



# Systematics and Phylogeny of the Ancorabolidae (Copepoda: Harpacticoida). IV. Redescription, ontogeny and position of *Echinopsyllus normani*

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**Abstract:** *Echinopsyllus normani* (Harpacticoida: Ancorabolidae) is redescribed on the basis of topotypic females from the Sars collection (Oslo, Norway) and males from newly collected Norwegian material. Aspects of copepodid development from CIII stage to adult are described and illustrated for both sexes. The monotypic genus *Echinopsyllus* is characterized by the highly ornate nature of the cephalothorax and body, the dorsal conical processes on first and second abdominal somites arising from a common middorsal base, the presence of dorsal processes on the second abdominal somite, the mandibular palp with 4 setae and the sexual dimorphism displayed in P5 exopodal armature. The isolated position of *Echinopsyllus* within the Ancorabolinae is briefly discussed.

**Résumé:** *Systématique et phylogénie des Ancorabolidae (Copepoda: Harpacticoida). IV. Redescription, ontogénie et position systématique de Echinopsyllus normani.* *Echinopsyllus normani* (Harpacticoida: Ancorabolidae) est redécrit sur la base des femelles topotypiques provenant de la collection de Sars (Oslo, Norvège) et les mâles de matériel récemment récolté en Norvège. Des aspects du développement des copépodites du stade III jusqu'à l'adulte sont décrits et illustrés pour les deux sexes. Le genre monotypique *Echinopsyllus* est caractérisé par l'importante ornementation du céphalothorax et du corps, les protubérances coniques dorsales des premier et second somites abdominaux insérées sur une assise médiadorsale commune, la présence de protubérances dorsales sur le second somite abdominal, le palpe mandibulaire portant quatre soies et le dimorphisme sexuel de l'armature de l'exopodite du P5. La position systématique isolée d'*Echinopsyllus* au sein des Ancorabolinae est brièvement discutée.

**Keywords:** Copepoda, Harpacticoida, Ancorabolidae, *Echinopsyllus*, systematics, ontogeny.

## Introduction

Recent contributions to the evolutionary systematics of the subfamily Ancorabolinae (Copepoda, Ancorabolidae) have addressed the taxonomic status of the genus *Ceratonotus* Sars, 1909 (Conroy-Dalton, 2003) and the phylogenetic

relationships at generic level within the *Ancorabolus*-lineage (Conroy-Dalton & Huys, 2000; Gómez & Conroy-Dalton, 2002) and the *Ceratonotus*-lineage (Conroy-Dalton, 2001). The two remaining genera, *Echinopsyllus* Sars, 1909 and *Echinocletodes* Lang, 1936, both hold an unresolved position in the Ancorabolinae. The former is dealt with in detail here while the relationships of the polyphyletic *Echinocletodes* will be the subject of a forthcoming paper (Conroy-Dalton & Huys, in press).

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The monotypic genus *Echinopsyllus* was described by Sars (1909) on the basis of two females from southern Norway. Lang (1936), Wells (1965) and Drzycimski (1969) reported males of *E. normani* Sars, 1909 but none provided a proper description. Lang's (1936) comments are confined to the 3-segmented P3 endopod and Wells' (1965) illustration of this undoubtedly refers to a juvenile male stage. In this paper a complete redescription of both sexes of *E. normani* and a concise re-assessment of its phylogenetic relationships are presented.

### Material and methods

Norwegian material: meiofaunal core samples were collected from Frierfjord/ Langesundfjord Norway, as part of the GEEP surveys during Spring 1985, and the harpacticoid copepods picked out and preserved in alcohol.

Specimens were dissected in lactic acid, and the dissected parts mounted in lactophenol. Preparations were sealed with transparent nail varnish. All drawings have been prepared using a camera lucida on a Leitz Diaplan microscope equipped with differential interference contrast.

Scale bars in figures are indicated in  $\mu\text{m}$ .

The descriptive terminology for body and appendage morphology is adopted from Huys & Boxshall (1991). Abbreviations used in the text and figures are: ae, aesthetasc; P1-P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus. The term acrothek is used to denote the trifid setal complement found apically on the distal antennular segment.

### Systematics

Family ANCORABOLIDAE Sars, 1909  
Subfamily ANCORABOLINAE Sars, 1909  
Genus *Echinopsyllus* Sars, 1909

Diagnosis. Ancorabolinae. Body cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome; body ornate with series of produced conical processes, each bearing an unmodified sensilla apically. Cephalothorax with 3 pairs of lateral and 2 pairs of dorsal conical processes; with distinctly raised area present immediately posterior to anterodorsal paired processes. Anterior corners of cephalothorax with sensory tube-pore. Thoracic somites bearing P2-P5 each with paired dorsal conical processes; P6-bearing somite (genital half of double-somite in ♀) without produced processes. First

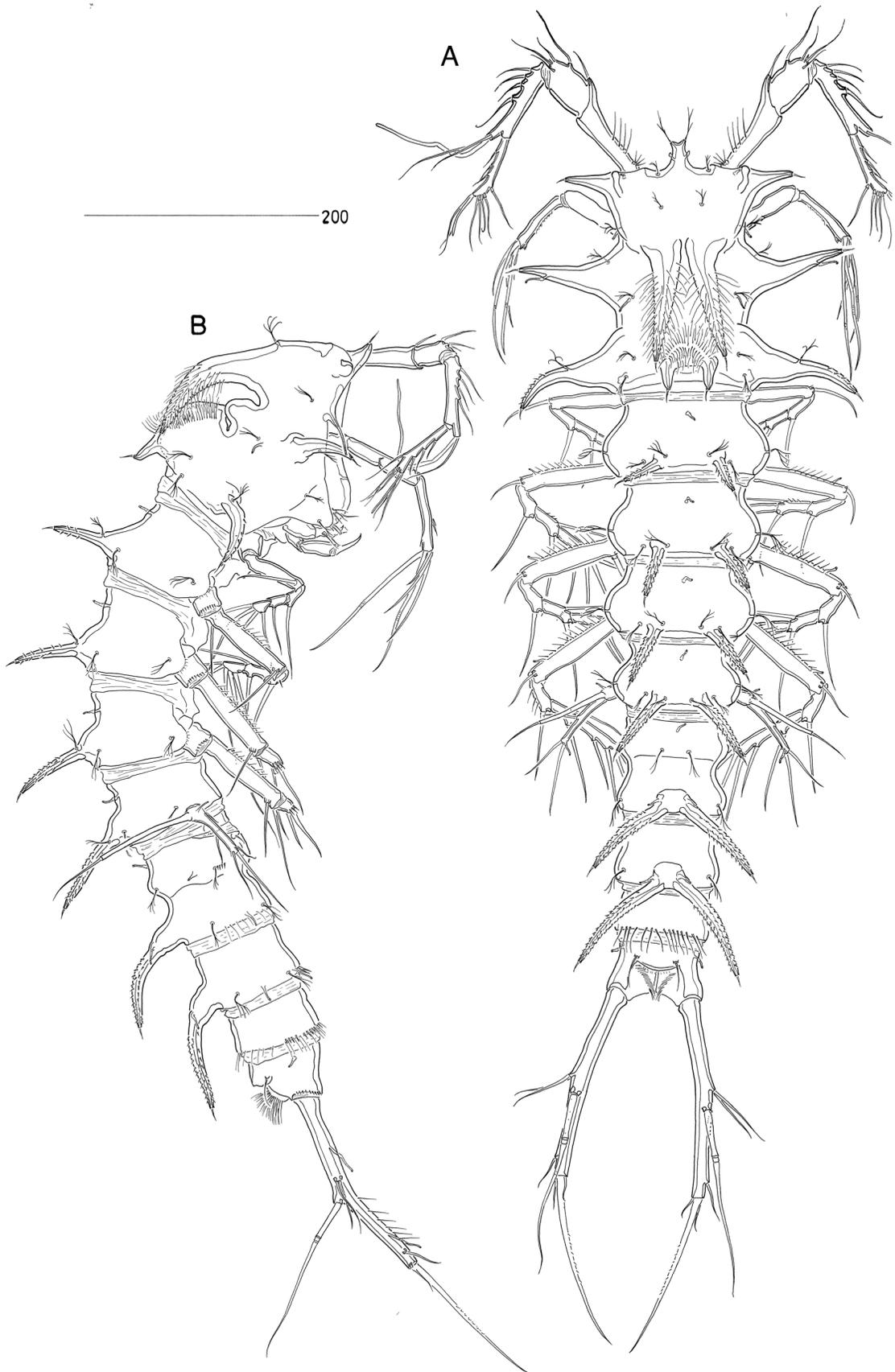
abdominal somite (abdominal half of double-somite in ♀) and second abdominal somite with basally fused pair of divergent, conical processes. Remaining integumental sensillae modified, branched. Somatic hyaline frills weakly developed and smooth. Body somites, swimming legs, P5 and caudal rami with conspicuous tube-pores. Anal operculum rounded with fine setules. Caudal rami elongate and divergent, with 7 setae; setae I and II inserted in median third of ramus, seta III sub-distal; seta IV reduced, fused basally to seta V; seta V well developed, pinnate; seta VI reduced; seta VII inserted in median third of ramus, triarticulate at base. Sexual dimorphism in body size, degree of development of cephalothoracic posterodorsal processes and dorsal processes of P2- P3 bearing somites, rostrum size, antennule, P3 endopod, P5, P6, genital segmentation and abdominal ornamentation.

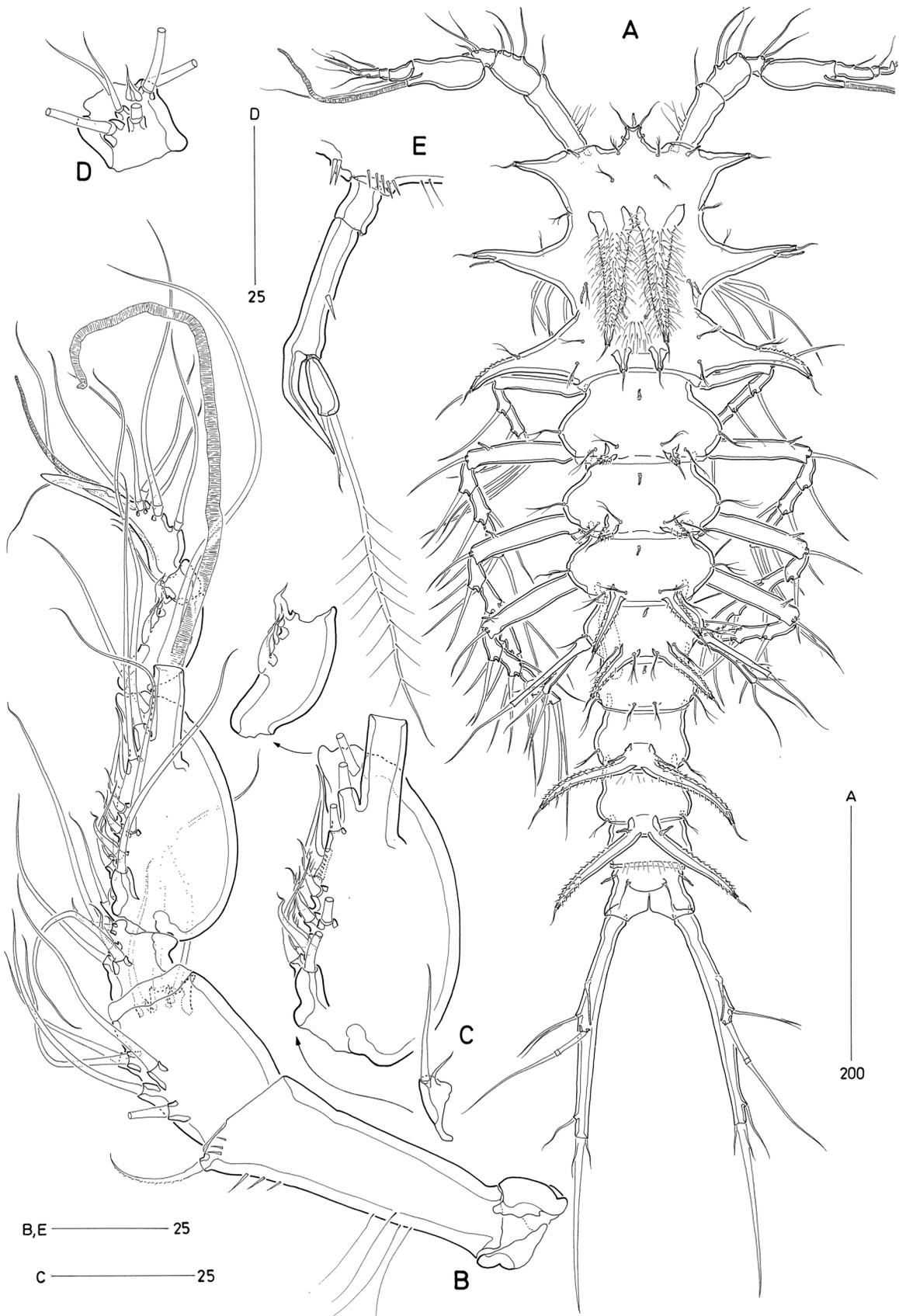
Rostrum moderate in size, discernible in dorsal aspect; fused to cephalic shield; with paired bulbous membranous projections proximal to sensillae; with long distinctive midventral tube-pore subdistally. Antennule 4-segmented in ♀, 8-segmented and subchirocer in ♂ (with three segments distal to geniculation); aesthetasc arising from segments 3 and 4 in ♀, segments 5 and 8 in ♂; segment 2 (both sexes) with 1 subapical anterior seta arising from distinctive spinous projection. Antenna with allobasis showing partial suture along exopodal margin, abexopodal margin with 2 setae of which endopodal one reduced; exopod entirely absent; endopod with 3 lateral and 6 distal elements (2 spines and 3 geniculate setae, longest one fused basally to tiny naked seta). Mandible with robust coxa bearing short pinnate dorsal seta; palp 1-segmented, uniramous with 4 setae (3 endopodal and 1 basal). Maxillule with 1 element on coxal endite; basis with 3 elements on proximal endite; exopod and endopod completely incorporated into basis, each represented by 1 seta. Maxillary syncoxa with 2 well developed endites, each with 2 elements; allobasis drawn out into claw with 3 accessory elements; endopod minute with 2 setae. Maxilliped subchelate, slender; syncoxa without armature; endopod drawn out into long narrow, curved claw with 1 reduced accessory seta.

P1-P4. Intercoxal sclerites wide and narrow; praecoxae moderately developed; coxae small, quadrangular, bases extremely transversely elongate. P1 exopod 3-segmented; exp-3 with 3 geniculate setae and 1 outer spine; endopod absent, original position indicated by slightly membranous area. P2-P4 exopods 3-segmented; endopods absent (P2), 1-segmented (P4) or 2-segmented (P3, except in ♂); without inner setae on exp-1, exp-3 and endopodal segments; exp-3 with 2 outer spines. P3 endopod ♂

Figure 1. *Echinopsyllus normani* (♀). A. habitus, dorsal; B. habitus, lateral.

Figure 1. *Echinopsyllus normani* (♀). A. habitus, vue dorsale ; B. habitus, vue latérale.





3-segmented; enp-2 elongate, anterior surface produced distally into recurved apophysis; enp-3 with 2 apical setae. Armature formula as follows:

	Exopod	Endopod
P1	0.0.022	absent
P2	0.1.022	absent
P3	0.1.022	0.020 (♀)
	0.1.022	0.0.020 (♂)
P4	0.1.022	010

P5 biramous in both sexes; basal setophore elongate and demarcated at base; endopodal lobe vestigial, represented by 1 seta and 1 conspicuous tube-pore; exopod discrete in both sexes and elongate without inner setae, with 1 apical and 3 (♀) or 2 (♂) outer elements. Female genital field located anteriorly; gonopores covered by common, unarmed genital operculum derived from medially fused P6, with 1 reduced seta on either side. Male P6 asymmetrical; without armature; functional member represented by small membranous flap.

Type and only species. *Echinopsyllus normani* Sars, 1909 (by monotypy)

*Echinopsyllus normani* Sars, 1909

*Echinopsyllus Normani* Sars, 1909:  
incorrect original notation

Type locality. Neither a precise type locality nor type specimen was designated by Sars (1909), who found one female in Farsund and another one in Korshavn. A neotype is designated here (from additional material of the G.O. Sars collection, collected from Korshavn and labelled "type locality"). In accordance with ICZN Art. 76.3, the type locality becomes Korshavn, Norway.

Material examined. (a) Zoologisk Museum, Oslo, Norway: 117 adults (both sexes) [ZMO reg. no. F20373a] and 7 copepodids (5 ♂♂ and 2 ♀♀; all CV) [ZMO reg. no. F20373b] in alcohol from Korshavn, Norway; coll. and det. G.O. Sars; 1 ♀ dissected on 12 slides and designated as neotype [ZMO reg. no. F22914a-1]; (b) Naturhistoriska Riksmuseet, Stockholm, Sweden: 101 adults (both sexes) and 2 copepodids (1 ♂ and 1 ♀ CV stage) in alcohol [SMNH reg. no. 15353 (old no. 496)] from Gullmarfjord, Sweden; 30 m, mud; coll. K. Lang, 10.04.1934; (c) The Natural History Museum, London, UK: 1 ♂ CV mounted whole on 1 slide [NHM reg. no. 1965.3.26.20] from the Fladen Bank, North Sea; 140 m, silty sand and detritus; coll.

A.D. McIntyre, 1962; det. J.B.J. Wells, 1965; (d) The Natural History Museum, London, UK: 182 adults (both sexes) and 17 copepodids (1 CIII, 1 ♀ CIV, 1 ♂ CIV, 3 ♂♂ and 11 ♀♀ CV) in alcohol [NHM reg. no. 2002.392-412]; all from meiofauna samples collected at Frierfjord/Langesundfjord, Norway; 99 m deep mud; coll. R. Huys, Spring 1985.

Individuals from (d) were in better condition, cleaner and less damaged and are therefore used for the description of the male and copepodid stages below.

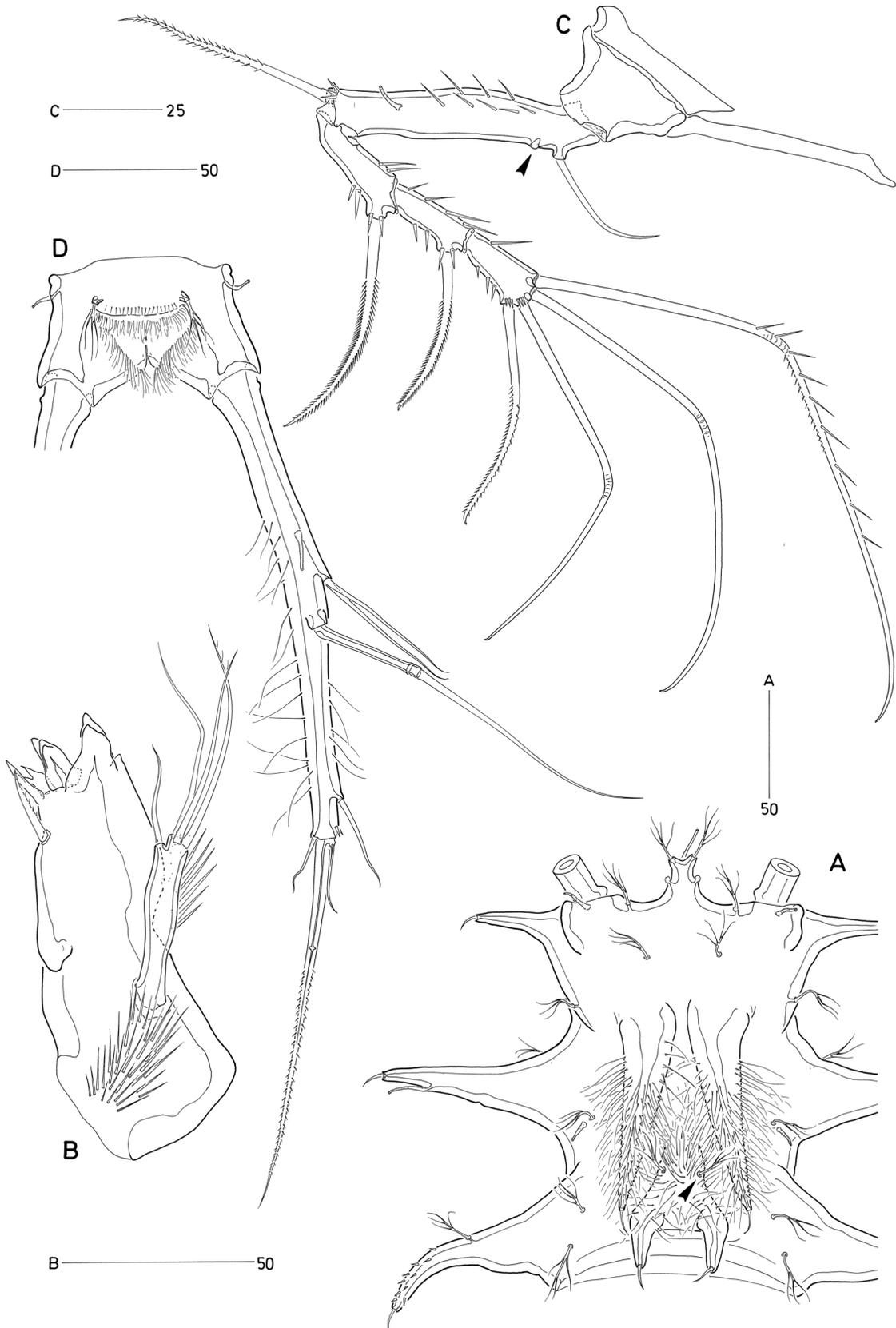
#### Re-description

*Female* (Figs 1; 3; 4; 5; 6A-B; 8A-B; based on neotype (a)). Total body length 988 µm (mean = 989; n = 13) measured from anterior tip of rostrum to posterior margin of caudal rami. Body (Fig. 1) cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome; integument moderately chitinized and ornate with series of produced conical processes; processes bearing unmodified sensillae. Somatic hyaline frills weakly developed and smooth (Figs 1; 6A). Cephalothorax (Figs 1; 3A; 8A-B) with 3 pairs of lateral and 2 pairs of dorsal conical processes, each bearing apical sensilla. Lateral processes comprising short anterior pair (Figs 1A; 3A) at outer corners, middle pair (Figs 1B; 3A) halfway cephalothorax length bearing conspicuous tube-pore subterminally and additional ventral sensilla, and backwardly recurved posterior pair (Fig. 3A) at outer corners with associated dorsal sensilla. Dorsal processes posteriorly directed, comprising large anterodorsal pair furnished with setules (Figs 1; 3A) and small posterodorsal pair (Figs 3A; 8A-B) arising from common swollen base furnished with setules and paired sensory triplet consisting of 2 sensillae and large pore (see Fig. 8A right side with setules omitted for clarity); distinct raised bulge present immediately posterior to anterodorsal pair (Figs 1B; 8B). Anterior corners of cephalothorax with tube-pore.

Free thoracic somites bearing P2-P5 (Fig. 1) with dorsal pair conical sensillate processes with associated proximal sensilla; genital half of double-somite without produced processes; abdominal half of double-somite and second abdominal somite with paired, divergent conical processes arising from common mid dorsal base, with paired tube-pores proximally; all dorsal processes furnished with spinules. All remaining integumental sensillae branched. Body, P1-P5 and caudal rami with conspicuous tube-pores (Figs 1; 3A; C-D; 5; 6B). Original segmentation of genital

←  
**Figure 2.** *Echinopsyllus normani* (♂). **A.** habitus, dorsal; **B.** antennule, ventral; **C.** antennule segments 4-6, disarticulated, ventral; **D.** antennule segment 3, lateral; **E.** P3 right endopod, anterior.

**Figure 2.** *Echinopsyllus normani* (♂). **A.** habitus, vue dorsale; **B.** antennule, vue ventrale; **C.** articles antennulaires 4-6, désarticulés, vue ventrale; **D.** article antennulaire 3, vue latérale; **E.** endopodite droit de P3, vue antérieure.



double-somite indicated by bilateral constriction and faint dorsal/dorsolateral ridge (Figs 1; 6B); posterior half with fine setules around hind margin. Second abdominal somite (Figs 1B; 6B) with paired sensilla and closely associated tube-pore laterally and lateroventrally; with 2 ventral spinule patches as figured (Fig. 6B) around posterior margin. Third abdominal somite (Figs 1A; 6B) posterior margin with spinules ventrally and setules dorsally. Anal somite partly cleft medially (Fig. 3D); 2 tube-pores and small spinules present around ventral hind margin (Fig. 6B); anterolateral margin with tube-pore; anal operculum (Fig. 3D) rounded with few small, fine setules; anal frill finely setulose.

Caudal rami (Figs 3D; 6B) elongate and divergent furnished with few fine setules. Seta I positioned ventral to seta II, both of equal length and bare, inserted in median third of ramus; seta III bare, inserted sub-distally; seta IV reduced and fused basally to well developed, finely pinnate seta V; seta VI shortest, bare; seta VII triarticulate at base, first socle elongate, arising from minute dorsal pedestal in medial third of ramus.

Rostrum (Fig. 4B) fused to cephalic shield; moderate size; basally constricted and elongate with paired branched sensillae arising from tiny pedestals forming vaguely bifid apical margin; with paired bulbous membranous projections laterally; midventral tube-pore, well developed and subdistal.

Antennule (Fig. 4A) 4-segmented. Segments 1, 3 and 4 elongate. Segment 2 shortest with 1 dorsal sub-apical seta arising from spinous projection (arrowed in Fig. 4A). Segment 3 with aesthetasc (length 124  $\mu\text{m}$ ). Segment 4 with apical acrothek consisting of aesthetasc and 2 slender setae. Armature formula: 1-[1 pinnate], 2-[5], 3-[7 + (1+ae)], 4-[9 + acrothek].

Antenna (Fig. 6A). Coxa represented by well developed sclerite. Basis and proximal endopod segment fused forming allobasis; membranous insert along exopodal margin marking original position of exopod; exopod completely absent; abexopodal margin with few strong spinules proximally, with 1 small pinnate seta in basal half and vestigial seta in endopodal half. Endopod with 1 distal surface frill and 2 spinule rows along outer margin; with spinules along medial margin; lateral armature consisting of 2 pinnate spines and 1 minute seta; distal armature consisting of 2 unipinnate spines and 3 distally pinnate geniculate setae, longest one with additional pinnules

around geniculation and fused basally to vestigial seta.

Labrum well developed (Fig. 4C), with lappet-like ornamentation along distal margin, flanked on either side by 1 tooth and few spinules; anterior face with large median tube-pore sub-distally and patches of tiny fine pinnules as in Fig. 4C.

Mandible (Fig. 3B). Coxa robust, with patch of long spinules proximally, expanding distally to gnathobase bearing 2 multicuspidate teeth and 2 thin blades; 1 sparsely pinnate seta at dorsal corner. Palp well developed, 1-segmented, with row of long spinules; with 1 setae along inner margin (representing basal element), 3 apical setae (representing incorporated endopod) and outer margin without armature.

Maxillule (Fig. 4D). Praecoxal arthrite subrectangular with 2 setae on anterior surface and few long spinules on posterior surface; distal armature consisting of 3 bare and 4 crenulate spines as figured. Coxal endite with 1 pinnate spine; outer margin with tuft of fine spinules. Basis with spinule row; proximal endite with 3 elements. Rami completely incorporated into basis, each represented by 1 bare seta.

Maxilla (Fig. 4F). Syncoxa with 3 spinule patches as figured; with 2 coxal endites, arising from membranous area, each with 1 pinnate, apically bifid spine and 1 blunt seta. Allobasis drawn out into pectinate claw; accessory armature consisting of 2 naked, blunt seta and 1 spine. Endopod minute, with 2 blunt setae.

Maxilliped (Fig. 4G). Subchelate and slender. Syncoxa with 3 spinule patches as figured and without armature. Basis with spinules along outer margin and spinule row along palmar margin. Endopod drawn out into long narrow, curved claw; claw finely serrate in middle third and with 1 accessory seta at base.

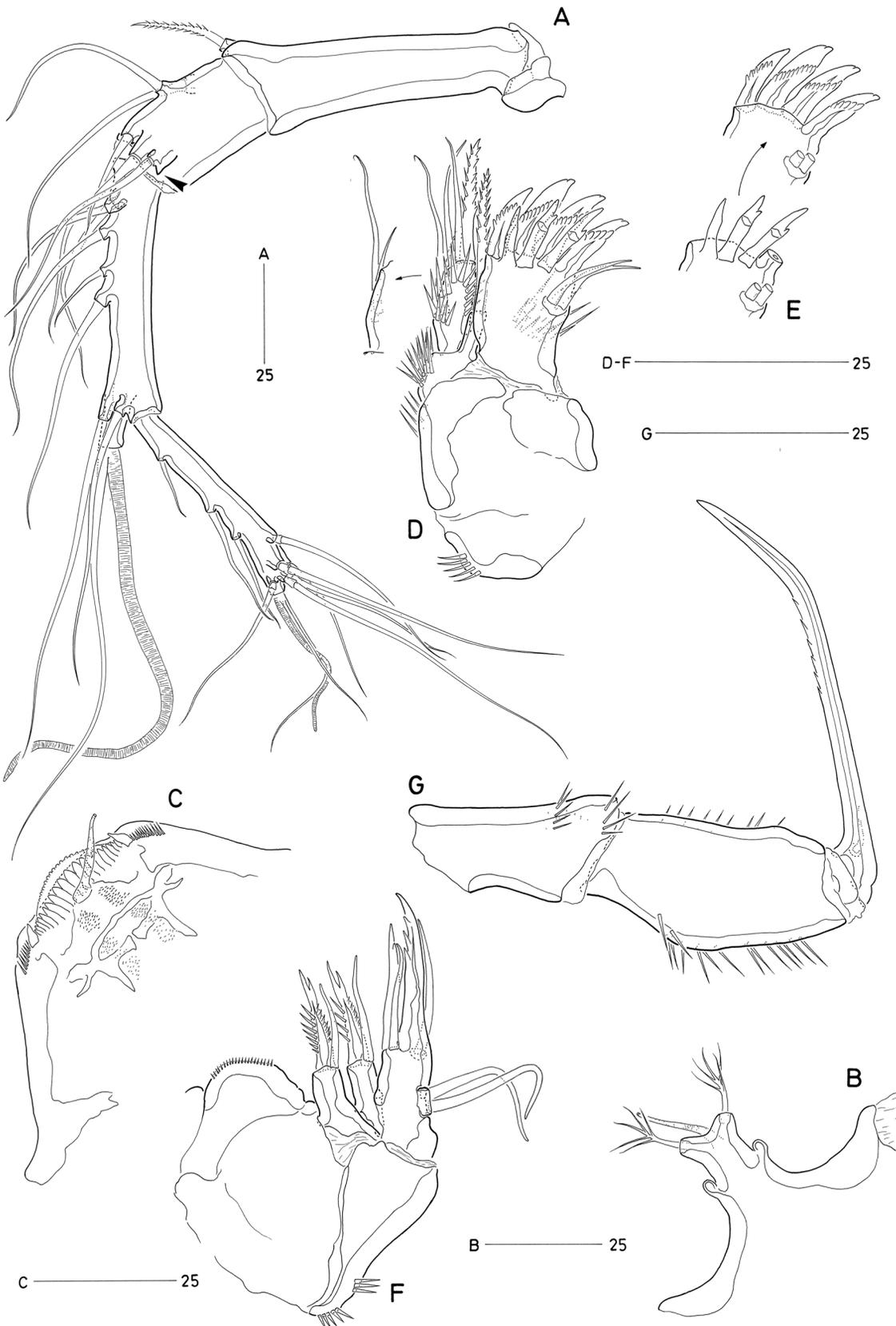
P1 (Fig. 3C). Intercoxal sclerite wide and narrow. Praecoxa moderately developed. Coxa trapezoid. Basis transversely elongate with conspicuous anterior tube-pore and spinule pattern as indicated in Fig. 3C; with pinnate outer spine and bare inner seta. Exopod 3-segmented, with few spinules along inner margins; outer spines finely pinnate; exp-3 with 3 geniculate setae and 1 pinnate outer spine. Endopod absent; original position represented by slightly membranous area arrowed in Fig. 3C.

P2-P4 (Fig. 5A-C) with wide intercoxal sclerites without ornamentation (see Fig. 5A as for P2). Praecoxae moderately developed, with few fine setules. Coxae

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**Figure 3.** *Echinopsyllus normani* (♀). **A.** cephalothorax, dorsal; **B.** mandible; **C.** P1, anterior (original position of endopod arrowed); **D.** anal somite and right caudal ramus, dorsal.

**Figure 3.** *Echinopsyllus normani* (♀). **A.** céphalothorax, vue dorsale; **B.** mandibule; **C.** P1, vue antérieure (la flèche indique la position originale de l'endopodite); **D.** somite anal et rame caudale droite, vue dorsale.



quadrangular with few spinules (P3-P4). Bases transversely elongate with long slender spinules along outer margins, inner margins with fine setules; with anterior tube-pore in distal half; outer distal seta bipinnate (P2) or short and bare (P3-P4). Exopods 3-segmented; exp-2 with inner seta. P2 endopod absent, position represented by slightly membranous area, with small nodule and few spinules. P3-P4 endopods reduced, 2-segmented (P3) or 1-segmented (P4). Armature formula as for genus.

P5 (Fig. 5D-E). Baseoendopod with tube-pore and few spinules sub-distally; setophore elongate, demarcated at base, bearing bare outer basal seta. Endopodal lobe partially absorbed, represented by small raised pedestal (Fig. 5E), with conspicuous tube-pore and 1 vestigial seta. Exopod discrete, long and slender; with sub-distal tube-pore, 1 distal pinnate seta and 3 outer setae (proximal and distal setae pinnate, median seta bare); without inner setae.

Genital field (Fig. 6B) with fused gonopores opening via common midventral slit covered by genital operculum derived from vestigial sixth legs; with conspicuous paired tube-pore just posterior to each gonopore. P6 each with 1 tiny seta. Copulatory pore moderately large.

*Male* (Figs 2; 6C-E). Smaller than ♀ (Fig. 2A); total body length 808 µm (mean = 871; n = 8) measured from anterior tip of rostrum to posterior margin of caudal rami. Sexual dimorphism in body size, degree of development of cephalothoracic posterodorsal processes and dorsal processes of P2- P3 bearing somites, rostrum size, antennule, P3 endopod, P5, P6, in genital segmentation and abdominal ventral ornamentation.

Pattern of body processes and sensillae as in ♀ (Fig. 2A). Cephalothoracic posterodorsal processes and dorsal processes of P2- P3 bearing somites relatively smaller than in ♀ (Fig. 2A). Abdominal ornamentation (Fig. 6C) as in ♀ except: first abdominal somite ventrally with short, anterior and posterior row of fine spinules; second abdominal somite without additional ventrolateral spinule patches present in ♀; and third abdominal somite hind margin with mid ventral tube-pore.

Rostrum structure as in ♀ except shorter and basally wider (Fig. 2A).

Antennule (Fig. 2B-D) 8-segmented and sub-chirocer, geniculation between segments 5 and 6; segment 4

represented by a U-shaped sclerite (Fig. 2C); segment 1 longest; segment 2 with 1 subapical anterior seta arising from distinctive spinous projection; aesthetasc present on segment 5 and as part of apical acrothek on segment 8. Armature formula: 1-[1 minutely pinnate], 2-[8 bare], 3-[6 bare + 1 vestigial], 4-[1 bare + 1 vestigial], 5-[6 bare + 5 spiniform with flagellate tip + 1 modified spine + (1 + ae)], 6-[3 modified], 7-[1], 8-[7 bare + acrothek]. Modified elements on segment 6 fused to segment and with flagellate tip. Acrothek consisting of 2 bare setae plus aesthetasc.

Antenna, mandible, maxillule, maxilla, maxilliped, P1-P2, P3 exopod, P4 as in ♀.

P3 endopod (Fig. 2E) 3-segmented; enp-2 elongate, anterior distal surface produced into small, recurved apophysis; enp-3 with 1 plumose and 1 small seta apically.

P5 (Fig. 6D). Baseoendopod as in ♀. Exopod discrete, long and slender; with sub-distal tube-pore, 1 distal and 2 outer pinnate setae; without inner setae.

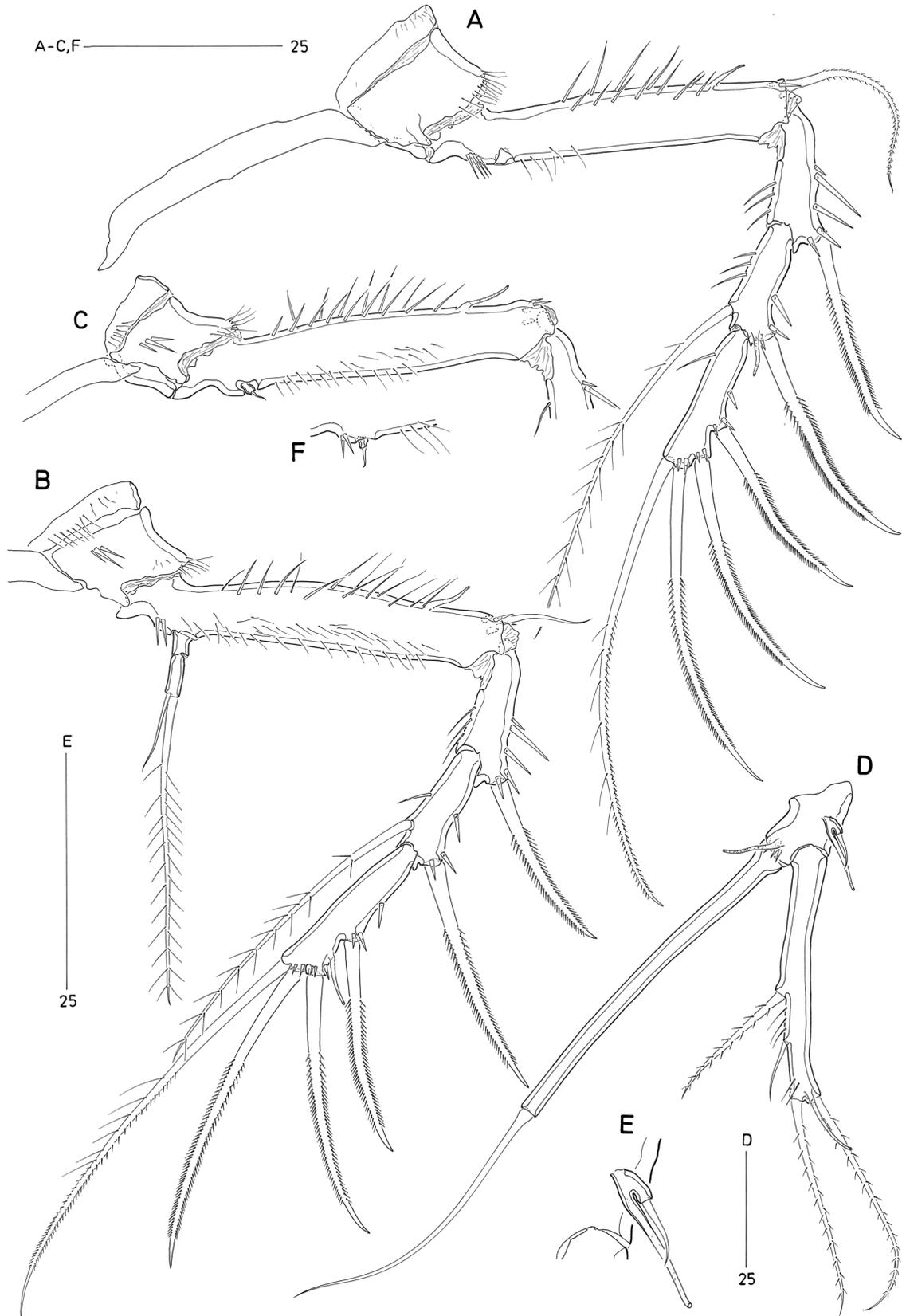
Sixth pair of legs asymmetrical (Fig. 6C), with only 1 functional member, represented by membranous flap; P6 without armature. Spermatophore small (Fig. 6C), 54 µm.

*Copepodid III* (Figs 7C; 8C-D; 9). Body (Fig. 7C) comprising cephalothorax and six body somites; integument weakly chitinized and body basically cylindrical; sensillae unmodified. Cephalothorax (Fig. 7C) not sculptured; with paired lateral conical processes present halfway cephalothorax length bearing conspicuous tube-pore subterminally and additional ventral sensilla; anterior and posterior outer corners without produced processes; anterior corners without tube-pore. Precursor of anterodorsal processes found in adult represented by small tubercles. Paired posterodorsal sensillae (precursor of paired posterodorsal produced conical processes in adult) absent. Posterodorsal paired sensory triplet present (arrowed in Fig. 7C), comprising proximally reinforced conspicuous tube-pore, and 2 sensillae. Free thoracic somites (bearing P2-P5) with sensillar pattern as that in adult except without 1 pair laterodorsal sensillae; precursor of posterodorsal processes found in adult represented by small sensillate tubercles. Penultimate (last thoracic) somite without sensory structures; with fine setules along hind margin. Anal somite anterolateral margin with tube-pore; anal operculum



**Figure 4.** *Echinopsyllus normani* (♀). **A.** antennule, dorsal (spinous projection bearing anterior seta arrowed); **B.** rostrum, dorsal; **C.** labrum, anterior; **D.** maxillule; **E.** maxillule, distal portion of arthrite with 3 anteriormost elements (inset showing 4 posteriormost elements); **F.** maxilla; **G.** maxilliped.

**Figure 4.** *Echinopsyllus normani* (♀). **A.** antennule, vue dorsale (la flèche indique la projection épineuse portant la soie antérieure) ; **B.** rostre, vue dorsale ; **C.** labre, vue antérieure; **D.** maxillule ; **E.** maxillule, portion distale de l'arthrite montrant les 3 épines antérieures (l'encart indique les 4 épines postérieures) ; **F.** maxille; **G.** maxillipède.



rounded with few fine setules. Caudal rami elongate and divergent; general morphology and position of caudal setae I-VII as in adult; seta V longest, bare.

Rostrum (Fig. 7C) fused to cephalic shield; small, without basal constriction and elongation; paired unmodified sensillae arising from tiny raised pedestal, forming vaguely bifid apical margin; with paired bulbous membranous projections laterally; with midventral tube-pore.

Antennule (Fig. 7C) 4-segmented. Segment 4 longest, segment 2 shortest. Aesthetasc present on segments 3 and 4. Segment 2 without sub-apical spinous projection bearing 1 dorsal seta. Segment 4 with apical acrothek consisting of aesthetasc and 2 slender setae. Armature formula: 1-[1], 2-[3], 4-[6 + (1+ae)], 4-[9 + acrothek].

General morphology and armature formula of antenna, mandible, maxillule, maxilla and maxilliped as in adult.

P1 basis transversely elongate, inner basal seta arising from small pedestal. Exopod 2-segmented; exp-2 and exp-3 forming compound segment; full complement of armature present as in adult; exp-1 with 1 outer spine; exp-2 with 3 geniculate setae and 2 outer spines. Endopod absent. For schematic see Fig. 9.

P2-P4 with wide intercoxal sclerites. Bases transversely elongate. P2-P3 exopods 2-segmented, P4 1-segmented. Exp-2 with inner seta P2, without P3-P4. P2 endopod absent. P3 endopod (Fig. 8C) 2-segmented, segments minute and of equal size; exp-2 with 2 reduced apical setae. P4 endopod represented by minute segment, fused to basis with 1 vestigial seta apically. Schematic of armature formula see Fig. 9.

P5 (Fig. 8D) minute lobe, not discrete; with 2 setae apically.

*Copepodid IV* ♀ (Figs 7B; 8E, G; 9). Body (Fig. 7B) with cephalothorax and seven body somites; integument weakly chitinized and body basically cylindrical. Cephalothorax (Fig. 7B) weakly sculptured; with paired lateral conical processes present halfway cephalothorax length bearing conspicuous tube-pore subterminally and additional ventral sensilla; anterior outer corners slightly produced; posterior outer corners with small conical process. Anterodorsal backwardly projecting processes moderately developed. Posterodorsal paired processes represented by small sensillate tubercles (arrowed in Fig. 7B); paired posterodorsal sensory triplet present, comprising proximally reinforced conspicuous tube-pore, and 2 sensillae. Anterior

corners of cephalothoracic with tube-pore. Free thoracic somites (bearing P2-P5) with sensillar pattern as in adult; with small paired dorsal tubercles bearing sensilla representing precursors of dorsal conical processes in adult. Last thoracic somite with pair of dorsal sensillae. Penultimate (first abdominal) somite with paired dorsal tube-pores and with fine setules along hind margin. Anal somite with anterolateral tube-pore; anal operculum rounded with few fine setules. Caudal rami elongate and divergent; general morphology and position of caudal setae I-VII as in adult; seta V longest, pinnate.

Rostrum (Fig. 7B) fused to cephalic shield; small, without basal constriction and elongation; paired sensillae arising from tiny raised pedestal, forming vaguely bifid apical margin; with paired bulbous membranous projections laterally; with midventral tube-pore.

Antennule (Fig. 7B) 4-segmented. Segments 1, 3 and 4 elongate, segment 2 shortest. Aesthetasc present on segments 3 and 4. Segment 2 with sub-apical projection bearing dorsal seta. Segment 4 with apical acrothek consisting of aesthetasc and 2 slender setae. Armature formula: 1-[1], 2-[5], 4-[6 + (1+ae)], 4-[9 + acrothek].

General morphology and armature formula of antenna, mandible, maxillule, maxilla and maxilliped as in adult.

P1 basis transversely elongate, inner basal seta arising from small pedestal. Exopod 2-segmented; exp-2 and exp-3 not separated; full complement of armature present as in adult; exp-1 with 1 outer spine; exp-2 with 3 geniculate setae and 2 outer spines. Endopod absent. For schematic see Fig. 9.

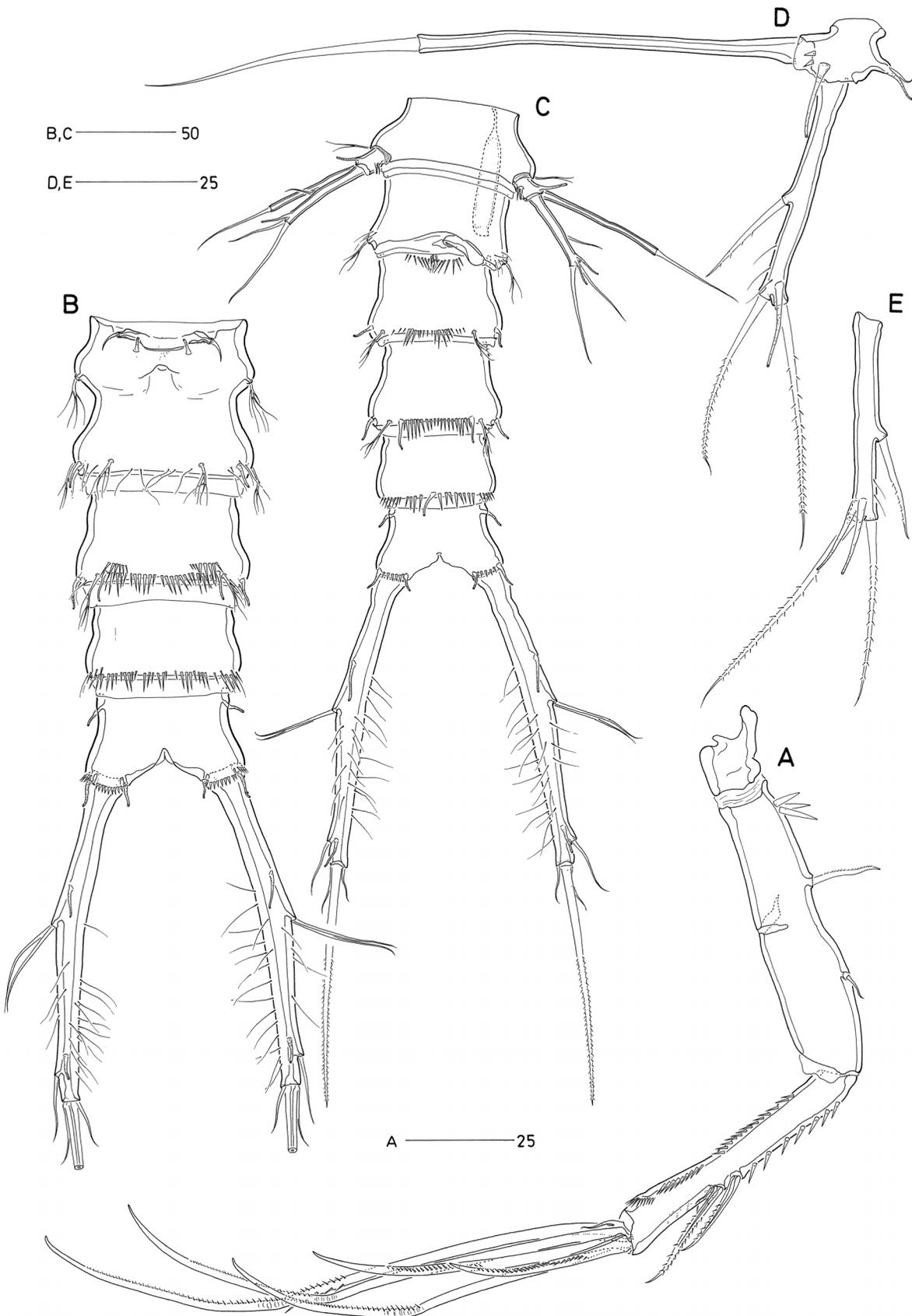
P2-P4 with wide intercoxal sclerites. Bases transversely elongate. P2-P4 exopods 2-segmented; exp-2 with inner seta (minute in P4). P2 endopod absent. P3 endopod (Fig. 8E) 2-segmented; exp-2 with 2 small apical setae. P4 endopod 1 minute discrete segment, with 1 vestigial seta apically. Schematic of armature formula see Fig. 9.

P5 (Fig. 8G). Baseoendopod with tub-pore; with basal setophore demarcated at base; with 1 minute seta and tube-pore representing endopodal elements. Exopod not separated, represented by sub-rectangular lobe, with 3 outer setae (proximal 2 reduced), 1 seta apically and sub-distal tube-pore.

*Copepodid IV* ♂ (Fig. 8F, H). General structure and morphology of body and all appendages as in CIV ♀ except for the following:

**Figure 5.** *Echinopsyllus normani*. **A.** (♀) P2, anterior; **B.** (♀) P3, anterior; **C.** (♀) P4 protopod and endopod, anterior; **D.** (♀) P5, anterior; **E.** (♀) P5 endopodal lobe; **F.** (♂) P4 endopod, anterior.

**Figure 5.** *Echinopsyllus normani*. **A.** (♀) P2, vue antérieure; **B.** (♀) P3, vue antérieure; **C.** (♀) P4 protopodite et endopodite, vue antérieure; **D.** (♀) P5, vue antérieure; **E.** (♀) P5, lobe de l'endopodite; **F.** (♂) endopodite de P4, vue antérieure.



P3 endopod (Fig. 8F) 2-segmented; enp-1 slightly smaller than enp-2; enp-2 outer margin with tiny notch sub-distally, with 2 apical setae.

P5 (Fig. 8H) with 2 outer setae, proximal one reduced.

*Copepodid V* ♀ (Figs 7A; 8I, K; 9). Body (Fig. 7A) with cephalothorax and eight body somites; integument weakly chitinized and body basically cylindrical. Cephalothorax (Fig. 7A) moderately sculptured. Body sensillar and produced process patterns as that of adult except: (a) dorsal processes in general less well developed, represented by produced tubercles without ornamentation; (b) cephalothoracic paired posterodorsal sensory triplet comprising distinctive tube-pore and 2 sensillae (cf adult with large pore and 2 sensillae); (c) first abdominal somite with 1 pair separated dorsal conical processes, with tube-pore basally and (d) second abdominal somite (penultimate) without produced sensillate processes. Anal somite anterolateral margin with tube-pore; anal operculum rounded with few fine setules. Caudal rami elongate and divergent; general morphology and position of caudal setae I-VII as in adult; seta V longest, pinnate.

Rostrum (Fig. 7A) fused to cephalic shield; small, with slight basal constriction and elongation; paired branched sensillae arising from tiny raised pedestal, forming vaguely bifid apical margin; with paired bulbous membranous projections laterally; with midventral tube-pore.

Antennule (Fig. 7A) 4-segmented. Segments 1, 3 and 4 elongate, segment 2 shortest. Aesthetasc present on segments 3 and 4. Segment 2 shortest, with sub-apical spinous projection bearing dorsal seta. Segment 4 with apical acrothek consisting of aesthetasc and 2 slender setae. Armature formula: 1-[1], 2-[5], 4-[7 + (1+ae)], 4-[9 + acrothek].

General morphology and armature formula of antenna, mandible, maxillule, maxilla and maxilliped as in adult.

P1-P4 segmentation and armature formula as in adult (Fig. 9) except P3 endopod (Fig. 8I) 2 segmented, both segments virtually equal in size, setae less developed.

P5 (Fig. 8K). Baseoendopod with tube-pore; basal setophore elongate and demarcated at base; endopodal lobe represented by small raised pedestal, with 1 minute seta and tube-pore. Exopod not separated, sub-rectangular in shape, with 3 outer setae, 1 seta apically and sub-distal tube-pore.

*Copepodid V* ♂ (Figs 8J, L; 9). General structure and

morphology of body and appendages as in CV ♀ except for the following:

Antennule 4-segmented; aesthetasc arising from segments 3 and 4. Segment 2 shortest, with sub-apical spinous projection bearing dorsal seta. Segment 4 tapering apically, with acrothek (comprising 2 setae and aesthetasc) arising sub-distally. Armature formula 1-[1], 2-[8], 3-[16 + (1+ae)], 4-[10 + acrothek].

P3 endopod (Fig. 8J) 2-segmented; enp-1 small, unarmed; enp-2, 2.85 times as long as enp-1, outer margin produced sub-distally into small pointed apophysis, with 2 setae apically.

P5 (Fig. 8L) Basic structure as in CV ♀ except: exopodal lobe more slender and proportionally more elongate, with tube-pore sub-distally, 1 apical and 2 outer setae.

*Variability.* The adult male specimen figured and described here exhibited an asymmetrical condition in the P5, with the left exopod being slightly shorter and bearing 2 sub-distal tube-pores (Fig. 6E).

*Distribution.* Norway: Farsund and Korshavn, depth 37 m (Sars, 1909); Korsfjord, Bömlafjord, Björnefjord, Fanafjord and Husnesfjord, depth 340-680 m (Drzycimski, 1969); Frierfjord/Langesundfjord, depth 99 m (present account). Sweden: Gullmarfjord, depth 30-110 m (Lang, 1936, 1948). Scotland: Fladen Bank, depth 146 m (Wells, 1965).

Coull (1973) identified 1 ♀ of *Echinopsyllus* sp. from 3000 m depth off North Carolina (34°14.0' N, 75°20.0' W). This is the only record of the genus outside NW Europe and may well represent a different species considering the limited geographical distribution of most ancorabolids. The North Carolina material is unfortunately lost (B.C. Coull, pers. comm.).

## Discussion

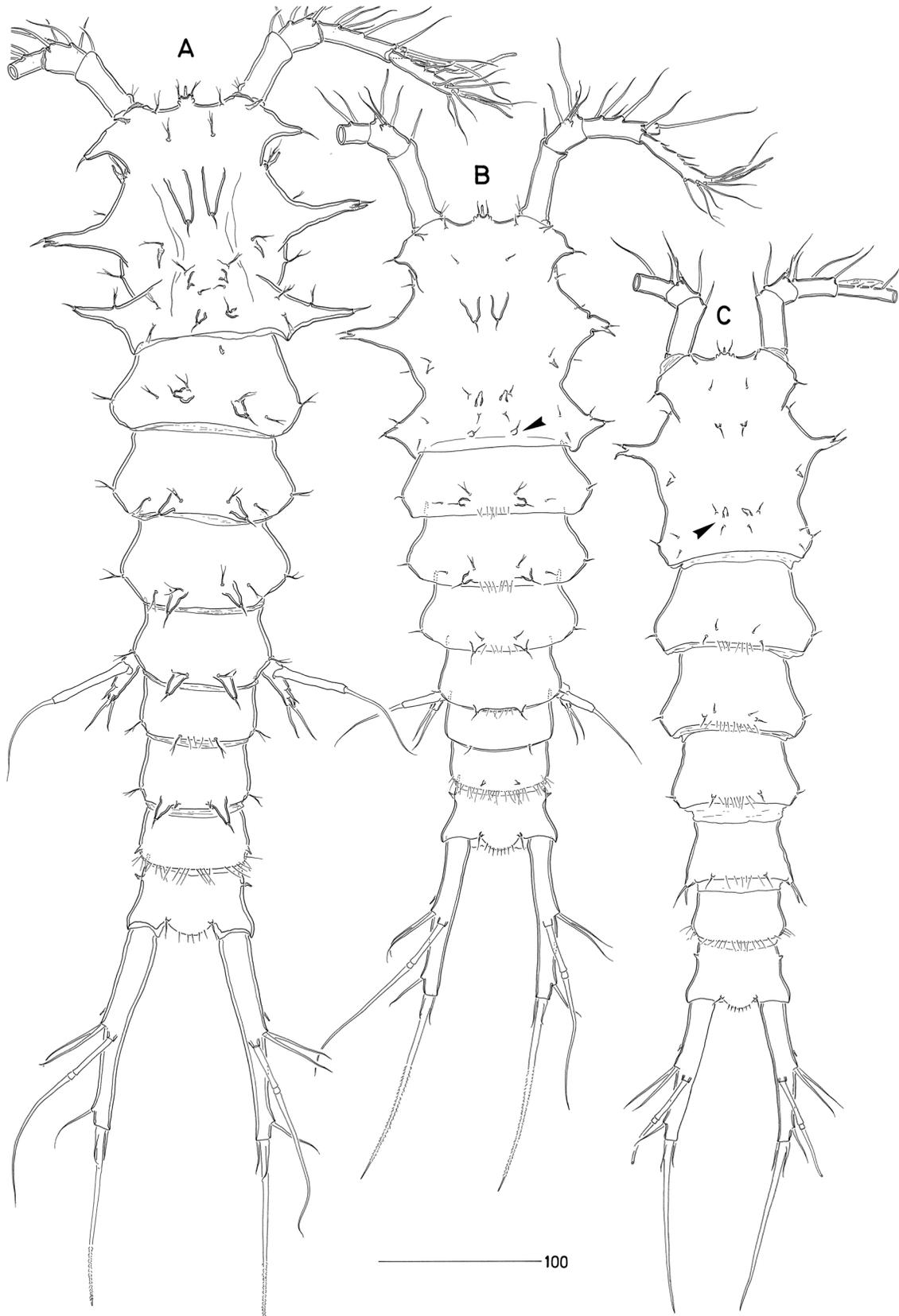
In his account of the Crustacea of Norway Sars (1909) described the new genus and species *Echinopsyllus normani* based on two female specimens, one collected from Farsund and the other from Korshavn. Without describing the male in any detail or providing any figures, Lang on two separate occasions (1936, 1948) provided some cursory information on males of *E. normani* he collected from Gullmarfjord, Sweden. Firstly, Lang (1936) noted that the male P3 endopod is 3-segmented with a process arising from the

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**Figure 6.** *Echinopsyllus normani*. A. (♀) antenna; B. (♀) urosome, ventral (excluding P5-bearing somite); C. (♂) urosome, ventral; D. (♂) P5, anterior; E. (♂) P5 aberrant exopod, anterior.

**Figure 6.** *Echinopsyllus normani*. A. (♀) antenne; B. (♀) urosome, vue ventrale (sauf le somite portant P5); C. (♂) urosome, vue ventrale; D. (♂) P5, vue antérieure; E. (♂) P5 exopodite aberrant, vue antérieure.



second segment, and subsequently (Lang, 1948) added that the male is slightly smaller than the female and that the size (but not structure) of the P5 is slightly different between the sexes. Wells (1965) stated that the male specimen collected from the Fladen Bank, North Sea is identical to the female except in the following characters: (a) 4-segmented antennule, segment 3 broader than in ♀, segment 4 with curved distal portion; (b) 2-segmented P3 endopod, enp-2 apically with 1 spine and 2 setae (which he figured) and (c) P5 exopod with only 1 outer seta. Re-examination of Wells' slide material (NHM reg. no. 1965.3.26.20) and morphological comparison with the adult and copepodid stages described above, shows the North Sea specimen to be a male copepodid V stage. The three sexually dimorphic characters listed by Wells (1965) are confirmed here as juvenile and diagnostic for a ♂ CV, although it appears that the apophysis arising from enp-2 was misinterpreted as a spine in his Fig. 110 (see above description for CV ♂ and Fig. 8J for comparison).

The present study also removes the historical confusion surrounding the nature of the endopods of the swimming legs. It is shown that for the P1, what has consistently been interpreted as a rudimentary unisetose endopod, is in fact the inner basal seta arising from a small pedestal. The P1 endopod is completely absent, as is that of the P2. The original position of this ramus is marked by a membranous insert on the distal margin of the basis of both P1 and P2 (Figs 3C, 5A). The P3 possesses a small 2-segmented endopod in the ♀, and a 3-segmented endopod in the ♂ (with the apophysis arising from segment 2). The P4 endopod is a minute segment bearing 1 vestigial seta in both sexes.

The ontogenetic data presented here, demonstrates the gradual development of body processes, being correlated with a remarkable consistency in body sensillar patterns between stages. The copepodid III stage (Fig. 7C) shows a very simple body morphology, displaying only the middle pair of cephalic lateral conical processes. The general sensillar pattern is however, very similar to that found in the adult with only a few exceptions. Most notably, the CIII stage lacks one pair of sensillae around the posterior margins of the cephalothorax and body somites bearing P2-P5. On the cephalothorax one pair of dorsal sensillate tubercles is added in the CIV stage (arrowed in Fig. 7B).

Vertical tracking of these structures through later phases of copepodid development, show them to be the precursors of the posterodorsal conical processes found in the adult. Hence, the absence of dorsal tubercles at the CIII stage is directly related to the absence of the posterodorsal pair of sensillae. On the pedigerous somites (P2-P5) one additional pair of laterodorsal sensillae becomes expressed at CIV stage, but these are not involved in the subsequent elaboration of the dorsal conical processes (the precursors of which are present from at least CIII stage, see Fig. 7C). The posterodorsal sensory triplet isolated in the adults is shown to be expressed from at least the CIII stage (arrowed in Fig. 7C) onwards.

The pattern of swimming leg development from CIII stage to adult is presented in Fig. 9 in schematic form. Note that the male P3 endopodal development has been omitted (refer to Figs 2E, 8F, J for adult, CIV and CV stages respectively).

The genus *Echinopsyllus* occupies an isolated position in the Ancorabolinae. Two distinct lineages have already been recognised within the sub-family, the *Ancorabulus*-group and the *Ceratonotus*-group. Based on the characters used to define these two groups (Conroy-Dalton & Huys, 2000; Conroy-Dalton, 2001) *Echinopsyllus* cannot be readily accommodated in either of them. *Echinopsyllus* appears to be more closely related to the *Ceratonotus*-group on account of the absence of wing-like lateral body processes, the cylindrical nature of the body in general, the antennule segmentation, the ♀ P5 with vestigial endopodal lobe. However, *Echinopsyllus* can be readily characterised by: (a) cephalothorax with 3 pairs of well developed lateral conical processes; (b) dorsal conical processes on first and second abdominal somites arising from a common mid dorsal base; (c) presence of dorsal processes on second abdominal somite; (d) the mandibular palp with 4 setae; and (e) the sexual dimorphism displayed in P5 exopodal armature. Its precise position within the ancorabolid-cletodid complex will be addressed in a forthcoming phylogenetic analysis evaluating the potentially polyphyletic status of the Ancorabolidae (Conroy-Dalton & Huys, in prep.).

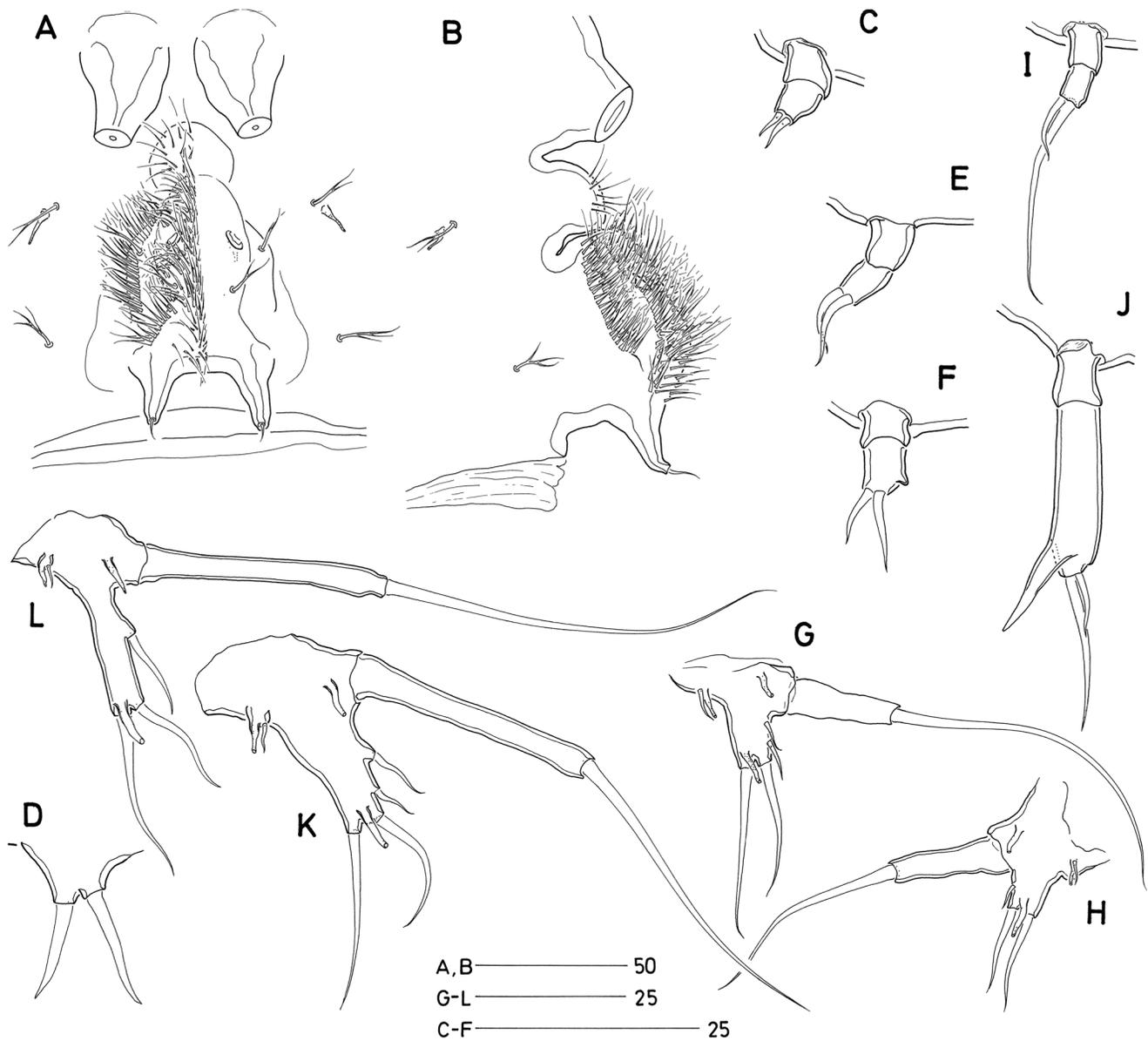
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**Figure 7.** *Echinopsyllus normani*. **A.** (♀) copepodid V habitus, dorsal; **B.** (♀) copepodid IV habitus, dorsal (posterior dorsal sensillate tubercle arrowed); **C.** copepodid III habitus, dorsal (sensory triplet arrowed).

**Figure 7.** *Echinopsyllus normani*. **A.** (♀) copépodite V habitus, vue dorsale; **B.** (♀) copépodite IV habitus, vue dorsale (la flèche indique le tubercule sensillaire postérodorsal); **C.** copépodite III habitus, vue dorsale (la flèche indique le triplé sensoriel).

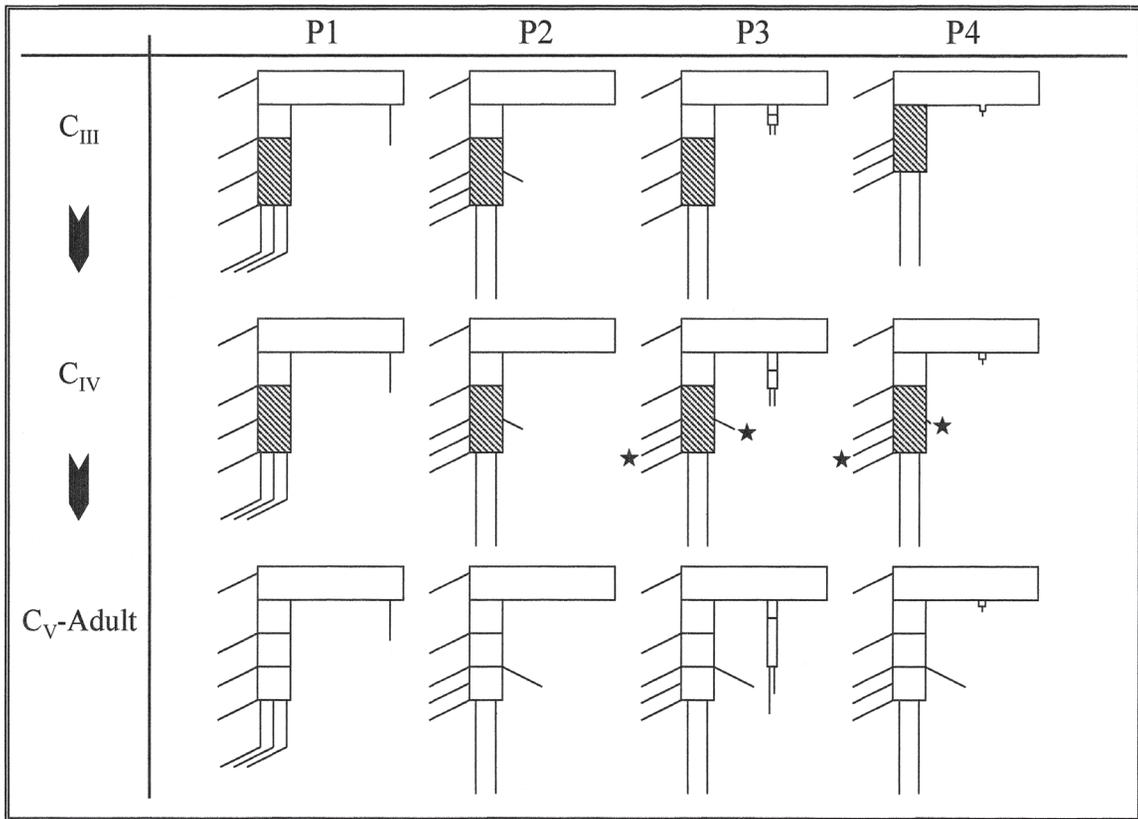


**Figure 8.** *Echinopsyllus normani*. Adult (♀): **A.** cephalothorax posterior part (setules on right side omitted for clarity), dorsal; **B.** same lateral. Copepodid III: **C.** left P3 endopod, anterior; **D.** right P5, anterior. Copepodid IV: **E.** (♀) left P3 endopod, anterior; **F.** (♂) same; **G.** (♀) left P5, anterior; **H.** (♂) right P5, anterior. Copepodid V: **I.** (♀) left P3 endopod, anterior; **J.** (♂) right P3 endopod, anterior; **K.** (♀) left P5, anterior; **L.** (♂) same.

**Figure 8.** *Echinopsyllus normani*. Adulte (♀) : **A.** partie postérieure du céphalothorax (sétules de la partie droite omises pour plus de clarté), vue dorsale; **B.** idem, vue latérale. Copépodite III : **C.** endopodite gauche de P3, vue antérieure ; **D.** P5 droite, vue antérieure. Copépodite IV : **E.** (♀) endopodite gauche de P3, vue antérieure ; **F.** (♂) idem ; **G.** (♀) P5 gauche, vue antérieure ; **H.** (♂) P5 droite, vue antérieure. Copépodite V : **I.** (♀) endopodite gauche de P3, vue antérieure ; **J.** (♂) endopodite droit de P3, vue antérieure ; **K.** (♀) P5 gauche, vue antérieure ; **L.** (♂) idem.

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**Figure 9.** *Echinopsyllus normani* (♀). Schematic depicting swimming leg (P1-P4) development C III - adult. Asterisks indicate newly acquired setae. Shaded areas indicate compound segments that subdivide later in development.

**Figure 9.** *Echinopsyllus normani* (♀). Schéma montrant le développement des pattes natatoires (P1-P4) du CIII à adulte. Les astérisques indiquent les soies nouvellement apparues. Les surfaces hachurées indiquent les segments qui se subdivisent ultérieurement au cours du développement.

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