DESCRIPTIONS OF THE LARVAE OF FOUR NORTH PACIFIC PORCELLANIDAE (CRUSTACEA: ANOMURA)[1]

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ABSTRACT

Complete descriptions are given of the zoea and megalopa stages of four porcelain crabs common in the rocky intertidal regions of the Pacific coast of North America. Both larvae reared in the laboratory and larvae taken from the plankton were available for the species *Petrolisthes cinctipes* (Randall), *Petrolisthes eriomerus* Stimpson, *Pachycheles pubescens* Holmes, and *Pachycheles rudis* Stimpson. All four species have a short prezoea stage, two zoeae, and a planktonic megalopa stage. Extensive variation was found in setal numbers between left and right members of appendage pairs and between individuals in these larvae. Setal counts characteristics of species cannot be obtained from one or a few larvae, and ranges in the counts overlap considerably between species. The criteria of Lebour for grouping zoeal types in the Porcellanidae are applied to these four species and comparisons made between all available descriptions of porcellanid larvae. Intermolt growth of appendage buds occur in these four species, and it is concluded that this type of growth is the cause of most of the differences described previously as larval substages. Tabulations of species showing stage variation and intermolt growth are given.

All larval stages of four common Pacific coast rocky intertidal porcelain crabs have been reared in this laboratory. Material obtained from cultures and from the plankton was used for the descriptions given here of the larvae of each species. One of these species, *Pachycheles rudis*, has been described previously (Knight, 1966), and in this case the available material permitted this description to be expanded. Attention was also directed to variation in larval characteristics since adequate numbers of specimens were available for examination.

Gravid female porcelain crabs of the species *Petrolisthes cinctipes* (Randall), *Petrolisthes eriomerus* Stimpson, *Pachycheles rudis* Stimpson, and *Pachycheles pubescens* Holmes were collected from rocky intertidal shores at Boiler Bay and Yaquina Head on the central Oregon coast. *P. rudis* was collected from the lower intertidal (—0.8 to —2.5 ft below mean lower low water) beneath *Phyllospadix* root mats on the seaward sides of large boulders. *Pachycheles pubescens* was collected from burrows and crevices in rock at the same tide level. The *Petrolisthes* species were gathered somewhat higher in the intertidal regions of the two sites beneath loosely bedded rocks and rubble. All four species occur in various other habitats as well (Haig, 1960) but were taken from these areas for convenience. Egg-carrying *Pachycheles rudis* were collected in May and June of 1968. In the same months of 1969, egg-bearing females of the other species were obtained for larval studies. Gravid females were also noted during other months of the year, in agreement with Knudsen's (1964) observations on the reproductive cycles of these species. The specific identity of the females used was confirmed by comparing them to the descriptions given by Haig (1690).

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Female crabs were held individually in 1-liter beakers containing 600 ml of aerated, unfiltered seawater, standing in trays of running seawater ranging in temperature from 10.8° to 15.2°C. The water in the beakers was changed every 2 days. Larvae released by the females were removed from the beakers as soon as a hatch was discovered. Only actively swimming larvae of normal appearance were used.

Glassware for handling and culturing larvae was washed in fresh water, rinsed with distilled water, and steam autoclaved to minimize microbial contamination of the cultures. Seawater used for culturing was collected at high tide from the laboratory seawater system, passed through a sintered glass filter of pore size 40-60 mμ, and stored at 9°C in darkness. The salinity of this water ranged from 32.8 to 33.7‰.

Laboratory-hatched larvae of *Pachycheles rudis* and *Petrolisthes eriomerus* were cultured in flasks, while *P. cinctipes* larvae were reared in mass cultures only. Larvae from a single *Pachycheles pubescens* female were divided between flask and mass cultures. Light received by the larvae was not controlled. In all flask cultures larvae were maintained without aeration, initially with six to eight zoea I larvae per Erlenmeyer flask. The seawater volume allowance ranged from 25 ml per larva for early stages to 50 ml per larva for the larger later stages. Flasks were maintained at either 12°C or 15°C (± 0.01°C) in refrigerated baths of circulating water. All flask cultures were examined daily, mortality recorded, and newly molted larvae transferred to new cultures. Plankton tows were made intermittently from May through September of 1968 in Yaquina Bay and 1 mile outside the estuary along a rocky reef paralleling the shore. The catch was immediately resuspended in cold seawater and kept under refrigeration while being taken to the laboratory. Live porcellanid larvae obtained in these hauls were removed to fresh seawater, sorted by zoeal stage, and further separated into four groups on the basis of differences in the patterns of the primary red chromatophores. Larvae within each group were further divided and placed in flask cultures.

Mass cultures of laboratory-hatched *Petrolisthes cinctipes* larvae were maintained in 5-gal carboys filled with filtered seawater, with 150 or fewer larvae per carboy. Aerated mass cultures were immersed in baths of running seawater and experienced a temperature range of 10.8° to 15.2°C during the culture period and a maximum daily fluctuation of 2.5°C due to tidal influence. Larvae in mass culture were transferred to clean containers and fresh seawater every 14 days.

Zoea larvae were fed *Artemia salina* nauplii not more than 3 days old daily if required so that excess food was always present. The megalopa larvae required suspended algal material as food. Several monoalgal (*Tetraselmis* sp., *Isochrysis* sp.) and diatom (unidentified) cultures were tried singly and in combinations as a food source. Nutrient culture medium inoculated with raw seawater was also used as a source of food organisms. Small stones were introduced into the flasks to provide the megalopae with a surface for settling.

The larvae of the two *Petrolisthes* species and *Pachycheles rudis* were reared to the megalopa stage in cultures from embryos obtained from females held in the laboratory. Live larvae of these species taken from the plankton were reared to confirm stages obtained from the laboratory-hatched broods and to supplement laboratory-grown material for descriptive purposes. The larval history of *P. pubescens* was first described from larvae captured in the plankton and placed in laboratory cultures. Three gravid females of this species were collected later, and the identity of the planktonic larvae was confirmed by comparison with larvae released by one of the females and reared to the second zoeal stage.

Larvae in various stages of development were preserved for dissection primarily in 70% ethanol, but a few larval specimens were preserved in a mixture of 50% glycerine and 50% ethanol for chromatophore examinations. Both temporary and permanent slides were made of the dissected materials. Temporary mounts were made in glycerine, and permanent mounts were made in Zeiss hardening phase medium as well

as in Turtox CMC-9AB and CMC-10 media.[8] Drawings were made from both types of material with the aid of a Wild M-20 compound microscope and camera lucida attachment. Since the length of the rostral and posterior spines of zoeae is highly variable and dependent on a number of factors, only the carapace proper was measured to serve as an indication of zoeal size. This measurement was made from the point of junction of the posterior spines to the posterior margin of the orbital arch, using an ocular micrometer.

The term "seta" is used to indicate any firm-walled process, located on an appendage or other body surface, which is distinctly articulate at its base or attachment point (Figure 1). The figures are in part schematic and represent typical setal counts only. Setules are not represented in actual numbers and are often omitted entirely for clarity. Only one member of each setal pair present is figured for the exopodites of zoeal maxillipeds. Only the right member of each appendage pair is figured except for mandibles, which are sometimes drawn in pairs from the dorsal view.

Sexually mature females of the two genera considered in this study produce eggs of distinctly different types. *Pachycheles rudis* and *P. pubescens* females carry eggs which are 0.50 to 0.58 mm in size and brilliant yellow-orange when they are newly extruded. The eggs of *P. rudis*, as Knudsen (1964) and Knight (1966) observed, gradually change to a translucent amber color as the embryos develop and the yolk is absorbed. The color change with development is similar in *P. pubescens*. The age of the egg masses of the individual females collected in the field was unknown; however, the maximum length of time any female *P. rudis* carried eggs was 47 days, and two others carried eggs for 43 days before releasing larvae. This time may approach the length of time eggs are carried in this species. In both *Pachycheles* species, eggs hatched and all the larvae were released in a period of 10 to 20 hr. A hatch from a large female (carapace width 14.2-15.0 mm) may yield between 2,000 and 3,000 larvae but brood size varies (Knudsen, 1964).

In contrast, the eggs of *Petrolisthes cinctipes* and *P. eriomerus* are somewhat larger, 0.80 to 0.84 mm, and are deep scarlet to maroon in color, when newly extruded, similar to those of other species in the genus (Wear, 1965b; Greenwood, 1965). As Boolootian et al. (1959) also observed, the eggs gradually change to a translucent brownish red color as the embryos develop and the yolk is absorbed. Females of these two species were deliberately collected close to the hatching time; consequently, no information on the length of the brooding period was obtained. The time required for a female to complete a hatch is similar in these two *Petrolisthes* species but differs considerably from that observed for the *Pachycheles* species. Female *Petrolisthes* require 40 to 70 hr to release an entire group of larvae in the laboratory. Release of the larvae in these two species occurs in spurts with "resting" periods between each period of concentrated release.

The embryonic and larval histories of all four species observed in the laboratory have a number of characteristics in common. Fully developed embryos examined prior to eclosion possessed the full complement of primary red chromatophores found throughout the active larval life of these crabs. Although occasional minor variations were noted both in laboratory hatches and in larvae from the plankton, the occurrence and placement of the chromatophores is generally stable and is species specific, as various workers have noted in other species (Wear, 1964a, b, 1965a, b; Greenwood, 1965; Gore, 1968; Gurney, 1942). The primary chromatophores can thus be used to identify a larva to the species level at any stage of development.

In the hatching of all four species, females released larvae in the form of prezoeae. This has been observed in other porcellanid species, for example, by Lebour (1943), Greenwood (1965), Wear (1965b, 1966), and Gore (1968). The duration of this stage in the laboratory varies considerably and lasts from 10 min to about 1 hr in the species studied here. Prezoeae were never collected in the plankton.

[8] Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

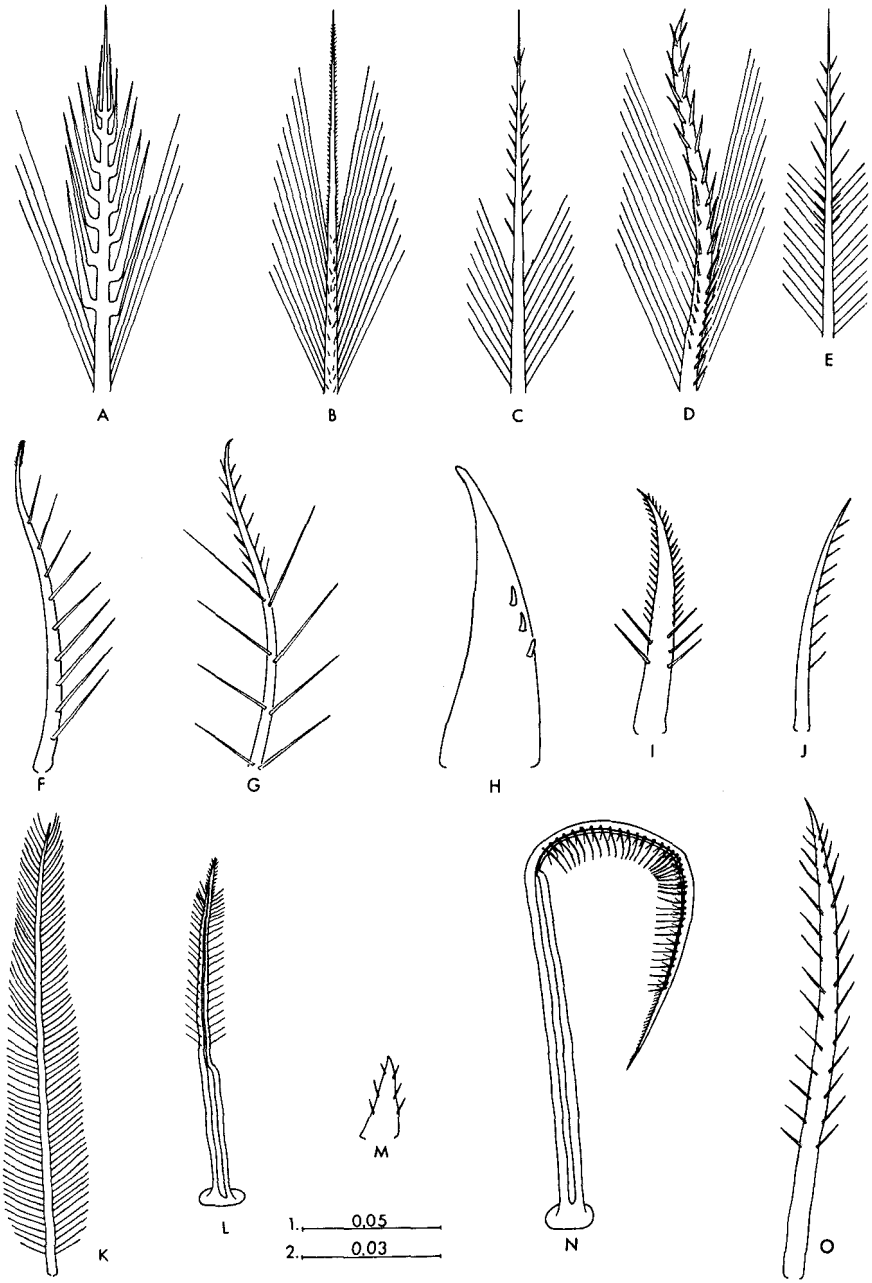

FIGURE 1.—Setal types in four porcellanid species studied: A-E (Scale 1), zoeal telson processes, distal portions: A - processes 3 and 4, *Pachycheles* spp.; B - processes 5, 6, and 7, *Pachycheles* spp.; C - median spine, Zoea II, *Pachycheles* spp.; D - processes 3 through 7, *Petrolisthes* spp.; E - median spine, Zoea II, *Petrolisthes* spp. F-K (Scale 2), zoeal maxillary setae, all four species. L, N (Scale 2), scythelike cleaning setae, straight and hooked, megalopa, pereiopod 5, all four species. M, O (Scale 2), "spikelike" and "brushlike" setae, megalopa, maxilliped III, all four species. Scales in millimeter.

After the larva has spent a period of time as a prezoea, the cuticle over the carapace is ruptured dorsally along the midline and the prezoea molts to the first true zoeal stage. The rostrum is the first portion of the body to be freed, followed by the functional mouth parts and natatory maxillipeds. The abdomen and telson are the last portions to be withdrawn from the cuticle. When the molt is completed, the natatory setae and setae of the telson, previously compacted and confined by the prezoeal cuticle, become fully extended and serve to keep the larva afloat and propel it through the water. The rostral spine, partially invaginated into the carapace in the prezoea, straightens out almost immediately following the molt. The posterior carapace spines which often, but not always, become tightly coiled immediately after the cuticle is shed may take several minutes to several hours to uncoil. The cuticle is shed virtually intact except for the original dorsal split. Often in later molts, the delicate elastic cuticle covering the pereiopod and pleopod buds is shriveled or damaged in the cast exoskeleton.

Larvae of all four species always pass through two true zoeal stages and one megalopal stage (terminology of Williamson, 1957) in the laboratory as do certain other porcellanids (Le Roux, 1961, 1966; Knight, 1966; Boschi, Scelzo, and Goldstein, 1967; Gore, 1968, 1970, 1971a, b, 1972). This was true of larvae hatched in the laboratory as well as those taken from the plankton.

In these four species, both zoeal stages demonstrate the remarkable property of intermolt growth in which certain of the larval appendages increase in size, apparently throughout the duration of a stage, while the larval cuticle remains intact. This phenomenon has been reported for various other porcellanid larvae (Le Roux, 1961, 1966; Kurata, 1964; Knight, 1966; Gore, 1968, 1970, 1971a, b, 1972) but has not yet been thoroughly investigated. Appendages may increase in size as much as threefold between molts as a result of this growth pattern.

The number of specimens of each stage dissected and examined is given in Table 1. The ranges given in the descriptions refer only to variations found within these specimens. Many other specimens were examined but not dissected.

LARVAL DEVELOPMENT OF *PETROLISTHES CINCTIPES* (RANDALL)

Larvae of *P. cinctipes* were reared using the mass culture method. The single megalopa thus obtained as well as one megalopa from the plankton were preserved and dissected for purposes of description.

PREZOEA
(Figure 2)

The prezoea of *P. cinctipes* is virtually spineless and hairless. The carapace has a generally rounded appearance because the rostral and posterior spines are curved downward and inward toward the center of the body. These spines are further compacted by being telescoped and invaginated into their respective portions of the carapace. The natatory setae are nonfunctional, withdrawn into the ends of the maxillipeds, and held in place by the prezoeal cuticle. The primary red chromatophores appear in the following locations: one on either side of the mouth; one distally on the basipodite of each second maxilliped; one distally in abdominal segment number two or between segments two and three; and one on either side of the body between the bases of maxillipeds one and two. The rostrum and posterior spines are tipped with red, and an additional red band appears on the rostrum proximal to the red tip and separated from it by a white or colorless band.

With the exception of the chromatophore numbers and arrangement, the prezoeal stages of the four species do not differ significantly. For this reason, a prezoea will be figured only

TABLE 1.—Number of porcelain crab larvae dissected and examined for this study.

Species	Zoea I	Zoea II	Megalopa
Petrolisthes cinctipes	11	4	2
Petrolisthes eriomerus	16	4	9
Pachycheles pubescens	9	6	9
Pachycheles rudis	12	12	7

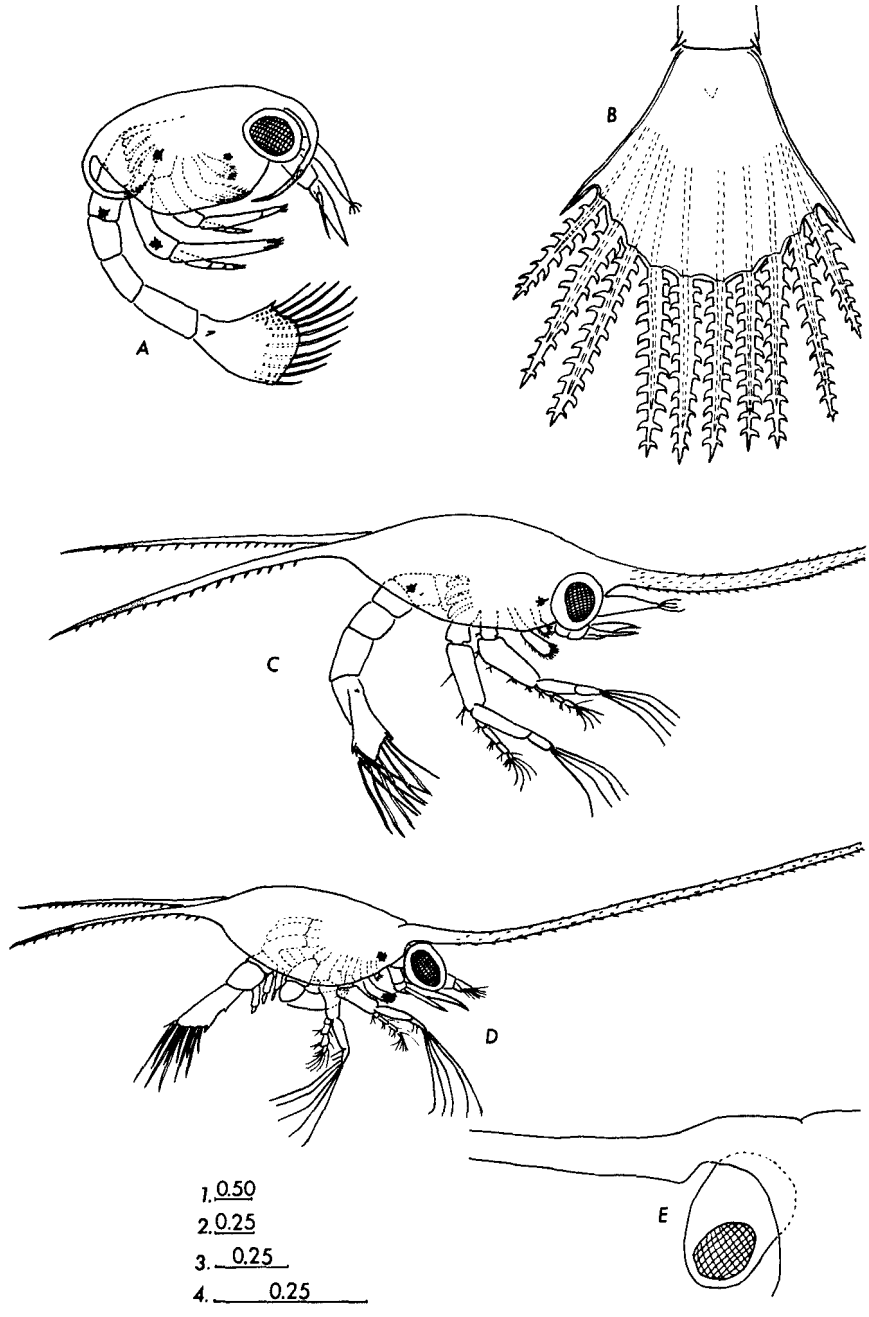

FIGURE 2.—Prezoea, Zoea I, Zoea II, entire: A - prezoea, *Petroli...* *inctipes* with primary chromatophores (Scale 3); B - prezoeal telson with modified cuticle, *Pachycheles pubescens* (Scale 4); C - *Petrolisthes eriomerus*, Zoea I with chromatophores (Scale 2); D - *Pachycheles pubescens*, Zoea II with chromatophores (Scale 1); E - *Petrolisthes* spp., Zoea II, ventral rostral bulge (Scale 3). Scales in millimeter.

once, and specific variations will be indicated in the text. Prezoeae were not dissected.

ZOEA I
(Figure 3)

Antennule unsegmented with five or six terminal processes including three aesthetascs and two or three setae.

Antenna biramous; endopodite fused with protopodite and bearing a terminal point and subterminal tubercle with a fine seta between; exopodite mobile, about 1½ times as long as endopodite, with three or four prominent distal spines and one long seta proximal to the spines.

Mandibles strongly sclerotized, heavily toothed, asymmetrical appendages.

Maxilla I with unsegmented endopodite bearing three or four terminal setae and a number of fine hairs along the anterior margin; basal endite with 9 or 10 stout spinous processes; coxal endite with 9 or 10 stout setae.

Maxilla II with unsegmented endopodite bearing eight or nine setae, grouped 3, 1-2, 3-4 proximal to distal, 3-2-4 being the most common grouping. Basal endite bilobed: distal lobe with 7 to 10 setae; proximal lobe with seven to nine setae. Coxal endite bilobed: distal lobe with four to six setae; proximal lobe with 8 to 11 setae. Scaphognathite with six or seven long plumose marginal setae, and one apical seta; numerous fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite with one or two distal setae. Basipodite with 9 to 11 setae most commonly grouped 2, 2, 3, 3 proximal to distal. Endopodite four-segmented: segment 1 with one to three distal setae, inner margin; segment 2 with two or three distal setae, inner margin; segment 3 with four to seven setae including two or three medial, one or two distal, inner margin, occasionally one long medial seta, outer margin; segment 4 with five to seven terminal setae and one proximal on outer margin. Exopodite two-segmented with four terminal natatory setae on distal segment. Additional groups of very fine hairs appear on endopodite segments 2, 3, and 4 and on segment 2 of exopodite as figured.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite with three setae on inner margin grouped 1, 2 proximal to distal. Endopodite four-segmented: segment 1 with one or two distal setae, inner margin; segment 2 with one or two distal setae, inner margin; segment 3 with one medial and one or two distal setae, inner margin; segment 4 with three to five (usually five) terminal setae and one proximal seta, outer margin. Exopodite two-segmented with four terminal natatory setae on distal segment. Groups of very fine hairs appear on endopodite segments 2, 3, and 4 and on both segments of exopodite as figured.

Maxilliped III present as small bilobed bud which undergoes growth throughout stage.

Pereiopods present as five pairs of short limb buds, all without setae; none chelate; undergo growth during entire stage.

Abdominal somites numbering five; segments 3, 4, and 5 with serrated dorsal posterior margins; segments 4 and 5 each with a pair of strong ventrolateral spines on posterior margin.

Telson with seven symmetrically arranged pairs of processes, with central pair located on central prominence; outer margin to center line: one heavy, articulated lateral process with few spinules (not figured), one short fine seta, and five long plumose articulating setae; all long plumose setae armed distally with fixed curved spines (Figure 1D); fine hairs (not figured) on margin of telson between all major plumose setae and on central prominence; anal spine present.

Chromatophores as described in the prezoea; carapace 1.23 to 1.39 mm in length.

ZOEA II
(Figure 4)

Antennule biramous; exopodite with six or seven terminal processes including four aesthetascs and two or three setae, followed by five tiers of subterminal aesthetascs grouped 2, 3, 3, 4, 3 progressing proximally; three or four fine setae present on distal margin of protopodite.

Antenna biramous; endopodite same form as in zoea I; exopodite similar to zoea I, with three spines and one seta distally; exopodite and endopodite approximately equal in length.

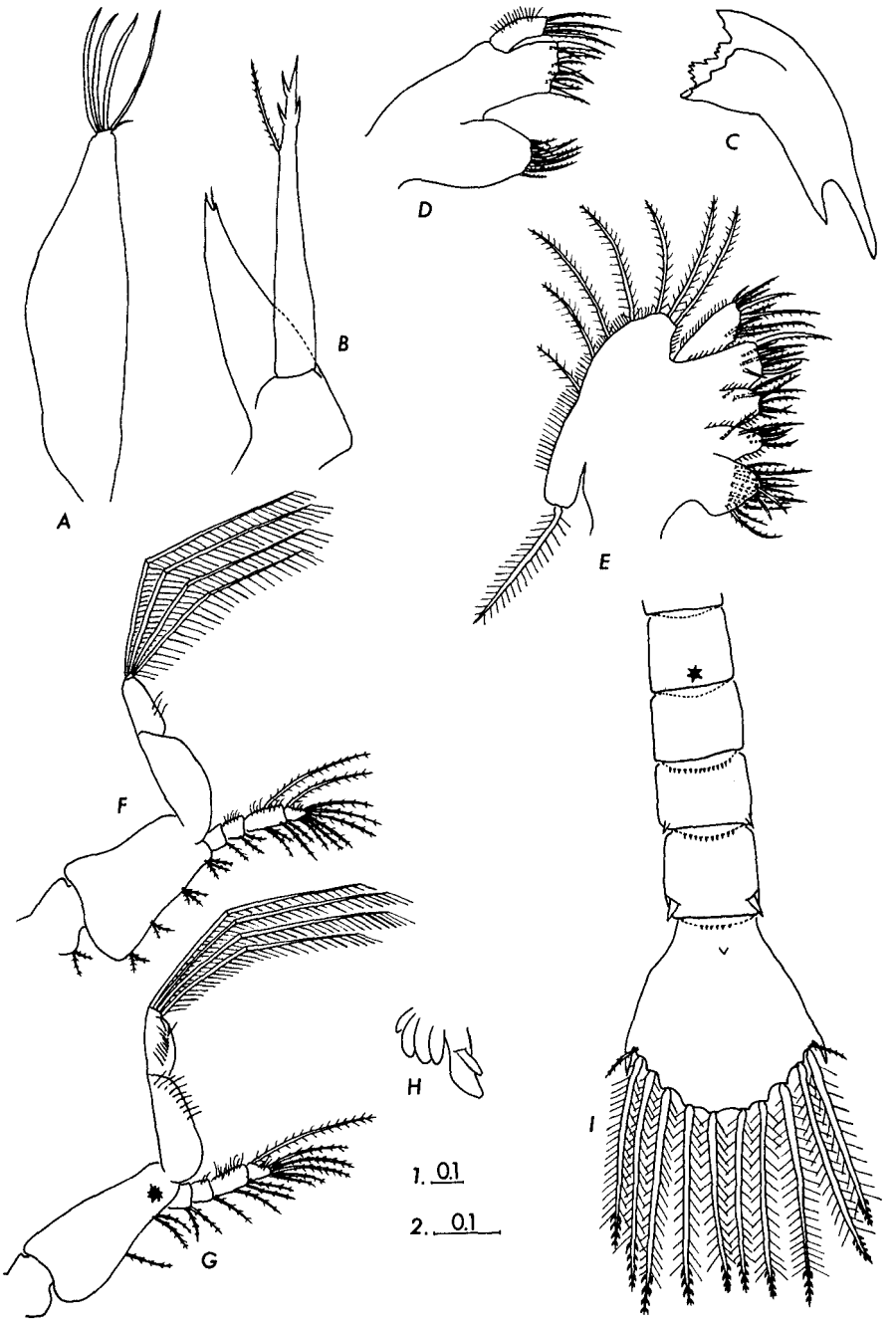

FIGURE 3.—*Petrolisthes cinctipes*, Zoea I: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II (A-E, Scale 2); F - maxilliped I; G - maxilliped II (F and G, Scale 1); H - maxilliped III and pereiopod buds (Scale 2); I - abdomen and telson, ventral (Scale 1). Scales in millimeter.

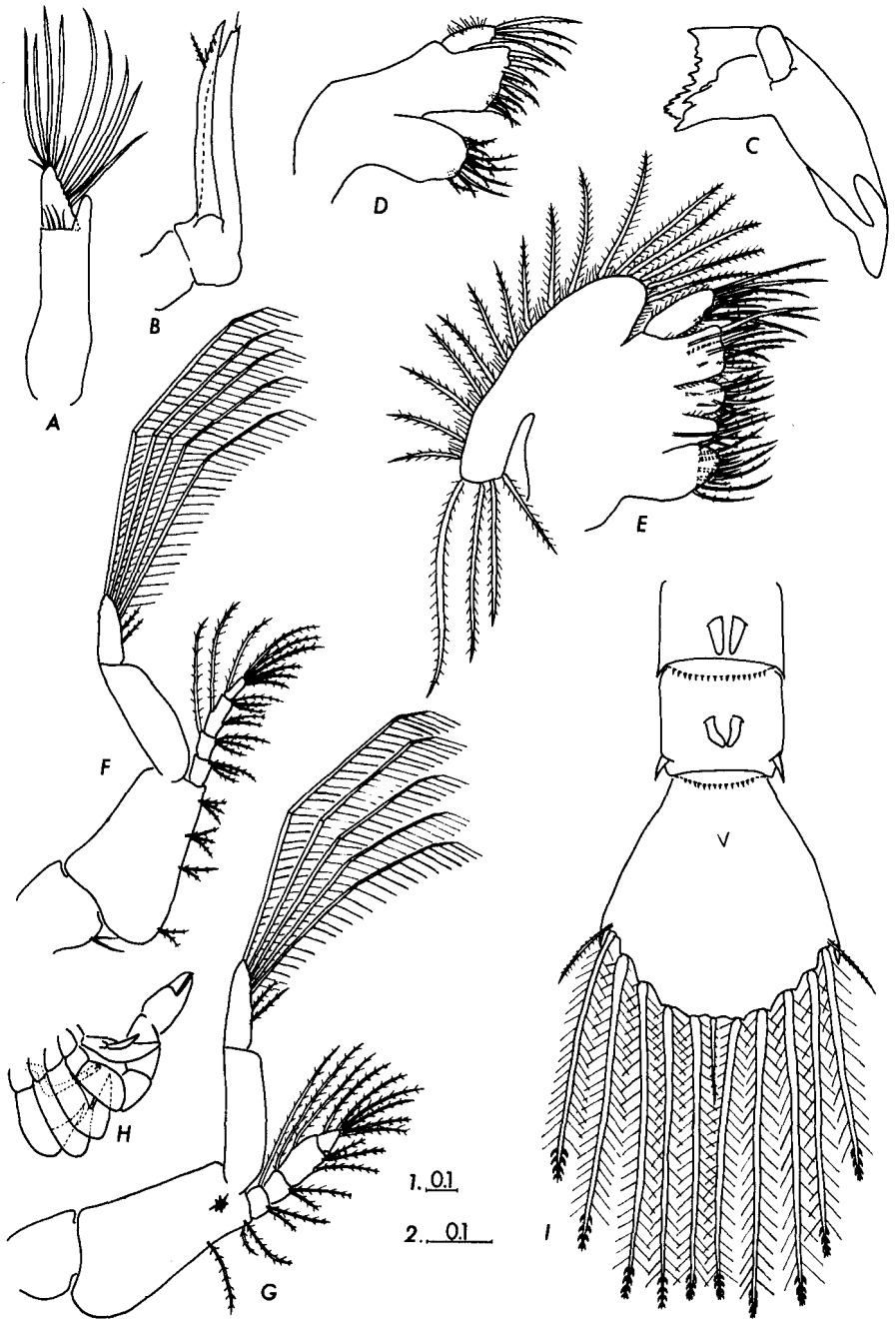

FIGURE 4.—*Petrolisthes cinctipes*, Zoea II: A - antennule with only one aesthetasc shown for each of the five subterminal tiers; B - antenna; C - mandible; D - maxilla I; E - maxilla II (A-E, Scale 2); F - maxilliped I; G - maxilliped II; H - maxilliped III and pereiopods; I - abdomen and telson (F-I, Scale 2). Scales in millimeter.

Mandibles larger than in zoea I and with prominent palp bud.

Maxilla I with unsegmented endopodite bearing four or five terminal setae and a number of fine hairs along anterior margin; basal endite with 10 or 11 setae; coxal endite with 11 to 13 setae.

Maxilla II with unsegmented endopodite bearing nine setae grouped 3, 2, 4 progressing distally. Basal endite bilobed; both distal and proximal lobes with 11 or 12 setae each. Coxal endite bilobed: distal lobe with seven setae; proximal lobe with 11 to 15 setae. Scaphognathite with 16 to 18 outer marginal setae, three apical setae and one on internal margin of posterior lobe (total 20 to 22 setae), all plumose. Fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite with one or two distal setae. Basipodite with setae grouped 2, 2, 3, 3 proximal to distal. Endopodite four-segmented: segment 1 with three distal setae, inner margin; segment 2 with three distal setae, inner margin and one distal seta, outer margin; segment 3 with two medial and three distal setae, inner margin and one medial seta, outer margin; segment 4 with five or six terminal setae and one proximal seta, outer margin. Exopodite two-segmented with 14 natatory setae on distal segment.

Maxilliped II biramous. Coxopodite lacks setae. Basipodite with three setae grouped 1, 2 proximal to distal. Endopodite four-segmented: segments 1 and 2 each with two distal setae, inner margin and one distal, outer margin; segment 3 with one medial, two distal, inner margin and one medial seta, outer margin; segment 4 with four to six (usually five) terminal setae and one proximal seta on outer margin. Exopodite two-segmented with 14 natatory setae on distal segment.

Maxilliped III biramous, larger than in zoea I; endopodite curved anteriad; appendage grows and additional segments become defined during stage.

Pereiopods present as five pairs of limb buds, pairs one and five distinctly chelate; buds expand in size throughout stage and become distinctly segmented in a late zoea II.

Abdominal somites larger but otherwise similar to those in zoea I; pairs of pleopods, unequal in length, occur ventrally on segments 2, 3, 4, and 5; pleopods increase in length throughout stage.

Telson similar to form in zoea I but with single median seta (Figures 1E and 4I) added to central prominence and size increased; anal spine present.

Basic pattern of primary red chromatophores same as in prezoea and zoea I; however, new chromatophores appear in the late second stage zoea on the growing pereiopods and on body beneath carapace. Carapace 1.72 to 1.98 mm in length. Rostrum bears distinct ventral bulge just anterior to eyes (Figure 2E).

MEGALOPA
(Figures 5 and 6)

Antennule biramous with three-segmented peduncle. Dorsal ramus with six segments; segments 2, 3, and 4 each bear two tiers of aesthetascs and segment 5 bears one tier; numbers of aesthetascs per tier are approximately 3-4, 2-3, 3, 2, 2-3, 2, 2 progressing distally (specimens damaged); one long seta present on each of segments 3 and 4 associated with the distal aesthetasc tier. Ventral ramus with three distinct segments, the distal segment itself appearing indistinctly divided; setation as figured.

Antennal flagellum usually composed of 17 segments; peduncle three-segmented; hairs and bristles associated with the distal end of each segment along the length of the flagellum vary in number and pattern of distribution.

Mandible strongly sclerotized, partially cup-shaped appendage with bladelike leading edge which may be somewhat irregular but is not strongly toothed as in the zoea; three-segmented palp present with about six spinelike setae on terminal segment.

Maxilla I with probably two-segmented endopodite (specimens damaged) bearing one or more setae; basal endite with a total of 21 or 22 spines and setae arranged predominantly along the distal margin; coxal endite with approximately 26 processes, most of them slender setae in contrast to the spinelike processes of the basal

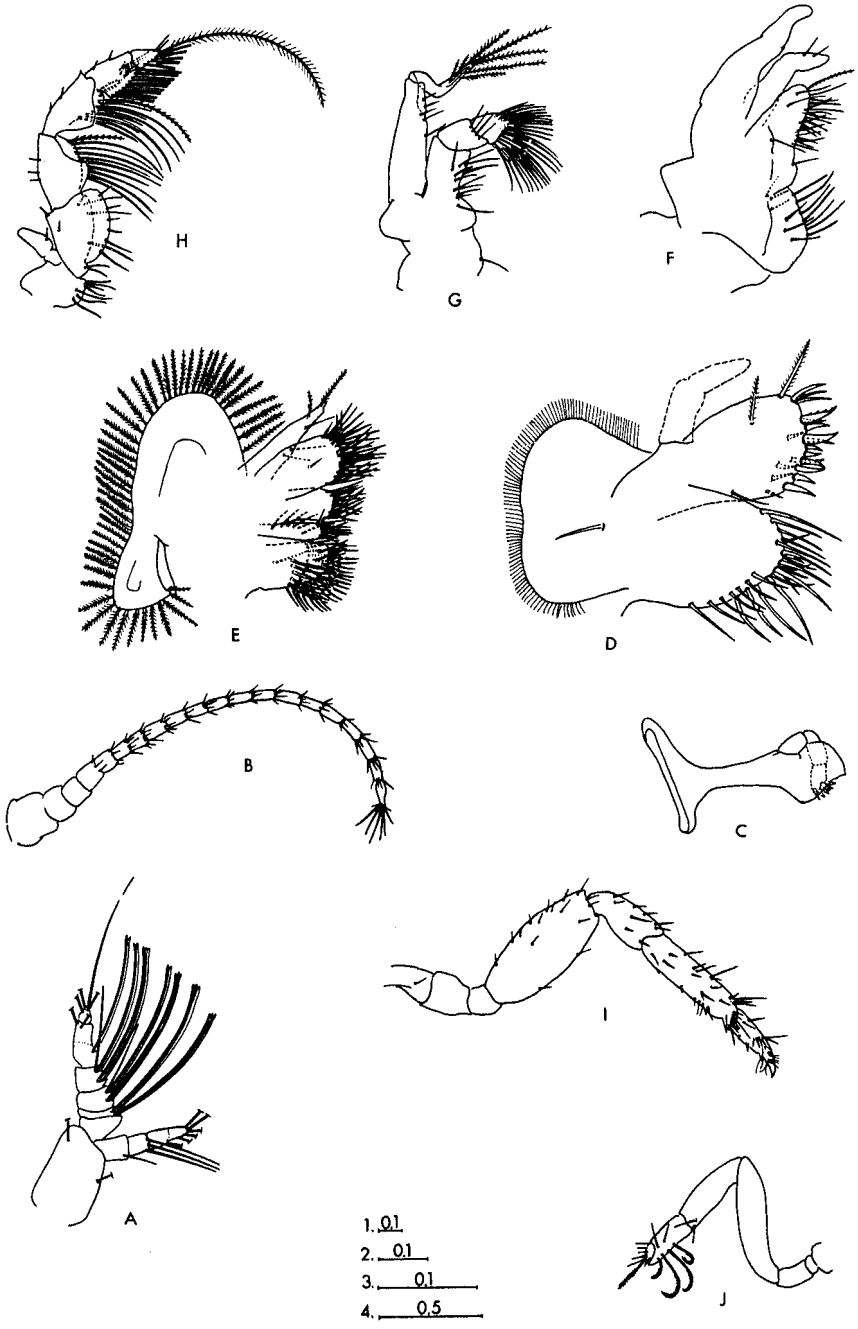

FIGURE 5.—*Petrolisthes cinctipes* megalopa: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III; I - pereiopod III; J - pereiopod V (B, G, H, J, Scale 1; A, C, E, F, Scale 2; D Scale 3; I, Scale 4). Scales in millimeter.

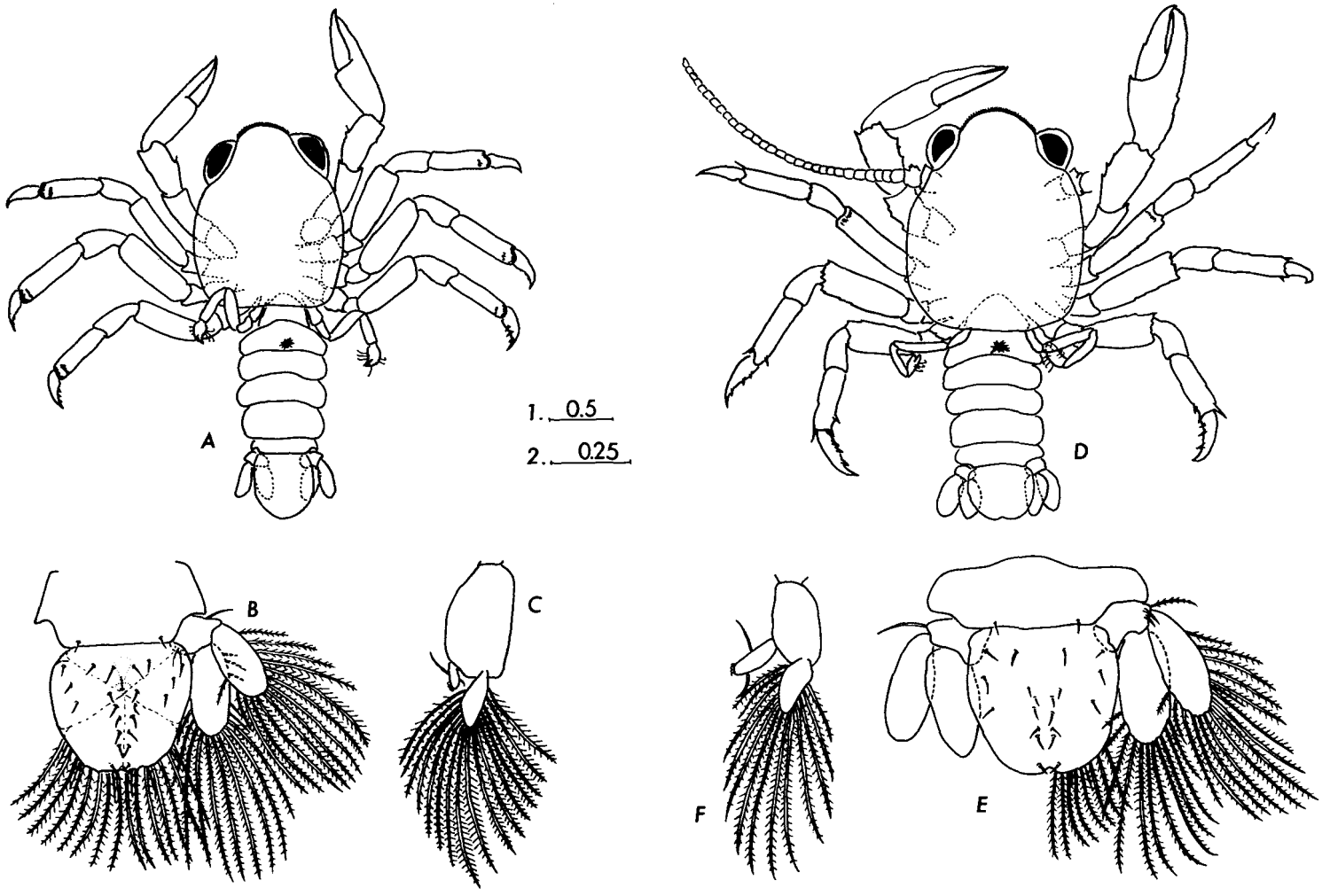

FIGURE 6.—*Petrolisthes cinctipes* and *P. eriomerus* megalopae: A - *P. cinctipes* megalopa, generalized, with chromatophore; B - *P. cinctipes* telson and uropods; C - *P. cinctipes* right third pleopod; D - *P. eriomerus* megalopa, generalized, with chromatophore; E - *P. eriomerus* telson and uropods; F - *P. eriomerus* right third pleopod (A, D, Scale 1; B, C, E and F, Scale 2). Scales in millimeter.

endite; a small fanlike exite also present, rimmed with very fine hairs.

Maxilla II with unsegmented endopodite bearing five setae. Basal endite bilobed: distal lobe with approximately 26 setae; proximal lobe with 13 to 15 setae. Coxal endite bilobed: distal lobe with nine marginal setae and six submarginal setae, dorsal surface; proximal lobe with about 20 marginal setae, 13 submarginals, dorsal surface, and 8 submarginal setae, ventral surface. Scaphognathite with approximately 50 marginal setae.

Maxilliped I biramous. Exopodite devoid of setae or hairs in specimens examined (two). Endopodite two-segmented in appearance, but indistinctly so; distal segment bears two short setae. Basal endite with 19 or 20 major marginal setae, 5 to 8 submarginal setae, dorsal surface. Coxal endite with about seven major marginal setae and six submarginal setae, three on dorsal surface and three on ventral surface.

Maxilliped II biramous. Exopodite consists of two distinct segments, the distal segment itself appearing indistinctly segmented; there are five to seven plumose setae on the distal segment and five setae on the internal margin of the first segment. Endopodite four-segmented, the distal two segments each bearing dense brushes of approximately 20 to 30 setae; segment 2 with four or five setae along distal margin; segment 1 with approximately 11 setae along the internal margin.

Maxilliped III biramous. Exopodite incompletely formed with two segments only; segment 2 with one small proximal seta. Endopodite specialized for filter feeding and consists of five segments; segment 2 with 10 to 12 major setae, dorsal internal margin; segment 3 with 9 or 10 major feeding setae, 3 or 4 short, stout brushlike setae, and 2 or 3 very short, spikelike setae all on the dorsal internal margin; segment 4 with nine major feeding setae along the internal ventral margin, six or seven minor feeding setae along dorsal internal margin; four or five major brush setae and two spikes, all along internal dorsal margin; segment 5 with six pairs of feeding setae and two minor brush setae terminally; other setation as pictured.

Pereiopods well developed and functional. Chelipeds slender and streamlined, generally dorsoventrally flattened with fine bristles over entire surface; outer margin of chelae produced in a series of spines; anterior margin of carpus with one major spine and a fine bristle associated with it. Pereiopods 2, 3, and 4 similar to each other in shape and setation as figured (Figure 5I). Pereiopod 5 chelate and armed with setae and bristles as shown; four to eight scythelike cleaning setae (Figure 1L, N) are also present.

Abdomen six-segmented; segments 2 through 5 each bearing one pair of pleopods. Pleopods biramous; exopodite with 16 plumose marginal setae; endopodite with two short setae and four hooks on margin. A single primary red chromatophore located on segment 2 or between 2 and 3. Segment 6 of the abdomen bears a pair of biramous uropods, the outer ramus usually having 14 and inner ramus with 15 marginal setae. Telson with 14 to 16 major plumose setae and 14 to 16 minor setae located between the major marginal setae. The dorsal surface of the telson bears a number of symmetrically placed pairs of fine hairs. In megalopae of advanced age, the beginning of the division of the telson into five plates can be seen beneath the cuticle. Upon molting to the first crab stage, the division of the telson is complete and distinct.

LARVAL DEVELOPMENT OF *PETROLISTHES ERIOMERUS* STIMPSON

Larvae of *P. eriomerus* were reared in unaerated Erlenmeyer flask cultures.

PREZOEA

The prezoea has essentially the same form as that described for *P. cinctipes* and differs only in one pair of primary chromatophores. *P. eriomerus* prezoeae lack the chromatophore on either side of the body between the bases of maxillipeds I and II which occurs in *P. cinctipes* larvae.

ZOEA I
(Figure 7)

Antennule unsegmented; five to six terminal processes including four aesthetascs and one or two setae.

Antenna biramous, with endopodite and protopodite fused; endopodite with terminal point, subterminal tubercle and fine seta between; exopodite approximately 1⅓ times as long as endopodite with one, two, or three prominent distal spines and one long seta proximal to spines.

Mandibles strongly sclerotized asymmetrical appendages, heavily armed with teeth and tubercles on leading edges.

Maxilla I with unsegmented endopodite bearing three to six terminal and subterminal setae and a number of fine hairs along anterior margin; basal endite with 9 or 10 setae; coxal endite with 8 to 10 setae.

Maxilla II with unsegmented endopodite which bears 7 to 10 setae, grouped 2-3, 2, 3-4 progressing distally. Basal endite bilobed: distal lobe with 8 to 10 setae; proximal lobe with 6 to 10 setae. Coxal endite bilobed: distal lobe with four to eight setae; proximal lobe with 7 to 11 setae. Scaphognathite with six to eight long plumose marginal setae and one strong apical seta. Numerous fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite with two or rarely three distal setae. Basipodite with 10 setae usually grouped 2, 2, 3, 3 proximal to distal. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin; segment 2 with three distal setae, inner margin; segment 3 with usually two medial and three or rarely four distal setae, inner margin; segment 4 with five to seven terminal setae and one proximal seta, outer margin; segments 2 and 3 also bear groups of fine hairs as figured. Exopodite two-segmented, the distal segment bearing four terminal natatory setae.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite with usually two but sometimes one distal seta and one medial seta, inner margin. Endopodite four-segmented: segment 1 with usually two but sometimes with one distal seta, inner margin; segment 2 usually with two but rarely one or three distal setae, inner margin; segment 3 with one medial seta or occasionally two setae, and usually two, but sometimes three distal setae, inner margin; segment 4 with three to five terminal setae and one proximal seta, outer margin; segments 2 and 3 also bear groups of fine hairs as figured. Exopodite two-segmented, the distal segment bearing four terminal natatory setae.

Maxilliped III a small bilobed bud which grows throughout stage.

Pereiopod buds simple, five pairs in number, growing throughout the duration of the stage.

Abdominal segments five in number; segments 3, 4, and 5 having serrations on dorsal posterior margins; segments 4 and 5 with strong ventrolateral spines on posterior margin.

Telson with seven symmetrically placed pairs of processes, with seventh pair on central prominence. Outer margin to center line: one heavy lateral spine fused with telson, one short fine seta, and five long plumose articulating setae, all armed distally with a series of short, curved fixed spines (Figure 1D); numerous fine hairs on telson margin (not figured) between all major plumose setae; anal spine present.

Chromatophore pattern as noted for the prezoea; extended rostrum with one terminal and one subterminal band of red color; posterior spines each with one terminal red band. Carapace 1.31 to 1.48 mm in length.

ZOEA II
(Figure 8)

Antennule biramous; exopodite with six or seven terminal processes including four aesthetascs and two or three setae followed by five tiers of subterminal aesthetascs grouped 3, 4, 3, 3, 2 proximal to distal.

Antenna biramous; endopodite same form as in zoea I; exopodite similar to that in zoea I with one to three spines, one seta distally; spines somewhat less prominent than in zoea I; exopodite approximately three-quarters length of endopodite.

Mandibles larger than in zoea I and with prominent palp bud.

FIGURE 7.—*Petrolisthes eriomerus* zoea I: A - antennule; B - antenna; C - mandibles; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III and periopod buds; I - abdomen and telson (A-E, H, Scale 2; F, G, I, Scale 1). Scales in millimeter.

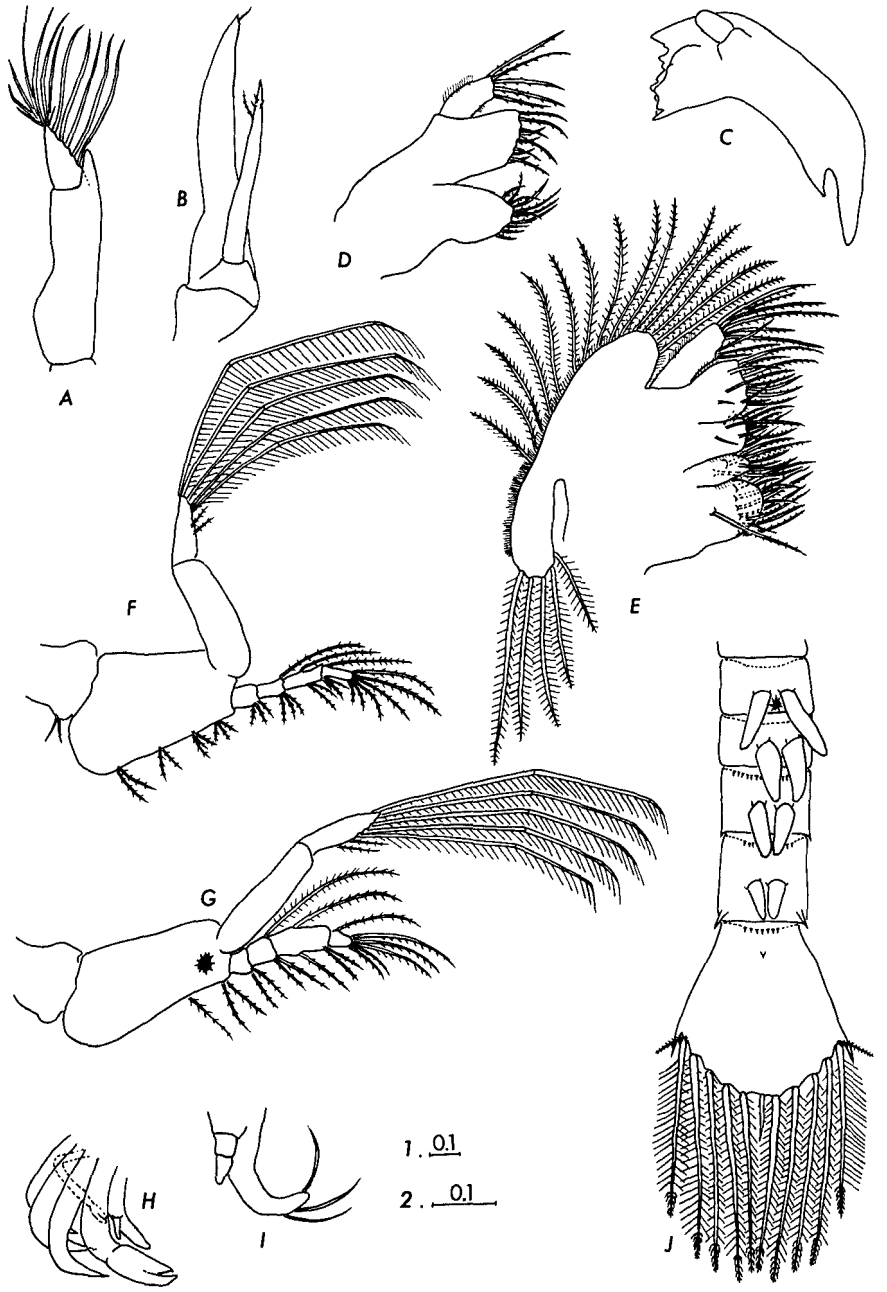

FIGURE 8.—*Petrolisthes eviomerus* zoea II: A - antennule with only one aesthetasc shown for each of the five subterminal tiers; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III and pereiopods; I - maxilliped III, late zoea II; J - abdomen and telson (A, B, F-H, J, Scale 1; C-E, I, Scale 2). Scales in millimeter.

Maxilla I with unsegmented endopodite bearing four to seven terminal and subterminal setae and a group of fine hairs along anterior margin; basal endite with 10 or 11 setae; coxal endite with 9 to 11 setae.

Maxilla II with unsegmented endopodite bearing nine setae grouped 3, 2, 4 progressing distally. Basal endite bilobed: distal lobe with 12 or 13 setae; proximal lobe with 11 or 12 setae. Coxal endite bilobed: distal lobe with five to seven setae; proximal lobe with 12 to 15 setae. Scaphognathite with 13 to 16 marginal, 3 apical, and 1 or 2 internal lateral setae (total 17 to 21); fine hairs present on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite with two distal setae. Basipodite with setae usually grouped 2, 2, 3, 3 proximal to distal along inner margin. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin; segment 2 with three or four distal setae, inner margin and one distal seta, outer margin; segment 3 usually with two medial and three distal setae, inner margin and one medial, outer margin; segment 4 with four to seven terminal and one proximal seta, outer margin. Exopodite two-segmented, the distal segment bearing 14 natatory setae.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite with three distal setae grouped 1, 2 proximal to distal. Endopodite four-segmented: segment 1 with two (occasionally one) distal setae, inner margin; segment 2 with two distal setae, inner margin and one distal setae, outer margin; segment 3 with one medial, two or rarely three distal, inner margin, and one medial seta, outer margin; segment 4 with five terminal setae and one proximal seta, outer margin. Exopodite with two segments, the distal segment bearing 14 natatory setae.

Maxilliped III biramous. Exopodite indistinctly divided with two segments; zero to three setae have been observed on endopodite. Endopodite with up to five segments apparent beneath cuticle, depending on the age of the zoea.

Pereiopod buds five pairs in number with first and fifth pairs distinctly chelate; buds increase in length throughout the stage.

Abdominal somites numbering five, similar to form in zoea I but larger and with paired pleopod buds of unequal length on segments 2 through 5; pleopods increase in length throughout the stage.

Telson similar to form in zoea I but larger and with one unpaired median seta on the central prominence (Figures 1E and 8J).

Pattern of primary chromatophores same as that in zoea I but new ones may be added on the growing pereiopods. Carapace 1.80 to 1.89 mm in length. Rostrum bears distinct ventral bulge just anterior to eyes.

MEGALOPA
(Figures 6 and 9)

Antennule biramous with three-segmented peduncle. Dorsal antennular ramus six-segmented; segments 2, 3, 4, and 5 with 2, 2, 2, 1 tiers of aesthetascs respectively; tiers, progressing distally, contain approximately 6-7, 6-7, 6-7, 3-4, 3, 2, 3 aesthetascs respectively; one long slender seta associated with the distal tier on each of segments 3 and 4. Ventral ramus with three segments; setation as figured.

Antenna long and slender with three-segmented peduncle; flagellum with 28 to 30 segments; most segments armed distally with variable numbers of short bristles and hairs as figured.

Mandible differs from toothed form in zoeal stages and is partially cup-shaped with slightly irregular bladelike leading edge; three-segmented palp has seven to ten spines on distal segment.

Maxilla I with indistinctly two-segmented endopodite bearing a single terminal seta on the distal segment and a single seta situated at base; basal endite with a total of about 25 stout spines and setae; coxal endite with a total of 32 stout setae. In addition, there is a single long seta proximally on the exopodite and a delicate exite edged with fine hairs associated with coxal portion of appendage.

Maxilla II with slender, indistinctly segmented endopodite bearing three terminal setae and one

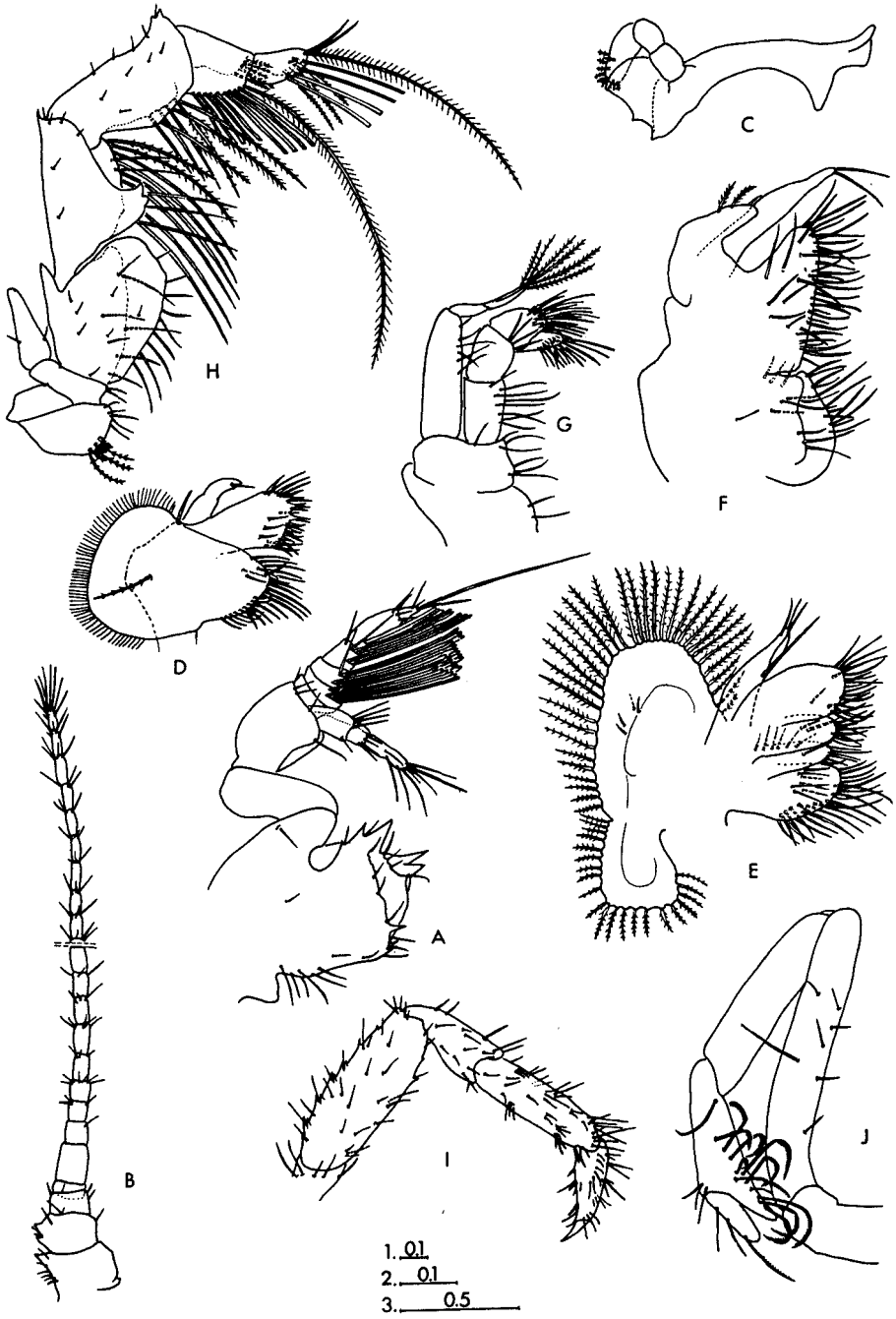

FIGURE 9.—*Petrolisthes eriomerus* megalopa: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III; I - pereiopod III; J - pereiopod V (B, G, H, Scale 1; A, C-F, J, Scale 2; I, Scale 3). Scales in millimeter.

lateral seta. Basal endite bilobed: distal lobe with 32 to 34 setae; proximal lobe with about 19 setae. Coxal endite bilobed: distal lobe with about 19 setae; proximal lobe with about 39 setae.

Maxilliped I with exopodite bearing three marginal setae; endopodite with two terminal setae in specimens dissected; basal portion of protopodite produced into triangular lobe bearing 35 to 42 setae; coxal lobe with numerous setae numbering 16 to 21 in specimens counted.

Maxilliped II with two-segmented exopodite usually bearing six setae on terminal segment and six internal marginal setae on proximal segment. Endopodite composed of four segments the distal two of which are armed with dense setal brushes each containing about 16 to 20 setae. Other setation as figured.

Maxilliped III with single-segmented exopodite bearing two very fine setae. Endopodite with five well-developed segments; segments 2 through 5 armed with filtering setae; segment 2 with 13 major setae along dorsal inner margin; segment 3 with three major ventral and four or five major dorsal internal marginal feeding setae, seven or eight minor submarginal brushlike setae dorsally and five ventral major submarginal brush setae; segment 4 with 10 major ventral marginal feeding setae, 9 minor dorsal marginal feeding setae, protuberance distally and dorsally on segment bearing a row of 5 major brush setae and a subordinate row of 4 spikelike setae and 1 fine seta; segment 5 with five major ventral and four or five dorsal (mixed major and minor) feeding setae, two slender terminal brush setae; three major brushes and two spikes on dorsal, submarginal bulge.

Pereiopods well developed and functional. Chelae slender, narrow, dorsoventrally flattened with two fixed spines present on internal margin of carpus. Walking legs all similar in form and setation as figured. Pereiopod 5 chelate with bristles and hooked setae for cleaning as figured.

Abdomen segments numbering 6, segments 2 through 5 with paired biramous pleopods; marginal setation of pleopod exopodites varies from 10 to 13, the higher numbers generally being found on the more proximal pleopods; each pleopod endopodite is armed with four small hooks and two setae. Segment 2 bears one chromatophore distally. A pair of biramous uropods articulate with segment 6; the outer ramus with 15 or 16 marginal setae, inner ramus with 10 or 11 marginal setae.

Telson with 15 or 16 major marginal plumose setae and usually four minor setae placed approximately symmetrically with respect to the center line of the telson between the major marginal setae; dorsal surface of telson bears about 10 pairs of fine setae in approximately symmetrical positions.

LARVAL DEVELOPMENT OF *PACHYCHELES PUBESCENS* HOLMES

Larvae taken from the plankton were reared in unaerated Erlenmeyer flask cultures and identified at a later date by comparison with laboratory hatched larvae.

PREZOEA

The general body form of *Pachycheles pubescens* is the same as that described for *Petrolisthes cinctipes* prezoeae; however, certain details of the prezoeal cuticle of the telson differ from *P. cinctipes*. The prezoeal cuticle of *Pachycheles pubescens* is produced into flat spines with toothed margins (Figure 2), an additional adaptation for swimming by abdominal flexion. Chromatophores occur as follows: one on either side of the mouth; one each on abdominal segments 1, 2, 3, and 5; and one on the telson.

ZOEA I
(Figure 10)

Antennule unsegmented with five or six terminal processes including three or four aesthetascs and one or two setae.

Antenna biramous with endopodite and protopodite fused; endopodite without subterminal tubercle or fine seta; exopodite 1¾ to 2 times as long as endopodite; usually three short stout, curved spines along internal lateral margin distally on exopodite, but spines occasionally number one or two and rarely four.

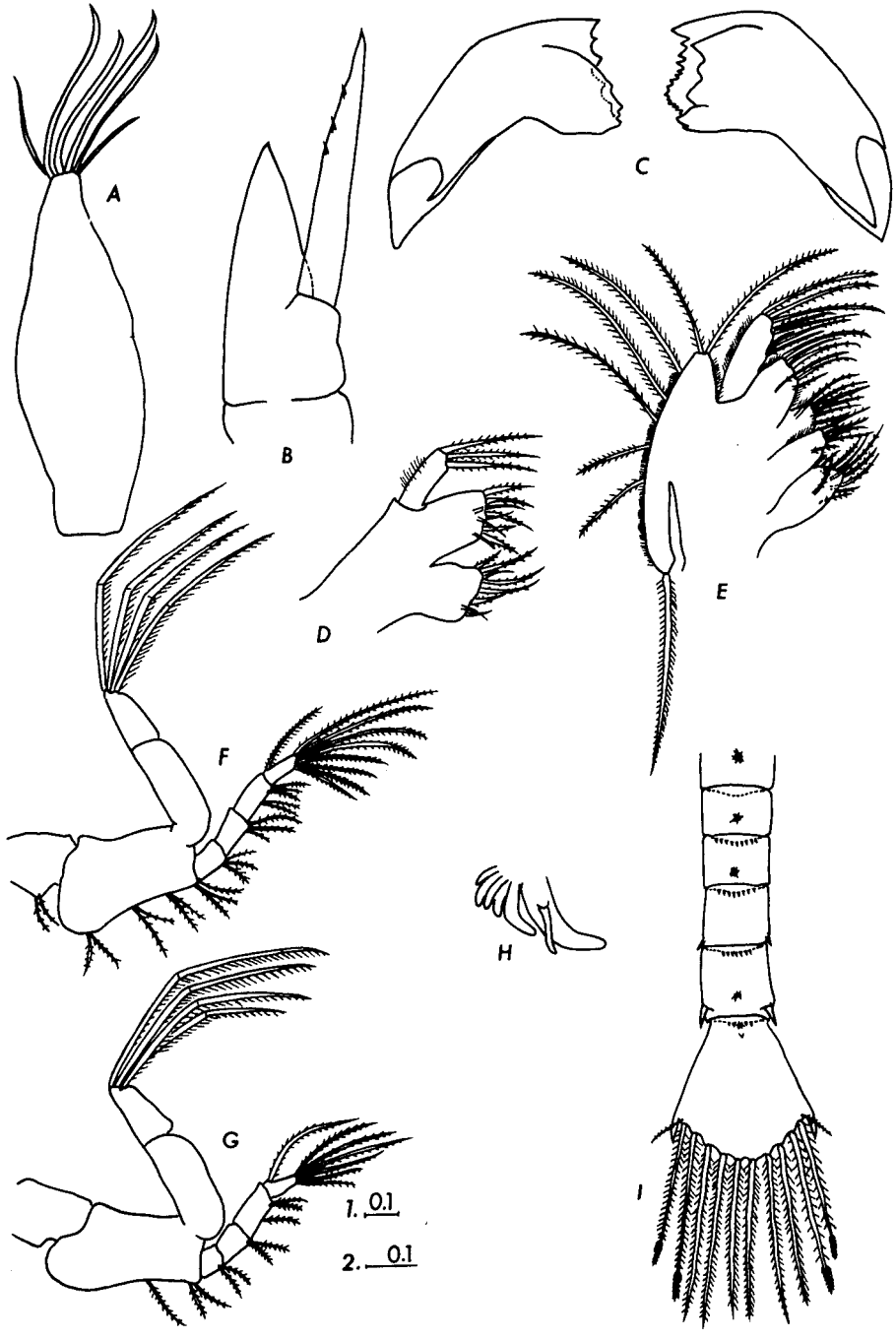

FIGURE 10.—*Pachycheles pubescens*, zoea I: A - antennule; B - antenna; C - mandibles; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III and pereiopod buds; I - abdomen and telson (A-E, H, Scale 2; F, G, I, Scale 1). Scales in millimeter.

Mandibles strongly toothed, heavily sclerotized asymmetrical appendages.

Maxilla I with unsegmented endopodite bearing three to five terminal setae and a number of fine hairs along anterior margin; basal endite with eight or nine setae; coxal endite with seven to nine setae.

Maxilla II with unsegmented endopodite bearing eight or nine setae grouped 3, 2, 3-4 progressing distally. Basal endite bilobed: distal lobe with six to eight setae; proximal lobe with six to eight setae. Coxal endite bilobed: distal lobe with three to five setae; proximal lobe with six to nine setae. Scaphognathite with seven long plumose marginal setae and one apical seta on posterior lobe. Numerous fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

Maxilliped I biramous. Coxopodite usually with two distal setae. Basipodite usually with nine setae arranged 2, 2, 2, 3 proximal to distal along inner margin. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin; segment 2 with three distal setae, inner margin; segment 3 usually with one, sometimes two medial setae, and usually three, sometimes two or four distal setae, inner margin; segment 4 with seven to nine terminal setae and one long proximal seta, outer margin. Exopodite two-segmented with four natatory setae on distal segment.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite with one medial, two distal setae, inner margin. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin; segment 2 with two distal setae, inner margin; segment 3 with one medial and one or two distal setae, inner margin; segment 4 with five or six terminal and one proximal seta, outer margin. Exopodite two-segmented with four terminal natatory setae.

Maxilliped III present as small bilobed bud which increases in size during the stage.

Pereiopod buds numbering five pairs, simple; none chelate; buds increase in size throughout stage.

Abdominal somites five in number; segments 4 and 5 with prominent paired ventrolateral spines on posterior margin; segments 2 through 5 with serrated dorsal posterior margins.

Telson with seven symmetrically arranged pairs of processes with seventh pair on central prominence. Outer margin to center line: one heavy lateral spine fused with telson; one short, fine seta; five long plumose articulating setae, the outer two armed distally with fixed, curved spines (Figure 1A, B); fine hairs on margin of telson (not figured) between all major plumose setae and on central prominence.

Chromatophore pattern same as that described for prezoea. Rostrum commonly with three bands of red, one terminal and two subterminal, occasionally with only one subterminal band; both posterior spines tipped with red. Carapace 1.31 to 1.56 mm long.

ZOEA II
(Figure 11)

Antennule biramous; exopodite with six or seven terminal processes including three or four aesthetascs and two or three setae followed by five tiers of aesthetascs grouped 2, 3, 3, 4-5, 4-6 proceeding proximally. One long seta projects from distal portion of protopodite.

Antenna biramous; endopodite pointed terminally and armed subterminally with one fine seta and two small spines; exopodite unarmed and about two-thirds length of endopodite.

Mandibles increased in size; prominent palp bud present.

Maxilla I with unsegmented endopodite bearing three or four terminal setae and a group of fine hairs along anterior margin; basal endite with 9 or 10 heavy spinous setae; coxal endite with 8 to 11 heavy spinous setae.

Maxilla II with unsegmented endopodite bearing nine setae. Basal endite bilobed: distal and proximal lobes each with 9 to 11 setae. Coxal endite bilobed: distal lobe with four to seven setae; proximal lobe with 10 to 13 setae. Scaphognathite with 18 setae on outer margin and 3 strong apical setae on posterior lobe. Numerous fine hairs occur on scaphognathite margin between plumose setae and elsewhere on appendage as figured.

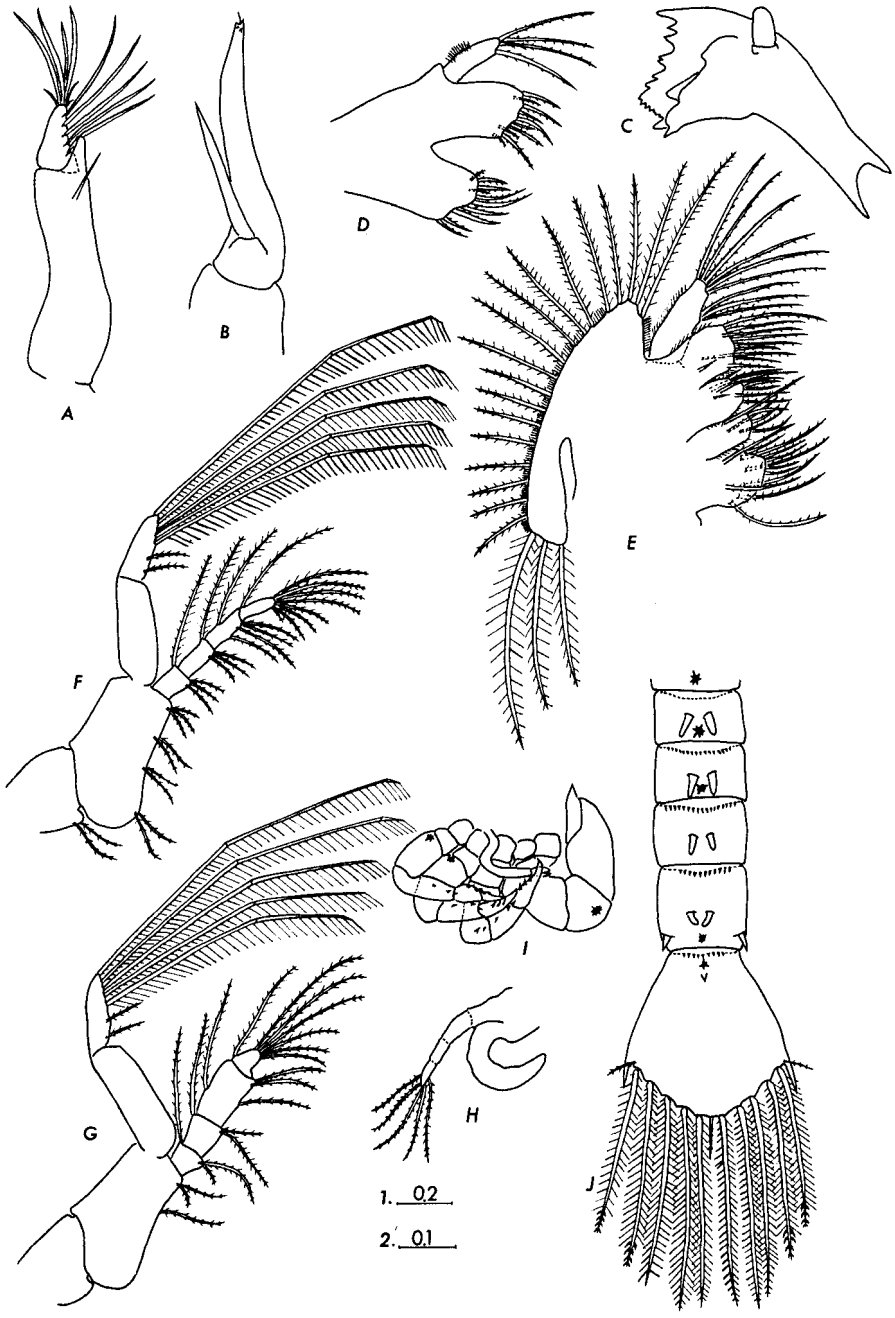

FIGURE 11.—*Pachycheles pubescens*, zoea II: A - antennule with only one aesthetasc shown for each of the five subterminal tiers; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III, late zoea II; I - pereiopods; J - abdomen and telson, early zoea II (A, B, F-J, Scale 1; C-E, Scale 2). Scales in millimeter.

Maxilliped I biramous. Coxopodite usually with two distal setae. Basipodite usually with nine setae along inner margin grouped 2, 2, 2, 3 proximal to distal. Endopodite four-segmented: segments 1 and 2 each usually with three distal setae (segment 2 occasionally with four), inner margin and one distal seta, outer margin; segment 3 most commonly with one but occasionally two medial, two to four distal setae, inner margin and one medial seta, outer margin; segment 4 with 8 to 11 terminals and 1 proximal seta, outer margin. Exopodite two-segmented with 14 natatory setae on distal segment.

Maxilliped II biramous. Coxopodite lacking setae. Basipodite usually with three setae grouped 1, 2 proximal to distal. Endopodite four-segmented: segment 1 with two or three distal setae, inner margin and one distal seta, outer margin; segment 2 with one or two distal setae, inner margin and one distal seta, outer margin; segment 3 usually with one (occasionally none) medial, two distal setae, inner margin, and one medial seta, outer margin; segment 4 with five terminals and one proximal seta, outer margin. Exopodite two-segmented with 14 natatory setae on distal segment.

Maxilliped III a bilobed bud. Exopodite increases in size throughout stage; four to six setae present; one or two definite segments present beneath cuticle, depending on age of zoea. Endopodite entire or segmented with up to five segments beneath cuticle, depending on age; setae of megalopa stage visible beneath cuticle of advanced zoea.

Pereiopod buds enlarge during stage and become well developed; first and fifth pairs distinctly chelate. Spines and claws appear on pereiopods in advanced, premolt larva.

Abdominal somites larger than in zoea I but similar in form; segments 2, 3, 4, and 5 each bear a pair of pleopods of unequal length.

Telson increased in size; an unpaired median seta added on central prominence (Figures 1C and 11J); anal spine present.

Basic color pattern same as in zoea I; red chromatophores added to pereiopods and beneath carapace in zoeae of advanced age. Carapace 2.37 to 2.54 mm in length.

MEGALOPA
(Figures 12 and 13)

Antennule biramous, consisting of a three-segmented peduncle, a dorsal ramus with six segments, and a ventral ramus with three segments. Segments 2, 3, and 4 of dorsal ramus each bear two tiers of aesthetascs; segment 5 with only 1 aesthetasc tier. Numbers of aesthetascs per tier proximal to distal 7-8, 8, 6-7, 5, 4, 2, 3. One long seta associated with distal tier of aesthetascs on segments 2, 3, and 4. Other setation as figured.

Antennal flagellum composed of 29 to 30 segments in addition to the three-segmented peduncle; most segments bear variable numbers of fine bristles around the distal margin as figured.

Mandible highly sclerotized with three-segmented palp; terminal segment of palp with about 17 spines; grinding edge only slightly irregular with a generally bladelike form.

Maxilla I with a two-segmented endopodite bearing a single distal seta on terminal segment. Basal endite with 7 slender setae and 14 heavy spinelike setae along distal margin; also seven short, stout, spinelike setae submarginally on dorsal surface of segment. Coxal endite with four setae on dorsal surface and about 29 marginal and near submarginal setae; delicate fanlike coxal exite rimmed with hairs is present.

Maxilla II with unsegmented endopodite which bears five or six setae. Basal endite bilobed: distal lobe with 33 to 36 setae; proximal lobe with about 22 setae. Coxal endite bilobed: distal lobe with about 20 setae; proximal lobe with about 38 setae. Scaphognathite with about 68 marginal plumose setae and 5 short fine hairs on the surface of the fan.

Maxilliped I with exopodite bearing nine setae. Endopodite indistinctly two-segmented, bearing one seta on distal segment. Protopodite with about 52 setae. Coxal endite with about 23 setae.

Maxilliped II biramous; exopodite indistinctly two-segmented with eight or nine terminal setae; endopodite four-segmented, segments 3 and 4 having heavy terminal brushes of about 26 and 30 setae respectively; other setation as figured.

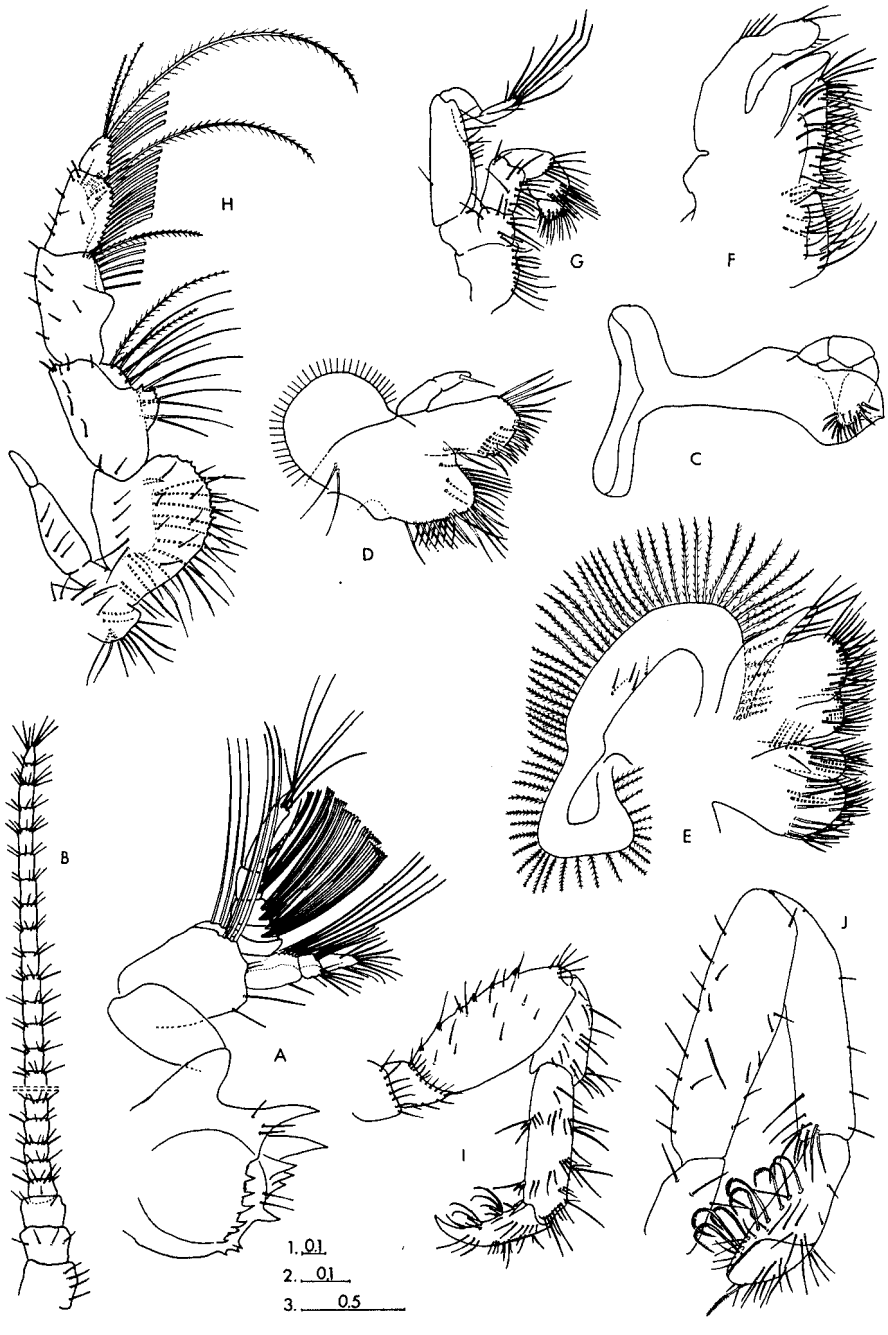

FIGURE 12.—*Pachycheles pubescens*, megalopa: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III; I - pereiopod III; J - pereiopod V (A, C-F, J, Scale 2; B, G, H, Scale 1; I, Scale 3). Scales in millimeter.

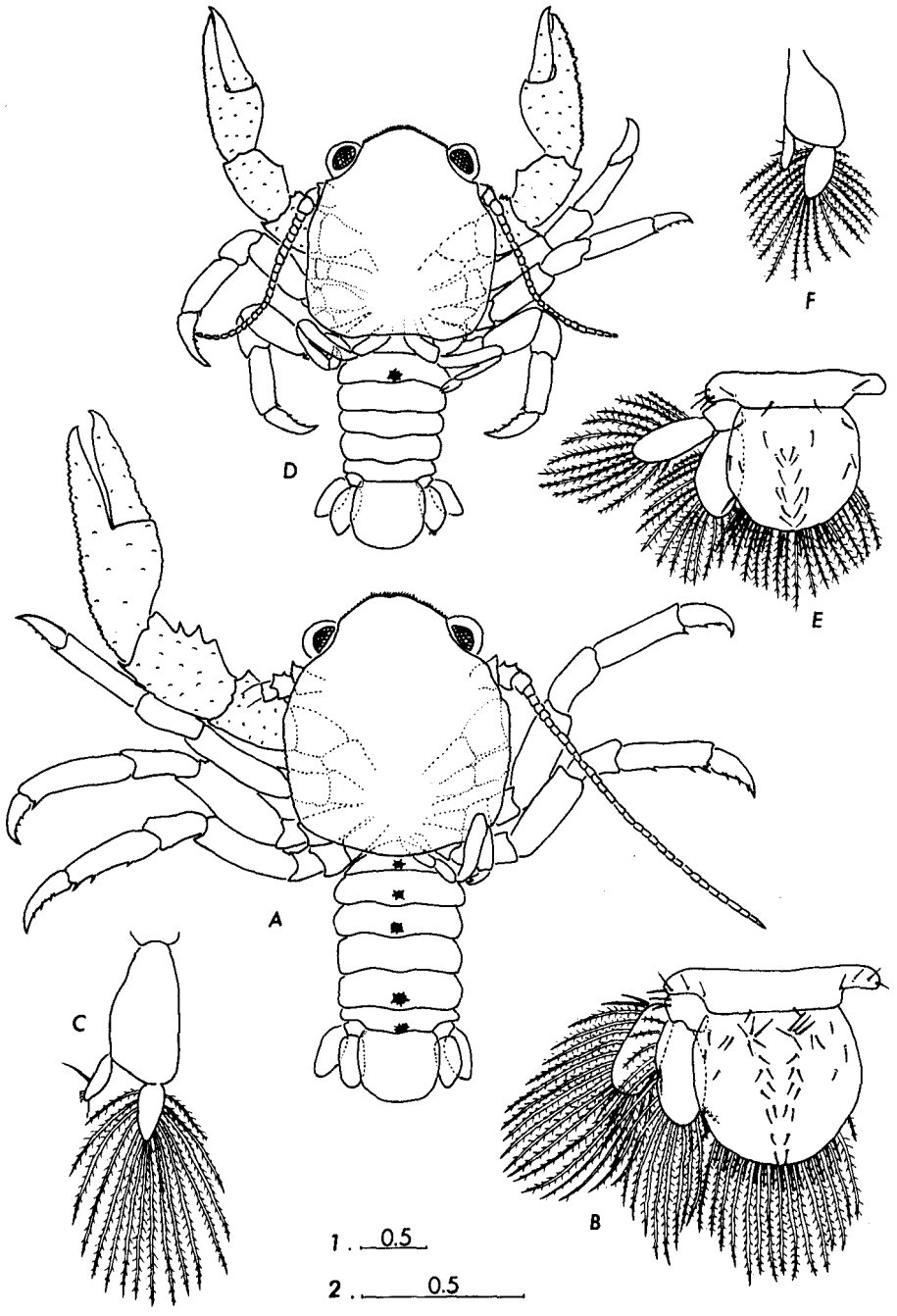

FIGURE 13.—*Pachycheles pubescens* (A-C) and *P. rudis* (D-F) megalopae, whole mounts: A - *P. pubescens* megalopa, whole mount; B - telson and uropods; C - right third pleopod; D - *P. rudis* megalopa, whole mount; E - telson and uropods; F - right third pleopod (A, D, Scale 1; B, C, E, F, Scale 2). Scales in millimeter.

Maxilliped III biramous; exopodite two-segmented, terminal segment being incomplete and lacking setae. Endopodite with five segments; segment 2 with 13 major marginal setae in double row (7, 6); segment 3 with five or six slender minor setae, outer margin, six major inner marginals, and nine brush setae, inner margin; segment 4 with five major and three spike-like brush setae, inner margin, 11 outer major marginals, and 7 inner minor auxiliaries; segment 5 with five pairs of major feeding setae, one or two pairs of minor terminal setae.

Pereiopods well developed and functional. Chelipeds large, swollen and bristly; two or three prominent fixed spines on the anterior margin of carpus. Three pairs of walking legs similar in form and setation as figured. Pereiopod 5 with 8 to 10 sickle-shaped setae and a number of other bristles.

Abdominal segments six in number, segments 2 through 5 with paired biramous pleopods bearing setae as follows: 16 marginal setae on exopodite; endopodite armed with four small hooks and two setae. Chromatophores appear posteriorly in segments 1, 2, 3, 5, and 6. Segment 6 bears a pair of biramous uropods, the outer rami each with about 19 plumose marginal setae and the inner with 17 or 18 such setae.

The telson has 15 or 16 major marginal setae. Minor marginal setae are present between almost all major setae. The dorsal surface of the telson is equipped with a number of very fine short hairs arranged in approximate symmetry as figured. Frontal margin of carapace as figured (Figure 13A).

LARVAL DEVELOPMENT OF *PACHYCHELES RUDIS* STIMPSON

In the laboratory, only a single *P. rudis* larva reared at 15°C and 33‰ salinity reached the megalopa stage. Laboratory-reared material was extensively supplemented with larvae from the plankton for purposes of examination.

Knight (1966) has dissected and accurately described the two true zoeal stages of *P. rudis*. She also adequately described the gross external morphology of the megalopa stage. Owing to high mortality in her cultures, she was forced to describe the larvae of this species on the basis of very few specimens. In this study, numbers of laboratory-hatched larvae surviving each stage in cultures were comparable to numbers obtained by Knight (1966), but the various stages were extremely abundant in the plankton. Knight's description of the species is expanded here using this more plentiful material.

PREZOEA

Body form is the same as that described for *Petrolisthes cinctipes* (Figure 2). Chromatophores occur as follows: one on either side of the mouth; one posteriorly in abdominal segment 2 or between segments 2 and 3. This is the least colorful of the species discussed here. Knight (1966) does not mention a prezoeal stage.

ZOEA I AND II

Table 2 indicates points in which the larvae studied here differ from those described by Knight (1966). Differences are minor but are included to establish a more accurate range of variability for this species.

MEGALOPA
(Figures 13 and 14)

Antennule biramous with three-segmented peduncle. Dorsal ramus with six segments, segments 2 through 5 bearing 2, 2, 2, and 1 tier of aesthetascs respectively. Aesthetascs are arranged 6, 6-7, 5-6, 3-4, 3-4, 2, 3 in tiers progressing distally. A single long plumose seta is associated with the distal tier on segments 2, 3, and 4. Ventral ramus distinctly three-segmented, the most distal segment being indistinctly divided. Other setation and spination as figured.

Antenna long, slender, with three-segmented peduncle; flagellum with 20 to 21 segments; variable numbers of fine hairs and bristles arranged distally on most segments as figured.

Mandible strongly sclerotized, partially cup-shaped appendage with three-segmented palp; distal segment of palp with about 13 terminal spines as figured.

TABLE 2.—Comparison of species descriptions of *Pachycheles rudis*.

Stage	Appendage	Knight (1966)	This study
Zoea I	Antennule	6 processes including 3 aesthetascs, 2 setae	6-7 processes including 4 aesthetascs, 1-2 setae
Zoea II	Antennule	7 processes, including 3 aesthetascs, 2 setae	6-7 processes including 4 aesthetascs, 2-3 setae
Zoea II	Maxilla I: Coxal endite	5 spines, 6 setae	10 setae
Zoea II	Maxilla II:		
	Basal endite, distal lobe	10-12 setae	11-12 setae
	Basal endite, proximal lobe	10 setae	10-11 setae
	Coxal endite, distal lobe	6 setae	6-7 setae
	Coxal endite, proximal lobe	10-12 setae	9-10 setae
Zoea II	Maxilliped I:		
	Basipodite	Setae grouped 2, 2, 3, 3	Setae grouped 2, 2, 2, 3
	Endopodite, segment 3	2 medial setae	1-2 medial setae
	Endopodite, segment 3	3 distal setae	3-4 distal setae[1]
	Endopodite, segment 4	7-8 terminal setae[1]	8-9 terminal setae[1]
Zoea II	Maxilliped II: Endopodite, segment 1	2 distal setae, inner margin	2-3 distal setae, inner margin
Zoea II	Maxilliped III: Exopodite	2 slender setae	2 slender setae, and 2-3 fine setae
All larval stages	Abdominal segment 2 or between 2 and 3	--	1 chromatophore
	Either side of mouth	--	1 chromatophore

[1] Most common occurrence in bold face.

Maxilla I with indistinctly two-segmented endopodite bearing two stout setae on distal segment. Basal endite with 8 long, slender and 16 stout, spinous setae on margin and 6 short setae on ventral surface. Coxal endite with about 26 marginal setae and 4 fine setae on ventral surface. Coxal exite present as delicate fleshy lobe rimmed with fine hairs. One proximal seta on appendage near articulation with gnathal skeleton.

Maxilla II with large numbers of setae. Endopodite unsegmented with five setae. Basal endite bilobed: distal lobe with about 35 setae; proximal lobe with 9 or 10 marginal and 4 submarginal setae. Coxal endite bilobed: distal lobe with 20 to 21 setae arranged as figured; proximal lobe with 30 to 35 setae arranged as figured. Scaphognathite with about 58 setae around the margin and 2 fine submarginal setae on the anterior lobe.

Maxilliped I with numerous setae. Exopodite fleshy with one seta on margin. Endopodite indistinctly two-segmented, bearing a single seta proximally. Protopodite produced into triangular lobe with about 35 to 45 marginal setae and 3 proximal setae as figured. Coxal lobe with a total of about 18 setae arranged as figured.

Maxilliped II biramous. Setation of coxopodite and basipodite variable, approximately as figured. Exopodite two-segmented with setae as figured, with eight or nine setae on terminal segment. Endopodite with four segments; segments 3 and 4 having distal brushes of short setae numbering about 24 to 28 and 16 to 20 respectively. Other setation as figured.

Maxilliped III biramous. Exopodite two-segmented but incompletely formed. Segments 2 through 5 of endopodite equipped with major feeding setae; segment 2 with 11 or 12 feeding setae of two lengths, dorsal margin; segment 3 with five or six feeding setae on ventral margin, seven feeding setae or dorsal margin, and seven brush setae of varying lengths; no spikelike setae on dorsal protuberance; segment 4 with 2 short setae, 5 major brushes and 4 spike setae on dorsal protuberance, 10 long feeding setae on ventral margin, and 9 scattered minor submarginal setae on ventral surface; segment 5 with 10 or 11 marginal setae and 2 or 3 short terminal setae. Other setation as figured.

Details of setation and form of the walking

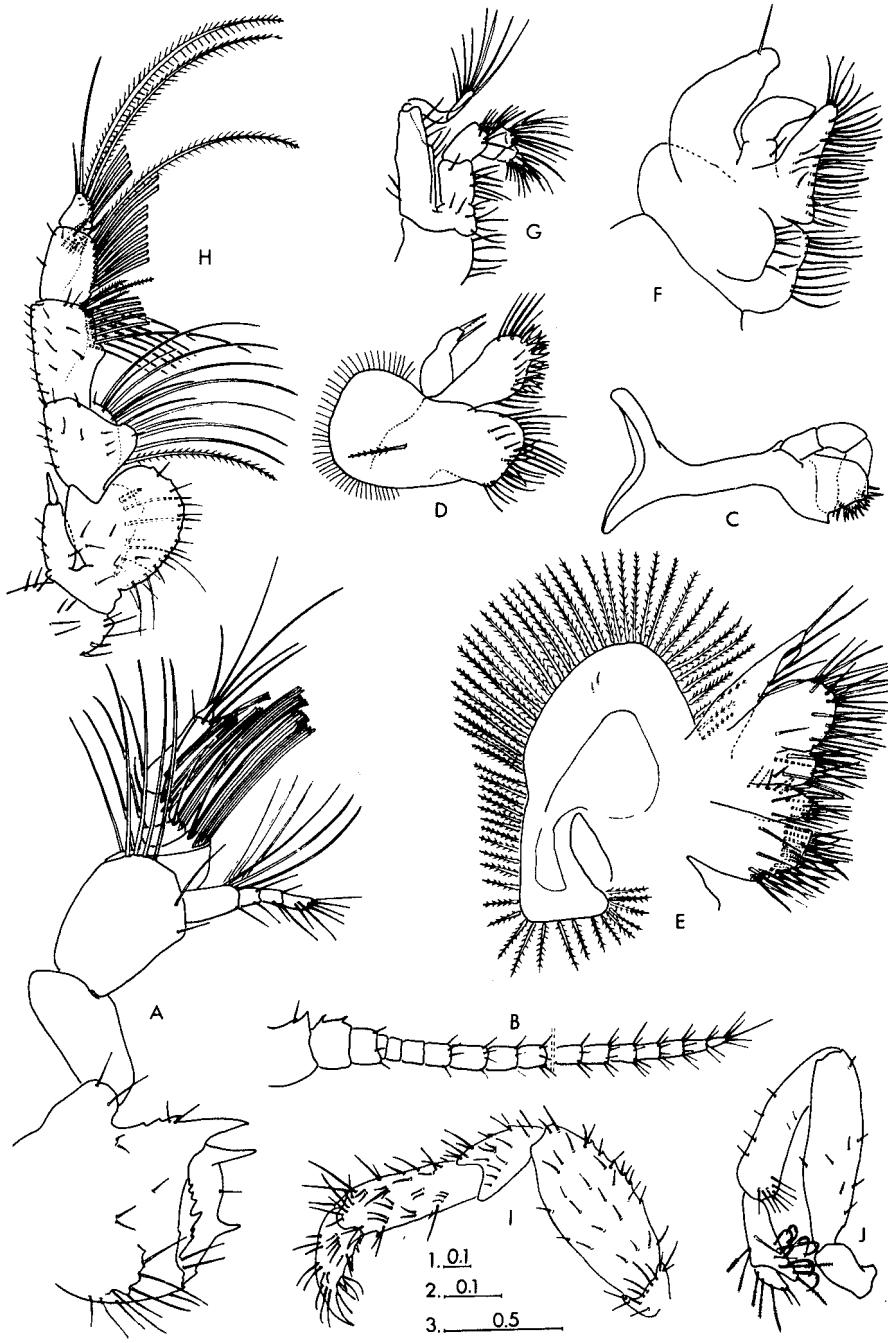

FIGURE 14.—*Pachycheles rudis* megalopa: A - antennule; B - antenna; C - mandible; D - maxilla I; E - maxilla II; F - maxilliped I; G - maxilliped II; H - maxilliped III; I - pereiopod III; J - pereiopod V (A, C-F, Scale 2; B, G, H, J, Scale 1; I, Scale 3). Scales in millimeter.

legs, the fifth pereiopods, the telson and sixth segment, and the frontal margin of the carapace are as figured.

DISCUSSION

The four species whose larvae are described here are the only porcellanids known (Haig, 1960) on the Pacific coast of North America north of Bodega Head, Calif., and we have found their larvae simultaneously in the plankton off the central Oregon coast. Both preserved and live zoea larvae of these four species can be readily assigned to genus on the basis of the number of long telson setae bearing conspicuous distal spines and the nature of these spines (Table 3). Once live or freshly killed zoeae are separated by genus using telson characters, individuals of the congeneric species can be separated to species on the basis of the distribution of the primary red chromatophores. Zoea larvae from preserved plankton samples cannot be identified to species easily once the chromatophores have faded. The only other nonvariable character found which distinguishes the species was maxillipedal setal counts, and it is possible that further study will indicate that these counts are also variable.

The two *Pachycheles* species differ in both zoeal stages by a single seta on the inner margin of segment two of the endopodite on maxilliped I (Table 4). In addition, second zoea larvae of these two species differ by a single seta on the outer margin of endopodite segment 1 on maxillipeds I and II (Table 4). Similar characters separate the larvae of the two *Petrolisthes* species. First zoeae differ by one seta on the inner margin of segment two of the endopodite of both maxillipeds I and II (Table 5). Second zoeae of these *Petrolisthes* differ by a single seta on the outer margin of the first segment of the endopodite on maxilliped II (Table 5). Megalopae of all four species can be readily differentiated on the basis of cheliped form and other finer characters (Figures 12-14).

Available knowledge of the larvae of *Pachycheles* species does not support Haig (1960) who, studying adult animals, suggested that *P. rudis* is most closely related to *P. stevensii*. A comprehensive comparison (Table 4) of the four most similar larvae of the *Pachycheles* species studied thus far does not definitely indicate such a relationship. On the basis of larval form and setal numbers, all four of the species are equally similar.

At this time too few porcellanid larvae have been described to use larval characters to draw firm conclusions about generic and specific relationships. There is however a need for means to identify as closely as possible porcellanid zoea larvae taken from the plankton in regions where larvae of all of the porcellanid species have not been reared. For all known porcellanid larvae of established specific identity, we have listed in Table 3 three morphological characteristics which appear to assign porcellanid zoeae to genera or generic groups. The following discussion evaluates the usefulness of these characteristics in grouping presently known larvae systematically. Planktonic larvae of uncertain adult origin are included and grouped with known larvae they most closely resemble, but are not discussed further. Two New Zealand porcellanids for which larvae have been described, *Petrolisthes novaezelandiae* and *P. elongatus*, have some unusual characteristics in both the larval and adult forms which distinguish them from all other porcellanids known. For this evaluation, they are conditionally placed with groups with which they share the larval characters listed in Table 3.

All presently known porcellanid zoeae can be placed in one of three groups on the basis of telson form. Lebour (1943) originally established two of these groups (A and B, Table 3) by distinguishing larvae of the genus *Porcellana* from larvae of the genus *Petrolisthes* as the genera were known at that time. Lebour's original *Petrolisthes* type telson group (B, Table 3) now includes all described species of the genera *Pachycheles* and *Megalobrachium* and all but one of the described *Petrolisthes* larvae, *P. novaezelandiae*. Wear (1964a) has suggested that the exceptional *P. novaezelandiae* be placed in the genus *Pisidia* on the basis of both larval and adult characters. Lebour's original *Porcellana* type telson group (A, Table 3) now includes all described larvae of the genera *Euceramus, Poly-*

TABLE 3.—Comparison of porcellanid larvae on the basis of distal armature of telson processes and telson form.[1]

Species	Position of armed telson processes		Type of armature on setae	Telson form	Author
	Zoea I	Zoea II			
Pachycheles rudis	3,4	3,4	All *Pachycheles* spp. have equal number of spines on inner and outer margins.	B	Knight, 1966
Pachycheles pubescens	3,4	3,4		B	This study
Pachycheles stevensii	3,4	3,4		B	Kurata, 1964
Pachycheles haigae	3,4	3,4		B	Boschi et al., 1967
Pachycheles natalensis	3-7	?	Spines most prominent on 5th process.	B	Sankolli, 1967
Megalobrachium poeyi	0	0		B	Gore, 1971
Petrolisthes cinctipes	3-7	3-7	Spines, equal number inner and outer margins (first 5 species listed).	B	This study
Petrolisthes eriomerus	3-7	3-7		B	This study
Petrolisthes armatus	3-7	3-7		B	Lebour, 1943, 1950 Gurney, 1938 Gore, 1970, 1972
Petrolisthes lamarckii	3-7	?	Spines most prominent on 5th process.	B	Sankolli, 1967
Petrolisthes boscii	3-7	3-7	Spines most prominent on 5th process.	B	Shenoy and Sankolli, 1967
Petrolisthes rufescens	?	?	Not mentioned.	B	Gohar and Al-Kholy, 1957
"Porcellanella" sp.	?	?	Not mentioned.	B	Menon, 1937
Petrolisthes elongatus	3-7	3-7	6 prominent spines, inner margin; less prominent spines, outer margin.	B	Wear, 1964b Greenwood, 1965
Petrocheles spinosus	4,5	4,5	6-8 spines, inner margin.	C	Wear, 1966
Petrolisthes novaezelandiae	3	3,4	5-6 spines, inner margin.	A	Wear, 1964a Greenwood, 1965
?Petrolisthes sp. I	?	?	Not mentioned.	A	Menon, 1937
?Petrolisthes sp. II	?	?	Not mentioned.	A	Menon, 1937
Porcellana platycheles	3	3	Long fine spines inner margin only (?)	A	Lebour, 1943
Porcellana ornata	3-7	?	"Hooks" minute, most prominent on 3rd process.	A	Sankolli, 1967
Porcellana sigsbeiana	3-7	3-7	Finely dentate	A	Gore, 1971b
Porcellana sayana (as *P. ocellata*)	3-7	?	According to figures, tips are similar, smooth, or finely serrated(?)		Brooks and Wilson, 1883
Pisidia longicornis	3	3	Well-defined spines, equal number inner and outer margins (first 3 species listed).	A	Lebour, 1943 Sars, 1889
Pisidia bluteli	3	3		A	Bourdillon-Casanova, 1956
Pisidia inaequalis	3	3		A	Gurney, 1938
Pisidia spinulifrons	3	?	Minute "hooks", more developed on outer than on inner margin.	A	Sankolli, 1967
Polyonyx gibbesi	0	0		A	Gore, 1968
Polyonyx quadriungulatus	3	3	More spines on outer than on inner margin.	A	Knight, 1966
Polyonyx hendersoni	3-7	?	Minute spines, most prominent on 3rd process.	A	Sankolli, 1967
Euceramus praelongus	3,4	3,4	Well-defined spines, equal number inner and outer margins.	A	Roberts, 1968

[1] A = Lebour's (1943) definition of *Porcellana* telson. Telson about 1½ times as wide as long with seventh pair of processes situated outside and below central prominence in stage I. In stage II, an eighth pair of processes is added on the central prominence.
B = Lebour's (1943) definition of *Petrolisthes* telson. Telson about as long as wide with seventh pair of processes situated on central prominence in stage I. In stage II, a single median spine (or setae) added.
C = Fits neither A nor B exactly.

onyx, Porcellana, and *Pisidia.* A third telson type (C, Table 3) has since been described and to date includes only the larvae of *Petrocheles spinosus* from New Zealand.

Among larvae possessing a similar telson form, further systematic separation following generic lines appears to be possible on the basis of the position of the long telson setae (processes 3 through 7) armed distally with conspicuous spines. This is particularly true of 13 larvae of known adult origin possessing the *Petrolisthes* type telson. Of these 13 species, only the larvae attributed to *Pachycheles natalensis* differ from other larvae of the same genus.

The known larvae possessing the *Porcellana* type telson are more difficult to group using telson seta armature alone. Only larvae of the single known species of *Euceramus* can be distinguished from other known larvae of this telson type on the basis of setal armature. In

TABLE 4.—Comparison of larvae of four *Pachycheles* species.
(All unlabeled figures are setal numbers; all serial listings are proximal to distal.)

Appendage	Zoea I				Zoea II			
	P. rudis Knight 1966 and this study	*P. pubescens* This study	*P. haigae* Boschi et al., 1967	*P. stevensii* Kurata 1964	*P. rudis*	*P. pubescens*	*P. haigae*	*P. stevensii*
Antennule	3-4 aesthetascs; 1-2 setae	3-4 aesthetascs; 1-2 setae	3 aesthetascs; 2-3 setae	?	biramous; aesthetasc tiers 4, 5, 3, 3, 2	biramous; aesthetasc tiers 4-6, 4-5, 3, 3, 2	biramous; aesthetascs 8-14, 3 terminals	
Antenna:								
Endopodite	1 fine seta	0	1 fine seta	1 fine seta	1 seta	1 seta, 2 small spines	1 seta	
Exopodite	3 spines	1-4 spines	4 spines	3 spines	(3) spines rudimentary or absent	0 spines	0 spines	
Mandible	no palp bud	no palp bud	no palp bud	no palp bud	pulp bed present	palp bud present	palp bud present	palp bud present
Maxilla I:								
Coxal endite	9	7-9	8	8	10-11	8-11	10	NOT
Basal endite	9	8-9	9	6	10	9-10	11	
Endopodite	4	3-5	4	4	4	3-4	4	
Maxilla II:								
Coxal endite, PL[1]	6-8	6-9	9	7	9-12	10-13	7-8	MENTIONED
Coxal endite, DL[1]	4	3-5	7	3	6-7	4-7	5-7	
Basal endite, PL	7	6-8	7	5	10-11	9-11	6-7	
Basal endite, DL	7-8	6-8	7	6	10-12	9-11	8-10	
Endopodite	9	8-9	7	9	9	9	8	OR
Scapognathite	6 + 1 apical	7 + 1 apical	8 + 1 apical	6 + 1 apical	20-22	21	21-24	
Maxilliped I:								
Coxopodite	2	2	none?	NOT	2	2	2	FIGURED
Basipodite	2, 2, 2, 3	2, 2, 2, 3	2, 2, 3, 3		2, 2, 2-3, 3	2, 2, 2, 3	2, 2, 2, 3	?, 2, 2, 3
Exopodite	4	4	4		14	14	14	14
Endopodite:								
Inner margin	3, 2, 5, 7-8	2-3, 3, 3-6, 7-9	2, 4, 7, 10	MENTIONED	3, 2, 5, 7-9	3, 3-4, 3-6, 8-11	2, 4, 7, 10	3, 3, 2, 10
Outer margin	0, 0, 0, 1	0, 0, 0, 1	0, 0, 0, 1		0, 1, 1, 1	1, 1, 1, 1	1, 1, 1, 1	1, 1, 1, 1
Maxilliped II:								
Coxopodite	0	0	0		0	0	0	0
Basipodite	1, 2	1, 2	2	OR	1, 2	1, 2	1, 2	1, 2
Exopodite	4	4	4		14	14	14	14
Endopodite								
Inner margin	2, 2, 3, 5	2-3, 2, 3, 5-6	3, 3, 2, 7		2, 2, 3, 5	2-3, 1-2, 2-3, 5	3, 3, 2, 7	2, 2, 1, 6
Outer margin	0, 0, 0, 1	0, 0, 0, 1	0, 0, 0, 1	FIGURED	0, 1, 1, 1	1, 1, 1, 1	0, 1, 1, 1	1, 1, 1, 1
Maxilliped III	bilobed bud	bilobed bud			bilobed; 2 setae	bilobed; 4-6 setae	bilobed; 2 setae	bilobed; 2 setae
Pereiopods	5 pairs buds	5 pairs buds			5 pairs; 1 and 5 chelate	5 pairs; 1 and 5 chelate	5 pairs; 1 and 5 chelate	5 pairs; 1 and 5 chelate
Abdomen	5 segments, no pleopods	5 segments, no pleopods	5 segments, no pleopods	5 segments, no pleopods	5 segments, pleopods on 2-5	5 segments, pleopods on 2-5	5 segments, pleopods on 2-5	5 segments, pleopods on 2-5
Primary chromatophores	Total 3	Total 7	Total 5?	?	Total 3	Total 7	Total 5(?)	?

[1] PL = proximal lobe.
DL = distal lobe.

TABLE 5.—Comparison of maxilliped setation in *Petrolisthes cinctipes* and *P. eriomerus*. (All serial listings are numbers of setae, arranged proximally to distally.)

Appendage	Zoea I		Zoea II	
	P. cinctipes	*P. eriomerus*	*P. cinctipes*	*P. eriomerus*
Maxilliped I:				
Coxopodite	1-2	2	1-2	2
Basipodite	2, 2, 3, 3	2, 2, 3, 3	2, 2, 3, 3	2, 2, 3, 3
Exopodite	4	4	14	14
Endopodite:				
Inner margin	1-3, 2-3, 4-7, 5-7	2-3, 3, 5-6, 5-7	3, 3, 5, 5-6	2-3, 3-4, 5, 4-7
Outer margin	0, 0, 0-1, 1	0, 0, 0, 1	0, 1, 1, 1	0, 1, 1, 1
Maxilliped II:				
Coxopodite	0	0	0	0
Basipodite	1, 2	1, 1-2	1, 2	1, 2
Exopodite	4	4	14	14
Endopodite:				
Inner margin	1-2, 1-2, 2-3, 3-5	1-2, 1-3, 3-4, 3-5	2, 2, 3, 4-6	1-2, 2, 3-4, 5
Outer margin	0, 0, 0, 1	0, 0, 0, 1	1, 1, 1, 1	0, 1, 1, 1

contrast, larvae belonging to species of the present genera *Porcellana, Pisidia,* and *Polyonx* exhibit several different patterns of armed telson setae, a fact which, when coupled with the confusion of adults of these genera in the past, suggests that systematic problems still exist among these groups. The only point worth noting at this time is that second zoeae of two of the three species currently bearing the genus name of *Pisidia* and the second zoea of *Petrolisthes novaezelandiae,* which Wear suggests is actually a *Pisidia,* all have similar setal armatures and possess three pairs of pleopod buds on the abdomen. All other porcellanid zoea II larvae known to species have four pairs of pleopod buds. In order to determine whether these two characters are of any value in distinguishing the larvae of the genus *Pisidia* from other larvae with the *Porcellana* type telson, the second zoea of *Pisidia spinulifrons* must be described, the identity of Menon's (1937) *"Petrolisthes"* species I and II, with three pleopod pairs, resolved and *Pisidia inaequalis,* with four pleopod pairs, reexamined as a member of the genus.

In the course of this study, a number of specimens of each stage were examined, and particular attention paid to morphological variation, especially in setal counts for the larval appendages, since larval variability has caused a great deal of confusion in the literature on porcellanid and other anomuran larvae. Morphological variations in setal numbers, spine lengths, etc. were found within individuals from the left to the right sides, between individuals of the same species, and between individuals of the different species studied. These findings emphasize the necessity of basing larval descriptions, especially setal counts, on examination of adequate numbers of larvae of each stage. Throughout the descriptions given here, only the range of setal numbers found is indicated. Because of the importance placed on setation formulae in descriptions of crustacean larvae, some of the setal count variations found and their implications will be analyzed in a separate paper.

Variability in the number of larval molts required to reach a specific point in development, apparently in response to varying environmental conditions, occurs in many Anomura (Table 6) and other decapod groups as well (e.g., Broad, 1957; Costlow, 1965). This type of variation has caused difficulties among larval systematists for some time and has in part given rise to the idea that either larvae produced under laboratory conditions are abnormal and should be discounted altogether or that such stages are extraneous and should be subgrouped under larval stages most commonly noted. This concept of substages or extra stages has served to confuse the developmental picture (Efford, 1970), particularly among the porcellanids, where another type of variability has been discovered which, unfortunately, has lent further support to the "substage" concept.

Intermolt growth in which certain appendages increase in size within a single larval stage without molt is a type of variability prevalent in porcellanids. All four species described here show

this type of growth. Lebour (1943, 1950) was probably the first author to notice specimens showing this phenomenon. Lebour observed some substage molting and concluded that each substage she found in plankton collections must necessarily have been separated from less advanced substages by a discrete molt. She subsequently proposed that *Pisidia longicornis* and *Porcellana platycheles* probably possessed a variable number of stages with two "essential" stages. She assumed that a molt always separated the "alternative" stages, or substages from each other. The variable molting sequence may indeed occur in these species under certain circumstances, as it does in other Anomura (Table 6), but it is probable that Ib and IIc substages in *Pisidia longicornis* and IIc in *Porcellana platycheles*, which were taken in plankton samples but never obtained by molt in the laboratory, were products of intermolt growth.

LeRoux (1961, 1966) subsequently reared the larvae of both species and reported only two "true" zoeal stages each of which underwent growth in certain appendage buds without molting. It is likely that these species have the potential for both intermolt growth and stage number variability and that Lebour found a combination of both while LeRoux did not. A similar case might also exist in the *Petrolisthes* larvae studied by Wear (1964a, b), although he reports definite ecdysis between each of his substages. Larvae of these species, like the *Pisidia* and *Porcellana* species mentioned above, may show both intermolt growth and variable stage numbers, depending on environmental circumstances, a possibility not considered for example, by Roberts (1968) and Gore (1970) in discussing substages.

Other authors have subsequently supported Lebour's original substage designation of growth forms even though no molting was observed (e.g., Boschi et al., 1967). This is a needless and confusing subdivision of an apparently continuous process and it obscures the nature of the flexibility of the animals. The term substage is now used in such a variety of ways that it should be abandoned altogether, as Gore (1970) has suggested, and attention directed to the possible occurrence of variation in both molting and development rates as observed by Costlow (1965) in the portunid *Callinectes sapidus*.

Intermolt growth to date has been recorded directly or indirectly in the larvae of 70% of the porcellanids studied for which two or more zoeal stages are known (Table 7). All these species have demonstrated abbreviated development (fewer number of molts necessary to attain juvenile adult form) compared to most other

TABLE 6.—Species of Anomura other than Porcellanidae for which stage number variability has been reported.[1]

Species of Anomura	Source
Pleuroncodes planipes	Boyd and Johnson, 1963
Emerita talpoida	Rees, 1959
Emerita analoga	Johnson and Lewis, 1942; Efford, 1970
Emerita rathbunae	Knight, 1967
Hippa cubensis	Hanson, 1969
Blepharipoda occidentalis	Knight, 1968; Johnson and Lewis, 1942
Calcinus tibicen	Provenzano, 1962a
Coenbita clypeatus	Provenzano, 1962b
Trizopagurus magnificus	Provenzano, 1967
Petrochirus diogenes	Provenzano, 1968
Birgus latro	Reese and Kinzie, 1968
Paralithodes camtschatica	Kurata, 1960

[1] Intermolt growth has not been reported in the larvae of any of the above species.

TABLE 7.—Species of Porcellanidae for which intermolt growth or stage number variability have been reported. Includes only species with both zoeae known.

Species	Intermolt growth[1]	Stage variability[1]	Author
Petrolisthes cinctipes	+	—	This study
Petrolisthes eriomerus	+	—	This study
Petrolisthes armatus	—	+	Gurney, 1938
	—	+	Lebour, 1943, 1950
	+	—	Gore, 1970, 1972
Petrolisthes elongatus	O	+	Wear, 1964b
Petrolisthes novaezelandiae	O	+	Wear, 1964a
Petrolisthes rufescens	O	—	Gohar and Al-Kholy, 1957
Petrolisthes sp. I	O	—	Menon, 1937
Petrolisthes sp. II	O	—	Menon, 1937
Porcellana sp.	O	—	Menon, 1937
Porcellana platycheles	+	—	Le Roux, 1961
	—	+	Lebour, 1943
Porcellana sigsbeiana	+	—	Gore, 1971b
Pisidia longicornis	+	—	Le Roux, 1966
	—	+	Lebour, 1943
Pisidia bluteli	O	—	Bourdillon-Casanova, 1956
Pisidia inaequalis	O	—	Gurney, 1938
Polyonyx gibbesi	+	—	Gore, 1968
Polyonyx quadriungulatus	+	—	Knight, 1966
Pachycheles pubescens	+	—	This study
Pachycheles rudis	+	—	Knight, 1966; this study
Pachycheles haigae	+	—	Boschi et al., 1967
Pachycheles stevensii	+	—	Kurata, 1964
Euceramus praelongus	+	—	Roberts, 1968
Petrocheles spinosus	—	—	Wear, 1965a
Megalobrachium poeyi	+	—	Gore, 1971a

[1] + = Occurrence reported.
— = Occurrence not reported.
O = Occurrence probable but not directly reported.

Anomura studied but not necessarily reduced time spent in the plankton. This suggests that intermolt growth might permit larvae of these species to develop to metamorphosis under a variety of conditions without passing through a large number of molts. This mechanism might thus be of survival value in reducing larval loss at molt by effectively decreasing the number of molts required under various conditions to reach the juvenile form.

As more larval histories are studied, it may be found that intermolt growth occurs in Anomura other than the Porcellanidae. If the function and value of intermolt growth has been correctly interpreted here, this form of variability might be expected among species with low numbers of larval molts required to attain the subadult. Only careful studies of more life histories can reveal the possible relationship of intermolt growth and variable stage numbers.

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