

COMPARATIVE ANALYSIS OF VERMIFORM GENERA (COPEPODA: HARPACTICOIDA: CYLINDROPSYLLIDAE), INCLUDING DESCRIPTIONS OF *BOREOVERMIS*, NEW GENUS AND *BOLBOTELOS*, NEW GENUS, FROM THE SOUTHERN NORTH SEA

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A B S T R A C T

Two new monotypic genera of Cylindropsyllidae (Copepoda, Harpacticoida), *Boreovermis* and *Bolbotelos*, are described from subtidal sandy sediments in the Southern Bight of the North Sea. *Boreovermis bilobata* new genus, new species is primarily characterized by its conspicuous sexual dimorphism on P2 and P3. *Bolbotelos longisetosus*, new genus, new species is unique in its vermiform body morphology, bi-laterally compressed bulbous caudal rami, loss of inner basal spine on P1 and secondarily elongated geniculate setae on both P1 rami. Both genera are related to *Navalonia* Huys and Conroy-Dalton, 1993 and *Willemsia* Huys and Conroy-Dalton, 1993, with which they form a well supported clade of vermiform taxa within the Cylindropsyllidae. The relationships within this *Navalonia*-clade are analysed and apomorphic character states for each internal node and terminal taxon are discussed.

INTRODUCTION

In addition to forming an integral part of the plankton of both freshwater and marine water bodies, copepods constitute an important group in the benthic environment. Harpacticoid copepods are usually the second most abundant metazoan taxon in marine sediments (Hicks and Coull, 1983) where they are typically outnumbered only by the nematodes. They occur from the intertidal zone to the deepest oceanic ooze, colonizing a wide range of sediment types from mud substrata to coarse shelly gravels. Harpacticoids have been known since the late 1700s (O.F. Müller, 1776), yet it was not until the nineteen-thirties that carcinologists started to fully appreciate their sheer diversity in the microfauna of sandy beaches. Ironically, the discovery of small-sized copepods was first made by Nathan Cobb, government specialist on nematodes and widely regarded as the founder of nematology. His contemporary, Charles Branch Wilson, discovered in the Woods Hole region that these harpacticoids genuinely lived in the interstitial water between sediment particles and called this fauna “terraqueous” (Wilson, September 1935). Nicholls (August 1935), who studied the intertidal harpacticoids of Millport (Isle of Cumbrae, Scotland) beaches, inadvertently stole Wilson’s thunder by introducing the term “interstitial” for the sand microfauna, a definition which has now gained general acceptance. The interstitial fauna inhabits the labyrinthic space between sand grains and thus is potentially present in almost all benthic substrata, freshwater and marine. By definition, these animals crawl or swim within the lacunae with no, or negligible, disturbance to the arcade structure of the sediment (Wells, 1986).

Colonization of the interstitial environment by harpacticoid copepods has been achieved by three different trajectories of morphological adaptation, i.e., miniaturization, adoption of a cylindrical body shape, or a combination of both. In many Paramesochridae and some interstitial Ectinosomatidae the regressive evolution in body size has reached a limit below which it is difficult to comprehend how

an adequately sized egg could be produced or a functional spermatophore could be extruded. Excessive miniaturization does not occur in the Cylindropsyllidae; however, their successful radiation in the interstitial realm can be attributed to substantial elongation along the main body axis, resulting in an almost perfectly cylindrical habitus with no marked transition between the prosome and urosome. Within the Cylindropsyllidae this evolutionary trend has led to extreme vermiformity as in *Willemsia calceola* Huys and Conroy-Dalton, 1993. Typically, accompanying these ultimate changes in body form are two opposite morphological trends displayed in the swimming legs: progressive reduction and simplification in females, and, incremental increase in complexity and transformation in males. This asymmetry in character evolution has resulted in extreme sexual dimorphism in the genera *Navalonia* Huys and Conroy-Dalton and *Willemsia* Huys and Conroy-Dalton, 1993.

Intensive research on the subtidal meiofauna of the Southern Bight of the North Sea over the last 25 years has led to the discovery of several new genera and species of interstitial harpacticoids (Willems, 1981; Willems and Claeys, 1982; Huys, 1987, 1988, 1992; Huys and Conroy-Dalton, 1993, 1996, in press). Here we present detailed descriptions of another two new species of Cylindropsyllidae from this region and review the relationships between the four vermiform genera of the family: *Navalonia*, *Willemsia*, *Bolbotelos*, new genus and *Boreovermis*, new genus.

MATERIALS AND METHODS

Before dissection the habitus was drawn from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactic acid and the parts individually mounted in lactophenol under coverslips which were subsequently sealed with transparent nail varnish. All drawings were prepared using a camera lucida on a Leica Diaplan or Leica DMR differential interference contrast microscope. The terminology for body and appendage morphology follows that of Huys and Boxshall (1991) and Huys et al. (1996). Abbreviations used: *P1-P6* for swimming legs 1-6; *exp(enn)-1(-2-3)* to denote the proximal (middle, distal) segment of a ramus; and *ae* for

aesthetasc. Body length was measured along the dorsal curvature in lateral aspect, from the anterior margin of the rostrum to the posterior margin of the caudal rami. Scale bars in all illustrations are in μm . Type material has been deposited in the Natural History Museum, London (NHM).

RESULTS

Family Cylindropsyllidae Sars, 1909

Martínez Arbizu & Moura (1994) incorporated the nominate subfamily Cylindropsyllinae in the Canthocamptidae. Huys & Conroy-Dalton (in press) showed the grounds for this course of action to be unsound and provided justification for its resurrection. The family currently contains the following genera: *Cylindropsyllus* Brady, 1880; *Evansula* T. Scott, 1906; *Stenocaris* Sars, 1909; *Cylinula* Coull, 1971; *Boreopontia* Willems, 1981; *Stenocaropsis* Apostolov, 1982; *Willemsia* Huys & Conroy-Dalton, 1993; *Navalonia* Huys & Conroy-Dalton, 1993; and *Selenopsyllus* Moura & Pottek, 1998.

Boreovermis, new genus

Diagnosis.—Cylindropsyllidae. Body slender, vermiform. Rostrum triangular, defined at base. Genital double-somite ♀ without chitinous traces marking original segmentation. Copulatory pore small, positioned slightly anterior to gonopores. Seminal receptacles weakly chitinized, with long anteriorly directed paired reservoirs. Caudal ramus elongate; with 7 setae; seta I vestigial; seta V without defined flexure zone, somewhat more swollen proximally in ♀, fused to seta IV; seta VI vestigial.

Sexual dimorphism in antennule, P2-P3 (protopod and both rami), P5, P6, genital segmentation, and in the caudal rami (slightly in seta V).

Antennule with segment 1 distinctly shorter than segment 2; segment 2 with 8 setae; segment 6 with 3 setae in ♀; 7-segmented and with aesthetasc on segments 4 and 7 in ♀; indistinctly 9-segmented, haplocer and with aesthetasc on segments 5 and 9 in ♂; apical segment in both sexes with terminal acrothek consisting of 2 long setae fused basally to slender aesthetasc. Antenna with incompletely fused allobasis and bisetose 1-segmented exopod. Mandible with 2-segmented, uniramous palp consisting of unisetose basis and endopod bearing 1 lateral and 4 distal setae. Maxillule with 1 claw and 1 seta on coxa, 4 setae plus 1 claw on basis; endopod and exopod represented by 2 and 1 setae, respectively. Maxillary endopod discrete, 1-segmented, with 4 setae; proximal endite of syncoxa with 3 setae/spines. Maxillipeds well developed, subchelate, syncoxa without seta, endopod represented by relatively short claw. P1-P4 with 3-segmented exopods and 1- (P2-P3) or 2-segmented (P1, P4) endopods. P1 with outer and inner seta on basis; exopod with outer spine on exp-2 and 2 geniculate setae plus 2 spines on exp-3; endopod not prehensile, slightly shorter than exopod; enp-1 about as long as enp-2, with inner seta being serrate distally; enp-2 with 2 geniculate setae and 1 setule. P2-P4 bases with outer seta. P3 endopod of ♀ with 1 distal spine. Inner distal spine of P2-P3 exp-3 shorter than outer distal one and somewhat displaced to subdistal position, that of P4 exp-3 distinctly longer. Inner

setae of P3-P4 exp-3 serrate. Armature formula of swimming legs:

	Exopod	Endopod
P1	0.0.112	1.111
P2	0.0.021	010
P3	0.0.121	010
P4	0.0.121	0.010

P2 protopod ♂ with incompletely fused basis and coxa; inner distal corner of basis with two small spinous processes. P2 exopod ♂ 2-segmented and strongly modified; exp-1 and -2 forming compound segment; exp-3 with massive claw (positional homologue of inner distal spine in ♀). P2 endopod ♂ 2-segmented; enp-1 with serrate inner seta; enp-2 with pinnate apical seta. P3 protopod ♂ with basis and coxa reduced to isolated sclerites. P3 exopod ♂ with exp-1 shorter than in ♀; exp-2 with long tube-pore; exp-3 swollen in proximal half. P3 endopod ♂ 2-segmented; enp-1 small, largely incorporated into basis, with long, typically sigmoid apophysis; enp-2 produced into robust spinous process.

P5 baseoendopod and exopod completely fused forming triangular plate in both sexes; in ♀ with 6 setae and 1 strong, pectinate spine; in ♂ with 3 setae and 1 bare spine. P6 asymmetrical in ♂, with 2 setae each; represented by operculum with 1 setule and 2 minute spiniform processes in ♀.

Type Species.—*Boreovermis bilobata*, new species.

Etymology.—The generic name is derived from the Latin *boreas*, meaning north wind, and *vermis*, meaning worm, and alludes to the boreal distribution of this vermiform genus. Gender: feminine.

Boreovermis bilobata, new species

Figures 1-7

Type Locality.—North Sea, Southern Bight, off Dutch Delta; 52°00'00"N, 3°00'00"E; depth 40.8 m.

Material Examined.—Holotype ♀ (dissected on 8 slides; NHM reg. no. 1995.397), paratype ♂ (dissected on 7 slides; NHM reg. no. 1995.398) and additional paratypes (12 ♀♀, 14 ♂♂, 1 Cop.V♀) in alcohol (NHM reg. no. 1995.399-425); all collected at type locality; coll. R. Huys, 29 April 1986. Additional non-registered material examined is listed in Table 1.

Description of Female.—Total body length: 440-475 μm ($n = 10$; mean = 462 μm). Body slender, cylindrical (Fig. 1), semi-transparent, colourless; no distinct separation between prosome and urosome. Integument of cephalothorax and body somites pitted. Except for P5-bearing somite all urosomites with minutely serrate hyaline frill (Figs. 5D, 7A). Genital double-somite completely fused (Figs. 5D, 7A). Anal somite distinctly longer than wide (40 $\mu\text{m} \times 85 \mu\text{m}$), with 3 pairs of secretory pores laterally (Fig. 6D); posterior margin with small lappets laterally (Fig. 6D-E) and short spinular row on either side of ventral midline (Fig. 7A). Anal operculum well developed, rounded, smooth (Fig. 6E).

Caudal ramus conical (Figs. 6D-E, 7A), distinctly wider at level of seta VII insertion site; length (measured along the

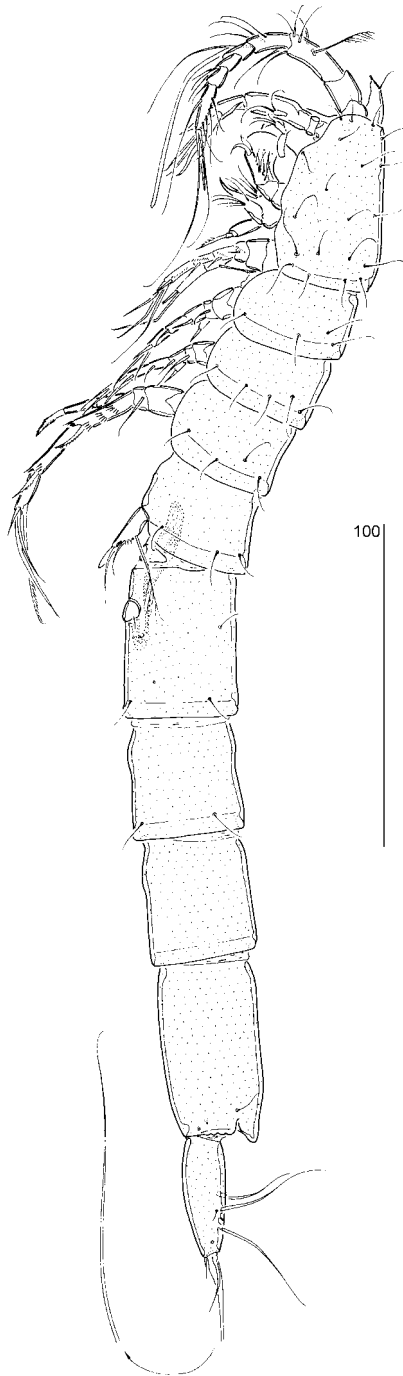


Fig. 1. *Boreovermis bilobata*, new genus, new species (♀): habitus, lateral.

outer margin) about 3.9 times the proximal width; dorsal surface without chitinous spur; with 7 setae, setae I-VI in distal half and seta VII at about half way the caudal ramus length (Fig. 6E); seta I diminutive; setae II-III long and bare; seta IV short and naked; seta V long, without distinct flexure zone, swollen at base and fused proximally to vestigial seta IV; seta VI vestigial; seta VII tri-articulate at base and located along proximal inner margin; ventral surface with 1 secretory pore (Fig. 6D), dorsal surface with 3 pores (Fig. 6E).

Rostrum triangular (Fig. 3A); slightly shorter than first antennular segment; demarcated at base; base surrounded

by area of flexible integument; with 2 long sensilla; median tube-pore positioned ventrally near apex of rostrum.

Antennule 7-segmented (Figs. 2A, 3A). Segment 1 distinctly shorter than segment 2, with small sclerite around proximal posterior margin, 2 spinular rows along anterior margin and 1 pore on dorsal surface; segment 2 longest and much wider than segments 3-7, with secretory pore; segment 4 with distal cylindrical process bearing large aesthetasc (50 μ m). Armature formula: 1-[1], 2-[7 + 1 pinnate], 3-[4], 4-[1 + (1 + ae)], 5-[1], 6-[3], 7-[7 + acrothek]. Apical acrothek consisting of 2 long setae and 1 slender aesthetasc (20 μ m).

Antenna (Fig. 2A-B) with small unarmed coxa; basis and first endopod segment incompletely fused forming allobasis, leaving transverse suture around abexopodal margin; allobasis with spinular pattern along abexopodal margin as illustrated in Fig. 2B; exopod a small segment, with 2 apical setae of equal length (1 naked, 1 pinnate); endopod with 2 lateral pinnate spines and distal armature consisting of 2 pinnate spines, 2 geniculate setae and 1 large geniculate spine bearing spinules at about mid-margin and fused at base with short seta; tube-pore (arrowed in Fig. 2B) discernible at base of geniculate spine.

Labrum (arrowed in Fig. 2A) a well-developed, ventrally produced extension; distal margin with short, blunt spinules; lateral margins with finer setules.

Mandible (Fig. 2C-D). Gnathobase relatively small, with fine teeth and unipinnate spine at dorsal distal corner; uniramous palp, consisting of basis and 1-segmented endopod; basis elongate, with 1 lateral, pinnate seta; endopod with 1 outer and 4 apical setae fused in 2 clusters, each cluster comprising 1 long and 1 short seta.

Maxillule (Fig. 6F). Praecoxal arthrite with 9 spines/setae around distal margin and 1 tubular seta on anterior surface. Coxal endite with 1 geniculate claw and 1 seta. Basis and rami largely fused into elongate palp; basal armature represented by 1 lateral seta, and 3 setae plus a geniculate claw apically. Endopod represented by 2 basally fused setae, exopod by 1 small seta.

Maxilla (Fig. 3D). Syncoxa with 2 endites, each with 1 pinnate and 2 naked setae, all articulating at base. Allobasis drawn out into a claw-like pinnate endite armed with 2 accessory setae; with distinct tube-pore. Endopod a discrete segment with 4 long, basally fused setae.

Maxilliped (Fig. 2A, E) small, subchelate, outwardly directed. Syncoxa short, without armature but with 1 spinular row. Basis elongate, without ornamentation. Endopod represented by a straight, acutely curved claw provided with few spinules along distal margin.

P1 (Figs. 2A, 4A). Praecoxa a small, bare sclerite. Coxa with 3 spinular rows on posterior surface. Basis with short, naked, inner seta and short, pinnate, outer spine. Exopod 3-segmented; with outer spine on exp-2 and 1 spine plus 3 geniculate setae on exp-3. P1 endopod not prehensile, slightly shorter than exopod; exp-1 slightly longer than exp-2, with distally serrate inner seta; exp-2 with subapical setule and 2 geniculate setae apically.

Swimming legs P2-P4 (Fig. 4B-D). P4 much longer than P2-P3. Praecoxae well developed, with spinular row on anterior surface of P4. Coxae with pattern of spinules as in

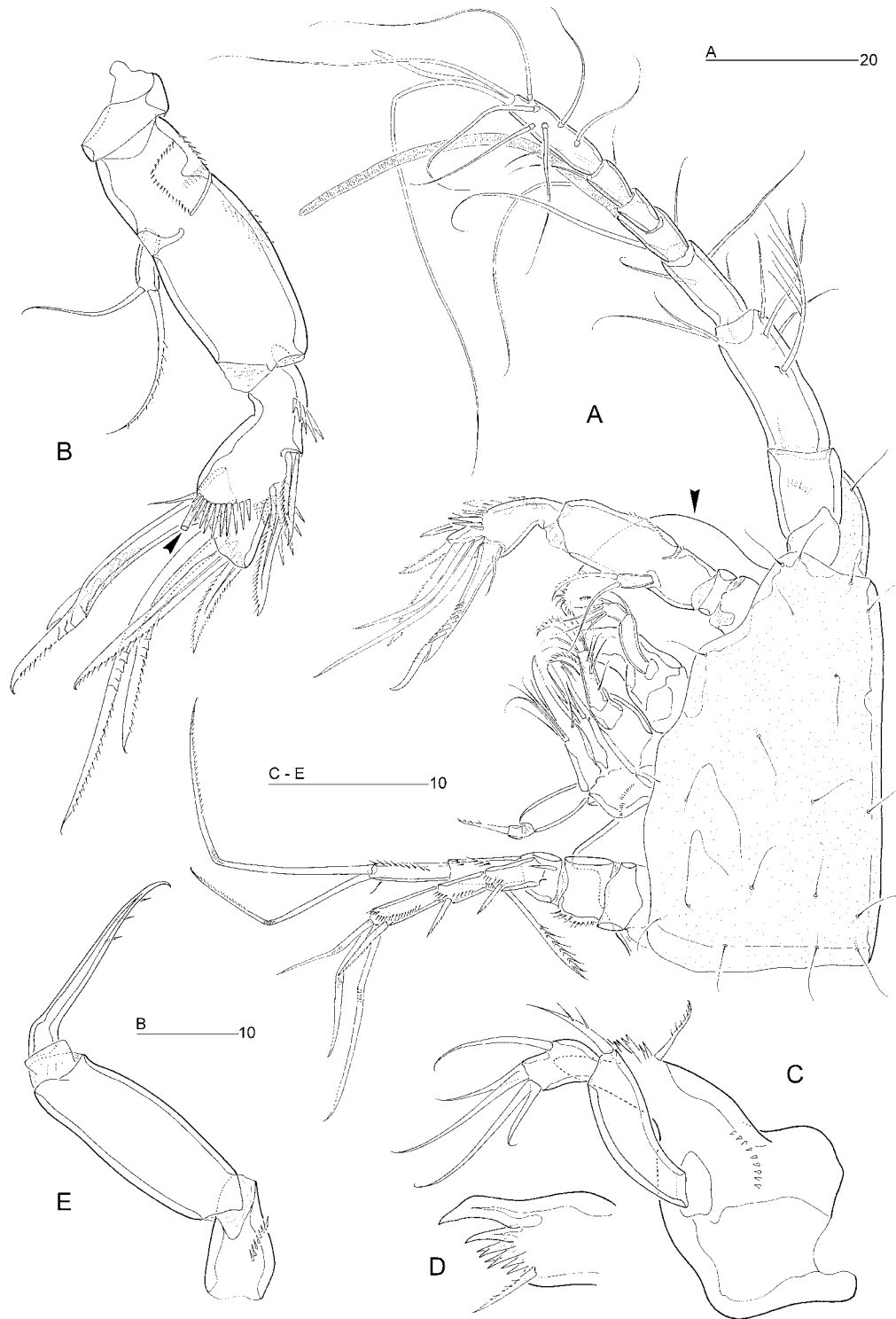


Fig. 2. *Boreovermis bilobata*, new genus, new species (♀): A, cephalothorax, lateral [labrum arrowed]; B, antenna [tube-pore arrowed]; C, mandible; D, mandibular gnathobase; E, maxilliped.

Fig. 4B-D. Bases with outer seta; with spinular rows on anterior surface only; with pore on anterior surface of P3 and P4. Exopods 3-segmented, endopods 1- (P2-P3) or 2-segmented (P4). P2-P3 exp-3 with inner distal spine shorter than outer distal one. Inner setae of P3 exp-3 and P4 exp-3 serrate. Inner setule on P4 exp-2 absent. Distal spine of

endopods pinnate in P2-P3, pectinate in P4. Seta and spine formulae as for genus.

Fifth pair of legs (Figs. 5D, 7A, C) relatively small; not fused medially, no distinct intercoxal sclerite. Baseoendopod and exopod fused into a common subtriangular plate, tapering distally; apex with stout, pectinate spine, distinctly



Fig. 3. *Boreovermis bilobata*, new genus, new species: A, antennule and rostrum (♀), dorsal; B, antennule (♂), ventral; C, antennular segments 3-9 (♂), anterior; D, maxilla.

shorter than plate; outer margin with 1 sparsely plumose seta (derived from baseoendopod), 2 naked setae and 3 vestigial ones; inner margin with 1 tube-pore; anterior surface with 1 simple pore.

Sixth legs (Figs. 5D-E, 7A) represented each by small operculum closing off gonopore; armature consisting of 1 fine setule and 2 minute dentate processes. Genital apertures

not fused medially; copulatory pore small (arrowed in Fig. 5E), located midventrally, anterior to gonopores; leading via short chitinized copulatory duct to large paired seminal receptacles, each comprising small ventral chamber and long, anteriorly directed reservoir.

Single egg-sac containing about 4-6 eggs arranged in uniserial way, enclosed in common egg-sac membrane;

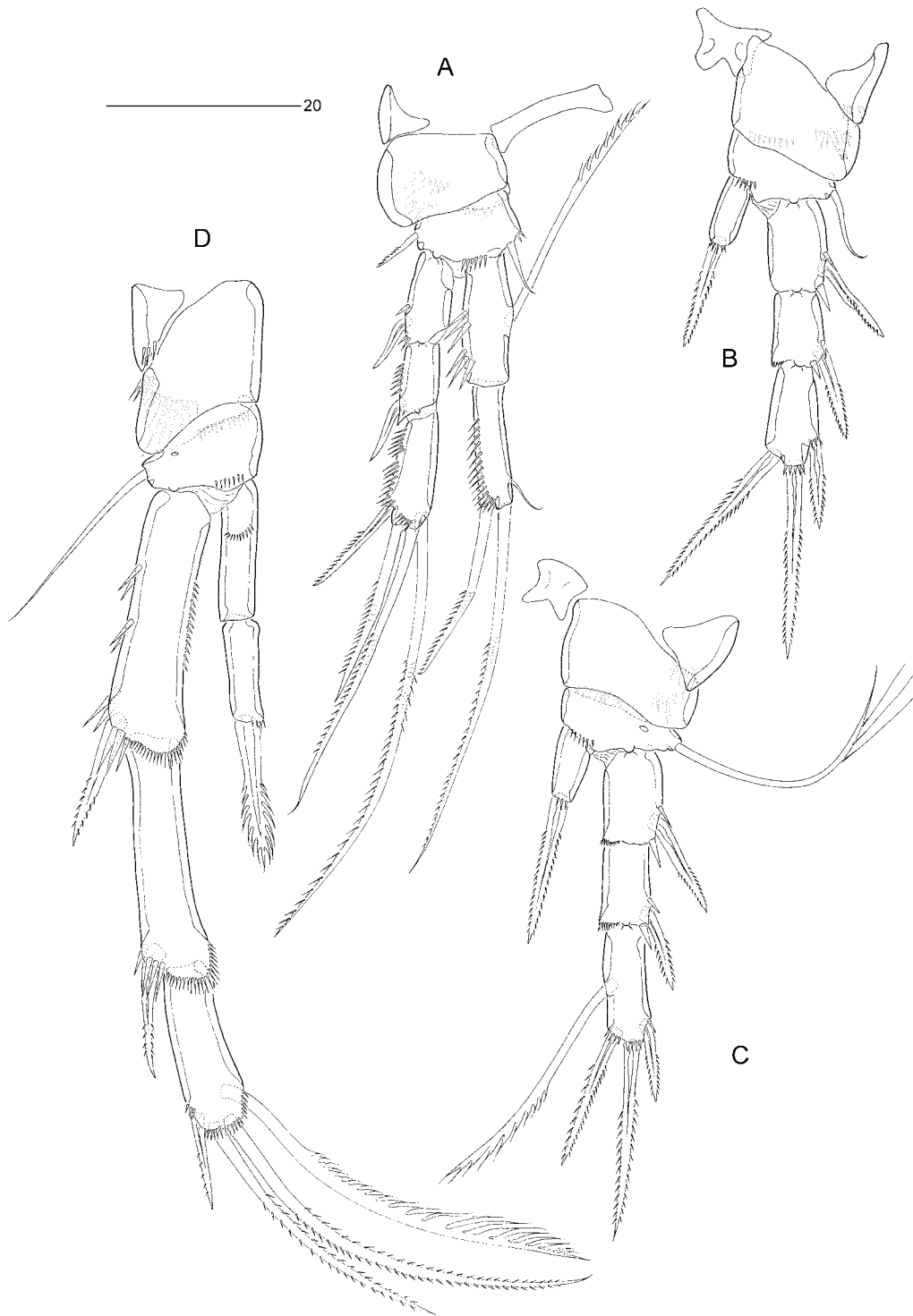


Fig. 4. *Boreovermis bilobata*, new genus, new species (♀): A, P1, anterior; B, P2, anterior; C, P3, anterior; D, P4, anterior.

egg-sac connected with each genital aperture via transparent string.

Description of Male.—Total body length: 440–470 μm ($n = 5$; mean = 458 μm).

Antennule (Fig. 3B–C) indistinctly 9-segmented; geniculation between segments 6 and 7; segment 1 with 1 minute

seta and spinular pattern as in Fig. 3B; segment 2 longest, with 1 plumose plus 8 naked setae, ventral surface with small pore; segment 3 with 6 setae; segment 4 minute, forming an incomplete ring, with 2 short setae; segment 5 distinctly swollen, with 6 elements along the anterior margin and with distal cylindrical process bearing basally fused seta and large aesthetasc (60 μm); segment

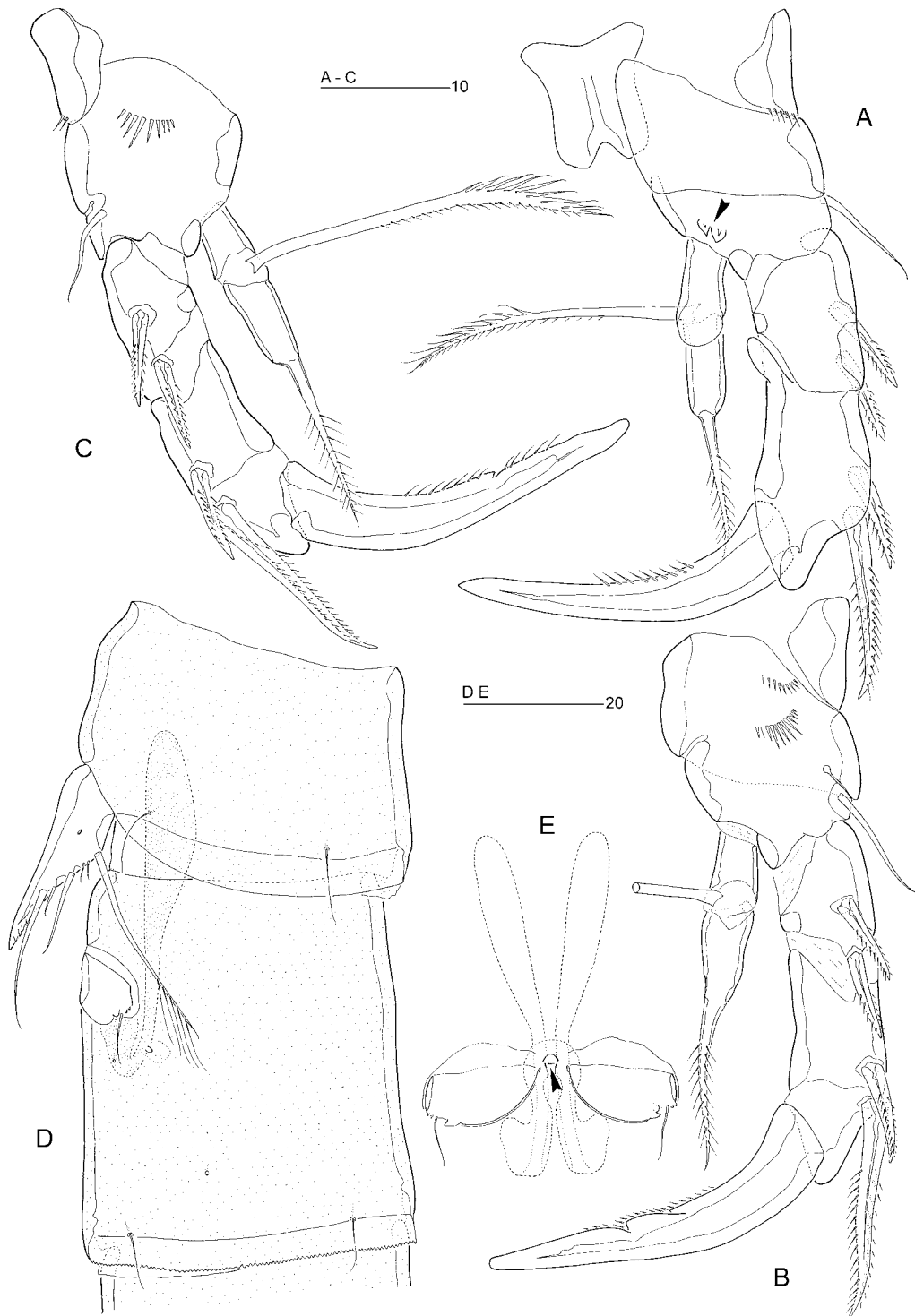


Fig. 5. *Boreovermis bilobata*, new genus, new species: A, P2 (♂), anterior [basal processes arrowed]; B, P2 (♂), posterior; C, P2 (♂), outer lateral; D, P5-bearing somite and genital double-somite (♀), lateral; E, Genital field (♀), ventral [copulatory pore arrowed].

6 with 1 short pinnate spine, 2 modified elements and 1 setule; segment 7 with 2 modified elements; segment 8 minute, with 1 setule (Fig. 3C); segment 9 with 6 posterior setae, 1 anterior seta and an acrothek apically. Apical acrothek consisting of 2 naked setae and 1 slender aesthetasc (23 μ m).

P2 with large intercoxal sclerite and well developed praecoxa (Fig. 5A). Basis and coxa separated anteriorly (Fig. 5A) but largely fused posteriorly (Fig. 5B); coxa with 2 spinular rows on posterior surface; basis with double spinous process near inner distal corner of anterior surface (arrowed in Fig. 5A) and naked seta along outer margin.

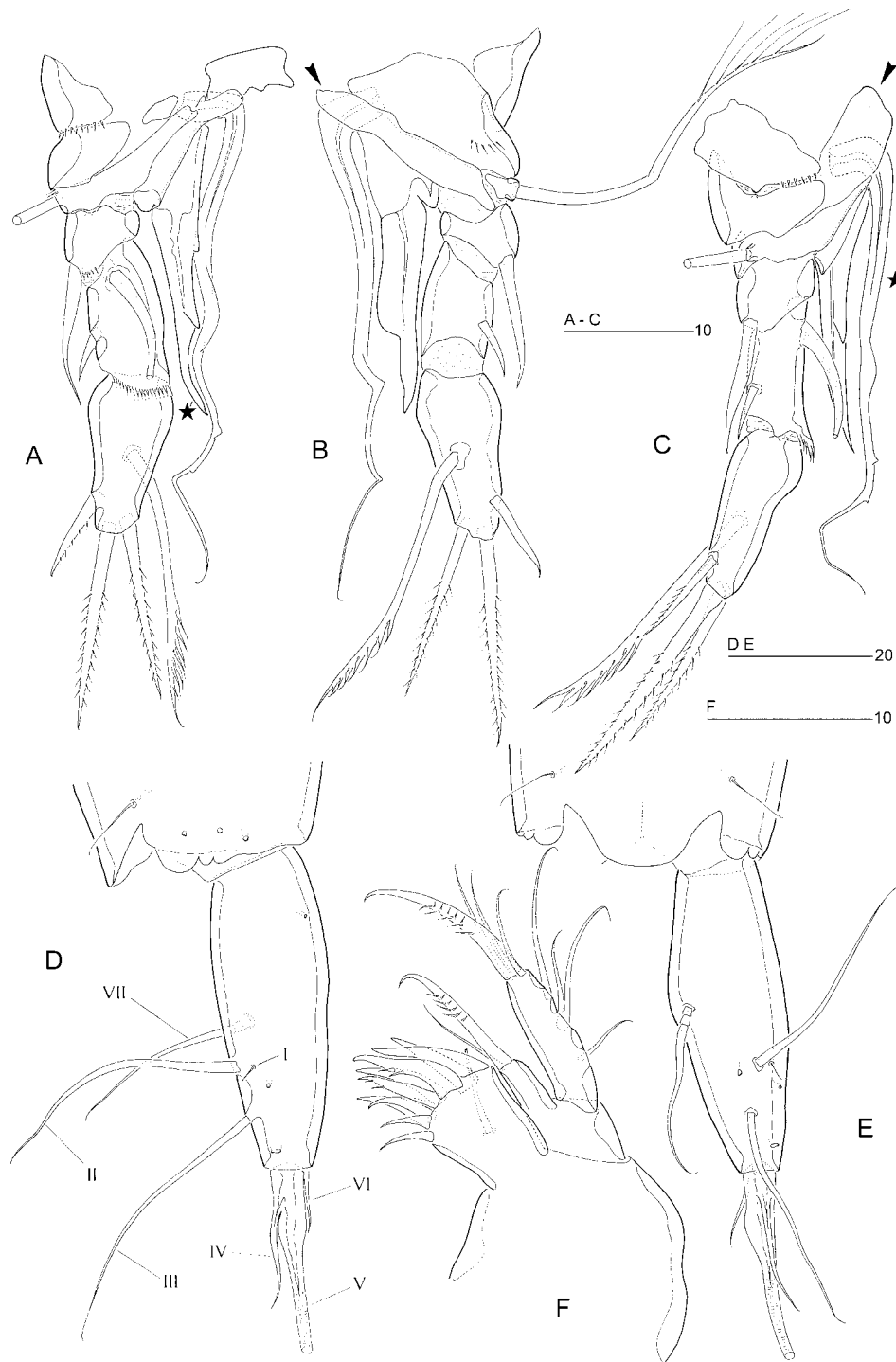


Fig. 6. *Boreovermis bilobata*, new genus, new species: A, P3 (♂), anterior [star indicating enp-2]; B, P3 (♂), posterior [enp-1 arrowed]; C, P3 (♂), outer lateral [enp-1 arrowed; star indicating apophysis]; D, right caudal ramus, lateral; E, anal operculum and right caudal ramus, dorsal; F, maxillule.

Endopod larger than in ♀, 2-segmented; enp-1 with serrate inner seta arising from posterior surface; enp-2 with apical pinnate seta partly fused to segment (Fig. 5B-C). Exopod robust, 2-segmented. Proximal exopod segment compound (derived by fusion of exp-1 and exp-2 expressed in ♀); posterior surface with 2 bipinnate outer spines and large membranous articulation zone distally. Distal exopod

segment longer than proximal one; with 2 bipinnate outer spines, distal one of which being much longer; apex with massive, unipinnate, inner claw which is both inwardly (Fig. 5A-B) and posteriorly (Fig. 5C) directed and homologous to inner distal spine expressed in ♀; inner proximal corner with elongate, dorsally directed condyle (Fig. 5A).

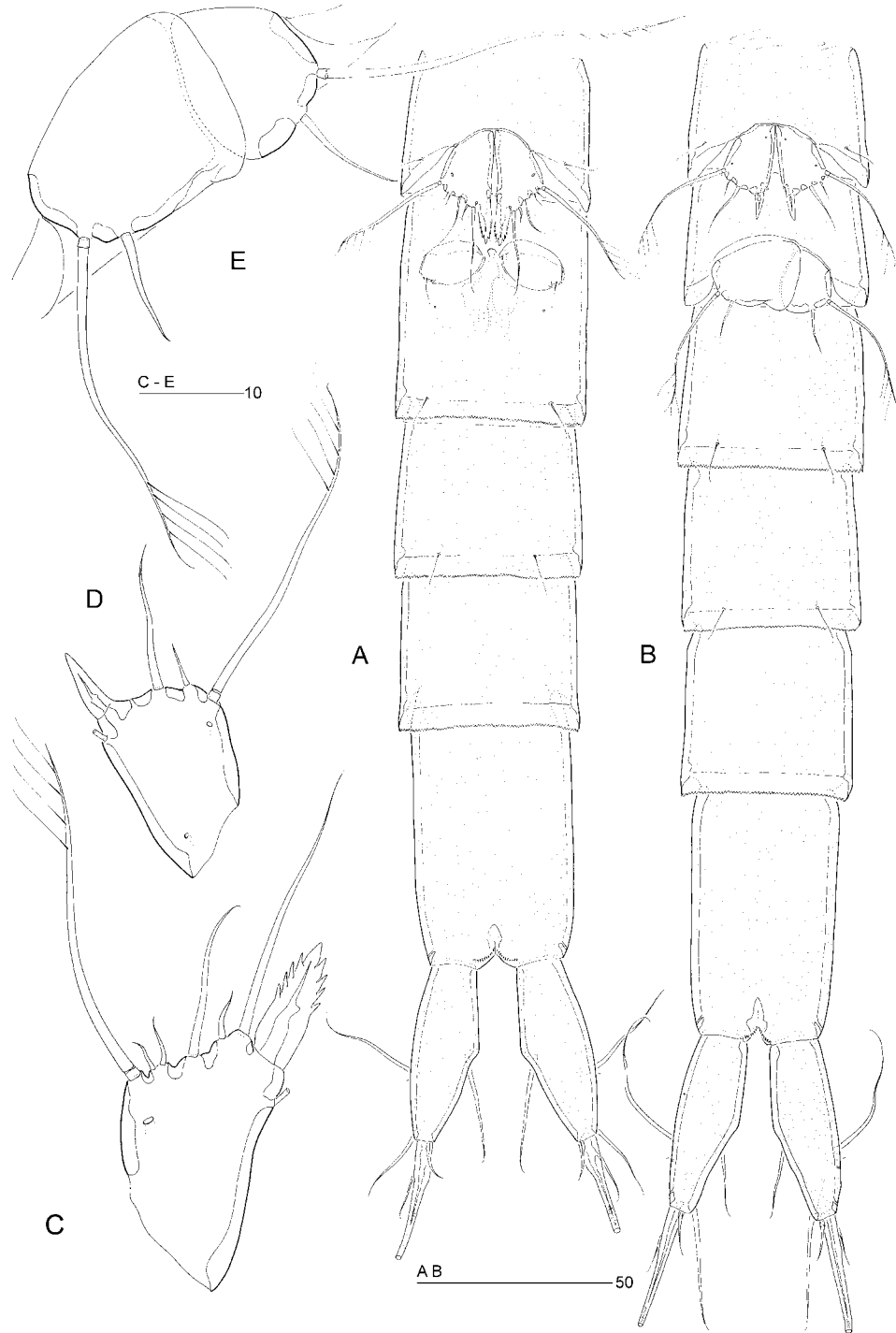


Fig. 7. *Boreovermis bilobata*, new genus, new species: A, urosome (♀), ventral; B, urosome (♂), ventral; C, P5 (♀), anterior; D, P5 (♂), anterior; E, sixth pair of legs (♂), anterior.

P3 with protopod and rami highly modified. Praecoxa represented by small sclerite with distal spinular margin (Fig. 6A). Coxa triangular in posterior view (Fig. 6B) and represented by individualized chitinized areas anteriorly (Fig. 6A), with spinular row on posterior surface (Fig. 6B). Basis strongly reduced in size; represented by an incomplete, U-shaped sclerite, tapering and defined medially on

anterior surface (Fig. 6A), virtually absent and reduced to small area around outer basal seta posteriorly where it is delimited from the posterior face of enp-1 by small membranous insert (Fig. 6B). Exopod 3-segmented; exp-1 short, with curved, naked outer spine; exp-2 with small outer spine and long tube-pore arising proximally from anterior surface (Fig. 6A, C); exp-3 swollen proximally, distinctly tapering

distally with 3 pinnate spines around apical margin and serrate inner seta arising from posterior surface. Endopod 2-segmented; enp-1 short but extremely enlarged transversely, covering most of distal part of protopod where it replaces the strongly reduced basis and consequently adjoins the coxa (arrowed in Fig. 6B-C), with very long, twisted apophysis deeply embedded in medially produced part of segment (indicated by star in Fig. 6C); enp-2 a strongly chitinized triangular segment with spinous apex and 2 barbs along the inner margin (indicated by star in Fig. 6A).

Fifth legs (Fig. 7B, D) small, not fused medially, no distinct intercoxal sclerite. Baseoendopod and exopod fused into a common plate, tapering distally towards apex with short naked spine (incompletely delimited at base); outer margin with 1 naked seta, 1 setule and 1 sparsely plumose seta (derived from baseoendopod); inner margin with 1 tube-pore subapically; anterior surface with 2 simple pores.

Sixth pair of legs (Fig. 7B, E) asymmetrical, each with sparsely plumose outer seta and short, naked inner seta. Left or right leg articulating according to sinistral or dextral development of testis and vas deferens.

Caudal ramus conical (Fig. 7B) slightly more slender than in ♀; seta V less swollen at base.

Etymology.—The species name is derived from the Latin *bis*, meaning twice, and *lobus* (Late Latin), meaning lobe, and refers to the characteristic subdivision of the seminal receptacles.

Distribution.—*Boreovermis bilobata* was found exclusively in the Southern Bight of the North Sea (Table 1).

***Bolbotelos*, new genus**

Diagnosis [based on ♀ only].—Cylindropsyllidae. Body slender, vermiform. Rostrum triangular, defined at base. Genital double-somite ♀ with virtually no chitinous traces marking original segmentation. Copulatory pore very large, positioned at level of gonopores. Seminal receptacles not very well chitinized. Caudal ramus bulbous, elongate, distinctly compressed bi-laterally; attachment site with anal somite very small; with 7 setae; seta I vestigial; seta V swollen at base, without well defined flexure zone, fused to seta IV; seta VI vestigial.

Sexual dimorphism unconfirmed but at least present in antennule, P6 and in genital segmentation.

Antennule ♀ 7-segmented; with segment 1 distinctly shorter than segment 2; segment 2 with 8 setae; segment 6 with 3 setae; with aesthetasc on segments 4 and 7; apical segment with terminal acrothek consisting of 2 setae fused basally to slender aesthetasc. Antenna with incompletely fused allobasis and bisetose 1-segmented exopod. Mandible with 2-segmented, uniramous palp consisting of unisetose basis and endopod bearing 1 lateral and 4 distal setae. Maxillule with 1 claw and 1 seta on coxa, 4 setae plus 1 claw on basis; endopod and exopod represented by 2 setae each. Maxillary endopod discrete, 1-segmented, with 4 basally fused setae; proximal endite of syncoxa with 3 setae/spines. Maxillipeds well developed, subchelate, syncoxa without seta, endopod represented by short claw. P1-P4 with 3-segmented exopods and 1- (P2-P3) or 2-

Table 1. Non-type material of *Boreovermis bilobata*, new genus, new species collected from southern part of North Sea.

Latitude	Longitude	Date	Depth (m)	Material
51°15'00"N	1°30'00"E	8 April 1986	12.6	2 ♀♀, 4 ♂♂
51°15'00"N	2°30'00"E	2 April 1986	18.0	1 ♀
51°43'06"N	3°06'15"E	30 March 1992	32.8	11 ♀♀, 8 ♂♂
51°45'00"N	3°30'00"E	17 April 1986	14.0	10 ♀♀, 6 ♂♂
51°57'24"N	2°40'57"E	30 March 1992	42.7	1 ♀, 6 ♂♂, 1 juv.
52°02'30"N	3°25'00"E	24 June 1987	37.2	8 ♀♀, 4 ♂♂
52°15'00"N	2°30'00"E	18 April 1986	29.9	2 ♀♀
52°30'00"N	4°00'00"E	2 May 1986	24.6	1 ♂
52°34'10"N	3°31'53"E	26 April 1991	32.5	4 ♀♀, 2 ♂♂

segmented (P1, P4) endopods. P1 with outer but without inner seta on basis; exopod with outer spine on middle segment and 2 very long geniculate setae plus 2 spines on distal segment; endopod not prehensile, slightly shorter than exopod; enp-1 shorter than enp-2, with inner seta being serrate distally; enp-2 with 2 geniculate setae (1 very long) and 1 setule. P2-P4 bases with outer seta. P3 endopod with 1 distal spine. Inner distal spine of P2-P3 exp-3 distinctly shorter than outer distal one, that of P4 exp-3 distinctly longer. Inner setae of P3-P4 exp-3 serrate. Armature formula of swimming legs:

	Exopod	Endopod
P1	0.0.022	1.111
P2	0.0.021	010
P3	0.0.121	010
P4	0.0.121	0.010

P5 baseoendopod and exopod completely fused; with 4 setae/spines and 2 tiny setules; P6 represented by unarmed operculum.

Type Species.—*Bolbotelos longisetosus*, new species.

Etymology.—The generic name is derived from the Greek *bolbos*, meaning bulb, and *telos*, meaning end, and refers to the bulbous caudal rami. Gender: masculine.

***Bolbotelos longisetosus*, new species**

Figures 8-11

Type Locality.—North Sea, 53°00'00"N, 3°00'00"E, depth 49.1 m.

Material Examined.—Holotype ♀ dissected and mounted on 9 slides (NHM reg. no. 1995.426); coll. R. Huys, 19 April 1986.

Description of Female.—Total body length: 480 µm. Cuticle smooth. Body very slender, vermiform (Fig. 8A-B), semi-transparent, colourless; no distinct separation between prosome and urosome. Urosomites slightly wider than cephalothorax and prosomites. Genital double-somite about 1.5 times as long as wide; completely fused (Figs. 8A-B, 11C), original segmentation marked by small chitinous ribs laterally and paired sensilla dorsally (Fig. 8A-B). Anal somite elongate, about twice as long as wide (70 µm × 34 µm), with 1 pair of secretory pores laterally (Fig. 8E); posterior margin with tiny spinular rows dorsally on either

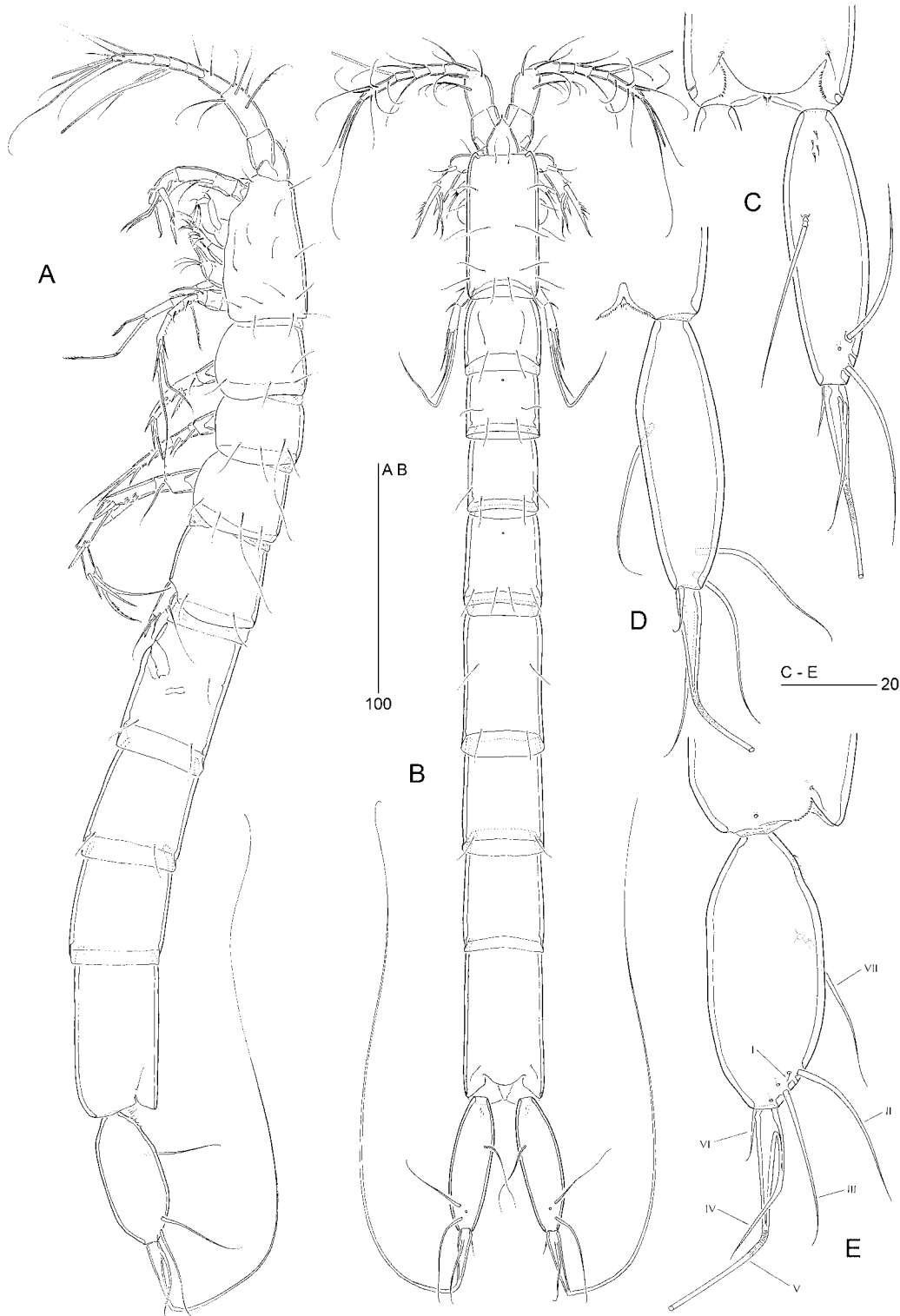


Fig. 8. *Bolbotelos longisetosus*, new genus, new species (♀): A, habitus, lateral; B, habitus, dorsal; C, anal somite (posterior part) and right caudal ramus, dorsal; D, anal somite (posterior part) and left caudal ramus, ventral; E, anal somite (posterior part) and caudal ramus, lateral.

side of the anal opening (Fig. 8C, E), and ventrally on either side of the midline (Fig. 8D). Anal operculum well developed, strongly convex, unarmed (Fig. 8C).

Caudal ramus conspicuous and large (Fig. 8A-E); bulbi-form and strongly constricted at proximal margin, leaving

only small articulation area with anal somite (particularly in lateral aspect: Fig. 8A, E); distinctly bi-laterally compressed (compare Fig. 8C and E), maximum width in lateral aspect 26 μm , in dorsal aspect 16 μm ; length about 0.8 times the anal somite length; dorsal surface without chitinous spur but

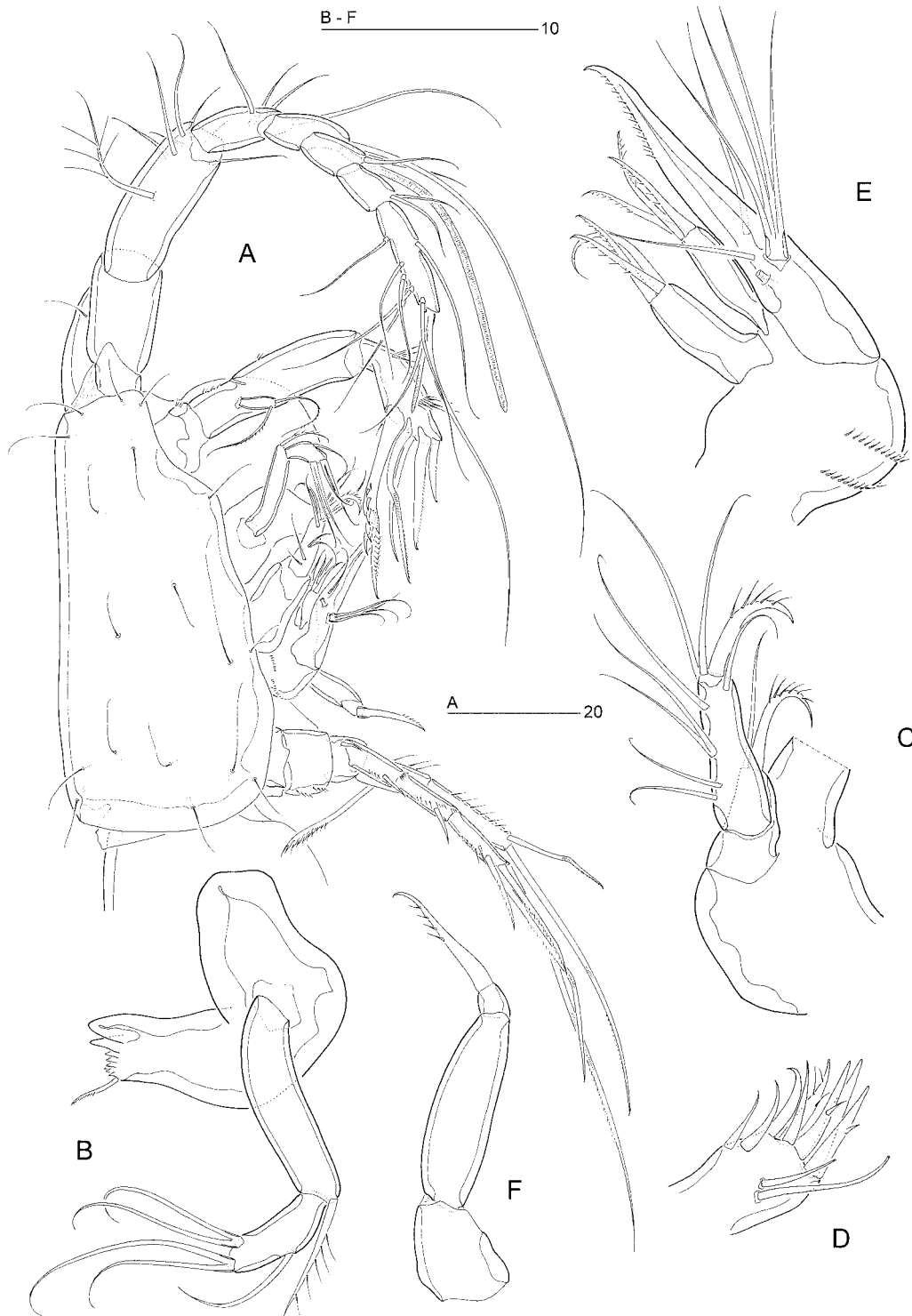


Fig. 9. *Bolbotelos longisetosus*, new genus, new species (♀): A, cephalothorax, lateral; B, mandible; C, maxillule [arthrite omitted], posterior; D, maxillular arthrite, anterior; E, maxilla; F, maxilliped.

with patch of spinules near anterior rim (Fig. 8C); with 7 setae, setae I-VI positioned in distal fifth and seta VII at boundary between proximal and middle third (Fig. 8E); seta I diminutive; setae II-III moderately long and bare; seta IV short and naked; seta V long, without defined flexure zone but with swollen basal part, fused proximally to seta IV; seta

VI vestigial; seta VII tri-articulate at base and located along proximal inner margin; lateral surface with 2 pores near posterior margin (Fig. 8E), dorsal surface with 1 pore near insertion site of seta II (Fig. 8C).

Rostrum triangular (Fig. 11A), longer than wide but distinctly shorter than first antennular segment; demarcated

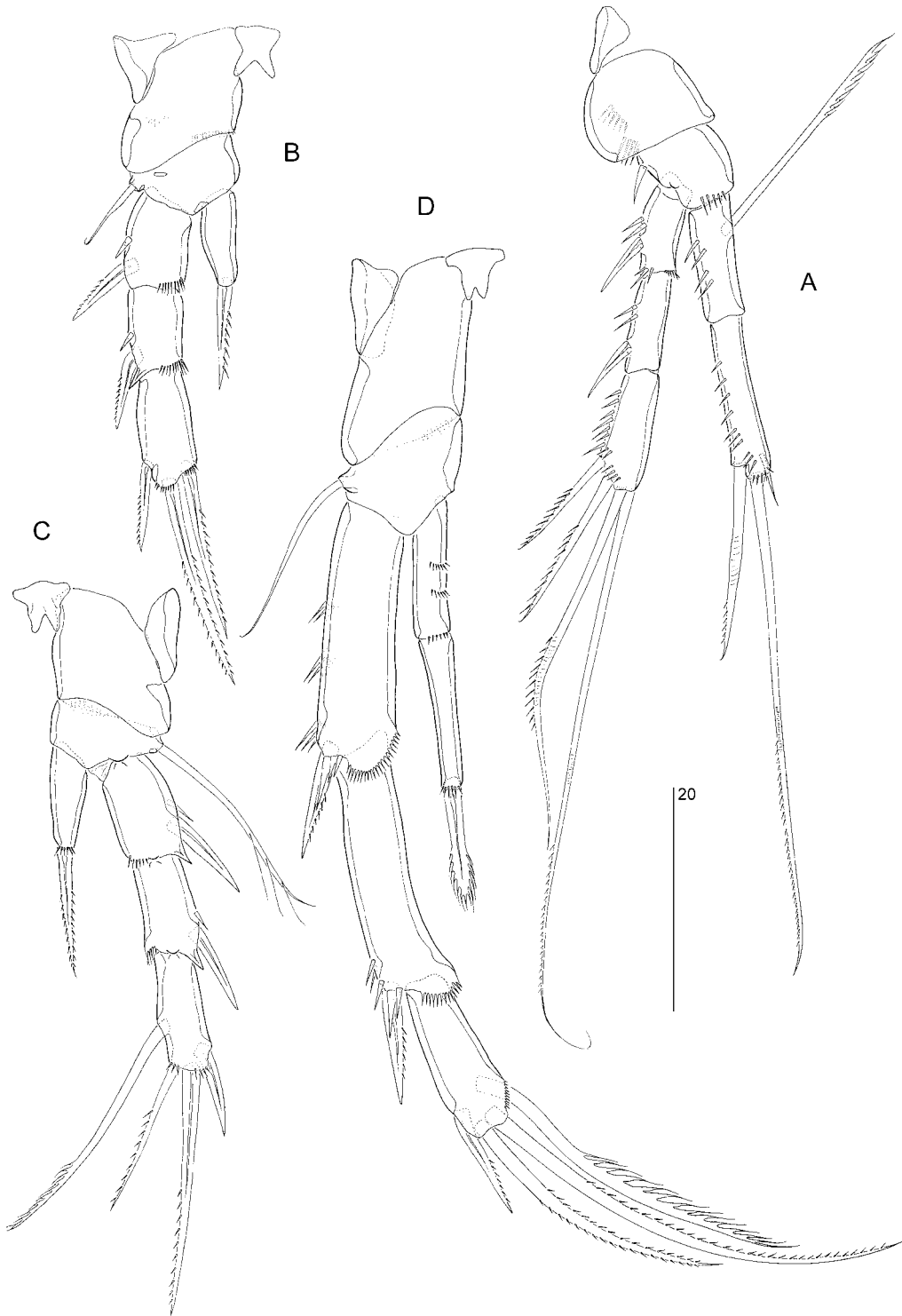


Fig. 10. *Bolbotelos longisetosus*, new genus, new species (♀): A, P1, anterior; B, P2, anterior; C, P3, anterior; D, P4, anterior.

at base; base surrounded by area of flexible integument; with 2 long sensilla; median tube-pore positioned ventrally near apex of rostrum.

Antennule 7-segmented (Figs. 9A, 11A). Segment 1 distinctly shorter than segment 2, with small sclerite around proximal posterior margin, no spinular rows discernible along anterior margin; segment 2 longest, without secretory

pore; segment 4 with distal cylindrical process bearing slender aesthetasc (50 μ m). Armature formula: 1-[1], 2-[7 + 1 pinnate], 3-[4], 4-[1 + (1 + ae)], 5-[1], 6-[3], 7-[7 + acrothek]. Apical acrothek consisting of 2 long setae and 1 slender aesthetasc (20 μ m).

Antenna (Figs. 9A, 11B) with small unarmed coxa; basis and first endopod segment incompletely fused

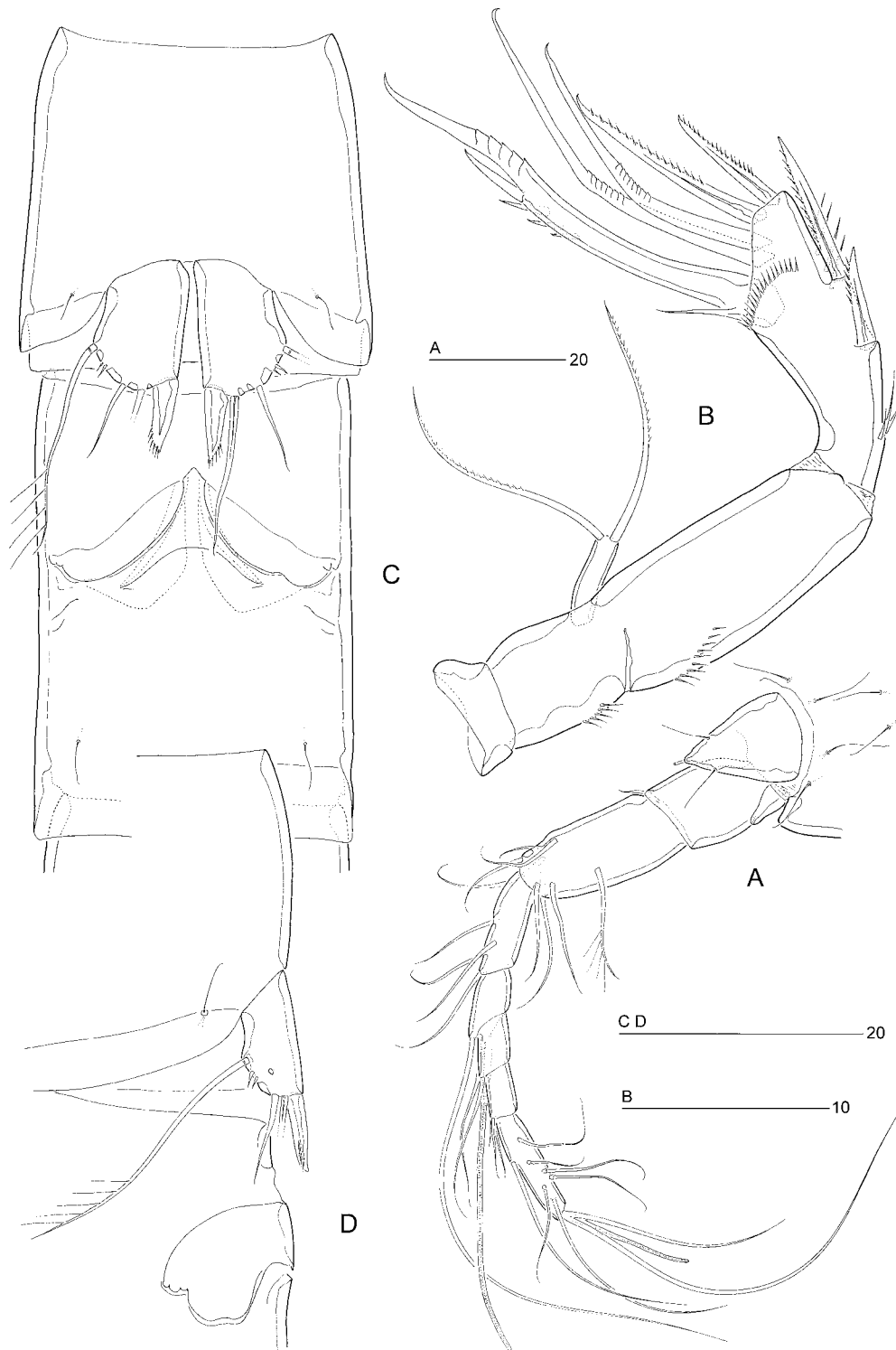


Fig. 11. *Bolbotelos longisetosus*, new genus, new species (♀): A, rostrum and antennule, dorsal; B, antenna; C, P5-bearing somite and genital double-somite, ventral; D, P5-bearing somite and anterior half of genital double-somite, lateral.

forming allobasis, abexopodal margin with 2 spinular rows; exopod a narrow segment, with 2 long pinnate setae apically; endopod with 2 lateral spines and distal armature consisting of 2 pinnate spines, 2 geniculate setae and 1 large geniculate spine bearing spinules at about mid-

margin and fused at base to short, naked seta; no tube-pore discernible.

Labrum (Fig. 9A) a well-developed, ventrally produced extension; distal margin with short, blunt spinules; lateral margins with finer setules.

Mandible (Fig. 9A-B). Gnathobase well developed, with 1 pinnate seta dorsally. Uniramous palp, consisting of basis and 1-segmented endopod; basis elongate, with 1 lateral, pinnate seta; endopod with 1 outer and 4 apical setae fused in 2 clusters.

Maxillule (Fig. 9C-D). Praecoxal arthrite with 8 spines/ setae around distal margin and 2 tubular setae (1 long, 1 short) on anterior surface. Coxal endite with 1 pinnate claw and 1 seta. Basis and rami fused into elongate palp; basal armature represented by 1 lateral seta, and 3 setae plus a pinnate claw apically. Endopod represented by 2 basally fused setae, exopod by 2 setae.

Maxilla (Fig. 9E). Syncoxa with 2 cylindrical endites, proximal endite with 1 naked and 2 pinnate setae, distal endite with 3 pinnate setae, all articulating. Allobasis drawn out into a claw-like pinnate endite armed with 2 accessory setae; with distinct tube-pore. Endopod a discrete segment with 4 basally fused setae.

Maxilliped (Fig. 9A, F) well developed, subchelate, directed outwards. Syncoxa well developed, without seta or spinular rows. Basis elongate, without ornamentation. Endopod represented by a small discrete segment with short, pinnate, acutely recurved claw.

P1 (Figs. 9A, 10A). Praecoxa represented by small sclerite. Coxa with 2 spinular rows on posterior surface; outer margin expanded forming distinct bulge. Basis with short outer seta and 1 spinular row near articulation with endopod; inner seta absent. Exopod 3-segmented; with outer spine on exp-2, and 2 spines plus 2 very long geniculate setae on exp-3. P1 endopod not prehensile, slightly shorter than exopod; enp-1 shorter than enp-2, with serrate inner seta; enp-2 with inner subdistal setule, 1 very long geniculate seta apically and 1 geniculate spine on subdistal outer margin.

Swimming legs P2-P4 (Fig. 10B-D). P4 much larger than P2-P3. Intercoxal sclerites small. Praecoxae well developed, without spinular row. Coxae with posterior row of tiny spinules near articulation with basis and with additional spinular row in P2. Bases with outer seta; without spinular rows; with anterior secretory pore in P2. Exopods 3-segmented, endopods 1-segmented (P2-P3) or 2-segmented (P4). Exopods of P2-P3 short and stout; inner distal spine of exp-3 shorter than outer distal one and displaced to subdistal position (Fig. 10B-C). P4 exp-3 inner distal spine longer than outer distal one (Fig. 10D). Inner setae of P3-P4 exp-3 serrate. P4 enp-1 shorter than enp-2, with 3 spinular rows on anterior surface; enp-2 with pectinate apical spine. Seta and spine formulae as for genus.

Fifth pair of legs (Fig. 11C-D) relatively small; not fused medially; no intercoxal sclerite present. Baseoendopod and exopod fused into a common plate with straight inner margin and convex outer margin; inner distal corner with strong, unipinnate spine, shorter than plate; armature consisting of 1 sparsely plumose seta (derived from baseoendopod), 2 naked setae and 2 closely set spinules (or setules?).

Sixth legs (Fig. 11C-D) represented each by large operculum closing off crescent-shaped gonopore; armature absent, replaced by 3 minute, lobate processes (Fig. 11D). Gonopores not fused medially; copulatory pore very large and wide, located slightly posterior to gonopores; copulatory duct short; seminal receptacles paired, elongate, thin-

walled reservoirs, extending over almost the entire length of genital double-somite, subdivided in dorsal and ventral chambers [note: most internal tissues in the anterior urosomites were destroyed during dissection. An accurate illustration of the seminal receptacles could therefore not be presented, but Fig. 5E of the genital field in *Boreovermis bilobata* gives an approximate view of what they looked like in situ.]; no secretory pores discernible on ventral face of genital double-somite.

Male.—Unknown.

Etymology.—The species name is derived from the Latin *longus*, meaning long, and *seta*, meaning bristle, and refers to the very long setae on the P1 exopod and endopod.

Distribution.—Known from the type locality only.

DISCUSSION

Huys and Conroy-Dalton (1993) recognized a well-supported sister group relationship between the vermiform monotypic genera *Willemsia* and *Navalonia*, based primarily on the elaborate sexual dimorphism of the swimming legs. *Navalonia kerguelensis* (Bodiou, 1977) is known only from its type locality in the Kerguelen Archipelago. In the North Sea, *Willemsia calceola* Huys and Conroy-Dalton, 1993 appears to be restricted to the shallow coastal areas of Belgium and the Netherlands (Huys and Conroy-Dalton, 1993), but our examination of Bodin's (1984) unidentified cylindropsyllid material from the Bay of Douarnenez (Finistère) revealed that its distribution extends further southwards to at least the coast of Brittany. The discovery of *Bolbotelos longisetosus* and *Boreovermis bilobata* from the southern North Sea adds two more vermiform members to the family and their morphology suggests they form a coherent clade with *W. calceola* and *N. kerguelensis*, hereafter called the *Navalonia*-clade. This clade groups species that have adapted to the interstitial habitat by the adoption of extreme vermiformity, reduction of swimming legs in the female, and usually modification of the caudal rami into bulbous or bulbiform appendages. This trend culminates in the very slender *B. longisetosus* where the integument has become very pliable so that one may suspect worm-like wriggling to be the primary mode of locomotion. Accompanying these changes in body facies is the progressive elaboration and complexity of sexually dimorphic structures on the swimming legs.

The monophyly of the *Navalonia*-clade is supported by at least four synapomorphies (Fig. 12; Table 2: characters 1-5) and we envisage it to gain even more robustness upon the discovery of the male of *Bolbotelos* and the redescription of the female of *Navalonia* (the type material of *N. kerguelensis* is no longer extant; J.-Y. Bodiou, personal communication):

- (1) The female plesiomorphic 2-segmented condition of the endopods in P2-P3 is retained in the genera *Cylindropsyllus* Brady, 1880, *Cylinula* Coull, 1971, *Stenocaropsis* Apostolov, 1982 and *Selenopsyllus* Moura and Pottek, 1998. The genus *Boreopontia* Willems, 1981 shows the ancestral segmentation for the P2 but the apomorphic 1-

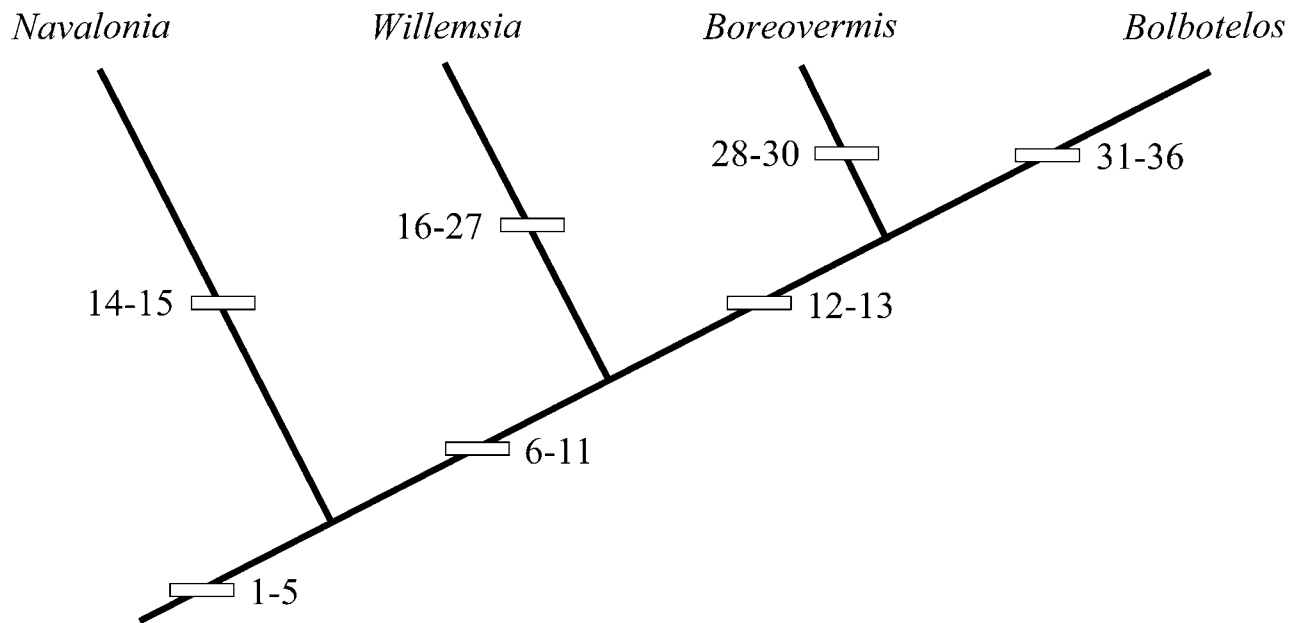


Fig. 12. Phylogenetic relationships between vermiform genera. Numbers refer to apomorphic character states listed in Table 2.

segmented condition for the P3. In *Evansula* T. Scott, 1906, *Stenocaris* Sars, 1909 and the four genera of the *Navalonia*-clade, both P2 and P3 possess a 1-segmented endopod, but only in the latter is the setation pattern of the P2 endopod sexually dimorphic. Males of the *Navalonia*-clade possess an inner serrate seta on enp-1 (in *Willemsia*, the endopod is reduced to a single segment but the seta is still present). In females, the expression of this element is suppressed during ontogeny, possibly as the result of post-displacement. In all other genera, the inner serrate seta is expressed in both sexes except for *Evansula* where it is absent in females and males. Huys and Conroy-Dalton (in press) provided robust morphological grounds for the basal position of this genus in the Cylandropsyllidae and consequently we regard the loss of this setal element in female *Evansula* as an independent event due to convergence.

- (2) Males of the *Navalonia*-clade have a 2-segmented P2 exopod. The outer spine pattern indicates the proximal segment is a compound segment homologous to exp-1 and exp-2 in the female. In the absence of ontogenetic data, it is impossible to decide whether these segments have failed to separate or became secondarily fused during the last moult as in the P2 endopod of Miraciidae and allied families.
- (3) The extreme displacement of the male P3 endopod, in particular of the proximal segment, in conjunction with the excessive reduction of the basis is unique among harpacticoids. The unusual configuration of enp-1 bordering the distal margin of the coxa creates the impression that the apophysis is derived from the coxa, but scrutinous examination of the segment boundaries from all angles demonstrates that it is firmly anchored in the endopodal component of the leg. In light of this observation, the "coxal spine" observed by Bodiou (1977) in the male P3 of *N. kerguelenensis* can now be

re-interpreted. This element was previously assumed to be the homologue of the raised complex pore in *Willemsia* that was believed to be a derivative of the coxa (Huys and Conroy-Dalton, 1993); however, the similar position of the apophysis at the inner margin of the putative basis in *Boreovermis* strongly suggests that these modifications are of endopodal origin in all three genera. It appears that the *Willemsia* condition is the most derived state in the modification of the P3, causing the endopod to be almost completely integrated in the coxa forming a unique copulatory device with a raised coxal pore. The allometric growth of the proximal part of the endopod represents a synapomorphy linking *Navalonia*, *Willemsia* and *Boreovermis* in a monophyletic clade. Given the close morphological similarity between the females of *Boreovermis* and *Bolbotelos*, it is conceivable that the as yet undiscovered male of *B. longisetosus* also displays a similarly modified P3 endopod.

- (4) The terminal caudal ramus seta V is typically composite in cylindropsyllids, comprising a proximal styliform part and a distal flagellate part with a distinct flexure zone in between. This condition was considered plesiomorphic by Huys and Conroy-Dalton (in press). In all four genera of the *Navalonia*-clade, seta V (at least in the ♂) is reduced to a slender, basally swollen element without distinct flexure zone. The modification of this seta into a bulbiform element in the female of *N. kerguelenensis* is reminiscent of the condition found in female *Stenocaris intermedia* Itô, 1968 and *S. minor* (T. Scott, 1892); however, the usefulness of this character in phylogenetic inference is limited since traces of such sexual dimorphism of the same seta are also found in some species of *Evansula*, the *minuta*-group of *Stenocaris*, and *Boreovermis*. It is conceivable that caudal ramus sexual dimorphism is the ancestral state

Table 2. Apomorphic and plesiomorphic [in square brackets] character states of phylogenetically informative characters numbered in Fig. 12.

1	P2 enp-1 inner serrate seta suppressed in ♀ [expressed in both sexes]
2	P2 exopod ♂ 2-segmented (proximal segment compound) [3-segmented]
3	P3 endopod ♂ extremely displaced, in particular the proximal segment, in conjunction with the excessive reduction of the basis [endopod not displaced, basis of normal size and shape]
4	Caudal ramus seta not composite [with styliform proximal and flagellate distal parts, separated by distinct flexure zone]
5	Seminal receptacles forming paired elongate reservoirs which are compartmentalized in ventral and anteriorly directed dorsal chambers [oval/round sacs, not subdivided]
6	P2-P4 exp-3 with one outer spine [two]
7	P2-P3 endopod inner distal seta absent [present]
8	P2-P3 exp-3 ♀ inner distal spine secondarily reduced in size, shorter than the outer distal one [inner distal spine longer than outer distal one]
9	P5 ♀ with reduced setation and inner spine displaced to distal position [maximum complement of eight setae present; inner spine in proximal position along inner margin]
10	P2 ♂ with partly fused basis and coxa [all protopodal segments discrete]
11	P3 endopod ♂ apophysis slender, very long and twisted [apophysis spinous and not twisted]
12	Maxilliped syncoxal seta absent [present]
13	P4 enp-2 inner seta absent [present]
14	Caudal ramus seta V strongly sexually dimorphic (flask-shaped with dorsal bulbiform process) [sexual dimorphism absent or only slightly expressed]
15	P4 enp-1 ♂ with strong dentiform process arising from inner margin [not sexually dimorphic]
16	Mandibular palp 1-segmented with reduced setation [2-segmented, with 1 seta on basis and 5 setae on endopod]
17	P1 basis outer seta absent [present]
18	P2-P3 endopods ♀ strongly reduced [represented by moderately-sized segment]
19	P2 outer exopodal elements ♂ setiform [spiniform]
20	P2 exp-1 ♂ with bulbiform (secretory) structure on inner margin [without]
21	P3 exp-2 outer spine absent in both sexes [present]
22	P3 exp-3 inner serrate seta absent in both sexes [present]
23	P3 endopod ♂ with large raised pore on apophysis [without]
24	P3 exp-2 ♂ without sexually dimorphic tube-pore but with setular tuft at inner distal corner [with sexually dimorphic tube-pore; no tuft]
25	P5 inner basal spine forming foot-shaped endopodal process in both sexes [inner basal spine discrete]
26	P5 without sexual dimorphism [sexually dimorphic]
27	Genital field ♀ without isolated copulatory pore(s) [copulatory pore discrete]
28	P2 basis ♂ with double spinous process [single]
29	P3 exp-1 ♂ strongly reduced [normal size]
30	P3 exp-2 ♂ with very large tube-pore and reduced outer spine [tube-pore small, outer spine not reduced]
31	Body extremely vermiform [moderately vermiform]
32	Caudal ramus bi-laterally compressed and bulbous [not modified]
33	Copulatory pore extremely wide [small or of moderate size]
34	P1 basis inner spine absent [present]
35	P6 ♀ without armature [armature represented by at least one seta]
36	Inner geniculate setae on P1 exp-3 and enp-2 very long and slender [short and not slender]

in the family which subsequently disappeared convergently in different lineages.

- (5) Moura and Pottek (1998) convincingly demonstrated that the paired crescent-shaped structures commonly found in the anterior part of the female genital double-somite of many canthocamptids and cylindropsyllids are in reality labyrinthic extensions of the copulatory duct

and not the seminal receptacles as previously assumed. The true receptacles are non-chitinized rounded sacs, which are difficult to discern in fixed specimens unless they are filled with sperm. In females of *Willemsia*, *Boreovermis* and *Bolbotelos*, the seminal receptacles form paired elongate reservoirs, which are compartmentalized in ventral and anteriorly directed dorsal chambers. Bodiou (1977) did not describe the genital field of *N. kerguelensis* and thus this character can only be considered as a potential synapomorphy of the *Navalonia*-clade.

Navalonia represents the first offshoot in this clade (Fig. 12). Supporting evidence for its basal position is found in the more primitive swimming leg armature, including the presence of two outer spines on the distal exopod segment of P2-P4 (instead of one) and two distal elements on the endopod of P2-P3 (instead of one spine). *N. kerguelensis* has also retained the ancestral complement of eight setae/spines of the female P5 and none of these elements is modified (as in *Cylindropsyllus* and *Cylinula*). The other three genera of the *Navalonia*-clade exhibit reduction in the number of setation elements (and occasionally modification; *Willemsia*). Bodiou (1977) showed two lateral setae on the distal segment of the mandibular palp of *N. kerguelensis*; this observation requires confirmation since no other member of the family possesses more than one element in this position. Autapomorphies for *Navalonia* (Table 2: characters 14-15) include the strongly sexually dimorphic seta V on the caudal ramus. Caudal ramus sexual dimorphism is not uncommon among cylindropsyllids (see above) but the peculiar flask shape of the principal seta in addition to the presence of a dorsal bulbiform process (constant in all specimens according to Bodiou (1977)) represents a unique modification. With the exception of *Evansula arenicola* Nicholls, 1939 (1-segmented in ♀, 2-segmented in ♂; see Huys and Conroy-Dalton, in press), *N. kerguelensis* is the only cylindropsyllid that displays distinct sexual dimorphism on the male P4 endopod. The strong dentiform process arising from the inner margin of the proximal endopod segment is an additional autapomorphy for the genus. Other similarities or differences with the residual genera of the *Navalonia*-clade are likely to emerge when information becomes available about the female genital field (copulatory pore, seminal receptacles) and the male sixth legs.

Willemsia, *Boreovermis*, and *Bolbotelos* form a strongly supported clade characterized by the following synapomorphies (Fig. 12 and Table 2: characters 6-11): (1) P2-P4 exp-3 with one outer spine (instead of two); (2) P2-P3 endopods without inner distal seta (present in *Navalonia*); (3) secondary reduction in size of the inner distal spine of P2-P3 exp-3 in the ♀ so that it is shorter than the outer distal one (a similar reduction is found on P3-P4 exp-3 in *Evansula*); (4) P5 ♀ with reduced setation and inner spine displaced to distal position (forming foot-shaped process in *Willemsia*); (5) P2 ♂ with partially fused basis and coxa (anteriorly in *Willemsia*, posteriorly in *Boreovermis*, unknown in *Bolbotelos*); and, (6) P3 endopod ♂ with very long twisted apophysis. The latter two character states are only listed here as potential synapomorphies pending the description of the

male of *B. longisetosus*. Huys and Conroy-Dalton (1993) identified *Navalonia* as the out-group of *Willemsia*. The discovery of both *Bolbotelos* and *Boreovermis* shows that *Willemsia* does not share such a sister group relationship but instead holds an intermediate position between *Navalonia* and the former genera. *Boreovermis* and *Bolbotelos* share the loss of the syncoxal seta on the maxilliped and the secondary absence of the inner seta on P4 enp-2.

Willemsia displays a wide array of autapomorphic character states (Table 2: characters 16-27): (1) mandibular palp 1-segmented with reduced setation; (2) P1 basis without outer seta (surprisingly it is the inner one that is lost in *Bolbotelos* while both setae are retained in *Boreovermis*); (3) P2-P3 endopods ♀ strongly reduced; (4) P2 exp-1 ♂ with bulbiform (secretory) structure on inner margin; (5) outer exopodal elements of ♂ P2 setiform; (6) P3 endopod ♂ with large raised pore on apophysis; (7) P3 exp-2 without outer spine in both sexes; (8) P3 exp-3 without inner serrate seta in both sexes; (9) P3 exp-2 ♂ without sexually dimorphic tube-pore but with setular tuft at inner distal corner in ♂; (10) inner basal spine of P5 forming foot-shaped endopodal process in both sexes; (11) P5 without sexual dimorphism; and (12) ♀ genital field without isolated copulatory pore(s).

Bolbotelos can readily be differentiated from all other genera by its extremely vermiform body and the conspicuous, bi-laterally compressed, bulbous caudal rami. In addition to the caudal ramus, *Bolbotelos* can be defined based on the extremely wide copulatory pore positioned in between the gonopores, the loss of the inner basal spine on P1, the elongation of the inner geniculate setae on P1 exp-3 and enp-2, and the reduced armature on the ♀ P6 (Fig. 12 and Table 2: characters 31-36). These unique character states are not found elsewhere in the family. The genus *Boreovermis* exhibits very distinctive sexual dimorphism on both P2 and P3. Unlike other known cylindropsyllids the male possesses a double spinous process on the P2 basis. Likewise, the male P3 is unique in the presence of a very large tube-pore on exp-2 and strong reduction in size of exp-1.

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