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Studies on the Cylindropsyllidae (Copepoda, Harpacticoida). 2. A revision of the genus *Cylindropsyllus* Brady

RONY HUYS

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The cylindropsyllid type genus *Cylindropsyllus* Brady, 1880 is revised and a new species *C. kunzi* sp.n. from the North Sea is added. Of the other species a detailed redescription and figures are given, distribution records are compiled and some phylogenetic data are presented. It is suggested that *Cylindropsyllus* and the monotypic *Cylinula* Coull, 1971 are sister groups, the latter being the apomorphous lineage because of the unisegmented mandibular palp and the prehensile endopodite P1. *Cylindropsyllus* sp. Monard, 1935 cannot be assigned to any known species. An amended diagnosis of the genus *Cylindropsyllus* and a comparison with *Cylinula* are presented.

Rony Huys, Marine Biology Section, Instituut voor Dierkunde, Rijksuniversiteit Gent, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium.

Introduction

Sand dwelling organisms, particularly crustaceans and worms, are usually regarded as burrowers, since in their migrations they displace the particles of their environment. In contrast to the sand burrowing animals, interstitial copepods do not transpose the particles of the sand through which they move but crawl over the surface of the grains, which by capillarity always hold more or less water, even high up on the beach at low tide (Pennak 1951). Copepods of this type, though frequently represented in several other families through analogous adaptations, can in general be referred to two 'Lebensformtypen' (Noodt 1971), corresponding with as many exclusively mesopsammic families. Paramesochridae are usually small, cyclopiform to (secondarily) vermiform and dorsoventrally flattened in cross-section (Huys 1987*a*, in press). Cylindropsyllidae, in contrast, are all slender, elongate, vermiform and round in cross-section, however, some forms obviously found adequate living conditions in the detritus layer of soft sediments and attained secondarily an extreme body size (e.g. *Cylindropsyllus laevis* Brady, 1880; *Stenocaris gracilis* G. O. Sars, 1909).

Sars (1909) established the family Cylindropsyllidae to comprise the genera *Cylindropsyllus* Brady, 1880, *Stenocaris* G. O. Sars, 1909, *Darcythompsonia* T. Scott, 1906 and *Leptocaris* T. Scott, 1899. Later on, Lang (1936) removed the latter two genera to a newly erected family Darcythompsoniidae, in which he included also *Horsiella* Gurney, 1920, originally assigned to the Cylindropsyllidae by its nominal author. In his comprehensive revision of the Cylindropsyllidae Lang (1948) emended Sars' familiar diagnosis. As a result, seven canthocamptid genera were added to the family, which he subsequently divided into three subfamilies: Cylindropsyllinae, Leptastacinae and Leptopontiinae.

The Cylindropsyllinae, characterized by the sexual dimorphism in both exopodite P2 and endopodite P3, grouped the genera *Cylindropsyllus*, *Stenocaris* and *Evansula* T. Scott, 1906, the latter being a replacement name for the preoccupied *Evansia* T. Scott, 1906, originally referred to the Canthocamptidae by several authors (Sars 1909; Monard 1927; Gurney 1932).

Brady (1878) at first proposed the name *Cylindrosoma*, yet altered it soon (Brady 1880) into *Cylindropsyllus*, since it was already appropriated for an amphibian genus (*C. longicaudata* Tschüdi, 1838). In his monograph of the British Copepoda Brady (1880) removed the genus from the 'Harpacticidae' and described it provisionally under the group Poecilostoma Thorell. Due to a lack of knowledge concerning the mouth parts, no distinct place in the classification was assigned to it. The author mentioned a similarity in general appearance with the genus *Ophthalmopachus* Hesse and suggested *Cylindropsyllus* ". . . may be found to be of parasitic or semi-parasitic habits". Scott (1892) redescribed the type species *C. laevis*, favouring a closer affinity with the Harpacticidae than with either the Poecilostoma or the Siphonostoma by reason of the male antennula, the biramous antenna and the form of the mandible. In order to complete Brady's description, Scott (1892) placed special emphasis on the structure of the head appendages, however, as Sars (1909) pointed out, an erroneous interpretation of the post-mandibular mouth parts was given. Furthermore, a peculiar organ situated anterior to the mandibles and possessing two subtriangular appendages ('sucking disks') was described (but not figured). According to Scott (1892), this structure would indicate a tendency towards parasitism, as Brady (1880) had stated before.

Sars (1909) was the first to assign a distinct place within the Harpacticoida to *Cylindropsyllus* and therefore erected a new family Cylindropsyllidae. Monard (1927) and later Gurney (1932) agreed with Sars, however, their

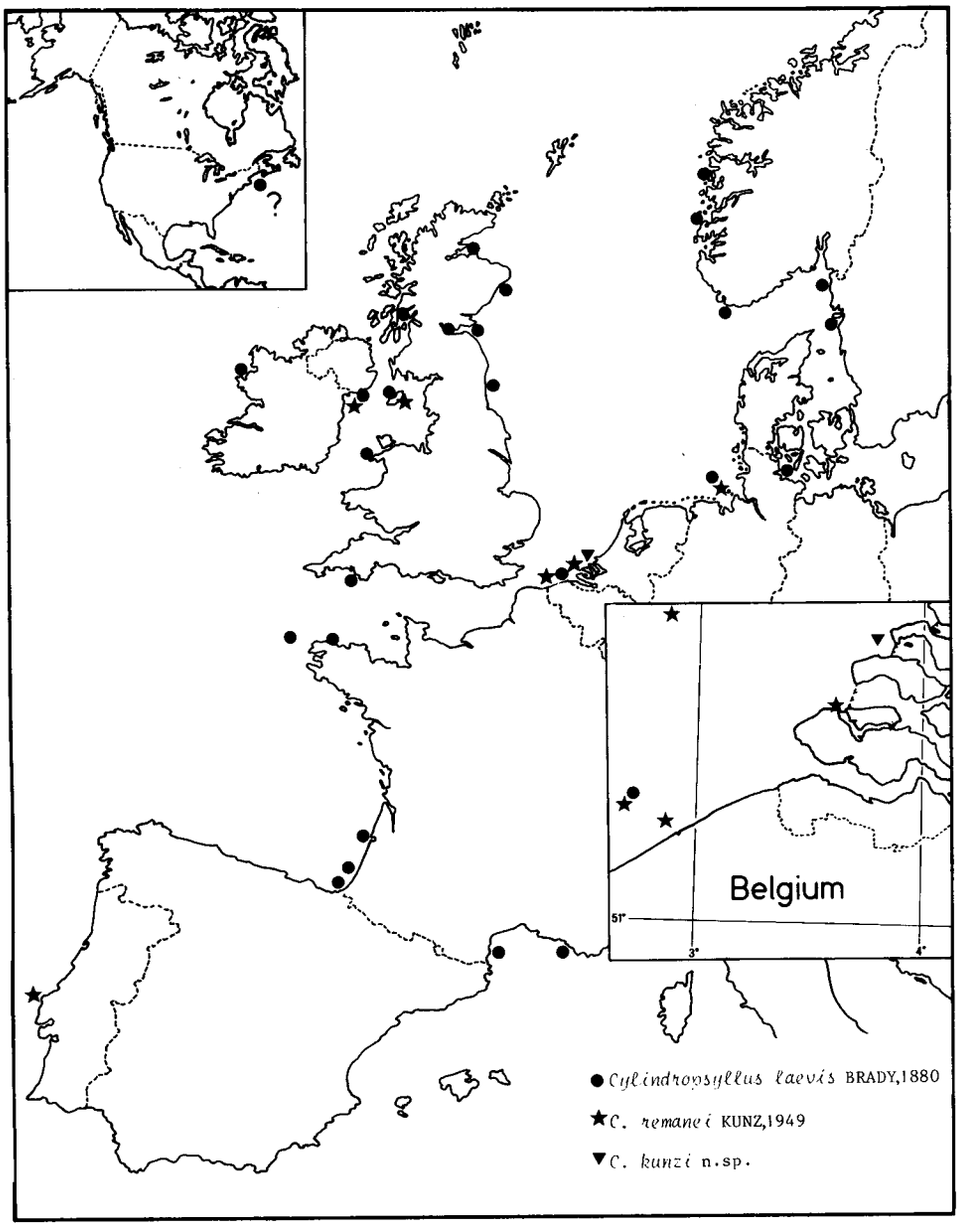

Fig. 1. Distribution of the genus *Cylindropsyllus* Brady, 1880.

familiar diagnosis of the Cylindropsyllidae and subsequently the genera referred to differed fundamentally. Following these authors, cylindropsyllid genera were characterized by the loss of maxillipeds (*Cylindropsyllus*, *Darcythompsonia*, *Horsiella*), which implied the transfer of *Stenocaris* to a separate family Stenocaridae. Accordingly, Monard (1927) established a section Agnatha which comprised the Cylindropsyllidae, Metidae and Lourinhidae because of the shared reduced maxillipeds. Lang (1936) argued strongly against the recognition of the Agnatha and the Cylindropsyllidae *sensu* Monard, as these taxa were unquestionably based on a convergence phenomenon.

The following species have been referred to the genus *Cylindropsyllus*: *C. laevis* (type species), *C. minor* T. Scott, 1892, *C. fairliensis* T. Scott, 1899, *C. brevicornis* Douwe, 1904, *C. remanei* Kunz, 1949. Sars (1909) considered *C. minor* as type species of a new genus *Stenocaris*, closely allied to *Cylindropsyllus*. *C. fairliensis* and *C. brevicornis* have been included in the family Darcythompsoniidae, the former being designated as the type species of the genus *Darcythompsonia* by Scott (1906*a*), the latter as type species of Gurney's (1920) new genus *Horsiella*, more recently being synonymized with *Leptocaris* by Kunz (1961).,

Since Sars' (1909) redescription, additional information on *C. laevis* has been given only by Kunz (1949) and Bodin (1968), however, their contributions were focused mainly on the setation of the swimming legs and/or the structure of the fifth leg. In the present paper a detailed redescription and a compilation of the distribution records (Fig. 1) of *C. laevis* and *C. remanei* are presented. A further new species, *C. kunzi* sp.n., from the Southern Bight of the North Sea is described.

Material and methods

The original type material of *C. laevis* apparently no longer exists. The redescription is based on Norman's specimens from the Firth of Forth, in the British Museum (Natural History), London [BM(NH)], though these are neither topotypes nor cotypes (for the explanation of the term cotype I refer to Huys 1987*b*). Kunz' type material of *C. remanei* was lost when the Institut für Meereskunde at Kiel was bombed in 1944. New

material collected from the Southern Bight of the North Sea was used for the redescription. Since the material upon which the redescription of both species is based did not come from the original type locality, a neotype cannot be designated (International Code of Zoological Nomenclature, Third Edition, Article 75d5).

Before dissection the habitus was drawn in lactophenol and body length measurements were made. Specimens were dissected in lactic acid and the dissected parts were placed in polyvinyl lactophenol mounting medium, between two coverslips, and individually positioned on Cobb aluminium slide frames. This mounting procedure allows the slide to be placed on either of its surfaces, so that both anterior and posterior aspects can be observed.

Cylindropsyllus laevis and *C. remanei* were examined by scanning electron microscopy (SEM) with a JEOL JSM-840 microscope. Specimens of both sexes were prepared by dehydration through graded ethanol, critical point dried, mounted on stubs and sputter coated with gold.

All figures have been prepared using a camera lucida. Abbreviations used in the text and figures are: *A2* antenna; *Md* mandible; *Mx* maxilla; *P1–P6* first to sixth leg: *exp* exopodite; *enp* endopodite. The terminology and presentation of the setal formulae are adopted from Lang (1948, 1965). The terms pars incisiva, pars molaris and lacinia mobilis are omitted in the description of the mandibular praecoxa (cf. Mielke 1984).

Systematics

Family Cylindropsyllidae

Genus *Cylindropsyllus* Brady, 1880

Cylindrosoma Brady, 1878

Amended diagnosis

Body slender, cylindrical and vermiform. Integument pitted. Rostrum triangular, well defined at base. Antennula 7-segmented in female, 1st segment shorter than 2nd, furnished with aesthetasc on 4th segment; 8-segmented and haplocer in male. Antenna with allobasis; 1-segmented exopodite with 1–2 distal setae. Mandible with well developed praecoxa; coxa-basis bare; 1-segmented endopodite with 4 setae; exopodite absent. Endopodite and exopodite of maxillula represented as a seta. Maxillar syncoxa with 2 subcylindrical endites; endopodite represented by 2–3 setae. Maxillipeds obsolete. Exopodite of P1 3-segmented, with outer seta on middle segment and 3–4 setae on distal segment; endopodite 2-segmented, 1st segment with 1 seta on middle inner edge, distal segment with 2–3 setae. P2–P4 with 3-segmented exopodites 2-segmented endopodites and following setal formula:

	Exopodite	Endopodite
P2	[0.0.0 2 (1–2)]	[1.0 1 0]
P3	[0.0.1 2 (1–2)]	[0.2 1 0]
P4	[0.0.1 2 (1–2)]	[0.1 1 0]

Baseoendopodite and exopodite P5 forming a common plate in both sexes, furnished with 8 setae in female, 6 in male. Genital double somite not subdivided. Caudal rami short, inner terminal seta strongly developed with basal styliform processus. Sexual dimorphism in antennula, 5th and 6th legs, basis and exopodite P2, endopodite P3 and in genital segmentation. 6th pair of legs asymmetrical in male.

Type species: *Cylindropsyllus laevis* Brady, 1880.

Cylindropsyllus laevis Brady, 1880 (Figs. 2–6)

Type locality. Muddy sand at 5 fathoms (9 m) depth off Hartlepool, Co. Cleveland (U.K.).

Material. (1) Scotland, Firth of Forth and Loch Fyne (coll. T. Scott): several females and males deposited (spirit preserved) in the BM(NH), nos. 45253–5 and 45248–52 as part of the Cannon A.M. Norman collection (no. 1911.11.8).

(2) Isle of Man, Port Erin Bay (coll. I. C. Thompson): 1 undissected female on slide, deposited in the BM(NH), no. 1959.2.9.95.

(3) Sweden, Bonden (Bohuslän) (coll. K. Lang): 2 specimens deposited (formalin preserved) in U.S. National Museum of Natural History, Washington, D.C., no. 90882.

(4) F.R.G., Kiel Bay (coll. A. Remane): 2 females deposited (pycrine–glycerine preserved) in the Zoologisches Museum, Kiel, no. 1917 as part of the Walter Klie collection.

(5) One dissected female (slide in a poor state, useless) deposited in the Zoologisches Museum, Kiel, no. 1210 as part of the Walter Klie collection; locality and collector unknown.

(6) From Dr H. Kunz: 2 females, 5 males and 6 copepodid stages (spirit preserved); collected from Sweden, Bonden (Bohuslän), depth 20 m (see Wells *et al.* 1975). Two males and 1 female (spirit preserved) have been deposited in the collection of the Recent Invertebrate Section of the Koninklijk Belgisch Instituut voor Naturrwetenschappen, Brussels, no. IG 27143.

Redescription

FEMALE. Body length 1280–1288 μm ($n = 3$; $\bar{x} = 1285$ μm) excluding rostrum and caudal rami; 1365–1372 μm ($n = 3$; $\bar{x} = 1370$ μm) including rostrum and caudal rami.

Body (Fig. 2A) slender, cylindrical, brownish-yellow and semi-transparent. Thoracic somites slightly broader than urosoma; no distinct separation between anterior and posterior body; anal somite narrowest. Cephalothorax as long as the two succeeding somites combined; 1st thoracic somite shortest. Nauplius eye wanting.

Rostrum prominent, not exceeding 1st antennular segment, not fused with cephalosoma, well defined at base; triangular, greatest width at 1/3 distance of base; tip pointing forwards and downwards; with a pair of delicate sensillae at 1/3 distance of tip; integument pitted.

Somitic hyaline frill smooth, equally developed in thoracic and abdominal somites. Integument of all body somites, caudal rami and proximal segments of antennula dorsally, laterally and ventrally densely pitted.

Cephalic shield rectangular, with 7 groups of sensillae and a central triradiate cuticular thickening dorsally. Thoracic somites 1–4 with 8 (4 dorsal, 2 lateral, 2 ventrolateral), 10 (4 dorsal, 4 lateral, 2 ventrolateral), 8 (4 dorsal, 2 lateral, 2 ventrolateral) and 6 (2 dorsal, 2 dorsolateral, 2 ventrolateral) sensillae, respectively.

Genital double somite without any trace of subdivision, anteriorly with 2 dorsal sensillae, posteriorly with 2 dorsolateral and 2 ventrolateral sensillae. Antepenultimate somite posteriorly likewise with 2 dorsolateral and 2 ventrolateral sensillae. Penultimate somite without sensillae. Anal somite posteriorly with 2 dorsolateral sensillae; anal operculum rounded, thin.

Caudal rami (Figs. 2A, B, D, 6A) slightly divergent, inner margin convex, approximately 2× as long as proximal diameter. Inner terminal seta with styliform cylindrical base from which a delicate seta arises near outer proximal margin; accompanied by a short accessory inner seta. Three bare setae arise from dorsal side. Outer lateral surface provided with 3 secretory pores.

Antennula (Fig. 3A). 7-segmented, slender; antennular

hyaline frill slightly developed, plain; 1st segment partially subdivided, with 4 rows of minute spinules and 1 bare seta near distal edge; 2nd one longest, 2× as long as greatest width, with 8 (1 plumose) setae and a pore on the distal half; 3rd segment with 4 bare setae; anterior edge of 4th segment with an inner seta and a long aesthetasc (*L*: ±100 μm) accompanied with a bare seta on outer edge; 5th segment with 1 seta on inner distal corner; 6th segment smallest with 2 subterminal setae; last segment prolonged, with 10 setae (1 trifurcate terminal seta representing 3 basally fused setae).

Antenna (Figs. 3B, 6B, E). Coxa small, much shorter than width, bare. Allobasis about 2.7× as long as greatest width, longer than endopodite, with a spinular row at about middle inner margin. Exopodite implanted 1/4 the length from proximal margin, 1-segmented; approximately 3× as long as greatest diameter, a little thickened distally; distally with a long bare seta. Endopodite about 2/3 the length of allobasis; anterior margin with some spinules in proximal part and 2 strong juxtaposed spines (of which distal-most accompanied by some spinules and a setula at base) in distal part; posterior margin with 2 spinular rows; distal edge with a slightly curved spine, a longer straight spine and 3 geniculate setae, the posterior one spinulose along middle part and confluent at base with a short slender seta. Antennal hyaline frill around proximal articulation of allobasis not observed.

Labrum (Fig. 6C). Strongly developed, armed with several rows of closely set spinules.

Mandible (Fig. 3C). Praecoxa (corpus mandibulae) well developed; distal end (cutting edge) with 2 bidentate thick spines, 7–8 small teeth and a strong one-sided spinulose seta. Palp 2-segmented. Coxa-basis 2× as long as greatest width, shorter than endopodite; not ornamented. Endopodite armed with a bare seta on subproximal edge; 3 bare setae of different lengths arising from distal edge.

Maxillula (Fig. 3D). Praecoxa thickly chitinous along outer edge. Arthrite of praecoxa with 8 claws or spines, of which at least 6 are pectinate along inner edge; anterior surface with 2 parallel setae, innermost one dwarfed. Coxa with strong medially geniculate claw accompanied at base by minute spinules. Basis with 1 strong claw accompanied by 2 slender setae basally. Exopodite and endopodite represented each by a slender seta.

Maxilla (Fig. 3E). Syncoxa thickly chitinous at outer edge, with 2 well developed cylindrical endites. Proximal endite shortest, distally with 1 spinulose claw and 1 terminally spinulose seta. Distal endite closely set to the basis, with 1 terminal claw and 2 spinulose setae. Basis forming into a strong claw which is acutely recurving dorsally and provided with several delicate spinules; with 2 bare setae (one each on dorsal and ventral side) at base. Endopodite represented by 3 juxtaposed setae, all bare and slender.

Maxilliped (Figs. 6B, G). Obsolete. Represented by a small triangular plate along dorsal edge of syncoxa of maxilla.

Natatorial legs (Fig. 4). With 3-segmented exopodites; endopodites 3-segmented, always shorter than outer rami. Succeeding legs increasing in length.

P1 (Fig. 4A). Coxa well developed, ornamented with a spinular row near outer distal margin. Basis shorter than coxa; with 2 rows of spinules on anterior surface; neither inner nor outer seta. Rami divergent. First 2 exopodite segments each with 1 outer spinulose spine at subdistal corner and several spinules along outer margin; 2nd slightly shorter than 1st. 3rd segment with 2 outer spinulose spines subdistally and 2 long geniculate spinulose setae. Endopodite a little shorter than outer ramus; 1st segment narrowing distally, with 1 apically serrate long seta on about middle inner edge, an arched row of diminutive spinules in the proximal half and several long slender spinules along outer margin; 2nd segment a little longer than proximal one, with a setula near inner distal corner and 2 long geniculate spinulose setae distally, inner one of which longer than outer.

P2 (Fig. 4B). Coxa strongly developed, more than 2× as long as preceding one; with parallel margins; not ornamented. Basis short, with 1 plumose seta on outer margin near junction with coxa. Exopodite about 2.5× as long as endopodite; all segments spinulose along each outer margin. First 2 segments each furnished with 1 outer spinulose spine and a strong spinule on outer distal corner. 3rd segment with a long spinulose seta and a shorter one at distal end and 2 shorter spinulose setae on outer subdistal margin. 1st endopodite segment thickest with a long serrate inner seta subdistally. Distal segment much slenderer than preceding one, furnished with a long terminal seta.

P3 (Fig. 4C). Coxa as in preceding leg. Basis with a plumose outer seta and a spinular row near inner edge. First 2 exopodite segments ornamented almost as in P2; proximal one shortest. 3rd segment with 1 serrate seta on about middle inner edge, a long slender seta on inner distal corner, a shorter spinulose seta at distal end and 2 spinulose spines on outer subdistal margin. Both endopodite segments combined exceeding 1st segment of exopodite; 1st one entirely bare; 2nd a little longer than preceding one, furnished with 2 terminal bare spines of different lengths and a slender plumose seta at inner subdistal corner.

P4 (Fig. 4D). Strikingly developed. Coxa longer than wide, not ornamented. Basis short, with a long plumose seta on a small outer projection. Exopodite more than 3× as long as endopodite; 1st segment thickest, with some spinules along outer edge and 1 spinulose outer spine subdistally, appendicular hyaline frill strongly developed; 2nd segment as long as preceding one, with 1 spine and several spinules on subdistal outer edge; last segment much shorter, with 2 spinulose slender setae and 1 two-sided spinulose, dilated long seta distally and 1 apically serrate inner seta just inside of subdistal edge. Endopodite not exceeding 1st exopodite segment; proximal segment with 2 oblique spinular rows on anterior surface; 2nd a little shorter than first, with a spinulose seta distally and a minute plumose seta near subdistal inner edge.

Setal formula.

	Exopodite	Endopodite
P1	(0.0.112)	(1.111)
P2	(0.0.022)	(1.010)
P3	(0.0.122)	(0.210)
P4	(0.0.122)	(0.110)

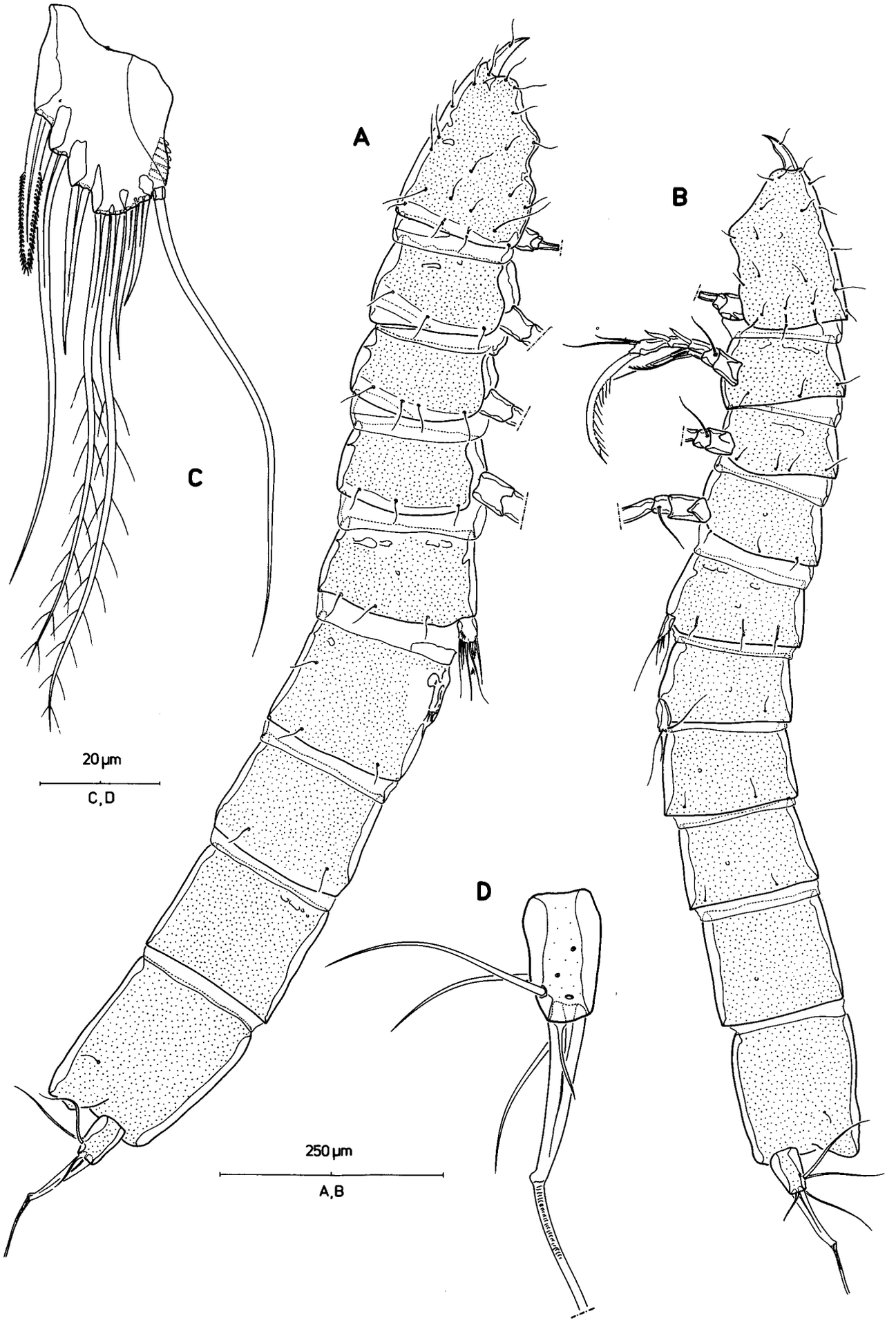

Fig. 2. Cylindropsyllus laevis Brady, 1880.—*A*. Habitus, lateral (♀).—*B*. Habitus, lateral (♂).—*C*. P5 (♀).—*D*. Caudal ramus, lateral.

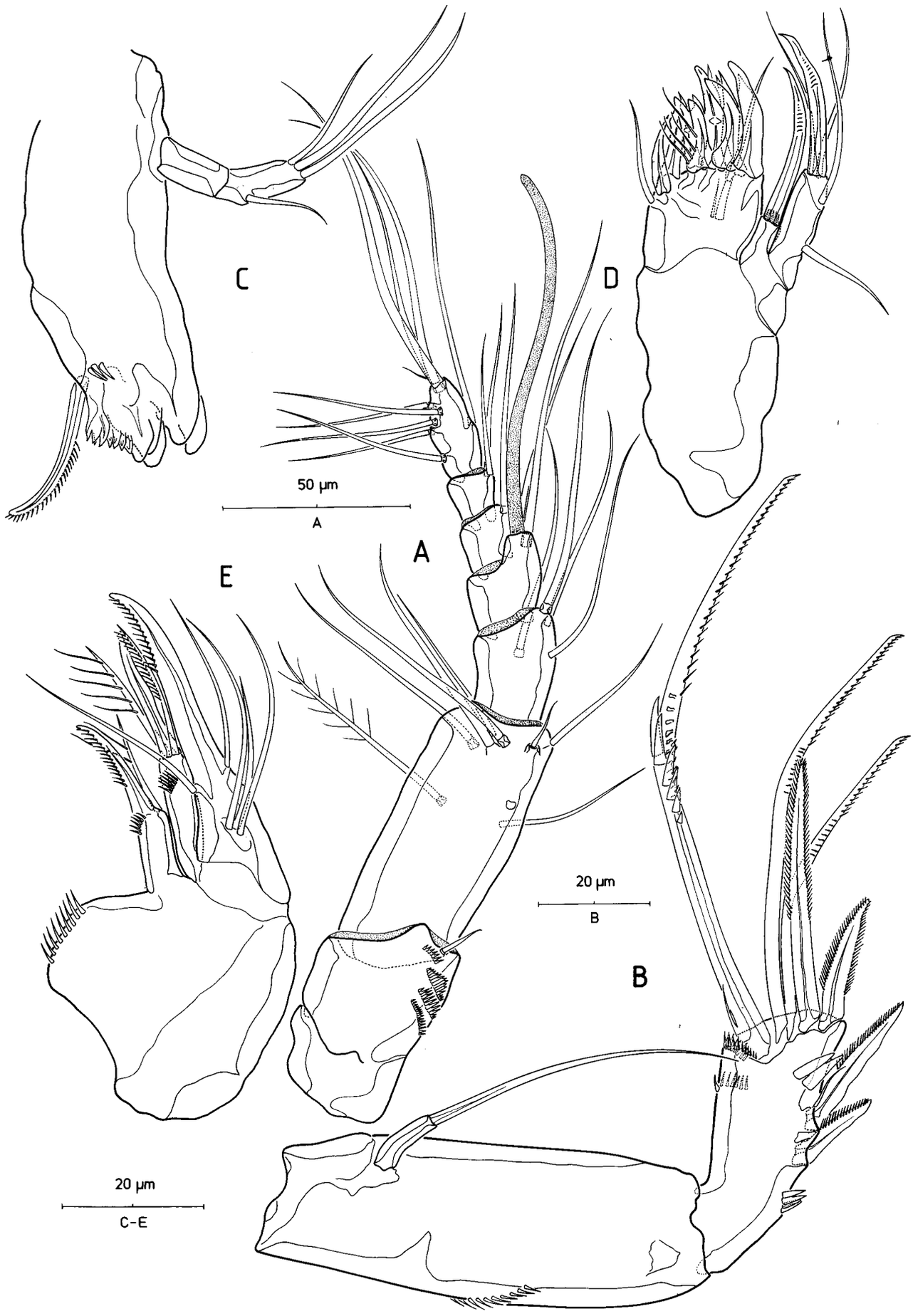

Fig. 3. Cylindropsyllus laevis Brady, 1880 (♀).—*A*. Antennula.—*B*. Antenna.—*C*. Mandible.—*D*. Maxillula.—*E*. Maxilla.

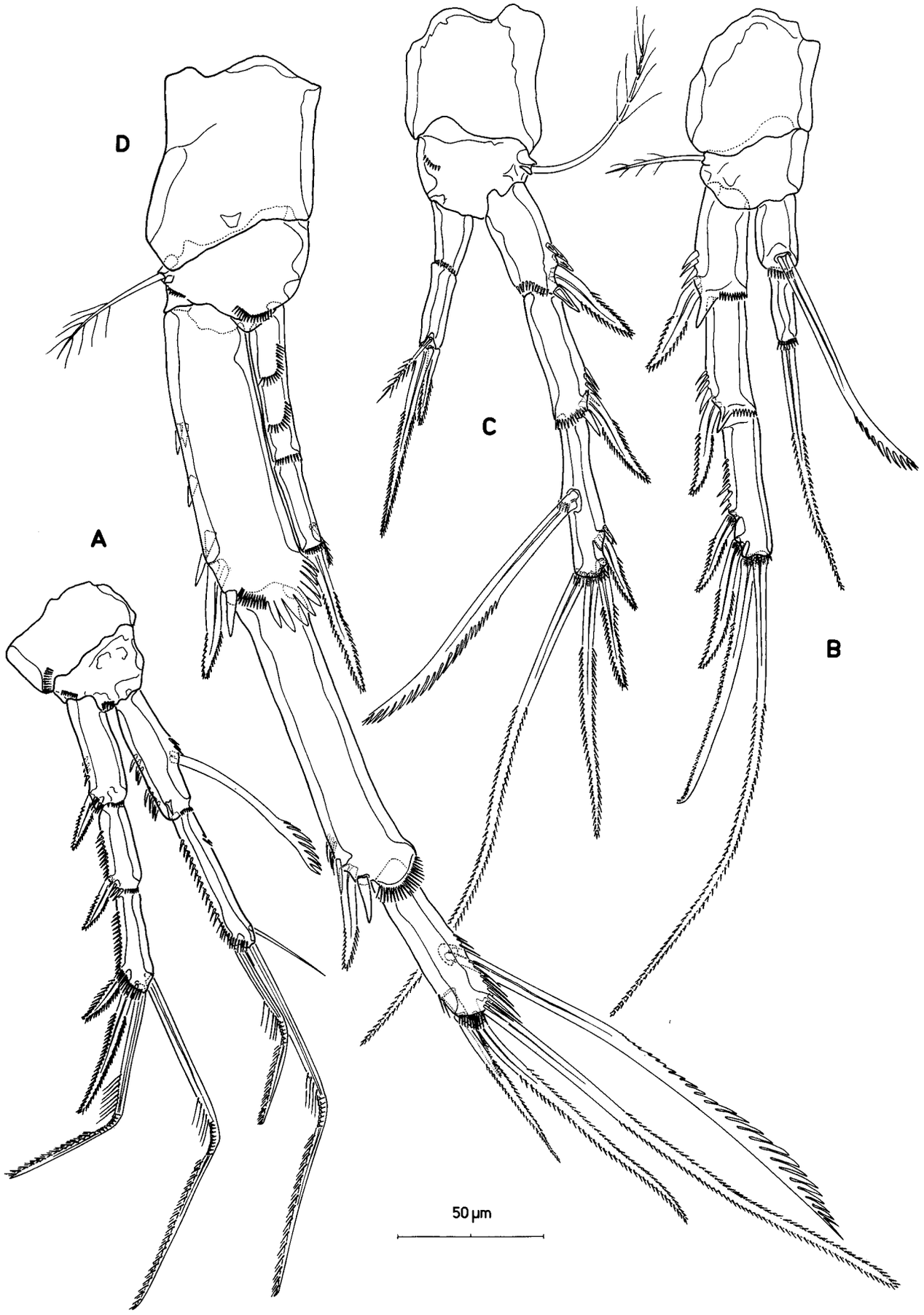

Fig. 4. Cylindropsyllus laevis Brady, 1880 (♀).—*A*. P1.—*B*. P2.—*C*. P3.—*D*. P4.

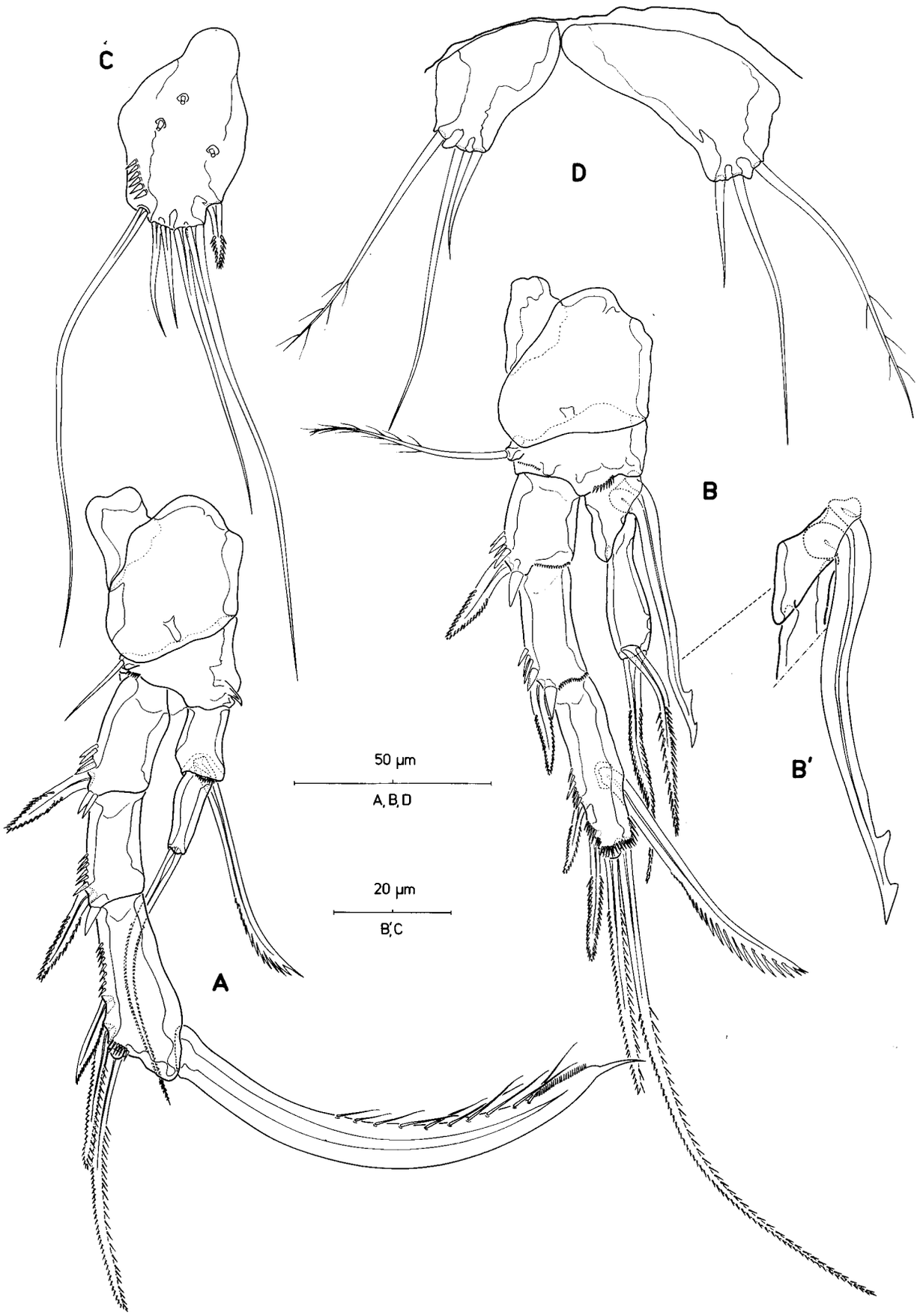

Fig. 5. Cylindropsyllus laevis Brady, 1880 (♂).—*A*. P2.—*B*. P3.—*B'*. Modified spine of proximal endopodite segment P3.—*C*. P5.—*D*. P6.

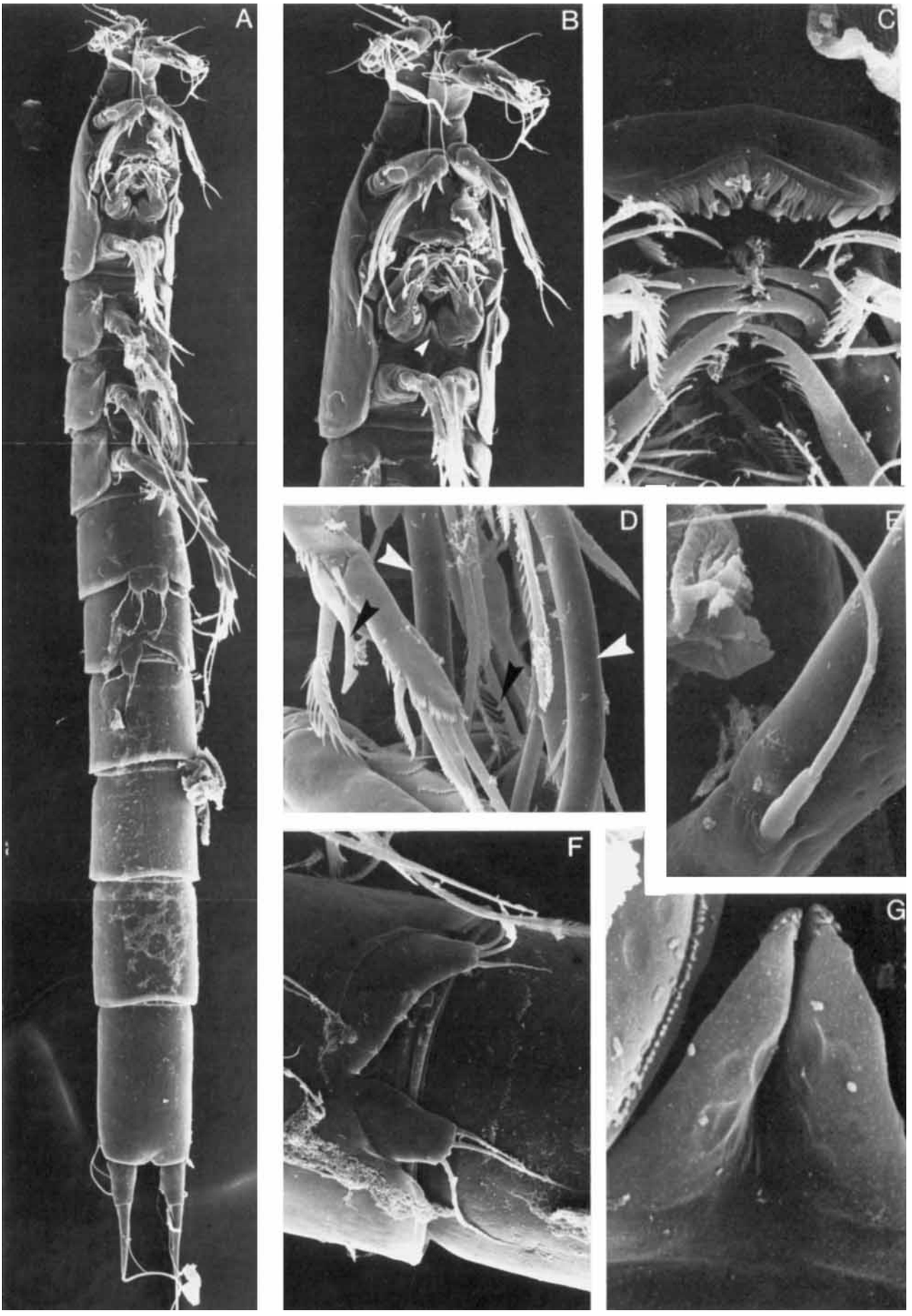

Fig. 6. Cylindropsyllus laevis Brady, 1880 (SEM micrograph).—*A*. Habitus, ventral (♂), ×370.—*B*. Cephalothorax, ventral (♂), ×590.—*C*. Labrum, ×4100.—*D*. Sexual dimorphism in leg 2 (*white arrow*) and leg 3 (*black arrow*) (♂), ×2000 .—*E*. Antennal exopodite, ×3400.—*F*. Leg 6 (♂), ×1250.—*G*. Maxillipeds, ×10,500.

Leg 5 (Fig. 2C). Represented by a robust plate with thickly chitinous margins; 2 plumose setae at distal end; inner edge stepped and furnished with 3 setae in total, proximal-most strong and spinulose, succeeding one slender and distal-most spiniform and short; outer edge with a spinular row and 3 setae in total, proximal-most well developed and biarticulated at base, succeeding two much shorter and spiniform.

MALE. Body length 1105–1135 μm ($n = 5$; $\bar{x} = 1120$ μm) excluding rostrum and caudal rami; 1190–1215 μm ($n = 5$; $\bar{x} = 1200$ μm) including rostrum and caudal rami. General body shape, ornamentation, colour and sensillar pattern as in female. Sexual dimorphism in antennula, 2nd, 3rd, 5th and 6th legs and in genital segmentation (Fig. 2B).

Antennula. 8-segmented, robust; haplocer; antennular hyaline frill somewhat weaker developed than in female, plain; first 2 segments as in female. Inner distal corner of 3rd segment with 3 spiniform setulae and 4 long slender setae, of which all but one geniculate at base. 4th segment swollen, with 2 juxtaposed spiniform outgrowths on surface; inner subdistal corner with a long seta, accompanied at base with 2 short ones of different lengths; provided with a long aesthetasc (L: +90 μm) accompanied at base by a slender seta. 5th segment shortest, with a slender seta at inner subdistal corner. 6th with a bare seta at about middle inner edge. Inner margin of 7th segment thickly chitinous; without setae. Last segment furnished as in female.

P2 (Figs. 5A, 6D). Basis forming a hook-shaped projection at inner subdistal corner. General outline and ornamentation of endopodite and first 2 exopodite segments as in female. Distal exopodite segment modified, widening distally and prolonged into a median apical projection from which a remarkable claw arises. This extraordinarily developed claw (homologous with inner distal seta in female) directed both posteriorly and inwards and furnished with long spinules along distal 2/3 of inner margin, except for ultimate part which has 2 parallel rows of diminutive spinules.

P3 (Figs. 5B, B′, 6D). Exopodite somewhat stronger and 1st segment shorter than in female. Endopodite longer than in female, 2-segmented; proximal segment short, with a strong spiniform process at inner margin, 2-barbed near end; distal segment longest, widening distally, terminally with 2 long, spinulose setae, inner chitinous rim divided into 3 parts by 2 small pits.

P5 (Fig. 5C). Baseoendopodite and exopodite forming a robust plate, with 3 secretory tube pores and an outer oblique spinular row on anterior surface and 6 setae at distal margin of which innermost is shortest and bilaterally spinulose along distal half.

P6 (Figs. 5D; 6A, F). 6th pair of legs asymmetrical in shape; each plate with 3 setae on outer part, innermost shortest, succeeding one long and slender, outermost plumose.

Distribution (Fig. 1)

Norway: Korshavn, Lindesnes (Sars 1909) Korsfjorden (Drzycimski 1969); Bergen area (Clausen 1967). Sweden: Bonden, Bohuslän (Lang 1948; Por 1964; Wells *et al.* 1975); Koster fjord (Por 1964). F.R.G.: Helgoland (Kunz 1949); Kiel Bay (Klie 1950). Scotland: Moray Firth (Scott 1902); Firth of Forth (Scott 1890, 1892); St. Monans and Forth estuary (Scott 1906*b*); Loch Fyne (Scott 1890, 1896); River Ythan in Aberdeenshire (Hockin & Ollason 1981; Hockin 1982). England: Hartlepool, Co. Cleveland (Brady 1880; Norman & Brady 1909; Bossanyi & Bull 1971); Plymouth (Scott 1890); 48°34′N, 05°13′W (Knudsen 1905). Wales: Porth-y-post (Geddes 1972). Isle of Man: Port Erin (Thompson 1893). Northern Ireland: Rock Angus (Wells 1963). Ireland: Killary Harbour in Mayo (Farran 1913). Belgium: North Sea coastal zone (Govaere *et al.* 1980); Kwinte Bank (Willems *et al.* 1982). France: Roscoff (Monard 1935); Bassin d'Arcachon (Renaud-Debyser & Salvat 1963); Banyuls-sur-Mer (Soyer 1970; Bodiou & Soyer 1973); Marseille (Bodin 1968); Lacanau-Océan, Contis-Plage (Noodt 1955*a*, *b*; Delamare Debouteville 1960).

?U.S.A.: Gulf of Maine, northern New England (Coffin 1979).

Cylindropsyllus remanei Kunz, 1949 (Figs. 7–12)

Type locality. Helgoland (*Amphioxus* sand).

Material. (1) The Netherlands, Southern Bight of North Sea, 51°50′50″N, 02°52′00″E (coll. R. Huys, 4 June 1985), medium sand (median grain size: 0.290 mm; 0.25% mud), depth 39 m: 7 females, 3 males. Two whole specimens (spirit preserved) and 1 dissected specimen (on 10 slides) of each sex have been deposited in the collection of the Recent Invertebrates Section of the Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, no. IG 27142.

(2) The Netherlands, SW coast, off Delta region, 51°36′04″N, 03°35′47″E (coll. R. Huys, 6 September 1984), medium sand (median grain size: 0.310 mm; 5.06% mud), depth 12 m: 2 females, 2 males.

(3) Belgium, coastal zone off Ostend, 51°16′32″N, 02°51′08″E (coll. R. Herman, 6 May 1980), medium sand (median grain size: 0.290 mm; 0.07% mud), depth 10 m: 1 male.

(4) Portugal, Peniche, sandy beach: 1 undissected male on slide (coll. J. B. J. Wells), deposited in the BM(NH), no. 1964.12.1.14.

Redescription

FEMALE. Body length 689–695 μm ($n = 5$; $\bar{x} = 693$ μm) excluding rostrum and caudal rami; 726–735 μm ($n = 5$; $\bar{x} = 730$ μm) including rostrum and caudal rami.

Body (Figs. 7A–C, 12A) more slender than that of *C. laevis*, cylindrical, vermiform, brownish-yellow and semitransparent. Approximately 11.3× longer than broadest part. Anal somite strongly prolonged, slightly longer than cephalosoma. Integument pitted. Rostrum (Fig. 9C), somitic hyaline frill, sensillar pattern, genital field (Figs. 7D, 12C) and caudal rami (Figs. 11F, 12F) as in preceding species.

Antennula (Fig. 8C). 7-segmented; 2nd segment with obvious brownish pigment spot; 4th segment with slender aesthetasc (±55 μm); ornamentation as in *C. laevis*.

Antenna (Figs. 9A, 12B, E). Allobasis spinular along middle inner margin and bearing a 1-segmented exopodite with 2 plumose setae, outer one swollen at base.

Mandible (Figs. 9B, B′) *and maxillula* (Fig. 9D). Exactly as in *C. laevis*.

Maxilla (Fig. 9E). Distal endite with a spinulose claw and 1 bare seta; endopodite represented by 2 juxtaposed setae.

Maxilliped (Figs. 9E, 12D). A small triangular plate with a minute protrusion on its posterior surface.

Natatorial legs (Figs. 10A–D). Distal segment of endopodite P1 with 2 geniculate setae and distal segment of exopodite P1–P4 with only 1 outer seta, resulting in following setal formula:

	Exopodite	Endopodite
P1	(0.0.111)	(1.011)
P2	(0.0.021)	(1.010)
P3	(0.0.121)	(0.210)
P4	(0.0.121)	(0.110)

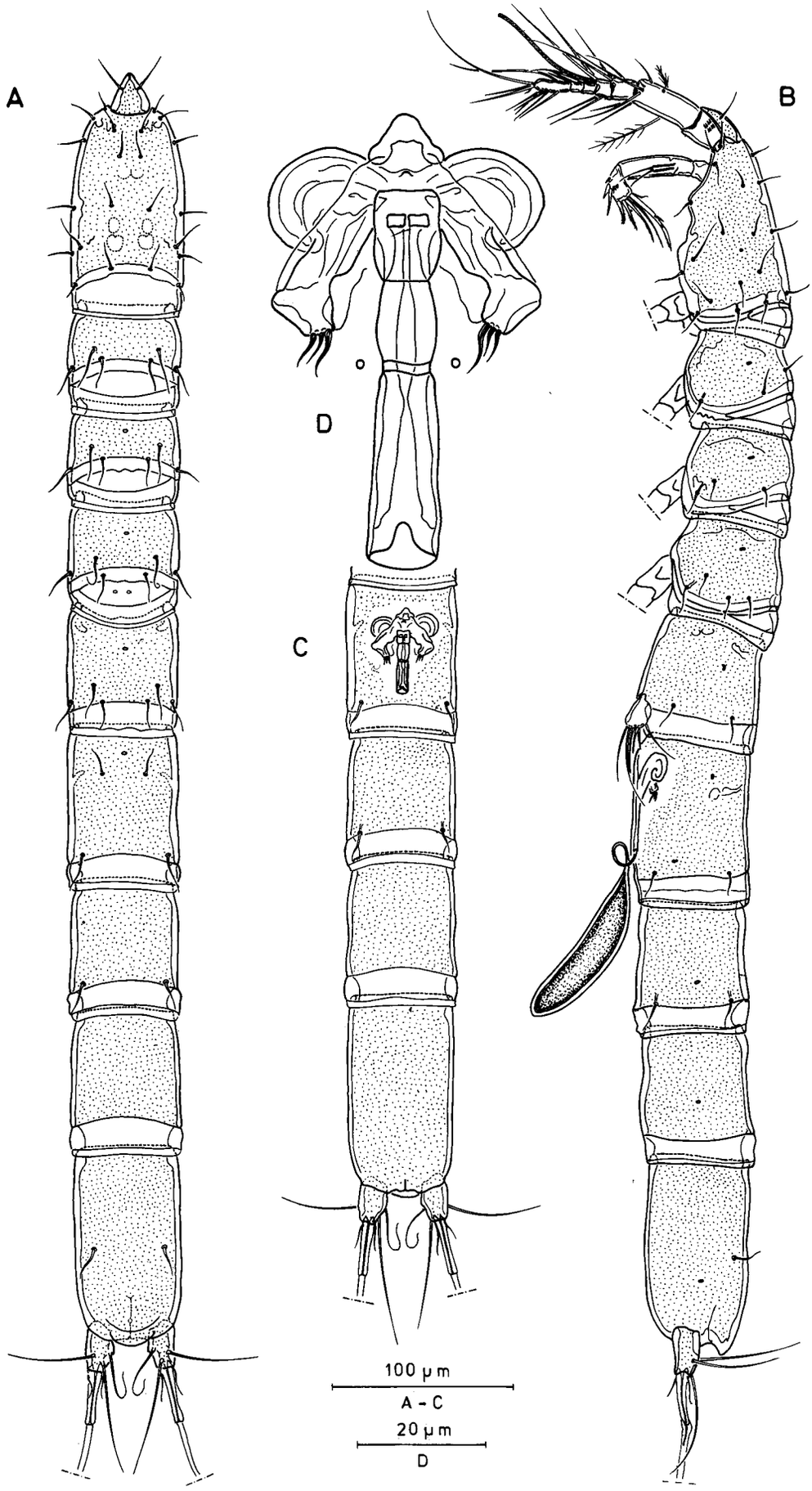

Fig. 7. Cylindropsyllus remanei Kunz, 1949 (♀).—*A*. habitus, dorsal.—*B*. Habitus, lateral.—*C*. Abdomen, ventral.—*D*. Genital field.

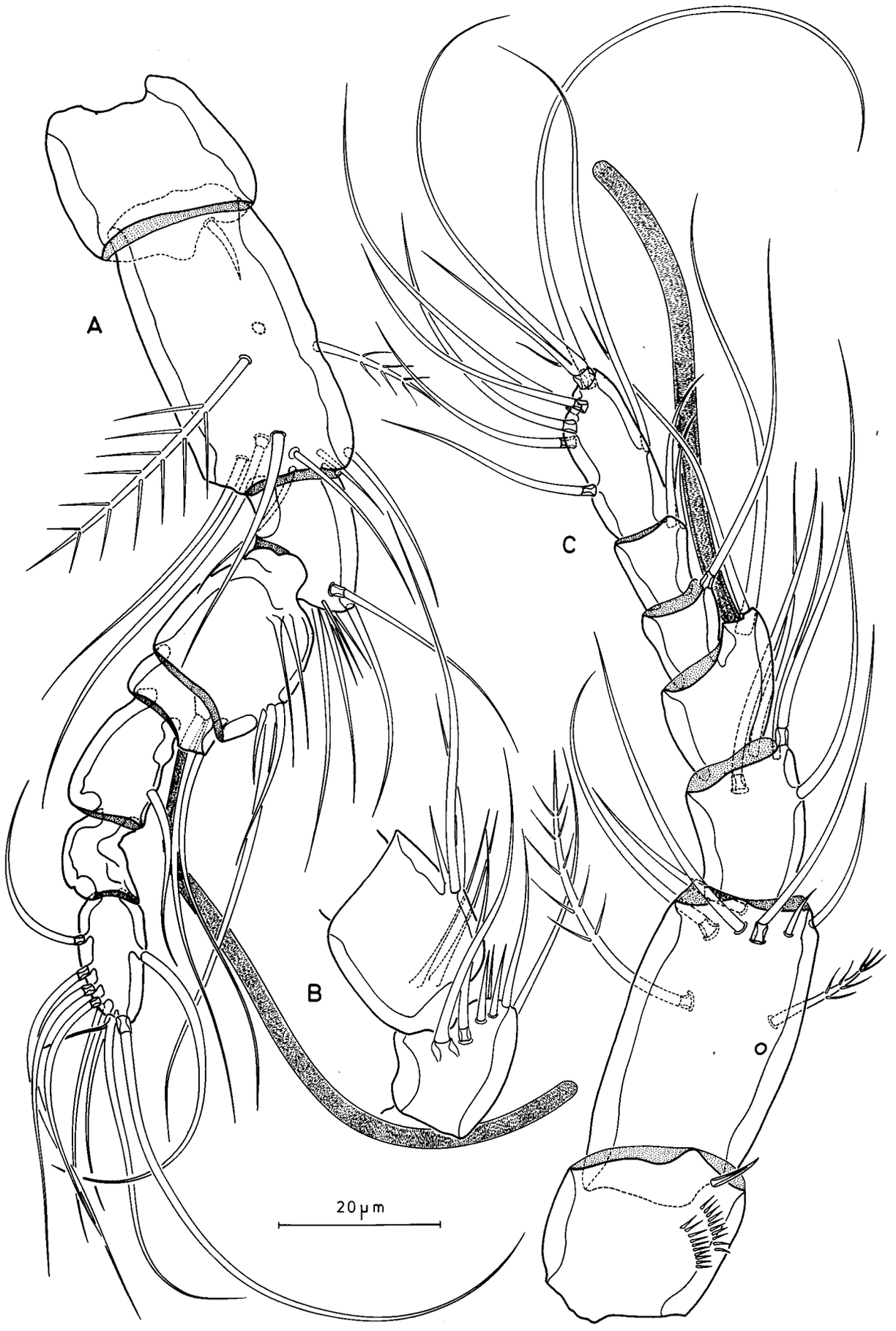

Fig. 8. Cylindropsyllus remanei Kunz, 1949.—*A*. Antennula (♂).—*B*. Antennula, detail of 3rd and 4th segments (♂) (aesthetasc not drawn).—*C*. Antennula (♀).

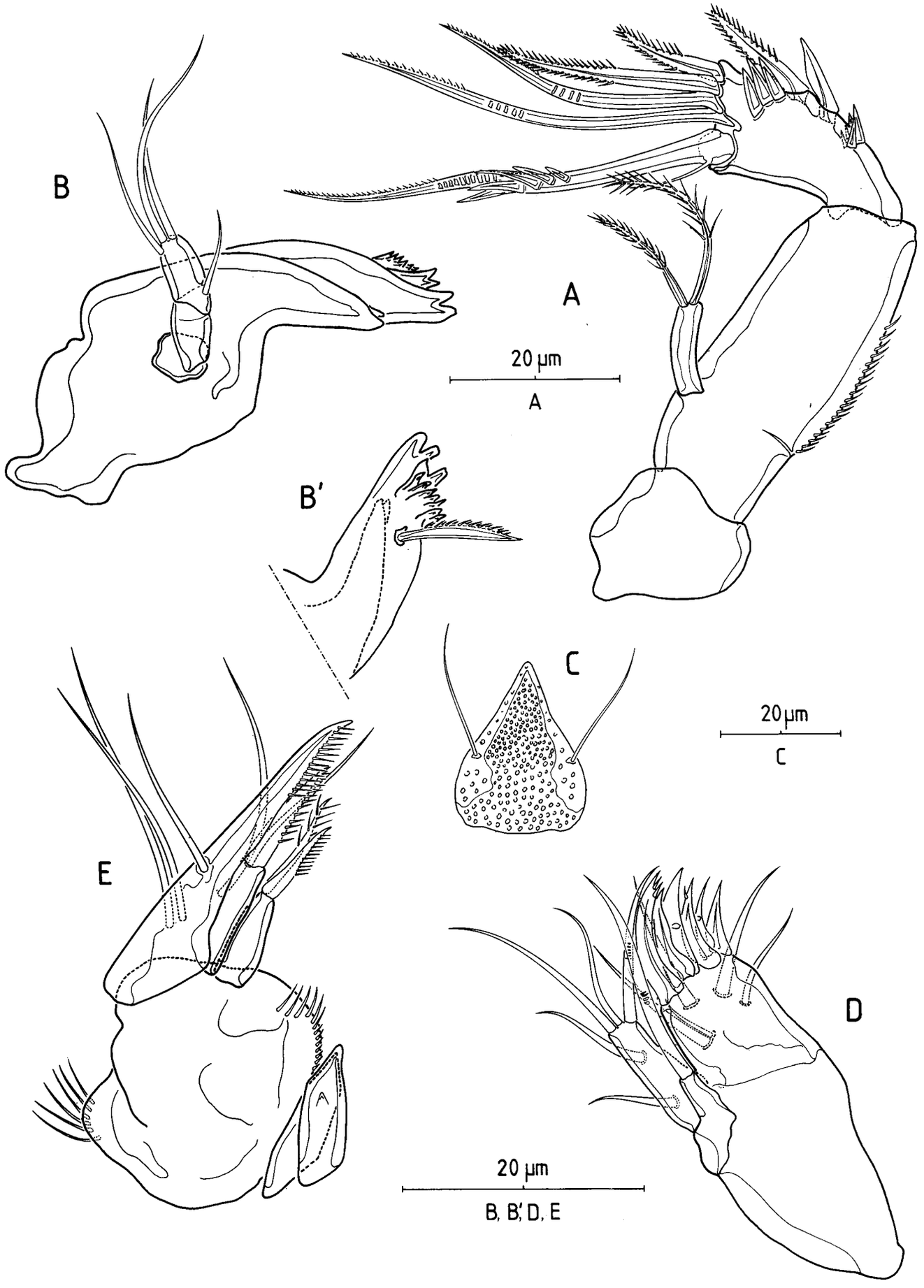

Fig. 9. Cylindropsyllus remanei Kunz, 1949 (♀).—*A*. Antenna.—*B*. Mandible.—*B'*. Cutting edge of mandibular praecoxa.—*C*. Rostrum.—*D*. Maxillula.—*E*. Maxilla and maxilliped.

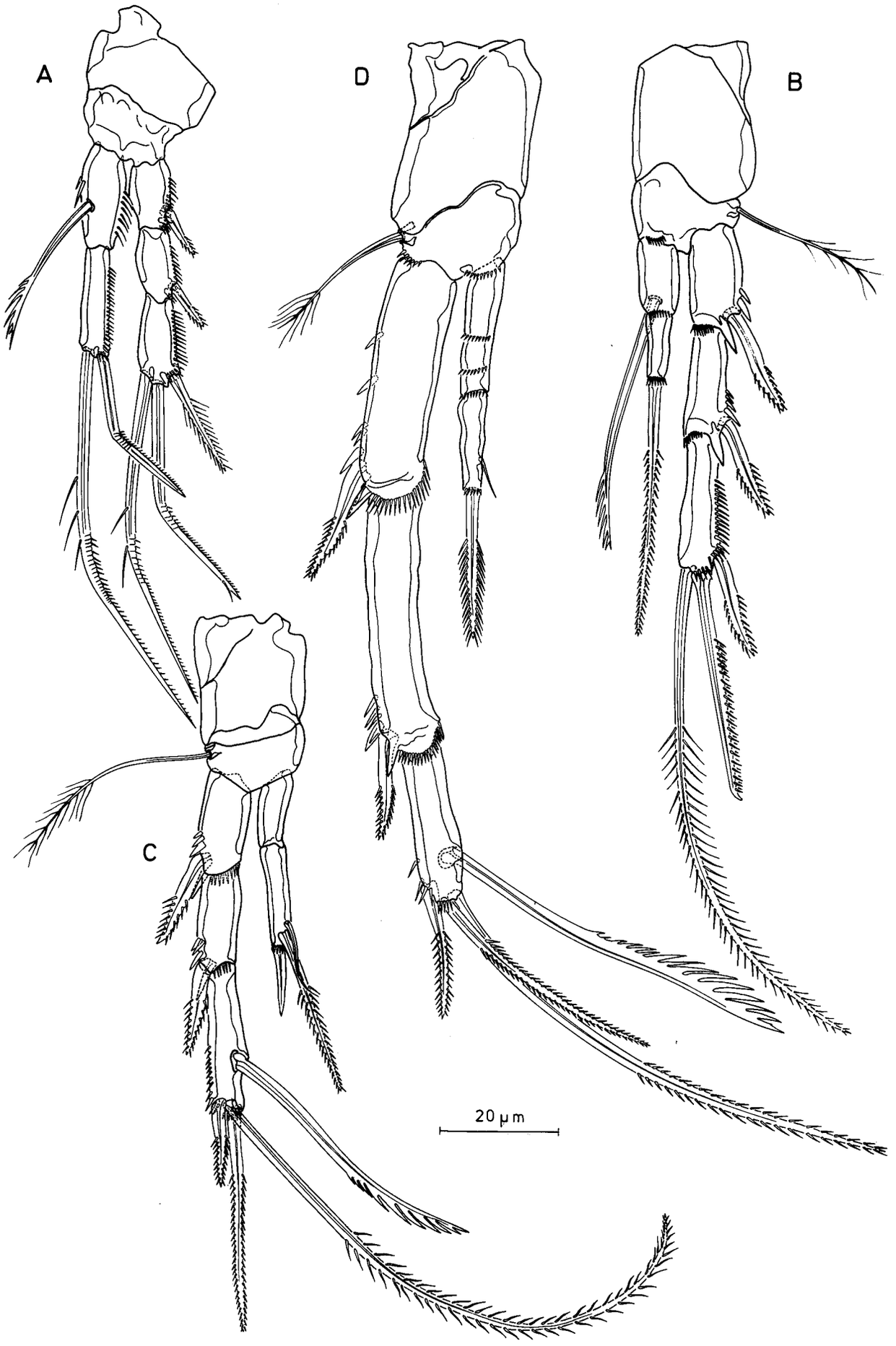

Fig. 10. Cylindropsyllus remanei Kunz, 1949 (♀).—*A*. P1.—*B*. P2.—*C*. P3.—*D*. P4.

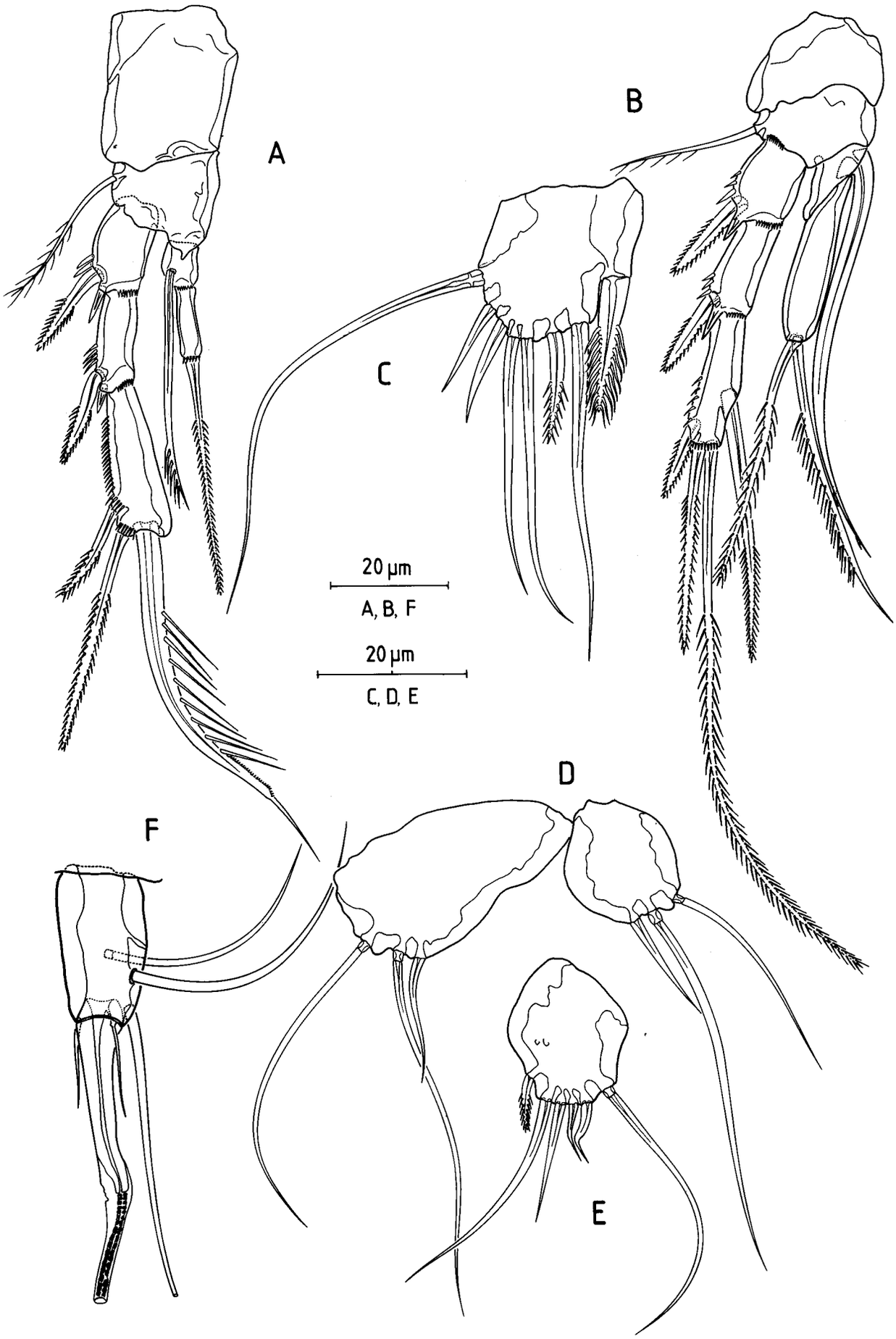

Fig. 11. Cylindropsyllus remanei Kunz, 1949.—*A*. P2 (♂).—*B*. P3 (♂).—*C*. P5 (♀).—*D*. P6 (♂).—*E*. P5 (♂).—*F*. Caudal ramus, lateral.

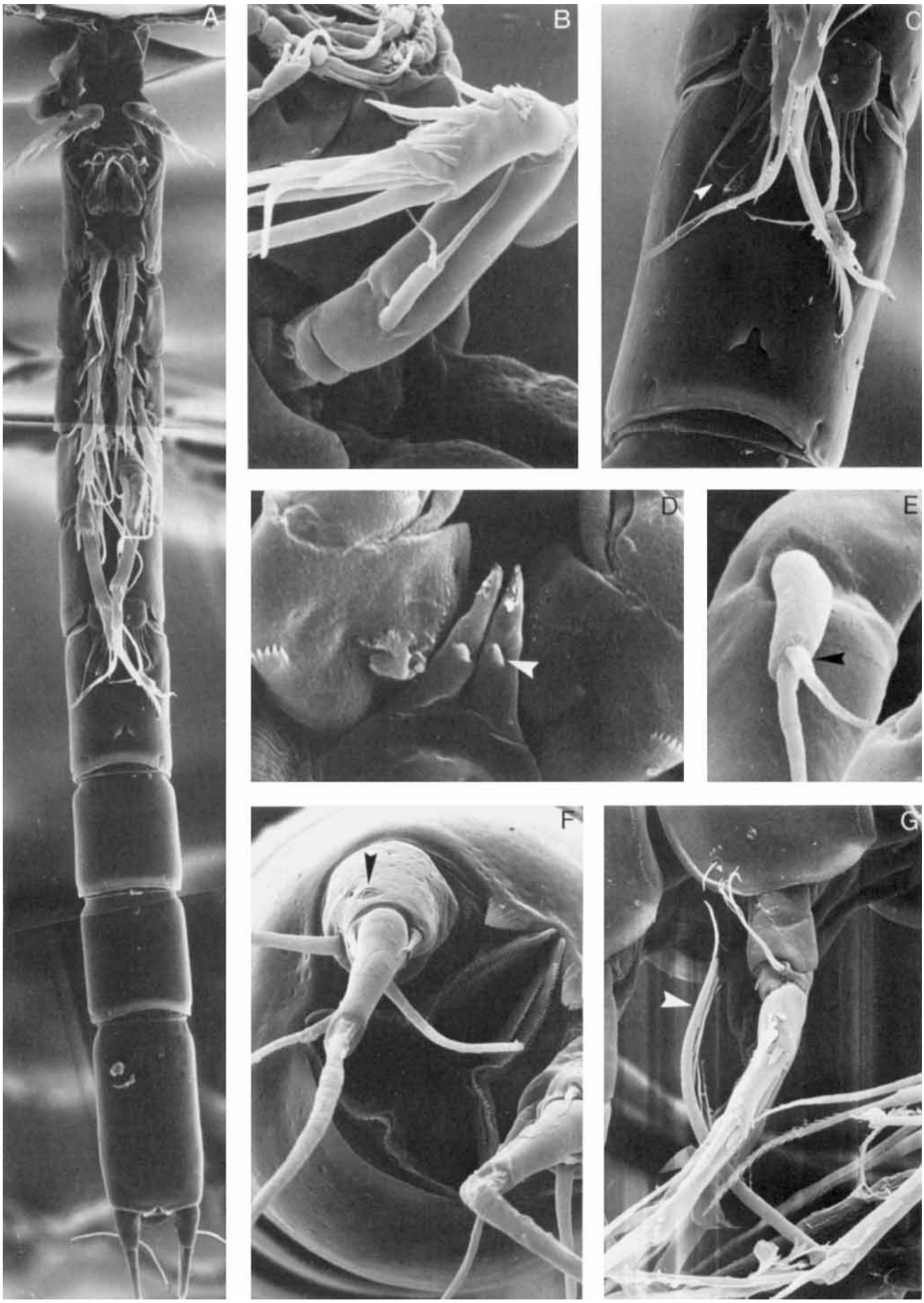

Fig. 12. Cylindropsyllus remanei Kunz, 1949 (SEM micrograph).—*A*. Habitus, ventral (♀), ×550.—*B*. Antenna., ×3000—*C*. Genital double somite and P5 (♀)1400.—*D*. Maxillipeds, ×8900.—*E*. Antennal exopodite, ×6800.—*F*. Caudal rami and triradiate anal aperture, ×2700.—*G*. Sexual dimorphism in leg 2 (♂), ×1900.

Endopodite of P3 extending as far as first 2 exopodite segments combined. Endopodite of P4 as long as proximal exopodite segment.

Leg 5 (Fig. 11C). Exopodite and baseoendopodite confluent; furnished with 8 setae in total, innermost stout and densely spinulose; outer margin without spinular row.

MALE. Body length 639–657 μm (n = 5; $\bar{x}$ = 648 μm) excluding rostrum and caudal rami; 681–694 μm (n = 5; $\bar{x}$ = 690 μm) including rostrum and caudal rami.

General body shape, ornamentation, colour and sensillar pattern as in female. Sexual dimorphism in antennula, 2nd, 3rd, 5th and 6th legs and in genital segmentation.

Antennula (Figs. 8A, B). 8-segmented; 2nd segment with dark pigment spot; 4th with a slender aesthetasc (±70 μm); ornamentation as in *C. laevis*.

P2 (Figs. 11A, 12G). Basis forming a pointed processus at inner distal edge. 1st endopodite segment squarish, shorter than in female. General outline and ornamentation of proximal and middle podomeres of exopodite as in female; distal segment dilating terminally and furnished with 2 spinulose setae at outer subdistal corner and a strikingly developed unilaterally spinulose claw at distal end.

P3 (Figs. 11B, 12G). Endopodite exceeding first 2 exopodite segments combined; 2-segmented; proximal segment small, armed at inner margin with a long spiniform process, indistinctly 2-barbed near distal end; 2nd segment long, with 2 bilaterally spinulose setae; suture between both segments running diagonally towards inner subdistal corner of basis.

P5 (Fig. 11E). Baseoendopodite and exopodite forming a semi-circular plate, armed with 6 setae, innermost short and spinulose, outer one longest and biarticulated at base.

P6 (Fig. 11D). 6th pair of legs asymmetrical in shape, each plate with 3 bare setae.

Distribution (Fig. 1)

British Isles: Isle of Man, Irish Sea (Moore 1979); Northern Ireland: Strangford Harbour (Wells 1963). F.R.G.: Helgoland (Kunz 1949). The Netherlands: Southern Bight of North Sea (present paper), SW coast, off Delta region (present paper). Belgium: Kwinte Bank (Willems *et al.* 1982), coastal zone off Ostend (present paper). Portugal: Peniche (Wells & Clark 1965).

Cylindropsyllus kunzi sp.n. (Figs. 13–16)

Material. Holotype (female) and paratype (1 female) dissected and mounted on 9 and 8 slides, respectively. The type-series is deposited in the collections of the Recent Invertebrates Section of the Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, no. IG 26953. Of holotype were drawn: habitus, antennula, antenna, maxilla, P1–P5, genital field and urosoma.

Type locality. The Netherlands, S.W. Dutch coast, off Delta region, 51°48′02″N, 03°45′35″E (coll. R. Huys, 2 November 1984), fine sand (median grain size: 0.183 mm; 0.65% mud), depth 3 m; associated harpacticoid fauna: *Kliopsyllus constrictus constrictus* (Nicholls, 1935), *Paraleptastacus espinulatus* Nicholls, 1935 and *Arenocaris bifida* Nicholls, 1935.

Description

FEMALE. Body length 546–552 μm (n = 2; holotype: 546 μm) excluding rostrum and caudal rami; 586–590 μm (n = 2; holotype: 586 μm) including rostrum and caudal rami.

Body (Figs. 13A–C) slender, cylindrical, vermiform, colourless and transparent; approximately 12× as long as maximum width; no separation between anterior and posterior body. Cephalothorax as long as 2 succeeding thoracic somites combined; anal somite strongly prolonged, longer than 1/6 of total body length. Nauplius eye wanting. Genital double somite without any trace of subdivision. Genital field as in Fig. 16B. Caudal rami (Figs. 16D–F) about 1.9× as long as proximal diameter. Integument pitted. Sensillar pattern, rostrum (Fig. 13D) and setation of caudal rami as in preceding species.

Ornamentation of *antennula* (Fig. 14A), *antenna* (Fig. 16A), *mandible* (Fig. 14B), *maxillula* (Figs. 14C1, C2) and *maxilliped* as in *C. remanei*.

Maxilla (Fig. 14D). Endopodite represented by 3 setae. Distal endite with 1 spinulose claw and a slender seta.

Natatorial legs (Figs. 15A–D). With 3-segmented exopodites and 2-segmented endopodites. Distal segment of endopodite P1 with an inner subdistal setula and 2 terminal geniculate setae, distal segment exopodite P1–P4 with only 1 outer seta, resulting in following setal formula:

	Exopodite	Endopodite
P1	(0.0.111)	(1.111)
P2	(0.0.021)	(1.010)
P3	(0.0.121)	(0.210)
P4	(0.0.121)	(0.110)

Endopodite P3 hardly exceeding proximal exopodite segment. Endopodite P4 fairly exceeding 1st exopodite segment; distal podomere with a strong spinulose seta instead of a diminutive setula. Innermost apical seta of distal exopodite segment P4 relatively short and strikingly dilated.

Leg 5 (Fig. 16C). Represented by a robust plate with thickly chitinous margins and 8 setae in total, innermost 2 spinulose along subdistal margin, outermost plumose and arising from a small protuberance.

Variability. The paratypical female displayed one aberrant endopodite of leg 4 (Fig. 15E) with two spinulose setae distally. Except for this aberrant case, no conspicuous variability in the size and the ornamentation of all appendages was detected.

MALE. Unknown.

Etymology. This species is named in honour of my colleague Dr Helmut Kunz.

Cylindropsyllus sp. *sensu* Monard (1935)

Monard (1935) reported a single (juvenile!) specimen among the material of *C. laevis* from Roscoff. He considered that this species differed from the latter in the 5-segmented antennula and in many other respects. The little information given (Monard presented drawings only of the antennula and the antenna) raises grave doubts that it belongs to this genus at all. Having examined copepodid

Table I. *Comparison of* Cylindropsyllus *species with* Cylinula proxima *Coull, 1971*

	laevis	*remanei*	*kunzi* sp.n.	*Cylinula proxima*
Exp A2	1 seta	2 setae	2 setae	2 setae
Palp Md	2-segmented enp + 4 setae	2-segmented enp + 4 setae	2-segmented enp + 4 setae	1-segmented 5 setae
Enp Mx	3 setae	2 setae	3 setae	3 setae
P1	Non-prehensile	Non-prehensile	Non-prehensile	Prehensile
Distal segment exp P1–P4	2 outer setae	1 outer seta	1 outer seta	2 outer setae
Distal segment Enp P1	2 geniculate setae + 1 setula	2 geniculate setae	2 geniculate setae + 1 setula	1 geniculate seta + 1 claw + 1 setula
Length of ♀ (μm)	1370	730	590	610
Length of ♂ (μm)	1200	690	?	540

stages I do not reject the possibility that Monard's specimen belongs to *C. laevis*. Consequently *Cylindropsyllus* sp. *sensu* Monard (1935), having no nomenclatural status, cannot be assigned to any of the currently known species of the genus.

Discussion

The phylogeny of the family Cylindropsyllidae as compiled by Lang (1948, p. 1214) divides the family into three branches. Working from the literature, Lang (1948) recognized three genera within the subfamily Cylindropsyllinae: *Cylindropsyllus, Evansula* and *Stenocaris*. Coull (1971) described the intermediary genus *Cylinula* from coarse sandy sediments of the North Carolina continental shelf and a fifth genus was added, with hesitation however, by Willems (1981): *Boreopontia* Willems, 1981.

Most recently, Apostolov (1982) removed *S. pristina* Wells, 1968 and *S. valkanovi* Marinov, 1974 from the genus *Stenocaris*, resulting in the erection of the genus *Stenocaropsis* Apostolov, 1982. It is clear that *Stenocaris* urgently needs revision and, pending this, Apostolov's split remains highly speculative. Moreover, his statement that ". . . les deux espèces sont isolées des autres formes du genre *Stenocaris* qui se caracterise par un endopodite uniarticulé au P2–P4 tandis que l'endopodite de ces deux espèces est biarticulé" cannot be supported, since *S. abyssalis* and *S. profundus*, both described from the Iberian deep sea by Becker *et al.* (1979) also display a two-segmented endopodite P2–P4.

The subfamily Cylindropsyllinae was defined on the basis of cylindropsyllid genera having (1) sexual dimorphism in the exopodite P2 and endopodite P3, (2) a three-segmented exopodite P1 in which the middle segment possesses an outer seta and the distal segment 4 setae, (3) baseoendopodite and exopodite fused in leg 5 and (4) a normally developed or obsolete maxilliped. Except for (2) (*Boreopontia* shows no outer seta on the middle segment; *C. remanei* and *C. kunzi* sp.n. have only 3 setae on the distal segment), all other diagnostic characters remain valid. Moreover, a fifth character, usually overlooked due to less precise descriptions, is the sexual dimorphism of the basis in leg 2. According to the author's knowledge such a situation is unique among harpacticoids (thus far sexual dimorphism in the basis, i.e. the inner spine and/or subdistal margin, has only been recorded in leg 1; e.g. in Thalestridae, Diosaccidae, Metidae, Ameiridae). The presence of a spinous processus at the inner distal corner of the male basis in leg 2 is reported in *Cylindropsyllus* (this study), *Cylinula* (Huys unpubl.), *Stenocaris* (see *S. gracilis*; Sars 1909; *S. intermedia*; Itô 1972) and *Boreopontia* (see *B. heipi*; Willems 1981), yet is absent in all other cylindropsyllids and consequently could be a feature of central importance in the evolution of the family.

Amongst the six genera described, *Cylinula* is without doubt the one most closely related to *Cylindropsyllus*, because of the shared obsolete maxilliped, the short caudal rami, the curious sexual dimorphism in P2 and P3, the genital field, the structure of the antennula and maxillula (exo- and endopodite represented as a seta, innermost surface seta of arthrite dwarfed) and the fifth pair of legs in both sexes.

When describing *Cylinula proxima* Coull (1971) suspected affinities (cf. generic name) with *Cylindropsyllus* and *Evansula*. Re-examination of *C. proxima* (Huys, in prep.), however, showed that *Cylinula* and *Cylindropsyllus* are close relatives and a direct relationship with *Evansula* now seems dubious. Because of the unisegmented mandibular palp and the prehensile endopodite P1, *Cylinula* can be considered as the apomorphous branch. Within the genus *Cylindropsyllus C. laevis* is undoubtedly more plesiomorphous than any other species. The primitive setation of exopodite P1–P4 (2 outer setae on distal segment) relates the species closely to the genus *Cylinula*. Apart from the exopodal chaetotaxy, *C. laevis* differs fundamentally from the other *Cylindropsyllus* species in its extreme body size and the unisetose antennal exopodite.

Cylindropsyllus kunzi in various aspects resembles *C. remanei*. The latter, however, shows no inner setule on the distal endopodite segment P1, the maxillar endopodite has only two setae, a dark pigment spot occurs on the antennula and there is a difference in body length. *Cylindropsyllus kunzi* seems to be clearly differentiated from the other members of the genus by the characteristic dilated seta on the distal exopodite segment of leg 4 and by the short endopodite of leg 3.

The slender seta at the inner subdistal corner of the second endopodite segment P3 and the minute seta near the inner subdistal edge of second endopodital segment P4 have been overlooked by some authors (Sars 1909; Kunz 1949) and in consequence their setal formulae have to be amended. In Table I the salient features of *C. kunzi* are summarized and compared with those of its cognates and *C. proxima*.

Whilst *C. remanei* and *C. kunzi* have been reported

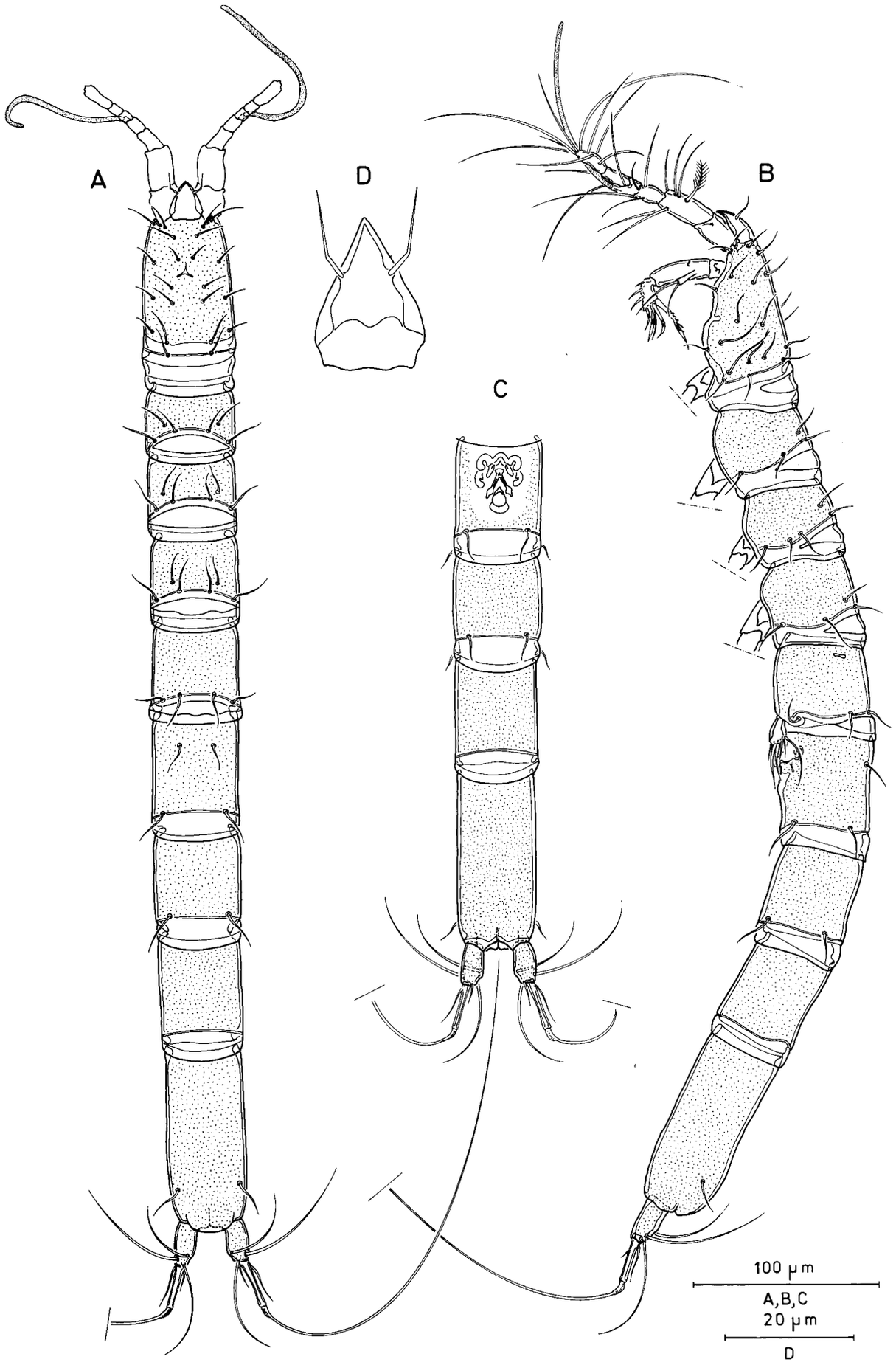

Fig. 13. Cylindropsyllus kunzi sp.n. (♀).—*A*. Habitus, dorsal.—*B*. Habitus, lateral.—*C*. Abdomen, ventral.—*D*. Rostrum.

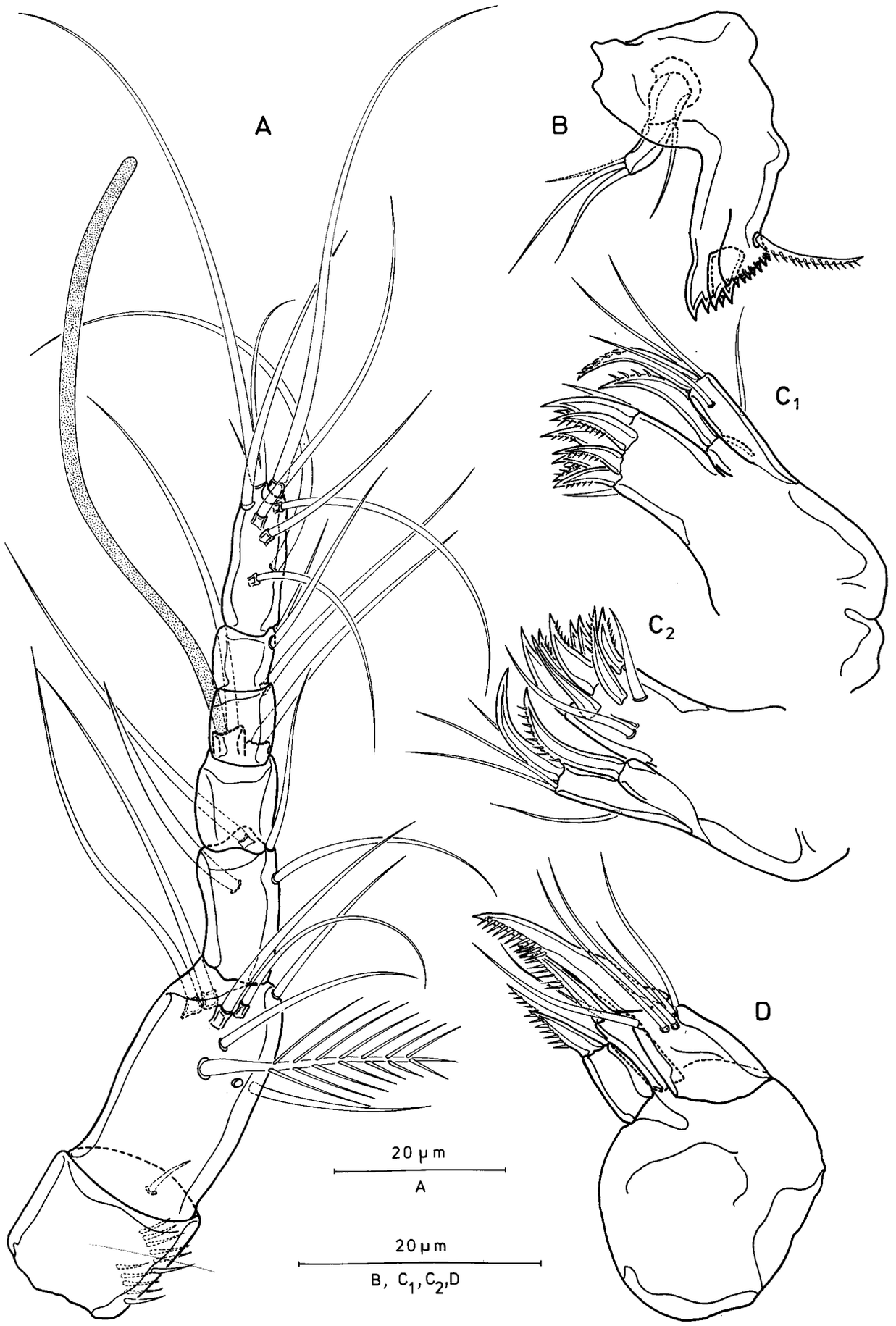

Fig. 14. Cylindropsyllus kunzi sp.n. (♀).—*A*. Antennula.—*B*. Mandible.—*C1*. Maxillula, posterior.—*C2*. Maxillula, anterior.—*D*. Maxilla.

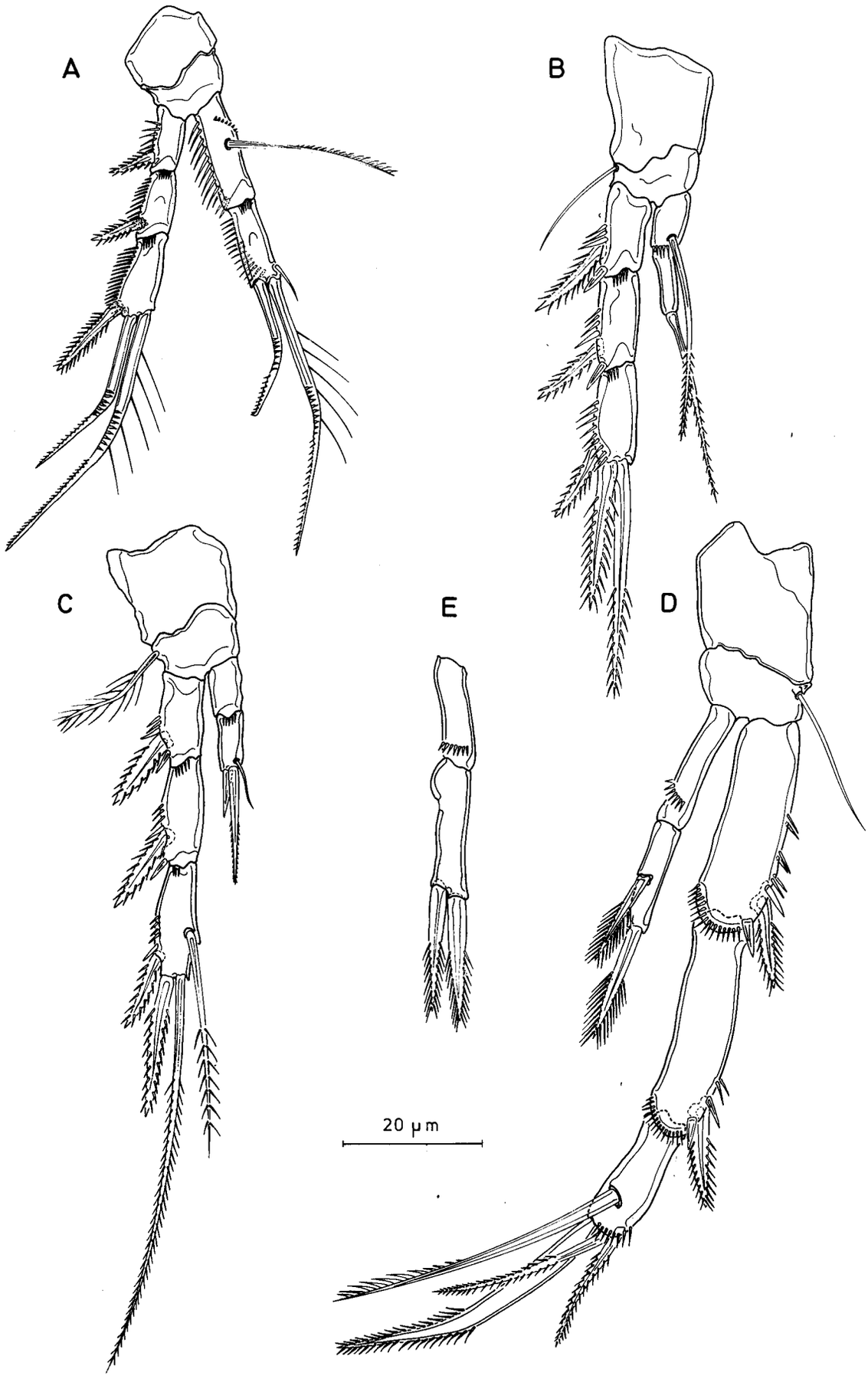

Fig. 15. Cylindropsyllus kunzi sp.n. (♀).—*A*. P1.—*B*. P2.—*C*. P3.—*D*. P4.—*E*. Aberrant endopodite P4 of paratypical female.

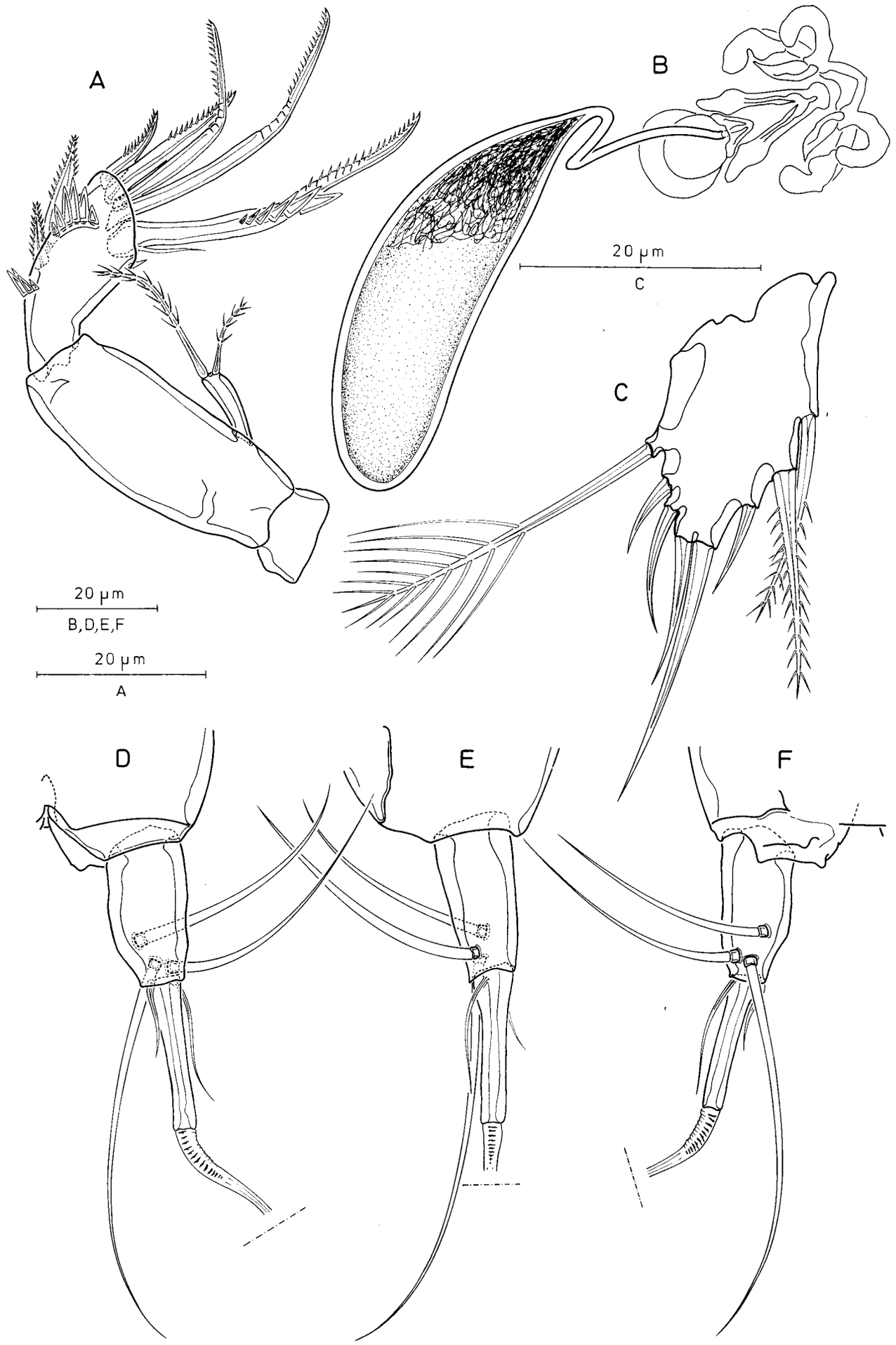

Fig. 16. Cylindropsyllus kunzi sp.n. (♀).—*A*. Antenna.—*B*. Genital field and attached spermatophore.—*C*. P5.—*D*. Caudal ramus, ventral.—*E*. Caudal ramus, lateral.—*F*. Caudal ramus, dorsal.

exclusively from medium to coarse sandy sediments in both intertidal (e.g. Wells & Clark 1965) and subtidal localities, *C. laevis*, pre-adapted for an epibenthic existence by its extreme body size, is often found in muddy deposits (e.g. Thompson 1893; Sars 1909; Por 1964).

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