

Developmental stages of *Oncaea media* Giesbrecht, 1891 and *Oncaea subtilis* Giesbrecht, 1892

S. J. Malt

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Introduction

Few studies have been made of the life-cycles of copepod species belonging to the cyclopoid family Oncaeidae although they are common in the plankton. Björnberg (1972) described some of the developmental stages of *Oncaea venusta* Philippi, 1843 and *O. media* Giesbrecht, 1891 using material from the coastal waters of Brazil and Curaçao, and from rearing experiments, but could not assign the wild copepodids to a species. Digby (1950) encountered a similar problem in which *O. venusta* and *Corycaeus* in the Plymouth plankton were '... accompanied by large numbers of nauplii which were counted *in toto*: they probably comprised nauplii of these two species together with possibly *Euterpina* and other harpacticoids'. Since the larval stages could not be identified Digby was unable to estimate the local population of *O. venusta*. Hanaoka (1952) described the third, fourth and fifth nauplii of *O. mediterranea* Claus, 1863.

There have been many studies of development in the Oithonidae (Oberg, 1906; Murphy, 1923; Gibbons & Ogilvie, 1933; Krishnaswamy, 1950; Rao, 1958; Sazhina, 1960; Haq, 1965; Faber, 1966; Björnberg, 1968, 1972; Goswami, 1975; Fanta, 1976; Fonseca, 1976; Fonseca & Prado, 1979; Uchima, 1979), but few for the Corycaeidae (Hanaoka, 1952; Johnson, 1969; Björnberg, 1972; Gibson & Grice, 1978) and only those mentioned above for the Oncaeidae. Members of all three families exhibit the same sequence of developmental stages, six nauplius and five copepodid. The lack of data for *Oncaea* can be attributed to the small size of the nauplii and the difficulties of rearing them in the laboratory.

Materials and methods

Copepodids and adults of both species were collected in September 1979 at the mouth of the English Channel (48°N 7°30' W, 48°30' N 7°W and 49°N 6°30' W) during a cruise of the R.V. 'Sarsia', and donated to the British Museum (Natural History) by the Marine Biological Association, Plymouth. The material was taken using a pump system with 80 µm and 200 µm mesh filters. Adults were also collected in September 1979 and August to October 1980 in Plymouth Sound using 170 µm and 343 µm nets fished at the surface and at 30 m depth. All this material was preserved in 10% sea-water formalin. Further nauplii and copepodids of *O. media* and nauplii of *O. subtilis* were reared from ovigerous females in the laboratory. Single ovigerous females were placed in phials containing approximately 20 ml of filtered sea water containing dense cultures of one species or a combination of two or more species of the following unicellular algae: *Peridinium trochoideum* (Stein) Lemmermann, *Thalassiosira rotula* Meunier and *Isochrysis galbana* Parke. The phials were maintained at 12, 15, 18 and 20°C on a 12:12 hour light:dark cycle. The larvae were harvested periodically and preserved in 10% sea-water formalin. Adults and copepodids were measured and dissected in lactophenol; all material was stained with chlorazol black and mounted in polyvinyl lactophenol. Drawings were either made with the aid of a *camera lucida* or traced from SEM micrographs. Specimens were measured using an eyepiece

micrometer, total copepodid body length being the distance from the tip of the rostrum to the apex of the caudal rami. Specimens were prepared for scanning electron microscopy by critical-point drying, coated with gold-palladium, and examined using an ISI 60A Stereoscan microscope.

Descriptions of developmental stages

The formulae used to describe the armature of nauplius mouthparts are derived as follows. Setae are given in arabic and spines in roman numerals. The armature of each segment is written between colons and each limb is given a separate grouping; thus 1+I: 0: 3+3 terminal, describes a limb whose first segment bears a seta and a spine, whose second segment is unarmed and whose terminal segment bears two groups of three setae, of which one group is terminal. A question mark indicates that an armature formula is uncertain and is used when a segment bears fewer elements than the previous stage, or if the limb of a specimen is obscured. Each formula is derived from the study of several individuals, where possible, and may not tally precisely with the figured specimen. Some of the segmentation is poorly defined, especially in early developmental stages and may apparently differ in the figures between left and right sides of the same individual.

Oncaea media Giesbrecht, 1891

NAUPLIUS STAGES. *Nauplius 1* (Fig. 1a). Length 0.06 to 0.07 mm (7 reared specimens). Oval body. First antenna, 1: 1: 3. Second antenna: coxopodite, 1; basipodite, 1; endopodite, 2 terminal; exopodite 5-segmented, 1: 1: 1: 1: 3. Mandible: coxopodite, 0; basipodite, 0; endopodite, 5; exopodite 2-segmented, 1?: 2 terminal. Caudal armature, a pair of fine setae.

Nauplius 2 (Fig. 1b). Length 0.07 to 0.09 mm (8 reared specimens). Oval body. First antenna, 1: 1: 2? Second antenna: coxopodite, I; basipodite, 2; endopodite, 2; exopodite, 1: 1: 1: 1: 3. Mandible (Fig. 1c): coxopodite, 1; basipodite, 1; endopodite, internal lobe, 3, external lobe, 3; exopodite, 2 terminal. Caudal armature, a pair of long setae.

Nauplius 3 (Fig. 1d). Length 0.08 to 0.1 mm (4 reared specimens). Rounded oblong body. First antenna, 1: 1: 4. Second antenna: coxopodite, I+1; basipodite, 3; endopodite 2-segmented, 2: 3; exopodite, 2: 1: 1: 1: 3. Mandible (Fig. 1e): coxopodite, 1; basipodite, 1; endopodite, internal lobe, 3, external lobe, 4; exopodite, 2 terminal. Caudal armature, 2 pairs of long setae.

Nauplius 4 (Fig. 1f). Length 0.09 to 0.13 mm (28 reared specimens). Long oblong, or oval body; internal body division visible. First antenna, 1: 2: 2+4 terminal. Second antenna: coxopodite, I+1; basipodite, 3; endopodite, 2: 3; exopodite, 2: 1: 1: 1: 3. Mandible: coxopodite, 1; basipodite, 1; endopodite, internal lobe 4, external lobe, 4; exopodite (obscured Fig. 1f), 2 terminal. First maxilla represented by a ventral spine. Caudal armature, 2 or 3 pairs of long setae.

Nauplius 5 (Fig. 1g). Length 0.09 to 0.15 mm (17 reared specimens). Long oblong, or oval body; internal body divisions visible. First antenna, 1: 3: 2+3? terminal. Second antenna: coxopodite, I long +1; basipodite, 3; endopodite, 3+3 terminal; exopodite, 2: 1: 1: 1: 4. Mandible (Fig. 1h): coxopodite, 1; basipodite, 1; endopodite, internal lobe, 3? (2 bearing paired spinules), external lobe, 5; exopodite, 1+2 terminal. First maxilla, single lobe bearing a long and a short seta. Caudal armature, 2 or 3 pairs of long setae and a pair of medial spinules.

Nauplius 6 (Fig. 1i). Length 0.11 to 0.14 mm (5 reared specimens, smallest measured from critical point dried specimen). Rectangular, segmented body. Posterior labral margin bearing row of setules. First antenna, I: 1?: 2+3? terminal. Second antenna: coxopodite, I+1, both pinnate; basipodite, 2?; postero-ventral surfaces of coxopodite and basipodite covered with clusters of spinules; endopodite, 4+4 terminal; exopodite 2: 1: 1: 1: 4. Mandible: coxopodite, I pinnate; basipodite, II pinnate; endopodite, internal lobe, 4 (3 bearing paired

spinules), external lobe, 4; exopodite, 5 (1 pinnate). First maxilla 2-segmented, terminal segment bilobed, inner lobe, II, outer lobe, a very long terminal seta (broken in Fig. 1i)+2 terminal. Pair of small spines situated postero-laterally to first maxillae. Caudal armature, 2 pairs of robust setae (1 pair setose) and a pair of medial spinules; postero-ventral surface bearing 2 subterminal rows of setules.

COPEPODID STAGES. *Copepodid 1* (Fig. 2a). Length 0.22 mm (1 reared specimen). Prosome 5-segmented, urosome single-segmented. First antenna 3-segmented; appendage damaged in dissection, therefore armature uncertain. Second antenna 3-segmented (Fig. 3a); first segment bearing a long distal seta; second segment unarmed; terminal segment bearing 3 proximal setae and a proximal spine and 5 distal setae. Mandible, first and second maxillae and maxilliped lost in dissection. Armature of natatory legs (Fig. 4a–d) given in table 1; first natatory legs damaged in dissection; endopodite of second natatory leg bilaterally setose, seta on internal margin pinnate; seta on internal margin of exopodite pinnate; external spines of exopodite bilaterally serrate.

Copepodid 2 (Fig. 2b). Length 0.25 to 0.32 mm (1 reared specimen and 2 from pump samples). Urosome 2-segmented. Caudal rami bearing 3 distal setae (2 longest pinnate), a distal spine and a dorsal seta. First antenna 3-segmented (Fig. 3b); armature, 0: 4: 8. Armature of second antenna similar to copepodid 1. Mandible, first and second maxillae lost in dissection. Maxilliped 3-segmented (Fig. 3c); first segment unarmed; internal surface of second segment bearing 2 spines and 3 setae; terminal segment produced as a curved claw. Armature of natatory legs (Fig. 4e–g) given in table 1; second natatory legs lost in dissection; terminal spines of exopodites unilaterally serrate, those of endopodites bilaterally serrate; external spines of exopodites bilaterally serrate; all setae pinnate.

Copepodid 3 (Fig. 2c). Length 0.36 to 0.42 mm (4 specimens from pump samples). Urosome 3-segmented (Fig. 3d). Caudal rami bearing 3 distal setae (2 longest pinnate), a distal setose spine and a dorsal seta. First antenna 5-segmented (Fig. 3e); armature, 2: 4: 3: 3: 7+1 esthete. Armature of second antenna similar to copepodid 1 (Fig. 3f). Mandible single-segmented (Fig. 3g), bearing 2 broad, dentate blades and a spine. First maxilla also single-segmented (Fig. 3h), bearing 4 stout, terminal setae. Second maxilla 2-segmented (Fig. 3i); first segment unarmed; second segment produced distally as a unilaterally spinulose claw, also having an external seta and an internal bilaterally spinulose element. Maxilliped 4-segmented (Fig. 3j); first and third segments unarmed; internal surface of second segment bearing 2 spines, proximal smooth, distal setose; fourth segment produced as a curved claw. Armature of natatory legs (Fig. 4h–k) given in table 1; external margins of endopodites setulose; terminal spines of exopodites unilaterally serrate, those of first, second and third endopodites bilaterally serrate; external spines of exopodites bilaterally serrate; all setae pinnate except those on basipodites; first, second and third endopodites terminating in conical projections. Fifth leg represented by a single seta on first urosome segment (Fig. 3d).

Copepodid 4 (Fig. 2d). Length 0.33 to 0.49 mm (1 reared specimen and 9 from pump samples). Urosome 4-segmented (Fig. 3k). Caudal rami bearing lateral setose spine in addition to dorsal and distal armature mentioned above. First antenna 6-segmented (Fig. 3l); armature, 1: 1: 3: 2: 0: 5 (some elements may be missing). Proximal armature of second antenna similar to copepodid 1, distal armature of terminal segment comprising 6 setae (Fig. 3m). Mandible and second maxilla lost in dissection. First maxilla single-segmented (Fig. 3n), bearing 2 stout setae plus a long seta and a shorter pinnate seta. Armature of maxilliped similar to copepodid 3. Armature of natatory legs (Fig. 4l–o) given in table 1; exopodites and endopodites 2-segmented; all setae pinnate except those on basipodites. Armature of fifth leg similar to copepodid 3.

Copepodid 5: Female (Fig. 2e and f). Length 0.5 to 0.59 mm (1 reared specimen, 1 netted specimen and 3 from pump samples). Urosome 4-segmented (Fig. 3o); genital setules situated laterally on second segment, anterior to midpoint; genital segment approximately uniform in width. Armature of caudal rami similar to copepodid 3; all distal setae pinnate. First antenna 6-segmented (Fig. 3p); armature, 3: 6: 4: 2: 2: 6 (some elements may be

Table 1 Armature of legs 1 to 4 in the copepodid stages and adults of *Oncaea media* (i = internal; e = external; t = terminal)

Copepodid stage: I		II	III	IV	V	ADULT (VI)
Leg 1						
coxopodite	0	0	0	0	0	0
basipodite	0	?	li, 1e	li, 1e	li, 1e	li, 1e
endopodite						
segment 1	—	—	—	—	li	li
segment 2	—	0	li	li	li	li
segment 3	li, 1e, 1t	2 + li, 2e, 1t	6i, 1t	5i, 1t	5i, 1t	5i, 1t
exopodite						
segment 1	—	—	—	—	1e	1e
segment 2	—	1e	1e	1e	li, 1e	li, 1e
segment 3	?	4i, 11e, 1t	4i, 111e, 1t	4i, 111e, 1t	4i, 111e, 1t	4i, 111e, 1t
Leg 2						
coxopodite	0		0	0	0	0
basipodite	0	L	1e	1e	1e	1e
endopodite		O				
segment 1	—	S	—	—	li	li
segment 2	—	T	li	li	2i	2i
segment 3	li, 1e, 2t		4i, 11e, 1t	5i, 11e, 1t	3i, 11e, 1t	3i, 11e, 1t
exopodite						
segment 1	—		—	—	1e	1e
segment 2	—		1e	1e	li, 1e	li, 1e
segment 3	3i, 111e, 1t		5i, 111e, 1t	5i, 111e, 1t	5i, 111e, 1t	5i, 111e, 1t
Leg 3						
coxopodite	} single lobe bearing 2 setae 1 spine	0	0	0	0	0
basipodite		0	1e	1e	1e	1e
endopodite						
segment 1		—	—	—	li	li
segment 2		li	li	li	2i	2i
segment 3		li, 1e, 1t	2i, 11e, 1t	3i, 11e, 1t	2i, 11e, 1t	2i, 11e, 1t
exopodite						
segment 1		—	—	—	1e	1e
segment 2		1e	1e	1e	li, 1e	li, 1e
segment 3	4i, 11e, 1t	4i, 11e, 1t	5i, 111e, 1t	5i, 11e, 1t	5i, 11e, 1t	
Leg 4						
coxopodite	} single lobe bearing 3 setae 1 spine	} single lobe bearing 1? seta 1 spine	0	0	0	0
basipodite			0	0	1e	1e
endopodite						
segment 1			—	—	li	li
segment 2			—	li	2i	2i
segment 3			2i, 1e, 1t	2i, 11e, 1t	li, 11e, 1t	li, 11e, 1t
exopodite						
segment 1			—	—	1e	1e
segment 2			—	1e	li, 1e	li, 1e
segment 3	3i, 111e, 1t	5i, 111e, 1t	5i, 11e, 1t	5i, 11e, 1t		

missing). Internal surface of second segment of second antenna armed with a distal row of setules (Fig. 3q). Armature of mandible similar to copepodid 3 (Fig. 3r). Internal margin of first maxilla bearing 5 terminal elements and a seta (Fig. 3s). Armature of second maxilla similar to copepodid 3 (Fig. 3t). Internal surface of second maxilliped segment setulose (Fig. 3u), also bearing 2 setose spines; terminal claw bearing row of spinules on concave margin, a stout spine on internal base and a small seta on external base. Armature of natatory legs (Fig. 5a–d) given in table 1; exopodites and endopodites 3-segmented; all setae pinnate except those on basipodites. Fifth leg consisting of a small cylindrical segment bearing 2 terminal setae and a seta on dorsal surface of first urosome segment (Fig. 3o).

Male. Length 0.55 mm (1 specimen from pump samples). Armature of mouthparts and natatory legs similar to female copepodid 5. Urosome 5-segmented (Fig. 3v). Armature of fifth leg and caudal rami similar to female copepodid 5, except that cylindrical segment of female leg 5 is replaced in male by protuberance fused to first urosome segment.

ADULT. Female (Fig. 2g and h). Length 0.49 to 0.76 mm, mean 0.62 mm (500 specimens from pump and net samples). Ratio of prosome and urosome lengths 1.6: 1. Third prosome segment without a dorsal projection. Head (first prosome division) equal in length to width. Proportional lengths of urosome segments and caudal rami 13: 42: 8: 7: 12: 18 (Fig. 3v'); genital apparatus situated anterior to midpoint on dorsal surface of genital segment, each aperture armed with a setule; length to width ratio of genital segment 1.6: 1; maximum width anterior to genital apparatus. Caudal rami 2.5 to 3 times as long as wide; armature similar to female copepodid 5. First antenna 6-segmented (Fig. 3w); armature, 3: 6: 4 + I; 3: 2: 6; ratio of segment lengths 12: 18: 32: 9: 5: 7. Armature of second antenna similar to female copepodid 5 (Fig. 3w'), distal seta on first segment setose; terminal segment shorter than second segment. Armature of mandible similar to female copepodid 5 (Fig. 3x). First maxilla bearing 6 terminal elements and an internal seta (Fig. 3x'). Armature of second maxilla (Fig. 3y) and maxilliped (Fig. 3y') similar to female copepodid 5. Armature of natatory legs (Fig. 5e–h) given in table 1. Armature of fifth leg similar to female copepodid 5.

Male (Fig. 2i and j). Length 0.37 to 0.58 mm, mean 0.48 mm (100 specimens from pump and net samples). Ratio of prosome and urosome lengths 2: 1. Head equal in length to width. Proportional lengths of urosome segments and caudal rami 14: 50: 3: 2: 2: 7: 9 (Fig. 3z); genital lappets produced as small postero-ventral processes; length to width ratio of genital segment 1.2: 1. Caudal rami 1.5 to 2 times as long as wide; armature similar to female. Armature of mouthparts similar to female, except first antenna and maxilliped. First antenna 4-segmented (segments corresponding to 3 terminal segments of female first antenna fused in male). Maxilliped 3-segmented (Fig. 3z'); second segment bearing 2 rows of stout setules on internal surfaces; terminal claw bearing a setose spine on internal base. Armature of natatory legs similar to female adult. Armature of fifth leg similar to male copepodid 5.

MATERIAL EXAMINED. 79 nauplii reared from adults caught in Plymouth Sound, 1981: 221. 4 Reared copepodids, 1981: 222 and 1981: 223. 19 copepodids, 5♀♀ adults and 113♂♂ adults from samples F150, F152–155 and F165–173, 90–10 m, 48°N 7°30'W and 48°30'N 7°W, 1981: 224 and 1981: 225. 1 Copepodid, 493♀♀ adults and 103♂♂ adults from Plymouth Sound, 0–30 m, 1981: 226–232.

REMARKS. Sexual dimorphism in the length of the second urosome segment of *Oncaea* sp. has been reported at copepodid stage 4 by Björnberg (1972), but she does not assign the morphs to sexes. However, the small postero-lateral processes of the shorter segmented morph, shown in figure 600 (Björnberg, 1972) may be precursors of the male genital lappets. Only one copepodid 4 morph was found in the present material. Dimorphism at copepodid stage 5 is also restricted to the posterior body segments; the well-documented sexual dimorphism in the first antenna and the maxilliped does not emerge until the adult stages.

Sewell (1947) reports two forms of female adult *O. media*: *O. media minor* and *O. media major*, and separates them by body length and structure of the caudal rami. According to these criteria the present material is *O. media minor*.

Oncaea subtilis Giesbrecht, 1892

NAUPLIUS STAGES. *Nauplius 1* (Fig. 6a). Length 0.07 mm (3 reared specimens). Oval body. First antenna, 0: 1: 3/4. Second antenna: coxopodite, 1; basipodite, 2; endopodite single-segmented, 1+2 terminal; exopodite 5-segmented, 1: 1: 1: 1: 3. Mandible: coxopodite, 0; basipodite, 0; endopodite, 2+4; exopodite 2-segmented, 0: 2. Caudal armature, a pair of setae. Segmentation of appendages more pronounced than nauplius 1 of *O. media*.

Nauplius 2 (Fig. 6b). Length 0.07 and 0.08 mm (2 reared specimens). Oval body. First antenna, 0: 2: 5. Second antenna: coxopodite, 0?; basipodite, 2; endopodite, 1: 0: 3; exopodite 4?-segmented, 1: 1: 1: 4. Mandible: coxopodite, 0; basipodite, 0; endopodite, internal lobe, 3, external lobe, 3; exopodite 2-segmented, 2 terminal. Caudal armature, a pair of long setae. Segmentation of appendages more pronounced than nauplius 2 of *O. media*.

Nauplius 3 (Fig. 6c). Length 0.08 mm (1 reared specimen). Rounded oblong body. First antenna, 1: 2: 2+4 terminal. Second antenna: coxopodite, I+1 (seta bearing paired spinules); basipodite, 3; endopodite, 2+2 terminal; exopodite 5-segmented, 0?: 0?: 1: 2: 4. Mandible: coxopodite, 0; basipodite, 1; endopodite, internal lobe, 3 (1 bearing paired spinules), external lobe, 2?; exopodite, 2 terminal. Caudal armature, 2 pairs of setae.

Nauplius 4 (Fig. 6d). Length 0.12 mm (1 reared specimen). Long oblong body. First antenna, 1: 3: 3? Second antenna: Coxopodite, I+1; basipodite, 3; endopodite single segmented, 2+2 terminal; exopodite, 0?: 0?: 1: 0?: 3? Mandible: coxopodite, 0; basipodite, 0?; endopodite, internal lobe, 3 (bearing paired spinules), external lobe, 3 (2 bearing paired spinules); exopodite 3-segmented, 0: 1: 3. Caudal armature, 2 pairs of setae.

Nauplius 5 (Fig. 6e). Length 0.14 mm (1 reared specimen). Rotund body. First antenna, 1: 1?: 2+4. Second antenna: coxopodite, 0?, basipodite, I+2, endopodite, 4 terminal; exopodite, 2: 1: 1: 1: 3? Mandible: coxopodite, 0; basipodite, 0?, endopodite, internal lobe, 3 (2 bearing paired spinules), external lobe, 1?; exopodite 3-segmented, 0: 1: 3. First maxilla single-segmented, bearing a lateral and 2 terminal setae (1 very long). Caudal armature, 2 pairs of setae.

Nauplius 6 (Fig. 6f and g). Length 0.11 to 0.14 mm (4 reared specimens). Rotund body. First antenna, 2: 1?: 2+4 terminal. Second antenna: coxopodite, 0?; basipodite, 1?; endopodite, 2+4; exopodite, 2: 1: 1: 1: 5. Mandible: coxopodite, 0; basipodite, 1; endopodite, internal lobe, 3 (bearing paired spinules), external lobe, 4; exopodite 3-segmented, 0: 1: 3. First maxilla 2-segmented, basal segment bearing 1 long and 2 short terminal setae; terminal segment bearing a long and a short seta. Pair of setose spines situated postero-laterally to first maxillae. Caudal armature, 2 pairs of setae.

COPEPODID STAGES. *Copepodid 2* (Fig. 7a). Earliest copepodid found in the plankton. Length 0.28 mm (1 specimen from pump samples). Prosoma 5-segmented, urosome 2-segmented, (Fig. 8a). Caudal rami bearing 3 distal setae, a distal and a lateral spine, and a dorsal seta. First antenna 6-segmented (Fig. 8b); armature, 1: 1: 5: 1: 2: 7. Second antenna 3-segmented (Fig. 8c); first segment bearing a long distal seta; second segment unarmed; terminal segment bearing 3 proximal setae, a proximal curved, pinnate spine and 4 distal curved setae. Mandible single-segmented (Fig. 8d), bearing 2 broad blades and 2 spines. First maxilla lost in dissection. Second maxilla 2-segmented (Fig. 8e); first segment unarmed; second segment produced distally as a unilaterally setose claw, also having an external spinulose seta, an internal pinnate element and a thin seta. Maxilliped 4-segmented (Fig. 8f); first and third segments unarmed; internal surface of second segment bearing 2 spinulose spines and a row of spinules; fourth segment produced as a curved claw, bearing a row of spinules on concave surface. Armature of natatory legs (Fig. 9a-d) given in table 2; terminal spines of first and second exopodites and second endopodite unilaterally serrate; external spines of first and second exopodites bilaterally serrate; terminal spine of first endopodite bilaterally serrate; all setae pinnate except those on basipodites.

Copepodid 3 (Fig. 7b). Length 0.28 to 0.34 mm (5 specimens from pump samples). Urosome 3-segmented (Fig. 8g). Caudal rami bearing 3 distal setae (2 longest setose), a distal and a lateral spine, and a dorsal seta. First antenna 6-segmented (Fig. 8h); armature, 1: 4: 2: 1: 1:

Table 2 Armature of legs 1 to 4 in the copepodid stages 2 to 5 and adults of *Oncaea subtilis*, (notation as for Table 1)

Copepodid stage:	II	III	IV	V	ADULT (VI)
Leg 1					
coxopodite	0	0	0	0	0
basipodite	li,le	li,le	li,le	li,le	li,le
endopodite					
segment 1	—	—	—	0	0
segment 2	li	li	li	li	li
segment 3	5i,It	5i,It	5i,It	5i,It	5i,It
exopodite					
segment 1	—	—	—	le	le
segment 2	le	le	le	le	li,le
segment 3	4i,IIIe,It	4i,IIIe,It	5i,IIIe,It	4i,IIIe,It	4i,IIIe,It
Leg 2					
coxopodite	0	0	0	0	0
basipodite	le	le	le	le	le
endopodite					
segment 1	—	—	—	li	li
segment 2	li	li	li	2i	2i
segment 3	4i,le,It	4i,le,It	4i,le,It	3i,le,It	3i,le,It
exopodite					
segment 1	—	—	—	le	le
segment 2	le	le	le	li,le	li,le
segment 3	4i,IIIe,It	5i,IIIe,It	5i,IIIe,It	5i,IIIe,It	5i,IIIe,It
Leg 3					
coxopodite	0	0	0	0	0
basipodite	le	le	le	le	le
endopodite					
segment 1	—	—	—	li	li
segment 2	—	li	li	2i	2i
segment 3	2i,le,It	2i,le,It	3i,le,It	2i,le,It	2i,le,It
exopodite					
segment 1	—	—	—	le	le
segment 2	—	le	le	li,le	li,le
segment 3	3i,IIIe,It	4i,IIe,It	5i,IIIe,It	5i,IIe,It	5i,IIe,It
Leg 4					
coxopodite	} single lobe bearing 1 seta 2 spines	0	0	0	0
basipodite		le	le	le	le
endopodite					
segment 1		—	—	li	li
segment 2		—	li	2i	2i
segment 3		2i,It	3i,It	li,le,It	li,le,It
exopodite					
segment 1		—	—	le	le
segment 2		—	—	li,le	li,le
segment 3		3i,IIIe,It	5i,IVe,It	5i,IIe,It	5i,IIe,It

Table 3 Size in microns of *Oncaea* nauplii, data from Hanaoka (1952), Björnberg (1972) and present study

	<i>Oncaea media</i> (present account)	<i>Oncaea subtilis</i> (present account)	<i>Oncaea mediterranea</i> (Hanaoka)	<i>Oncaea media</i> (Björnberg)	<i>Oncaea venusta</i> (Björnberg)
Nauplius 1	60–70	70	–	50–60	90
Nauplius 2	70–90	70–80	–	80	90
Nauplius 3	80–100	80	125*	90	–
Nauplius 4	90–130	120	150*	100	–
Nauplius 5	90–150	140	185*	130–150	–
Nauplius 6	110–140	110–140	–	150–180	–

*These are probably stages 4 to 6.

6 + 1 esthete (some elements may be missing). Second antenna 3-segmented (Fig. 8i); first segment bearing a long distal pinnate seta; second segment unarmed; proximal armature of terminal segment similar to copepodid 2; distal armature comprising 3 long curved, pinnate setae and a short seta. Armature of mandible similar to copepodid 2 (Fig. 8j), both spines setose. First maxilla single-segmented (Fig. 8k), bearing 6 terminal setae (1 setose). Second maxilla 2-segmented (Fig. 8l); first segment unarmed; second segment produced distally as a unilaterally setose claw, additional armature similar to copepodid 2. Armature of maxilliped similar to copepodid 2 (Fig. 8m), internal surface of second segment bearing 2 rows of setules and 2 pinnate setae. Armature of natatory legs (Fig. 9e–h) given in table 2; terminal exopodite spines unilaterally serrate; external spines of first, second and third exopodites bilaterally serrate; terminal spines of first, second and third endopodites bilaterally serrate; all setae pinnate except those on bases. Fifth leg represented by a single seta on first urosome segment (Fig. 8g).

Copepodid 4 (Fig. 7c and d). Length 0.32 to 0.36 mm (13 specimens from pump samples). Urosome 4-segmented. Armature of caudal rami similar to copepodid 3. First antenna 6-segmented (Fig. 8n); armature 2: 4: 2: 3: 2: 5 + 1 esthete. Armature of second antenna similar to copepodid 3. Mandible and first maxilla lost in dissection. Armature of second maxilla (Fig. 8o) and maxilliped similar to copepodids 2 and 3. Armature of natatory legs (Fig. 9i–l) given in table 2; terminal exopodite spines unilaterally serrate; external exopodite spines bilaterally serrate; terminal endopodite spines bilaterally serrate; all setae pinnate except those on basipodites. Fifth leg represented by 2 setae on first urosome segment.

Copepodid 5: Female (Fig. 7e). Length 0.36 to 0.48 mm (12 specimens from pump samples). Urosome 4-segmented (Fig. 8p); genital setules situated laterally on second segment. Armature of caudal rami similar to copepodid 3. First antenna 6-segmented (Fig. 8q); armature, 2: 6: 4: 2: 2: 5 + 1 esthete. Second antenna 3-segmented (Fig. 8r); first segment bearing a long distal setose seta and a row of denticles on external margin, external margin of second segment bearing a row of spinules; proximal armature of terminal segment similar to copepodid 4; distal armature comprising 5 curved, pinnate setae and a spine. Armature of mandible similar to copepodid 2 (Fig. 8s), and of first and second maxilla similar to copepodid 3. Internal surface of second segment of maxilliped bearing row of setules (Fig. 8t); terminal claw having a stout, setose spine on internal base and a small seta on external base. Armature of natatory legs (Fig. 9m–p) given in table 2. Fifth leg consisting of a pair of setae on postero-lateral margin of first urosome segment and a single seta on the dorsal surface (Fig. 8p).

Male (Fig. 7f and g). Length 0.34 to 0.4 mm (7 specimens from pump samples). Armature of mouthparts and natatory legs similar to female copepodid 5. Urosome 5-segmented (Fig. 8u). Armature of caudal rami similar to female copepodid 5. Fifth leg consisting of 2 setae on a tubercle.

ADULT. Female (Fig. 7h). Length 0.46 to 0.69 mm, mean 0.5 mm (75 specimens from pump and net samples). Ratio of prosome and urosome lengths 3: 2. Third prosome segment without a dorsal projection. Head 1.1 times longer than wide. Proportional lengths of urosome segments and caudal rami 5: 23: 10: 9: 8: 8 (Fig. 8v); genital apparatus situated anterior to midpoint of dorsal surface of genital segment; each aperture armed with a setule; 1 specimen bearing spermatophores (Fig. 7i); length to width ratio of genital segment 1.2: 1; maximum width at level of genital apparatus. Caudal rami twice as long as wide; armature similar to copepodid 3. First antenna 6-segmented (Fig. 8w); armature, 3: 8: 4: 3: 1: 5+1 esthete; ratio of segment lengths 9: 11: 31: 6: 4: 5. Armature of second antenna (Fig. 8w') and mandible (Fig. 8x) similar to copepodid 5. Terminal segment of second antenna longer than second segment. First maxilla bilobed (Fig. 8x'), bearing 3 setae on internal lobe (1 setose), 4 setae on external lobe (1 setose), and a seta on internal margin. Second maxilla 2-segmented (Fig. 8y); second segment produced distally as a unilaterally spinulose claw, also having an external pinnate seta and an internal bilaterally spinulose element. Maxilliped 4-segmented (Fig. 8y'); armature similar to female copepodid 5. Armature of natatory legs (Fig. 7j-m) given in table 2. Armature of fifth leg similar to female copepodid 5.

Male (Fig. 7n). Length 0.38 to 0.44 mm, mean 0.41 mm (32 specimens from pump and net samples). Ratio of prosome and urosome lengths 1.8: 1. Proportional lengths of urosome segments and caudal rami 8: 51: 2: 2: 3: 13: 11 (Fig. 8z); genital lappets produced as small postero-ventral processes; length to width ratio of genital segment 1.9: 1. Caudal rami 2.5 times as long as wide; armature similar to copepodid 3. Armature of mouthparts similar to female adult, except first antenna and maxilliped. First antenna 4-segmented (segments corresponding to 3 terminal segments of female first antenna fused in male). Maxilliped 3-segmented (Fig. 8z'); second segment bearing a row of stout setules and 2 spines on internal surface; terminal claw having a spine on internal base. Armature of natatory legs similar to female adult. Armature of fifth leg similar to male copepodid 5, but with additional seta on dorsal surface of first urosome segment.

MATERIAL EXAMINED. 13 nauplii reared from adults caught in Plymouth Sound, 1981 : 234. 706 copepodids, 421♀♀ adults and 576♂♂ adults from samples F89-92, F125-129, F150-155 and F165-173, 48°N 7°30' W, 48°30' N 7°W and 49°N 6°30' W, 1981 : 235 and 1981 : 236. 88♀♀ adults and 1♂ adult from Plymouth Sound 0-30 m, 1981 : 237-241.

REMARKS. All but the largest specimens of the earlier stages would have passed through the filtering mesh of the pump system, thus few of the specimens examined were stage 2, and none were stage 1. Also the quoted size ranges for copepodids 2 and 3 may be biased by this sampling method, towards the largest individuals. Few stage 4 individuals were caught, but this stage may be relatively brief and therefore infrequently caught in the plankton. All of the stage 4 copepodids examined bear small postero-lateral processes on the second urosome segment. It is assumed that this is the male morph. Sexual dimorphism at copepodid 5 is restricted to the posterior body segments; dimorphism of the first antenna and maxilliped does not emerge until the adult stages. All the present material has orange colouration; the caudal setae are especially brightly pigmented.

Comparison with other Oncaeid larvae

The nauplii of *O. media*, *O. subtilis* and early *O. venusta* are similar in size (Table 3), but according to Hanaoka (1952), those of *O. mediterranea* are larger. Adults of these species differ greatly in size and present data indicate that such divergence is not initiated until copepodid 3 in *O. media* and *O. subtilis*. Inter- and intra-specific morphological differences between nauplii of *Oncaea* are mainly confined to variations in the armature and segmentation of the appendages (Table 4). Björnberg (1972) noted several minor variations among *O. media* nauplii.

Table 4 (continued)

Nauplius stage:	<i>Oncaea mediterranea</i> (Hanaoka*)	<i>Oncaea media</i> (Björnberg)	<i>Oncaea venusta</i> (Björnberg)
First antenna	0:0:1:3 3	0:I:I+1:4 1	1:1:3 2
Second antenna	0:I:1:4 4	1:1:3/4 1	1:2:6/7 D
Coxopodite II	II	I+1 I	0:II A
Basipodite I	I	II I+1	I+1 T
Endopodite II+2	2+2	1/2+3/2 2:3	2+1/0 O
Exopodite 1:1:1:2	1:1:1:2	4 segm. 7/8	2+4 T
Mandible	0	1:1:1:3 1	6 segm. 8 6/7
Coxopodite	0	1/2 2	A
Basipodite	2	1/2 3:4	V
Endopodite	3:3	3:4 1:1:1:2	I A
Exopodite 1:1:1:1	1:1:1:2	3 - bas. 2 end. 3 ex. 0:0:1	L A B L E
First maxilla	1	-	5 segm. 5/6 2pr + lpr lpr
Caudal rami	2pr	1pr	2pr + lpr lpr

*These are probably stages 4 to 6, armatures taken from 1952: Figures 2-6.

Early *O. mediterranea* and *O. venusta* nauplii are more advanced than those of other species, the first maxilla and the labral row of setae appearing simultaneously in *O. venusta* at nauplius 2 and sequentially in *O. mediterranea* at nauplii 3 and 4. In contrast to this, the labral setae first appear in *O. media* at nauplius 6, but do not appear at all in *O. subtilis*. The first maxilla appears at nauplius 5 in *O. media* and *O. subtilis* (the precursor at nauplius 4 is a ventral spine), developing into a two-segmented structure in each case, whilst Hanaoka (1952) reports it to be multi-segmented in *O. mediterranea* nauplius 5. In my opinion Hanaoka assigns the nauplii wrongly, describing stage 4 as stage 3, stage 5 as stage 4 and stage 6 as stage 5. Björnberg reports maxillulary spines for *O. media* nauplius 3. Caudal spines first appear at *O. media* nauplius 5, but at nauplius 4 (*sensu* Hanaoka) of *O. mediterranea* and do not appear at all in *O. subtilis*. Variation in the caudal armature of *O. media* nauplii 4 and 5 is a newly reported phenomenon. A key to the stages of *O. media* and *O. subtilis* nauplii has been constructed from present data, but it is doubtful whether young nauplii from the plankton could be assigned to species purely on present knowledge of their morphology.

Several authors have described, but not identified stage 5 *Oncaea* copepodids (Vilela, 1968; Björnberg, 1972; Boxshall, 1977), but only Björnberg has described stages 2 to 4. She depicted the first antenna as being seven and latterly six-segmented. Early copepodids, 1 and 2, of *O. media* have a three-segmented first antenna, those of *O. subtilis* copepodids, 2 to 5, are all six-segmented. Similarly the armature of the second antenna is different in the second copepodids of these and Björnberg's species, becoming more alike in later stages. The maxilliped of *O. media* copepodid 2 is three-segmented, expanding to four segments at copepodid 3; both *Oncaea* sp. (Björnberg, 1972) and *O. subtilis* second copepodids have a four-segmented maxilliped. The armature of the other mouthparts of *Oncaea* sp. (Björnberg) is inadequately described for comparison with the other species. The armature of the first leg endopodite and the segmentation of the third leg endopodite of *O. media* copepodid 2 (Table 1) are very different to those of *O. subtilis* (Table 2) and *Oncaea* sp. (Björnberg); the figured specimen of *O. media* may be abnormal in these respects. Figured specimens of *Oncaea* sp. lack the basipodite seta common to all copepodids of *O. media* and *O. subtilis*. All other differences of the natatory legs are minor. There are no data on the early development of the fifth leg of *Oncaea* sp. Also Björnberg (1972: Figures 596–602) shows *Oncaea* sp. copepodids which lack the dorsal setae of the caudal rami. In contrast to the nauplii the copepodids are relatively easy to assign to species; those of *O. subtilis* being more slender and smaller than those of *O. media*. A key to the stages based on all available data is presented below. The descriptions of females of *Oncaea obscura* Farran, 1908, *O. neobscura*, Razouls, 1969 and *O. parobscura*, Shmeleva, 1979 are similar to those of stage 5 male copepodids. None of the authors mention or figure the external genital openings which are common to all female adults other than those of these three species, but their figures show postero-lateral processes on an almost parallel-sided genital segment; these processes are common to *O. media* and *O. subtilis* stage 5 males. Significantly only one male adult is described: that of *O. obscura*, but Farran notes morphological differences of the second antenna and fourth endopodite which suggest that it is the male of a different species. In my opinion the descriptions of females of *O. obscura*, *O. neobscura* and *O. parobscura* are descriptions of stage 5 males of unidentified species of the genus *Oncaea*.

Key to nauplius stages

1	One pair of caudal setae	2
	Two or more pairs of caudal setae	3
2	Mandibular endopodite single-lobed	STAGE 1*
	Mandibular endopodite bilobed	STAGE 2
3	First maxilla absent, body rounded oblong or long oblong	4
	First maxilla present, body oval or rotund	5

4	Ventral spines absent	STAGE 3
	Ventral spines (precursor of first maxilla) present	STAGE 4
5	First maxilla single-lobed	STAGE 5
	First maxilla composed of more than one segment	STAGE 6

*Björnberg describes a stage 1 *O. media* nauplius which has bilobed mandibular endopodites.

Key to copepodid stages

1	Urosome one-segmented, two pairs of natatory legs	STAGE 1
	Urosome two- or more segmented, three or more pairs of natatory legs	2
2	Urosome two-segmented, three pairs of natatory legs	STAGE 2
	Urosome three- or more segmented, four pairs of natatory legs	3
3	Urosome three-segmented, fourth natatory endopodites single-segmented	STAGE 3
	Urosome four- or more segmented	4
4	Urosome four-segmented	5
	Urosome five- or more segmented, fourth natatory endopodites three-segmented	6
5	Second urosome segment parallel-sided, fourth natatory endopodites two-segmented	STAGE 4
	Second urosome segment usually convex-sided, bearing lateral setules fourth natatory endopodites three-segmented	STAGE 5♀
6	Urosome five-segmented	7
	Urosome six-segmented, second segment bearing genital lappets	STAGE 6 (ADULT) ♂
7	Second urosome segment bearing setules on dorsal surface over genital apertures	STAGE 6 (ADULT)♀
	No external openings on dorsal surface of second urosome segment, but having small postero-lateral processes	STAGE 5♂

Acknowledgements

I wish to thank Dr R. P. Harris (M.B.A.) for his help and advice with the larval rearing programme, and for arranging for preserved material to be donated to the BM(NH); Dr P. Carey for his help with the preparation of specimens for electron microscopy; and Drs G. A. Boxshall and R. J. Lincoln for commenting upon the manuscript. This work was undertaken while the author was in receipt of a BM(NH) postgraduate studentship.

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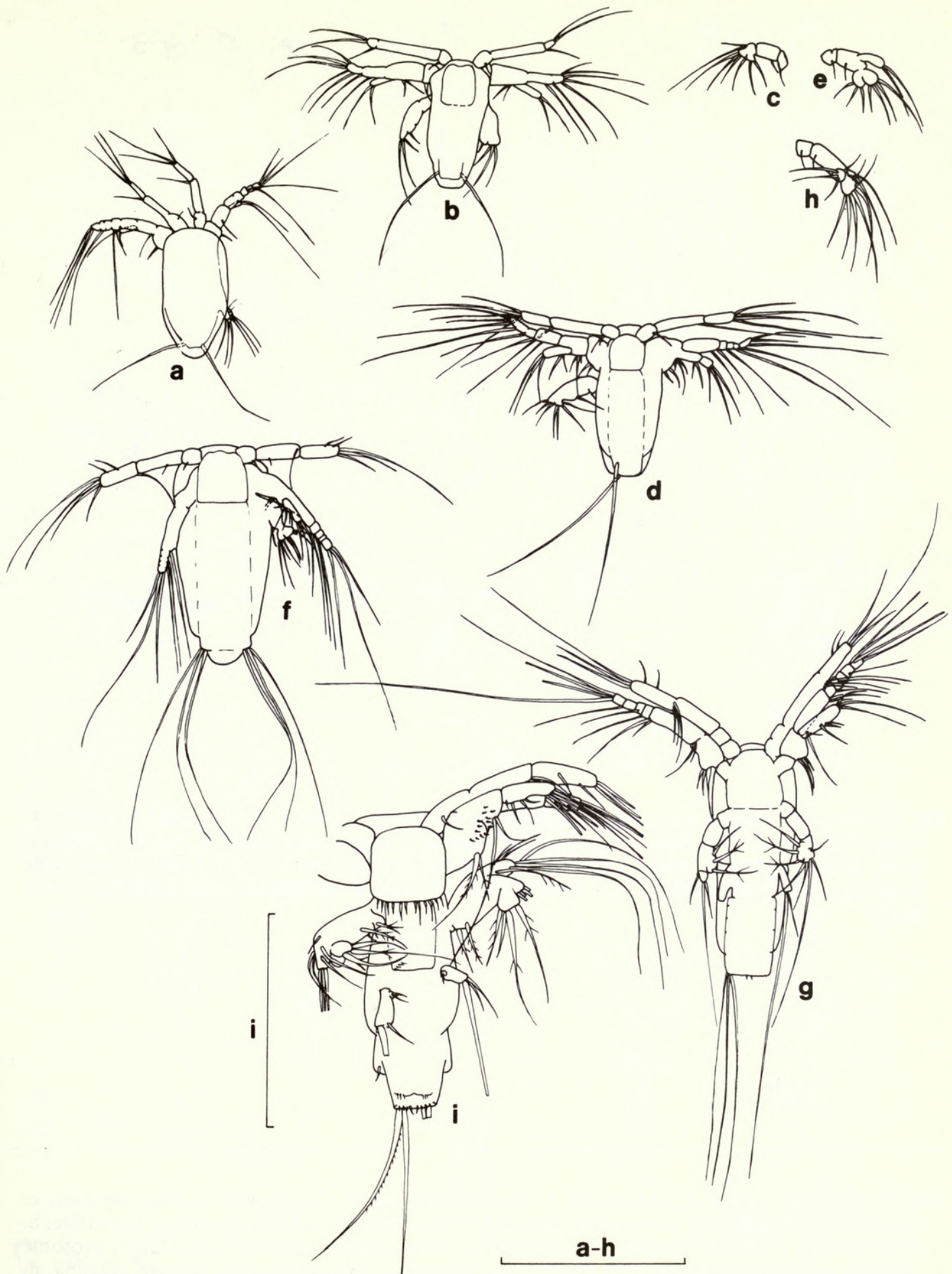


Fig. 1 *Oncaea media*. a. nauplius 1, dorsal (only right mandible shown); b. nauplius 2, dorsal; c. nauplius 2, mandible; d. nauplius 3, ventral (only right mandible shown); e. nauplius 3, mandible; f. nauplius 4, ventral (only left mandible shown); g. nauplius 5, ventral; h. nauplius 5, mandible; i. nauplius 6, ventral. Scales 100 microns, scale for nauplii 1 to 5 and mandibles at base of figure.

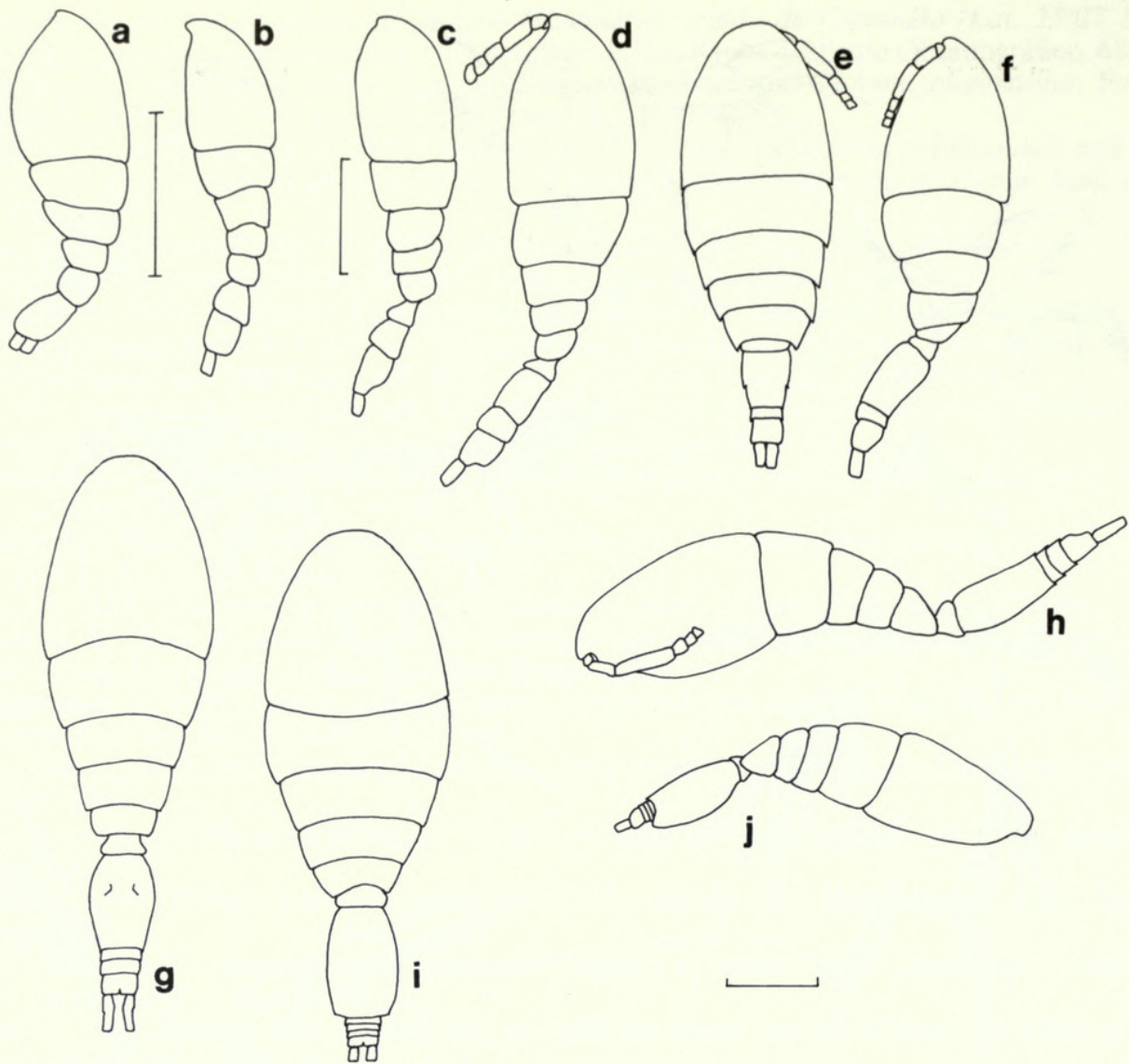
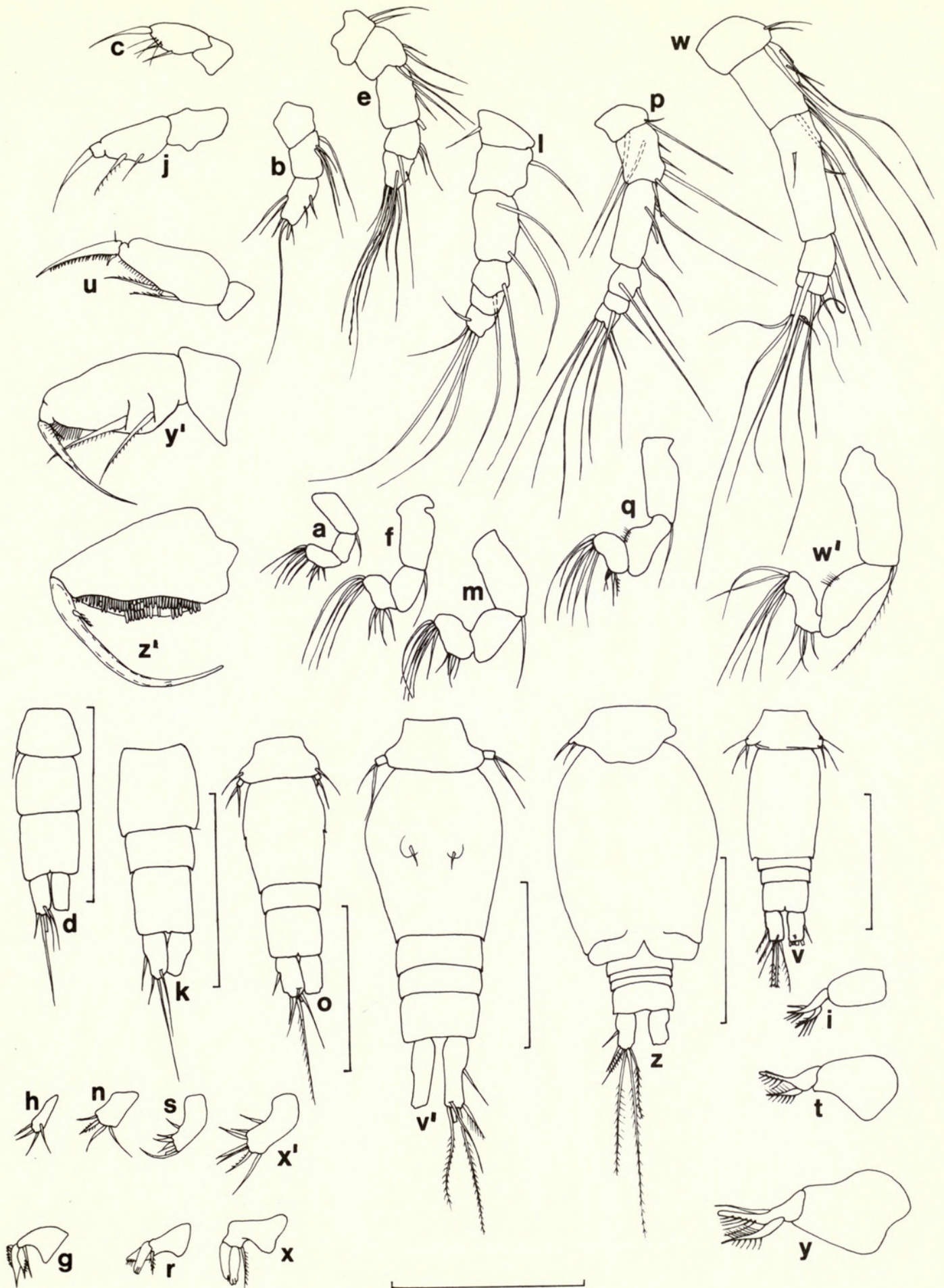


Fig. 2 *Oncaea media*. a. copepodid 1, lateral; b. copepodid 2, lateral; c. copepodid 3, lateral; d. copepodid 4, lateral; e. female copepodid 5, dorsal; f. female copepodid 5, lateral; g. female adult, dorsal; h. female adult, lateral; i. male adult, dorsal; j. male adult, lateral. Scales 100 microns, scale for copepodids 3 and 4 next to Fig. 2c, scale for copepodid 5 and adults at base of figure.

Fig. 3 *Oncaea media*. a. copepodid 1, second antenna; b. copepodid 2, first antenna; c. maxilliped; d. copepodid 3, urosome, dorsal; e. first antenna; f. second antenna; g. mandible; h. first maxilla; i. second maxilla; j. maxilliped; k. copepodid 4, urosome, dorsal (first urosome segment and some elements from caudal rami missing); l. first antenna; m. second antenna; n. first maxilla; o. female copepodid 5, urosome, dorsal; p. first antenna; q. second antenna; r. mandible; s. first maxilla; t. second maxilla; u. maxilliped; v. male copepodid 5, urosome, dorsal; v'. female adult, urosome, dorsal (dorsal seta of fifth leg missing); w. first antenna; w'. second antenna; x. mandible; x'. first maxilla; y. second maxilla; y'. maxilliped; z. male adult, urosome, ventral; z'. maxilliped. Scales 100 microns, scale for mouthparts at base of figure.



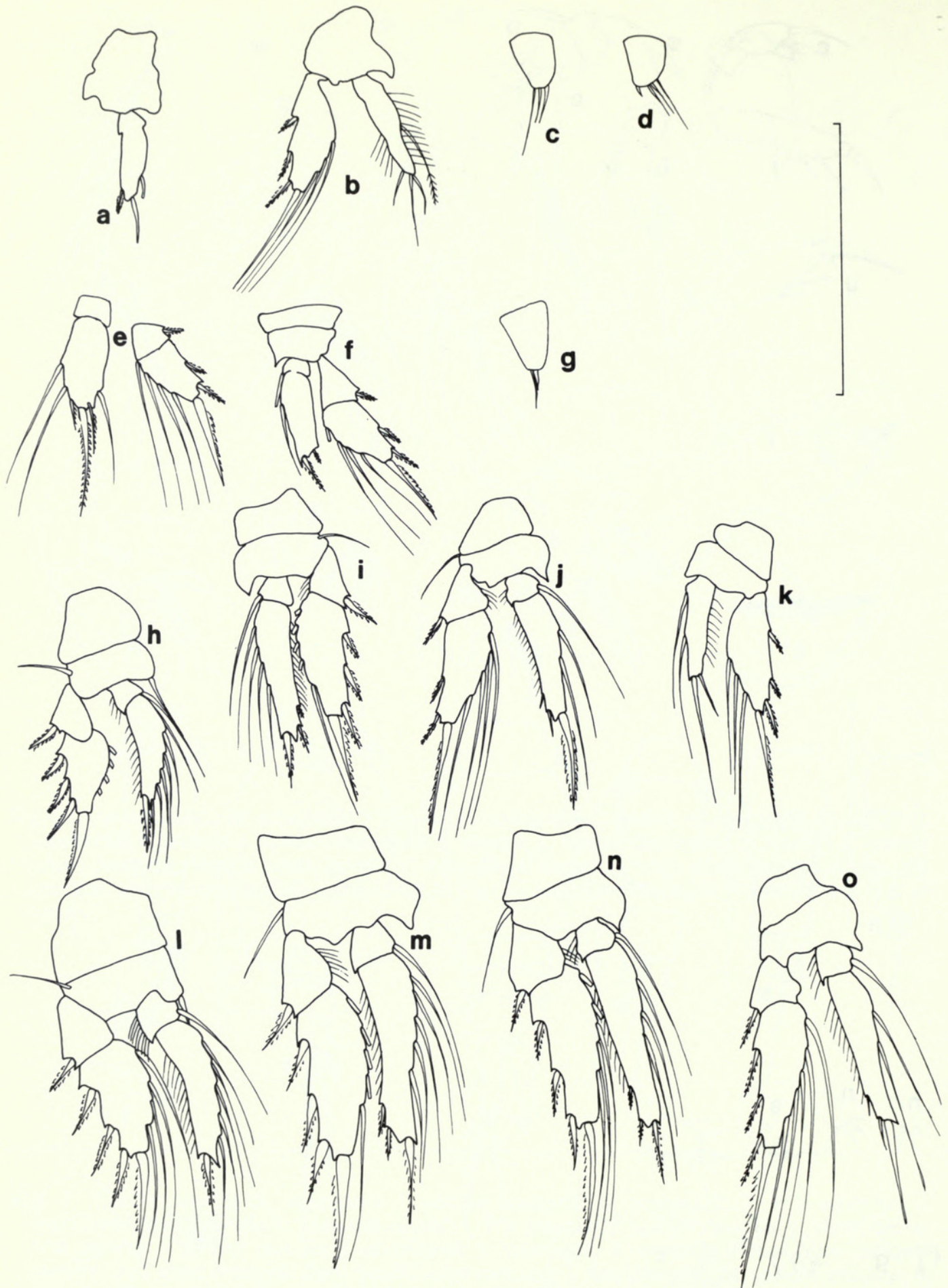


Fig. 4 *Oncaea media*. a. copepodid 1, leg 1 (damaged in dissection); b. leg 2; c. leg 3; d. leg 4; e. copepodid 2, leg 1 (coxapodite and basipodite missing); f. leg 3; g. leg 4; h. copepodid 3, leg 1; i. leg 2; j. leg 3; k. leg 4; l. copepodid 4, leg 1; m. leg 2; n. leg 3; o. leg 4. Scale 100 microns.

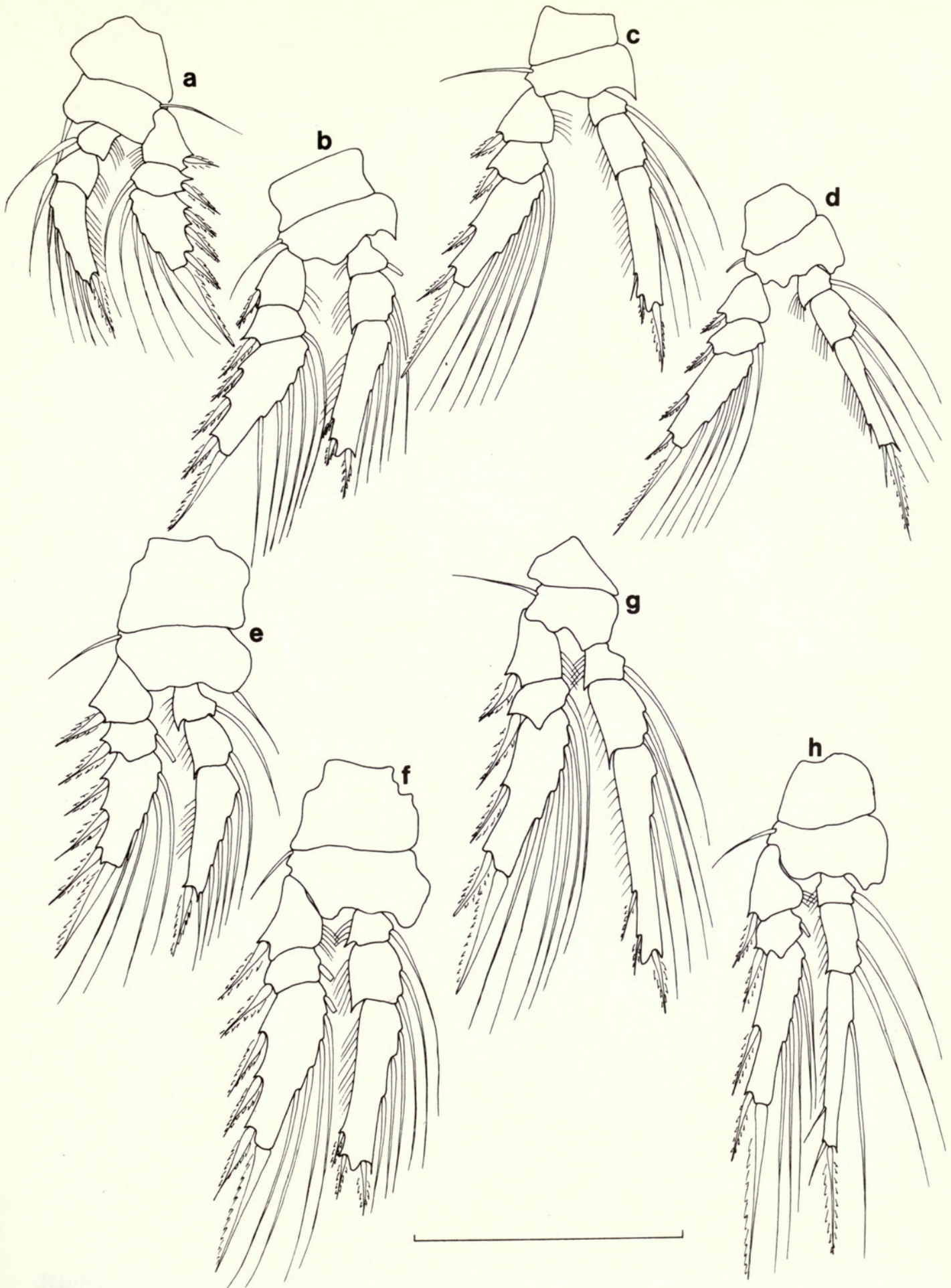


Fig. 5 *Oncaea media*. a. female copepodid 5, leg 1; b. leg 2; c. leg 3; d. leg 4; e. female adult, leg 1; f. leg 2; g. leg 3; h. leg 4. Scale 100 microns.

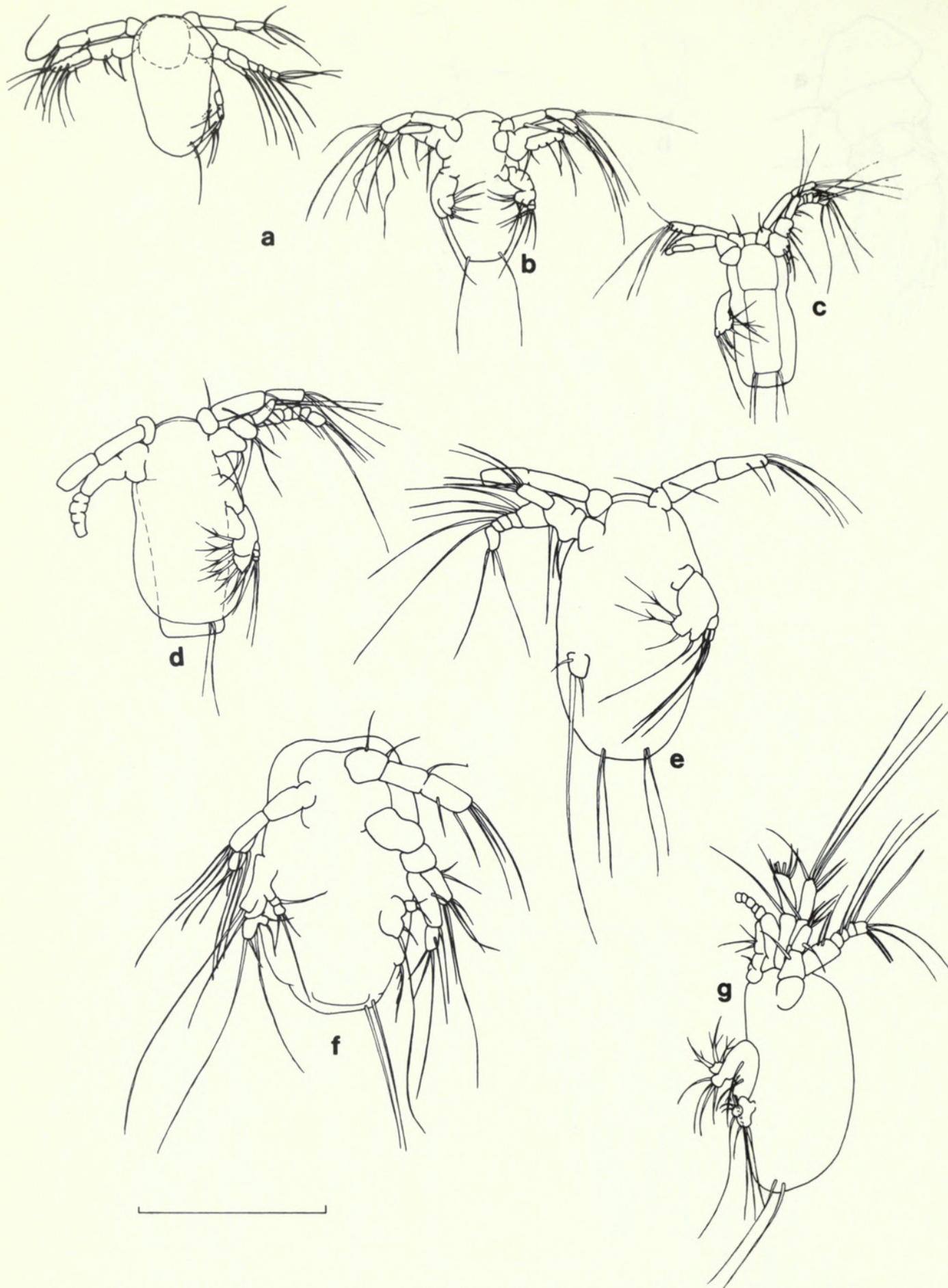


Fig. 6 *Oncaea subtilis*. a. nauplius 1, dorsal (only right mandible shown); b. nauplius 2, ventral; c. nauplius 3, ventral (only right mandible shown); d. nauplius 4, ventral (only left mandible shown); e. nauplius 5, ventral (right second antenna, left mandible and right first maxilla shown); f. nauplius 6, ventral (left first antenna, right mandible, left first maxilla and left second maxilla shown); g. nauplius 6, lateral. Scale 100 microns.

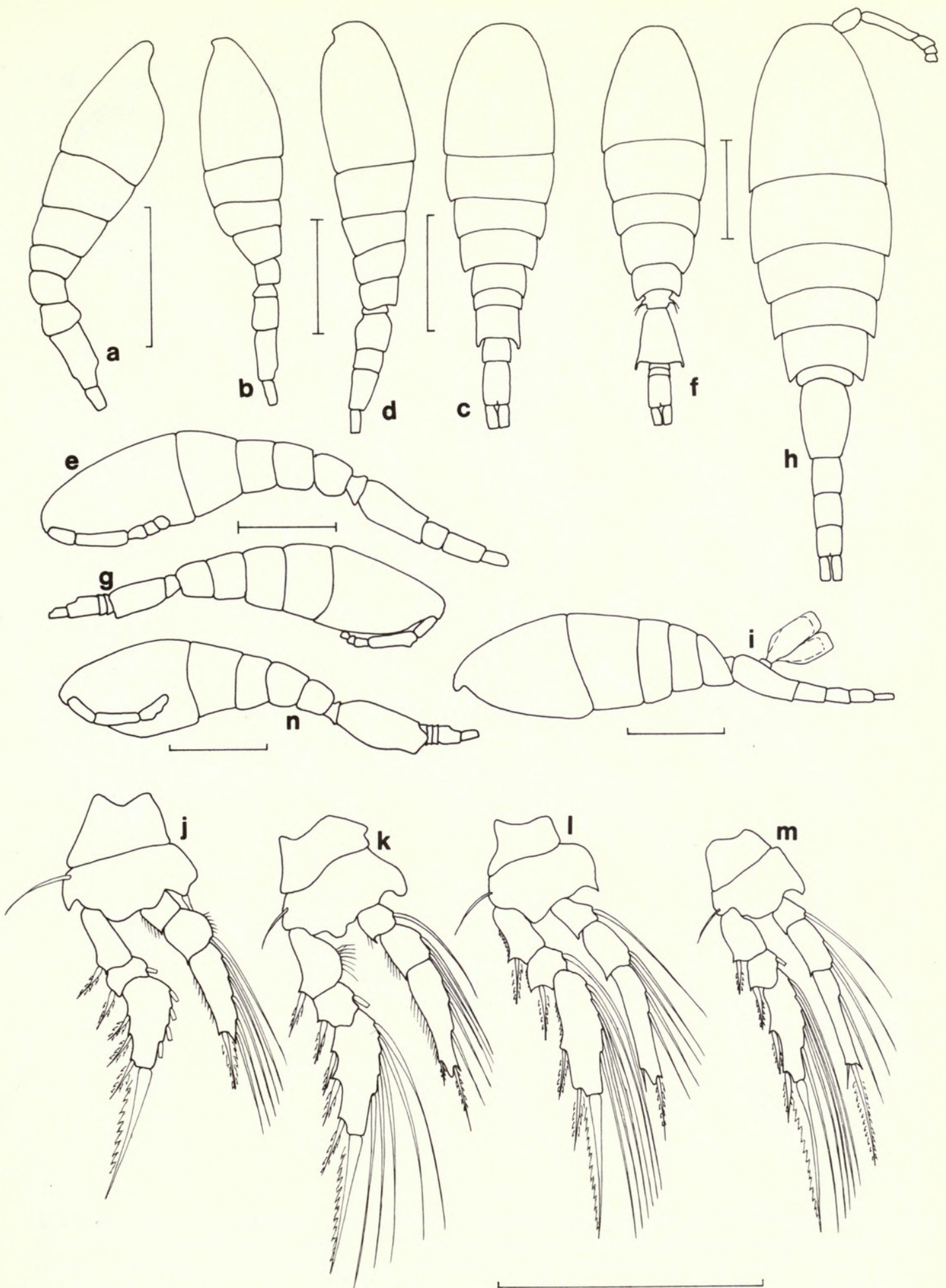


Fig. 7 *Oncaea subtilis*. a. copepodid 2, lateral; b. copepodid 3, lateral; c. copepodid 4, dorsal; d. copepodid 4, lateral; e. female copepodid 5, lateral; f. male copepodid 5, dorsal; g. male copepodid 5, lateral; h. female adult, dorsal; i. female adult bearing spermatophores on genital spines, lateral; j. female adult, leg 1; k. leg 2; l. leg 3; m. leg 4; n. male adult, lateral. Scales 100 microns, scale for natatory legs at base of figure.

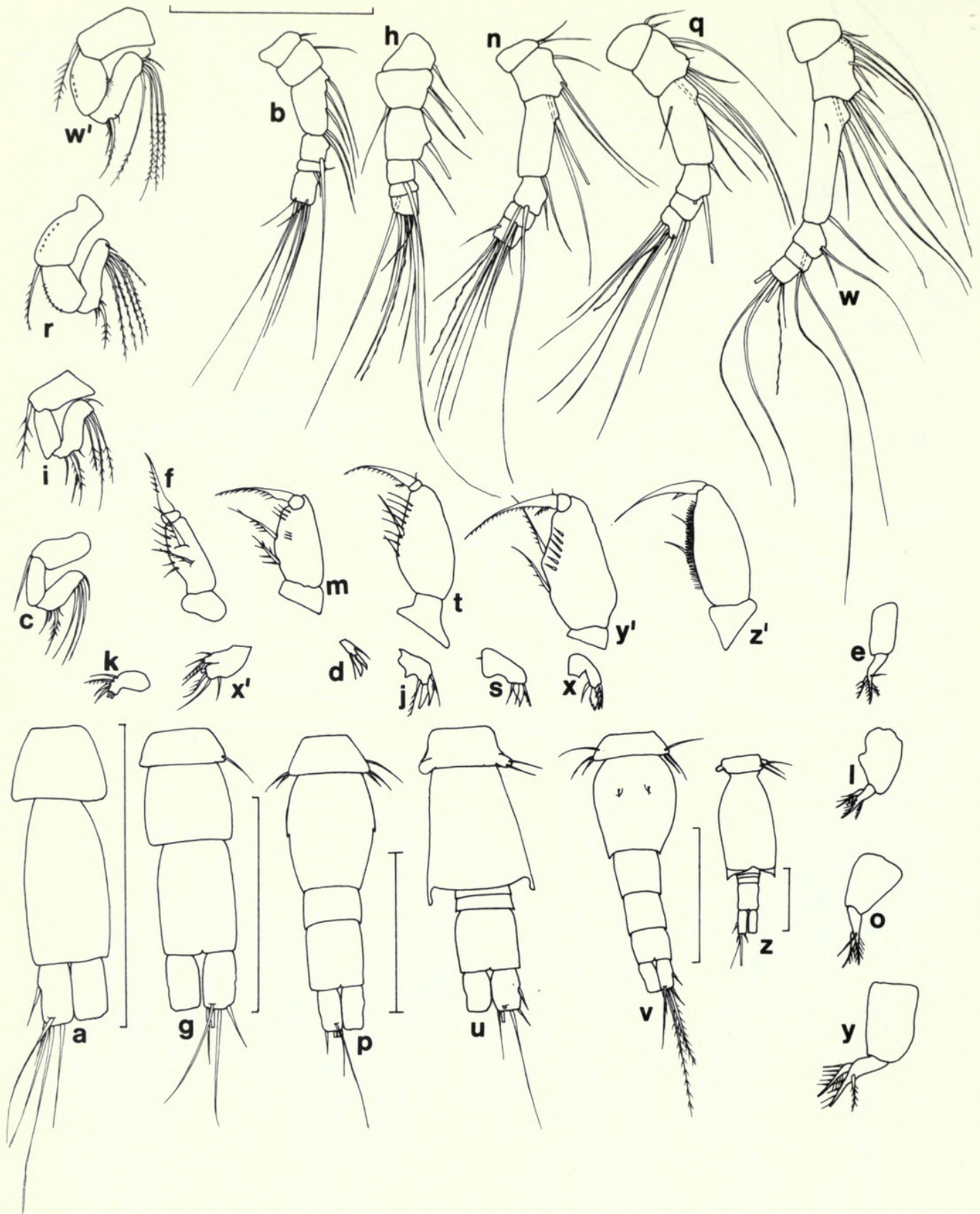


Fig. 8 *Oncaea subtilis*. a. copepodid 2, urosome, dorsal; b. first antenna; c. second antenna; d. mandible; e. second maxilla; f. maxilliped; g. copepodid 3, urosome, dorsal (lateral spine missing from caudal rami); h. first antenna; i. second antenna; j. mandible; k. first maxilla; l. second maxilla; m. maxilliped; n. copepodid 4, first antenna; o. second maxilla; p. female copepodid 5, urosome, dorsal (lateral spine missing from caudal rami); q. first antenna; r. second antenna; s. mandible; t. maxilliped; u. male copepodid 5, urosome, dorsal; v. female adult, urosome, dorsal; w. first antenna; w'. second antenna; x. mandible; x'. first maxilla; y. second maxilla; y'. maxilliped; z. male adult, urosome, ventral; z'. maxilliped. Scales 100 microns, scale for mouthparts at top of figure.

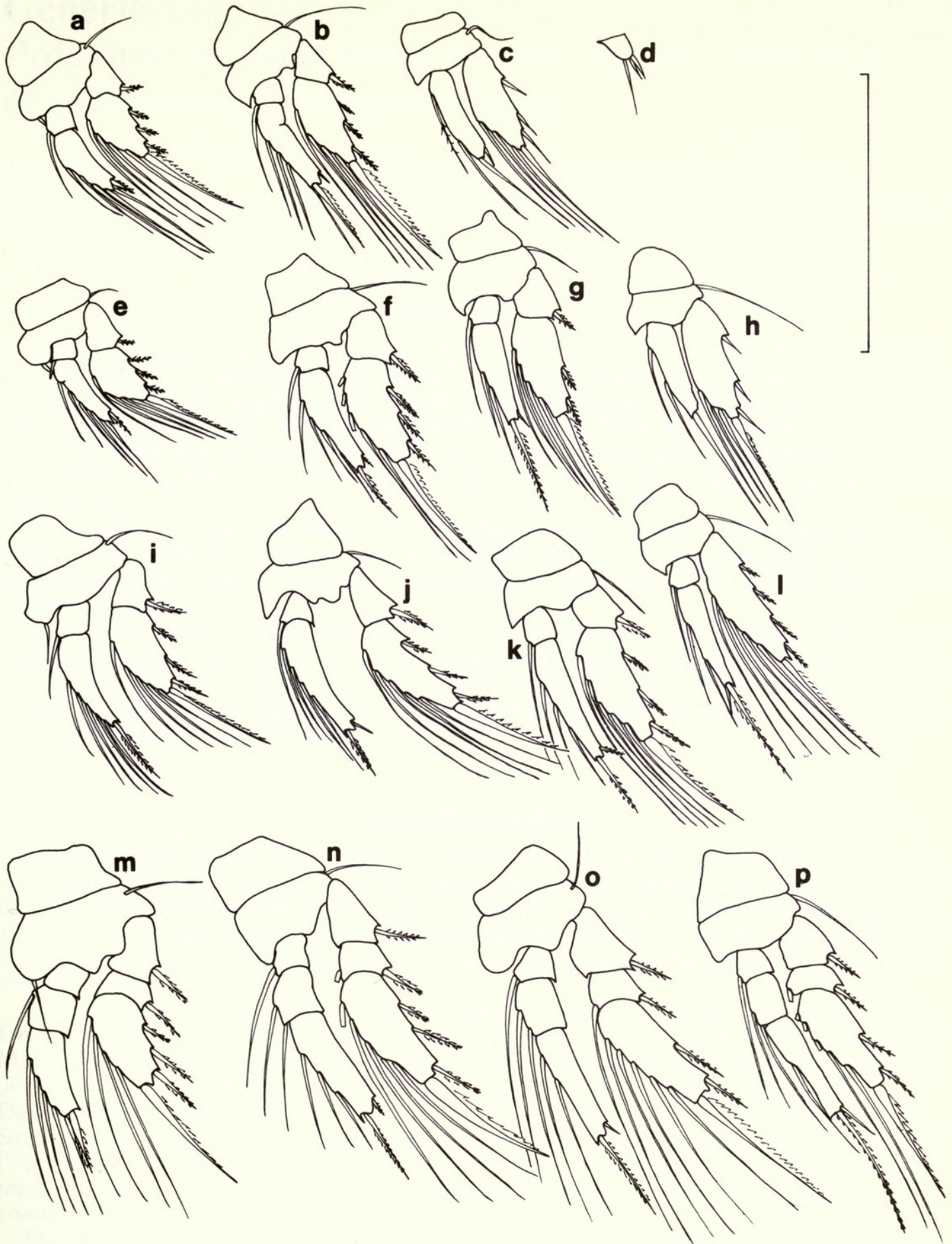


Fig. 9 *Oncaea subtilis*. a. copepodid 2, leg 1; b. leg 2; c. leg 3; d. leg 4; e. copepodid 3, leg 1; f. leg 2; g. leg 3; h. leg 4; i. copepodid 4, leg 1; j. leg 2; k. leg 3; l. leg 4; m. female copepodid 5, leg 1; n. leg 2; o. leg 3; p. leg 4. Scale 100 microns.



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