LARVAL MORPHOLOGY OF *PANDALUS TRIDENS* AND A SUMMARY OF THE PRINCIPAL MORPHOLOGICAL CHARACTERISTICS OF NORTH PACIFIC PANDALID SHRIMP LARVAE

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ABSTRACT

Larval stages I-VII of *Pandalus tridens* from plankton of lower Cook Inlet, Alaska, are most similar morphologically to larvae of *P. borealis*, *P. goniurus*, *P. jordani*, and *P. stenolepis* from the North Pacific Ocean. Larvae of *P. tridens* are distinguished from larvae of *P. borealis*, *P. goniurus*, and *P. jordani* by the shape of the rostrum and antennal scale, and spination of the abdominal somites. Larvae of *P. tridens* differ from larvae of *P. stenolepis* by shape of the carapace, abdominal somites, and telson; length of the antennal flagellum and rostrum; and setation of the antennal scale. Differences in larval morphology support classification of *P. tridens* as a species rather than a subspecies of *P. montagui*. A summary of the principal morphological characteristics of the described larvae of pandalid shrimp found in the North Pacific Ocean is provided.

In 1976, the Northwest and Alaska Fisheries Center Auke Bay Laboratory of the National Marine Fisheries Service and the Alaska Department of Fish and Game conducted a survey to determine the seasonal distribution of larvae of king crab and pandalid shrimp in the Kachemak Bay-lower Cook Inlet area (Haynes[2]). During the survey, Stages I-VII zoeae of *Pandalus tridens* (= *P. montagui tridens* Rathbun 1902) were captured in plankton tows in lower Cook Inlet. Except for Stage I, zoeae of *P. tridens* have not been described in the literature. In this report I describe and illustrate each of the seven zoeal stages captured and compare my descriptions with those of pandalid shrimp zoeae given by other authors. I also discuss the evidence from larval morphology that supports raising the subspecies, *P. montagui tridens*, to full species status, *P. tridens* Rathbun 1902. A summary of the principal morphological characteristics of described pandalid shrimp larvae of the North Pacific Ocean is also given.

METHODS

During the 1976 survey, plankton was collected by hauling 61 cm bongo samplers vertically from about 1 m above the ocean bottom to the surface at a velocity of slightly <1 m/s. Nets with 0.333 mm mesh and cod end jars with 0.571 mm mesh were used. Zoeae of *P. tridens* were collected in water 120-160 m deep about 16 km west of the Kenai Peninsula in lower Cook Inlet.

The terminology, methods of measurement, techniques of illustration, and nomenclature of gills and appendages are those used by Haynes (1979). Identification of the zoeae is based on description of Stage I zoeae hatched from known parentage by Ivanov (1971) and undescribed Stage I specimens hatched from known parentage by Ethelwyn Hoffman of the Auke Bay Laboratory's staff. Only those morphological characteristics useful for readily identifying each stage are given. For clarity, setules on setae are usually omitted from the figures, but spinulose setae are shown.

STAGE I ZOEA

Total length of Stage I zoea (Figure 1A) 3.2 mm (range 3.1-3.5 mm; 6 specimens). Rostrum slender, somewhat sinuate, without teeth, about two-thirds length of carapace, and projects horizontally. Carapace with small, somewhat angular dorsal prominence at base of rostrum and smaller

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[2]Haynes, E. 1977. IV Summary status on the distribution of king crab and pandalid shrimp larvae in Kachemak Bay-lower Cook Inlet, Alaska, 1976. *In* L. L. Trasky, L. B. Flagg, and D. C. Burbank (editors), Environmental studies of Kachemak Bay and lower Cook Inlet, vol. 4, 52 p. Alaska Dep. Fish Game, Anchorage.

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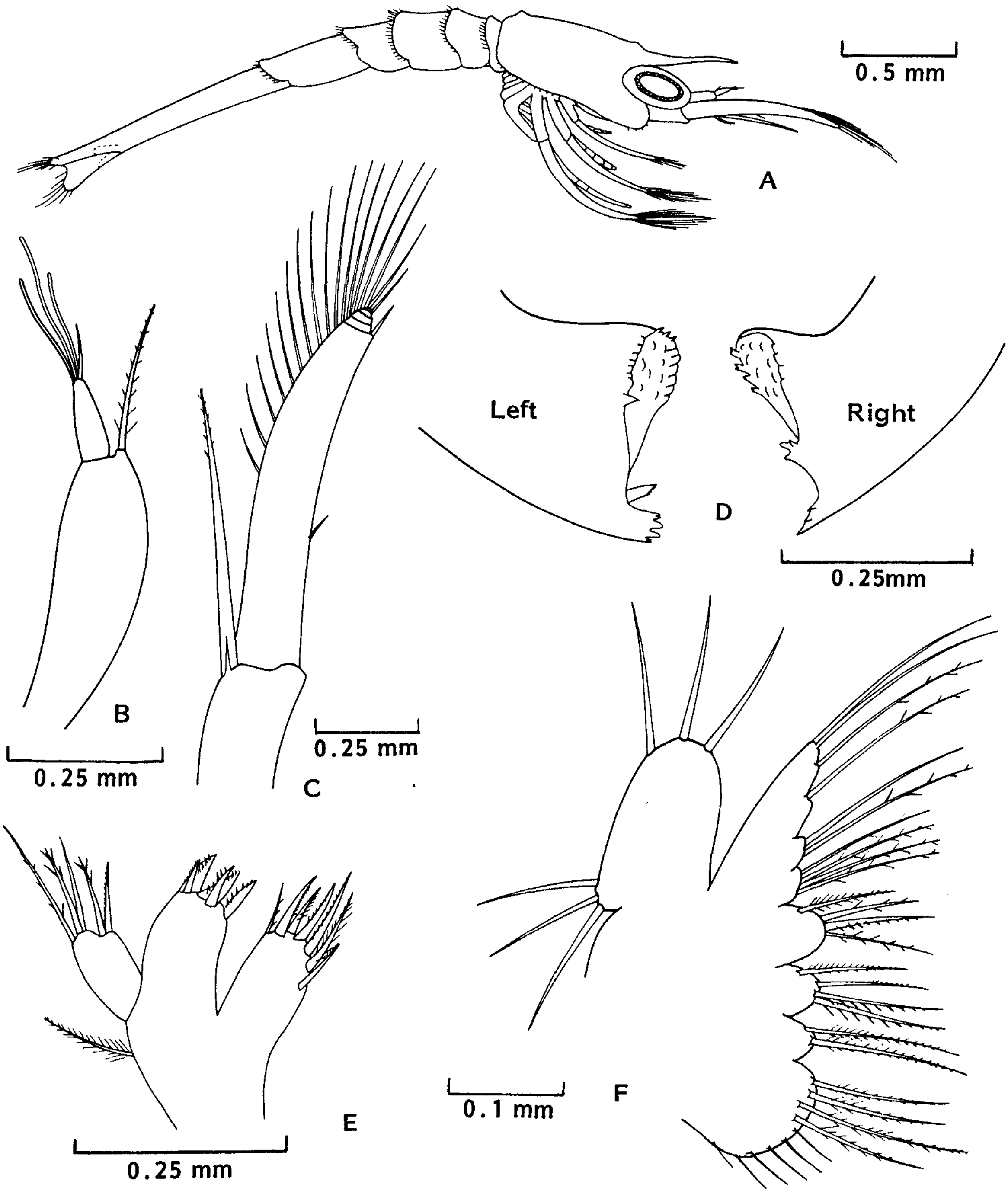
rounded prominence near posterior edge. These two prominences occur in all seven zoeal stages. Pterygostomian spines present, but minute and usually hidden by sessile eyes. Three to four minute denticles on ventral margin of carapace immediately posterior to pterygostomian spine, and about 12 somewhat larger denticles along posteroventral margin of carapace. Denticles in Stages I-III, but rarely in Stage IV. Denticles vary in number among stages and among individuals in



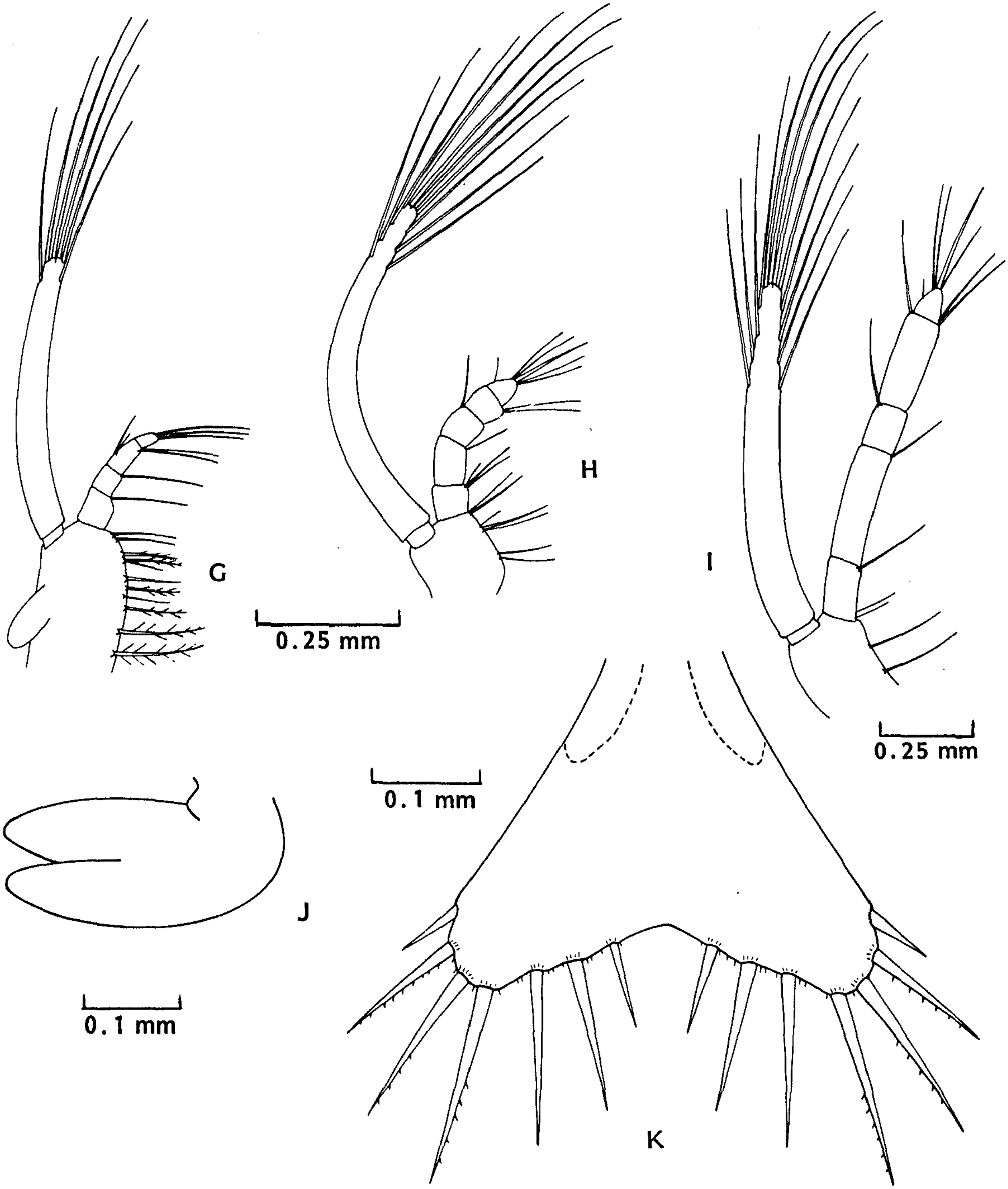


FIGURE 1.—Stage I zoea of *Pandalus tridens*: A, whole animal, right side; B, antennule, dorsal; C, antenna, ventral; D, mandibles (left and right), posterior; E, maxillule, dorsal; F, maxilla, dorsal; G, first maxilliped, lateral; H, second maxilliped, lateral; I, third maxilliped, lateral; J, second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

each stage. Posterior margins of abdominal somites fringed with spines.

ANTENNULE (Figure 1B).—First antenna, or antennule, has a simple, unsegmented, tubular basal portion; plumose seta terminally; and terminal 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 spiniform, unsegmented, about three-fourths length of scale, and spinulose distally. Protopodite bears spinous seta at base of flagellum, but no spine at base of scale. Antennal scale distally divided into four joints, fringed with 17 heavily plumose setae along terminal and inner margins. Distinct seta on outer margin at base of terminal segments; another seta on outer margin, near the protopodite.

MANDIBLES (Figure 1D).—Without palps in this stage and all later zoeal stages examined. Incisor process of left mandible has six teeth in contrast to triserrate incisor process of right mandible. Left mandible bears movable premolar denticle (lacinia mobilis) and subterminal tooth only on left mandible in all zoeal stages examined.

MAXILLULE (Figure 1E).—First maxilla, or maxillule, bears coxal and basial endites and an endopodite. Proximal lobe (coxopodite) has seven spinulose spines terminally. Median lobe (basipodite) bears five spinulose spines and a large setose seta proximally. Endopodite originates from lateral margin of basipodite and has three terminal and two subterminal spines; two of the spines have especially long spinules.

MAXILLA (Figure 1F).—Bears platelike exopodite (scaphognathite) with six long plumose setae: three on distal margin and three on proximal margin. Endopodite has 10 nonplumose setae: 7 bear distinct setules. Basipodite and coxopodite bilobed. Basipodite bears four setae on each lobe; each seta has distinct pattern of setules. Coxopodite bears 12 setae: 2 on distal lobe and 10 on proximal lobe; 6 distal setae of coxopodite somewhat plumose, remaining 6 setae have few, if any, setules.

FIRST MAXILLIPED (Figure 1G).—Most setose of natatory appendages. Protopodite not segmented, bears 11 setae (7 of them spinulose). Endopodite distinctly four-segmented; setation formula 3, 4, 1, 1. Exopodite is long slender ramus, segmented at base; exopodite bears two terminal and four lateral natatory setae. Epipodite a single lobe.

SECOND MAXILLIPED (Figure 1H).—Protopodite not segmented; bears seven sparsely plumose setae. Endopodite distinctly five-segmented; fourth segment expanded somewhat laterally; setation formula 5, 2, 1, 1, 3. Exopodite with two terminal, eight lateral natatory setae. No epipodite.

THIRD MAXILLIPED (Figure 1I).—Protopodite unsegmented, bears two setae. Endopodite distinctly five-segmented, about the same length as exopodite; setation formula 5, 3, 1, 1, 3. Exopodite has 2 terminal and 10 lateral natatory setae. No epipodite.

PEREOPODS.—Poorly developed, not segmented, directed under body somewhat anteriorly (Figure 1A). First three pairs biramous (second pereopod shown in Figure 1J), last two pairs uniramous and slightly smaller than pairs 1-3. All pereopods without setae.

PLEOPODS.—Absent until Stage IV.

TELSON (Figure 1K).—Continuous with sixth abdominal somite; slightly emarginate distally; bears seven pairs of densely plumose setae. Fourth pair of setae longest: length about one-half maximum width of telson. Minute spinules at base of each seta except lateral pair. A few larger spinules on distal margin between bases of four inner pairs. Enclosed uropods visible. No anal spine.

STAGE II ZOEA

Total length of Stage II zoea (Figure 2A) 4.2 mm (range 3.9-4.6 mm; 5 specimens). Rostrum without teeth, sinuate, projects somewhat dorsally. Carapace bears two prominent, supraorbital spines, one on each side of carapace; antennal and pterygostomian spines clearly visible. All zoeal stages examined except Stage I bear supraorbital, antennal, and pterygostomian spines. Epipodite slightly larger than in Stage I, but not bilobed. No pleurobranchiae. Spines on posterior margins of abdominal somites similar in size and number to spines in Stage I.

ANTENNULE (Figure 2B).—Three-segmented; bears large lateral flagellum and smaller inner flagellum on terminal margin. Inner flagellum unsegmented, conical, and has one long spine terminally. Outer flagellum has five aesthetascs of various lengths and one plumose seta. Proximal segment bears four setae laterally near base, single seta subdistally, and two setae distally. Second segment has two setae distally. Distal segment has four plumose setae laterally near inner flagellum and has small seta laterally and subdistally.

ANTENNA (Figure 2C).—Flagellum styliform, about one-third length of scale. Antennal scale about 5½ times as long as wide and fringed along distal and inner margins with 22 long, thin plumose setae. Antennal scale still divided distally into four joints; bears two setae on lateral margin: one at base of proximal joint, one proximally. Protopodite bears spine at base of flagellum but no spine at base of scale.

MANDIBLES (Figure 2D).—Incisor processes of both mandibles more pronounced and have more teeth than in Stage I. Molar processes somewhat more developed than in Stage I, especially forward lip of truncated end.

MAXILLULE.—Similar in shape to maxillule of Stage I, except coxopodite and basipodite each bear additional spine.

MAXILLA.—Shape similar to Stage I maxilla, except scaphognathite is slightly longer proximally, bears 9-11 marginal plumose setae, and large plumose seta at proximal end. Endopodite same as endopodite of Stage I. Lobes of basipodite bear either 6 + 6 or 7 + 5 setae; lobes of coxopodite bear 3 + 11 or 3 + 12 setae.

FIRST MAXILLIPED (Figure 2E).—Epipodite of first maxilliped longer than in Stage I. Setation formula of endopodite 3, 2, 1, 3. Protopodite unsegmented, bears about 20 setae.

SECOND MAXILLIPED.—Same as Stage I, except each segment of endopodite may have an additional seta.

THIRD MAXILLIPED.—Dactylopodite (Figure 2F) narrower, longer than in Stage I.

FIRST AND SECOND PEREOPODS (second pereopod shown in Figure 2G).—Endopodites of first and second pereopods functionally developed, five-segmented and terminating in simple conical dactylopodite. Exopodite of first pereopod is longest exopodite of pereopods. Exopodites of first and second pereopods have two terminal and eight lateral natatory setae.

THIRD PEREOPOD (Figure 2H).—Exopodite and endopodite nonfunctional but segmented at base. Endopodite tipped by four simple setae.

FOURTH AND FIFTH PEREOPODS (Figure 2I).—Poorly developed, unsegmented, and without exopodites.

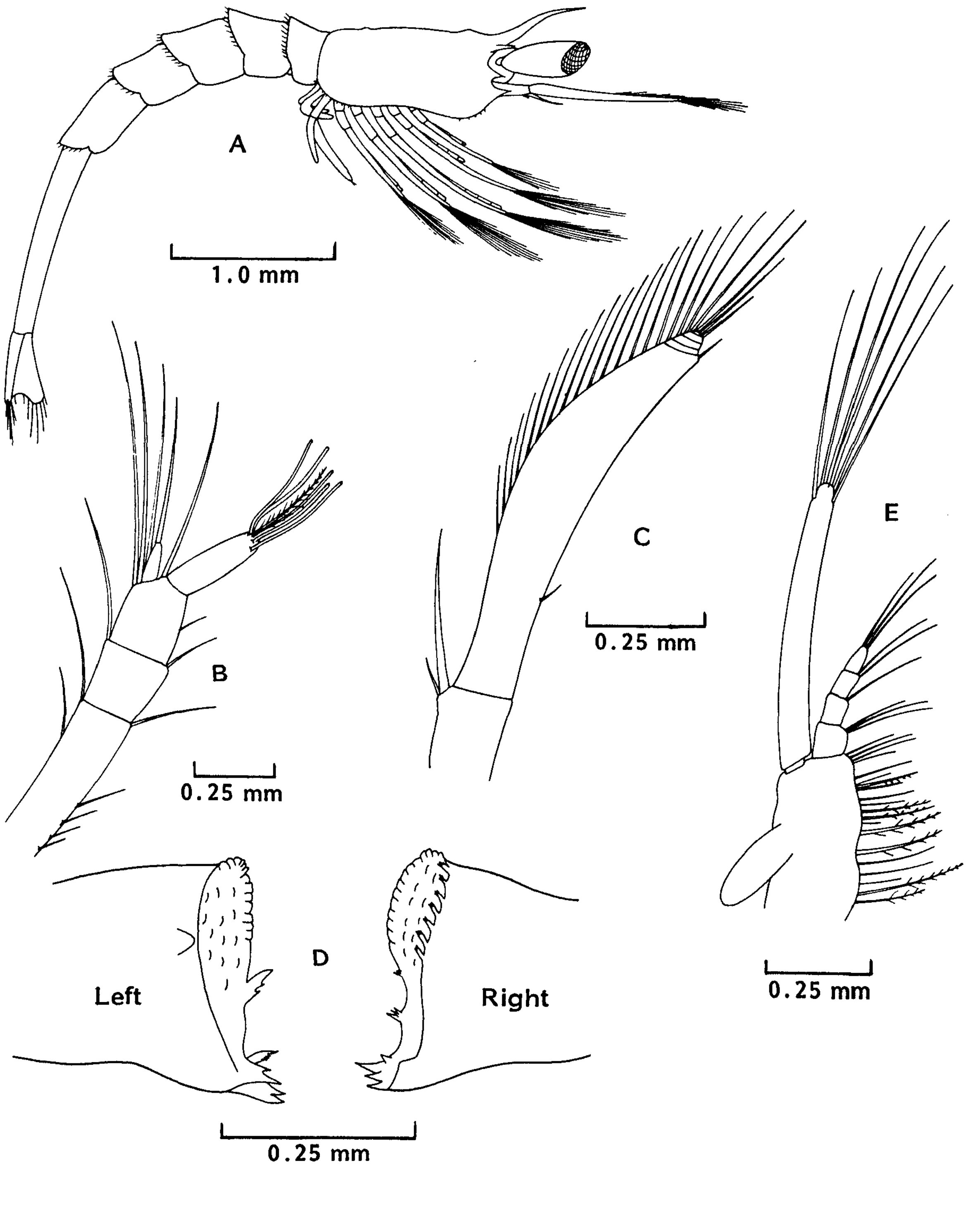
TELSON (Figure 2J).—Telson similar in shape to Stage I, but distinctly segmented from sixth abdominal somite. Telson has eight pairs of densely plumose setae. Uropods still enclosed. Anal spine present but minute.

STAGE III ZOEA

Total length of Stage III zoea 5.9 mm (range 5.6-6.3 mm; 7 specimens). No change in shape of rostrum from Stage II. Spines along anteroventral and posteroventral margin of carapace still present, but minute and fewer than in Stage II. Epipodite on first maxilliped still only gill structure present. Spines on posterior margins of abdominal somites smaller than in Stage II.

ANTENNULE.—Similar in shape to antennule of Stage II but bears several additional setae; a spine projects downward from ventral surface of proximal segment. From this stage on, change in antennule slight: inner flagellum lengthens, more setae on antennule.

ANTENNA.—Flagellum styliform, two-segmented, still only about one-third length of scale. Antennal scale about six times as long as wide; two complete joints at tip (Figure 3A). Terminal spine on lateral margin of scale does not quite reach tip of scale. Protopodite bears small spine at base of flagellum and minute projection at base of scale.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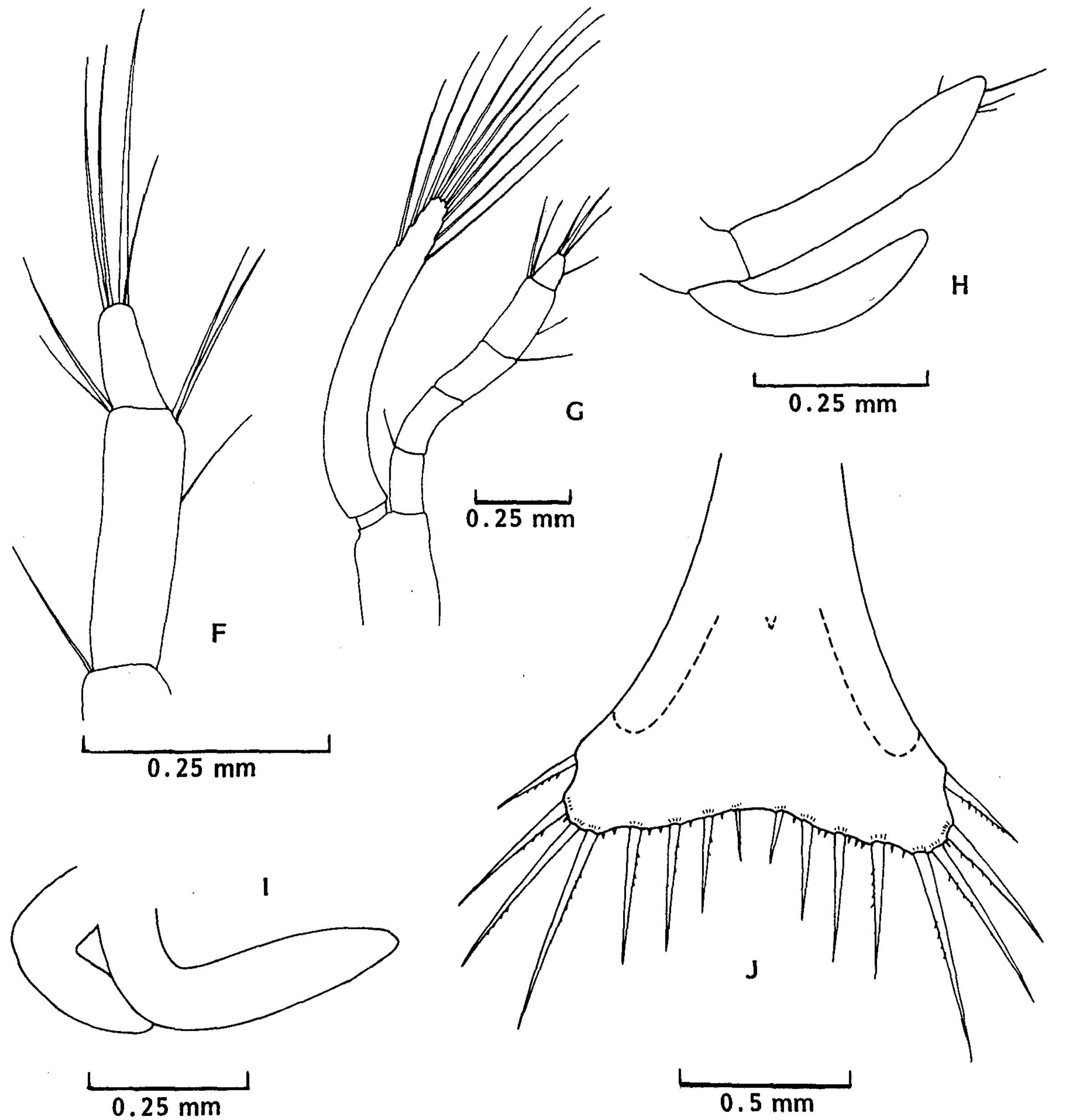

FIGURE 2.—Stage II zoea of *Pandalus tridens*: A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles (left and right), posterior; E, first maxilliped, lateral; F, third maxilliped (distal segments), lateral; G, second pereopod, lateral; H, third pereopod, lateral; I, fourth and fifth pereopods, lateral; J, telson, dorsal.

FIRST AND SECOND PEREOPODS.—Essentially same as Stage II, except exopodite of second pereopod bears additional pair of setae.

THIRD PEREOPOD (Figure 3B).—Functional, five-segmented. Exopodite bears two terminal and eight lateral natatory setae.

FOURTH PEREOPOD (Figure 3C).—Functional. Dactylopodite tipped by spine and simple seta.

FIFTH PEREOPOD.—Similar to fourth pereopod except terminal spine not as fully developed.

TELSON (Figure 3D).—Uropods free. Endopodite

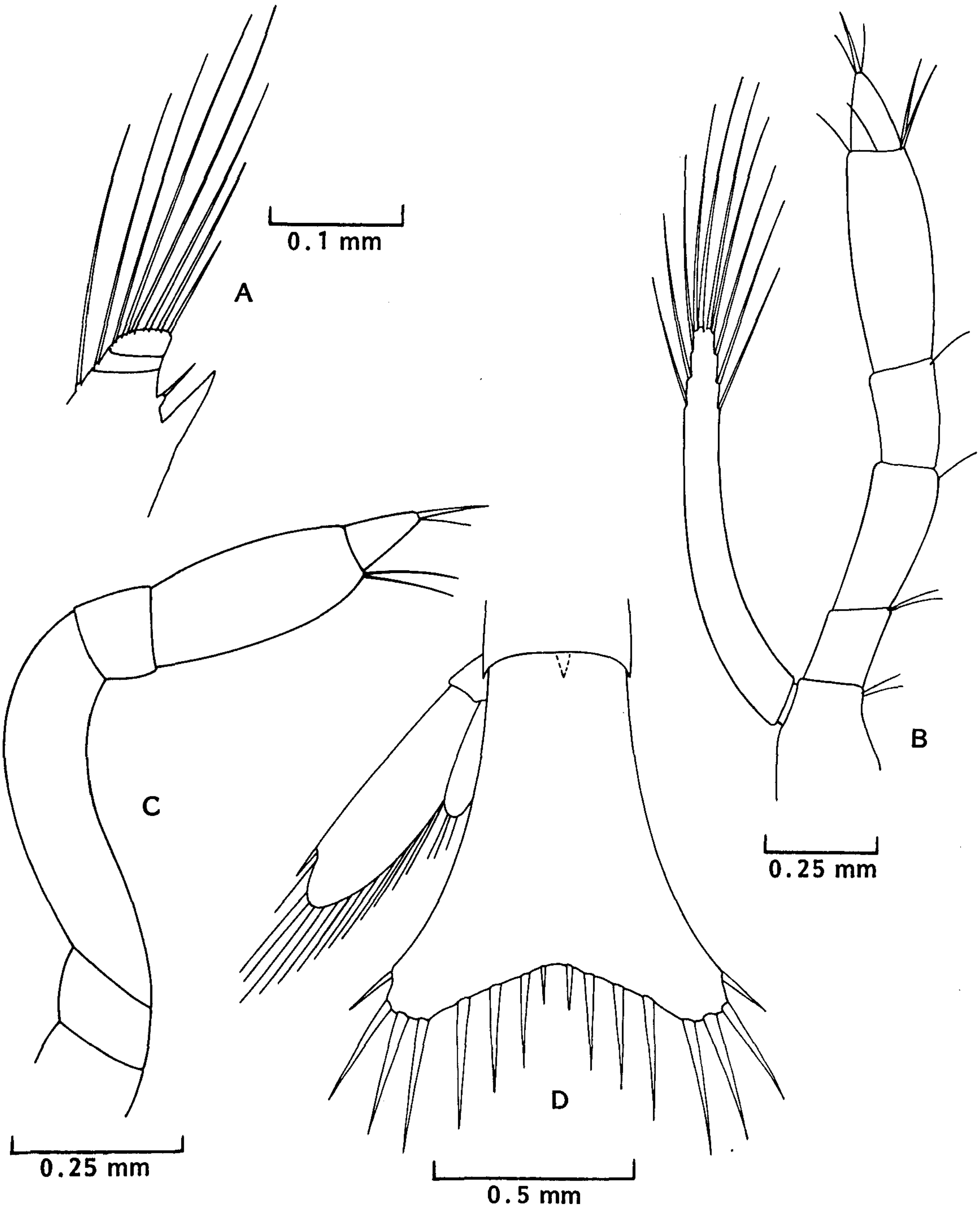

FIGURE 3.—Stage III zoea of *Pandalus tridens*: A, antennal scale (distal portion), ventral; B, third pereopod, lateral; C, fourth pereopod, lateral; D, telson, dorsal.

undeveloped, less than one-half length of exopodite, bears three setae distally. Anal spine clearly visible.

STAGE IV ZOEA

Total length of Stage IV zoea 7.8 mm (range 7.0-8.4 mm; 9 specimens). Rostrum (Figure 4A) projects horizontally but curves slightly downward at tip, bears two teeth at base. A few minute spines still on anteroventral and posteroventral margins of carapace. Epipodite of first maxilliped bilobed. Posterior margins of abdominal somites fringed as in Stage III.

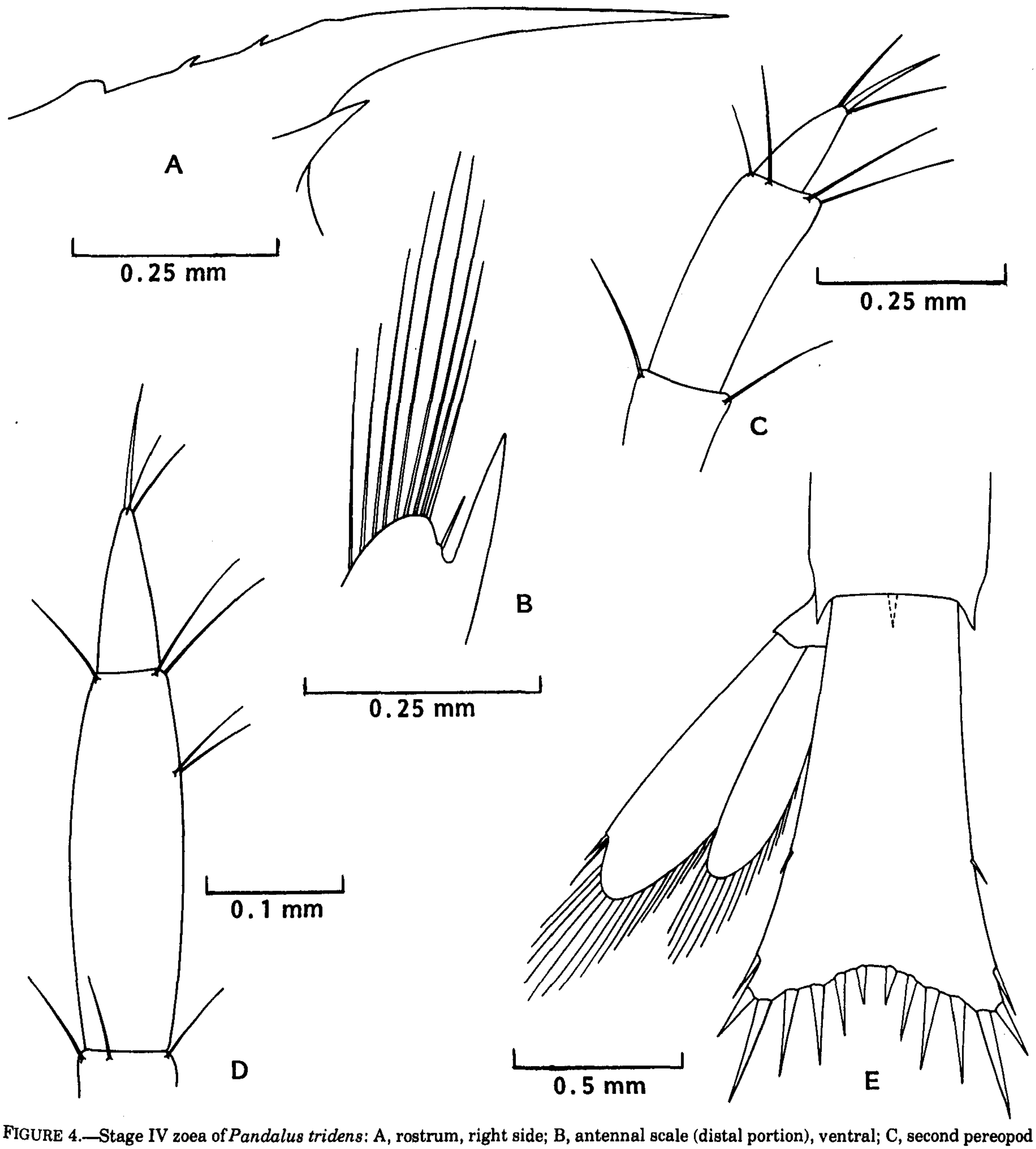

FIGURE 4.—Stage IV zoea of *Pandalus tridens*: A, rostrum, right side; B, antennal scale (distal portion), ventral; C, second pereopod (terminal segments), lateral; D, third pereopod (distal segments), lateral; E, telson, dorsal.

ANTENNA.—Flagellum still styliform, only about one-third length of scale. Antennal scale about seven times as long as wide, no joints at tip; terminal spine projects considerably beyond tip of scale (Figure 4B). Protopodite bears small spine at base of flagellum and antennal scale.

SECOND PEREOPOD.—Distal joint of propodite (Figure 4C) widened, projects distally in later stages.

THIRD PEREOPOD.—Dactylopodite lengthened (Figure 4D); exopodite has an additional pair of setae.

PLEOPODS.—Minute buds.

TELSON (Figure 4E).—Endopodite of uropod about three-fourths length of exopodite and fringed with about 15 setae. Lateral margins of telson widen posteriorly, have two spines each. Distal margin emarginated, bears 6 + 6 spines.

STAGE V ZOEA

One specimen with rostrum broken and exopodites of third pereopods missing. Posterior margins of abdominal somites minutely fringed.

ANTENNA.—Flagellum slightly rounded at tip, two-thirds length of antennal scale, five-segmented.

SECOND PEREOPOD.—Chela partially formed; distal joint of propodite projected somewhat distally, tipped by spine (Figure 5A).

SECOND PLEOPODS.—About one-fourth height of second abdominal somite.

TELSON (Figure 5B).—Uropods fully developed, no evidence of transverse hinge. Lateral margins somewhat parallel but widen slightly posteriorly.

STAGE VI ZOEA

Total length of Stage VI zoeae 10.7 mm (range 10.2-11.2 mm; 2 specimens). Rostrum (Figure 6A) about one-third length of carapace, projects horizontally, bears six teeth dorsally, tip bears hump indicating future location of distal tooth. A few minute spines on posterior margin of fifth somite.

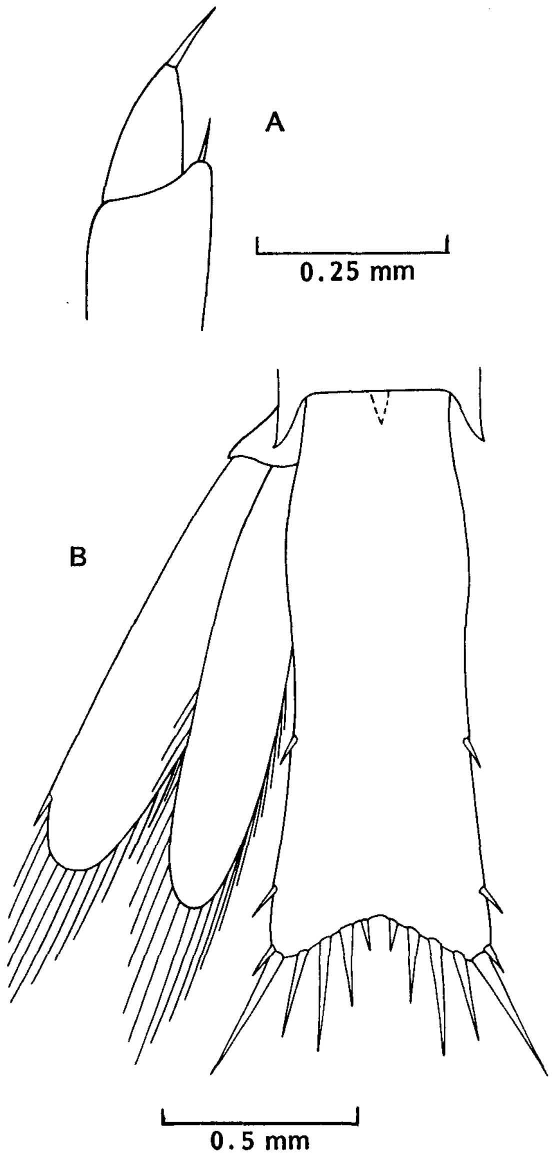

FIGURE 5.—Stage V zoea of *Pandalus tridens*: A, second pereopod (distal segments), lateral; B, telson, dorsal.

Bud of epipodite on second maxilliped. Pleurobranchiae at base of all five pereopods.

ANTENNA.—Inner flagellum nearly as long as antennal scale, about 25-segmented.

SECOND PEREOPOD.—Chela well formed (Figure 6B). Terminal spines of propodite and dactylopodite each bear single spine at base.

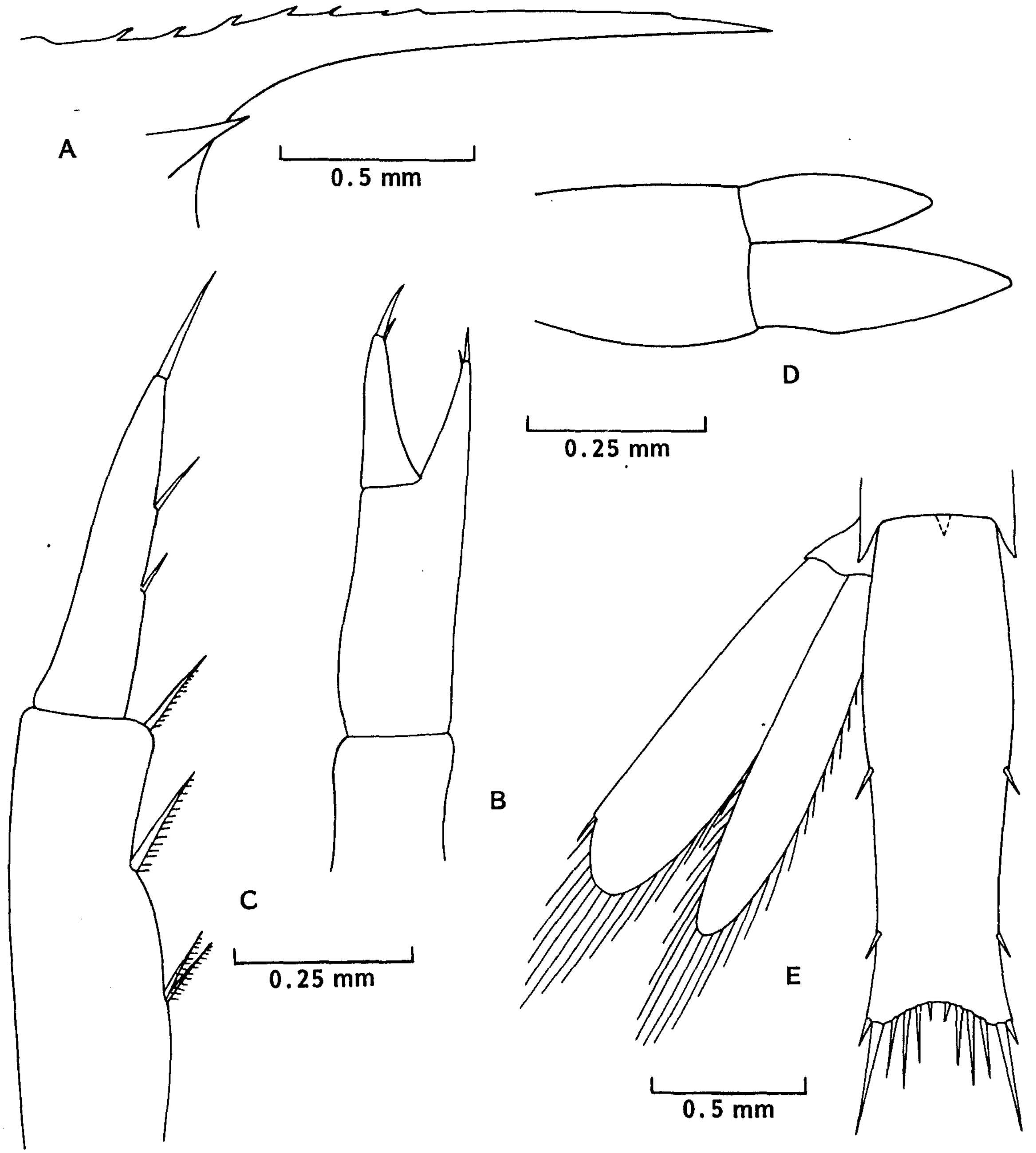

FIGURE 6.—Stage VI zoea of *Pandalus tridens*: A, rostrum, right side; B, second pereopod (distal segments), lateral; C, third pereopod (distal segments), lateral; D, second pleopod, lateral; E, telson, dorsal.

THIRD PEREOPOD.—Dactylopodite well developed; has two distinct spines along inner margin (Figure 6C).

PLEOPODS.—Pleopods segmented at base; no setae or appendices internae. Second pleopod about one-half height of second abdominal somite (Figure 6D).

TELSON (Figure 6E).—Lateral margins somewhat parallel, but not as much as in Stage VII; each margin bears two spines. Posterior margin slightly emarginated and bears 6 + 6 spines distally. Transverse hinge of exopodite of uropod not evident.

STAGE VII ZOEA

Total length of Stage VII zoea 13.0 mm (1 specimen). Rostrum (Figure 7A) curved slightly upward, slightly less than one-half length of carapace; bears seven teeth dorsally, tooth near tip not developed. No change in number of gill structures from Stage VI.

SECOND PEREOPOD.—Terminal spine of dactylopodite may bear two spines at base instead of one spine, as in Stage VI; carpopodites unsegmented.

PLEOPODS.—Exopodite and endopodite of pleopods tipped by a few setae; no appendices internae. Second pleopod (Figure 7B) about two-thirds height of second abdominal somite.

TELSON (Figure 7C).—Lateral margins essentially parallel, each bears two spines. Transverse hinge of exopodite of uropod partially complete.

COMPARISON OF LARVAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

The only previously published description of larvae of *Pandalus tridens* is that of Ivanov (1971) who described and figured Stage I zoeae reared from known parentage. My description of the

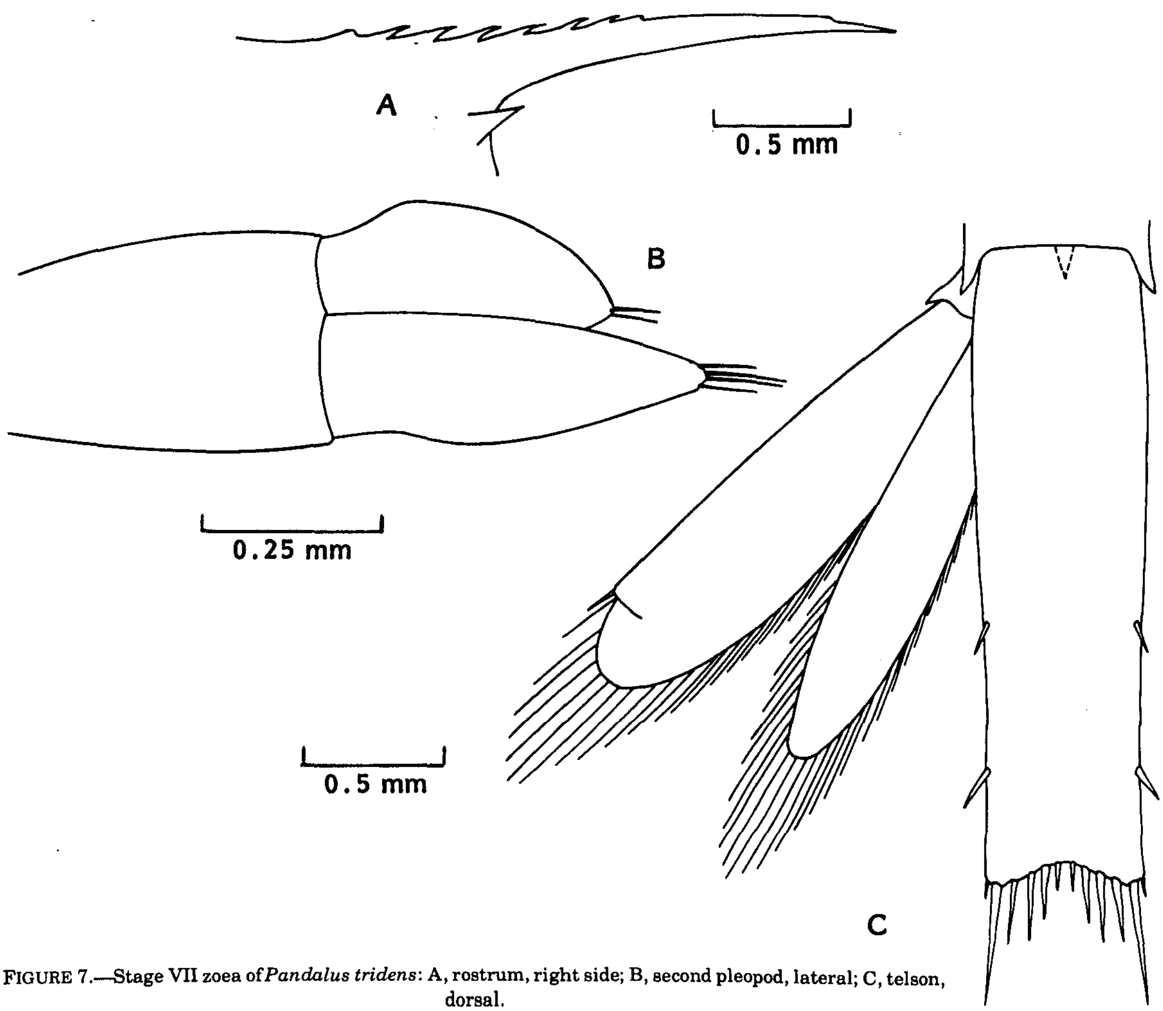

FIGURE 7.—Stage VII zoea of *Pandalus tridens*: A, rostrum, right side; B, second pleopod, lateral; C, telson, dorsal.

Stage I zoeae agrees in all essential aspects with Ivanov's description.

Larvae of *P. tridens* are similar to larvae of *P. borealis*, *P. goniurus*, *P. jordani*, and *P. stenolepis*: all have poorly developed pereopods and exopodites on pereopods 1-3 in Stage I. Larvae of *P. borealis* (described by Haynes [1979]), and *P. goniurus* (described by Haynes [1978]), and *P. jordani* (described by Modin and Cox [1967]) are readily distinguishable from larvae of *P. tridens* by the lack of spines on the posterior margins of the abdominal somites and by the rostrum, which in early stages is spiniform and projects downward rather than being sinuate and projecting upwards as in *P. tridens*. In addition, the antennal scales of larvae of *P. borealis*, *P. goniurus*, and *P. jordani* are markedly shorter and wider than in larvae of *P. tridens*.

Zoeae of *P. tridens* described in this report are most similar to zoeae of *P. stenolepis* described by Needler (1938), especially in Stage I. In Stage I zoeae of both species the carapace bears denticles, the abdominal somites are fringed with spines, and the antennal scale is relatively long and narrow. The Stage I zoeae of these species differ: the carapace and abdominal somites of Stage I zoeae of *P. stenolepis* are flared laterally, and the antennal scale bears 9-12 plumose setae; the carapace and abdominal somites of Stage I zoeae of *P. tridens* are not flared, and the antennal scale bears 17 plumose setae. Also, the telson of Stage I zoeae of *P. stenolepis* is considerably wider and the posterior margin more emarginate than the telson of Stage I zoeae of *P. tridens*. Other morphological differences between zoeae of the two species are the antennal flagellum and rostrum. The antennal flagellum in all zoeal stages of *P. stenolepis* is longer than the antennal scale; the antennal flagellum of zoeae of *P. tridens* remains shorter than the antennal scale through at least Stage V. The rostrum of *P. stenolepis* zoeae is as long as, or longer than, the carapace and bears teeth as early as Stage II; the rostrum of *P. tridens* zoeae remains shorter than the carapace as late as Stage VII and does not bear teeth until Stage IV.

The morphology of Stages I-VII zoeae of *P. tridens* from lower Cook Inlet confirms the opinion (Ivanov 1971; Squires[3]) that *P. montagui tridens*, the Pacific subspecies of *P. montagui* Leach, should be given the full specific rank of *P. tridens* Rathbun 1902. Rathbun's (1902, 1904) separation of the Pacific subspecies, *P. montagui tridens*, from the Atlantic species, *P. montagui*, was based on slight differences in adult morphology. For instance, the rostrum of the Pacific subspecies was 1½-1⅔ times the length of the carapace compared with 1²/₅-1½ times the length of the carapace for the Atlantic species. Also, termination of the dorsal rostral spines of the Pacific subspecies was behind the middle of the carapace rather than in the middle or in front of the middle of the carapace as in the Atlantic form. Squires' (see footnote 3) conclusion that the Pacific subspecies should be given specific status was based on coloration of adults. Ivanov's (1971) conclusion was based on morphological differences between Stage I larvae of *P. tridens* from the Gulf of Alaska and Pike and Williamson's (1964) description of Stage I larvae of *P. montagui* from the North Atlantic. In Stage I *P. montagui* the margins of the carapace and abdominal somites are smooth; in Stage I *P. tridens* the carapace bears pterygostomian spines, the antero- and posterolateral margins of the carapace bear denticles, and the posterior margins of the abdominal somites bear minute spines. In *P. tridens*, the rostrum is longer and the number of setae and spines on the antennal scale is greater than in *P. montagui*. Also, *P. tridens* larvae are larger than larvae of *P. montagui*. My comparison of the seven zoeal stages of *P. tridens* from Cook Inlet with the zoeae of *P. montagui* raised in the laboratory and collected from North Atlantic plankton by Pike and Williamson (1964) confirms the morphological differences found by Ivanov (1971) for Stage I and shows that these differences persist through later stages.

SUMMARY OF PRINCIPAL MORPHOLOGICAL CHARACTERISTICS

Certain characteristics of larvae of pandalid shrimp from the North Pacific Ocean change form as the larvae develop. I discuss changes of these characteristics and categorize the larvae by number of stages. I also discuss the probable morphology of larvae of *Pandalopsis ampla* Bate, *P. aleutica* Rathbun, and *P. longirostis* Rathbun and larvae tentatively identified as *Dichelopandalus leptocerus* (Smith).

Although the number of pereopods bearing exopodites does not change during larval development, the exopodites themselves degenerate

[3]Squries, H. J. 1965. Decapod crustaceans of Newfoundland, Labrador and the Canadian Eastern Arctic. Fish. Res. Board Can., MS Rep. Ser. Biol. 810:1-212. Biological Station, Nanaimo, B.C. V9R-5K6.

during later stages, usually at the molt to the megalopa. In Table 1, poorly developed pereopods in Stage I are unsegmented pereopods that are directed anteriorly under the cephalothorax. Usually pereopods become functional by Stage III.

Denticles on the carapace and spines on the abdominal somites are most prevalent in Stage I and tend to disappear during larval development. Thus, in *Pandalus platyceros* most of the denticles and spines have disappeared by Stage III; in *P. stenolepis* and *P. tridens* most have disappeared by Stage VI.

For most pandalid shrimp larvae, the typical number of telsonic spines is 7 + 7 in Stage I and 8 + 8 in later stages. In the latest stage another pair may be added. The total number of telsonic spines of *P. kessleri* varies from 30-34 (Stage I) to 14-15 (Stage V); *Pandalopsis coccinata* has 55-56 telsonic spines in Stage I (Kurata 1955, 1964). Stage I *Pandalus kessleri* and *Pandalopsis coccinata* usually have 16 + 16 and 28 + 28 telsonic spines, respectively (Table 1).

The number of larval stages of *Pandalopsis dispar*, *P. coccinata*, *Pandalus tridens*, and *P. jordani* has not been verified. Seven zoeal stages are known for *Pandalopsis dispar* and *Pandalus tridens*. Based on morphological development, Stage VII of *Pandalopsis dispar* is probably the last larval stage. *Pandalus tridens* probably has an additional stage before the larvae molt to the first juvenile stage. Only the first zoeal stage of *Pandalopsis coccinata* is known, but development of this stage is so far advanced that only one or, at the most, two more stages probably appear before the larvae molt to the first juvenile stage. For *Pandalus jordani*, I have estimated six larval stages based on development of larvae of morphologically similar species, *P. borealis*, *P. goniurus*, and *P. tridens*, rather than the 11-13 stages obtained by Modin and Cox (1967) or the 8+ stages obtained by Lee (1969) in the laboratory. Modin and Cox (1967) noted that the 11-13 larval stages of *P. jordani* obtained by them in the laboratory were nearly twice the number of larval stages of the closely related *P. borealis*. Artificial laboratory conditions may have caused a greater number of larval stages than natural conditions.

The numbers of larval stages cited in Table 1 include the megalopa stage because the transition from zoea to megalopa is not always abrupt and may extend over several molts. For example, *P. hypsinotus* has functional pleopods in Stage VII, but other morphological characteristics normally associated with postzoea occur earlier (Haynes 1976). Also, the number of larval stages of some species vary slightly depending on geographical origin. Larvae of *P. hypsinotus*, *P. goniurus*, and *P. borealis* from the western North Pacific Ocean and *P. borealis* from British Columbia waters have one or two more stages than larvae of these species from Alaskan waters (Haynes 1976, 1978, 1979). Geographical variation in larval morphology has not been verified for other species of pandalids from the North Pacific.

The number of larval stages given in Table 1 refers to development in the sea rather than in the laboratory. Development in the laboratory often results in molt retardation and extra stages. Although the number of molts required to reach a specific point in development may vary in wild pandalid shrimp (Haynes 1978), the stages are, for the most part, remarkably constant and limited in number (Gurney 1942).

For identification purposes, pandalid shrimp larvae of the North Pacific Ocean can be categorized into two groups on the basis of morphological

TABLE 1.—Principal morphological characteristics and number of larval stages of known larvae of pandalid shrimp of the North Pacific Ocean. + = yes; − = no. (Only the most complete references on larval morphology are given.)

Species	Pereopods bearing exopodites	Pereopods poorly developed in Stage I	Spines on abdominal somites	Denticles on carapace margin	No. of telson spines in Stage I	No. of larval stages	References[1]
Pandalopsis coccinata	1-2	−	−	−	28 + 28	3	4
P. dispar	1-2	−	−	−	12 + 12	7	1
Pandalus kessleri	1-2	−	−	−	16 + 16	4	3, 4
P. danae	1-2	−	−	−	7 + 7	6	1
P. hypsinotus	1-2	−	−	−	7 + 7	7	1, 10
P. platyceros	1-3	−	+	+	8 + 8	5	1, 9
P. tridens	1-3	+	+	+	7 + 7	8	8, 13
P. stenolepis	1-3	+	+	+	7 + 7	6	2
P. borealis	1-3	+	−	−	7 + 7	6	1, 4, 12
P. goniurus	1-3	+	−	−	7 + 7	6	5, 11
P. jordani	1-3	+	−	−	7 + 7	6	6, 7

[1]References: 1) Berkeley (1930); 2) Needler (1938); 3) Kurata (1955); 4) Kurata (1964); 5) Ivanov (1965); 6) Modin and Cox (1967); 7) Lee (1969); 8) Ivanov (1971); 9) Price and Chew (1972); 10) Haynes (1976); 11) Haynes (1978); 12) Haynes (1979); 13) this report.

characteristics: species with exopodites on pereopods 1-3 and species with exopodites only on pereopods 1 and 2. Species with exopodites on pereopods 1 and 2 are characterized by well-developed pereopods in Stage I, and no spines on the abdominal somites or denticles on the carapace margin. For three of the species with exopodites on pereopods 1 and 2 (*Pandalopsis coccinata*, *P. dispar*, and *Pandalus kessleri*), the numbers of telsonic spines in Stage I are considerably greater than for species with exopodites on pereopods 1-3.

Fewer thoracic exopodites usually indicate fewer stages before the megalopa (Pike and Williamson 1964). This is not always true for pandalid shrimp larvae of the North Pacific Ocean. For instance, larvae of *P. danae, P. hypsinotus,* and *Pandalopsis dispar* also bear exopodites on first and second pereopods; but, the number of their larval stages is 6, 7, and 7, respectively. Also, Stage I larvae of *P. dispar* have dorsal and ventral teeth on the rostrum, 12 + 12 spines on the telson, and a long, jointed antennal flagellum that is about six times the length of the antennal scale; but the pleopods are not tipped with setae until Stage V, and Stage VII zoeae still bear a supraorbital spine.

A greater number of telsonic spines in Stage I is associated with fewer larval stages in development of the Caridea (Gurney 1942; Pike and Williamson 1964). This is true for *Pandalus platyceros*, *P. kessleri*, and *Pandalopsis coccinata*, which have 8 + 8, 16 + 16, and 28 + 28 telsonic spines in Stage I and 5, 4, and 3 larval stages, respectively. An exception is *P. dispar*, which has 12 + 12 telsonic spines in Stage I, but may have as many as seven larval stages.

Four species of pandalid shrimp in the North Pacific Ocean are not listed in Table 1: *Pandalopsis ampla*, *P. aleutica*, *P. longirostris*, and *Dichelopandalus leptocerus*. Larvae of *P. ampla*, *P. aleutica*, and *P. longirostris* have not been described. If larvae of *P. ampla*, *P. aleutica*, and *P. longirostris* undergo typical development of larvae of the genus *Pandalopsis* (Kurata 1964; Berkeley 1930), they will be characterized by advanced development, especially their large size and long antennal flagellum. Stage I *Pandalopsis* spp. larvae are at least 10.0 mm long and the antennal flagellum is longer than the body and segmented throughout its length. For comparison, Stage I larvae of *Pandalus* are 8.0 mm or less in length and the antennal flagellum is usually unsegmented and shorter than the length of the carapace. Stage I and II larvae of *D. leptocerus* have been tentatively identified from western Greenland waters (Pike and Williamson 1964). The larvae identified as *D. leptocerus* are most similar to larvae of *P. stenolepis* and *P. platyceros*: in Stage I and II, *D. leptocerus*, *P. stenolepis*, and *P. platyceros* bear prominent denticles on the anteroventral margin of the carapace, the anteroventral margin of the carapace and posterior margin of the third abdominal somite are flared, the rostrum is about as long as the carapace, and exopodites are present on pereopods 1-3. Larvae of *D. leptocerus* can be distinguished, however, from the identified pandalid shrimp larvae of the North Pacific Ocean, including larvae of *P. stenolepis* and *P. platyceros*, by the presence of posterolateral spines on the fifth abdominal somite.

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