

DESCRIPTION OF LARVAE OF THE HUMPY SHRIMP, *PANDALUS GONIURUS*, REARED IN SITU IN KACHEMAK BAY, ALASKA

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ABSTRACT

Except for Stage I, identification of larval stages of *Pandalus goniurus* has not been verified by rearing the larvae from known parentage. Larvae of *P. goniurus* were reared in situ in Kachemak Bay, Alaska, from the first zoea (Stage I) through the first juvenile stage (Stage VII). Each of the seven stages is described and illustrated. The descriptions are compared with descriptions of larval stages of *P. goniurus* given by other authors.

Studies on the early life history of pandalid shrimp in Alaskan waters were begun in 1972 by the National Marine Fisheries Service with the initial objective of describing pandalid shrimp larvae reared in the laboratory from known parentage. I have reported on larvae of coonstripe shrimp, *Pandalus hypsinotus* Brandt, reared in the laboratory (Haynes 1976). In the present report I describe and illustrate larvae of humpy shrimp, *P. goniurus* Stimpson, reared in situ in Kachemak Bay, Alaska. A third report will describe larvae of pink shrimp, *P. borealis* Krøyer, and compare the larvae of *P. borealis* with larvae of other local pandalid species, including *P. goniurus*.

MATERIALS AND METHODS

The laboratory technique used successfully for rearing larvae of *P. hypsinotus* (Haynes 1976) proved unsuitable for rearing *P. goniurus* beyond Stage II. Beginning with Stage III, molting frequency and number of larval stages of *P. goniurus* reared in the laboratory were inconsistent, mortality was high, and the larvae of a given stage were not always morphologically identical. Rearing *P. goniurus* in situ reduced mortalities and yielded larvae essentially identical morphologically within each stage.

Larvae were reared in situ from the first zoea (Stage I) through the megalopa and first juvenile (Stages VI and VII) in the following manner. Stage

I zoeae of known parentage were obtained using the laboratory technique described by Haynes (1976). The Stage I zoeae were then transported to sea and placed in 500-ml flasks containing seawater of about 35‰ salinity and 4°C obtained from about 6 m depth with a plastic hand pump and hose. Subsurface seawater was used to avoid the lower salinity (about 28‰) of surface waters derived from local runoff which, as I had found during previous rearing studies, adversely affects larval development by resulting in delayed molting and variable numbers of stages. One larva was placed in each flask. The mouths of the flasks were then covered with nylon screening of #0 mesh (0.571 mm); the flasks were placed in holding containers and suspended upright at 15-20 m depth in water about 40 m deep. The #0 mesh size allowed plankton to collect in the flasks for food but prevented the larvae from escaping. Each flask was numbered and a record kept of the molting history of each larva in each flask. Flasks were checked at least every other day for cast skins and refilled with fresh subsurface seawater. When a larva molted, the cast skin was removed from the flask with a large-bore pipette and preserved in 5% formaldehyde for subsequent examination ashore.

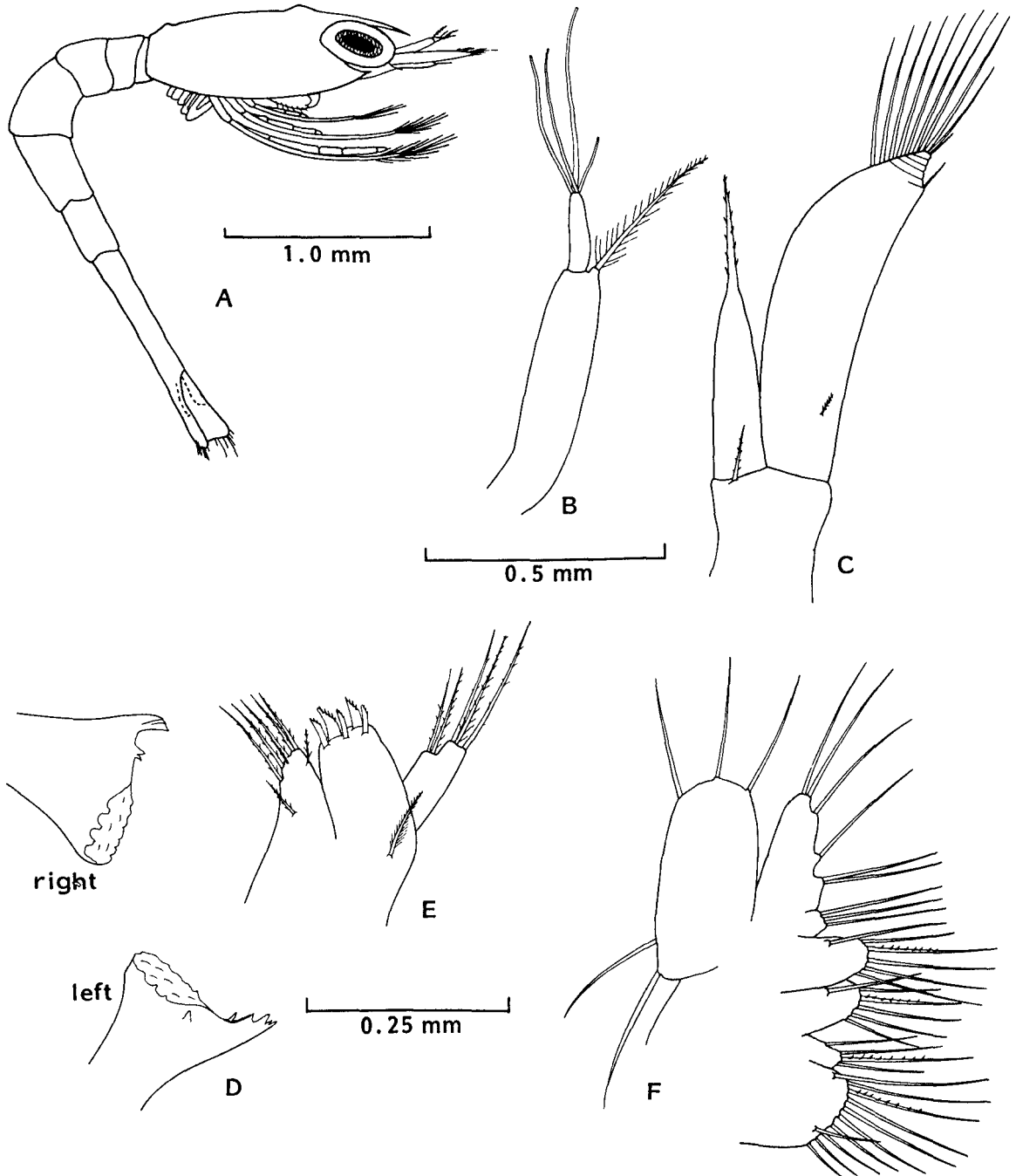
Identification of larval sequence and stage was verified using larvae obtained from plankton with a net of #0 mesh towed near the bottom at about 2 kn in water 60 m deep. The plankton sample was immediately placed in a glass receptacle containing several liters of subsurface seawater. Stage I zoeae of *P. goniurus* were removed from the glass receptacle using a large-bore pipette, placed in 500-ml flasks, one zoea to a flask, and reared to

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postlarvae in the same manner as the Stage I zoeae obtained in the laboratory.

To verify the validity of the sequence of the larval stages obtained from flasks, larvae of each stage were obtained from plankton and reared in flasks in the same manner for one molt. They were

then removed from the flasks along with their cast skins, preserved, and replaced with a larva of the same stage. Thus, a Stage II zoea that had molted to Stage III in a flask was replaced with a Stage III zoea from plankton, the Stage III zoea being replaced in like manner when it had molted to Stage



IV. This procedure was done for each stage including the megalopa (Stage VI). In addition to the larvae and cast skins obtained from rearing in flasks, molting sequence and stage were verified by monitoring the sequence of larval stages from

local collections, obtained at least weekly in areas where larvae were abundant, and by examining larvae caught while in the process of molting.

Only those morphological characteristics useful for readily identifying each stage are given.

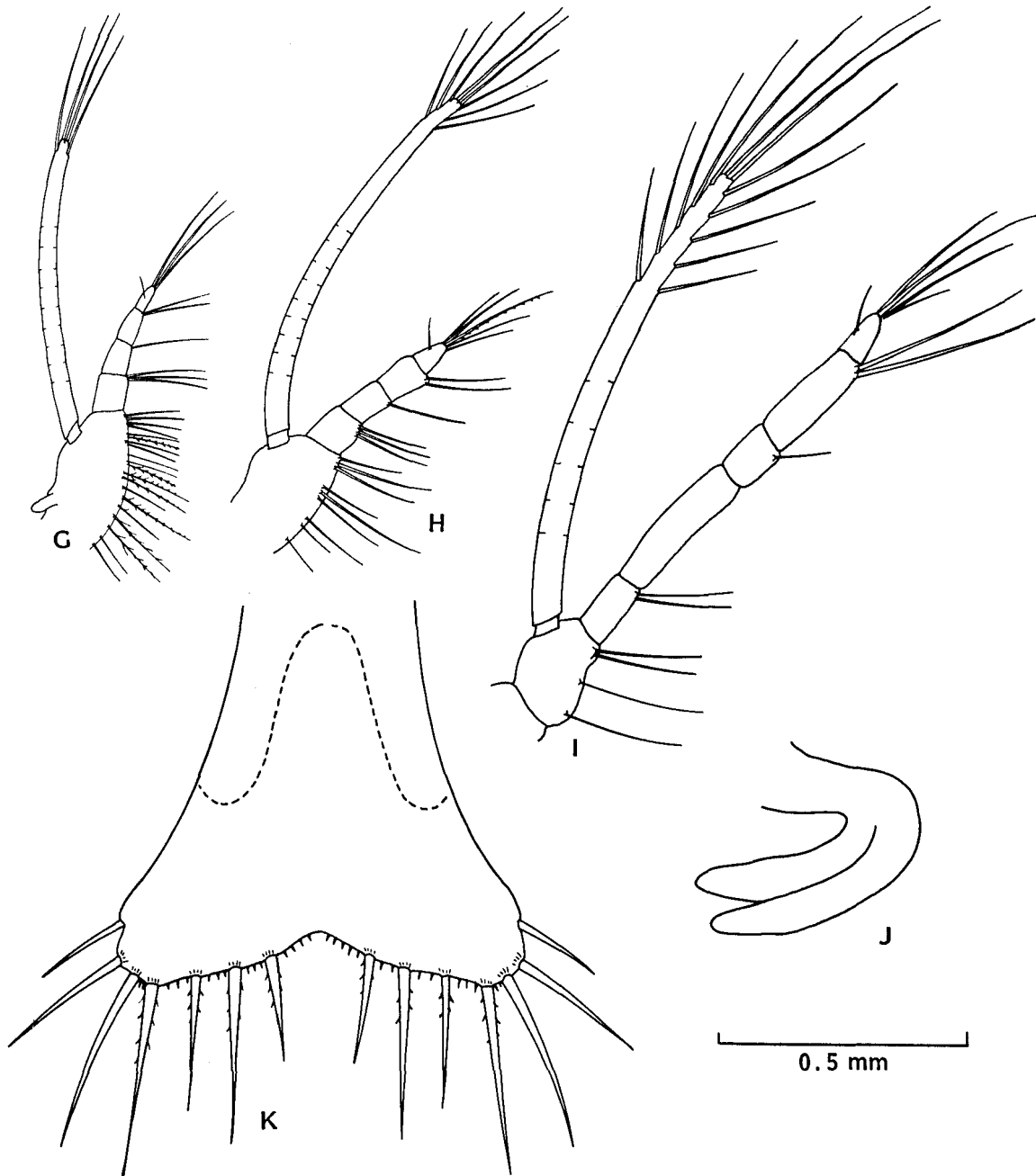


FIGURE 1.—Stage I zoea of *Pandalus goniurus*: A, whole animal; B, antennule; C, antenna; D, mandibles (right and left); E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, second pereopod; K, telson.

Stages I and II are described in greatest detail because these stages are the most difficult to identify. Terminology, methods of measuring, techniques of illustration, and nomenclature of gills and appendages follow Haynes (1976). Comparison of larvae from plankton with cast skins from flasks was facilitated by first clearing the larvae in 10% KOH. For each pair of appendages the left member is figured except for the mandibles, which are drawn in pairs and figured from the right side. For clarity, setules on setae are usually omitted but spinulose setae are shown.

STAGE I ZOEAE

Total length of Stage I (Figure 1A) 4.0 mm (range 3.7-4.2 mm; 10 specimens). Live specimens translucent with isolated areas of color: mouthparts orange with a bright yellow chromatophore at base; internal thoracic organs greenish, especially heart area; base of maxillipeds greenish orange; distinct yellow chromatophore at anus. Rostrum slender, spiniform, without teeth, about one-third length of carapace, and projects horizontally or slightly downward. Carapace with small, somewhat angular dorsal prominence at base of rostrum and a smaller rounded prominence near posterior edge. These two prominences occur in all zoeal stages. Pterygostomian spines present but usually hidden by sessile eyes. Three to four minute spinules along ventral margin of carapace immediately posterior to pterygostomian spine (spinules not shown in Figure 1A). These spinules usually occur in all zoeal stages but may vary in number from two to five not only between stages but among individuals within a given stage.

ANTENNULE (Figure 1B).—First antenna, or antennule, consists of a simple unsegmented tubular basal portion with a heavily plumose seta terminally and a distal conical projection bearing four aesthetascs: one long, one short, and two of intermediate length.

ANTENNA (Figure 1C).—Consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum unsegmented, slightly shorter than scale, styliform, and tipped by a spinulose spine. Antennal scale distally divided into five joints (the proximal joint incomplete) and fringed with nine heavily plumose setae. Two simple setae occur on outer margin, one terminal and adjacent to plumose setae and the other near

base of terminal segments. A small plumose seta usually occurs proximally near lateral margin in all zoeal stages. Protopodite bears spinous seta at base of flagellum but no spine at base of scale.

MANDIBLES (Figure 1D).—Without palps in all zoeal stages. Incisor process of left mandible bears four teeth in contrast to triserrate incisor process of right mandible. Left mandible bears a movable premolar denticle (*lacinia mobilis*) whereas right mandible bears two immobile premolar denticles. Truncated molar process of left mandible bears a subterminal tooth that occurs throughout all zoeal stages.

MAXILLULE (Figure 1E).—First maxilla, or maxillule, bears coxal and basial endites and an endopodite. Proximal lobe (coxopodite) bears stout seta near base, and seven spinulose spines terminally. Median lobe (basipodite) bears five stout spinulose spines on terminal margin, two of them especially thick with projecting teeth, and a large setose seta proximally. Endopodite originates from lateral margin of basipodite and bears three terminal and two subterminal setae; two of the setae are especially spinulose.

MAXILLA (Figure 1F).—Bears platelike exopodite (scaphognathite) with four long plumose setae along distal and outer margins, and one slightly longer and thicker seta at proximal end. Endopodite gives indication of four partly fused segments and bears nine large plumose setae. Basipodite bilobed; each lobe bears six setae. Bilobed coxopodite bears 15 setae, 4 on distal lobe and 11 on proximal lobe. Four setae, one on each lobe of basipodite and coxopodite, bear a row of little spines along entire length.

FIRST MAXILLIPED (Figure 1G).—Most heavily setose of natatory appendages. Protopodite not segmented; bears 17-20 setae, several of them especially spinulose. Endopodite distinctly four-segmented; setation formula 4, 2, 1, 3. Exopodite a long slender ramus segmented at base; has two terminal and two lateral natatory setae. Epipodite a single lobe.

SECOND MAXILLIPED (Figure 1H).—Protopodite not segmented; bears nine sparsely plumose setae. Endopodite distinctly four-segmented; setation formula 6, 2, 1, 3. Exopodite with two terminal, six lateral natatory setae. No epipodite.

THIRD MAXILLIPED (Figure 1I).—Protopodite bears four setae. Endopodite distinctly five-segmented; nearly as long as exopodite; setation formula 5, 2, 1, 0, 2. Exopodite with 2 terminal, 10 lateral natatory setae. No epipodite.

PEREPODS.—Poorly developed, directed under body somewhat anteriorly. First three pairs biramous (second pereopod shown in Figure 1J), last two pairs uniramous and slightly smaller than pairs 1-3.

PLEOPODS.—Not evident.

TELSON (Figure 1K).—Not segmented from sixth abdominal somite; slightly emarginate distally; bears seven pairs of densely plumose setae. Fourth pair of setae longest, length about one-half width of telson. Minute spinules at base of each seta except possibly last pair. Larger spinules along terminal margin between bases of four inner pairs and on setae themselves. Enclosed uropods visible. No anal spine.

STAGE II ZOEAE

Total length of Stage II (Figure 2A) 4.9 mm (range 4.5-5.3 mm; 10 specimens). Chromatophore color and pattern essentially identical to Stage I except chromatophores larger and color more pronounced, especially in mouth parts. From this stage on, zoeae become increasingly more orange and color pattern is not useful as an aid to specific identification. Rostrum still without teeth but not curved downward as strongly as in Stage I. Carapace has prominent supraorbital spine; antennal and pterygostomian spines clearly visible. These spines persist throughout all zoeal stages. Epipodite still not bilobed; pleurobranchiae not yet present.

ANTENNULE (Figure 2B).—Three-segmented; bears on terminal margin a large outer and a smaller inner flagellum. Inner flagellum not segmented, conical, and bears one long spine terminally. Outer flagellum bears two groups of aesthetascs, one group terminally consisting of seven aesthetascs, two of them larger than remaining five, and a second group of two aesthetascs on inner margin. A small budlike projection (not shown in Figure 2B) originates at base of the two flagella and bears three simple setae. Joint of proximal segment faint and may not be complete;

bears about five dorsally projecting small plumose setae. Second segment has one lateral plumose seta and about five dorsally projecting plumose setae ringing terminal margin. Third segment has five lateral plumose setae.

ANTENNA (Figure 2C).—Flagellum unsegmented, still shorter than scale, styloform, and tipped by a short spine. Antennal scale fringed with 19 long, thin, plumose setae along terminal and inner margins; small seta on outer margin near base of terminal segments; has four joints distally but only the three most distal joints are complete. Protopodite bears minute spine at base of scale in addition to spine at base of flagellum.

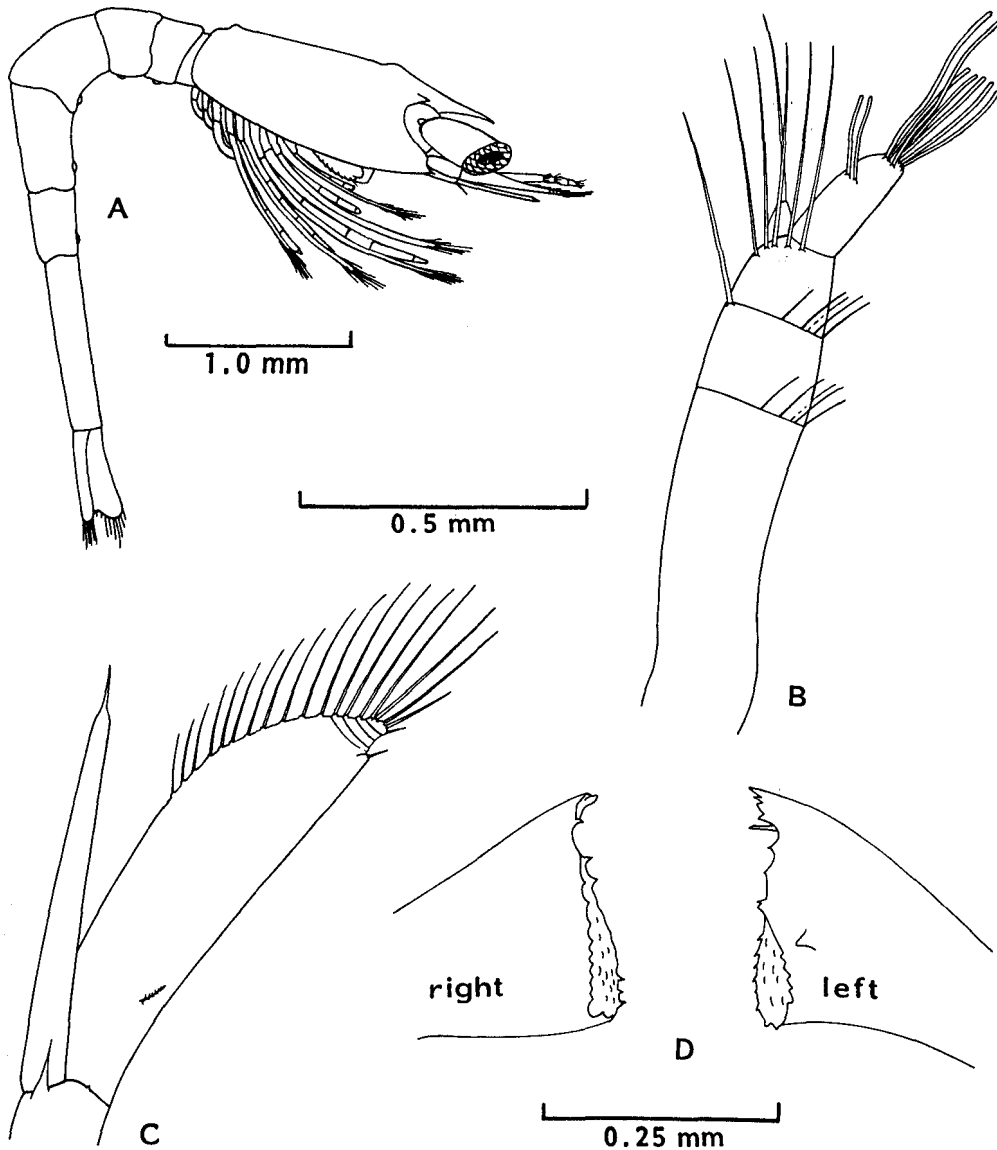
MANDIBLES (Figure 2D).—More massive than in Stage I. Both mandibles bear additional denticles and molar processes more developed. Curved lip of truncated end of molar process of right mandible more developed.

MAXILLULE.—Unchanged from Stage I except basipodite now bears two additional spinulose spines.

MAXILLA.—Shape similar to Stage I except exopodite slightly longer proximally and now bears nine marginal plumose setae in addition to plumose seta at proximal end. No change in number of setae on basipodite or coxopodite.

MAXILLIPEDS.—Essentially identical to Stage I but bear additional setae as follows. First maxilliped bears 17-20 setae on protopodite; exopodite bears 6 natatory setae rather than 4 as in Stage I; no change in epipodite. Second maxilliped bears 7 setae on protopodite; exopodite bears 10 lateral natatory setae in addition to the 2 terminal setae; endopodite five-segmented, setation formula 5, 2, 1, 1, 3. Third maxilliped bears 2 setae on protopodite; exopodite bears 10 lateral natatory setae in addition to the 2 terminal setae; segments of endopodite may or may not bear an additional seta or 2, setation formula usually 5, 4, 0, 1, 2.

FIRST PEREOPOD (Figure 2E).—Endopodite functionally developed; five-segmented and terminating in a simple conical dactylopodite; setation formula 4, 2, 1, 0, 0. Protopodite bears no setae. Exopodite, longest among pereopods, has 2 terminal and 10 lateral natatory setae.



SECOND PEREPOD (Figure 2F).—Similar to first pereopod except endopodite shorter, setation formula 3, 2, 0, 0, 1. Protopodite bears no setae. Exopodite with two terminal and six lateral natatory setae.

THIRD PEREPOD (Figure 2G).—Endopodite five-segmented; one-fourth to one-third longer than exopodite. Dactylopodite slightly longer than in first two pereopods; bears two setae terminally. Propodite bears two setae; remaining segments without setae. Exopodite noticeably shorter than exopodites of first two pereopods; bears six lateral

natatory setae in addition to two terminal natatory setae.

FOURTH AND FIFTH PEREPODS.—Unsegmented except at base; without exopodite or setae; directed under body somewhat anteriorly as in Stage I (Figure 2A).

PLEOPODS (Figure 2A).—Present as minute buds.

TELSON (Figure 2H).—Similar in shape to Stage I but distinctly segmented from sixth abdominal

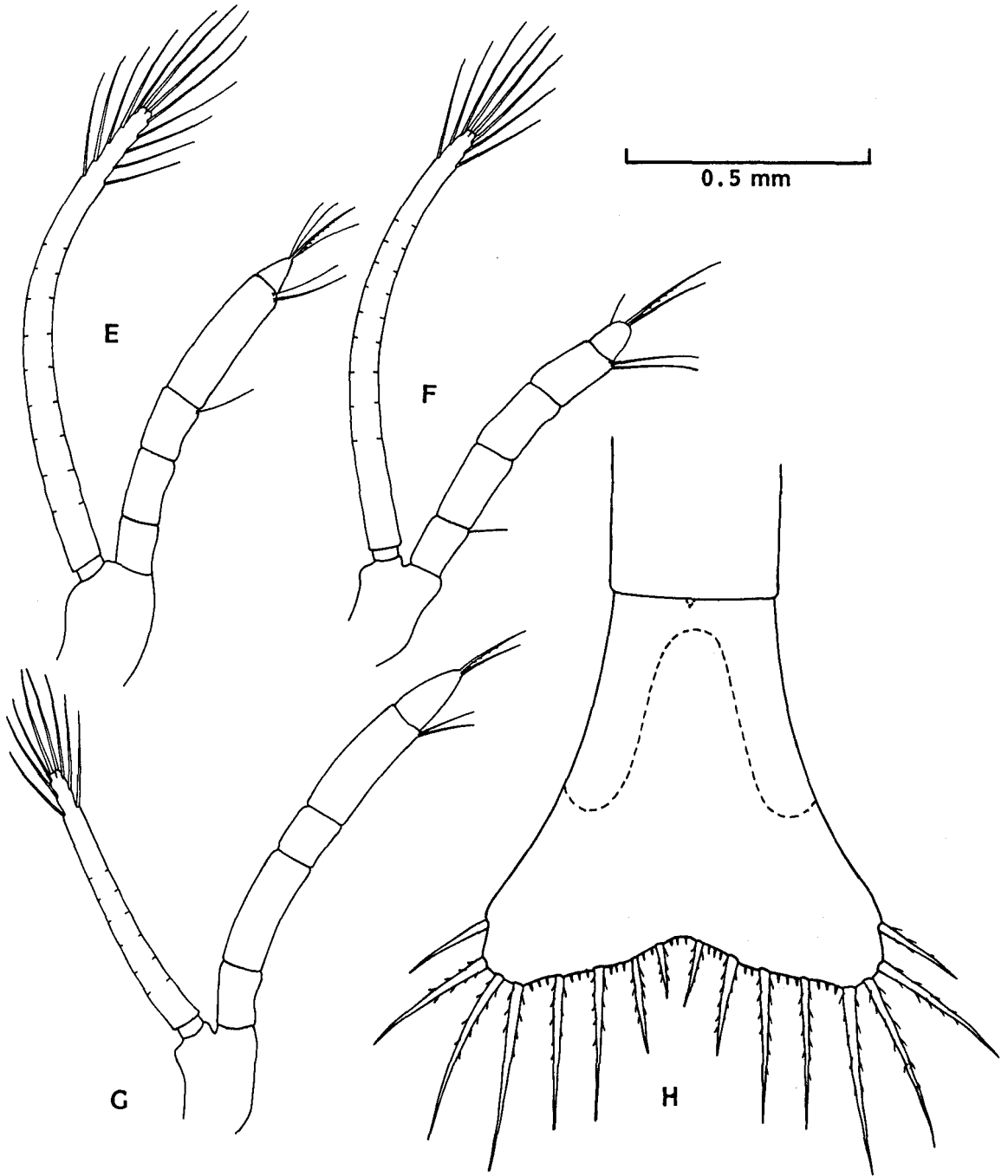


FIGURE 2.—Stage II zoea of *Pandalus goniurus*: A, whole animal; B, antennule; C, antenna; D, mandibles (right and left); E, first pereopod; F, second pereopod; G, third pereopod; H, telson.

somite; bears eight pairs of densely plumose setae. Uropods still enclosed. Anal spine present but minute.

STAGE III ZOEAE

Total length of Stage III 6.2 mm (range 6.0-6.6 mm; 10 specimens). Rostrum (Figure 3A) projects horizontally but curves slightly downward at tip; bears the beginning of a tooth at base. Epipodite of first maxilliped minutely bilobed; pleurobranchiae present as minute buds.

ANTENNULE (Figure 3B).—Inner flagellum unsegmented; about one-half to two-thirds length of outer flagellum. Outer flagellum unsegmented; bears three long and three shorter aesthetascs terminally and one group of two aesthetascs proximally. Each segment bears additionally one or two long plumose setae. Large spine projects ventrally from proximal segment.

ANTENNA (Figure 3C).—Flagellum three-segmented; about two-thirds length of scale and tipped by remnant terminal spine. Antennal scale slightly narrower than in Stage II and fringed with 21 plumose setae; two complete joints at tip. Spine on protopodite at base of scale somewhat larger than in Stage II.

FIRST PEREOPOD (Figure 3D).—Has begun to acquire adult shape, particularly in widened propodite and carpopodite segments. Exopodite bears 12 natatory setae in addition to terminal pair.

SECOND PEREOPOD (Figure 3E).—Endopodite bears a few additional setae and dactylopodite slightly more conical than in Stage II. Propodite not yet projected anteriorly. Exopodite of second pereopod bears 9-10 natatory setae in addition to terminal pair.

THIRD PEREOPOD.—Essentially identical to third pereopod of Stage II except each segment of endopodite bears an additional seta or two.

FOURTH (Figure 3F) AND FIFTH PEREOPODS.—Have begun to acquire adult shape, especially in lengthened dactylopodite and slightly widened propodite.

PLEOPODS (Figure 3G).—Bilobed, unsegmented, and without setae.

TELSON (Figure 3H).—Uropods free. Endopodite undeveloped; about one-third length of exopodite and bearing two simple setae terminally. Anal spine clearly visible.

STAGE IV ZOEAE

Total length of Stage IV 7.7 mm (range 6.8-8.3 mm; 10 specimens). Rostrum (Figure 4A) bears two teeth dorsally, no teeth ventrally; tip not yet bifid. Epipodite of first maxilliped fully bilobed; pleurobranchiae small but readily visible, project anteriorly. Epipodite on second maxilliped present as a small bud. No mastigobranchiae.

ANTENNULE.—Shaped as in adult. Neither inner nor outer flagellum segmented. Outer flagellum bears an additional group of three aesthetascs proximally.

ANTENNA (Figure 4B).—Flagellum six-segmented; longer than scale but does not extend past terminal setae of scale. Antennal scale without joints at tip. Other than increase in size, changes in antennal scale from Stage IV onward are negligible.

FIRST PEREOPOD.—Essentially no change from Stage III except exopodite may have an additional pair of natatory setae.

SECOND PEREOPOD (Figure 4C).—Distal joint of propodite projects slightly anteriorly. Exopodite has 10-12 natatory setae in addition to terminal pair.

THIRD PEREOPOD.—Shaped as in adult; exopodite with five pairs of natatory setae in addition to terminal pair.

FOURTH AND FIFTH PEREOPODS.—Shaped as in adult.

PLEOPODS (Figure 4D).—Still unsegmented; length of second pleopod about one-third height of second abdominal segment. Neither setae nor appendix internae present.

TELSON (Figure 4E).—Endopodite of uropod nearly as long as exopodite and fringed with about 20 setae. Lateral margins of telson nearly parallel but slightly wider posteriorly and bear two spines each. Terminal margin still slightly emarginate;

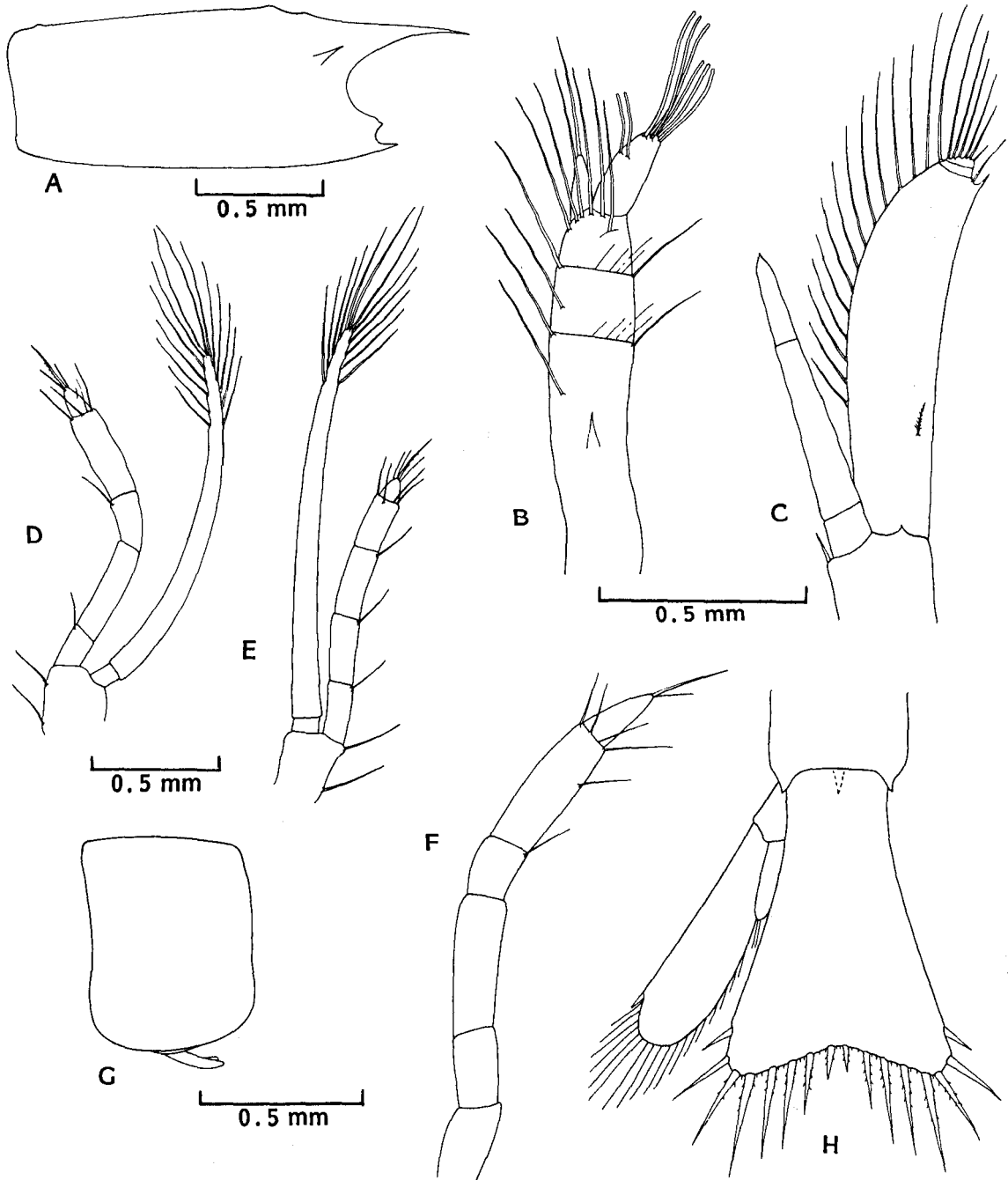


FIGURE 3.—Stage III zoea of *Pandalus goniurus*: A, carapace; B, antennule; C, antenna; D, first pereopod; E, second pereopod; F, fourth pereopod; G, second abdominal segment and pleopod; H, telson.

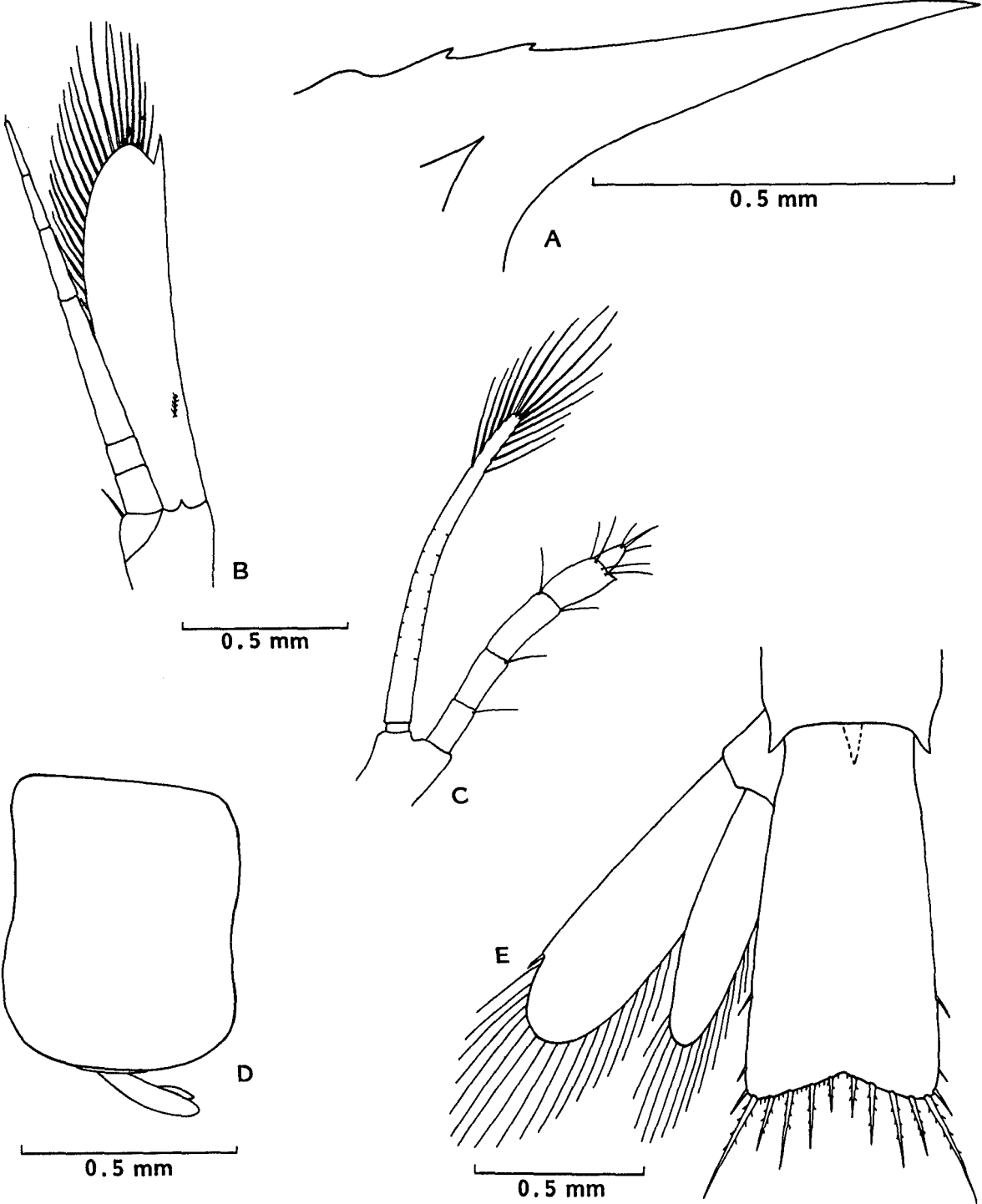


FIGURE 4.—Stage IV zoea of *Pandalus goniurus*: A, rostrum; B, antenna; C, second pereopod; D, second abdominal segment and pleopod; E, telson.

bears six pairs of spines, the outermost (sixth) pair usually without spinules.

STAGE V ZOEAE

Total length of Stage V 10.3 mm (range 8.2-11.3 mm; 10 specimens). Rostrum (Figure 5A) with five or six dorsal teeth and no ventral teeth; tip smooth but may bear small hump indicating future location of bifid tooth. Epipodite of second maxilliped lobed. Mastigobranchiae occur as minute buds on third maxilliped and pereopods 1-3.

ANTENNULE.—Inner flagellum usually four-segmented; still bears terminal spine. Outer flagellum three-segmented; bears four groups of three aesthetascs each in addition to terminal aesthetascs.

ANTENNA (Figure 5B).—Flagellum about 1.7 times length of scale; 11-12 segments.

FIRST PEREPOD (Figure 5C).—Propodite projects anteriorly but not as much as in second pereopod; projection bears small spine terminally. Neither dactylopodite nor propodite projection bear subterminal spines.

SECOND PEREPOD (Figure 5D).—Chela well formed. Dactylopodite bears two spines subterminally, and propodite projection one spine subterminally. Carpopodite not segmented.

PLEOPODS (Figure 5E).—Segmented; length about two-thirds height of second abdominal segment. Flagella tipped with several simple setae, except first pair of pleopods bears setae only on outer flagellum.

TELSON (Figure 5F).—Uropods similar in shape to adult; telson margins somewhat parallel, bear two spines each. Terminal margin straight or only slightly emarginated, bears six pairs of spines. No evidence of transverse hinge of exopodite of uropod.

STAGES VI AND VII (MEGALOPA AND FIRST JUVENILE)

Total length of Stage VI (megalopa) 13.8 mm (11.1-15.8 mm; 6 specimens). Carapace without

supraorbital spine. Rostrum (Figure 6A) shaped as in adult; posterior dorsoventral width not as pronounced nor ventral teeth as fully developed as in Stage VII; bears eight or nine teeth dorsally in addition to distinct bifid tip and four or five teeth ventrally. Usually one or two setae occur between several of the posterior dorsal teeth. Exopodites on third maxilliped and pereopods reduced. Mastigobranchiae larger but still not evident on fourth pereopod. Pleurobranchiae clearly lobulated. Inner flagellum of antennule five- or six-segmented and outer flagellum four-segmented. Inner flagellum lacks terminal spine. Outer flagellum bears subterminally six groups of three aesthetascs each; terminal segment lengthened, without aesthetascs. Mouthparts shaped as in adult; mandibular palp present, two-segmented, without setae. Chelae of first and second pereopods shaped as in adult; carpal joints of left and right second pereopods 20 to 25 and 7 to 9, respectively. Meropodite of left second pereopod three-segmented. Pleopodal setae extend along entire lateral margins of both flagella; tips of appendix internae bear several distinct cincinnuli. Telson (Figure 6B) shows, for first time, shape and spination similar to adult; lateral margins narrow posteriorly but widen slightly at terminal margin. Typically three pairs of spines on lateral margins of telson but often a spine, rarely two, lacking. Terminal margin of telson rounded but not as much as in Stage VII; bears three pairs of stout spines. Transverse hinge of uropod exopodite complete.

Total length of Stage VII (first juvenile) 14.9 mm (range 13.7-15.8 mm; 3 specimens). Rostrum (Figure 7A) typically adult; posterior dorsoventral width slightly greater than in Stage VI; ventral teeth fully formed and one or two setae between most, if not all, teeth including bifid tip. No exopodite on third maxilliped or pereopods. Mastigobranchia evident on fourth pereopod. Flagella of antennules lengthened as in adult; outer flagellum nine-segmented, bears nine groups of three aesthetascs each; inner flagellum six-segmented. Mandibular palp three-segmented, with spinous setae. Carpal joints of left and right second pereopods 29 and 11, respectively. Meropodite of left second pereopod 11-segmented. Telson (Figure 7B) adult in shape, typically bears four pairs of lateral spines although often lacks a single lateral spine.

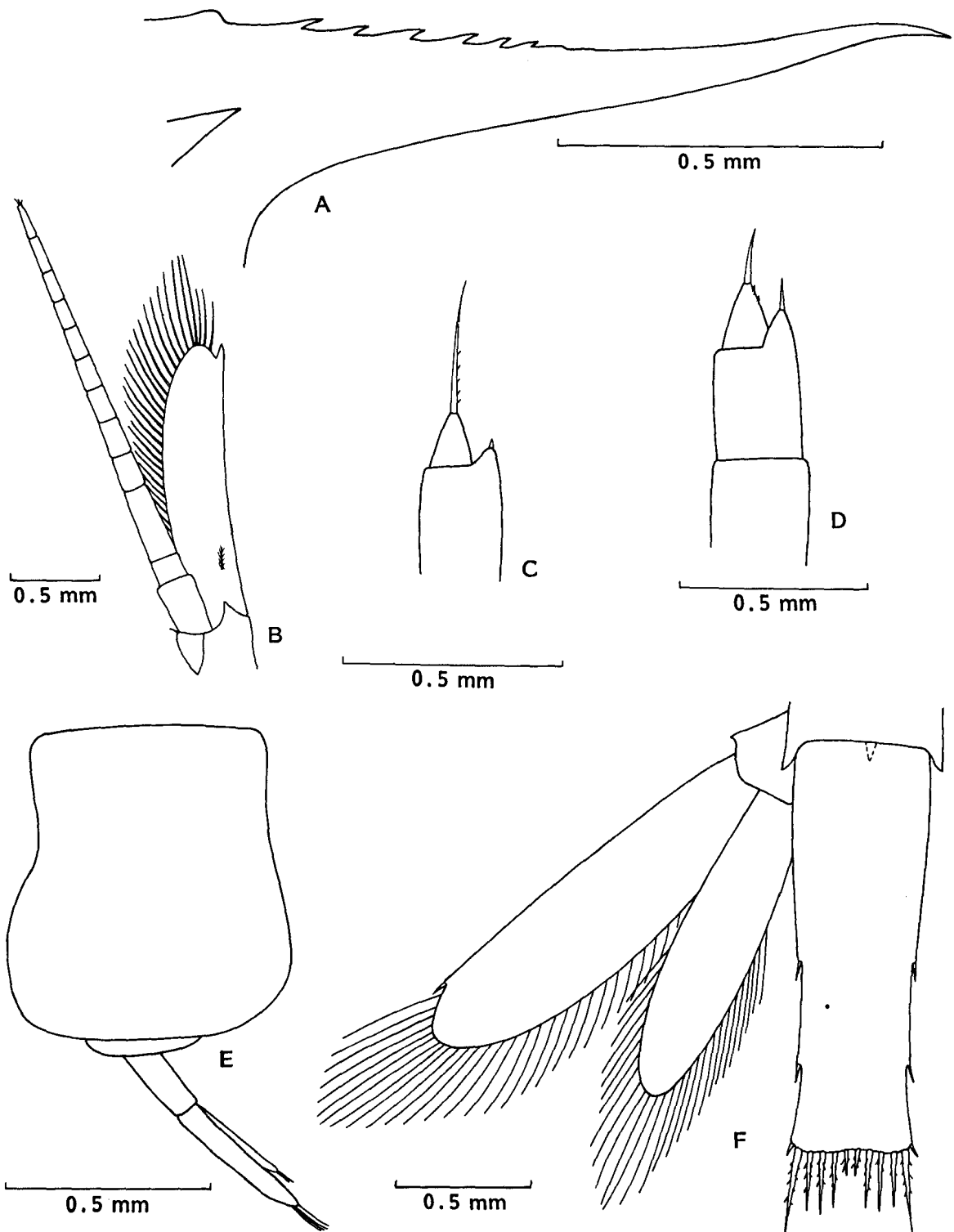


FIGURE 5.—Stage V zoea of *Pandalus goniurus*: A, rostrum; B, antenna; C, first pereopod (terminal segments only); D, second pereopod (terminal segments only); E, second abdominal segment and pleopod; F, telson.

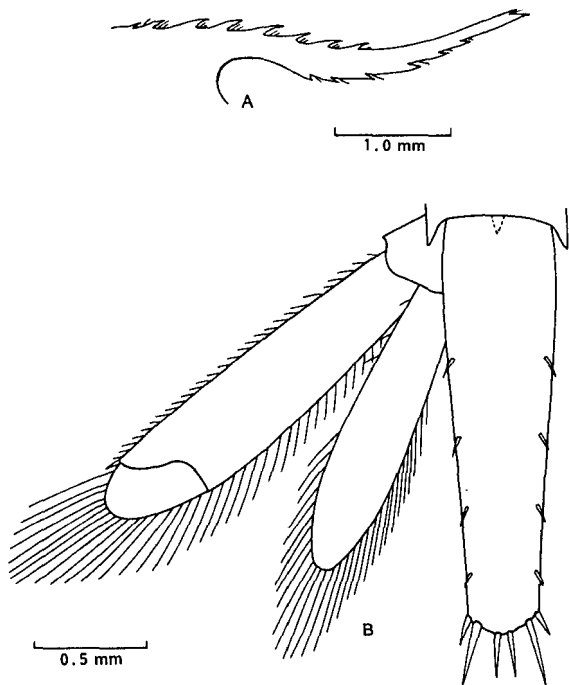


FIGURE 6.—Stage VI (megalopa) of *Pandalus goniurus*: A, rostrum; B, telson.

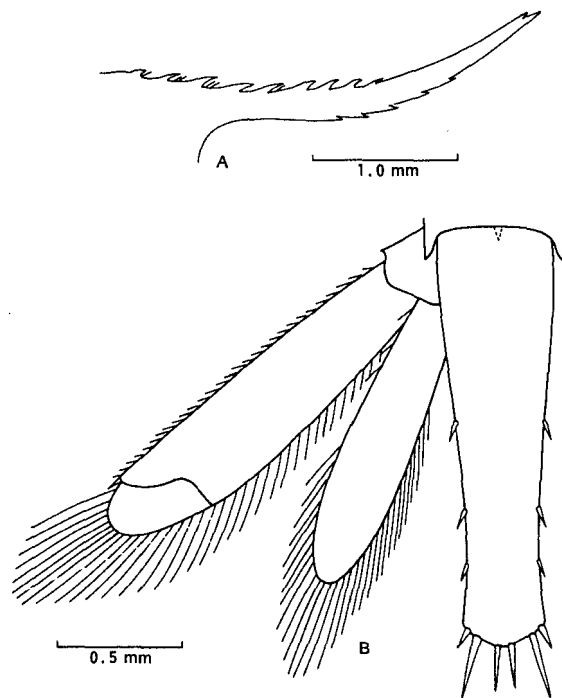


FIGURE 7.—Stage VII (first juvenile) of *Pandalus goniurus*: A, rostrum; B, telson.

COMPARISON OF LARVAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

Ivanov (1965) described and illustrated the first stage zoeae of *P. goniurus* that he reared in the laboratory from known parentage. His descriptions agree in all aspects with mine except for the third maxillipeds: Ivanov's zoeae had 9 natatory setae on the exopodite compared with 12 natatory setae in my zoeae.

The only other description of *P. goniurus* larvae known to me is that of Makarov (1967) who constructed a series of zoeal stages from plankton of the western Kamchatka coast based on Ivanov's description of Stage I. Makarov's descriptions of each stage are brief and include primarily development of the rostrum, antennal flagellum, dactylopodite of the second pereopod, pleopods, and telson. Makarov's zoeae are essentially identical to mine through Stage V but Makarov's Stages VI and VII possess mostly zoeal characteristics, rather than postzoeal as mine do. For instance, in Stage VI the rostrum of Makarov's specimens is not bifid and does not bear ventral

teeth, and the telson still bears six pairs of spines terminally. In my Stage VI specimens, the rostrum is bifid, bears five or six distinct ventral teeth, and the telson bears only four pairs of spines terminally. In Stage VII, the rostrum of Makarov's specimens is bifid but bears only three or four poorly developed teeth ventrally and the telson still bears six pairs of spines terminally. In my Stage VII specimens both the rostrum and telson are essentially fully developed as in the adult. Apparently *P. goniurus* from the western Kamchatka coast has at least two more zoeal stages than *P. goniurus* from Kachemak Bay.

The morphological differences between larval Stages VI and VII of *P. goniurus* from the western Kamchatka coast and from Kachemak Bay, Alaska, may reflect variation in number of molts in response to environmental conditions. Variability in number of molts required to reach a specific point in development in the Crustacea is well known. In a review of the literature, Costlow (1965) showed that variability in number of molts occurs in the Cirripedia, Euphausiacea, Natantia, Reptantia, Anomura, and Brachyura regardless of whether the larvae are reared in the laboratory or

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from the natural environment. Regarding the Pandalidae, Pike and Williamson (1964) have shown variability in number of molts required to reach the megalopa stage in the plankton for *Pandalina brevirostris* (Rathke) and *Pandalus propinquus* G. O. Sars, and that larvae of *Dichelopandalus bonnieri* (Cautlery) and *Pandalus montagui* Leach reared in the laboratory have more larval stages than specimens from plankton. Berkeley (1931) mentioned the possibility of variation in number of molts in larvae of *Pandalus danae* Stimpson. Kurata (1964) speculated that larvae of *P. borealis* Krøyer in Japanese waters may have six or seven stages.

I have observed that both *P. borealis* and *P. goniurus* reared in the laboratory are capable of prolonging their normal interval between zoeal moltings (about 10-15 days) to as much as 5 wk, and that *P. borealis* may have as many as 11 zoeal stages before reaching the megalopa stage. Although the causes of molt retardation and morphological variation in pandalid larvae have not been established, the potential for variability exists not only in *P. goniurus* but in other pandalids as well. Variability in larval development from different geographical areas, therefore, is to be expected.

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