DESCRIPTION OF ZOEAE OF COONSTRIPE SHRIMP, *PANDALUS HYPSINOTUS*, REARED IN THE LABORATORY

EVAN HAYNES[1]

ABSTRACT

Zoeae of *Pandalus hypsinotus* from ovigerous females caught in Kachemak Bay, Alaska, were reared in the laboratory. Each of the six zoeal stages is described and illustrated, and a brief description is given for postzoeal Stages VII-IX. The descriptions are compared with descriptions of zoeal stages of *P. hypsinotus* given by other authors.

Although pandalid shrimp form a major fishery resource along the Pacific coast of North America, little has been published on their early life history, especially on identification of the larval stages. Berkeley (1930) described the zoeal stages of five pandalid species from British Columbia, *Pandalus borealis* Krøyer, *P. danae* Stimpson, *P. hypsinotus* Brandt, *P. platyceros* Brandt, and *Pandalopsis dispar* Rathbun. The first zoeal stage of each species was obtained in the laboratory, and various remaining stages were obtained from the plankton. Berkeley also mentioned briefly the growth and distribution of the zoeae. Of 14 species of pandalid shrimps known to occur along the Pacific coast of North America, only two species, *Pandalus jordani* Rathbun and *P. platyceros*, have been reared through all their zoeal stages in the laboratory (Modin and Cox 1967; Price and Chew 1972).

In 1972, the National Marine Fisheries Service began an intensive investigation at its field station at Kasitsna Bay, Alaska, on the early life history of pandalid shrimp in Alaskan waters. The initial objective of the investigation was to describe in detail laboratory-reared zoeae of each pandalid species previously unverified. This report describes and illustrates each of the six zoeal stages of coonstripe shrimp, *P. hypsinotus*, and compares the stages obtained from laboratory-reared zoeae with stages obtained from the plankton by other authors. Brief descriptions of postzoeal Stages VII through IX are also included.

MATERIALS AND METHODS

Ovigerous *Pandalus hypsinotus* were caught at depths of 54 m (30 fathoms) in shrimp pots in late April 1973. They were kept in plastic buckets filled with seawater for about ½ h and then were put in plastic glass hatching boxes similar to those used by Price and Chew (1972) for rearing zoeae of spot shrimp, *P. platyceros*. The hatching boxes were kept in a biologically filtered recirculating aquarium system containing 190 liters (50 gallons) of refrigerated seawater, of which 19 liters (5 gallons) were exchanged for fresh seawater every other day. Salinity was maintained between 32 and 34‰ and temperature between 6° and 8°C. The quality and quantity of light were not controlled, but direct sunlight was avoided. Most zoeae were released at night but some were released during daytime whenever a female shrimp was stimulated to flex her abdomen rapidly. No predation of zoeae by female shrimp or by the zoeae themselves was noted. No prezoeae were seen.

About 50 zoeae were transferred by large-bore pipette to each of 25 500-ml beakers containing about 400 ml of aquarium seawater. In addition, a zoea was placed in each of 50 25- by 50-mm numbered plastic vials held in compartmented trays. The zoeae in the beakers provided both individual specimens and cast skins of various stages for dissection, and the individual zoeae in the vials provided a continuous sequence of cast skins with a known history. The beakers and vials were both checked daily for exuviae. Seawater in the holding containers was changed every other day and the zoeae were fed newly hatched nauplii of brine shrimp, *Artemia salina*, from San Francisco Bay.

[1]Northwest Fisheries Center Auke Bay Fisheries Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 155, Auke Bay, AK 99821.

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The density of nauplii was controlled only to the extent that a few nauplii remained in the container at the end of each feeding period. The original beakers and vials were used throughout the study because the zoeae also fed on the algae that grew on the sides and bottoms.

All zoeae molted at night. Of the deaths noted, most were caused by failure to complete the molting process; the posterior half was shed successfully, but the anterior half remained attached to the mouth parts and pereopods. Survival was about 90%.

Illustrations were drawn from unstained zoeae and from exuviae stained red with Turtox CMC-S[2] (acid fuchsin stain mountant). Stained exuviae show segmentation and setation more clearly than unstained. Zoeae and exuviae were dissected with the aid of a binocular dissecting microscope. The dissected material was mounted on a slide and drawn to scale with the aid of a camera lucida. Detail was checked with a compound microscope up to 430×.

In the final illustrations (Figures 1-6), for clarity, setules on the setae are usually omitted but spinulose setae are shown. Because the numbers of setae on the surface of the carapace and abdomen are highly variable, especially from Stage IV onward, they are figured only when useful in identification of a stage. 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. Whole zoeae are also figured from the right side. The figures are in part schematic and represent typical setal counts. The setation formulas proceed from the distal to the proximal ends of appendages. Gill development is mentioned in the text but usually not shown in the figures. The terms are defined as follows:

spinose—bearing many spines
spinous—spinelike
setose—set with bristles (setae)
spinulose—set with little spines.

Total length was measured from the anterior tip of the rostrum to the posterior tip of the telson with the aid of a dissecting microscope; the number of specimens used to determine total lengths is given for each stage. A minimum of 10 exuviae of each stage was used to verify segmentation and setation unless noted otherwise. The term "stage" denotes the intermolt period. Nomenclature of larval appendages and gills follows Pike and Williamson (1964) and Berkeley (1930) respectively.

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

STAGE I ZOEA

Total length of Stage I zoea (Figure 1A) 5.8 mm (range 5.5-6.2 mm; 50 specimens). Live specimens brightly colored by numerous yellow chromatophores edged reddish brown. A conspicuous yellow chromatophore occurs dorsally on each eyestalk and at base of telson. Smaller but distinct chromatophores occur on nearly all appendages, especially maxillipeds and pereopods. Tips of antennule and antennal scale are tinged reddish brown. Chromatophore pattern of specimens preserved in 5% solution of Formalin and seawater for several days identical to the pattern on live specimens except that yellow color changes to reddish brown after preservation. 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; prominences occur in all zoeal stages. Antennal and pterygostomian spines present, but both usually hidden by sessile eyes; no supraorbital spine.

ANTENNULE (FIGURE 1B).—Antennule (first antenna) consists of a simple unsegmented tubular basal portion, distal conical base, distal conical projection, and a heavily plumose seta on a small conical base; distal conical projection bears four aesthetascs—one long, one short, and two of intermediate length.

ANTENNA (FIGURE 1C).—Antenna consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum two segmented and about one-fourth longer than scale; distal segment is styliform, tipped by a plumose seta and a spine. Distal segment may be partially segmented proximally. Protopodite bears spinous seta at base of flagellum and a spine at base of scale, both of which persist throughout zoeal development. Antennal scale distally divided into six segments (two proximal joints incomplete) and fringed with 10 heavily plumose setae along terminal and inner margins. A small seta occurs on outer margin near base of terminal segments.

MANDIBLES (FIGURE 1D).—Mandibles without palps. Incisor process of left mandible usually bears four teeth in contrast to the distinctly triserrate incisor process of right mandible. Left mandible bears one premolar denticle and right mandible bears two. Two subterminal processes occur on truncated molar process of left mandible but not on right mandible.

MAXILLULE (FIGURE 1E).—Maxillule (first maxilla) bears coxal and basial endites and an endopod. Proximal lobe (coxopodite) bears a stout seta near base and 12 spinulose setae terminally along with a series of extremely fine hairs. Median lobe (basipodite) bears 11 spinulose spines in two rows on terminal margin and several fine hairs subterminally. Endopodite originates from lateral margin of basipodite and bears three terminal and two subterminal setae; three of the five spines are sparsely plumose, the remaining two spinulose. There is no evidence of an outer seta (representing a vestigial exopodite) on maxillule.

MAXILLA (FIGURE 1F).—Maxilla bears platelike exopodite (scaphognathite) with 16 long, approximately equal, evenly spaced plumose setae along outer margin and one longer and slightly thicker seta (at proximal end). Endopodite has four partly fused segments and bears nine large plumose setae. Basipodite bilobed; each lobe bears eight setae. Bilobed coxopodite bears 16 setae, 4 on distal lobe and 12 on proximal lobe.

FIRST MAXILLIPED (FIGURE 1G).—First maxilliped most heavily setose of natatory appendages. Protopodite partially segmented; bears 7 setae on proximal segment and 18 slightly smaller setae on distal segment; most setae on protopodite plumose but some simple or spinulose. Endopodite distinctly four segmented; setation formula—4, 2, 1, 3. Exopodite a long slender ramus segmented at base; has four terminal and five or six lateral natatory setae. Epipodite a single lobe.

SECOND MAXILLIPED (FIGURE 1H). —Protopodite bisegmented; distal segment bears eight sparsely plumose setae, and proximal segment bears a simple seta. Endopodite distinctly five segmented; fourth segment expanded laterally; terminal segment has at least two spinulose setae; remaining setae on endopodite usually sparsely plumose; setation formula—7, 2, 1, 1, 3. Exopodite similar to exopodite of first maxilliped but slightly larger; has 4 terminal setae, 11 or 12 lateral natatory setae. No epipodite.

THIRD MAXILLIPED (FIGURE 1I).—Protopodite bisegmented; distal segment bears four setae. Endopodite distinctly five segmented and nearly as long as exopodite, giving it more pediform appearance than either of the two preceding appendages; setation formula —4, 8, 2, 2, 2. Exopodite similar to second maxilliped but slightly longer; has 3 or 4 terminal setae and 14 lateral natatory setae. No epipodite.

FIRST PEREOPOD (FIGURE 1J).—Endopodite functionally developed and similar in form to third maxilliped but slightly smaller. Endopodite distinctly five segmented; ends in simple conical dactylopodite; setation formula—3, 7, 2, 2, 2. Exopodite naked. Protopodite bisegmented; has four setae. Neither this nor remaining pereopods of this stage have any evidence of epipodite.

SECOND PEREOPOD (FIGURE 1K).—Second pereopod similar to first except that it has fewer setae and fourth or propodal joint is slightly extended to form beginning of chela.

THIRD, FOURTH, AND FIFTH PEREOPODS (FIGURE 1L-N).—These three pereopods essentially identical to each other except that they decrease slightly in size from third to fifth. No exopodites.

PLEOPODS.—No pleopods evident, not even as small buds.

TELSON (FIGURE 1O).—Telson not segmented from sixth abdominal segment; slightly emarginate distally; bears 14 densely plumose setae. Minute spinules at base of each seta; larger spinules along terminal margin between bases of four inner pairs and on the four inner pairs of setae themselves. Enclosed uropods visible. No anal spine.

STAGE II ZOEA

Total length of Stage II zoea (Figure 2A) 6.1

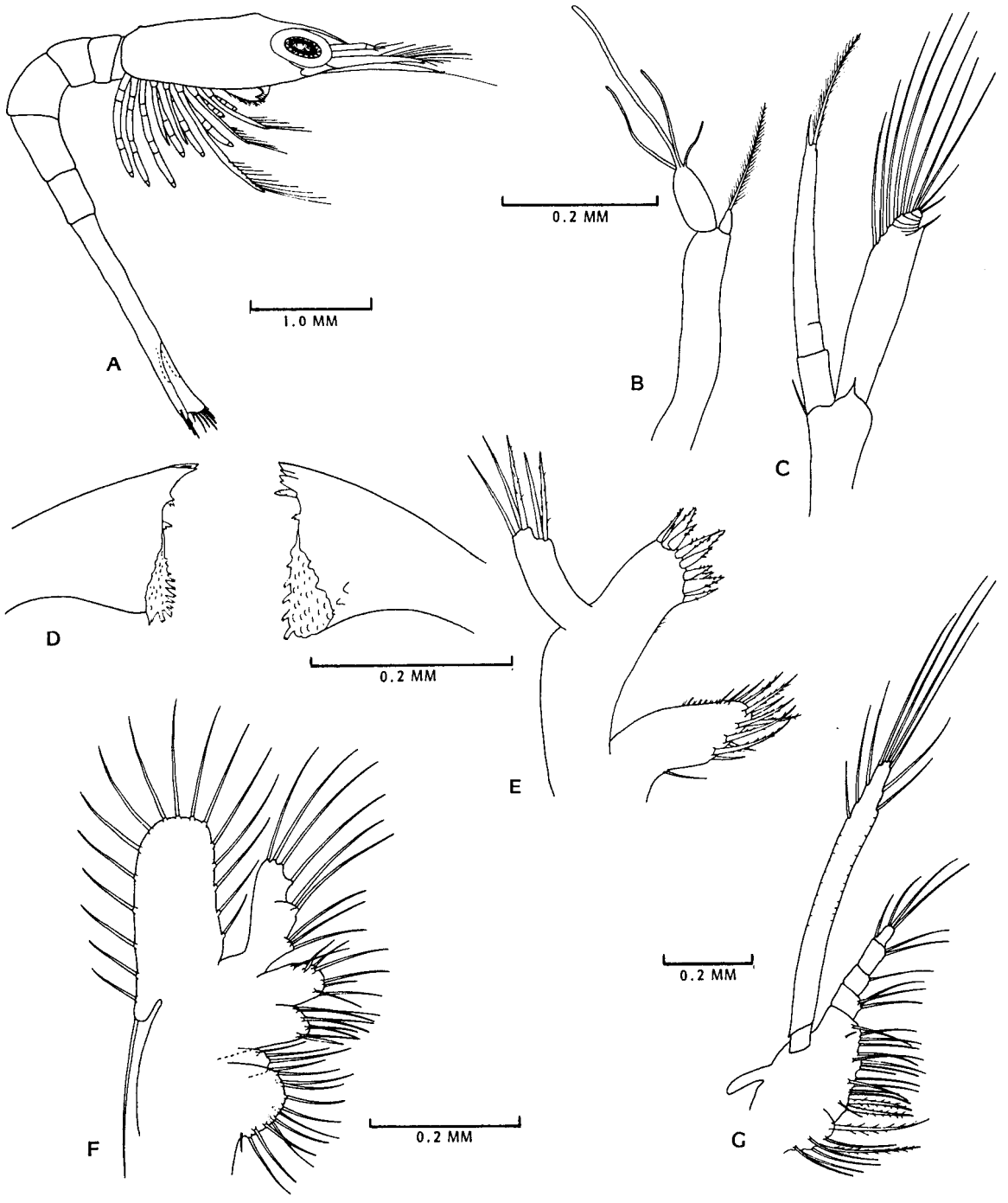
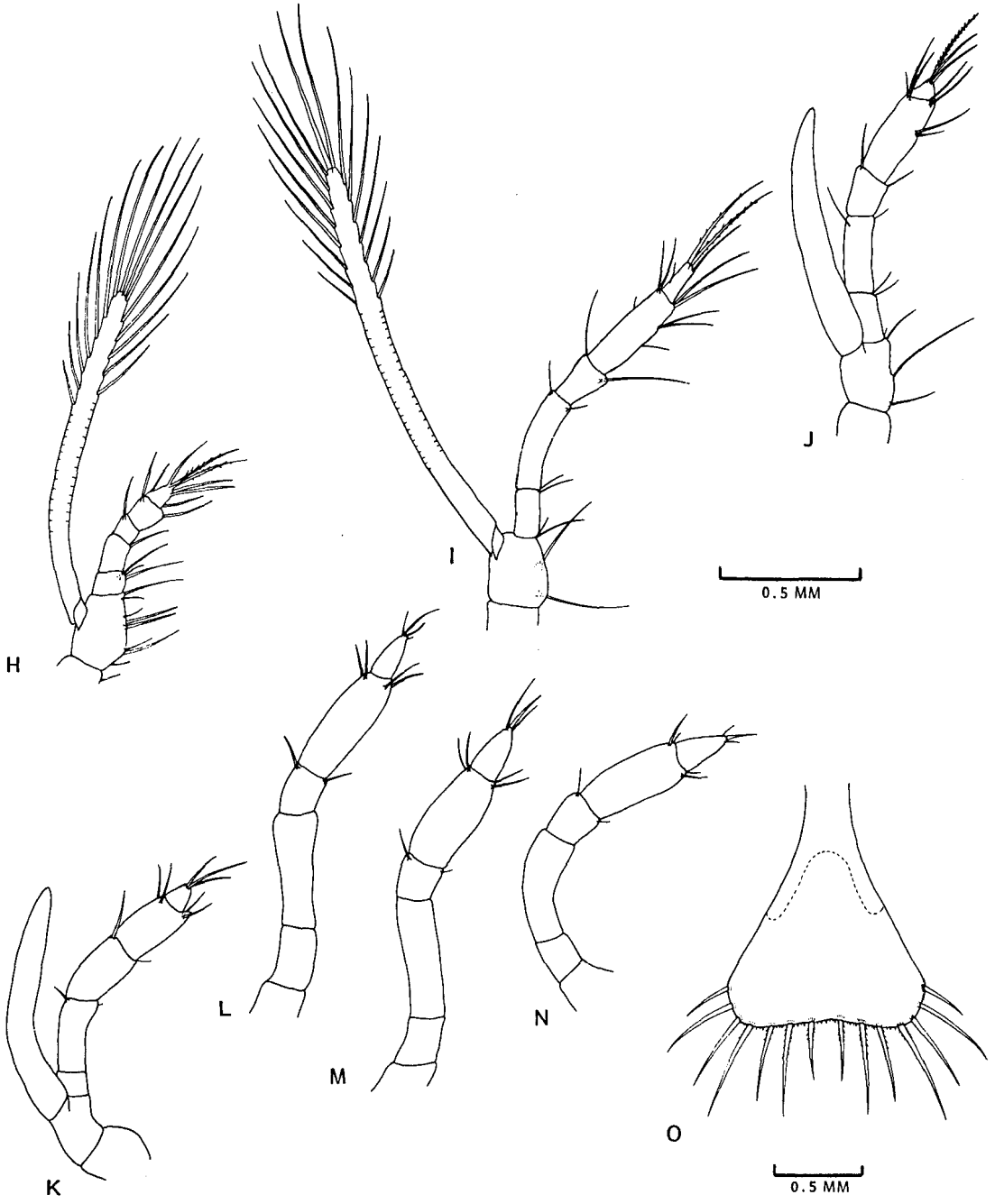


FIGURE 1.—Stage I zoea of *Pandalus hypsinotus:* (A) whole animal, (B) antennule, (C) antenna, (D) mandibles (right and left), (E) maxillule, (F) maxilla, (G) first maxilliped, (H) second maxilliped, (I) third maxilliped, (J) first pereopod, (K) second pereopod, (L) third pereopod, (M) fourth pereopod,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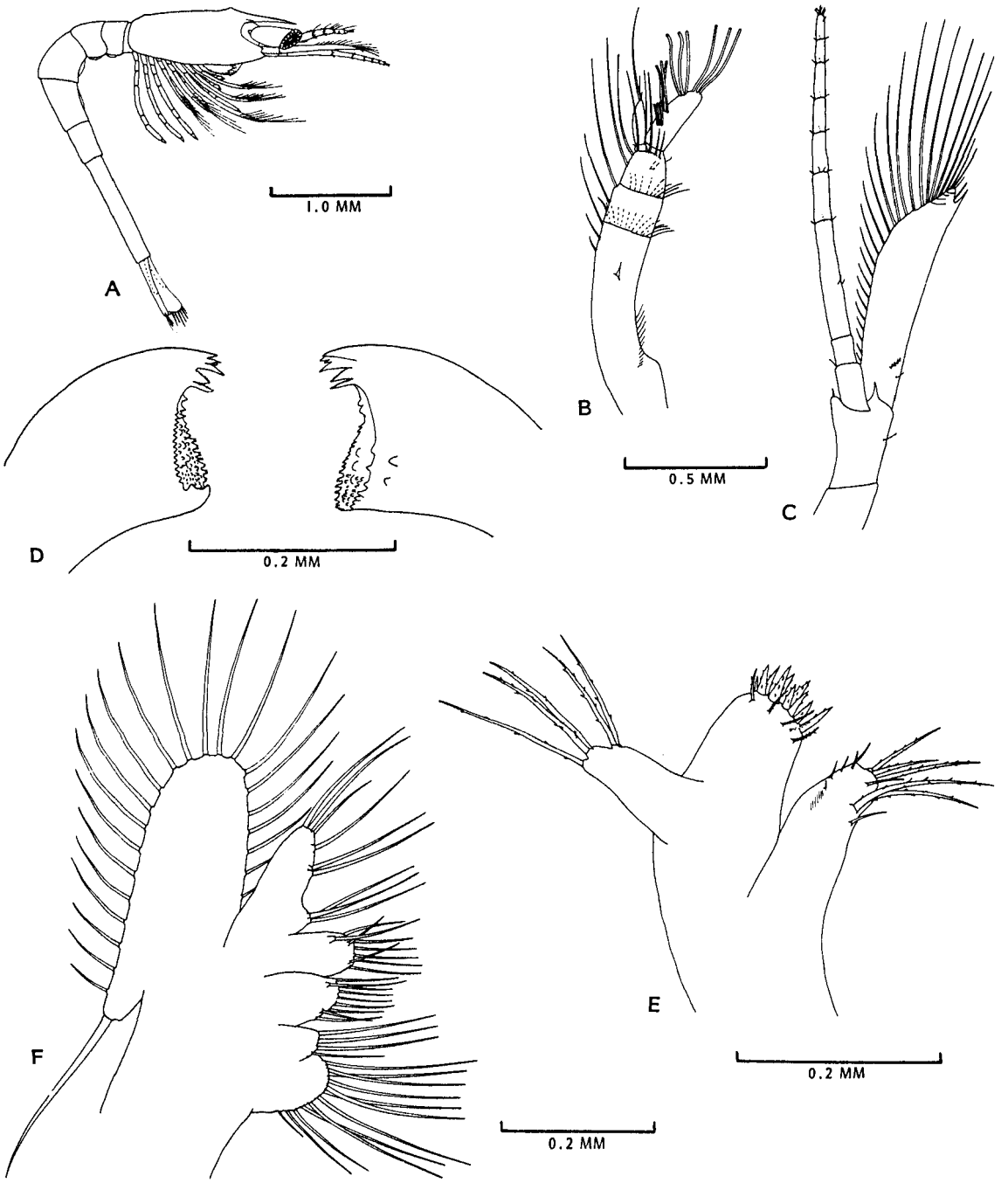
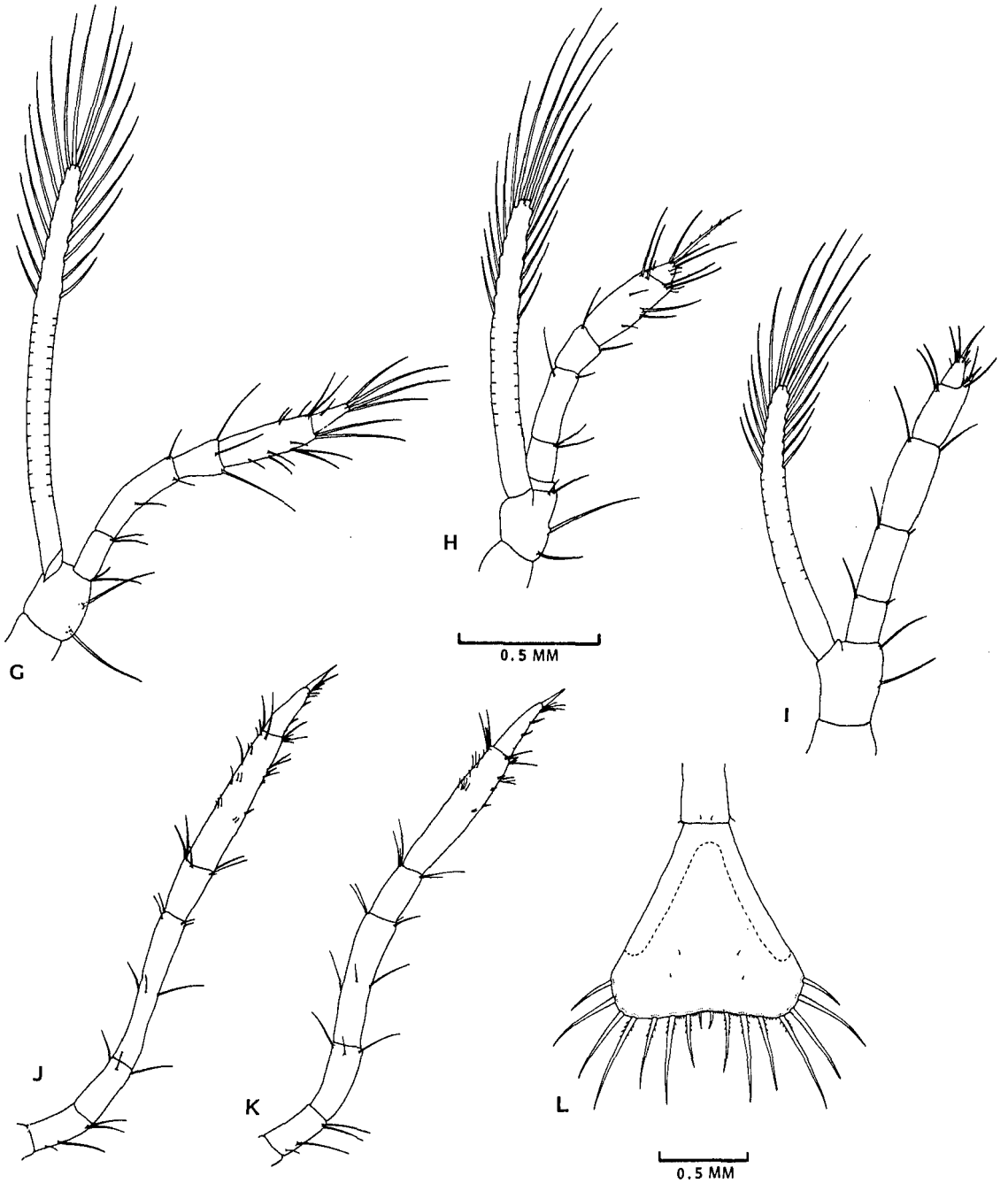


FIGURE 2.—Stage II zoea of *Pandalus hypsinotus:* (A) whole animal, (B) antennule, (C) antenna, (D) mandibles (right and left), (E) maxillule, (F) maxilla, (G) third maxilliped, (H) first pereopod, (I) second pereopod, (J) third pereopod, (K) fourth pereopod, (L) telson.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mm (range 5.6-6.5 mm; 50 specimens). Chromatophore color and pattern essentially identical to Stage I except ventral surface of abdomen now greenish. Rostrum still without teeth; not curved downward as strongly as in Stage I. Carapace same as Stage I except now has prominent supraorbital spine; antennal and pterygostomian spines clearly visible. Eyes, sessile in Stage I, now stalked.

ANTENNULE (FIGURE 2B).—Antennule shows considerable change from Stage I, now three segmented. It bears on terminal margin a large outer and a smaller inner flagellum, outer flagellum bears four groups of three aesthetascs each, one group terminally and three groups along inner margin; inner flagellum bisegmented and bears three setae terminally, one long and two short; originating at base of these two flagella is a dorsal budlike projection bearing four simple setae (projection and setae not shown in Figure 2B). Proximal segment of antennule laterally expanded at base, with about 12 small setae arranged laterally near expansion; 3 lateral plumose setae and about 14 dorsally projecting but smaller plumose setae ring terminal margin; large spine projects downward from ventral surface. Second segment has 4 lateral plumose setae, 2 long and 2 short, and about 10 dorsal plumose setae ringing terminal margin. Third segment has seven lateral plumose setae—five originating ventrally and the remaining two dorsally—and three simple setae—two dorsal and one lateral.

ANTENNA (FIGURE 2C).—Inner flagellum nine segmented, about twice as long as scale; distal segment tipped by about six small setae. Spine on basipodite at base of inner flagellum reduced in size. Antennal scale fringed with 28-30 long, thin plumose setae along terminal and inner margins. Joints at distal tip reduced to four, three of them incomplete. Distal outer seta of scale a stout spine.

MANDIBLES (FIGURE 2D).—More massive than in Stage I but still without palps. Both mandibles bear pair of premolar serrated denticles, and molar processes are more developed. Truncated end of molar process of right mandible formed into curved lip. Subterminal processes still present on left mandible.

MAXILLULE (FIGURE 2E).—Endopodite essentially unchanged from previous stage. Basipodite bears 10 spinose spines in two rows and five spinous setae on terminal margin, but no fine hairs. Coxopodite bears 12 setae terminally, 5 spinous and considerably longer than remaining 7.

MAXILLA (FIGURE 2F).—Similar to Stage I except exopodite larger and now bearing 21 or 22 marginal plumose setae in addition to plumose seta at proximal end. Lobes of basipodite bear nine setae each instead of eight as in Stage I.

FIRST, SECOND, AND THIRD (FIGURE 2G) MAXILLIPEDS.—Maxillipeds essentially identical to each other and nearly identical to first stage except for an increase in size and a slight variation in numbers of setae.

FIRST PEREOPOD (FIGURE 2H).—First pereopod functionally developed and similar in form to third maxilliped. Exopodites fringed with 15-17 plumose setae. Endopodite six segmented. Propodite projected slightly distally. Setae more numerous than in Stage I, especially on last two segments. This pereopod and the remaining four have a pleurobranchia bud at their base.

SECOND PEREOPOD (FIGURE 2I).—Similar to first pereopod except propodite projection longer and ischiopodite not segmented.

THIRD, FOURTH, AND FIFTH PEREOPODS (FIGURE 2J, K).—Third, fourth, and fifth pereopods essentially identical except for slight differences in size, fifth being smallest. Seven functional segments including dactylopodite. Dactylopodite bears spine at tip and three spines laterally. No exopodite.

PLEOPODS (FIGURE 2A).—Pleopods evident only as slightly swollen areas on abdominal segments.

TELSON (FIGURE 2L).—Telson distinct from sixth abdominal segment; bears 16 densely plumose setae along margin. Spinule arrangement essentially same as Stage I. Dorsal surface bears four small simple setae. Uropods still enclosed but longer than in first stage. No anal spine.

STAGE III ZOEA

Total length of Stage III zoea (Figure 3A) 6.7 mm (range 6.2-7.7 mm, 25 specimens).Chromatophore pattern similar to first two stages but less yellow color and more reddish brown. Rostrum pointing slightly upward with one or two small teeth at base. Supraorbital, antennal, and pterygostomian spines still present on carapace.

ANTENNULE (FIGURE 3B).—Outer flagellum distinctly three segmented; first and second segments have two groups of three aesthetascs each; distal segment has four aesthetascs. Inner flagellum still bisegmented but about twice as long as in Stage II. Remainder of antennule similar to Stage II except it is larger and more setose, and lateral projection on proximal segment is more arcuate.

ANTENNA (FIGURE 3C).—Antennal scale with 32-36 lateral plumose setae; no segmentation at tip in this or later stages. Lateral margin near base now has four additional simple setae. Flagellum about 3 times length of scale; has several additional segments and setae near base.

MANDIBLES (FIGURE 3D).—Both mandibles without palps. Right mandible bears three premolar processes; projections along anterior molar edge stronger and truncated end not curved into lip as in Stage II. Left mandible molar processes also stronger, and subterminal processes present.

MAXILLULE (FIGURE 3E).—Endopodite unchanged from Stage II except two setae particularly spinulose. Basipodite bears an additional plumose seta and a group of small fine hairs subterminally. Coxopodite now bears 14 instead of 12 setae and has more fine hairs than Stage II.

MAXILLA (FIGURE 3F).—Exopodite longer than in Stage II, slightly curved, and bears 27 marginal plumose setae in addition to plumose seta at proximal end. Lobes of basipodite bear 10 setae instead of 9 as in Stage II.

FIRST AND SECOND MAXILLIPEDS.—Epipodite on first maxilliped has rudiment of second lobe. Otherwise, first and second maxillipeds same as Stage II but slightly larger.

THIRD MAXILLIPED (FIGURE 3G).—Similar in shape to third maxilliped at Stage II but larger and more spinous and propodite bears two small spinulose spines. Numbers of setae on endopodites of maxillipeds and pereopods on this and succeeding stages are so highly variable that a specific description of them would not be an aid in identification of stage or species.

FIRST PEREOPOD (FIGURE 3H).—Exopodite still present, more setose than Stage II. Propodite bears a small spinulose spine near base. Pleurobranchia at base of this appendage and remaining four pereopods barely larger than in Stage II.

SECOND PEREOPOD (FIGURE 3I).—Most significant changes are presence of chela on endopodite and an additional segment on base of ischiopodite.

THIRD (FIGURE 3J), FOURTH, AND FIFTH PEREOPODS.—Essentially similar; fifth smallest as usual. Greater development from Stage II shown by well-formed dactylopodite and more setae. An additional segment occurs at base of ischiopodite.

PLEOPODS (FIGURE 3A).—Pleopods evident as small buds.

TELSON (FIGURE 3K).—Uropods free; bear plumose setae and small, randomly located setae on dorsal surface. Telson broader at tip than at base and still slightly emarginate; bears seven pairs of spinous setae and two pairs of lateral spines. Base of telson bears a pair of simple setae that increase in number in later stages and persist in adults. Anal spine appears at this stage.

STAGE IV ZOEA

Total length of Stage IV zoea (Figure 4A) 7.5 mm (range 7.3-8.1 mm, 10 specimens). Chromatophore pattern and color considerably different from previous stages. In general, numerous small wine-red chromatophores occur on carapace, pereopods, and ventral surface of abdomen; small yellow chromatophores occur on carapace, antennules, antennal scale, uropods, telson, and third abdominal segment. Rostrum beginning to acquire adult shape; 11-13 dorsal spines, 2 or 3 small ventral spines, and 1 dorsal spine that may be

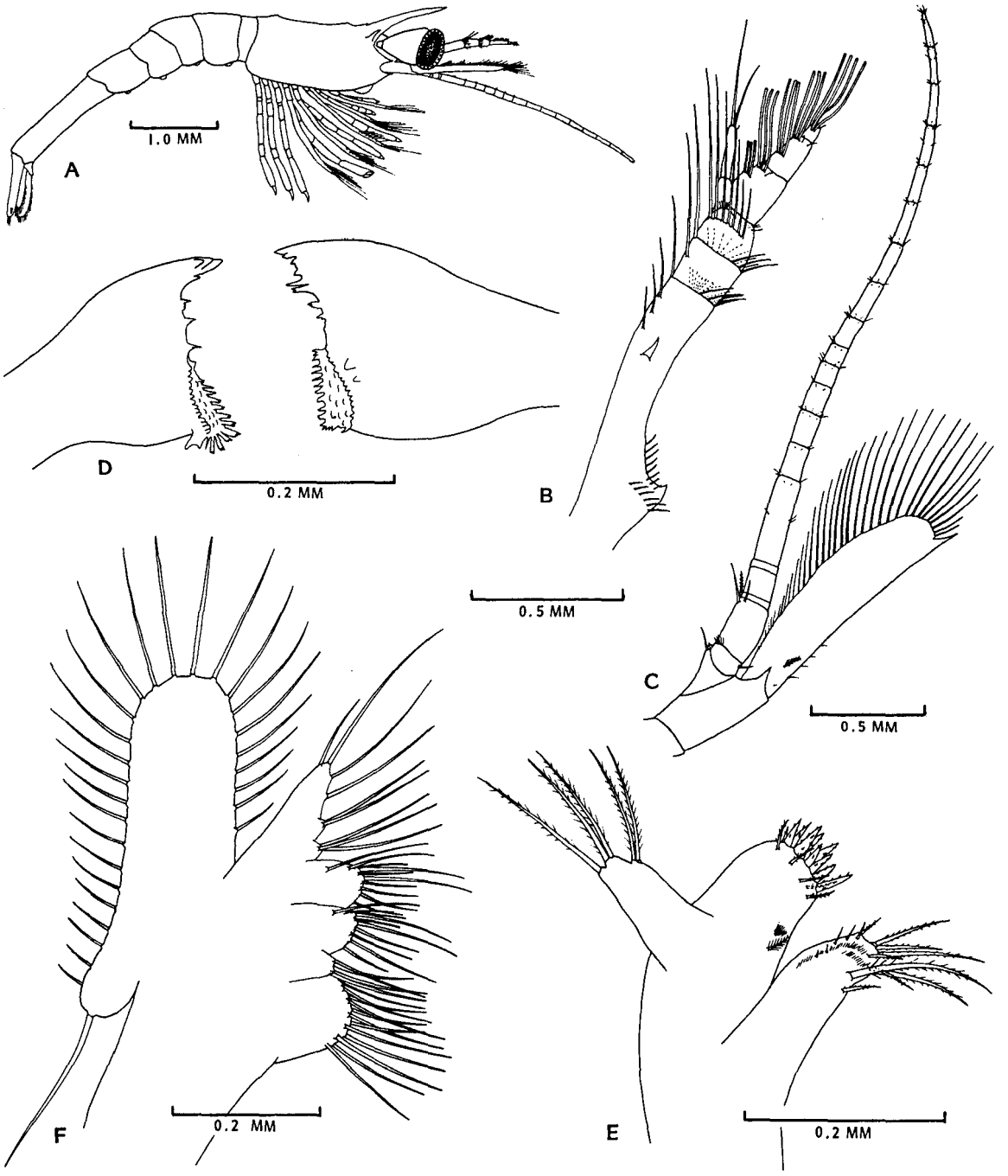
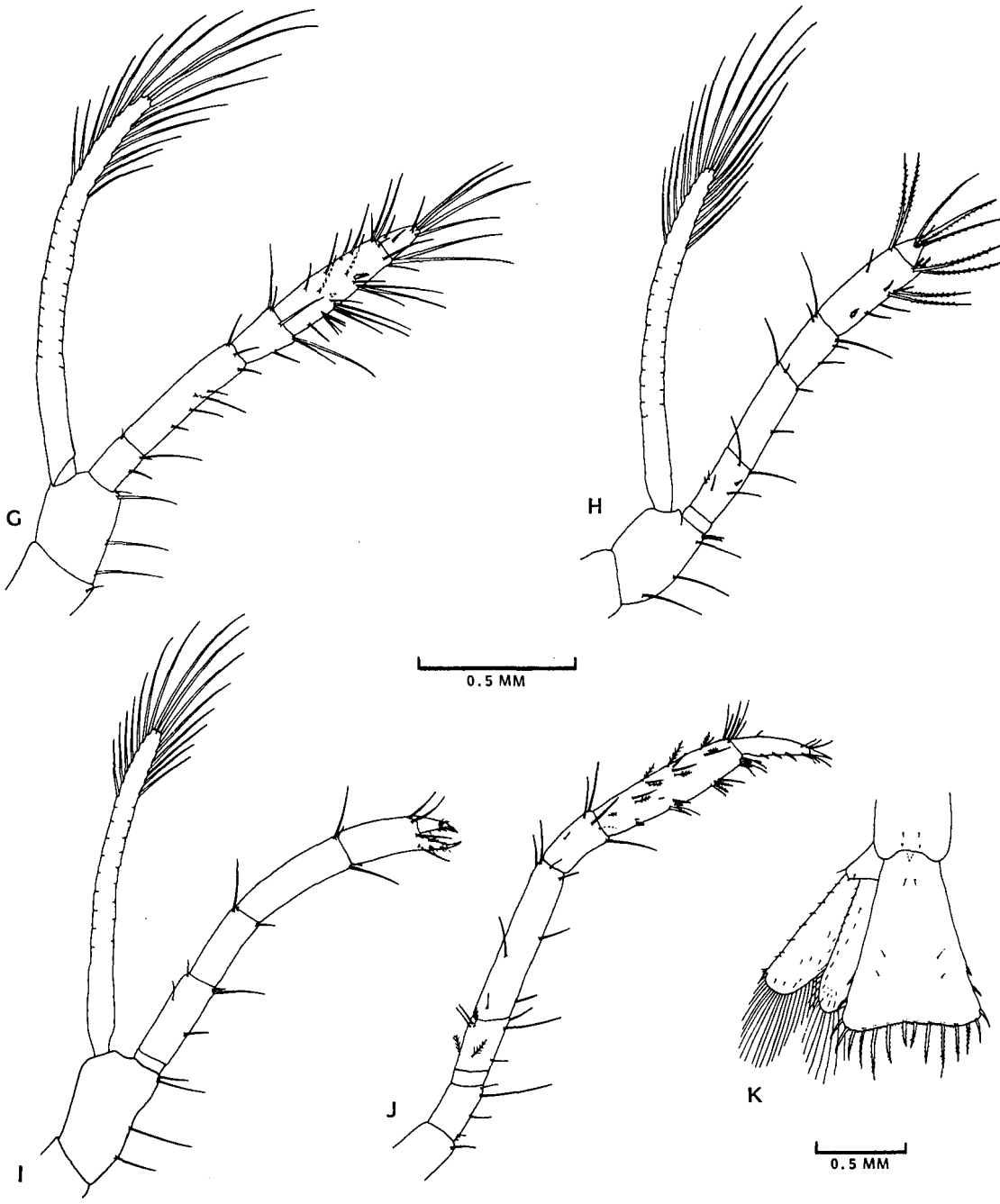


FIGURE 3.—Stage III zoea of *Pandalus hypsinotus:* (A) whole animal, (B) antennule, (C) antenna, (D) mandibles (right and left), (E) maxillule, (F) maxilla, (G) third maxilliped, (H) first pereopod, (I) second pereopod, (J) third pereopod, (K) telson.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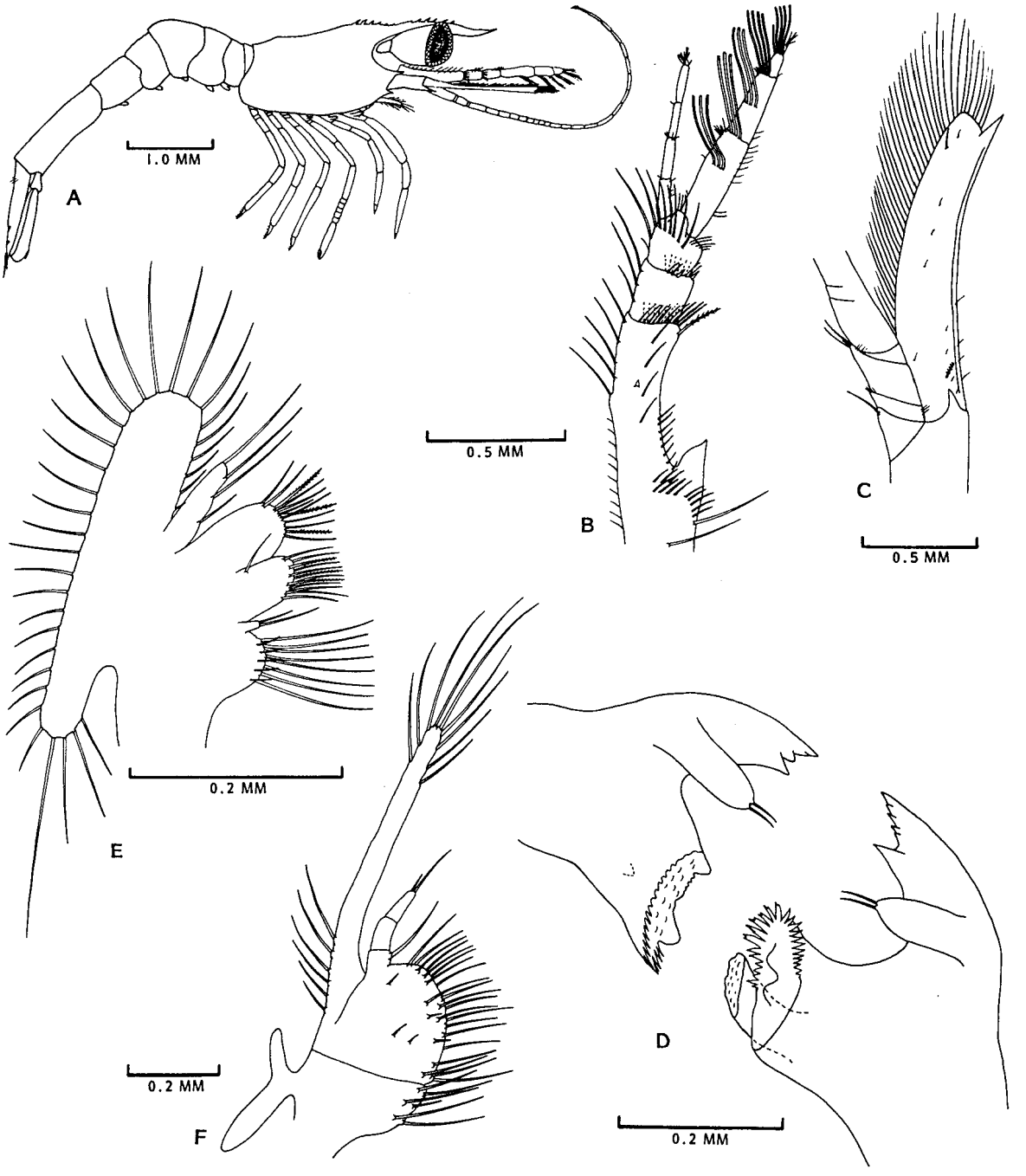
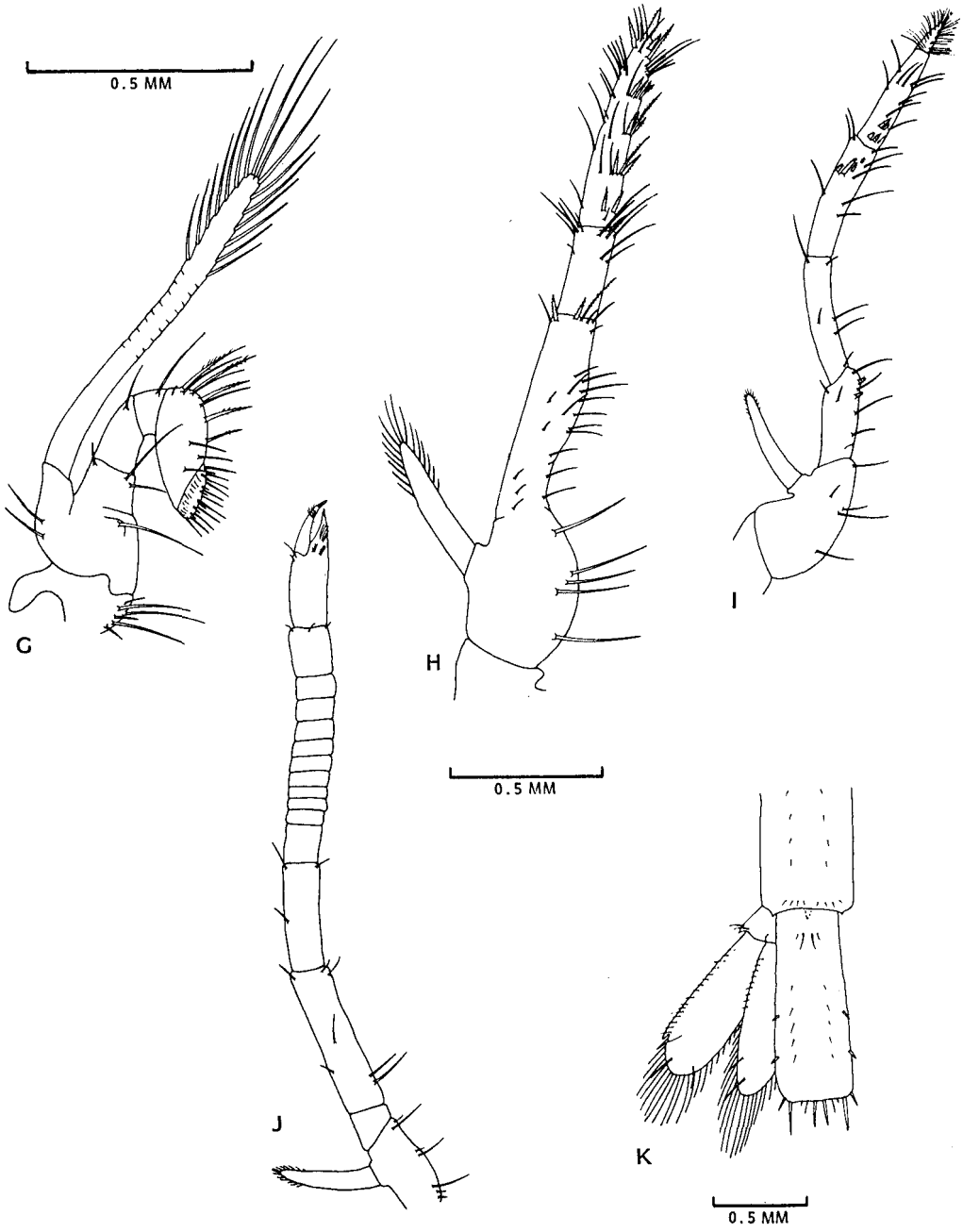


FIGURE 4.—Stage IV zoea of *Pandalus hypsinotus:* (A) whole animal, (B) antennule, (C) antenna, (D) mandible (right and left), (E) maxilla, (F) first maxilliped, (G) second maxilliped, (H) third maxilliped, (I) first pereopod, (J) second pereopod, (K) telson.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faint or distinct near acute tip. No supraorbital spine in this or remaining stages (Figure 4A). Small setae and groups of minute hairs irregularly located on carapace.

ANTENNULE (FIGURE 4B).—Outer flagellum four segmented and longer than in Stage III beginning to acquire slender terminal portion as in adult; five groups of aesthetascs, two groups on first and second segments each and one group on third; groups composed of 3, 3, 3, 4, and 5 aesthetascs. Inner flagellum four segmented, nearly as long as outer flagellum. Rest of antennule similar in shape to Stage III but larger; bears additional spines and setae; lateral projection on proximal segment more pronounced, and ventral spine on proximal segment noticeably smaller than in Stage III.

ANTENNA (FIGURE 4C).—Antennal scale with 32-39 lateral plumose setae and is assuming narrow, slightly curved form of adult; scale bears a few simple setae medially and usually a large seta on inner margin near tip. Inner flagellum not much longer than Stage III, about 3½ times length of scale.

MANDIBLES (FIGURE 4D).—Incisor and molar processes of both mandibles separated by deep cleft, and each mandible has unsegmented palp bearing two setae terminally. Curved lip of right mandible considerably larger than in Stage III.

MAXILLULE.—Similar to Stage III except number of setae somewhat variable. Endopodite usually has one seta but may bear additional small setae. Basipodite has 12 spines and 9-13 setae terminally, 2 or 3 setae subterminally. Coxopodite usually has 15 setae.

MAXILLA (FIGURE 4E).—Exopodite fringed, has 32 plumose setae in addition to plumose seta at proximal end; separated from protopodite by cleft and bears 3 setae along inner margin. Number of setae on endopodite reduced to four. Basipodite bears 12 setae on each lobe; proximal lobe bears additional seta subterminally. Distal lobe of coxopodite reduced in size and bears two setae instead of four as in Stage III; proximal lobe of coxopodite bears eight long and five short setae.

FIRST MAXILLIPED (FIGURE 4F).—Epipodite distinctly bilobed. Protopodite clearly two segmented and bears 6 setae on proximal segment, 26 smaller setae on distal segment. Endopodite three segmented and bears one long seta on first segment and one long and one short setae terminally on third segment. Exopodite bears 6 long plumose setae along proximal outer margin and 9 or 10 natatory setae.

SECOND MAXILLIPED (FIGURE 4G).—Second maxilliped has undergone considerable change from Stage III and now is similar in shape to adult. Endopodite five segmented; terminal segment flattened with many short spinous setae on lateral margins. Epipodite arises from coxopodite and is single lobed.

THIRD MAXILLIPED (FIGURE 4H).—Exopodite considerably reduced. Endopodite heavily setose and spinous. Meropodite slightly enlarged medially; not distinctly segmented from ischiopodite. Basipodite enlarged medially somewhat more than meropodite. Bud of mastigobranchia arises from coxopodite.

FIRST PEREOPOD (FIGURE 4I).—Exopodite reduced as in preceding appendage. Endopodite ends in simple, heavily setose conical dactyl, as in the third maxilliped; ischiopodite articulates somewhat laterally with meropodite. Pereopods of this stage, except fifth pair, bear bud of mastigobranchia. Each pleurobranchia adult in shape and clearly lobulated.

SECOND PEREOPOD (FIGURE 4J).—Exopodite reduced in size as in third maxilliped and first pereopod. Joints appear on carpal segment for first time, 10 or 11 on left and 5-7 on right. Left pereopod slightly longer (about one-tenth) than right pereopod.

THIRD, FOURTH, AND FIFTH PEREOPODS.—Essentially similar to pereopods of Stage III.

PLEOPODS (FIGURE 4A).—Pleopods cleft slightly and without joints or setae.

TELSON (FIGURE 4K).—Lateral margins nearly parallel but spaced slightly wider posteriorly and bear two spines on each margin. Terminal margin straight and bears three pairs of feathered spines, the second pair longest; two

simple setae—one long, one short—occur between first and second pairs of spines. Two pairs of simple setae (inner pair stouter) occur at base of telson and project noticeably at nearly right angles to telson surface (Figure 4A). Both pairs of uropods nearly as long as telson and fully developed; both bear numerous small setae irregularly located on dorsal and ventral surfaces of both pairs in addition to setae figured. Beginning of transverse hinge (diaeresis) of exopodite of uropod faintly evident.

STAGE V ZOEA

Total length of Stage V zoea (Figure 5A) 9.2 mm (range 8.4-10.1 mm, 10 specimens). Numerous small wine-red chromatophores occur primarily on cephalothorax but also along surface of abdomen to base of telson and on dorsal hump of third abdominal segment; large wine-red chromatophore on side of carapace especially pronounced; yellow chromatophores few and minute; occur in head region at base of antennae, on antennules, and on dorsal surface of eyes. Rostrum similar in shape to adult; 15-17 dorsal teeth, in addition to 1 (rarely 2) near acute tip; 4 or 5 ventral teeth. Still no setae between dorsal rostral teeth (Figure 5A).

ANTENNULE AND ANTENNA.—Essentially similar to Stage IV. Inner flagellum of antenna approximately 4 times length of scale.

MANDIBLES.—Mandibles larger but morphology unchanged from Stage IV; mandibular palp row three segmented and bears three or four setae terminally (Figure 5B).

MAXILLULE (FIGURE 5C).—Maxillule adult in shape. Endopodite bears one long seta terminally, sometimes an additional short seta. Basipodite bears 13 spines in two rows along terminal margins: 5 of the spines are relatively long and the remaining 8 short. Seventeen setae of various lengths are distributed terminally and along lateral margin of basipodite. Coxopodite bears five long spinulose setae terminally and a row of five shorter sparsely plumose setae extending proximally; row of fine hairs and a medial seta occur ventrally.

MAXILLA (FIGURE 5D).—Maxilla more adult in shape than previously. Exopodite fringed with 40-44 plumose setae; proximal expansion of exopodite and setae along its inner margin, especially proximal seta, considerably longer than in previous stages. Endopodite shaped as adult; bears three setae. Shape and setation of basipodite and coxopodite similar to Stage IV except distal lobe of basipodite bears 15 setae and proximal lobe of coxopodite bears 7 long and 5 short setae.

FIRST AND SECOND MAXILLIPED.—Similar to Stage IV except endopodite of first maxilliped bears two setae on second segment and three or four on proximal segment.

THIRD MAXILLIPED.—Similar to Stage IV except for a few additional setae, and exopodite is reduced to remnant. Mastigobranchia similar in shape to adult. Arthrobranchia small bud.

FIRST PEREOPOD.—Appendage with few additional setae and spines. Exopodite remnant, distal joint of ischiopodite more pronounced than in Stage IV (Figure 5E). Arthrobranchia minute bud. Mastigobranchia on this and pereopods two to four; adult in shape.

SECOND PEREOPOD.—Exopodite remnant, carpal joints of left and right pereopods 14-16 and 7. No arthrobranchia on this or remaining pereopods.

THIRD, FOURTH, AND FIFTH PEREOPODS.—Distal joints of carpal and basial segments pointed (Figure 5F), no additional joint at basis. Setation essentially as shown in Figure 3J except carpopodite and meropodite each bear a spine.

PLEOPODS (FIGURE 5A).—Pleopods bilobed, segmented, and without setae.

TELSON (FIGURE 5G).—Lateral margins nearly parallel but slightly farther apart at center and bear two spines on each margin. Terminal margin straight; arrangement of spines and setae on margin similar to Stage IV. The two pairs of setae at base of telson noticeably longer than in Stage IV. Transverse hinge of exopodite of uropod complete; numerous small setae located randomly on dorsal and ventral surfaces in addition to those figured.

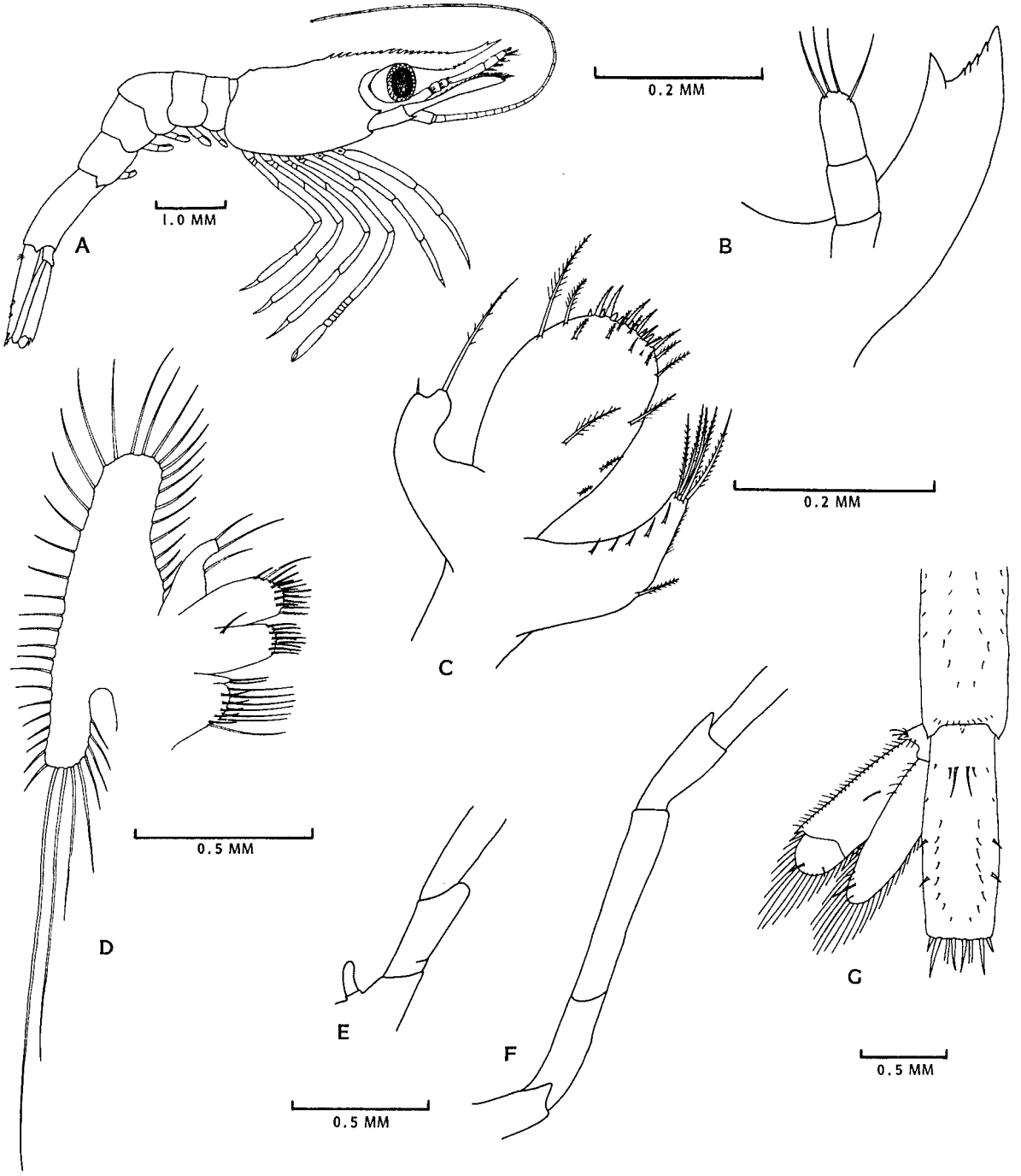

FIGURE 5.—Stage V zoea of *Pandalus hypsinotus:* (A) whole animal, (B) mandibular palp, (C) maxillule, (D) maxilla, (E) first pereopod, (F) fifth pereopod (segmentation only), (G) telson.

STAGE VI ZOEA

Total length of Stage VI zoea (Figure 6A) 10.8 mm (range 10.0-11.8 mm, 10 specimens). General color wine-red, particularly on carapace and pereopods and along ventral abdomen; remainder of telson greenish hue. Most appendages of this stage differ in shape only slightly from those of Stage V and succeeding stages and are not figured in detail. Rostrum with 15-19 dorsal teeth in addition to 1 (usually) but sometimes 2 dorsal teeth near acute tip; 4-7, usually 5, ventral teeth. A seta may occur between two or three dorsal teeth (Figure 6A).

ANTENNULE.—Inner flagellum six segmented (rarely five). Outer flagellum eight segmented; bears seven (rarely eight) groups of three (usually) aesthetascs each.

ANTENNA.—Antennal scale fringed with 40-45 plumose setae; flagellum about 6 times length of scale.

MANDIBULAR PALP.—Three segmented; number of setae variable; setation formula—6-8, 2-3, and 1-3.

MAXILLULE.—Endopodite unchanged from Stage V. Basipodite bears about 20 setae and 13 spines; coxopodite bears 18 setae.

MAXILLA.—Exopodite fringed with 61 or 62 plumose setae. Three setae on endopodite. Setation formula of lobes of basipodite and coxopodite 21-22, 17-19, 2, 11-12.

FIRST MAXILLIPED.—Exopodite has 10 or 11 setae along proximal margin. Setation formula of endopodite 2, 4, 5. Number of setae on protopodite variable—38-61 on basipodite, 7-12 on coxopodite.

SECOND MAXILLIPED.—More setose than in preceding stages; about 50 setae on terminal segment. No podobranchia.

THIRD MAXILLIPED.—No exopodite. Arthrobranchia as two minute rounded buds.

FIRST PEREOPOD.—No exopodite. Arthrobranchia bud at base of each pereopod except fifth.

SECOND PEREOPOD.—No exopodite; carpal joints of left and right pereopods 19 and 7 or 8 respectively. Left and right meropodites with three or four and one or two joints respectively.

THIRD, FOURTH, AND FIFTH PEREOPODS.—Meropodite bears 4-6 spines. Fifth pereopod bears neither bud of arthrobranchia nor epipodite.

PLEOPODS (FIGURE 6B).—All five pairs segmented, biramus, and tipped with setae but nonfunctional. Appendix interna small bud on inner lamella of second and third pleopods only.

TELSON (FIGURE 6C).—Telson shows, for first time, narrow shape similar to adult and bears three pairs of dorsolateral spines. Terminal margin rounded slightly; bears three pairs of feathered spines and a pair of large setae dorsally. Three pairs of stiff setae at base of telson instead of two as in Stage V.

POSTZOEAL STAGES VII-IX

Total length of Stage VII zoea 12.1 mm (range 11.5-12.8 mm, four specimens). Pleopods functional and appendix interna distinct on all pleopods except first pair. Because abdominal propulsion is evident at this stage, it is considered the first postzoeal (megalopa) stage (Williamson 1969). Dorsal rostral spines 19 or 20, 1 or 2 at acute tip; 7 or 8 ventral spines. Seta (usually 1, rarely 2) occurs between each pair of rostral spines. Bud of podobranchia distinct, arises at base of epipodite of second maxilliped; buds of arthrobranchiae on third maxilliped distinct, pointed. Telson bears four pairs of spines along lateral margin, rarely an additional small spine on either margin. Left and right carpal joints of second pereopods 24 or 25 and 10 respectively.

Stages VIII and IX differ only slightly from VII. Total length of Stage VIII zoea 12.4 mm (range 11.1-13.0 mm, four specimens). Gill buds more fully developed in VIII than in VII but not yet lobulated. Left and right carpal joints of second pereopod 28 and 10 or 11 respectively. Total length of Stage IX zoea 13.6 mm (range 13.4-13.8 mm, three specimens). Rostrum with one to three setae between dorsal rostral spines and one to five setae between ventral spines; seta between the two spines at rostral tip. Buds of both podobranchiae and arthrobranchiae nearly lobulated.

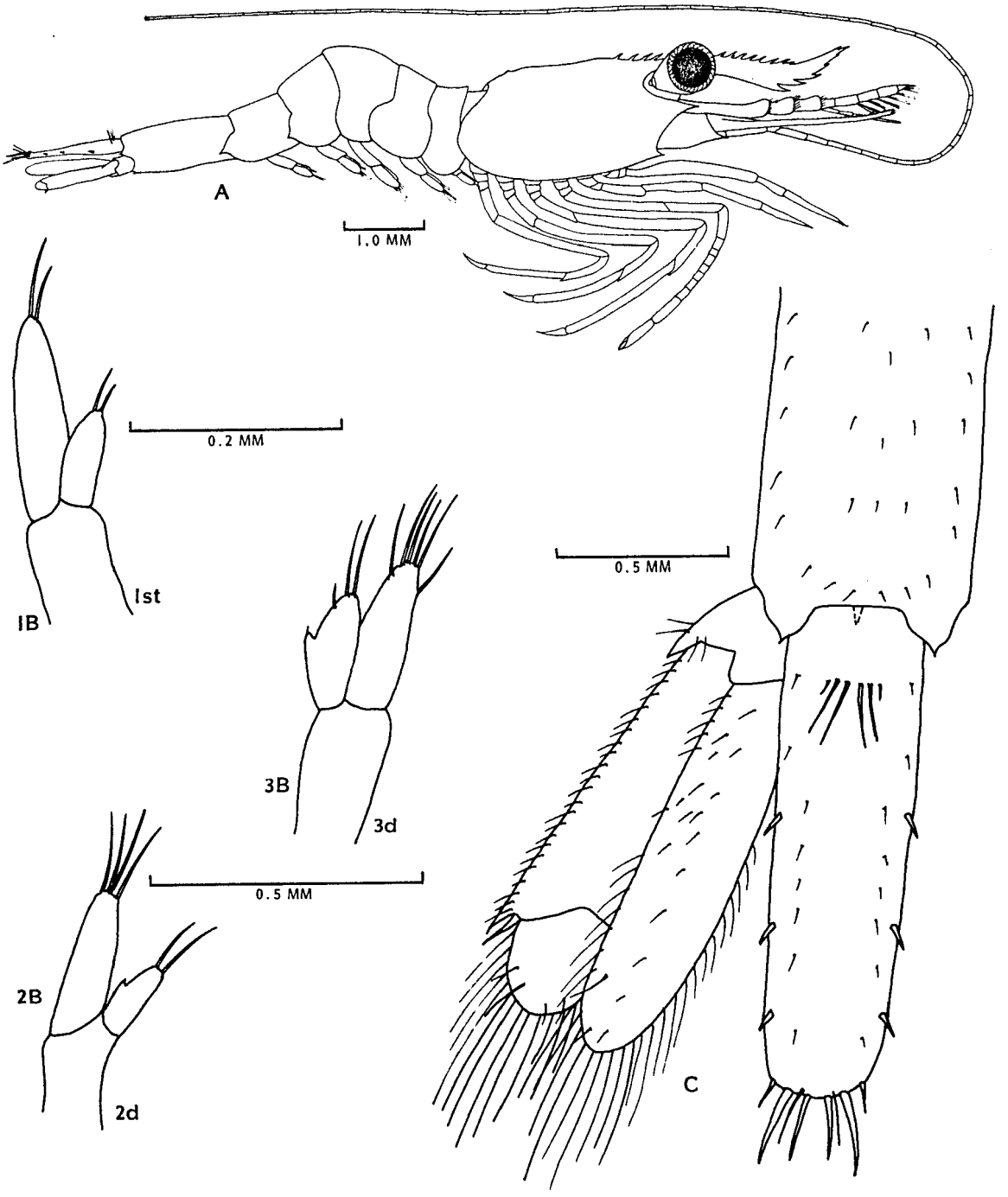

FIGURE 6.—Stage VI zoea of *Pandalus hypsinotus:* (A) whole animal, (B) pleopods (1, 2, and 3), (C) telson.

COMPARISON OF ZOEAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

Berkeley (1930) described and figured the first stage zoeae of *P. hypsinotus* that she reared in the laboratory. She also obtained the probable second and third stages from the plankton, but these were not described. Stage I zoeae reared by Berkeley differed in several respects from mine, but mostly in segmentation and setation of appendages. For instance, Berkeley showed the telson separated from the sixth abdominal segment by a joint whereas I do not. She described the tip of the antennal scale as unsegmented, but my zoeae have the tip divided into six segments. The endopodites of the first and second maxillipeds of her zoeae are unsegmented, and the exopodites of the maxillipeds and first and second pereopods are unjointed at their bases. In my zoeae, the endopodites of the first and second maxillipeds are segmented, and the exopodites of the maxillipeds and first and second pereopods are jointed at their bases. Segmentation of appendages, especially in the early zoeal stages, is most clearly seen in exuviae. Because Berekeley was unable to obtain exuviae from her laboratory-reared specimens, she probably missed seeing the segmentation of most appendages.

Kurata's (1964) description of Stage I zoeae of *P. hypsinotus* was also based on specimens reared in the laboratory; the remaining stages (II-V) he described were obtained from the plankton. The most important differences between Kurata's description and mine are: Stage I—Kurata's zoeae bear a chela on the second pereopod and the antennal scale is four segmented. In my zoeae the chela does not appear until Stage III and the antennal scale is six segmented. Stage II—The tip of the antennal scale is two segmented in Kurata's zoeae but four segmented in mine. Stage III—On Kurata's zoeae, the marginal spines of the telson vary from one to three pairs, and the inner flagellum of the antenna is twice as long as the antennal scale and has 9 or 10 joints. My Stage III zoeae always have two pairs of marginal spines and the inner flagellum of antenna is 3 times the length of the antennal scale and has 19 joints. Stage IV—The telson of Kurata's zoeae decreases in width posteriorly; the inner flagellum of antennule is two segmented; the tip of the first pereopod bears a small chela; and the carapace bears a supraorbital spine. The telson of my Stage IV zoeae increases in width posteriorly; the inner flagellum of antennule is four segmented; the tip of the first pereopod bears a simple dactylopodite in all stages (including adults); and the supraorbital spine occurs only in Stages II and III. Stage V—The telson of Kurata's zoeae bears 6+6 spines terminally; the carpopodites of the second pereopods and the pleopods are without joints; and the carapace still bears a supraorbital spine. In my specimens, the telson bears 3+3 spines terminally; the carpopodites of the left and right second pereopods bear 14-16 and 7 joints respectively; the pleopods are jointed; and the carapace does not bear a supraorbital spine.

The cause for the morphological differences between Kurata's description of the morphology of the zoeae and mine is unknown but apparently is not a result of my zoeae being reared in the laboratory. My zoeae showed no variation in number of zoeal stages and only negligible morphological variation between individuals of the same stage. Also, there were no morphological differences between my zoeae reared in the laboratory and the zoeae of *P. hypsinotus* available from local plankton collections (Stages I-III). The morphological differences between Kurata's zoeae and mine may be due to geographical variation. Berkeley (1930) has shown that pandalid zoeae from the northeast Pacific are further advanced on hatching than those from the Atlantic, although she did not have enough information to compare identical species from both areas. Unfortunately, Kurata's descriptions from Stage II onward were based on specimens from the plankton. Verification of geographical variation in zoeal morphology will be possible only when identification is based upon zoeae of known parentage and the magnitude of variation is established for each stage.

Segmentation of the antennal scale was used by Lebour (1940) as one criterion for classifying the early stages of pandalid zoeae into two groups. The first group includes pandalid species described by various authors as possessing a segmented scale (*Dichelopandalus bonnieri* (Caullery), *Pandalus montagui* Leach, and *P. propinquus* G. O. Sars). The second group includes pandalid species described by Berkeley (1930) as possessing an unsegmented scale (*P. stenolepis* Rathbun, *P. hypsinotus, P. danae,* and *P. platyceros*). Price and Chew (1972) showed Lebour's grouping to be invalid for *P. platyceros*. Kurata (1964) described zoeae of *P. hypsinotus* as hav-

ing a segmented scale. Laboratory-reared Stage I zoeae known by me to possess a segmented scale are *Pandalopsis dispar, Pandalus stenolepis, P. goniurus, P. borealis, P. danae, P. hypsinotus,* and *P. platyceros.* Berkeley obviously failed to recognize the segmented scales on her specimens. Therefore, Price and Chew's (1972) suggestion that Lebour's grouping for classifying the early stages of pandalid zoeae using segmentation of the antennal scale be disregarded is valid.

In most Decapoda, the development of functional pleopods provides a convenient and clear distinction between the zoeal and postzoeal stages because it is accompanied by several other abrupt changes in morphology, such as loss or reduction of some or all of the thoracic exopodites and changes in shape and body proportions. In the Pandalidae, however, there is not always an abrupt metamorphosis at this molt. Pike and Williamson (1964) discussed how in *P. montagui* the pleopods may become fully functional before the exopodites on the pereopods show any reduction; in *P. danae* the exopodites on the pereopods and the third maxilliped degenerate before the pleopods become functional; and in *P. kessleri* Czernaivski the exopodites on the pereopods never become functional. In my zoeae the development of functional pleopods occurred at Stage VII, but other morphological changes normally associated with postzoeal metamorphosis occurred earlier, especially at the molt to Stage IV. Morphological changes that occurred at the molt to Stage VI are reduction of thoracic exopodites; loss of supraorbital spines; changes in color; changes in shape of rostrum, mandibles, and second maxilliped; and segmentation of carpopodite of the second pereopod. Depending upon one's definition of "megalopa," it may be valid to consider Stage VII of *P. hypsinotus* as the megalopa; or one may consider stages IV through VII are all megalopal or the term "megalopa" is not strictly applicable to *P. hypsinotus.*

In addition to the morphological changes noted above, abbreviated development of zoeae of *P. hypsinotus* is also indicated by the occurrence of thoracic exopodites on pereopods 1 and 2. In contrast, most Pandalidae without abbreviated development have thoracic exopodites on pereopods 1-3. A notable exception is zoeae of *P. platyceros,* which have thoracic exopodites on pereopods 1-3 but only four zoeal stages and 8+8 telson setae in Stage I rather than the usual 7+7. Another feature of abbreviated development in *P. hypsinotus* is the proximal extension and occurrence of 17 setae on the exopodite of the maxilla in Stage I. Usually the exopodite of the maxilla in Stage I of the Caridea has no proximal extension and only five setae, as in the protozoea of the Peneidea and most British Pandalidae (Lebour 1940; Gurney 1942). The abbreviated development of zoeae of *P. hypsinotus* agrees with the findings of Berkeley (1930), who noted that zoeae of most Pandalidae of the northeast Pacific tend to be more developed when they hatch than is normal for Caridea.

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