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WILLEMSIA GEN. NOV. AND BOREOPONTIA WILLEMS, 1981 REVISITED (HARPACTICOIDA: CYLINDROPSYLLIDAE)

RONY HUYS & SOPHIE CONROY-DALTON

SARSIA

A new genus and species of Cylindropsyllidae (Copepoda, Harpacticoida), collected from shallow subtidal sand in the Southern Bight of the North Sea, is described and illustrated. *Willemsia calceola* gen. et sp. n. exhibits a unique kind of sexual dimorphism on the male P3 not observed thus far in any other harpacticoid. It is further distinguished from all known Cylindropsyllinae by the absence of an isolated midventral copulatory pore, the facies of the P2–P3 in the female and the peculiar shape and orientation of the fifth pair of legs in both sexes. Based on the sexual dimorphism of the P2 exopod and P3 endopod, it is suggested that *W. calceola* shares a sistergroup relationship with *Stenocaris kerguelenensis* BODIOU, 1977 which is transferred to a new genus *Navalonia*.

Boreopontia heipi WILLEMS, 1981 is redescribed and an update of its distribution in the North Sea is given. *Stenocaris pygmaea* NOODT, 1955, previously ranked as a junior subjective synonmy of *S. pontica* CHAPPUIS & SERBAN, 1953, is reinstated.

The homology of spinous processes on the caudal rami in species of *Boreopontia* WILLEMS, *Stenocaris* SARS and *Stenocaropsis* APOSTOLOV is assessed.

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INTRODUCTION

The high level taxonomy of the family Cylindropsyllidae is currently in a state of flux. LANG (1944) divided the family into three 'Reihen', which were subsequently formalised as subfamilies in his monograph (LANG 1948): Cylindropsyllinae, Leptastacinae and Leptopontiinae. In addition, KRISHNASWAMY (1956) proposed a fourth subfamily Psammopsyllinae to accommodate *Psammopsyllus* NICHOLLS and the newly discovered *Sewellina* KRISHNASWAMY. Though this division apparently gained wide acceptance, the actual relationships of the respective subfamilies have never been demonstrated as such. A survey of the morphological characters contained in LANG's (1948: 1192) family diagnosis shows that only a few are displayed by all four subfamilies. The majority of these shared features either represent plesiomorphic character states being of negligible phylogenetic significance, or morphological reductions acquired convergently through independent invasion events into the same habitat – the interstitial environment. The fact that a number of 'floating' genera (e.g. *Syrticola* WILLEMS & CLAEYS) could not be satisfactorily allocated to any of the four subfamilies (the highest number in any harpacticoid family) has added to the confusion and indicates that the current subfamily concept is no longer tenable.

With the possible exception of the Leptopontiinae (HUYS & OHTSUKA 1993) all other subfamilies represent natural lineages which have successfully invaded the interstices of marine sands independently. The Leptastacinae, recently upgraded to full family rank (HUYS 1992), is perhaps the most speciose group. They are characteristic of high energy beaches world-wide though many species inhabit sandy sublittoral sediments. As a result of the North Sea Benthos Survey (NSBS), HUYS & al. (1992) found (a) that a constant relationship between the distribution of the Leptastacidae and the actual grain size of the sand fraction or the amount of silt did not exist, and (b) that the Leptastacidae were the only interstitial copepods whose distribution extended into the Central North Sea where finer sediments prevail. HUYS & al. (1992) suggested that the unique feeding biology partly based on mucus trap feeding probably represented the underlying reason for this unexpected distribution pattern. The Cylindropsyllinae differ in all these aspects: they are genuinely interstitial with the exception of a few species that inhabit abyssal muds (BECKER 1979), their feeding appendages are designed for rasping diatoms from sand grains rather than for manipulating a mucilage food bolus, and, body size and distribution are to a large extent correlated with the size of the interstices of the sediment. Hence, in the course of the NSBS Cylindropsyllinae were only

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recorded from clean sandy deposits in the south of the North Sea and were therefore regarded as an indicator group for the Southern Bight community (TWIN A in HUYS & al. 1992).

Leptastacidae and Cylindropsyllinae are also clearly different phylogenetically, however, a detailed analysis of the generic relationships of the latter group is severely hampered by the lack of morphological detail in the majority of the species descriptions. Revisions of *Cylindropsyllus* BRADY and *Cylinula* COULL were already published elsewhere (HUYS 1988; HUYS & WILLEMS 1993), however, a critical revision of the other genera, in particular the genus *Stenocaris* SARS, remains vital before such an analysis can be undertaken. This paper redescribes *Boreopontia heipi* WILLEMS, 1981, the type and only species of the genus, and presents a full description of a new genus and species, *Willemsia calceola,* also collected from the Southern Bight of the North Sea.

MATERIAL AND METHODS

Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, England).

All drawings have been prepared using a camera lucida on a Leitz Diaplan or Dialux 20 microscope equipped with differential interference contrast.

The descriptive terminology applied to segmentation and setation of body appendages is adopted from HUYS & BOXSHALL (1991). Abbreviations used in the text and figures are: P1–P6; first to sixth thoracopods; exp., exopod; exp(enp)–1(-2, -3), to denote the proximal (middle, distal) segment of a ramus.

The type series of *Willemsia calceola* gen. et sp. n. and specimens of *Boreopontia heipi* are deposited in the collections of the Natural History Museum, London (BMNH).

SYSTEMATICS

Family Cylindropsyllidae G.O. SARS, 1909

Boreopontia WILLEMS, 1981

Diagnosis (amended). Cylindropsyllidae. Body slender, cylindrical and vermiform. Rostrum triangular, defined at base. Antennule 7-segmented and with aesthetasc on segment 4 in ♀; 9-segmented, haplocer and with aesthetasc on segment 5 in ♂. Antenna with allobasis and bisetose 1-segmented exopod. Mandible with 2-segmented, uniramous palp bearing 1 lateral seta on basis and 5 setae on endopod. Maxillule with 2 setae on coxa, 5 setae plus 1 claw on basis, 3 setae on endopod and 2 setae on exopod. Maxillary endopod discrete. Maxillipeds subschelate, syncoxa with 1 seta, endopod represented by geniculate claw. P1–P4 with 3-

segmented exopods and 1- (P3) or 2-segmented (P1, P2, P4) endopods. P1 exopod without outer spine on middle segment and 3 geniculate setae plus 1 spine on distal segment; endopod not prehensile, proximal segment about as long as distal, with inner seta, distal segment with setule and 2 geniculate setae. Armature formula of swimming legs:

	coxa	basis	exopod segment			endopod segment	
			1	2	3	1	2
P1	0–0	1–1	I–0;	0–0;	I1,1,1	0–1;	1,1,1
P2	0–0	I–0	I–0;	I–0;	I,I,I	0–1;	0,I,0
P3	0–0	1–0	I–0;	I–0;	I,II,1	0,I,0	
P4	0–0	1–0	I–0;	I–0;	I,I1,1	0–0;	0,I,1

P5 baseoendopod and exopod fused, forming triangular plate in both sexes; with 7 setae/spines in ♀, 6 in ♂; distal element a strong spine. P6 asymmetrical in ♂, with 3 setae each; represented by small operculum without armature in ♀. Copulatory pore large, midventral, at about level of gonopores.

Sexual dimorphism in antennule, P2 basis (with hook-shaped process at inner corner) and exopod (inner spine of distal segment transformed into slender claw), P3 endopod (indistinctly 2-segmented; proximal segment minute, with short, barbed apophysis; apical spine of distal segment reduced in size), P5, P6 and in genital segmentation.

Caudal ramus 3–4 times longer than wide; with dorsally recurved, spinous process in distal third; with 7 setae, seta I diminutive; seta V with defined flexure zone between proximal styliform and distal flagellate parts, fused to vestigial seta IV.

Type and only species. *Boreopontia heipi* WILLEMS, 1981.

Boreopontia heipi WILLEMS, 1981

WILLEMS' (1981) description was based on specimens (originally referred to as *Arenopontia* sp. A in WILLEMS & al. (1982)) from the Kwinte Bank, one of the Flemish Banks situated in a southwest-northeastern direction off the Belgian coast. With the exception of a single record by BODIN (1984) from the Bay of Douarnenez (Finistère), the species has not been reported again in the published literature since its original description. Compilation of the unpublished data (Table 1) contained in the numerous Government Reports and other grey literature published by the Marine Biology Section (University of Gent) during the 1980s and early 1990s revealed that *B. heipi* is relatively common in clean, well sorted, coarse sandy sediments and

Table 1. Distribution records of *Boreopontia heipi* and *Willemsia calceola*.

Boreopontia heipi

Station	Latitude (N)	Longitude (E)	Date	Depth (m)	Specimens
1	51°15′00″	1°30′00″	8 Apr 86	12.6	4 ♀♀, 2 ♂♂
2	51°15′00″	2°30′00″	2 Apr 86	18.0	2 ♀♀
3	51°30′00″	2°00′00″	8 Apr 86	14.1	1 ♀, 3 ♂♂
4	51°30′00″	3°00′00″	1 Apr 86	18.7	2 ♀♀
5	51°43′06″	3°06′15″	30 Mar 92	32.8	7 ♀♀, 3 ♂♂
6	51°43′06″	3°06′49″	7 May 91	32.9	6 ♀♀, 1 ♂
7	51°45′00″	2°30′00″	29 Apr 86	36.5	3 ♀♀, 3 ♂♂
8	51°45′00″	3°30′00″	17 Apr 86	14.0	19 ♀♀, 14 ♂♂, 13 cop.
9	51°57′24″	2°40′57″	30 Mar 92	42.7	4 ♂♂
10	51°57′25″	2°40′45″	8 May 91	44.5	5 ♀♀, 4 ♂♂
11	52°00′00″	3°30′00″	29 Apr 86	40.8	4 ♀♀, 1 ♂
12	52°02′30″	3°25′00″	24 Jun 87	37.2	2 ♀♀, 1 ♂
13	52°15′00″	2°30′00″	18 Apr 86	29.9	3 ♂♂
14	52°28′48″	3°47′12″	31 Mar 92	30.4	2 ♀♀
15	52°30′00″	2°00′00″	8 Apr 86	14.3	1 ♀
16	52°30′00″	4°00′00″	2 May 86	24.6	4 ♀♀, 1 ♂
17	52°34′10″	3°31′53″	26 Apr 91	32.5	5 ♀♀, 1 ♂
18	53°34′11″	3°31′53″	31 Mar 92	31.3	9 ♀♀, 2 ♂♂
19	53°00′00″	2°00′00″	19 Apr 86	22.3	2 ♀♀, 1 ♂
20	53°00′00″	3°00′00″	19 Apr 86	49.1	7 ♀♀, 3 ♂♂, 6 cop.

Willemsia calceola

Station	Latitude (N)	Longitude (E)	Date	Depth (m)	Specimens
4	51°30′00″	3°00′00″	1 Apr 86	18.7	3 ♀♀, 1 ♂
5	51°43′06″	3°06′15″	30 Mar 92	32.8	1 ♀, 1 ♂
6	51°43′06″	3°06′49″	7 May 91	32.9	6 ♀♀, 5 ♂♂
9	51°57′24″	2°40′57″	30 Mar 92	42.7	5 ♀♀
10	51°57′25″	2°40′45″	8 May 91	44.5	10 ♀♀
11	52°00′00″	3°00′00″	29 Apr 86	40.8	4 ♀♀
13	52°15′00″	2°30′00″	18 Apr 86	29.9	3 ♀♀, 2 ♂♂
16	52°30′00″	4°00′00″	2 May 86	24.6	3 ♂♂
21	52°30′00″	3°00′00″	29 Apr 86	48.1	2 ♀♀, 3 ♂♂
22	52°45′00″	3°30′00″	17 Apr 86	43.2	2 ♀♀, 1 ♂
23	52°59′53″	3°55′01″	31 Mar 92	17.0	2 ♀♀
24	53°42′05″	4°30′00″	28 May 91	37.0	5 ♀♀

is distributed throughout the Southern Bight of the North Sea, roughly demarcated in the north at 53.5° N (Fig. 1).

Material examined. See Table 1; 10 ♀♀ and 10 ♂♂ collected during North Sea Benthos Survey at Stn 8 (51°45′00″ N 03°30′00″ E), 17 April 1986, 14.0 m depth are deposited under reg. nos 1993.3398–3407.

Redescription

Female (Figs 3; 4A, E, F; 5–6; 8A–C; 16A–C)

Total body length from the tip of the rostrum to the posterior margin of the caudal rami: 525–710 μm (n = 15; x̄ = 605 μm). Body slender, cylindrical (Fig. 3A, B), transparent; no distinct separation between prosome and urosome. Genital double-somite completely fused, original segmentation marked by small internal ribs dorsolaterally, and paired dorsal sensillae (Fig. 3A). Anal somite 1.8 times as long as wide (75 × 40 μm), with 2 pairs of large pores ventrolaterally. Anal operculum weakly developed, unarmed. Caudal ramus (Fig. 16A–C) about 3.6 times as long as average width (measured in dorsal aspect), slightly tapering distally; dorsal surface with distinct chitinous spur in distal third, slightly bent outwards, anterior face membranous; with 7 setae (seta I diminutive) in distal quarter and 3 secretory pores; seta VII triarticulate at base and located immediately posterior to spur; seta III displaced to dorsal rear margin; seta V long, with distinct flexure zone between styliform part and long distal flagellate part, fused at base with vestigal seta IV.

Rostrum triangular (Figs 3A; 4B), about as long as first antennulary segment; demarcated at base; base surrounded by area of flexible integument, with 2 long sensillae; median pore positioned ventrally near apex of rostrum.
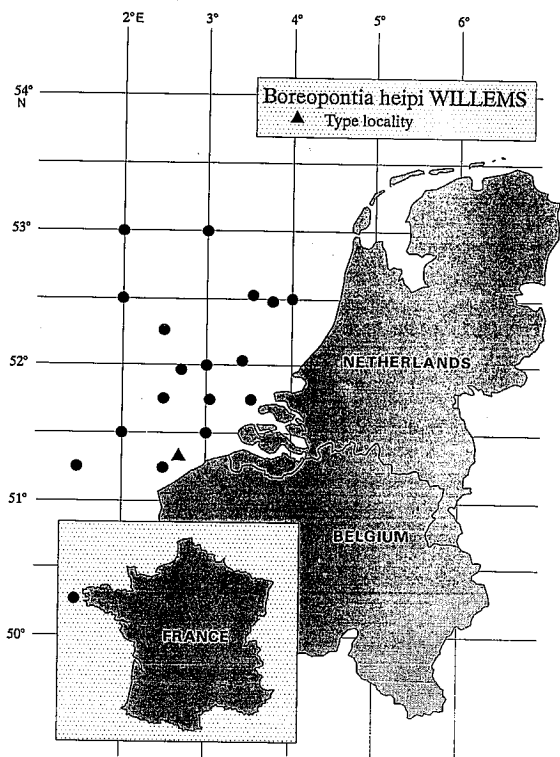
Fig. 1. Compilation of distribution records of *Boreopontia heipi* WILLEMS, 1981.

Fig. 2. Compilation of distribution records of *Willemsia calceola* gen. et sp. n.

Antennule 7-segmented (Fig. 4A). Segment 1 without spinular rows; segment 2 longest, with secretory pore; segment 4 with distal cylindrical process bearing large aesthetasc (80 μm). Armature formula: 1–[1], 2–[7 + 1 pinnate], 3–[4], 4–[2 + ae], 5–[1], 6–[2], 7–[7 + trithek]. Apical trithek consisting of 2 long setae and 1 vestigial process (probably representing aesthetasc).

Antenna (Fig. 4E, F) with small unarmed coxa; basis and first endopod segment fused to form allobasis, abexopodal margin without ornamentation; exopod a narrow segment, with 2 apical, pinnate setae; endopod with 2 lateral spines and distal armature consisting of 2 bipinnate spines, 2 geniculate setae and 1 large geniculate spine bearing spinules at about mid-margin and fused at base with vestigal seta.

Labrum (arrowed in Fig. 5A) a well developed, ventrally produced extension; distal margin with short, blunt spinules (see *Cylindropsyllus*; HUYS 1988).

Mandible (Fig. 5B).Gnathobase well developed; uniramous palp, consisting of basis and 1-segmented endopod; basis with 1 lateral, pinnate seta; endopod with 1 outer, 2 inner (basally fused) and 2 apical (basally fused) setae.
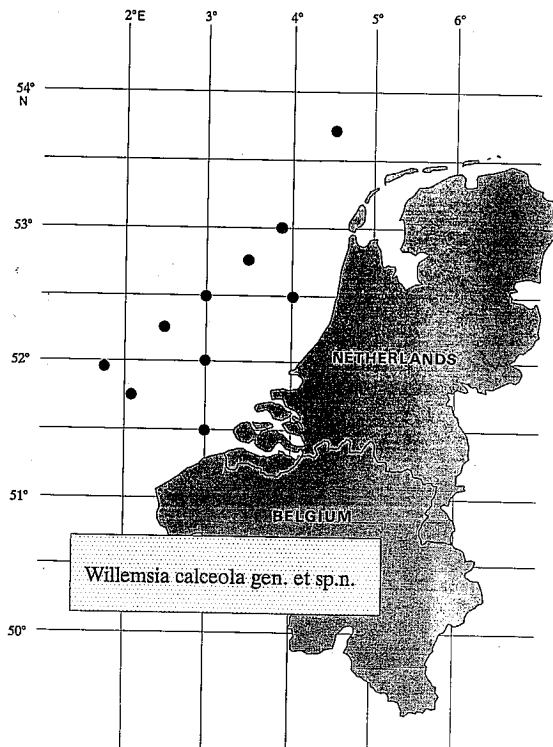
Maxillule (Fig. 5C). Praecoxal arthrite with 10 spines/setae around distal margin and 1 tubular seta on anterior surface. Coxal endite with 1 geniculate claw and 1 seta. Basis and rami fused into elongate palp; basal armature represented by inner seta, apical geniculate claw, and 4 outer setae fused in 2 clusters. Endopod represented by 3 setae, exopod by 2 small setae.

Maxilla (Fig. 5D). Syncoxa with 2 endites, proximal endite with 2 articulating setae and 1 spine fused to endite, distal endite with 1 claw and 2 setae, all articulating and pinnate. Allobasis drawn out into a claw-like pinnate endite armed with 2 additional setae. Endopod a discrete segment with 3 long setae, 1 being pinnate.

Maxilliped (Fig. 5E) small, subchelate, directed inwards. Syncoxa well developed, with 1 pinnate seta. Basis elongate, unarmed. Endopod represented by pinnate claw with distinct flexure zone at about half its length.

Swimming legs P1–P4 (Fig. 6A–D). Length of legs increasing in antero-posterior direction. Intercoxal sclerites minute. Praecoxae well developed. All protopodal segments without ornamentation but bases with outer seta. Exopods 3-segmented, endo-
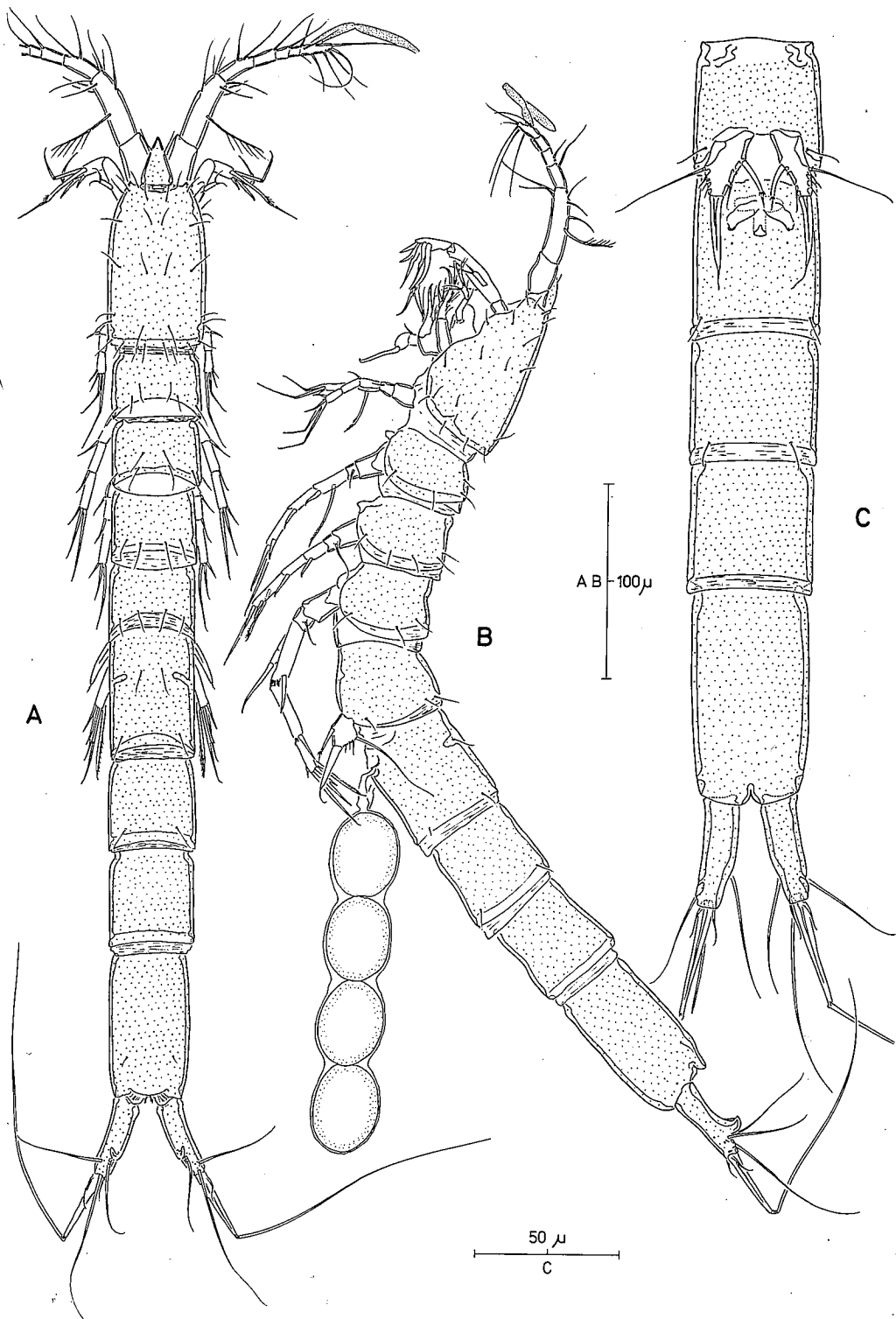
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Fig. 3. *Borepontia heipi* WILLEMS, 1981. Female. A. Habitus, dorsal. B. Habitus, lateral. C. Urosome, ventral.
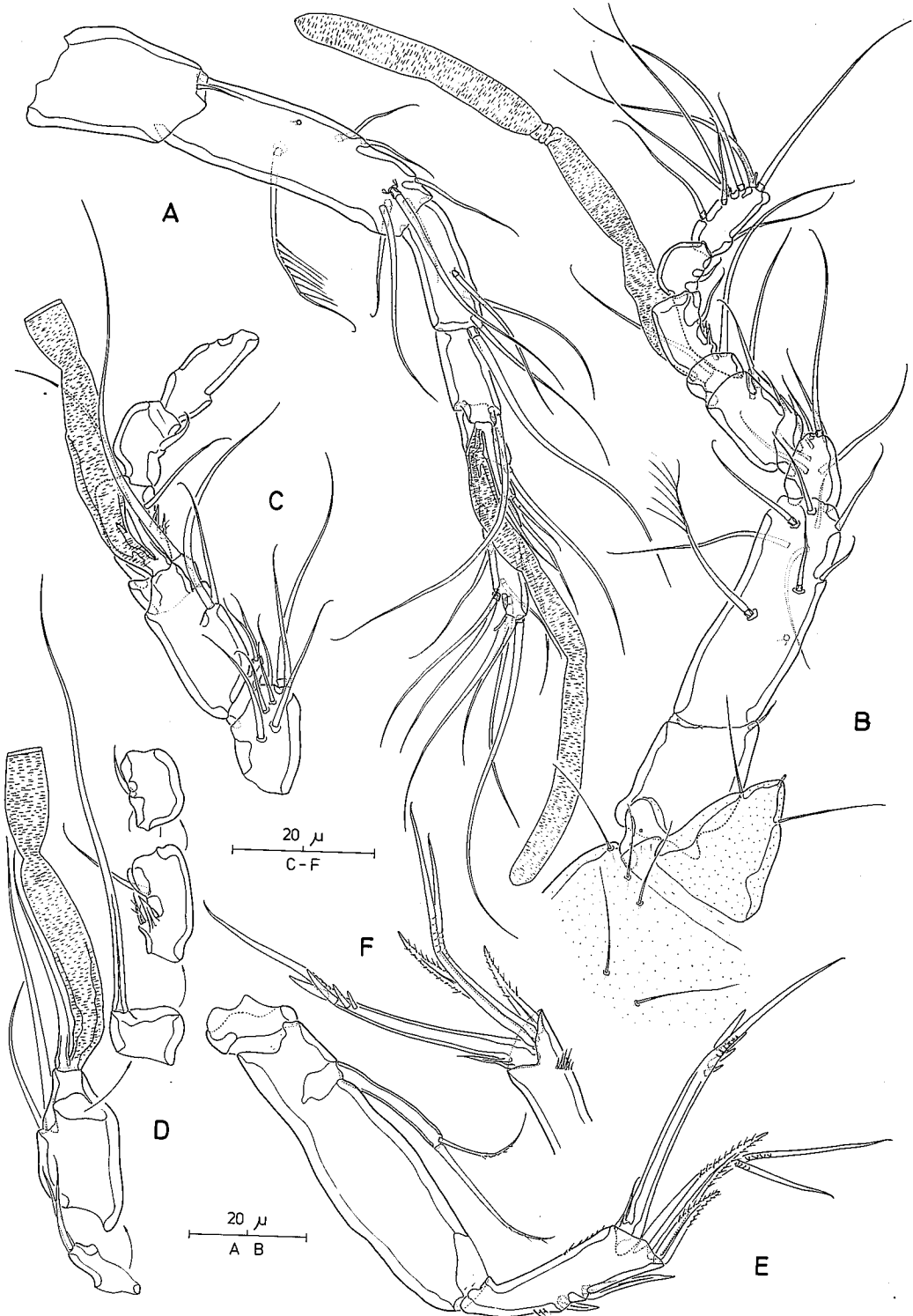
Fig. 4. *Boreopontia heipi* WILLEMS, 1981. Female. A. Antennule. B. Rostrum and antennule, dorsal. C. Antennulary segments 3–9, ventral. D. Antennulary segments 4–8, disarticulated, ventral. E. Antenna, ventral. F. Distal part of antennary endopod, dorsal. Male.

Fig. 5. *Boreopontia heipi* WILLEMS, 1981. Female. A. Cephalothorax, lateral (distal segments of antennule and P1 omitted; labrum arrowed). B. Mandible. C. Maxillule. D. Maxilla. E. Maxilliped.
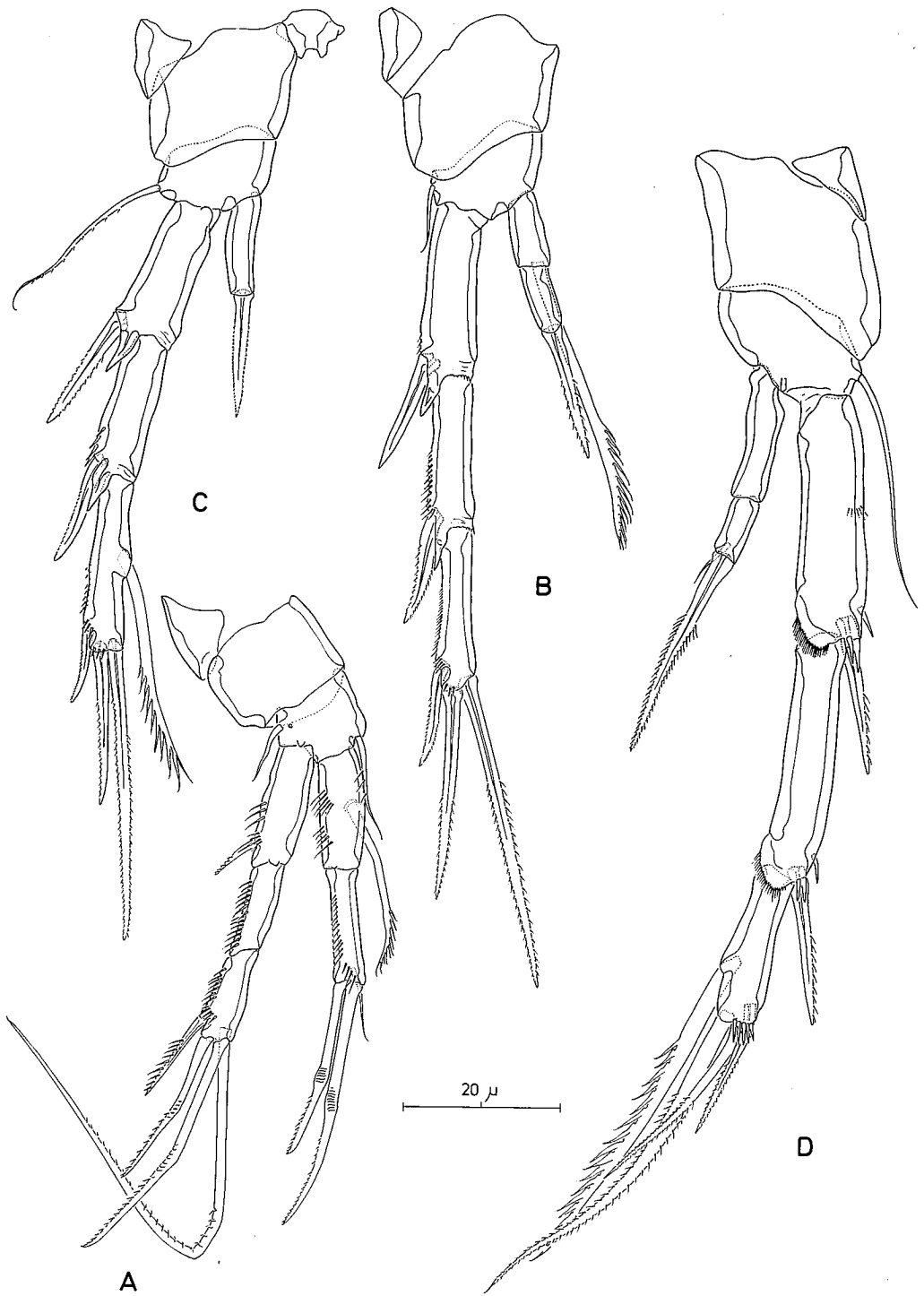
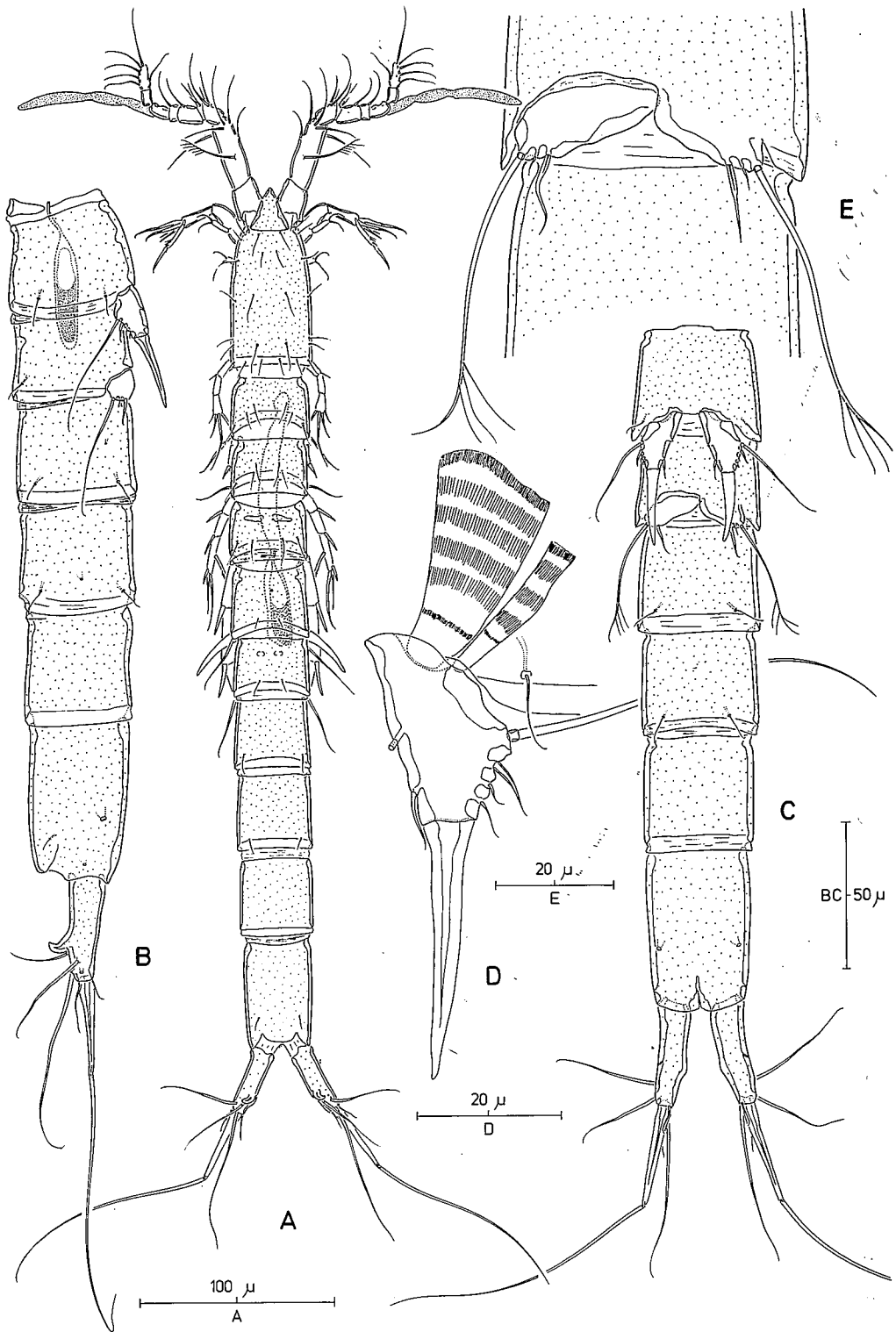Fig. 6. *Boreopontia heipi* WILLEMS, 1981. Female. A. P1. B. P2. C. P3. D. P4.

Fig. 7. *Boreopontia heipi* WILLEMS, 1981. Male. A. Habitus, dorsal. B. Urosome, lateral. C. Same, ventral. D. P5. E. Sixth pair of legs.
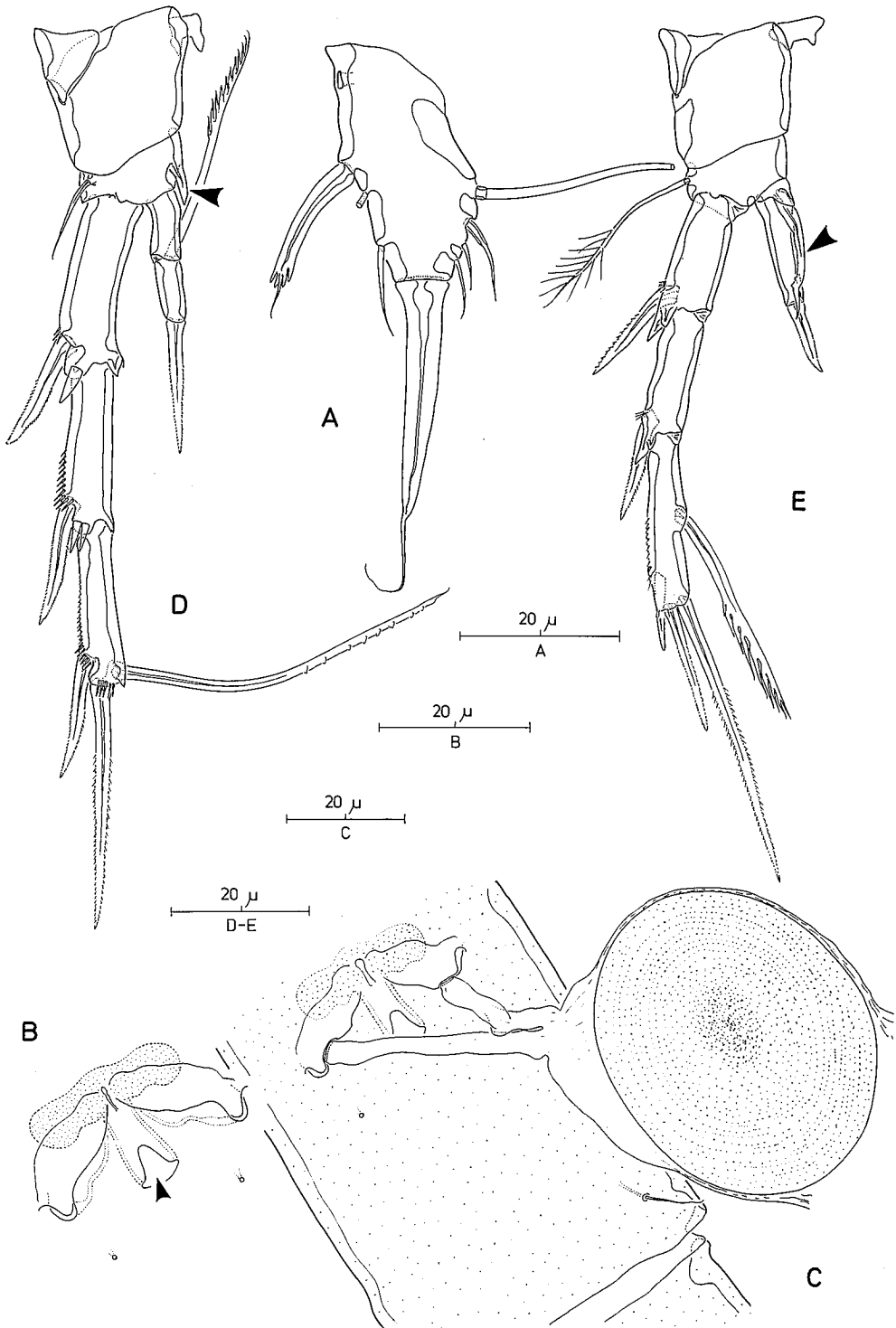
Fig. 8. *Boreopontia heipi* WILLEMS, 1981. Female. A. P5. B. Genital field (copulatory pore arrowed). C. Genital field of ovigerous female showing attachment sites of egg-sac. Male. D. P2 anterior (basal spinous process arrowed). E. P3, anterior (apophysis arrowed).

pods 1- (P3) or 2-segmented (P1, P2, P4). P1 basis with outer seta naked and inner seta pinnate. P1 exopod without outer spine on middle segment. P1 endopod not prehensile, distinctly shorter than exopod; proximal segment only slightly longer than distal one; with serrate inner seta; distal segment with subdistal setule, and 2 geniculate setae distally. Seta and spine formulae as for genus.

Fifth pair of legs (Figs 3C; 8A) not fused medially, no distinct intercoxal sclerite. Baseoendopod and exopod fused into commom elongate plate, tapering distally; apex with strong, articulate spine, about as long as the plate and with flagellate tip; outer margin with 3 small setae and long plumose seta derived from baseoendopod; inner margin with 2 secretory pores, 1 small seta and 1 strong spine with modified tip.

Sixth legs (Fig. 8B, C) represented each by small operculum closing off gonopore; no armature discernible. Genital apertures not fused medially; copulatory pore large at about level of gonopores; leading via short chitinized copulatory duct to paired seminal receptacles positioned anterior to genital apertures; copulatory pore flanked by 2 small secretory pores.

Single egg-sac (Figs 3B; 8C) containing 4 or 6 eggs arranged in uniserial way, enclosed in common egg-sac membrane; egg-sac connected with each genital aperture via transparent string.

Male (Figs 4B–D; 7; 8D, E)

Body length 460–575 μm (n = 15; $\bar{x}$ = 535 μm) measured from tip of rostrum to posterior margin of caudal rami. Spermatophore 50 μm long (Fig. 7B).

Antennule (Fig. 4B–D) distinctly 9-segmented; geniculation between segments 7 and 8; segment 1 with 1 minute seta, posterior margin forming bulbous extension partly covered dorsally by small sclerite bearing minute pore (Figs 4B; 5A); segment 2 longest, with 1 plumose and 8 naked setae; segment 3 with 7 setae; segment 4 diminutive, with 2 short setae; segment 5 not distinctly swollen, with 2 setae along the anterior margin and with distal cylindrical process bearing basally fused seta and large, constricted aesthetasc (95 μm); segment 6 with 1 long seta; segment 7 with 1 seta, 1 spinous process (modified seta) and 1 small pinnate spine; segment 8 with 1 small seta; segment 9 with 5 posterior setae, 1 anterior seta and 1 seta plus a trithek apically.

P2 (Fig. 8D) with modified basis and exopod. Inner margin of basis forming a distinct spinous process on the anterior surface. Inner distal spine of exp-3 modified into slender claw; directed medi-

ally and posteriorly; distal half barbed and tapering to a fine tip.

P3 endopod (Fig. 8E) indistinctly 2-segmented; enp-1 small, with short sigmoid apophysis arising from the anterior surface: enp-2 as in the female except for distal spine which is distinctly shorter.

Fifth legs (Fig. 7C–D) not fused medially, no distinct intercoxal sclerite. Baseoendopod and exopod fused into a common elongate plate, tapering distally; apex with strong, articulate spine, about 1.5 times as long as the segment; without flagellate tip; outer margin with 3 small setae and long plumose seta derived from baseoendopod; inner margin with 1 secretory pore and 1 small seta.

Sixth pair of legs (Fig. 7C, E) asymmetrical, with 3 setae each: outer one plumose and longest, middle one vestigal. Left or right leg articulating according to sinistral or dextral development of testis and vas deferens.

Variability. Except for body size no variability was encountered in the material under study.

Willemsia gen. nov.

Diagnosis. Cylindropsyllidae. Body slender, cylindrical and vermiform. Rostrum triangular, defined at base, with long apical tube pore. Antennule 7-segmented and with aesthetasc on segment 4 in $\female$; indistinctly 9-segmented, haplocer and with aesthetasc on segment 5 in $\male$. Antenna with allobasis and bisetose 1-segmented exopod. Mandibular palp 1-segmented, small. Maxillule with 2 setae on coxa, 4 setae plus 1 claw on basis, 2 setae on endopod and 1 seta on exopod. Maxillary endopod incorporated into allobasis. Maxillipeds subchelate, syncoxa with 1 seta, endopod represented by serrate geniculate claw. P1–P4 with 3-segmented exopods and 1-(P2, P3) or 2-segmented (P1, P4) endopods. P1 exopod with outer spine on middle segment and 1 simple seta, 2 geniculate setae plus 1 spine on distal segment; endopod not prehensile, proximal segment slightly shorter than distal, with inner seta, distal segment with setule and 2 geniculate setae. P2–P3 small, with abbreviated exopods and minute endopods. Armature formula of swimming legs:

	coxa	basis	exopod segment			endopod segment	
			1	2	3	1	2
P1	0–0	0–1	I–0;	I–0;	I1,1,1	0–1;	1,1,1
P2	0–0	0–0	I–0;	I–0;	I,I,I	0,1,0	
P3	0–0	1–0	I–0;	0–0;	I,I,I	0,1,0	
P4	0–0	1–0	I–0;	I–0;	I,I1,1	0–0;	1,I,0

P5 baseoendopod and exopod fused, forming bilobate plate with inner foot-shaped process; with 5 setae/spines in both sexes; no distinct sexual dimorphism. P6 asymmetrical in ♂, with 3 setae each; represented by small operculum without armature in ♀. Copulatory pore lying within genital aperture, concealed beneath the lobe of the genital operculum. Seminal receptacles subdivided in two chambers.

Sexual dimorphism in antennule, P2 basis (with hook-shaped process at inner corner), endopod (extra inner setae) and exopod (exp-1 and exp-2 fused into compound segment with inner hyaline appendage, exp-3 with outer and distal spines reduced and inner spine transformed into robust claw), P3 coxa (with complex raised pore), basis (with lobate process near inner margin), endopod (with short distal apophysis) and exopod (exp-2 without outer spine but with inner tuft of long setules, exp-3 with extra seta), P5 (slight), P6 and in genital segmentation.

Caudal ramus slightly swollen, about 3 times longer than wide; with 7 setae, seta I diminutive; seta V long, swollen proximally, fused to vestigial seta IV.

Type and only species. *Willemsia calceola* gen. et sp. n.

Etymology. The genus is named after Dr Kris Willems in recognition of his contributions to harpacticoid taxonomy and ecology. Gender: feminine.

Willemsia calceola gen. et sp.n.

Material examined. See Table 1. Type series (3 ♀♀, 2 ♂♂) taken from Stn 13. Holotype ♀ dissected and mounted on 6 slides (reg. no. 1993.3393), paratypes (2 ♀♀ and 1 ♂ in alcohol, 1 ♂ dissected and mounted on 5 slides) deposited under reg. nos 1993.3394–3397.

Distribution. *W. calceola* seems to be restricted to the shallow coastal areas of Belgium and The Netherlands (Fig. 2), particularly to localities where the median grain size of the sand fraction exceeds 250 μm. Sandy samples collected at the Dogger Bank and in the German Bight during the North Sea Benthos Survey did not contain any specimens of *W. calceola*.

Description

Female (Figs 9A, B; 10A; 11–13; 15D)
Total body length from the tip of the rostrum to the posterior margin of the caudal rami: 480–485 μm (n = 2). Body slender, cylindrical (Fig. 9A, B), transparent; no distinct separation between prosome and urosome, all somites equally wide. Geni-

tal double-somite completely fused, original segmentation marked by paired dorsal sensillae only (Fig. 9B). Anal somite 2.2 times as long as wide (80 × 36 μm). Anal operculum well developed, rounded, unarmed. Caudal ramus (Fig. 13D–F) about 2.8 times as long as maximum width (measured in dorsal aspect); moderately bulbous in lateral aspect (2.2 times as long as maximum width), distinctly tapering proximally; with 7 setae (seta I diminutive) and 4 secretory pores; seta VII triarticulate at base and located near inner margin in anterior half of ramus; seta III not displaced; seta V long (about 340 μm), without distinct flexure zone but slightly swollen proximally, fused at base with vestigal seta IV.

Rostrum triangular (Figs 9B; 10A, B), shorter than first antennulary segment, wider than long; demarcated at base; with 2 sensillae and very long median tube pore arising from apex of rostrum.

Antennule 7-segmented (Fig. 10A), base surrounded by small sclerite at outer corner. Segment 1 without spinular rows; segment 2 longest, with ventral secretory pore; segment 4 with small cylindrical process distally bearing large aesthetasc (38 μm). Armature formula: 1-[1], 2-[7+1 pinnate], 3-[4], 4-[2+ae], 5-[1], 6-[2], 7-[7+trithek]. Apical trithek consisting of 2 long setae and 1 aesthetasc (16 μm).

Antenna (Fig. 11A) with small unarmed coxa; basis and first endopod segment fused to form allobasis, abexopodal margin without ornamentation but with furrow indicating original segmentation; exopod a narrow segment, with 2 apical, naked setae; endopod relatively short, with 2 lateral spines and distal armature consisting of 2 pinnate spines, 2 geniculate setae and 1 large geniculate seta bearing spinules at about mid-margin and fused at base with vestigial seta.

Labrum (Fig. 11B) a well developed, ventrally produced extension; distal margin serrate medially and with short, blunt spinules laterally.

Mandible (Fig. 11B, C). Gnathobase well developed, with several teeth and 1 dorsal seta; uniramous, 1-segmented palp; with 1 short outer and 2 long inner setae.

Paragnaths (Fig. 11B) well developed lobate structures; each with 2 serrate, non-articulating blades medially.

Maxillule (Fig. 11D). Praecoxal arthrite with 9 spines/setae around distal margin and 1 tubular seta on anterior surface. Coxal endite with 1 pinnate claw and 1 seta. Basis and rami fused into palp; basal armature represented by outer seta and 3 setae plus a pinnate spine apically. Endopod represented by 2 setae, exopod by 1 seta.
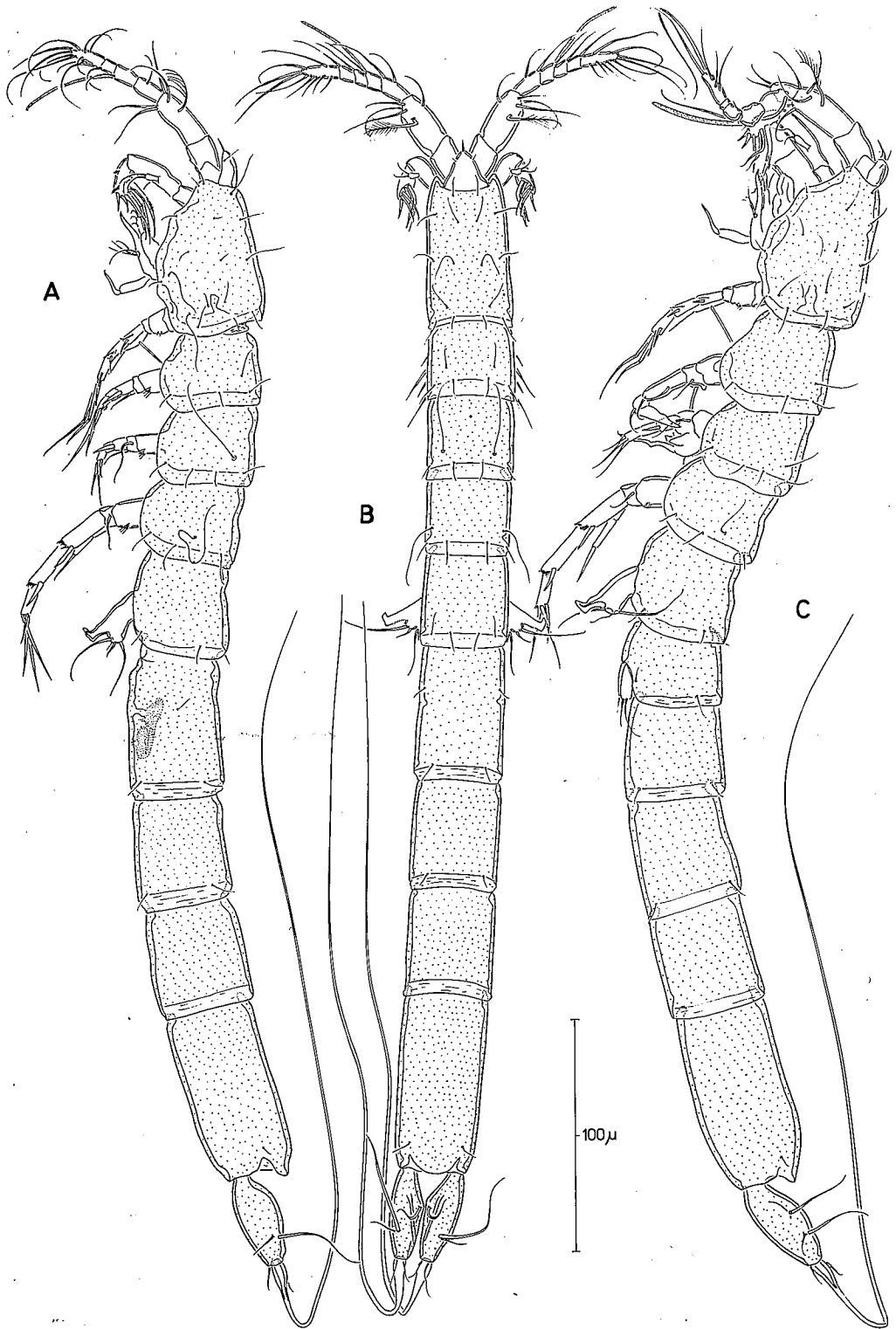
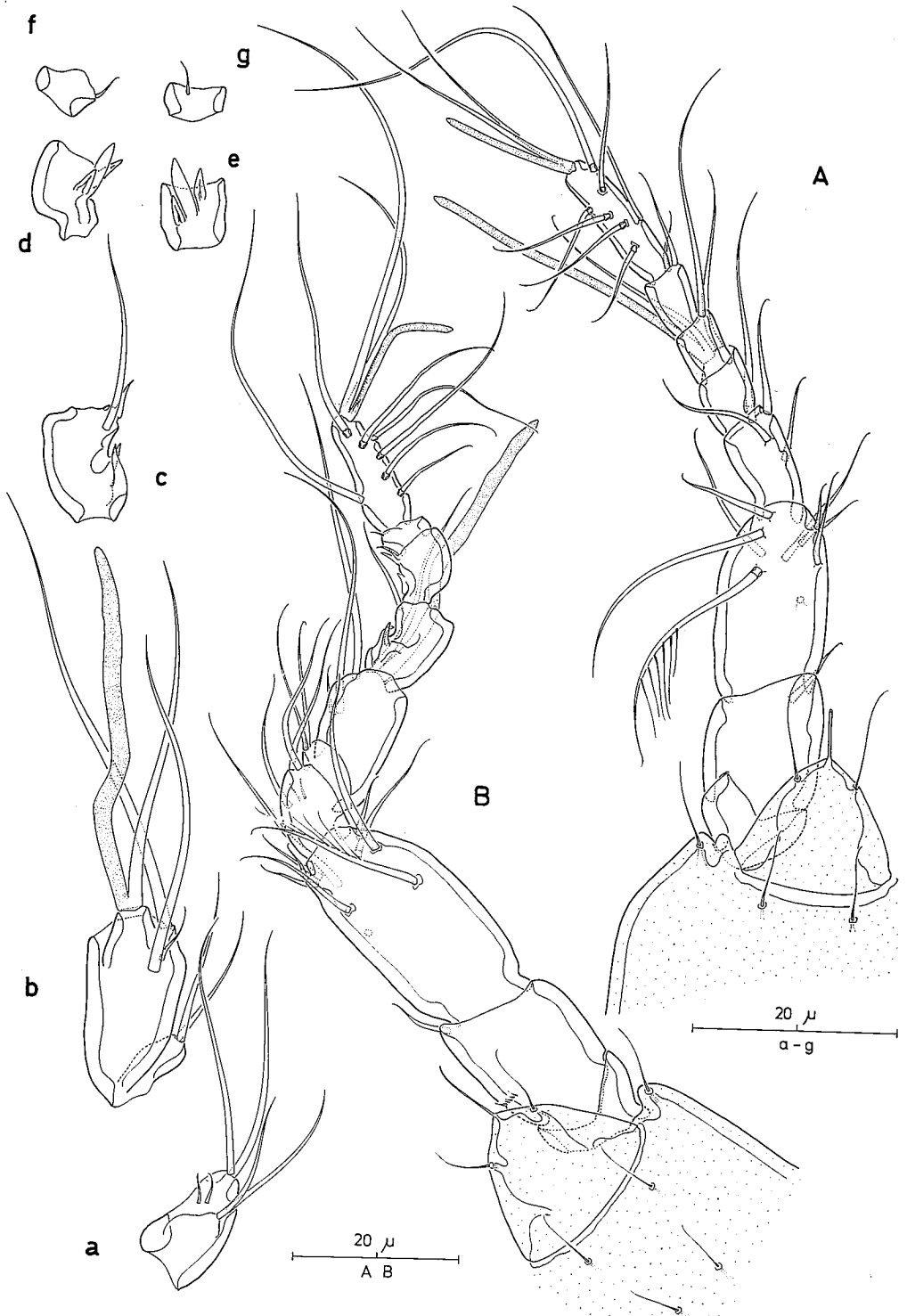Fig. 9. *Willemsia calceola* gen. et sp. n. Female. A. Habitus, lateral. B. Habitus, dorsal. Male. C. Habitus lateral.

Fig. 10. *Willemsia calceola* gen. et sp. n. Female. A. Rostrum and antennule, dorsal. Male. B. Rostrum and antennule, dorsal. a–d and f. Antennulary segments 3–8, ventral. e and g. Antennulary segments 7–8, anterior.
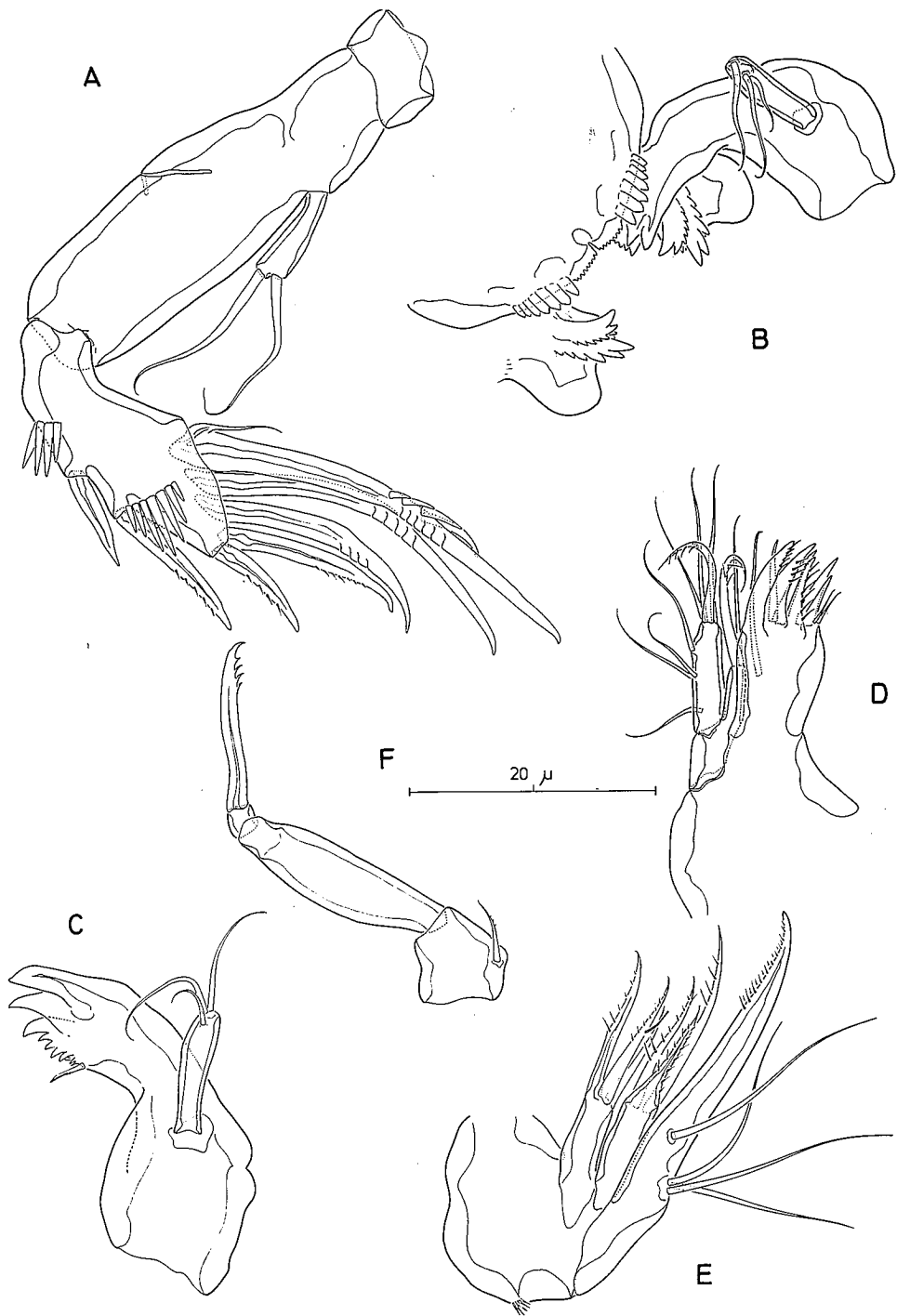
A

B

D

F

| 20 μ |

C

E

Fig. 11. *Willemsia calceola* gen. et sp. n. Female. A. Antenna. B. Labrum, left mandible and para-gnaths. C. Mandible. D. Maxillule. E. Maxilla. F. Maxilliped.
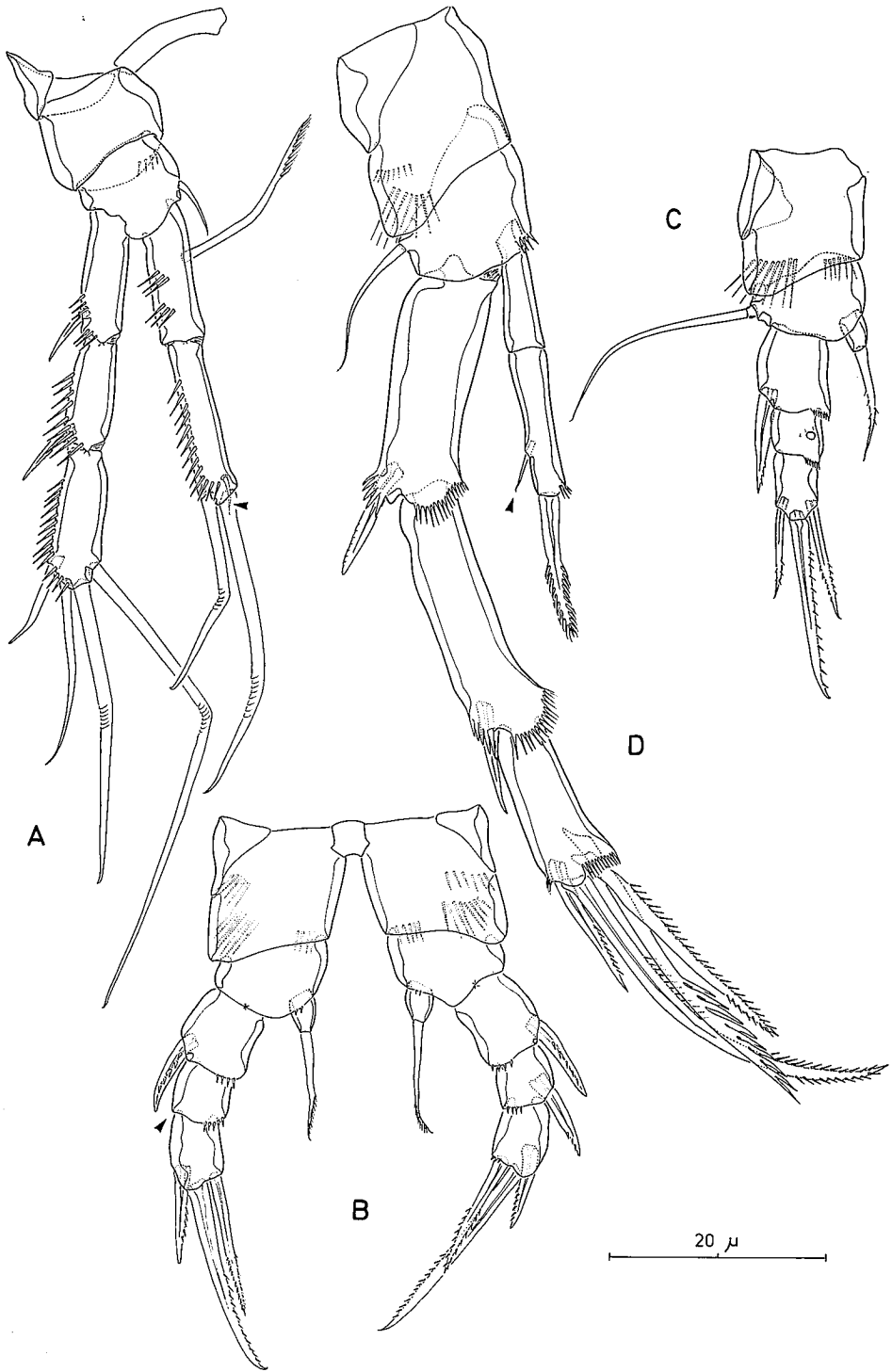
Fig. 12. *Willemsia calceola* gen. et sp. n. Female. A. P1 (minute seta arrowed). B. P2 (missing spine arrowed). C. P3. D. P4 (small seta on endopod arrowed).

Maxilla (Fig. 11E). Syncoxa with 2 endites, both with 2 articulating setae and 1 spine fused to endite. Allobasis drawn out into a claw-like pinnate endite armed with 1 additional seta. Endopod completely incorporated into allobasis; represented by 3 long setae.

Maxilliped (Fig. 11F) small, subchelate, directed inwards. Syncoxa well developed, with 1 pinnate seta. Basis elongate, unarmed. Endopod represented by small segment bearing strong, distally serrate claw.

Swimming legs P1–P4 (Fig. 12A–D). P2–P3 distinctly shorter than other legs. Intercoxal sclerites minute. Praecoxae well developed. Coxae with spinular row(s) on anterior surface. Outer basal seta present in P3–P4 only; P1 basis with inner seta. Exopods 3-segmented, distinctly abbreviated and compact in P2–P3; endopods 1- (P2, P3) or 2-segmented (P1, P4). P1 exopod with outer spine on middle segment, with 2 geniculate setae, 1 simple seta and 1 spine on distal segment. P1 endopod not prehensile, distinctly shorter than exopod; proximal segment only slightly shorter than distal one, with serrate inner seta; distal segment with subdistal setula, and 2 geniculate setae distally. P3 exp-2 without outer spine but with large secretory pore. Seta and spine formulae as for genus.

Fifth pair of legs (Fig. 13A–C) very distinctive, laterally and ventrally directed (Figs 9B, 13A); not fused medially, joined by trapezoid intercoxal sclerite. Entire leg extremely compressed bilaterally (Fig. 13B) with all armature elements being arranged in dorso-ventral sequence (the plumose outer basal seta is the dorsalmost one and appears to be positioned on the inner margin when viewed in ventral aspect: Fig. 13C). Baseoendopod and exopod fused into a common plate; inner (= dorsal) portion produced into foot-shaped apophysis with few spinules on the inner surface; all armature elements are located on a lobate process situated between this apophysis and the outer basal seta. Armature consisting of 4 setae, 2 of which being vestigial and arrowed in Fig. 13B, C. Outer surface with 3 secretory pores (Fig. 13B).

Sixth legs (Fig. 15D) represented each by small operculum closing off gonopore; no armature discernible. Genital apertures not fused medially. Copulatory pore not observed and probably lying within genital aperture, concealed beneath the lobe of the genital operculum. Seminal receptacles large, paired; largely positioned posterior to genital apertures; each consisting of narrow portion ventrally and recurved bulbous chamber dorsally; 2 small secretory pores located near ventral midline at level of genital apertures.

Male (Figs 9C; 10B, a–g; 14; 15A–C)

Body length 505–515 μm (n = 2) measured from tip of rostrum to posterior margin of caudal rami (Fig. 9C).

Antennule (Fig. 10B, a–g) indistinctly 9-segmented; geniculation between segments 6 and 7; segment 1 with 1 minute seta, posterior margin partly covered dorsally by small sclerite; segment 2 longest, with ventral secretory pore, 1 plumose and 8 naked setae; segment 3 (Fig. 10B, a) with 4 long and 2 minute setae; segment 4 diminutive, fused to ventral surface of segment 5 (Fig. 10B, b) but with distinct suture line dorsally (Fig. 10B), with 2 setae; segment 5 not distinctly swollen (Fig. 10B, b), with 3 setae along the anterior margin and with distal cylindrical process bearing basally fused seta and large aesthetasc (35 μm); segment 6 (Fig. 10B, c) with 1 long seta and 3 spinous processes (modified setae); segment 7 (Fig. 10B, d–e) with 3 spinous processes (modified setae); segment 8 (Fig. 10B, f–g) minute, with 1 vestigial seta; segment 9 with 5 posterior setae, 1 anterior seta and 1 seta plus a trithek apically.

P2 (Fig. 14A–C) with basis and coxa fused along the posterior surface (Fig. 14B–C). Basis forming a distinct spinous process on the posterior surface (arrowed in Fig. 14B, C). Exopod robust; proximal segment compound, derived by fusion of exp-1 and exp-2, with 2 outer setae and a hyaline bulbiform element along the inner margin (Fig. 14A); distal segment with inner distal spine modified into strong, naked claw and directed medially and posteriorly (Fig. 14A, B), other armature elements reduced in size compared to ♀. Endopod 1-segmented, with inner serrate seta and apical pinnate seta fused to segment along the posterior surface.

P3 (Fig. 14D–F) strongly modified. Coxa with large raised structure arising from the posterior surface and concealing most of basis and endopod (Fig. 14E, F). Basis with bulbous structure near the inner margin of the anterior surface (Fig. 14D). Exopod 3-segmented; exp-2 without outer spine but with tuft of 'hairs' probably surrounding secretory tube pore; exp-3 elongate, with extra serrate seta at the inner margin. Endopod indistinctly 2-segmented; distal half with inner pinnate seta and with small apical apophysis.

Fifth legs (Fig. 15A, C) largely as in female; foot-shaped process without spinules; long middle seta fused to segment.

Sixth pair of legs (Fig. 15A, B) strongly asymmetrical and slightly overlapping medially; with 3 setae each, outer and inner setae long, middle one vestigal. Both legs articulating.
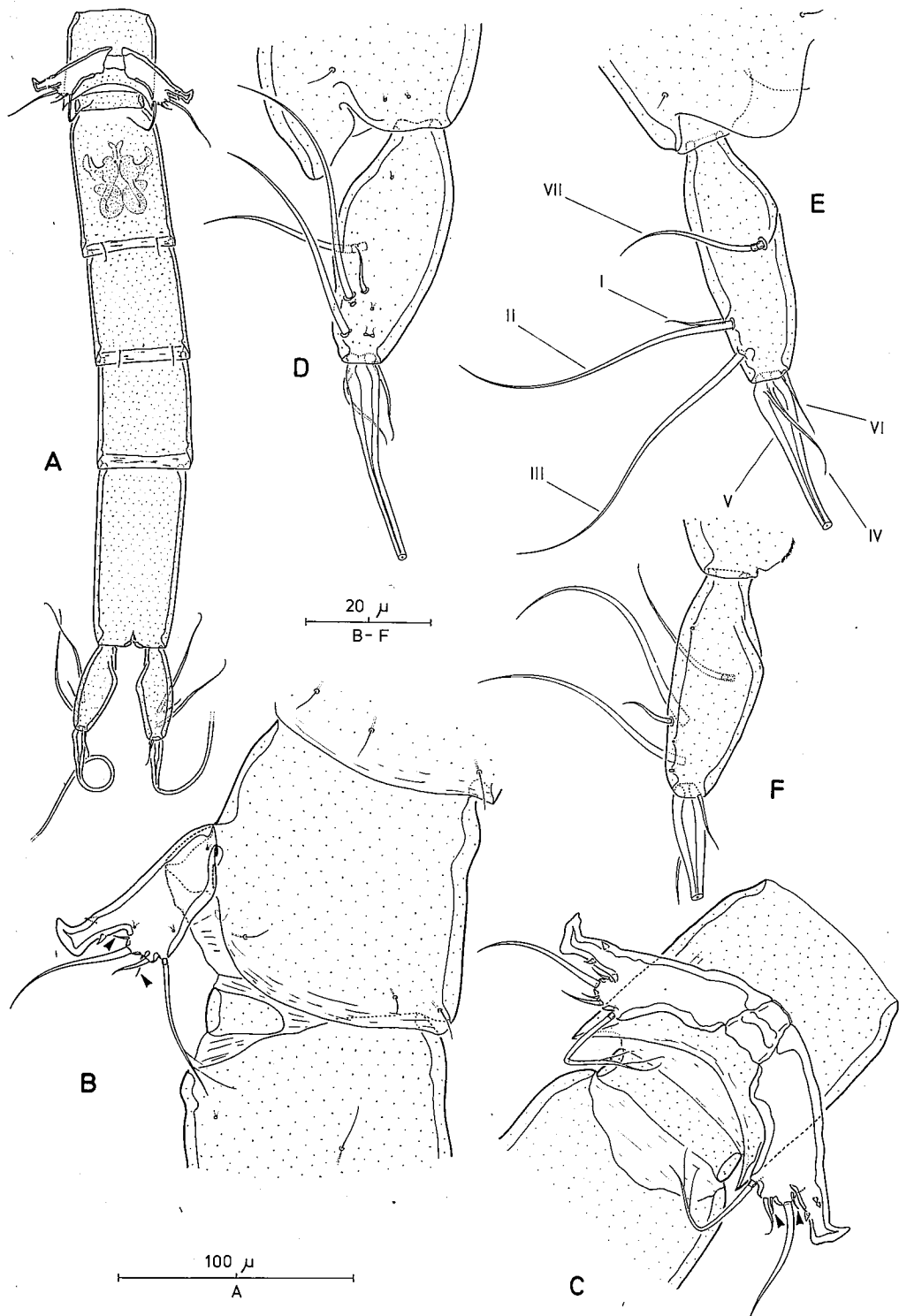
Fig. 13. *Willemsia calceola* gen. et sp. n. Female.   A. Urosome, ventral.   B. P5-bearing somite, lateral (setules on P5 arrowed).   C. Same, ventral.   D. Anal somite and right caudal ramus, lateral.   E. Anal somite and left caudal ramus, dorsal.   F. Right caudal ramus, ventral.
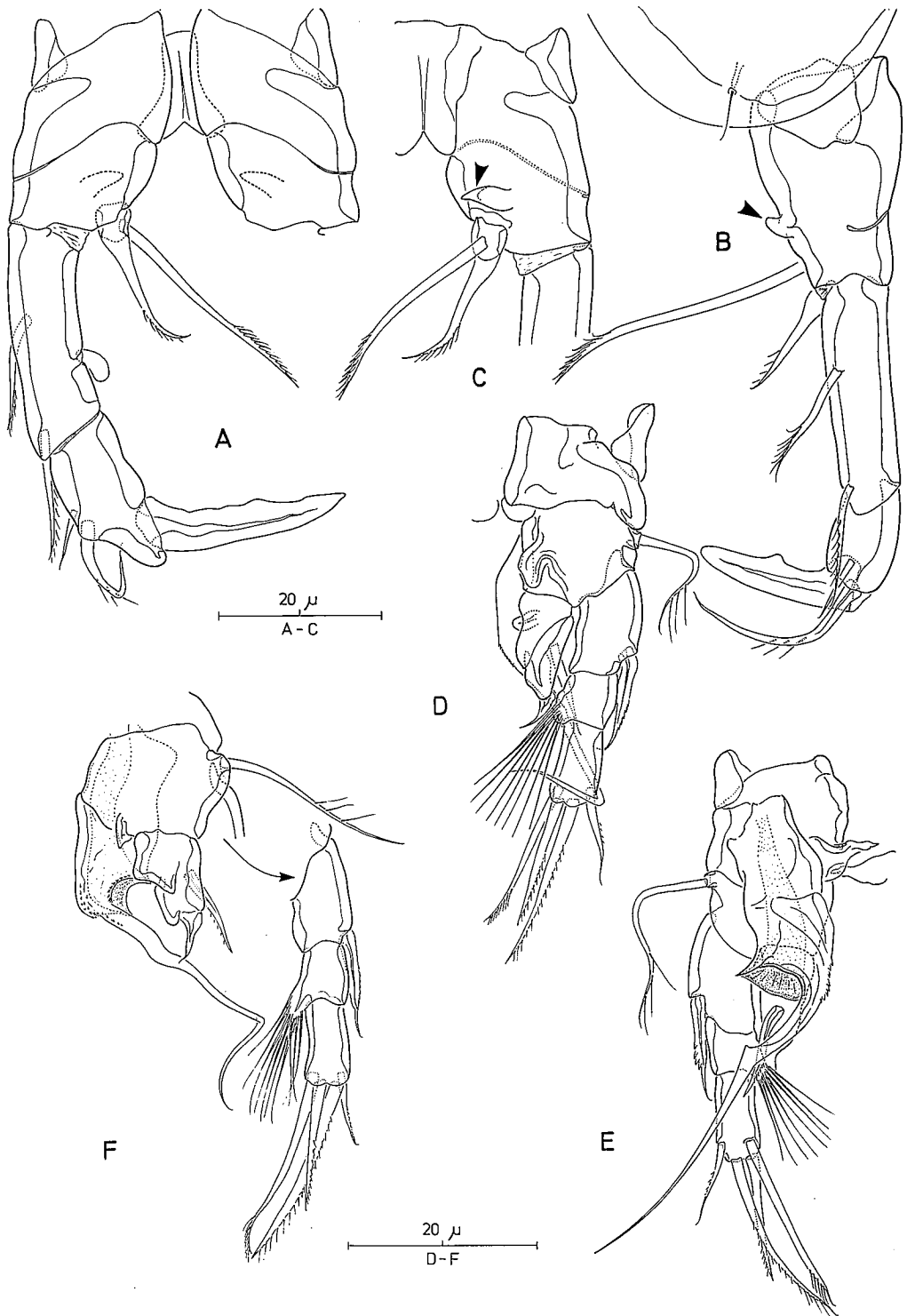
Fig. 14. *Willemsia calceola* gen. et · sp. n. Male. A. P2, posterior. B. P2, lateral (spinous process arrowed). C. P2 protopod, anterior (spinous process arrowed). D. P3, anterior. E. P3, posterior. F. P3, anterior with exopod disarticulated (other specimen).
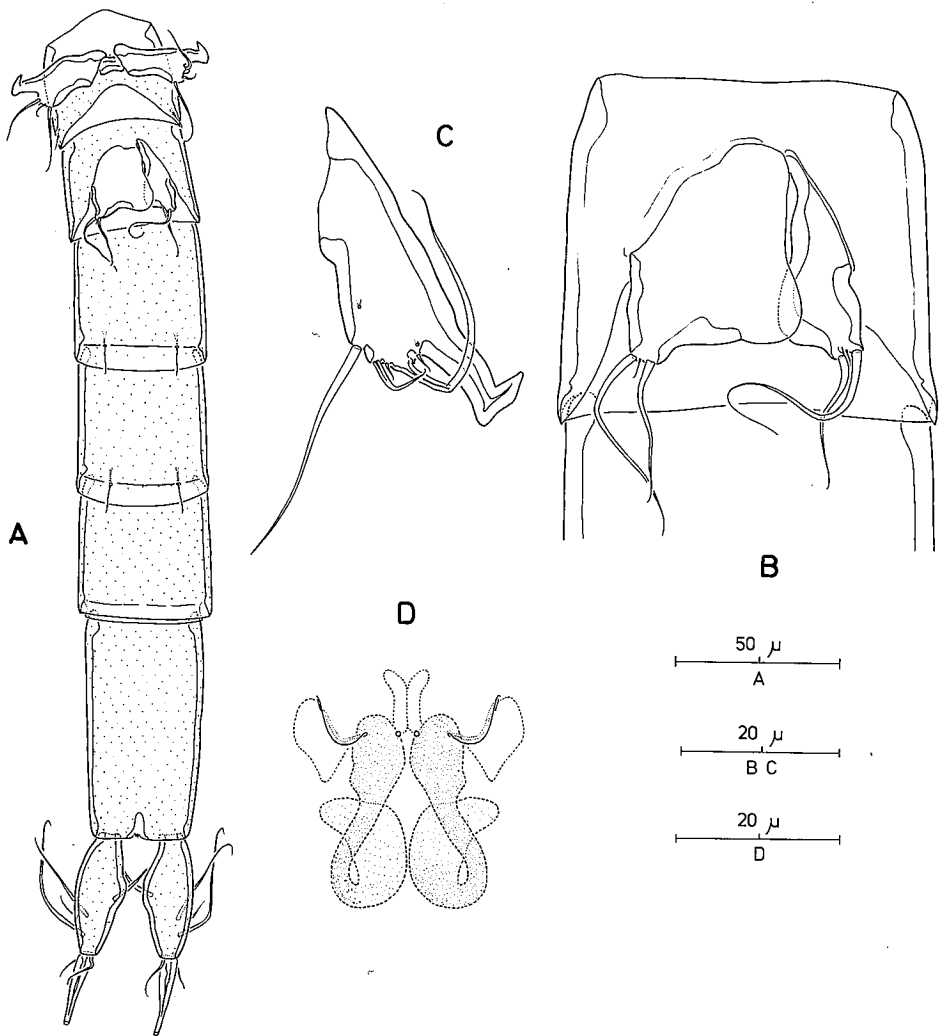
Fig. 15. *Willemsia calceola* gen. et sp. n. Male. A. Urosome, ventral. B. Sixth pair of legs. C. P5. Female. D. Genital field.

Variability. The outer spine on the middle exopod segment was missing from the right P2 in the holotype ♀ (arrowed in Fig. 12B).

Etymology. The species name is derived from the Latin *calceolus*, meaning small foot, and alludes to the peculiar shape of the fifth legs in both sexes.

DISCUSSION

Boreopontia heipi

The absence of the outer spine on the middle exopodal spine of P1 is confirmed by the present redescription and additional observations on copepodid

stages of *B. heipi* revealed that this armature element is not acquired (and subsequently lost) at any stage in the ontogeny. The loss of this spine is an unusual condition within the Harpacticoida, further being found only in the Parastenocarididae, a few Ameiridae (*Psammonitocrella* ROUCH, some species of *Leptomesochra* SARS) and a number of 'cylindropsyllid' genera, i.e. *Leptopontia* T. SCOTT, *Arenopontia* KUNZ and *Pararenopontia* BODIOU & COLOMINES. It was primarily this character that led WILLEMS (1981) to suggest that *Boreopontia* occupied an intermediate position between the Langian subfamilies Leptopontiinae and Cylindropsyllinae.

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However, a suite of other characters including the sexual dimorphism on P2–P3, the structure of the antenna and the mouthparts indicate a close affinity with the Cylindropsyllinae, a relationship also favoured by WILLEMS (1981) who suggested a link with *Stenocaris* to be likely. It is noteworthy that all harpacticoids lacking this outer exopodal spine belong to the interstitial fauna, however, the functional significance of this loss is as yet unknown. With respect to *Boreopontia* it is unlikely that this character indicates common ancestry with the genera of the Leptopontiinae since it (1) represents the only synapomorphy shared between *B. heipi* and the Leptopontiinae, (2) is highly outweighed by a number of apomorphies found only in the Cylindropsyllinae, and (3) has undoubtedly evolved convergently in a range of families each having a different phylogenetic history and ecological radiation (marine subtidal, sandy shores, subterranean).

The original description and figures of *B. heipi* contain a few inaccuracies, particularly in the setal counts of the antennules in both sexes, the maxillule and maxilla. As a rule in Cylindropsyllinae the male sixth pair of legs is asymmetrical with one member fused to the genital somite and the opposite one being discrete (thereby acting as an operculum closing off the genital aperture), usually smaller and of a different shape. WILLEMS' (1981) illustration of the male P6 in *Boreopontia* presumably shows only the articulating member of the leg pair. The tiny setule located in between the outer plumose seta and the inner smooth one was overlooked in the original description.

The present redescription has also revealed the true nature of the sexual dimorphism on the male swimming legs. The 'additional spine' noted by WILLEMS (1981) at the inner corner of the P2 basis is a cuticular extension of the inner basal margin. This modification is found in all male Cylindropsyllinae except for males of *Evansula* T. SCOTT (HUYS 1988; HUYS & WILLEMS 1993). The slightly modified inner distal spine of P2 exp-3 erroneously shown in the same position and orientation as its female homologue in WILLEMS' original illustrations (compare figs B₁, B₂: p. 205), is laterally displaced and both inwardly and posteriorly directed. This spine is homologous with the robust claw found in the same position in species of *Cylindropsyllus* and *Cylinula* (HUYS & WILLEMS 1993). Finally, the long curved seta figured in the proximal part of the 1-segmented P3 endopod proved upon re-examination to be a non-articulating sigmoid apophysis arising from the proximal segment of a 2-segmented endopod. This structure is homologous to the apophysis found in all other genera of the subfamily and

is probably derived from an anterior integumental outgrowth of the proximal half of the endopod.

Females of *B. heipi* produce a single, median egg sac which is attached via paired membranous strings to each of the genital apertures, probably suggesting that eggs contained in a single egg sac were released in an alternating sequence from both genital openings. Some species of Cylindropsyllinae such as *Cylindropsyllus laevis* BRADY, 1880 and *Stenocaris minor* (T. SCOTT 1892) possess paired egg sacs (T. SCOTT 1892; SARS 1909, 1911) and it is conceivable that this represents the ancestral condition for the group. Since females of *B. heipi* have paired functional oviduct openings, and the genital apertures are completely separate externally, the unpaired configuration of the egg sac can only be produced when the individual egg sac membranes merge at an early stage in the oviposition process, i.e. immediately after the first egg is released on both sides.

The fifth leg in *Boreopontia* has a modified, robust spine as the apical element and therefore resembles the condition in *Evansula* (see e.g. MIELKE 1975). This similarity is only superficial since it is not the same armature element that is modified. The ancestral number of setae on the female P5 in the subfamily Cylindropsyllinae is probably eight. This number is retained by some genera with unmodified fifth legs such as *Cylinula, Cylindropsyllus* and *Navalonia* (see below), but also in genera with modified ones such as *Stenocaropsis* APOSTOLOV and *Evansula*. Counting from the outermost (= basal) setae downwards, the modified spine can be identified as the fourth element in *Evansula*. *Boreopontia* has not retained all the armature elements on the P5 (one is missing) but the fact that the apical spine represents the fifth element (= the potential homologue of either the fifth or the sixth in *Evansula*) along the distal margin disproves its homology with the spine in *Evansula*.

Perhaps the most distinctive feature of *B. heipi* is the spur-like process on the caudal rami. Spinous modifications of the caudal rami can be common and of a diverse origin in certain families of interstitial copepods such as the Leptastacidae (HUYS 1992). In the Cylindropsyllinae distinct caudal processes have been recorded thus far only in *Stenocaris kliei* KUNZ, 1938 and in the various species of the genus *Stenocaropsis* (WELLS 1968; MARINOV 1974; COTTARELLI & VENANZETTI 1989). Detailed comparison (Figs 16, 17) reveals a number of obvious differences between both genera. In *Stenocaropsis pristina* (WELLS, 1968) the spinous process is distal in position and derived from a slightly dorsally directed cuticular outgrowth of the outer distal
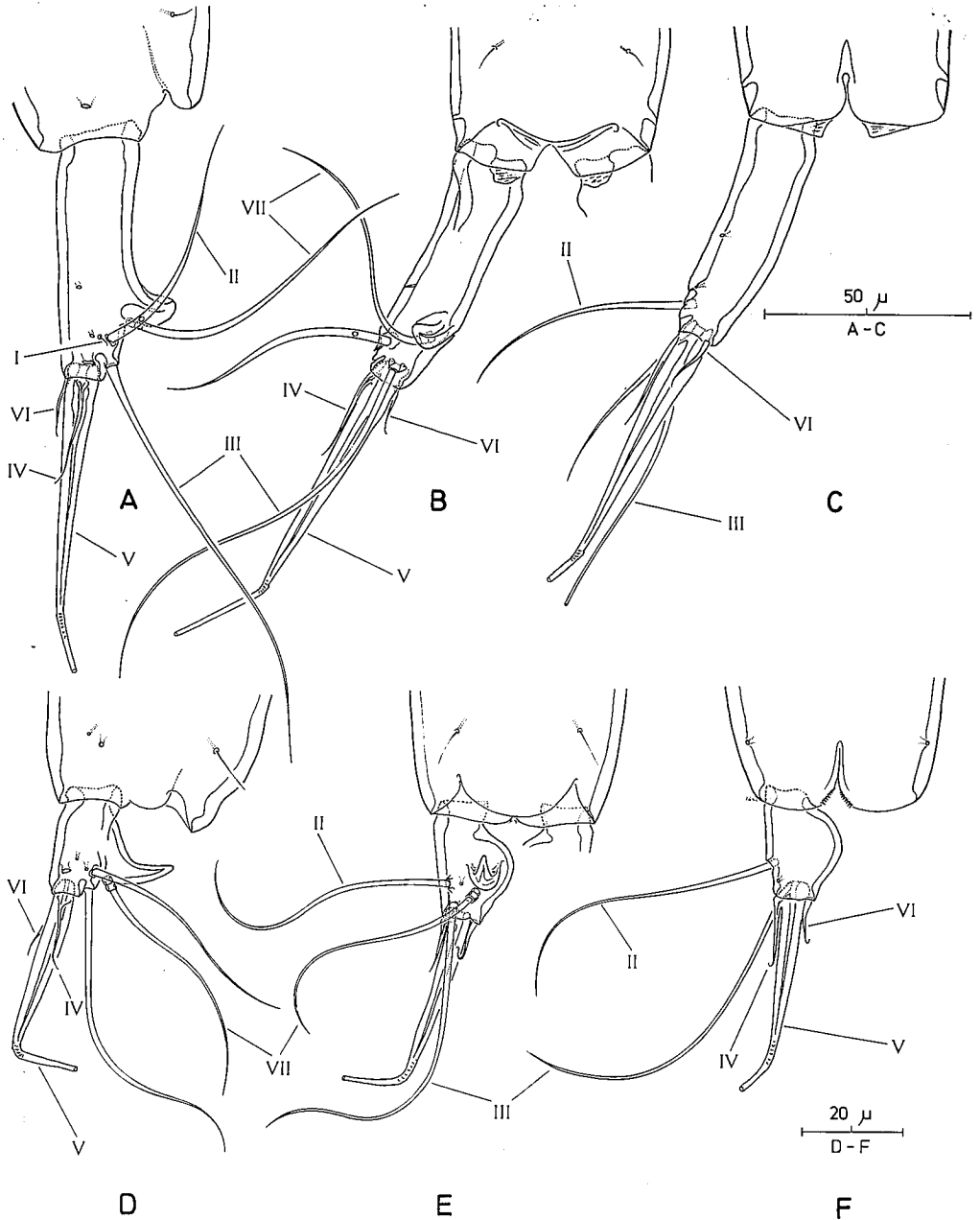
Fig. 16. *Boreopontia heipi* WILLEMS, 1981. A. Caudal ramus, lateral. B. Same, dorsal. C. Same, ventral. *Stenocaris kliei* KUNZ, 1938. D. Caudal ramus, lateral. E. Same, dorsal. F. Same, ventral.

corner, thereby displacing setae IV–VI to the inner distal corner (Fig. 17A–C). This type of process might well be homologous to the small pointed attenuation found in the same position in both of BECKER's (1979) deep-sea species *Stenocaris profundus* and *S. abyssalis*. It is interesting to note here that *Stenocaropsis* had originally been established by APOSTOLOV (1982) to accommodate those *Stenocaris* species with 2-segmented P2–P3 endopods. For some unknown reason APOSTOLOV did not consider BECKER's species which remained the only ones with this segmentation in the genus *Stenocaris* (HUYS
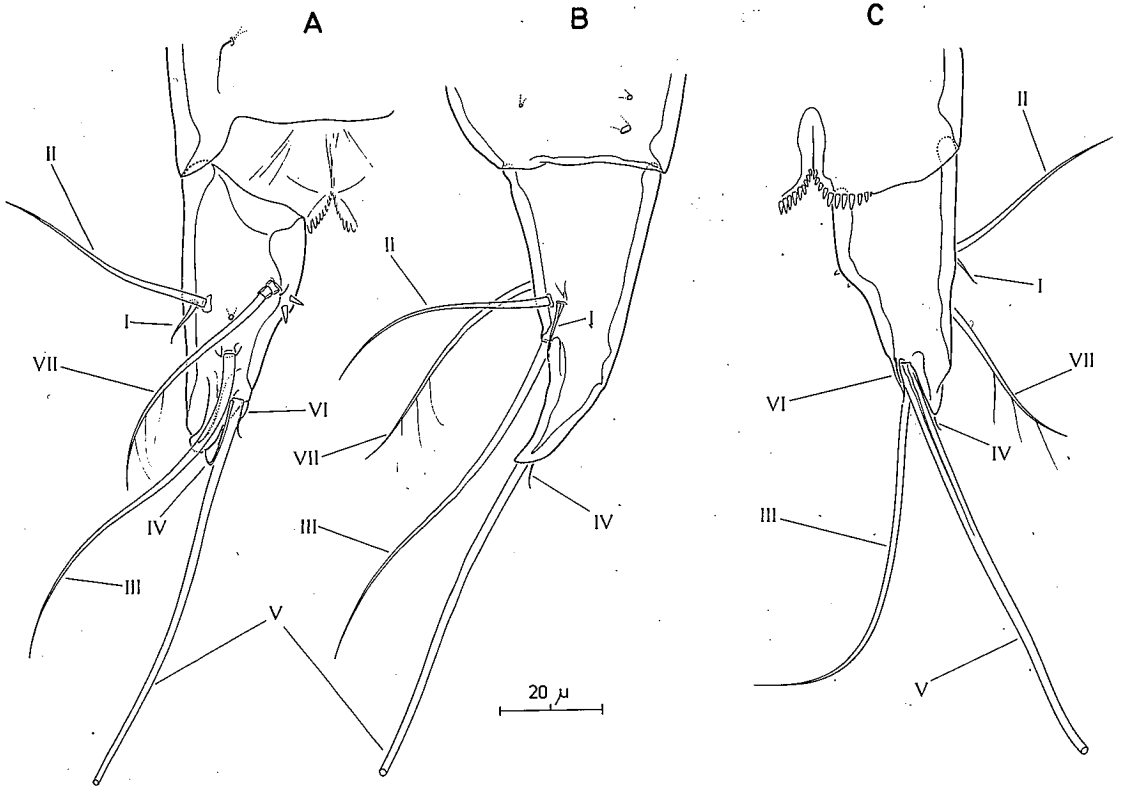
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Fig. 17. *Stenocaropsis pristina* (WELLS, 1968). A. Caudal ramus, dorsal. B. Same, lateral. C. Same, ventral.

1988). The relationships between *Stenocaropsis* and *S. profundus/abyssalis* will be discussed in a forthcoming revision of the genus *Stenocaris* (R. Huys in prep.).

In both *B. heipi* and *S. kliei* all ramal setae (seta I is missing in the latter) are located in the distal third of the ramus. The spinous process is entirely dorsal in position and derived from an integumental extension of the inner margin anterior to the implantation of seta VII (Fig. 16A–F). Re-examination of the types of *Stenocaris arenicola* WILSON, 1932 held in the collections of the National Museum of Natural History, Washington, D.C. (reg. no. USNM 063881) revealed a similar modification although WILSON (1932) did not mention such a dorsal process in the original description. As far as we can judge from the accompanying illustrations, he presumably had examined the specimens in dorsal and ventral view only, which might explain why such an obvious structure was overlooked. The structure of the sexual dimorphism and the P5 reinforces the close relationship between *S. arenicola* and *S. kliei*, but simultaneously almost certainly rules out a similar affinity between *Boreopontia* and

this species group, probably indicating that the dorsal process on the caudal ramus arose convergently.

The relationships of *Boreopontia* are enigmatic as ever. The primitive cephalic appendages, each displaying the maximum number of armature elements found in the family, are not very informative in resolving relationships. On the other hand, the segmentation of the P2–P4 endopods [2-1-2] represents an intermediate condition between the overall 2-segmented pattern [2-2-2] found in *Cylindropsyllus*, *Cylinula* and *Stenocaropsis* and the [1-1-2] pattern displayed by *Willemsia* and *Stenocaris* (part.). A revision of the heterogeneous genus *Stenocaris* will undoubtedly throw more light on the evolutionary history of *Boreopontia*.

The unusual [2-1-2] segmentation of the P2–P4 endopods is also found in *Stenocaris pygmaea* NOODT, 1955, described from the Gulf of Biscay (NOODT 1955). MARINOV (1971) presumed that the latter species was very closely related and probably identical to the Black Sea species *S. pontica* CHAPPUIS & SERBAN, 1953 which displays a [1-1-2] segmentation pattern. MARINOV's presumption was based on the examination of 'transitionary' speci-

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mens from the Bulgarian Black Sea coast, which had the same segmentation as CHAPPUIS & SERBAN's (1953) material from the Rumanian coast but were more similar to *S. pygmaea* in the structure of the P1 and P2. The similarities between the Biscayan and Bulgarian 'populations' listed by MARINOV (1971: 64), however, are shared by a whole group of *Stenocaris* species, and can therefore hardly be considered a basis for comparison. In this case they are rather more of a reflection of the inaccuracies (e.g. P1 enp-2 with 1 seta) contained in CHAPPUIS & SERBAN's (1953) original description. In view of the relatively narrow geographical separation of the Bulgarian and Rumanian populations it is conceivable that CHAPPUIS & SERBAN (1953) and MARINOV (1971) were dealing with the same species. MARINOV (1971) initially identified the Bulgarian material as *S. pygmaea* but APOSTOLOV (1972) and APOSTOLOV & MARINOV (1988) listed the latter as a junior subjective synonym of *S. pontica*. On the basis of the 2-segmented condition of the P2 endopod and pending the discovery of the male we suggest to reinstate *S. pygmaea* as a valid species.

Willemsia calceola

Willemsia gen. nov. displays a number of typical cylindropsyllid features including the cylindrical, vermiform body shape, the fine structure of the mouthparts (e.g. uniramous mandibular palp, maxilla with 2 syncoxal endites) and the general facies of the P1 and P4. Irrespective of the potential phylogenetic significance that can be attributed to each of these characters the familial position of *Willemsia* is unambiguously defined by its sexual dimorphism on the male P2. The latter is a powerful synapomorphy for the Cylindropsyllinae as a whole since it represents a compound character involving modifications on both the protopod (anterior spinous process on basis; except *Evansula*) and the exopod (inner distal spine of exp-3 transformed).

Willemsia clearly occupies an isolated and phylogenetically advanced position in the Cylindropsyllinae. This is illustrated by for instance the morphological reductions on the mouthparts including the vestigial 1-segmented mandibular palp, the complete incorporation of the maxillary endopod into the allobasis and the loss of setal elements on the maxillulary palp. However, the new genus also exhibits a number of highly distinctive and evolutionary novel characters associated with the P5, the female genital field and the swimming leg sexual dimorphism.

Unlike any other cylindropsyllinid genera, the fifth legs do not show noticeable sexual dimorphism

in general shape, size and in number and individual position of armature elements. The presence of a foot-shaped apophysis on the fifth leg is also unique among Cylindropsyllinae. A similar process occurs on the P5 of some species of *Leptastacus* T. SCOTT (Family Leptastacidae) (HUYS 1987a). On the basis of ontogenetic evidence HUYS (1992) showed that this structure is clearly a derivative of the exopod whereas in *Willemsia* it is most likely a modification of the endopodal lobe.

The female genital field of *W. calceola* is atypical in two respects. First, the absence of an isolated midventral copulatory pore as in for instance *Cylindropsyllus* and *Cylinula* is unique among the Cylindropsyllidae. This derived state suggests that the copulatory pore(s) is (are)·lying within the genital apertures, concealed beneath the lobe of the genital operculum (P6). Second, the seminal receptacles are subdivided in two chambers, ventral and dorsal, and are recurved. In other genera the receptacles are smaller, horseshoe-shaped and located anterior to or at about the level of the genital apertures.

The homology of the bulbiform, hyaline structure, located at the inner margin of the compound exopod segment in the male P2, is unclear. Similar to armature elements this process clearly arises from a gap in the cuticle, providing a connection with the underlying tissue. It is unlikely, however, that it is derived from a seta or a spine since an inner seta on the P2 exp-1 or -2 has not been reported thus far in any species of the subfamily Cylindropsyllinae. Presumably it represents a specialized secretory structure.

The most distinctive feature of the new genus is the extraordinary sexual dimorphism shown on the male P3. The large, conspicuous apophysis-like structure overlying most of the endopod and arising from the posterior surface of the protopod is obviously a derivative of the coxa. Unlike the rami which can display all kinds of transformations in male swimming legs, protopodal segments are less frequently involved in the sexual dimorphism. As far as we could ascertain, praecoxae and coxae never exhibit any differences between sexes apart from (a) slight variations in surface ornamentation (spinules, setules, denticles) usually falling well within the boundaries of intraspecific variability or (b) coxo-basal fusions as in the male P3 of *Forficatocaris* JAKOBI (Family Parastenocarididae; e.g. NOODT 1972). Bases can be sexually dimorphic in a range of families but gross modifications such as in *Amphiascopsis* GURNEY are exceptional. Usually it is the inner basal seta or spine that is transformed (e.g. Ameiridae, many Thalestridae, some Darcy-
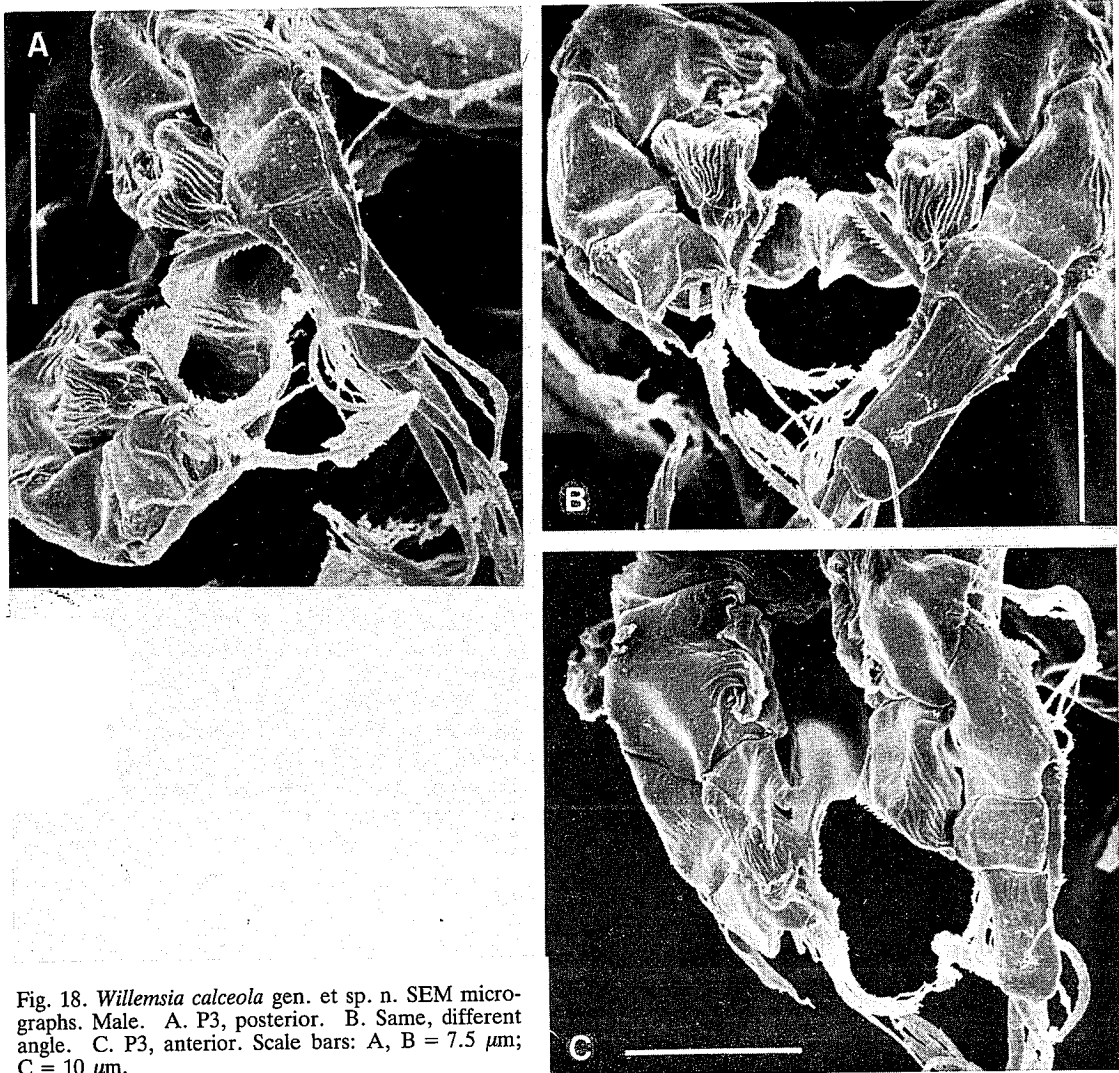
Fig. 18. *Willemsia calceola* gen. et sp. n. SEM micrographs. Male. A. P3, posterior. B. Same, different angle. C. P3, anterior. Scale bars: A, B = 7.5 μm; C = 10 μm.

thompsoniidae), or the inner basal margin (e.g. most Diosaccidae, Cancrincolidae, Cylindropsyllinae) or both (e.g. *Amphiascopsis*).

The elaborate structure in *Willemsia* proved upon examination with SEM (Fig. 18) to be a thin-walled tubular extension of the cuticle surrounding an integumental pore. The distal margin of this extension, delineating the wide, semicircular orifice of the presumptive secretory pore, is serrate anteriorly and equipped with an extremely long and flexible inner process distally.

Sexually dimorphic pores are rare among harpacticoids and until now they had not been discovered on protopodal sites. Some authors (Huys 1987b; Schminke & Dahms 1989) reported on the presence of a hyaline tube pore on the distal endopod segment of P3 in male Neobradyidae. Similarly, Gee & Fleeger (1990) documented for a wide range of diosaccid genera the distribution, size and ornamentation of sexually dimorphic tube pores on the distal exopod segment of P3. These pores, however, are relatively simple, cylindrical structures located exclusively on the anterior surface of the ramus and because of their small size and flaccid appearance are hard to discern without differential interference contrast microscopy.

The plethora of autapomorphies and numerous reductions in setal counts in *Willemsia* impedes the identification of an outgroup. Sexual dimorphism is often informative in elucidating phylogenetic rela-

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tionships, particularly when it involves multiple changes as in *W. calceola*. Within the Cylindropsyllinae only in males of *S. kliei* (and *S. arenicola*) and *S. kerguelenensis* BODIOU the P2 and P3 exhibit modifications of a comparable complexity. The sexual dimorphism in the former species is clearly of a different nature (KUNZ 1938) and will not be considered here. *S. kerguelenensis* described from fine subtidal sand in the Bay of Morbihan (Kerguelen Archipelago) (BODIOU 1977), however, displays a number of interesting features on the male P2 and P3: (a) ♂ P2 exp-1 and exp-2 are fused into a compound segment as in *Willemsia*; in all other Cylindropsyllinae the male exopods are 3-segmented; (b) the modified inner distal spine on exp-3 has the same outline and dimensions as in *Willemsia* but is provided with long spinules; (c) the inner seta on ♂ P2 enp-1 is absent in the female (though the pattern is somewhat obscured here by the 1-segmented condition and the presence of 2 setae on the apex instead of only 1 in the male). In the absence of conflicting ontogenetic evidence it is considered unlikely that the inner seta has migrated to an apical position in the female. Therefore we consider it to be more plausible that the seta was lost in the female, probably through an ontogenetic event. Comparison with the endopods of *Willemsia* shows the inner serrate seta also to be present in the male only. This pattern is unique since in all other Cylindropsyllinae where this inner seta is retained it seems to be present in both sexes irrespective of the endopodal segmentation; (d) BODIOU reported '... une trés forte épine interne ... à côté de l'endopodite' on the coxa of the P3; this 'spine' is almost certainly homologous to the coxal structure overlying the endopod in *Willemsia*. The combination of these apomorphic character states found only in *W. calceola* and *S. kerguelenensis* unquestionably indicates their close relationship and presents supporting evidence for the removal of the latter from the genus *Stenocaris*.

S. kerguelenensis displays a number of substantial differences preventing its inclusion in *Willemsia*: (a) the P2–P3 are not modified in the female; (b) *S. kerguelenensis* is the only cylindropsyllinid with distinct sexual dimorphism on the male P4 endopod [apomorphy]: (c) the P5 is not modified in both sexes (no foot-shaped process) and has the maximum number of armature elements (8) in the female; (d) the caudal ramus shows strong sexual dimorphism in the female [apomorphy]. Other similarities or differences might emerge when information becomes available about the female genital field (copulatory pore, seminal receptacles) and the male sixth legs.

As a result of all these considerations *S. kerguelenensis* is transferred as the type and only species to a new genus *Navalonia* gen. nov. which is currently regarded as the sistergroup of *Willemsia*. Since the types of *S. kerguelenensis* were not available for re-examination, some of the characters in the diagnosis given below remain unconfirmed due to incomplete data or inaccuracies in the original description.

Navalonia gen. nov.

Diagnosis. Cylindropsyllidae. Body slender, cylindrical. Rostrum triangular, defined at base. Antennule 7-segmented and with aesthetasc on segment 4 in ♀; at least 7-segmented, haplocer and with aesthetasc on segment 4 in ♂. Antenna with allobasis and bisetose 1-segmented exopod. Mandibular palp 2-segmented. Maxillule with 2 setae on coxa, 3(?) setae on basis, 2 setae on endopod and 1 seta on exopod. Maxillary endopod discrete. Maxillipeds subchelate, syncoxa without(?) seta, 1-segmented endopod with claw. P1–P4 with 3-segmented exopods and 1- (P2, P3) or 2-segmented (P1, P4) endopods. P1 exopod with outer spine on middle segment and 1 simple seta, 2 geniculate setae plus 1 spine on distal segment; endopod not prehensile, proximal segment slightly shorter than distal, with inner seta, distal segment with setule and 2 geniculate setae. Armature formula of swimming legs:

	coxa	basis	exopod segment			endopod segment	
			1	2	3	1	2
P1	0–0	0–1	I–0;	I–0;	I1,1,1	0–1;	1,1,1
P2	0–0	1–0	I–0;	I–0;	II,I1,0	0,I1,0	
P3	0–0	1–0	I–0;	I–0;	II,I1,1	0,I1,0	
P4	0–0	1–0	I–0;	I–0;	II,I1,1	0–0;	1,I,0

P5 baseoendopod and exopod fused, forming rectangular plate with 8 setae/spines in ♀ and 5 setae in ♂, P6 of both sexes, copulatory pore and seminal receptacles unconfirmed.

Sexual dimorphism in antennule, P2 basis (with hook-shaped process at inner corner), endopod (extra inner seta on proximal segment, loss of seta on distal segment) and exopod (exp-1 and exp-2 fused into compound segment, exp-3 with distal inner spine transformed into robust pinnate claw), P3 coxa (with complex raised pore), endopod (with short distal apophysis), P4 endopod (proximal segment with blunt apophysis), P5, P6, caudal rami and in genital segmentation.

Caudal ramus slightly conical, about twice as long as wide; with 7(?) setae (seta I diminutive?); seta V modified in ♀, short, distinctly swollen proximally and with dorsal bulbous process, fused to well developed seta IV.

Type and only species. *Navalonia kerguelenensis* (BODIOU, 1977) comb. nov.

Etymology. The genus alludes to the type locality at Port-Navalo situated in the southeast of the Gulf of Morbihan, Kerguelen Archipelago. Gender: feminine.

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