

EARLY ZOEAL STAGES OF *LEBBEUS POLARIS*, *EUALUS SUCKLEYI*,
E. FABRICII, *SPIRONTOCARIS ARCUATA*, *S. OCHOTENSIS*, AND
HEPTACARPUS CAMTSCHATICUS (CRUSTACEA, DECAPODA, CARIDEA,
HIPPOLYTIDAE) AND MORPHOLOGICAL CHARACTERIZATION OF
ZOEAE OF *SPIRONTOCARIS* AND RELATED GENERA

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ABSTRACT

Stage I and II zoeae of *Lebbeus polaris*, *Eualus suckleyi*, and *E. fabricii* and Stage I zoeae of *Spirontocaris arcuata*, *S. ochotensis*, and *Heptacarpus camtschaticus* are described from individuals of known parentage. Larval development of *L. polaris* is more abbreviated than larval development of other hippolytid shrimp. Early stage zoeae of *L. polaris* can be distinguished from zoeae of *L. groenlandicus* by differences in morphology of antennal flagellum, maxillipeds, pereopods, and pleopods. Early stage zoeae of *E. suckleyi*, *E. fabricii*, *S. arcuata*, *S. ochotensis*, and *H. camtschaticus* can be distinguished from each other and other known hippolytid zoeae by slight differences in morphology, especially length of rostrum, armature of carapace and abdomen, setation of antennule and mouthparts, and development of pereopods. These new descriptions extend the range of morphological characters of zoeae for each genus and support the proposal that the *Spirontocaris* sensu lato unit be accorded suprageneric status rather than generic status.

Larvae of only a few of the 87 known species of hippolytid shrimp in the northern North Pacific Ocean have been described. Needler (1934) described Stage I zoeae of *Hippolyte clarki* Chace under the name *Hippolyte californiensis* Holmes, and Stage I zoeae of *Eualus herdmani* (Walker), *Heptacarpus brevirostris* (Dana), *H. paludicola* (Holmes), and *H. tridens* (Rathbun) under the generic name *Spirontocaris*. These zoeae were hatched in the laboratory from ovigerous females collected in British Columbia waters. Zoeae and megalopa of *Spirontocaris spinus* (Sowerby) and *S. lilljeborgii* (Danielssen) were described from known parentage and from plankton of eastern Atlantic waters (Pike and Williamson 1961). Pike and Williamson (1961) also described Stage II zoeae of *S. phippisii* (Krøyer) collected from plankton in the western Atlantic and all larval stages of *E. pusiolus* (Krøyer), a species found in the western Atlantic and northern North Pacific Ocean. In addition, Pike and Williamson (1961) described several stages of zoeae presumed to be zoeae of *Lebbeus polaris* (Sabine). Ivanov (1971) described

Stage I zoeae of *Eualus macilentus* (Krøyer), *E. barbatus* (Rathbun), *Spirontocaris spinus* (= *S. spina intermedia* Kobjakova), and *Lebbeus groenlandicus* (Fabricius) hatched in the laboratory from ovigerous females collected in the Bering Sea and Gulf of Alaska. Haynes (1978) described the larval stages, including the megalopa, of *L. groenlandicus* from specimens hatched from ovigerous females collected in Kachemak Bay, Alaska.

In this paper, I describe and illustrate zoeal Stages I and II of *L. polaris*, *E. suckleyi* (Stimpson), and *E. fabricii* (Krøyer), and Stage I zoeae of *S. arcuata* (Rathbun), *S. ochotensis* (Brandt), and *H. camtschaticus* (Stimpson) hatched in the laboratory from ovigerous females collected in Kachemak Bay. I also compare the morphology of zoeae of *Spirontocaris* and related genera, and support Pike and Williamson's (1961) proposal to elevate *Spirontocaris* to suprageneric status.

METHODS

From late April to early May 1976, ovigerous *L. polaris*, *E. suckleyi*, *E. fabricii*, *S. arcuata*, *S. ochotensis*, and *H. camtschaticus* were caught in pots at depths of 20-30 m (11-16 fathoms) in Kachemak Bay. The females were transported

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to the laboratory and maintained as described by Haynes (1980) for ovigerous *Crangon franciscorum angustimana*. Most zoeae were released at night, about 1 wk after the females were captured. I do not know whether any of the larvae hatched as prezoaeae.

For each species, 100 zoeae in groups of 10 zoeae each were placed by large-bore pipette into 500 ml beakers containing about 400 ml of filtered seawater. Seawater in the beakers was changed every other day. Newly hatched nauplii of brine shrimp, *Artemia salina*, from San Francisco Bay were offered, but none were eaten by the zoeae. The zoeae of each species were preserved in 5% Formalin² about 10 d after their release. Some of the zoeae of *L. polaris*, *E. suckleyi*, and *E. fabricii* had molted to Stage II.

To study segmentation and setation, I cleared some zoeae in 10% KOH and stained the exoskeleton with Turtox CMC-S (acid fuchsin stain mountant). Because the paired appendages of the zoeae are symmetrical, only the left members are figured. The mandibles, an exception, are drawn as pairs. For clarity in the illustrations, setules on setae are usually omitted, but spinulose setae are shown. Illustrations are partly schematic and represent typical setal counts. Any variation in setal counts is noted in the text.

DESCRIPTION OF ZOEAE

Terms used in the text, nomenclature of gills and appendages, and techniques of measurement and illustration are those given by Haynes (1976). Carapace length refers to the straight-line distance from posterior margin of the orbit to mid-dorsal posterior margin of the carapace. Total body length refers to the distance from the tip of

the rostrum to the posterior margin of the telson, not including telsonic spines. Stage I zoeae of *S. ochotensis* lack a rostrum; therefore, for this species only, total body length refers to the distance from anterior middorsal margin of the carapace to posterior margin of the telson. Telsonic setae or spines are numbered from an inner (medial) to outer (lateral) direction. The setation formulas proceed from the distal to the proximal ends of appendages. Principal morphological characteristics used to separate the species of zoeae described in this report are summarized in Table 1.

Lebbeus polaris—Stage I Zoeae

Mean total length of Stage I (Figure 1A), 5.4 mm (range 5.2-5.6 mm, 3 specimens). Rostrum slightly sinuate, without teeth, about one-half length of carapace. Carapace with a rounded prominence at base of rostrum and near posterior margin. Ventral margin of carapace smooth except for pterygostomial spine. No supraorbital spines.

Antennule (Figure 1B).—First antenna, or antennule, an unsegmented peduncle with conical projection and heavily plumose seta. Conical projection with four aesthetascs of various lengths.

Antenna (Figure 1C).—An inner flagellum (endopodite) and outer scale (exopodite). Flagellum two-segmented, slightly longer than scale; distal segment styliform, with terminal plumose seta and short spine. Proximal segment of flagellum has simple seta near joint. Scale distally divided into four joints, fringed with 11 heavily plumose setae. Protopodite with two simple spines: one at base of flagellum, other at base of scale.

Mandibles (Figure 1D).—Well developed, without palps. Four teeth on incisor process of left mandible in contrast to diserrate incisor process

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

TABLE 1.—Principal morphological characteristics of hippolytid zoeae described in this report.

Species	Rostrum	Supraorbital spine in Stage I	Abdominal somites bearing posterolateral spines in all stages	Pereopods bearing exopodites	Pereopods in Stage I
<i>Lebbeus polaris</i>	long	no	4, 5	1, 2	5
<i>Eualus suckleyi</i>	long	no	5	2, 3	3, 5
<i>E. fabricii</i>	long	no	4, 5	2, 3	3, 5
<i>Spirontocaris arcuata</i>	short	no	4, 5	1, 2	3, 5
<i>S. ochotensis</i>	absent	yes	4, 5	1, 2	3, 5
<i>Heptacarpus camtschaticus</i>	minute	no	none	1, 2	3, 5

¹Small lobe in Stage I and II; absent in later stages.

²Poorly developed in Stage I and II; pereopods gradually develop in later stages.

³Undeveloped pereopods.

⁴Poorly developed in Stage I; pereopods gradually develop in later stages.

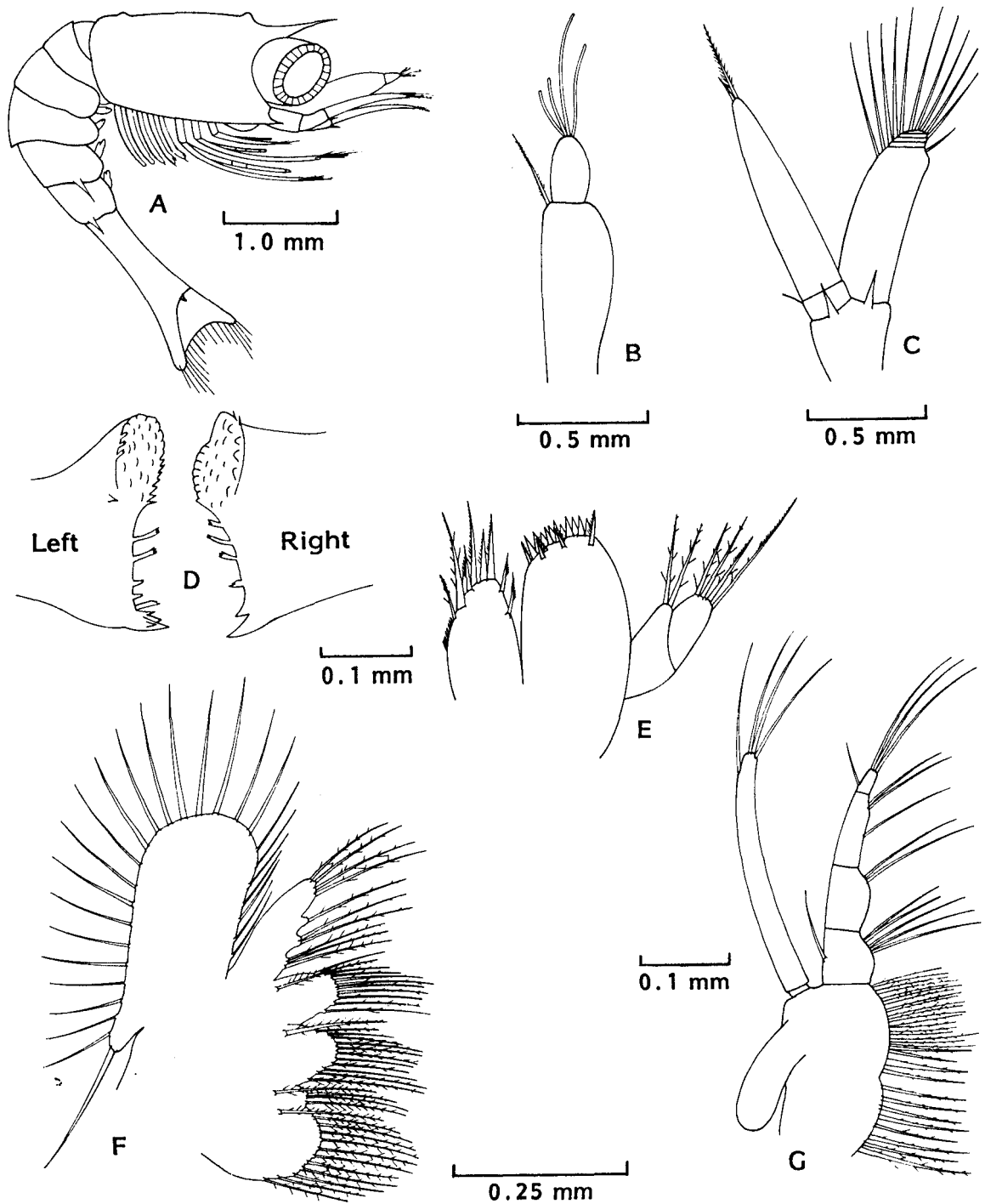


FIGURE 1.—Stage I zoea of *Lebbeus polaris*: A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles, left and right, posterior; E, maxillule, ventral; F, maxilla, dorsal; G, first maxilliped, dorsal.

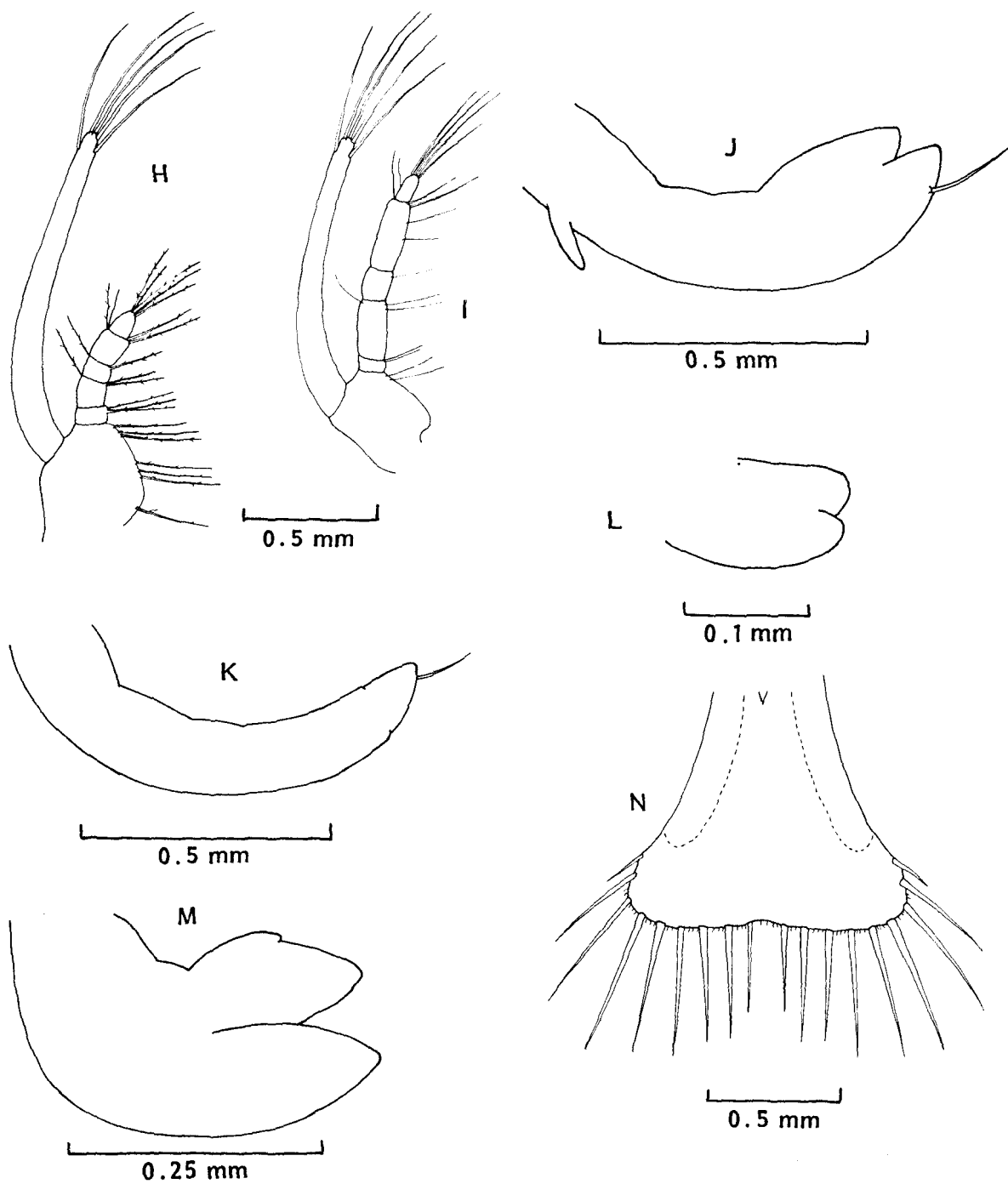


FIGURE 1.—Stage I zoea of *Lebbeus polaris*: H, second maxilliped, dorsal; I, third maxilliped, dorsal; J, first pereopod, right side; K, third pereopod, right side; L, first pleopod, right side; M, second pleopod, right side; N, telson, ventral.

of right mandible. Lacinia mobilis adjacent to incisor process and subterminal tooth on left mandible; neither structure on right mandible.

Maxillule (Figure 1E).—With coxal and basal endites and endopodite on maxillule (first maxilla). Eight setae, all spinulose, on proximal lobe (coxopodite). Fifteen spines terminally (four spines spinulose) on median lobe (basipodite). Two-segmented endopodite on lateral margin of basipodite: distal segment with four, sometimes three, spinulose setae terminally (one seta especially long; remaining three, or two, about equal length); two spinulose setae terminally on proximal segment. No outer seta on maxillule.

Maxilla (Figure 1F).—Platelike exopodite (scaphognathite) with 25 long plumose setae and long thicker seta at proximal end. Both coxopodite and basipodite bilobed. Ten setae on unsegmented endopodite—all setae distinctly setulose. Basipodite with 23 setae: 11 on distal lobe, 12 on proximal lobe. Most, if not all, setae on basipodite and coxopodite setulose. Sixteen setae on coxopodite: 4 on distal lobe, 12 on proximal lobe.

First maxilliped (Figure 1G).—Unsegmented protopodite with 31 spinulose setae: 23 on basipodite, 8 on coxopodite. Endopodite four-segmented; setation formula 4, 3, 2, 6. Exopodite segmented at base, has four natatory setae. Epipodite a single lobe.

Second maxilliped (Figure 1H).—Seven sparsely spinulose setae on unsegmented protopodite. Endopodite five-segmented; fourth segment expanded somewhat laterally; setation formula 5, 4, 2, 3, 3. Exopodite about three times longer than endopodite, not segmented at base. Five natatory setae on exopodite. No epipodite.

Third maxilliped (Figure 1I).—Two simple setae on unsegmented protopodite. Endopodite five-segmented, nearly as long as exopodite; setation formula 5, 5, 1, 3, 2. Setae simple and, except for few terminal setae, minutely spinulose. Exopodite unsegmented at base, has five natatory setae. No epipodite.

First pereopod (Figure 1J).—Endopodite relatively short, wide, unsegmented; chela partially formed; dactylopodite with simple spine. Exopodite, a small lobe.

Second pereopod.—Similar to first pereopod except narrower, exopodite smaller, and chela more deeply cleft.

Third (Figure 1K), *fourth*, and *fifth pereopods*.—Nearly identical, except size decreases slightly from third to fifth pair. No exopodites.

Pleopods.—First pleopod (Figure 1L) blunt, slightly bilobed. Second pleopod (Figure 1M) bilobed; inner lamella with bud of appendix interna. Third, fourth, and fifth pleopods same as second pleopod. All pleopods without joints or setae.

Abdomen and telson (Figure 1A, N).—Five somites and telson (somite 6 fused with telson). Fourth and fifth abdominal somites with pair of posterolateral spines about half as long as the somites themselves—pair on fifth somite slightly shorter than pair on fourth somite. Telson slightly emarginated distally, has 9 + 9 densely plumose setae; small spinules between bases of all setae except last outer pair of setae. Enclosed uropods visible. Anal spine present but minute.

Lebbeus polaris—Stage II Zoeae

Mean total length of Stage II, 5.7 mm (range 5.6–5.8 mm, 4 specimens). Rostrum (Figure 2A) styliiform, not sinuate, without teeth, about one-half length of carapace. Carapace with small supra-orbital spine and pterygostomian spine; no spinules along posteroventral margin. Eyes stalked.

Antennule (Figure 2B).—Similar to Stage I antennule, except heavily plumose seta arises from small conical projection. Spine, or seta, and four aesthetascs on tip of large conical projection. Three plumose setae ventrally on distal portion of peduncle.

Antenna (Figure 2C).—Flagellum of antenna three-segmented: terminal segment spined at tip; proximal segment has simple seta. Scale and protopodite similar to scale and protopodite of Stage I.

Mandibles, maxillule, and maxilla.—Nearly identical to Stage I, except molar process of left mandible has several spines along outer margin. Eighteen setae on basipodite of maxillule; 12 setae on coxopodite of maxillule. About 30 setae on scaphognathite of maxilla.

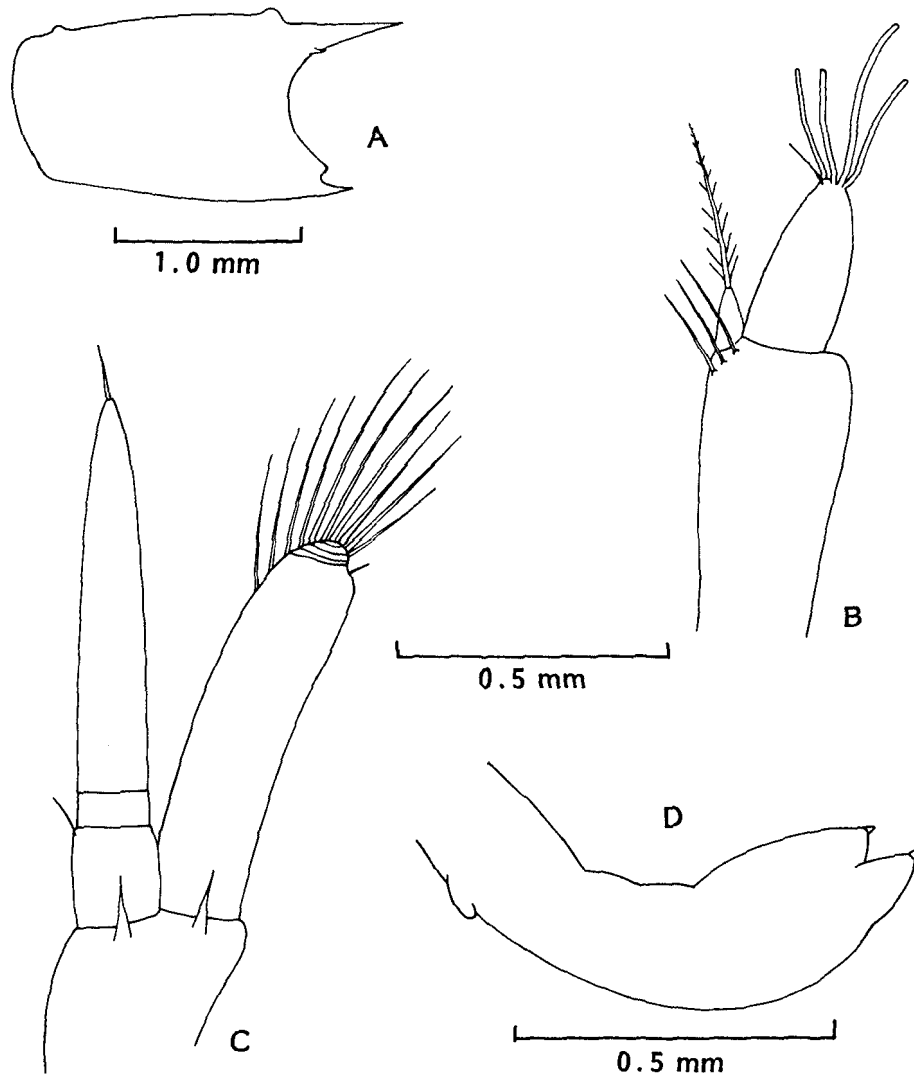


FIGURE 2.—Stage II zoea of *Lebbeus polaris*: A, carapace, right side; B, antennule, ventral; C, antenna, ventral; D, first pereopod, right side.

Maxillipeds.—Same as Stage I.

First pereopod (Figure 2D).—Unsegmented, slightly narrower than in Stage I. Propodite and dactylopodite tipped by small spine; dactylopodite without seta; exopodite remnant.

Second to fifth pereopods.—Similar to Stage I, except second pereopod slightly narrower, without exopodite. Third, fourth, and fifth pereopods with incipient segmentation.

Pleopods.—Similar to Stage I except more bilobed, appendices internae more distinct.

Abdomen and telson.—Nearly identical to Stage I, except sixth abdominal somite and telson jointed. Same number of telsonic setae as in Stage I. Uropods still enclosed.

Eualus suckleyi—Stage I Zoeae

Mean total length of Stage I (Figure 3A), 3.2

mm (range 3.0-3.5 mm, 10 specimens). Rostrum slender, spiniform, without teeth, slightly less than one-half length of carapace. Carapace with small, somewhat angular, dorsomedial promi-

nences at base of rostrum and near posterior edge. Pterygostomian spines present, not hidden by sessile eyes. Several minute spines adjacent to pterygostomian spine: three or four spines on

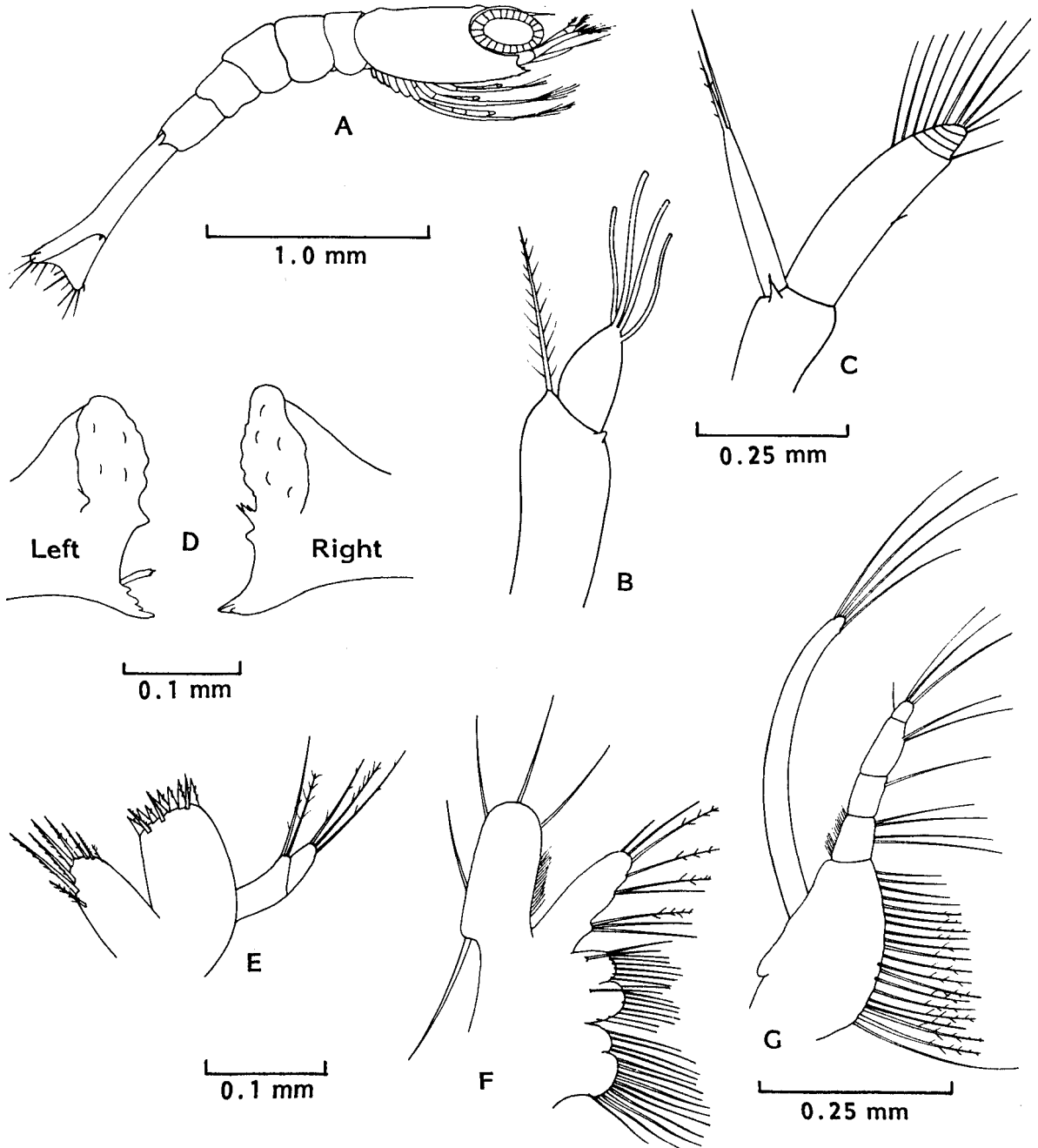


FIGURE 3.—Stage I zoea of *Eualus suckleyi*: A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles, left and right, posterior; E, maxillule, ventral; F, maxilla, dorsal; G, first maxilliped, dorsal.

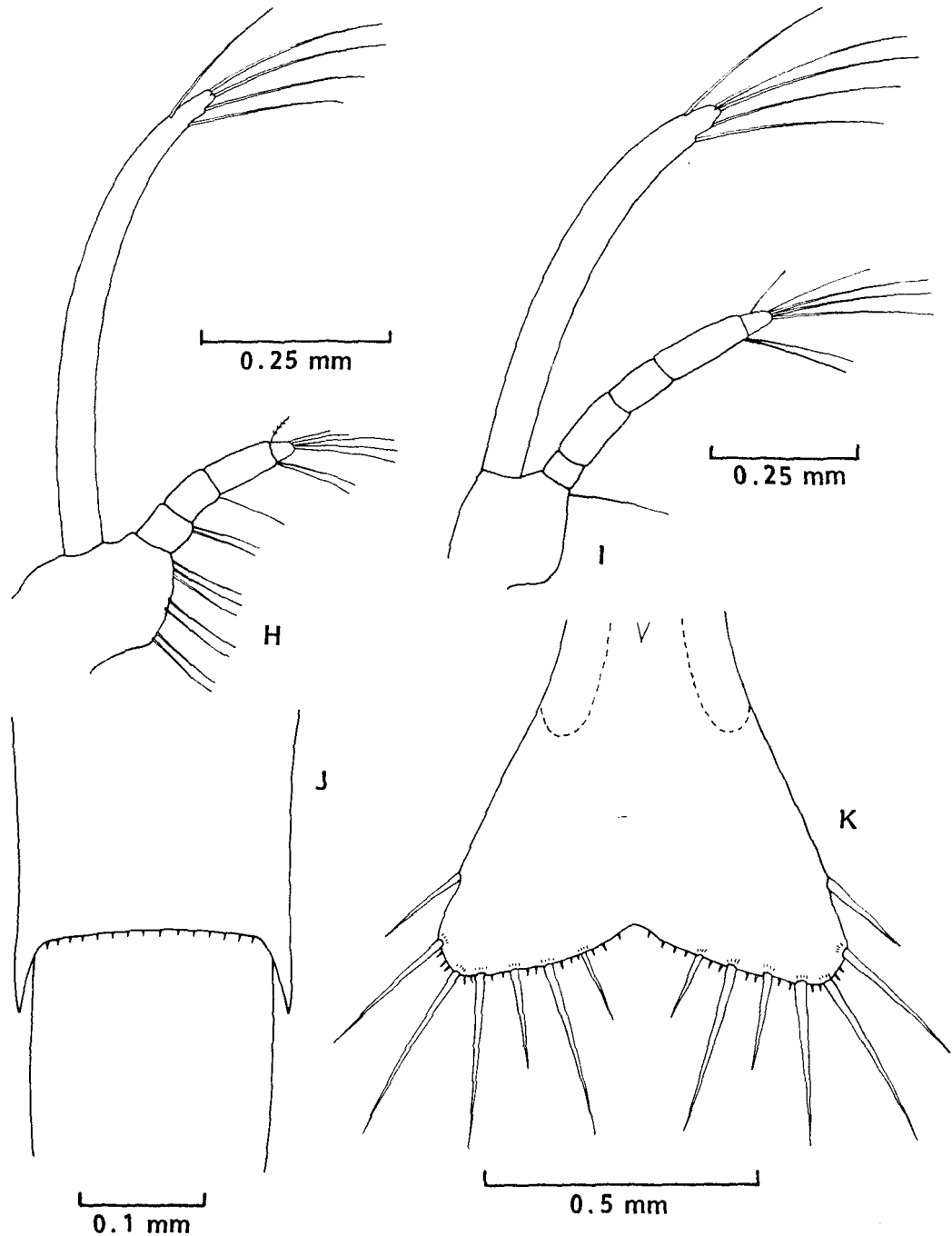


FIGURE 3.—Stage I zoea of *Eualus suckleyi*: H, second maxilliped, dorsal; I, third maxilliped, dorsal; J, fifth abdominal somite, dorsal; K, telson, ventral.

ventral margin of carapace, one spine on anterolateral margin. No supraorbital spines.

Antennule (Figure 3B).—Unsegmented peduncle

with conical projection and heavily plumose seta. Four aesthetascs of various lengths on conical projection. Small projection on peduncle near base of conical projection.

Antenna (Figure 3C).—Flagellum unsegmented, shorter and narrower than scale, terminally has plumose seta and shorter spinulose spine. Scale distally divided into four joints, fringed with 11 heavily plumose setae. Small plumose seta about midway on outer lateral margin. Protopodite with spine at base of flagellum but not at base of scale.

Mandibles (Figure 3D).—Well developed, without palps. Incisor process of left mandible with four teeth; incisor process of right mandible triserrate. Left mandible has lacinia mobilis adjacent to incisor process and subterminal tooth on truncated molar process.

Maxillule (Figure 3E).—Coxopodite with eight spinulose setae. Basipodite with 11 spinulose spines terminally. Two-segmented endopodite originating from lateral margin of basipodite has five spinulose setae: three on distal segment, two on proximal segment. Two setae especially spinulose, as shown. No outer seta on maxillule.

Maxilla (Figure 3F).—Scaphognathite with four long plumose setae, slightly longer thicker seta at proximal end, and series of fine hairs along inner margin of exopodite. Unsegmented endopodite with nine setae (four spinulose, as shown). Both basipodite and coxopodite bilobed. Basipodite with 17 setae: 8 on distal lobe, 9 on proximal lobe. Coxopodite with 14 setae: 4 on distal lobe, 10 on proximal lobe. Most, if not all, setae on basipodite and coxopodite setulose.

First maxilliped (Figure 3G).—Unsegmented protopodite with 20 setae; most setae heavily spinulose. Endopodite four-segmented; setation formula 4, 2, 1, 4; series of fine hairs on medial margin of proximal segment. Four natatory setae on exopodite. Epipodite, a small lobe.

Second maxilliped (Figure 3H).—Unsegmented protopodite with seven spinulose setae. Endopodite four-segmented; setation formula 6, 2, 1, 2. Exopodite about three times longer than endopodite, five natatory setae.

Third maxilliped (Figure 3I).—Usually one seta on unsegmented protopodite. Endopodite five-segmented, seven setae: five setae on distal, two on penultimate segment. Exopodite with five natatory setae.

Pereopods.—Poorly developed, unsegmented, and compacted tightly under cephalothorax. Pairs 1-3 biramous, 4 and 5 uniramous.

Pleopods.—Absent.

Abdomen and telson (Figure 3A, J, K).—Five somites and telson (somite 6 fused with telson). Fifth somite with pair of spines on posterolateral margin that extend posteriorly about one-fifth length of fifth somite. Minute spinules along posterodorsal border of fifth somite (Figure 3J) (spinules most easily seen in cleared specimens at $\geq 100\times$ magnification). Telson (Figure 3K) slightly emarginate distally, bears 7 + 7 densely plumose setae. Third setal pair shorter than second or fourth setal pair. Minute spinules along posterior margin and at base of all setal pairs except possibly outer (seventh) setal pair. Enclosed uropods visible. Anal spine present.

Eualus suckleyi—Stage II Zoeae

Mean total length of Stage II, 3.8 mm (range 3.5-4.2 mm, 8 specimens). Eyes stalked. Rostrum shaped as in Stage I. Carapace with small supra-orbital spine, no spinules (Figure 4A).

Antennule.—Similar to Stage I, except peduncle two-segmented with two setae at joint.

Antenna.—Flagellum with terminal spine, no setae, almost same length as scale (Figure 4B). Tip of scale four-segmented, proximal segment incomplete. Scale with 13 plumose setae—no proximal seta near outer lateral margin.

Mandibles, maxillule, and maxilla.—Same as Stage I.

Maxillipeds.—Epipodite of first maxilliped distinctly lobed. Exopodites of maxillipeds 1, 2, and 3 have four, five, and five natatory setae, respectively.

Pereopods.—Poorly developed, tightly compacted under cephalothorax; pairs 1-3 biramous, 4 and 5 uniramous.

Pleopods.—Absent.

Abdomen and telson.—Somite 6 fused with telson. Abdomen retains spines on fifth somite.

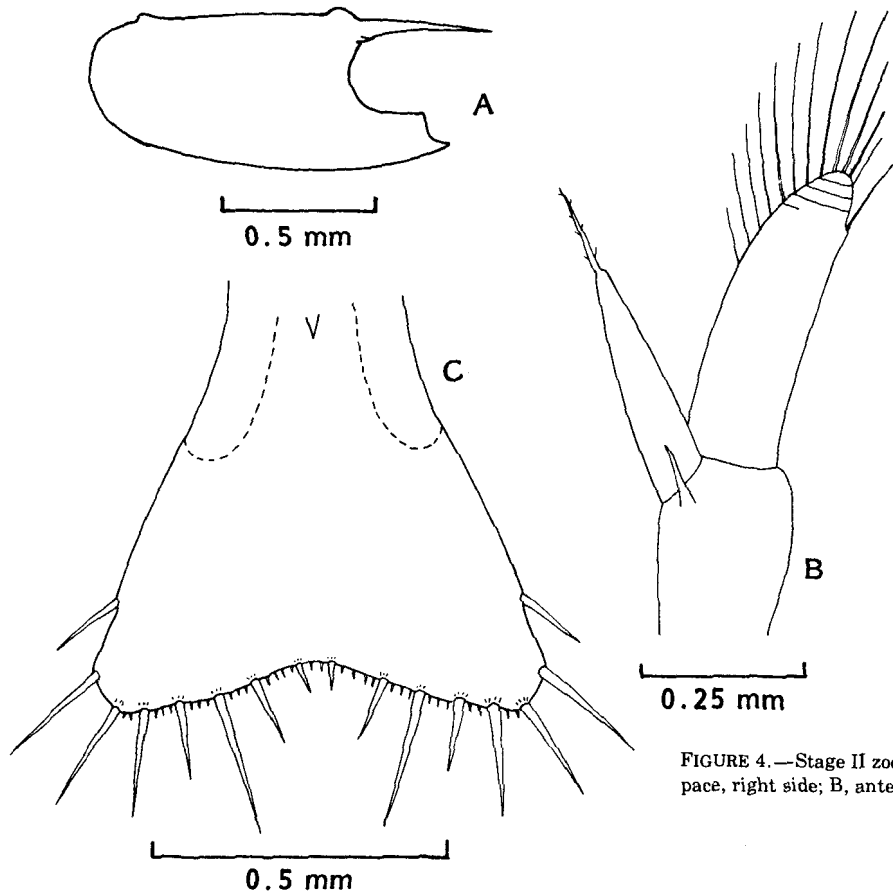


FIGURE 4.—Stage II zoea of *Eualus suckleyi*: A, carapace, right side; B, antenna, ventral; C, telson, ventral.

Telson with 8 + 8 plumose setae; setae noticeably shorter than in Stage I (Figure 4C). Uropods enclosed.

Eualus fabricii—Stage I and II Zoeae

Stage I and II *Eualus fabricii* are similar morphologically to Stage I and II *E. suckleyi*; however, they can be distinguished. Stage I and II of *E. fabricii* are slightly larger than Stage I and II *E. suckleyi*, and armature of the fourth and fifth abdominal somites and numbers of spines and setae differ between the two species.

Stage I Zoeae

Mean total length of Stage I, 3.7 mm (range 3.5–3.8 mm, 10 specimens). Carapace and rostrum similar to those of Stage I *E. suckleyi*, except no spines adjacent to pterygostomian spine on anterior margin of carapace.

Antennule.—Minute projection at base of conical projection of antennule (observable only under high [400×] magnification).

Antenna.—Same as antenna of Stage II *E. suckleyi* (Figure 4B), except flagellum about 1.5 times length of scale.

Mandibles.—Same as Stage I *E. suckleyi*.

Maxillule.—Seven spines on coxopodite; nine spines on basipodite.

Maxilla.—Three (sometimes 4) setae on distal lobe of coxopodite; 11 setae on proximal lobe. Six setae on each lobe of basipodite.

Maxillipeds.—Similar to Stage I *E. suckleyi* except no epipodite on first maxilliped.

Pereopods.—Same as Stage II *E. suckleyi*.

Pleopods.—Absent.

Abdomen and telson.—Pair of lateral spines on fourth and fifth somites. Lateral spines on fourth somite slightly smaller than lateral spines on fifth somite (Figure 5). Minute spinules on postero-dorsal margin of fourth and fifth somites: usually one to three on fourth somite, about eight on fifth somite. Minute spinules somewhat variable in size and number, slightly larger than spinules of *E. suckleyi*. Telson same as Stage I telson of *E. suckleyi*.

Stage II Zoeae

Mean total length of Stage II, 4.1 mm (range 4.0-4.3 mm, 10 specimens). Carapace with two spinules immediately posterior to pterygostomial spine; small supraorbital spine present.

Antennule and antenna.—Similar to Stage II *E. suckleyi*, except antennules have only 1 small seta at joint of peduncle and scale with 16 or 17 plumose setae.

Mandibles, maxillule, and maxilla.—Same as Stage I *E. fabricii*.

Maxillipeds.—Exopodites of maxillipeds 1, 2, and 3 have 4, 9, and 10 natatory setae, respectively. Epipodite on first maxilliped undeveloped, not lobed.

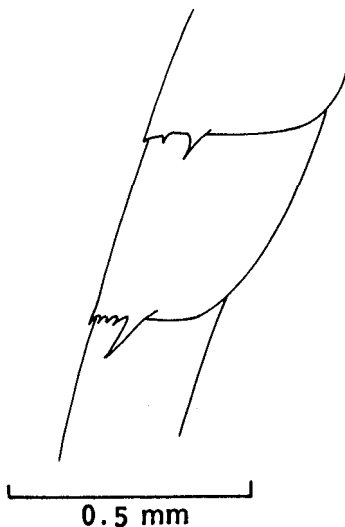


FIGURE 5.—Stage I zoea of *Eualus fabricii*: fourth and fifth abdominal somites, right side.

Pereopods.—Pairs 1-3 biramous, 4 and 5 uniramous.

Pleopods.—Absent.

Abdomen and telson.—Fourth and fifth somites with lateral spines, no spinules. Telson fused with sixth somite, has 8 + 8 densely plumose setae. Setae noticeably shorter than in Stage I *E. fabricii*. Uropods enclosed.

Spirontocaris arcuata—Stage I Zoeae

Mean total length of Stage I (Figure 6A), 4.2 mm (range 4.1-4.4 mm, 10 specimens). Rostrum (Figure 6B) spiniform, without teeth, about one-seventh length of carapace, projects downward paralleling contour of eyes. Carapace with small, somewhat angular, dorsal prominence at base of rostrum; another prominence near posterior edge. Pterygostomial spines present, not hidden by sessile eyes. Two or three minute spines along anteroventral margin of carapace. No supraorbital spines.

Antennule (Figure 6C).—Unsegmented peduncle with conical projection and several small simple setae (one seta especially longer than others). Four aesthetascs on small projection on peduncle near base of conical projection.

Antenna (Figure 6D).—Unsegmented flagellum shorter and narrower than scale. Flagellum with spinulose apical spine and several simple setae of various lengths. Scale distally divided into four segments, fringed with 11 heavily plumose setae, has small plumose seta proximally (near outer lateral margin). Protopodite with spine at base of flagellum but not at base of scale.

Mandibles (Figure 6E).—Well developed, without palps. Incisor process of left mandible has four teeth; incisor process of right mandible triserrate. Left mandible with relatively wide lacinia mobilis adjacent to incisor process, subterminal tooth on truncated molar process.

Maxillule.—Maxillule same shape as maxillule of Stage I *E. suckleyi* (Figure 3E). Coxopodite with seven spinulose setae. Basipodite with 10 (sometimes 11) spinulose spines terminally. Endopodite two-segmented, has five spinulose setae: three on

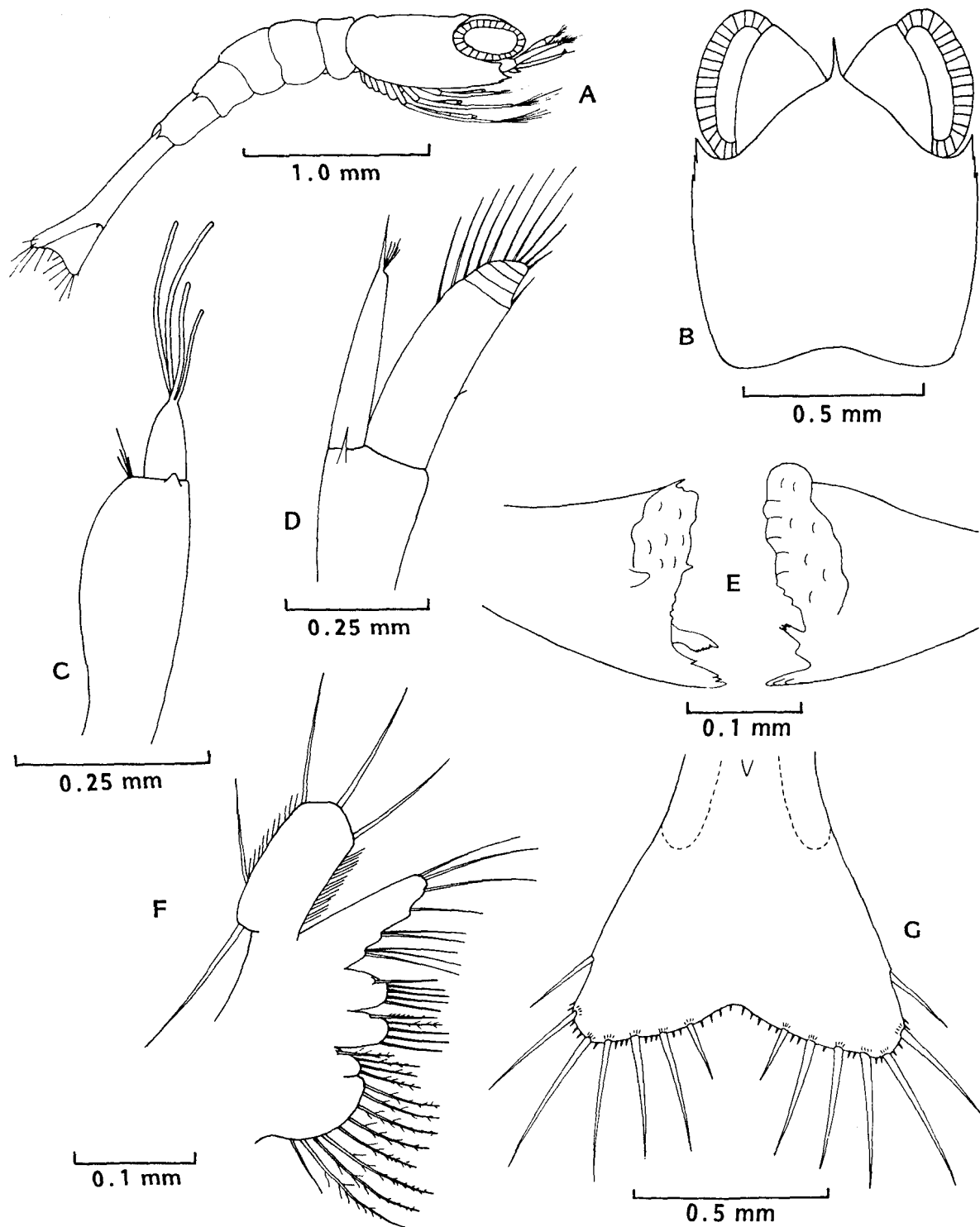


FIGURE 6.—Stage I zoea of *Spirontocaris arcuata*: A, whole animal, right side; B, carapace and eyes, dorsal; C, antennule, ventral; D, antenna, ventral; E, mandibles, left and right, posterior; F, maxilla, dorsal; G, telson, ventral.

distal segment, two on proximal segment. No outer seta on maxillule.

Maxilla (Figure 6F).—Four long plumose setae on scaphognathite; slightly longer, thicker seta at proximal end; series of fine hairs along inner margin; thinner series of hairs along outer margin. Nine setae on unsegmented endopodite. Basipodite and coxopodite bilobed. Basipodite with five setae on each lobe. Coxopodite with 13 setae: 4 on distal lobe, 9 on proximal lobe. Most setae on coxopodite setulose.

First, second, and third maxillipeds.—Maxillipeds similar to Stage I *E. suckleyi*; protopodite of first maxilliped has 25-27 setae; setation formula of endopodite of third maxilliped 5, 2, 1, 1, 4.

Pereopods (Figure 6A).—All five pairs present, poorly developed, unsegmented, and compacted under cephalothorax. Pairs 1 and 2 biramous, 3-5 uniramous.

Pleopods.—Absent.

Abdomen and telson (Figure 6A, G).—Five somites (somite six fused with telson). Fourth and fifth somites with spine but no spinules on posterolateral margins. Telson, shaped as in Stage I *E. suckleyi* (Figure 3K), has 7 + 7 densely plumose setae. Second and third pair of telsonic setae are same length. Minute spinules along terminal margin and at base of each seta except possibly last setal pair. Enclosed uropods visible. Anal spine present.

Spirontocaris ochotensis—
Stage I Zoeae

Stage I *S. ochotensis* similar to Stage I *S. arcuata*. *Spirontocaris ochotensis* smaller than *S. arcuata* and lacks rostrum; morphology of carapace, antenna, mandibles, and maxilla slightly different. Characters not mentioned are identical to Stage I *S. arcuata*.

Mean total length of Stage I, 2.8 mm (range 2.7-2.9 mm, 10 specimens). Carapace of *S. ochotensis* without rostrum. Pterygostomial spine and usually a spine along anteroventral margin of carapace (Figure 7A). Minute supraorbital spines present.

Antenna.—Plumose seta three times length of

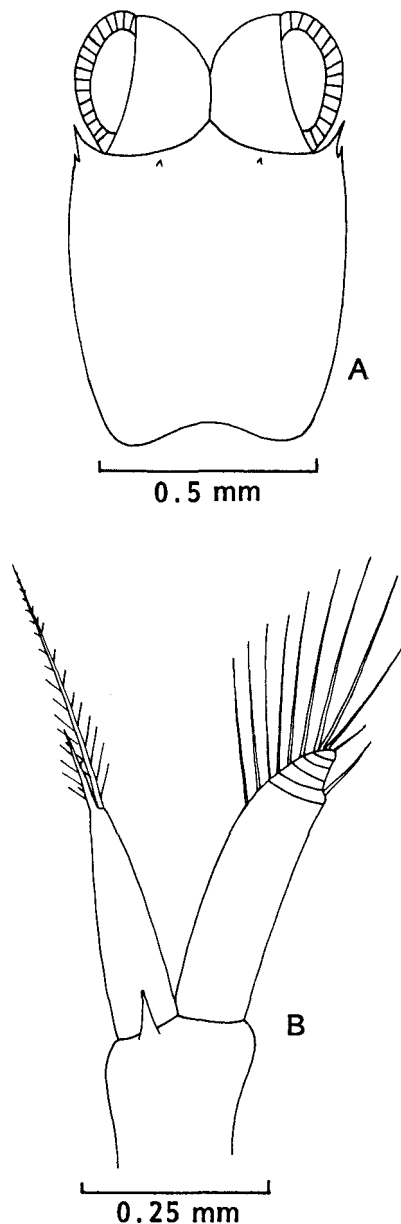


FIGURE 7.—Stage I zoea of *Spirontocaris ochotensis*: A, carapace and eyes, dorsal; B, antenna, ventral.

terminal spine on tip of flagellum (Figure 7B).

Mandible.—Narrow lacinia mobilis on left mandible (as in Stage I *E. suckleyi*, see Figure 3D).

Maxilla.—Seven (rarely eight) plumose setae on exopodite.

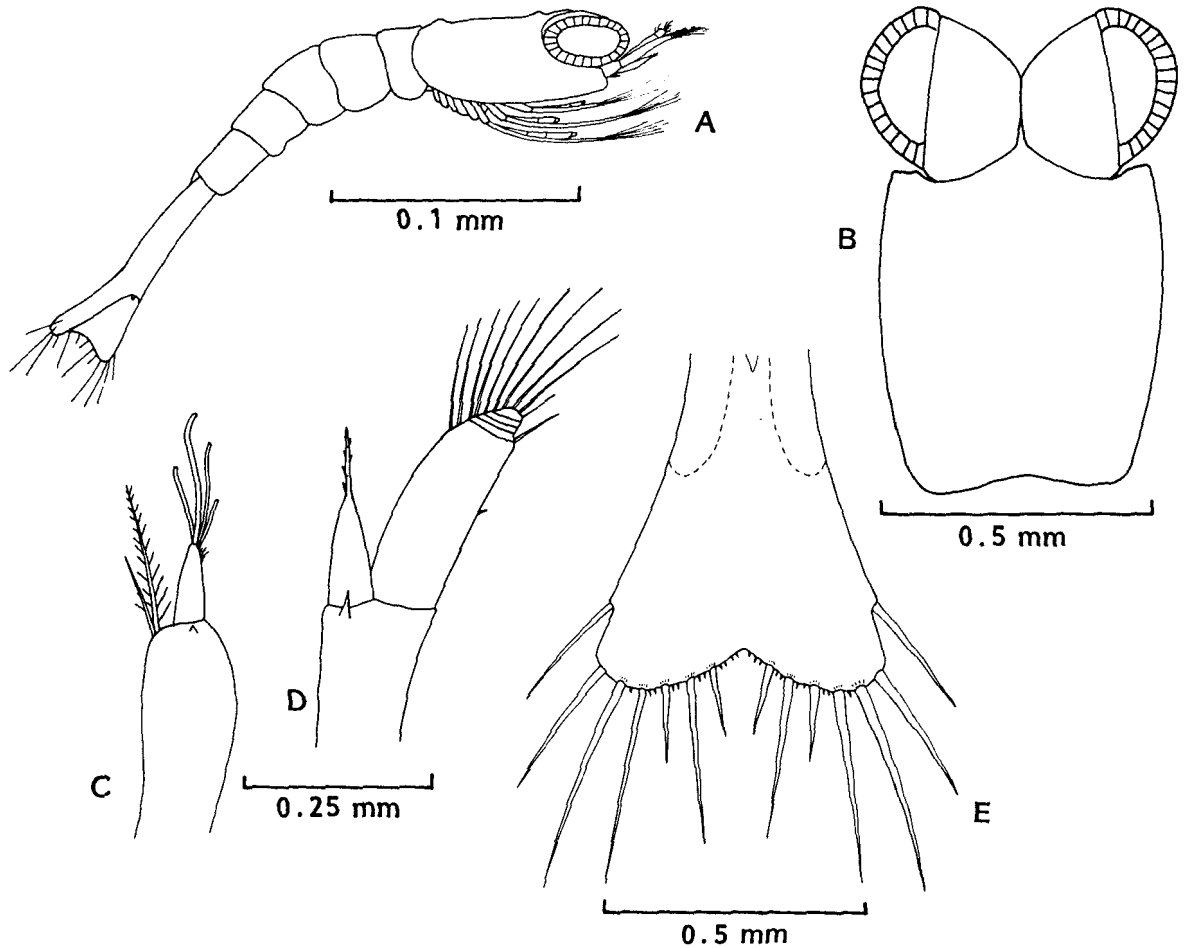


FIGURE 8.—Stage I zoea of *Heptacarpus camtschaticus*: A, whole animal, right side; B, carapace and eyes, dorsal; C, antennule, ventral; D, antenna, ventral; E, telson, ventral.

Heptacarpus camtschaticus—
Stage I Zoeae

Mean total length of Stage I (Figure 8A), 2.9 mm (range 2.8-3.1 mm, 10 specimens). Carapace without spines; minute rostrum curves slightly downward following dorsal contour of sessile eyes (Figure 8B).

Antennule (Figure 8C).—Unsegmented peduncle with conical projection, plumose seta, simple spine, and small projection. Plumose seta about twice length of conical projection. Conical projection has four aesthetascs terminally, three small aesthetascs subterminally.

Antenna (Figure 8D).—Unsegmented flagellum

about three-fourths length of scale, tipped by stout spinulose spine. Scale similar to scale of Stage I *E. suckleyi* (Figure 3C) except noticeably shorter and wider.

Mandibles, maxillule, maxilla, and maxillipeds.—Mouthparts similar to those of Stage I *E. suckleyi*, except coxopodite of maxillule has seven spinulose setae; basipodite of maxilla has six setae on each lobe; first maxilliped has no epipodite; setation formulas of the endopodites of the second and third maxillipeds are 5, 2, 1, 3 and 4, 2, 0, 0, 2, respectively.

Pereopods (Figure 8A).—All five pairs present: pairs 1 and 2 biramous; 3-5 uniramous.

Pleopods.—Absent.

Abdomen and telson (Figure 8A, E).—Abdomen similar in shape to abdomen of Stage I *E. suckleyi* except without spines or spinules. Telson emarginated, bears 7 + 7 relatively long densely plumose setae: longest (fifth) pair about three-fourths length of greatest telsonic width. Minute spinules along terminal margin of telson and at base of each seta to fifth setal pair. Anal spine present.

COMPARISON OF ZOEAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

In the literature, authors have identified or assigned names or stages to hippolytid larvae obtained from plankton. A comparison of their descriptions with my descriptions of zoeae of known parentage is useful in placing these earlier works in proper perspective (Table 2).

TABLE 2.—Presumed and corrected identities of hippolytid zoeae discussed in this report.

Author	Presumed identity	Conclusion from this study
Stephensen (1916)	<i>S. polaris</i> (= <i>L. polaris</i>)	Probably <i>L. polaris</i>
	Stage I	Stage III or later
	<i>Spirontocaris</i> -larva Nr. 3	Not <i>E. fabricii</i>
	<i>S. fabricii</i> (= <i>E. fabricii</i>)	
Stephensen (1935)	"youngest" stage (Stage I)	Stage III
	"intermediate" stage (Stage II)	Stage IV
	"oldest" ("last") stage (Stage III)	Stage V or VI
	<i>Spirontocaris</i> -larva No. 1	Unknown
Frost (1936)	<i>S. polaris</i> (= <i>L. polaris</i>)	—
	Stages not specified	—
Makarov (1967)	<i>E. fabricii</i>	Not <i>E. fabricii</i>
	Late-stage larvae	Stage VI or VII
Makarov (1967)	<i>Lebbeus</i> sp. "C"	<i>Lebbeus</i> sp.
	Stage II	Stage I
Makarov (1967)	<i>Lebbeus</i> sp. "D"	<i>Lebbeus</i> sp.; different species from <i>Lebbeus</i> sp. "C"
	Stage I	Stage I
	" <i>Eualus</i> sp. A"	Not <i>E. fabricii</i>
	<i>E. fabricii</i>	
	Stage I	Stage I
	" <i>Spirontocaris</i> sp. A"	Not <i>S. arcuata</i>
	<i>S. phippisii</i>	
	Stage I	Stage I
	" <i>Spirontocaris</i> sp. B"	Not <i>S. arcuata</i>
	Stage I	Stage I

Lebbeus polaris

Krøyer (1842, in Pike and Williamson 1961) described an advanced embryo of *L. polaris* with all appendages, except uropods, present and segmented. The fourth and fifth abdominal somites each have a pair of small posterolateral spines.

All three pairs of maxillipeds have natatory exopodites, but the pereopods have none. As far as can be compared, my Stage I zoeae of *L. polaris* are identical to Krøyer's embryo, except the pereopods and pleopods of my specimens are unsegmented.

Stephensen, in 1916, described a zoea from southern waters of Greenland that he assumed is a Stage I zoea of *S. polaris* (= *L. polaris*). As noted by Pike and Williamson (1961), Stephensen's zoea is similar to Krøyer's specimen. Stephensen's zoea has posterolateral spines on the fourth and fifth abdominal somites, lacks exopodites on the pereopods, and the appendages are larger and more developed than Krøyer's specimen. The carapace of Stephensen's zoea has supraorbital spines, and developing uropods are visible inside the telson. In addition, the chelae of the first and second pereopods of Stephensen's zoea are well developed; the carpopodite of the second pereopod had begun to develop joints; and the pleopods have well-developed appendices internae. The presence of appendices internae, well-developed chelae, and segmentation of carpopodite shows that Stephensen's zoea is in the last, or perhaps penultimate, zoeal stage and that the species passes through only three or, perhaps, four zoeal stages. Under the name "*Spirontocaris*-larva No. 1," Stephensen (1935) included several specimens collected from waters of western Greenland that he assumes are later stages of *S. polaris* (= *L. polaris*); one specimen bears exopodites on pereopods 1 and 2.

The characteristics of Stephensen's (1916) late-stage "*S. polaris*" zoea are typical of *Lebbeus* zoeae although his zoea differs somewhat from my *L. polaris* zoeae. Stephensen's zoea has an unsegmented antennal flagellum, and the telson is fused with the sixth somite; my zoeae of *L. polaris* have a two-segmented antennal flagellum in Stage I, and the sixth somite and telson are jointed in Stage II. If Stephensen was correct in assuming his specimen to be *L. polaris*, then *L. polaris* in Greenland waters has at least one more zoeal stage than *L. polaris* in Alaskan waters. Stephensen's (1935) descriptions of his "*Spirontocaris*-larva No. 1" zoeae are too brief to identify either the species or stage. At least one of Stephensen's specimens lacks the pair of spines on the antennal protopodite and must be a species other than *L. polaris*.

Makarov (1967) briefly described zoeae collected from plankton of the western Kamchatka Peninsula shelf. He thought these zoeae were probably

zoeal Stages I-IV of a species of *Lebbeus*. He also obtained one specimen each of "*Lebbeus* sp. D" and "*Lebbeus* sp. C"; these he thought were zoeal Stages I and II, respectively. My Stage I zoeae of *L. polaris* are similar to Makarov's Stage I zoea ("*Lebbeus* sp. D") except my zoeae are not as long (average length 5.4 mm compared with 6.4 mm). Makarov's Stage II zoea ("*Lebbeus* sp. C") is 7.6 mm long; the eyes are sessile; and the carapace lacks supraorbital spines. My Stage II zoeae of *L. polaris* are 5.7 mm (mean) long; the eyes are stalked; and the carapace has supraorbital spines. Development of Makarov's "*Lebbeus* sp. C" and "*Lebbeus* sp. D" zoeae shows that they are undoubtedly zoeae of the genus *Lebbeus*. Because his "*Lebbeus* sp. C" zoea has sessile eyes and does not have supraorbital spines, it must be a Stage I zoea rather than a Stage II zoea. "*Lebbeus* sp. C," therefore, is a species different from "*Lebbeus* sp. D."

Larvae of only one other species of *Lebbeus*, *L. groenlandicus*, have been completely described from known parentage (see Haynes 1978). At comparable zoeal stages, *L. groenlandicus* is more developed than *L. polaris*. The antennal flagellum of Stage I zoeae of *L. groenlandicus* is about twice as long as the scale and terminates in a narrow projection. In *L. polaris*, the antennal flagellum is only slightly longer than the scale and has a plumose seta and spine. Also, in Stage I zoeae of *L. groenlandicus*, the epipodite of the first maxilliped is bilobed; the second maxilliped has a single lobed epipodite; and pereopods and pleopods are either partially or fully segmented. In *L. polaris*, only the first maxilliped bears an epipodite (single lobed), and none of the pereopods or pleopods are either partially or fully segmented.

In Stage II zoeae of *L. groenlandicus*, the supraorbital spine is well developed; the antennule differs considerably from the antennule of Stage I; the antennal flagellum has setae; the antennal scale is fringed with plumose setae along nearly the entire inner margin; the pereopods are essentially adult in shape; and the pleopods are fully segmented. In Stage II *L. polaris*, the supraorbital spine is small; the antennule and antennae are similar to the antennule and antennae of Stage I; the pereopods are not adult in shape; and the pleopods are unsegmented.

Lebbeus groenlandicus has only three larval stages: two zoeal stages and one megalopal stage (Haynes 1978). Because larvae of *L. polaris* are somewhat less developed for a given stage than

those of *L. groenlandicus*, *L. polaris* probably has three zoeal stages before molting to the megalopa.

Eualus suckleyi

Zoeal Stages I and II of *E. suckleyi* are similar to the same zoeal stages of *E. gaimardii* (H. Milne Edwards), *S. spinus*, and *S. lilljeborgii* (as Pike and Williamson [1961] described them from eastern Atlantic specimens); however, there are slight differences in setation, development of pereopods, and armature of carapace and abdomen. The antennal flagellum of Stage I zoeae of *E. suckleyi* has a spine and a seta; the antennal scale has a plumose seta at the base of each of the four segments; and pereopods 1-5 are present (pereopods 1-3 biramous, other pereopods uniramous). The antennal flagellum of Stage I zoeae of *E. gaimardii* has only a spine; the antennal scale has a small outer spine at the base of the four segments; and pereopods 1-4 are present and uniramous. Stage I zoeae of *S. spinus* and *S. lilljeborgii* lack minute spines on the anteroventral margin of the carapace, have a rudimentary supraorbital spine, and only pereopods 1 and 2 are biramous. Also, *S. spinus* has posterolateral spines on abdominal somites 4 and 5 rather than only on somite 5 as in *E. suckleyi*.

In Stage II zoeae of *E. suckleyi*, an outer plumose seta is at the base of the distal joints of the antennal scale; and exopodites on maxillipeds 1-3 have four, five, and five natatory setae, respectively. In Stage II zoeae of *E. gaimardii*, a somewhat stout spine is at the base of the distal joints of the antennal scale, and exopodites on maxillipeds 1-3 have five, seven, and seven natatory setae, respectively. Stage II zoeae of both *S. spinus* and *S. lilljeborgii* have a tuft of dorsal setae on abdominal somite 4; Stage II zoeae of *E. suckleyi* do not have this tuft.

Eualus fabricii

Stephensen's (1916) "*Spirontocaris*-larva Nr. 3" were the most abundant spirontocarid larvae in his plankton samples from Greenland waters. He thought the larvae were the same species as the most abundant adult and described and illustrated them as the "youngest" stage, "intermediate" stage, and "oldest" ("last") stage of *Spirontocaris fabricii* (= *Eualus fabricii*). Stephensen (1935) later described additional characteristics for the "first" and "last" stages. Frost

(1936) illustrated a whole zoea she believed was a zoeal stage of *E. fabricii* later than Stephensen's "last" stage. Pike and Williamson (1961), from development of zoeae of the genus *Eualus*, showed that Stephensen's "youngest" stage is Stage III; the "intermediate" stage is Stage IV; and the "oldest" stage is Stage V or VI. They believed that the zoea illustrated by Frost (1936) is probably Stage VI or VII.

Although Stephensen's and Frost's *E. fabricii* zoeae are later stages than my zoeae, they can be compared with my zoeae by the presence of posterolateral spines on abdominal somites, length of the antennal flagellum, and number of setae fringing the antennal scale. My *E. fabricii* zoeae have posterolateral spines on abdominal somites 4 and 5; Stephensen's and Frost's zoeae do not. The antennal flagellum in Stages I and II of my *E. fabricii* zoeae is about 1.5 times the length of the antennal scale, and the antennal scale has 13 setae in Stage I and 16 or 17 setae in Stage II. In the "youngest" stage (Stage III zoeae) described by Stephensen, the length of the antennal flagellum is still only about one-half the length of the antennal scale, and the number of setae on the antennal scale does not exceed 11. Stephensen's and Frost's zoeae apparently belong to a species other than *E. fabricii*.

Pike and Williamson (1961) noted that the zoeae described by Stephensen (1916, 1935) and Frost (1936) as *S. fabricii* (= *E. fabricii*) are similar to zoeae of *E. pusiolus*. The zoeae of both species lack abdominal spines and have exopodites on pereopods 1-4. However, *E. fabricii* zoeae are larger, have a longer rostrum, and have a well-developed antennal spine on the anterior margin of the carapace in late zoeal stages (compared with *E. pusiolus* zoeae). On the basis of Pike and Williamson's comparison of zoeae of *E. fabricii* and *E. pusiolus*, Makarov (1967) suggested that his "*Eualus* sp. A" series of zoeae from the west Kamchatka shelf is either *E. pusiolus* or *E. fabricii*. According to Makarov, "*Eualus* sp. A" zoeae are nearly identical to zoeae of *E. pusiolus* described by Pike and Williamson (1961), but because Makarov's zoeae are larger, especially in the later stages, he speculated that "*Eualus* sp. A" zoeae might be *E. fabricii* zoeae.

Stage I and II zoeae of Makarov's "*Eualus* sp. A" differ considerably from my Stage I and II zoeae of *E. fabricii*. The zoeae of "*Eualus* sp. A" are markedly smaller (Stages I and II of "*Eualus* sp.

A" are 2.8 mm and 3.2 mm long, respectively; Stage I and II *E. fabricii* are 3.7 mm and 4.1 mm long, respectively). The rostrum of Makarov's zoeae is minute; the abdomen lacks spines; and the antennal flagellum is noticeably shorter than the antennal flagellum of my Stage I and II *E. fabricii*.

Spirontocaris arcuata

Pike and Williamson (1961) described a Stage I zoeae of *S. spinus* and *S. lilljeborgii* hatched from known parentage and a Stage II zoea of *S. phippisii* collected from plankton. My Stage I zoeae of *S. arcuata* are clearly different from these zoeae. Stage I zoeae of *S. arcuata* differ from those of *S. spinus* and *S. lilljeborgii* in shape of rostrum, armature of carapace and abdomen, and setation of antennule and antennae. Stage I *S. arcuata* zoeae have a short rostrum that does not project beyond the anterior margin of the eyes. In Stage I zoeae of *S. spinus* and *S. lilljeborgii* and Stage II zoeae of *S. phippisii*, a prominent rostrum projects anteriorly beyond the eyes to about three-fourths the length of the antennular peduncle. The carapace of my specimens of *S. arcuata* does not have supraorbital spines but has spines along the anteroventral margin. However, in Stage I *S. spinus* and *S. lilljeborgii* and Stage II *S. phippisii*, the carapace has a small supraorbital spine, and the anteroventral margin is smooth. Also, in Stage I zoeae of *S. arcuata*, the antennule and inner flagellum of the antenna have several setae terminally. Both the antennule and inner antennal flagellum of Stage I zoeae of *S. spinus* and *S. lilljeborgii* and Stage II zoeae of *S. phippisii* have a large seta terminally. Finally, Stage I zoeae of *S. lilljeborgii* have posterolateral spines only on the fourth abdominal somite; Stage I zoeae of *S. arcuata* have posterolateral spines on both fourth and fifth abdominal somites.

Makarov (1967) described Stage I zoeae of two unidentified species of *Spirontocaris* ("species A" and "species B") from plankton of the western Kamchatka Peninsula shelf. His zoeae can be separated from Stage I zoeae of *S. arcuata* by the relatively long rostrum in his species A and B. In addition, Makarov's Stage I zoeae of *Spirontocaris* sp. B are longer than those of *S. arcuata* (5.1 mm and 4.2 mm, respectively) and have pleopodal buds.

Ivanov (1971) briefly described four zoeae he assumed were *S. spina intermedia*. His zoeae are readily distinguishable from zoeae of *S. arcuata*

because *S. spina intermedia* has a tuft of setae on the dorsal surface of the fourth abdominal somite.

Spirontocaris ochotensis

When descriptions of hippolytid zoeae by other authors (Stephensen 1916, 1935; Webb 1921; Lebour 1931, 1932; Needler 1934; Frost 1936; Gurney 1942; Williamson 1957; Pike and Williamson 1961; Makarov 1967; Ivanov 1971; and Haynes 1978) are compared with my description of zoeae of *S. ochotensis*, my Stage I zoeae of *S. ochotensis* are the only described hippolytid zoeae of the northern North Pacific Ocean that have posterolateral spines on the fourth and fifth abdominal somites and lack a rostrum. Stage I zoeae of *S. arcuata* (described in this report) are similar to Stage I *S. ochotensis* zoeae but have a rostrum.

Heptacarpus camtschaticus

The only larvae of *Heptacarpus* identified are the first zoeal stages of three species that Needler (1934) described: *H. paludicola*, *H. tridens*, and *H. brevisrostris*. These zoeae differ from *H. camtschaticus*: Needler's zoeae lack a rostrum, a spine adjacent to the plumose seta of the antennule, and a long proximal seta on the scaphognathite of the maxilla. Also, Needler's zoeae have pterygostomian spines, which are absent in Stage I zoeae of *H. camtschaticus*.

Stage I zoeae that resemble Stage I zoeae of *H. camtschaticus* include *E. pusiolus* and *E. occultus* found in European waters (Pike and Williamson 1961) and *E. macilentus* found in the Bering Sea (Ivanov 1971). All these Stage I zoeae lack posterolateral spines on the fourth and fifth abdominal somites and have a minute rostrum (although Stage I zoeae of *E. occultus* from British waters may lack a rostrum [Pike and Williamson 1961]). Stage I zoeae of *H. camtschaticus* differ from the other Stage I zoeae because *H. camtschaticus* zoeae have all pairs of pereopods, and the antennal flagellum projects only about three-fourths the length of the antennal scale. In Stage I, the other species lack pereopods, and the antennal flagellum projects to the tip of the antennal scale or just beyond. In addition, Stage I zoeae of *E. occultus* have a small dorsal tuft of setae on the fourth abdominal somite and a row of fine denticles on the posterior margin of the fifth abdominal somite; these structures are absent in Stage I zoeae of *H. camtschaticus*.

CHARACTERIZATION OF ZOEAE OF *SPIRONTOCARIS* S. S. AND RELATED GENERA

Holthuis (1947) redefined the genus *Spirontocaris* sensu lato (s.l.) and divided it into six genera: *Birulia*, *Eualus*, *Heptacarpus*, *Lebbeus*, *Spirontocaris* sensu stricto (s.s.), and *Thoralus*. Pike and Williamson (1961) categorized the zoeae of *Spirontocaris* s.l. by the number of zoeal stages, number of pereopods, morphology of the rostrum in Stage I, and number of pereopods with exopodites in the last zoeal stage. Because of the wide range in morphology of the zoeae, Pike and Williamson (1961) suggested that *Spirontocaris* s.l. be given suprageneric status. My descriptions of hippolytid zoeae partially invalidate Pike and Williamson's categorization, extend the range of larval characters of the genus *Spirontocaris* s.l., and confirm Pike and Williamson's suggestion that *Spirontocaris* s.l. be given suprageneric status.

In Pike and Williamson's (1961) categorization, the known larvae of *Lebbeus* and *Spirontocaris* s.s. form separate generic groups. They categorize identified larvae of *Eualus* spp. into two distinct groups. Group 1 includes *E. gaimardii*, which has five zoeal stages. In Stage I zoeae of Group 1, the rostrum is large, and four pairs of undeveloped pereopods are present; in later zoeal stages, exopodites are present on pereopods one through three. Group 2 includes *E. pusiolus*, *E. occultus*, *E. fabricii*, and *E. herdmani*, which probably have six to nine zoeal stages. In Stage I zoeae of Group 2, the rostrum is minute or absent, and there are no pereopods. In later zoeae, exopodites are present on pereopods one through four (evidence was incomplete for *E. fabricii* and *E. herdmani*). The lack of information on larvae of *Heptacarpus* spp. prevents any comparison of *Heptacarpus* spp. larvae to those of Group 2 *Eualus*.

My descriptions of zoeae of *L. polaris*, *E. suckleyi*, *E. fabricii*, *S. arcuata*, *S. ochotensis*, and *H. camtschaticus* increase the range of morphological variations of zoeal "generic" characters used by Pike and Williamson (1961) for these genera (Table 3). Pike and Williamson list the rostrum of *Lebbeus* spp. zoeae in Stage I as small, but the rostrum may also be large (about one-half the length of the carapace). They list the rostrum in Stage I zoeae of *Spirontocaris* s.s. as large, but the rostrum of Stage I zoeae of *S. arcuata* is small (about one-seventh the length of the carapace), and the rostrum of Stage I zoeae of *S.*

TABLE 3.—Range of morphological and developmental characters used to define zoeae of *Spirontocaris* s.s. and related genera. (? = unknown.)

Genus	Characters				
	Number of zoeal stages	Number of pereopods in Stage I	Rostrum in Stage I	Pereopods bearing exopodites in later zoeal stages	References ¹
<i>Lebbeus</i> sp.	2, 3	5	long	0	1, 2, 3
<i>Eualus</i> sp.	5-9	0, 2 ⁴ , 2 ⁵	absent to long	3, 4	1, 3, 4, 5, 6, 7
<i>Spirontocaris</i> s.s.	5	2 ⁵	absent to long	2	1, 3, 4, 6, 8
<i>Heptacarpus</i> sp.	?	0, 2 ⁵	absent, minute	?	1, 5
<i>Thoralus</i> sp.	9	0	absent, minute	3	4, 9, 10

¹1) Haynes 1978, 2) this report, 3) Ivanov 1971, 4) Pike and Williamson 1961, 5) Needler 1934, 6) Williamson 1957, 7) Lebour 1940, 8) Lebour 1937, 9) Lebour 1932, 10) Lebour 1936.

²Undeveloped pereopods.

ochotensis is absent. Stage I zoeae of both *E. suckleyi* and *E. fabricii* have large rostrums (about one-half the length of the carapace) and, therefore, correspond to Pike and Williamson's *Eualus* Group 1 but also have some of the characters of Group 2. Additionally, zoeae of *E. suckleyi* and *E. fabricii* have five pairs of undeveloped pereopods rather than four pairs of undeveloped pereopods like Stage I zoeae of *E. gaimardii*. The genus *Heptacarpus* is characterized by Pike and Williamson (1961) by the absence of both rostrum and pereopods in Stage I, but Stage I zoeae of *H. camtschaticus* have both a minute rostrum and all five pairs of undeveloped pereopods.

Although my new descriptions of zoeae extend the range of morphological characters of the genus *Spirontocaris* s.l. and partially invalidate the generic groupings used by Pike and Williamson (1961), these new descriptions confirm their findings of great morphological variation of the zoeae of *Spirontocaris* s.l. The range of two to nine zoeal stages among the species is unequalled in any described genus. Usually Stage I zoeae of a caridean genus vary little in the degree of development at hatching, but *Spirontocaris* s.l. includes some species that have Stage I zoeae with all appendages, except uropods, present and segmented and other species of Stage I zoeae that have no trace of appendages posterior to the maxillipeds. The size of the zoeal rostrum is frequently of generic importance. Among species of the spirontocarid group, the rostrum varies from being absent to large. Also, the number of pereopods with exopodites in later zoeal stages is constant throughout known zoeae of nearly all caridean genera except *Spirontocaris* s.l., which may have 0, 2, 3, or 4 pereopods (Pike and Williamson 1961). The wide range in morphology of different species in the *Spirontocaris* s.l. supports Pike and Williamson's (1961) suggestion that it be accorded suprageneric, rather than generic, status.

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