Systematics and phylogeny of the Ancorabolidae (Copepoda : Harpacticoida). I. The Ancorabolus-lineage, with the description of three new genera.

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Systematics and Phylogeny of the Ancorabolidae (Copepoda: Harpacticoida). I. The *Ancorabolus*-lineage, with the description of three new genera.

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Abstract: The *Ancorabolus*-group is recognized within the sub-family Ancorabolinae (Harpacticoida, Ancorabolidae) comprising *Ancorabolus*, *Arthropsyllus* and three new genera: *Breviconia* gen. nov., *Juxtaramia* gen. nov and *Uptionyx* gen. nov. The common ancestry of these genera is supported by antennulary segmentation, rostral morphology, cephalothoracic sensillar patterns, presence of lateral body processes, elongation of P1 endopod, segmentation of ♂ P3 endopod and P5 armature in both sexes.

Two new species of *Ancorabolus* are described from Frierfjord/Langesundfjord in Norway. *A. inermis* sp. nov. and *A. confusus* sp. nov. occur sympatrically in southern Scandinavia and can be readily differentiated by the pattern of body processes. Re-examination of Sars' (1909) material revealed that his widely adopted redescription of the type species *A. mirabilis* was based on an amalgamate of these two species. All records of *A. mirabilis* from outside the Firth of Clyde (Scotland) which cannot be identified as *A. inermis* or *A. confusus* have to be regarded as unconfirmed. Norman's (1903) material of *A. mirabilis* collected in East Finmark (Norway) and erroneously designated as types, is radically divergent in cephalic process pattern, caudal ramus configuration, antennary armature and P1 morphology. It is allocated to a new genus and species, *Juxtaramia polaris*.

Both sexes of *Arthropsyllus serratus* are redescribed from new and existing material collected in southern Norway. Re-examination of Norman's (1911) material from the Firth of Clyde did not provide any conclusive evidence to maintain *A. serratus spinifera* as a valid subspecies. *A. australis* is transferred as the type species of a new genus *Breviconia*, since it deviates significantly from the revised diagnosis of *Arthropsyllus*. *Laophontodes echinatus* Brady, 1918 is regarded as *species inquirenda* in *Breviconia*.

A new genus and species, *Uptionyx verenae*, is described from a hydrothermal vent of the Juan de Fuca Ridge, northeastern Pacific Ocean.

Parsimony analysis of the *Ancorabolus*-group identifies *Arthropsyllus* as the most primitive offshoot and *Juxtaramia*-*Ancorabolus* as the terminal clade with both *Uptionyx* and *Breviconia* diverging from intermediate nodes. Evolution in the group is typified by progressive elaboration and ramification of integumental processes on the cephalothorax and free body somites, culminating in the complex body ornamentation of the most advanced genus *Ancorabolus*. Distribution records of all five genera are compiled.

Résumé : *Systématique et phylogénie des Ancorabolidae (Copepoda: Harpacticoida). I. Lignée des* Ancorabolus*, et description de trois nouveaux genres*. Dans la sous-famille des Ancorabolinae (Harpacticoida, Ancorabolinae) un groupe

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Ancorabolus est distingué. Il comprend les genres *Ancorabolus*, *Arthropsyllus* et trois nouveaux genres : *Breviconia* gen. nov., *Juxtaramia* gen. nov. et *Uptionyx* gen. nov. Le tronc commun de ces genres est fondé sur la segmentation de l'antennule, la morphologie du rostre, le modèle des éléments sensillaires céphalothoraciques, la présence d'excroissances latérales le long du corps, l'élongation de l'endopodite P1, la segmentation de l'endopodite P3 ♂ et l'armature des P5 des deux sexes.

Deux espèces nouvelles d'*Ancorabolus* sont décrites de Frierfjord/Langesundfjord en Norvège. *A. inermis* sp. nov. et *A. confusus* sp. nov. sont présentes conjointement dans le sud de la Scandinavie et peuvent être différenciées d'emblée par l'aspect des excroissances du corps. Un nouvel examen du matériel de Sars (1909) a révélé que sa redescription, largement adoptée, de l'espèce-type *A. mirabilis* est fondée sur un amalgame de deux espèces. En conséquence, tous les signalements de *A. mirabilis* ailleurs que dans l'estuaire de la Clyde (Écosse), et qui ne peuvent être identifiés comme étant soit *A. inermis* soit *A. confusus*, doivent être considérés comme incertains. Le matériel de Norman (1903) identifié sous le nom de *A. mirabilis* et collecté dans l'East Finmark (Norvège), et désigné par erreur comme espèce-type, diffère radicalement de cette espèce par la structure des excroissances céphaliques, la configuration des rames caudales, l'armature des antennes et la morphologie des P1. Ce matériel est donc placé dans un nouveau genre et une nouvelle espèce, *Juxtaramia polaris*.

Les deux sexes de *Arthropsyllus serratus* sont redécrits à partir d'un matériel existant et d'un matériel prélevé dans le sud de la Norvège. Un ré-examen du matériel de Norman (1911) provenant de l'estuaire de la Clyde n'a pas fourni de raisons sérieuses pour maintenir *A. serratus spinifera* comme sous-espèce valable. *A. australis* est transférée comme espèce-type dans le nouveau genre *Breviconia*, car elle diffère significativement de la nouvelle diagnose d'*Arthropsyllus*. *Laophontodes echinatus* est considérée comme *species inquirenda* dans le genre *Breviconia*.

Une nouvelle espèce, appartenant à un nouveau genre, *Uptionyx verenae*, est décrite d'un site hydrothermal de la dorsale de Juan de Fuca, dans le nord-est de l'océan Pacifique.

Une analyse, appliquant le principe de parcimonie, du groupe *Ancorabolus* identifie *Arthropsyllus* comme la lignée la plus primitive, et l'ensemble *Juxtaramia*-*Ancorabolus* comme la branche terminale, avec *Uptionyx* et *Breviconia* divergeant à partir de nœuds intermédiaires. A l'intérieur du groupe, l'évolution est caractérisée par l'élaboration progressive et la ramification des excroissances tégumentaires sur le céphalothorax et les segments libres du corps, aboutissant à l'ornementation complexe du genre le plus évolué *Ancorabolus*. La répartition géographique des signalements des cinq genres est indiquée.

Keywords: Copepoda, Harpacticoida, Ancorabolidae, *Ancorabolus*-group, systematics, phylogeny.

Introduction

The Ancorabolidae is one of the most visually striking families of harpacticoid copepods, readily identifiable by the distinctive morphology and typically characterized by conspicuous body processes and integumental outgrowths. Consequently, it is not surprising that this group has attracted attention quite early on from prolific natural historians such as the Rev. Canon A. M. Norman and G. O. Sars. The family Ancorabolidae was established in 1909 by Sars for *Ancorabolus mirabilis* Norman, 1903 and three new monotypic genera: *Arthropsyllus* Sars, 1909, *Ceratonotus* Sars, 1909 and *Echinopsyllus* Sars, 1909. Lang (1936) widened the diagnostic boundaries of the family to accommodate the genus *Laophontodes* T. Scott, 1894 which he had transferred from the Laophontidae. Lang (1944, 1948) subsequently divided the family into the Ancorabolinae and the Laophontodinae, separating the two subfamilies on the basis of body ornamentation (including produced body processes), ♀ antennulary segmentation, P1 morphology (with particular regard to the basis and endopod) and the number of outer spines on P2-P4 exp-3. Since Lang's (1948) review, the number of species in the Ancorabolidae has more than doubled, the family currently containing 42 species and subspecies in 13 genera.

Members of the Ancorabolinae have frequently been recorded from European waters and the subfamily has traditionally been thought of assuming a North Atlantic distribution. Recent investigations, however, suggest a more extensive distribution of the Ancorabolinae (and the Laophontodinae), possibly stretching almost continuously from the Arctic (Norman, 1903, 1911; Sars, 1909; Smirnov, 1946; George, 1998b) to the (sub-) Antarctic (Brady, 1918; George, 1998a; George & Schminke 1998). The subfamily currently comprises 7 genera with 18 species and subspecies. Although some species have occasionally been reported from brackish water (Kunz, 1935) and sandy sediments (Drzycimski, 1969; Moore et al., 1987), most Ancorabolinae typically inhabit the flocculent upper layers of muddy substrata. They have been reported from depths ranging from 22-1440 m and their densities are generally low to very low (Table 1).

The monophyly of the two ancorabolid subfamilies and their position within the Harpacticoida have not been readdressed since Lang (1948), neither have their phylogenetic relationships been analysed. The impetus for such an analysis was provided by the recent discovery of a new genus of Ancorabolinae during our ongoing investigations of hydrothermal vent copepods. Hydrothermal vents are among the most spectacular deep-

Table 1. Distribution records for species of *Ancorabolus*, *Arthropsyllus*, *Breviconia*, *Juxtaramia* and *Uptionyx*.
Tableau 1. Signalisations d'espèces des genres *Ancorabolus*, *Arthropsyllus*, *Breviconia*, *Juxtaramia* et *Uptionyx*.

Species	Locality	Depth	Sediment Type	Material	Reference
Ancorabolus mirabilis	Little Cumbrae island, Firth of Clyde, Scotland	36.6 m	dredge, high in particulate matter	?	Norman (1903, 1911)
A. inermis	Norwegian coast	29-55 m	high level detritus/ particulate matter	20 ♀♀	present study (Sars coll.)
	Frierfjord/Langesundfjord, Norway	99 m	mud	54 ♀♀, 4 ♂♂	present study
	Gullmarfjord, Sweden	60 m	mud	4 ♀♀	present study (Lang coll.)
	Off River Tyne, England	72 m	mud/fine sand	1 ♂	present study
A. confusus	Norwegian coast	29-55 m	high level detritus/ particulate matter	9 ♀♀	present study (Sars coll.)
	Fanafjord, Norway	100 m	sand/gravel	1 ♀	Drzycimski (1969)
	Husnesfjord, Norway	65 m	sand	1 ♂	Drzycimski (1969)
	Raunefjord, Norway	145 m	soft mud	1 copepodid	Drzycimski (1969)
	Frierfjord/Langesundfjord, Norway	99 m	mud	58 ♀♀, 3 ♂♂	present study
	Gullmarfjord, Sweden	60 m	mud	4 ♀♀	present study (Lang coll.)
Ancorabolus sp. indet.	Norwegian coast	29-55 m	high level detritus/ particulate matter	several	Sars (1909)
	Kosterfjord, Skagerak, Norway	72 m	sandy mud	?	Por (1964)
	North Koster, Skagerak, Norway	215 m	deep mud	?	Por (1964)
	Bjornehodenbukta, Oslofjord, Norway	35 m	fine silt	68	Gee et al. (1985)
	Gullmarfjord, Sweden	30-70 m	mud	{ 35 ♀♀ +	Lang (1948)
	Måseskär, Sweden	145 m	mud	1 ♂ in total	Lang (1948)
	Loch Nevis, Scotland	101 m	mud	1 ♀	Wells (1965)
	180 km southwest of Shetland Isles, Scotland	115 m	silty sand	several	Moore et al. (1987)
Arthropsyllus serratus	Karelian coast, White Sea, Russia	?	?	2 ♀♀	Chislenko (1967)
	Bejan, Trondhjem Fjord, Norway	22-55 m	mud	several ♀♀	Sars (1909)
	Repvaag, East Finmark, Norway	?	?	1 ♂	Sars (1909)
	Frierfjord/Langesundfjord, Norway	99 m	mud	4 ♀♀, 1♂	present study
	Kiel Bay, Germany	?	black mud	1 ♀	Kunz (1935)
	Kiel Bay, Germany	18-24 m	fine mud-muddy sand	several	Becker (1970)
	East of Darss Sill, Baltic Sea	45 m	grey mud	1♀	Arlt (1983)
	Little Cumbrae island, Firth of Clyde, Scotland	36.6 m	dredge, high in particulate matter	?	Norman (1911)
Breviconia australis	Gardiner Island, Beagle Channel, Chile	100 m	?	1 ♀	George (1998a)
B. echinata	Antarctica, off Wilkes Land, Australian Territory	82 m	tow-net among pack-ice	1 ♀	Brady (1918)
Juxtaramia polaris	Varanger Fjord, East Finmark, Norway	?	mud	4 ♀♀, 1♂	present study (Norman coll.)
Uptionyx verenae	Juan de Fuca Ridge, Northeastern Pacific Ocean	2417 m	macroinvertebrate washings	4 ♀♀	present study

sea features revealed during the last decades, and extensive explorations have led to the discovery of unusual and often bizarre vent faunal communities. Although harpacticoids have been collected from a wide range of vent fields, identified records from these habitats are still rare (Huys & Conroy-Dalton, 1997; Conroy-Dalton & Huys, 1999). *Uptionyx* gen. nov. was collected from a vent of the Juan de Fuca Ridge in the northeastern Pacific. It is the first ancorabolid to be described from a hydrothermal vent and its discovery at 2417 m represents a substantial depth range extension for the subfamily.

This paper is the first towards a revision of the Ancorabolidae and will deal with the systematics and phylogeny of the *Ancorabolus*-group. This monophyletic group of closely related species represents a distinct lineage within the subfamily Ancorabolinae consisting of: *Ancorabolus mirabilis*, *A. confusus* sp. nov., *A. inermis* sp. nov., *Arthropsyllus serratus* Sars, 1909, *Breviconia australis* (George, 1998a) comb. nov., *B. echinatus* (Brady, 1918) comb. nov. [*species inquirenda*], *Juxtaramia polaris* gen. et sp. nov. and *Uptionyx verenae* gen. et sp. nov.

Material and methods

Hydrothermal vent samples were taken at Peanut Vent by the submersible ALVIN on 27th June 1992, fixed in 5% formalin in seawater and the meiofauna picked out from the macro-invertebrates collected. Meiofaunal core samples were collected from Frierfjord/Langesundfjord Norway, as part of the GEEP surveys during the Spring of 1985 and the harpacticoid copepods picked out.

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.

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 seta complement found apically on the distal antennulary segment.

Type material was deposited in the Canadian Museum of Nature, Ottawa, Canada (CMNC) and/or the Natural History Museum, London, UK (NHM). Other material was examined from the collections in the Zoologisk Museum, Oslo, Norway (ZMO) and the Naturhistoriska Riksmuseet, Stockholm, Sweden (SMNH).

The phylogenetic software package PAUP 3.1.1, written by David Swofford of the Laboratory of Molecular Systematics, Smithsonian Institution (Swofford, 1993; Swofford & Begle, 1993), was used to analyse phylogenetic relationships within the *Ancorabolus*-group.

Scale bars in figures are indicated in μm.

Systematics

Family ANCORABOLIDAE Sars, 1909
Subfamily ANCORABOLINAE Sars, 1909

Type genus. *Ancorabolus* Norman, 1903.

Other genera. *Arthropsyllus* Sars, 1909; *Echinopsyllus* Sars, 1909; *Ceratonotus* Sars, 1909; *Dorsiceratus* Drzycimski, 1967; *Polyascophorus* George, 1998b; *Breviconia* gen. nov.; *Juxtaramia* gen. nov.; *Uptionyx* gen. nov.

Genus inquirendum. *Echinocletodes* Lang, 1936.

Genus *Ancorabolus* Norman, 1903
Anchorabolus Norman, 1903: unjustified subsequent spelling by Sars (1909).

Diagnosis. Ancorabolinae. Body dorsoventrally depressed, tapering posteriorly, without clear demarcation between prosome and urosome; body highly ornate with series of backwardly produced processes, each with spinules and bifid or unmodified sensillae. Processes never present on last 2 abdominal somites; other somites always with large lateral wing-like processes (except second abdominal somite in ♂). Cephalothorax with paired simple processes at anterior corners; lateral margins each with 3 branched processes; posterior margin with paired laterodorsal spinous projections each associated with 2 sensilla-bearing processes plus additional sensilla. Body with following pattern of paired produced processes: somites bearing P2-P4 with 8 processes (2 large lateral, 2 small dorsal and 4 dorsolateral processes arranged in 2 pairs); P5-bearing somite with 6 processes in ♀ (2 lateral, 2 dorsolateral and 2 dorsal) and 4 in ♂ (no dorsal); both genital and abdominal halves of genital double-somite (or genital and first abdominal somite in ♂) each with 1 lateral and 1 laterodorsal pair; second abdominal somite with 1 lateral and 1 laterodorsal pair in ♀, ♂ without lateral, sometimes with laterodorsal processes. Somatic hyaline frills weakly developed and smooth; somatic hind margins often with very fine setular extensions. Abdominal somites and caudal rami with conspicuous tube-pores ventrally and laterally. Anal somite partly cleft medially; anal operculum with long fine spinules. Caudal rami elongate and cylindrical with 7 setae. Sexual dimorphism in body size, rostrum, antennule, P3 endopod, P5, P6, genital segmentation, ventral abdominal ornamentation, and in pattern of body processes on P5-bearing and second abdominal somites.

Rostrum fused to cephalic shield; elongate with bifid tip; lateral paired pointed membranous projections arising proximal to sensillae; long midventral tube-pore subapically. Antennule 3-segmented in ♀, 7-segmented and subchirocer in ♂; first segment compound in both sexes, with 1 subapical anterior seta arising from distinctive spinous projection; ♀ segment 2 armature formula [7 + (1 + ae)]. Antenna with basis and proximal endopod segment fused forming allobasis with small partial suture along exopodal margin, abexopodal margin with 2 setae; exopod entirely absent; endopod with 3 lateral and 6 distal elements. Mandible with slender coxa; palp 1-segmented, uniramous with 3 setae apically. Maxillule with 1 element on coxal endite; basis with 3 elements on proximal and 2 on distal endite; exopod and endopod completely incorporated into basis, exopod represented by 2 setae. Maxillary syncoxa with 2 well developed endites, each with 3 elements; allobasis drawn out into claw with basal constriction and 3 accessory elements; endopod minute, with 2 setae. Maxilliped subchelate, slender and elongate; endopod drawn out into long narrow, curved claw with 1 accessory seta.

P1-P4. Intercoxal sclerites wide and narrow; praecoxae well developed; bases transversely elongate. P1 with 2-segmented rami; exp-2 with 3 geniculate setae and 2 outer spines; enp-1 elongate, much longer than enp-2 and exopod; enp-2 with 1 naked and 2 geniculate setae. P2-P4 exopods 3-segmented, endopods 2-segmented; without inner setae on exp-1, exp-3 and enp-1; exp-3 with only 2 outer spines. P3 endopod ♂ 2-segmented; enp-2 anterior surface produced subdistally into recurved apophysis; with 2 apical setae. Armature formula as follows:

	Exopod	Endopod
P1	I-0; II+1,2,0	0-0; 0,2,1
P2	I-0; I-1; II,2,0	0-0; 0,2,[0-1]
P3	I-0; I-1; II,2,0	0-0; 1,2,0 (♀)
		0-0; 0,2,0 (♂)
P4	I-0; I-1; II,2,0	0-0; 1,2,0

P5 biramous in both sexes; baseoendopod with 4 setae in ♀ and 2 spines in ♂; exopod with 5 elements in both sexes; endopodal lobe and exopod elongate in ♀, less so in ♂ Female genital field located anteriorly, with moderately large copulatory pore; gonopores covered by common genital operculum derived from medially fused P6 with 2-3 basally fused minute elements on either side. Male P6 asymmetrical; without armature; functional member represented by membranous flap.

Type species. *Ancorabolus mirabilis* Norman, 1903 (by monotypy)

Other species. *A. confusus* sp. nov., *A. inermis* sp. nov.

Remark.

Re-examination of the material of *A. mirabilis* held in the collections of G.O. Sars (Oslo) and K. Lang (Stockholm) revealed it to be based on an amalgamate of two species, neither of which being the type species. Both species are new to science and were also encountered in newly collected material from Frierfjord/Langesundfjord in Norway which serves as the basis for the descriptions below.

Ancorabolus inermis sp. nov.

Ancorabolus mirabilis Norman, 1903 *sensu* Sars (1909) [partim]: Plate CCXI, all drawings of ♀, except for habitus.

Type locality. Frierfjord/Langesundfjord, Norway; 99 m deep mud.

Type material. The Natural History Museum, London, UK: holotype ♀ dissected on 11 slides (NHM reg. no. 2000.1061); paratypes are 53 ♀♀ (2 ♀♀ damaged and stored in separate vial) and 3 ♂♂ in alcohol (NHM reg. no. 2000.1062-1117) and 1 ♂ dissected on 3 slides (NHM reg. no. 2000.1118); all from meiofauna samples collected at type locality; coll. R. Huys, Spring 1985.

Other material. (a) Naturhistoriska Riksmuseet, Stockholm, Sweden: 4 ♀♀ in alcohol labelled *Ancorabolus mirabilis* (SMNH reg. no. 15352 [old no. 495]) from Gullmarfjord, Sweden; 60 m, mud; coll. K. Lang, 03.08.1936; (b) Zoologisk Museum, Oslo, Norway: 20 ♀♀ in alcohol labelled *A. mirabilis* (ZMO reg. no. F20301) from unspecified locality in Norway; coll. and det. G.O. Sars; (c) from Dr J.M. Gee: 1 ♂ from off mouth of River Tyne, 55°00' N, 01°08' W, Northumberland; 72 m depth; fine muddy sand.

Description (based on type material)

Female

Total body length 758 μm ($\bar{x}$ = 715 μm, n = 12) measured from anterior tip of rostrum to posterior margin of caudal rami. Body (Fig. 1A-D) dorsoventrally depressed, tapering posteriorly, without clear demarcation between prosome and urosome; integument strongly chitinized and highly ornate. Somatic hyaline frills weakly developed and smooth (Fig. 1A, C-D); somatic margins often with very fine setular extensions (Fig. 1A). Cephalothorax and body somites with surface sculpturing forming irregular network of fine striations (not figured). Cephalothorax (Fig. 1A-B) with paired simple process at proximal outer corners and 3 branching processes around each lateral margin; processes furnished with spinules and bearing either bifid or unmodified sensillae; posterior margin with paired laterodorsal spinous projections (Fig. 1A, C) each associated with 2 sensilla-bearing produced processes plus 1 additional unmodified sensilla. Bifid sensillae consisting of spiniform main branch bearing flagelliform lateral branch

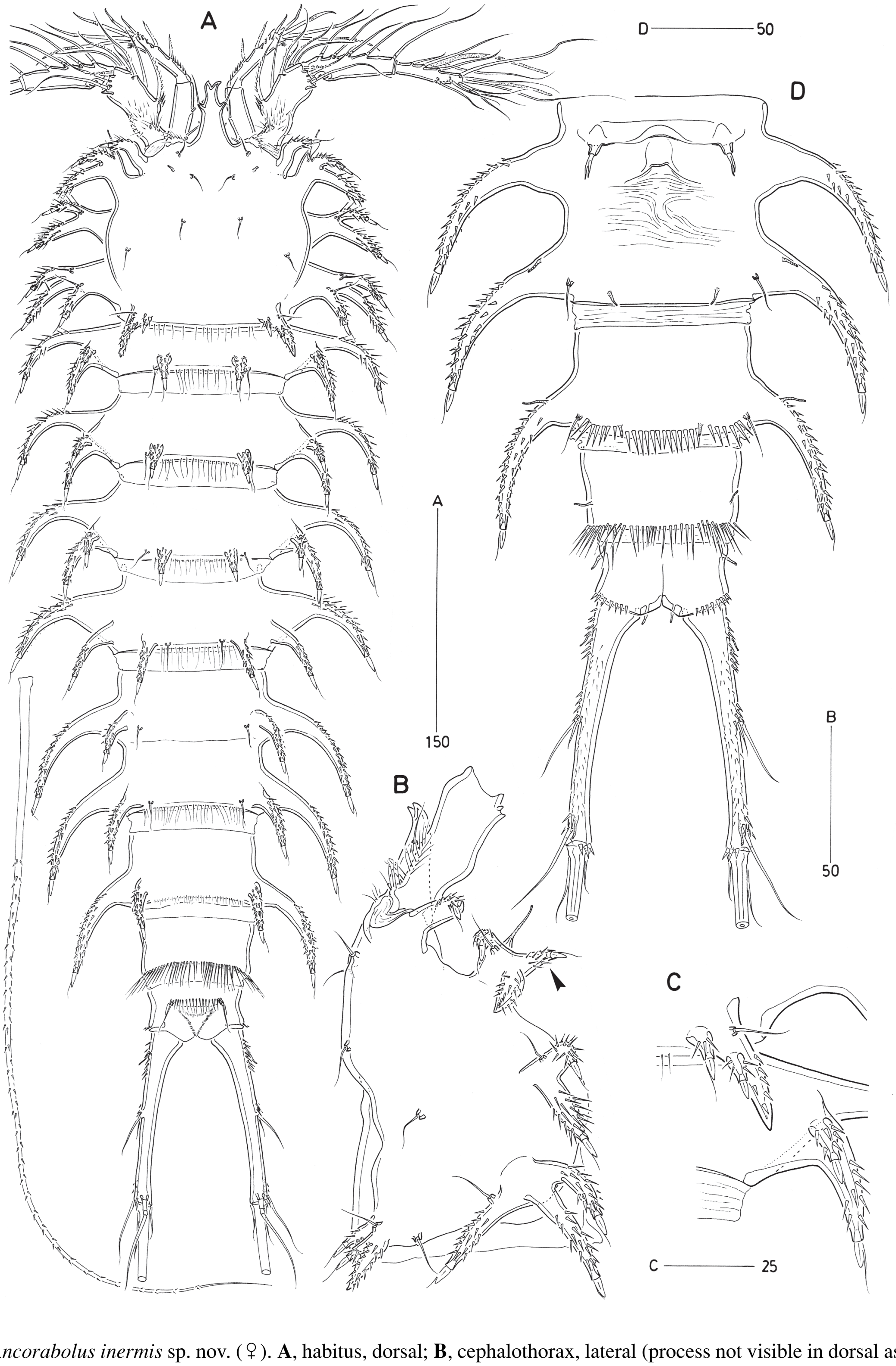

Figure 1. *Ancorabolus inermis* sp. nov. (♀). **A**, habitus, dorsal; **B**, cephalothorax, lateral (process not visible in dorsal aspect arrowed); **C**, dorsolateral projections of cephalothorax and P2-bearing somite, dorsal; **D**, urosome (excluding P5-bearing somite), ventral.

Figure 1. *Ancorabolus inermis* sp. nov. (♀). **A**, habitus, vue dorsale ; **B**, céphalothorax, vue latérale (la flèche indique la protubérance non visible en vue dorsale) ; **C**, projections dorsolatérales du céphalothorax et du somite portant P2, vue dorsale ; **D**, urosome (sauf le somite portant P5), vue ventrale.

(Fig. 1C). Body somites (Fig. 1A) with following pattern of paired produced processes: somites bearing P2-P4 with 4 pairs of processes (1 large lateral, 2 closely set dorsolateral and 1 smaller dorsal); P5-bearing somite with 1 lateral, 1 dorsolateral and 1 dorsal pair of processes; genital and abdominal halves of double-somite and second abdominal somite each with 1 lateral and 1 laterodorsal pair. Dorsal surfaces of pedigerous somites and genital double-somite (both halves) additionally with paired minute tubercles bearing unmodified sensillae (Fig. 1A).

Urosomites (except P5-bearing somite) and caudal rami with conspicuous tube-pores ventrally and laterally (Fig. 1D). Original segmentation of genital double-somite indicated by dorsal surface ridge and by position of lateral wing-like processes (Fig. 1A); posterior half with paired minute tubercles ventrolaterally (Fig. 1D) bearing unmodified sensilla. Second abdominal somite with sensilla arising from paired minute tubercles ventrolaterally (Fig. 1D); ventral posterior margin with median and paired ventrolateral spinule rows. Third abdominal somite with continuous fine spinule row along posterior margin (Fig. 1A-D). Anal somite partly cleft medially (Figs 1A, D; 4E); small spinules present around ventral hind margin (Fig. 1D); anal operculum furnished with long fine spinules (Fig. 4E).

Caudal rami elongate, divergent and slightly bent inwards, cylindrical (Figs 1A, D; 4E); with minute spinules ventrally; outer lateral margin with spinular patches in proximal quarter and around insertion sites of setae I - III; with 2 tube-pores (Figs 1D; 4E) and 7 setae. Setae I and II (Fig. 4E) arising midway outer margin; seta IV (Fig. 4E) diminutive and fused basally to seta V; seta V well developed, multipinnate (Fig. 1A); seta VI shortest (Fig. 4E); seta VII triarticulate at base and arising from minute dorsal pedestal, near posterior margin (Fig. 4E).

Rostrum fused to cephalic shield (Figs 1A; 6A-C); elongate with bifid tip; with paired pointed membranous projections laterally (arrowed in Fig. 6A) just proximal to sensillae; midventral tube-pore subapically.

Antennule (Figs 1A; 3A) 3-segmented. Segment 1 with small dorsal nodule near proximal margin bearing tuft of fine spinules; with 2 short spinule rows along anterior margin; 1 dorsal sub-apical seta arising from spinous projection (arrowed in Fig. 3A). Segment 2 longest, with aesthetasc (length 110 μm); posterior margin with recurved process proximally. Segment 3 with apical acrothek consisting of aesthetasc and 2 slender setae. Armature formula: 1-[5 + 5 pinnate], 2-[7 + (1+ae)], 3-[2 sparsely pinnate + 7 + acrothek].

Antenna (Fig. 3B). Coxa represented by sclerite. Basis and proximal endopod segment fused forming allobasis; membranous insert along exopodal margin marking original position of exopod (Fig. 3B); exopod absent; abexopodal margin with few spinules in basal half and 1 pinnate and 1 plumose seta. Endopod with distal surface frill and 3 fine spinule rows along outer margin; 2 spinule rows along medial margin; lateral armature consisting of 2 pinnate spines and 1 bare seta; distal armature consisting of 2 unipinnate spines and 3 geniculate pinnate setae, longest one with tube-pore (arrowed in Fig. 3B) and fused basally to vestigial seta .

Mandible (Fig. 4A). Coxa slender, expanding distally to gnathobase bearing thin incised blades; dorsal corner with robust, bifid, minutely pinnate element. Palp well developed, 1-segmented with 3 apical setae (probably of endopodal origin).

Maxillule (Fig. 3C). Praecoxal arthrite rectangular with 2 setae on anterior surface; distal armature consisting of 3 pinnate and 3 bare spines, proximalmost spine fused to arthrite. Transverse membranous zones present around base of praecoxal arthrite and coxa allowing for additional flexure. Coxal endite with 1 sparsely pinnate seta. Basis with 2 closely set endites and few spinules along medial margin; proximal endite with 3 elements; distal endite with 2 setae. Rami completely incorporated into basis; exopod represented by 2 setae; endopod represented by 1 sparsely plumose seta.

Maxilla (Fig. 3D). Syncoxa with 3 spinule rows as figured; with 2 endites, arising from membranous area and each with 1 strong pinnate spine, 1 pinnate seta and 1 naked seta. Allobasis drawn out into claw with basal constriction and few fine spinules at base; acutely tapering in distal half; accessory armature consisting of 2 pinnate setae and 1 pinnate spine. Endopod minute, with 2 setae.

Maxilliped (Fig. 4B). Subchelate, slender and elongate. Syncoxa unarmed, with few spinules. Basis with palmar row of long spinules. Endopod drawn out into long narrow, curved claw; with 1 accessory seta at base.

P1 (Fig. 4C). Intercoxal sclerite wide and narrow (only partially figured; see as for P2, Fig. 5A). Praecoxa very well developed with short anterior spinule row. Coxa small, trapezoid. Basis transversely elongate with pinnate outer seta and naked inner seta; anterior spinule pattern as indicated in Fig. 4C. Both rami 2-segmented; exp-1 outer spine very long and finely serrate; exp-2 with 3 geniculate setae and 2 finely serrate outer spines; all outer spines with setules in proximal portion. Enp-1 much longer than enp-2 (2.7 times as long) and 1.67 times as long as entire exopod, with fine setules along inner margin; enp-2 with 1 naked and 2 pinnate, geniculate setae.

P2-P4 with wide, narrow intercoxal sclerites without ornamentation (as figured for P2; see Fig. 5A). Praecoxae (see Fig. 5A) very well developed, with short anterior spinule row. Coxae with few spinules anteriorly. Bases transversely elongate; outer margin with sigmoid row of long spinules (as figured for P2; see Fig. 5A) and posterior

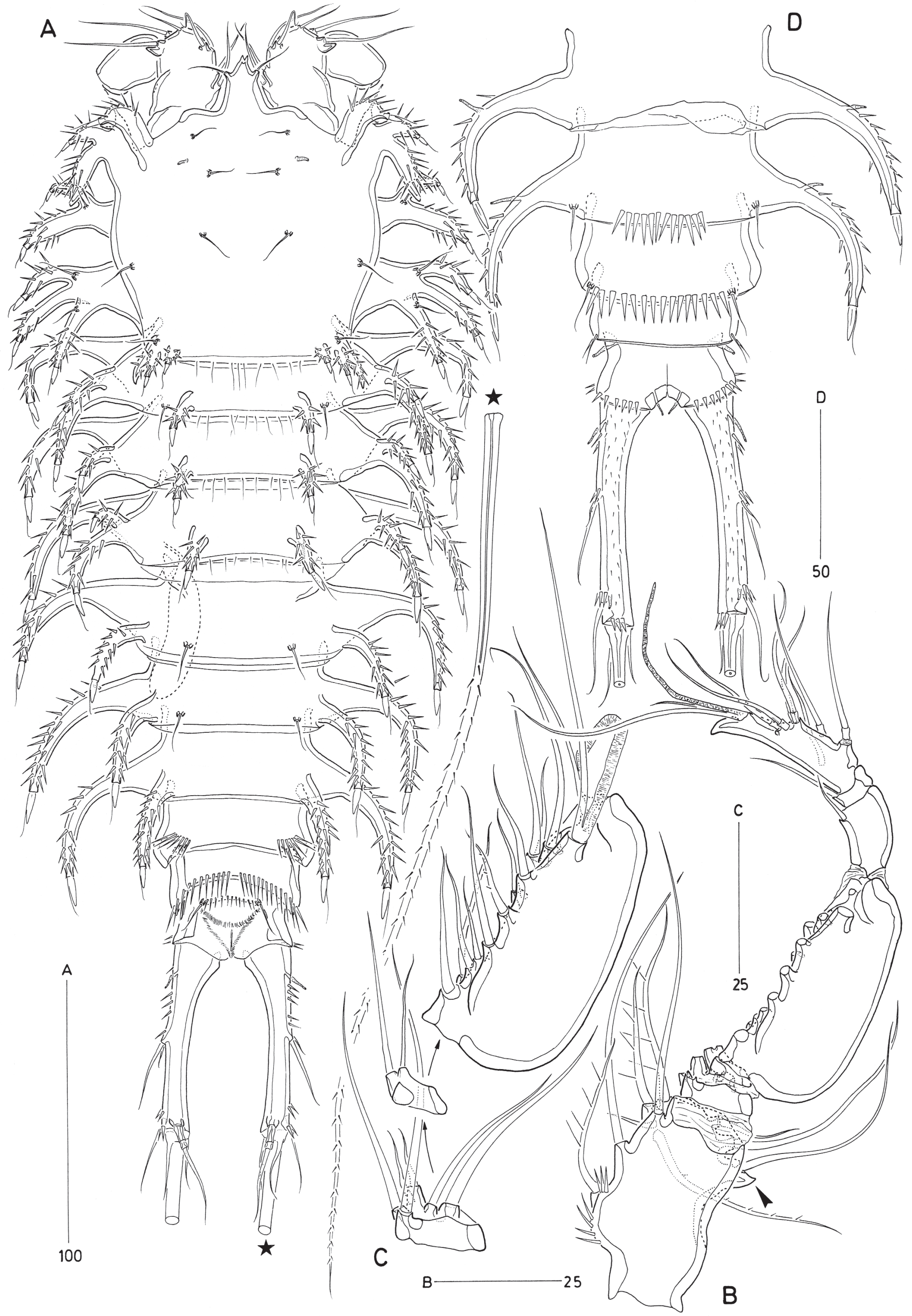

Figure 2. *Ancorabolus inermis* sp. nov. (♂). **A**, habitus, dorsal; **B**, antennule, ventral (spinous projection bearing anterior seta arrowed); **C**, antennulary segments 2-4 (disarticulated), ventral; **D**, urosome (excluding P5-bearing somite), ventral.

Figure 2. *Ancorabolus inermis* sp. nov. (♂). **A**, habitus, vue dorsale ; **B**, antennule, vue ventrale (la flèche indique la projection épineuse portant la soie antérieure) ; **C**, articles antennulaires 2-4 (détachés), vue ventrale ; **D**, urosome (sauf le somite portant P5), vue ventrale.

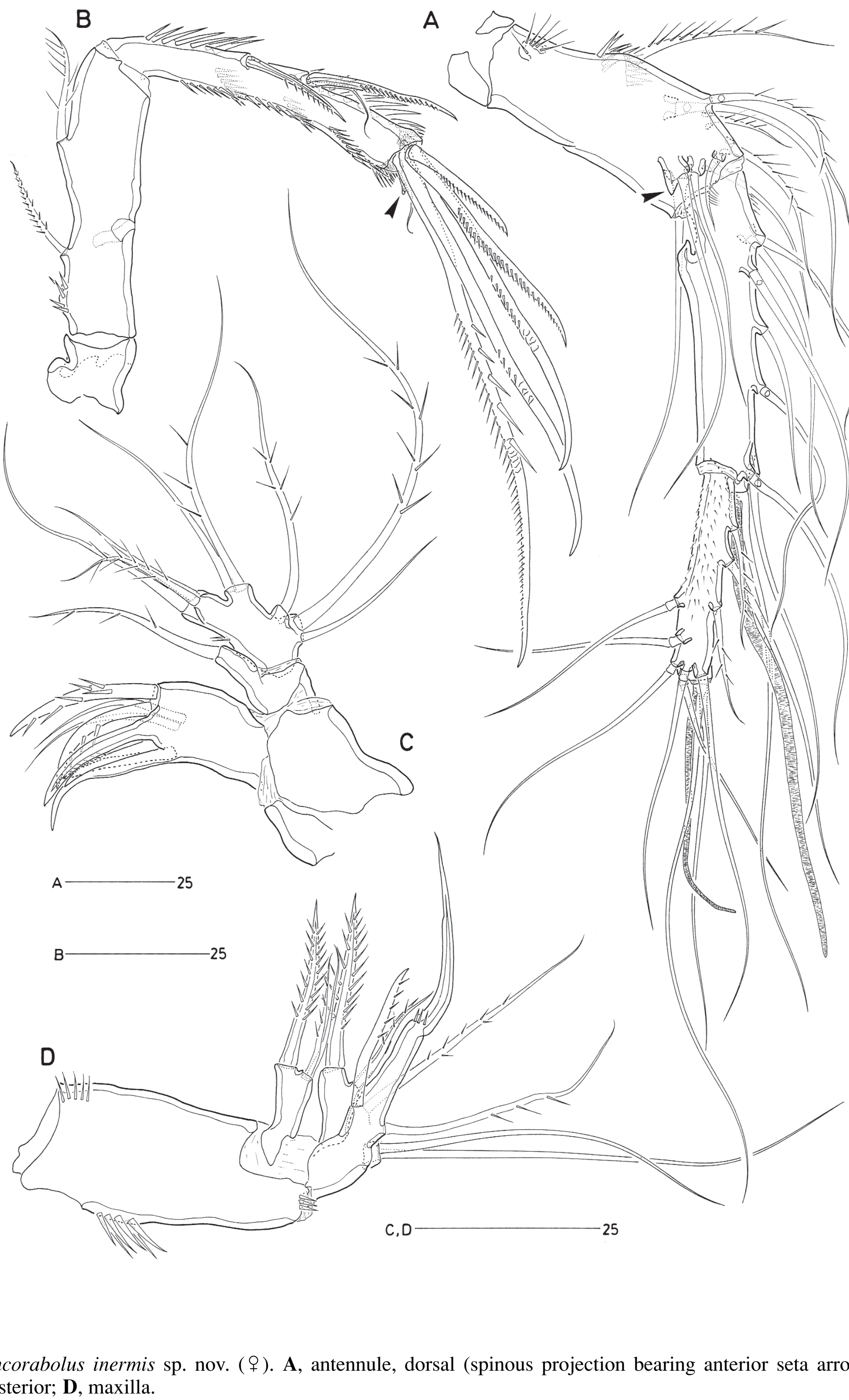

Figure 3. *Ancorabolus inermis* sp. nov. (♀). **A**, antennule, dorsal (spinous projection bearing anterior seta arrowed); **B**, antenna; **C**, maxillule, posterior; **D**, maxilla.

Figure 3. *Ancorabolus inermis* sp. nov. (♀). **A**, antennule, vue dorsale (la flèche indique la projection épineuse portant la soie antérieure) ; **B**, antenne ; **C**, maxillule, vue postérieure ; **D**, maxille.

Figure 4. *Ancorabolus inermis* sp. nov. (♀). **A**, mandible; **B**, maxilliped; **C**, P1, anterior; **D**, P5, anterior; **E**, anal somite and left caudal ramus, dorsal.

Figure 4. *Ancorabolus inermis* sp. nov. (♀). **A**, mandibule; **B**, maxillipède ; **C**, P1, vue antérieure ; **D**, somite anal et rame caudale gauche, vue dorsale.

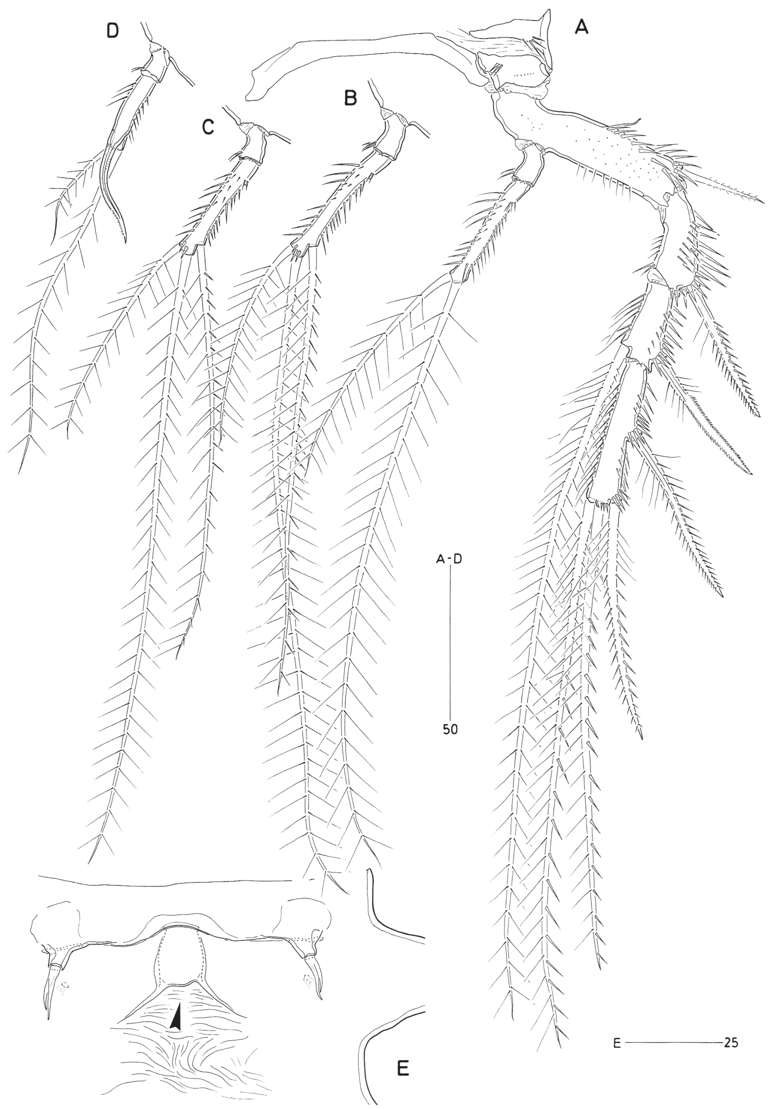

Figure 5. *Ancorabolus inermis* sp. nov. **A**, P2 (♀), anterior; **B**, P3 (♀) left endopod, anterior; **C**, P4 (♀) left endopod, anterior; **D**, P3 (♂) left endopod, anterior; **E**, genital field (♀), ventral (copulatory pore arrowed).

Figure 5. *Ancorabolus inermis* sp. nov. **A**, P2 (♀), vue antérieure; **B**, endopodite gauche de P3 (♀), vue antérieure ; **C**, endopodite gauche de P4 (♀), vue antérieure ; **D**, endopodite gauche de P3 (♂), vue antérieure ; **E**, aire génitale (♀), vue ventrale (la flèche indique l'orifice copulateur).

tube-pore mid-way down margin; distal margin with fine hair-like setules between rami; additional patches of minute spinules on anterior surface; outer distal seta bipinnate, arising from a tiny, posteriorly displaced setophore. Exopods 3-segmented, endopods 2-segmented. Exopodal spines elongate, those of exp-2 serrate. Endopods distinctly shorter than exopods, reaching to distal half of exp-2 (see Fig. 5A). P2-P4 enp-1 reduced in size, unarmed; enp-2 elongate (Fig. 5 A-C). Armature formula as follows:

	Exopod	Endopod
P2	I-0; I-1; II,2,0	0-0; 0,2,0
P3	I-0; I-1; II,2,0	0-0; 1,2,0 (♀) or 0-0; 0,2,0 (♂)
P4	I-0; I-1; II,2,0	0-0; 1,2,0

P5 (Fig. 4D) biramous. Baseoendopod outer corner with tube-pore; setophore demarcated and very long, bearing naked outer basal seta. Endopodal lobe slender and rectangular, with spinule row along outer margin; with 4 bipinnate setae and 1 anterior tube-pore at inner distal corner; reaching to proximal third of exopod. Exopod long and slender; fine setules along inner margin and some spinules along outer margin; with serrate inner spine, 2 pinnate setae and anterior tube-pore distally, and 2 pinnate outer setae.

Genital field (Figs 1D; 5E) with fused gonopores opening via common midventral slit covered by genital operculum derived from vestigial sixth legs. P6 each with 2 minute, basally fused elements. Copulatory pore moderately large (arrowed in Fig. 5E), flanked by paired pore triplet, just posterior to each gonopore. Area between P6 and copulatory pore slightly raised.

Male

Smaller and stubbier than ♀ (Fig. 2A); total body length 420 μm ($\bar{x}$ = 460 μm; n = 2) measured from tip of rostrum to posterior margin of caudal rami. Sexual dimorphism in body size, degree of development of body processes, pattern of body processes of P5-bearing and second abdominal somites, abdominal ornamentation, rostrum, antennule, P3 endopod, P5, P6 and in genital segmentation. Body processes (Fig. 2A) relatively more developed than in ♀. Ornamentation pattern of processes and sensillae same as for ♀ except: P5-bearing somite without dorsal pair of sensillae bearing processes; second abdominal somite (Fig. 2A, D) without processes and posterior margin with paired spinule row dorsolaterally. First and second abdominal somites (Fig. 2D), with median spinule row around ventral posterior margin. Penultimate somite with spinule row dorsally only.

Rostrum (Figs 2A; 6D) elongate, bifid apically but distinctly shorter than in ♀.

Antennule (Fig. 2B-C) 7-segmented and subchirocer, geniculation between segments 4 and 5; segment 3 represented by a U-shaped sclerite (Fig. 2C); segment 4 longest and swollen; aesthetasc present on segment 4 and as part of apical acrothek on segment 7. Segment 1 with 2 short anterior spinule rows, with 1 dorsal seta arising from spinous projection (arrowed in Fig. 2B). Segments around geniculation without modified elements. Armature formula: 1-[4 pinnate + 6], 2-[6], 3-[2], 4-[1 sparsely pinnate + 11 + (1 + ae)], 5-[1], 6-[1], 7-[7 + acrothek]. Apical acrothek consisting of 2 setae and aesthetasc.

P3 endopod (Fig. 5D) 2-segmented; enp-2 with 2 apical setae, anterior distal surface produced into recurved apophysis, finely denticulate in distal half.

P5 (Fig. 6E) biramous. Baseoendopod outer corner with tube-pore; setophore demarcated and very long, bearing naked outer basal seta. Endopodal lobe rectangular, much shorter than in ♀, with few spinules along outer margin; distally with 1 serrate and 1 pinnate spine; inner distal corner with 1 anterior tube-pore; reaching to proximal margin of exopod. Exopod long but shorter than in ♀; fine setules along inner margin and some spinules along outer margin; with serrate inner spine, 2 pinnate setae and anterior tube-pore distally and 2 pinnate outer setae.

Sixth pair of legs asymmetrical (Figs 2D; 6F), with only 1 functional member, represented by membranous flap; other member fused to somite. P6 without armature.

Spermatophore elongate, 57 µm.

Variability. - Some female specimens display size variation in rostrum (Fig. 6A-C).

Distribution. - See Table 1.

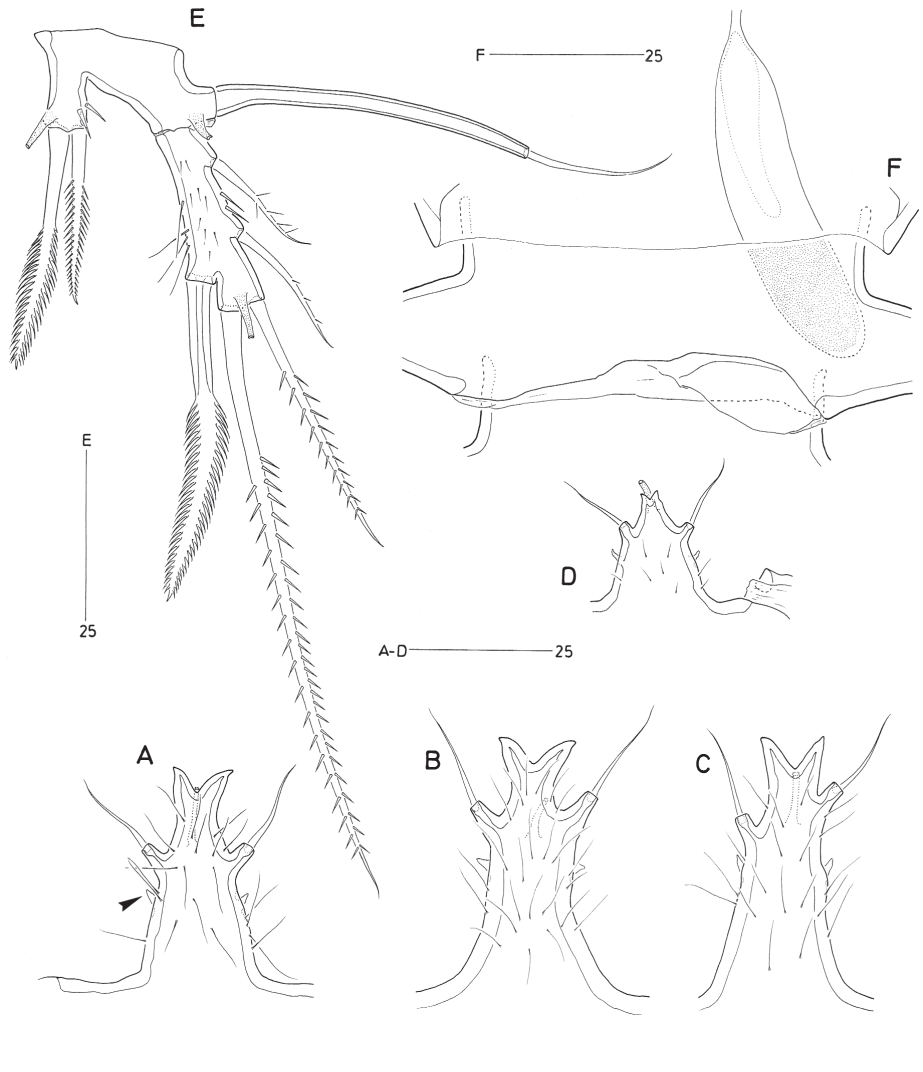

Figure 6. *Ancorabolus inermis* sp. nov. **A**, rostrum (♀), dorsal (lateral membranous projection arrowed); **B-C**, same, examples of variability; **D**, rostrum (♂), dorsal; **E**, P5 (♂), anterior; **F**, P6 (♂), ventral.

Figure 6. *Ancorabolus inermis* sp. nov. **A**, rostre (♀), vue dorsale (la flèche indique l'excroissance membraneuse latérale) ; **B-C**, idem, exemples de variabilité ; **D**, rostre (♂), vue dorsale ; **E**, P5 (♂), vue antérieure ; **F**, P6 (♂), vue ventrale.

Ancorabolus confusus sp. nov.
Ancorabolus mirabilis Norman, 1903 *sensu* Sars (1909) [partim]: Plate CCXI, habitus of ♀.

Type locality. Frierfjord/ Langesundfjord, Norway; 99 m deep mud.

Type material. The Natural History Museum, London, UK: holotype ♀ dissected on 10 slides (NHM reg. no. 2000.1120); paratypes are 48 ♀♀ (NHM reg. no. 2000.1121-1168) and 3 ♂♂ (NHM reg. no. 2000.1169-1171) in alcohol (1 side of A1 dissected from 1 ♂ and mounted separately on 1 slide) and 1 ♀ dissected on 4 slides (NHM reg. no. 2000.1172). Additional material are 8 ♀♀ in alcohol, all with aberrant P3 endopod armature. All NHM material from meiofauna samples collected at type locality; coll. R. Huys, Spring 1985.

Other material. (a) Naturhistoriska Riksmuseet, Stockholm, Sweden: 4 ♀♀ in alcohol labelled *A. mirabilis* (SMNH reg. no.15352 [old no. 495]); from Gullmarfjord, Sweden, 60m mud, coll. K. Lang, 03.08.1936; (b) Zoologisk

Museum, Oslo, Norway: 9 ♀♀ in alcohol labelled as *A. mirabilis* (ZMO reg. no. F20301); from unspecified locality in Norway; coll. and det. G.O. Sars.

Description (based on type material).
Female
Total body length for holotype 692 µm ($\bar{x}$ = 721 µm, n = 8) measured from anterior tip of rostrum to posterior margin of caudal rami. Body (Fig. 7 A, C) more robust and relatively shorter than in *A. inermis*; body processes generally longer and more developed. Somatic hyaline frills weakly developed and smooth (Fig. 7A, C); somatic margins often with very fine setular extensions (Fig. 7A). Pattern of cephalothoracic processes (Fig. 7A) similar to *A. inermis* except for: (1) presence of additional pair of dorsal backwardly directed processes in anterior half; (2) basal shafts of lateral branched processes being distinctly longer and more slender, and (3) posterior spinous processes being very large, extending to hind margin of P3-bearing somite. Free body somites with pattern of processes as in *A. inermis* but dorsal (somites bearing P2-P5) and dorsolateral (P5-bearing somite, genital double-somite and second abdominal somite) pairs much longer. Spinules on all these processes distinctly coarser. Pattern of tube-pores, sensillae and spinules on urosomites as in *A. inermis*.

Caudal rami elongate (Figs 7A, C; 9E) and divergent; with minute spinules dorsally and ventrally; outer lateral margin with few spinules in proximal half; with 2 tube-pores (Figs 7C; 9E) and 7 setae. Setae I and II (Fig. 9E) arising from midway outer margin; seta IV (Fig. 9E) diminutive and fused basally to seta V; seta V well developed, multipinnate (Fig. 7A); seta VI shortest (Fig. 9E); seta VII triarticulate at base and arising from small posterodorsal pedestal (Fig. 9E).

Rostrum (Fig. 7A-B) fused to cephalic shield and very elongate; with bifid tip apically and paired pointed membranous projections just posterior to sensillae; midventral tube-pore subapically.

Antennule (Figs 7A; 10A) 3-segmented, more slender than in *A. inermis*. Segment 1 with small dorsal nodule near proximal margin bearing tuft of fine spinules; with 2 short spinule rows along anterior margin; 1 dorsal sub-apical seta arising from spinous projection. Segment 2 longest with aesthetasc (length 125 µm). Segment 3 with apical acrothek consisting of aesthetasc + 2 slender setae. Armature formula: 1-[8 + 2 pinnate], 2-[7 + (1+ae)], 3-[9 + acrothek].

Antenna, mandible and maxilla as for *A. inermis*.

Maxillule (Fig. 9A). Praecoxal arthrite rectangular with 2 setae on anterior surface; distal armature consisting of 4 pinnate and 2 bare spines, most posterior spine fused to arthrite. Transverse membranous zones around proximal area of praecoxa and coxa allowing for additional flexure. Coxal endite with 1 sparsely pinnate seta. Basis with 2 endites; proximal endite with 3 elements; distal endite with 2 setae. Exopod completely incorporated into basis; represented by 2 setae; endopod not represented by any elements.

Maxilliped (Fig. 9B). Subchelate, proportionally more slender than in *A. inermis*. Syncoxa lacking armature and ornamentation. Basis with a few spinules. Endopod drawn out into long narrow, curved claw with 1 accessory seta at base.

P1 (Fig. 9C). Intercoxal sclerite wide and narrow (only partially figured). Praecoxa well developed with short anterior spinule row. Coxa small, sub-rectangular. Basis transversely elongate with pinnate outer seta and naked seta at inner distal corner; anterior spinule pattern as indicated in Fig. 9C. Both rami 2-segmented; exp-1 outer spine finely serrate; exp-2 with 3 geniculate setae and 2 finely serrate outer spines. Enp-1 much longer than enp-2 (3.5 times as long) and 1.4 times as long as entire exopod, with long spinules along inner margin and fine setules along outer margin; enp-2 with 1 naked and 2 pinnate, geniculate setae.

P2-P4 with wide, narrow intercoxal sclerites without ornamentation, praecoxae, coxae and transversely elongate bases as in *A. inermis*. Exopods 3-segmented, endopods 2-segmented. Endopods distinctly shorter than exopods; enp-1 (Fig. 10B-E) reduced in size, unarmed; enp-2 elongate. Armature formula as follows:

	Exopod	Endopod
P2	I-0; I-1; II,2,0	0-0; 0,2,1
P3	I-0; I-1; II,2,0	0-0; 1,2,0 (♀) or 0-0; 0,2,0 (♂)
P4	I-0; I-1; II,2,0	0-0; 1,2,0

P5 (Fig. 9D) biramous. Baseoendopod outer corner with tube-pore; setophore demarcated, very long, bearing naked outer basal seta. Endopodal lobe slender and rectangular, with spinules along inner and outer margins; with 4 pinnate setae and 1 anterior tube-pore at inner distal corner; reaching to proximal third of exopod. Exopod long and slender; fine spinules along inner margin and some along outer margin; with serrate inner spine, 2 pinnate setae and anterior tube-pore distally and 2 pinnate outer setae.

Genital field (Fig. 7C-D) with fused gonopores opening via common midventral slit covered by genital operculum derived from vestigial sixth legs. P6 (Fig. 5E) each with 3 minute, basally fused elements. Copulatory pore (arrowed in Fig. 7D) moderately large with less chitinous area posteriorly. Area between P6 and copulatory pore slightly raised.

Male
Smaller than ♀ (Fig. 8A); total body length 409 µm ($\bar{x}$ = 391 µm; n = 2) measured from tip of rostrum to

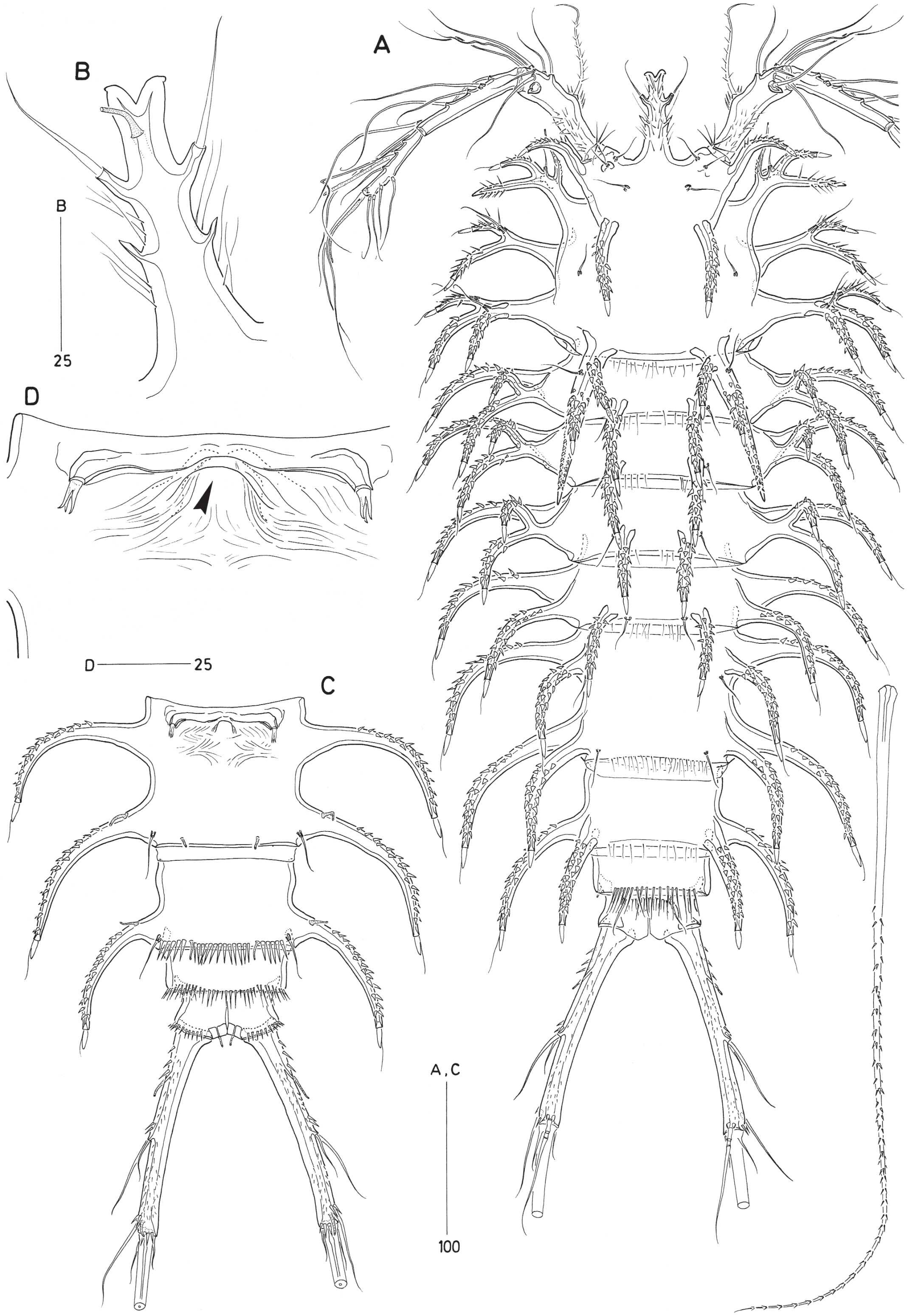

Figure 7. *Ancorabolus confusus* sp. nov. (♀). **A**, habitus, dorsal; **B**, rostrum, ventral; **C**, urosome (excluding P5-bearing somite), ventral; **D**, genital field, ventral (copulatory pore arrowed).

Figure 7. *Ancorabolus confusus* sp. nov. (♀). **A**, habitus, vue dorsale ; **B**, rostre, vue ventrale ; **C**, urosome (sauf le somite portant P5), vue ventrale ; **D**, aire génitale, vue ventrale (la flèche indique l'orifice copulateur).

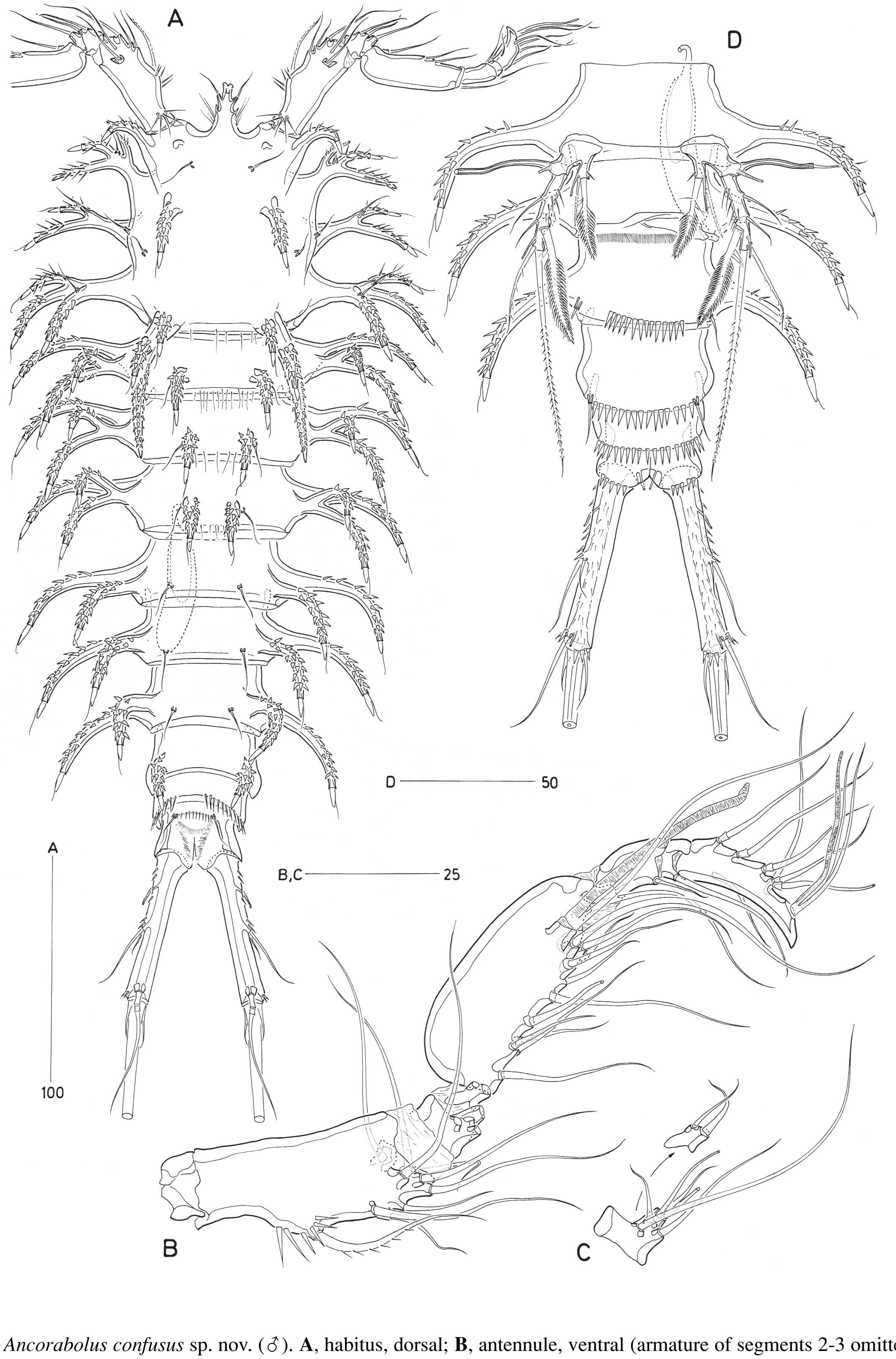

Figure 8. *Ancorabolus confusus* sp. nov. (♂). **A**, habitus, dorsal; **B**, antennule, ventral (armature of segments 2-3 omitted); **C**, disarticulated antennulary segments 2-3, ventral; **D**, urosome, ventral.

Figure 8. *Ancorabolus confusus* sp. nov. ♂). **A**, habitus, vue dorsale ; **B**, antennule, vue ventrale (armature des articles 2-3 omise) ; **C**, articles antennulaires 2-3 détachés, vue ventrale ; **D**, urosome, vue ventrale.

Figure 9. *Ancorabolus confusus* sp. nov. (♀). **A**, maxillule, posterior; **B**, maxilliped; **C**, P1, anterior; **D**, P5, anterior; **E**, anal somite and right caudal ramus, dorsal.

Figure 9. *Ancorabolus confusus* sp. nov. (♀). **A**, maxillule, vue postérieure ; **B**, maxillipède ; **C**, P1, vue antérieure ; **D**, P5, vue antérieure ; **E**, somite anal et rame caudale droite, vue dorsale.

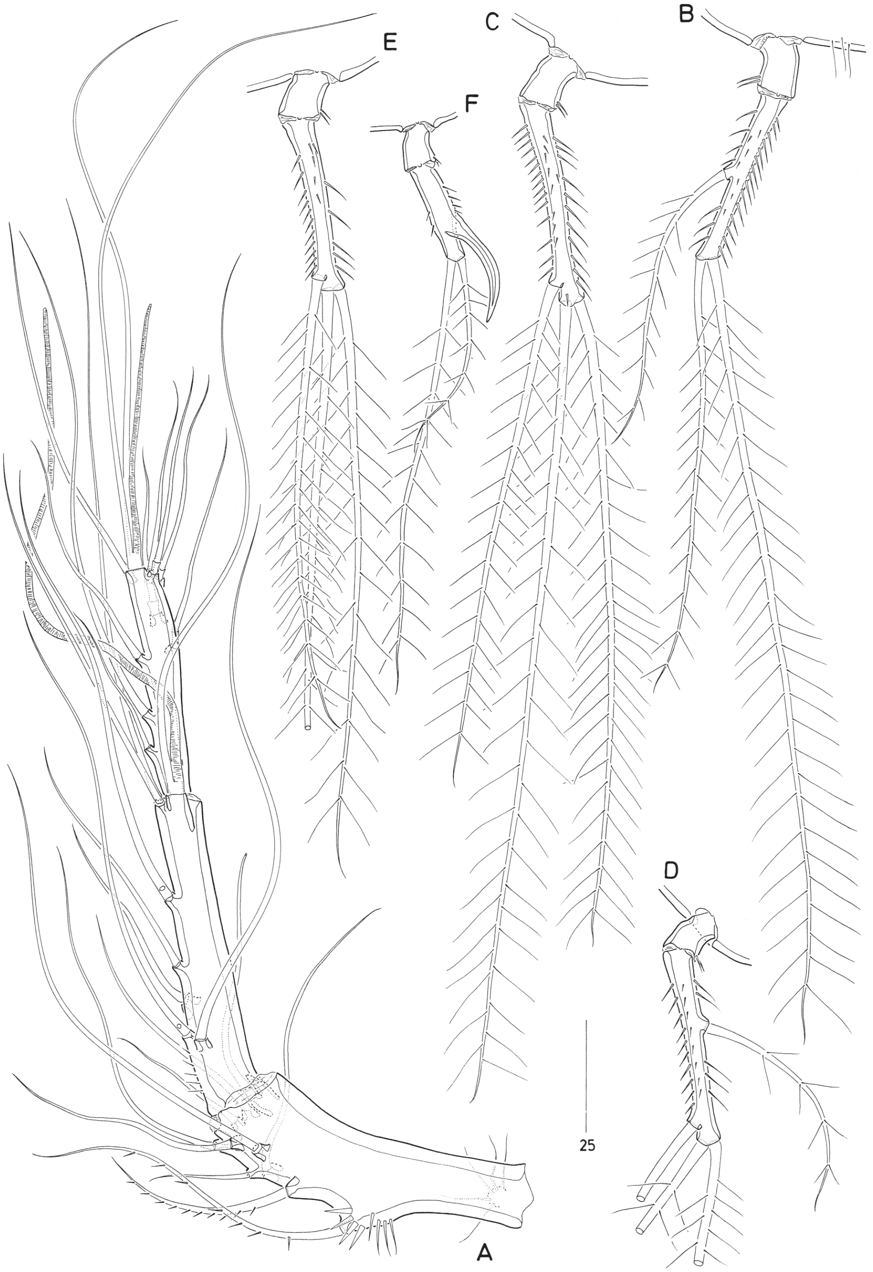

Figure 10. *Ancorabolus confusus* sp. nov. **A**, antennule (♀), ventral; **B**, P2 (♀) left endopod, anterior; **C**, P3 (♀) right endopod, anterior; **D**, P3 (♀) aberrant right endopod, anterior; **E**, P4 (♀) right endopod, anterior; **F**, P3 (♂) right endopod, anterior.

Figure 10. *Ancorabolus confusus* sp. nov. **A**, antennule (♀), vue ventrale ; **B**, endopodite gauche de P2 (♀), vue antérieure ; **C**, endopodite droit de P3 (♀), vue antérieure ; **D**, endopodite droit aberrant de P3 (♀), vue antérieure ; **E**, endopodite droit de P4 (♀), vue antérieure ; **F**, endopodite droit de P3 (♂), vue antérieure.

Body (Fig. 8A, D) ornamentation pattern of processes and sensillae same as for ♀ except: P5-bearing somite without dorsal pair of body processes; second abdominal somite without lateral processes but with paired dorsolateral processes. First and second abdominal somites (Fig. 8D), with median spinule row along ventral posterior margin; penultimate somite with almost continuous spinule row along posterior margin.

Rostrum (Fig. 8A) elongate; bifid extension less well developed than in ♀.

Antennule (Fig. 8A-C) 7-segmented and subchirocer, geniculation between segments 4 and 5. Segment 1 with short anterior spinule row, with 1 dorsal seta arising from spinous projection; segment 3 represented by U-shaped sclerite (Fig. 8C); segment 4 longest and swollen; with aesthetasc on segment 4 and as part of apical acrothek on segment 7. Segments around geniculation without modified elements. Armature formula: 1-[1 pinnate + 9], 2-[6], 3-[2], 4-[12 + (1 + ae)], 5-[1], 6-[1], 7-[7 + acrothek]. Apical acrothek consisting of 2 setae and aesthetasc.

P3 endopod (Fig. 10F) 2-segmented; enp-2 with 2 apical setae, distal anterior surface produced into smooth recurved apophysis.

P5 (Fig. 8D) biramous. Baseoendopod outer corner with tube-pore; setophore demarcated, very long, bearing naked outer basal seta. Endopodal lobe rectangular, much shorter than in ♀; distally with 1 serrate spine and 1 pinnate seta, outer distal corner with 1 anterior tube-pore; reaching to proximal margin of exopod. Exopod long (shorter than in ♀); fine setules along inner margin; with serrate inner spine, 2 pinnate setae and anterior tube-pore distally and 2 outer setae.

posterior margin of caudal rami. Sexual dimorphism in body size, abdominal ornamentation, pattern of body processes of P5-bearing and second abdominal somites, rostrum, antennule, P3 endopod, P5, P6 and in genital segmentation.

Sixth pair of legs asymmetrical (Fig. 8D) with only 1 functional member, represented by membranous flap; other member fused to somite. P6 without armature.

Spermatophore 68 µm.

Variability. Eight females displayed an aberrant setation of P3 endopod, either one or both endopods having an additional inner seta on enp-2 (Fig.10D). Three ♀ ♀ from the Sars collection (material (c)) were also found with the same aberrant setation of one of the P3 endopod rami.

Distribution. See Table 1.

Etymology. The specific name refers to the confusion surrounding Sars' (1909) description of *A. mirabilis* which in fact was based on a composite of *A. inermis* sp. nov. and this second sympatric species.

Remarks

A. confusus can be readily differentiated from *A. inermis* on the basis of the following characters (both sexes unless stated otherwise): (a) body processes more developed and elongate; (b) cephalothorax with additional pair of dorsal backwardly directed processes in anterior half; (c) A1 ♀ segment 2 more slender and without proximal recurved process near posterior margin; (d) P2 enp-2 with inner seta (absent in *A. inermis*; cf. name); (e) maxillule, incorporated endopod not represented by armature element. Males of both species can also be separated by the presence (*confusus*) or absence (*inermis*) of paired dorsolateral processes on the second abdominal somite and a ventral posterior spinule row on the third abdominal somite. Other morphometric characters such as the slenderness of the P5 exopod and caudal rami also have some discriminating value but are less significant.

Since both species are not only very closely related but also appear to be sympatric in Frierfjord/Langesundfjord, it is conceivable that they have been confused in the past. Sars (1909) recorded *A. mirabilis* "... in many different places on the Norwegian coast...", however, examination of his material from an unspecified locality (ZMO reg. no. F20301) revealed it to contain a mixture of *A. inermis* and *A. confusus* and not *A. mirabilis*. Inspection of Sars' (1909) illustrations (Plate CCXI) suggests that they were also based on an amalgamate of these two species. His figures of the habitus, maxillule, maxilliped and P1 are undoubtedly taken from *A. confusus* whereas those of the ♀ antennule (+ rostrum), P2 and possibly ♀ P5 are based on *A. inermis*. Sars' figure of the dorsal habitus is particularly confusing for two reasons. First, the specimen figured is completely stretched out with the intersomitic membranes being fully exposed. Sars obviously failed to distinguish between the broad membranous zone and the actual somite as he did not draw the posterior margin but only the anterior one of the following somite. This gives the false impression that the somites are much bigger than in reality, and more importantly, that the paired dorsal processes arise from a more anterior position. Secondly, Sars combined the antennules of both *A. inermis* (right) and *A. confusus* (left) in his habitus drawing. It is known that Sars achieved the virtually perfect symmetry commonly displayed in his dorsal body illustrations by drawing the left half of the animal and its subsequent mirroring onto the right half. It is likely that erroneous superimposing of the right antennule happened during the latter phase (and after its enlarged view was completed). Sars' illustrations of the male are confined to the antennule, P3 endopod (mistakenly cited P2 in text) and P5 so that it is impossible to identify which species was figured.

In his monograph, Lang (1948) made some ecological comments concerning *A. mirabilis* but no taxonomic notes, despite having collected material of *Ancorabolus* himself in 1936 from Gullmarfjord and Måseskär in Sweden. He reproduced Sars' (1909) illustrations and stated specifically that P2 enp-2 bears two apical setae, hence clearly referring to the *A. inermis* condition. His erroneous statement that P4 enp-2 also possesses two apical setae is probably a misinterpretation of Sars' (1909) text since the P4 was not illustrated. Re-examination of Lang's material showed the presence of both *A. inermis* and *A. confusus*.

Drzycimski (1969) recorded *A. mirabilis* from three fjords in the vicinity of Bergen, Norway. Contrary to Sars (1909) and Lang (1948), he correctly identified the armature of P4 enp-2 as [021] and described the ♂ P3 endopod as 2-segmented, with an apophysis and 2 apical setae arising from the distal segment (Sars figured only 1 seta). He noted a crucial difference to these authors in that his specimens had an inner seta on the P2 enp-2 which unequivocally identifies this material as *A. confusus*.

Ancorabolus mirabilis Norman, 1903

Type locality. North-eastern corner of the island of Little Cumbrae, Firth of Clyde, Scotland; 36.6 m.

Type material. According to the NHM registers the type-series of *Ancorabolus mirabilis* deposited as part of the Norman Collection (reg. no. 1911.11.8) consists of:

(a) 4 ♀♀ and 1 ♂ in alcohol labelled as "Types" of *A. mirabilis* (NHM reg. no. 44973-977); from Varanger Fjord, East Finmark (Norway); coll. A. M. Norman, 1890. Re-examination of this material proved that the 5 individuals were not conspecific with *A. mirabilis* and differ in the following key characters: (i) body size; (ii) pattern of processes on cephalothorax and free body somites; (iii) antennulary segmentation in both sexes; (iv) absence of armature on antennary allobasis; (v) caudal rami. The material from East Finmark represents a new genus and species which is described below as *Juxtaramia polaris* gen. et sp. nov.

(b) 1 slide labelled as "Type" of *A. mirabilis* (NHM reg. no. M.2265); from the northeastern corner of the island of Little Cumbrae, Firth of Clyde (Scotland), at 36.6 m; coll. A.M. Norman, 1888. This slide, despite a thorough search could not be located in the collections, and must be considered as lost to Science. No other material from Scotland was available for study.

History

Norman (1903) provided a preliminary description (text only) for the new genus and species *Ancorabolus mirabilis* in his paper on the natural history of East Finmark (Norway). According to Norman he had first encountered *A. mirabilis* together with a second species of the same genus (subsequently described as *Arthropsyllus serratus* var. *spinifera* by Norman (1911)) from dredge samples taken in 1888 from the Firth of Clyde, Scotland, and again (two years later in 1890) somewhat unexpectedly from Varanger Fjord in East Finmark. Norman's (1903) text description primarily documented the pattern and size of the various body processes but provided only little information on the appendages. The unpublished illustrations he referred to had already been completed in 1890 by Andrew Scott but other commitments had delayed their publication (Norman, 1903; T. Scott, 1903). It is highly conceivable that both text and illustrations were based on the Scottish material and not on the Norwegian specimens as Sars (1909) had mistakenly assumed. Since the erroneous identification of Norman's East Finmark specimens (see *Juxtaramia* gen. nov.) appears to substantiate this assumption we formally designate the Firth of Clyde (Little Cumbrae) as the type locality of *A. mirabilis*. Presumably prompted by Sars' (1909) illustrated description of "*A. mirabilis*", Norman (1911) finally published a more comprehensive account of the type species (♀ only) accompanied by A. Scott's illustrations.

Two important inferences can be made from Norman's (1903, 1911) text and illustrations.

First, conspecificity with either of the Scandinavian species described above can be ruled out on the basis of the following combination of characters illustrated in Norman's (1911) habitus drawing of the female: (a) antennule with recurved process on posterior margin of segment 2; (b) rostrum not particularly elongate; (c) presence of anterior pair of small dorsal processes on cephalothorax; (d) dorsal processes on somites bearing P2-P4 markedly developed; (e) inner and outer dorsolateral processes on somites bearing P2-P4 of about equal size; (f) laterodorsal processes on genital double-somite and second abdominal somite robust; (g) caudal rami not as slender as in *A. inermis* and *A. confusus*. This combination is partly a mozaic of characters exhibited by either *A. inermis* (a-b) or *A. confusus* (c). Since these characters have proven to be remarkably constant in the Scandinavian species their combination has to be considered as diagnostic for *A. mirabilis*, allowing its identification without prior dissection. The intermediate position of *A. mirabilis* is also expressed in the body processes which generally tend to be more robust than in *A. inermis* but less well developed than in *A. confusus*.

Secondly, Norman's (1911) statement that the recurved process on the posterior margin of antennulary segment 2 is present only in some specimens raises the suspicion that he (like Sars and Lang) was dealing with a composite of two species. Both antennule types were illustrated by Norman and appear to be correlated with differences in rostrum shape. The "smooth" type (his Pl. 29, Fig. 3) shows a rostrum which is distinctly longer than in the specimen shown in dorsal habitus (his Pl. 29, Fig. 2) but not as long as in *A. confusus* (Fig. 7A-B). Although the former type is remarkably similar to the condition found in *Juxtaramia polaris* gen. et sp. nov. (see below; Fig. 19A-B) and therefore suggesting that Norman's Fig. 3 was possibly based on East Finmark specimens, it is equally conceivable that two sympatric *Ancorabolus* species occur in the Firth of Clyde. In either case it is impossible to decide which of the appendages figured by Norman (except for Fig. 2) belong to the species depicted in the habitus drawing. In order to provide objective continuity in the future application of the name *A. mirabilis*, the specimen depicted in Norman's (1911) Plate 29, Figs 1-2 is formally designated as the lectotype in conformity with ICZN Art. 74.4. Whether or not Norman's other illustrations (Figs 4-9) can be attributed to *A. mirabilis* will have to await the collection of topotype material. Likewise, all records of *A. mirabilis* (Table 1) from outside the Firth of Clyde which cannot be identified as *A. inermis* or *A. confusus* have to be considered as unconfirmed.

Genus *Arthropsyllus* Sars, 1909

Diagnosis. Ancorabolinae. Body dorsoventrally depressed, tapering posteriorly, without clear demarcation between prosome and urosome; body with series of backwardly produced lateral processes. Cephalothorax with paired simple processes at anterior corners and 3 bulbous processes on lateral margins. Large lateral wing-like processes present on all but last 2 abdominal somites; with fine spinules and unmodified sensillae. Body somites (except penultimate) with pattern of paired tubercles bearing unmodified sensillae; dorsolateral pair on P5-bearing somite absent in ♂; laterodorsal pairs on all but last two somites more developed in ♂ forming small processes. Somatic hyaline frills weakly developed and smooth; somatic hind margins often with very fine setular extensions. Abdominal somites and caudal rami with conspicuous tube-pores ventrally and laterally. Anal somite partly cleft medially; anal operculum with fine spinules. Caudal rami long and cylindrical with 7 setae. Sexual dimorphism in body size, rostrum, antennule, P2-P4 endopods, P5, P6, genital segmentation, abdominal ornamentation, sensillar and process pattern of P5-bearing somite and in degree of development of laterodorsal body processes.

Rostrum fused to cephalic shield and broad; triangular in ♀, dome shaped in ♂; with bifid tip (less pronounced in ♂); lateral paired pointed membranous projections arising proximal to sensillae; midventral tube-pore subapically. Antennule 3-segmented in ♀, 7-segmented and subchirocer in ♂; first segment compound and with 1 sub-apical anterior seta arising from distinctive spinous projection; ♀ segment 2 armature formula [9 + (1 + ae)]. Antenna with basis and proximal endopod segment fused forming allobasis with small membranous insert along exopodal margin, abexopodal margin with 2 setae; exopod entirely absent; endopod with 3 lateral and 6 distal elements. Mandible with slender coxa; palp 1-segmented, uniramous with 2 lateral (basal) and 3 apical (endopodal) setae. Maxillule with membranous zones around proximal area of praecoxa and coxa, increasing flexure; 2 elements on coxal endite; basis with 3 elements on proximal endite, and 2 elements on distal endite; exopod and endopod completely incorporated into basis, each represented by 1 seta. Maxillary syncoxa with 2 well developed endites, each with 3 elements; allobasis drawn out into short robust claw with basal constriction and 3 accessory elements; endopod minute, with 2 setae. Maxilliped subchelate, slender and elongate; endopod drawn out into long narrow, curved claw with 1 accessory seta at base.

P1-P4. Intercoxal sclerites wide and narrow; praecoxae well developed; bases moderately transversely elongate. P1 with 2-segmented rami; endopod about as long as exopod; exp-2 with 2 geniculate setae and 3 outer spines; enp-1 slightly longer than enp-2; enp-2 with 1 naked and 2 geniculate setae. P2-P4 with 3-segmented exopods and 2-segmented endopods; without inner setae on exp-1, exp-3 and enp-1; exp-3 with only 2 outer spines. P2 enp-2 inner seta longer in ♂, inner distal seta shorter in ♂. P3 endopod ♂ 2-segmented; enp-2 anterior surface produced into recurved apophysis; with 2 apical setae. P4 enp-2 without inner seta in ♂. Armature formula as follows:

	Exopod	Endopod
P1	I-0; III,2,0	0-0; 0,2,1
P2	I-0; I-1; II,2,0	0-0; 0,2,1
P3	I-0; I-1; II,2,0	0-0; I,2,1 (♀)
		0-0; 0,2,0 (♂)
P4	I-0; I-1; II,2,0	0-0; I,2,1 (♀)
		0-0; I,2,0 (♂)

P5 biramous in both sexes; baseoendopod with 4 elements in ♀ and 2 setae in ♂; exopod with 5 elements in both sexes. Endopodal lobe and exopod elongate in ♀, less so in ♂. Female genital field located anteriorly, with moderately large copulatory pore; gonopores covered by common genital operculum derived from medially fused P6 with 3 minute elements on either side. Male P6 asymmetrical; without armature; functional member represented by membranous flap.

Type and only species. *Arthropsyllus serratus* Sars, 1909 (by monotypy)

Arthropsyllus serratus Sars, 1909

Arthropsyllus serratus var. *spinifera* Norman, 1911

Type locality. Bejan, outer part of Trondhjem Fjord, Norway.

Type material. Zoologisk Museum, Oslo, Norway: Syntypes, 3 ♀♀ in alcohol (ZMO reg. no. F20302); from Bejan, Trondhjem Fjord, Norway; coll. and det. G.O. Sars.

Other material. The Natural History Museum, London, UK: (a) 4 ♀♀ (1 ♀ damaged lacking urosome, 1 antennule dissected off and mounted on separate slide) in alcohol (NHM reg. no. 2000.1181-1184); 1 ♀ dissected on 12 slides (NHM reg. no. 2000.1185); all from meiofauna samples collected from Frierfjord/Langesundfjord, Norway, 99 m, mud; coll. R. Huys, Spring 1985; (b) Norman Collection (NHM reg. no. 1911.11.8): 1 ♂ in alcohol (reg. no. 45125) labelled as *Arthropsyllus serratus* var. *spinifera* and 6 slides (reg. no. M.2266-2271) labelled as *Arthropsyllus serratus*. Slide M.2271 containing whole mount of 1 ♀ and 1 ♂ which were restored and now preserved in 70% ethanol with added glycerine; 2 ♀♀ dissected onto 3 slides (M.2266, 2268 and 2270); slide M.2269 containing P1-P5 of dissected ♂; all material from northeastern corner of the island Little Cumbrae, Firth of Clyde, Scotland; 36.6 m; coll. A. M. Norman, 1888.

Redescription (♀ based on syntypes and ♂ on Norman's alcohol preserved material (b))

Female

Total body length 846 µm for specimen illustrated ($\bar{x}$ = 874 µm, n = 4) measured from anterior tip of rostrum to posterior margin of caudal rami. Body dorsoventrally depressed, tapering posteriorly, without clear demarcation between prosome and urosome; integument moderately chitinized, with series of backwardly produced lateral wing-like processes. Processes with fine spinules and unmodified sensillae; absent on last two abdominal somites (Fig. 11A-D). Somatic hyaline frills weakly developed and smooth (Fig. 11A, D); somatic margins often with very fine setular extensions. Cephalothoracic processes somewhat bulbous (Fig. 11B-C); with paired simple processes at anterior corners; lateral margins each with 3 complexes of processes plus several sensillae. Body somites (Fig. 11A)

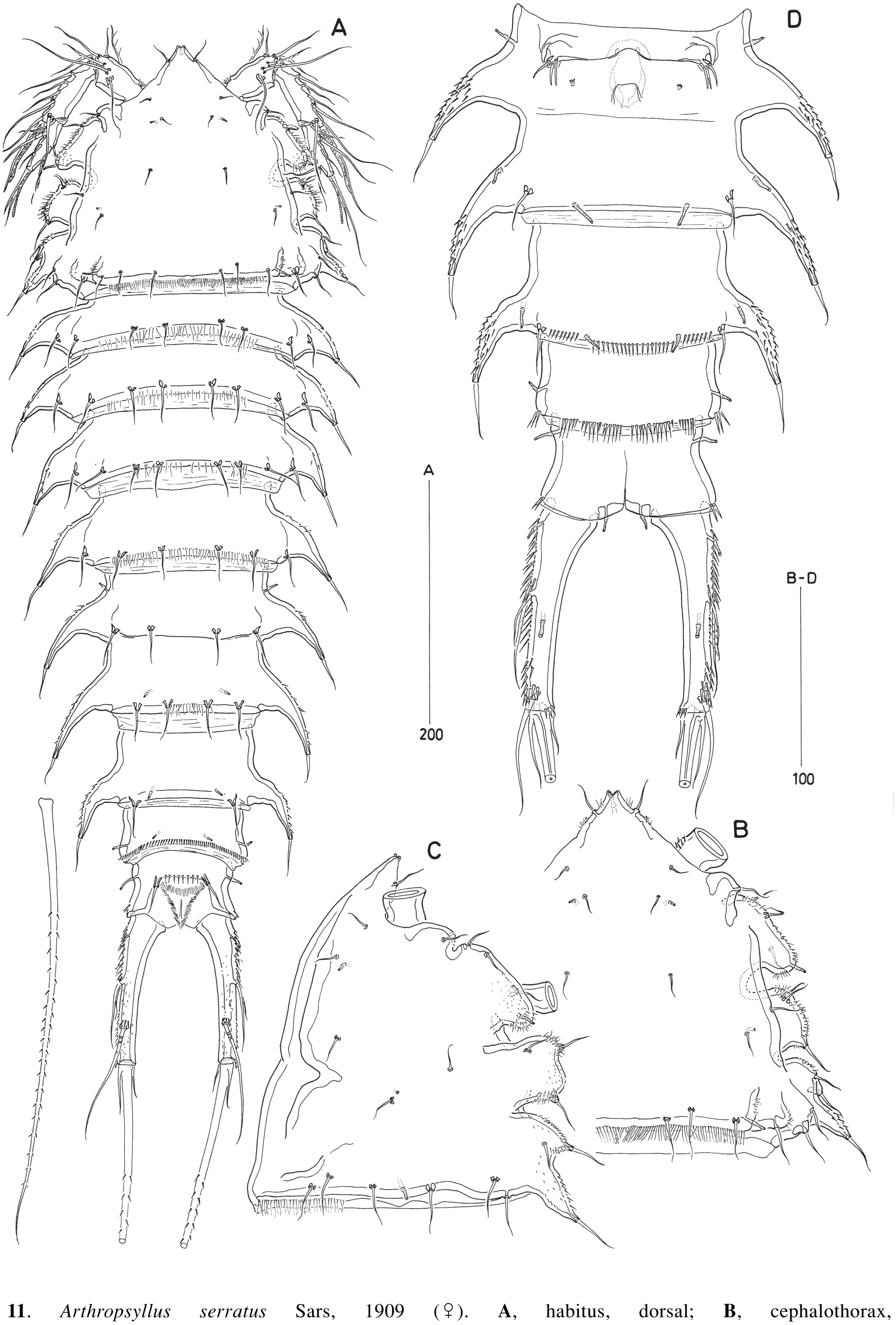

Figure 11. *Arthropsyllus serratus* Sars, 1909 (♀). **A**, habitus, dorsal; **B**, cephalothorax, dorsal; **C**, cephalothorax, lateral; **D**, urosome (excluding P5-bearing somite), ventral.

Figure 11. *Arthropsyllus serratus* Sars, 1909 (♀). **A**, habitus, vue dorsale ; **B**, céphalothorax, vue dorsale ; **C**, céphalothorax, vue latérale ; **D**, urosome (sauf le somite portant P5), vue ventrale.

with following pattern of processes: somites bearing P2-P5 with lateral pair of large conical processes in addition to 1 dorsolateral, 1 laterodorsal and 1 (P5) or 2 (P2-P4) dorsal pairs of minute tubercles bearing sensillae; genital double-somite (both genital and abdominal halves) and second abdominal somite each with 1 lateral pair of large processes, 1 dorsal (genital double-somite only) and 1 laterodorsal pair of minute tubercles bearing sensillae.

Urosomites (except P5-bearing somite) and caudal rami with conspicuous tube-pores ventrally and laterally (Fig. 11D). Original segmentation of genital double-somite indicated by dorsal surface ridge and by position of lateral wing-like processes (Figs 11A, D); posterior half with paired small tubercles ventrolaterally (Fig. 11D) bearing sensilla. Second abdominal somite (Fig. 11D) with sensilla arising from paired small tubercles ventrolaterally (Fig. 11D); ventral posterior margin with median and paired ventrolateral spinule rows. Third abdominal somite (Figs 11A, D; 12F) with almost continuous fine spinule row along posterior margin. Anal somite partly cleft medially (Figs 11A, D; 12F); anal operculum with fine spinule row (Fig. 12F).

Caudal rami elongate and slightly conical (Figs 11A, D; 12F); numerous spinules along outer lateral margin; few spinules around ventral hind margin; with 2 tube-pores and 7 setae, all setae bare except seta V (Fig. 11A): setae I and II arising halfway down outer margin (Fig. 12F); seta IV (Fig. 12F) diminutive and fused basally to seta V; seta VI shortest, not fused basally; seta VII triarticulate at base, arising from small dorsal pedestal (Fig. 12F).

Rostrum (Figs 11B; 13A) broad, triangular, not demarcated at base; with bifid tip; with paired pointed membranous projections laterally (Fig. 13A) just proximal to paired sensillae; midventral tube-pore subapically.

Antennule (Figs 11A, 12A) 3-segmented, arising from distinct pedestal. Segment 1 with 2 short spinule rows along anterior margin; 1 dorsal sub-apical seta arising from spinous projection. Segments 1 and 2 about equally long; segment 2 with aesthetasc. Segment 3 with apical acrothek consisting of short aesthetasc and 2 slender setae fused basally. Armature formula: 1-[5 pinnate + 5], 2-[9 + (1+ae)], 3-[9 + acrothek].

Antenna (Fig. 12B). Coxa represented by small unarmed sclerite. Basis and proximal endopod segment fused forming allobasis; small membranous insert along exopodal margin marking original position of exopod (Fig. 12B); abexopodal margin with spinules in basal half; with 1 pinnate and 1 plumose seta. Endopod with distal surface frill and 2 fine spinule rows along outer margin; 3 spinule rows laterally; lateral armature consisting of 2 pinnate spines and 1 naked seta (Fig. 12B insert); distal armature consisting of 2 pinnate spines and 3 geniculate setae, longest one bearing spinules both proximal and distal to geniculation and fused basally to vestigial seta.

Mandible (Fig. 13B). Coxa slender and elongate, expanding distally into gnathobase bearing, finely incised teeth; dorsal corner with serrate element. Palp well developed, 1-segmented; with 2 sparsely pinnate setae along inner margin (representing basal elements), 3 apical setae (representing incorporated endopod), exopodal seta absent.

Maxillule (Fig. 12C). Praecoxal arthrite rectangular with two setae on anterior surface; distal armature consisting of 3 pinnate and 3 unarmed spines, posteriormost spine fused to arthrite. Transverse membranous zone present around base of praecoxal arthrite and coxa allowing for additional flexure of arthrite. Coxal endite with 2 elements. Basis with 2 closely set endites and few spinules; proximal endite with 3 elements; distal endite with 2 setae. Rami completely incorporated into basis, each represented by 1 seta.

Maxilla (Fig. 12D-E). Syncoxa with 3 spinules rows along outer, inner and anterior distal margin; with 2 endites set in membranous area, each with 1 strong pinnate spine and 2 setae basally fused to endite (Fig. 12E). Allobasis drawn out into claw with basal constriction; tapering in distal half; accessory armature consisting of 2 sparsely pinnate setae and 1 pinnate spine. Endopod minute, 1-segmented, not well developed or clearly defined at base; with 2 setae.

Maxilliped (Fig. 13C). Subchelate and slender. Syncoxa unarmed, with few spinules. Basis with few spinules along outer and palmar margins, unarmed. Endopod drawn out into long narrow, curved claw, pinnate in distal half; 1 small accessory seta at base.

P1 (Fig. 13D). Intercoxal sclerite long and narrow. Praecoxa very well developed with short anterior spinule row. Coxa small and trapezoid with few spinules anteriorly. Basis transversely elongate with pinnate outer spine and naked inner seta; anterior surface with tube-pore and sigmoid row of spinules. Exopod and endopod 2-segmented; exp-2 with 2 geniculate setae and 3 pinnate spines. Endopod about as long as exopod; enp-1 with fine spinules along inner margin, slightly longer than enp-2 (1.36-1.42 times as long) and reaching to proximal half exp-2; enp-2 with 1 naked and 2 geniculate setae.

P2-P4 with long, narrow intercoxal sclerites without ornamentation (as figured for P2; Fig. 14A). Praecoxae well developed, with short anterior spinule row (Fig. 14A). Coxae represented by well developed sclerites, anteriorly with few spinules (as figured for P2; Fig. 14A). Bases moderately transversely elongate; outer margin with sigmoid row of spinules (Fig 14A) and anterior tube-pore in proximal half; outer seta bipinnate, arising from tiny, slightly posteriorly displaced setophore. Exopods 3-segmented, endopods 2-segmented. Exopodal spines pinnate. Endopods distinctly shorter than exopods, reaching almost to distal margin of exp-2. P2-P4 (Fig. 14A-C) enp-1 small, without armature or ornamentation; enp-2 elongate. Armature formula as for genus.

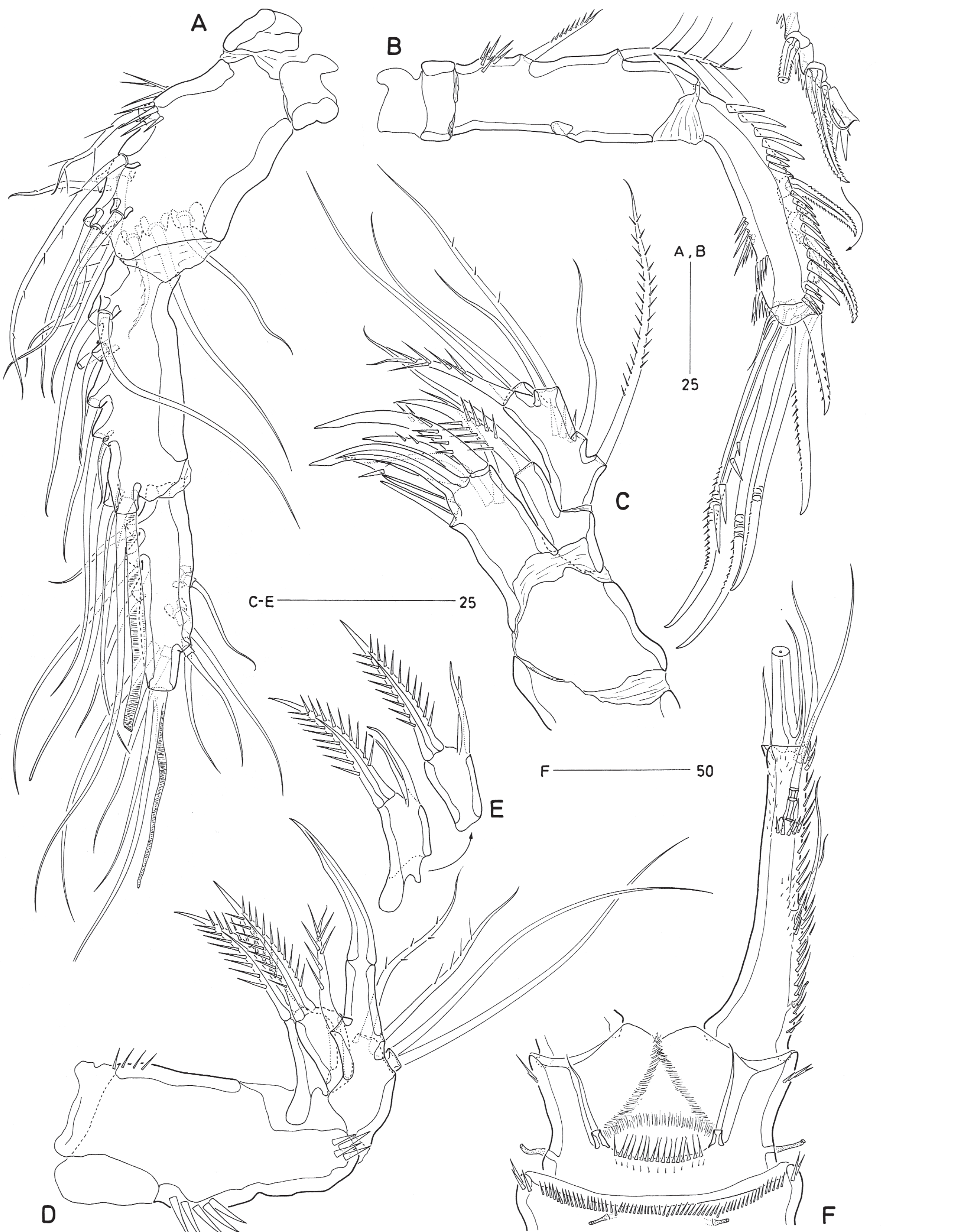

Figure 12. *Arthropsyllus serratus* Sars, 1909 (♀). **A**, antennule, ventral; **B**, antenna (inset showing distal portion of endopod, lateral); **C**, maxillule, posterior; **D**, maxilla; **E**, maxillary endites, disarticulated; **F**, anal somite and left caudal ramus, dorsal.

Figure 12. *Arthropsyllus serratus* Sars, 1909 (♀). **A**, antennule, vue ventrale ; **B**, antenne (l'encart indique la portion distale de l'endopodite, vue latérale) ; **C**, maxillule, vue postérieure ; **D**, maxille ; **E**, endites maxillaires, détachés ; **F**, somite anal et rame caudale gauche, vue dorsale.

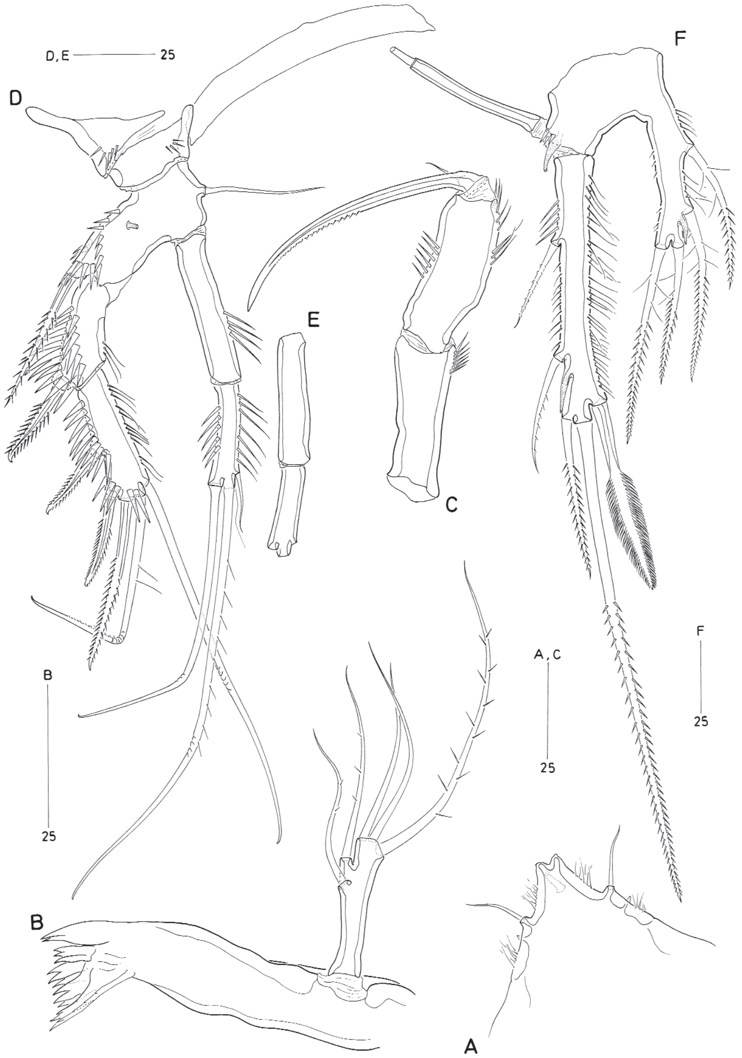

Figure 13. *Arthropsyllus serratus* (♀). **A**, rostrum, dorsal; **B**, mandible; **C**, maxilliped; **D**, P1, anterior; **E**, P1 endopod outline of second ♀, anterior; **F**, P5, anterior.

Figure 13. *Arthropsyllus serratus* (♀). **A**, rostre, vue dorsale ; **B**, mandibule ; **C**, maxillipède ; **D**, P1, vue antérieure; **E**, contours de l'endopodite de P1 d'une autre ♀, vue antérieure ; **F**, P5, vue antérieure.

P5 (Fig. 13F) biramous. Baseoendopod outer corner with tube-pore and short spinule row; setophore long and demarcated, bearing naked outer basal seta. Endopodal lobe slender, elongate and rectangular, with fine spinules along inner and outer margins; with 4 bipinnate elements (with setules in proximal part) and 1 anterior tube-pore between apical and inner distal setae; reaching to insertion level of proximal outer seta on exopod. Exopod long and slender, rectangular; with fine setules along inner margin and some fine spinules along outer margin; with serrate inner spine, 2 pinnate setae distally and 2 pinnate setae plus anterior tube-pore along outer margin.

Genital field (Figs 11D; 14D) with fused gonopores opening via common midventral slit covered by genital operculum derived from vestigial sixth legs. P6 (Fig. 14D) each with 3 reduced setae. Copulatory pore moderately large, flanked by paired tube-pore triplet.

Male

Smaller than ♀ (Fig. 15A), total body length for specimen illustrated 643 µm ($\bar{x}$ = 640, n = 2) measured from tip of rostrum to posterior margin of caudal rami.

Body (Fig. 15A-C) with pattern of processes and sensillae same as for ♀ except: P5-bearing somite without paired dorsolateral sensilla bearing tubercles; first abdominal somite without dorsal pair of sensilla bearing minute tubercles. Laterodorsal processes on all somites distinctly larger and more developed than in ♀ (cf: ♀ minute tubercles); with spinules. First abdominal somite (Fig. 15C) with median spinule row along posteroventral margin; second abdominal (Fig. 15C) somite posterior margin with median spinule row ventrally and paired dorsolateral short row; penultimate somite (Fig. 15C) with almost continuous spinule row along posterior margin.

Rostrum (Fig. 16E) fused to cephalic shield, dome-shaped, shorter than in ♀; apical bifid extension only slightly developed compared to ♀.

Antennule (Fig. 17D-E) 7-segmented and subchirocer, arising from distinct pedestal (arrowed in Fig. 17D), geniculation between segments 4 and 5; segment 4 longest and swollen; with aesthetasc on segment 4 and as part of apical acrothek on segment 7. Segment 1 with 2 short anterior spinule rows, with 1 dorsal seta arising from spinous projection. Segment 2 small with two elements fused to segment (Fig. 17E). Segment 3 represented by a U-shaped sclerite (insert Fig. 17D). Segments around geniculation without modified elements. Armature formula: 1-[3 pinnate + 7], 2-[8], 3-[2], 4-[12 + (1 + ae)], 5-[1], 6-[1], 7-[7 + acrothek]. Apical acrothek consisting of 2 setae and aesthetasc.

P1 (Fig. 16F) differing from ♀ in proportional lengths and shape of endopodal segments (♀ enp-1, 1.44 times as long as enp-2; ♂ enp-1, 1.3 times as long as enp-2).

P2 enp-2 (Fig. 18D) with inner seta distinctly longer and inner distal seta shorter than in ♀ (Fig. 18A).

P3 (Fig. 18E) endopod 2-segmented; enp-2 with 2 apical setae, anterior distal surface produced into recurved apophysis, denticulate in distal half; inner seta absent, inner distal seta markedly shorter than in ♀ (Fig. 18B).

Figure 14. *Arthropsyllus serratus* (♀). **A**, P2 (inset showing entire intercoxal sclerite), anterior; **B**, P3 left endopod, anterior; **C**, P4 left endopod, anterior; **D**, genital field, ventral.

Figure 14. *Arthropsyllus serratus* (♀). **A**, P2 (l'encart indique le sclérite intercoxal entier), vue antérieure ; **B**, endopodite gauche de P3, vue antérieure ; **C**, endopodite gauche de P4, vue antérieure ; **D**, région génitale, vue ventrale.

P4 endopod (Fig. 18F) somewhat more compact; enp-2 without inner seta, outer spine longer and distal setae shorter than in ♀ (Fig. 18C).

P5 (Fig. 17F) biramous. Baseoendopod outer corner with tube-pore; setophore demarcated, long, bearing naked outer basal seta. Endopodal lobe rectangular, much shorter than in ♀; distally with 2 pinnate setae, outer distal corner with 1 anterior tube-pore; reaching to proximal margin of exopod. Exopod rectangular, comparatively shorter than in ♀; fine setules along inner margin, and few spinules along outer margin; with serrate inner spine, 2 pinnate setae and anterior tube-pore distally and 2 outer setae.

Sixth pair of legs asymmetrical (Fig. 15C) with only 1 functional member, represented by membranous flap; other member fused to somite. P6 without armature.

Variability. Slight variation in proportional lengths of P1 enp-1 and -2 (Fig. 13D-E) were observed in the ♀♀ from Frierfjord/Langesundfjord.

Distribution. See Table 1.

Remarks

The Frierfjord/Langesundfjord material agreed in every aspect with Sars' female syntypes. There appear to be some slight deviations between the Frierfjord material compared to Sars' published description which were not, however, supported by observations made directly from the syntypes: (a) ♀ body length according to Sars 800 µm (855 µm from syntype); (b) mandibular coxa shorter and stouter in Sars' illustration (longer and more slender in syntype); (c) P1 proportional lengths of enp-1 to enp-2 (1.36-1.42 times as long present study; 1.1 times as long in Sars' (1909) Plate CCXIV; 1.37 times as long in ♀ syntype); (d) small dorsal tubercles bearing sensillae of body somites (except last two) not indicated by Sars but present in syntypes. Additional discrepancies in the armature of oral appendages were excluded as points of comparison since they undoubtedly result from imperfect observations made by Sars (1909). The author also erroneously claimed the sexually dimorphic apophysis to be

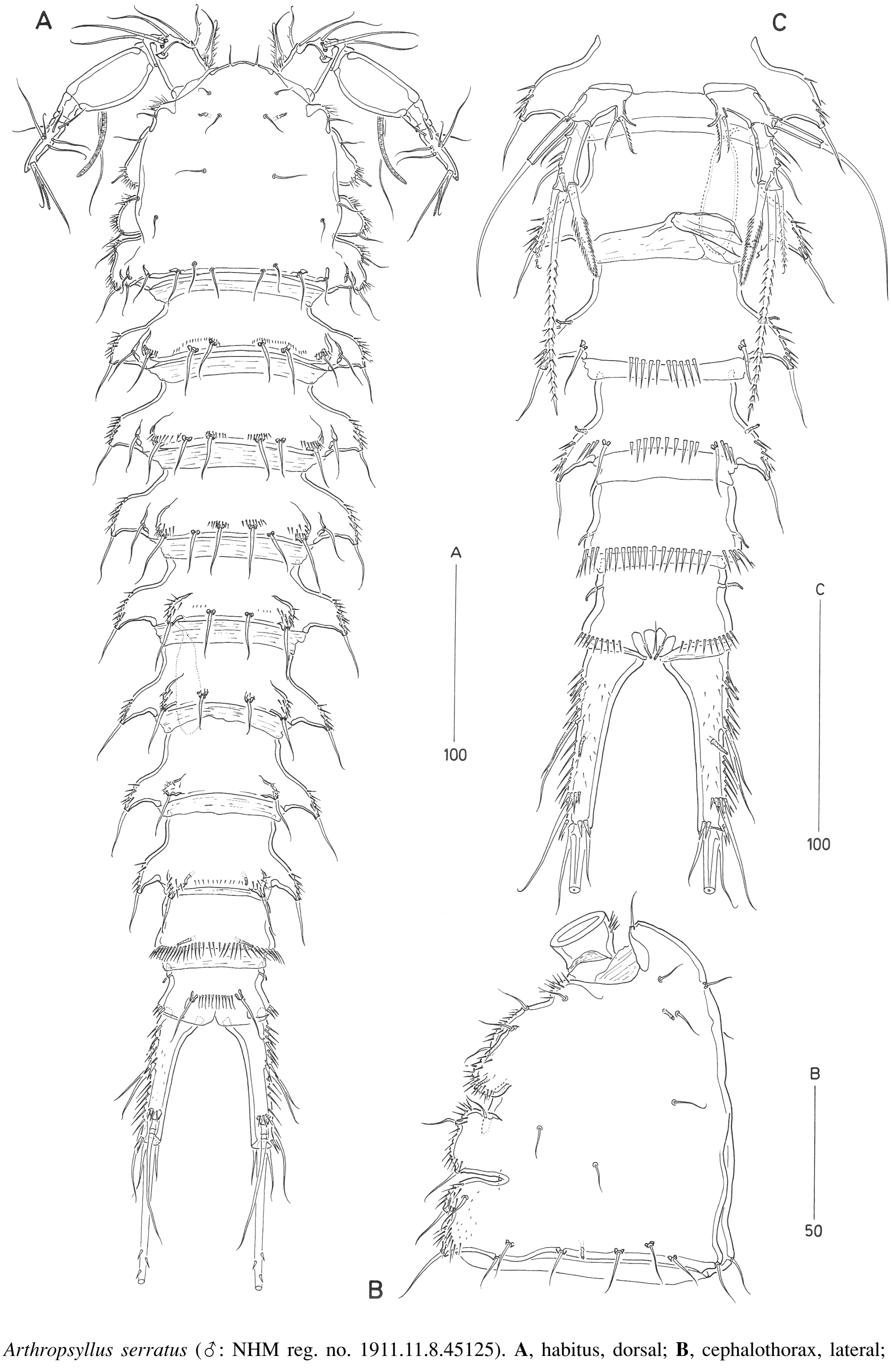

Figure 15. *Arthropsyllus serratus* (♂: NHM reg. no. 1911.11.8.45125). **A**, habitus, dorsal; **B**, cephalothorax, lateral; **C**, urosome, ventral.

Figure 15. *Arthropsyllus serratus* (♂: NHM reg. no. 1911.11.8.45125). **A**, habitus, vue dorsale ; **B**, céphalothorax, vue latérale ; **C**, urosome, vue ventrale.

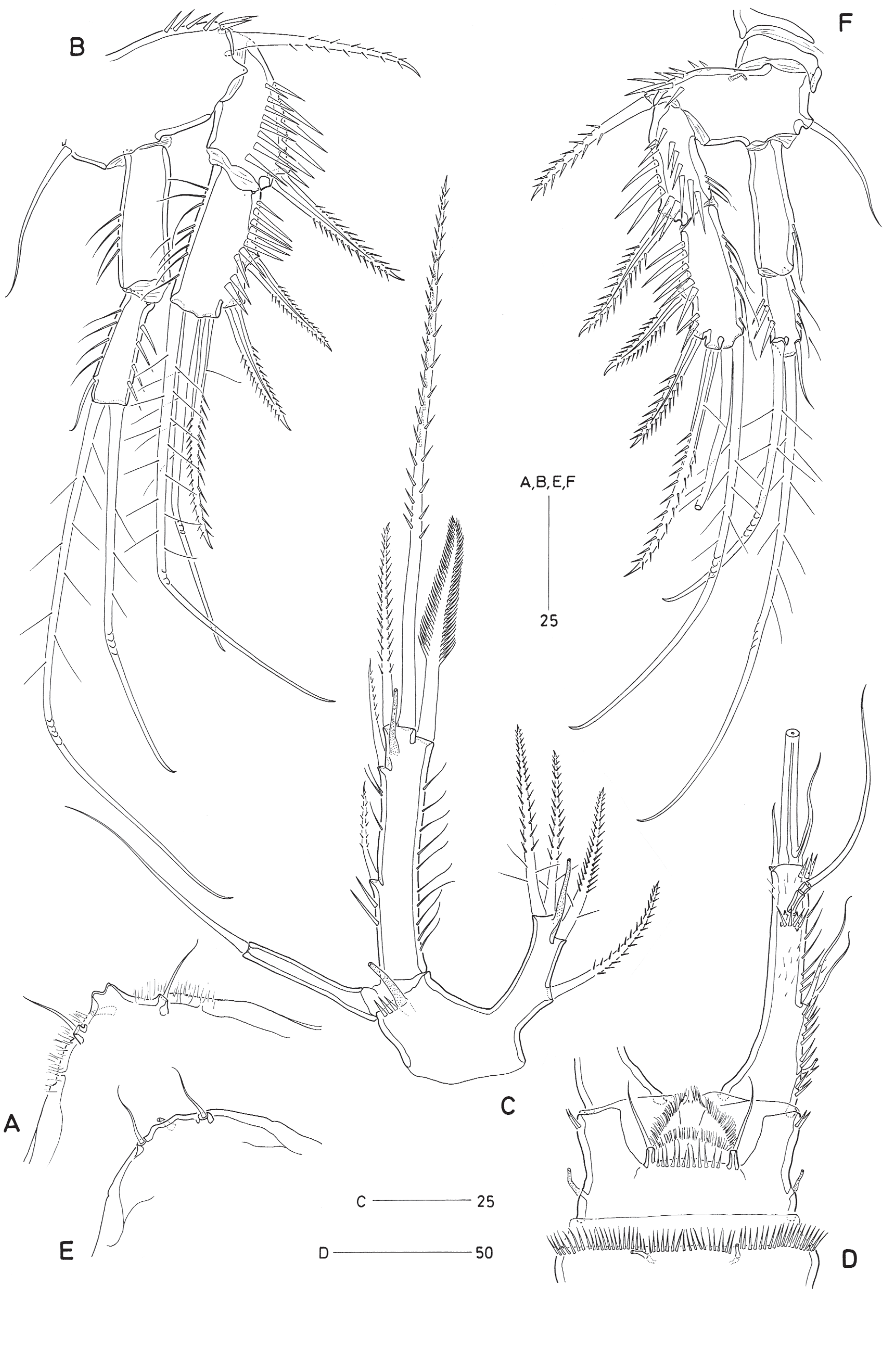

Figure 16. *Arthropsyllus serratus*. **A**, rostrum (♀), dorsal; **B**, P1 (♀), anterior; **C**, P5 (♀), anterior; **D**, anal somite and left caudal ramus (♀), dorsal; **E**, rostrum (♂), anterior; **F**, P1 (♂), anterior. A-D, Norman's slide material (♀: NHM reg. no. 1911.11.8.M2271); E-F, Norman's alcohol preserved material (♂: NHM reg. no. 1911.11.8.45125).

Figure 16. *Arthropsyllus serratus*. **A**, rostre (♀), vue dorsale ; **B**, P1 (♀), vue antérieure ; **C**, P5 (♀), vue antérieure; **D**, somite anal et rame caudale gauche (♀), vue dorsale ; **E**, rostre (♂), vue antérieure ; **F**, P1 (♂), vue antérieure. A-D, lames de Norman (♀: NHM reg. no. 1911.11.8.M 2271) ; E-F, matériel de Norman préservé dans l'alcool (♂: NHM reg. no. 1911.11.8.45125).

present on the endopod of P2, an observational error adopted by Norman (1911; text only) but rectified by Lang (1948).

Norman (1903) stated that he had found a second species of *Ancorabolus* from the same dredge sample as *A. mirabilis* taken near Little Cumbrae, Scotland. Subsequent to Sars' (1909) publication of *The Crustacea of Norway* and the description of *A. serratus*, Norman (1911) concluded that this second species in fact belonged to *Arthropsyllus* and not *Ancorabolus* as he first remarked. Norman (1911) regarded the only difference between the Scottish material and the nominal type species to be the presence of dorsal tubercles ("spines", cf. name) on most body somites, which appeared to be absent from Sars' (1909) illustrations. The illustrations presented in Norman's (1911) publication were made by Andrew Scott in 1890. Norman however, placed every trust in the accuracy of A. Scott's illustrations, but stated that he himself was "..unable to see.." these tubercles upon re-examination of the slide material. In anticipation of possible synonymy he attributed only infrasubspecific status to the Scottish material as *Arthropsyllus serratus* var. *spinifera*.

Re-examination of Norman's material (Figs 16A-D; 17A-C; 18A-C) showed the females to be very similar to the Norwegian syntypes and the Frierfjord/Langesundfjord material of *A. serratus*. For example, perfect agreement was found in the body ornamentation pattern and the detailed morphology of

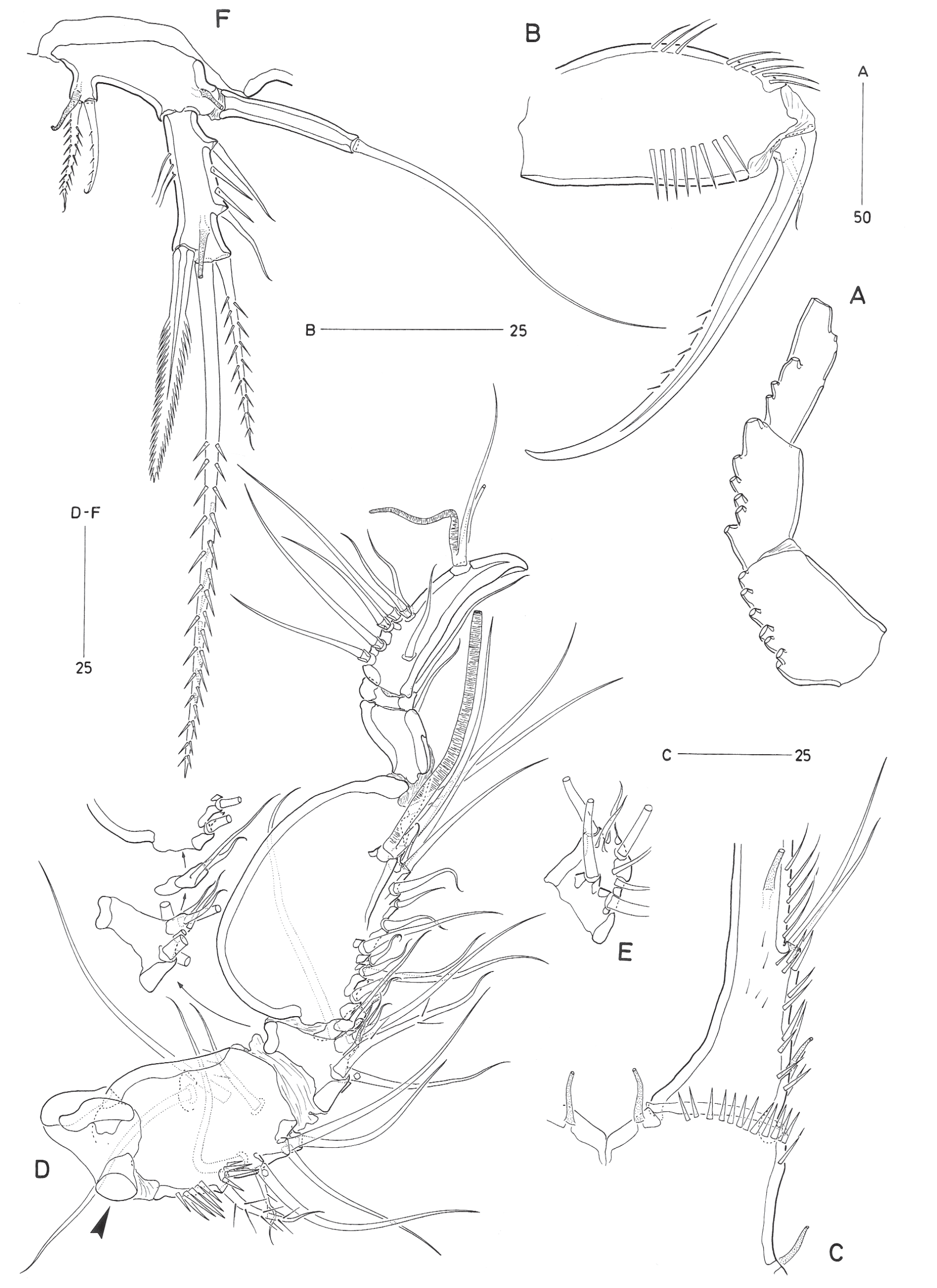

Figure 17. *Arthropsyllus serratus*. **A**, antennule (♀), armature omitted; **B**, maxilliped (♀), syncoxa omitted; **C**, anal somite (part) and right caudal ramus (♀), ventral; **D**, antennule (♂), ventral (well developed pedestal arrowed), inset showing detailed armature of disarticulated segments 2-3 and proximal portion of segment 4; **E**, antennule (♂) segment 2, anterior; **F**, P5 (♂), anterior. A-C, Norman's slide material (A, NHM reg. no. 1911.11.8.M 2266; B, NHM reg. no. 1911.11.8.M 2268; C, NHM reg. no. 1911.11.8.M 2271); D-F, Norman's alcohol preserved material (♂: NHM reg. no. 1911.11.8.45125).

Figure 17. *Arthropsyllus serratus*. **A**, antennule (♀), armature omise; **B**, maxillipède (♀) ; **C**, somite anal (part.) et rame caudale droite (♀), vue ventrale; **D**, antennule (♂), vue ventrale (la flèche indique le socle bien développé), l'encart indique l'armature détaillée des articles 2-3 et de la portion proximale de l'article 4 ; **E**, article antennulaire 2 (♂), vue antérieure ; **F**, P5 (♂), vue antérieure. A-C, lames de Norman (A, NHM reg. no. 1911.11.8.M 2266 ; B, NHM reg. no. 1911.11.8.M 2268 ; C, NHM reg. no. 1911.11.8.M 2271) ; D-F, matériel de Norman préservé dans l'alcool (♂: NHM reg. no. 1911.11.8.45125).

antennules, antennae and mouthparts. The few differences discerned mostly concern morphometric deviations: (1) total body length 799 µm; (2) rostrum (Fig. 16A) more obtuse, although general structure the same; (3) maxillipedal basis wider (but ornamentation identical); (4) P1 (Fig. 16B) length ratio of enp-1 to enp-2 (1.25 in Scottish ♀♀); (5) P2-P4 (Fig. 18) enp-2 slightly shorter and wider; (6) proportional length of P5 exopod and endopodal lobe (Fig. 16C) slightly shorter; (7) spinules of penultimate somite (Fig. 16D) longer, spinules present around ventral hind margin of anal somite (Fig. 17C). Caution must be exercised when considering points (1)-(6) since all measurements and drawings were made from slide mounted material (either whole or dissected specimens), hence body, appendages and related characters show distortion effects from squashing.

Unfortunately no males were obtained from the Frierfjord/Langesundfjord and Sars (1909) acquired only a single ♂ specimen from Repvaag in East Finmark which could not be traced in the type material. Sars figured only the male antennule, P5 and P3 endopod, misinterpreting the segmentation and/or setation of the former two. Comparison of his illustrations of the Repvaag male with males from the Norman collection indicates that: (a) the antennule is undoubtedly 7-segmented, Sars having misinterpreted the pedestal as segment 1 (see Fig. 17D, pedestal arrowed), and overlooked segments 3 and 6;

Figure 18. *Arthropsyllus serratus*. **A**, P2 (♀) left endopod, anterior; **B**, P3 (♀) left endopod, anterior; **C**, P4 (♀) left endopod, anterior; **D**, P2 (♂) right endopod, anterior; **E**, P3 (♂) left endopod, anterior; **F**, P4 (♂) left endopod, anterior. A-C, Norman's slide material (♀: NHM reg. no. 1911.11.8.M 2271); D-F, Norman's alcohol preserved material (♂: NHM reg. no. 1911.11.8.45125).

Figure 18. *Arthropsyllus serratus*. **A**, endopodite gauche de P2 (♀), vue antérieure ; **B**, endopodite gauche de P3 (♀), vue antérieure ; **C**, endopodite gauche de P4 (♀), vue antérieure ; **D**, endopodite droit de P2 (♂), vue antérieure ; **E**, endopodite gauche de P3 (♂), vue antérieure ; **F**, endopodite gauche de P4 (♂), vue antérieure. A-C, lames de Norman (♀: NHM reg. no. 1911.11.8.M 2271) ; D-F, matériel de Norman.

(b) Sars omitted the endopodal lobe of P5 and consequently also the 2 setal elements. Lang (1948) maintained *A. serratus* var. *spinifera* on the basis of ♀ body length (700 µm compared to 800 µm in *A. serratus*), the presence of dorsal tubercles on the body somites (except cephalothorax and last 2 abdominal somites) and the presence of a small trisetose endopodal lobe on the ♂ P5. As shown above, the latter two characters are displayed by *A. serratus* (although Norman (1911) and Lang (1948) had misinterpreted the distinctive tube-pore on the ♂ P5 endopodal lobe as a third element). In addition, our measurements of Norman's slide material show the ♀ to be at least 799 µm in length, despite telescoping and squashing. In the absence of any discriminating characters we formally synonymise *A. serratus* var. *spinifera* with *A. serratus*. This course of action requires confirmation by the examination of male *Arthropsyllus* from the Trondhjem area, since Sars' (1909) description of the male is only cursory, and observations of the Scottish material indicated some striking sexual dimorphism particularly with regard to the pattern and size of body processes and the endopodal armature of P4. Also, examination of both sexes on the basis of topotypes would be desirable in view of the wide separation of Sars' (1909) collecting sites of the single ♂ (East Finmark) and the ♀♀ syntypes (Trondhjem Fjord).

Kunz (1971, 1977) summarized previously published records of *A. serratus* in Kiel Bay (Germany), citing his own record of a single ♀ in black muds (Kunz, 1935) and those of Becker (1970) who found the species in three 3 localities and noted that Klie (unpubl.) had collected some material of *A. serratus* in May 1949. Becker's (1970) inconsistent usage of both names *A. serratus* and *A. serratus* var. *spinifera* throughout his paper is confusing but obviously refers to the same species.

Arlt (1983) reported 1 ♀ from the central Baltic Sea (East of Darss Sill) of which he illustrated the antennule, P1, P2, endopods of P3-P4, P5 and urosome. Arlt remarked on three main differences displayed by the Baltic specimen: (a) P1 enp-1 with a small inner seta: this most likely results from misinterpretation of the fine setules along the inner margin as a seta (see Fig. 13D); (b) P3 enp-2 without inner seta: this element has most probably either been broken off, or the ramus figured is aberrant (aberrant conditions in swimming leg armature have been observed in other Ancorabolinae, e.g. *A. confusus*); (c) endopodal lobe of ♀ P5 distally with 2 setae and 1 additional reduced element: the latter is probably the large tube-pore typically found in this position. Arlt's (1983) record is confirmed here as *A. serratus*, substantiating its penetration into the oligohaline waters of the Baltic.

Chislenko (1967) recorded 2 ♀♀ from the Karelian coast of the White Sea which is geographically close to the collecting site of Sars' (1909) single male. Chislenko's specimens are slightly larger, measuring 880-900 µm, however, comparison of the few appendages figured identify them as *A. serratus*.

Distribution. See Table 1.

Genus *Breviconia* gen. nov.

The following diagnosis is based on the original description and figures of George (1998a).

Diagnosis [based on ♀ only]. Ancorabolinae. Body slightly dorsoventrally depressed, tapering posteriorly, without clear demarcation between prosome and urosome. Body somites (except last 2) with large lateral wing-like processes. Somatic hyaline frills weakly developed. Cephalothorax with conical or thorn-like processes; anterior corners with small simple processes; lateral margins each with 2 isolated conical processes and set of 3 similar processes at posterolateral corners; posterior margin with paired dorsal and 2 closely set laterodorsal pairs of conical processes, plus additional sensillae. Somites bearing P2-P4 with lateral wing-like processes, 2 pairs of closely set dorsolateral conical processes (forming bipartite branch) plus 1 pair of dorsal conical processes; P5-bearing somite with large lateral wing-like processes, 1 dorsolateral and 1 laterodorsal pair of conical processes; genital double-somite (both genital and abdominal halves) and second abdominal somite each with 1 lateral (wing-like) and 1 dorsolateral (conical) pair of processes. Genital and first abdominal somites completely fused forming genital double-somite; original segmentation indicated by position of lateral wing-like processes and dorsal spinule row. Penultimate somite, posterior margin with spinule row. Anal somite partly cleft medially; anal operculum rounded. Caudal rami long and cylindrical with 7 setae: setae I and II positioned halfway down outer margin; seta IV diminutive, positioned very close to seta V; seta VI shortest; seta VII triarticulate at base, arising near posterior margin.

Rostrum fused to cephalic shield, triangular; with bifid tip; median tube-pore apically. Antennule 3-segmented in ♀; segment 1 longest; aesthetasc on segments 2 and 3. Armature formula: 1-[10], 2-[7 + (1+ae)], 3-[9 + acrothek]. Antenna with basis and proximal endopod segment fused forming allobasis, abexopodal margin with 2 setae; exopod absent; endopod with 3 lateral and 6 distal elements (1 element reduced and fused basally to longest geniculate seta). Mandible with slender coxa; palp 1-segmented, uniramous with 5 setae (1 exopodal, 1 basal, 3 endopodal). Maxillule with 1 element on coxal endite; basis with 3 elements on proximal endite, and 2 elements on distal endite; exopod and endopod completely incorporated into basis. Maxillary syncoxa with 2 well developed endites; allobasis drawn out into robust claw with 3 accessory elements; endopod represented by 2 setae. Maxilliped subchelate, slender and elongate; syncoxa and basis unarmed; endopod drawn out into long narrow, curved claw.

P1-P4. Intercoxal sclerites wide and narrow; bases transversely elongate. P1 with 2-segmented rami; endopod longer than entire exopod; enp-1 longer than enp-2; enp-2 with 1 naked and 2 geniculate setae; exp-2 with 3 geniculate setae and 2 outer spines. P2-P4 exopods 3-segmented, endopods 2-segmented; endopods about the same length or shorter than exopods; enp-1 small; without inner setae on exp-1, exp-3 and enp-1; exp-3 with only 2 outer spines. Armature formula as follows:

	Exopod	Endopod
P1	I-0; II+1,2,0	0-0; 0,2,1
P2	I-0; I-1; II,2,0	0-0; 0,2,1
P3	I-0; I-1; II,2,0	0-0; 1,2,1
P4	I-0; I-1; II,2,0	0-0; 1,2,1

P5 biramous; baseoendopod with long demarcated setophore bearing outer basal seta. Endopodal lobe and exopod long and rectangular with 4 and 5 elements, respectively. Exopod inner spine inserting in middle third. Female genital field located anteriorly, with moderately large copulatory pore; gonopores covered by common genital operculum derived from medially fused P6 with 2 minute elements on either side.

Type species. *Arthropsyllus australis* George, 1998a = *Breviconia australis* (George, 1998a) comb. nov.

Species inquirenda. *Laophontodes echinatus* Brady, 1918 = *Breviconia echinata* (Brady, 1918) comb. nov.

Etymology. The generic name is derived from the Latin *brevis* meaning short, and *conus* meaning cone, and refers to conical dorsal body processes. Gender: feminine.

Breviconia australis (George, 1998a) comb. nov.

Arthropsyllus australis George, 1998a

Type locality. Gardiner Island, Beagle Channel, 55° 00.4' S, 66° 53.6' W, Chile.

Material. None examined.

Remarks

This species was described on the basis of a single ovigerous female from the Beagle Channel (Southern Chile) as *Arthropsyllus australis*. Its placement in *Arthropsyllus* by George (1998a) was based on the lack of well developed dorsal/dorsolateral processes, the slightly dorsoventrally depressed body shape and the presence of lateral extensions ("epimeres") on all but the last two body somites. George (1998a) rightly expressed reservations about the application of the first character without prior assessment of its homology across genera, however, considered the other two characters as autapomorphies for *Arthropsyllus*. The present study has demonstrated that both characters are diagnostic of a wider group of taxa and in fact are synapomorphies shared by all genera in the *Ancorabolus*-lineage.

Comparison of the original description of *A. australis* revealed several deviations from the generic diagnosis of *Arthropsyllus* as redefined above: (a) cephalothoracic processes conical or thorn-like [bulbous]; (b) posterior margin of cephalothorax with pairs of distinct dorsal and laterodorsal conical processes [not developed]; (c) rostrum distinctly offset from anterior margin of cephalic shield [forming continuous outline]; (d) all laterodorsal, dorsolateral and dorsal sensilla-bearing processes conical and moderately developed [small tubercles]; (e) armature formula of ♀ A1 segment 2: [7 + (1 + ae)] instead of [9 + (1 + ae)]; (f) coxal endite of maxillule with only 1 element [2 elements], exopod represented by 2 setae [1 seta]; (g) P1 endopod longer than exopod [subequal]; (h) P1 exp-2 with 3 geniculate setae + 2 spines [2 geniculate setae + 3 spines]; (i) P2-P4 endopods reaching to at least halfway down exp-3 [to distal margin of exp-2]; (j) P5 exopod and endopodal lobe shorter, position of inner exopodal seta higher; (k) ♀ P6 with only 2 reduced elements [3 elements]. The majority of these character states represent discrete steps of major morphological transformations in the phylogeny of the *Ancorabolus*-lineage (see below). Maintaining *A. australis* in the genus *Arthropsyllus* and accepting this combination of character states as the result of intrageneric evolution is clearly a less parsimonious hypothesis and would require explaining multiple convergences within the *Ancorabolus*-lineage. Phylogenetic analysis (see below) clearly indicates that *A. australis* represents a separate clade, occupying an intermediate position between *Uptionyx* gen. nov. and the *Juxtaramia*-*Ancorabolus* lineage, justifying its transfer to a new genus *Breviconia*.

Several of the characters above were listed by George (1998a) to differentiate his new species from Sars' (1909) description of *A. serratus* and hence were only attributed specific status. Additional discrepancies observed by George are not valid and can be associated with misinterpretations and/or omissions made originally by Sars (1909). These include (a) the coxa of the mandible which is more slender and elongate than illustrated by Sars, and the curved nature of which can only be represented when mounted in the correct plane, (b) the geniculate nature of the terminal setae on P1 exp-2 and (c) the inner exopodal spine of P5 which is serrate as in *B. australis*.

George (1998a) claimed that the caudal rami of *A. australis* possess only 6 setae and inferred from their individual positions that seta IV is absent. This character clearly requires confirmation since it is almost certainly based on incorrect homologization. Reduction to 6 setae frequently occurs in harpacticoid copepods but is always the result of the loss of seta I (Huys & Boxshall, 1991). Setae can also migrate, but the displacement of seta II to the hind margin (according to George) is dubious. In general (Huys & Boxshall, 1991) seta I is located ventral to seta II and in the *Ancorabolus*-lineage the latter is typically positioned closely to former, overlying it when viewed in dorsal aspect (Figs 4E, 9E, 12F, 19D, 16D, 25D). It is therefore assumed that seta I was overlooked in George's (1998a) original description and figures, accounting for the erroneous numbering of setae II-IV.

Other anomalies in George's (1998a) illustrations which appear to be in conflict with all species of the *Ancorabolus*-lineage are: (a) maxillary endites with only 2 elements [3 elements], (b) maxilliped without accessory seta on endopod [present], and (c) posterior margins of body somites (except penultimate) with spinules [setular extensions].

Breviconia echinata (Brady, 1918) comb. nov.

Laophontodes echinatus Brady, 1918

Type locality. Tow net among pack ice at 82 m; 64°18' S, 132°24' E.
Material. None examined. The holotype no longer exists.

Remarks
The fragmentary descriptions given by Brady (1918) for three new *Laophontodes* species collected during the Australian Antarctic Expedition (1911-1914), compelled Lang (1936, 1948) to place them as *species incertae sedis* in this genus. Of these, *L. echinatus* was described on the basis of a single damaged ovigerous female. Lang (1936) explicitly excluded any affiliation to *Laophontodes*, citing the 2-segmented P5 exopod as the main obstacle. Brady's (1918) habitus illustration in ventral aspect is somewhat misleading, however the simple, not very well developed lateral processes of the cephalic shield can be discerned and also the lateral wing-like processes on the genital and abdominal somites (except the last two somites) which are figured in dorsal aspect. This pattern shows closest affinity to the *Breviconia* condition with Brady's (1918) lateral habitus illustration indicating some sort of dorsal projections on at least the cephalothorax and pedigerous somites. Unfortunately the specimen had lost the first swimming legs and hence a valuable diagnostic character. However several other similarities with *Breviconia* can be identified: (a) antennule short and 3-segmented from the habitus figured (which contradicts the text and the separate antennule figured; the latter was probably taken from another species since segment proportions appear quite different and the missing apical setae can be clearly distinguished from the habitus figure); (b) P3 endopod reaching beyond distal margin of exp-2, to proximal half exp-3; outer exopodal spines elongate; (c) P5 proportional

lengths of exopod and endopodal lobe (although Brady has misinterpreted the exopod as 2-segmented) and the position of the inner exopodal seta. On the basis of these similarities *L. echinatus* is removed from *Laophontodes* and transferred to *Breviconia* as *species inquirenda*. Both *B. australis* and *B. echinata* are found at high latitudes in the Southern Hemisphere. Despite the grossly deficient description of the latter, conspecificity is ruled out on the basis of differences in body size and caudal ramus length. *B. echinata* is about twice the size (0.86 mm according to Brady, 1.0-1.2 mm according to our measurements) of *B. australis* (0.53 mm).

Genus *Juxtaramia* gen. nov.

Diagnosis. Ancorabolinae. Body dorsoventrally depressed, tapering posteriorly, without clear demarcation between prosome and urosome; body ornate with series of backwardly produced processes, each with fine spinules and unmodified sensillae. Processes never present on last 2 abdominal somites; other somites always with large paired lateral wing-like processes. Cephalothorax, with paired simple processes at anterior corners; lateral margins each with 3 branching processes; posterior margin with dorsal pair of small tubercles bearing sensilla. Body somites with sexually dimorphic pattern of produced processes. In ♀: somites bearing P2-P4 with 8 processes (2 large lateral, 2 small dorsal and 4 dorsolateral arranged in 2 pairs); P5-bearing somite with 6 processes (2 lateral, 2 dorsolateral, 2 laterodorsal); genital double-somite, both genital and abdominal halves and second abdominal somite each with 1 lateral and 1 dorsolateral pair. In ♂: P2-bearing somite lacking dorsolateral processes (only lateral and dorsal present); somites bearing P3-P4 with only 2 dorsolateral processes; P5-bearing somite without dorsolateral processes (only lateral and laterodorsal present). Somatic hyaline frills weakly developed and smooth; somatic hind margins often with very fine setular extensions. Abdominal somites and caudal rami with conspicuous tube-pores ventrally and dorsally. Anal somite partly cleft medially; anal operculum without ornamentation. Caudal rami elongate, cylindrical and parallel with 7 setae. Sexual dimorphism in body size, rostrum, antennule, P2-P4 endopods, P5, P6, genital segmentation, abdominal ornamentation, caudal rami and in both pattern and size of body processes.

Rostrum fused to cephalic shield, with bifid tip; elongate in ♀, distinctly shorter and wider in ♂; lateral paired pointed membranous projections arising proximal to sensillae; long midventral tube-pore in distal half. Antennule indistinctly 4-segmented in ♀, indistinctly 8-segmented and subchirocer in ♂; boundary between segments 1-2 in both sexes represented by incomplete surface suture; segment 2 with 1 sub-apical anterior seta arising from distinctive spinous projection; ♀ segment 3 armature formula [7 + (1+ae)]. Antenna with basis and proximal endopod segment fused forming allobasis with small membranous insert along exopodal margin, abexopodal margin without armature; exopod entirely absent; endopod with 3 lateral and 6 distal elements. Mandible with slender coxa; palp 1-segmented, uniramous with 3 apical setae. Maxillule with 1 element on coxal endite; basis with 3 elements on proximal endite, and 2 elements on distal endite; endopod and exopod completely incorporated into basis, represented by 1 and 2 setae respectively. Maxillary syncoxa with 2 well developed endites, each with 3 elements; allobasis drawn out into claw with basal constriction and 3 accessory elements; endopod minute, with 2 setae. Maxilliped subchelate, slender and elongate; endopod drawn out into long narrow, curved claw with 1 accessory seta.

P1-P4. Intercoxal sclerites wide and narrow; praecoxae well developed; bases transversely elongate. P1 with 2-segmented rami; exp-2 with 4 geniculate setae and 1 outer spine; enp-1 elongate, much longer than enp-2 and exopod; enp-2 with 1 naked and 2 geniculate setae. P2-P4 with 3-segmented exopods and 2-segmented endopods; without inner setae on exp-1, exp-3 and enp-1; exp-3 with only 2 outer spines. P2 enp-2 inner distal seta shorter in ♂. P3 endopod ♂ 2-segmented; enp-2 anterior surface produced subdistally into recurved apophysis; with 2 apical setae. P4 enp-2 outer element setiform in ♀, spiniform in ♂; inner distal seta shorter in ♂. Armature formula as follows:

	Exopod	Endopod
P1	I-0; I+2,2,0	0-0; 0,2,1
P2	I-0; I-1; II,2,0	0-0; 0,2,0
P3	I-0; I-1; II,2,0	0-0; 1,2,0 (♀)
		0-0; 0,2,0 (♂)
P4	I-0; I-1; II,2,0	0-0; 1,2,0 (♀)
		0-0; I,2,0 (♂)

P5 biramous in both sexes; baseoendopod with 4 setae in ♀ and 2 setae in ♂; exopod with 5 elements in both sexes. Endopodal lobe and exopod elongate in ♀, less so in ♂. Female genital field located anteriorly, with moderately large copulatory pore; gonopores covered by common genital opercula derived from P6 with 3 basally fused minute elements on either side. Male P6 asymmetrical; without armature; functional member represented by membranous flap.

Type and only species. *Juxtaramia polaris* gen. et sp. nov.
Etymology. The generic name is derived from the Latin *iuxta*, meaning close by, near, and *ramus*, meaning branch, and refers to the parallel positioning of the caudal rami. Gender: feminine.

Juxtaramia polaris gen. et sp. nov.

Ancorabolus mirabilis Norman, 1903 *sensu* Norman (1911)

Type locality. Varanger Fjord, East Finmark, Norway.
Type material. The Natural History Museum, London, UK: Norman Collection (NHM reg. no. 1911.11.8): 4 ♀♀ and 1 ♂ erroneously deposited as "Types of *Ancorabolus mirabilis*" (NHM reg. no. 44973-977). Holotype ♀ designated (NHM reg. no. 44973) in alcohol; paratypes are 3 ♀♀ and 1 ♂ in alcohol (NHM reg. no. 44974-977); from Varanger Fjord, East Finmark, mud; coll. A. M. Norman, 1890.

Description
Female
Total body length 896 µm ($\bar{x}$ = 874 µm, n = 4) measured from anterior tip of rostrum to posterior margin of caudal rami. Body (Fig. 19A) slightly dorsoventrally depressed, tapering posteriorly, without clear demarcation between prosome and urosome; integument strongly chitinized and highly ornate. Somatic hyaline frills weakly developed and smooth (Fig. 19A, C); somatic margins often with very fine setular extensions (Fig. 19A). Cephalothorax (Figs 19A; 21A) with paired simple process at proximal outer corners and 3 branched processes around each lateral margin; processes furnished with spinules and bearing unmodified sensillae; posterior margin (Fig. 21A) with paired sensillae arising from small dorsal tubercles plus 1 additional unmodified sensilla; dorsal surface with pair of sensillate tubercles about halfway down the length of the cephalic shield. Body somites (Fig. 19A) with following pattern of paired produced processes: somites bearing P2-P4 with 4 pairs of processes (1 large lateral, 2 closely set dorsolateral and 1 very small dorsal); P5-bearing somite with 1 lateral, 1 dorsolateral and 1 laterodorsal pair of processes; genital and abdominal halves of double-somite and second abdominal somite each with 1 lateral and 1 dorsolateral pair. Dorsal surfaces of pedigerous somites and genital double-somite (both halves) additionally with paired minute tubercles bearing unmodified sensillae (Fig. 19A).

Body somites and caudal rami with conspicuous tube-pores (Fig. 19A, C-D). Original segmentation of genital double-somite indicated by dorsal surface ridge and by position of lateral wing-like processes (Fig. 19A); posterior half with paired minute tubercles ventrolaterally (Fig. 19C) bearing sensilla. Second abdominal somite with sensilla arising from paired minute tubercles ventrolaterally (Fig. 19C); ventral posterior margin with median and paired ventrolateral spinule rows. Third abdominal somite with continuous fine spinule row along posterior margin (Fig. 19A, C-D). Anal somite partly cleft medially (Figs 19A, C-D); spinules present around ventral hind margin (Fig. 19C); anal operculum bare (Fig. 19D).

Caudal rami elongate, cylindrical and juxtaposed (Fig. 19C-D); with minute spinules on surface and around insertion sites of setae I - III; with 2 tube-pores (Fig. 19C-D) and 7 setae. Setae I and II (Fig. 19D) arising in proximal half of ramus; seta IV (Fig. 19D) diminutive and fused basally to seta V; seta V well developed, pinnate (Fig. 19A); seta VI shortest (Fig. 19D); seta VII triarticulate at base and arising from minute dorsal pedestal, near posterior margin (Fig. 19D).

Rostrum (Fig. 19A-B) fused to cephalic shield, elongate; with bifid tip; with paired pointed membranous projections laterally (Fig. 19B) just proximal to sensillae; sensillae arising from long conical projections; midventral tube-pore.

Antennule (Figs 19A; 21B) indistinctly 4-segmented; boundary between segments 1-2 represented by incomplete surface suture. Segment 1 with small dorsal node near proximal margin bearing tuft of fine setules; with spinule rows along anterior margin. Segment 2 with 1 dorsal sub-apical seta arising from spinous projection. Segment 3 longest with aesthetasc. Segment 4 with apical acrothek consisting of aesthetasc and 2 slender setae. Armature formula: 1-[1 plumose], 2-[3 sparsely pinnate + 6], 3-[1 pinnate + 6 + (1+ ae)], 4-[9 + acrothek].

Antenna (Fig. 21C). Coxa represented by sclerite. Basis and proximal endopod segment fused forming allobasis; membranous insert along exopodal margin marking original position of exopod; abexopodal margin with 2 spinule rows; unarmed. Endopod with distal surface frill and 3 fine spinule rows along outer margin; 2 spinule rows along medial margin; lateral armature consisting of 2 spines and 1 bare seta; distal armature consisting of 2 unipinnate spines and 3 geniculate pinnate setae, longest one fused basally to small bare seta. Exopod entirely absent.

Mandible with slender coxa and gnathobase bearing thin incised blades. Palp (Fig. 21D) cylindrical, 1-segmented with 3 apical setae (probably of endopodal origin).

Maxillule. Praecoxal arthrite with 2 setae on anterior surface; distal armature consisting of 6 spines. Coxal endite with 1 seta (Fig. 21E). Basis with 2 closely set endites and few spinules along medial margin; proximal endite with 3 elements; distal endite with 2 setae. Rami completely incorporated into basis; endopod and exopod represented by 1 and 2 setae, respectively.

Maxilla (Fig. 21F). Syncoxa with 2 endites, arising from membranous area and each with 1 strong pinnate spine and 2 naked setae. Allobasis drawn out into claw with constriction and 3 fine spinules at base and acutely tapering in distal half; accessory armature consisting of 2 setae and 1 pinnate spine. Endopod minute; with 2 setae.

Maxilliped (Fig. 22A). Subchelate, slender and elongate. Syncoxa unarmed. Basis with few long spinules. Endopod drawn out into long narrow, curved claw; with 1 accessory seta at base.

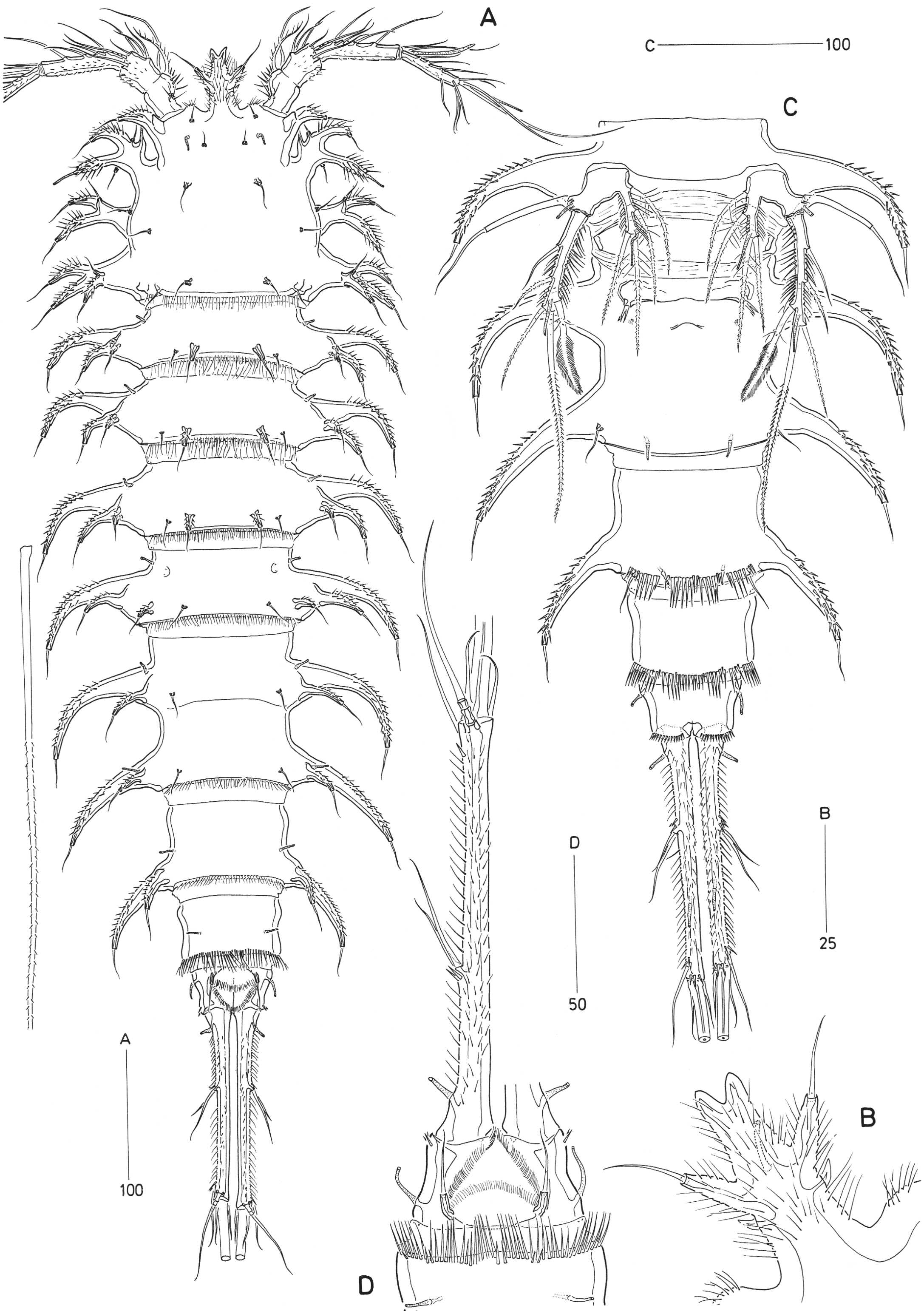

Figure 19. *Juxtaramia polaris* gen. et sp. nov. (♀). **A**, habitus, dorsal; **B**, rostrum, dorsal; **C**, urosome, ventral; **D**, anal somite and right caudal ramus, dorsal.

Figure 19. *Juxtaramia polaris* gen. et sp. nov. (♀). **A**, habitus, vue dorsale ; **B**, rostre, vue dorsale ; **C**, urosome, vue ventrale ; **D**, somite anal et rame caudale droite, vue dorsale.

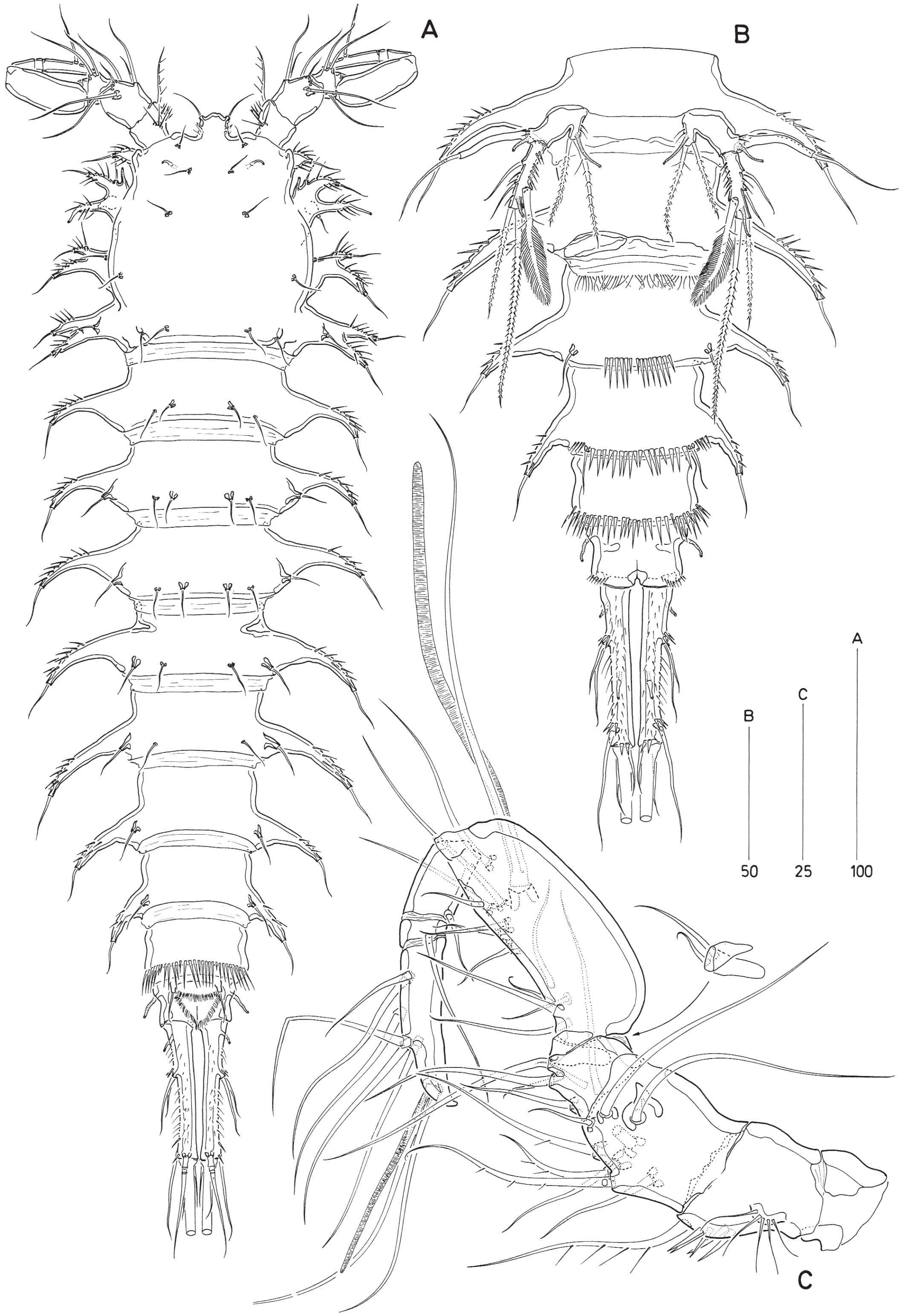

Figure 20. *Juxtaramia polaris* gen. et sp. nov. (♂). **A**, habitus, dorsal; **B**, urosome, ventral; **C**, antennule, dorsal (inset showing segment 4).

Figure 20. *Juxtaramia polaris* gen. et sp. nov. (♂). **A**, habitus, vue dorsale ; **B**, urosome, vue ventrale ; **C**, antennule, vue dorsale (l'encart indique article 4).

Figure 21. *Juxtaramia polaris* gen. et sp. nov. (♀). **A**, cephalothorax, dorsal; **B**, antennule, dorsal; **C**, antenna; **D**, mandible, gnathobase omitted; **E**, maxillule, praecoxal arthrite omitted; **F**, maxilla, inset showing armature of disarticulated syncoxal endites.

Figure 21. *Juxtaramia polaris* gen. et sp. nov. (♀). **A**, céphalothorax, vue dorsale ; **B**, antennule, vue dorsale ; **C**, antenne; **D**, mandibule, gnathobase omise ; **E**, maxillule, arthrite précoxale omise ; **F**, maxille, l'encart indique l'armature des endites syncoxaux détachés.

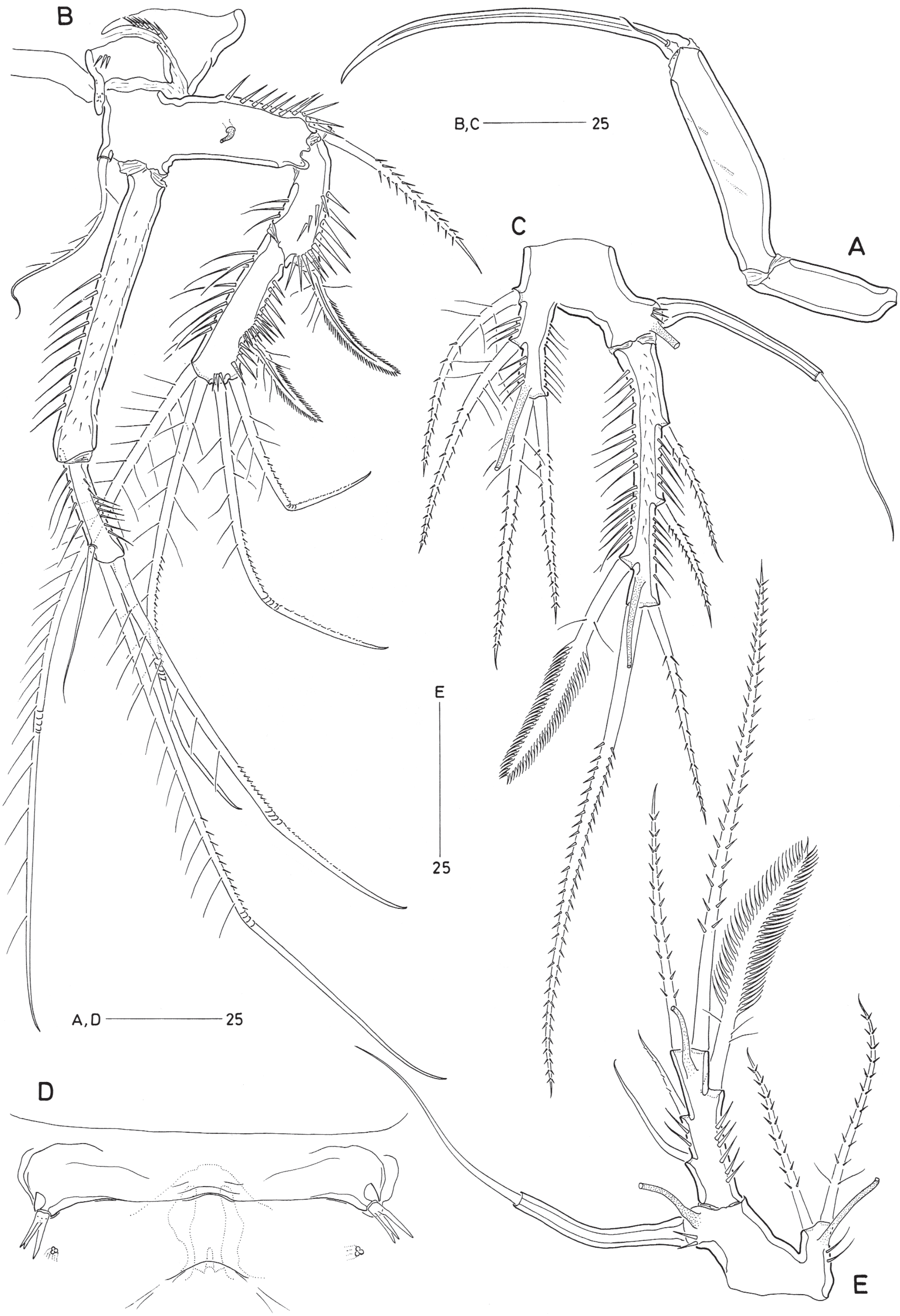

Figure 22. *Juxtaramia polaris* gen. et sp. nov. **A**, maxilliped (♀); **B**, P1 (♀), anterior; **C**, P5 (♀), anterior; **D**, genital field (♀), ventral: **E**, P5 (♂), anterior.

Figure 22. *Juxtaramia polaris* gen. et sp. nov. **A**, maxillipède (♀); **B**, P1 (♀), vue antérieure; **C**, P5 (♀), vue antérieure; **D**, région génitale (♀), vue ventrale; **E**, P5 (♂), vue antérieure.

P1 (Fig. 22B). Intercoxal sclerite wide and narrow (only partially figured; see as for P2, Fig. 23A). Praecoxa extremely well developed with short anterior spinule row. Coxa small, trapezoid with few spinules. Basis transversely elongate with pinnate outer spine and sparsely pinnate inner seta; anterior surface with tube-pore and spinule pattern as indicated in Fig. 22B. Both rami 2-segmented; exp-1 outer spine long and finely serrate; exp-2 with 4 geniculate setae and 1 finely serrate outer spine; outer spines with setules in proximal portion. Enp-1 much longer than enp-2 (2.95 times as long) and 1.1 times as long as entire exopod, with long spinules along inner margin; enp-2 with 1 naked and 2 geniculate setae.

P2-P4 with wide, narrow intercoxal sclerites without ornamentation (as figured for P2; see Fig. 23A). Praecoxae (see Fig. 23A) very well developed, with short anterior spinule row. Coxae with few spinules. Bases transversely elongate; outer margin with sigmoid row of long spinules (as figured for P2; see Fig. 23A) and posterior tube-pore halfway down margin; outer distal seta bipinnate, arising from tiny, posteriorly displaced setophore. Exopods 3-segmented, endopods 2-segmented. Exopodal spines elongate. Endopods distinctly shorter than exopods, reaching to proximal third of exp-3 (see Fig. 23A). P2-P4 enp-1 reduced in size, unarmed; enp-2 elongate (Fig. 23A-C). Armature formula as for genus.

P5 (Fig. 22C) biramous. Baseoendopod outer corner with tube-pore; setophore demarcated, long and bearing naked outer basal seta. Endopodal lobe slender, rectangular, with spinule rows along inner margin and fine setules along outer margin; with 4 bipinnate setae and 1 anterior tube-pore subapically; reaching to proximal quarter of exopod. Exopod long and slender; fine spinules along inner and outer margins; with serrate inner spine, 2 pinnate setae and anterior tube-pore distally, and 2 pinnate outer setae.

Genital field (Figs 19C; 22D) with fused gonopores opening via common midventral slit covered by genital operculum derived from vestigial sixth legs. P6 (Fig. 22D) each with 3 minute, basally fused elements. Copulatory pore moderately large, flanked by paired pore triplet, just posterior to each gonopore.

Male

Smaller than ♀ (Fig. 20A); total body length 493 µm measured from tip of rostrum to posterior margin of caudal rami

Body processes (Fig. 20A) relatively less well developed than in ♀ and pattern significantly reduced; P2-bearing somite without and P3-P5 bearing somites with only 1 pair of dorsolateral processes; dorsolateral processes on urosomites reduced. First abdominal somite (Fig. 20B) with paired median spinule rows along ventral posterior margin; second abdominal somite (Fig. 20B) with ventral spinule row; penultimate somite (Fig. 20B) with continuous spinule row around posterior margin.

Rostrum (Fig. 20A) shorter, wider and bifid extension less well developed than in ♀.

Antennule (Fig. 20A, C) indistinctly 8-segmented (boundary between segments 1-2 represented by incomplete surface suture) and subchirocer, geniculation between segments 5 and 6; segment 4 represented by U-shaped sclerite (Fig. 20C); segment 5 longest and swollen; aesthetascs on segment 5 and as part of apical acrothek on segment 8. Segment 1 with short anterior spinule rows and small dorsal node near proximal margin bearing tuft of fine setules. Segment 2 with 1 dorsal sub-apical seta arising from spinous projection. Segments around geniculation without modified elements. Armature formula (1 seta missing on segment 2 in Fig. 20C but presence confirmed on other side): 1-[1 pinnate], 2-[3 sparsely pinnate + 6], 3-[6], 4-[2], 5-[12 + (1+ae)], 6-[1], 7-[1], 8-[6 + acrothek]. Apical acrothek consisting of 2 setae and aesthetasc.

P1, P2-P4 protopods and exopods as in ♀. Inner distal seta of P2-P4 enp-2 distinctly shorter than in ♀ (Fig. 23D-F). P4 enp-2 outer element shorter than in ♀ and spiniform instead of setiform (Fig. 23F). P3 (Fig. 23E) endopod 2-segmented; enp-2 with 2 apical setae, anterior surface produced into smooth recurved apophysis subdistally.

P5 (Fig. 22E) biramous. Baseoendopod outer corner with tube-pore; setophore demarcated, long, bearing naked outer basal seta. Endopodal lobe much shorter than in ♀; distally with 2 pinnate setae and 1 anterior tube-pore. Exopod shorter than in ♀; fine spinules along inner margin; with serrate inner spine, 2 pinnate setae and anterior tube-pore distally and 2 outer setae.

Sixth pair of legs asymmetrical (Fig. 20B) with only 1 functional member, represented by membranous flap; other member fused to somite. P6 without armature.

Caudal rami distinctly shorter than in ♀ (Fig. 20A-B).

Variability. None observed.

Etymology. The species is named after the (north) polar type locality.

Remarks

This new genus and species is described from material collected by Norman in 1890 from Varanger Fjord, Norway and erroneously deposited in The Natural History Museum as “Types” of *Ancorabolus mirabilis*. Norman (1903) stated that he first discovered *A. mirabilis* from the Firth of Clyde, Scotland and then again two years later from East Finmark, Norway. It is incomprehensible why the author failed to distinguish between both sets of specimens since the Finmark material is radically different from any of the three *Ancorabolus* species recognized herein. Characters which preclude assignment to *Ancorabolus* include: (1) cephalic

Figure 23. *Juxtaramia polaris* gen. et sp. nov. **A**, P2 (♀), anterior; **B**, P3 (♀) left endopod, anterior; **C**, P4 (♀) left endopod, anterior; **D**, P2 (♂) left endopod, anterior; **E**, P3 (♂) left endopod, anterior; **F**, P4 (♂) left endopod, anterior.

Figure 23. *Juxtaramia polaris* gen. et sp. nov. **A**, P2 (♀), vue antérieure ; **B**, endopodite gauche de P3 (♀), vue antérieure ; **C**, endopodite gauche de P4 (♀), vue antérieure ; **D**,endopodite gauche de P2 (♂), vue antérieure ; **E**, endopodite gauche de P3 (♂), vue antérieure ; **F**, endopodite gauche de P4 (♂), vue antérieure.

shield without spinous and associated processes along posterior margin; (2) no sexual dimorphism in pattern of processes on abdominal somites; (3) antennule indistinctly 4-segmented in ♀ and 8-segmented in ♂; (4) absence of armature on antennary allobasis; (5) modification of middle outer spine of P1 exp-2 into geniculate seta; (6) caudal rami parallel. *J. polaris* is also unique in its sexual dimorphism expressed in the pattern of dorsolateral processes on the pedigerous somites (absent on P2-bearing somite, only 1 pair on somites bearing P3-P5).

Genus *Uptionyx* gen. nov.

Diagnosis [based on ♀ only]. Ancorabolinae. Body dorsoventrally depressed, tapering posteriorly, without clear demarcation between prosome and urosome; integument strongly chitinized and highly ornate with series of backwardly produced processes, each with spinules and bifid or unmodified sensillae. Processes never present on last two abdominal somites, other somites always with large paired lateral wing-like processes. Cephalothoracic processes notably bulbous, with paired simple processes at anterior corners; lateral margins each with 3 branching processes; posterior margin with paired laterodorsal spinous projections each associated with 2 sensilla-bearing small tubercles plus additional sensilla. Body with following pattern of produced processes: somites bearing P2-P4 with lateral and 2 dorsolateral processes all closely set; P5-bearing somite with 1 lateral, 1 dorsolateral and 1 dorsal pair of processes; genital double-somite (both genital and abdominal halves) and second abdominal somite each with 1 lateral and 1 laterodorsal pair. Somatic hyaline frills weakly developed and smooth; somatic hind margins often with setular extensions. Urosome and caudal rami with ventral and lateral pattern of conspicuous tube-pores. Female genital and first abdominal somites completely fused forming genital double-somite; without inner chitinous ribs, original segmentation indicated by position of laterally produced processes. Anal somite partly cleft medially; anal operculum rounded, with fine spinules. Caudal rami elongate and slightly conical; with 7 setae.

Rostrum fused to cephalic shield; broad, bell-shaped; lateral paired pointed membranous projections arising proximal to sensillae; midventral tube-pore in distal half. Antennule 3-segmented, with aesthetasc on segments 2 and 3; setae largely bare; segment 1 compound, with 1 subapical anterior seta arising from spinous projection; ♀ segment 2 armature formula [7 + (1 + ae)]. Antenna with basis and proximal endopod segment completely fused forming allobasis with small membranous insert along exopodal margin, abexopodal margin with 2 setae; exopod entirely absent; endopod with 3 lateral and 6 distal elements. Mandibular palp 1-segmented, uniramous with 6 setae, representing endopod, exopod and basis. Maxillule with 2 elements on coxal endite; basis with 3 elements on proximal and 2 elements on distal endite; exopod and endopod completely incorporated into basis, both represented by 2 setae. Maxillary syncoxa with 2 well developed endites, each with 3 elements; allobasis drawn out into claw with basal constriction and 3 accessory elements; endopod minute, 1-segmented with 2 setae. Maxilliped subchelate and elongate; syncoxa and basis unarmed; endopod drawn out into long curved claw with 1 accessory element at base.

P1-P4. Intercoxal sclerites long and narrow; praecoxae well developed; bases transversely elongate. P1 with 2-segmented rami; exp-2 with 3 geniculate setae and 2 outer spines; enp-1 elongate, much longer than enp-2 and entire exopod; enp-2 with 1 naked and 2 geniculate setae. P2-P4 exopods 3-segmented, endopods 2-segmented; without inner seta on exp-1, exp-3 and enp-1; exp-3 with only 2 outer spines. Armature formula as follows:

	Exopod	Endopod
P1	I-0; II+1,2,0	0-0; 0,2,1
P2	I-0; I-1; II,2,0	0-0; 0,2,1
P3	I-0; I-1; II,2,0	0-0; 1,2,1
P4	I-0; I-1; II,2,0	0-0; 1,2,1

P5 biramous; endopodal lobe long and rectangular with 4 setae; exopod with 5 setae. Female genital field with moderately large copulatory pore; gonopores fused forming common genital slit covered by common genital operculum derived from medially fused P6, with 3 small setae on either side.

Type and only species. *Uptionyx verenae* gen. et sp. nov.

Etymology. The generic name is derived from the Greek *aptest*, meaning bent backwards and *onyx*, meaning nail or claw, and refers to the numerous projections on the body somites. Gender: masculine.

Uptionyx verenae gen. et sp. nov.

Type locality. Peanut Vent, Middle Valley Segment, Juan de Fuca Ridge, Northeastern Pacific; 48°27.5' N, 128°42.5' W; sample collection site number R192-911; depth 2417 m.

Type material. (a) The Natural History Museum, London, UK: Holotype ♀ dissected on 10 slides (NHM reg. no. 1997.865); paratypes are 2 ♀ ♀ in 70% ethanol (NHM reg. no. 1997.866-867); (b) Invertebrate Collections of the Canadian Museum of Nature, Ottawa, Canada: 1♀ paratype in 70% ethanol (CMNC reg. no. 1997-0009). All above material was obtained from meiofauna picked out from macro invertebrate samples collected by the submersible *Alvin*; coll. V. Tunnicliffe, 27.06.1992.

Description

Female

Total body length 1034 µm for holotype ($\bar{x}$ =1106 µm, n = 4) measured from anterior tip of rostrum to posterior margin of caudal rami. Body (Fig. 24A-B) dorsoventrally depressed, tapering posteriorly, without clear demarcation between prosome and urosome; integument strongly chitinized and highly ornate with series of backwardly produced processes, each with spinules and bifid or unmodified sensillae; with little ornamentation dorsally. Bifid sensillae consisting of spiniform main branch bearing flagelliform lateral branch (Fig. 24C-D). Processes never present on last two abdominal somites (Figs 24A; 28C), other somites always with large paired lateral wing-like processes. Somatic hyaline frills weakly developed and smooth (Fig. 24A-B); somatic margins often with very fine setular extensions. Cephalothoracic processes notably bulbous (Fig. 24A,C). Cephalothorax with paired simple processes at anterior corners; lateral margins each with 3 branching processes; posterior margin with paired laterodorsal spinous projections each associated with 2 sensilla-bearing small tubercles and additional sensilla. Body somites (Figs 24A-B; 28C) with following pattern of produced processes: somites bearing P2-P4 with 1 lateral and 2 dorsolateral processes all closely set; P5-bearing somite with 1 lateral, 1 dorsolateral and 1 dorsal pair of processes; genital double-somite (both genital and abdominal halves) and second abdominal somite each with

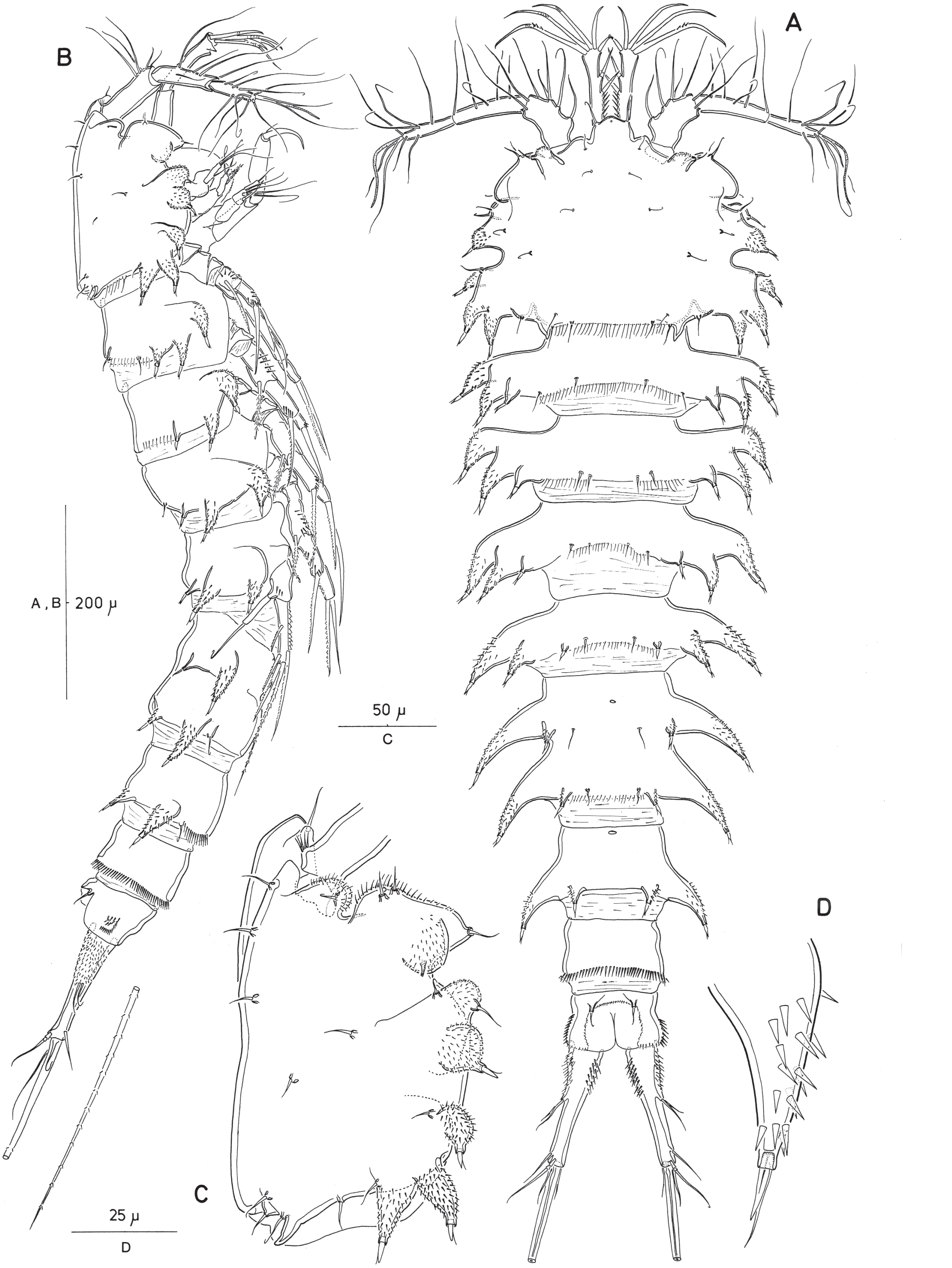

Figure 24. *Uptionyx verenae* gen. et sp. nov. (♀). **A**, habitus, dorsal; **B**, same, lateral; **C**, cephalothorax, lateral; **D**, lateral projection of P2-bearing somite, dorsal.

Figure 24. *Uptionyx verenae* gen. et sp. nov. (♀). A, habitus, vue dorsale ; **B**, habitus, vue latérale ; **C**, céphalothorax, vue latérale ; **D**, projection latérale du somite portant P2, vue dorsale.

1 lateral and 1 laterodorsal pair. Dorsal surfaces of pedigerous somites and genital double-somite (both halves) additionally with unmodified paired sensillae (Fig. 24A).

Urosomites (except P5-bearing somite) and caudal rami with conspicuous tube-pores ventrally and laterally (Fig. 28C). Genital double-somite original segmentation indicated laterally by position of large wing-like processes (Figs 24A; 28C); posterior half with paired small tubercles ventrolaterally (Fig. 28C). Second abdominal somite (Fig. 28C) with sensilla arising from paired small tubercles ventrolaterally (Fig. 28C); ventral posterior margin with paired median and paired ventrolateral spinule rows. Third abdominal somite (Figs 24A; 28C) with continuous fine spinule row along posterior margin. Anal somite partly cleft medially (Figs 24A; 25D; 28C), with transverse chitinous rib (Fig. 28C); posterior half (Fig. 25D) with spinules present laterally and around ventral hind margin; anal operculum rounded (Fig. 25D) with fine spinule row.

Caudal rami elongate and slightly conical (Figs 24A-B; 25D; 28C); proximal half with minute spinules dorsally and larger spinules along inner and outer lateral margins; some spinules present around ventral hind margin and outer distal corner; with 2 tube-pores and 7 setae, all setae bare except seta V (Fig. 24B): seta I and II arising from halfway down outer margin (Fig. 25D); seta IV (Fig. 25D) diminutive and fused basally to seta V; seta V pinnate in distal portion (Fig. 24B); seta VI shortest, not fused basally; seta VII triarticulate at base, arising from small posterodorsal pedestal.

Rostrum (Fig. 26C) broad, rounded anteriorly, not demarcated at base; with 1 pair of sensillae, and 1 median tube-pore ventrally; lateral paired pointed membranous projections arising proximal to sensillae.

Antennule (Figs 24A-B; 25A) 3-segmented. Segment 1 with dorsal spinule patch and 2 short spinule rows along anterior margin; 1 dorsal sub-apical seta arising from spinous projection. Segment 2 longest with aesthetasc (length 110 µm). Segment 3 with apical acrothek consisting of short aesthetasc and 2 slender setae fused basally. Armature formula: 1-[6 pinnate + 4], 2-[2 sparsely pinnate + 5 + (1+ae)], 3-[9 + acrothek].

Antenna (Fig. 27A). Coxa represented by small sclerite, with few tiny spinules. Basis and proximal endopod segment completely fused forming allobasis; membranous insert along exopodal margin marking original position of exopod; abexopodal margin with spinules in basal half and 2 pinnate setae. Endopod with distal surface frill and 3 fine spinule rows along outer margin; 2 spinule rows laterally; lateral armature consisting of 2 pinnate spines and 1 naked seta; distal armature consisting of 2 unipinnate spines and 3 geniculate setae, longest one fused basally to vestigial seta and bearing spinules both proximal and distal to geniculation.

Mandible (Fig. 26A). Coxa robust, expanding distally into gnathobase bearing complex, finely incised teeth either fused or free; dorsal corner with slender bifid extension overlying minutely serrate, basally fused element. Palp well developed, 1-segmented with some spinules; with 2 pinnate setae along inner margin (representing basal elements), 3 apical setae (representing incorporated endopod) and outer margin with 1 pinnate seta arising from tiny pedestal (representing exopod).

Maxillule (Fig. 26B). Praecoxal arthrite rectangular with spinules along inner lateral margin and two tube setae on anterior surface; distal armature consisting of 5 pinnate or serrate spines and 1 spiniform seta, 2 most posterior spines fused to arthrite. Coxa with transverse membranous zone proximally, allowing for additional flexure of arthrite (arrowed in Fig. 26B); endite with 2 pinnate setae. Basis with 2 closely set endites and anterior spinule row; proximal endite with 3 pinnate elements; distal endite with 2 plumose setae. Rami completely incorporated into basis; both exopod and endopod represented by 2 setae.

Maxilla (Fig. 25B). Syncoxa with spinule rows along outer margin, on proximal anterior and posterior surface and anterior distal margin; with 2 endites, area around endites membranous; proximal endite with strong pinnate spine and 2 pinnate setae; distal endite with strong pinnate spine and 2 bare setae. Allobasis drawn out into claw with basal constriction and 3 fine spinules at base; acutely tapering in distal half; accessory armature consisting of 1 bare and 1 pinnate seta, and 1 pinnate spine. Endopod minute, 1-segmented, not well developed or clearly defined at base; with 2 setae.

Maxilliped (Fig. 25C). Subchelate, slender and elongate, inserted on a small pedestal. Syncoxa unarmed and without ornamentation. Basis with few spinules along outer distal margin. Endopod drawn out into long narrow, curved claw; 1 small accessory seta at base.

P1 (Fig. 27B). Intercoxal sclerite long and narrow (only partially figured; see as for P3-P4, Fig. 29A-B). Praecoxa extremely well developed, larger in size and shape in posterior aspect (see as for P3, Fig. 29C); with short anterior spinule row. Coxa represented by well developed sclerite with several rows of minute spinules anteriorly and narrow membranous strip posteriorly between praecoxa and basis (Fig. 27B; see as for P3, Fig. 29C). Basis transversely elongate (Fig. 27B) with pinnate outer spine and naked seta at inner distal corner; conspicuous tube-pore in proximal half and anterior spinule pattern as indicated in Fig. 27B. Exopod and endopod 2-segmented. Exopod outer spines finely serrate; exp-2 with 3 geniculate setae and 2 serrate spines. Endopod distinctly longer than exopod; enp-1 with fine spinules along inner margin, much longer than enp-2 (3.3 times as long) and entire exopod (1.35 times as long); enp-2 with 1 naked and 2 geniculate setae.

P2-P4 (Figs 28A-B; 29A-C) with long, narrow intercoxal sclerites without ornamentation. Praecoxae very well

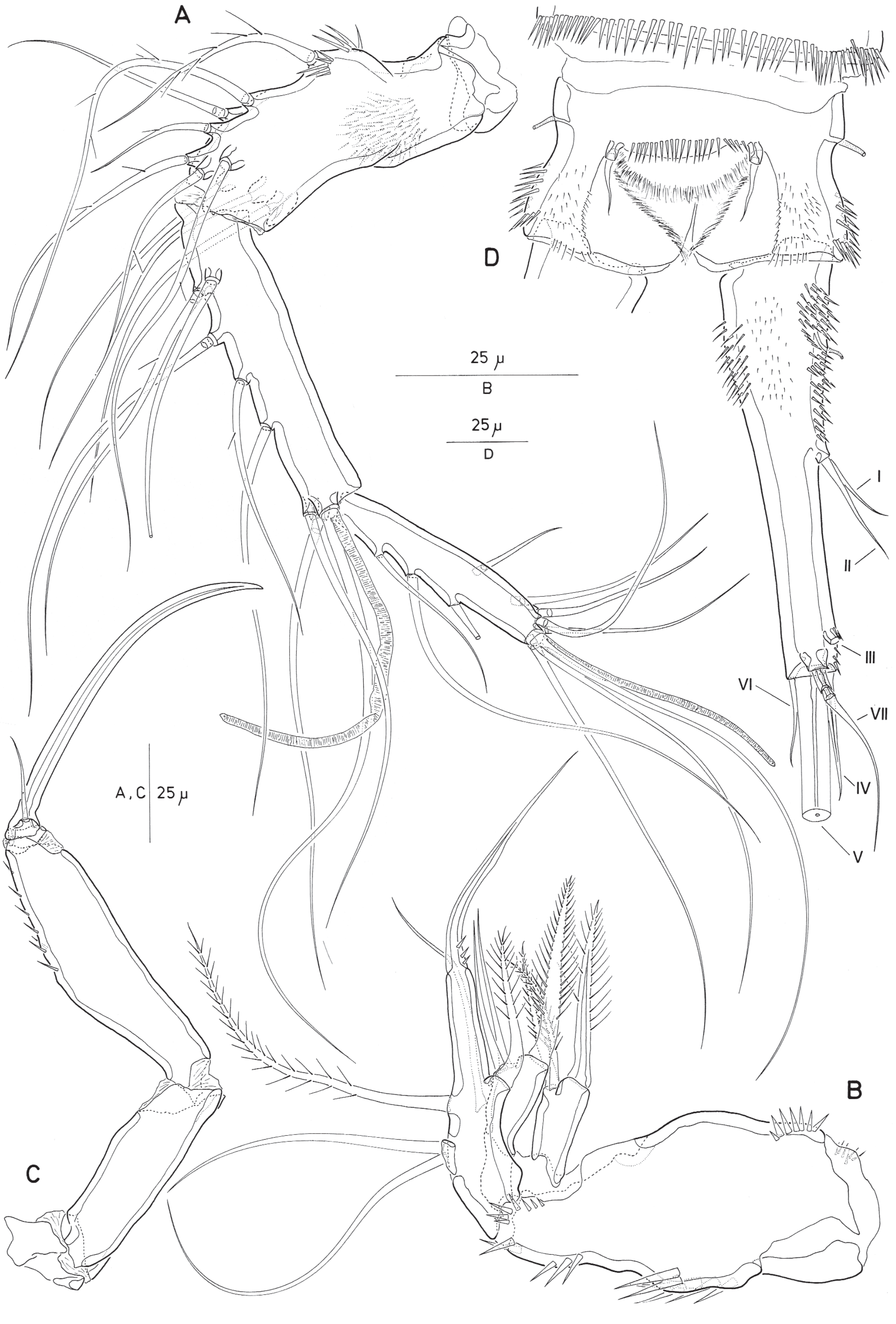

Figure 25. *Uptionyx verenae* gen. et sp. nov. (♀). **A**, antennule, ventral; **B**, maxilla; **C**, maxilliped; **D**, anal somite and right caudal ramus, dorsal.

Figure 25. *Uptionyx verenae* gen. et sp. nov. (♀). **A**, antennule, vue ventrale ; **B**, maxille ; **C**, maxillipède ; **D**, somite anal et rame caudale droite, vue dorsale.

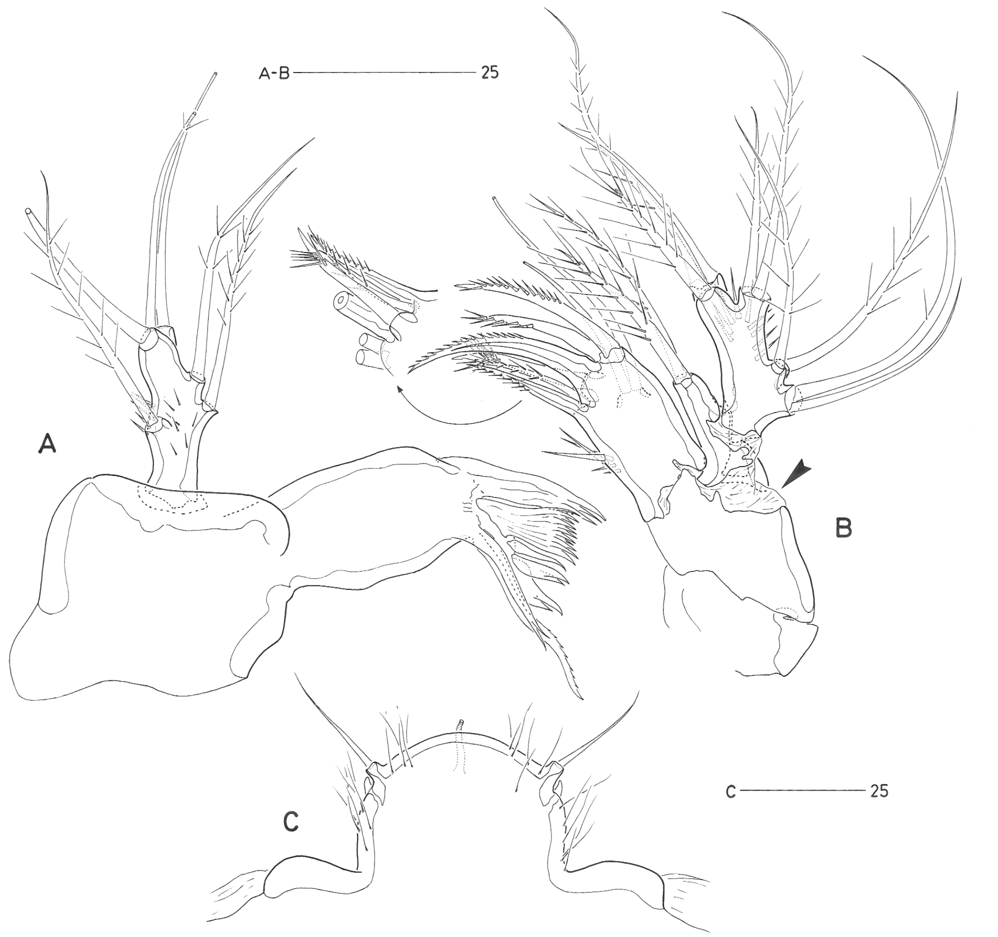

Figure 26. *Uptionyx verenae* gen. et sp. nov. (♀). **A**, mandible; **B**, maxillule, posterior (inset showing inner distal portion of arthrite, anterior); **C**, rostrum, dorsal.

Figure 26. *Uptionyx verenae* gen. et sp. nov. (♀). **A**, mandibule ; **B**, maxillule, vue postérieure (l'encart indique la portion disto-médiale de l'arthrite, vue antérieure) ; **C**, rostre, vue dorsale.

developed, sub-rectangular in posterior aspect (Fig. 29C) with short anterior spinule row. Coxae represented by well developed sclerites anteriorly with several spinule rows and narrow membranous strip posteriorly between praecoxa and basis (Fig. 29C). Bases transversely elongate; outer margin with sigmoid row of long spinules (Figs 28A; 29A-B) and posterior tube-pore in distal half; distal margin with fine hair-like setules between rami; additional patches of minute spinules on anterior surface; outer distal setae bipinnate, arising from tiny, slightly posteriorly displaced pedestal (Fig. 28B). Exopods 3-segmented, endopods 2-segmented. Exopodal spines elongate, those of exp-2 distinctly serrate. Endopods distinctly shorter than exopods reaching to proximal half of exp-3. P2-P4 (Figs 28A; 29A-B) enp-1 reduced in size without armature or ornamentation; enp-2 elongate. Armature formula as for genus.

P5 (Fig. 27C) biramous. Baseoendopod outer corner with tube-pore and row of spinules around base of demarcated, very long setophore bearing naked outer basal seta. Endopodal lobe slender and rectangular, with spinule rows along outer margin; with 4 bipinnate setae and 1 anterior tube-pore between apical and inner distal setae; reaching to proximal third of exopod. Exopod long and slender, rectangular in shape; fine setules along inner margin and some setules along proximal outer margin; with serrate inner seta, 2 pinnate setae and anterior tube-pore distally and 2 pinnate outer setae.

Genital field (Fig. 28C-D) with fused gonopores opening via common midventral slit covered by genital operculum derived from vestigial sixth legs. P6 (Fig. 28D) each bearing 3 reduced setae. Copulatory pore moderately large, slight groove leading to pore outlined by less chitinous area posterior to copulatory pore; with 2 triplet tube-pores anteriorly, just posterior to each gonopore. Area between P6 and copulatory pore slightly raised, thin and membranous (Fig. 28D).

Male. Unknown.

Variability. None observed.

Etymology. The type species is named after its collector Prof. Verena Tunnicliffe, University of Victoria, Canada, who put at our disposal the harpacticoid copepods collected from northeastern Pacific hydrothermal vents.

Remarks

U. verenae shows some superficial resemblance to *A. serratus*, however both species are clearly not congeneric. Several characters such as the basal constriction of the ♀ rostrum, the presence of dorsolateral and laterodorsal processes on the body somites, the more

Figure 27. *Uptionyx verenae* gen. et sp. nov. (♀). **A**, antenna; **B**, P1, anterior; **C**, P5, anterior.
Figure 27. *Uptionyx verenae* gen. et sp. nov. (♀). **A**, antenne ; **B**, P1, vue antérieure ; **C**, P5, vue antérieure.

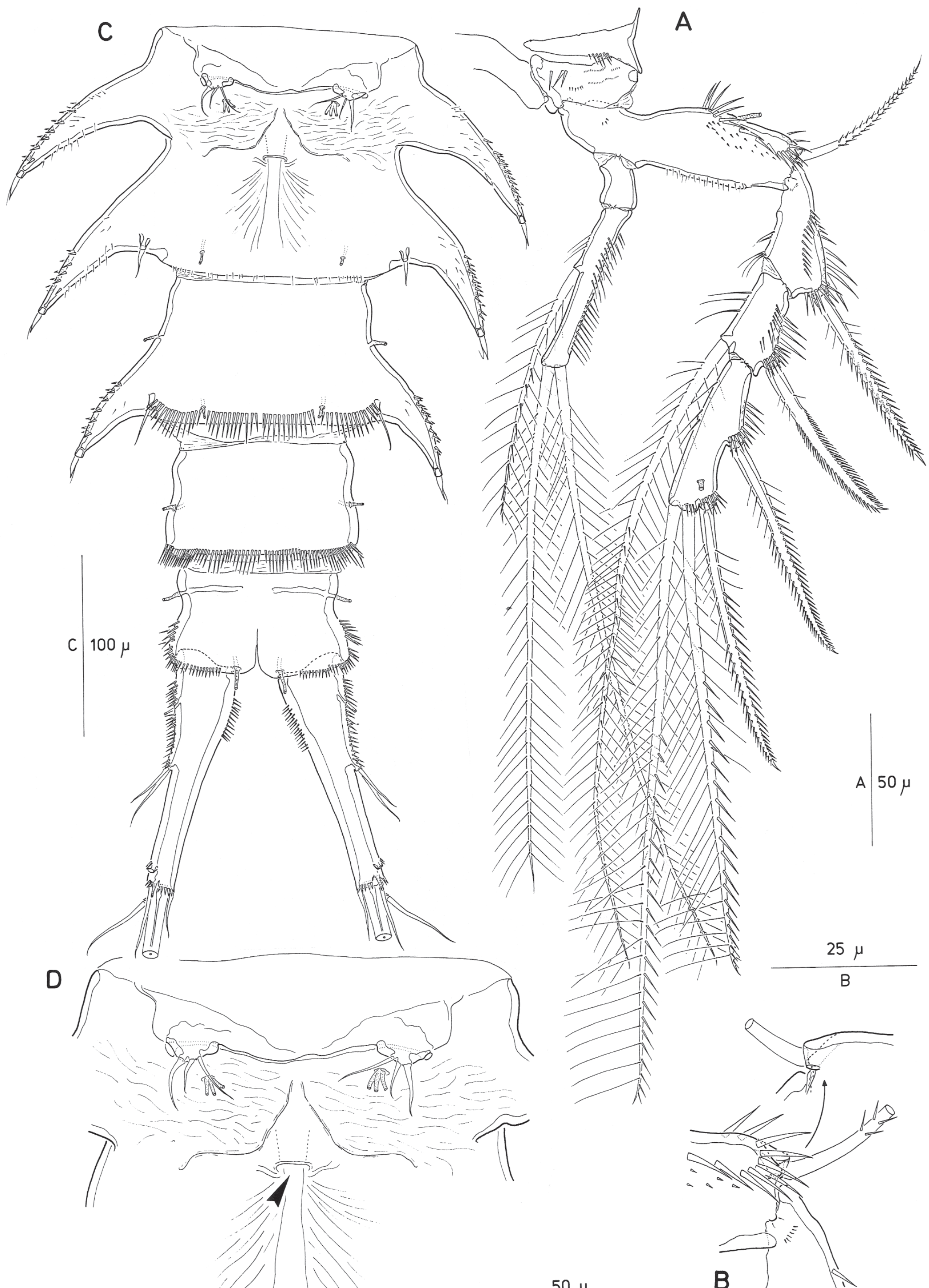

Figure 28. *Uptionyx verenae* gen. et sp. nov. (♀). **A**, P2, anterior; **B**, P2, outer basal seta, anterior (inset showing same, posterior); **C**, urosome (excluding P5-bearing somite), ventral; **D**, genital field, ventral (copulatory pore arrowed).

Figure 28. *Uptionyx verenae* gen. et sp. nov. (♀). **A**, P2, vue antérieure ; **B**, P2, soie extérieure du basipodite, vue antérieure (l'encart indique la même région en vue postérieure) ; **C**, urosome (sauf le somite portant P5), vue ventrale ; **D**, région génitale, vue ventrale (la flèche indique l'orifice copulateur).

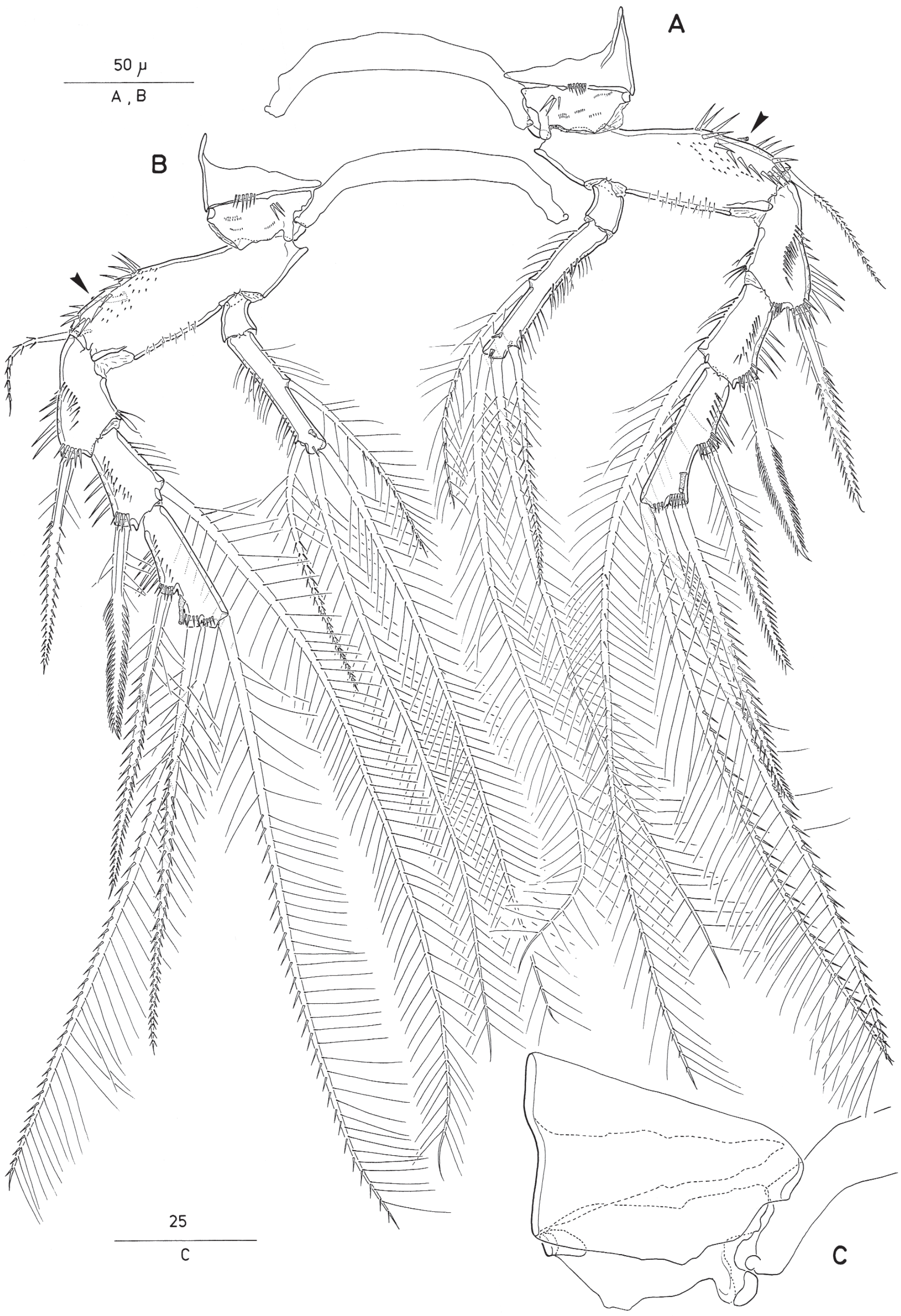

Figure 29. *Uptionyx verenae* gen. et sp. nov. (♀). **A**, P3, anterior (posterior tube-pore on basis arrowed); **B**, P4, anterior (posterior tube-pore on basis arrowed); **C**, P3, praecoxa and coxa, posterior.

Figure 29. *Uptionyx verenae* gen. et sp. nov. (♀). **A**, P3, vue antérieure (la flèche indique le pore tubulaire postérieur sur le basis); **B**, P4, vue antérieure (la flèche indique le pore tubulaire postérieur sur le basis) ; **C**, P3, précoxa et coxa, vue postérieure.

elaborate pattern of cephalothoracic processes (including the presence of a spinous extension along the rear margin), the reduced [7 + (1+ae)] formula on antennulary segment 2 in the ♀, and the modification of the distal outer element of P1 enp-2 into a geniculate seta all exclude *U. verenae* from *Arthropsyllus*.

Inclusion of *U. verenae* in any of the other genera of the *Ancorabolus*-group is untenable because of the retention of the ancestral setation of the mandibular and maxillulary palps, the simple process pattern on the body somites and cephalothorax, and the full complement of elements on P2-P4 endopods and rostrum shape. *Uptionyx* is readily distinguished by the subrectangular rostrum, the bulbous appearance of the cephalothoracic processes (particularly in lateral aspect; Fig. 24C) and the divergent caudal rami which possess a spinular patch along the proximal medial margin (no such ornamentation is found in any other species). A peculiar feature is the strongly serrated nature of the outer spine on P2-P4 exp-2.

Phylogenetic analysis of *Ancorabolus*-group

Monophyly of ingroup

The common ancestry of the *Ancorabolus*-group is supported by the following synapomorphies: (1) body dorsoventrally depressed,

(2) presence of lateral wing-like body processes on all except the last 2 abdominal somites (except last 3 somites in *Ancorabolus* males), (3) antennulary segments 1-2 fused (incompletely in *Juxtaramia*), resulting in 3-segmented condition in ♀ and 7-segmented condition in ♂, (4) P1 exopod 2-segmented (fusion of exp-2 and -3), (5) elongation of P1 enp-1, (6) male P3 endopod 2-segmented with apophysis arising from apical segment, (7) P5 (both sexes) with inner exopodal element modified. All genera possess the primitive P5 condition with a well developed rectangular endopodal lobe in the ♀ (smaller and sub-rectangular in ♂ where known), bearing 4 elements and a total of 5 elements on the exopod.

Characters and taxa

In total, 21 phylogenetically informative characters were available from the morphological data (Table 2). Apomorphic character states are explained inside square brackets using the multistate system. Characters are coded from 0-3, the character state scores for each taxon being compiled in matrix format in Table 3. Characters were polarized by outgroup-comparison with the Cletodidae *sensu* Por (1986). A question mark indicates missing data, either because the appendage or structure is unknown in that species (certain sexually dimorphic characters could not be scored because only females were known) or because it was impossible to score the character accurately due to incompleteness or lack of detail in the original descriptions. *Breviconia echinatus* was eliminated from the analysis because Brady's (1918) fragmentary description did not allow confident scoring for the majority of the characters. In view of the high extent of missing entries in this species (85%; only characters 2, 6 and 18 can be coded) it is unlikely that its removal caused any effect upon the parsimonious interpretation of relationships among the remaining taxa.

Huys & Boxshall's (1991) study of ordinal copepod phylogeny demonstrated that oligomerization was the dominant trend of evolutionary transformation within the Copepoda. Armature counts used in this analysis were scored according to this overall polarisation mode. All characters were set irreversible which suppresses reversals at the expense of introducing extra convergences and thereby increasing tree length. A BRANCH AND BOUND search was run, which guarantees finding all most parsimonious trees, and the ACCTRAN optimisation used.

Most characters in Table 2 are self-explanatory but additional notes are provided for the following:

Rostrum

Rostrum sexual dimorphism appears to be the rule in the *Ancorabolus*-group (♂♂ of *Breviconia* and *Uptionyx* are unknown), the rostrum of the male being generally less well developed and markedly shorter than in the female. Within this lineage, females in particular display a distinct gradient in the shape and size of the rostrum [character 1]. The plesiomorphic condition is retained in *Arthropsyllus* where the rostrum is least well developed and represented by a broadly triangular extension of the cephalic shield (Fig. 11B). The lateral margins of the rostrum form an almost rectilinear contour with the anterolateral portions of the cephalic shield. This state strongly resembles the rostral type found in various cletodid genera such as *Cletodes* Brady and *Intercletodes* Fiers, and is regarded here as the plesiomorphic condition. In all other genera of the *Ancorabolus*-group the rostrum has become more offset as a result of basal constriction. Constriction is least pronounced in *Uptionyx*, forming a subrectangular rostrum without raised sensillae (state 1: Fig. 26C). The further derived condition (state 2) is found in the remaining genera where the rostrum has developed into a more prominent feature through progressive constriction and elongation, extension of the apical part and lateral displacement of the rostral sensillae onto distinct conical projections (Figs. 6A-C; 7B; 19B). In all members of the *Ancorabolus*-group the rostrum possesses a pair of lateral, pointed membranous projections arising proximal to the sensillae. Their position is marked by a minute gap in the cuticle and their transparency seems to suggest that they are raised pores. If this observation is correct it is likely that they are homologous with the fourth unit of the sensory pore X-organ (organ of Bellonci) as described by Hosfeld (1995/96).

Cephalothoracic processes and associated sensillae

Within the *Ancorabolus*-group the overall consistency in the number of cephalothoracic sensillae is remarkable and their virtually constant relative position allows unequivocal homologization. Conversely, the number, size and shape of spinous processes on the cephalothorax can be radically divergent between genera. This variation, analyzed against the background of a consistent sensillar reference pattern, provides a useful tool for assessing phylogenetic relationships within the *Ancorabolus*-group. The sensillae distributed along the lateral and posterior margins of the cephalic shield can be allocated to five paired groups, according to their position and association with particular processes. The position and composition of these sensillar groups (indicated by Roman numerals I-V) are illustrated for one side in Fig. 30.

Sensillar group I (Fig. 30) primitively consists of 1 sensilla arising from a process at the anterolateral corner of cephalic shield. This process is small and blunt in both *Arthropsyllus* and *Uptionyx* (Figs 11B-C; 24C) and becomes thorn-like, recurved and more produced in *Juxtaramia* and all 3 species of *Ancorabolus* (Figs 1B; 7A; 21A). George's (1998a) habitus drawing of *B. australis* is inconclusive in

Table 2. Morphological characters used in the phylogenetic analysis. Apomorphic states are referred to in square brackets.
Tableau 2. Caractères morphologiques utilisés dans l'analyse phylogénétique. Les caractères apomorphes sont indiqués entre crochets.

1. Rostrum ♀ lateral margins forming rectilinear contour with anterolateral portions of cephalic shield [1: with clear basal constriction forming subrectangular rostrum; 2: additional constriction and elongation + sensillae on distinct conical projections].
2. Cephalic shield without pair of dorsal processes in anterior half [paired dorsal processes present].
3. Dorsolateral processes on P5-bearing somite present in both sexes [absent in ♂].
4. Lateral wing-like processes on second abdominal somite present in both sexes [1: absent in ♂].
5. Body somites ♀ without distinct laterodorsal and dorsolateral processes [2 pairs (1 laterodorsal, 1 dorsolateral) present on somites bearing P2-P5; additional development of 1 pair of laterodorsal processes in both anterior and posterior halves of genital double-somite; addition of 1 pair on second abdominal somite].
6. Pedigerous somites without dorsal processes [1 pair present on somites bearing P2-P4].
7. Process bearing cephalothoracic sensillar group I blunt and small [more produced and spinous].
8. Cephalothoracic sensillar group II: all sensillae and tube-pores arising from single lobate process [sensillae *b-c* and posterior tube-pore arising from individual thorn-like processes; anterior tube-pore raised].
9. Cephalothoracic sensillar group III: all sensillae arising from weakly or strongly bilobate process [processes thorn-like and elongate].
10. Cephalothoracic sensillar group IV: sensillae *c-e* arising from conical processes [1: development of third process bearing sensilla *a-b*; 2: constriction and allometric growth resulting in distad displacement of sensilla(e) *a* (and *d*)].
11. Cephalothoracic sensillar group V: all sensillae arising from posterior margin [1: formation of spinous extension between sensillae *c* and *d*, and development of tubercles bearing sensillae *a* and *c*; 2: enlargement of tubercles; 3: displacement of sensillae *a-c* (with associated processes) onto spinous extension].
12. Antennule ♀ segment 2 (or equivalent when segments 1 and 2 are indistinctly fused) with armature formula 9 + (1+ae) [loss of 2 setae resulting in 7 + (1+ae)].
13. Seta representing mandibular exopod present [absent].
14. Mandibular palp with 2 basal setae [1: with 1 seta; 2: both setae absent].
15. Coxal endite of maxillule with 2 setae [1 seta].
16. P1 exp-2 distal outer element spiniform, not modified [setiform and geniculate].
17. P2 enp-2 inner seta present [absent].
18. P3 enp-2 inner seta present [absent].
19. P4 ♀ enp-2 inner seta present [absent].
20. P4 enp-2 outer element not sexually dimorphic [setiform in ♀, spiniform in ♂].
21. P5 ♂ inner baseoendopodal seta not modified [spiniform and serrate].

Table 3. Character data matrix [0 = ancestral (plesiomorphic) state, 1-3 = derived (apomorphic) states, ? = missing data].
Tableau 3. Matrice de caractères [0 = état ancestral (plésiomorphe), 1-3 = états dérivés (apomorphes), ? = données absentes].

Character	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
Ancorabolus inermis	2	0	1	1	1	1	1	1	1	2	3	1	1	2	1	1	1	1	1	1	1
A. confusus	2	1	1	1	1	1	1	1	1	2	3	1	1	2	1	1	0	1	1	1	1
A. mirabilis	2	1	?	?	1	1	1	1	1	2	3	?	?	?	?	?	?	?	?	?	?
Arthropsyllus serratus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Breviconia australis	2	0	?	?	1	1	?	?	1	1	2	1	0	1	1	1	0	0	0	0	?
Juxtaramia polaris	2	0	1	0	1	1	1	1	1	2	?	1	1	2	1	1	1	1	1	1	0
Uptionyx verenae	1	0	?	?	1	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	?

this respect and the score for character 7 has therefore been treated as a missing entry. A small accessory process is present dorsally in *J. polaris* (Fig. 21A).

Sensillar group II (Fig. 30) comprises 3 sensillae

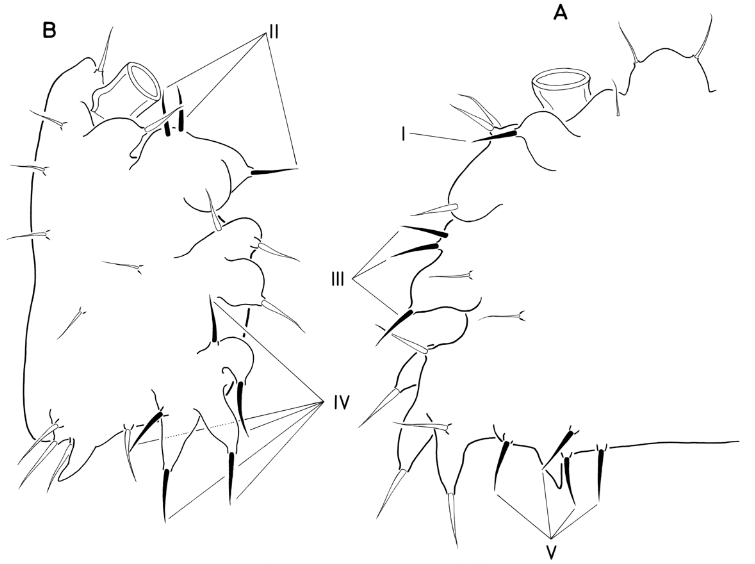

Figure 30. Position of cephalothoracic sensillar groups (♀). **A**, dorsal; **B**, lateral

Figure 30. Position des groupes sensillaires du céphalothorax (♀). **A**, vue dorsale ; **B**, vue latérale.

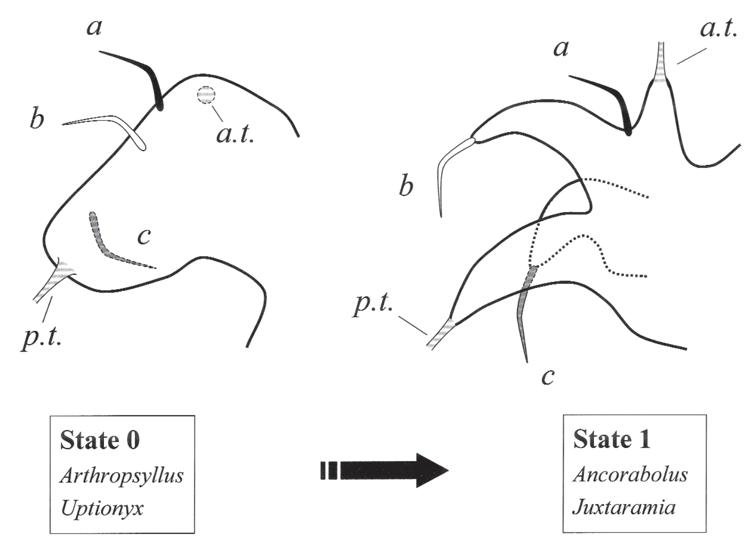

Figure 31. Evolution of cephalothoracic sensillar group II in *Ancorabolus*-group (a.t. = anterior tube-pore; p.t. = posterior tube-pore).

Figure 31. Evolution du groupe sensillaire II du céphalothorax dans le groupe *Ancorabolus* (a.t. = pore tubulaire antérieur ; p.t. = pore tubulaire postérieur).

(labelled *a-c* in Fig. 31), associated with a produced projection and 2 tube-pores which can be used as additional reference points. The anterior tube-pore and sensilla *c* are typically positioned ventrally. The simplest (plesiomorphic) condition is retained in *A. serratus* and *U. verenae* where all sensillae arise from the surface of a single lobate projection. In both *Juxtaramia* and *Ancorabolus* the projection has undergone secondary branching associated with displacement of sensillae and tube-pores (Fig. 31). Sensillae *b-c* and the posterior tube-pore arise from individual spinulose thorn-like processes arranged in a 3-D configuration (e.g. Fig. 1B) and the anterior tube-pore is distinctly raised. This transformation is most extreme in *A. confusus* (Fig. 7A). George (1998a) did not map the sensillae accurately nor was a potentially informative lateral view of the cephalothorax presented in his description of *B. australis* so that character 8 needs to be coded as missing for this taxon.

Sensillar group III (Fig. 30) consists of 3 sensillae (labelled *a-c* in Fig. 32), i.e. 1 dorsal (*a*) and 1 ventral one (*b*) anteriorly and 1 sensilla (*c*) posteriorly. In the most plesiomorphic condition all sensillae are located on a single weakly (*A. serratus*) or strongly (*U. verenae*) bilobate extension (Figs 11B; 24C). Subsequent elongation of both lobes displaced sensillae *b* and *c* onto subcylindrical processes (Fig. 32). This apomorphic state is found in both *Ancorabolus* and *Juxtaramia* (Figs 1B; 21A) and most probably also in *B. australis*.

Sensillar group IV (Fig. 30) includes 5 sensillae arranged around each posterolateral corner of the cephalic shield and labelled *a-e* in Fig. 33. In *Arthropsyllus* this corner is produced into two closely set conical processes which bear sensillae *c* and *e* (state 0) at their tips and sensilla *d* at the base of the anterior process (Fig. 11B-C). Sensillae *a-b* are not associated with processes, occupying a position along the posterior margin of the cephalothorax. An additional process has developed in *Uptionyx* (state 1), bearing sensilla *a* at the base and *b* at its apex (Figs 24C; 33). In both *B. australis* and *U. verenae* the three processes share a common base and can be regarded as the branches of a single trifid projection (Fig. 24A). In a further derived condition (state 2), both constriction and simultaneous allometric growth in the basal area of the projection has resulted independently in two different sensillar patterns according to the relative position of the growth field (State 2). In *Juxtaramia* allometric growth was confined to a narrow zone between sensillae *d* and *a* and consequently displaced only the latter (Figs 21A; 33) whereas in *Ancorabolus* the growth field was located clearly more

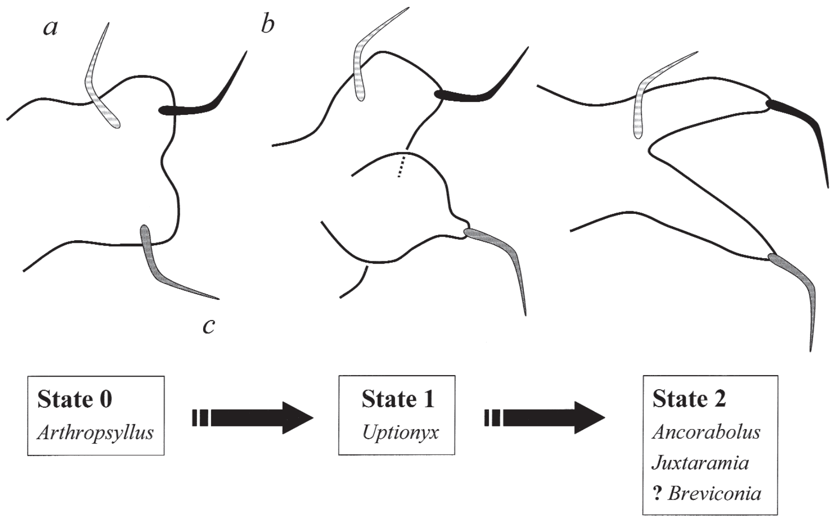

Figure 32. Evolution of cephalothoracic sensillar group III in *Ancorabolus*-group.
Figure 32. Evolution du groupe sensillaire III du céphalothorax dans le groupe *Ancorabolus*.

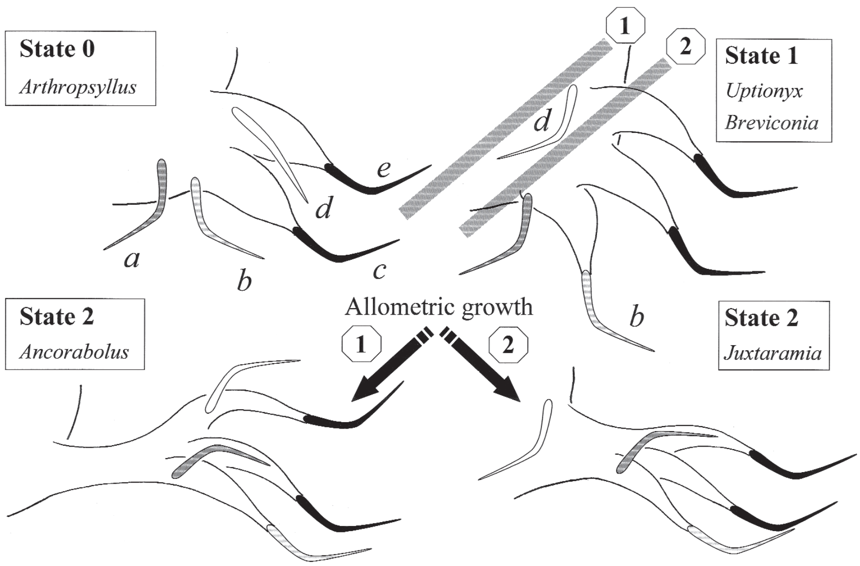

Figure 33. Evolution of cephalothoracic sensillar group IV in *Ancorabolus*-group.
Figure 33. Evolution du groupe sensillaire IV du céphalothorax dans le groupe *Ancorabolus*.

proximally and caused distal displacement of both sensillae (Figs 1A; 7A; 33).

Sensillar group V (Fig. 30) contains 4 sensillae labelled *a-d* in Fig. 34. In the most primitive configuration (state 0), displayed only in *Arthropsyllus* (Fig. 11B-C), all sensillae are arranged around the posterior margin of the cephalic shield and accessory processes are completely absent. The *Uptionyx*-condition (state 1; Fig. 24A, C) is characterized by a spinous extension of the posterior margin between sensillae *c* and *d* and by the formation of small tubercles bearing sensillae *a* and *c* (arrowed in Fig. 34). These tubercles can be considered as the precursors of the larger conical processes found in *B. australis* (state 2). Finally, both sensillate processes are secondarily displaced onto the spinous extension in the three known species of *Ancorabolus* (state 3; Figs 1C; 7A). The condition found in *J. polaris* is radically divergent since only 2 sensillae remain in group V which, by virtue of relative position, can be identified as *b* and *d*. The cephalic shield of *Juxtaramia* differs from that of *Ancorabolus* primarily in the complete absence of conical processes (and spinous extension) along the posterior margin (Fig. 21A). This loss is correlated with the absence of sensillae *a* and *c* and is postulated here to have evolved secondarily. Since character 11 does not apply to *J. polaris* we have coded the species as having missing data rather than coding it as having an extra state "not present". Although this practice can potentially lead to undesirable effects in parsimony analysis, such probability is eliminated here because the inapplicable coding is restricted to a single taxon on the tree.

Mandible

The plesiomorphic setation pattern of the mandibular palp is retained only in *Uptionyx* (Fig. 26A). The endopod is represented by 3 apical setae, the exopod by a single lateral seta and the 2 setae along the medial margin are regarded as basal in origin. The full complement of endopodal elements is preserved in all genera whereas the exopod is present only in *U. verenae* and *B. australis* (character 13). Reduction in the number of basal setae (character 14) is partial in *Breviconia* (1 seta left) and complete in both *Juxtaramia* and *Ancorabolus* (Figs 4A; 21D).

P1

The variation in P1 morphology in the Ancorabolidae is striking, being expressed in the transverse elongation of the basis, exopod segmentation and the prehensile nature of the endopod. "Prehensility" is a deceptive morphological concept, introduced by Lang (1948: 63) to define any leg or

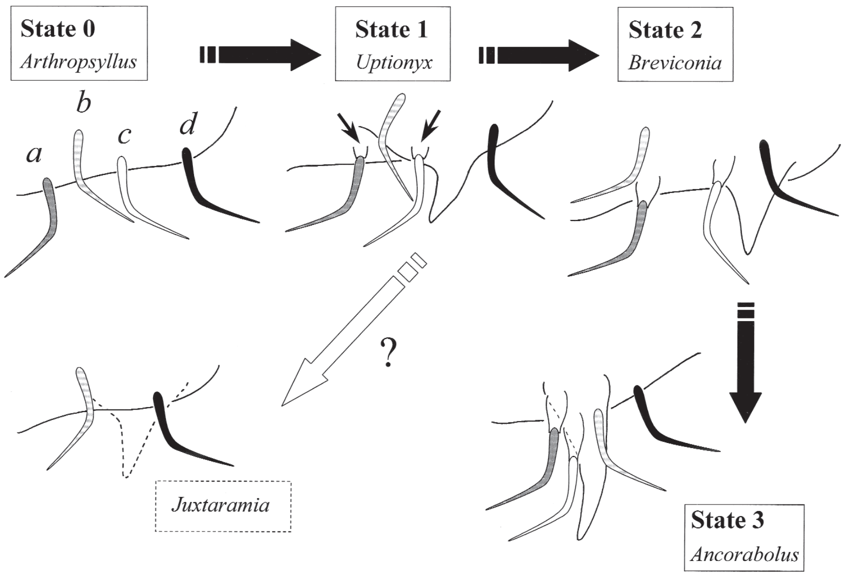

Figure 34. Evolution of cephalothoracic sensillar group V in *Ancorabolus*-group.
Figure 34. Evolution du groupe sensillaire V du céphalothorax dans le groupe *Ancorabolus*.

ramus that is modified for grasping ("Greiforgan"). This modification is usually a character complex involving any combination of (1) secondary elongation of one or more segments, (2) specialization of articulations and associated muscles, and (3) transformation of armature elements. A clear distinction should be made between these three character subsets when "prehensility" is to be coded in phylogenetic analysis. In the *Ancorabolus*-group there are obvious trends towards progressive elongation of the endopod and transverse expansion of the basis. Although their polarity is easily determined by outgroup comparison with the Cletodidae, such morphoclines cannot effectively be decomposed in discrete character states and are therefore intentionally omitted from the analysis.

In *Arthropsyllus* the distal exopod segment bears 3 outer spines and 2 geniculate apical setae (Fig. 13D; 16B, F). In *Uptionyx*, *Juxtaramia* and *Ancorabolus* the distal outer element is modified into an additional geniculate seta (Figs 4C; 9C; 22B; 27B). Although George (1998a) did not illustrate any flexure zones in his figure of leg 1, his text description of *B. australis* clearly confirms the presence of 3 geniculate setae. In *Juxtaramia* the middle outer spine is also modified and geniculate, resulting in a [I+2,2,0] formula for the distal exopod segment.

Swimming leg sexual dimorphism
Male *Arthropsyllus*, *Juxtaramia* and *Ancorabolus* have a modified 2-segmented P3 endopod (Figs 5D; 10F; 18E; 23E), bearing a spinous apophysis on the anterior surface of the distal segment which can be homologized with the outer seta/spine expressed in the female. This modification is derived from the groundpattern defining the "canthocamptoid complex" (Huys & Lee, 1998/99) and it is conceivable that the unknown males of *Breviconia* and *Uptionyx* exhibit the same condition.

Additional swimming leg sexual dimorphism is found in the P4 endopod of *Juxtaramia* and *Ancorabolus*. In both genera the outer element of the distal segment is setiform in the female but modified into a spine in the male and the inner distal seta is distinctly shorter in the male (Fig. 23C, F). In *A. serratus* the inner seta of P4 enp-2 is lost in the male (Fig. 18C, F). This modification is regarded here as an autapomorphy of the genus *Arthropsyllus*.

The inner distal seta of P2 enp-2 is generally shorter in the males of *Ancorabolus* (not figured), *Arthropsyllus* (Fig. 18D) and *Juxtaramia* (Fig. 23D), indicating that this character may well be a potential synapomorphy of the entire *Ancorabolus*-group.

Results and discussion

Parsimony analysis identified a single, fully resolved, most parsimonious tree with a tree length of 28 steps and consistency index 0.929 (Fig. 35). State changes occur predominantly on internal nodes which is reflected in the very high retention index (0.974). Homoplasy is encountered in only 2 characters (13, 17) and largely concentrated on branches leading to terminal taxa.

Arthropsyllus is the first offshoot in the cladogram characterized by two autapomorphies: (1) P4 sexual dimorphism involving the loss of the inner seta on the ♂ enp-2, and (2) loss of exopodal seta on mandibular palp (parallel evolution in the *Juxtaramia*-*Ancorabolus* clade). An additional autapomorphy may be the reduction in the lateral armature of the maxillulary palp, however, since there are as yet no criteria for the unequivocal identification of individual setation elements on this segment its significance is limited. For this reason similar setal reductions in the maxillules of *Ancorabolus*, *Juxtaramia* and *Breviconia* have been eliminated from the data set.

The basal position of *Arthropsyllus* is reflected in several plesiomorphic character states exhibited in the shape of the rostrum, the armature of antennulary segment 2 in the ♀, the short P1 basis and endopod, the number of geniculate setae on P1 exp-2 and the simple configurations of sensillae and integumental spinous processes.

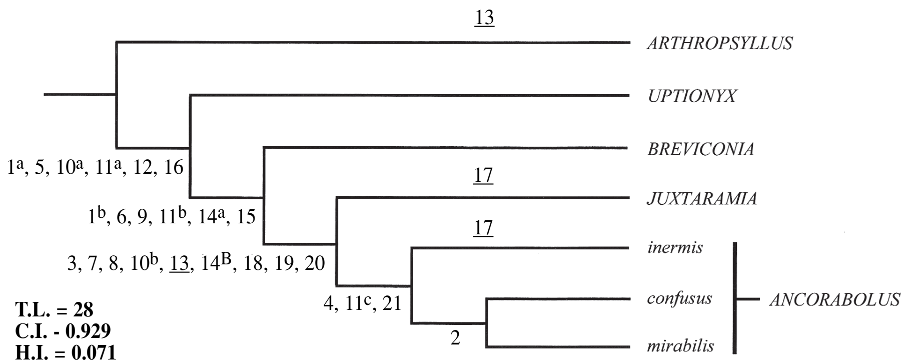

Figure 35. Phylogenetic tree depicting relationships between species of the *Ancorabolus*-group. Superscript letters refer to multistep character changes [^{a}: 0→1; ^{b}1→2; ^{c}2→3]. Underlined numbers refer to convergences. For explanation see tables 2-3 and text.

Figure 35. Arbre phylogénétique montrant les relations entre les différentes espèces du groupe *Ancorabolus*. Les lettres en exposant se réfèrent aux changements de caractère multiétats. Les chiffres soulignés se réfèrent aux convergences. Voir tableaux 2-3 et texte.

The common ancestry of the residual taxa is strongly supported by 6 synapomorphies: (1) basal constriction of the ♀ rostrum, (2) development of dorsolateral and/or laterodorsal processes on body somites, (3) addition of conical process in sensillar group IV, (4) formation of spinous extension in sensillar group V, (5) antennulary segment 2 in ♀ with reduced 7 + (ae + 1) formula, and (6) modification of distal outer element of P1 enp-2 into geniculate seta. Within this group, the genus *Uptionyx* represents the basal clade in opposition of the three remaining genera which form a monophyletic group. It is the only taxon that has retained the ancestral setation of the mandibular and maxillulary palps and its primitive position is further corroborated by the simple process pattern on the body somites and cephalothorax, the full complement of elements on P2-P4 endopods and rostrum shape. The genus is readily distinguished by the bulbous appearance of the cephalothoracic processes (Fig. 24C) and the characteristic caudal rami which possess a spinular patch along the proximal medial margin (Fig. 25D). Its sistergroup unites *Breviconia*, *Juxtaramia* and *Ancorabolus*, and is supported by the following suite of synapomorphies: (1) additional constriction and elongation of rostrum, (2) dorsal processes on somites bearing P2-P4, (3) modification of sensillar group III, (4) enlargement of tubercles in sensillar group V, (5) loss of basal seta on mandibular palp, and (6) maxillulary coxal endite with 1 element. The robustness of this clade unequivocally demonstrates the polyphyletic status of *Arthropsyllus* as defined in George's (1998a) sense. Our analysis at species level clearly refutes the alleged sistergroup relationship between *A. serratus* and *A. australis*, identifying the latter instead as a morphological intermediate between *Uptionyx* and the *Juxtaramia*-*Ancorabolus* clade. Although its transitionary position warrants designation of separate generic status as *Breviconia* gen. nov., substantial difficulties are encountered in identifying clearcut autapomorphies. This is partly attributable to the lack of data on sexual dimorphism (♂♂ are as yet unknown) and the deficiencies contained in George's description which cast doubt on the validity of certain unusual derived character states such as the presence of only 2 elements on the endites of the maxillary syncoxa. Based on the few distributional data currently available (Table 1) it appears that the phylogenetic divergence between *Arthropsyllus* and *Breviconia* is also reflected in their distinct zoogeographical separation.

The two most highly ornate genera, *Juxtaramia* and *Ancorabolus*, form the terminal clade of the tree. Robust evidence for their sistergroup relationship is provided by the following synapomorphies: (1) sexual dimorphism in dorsolateral processes on P5-bearing somite, (2) elongation of anterolateral process of sensillar group I, (3) sensillar group II with several thorn-like processes, (4) allometric growth in sensillar group IV, (5) mandibular palp with 3 setae, (6) loss of inner seta of P3 enp-2, and (7) sexual dimorphism in P4 enp-2 outer element. Although the close relationship with *Ancorabolus* is well founded, *Juxtaramia* is radically divergent from the three known species included in the latter. This distinction is expressed in the following combination of unique autapomorphies exhibited in *J. polaris*: (1) caudal rami juxtaposed and closely set together, (2) sensillar group I with small accessory process, (3) secondary loss of spinous extension and sensillate tubercles in sensillar group V, (4) loss of both abexopodal setae on antennary allobasis, (5) modification of middle outer spine of P1 exp-2 into geniculate seta, and (6) sexual dimorphism expressed in the pattern of dorsolateral processes on the pedigerous somites (absent on P2-bearing somite, only 1 pair on somites bearing P3-P5). In addition, *J. polaris* has also lost the inner seta on P2 enp-2, a loss that evolved convergently in *A. inermis*.

The progressive ramification and elaboration of integumental processes on the cephalothorax and free body somites clearly culminated in *Ancorabolus* which represents the most advanced genus in the group. Its monophyletic status is substantiated by (1) the absence of lateral wing-like processes on the second abdominal somite in ♂, (2) displacement of sensillae *a-c* of group V (with associated tubercles) onto the spinous extension, and (3) modification of P5 ♂ inner endopodal element into spiniform and serrate spine. Within the genus, *A. mirabilis* and *A. confusus* appear to be most closely related by virtue of the presence of paired dorsal processes on the cephalothorax, whereas the shared presence of a recurved process on the second antennulary segment points to affinity between *A. mirabilis* and *A. inermis*. Finer resolution of intraspecific relationships within *Ancorabolus* will have to await detailed re-examination of the type species.

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