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Petrolisthes zacae Haig, 1968 (Crustacea, Decapoda, Porcellanidae): The Development of Larvae in the Laboratory[1]

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ABSTRACT: The larval development of *Petrolisthes zacae* Haig, 1968, an eastern Pacific species of porcellanid crab that inhabits mangrove forests, is completely described and illustrated. Development consists of a prezoeal stage, two zoeal stages, and a megalopal stage. The zoeae and megalopae of *P. zacae* are quite similar to those of *P. armatus* but can be distinguished from the latter by several morphological features. The larvae of *P. zacae* are compared to those of both Atlantic and Pacific *P. armatus*, wherein the close relationship exhibited by the larvae of all three forms reaffirms that already noted for adults of the two species.

Petrolisthes zacae is a small, intertidal, eastern Pacific species of porcellanid crab commonly collected along muddy fringes of mangrove swamps in Costa Rica and Panama. The species was originally described from three specimens collected in 1938 from Ballenas Bay, Gulf of Nicoya, Costa Rica. Additional collections of the species were made by Dr. Lawrence G. Abele during visits and tenure at the Smithsonian Tropical Research Institute, Balboa, Canal Zone, from 1970 through 1973. The abundance of *Petrolisthes zacae* throughout the deep muddy regions of the mangrove forests in this area (see Abele 1972) and the close relationship of adults of the species to *Petrolisthes armatus* (Gibbes 1850), another extremely common intertidal species, suggested that examination of the larvae of *P. zacae* might prove interesting when compared to larvae of *P. armatus*. Consequently, a collecting trip to the Pacific side of Panama was made during the week of 8–13 August 1973, wherein several ovigerous female specimens were procured. The complete larval development, from hatching to megalopal stage, was followed in the laboratory and is the subject of this report.

MATERIALS AND METHODS

Ovigerous females, and the males occurring with them, were collected on 10 August 1973 in the vicinity of the Diablo Boat Ramp, Balboa, Canal Zone. The crabs usually occurred in small niches or eroded cavities in hip-deep mud along a mangrove strand (*Rhizophora mangle* L.) fringing the mouth of the Panama Canal, east of the Bridge of the Americas. The specimens were returned to the laboratory at Fort Pierce where six females yielded larvae. The description that follows is based on a series of 72 larvae which hatched from two isolated females on 17 August 1973 (= series I). Additional larvae produced 3 and 4 days later by other females (including series II and III, see below) were examined periodically to determine whether morphological variation was occurring. None was found. Larvae obtained from all of the females were reared in 24-compartmented plastic trays by methods previously described for other porcellanid crabs (see, e.g., Gore 1970). Seawater stored in 13-gallon containers and used throughout the study varied from 31–33‰. Controlled temperature units were unavailable and, because the room temperature could not be adjusted to a constant value due to the type of air-conditioning present, room temperatures recorded at time of water change ranged from a low of 18° C in two instances, to a high of 26° C in a single instance. Temperatures almost never fluctuated faster than 4° C over any given 24-hour period, however, and the mean value for the 46-day rearing experiment was 22.5° C. Seawater was changed and *Artemia* nauplii were provided as food every day in series I, and every other day in series II and III. All trays were exposed to diurnal illumination. Measure-

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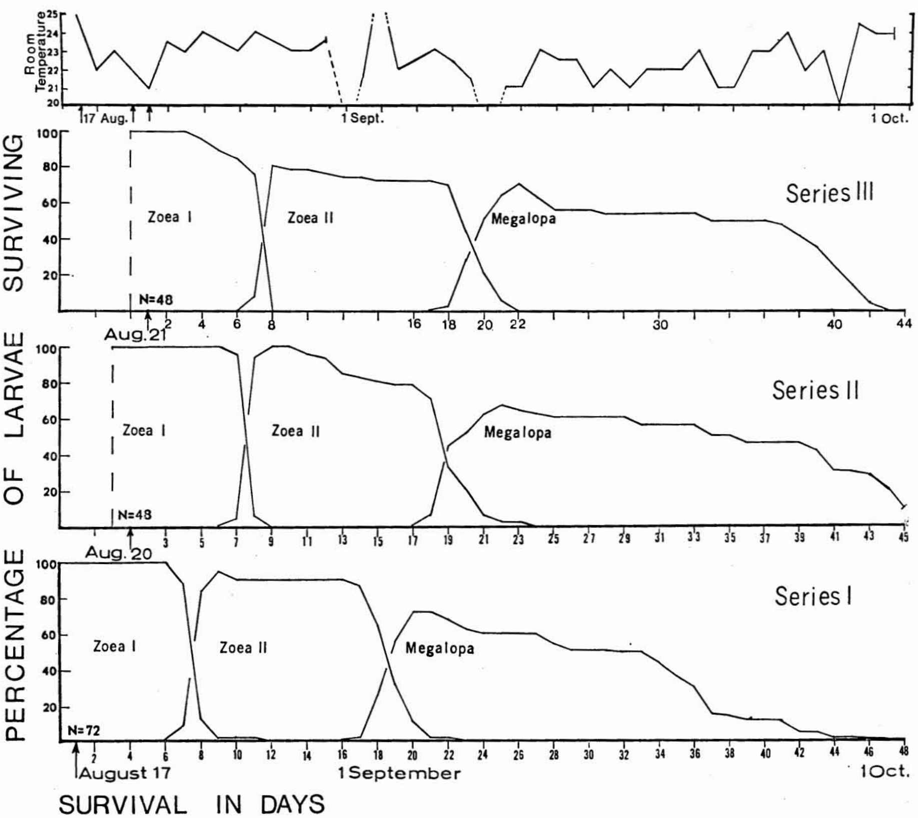

FIGURE 1. Percentage and duration of survival in three series of larvae of *Petrolisthes zacae*, reared under laboratory conditions. The calendar scale and the temperature record (C°) are the same for all three series. Arrows denote day 1, and N is the number of larvae cultured, in each series (see text).

ments of zoeae and megalopae, as in previous studies, are expressed as the arithmetic average of the specimens examined.

The two spent females, two males collected with them, and a complete series of larval and postlarval stages are deposited in the National Museum of Natural History, USNM 149176, 149177; a second series of a female, a male, and larvae is deposited in the British Museum of Natural History; a third series with a single female is deposited in the museum of the Allan Hancock Foundation, University of Southern California, Los Angeles, California.

REARING EXPERIMENT

Petrolisthes zacae hatches as a prezoea, a stage never lasting longer than about 30 minutes; this stage is not described. As in nearly all other porcellanid crabs, there follows two zoeal stages and one megalopal stage. Unfortunately, first crab stage was not attained in this study, although several megalopae died either while molting to that stage or entering the premolt state.

The females used in this study produced larvae over a 5-day period, those larvae hatching on 17 August from two females being termed series I, those on 20 August from a third female as series II, and those on 21 August from a fourth female as series III. Because of the irregularity in room temperature and the differences in hatching dates, each series was subjected to a slightly different temperature regimen. As can be seen in Figure 1, larvae in series I hatched at 25° C, whereas those in series II and III hatched at 21.5° C and 21° C, respectively. Consequently, though the temperature was the same for all series on any given calendar day, the larvae in each series were subjected to slightly different temperature sequences as their respective development progressed. For example, 4-day-old larvae in series I would be in water of about 22° C, whereas 4-day-old larvae in series II and III would be in water of about 23° and 24° C, respectively, as noted at time of water change. This minor temperature fluctuation apparently had no effect on early zoeal development, since first-stage zoeae in each series began to molt to stage II 7 days after hatching (Figure 1). More drastic temperature fluctuations occurred during early second zoeal stage and in the terminal days during the subsequent molt to megalopa. Temperatures dropped to 18° C on 1 and 9 September and rose to 26° C on 3 September. These changes are indicated by dashed lines on the room temperature record in Figure 1. It is impossible to determine the effects of such temperature fluxes on the duration of subsequent zoeal development. Again, no apparent effect on initiation of molting was noted. In each series, stage II zoeae began to molt to megalopal stage about day 17 or 18. However, the molting period for each series might have been extended at this time, since individual zoeae continued to attain megalopal stage as long as 23 days after hatching (see series II, Figure 1). It was during the latter part of this molting period in series II and III that the water temperature again dropped to 18° C.

As to whether or not the temperature changes observed previously during early stage II or subsequently during the molt to megalopa in series II and III affected postlarval survival or the ability of the megalopae to attain crab stage I must also remain speculative. Megalopae first appeared on day 18 and remained as such for as long as 27 additional days (day 45) before dying in that stage. Three megalopae from series III, however, died on day 38, 40, and 44, respectively, while molting to crab stage I. These were the only postlarvae actually to undergo visible ecdysis. Several other megalopae of similar age (greater than 35 days), upon postmortem microscopic examination, exhibited typical setal and appendage withdrawal and resorption indicative of late premolt condition. Otherwise these megalopae showed no outward signs of molting.

DISCUSSION OF REARING EXPERIMENT

In the Bay of Panama where the species was collected, water temperatures range between 25° and 32° C, with a mean of about 28° C during the months of August and September (Glynn 1972). The mean yearly surface seawater temperature is about 26.6° C, but a range of over 18° C can occur in a single day (Abele, unpublished). Mean seawater salinity for August-September is about 30‰, with monthly extremes from about 28 to 33‰.

Larvae in this study were cultured at an average temperature of 22.5° C in seawater of 31–33‰ salinity. They were thus exposed to what, in nature, would be high or extreme salinity values on the one hand, and on the other, to seawater the mean temperature of which was substantially lower than that occurring in the Bay of Panama at that time of year. The lowest temperature reported in the Bay of Panama for August–September was still about 3° C higher than the mean temperature of laboratory culture, although one laboratory extreme (26° C on 3 September) approached that normally occurring in Pacific Panama at that time of year. It appears, however, that the larvae of *Petrolisthes zacae* can tolerate these rather severe conditions, at least in the laboratory, and develop to the megalopal stage.

This tolerance is further reflected in larval survival, the percentage of which is remarkable. As can be seen in Figure 1, more than 70 percent of all larvae hatched and reared in each series attained the megalopal stage. The individual megalopae also survived reasonably well, and 50 percent mortality level was not reached until about halfway through the survival period, some 32 days after hatching. This again suggests that the temperatures and salinities to which the larvae were subjected in the laboratory (about 23° C, 31–33‰), although not necessarily those which would be encountered in nature, are not detrimental to larval survival. What remains unclear, however, is whether such temperatures and/or salinities inhibit in some way the postlarval molt to the first crab stage.

I have noted a similar occurrence in larvae of two other porcellanid crabs collected in the Bay of Panama and reared in the laboratory. Both

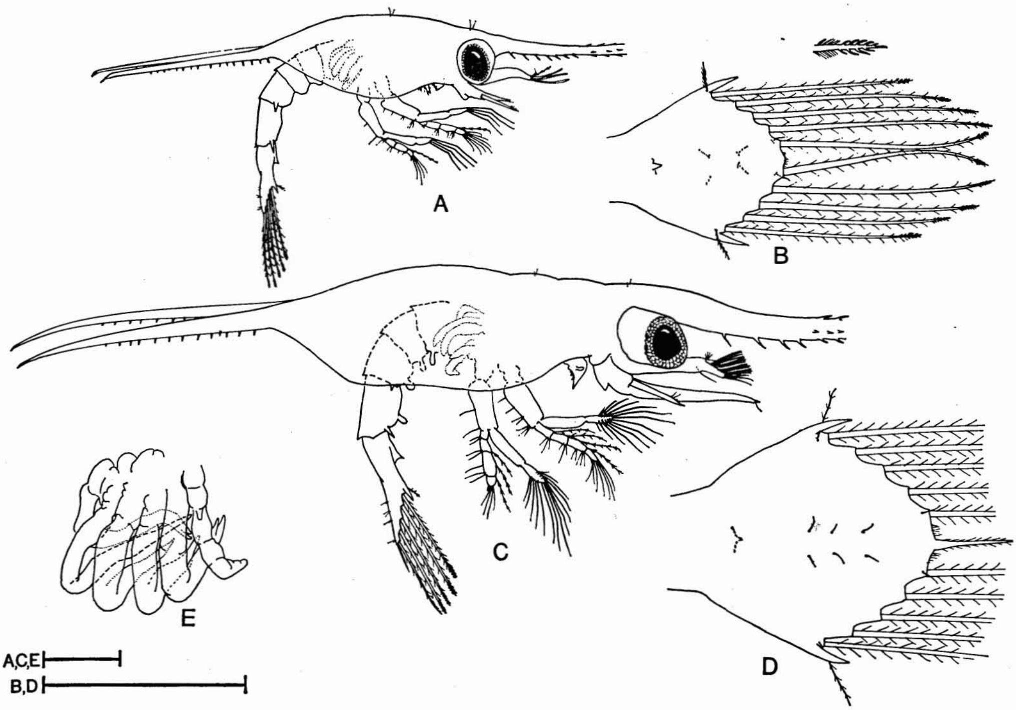

FIGURE 2. The zoeal stages of *Petrolisthes zacae* Haig. *A*, first zoea, early stage; *B*, telson of same, ventral view, and setal detail; *C*, second zoea, early stage; *D*, telson of same, dorsal view; *E*, third maxilliped and pereiopods, late second stage zoea. Scale line equals 0.5 mm.

Petrolisthes armatus and *P. tridentatus* exhibited greater than 50 percent survival well into the megalopal stage when cultured at lower temperatures and higher salinity (about 20° C, and greater than 32‰, respectively). However, only *P. tridentatus* attained crab stage I, with 11- and 17-day-old megalopae molting. Thus, the question posed is: Are the porcellanid postlarvae subject to molting difficulties when they encounter extreme conditions in the natural environment? And, if so, are they able to overcome such difficulties or do they simply "mark time" as megalopae until they die?

DESCRIPTION OF THE LARVAE

First Zoea

NUMBER OF SPECIMENS EXAMINED: Fifteen specimens were examined.

CARAPACE LENGTH: Carapace length is 1.4 mm (range 1.3–1.6 mm).

CARAPACE (Figure 2*a*): Typically porcellanid; shallow, not much inflated, long rostral spine up to 5 × carapace length, usually about 3.2 × carapace length, generally straight or slightly curved downward distally, armed with series of five to seven larger spines proximally, followed by numerous, smaller, distally directed spinules to tip. Posterior carapace spines straight or curved slightly downward, usually 0.6–0.7 × carapace length, armed with about 15 spinules ventrally progressing interiorad about midlength distally; none on posterolateral margin of carapace; tips of posterior spines naked, curved downward. Two pairs setae dorsally on carapace, over eyes and over midgut, respectively. Eyes sessile.

ANTENNULE (Figure 3*A*): Simple, elongate rod, three aesthetascs, two or occasionally three setae of decreasing size at tip.

ANTENNA (Figure 3*B*): Endopodite fused to protopodite, about 0.8 × length of exopodite,

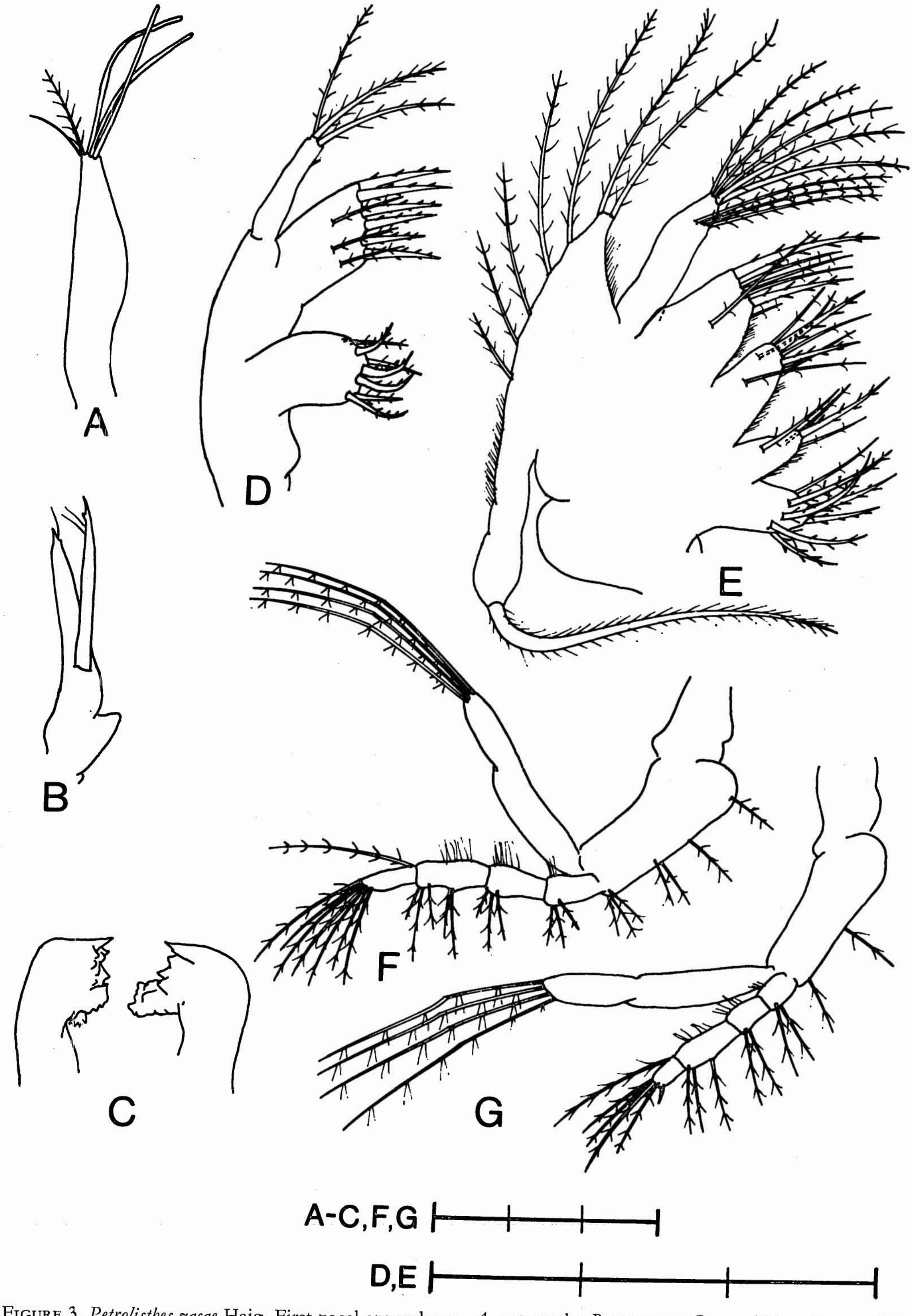

FIGURE 3. *Petrolisthes zacae* Haig. First zoeal appendages. *A*, antennule; *B*, antenna; *C*, mandibles; *D*, maxillule; *E*, maxilla; *F*, maxilliped 1; *G*, maxilliped 2. Scale lines equal 0.3 mm.

a single small seta distally; exopodite a slender spine overreaching endopodite, two small setae distally, followed by single small spinule.

MANDIBLES (Figure 3*C*): Asymmetrical dentate processes, left with well-developed molar process; no palp.

MAXILLULE (Figure 3*D*): Endopodite a single segment, three terminal setae plus small subterminal spinule. Coxal and basal endites with 6, 1, and 6, 3, spines and setae, respectively.

MAXILLA (Figure 3*E*): Endopodite unsegmented, five terminal (appearing as three apical, two slightly lower), three subterminal setae. Endites with spines and setae, respectively, as follows: coxal endite, proximal and distal lobes, 4, 3, and 1, 3; basal endite, proximal and distal lobes, each with 2, 5. Scaphognathite with seven or eight setae around margin, plus one long apical seta on posterior lobe. All processes placed as illustrated.

MAXILLIPED 1 (Figure 3*F*): Coxopodite naked. Basipodal ventral setae progressing distally, 1, 1, 2, 3; endopodal setae, 3, 3, 2+3, 7+I (Roman numerals denote dorsal setae only), plus fine hairs dorsally on segments two, three. Exopodite two-segmented, four natatory setae.

MAXILLIPED 2 (Figure 3*G*): Coxopodite naked. Basipodal ventral setae 1, 1; endopodal setae progressing distally, 2, 2, 1+2, 4+I, plus small distinct spinule terminally; fine hairs dorsally on segments two, three. Exopodite two-segmented, four natatory setae.

MAXILLIPED 3 (Figure 2*A*): Small naked bifid bud in early stage, future exopodite longer than endopodite. Appendage enlarges as zoea progresses toward stage II.

PEREIOPODS (Figure 2*A*): Simple, unsegmented buds, enlarging as stage progresses.

ABDOMEN (Figure 2*A*): Five somites, numbers four and five with distinct lateral spine.

PLEOPODS: Absent throughout stage I, but primordia distinctly noticeable in latter part of stage.

TELSON (Figure 2*B*): Seventh pair of telsonal processes (i.e., the fifth pair elongate plumose setae) situated on central prominence; latter with several fine hairs posteriorly, plus two fine setae dorsally. Elongate plumose setae (i.e., telsonal processes 3–7) with distinct spinules (see detail), more developed on process 3. Other setae located as illustrated. Anal spine present.

COLOR: Rostral spine orange, appearing faintly banded proximally and medially; posterior carapace spines orange but without banding. Red chromatophores appear as follows: on mandibles, scattered on zoeal mouthparts; interiorly in gut; as elongate bands ventrally, and extending vertically along posterior margins of abdominal somites 2, 3, 4, 5; a pair dorsally on telson; one on coxopodite, maxilliped 2. Developing pereiopods and maxilliped 3 tinged with blue; eyes pale green with dark eyespots. Rostrum becomes completely suffused with orange prior to ensuing molt.

Second Zoea

NUMBER OF SPECIMENS EXAMINED: Ten specimens were examined.

CARAPACE LENGTH: Carapace length is 2.3 mm (range 2.2–2.5 mm).

CARAPACE (Figure 2*C*): Now larger, more inflated transversely. Rostral spine up to 5× carapace length, usually about 4× carapace length, armed as in stage I with four to six large distinct spines proximally, followed by numerous smaller spinules to tip. Posterior carapace spines about 0.4–0.6× carapace length, armed as in stage I. Dorsal setae on carapace unchanged; eyes now mobile.

ANTENNULE (Figure 4*A*): Biramous; exopodite elongate, about twice endopodite length, with aesthetascs progressing distally 4, 3, 3, 3, 2, plus three terminally and three setae of decreasing size. Endopodite rounded, naked, four setae at junction with protopodite; latter with one long seta distally, two smaller spinules proximally, placed as illustrated.

ANTENNA (Figure 4*B*): Endopodite now greatly elongate, about 2.5× longer than exopodite, with single subterminal seta. Exopodite retains two subterminal setae and small spinule distally.

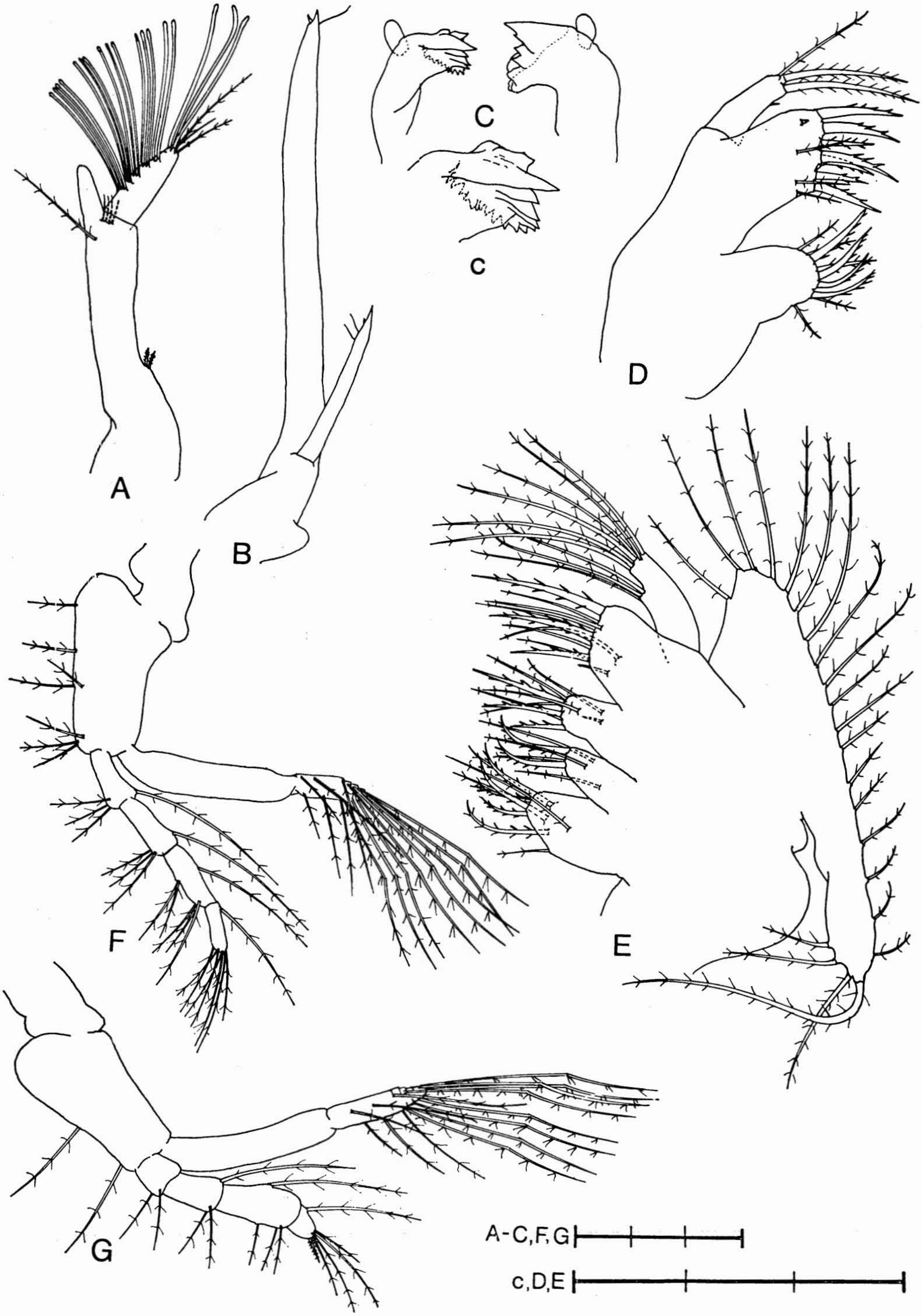

FIGURE 4. *Petrolisthes zacae* Haig. Second zoeal appendages. *A*, antennule; *B*, antenna; *C*, mandibles; *c*, detail illustrating dentition; *D*, maxillule; *E*, maxilla; *F*, maxilliped 1; *G*, maxilliped 2. Scale lines equal 0.3 mm.

MANDIBLES (Figure 4*C*, *c*): Now enlarged, more noticeably dentate than stage I, both with unsegmented palp.

MAXILLULE (Figure 4*D*): Endopodite and processes thereon remain as in stage I. Coxal and basal endites with 6, 3, and 7, 3, spines and setae, respectively; a small spinous nub may appear on basal endite as illustrated.

MAXILLA (Figure 4*E*): Endopodite unsegmented, 6, 3 setae, placed four terminally, two slightly lower, three subterminally as illustrated. Processes on basal endite as follows: distal and proximal lobes with 3, 7, and 3, 6, spines and setae, respectively. Coxal endite with 2, 4, and 3, 6, spines and setae on distal and proximal lobes, respectively. Scaphognathite with about 21 setae around margin, plus one long apical seta on posterior lobe.

MAXILLIPED 1 (Figure 4*F*): Coxopodite naked. Basipodite setae as in stage I, namely, 1, 1, 2, 3; endopodal setae formula 3+I, 3+I, 2+3+I, 7+I. Exopodite two-segmented; 14 natatory setae.

MAXILLIPED 2 (Figure 4*G*): Coxopodite naked. Basipodal setae remain as in stage I, 1, 1; endopodal setae formulae 2, 2+I, 1+2+I, 4+I plus distinct spinule terminally. Exopodite two-segmented, 14 natatory setae.

MAXILLIPED 3 (Figure 2*C*, *E*): Endopodite continues to increase in size as stage progresses; exopodite enlarges little, if at all; both appendages without setae.

PEREIOPODS (Figure 2*C*, *E*): Changing from short amorphous buds to elongate, distinctly segmented appendages as stage progresses; pereiopods 1 and 5 noticeably chelate at end of stage II. Gill buds enlarge concomitantly; entire mass protrudes from under carapace before molt to megalopa.

PLEOPODS (Figure 2*C*): Small buds at beginning of stage on somites 2, 3, 4, 5, lengthening noticeably throughout stage, becoming indistinctly segmented just prior to ensuing megalopal molt.

TELSON (Figure 2*D*): Stage I setation retained, fifth plumose pair remaining on central prominence, but with addition of median spine as illustrated.

COLOR: Similar to stage I; pleopods of somites 2, 3, 4, with spidery red chromatophores; pleopod 5 colorless. Rostral and posterior carapace spines become suffused with orange just prior to molt.

Megalopa

NUMBER OF SPECIMENS EXAMINED: Twenty specimens were examined.

CARAPACE LENGTH × WIDTH: Carapace length × width is 1.5 × 1.1 mm (range 1.4–1.5 × 1.0–1.1 mm).

CARAPACE (Figure 5): Subovate, moderately inflated, longer than wide. Frontal region broadly triangular, unarmed or with very minute teeth placed irregularly, visible only under high magnification (40× objective); a shallow median depression; numerous hairs dorsally. Small, distinct, epibranchial spine present, remainder of carapace covered with scattered short setae. Megalopa resembles adult in miniature except for enlarged eyes; latter each with single small palplike protuberance dorsoanteriorly.

ANTENNULE (Figure 6*A*, *a*): Biramous. Peduncle three-segmented, basal segment enlarged, flattened dorsally, rounded anteriorly, distinctly dentate, with setae placed as illustrated. Dentition of basal segment when projecting beyond frontal margin of carapace is easily seen from above. Lower ramus three-segmented, setae as illustrated. Upper ramus six-segmented, aesthetascs on segments two through five usually in following sequence of rows and numbers: one row (6), two rows (4, 3, +2 setae), two rows (3, 2, +2 setae), one row (3). Other setae somewhat variable but usually appearing as shown.

ANTENNA (Figure 6*B*): Peduncle three-segmented. Basal article expanded laterally as illustrated; first movable segment with distinct spine distally, followed by row of six to seven short spinules, a small lobe ventrolaterally; second and third segments smooth; flagellum with 30–34 short, subequal segments with setae as illustrated.

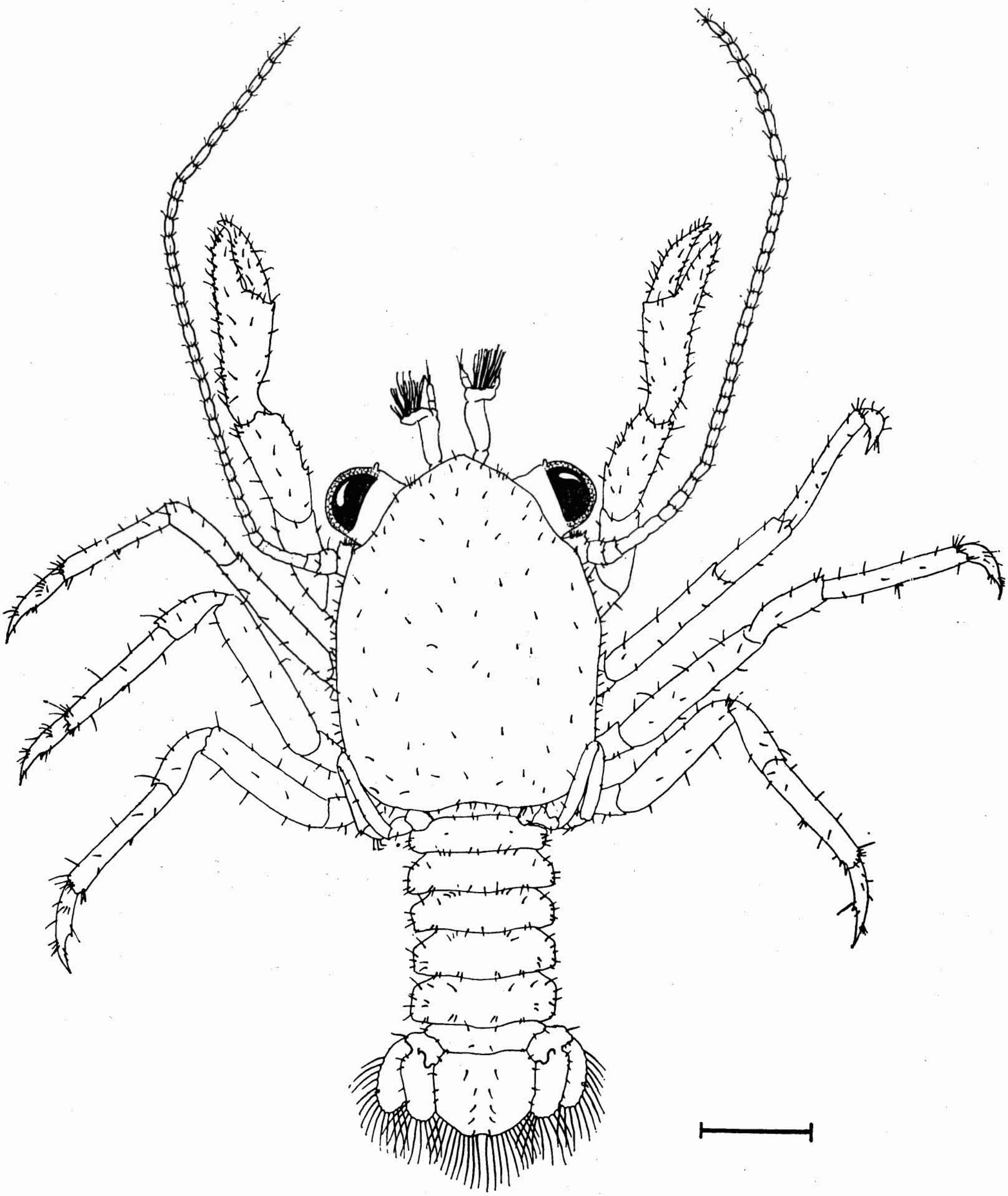

FIGURE 5. The megalopal stage of *Petrolisthes zacae* Haig. Scale line equals 0.5 mm.

MANDIBLES (Figure 6*C*): Cupped processes with thin blades. Each with three-segmented palp; basal segment with a single spine, terminal segment with 12–14 stiff setae and spines.

MAXILLULE (Figure 6*D*): Endopodite unsegmented, one or two setae terminally. Basal endite with about 13 sharp spines, about 15 setae; coxal endite distally with about nine sharp spines, one strongly spinous seta, 13 smaller

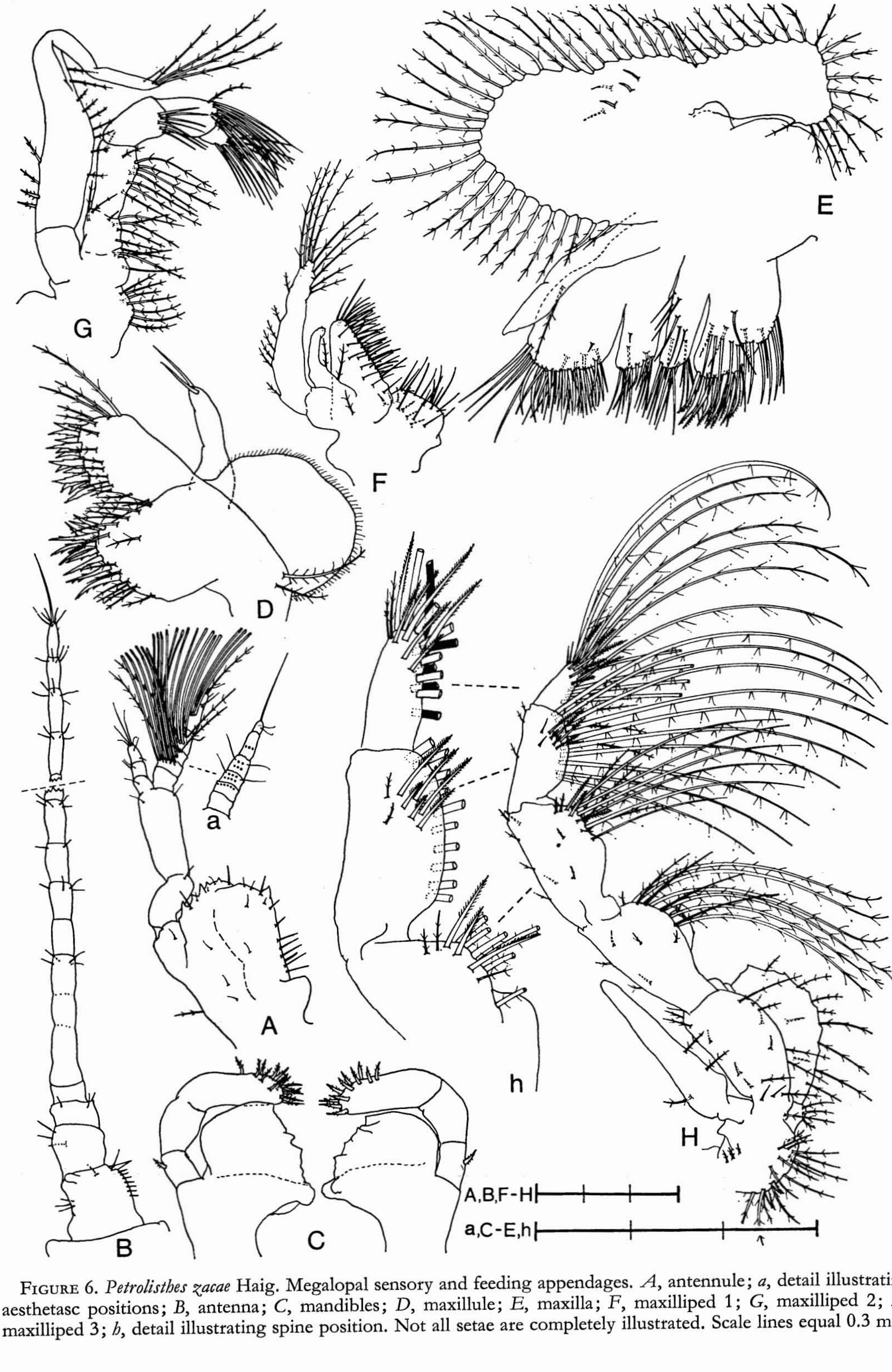

FIGURE 6. *Petrolisthes zacae* Haig. Megalopal sensory and feeding appendages. *A*, antennule; *a*, detail illustrating aesthetasc positions; *B*, antenna; *C*, mandibles; *D*, maxillule; *E*, maxilla; *F*, maxilliped 1; *G*, maxilliped 2; *H*, maxilliped 3; *h*, detail illustrating spine position. Not all setae are completely illustrated. Scale lines equal 0.3 mm.

setae, two additional setae proximally near base; elongate basal lobe of coxal endite fringed with fine hairs.

MAXILLA (Figure 6*E*): Endopodite obscurely two-segmented, one subterminal seta. Basal endite proximal and distal lobes heavily armed with about 14 and 40 strong setae and spines, respectively. Numbers difficult to count and may vary by two or more on each lobe. Coxal endite distal and proximal lobes densely covered with setae, spinous setae, and sharp spines; distal lobe with about 18 processes, including six to seven laterally down lobe, proximal lobe with about 32 processes, 16 of which encircle lobe medially, plus about 10 strong spines terminally. Scaphognathite with over 50 marginal setae, plus additional smaller setae on dorsal and ventral surface as illustrated.

MAXILLIPED 1 (Figure 6*F*): Appendage poorly calcified. Exopodite inconsistently armed, usually with about seven marginal setae and up to nine terminal setae; exopodite with two setae as illustrated; protopodite heavily armed with at least 40 setae on basal lobes and about 20 setae on coxal lobes.

MAXILLIPED 2 (Figure 6*G*): Exopodite indistinctly three-segmented, with four or five terminal setae, plus eight to nine setae on basal segment. Coxopodite, basipodite, and ischium fused, with six to seven, four, and five setae, respectively. Four-segmented endopodite with major spines or setae progressing distally as: 6–7, 7, about 14 (two of which are pectinate spines), about 12.

MAXILLIPED 3 (Figure 6*H*, *h*): Coxal and basal lobes with numerous setae, former with two strong spines. Exopodite with three setae as illustrated. Endopodite five-segmented, with major processes as follows: ischium, with flattened dentate blade, about 25 setae; merus with reduced, flattened dentate blade, six long, four shorter plumose setae; carpus, with proximal swelling, three daggerlike spines, 10 long, three or four shorter plumose setae; dactylus, seven daggerlike spines, 10 long, several shorter plumose setae. Daggerlike spines occasionally vary by one; longer plumose setae may vary in same specimen by one or two. Detail shows usual position of daggerlike spines to major plumose setae.

PEREIOPODS (Figures 5; 7*A*, *B*): Chelipeds not overly large, about equal, flattened, covered with setae; anterior margin of carpus with two or three unequal spines, posterodistal angle of same with single spine; outer margin of hand with numerous small, spinelike teeth. Walking legs as illustrated; merus with one or more reduced teeth along anterior margin, often visible only under high magnification (40× objective), carpus with small tooth anterodistally, propodus with single spinule ventrally about midlength, two elongate spines at posterodistal angle, dactylus with single, small movable tooth ventrally at midlength. Single dactylar tooth conforms to specific taxonomic feature characterizing adult of the species. Pereiopod 5 chelate, gape distinctly dentate, about seven scythelike pectinate setae as illustrated.

PLEOPODS (Figure 7*C*, *D*): Biramous, on somites 2, 3, 4, 5, shorter appendages nearer telson; exopodal and endopodal setae numbers inconsistent in same specimen, generally appearing as 10+0, 12+1, 12+2, 12+2, respectively, approaching telson. All endopodites with small hooks terminally, functioning as appendix interna.

ABDOMEN (Figure 5): Pleura as illustrated, covered with scattered setae.

TAIL FAN (Figure 7*E*): Telson with about 10+10 large marginal setae plus smaller setae interspersed among them; other paired setae dorsally and ventrally as illustrated. Uropodal exopodite with 17–19 large, marginal setae plus a distinct spinule on posterolateral margin; exopodite with 14–17 large, marginal setae.

COLOR: Eyes bronze-gold in reflected light. Body transparent overall, but carapace covered with numerous large red chromatophores, placed as follows: frontally, forming a V extending inward from each orbit; marginally along left and right sides of carapace, extending in interrupted line around posterolateral margin; gastric, cardiac, hepatic regions with several large coalesced chromatophores, also

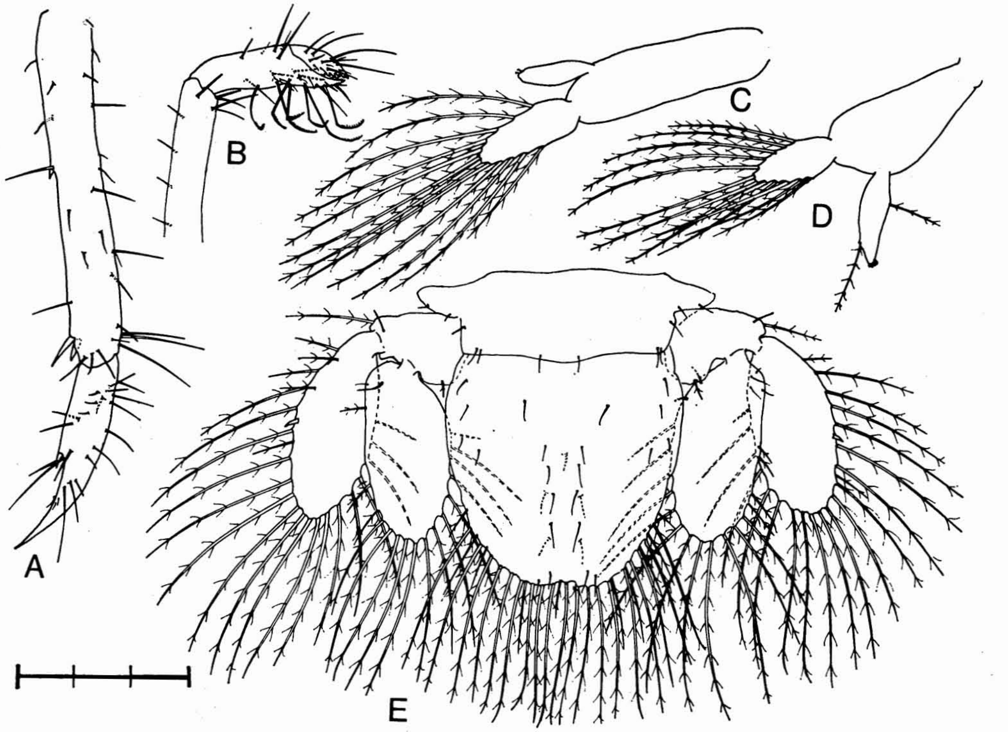

FIGURE 7. *Petrolisthes zacae* Haig. Megalopal locomotory appendages and tail fan. *A*, pereiopod 2; *B*, pereiopod 5; *C*, pleopod 1; *D*, pleopod 4; *E*, tail fan, dorsal view. Scale lines equal 0.3 mm.

extending obliquely outward in more or less interrupted line from mesobranchial region; additional large coalesced chromatophores appear on metabranchial area, and to lesser extent on intestinal region. Walking legs and chelipeds heavily speckled with red, abdominal somites with paired red chromatophores dorsally except for somite 5; pleopods except those on somite 5, with single red chromatophore basally. Lower lateral margin of carapace viewed from above appears deep blue; a small area of whitish yellow chromatophores anterior to red V on frontal margin. When viewed without magnification, megalopa appears distinctly mottled and speckled with red.

DISCUSSION

Haig (1968:64) has previously noted the close relationship between adult *Petrolisthes zacae* and *P. armatus*, a relationship now also exhibited in the zoeal and megalopal stages of both species. The zoeal stages of *P. zacae* are indeed nearly identical to those of both Atlantic and Pacific specimens of *P. armatus*, but may be distinguished from the latter by several features.

In live specimens of *P. zacae*, the most distinctive difference is in coloration, with the rostral spine indistinctly banded with orange, not pale green; with a red chromatophore only on the coxopodite of maxilliped 2, not on both maxillipeds; and with more intense color on the abdominal somites, with distinct bands, not widely scattered spots, being formed.

First zoeae of *P. zacae* differ from those of *P. armatus* in several morphological features. These include the more numerous spinules on the posterior carapace spines (compared with eastern Pacific *P. armatus*), greater lengths of the rostral and posterior carapace spines in relation to carapace length, the longer exopodite to endopodite length in the antenna, the presence of a single small spinule distally on the antennal exopodite, the greater number of setae on the maxillary scaphognathite, the slightly different setae formulae in the maxillipeds, and the presence of a small, distinct spine on the terminal endopodal segment of maxilliped 2.

In the second zoeal stage, *P. zacae* differs from *P. armatus* in the aesthetasc formula on the antennular exopodite, in the shorter relative length of the exopodite to the endopodite in the antenna (about $\frac{1}{3}$ as long), and in the retention of the small distal spinule on the exopodite of same; whereas both the Atlantic and Pacific second zoeae of *P. armatus* increase the terminal setae on the endopodite of maxilliped 1 by two, *P. zacae* still retains the basic stage I formula on the terminal segment. However, like the Atlantic form of *P. armatus* (but not the Pacific), *P. zacae* lacks the dorsal seta on the first endopodal segment of maxilliped 2, giving a formula of 2, 2+I, 1+2+I for the first three segments; and neither Atlantic nor Pacific specimens of *P. armatus* possess the single distinct spine in addition to four terminal setae seen on the last segment of this appendage in *P. zacae*.

Live megalopae of *P. zacae* may be identified in the plankton by the bright red V-shaped band across the frontal region of the carapace; and by the irregular red streaks along each lateral margin, which produce a distinctly mottled appearance in the postlarvae. Moreover, the megalopal stage of *P. zacae* may be immediately distinguished by a major morphological feature used to characterize adults of the species, namely, the single movable spine midway down the length of the elongate dactylus of each pereiopod. Haig (1968) noted this feature to be unique in adults of the genus *Petrolisthes*, and such is also the case in the megalopae of the genus known to me.

Additional features for comparison between *P. zacae* and *P. armatus* megalopae include the different aesthetasc formula on the antennule of the former species, as well as the more reduced armature of the basal antennal segment, the greater number of segments in the antennal flagellum, the different number of daggerlike spines on maxilliped 3, and, most noteworthy, the presence of a single small spine on the posterolateral margin of each uropodal exopodite. This last feature has not been noted in any other megalopa in the family Porcellanidae, so far as they have been described. These and other differences among both the zoeal and megalopal stages are summarized in Tables 1 and 2.

A comparison of larval mouthparts between *P. zacae* and eastern Pacific *P. armatus* thus reaffirms the close relationship held by the adults of the two species (see Table 1 and Gore 1972). The mandibles, maxillules, and maxillae reveal either no differences in setation, or only slight variation between the two species. Indeed, in the first zoeal stage the only consistent differences seemed to be in the higher number of marginal setae on the scaphognathite of the maxilla and in the relative length of the endopodite to the exopodite of the antenna. Maxilliped setation must be used with some caution inasmuch as both *P. zacae* and the Pacific form of *P. armatus* have the same formula on maxilliped 1. The presence, however, of a small spinule on the terminal endopodal segment of maxilliped 2 allows *P. zacae* to be easily distinguished not only from both zoeal stages of eastern Pacific *P. armatus*, but from those of the Atlantic form as well. In the second zoeal stage, of course, the setation on the maxillipeds is sufficiently different in the three forms to present no problem in identification at the present time.

Further comparison between the larvae of the two species reveals several other interesting features. For example, in the second zoeal stage, both *P. zacae* and Atlantic *P. armatus* lack a dorsal seta on the first endopodal segment of maxilliped 2; this seta is present in Pacific *P. armatus*. Zoeal stages of both *P. zacae* and Atlantic *P. armatus* possess similar posterior carapace spines armature; this armature is decidedly different in Pacific *P. armatus*. In the zoeal stage the antennular aesthetasc formula decreases by one, progressing from Atlantic *P. armatus*, to *P. zacae*. This tendency toward reduction is carried still further in *P. zacae* in the reduced setal formula on the first maxillipeds, as noted above. In this last respect, *P. zacae* is closer to Pacific *P. armatus* than to the Atlantic form.

Reduction in appendage adornment is also seen in the megalopae of *Petrolisthes zacae*. This reduction is exhibited, for example, in the antennular aesthetasc formulae, in the number of processes on the mandibular palp, in the

TABLE 1

COMPARISON OF ZOEAL FEATURES IN TWO SPECIES OF *Petrolisthes*

		P. armatus	
STAGE AND BODY PART	*P. zacae*	PACIFIC	ATLANTIC
Zoea I			
Carapace			
Length	1.4 mm	1.16 mm	1.6 mm
Rostral Spine	to 5 × carapace length (3.2 ×)	to 3 × carapace length	to 4 × carapace length
Posterior Spine	unarmed dorsally ca. 15 ventral spinules 0.6–0.7 × carapace length	small nubs ca. 4–6 ventral spinules 0.7 × carapace length	small nubs ca. 15 ventral spinules about equal carapace length
Antenna			
Exopodite	2 setae, 1 spinule	2 setae	2 setae
Endopodite	0.8 × exopodite length	2/3 exopodite length	1/2 exopodite length
Maxilla			
Scaphognathite	7–8 marginal setae	5 marginal setae	5 marginal setae
Maxilliped 1			
Basipodite	1, 1, 2, 3, setae	1, 1, 2, 3, setae	1, 2, 2, 3, setae
Endopodite	3, 3, 2+3, 7+I	3, 3, 2+3, 7–8+I	3, 3, 2+4, 9+I
Maxilliped 2	2, 2, 1+2, 4+I, plus small spine	2, 2, 1+2, 5+I	2, 2, 1+2, 5+I
Zoea II			
Carapace			
Length	2.3 mm	1.77 mm	2.0 mm
Rostral Spine	to 5 × carapace length (4 ×)	to 3.5 × carapace length	to 5 × carapace length
Posterior Spine	armed as stage I 0.4–0.6 × carapace length	armed as stage I 0.6 × carapace length	armed as stage I about equal carapace length
Antennule			
Endopodite	1/2 exopodite length	<1/2 exopodite length	2/3 exopodite length
Aesthetascs	4, 3, 3, 3, 2, +3 terminally	4, 4, 3, 3, 2, +3 terminally	4, 5, 3, 3, 2, +3 terminally
Antenna			
Exopodite	1/3 endopodite length	2/3 endopodite length	1/2 endopodite length
Maxilliped 1			
Endopodite	3+I, 3+I, 2+3+I, 7+I	3+I, 3+I, 2+5+I, 9+I	3+I, 3+I, 2+5+I, 11+I
Maxilliped 2			
Endopodite	2, 2+I, 1+2+I, 4+I, plus spine	2+I, 2+I, 1+2+I, 5+I	2, 2+I, 1+2+I, 5+I

Note: Data for *P. armatus* from Gore (1970, 1972). Parentheses indicate most common value.

setae on the maxillulary endopodite and coxopodite, in the daggerlike spines on maxilliped 3, and in the single ventral spinule on the dactyl of the walking legs. On the other hand, *P. zacae* has more segments in the antennal flagellum than either Atlantic or Pacific *P. armatus*, and possesses a spinule on the uropodal exopodite of the tail fan which both forms of *P. armatus* lack. However, if a trend toward progressive reduction in appendage adornment in zoeae and megalopae can be considered indicative of close relationships, then the larvae and postlarvae of *P. zacae* would appear to be more closely related to those of Atlantic *P. armatus* than to the Pacific form of that species.

Petrolisthes zacae is one of a small group of allied species that include *P. armatus*, *P. nobilii* Haig 1960, *P. robsonae* Glassell 1945 in the eastern Pacific, and perhaps the western Atlantic *P. politus* (Gray 1831), the geminate relative of *P. nobilii*. A fifth species described from the eastern Pacific, *P. lindae* Gore &

TABLE 2

COMPARISON OF MEGALOPAL FEATURES IN TWO SPECIES OF *Petrolisthes*

BODY PART	*P. zacae*	*P. armatus* PACIFIC	*P. armatus* ATLANTIC
Carapace			
Length × width	1.4 × 1.1 mm	1.5 × 1.2 mm	1.5 × 1.2 mm
Frontal region	unarmed*	sparsely serrate	serrate
Antennule			
Aesthetascs	(6), (4, 3, +2 setae), (3, 2, +2 setae), (3)	(4, 7–8), (6, 3, +2 setae), (3, 2, +1 seta), (3)	(8), (7, 3, +2 setae), (3, 3, +2 setae)
Antenna			
Flagellum	30 or more segments	about 25 segments	25 or more segments
Mandibles			
Palp	12–14 processes	10 processes	14 processes
Maxillule			
Endopodite	1–2 terminal setae	2 terminal, 1 subterminal setae	2 terminal setae
Basal Endite	2 basal setae, 28 processes	1 basal seta, 24 processes	2 basal setae, 25 processes
Coxal Endite	23 processes	18 processes	26–27 processes
Maxilla			
Endopodite	1 subterminal seta	2 unpaired setae	2 paired setae
Maxilliped 3			
Coxal lobe	2 strong spines	1 strong spine	2 strong spines
Endopodite Carpus	3 daggerlike spines*	3–4 daggerlike spines	6 daggerlike spines
Endopodite Propodus	6 daggerlike spines*	6 daggerlike spines	7 daggerlike spines
Endopodite Dactylus	7 daggerlike spines*	5 daggerlike spines	8 daggerlike spines
Pereiopods			
Dactyls	single movable spine	3 movable spines	3 movable spines
Tail fan			
Uropodal Exopodite	single spinule posterolaterally	no spinule present	no spinule present

Note: Data for *P. armatus* from Gore (1970, 1972).
* See text for variation.

TABLE 3

A COMPARISON OF SOME MORPHOLOGICAL FEATURES IN FIVE SPECIES OF *Petrolisthes*

SPECIES	EPIBRANCHIAL SPINE	CHELIPED CARPAL SPINES	WALKING LEG MERAL SPINES	WALKING LEG DACTYLAR SPINES
P. armatus	present	3–4	2–6	3 accessory
P. zacae	present	3	2–4	1 accessory
P. robsonae	present	2	0–1–2	3 accessory
P. nobilii	absent	3–4	1–8	3 accessory
P. lindae	vestigial or absent	1–2 plus lobe	0–1	3 accessory

Abele, 1973, appears to be intermediate in several features to *P. nobilii* and *P. robsonae*, and thus is probably also related to *P. zacae*. Relationships among these species are exhibited in the presence, reduction, or absence of epibranchial spines, a progressive reduction in the number of wide-set teeth on the anterior margin of the cheliped carpus, and by the varying number of spines on the anterior margin of the merus of the walking legs (see Table 3).

Only the larvae of *P. armatus* and *P. zacae* are known at present. It is tempting, but admittedly premature, to speculate on the possible evolution occurring in the species-complex mentioned above. Studies on the larvae of *P. nobilii*, *P. robsonae*, and *P. lindae* might provide further insight into both evolutionary trends and in determining species relationships across the Panamanian isthmus within this small, but notoriously variable, porcellanid group. It is to be hoped that such studies will be completed before the proposed sea-level canal is opened.

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