External morphology and larval development of *Derocheilocaris remanei* Delamare-Deboutteville & Chappuis, 1951 (Crustacea, Mystacocarida), with a comparison of crustacean segmentation and tagmosis patterns

By JØRGEN OLESEN

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Abstract

The external morphology of the adult and various larval stages of the mystacocarid *Derocheilocaris remanei* Delamare-Deboutteville & Chappuis, 1951 has been described by SEM. The study confirms and supplements earlier descriptions by light microscopy. New information for the adult includes: 1) the description of a large number of different types of setae; 2) the first detailed description of the 'boot-shaped' coxal process of the mandible; 3) the first description of the type of setation and ornamentation of the cephalic sternites under the labrum, where there appear still to be remnants of the segmentation; 4) an extra segment of the endopod of antenna 2, yielding six segments in all; 5) setae and pore patterns on the cephalon and the trunk segments. Some details for the adult were known earlier but are now described in more detail. Among these are: 1) the basic segmentation of the cephalic limbs and the maxilliped; 2) an unusual claw on the tip of the endopod of antenna 2; 3) the female gonopores at the inner side of trunk limbs 4; 4) a pair of setulated setae on the inner side of trunk limbs 5 in the males of probable sexual nature; 5) the setation and ornamentation of the telson and the furcal rami. Four larval stages are described in detail. These are stages 1, 2, 4 and 5. The descriptions focus on the addition and development of body segments and appendages and on the development of the telson and the furcal rami. Important results are: 1) there are eight segments in the exopod of the mandible of the larvae, the most proximal of which has disappeared in the adult; 2) segments 2 and 3 of the endopod of antenna 2 appear late in development from the subdivision of an earlier and larger segment; 3) the protopod of maxilla 1 appears, in early stages, to be divided only into two segments, interpreted as the coxa and the basis (in contrast to the adult where three segments are present). The largest change in morphology of the telson and furcal rami takes place between stages 1 and 2. It is concluded that the Mystacocarida probably is closest related to the Upper Cambrian, 'Orsten' fossil taxa, Skaracarida and the Copepoda. A comparison between crustacean segmentation and tagmosis patterns is provided.

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Introduction

The minute Mystacocarida was established as a new order of the Crustacea in 1943 by Pennak and Zinn on the basis of *Derocheilocaris typicus* Pennak & Zinn, 1943, collected at Nobska Beach, Woods Hole, Massachusetts. Since then, additional 12 species have been described, placed in two genera, *Derocheilocaris* (eight species) and *Ctenocheilocaris* (five species). *Derocheilocaris* has been found at the east coast of North America, south west coast of Africa, and in southern Europe, while *Ctenocheilocaris* has been found only in the southern hemisphere, in South America and recently also in Australia (summarised by Boxshall and Defaye 1996). All species live interstitially among sand grains.

Despite the fact that many species are separated by large geographical distances they differ only slightly morphologically. The two most well-studied species, *Derocheilocaris typica*, from the east coast of North America, and *D. remanei* Delamare-Deboutteville & Chappuis, 1951, primarily from the Mediterranean coast of Europe, are separated only by a few morphological features (Hessler & Sanders 1966). They were earlier believed to differ in their larval sequence (summarized by Hessler & Sanders 1966), but later examination has demonstrated that the two species are very similar also in this respect (Cals & Cals-Usciati 1982), which is confirmed by the present study.

This study provides new information about the Mystacocarida by using SEM to examine the adult and a wide spectrum of larval stages of *Derocheilocaris remanei*. The purpose is to facilitate future comparison with other crustacean taxa by using external morphology.

Materials & methods

The material for the study was collected in February, 1996 at Canet Plage (close to Perpignan), France, which is the type locality for the species. Numerous specimens were obtained by digging a large hole in the beach close to the upper tide zone and then filtering the seawater sieving into the hole from below. The material was brought alive to Laboratoire Arago, Banyuls-sur-Mer, where it was sorted and fixed in glutaraldehyde. The material for SEM was dehydrated and critical-point dried, mounted and coated following standard procedures. Best results were obtained when the material was postfixed in Osmium. The light-microscopy drawings were made on a Zeiss Axioscope, using a camera lucida. The SEM used was a JEOL JSM-840 situated at the Zoological Museum, University of Copenhagen. One single photograph (Plate 11I) was taken with a LEO electron microscope during a demonstration in Cambridge, England. Dozens of adults of both genders were examined by SEM, some as complete specimens, some after dissection with fine needles to get a view of various mouthparts. Additionally, 5-10 specimens for each larval stage were examined. The larval stages were numbered according to Hessler & Sanders (1966) (see note on this in Results section on larval development).

Note on terminology

Most of the terminology is standard and known by those familiar with crustacean external morphology. However, to facilitate the reading, some terminology is explained in the following. *Postmaxillary segments* are referred to as *trunk segments.* Trunk segment 1 is also named maxilliped segment due to the special function of its legs as a 'maxilliped' (=mouth part). The basal part of the limbs from which the rami arises is referred to as the *'protopod'.* When terms like *'coxa'* and *'basis'* are used, it is intended to indicate homology with corresponding limb parts in other taxa.

Abbreviations used in figures

a1	antenna 1
a2 en	endopod of antenna 2
a2 ex	exopod of antenna 2
ant ceph	anterior part of cephalon
ba	basis
co	coxa
co pro	coxa process
en	endopod
ex	exopod
fuc	furcal claw
fur	furcal rami
la	labrum
md ba	basis of mandible
md co	coxa of mandible
md en	endopod of mandible
md ex	exopod of mandible
md	mandible
mx1	maxilla 1
mx2	maxilla 2
mxp	maxilliped (=t1)
nau pro	'naupliar process' (endite)
pgn	paragnath
post ceph	posterior part of cephalon
pro	protopod
sup an	supra-anal process
t1-t10	trunk segments 1-10
te	telson

Results

I. External morphology of the adult

General – body segmentation and tagmatisation

Cephalon dorsally divided in a small *anterior portion*, corresponding to the segment of antennae 1, and a larger *posterior portion*, corresponding to the segments of antennae 2, mandibles and maxillae 1 and 2 (see Plate 4A). Trunk made of 10 segments plus the telson. Anterior-most trunk segment (=maxilliped segment) significantly smaller than the nine following ones (Plate 3A, 4). Telson terminating in a pair of articulated furcal rami, each with a distal claw.

Cephalon with five pairs of limbs. Anterior-most five trunk segments bearing limbs. Limbs on the first trunk segment well-developed and usually termed maxillipeds. The remaining four trunk limbs (on trunk segments 2-5) are small, unsegmented lobes.

Cephalon, dorsal (head shield) (Plate 4)

Anterior portion of head shield with a pair of anterior lobes, overhanging the first segments of the first antennae and with a pair of broad, slightly larger, rounded lateral lobes, partly overhanging the basal parts of the second antennae (Plates 2, 6A, 11A). Anterior and lateral lobes separated by deep anterolateral notches; two anterior lobes separated by an anteromedial notch. The lateral lobes each have a ventroanteriorly directed protuberance with spines (marked by a black arrow on Plate 6A). Anterior portion of the head shield with 10 setae, one submarginal pair on each of the anterior lobes, one submarginal pair on each of the lateral lobes, and one dorsal pair (Plate 4A, Fig. 8).

Posterior portion of the head shield with a pair of X-shaped, toothed furrows posterolateral (Plates 3A, 4, 6A). Head shield with six median setae (three pairs) and six submarginal setae along the edge (Fig. 8, schematised; not all setae shown illustrated by SEM but see Plates 4, 6A). Between the anterior pair of median setae is a small depression (marked by a white arrow on Plate 4A).

Cephalon, ventral (Plate 7, mostly)

Remnants of possible segment boundaries are present (marked by arrows on Plate 7C). The paragnaths are two flattened, upright lobes situated laterally between the mandibles and maxillae 1, immediate posterior to the coxal process of the mandibles, apparently arising from the segment of maxilla 1. Posterior to the paragnaths, at the presumed maxilla 2 segment, is a median heart-shaped setal structure and more posteriorly are four lateral setal scales ventrally on each side of the segment (Plates 7B, C, E, 16C). The separate maxilliped segment (trunk segment 1) appears functionally to be connected to the cephalon (e.g., Plate 7B), but is described in the following section.

Trunk segments (Plates 1, 3, 4, 5, 6A-D, Fig. 8)

Dorsal side of each body segment consists of longitudinal bars (at least after critical point drying) (Plate 4; schematised in Fig. 8). Dorsal side of trunk segment 1 (maxilliped segment) with one bar extending in the whole length of the segment, posteriorly flanked by small triangular sections; segment 2 dorsally with three bars; segment 3 with four bars; segments 4-10 with five bars each. Only segment 3 lacks a bar in the mid-axis of the segment. One pair of setae is present posteriorly on the dorsal side of each of trunk segments 1-3. On segments 1 and

2 these are on either side of one bar, while on segment 3 they are separated by 2 bars. Segments 4-10 have 6 setae dorsally; one pair is situated close to the posterior margin on the segment and separated by 3 bars (these are probably serially homologous to the setal pairs on the 3 previous segments); a row of 4 setae is present more anteriorly on the segment: two central setae separated by the central longitudinal cuticular bar and two placed widely apart, lateral to the five cuticular bars (see Fig. 8 for a schematic representation of the setal distribution).

Laterally, each trunk segment has a furrow fringed with small teeth. On trunk segment 1 (maxilliped segment) the toothed furrow is more or less X-shaped, quite similar in morphology to the toothed furrow at the posterolateral margin of the cephalon (Plates 4A, 6A). The nine pairs of toothed furrows on trunk segment 2-10 are similar in shape (Plates 3A, 6B-D). They are all situated slightly anterior to the midlength of the segment. All are 20-25 µm long, narrow furrows with rows of teeth on the anterior and posterior margin and with slight expansions without teeth at each end. The anterior row always overlap the posterior row. The setation of the lateral side is similar for trunk segments 2-10 (Plate 6B-D, Fig. 8). All have two ventral setae, one close to the ventral end of the toothed furrow, another one close to the posterior margin of the segment. Segment 1 only has one seta laterally (Plate 6A, Fig. 8), near the posterior margin of the segment. On segments 2-10 there is a small depression (pore) situated in the dorsal third of the segment, between the toothed furrow and the posterior margin (Plate 6B-D).

The *ventral* side of the trunk segments have the following morphology. In the midline of trunk segment 1 (=maxilliped segment) is a furrow which on each side is flanked by a dense setation (Plate 7A-C); laterally a pore is present (Plate 7C, black arrow). Trunk segment 2 is ventrally smooth and triangular of shape, with the apex pointing anteriorly; the anterior part of the segment is slightly depressed with a pair of elevations in the midline (Plates 5B, 7A). Trunk segments 3-5 are similar to each other (Plates 1, 5A); ornamentation absent except for the granulation typical for most segments. Trunk segment 6 is similar to trunk segments 3-5 except for the presence of a pair of widely separated setae which are absent at the preceding segments (Plate 5A). Trunk segments 7 and 8 are similar to each other (Plate 5A, C): A pair of widely separated setae are present together with two pairs of serrate combs. Trunk segments 9-10 are similar to the two preceding segments except for a pair of pores situated anterior to the serrate combs (Plate 5A, D).

Labrum (Plate 6E-J)

Labrum large, elongate and dorsoventrally flattened, extending freely over the ventral body surface from antenna 2 to trunk limb 1 (=maxilliped); distal part with a wide and rounded profile compared to anterior part, which is more narrow (Plate 6E, G). There are two lateral 'shoulders' at the level of antenna 2 (arrow on Plate 6E). Distal edge with a dense submarginal setation (Plate 6E, I, J). Inner side of labrum (facing the atrium oris) with dense setation, most pronounced under the rounded tip of the labrum; with two pairs of pores at the distal part of the labrum close to midline (Plate 6F, H).

Appendages

Antenna 1 (Plates 2, 9)

Uniramous. Eight segments. Segments 1-3 of irregular shape (see below). Segments 4-8 tubular and smooth. Ventral surfaces of segments 1-3 divided into a number of sclerites, most pronounced for segment 2 (not shown in pictures). Segments 1 and 2 each with a hook-shaped spine, pointing anteriorly, positioned dorsally at segment 1 and medio-dorsally at segment 2 (Plate 2A). Segment 1 with one seta; segment 2 with four setae; segment 3 with eight setae; segment 4 with five setae; segment 5 with eight setae; segment 6 with five setae; segment 7 with five setae; segment 8 with four setae, and one subterminal aesthetasc.

Most setae of a smooth, simple type with two annulations (10-70 µm). Some have a different morphology: the ventral setae at the basis of segment 2 have a row of setules and a slender acute tip; each of segments 3, 5, 7 have one small seta (3-5 µm) without annulations.

Antenna 2 (Plates 10, 11)

Biramous. *Protopod* divided into a large coxa and a small basis (Plate 10G-I). Inner side of coxa with three blunt, cuticular processes (marked by 'A'-'C', probably the remains of the naupliar processes, Plate 10G-I), the posterior of which (process 'A') bears a small seta, the median of which (process 'B') bears a large, slender seta (15 µm) (Plate 11D). Anteromedian side of basis with two 'denticle-scales' (small group of 3-7 denticles) and a small, smooth seta with a distinct slender tip (4-5 µm).

Endopod curved, and situated ventral to the body; with six segments of unequal size and morphology (Plates 10A, 11). The true nature of all six segments can be questioned, but in this treatment they are considered as such. In previous literature, segments 4 and 5 (herein) are sometimes counted as one segment, and sometimes segment 6 (herein) is viewed as a modified seta. Segment 1 (counting from proximal) with one asymmetrically bifid, robust seta; a slender unornamented acute seta; and a denticle-scale close to the basis of the first-mentioned setae (Plate 11E). Segment 2 lacks ornamentation or setation. Segment 3 is small with an asymmetrically bifid, stout seta with a denticle-scale close to its basis (Plate 11F). Segment 4, small, lacks ornamentation or setation (has sometimes not been recognised as a separat segment). Segment 5 with two small setae, both slender distally (Plate 11G). Segment 6 long and slender, inflated proximally (Plate 11G). The tip of the endopod (segment 6) is modified into a characteristic, symmetrical double-sided comb like structure, composed of two rows of opposing denticles and a slender denticle between the two rows of denticles (Plate 11H, I). There are 5-8 denticles in each row that gradually become larger towards the tip of the endopod.

Exopod bent dorsally in relation to the body (e.g., Fig. 3, Plates 2, 10A, 11A), with nine almost identical segments. Segments 1, 2 and 4-8 each with one seta; segment 9 with three terminal setae; segment 3 lacks setation. Setae on segments 1 and 4-6 robust, tip bifid with a terminal slender process; the most proximal setae are smallest (Plates 10A, C, F, 11A). The seta on segment 2 is unornamented, with a proximal annulus, and a long slender tip (Plate 10D). Setae on segment 7-9 long and bilaterally serrated; the longest are the seta on segment 8 and two of those on segment 9; tips of these setae each with a slender process (Plate 10A, B, E). All setae, except on the distal segment, arising from posteromedian face of the exopod. Two denticle-scales present on the median side of each of segments 3-9.

Mandible (Plates 7A, C, D, 12, 13)

Biramous. *Protopod* divided into a coxa and basis (Plate 12D). Coxa with a large, flattened, anteriorly curved coxal process (Plates 7A, C, D, 12A, B). Posterior edge of coxal process with a large pointed tooth anterior to which is a tubular seta with a bifurcate tip (Plate 12A, C; indicated by arrow); anterior inner margin with 8-9 double or triple teeth (Plates 7A, C, D, 12A, B); anterior tip of coxal process with a large multiserrate process (Plate 12B). Inner side of basipod with 4 denticle-scales and two setae, a small smooth type and a large annulated type with a row of setules (Plate 12D-F, not all denticle-scales shown).

Endopod with three segments (Plate 13). Segment 1 with one small, asymmetrically bifid seta; inner face with four denticle-scales. Segment 2 with two setae, one which is bilaterally setulated and another which is unilaterally serrated; inner surface with two denticle-scales. Segment 3 with three unilaterally serrated setae and two denticle-scales.

Exopod bent dorsally in relation to the body, with seven segments (Plates 11A, 12H-J). Segments 1-2 lack setation; segments 3-6 with one seta each; segment 7 with three setae; all setae are unilaterally or occasionally bilaterally setulated and with a slender terminal process. Segments 1-5 each with a pair of denticle-scales.

Maxilla 1 (Plates 14, 15)
Uniramous. With a three-segmented protopod and and four-segmented endopod. Three proximal segments sometimes termed 'precoxa', 'coxa', 'basis', see Boxshall, 1997). Segment 1 of the protopod with six setae situated on one large endite; the two proximal setae are long and slender with bilateral sparsely set serrations on distal half; two other setae are stout and bifid with a long tubular terminal process; two remaining setae are stout and heavily plumose distally. Segment 2 of the protopod is small with one endite with a stout, densely circum-plumose seta (this segment appears late in ontogeny, see below). Segment 3 of the protopod with two endites, the proximal one with two stout distally circum-plumose setae; the other endite with three setae, one small and two larger, all with some setules distally. Segment 1 of the endopod with two setae; one is slender with many setules (Plate 15B), the other is short and stout. Segment 2 of the endopod with same setation as segment 1 (Plate 15F). Segment 3 of the endopod: inner margin with one short, stout seta with a dense row of denticles on one side (Plates 14A, 15E, F); outer margin with a asymmetrically bifid, smooth seta (Plate 15D). Segment 4 of the endopod with eight setae of varying lengths, all with same basic morphology: a stout basal part (about 1/3 of length) followed by a long, slender, somewhat blade-shaped part with denticles on one side (Plates 14A, 15C, E, G, H).

Maxilla 2 (Plates 16, 17)
Uniramous. *Protopod* with 2-3 segments. The true segmental status of all protopodal segments is uncertain and needs verification by other methods than SEM. The most proximal 'segment' of the protopod (indicated by '?') in Plate 17) lacks setae. Protopod with numerous dense clusters of setae pointing towards ventral side of the cephalon. All setae are ornamented; some are densely circum-plumose, some are flattened and serrate distally, and some are armed with sparsely placed setules (Plates 16A-D, 17A, B, E).

Endopod segment 1 with two setae, one short and stout with a row of setules, the other long and slender with widely separated setules. Segment 2 with setation identical to segment 1. Segment 3 with two setae, one short, stout and serrate along one side, the other long and slender with widely separated setules. Segment 4 (distal segment) with five setae of varying lengths, ornamentation is the same as the stout seta on segment 3 of the endopod and the setae on the distal segment of maxilla 1.

Trunk limb 1 **(Maxilliped)** (Plate 18)
Biramous. *Protopod* divided into 2-3 segments. The true segmental status of the protopod limb portions is uncertain. The small basal 'segment' lacks setation. The second segment is twice the size of the basal segment; laterally with one short, stout, plumose seta; anterior face with a dense cluster of setules and two large setae with a very dense setulation pointing towards the sternitic surface of the cephalon. The third segment is the largest part of the protopod; laterally there is a long slender seta with two rows of setules; the inner margin is di-

vided into a number of endites (at least 4) with at least 12 setae, some of which are small and smooth, and some of which are long and slender with a dense row of setules; inner margin of posterior face with a small cluster of acute denticles.

Endopod with three segments; segment 1 without setae; segment 2 with two slender setae, both with long setules along distal half; segment 3 with two setae similar to those of segment 2.

Exopod unsegmented; with two slender, distal setae with dense setulation.

Trunk limbs 2-5 (Plates 19, 20)

Trunk segments 2-5 in both sexes with four pairs of small, unsegmented and lobate limbs.

Female (Plate 19). Trunk limb 2 with two distal setae, one smooth and small and another long, smooth and with bifid tip (Plate 19C). Trunk limb 3 with three distal setae; two small with bifid tips, both with a basal annulation (Plate 19F, G); one large with a sparse row of setules on distal half and a bifid tip (Plate 19E). Trunk limb 4 with an oval gonopore on the median side and with three distal setae (Plate 19A-C); one seta small with a bifid tip, a terminal tubular process and a basal annulus (Plate 19C); two long setae with one row of setules along distal half and a terminal tubular process (Plate 19A, B). Trunk limb 5 with three setae similar to those on trunk limb 4.

Male (Plate 20). Similar to female, except for the absence of external indication of gonopores on trunk limbs 4, and two additional circum-plumose setae on the inner side of trunk limb 5, one small and one larger.

Telson, furcal rami and furcal claws (Plates 21, 22)

Telson dorsally with a large, elongate supra-anal bar extending in the full length of the telson and terminating in an acute process (supra-anal process) (Plate 21A). Ventral to this process there are 10-12 spines (Plate 21E) and dorsally a long, slender seta with irregular annulations on the proximal half (Plate 21E, F, H); dorsal to the large seta is a small, simple seta (4 μm) (Plate 21F, arrow), on each side of which is an oval pore with a blade-shaped seta in the middle (Plate 21E, arrow). A pair of triangular acute processes are present on each side of the supra-anal process, each with a subterminal oval pore. Telson ventrally with a number of serrated scales and lobes, so that it appears superficially subdivided into two parts, an *'anterior part'* and a *'posterior part'* ('ap' and 'pp' on Plate 22A). The serrated posterior margin of the *anterior part* is subdivided into a central large scale and two lateral lobes. On the posterior part is a pair of serrated scales between the furcal rami and another larger pair of serrated scales at the basis of the furcal rami; lateral to these on each side is a serrated margin. Additional ornamentation ventrally on the telson is a pair of oval pores (arrow on Plate 22A) and a pair of setae more laterally. On the sides of the telson there is also a small seta on each side.

The furcal rami articulate to the telson. Each ramus has three long setulated setae laterally projecting in three different directions: dorsal, lateral, and ventral; a smaller dorsal seta (10-12 μm) with a wide basal part (arrow on Plate 21A, H and Plate 21D); a very small ventrolateral simple seta (Fig. 21B). Each ramus has seven comb-like scales, five along the mediolateral side of the ramus, two partly covering the bases of the furcal claws (numbered on Plate 21A, B). Furcal claws smooth, acutely pointed and attached to rest of the furcal rami at a 90° angle; the distal 1/4 is hollow (Plates 21A-C; 22C). Each ramus with six oval pores in which there is a central blade-like sensillum; four pores are located ventrolaterally, close to where two of the large setae originates (Plate 22A); one pore is located dorsally, close to the basis of the furcal ramus (Plate 21A); another dorsal pore is immediate behind the furcal claw (hidden on Plate 21A).

II. External morphology of larvae

No complete description of all larval stages has been attempted in this paper which focuses on the change in segmentation of the body and the appendages during development. The larval stages have been numbered according to the larval sequence of *Derocheilocaris typicus* Pennak & Zinn as described by Hessler & Sanders (1966). This numbering system was chosen because there still is some uncertainty with respect to the actual larval sequence for *D. remanei*. Originally 10 preadult stages were described by Delamare-Deboutteville (1954), which is in contrast to the seven described for *D. typicus*. Later this was modified by Cals & Cals-Usciati (1982), who found that the earliest stage of *D. remanei* was not a 'true' nauplius, but already had the limb buds of one extra pair of cephalic limbs. All larvae investigated of *D. remanei* in this study conformed with those in the sequence of *D. typicus*. Thus, it is very likely that both larval sequences are identical. Accordingly, Hessler & Sanders (1966) can be consulted for other details of the sequence of *Derocheilocaris* than those mentioned in this account.

Antenna 1 (Figs 4-7, Plates 23-26)
There is no change in segmentation of antenna 1 during development. Eight segments are present in all stages. The setation of the segments changes but has not been followed in detail this study.

Antenna 2 (Plate 27)
The protopod in all stages is divided into two segments, the coxa and basis. The second antenna of both sides in the larvae has two bifid naupliar processes, actually endites, arising from the median surface of the coxa (Plates 23, 24A, 26B, 27B, F, and various line drawings Figs. 4, 6, 7). The coxae of the adult each have a pair of lobes in the same position as the naupliar processes (Plate 10G-I, indicated by 'A'-'C') which are intepreted as the vestigia of the naupliar processes. The endopod has five segments in all larval stages (if segment 4 is interpreted as a separate segment and if the distalmost segment is not interpreted as a modified seta, see Plate 27). In the adult, segment 2 has become subdivided into two segments, so that the endopod in the adult has a total of six segments (Plates 10A, 11A-C). The segmentation of the exopod does not change during development.

Mandible (Plate 28A, B)
The larval stages have an elongate naupliar process (endite) arising from the mandibular coxa and another, larger one, arising from the basis (not shown in SEM). The endopod is three-segmented in all stages. The exopod has eight segments in the larval stages (Plate 28A, B), whereas in the adult there are only seven. By comparing the ornamentation of the exopod segments of the larvae and the adult, it becomes apparant that the most proximal segment of the larvae has disappeared during development (extra segment in larval stages marked by '0' on Plate 28A, B).

Maxilla 1 (Plates 28D-F, 29)
In the first larval stage, maxilla 1 is a flattened lobe with five medial, rounded processes and one lateral seta (not shown in SEM, see Hessler & Sanders,1966: fig. 3e). In stage 2, more setation has appeared and the limb has become subdivided into 2-3 portions (lateral side and distal ends of maxilla 1 shown in Plate 29A, B; whole limb shown by Hessler & Sanders, 1966: fig. 4d). In stage 3 the limb is subdivided into 3-4 portions (Plate 29C, D). The *two* proximal portions in stage 2 and 3 appear to correspond to the *three* first segments in the adult. The

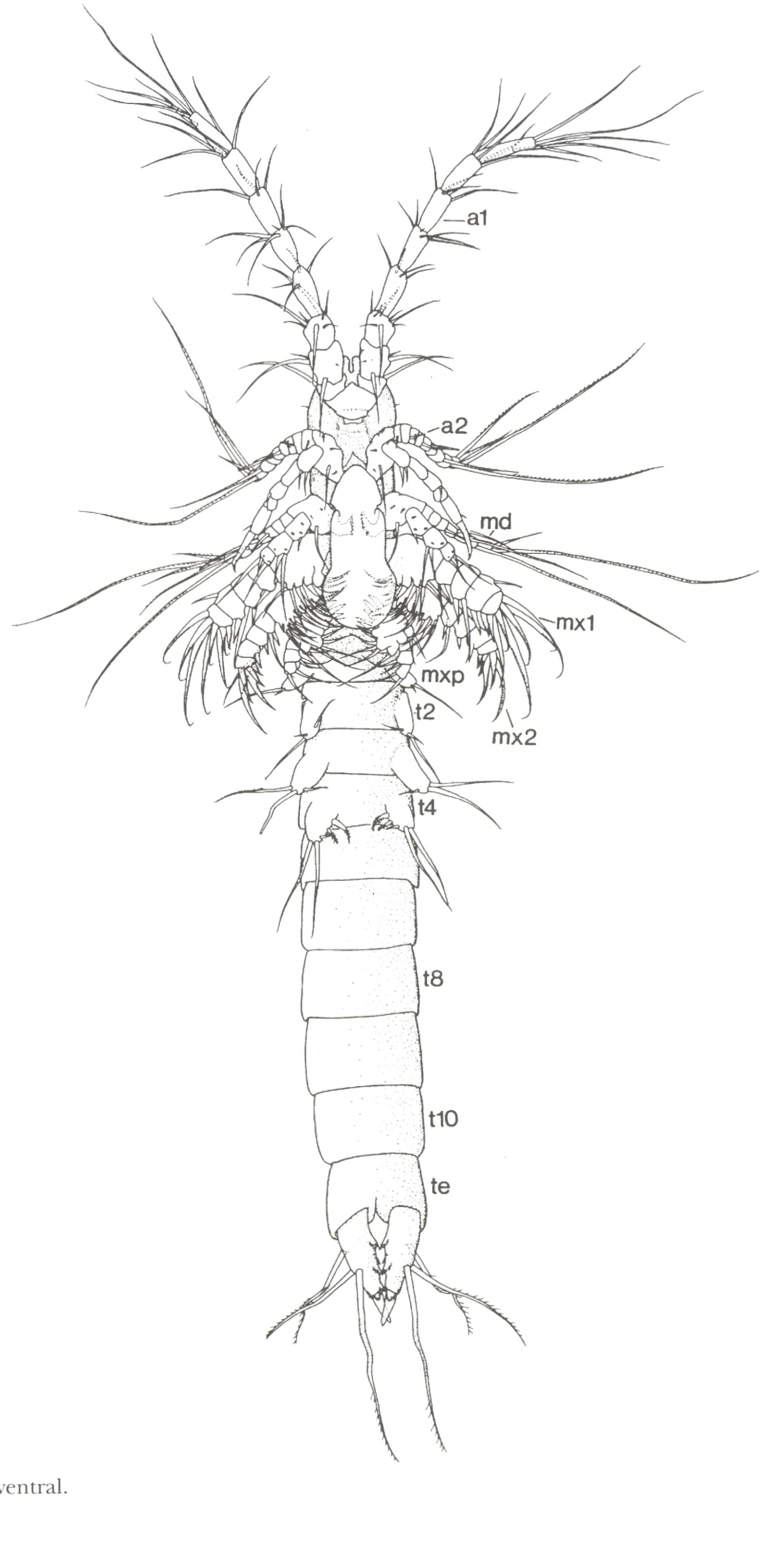

Figure 1. Adult male, ventral.

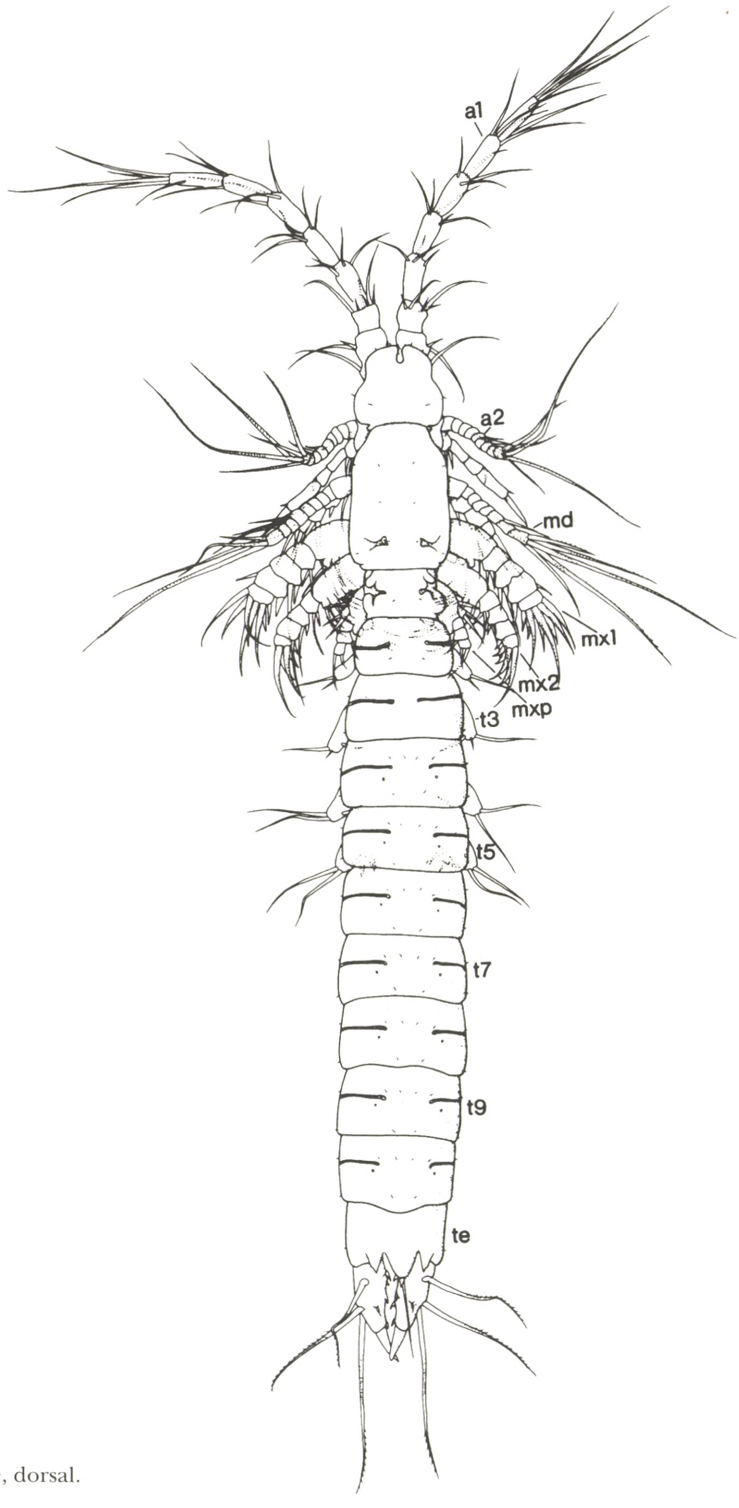

Figure 2. Adult male, dorsal.

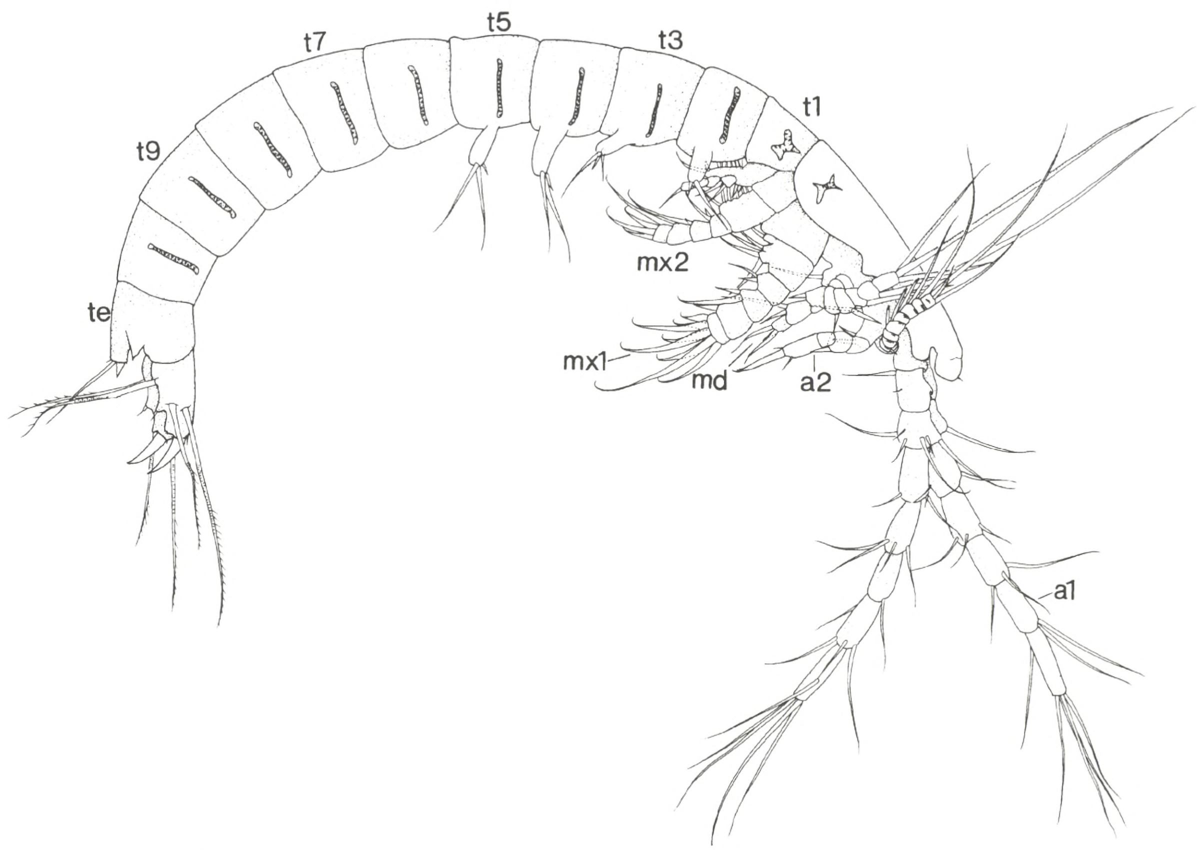

Figure 3. Adult female, lateral.

small, second segment, present in the adult, apparantly appears late in the ontogeny of the limb. It is yet uncertain whether this small segment appears from a subdivision of the larval coxa or basis.

Maxilla 2 (Plates 28C-F, 29A-F)
No certain information as to the origin and homologies of the segmentation of the protopod has become available by this study. The two most proximal segments in the larval maxilla 2 at stage 4 are tentatively interpreted as the coxa and basis (Plate 30C). The segmentation is difficult to follow in the material of stage 5 (Plate 30E, F). The protopod of the adult appears to be divided into 2-3 segments (Plates 8C-F 17A-C), but the most proximal segment lacks setation and may therefore be of secondary origin.

***Maxilliped* (trunk limb 1)** (Plates 28C-F, 30G)
The protopod of the adult appears to be divided into 2-3 segments. Three segments are seen at least at the lateral margin of the limb and partly also at the posterior face. I have found no certain information as to the origin and homologies of the segmentation of the protopod.

Trunk limbs
The trunk limbs on trunk segment 4 appear earlier than limbs 2 and 3. They are first visible

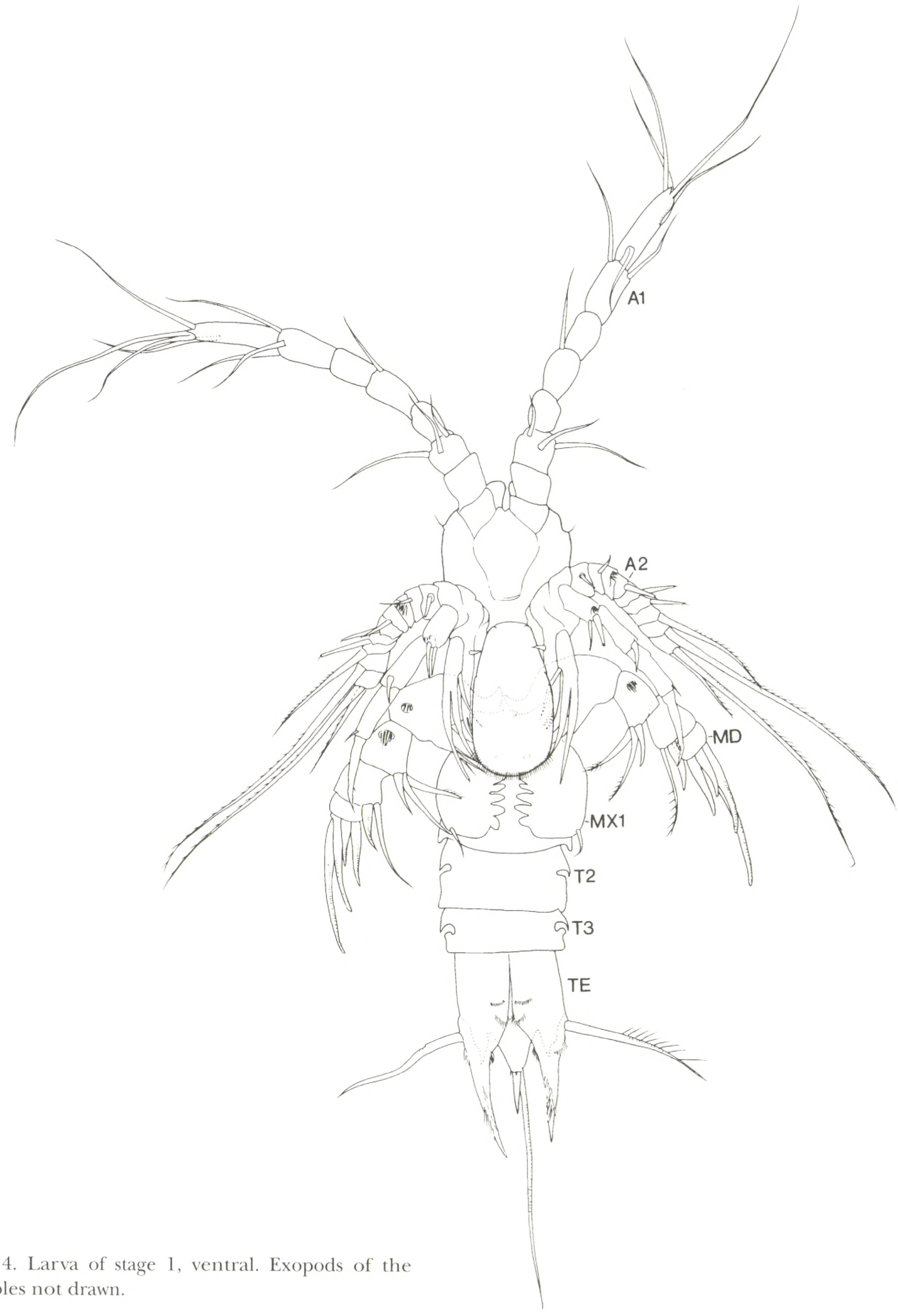

Figure 4. Larva of stage 1, ventral. Exopods of the mandibles not drawn.

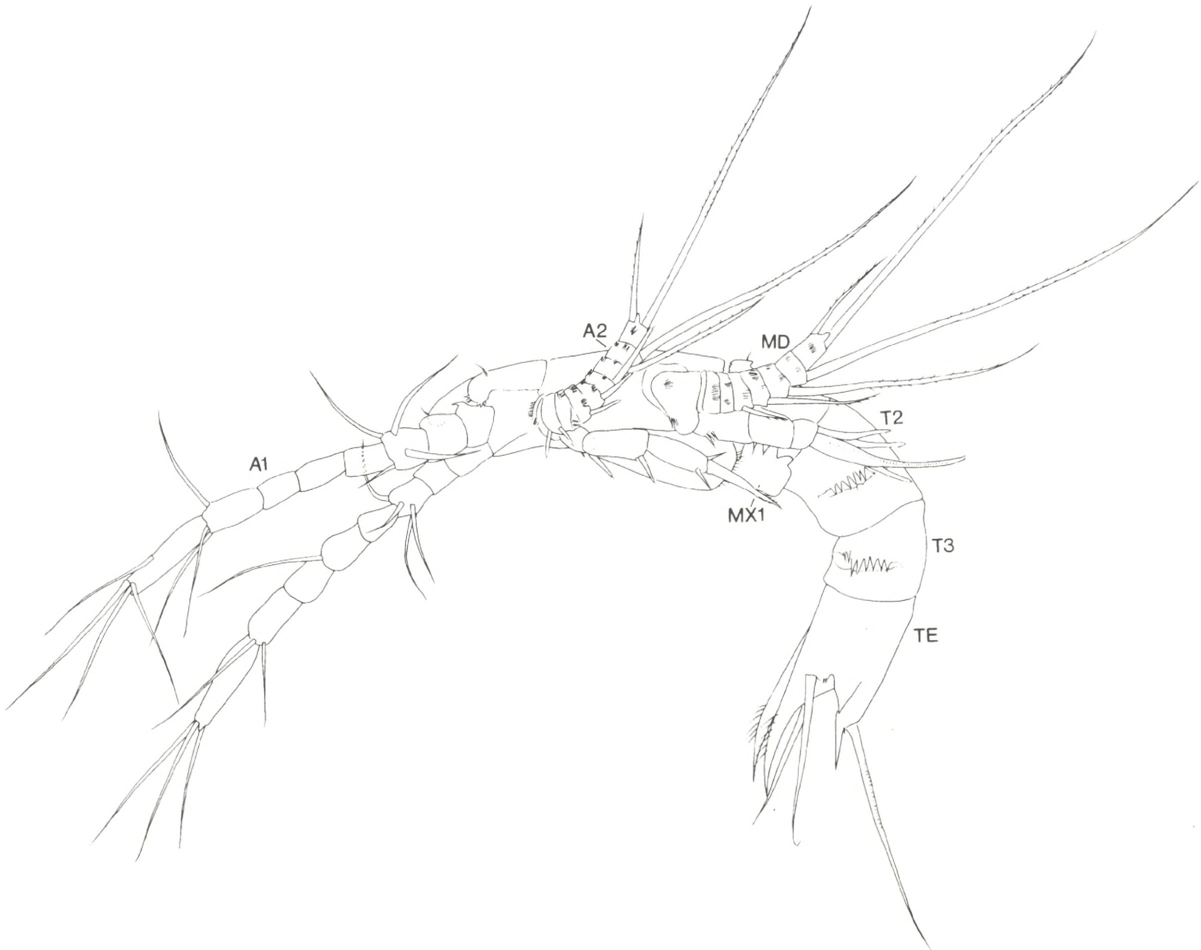

Figure 5. Larva of stage 1, lateral.

as small lobes in stage 3 (Hessler & Sanders, 1966: fig. 4i; not shown in the present paper). The remaining four trunk limbs develop slightly later than the limbs of trunk segment 4. In stage 4, the limbs of trunk segment 4 have developed to larger lobes with one developed seta and one rudimentary seta distally; trunk limbs 2 and 3 are small lobes, while trunk limbs 5 are not yet present (Fig. 7, Plates 25, 30A,B, 31G). In stage 5 the limbs of trunk segment 4 approach their final shape, with three setae present; trunk limbs 2 and 5 are lobes only, the latter triangular; trunk limbs 3 have two rudimentary setae (Plate 26).

Segment addition

As is typical for crustaceans, there is a growth zone anterior to the telson. In stage 1 (the hatching larva) has already three trunk segments (including the maxilliped segment) and a distinct telson (Fig. 4, 5, Plate 23). In stage 2 there are 5 trunk segments (including the maxilli-

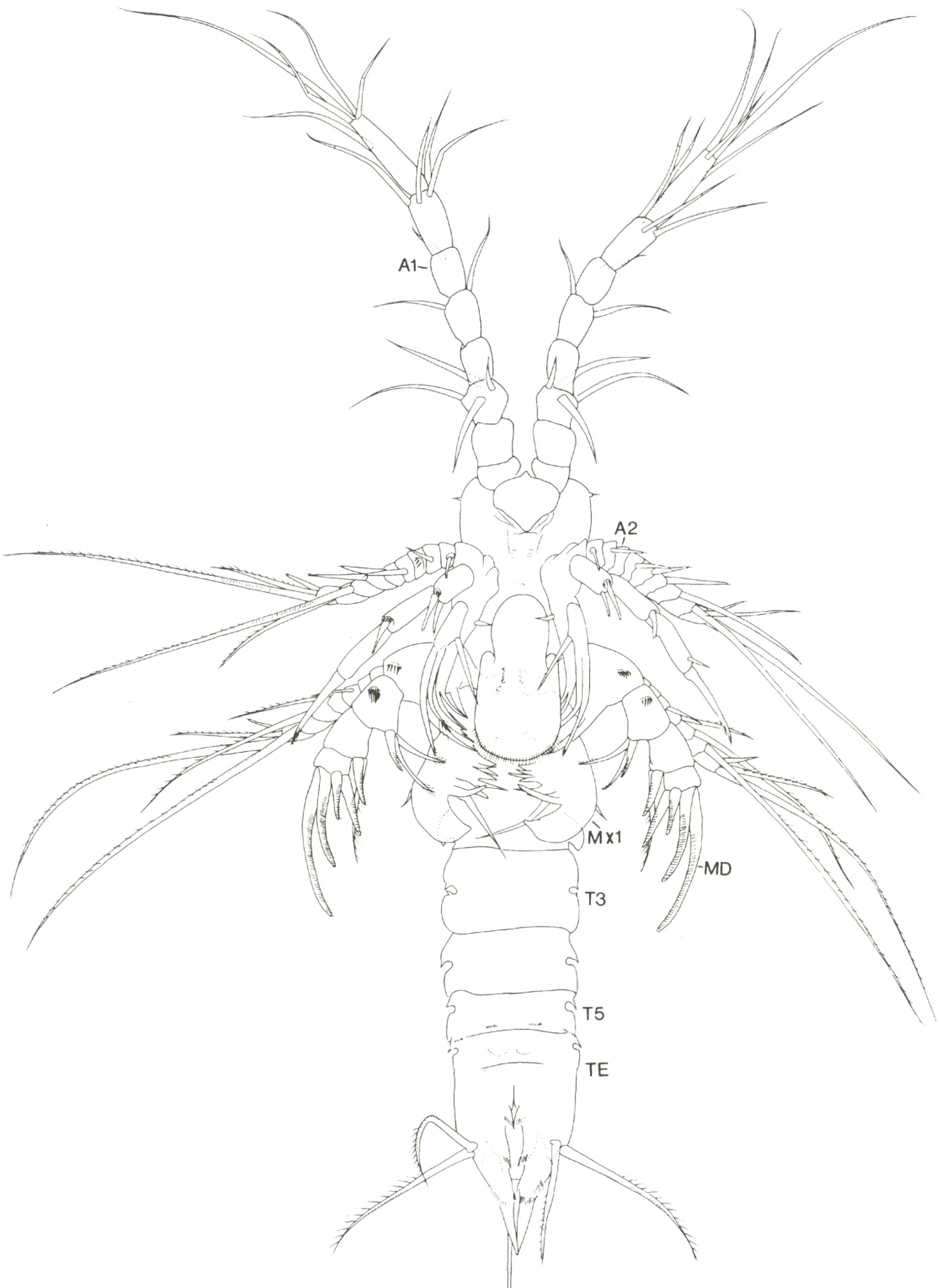

Figure 6. Larva of stage 2, ventral.

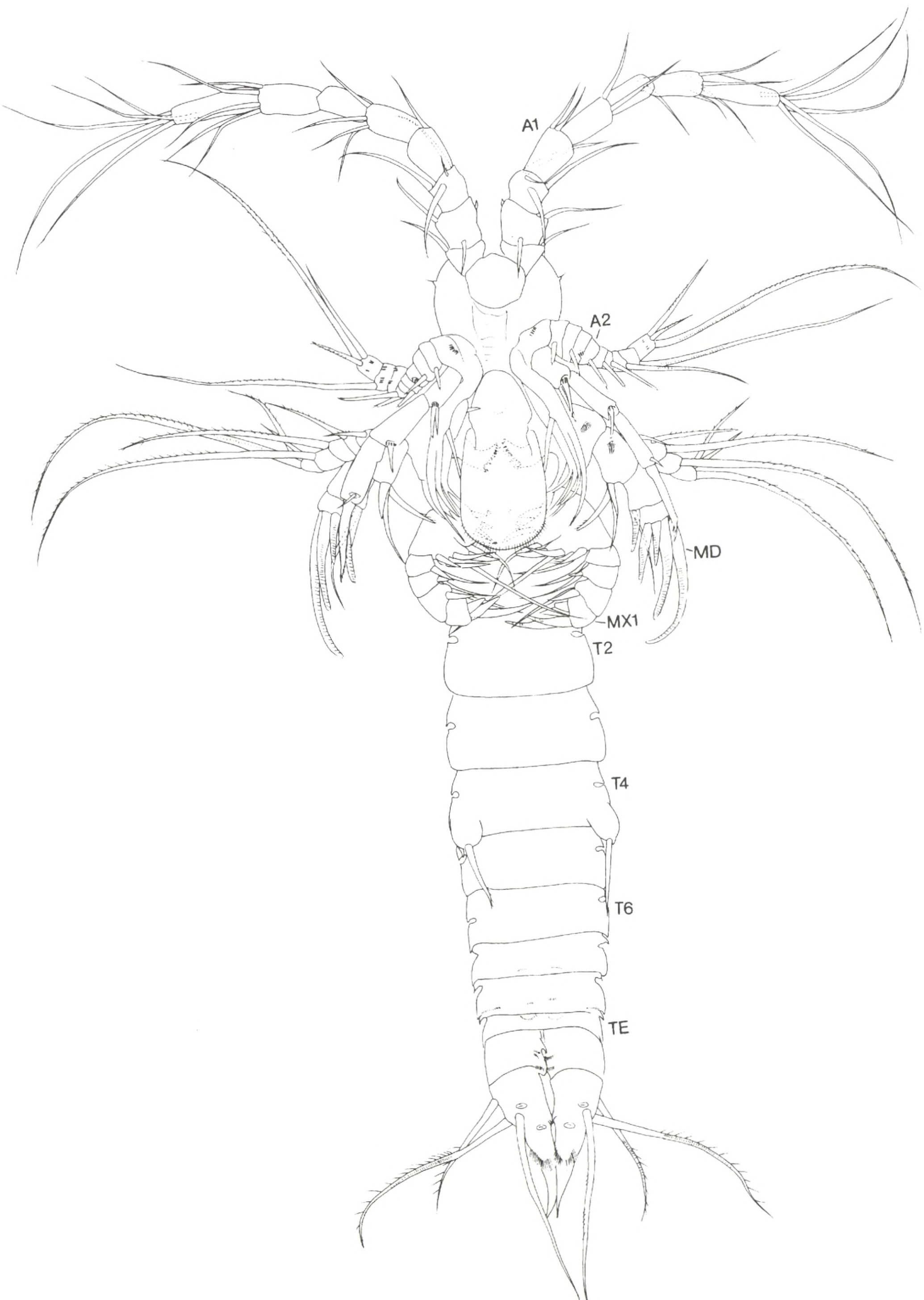

Figure 7. Larva of stage 4, ventral.

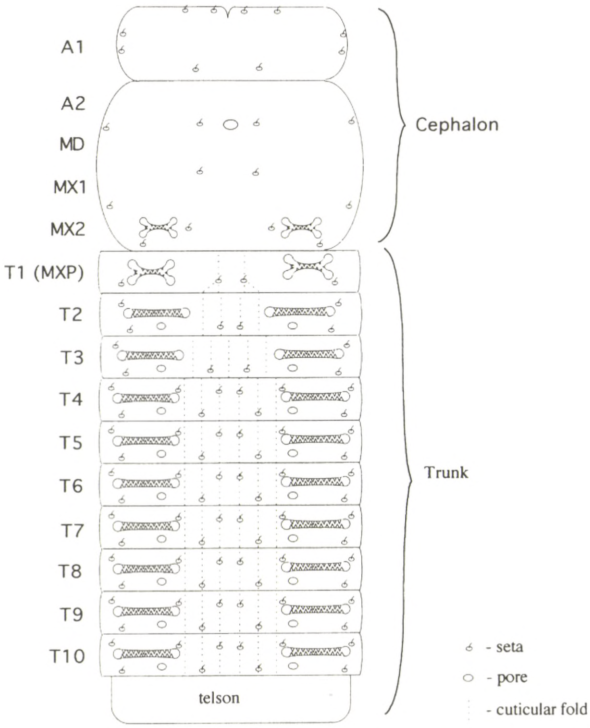

Figure 8. Setae and pores on lateral and dorsal sides of trunk and cephalon.

ped segment) plus the telson (Fig. 6, Plates 24B, 31C-E). In the same stage, the lateral toothed furrows of the future trunk segment 6 are present on the telson, and also the future segment margin is indicated laterally. The same developmental pattern is repeated in stages 4 and 5, only do the stages have eight and nine trunk segments respectively. So, between stages 1 and 4, two segments are added between each stage, while only one segment is added between stages 4 and 5. In stage 5, the full body segmentation of the adult is approached, and only trunk segment 10 is not yet fully separated from the telson. As noted earlier, there are reasons to believe that the development of *D. remanei* is very similar to that of *D. typicus*. The development of the latter is summarised by Hessler & Sanders (1966: fig. 8, lower part).

Interestingly, there is some delay in the posterior elongation of the cephalon relative to the development of the post-cephalic segments. In stage 1 (this aspect is not shown in SEM) and stage 2 (Plate 29A), the segment of maxilla 1 forms the rear of the cephalon. In later stages the cephalon elongates to include maxilla 2 (e.g., stage 5, Plate 28D-F).

Telson and furcal rami – changes in morphology during development (Plate 31)
During development, the telson morphology changes in several ways. As stage 1 and the adult are the two extremes, the comparison will focus on these two stages (compare Plate 31A,B and Plate 21A). In the adult the telson has a longitudinal cuticular bar dorsally extending in the whole length of the telson, posteriorly continuing into an acute process (Plate 21A, E, F). Such a bar is not present in stage 1, where the telson is smooth dorsally (Plate 31A), posteriorly extending into a dorsal supra-anal process, also with an acute process but more slender than in the adult. During development the supra-anal process (homologous to 'dorso-caudal spine' of e.g., *Rehbachiella*, see Walossek, 1993) develops in anterior direction and end up constituting an elongate cuticular bar at the telson.

With respect to the development of the furcal rami some significant changes take place. By using the single long seta present on each furcal ramus in stage 1 as a positional marker during development (marked by 'a' on Plate 31), the various steps in the development can be outlined as follows. In stage 1 the furcal rami are slender, straight with acute tips and with various rows of short and long setules along the length and the articulation with the telson is only weakly indicated (Plate 31A, B). From stage 1 to 2, the articulation between the telson and the furcal rami becomes clearer; an

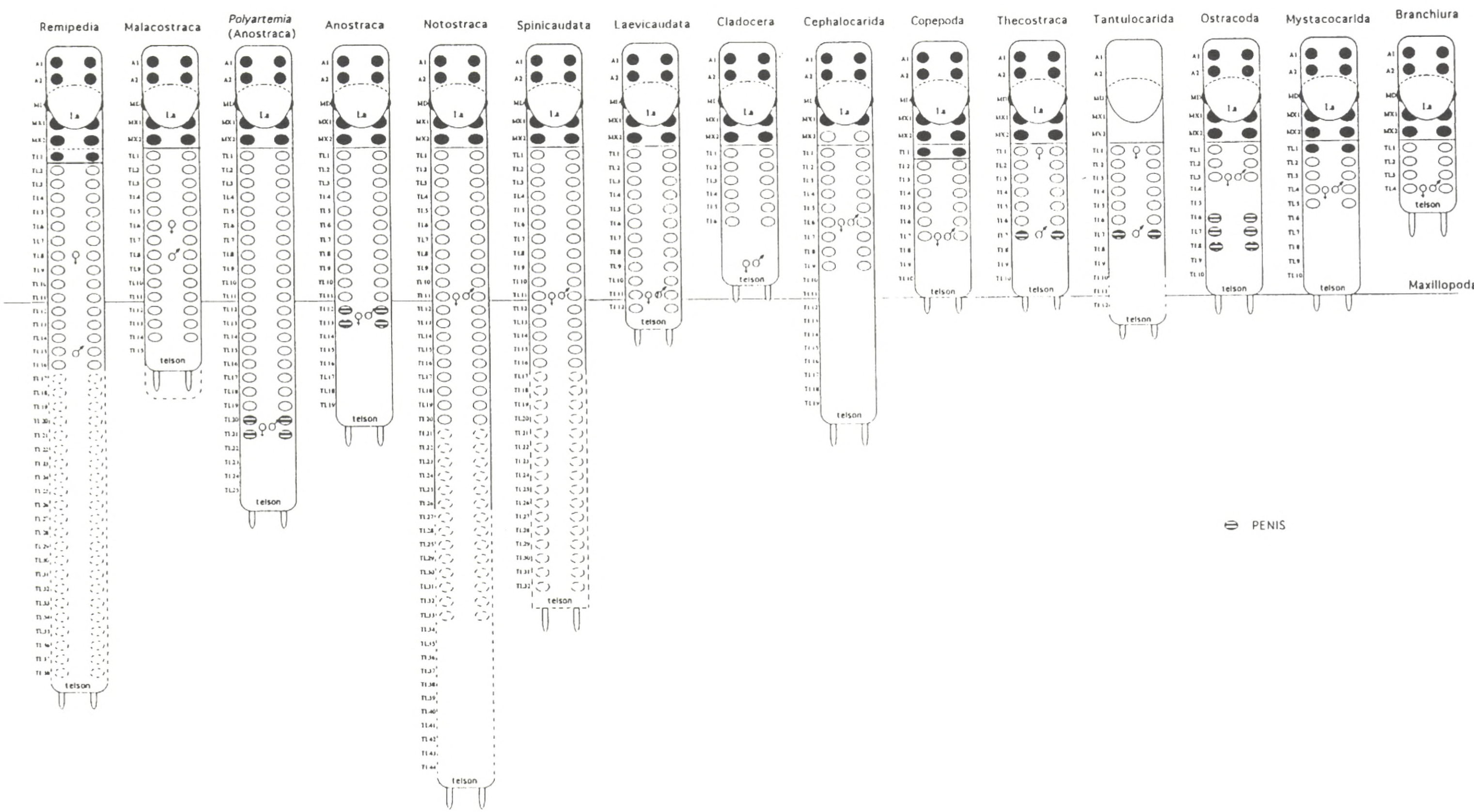

Figure 9. Tagmosis and other patterns within the Recent Crustacea. Included are information about length, tagmosis, position of gonopores and male reproductive organ, fusion of anterior trunk segment to head shield and presence of maxillipeds. For some taxa the variation in length etc. within the taxon is indicated by dashed lines (Remipedia, Notostraca, Spinicaudata, Tantulocarida). The variation within the Anostraca is shown by two examples. The remaining are supposed to represent ancestral body plans.

additional long seta appears laterally close to the original one (which one is the new seta is uncertain; both marked with 'a' on Plate 31) (compare Plates 31A,B and 31C-F); dorsally appears, on each ramus, a small seta with a wide basis (Plate 31D; shown for the adult in Plate 21D); each ramus elongates and the distal half bends dorsally to form claws; the setation on the rami, found in stage 1, disappears from the claws; the tip of the claw becomes hollow (shown for the adult in Plate 21C). From stage 2 to stage 4 (stage 3 not examined in detail), the furcal rami elongate further and an additional long seta appears near the basis of each (present also in stage 3; Hessler & Sanders, 1966). The morphology of the furcal rami in stage 4 approaches that of the adult, except for the addition of some more denticle-scales on the median sides eventually.

In general, the most significant changes with respect to the furcal rami take place between stage 1 and 2 (see above). With respect to the telson (dorsal side), the most significant changes takes place between stage 4 and 5.

Discussion

Larval development of *Derocheilocaris remanei*

Characteristic for all Mystacocarida, where larvae have been examined, is the great similarity between these and the adult; something which is confirmed by this study. This is probably due to the similar lifestyle of the larvae and the adults as components of the interstitial fauna among sand grains. However, some changes do take place during development in *Derocheilocaris remanei*, other than the simple addition of body segments and appendages.

Between stage 1 and 2 significant changes are seen in the morphology of the furcal rami which must have an important functional impact (compare Plate 31A, B and Plate 31C, D). The rami elongate and the tips bend, loose the setation, become hollow and more claw-like. An additional pair of long lateral setae, closely placed to the ones already present, and a pair of small dorsal setae, also appears. As a consequense of the more claw-like furcal rami, it appears likely that stage 2 is better equipped for the 'turning-escape reaction' described for the adult of *Derocheilocaris typicus* by Lombardi & Ruppert (1982), than is stage 1. The rami are mentioned by Lombardi & Ruppert (1982) to be important *points d'appuis* during the turning and escape movement in which the trunk curls ventrally and anteriorly until the telson and furca are approximately at the level of the head appendages. The dorsal trunk is then, using the furcal claws as *points d'appui*, pressed against the substrate which causes the head to roll around so that the animal makes a 180° turning. One can speculate that a 'turning-escape reaction' may not be necessary in the short bodied stage 1 in which the furcal claws for that reason are not yet developed.

Another significant change in morphology takes place between larval stage 6 and the adult (or 'juvenile', after Hessler & Sanders 1966) where the naupliar processes are lost from antennae 2 and the mandibles.

Phylogenetic position of the Mystacocarida – summary of earlier ideas

No consensus has been reached with regard to the phylogenetic position of the Mystacocarida within the Crustacea. They have generally been accepted as constituting a separate crustacean taxon, sometimes at ordinal level, sometimes at class level, depending on the preferred crustacean classification. Only Armstrong (1949) believed differently, as he stated that *Derocheilocaris* should be considered as belonging to a new order of the Copepoda which he termed 'Derocheilocarida'. Several authors have advocated a position within the weakly supported class (or super-class) Maxillopoda (Dahl 1956, Grygier 1983, Newman 1983, Schram 1986, Boxshall & Huys 1989, Walossek & Müller 1998), most often close to the Copepoda. Dahl (1956) depicted the Mystacocarida as sister group to the Copepoda/Archicopepoda/Branchiura clade. Grygier (1983) suggested, based on spermatological evidence, that the Mystacocarida possibly are more closely related to the Branchiura/Pentastomida and the thecostracan taxa than to any other maxillopodan taxa, but also stated that the Mystacocarida probably are the weakest component of the Maxillopoda. Newman (1983) suggested a precaridoid malacostracan origin for the Maxillopoda (and thereby also for the Mystacocarida). Schram (1986) suggests the Mystacocarida and Ostracoda as sister groups based on a similar position of the gonopores (4th somite, not specified on the cladogram of Schram but mentioned in his text). Boxshall & Huys (1989) suggest a sistergroup relationship to the Copepoda. Walossek & Müller (1998) propose a monophyletic group consisting of the Mystacocarida and Copepoda and the 'Orsten' fossil *Skara* (unresolved trichotomy). Other analyses not supporting the 'Maxillopoda' include those of Wilson (1992) who, depending on the rooting of the obtained cladogram, shows the Mystacocarida as either sister group to the Ostracoda and Copepoda or as sister group to the Copepoda alone. Boxshall & Defaye (1996) suggests a close relationship between the Mystacocarida and Remipedia, based on a similar, uniramous first maxilla with a 3-segmented protopodite and a 4-segmented endopod. Wills (1997) shows *Derocheilocaris* as sister group to *Calanus* (Copepoda), *Lepas* (Cirripedia) and *Argulus* (Branchiura) in the tree on which they base most of their discussion (their fig. 2.1).

Comparison of *Derocheilocaris* (Mystacocarida) with other crustacean taxa, mainly with respect to tagmosis patterns

General

As seen from the previous section, the precise phylogenetic position of the Mystacocarida has been difficult to find. This is partly due to the peculiar morphology of the taxon with its characteristic combination of many unique characters and many general crustacean characters, and partly because of the uncertainty about crustacean phylogeny in general. Among the unique characters can be mentioned 1) the characteristic serrated lateral furrows on the trunk segments and on the posterior part of the cephalon (see Plate 6A), 2) the subdivided head shield into a anterior and a posterior part (see Plate 4A, possibly a crustacean plesiomorphy), 3) the 'comb'-like tip of the endopod of antenna 2 (see Plate 11H, I), 4) the lobate trunk limbs (see Plates 19, 20). Some of the characters that the Mystacocarida share with subgroups of the Crustacea will be mentioned in the following sections.

Cephalocarida Sanders, 1955

There are both similarities and differences between the Mystacocarida and Cephalocarida. Some of of the similarities can easily be dismissed as plesiomorphies as they are also found in a large assemblage of other Recent or fossil crustaceans. This is the case for the many-segmented exopods of antenna 2 and the mandible, and the presence of a 'naupliar process' of the antenna 2 in a large part of the larval sequence.

One similarity, however, is quite remarkable. The coxal process of the mandible in the adult of *Derocheilocaris remanei* (Plates 7A, C, D, 12A, B) appears to be very similar to that of certain larvae of *Hutchinsoniella macracantha* Sanders, 1955 (Sanders 1963, fig. 16). In both taxa the coxal process is boot-shaped with a large spine posteriorly and with a row of spines anteriorly, while in the adult of *Hutchinsoniella* it is different. SEM of any cephalocarids would facilitate comparison, but unfortunately none are available.

Apart from that, there are not many similarities. The segmentation and tagmosis patterns of the body in the adults are very different. *Derocheilocaris* has 10 trunk segments (telson exclusive), while *Hutchinsoniella* have 19 (excluding the telson). Only five trunk segments are limb-bearing in the mystacocarids, while there is are nine limb-bearing trunk segments in the Cephalocarida (egg-limbs included). In *Derocheilocaris* four pairs of trunk limbs (t2-t5) are reduced to unsegmented lobes which prevents comparison with *Hutchinsoniella*.

Skaracarida Müller & Walossek, 1985

Skara Müller, 1983 and *Derocheilocaris* are in the general appearance quite similar to each other. Both are long slender animals, *Skara* with 11 postcephalic body segments, *Derocheilocaris* with 10 (telson excluded in both). Both have the limbs concentrated anteriorly in the body. *Skara* has six pairs of limbs, five cephalic and one pair of maxillipeds, the remaining trunk segments are apodous. *Derocheilocaris* has 10 pairs of limbs, but only the six anterior pairs – the cephalic limbs and the maxilliped (as in *Skara*) – are well-developed, the remaining 4 pairs being small, unsegmented lobes (t2-t5). All limbs in *Skara*, except antennae 1, are biramous, while in *Derocheilocaris* maxillae 1 and 2 are uniramous. In both taxa, the maxilliped segment is not fused to the cephalon, and has a different morphology compared to the more posterior trunk segments. The ventral side of trunk segment 2 is also modified in both taxa. In *Skara* there is a pliable membrane (Müller & Walossek, 1985, p. 9), in *Derocheilocaris* the surface is more smooth than the succeeding segments. Walossek & Müller (1998) suggested, together with other characters, the achievement of a cephalo-thoracic feeding apparatus as a synapomorphy for the Mystacocarida, Skaracarida and Copepoda.

Branchiopoda Latreille, 1817

There for the most part no similarities to the Branchiopoda apart from general crustacean features. One major difference is the possession of thoracic feeding appendages in the Branchiopoda, which are absent in *Derocheilocaris*. As such, the Mystacocarida and the Branchiopoda represent two opposite extremes.

Remipedia Yager, 1981

Derocheilocaris is also very different from the Remipedia. With respect to the distribution of limbs along the body, the two taxa represent two different extremes as all remipedes have limbs along the whole body, while these are concentrated in the anterior end of *Derocheilocaris*. Boxshall & Defaye (1996) suggest a close relationship between the Mystacocarida and the Remipedia based on a similar possession of a maxilla 1 with 7 segments.

Copepoda Milne-Edwards, 1840

Derocheilocaris is similar to the Copepoda with respects to the number of body segments, i.e., 10 excluding the telson (as proposed for the 'ancestral copepod' by Boxshall *et al.* 1984). In the 'ancestral copepod' the first trunk segment is fused to the cephalon, which is not the case in *Derocheilocaris*. As in *Derocheilocaris* the limbs of the first trunk segment are cephalised and form maxillipeds; they are uniramous in the Copepoda while they are biramous in *Derocheilocaris*. Another similarity is the uniramous maxilla 2.

Other 'maxillopodans'

With respect to body length or tagmatisation *Derocheilocaris* is more different from the remaining 'maxillopods' than they are from the Copepoda. It should be mentioned that the Thecostraca (and most of the Tantulocarida) have the same number of segments in the trunk as the Mystacocarida (10, excluding the telson). This has also been demonstrated for at least some ostracods (Schultz 1976), while punciid ostracods, despite their primitive appearance, seem to be one segment shorter in total (counting based on fig. 3 of Swanson 1990). In the Branchiura and the Mystacocarida the gonopores are associated with the fourth trunk segment. However, as this is the most posterior trunk segment in branchiurans, only limited attention should probably be paid to this similarity. A more posteriorly positioned gonopore in a longer-bodied ancestor to the Recent branchiurans would most likely end up in this position.

Conclusion on phylogenetic position of the Mystacocarida

The external morphology of the Mystacocarida is a mixture of characters unique to the taxon and characters found in a very wide spectrum of crustaceans.

Some similarities in number of trunk segments and cephalisation of trunk limbs are found between *Derocheilocaris* and other 'maxillopods' like the Copepoda, Thecostraca and the Upper Cambrian *Skara*. Indeed, the closest relatives to the Mystacocarida may be the Skaracarida and the Copepoda as suggested by Boxshall & Huys (1989) and Walossek & Müller (1998).

General note on segmentation and tagmatisation within Crustacea

Walossek & Müller (1997) hypothesised that the tagmatised limb-bearing section in the Malacostraca (thorax + pleon) is homologous to the un-tagmatised limb-bearing section in other crustaceans. Evidence provided for *Nebalia* (Malacostraca, Leptostraca) (Olesen & Walossek 2000) illustrates that there are deep-founded similarities in the limb development in the thorax and pleon tagma in malacostracans. It is therefore possible, as do Walossek & Müller(1997), to homologise the malacostracan pleon with a sub-part of the limb-bearing tagma seen in other Crustacea, and not with the limb-less abdomen of these. However, the suggested homologisation, between the 14 limb bearing trunk segments in the Malacostraca and, for instance, the limb bearing tagma in Anostraca, Cephalocarida or Copepoda, implies either the evolutionary loss or gain (depending on what is plesiomorphous) of trunk segments *within* the trunk, and not only at the end of the body where ontogenetic growth takes place. This raises an important question. Are trunk segments homologous in a strict sense, that is for instance, is trunk segment 14 in the Malacostraca homologous to trunk segment 14 in the Cephalocarida? (depicted in Fig. 9), or is simple counting a completely unreliable homologisation tool in this respect? The answer probably is that sometimes simple counting *is* reliable, and sometimes not, but that we have yet to identify when simple counting is insufficient. Fig. 9 and Table 1 summarise various information related to segmentation and tagmatisation of Crustacea, such as total body length, limb-bearing segments, position of gonopores, presence of maxillipeds, etc. Despite the overall large variation, tagmosis patterns have traditionally played an important role as a key character for the Malacostraca, where a very constant tagmosis pattern is seen, in addition to an almost unvariable position of the gonopores. Attention has also been paid to tagmosis patterns, gonopore position and total body length in establishing, supporting or discussing the 'Maxillopoda' concept (Dahl, 1956; Grygier, 1983; Boxshall, 1992; Walossek & Müller, 1998). Many of the taxa included in the 'Maxillopoda' – Copepoda, Thecostraca, Tantulocarida, Ostracoda, Mystacocarida – share the same number of trunk segments (10, excluding the telson),

Additional information on segmentation and tagmosis with a possible phylogenetic value, is the same position of gonopores (trunk segment 11) in some of the branchiopod taxa, the Notostraca, Spinicaudata and Laevicaudata. Also the Mystacocarida and Branchiura have a similar position of the gonopores (trunk segment 4, see above), as do the Thecostraca and Tantulocarida (female gonopore on segment 1, male on segment 7). Other segmental information of possible value is the possession of maxillipeds. Outside the Malacostraca, maxillipeds are found only in three Recent crustacean taxa, Remipedia, Copepoda and Mystacocarida, and in one fossil taxon, Skaracarida. Yet another possible phylogenetically valuable character is the fusion of the anterior trunk segments to the cephalon. Outside the Malacostraca, this is seen only in the Copepoda and Remipedia.

From a morphological point of view, it appears to be the simplest starting point to assume that the crustacean trunk segments are homologous between taxa in a strict sense (that is, simple counting can be used as a homologisation tool). Further insights from work with expression zones of various segmentation genes within the Crustacea may in the future offer a different conclusion (see review by Zrzavy &

	Postmaxillary segments (telson excluded)	**Limb-bearing postmaxillary segments**	**Position of genital openings**
Remipedia	15-37 (Yager, 1991).	All (except telson).	Hermaphrodite - Paired female genital opening on appendages of trunk segment 8 - Paired male openings on appendages of trunk segment 15 (e.g., Itô & Schram, 1988; Felgenhauer *et al.*, 1992).
Anostraca	19 or 25 (*Polyartemia*, male) (Sars, 1896).	13 or 21 (*Polyartemia*, male) (genital segments incl.) (Sars, 1896).	Female genital openings unpaired and open in ventral brood chamber on segment 12 or 13 (Calman, 1909), or on segment 20 or 21 (*Polyartemia*). Paired male genital openings situated distally on the paired penis (at least in *Branchinecta paludosa* after Sars, 1896).
Notostraca	32-44 in *Triops*, 26-34 in *Lepidurus* (Longhurst, 1955).	Variable. Anterior 11 segments bear one pair of limbs each (often termed 'thoracic limbs'). The following limb bearing segments bear 2-6 limbs each. In *Lepidurus* this is approximately 10-13 segments, in *Triops* it is approximately 16-18. Information form Linder (1952), Longhurst (1955).	Female genital opening at the base of appendages on trunk segment 11 (*Lepidurus arcticus*, information from Sars, 1896). This is apparently also the position for the male genital opening.
Spinicaudata	15-31 (Martin, 1992).	All (except telson).	Paired female/male genital openings at the base of appendages of trunk segment 11 (Martin, 1992)
Laevicaudata	10 (male) or 12 (female) (Martin, 1992).	All (except telson).	Paired female genital openings on the basal part of appendages on trunk segment 11 (Linder, 1945). Paired male genital openings openings on the telson on each side of the anal opening (Linder, 1945).
Cladocera	4 (Onychopoda)-6 (Ctenopoda) or 9 (Haplopoda).	4-6	Female/male paired genital openings dorsolateral anteriorly at trunk segment 9 (apodous segment 3) in Haplopoda (Weismann, 1874). In other cladocerans the female gonopores open dorsolateral on a short apodous section (Weismann, 1874), the male gonopores open lateral or ventral, and are sometimes unpaired (Calman, 1909).
Cephalocarida	19 (e.g., Sanders, 1963; Hessler & Elofsson, 1992).	9	Hermaphrodites - Paired, common female/male genital openings on appendages of trunk segment 6 (Hessler *et al.*, 1995).
Copepoda	10 (in 'ancestral copepod', according to Boxshall *et al.*, 1984).	7 (in 'ancestral copepod', according to Boxshall *et al.*, 1984).	Female/male paired genital openings on ventral surface of trunk segment 7 (in 'ancestral copepod' by Boxshall *et al.* (1984).

	Postmaxillary segments (telson excluded)	**Limb-bearing postmaxillary segments**	**Position of genital openings**
Thecostraca	10	7 pair of legs as and unpaired penis (see Boxshall & Huys, 1989)	Female opening at trunk segment 1. Male at trunk segment 7.
Tantulocarida	10-12 (Boxshall & Huys, 1989).	7 (Boxshall & Huys, 1989). Seventh pair of legs as and unpaired penis (see Boxshall & Huys, 1989)	Unpaired medial female genital opening ventrally at the cephalothorax at about the level of the incorporated first thoracic somite (Huys *et al.*, 1993).
Ostracoda	10 (or less). *Cytherella pori* Lerner-Seggev, 1964, has 10 postmax. segments (see Schultz, 1976).	Penis in *Cythorella pori* Lerner-Seggev, 1964, is derived from sixth trunk somite (Schultz, 1976), but receives support from seventh and eighth trunk somite (Grygier, 1984).	?
Mystacocarida	10	5	Paired female/male genital openings on appendages of trunk segment 4.
Branchiura	4	4	Paired female genital openings on ventral side of trunk segment 4 (Calman, 1909). Unpaired median male genital opening on ventral side of segment 4 (Calman, 1909).
Malacostraca	14 (Eumalacostraca) or 15 (Leptostraca).	14	Paired female genital openings on base of appendages on trunk segment 6. Paired male genital openings on base of trunk appendages of trunk segment 8.

Table 1. Sources of information for tagmosis and segmentation patterns showed in Fig. 9.

Stys, 1997). Detailed knowledge about homology zones between taxa (if simple counting in some cases is unreliable) is a pivotal basis for the construction of reliable character matrices for the Crustacea, if information about tagmatisation, gonopore position, limb morphology etc. are to be included.

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Litterature

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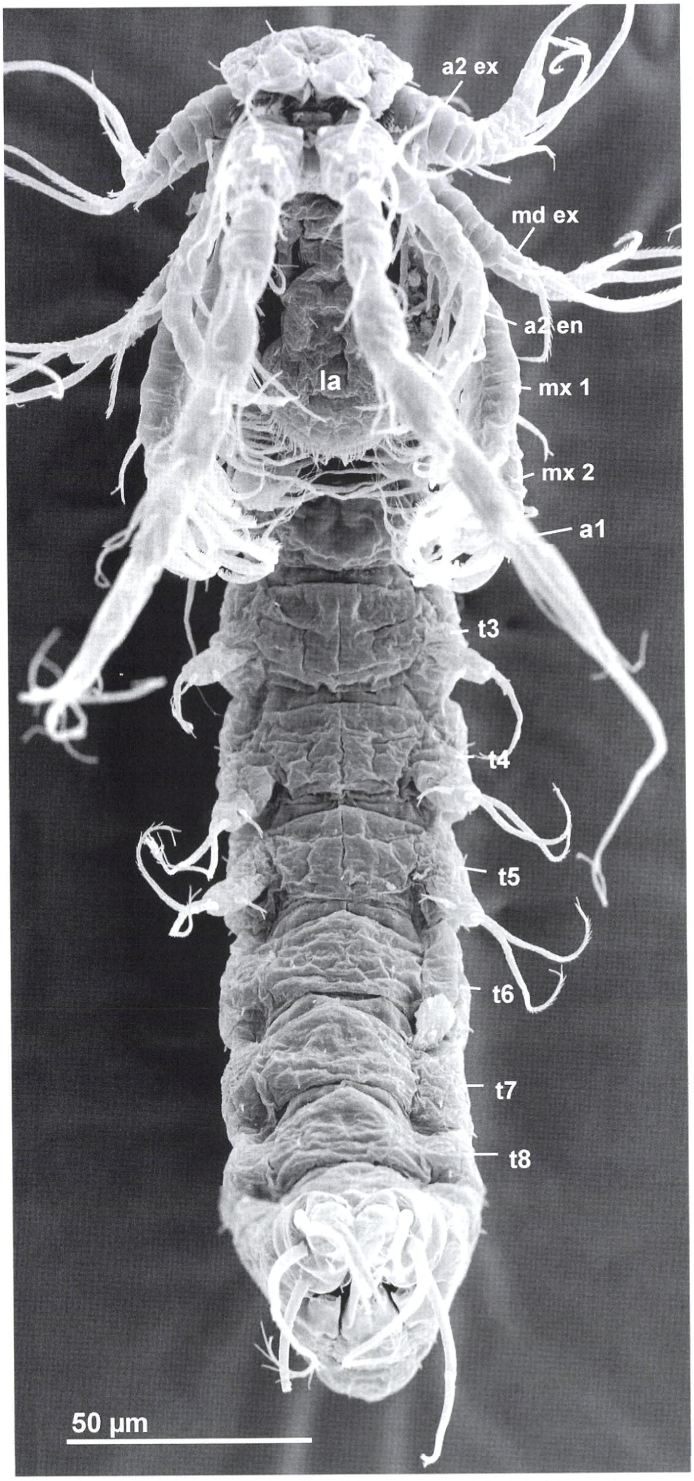


Plate 1. Adult female, ventral.

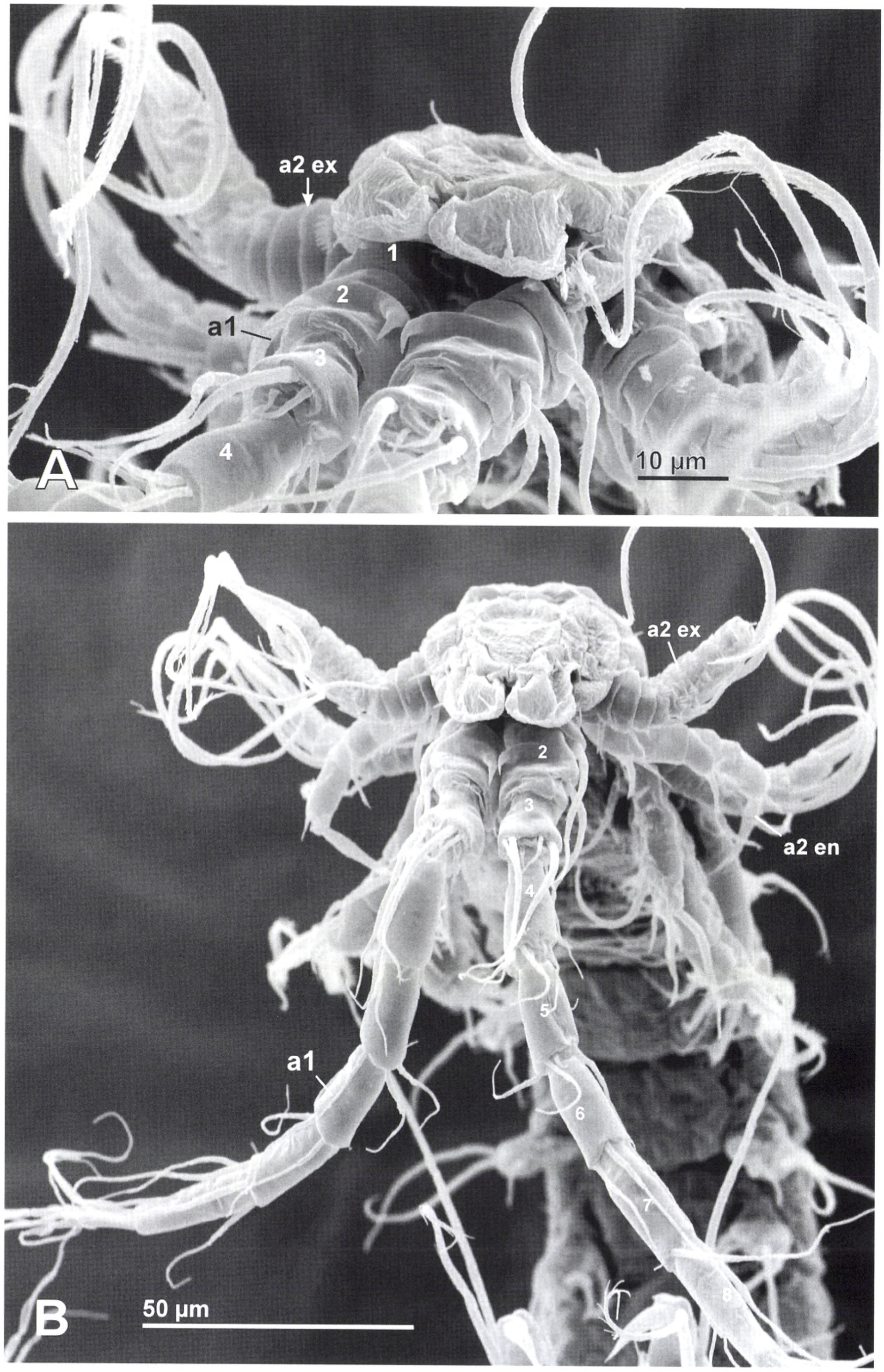


Plate 2. Adult. A. Frontal view. – B. Adult, frontal/ventral view

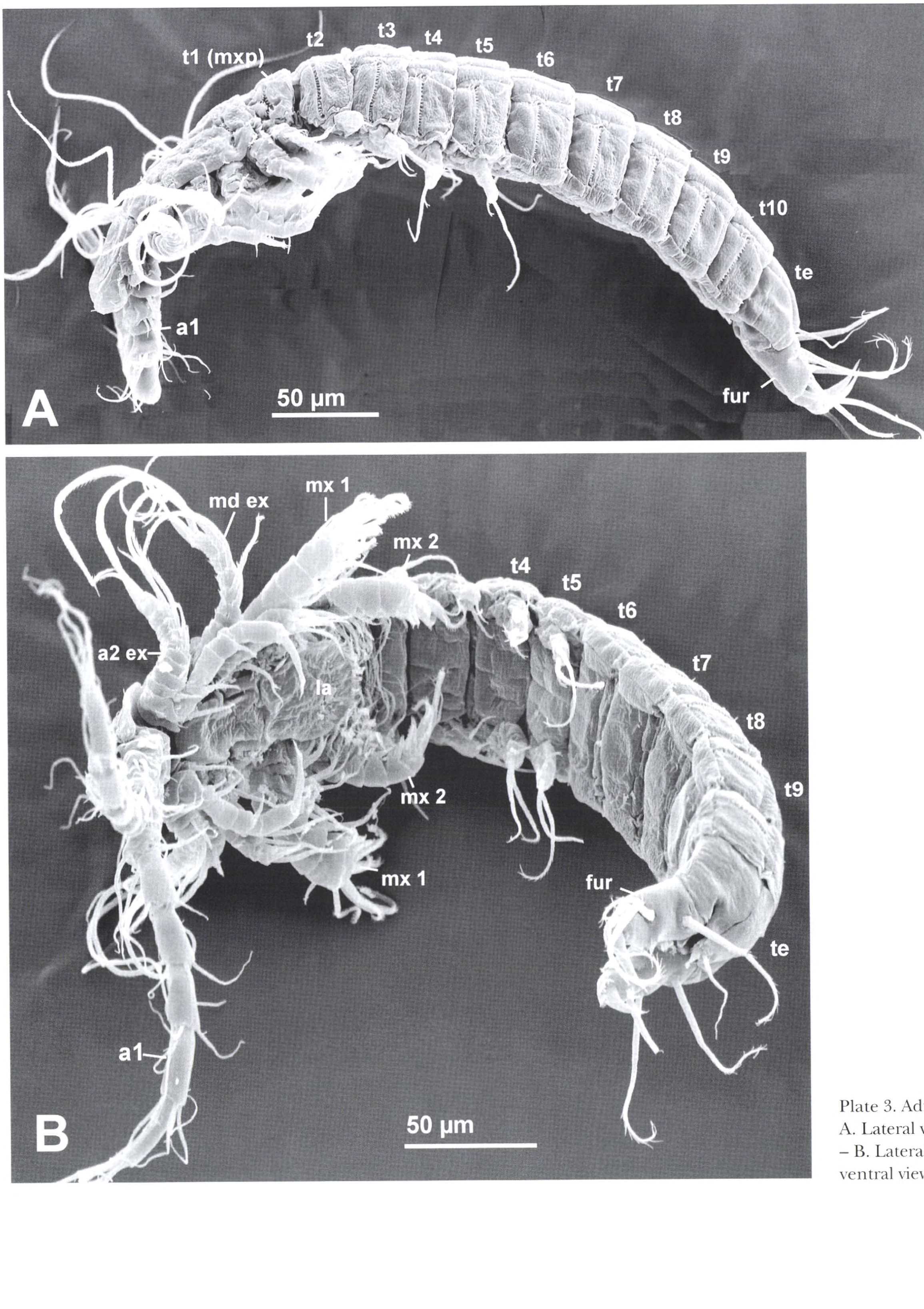


Plate 3. Adult. A. Lateral view – B. Lateral/ ventral view.

Plate 4. Adult, dorsal. A. Cephalon and trunk segments 1 to 6. – B. Cephalon (in part) and trunk segments 1 to 9.

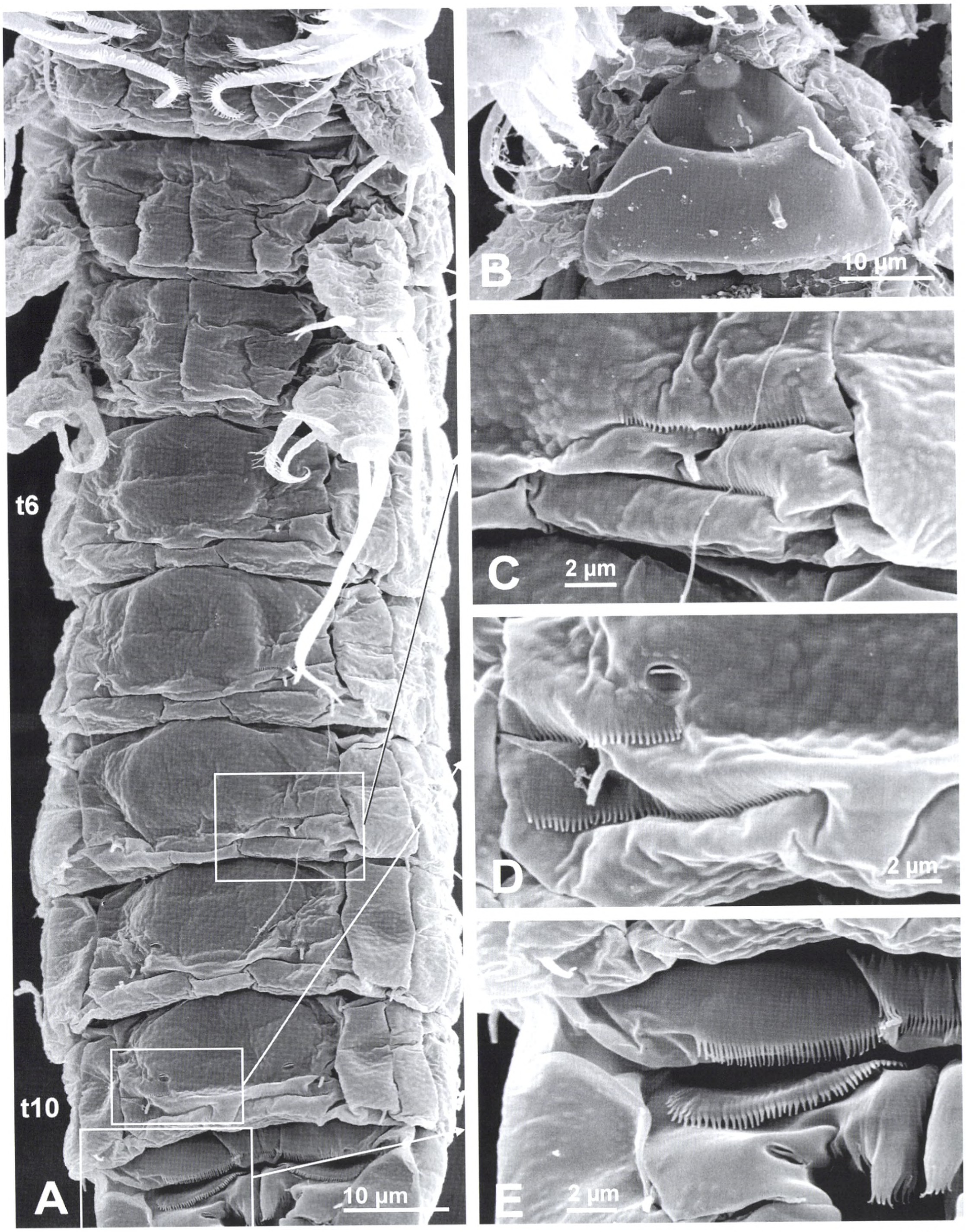


Plate 5. Adult, ventral. A. Male, trunk segments 3-10 and telson. – B. Trunk segment 2. – C. Trunk segment 8, left side. – D. Trunk segment 10, right side. – E. Telson, right side.

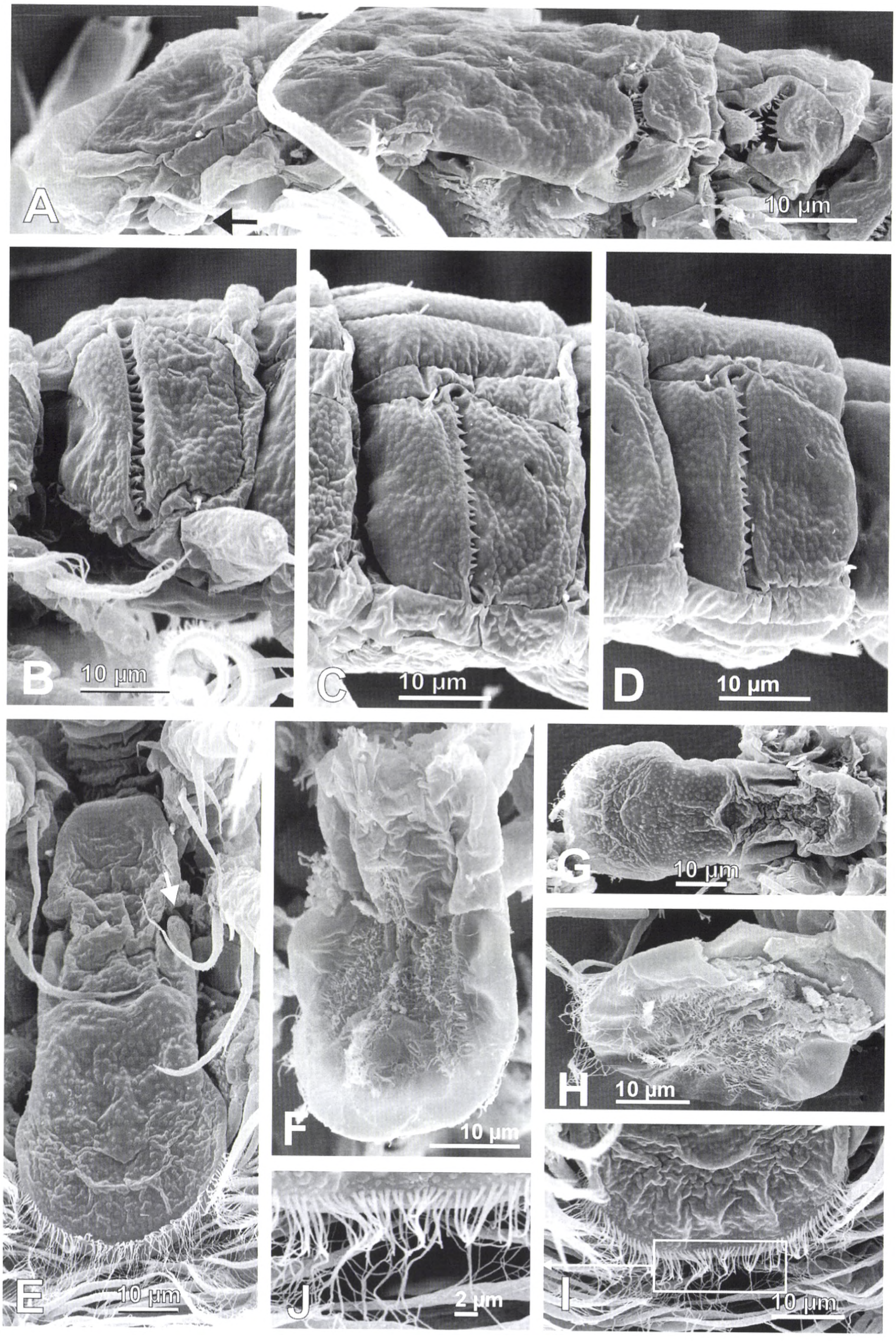


Plate 6. Adult, lateral view (A-D) and labrum of adult (E-J). A. Cephalon and trunk segment 1 (maxilliped segment). Arrow indicates spine bearing, anterior part of lateral cephalic lobe. – B. Segment 2. – C. Segment 6. – D. Segment 10. E. Outer side of labrum, arrow indicates lateral 'shoulder' of labrum. – F. Inner side of labrum. – G. Outer side of labrum. – H. Inner side of labrum. – I. Distal margin of labrum with setae. – J. Close-up of E.

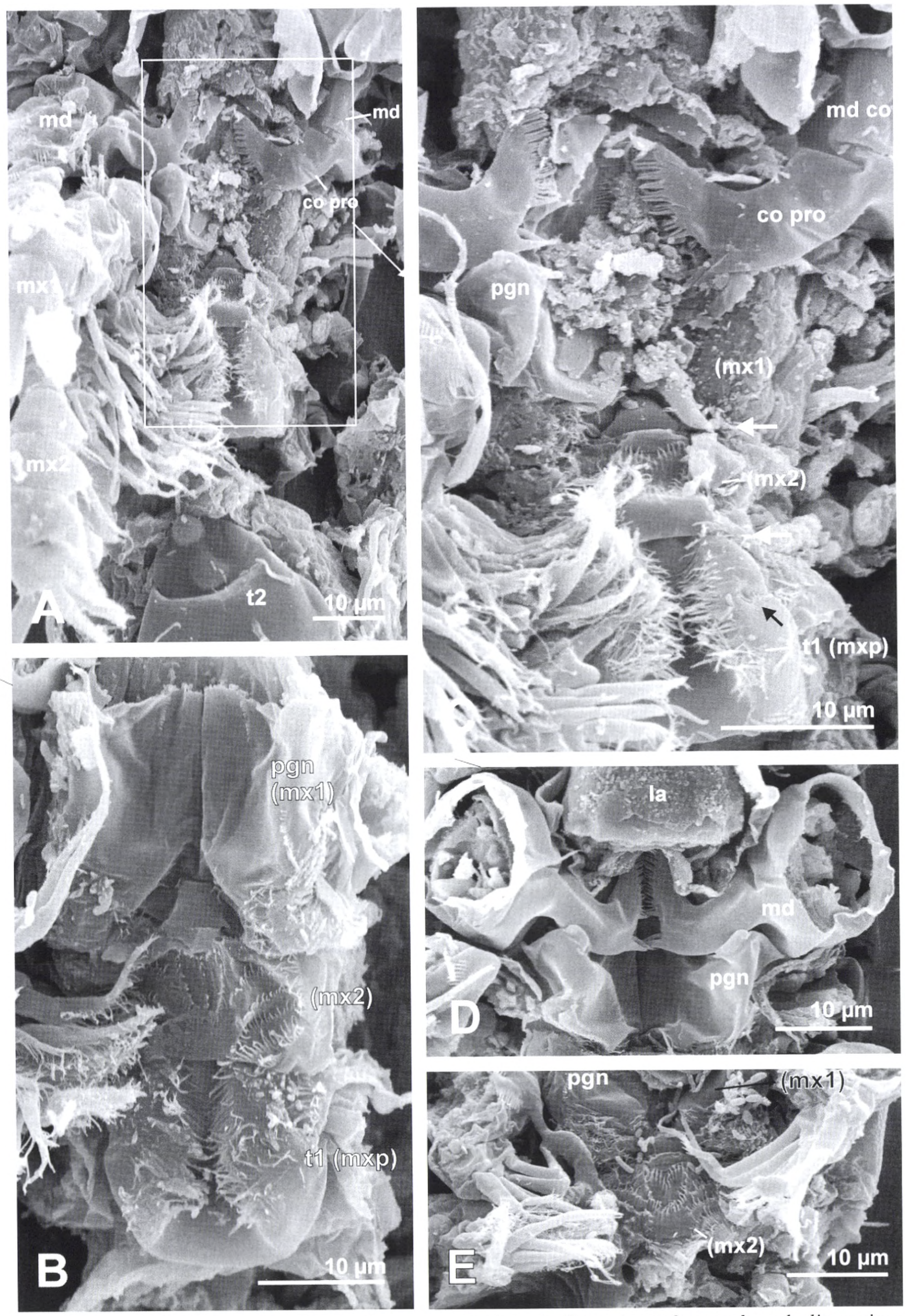


Plate 7. Ventral side of cephalon, segmentation and ornamentation. A. Overview of ventral cephalic region and two anteriormost trunk segments. – B. Segments of maxillae 1 and 2 and maxillipeds (trunk segment 1) – C. Close-up of A, arrows indicate possible cephalic segmentation borders. – D. Segments of mandible and maxilla 1; basis and rami of mandible broken off. – E. Segments of maxilla 1 (in part) and maxilla 2.

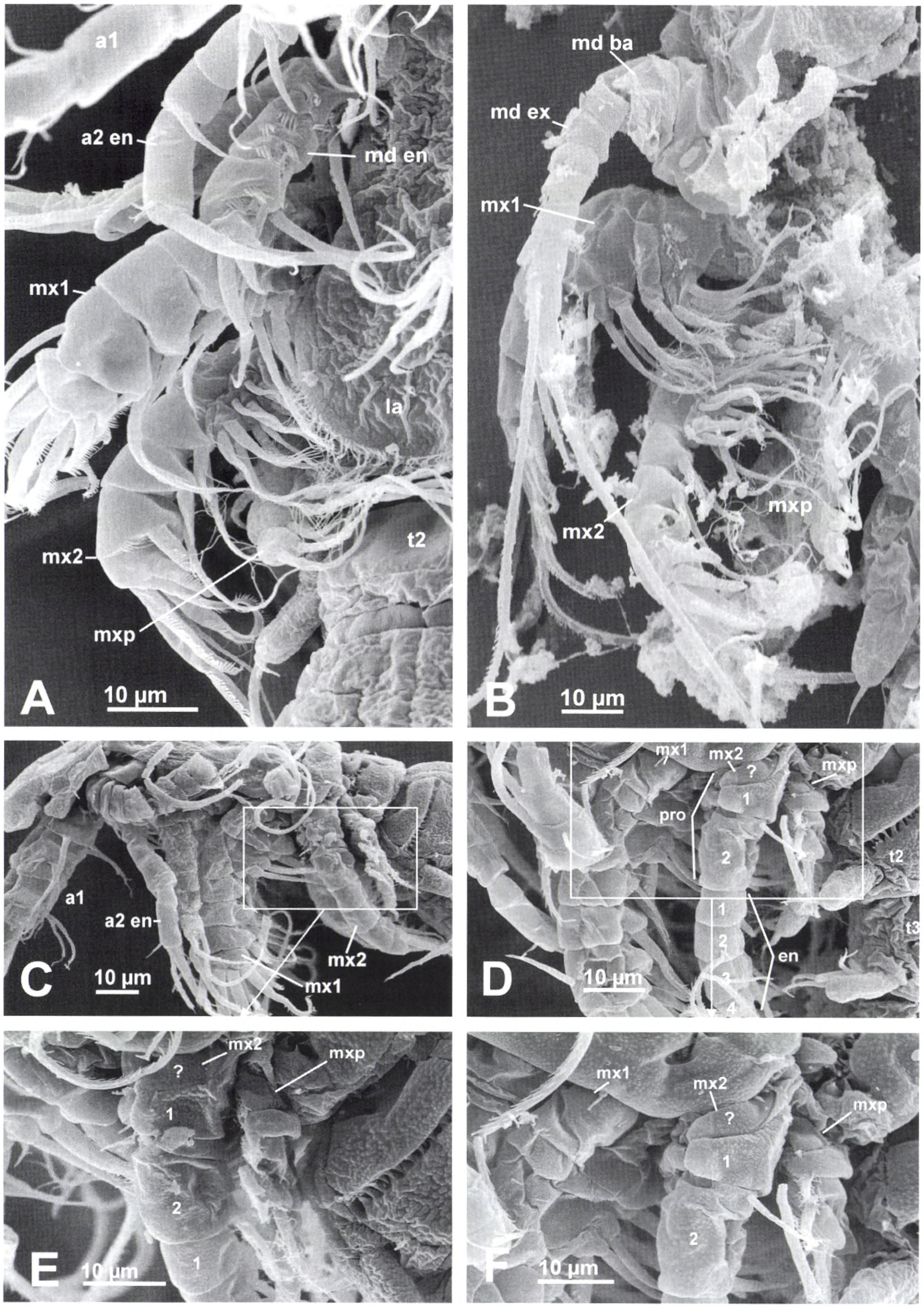


Plate 8. Cephalic appendages. A. Ventral view of antenna 2 (in part), mandible, maxilla 1 and 2, maxilliped (trunk limb 1), trunk limb 2; all from right side. – B. Ventral view of mandible (endopod missing), maxilla 1 and 2, maxilliped and trunk limb 2 after labrum has been removed; all from right side. – C. Lateral view of antenna 1 (in part), antenna 2, mandible, maxilla 1 and 2, maxilliped and trunk limb 2; all left side. – D. Lateral view of maxillae 1 and 2, maxilliped (t1) and trunk limb 2 and 3. – E. Close-up of C. – F. Close-up of D.

Plate 9. Antenna 1. A. Lateral view. – B. Dorsal view. – C. Ventral view.

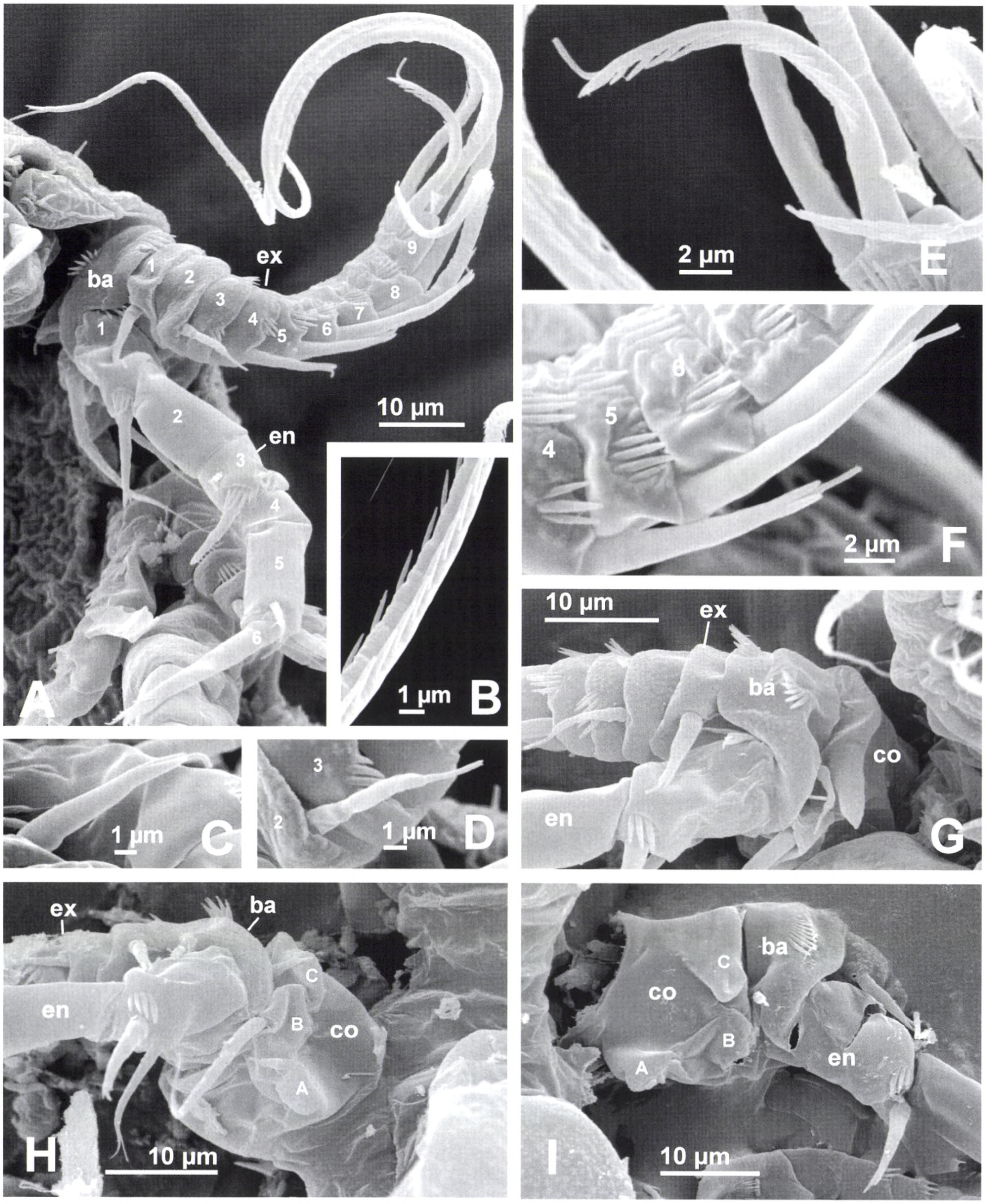


Plate 10. Antenna 2. A. A2, left. – B. Seta from distal exopod segment. – C. Seta from exopod segment 1. – D. Seta from exopod segment 2. – E. Seta from distal exopod segment. – F. Setae from exopod segments 4 and 5. – G. Coxa, basis and proximal rami segments of right A2; inner view. – H. Coxa, basis and proximal rami segments of right A2; inner/posterior view. – I. Coxa, basis and proximal endopod segments of left A2, setae on coxa lost; inner view. Three cuticular processes on innerside of coxa marked by 'A'-'C'.

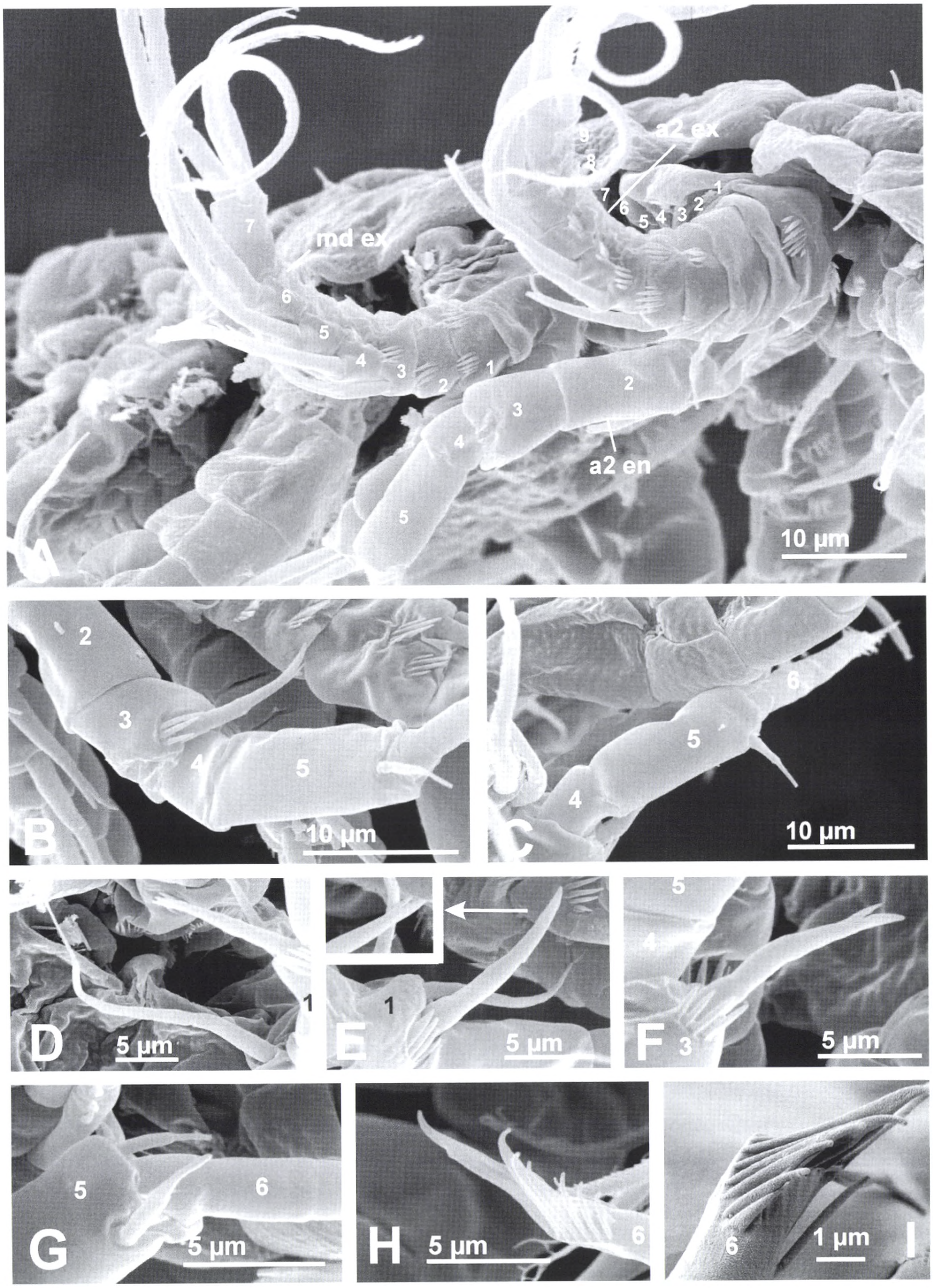


Plate 11. Antenna 2. A. A2 and MD (in part), right. – B. Endopod. – C. Endopod. – D. Seta on coxa and setae on endopod segment 1. – E. Setae on endopod segment 1; insertion is the tip of the seta seen from another angle. – F. Seta on endopod segment 3. – G. Setae on endopod segment 5. – H. Tip of segment 6. – I. Tip of segment 6

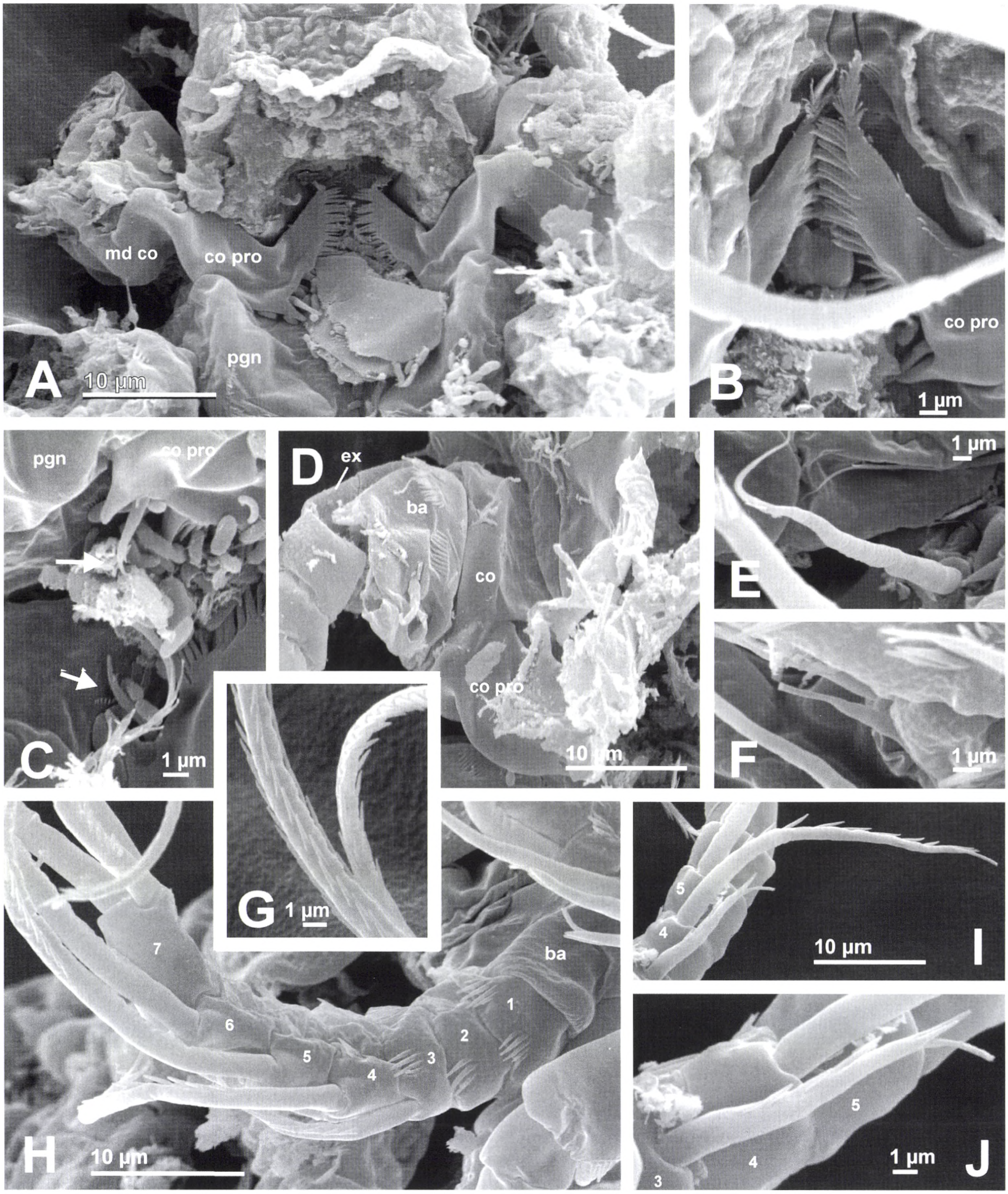


Plate 12. Mandible, coxa, basis and exopod. A. Mandibular coxae (basis and rami broken off) and paragnaths; labrum removed. – B. Tips of mandibular coxae. – C. Tips of mandibular coxae, posterior parts; arrows indicate small bifurcate setae. – D. Coxa and basis, inner view, right side. – E. Seta on basis. F. Seta on basis. – G. Setae on distal exopod segment. – H. Exopod, right. – I. Setae on exopod segment 3 and 4. – J. Seta on exopod segment 3.

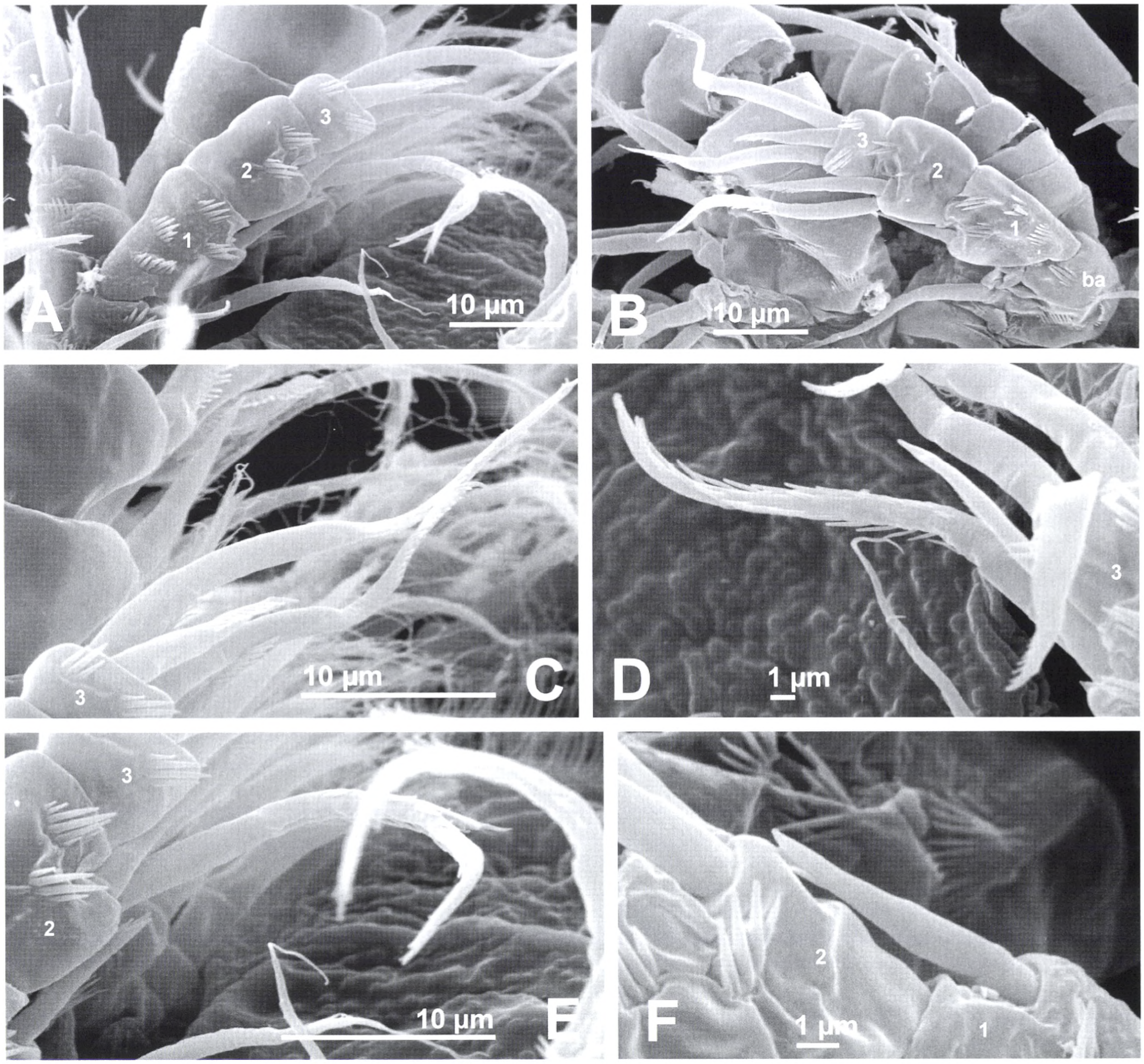


Plate 13. Mandible, endopod. A. Endopod, left. – B. Endopod, right. – C. Setae on distal segment, close-up of A. – D. Setae on segment 2 and 3. – E. Seta on segment 2. – F. Seta on segment 1.

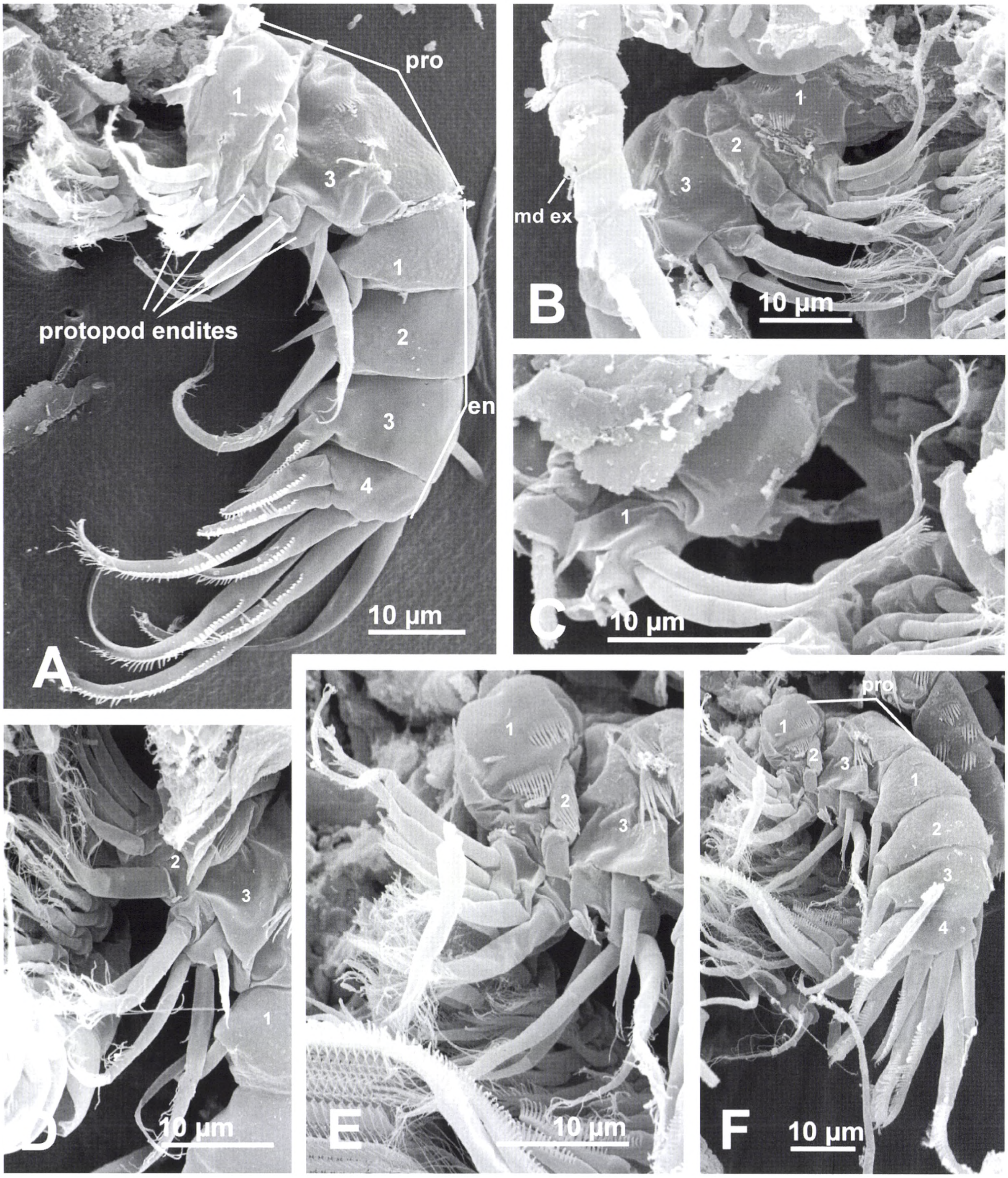


Plate 14. Maxilla 1. A. Left side, anterior face. – B. Protopod, right side, anterior face. – C. Setae on the most proximal endite. – D. Setae on protopod. – E. Setae on protopod. – F. Left side, anterior face.

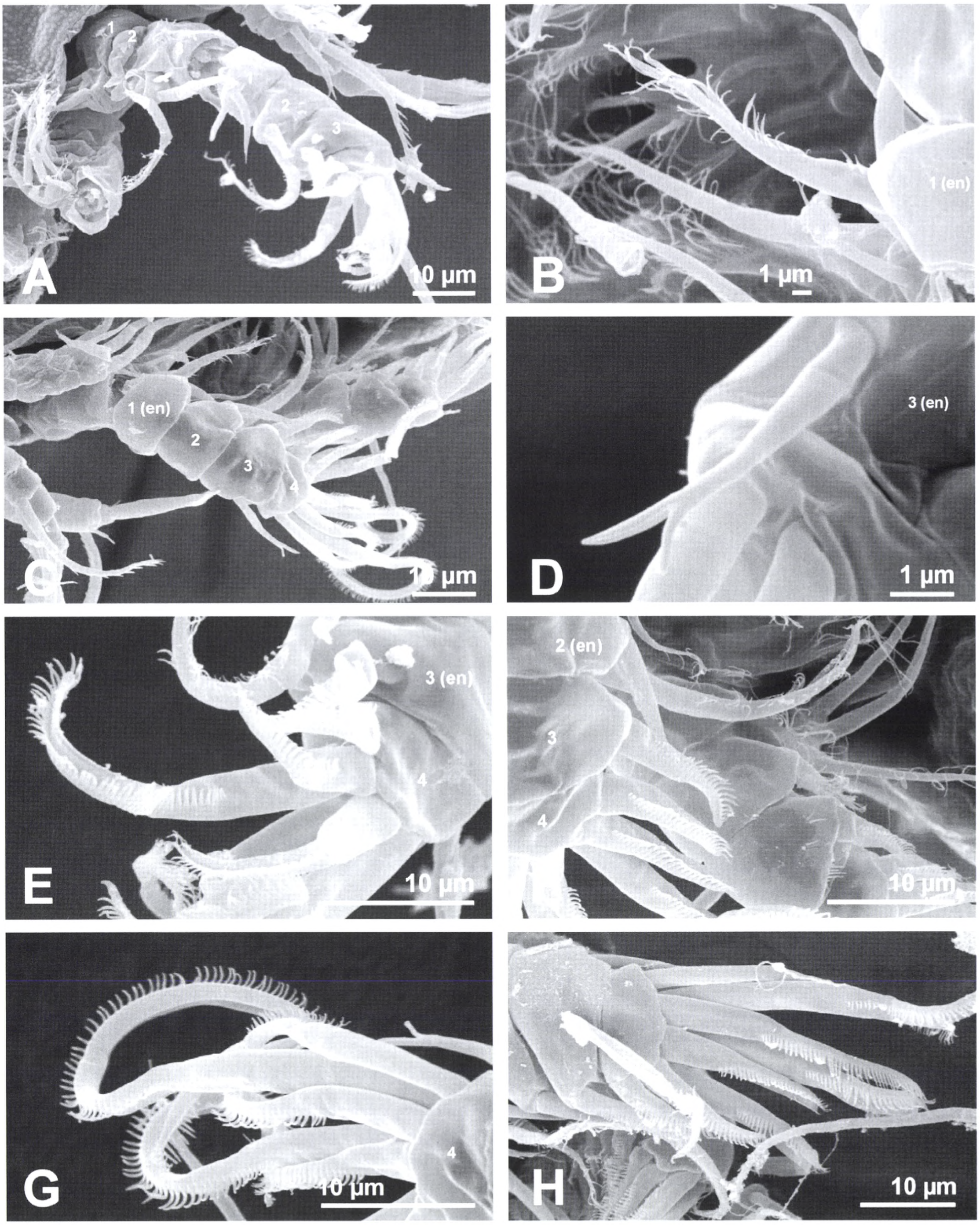
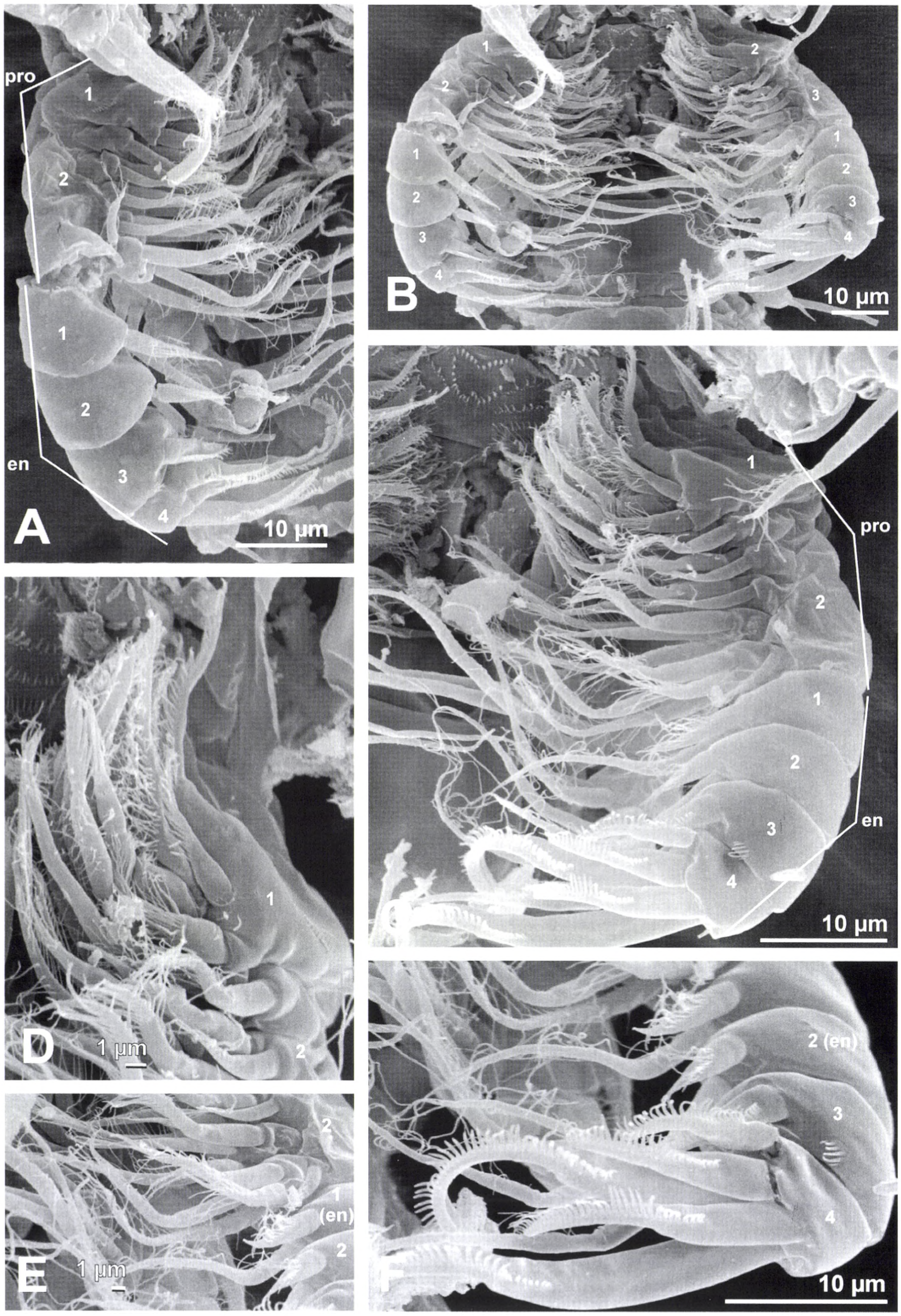


Plate 15. Maxilla 1. A. Whole view, left side. – B. Seta on protopod and segment 4. – C. Segment 4 to 7. – D. Seta lateral on segment 6. – E. Setae on segment 6 and 7. – F. Setae on segment 5 to 7. – G. Setae on segment 7. – H. Setae on segment 6 to 7.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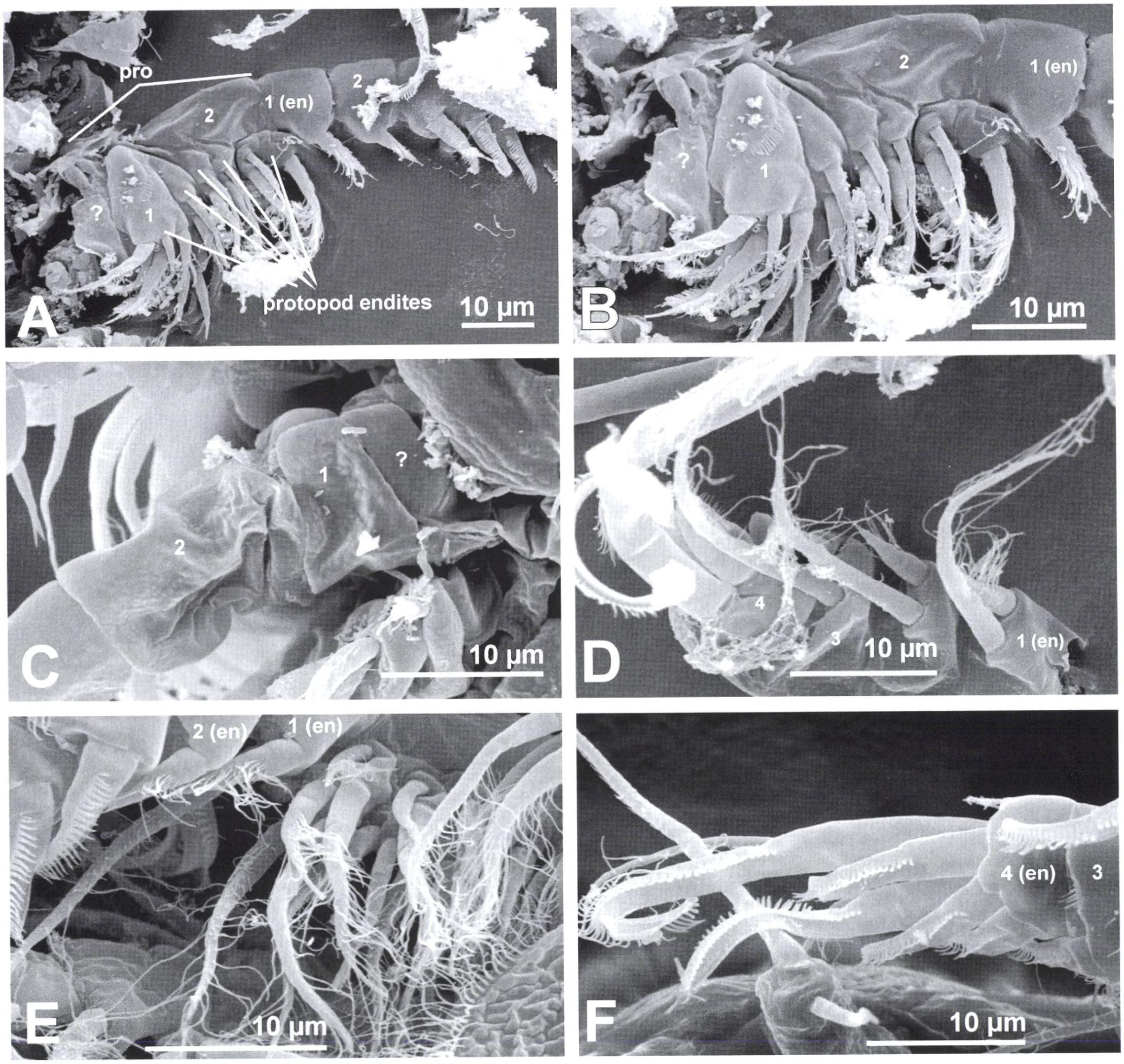


Plate 17. Maxilla 2. A. Left side, anterior face. – B. Close-up of A. – C. Lateral view of protopod. – D. Setae on endopod segments 1-4. – E. Setae on various segments. – F. Setae on endopod segment 4.

◀ Plate 16. Maxilla 2. A. Right side, anterior face. – B. Maxillae, right and left side, anterior face. – C. Left side, anterior face. – D. Setation on proximal part of protopod, close-up of C. – E. Setae on distal part of protopod and proximal segments of ramus. – F. Setae on distal segments.

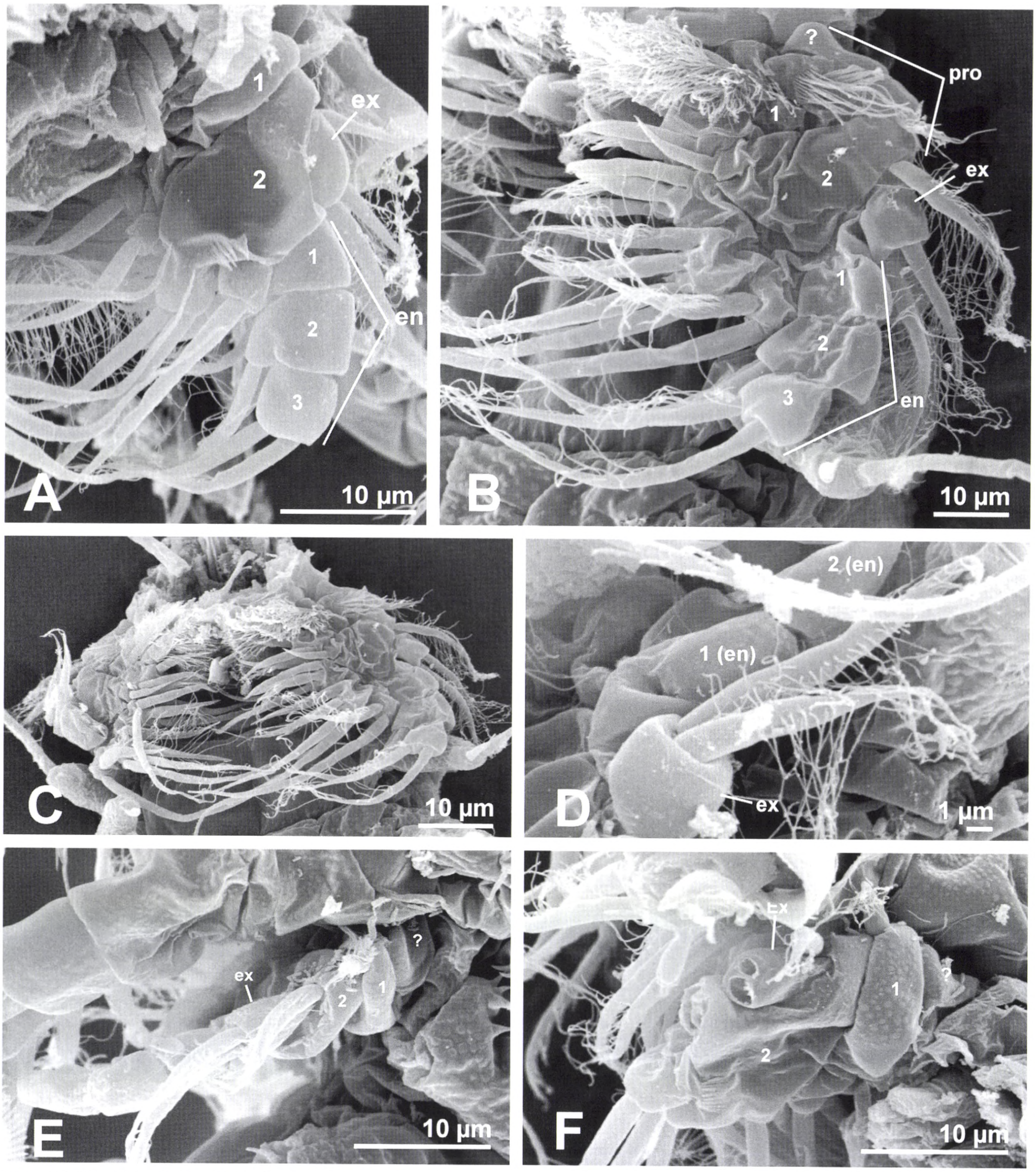


Plate 18. Maxilliped (trunk limb 1). A. Right side, posterior face. – B. Left side, anterior face. – C. Maxillipeds, left and right anterior face. – D. Exopod and endopod (in part). – E. Lateral view of left side maxilliped. – F. Lateral view of protopod.

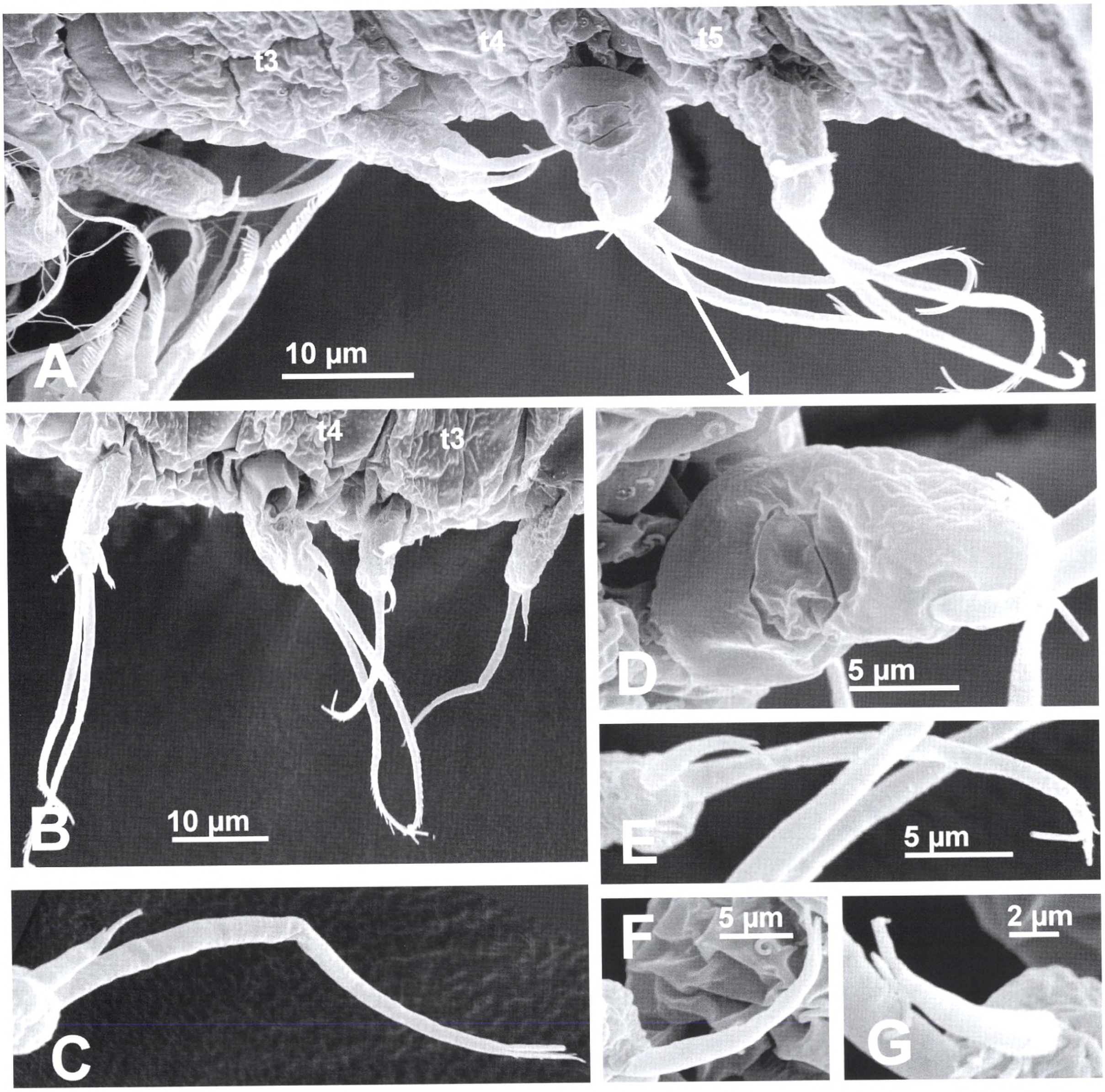


Plate 19. Trunk limbs 2-5, female. A. Inner side of trunk limbs 2-5, right side. – B. Inner side of trunk limbs 2-5, left side. – C. Setae on trunk limb 2. – D. Trunk limb 4 with gonopore. – E. Setae on trunk limb 3. – F. Small, median seta on trunk limb 4. – G. Small, distal seta on trunk limb 3.

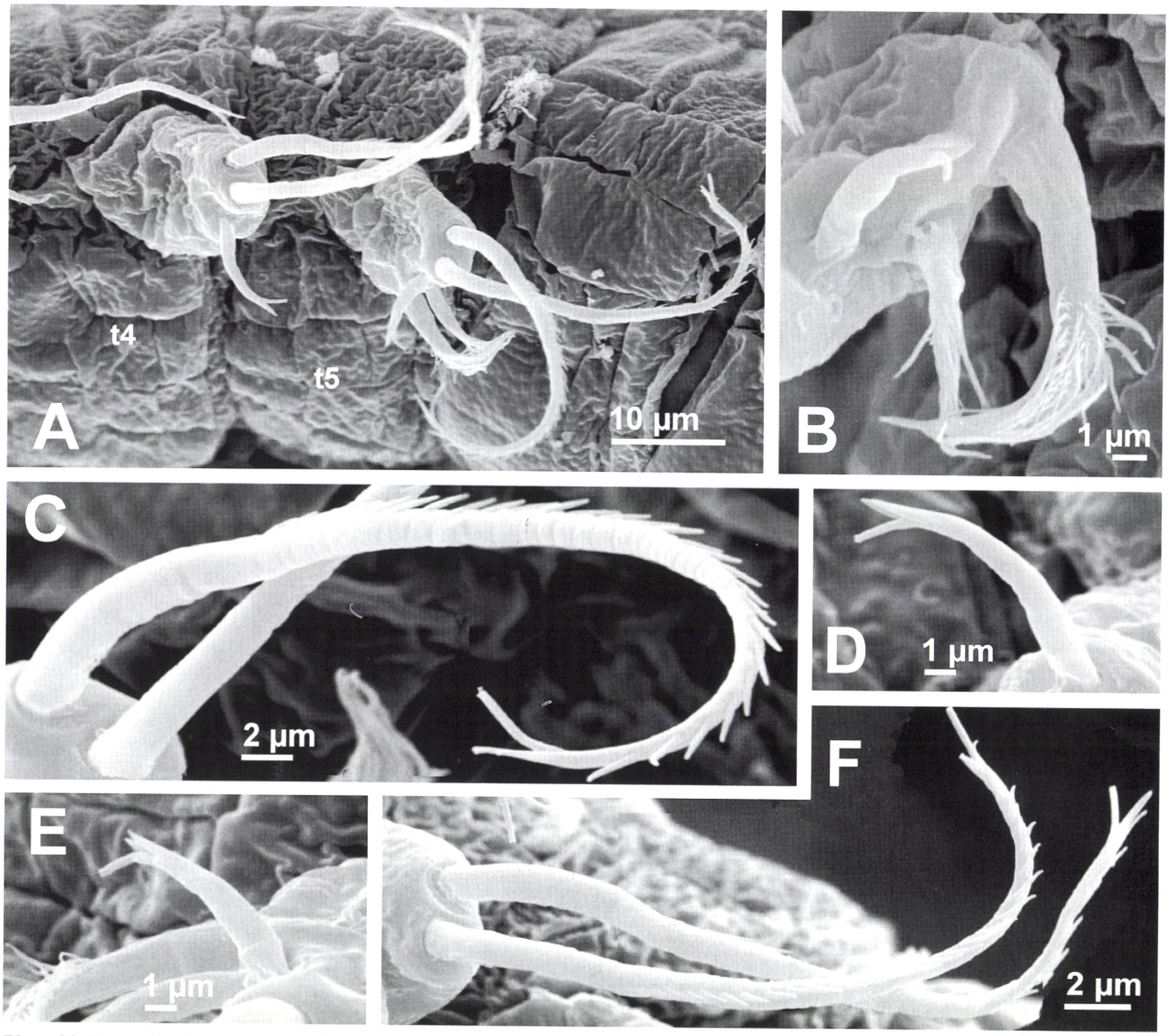
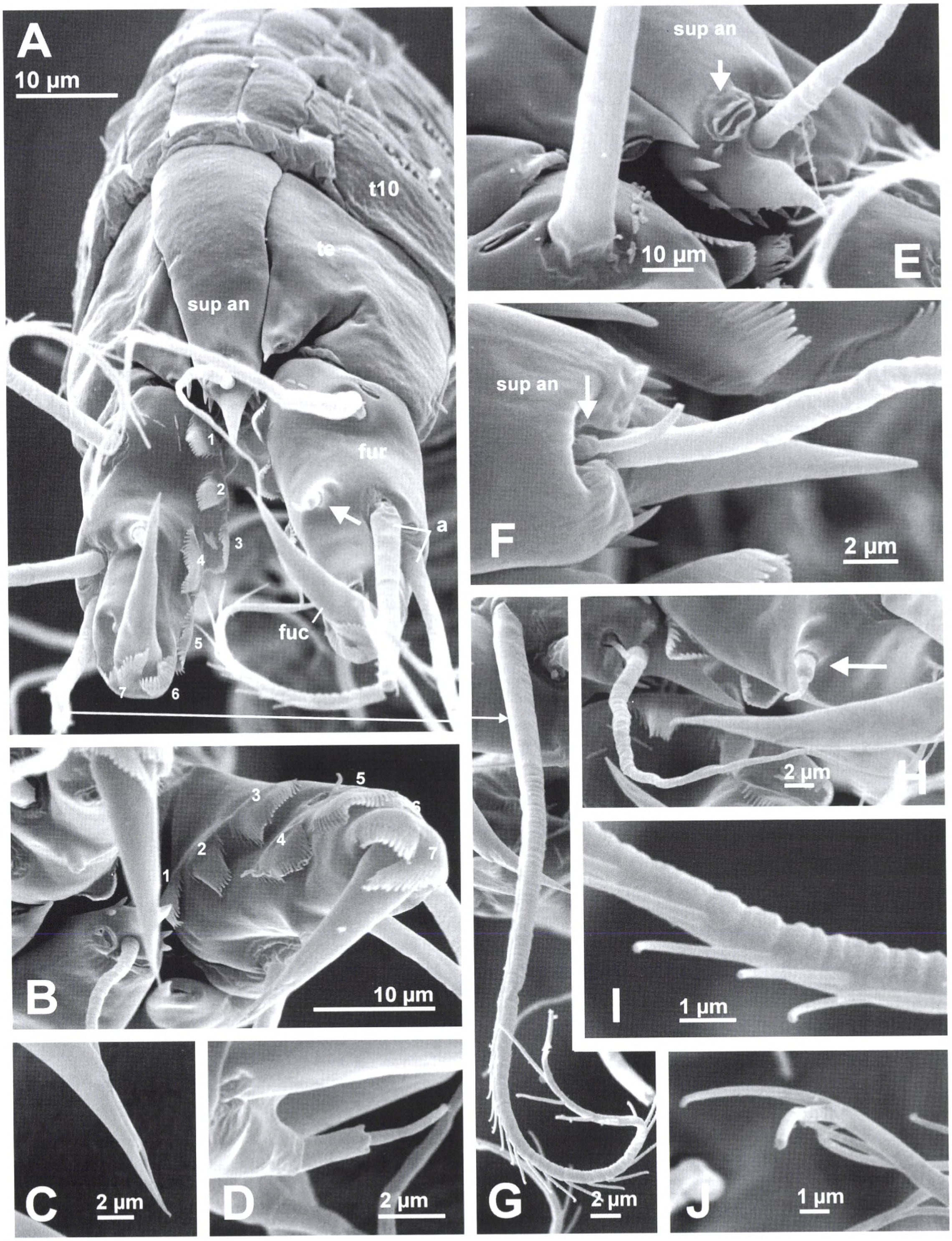


Plate 20. Trunk limbs 4 and 5, male. A. Trunk limbs 4 and 5, left side. – B. Median setae on trunk limb 5; the two setulated setae are of probable sexual nature. – C. Seta on trunk limb 5, enlargement of A. – D. Seta on trunk limb 4, enlargment of A. – E. Seta on trunk limb 5, enlargement of A. – F. Setae on trunk limb 4.

Plate 21. Telson and furcal rami. A. Dorsal view of telson and furcal rami, arrow indicates small dorsal seta shown in D. – B. Furcal ramus, left, inner side. – C. Tip of furcal claw. – D. Small dorsal seta on furcal ramus. – E. Supra-anal process, lateral/posterior view. – F. Supra-anal process, dorsal view, arrow indicates small dorsal seta. – G. Seta on left furcal ramus. – H. Long seta on supra-anal process. – I. Same seta as in G. – J. – Tip of most proximal large seta on left furcal ramus.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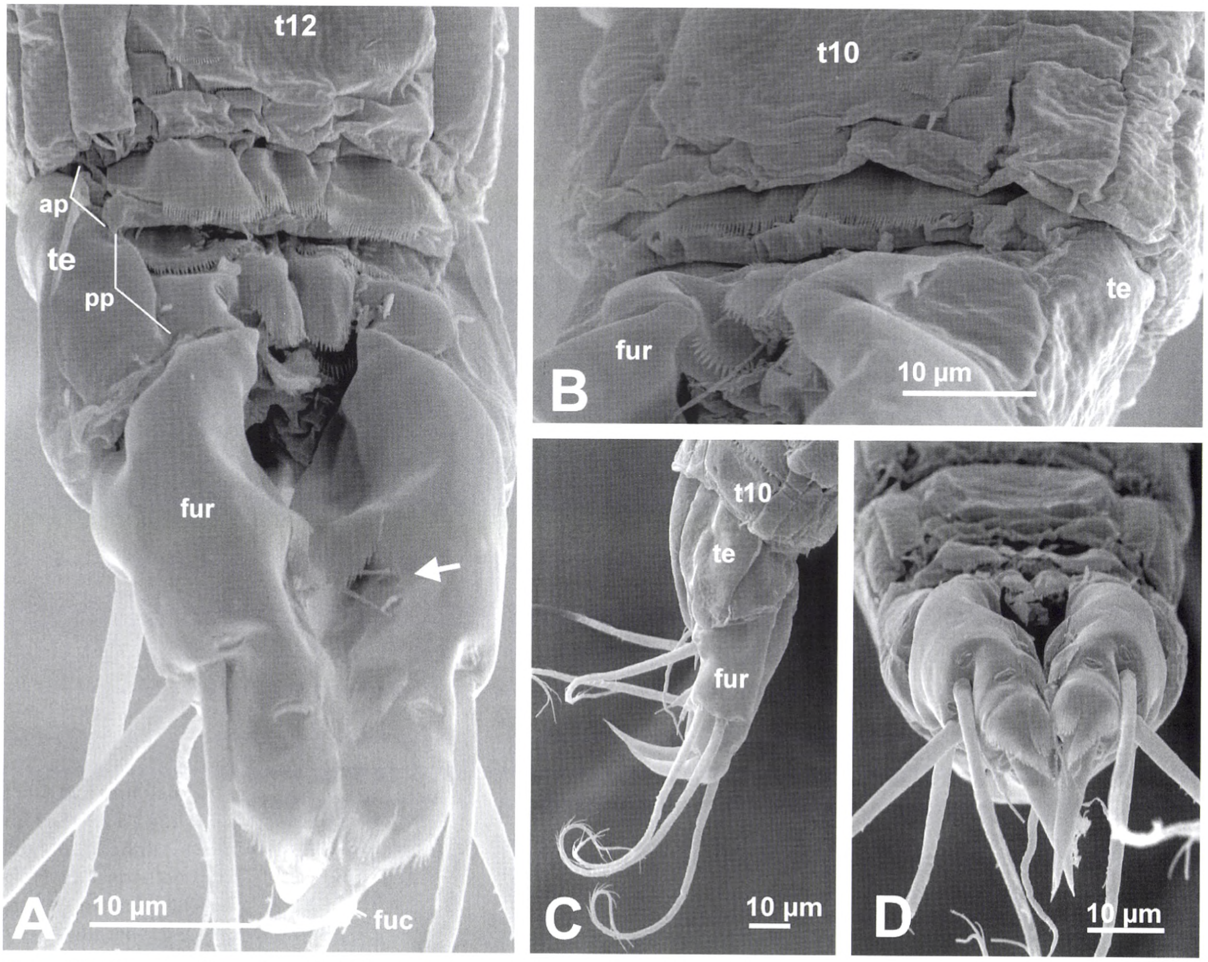

Plate 22. Telson and furcal rami. A. Ventral view of telson and furcal rami, 'ap' is anterior part of telson, 'pp' is posterior part. – B. Ventral view of telson and furcal rami. – C. Lateral view of telson and furcal rami. – D. Ventral view of telson and furcal rami.

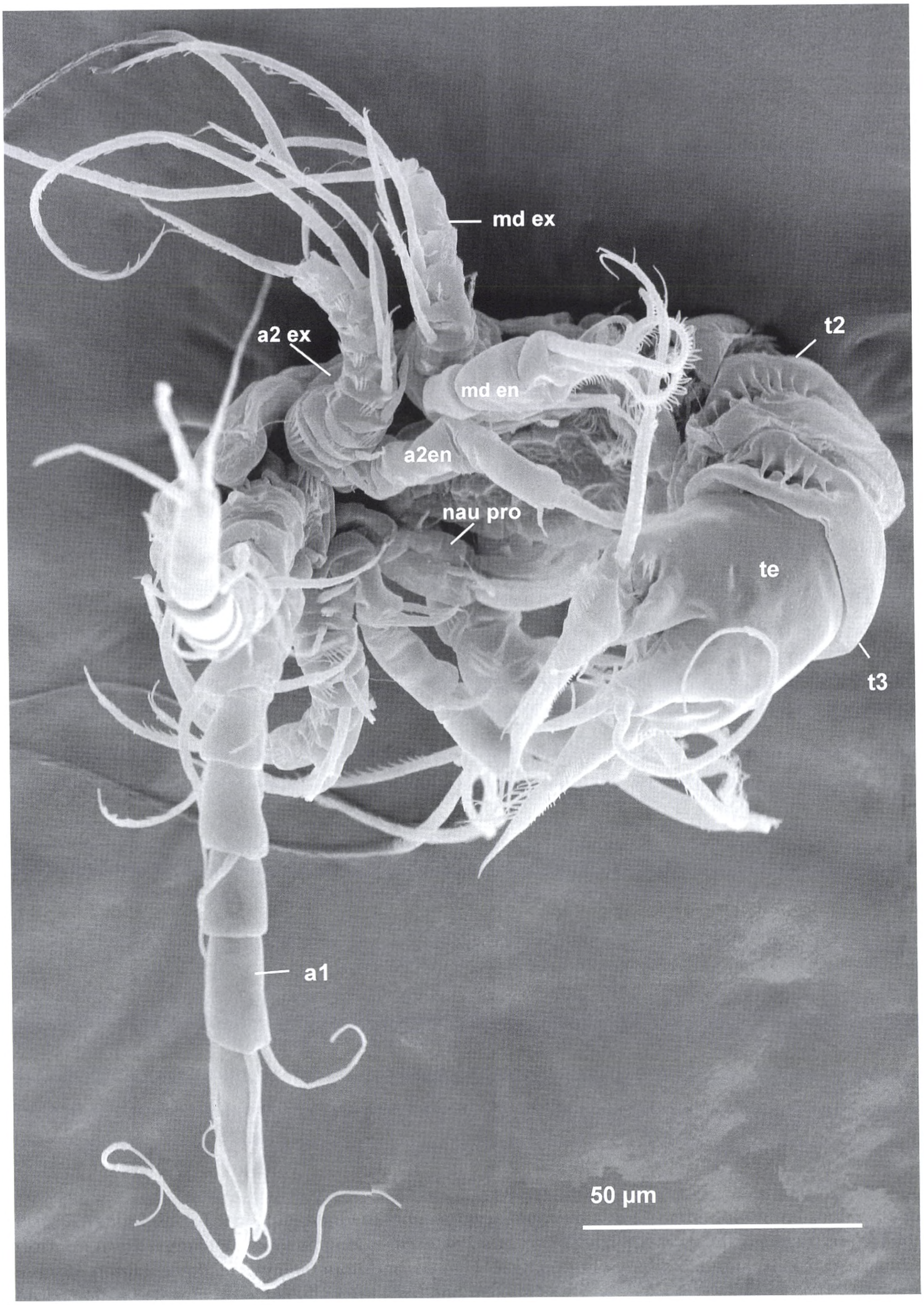

Plate 23. Larva of stage 1, left lateral view.

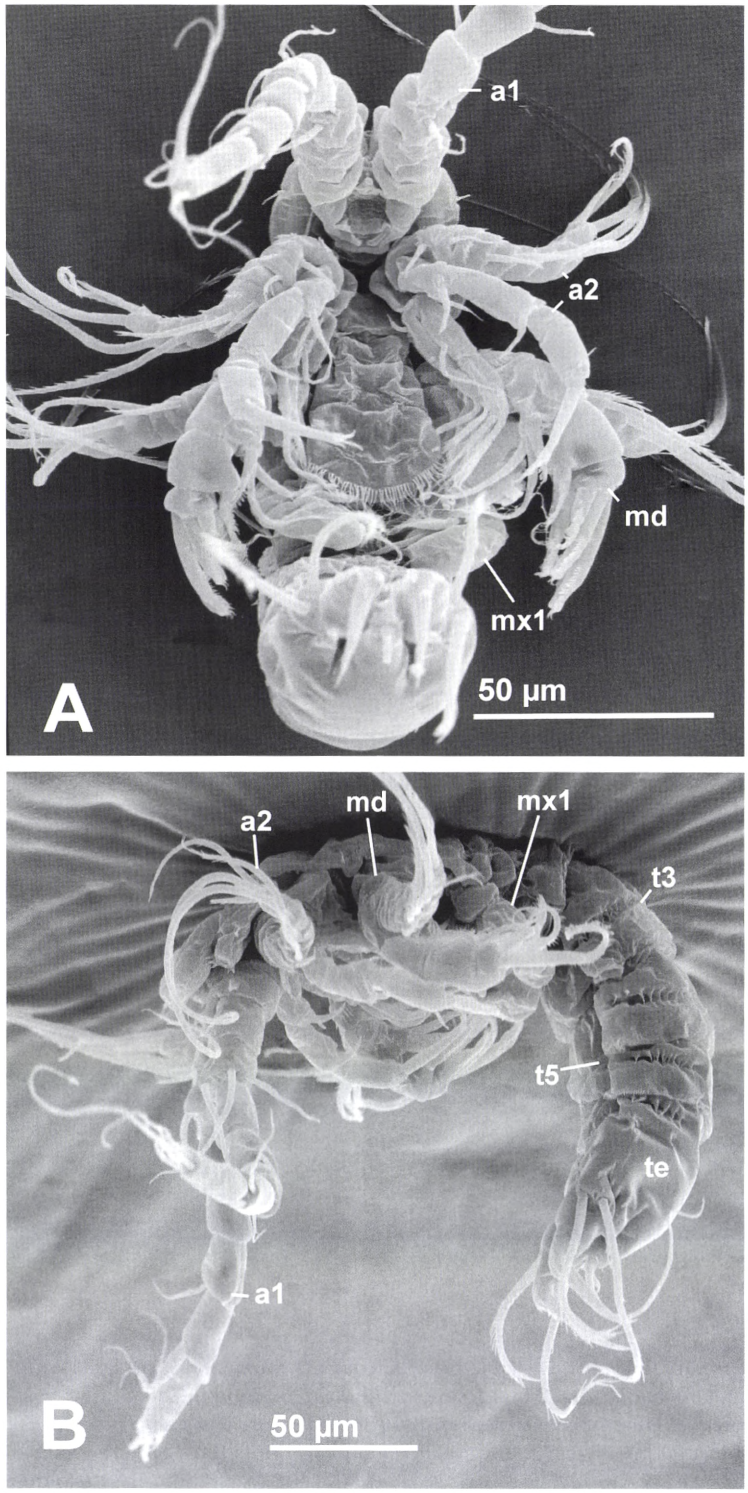

Plate 24. Larvae of stage 2. A. Ventral view – B. Left lateral view.

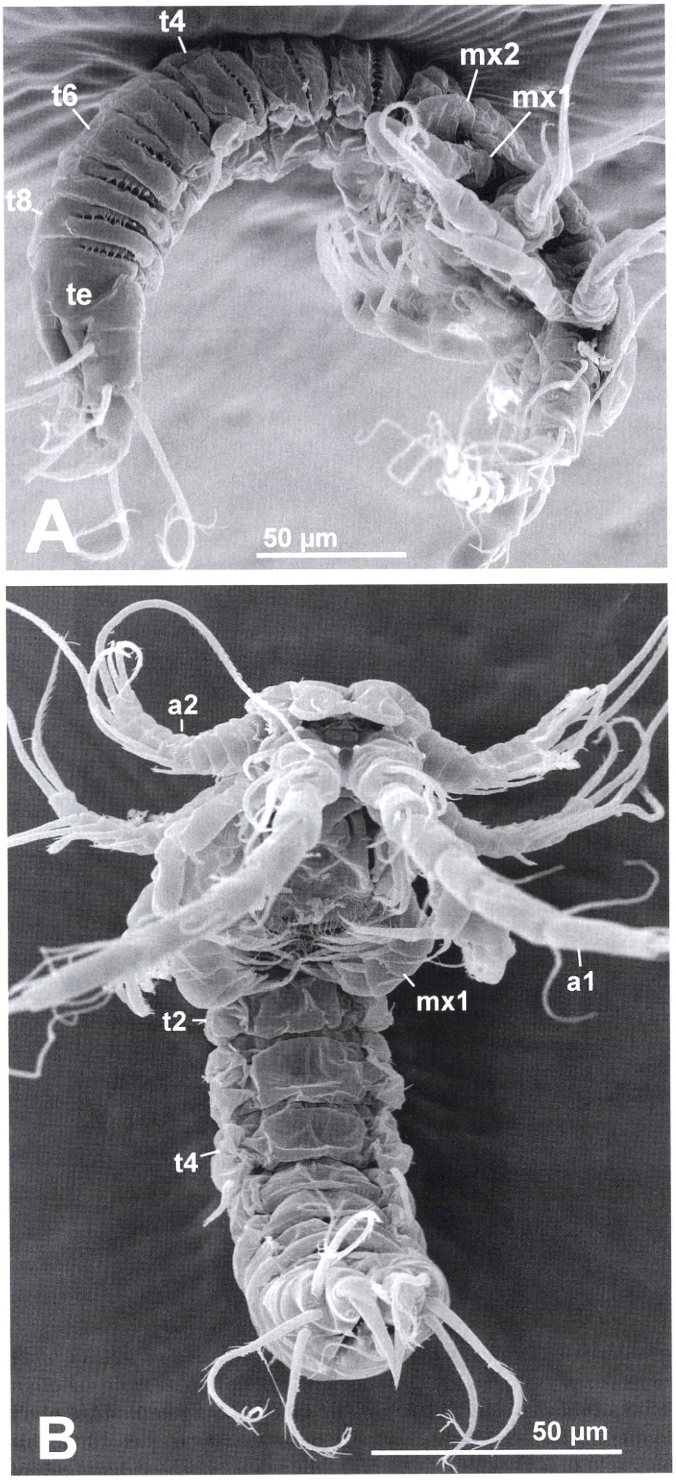

Plate 25. Larvae of stage 4. A. Right lateral view. -C. Ventral view.

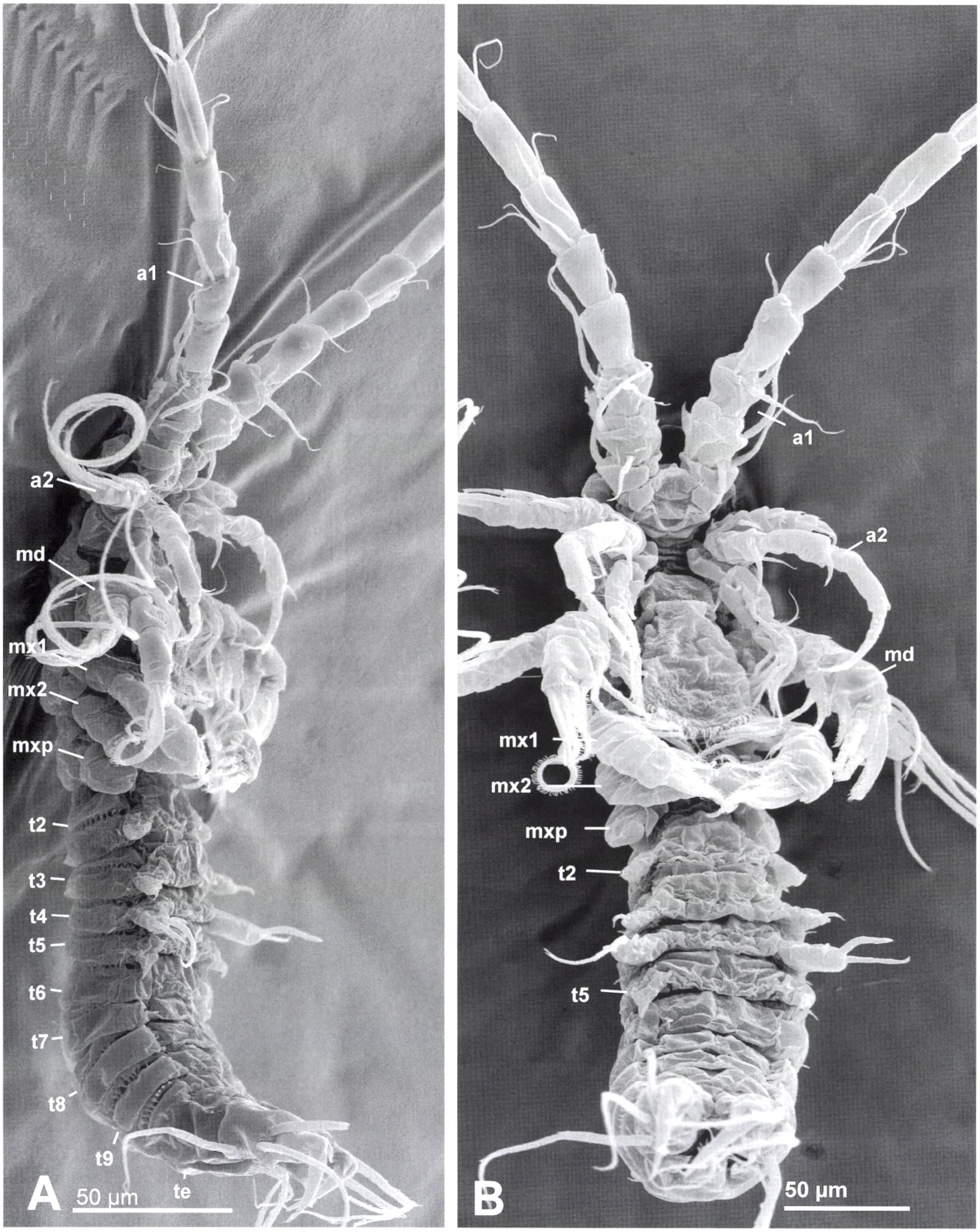

Plate 26. Larvae of stage 5. A. Right lateral view. – Ventral view.

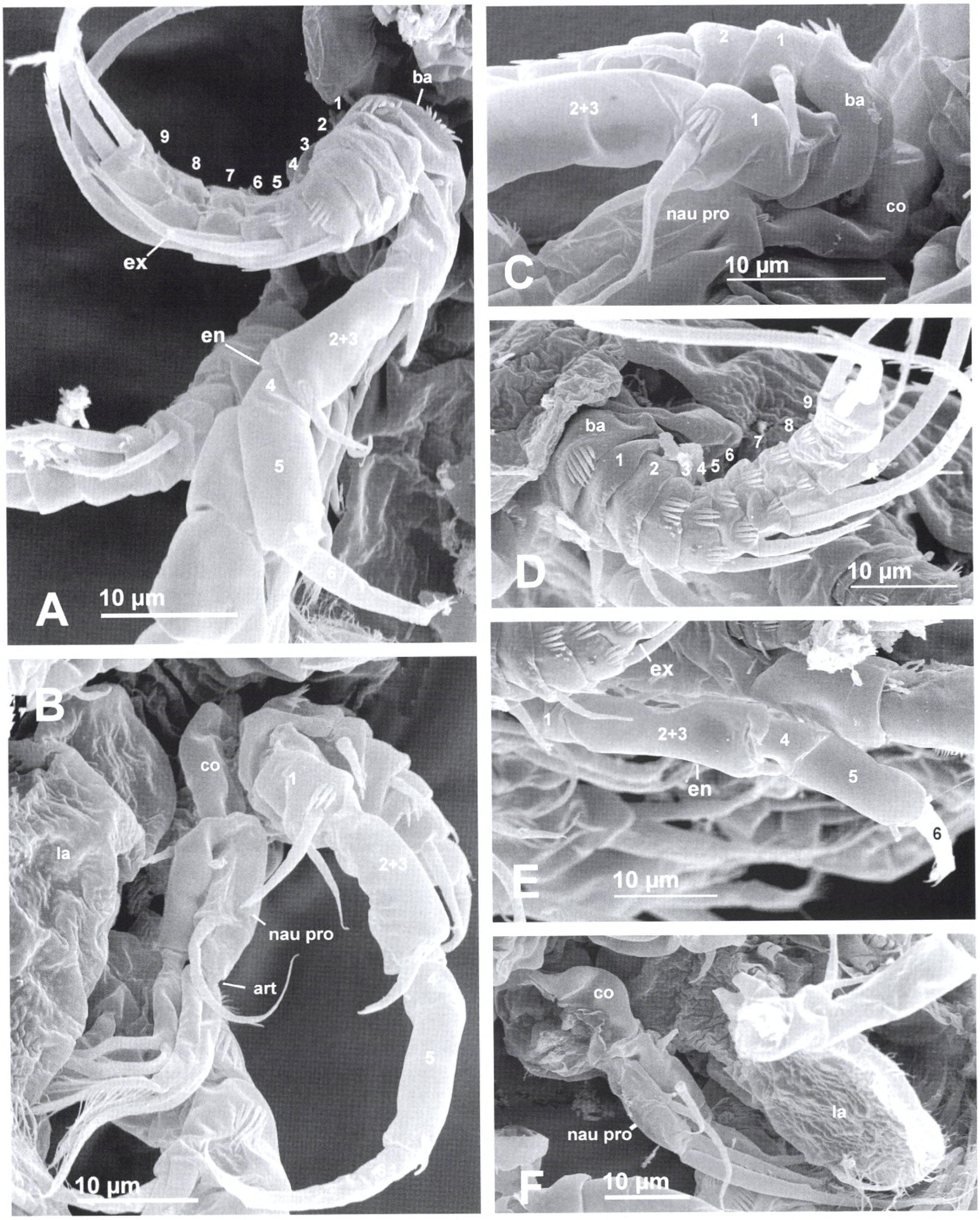

Plate 27. Larvae, antenna 2. A. A2 of stage 2, exopod and endopod, right side. – B. A2 of stage 5, left side, coxa, basis, naupliar process, endopod and exopod (in part). – C. A2 of stage 2, right side, basis, naupliar process, proximal parts of endopod and exopod. – D. A2 og stage 5, left side, exopod. – E. A2 of stage 5, left side, endopod. – F. A2 of stage 5, right side, naupliar process; basis and rami removed. The Arabic numerals used on segments of the endopod and exopod refer to the numbers used for the adult.

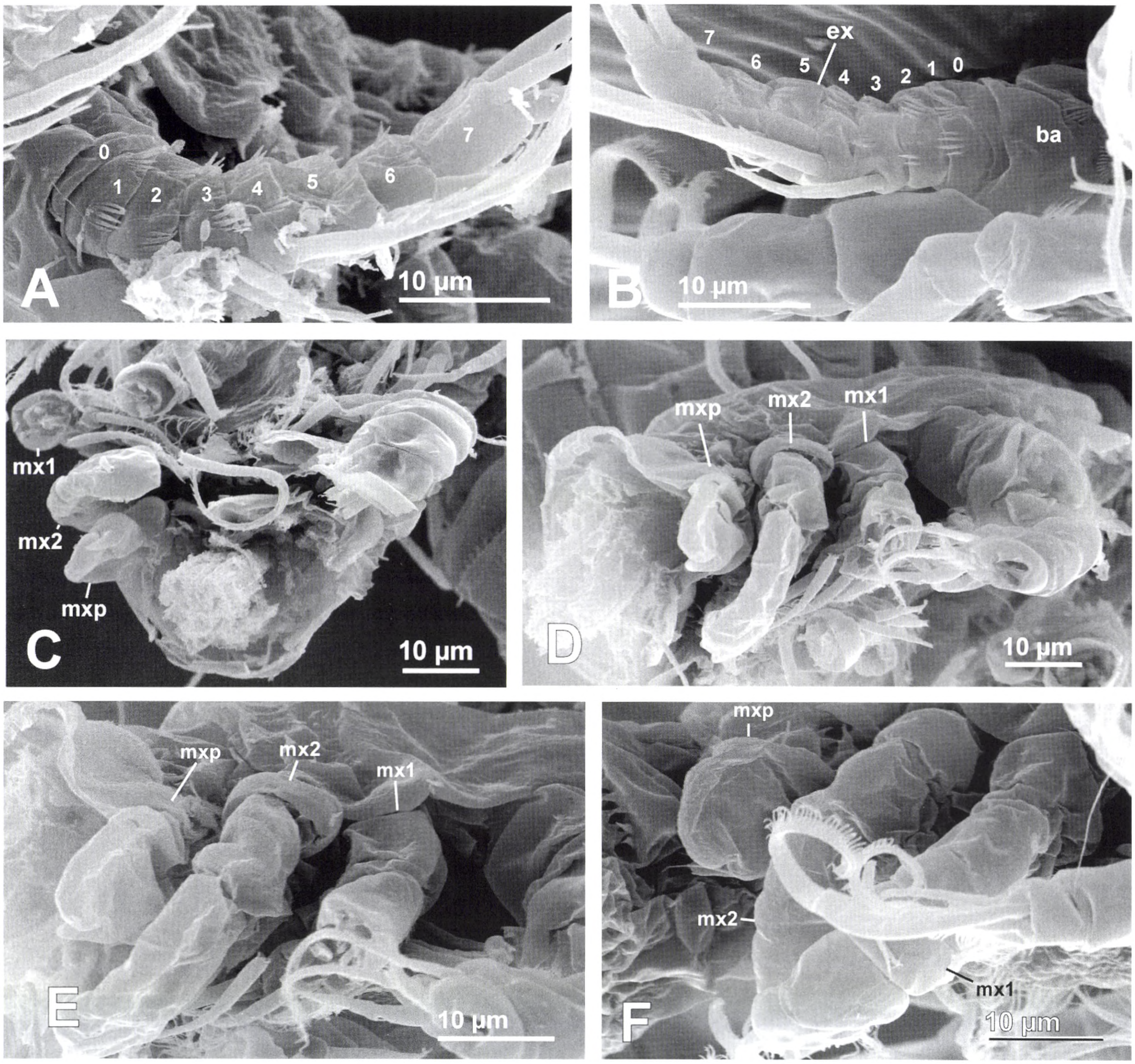

Plate 28. Larvae, various cephalic appendages. A. Md of stage 5, exopod, left side. – B. Md of stage 2, exopod and endopod, right side. – C. Mx1, mx2 and mxp of stage 5, view from posterior/ventral. – D. A2, mx1, mx2 and mxp of stage 5, right side, lateral. – E. Mx1, mx2 and mxp og stage 5, right side, lateral. – F. Mx1, mx2 and mxp og stage 5, right side, lateral.

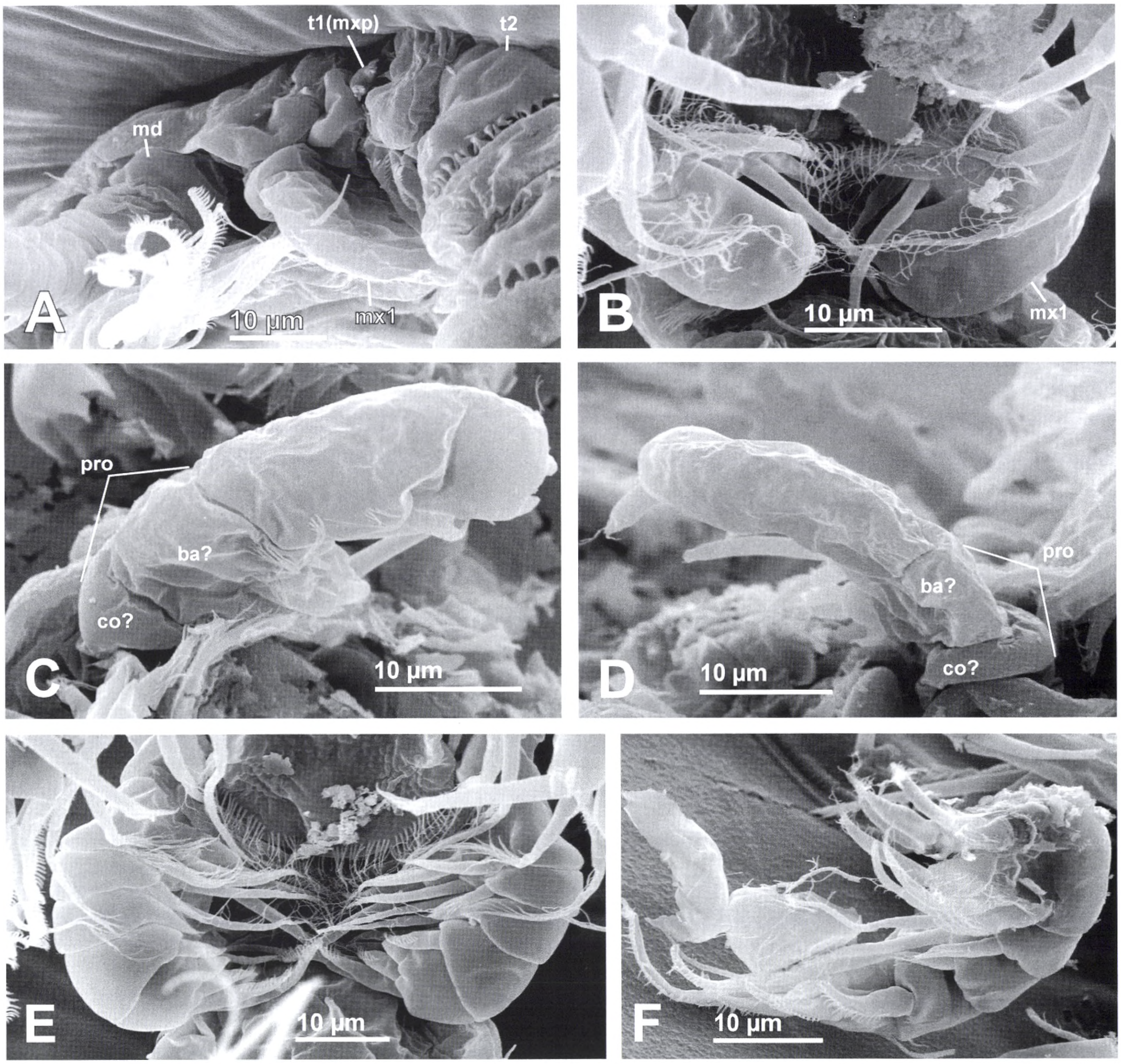

Plate 29. Larvae, maxilla 1. A. Stage 2, left side, lateral view. – B. Mx1 of stage 2, right and left, ventral view. – C. Mx1 of stage 3, left side, lateral/anterior side. – D. Mx1 of stage 3, left side, lateral. – E. Mx1 of stage 4, right and left, ventral view. – F. Mx1 of stage 5, left side, anterior face.

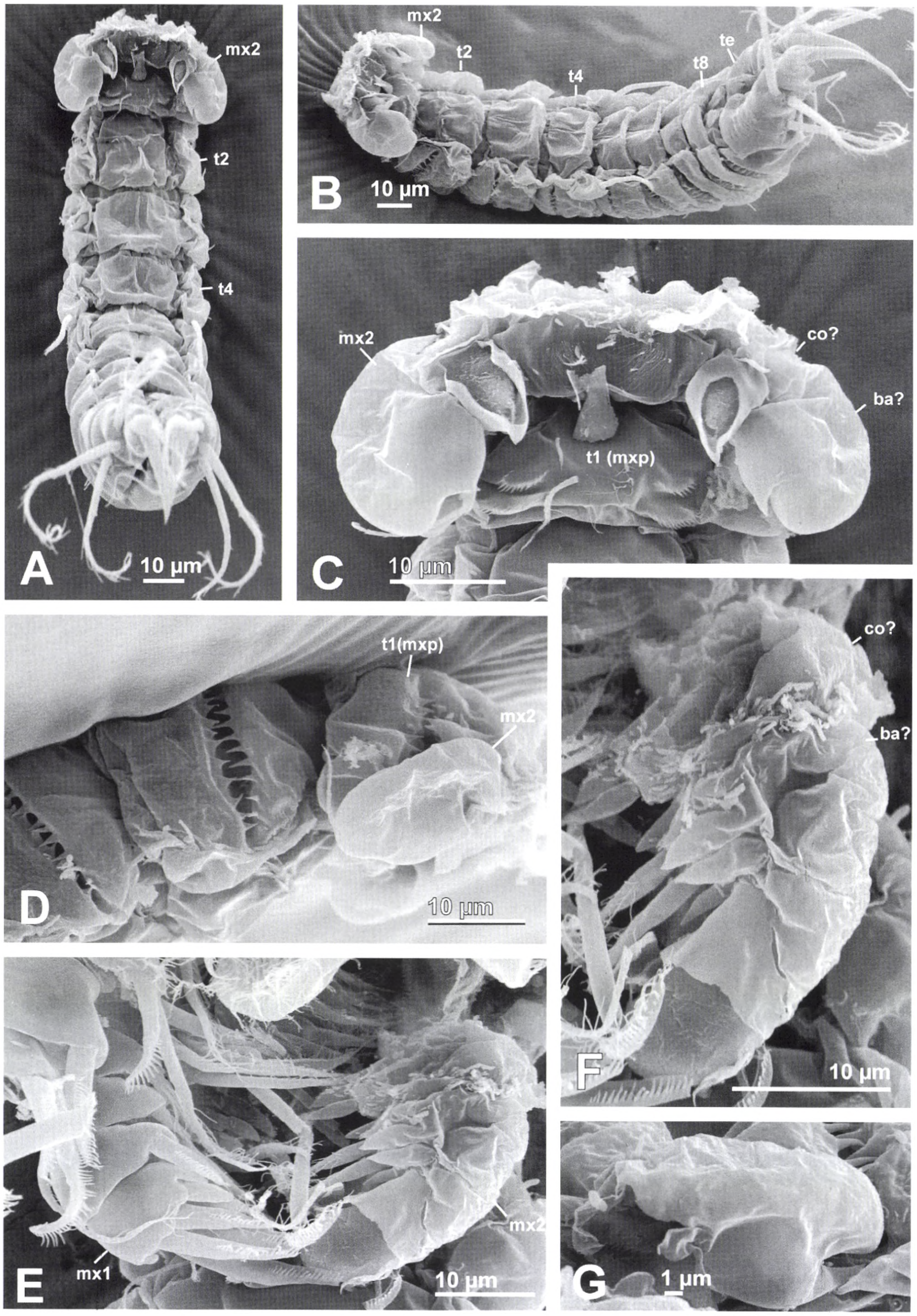

Plate 30. A-F maxilla 2, G Maxilliped. A. Ventral view of stage 4, cephalon anterior to mx2 removed. – B. Same as A seen from slightly different angle. – C. Close-up of A. – D. Lateral view of right mx2, stage 4, same specimen as in A-C. – E. Stage 5, ventral view showing right mx1 and left mx2. – F. Stage 5, left mx2, close-up of E. – F. Stage 5, mxp, left side.

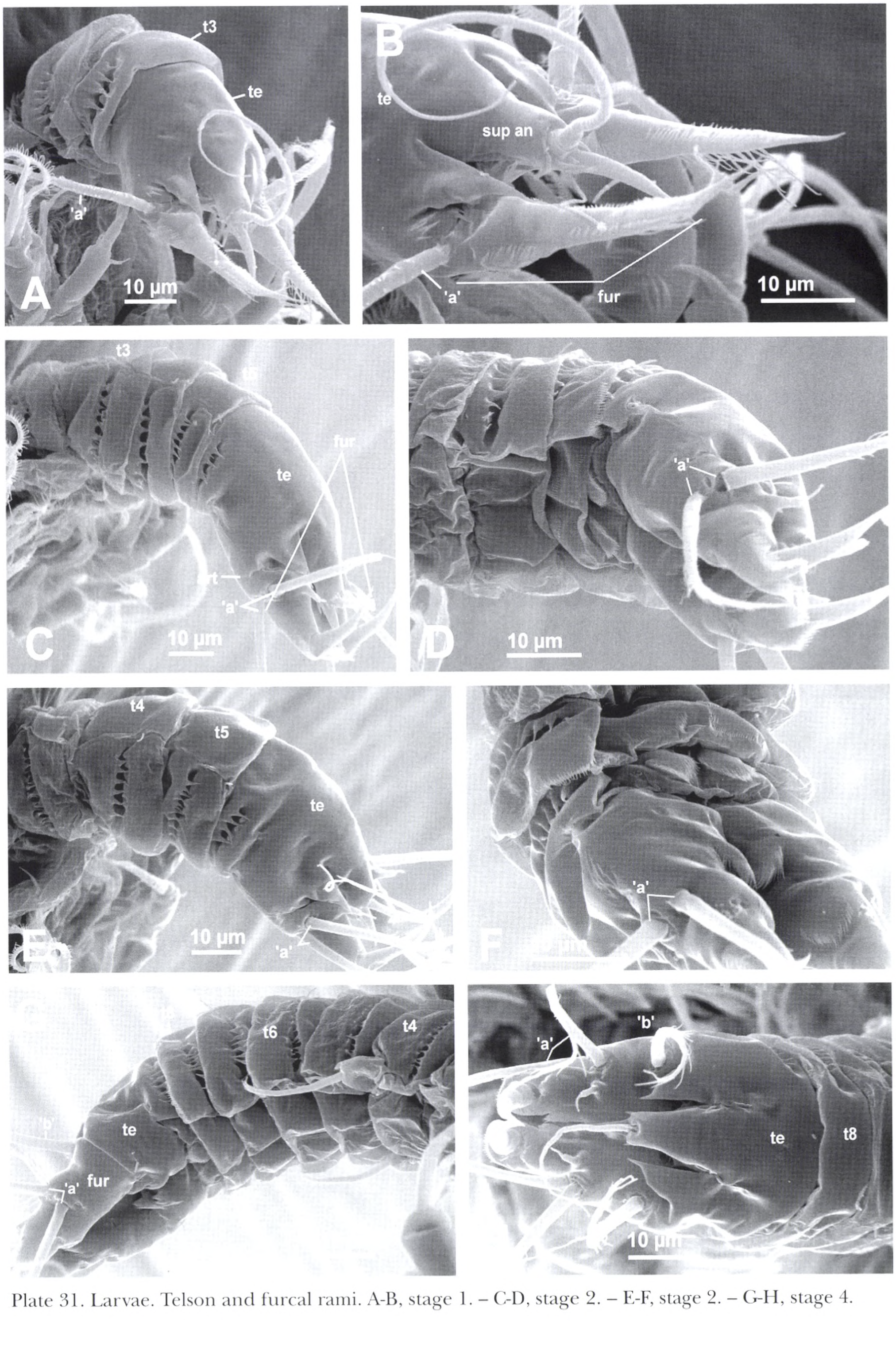

Plate 31. Larvae. Telson and furcal rami. A-B, stage 1. – C-D, stage 2. – E-F, stage 2. – G-H, stage 4.

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