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SCOPALATUM VORAX (ESTERLY, 1911) AND *SCOLECITHRICELLA LOBOPHORA* PARK, 1970, CALANOID COPEPODS (SCOLECITRICHIDAE) ASSOCIATED WITH A PELAGIC TUNICATE IN MONTEREY BAY

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Abstract.—The last five copepodid stages of *Scopalatum vorax* and the last three of *Scolecithricella lobophora* are described from specimens collected in association with the pelagic tunicate *Bathochordaeus* sp. A non-feeding, stage six nauplius of the former species has three anterior naupliar appendages, five posterior appendage buds, and no mouth. The addition of setae during copepodid development to the uniramal appendages of *S. vorax* suggests that distal segments of maxilla 2 are exopodal while those of the maxilliped are endopodal; addition of setae on antenna 1 are endopodal in pattern. The developmental pattern of the maxilliped of *S. vorax* suggests that it consists of a coxa, a basis with a distomedial lobe, and five endopodal segments.

During the last three years, scientists at the University of California, Santa Cruz and Monterey Bay Aquarium Research Institute (MBARI) have undertaken a study of marine snow in Monterey Bay (Pilskaln et al. 1991, Silver et al. 1991). One of us (DKS) is studying the ecological role of metazoans associated with large mucus structures which contribute significantly to marine snow in Monterey Bay. These mucus structures, which are on the order of tens of centimeters in diameter, are derived from the house and filtering apparatus of a midwater larvacean, *Bathochordaeus* sp. (Barham 1979, Galt 1979, Hamner & Robison 1992).

We have found several copepods associated with the house and filtering apparatus of the larvacean. These include the poecilostomatoids *Oncaea conifera* and *O. similis,* an harpacticoid, *Microsetella rosea,* and *Metridia pacifica,* a calanoid common in the pelagic waters. One of the most abundant calanoid associated with larvacean houses is a large, bright-red scolecitrichid, *Scopalatum vorax* (Esterly 1911), which previously was known from a single adult female. *Scolecithricella lobophora* Park, 1970, another rare scolecitrichid also was collected around the houses.

Adult females and several other copepodid stages of both species are described from specimens collected in the field. A fifth copepodid of *Scottocalanus thomasi* is the only juvenile scolecitrichid described (Sewell 1929). A nauplius of *Scopalatum vorax* which hatched from an egg produced by one of several females in culture is described; this is the first report of a scolecitrichid nauplius. We also analyse the developmental patterns of setal addition to the first six appendages of *Scopalatum vorax,* and from these patterns develop hypotheses about the identity and homologies of antenna 1, maxilla 2, and the maxilliped.

The family Scolecitricidae initially was established as a subfamily, Scolecithrichina, of the Calanidae by Giesbrecht (1892). Sars (1902) used the now widely-accepted name, Scolecithricidae; Bowman & Abele (1982) changed the family name to Scolecitrichidae, using the correct latin transliteration of the genitive of the Greek word for "thrix."

Bradford (1973) recently redefined the family and its genera. Roe (1975) established *Scopalatum* for the "*Amallophora*" *altera* group of scolecitrichids defined by Bradford (1973); that group included Esterly's *Scolecithrix vorax*. Esterly's species has not been recorded since its initial description. Sars (1902) established *Scolecithricella*. *S. lobophora* Park, 1970 has been recorded once, as *Amallothrix lobophora* by Roe (1975).

Methods

Copepods were collected with houses of *Bathochordaeus* sp. in Monterey Bay in water deeper than 1000 m over a submarine canyon (36°42′N, 122°02′W) on seven different occasions between 8 October 1989 and 20 December 1991. Depths of samples ranged from 198–310 m in temperatures of 7.6°–9.0°C and salinities 33.95–34.07‰. Samples were collected during the day using a remotely-operated submersible, the *Ventana*. Two different types of samplers on the submersible were used to collect the larvacean houses and associated copepods. The "detritus sampler," from Harbor Branch Oceanographic Institution, is a 7.5 liter plexiglass cylinder with an opening/closing lid at either end. The "suction sampler" is a vacuum system; samples are drawn through a vacuum nozzle and deposited onto a rotating carousel containing canisters, each of which is fitted with a 165 μm mesh net and cod end. Larvacean houses were fixed with buffered 4% formaldehyde and their associated copepods subsequently were separated. In a few cases, living specimens of *Scopalatum vorax* were pipetted from house samples before fixation and placed in 0.2 μm filtered seawater in a dark, 10°C cold room. These copepods were fed a mixture of the algae *Dunaliella tertiolecta, Isochrysis galbana,* and *Thalassiosira weissflogii.* One nauplius hatched from several eggs produced by a female in culture.

Specimens were preserved in the laboratory in 0.5% propylene phenoxytol/4.5% proplylene glycol/95.0% water. They were clared in steps through 50.0% lactic acid/50.0% water to 100% lactic acid, and stained by adding a solution of chlorazol black E dissolved in 70.0% ethanol/30.0% water.

The naupliar stage is presumed to be the sixth and is abbreviated N6; second through sixth copepodid stages are CII to CVI. Thoracic and abdominal somites are numbered according to their relative developmental age as interpreted from data of Hulsemann (1991). The first and oldest thoracic somite bears the maxilliped and is fused with the cephalon. The youngest is the seventh; it is the only thoracic somite without an appendage. In adult calanoids it is the first somite of the urosome, and in adult females it is fused to the second abdominal somite. The first, and oldest, abdominal somite is the last; it bears the caudal rami. The youngest is immediately anterior to the oldest, and the remaining abdominal somites increase in age anteriorly.

Appendages are A1 = antennule; A2 = antenna; Mn = mandible; Mx1 = maxillule; Mx2 = maxilla; Mxp = maxilliped; appendages on thoracic somites are P1–5; caudal ramus = CR. Designations of appendage segments generally follow Huys & Boxshall (1991) except for Mx2 and Mxp; exopods = Re; endopods = Ri; medial lobes of a segment = li, lateral lobe = le. Terminal segments of Mx2 are exopodal. Mxp has at most 5 endopodal segments.

Ramal segments on P1–4 are numbered by their developmental age (see Hulsemann 1991, Ferrari & Ambler 1992, for a discussion of the age of these segments) and not proximal-to-distal as is the usual case for copepod descriptions. The distal-most segment of a ramus is the *first* segment. The *second* segment is immediately distal to the basipod. If present, the *third* segment is immediately proximal to the distal (or first) segment of a 3-segmented ramus. For a 3-segmented ramus, the proximal segment is the *second* segment, the middle segment is the *third* segment, and the distal segment is the *first* segment. Thus, developmentally homologous segments are given the same number in this system. The number of setae recorded for the segments follows this same scheme.

Armament elements of appendages are setae. Examples of the quality of setae are illustrated. Three setae and one aesthetasc on a segment of A1 are designated 3+1; if these elements are broken, one number is given for setae plus aesthetascs. Bradford's setae are those modified setae on Re of Mx2 and syncoxa of Mxp; their diversity and taxonomic value were described by Bradford (1973). Breaking planes are annular regions on a seta where the cuticular wall is thinner (Von Vaupel Klein 1982:112). Setules are epicuticular extensions of a seta and denticles are epicuticular extensions of an appendage segment; spinules, epicuticular extensions of a somite, are not found on these species. Groups of denticles are distally polarized if their tips point distally; they are radially polarized if their longitudinal axes appear to diverge from a central point. Von Vaupel Klein's organ on P1 (the appendage of thoracic somite 2) consists of the curved basipodal seta and tubercle with denticles on the endopodal segment; its taxonomic value was described by Von Vaupel Klein (1972).

Results

Scopalatum vorax (Esterly, 1911)
Figs. 1–9

Scolecithrix vorax.—Esterly, 1911:327–328, figs. 15, 21, 29, 45, 68, 93, 96, 99.
?*Amallophora smithae.*—Grice, 1962:205–206, plt. 15, figs. 12–22 (see remarks).

CVI female.—Length of 8 specimens 2.64, 2.66, 2.68, 2.70 (2), 2.75 (2), 2.93 mm; average Pr length/Ur length = 4.6; average Pr length/Pr depth = 2.5.

Pr (Fig. 1A): 4 segments; 1st a complex of 5 cephalic somites plus thoracic somites 1 and 2; thoracic somites 3 and 4 simple and articulated; fourth segment a complex of thoracic somites 5 and 6.

Ur (Fig. 1B): 4 segments; 1st a genital complex of thoracic somite 7 and abdominal somite 2 (Fig. 1C); abdominal somites 3, 4, 1 articulated.

Rostrum (Fig. 1H): 2 long filaments; armament of labrum and paragnath as in Fig. 1E.

A1: (Fig. 2A–E) 23 articulated segments with 3, 6+1, 2+1, 2, 2+1, 2+1, 2+1, 4+1, 1, 1, 2+1, 1, 2+1, 1, 1, 1, 2, 1+1, 1, 1, 2, 2, 7+1 setae + aesthetascs; 1st segment with 2 rows of small denticles.

A2 (Fig. 3A, B): Coxa with 1 seta and a row of long denticles; basis with 2 setae. Re 7-segmented with 0, 1, 1, 1, 1, 1, 4 setae with thick, dense setules above breaking plane and few scattered setules below; terminal 3 setae 1.5 times length of medial ones. Ri 2-segmented with 3, 15 (7 terminal, 8 subterminal) setae.

Mn (Fig. 3C, D): Coxa with a row of thin and a row of thick denticles; basis with 2 setae. Re 5-segmented with 1, 1, 1, 1, 3 setae, each with breaking plane. Ri 2-segmented with 1, 9 setae.

Mx1 (Fig. 3E, F): Le with 9 setae, largest 7 with breaking plane. Re 1-segmented with 8 setae; baseoendopod with medial sets of 5 and 3, and 6 terminal setae. Li 2 and 3 with 2 and 4 setae. Li 1 with 9 apical and 2 posterior setae; denticles on anterior and posterior surfaces.

Mx2 (Fig. 3G, H, I): Li 1–4 of coxa each with 3 setae and posterior denticles; li of basis with 4 setae. Re indistinctly segmented with 8 Bradford's setae; 1 thick with long apical setules, 4 thin with short apical setules, and 3 thin with tiny apical setules.

Mxp (Fig. 4A, B): Coxa with 7 (1 Bradford's) setae, basis with 5 (2 on a subterminal medial lobe). Ri with 4, 4, 3, 4 (1 lateral), 4 setae. 3 areas of denticles on coxa and a longitudinal row of denticles on basis.

P1 (Fig. 4C): Coxa with medial denticles, and basis with medial and lateral denticles. Re 3-segmented with 5, 1, 2 setae; segments

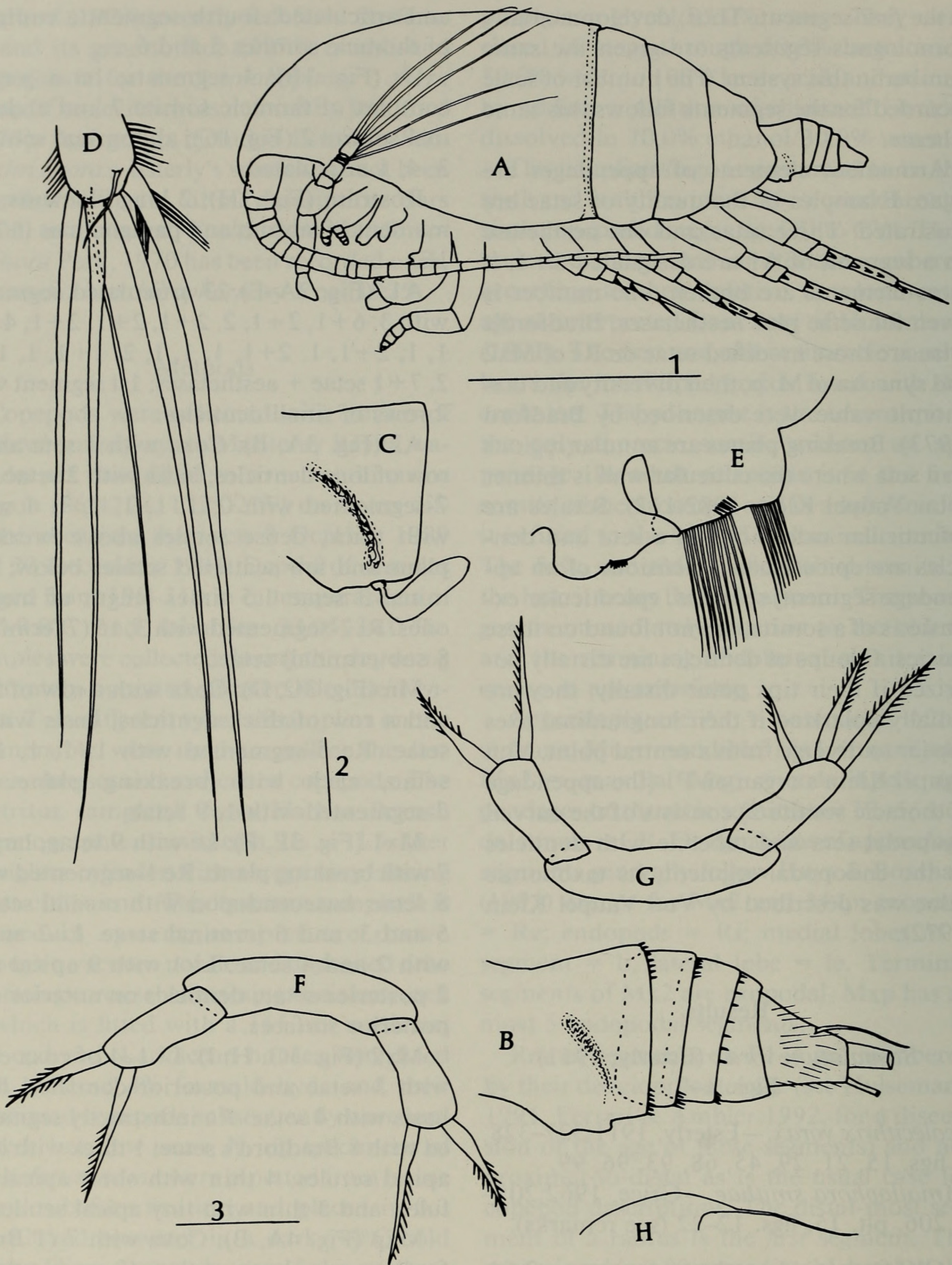

Fig. 1. *Scopalatum vorax,* CVI female: A, animal, lateral; B, Ur, lateral; C, genital segment with attached spermatophore, lateral; D, CR, dorsal; E, labrum and labium, lateral; F, P5, posterior; G, unusual P5, posterior; H, rostrum, lateral. Line 1 = 1.0 mm for A; line 2 = 0.1 mm for B–D; line 3 = 0.1 mm for E–G.

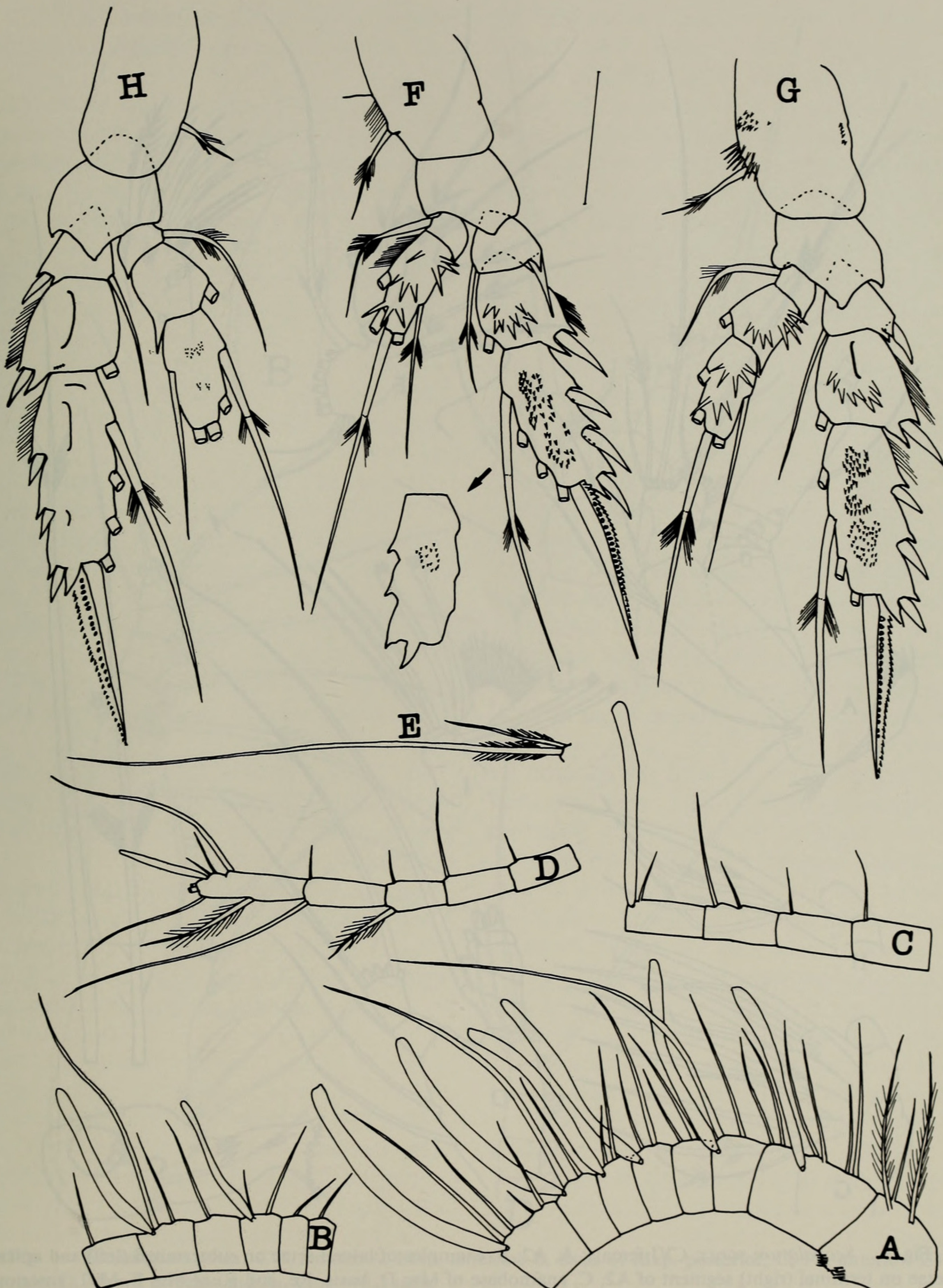

Fig. 2. *Scopalatum vorax,* CVI female: A, free segments 1–8 of A1; B, free segments 9–14 of A1; C, free segments 15–18 of A1; D, free segments 19–23 of A1; E, teminal setae of last segment of A1; F, P2, posterior, arrow to Re3 anterior; G, P3, posterior; H, P4, posterior. Line = 0.2 mm; letters on proximal-most segments of A–D.

Fig. 3. *Scopalatum vorax,* CVI female: A, A2; B, examples of lateral setae on subterminal (left) and apical setae on terminal (right) segment of A2; C, gnathobase of Mn; D, basis, Re, and Ri of Mn; E, Mx1, anterior; F, li of Mx1 with posterior setae darkened; G, coxa of Mx2; H, basis of Mx2; I, Re of Mx2. Line = 0.2 mm.

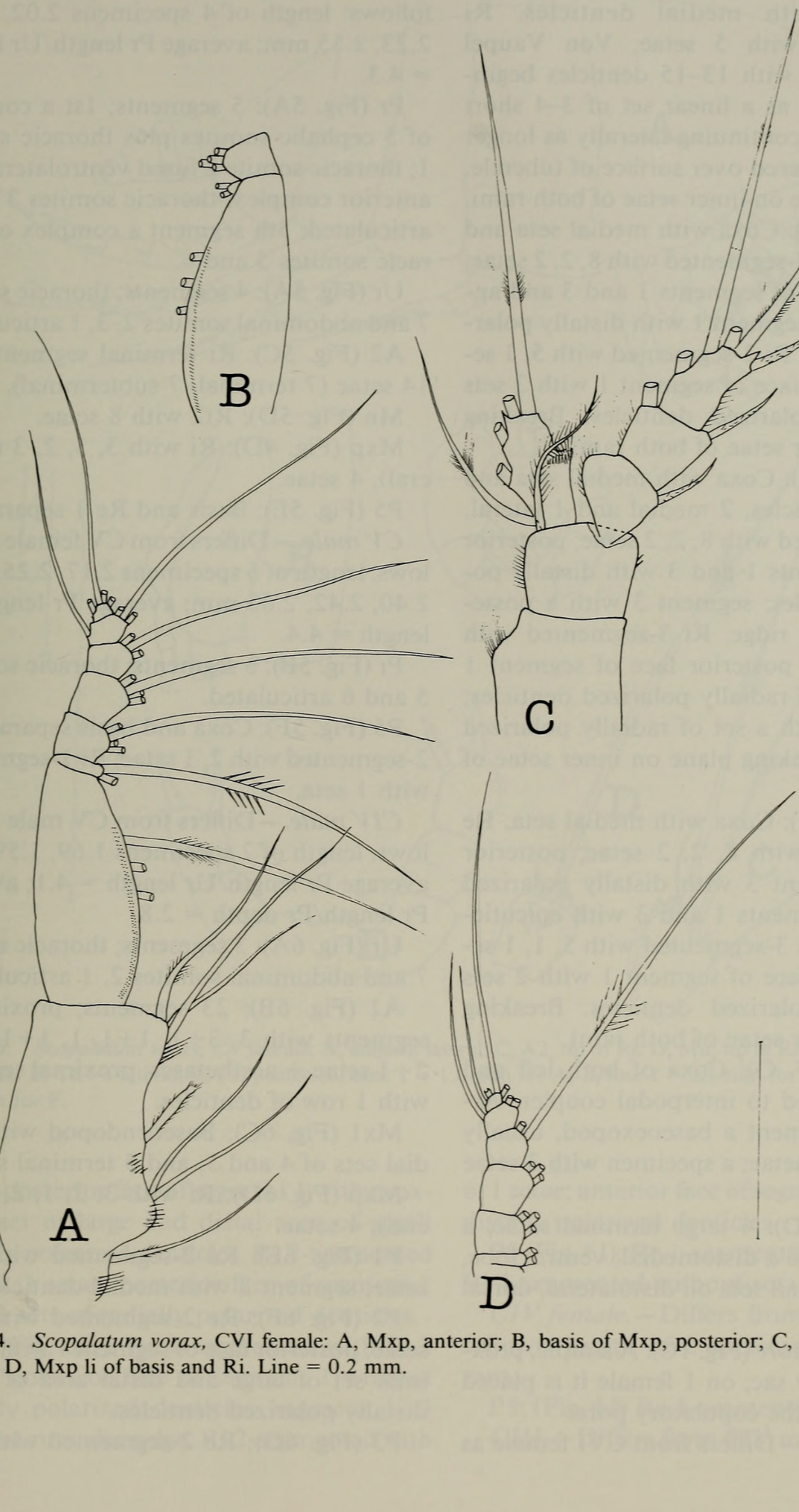

Fig. 4. *Scopalatum vorax,* CVI female: A, Mxp, anterior; B, basis of Mxp, posterior; C, P1, anterior. CV female: D, Mxp li of basis and Ri. Line = 0.2 mm.

2 and 3 with medial denticles. Ri 1-segmented with 5 setae; Von Vaupel Klein's organ with 13–15 denticles beginning medially as a linear set of 3–4 short denticles and continuing laterally as longer denticles scattered over surface of tubercle. Breaking plane on inner setae of both rami.

P2 (Fig. 2F): Coxa with medial seta and denticles. Re 3-segmented with 8, 2, 2 setae; posterior face of segments 1 and 3 and anterior face of segment 1 with distally polarized denticles. Ri 2-segmented with 5, 1 setae; posterior face of segment 1 with 3 sets of distally polarized denticles. Breaking plane on inner setae of both rami.

P3 (Fig. 2G): Coxa with medial seta and 3 sets of denticles, 2 medial and 1 lateral. Re 3-segmented with 8, 2, 2 setae; posterior face of segments 1 and 3 with distally polarized denticles; segment 3 with a posterior, cuticular ridge. Ri 3-segmented with 5, 1, 1 setae; posterior face of segment 1 with 2 sets of radially polarized denticles; segment 3 with a set of radially polarized denticles. Breaking plane on inner setae of both rami.

P4 (Fig. 2H): Coxa with medial seta. Re 3-segmented with 8, 2, 2 setae; posterior face of segment 3 with distally polarized denticles; segments 1 and 3 with epicuticular ridges. Ri 3-segmented with 5, 1, 1 setae; anterior face of segment 1 with 2 sets of distally polarized denticles. Breaking plane on inner setae of both rami.

P5 (Fig. 1F, G): Coxa of both left and right legs fused to interpodal coupler. Articulating segment a baseoexopod, usually with 2 apical setae; a specimen with 3 setae on left P5.

CR (Fig. 1D): 4 large terminal setae, a smaller seta on a distomedial, ventral lobe, and a very small seta on distolateral, dorsal lobe.

Spermatophore (Fig. 1C): A simple, proximally narrow sac; on 1 female it is placed directly over the copulatory pore.

CV female.—Differs from CVI female as follows: length of 4 specimens 2.02, 2.13, 2.23, 2.55 mm; average Pr length/Ur length = 4.3.

Pr (Fig. 5A): 5 segments; 1st a complex of 5 cephalic somites plus thoracic somite 1; thoracic somite 2 fused ventrolaterally to anterior complex; thoracic somites 3 and 4 articulated; 5th segment a complex of thoracic somites 5 and 6.

Ur (Fig. 5A): 4 segments; thoracic somite 7 and abdominal somites 2, 3, 1 articulated.

A2 (Fig. 5C): Ri terminal segment with 14 setae (7 terminal, 7 subterminal).

Mn (Fig. 5D): Ri2 with 8 setae.

Mxp (Fig. 4D): Ri with 3, 3, 2, 3 (1 lateral), 4 setae.

P5 (Fig. 5E): Basis and Re 1 separate.

CV male.—Differs from CV female as follows: length of 6 specimens 2.17, 2.25, 2.30, 2.40, 2.42, 2.63 mm; average Pr length/Ur length = 4.4.

Pr (Fig. 5B): 6 segments; thoracic somites 5 and 6 articulated.

P5 (Fig. 5F): Coxa and basis separate; Re 2-segmented with 2, 1 setae; Ri 1-segmented with 1 seta.

CIV male.—Differs from CV male as follows: length of 2 specimens 1.69, 1.59 mm; average Pr length/Ur length = 4.1; average Pr length/Pr depth = 2.8.

Ur (Fig. 6A): 3 segments; thoracic somite 7 and abdominal somites 2, 1 articulated.

A1 (Fig. 6B): 23 segments; proximal 8 segments with 3, 3+1, 1+1, 1, 1+1, 1, 1, 2+1 setae + aesthetascs; proximal segment with 1 row of denticles.

Mx1 (Fig. 6C): Baseoendopod with medial sets of 4 and 3, and 5 terminal setae.

Mxp (Fig. 6D): Ri with 3, 2, 1, 2 (1 lateral), 4 setae.

P1 (Fig. 6E): Re 2-segmented with 7, 1 setae; segment 2 with medial denticles.

P2 (Fig. 6F): Re 2-segmented with 9, 2 setae; posterior face of segment 1 with proximal set of large and distal area of small distally polarized denticles.

P3 (Fig. 6G): Re 2-segmented with 9, 2

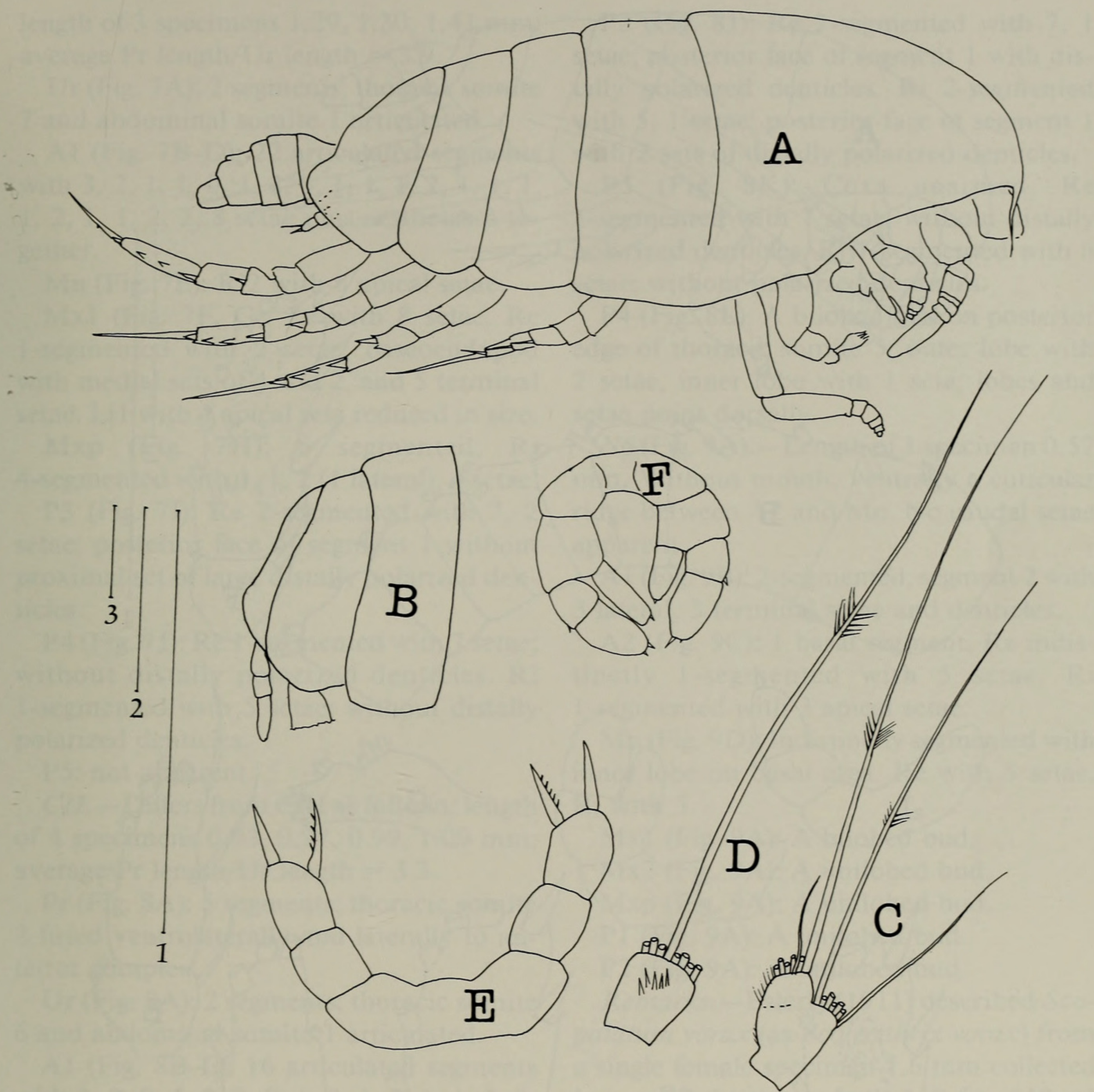

Fig. 5. *Scopalatum vorax,* CV female: A, animal, lateral; C, A2, tip of Ri; D, Mn, tip of Ri; E, P5, posterior. CV male: B, Th4-6 lateral; F, P5, posterior. Line 1 = 1.0 mm for A, B; line 2 = 0.1 mm for C, D, E; line 3 = 0.1 mm for F.

setae; posterior face of segment 1 with proximal set of large and distal area of small distally polarized denticles. Ri 2-segmented with 6, 1 setae; posterior face of segment 1 with 3 sets of radially polarized denticles.

P4 (Fig. 6H): Re 2-segmented with 9, 2 setae; posterior face of segment 1 without distally polarized denticles; segment 1, 3 without cuticular ridge. Ri 2-segmented with 6, 1 setae; anterior face of segment 1 without distally polarized denticles.

P5 (Fig. 6I): Re 1-segmented with 2 setae; Ri 1-segmented without seta.

CIV female.—Differs from CIV male as follows: length of 2 specimens 1.78, 1.65 mm.

P5: (Fig. 6J) Re 1-segmented with 1 seta.

CIII.—Differs from CIV male as follows:

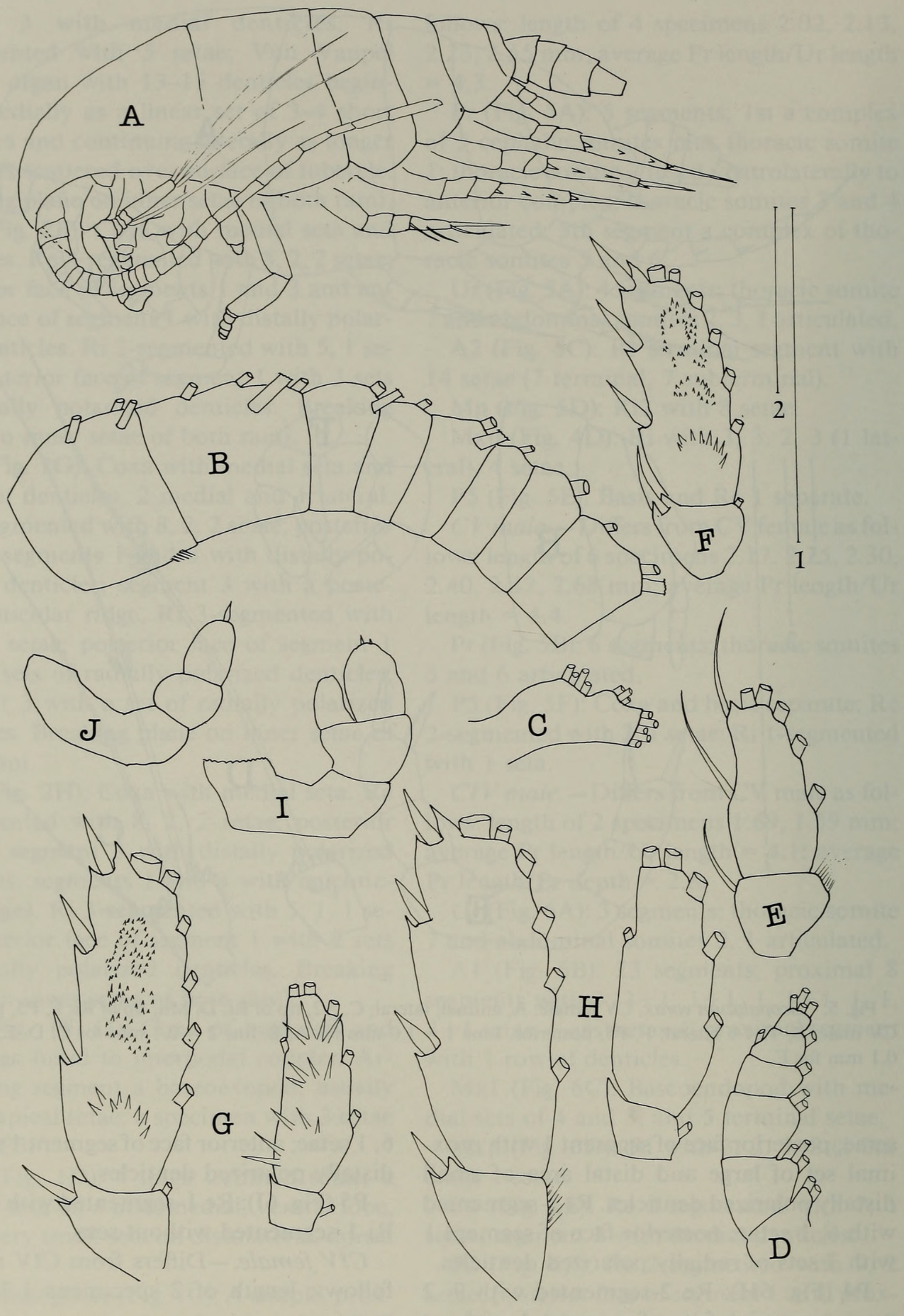

Fig. 6. *Scopalatum vorax,* CIV male: A, animal, lateral; B, proximal 8 segments of A1; C, Ri of Mx1; D, end of basis and Ri of Mxp; E, Re of P1; F, Re of P2; G, Re (left) and Ri (right) of P3; H, Re (left) and Ri (right) of P4; I, P5. CIV female: J, P5. Line 1 = 1.0 mm for A; line 2 = 0.1 mm for B–J.

length of 3 specimens 1.29, 1.30, 1.41 mm; average Pr length/Ur length = 3.9.

Ur (Fig. 7A): 2 segments; thoracic somite 7 and abdominal somite 1 articulated.

A1 (Fig. 7B–D): 22 articulated segments with 3, 2, 1, 1, 0, 1, 2, 0, 1, 1, 1, 2, 1, 1, 1, 1, 2, 1, 1, 2, 2, 8 setae plus aesthetascs together.

Mn (Fig. 7E): Ri2 with 6 apical setae.

Mx1 (Fig. 7F, G): Le with 8 setae. Re 1-segmented with 7 setae; baseoendopod with medial sets of 4 and 2, and 5 terminal setae. Li1 with 1 apical seta reduced in size.

Mxp (Fig. 7H): 6 segmented; Ri 4-segmented with 1, 1, 2 (1 lateral), 4 setae.

P3 (Fig. 7I): Re 2-segmented with 7, 2 setae; posterior face of segment 1 without proximal set of large distally polarized denticles.

P4 (Fig. 7J): Re 1-segmented with 7 setae; without distally polarized denticles. Ri 1-segmented with 5 setae; without distally polarized denticles.

P5: not apparent.

CII.—Differs from CIII as follows: length of 4 specimens 0.93, 0.97, 0.99, 1.09 mm; average Pr length/Ur length = 3.3.

Pr (Fig. 8A): 5 segments; thoracic somite 2 fused ventrolaterally and laterally to anterior complex.

Ur (Fig. 8A): 2 segments; thoracic somite 6 and abdominal somite 1 articulated.

A1 (Fig. 8B–E): 16 articulated segments with 3, 3, 0, 1, 0, 2, 0, 1, 0, 1, 2, 1, 1, 2, 2, 8 setae plus aesthetascs together.

A2 (Fig. 8F): Ri terminal segment with 10 (6 terminal, 4 subterminal) setae.

Mn (Fig. 8G): Ri2 with 5 setae.

Mx1 (Fig. 8H): Le with 6 setae. Re 1-segmented with 6 setae; baseoendopod with medial sets of 3 and 2, and 5 terminal setae. Li1 with 7 apical and 2 posterior setae.

Mxp (Fig. 8I): 5 segments with 7 (1 Bradford's) setae on coxa, 4 (2 on a subterminal medial lobe) on basis. Ri 3-segmented with 1, 1, 4 setae.

P1: basis with 1 medial seta.

P2 (Fig. 8J): Re 2-segmented with 7, 1 setae; posterior face of segment 1 with distally polarized denticles. Ri 2-segmented with 5, 1 setae; posterior face of segment 1 with 2 sets of distally polarized denticles.

P3 (Fig. 8K): Coxa unarmed. Re 1-segmented with 7 setae; without distally polarized denticles. Ri 1-segmented with 6 setae; without polarized denticles.

P4 (Fig. 8L): A bilobed bud on posterior edge of thoracic somite 5; outer lobe with 2 setae, inner lobe with 1 seta; lobes and setae point dorsally.

N6 (Fig. 9A).—Length of 1 specimen 0.57 mm. Without mouth; ventrally a cuticular ridge between A2 and Mn. No caudal setae apparent.

A1 (Fig. 9B): 2-segmented; segment 2 with 3 lateral, 3 terminal setae and denticles.

A2 (Fig. 9C): 1 basal segment. Re indistinctly 1-segmented with 5 setae. Ri 1-segmented with 3 apical setae.

Mn (Fig. 9D): Indistinctly segmented with inner lobe on basal area. Re with 5 setae, Ri with 3.

Mx1 (Fig. 9A): A bilobed bud.

Mx2 (Fig. 9A): A unilobed bud.

Mxp (Fig. 9A): A unilobed bud.

P1 (Fig. 9A): A unilobed bud.

P2 (Fig. 9A): A unilobed bud.

Remarks.—Esterly (1911) described *Scopalatum vorax* (as *Scolecithrix vorax*) from a single female specimen 1.6 mm collected in a vertical net tow from 310 fm (558 m) off San Diego; the location of that specimen is unknown. Our specimens agree in general with Esterly's description and illustrations of the appendages, except that our specimens are larger and thoracic somites 5 and 6 are fused.

Of the remaining nominal species (Roe 1975) in the genus, *S. dubia* (T. Scott, 1894), *S. farrani* Roe, 1975, *S. gibbera* Roe, 1975, and *S. smithae* (Grice, 1962), only *S. smithae* has been reported from the Pacific Ocean. It was described as *Amallophora smithae* by Grice (1962) from one adult female, 1.40 mm, collected from the equa-

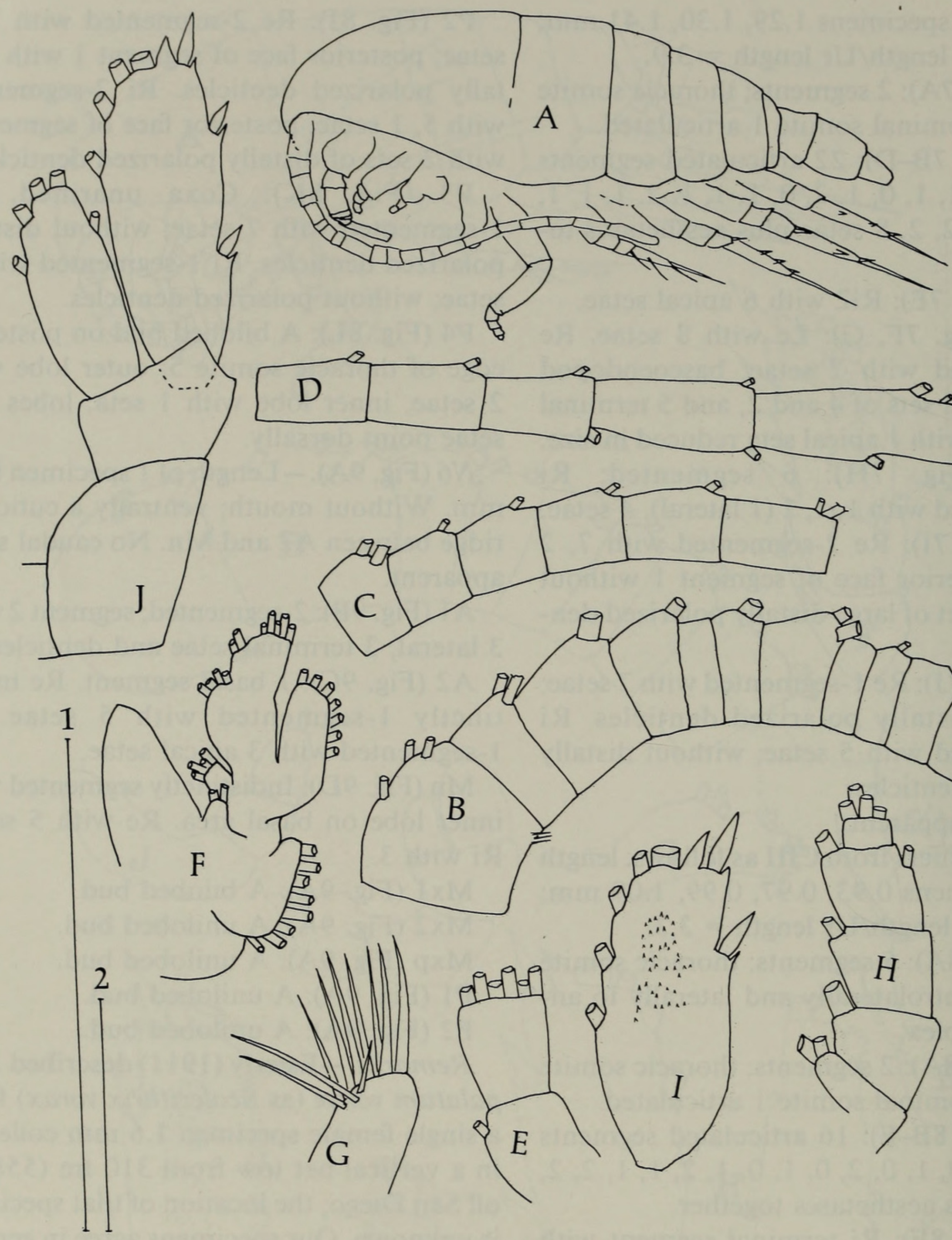

Fig. 7. *Scopalatum vorax,* CIII: A, animal, lateral; B, free segments 1–11 of A1; C, free segments 12–17 of A1; D, free segments 18–22 of A1; E, Mn, tip of Ri; F, Mx1; G, Mx1, armament of li1; H, end of basis and Ri of Mxp; I, Re1 of P3; J, P4. Line 1 = 1.0 mm for A; line 2 = 0.1 mm for B–J; letters on proximal-most segments of B–D.

torial Pacific Ocean southeast of Hawaii. The description of that specimen agrees in most character states with ours, including the fusion of thoracic somites 5 and 6, and the armament of most appendages; however, P5 of that specimens has only one terminal seta. The dissected type specimen is mounted on a slide and consists of 10 submounts with 1 A1, 2 A2; 1 Mn; 2 Mx1; 2 Mx2; 2 Mxp; nothing; 2 P2 complete with coupler; 2 P3 missing left Re2-3; 2 P4 missing right Re2-3 and Ri2-3; nothing.

The type localities of *S. farrani* and *S. gibbera* are in the Atlantic Ocean. P5 of the

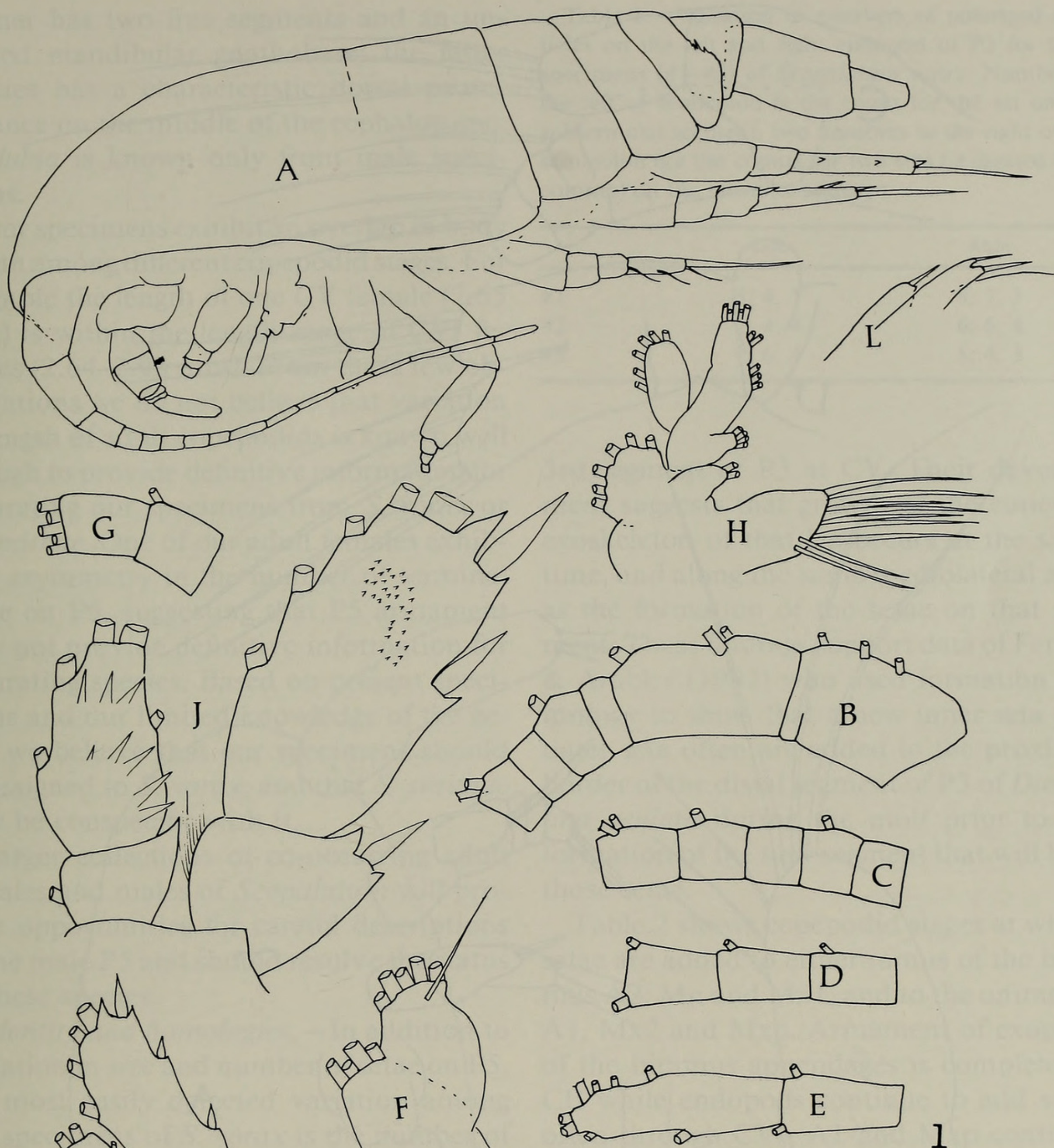

Fig. 8. *Scopalatum vorax,* CII: A, animal, lateral; B, free segments 1–6 of A1; C, free segments 7–11 of A1; D, free segments 12–14 of A1; E, free segments 15–16 of A1; F, A2, tip of Ri; G, Ri of Mn; H, Mx1; I, basis and Ri of Mxp; J, Re (right) and Ri (left) of P2; K, P3; L, right P4 (dorsal is up). Line 1 = 0.3 mm for A; line 2 = 0.1 mm for B–L; letters on proximal-most segments of B–D.

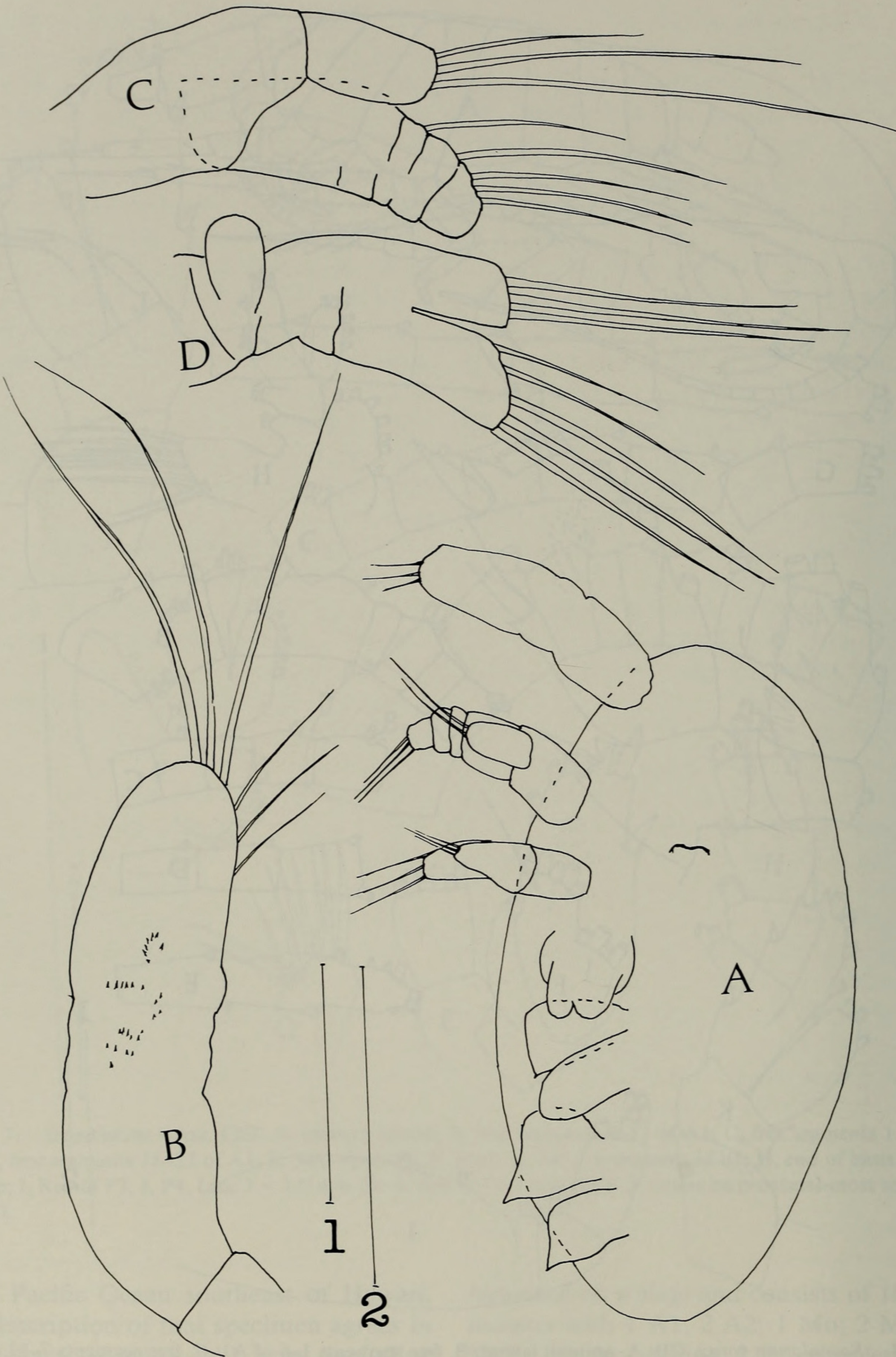

Fig. 9. *Scopalatum vorax,* N6: A, animal, ventral; B, A1; C, A2; D, Mn. Line 1 = 0.2 mm for A; line 2 = 0.1 mm for B–D.

former has two free segments and an unarmed mandibular gnathobase; the latter species has a characteristic dorsal protuberance on the middle of the cephalosome. *S. dubia* is known only from male specimens.

Our specimens exhibit an overlap in body length among different copepodid stages. For example the length of one CV female (2.65 mm) is within the length range of CVI females (2.64–2.93 mm). From these few observations we do not believe that variation in length of adult copepodids is known well enough to provide definitive information for separating our specimens from *S. vorax* or *S. smithae.* One of our adult females exhibited asymmetry in the number of terminal setae on P5, suggesting that P5 armament may not provide definitive information for separating species. Based on present specimens and our limited knowledge of the genus we believe that our specimens should be assigned to *S. vorax,* and that *S. smithae* may be conspecific with it.

Larger collections of co-occurring adult females and males of *Scopalatum* will provide opportunities for careful descriptions of the male P5 and should resolve the status of these species.

Identity and homologies.—In addition to variation in size and number of setae on P5, the most easily detected variation among our specimens of *S. vorax* is the number of polarized denticles on rami of P2-4. For example, denticle numbers on left and right endopodal segments 1 and 3 of P3 from 3 specimens are given in Table 1. The difference in counts between left and right appendages and among specimens suggests that the numbers of denticles may not have specific taxonomic value.

The position of surface denticles on P2-4 during copepodid development, however, does provide information about the growth of the appendage cuticle. Denticles initially appear on the posterior surface of segment 1 of leg 3 at CIII. We believe that these denticles are homologous to those on the

Table 1.—Variation in numbers of polarized denticles on the left and right endopod of P3 for three specimens (#1–#3) of *Scopalatum vorax.* Number to the left of semicolon is the count for the set on the subterminal segment; two numbers to the right of the semicolon are the counts for two sets (separated by a comma) on the terminal segment.

	Left	Right
#1	5; 4, 3	8; 7, 3
#2	7; 4, 4	6; 6, 4
#3	7; 6, 4	8; 4, 3

3rd segment of P3 at CV. Their development suggests that growth of the cuticular exoskeleton of that leg occurs at the same time, and along the same mediolateral axis, as the formation of the setae on that segment. These findings support data of Ferrari & Ambler (1992) who used formation homology to show that a new inner seta and outer seta often are added to the proximal border of the distal segment of P3 of *Dioithona oculata* during the molt prior to the formation of the new segment that will bear those setae.

Table 2 shows copepodid stages at which setae are added to either ramus of the biramus A2, Mn and Mx1, and to the uniramus A1, Mx2 and Mxp. Armament of exopods of the biramus appendages is complete by CII while endopods continue to add setae often through CVI. A1 and Mxp continue to add setae late in development while Mx2 does not. These results suggest that the terminal segments of Mx2 are exopodal, not endopodal as has been suggested by Giesbrecht (1894) and Huys & Boxshall (1991), and the terminal segments of Mxp are endopodal. The developmental pattern of setal addition to A1 is similar to that of an endopod.

Table 3 gives two interpretations of the number of setae on the terminal and 4 subterminal endopodal segments, and on the basal lobe of the Mxp. This latter structure has recently been called an endopodal segment by Huys & Boxshall (1991). During

Table 2.—Stages of development of *Scopalatum vorax* at which setae are added (A) to rami of A2, Mn, Mx1, and to A1, Mx2, Mxpd.

	A1	A2		Mn		Mx1		Mx2	Mxpd
		Re	Ri	Re	Ri	Re	Ri		
CII	—	—	—	—	—	—	—	—	—
CIII	A		A		A		A		A
CIV	A				A		A		A
CV	A						A		A
CVI			A		A				A

copepodid development, setae are added to the 4 subterminal endopodal segments but there is no change in number of setae on the lobe of the basis. These data and Von Vaupel Klein (1982) suggest that this latter structure is a true lobe of the basis, and not subterminal, endopodal segment fused to the basis.

Based on its developmental pattern, we have interpreted P5 of the adult female as the coxa of both left and right legs which are fused to the interpodal coupler; the articulating segment is the basis fused to exopod 1. Post-maxillipedal appendages usually are transformed from a bud to an appendage having a basis articulating with the coxa and 1-segmented rami (Ferrari 1988, Ferrari & Ambler 1992). For P5 of calanoids this transformation usually occurs during the molt to CIV (Ferrari 1988). P5 of CIV male (Fig. 6I) exhibits this transformed morphology. Its exopod has 2 setae and its endopod is unarmed. P5 of CIV females (Fig. 6J) is similar but has one ramal segment which, we believe, is an exopod because it is armed with a seta. P5 of CV female (Fig. 5E) is morphologically similar; the unarmed basis articulates with the coxa and with a 1-segmented exopod now armed with 2 setae. An alternate explanation is that the basis has fused to the coxa and the exopod has gained an unarmed, second segment; CV male has a 2-segmented exopod but the second segment has an outer seta (Fig. 5F). For CVI female the basis of P5 has fused with the exopodal segment, while the fused coxa and coupler remain. In the alternate developmental pattern, the articulating segment would incorporate two or three fused exopodal segments. We prefer the first developmental pattern and its interpretation of the articulating segment, a basis fused to exopod 1.

Table 3.—Two interpretations of the number of setae on the distal inner lobe of the basis (L) and on the five endopodal segments (numbered proximally to distally) of the maxilliped of *Scopalatum vorax* for stages CII–CVI. A—when new segments are armed with only one seta; B—when new segments are added proximally to the distal-most segment. a = segment presumed absent.

	L	1st	2nd	3rd	4th	5th
			A			
CII	2	1	a	a	1	4
CIII	2	1	1	a	2	4
CIV	2	3	2	1	2	4
CV	2	3	3	2	3	4
CVI	2	4	4	3	4	4
			B			
CII	2	1	1	a	a	4
CIII	2	1	1	2	a	4
CIV	2	3	2	1	2	4
CV	2	3	3	2	3	4
CVI	2	4	4	3	4	4

Behavior and ecology.—Houses of shallower living larvaceans are known to serve as surface habitat for a variety of zooplankton and can be used as a food source for some copepods (Alldredge 1972, 1976; Ohtsuka & Kubo 1991). *S. vorax* could be seen clearly with the submersible's video camera moving around the inner food collecting filter of larvacean houses and less often near its outer house or "sheet" (Hamner & Robison 1992). Preliminary analyses of the gut contents of *S. vorax* show similarities between food items, diatom and crustacean skeletal parts, and diatom and crustaceans associated with the houses. These data suggest that the community of organisms associated with larvacean houses is being utilized as a food source by a *S. vorax*.

The presence of lobes of Mx1, Mx2, Mxp, P1, and P2, suggests that our nauplius is a stage 6 calanoid nauplius. Absence of a mouth opening, labrum, paragnaths and gnathobase on A2 suggests that this nauplius cannot feed. If the rules of Izawa (1987) for a reduced number of naupliar stages can be extended to calanoids, we expect *S. vorax* to develop through six naupliar stages. We do not expect these lecithotrophic nauplii to occur in shallow depths.

Scolecithricella lobophora Park, 1970
Figs. 10–13

Scolecithricella lobophora.—Park, 1970:511, 515, figs. 188–201. not *Amallothrix lobophora*.—Roe, 1975:329, fig. 17 (see remarks).

CVI female.—length of 4 specimens 1.26, 1.52, 1.75, 1.85 mm; average Pr length/Ur length = 3.7.

Pr (Fig. 10A): 4 segments; 1st a complex of 5 cephalic somites plus thoracic somites 1 and 2; thoracic somites 3 and 4 simple and articulated; fourth segment a complex of thoracic somites 5 and 6.

Ur (Fig. 10B): 4 segments; 1st a genital complex of thoracic somite 7 and abdominal somite 2; abdominal somites 3, 4, 1 articulated.

Rostrum (Fig. 10A): 2 short points.

A1 (Fig. 11B–E): 22 articulated segments with 3, 7+1, 2+1, 2, 2+1, 2+1, 2+1, 4, 1, 2+1, 1, 2+1, 1, 2, 1, 2, 1+1, 1, 1, 2, 2, 7+1 setae + aesthetascs; segments 1, 8–11 distally with circumferential denticles.

A2: Coxa with 1 seta and row of long denticles; basis with 2 setae. Re 7-segmented with 0, 1, 1, 1, 1, 1, 4 setae with breaking planes. Ri 2-segmented with 2, 15 (7 terminal, 8 subterminal) setae and lateral denticles.

Mn (Fig. 10C, D): Coxa with 2 rows of thin and 1 row of thick denticles; basis with 2 setae; denticles medially and laterally. Re 4-segmented with 1, 1, 1, 3 setae. Ri 2-segmented with 1, 9 setae.

Mx1 (Fig. 10E, F): Le with 9 setae. Re 1-segmented with 8 setae; baseoendopod with medial sets of 5 and 3, and 6 terminal setae. Li 2 and 3 with 2 and 4 setae. Li 1 with 9 apical and 2 posterior setae; denticles on anterior and posterior surfaces.

Mx2: Li 1–4 of coxa each with 3 setae and posterior denticles; li of basis with 4 setae. Re indistinctly segmented with 8 Bradford's setae: 5 thin with short apical setules, and 3 thin with tiny apical setules.

Mxp: Coxa with 6 (1 Bradford's) setae, basis with 5 (2 on a subterminal medial lobe). Ri 5-segmented with 4, 4, 3, 4 (1 lateral), 4 setae; 3 areas of denticles on coxa and a longitudinal row of denticles on basis.

P1: Coxa and basis with medial denticles. Re 3-segmented with 5, 0, 2 setae; segment 2 with medial denticles. Ri 1-segmented with 5 setae; Von Vaupel Klein's organ with 8–10 denticles below crest of tubercle. Breaking plane on inner setae of both rami.

P2 (Fig. 12A): Coxa with medial seta; basis with distolateral denticles. Re 3-segmented with 8, 2, 2 setae; posterior face of segments 1 and 3 with distally polarized denticles. Ri 2-segmented with 5, 1 setae; posterior face of segment 1 with 3 sets of radially polarized denticles. Breaking plane on inner setae of both rami.

P3 (Fig. 12B, C): Coxa with medial seta and 2 medial sets of denticles; basis with distolateral set of denticles. Re 3-segmented with 8, 2, 2 setae; posterior face of segments 1 and 3 with distally polarized denticles; anterior face of segment 2 with distally polarized denticles. Ri 3-segmented with 5, 1, 1 setae; posterior face of segment 3 with a set of radially polarized denticles and of seg-

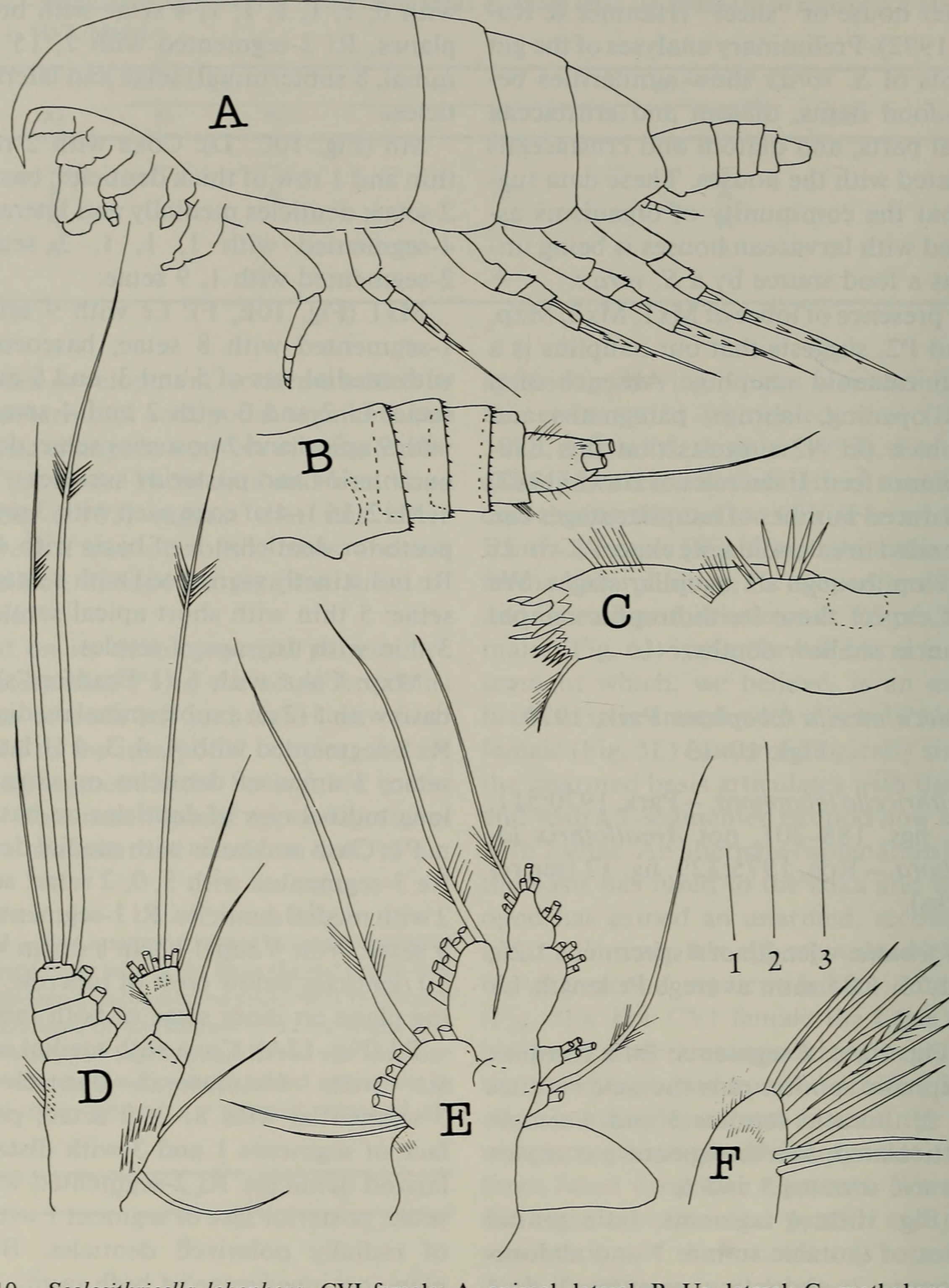

Fig. 10. *Scolecithricella lobophora,* CVI female: A, animal, lateral; B, Ur, lateral; C, gnathobase of Mn, anterior; D, basis, Re and Ri of Mn, posterior; E, Mx1; F, li1 of Mx1. Line 1 = 0.2 mm for A; line 2 = 0.2 mm for B; line 3 = 0.1 mm for C-F.

ment 1 with 2 sets of radially polarized denticles. Breaking plane on inner setae of both rami.

P4 (Fig. 12D, E): Coxa with medial seta and basis with distolateral denticles. Re 3-segmented with 8, 2, 2 setae; posterior face of segment 1 with distally polarized denticles. Ri 3-segmented with 5, 1, 1 setae;

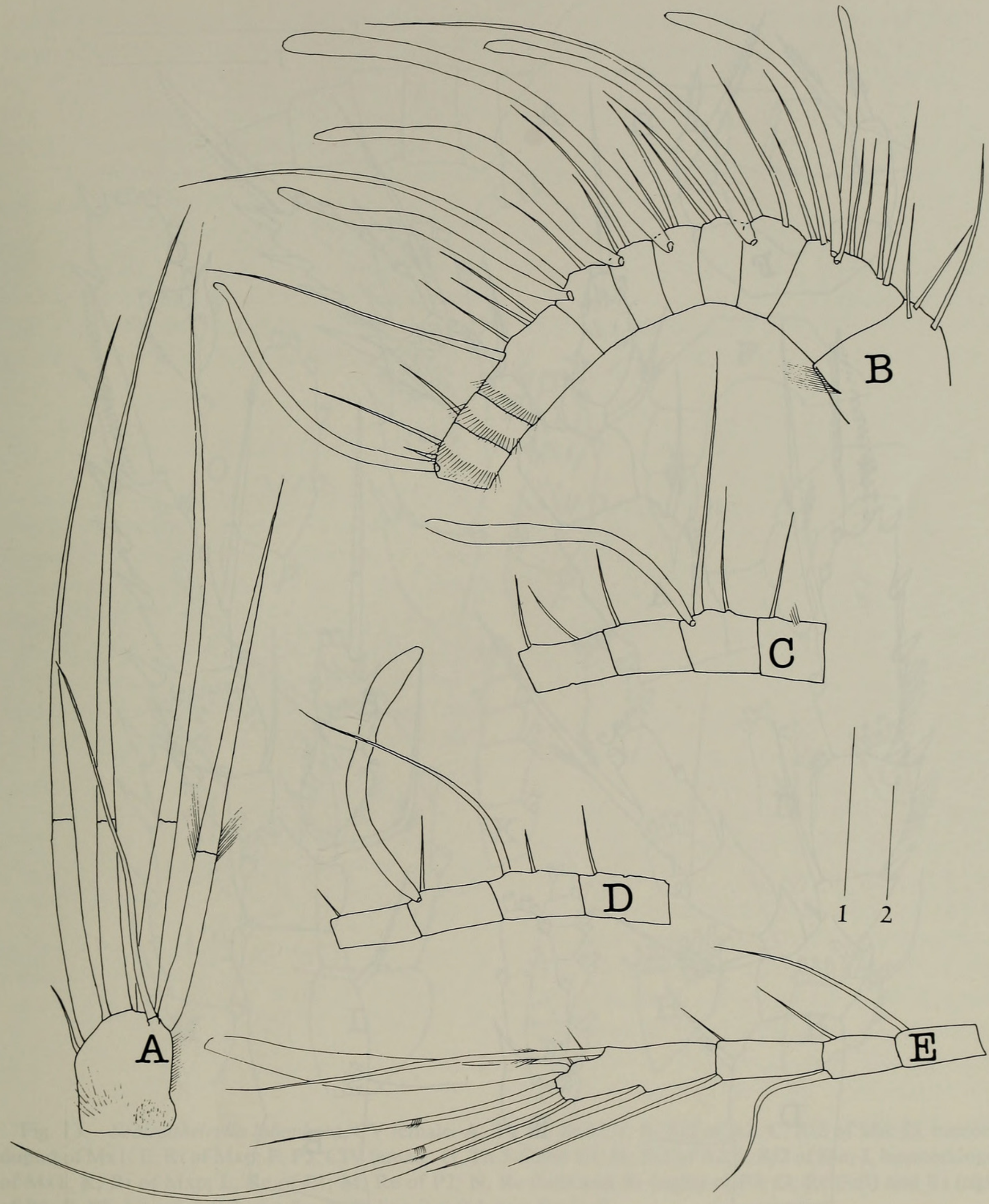

Fig. 11. *Scolecithricella lobophora,* CVI female: A, CR, ventral; B, free segments 1–10 of A1; C, free segments 11–14 of A1; D, free segments 15–18 of A1; E, free segments 19–22 of A1. Line 1 = 0.2 mm for A; line 2 = 0.1 mm for B–E; letters on proximal-most segments of D–G.

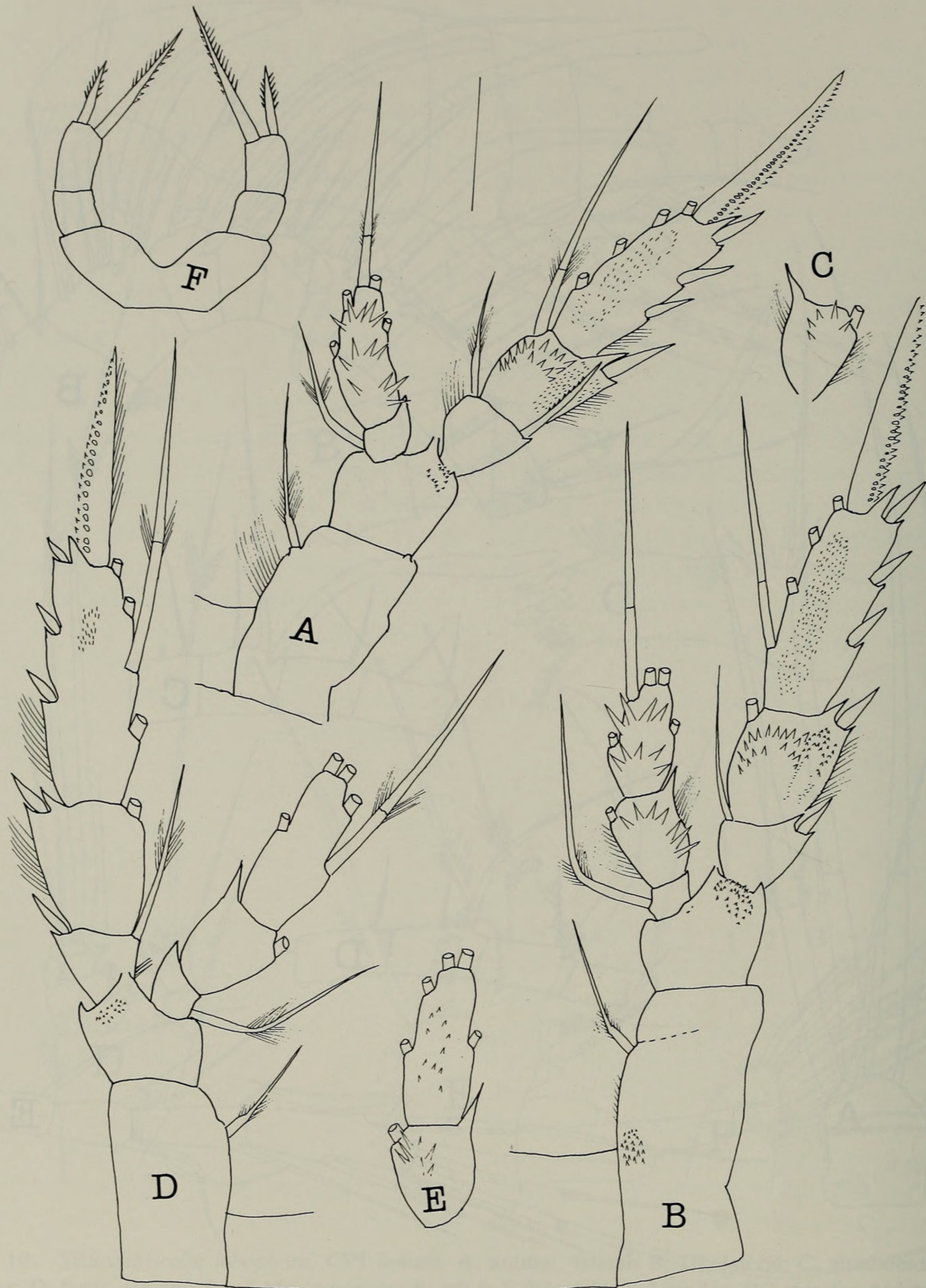

Fig. 12. *Scolecithricella lobophora,* CVI female: A, P2, posterior; B, P3, posterior; C, Re2 of P3, anterior; D, P4, posterior; E, Ri1, 3 of P4, anterior; F, P5, posterior. Line = 0.1 mm.

anterior face of segments 1 and 3 with distally polarized denticles. Breaking plane on inner setae of both rami.

P5 (Fig. 12F): Coxa of both left and right legs fused to interpodal coupler; basis separate. Re 1-segmented with 2 apical setae.

CR (Fig. 11A): 4 large terminal setae, and a smaller seta on dorsal and on lateral sur-

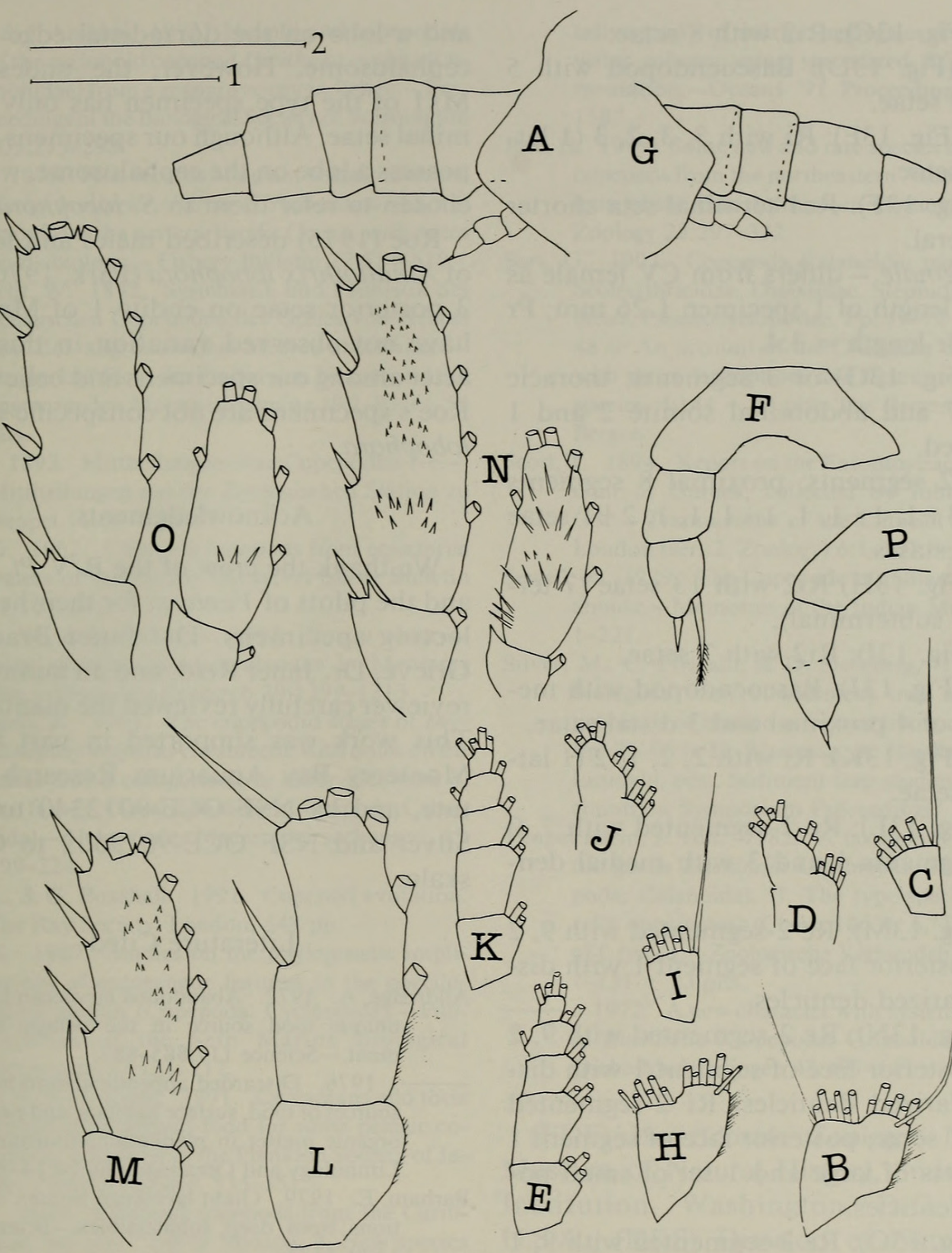

Fig. 13. *Scolecithricella lobophora,* CV female: A, Th 5-6 and Ur; B, Ri2 of A2; C, Ri2 of Mn; D, baseoendopod of Mx1; E, Ri of Mxp; F, P5. CIV female: G, Th 5-6 and Ur; H, Ri2 of A2; I, Ri2 of Mn; J, baseoendopod of Mx1; K, Ri of Mxp; L, Re of P1; M, Re of P2; N, Re (left) and Ri (right) of P3; O, Re (left) and Ri (right) of P4; P, P5. Line 1 = 0.2 mm for A, B; line 2 = 0.1 mm for C–P.

faces; medially and dorsally with denticles. Terminal setae each with breaking plane.

CV female.—differs from CVI female as follows: length of 1 specimen 1.52 mm; Pr length/Ur length = 4.1.

Ur (Fig. 13A): 4 segments; thoracic somite 7 and abdominal somites 2, 3, 1 articulated.

A2 (Fig. 13B): Ri2 with 14 setae (7 terminal, 7 subterminal).

Mn (Fig. 13C): Ri2 with 8 setae.

Mx1 (Fig. 13D): Baseoendopod with 5 terminal setae.

Mxp (Fig. 13E): Ri with 3, 3, 2, 3 (1 lateral), 4 setae.

P5 (Fig. 13F): Re1 terminal seta shorter than lateral.

CIV female.—differs from CV female as follows: length of 1 specimen 1.26 mm; Pr length/Ur length = 3.4.

Ur: (Fig. 13G) of 3 segments; thoracic somite 7 and abdominal somite 2 and 1 articulated.

A1: 22 segments; proximal 8 segments with 3, 3+1, 1+1, 1, 1+1, 1, 1, 2+1 setae + aesthestascs.

A2: (Fig. 13H) Ri2 with 13 setae (7 terminal, 6 subterminal).

Mn (Fig. 13I): Ri2 with 7 setae.

Mx1 (Fig. 13J): Baseoendopod with medial sets of 4 proximal and 3 distal setae.

Mxp (Fig. 13K): Ri with 2, 2, 1, 2 (1 lateral), 4 setae.

P1 (Fig. 13L): Re 2-segmented with 7, 0 setae; segments 1 and 3 with medial denticles.

P2 (Fig. 13M): Re 2-segmented with 9, 2 setae; posterior face of segment 1 with distally polarized denticles.

P3 (Fig. 13N): Re 2-segmented with 9, 2 setae; posterior face of segment 1 with distally polarized denticles. Ri 2-segmented with 6, 1 setae; posterior face of segment 1 with 3 sets of large and 1 set of small polarized denticles.

P4 (Fig. 13O): Re 2-segmented with 9, 1 setae; posterior face of segment 3 without distally polarized denticles. Ri 2-segmented with 6, 1 setae; anterior face of segment 1 with distally polarized denticles.

P5 (Fig. 13P): Re indistinctly separate from basis with 1 seta.

Remarks.—*Scolecithricella lobophora* was described by Park (1970) from a single adult female collected in the southern Gulf of Mexico. Our specimens differ from Park's description and illustration of 7 terminal setae on an articulating endopod of Mx1 and a lobe on the dorsodistal edge of the cephalosome. However, the undescribed Mx1 of the type specimen has only 5 terminal setae. Although our specimens do not possess a lobe on the cephalosome, we have chosen to refer them to *S. lobophora.*

Roe (1975) described males and females of *Amallothrix lobophora* (Park, 1970) with 3 posterior setae on endite 1 of Mx1. We have not observed variation in this character among our specimens and believe that Roe's specimens are not conspecific with *S. lobophora.*

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Literature Cited

Alldredge, A. 1972. Abandoned larvacean houses: a unique food source in the pelagic environment.—Science 117:885–887.

———. 1976. Discarded appendicularian houses as sources of food, surface habitats, and particulate organic matter in planktonic environments.—Limnology and Oceanography 24:14–23.

Barham, E. 1979. Giant larvacean houses: observations from deep submersibles.—Science 205: 1129–1131.

Bowman, T., & L. Abele. 1982. Classification of the recent Crustacea. Pp. 1–27 *in* D. E. Bliss, ed., The biology of Crustacea 1:xx + 319.

Bradford, J. 1973. Revision of family and some generic definitions in the Phaennidae and Scolecithricidae (Copepoda: Calanoida).—New Zealand Journal of Marine and Freshwater Research 7:133–153.

Esterly, C. 1911. Third report on the Copepoda of the San Diego region.—University of California Publications in Zoology 6:313–352.

Ferrari, F. 1988. Developmental patterns in numbers of ramal segments of copepod post-maxillipedal legs.—Crustaceana 54:256–293.

———, & J. Ambler. 1992. Nauplii and copepodids of the cyclopoid copepod *Dioithona oculata* (Oithonidae) from a mangrove cay in Belize.—Proceedings of the Biological Society of Washington 105:275–298.

Galt, C. 1979. First records of a giant pelagic tunicate, *Bathochordaeus charon* (Urochordata, Larvacea), from the eastern Pacific Ocean, with notes on its biology.—Fishery Bulletin 77:514–519.

Giesbrecht, W. 1892. Systematik und Faunistik des pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeres-abschnitte.—Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-abschnitte 19:1–831 + 54 plts.

———. 1893. Mittheilungen über Copepoden 1-6.—Mittheilungen aus der Zoologischen Station zu Neapel 11:56–106.

Grice, G. 1962. Calanoid copepods from equatorial waters of the Pacific Ocean.—Fishery Bulletin 61:167–246.

Hamner, W., & B. Robison. 1992. In situ observations of giant appendicularians in Monterey Bay.—Deep-Sea Research 39:1299–1313.

Hulsemann, K. 1991. The copepodid stages of *Drepanopus forcipatus* Giesbrecht, with notes on the genus and a comparison to other members of the family Clausocalanidae (Copepoda Calanoida).—Helgoländer Meeresuntersuchungen, 45: 199–224.

Huys, R., & G. Boxshall. 1991. Copepod evolution. The Ray Society, London, 648 pp.

Izawa, K. 1987. Studies on the phylogenetic implications of ontogenetic features in the poecilostome nauplii (Copepoda: Cyclopoida).—Publications of the Seto Marine Biological Laboratory 32:151–217.

Ohtsuka, S., & N. Kubo. 1991. Larvaceans and their houses as important food for some pelagic copepods.—Bulletin of the Plankton Society of Japan, Special Volume, 535–551.

Park, T. 1970. Calanoid copepods from the Caribbean Sea and Gulf of Mexico. 2. New species and new records from plankton samples.—Bulletin of Marine Sciences 20:472–546.

Pilskaln, C., M. Silver, D. Davis, K. Murphy, B. Gritton, S. Lowder, & L. Lewis. 1991. A quantitative study of marine aggregates in the mid-water column using specialized ROV instrumentation.—Oceans '91 Proceedings 2:1175–1182.

Roe, H. 1975. Some new and rare species of calanoid copepods from the northeastern Atlantic.—Bulletin of the British Museum (Natural History), Zoology 28:297–372.

Sars, G. 1902. Copepoda Calanoida, part V & VI Scolecithricidae, Diaixiidae, Stephidae, Tharybidae, Pseudocyclopiidae. Pp. 49–72 + plts 34–48 *in* An account of the Crustacea of Norway, with short descriptions and figures of all of the species, 4:144 + 96 plts. The Bergen Museum, Bergen.

Scott, T. 1894. Report on the Entomostraca from the Gulf of Guinea, collected by John Rattray, GSc.—Transactions of the Linnean Society of London (ser. 2, Zoology) 6:1–161 + plts 1–15.

Sewell, R. 1929. The Copepoda of Indian Seas. Calanoida.—Memoires of the Indian Museum 10: 1–221.

Silver, M., C. Pilskaln, & D. Steinberg. 1991. The biologists' view of sediment trap collections: problems of marine snow and living organisms. Pp. 76–93 *in* H. Wassman, A. Heiskaven, & O. Linidahl, eds., Sediment trap studies in nordic countries, Symposium Proceedings.

Vaupel Klein, J. von. 1982. A taxonomic review of the genus *Euchirella* Giesbrecht, 1888 (Copepoda, Calanoida). II. The type-species *Euchirella messinensis* (Claus, 1863). A. The female of f. *typica*.—Zoologische Verhandelingen, 198: 1–131 + 23 plts.

———. 1972. A new character with systematic value in *Euchirella* (Copepoda, Calanoida).—Zoologische Mededelingen 47:497–512 + 6 plts.

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