REMIPEDIA. PART I. SYSTEMATICS

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Speleonectes ondinae, ventral surface. Animal swimming and executing a 180° turn. From a photograph by Dennis Williams.

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SYNOPSIS

The order Nectiopoda is a relatively new taxonomic addition to crustacean biology. First collected during the early 1980s from caves in the Bahamas and Turks and Caicos Islands, these living representatives of the apparently ancient class Remipedia are known from analogous habitats on both sides of the Atlantic.

The three known nectiopodans are reviewed here, and one species is described: *Godzillius robustus* gen. & sp. nov., sole representative of the Godzilliidae. A detailed, illustrated analysis of each species, based on SEM and light microscopy, is given with known data on natural history, distribution, and relationships within the Nectiopoda. A new study of the Carboniferous fossil *Tesnusocaris goldichi* Brooks from West Texas reveals additional details of cephalic morphology in the monotypic order Enantiopoda that suggest a closer affinity with the living nectiopodans than previously indicated.

These five living and fossil species are compared with each other and all other Crustacea, using cladistic analysis to identify the most parsimonious relationships possible. The resulting implications for crustacean evolution are discussed with reference to existing theories.

Remipedia. Part I. Systematics

Frederick R. Schram,[1] Jill Yager[2] and Michael J. Emerson[1]

INTRODUCTION

In 1981, Yager described a new crustacean from Lucayan Cavern, an anchialine cave in Grand Bahama. It was so unlike any other known crustacean that establishment of a new class was necessary, the Remipedia. This animal, *Speleonectes lucayensis,* seemed to bear some resemblance to a problematic Carboniferous species, *Tesnusocaris goldichi* Brooks (Schram 1983*a*), which had been placed in its own order Enantiopoda (Birshtein 1960). Though the two animals are distinct, the overall similarities proved so striking that a sister group relationship was indicated, and Schram (1986) erected a separate order, the Nectiopoda, for the speleonectids allying both groups within the class Remipedia.

Since the first remipede was described, other nectiopodan taxa have been discovered from the West Indies and the Canary Islands (Garcia-Valdecasas 1984, Yager and Schram 1986). Several features of all these taxa, fossil and living, denote these as a most intriguing group. The complete lack of tagmosis in the trunk, as well as the serial nature of several organ systems (such as limbs, gut, and possibly reproductive system and cephalic glands) marks the remipedes as among the most primitive of known crustaceans (Schram 1986). The phylogenetic importance of this group requires a detailed series of diagnoses and descriptions for the known taxa, based on more extensive materials than was available before. A summary taxonomy of the class as currently understood is as follows:

Phylum Crustacea Pennant, 1777
  Class Remipedia Yager, 1981
    Order Nectiopoda Schram, 1986
      Family Speleonectidae Yager, 1981
      Family Godzilliidae new

    Order Enantiopoda Birshtein, 1960
      Tesnusocarididae Brooks, 1955

An analysis of internal anatomy will follow in Part II of this monograph. It will be based on study of *Lasionectes entrichoma,* the only nectiopodan so far known from sufficient numbers of specimens to allow for sectioning and staining of many individuals.

The present study is concerned only with the description and analysis of adult nectiopodans. Apparently, these animals reach maturity when the body grows to approximately 30 trunk segments. At that size the animals have developed the trunk pleural lobes, into which the midgut diverticula extend. Preliminary study of serial sections of *Lasionectes entrichoma* indicates that nectiopodans may be hermaphroditic. Several localities have yielded specimens of juvenile Nectiopoda (see table 5), but, these exist in insufficient numbers for a detailed study at this time.

Specimens of Remipedia are located in several different collections. These are indicated by a prefix to the catalog numbers as follows:

K   —Zoologisches Institut, Hamburg, West Germany.
MNCN —Museo Nacional de Ciencias Naturales, Madrid, Spain.
SDSNH —San Diego Society of Natural History, Crustacean collections.
USNM —National Museum of Natural History, Washington, Crustacean collections.
USNMP—National Museum of Natural History, Washington, Paleobiology collections.

Additional material was also used from Yager's private collection, and is so designated when referenced.

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SYSTEMATICS

Class REMIPEDIA Yager, 1981

Diagnosis.—Crustaceans without trunk tagmosis; lacking carapace but possessing well-developed subquadrangular cephalic shield; labrum well developed, forming large atrium oris behind mouth; (?) mandibles lacking palps; raptorial posterior mouthparts; biramous, paddle-like trunk limbs, rami of trunk limbs with three or more segments.

Remarks.—The query on mandibular palps is discussed below under Remarks on *Tesnusocaris goldichi.*

Order NECTIOPODA Schram, 1986

Diagnosis.—No eyes; cephalon with ventral, spined frontal processes; large biramous antennules with basal pad of aesthetascs; paddle-like biramous antennae; mandibles "internalized" into atrium oris; maxillules, maxillae and maxillipedes as well-developed, uniramous, raptorial mouthparts with elbows; maxillules with terminal claw or "fang," basal maxillulary endites functioning in place of "external" mandibles; maxillae with basal complex of three digitiform endites; maxillipedal segment fused to cephalon; trunk limbs ventro-laterally directed from body, gonopores located on bases of fourteenth trunk limbs; anal segment with simple oval caudal rami.

Family SPELEONECTIDAE Yager, 1981 (=Morlockiidae Garcia-Valdecasas, 1984)

Diagnosis.—Head shield subrectangular; ventral ramus of antennules with many segments; antennal segments generally with single rows of setae along margins, except for double row along distal edge of third endopodal segment; mandibles markedly asymmetrical; maxillule second segment with broad, ventral, pad-like setose, endite; maxillule third segment as broad, long, subtriangular endite; maxillae with four segments beyond elbow of limb; maxillipede basal endite broad and pad-like, with five segments beyond elbow of limb; posterior trunk segments generally without sternal plates, but with differentiated sternal bars.

Remarks.—The collection of more material of *Speleonectes lucayensis,* as well as recognition of an additional family of nectiopodan remipedes allows a more detailed diagnosis to be provided here than was possible by Yager (1981).

Genus SPELEONECTES Yager, 1981

Speleonectes Yager, 1981:328.
Morlockia Garcia-Valdecasas, 1984:329.

Diagnosis.—Third endite of maxillule large with robust setae, fourth endite moderately developed and bearing pair of robust apical setae; second endite of maxillae with long simple setae as well as apical seta; maxillae and maxillipedes prehensile, with long simple setae on distal segments of limb, terminal claws developed as horseshoe-shaped scraper with dense comb-like row of spines (Fig. 7).

Type species.—*Speleonectes lucayensis* Yager, 1981.

SPELEONECTES LUCAYENSIS Yager, 1981

Speleonectes lucayensis Yager 1981:328.

Diagnosis.—Apical setae on mouthpart endites robust and without subsetules; sternite bar on fourteenth trunk segment with sub-triangular flaps extending over genital pores located on limb protopod; posterior trunk segments with sternite bars somewhat wide and convex posteriorly.

Holotype.—USNM 184343, coll. March 13, 1980.

Type locality.—Lucayan Cavern, Grand Bahama Island.

Additional material.—Yager Private Collection, 3 adults, from type locality, coll. between Oct. 1979–Nov. 1980. SDSNH 2189, from type locality, coll. Nov. 10, 1983.

Description.—The cephalon is approximately $\frac{1}{12}$ the total body length (Fig. 1A). The cephalic shield tapers anteriorly where it bears a faint median transverse groove in addition to a prominent transverse groove about midlength on the head shield. The adult animal has 29 to 32 free segments in the trunk. The tergite of the first trunk segment is reduced in size from those which follow, and is usually partially covered by the posterior margin of the cephalic shield. The trunk segments are produced laterally as prominent pleurites that are rounded anteriorly and somewhat concave posteriorly. The last tergite is reduced and appears to be partially fused to the anal segment. The sternites of the trunk segments are reinforced with well-developed transverse bars. The bar on the fourteenth segment bears sub-triangular flaps that extend over the genital pores located on the bases of the limb protopods. The sternal bars posterior to the fourteenth segment are some-
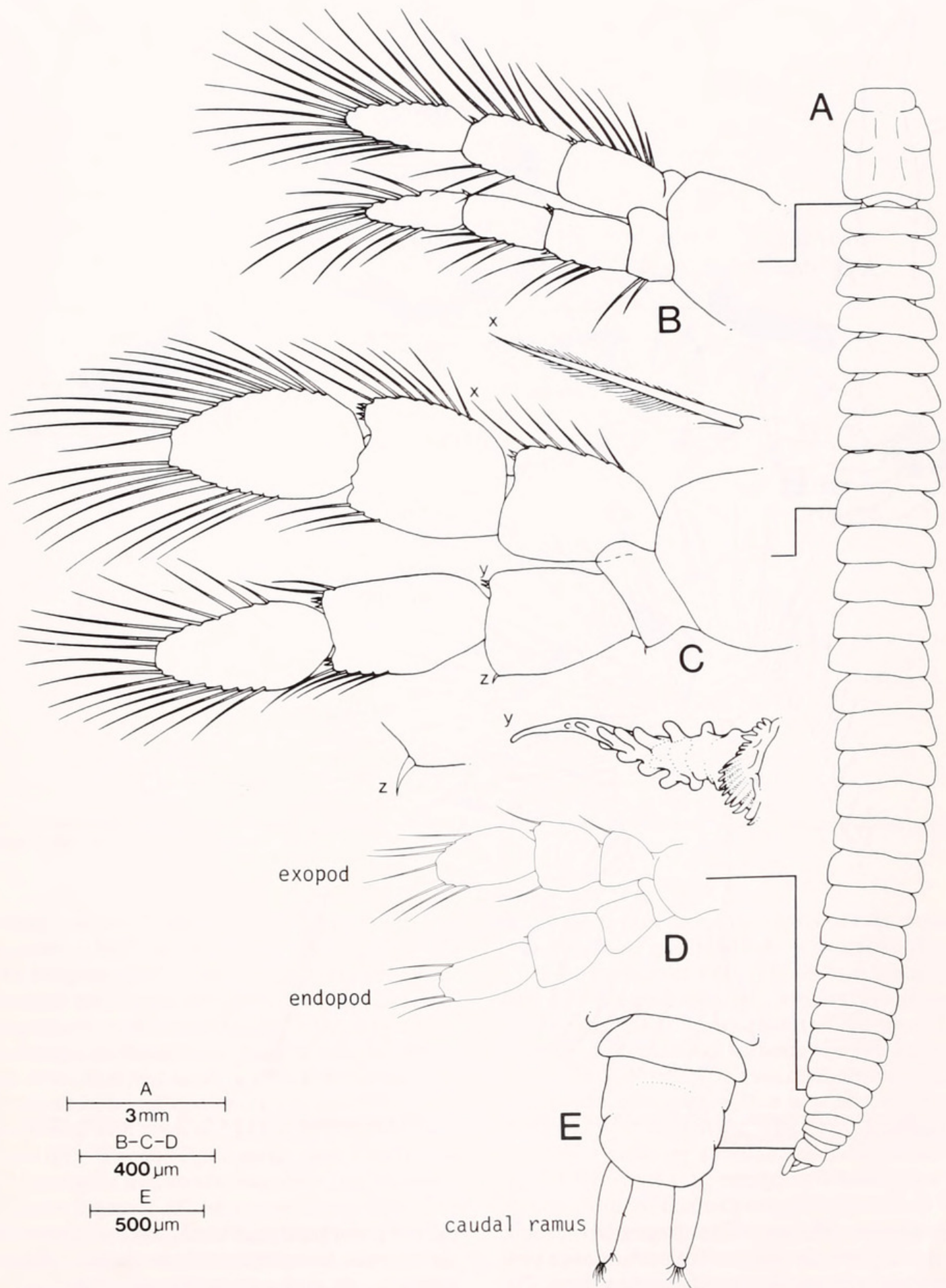
A
3mm
B–C–D
400μm
E
500μm

exopod

endopod

caudal ramus

Fig. 1. *Speleonectes lucayensis.* A) dorsal surface of body; B) posterior view of first trunk limb; C) tenth trunk limb, with x, y, and z as variant setal types; D) twenty-eighth trunk limb; E) anal segment with caudal rami.
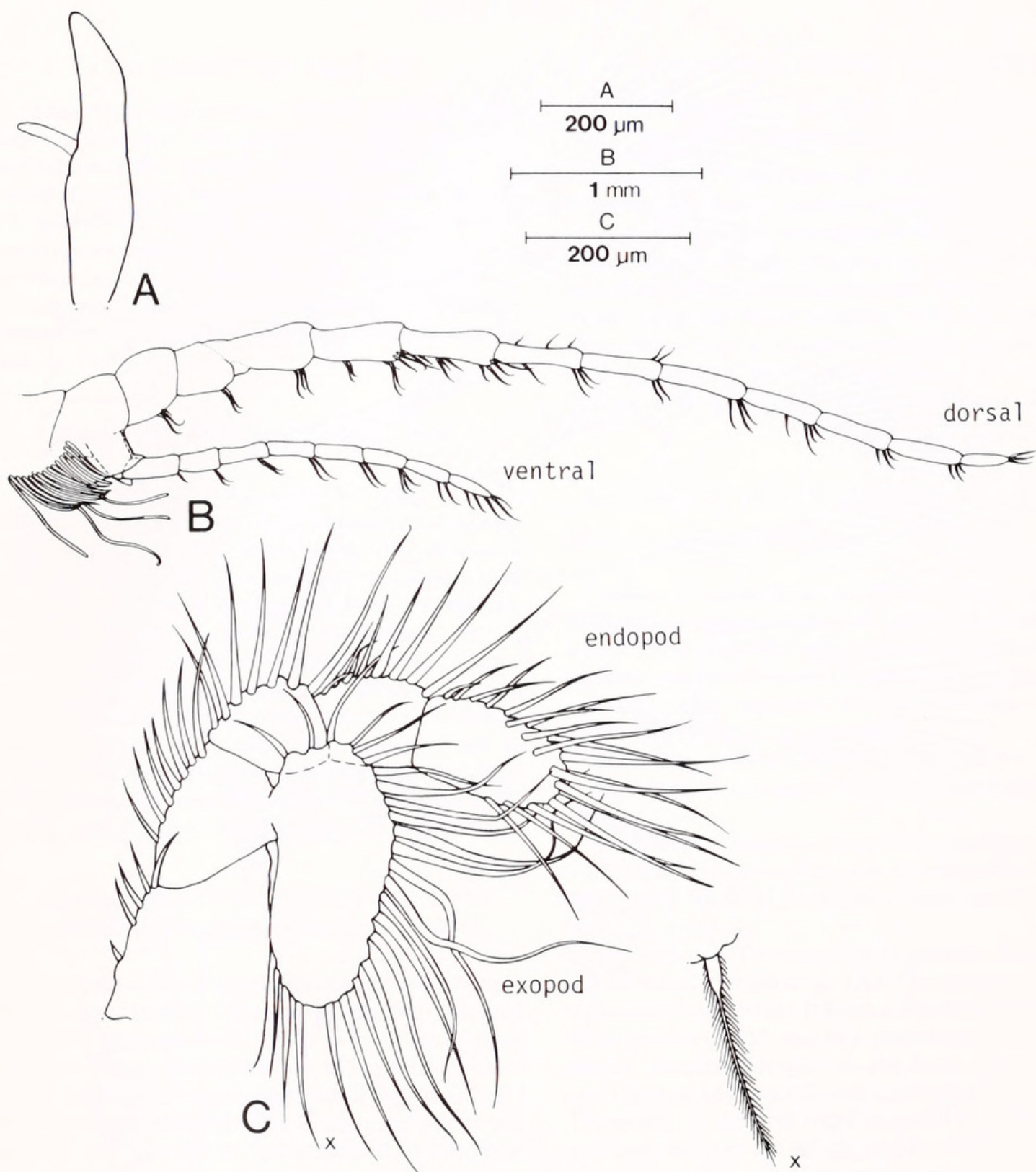
Fig. 2. *Speleonectes lucayensis.* A) left frontal filament, lateral view; B) left antennule, anterior view; C) left antenna, ventral view, with x as plumose seta on margins.

what concave on their posterior margins, but at about segment 26 the bars become distinctly convex posteriorly and have an almost subtriangular form. The anal segment (Fig. 1E) is slightly longer than wide. The caudal rami are slightly shorter than the length of the anal segment. The caudal rami terminate in

tufts of about six simple setae, and bear two or three simple setae along their median margins. Measurements of specimens are provided in Table 1.

There is a small pair of frontal processes (Fig. 2A) on the anterior part of the ventral cephalon, located near the base of the antennules. They are rod-like,
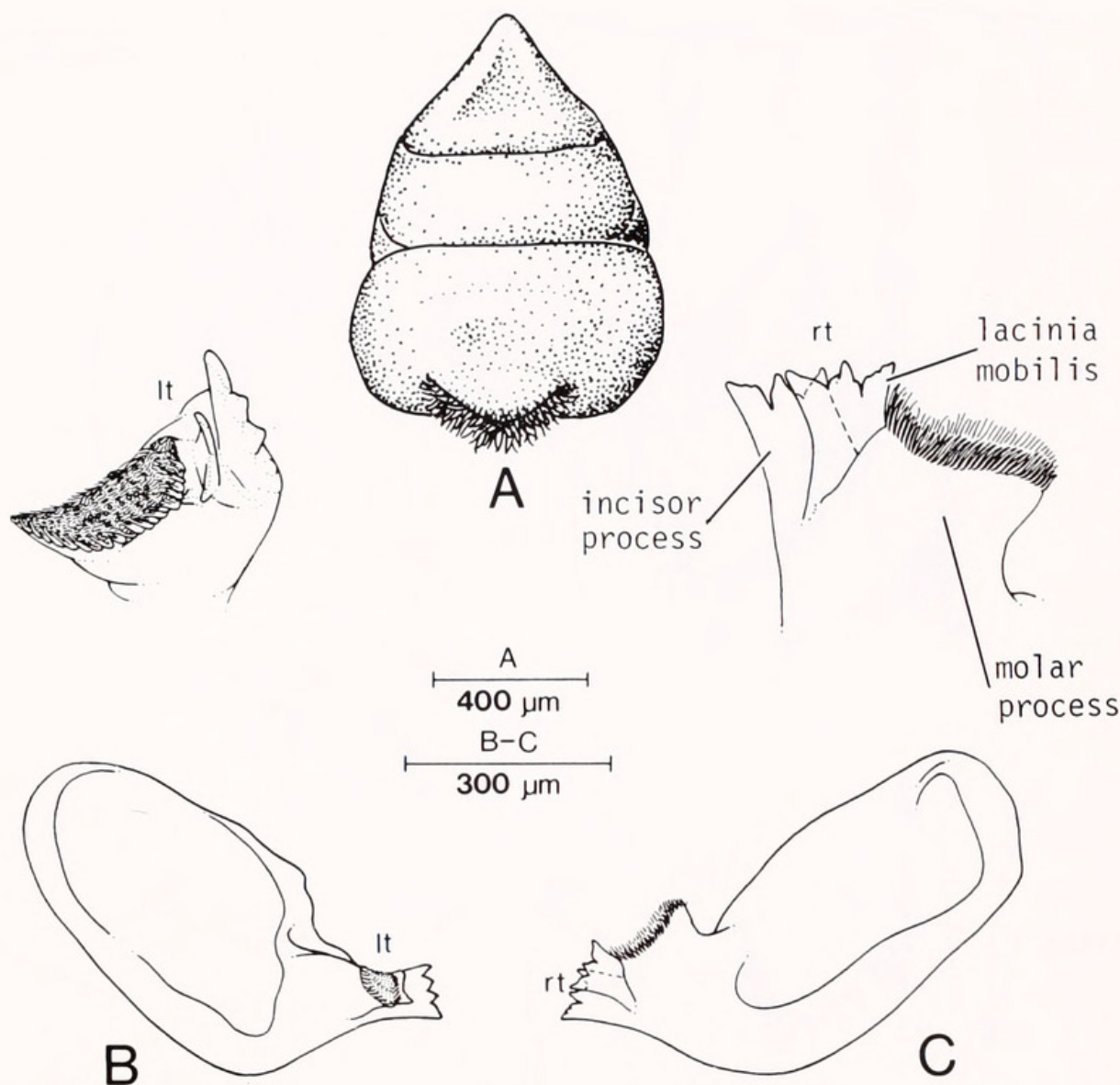
Fig. 3. *Speleonectes lucayensis.* A) labrum, ventral surface; B) left mandible dorso-posterior view with enlargement; C) right mandible dorso-posterior view with enlargement.

terminally tapered, and equipped with thumb-like spines about half way along their length (Fig. 6A).

The biramous antennules (Fig. 2B) are very well-developed and somewhat ventro-laterally directed. The peduncle is composed apparently of two articles, though the separating suture is not well developed. The proximal joint is enlarged ventrally to accommodate a pad that bears a battery of closely packed rows with from two to four long aesthetascs per row (Fig. 6 A, B). These aesthetascs extend posteriorly towards the labrum and cover the antennae. The distal segment of the antennular peduncle is bifurcate, each branch bearing a flagellum. The dorsal flagellum is robust and composed of 12 segments. The ventral flagellum is shorter than the dorsal by half and is composed of eight segments. Each segment of these flagella has a tuft of two to four short, simple setae on the disto-ventral margin, in addition

to scattered setae along the shafts of each segment. Both flagella terminate in tufts of short simple setae.

The biramous antennae (Fig. 2C) are moderate in size. The protopod has two articles, the proximal joint is somewhat longer than the distal unit, and the line of articulation between the two articles is somewhat oblique. The proximal segment of the protopod is equipped with a row of 5 short setae along the median margin, whereas the distal joint has a row of seven short to moderate setae. The exopod is an oval scale extending medially and posteriorly from the second protopod segment. It bears along its margins about 21 setae, the bases of which are more robust than the distal shafts. The endopod is composed of three broad, subequal segments which arc laterally from their origin on the distal aspect of the protopod. Each segment is equipped with setae along its margins; the most proximal with approx-
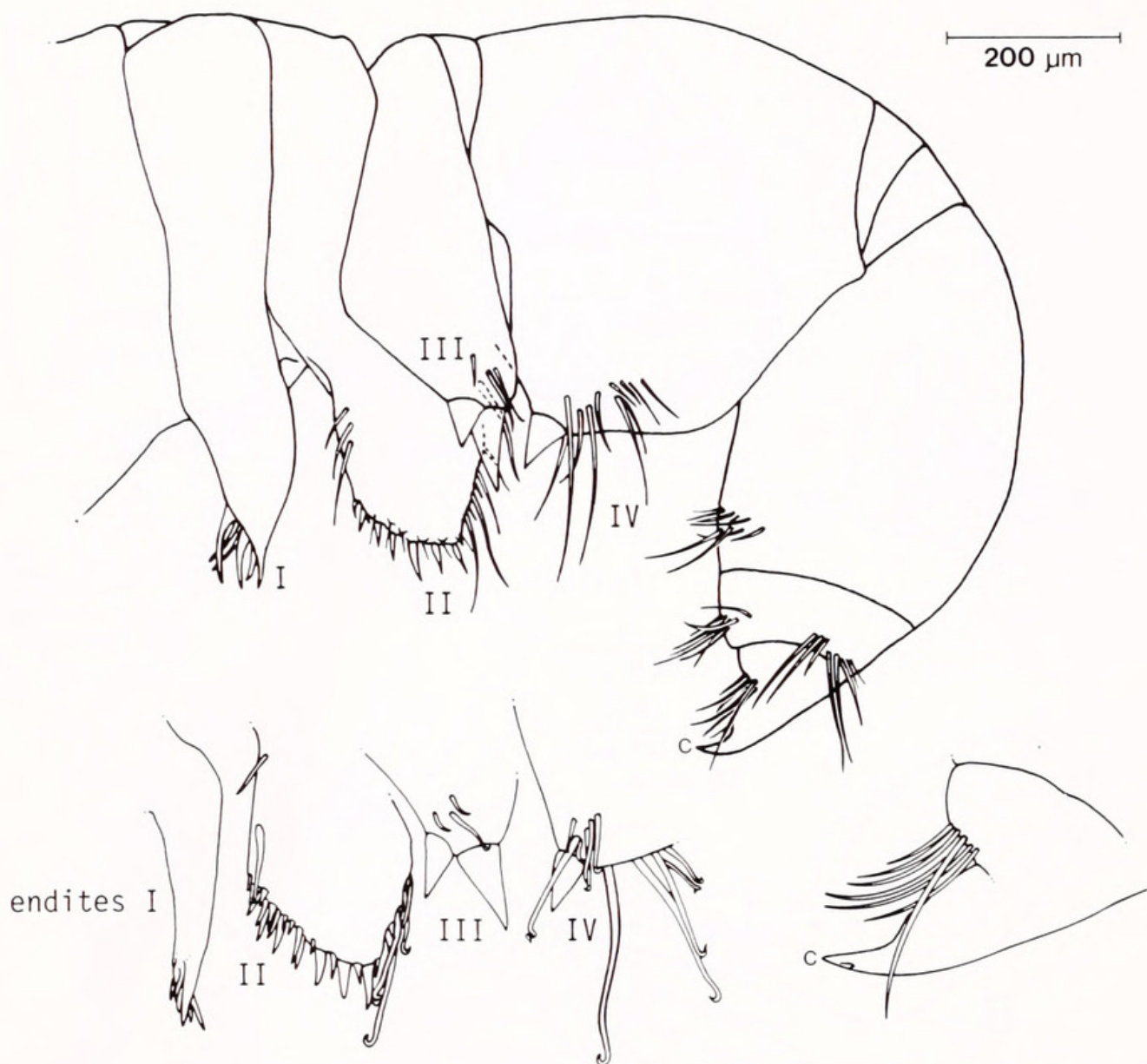
Fig. 4. *Speleonectes lucayensis*. Right maxillule, posterior surface, with I–IV and c providing details of designated endites and limb tip.

imately seven, the next with about eight, and the most distal with 19. These distal 19 are not in a single row, rather 10 are arranged in a double row along the distal margin, whereas the proximal anterior and posterior margins of this segment bear single rows of setae. All the setae on the antennal segments are plumose (Fig. 2C-x).

The labrum (Fig. 3A) is a large fleshy structure. It narrows anteriorly to form a subtriangular portion marked off posteriorly by a slight furrow. The bulbous posterior portion extends over the mouth proper to form an atrium oris. The posterior margin of the labrum bears a median setose lobe.

The mandibles (Fig. 3B, C) are asymmetrical. They take origin on the side of the cephalon and extend ventrally under the posterior lobe of the labrum into the atrium oris. The molar processes are located on pedestals, and are composed of broad flat basins

covered with a dense row of spines. The left incisor process is a row of four large denticles. The right incisor process is formed by a row of three large denticles. Between the incisor and molar processes are prominent laciniae mobiles; that on the left is concave and sickle-like, that on the right is formed by a row of three large denticles.

The paragnaths flank the atrium oris, and are covered by fine, densely packed setae.

The maxillules (Fig. 4) are very robust, uniramous, prehensile, and seven-segmented. Segments one to four are equipped with robust endites (Fig. 6C). Although all segments are capable of movement in relation to adjacent segments, the principal point of flexure for an elbow occurs between segments four and five. The first four segments bear one endite each. The most proximal of these (Fig. 4, endite I) terminates in a stout spine, adjacent to

endites I

II III IV

A
200 µm
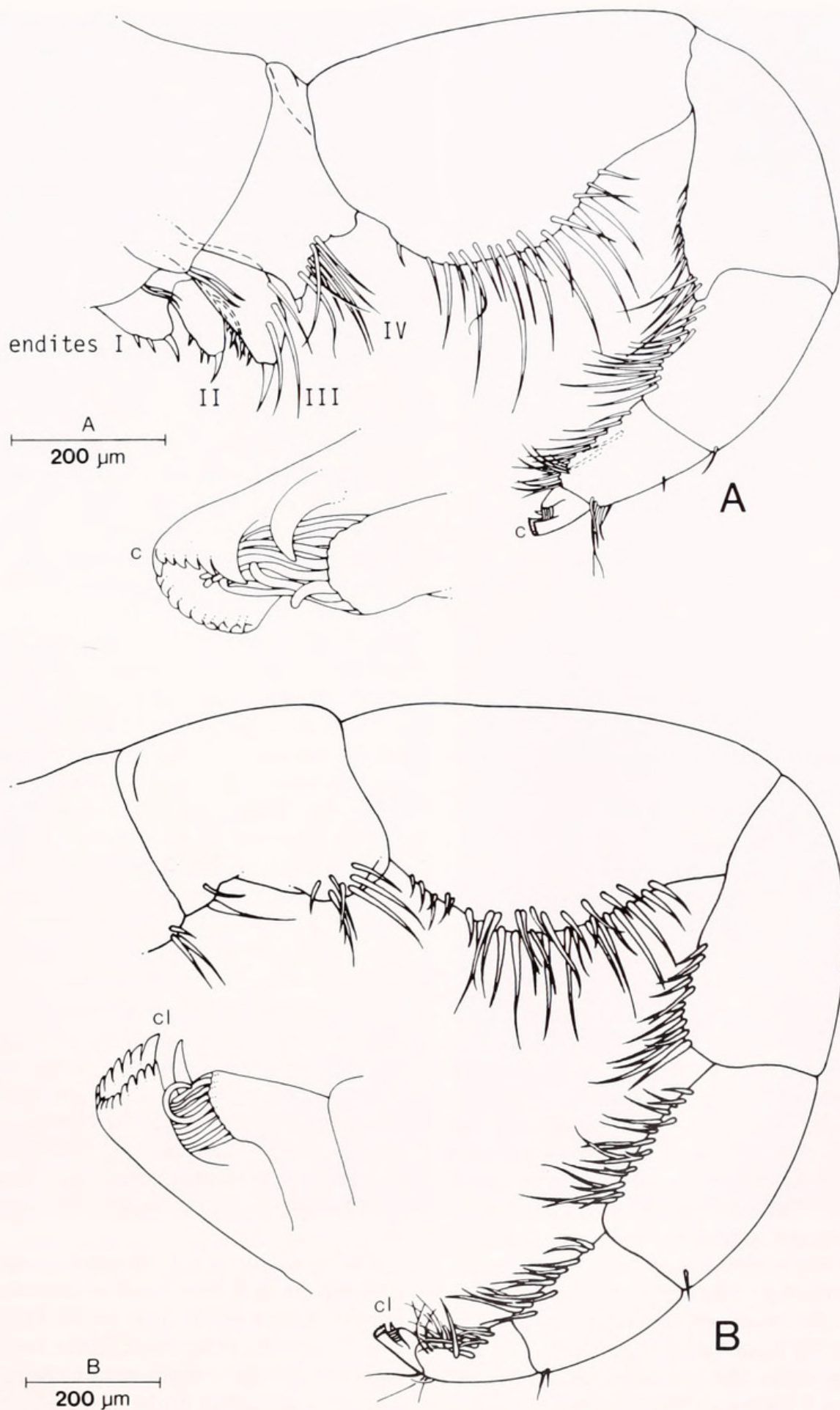
c

A

c

cl

cl

B
200 µm

B

Fig. 5. *Speleonectes lucayensis*. A) left maxilla, anterior surface, with c as postero-oblique view of limb tip; B) left maxillipede, anterior view, with cl as anterior view of limb tip.

TABLE 1. Representative measurements in mm of *Speleonectes lucayensis*. Not all dimensions could be measured on all the specimens at hand.

Feature	Range	n	$\bar{x}$	s	V
Body length	15.0–23.8	3	20.0	4.5 ± 3.2	22.5
Head length	1.5–2.5	4	2.0	0.4 ± 0.2	20.0
Head width	1.6–1.8	2	1.7	0.1 ± 0.1	5.9
Trunk segs.	29–32	4	30	1.3 ± 0.7	4.3
T1 length	0.3–0.4	3	0.4	0.1 ± .04	25.0
T1 width	1.2–1.2	2	1.2		
T2 length	0.4–0.5	4	0.5	0.1 ± .04	20.0
T2 width	1.4–1.9	3	1.6	0.2 ± 0.2	12.5
T14 length	0.6–0.8	4	0.7	0.1 ± 0.1	14.3
T14 width	1.4–2.1	3	1.8	0.4 + 0.2	22.2
Anal seg. length	0.5–0.6	4	0.5	0.1 ± 0.1	20.0
Anal seg. width	0.3–0.6	3	0.5	0.2 ± 0.1	40.0
Caudal ramus length	0.3–0.5	4	0.4	0.1 ± .05	25.0
Caudal ramus width	0.1–0.2	4	0.1	.05 ± .03	50.0

which is a row of six stout simple setae. The next endite (Fig. 4, endite II) is rather broad and flap-like; the proximal margin has three simple setae, the distal margin has four long simple setae, and the apical margin has eight to nine robust spine-like setae each flanked by small simple setae. The third segment of the limb has two short, robust setae at the apex of its cone-like endite (Fig. 4, endite III). The flanks of the cone have six slender, simple setae scattered around the anterior and posterior surfaces. The fourth segment is relatively long, and bears a large lobate endite (Fig. 4, endite IV) that has a single, robust seta at its apex. This apical seta, when the segment is flexed, interlocks with the two apical setae on endite III (Fig. 6C). Distal to the apical seta on endite IV are 12 variously short and long simple setae extending in rows toward the articulation with the fifth segment. The fifth segment has a cluster of six to eight simple setae on the disto-ventral surface of the segment. The sixth segment has a cluster of eight simple setae about ⅔ the length of the joint on the ventral surface and another cluster of eight simple setae along the anterior aspect of the disto-dorsal margin of the segment. The seventh joint terminates in a prominent talon-like structure (Fig. 4, inset) which is surmounted by a large pore. At the base of this claw, along the ventral surface of the segment, is a cluster of seven medium to large simple setae.

The maxillae (Fig. 5A) are robust, uniramous, prehensile limbs, composed of seven segments. The principal point of flexure occurs between the third and fourth segments. The first segment is relatively long and bears a series of three endites (Fig. 5A, endites I to III). The first endite is small and has a modestly robust simple seta at its apex, and two short simple setae proximally. The second endite is modest in size and has a robust simple seta at its apex, and three short simple setae proximally. The third endite is relatively large, has a robust, simple seta at its apex that is flanked proximally by a row of four or five small simple setae, and distally by a row of three large simple setae. The second segment of the limb is almost thumb-like and bears a large, lobe-like endite. This endite is surmounted by a small, spine-like seta that is abutted distally along the margin of the endite by a row of about 12 densely packed moderate to long simple setae. The third segment of the limb is very long, and has its ventral surface developed as an arcuate double crested endite. Each crest is marked by a row of 14 to 15 moderate to long simple setae. The third to sixth segments decrease in length as one proceeds distally in the series. These segments do not have endites, but do bear rows of moderate to long simple setae along their ventral margins. The seventh segment terminates in a distinctive claw composed of a row of densely spaced spines arranged in an arcuate or horseshoe-shaped crest. This spine row is opposed by a setose thumb-like pad. Between the setal pad and the spine row on the posterior surface of the claw is a separate arcuate spine (Fig. 5A-c).

The maxillipedes (Fig. 5B) are very long, uniramous, robust, prehensile limbs composed of eight segments. The principal flexure occurs between the third and fourth segments. With the exception of the basal endites, these limbs are very similar in form to that of the maxillae. The two most proximal segments each bear a weakly developed endite with moderate to long simple setae. The endite of the second segment is somewhat better developed than that of the first. The third segment bears an arcuate, double-crested endite, each crest with 16 to 18 moderate to long simple setae along its length. The fourth through seventh segments are progressively shorter as one proceeds distally in the series, and each segment has a row of moderate to long setae along its medial edge. The eighth segment of the limb is equipped with a distinctive claw identical to that seen on the maxilla terminus (Fig. 5B-c1; Fig. 7 A, B).

The trunk limbs are all biramous and nearly homonomous in form. The first limb has somewhat narrower rami than those which follow (Fig. 1B). The majority of the trunk limbs have broad subrectangular to oval segments on the rami (Fig. 1C). The most posterior limbs in the series, while biramous, are somewhat less setose than the larger anterior limbs, and are also smaller in size. All trunk limbs present a basic similarity in regard to the ar-
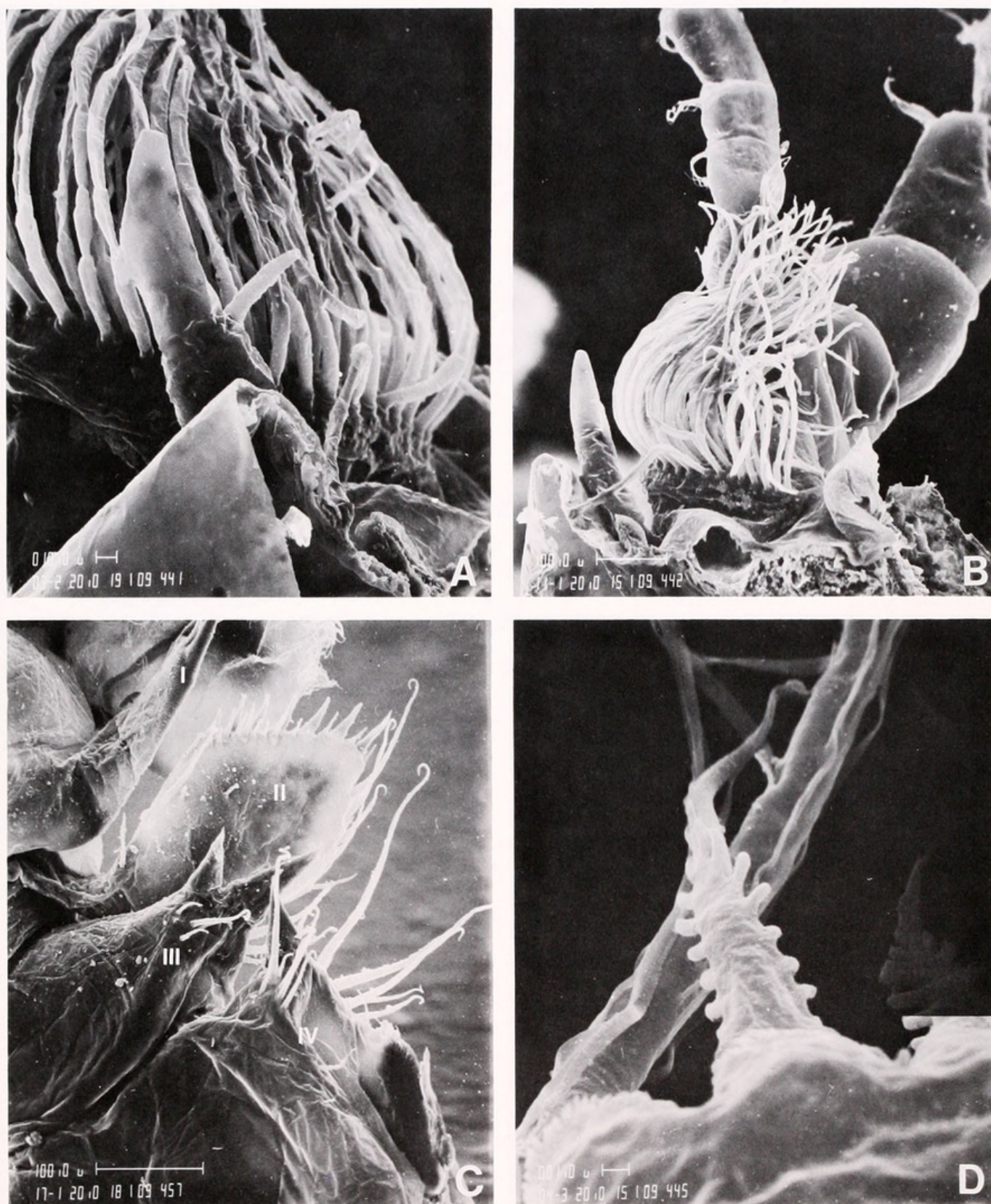
Fig. 6. *Speleonectes lucayensis.* A) anterior view of front edge of cephalon (specimen cut along midline), with anterior margin of head shield in front of frontal filament and aesthetascs of antennule behind; B) lateral view of A, showing pad of aesthetascs at base of biramous antennules; C) endites of maxillule (numbered I–IV), note apical setae on endites III and IV lack subsetules; D) comb seta of tenth trunk limb.
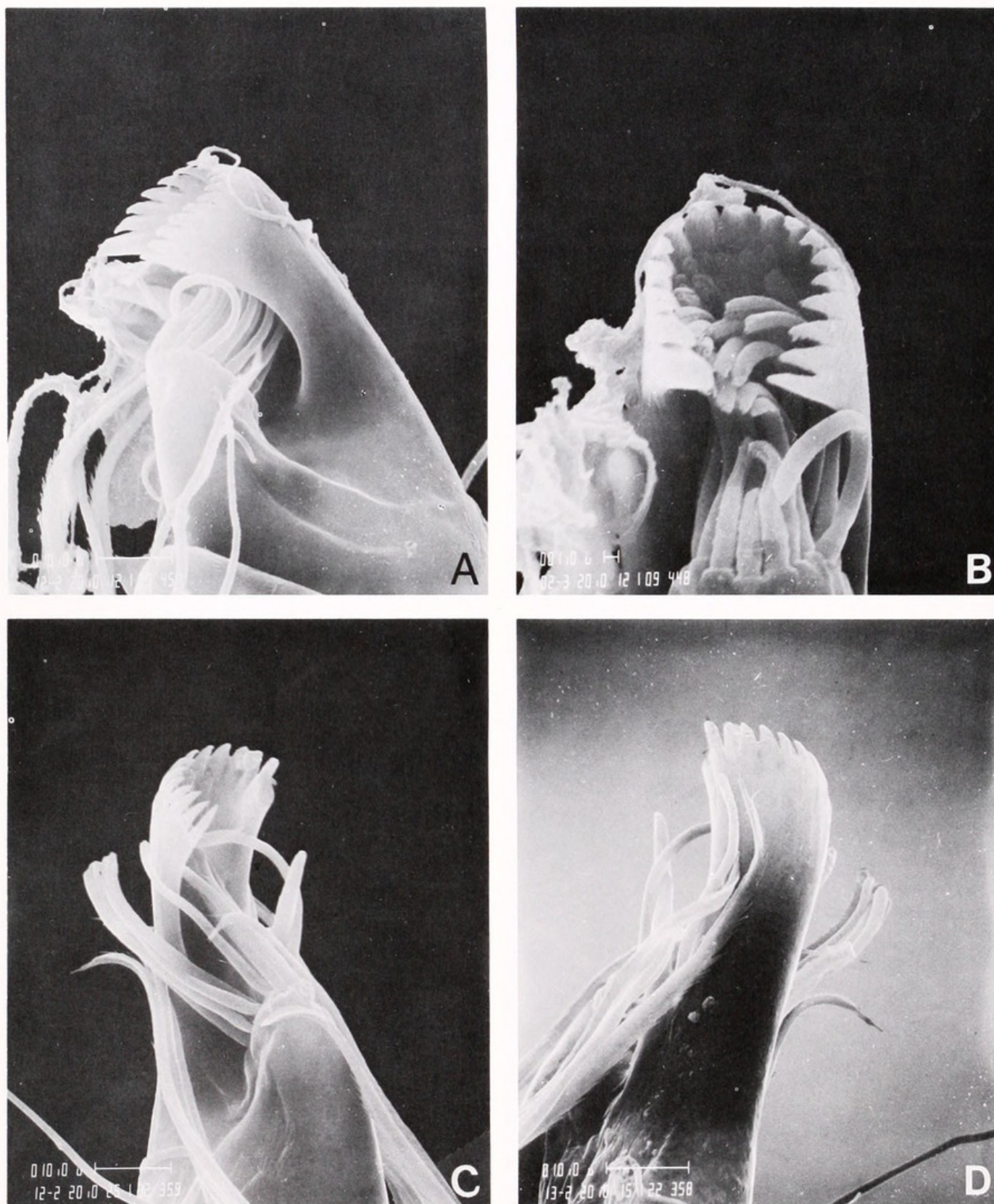
Fig. 7. *Speleonectes* maxilla and maxillipede limb tips. A, B) *S. lucayensis* maxillipede. A) lateral oblique view, B) ventral view; C, D) *S. ondinae* maxilla, C) lateral oblique view, D) lateral view.
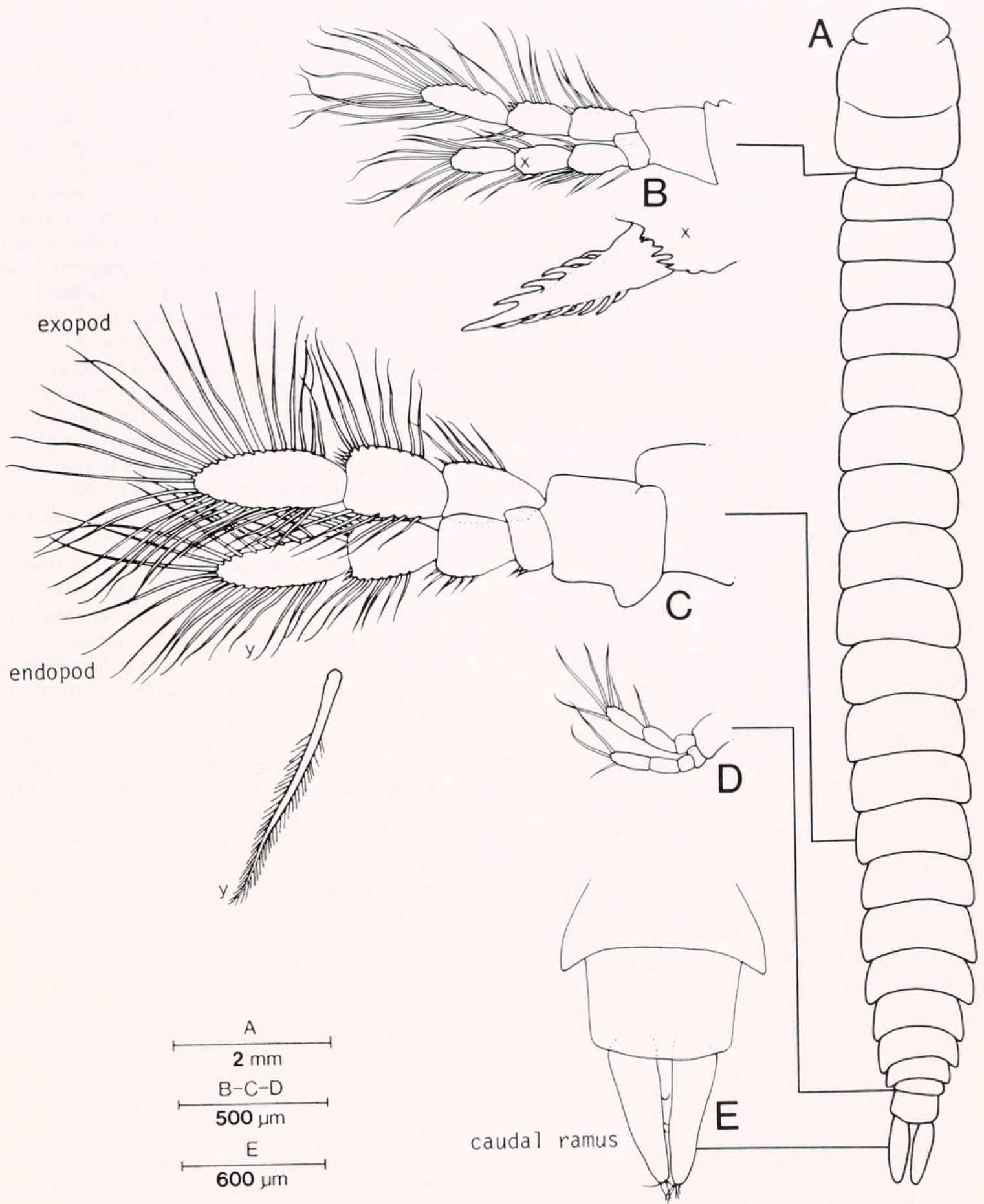
exopod

endopod

caudal ramus

A
2 mm
B-C-D
500 μm
E
600 μm

Fig. 8. *Speleonectes ondinae.* A) dorsal surface of body; B) posterior view of first trunk limb, with x as comb seta; C) fourteenth trunk limb, with y as plumose seta of margins and genital flap on protopod; D) last trunk limb; E) anal segment with caudal rami.

TABLE 2. Representative measurements in mm of available specimens of *Speleonectes ondinae*.

Feature	Range	n	$\bar{x}$	s	V
Body length	8.3–16.1	6	11.2	2.7 ± 1.2	24.1
Head length	1.2–2.2	6	1.6	0.3 ± 0.1	18.8
Head width	0.7–1.5	6	1.2	0.3 ± 0.1	25.0
Trunk segs.	19–25	6	21	2.2 ± 1.0	10.5
T1 length	0.2–0.4	6	0.3	.08 ± .04	26.7
T1 width	0.3–1.1	6	0.8	0.3 ± 0.1	37.5
T2 length	0.3–0.6	6	0.4	0.1 ± .04	25.0
T2 width	0.7–1.5	6	1.0	0.3 ± 0.1	30.0
T14 length	0.4–0.8	6	0.6	0.1 ± .06	16.7
T14 width	0.7–1.6	6	1.1	0.3 ± 0.1	27.3
Anal seg. length	0.3–0.4	6	0.4	.05 ± .02	12.5
Anal seg. width	0.3–0.6	6	0.4	0.1 ± .05	25.0
Caudal ramus length	0.4–0.8	6	0.7	0.2 ± .07	28.6
Caudal ramus width	0.1–0.2	6	0.2	.04 ± .02	20.0

rangement of different setal types on the rami. The most prominent setae are of the large plumose type and occupy most of the margins of the segments (Fig. 1C-x). A second type of seta has a comb-like form (Fig. 1C-y) in which a tall tapering shaft has round processes arranged along the margins of the shaft. The base of the seta is marked by a fan or crest of densely arranged comb-like spines (Fig. 6D). These distinctive comb setae are placed on the distal corners of the intermediate rami of the trunk limbs. They resemble similar comb-like setae in other groups of crustaceans that appear to be used in combing out or carding the subsetules of plumose setae. One additional kind of seta is noted on the disto-median corners of the two proximal segments of the endopods on the middle segments of the body. These are short, simple, spine-like setae (Fig. 1C-z).

Remarks. — The above description is considerably more detailed than that found in Yager (1981). This is due not only to the fact that more material of this species is now available, but also to new insight into understanding the anatomy of the species, derived from the discovery of additional taxa of nectiopodans.

SPELEONECTES ONDINAE
(Garcia-Valdecasas), 1984

Morlockia ondinae Garcia-Valdecasas, 1984:329.

Diagnosis. — Robust apical setae on endites of mouthparts with subsetules (Fig. 13C); fourteenth limb protopod with subtriangular flap over opening to gonopore; no differentiation of posterior sternite bars; rami of trunk limbs with segments longer than broad.

Holotype. — MNCN 14-VIII-84.

Type locality. — Tunel de la Atlantida, Jameos del Agua, Lanzarote, Canary Islands.

Additional material (examined by us). — USNM 216979 (dissected for SEM), K 32945-7. Yager Private Collection, 6 specimens, coll. from type locality between 1982–1984.

Description. — The cephalon is approximately $\frac{1}{7}$ the total length of the body (Fig. 8A). The cephalic shield tapers only slightly anteriorly; it bears a faint transverse groove about mid-length, and also a pair of short lateral grooves at the extreme anterior end of the cephalon. The animals at hand have 19 to 25 trunk segments (Table 2), with a mode of 20. The first tergite of the trunk is reduced in length and width over those that follow, and it is partially covered by the posterior margin of the cephalic shield. The trunk segments are produced laterally as broadly rounded pleurites, including the last tergite, which has moderately prominent pleura. The sternites of the trunk are reinforced with well-developed bars that are not particularly differentiated from each other along the length of the body (Frontispiece). The anal segment is wider than long (Fig. 8E). The caudal rami are somewhat longer than the anal segment, terminate in tufts of four simple setae, and bear two or three simple setae along their median margin. Measurements of available specimens are provided in Table 2.

There is a pair of short and relatively robust frontal processes (Fig. 9A) on the anterior part of the cephalon near the base of the antennules. These processes are almost club-like, terminally rounded, and have a small, thumb-like spine that arises half way along their length.

The biramous antennules (Fig. 9B) are well developed, ventro-laterally directed, and extend well beyond the cephalon. The peduncle is composed of two segments, though the separating suture is weakly developed. The proximal joint bears a large pad ventrally, which contains a battery of closely packed rows of long aesthetascs. These extend posteriorly over the antennae. The distal segment of the peduncle is somewhat bifurcate terminally where the flagella attach. The dorsal flagellum is the longer, and is composed of 12 articles. The ventral flagellum is composed of eight joints and is less than half the length of the dorsal ramus. Each segment of these flagella bear tufts of at least four simple setae along their disto-ventral margins, and both rami terminate in a tuft of three or four simple setae.

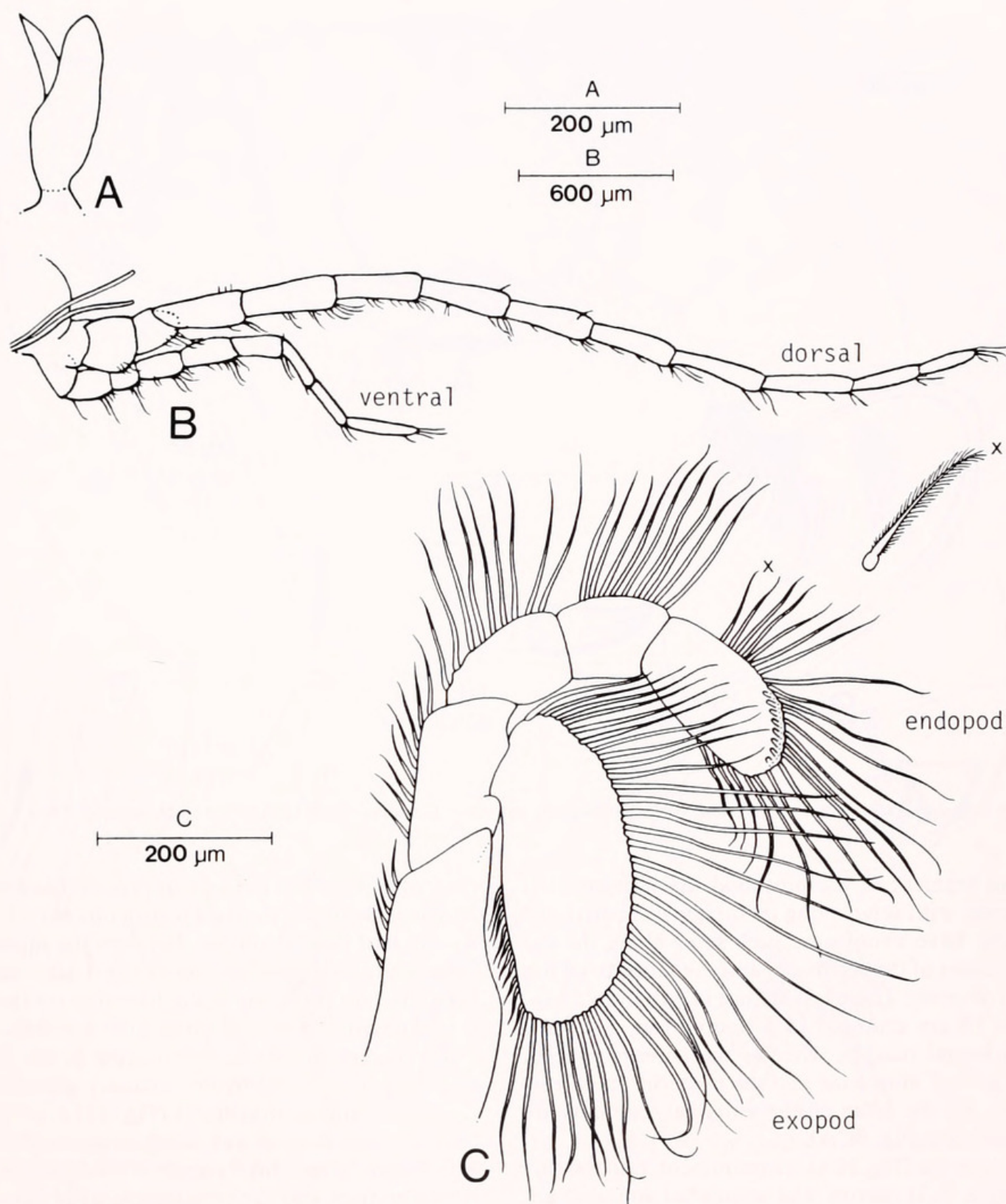The biramous antennae (Fig. 9C) are small to modest in size. The protopod is composed of two

Fig. 9. *Speleonectes ondinae.* A) left frontal filament, lateral view; B) left antennule, anterior view, with few aesthetascs of basal pad drawn; C) left antenna, ventral view, with x as plumose seta of margins.

articles. The proximal segment is much longer than the distal segment, and the line of articulation between them lies at an oblique angle. The proximal segment is equipped with a row of six short setae along the medial margin near the distal end of the limb. The distal segment of the protopod has a row of eight setae on the medial margin. The exopod is an oval scale extending medially and posteriorly from the lateral edge of the distal protopodal segment. The exopod bears along its margins about 50 setae, the bases of which are only slightly more robust than the distal shafts. The endopod is composed of three subequal segments which arc laterally from their point of origin on the distal end of the
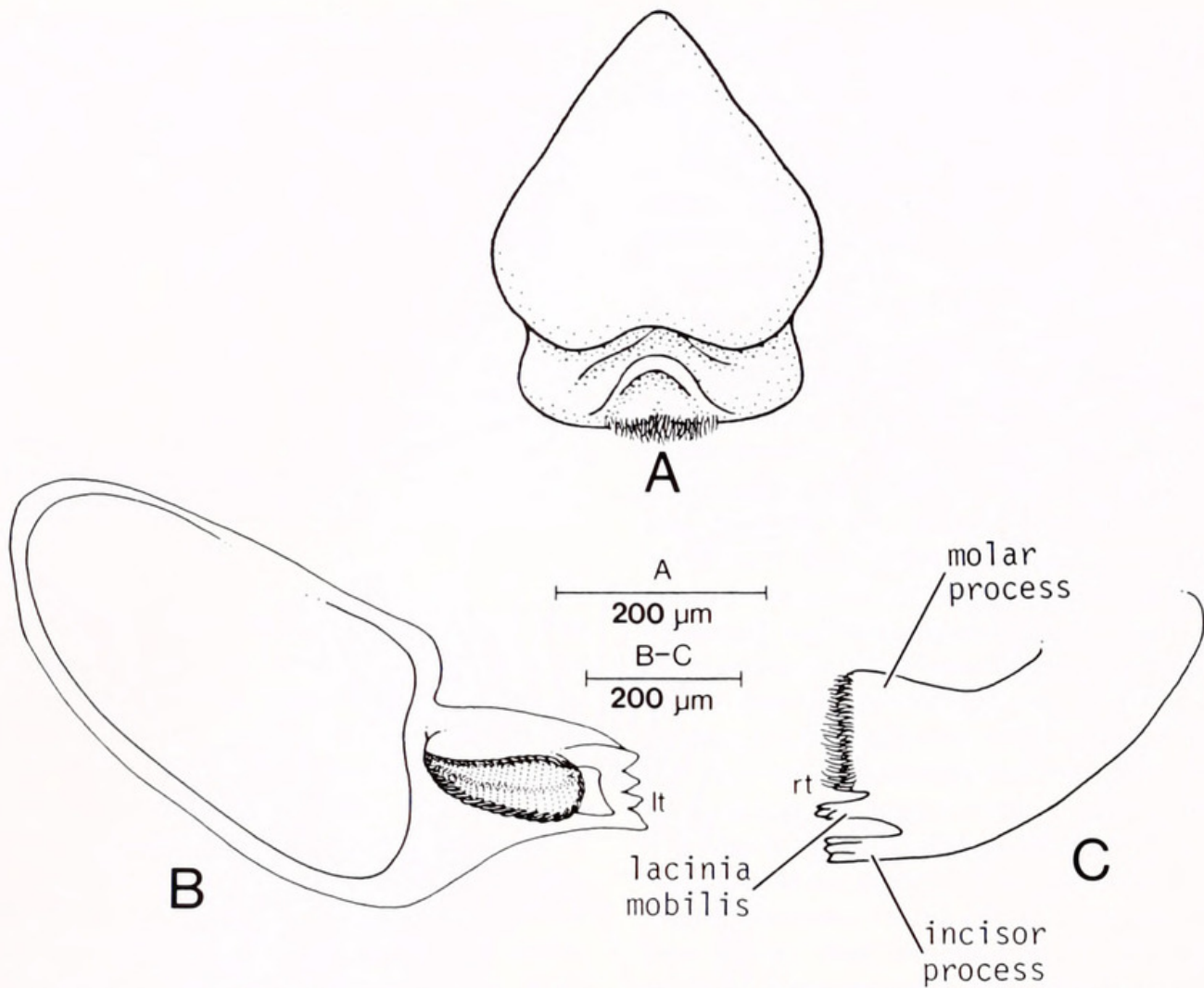
Fig. 10. *Speleonectes ondinae.* A) labrum, ventral surface; B) left mandible dorsal view; C) right mandible anterior view.

second segment of the protopod. Each segment is equipped with setae along its margins; the first two of these have about nine such setae along the anterior edges of the segments, and the most distal has about 30 setae. These last are not in one simple row, rather 16 are arranged in a double row along the distal lateral margin, whereas the anterior margin has a row of nine setae and the posterior has a row of five. All the setae on the antennal segments are plumose (see Fig. 9C-x).

The labrum (Fig. 10A) is a prominent, rather fleshy structure. It is narrow and somewhat rounded anteriorly, and dilineated by a furrow from the posterior portion that forms the atrium oris. The posterior margin of the labrum is equipped with a dense array of ribbon-like setae, and the surface just anterior to this is decorated with a slight fossa.

The mandibles (Fig. 10B, C) are asymmetrical. The body of the limbs are very large and occupy the sides of the cephalon. The working ends of the limbs insert under the labrum into the atrium oris. The molar processes are located on pedestals, and are composed of a broad flat basin covered by dense

rows of spines. The left incisor process has a row of four large denticles; the right incisor process is formed by a row of three denticles. Between the molar and incisor processes are well-developed laciniae mobiles; that on the left is sickle-like, that on the right is composed of a row of three large denticles.

The paragnaths flank the opening to the atrium oris, and are covered by fine, densely packed setae.

The uniramous maxillules (Fig. 11) are very robust, prehensile, and composed of seven segments. The four most proximal segments are equipped with robust endites, and the principle point of flexure for the limb occurs between the fourth and fifth segments. The most proximal segment bears an endite (Fig. 11, endite I) that is rather long and narrow, and terminates in a stout spine located somewhat anteriorly on the distal end of the endite. Adjacent to this spine is a double row of six shorter, stout, spine-like setae located along the apical edge of the endite. The most posterior of these is subsetulate (Fig. 13C). The endite of the second segment (Fig. 11, endite II) is rather broad and flap-like. It bears a row of five spine-like setae along the proximal
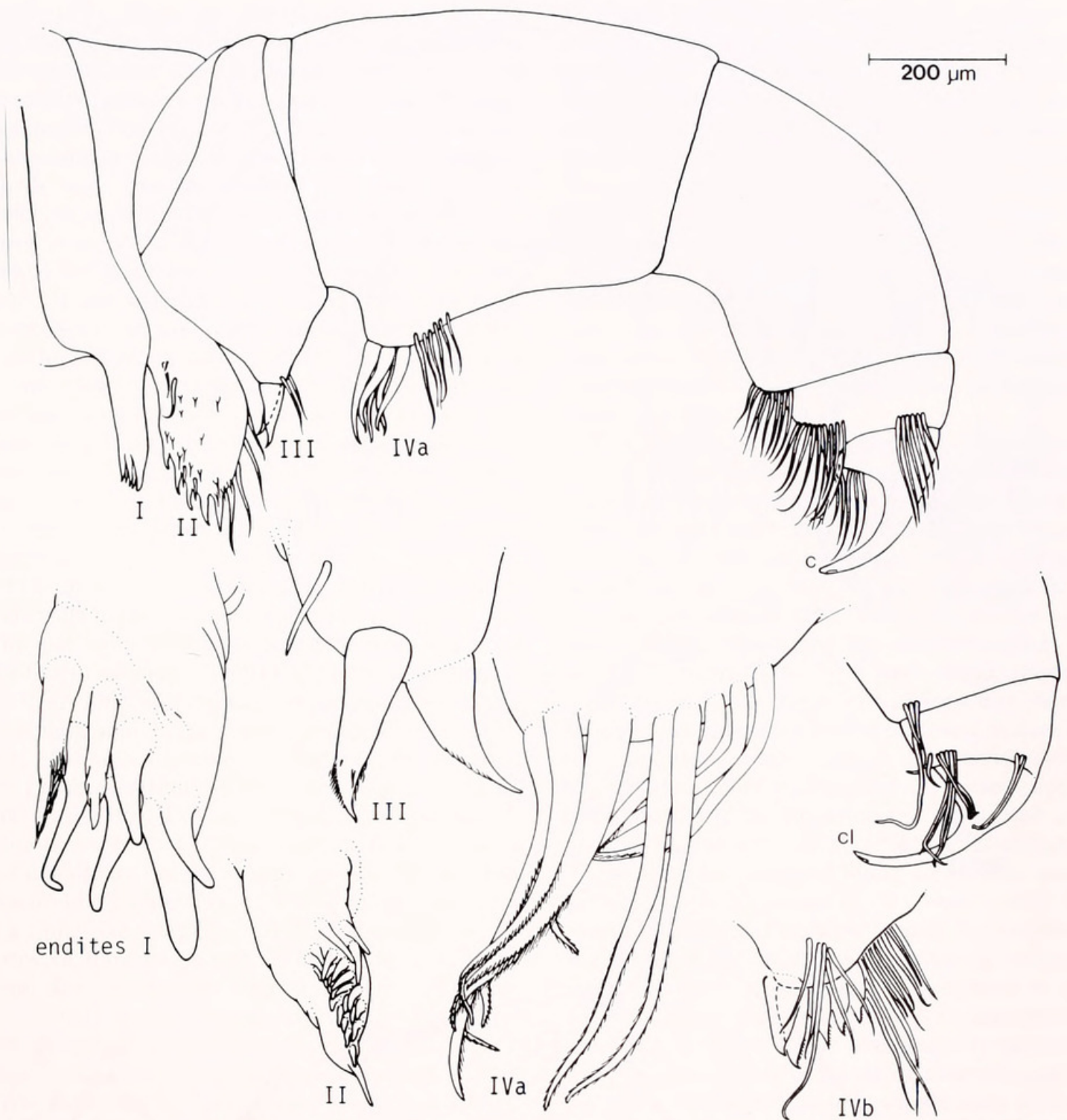
Fig. 11. *Speleonectes ondinae.* Left maxillule, anterior surface, with I–IV providing details of designated endites and limb tip; IVa detail of left limb illustrated, IVb and cl details of right limb posterior surface.

margin; a row of four moderate to long, simple setae along the distal margin; short to moderate simple setae scattered on the anterior face, especially near the outer margin; and several additional simple setae in one or more rows near the outer margin of the posterior face. The lobes of the paragnaths are inserted between the first two endites of this limb, and the whole complex flanks the mouth laterally. The third segment of the limb is rather short and is developed ventrally as a cone-shaped endite (Fig.

11, endite III). This endite is surmounted at its apex by two short, very stout, spine-like, subsetulate setae (Fig. 13C) that are flanked by a few, short, simple setae. The fourth segment of the limb is relatively long and bears a large, lobate, subtriangular endite whose apex is located proximally on the segment (Fig. 11, endite IV). The apex is equipped with five robust subsetulate setae. These vary in different individuals from being rather long and slender (Fig. 11, endite IVa) to quite short and stout (Fig. 11,
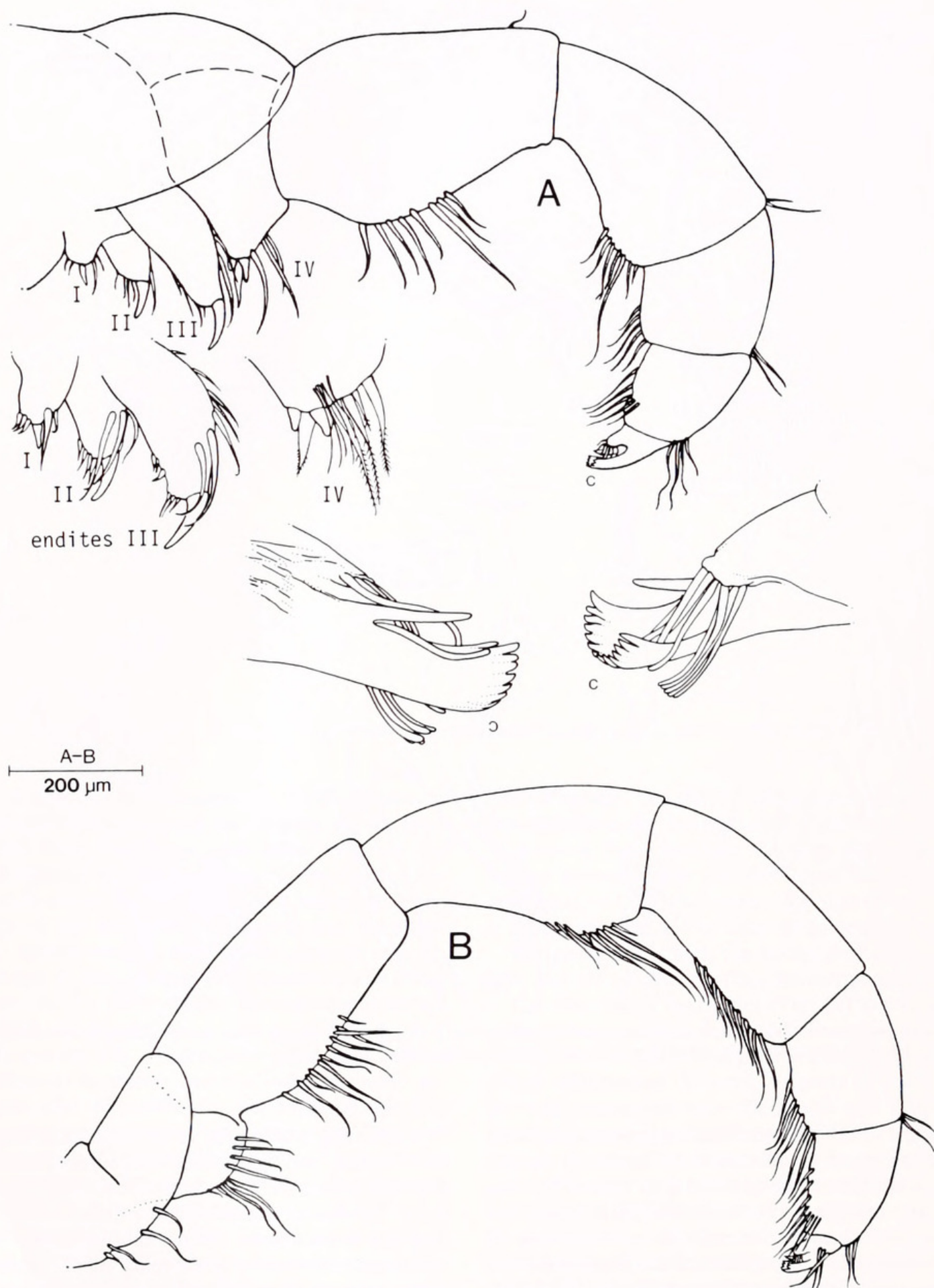
Fig. 12. *Speleonectes ondinae.* A) left maxilla, anterior surface, wtih I–IV and c providing details of designated endites and limb tip; B) left maxillipede, anterior surface.

endite IVb). These apical setae are flanked distally by a double row of six to ten moderately long, weakly subsetulate setae. An additional cluster of five of these setae appears on the posterior face of some specimens (Fig. 11, endite IVb). The fifth segment of the limb is slightly shorter and narrower than the fourth, and bears two clusters of at least 12 moderately long, simple setae on the anterior and posterior faces of the disto-ventral margin of the segment. The sixth segment of the maxillule is very short. It has anterior and posterior rows of long, simple setae on the ventral surface approximately ⅔ of the way along the length of the segment, as well as matching rows on the lateral surface about ¾ of the way along the length of the article. The seventh segment is short, and developed as a single, long, talon-like claw or fang (Fig. 13B) terminating in a large pore (Fig. 11-cl). There are small clusters of densely packed, short to moderate, simple setae arranged around the base of the claw.

The uniramous maxillae (Fig. 12A) are robust, prehensile limbs composed of seven segments. The principal point of flexure occurs between the third and fourth articles of the limb. The first segment is relatively long, somewhat bent about midway along its length, and bears three digitiform endites directed towards the mouth. These increase in size as one proceeds distally in the series. The most proximal endite (Fig. 12A, endite I) has a single, apical, spine-like seta that is flanked proximally by three and distally by two short to moderate simple setae. The middle endite (Fig. 12A, endite II) terminates in a spine-like seta, which is flanked proximally by a row of four short, simple setae and distally by about three moderately long, simple setae. The distal endite (Fig. 12A, endite III) is surmounted apically by a single spine-like setae that is flanked proximally by six short, simple setae and distally by about seven moderate to long simple setae. The second segment of the limb, lying at an angle to the distal joint, bears a somewhat conical endite (Fig. 12A, endite IV) that bears three stout setae on the apex, the middle one subsetulate, with two groups of moderately long setae arranged distally. The more anterior cluster is composed of about five very fine setae and the more posterior row has about five robust setae. These latter are subsetulate. The third segment of the limb is long, with a gently convex ventral surface bearing two rows of about eight to 12 long simple setae. The fourth segment is somewhat shorter than the third, with the ventral margin convex distally, where it bears seven or more moderate to long simple setae. The distodorsal margin

is armed with two moderately long, simple setae. The fifth segment of the maxilla is about ½ the length of the fourth and bears a cluster of setae of varying lengths distoventrally, and two simple setae on the distodorsal margin. The sixth segment has several small clusters of moderate to long simple setae along the ventral surface and another cluster on the distodorsal margin. The seventh segment is short and terminates in a complex claw (Fig. 12A-c). The terminus of the claw is an arcuate or horseshoe-shaped row of densely spaced spines that is flanked posteriorly by a single stout arcuate spine. These are opposed by a thumb-like setose pad whose filamentary elements typically lie within the basin of the arcuate spine row (Fig. 7C, D).

The uniramous maxillipedes (Fig. 12B) are long, robust, prehensile limbs, and are composed of eight segments. The principal point of flexure occurs between the third and fourth segments. The most proximal segment is short, showing complex folding on its surface, or what may be the very weak development of a ventral lobe. There are several moderate, simple setae along the ventral surface. The second segment of the limb has a small, rounded, distinctly pad-like endite with at least five short to moderate simple setae on the posterior surface and about four long simple setae on the anterior surface. The third segment is long, and the ventral surface has about 23 to 24 moderate to long, simple setae arranged in two rows of about 11 to 13 setae each. These setae are arranged along an arcuate convex surface that forms a sort of very weak endite. The fourth maxillipedal segment is long, but somewhat shorter than the third. Its distoventral surface is slightly inflated, with about 17 moderate to long simple setae in two rows. The fifth through seventh segments of the limb are progressively shorter as one proceeds distally in the series, and each segment has rows of moderate to long simple setae arranged along the distoventral edges of the articles. The eighth segment of the limb is equipped with a distinctive claw identical to that seen on the terminus of the maxillae.

The trunk is composed of from 19 to 25 homonomous segments (Fig. 8A), each bearing a pair of biramous, paddle-like limbs. Most of the limbs bear oval segments on the rami (Fig. 8C) and are all similar to each other, except in the first pair the rami are rather slender (Fig. 8B) and in the posterior limbs the segments are small and have fewer setae (Fig. 8D). All the trunk limbs present basically the same arrangements and kinds of setae. The most prominent and common are the plumose setae along
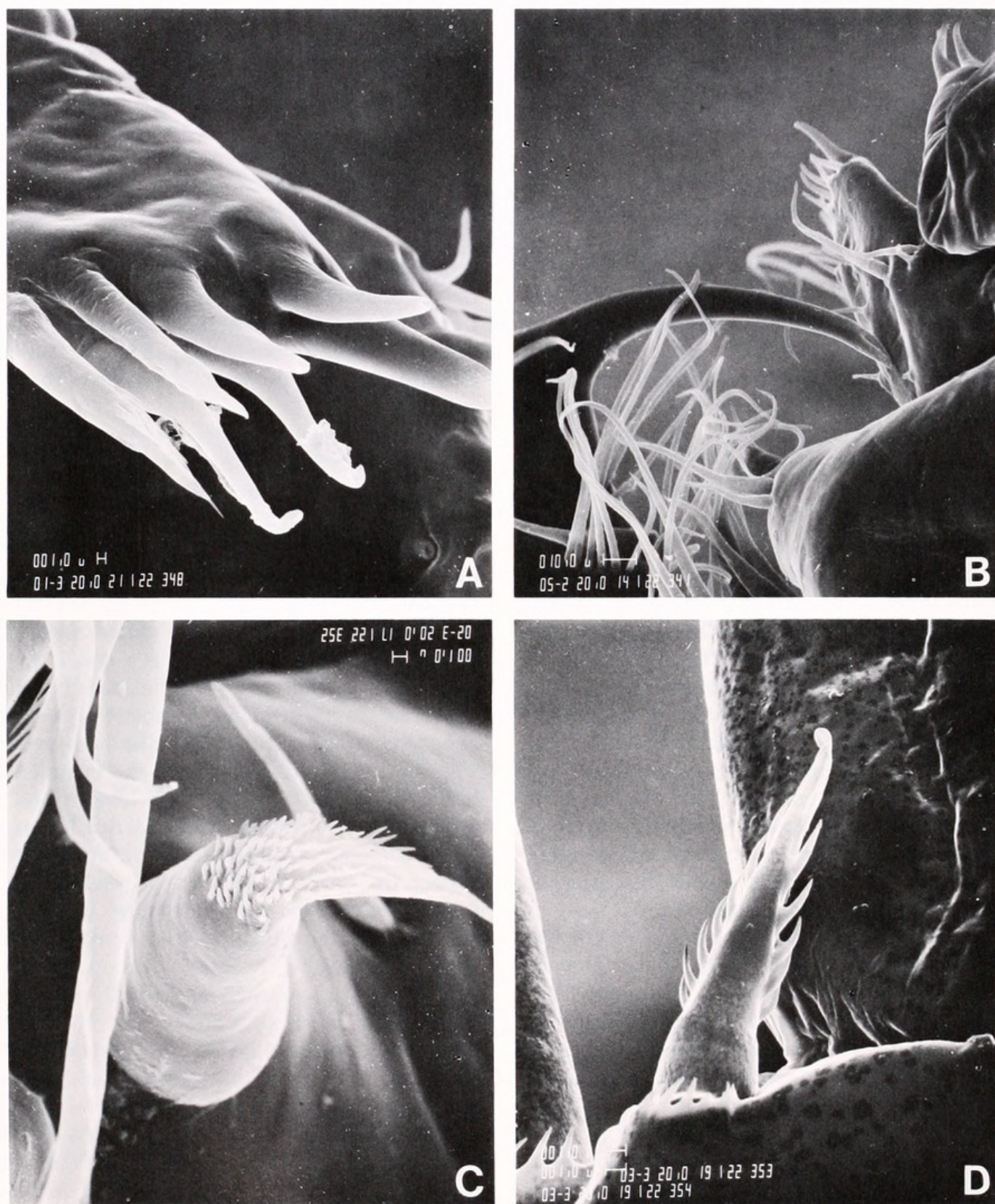
Fig. 13. *Speleonectes ondinae.* A) first endite of maxillule showing subsetulate setae; B) maxillule limb tip showing talon-like claw with terminal pore, limb tightly flexed with tip opposed to basal endites; C) subsetulate apical seta of third endite of maxillule; D) comb seta of second trunk limb.

the margins of the segments (Fig. 8C-y). A second setal type has a comb-like form (Fig. 8B-x), in which a tall, tapering shaft has pointed processes arranged along it margins. The bases of these comb setae are marked with a fan or crest of densely arrayed spines (Fig. 13D). This distinctive setal type is found at the distal and outer corners of the intermediate segments of the rami.

Remarks.—In the original description of this species Garcia-Valdecasas (1984) placed this taxon in its own genus, *Morlockia,* and in a separate monotypic family. However, our analysis reveals this species to be a close relative of *Speleonectes lucayensis.* Both taxa share several derived features evident in the diagnosis of *Speleonectes* provided above. The most notable of these is the distinctive horseshoe shaped comb on the claws of the maxillae and maxillipedes. Knowledge of these claws in other genera of nectiopodans, to be described below, shows that these structures are especially diagnostic. The sharing of such a derived feature probably indicates the common ancestry of *S. lucayensis* and *S. ondinae.* Separate generic and familial placement is therefore not justified for these two species.

Specimens examined in the present study exhibit considerable variation, not only in segment number but also body size (Table 2), more so than that in other known species of nectiopodans (see e.g., Tables 1 or 3). Most adult nectiopodans vary in segment number by only one or two, with body sizes varying in a similar manner. In *S. ondinae,* the ratio of head length to total body length is relatively large, about 1:7, while a more typical ratio is that seen for *S. lucayensis,* about 1:12. The larger ratio is actually more akin to that noted in juveniles of several nectiopodan species currently being studied by us. It may be of importance that the subsetulation characteristic of setae on mouthparts of *S. ondinae* is also seen on mouthparts of juveniles that appear to belong to *S. lucayensis.* Finally, the last limbs in the trunk series are especially small and lacking in setation, again more like that seen in juvenile nectiopodans than in adults (compare e.g., Fig. 8D to 1D).

Taken together, these observations suggest that specimens of *S. ondinae* are possibly immature individuals. However, the specimens appear to be beyond a juvenile stage: they have well-developed trunk pleurites and segmental digestive diverticula (features that are generally absent from juvenile forms). Therefore, it would not be surprising if future collections of the Canary Island nectiopodans produce larger animals of around 30 trunk segments,

with relatively small head to body length ratios. However, because of the strong suspicion on our part that the known specimens of *S. ondinae* are subadults, we have chosen at this time not to include the head/body ratio and the low trunk segment number in the diagnosis of this species. It is conceivable, however, that *S. ondinae* may be a paedomorphic derivative exhibiting a "juvenilized" head/body ratio and subsetulate setae as a result of evolution from some form more akin to *S. lucayensis.*

Genus LASIONECTES Yager and Schram, 1986

Lasionectes Yager and Schram, 1986:65.

Diagnosis.—Maxillae and maxillipedes subchelate, with segments three and those distal having rows of fine hair-like setae along medial edges, endites of second segments with central basin flanked by arrays of setae and pores, termini with distinctive trifid claw opposed to thumb-like setal pad.

Type species.—*Lasionectes entrichoma* Yager and Schram, 1986.

LASIONECTES ENTRICHOMA Yager and Schram, 1986

Lasionectes entrichoma Yager and Schram, 1986: 65.

Diagnosis.—Since there is only a single species currently recognized, the diagnosis is the same as that of the genus.

Holotype.—USNM 216978, coll. April 6, 1983.

Type locality.—Old Blue Hill Cave (tannic pool), Providenciales Island, Turks and Caicos, British West Indies.

Additional material.—Type locality. Yager Private Collection: 2 individuals, coll. Dec. 1982; 1 individual, coll. Oct. 29, 1982; 2 individuals, coll. Oct. 30, 1982. SDSNH Crustacean Collection: 2191, 7 individuals, coll. April 6, 1983; 2196, 2 individuals, coll. April 7, 1983; 2195, 4 individuals, coll. Oct. 1983; 2002, 1 sectioned individual, coll. April 6, 1983; 2003–2008, 6 sectioned individuals, coll. April 7, 1983; 2217, dissected and parts mounted for SEM.

Old Blue Hill cave (clear water pool), Providenciales, Turks and Caicos Islands. SDSNH Crustacean Collection: 2192, 4 individuals, coll. April 6, 1983; 2194, 6 individuals, coll. Oct. 17, 1983; 2009–2011, 3 sectioned individuals, coll. April 6, 1983; 2012–2013, 2 sectioned individuals, coll. April 7, 1983; 2014, 1 sectioned individual, coll. Oct. 17, 1983; 2216, whole mounted for SEM.
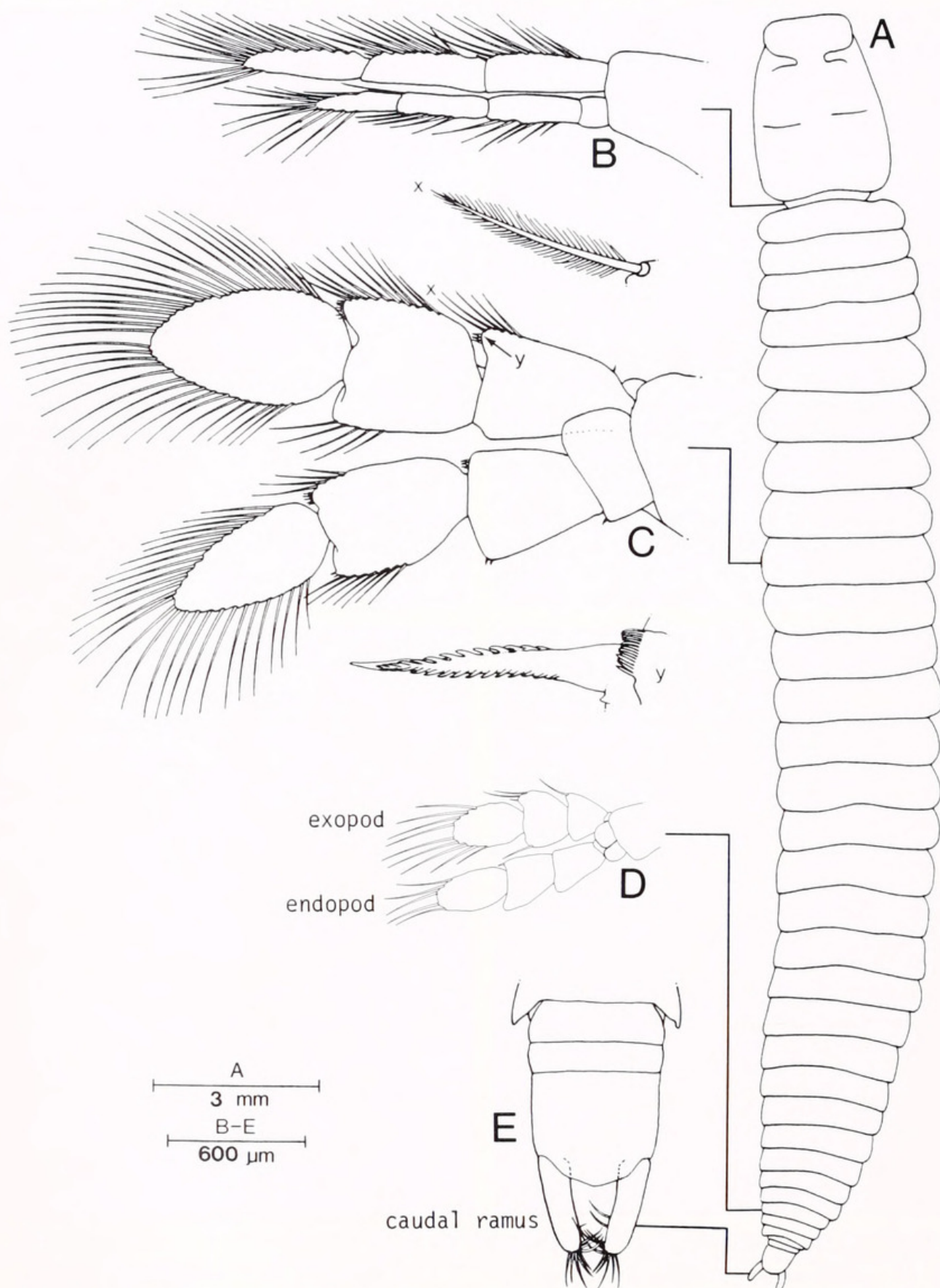
Fig. 14. *Lasionectes entrichoma.* A) dorsal surface of body; B) posterior view of first trunk limb; C) tenth trunk limb, with x and y as variant setae found along trunk limb margins; D) twenty-ninth trunk limb; E) anal segment with caudal rami.

Cottage Pond, North Caicos, Turks and Caicos Islands. SDSNH Crustacean Collections: 2197, 3 individuals, coll. Oct. 20, 1983; 2198, 2 individuals, Oct. 22, 1983.

Description.—The cephalon is about $\frac{1}{13}$ the total length of the body (Fig. 14A). The cephalic shield is slightly narrower anteriorly than posteriorly and, at the point of narrowing, bears a faint transverse
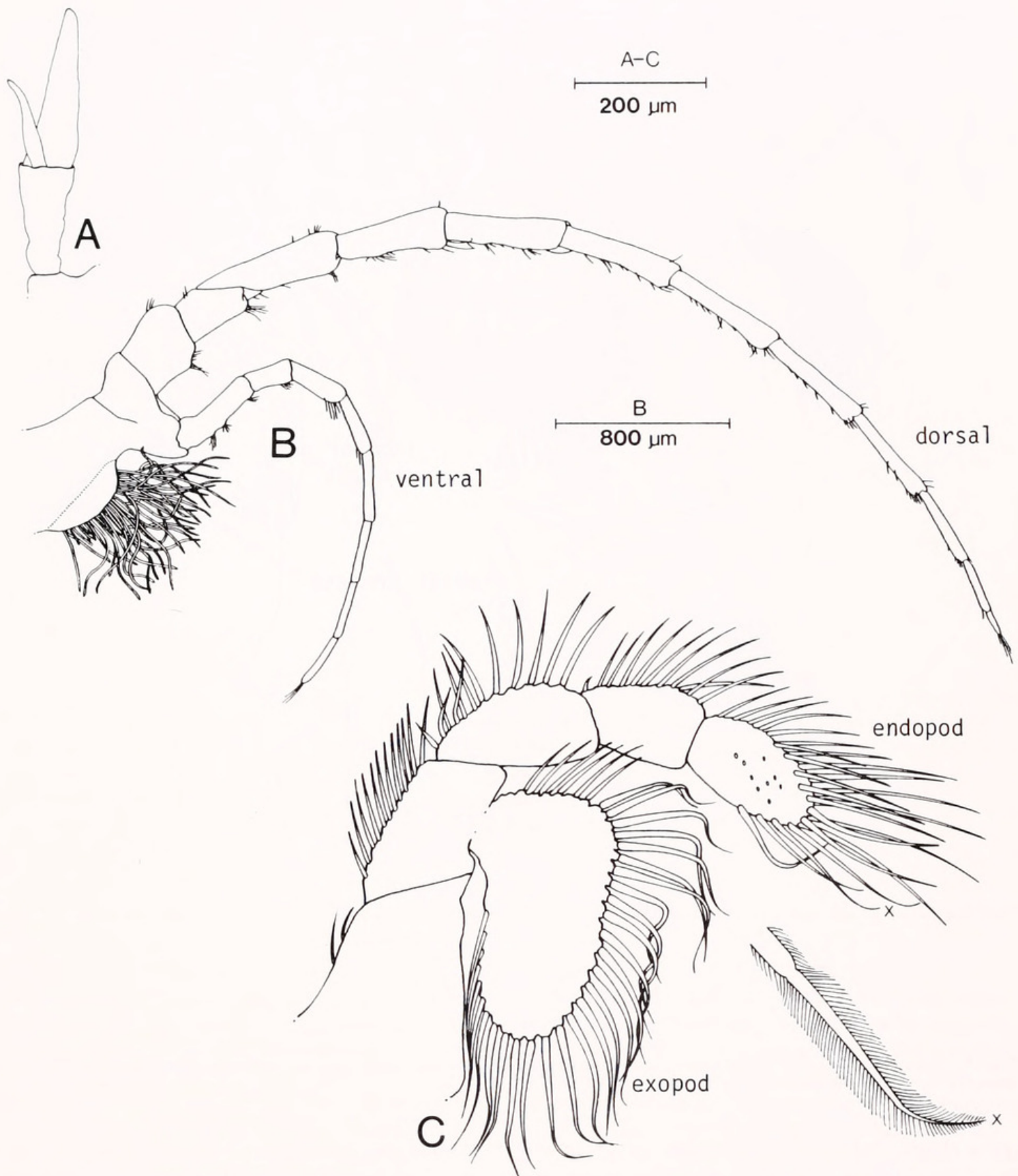
Fig. 15. *Lasionectes entrichoma.* A) left frontal filament, posterior view; B) left antennule, anterior view; C) left antenna, ventral view, with x as plumose seta found along margins.

groove that does not quite meet in the midline. There is an additional transverse groove on the shield about half way along its length. The anterior margin of the shield folds ventrad over the front of the cephalon. The adult trunk has a maximum of 32 segments.

The tergite of the first trunk segment is narrower and shorter than those that immediately follow, and is frequently covered in whole or in part by the posterior margin of the head shield. The trunk segments of the adult are produced laterally as prom-
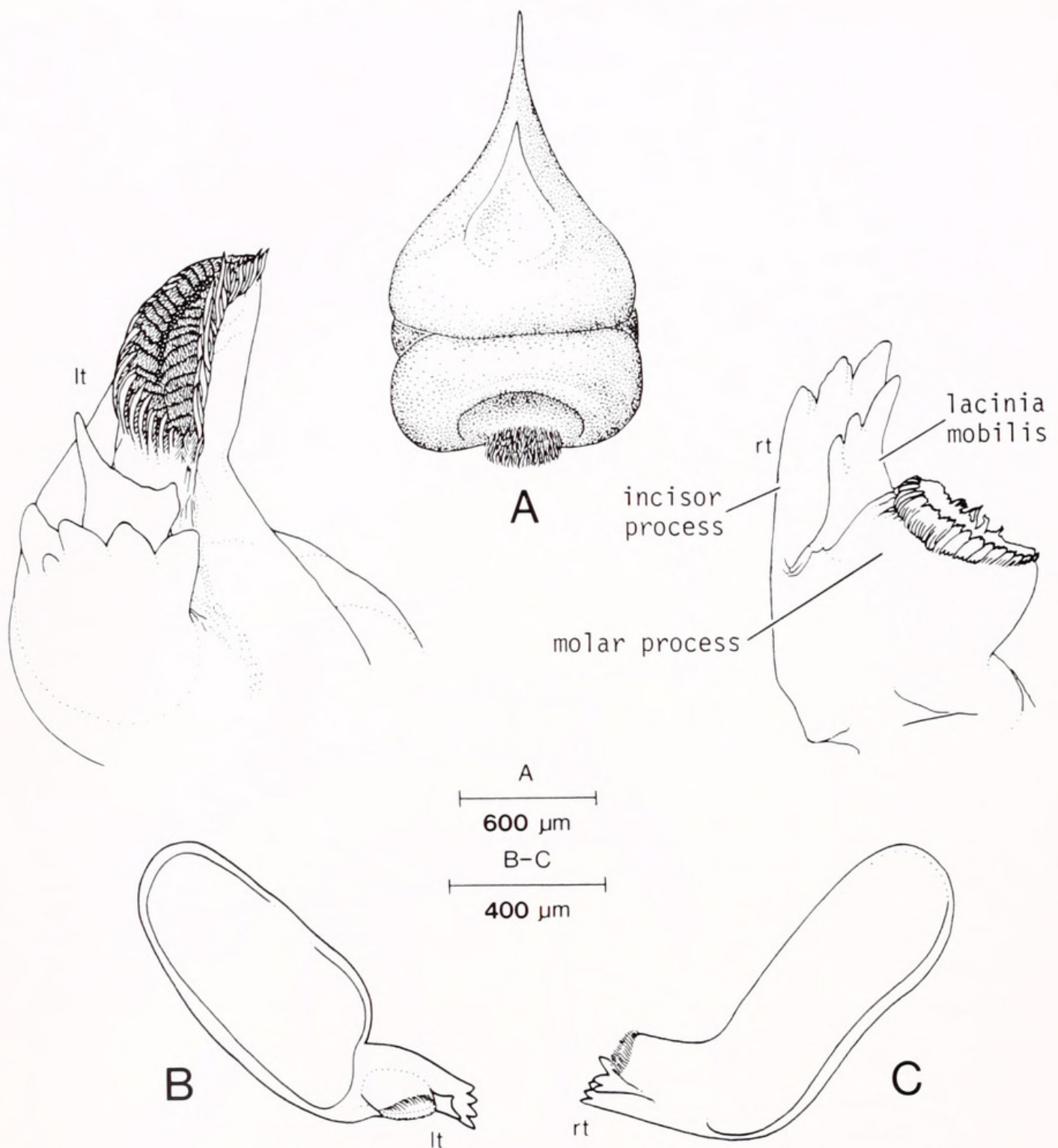
Fig. 16. *Lasionectes entrichoma.* A) labrum, ventral surface; B) left mandible dorsal view with enlargment; C) right mandible dorso-posterior view with enlargement.

inent pleura, and are rounded on their anterior and posterior corners. The most posterior trunk segments are greatly reduced (Fig. 14E). The sternites of the trunk segments bear distinct transverse bars along their posterior aspect (Fig. 27A). The bar of the fourteenth segment is developed at its lateral extent as triangular flaps that shield the gonopores located on the bases of the protopods of the fourteenth trunk limbs. The sternal bars from segments 24 posteriad are concave. The anal segment is about as wide as it is long, and the terminal anus is protected by a small anal flap (Fig. 27D). The caudal rami are slightly shorter than the length of the anal segment, and bear a cluster of short to moderate setae on their termini and 2 moderate setae along the medial surfaces (Fig. 14E). Measurements of a representative series of specimens are provided in Table 3.

A small pair of frontal filaments or processes are located on the anterior part of the ventral cephalon,
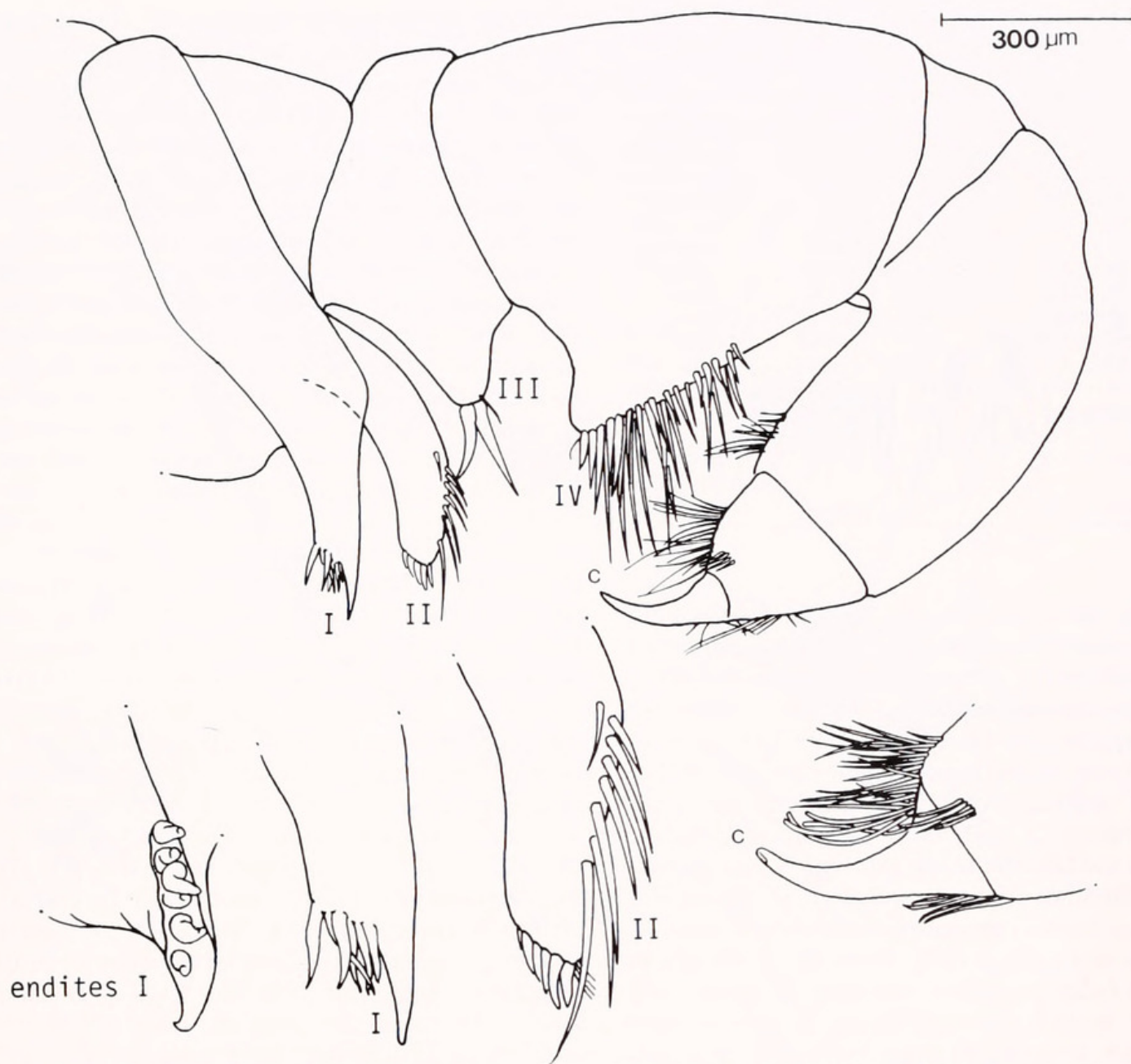
Fig. 17. *Lasionectes entrichoma.* Left maxillule, anterior surface, with I–II and c providing details of designated endites and limb tip.

near the bases of the antennules (Fig. 19A). These rod-like structures appear to have the cuticle of the basal portion somewhat less sclerotized than that of the distal portion (Fig. 19B). The thinner distal part of the filament is tapered, and a small spine-like process arises at the point of transition from the basal to distal portions of the filament (Fig. 15A).

The biramous antennules (Fig. 15B) are well developed and of the typical speleonectid form. The peduncle is composed apparently of two segments, though the suture marking the articulation is weakly developed. The most proximal bears a pad which has three to four rows of densely packed aesthetascs (Fig. 19C) draped back over the antennae (Fig. 20A). The distal segment is bifurcate at its terminus. The long dorsal ramus is composed of 12 segments; and

the ventral ramus, ½ to ⅔ the length of the dorsal, is composed of eight segments. Except for the proximal two articles of the dorsal ramus, the elements are long and slender, and are equipped with fine setae arranged in rows along their ventral margins in tufts distoventrally, and scattered distodorsally. The terminal segments of each ramus bear distal tufts of four to six hair-like simple setae.

The biramous antennae (Fig. 15C) are well developed but modest in size. They do not extend beyond the margin of the cephalic shield. The proximal segment of the protopod is somewhat longer than the distal unit, and is wider at its base than at its terminus. It bears two setae along its medial margin. The distal segment of the protopod is equipped with about 12 setae medially, and laterally bears the
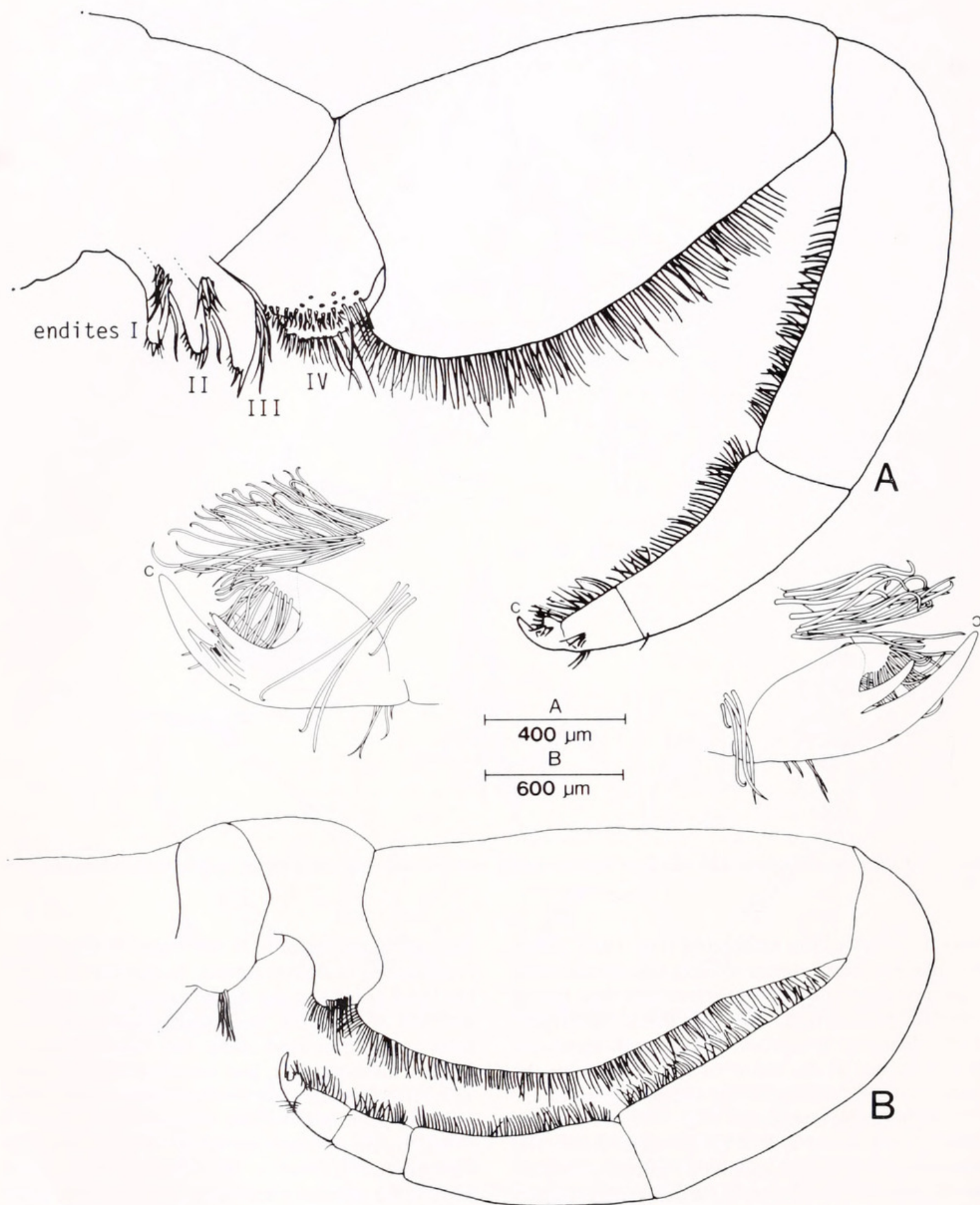
Fig. 18. *Lasionectes entrichoma*. A) left maxilla, anterior surface, with c providing anterior and posterior details of limb tip; B) left maxillipede, anterior view.

oval exopod. The exopod is a scale-like structure with about 35 to to 40 long setae arranged around its margins. The three-segmented endopod arcs laterally from the distal end of the protopod. The first segment bears about 12 or 13 setae along its anterior margin; the second is equipped with about 11 or 12 setae along its anterior edge; the third segment has some 24 setae arranged along its margins. With regard to the latter, the setae along the proximal anterior and the posterior margins are in single rows, and those along the distal anterior and distal margins are in a double row (Fig. 20B). The anterior surface of the third endopodal segment is equipped with an array of large pores (Fig. 20C). All the marginal setae of the antennae are of the plumose type (Fig. 15C-x), distinctly enlarged at their bases (Fig. 20D).

The labrum (Fig. 16A) is a large fleshy lobe. Anteriorly it narrows to a point, and posteriorly is marked by a furrow where it folds back to form the atrium oris. This bulbous posterior portion is marked with a fossa on its margin which bears a dense array of ribbon setae (Fig. 21A).

The mandibles (Fig. 16B, C) are asymmetrical. They take origin on the side of the cephalon (Fig. 19D), extending ventrally to insert distally under the posterior lobe of the labrum and into the atrium oris (Fig. 21B). The molar processes (Fig. 22A, B) are located on pedestals. They are composed of broad, flat basins with a complex array of spines. Along the edges are located long, thin, densely packed spines (Fig. 22C) that mark the edge of the basin. Within the basin the spines are arranged in rows (Figs. 23A) and are of two types: flanking the axes of the basins are densely packed short spines, and along the axes of the basins are low round tubercles (Fig. 22D). Near the lateral extent of the central axes the tubercles are mixed with four low cones with apical pores (Fig. 23A, B). (That these pores produce some kind of secretion is indicated by the fact that the spines in the basin of the molar process can sometimes be clogged with an amorphous substance, see e.g., Fig. 21D). The right incisor process is composed of a row of three large denticles (Figs. 16C, 22A); the left incisor process is composed of four large denticles with a smaller tooth between the two posterior major teeth (Figs. 16B, 22B). Prominent laciniae mobiles are found between the incisor and molar processes: the right one is formed by three large denticles, the left is concave and sickle-like.

The paragnaths flank the atrium oris (Fig. 21B). Their margins are covered by densely packed ribbon

TABLE 3. Representative measurements in mm of specimens of *Lasionectes entrichoma*. (Not all dimensions could be measured on all specimens.)

Feature	Range	n	$\bar{x}$	s	V
Body length	11.8–31.5	47	20.4	4.7 ± 0.7	23.0
Head length	1.4–3.3	50	2.4	0.5 ± 0.1	20.8
Head width	1.1–2.6	50	2.0	0.4 ± .05	20.0
Trunk segs.	26–32	50	30	1.5 ± 0.2	5.0
T1 length	0.2–0.6	47	0.4	0.1 ± .02	25.0
T1 width	0.8–1.7	50	1.4	0.2 ± .03	14.3
T2 length	0.4–0.8	50	0.6	0.1 ± .02	16.7
T2 width	1.1–2.7	50	2.1	0.4 ± .06	19.0
T14 length	0.5–1.0	50	0.8	0.1 ± .02	12.5
T14 width	1.3–3.2	50	2.4	0.4 ± .06	16.7
Anal seg. length	0.3–0.7	48	0.5	0.1 ± .02	20.0
Anal seg. width	0.3–0.6	48	0.5	0.1 ± .01	20.0
Caudal ramus length	0.2–0.5	48	0.4	0.1 ± .01	25.0
Caudal ramus width	.06–0.1	48	0.1	.01 ± .001	10.0

setae (Fig. 21C), and they insert into the space between the two basal-most endites of the maxillules.

The uniramous maxillules (Fig. 17) are robust and prehensile. They are composed of seven segments, of which the three most basal are equipped with well-developed endites. The principal point of flexure occurs between segments four and five. The first segment bears a large endite (Figs. 17, endite I; 23C) that terminates in a long stout spine flanked postero-proximally by a row of six stout spine-like setae. The endite of the second segment is broad and plate-like (Figs. 17, endite II, 23C). It has six short, stout setae along its posterior margin, paralleled by an irregular row of many tiny setae distally. In turn, this array is flanked along the anterior margin by eight moderate to long simple setae. The third segment of the limb is developed into a cone-like endite (Fig. 17, endite III) that is surmounted apically by two robust, spine-like setae and one or two small, simple setae. The fourth segment of the limb is rather long, with a subtriangular endite whose apex is near the proximal end of the limb (Fig. 17, endite IV). The endite is double crested and bears a row of moderate to long, simple setae along each crest. At the apex is a short, stout, spine-like seta which interdigitates with the two apical setae on endite III when the limb is flexed. The fifth segment is as long as the third, but is not equipped with any endites. It does bear two clusters of eight to ten simple setae on the antero- and postero-distal margins of the segment. The sixth maxillulary segment is short and bears two clusters of about 12 moderately long, simple setae distally on the antero- and postero-ventral
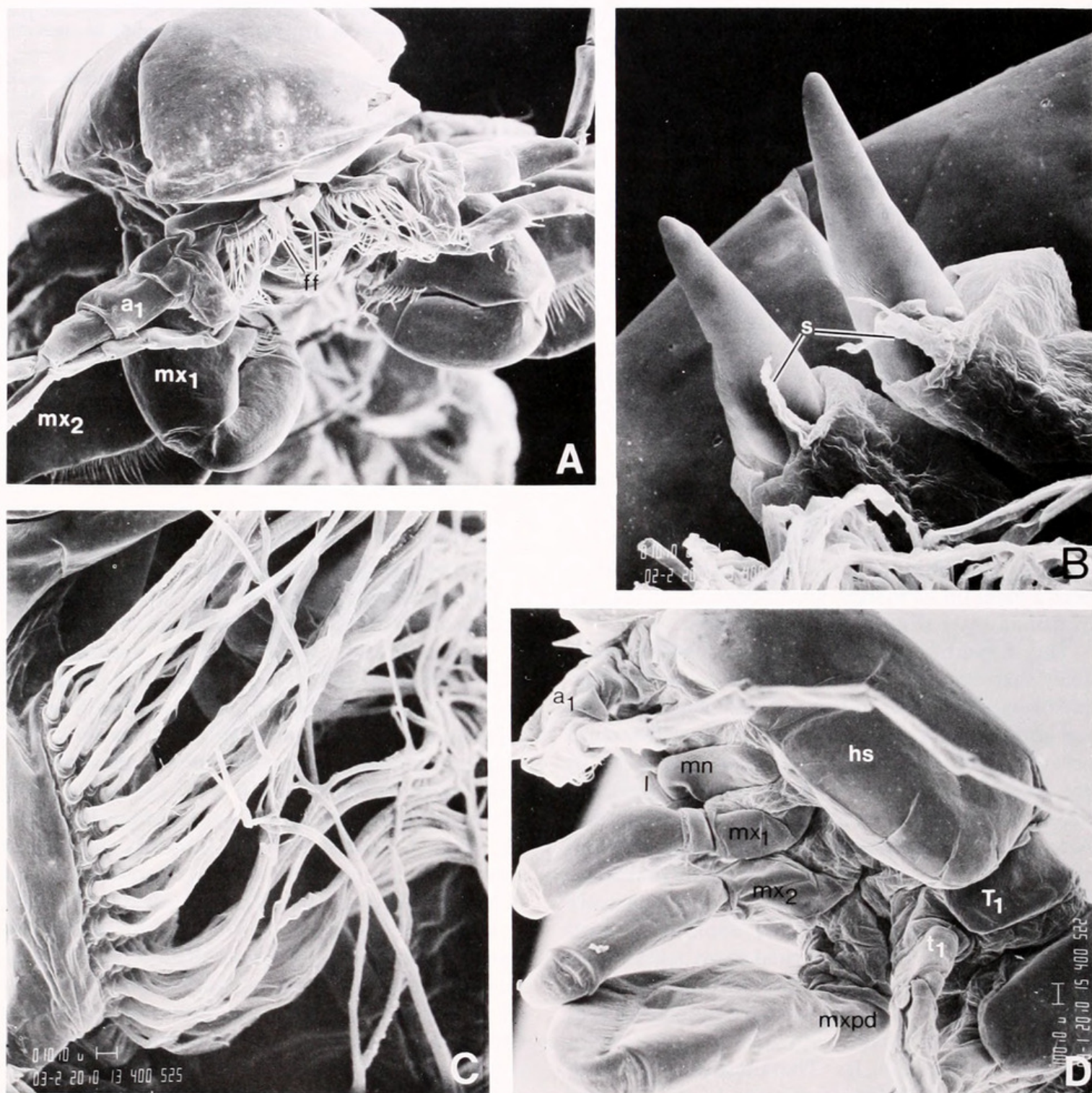
Fig. 19.   *Lasionectes entrichoma.* A) view of anterior body, ff—frontal filaments, a1—antennule, mx1—maxillule, mx2—maxilla; B) posterior views of frontal filaments, note thinner cuticle of filament base and spine (s) allowing cuticle to shrivel and distort; C) antero-oblique view of aesthetasc pad of antennule; D) lateral view of cephalon, a1—antennule, l—labrum, mn—mandible, mx1—maxillule, mx2—maxilla, mxpd—maxillipede, T1—first trunk segment, t1—first trunk limb, hs—head shield.
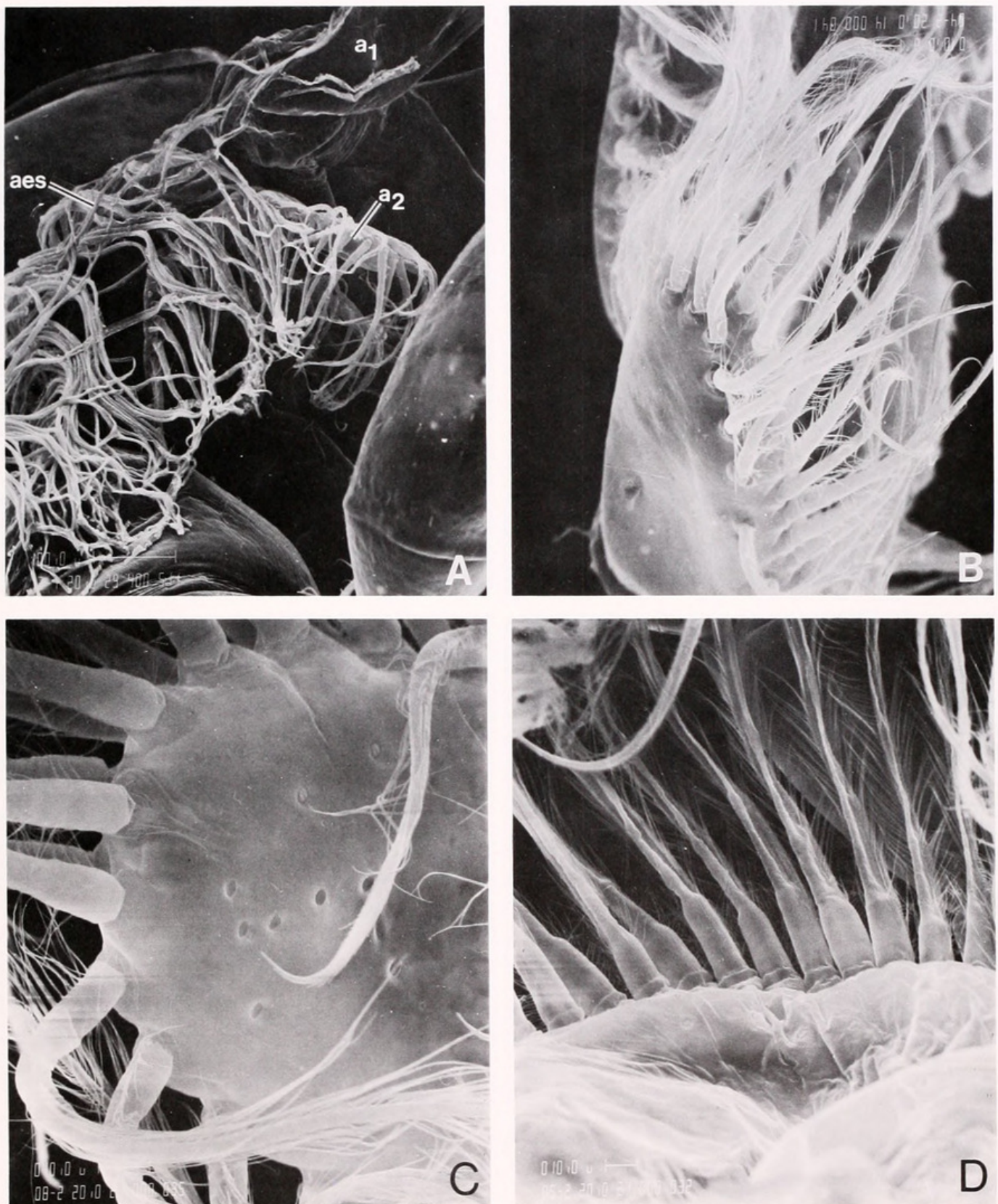
Fig. 20. *Lasionectes entrichoma.* A) ventral view of anterior part of cephalon showing relationship of antennule and antenna beneath it, aes—aesthetascs, a1—antennule, a2—antenna; B) on end view of distal margin of third segment of antennal endopod showing double row of plumose setae; C) ventral surface of third segment of antennal endopod showing surface pores; D) detail of basal aspect of antennal plumose setae.
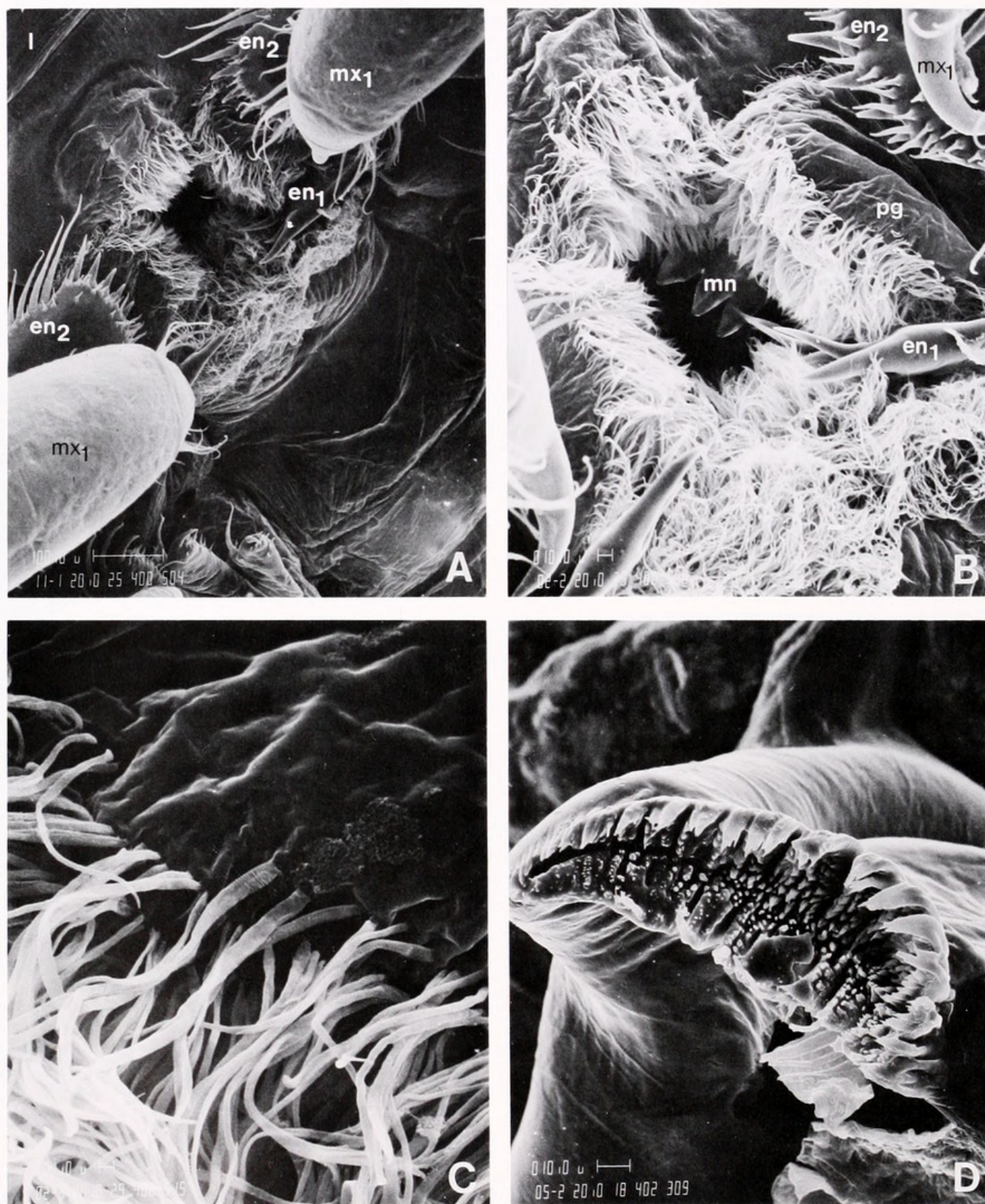
Fig. 21. *Lasionectes entrichoma.* A, B) mouth region, l—labrum, mn—mandible, en1—first maxillulary endite, en2—second maxillulary endite, mx1—distal portion of maxillule, pg—paragnaths; C) detail of paragnaths showing ribbon setae; D) surface view of right molar process, note secretory material clogging spines on lower aspect of process.
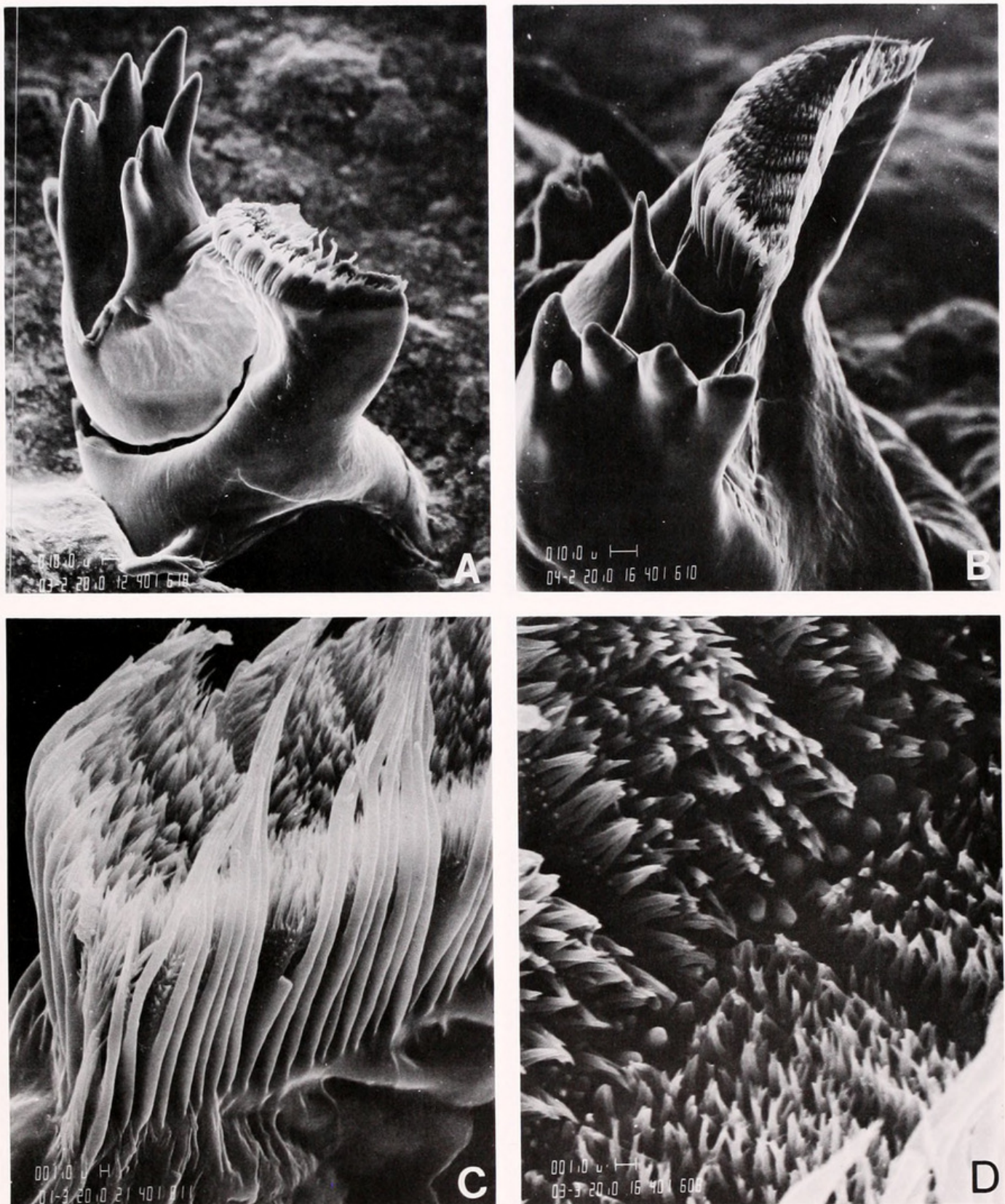
Fig. 22. *Lasionectes entrichoma*. A) right mandible; B) left mandible; C) lateral oblique view of left mandible molar process showing differences between spines on edge and those of basin; D) detail of Systral axis of left molar process basin.
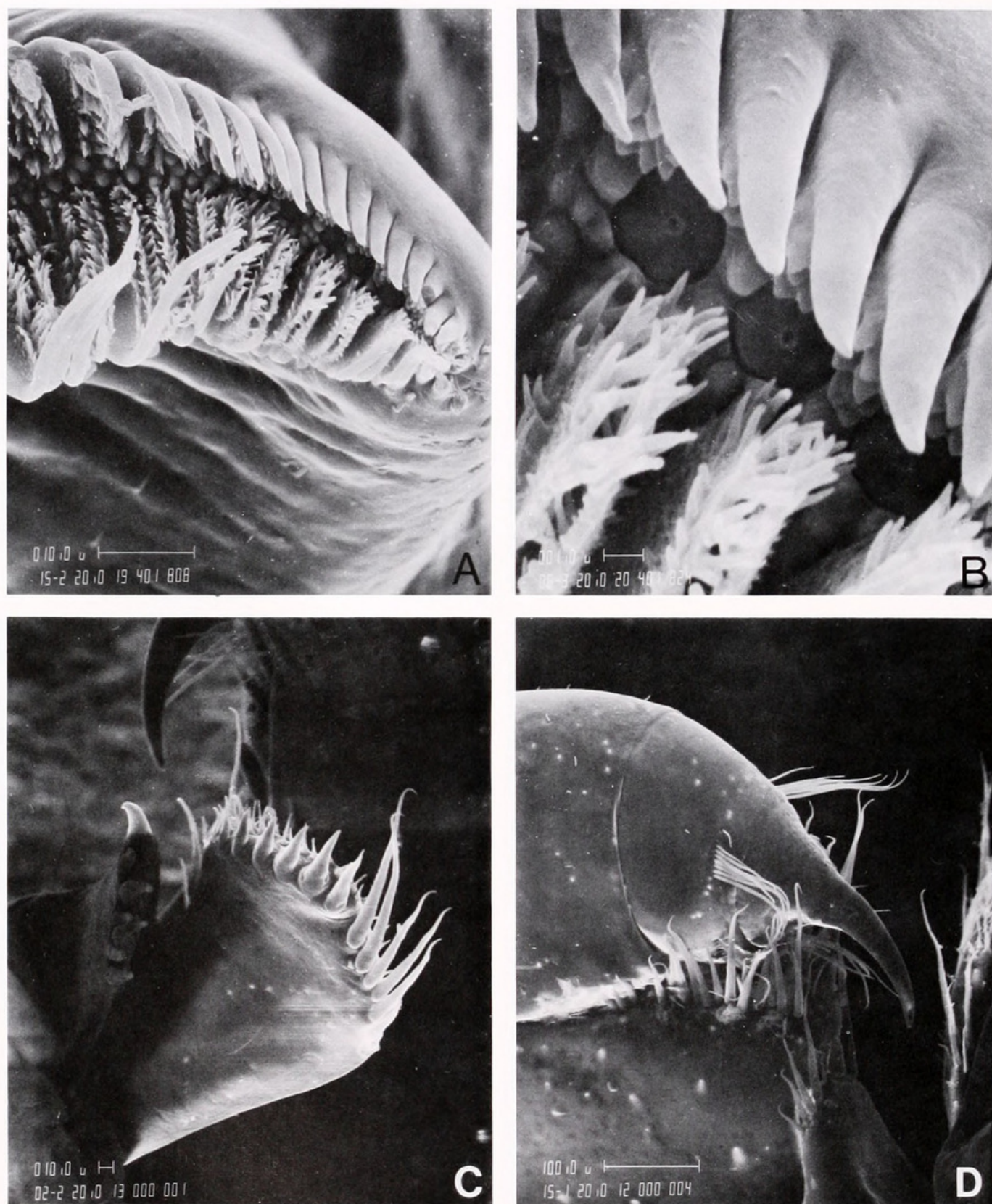
Fig. 23. *Lasionectes entrichoma.* A) surface view of dorsal portion of molar process of left mandible; B) detail of A showing cones with pores; C) first and second endites of maxillule with talon-like tip of limb projecting down from above; D) tip of maxillule with terminal pore.
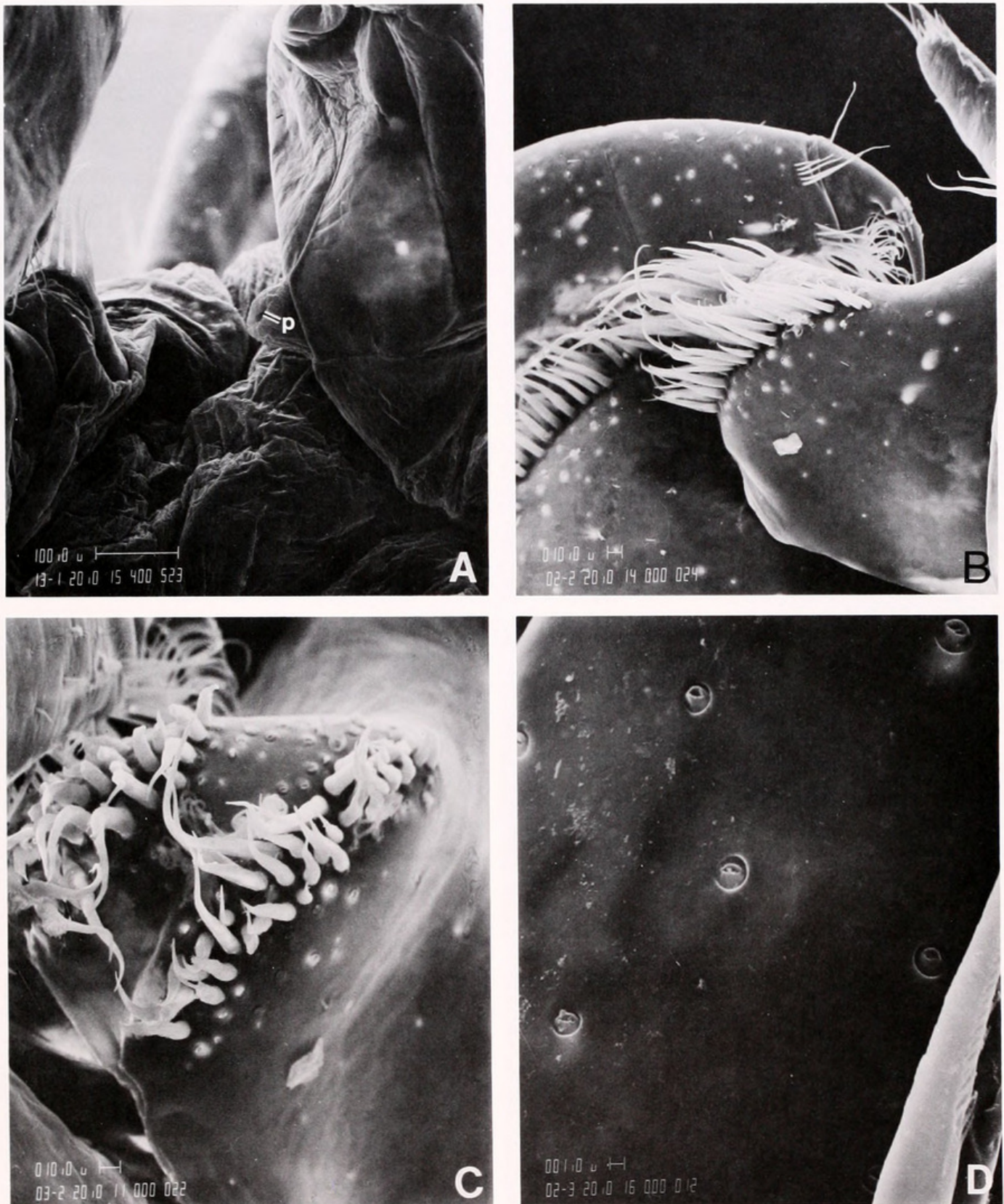
Fig. 24. *Lasionectes entrichoma.* A) lateral view of maxilla base showing opening (p) of maxillary pore; B) lateral view of tightly flexed maxilla showing how tip becomes opposed to basal pads; C) oblique view of maxilla endite IV showing setae flanking porous central trough; D) detail of some pores on maxillary endite IV.

Fig. 25. *Lasionectes entrichoma.* A) antero-lateral view of digitiform endites at base of maxilla; B) medial view of endites in A; C) posterior aspect of tip of maxilla; D) anterior aspect of tip of maxilla (see text for discussion).
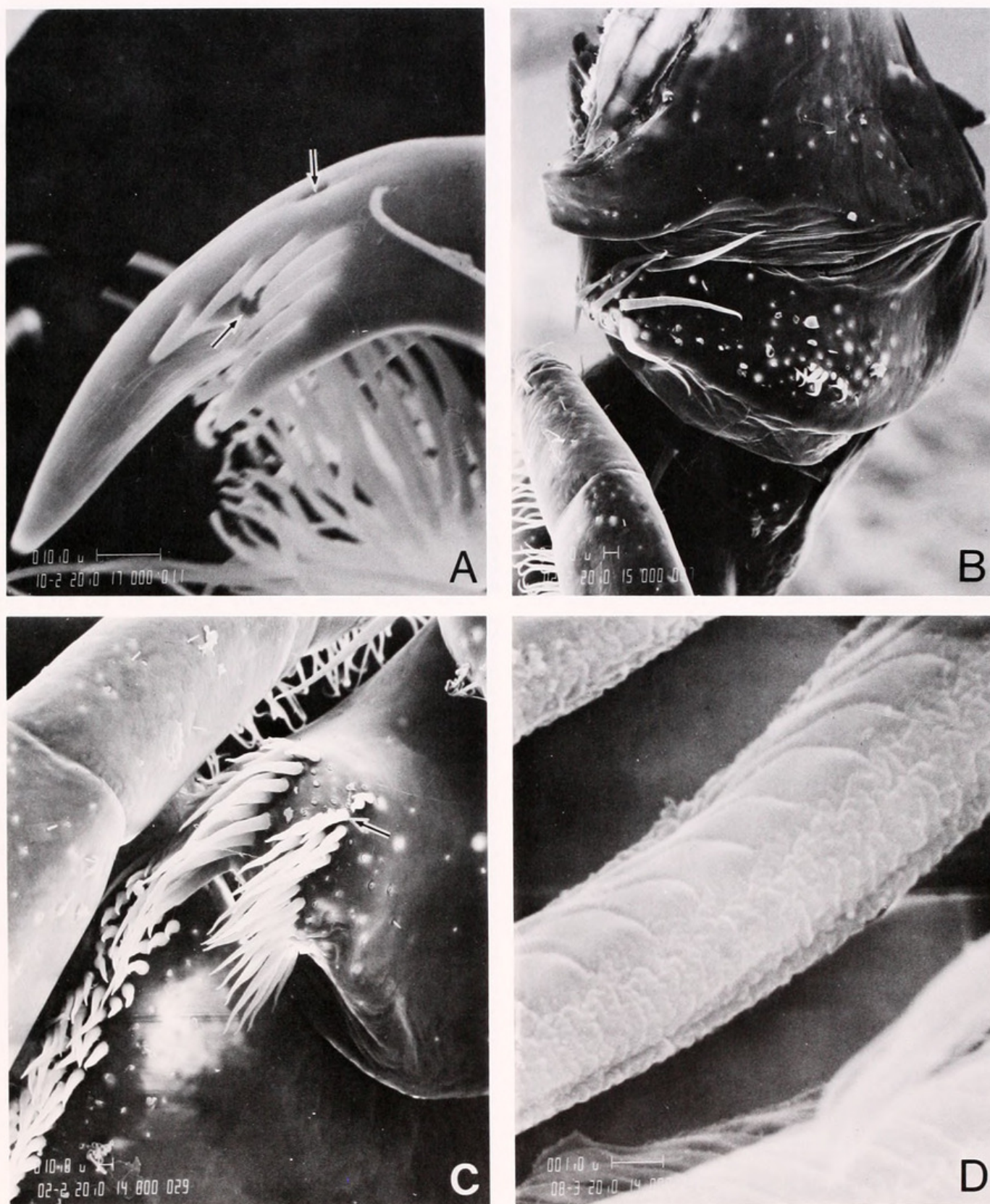
Fig. 26. *Lasionectes entrichoma*. A) anterior aspect of tip of maxillipede showing location of pores on claw; B) ventral view of weak basal endite of maxillipede; C) oblique view of second pad-like endite of maxillipede showing rows of simple setae flanking central porous trough; D) detail of setae in C.
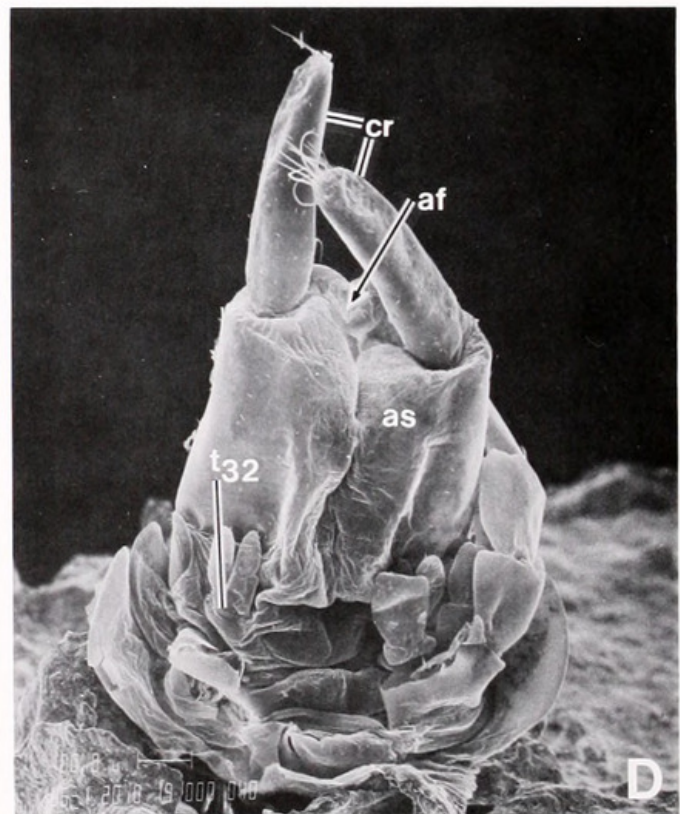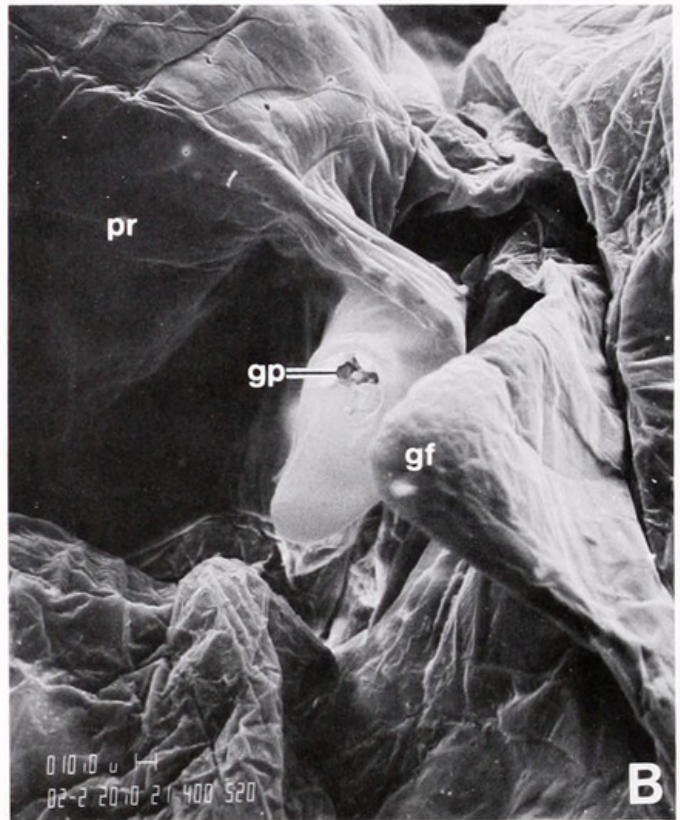
Fig. 27. *Lasionectes entrichoma.* A) ventral surface of anterior portion of trunk; mxpd—maxillipede, t1—first trunk limb, t2—second trunk limb, t3—third trunk limb, sb—sternite bar; B) gonopore region on fourteenth trunk somite, pr—protopod of fourteenth limb, gp—gonopore, gf—genital flap on the lateral most aspect of the sternite bar; C) comb setae seen on trunk limbs; D) ventro-posterior aspect of posterior end of body, t32—thirty-second trunk limb, as—anal segment, af—anal flap, cr—caudal rami.

margins and two clusters of six short, simple setae distally on the antero-and postero-lateral margins. The seventh segment of the limb is short and terminates in a long, gently arcing, talon-like claw. This bears a large pore at its apex (Fig. 23D). Rows of seven to ten simple setae flank the bases of the claw on the anterior and posterior surfaces of the segment.

The uniramous maxillae (Fig. 18A) are robust, subchelate limbs. They bear a prominent maxillary gland pore on the posterior surface of the limb base (Fig. 24A). They are composed of seven segments, and the principal point of flexure occurs between the third and fourth segments. The most proximal segment bears a series of three digitiform endites (Figs. 18, endites I–III, 25A, B) that increase in size distally. The second and third endites have clusters of four to five short simple setae on their anterior surfaces (Fig. 25A). The first endite has a short, spine-like seta at the apex, a cluster of up to twelve short, simple setae proximal to this, and a long, simple seta on the lateral margin with some short simple setae clustered around its base. The second endite has a moderately long, spine-like seta at the apex, up to a dozen simple setae along the proximal margin of the endite, and a long, simple seta on the lateral margin. The third endite has a large spine-like seta at the apex, a dozen or more short, simple setae along the proximal margin, and three long, simple setae along the lateral margin. The second segment of the limb bears a prominent pad-like endite (Fig. 18, endite IV; 24B, C). This bears clusters of short setae in two rows along a central basin well equipped with secretory pores (Fig. 24C). When the limb is tightly flexed the terminal claw rests in or close to the basin of this endite. The third segment of the limb is very long, and has an arcuate endite with two rows of densely packed, simple setae along two crests. Segments four through six of the maxillae are narrow and progressively shorter distally. Their ventral margins are decorated with a densely packed row of short, hair-like setae. Segment five has one or two simple setae at the disto-dorsal margin of the rim, and segment six has two clusters of about four simple setae, each located distally on the antero- and postero-dorsal surfaces of the segment. The seventh segment of the limb is rather short and armed with a distinctive claw (Figs. 18A-c, 25C, D). This is basically a trifid structure of three denticles, the central one being the longest. Between the central and anterior denticles is a comb-like row of about five or six short, delicate spines. A large pore is located on the dorsal surface of the base of the central tooth and another on the side of the central tooth beneath the comb row (Fig. 26A). Opposed to this complex is a thumb-like pad bearing long, simple setae.

The uniramous maxillipedes (Fig. 18B) are similar to the maxillae, but are markedly longer. They are composed of eight segments, with the subchelate flexure occurring between the third and fourth segments. The first segment is relatively long and has a weakly developed lobe on its ventral surface (Fig. 26B) that bears some simple setae and pores. The second segment of the limb bears a pad-like process similar in many respects to endite IV of the maxillae in that it bears two rows of setae along a central basin equipped with numerous pores (Fig. 26C). These setae are actually terraced (Fig. 26D). Both these endites are opposed by the terminal claw of the maxillipede when the limb is tightly flexed. The long, third segment is similar to that of the maxillae. Beyond the flexure, however, there are five segments on the maxillipede. The first four are similar to the first three on the maxillae. The eighth maxillipede segment is almost identical to the seventh on the maxillae, including the complex trifid claw.

The trunk limbs are all biramous paddles. The first pair are somewhat more slender (Fig. 14B) and are located slightly more dorsally on the segment than any of the following trunk limbs (Figs. 19D, 27A). The more posterior trunk limbs have rami with subrectangular intermediate segments and oval terminal ones (Fig. 14C). The posterior trunk limbs are much like those anterior to them except that they are smaller and bear few setae (Fig. 14D). The arrangement of setal types around the margins of the limbs are similar for all limbs, though the exact number on each limb (and even each member of a pair) varies. The most common are plumose setae (Fig. 14C-x) occupying most of the margins. Next are the comb-like setae found on the distal corners of the intermediate segments. These have a long, thin shaft with small, sharp, curved denticles along the margins of the shaft (Figs. 14C-y, 27C), and a fan-like comb of densely packed spines at the base (Fig. 27C). As mentioned above, it is assumed these setae are used in combing out or carding the setules of the plumose setae.

Remarks.—The description and illustrations of this species presented here are considerably more detailed than for those of any other nectiopodan because the available material is so abundant. Indeed, though species of the genus *Speleonectes* were
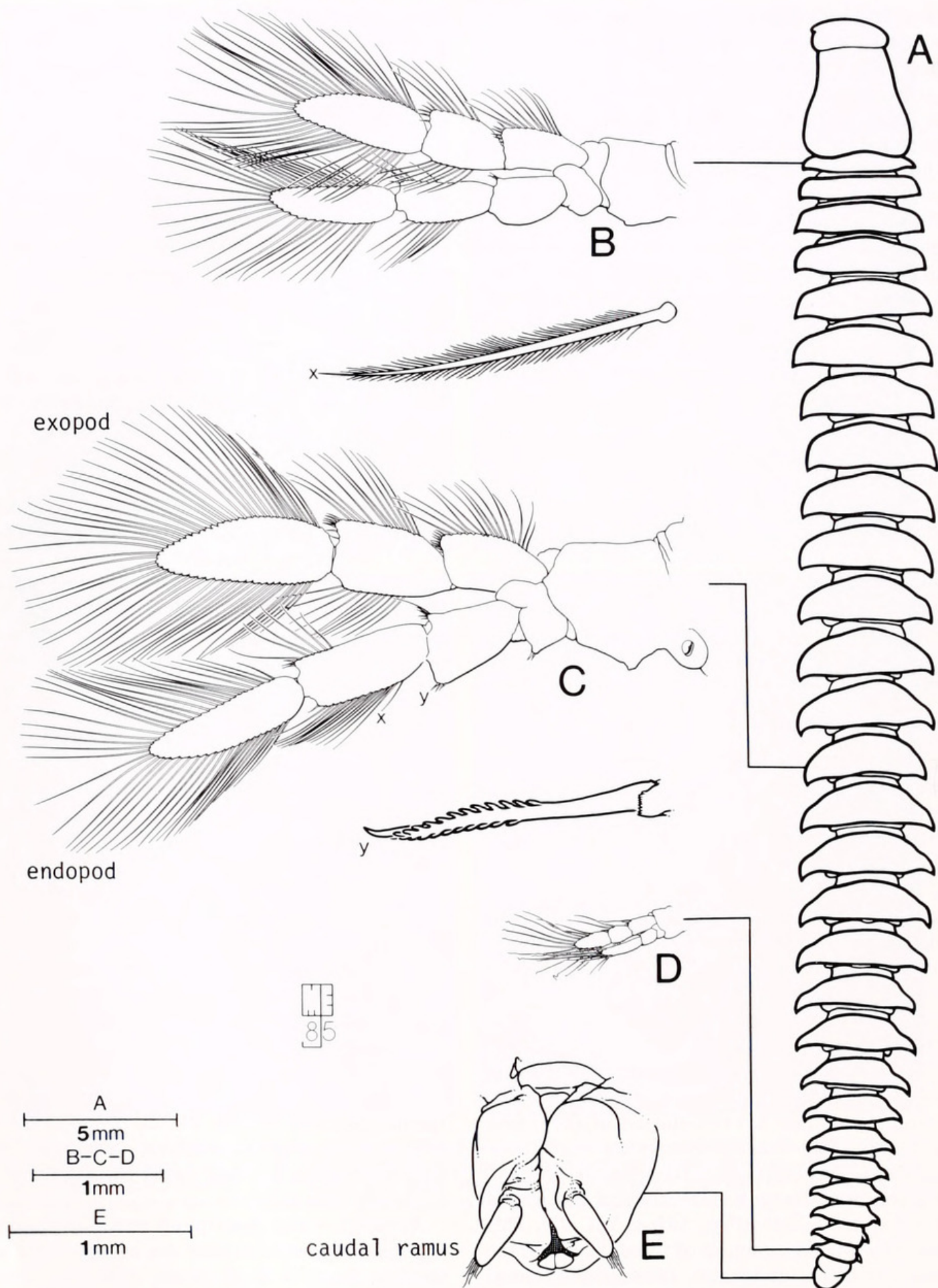
exopod

endopod

caudal ramus

A
5mm
B-C-D
1mm
E
1mm

Fig. 28. *Godzillius robustus.* A) dorsal surface of body; B) posterior view of first trunk limb; C) fourteenth trunk limb, with x and y as variant setae from margins, and genital flap with pore at base; D) twenty-ninth trunk limb; E) ventral view of anal segment with caudal rami.

the first to be discovered, because those species are so rare, *L. entrichoma* will undoubtedly become the standard morphological type of reference for the order.

One interesting fact noted in the course of SEM study of this material is the porous nature of the cuticle. Pores are found everywhere: the cephalic shield (Fig. 19A), body segments, and the surfaces of endites and limbs (Fig. 24D). In addition, the cuticle surface is often equipped with fine sensillia; these are especially common on the surfaces of the anal segment and caudal rami. These latter are probably related to mechanoreception, but the determination of whether the pores are chemo- or mechanoreceptors, or secretory must await TEM studies of these structures and their underlying cuticle.

Family GODZILLIIDAE nov.

Diagnosis. — Cephalic shield subtrapezoidal, wider posteriorly than anteriorly; frontal filaments with several "joints"; ventral ramus of antennules with few segments, terminal segment very long and blade-like; antennae with multiple rows of plumose setae on all segments of endopod; mandibles only slightly asymmetrical; maxillule endite III weakly developed, endite IV club-like; maxillae and maxillipedes subchelate, subtriangular endites on third segments massive and densely setose, with segments distal to elbow relatively thin and delicate, terminal claws seven-pronged; maxillae with three segments beyond elbow; maxillipede with four segments beyond elbow; trunk tergites laterally pointed; protopod of fourteenth trunk limb with flap protecting genital pore; trunk sternites developed as plates.

Remarks. — Besides the large adult size of these nectiopodans (at least twice that of any other known species in the order), the morphology, especially of the cephalic limbs, is so distinctive as to warrant separate familial status.

Genus GODZILLIUS nov.

Diagnosis. — Since only one genus is currently recognized, the diagnosis is the same as that of the family.

Etymology. — A reference to the almost monstrously large size of these animals as adults, the extreme styliform talon on the maxillule, and the grappling-like claws on the maxillae and maxillipedes.

Type species. — *Godzillius robustus* nov.

GODZILLIUS ROBUSTUS nov.

Diagnosis. — Since only one species is currently recognized, the diagnosis is the same as that of the family and genus.

Etymology. — A reference to the large size of this species.

Holotype. — USNM 216980, coll. Oct. 22, 1983.

Type locality. — Cottage Pond, North Caicos, Turks and Caicos Islands, British West Indies.

Additional material. — SDSNH 2215, coll. Oct. 22, 1983 from the type locality.

Description. — The cephalon is about $\frac{1}{9}$ the total length of the body (Fig. 28A). The cephalic shield is subtrapezoidal, the widest portion is posterior, the narrowest part in the middle, and the anterior part wider than the middle but narrower than the posterior. The adult is composed of about 29 trunk segments. The trunk tergites are very prominent and somewhat pointed postero-laterally. The first trunk segment is shorter than those which immediately follow, but is not especially narrower, and is apparently not covered to any degree by the posterior margin of the head shield. The sternites of the trunk segments are developed as plates. The protopod of the fourteenth trunk limb bears a triangular flap on the ventral margin near the base of the limb which serves to protect the opening of the genital pore (Fig. 28C). The anal segment is markedly wider than long (Fig. 28E). The caudal rami are shorter than the anal segment, situated and directed ventro-posteriorly on the distal end of the segment, and bear terminal clusters of setae. Short, fine setae are scattered over much of the cuticle, and these frequently issue from papilla-like structures embedded in the semi-transparent epicuticle. Measurements of the specimens at hand are provided in Table 4.

There is a relatively prominent set of frontal filaments (Fig. 29A) on the anterior portion of the ventral cephalon near the base of the antennules. The main shaft is rather long, and appears to be divided into three subequal "articles" by two joints or points of flexion. The distal "article" bears a small spine about ¼ its length from its base.

The biramous antennules (Fig. 28B) are well developed. The peduncle is composed of two segments. The proximal one is relatively long, and ventrally bears the characteristic nectiopodan pad with several rows of long aesthetascs. The distal segment of the peduncle is relatively short and deeply bifurcate at its tip. The dorsal ramus is very long; the three basal segments are of modest length; the next seven segments are very long and narrow; the elev-
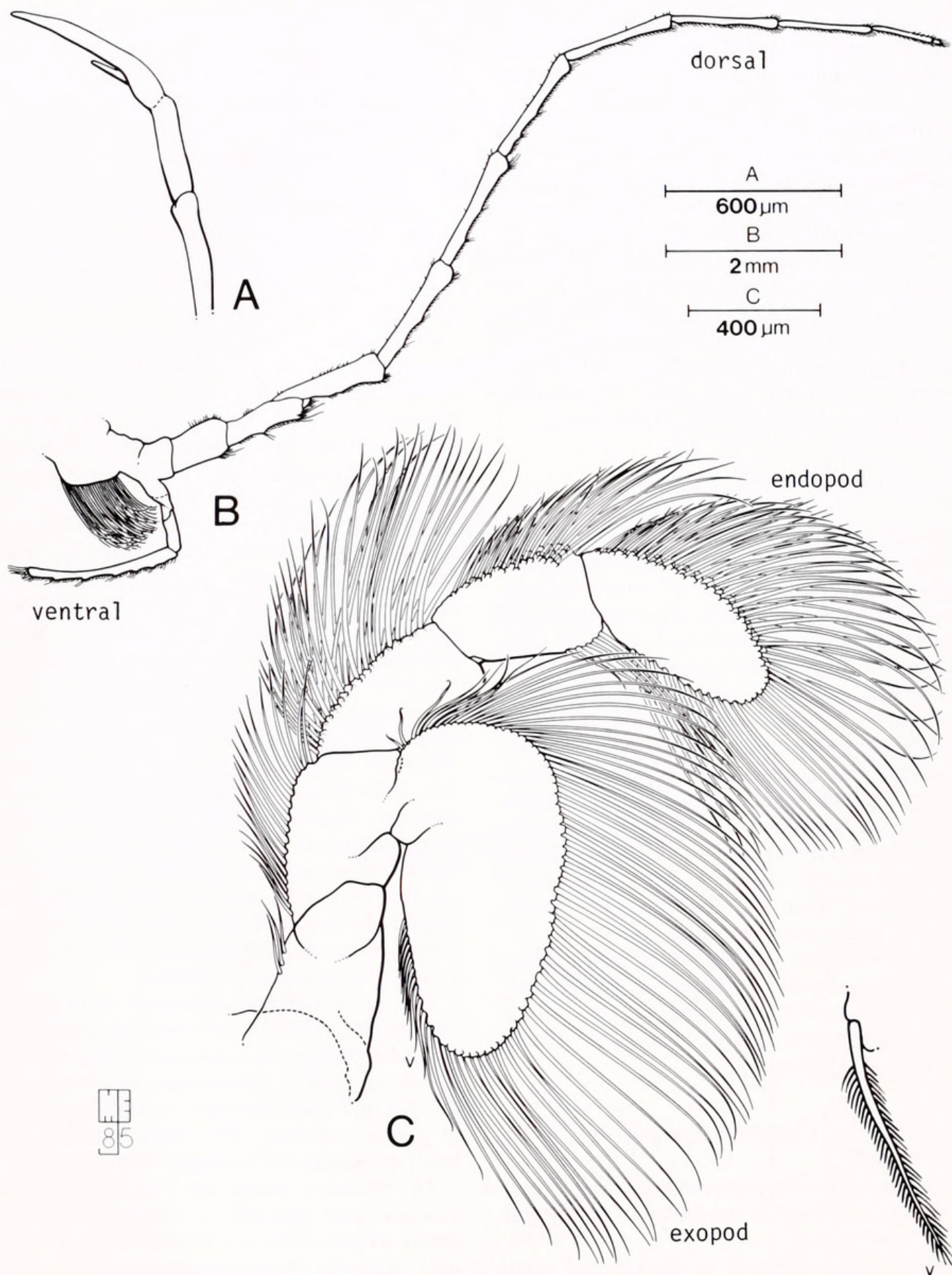
dorsal

A
600 μm
B
2 mm
C
400 μm

ventral

endopod

exopod

Fig. 29. *Godzillius robustus.* A) left frontal filament, lateral view; B) left antennule, anterior view; C) left antenna, ventral view, with x as plumose seta of the margins.
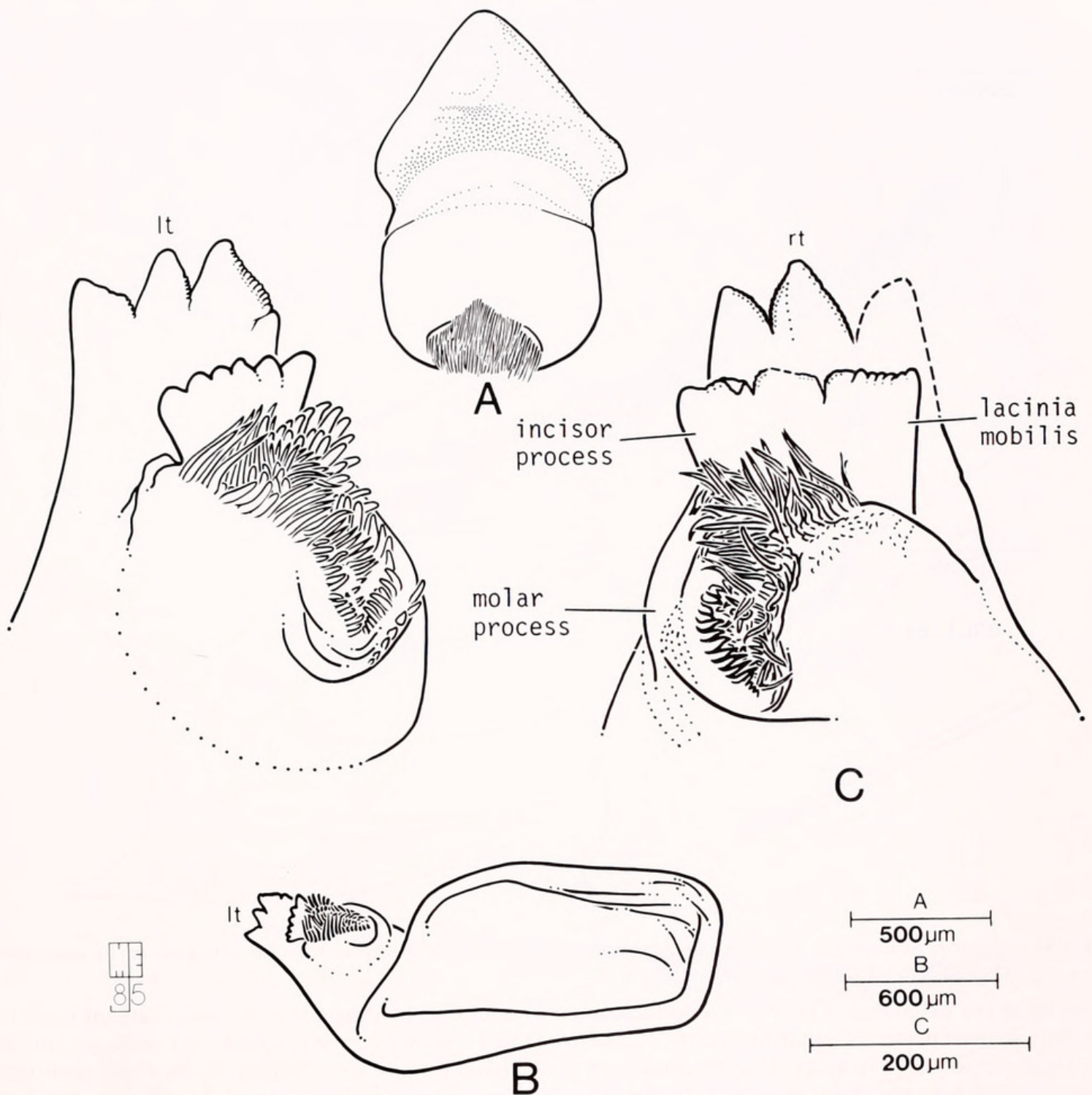
Fig. 30. *Godzillius robustus.* A) labrum, ventral surface; B) left mandible dorso–posterior view with enlargement; C) detail of right mandible.

enth and terminal segment is very short. The basal-most segment tends to have its rows of short hair-like setae closer to the distal ends. The intermediate segments have rows of short, hair-like setae all along their medial margins. The terminal segment is setose on all its margins. The lateral margins of most segments can have tiny hair-like setae near their distal ends. The ventral ramus of the limb is quite short and apparently composed of only three segments. What appear to be the two most proximal segments are short and do not seem to bear any

setae. Most of the length of the ramus is made up by the distal-most third segment, which bears a row of fine hair-like setae along its undulate, lateral margin and its terminus.

The biramous antennae (Fig. 29C) are noteworthy for their extremely setose margins. The limb is of modest size with a two-segmented peduncle. The peduncular segments are subequal: the proximal segment has only three setae located on its distal medial aspect; the distal segment has about 17 setae along its medial margin with an extra seta set slightly
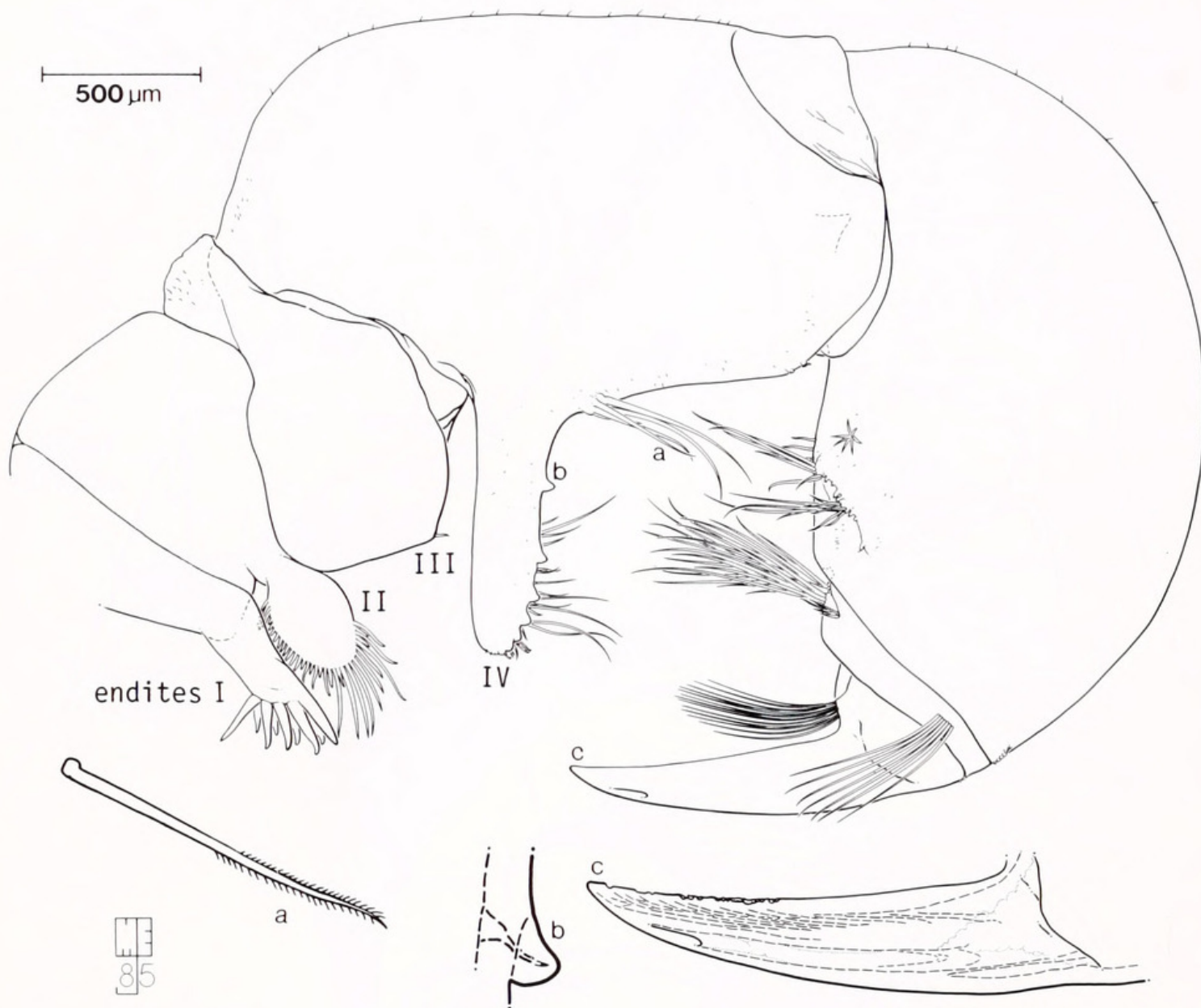
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Fig. 31. *Godzillius robustus.* Left maxillule, anterior surface, with a–c as details of subsetulate seta, papilla, and limb tip respectively.

dorsal at the distal end. The oval exopod is somewhat narrower posteriorly than anteriorly, and bears a single row of 60 to 70 setae along its margins. The articulation between the exopod and the distal peduncular segment is not well developed. The three endopodal segments arc laterally, and all bear multiple rows of setae along their anterior margins, and, where they occur, only a single row along the posterior margins. The first or most proximal segment has a total of 33 setae in three unequal rows along the margin, and what appears to be four additional setae near the proximal end. The intermediate segment has close to 35 setae along its anterior margin. Twenty of these are arranged primarily in three unequal rows, and the remaining setae are clustered in a dense array at the distal end of the segment. This intermediate segment also has an additional row of five or six setae located distally on the posterior

margin. The third or most distal segment has close to 55 setae in three unequal rows along its anterior margin, with what appear to be three additional setae near the proximal end. In addition, the distal and posterior margins of the segment have a single row of about 17 setae. All these marginal setae on the antennae are very long and plumose in form (Fig. 29C-v).

The labrum (Fig. 30A) is a large, lobate structure. The anterior portion is subtriangular, with the apex pointed anteriorly. This is separated from the posterior portion by a deep furrow, which acts to pinch off the anterior portion of the labrum from the posterior. Ridges on both the anterior and posterior portions flank the furrow. The posterior free margin of the labrum is marked by a large, broad fossa which bears a dense array of setae.

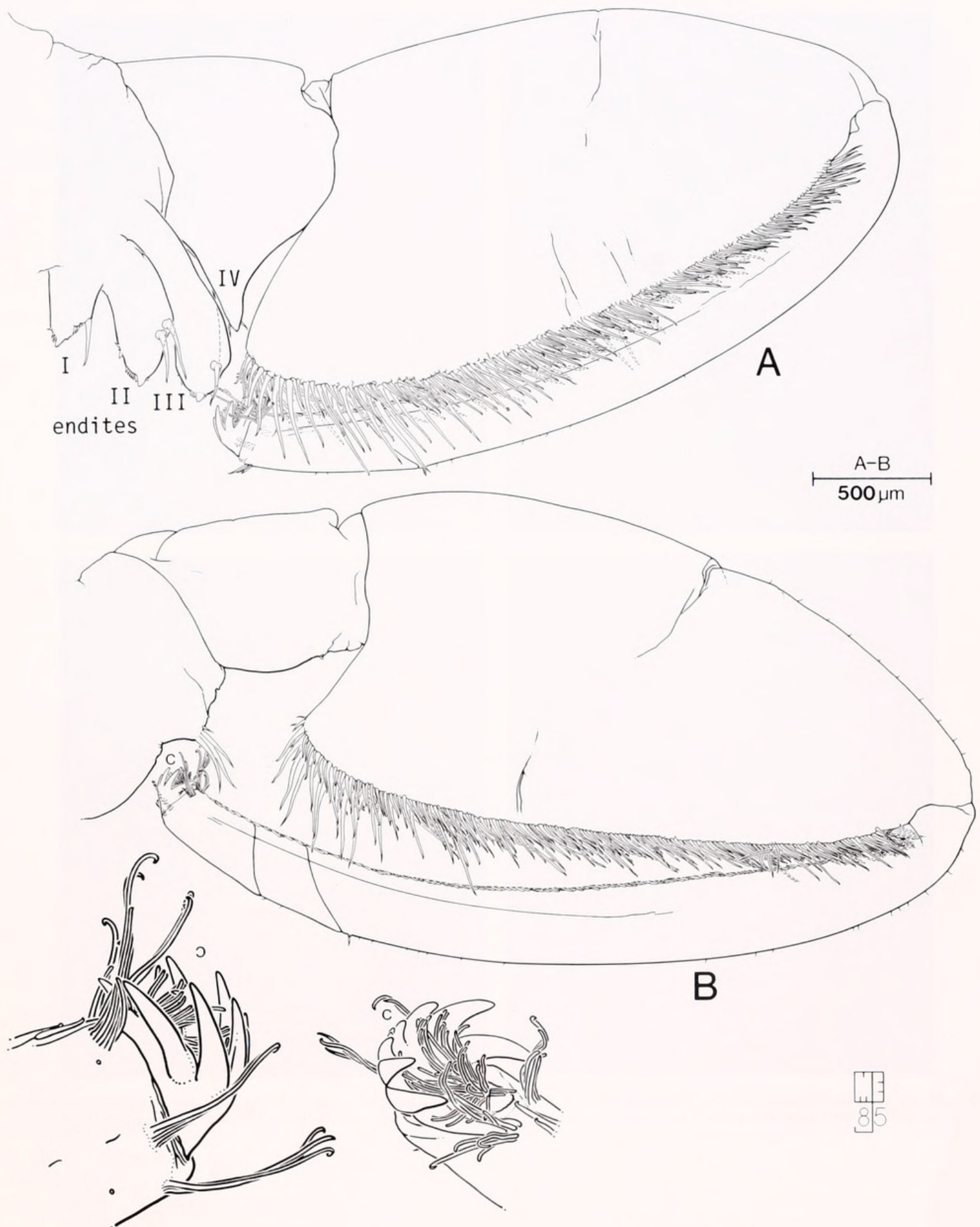The mandibles (Fig. 30B, C) are only slightly

Fig. 32. *Godzillius robustus.* A) left maxilla, anterior surface; B) left maxillipede, with c as detail of limb tip.
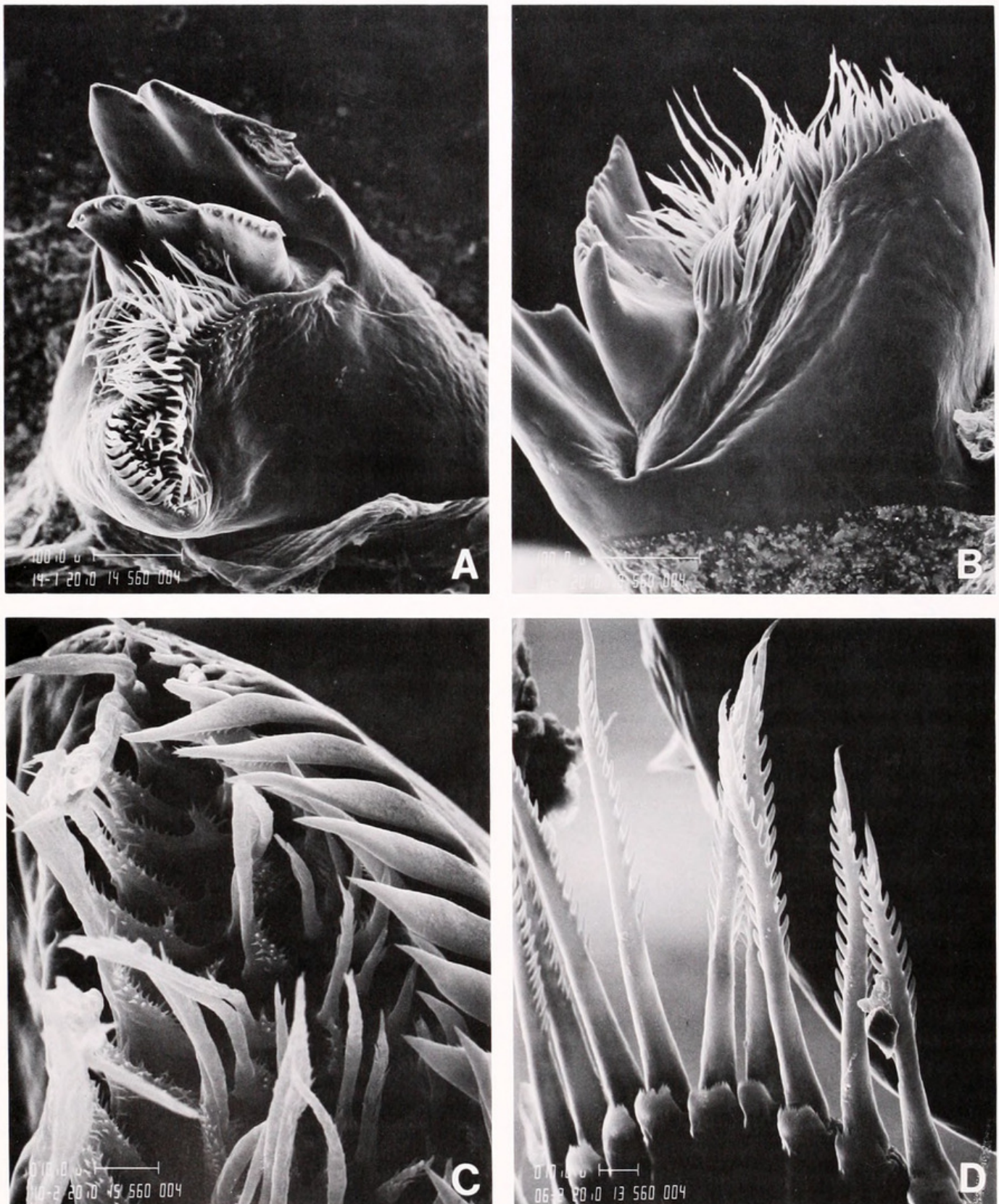
Fig. 33.   *Godzillius robustus.* A–C) tip of right mandible; A) dorsal view; B) anterior view; C) lateral-most portion of molar process, note spike-like spines along margin and shorter spines of basin with basal accessory spinose lobes; D) comb seta of second trunk limb.
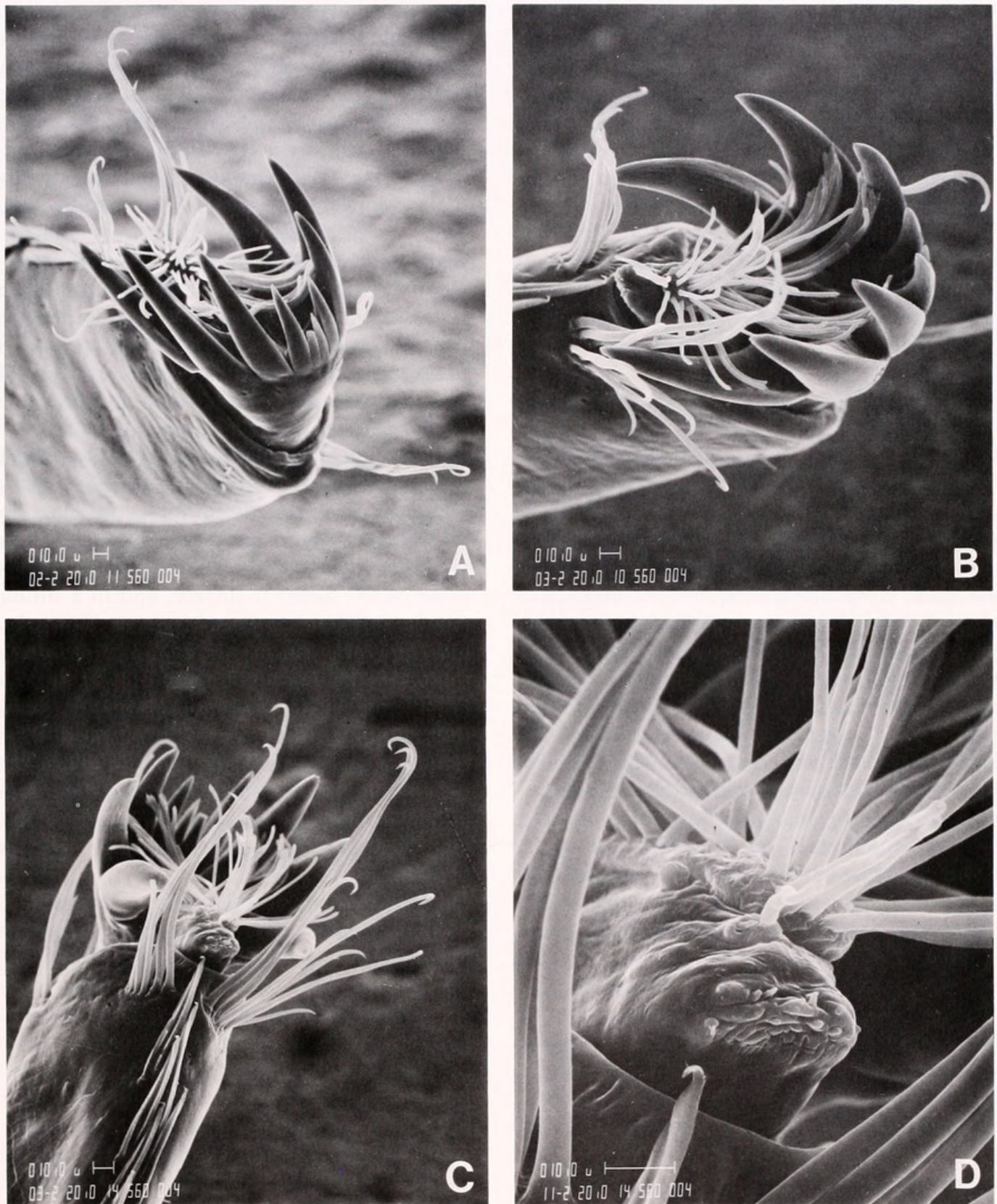
Fig. 34. *Godzillius robustus.* Right maxillipede claw; A) disto-oblique view; B) ventral view; C) proximo-oblique view; D) closeup of fleshy setose pad of C.

TABLE 4. Representative measurements in mm of the two available specimens of *Godzillius robustus*. Not all measurements could be taken on SDSNH 2215, since the specimen was dissected before detailed laboratory study could be undertaken.

Feature	USNM 216980	SDSNH 2215
Body length	43.2	—
Head length	4.9	—
Head width	3.6	3.7
Trunk segs.	29	
T1 length	0.6	0.5
T1 width	3.7	3.6
T2 length	0.8	0.7
T2 width	4.0	—
T14 length	1.7	1.5
T14 width	4.2	—
Anal seg. length	0.7	1.2
Anal seg. width	1.0	1.1
Caudal ramus length	0.5	0.5
Caudal ramus width	0.1	0.2

asymmetrical. The left incisor process is composed of a row of three large denticles that are developed with serrated crests along their anterior edges. The most anterior tooth has a small accessory denticle near its base on the anterior surface. The right incisor process (Fig. 33A) has three denticles (one broken off on the specimen SDSNH 2215), but the median tooth is serrated along both its edges. The left lacinia mobilis is composed of six denticles. The right lacinia is formed by three denticles with broadly serrate surfaces (Fig. 33A, B). The molar processes are situated on pedestals, and have broad flat basins covered with dense rows of spines. Those along the edges are spike-like; those in the basins are smaller but these bear spinose lobes near their individual bases (Fig. 33C). The surfaces of the molar processes are somewhat T-shaped, with the top of the T paralleling the laciniae mobiles.

The paragnaths flank the opening to the atrium oris and are covered by dense arrays of setae.

The uniramous maxillules (Fig. 31) are robust prehensile limbs. They are composed of seven segments, with the principal point of flexure between the fourth and fifth segments. Segment one bears a large endite (Fig. 31, endite I) surmounted at its apex by a robust spine flanked by a cluster of eight highly sclerotized, tooth-like setae arranged in a row. The teeth of these endites on either side of the animal are opposed to each other at the opening to the atrium oris. The endite of the second segment is a broad, thin, lobate structure (Fig. 31, endite II). Its apical margin is marked with about 12 moderate to long, relatively robust simple setae. The third segment of the maxillule essentially lacks an endite,

though its ventral surface is broadly rounded and bears one short, simple seta (Fig. 31, endite III). The fourth segment of the limb is relatively long and bears a large, club-like process as an endite near the proximal end of the segment (Fig. 31, endite IV). This is marked on its distal surface by six or so rounded, tooth-like papillae interspersed with moderate to long, simple setae. These papillae appear to have a duct through the cuticle connecting their tips with underlying tissue (Fig. 31-b). At the base of the club is a small cluster of five long, subsetulate setae (Fig. 31-a). The fifth segment of the limb is long and bears a diagonal row of moderate to long, simple setae and small papillae that extend across the ventral anterior surface of the segment. Near the proximal end of the antero-ventral surface is a cluster of seven small, simple setae. The sixth segment is very short and has a row of about 19 moderate to long simple setae clustered on the ventral margin, and a row of about four short simple setae anterior to that. Near the dorsal margin is a row of seven long, simple setae on the anterior surface, and in a similar spot on the posterior surface is a pair of simple setae. The seventh segment of the limb is a long, styliform, talon-like claw surmounted by a large pore. At the base of the claw on the medial surface of the segment is a cluster of about 13 long, simple setae. Light microscopy reveals a large, membrane-lined duct leading from the pore to a granular mass of tissue and the presence of many structural grooves within the talon, the outer surface of which is abraded (Fig. 31-c).

The uniramous maxillae (Fig. 32A) are subchelate limbs composed of six segments, the principle point of flexure being between the third and fourth segments. The proximal three segments are very robust; the distal three segments are long, thin, and delicate. A prominent groove appears on the anterior surface of the fourth and fifth segments. The most proximal segment of the limb bears three digitiform endites (Fig. 32A, endites I–III); the smallest is most proximal; the largest most distal. Each endite is surmounted with a short, rounded, tooth-like spine. These are flanked by two to seven short, spine-like setae along the crests of the apical margins. Each endite also bears one or two large, simple setae with disc-like bases located along the antero-distal margins of the endites. The second segment of the maxilla is developed as a simple, tall, cone-like endite with two small, simple setae near the apex (Fig. 32A, endite IV). When the limb is tightly flexed, this cone appears to fit into a groove along the postero-distal margin of the third of the digitiform endites. The

third segment of the limb is extremely wide, especially at its proximal end. The ventral surface is developed as a long, double-crested endite with dense rows of moderate to long, simple setae along its crests. Internally, this segment accommodates a well-developed musculature to flex the distal segments of the limb. The fourth segment of the limb is almost as long as the third, but is a long, thin, narrow element that lies in the valley between the two crests of the third segment. The ventral surface is covered with a dense row of small, appressed, simple setae, and the dorsal surface bears two short setae at the distal margin. The fifth segment of the limb is relatively short and bears setae similar to the fourth, with additional clusters of short to moderate, simple setae near the distal margin on the posterior surface and flanking the appressed ventral setae. The sixth segment is very short and is developed as a distinctive ten pronged, grappling hook-like claw. The ten denticles are arranged in an arc, directed ventrally, and are opposed by a fleshy pad bearing an array of setae.

The uniramous maxillipedes (Fig. 32B) are very similar to the maxillae in form, but are composed of seven segments. The limb is subchelate, with its principal point of flexure between the third and fourth segments. The three basal segments are very robust, the four distal segments are thin and delicate. The first segment of the limb bears a weakly developed endite with four or five short to moderate simple setae. The short second segment of the limb bears no endites. The third segment of the limb is very long and wide, and has its ventral surface developed as a double crested endite bearing rows of moderate to long simple setae. As in the maxilla, this segment accommodates a very robust musculature to flex the distal segments of the limb, and bears an intermittent groove on the dorsal and anterior surfaces. The fourth through sixth segments of the limbs are thin and delicate and appear to act as a unit in opposition to the endite on the third segment. These segments bear an anterior groove and ventral setation similar to those of the maxillae. The distal setation of the sixth segment resembles that of the maxilla's fifth, but the dorsal setae are reduced to a single seta at the distal margin of the fourth segment. As with the juncture of the maxilla's fourth and fifth segments, the articulations between the fourth, fifth, and sixth segments of the maxillipede are diagonal. The seventh segment of the limb is developed with a ten-pronged claw (Fig. 32B-c, 34 A–D) similar to that seen on the maxilla.

The trunk limbs are all biramous paddles. The first pair is somewhat shorter but not markedly narrower than those that immediately follow (Fig. 28B, C). The last trunk limb is much reduced (Fig. 28D). The trunk limb rami are elongate and subrectangular. The terminal segments of the rami are distinctly oval. The most common setae along the margins of the rami are plumose (Fig. 28C-x). On the distal corners of the intermediate rami are located the comb-like setae so characteristic of these limbs (Fig. 28C-y). In *Godzillius* these are characterized by a very long shaft with laterally directed, sharp, curved denticles restricted to the distal half of the shaft (Fig. 33D).

Order ENANTIOPODA Birshtein, 1960

Diagnosis.—Compound eyes sessile; (?) antennules and antennae biramous; mouthparts raptorial; trunk segments with pairs of homonomous, paddle-like limbs bearing five- or six-segmented "exopods" and flap-like "endopods."

Remarks.—The published report with illustrations and reconstruction of Brooks (1955) presented an animal with simple flap-like mouthparts. Detailed restudy of the type and only known specimen now indicates that the previous description of this animal was not entirely accurate. Though the material is too poorly preserved to allow a complete reconstruction, sufficient evidence is at hand that casts doubt on earlier diagnoses of this taxon.

Brooks (1955:853) originally described *Tesnusocaris goldichi* as "unlike any known arthropod." To this end he employed a rather non-specific terminology for the appendages, e.g., referring to a "first cephalic appendage" rather than calling it an antennule or antenna, but nonetheless placed the animal, for no particular reason, within the Branchiopoda *incerta sedis*. However, while Brook's paper was in press, Sanders (1955) described the cephalocarid *Hutchinsoniella macracantha*. In a footnote to his publication, Brooks (1955:853) assigned *Tesnusocaris* to the cephalocarids on ". . . the basis of the unspecialized nature of the postcephalic tagma and the presence of jointed appendages." It was Birshtein (1960) who then formally recognized the separate status of these two genera and erected ordinal names to accommodate them: Brachypoda for *Hutchinsoniella* and allies, Enantiopoda for *Tesnusocaris*. However, Hessler (1969) rejected *Tesnusocaris* as having any relationship to brachypodans.

The discovery of living nectiopodans sheds new light on the question of enantiopodan affinities. Of
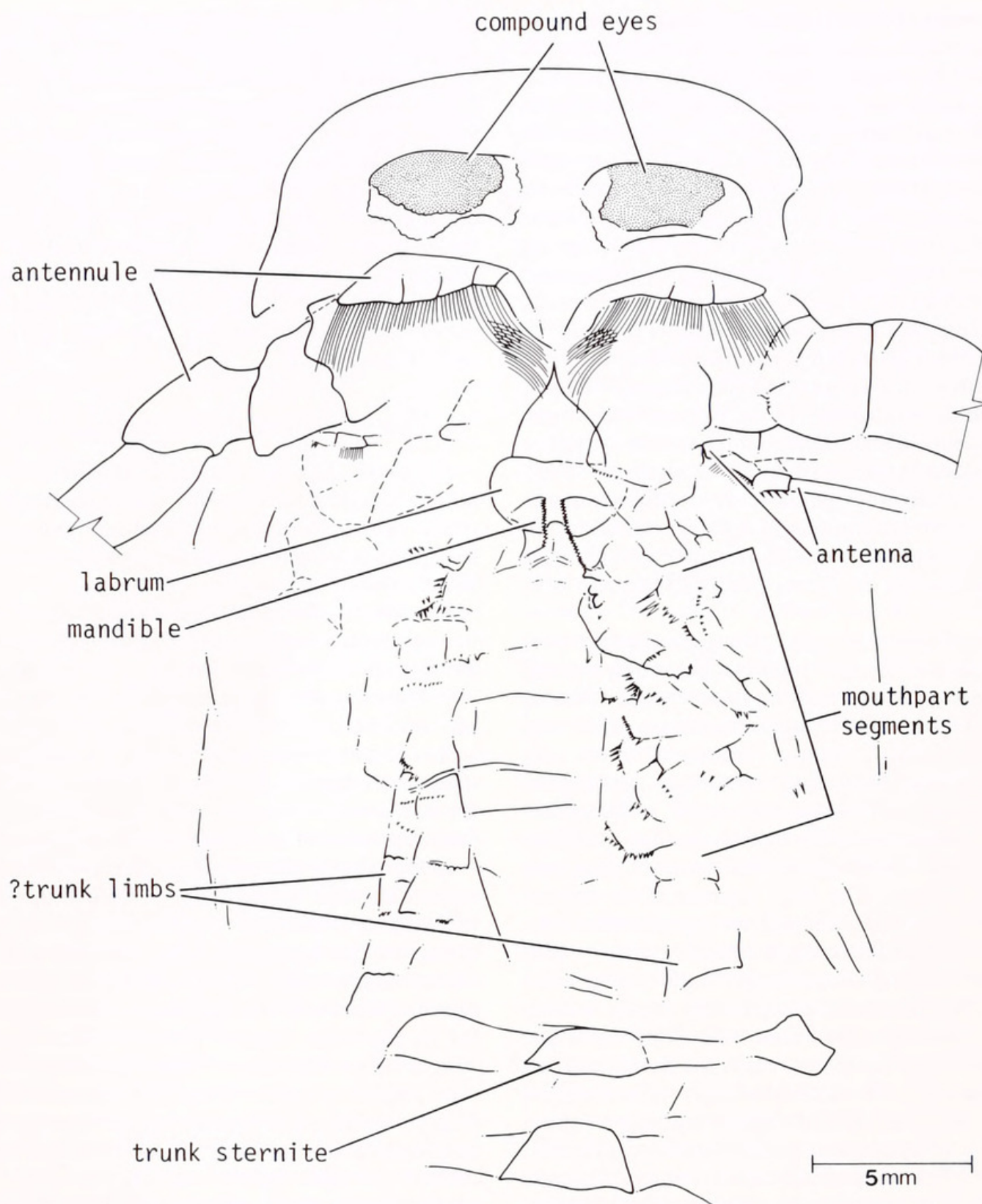
Fig. 35. *Tesnusocaris goldichi.* Camera lucida drawing of holotype, USNMP 124173.

the two characters used by Brooks to define *Tes-nusocaris* vis-à-vis the brachypodans, one—presence of jointed limbs—is a general feature of *all* arthropodous groups (see Schram, 1986:chapter 2). The other feature—unspecialized post-cephalic tag-mata—is not a characteristic of cephalocarids, even *sensu lato.* All crustaceans, except for the remipedes and conchostracans, exhibit some degree of trunk

tagmosis. In the case of brachypodans, the thorax is marked by the possession of multiramous leaf-like limbs, but the abdomen lacks appendages altogether. The presence of unspecialized post-cephalic tagma *is* distinctive, but not of cephalocarids—or for that matter any phyllopodans. It is, however, a diagnostic feature of the remipedes!

This latter fact suggested to Schram (1983a) that

Tesnusocaris and the living remipedes were possibly sister-groups. Further analysis (Schram, 1986) indicated that nectiopodans and enantiopodans form a primitive clade near the base of the crustacean lineage (see below).

Family TESNUSOCARIDIDAE Brooks, 1955

Diagnosis. — Since there is only one family, the diagnosis is the same as that of the order.

Type genus. — *Tesnusocaris* Brooks, 1955

Genus TESNUSOCARIS Brooks, 1955

Diagnosis. — Since there is only one genus, the diagnosis is the same as that of the family.

Type species. — *Tesnusocaris goldichi* Brooks, 1955

TESNUSOCARIS GOLDICHI Brooks, 1955

Diagnosis. — Since there is only one species currently recognized, the diagnosis is the same as that of the genus.

Holotype. — USNMP 124173, concretion with two counterparts.

Locality. — West of Rough Creek, 4300 ft. S 51 E of Hill 4334, Dove Mountain Quadrangle, Brewster County, Texas.

Stratum. — Tesnus Formation, Lower Pennsylvanian.

Remarks. — The description of this species by Brooks (1955) is generally accurate regarding gross body form. However, certain observations concerning the cephalic limbs have proven to be inaccurate and are corrected here. The preservation of this fossil leaves much to be desired. Body outline and shape are clearly discernable (Fig. 36A), but details of appendage structure are obscure. Generally, best results were obtained (FRS) by immersing the fossil in alcohol, but the details thus revealed are difficult to photograph (Fig. 36). To assist future workers in study of this specimen, a camera lucida drawing of the holotype (Fig. 35) is presented.

The shape of the cephalic shield and the sessile compound eyes are as Brooks described. The separate first and second cephalic appendages of Brooks, however, appear to form together a single biramous limb. The short anterior branch (first cephalic appendage of Brooks) is not the single-segment flap-like structure originally described, rather it appears to be composed of at least five segments. The posterior margin is setose, with the distal and basal segments bearing longer setae than the intermediate segments. This branch appears to arise from an obscure basal portion that is closely associated with the most proximal segment of the posterior branch of the limb. This posterior branch (second cephalic appendage of Brooks) is as originally described; and the long, medially directed, somewhat curved setae near the base are overlain by the long setae on the base of the anterior branch. These branches taken together would seem to be the antennules.

The real second cephalic limb of this animal was not noted at all by Brooks. It is best observed with very oblique lighting. The basal and distal parts of the limb are not preserved on this specimen. However, just posterior to the base of the large posterior branch of the antennules are a series of laterally directed, setose and spinose segments that seem to form parts of a pair of modest sized, biramous, subflagellate limbs. These appear to represent the antennae.

The labrum generally corresponds to the "bell-shaped" form described by Brooks (Fig. 36B, C). However, it should be noted that the anterior extremity is rather pointed, extending anteriorly between the bases of the antennules and antennae. In addition, the posterior portion of the labrum is delineated by a groove that appears to mark off a structure that forms a large atrium oris. Under this lobate posterior portion of the labrum can be clearly seen the large molar processes of the mandibles described by Brooks. These are so large, however, that they do not seem to have been completely enclosed within the atrium oris. Some material seems to have fallen out of the fossil on the right side of the better preserved counterpart, and the outline of these missing items is reminiscent of the form of the lacinia mobilis and incisor process seen on nectiopodan mandibles. No palp can be seen on the mandibles.

The fourth and fifth cephalic limbs outlined by Brooks do not appear to exist at all in the forms he described and reconstructed. Rather this region, lateral to and posterior of the mandibles, is a complex jumble of very setose and spinose segments with their armatures directed medially (Fig. 36B). The exact form, length, and number of the limbs represented by these segments can not be discerned on the holotype. There are probably at least three pairs of these limbs that seem to be directed somewhat laterally. Posterior to these laterally oriented appendages there are an undeterminable number of limbs that are directed posteriorly. These latter appear to have short, broad, and faintly setose joints; and are actually rather similar in form to what is known of the more clearly preserved trunk limbs seen more posteriad on the body. It would appear that the region just posterior to the mouth was
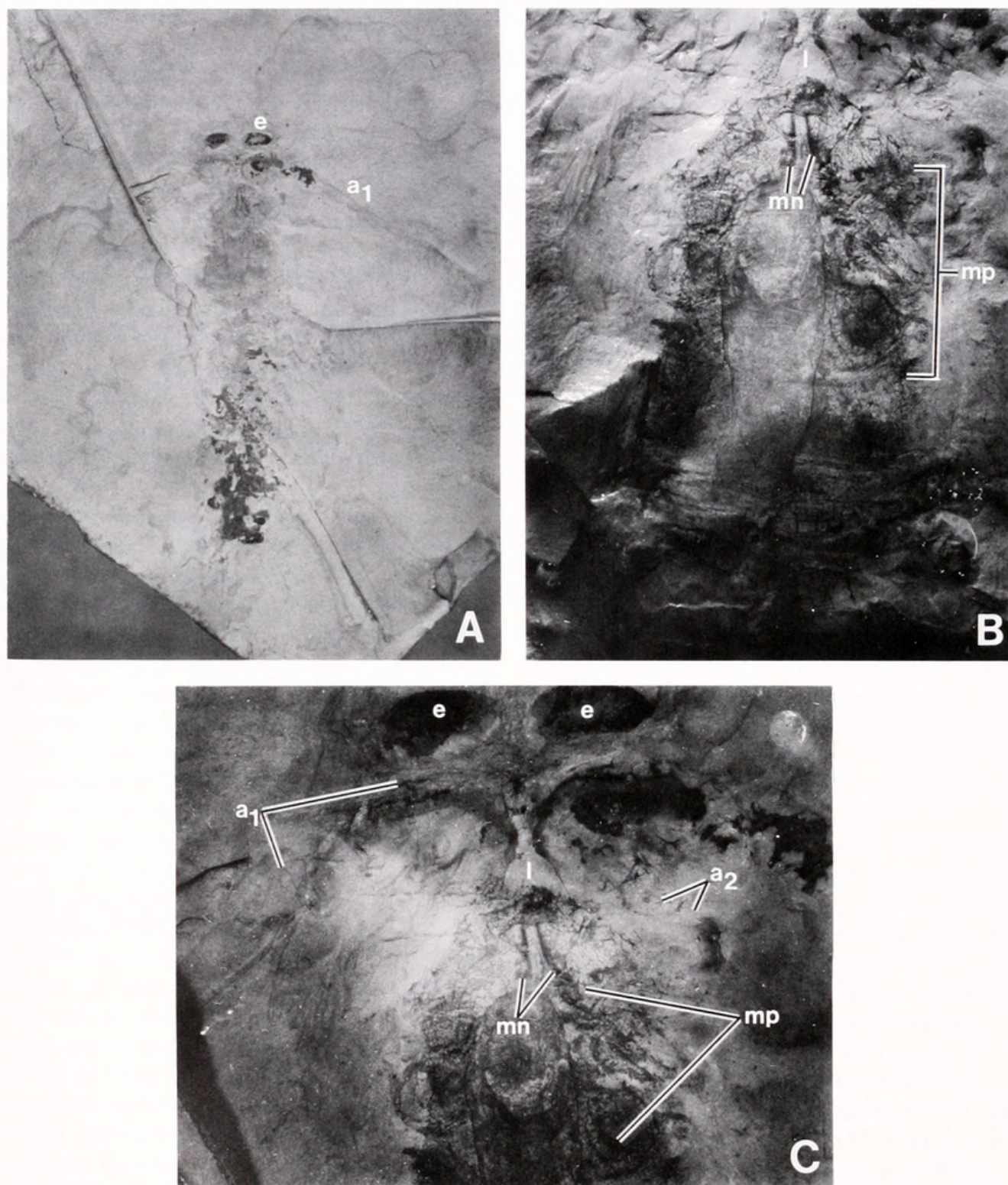
Fig. 36.   *Tesnusocaris goldichi.* Holotype, USNMP 124173; A) whole body, 1.0×; B) closeup of postoral region, 4.3×; C) closeup of anterior head, 5.4×. a1—antennule, a2—antenna, 1—labrum, mn—mandible, e—eyes, mp—mouthparts.

equipped with an array of robust mouthparts, and that these were closely followed by the flap-like trunk limbs that were already known from Brooks' description.

Unfortunately, the preservation of USNMP 124173 does not allow an accurate reconstruction to be made of the ventral cephalon of *Tesnusocaris*. However, the interpretation of the specimen that is presented here (Fig. 35) does suggest that even more clearly resolved relationships to the nectiopodans may be drawn. The antennules and antennae seem to be biramous, and the antennules bear long setae on their bases that are suggestive of the aesthetasc pads so characteristic of living remipedes. The labrum, now that distinct anterior and posterior areas can be delineated, is very similar to that seen in nectiopodans, as is the relationship of the molar process of the mandible to the atrium oris. The limbs in proximity to the mouth and mandibles, with their robust setose and spinose endites, are evocative of the grappling mouthparts of the Nectiopoda. Of course, the significance of the apparent lack of trunk tagmosis and the possession of simple, biramous, paddle-like limbs on the segments of this region have already been discussed by Schram (1983a, 1986).

More and better material of this species must be sought in order to clarify our understanding of the pertinent features of cephalic anatomy of this group. Several characters declaim a separate status for enantiopodans from nectiopodans. The sessile compound eyes, possible flagellar form of the antennae, large size of the mandibular molar processes and their apparently incomplete incorporation into the atrium oris, and the possibly robust (but not necessarily prehensile or subchelate) posterior mouthparts would appear to be unique.

DISCUSSION

The recognition and detailed description of several species of nectiopodans now allow an outline of the phylogenetic relationships within the order to be proposed. At this stage, a phylogenetic scheme of remipedes is tentative, and should be treated as a working hypothesis. For this reason we have deliberately kept the supraspecific taxonomy of the group rather simple, recognizing only three genera in two clearly delineated families within the order Nectiopoda.

Polarization of characters in a "new" group such as this is difficult, especially because so many features indicate that the taxon in question is a primitive one near the base of the crustacean clade. Under such a constraint, the sister group—all other crustaceans—happens to contain what are commonly thought to be advanced taxa. However, no group is ever completely derived nor completely primitive in all its characters. One therefore cannot make blanket judgements about individual characters among taxa. To mitigate against this, one should establish outgroups beyond the Crustacea, but as Anderson (1973), Manton (1977), and Schram (1978, 1986) have pointed out, the position of the Crustacea (whether one accepts a distinct phylum status or not) is so distinct from other arthropodous types that selection of an outgroup from among the many potential living and fossil groups is nearly impossible. However, one can use the array of known living and fossil articulates to construct some kind of ancestral structural plan from which all crustaceans could be derived. Conclusions drawn from such an animal should be tempered by the caveats of the uncertainty principle outlined by Schram (1983b).

As an example of the problems to be encountered, let us consider polarization of some prominent remipede features. The chief distinguishing features of remipedes are the presence of limbs on every trunk segment and the lack of trunk tagmosis (features homoplastic with similar conditions in Conchostraca). Comparison to other crustaceans reveals some ambiguous insights. For example, malacostracans also have limbs on every trunk segment, but like most other crustaceans the Malacostraca have trunk tagma. Clearly, scoring of the polarity of these remipede characters on the basis of this comparison would have to be uncertain. Considering outgroups to Crustacea, both living (e.g., myriapods, primitive uniramians) and fossil types (e.g., trilobites as well as some of the Middle Cambrian, Burgess Shale articulates, like *Branchiocaris*), would seem to indicate that a condition with limbs on all segments and no trunk tagmosis is a primitive one, that is, classic theory for ancestral arthropod types (Hessler and Newman 1975). In this case, remipedes would be scored as primitive in limb location and lack of trunk tagmosis.

A prominent nectiopodan feature is the development of robust, uniramous, grappling mouth-

Tesnusocaris goldichi   Godzillius robustus   Lasionectes entrichoma   Speleonectes lucayensis   ondinae
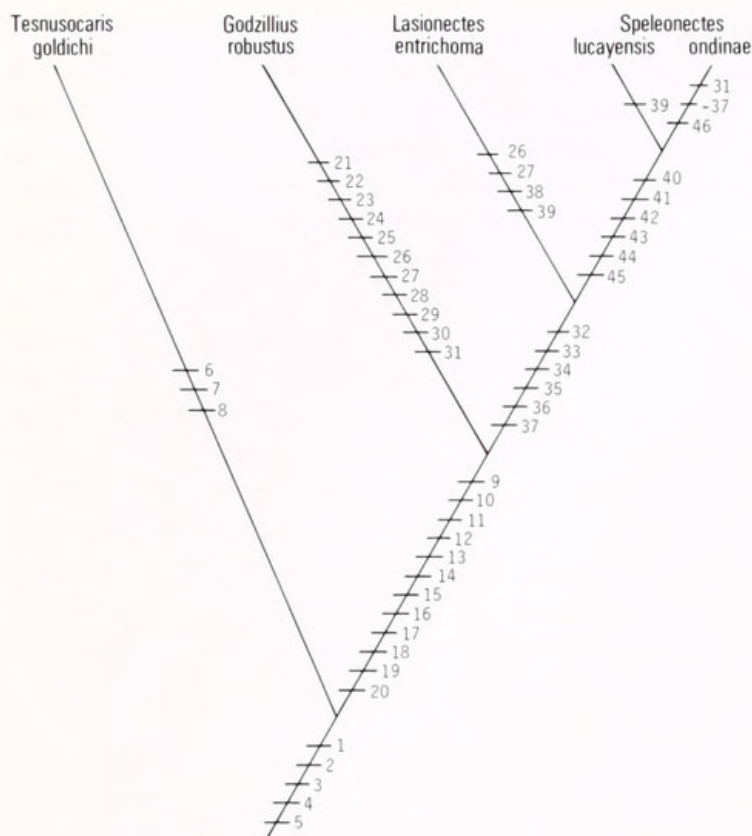
Fig. 37. Cladogram of relationships of currently recognized Remipedia. Apomorphic features: 1—broad, subquadrangular, cephalic shield; 2—bulbous labrum forming large atrium oris; 3—mandible at least partly within the atrium oris; 4—(?) mandible lacking palp; 5—(?) mouthparts raptorial; 6—(?) frontal filaments absent; 7—huge mandibular molar process; 8—trunk limb endopods with seven segments; 9—no eyes; 10—frontal filaments with spines; 11—antennular aesthetasc pad; 12—antenna paddle-like; 13—mandible tip completely within atrium oris; 14—mouthparts uniramous; 15—mouthparts with elbow to allow grappling; 16—maxillule with terminal fang; 17—basal maxillulary endites mandible-like; 18—maxilla with three ditiform endites; 19—maxillipedal segment fused to cephalon; 20—gonopores on base of fourteenth trunk limb; 21—cephalic shield subtrapezoidal; 22—frontal filaments with "joints"; 23—antennular ventral ramus blade-like; 24—antenna with multiple rows of setae on margins of endopod; 25—third maxillulary endite club-like; 26—maxilla and maxillipede subchelate; 27—maxilla and maxillipede third segment wide with dense rows of setae on crests; 28—maxilla and maxillipede with grappling hook-like terminal claws; 29—maxilla with three segments beyond elbow; 30—maxillipede with four segments beyond elbow; 31—genital flap on leg base; 32—maxillule with subtriangular endite on segment three; 33—maxillule third endite cone-like; 34—maxilla with four segments beyond elbow; 35—maxillipede with five segments beyond elbow; 36—loss of sternal plates; 37—posterior segments at least with differentiation of sternal bars; 38—maxilla and maxillipede with trifid terminal claws; 39—genital flap on fourteenth sternal bar; 40—maxillules with robust apical setae on endites of second and (41) third segments; 42—maxilla and maxillipede prehensile; 43—maxilla and maxillipede bear arcuate endites on third segment; 44—maxilla and maxillipede have rows of widely spaced simple setae on distal segments of limb; 45—maxilla and maxillipede with comb-like, semi-circular, terminal claws; 46—apical setae on maxillulary endites subsetulate. A negative character (−) denotes reversal of feature.

parts. In the analysis of this feature, changes in our understanding of nectiopodan outgroups has caused some problems. Schram (1986:chapter 43) considered the sister group of the Nectiopoda, the enantiopodan *Tesnusocaris goldichi*. He noted that Brooks described and reconstructed the first two post-mandibular appendages as simple setose lobes. Examination of the outgroup to remipedes, i.e., all other crustaceans, revealed simple setose mouthparts was the norm. Hence, it might have been assumed that the grappling form of the mouthparts of the nectiopodans is an advanced condition.

However, the recognition herein that *Tesnusocaris* also may have had raptorial mouthparts makes the issue of the form of ancestral crustacean mouthparts an open one. Though other crustaceans generally have simple setose lobes for maxillules and maxillae, there are some exceptions (e.g., some copepods and ostracodes) in which the mouthparts are raptorial. Furthermore, in light of the discussion of the evolution of crustacean feeding types by Schram (1986:chapter 44) it would appear that a series of raptorial type mouthparts may prove primitive, and that the simple setose lobes so common among other crustaceans may be derived. In light of this possibility, reliance for the time being is placed on the tendency of evolution to go frequently from the simple to the more complex. In this instance, simple mouthparts are scored primitive and raptorial forms are considered derived; thus the form of the mouthparts in nectiopodans, and possibly enantiopodans as well, are judged as an autapomorphy.

In the present study, we utilized 46 characters for five species. However, our analysis was tempered by the recognition of two (possibly three) additional nectiopodan species not described. These taxa are known only from single specimens, and we have chosen not to describe them at this time pending the collection of more material. These taxa appear to be related rather closely to the genus *Speleonectes* and were useful in delineating the order of appearance of certain characters in the cladogram of Figure 37. The analysis was done using the computer facilities of the California State University system; and employed PIMENTEL, an option within the PHYSYS package. This is basically a modification of the well-known WAGNER 78 program that seeks to produce the most parsimonious arrangement of taxa with the highest degree of congruence and lowest amount of homoplasy of the characters used.

The class Remipedia is distinguished by a broad, rectangular cephalic shield (1); a bulbous, well-developed labrum which extends posteriorly to form

a large atrium oris (2); mandibles that are at least partially within the atrium oris (3); (?) mandible lacking a palp (4); and (?) raptorial mouthparts (5). Recognition of characters 2 and 3 have resulted from the present study, but the resolution of characters 4 and 5 must await the discovery of more and better material of *Tesnusocaris*.

The order Enantiopoda is characterized by a possible lack of frontal filaments (6), an enlarged molar process on the mandible (7), and the trunk limb endopods with 5 or possibly 6 segments (8). The possession of eyes, biramous antennules, and subflagelliform biramous antennae are ajudged as primitive features (though the sessile and compound nature of the eyes might be apomorphic). The fact that the mandibles of *Tesnusocaris* are only partially incorporated into the atrium oris might be an intermediate step between a condition where the mandibles are a completely external set of limbs—as seen in almost all other crustaceans—and one in which the mandibles are completely incorporated into the atrium oris—as seen in the Nectiopoda. The long, lash-like setae seen on the basal segments of the antennular rami of *Tesnusocaris* could also be interpreted as an intermediate stage towards the development of the prominent aesthetasc pad seen at the base of the nectiopodan antennules. In short, the Enantiopoda seem to provide insight into how the class Remipedia evolved.

The order Nectiopoda is characterized by a lack of eyes (9); frontal filaments with an accessory spine (10); an aesthetasc pad on the antennules (11); paddle-like form of the very setose antennae (12); mandibles with their distal ends completely incorporated into the atrium oris (13); uniramous mouthparts (14); mouthparts developed with an elbow to allow some kind of flexion of the limbs for grappling (15); maxillules developed as a fang-like claw (16); the two most proximal maxillulary endites "mandibulariform," and these endites flanking the mouth in the place of the mandibles (17); the maxillae with the proximal-most endites as three digitiform structures (18); fusion of the maxillipedal segment to the cephalon (19); and gonopores located on the bases of the fourteenth trunk limbs (20). Most of these diagnostic features are directed towards the specialized mode of carnivorous feeding seen in nectiopodans (further discussion in this regard will await the analysis of internal anatomy now under way).

The family Godzilliidae possesses a number of very distinct features. The head shield is subtrapezoidal, i.e., rather narrow in its anterior aspect (21); the frontal filaments are very long and seem to have a number of "joints" along their length (22); the antennular ventral ramus is blade-like (23); the antenna bears multiple rows of plumose setae along the margins of the endopod (24); the maxillulary third endite is a large club-like process (25); the maxillae and maxillipedes are subchelate (26); the maxillae and maxillipedes have very wide third segments, and bear dense rows of simple setae along their entire lengths (27); the maxillae and maxillipedes have terminal claws in the form of multipronged grappling hooks (28); the maxillae have three segments beyond the elbow (29); the maxillipede has four segments beyond the elbow (30); and the genital flap that protects the opening of the genital pore is located on the base of the leg (31). Several of the aptations of this creature, especially those of the maxillules, seem to indicate a large animal having to locate and immobilize large prey items.

The family Speleonectidae can be characterized generally, vis-à-vis godzilliids, as more delicately structured beasts. They are defined by the maxillules having a modestly well-developed, thumb-like endite on the second segment (32) and a subtriangular endite on the third segment (33), the maxillae have four segments beyond the elbow (34), the maxillipedes have five segments beyond the elbow (35), the sternites generally are not developed as plates (36) though the form of the sternal bars is differentiated (37).

The genus *Lasionectes* bears certain similarities to *Godzillius*. The maxillae and maxillipedes are subchelate (26) and the third segment of these limbs is quite wide, having dense rows of simple setae all along the edge (27). However, the terminal claws of the maxillae and maxillipedes are trifid (38) and the genital flap that protects the genital opening is located on the lateral aspect of the sternal bar of the fourteenth segment (39).

The genus *Speleonectes* is characterized by the maxillules with robust apical setae on the endites of the second (40) and third segments (41); the maxillae and maxillipedes are prehensile (42), bear rather arcuate endites on the third segments (43), have widely spaced rows of simple setae along the margins of the distal segments (44), and have terminal claws that are a semicircular row of comb-like spines (45).

Speleonectes lucayensis is distinguished from its sister species largely by a feature that it shares with *Lasionectes*, i.e., it possesses a genital flap on the lateral aspect of the fourteenth sternal bar (39). On the other hand, *S. ondinae* is characterized by the possession of a genital flap located on the base of
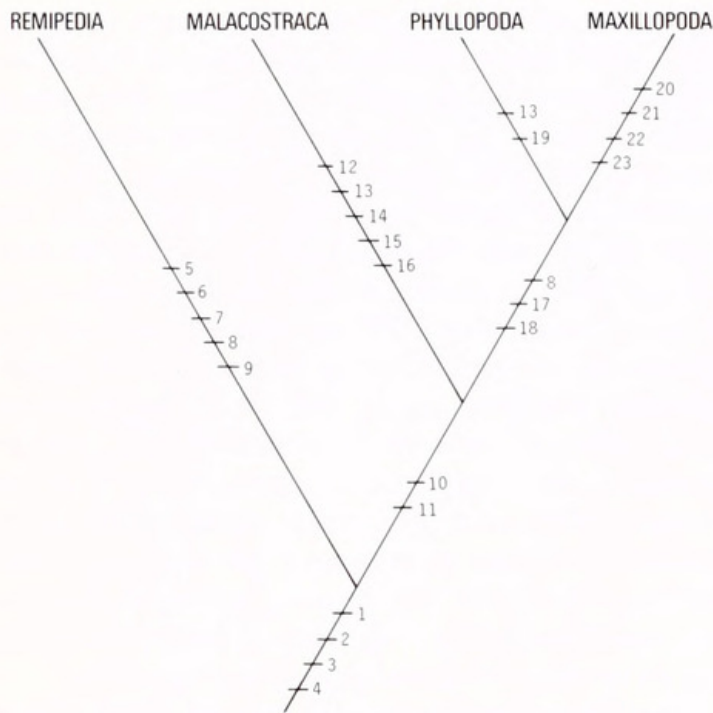
Fig. 38.   Cladogram of crustacean classes modified from Schram
(1986). Apomorphic features: 1—two pair of antennae; 2—bira-
mous antennules; 3—two pairs of maxillae; 4—nauplius larva or
egg-nauplius stage; 5—broad subquadrangular cephalic shield;
6—labrum forming large atrium oris; 7—mandible at least par-
tially enclosed within atrium oris; 8—mandibular palp lacking;
9—(?)raptory mouthparts; 10—postcephalic tagmosis; 11—typ-
ically at most eight thoracic segments; 12—malacostracan nau-
pliar eye; 13—polyramous limbs; 14—stenopodous thoracic en-
dopods; 15—uropods; 16—carapace that covers only, or at least
parts of, thorax; 17—abdomen typically lacks limb; 18—unira-
mous antennules; 19—leaf-like (foliaceous) thoracopods; 20—at
most 11 trunk segments; 21—no more than six thoracic segments;
22—short, bulbous heart; 23—maxillopodan naupliar eye.

the fourteenth limb (31), a loss of differentiation in
the form of the sternal bars of the posterior trunk
segments (−37), and the apical setae on the max-
illulary endites being subsetulate (46). As mentioned
above in remarks on *S. ondinae*, it remains to be
determined whether the body form of this species,
i.e., the high head to body ratio and relatively low
number of body segments, is due to some paedo-
morphic process in the evolution of the taxon or
merely to our only having subadult specimens at
hand.

Recognition of the class Remipedia has had a
profound effect on understanding the phylogeny of
the Crustacea (Schram 1986). It was thought pre-
viously that the brachypodan cephalocarids repre-
sented something close to an ancestral type, an idea
derived from the mixopodial theory of crustacean
limb evolution developed by Borradaile (1917,
1926). He postulated that polyramous, leaf-like limbs
gave rise to biramous forms (see Schram 1983*a* for
details). This idea stood in contrast to the biramous
theory of Cannon and Manton (1927), which had

the advantage of moving from the simple to the
complex in regard to limb form. However, until the
discovery of the nectiopodans in 1981, the only
known living forms in which adults possessed bira-
mous limbs (various maxillipodan types) were all
considered to be derived in regard to body plan, i.e.,
copepods, ostracodes, barnacles and their allies. The
delineation of a class Remipedia placed a biramous
limb type onto what is generally conceded to be a
primitive *Bauplan*; i.e., one in which there is a pair
of limbs on every trunk segment and no tagmosis
or regionalization of the trunk.

The concept of a cephalocarid-like ancestor had
a rather inconvenient side effect. Attempts at draw-
ing a phylogenetic tree of crustacean relationships
typically resulted in the production of a "phyloge-
netic grass." That is, with cephalocarids as an ances-
tor, no clear view could be developed as to rela-
tionships of basic crustacean types; indeed, there
was no consensus as to just what were the basic
Baupläne of the groups. Crustacean taxonomies
usually contained six or more classes, and the dis-
covery of new groups (e.g., mystacocarids or tan-
tulocarids) usually resulted in their arbitrarily being
installed at a class level. This sort of scheme stood
in stark contrast to the accepted phylogenies within
other arthropodous groups, such as uniramians and
cheliceriforms, in which generally clear concepts of
relationships had developed, and for which a rela-
tively few basic classes were accepted.

Schram (1986) utilized methods of cladistic anal-
ysis to evaluate characters in an attempt to arrive
at a parsimonious tree of relationships for all crus-
taceans. The method was not used slavishly, how-
ever, since it was recognized that any kind of cla-
distic analysis must be tempered with consideration
of functional morphology. Schram (1986) also at-
tempted to evaluate the effectiveness of a remipede
versus a cephalocarid ancestral type. Both groups
have derived features (i.e., autapomorphies) which
preclude their being viewed as direct ancestors of
all other crustaceans. However, cladistic analyses
are based on character matrices. Characters are
scored as primitive or derived based on the outgroup
analysis of the individual features rather than in
which group the features may happen to occur.
Schram (1986) can be consulted for details, but one
conclusion of that study was that cladograms with
remipedes as ancestral types were shorter and more
highly resolved (i.e., more parsimonious) than ones
with cephalocarids as ancestral types.

Indeed, a consequence of developing a remipede
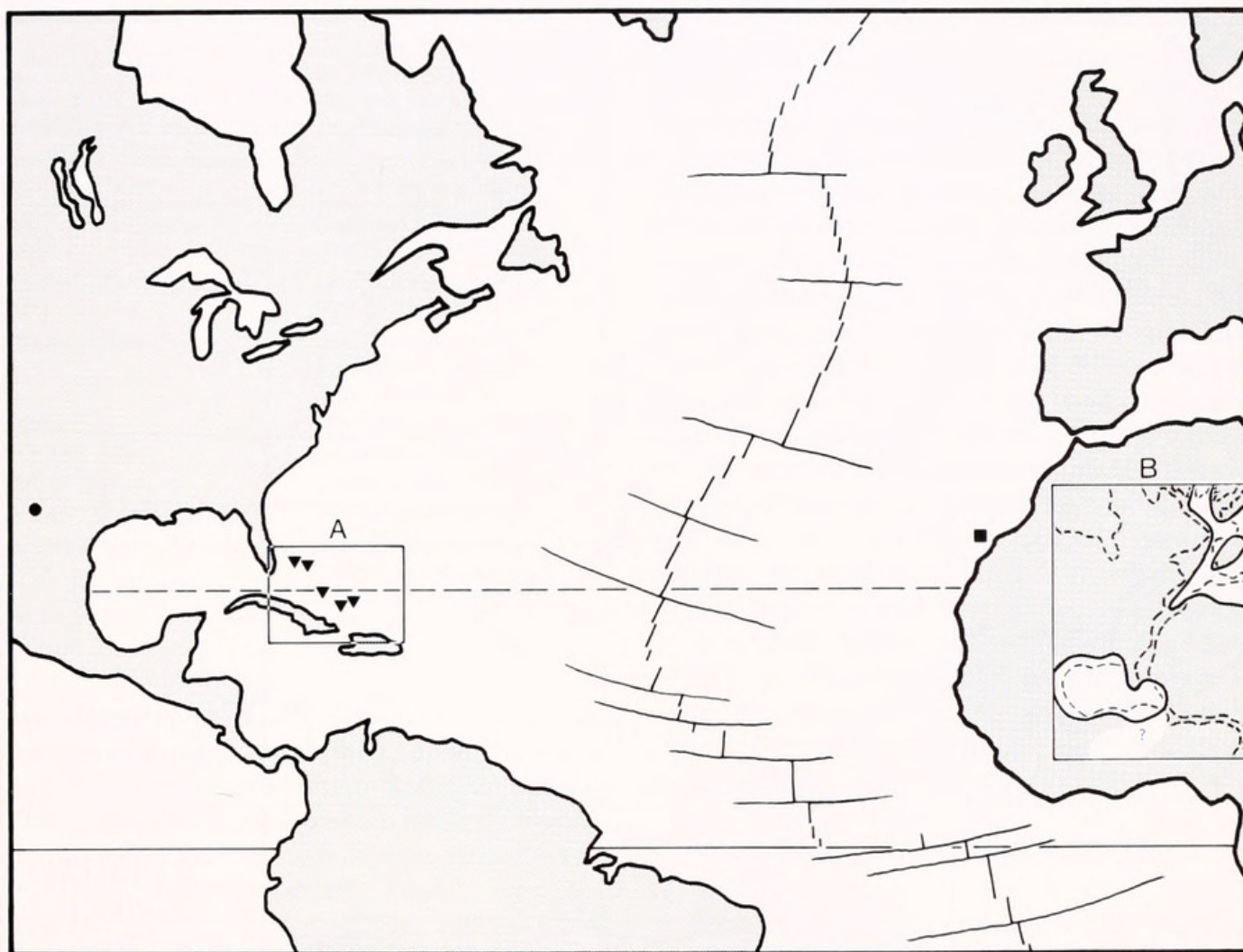rooted phylogenetic tree (Fig. 38) is to suggest a

Fig. 39.   Distribution of fossil and living Remipedia. Atlantic basin shown with mid-ocean ridge and fracture system. ● *Tesnusocaris goldichi,* lowermost Pennsylvanian of Texas; ▼ various Nectiopoda, West Indies; ■ *Speleonectes ondinae,* Lanzarote, Canary Islands. Inset A—see Figure 40 for details; Inset B—location of continents 165 million years ago before opening of Atlantic Ocean.

more logical scenario for crustacean evolution than had been available previously. An essentially long bodied, unregionalized, cephalic feeding animal with mandibular palps was seen to give rise to Remipedia on one hand as well as other types of crustaceans on the other. The first step in the evolution of higher crustaceans was to regionalize the body. This apparently allowed several things to occur. Reproductive and locomotory functions could be clearly delineated in the somite division of labor. Locomotory subspecializations could be achieved with some limbs and regions being specialized for swimming (e.g., uropods) and others for walking (e.g., stenopodous endopods). Furthermore, other methods of food procurement could be developed, with some lines experimenting with various cephalic strategies and others incorporating the thorax into feeding behaviors. Reduction in total number of body segments climaxed in fixation on no more than eight segments in the thorax.

The first offshoot of this initial differentiation resulted in the evolution of the immensely successful Malacostraca. In this class most variations on the above options were explored. In connection with this radiation, a type of multiramous limb—that with a stenopodous endopod—was evolved.

Subsequently, the main theme of crustacean evolution was directed at further reduction of the trunk, both in numbers of segments as well as a strong tendency to lose limbs on the abdomen. Perhaps as a consequence of this paedomorphosis, most of the following crustaceans share the possession of uniramous antennules and many lack mandibular palps. Two main lines developed, each exploiting different modes of food procurement, and these lineages contain the most highly derived of crustaceans.

The class Phyllopoda (similar to the Thoracopoda of Hessler and Newman, 1975) developed polyramous leaf-like limbs that function in a unique method of thoracic filtration. The major groups within
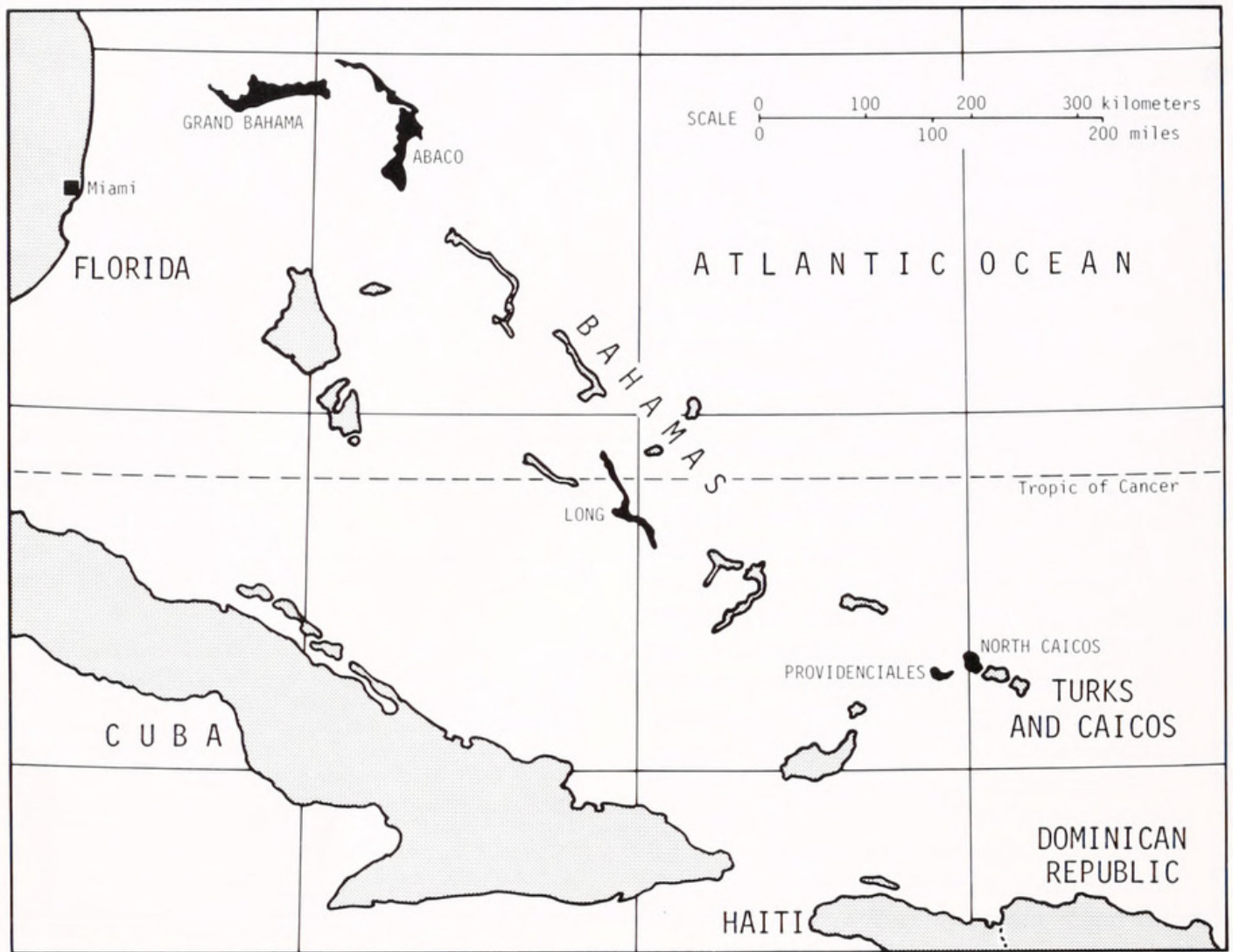
Fig. 40.   Islands in West Indies (shaded) currently known to harbor Nectiopoda. See Table 5 for details.

this class are: the Phyllocarida, a group that still retains most of the abdominal limbs, and developed a unique flap-like branch to the antennule; the Cephalocarida, which contains the living brachypodans and the Devonian lipostracan *Lepidocaris*; the Sarsostraca or Anostraca, which lack not only a carapace but a head shield as well; and the Calmanostraca, i.e., the branchiopods with carapaces such as notostracans and diplostracans.

The class Maxillopoda contains crustaceans that, with the one major exception of the barnacles, exploit cephalic feeding modes. However, maxillopodans tend to have repeatedly evolved various methods of parasitism and the class is generally marked by distinct reductions in the development of the trunk and limbs. The Cirripedia *sensu stricto* evolved yet another special mode of thoracic feeding, the filtratory cirri. The maxillopodan trunk generally does not exceed 11 segments, and the thorax seems fixed at no more than six somites. The constituent groups of the Maxillopoda are frequently so highly derived that proposed relationships of the

group are rather unresolved (see e.g., Grygier 1983, or Schram 1986). The major maxillopodan groups are: Tantulocarida, Branchiura, Mystacocarida, Ostracoda, Copepoda, and Thecostraca. The first three of these may bear some relationship to each other. The last of these includes the barnacles and their relatives. To these should now be added the Skaracarida of Müller and Walossek (1985), but the exact affinity of these Cambrian beasts within the class is uncertain at this time.

One final matter requires some comment. Though the remipedes are a primitive group, apparently a very ancient one, they are not widely distributed. Though nectiopodan studies are still few, all forms discovered to date have been part of a well-established western Tethyan distribution. The Canary Islands and British West Indies, where nectiopodans have been collected (Figs. 39, 40), are part of a region (the Caribbean, central west Atlantic, west Africa, and the Mediterranean) which is known to contain a common fauna of interesting crustaceans. In addition to nectiopodans, this region is noted for such

TABLE 5. Nectiopodans collected in known localities for the group in the West Indies. New species I has been collected from two caves on different islands (Ia & Ib), and the single specimen from each may or may not be in the same species.

Locality	Nectiopodan taxa
Lucayan Cavern, Grand Bahama	*Speleonectes lucayensis* adults and juveniles
Old Freetown Cave, Grand Bahama	*Speleonectes* juveniles New species Ia
Dan's Cave, Abaco	*Godzillius* juveniles *Speleonectes* juveniles New species Ib
Long Island	unidentified nectiopod
Old Blue Hill Cave, Providenciales	*Lasionectes entrichoma* adults and juveniles
Airport Cave, Providenciales	*Lasionectes* juveniles
Cottage Pond, North Caicos	*Lasionectes entrichoma* *Godzillius robustus* New species II

phylogenetically interesting crustacean forms as thermosbaenaceans, stygiomysids, procarid eukyphidans, mictaceans, and certain hypogean amphipods. Interestingly, the only known fossil remipede, the enantiopodan *Tesnusocaris,* also occurs adjacent to this Tethyan realm in western Texas.

This distribution indicates several things. First, the group's history seems to be closely linked with the ancient Tethyan Sea and the subsequent formation of the Atlantic Ocean (Fig. 39B). Second, their restriction to caves in just this area implies that nectiopodans have rather limited powers of dispersion and/or highly specific environmental requirements. Though some cohabitants of their fauna are found in the open ocean as well as in caves, e.g., the mictaceans and some amphipods, it would seem that the deep-ocean origin postulated for at least some of this fauna (Hart et al. 1984) may not apply to the nectiopodans. Third, though one can never rule out a serendipitous discovery of a nectiopodan outside this realm (witness *Procaris* spp. on the Hawaiian Islands juxtaposed against their occurrence on Ascension Island and Bermuda), it appears that the greatest opportunity to find more nectiopodans would be to explore caves in the Greater Antilles, Mediterranean, and other islands in the archipelagos where they have already been collected.

Another important aspect of nectiopodan distribution also holds great promise for future discoveries. Nectiopoda usually do not occur in isolation, but are more often found sympatrically with other nectiopodans (Table 5). The ecological explanation for this is difficult to understand. All nectiopodans share the same body plan, and differences between taxa are not that great. With the exception of the large form, *Godzillius robustus,* all the animals are in the same size range and presumably dine on similar prey. How these animals have subdivided cave niches so that several species can coexist is not known. To resolve this question will require prolonged and repeated observation of nectiopodans, both in their native habitat as well as in the laboratory. For the time being, however, it is useful to note that, though they are not typically abundant in absolute numbers, where one nectiopodan species occurs, more will probably be found.

ACKNOWLEDGMENTS

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