* (CRUSTACEA, STOMATOPODA), WITH AN ASSESSMENT OF LARVAL CHARACTERS WITHIN THE SQUILLIDAE

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ABSTRACT

Larvae of the predatory crustacean *Squilla empusa* were collected from the plankton in Chesapeake Bay and reared in the laboratory to permit description of the pelagic stages before the postlarval stage.

Characters such as rostral length and spinulation, carapace spinulation, relative size of telson, overall body size, and appearance probably are of more value for specific than for generic identification. The presence or absence of teeth on the dactylus of the second maxilliped, the presence or absence of a spine on the basis of the second maxilliped, and the number of epipods may be useful characters in determining generic alliances of larvae belonging to the Squillidae, but present data are not adequate for construction of generic keys to stomatopod larvae.

Mantis shrimps are formidable predators, able to slice a swimming shrimp in half or smash open a bivalve with enlarged second maxillipeds (MacGinitie and MacGinitie 1968). Even though the strike occurs under water, it is one of the fastest movements known in the animal kingdom taking 4 to 8 ms to complete and traveling at a velocity of 1,000 cm/s (Burrows 1969). Basically, any animal of appropriate size may fall prey to a stomatopod including fish, shrimp, crabs, annelids, clams, mussels, snails, squids, and echinoderms (Piccinetti and Manfrin 1970).

Stomatopod larvae are often met with in great swarms, particularly in tropical waters. The planktonic larval stages constitute a considerable portion of the diet of reef fishes and commercially important pelagic fishes such as the tunas, skipjack tuna, mackerel, herring, and snapper (Sunier 1917; Fish 1925; Reintjes and King 1953; Randall 1967; Dragovich 1970).

Squilla empusa Say 1818 is found in the western Atlantic Ocean and ranges from Massachusetts, U.S.A. to northern South America, including Trinidad, Venezuela, Surinam, and French Guiana (Manning 1969). It is abundant throughout its range, but is especially prevalent in commercial shrimp beds, and is believed to be a serious predator of the shrimp. Hildebrand (1954) observed that it is the most abundant crustacean in the offshore trawl fishery of the Gulf of Mexico except for *Penaeus* sp. and *Callinectes* sp. Stomatopods are fished and eaten in most Mediterranean countries, Japan, and the tropical Pacific (Kaestner 1970).

Like the adult, the larvae of *S. empusa* are rapacious predators. Able to attain a length of 17 mm, they can capture zooplankters as large as themselves by using their second maxillipeds (Lebour 1924). *Squilla empusa* larvae not only fill a role as predators, but also as prey. To date very little has been published on the ecology of the larvae nor has the sequence of pelagic stages been established for this species.

Of the 350 known species of stomatopods, only 1 in 10 can be identified with their larvae and only 1 has been reared from hatching to metamorphosis. Difficulty in rearing the larvae has forced investigators to base their accounts on reconstructions made from preserved specimens or from holding planktonic larvae through one ecdysis to connect successive stages. The species of stomatopods for which larvae are definitely known by the rearing of late stage larvae through metamorphosis were listed by Provenzano and Manning (1978). Stomatopod species for which larvae are definitely known by the hatching of eggs also are listed by Provenzano and Manning.

The only description of the developmental sequence of *S. empusa* was made almost 100 yr ago by Brooks (1878) who captured larvae at Fort Wool near the mouth of the Chesapeake Bay. Because

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none of Brooks' larvae metamorphosed into postlarvae, he could not be sure of their identity. However, of the thousands he collected, all appeared to Brooks to be "specifically identical" and the series of forms were so complete with the differences between the successive stages so slight that he concluded there was "no reason to doubt that they are all of the same species, and that species the only one which is known to occur in the Chesapeake Bay." However, we now know that early larval stages of at least one other species of stomatopod occur at the mouth of Chesapeake Bay (Provenzano and Goy, pers. obs.) Brooks' description is inadequate to permit stages to be adequately assigned to larvae.

Brooks apparently was unable to obtain successful molting in his larvae, but instead had to rely on reconstruction to describe the larval history. He provided no conjecture as to the number of pelagic stages, and only partially described four stages. Furthermore, the illustrations which Brooks included were of whole specimens only; detailed figures of appendages, necessary for accurate species identification, were not made.

Faxon (1882), working in Rhode Island, held what he considered to be the last pelagic stage of *S. empusa* until it metamorphosed and could be identified. However, the last stage larva and postlarva appear to belong to another species, not *S. empusa* (see Discussion).

In this paper we describe the pelagic larval development and postlarval stage of *S. empusa*. Because egg masses were not collected, hatched, and reared, the propelagic stages remain undescribed. Furthermore, because larvae were obtained from the plankton, we are not positive that the larvae described as stage I are the true first pelagic stage. However, of the hundreds of larvae collected these stage I larvae are the least developed and closely resemble stage I larvae of other species reared from eggs.

A brief review of previous efforts to associate stomatopod larvae with adults and a discussion of possible specific and generic larval characters within the Squillidae is presented.

METHODS

Larval specimens of *S. empusa* were collected weekly 1 to 2 km north of Cape Henry at the mouth of the Chesapeake Bay where we have determined that a population of adults exists. A ½-m plankton net (153-μm mesh) was used to make 10-min stepped oblique tows, as the ship circled the collection site at idle speed.

Each plankton sample was placed into one or two 1.9-l (½-gal) jars filled with seawater until stomatopod larvae could be separated from the sample. Separation of larvae from the samples was started aboard ship and completed in the laboratory. Larvae were sorted according to size to minimize cannibalism, and held temporarily in aerated 1.9-l jars filled with seawater.

The larvae were then placed in compartmentalized plastic trays, one per compartment. Each tray contained 18 compartments measuring 4.5 × 5 × 4 cm. Medium for rearing the larvae was made from Instant Ocean Synthetic Sea Salts[2] (Aquarium Systems, Inc., Eastlake, Ohio) and tapwater.

Larvae were reared over a range of temperatures (10° to 25°C) and salinities (10 to 35‰) in an attempt to insure survival of at least some larvae since optimum conditions were unknown. Because the larvae were not hatched in the laboratory under the temperature-salinity combination at which they were reared, some larvae had to be acclimated to the test conditions. Lavae were never acclimated to temperature changes of more than 5°C and 10‰/day. The larvae were maintained in total darkness except for brief periods (15 to 20 min/day) when they were examined and transferred to newly prepared trays.

Each larva was reared in 25 ml of water and given approximately 30 *Artemia salina* nauplii/ml daily. Decapod larvae and *A. salina*, grown on yeast or an algal culture of *Dunaliella*, were fed to larvae that became too large to capture or obtain substantial nutrition from the *A. salina* nauplii. Larvae were transferred daily, early stages by means of a pipette, later stages with a spoon, into compartments containing freshly prepared seawater and food. During this transfer, frequency of molting, duration of larval development, survival, and the stage of development were recorded. Dead larvae were preserved in 70% ethyl alcohol and 10% glycerin. Preserved larvae were heated in a 5% potassium hydroxide solution to dissolve the tissue so that only the exoskeleton remained. The larvae were then stained in acid fuchsin red to facilitate description and illustration. Larvae and exuviae were dissected in lactic acid. All larval appendages were illustrated using a Tasco camera lucida on a Unitron binocular compound scope,

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

while the postlarval appendages were illustrated with the aid of a Bausch and Lomb microprojector.

The descriptions of all larval stages were based on five specimens; four specimens were used to describe the postlarva. Carapace length (CL) indicates the distance from the tip of the rostrum to the median posterior margin of the carapace, exclusive of the median spine; telson length (tL), distance from the articulation with the sixth abdominal somite to the median posterior margin of the telson. The term pleotelson (Kaestner 1970) is used to refer to the telson before the sixth abdominal somite has become completely articulated. Pleotelson length (PL) indicates the distance from the articulation with the fifth abdominal somite to the median posterior margin of the pleotelson; telson width (TW) and pleotelson width (PW), distance across the widest portion; rostral length (RL) of the larva, distance from the tip of the rostrum to the base of the anterolateral spines of the carapace; rostral length of the postlarva, distance from the tip of the rostrum to the posterior margin of the rostrum; rostral width (RW) of the postlarva, distance from the tip of the rostrum to the median posterior margin of the telson; and total length (TL) of the postlarva, distance from the anterior margin of the rostrum to the median posterior margin of the telson.

Maxillules, maxillae, pleopods, distal spinules of the rostrum, and most epipods were omitted from illustrations of the whole animal for the sake of clarity.

RESULTS

The pelagic larval development of *S. empusa* was found to include nine stages before the postlarval stage. Juvenile stages reared for several months after metamorphosis attained sizes of approximately 30 to 40 mm TL and could be positively identified with the adult. Although none of the 576 larvae reared at the 16 different temperature and salinity combinations was reared through the entire pelagic development to metamorphosis, larvae survived well and molted frequently at two of the test combinations. Of larvae kept at 20°C, 25‰ salinity, or at 25°C, 25‰ salinity, 47% molted three or more times, 24% underwent at least five ecdyses, and 3% molted seven times over a 6-wk period. Thirty-four animals molted to postlarva. Great increases in size from the first to the last stage necessitated adjustments in food size and quantity. Detailed results of effects of various experimental conditions are being prepared by Morgan for publication elsewhere.

The difficulty in rearing the larvae through the lengthy pelagic development made it necessary to reconstruct the developmental sequence by observing the larvae molt through successive stages.

Stage I (Figure 1A)

Measurements (mm): RL, 0.70 to 1.10; PL, 0.4 to 0.8; TL, 2.9 to 3.3; CL, 0.80 to 1.30; PW, 0.3 to 0.6.

Rostrum deflexed, extending slightly beyond antennular flagella, ventral spinules absent.

Carapace with one pair of supraorbital spines. Lateral margins of carapace convex, armed ventrally with four spinules. Posterior margin of carapace deeply notched, armed with a median dorsal spine. Posterolateral spines, armed with one ventral spinule, extending to fourth abdominal somite.

Ocular somite articulated, armed with one spine on median ventral margin. Antennular somite not articulated.

Antennule (Figure 2A) with long two-segmented inner flagellum, apical segment armed with one strong and one weak seta distally and a pair of weak setae medially, proximal segment armed with one strong and two weak setae distally. Outer flagellum armed with one large and one small seta distally, followed by one weak seta and six aesthetascs arranged 1-2-3 along inner margin. Median flagellum absent.

Antenna (Figure 3A) armed with nine plumose setae, endopod absent.

Mandible (Figure 4A) serrate, mandibular palp absent.

Maxillule (Figure 5A) with coxal endite bearing three spinules and one seta, basal endite with one strong tooth flanked by two strong setae, palp with one long seta, endopod absent.

Maxilla (Figure 6A) unsegmented, armed with six setae.

First maxilliped (Figure 7A) with dactylus small, pointed. Propodus with two extremely minute spinules, inner margin bearing seven strong setae arranged 2-3-2. Carpus with one strong seta distally, merus without setae, epipod absent.

Second maxilliped (Figure 8A) large, basis with stout proximal spine. Propodus with 1 strong terminal tooth followed by 17 to 20 denticles on inner margin. Dactylus armed with spinules, distal

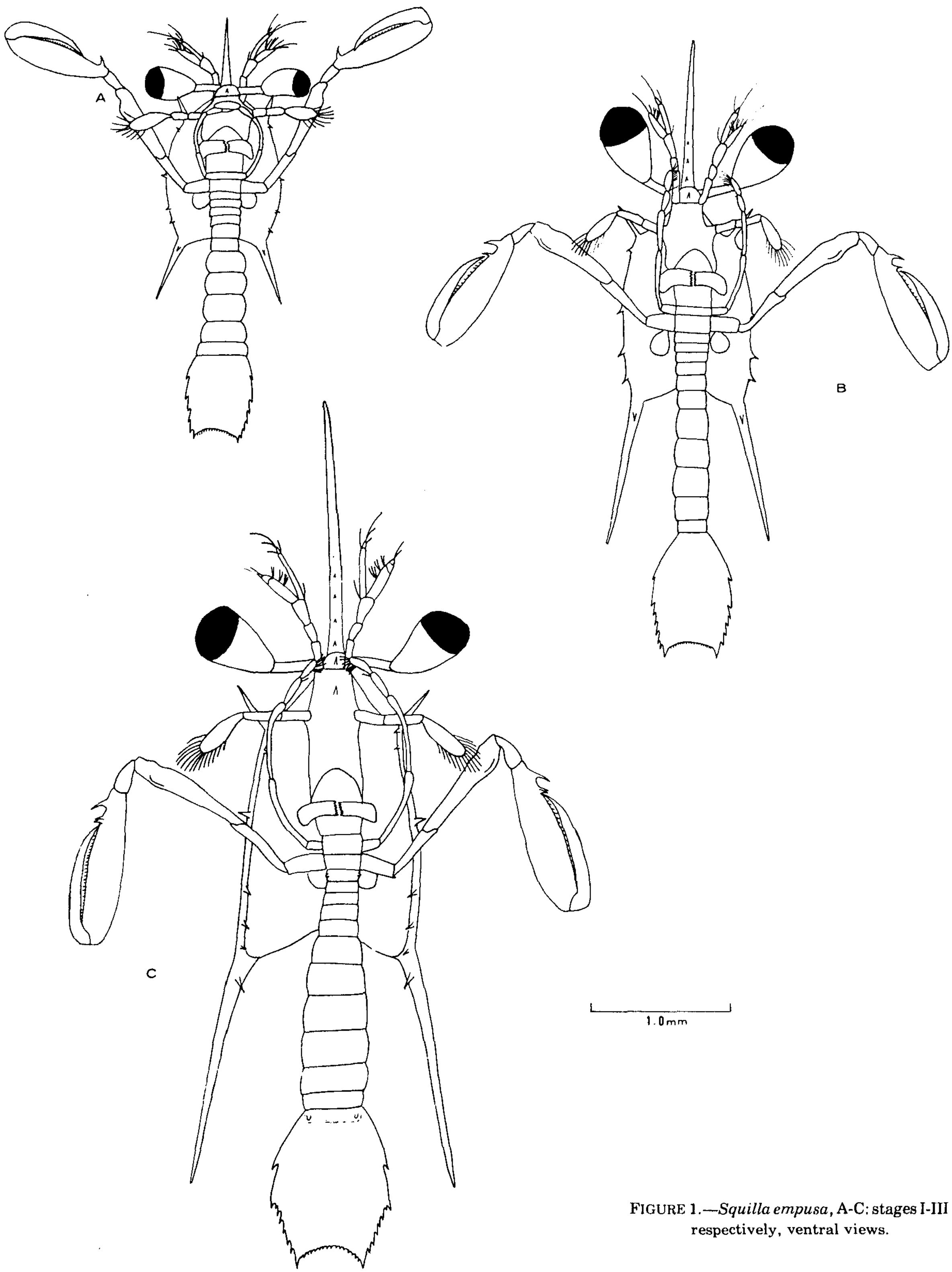

FIGURE 1.—*Squilla empusa*, A-C: stages I-III respectively, ventral views.

FIGURE 2.—*Squilla empusa*, A-I: stages I-IX respectively, antennules.

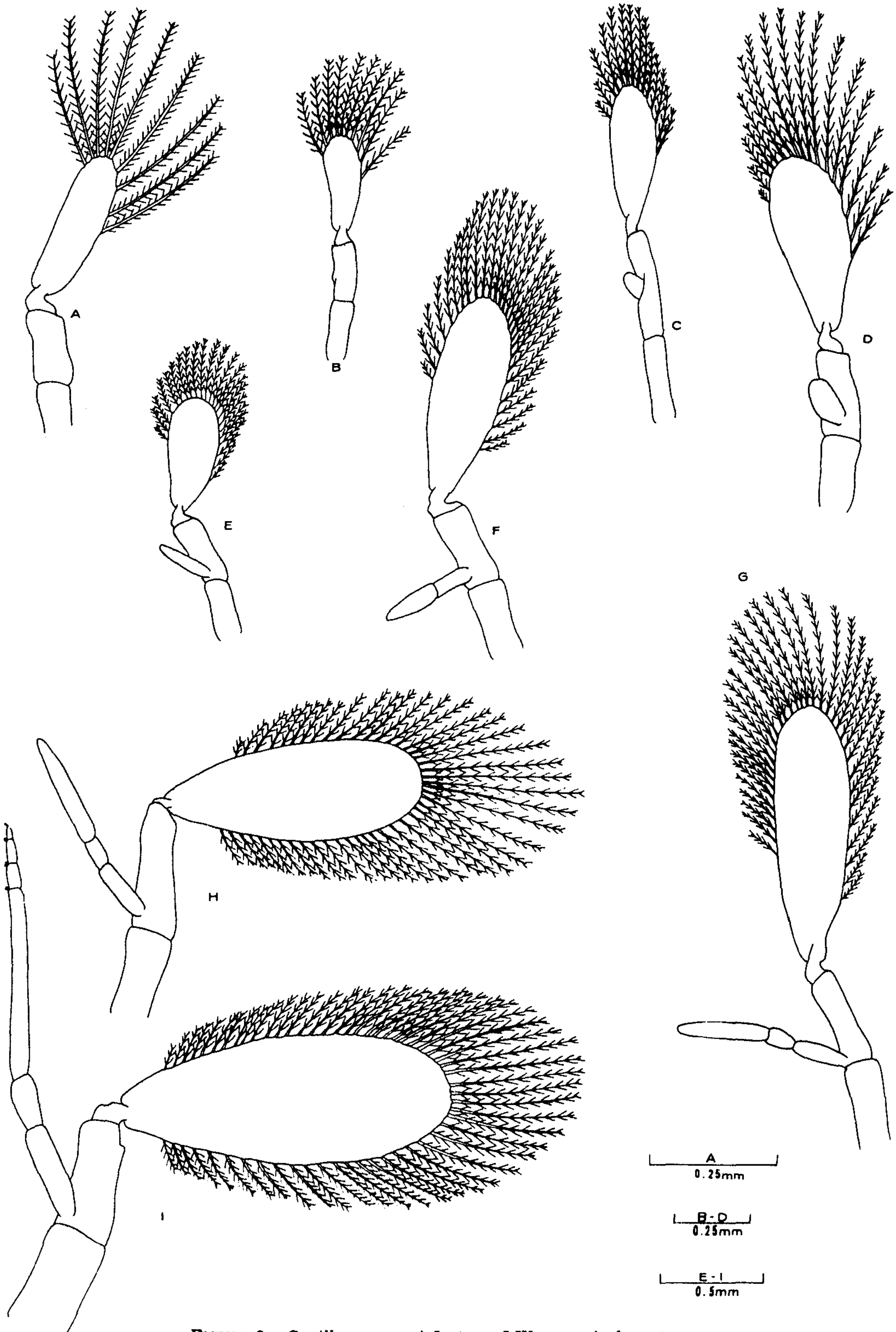

FIGURE 3.—*Squilla empusa*, A-I: stages I-IX respectively, antennae.

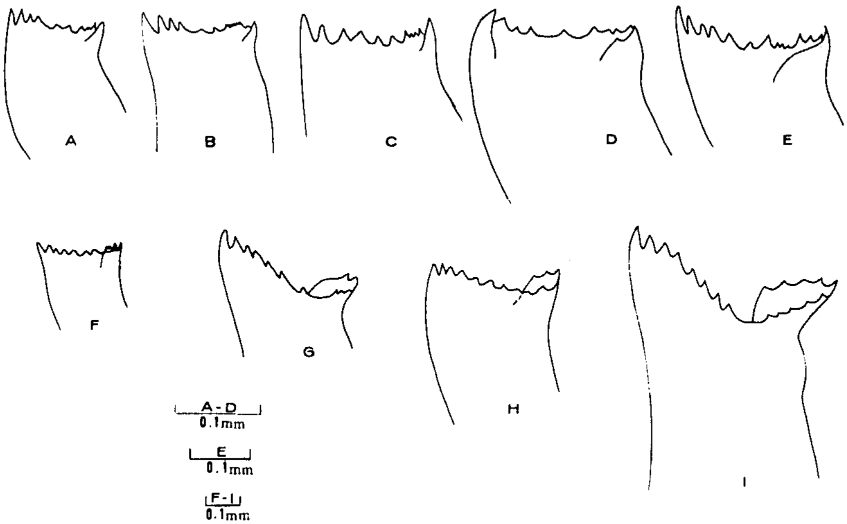

FIGURE 4.—*Squilla empusa*, A-I: stages I-IX respectively, mandibles.

FIGURE 5.—*Squilla empusa*, A-I: stages I-IX respectively, maxillules

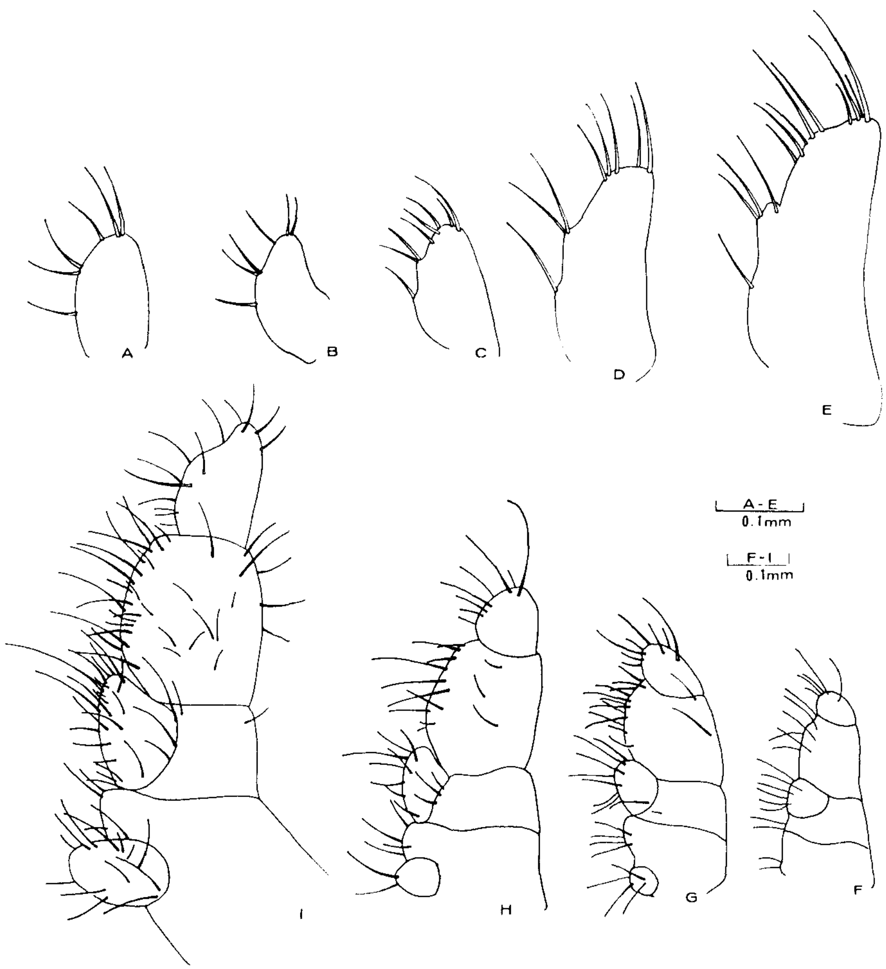

FIGURE 6.—*Squilla empusa*, A-I: stages I-IX respectively, maxillae.

portion of cutting edge minutely serrate. Epipod present.

Third, fourth, and fifth maxillipeds absent.

Pereiopods absent.

Posterolateral angles of pleomeres rounded. Pleopods (Figure 9A to 9D) one through four present with appendix interna. Pleopod setation of this and other larval stages presented in Table 1.

Sixth pleomere not articulated, submedian spines absent, uropods absent.

Pleotelson (Figure 10A) with paired lateral, intermediate, and posterolateral spines, 4 pairs of intermediate denticles, 15 submedian denticles bearing spinules.

Stage II (Figure 1B)

Measurements (mm): RL, 1.35 to 1.55; PL, 0.70 to 0.90; TL, 4.20 to 4.60; CL, 1.05 to 1.30; PW, 0.55 to 0.75.

Rostrum extending well beyond end of antennular flagellum, armed with one to four ventral spinules.

Carapace slightly convex, posterolateral spines extend to anterior section of telson.

Antennule (Figure 2B) as in previous stage.

Antenna (Figure 3B) with 10 to 13 plumose setae, endopod present as incipient bud.

FIGURE 7.—*Squilla empusa*, A-I: stages I-IX respectively, first maxillipeds.

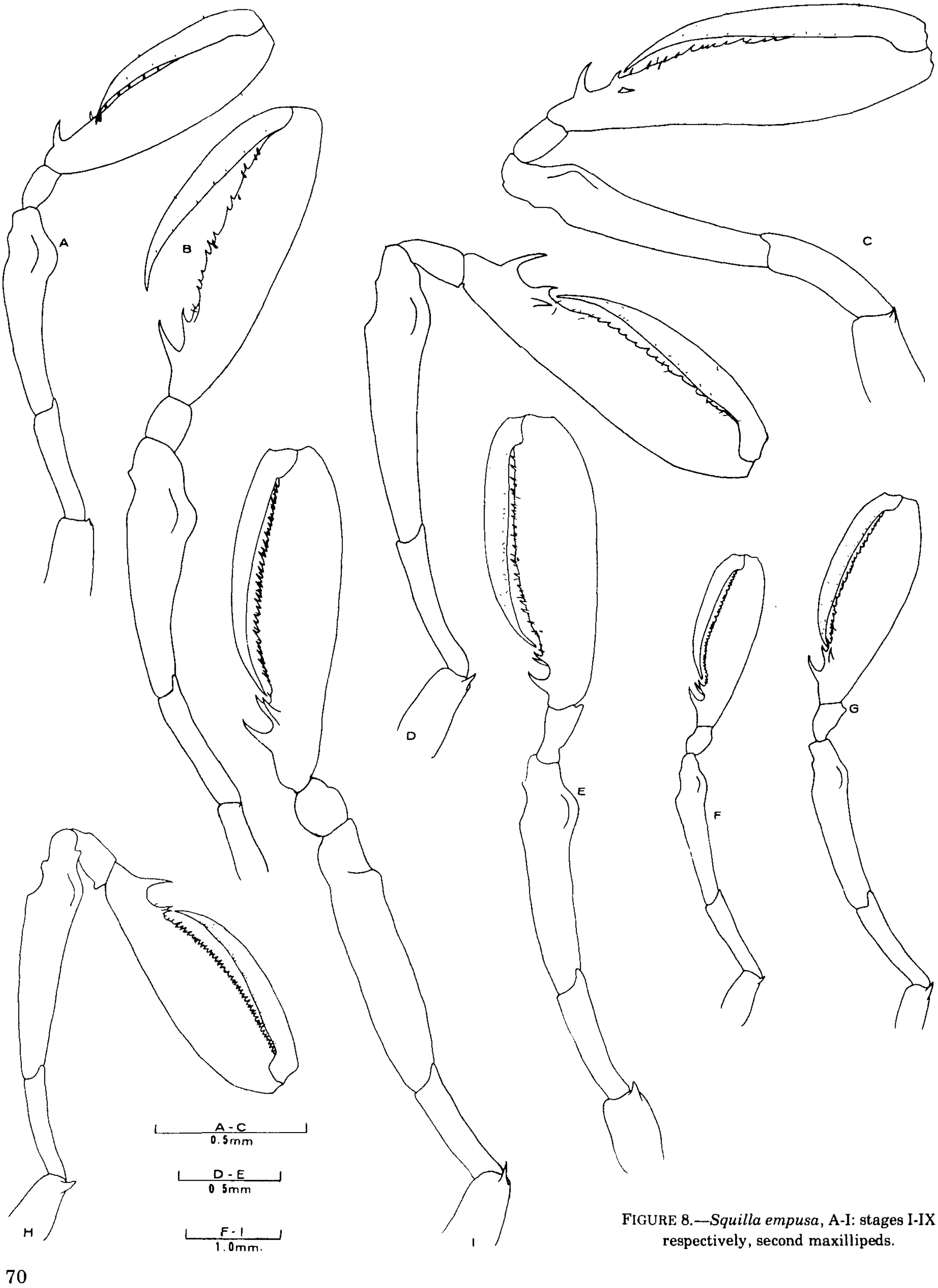

FIGURE 8.—*Squilla empusa*, A-I: stages I-IX respectively, second maxillipeds.

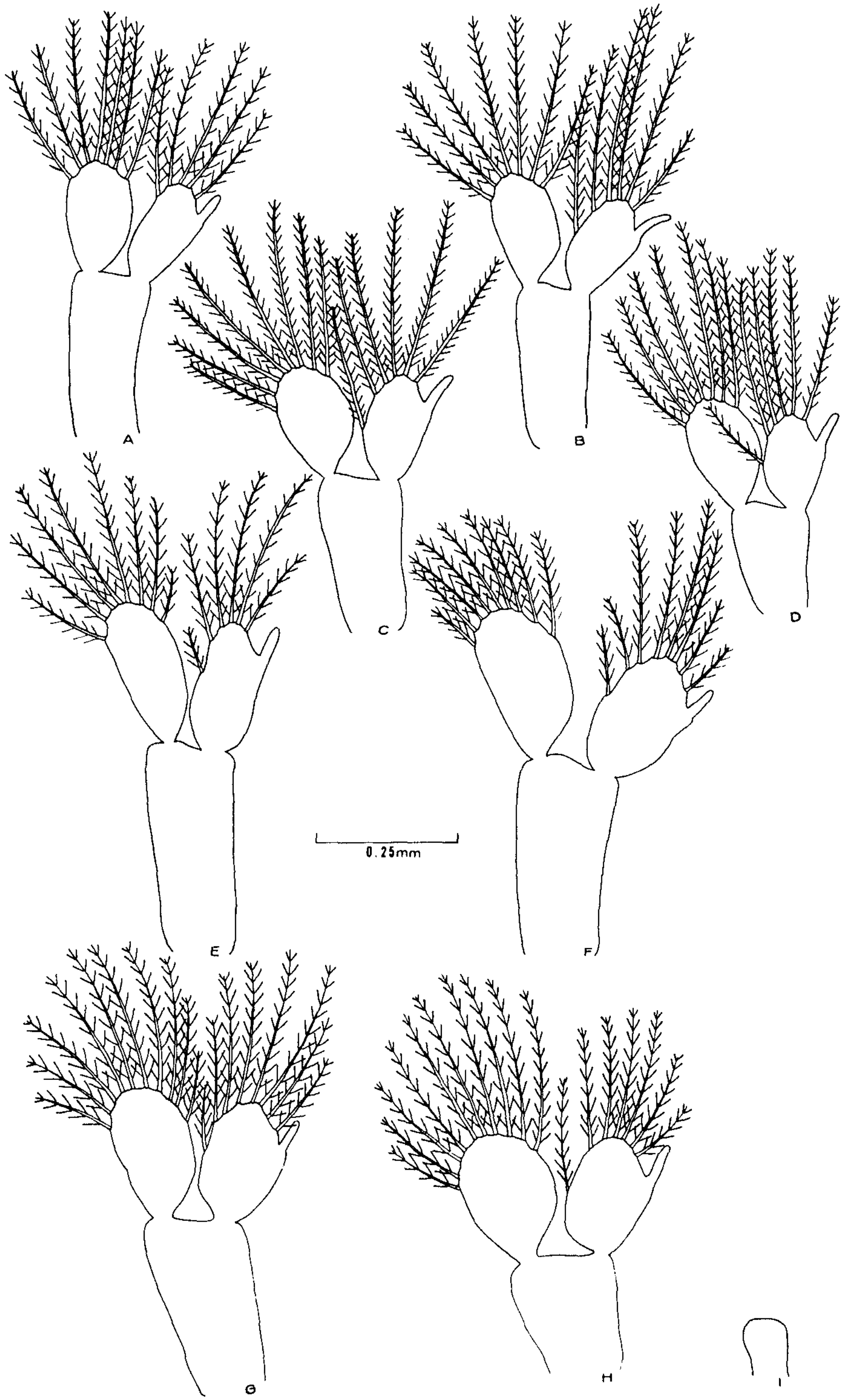

FIGURE 9.—*Squilla empusa*, A-D: stage I, first to fourth pleopods respectively, E-I: stage II, first to fifth pleopods respectively.

TABLE 1.—Number of setae on margins of pleopods for pelagic larval stages I to IX of *Squilla empusa*. Fifth pleopod does not appear until stage V.

	Abdominal somite									
	Endopod					Exopod				
Stage	1	2	3	4	5	1	2	3	4	5
I	6	6	6-7	6-7	—	7	7	7-9	7-9	—
II	6	7-8	7-8	7	—	7-8	9-10	9-11	9-10	—
III	8-10	9-13	10-14	9-14	—	9-10	12-13	13-14	11-14	—
IV	12-13	14-15	15-16	15-17	—	12	16-17	17-18	16-17	—
V	14-15	15-18	16-18	16-20	—	14-15	17-19	19-20	18-19	7-8
VI	16-20	18-25	20-27	20-27	3-8	15-20	21-26	23-29	21-27	12-16
VII	22-28	26-28	26-31	26-32	23-28	22-30	26-31	29-33	28-31	20-23
VIII	25-29	27-32	28-36	31-38	30-39	24-30	32-36	32-38	31-38	24-31
IX	27-31	32-39	35-42	36-45	40-47	36-41	36-41	38-46	37-45	33-39

Mandible (Figure 4B), maxillule (Figure 5B), maxilla (Figure 6B), and first maxilliped (Figure 7B) as in previous stage.

Second maxilliped (Figure 8A) with propodus bearing proximal tooth followed by another large tooth and 19 to 21 denticles along inner margin.

Pleopods one through four (Figure 9E to 9H) increase setation slightly (Table 1). Fifth pleopod (Figure 9I) present as bifurcated bud.

Pleotelson (Figure 10B) as in previous stage.

Stage III (Figure 2C)

Measurements (mm): RL, 1.90 to 2.10; PL, 1.00 to 1.10; TL, 5.80 to 6.50; CL, 1.50 to 1.78; PW, 0.75 to 0.95.

Rostrum with four to eight spinules ventrally for stages III to VIII.

Carapace with lateral margins straight, armed with two anterior and three posterior spinules all ventrally directed, and one median spinule laterally directed. Posterolateral spines extend to posterior region of pleotelson.

Antennule (Figure 2C) with two-segmented inner flagellum, proximal segment armed with one strong distal seta. Outer flagellum two-segmented with 9 or 10 mesial aesthetascs arranged in three groups of 2 or 3, each group with a weak seta.

Antenna (Figure 3C) with 13 to 16 plumose setae, length of unsegmented endopod increased.

One median ventral spine situated between base of antennules and antennae.

Mandible (Figure 4C) essentially unchanged.

Maxillule (Figure 5C) with coxal endite bearing four to eight teeth.

Macilla (Figure 6C) with six to eight setae.

First maxilliped (Figure 7C) with 9 or 10 strong setae arranged in four groups of 2 or 3 on propodus, carpus with 1 or 2 strong setae distally.

Second maxilliped (Figure 8C) with propodus bearing 23 to 27 denticles, basis with proximal spine well developed.

Third maxilliped present as bud.

Pleopods one through four (Figure 11A to 11D) increase setation (Table 1). Fifth pleopod (Figure 11E) biramous, nonsetose.

Sixth pleomere partially articulated, one pair of small submedian spines present. Uropods (Figure 10C) present as buds.

Pleotelson (Figure 10C) with 8 to 10 pairs of intermediate denticles, including 1 pair in axis of intermediate spines 15 to 27 submedian denticles.

Stage IV (Figure 12)

Measurements (mm): RL, 2.50 to 2.90; PL, 1.20 to 1.40; TL, 6.50 to 6.90; CL, 1.80 to 2.25; PW, 1.00 to 1.20.

Rostrum with a row of minute spinules distally for stages IV to VIII.

Antennule (Figure 2D) with three-segmented inner flagellum armed with two strong setae on distal half of proximal segment. Outer flagellum divided into a two-segmented median flagellum, and a broader outer flagellum with 10 or 11 aesthetascs arranged in four groups of 2 or 3, a small seta with each group. Antennular somite articulated.

Antenna (Figure 3D) with 17 to 19 plumose setae, length of unsegmented endopod increased slightly.

Mandible (Figure 4D) essentially unchanged.

Maxillule (Figure 5D) with coxal endite bearing seven to nine teeth, palp with two setae.

Maxilla (Figure 6D) with eight to nine setae.

First maxilliped (Figure 7D) with 12 or 13 strong setae arranged in five groups of 2 or 3 on propodus, carpus with 4 distal setae, merus with 1 strong distal seta.

Second maxilliped (Figure 8D) with propodus bearing proximal tooth followed by 2 strong teeth in opposition and 25 to 33 denticles along inner margin.

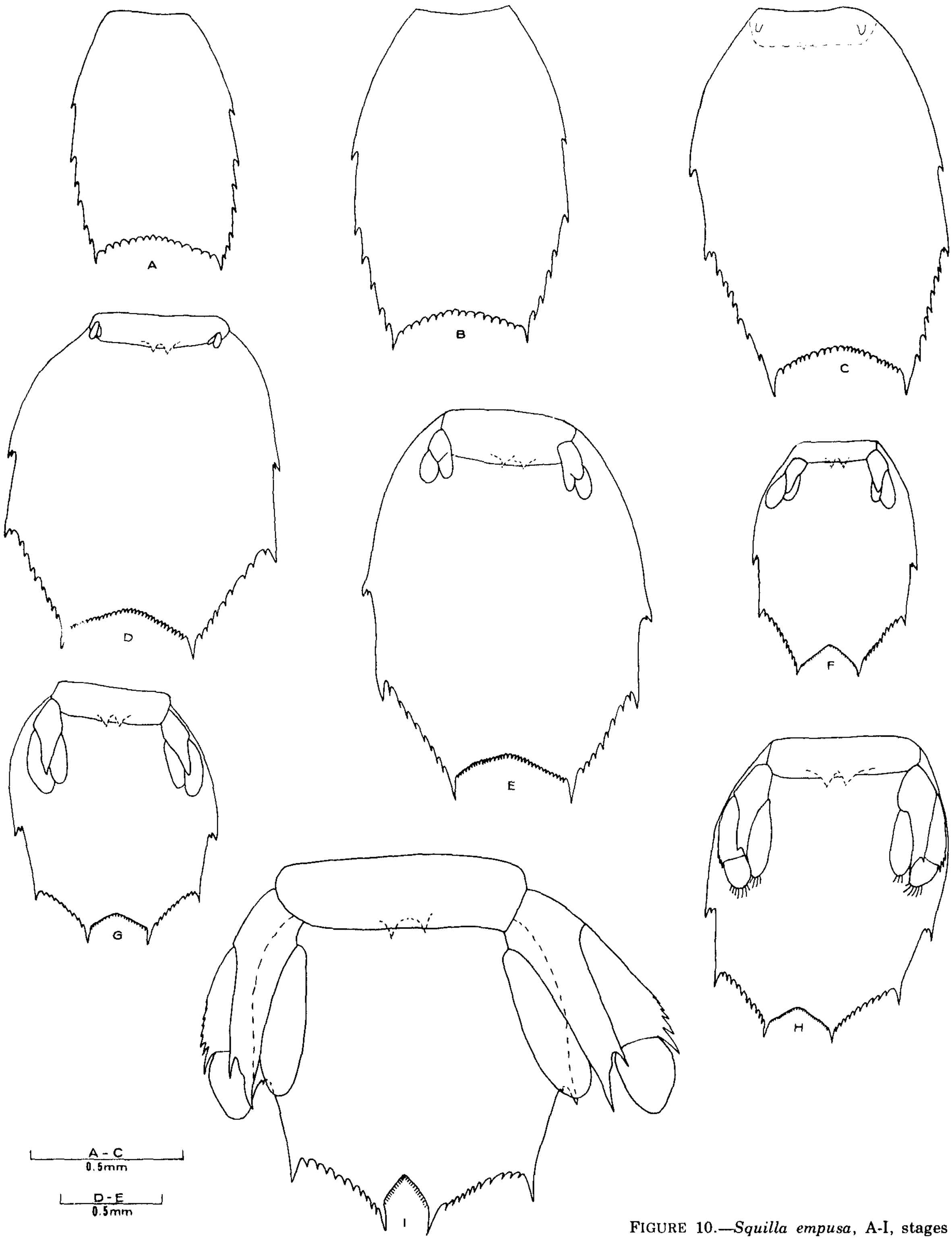

FIGURE 10.—*Squilla empusa*, A-I, stages I-IX respectively, tail fans. Setae omitted from uropods of stage IX.

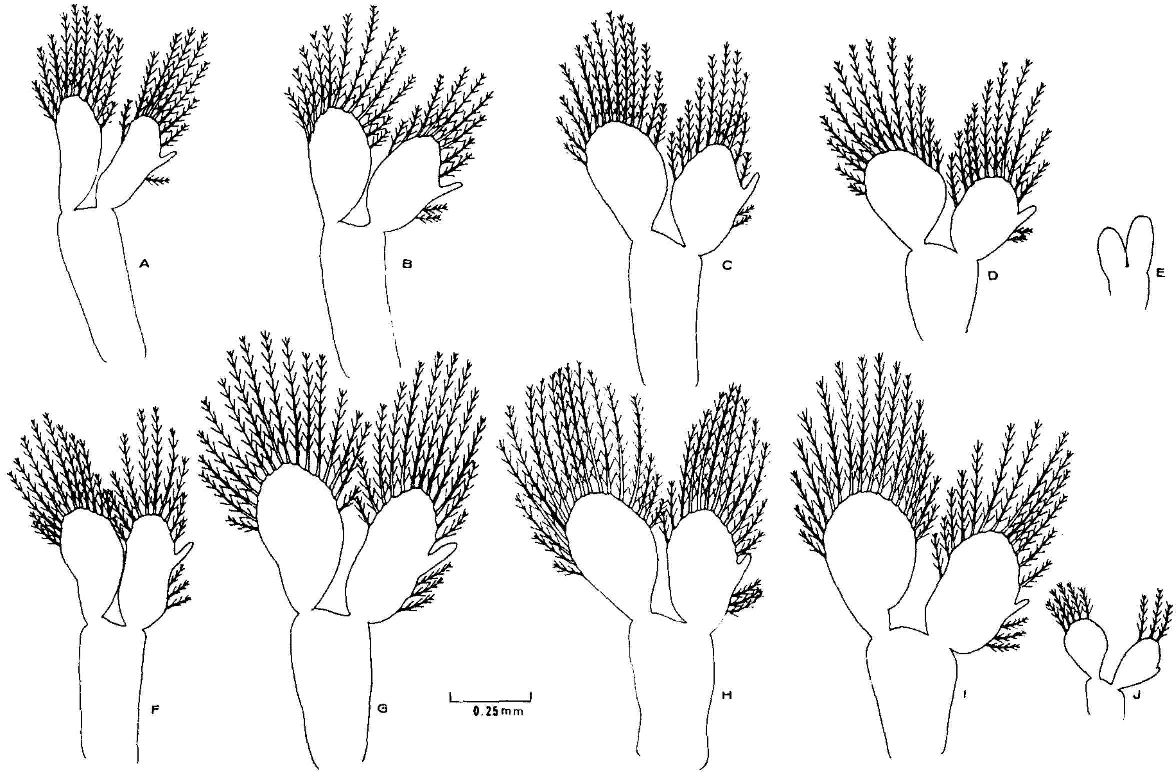

FIGURE 11.—*Squilla empusa*, A-E: stage III, first to fifth pleopods respectively, F-J: stage IV, first to fifth pleopods respectively.

Third, fourth, and fifth maxillipeds (Figure 13A to 13C) unsegmented buds.

Pereiopods (Figure 14A to 14C) present as buds.

Posterolateral angles of pleomeres acute. Pleopods one through four (Figure 11F to 11I) increase setation. Fifth pleopod (Figure 11J) setose and possessing appendix interna.

Sixth abdominal somite articulated. Uropods (Figure 10D) biramous.

Pleotelson (Figure 10D) with 1 denticle in axis of lateral spine, 8 or 9 pairs of intermediate denticles, 23 to 30 submedian denticles.

Stage V (Figure 15)

Measurements (mm): RL, 2.50 to 3.25; PL, 1.50 to 1.65; TL, 8.50 to 9.00; CL, 2.30 to 2.50; PW, 1.40 to 1.60.

Antennule (Figure 2E) with three-segmented inner flagellum armed with two to four setae on distal half of proximal segment; median flagellum also three-segmented.

Antenna (Figure 3E) with 19 to 23 plumose setae, length of unsegmented endopod now nearly equal to segments bearing it.

Epistome with small apical spine.

Mandible (Figure 4E) essentially unchanged.

Maxillule (Figure 5E) with coxal endite bearing 8 to 12 teeth.

Maxilla (Figure 6E) with 10 or 11 setae.

First maxilliped (Figure 7E) with 13 to 17 strong setae arranged in five or six groups of 2 to 4, carpus with 5 to 8 distal setae.

Second maxilliped (Figure 8E) with propodus armed with 30 to 43 denticles.

Third, fourth, and fifth maxillipeds (Figure 13D to 13F) still unsegmented, but increased in length.

Pereiopods (Figure 14D to 14F) present as bifurcated buds.

Uropods (Figure 10E) with basal prolongation present.

Pleotelson (Figure 10E) with 8 to 10 pairs of intermediate denticles, 28 to 33 submedian denticles.

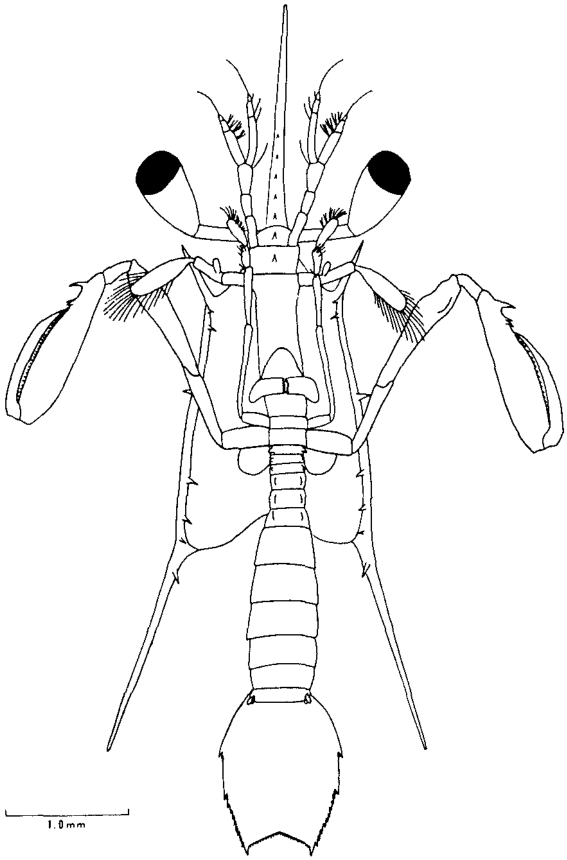

FIGURE 12.—*Squilla empusa*, stage IV, ventral view.

Stage VI (Figure 17A)

Measurements (mm): RL, 3.00 to 3.50; PL, 1.65 to 2.00; TL, 9.80 to 10.60; CL, 2.65 to 2.95; PW, 1.45 to 1.75.

Antennule (Figure 2F) with four-segmented inner flagellum. Median flagellum with three segments. Outer flagellum with 12 to 14 aesthetascs arranged in four groups of 2 or 3, each group with a seta.

Antenna (Figure 3F) with 22 to 25 plumose setae, endopod now two-segmented.

Mandible (Figure 4F) essentially unchanged.

Maxillule (Figure 5F) with coxal endite bearing 10 to 12 marginal teeth and 1 or 2 very short medial setae, palp well developed, armed with 2 setae.

Maxilla (Figure 6F) five-segmented, subproximal segment with endite bearing 14 to 19 setae. Palp articulated.

First maxilliped (Figure 7F) with 18 to 22 strong setae arranged in six or seven groups of 2 to 4 on propodus, carpus with 8 to 12 distal setae, conspicuous epipod present.

Second maxilliped (Figure 8F) with 33 to 47 denticles along inner margin of propodus.

Third maxilliped (Figure 13G) with endopod four-segmented, dactylus not reflected against propodus.

Fifth maxilliped (Figure 13I) with endopod unsegmented.

Pereiopods (Figure 14G to 15I) unsegmented, distally bifurcate, increased in length.

Pleopods one through five (Figure 16F to 16J) with gills present as buds on inner proximal margin of exopod.

Uropods (Figure 10F) with basal prolongation half length of endopod, exopod with or without one spine on outer margin.

Pleotelson (Figure 10F) with 8 to 10 pairs of intermediate denticles. 29 to 33 submedian denticles.

Stage VII (Figure 17B)

Measurements (mm): RL, 3.20 to 3.70; PL, 2.00 to 2.20; TL, 11.60 to 13.60; CL, 2.85 to 3.55; PW, 1.85 to 2.30.

Antennule (Figure 2G) with seven-segmented inner flagellum, median flagellum five-segmented, outer flagellum with 18 or 19 aesthetascs arranged in five or six groups of 2 or 3, each with a seta.

Antenna (Figure 3G) with 32 to 39 plumose setae, endopod with three segments.

Mandible (Figure 4G) essentially unchanged.

Maxillule (Figure 5G) with coxal endite bearing 13 marginal teeth and 2 medial setae, endite with spine flanked by 1 strong seta. Palp unchanged.

Maxilla (Figure 6G) four-segmented, the two more proximal segments each with one endite. Maxilla armed with 32 to 34 setae.

First maxilliped (Figure 7G) with 23 to 26 strong setae on propodus, in seven or eight groups of 2 to 4, carpus with 21 to 27 setae.

Second maxilliped (Figure 8G) with 52 to 60 denticles along inner margin of propodus.

Third, fourth, and fifth maxillipeds (Figure 13J to 13L) fully articulated.

Third maxilliped (Figure 13J) with dactylus armed with spinules and reflected against propodus, latter armed with 10 or 11 spinules, carpus with 4 to 6 spinules.

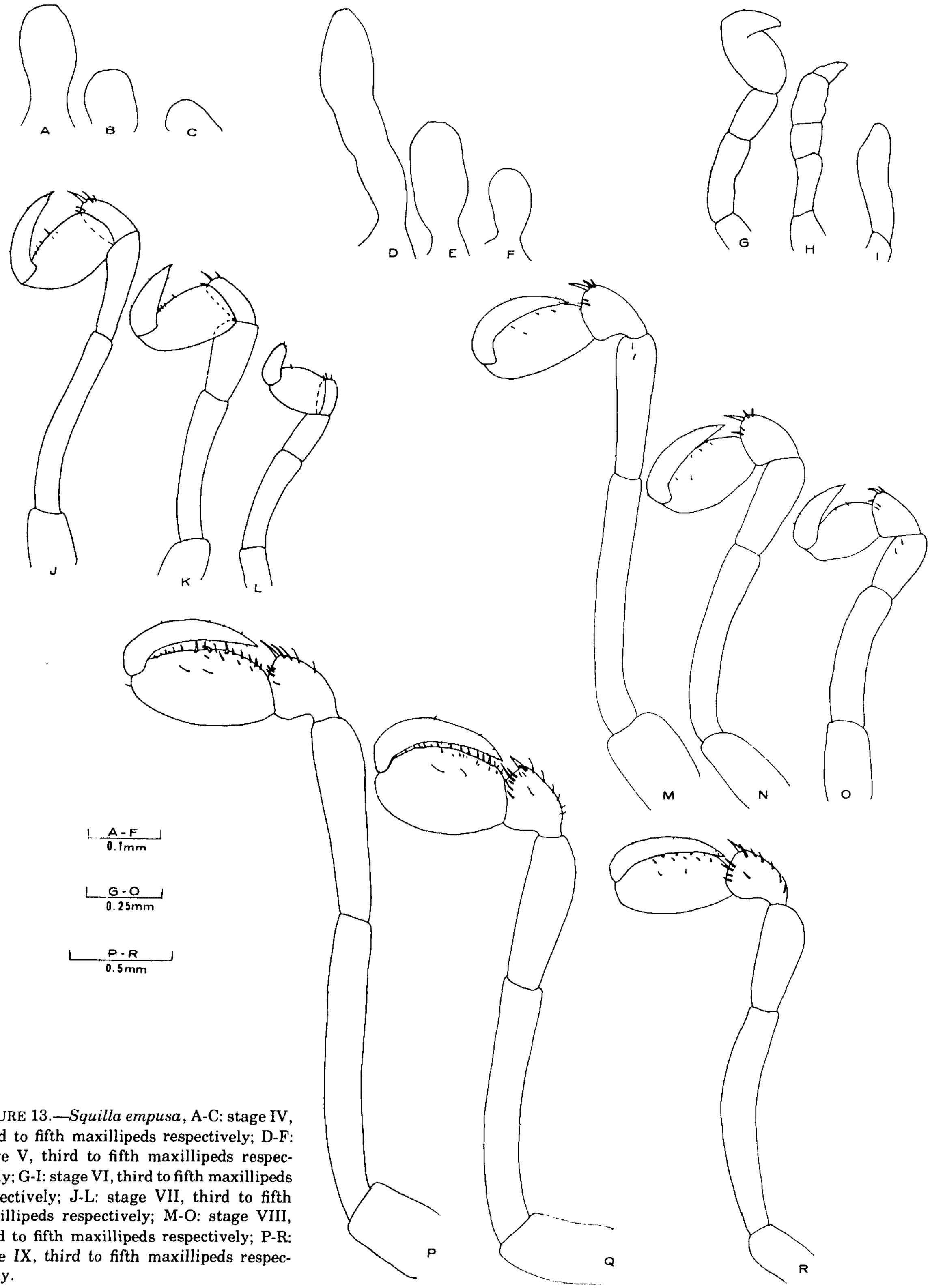

FIGURE 13.—*Squilla empusa*, A-C: stage IV, third to fifth maxillipeds respectively; D-F: stage V, third to fifth maxillipeds respectively; G-I: stage VI, third to fifth maxillipeds respectively; J-L: stage VII, third to fifth maxillipeds respectively; M-O: stage VIII, third to fifth maxillipeds respectively; P-R: stage IX, third to fifth maxillipeds respectively.

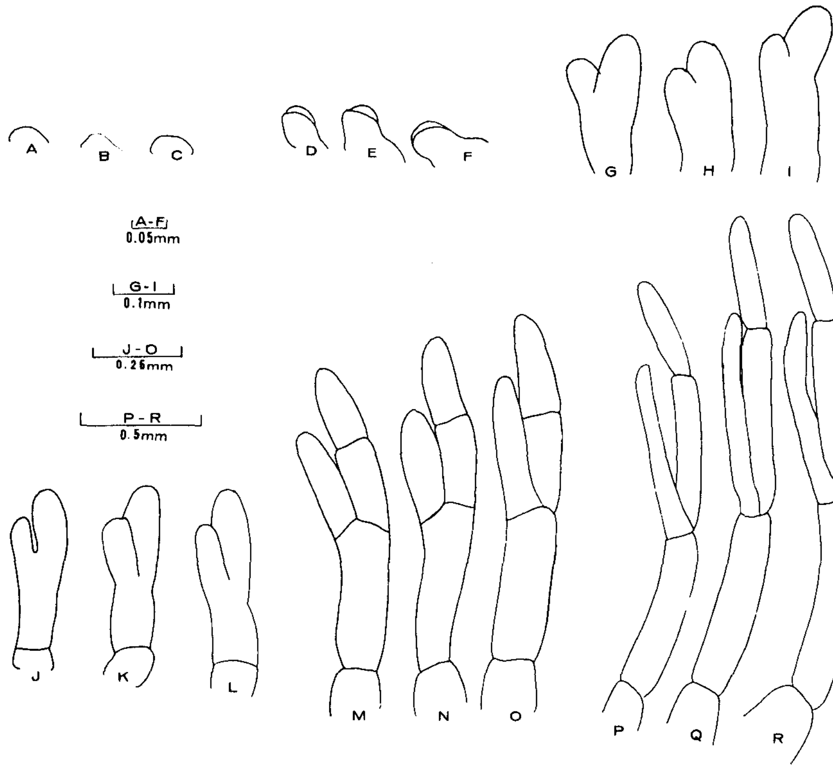

FIGURE 14.—*Squilla empusa*, A-C: stage IV, first to third pereiopods respectively; D-F: stage V, first to third pereiopods respectively; G-I: stage VI, first to third pereiopods respectively; J-L: stage VII, first to third pereiopods respectively; M-O: stage VIII, first to third pereiopods respectively; P-R: stage IX, first to third pereiopods respectively.

Fourth maxilliped (Figure 13K) with dactylus armed with spinules and partially reflected against propodus, latter armed with four to eight spinules, carpus with four to six spinules, epipod present.

Fifth maxilliped (Figure 13L) segmented, dactylus unarmed and not reflected against unarmed propodus, carpus with zero to three spinules.

Pereiopods (Figure 14J to 14L) with clearly differentiated endopods and exopods, though segmentation not yet distinct.

Pleopods (Figure 18A to 18E) with bilobed rudimentary gills.

Sixth pleomere partially separated from telson. Uropods (Figure 10G) with basal prolongation acute. Exopod with one or two spines on outer margin, armed with zero to five plumose setae. Endopod with zero to two plumose setae.

Pleotelson (Figure 10G) with 9 or 10 pairs of intermediate denticles, 32 to 35 submedian denticles.

Stage VIII (Figure 19)

Measurements (mm): RL, 3.25 to 3.45; tL, 2.30 to 2.50; TL, 13.90 to 15.30; CL, 3.90 to 4.35; TW, 2.25 to 2.65.

Antennule (Figure 2H) with inner flagellum bearing 9 to 11 distinctly articulated segments. Median flagellum with five to seven distinct segments. Outer flagellum with 21 to 23 aesthetascs arranged in six or seven groups of 2 or 3, each group with a seta in addition.

Antenna (Figure 3H) with 40 to 55 plumose seta.

Mandible (Figure 4H) essentially unchanged.

Maxillule (Figure 5H) with coxal endite bearing 15 to 19 marginal teeth and 2 to 4 medial setae, distal margin of basis with 1 median seta.

Maxilla (Figure 6H) armed with 40 to 58 setae.

First maxilliped (Figure 7H) with 29 to 31 strong setae on propodus arranged in eight groups of 2 to 5, carpus with 37 to 44 setae.

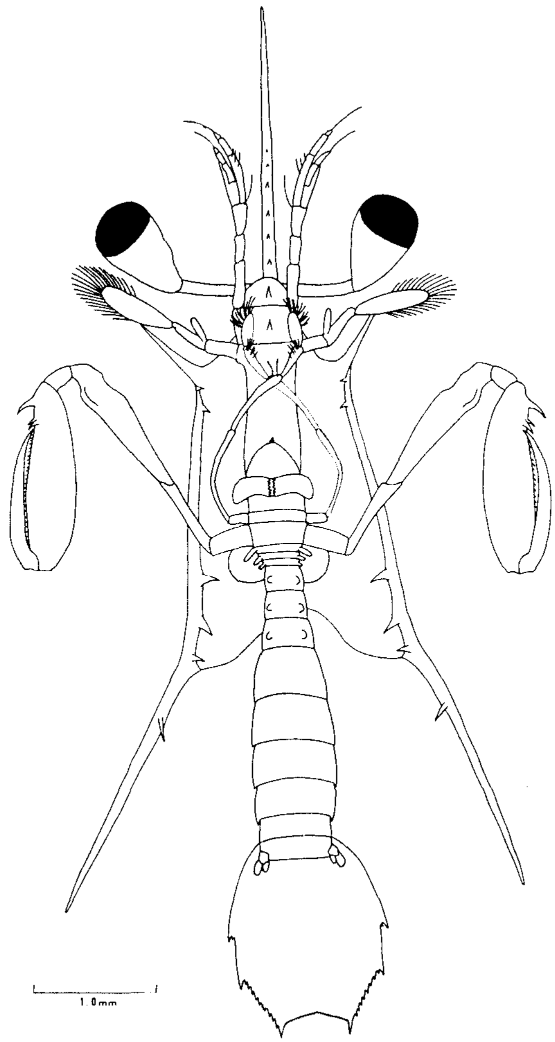

FIGURE 15.—*Squilla empusa*, stage V, ventral view.

Second maxilliped (Figure 8H) with 61 to 75 denticles on propodus.

Third, fourth, and fifth maxillipeds (Figure 13M to 13O) with dactylus armed with spinules and reflected against propodus, epipods present.

Third maxilliped (Figure 13M) with propodus armed with 12 to 21 spinules, carpus with 6 to 9 spinules.

Fourth maxilliped (Figure 13N) with propodus armed with 12 to 16 spinules, carpus with 5 to 8 spinules.

Fifth maxilliped (Figure 13O) with propodus armed with 6 to 11 spinules, carpus with 4 to 7 spinules.

Pereiopods (Figure 14M to 14O) with two-segmented exopods, endopods shorter, unsegmented.

Pleopods (Figure 20A to 20E) with trilobed gills.

Sixth abdominal somite completely separated from telson. Uropods (Figure 10H) with two-segmented exopod. Basal segment with 2 to 4 spines on outer distal margin, apical segment with 4 to 14 plumose setae on distal margin. Endopod of uropod with four to eight plumose setae on distal margin.

Telson (Figure 10H) with 10 pairs of intermediate denticles and 31 to 35 submedian denticles.

Stage IX (Figure 21)

Measurements (mm): RL, 2.40 to 4.50; tL, 2.30 to 2.60; TL, 13.00 to 17.50; CL, 3.00 to 3.90; TW, 2.10 to 2.80.

Rostrum with decrease in number of spinules, now with two to six spinules; with or without minute distal spinules.

Antennule (Figure 2I) with inner flagellum bearing 14 to 20 distinctly articulated segments. Median flagellum with 8 to 11 distinctly articulated segments. Outer flagellum with 23 to 33 aesthetascs arranged in seven to nine groups of 2 to 7, each group with a seta.

Antenna (Figure 3I) with 48 to 60 plumose setae, endopod with 6 to 9 segments.

Mandible (Figure 4I) essentially unchanged.

Maxillule (Figure 5I) with coxal endite bearing 20 to 25 marginal teeth and 1 or 2 medial setae, margin of basal endite with 1 or 2 setae.

Maxilla (Figure 6U) with 78 to 131 setae.

First maxilliped (Figure 7I) with 35 to 44 setae arranged in 9 or 10 groups of 2 to 5, carpus with 59 to 107 setae, dactylus with or without cluster of setae on median outer margin, propodus with or without cluster of setae on distal outer margin.

Second maxilliped (Figure 8I) with 71 to 92 denticles on propodus.

Dactylus of third, fourth, and fifth maxillipeds (Figure 13P to 13R) with or without regularly spaced setae along outer margin, propodus with or without a cluster of setae on distal outer margin.

Third maxilliped (Figure 13P) with propodus bearing 19 to 56 spinules, carpus with 11 to 22 spinules.

Fourth maxilliped (Figure 13Q) with propodus bearing 17 to 51 spinules, carpus with 10 to 28 spinules.

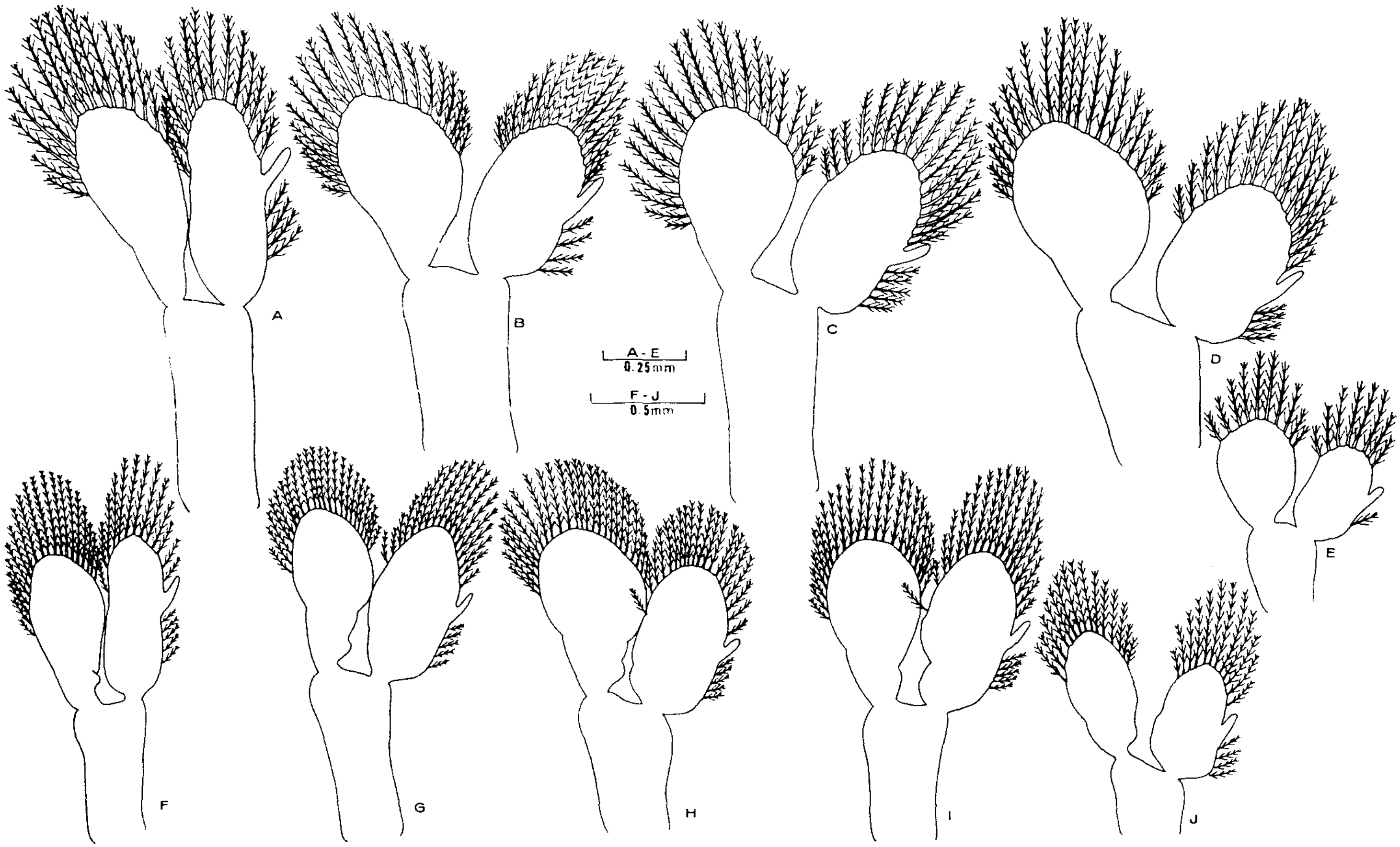

FIGURE 16.—*Squilla empusa*, A-E: stage V, first to fifth pleopods respectively; F-J: stage VI: first to fifth pleopods respectively.

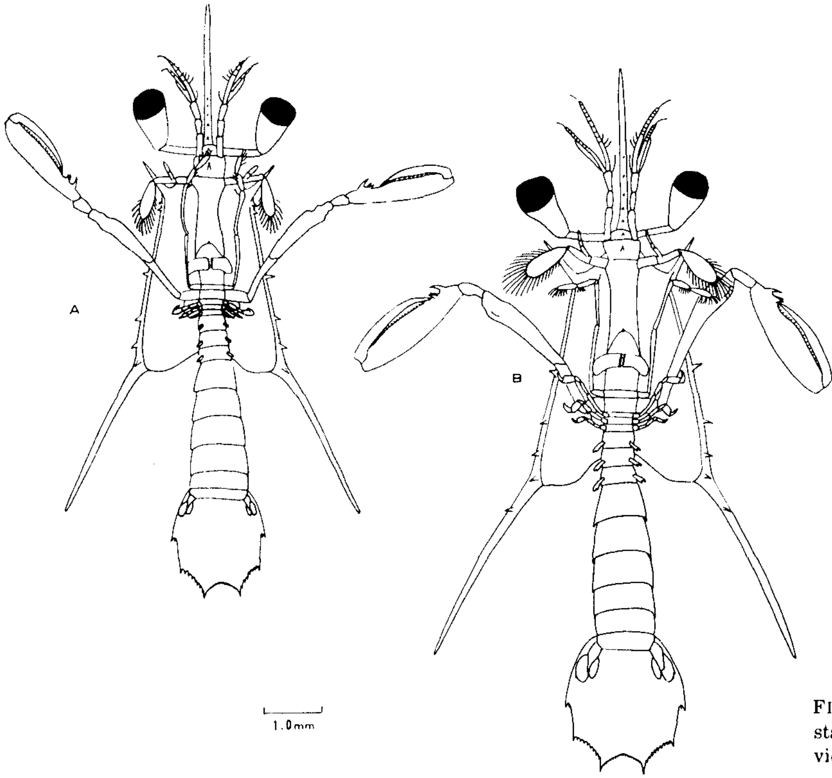

FIGURE 17.—*Squilla empusa*, A-B: stages VI and VII respectively, ventral views.

Fifth maxilliped (Figure 13R) with propodus bearing 18 to 40 spinules, carpus with 9 to 20 spinules.

Pereiopods (Figure 14P to 14R) slender with or without distal segment of exopods setose.

Pleopods (Figures 22A to 22C; 23A, 23B) with distal lobe of gill pinnate.

Uropod (Figure 26C) with basal segment of exopod armed with 6 to 8 spines, apical segment of exopod with 17 to 60 plumose setae. Endopod of uropod with 10 to 38 plumose setae. Inner spine of basal prolongation with blunt spine on outer proximal margin. Basal uropod segment with a dorsal spine on distal margin.

Telson (Figure 14I) with 8 to 10 pairs of intermediate denticles, 26 to 34 submedian denticles.

Postlarva (Figure 24)

Measurements (mm): RL, 0.50 to 0.60; CL, 2.90 to 3.30; TW, 2.55 to 3.10; RW, 0.65 to 0.75; tL, 1.95 to 2.55; TL, 12.3 to 14.20.

Eyes large, extending to middle of second segment of antennular peduncle. Cornea bilobed, set obliquely on stalk. Ocular scales rounded, anterior margin of opthalmic somite evenly rounded.

Antennular process produced into blunt spine directed anterolaterally, antennular peduncle slightly shorter than carapace, antennule (Figure 25A) with inner flagellum bearing 34 segments, median flagellum with 30 segments, outer flagellum with 15 segments and 22 aesthetascs arranged in eight groups of 2 or 3.

Antenna (Figure 25B) with 63 to 75 plumose setae, endopod with 16 segments.

Rostral plate wider than long, lateral margins tapering to rounded apex. Median carina present.

Anterolateral angle of carapace without spine, almost forming right angle, posterolateral margins broadly rounded, carinae poorly developed, median carina not bifurcate anteriorly or posteriorly, intermediate and lateral carinae present, reflected carinae absent.

Mandible (Figure 25C) serrate, mandibular palp absent.

Maxillule (Figure 25D) with coxal endite bearing 26 to 27 strong marginal teeth and 6 to 9 small medial teeth. Basal endite with one spine flanked

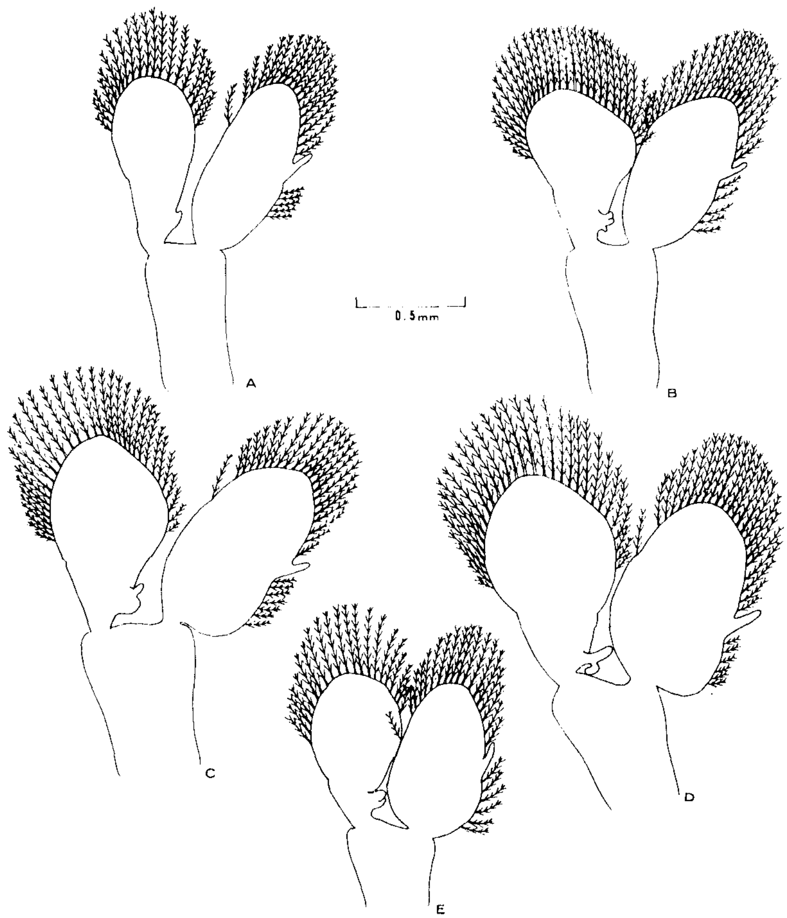

FIGURE 18.—*Squilla empusa*, A-E: stage VII, first to fifth pleopods respectively.

by one strong seta. Distal margin of basis with three setae. Endopod present as palp on distal margin of basis, armed with two setae.

Maxilla (Figure 25E) four-segmented, two proximal segments with endites, second bilobed.

Five pairs of maxillipeds (Figure 25F to 25J) each maxilliped with one epipod. First maxilliped (Figure 25F) with distal margin of propodus bearing 14 teeth, inner margin with 48 to 50 strong setae arranged in 10 transverse rows, 2 or 3 most distal setae spatulate with strong setules.

Second maxilliped (Figure 25G) with dactylus bearing six teeth, pectinate propodus with three moveable proximal spines, dorsal ridge of carpus undivided.

Pereiopods (Figure 26A) with setose endopod and exopod.

Last three thoracic somites with unarmed submedian and intermediate carinae. Lateral process of fifth thoracic somite subacute, sloping posteriorly. Lateral processes of next two somites bilobed each with a small anterior lobe and a large broadly rounded posterior lobe. Median ventral keel of eighth somite with rounded apex.

Abdomen broad, depressed, Submedian, intermediate, lateral, and marginal carinae present. Abdominal spines in submedian carinae of sixth somite, intermediate and lateral carinae of fifth and sixth somites, and marginal carinae of fifth somite, formula: submedian 6; intermediate 5 to 6; lateral, 5 to 6; marginal, 5. Sixth abdominal somite with sharp ventral spine anterior to uropod articulation.

Pleopods (Figure 26B to 26F) with gills. Pleopod setation presented in Table 2.

Uropod (Figure 26G) with eight graded moveable spines on outer margin of proximal segment of exopod, last extending to middle of apical segment. Apical segment of exopod extending posteriorly to apex of intermediate spine. Basal seg-

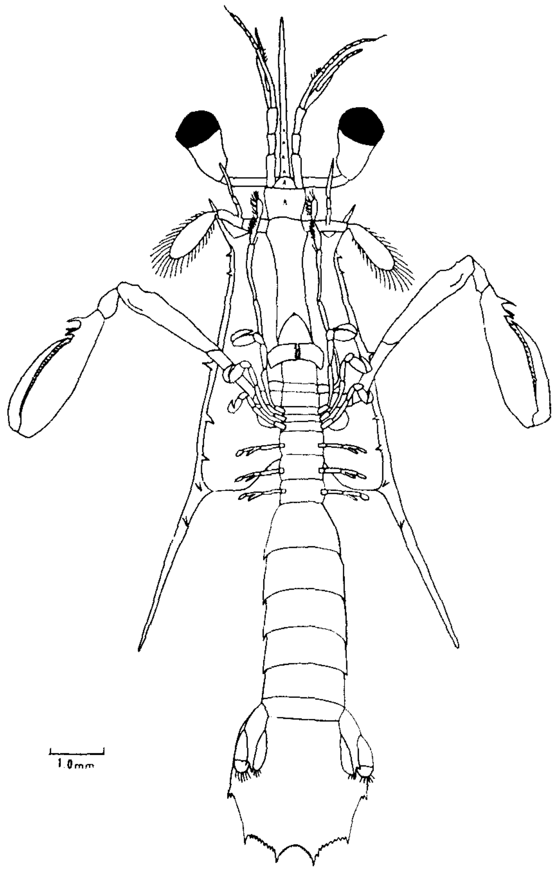

FIGURE 19.—*Squilla empusa*, stage VIII, ventral view.

ment of uropod with dorsal spine on distal margin. Basal prolongation of uropod with two spines, mesial longer. Single rounded lobe between spines of prolongation. Mesial margin of basal prolongation sinuate.

Telson (Figure 24) as wide as long, median carina with sharp posterior spine, prelateral lobes absent, postanal ventral carina absent, submedian teeth with moveable apices, denticle formula: submedian, 8 to 10; intermediate, 7 to 10; lateral, 1.

Postlarva white with brown chromatophores on eyes and all appendages except mouthparts. Carapace with few chromatophores. Exposed thoracomeres with chromatophores along posterior margin. Pleomeres with chromatophores along intermediate and lateral carinae and posterior margin. Telson with chromatophores along curved dorsal striations and posterior spine.

TABLE 2.—Number of setae on margins of pleopods of the postlarva of *Squilla empusa*.

	Abdominal somite				
Structure	1	2	3	4	5
Protopod	12-15	12-15	12-15	12-14	8-11
Endopod	55-60	60-71	65-72	63-72	59-67
Exopod	55-59	61-64	62-64	61-63	53-56

DISCUSSION

Brooks (1878) and Faxon (1882) have produced the only prior publications on the larvae of *Squilla empusa*. Brooks partially described the development by reconstruction, and Faxon held an unidentified last stage through metamorphosis to attempt to identify it with the adult. Although Brooks' illustrations and descriptions indicate that he probably was working with *S. empusa*, Faxon's do not. The carapace of Faxon's last stage larvae appears to be too broad, the posterolateral spines are too short, and a spinule is present on the posterior margin of the carapace midway between the dorsal and posterolateral spines. Furthermore, in Faxon's illustrations both the last larval stage and postlarva have broad abdomens with the first pleomere being as wide as the sixth, but in *S. empusa*, the abdomen is tapered with smaller anterior pleomeres grading into larger posterior ones.

Faxon collected his larva from Newport, R.I., where only four species of stomatopods are known to reside: *S. empusa*, *Nannosquilla grayi*, *Heterosquilla armata*, and *Platysquilla enodis* (Manning 1974). Because the telson of Faxon's postlarva bears four intermediate denticles, it can be attributed to the Squillidae, and *S. empusa* is the only squillid known to inhabit the area; the other three species belong to the Lysiosquillidae. Few larval descriptions have been made on southern species of squillid larvae, and of these none possesses the pair of spines on the posterior margin of the carapace, seen in Faxon's larva, nor does *S. empusa*. If Alikunhi (1952, 1967) was correct in his identification of the late larva and postlarva, these spines occur on *Cloridopsis scorpio* from the Indian Ocean. The spines may be only a specific character or they may be diagnostic for the genus *Cloridopsis*. The only member of that genus inhabiting the waters of the Western Atlantic is *C. dubia* which ranges from South Carolina to Brazil. Perhaps Faxon collected a larva of *C. dubia* which drifted north with the Gulf Stream. Until more larval descriptions are worked out for western At-

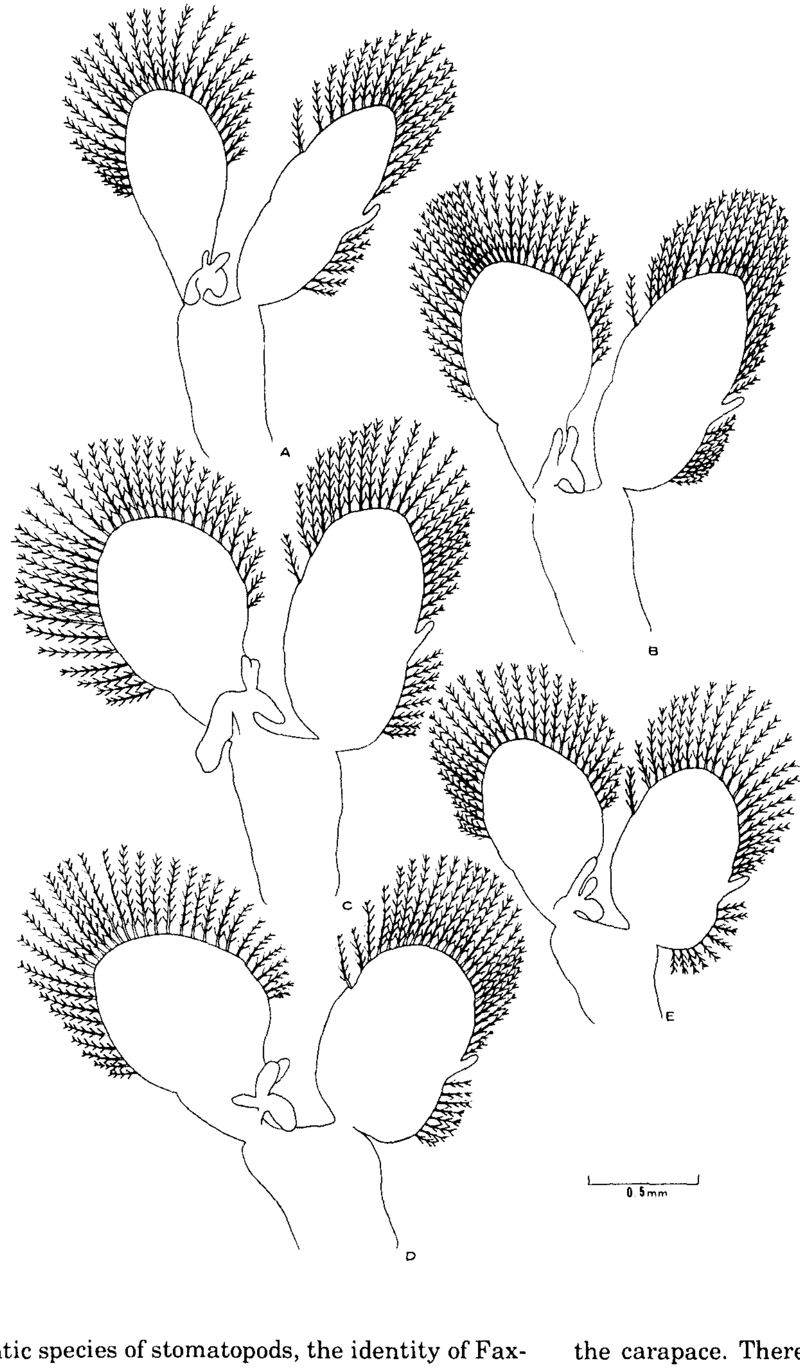

FIGURE 20.—*Squilla empusa*, A-E: stage VIII, first to fifth pleopods respectively.

lantic species of stomatopods, the identity of Faxon's larva will remain uncertain.

To identify larvae of *S. empusa* the spinules of the carapace and denticles of the telson should be examined. Stages I and II possess four spinules on the lateral margin of the carapace and four intermediate denticles. The third to ninth stages are armed with six spinules on the lateral margin of the carapace. There are two anterior and three posterior spinules all ventrally directed, and one median spinule laterally directed. The telsons of stages III to IX have 8 to 10 intermediate denticles.

Except for Provenzano and Manning (1978), who reared *Gonadactylus oerstedii* from hatching to metamorphosis, experimenters who have at-

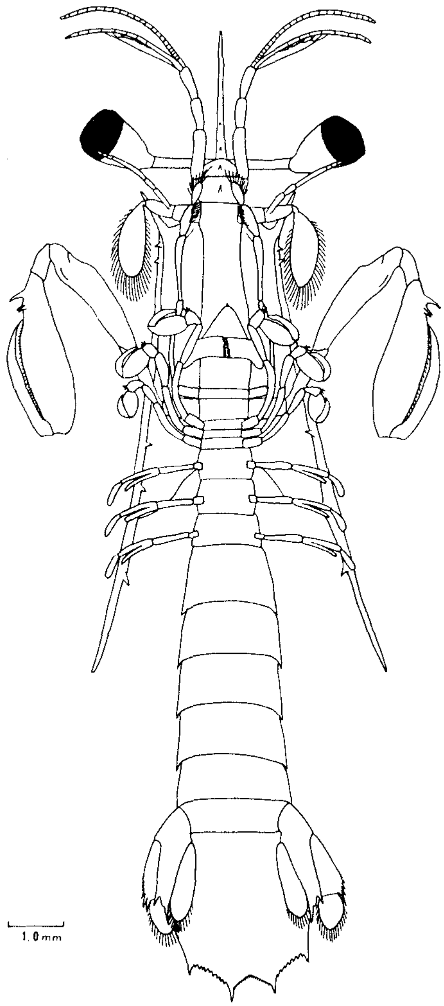

FIGURE 21.—*Squilla empusa*, stage IX, ventral view.

tempted to hatch and rear larvae either to link them with an adult or to describe the entire larval development have been unsuccessful at rearing larvae past the first pelagic stage because the larvae could not be induced to feed (Manning and Provenzano 1963). Pyne (1972) was unable to rear *Pterygosquilla armata schizodontia* eggs past the first pelagic stage, but did hold stages I to VII larvae taken from the plankton for periods as long as 10 to 16 days wherein the larvae passed through at least one ecdysis. Pyne also found it possible to keep later stage larvae for very much longer periods of up to 165 days during which time they molted as many as six times. Pyne reared his larvae in mass culture using 4-in (10.2-cm) finger bowls. Alikunhi (1975) reared planktonic larvae of *Oratosquilla nepa* in aquaria through metamorphosis until they reached adulthood, bred, and produced eggs.

The manner in which all species of Squillidae develop is similar. All Squillidae hatch as pseudozeae with four pairs of pleopods and develop into the alima form. Some, if not all, pass through two propelagic stages before the first truly planktonic stage. The alima is characterized by a telson with four or more intermediate denticles, the distance between the submedian spines in later stages being not larger than that between the intermediate and submedian spines, the propodus of the second maxilliped bearing three basal spines, the antennular somite generally having a median spine, the posterolateral spine of the carapace having a basal accessory spine, the eyestalks long, and the exopod of the uropod being longer than the endopod (Gurney 1942, 1946). Alikunhi (1952) added that alima larvae possess carapaces armed with a varying number of spinules on the lateral margins, the sixth abdominal somite usually being equipped with a pair of submedian dorsal spines, and in advanced larvae, the posterolateral angles of the abdominal somites ending in acute or subacute spines.

Alikunhi (1952) noted that between allied species, the specific differences are often "trivial" but remarkably constant. He determined that some features, such as the size of the final pelagic stage, the shape and spinulation of the carapace, telson, and uropods, and the presence or absence of teeth other than the terminal on the dactylus of the second maxilliped, hardly show any variation within a species. These characters may be used for specific determinations but are presently of little aid in defining generic alliances for three reasons.

First, relatively few stomatopods have been associated definitely with the adult of the species.

Second, most of these have had described only one larval stage of the entire development. Only 19 of the Squillidae have been definitely connected with their larval forms. Provenzano and Manning (1978) listed 17 species of identified stomatopod larvae, but *O. massavensis* was omitted and *S. empusa* has now been added to the list. Of the 19 species, only 2, *P. armata schizodentia* and *S. empusa*, have been reared in the laboratory through essentially their entire pelagic development. Two additional species have been hatched from eggs obtained from a known adult and the first pelagic stage described, i.e., *Clorida choprai* by Gurney

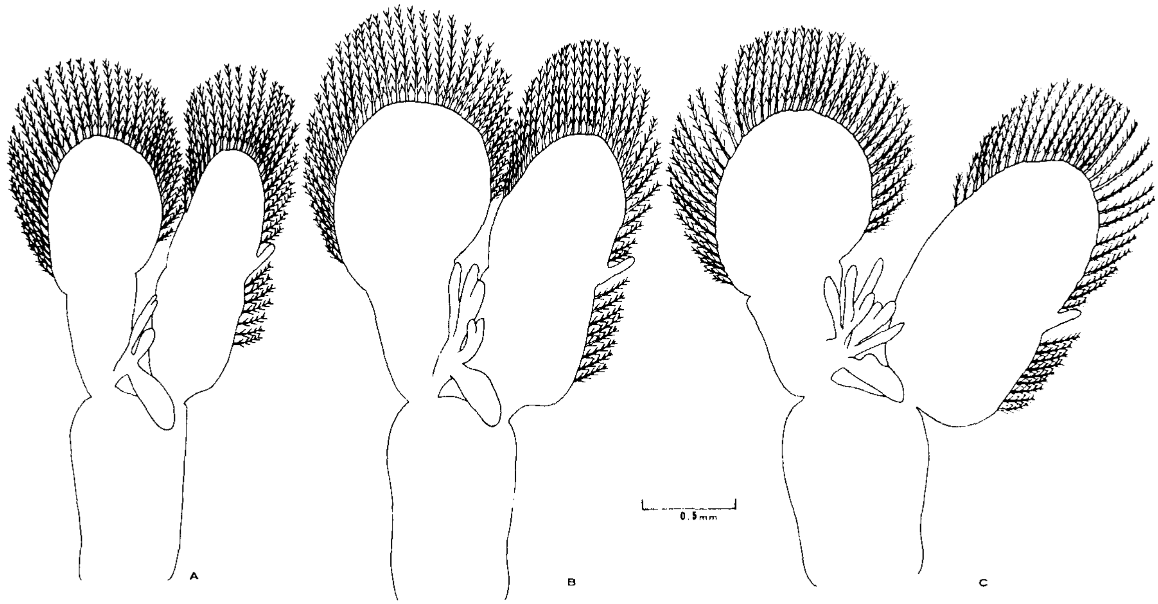

FIGURE 22.—*Squilla empusa*, A-C: stage IX, first to third pleopods respectively.

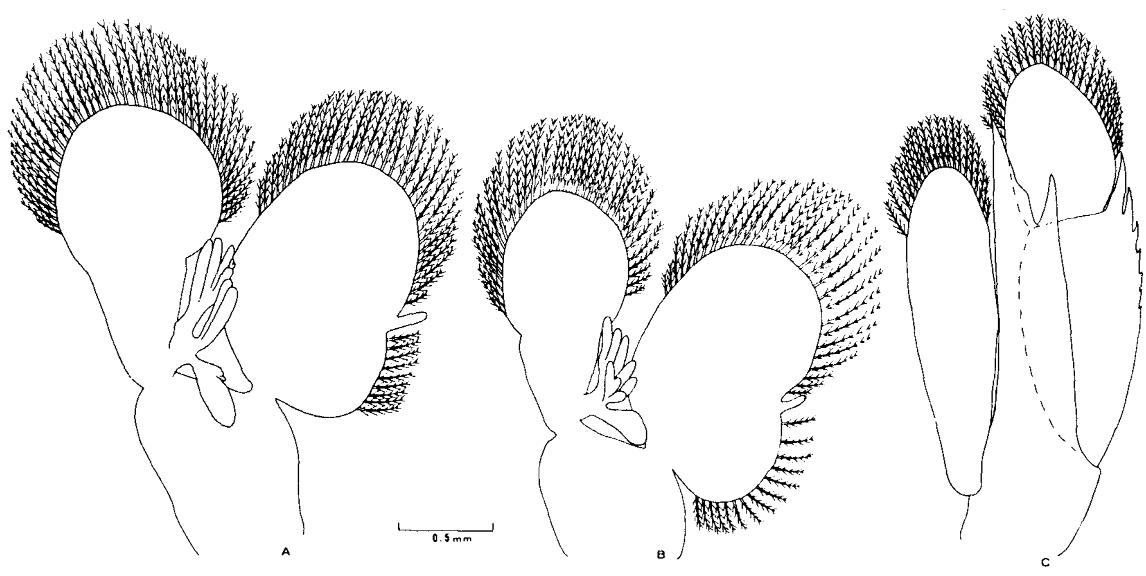

FIGURE 23.—*Squilla empusa*, A-B: stage IX, fourth to fifth pleopods respectively; C: stage IX, uropod.

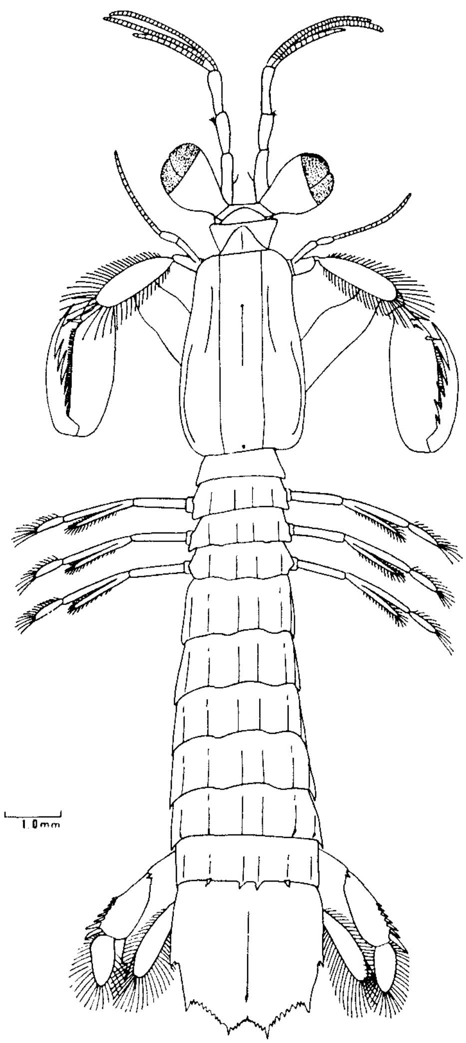

FIGURE 24.—*Squilla empusa*, postlarva, dorsal view.

(1946) and *S. mantis* by Giesbrecht (1910), and the remainder have had the last stage described by holding the final pelagic stage until metamorphosis occurred and the stomatopod could be correlated with an adult of the species. Reconstructions of the larval development of three species, *S. mantis* by Giesbrecht (1910), *O. oratoria* by Komai and Tung (1929), and *O. massavensis* by Gohar and Al-Kholy (1957), were attempted by collecting larval stages from the plankton and piecing them together. Metamorphosis from the last larval stage was obtained for *O. massavensis*, but since the larvae were not reared, the larval histories may not be entirely factual. Thus, because so few larval forms have been identified and because most of these have had only one stage described, it is difficult to discover which characters are shared by all members of a genus and which characters are only specific. Of the nine genera of Squillidae which have had larvae described, four genera have had one or more larval stages of a single species described, four more genera have had two species identified, and one genus has had larvae of eight species described. A determination of generic characters is difficult at best for those genera for which only one or two species have been described, especially since there are no adequately represented genera with which to compare characters.

The third reason why specific characters are of little help in generic definition lies in the incomplete descriptions of the larval stages. Characters noted by one author are frequently omitted by another, so that even for the genus *Oratosquilla*, represented by larval descriptions of eight species, consistent characters are difficult to recognize.

An assessment of larval characters was attempted to determine which ones were constant within each genus. Most characters mentioned in the descriptions appeared to vary a great deal for the species within a genus, or the characters that varied relatively little within a genus were frequently found in other species of different genera. Of possible value in defining generic associations is the presence or absence of teeth (other than the terminal) on the dactylus of the second maxilliped. These teeth occur during the last stage in the genera *Anchisquilla*, *Clorida*, *Pterygosquilla*, and *Squilloides*, although for each of these genera larvae of only one species have been described. The dactylus of *P. armata schizodontia* is armed with 5 to 8 teeth and the first stage is easily diagnosed by the posterior spines of the carapace which bear 6 to 16 spirally arranged, proximal spinules. The spinules are replaced by three ventral spinules in the remaining stages (Pyne 1972). The dactyl of the second maxilliped is equipped with two free teeth in *A. fasciata*, three teeth in *S. lata*, and in *C. latreillei* is usually armed with one tooth, rarely with two (Alikunhi 1952). Newly hatched larvae of *C. choprai* were too inadequately described to be compared with *C. latreillei* (Tweedie 1935; Gurney 1946), but the dactylus of the second maxilliped was observed to be unarmed. This is not surprising since *C. latreillei* and *S. lata* develop teeth on the dactylus of the second maxilliped in the later stages and *P. armata schizodontia* develops its first tooth in the third stage.

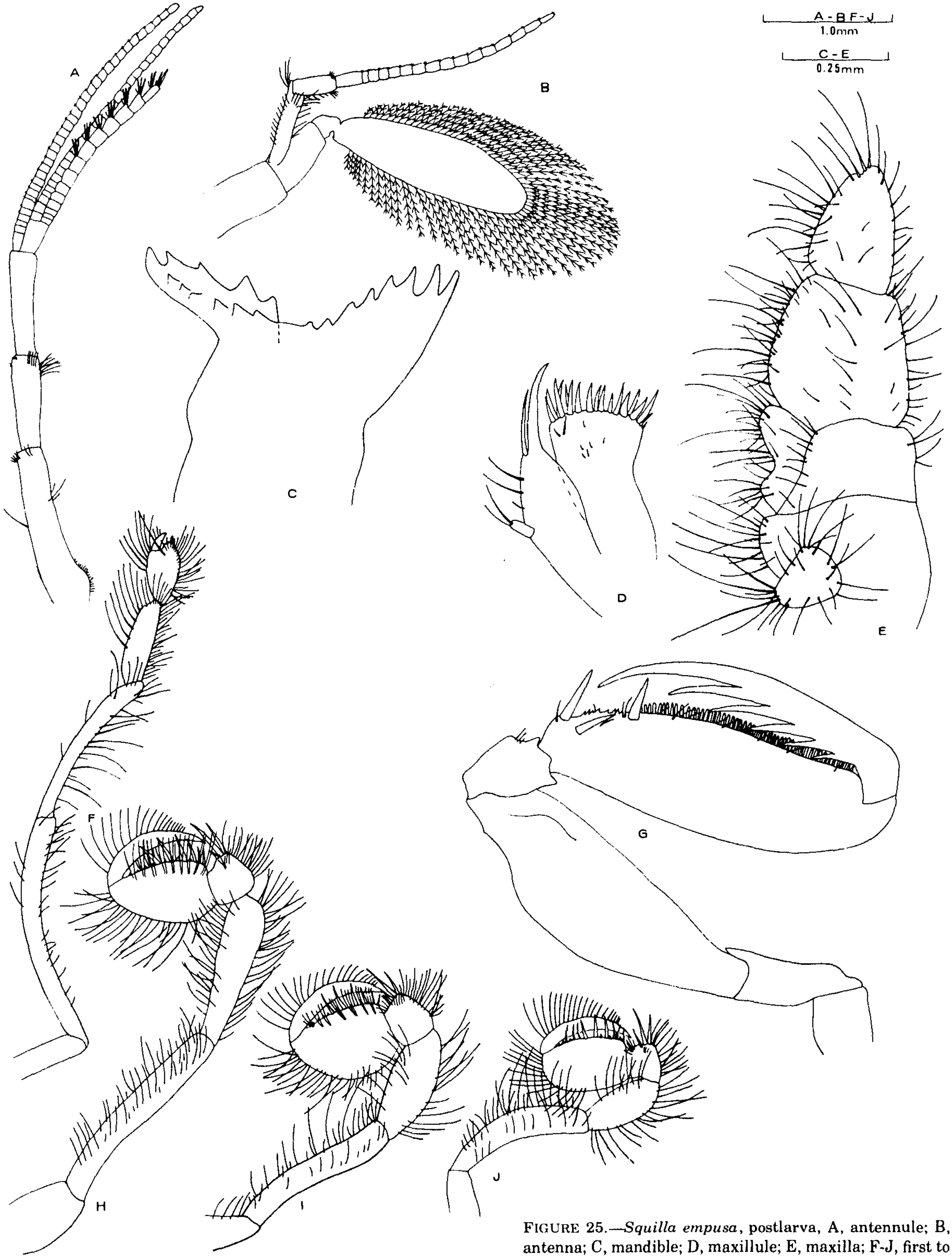

FIGURE 25.—*Squilla empusa*, postlarva, A, antennule; B, antenna; C, mandible; D, maxillule; E, maxilla; F-J, first to fifth maxillipeds respectively.

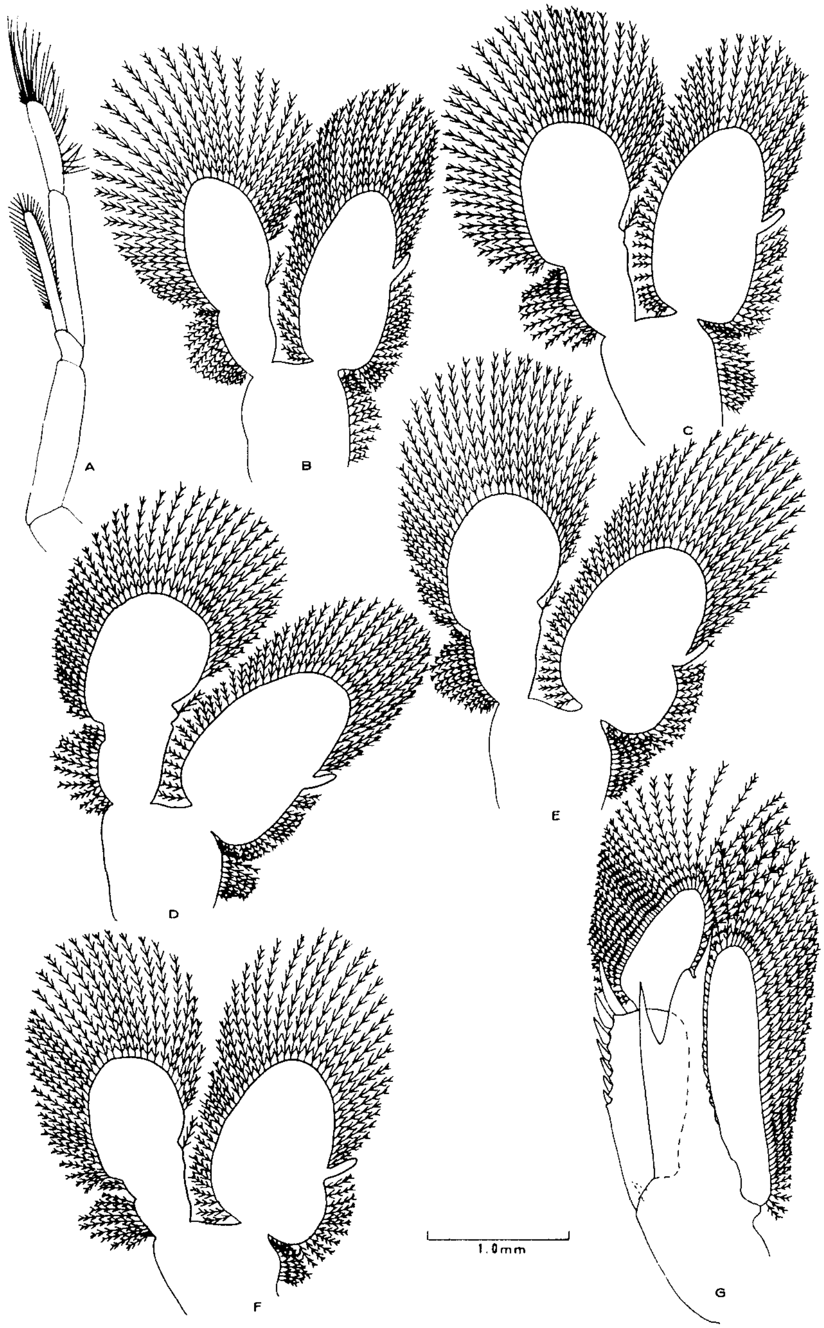

FIGURE 26.—*Squilla empusa*, postlarva, A, first pereipod; B-F, first to fifth pleopods respectively; G, uropod.

The second maxilliped of the remaining described larvae is unarmed throughout the larval development. To distinguish these genera, other characters, such as the presence or absence of a spine on the basis of the second maxilliped, must be relied on. The spine is definitely born by seven of the eight species of *Oratosquilla*, but was not mentioned for *O. massavensis*. Other species, *Squilla empusa*, *P. armata schizodontia*, *Alima hyalina*, and *Meiosquilla lebouri* have the spine, while *Harpiosquilla harpax* and *A. fasciata* definitely do not.

The development of epipods on five pairs of maxillipeds in older larvae appears to be a generic character of *Squilla* as most other genera bear four pairs of epipods.

Characters such as rostral length and spinulation, carapace and telson shape, size, and spinulation, and overall body size and appearance have been too variable within the limited number of species presently described to use them in defining generic associations of the larvae. Deriving characters which apply to the youngest larvae as well as the old will be difficult since far fewer characters are present in the early stage larvae, and the gross appearance of the young larvae is very similar due to the small degree of differentiation. Other characters such as antennular segmentation, mouthpart morphology, setation, spination of the maxillipeds, or the presence of ocular, antennular, epistomal, or basal uropodal spines may also need to be examined. The setation and spination of the first maxilliped may be of great value in defining alliances of the species as well as in making specific determinations. However, many more complete descriptions of the larval developments undergone by the various species must be accomplished before larval characters can be used in establishing generic relationships.

The postlarva of *Squilla empusa* exhibited the basic features of first stage postlarva as determined for other species by Alikunhi (1967). These include the absence of anterolateral spines on the carapace, the extremely poorly developed carination of the carapace, acutely pointed marginal denticles of the telson, and moveable apices of the submedian spines of the telson. As with the adult, the postlarva possesses the full complement of teeth on the raptorial dactylus, just as Alikunhi (1967) found. Furthermore, the five pairs of epipods found in the adult are also possessed by the postlarva. Other adult characters were developed upon the next molt. The dorsal carinations of the carapace were developed, the lateral processes of the exposed thoracic somites five through eight resembled those of the adult, the marginal denticles of the telson were not as acute, and the submedian spines were fixed. The abdominal spinal formula was still not equal to that of the adult. Nevertheless, after the postlarva had undergone its first molt more than enough characters were shared with the adult to make a definite determination of the species.

CONCLUSIONS

1. *Squilla empusa* undergoes nine pelagic stages before attaining the postlarval stage.
2. The last stage stomatopod larva and postlarva described by Faxon (1882) are not *S. empusa*.
3. Larvae of *S. empusa* may be identified by the spinules of the carapace and the intermediate denticles of the telson. Stages I and II possess four spinules on the lateral margin of the carapace and four intermediate denticles. The third to ninth stages are armed with six spinules on the lateral margin of the carapace. There are two anterior and three posterior spinules all ventrally directed, and one median spinule laterally directed. The telsons of stages III to IX have 8 to 10 intermediate denticles.
4. Rostral length and spinulation, carapace and telson size and spinulation, and overall body size and appearance probably are specific rather than generic characters.
5. The presence or absence of teeth on the dactylus of the second maxilliped, the presence or absence of a spine on the basis of the second maxilliped, and the number of epipods may all be useful characters in determining generic status of larvae belonging to the Squillidae. However, many more complete descriptions of the larval developments undergone by the various species are needed before larval characters can be used in establishing generic relationships.

ACKNOWLEDGMENTS

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