

**COPEPODIDS AND ADULTS OF
LEPTINOGASTER MAJOR (WILLIAMS, 1907), A POECILOSTOMATOID
COPEPOD LIVING IN MYA ARENARIA L. AND
OTHER MARINE BIVALVE MOLLUSKS**

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ABSTRACT

The five copepodid stages and adults of *Leptinogaster major* (Williams, 1907), a poecilostomatoid copepod (family Clausidiidae) living in the mantle cavity of *Mya arenaria* L. and other marine bivalve mollusks along the coast of eastern North America from Prince Edward Island, Canada, to Louisiana, are described. Copepodid I is *Saphirella*-like in body form. In the adult female the maxilliped is present though much reduced. Sexual differentiation first occurs in Copepodid IV, where the male and female maxillipeds are differently formed.

The poecilostomatoid copepod *Leptinogaster* (= *Myocheeres*) *major* (Williams, 1907) has been reported from the mantle cavity of various marine bivalve mollusks along the eastern shore of North America, from Prince Edward Island, Canada (J. C. Medcof in correspondence with M. S. Wilson) to Louisiana (Causey 1953). This copepod has undergone several name changes, but it seems generally agreed now that it properly belongs in the genus *Leptinogaster* (see Bocquet and Stock 1958, and Table 1). The seasonal population changes and host relationships of this species have been described by Humes and Cressey (1960), who listed as hosts *Mya arenaria* L., *Tagelus gibbus* (Spengler), *Venus mercenaria* L., and *Ensis directus* (Conrad). Other hosts include *Mactra solidissima* Dillwyn (reported by Williams 1907), *Dosinia gibbus* Reeve (reported by Pearse

1947), and *Pholas costata* L. (reported by Causey 1953). For a list of bivalve hosts and localities see Table 2.

The copepodid development of *Leptinogaster* has not been fully described. Bocquet and Stock (1958) mentioned finding copepodids of *Leptinogaster histrio* (Pelseneer 1929) and figured the maxillipeds of an unknown stage (their fig. 3d, e); they also reported a Copepodid V of *Leptinogaster* sp. and il-

TABLE 1.—Taxonomic history of *Leptinogaster major* (Williams, 1907).

Lichomolgus major Williams, 1907, p. 77, pl. III, 8 figs.; Sharpe 1910, p. 408, placed in Lichomolgidae.
Mycicola major; C. B. Wilson, 1932, p. 347, fig. 208, genus wrongly assigned; Monod and Dollfus 1934, p. 316, placed in Clausidiidae; Deevey 1948, p. 22, 1960, p. 34; Sewell 1949, p. 156, placed in Lichomolgidae; Causey 1953, p. 12.
Mycicola spinosa Pearse, 1947, p. 5, figs. 26-31, placed in Mycolidae.
Myocheeres major, M. S. Wilson, 1950, p. 299; M. S. Wilson and Ilig 1955, p. 136, 138; Allen 1956, p. 62, placed tentatively in Lichomolgidae; Bocquet and Stock 1957a, p. 213, 221, placed in Clausidiidae; Humes and Cressey 1958, p. 932, 934, placed in Clausidiidae; Băcescu and Por 1959, p. 20, placed in Clausidiidae; Humes and Cressey 1960, p. 307-325.
Leptinogaster major, Bocquet and Stock, 1958, p. 86-88, placed in Clausidiidae; Gooding 1963, p. 132-136, pl. 17, figs. a-n.

TABLE 2.—Localities and hosts of *Leptinogaster major*.

Locality	Host(s)	Source
Ellerslie, Prince Edward Island, Can.	<i>Mya arenaria</i> L.	J. C. Medcof in correspondence (23 May 1950) with M. S. Wilson
Bideford River, Prince Edward Island, Can.	<i>Mya arenaria</i> L.	J. C. Medcof in correspondence (31 July 1948) with M. S. Wilson
Cotuit, MA	<i>Mya arenaria</i> L. <i>Tagelus gibbus</i> (Spengler) <i>Venus mercenaria</i> L. <i>Ensis directus</i> (Conrad)	Humes and Cressey (1960)
Marthas Vineyard, MA	in plankton	Deevey (1948)
Wickford and Matunuck, RI	<i>Mya arenaria</i> L. <i>Venus mercenaria</i> L. <i>Mactra solidissima</i> Dillwyn	Williams (1907)
Delaware Bay	in plankton	Deevey (1960)
Beaufort, NC	<i>Tagelus gibbus</i> (Spengler) <i>Dosinia discus</i> Reeve <i>Venus mercenaria</i> L.	Pearse (1947)
Grand Isle, LA	<i>Pholas costata</i> L.	Causey (1953)

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lustrated its maxilliped (their fig. 6b, c). Gooding (1963) described features of Copepodid I of *Leptinogaster major*.

Before her death Mildred S. Wilson had studied specimens of *Leptinogaster* (= *Myocheeres*) *major* that had been sent to her from Rhode Island and Prince Edward Island, and had prepared the first draft of a redescription. She recognized the need for a thorough redescription of this species whose original description by Williams (1907) is very incomplete. Although she wrote (1950) that a detailed description of adults and developmental forms was then in preparation, this study apparently was never completed. In a letter to J. C. Medcof dated 24 August 1948 she stated that she had found two early stages of *Myocheeres*. Presumably descriptions of these copepodids would have been part of her projected study if she had lived.

During the study by Humes and Cressey (1960) a large number of *Leptinogaster major* (1,535) were collected from *Mya arenaria* over a period of almost 2 yr at Cotuit, MA. The copepodids and adults described below came from collections made during the summer of 1957. All five copepodid stages, distinguished on the basis of the number of body segments, as well as adults, were obtained. This paper deals with the detailed description of the external morphology of these immature stages and adults.

Although the copepodids described here were not obtained by rearing, it seems certain that the copepodids found in such large numbers are those of *Leptinogaster major*. No other species of copepods occurred in the *Mya arenaria* examined.

MATERIALS AND METHODS

The copepodids and adults described here were selected from a pool of 305 copepodids and 195 adults found in 125 *Mya arenaria* during May-September at Cotuit, MA. The successive Copepodids I-V and the adults were cleared in lactic acid and sorted by size and external morphology into their respective groups.

All measurements and dissections were made on specimens cleared in lactic acid, following the method of Humes and Gooding (1964). The body length does not include the setae on the caudal rami. The measurements of certain parts, such as the length of the first antenna, maxilliped, and various setae and claws, and the dimensions of leg 5, the caudal ramus, and the urosomal segments, are based on dissected specimens from which the drawings were made, and may be considered representative

of nearly average body size. Such measurements are intended more to show relative changes in size during successive instars rather than to represent absolute size. The drawings were made with the aid of a camera lucida. The abbreviations used are as follows: A_1 = first antenna, A_2 = second antenna, L = labrum, MD = mandible, MX_1 = first maxilla, MX_2 = second maxilla, P_3 = leg 3, P_4 = leg 4, and P_5 = leg 5.

DESCRIPTIONS

Copepodid I

Figures 1a-n, 2a-c

Size.—Length 0.57 mm (0.45-0.60 mm) and greatest width 0.17 mm (0.16-0.18 mm) based on 38 specimens.

Body form (Fig. 1a, b, c).—*Saphirella*-like, with cephalosome bluntly pointed anteriorly. Five body segments including and posterior to segment bearing leg 1. Anal segment with 4 groups of spines, 2 ventral groups and 2 ventrolateral groups (Fig. 1d).

Caudal ramus (Fig. 1e).—Relatively short, $36 \times 18 \mu\text{m}$, ratio 2:1, with 6 setae. Outer lateral seta $18 \mu\text{m}$, dorsal seta $20 \mu\text{m}$, 4 terminal setae from outer to inner 23, 17, 39, and $176 \mu\text{m}$, the last with minute lateral spinules.

Rostrum (Fig. 1f).—Broad ridge, prominent in lateral view (Fig. 1g).

First antenna (Fig. 1h).—Five-segmented, $83 \mu\text{m}$ long. Armature: 2, 2, 3 + 1 aesthete, 2 + 1 aesthete, and 5 + 1 aesthete. All setae smooth.

Second antenna (Fig. 1i).—Indistinctly 4-segmented, last segment obscure. First segment with 1 distal seta. Second segment with 1 seta and group of small spines. Third segment with outer row of spines and 2 slender inner setules, with outer stout curved seta having expanded serrate distal half and 1 short inner blunt seta. Fourth segment small and indistinctly set off from third segment, with 1 blunt short seta, 1 long stout smooth seta, 1 slender smooth seta, and 1 long stout seta with prominent lateral setules.

Labrum (Fig. 1j).—Broad, with ventral surface bearing 2 medially interrupted rows of spines and with posteroventral margin having row of small

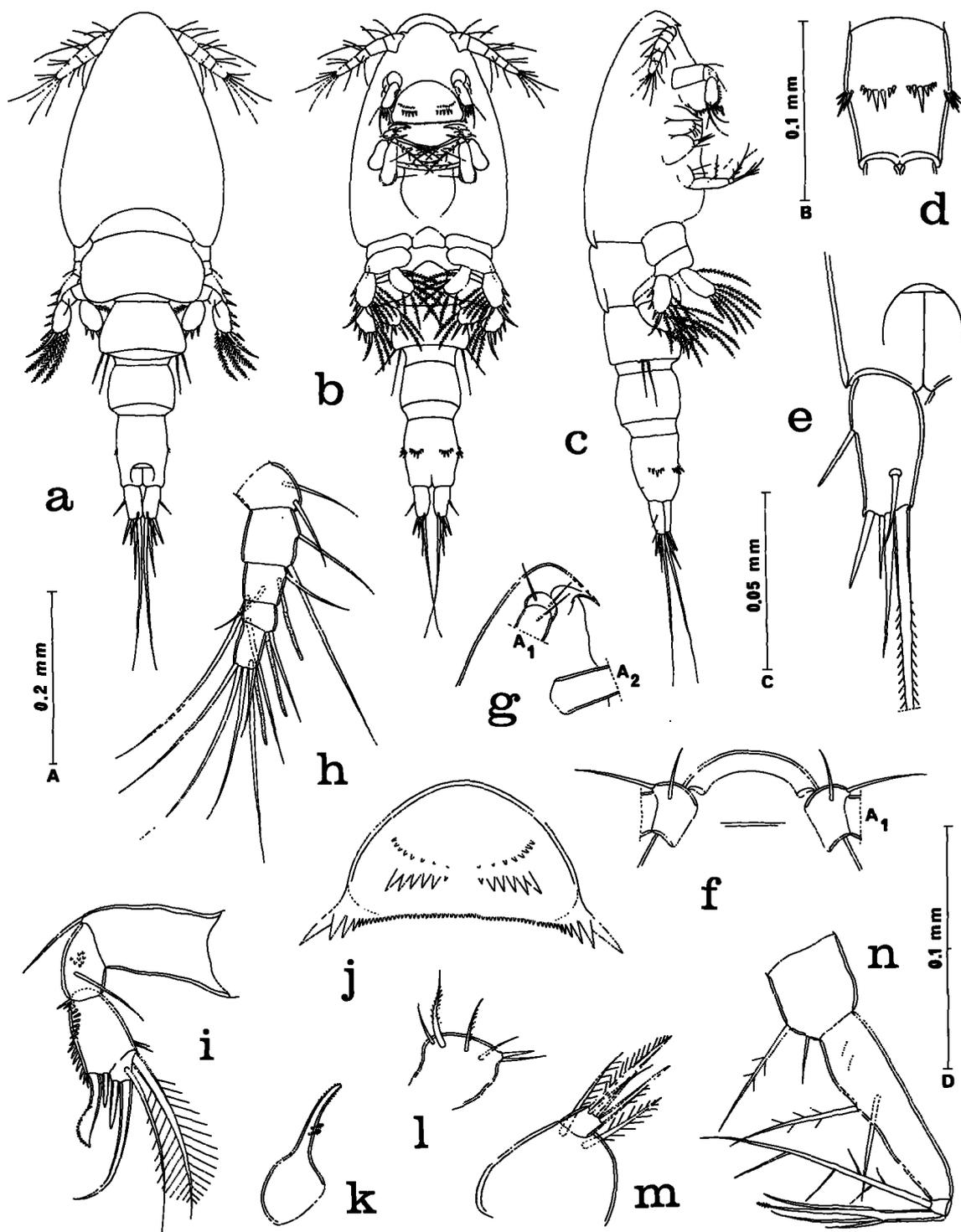


FIGURE 1.—Copepodid I of *Leptinogaster major*. a, dorsal (scale A); h, ventral (A); c, lateral (A); d, anal segment, ventral (B); e, caudal ramus, dorsal (C); f, rostral area, ventral (D); g, rostral area, lateral (B); h, first antenna, dorsal (D); i, second antenna, dorsal (C); j, labrum, in situ, ventral (C); k, mandible, ventral (C); l, first maxilla, ventral (C); m, second maxilla, ventral (C); n, maxilliped, posterior (D).

spines, these spines becoming much larger at both corners.

Mandible (Fig. 1k).—Simple form, small, about 42 μm long, with expanded base but slender distal portion bearing 2 minute setae midway and having minutely pectinate tip.

Paragnath.—Minute smooth lobe.

First maxilla (Fig. 1l).—Small lobe bearing 6 setae.

Second maxilla (Fig. 1m).—Two-segmented, large first segment with 2 setae, small second segment with 3 setae.

Maxilliped (Fig. 1n).—Elongate, slender, 4-segmented. First segment with 2 setae. Elongate second segment with 2 setae and 2 small setules. Small third segment with 1 long seta having few prominent lateral setules. Fourth segment bearing 3 setae near midregion and extended beyond as setiform process with few minute barbs near tip.

Leg 1 (Fig. 2a).—Both rami 1-segmented. Formula for armature: coxa 0-0; basis 1-0; exopod III,I,4; endopod 1,5,1. Exopod with 3 outer spines having prominent lateral spinules and terminal outer spine and adjacent seta with outer denticulations.

Leg 2 (Fig. 2b).—Both rami 1-segmented. Armature: coxa 0-0; basis 1-0; exopod III,I,3; endopod III,2,1. Exopod spines with lateral spinules or denticulations as in leg 1; endopod spines finely barbed.

Leg 3 (Fig. 2c).—Consisting of 2 setae, 70 and 57 μm , with 2 very small spines near their insertions.

Legs 4, 5, and 6.—Absent.

Copepodid II

Figures 2d-m, 3a-e

Size.—Length 0.68 mm (0.59-0.72 mm) and greatest width 0.19 mm (0.18-0.20 mm), based on 31 specimens.

Body form (Fig. 2d).—No longer *Saphirella*-like. Suggesting form of later instars. Six body segments including and posterior to segment bearing leg 1. Segment bearing leg 4 ventrally with 2 transverse rows of spines (Fig. 2e). Anal segment ventrally with distal spines in addition to 4 groups of proximal

spines. Ventrolateral areas of cephalosome at level of mouthparts with strip of small spinules (Fig. 3a).

Caudal ramus.—Similar to Copepodid I but few small ventral spines distally.

Rostrum (Fig. 2f).—Suggesting rounded form seen in later instars.

First antenna (Fig. 2g).—Five-segmented, 107 μm long. Armature: 2, 3, 3 + 1 aesthete, 2 + 1 aesthete, and 6 + 1 aesthete.

Second antenna (Fig. 2h).—Four-segmented. Third segment with 2 strong recurved outer clawlike spines. Small fourth segment with 4 smooth setae, 2 middle setae curved.

Labrum (Fig. 2i).—Posteroventral margin sharply pointed. No surficial or marginal ornamentation.

Mandible (Fig. 2j).—Elongate, 43 μm , distally with 3 elements, 2 helmet-shaped and 1 stoutly spiniform, all with minute marginal barbs.

Paragnath.—As an adult (see Fig. 7f).

First maxilla (Fig. 2k).—Small lobe bearing 5 setae.

Second maxilla (Fig. 2l).—Two-segmented, its form suggesting later instars. First segment expanded with outer patch of small spines. Second segment clawlike, 30 μm long, with 1 inner seta.

Maxilliped (Fig. 2m).—Delicately sclerotized and weakly 4-segmented, length 40 μm . Relative positions of maxillipeds and head appendages as in Figure 3a.

Leg 1 (Fig. 3b).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-I; exopod I-0; III,5; endopod 0-1; I,5.

Leg 2 (Fig. 3c).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-0; exopod I-0; III,4; endopod 0-1; III,3.

Leg 3 (Fig. 3d).—Both rami 1-segmented. Armature: coxa 0-0; basis 1-0; exopod III,4; endopod III,3.

Leg 4 (Fig. 3e).—Consisting of 2 setae, 52 and 39 μm .

Legs 5 and 6.—Absent.

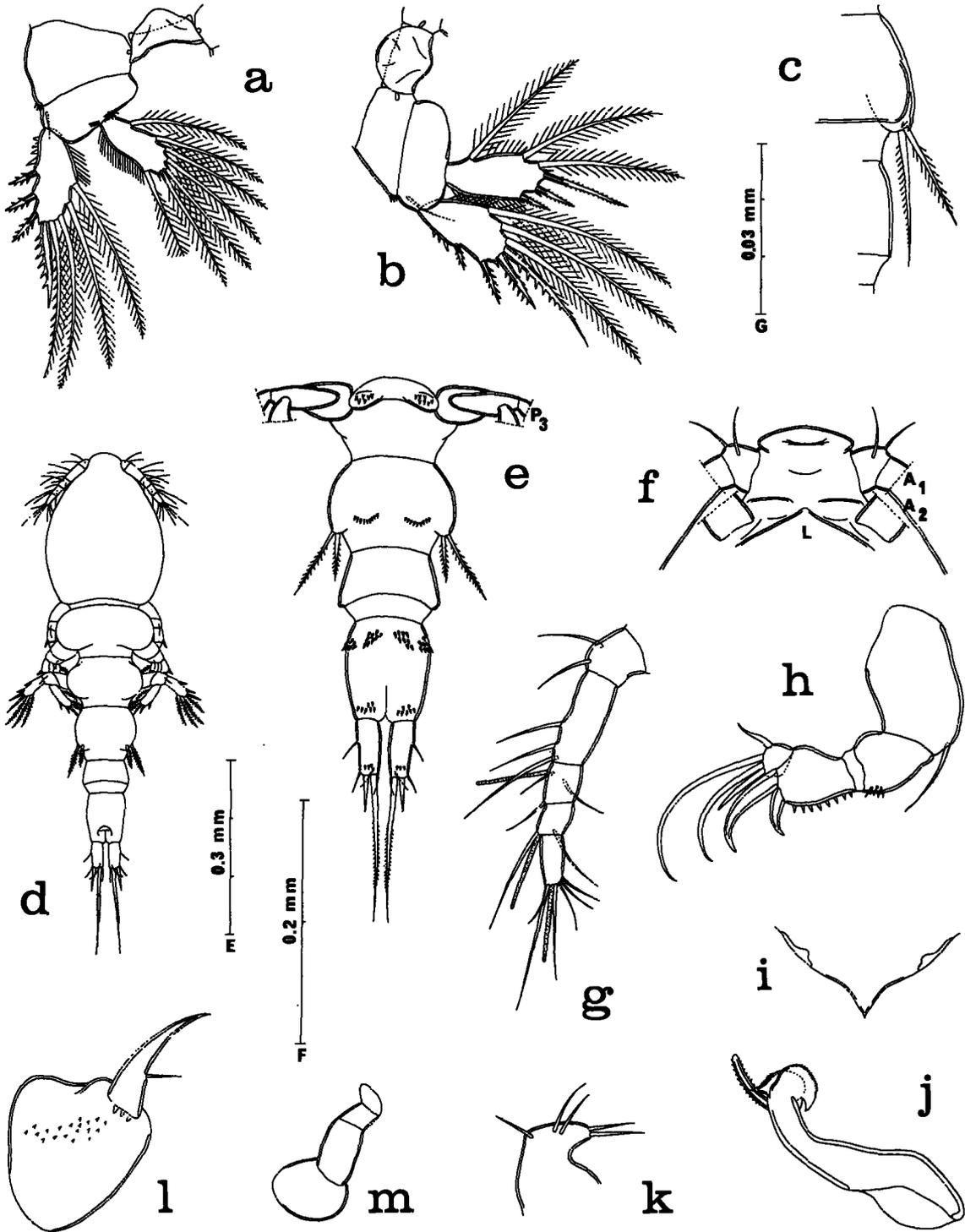


FIGURE 2.—Copepodid I of *Leptinogaster major*, a-c: a, leg 1 and intercoxal plate, anterior (scale B); b, leg 2 and intercoxal plate, anterior (B); c, leg 3, dorsal (B). Copepodid II of *Leptinogaster major*, d-m: d, dorsal (E); e, body posterior to leg 4, ventral (F); f, rostral area, ventral (B); g, first antenna, dorsal (D); h, second antenna, anteromesial (C); i, labrum, ventral (D); j, mandible, ventral (G); k, first maxilla, anterior (C); l, second maxilla, posteroventral (C); m, maxilliped (C).

Copepodid III

Figures 3f-k, 4a-d

Size.—Length 0.85 mm (0.72-0.95 mm) and greatest width 0.24 mm (0.21-0.26 mm), based on 37 specimens.

Body form (Fig. 3f).—Spinules on ventral surface of segment of leg 5 (Fig. 3g) continuous across segment. Seven body segments including and posterior to segment bearing leg 1. (One specimen, 0.62 × 0.24 mm, with segments behind leg 4 telescoped as in Figure 3h.)

First antenna (Fig. 3i).—Five-segmented, 145 μ m long. Armature: 3, 10, 3 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete.

Second antenna (Fig. 3j).—Similar to Copepodid II but outermost seta on fourth segment longer and recurved.

Maxilliped.—As in Copepodid II.

Leg 1 (Fig. 3k).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-I; exopod I-0; III, 5; endopod 0-1; I, 6.

Leg 2 (Fig. 4a).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-0; exopod I-0; III, 6; endopod 0-1; III, 4.

Leg 3 (Fig. 4b).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-0; exopod 0-1; II, 5; endopod 0-1; III, 3.

Leg 4 (Fig. 4c).—Both rami 1-segmented. Armature: coxa 0-0; basis 1-0; exopod II, 4; endopod III, 3. (Distal outer seta on exopod somewhat spiniform.)

Leg 5 (Fig. 4d).—Represented by 2 setae, 42 and 29 μ m.

Leg 6.—Absent.

Copepodid IV, female

Figures 4e-k, 5a-c

Size.—Length 1.19 mm (0.93-1.33 mm) and greatest width 0.32 mm (0.28-0.35 mm), based on 42 specimens.

Body form (Fig. 4e).—Eight body segments including and posterior to segment bearing leg 1. Spinules on ventral surface of segment bearing leg 5 and on anal segment (Fig. 4f) as in Copepodid III.

First antenna (Fig. 4g).—Five-segmented, 179 μ m long, but slight notch on posterior edge of second segment suggesting division of segment. Armature: 4, 15, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete.

Maxilliped (Fig. 4h).—Two-segmented, weakly sclerotized, distal segment lobelike. Relative position of maxillipeds as in Figure 4i.

Leg 1.—Both rami 2-segmented. Armature (as in Copepodid III): coxa 0-0; basis 1-0; exopod I-0; III, 5; endopod 0-1; I, 6.

Leg 2 (Fig. 4j).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-0; exopod I-0; III, 6; endopod 0-1; II, 6. Distalmost outer seta on endopod somewhat spiniform.

Leg 3 (Fig. 4k).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-0; exopod I-0; III, 6; endopod 0-1; II, 5. Distalmost outer seta on endopod somewhat spiniform.

Leg 4 (Fig. 5a).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-0; exopod I-0; III, 5; endopod 0-1; III, 3.

Leg 5 (Fig. 5b).—Two-segmented, but first segment, armed with 1 seta, not clearly set off from body; second segment oval, 60 × 30 μ m, bearing 3 spines and 1 seta, with few small spinules near insertion of proximalmost and distalmost spines.

Leg 6 (Fig. 5c).—Represented by 1 seta 32 μ m long, with minute spinules near insertion.

Copepodid IV, male

Figure 5d-g

Size.—Length 1.07 mm (0.90-1.19 mm) and greatest width 0.28 mm (0.25-0.31 mm), based on 38 specimens.

Body form.—As in female, with same number of body segments and similar arrangement of ventral spinules (Fig. 5d).

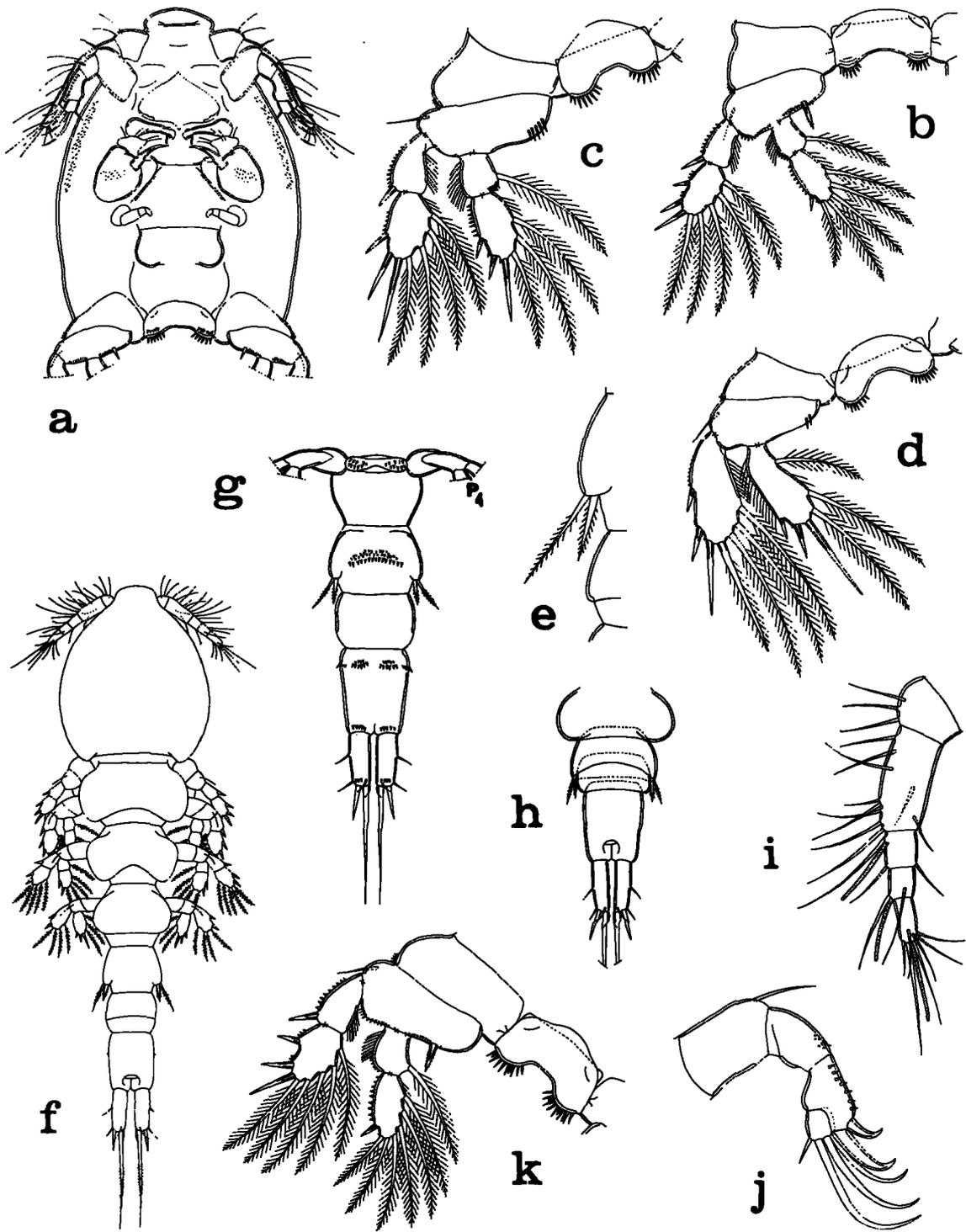


FIGURE 3.—Copepodid II of *Leptinogaster major*, a-e: a, cephalosome, ventral (scale F); b, leg 1 and intercoxal plate, anterior (B); c, leg 2 and intercoxal plate, anterior (B); d, leg 3 and intercoxal plate, anterior (B); e, leg 4, ventral (B). Copepodid III of *Leptinogaster major*, f-k: f, dorsal (E); g, body posterior to leg 4, ventral (A); h, posterior part of body showing telescoped segments, dorsal (A); i, first antenna, ventral (B); j, second antenna, anteromesial (D); k, leg 1 and intercoxal plate, anterior (B).

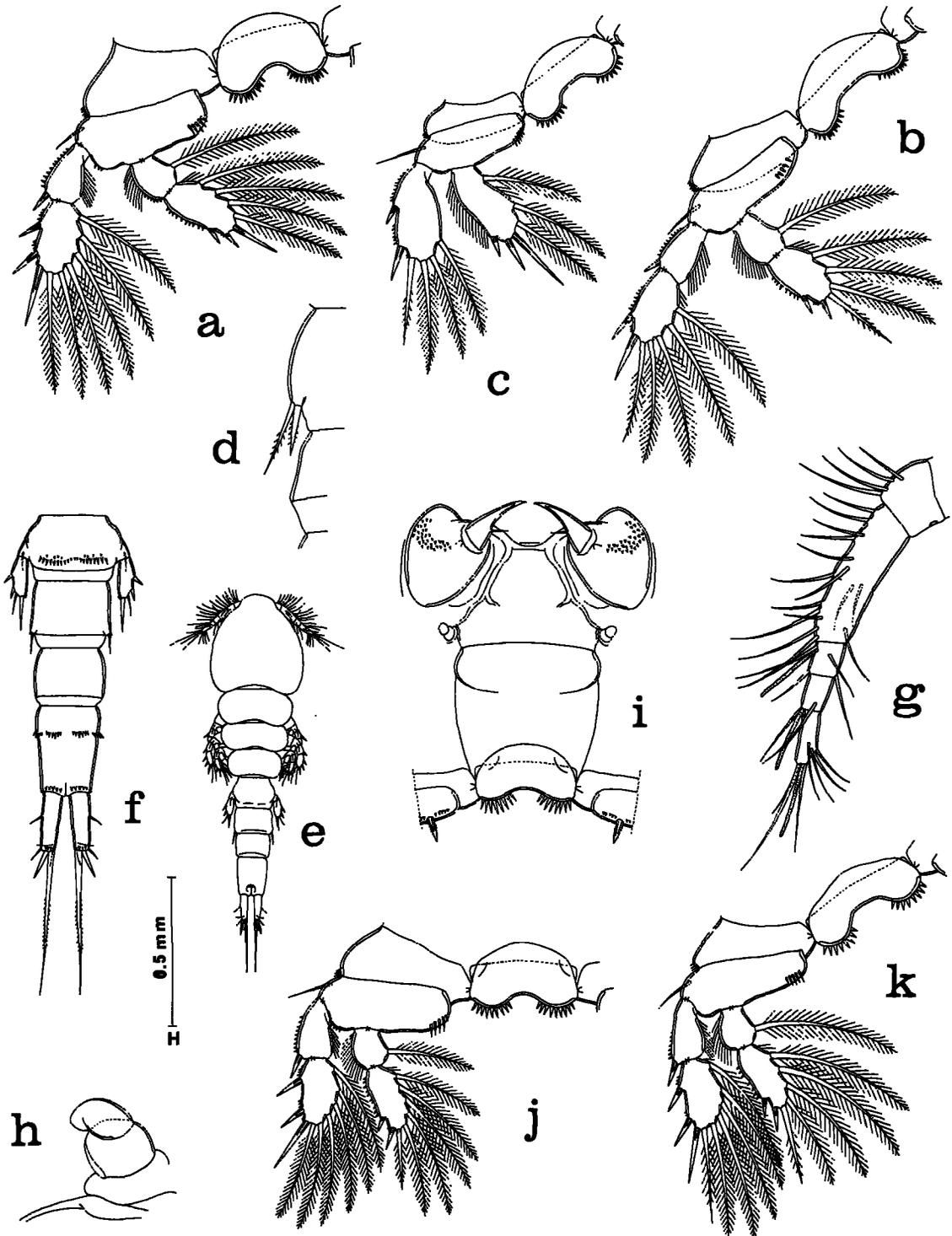


FIGURE 4.—Copepodid III of *Leptinogaster major*, a-d: a, leg 2 and intercoxal plate, anterior (scale B); b, leg 3 and intercoxal plate, anterior (B); c, leg 4 and intercoxal plate, anterior (B); d, leg 5, ventral (B). Copepodid IV of *Leptinogaster major*, female, e-k: e, dorsal (H); f, urosome, ventral (E); g, first antenna, ventral (B); h, maxilliped, ventral (C); i, ventral region from second maxillipeds to first pair of legs, showing maxillipeds (F); j, leg 2 and intercoxal plate, anterior (F); k, leg 3 and intercoxal plate, anterior (F).

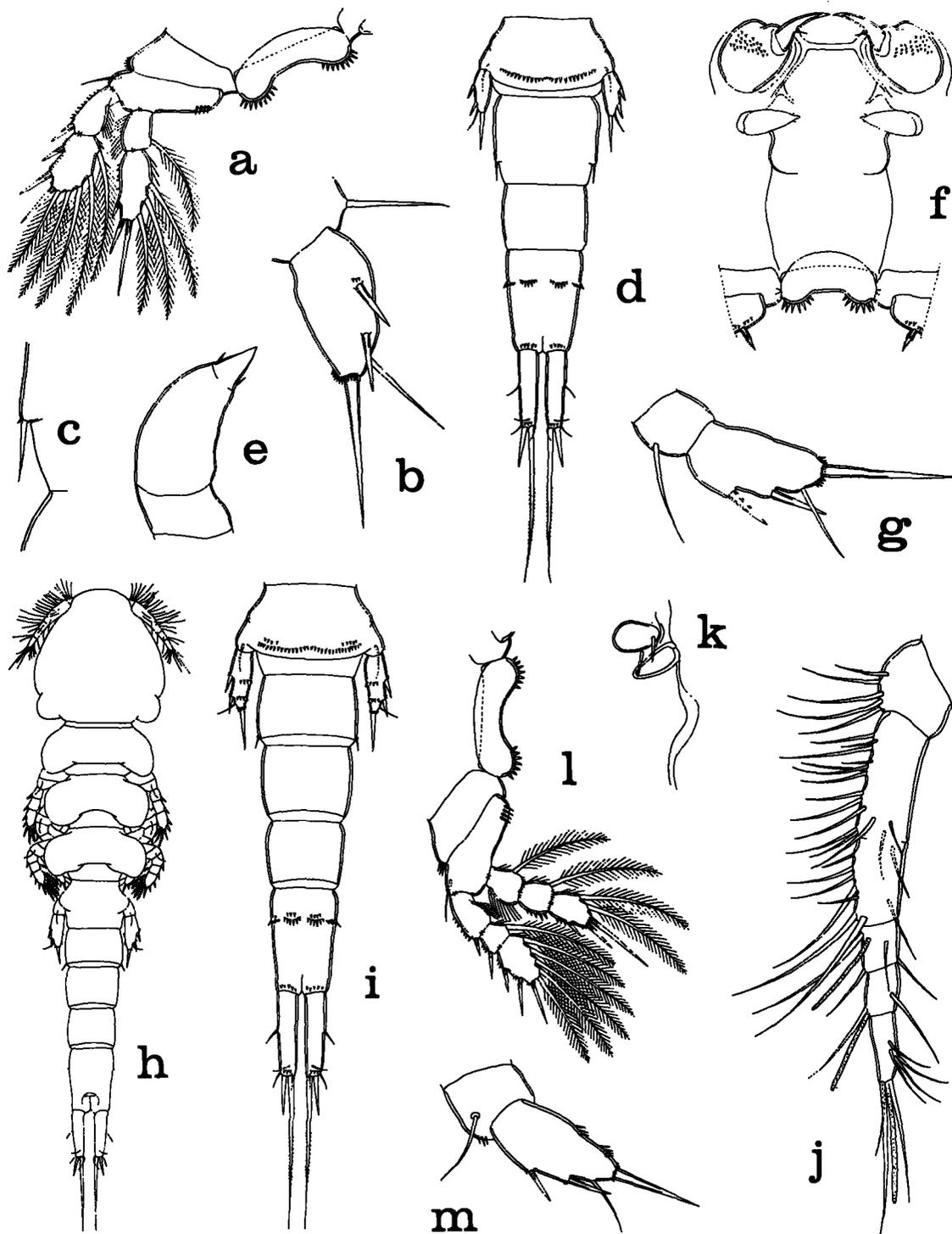


FIGURE 5.—Copepodid IV of *Leptinogaster major*, female a-c: a, leg 4 and intercoxal plate, anterior (scale F); b, leg 5, lateral (D); c, leg 6, ventral (D); male, d-g: d, urosome, ventral (A); e, maxilliped, ventral (C); f, ventral region from second maxillae to first pair of legs, showing maxillipeds (F); g, leg 5, dorsal (D). Copepodid V of *Leptinogaster major*, female, h-m: h, dorsal (H); i, urosome, ventral (E); j, first antenna, posteroventral (B); k, maxilliped, ventral (C); l, leg 4 and intercoxal plate, anterior (A); m, leg 5, dorsal (F).

Maxilliped (Fig. 5e).—Three-segmented, 50 μ m long, with small pointed third segment weakly set off from second segment and bearing 2 small setae. Relative position of maxillipeds as in Figure 5f.

Leg 5 (Fig. 5g).—Two-segmented. First segment set off from body. Second segment 55 \times 29 μ m. Armature similar to female.

Leg 6 (Fig. 5d).—Represented by single seta.

Copepodid V, female

Figures 5h-m, 6a-c

Size.—Length 1.62 mm (1.42-1.87 mm) and greatest width 0.41 mm (0.37-0.44 mm), based on 13 specimens.

Body form (Fig. 5h).—Nine body segments including and posterior to segment bearing leg 1. Segment of leg 5 and more posterior segments as in Figure 5i.

Caudal ramus (Fig. 5i).—Noticeably longer than in preceding instars.

First antenna (Fig. 5j).—Incompletely 6-segmented. Armature: 5, 15 + 9, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete.

Maxilliped (Fig. 5k).—Reduced to slightly raised lobe with 2 small setae.

Leg 1.—Both rami 3-segmented. Armature (as in adult): coxa 0-0; basis 1-1; exopod I-0; I-1; III,5; endopod 0-1, 0-1; I,5.

Legs 2 and 3.—Both rami 3-segmented. Armature (as in adult): coxa 0-0; basis 1-0; exopod I-0; I-1; III,6; endopod 0-1; 0-2; III,3.

Leg 4 (Fig. 5l).—Both rami 3-segmented. Armature: coxa 0-0; basis 1-0; exopod I-0; I-1; III,5; endopod 0-1; 0-1; III,2. Distal-most spine on exopod more slender than other exopod spines; outer of 2 terminal spines on endopod only about one-half length of inner terminal spine.

Leg 5 (Fig. 5m).—Second segment 99 \times 49 μ m. Few outer spinules on first segment. Two groups of spinules on inner side of second segment. Principal armature as in Copepodid IV.

Leg 6 (Fig. 5i).—Represented by 1 seta with minute spinule near its insertion.

Copepodid V, male

Figure 6a-c

Size.—Length 1.41 mm (1.22-1.57 mm) and greatest width 0.34 mm (0.31-0.39 mm), based on 30 specimens.

Body form.—As in female, with same number of body segments. Similar arrangement of ventral spinules on urosomal segments (Fig. 6a).

Maxilliped (Fig. 6b).—Four-segmented. First segment with 1 inner seta. Long second segment and short third segment unarmed. Pointed fourth segment with 2 setae.

Legs 1-4.—Similar to those of female. Endopod of leg 2 (Fig. 6c) not showing sexual dimorphism.

Leg 5.—As in female; second segment 75 \times 31 μ m.

Leg 6.—Represented by single seta with few very small spinules near its insertion.

Adult Female

Figures 6d-m, 7a-l, 8a-e, 9a-j

Size.—Length 2.18 mm (1.92-2.45 mm) and greatest width 0.52 mm (0.47-0.56 mm), based on 10 specimens. Dorsoventral thickness at level of leg 1, 0.25 mm.

Body form (Fig. 6d, e).—Elongate and flattened dorsoventrally. Nine body segments including and posterior to segment bearing leg 1. Urosome 5-segmented (Fig. 6f). Segment bearing leg 5 220 \times 319 μ m in dorsal view, smooth on dorsal surface, but ventral surface with transverse groups of spines (Fig. 6g); dorsally this segment with posterodorsal hump (Fig. 6e, h). Genital segment 270 \times 264 μ m, wider in anterior half than in posterior half. Three post-genital segments from anterior to posterior 143 \times 165, 143 \times 160, and 200 \times 143 μ m. Genital areas situated dorsolaterally, each area (Fig. 6i) bearing 2 very small setae about 16 μ m long. Ventral surfaces of genital segment and first and second post-genital segments smooth. Anal segment ventrally with few small spines at postero-outer corners, with row of 5 spines on each side distally, and with 2

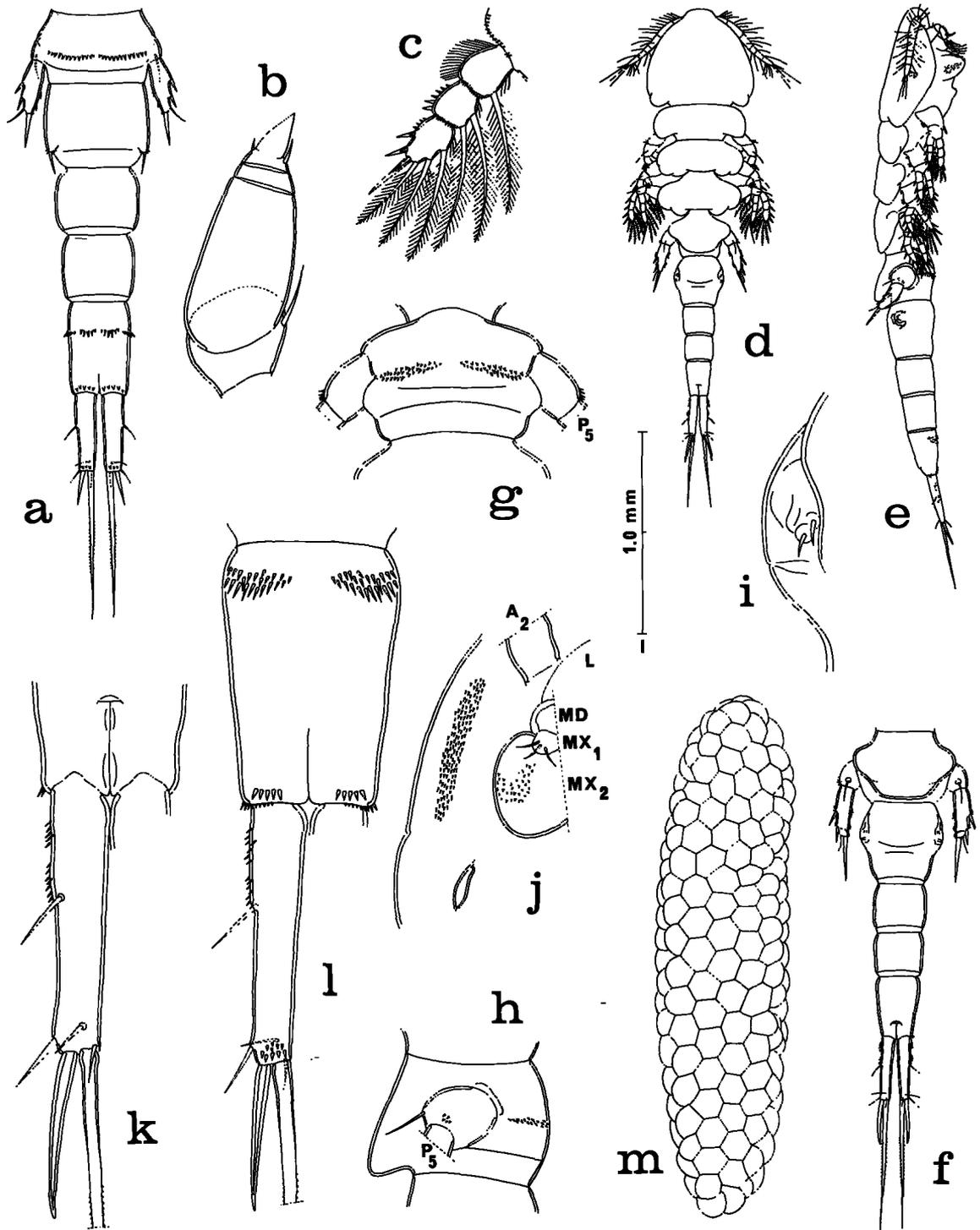


FIGURE 6.—Copepodid V of *Leptinogaster major*, male, a-c: a, urosome, ventral (scale E); b, maxilliped, ventral (D); c, endopod of leg 2, anterior (F). Adult female of *Leptinogaster major*, d-m: d, dorsal (I), e, lateral (I); f, urosome, dorsal (H); g, segment bearing fifth pair of legs, ventral (A); h, segment bearing leg 5, lateral (E); i, genital area, dorsal (B); j, patch of spinules and sclerotized area on side of cephalosome, ventral (E); k, caudal ramus, dorsal (F); l, anal segment and caudal ramus, ventral (F); m, egg sac, ventral (E).

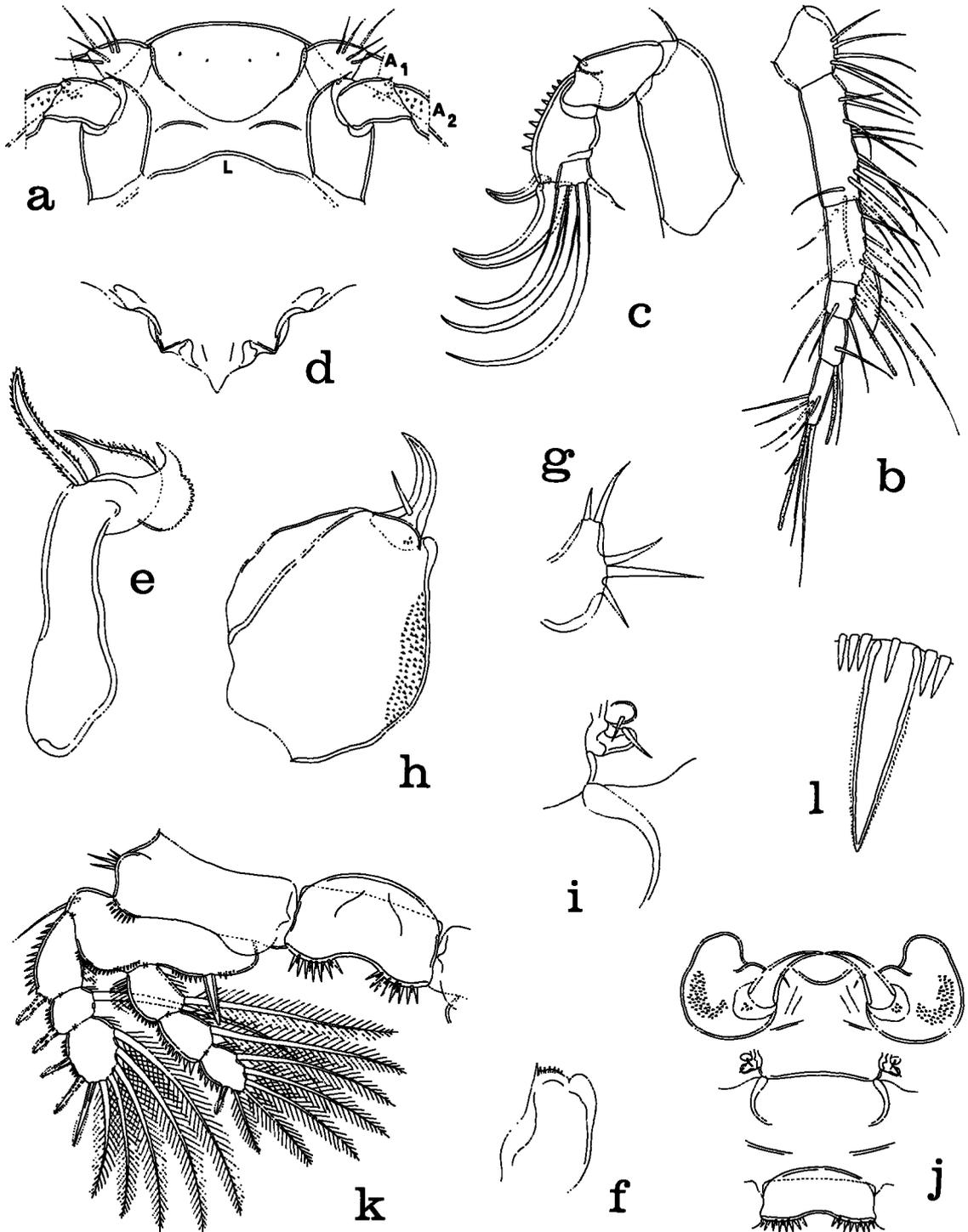


FIGURE 7.—Adult female of *Leptinogaster major*: a, rostrum, ventral (scale F); b, first antenna, posteroventral (F); c, second antenna, posteromesial (B); d, labrum, ventral (B); e, mandible, anteroventral (C); f, paragnath, ventral (D); g, first maxilla, anterior (D); h, second maxilla, posterior (B); i, maxilliped, ventral (D); j, ventral region from second maxillae to first pair of legs, showing maxillipeds (E); k, leg 1 and intercoxal plate, anterior (F); l, inner spine on basis of leg 1, anterior (G).

prominent groups of spines anteriorly. Cephalosome ventrally with elongate oblique strip of small spines between edge of body and region of mouthparts, and with small elongate oval sclerotized area lateral to level of maxillipeds (Fig. 6j).

Caudal ramus (Fig. 6k, l).—Elongate, 221 μm long, greatest width 44 μm , least width 35 μm , ratio about 5.5:1. Outer lateral seta 50 μm . Dorsal seta 26 μm . Outermost terminal seta 52 μm . Innermost terminal seta 26 μm . Outer of 2 median terminal setae 130 μm and almost spinelike. Inner of 2 median terminal seta 440 μm , with extremely small lateral spinules. Other setae smooth. Outer margin of ramus proximal to outer lateral seta with 2 groups of spinules. Distal end of ramus ventrally with patch of small spines.

Egg sac (Fig. 6m).—Elongate, various sacs 693 \times 209 μm , 781 \times 242 μm , 860 \times 220 μm (as in figure), and 1,023 \times 231 μm , average dimensions 839 \times 226 μm ; containing many small eggs with diameter 47-57 μm .

Rostrum (Fig. 7a).—Broad with weakly sclerotized rounded posteroventral margin.

First antenna (Fig. 7b).—Six-segmented, 320 μm long. Lengths of segments (measured along their posterior nonsetiferous margins): 29 (49 μm along anterior margin), 88, 55, 26, 36, and 52 μm , respectively. Armature: 5, 15, 9, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All setae smooth.

Second antenna (Fig. 7c).—Four-segmented. First segment with distal seta. Second segment with distal seta and crescentic row of small spines. Third segment with outer marginal row of spines and 2 large recurved clawlike spines, 34 and 70 μm . Small fourth segment 13 \times 21 μm , bearing 3 long recurved almost clawlike setae and 1 smaller inner seta.

Labrum (Fig. 7d).—Posteroventral edge sharply pointed medially. No surface ornamentation.

Mandible (Fig. 7e).—Elongate with distal end bearing 2 helmet-shaped elements and 1 stout pectinate spine.

Paragnath (Fig. 7f).—Small lobe with few distal spinules.

First maxilla (Fig. 7g).—Small lobe bearing 5 setae.

Second maxilla (Fig. 7h).—Two-segmented. Large first segment with patch of outer spinules (Fig. 7j). Second segment clawlike and bearing 1 seta.

Maxilliped (Fig. 7i).—Reduced to 2 small setae, located as in Figure 7j.

Legs 1-4 (Figs. 7k, 8a, b, c).—Intercoxal plates with 2 groups of spines on distal (ventral) margin. Exopods and endopods 3-segmented. Armature as follows (Roman numerals indicating spines, Arabic numerals representing setae):

P ₁	coxa	0-0	basis	1-I	exp	I-0; I-1; III,5
					enp	0-1; 0-1; I,5
P ₂	coxa	0-0	basis	1-0	exp	I-0; I-1; III,6
					enp	0-1; 0-2; III,3
P ₃	coxa	0-0	basis	1-0	exp	I-0; I-1; III,6
					enp	0-1; 0-2; III,3
P ₄	coxa	0-0	basis	1-0	exp	I-0; I-1; III,5
					enp	0-1; 0-1; III,2

Leg 1 (Fig. 7k).—Coxa with 2 groups of outer spines. Basis with row of small spines between bases of rami and another row near large inner spine. This inner spine delicately barbed (Fig. 7l) and 33 μm long; smaller spines near its base 7.5 μm . First segment of endopod with outer margin having hairlike setules along proximal half but small spines along distal half.

Leg 2 (Fig. 8a).—Basis without inner spine. First segment of endopod with hairlike setules along outer margin.

Leg 3 (Fig. 8b).—Fine ornamentation resembling that of leg 2.

Leg 4 (Fig. 8c).—Coxa with only 1 group of outer spines.

Leg 5 (Fig. 8d).—Two-segmented. First segment 130 \times 125 μm , with distal outer seta and group of spines. Second segment elongate, 161 \times 68 μm , with 2 outer smooth spines, 52 and 55 μm , distal smooth seta 70 μm , and terminal finely barbed spine 147 μm . These 3 spines with small spines near their insertions. Two groups of small spines on inner side of segment.

Leg 6 (Fig. 6i).—Probably represented by 2 setae on genital area.

Color.—Living specimens in transmitted light with opaque gray body, eye red.

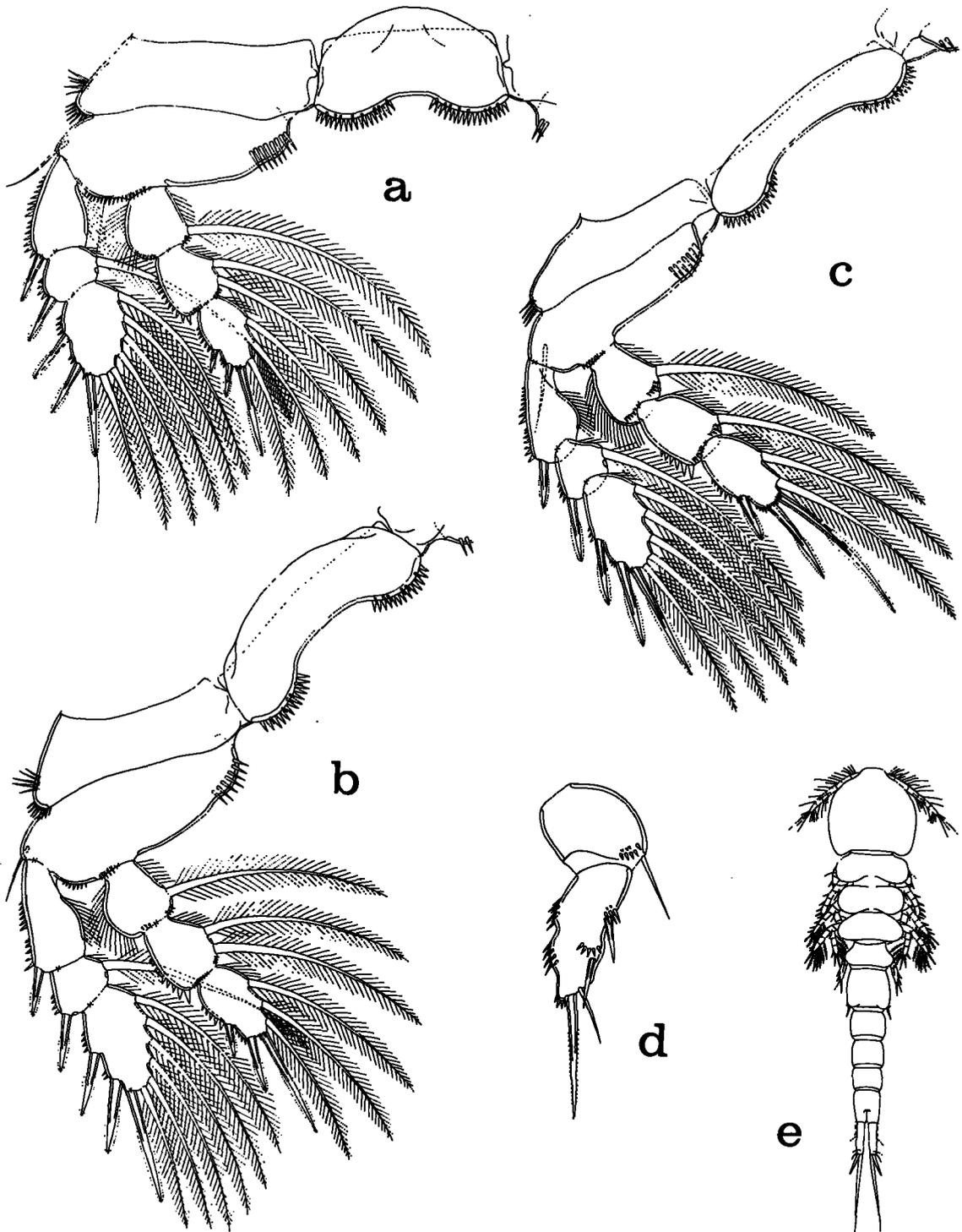


FIGURE 8.—Adult female of *Leptinogaster major*, a-d: a, leg 2 and intercoxal plate, anterior (scale F); b, leg 3 and intercoxal plate, anterior (F); c, leg 4 and intercoxal plate, anterior (F); d, leg 5, lateral (A). Adult male of *Leptinogaster major*: e, dorsal (I).

Adult Male

Figures 8e, 9a-j

Size.—Length 1.82 mm (1.70-2.04 mm) and greatest width 0.43 mm (0.40-0.47 mm), based on 10 specimens.

Body form (Fig. 8e).—Similar to female but 10 body segments including and posterior to segment of leg 1. Urosome (Fig. 9a) 6-segmented. Segment of leg 5 $135 \times 236 \mu\text{m}$ in dorsal view, with spines on ventral surface as in female. Four postgenital segments from anterior to posterior 140×166 , 135×143 , 113×128 , and $151 \times 109 \mu\text{m}$. Anal segment with spines as in female. Cephalosome ventrally with outer strip of small spines and small sclerotized area as in female.

Caudal ramus (Fig. 9a).—As in female but dimensions $174 \times 38 \mu\text{m}$, ratio 4.6:1.

Rostrum, first antenna, second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla as in female.

Maxilliped (Fig. 9b).—Four-segmented. First segment with 1 inner smooth seta $50 \mu\text{m}$. Elongate second segment with 2 inner setae and 2 groups of short spines. Small third segment unarmed. Claw $208 \mu\text{m}$, proximal part representing fourth segment bearing 3 setae. Concave margin of claw striated.

Legs 1-4.—With segmentation and armature as in female, and ornamentation as in that sex except for endopod of leg 2.

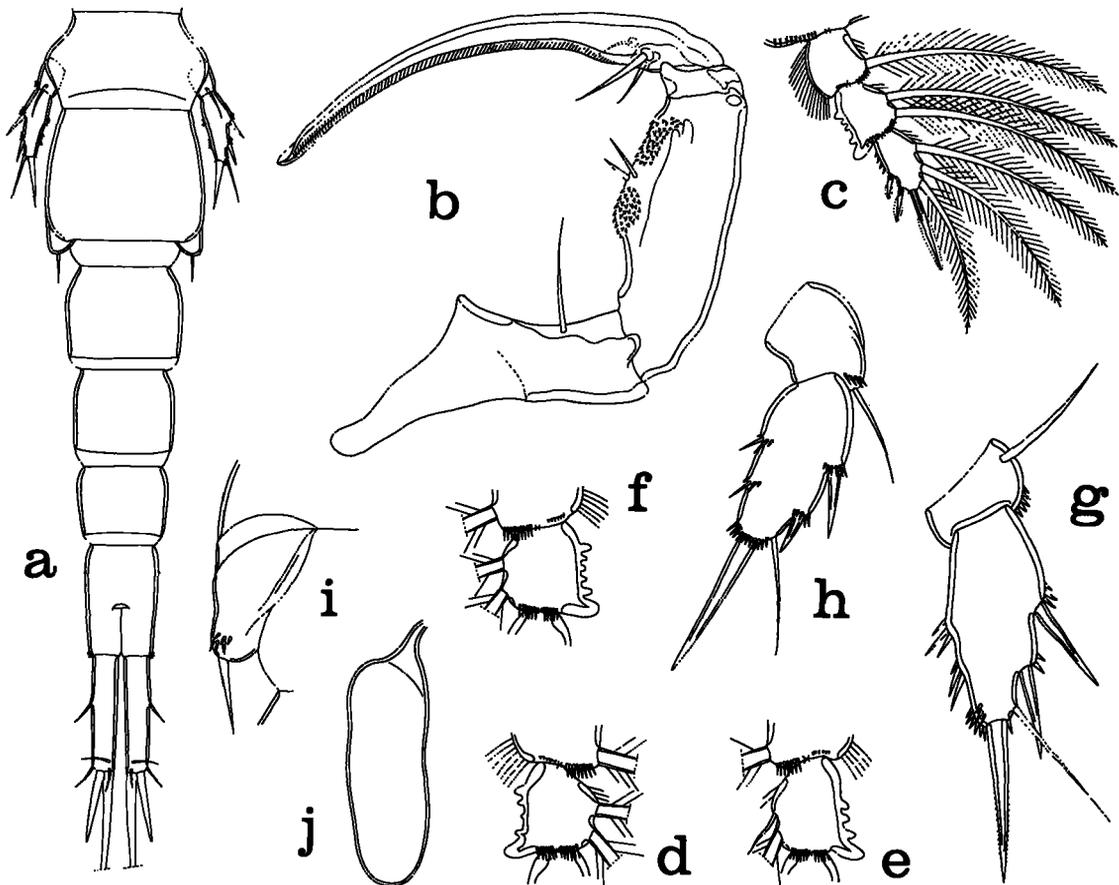


FIGURE 9.—Adult male of *Leptinogaster major*: a, urosome, dorsal (scale H); b, maxilliped, posterior (B); c, endopod of leg 2, anterior (F); d, second segment of endopod of right leg, anterior (B); e, second segment of endopod of left leg (same individual as in d), anterior (B); f, second segment of endopod of leg 2, anterior (B); g, leg 5, dorsal (B); h, leg 5, ventrolateral (B); i, leg 6, ventral (F); j, spermatophore, attached to female, ventral (A).

Leg 2 (Fig. 9c).—Endopod showing sexual dimorphism in having variable nodose outer margin on second segment (Fig. 9d, e, f). Number of nodes from 4-6, and not always same in 1 individual, as in Fig. 9d, e.

Leg 5 (Fig. 9g, h).—Resembling that of female. Second segment in 2 individuals $101 \times 47 \mu\text{m}$ (Fig. 9g) with 4 major elements from proximal to distal 45, 42, 80, and $78 \mu\text{m}$, and $86 \times 42 \mu\text{m}$ (Fig. 9h) with elements 22, 26, 65, and $73 \mu\text{m}$.

Leg 6 (Fig. 9i).—Represented by single smooth seta $49 \mu\text{m}$ and adjacent group of small spines on corner of genital area.

Spermatophore (Fig. 9j).—Elongate, approximately $220 \times 78 \mu\text{m}$ without neck.

Color.—As in female.

DISCUSSION

This study permits certain observations to be made concerning the postnaupliar development of *Leptinogaster major*. A summary of these is given in Table 3.

1) All five copepodid stages are present in the mantle cavity of *Mya arenaria*.

2) The presence of Copepodid I in *Mya* suggests that either the last nauplius molts outside the clam and then enters, or that this nauplius enters the clam and then molts.

3) Copepodid I is *Saphirella*-like in body form; Copepodid II and later copepodids have a body form more like the adult.

4) The number of body segments increases from 5 in Copepodid I to 9 in the adult female and 10 in the adult male.

5) The armature of the caudal ramus remains unchanged from Copepodid I onward, but the caudal ramus lengthens in successive copepodid stages and in the adults.

6) The first antenna is slow in reaching final form, being 5-segmented in Copepodid I and not reaching its fully 6-segmented condition until the adult.

7) The second antenna has an indistinct fourth segment in Copepodid I, but is clearly 4-segmented thereafter.

8) The labrum of Copepodid I is broad and ornamented with spines, but in Copepodid II and subsequently it is pointed and smooth.

9) The mandible of Copepodid I is a simple

blade, but in Copepodid II and succeeding stages there are 3 terminal elements as in the adult.

10) The first maxilla of Copepodid I is similar to that of Copepodid II and following stages.

11) The second maxilla has terminal setae in Copepodid I but a terminal claw thereafter.

12) The maxilliped in Copepodid I is elongate and 4-segmented with long setae, but in Copepodid II and Copepodid III it is small with 4 weak unarmed segments. From this point on, the maxilliped in the female shows further reduction, while in the male it undergoes enlargement and specialization. In the female of Copepodid IV it is minute, 2-segmented, and unarmed; in Copepodid V and in the adult it is reduced to 2 small setae. In the male of Copepodid IV the maxilliped is 3-segmented, pointed, with 2 setae; in Copepodid V it is 4-segmented, pointed, with 3 setae; in the adult male it is 4-segmented with a long terminal claw.

13) The full complement of 4 biramous 3-segmented legs is not reached until Copepodid V.

14) The inner spine on the basis of the endopod of leg 1 first appears in Copepodid II.

15) Leg 5 is absent in Copepodid I and Copepodid II, is represented by 2 setae in Copepodid III, and abruptly becomes 2-segmented with full armature in Copepodid IV.

16) Sexual dimorphism in legs 1-4 occurs only in the endopod of leg 2 in the adult male.

17) Sexual differentiation during copepodid development first occurs in Copepodid IV, where the male and female maxillipeds are differently formed.

The maxilliped in the adult female is said to be absent in *Leptinogaster histrio* (Bocquet and Stock 1958; Băcescu and Por 1959), in the genus *Myocheres* (Wilson 1950), in *Leptinogaster inflata* (Allen 1956), in *Leptinogaster scobina* (Humes and Cressey 1958), and in *Leptinogaster dentata* (Humes and Cressey 1958). The maxilliped has now been traced throughout copepodid development, and it is apparent that a remnant of this appendage exists in the adult female of *L. major*.

This discovery prompted a reexamination of adult females of two species of *Leptinogaster*, *L. scobina* and *L. dentata*. In both the maxilliped is represented by two very small setae, as in *L. major*. It is not surprising that these setae were overlooked, since they are very minute and readily seen only in well-cleared specimens.

Although the remaining species of *Leptinogaster*, *L. histrio* (Pelseneer, 1929), *L. pholadis* (Pelseneer, 1929), *L. inflata* (Allen, 1956), and a new species con-

TABLE 3.—Comparison of selected external features during copepodid stages and adults of *Leptinogaster major*.

	Copepodid I	Copepodid II	Copepodid III	Copepodid IV ♀	Copepodid IV ♂	Copepodid V ♀	Copepodid V ♂	Adult ♀	Adult ♂
No. of body segments	5	6	7	8	8	9	9	9	10
First antenna	5-segmented	5-segmented	5-segmented	5-segmented	5-segmented	incompletely 6-segmented	incompletely 6-segmented	6-segmented	6-segmented
Second antenna	indistinctly 4-segmented	4-segmented	4-segmented	4-segmented	4-segmented	4-segmented	4-segmented	4-segmented	4-segmented
Labrum	broad, spined	pointed, smooth	pointed, smooth	pointed, smooth	pointed, smooth	pointed, smooth	pointed, smooth	pointed, smooth	pointed, smooth
Mandible	simple blade	3 terminal elements	3 terminal elements	3 terminal elements	3 terminal elements	3 terminal elements	3 terminal elements	3 terminal elements	3 terminal elements
Second maxilla	terminal setae	terminal claw	terminal claw	terminal claw	terminal claw	terminal claw	terminal claw	terminal claw	terminal claw
Maxilliped	slender, 4-segmented, long setae	small, 4 weak unarmed segments	small, 4 weak unarmed segments	minute, 2 weak unarmed segments	3-segmented, pointed, 2 setae	2 setae on slight lobe	4-segmented, pointed, 3 setae	2 setae	4-segmented, long terminal claw
Rami of leg 1	1-segmented	2-segmented	2-segmented	2-segmented	2-segmented	3-segmented	3-segmented	3-segmented	3-segmented
Rami of leg 2	1-segmented	2-segmented	2-segmented	2-segmented	2-segmented	3-segmented	3-segmented	3 segmented	3 segmented, sexual dimorphism in endopod
Rami of leg 3	2 setae only	1-segmented	2-segmented	2-segmented	2-segmented	3-segmented	3-segmented	3-segmented	3-segmented
Rami of leg 4	absent	2 setae	1-segmented	2-segmented	2-segmented	2-segmented	3-segmented	3-segmented	3-segmented
Leg 5	absent	absent	2 setae	2-segmented	2-segmented	2-segmented	2-segmented	2-segmented	2-segmented
Leg 6	absent	absent	absent	1 seta	1 seta	1 seta	1 seta	2 setae on genital area	1 seta

tained in Gooding's thesis (1963) have not been re-examined, it appears likely that the presence of a very reduced maxilliped in the adult female is a generic character in *Leptinogaster*.

Gooding (1963:218-220) discussed the generic status of *Saphirella* T. Scott, 1894, pointing out that species of *Saphirella* may represent Copepodid I stages of clausidiids. In his thorough description of Copepodid I of *Leptinogaster* a significant difference seems to be in the body length, which Gooding gave as 0.45 mm, while in this study the length is 0.57 mm (0.45-0.60 mm).

Although the genus *Leptinogaster* has been assigned to various families (Table 1), its presently agreed location appears to be in the Clausidiidae Embleton, 1901, along with *Clausidium* Kossmann, 1874, *Conchyliurus* Bocquet and Stock, 1957a, *Giardella* Canu, 1888, *Hemicyclops* Boeck, 1873, *Hersiliodes* Canu, 1888, and *Hippomolgus* G.O. Sars, 1917. [According to the phylogenetic analysis of Ho (1984), the genus *Myzomolgus* Bocquet and Stock, 1957b, should be removed from the Clausidiidae and placed close to the Catiniidae Bocquet and Stock, 1957b.] The family Clausidiidae, containing seven genera of certain status, shows several features: first antenna 6- or 7-segmented; second antenna 4-segmented with third segment having in some cases prehensile elements and fourth segment without a strong claw; mandible with spine (or spinelike process) and 2 or 3 accessory elements (setae, spines); labrum with rounded margin, mostly entire without median indentation, except triangular in *Leptinogaster*; first maxilla often with 2 lobes, but with 1 lobe having 2 groups of setae in *Leptinogaster* and 1 lobe with a few setae in *Clausidium*; maxilliped in female mostly 2-, 3-, or 4-segmented, but in *Leptinogaster* reduced to 2 setae; maxilliped in male 2- or 3-segmented plus claw (in *Hippomolgus* male unknown); legs 1-4 biramous and 3-segmented (endopod of leg 1 bearing suckers in *Clausidium*); leg 5 2-segmented (though in some first segment not clearly separated from body).

Leptinogaster falls within this concept of the family Clausidiidae. Neighboring families have fundamentally different features, e.g., the Clausiidae (first antenna 3-6 segmented; legs 1-4 showing various degrees of reduction (as characterized by Wilson and Illg (1955)), the Mycolidae (3-segmented second antenna with strong terminal claw, maxilliped in female a small unarmed lobe), and the Ergasilidae (second antenna with a strong terminal claw, maxilliped often absent in female, legs 1-4 with some reduction). More information on the developmental stages of the members of these families

would contribute greatly to understanding their interrelationships.

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LITERATURE CITED

- ALLEN, J. A.
1956. *Myochoeres inflata* a new species of parasitic copepod from the Bahamas. *J. Parasitol.* 42:60-67.
- BĂCESCU, M., AND F. POR.
1959. Cyclopoide comensale (Clausidiide si Clausiide) din Marea Neagră și descrierea unui gen nou, *Pontoclausia* gen. nov. In *Omagiul lui Traian Săvălescu cu prilejul împlinirii a 70 e ani*, p. 11-30. *Acad. Rep. Pop. Rom.*
- BOCQUET, C., AND J. H. STOCK.
1957a. Copépodes parasites d'invertébrés des côtes de France I. Sur deux genres de la famille des Clausidiidae, commensaux de mollusques: *Hersiliodes* Canu et *Conchyliurus* nov. gen. *Proc. K. Ned. Akad. Wet., Ser. C Biol. Med. Sci.* 60: 212-222.
1957b. Copépodes parasites d'invertébrés des côtes de France. IVa. Le double parasitisme de *Sipunculus nudus* L. par *Myzomolgus stupendus* nov. gen., nov. sp., et *Catinia plana* nov. gen., nov. sp., copépodes cyclopoïdes très remarquables. *Proc. K. Ned. Akad. Wet., Ser. C Biol. Med. Sci.* 60:410-431.
1958. Copépodes parasites d'invertébrés des côtes de la Manche. IV. Sur les trois genres synonymes de copépodes cyclopoïdes, *Leptinogaster* Pelseneer, *Strongylopleura* Pelseneer et *Myochoeres* Wilson (Clausidiidae). *Arch. Zool. Exp. Gen.* 96:71-89.
- BOECK, A.
1873. Nye Slaegter og Arter af Saltvands-Copepoder. *Forh. Vidensk.-Selsk. Christiania* (1872), p. 35-60.
- CANU, E.
1888. Les copépodes marins du Boulonnais. III. Les Hersiliidae, famille nouvelle de copépodes commensaux. *Bull. Sci. Fr. Belg.* 19:402-432.
- CAUSEY, D.
1953. Parasitic Copepoda from Grand Isle, Louisiana. *Occas. Pap. Mar. Lab., La. State Univ.* No. 7, 18 p.
- DEEVEY, G. B.
1948. The zooplankton of Tisbury Great Pond. *Bull. Bingham Oceanogr. Collect., Yale Univ.* 12:1-44.
1960. The zooplankton of the surface waters of the Delaware Bay region. *Bull. Bingham Oceanogr. Collect., Yale Univ.* 17:5-53.
- EMBLETON, A. L.
1901. *Goidelia japonica* - a new entozoic copepod from Japan, associated with an infusorian (*Trichodina*). *Trans. Linn. Soc. Lond.* 2d Ser., Zool. 28:211-228.

- GOODING, R. U.
1963. External morphology and classification of marine poecilostome copepods belonging to the families Clausidiidae, Clausiidae, Nereicolidae, Eunicicolidae, Synaptiphilidae, Catiniidae, Anomopsyllidae, and Echiurophilidae. Ph.D. Thesis, Univ. Washington, Seattle, 247 p.
- HO, J.-S.
1984. New family of poecilostomatoid copepods (Spiophanicolidae) parasitic on polychaetes from southern California, with a phylogenetic analysis of nereicoliform families. *J. Crustacean Biol.* 4:134-146.
- HUMES, A. G., AND R. F. CRESSEY.
1958. Copepod parasites of mollusks in West Africa. *Bull. Inst. Fr. Afr. Noire* 20(A):921-942.
1960. Seasonal population changes and host relationships of *Myocheres major* (Williams), a cyclopoid copepod from pelecypods. *Crustaceana* 1:307-325.
- HUMES, A. G., AND R. U. GOODING.
1964. A method for studying the external anatomy of copepods. *Crustaceana* 6:238-240.
- KOSSMANN, R.
1874. Ueber *Clausidium testudo*, einen neuen Copepoden, nebst Bemerkungen über das System der halbparasitischen Copepoden. *Verh. Phys.-Med. Ges. Würzburg*, n.f. 7:280-293.
- MONOD, T., AND R.-PH. DOLLFUS.
1934. Des copépodes parasites de mollusques (deuxième supplément). *Ann. Parasitol. Hum. Comp.* 12:309-321.
- PEARSE, A. S.
1947. Parasitic copepods from Beaufort, North Carolina. *J. Elisha Mitchell Sci. Soc.* 63:1-16.
- PELSENEER, P.
1929. Copépodes parasites de mollusques. *Ann. Soc. R. Zool. Belg.* (1928) 59:33-49.
- SARS, G. O.
1917. An account of the Crustacea of Norway with short descriptions and figures of all the species. *In* Vol. VI Copepoda Cyclopoida Parts XI and XII Clausidiidae, Lichomolgidae (part), p. 141-172. Bergen Museum, Bergen.
- SCOTT, T.
1894. Report on Entomostraca from the Gulf of Guinea, collected by John Rattray, B.Sc. *Trans. Linn. Soc. Lond.* 2d Ser., Zool. 6:1-161.
- SEWELL, R. B. S.
1949. The littoral and semi-parasitic Cyclopoida, the Monstriloida and Notodelphyoida. *Sci. Rep. John Murray Exped.* 9(2):17-199.
- SHARPE, R. W.
1910. Notes on the marine Copepoda and Cladocera of Woods Hole and adjacent regions, including a synopsis of the genera of the Harpacticoida. *Proc. U.S. Nat. Mus.* 38:405-436.
- WILLIAMS, L. W.
1907. A list of the Rhode Island Copepoda, Phyllopoda, and Ostracoda, with new species of Copepoda. *In* Thirty-seventh Annual Report of the Commissioners of Inland Fisheries of Rhode Island, p. 69-79. Spec. Pap. 30.
- WILSON, C. E.
1932. The copepods of the Woods Hole region Massachusetts. *U.S. Nat. Mus. Bull.* 158, 635 p.
- WILSON, M. S.
1950. A new genus proposed for *Lichomolgus major* Williams (Copepoda, Cyclopoida). *J. Wash. Acad. Sci.* 40:298-299.
- WILSON, M. S., AND P. L. ILLG.
1955. The family Clausiidae (Copepoda, Cyclopoida). *Proc. Biol. Soc. Wash.* 68:129-141.