

THE LARVAL DEVELOPMENT OF *SERGESTES SIMILIS* HANSEN (CRUSTACEA, DECAPODA, SERGESTIDAE) REARED IN THE LABORATORY

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ABSTRACT

The larval development of *Sergestes similis* Hansen reared in the laboratory includes the following stages: nauplius I-IV, protozoa I-III, and zoea I-II. These forms together with the first two postlarval stages are described and illustrated.

Sergestes similis and *S. arcticus*, closely related species which comprise the *arcticus* species group, are very similar in larval as well as adult morphology especially in the ornate armature of protozoal carapace apparently specific to the group. In contrast, the two species of the *atlanticus* group, *S. atlanticus* and *S. cornutus*, differ distinctly from each other in carapace armature of the protozoal stages. The difference between these two species groups in variation within each group indicates that larval morphology may be of value in the study of interspecific relationships within *Sergestes*. *Sergestes similis* and *Sergia lucens*, species of closely related genera, differ in number of naupliar stages, in armature of body in protozoal and zoeal phases, and in development of some appendages.

The pelagic shrimp *Sergestes similis* is abundant in the North Pacific Drift ranging from Japan to North America between 40° and 50°N, and is a prominent constituent of the plankton in the cooler waters of the California Current.

Within the genus *Sergestes* (Omori 1974), *S. similis* is located in the *arcticus* species group, as defined by Yaldwyn (1957), which includes only the two species *S. arcticus* Krøyer and *S. similis* Hansen. *Sergestes arcticus* is widely distributed, occurring in the North Atlantic, the Mediterranean, and all sectors of the Southern Ocean, while *S. similis* is restricted to the subarctic and transitional zones of the North Pacific; available data indicates that the species are geographically isolated from one another (Judkins 1972). The life history and distribution of *S. similis* and its importance in oceanic ecosystems of the Pacific have been discussed by Percy and Forss (1969), Omori et al. (1972), and Omori and Gluck (1979).

The purpose of this paper is to describe and illustrate the larval development of *S. similis* and to compare the larvae with those of the closely related species *S. arcticus* described by Wasserloos (1908), Hansen (1922), and Gurney

and Lebour (1940). The larvae of *S. similis* are also compared with the early stages of *S. atlanticus* and *S. cornutus* (Gurney and Lebour 1940), which comprise the *atlanticus* group, to note the difference in variation within species groups in protozoal morphology, and with the larvae of *Sergia lucens* (Omori 1969) to note the differences between species of closely related genera. The description of *Sergestes similis* is based on both individuals reared in the laboratory by Omori (1979) during his study of the growth, feeding, and mortality of larval and postlarval stages of the species off southern California, and on specimens from preserved plankton samples.

Gurney and Lebour (1940), in the major work on larvae of the genus, remarked that "perhaps the most interesting feature of the development of *Sergestes* is the striking difference which exists between the larvae of the different species, while the adults are often separable with difficulty," and suggested that knowledge of the larvae, when complete, may give a better indication of the relationships of species than adult morphology.

METHODS

Omori (1979) described the procedures used for rearing the larvae of *S. similis* in the laboratory. Larvae from the population of the

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species off the coast of southern California were obtained for study from preserved plankton samples taken on Scripps Institution of Oceanography Expedition X and CalCOFI Cruises 6904 and 6905 during April and May of 1964 and 1965.

At least five individuals of each developmental stage were dissected in glycerine for study of appendages. Some specimens of each stage were prepared for study and dissection by digesting away all soft tissue in heated aqueous KOH and then staining with Chlorazol Black E. Drawings were prepared with the drawing attachment of a Wild M20³ microscope.

Measurements of reared and planktonic larvae of *S. similis* were compared by Omori (1979, table 6); the mean body lengths (with standard deviation in parentheses) of larval stages obtained at 14°C are repeated here by stage for convenience. The larvae were measured along the midline from anterior margin of forehead to posterior margin of telson.

The postnaupliar developmental phases have been named protozoa, zoea, and postlarva following Omori (1979), and the terminology of Gurney and Lebour (1940) has been followed in describing the armature of carapace. In the protozoal phase the outgrowths of the carapace are referred to as processes with secondary spines and spinules, while in the zoeal and postlarval stages the outgrowths are called spines with secondary spinules.

Segmentation of two of the appendages proved difficult to determine. The basal segmentation of the exopod of the second antenna in protozoal stages I-III was not clear. In *S. similis* it appeared that there were incomplete sutures within segments 1 and 3, giving 12 outer margin and 10 inner margin sutures; we have numbered the segments along the inner margin. The articulation of coxa, basis, and endopod of the second maxilla in protozoal and zoeal phases also proved confusing. We have followed Gurney (1942) in referring to the medial lobes as bifid endites of coxa and basis, and have assumed from the morphology of the postlarval appendage that the endopod consists of 5 segments, although the articulation of segment 1 and basis was not clear.

In the description of larval stages, only changes in structure and armature of body and appendages are discussed; if an appendage is not

mentioned, it may be assumed that there has been no change from the preceding stage except increase in size.

In order to compare the basic pattern of development between *Sergestes similis* and *Sergia lucens*, we reexamined a number of larvae and postlarvae of *S. lucens* from the rearing experiment in July 1965.

RESULTS

The larval development of *Sergestes similis* includes the following stages: nauplius I-IV, protozoa I-III, and zoea I-II. The first two postlarval stages are also described.

Nauplius I (Fig. 1a, e)

Body length: 0.34 mm (0.01).

Body ovoid with two posterior spines which curve posterodorsally and are slightly swollen basally.

Antennule (Fig. 2a) unsegmented with 4 smooth setae, 2 terminal and 2 subterminal, and small terminal spine.

Antenna (Fig. 3a) unsegmented; exopod with 5 setae; endopod with 3 setae, 2 terminal and 1 subterminal; all setae smooth.

Mandible (Fig. 4a) biramous and unsegmented, each ramus with 3 smooth setae.

Nauplius II (Fig. 1b)

Body length: 0.38 mm (0.01).

Body slightly longer and narrower posteriorly than in stage I, with 2 pairs of spines on posterior margin, outer pair very short, tiny rudiments of third inner pair sometimes visible.

Antennule (Fig. 2b) with 1 subterminal medioventral seta and 3 terminal processes including 2 setae with setules and 1 small aesthetasc.

Antenna (Fig. 3b) unsegmented; exopod with 6 setae and sometimes with small distal spine, distolateral seta smooth and others plumose; endopod with 2 plumose setae and 1 small spine terminally.

Mandible (Fig. 4b) with 3 plumose setae on each ramus.

Nauplius III (Fig. 1c, f)

Body length: 0.42 mm (0.02).

Body with posterior portion tapering, posterior margin slightly indented medially with 4

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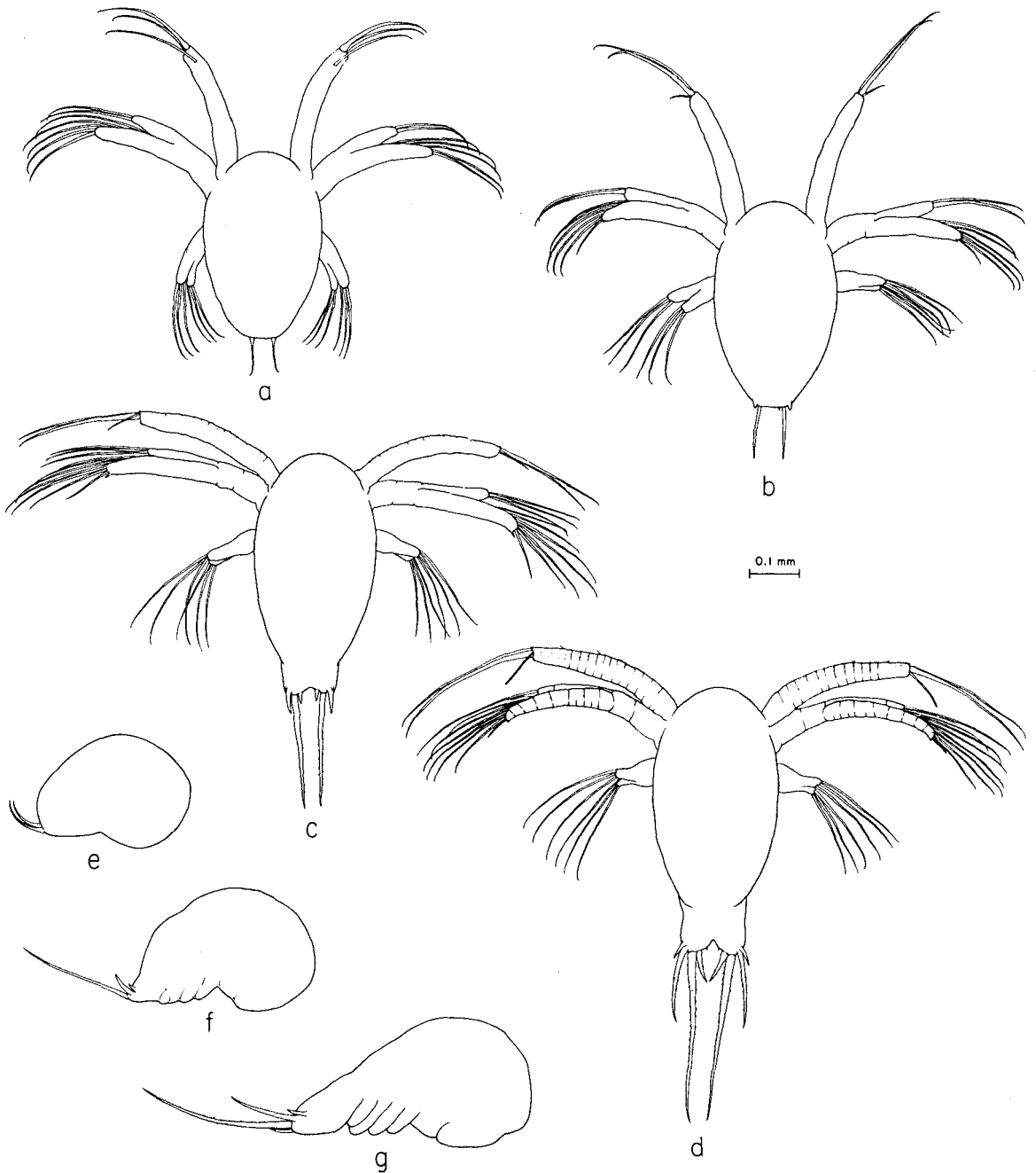


FIGURE 1.—*Sergestes similis*. Nauplius I-IV, a-d, dorsal view; nauplius I, III-IV, e-g, lateral view without appendages.

pairs of spines, outer pair tiny, relatively long third pair armed with spinules and articulated basally.

Antennule (Fig. 2c) sometimes with a second seta on inner margin, incipient segmentation, and few rows of tiny spinules.

Antenna (Fig. 3c) with incipient segmentation of protopod and exopod sometimes visible; exopod with 7 setae and small distal spine, distal 2 setae with small setules, other setae plumose; endopod with 3 terminal setae and 1 seta on inner margin.

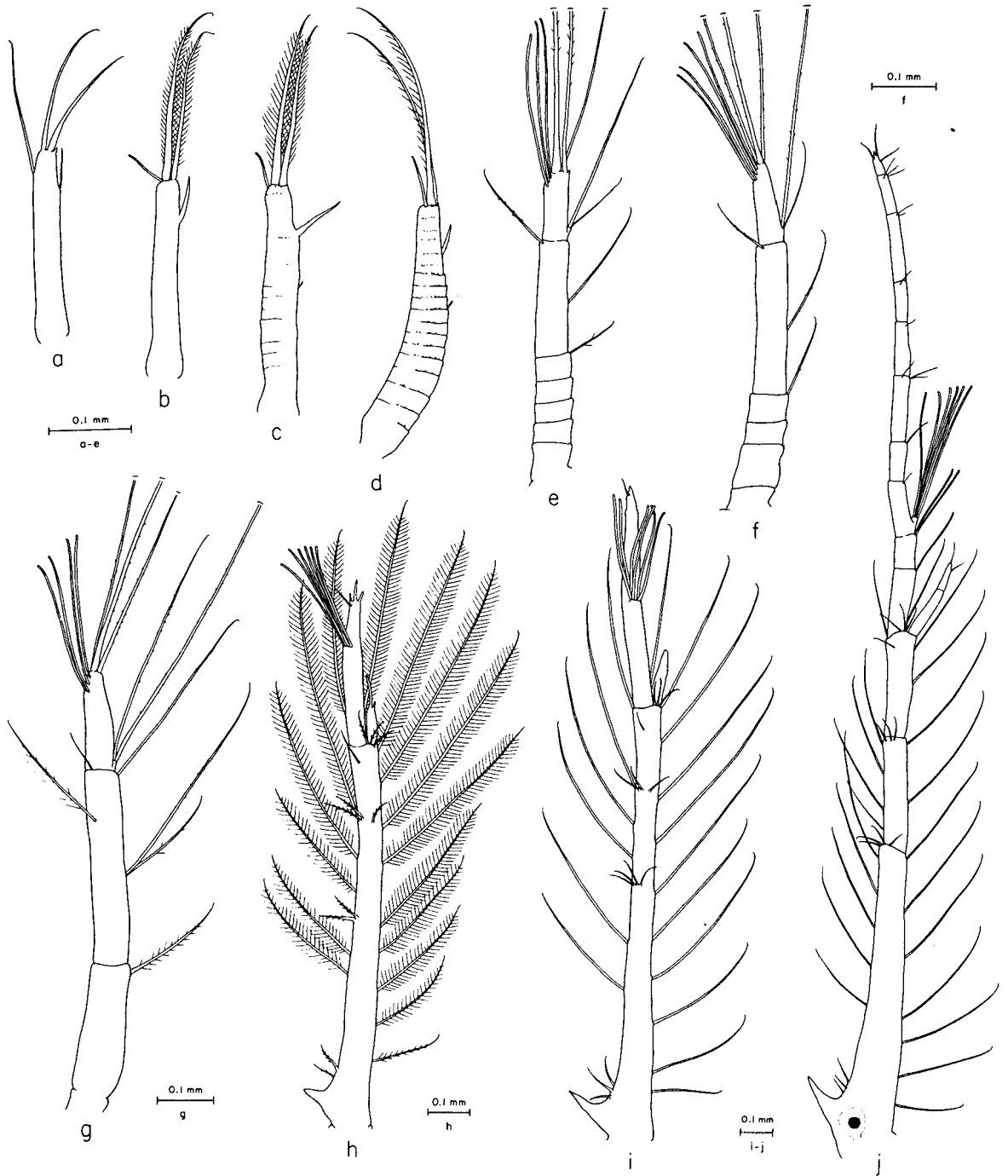


FIGURE 2.—*Sergestes similis*. Antennules: a-d, nauplius I-IV; e-g, protozoa I-III; h-i, zoea I-II; j, postlarva I; setules omitted on i and j.

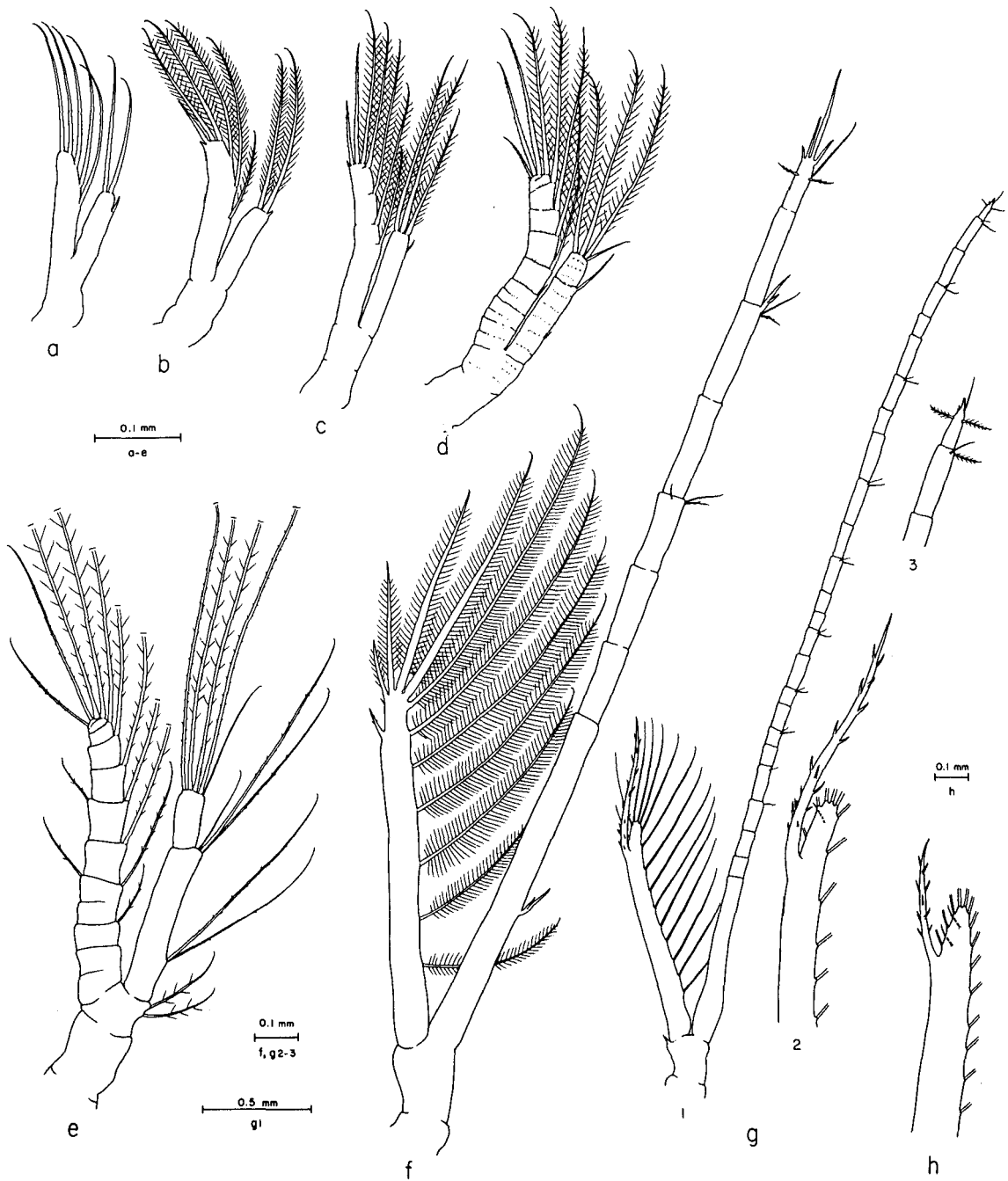


FIGURE 3.—*Sergestes similis*. Antenna: a-d, nauplius I-IV; e, protozoa I; f-g, zoea I-II; h, postlarva I, tip of scale; setules omitted on g.

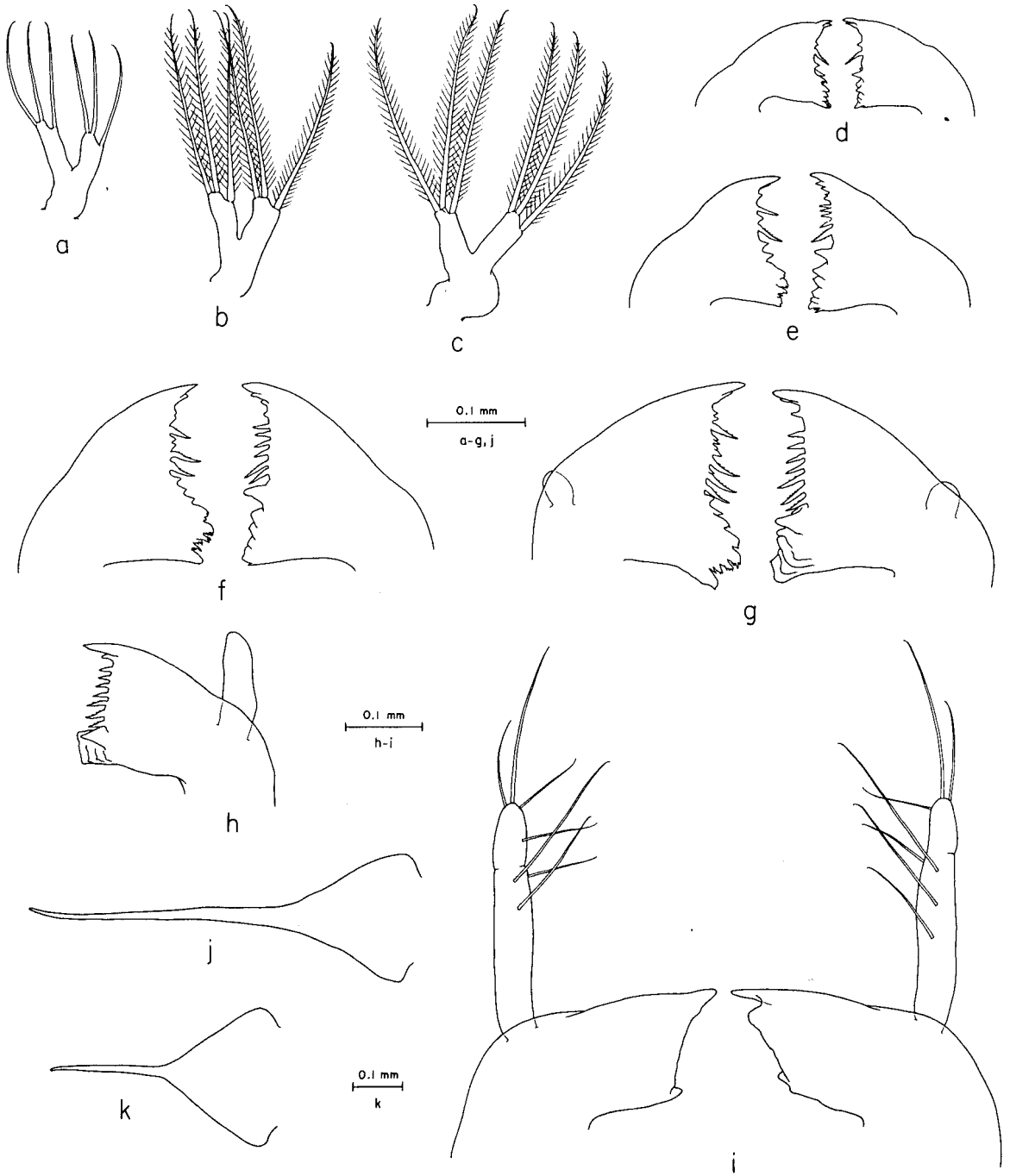


FIGURE 4.—*Sergestes similis*. Mandibles: a-c, nauplius I-II, IV; d-f, protozoa I-III; g-h, zoea I-II; i, postlarva I. Labrum: j, protozoa I; k, zoea I.

Mandible unchanged.

Anlagen of maxillules, maxillae, and first and second maxillipeds visible.

Nauplius IV (Fig. 1d, g)

Body length: 0.49 mm (0.03).

Body with abdomen forming, posterior margin with distinct medial indentation and 4 pairs spines, third pair still relatively long, rudiments of fifth inner pair sometimes visible, spinules present on spines 2-4, and sometimes on 1; third pair articulated, other spines fused with telson.

Antennule (Fig. 2d) with 2 inner setae, terminal setation unchanged; proximal two-thirds with indistinct segmentation most clearly visible along inner margin; about 17 rows of tiny spinules encircle antennule associated, in segmented section, with distal margin of segment.

Antenna (Fig. 3d) with protopod of 2 indistinct segments; exopod with approximately 8 segments (basal segmentation unclear, specimens cleared and stained have indication of 10 segments on outer margin and about 8 on inner margin), with 8 or 9 setae and sometimes a small distal spine, distal 3 setae with small setules, others plumose; endopod at least 2-segmented, small distinct distal segment with 4 terminal setae, proximal segment with 2 setae on outer margin and sometimes with incomplete basal segmentation; both rami encircled with rows of tiny spinules.

Mandible (Fig. 4c) with basal portion swelling with development of gnathal lobe, tissue withdrawing from rami.

Rudiments of maxillules, maxillae, and 2 pairs of maxillipeds present posterior to mandibles.

Protozoa I (Fig. 5a, b)

Body length: 0.82 mm (0.02).

Carapace with following processes: 1 pair anterolateral, each branching to 3 large spines and occasionally 1-3 small spines (5 of 20 reared larvae with small spines on one or both processes, 20 larvae from the plankton with 3 large spines only); 1 pair lateral with 1-3 large basal spinules; 1 posterodorsal with few large basal spinules, usually 2; all processes with small spinules to tip. Anterior margin of forehead with pair of small papillae. Prominent, round dorsal organ present in protozoal phase. Thorax with evidence of

segmentation, abdomen unsegmented. Telson forked, each fork with 2 small smooth ventral spines and 4 long curving processes armed with spinules.

Antennule (Fig. 2e) of 3 segments, proximal segment subdivided into 5 small segments; proximal and middle segments with 1 and 2 setae, distal segment with 8 processes including 5 setae, 3 terminal and 2 proximal, and 3 aesthetascs. Gurney (1942) noted that distal segment with aesthetascs is homologous with outer flagellum of later stages and that peduncle is therefore of 2 segments.

Antenna (Fig. 3e) with exopod of 10 segments, terminal segment with 3 setae, segments 2-9 with 1 distal seta on inner margin, segments 3 and 5 with 1 distal seta on outer margin as well; endopod 2-segmented, distal segment with 5 terminal setae, long proximal segment with 5 setae on inner margin—3 distal and 2 proximal on slight protuberance; basis with 2 setae on inner margin; structure unchanged in protozoal phase.

Mandibles (Fig. 4d) without palp, gnathal lobe of each mandible with 1 strong serrated spine on cutting edge between incisor teeth and molar area. Labrum (Fig. 4j) with long anteroventral spine in protozoal phase.

Maxillule (Fig. 6a) with exopod a small round lobe bearing 4 plumose setae; endopod 3-segmented with 3-2-5 setae progressing distally; basal and coxal endites with 4 and 5 setae, respectively.

Maxilla (Fig. 7a) with segmentation indistinct; exopod small and oblong with 5 long plumose setae; endopod 5-segmented with setation of 4-2-2-2-3, segment 1 rarely with 3 setae; basal and coxal endites bifid, the 4 median lobes with 8-4-4-4 setae.

First maxilliped (Fig. 8a) with exopod of 1 segment bearing 7 long plumose marginal setae; endopod 4-segmented with 3-2-2-5 setae; basis with 12 setae in groups of 3 along medial margin; coxa with 5 setae; inner margins with fine setules as well.

Second maxilliped (Fig. 9a) with exopod of 1 segment bearing 6 marginal plumose setae; endopod 4-segmented with 2-1-2-5 setae; basis with 5 and coxa with 2 setae.

Third maxilliped a small bud.

Protozoa II (Fig. 10a, b)

Body length: 1.21 mm (0.10).



FIGURE 5.—*Sergestes similis*. Protozoa I: a, dorsal view; b, lateral view.

Carapace with rostrum but without pair of anterolateral processes; all processes with relatively large spines which branch distally into several small spinules, the processes themselves do not branch distally but bear small spinules to

tip; rostral process with 3 pairs of spines, each lateral process usually with 7, rarely 6 or 8, spines, and posterior process with 2-4, usually 3 or 4, pairs of spines. Eyes stalked and moveable with papilla on anterior margin of stalk. Thorax

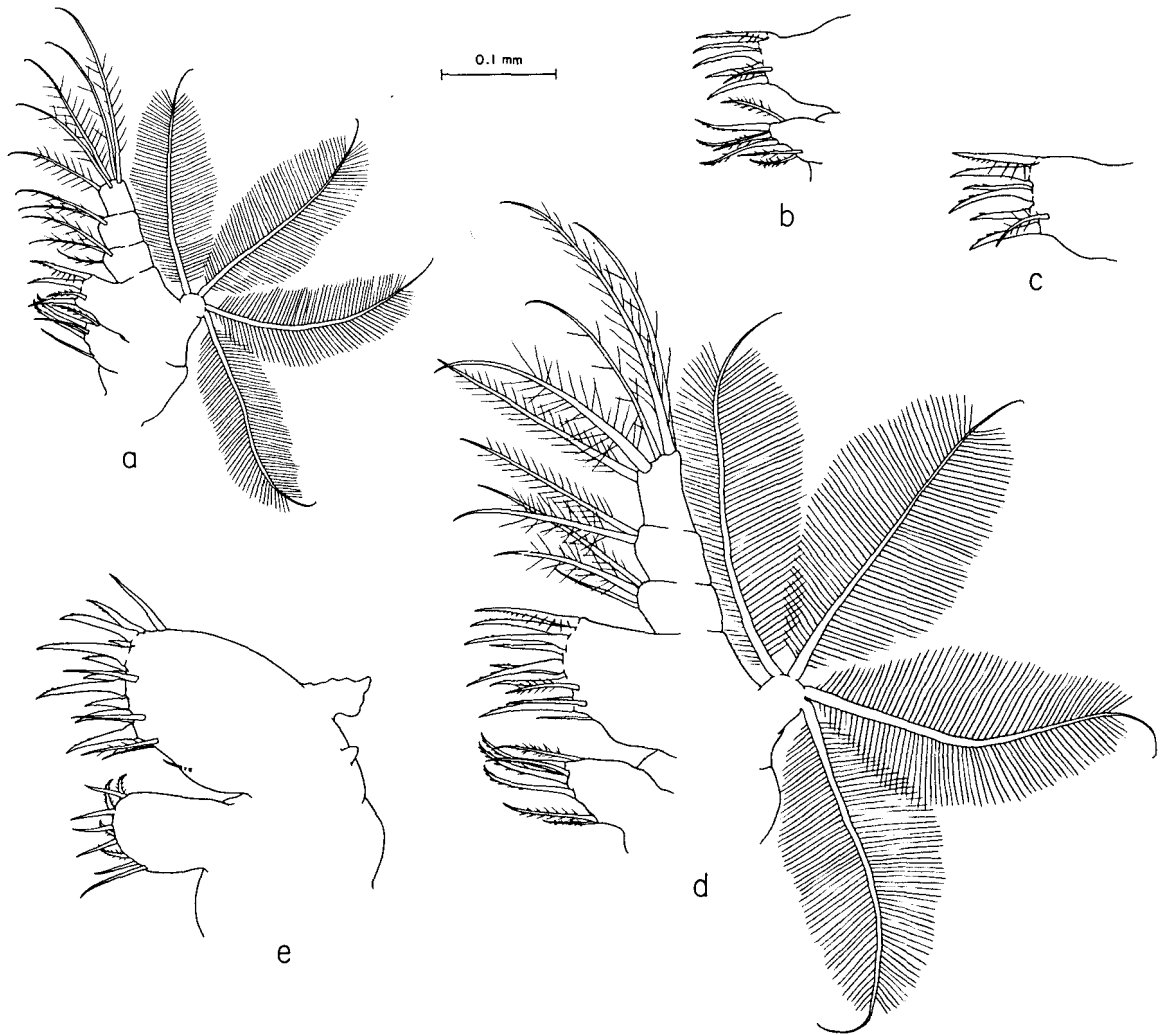


FIGURE 6.—*Sergestes similis*. Maxillule: a, protozoa I; b, protozoa II, coxal and basal endites; c, protozoa III, basal endite; d, zoea I; e, postlarva I.

with segments delineated; abdomen and telson as in preceding stage.

Antennule (Fig. 2f) with 4 subdivisions of proximal segment and distal segment with 9 processes, including 5 setae and 4 aesthetascs.

Mandibles (Fig. 4e) with median armature asymmetrical, right mandible with 2 and left mandible with 5 strong spines, the spine nearest molar area is strongest on each mandible, 2 long spines on right mandible separated by short tooth.

Maxillule (Fig. 6b) with 6 setae on basal endite and 6 or 7, usually 7, setae on coxal endite.

Maxilla (Fig. 7b) with setation of 8-4-5-5 on medial lobes.

First maxilliped with 7 or 8, usually 8, setae on coxa.

Second maxilliped with endopod setation of 2-2-2-5; basis with 5 or 6, rarely 6, setae.

Third maxilliped a small rudiment, sometimes slightly bifid at tip.

Anlagen of thoracic legs 1-5 may be visible.

Protozoa III (Fig. 11a, b)

Body length: 1.90 mm (0.18).

Carapace with 1 pair supraorbital processes which curve dorsolaterally in addition to armature of preceding stage; all processes but rostrum armed with strong spines which branch



FIGURE 7.—*Sergestes similis*. Maxilla: a, protozoa I; b, protozoa II, basal endite; c, zoea I; d, postlarva I.

distally into spinules, all processes terminate in single spine and bear spinules to tip; supra-orbital processes each with 9-14, usually 10-12, spines; each lateral process with 5-8, usually 7, spines; and posterodorsal process with 7-13,

usually 10-12, spines. Eyestalks longer than in stage II. Abdomen with 5 segments articulated, segment 6 still fused with telson; segments 1-5 with 1 pair lateral spines, segment 6 with biramous, unsegmented, nonsetose uropods and 1

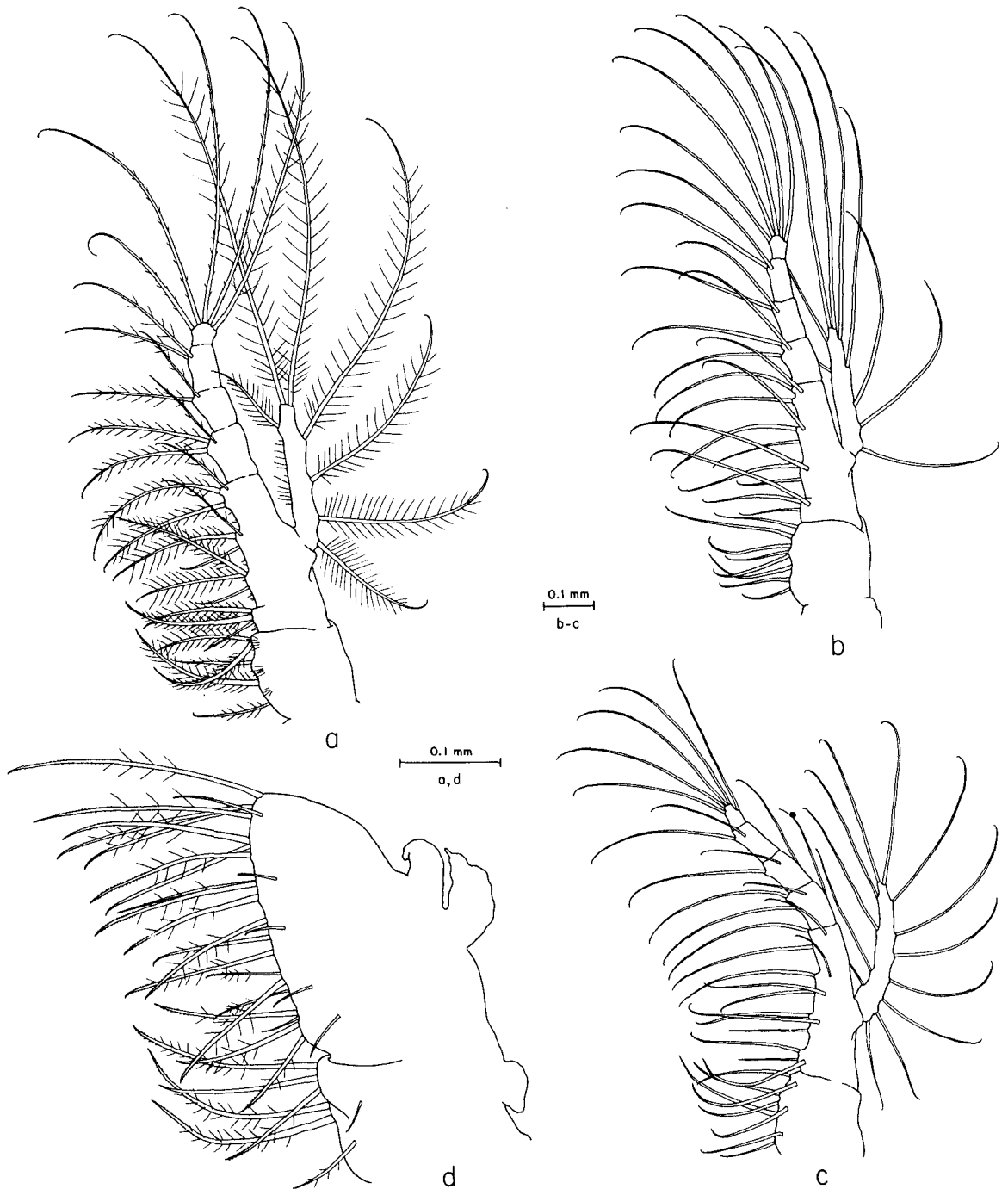


FIGURE 8.—*Sergestes similis*. First maxilliped: a-b, protozoaea I, III; c, zoea I; d, postlarva I; setules omitted on b and c.

pair small ventrolateral spines proximal to uropods; smooth ventral spines of telson relatively larger than in stage I.

Antennule (Fig. 2g) with proximal of 3 seg-

ments without subdivisions and segment 2 with 5 setae, otherwise setation unchanged.

Mandibles (Fig. 4f) usually with 3 and 6 spines on right and left cutting edges, 1 of 10 larvae

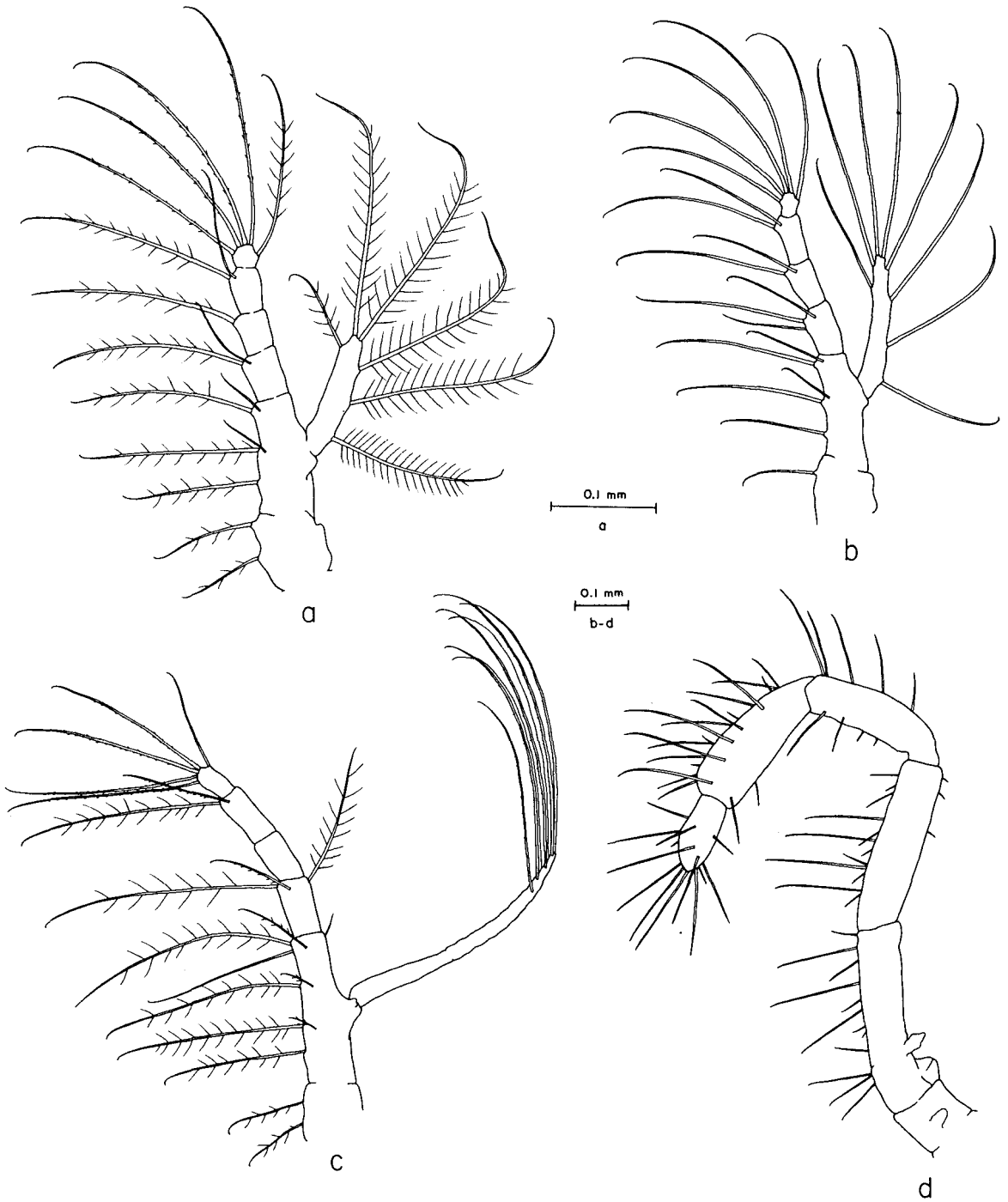


FIGURE 9.—*Sergestes similis*. Second maxilliped: a-b, protozoaea I, III; c, zoea I; d, postlarva I; setules omitted on b.

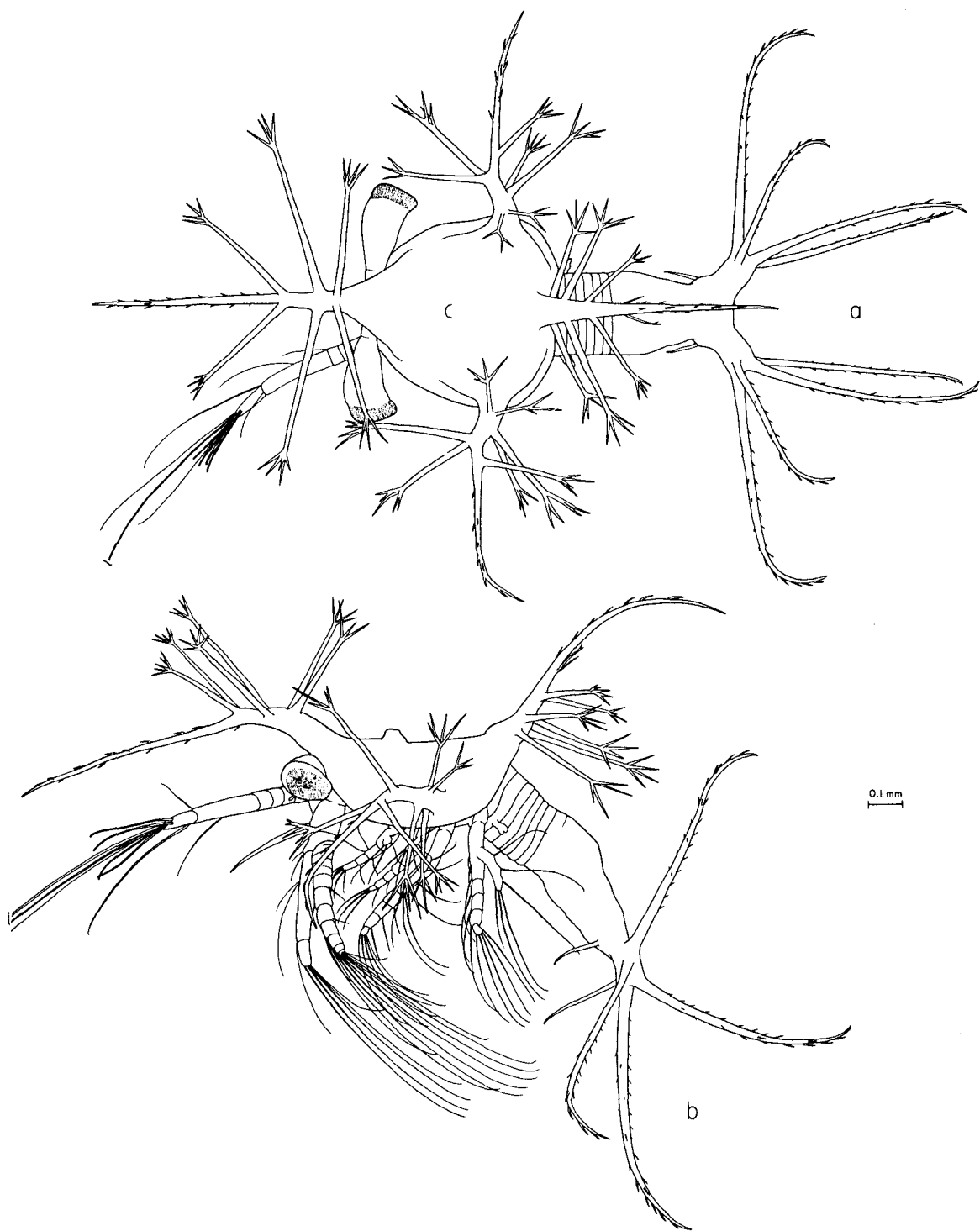


FIGURE 10.— *Sergestes similis*. Protozoa II: a, dorsal view; b, lateral view.



FIGURE 11.—*Sergestes similis*. Protozoa III: a, dorsal view; b, lateral view; c, third maxilliped and thoracic legs of late stage larva.

with armature of stage II, long spine nearest incisor teeth on right mandible separated from other long spines by several small teeth.

Maxillule (Fig. 6c) with 7 setae on both basal and coxal endites; as in earlier stages distal stout seta on basal endite with long basal spinules, other stout setae with short spinules.

Maxilla with setation of 9-5-6-5 on medial lobes, rarely with 8 setae on proximal lobe of coxal endite.

First maxilliped (Fig. 8b) with 9 setae on exopod.

Second maxilliped (Fig. 9b) with endopod setation of 3-2-2-5 and exopod with 8 setae; coxa with 1 or 2 setae.

Third maxilliped and thoracic legs 1-5 (Figs. 11c, 12a, d) biramous, unsegmented, and nonsetose with exopod slightly longer than endopod.

Zoea I (Figs. 13, 14a)

Body length: 3.25 mm (0.13).

Carapace altered with change in phase, now with 10 spines including rostrum, 1 pair supra-orbital, 1 pair hepatic, 2 pairs lateral, and 1 posterodorsal, all spines armed only with spinules except rostrum which bears a strong basal dorsal spine with spinules; dorsal organ present in zoeal phase but smaller than in preceding stages. Eyes with long slender stalk bearing single ventral papilla in both stages of phase.

Abdomen of 6 segments with following armature: segments 1-5 with 1 pair lateral spines which decrease in length posteriorly, segments 1-6 with 1 posterodorsal spine longest on segments 3-5, segment 6 with 1 pair small ventrolateral spines and segment 1 with 1 pair triangular dorsolateral processes; posterodorsal and lateral spines armed with spinules, lateral spines of segments 1 and 2 with relatively long spinules proximally on posterior margin, segments with dorsal and lateral setae as figured. Telson (Fig. 15e) slender with 1 pair lateral spines on rounded margin and produced distally into 2 long slender spines which bear 4 spinules near one-third their length and tiny spinules distally.

Antennule (Fig. 2h) with peduncle unsegmented and with following armature: basal lateral spine; 13-16, usually 15, long plumose setae along inner, outer, and distal ventral margins; smaller setae distributed near basal

spine and along dorsal surface of peduncle in clusters of 2-2-3-1-3. Flagella unsegmented; outer flagellum with 3 small spines and 1 seta distally, and dorsal tier of 6 aesthetascs near two-thirds the length of flagellum; inner ramus very small with 2 terminal spines.

Antenna (Fig. 3f) with scale (exopod) slender bearing 1 small subterminal ventral seta, 1 subterminal seta on outer margin, and 10 or 11, usually 11, setae on distal and inner margins, all setae with setules, terminal setae relatively stout and graded in size from short lateral to long medial seta; flagellum (endopod) with about 8 segments, proximal segment about the length of scale, distal segment with 4 terminal spines, 1 seta projecting laterally from each side, and 1 seta directed anteriorly; a strong spine with basal spinule appears on inner margin of flagellum before midpoint of segment 1 and distally on segment 6.

Mandibles (Fig. 4g) with 4 and 7 relatively long spines on right and left blades between incisor teeth and molar surfaces, bud of palp present. Labrum (Fig. 4k) with anteroventral spine present but shorter than in preceding phase.

Maxillule (Fig. 6d) with 11 setae on basal endite.

Maxilla (Fig. 7c) with exopod modified bearing 1 long plumose seta on proximal lobe and 4 small processes approximately in position of plumose setae of preceding stage; endopod unchanged; medial lobes with setation of 9-5-6-6.

First maxilliped (Fig. 8c) with form as in protozoeal phase; exopod with 13 marginal setae; endopod with setation of 4-3-2-5; basis with 13 and coxa with 8 setae.

Second maxilliped (Fig. 9c) somewhat modified, long flexible exopod with 7 or 8, rarely 8, setae and resembling exopod of thoracic leg rather than form of preceding phase; endopod 4-segmented with 3-0-2-5 setae; basis with 9 and coxa with 2-4 setae.

Third maxilliped (Fig. 12b) functional and pediform; exopod with 19-23, usually 21, setae; endopod 4-segmented, usually with setation of 3-4-4-5, rarely with 5 setae on segment 2; basis with 4 setae, coxa nonsetose.

Legs 1-5 functional; legs 1-3 (Fig. 12e) similar, shorter than third maxilliped; exopods with 20-22, frequently 21, setae; endopods 4-segmented with 3-4-4-4 setae and bases with 3 or 4 setae. Legs 4 and 5 (Fig. 16c, d) smaller than first three pairs; exopods with 17-19 setae; endopods

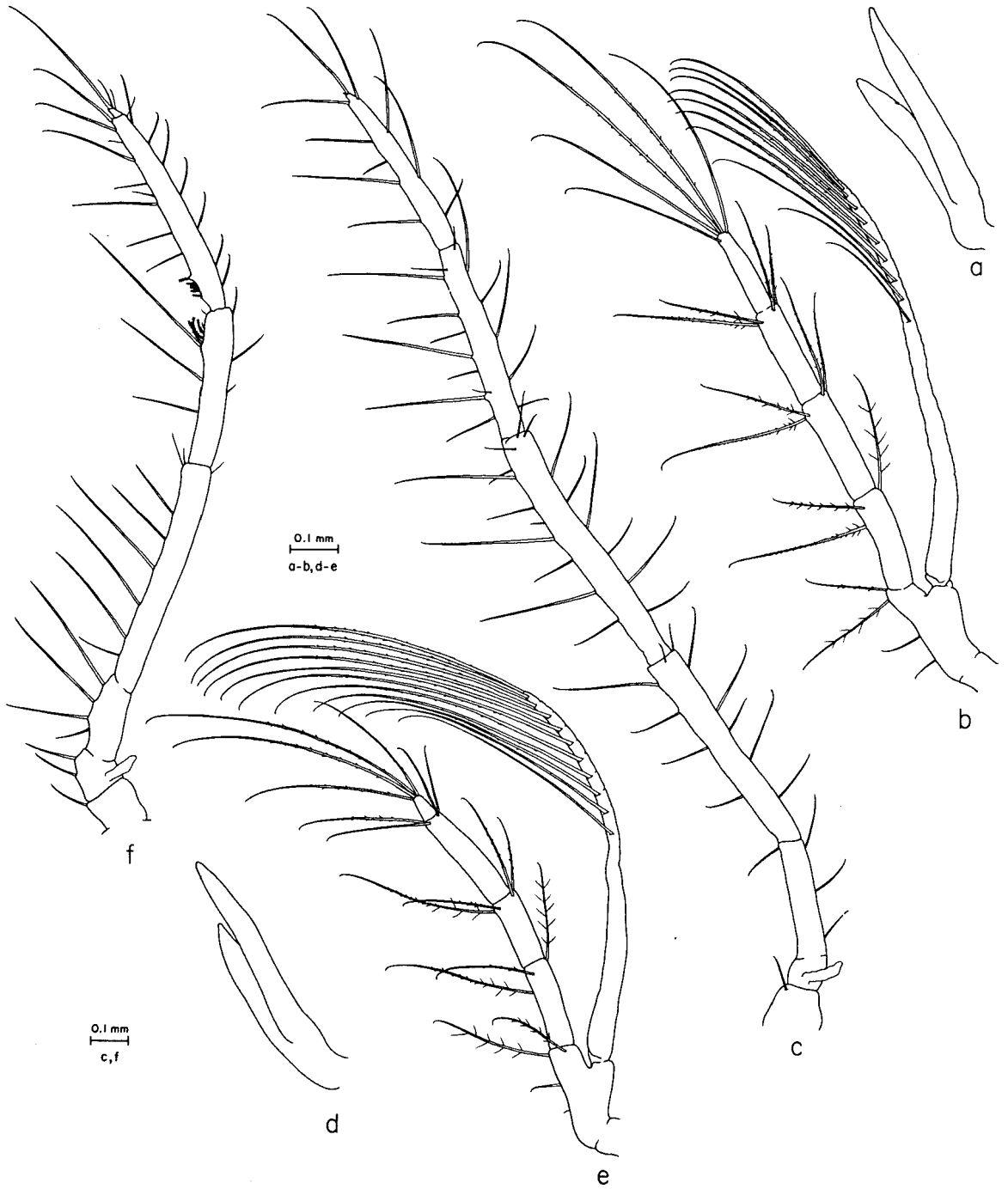


FIGURE 12.—*Sergestes similis*. Third maxilliped: a, protozoa III; b, zoea I; c, postlarva I. Leg 1: d, protozoa III; e, zoea I; f, postlarva I.

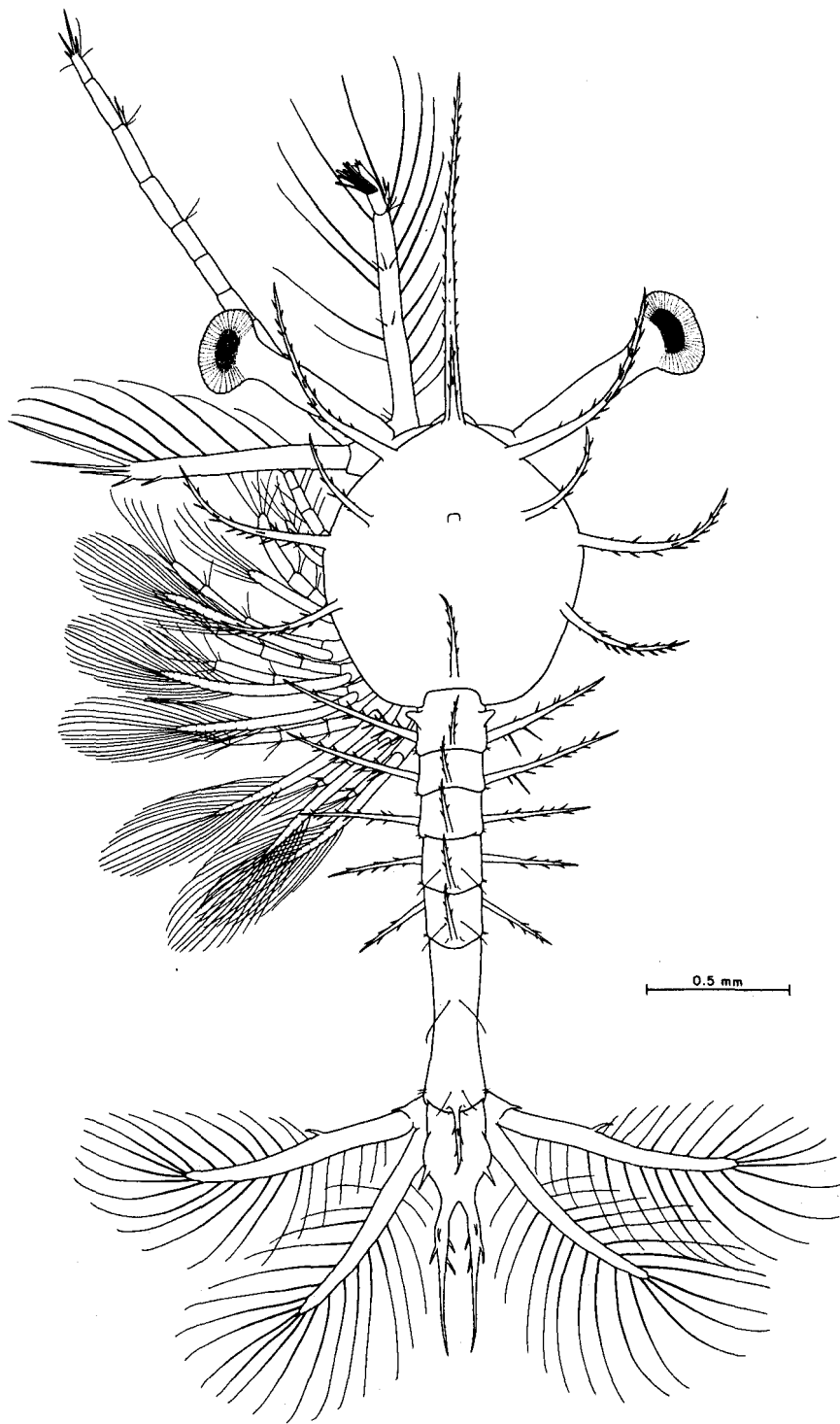


FIGURE 13.—*Sergestes similis*. Zoea I, dorsal view.

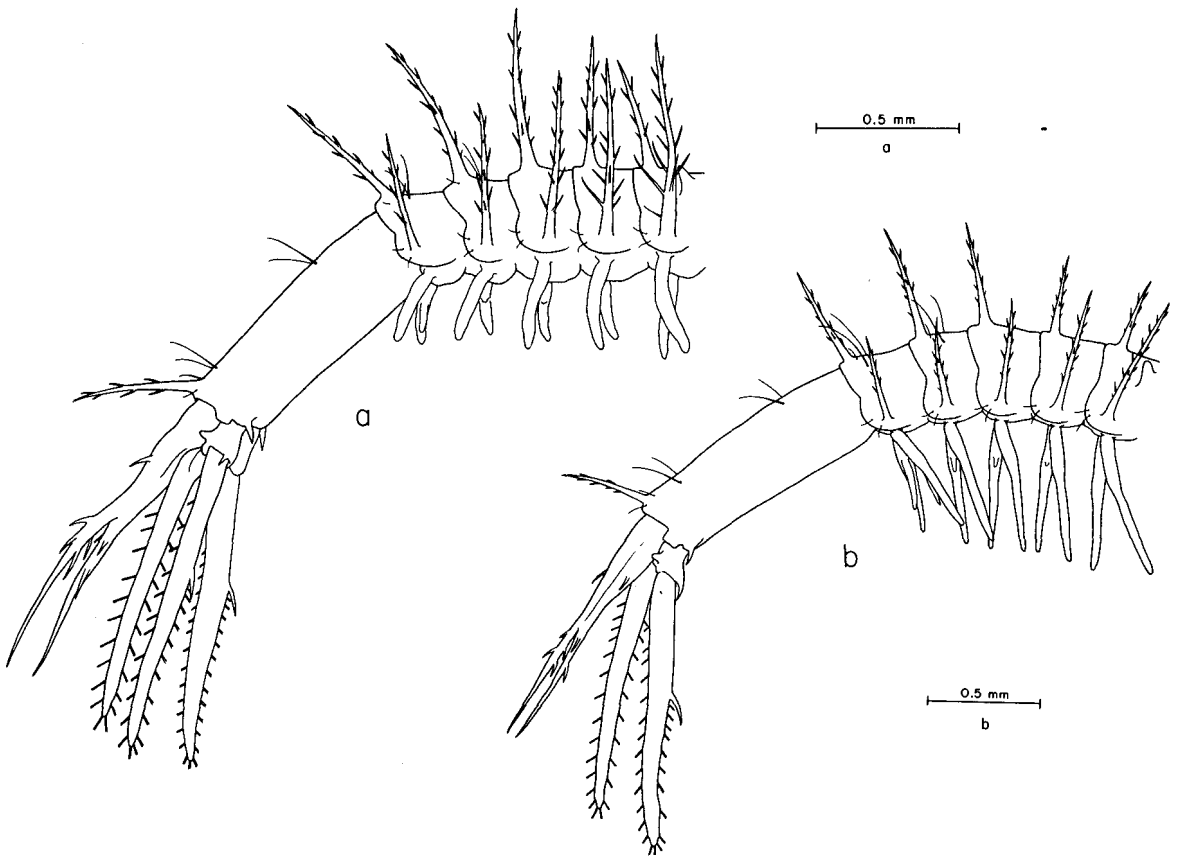


FIGURE 14.—*Sergestes similis*. Abdomen, lateral view: a, zoea I; b, zoea II.

3-segmented with 3-3-4 setae on leg 4, rarely 4 setae on segment 2, and 2-3-4 setae on leg 5; bases with 1 seta, coxae nonsetose.

Pleopods (Fig. 15a) present on abdominal segments 1-5 and variable in size within stage; exopods nonsetose decreasing in length from pleopod 1 to 5; pleopod 5 with nonsetose endopod about two-thirds length of exopod, pleopod 4 with small bud of endopod, pleopods 2 and 3 sometimes with some swelling in position of endopod.

Uropods with rami articulated; protopod with lateral spine and posterior projection (Fig. 14a); exopod and endopod long, slender, and fringed with plumose setae except proximal to smooth spine on lateral margin of exopod.

Zoea II (Figs. 14b, 17)

Body length: 4.42 mm (0.20).

Carapace, abdomen, and telson (Fig. 15f) with armature as in preceding stage; spines shorter

relative to size of larva and lateral spines of abdominal segments 1 and 2 without long posterior spinules.

Antennule (Fig. 2i) with peduncle bearing 16-19, usually 17 or 18, marginal plumose setae and small setae in clusters of 3-4-3-1-3; outer flagellum with 1 distal seta and usually unsegmented, sometimes constricted at two points distal to tier of 6 aesthetascs, rarely with weak sutures; inner ramus without spines.

Antenna (Fig. 3g) with scale armed with long subterminal spine on outer margin bearing spinules, a small subterminal ventral seta, and 14 or 15 marginal plumose setae, terminal setae no longer stout; flagellum long, with 19-25 segments in three reared larvae, terminal segment with 2 spines and 3 setae, 1 seta projects laterally from each side.

Mandibles (Fig. 4h) with armature unchanged; palp larger than in zoea I, unsegmented and nonsetose. Labrum with short remnant of anteroventral spine.

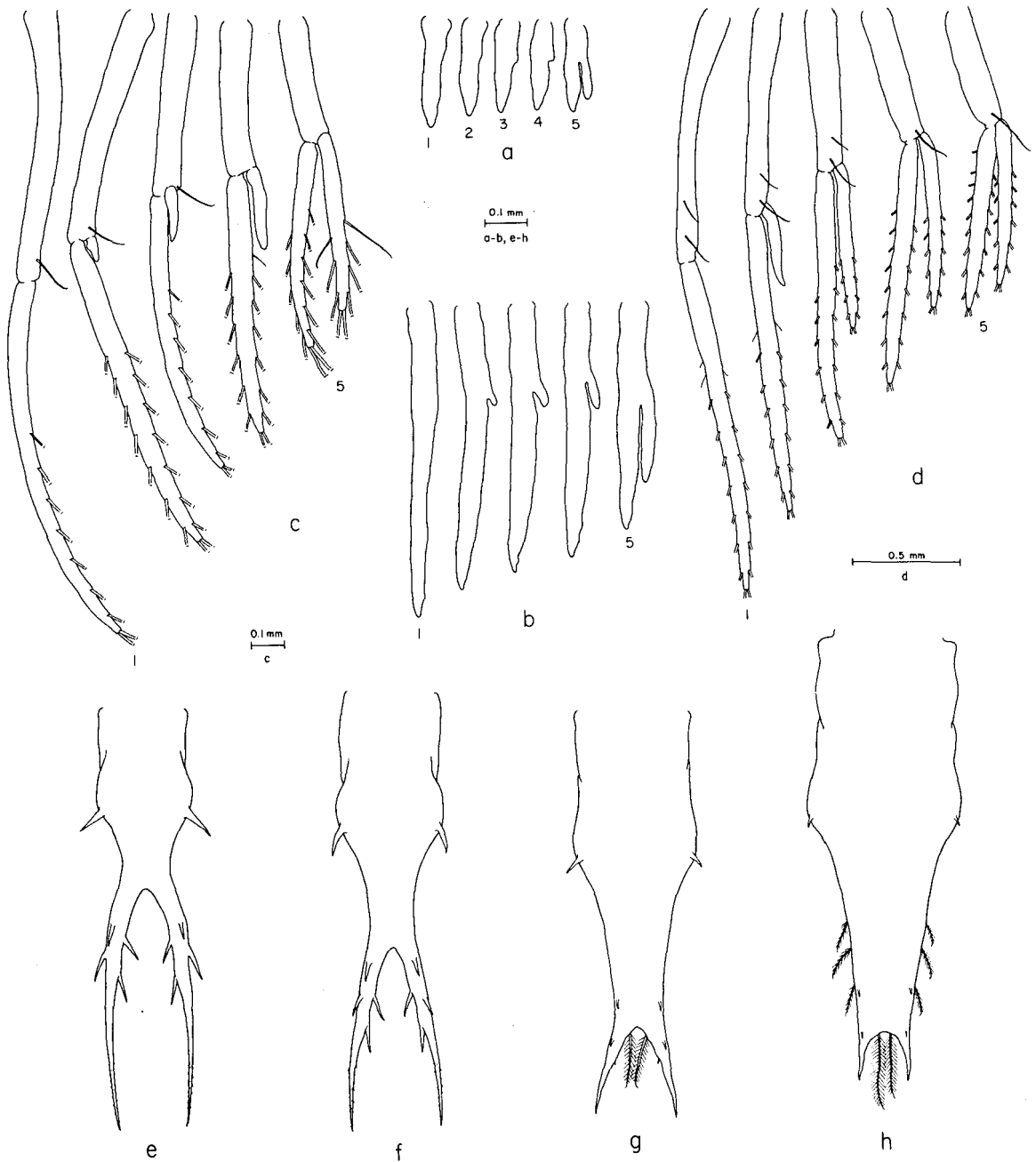


FIGURE 15.—*Sergestes similis*. Pleopods: a-b, zoea I-II; c-d, postlarva I-II. Telson: e-f, zoea I-II; g-h, postlarva I-II.

Maxillule with 12 or 13, usually 12, setae on basal endite and 8 or 9 setae on coxal endite.

Maxilla unchanged except that exopod relatively larger with small processes now tiny.

First maxilliped with 13 or 14, usually 13, setae on exopod.

Second maxilliped with endopod setation of 4-

2-3-5, rarely 5 and 4 setae on segments 1 and 3; exopod with 7 setae; basis with 9 or 10 and coxa with 3 or 4 setae.

Third maxilliped with 4 or 5, rarely 4, setae on distal segment of endopod and 3 setae on basis.

Legs 1-3 with endopod slightly longer than exopod, legs 2 and 3 with distal margin of

endopod segment 3 swelling in formation of chela (Fig. 16a); exopods with 20-24, usually 22, setae; endopods usually with setation of 3-4-5-4, rarely 5 and 4 setae on segments 2 and 3; bases with 3 or 4 setae. Leg 4 exopod with 18-21 setae, endopod usually with setation of 3-3-4, rarely with 2 and 4 setae on segments 1 and 2. Leg 5 exopod with 16-19 setae, endopod usually

with setation of 2-3-4, rarely with 3 setae on segment 1.

Pleopods (Fig. 15b) nonsetose but longer than in preceding stage, exopods again decreasing in length from anterior to posterior pairs; pleopods 2-5 with endopod which increases in size posteriorly with variation in size within stage with age.

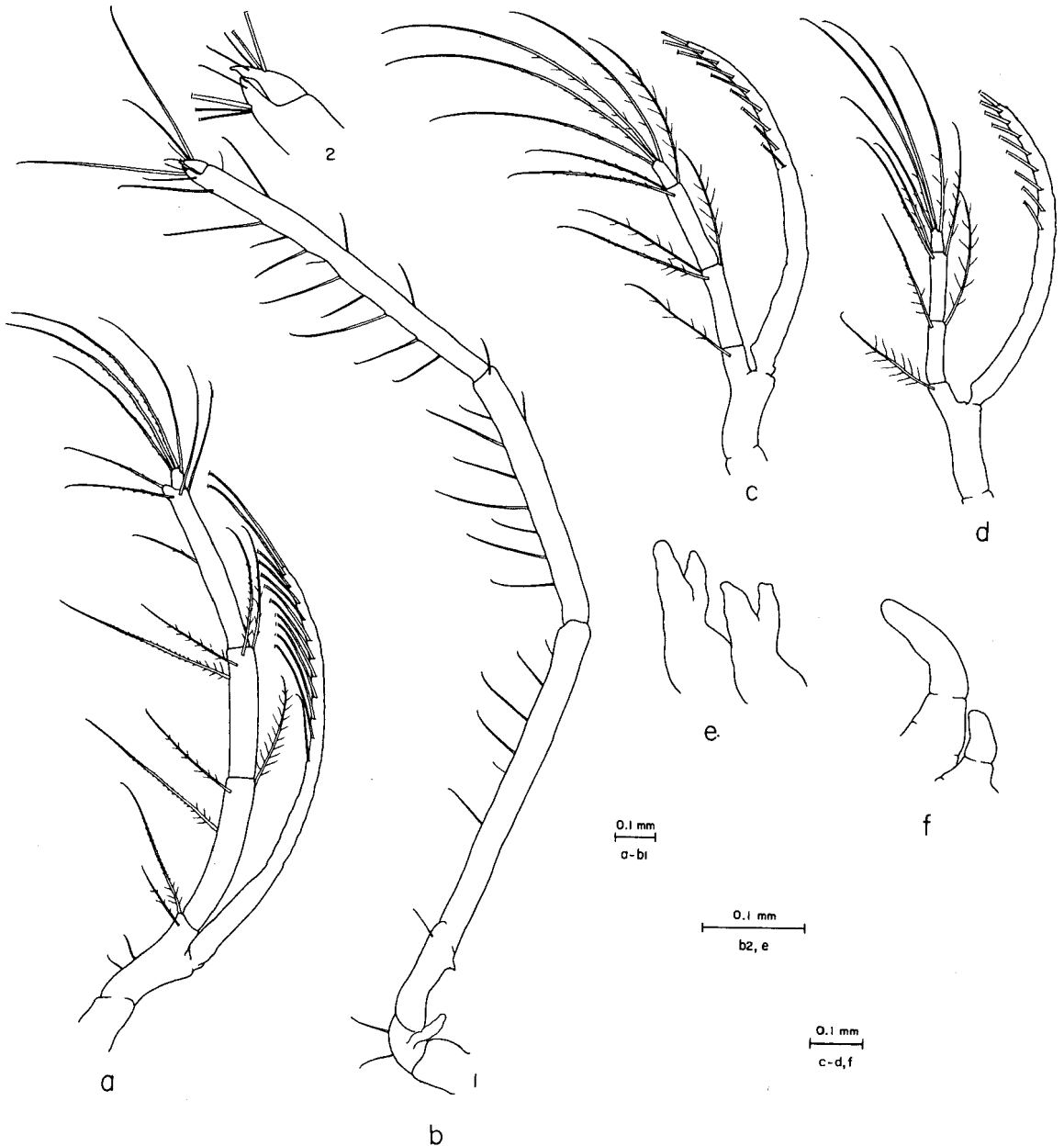


FIGURE 16.—*Sergestes similis*. Leg 2: a, zoea II; b, postlarva I. Leg 4: c, zoea I. Leg 5: d, zoea I. Legs 4 and 5: e-f, postlarva I-II.

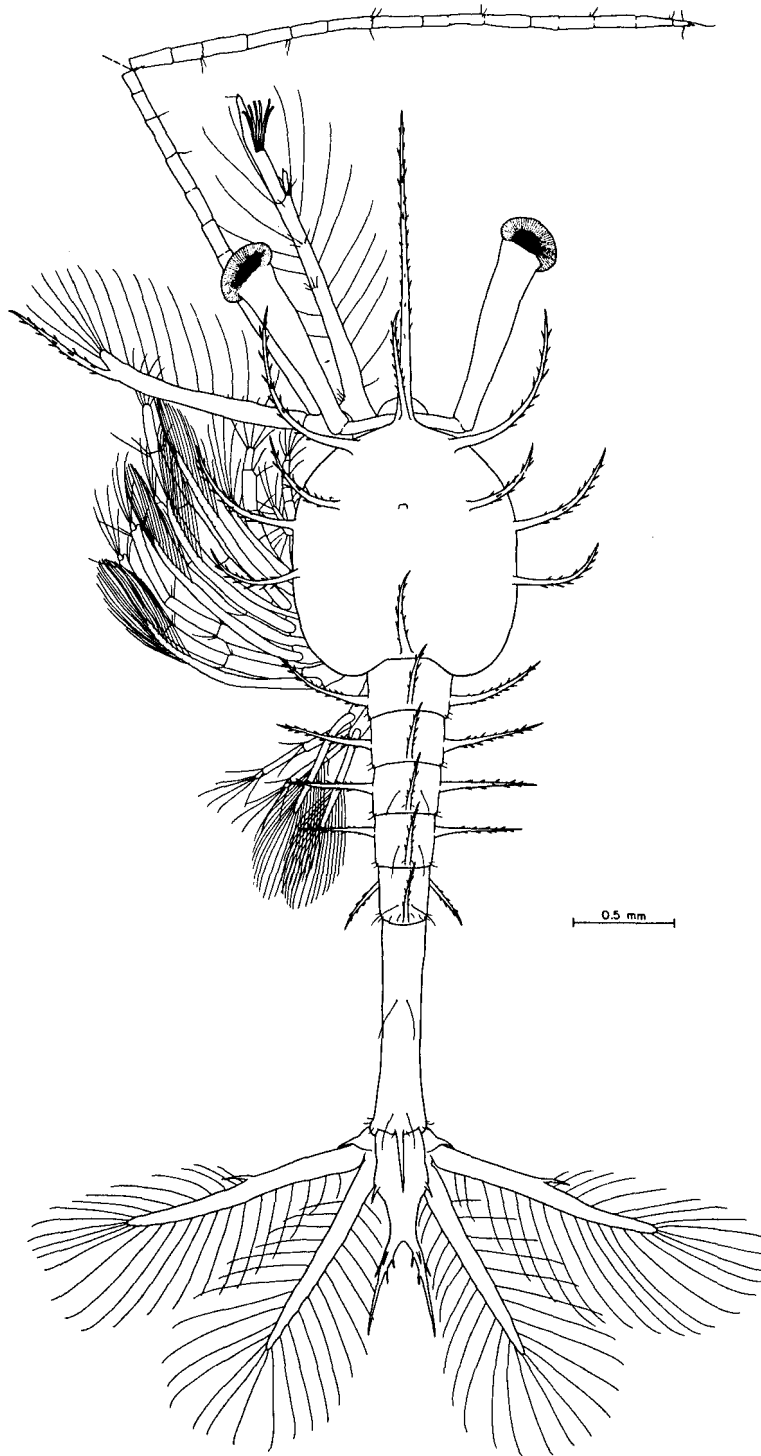


FIGURE 17.—*Sergestes similis*. Zoea II, dorsal view.

Postlarva I (Fig. 18a)

Body length: 5.07 mm (0.26).

Carapace with armature reduced, 2 pairs of lateral spines of preceding phase missing or only tiny remnants; rostrum, supraorbital, and hepatic spines, and posterodorsal spine shorter relative to length of carapace. Abdomen with lateral spines of segments 1-5 and posterodorsal spines of segments 1 and 2 small and without spinules. Telson (Fig. 15g) with posterior fork spines much shorter in relation to body of telson than in zoeal phase, with spinules reduced and with pair of plumose setae on inner margin near base of fork; relative length of terminal setae and fork spines vary within stage.

Antennule (Fig. 2j) with peduncle 3-segmented and fringed with marginal plumose setae, basal segment with statocyst and lateral spine; rows of small setae now situated on distal margins of segments; outer flagellum with 10 segments, proximal segments 1-3 with 1-2-6 medioventral aesthetascs, 6 aesthetascs of segment 3 set proximally on small protuberance; inner flagellum with 2 segments.

Antenna (Fig. 3h) with subterminal lateral spine of scale smaller than in zoea II, scale with 20-22 marginal setae; flagellum very long, about 2.6 times body length in one reared larva.

Mandibles (Fig. 4i) with cutting edges smooth between simplified incisor and molar processes, left mandible with notch opposing incisor tooth of right mandible; palp with 5-7 setae and sometimes indistinctly 2-segmented. Labrum without spine.

Maxillule (Fig. 6e) with endopod reduced to small nonsetose rudiment and with tiny vestige of exopod, basal and coxal endites with increased numbers of setae.

Maxilla (Fig. 7d) with endopod reduced to small nonsetose rudiment; scaphognathite (exopod) large with 17 or 18 marginal setae, 1 posterior seta relatively long; coxal and basal endites bifid, medial lobes with 2-2-4-4 to 6 setae.

First maxilliped (Fig. 8d) with small nonsetose exopod and endopod, coxa with medial setae and small epipodite, basis with broad flat medial lobe armed with setae along inner margin.

Second and third maxillipeds and legs 1-3 with small nonsetose remnant of exopod.

Second maxilliped (Fig. 9d) with endopod long, 5-segmented, recurved at articulation of merus and carpus, and armed with strong setae,

articulation of ischium and basis indistinct if visible; coxa with bud of epipodite.

Third maxilliped (Fig. 12c) with endopod long, 5-segmented, and with strong marginal setae.

Leg 1 (Fig. 12f) with clusters of strong barbed setae at articulation of propodus and carpus, legs 2 (Fig. 16b) and 3 with small setose chela, leg 2 with small spine on lateral margin of ischium. Leg 3 slightly longer than first maxilliped. Legs 4 and 5 (Fig. 16e) reduced to irregular, nonsetose bifid rudiments.

Pleopods (Fig. 15c) with setose exopods; endopod of pleopod 5 setose, rarely endopod 4 with 1 or 2 terminal setae, as before endopods increase and exopods decrease in length from anterior to posterior pairs; protopod with 1 distal seta on inner margin of pleopods 1-3; endopods vary in size within stage.

Postlarva II (Fig. 18b)

Body length: 5.80 mm (0.20).

Carapace and abdomen with armature reduced in size, small posterodorsal spine of carapace may be missing and dorsal spines of abdomen segments 1 and 2 very small. Telson (Fig. 15h) with posterolateral spines reduced in length and usually with 3 pairs plumose lateral setae in addition to terminal pair.

Antennule with outer flagellum, in exuvia of one reared larva, with about 17 segments and increased number of aesthetascs on proximal segments; inner flagellum with 2 or 3 segments.

Antenna with subterminal lateral spine of scale smooth or with few spinules and reduced in length, scale with 24-28 marginal setae.

Mandibles with palp 2-segmented bearing 11-14, usually 11 or 12, setae.

Maxillule with endopod more distinctly shaped; vestige of exopod not present.

Maxilla with 25-27 setae on scaphognathite; endopod larger than in preceding stage with outer basal seta and sometimes inner seta; medial lobes with setation of 2-3-5 to 8-8 or 9.

First maxilliped with endopod, exopod, and epipodite larger than in postlarva I, rarely endopod slightly longer than exopod with some indication of segmentation.

Second and third maxillipeds and legs 1-3 without vestige of exopod; legs 1 and 2 with small ischial spine; legs 4 and 5 (Fig. 16f) more distinctly formed, nonsetose, and with leg 4 longer than leg 5.

Pleopods 3-5 (Fig. 15d) with setose endopods,

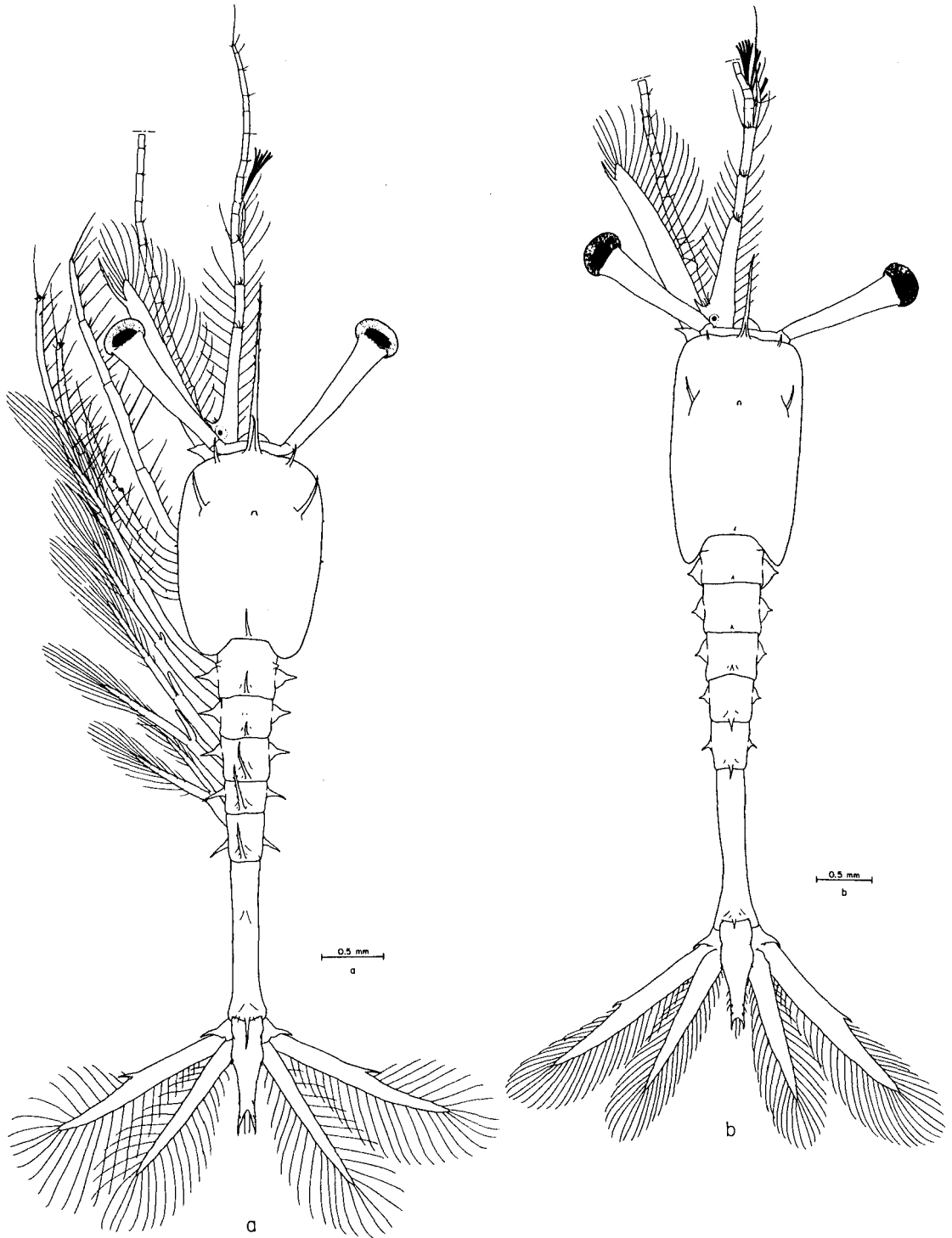


FIGURE 18.—*Sergestes similis*. a, postlarva I; b, postlarva II.

rarely endopod of pleopod 2 with 1 or 2 small setae; protopods of pleopods 1-3 with 2 setae; those of pleopods 4 and 5 with or without 1 seta on protopod.

DISCUSSION

Yaldwyn (1957) defined two subgenera, *Sergestes* s.s. and *Sergia*, within what he termed the rather unwieldy genus *Segestes* s.l. Recently, the subgenera were raised to full genera by Omori (1974). The species of *Sergestes* have specialized luminescent modifications of the gastrohepatic gland called organs of Pesta and are without cuticular pigmentation and dermal photophores, while species of *Sergia* are without organs of Pesta and, with some exceptions, have uniform cuticular pigmentation and often dermal photophores. The two genera are themselves divided into species groups, six in *Sergestes* and three in *Sergia*, which appear to be easily distinguished and are considered to be natural phyletic units (Judkins 1978).

The *arcticus* group includes only two species, *Sergestes arcticus* and *S. similis*, and is characterized by the morphology of third maxilliped, fifth pereopod, antennular peduncle, and petasma (Yaldwyn 1957). *Sergestes similis* differs from *S. arcticus* in having a more slender and fragile body and antennular peduncle, in a longer and more upwardly directed rostrum, in proportions of posterior arthrobranches above the third and fourth pereopods, and in some proportions and armature of petasma and thelycum (Milne 1968).

The close relationship of *S. similis* and *S. arcticus* which has been inferred from adult morphology may also be seen in their larval morphology, especially in the shape of eye, in the ornate armature of protozoal carapace, and in the armature of carapace, abdomen, and telson in the zoeal phase. Gurney and Lebour (1940) described larvae now known to be representative of all of the species groups within *Sergestes* s.l. and noted that the protozoa II and III of *S. arcticus* were very distinct in form of eye and peculiarly branched spines. They described some features of protozoa II and III, zoea I and II, and postlarva I of *S. arcticus* and gave figures of the second protozoa and zoea, with telson of postlarva I. They stated that the "brushlike endings" of the long spines on rostral, lateral, and posterior processes of protozoa II and on supraorbital, lateral, and posterior processes of

protozoa III were most characteristic of the species. The protozoa II and III of *S. similis*, identified in this study, have the same distinctive armature of carapace spines.

The larval stages of *S. arcticus* discussed by Gurney and Lebour (1940) resemble the comparable stages of *S. similis* in the details they described and figured. Gurney and Lebour, however, do not deal with the structure of mouthparts and thoracic appendages; rather, they note that these appendages seem to be uniform throughout the genus and refer the reader to the earlier descriptions of *S. arcticus* by Wasserloos (1908) and Hansen (1922). Gurney, in a later work (1942), does figure the appendages of protozoa III of *S. cornutus*, an *atlanticus* group species, and they appear very similar to those of the same stage of *S. similis*.

The protozoal stages of *S. arcticus* described by Wasserloos (1908), on the other hand, differ from those of *S. similis* in setation and/or segmentation of antennule, antenna, and mouthparts, but appendages are not figured; the armature of carapace differs in protozoa II and III on lateral and supraorbital processes, respectively. The species appear similar in described and figured features of the zoeal phase.

Hansen (1922) offered a brief summary of Wasserloos' description of the protozoal phase and added both generic and specific comments, with figures, on the zoea and postlarva of *S. arcticus* from his own observations. He noted that the mouthparts of the protozoa are like those of the zoeal stages which he described in some detail but which do not always agree with details of the protozoal phase described by Wasserloos. Hansen also noted that the rostrum in protozoa III is little modified from stage II, yet conspicuous secondary spines are lost in this molt. In the zoeal phase, *S. similis* larvae differ from those of *S. arcticus*, as described by Hansen, in segmentation of maxillule and first maxilliped.

Unfortunately, because the descriptions of *S. arcticus* by Wasserloos (1908) and Hansen (1922) were found to be inconsistent with each other and with that of Gurney and Lebour (1940), and they could not be interpreted with confidence, a detailed comparison with *S. similis* was not possible. A reexamination of the larval stages of *S. arcticus* is needed to detect specific differences that may exist between the apparently very similar *arcticus* group species.

Gurney and Lebour (1940) believed the elaborate protozoal phase of *Sergestes* s.l. to be of particular importance, as it might "point to a satisfactory subgeneric grouping of the adults." They separated the second and third protozoae of thirteen species of *Sergestes* s.l., representative of all of the nine species groups later defined by Yaldwyn (1957), into three types: *dohrni*, *ortmanni*, and *hispida*. The carapace has the same number of processes in all three types but the armature of the processes differs as follows: *dohrni* type with numerous long lateral spines on supraorbital, lateral, and posterior processes; *ortmanni* type with long spines on supraorbital processes but with long spines only at the bases of lateral and posterior processes on carapace; *hispida* type without long spines on supraorbital, lateral, or posterior processes, although there may be basal spines on lateral and posterior processes. Gurney and Lebour observed that the *ortmanni* armature seems to be derived from the *dohrni* type in that it retains long lateral spines on supraorbital processes.

These larval types do correspond with three divisions of species within *Sergestes* s.l. Of the species described by Gurney and Lebour (1940), the *hispida* type larvae all belong to the genus *Sergia*, while the *dohrni* and *ortmanni* types belong to *Sergestes*; *S. corniculum* is of the *ortmanni* type, but all other species of *Sergestes* identified are of the *dohrni* type. The zoeal stages could not be separated into groups which corresponded to the protozoal types.

Gurney and Lebour (1940) noted that the *dohrni* type carapace was found in a number of species which were not supposed to be particu-

larly closely related and which could not be grouped further by structure of the protozoal phase. The identification of *S. similis* larvae has proved this untrue with respect to the *arcticus* group species, but apparently it does apply to species of the *atlanticus* group, the only other species group within *Sergestes*, or *Sergia*, all of whose protozoal stages are identified. Gurney and Lebour described the larvae of *Sergestes atlanticus* and *S. cornutus*, the two species which comprise the *atlanticus* group, and observed that larval morphology did not corroborate the close relationship implied by the morphology of adult petasma. The carapace armature in protozoa II and III of the *arcticus* and *atlanticus* groups is compared in Table 1 to show the range of variation within each group; the species groups themselves are not considered to be closely related within the genus (Judkins 1972). *Sergestes arcticus* and *S. similis* may have the same armature in both protozoal stages, while *S. atlanticus* and *S. cornutus* differ in each stage; all of the lateral spines of the *atlanticus* group have smooth tips rather than the brushlike endings characteristic of the *arcticus* group.

The difference in larval morphology within the *atlanticus* group is in accordance with the significant difference described by Foxton (1972) between *S. atlanticus* and *S. cornutus* in morphology of the organs of Pesta. This discrepancy was one of two exceptions noted by Foxton to a generalization that species of *Sergestes* that are the most similar in other adult diagnostic characters usually have identical or closely similar organs of Pesta; he does not note any difference between the *arcticus* group

TABLE 1.—Comparison of the number of long lateral spines which arm carapace processes in protozoa II and III of two species groups of *Sergestes*; the lateral spines have smooth tips in the *atlanticus* group and branching tips ("brushlike endings") in the *arcticus* group (descriptions of the *atlanticus* group and *S. arcticus* are taken from Gurney and Lebour (1940)).

Carapace processes	arcticus group		atlanticus group	
	<i>S. similis</i>	<i>S. arcticus</i>	<i>S. atlanticus</i>	<i>S. cornutus</i>
Protozoa II:				
Rostrum	6 in 3 pairs	as <i>similis</i>	7 rather irregularly arranged	8 in 4 pairs + 2 ventral
Lateral, each	6-8, usually 7	¹ 7	9	8
Posterior	4-8, with 3 large pairs	6 in 3 pairs	6, process swollen basally	4 in 2 pairs
Protozoa III:				
Rostrum	with spinules only	as <i>similis</i>	3 ventral	7 ventral
Supraorbital, each	9-14, usually 10-12; processes curve posterolaterally	9, orientation as in <i>similis</i>	ca. 15; processes curve inward to meet and overlap	12-19; processes directed anterolaterally
Lateral, each	5-8, usually 7	7	17-20	12-14
Posterior	7-13, usually 10-12 in 5-6 pairs	10 in 5 pairs	16 arranged in circle on large basal swelling	8 in 4 pairs

¹Gurney and Lebour (1940) report eight long spines on the lateral carapace process, but their figure shows seven with brushlike endings and the simple spinulose tip of process, the common armature in *S. similis*.

species in morphology of this feature. The correspondence between variation in morphology of protozoal stages and organs of Pesta within the two species groups indicates that, with identification of additional species, larval morphology may prove useful in the study of interspecific relationships within *Sergestes*, as predicted by Gurney and Lebour (1940).

The larvae of *S. similis* were also compared with those of *hispida* type *Sergia lucens* (Omori 1969), one of the seven species comprising the *challengeri* group. They were found to differ in body armature, as expected from difference in protozoal type, in form of telson, and in development of some appendages, as shown in Table 2. They also differ in number of naupliar stages. Four distinct stages were observed in the naupliar phase of *Sergestes similis*, while in *Sergia lucens* nauplius I and II were found and the latter developed gradually to molt into protozoa I. When this finding is coupled with the observations by Nakazawa (1916, 1932), they suggest that there are zero to two molts during the naupliar phase of *S. lucens*. An assessment of the significance of these observations requires additional knowledge of larval development within the two closely related genera and their species groups.

ACKNOWLEDGMENTS

This work was supported by the Marine Life Research Program, the Scripps Institution of Oceanography's component of the California Cooperative Oceanic Fisheries Investigations.

We are very grateful to Kuni Hulsemann and her colleagues for a translation of Wasserloos (1908), to A. Fleminger for the method and materials to treat larvae with KOH and Chlorazol Black E, and to E. Brinton for criticism of the manuscript.

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TABLE 2.—Some differences between larvae of *Sergestes similis* and *Sergia lucens*.

Feature	<i>Sergestes similis</i>	<i>Sergia lucens</i>
Carapace armature:		
Protozoa I	anterolateral process branches to 3 spines posterodorsal process a single spine with basal spinules	anterolateral process branches to 4 spines posterodorsal process branches to 3 spines
Protozoa II	all processes with long spines which branch to spinules distally	all processes with small spinules only
Protozoa III	rostrum with small spinules, armature of other processes as in II	as in II
Zoea I-II	with 2 pairs lateral spines	with 3 pairs lateral spines
Postlarva I	lateral spines remnants only, other spines present	rostrum and small posterodorsal spine present; supra-orbital spine and basal spine of rostrum sometimes present, lateral and hepatic spines missing
Abdomen armature:		
Zoea I-II	lateral spines decrease in length posteriorly, spines 1 and 2 with relatively long spinules in I	lateral spines increase in length posteriorly, without long spinules in I
Telson:		
Zoea I-II	fork with 2 outer and 2 inner spinules, invagination does not reach lateral spines	fork with 1 outer and 5/6 inner spinules in I, with 2 outer spinules in II, invagination about as deep as lateral spines
Postlarva I	fork relatively wide with tiny spinules	fork narrow, with 2 large inner setae
Antennule:		
Zoea I-II	outer flagellum unsegmented in rarely 2- or 3-segmented in II and shorter than peduncle	outer flagellum 2-segmented in I, ca. 8-segmented in II, and longer than peduncle
Antenna:		
Zoea I	endopod 8-segmented and longer than rostrum	endopod 2-segmented and shorter than rostrum
Mandible:	palp appears in zoea I	palp appears in zoea II, rarely in zoea I
First maxilliped:		
Zoea I-II	exopod with 13 or 14 setae	exopod with 12 setae

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