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LARVAL, POSTLARVAL, AND EARLY JUVENILE DEVELOPMENT IN *PAGURUS VENTURENSIS* COFFIN, 1957 (DECAPODA: ANOMURA: PAGURIDAE) REARED IN THE LABORATORY, WITH A REDESCRIPTION OF THE ADULT

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ABSTRACT

The taxon originally described from southern California as *Pagurus hirsutiusculus venturensis* Coffin, 1957 has been critically reexamined. Comparison with a Puget Sound, Washington, population of *P. hirsutiusculus hirsutiusculus* (Dana) has shown that the two taxa represent distinct species. *Pagurus venturensis* is redescribed and illustrated. The zoeal, megalopal, and early juvenile stages of this species are described and illustrated for the first time from specimens reared under laboratory conditions. Zoeae and megalopae of *P. venturensis* are compared with similar stages of *P. hirsutiusculus* from Puget Sound and northern California populations. These data provide additional evidence of the distinctiveness of the two taxa.

Pagurus hirsutiusculus was described (as *Bernhardus hirsutiusculus*) by Dana (1851) from the Puget Sound region of Washington. It was subsequently reported from as far west as Hokkaido, Japan (Stimpson, 1858, 1907), as far north as the Bering Sea (Rathbun, 1904, 1910), and as far south as southern California (Holmes, 1900; Hilton, 1916). Coffin (1957) was the first to recognize differences between northern and southern populations; he designated the latter as a new subspecies, *P. hirsutiusculus venturensis* Coffin.

Pagurus h. hirsutiusculus is reported from Monterey Bay, California, northward (Haig, 1977) while *P. h. venturensis* is found from Monterey County southward (Coffin, 1957). Coffin recorded no area of overlap between the two subspecies, and there has been no documented evidence of a clinal distribution of characters, although Blackstone (1989) purportedly demonstrated a north to south decrease in carcinization. The two taxa are easily differentiated by observation of the length : width ratio of the anterior carapace shield. In *P. h. hirsutiusculus*, the shield width is equal to or greater than its length, whereas in *P. h. venturensis* shield length exceeds width. Other morphological differences have been noted, such as the length of the eyestalks (Coffin, 1957) and the armature of the telson (McLaughlin, 1974). Coffin provided a comparison of shield measurements along with a brief diagnosis of *P. h. venturensis*; McLaughlin (1974) gave a complete description of *P. h. hirsutiusculus* and mentioned the major characters that separated the two subspecies.

In recent years, there has been increasing interest in the role of larval development in phylogeny (Rice, 1980; Gore and Scotto, 1983). Characters observed during ontogeny may play significant roles in determining relationships among taxa. In the present study we have used both adult morphology and larval–postlarval developmental sequences to evaluate the taxonomic position of *P. h. venturensis*. From these data we have determined that Coffin's (1957) subspecies is a distinct, albeit closely related, taxon. It is herein elevated to specific rank.

LARVAL–POSTLARVAL DEVELOPMENT

Materials and Methods.—Four ovigerous females of *P. venturensis* were collected during low tide at Cabrillo Beach, Los Angeles Harbor, California, on 16 December 1990. Upon capture they were placed in a container of aerated local seawater and the following day they were transferred to individual plastic Whirl-Pak® bags, each containing a small amount of the same seawater. Each bag was then enclosed in a second Ziplock® plastic bag and the bags placed in an insulated styrofoam container for shipment by over-night express to the Shannon Point Marine Center. Upon their arrival, the crabs, still in their Whirl-Pak bags, were placed in a large bowl of local seawater until they were acclimated to the culture temperature of 20°C. Once acclimated, these females, now designated A–D, were removed from the plastic bags and placed in individual glass culture dishes, each with approximately 500 ml filtered local seawater (29‰). The crabs were provided with bits of fish daily, and water in the culture dishes was changed two to three hours after feeding. Thirty-five zoeae from female A and 50 from female B hatched on 21 December. Of these 24 larvae from female A and 48 from female B were compartmentalized for individual rearing. Larvae from female C hatched on 22 December and larvae from female D on 24 December. Twenty-four of female C's zoeae and 24 of female D's were also placed in individual compartments in 24-compartmented plastic trays. Each compartment was filled with approximately 50 ml of natural, filtered seawater (29–31‰). All remaining larvae were reared in mass culture dishes (approximately 10 individuals per 500-ml filtered-natural seawater). The trays and dishes were kept in a constant temperature unit (20°C ± 1°) without light during the entire rearing period. Water was changed daily and the larvae were provided with a diet of rotifers (*Brachionus plicatilis* Müller) and algae (*Isochrysis galbana* Parke). When the megalopal stage was reached the diet was supplemented with freshly hatched *Artemia* nauplii. Terminology for the descriptions follows that of McLaughlin and Gore (1988). Descriptions are based on molts and on preserved and living stages examined throughout development. Some specialized setal forms were observed; however, no attempt was made to classify them (cf. Ingle, 1990). The letter N refers to the number of individuals reported for each stage that survived through that stage and successfully molted to the next; n refers to the number of individuals measured and/or dissected. The abbreviation CL refers to carapace length, as measured by an ocular micrometer, from the rostral tip to the posterior midpoint of the carapace; TL refers to the total length, as measured from the tip of the rostrum to the midpoint of the telson margin, excluding the telsonal spines. In megalopae and juveniles SL (shield length), as measured from the midpoint or tip of the rostrum to the midpoint of the posterior margin of the shield, is the indicator of size. Illustrations were made with the aid of camera lucidas mounted on Wild M-5 dissecting and M-20 compound microscopes. Setal formulae are all given from proximal to distal. Stage durations for Zoeae I and II are approximate, as the laboratory was operating on only emergency power for the period 26 to 30 December as the result of severe storms. Although larvae were changed daily during this period, the likelihood of missed exuviae is very high. Surviving larvae were maintained for a total of 60 days, during which time most had reached crab stages 2 or 3. Voucher specimens have been deposited in the National Museum of Natural History, Smithsonian Institution.

Zoeal Stages

Zoea I

Size.—CL = 0.76–0.98 mm; TL = 1.74–2.03 mm; n = 10.

Duration.—3–6 days. N = 95.

Carapace (Fig. 1A, B).—Rostrum moderately well developed, slightly shorter than or approximately equal to length of antennae; posterolateral carapace spines small; eyes sessile.

Abdomen (Fig. 2A).—Five somites and telson; posterodorsal margin of first with 3 pairs of minute spinules, second and third with 3 pairs of spines, outermost pair smallest, fourth with 2 pairs of strong spines and occasionally outer pair of protuberances or spinules, fifth with only 2 pairs of strong spines; second through fifth somites also with pair of small posterolateral spines.

Telson (Fig. 2A).—Elongate, moderately slender, fused with sixth somite; posterior margin with 7 + 7 processes (1, ii, 3–7), outermost smooth, faintly articulated spine (1), second, anomuran hair (ii), third through seventh articulated, plumodenticulate spines or setae, of which fourth is approximately as long as maximum telson width; posterior margin slightly convex and with small median cleft. Anal spine present.

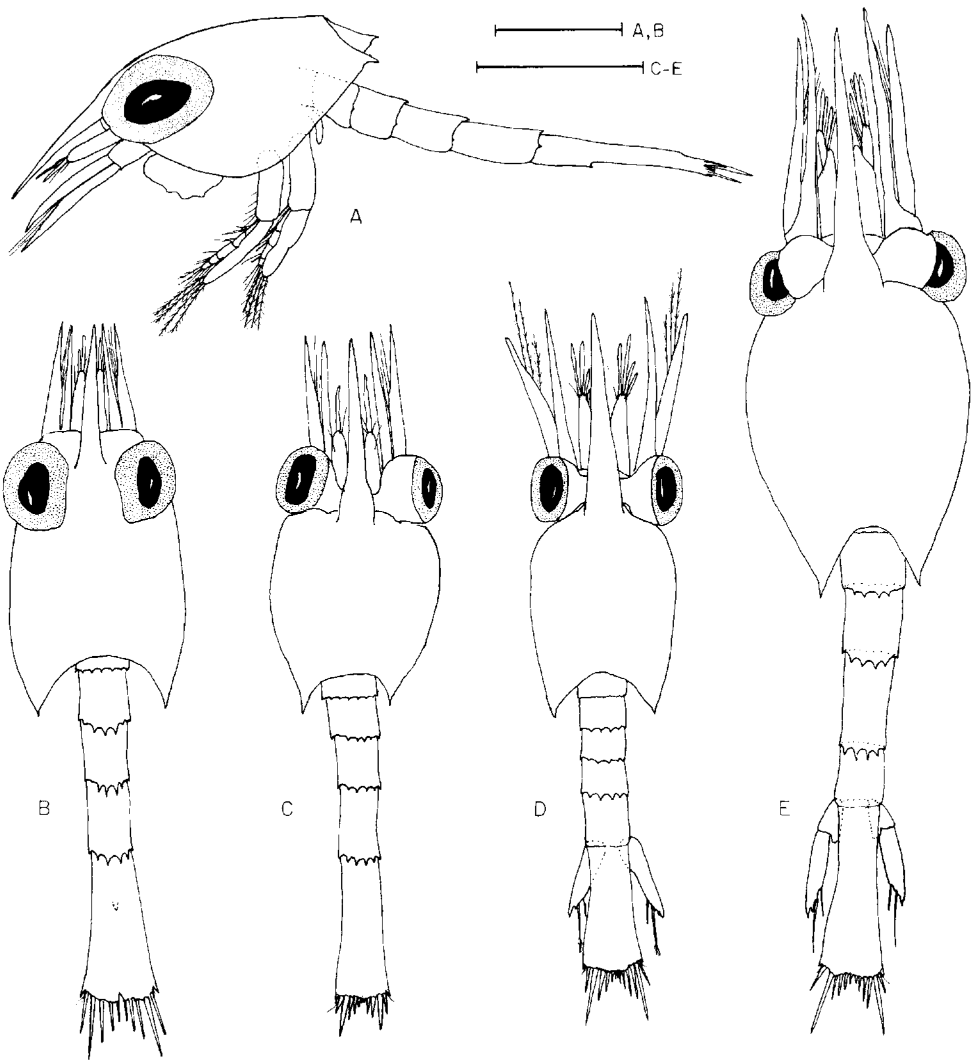

Figure 1. *Pagurus venturensis* Coffin. A, Lateral view of zoeal stage I; B–E, Dorsal view of zoeal stages I–IV. Scales: 0.5 mm.

Antennule (Fig. 2B).—Conical, unsegmented, one-half length of antenna or slightly longer; 1 or 2 aesthetascs and 3 or 4 simple setae terminally; 1 long plumose seta at site of future endopodal bud.

Antenna (Fig. 2C).—Scaphocerite slightly more than 4 times longer than wide, with elongate distal spine; inner margin with 3 or 4 plumose setae; endopod fused to protopod, approximately as long as scaphocerite, naked; 1 strong, unarmed or only faintly denticulate protopodal spine.

Mandible (Fig. 2D, E).—Asymmetrically dentate; incisor process with 1 strong prominent tooth and few denticles, often also 1 smaller bifid or blunted tooth; molar process serrate or spinose; no palp bud.

Maxillule (Fig. 2F).—Endopod 3-segmented; setal formula 0 or 1, 1, 3; coxal endite with 1 simple and 4 plumose setae marginally and 1 short simple seta

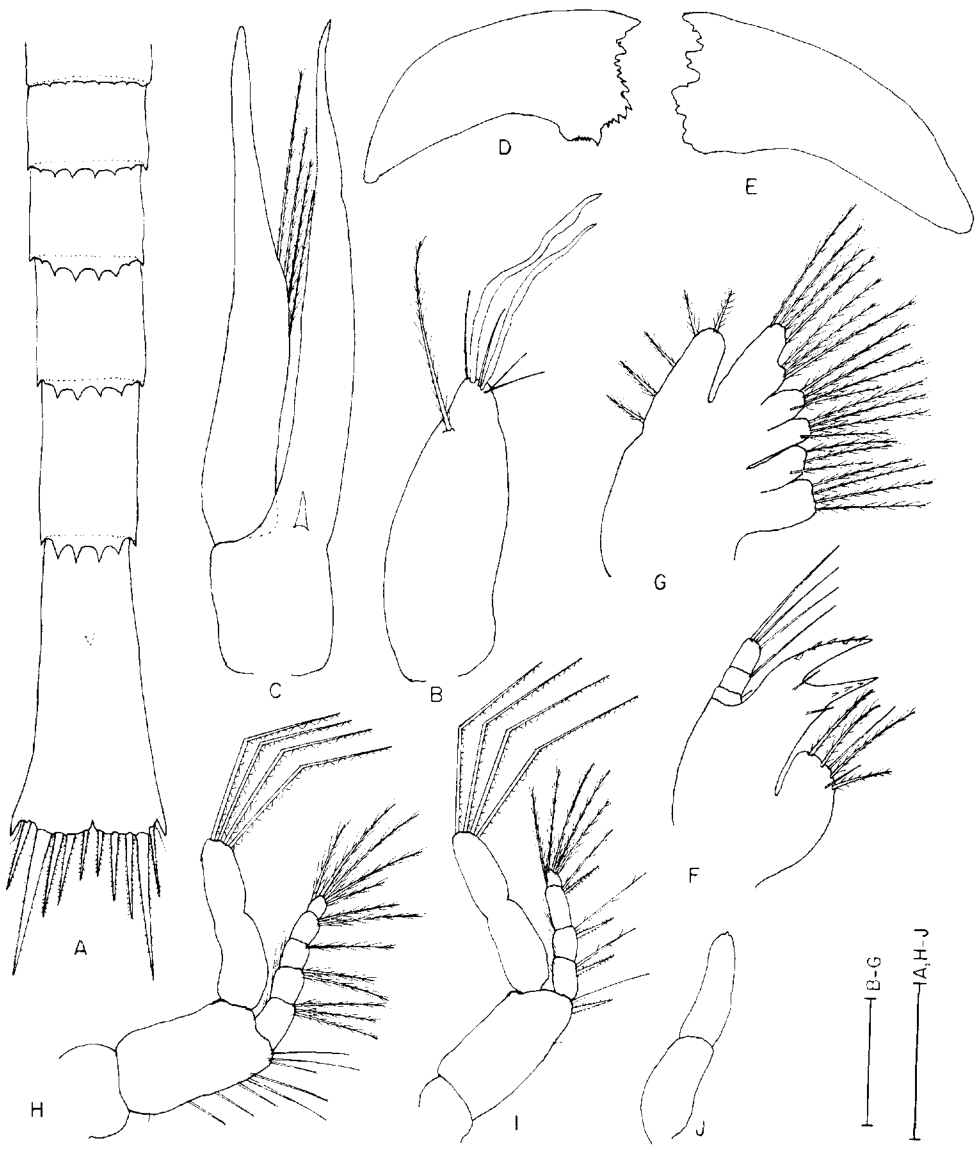

Figure 2. *Pagurus venturensis* Coffin: Zoeal stage I: A, abdomen and telson; B, antennule; C, antenna; D, left mandible, E, right mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped. Scales: 0.1 mm (B–G), 0.25 mm (A, H–J).

submarginally; basal endite with 2 elongate spine-like teeth, each armed with 3–6 moderately strong spinose denticles and 2 short simple setae submarginally.

Maxilla (Fig. 2G).—Endopod bilobed, with 2 or 3 plumose setae on proximal lobe and 3 or 4 plumose setae on distal lobe; coxal and basal endites also bilobed, coxal endite with 4 marginal plumose setae on proximal lobe and 2 or 3 marginal and 1 submarginal setae on distal lobe; basal endite usually with 3 marginal and 1 submarginal plumose setae on both proximal and distal lobes, occasionally only 3 marginal setae on distal lobe; scaphognathite fused to protopod proximally, distal lobe with 5 short, marginal, plumose setae.

First Maxilliped (Fig. 2H).—No coxal setae; setal formula of basipod usually 1, 1, 1, 3, 3, occasionally most proximal seta absent. Endopod 5-segmented, with setal formula of 3, 2, 1, 2, 4+I (I denoting dorsolateral seta) plus additional fine setae on lateral margins of proximal three segments; exopod incompletely 2-segmented, with 4 natatory terminal setae.

Second Maxilliped (Fig. 2I).—No coxal setae; basipod with 1 strong spine armed with marginal denticles and 1 long, usually simple, seta at or near distal angle, 1 additional short seta in distal half; endopod 4-segmented, first three segments each with 1 strong spine armed with marginal denticles and 1 long, usually only weakly plumose seta, fourth segment with 4+I plumose setae; exopod incompletely 2-segmented, with 4 natatory terminal setae.

Maxilliped 3 (Fig. 2J).—Exopod unsegmented, with rounded or slightly pointed, occasionally bifurcate tip.

Color.—Not recorded for this stage.

Zoea II

Size.—CL = 1.01–1.10 mm; TL = 1.91–2.32 mm; n = 10.

Duration.—4–6 days; N = 81.

Carapace (Fig. 1C).—Slightly larger but otherwise unchanged; rostrum varying from slightly shorter to slightly longer than antennae; eyes stalked.

Abdomen (Fig. 1C).—Posterodorsal marginal spines no longer apparent on somite 1, reduced on somite 2; posterolateral spines usually slightly smaller.

Telson (Fig. 3A).—Posterior marginal formula now 8 + 8 (1, ii, 3–8) with addition of short median pair of spines, first pair now clearly articulated, fourth still nearly as long as maximum telson width; median cleft obsolescent or absent; anal spine usually absent, occasionally still present as minute spinule.

Antennule (Fig. 3B).—Endopod bud now apparent, with 1 terminal plumose seta; exopod with 1 prominent and 1 smaller aesthetasc and 2 or 3 short, simple setae.

Antenna (Fig. 3C).—Spine of scaphocerite still very prominent, slightly overreaching endopod, inner margin with 1 simple and 3 plumose setae; protopod now with tiny spine near scaphocerite junction.

Mandible (Fig. 3D, E).—Larger, but generally unchanged from previous stage.

Maxillule (Fig. 3F).—Endopod and coxal endite unchanged; basal endite still with 2 simple submarginal setae, but now with 4 strong, spine-like teeth, each usually with 2–5 denticles, smaller than in preceding stage.

Maxilla (Fig. 3G).—Endopod, coxal and basal endites unchanged; scaphognathite now with 6–8 short, marginal plumose setae.

First Maxilliped (Fig. 3H).—Basipod setation unchanged; endopod setal formula now 3+I, 2+I, 1+I, 2, 4+I; exopod with 7 natatory terminal setae.

Second Maxilliped (Fig. 3I).—Basipod unchanged; endopod setal formula now 2, 2+I, 2, 4+I; exopod with 7 natatory terminal setae.

Third Maxilliped (Fig. 3J).—Exopod now incompletely 2-segmented and with 6 terminal natatory setae; endopod bud developing and with 1 simple terminal seta.

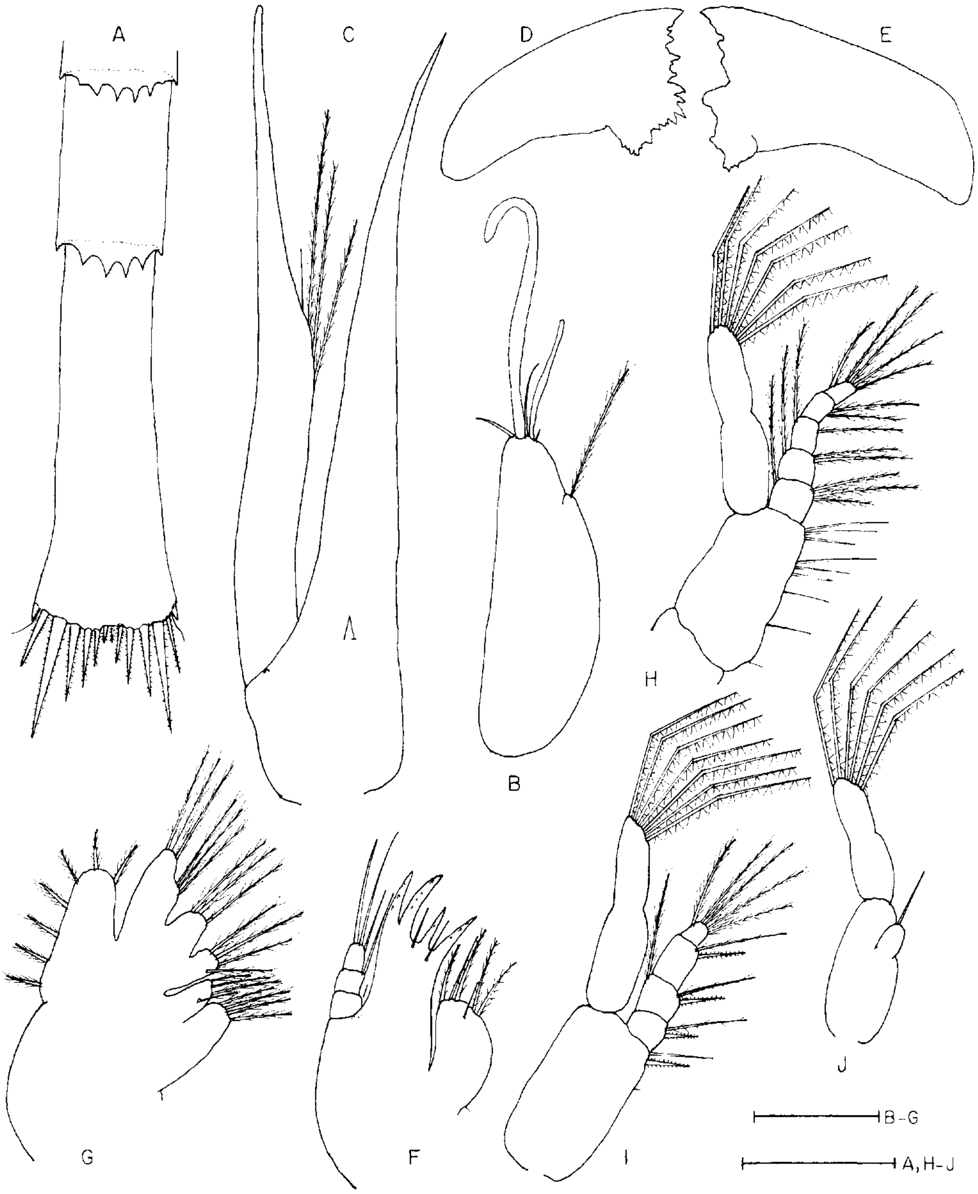

Figure 3. *Pagurus venturensis* Coffin: Zoeal stage II: A, fifth somite and telson; B, antennule; C, antenna; D, left mandible, E, right mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped. Scales: 0.1 mm (B–G), 0.25 mm (A, H–J).

Color.—Zoeae generally transparent, with red chromatophores on carapace behind eyes and at bases of antennae, maxillae and protopods of first and second maxillipeds; yellow chromatophores at base of rostrum and on antennal peduncles, on lateral margins of carapace, posteriorly on fifth abdominal somite, near anal opening and at terminal margin of telson.

Zoea III

Size.—CL = 1.46–1.55; TL = 2.81–2.98; n = 12.

Duration.—4–10 days; N = 73.

Carapace (Fig. 1D).—Increased in size but otherwise unchanged; rostrum now shorter than antennae.

Abdomen (Fig. 1D).—Posterodorsal spines very much reduced or absent on somite 2, generally unchanged on somites 3–5, or with some reduction in strength of posterodorsal spines; sixth somite now delineated from telson by weak dorsal and ventral sutures; uniramous uropods present, inner margins each with 1 long and 1 shorter plumose seta, 1 small and 1 strong acute spine and strong terminal spine, or 1 small spine and strong bifid terminal spine. Anal spine absent.

Telson (Fig. 4A, B).—Still with all processes clearly articulated, fourth remaining approximately as long as maximum telson width.

Antennule (Fig. 4C).—Exopod with 2 or 3 simple setae and 3 or 4 terminal aesthetascs and occasionally 1 subterminal aesthetasc; endopod still fused to protopod and with 1 terminal plumose seta; protopod with 2 or 3 short simple setae at endopodal base.

Antenna (Fig. 4D).—Scaphocerite spine appreciably shortened, inner margin with 3 or 4 plumose setae; endopod considerably overreaching scaphocerite; protopod still with 1 large and 1 very small spine.

Mandible (Fig. 4E, F).—Larger but otherwise unchanged.

Maxillule (Fig. 4G).—Unchanged.

Maxilla (Fig. 4H).—Endopod unchanged; coxal endite now with 5 marginal plumose setae on proximal lobe; basal endite now usually with 4 marginal plumose setae on proximal lobe, distal lobe routinely with 3 marginal and 1 submarginal plumose setae; scaphognathite with 9 or 10 short, marginal plumose setae.

First Maxilliped (Fig. 4I).—Unchanged.

Second Maxilliped (Fig. 4J).—Basipod and endopod unchanged; exopod now often with 8 natatory, terminal setae.

Third Maxilliped (Fig. 4K).—Exopod with 6 or 7 terminal natatory setae, endopod enlarged but still with 1 simple seta.

Color.—Changed from previous stage by presence of additional yellow chromatophores on antennules, on protopod of 3rd maxilliped, and in carapace midline above gut.

Zoea IV

Size.—CL = 1.58–2.44 mm; TL = 3.56–4.22 mm; n = 14.

Duration.—4–13 days; N = 70.

Carapace (Fig. 1E).—Larger but otherwise unchanged.

Abdomen (Fig. 1E).—Posterolateral spines reduced or absent on third through fifth somites; uropods with endopod buds apparent but fused to protopods; exopods each 2 plumose setae and 2 or 3 spines on inner margins, terminating in strong spine. Pleopods present on somites 2–5.

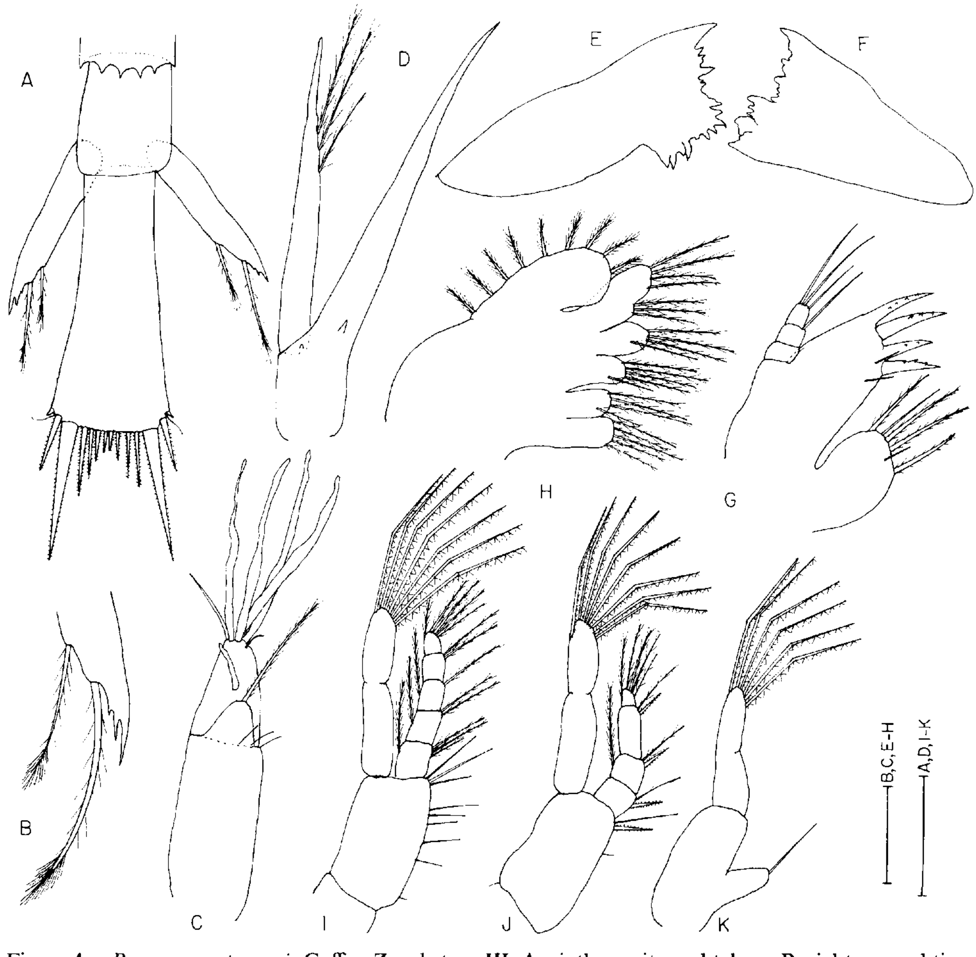

Figure 4. *Pagurus venturensis* Coffin: Zoeal stage III: A, sixth somite and telson; B, right uropod tip; C, antennule; D, antenna; E, left mandible; F, right mandible; G, maxillule; H, maxilla; I, first maxilliped; J, second maxilliped; K, third maxilliped. Scales: 0.1 mm (B, C, E–H), 0.25 mm (A, D, I–K).

Telson (Fig. 5A).—Unchanged from previous stage.

Antennule (Fig. 5B).—Endopod bud approximately half length of exopod, terminating acutely, naked, or rarely with short simple seta; aesthetascs of exopod 2, 0 or 1, 2, 3 or 4 plus 1 or 2 simple setae, protopod with 1 plumose seta at endopodal junction.

Antenna (Fig. 5C).—Scaphocerite still with 3 or 4 plumose and simple setae on inner margin; endopod unchanged; larger of protopodal spines appreciably reduced.

Mandible (Fig. 5D, E).—Larger; palp bud now present, well developed.

Maxillule (Fig. 5F).—Endopodal setation unchanged; coxal endite with 4 or 5 plumose and usually 2 simple marginal setae and 1 short, simple submarginal seta; basal endite now usually with 6, occasionally only 5 or very rarely 7, strong spinose teeth and 2 short, simple submarginal setae.

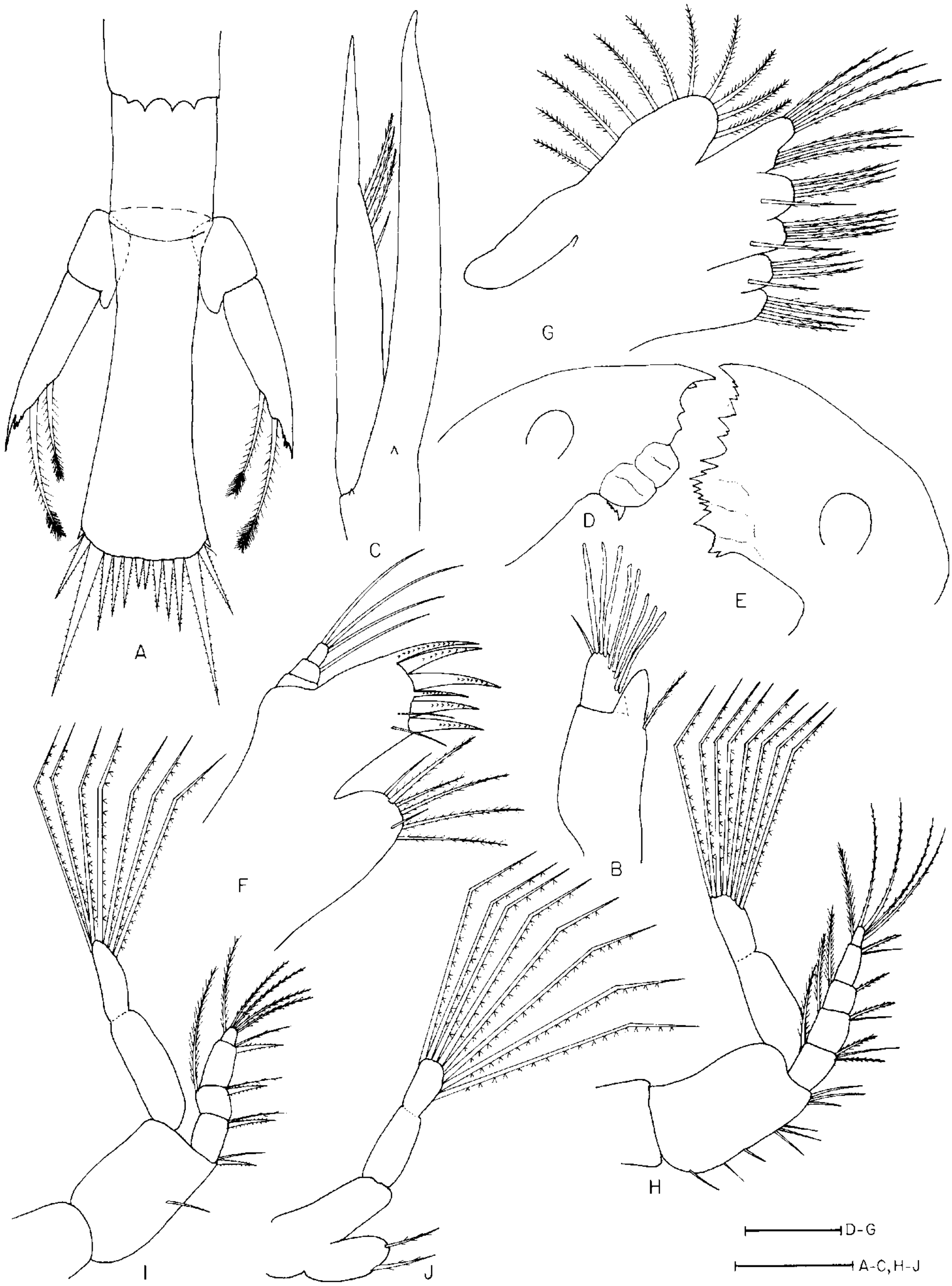

Figure 5. *Pagurus venturensis* Coffin: Zoeal stage IV: A, sixth somite and telson; B, antennule; C, antenna; D, left mandible; E, right mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped. Scales: 0.1 mm (D–G), 0.25 mm (A–C, H–J).

Maxilla (Fig. 5G).—Scaphognathite with 11–13 marginal plumose setae on distal lobe, proximal lobe distinct, elongate, naked; endopod and coxal and basal endites as in previous stage.

First Maxilliped (Fig. 5H).—Basipod and endopod unchanged from previous stage; exopod weakly 2-segmented, with 7 or 8 natatory setae.

Second Maxilliped (Fig. 5I).—Unchanged.

Third Maxilliped (Fig. 5J).—Endopod with 1 terminal and 1 subterminal simple or plumose seta; exopod incompletely 2-segmented, with 7 or 8 natatory setae.

Pereopods.—Cheliped with chela enlarged, dactyl distinct; ambulatory legs moderately elongate.

Color.—Little change from previous stage, except yellow chromatophores of abdomen and telson no longer apparent.

MEGALOPA

Size.—SL = 0.38–0.55 mm; n = 15

Duration.—8–16 days; N = 45.

Carapace (Fig. 6A).—Shield approximately two-thirds total carapace length, longer than broad; rostrum bluntly produced, slightly overreaching very weakly developed ocular acicles. Ocular peduncles short, broadened distally and with corneae slightly dilated.

Abdomen (Fig. 6A).—With six somites, all unarmed but with scattered short setae on dorsal and lateral surfaces, sixth with prominent median transverse thickening and pair of stiff bristles on posterodorsal margin; biramous pleopods (Fig. 7G) on somites 2–5, exopods well developed, setal formula progressing posteriorly 9 or 10, 9 or 10, 9, 9; endopods one-half to two-thirds length of exopods, each with appendix interna of 2 apical hooks.

Tail Fan (Fig. 7H).—Telson with few pair of setae on dorsal surface, posterior margin straight or slightly rounded, occasionally with 1–3 small tubercles or denticles, setal formula 3+3; uropods biramous; protopods each with acute spine or protuberance at posterior inner margin; exopods with 6–8 corneous scales and 9–11 plumose and simple setae marginally, endopods with 2–4 corneous scales and 1 or 2 simple setae.

Antennule (Fig. 6B).—Biramous, peduncle 3-segmented, considerably overreaching ocular peduncles; statocyst apparent, each segment with few setae as shown; exopod (upper ramus) 4-segmented, first segment without aesthetascs or setae, second with 2 pair of aesthetascs, third with 2 pair of aesthetascs and 2 or 3 short simple setae, fourth elongate, with 3 aesthetascs proximally and 2 or 3 short and 1 long simple setae distally; endopod (lower ramus) 2-segmented, with 2 short setae on basal segment and 2–4 short and 2 or 3 long setae on distal segment.

Antenna (Fig. 6C).—With supernumerary segment apparent; first segment unarmed, second segment with small spine at dorsomesial angle, segments 3–5 each with 2 or 3 simple setae, acicle blunt, and with 1–3 terminal setae; flagellum usually with 10 articles, first without setae, following articles all with 3–7 short, simple setae, terminal segment also with 1 or 2 long setae.

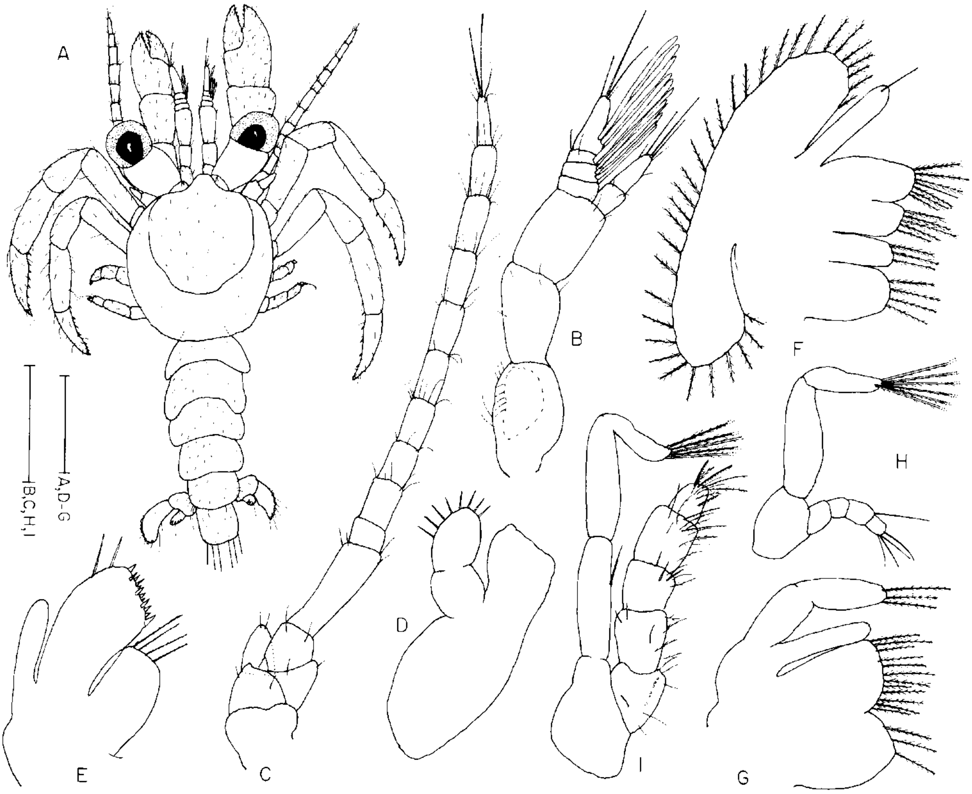

Figure 6. *Pagurus venturensis* Coffin: Megalopa: A, dorsal view of megalopa; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped. Scales: 0.5 mm (A), 0.1 mm (D–G), 0.25 mm (H, I).

Mandible (Fig. 6D).—Reduced, simple; palp 2-segmented, terminal segment with 7 or 8 marginal bristles.

Maxillule (Fig. 6E).—Endopod unsegmented, naked; coxal endite with 4 simple setae; basal endite with 9–11 small teeth and 1 or 2 simple setae.

Maxilla (Fig. 6F).—Endopod unsegmented, with 1 short, simple terminal seta; lobes of coxal endite each with 3 or 4 plumose setae; basal endite with 5 and 7 plumose setae on proximal and distal lobes, respectively; scaphognathite with 32 or 33 short, marginal plumose setae.

First Maxilliped (Fig. 6G).—Exopod indistinctly 2-segmented, with 3 short terminal plumose setae; endopod unsegmented, naked; coxal endite with 3 or 4 plumose setae; basal endite with 10–12 marginal plumose setae.

Second Maxilliped (Fig. 6H).—Exopod 2-segmented, with 6 terminal plumose setae; endopod 4-segmented, ultimate segment with 3 short terminal setae, penultimate segment with 1 short seta distally.

Third Maxilliped (Fig. 6I).—Exopod 2-segmented, basal segment with 1 long seta on mesial margin, flagellum with 5 terminal plumose setae; endopod 5-segmented,

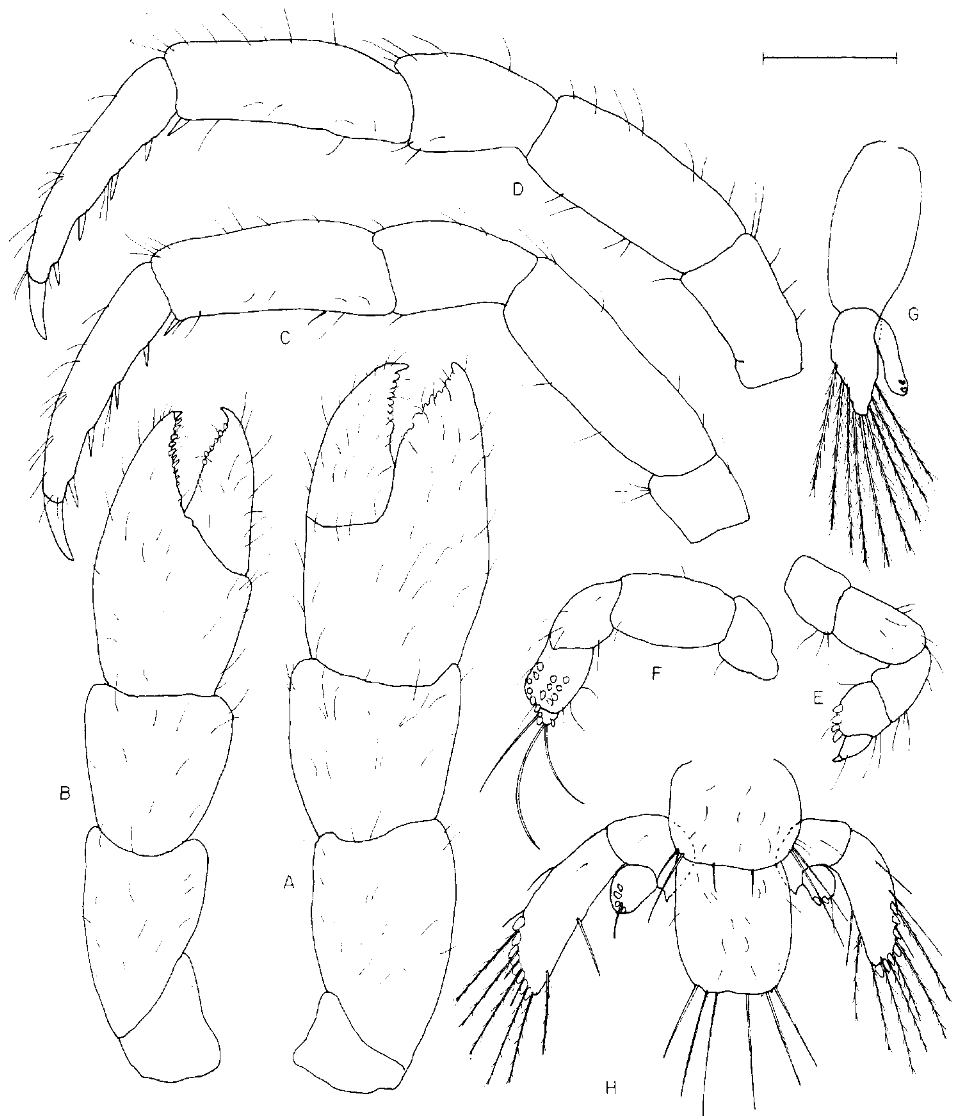

Figure 7. *Pagurus venturensis* Coffin: Megalopa: A, right cheliped; B, left cheliped; C, second pereopod; D, third pereopod; E, fourth pereopod; F, fifth pereopod; G, left pleopod of third abdominal somite; H, telson and uropods. Scale 0.25 mm.

ultimate and penultimate segments with numerous setae, many barbed or serrate, remaining segments with scattered short setae, ischium with 5–7 teeth on developing crista dentata.

Gills.—Pair of arthrobranch buds developing on chela and pereopods 2–4, also one pleurobranch bud on pereopod 4.

Pereopods (Fig. 7A–F).—Chelipeds unequal, right slightly larger, unarmed but with scattered setae. Ambulatory legs moderately long; dactyls each with 4 or 5 corneous spines on ventral margin, propodi each with 2 (second) or 1 (third) corneous spines at ventrodistal angle, all segments with numerous short to moderately long setae. Fourth pereopods with dactyls unarmed, propodi each with 3 or 4 corneous scales on ventral margin. Fifth pereopods with 3 or 4 corneous scales on dactyls, propodi each with numerous corneous scales.

Color.—Cephalothorax translucent except for reddish tint to branchiostegal region; antennular, antennal and ocular peduncles all translucent, corneae black with sliver flecks; chelae translucent, meri, carpi and propodi of ambulatory legs translucent with flecks of red.

Juvenile Stages

First Crab

Size.—SL = 0.49–0.56 mm; n = 12.

Duration.—5–20 days, N = 40 (by termination of rearing).

Shield and Ocular Peduncles (Fig. 8A).—Shield longer than broad, approximately two-thirds total carapace length; rostrum produced as rounded prominence. Ocular peduncles short, bulbous, corneae not dilated. Ocular acicles small, triangular, terminating acutely.

Abdomen.—Slightly twisted; segmentation becoming obscured; first somite now indistinguishable from eighth thoracic somite; second to fifth somites lacking calcification, weakly delineated by transverse fibrils, dorsal and lateral surfaces with scattered setae, sixth somite sometimes weakly calcified, still with prominent median transverse thickening and also with numerous short setae; paired, but markedly reduced pleopods (Fig. 9G–N) present on somites 2–5; both left and right second pleopods uniramous and reduced to stumps; pleopods 3–5 of left side biramous, endopods reduced, exopods each with 9 or 10 plumose setae, pleopods 3–5 of right side uniramous, markedly reduced and naked.

Telson and Uropods (Fig. 9O).—Telson with scattered setae on dorsal surface; transverse suture faintly delineated; terminal margin very weakly concave, with 2 or 3 small spines on either side of anal opening, outermost strongest, median cleft not apparent. Uropods asymmetrical; protopods each often with acute prominence or spine at posterior inner angle; exopods with 7–14 marginal and scattered surface setae, left with 10–14 corneous scales, right with 8–10; endopods naked or with 1–3 marginal setae, left also with 6–9 corneous scales, right with 3–5.

Antennules (Fig. 8B).—Biramous, peduncle 3-segmented, basal segment with short row of stiff setae marking developing statocyst, penultimate and ultimate segments with scattered setae; exopod (upper ramus) 5-segmented, first segment without aesthetascs or setae, second and third each with 2 or 3 pairs of aesthetascs, third also with 4 or 5 setae, fourth with 2 pair of aesthetascs, ultimate segment with 5 or 6 terminal setae of which 1 is noticeably longer; endopod (lower ramus) 2-segmented, proximal segment with 2 or 3 setae, distal segment with 7–10 setae.

Antenna (Fig. 8C).—Supernumerary segment distinct; fifth and fourth segments with few scattered setae; third segment with few scattered setae and with or without small spine at ventrodistal angle; second segment with somewhat produced and spinose dorsolateral distal angle and small spine at dorsomesial distal angle; first segment with prominent protuberance or small spine at mesial margin ventrally; acicle acutely triangular, usually with terminal spine and few setae; flagellum with 10 or 11 articles, first or first and second articles naked, remainder with 2–8 short setae.

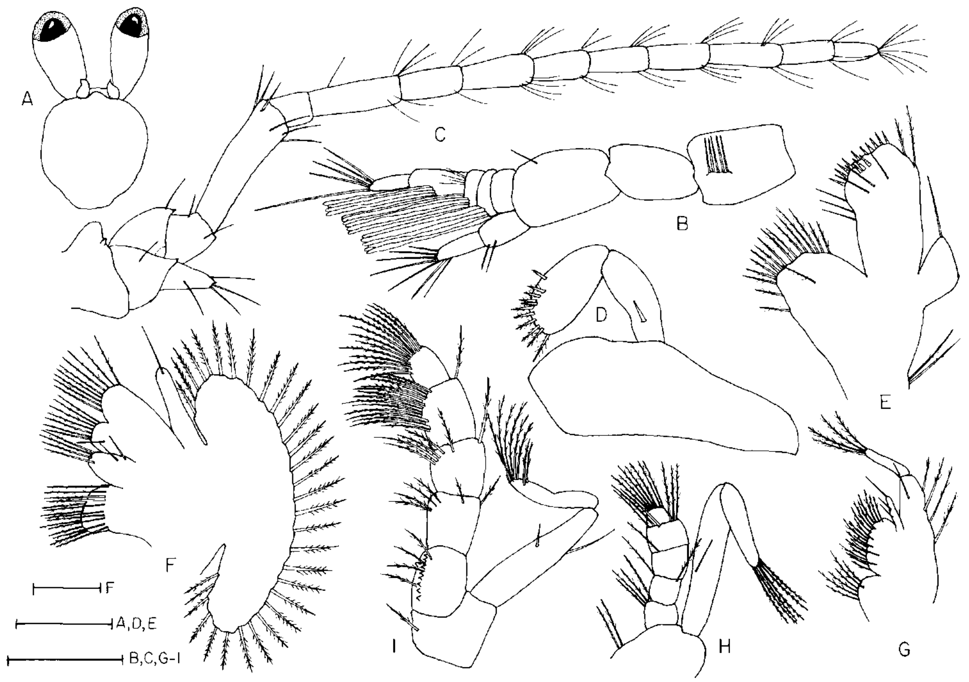

Figure 8. *Pagurus venturensis* Coffin: Crab stage I: A, shield and ocular peduncles; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped. Scales: 0.1 mm (D–F), 0.25 mm (B, C, G–I), 0.5 mm (A).

Mandible (Fig. 8D).—Generally as in megalopa, palp 2- or indistinctly 3-segmented, proximal segment with 1 short stiff seta, terminal segment with 10–13 short bristles.

Maxillule (Fig. 8E).—Endopod with internal and external lobes obsolete or weakly developed, internal lobe with 1 terminal seta; coxal endite with 6–9 simple or plumose, stiff and 7–9 plumose marginal setae plus 1 or 2 submarginal setae; basal endite with 11–17 small teeth, 2 or 3 plumose marginal setae and 3 or 4 submarginal setae plus 3 or 4 simple lateral setae.

Maxilla (Fig. 8F).—Endopod with 1 subterminal seta; coxal endite with 5–8 marginal and 10–12 submarginal plumose setae on proximal lobe, 3 or 4 marginal plumose and 3 submarginal setae on distal lobe; proximal lobe of basal endite with 1 simple submarginal and 6–8 plumose marginal setae, distal lobe with 7–10 marginal plumose setae; scaphognathite elongate, with 31–38 marginal plumose setae.

First Maxilliped (Fig. 8G).—Exopod 2-segmented, proximal segment with 1–3 setae on surface and 5 or 6 on lateral margin, distal segment with 4 or 5 terminal natatory setae; endopod unsegmented, with 1 terminal and 2 or 3 subterminal simple or plumose setae; coxal endite with 1 submarginal and 5 or 6 marginal plumose setae; basal endite with 11–14 marginal and 3–7 submarginal plumose setae.

Second Maxilliped (Fig. 8H).—Exopod 2-segmented, proximal segment with 1 or 2 setae, distal segment with 2 or 3 subterminal and 5 or 6 natatory terminal setae; endopod 5-segmented, setal formula 3–6, 1 or 2, 1, 5–8, 6–8.

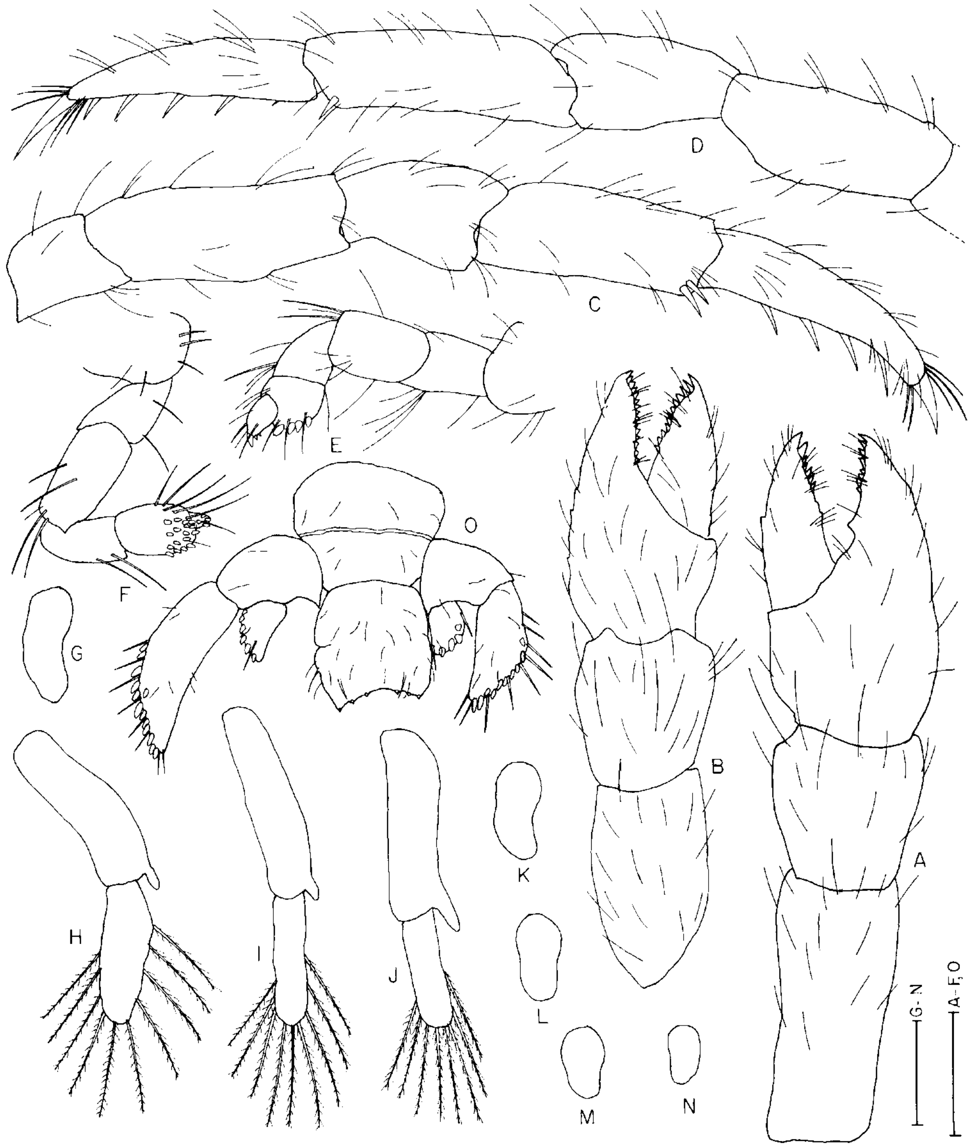

Figure 9. *Pagurus venturensis* Coffin: Crab stage 1: A, right cheliped; B, left cheliped; C, second pereopod; D, third pereopod; E, fourth pereopod; F, fifth pereopod; G–J, left pleopods of second, third, fourth, and fifth abdominal somites; K–N, right pleopods of second, third, fourth, and fifth abdominal somites; O, telson and uropods. Scales: 0.1 mm (G–N), 0.25 mm (A–F, O).

Third Maxilliped (Fig. 8I).—Exopod 2-segmented, flagellum with 4–6 terminal and 2 subterminal setae, proximal segment with 1 or 2 setae; basis-ischium incompletely fused, ischium with crista dentata of approximately 9 teeth and 1 accessory tooth, setal setation of merus to dactyl as illustrated.

Gills.—Well developed lobular arthrobranchs above pereopods 2–4, fourth also with developing pleurobranch; still small arthrobranchs on chelipeds, none discernible on third maxillipeds.

Pereopods (Fig. 9A–F).—Chelipeds unequal, right somewhat larger. Merus of right cheliped unarmed or with 1 or 2 subacute spines on ventromesial margin; carpus and palm unarmed but with scattered setae; fixed finger and dactyl with cutting edges armed with several strong corneous teeth, dorsomesial margin of dactyl often with small spine in proximal half. Merus of left cheliped unarmed or with 1 or 2 spines on ventromesial margin; corpus and palm unarmed but with scattered setae; dactyl and fixed finger each with several corneous teeth on cutting edges. Ambulatory legs with few changes from previous stage; corneous spines at ventrodistal margins of propodi frequently increased by 1. Fourth pereopods with 2–4 corneous spinules on propodus and 1 or 2 on ventral margin of dactyl. Fifth pereopods unchanged or with additional 1 or 2 scales on dactyls and propodi.

Color.—Generally as in megalopa.

Second Crab

Size.—SL = 0.64–0.70 mm; n = 15.

Duration.—9–14 days (those molting to Crab 3 by rearing's end); N = 15.

Shield and Ocular Peduncles (Fig. 10A).—Larger, but similar to previous stage; rostrum better developed, still terminally rounded. Ocular acicles now frequently with terminal spinule.

Abdomen.—More strongly twisted, but generally unchanged. Pleopods of second somite now completely absent; pleopods 3–5 of left (Fig. 10B–D) still with 9 or 10 plumose setae on exopods, endopods still markedly reduced, but fifth occasionally with single simple seta.

Telson and Uropods (Fig. 10E).—Terminal margin of telson now with 4 or 5 small spines on either side of anal opening. Exopods of uropods each with irregular double row of corneous scales; endopods each with increased number of scales.

Antennule.—Exopod now with 5 or 6 segments, terminal segment usually with 7 setae; endopod 3-segmented, setal formula 1 or 2, 0, 9 or 10.

Antenna.—Spines of first to third segments and acicle more acute; flagellum with 12 or 13 articles.

Mandible.—Palp now sometimes 3-segmented.

Maxillule.—Unchanged except for addition of few processes and setae.

Maxilla.—Endopod unchanged; endites with few additional setae; scaphognathite with 34–41 marginal plumose setae.

First Maxilliped.—Endopod with 2 subterminal setae.

Second Maxilliped.—Unchanged except for additional setal processes.

Third Maxilliped.—Basis-ischium fusion still incomplete; basis frequently with 1 tooth, crista dentata with 9 or 10 teeth; merus to dactyl with increased setation and setal processes.

Gills.—Generally increased in size and complexity on pereopods 2–4, still poorly developed on chelipeds, not apparent on third maxillipeds.

Pereopods.—Chelae now with few to several small spines on dorsal surfaces; left also with 1–3 spines dorsally on carpus and 2 or 3 spines or tubercles ventrally

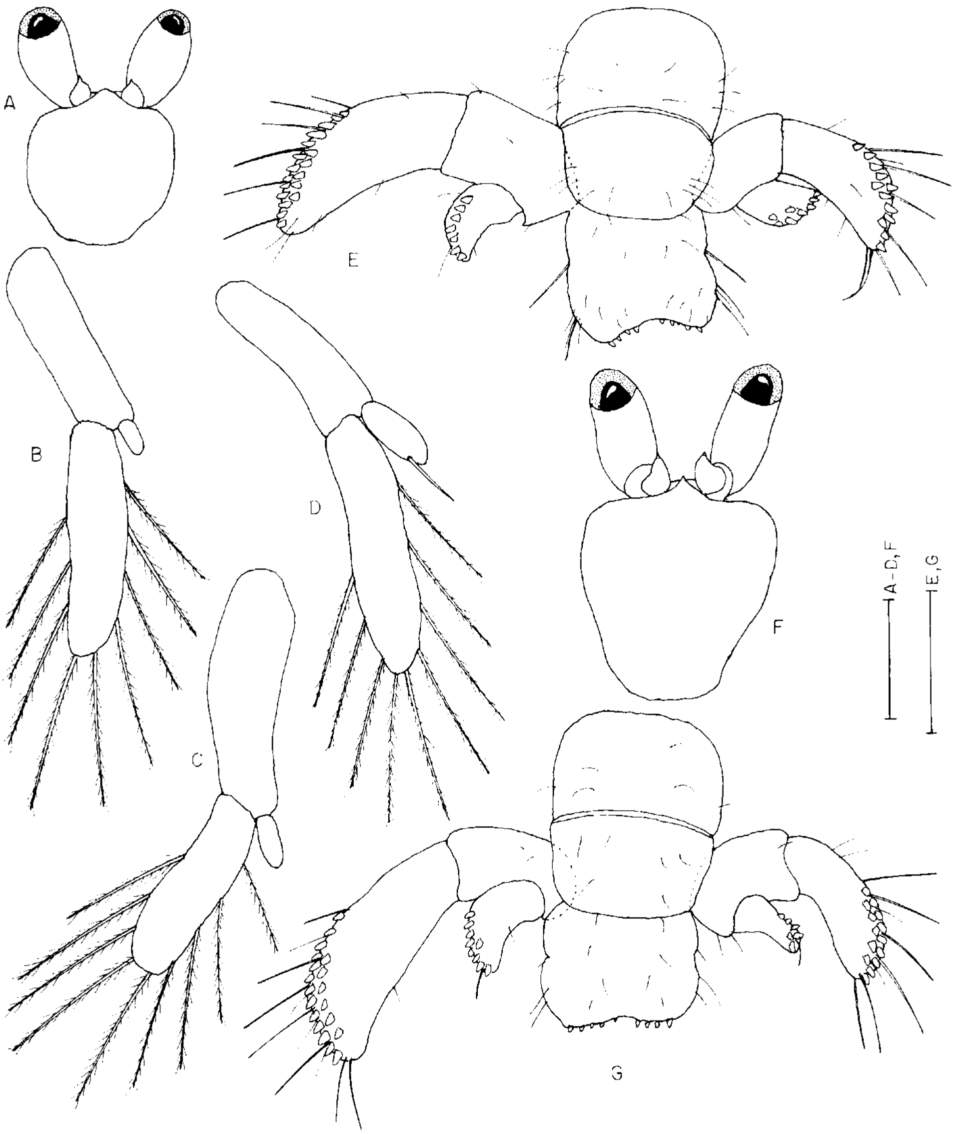

Figure 10. *Pagurus venturensis* Coffin: Crab stage 2: A, shield; B–D, left pleopods of third, fourth, and fifth abdominal somites; E, telson. Crab stage 3: F, shield; G, telson and uropods. Scales: 0.1 mm (B–D), 0.25 mm (E, G), 0.5 mm (A, F).

on merus. Ambulatory legs each sometimes with additional corneous spine on ventral margin of dactyl and 1 or 2 additional corneous spines on ventral margins of propodus. Fourth pereopod with 3 or 4 corneous spinules on ventral margin of dactyl.

Color.—Branchiostegites and shield margins reddish orange. Ocular peduncles translucent. Antennal peduncles with red basal segment. Chelipeds with ischia and meri red or reddish orange. Ambulatory legs with reddish-orange irregular bands or splotches on meri, carpi and propodi (proximally).

Third Crab

Size.—SL = 0.76–0.82; n = 7.

Shield and Ocular Peduncles (Fig. 10F).—Larger, appreciably longer than broad; rostrum triangular, terminating acutely. Ocular acicles larger and with well developed terminal spine.

Abdomen.—Segmentation of somites 2–5 only faintly discernible by transverse fibrils; sixth somite as in previous stage. Pleopods of left somites 3–5 as in previous stage, one individual (presumably incipient female) now with small bud of left Pl_2.

Telson and Uropods (Fig. 10G).—Telson as in previous stage or with 1 or 2 added spinules on terminal margin. Uropodal protopods with posterior inner margins now rounded; exopod of left uropod with 18 or 19 scales and 11–15 setae, endopod with 7–9 scales and 2–4 setae; exopod of right uropod with 11–15 scales and 9–11 setae, endopod with 5–7 scales and 1–3 setae.

Antennule.—Exopod still 5- or 6-segmented, aesthetasc number increased to 4 or 5 pairs on second segment.

Antenna.—Flagellum usually with 14 articles; acicle more elongate.

Mandible.—No change from previous stage.

Maxillule.—Internal lobe of endopod occasionally with 2 terminal setae.

Maxilla.—Endopod unchanged; coxal endite with 7–10 marginal setae on proximal lobe; basal endite with 8–10 setae on proximal lobe and 9–14 on distal lobe; scaphognathite with 40–45 marginal plumose setae.

First Maxilliped.—Generally unchanged.

Second Maxilliped.—Generally unchanged.

Third Maxilliped.—Generally unchanged.

Gills.—Larger and more lobular on pereopods 2–4, still weakly developed on chelipeds; arthropod buds now apparent at bases of third maxillipeds.

Pereopods.—Spination generally stronger, but otherwise generally unchanged.

Color.—Shield cream centrally, branchiostegites and shield margin reddish orange. Ocular peduncles red, corneae black with white flecks. Antennular peduncles red, flagella translucent. Antennal peduncles with first two basal segments reddish, distal segments translucent; flagella translucent, but with white chromatophores every 4th article in proximal half. Maxillipeds with reddish orange tint. Right cheliped with chela and carpus white, merus and ischium reddish; left cheliped with all segments reddish. Ambulatory legs with reddish-orange dactyls, propodi white distally and dark red proximally; carpi whitish in distal half, with splotches of red proximally and on meri.

Morphological Comparisons.—Larval development in *P. venturensis* is quite similar to that of both *P. hirsutiusculus* as described by McLaughlin et al. (1988) and *P. samuelis* as described by MacMillan (1971). The setal formula of the endopod of the second maxilliped links these three species, and distinguishes them, as a group, from most other *Pagurus* species. As pointed out by McLaughlin et al. (1988) for *P. hirsutiusculus* and *P. samuelis,* the setal formula (progressing distally) is 2, 2+I, 2, 4+I in zoeal stages II through IV. This same setal formula occurs in *P. venturensis.* Only in Zoeae III and IV of the Japanese *P. dubius* Ortmann (cf. Hong, 1981) does a similar condition exist. In all other species for which Zoea II and subsequent stages are known, the setal formula is 2, 2+I, 2+I, 4+I. One character that distinguishes *P. venturensis* and *P. samuelis* from *P. hirsutiusculus* is the absence, in the former two species, of accessory denticles on the primary spine of the scaphocerite of the antenna. *Pagurus venturensis* and *P. samuelis* differ in scaphocerite spination, in that a second, albeit very small, spine is present in zoeal stages II through IV only in *P. venturensis.* MacMillan (1971) indicated that no second spine is developed in any of the four zoeal stages, and the primary spine undergoes reduction and ultimate loss by stage IV. MacMillan also stated that no mandibular palp is present in Zoea IV, and illustrated the proximal lobe of the maxillary scaphognathite as fused to the protopod in this stage. In both *P. venturensis* and the Washington population of *P. hirsutiusculus* described by McLaughlin et al. (1988), a mandibular palp is present; the proximal lobe of the scaphognathite is free of the protopod. Neither Fitch and Lindgren (1979) in their description of development in another Washington population nor Hall (1972) for larvae of a northern California population of *P. hirsutiusculus* reported the presence of a mandibular palp in Zoea IV; however, this is thought to have been an oversight by these authors. They all agree that the proximal lobe of the scaphognathite is free at this stage. In development of the antennular endopod in the last zoeal stage, both species also differ from *P. samuelis.* The antennular endopod remains fused to the protopod in *P. venturensis* and *P. hirsutiusculus,* but is distinctly separated in *P. samuelis. Pagurus venturensis* is distinguished from *P. hirsutiusculus* not only by the absence of denticles on the primary spine of the scaphocerite, but by the articulated first telsonal process, the fewer number of scaphocerite setae, and the complete delineation of the sixth somite and telson in stages III and IV.

Among the three species, the most notable difference in megalopal characters is the telson setation. Both *P. venturensis* and *P. hirsutiusculus* have three pairs of long setae on the posterior margin; four pairs are described for *P. samuelis.* No ocular acicles are described or illustrated by MacMillan (1971) for *P. samuelis,* and none were described by either Fitch and Lindgren (1979) or Hall (1972) for *P. hirsutiusculus*; however, McLaughlin et al. (1988) described small acicles in their megalopae of that species. Ocular acicles are clearly developed in the megalopae of *P. venturensis.* Megalopae of *P. venturensis* are appreciably smaller (SL = 0.38–0.55 mm) than those of either the Washington or California populations of *P. hirsutiusculus* (SL = 1.1–1.22 mm), the antenna has fewer articles, and the palp of the mandible is 2-segmented. In *P. hirsutiusculus* the mandibular palp is described as incompletely segmented (Fitch and Lindgren, 1979) or incompletely 3-segmented (McLaughlin et al., 1988), and illustrated as unsegmented by Hall (1972). Early juvenile stages have not been described for *P. hirsutiusculus.*

Adult Morphology

Methods and Materials.—Adult specimens for this study have come from the collections of the Allan Hancock Foundation, University of Southern California (AHF), Naturhistoriska Rijksmuseet, Stockholm, Sweden (NHRM), and collections by the senior author. As in the megalopae and juveniles, one measurement, SL, provides an indication of specimen size. Measurements were obtained using a Mitutoyo calipers calibrated to 0.05 mm, and rounded to the closest 0.1 mm. Specimens have been returned to their institutions of origin and/or deposited in the National Museum of Natural History, Smithsonian Institution (USNM) and the Zoological Laboratory, Kumamoto University, Japan (ZLKU).

Type Series.—♂ (SL = 4.1) AHF 464, holotype, 12 miles N of Ventura, CA, 9 December 1946. Paratypes: 5 ♂, 2 ♀, 1 ovigerous (SL = 1.4–3.0 mm), AHF 475, 4.5 miles W to Cayucos, mouth of

Villa Creek, CA, 7 January 1947. 2 ♂ (SL = 1.6, 2.7 mm) AHF 474, Breaker Point, Piedras Blancas, CA, 1 April 1947. 1 ♂ (SL = 4.6 mm) AHF 291, Mission Bay, CA, 28 December 1929, collector, R. L. Morrison.

Other Material Examined.—1 ♂, 2 ovigerous ♀ (SL = 3.4–4.6 mm), NHRM 13415, Gislens Pacific-Expedition (1920–1931), Morro Bay, CA, 1 February 1931. 9 ♂, 1 ♀ (SL = 2.3–3.9 mm) AHF, ZLKU, VELERO III station 1216-40, Point Fermin, CA, 30 November 1940. 1 ♂, 1 ♀ (SL = 4.9, 5.9 mm) AHF, VELERO IV station 2131-52, Corona del Mar side, Newport Bay, CA, 8 July 1952. 1 ♂, 1 ♀ (SL = 2.9, 3.9 mm) AHF, SEARCHER station 64, Hidden Harbor, Santa Catalina Id., CA, 22 March 1972. 14 ♀, 10 ovigerous (SL = 2.3–3.3 mm) USNM, ZLKU, Cabrillo Beach, Los Angeles Harbor, CA, 16 December 1990, collectors, J. A. Crain, M. K. Wicksten.

Pagurus venturensis Coffin, 1957

Pagurus hirsutiusculus venturensis Coffin, 1957:1, fig. 2.—McLaughlin, 1974:185, figs. 43d, 44i.—Haig, 1977:16.—Haig and Abbott, 1980:585.—Taylor, 1981:207.—Wicksten, 1982:610.—Blackstone, 1989:478.

Pagurus (Trigonocheirus) hirsutiusculus: Holmes, 1900:143 (in part) (by implication; misspelling of *Trigonochirus* Benedict, Holmes, 1900:134).

Pagurus hirsutiusculus: Hilton, 1916:65.—Reese, 1962:347; 1969:347.—Ghiradella, Case and Cronshaw, 1968a.—Ghiradella, Cronshaw and Case, 1968b; not *Pagurus hirsutiusculus* (Dana, 1851).—Wicksten, 1977a:24, 27 (in part).—Hart, 1982:138 (in part, not fig. 51); see remarks.

?*Pagurus hirsutiusculus*: MacGinitie, 1935:712 (in part).—Bollay, 1964:71 (in part); see remarks.

Pagurus hirsutiusculus hirsutiusculus: McLaughlin, 1974:185 (in part, see remarks).

Redescription.—Shield (Fig. 11A) longer than broad; anterolateral margins terraced; anterior margin between lateral projections and rostrum concave; posterior margin rounded; dorsal surface and anterior margin with numerous tufts of moderately long setae (not illustrated); rostrum triangular, reaching beyond bases of ocular acicles, terminating acutely or subacutely, unarmed or with small spine or spinule and tuft of setae; lateral projections usually rounded, occasionally obtusely triangular, unarmed or sometimes with 1–5 small tubercles extending laterally and often obscured by long marginal setae; interocular lobes weakly developed.

Ocular peduncles one-third to one-half shield length; inflated basally, corneae usually weakly dilated; dorsal surface with few tufts of setae. Ocular acicles prominent; subovate; terminating subacutely and with strong submarginal spine; dorsal surface flattened or slightly concave, with few short setae; lateral and mesial margins also with few short setae; separated basally by approximately basal width of 1 acicle.

Antennular peduncles overreaching ocular peduncles by one-third to two-thirds length of ultimate segment; all segments unarmed but with scattered tufts of short setae.

Antennal peduncles exceeding ocular peduncles by approximately three-fourths to full length of ultimate segment; supernumerary segment present. Fifth and fourth segments unarmed but with scattered tufts of short setae. Third segment with scattered tufts of moderately long setae and spine at ventromesial distal angle. Second segment with dorsolateral distal angle produced, terminating in simple or bifid spine, mesial margin slightly inflated, unarmed or with 1–4 spinules distally, lateral margin with tufts of short setae, dorsal surface also with few tufts of short setae; dorsomesial distal angle usually terminating in moderately strong spine, occasionally unarmed. First segment unarmed or with 1 or 2 very small spines and tufts of short setae on distolateral margin, ventromesial distal angle produced and with 1–3 small spines. Antennal acicle not reaching to distal half of ultimate peduncular segment, arcuate, terminating in tuft of moderately long setae usually obscuring terminal spine, mesial margin with row of tufts of moderately short setae. Antennal flagellum overreaching tip of right cheliped; each article with 2 to several very short setae.

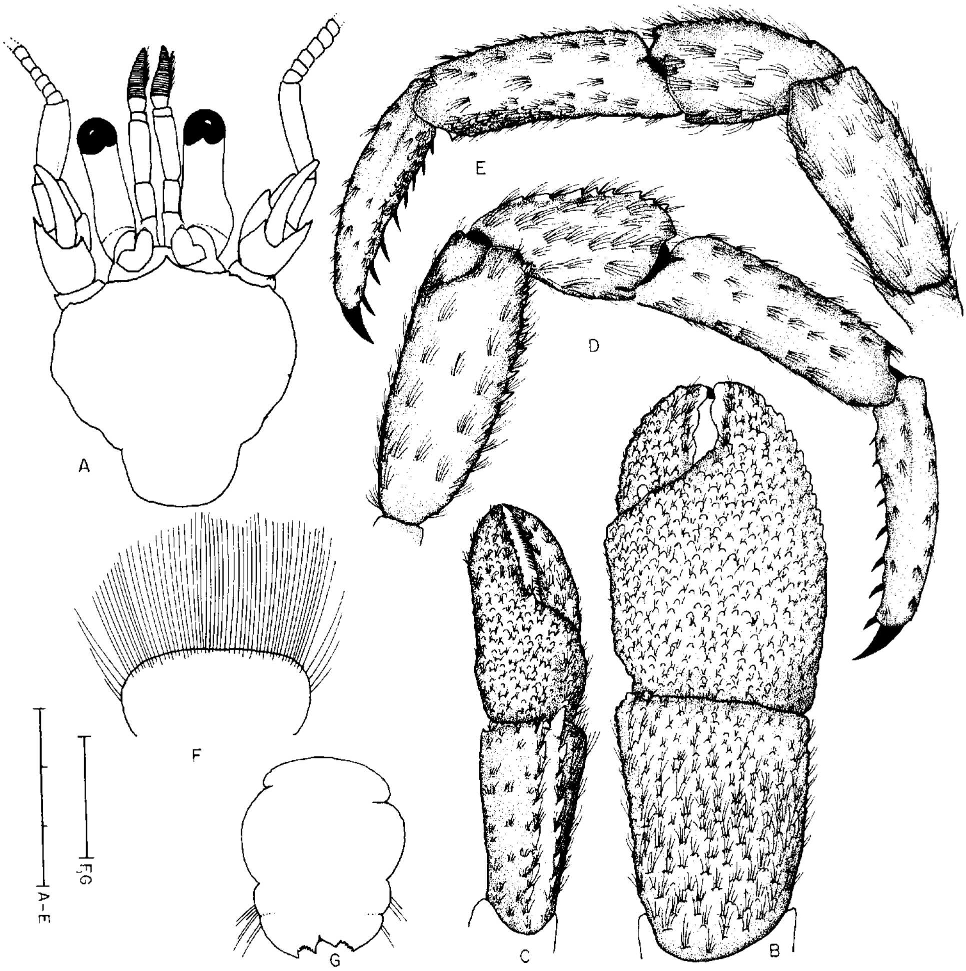

Figure 11. *Pagurus venturensis* Coffin, adult male from Point Fermin, CA: A, shield and cephalic appendages; B, right chela and carpus; C, left chela and carpus; D, right second pereopod; E, left third pereopod; F, sternite of third pereopods; G, telson. Scales equal 0.5 mm (F), 1 mm (G), 3 mm (A–E).

Maxillule with 1 or 2 bristles on produced internal lobe of endopod, external lobe obsolete. Maxilla with endopod inflated basally, narrowing distally, exceeding scaphognathite in distal extension. First maxilliped with endopod one-third to one-half length of exopod, basal segment of exopod moderately broad. Third maxilliped with basis-ischium fusion incomplete; basis with 1 or 2 small spines; ischium with crista dentata well developed and 1 accessory tooth; merus and campus each with spine on dorsodistal margin. Sternite of third maxillipeds with low protuberance, tubercle, or spinule, occasionally prominent spine, and tuft of setae on each side of midline.

Right cheliped (Fig. 11B) often with longitudinal hiatus between dactyl and fixed finger; dactyl three-fourths to entire length of palm, moderately broad; cutting edge with row of strong calcareous teeth, tufts of short stiff bristles and frequently also few small corneous denticles distally, terminating in strong corneous claw; not overreached or overlapped by fixed finger; dorsal surface tuberculate or spinose and with scattered tufts of short setae, midline slightly elevated and often marked by low tuberculate ridge, 1 usually more prominent tubercle at proximal margin; dorsomesial margin delineated by row of broad tubercles; ventral surface with scattered small tubercles or low protuberances and tufts of short setae. Palm inflated dorsoventrally; convex dorsal surface armed with relatively closely-spaced blunt or acute tubercles and scattered tufts of setae; dorsomesial margin usually not delineated, dorsolateral margin with row of blunt spines or prominent tubercles, strongest on fixed finger; mesial and lateral surfaces tuberculate; ventral surface convex and with scattered very low tubercles; cutting edge of fixed finger with few calcareous teeth, prominent broad tooth distally; terminating in corneous claw. Carpus approximately three-fourth length of merus, slightly exceeding palm in length; dorsal surface convex and with moderately closely-spaced blunt tubercles becoming more acute and spinose distally, sometimes also with few low transverse ridges and short setae proximally, dorsomesial margin sometimes delineated by irregular single or double row of blunt or spinulose tubercles, strongest distally, dorsolateral margin rounded, distal margin with row of blunt spines or tubercles; mesial and lateral faces with scattered blunt tubercles and few tufts of short setae, distal margins tuberculate; ventral surface with blunt tubercles and few tufts of short setae. Merus subtriangular; dorsal surface with transverse setose ridges, distal margin with row of small spines; mesial and lateral faces with transverse setose ridges, weaker proximally, distal margins minutely denticulate; ventral surface with simple tubercles sometimes becoming multifid mesially and laterally, ventromesial distal margin with 2 or 3 small spines or tubercles, ventrolateral margin with blunt or acute tubercles becoming spinules distally. Ischium with smooth ventral surface, ventromesial margin with row of small spines, decreasing in size distally; ventrolateral margin with 2 tubercles proximally.

Left cheliped (Fig. 11C) not reaching base of dactyl of right cheliped. Dactyl exceeding palm in length; cutting edge with row of small corneous teeth, terminating in strong corneous claw; not overlapped or overreached by fixed finger; dorsal surface with scattered tufts of setae and 2 or 3 irregular rows of tubercles at least in proximal half, dorsomesial margin delineated proximally by row of blunt tubercles; mesial face and ventral surface with tufts of moderately long setae. Palm approximately one-half length of carpus, subtriangular in cross-section; dorsal surface elevated in midline and armed with usually double row of blunt or acute tubercles, not extending onto fixed finger, dorsomesial and dorsolateral surfaces of palm and dorsal surface of fixed finger all with relatively closely-spaced blunt or spinulose tubercles and tufts of short setae; dorsomesial margin weakly tuberculate, lateral and ventral surfaces tuberculate and with scattered tufts of moderately long setae. Carpus three-fourths to equaling length of merus, broadened distally; dorsodistal margin with few small spines or spinules, dorsomesial and dorsolateral margins each with row of moderate to strong spines; mesial face with several irregular rows of transverse setose ridges, distal margin with few small tubercles or spinules, ventromesial margin with a row of moderately strong subacute spines, increasing in size distally; lateral face usually with several irregular rows of low ridges becoming tubercles distally and tufts of moderately long setae, distal margin usually with few tubercles, becoming spinose ventrally; ventral surface with few short transverse setose ridges and several simple or multifid tubercles in distal half, distal margin denticulate. Merus subtriangular; dorsal margin sometimes with row of closely-spaced transverse setose ridges; mesial and lateral faces each with few transverse setose ridges ventrally; ventromesial margin with irregular row of spines or tubercles, decreasing in size distally, and tufts of moderately long setae, ventrolateral margin with row of blunt or acute spines and tufts of moderately long setae; ventral surface with few scattered spinulose tubercles and transverse setose ridges, often also 1 prominent spine proximally. Ischium with row of small spines on ventromesial margin, increasing in size distally; lateral face often with spinulose distal margin, ventrolateral margin sometimes with prominent tubercle proximally.

Second (Fig. 11D) and third right pereopods generally similar; second pair slightly overreaching right cheliped; dactyls approximately equal to propodi in length; in lateral view, curved ventrally; in dorsal view straight or slightly twisted; terminating in strong corneous claws; dorsal surfaces each with 2 rows of tufts of short setae and frequently also few small corneous spinules partially obscured by mesial row of setae; mesial and lateral faces each with faint longitudinal sulcus flanked dorsally and ventrally by row of tufts of setae sometimes accompanied by small corneous spinules (mesial face); ventral margins each with row of 7 to 12 strong corneous spines, increasing in size distally. Propodi slightly longer than carpi; dorsal margins each with 3 or 4 rows of transverse setose ridges, distal margins usually with 2 or 3 spinules mesially, occasionally unarmed; mesial faces each with 3 to 4 irregular rows of transverse setose ridges; lateral and ventral surfaces each with 2 or 3 irregular rows of transverse setose ridges, ventral surfaces each with 2 or 3 small corneous spinules in distal half and 1 or 2 prominent corneous spinules at distal margin. Carpi approximately three-fourths length of meri; dorsal surfaces each with 2 or 3 irregular rows of spines, tubercles or spinose ridges, usually increasing in size distally (strongest on right 2nd) and tufts of moderately long setae; dorsodistal margins with 2 or 3 acute spines; mesial faces with few tufts of long setae distally and ventrally; lateral faces each with 1–3 rows of transverse setose ridges; ventral surfaces with scattered small tufts of moderately long setae, distal margins often with row of moderately long setae. Meri laterally compressed; dorsal surfaces each with 1 or 2 rows of transverse setose ridges; lateral and mesial faces each with several irregular rows of transverse setose ridges, ventrolateral distal margins with 0–4 spinules or small spines; ventral margins sometimes each with row of spines, increasing in size distally (2nd) or only transverse rows of setae. Ischia with low transverse setose ridges on all surfaces. Left third pereopod (Fig. 11E) with dactyl and propodus slightly shorter and deeper than third right and both second pereopods; dactyl approximately equal to length of propodus; in lateral view, curved ventrally; in dorsal view, very slightly twisted; terminating in strong corneous claw; dorsal surface with single or double row of corneous spinules mesially and 2 irregular rows of tufts of short setae; mesial face with moderately shallow longitudinal sulcus, flanked 1 or 2 single or double rows of small corneous spinules and tufts of moderately long setae; lateral face with moderately shallow longitudinal sulcus, deeper proximally, few to numerous blunt tubercles ventrally and tufts of moderately long setae; ventral margin with row of 9 or 10 strong corneous spines, increasing in size distally. Propodus slightly exceeding carpus in length; dorsal surface with 3 or 4 rows of transverse setose ridges, distal margin with row of moderately long setae; mesial face with 2 or 3 irregular rows of transverse setose ridges, often also with small corneous spinule distally, partly obscured by tuft of setae, distal margin with row of long setae; lateral face with 1 or 2 rows of low transverse setose ridges, few to numerous usually closely-spaced blunt tubercles in ventral half distally, distal margin usually with 1 or 2 small spinules ventrally; ventral margin tuberculate or with transverse, spinose ridges and tufts of moderately long setae; ventrodistal margins each with 1 prominent corneous spine mesially and 1 calcareous or occasionally corneous spine laterally. Carpus, merus, and ischium similar to third right. Fourth pereopods with no preungual process apparent; propodal rasp with several rows of corneous scales. Fifth pereopods typical of shell inhabiting pagurids. Sternite of third pereopods (Fig. 11F) sub-semicircular; anterior margin rounded, and with long dense setae.

Pleopods of males unpaired; pleopods of somites 3 to 5 with well developed exopods and reduced endopods, both rami with long plumose setae. Pleopods of females unpaired; pleopods of somites 2–4 with both rami well developed and with long plumose setae; pleopod of somite 5 with well developed exopod, reduced endopod, long plumose setae on both rami.

Telson (Fig. 11G) with posterior lobes slightly asymmetrical, separated by small narrow median cleft, terminal margins concave and with small spine on inner and outer edge of concavity separated by row of small spinules; lateral margins weakly calcified and entire; anterior lobes unarmed but with moderately long marginal setae.

Color.—Generally light gray or tan to olive brown; the actual color sometimes obscured by hair or dirt; dactyl usually blue with four longitudinal red stripes, one on either side, one on dorsal edge, and one on ventral edge (after Coffin, 1957).

Distribution.—Vicinity of Monterey Peninsula to San Diego, CA; low intertidal (Haig and Abbott, 1980).

Affinities.—*Pagurus venturensis* is quite similar to both *P. hirsutiusculus* and *P. samuelis.* The range of *P. venturensis* appears restricted to the southern California coast, whereas *P. hirsutiusculus* is distributed from south central (Monterey area) California to Alaska and Japan. Only in the Monterey Bay region are these two species likely to overlap. The longer and narrower shield and the tuberculate armature of the dactyl and propodus of the third left pereopod immediately distinguish *P. venturensis* from *P. hirsutiusculus.* In contrast, *P. samuelis* and *P. venturensis* occur sympatrically throughout the range of the latter species (Haig and Abbott, 1980). *Pagurus venturensis* is best distinguished from *P. samuelis* by the unarmed anterior lobe of the sternite of the third pereopods in the former species, the presence of a spine on the dorsodistal margin of both the merus and carpus of the third maxilliped, and the configuration and armature of the telson. In *P. samuelis,* the anterior margin of the anterior lobe of the sternite of the third pereopods is armed with two or three spinules or tubercles, the dorsodistal margins of the merus and carpus of the third maxilliped are unarmed, the lateral margins of the telson lack a distinct plate, the median cleft dividing the telson into two posterior lobes is poorly defined, and each rounded terminal margin is armed with a short row of small spines. Haig (1977) separated the two taxa by the presence of one prominent tubercle on the ventral surface of the merus of the right cheliped in *P. venturensis* and two in *P. samuelis,* however, we have found the tubercle in the former species sometimes not appreciably larger than the marginal tubercles.

Remarks.—In the synonymy, the citations by Holmes (1900), Wicksten (1977a) and Hart (1982) of *P. hirsutiusculus* are listed as "in part" because their general accounts include the ranges of both species. The reports by Hilton (1916), Reese (1962, 1969) and Ghiradella et al. (1968a, 1968b) of *P. hirsutiusculus* pertain exclusively to the taxon occurring in southern California and, therefore, are referable to *P. venturensis.* As may be seen from the discussion following, we believe that MacGinitie (1935) and Bollay (1964) may have confounded both taxa in the Monterey Bay area. McLaughlin (1974) mistakenly included Hilton (1916) in her synonymy of *P. h. hirsutiusculus*; his specimens from Laguna Beach, California are correctly referred to *P. venturensis.*

Discussion

Despite the several species concepts being debated currently (see Otte and Endler, 1989 for recent review), a species to most early carcinologists was a typological species. Any deviation from the morphological type was usually distinguished by a named *form* or *variety*. Generally such forms and varieties named before 1961 were subsequently elevated to subspecific rank (International Commission for Zoological Nomenclature, Art. 45g, 1985); however, in the case of *P. venturensis,* Coffin (1957) specifically designated this taxon as a subspecies of *P. hirsutiusculus.* Mayr (1969) defined a subspecies as "an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species." In this context, reproductively isolated species might overlap in their geographic ranges, but two subspecific taxa of a single species could not.

In modern hermit crab systematics, subspecies are not commonly distinguished, and those so designated have been considered only as morphological variants (De Saint Laurent, 1972). Blackstone (1989) compared shell-living and size between the two presumed subspecies, *P. h. hirsutiusculus* and *P. h. venturensis* and found significant differences, which he hypothesized to be the result of decreasing carapace carcinization from north to south. Blackstone based his study on collections of *P. hirsutiusculus* from Alaska, Puget Sound, Washington, and northern California. He was of the opinion that Point Conception, California most probably acted as a significant barrier to gene flow between the subspecies, consequently his samples of *P. venturensis* were taken south of Pt. Conception. This is unfortunate, since the range of *P. venturensis* had been confirmed as far north as Morro Bay in San Luis Obispo County (Taylor, 1981) and Point Sur in Monterey county (Coffin, 1957). Had Blackstone (1989) sampled further to the north, he well might have found both taxa occurring sympatrically in the Monterey area. For example, MacGinitie (1935) reported the rather uncommon occurrence of "*P. hirsutiusculus*" at Elkhorn Slough, a tributary of Monterey Bay. He noted that "adults" inhabited *Nassarius fossatus* (Gould) (as *Nassa fossata*) shells and smaller specimens were found in shells of *Olivella biplicata* (Sowerby) and *Littorina scutulata* Gould. Bollay (1964) studied the distribution and shell use of three pagurid species, including *P. hirsutiusculus* (sensu lato) in Monterey Bay. Some differences in shell preference among individuals of *P. hirsutiusculus* were noted, e.g., larger individuals occupied shells of *Tegula brunnea* (Philippi), *T. funebralis* (A. Adams), and *Nucella emarginata* (Dehayes) (as *Thais emarginata*), while smaller individuals were found in *Acanthina spirata* (Blainville), *Littorina* spp. and small unspecified shells. As Blackstone demonstrated, *P. hirsutiusculus* adults reach much larger sizes than adults of *P. venturensis.*

Reese (1962), in his study of shell preferences among southern California intertidal hermit crabs, found that when given a choice of shells, "*P. hirsutiusculus*" (=*P. venturensis*) for the most part selected either *Olivella biplicata* or *Acanthina spirata* shells. In contrast, Orians and King (1964) described the shell preference of a northern California population of *P. hirsutiusculus* as consistently for *Nucella emarginata.* Reese (1969) remarked on the differences in shell preferences between the northern and southern populations, but apparently was not aware that the latter had been designated as a distinct subspecies. An entirely different pattern of shell use was reported for another northern population of *P. hirsutiusculus* by Wicksten (1977b). However, she pointed out that virtually all of the shells utilized by this hermit crab in San Francisco Bay were of gastropod species introduced into the Bay from the Atlantic coast that essentially had replaced the native species.

Wicksten proposed that prior to the arrival of introduced species, the shells of choice for *P. hirsutiusculus* were the comparably large, congeneric species *Nucella lamellosa* (Gmelin) (as *Thais lamellosa*) and *Nassarius mendicus* (Gould) (as *Nassa mendica*). We concur with Haig's (1977) suggestion that *P. hirsutiusculus* does not occur "much south of Monterey Bay." However, it would appear that a small area of sympatry exists, or did exist at one time, in the Monterey Bay area.

Adult morphological differences that distinguish *P. venturensis* from *P. hirsutiusculus*, e.g., shield length, telson configuration and armature, and the armature of the dactyl and propodus of the third left pereopods, do not appear to exhibit any north-south cline. Similarly, differences in larval characters between the two taxa support the proposition that specific rank for the former taxon is justified. Differences of particular significance in *P. venturensis* are the fewer setae on the scaphocerite of the antenna, the articulation of the first telsonal process, and the weak, but distinct delineation of the telson from the sixth somite in zoeal stages III and IV. Although variations in larval development in populations of *P. hirsutiusculus* have been described from both Washington and northern California (cf. McLaughlin et al., 1988), none that could be indicative of clinal character shifts have been observed.

There is little doubt, as Blackstone (1986, 1989) and Cunningham et al. (1992) have suggested, that a correlation exists between shield and/or carapace carcinization and the ability of taxa to utilize shells that primarily protect only the abdomen. However, in Blackstone's (1989) study of *P. hirsutiusculus* he was actually dealing with two distinct species. Clearly, that study can not be used to substantiate the hypotheses that ecological conditions at polar latitudes may favor shell loss and carcinization or that size increase may be an integral part of carcinization.

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