



New Normanellidae (Copepoda: Harpacticoida) from western Pacific cold seeps including a review of the genus *Normanella*

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Abstract: Two new species of Normanellidae are described from cold seeps at the southeast side of Hatsushima Island in Sagami Bay, Japan. A new genus *Sagamiella* is proposed to accommodate *S. latirostrata* sp. nov. and *Normanella aberrans* Bodin, 1968, originally described from 1200 m depth in the Bay of Biscay. The second cold seep species, *N. bifida* sp. nov., is placed in the genus *Normanella* and shows affinity to the species of the *mucronata*-lineage.

The taxonomy of *Normanella* in NW Europe is thoroughly revised and several lineages are recognized within the genus. Both sexes of the problematic type species *N. dubia* Brady & Robertson in Brady (1880) are completely redescribed on the basis of material from the Isles of Scilly and Northumberland; a neotype has been designated. Material from Exmouth and Eddystone Lighthouse, identified by Norman & T. Scott (1906) as *N. dubia*, is redescribed as *N. obscura* sp. nov.

The controversy over the antennule segmentation in *N. minuta* (Boeck, 1873) is reviewed and new diagnostic features for this species are illustrated. *N. cf. minuta* sensu Arlt (1983) from the Baltic is based on a copepodid V stage. The male from La Rochelle described as *N. minuta* (?) by Bodin (1972) does not belong to Boeck's species and is ranked *species inquirenda* in the genus. The presumed amphiatlantic distribution of *N. minuta* is based on unsubstantiated evidence. Willey's (1930) material from Bermuda does not belong to *N. minuta* and is considered *species inquirenda* in the *minuta*-lineage. *N. minuta* sensu Pallares (1975) from Argentina is regarded as a sibling species of the NW European species and renamed *N. pallaresae* sp. nov.

The Norfolk material, originally identified as *N. tenuifurca* Sars, 1909, is described as a new species *N. paratenuifurca* which is closely related to the Norwegian one. The three illustrated records of *N. serrata* Por, 1959 refer to three different species. *N. serrata* sensu Božić (1964) from La Réunion is considered *species inquirenda* in the *minuta*-lineage and Marinov & Apostolov's (1985) material from off the Spanish Sahara belongs to a different lineage which also includes *N. sarsi* sp. nov. from Norway.

The intricate taxonomy of the *mucronata*-lineage is reviewed, resulting in the upgrade of *N. mucronata reducta* Noodt, 1955 to full species rank and the placement of Monard's (1928) *N. mucronata* var. *quinquesetata* as variety *incertae sedis* in the Normanellidae.

The swimming leg sexual dimorphism in the family Normanellidae is re-evaluated and its phylogenetic significance reassessed. The taxonomic concept of the family is restricted to include only the Normanellinae as defined by Huys & Willems (1989).

Résumé : *Nouveaux Normanellidae (Copepoda : Harpacticoida) des suintements froids du Pacifique Ouest et révision du genre Normanella.*

Deux nouvelles espèces de Normanellidae sont décrites; elles proviennent d'infiltrations froides situées au sud-est de l'île de Hatsushima, dans la baie de Sagami (Japon). Un nouveau genre, *Sagamiella*, est proposé pour *S. latirostrata* sp. nov. et *Normanella aberrans* Bodin, 1968, décrite du Golfe de Gascogne (profondeur : 1 200 m). La seconde espèce d'infiltration froide, *N. bifida* sp. nov., est placée dans le genre *Normanella* et montre des affinités avec les espèces de la lignée *mucronata*.

La taxonomie des *Normanella* de l'Europe du N-O est minutieusement révisée et plusieurs lignées sont identifiées dans ce genre. Une redescription complète des deux sexes et espèce-type problématique *N. dubia* déterminée par Brady (1880), est donnée à partir de spécimens des Iles Scilly et du Northumberland ; un néotype est désigné. Des spécimens d'Exmouth et du phare d'Eddystone, désignés sous le nom de *N. dubia* par Norman & T. Scott (1906), sont redécrits sous le nom de *N. obscura* sp. nov.

La controverse à propos de la segmentation des antennules de *N. minuta* (Boeck, 1873) est discutée et de nouveaux caractères, illustrés, sont fournis pour l'identification de cette espèce. *N. cf. minuta* sensu Arlt (1983), de la mer Baltique, est fondée sur un stade copépodite V. Le mâle provenant de La Rochelle et décrit sous le nom de *N. minuta* (?) par Bodin (1972) n'appartient pas à l'espèce de Boeck et est classée *species inquirenda* dans le genre. La distribution supposée amphiatlantique de *N. minuta* est en fait fondée sur des affirmations sans preuve. Le matériel de Willey (1930), des Bermudes, n'appartient pas à *N. minuta* et est considéré *species inquirenda* dans la lignée *minuta*. *N. minuta* sensu Pallares (1975), d'Argentine, est considérée comme espèce jumelle de l'espèce du N-O de l'Europe et renommée *N. pallaresae* sp. nov.

Le matériel du Norfolk, identifié à l'origine sous le nom de *N. tenuifurca* Sars, 1909, est décrit en tant que nouvelle espèce sous le nom de *N. paratenuifurca*, très proche de l'espèce norvégienne. Les trois signalements avec illustrations de *N. serrata* Por, 1959 correspondent à trois espèces différentes. *N. serrata* sensu Božić (1964), de la Réunion, est considérée comme *species inquirenda* dans la lignée *minuta*, et le matériel de Marinov & Apostolov (1985), provenant des fonds au large du Sahara Espagnol, appartient à une lignée différente qui inclut également l'espèce norvégienne *N. sarsi* sp. nov.

La taxonomie complexe de la lignée *mucronata* est révisée; il en résulte la promotion de *N. mucronata reducta* Noodt, 1955 au rang d'espèce à part entière et le classement de *N. mucronata* var. *quinqusetata* comme variété *incertae sedis* dans les Normanellidae.

Le dimorphisme sexuel des pattes natatoires, dans la famille des Normanellidae, est réévalué et sa signification phylogénétique réestimée. Le concept taxonomique de la famille est restreint de manière à ne plus inclure que les Normanellidae tels que définis par Huys & Willems (1989).

Keywords : Normanellidae - cold seeps - hyperbenthos - taxonomy - copepod - Western Pacific.

Introduction

The Normanellidae is one of the smaller families of marine harpacticoid copepods which has received only little attention in recent literature. The family was first proposed by Nicholls (1945) for the genera *Normanella* Brady and *Cletopsyllus* Willey but this course of action was refuted by Lang (1948). In an earlier short communication Lang (1944) had already introduced the subfamily name Normanellinae for four genera in the Laophontidae: *Normanella*, *Cletopsyllus*, *Pseudocleta* Lang and *Laophontopsis* Sars. In a recent attempt to gradually redefine the taxonomic concept of the Laophontidae, Huys & Willems (1989) excluded the subfamily Normanellinae and upgraded it to full family rank. They designated *Laophontopsis* as the type genus of a new family Laophontopsidae and allocated the remaining genera to two subfamilies within the upgraded Normanellidae. The Cletopsyllinae included *Cletopsyllus* and the doubtful genus *Pseudocletopsyllus* Vervoort which was regarded as *genus incertae sedis*. The Normanellinae was restricted to its type genus *Normanella*.

There are a number of fundamental problems surrounding the phylogenetic and taxonomic status of both the family Normanellidae and its type genus *Normanella*:

(1) Huys & Willems (1989) pointed out that the family is clearly diphyletic and established two monophyletic subfamilies in order to reflect this phylogenetic incongruence.

(2) The phylogenetic relationships of both the Normanellinae and Cletopsyllinae have remained unclear.

(3) The detailed morphology and sexual dimorphism in the Normanellinae are not well documented.

(4) A clear diagnostic concept of the genus *Normanella* is unavailable since the type species *N. dubia* Brady & Robertson in Brady (1880), the sole objective standard of reference by which the application of the name *Normanella* is determined (ICZN Art. 61(a)), has been declared *species incerta* by Lang (1948) due to its grossly deficient description.

The discovery of two new species of Normanellidae resulting from our ongoing study of the harpacticoids from hydrothermal vents and cold seeps in the western Pacific

(Lee & Huys, in press; Lee & Yoo, 1998) has prompted us to re-address some of these problems in the present paper. In addition, particular attention has been paid to the taxonomy of the genus *Normanella* in northwest Europe in order to provide a sound taxonomic base, facilitating future revisionary work on the family elsewhere.

Methods

Specimens were dissected in lactic acid and the dissected parts were mounted on slides in lactophenol mounting medium. Preparations were sealed with Glyceel or transparent nail varnish. All drawings have been prepared using a camera lucida on an Olympus BH-2 or a Zeiss Axioskop differential interference contrast microscope.

The descriptive terminology is adopted from Huys et al. (1996). Abbreviations used in the text are: ae, aesthetasc; P1-P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus. Type series are deposited in the collections of The Natural History Museum (NHM). Scale bars in figures are indicated in μm .

Cold seep harpacticoids were collected at the southeast side of Hatsushima Island in Sagami Bay by two methods. One set of specimens was collected by a multiple plankton sampler (DT-MPS) attached to the lower part of the Deep Tow system which was used to collect benthopelagic samples from 0.5 to 3 m above the bottom, during 21 February 1992. The DT-MPS is an opening/closing sampler with four plankton nets (for more technical details, see Terazaki (1991) and Toda et al. (1995)). Other specimens were collected by the deep-sea submersible *Shinkai 2000* of the Japan Marine Science and Technology Center (JAMSTEC) at about 0.8 - 1.1 km depth in Sagami Bay off Tokyo. The Hatsushima area is known for its cold seep sites dominated by large colonies of the giant vesicomid clam *Calyptogena soyoae* Okutani (Hashimoto et al., 1989). Five transects in the area were sampled during the *Kaiyo Maru* DK-92-2-SGM-OGS cruise. Detailed sampling characteristics of the individual transects and preliminary results of the benthopelagic plankton samples are given by Toda et al. (1995).

Systematics

Family NORMANELLIDAE Lang, 1944

The family is redefined here to include only the nominotypical subfamily Normanellinae. The systematics and relationships of the Cletopsyllinae are dealt with elsewhere (Huys & Lee, 1999).

Diagnosis.

Harpacticoida. Body elongate, sub-cylindrical. First

pedigerous somite fused to cephalosome forming cephalothorax. Rostrum triangular, completely defined at the base. Genital double-somite ♀ with internal, transverse, chitinous rib both laterally and dorsally. Anal operculum well developed, rounded; pseudoperculum absent. Caudal rami cylindrical, with 7 setae (V well developed). Sexual dimorphism in antennule, P2 endopod (enp-2 distal setae reduced in ♂), P3 endopod (enp-2 ♂ forming anterior apophysis being homologous to outer spine of ♀; distal setae extremely reduced), P5, P6, and in genital segmentation; occasionally also in P4 endopod.

Antennule without conical projections or spinous processes on posterior margin of proximal segments; with numerous pinnate and few smooth setae and spines; 5- or 6-segmented in ♀, with aesthetasc on segment 3 and as part of apical acrothek on distalmost segment (5 or 6); 7-segmented and subchirocer in ♂ with geniculation between segments 5 and 6 and with aesthetasc on segment 5 and 7. Antenna with allobasis bearing 1 abexopodal seta and 1-segmented exopod with 3-4 setae; endopod with 6 distal elements (2 spines, 2 geniculate setae, 1 strong spine fused basally to short seta) and 2 spines laterally. Mandible with biramous palp; basis with 1-2 setae; exopod and endopod 1-segmented or fused to basis (endopod in *Sagamiella*), with 1 and 4 setae, respectively. Maxillule with 1-segmented bisetose exopod; endopod incorporated in basis and represented by 3 setae; with 1-2 basal endites. Maxillary syncoxa with 3 endites, formula [1,3,3]; endopod 1-segmented (possibly 2-segmented in *N. confluens*), with 3 setae. Maxilliped with 2 setae on syncoxa; basis unarmed; endopod 1-segmented, drawn out into claw bearing 1 short and 1 long seta.

P1 with well developed 3-segmented protopod; basis forming long pedestal for endopod, with inner spine located at inner distal corner and outer spine; exopod 3-segmented, exp-2 with inner seta, exp-3 with 3 spines and 2 geniculate setae; endopod prehensile, 2-segmented with elongated enp-1 bearing inner seta and short enp-2 with 1 claw, 1 geniculate seta and 1 short seta. P2-P4 with 3-segmented exopods and 2-segmented endopods; bases with outer spine (P2) or seta (P3-P4); tube-pore present in P2 enp-1 at outer distal corner, and in P3-P4 enp-2 inner distal corner; spine- and seta formulae as follows:

	Exopod	Endopod
P2	0.1.123	1.[2-3]21
P3	0.1.223	1.321
P4	0.1.223	1.22[0-1]

Female fifth pair of legs not fused medially, defined at the base, intercoxal sclerite absent; exopod and baseoendopod

separate; exopod oval or elongate, with 6 setae; endopodal lobe triangular and narrow, with 5 setae; basal seta on short setophore. Male fifth pair of legs fused medially; endopodal lobe with 2 setae; exopod with 4 setae; basal seta arising from short setophore.

Gonopores ♀ fused medially forming genital slit; each covered laterally by vestigial P6 bearing 2 setae; copulatory pore of moderate size. Sixth pair of legs ♂ asymmetrical with dextral and sinistral configurations; each with 2-3 setae.

Male grasping terminal setae of ♀ caudal rami during precopulatory phase. One egg-sac.

Marine, freeliving.

Type genus. - *Normanella* Brady, 1880.

Other genera. - *Sagamiella* gen. nov.

Genus *Normanella* Brady, 1880

Brady (1880) proposed this genus for *N. dubia* Brady & Robertson in Brady (1880) and placed it in the subfamily Canthocamptinae. Sars (1909) synonymised *N. dubia* with *Mesochra minuta* Boeck, 1873, a species known only from a brief text description written in old Danish and totally lacking in illustrations (Boeck, 1873), and renamed it *Normanella minuta*. Lang (1936) rejected this course of action, regarded *N. minuta* (Boeck, 1873) as a distinct species and considered *N. dubia* virtually indeterminable on the basis of Brady's (1880) description. Later, Lang (1948) ranked the type species as *species incerta* whereas Huys & Willems (1989) placed it as *species inquirenda* in *Normanella*. The genus has seen the addition of 12 species (and subspecies) since. *N. attenuata* A. Scott, 1896 was transferred to the genus *Leptomesochra* Sars (Ameiridae) by Sars (1911). *N. aberrans* Bodin, 1968 is removed from *Normanella* and allocated to a new genus *Sagamiella* below.

Diagnosis.

Normanellidae. Antennule ♀ 5- or 6-segmented. Antennary exopod with 4 setae. Mandible with discrete endopod; basis with 2 setae. Maxillule with 2 basal endites. Maxilla with allobasis accompanied by 2 setae and 1 spine. P6 ♂ with 3 setae. Swimming leg setal formulae:

	Exopod	Endopod
P2	0.1.123	1.[2-3]21
P3	0.1.223	1.321
P4	0.1.223	1.22[0-1]

Type species. - *Normanella dubia* Brady & Robertson in Brady (1880) [by monotypy].

Other species. - *Mesochra minuta* Boeck, 1873 = *Normanella minuta* (Boeck, 1873); *Normanella tenuifurca* Sars, 1909; *N. mucronata* Sars, 1909; *N. incerta* Lang,

1934; *N. quarta* Monard, 1935a; *N. semitica* Monard, 1935b; *N. similis* Lang, 1936; *N. mucronata reducta* Noodt, 1955 = *N. reducta* Noodt, 1955 grad. nov.; *N. serrata* Por, 1959; *N. porosa* Noodt, 1964; *N. bolini* Lang, 1965; *N. confluens* Lang, 1965; *N. bifida* sp. nov.; *N. obscura* sp. nov.; *N. pallaresae* sp. nov.; *N. paratenuifurca* sp. nov.; *N. sarsi* sp. nov.

Species inquirendae. - *N. minuta* sensu Willey (1930); *N. serrata* sensu Bözic (1964); *N. minuta* (?) sensu Bodin (1972); *N. mucronata* sensu Marinov (1977); *N. serrata* sensu Marinov & Apostolov (1985).

Several lineages can be identified within this heterogeneous genus (Table 1), however, proper delimitation is severely hampered by the many reports of substantial intraspecific variability (e.g. Klie, 1950; Por, 1959, 1964a). Our observations on a range of species in NW Europe have revealed remarkably little variability (with the exception of ontogenetic aberrations of the ♂ P5). In one case «populations» from Britain and Norway were different enough for them to be considered as distinct species

Table 1. Lineages within *Normanella* Brady, 1880.

Tableau 1. Différentes lignées dans le genre *Normanella* Brady, 1880.

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1. *dubia*-lineage
 - N. dubia* Brady & Robertson in Brady (1880)
 - N. semitica* Monard, 1935a
 - N. quarta* Monard, 1935b
 2. *mucronata*-lineage
 - N. mucronata* Sars, 1909
 - N. reducta* Noodt, 1955
 - N. confluens* Lang, 1965
 - N. mucronata* sensu Marinov (1977)
 - N. bifida* sp. nov.
 3. *minuta*-lineage
 - N. minuta* (Boeck, 1873)
 - N. tenuifurca* Sars, 1909
 - N. minuta* sensu Willey (1930)
 - N. incerta* Lang, 1936
 - N. serrata* Por, 1959
 - N. porosa* Noodt, 1964
 - N. serrata* sensu Bözic (1964)
 - N. obscura* sp. nov.
 - N. pallaresae* sp. nov.
 - N. paratenuifurca* sp. nov.
 4. *sarsi*-lineage
 - N. sarsi* sp. nov.
 - N. serrata* sensu Marinov & Apostolov (1985)
 5. *bolini*-lineage
 - N. similis* Lang, 1934
 - N. bolini* Lang, 1965
 6. *species inquirendae*
 - N. minuta* (?) sensu Bodin (1972)
 7. Normanellidae *incertae sedis*
 - N. mucronata* var. *quinquesetata* Monard, 1928
 - N. cf. minuta* sensu Arlt (1983)
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(*tenuifurca-paratenuifurca*). This leads to our suspicion that many more sibling species or species pairs are yet to be recognized, which would account for at least part of the gross variability reported for some species such as *N. minuta* and *N. serrata*. Linked to this is another misconception, that of the disjunct distribution of certain species such as *N. minuta* (NW Europe, Argentina, Bermuda) and *N. serrata* (Black Sea, Spanish Sahara, La Réunion), which is conceivably based on erroneous identification. A complete revision of the genus *Normanella* is desirable but beyond the scope of this paper. However, we have provided concise standard descriptions of most known NW European species which can serve as a reference in future revisionary work. A review of the literature seems to lend support to our contention that some of the more widely distributed species in fact represent species complexes, the diversity of which is yet to be revealed.

(a) The *dubia*-lineage.

This lineage comprises *N. dubia*, *N. semitica* Monard, 1935a and *N. quarta* Monard, 1935b, all of which have a smooth cephalic shield without surface areolation, a rostrum with concave lateral margins, a 6-segmented ♀ antennule, caudal rami with reduced terminal setae and a typical P5 exopod shape in the ♀.

Normanella dubia Brady & Robertson in Brady (1880)

Laophonte dubia Brady & Robertson, 1876: 196 [*nomen nudum*].

Normanella dubia Brady & Robertson in Brady (1880): 87-88, Pl. LXXVIII, figs. 12-22.

This species was first mentioned in a checklist by Brady & Robertson (1876) as a new species *Laophonte dubia* dredged off Marsden and Hartlepool. Since this species name was not accompanied by a description, definition or indication it does not satisfy the provisions of availability (ICZN Art. 12(a)) and must be regarded a *nomen nudum*. The type material of *N. dubia* is no longer extant and hence a neotype has been designated from material collected off the mouth of the River Tyne which becomes the new type locality (ICZN Art. 75(f)).

Material. - (a) The Natural History Museum, London: 30 ♀♀ and 2 ♂♂ in alcohol (reg. no. 1967.10.31.76), labelled *Normanella quarta* Monard; from sandy substrate off Innisidgen (10-12 m depth) and Peninnis Inner Head (24-27 m depth), Isles of Scilly; coll. University of London Sub-Aqua Club; det. J.B.J. Wells. From the deposited specimens: 1 ♀ dissected on 15 slides (reg.no.1998.2129); 1 ♂ dissected on 7 slides (reg.no.1998.2130); 1 ♂ partially dissected and preserved in alcohol (reg.no.1998.2131);

(b) From Dr M. Austen: 61 ♀♀ and 6 ♂♂; collected off the mouth of the River Tyne, Northumberland, England

(55° 00'N, 01° 15'E), 50 m depth; coll. M. Kendall & M. Austen, May 1989. One ♀ (in alcohol) designated as neotype (reg. no. 1998.2143); other material (59 ♀♀ and 6 ♂♂ in alcohol, 1 ♀ dissected on 14 slides) deposited under reg. nos 1998.2132-2142.

(c) From Dr J.M. Gee: 2 ♀♀ and 1 ♂ in alcohol; collected off Wilcove in River Tamar; deposited under reg. nos 1998.2144-2146.

All British records of the genus predating Sars (1909) have been identified as *N. dubia*, however, it is conceivable that many are unreliable and require confirmation. The true diversity of the genus in northwest European waters was not disclosed until Sars (1909) described three additional species from Norway and pointed out their occasional co-existence. This sympatry had clearly not been appreciated in earlier studies but appears to be quite common as illustrated by Monard (1935b) who lists four species from the Roscoff area (*N. minuta*, *N. tenuifurca*, *N. mucronata*, *N. quarta*) and by Lang (1948) who recorded a similar number (*N. minuta*, *N. tenuifurca*, *N. mucronata*, *N. similis*) from the Gullmar Fjord. Soyer (1971) even lists 5 species off Banyuls-sur-Mer (*N. minuta*, *N. tenuifurca*, *N. mucronata*, *N. quarta*, *N. confluens*). The material collected in the Moray Firth (Scotland) by T. Scott (NHM reg. no. 1956.9.25.64; 11 ♀♀) and identified by him as *N. dubia* proved upon re-examination to belong to *N. mucronata*. Similarly, *N. dubia* identified by Norman & T. Scott (1906) from Eddystone Lighthouse (7 ♀♀ in alcohol, 1 ♀ on 8 slides; NHM reg. no. 1911.11.8 - 45131-140) and Exmouth (1 ♀ in alcohol; NHM reg. no. 1911.11.8 - 45126-130) belongs to another as yet undescribed species displaying similarities with *N. incerta* Lang, 1934 described from the Campbell Islands (see below: *N. obscura* sp. nov.).

Female

Total body length 626 - 696 µm (n=11; \bar{x} = 669 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 169 µm. Urosome narrower than prosome (Fig. 1A).

Cephalothorax with smooth posterior margin and 3 pairs of weakly developed longitudinal ridges dorsally and laterally; pleural areas well developed, rounded, posterolateral angles minutely crenated; ornamentation consisting of sensillae and few pores as illustrated in Fig. 1A-B. Cephalothorax without minute denticles as found on free body somites; no areolate surface pattern present. Rostrum bell-shaped (Fig. 3A), with distinctly concave lateral margins and rounded anterior margin; completely defined at the base; with pair of tiny sensillae and a midventral tube-pore near the apex; dorsal surface with minute denticles (Fig. 1A).

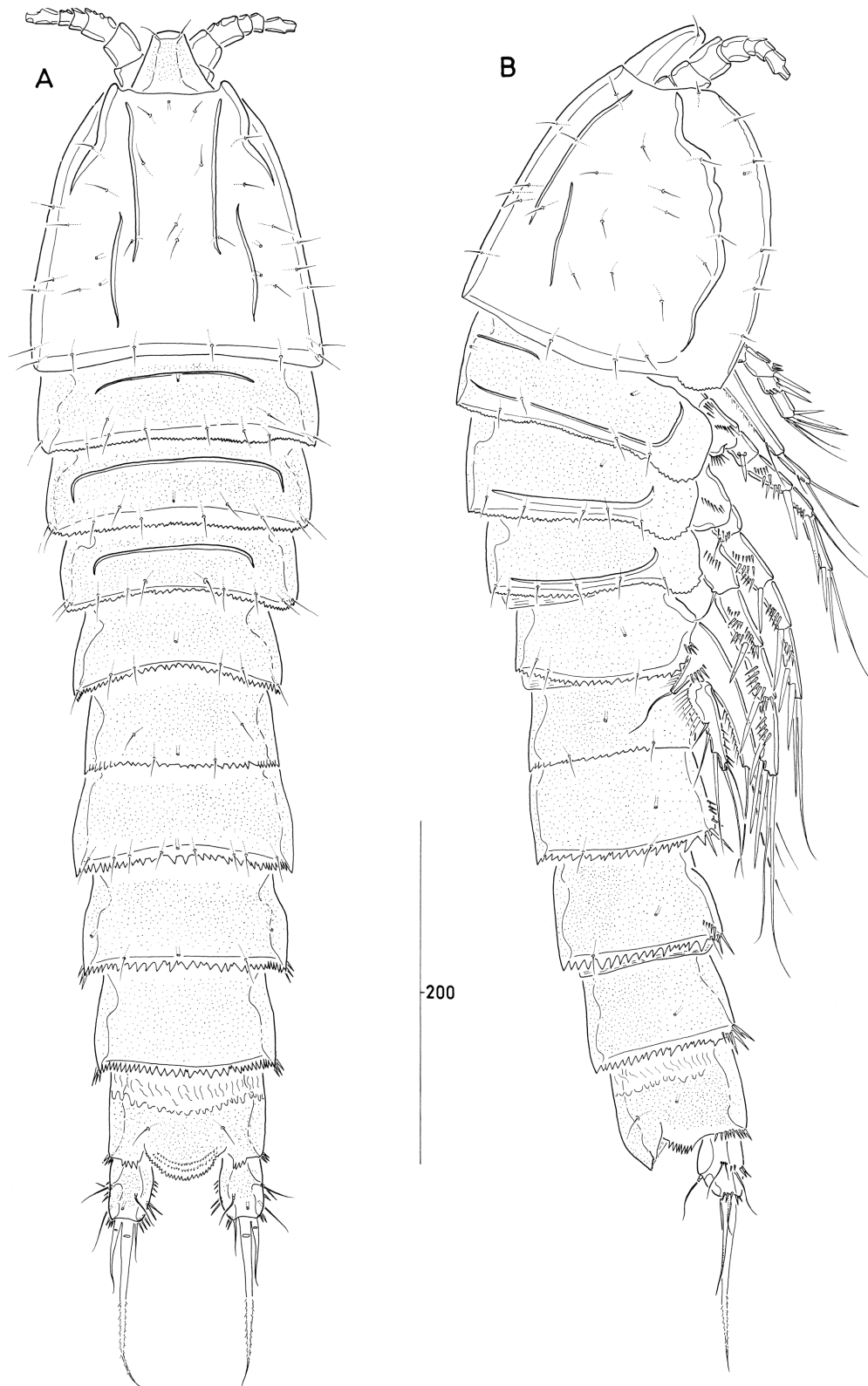


Figure 1. *Normanella dubia* Brady & Robertson in Brady (1880) (♀). A, habitus, dorsal; B, habitus, lateral.

Figure 1. *Normanella dubia* Brady & Robertson in Brady (1880) (♀). A, habitus, vue dorsale ; B, habitus, vue latérale.

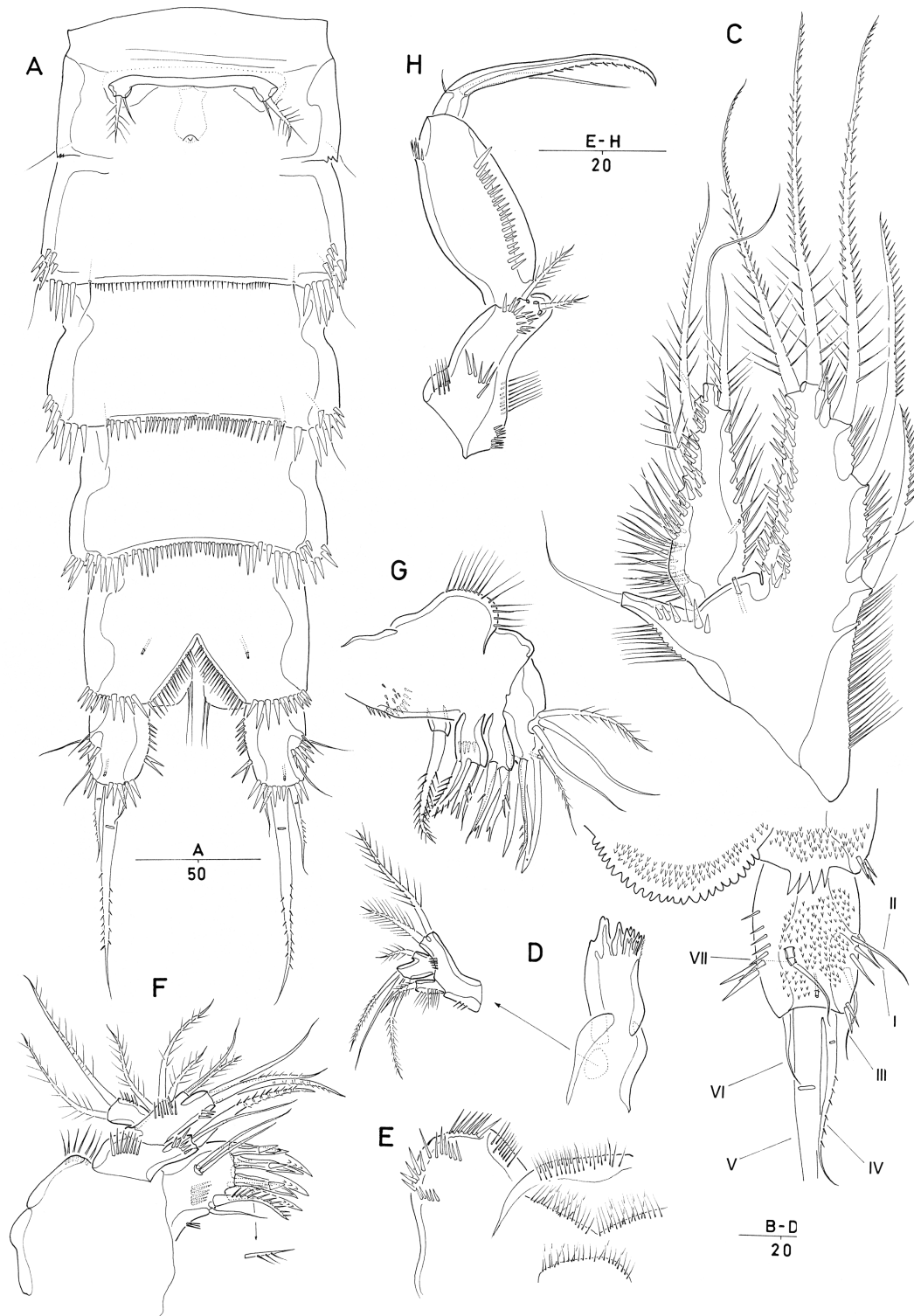


Figure 2. *Normanella dubia* Brady & Robertson in Brady (1880) (♀). A, urosome, ventral [excluding P5-bearing somite]; B, anal somite and right caudal ramus, dorsal; C, P5, anterior; D, mandible [with disarticulated palp]; E, paragnath; F, maxillule; G, maxilla; H, maxilliped.

Figure 2. *Normanella dubia* Brady & Robertson in Brady (1880) (♀). A, urosome, vue ventrale [sauf le somite portant P5]; B, somite anal et rame caudale droite, vue dorsale; C, P5, vue antérieure; D, mandibule [avec palpe détaché]; E, paragnathe; F, maxillule; G, maxille; H, maxillipède.

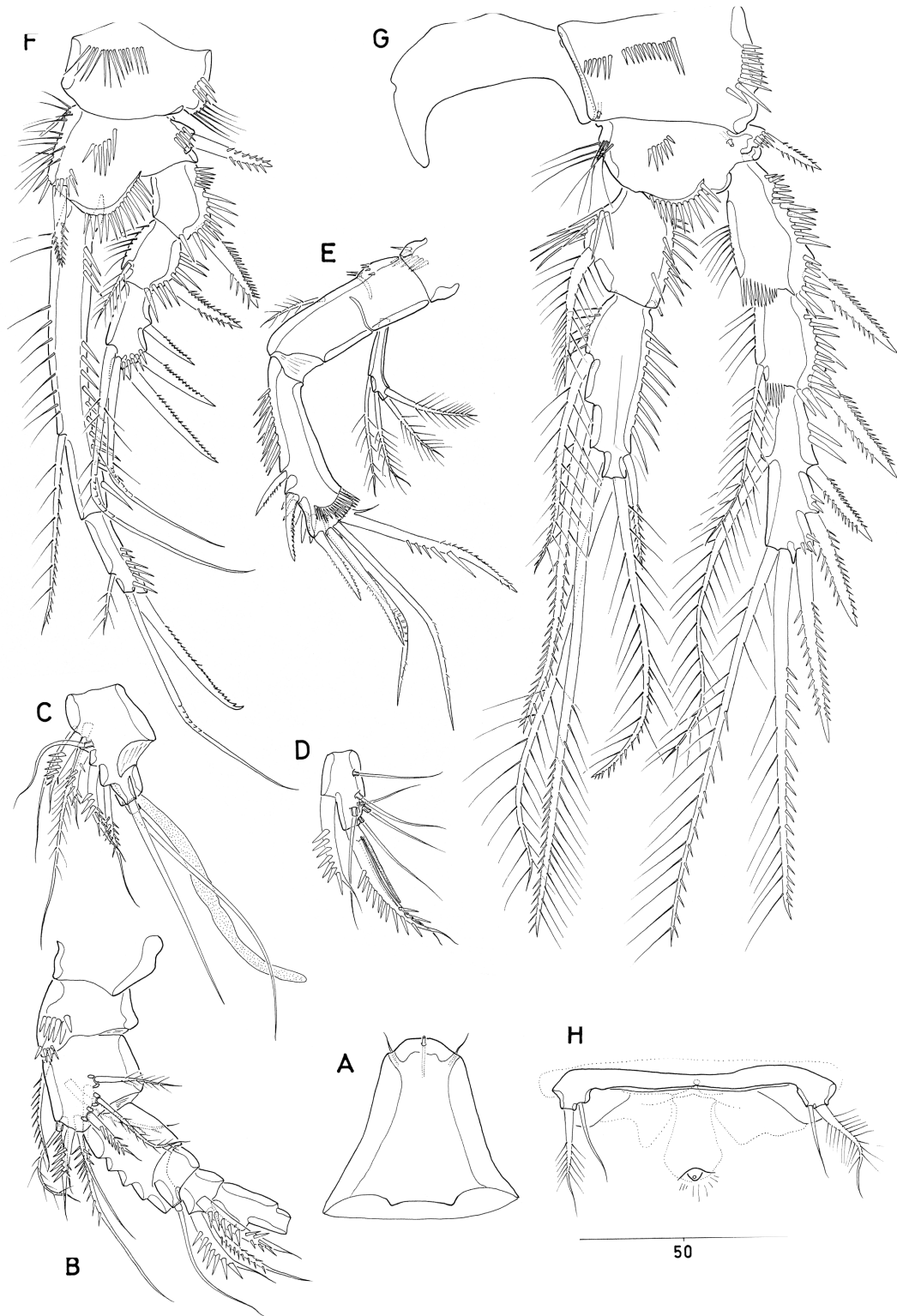


Figure 3. *Normanella dubia* Brady & Robertson in Brady (1880) (♀). A, rostrum, ventral; B, antennule [armature on segments 3 and 6 omitted]; C, 3rd antennular segment; D, 6th antennular segment; E, antenna; F, P1, anterior; G, P2, anterior; H, genital field.

Figure 3. *Normanella dubia* Brady & Robertson in Brady (1880) (♀). A, rostre, vue ventrale ; B, antennule [armature des articles 3 et 6 omise] ; C, article antennulaire 3 ; D, article antennulaire 6 ; E, antenne ; F, P1, vue antérieure ; G, P2, vue antérieure ; H, aire génitale.

Pedigerous somites covered with minute denticles. All prosomites without defined hyaline frills; hind margin minutely denticulate. Body not markedly constricted between individual somites.

Urosome (Figs 1A-B; 2A-B) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites with surface ornamentation consisting of small spinules or denticles dorsally and laterally; ventral surface completely smooth. Hyaline frills of urosomites not developed but hind margin distinctly serrate dorsally. Ventral hind margin with large spinules laterally and fine or minute spinules medially.

Genital double-somite (Fig. 2A) with transverse, serrate surface ridge dorsally and laterally, indicating original segmentation; completely fused ventrally. Genital field (Fig. 3H) with small copulatory pore located in median depression and covered anteriorly by concave, cuticular eminence; gonopores fused medially forming single genital slit covered on both sides by opercula derived from sixth legs; P6 with small protuberance bearing 1 long pinnate outer seta and 1 bare inner seta apically.

Anal somite (Fig. 2A-B) with crenate, well developed operculum flanked by row of spinous processes overlying dorsal anterior margin of caudal rami; anterior half wrinkled and without denticles dorsally and laterally (Fig. 1A-B).

Caudal rami (Fig. 2A-B) short, cylindrical, 1.4 times longer than wide; each ramus with 7 setae: seta I bare, shortest (Fig. 2B); seta II bare; seta III bare, positioned ventrolaterally; setae IV and V fused basally, strongly reduced in comparison to other members of the family, with internal fracture planes (seta IV unipinnate; seta V bipinnate, longest, and about as long as anal somite and caudal rami combined); seta VI bare and small; seta VII tri-articulate at base. Each ramus with minute denticles on dorsal surface; additional spinular ornamentation present along inner and outer margins and around ventral hind margin.

Antennule (Fig. 3B-D) 6-segmented; with well developed sclerite around base of segment 1. Segment 3 longest. Armature formula: 1-[1 pinnate], 2-[9 pinnate], 3-[3 + 5 pinnate + (1 + ae)], 4-[1], 5-[1 pinnate + 2 pinnate spines], 6-[6 + 1 pinnate spine + acrothek]. Apical acrothek consisting of small aesthetasc fused basally to 1 short slender seta and 1 strong pinnate spine. Segment 1 with 2 spinular rows around anterior margin. Segment 3 with aesthetasc fused basally to seta and set on distinct pedestal. Anterior elements on segments 5 and 6 spiniform and coarsely pinnate.

Antenna (Fig. 3E) 3-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa small, with 1 row of spinules. Basis and proximal endopod segment fused forming elongate allobasis with transverse surface sutures marking original segmentation anteriorly and posteriorly;

with 1 abexopodal pinnate seta in distal half. Exopod small, 5 times longer than width, with 2 plumose setae laterally, and 2 plumose setae apically. Endopod subequal to allobasis; lateral armature arising in proximal half, consisting of 2 short pinnate spines; apical armature consisting of 2 pinnate spines, 2 geniculate setae, and 1 strong pinnate spine (fused basally to short seta). Allobasis with small spinules on abexopodal lateral surface. Endopod with 2 rows of long spinules laterally and 1 transverse hyaline frill subapically.

Labrum with elaborate spinular ornamentation and pores as in Fig. 5J.

Mandible (Fig. 2D) with well developed gnathobase bearing several multicuspidate teeth around distal margin and 1 small pinnate spine at dorsal corner. Palp small, biramous. Basis with 2 plumose setae; with few minute spinules along outer margin and around base of endopod. Exopod 1-segmented, smaller than endopod, with 1 plumose seta apically and 2 rows of setules laterally. Endopod 1-segmented, with 1 naked and 2 plumose setae apically, and 1 short pinnate seta laterally.

Paragnaths (Fig. 2E) strongly developed lobes with medially directed hair-like setules, separated by medial lobe covered with dense pattern of short setules.

Maxillule (Fig. 2F). Praecoxa with few long spinules around distal outer margin; arthrite strongly developed, with 2 naked setae on anterior surface and 9 spines/setae around distal margin. Coxa with cylindrical endite bearing 1 naked seta and 1 curved, pinnate spine. Basis with 2 closely set endites (distal with 2 plumose setae, proximal with 1 naked, and 1 pinnate seta, and 1 curved, pinnate spine). Endopod incorporated in basis, represented by 3 plumose setae; exopod 1-segmented, with 2 plumose setae.

Maxilla (Fig. 2G) with 3 endites on syncoxa; praecoxal endite small and cylindrical, with 1 strong, pinnate seta; proximal coxal endite with 1 row of spinules posteriorly, 1 strong spine fused to endite, 1 pinnate seta with subapical tubular extension, and 1 naked seta; distal coxal endite with 2 pinnate setae armed with subapical tubular extension, and 1 sparsely pinnate seta. Allobasis drawn out into strong, slightly curved, sparsely pinnate claw; accessory armature consisting of 1 spine on anterior surface, 1 naked seta on posterior surface, and 1 plumose seta and short tube-pore along outer margin; endopod represented by 1 plumose and 2 naked setae.

Maxilliped (Fig. 2H) with 2 plumose setae and several patches of spinules on syncoxa. Basis with 1 row of spinules on outer distal region and 1 longitudinal spinular row along palmar margin. Endopod a minute segment drawn out into long, sparsely pinnate claw; accessory armature consisting of long naked seta and minute outer seta.

Swimming legs P1-P4 (Figs 3F-G; 4A, C) with wide intercoxal sclerites and well developed praecoxae. Coxae

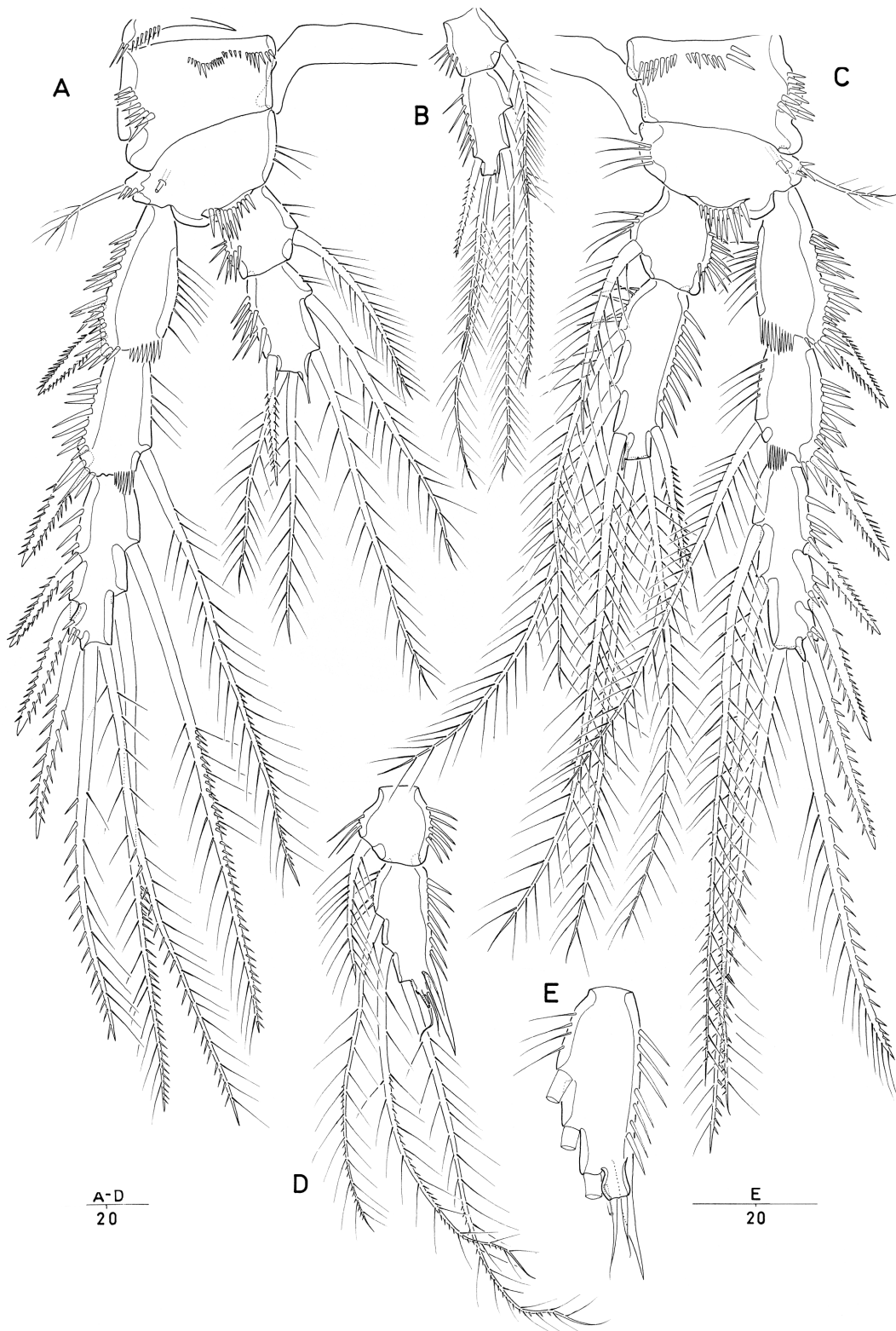


Figure 4. *Normanella dubia* Brady & Robertson in Brady (1880). A, P4 ♀, anterior; B, P4 endopod ♂, anterior; C, P3 ♀, anterior; D, P3 endopod ♂, anterior; E, P3 enp-2 ♂, posterior.

Figure 4. *Normanella dubia* Brady & Robertson in Brady (1880). A, P4 ♀, vue antérieure ; B, endopodite de P4 ♂, vue antérieure ; C, P3 ♀, vue antérieure; D, endopodite de P3 ♂, vue antérieure; E, P3 enp-2 ♂, vue postérieure.

and bases with anterior rows of surface spinules as figured. Exopods 3-segmented, endopods 2-segmented.

P1 (Fig. 3F) with large coxa; with long spinules along outer margin and on anterior surface; with additional row of short spinules anteriorly. Basis with strong, bipinnate spine and long setules along inner margin and with 1 stout bipinnate spine and few spinules along outer margin. Exp-1 with 1 stout bipinnate spine (about as long as outer spine of exp-2); exp-2 with 1 bipinnate, outer spine and 1 short, plumose, inner seta (not extending beyond exp-3 distal margin); exp-3 with 3 unipinnate spines and 2 geniculate setae. Endopod 1.8 times as long as exopod, enp-1 with 1 long, plumose inner seta, enp-2 with 1 slender, denticulate claw, 1 geniculate seta, and 1 small plumose seta.

P2-P4 (Figs 3G; 4A,C). Coxa and basis with secretory pores at anterior surface and spinular rows along outer margin; outer margin of basis with bipinnate spine (P2) or plumose seta (P3-P4); exp-1 and -2 with coarse frill at inner distal corner; all segments with pattern of spinules as figured; inner margins of exopod and endopod segments with long setules or spinules. P2 enp-2 twice longer than enp-1; endopod reaching to middle of exp-3. P3 enp-2 twice longer than enp-1; endopod reaching to distal margin of exp-2; inner distal corner of enp-2 produced into short tubular extension. P4 enp-2 short, 1.4 times longer than enp-1; endopod reaching to just beyond distal margin of exp-1; inner distal corner of enp-2 produced into long tubular extension. Spine and setal formula as in Table 2.

Fifth pair of legs (Fig. 2C) not fused to supporting somite; rami separate. Baseoendopod forming short, outer setophore bearing basal seta and row of spinules; with 3 tube-pores along inner margin and 1 tube-pore near articulation with exopod. Endopodal lobe extending to distal margin of exopod, with 1 bipinnate and 2 unipinnate setae laterally and 2 bipinnate setae apically; rows of short spinules along outer margin, and long spinules or setules along inner margin. Exopod elongate, distinctly tapering

Table 2. Swimming leg armature formulae of Normanellidae (♀ ♀ unless stated otherwise).

Tableau 2. Formules de l'armature des pattes natatoires des Normanellidae (♀ ♀ sauf autre indication).

	P2		P3		P4	
<i>Normanella</i>						
<i>mucronata reducta</i> [♀]	0.1.123	1.221	0.1.223	1.321	0.1.223	1.220
[♂]	0.1.123	<u>1.220</u>	0.1.223	1.321	0.1.223	1.220
<i>mucronata</i> sensu Griga (1963)*	?	?	0.1.223	1.321	0.1.223	1.220
<i>mucronata</i> sensu Marinov (1977)	0.1.123	1.321	0.1.223	1.321	0.1.223	1.220
<i>bifida</i> sp. nov.	0.1.123	1.221	0.1.223	1.321	0.1.223	1.221
all other species	0.1.123	1.321	0.1.223	1.321	0.1.223	1.221
<i>Sagamiella</i> gen. nov.	0.1.123	1.221	0.1.223	1.321	0.1.223	1.221

* reinterpreted (see text)

distally; with 1 naked terminal seta, 1 bipinnate inner seta, and 2 short bare setae, plus 2 pinnate setae along outer margin; terminal seta arising from small cylindrical process; 1 secretory pore on anterior surface; several rows of long setules along inner margin, short spinules anteriorly, and dense long setules along proximal outer margin.

Male

More slender than female. Body length 507 - 563 µm (n=7; \bar{x} = 533 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 121 µm. Urosome narrower than prosome (Fig. 5A).

Prosoma (Fig. 5A) 4-segmented, comprising cephalothorax and 3 free pedigerous somites. Rostrum distinct at base as in ♀. Cephalothorax with posterior margin weakly crenulated; 3 pairs of longitudinal ridges present as in ♀; ornamentation consisting of sensillae, and pores as figured. Pedigerous somites covered with minute denticles. Prosomites with crenulated hind margin.

Urosome (Figs 5A-B) 6-segmented, comprising P5-bearing somite, genital somite and 4 abdominal somites. Surface ornamentation pattern consisting of patches of minute denticles present dorsally and laterally; posterior margin irregularly serrate dorsally and laterally.

Antennule (Fig. 5C-G) 7-segmented; subchirocer with geniculation between segments 5 and 6. Segment 1 with 2 rows of spinules along anterior margin. Segment 4 represented by small sclerite along anterior margin (insert in Fig. 5E). Segment 7 triangular. Segment 5 largest; swollen. Segment 6 forming dorsal spinous process overlying anterior part of segment 7. Segmental homologies: 1-I, 2-(II-VIII), 3-(IX-XII), 4-XIII, 5-(XIV-XX), 6-(XXI-XXIII), 7-(XXIV-XXVIII). Armature formula: 1-[1 pinnate], 2-[2 + 9 pinnate], 3-[5 + 3 pinnate], 4-[1 + 1 pinnate], 5-[7 + 5 pinnate + 3 spinous processes + (1 + ae)], 6-[1 + 3 spinous processes], 7-[6 + acrothek]. Apical acrothek consisting of minute aesthetasc and 2 naked setae.

P2 endopod (Fig. 30B) 2-segmented; both apical setae of enp-2 distinctly shorter than in ♀; outer apical seta shortest and about 1.3 times as long as outer spine.

P3 endopod (Fig. 4D-E) 2-segmented; modified. Enp-2 shorter than in ♀; outer margin with short mucroniform process being homologous with outer spine of enp-2 of ♀; both apical setae strongly reduced and set on small lobe together with tube-pore; inner setae not modified.

P4 endopod (Fig. 4B) 2-segmented; slightly modified. Enp-1 and -2 slightly narrower than in ♀; inner distal seta of enp-2 distinctly longer than in ♀; apical tube-pore reduced.

Fifth pair of legs (Fig. 5B, H) fused medially; P5 defined at base. Baseoendopod with short setophore bearing outer basal seta, and well developed trapezoid endopodal lobe

with 2 pinnate setae apically; 2 tube-pores along inner margin and 1 tube-pore near articulation with exopod. Exopod about twice as long as maximum width; with 1 bipinnate inner seta, 1 bipinnate apical seta, and 1 naked plus 1 pinnate seta along outer margin.

Sixth pair of legs (Figs 5B, I) asymmetrical; represented on both sides by a small plate (fused to ventral wall of supporting somite along one side; articulating at base and covering gonopore along other side); outer distal corner produced into cylindrical process bearing 1 bipinnate, and 2 naked setae.

Notes. - Although *N. dubia* was originally reported from the Durham coast as a *nomen nudum* (Brady & Robertson, 1876), the precise type locality of the material upon which Brady's (1880) original description was based is unknown. Brady (1880) recorded the species from New Grimsby harbour (Tresco) and Porth Cressa Bay (St Mary's) on the Isles of Scilly, off Marsden and Hartlepool in Durham, and from a third locality in Clew Bay in Ireland. We have examined *Normanella* material from Innisidgen on the Isles of Scilly and from off Northumberland (i.e. north of Durham) and found only few differences with Brady's illustrations. These can be attributed to imperfect dissection or interpretation. For example, Brady (1880) interpreted the basal pedestal and surrounding sclerite (Fig. 3B) of the ♀ antennule as an additional segment, explaining why the antennule was originally described as 7-segmented. He also overlooked the inner seta of P1 enp-2 but this element is relatively small and can easily be missed when closely addressed to the segment. Of critical importance in our identification is the morphology and size of the caudal ramus. Its small size in conjunction with the markedly short, almost spiniform terminal setae unequivocally identify *N. dubia* among other NW European species. In addition, *N. dubia* exhibits a number of distinctive features such as the 6-segmented antennule in the ♀, the conspicuous shape of the rostrum with concave lateral margins and rounded anterior margin, and the absence of an areolate surface pattern on the cephalic shield. *N. dubia* is among the larger species of the genus and clear consistency in body size was found between the original description (0.68 mm) and the present study (0.67 mm).

Holmes & O'Connor (1990) pointed out that the *N. minuta* material held in the National Museum of Ireland collections closely resembles *N. dubia* and differs in a number of features from *N. minuta* described by Sars (1909). They speculated that *N. dubia* might well be the predominant *Normanella* around Ireland.

There is an undeniable relationship between the type species and *N. quarta* described from Brittany (Monard, 1935a) and *N. semitica* described from Salammbô, Tunisia (Monard, 1935b). The similarities with these species are

striking and in view of Monard's (1935a-b) incomplete original descriptions it is difficult to ascertain whether *N. quarta* and *N. semitica* are either distinct or conspecific with *N. dubia*. In fact, the material that we examined from the Isles of Scilly was originally identified as *N. quarta* by Wells (1970). According to Lang (1948) both *N. quarta* and *N. semitica* were possibly described on the basis of copepodid stages. His suspicion was based on the serrate nature of the anal operculum and posterior margins of the urosomites in these species but the present redescription of the closely related *N. dubia* has proven this to be unfounded. Monard (1937) regarded *N. semitica* as a vaguely characterised variety of *N. quarta* but Lang (1948) decided to maintain it as a valid species. It is preferred here to consider both species as potentially distinct from *N. dubia* until further evidence becomes available. They are ranked as *species inquirendae* in the *dubia*-lineage.

The published records indicate a distribution restricted to the British Isles but this could be extended to the French Atlantic coast if *N. quarta* proves synonymous: Ireland: Clew Bay (Brady, 1880; probably also Roe (1958, 1960) and Holmes (1985) - as *N. minuta*); Scotland: NE of Shetland Islands (T. Scott, 1904), E of Orkney Islands (T. Scott, 1907); Firth of Forth (T. Scott, 1894; T. Scott, 1906), Loch Fyne (T. Scott, 1897); England: Durham (Brady & Robertson, 1876; Brady, 1880; Norman & Brady, 1909), Northumberland (present account), River Tamar (present account), Devon and Cornwall (Norman & T. Scott, 1906), Isles of Scilly (Brady, 1880; Norman & T. Scott, 1906; Wells, 1970); Isle of Man (Thompson, 1893). *N. quarta* has been recorded from Brittany (Monard, 1935b; Bodin, 1984), Banyuls-sur-Mer (Soyer, 1971; Bodiou, 1976, 1982) and Algeria (Monard, 1937). With the exception of Marinov's (1977) record from off the Spanish Sahara, *N. semitica* has not been recorded again since its initial discovery in Tunisia (Monard, 1935a).

(b) The *mucronata*-lineage

This species group can be readily identified by the structure of the caudal ramus, in particular the form and shape of the inner terminal seta V. This seta, unlike in *Sagamiella* or other species groups of *Normanella*, lacks an internal fracture plane and is usually swollen in its proximal half. It is typically fused to seta IV which is reduced in length and also lacks an internal fracture plane.

All species of this group have a characteristic areolated surface pattern on the cephalic shield, a pointed (or bifid) rostrum, a 5-segmented ♀ antennule and a slender endopodal lobe on leg 5. The inner distal corner of this lobe bears a characteristic tube-pore surrounded at the base by spinules. This pore was misinterpreted as a pinnate seta by Lang (1965) in his description of *N. confluens* and this

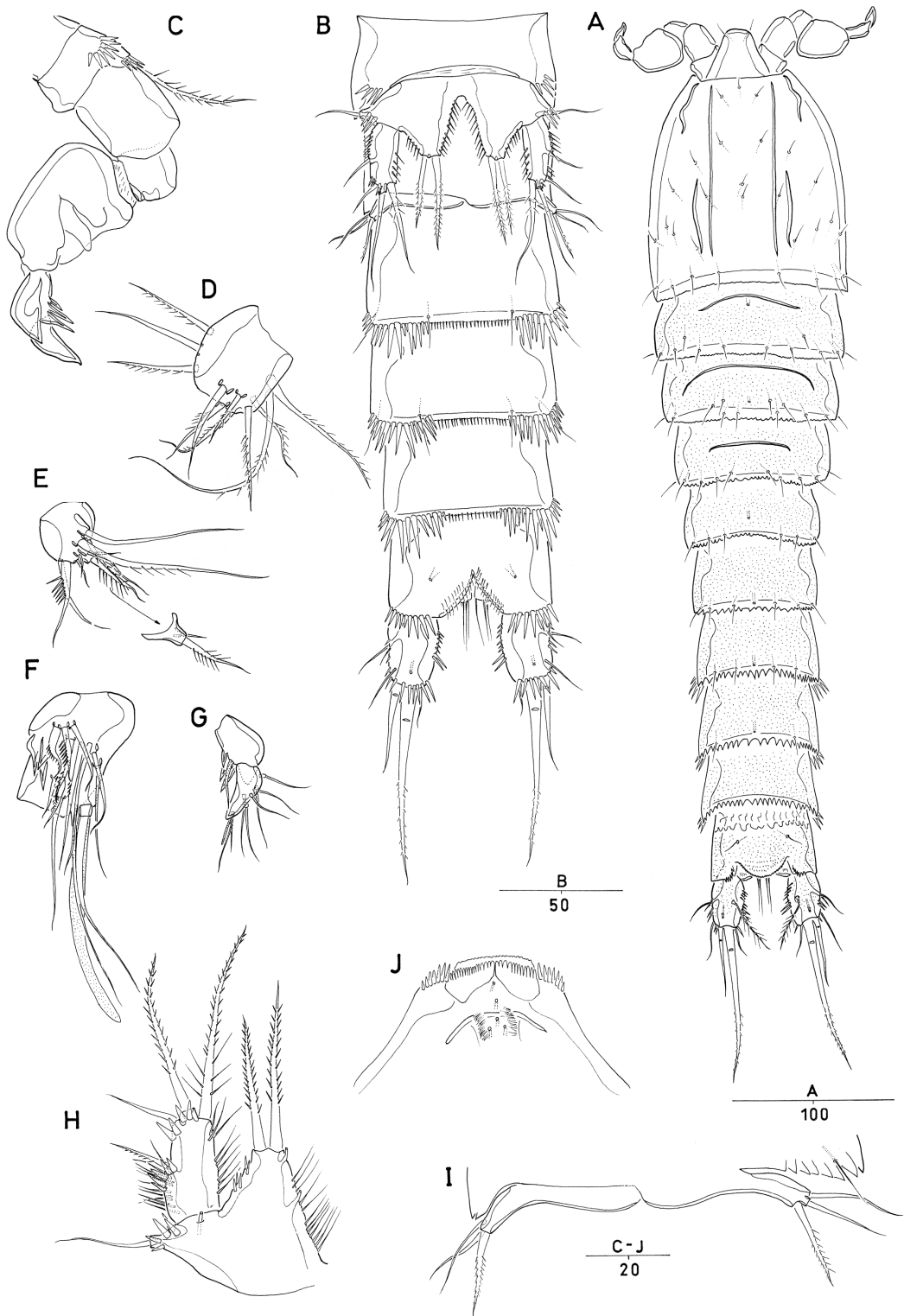


Figure 5. *Normanella dubia* Brady & Robertson in Brady (1880). A, habitus ♂, dorsal; B, urosome ♂, ventral; C, antennule ♂ [armature of segments 2-7 omitted]; D, 2nd antennular segment ♂; E, 3rd and 4th antennular segments ♂; F, 5th antennular segment ♂; G, 6th and 7th antennular segments ♂; H, P5 ♂, anterior; I, P6 ♂; J, labrum ♀, posterior.

Figure 5. *Normanella dubia* Brady & Robertson in Brady (1880). A, habitus ♂, vue dorsale; B, urosome ♂, vue ventrale; C, antennule ♂ [armature des articles 2-7 omise]; D, article antennulaire 2 ♂; E, articles antennulaires 3- 4 ♂; F, article antennulaire 5 ♂; G, articles antennulaires 6-7 ♂; H, P5 ♂, vue antérieure; I, P6 ♂; J, labre ♀, vue postérieure.

misinterpretation also explains the alleged variability encountered in the armature of the baseoendopod of leg 5 (Lang, 1965: 537).

The *mucronata*-group comprises *N. mucronata* Sars, 1909, *N. reducta* Noodt, 1955 grad. nov., *N. confluens* Lang, 1965 and a new species from cold seeps, *N. bifida* sp. nov.

Normanella mucronata Sars, 1909

Type locality. - South coast of Norway. Sars (1909) collected the material for the original description in two localities, Flekkerø and Farsund, but did not specify a type locality.

Material. - (a) The Natural History Museum, London: 12 ♀♀ (11 ♀♀ in alcohol, 1 ♀ dissected on 9 slides); Frierfjord/Langesundfjord, Norway, 99 m deep mud, coll. R. Huys, 1985; reg. nos 1998.2152-1261;

(b) The Natural History Museum, London: 11 ♀♀ (in alcohol); Moray Firth, Scotland, coll. T. Scott, 1898; labelled as *Normanella dubia*; reg. nos 1956.9.25.64.

Female.

Total body length 569 - 665 µm (n=10; \bar{x} = 585 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 125 µm. Urosome slightly narrower than prosome (Fig. 6A).

Cephalothorax with serrulate posterior margin; pleural areas well developed, rounded; posterolateral angles weakly crenate; ornamentation consisting of sensillae as illustrated in Figs. 6A, 7E and distinct, symmetrical, areolated pattern dorsally and laterally. Cephalothorax without minute denticles as found on free body somites. Rostrum (Fig. 7B) triangular, prominent; with almost straight lateral margins but abruptly tapering distal to sensillae; apex pointed and bordered by membranous flanges; completely defined at the base; with pair of tiny sensillae and a midventral tube-pore near the apex; dorsal and ventral surface smooth, without denticles.

Pedigerous somites covered with minute spinules. All prosomites without defined hyaline frills; hind margin irregularly serrulate.

Urosome (Figs 6A; 7A) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites with dense surface ornamentation consisting of small spinules dorsally and laterally; also present ventrally on penultimate urosomite (Fig. 7A). Hyaline frills of urosomites not developed but hind margin distinctly serrate dorsally and laterally. Ventral hind margin of urosomites 2-4 with setular extensions medially and large spinules laterally; those of urosomites 3-4 also with fine spinules medially.

Genital double-somite (Figs 6A;7A) with original segmentation indicated by transverse, serrulate surface

ridge dorsally and laterally and short surface suture ventrolaterally; completely fused ventrally. Genital field with small copulatory pore located in median depression; gonopores fused medially forming single genital slit covered on both sides by opercula derived from sixth legs; P6 with small protuberance bearing 1 short, bipinnate, outer seta and 1 minute, bare, inner seta (Fig. 7A).

Anal somite (Figs 6B; 7A) with well developed, serrate anal operculum flanked by row of spinous processes overlying anterior margin of caudal rami; midventral surface without ornamentation; anal opening with fringe of long setular extensions, bordered by spinules ventrally.

Caudal rami (Figs 6B; 7A) moderately long, 2.5 times longer than maximum width; tube-pores present on subdistal ventral and dorsal surfaces; each ramus with 7 setae; seta I bare and shortest, closely set to bare seta II; seta III bare, positioned ventrolaterally; setae IV and V fused basally, bipinnate (seta V longest and strongly developed, slightly longer than last 3 urosomites and caudal rami combined; without internal fracture plane); seta VI bare, unipinnate, without internal fracture plane; seta VII tri-articulate at base. Each ramus with minute spinules, dorsally and ventrally; sparse additional spinular ornamentation present along inner and outer margins and around ventral hind margin.

Antennule (Fig. 7B) 5-segmented, segment 3 longest (measured along anterior margin). Armature formula: 1-[1 pinnate], 2-[3 + 5 pinnate], 3-[3 + 5 pinnate + (1 + ae)], 4-[1], 5-[2 pinnate], 6-[7 + 1 pinnate spine + acrothek]. Anterior elements on segments 5 and 6 more setiform and less coarsely pinnate than in *N. dubia*.

Antennary exopod with 2 lateral and 2 apical bipinnate setae.

Mandibular palp (Fig. 6C) small, as in *N. dubia*.

P1 (Fig. 7C) with large coxa; with several spinules along outer margin and on anterior surface. Basis with stout, unipinnate spine but no long setules along inner margin and with 1 stout, bipinnate spine and few spinules along outer margin. Exp-1 with 1 long, bipinnate spine (distinctly longer than other exopodal spines); exp-2 with 1 bipinnate, outer spine and 1 short, plumose, inner seta (extending to insertion level of middle outer spine of exp-3); exp-3 with 3 bipinnate spines and 2 geniculate setae. Endopod 2.2 times as long as exopod, enp-1 with 1 short, plumose inner seta, enp-2 with 1 slender, smooth, curved claw and 1 geniculate seta apically, and 1 small plumose seta along inner margin.

P2-P4 armature formula as in *N. dubia* (Table 2). P3 endopod as in Fig. 7D.

P5 (Fig. 6D). Baseoendopod forming short, outer setophore bearing basal seta and rows of setules and spinules; with tube-pore near boundary with exopod. Endopodal lobe extending to insertion level of 3rd outer seta of exopod; with 3 bipinnate setae laterally and 2 bipinnate

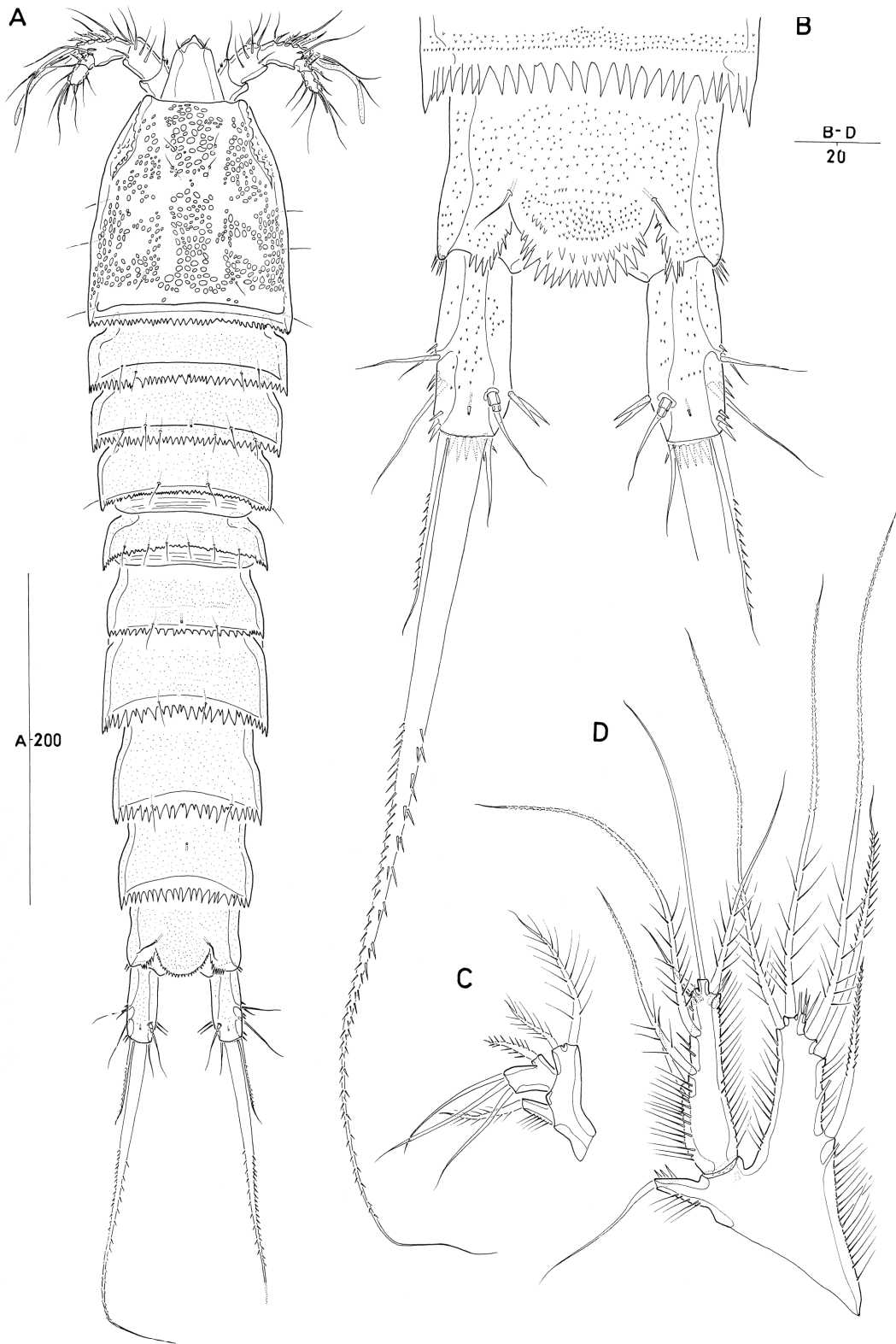


Figure 6. *Normanella mucronata* Sars, 1909. (♀). A, habitus, dorsal; B, anal somite and caudal rami, dorsal; C, mandibular palp; D, P5, posterior.

Figure 6. *Normanella mucronata* Sars, 1909. (♀). A, habitus, vue dorsale; B, somite anal et rames caudales, vue dorsale; C, palpe mandibulaire; D, P5, vue postérieure.

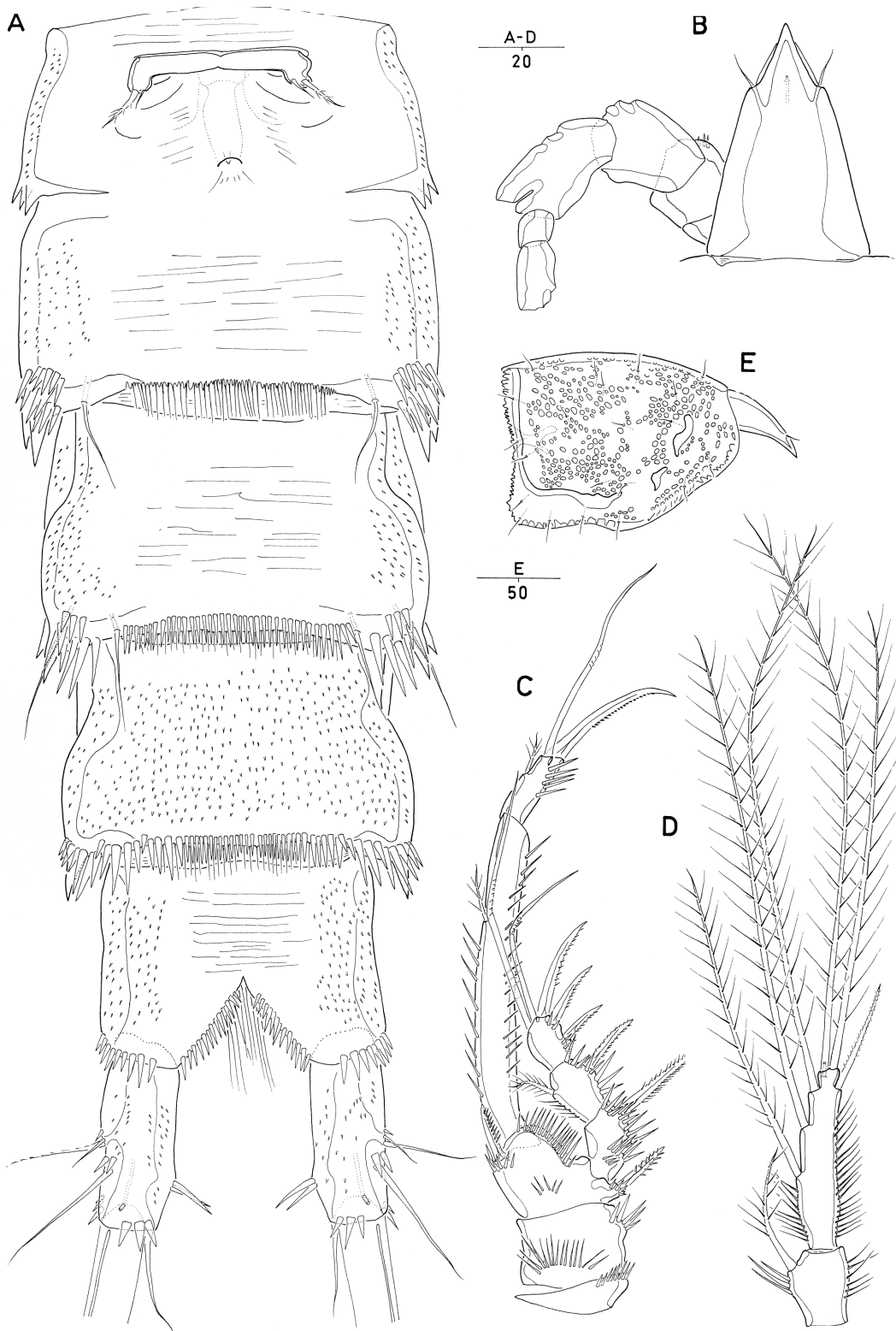


Figure 7. *Normanella mucronata* Sars, 1909. (♀). A, urosome [excluding P5-bearing somite], ventral; B, rostrum and left antennule [armature omitted], dorsal; C, P1, anterior; D, P3 endopod, posterior; E, cephalothorax and rostrum, lateral.

Figure 7. *Normanella mucronata* Sars, 1909. (♀). A, urosome [sauf le somite portant P5], vue ventrale ; B, rostre et antennule gauche [armature omise], vue dorsale ; C, P1, vue antérieure ; D, endopodite de P3, vue postérieure ; E, cephalothorax et rostre, vue latérale.

setae apically; rows of long spinules along outer margin, and long setules along proximal inner margin; with characteristic tube-pore (surrounded by spinules) at apex. Exopod elongate, distinctly tapering distally; with 1 naked terminal seta, 1 bipinnate inner seta, and 4 setae of different length along outer margin (middle 2 ones bipinnate, others bare); terminal seta arising from small cylindrical process; outer margin and inner margins with numerous long setules.

Male

Not examined.

Notes. - Sars (1909) distinguished this species from *N. tenuifurca* and *N. minuta* by the more robust appearance, the acutely produced rostrum and the structure of the caudal ramus, particularly the unusually strongly developed seta V. Our redescription agrees closely with Sars' illustrations, except for the areolated surface pattern on the cephalic shield which was overlooked by Sars (1909) (but noticed by Monard (1935b)) and proportional length differences in the exopodal setae of leg 5. Although the species name *mucronata* alludes to the sharply produced rostrum and our study has confirmed the shape described by Sars (1909), it should be noted that only dissection and flat mounting can reveal the true shape of the rostrum. The rostrum is typically ventrally deflected (Fig. 7E) so that viewing this structure *in toto* in specimens mounted in dorsal aspect may produce a misleading foreshortened image (Fig. 6A), disguising the real contours of the apex. Scrutinous examination of our material from Frierfjord/Langesundfjord and Moray Firth has failed to reveal the longitudinal dorsal keel on the caudal ramus, mentioned and illustrated by Sars (1909) in his Norwegian material. Since the author did not illustrate the caudal ramus in lateral aspect we suspect that this observation is based on a misinterpretation of the heavily (internally) chitinized inner margin. His statement that the anal somite is much shorter than the preceding one is probably based on a strongly telescoped specimen.

Monard's (1928) variety *quinquesetata* from Banyuls-sur-Mer is clearly smaller than the «typical» form (0.4 mm) and differs in the morphology of the P5 exopod which bears only 5 setae and is slightly shorter than the endopodal lobe. Although Lang (1948) recognized Monard's specimens as a valid variety of *N. mucronata* and subsequently regarded it as a distinct subspecies (Lang, 1965: 529), there appears to be little evidence in favour of this status. The original description is deficient in several aspects (e.g. armature of P1) and it is more than likely that Monard (1928) overlooked the small proximal seta on the P5 exopod. The swollen seta V supports placement in the *mucronata*-complex, however, since there is no illustrated information on the rostrum and the proportional lengths of the P5 exopod and endopodal lobe appear to be the opposite from those recorded in other members of the complex, this

assignment has to be regarded as tentative. The exopod is shorter in *N. sarsi* and in some species of the *dubia*-group. Pending the redescription of this form we rank it as *variety incertae sedis* in the Normanellidae. It is possible that Bodiou's (1976, 1982) records of *N. mucronata* from Banyuls-sur-Mer refer to this species. Arlt (1983) ascribed one female of *N. mucronata* from the Kattegat to the variety *quinquesetata* but this record requires confirmation. For a second female Arlt (1983) remarked that the inner seta of P1 enp-1 was much shorter than in Sars' (1909) description (which agrees with our observation: Fig. 7C), and that the distalmost seta on the P5 exopod was not at the extreme edge but more on the surface of the segment which indicates that he was referring to the tube-pore found in this position. Arlt's (1983) specimen described under the name *N. cf. minuta* is based on a copepodid V stage, possibly of *N. mucronata*.

N. mucronata assumes a NW European distribution: Scandinavia (Sars, 1909; Lang, 1948; Por, 1964b, 1965; Drzycimski, 1969), Ireland (Holmes, 1985), Scotland (present account), Northumberland (Bossanyi & Bull, 1971), Isle of Man (Moore, 1979), Southern Celtic Sea (Gee, unpubl.), Brittany (Monard, 1935b; Chamroux et al., 1977; Bodin, 1984; Bodin & Le Guellec, 1992). The mediterranean and Black Sea records of this species are considered uncertain. Apostolov & Marinov (1988) misleadingly reproduced Sars' (1909) drawings in their handbook of the Bulgarian harpacticoids; these illustrations do not refer to the *N. mucronata* recorded in earlier Bulgarian studies (Apostolov, 1969; Marinov, 1971, 1977; see below). A similar misleading reproduction was adopted by Griga (1969).

Coull (1971) recorded «*N. mucronata typica*» from several localities between 20 and 90 m depth on the North Carolina shelf, however, validation of this record would require re-examination of the original material. Rouch's (1962) record of *N. mucronata* from the Buenos Aires area (Argentina) is equally doubtful.

Normanella reducta Noodt, 1955 grad. nov.

Normanella mucronata reducta Noodt, 1955

Normanella mucronata sensu Griga (1963)

Normanella mucronata sensu Marinov (1971) [but not (1977)]

Type locality. - Sea of Marmara, detritus-rich *Amphioxus*-sand (Noodt, 1955).

Noodt (1955) established this subspecies for specimens which displayed a reduced setation on the endopods of P2 and P4 (Table 2). In comparison to the typical form *N. mucronata reducta* has lost 1 inner seta on P2 enp-2 (formula 221 instead of 321) and the outer spine on P4 enp-2 (formula 220 instead of 221). Noodt (1955) illustrated

the typical modification of the male P3 endopod, however, also claimed that additional sexual dimorphism was expressed on the P2 endopod, displaying a armature formula [1.220] (Table 2). This modification is clearly unique within the family and requires re-examination. Noodt's practice of mounting and dissecting multiple specimens on a single slide raises the suspicion that he had actually observed the P4 of a second specimen instead of the P2. Alternatively, it is possible that the outer distal seta is extremely reduced in the ♂ (even more so than in *N. minuta*) and Noodt was really referring to a [1.211] formula in which the outer spine is retained but the equivalent of the outer distal seta was overlooked. Another enigma concerns the male P5 exopod which according to Noodt (1955) is well over twice as long as wide, «... wie von Sars gezeichnet». This reference to Sars' (1909) original drawings is inexplicable since the type material consisted exclusively of females. In fact, the male of *N. mucronata* has remained undescribed apart from Lang's (1948) cursory comments on size and P5 exopod which must have been based on his personal material from the Gullmar Fjord and Måseskär. Males of *N. mucronata reducta* also differ from their females in the caudal rami which are about 3 times instead of twice (as in the typical form) as long as wide.

Griga (1963) presented a fragmentary description of specimens from the Ukrainian coast which she ascribed to *N. mucronata*. Bodin (1997 and previous editions) remarked that the setal formula of P2 and P4 presented an intermediate between *N. mucronata reducta* and the typical form, but that Griga (1963) had obviously been unaware of Noodt's (1955) paper. The pointed rostrum and the well developed seta V leave no doubt that her material belongs to the *mucronata*-complex, however, reinterpretation of the illustrations of the swimming legs provides strong evidence that it is attributable to *N. mucronata reducta*. Using the exopodal setation as reference it is obvious that the leg figured as P2 is in fact the P3 and that the real P2 had not been figured. The [1.220] formula of the P4 relate the species to *N. mucronata reducta* which, based on Por's (1959) Romanian record and Marinov's (1971, 1977) records from Bulgaria, appears to assume a continuous distribution throughout the Black Sea basin from the Sea of Marmara to at least Crimea.

Marinov (1971) found the P2 endopodal setation to be variable within a single specimen, with the typical pattern [1.321] expressed on one side and the reduced pattern [1.221] on the other, and therefore doubted the validity of *N. mucronata reducta* and subsumed it in the nominal form. Whether the observed deviation from the typical condition is an expression of intraspecific variability or simply teratological is a crucial issue in this context which is hard to resolve in practice. From Marinov's (1971) illustration other differences between the left and right counterpart

(length of inner seta on exp-2, shape of outer spine on enp-2) can be detected indicating that he was probably dealing with a malformation. In a later paper Marinov (1977) figured another female displaying the reduced pattern [1.220] on the P4 but the typical pattern [1.321] on the P2. This would have given further credence to his earlier hypothesis on intraspecific variability, provided that he was dealing with the same species. The difference in leg 5 shape, however, indicates that his *N. mucronata typica* is not conspecific with his 1971 material and that there are at least two *Normanella* species with reduced swimming leg armature in the Black Sea. Marinov & Apostolov (1981), referring to Marinov's findings, continued to regard *N. mucronata* as a highly variable species even though no such variability was detected in their material from the Bay of Piran in which only the *reducta* form was represented. It is conceivable that Marcotte & Coull's (1975) *N. mucronata* from the same area also belongs to *N. mucronata reducta*. Since we have not encountered any swimming leg variability during the course of this study and other species (*N. bifida*, *Sagamiella* species) are known to display setal reductions we regard the differences as pointed out by Noodt (1955) as sufficient evidence to warrant full specific status for *N. mucronata reducta*.

Normanella confluens Lang, 1965

Type locality. - Monterey Bay, California; off Hopkins Marine Station; tidal pools, shell-sand, stones (Lang, 1965).

Lang (1965) has already pointed out the close similarity with *N. mucronata*. Both species can be differentiated by the areolated pattern on the cephalic shield, the shape of the rostrum, the relative proportions of the female P5, and to a lesser extent, urosomal ornamentation and shape of seta V. The 2-segmented condition of the maxillary endopod in *N. confluens* is unique within the family.

The Mediterranean records from Banyuls-sur-Mer (Bodiou, 1976, 1982; Soyer, 1971) and Marseilles (Nodot, 1978; Dinet et al., 1982) probably refer to another species of the *mucronata*-complex.

Normanella bifida sp. nov.

Type locality. - Sagami Bay, Stn DT1-2, depth 625.6 m.

Material. - Holotype ♀ dissected on 15 slides (reg. no. 1998.2162); coll. 22-23 February 1992.

Female

Total body length 787 µm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured halfway the cephalic shield length: 175 µm. Urosome narrower than prosome (Fig. 8A).

Cephalothorax with distinct areolated pattern of surface pits delineating H-shaped smooth area dorsally; posterior

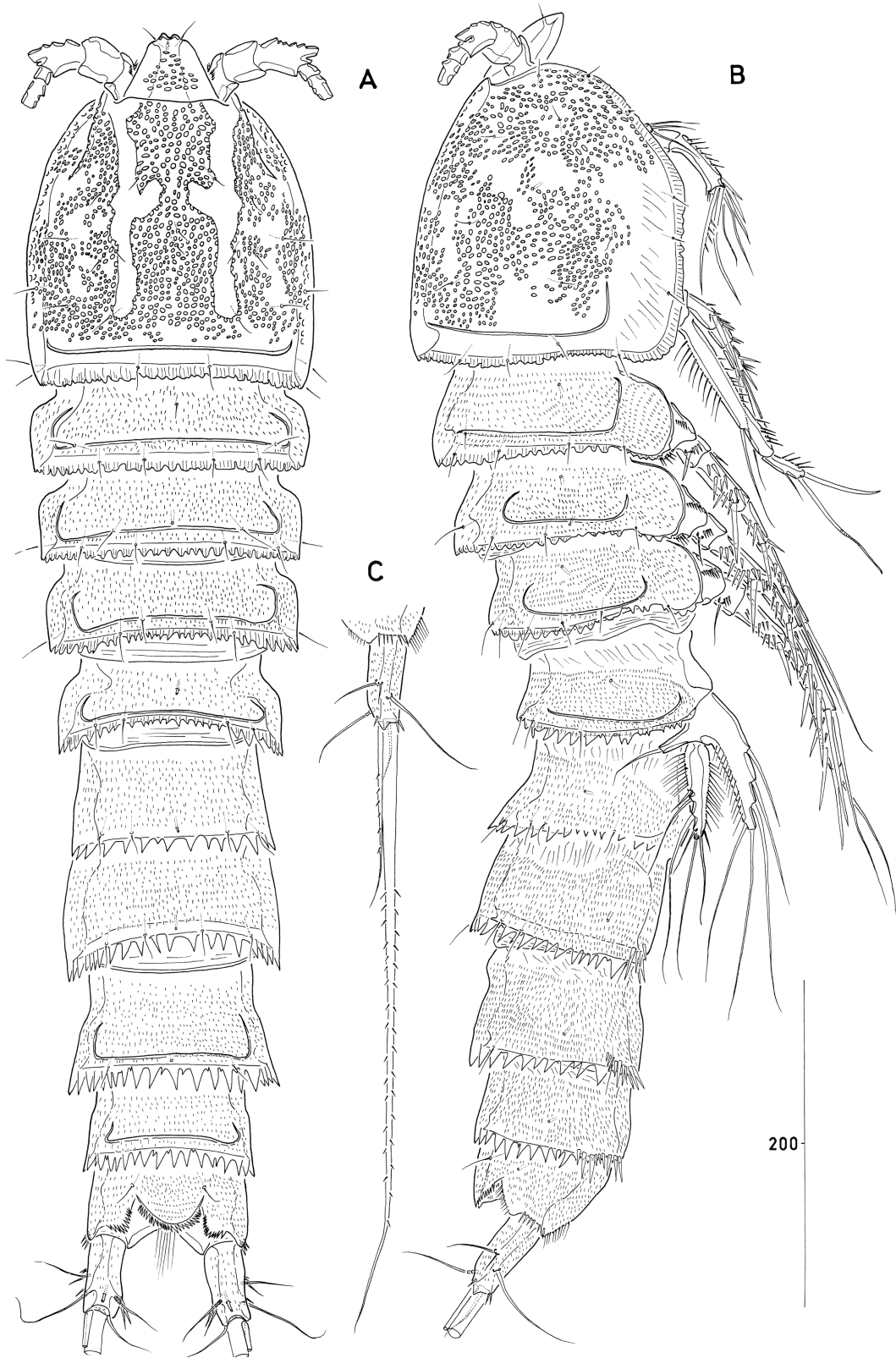


Figure 8. *Normanella bifida* sp. nov. (♀). A, habitus, dorsal; B, habitus, lateral; C, right caudal ramus, lateral.
Figure 8. *Normanella bifida* sp. nov. (♀). A, habitus, vue dorsale ; B, habitus, vue latérale ; C, rame caudale droite, vue latérale.

margin crenulate; pleural areas strongly developed, with rounded posterolateral angles weakly crenulate; additional ornamentation consisting of sensillae and few pores as illustrated in Fig. 8A-B; cephalothorax without minute spinules as found on free body somites. Rostrum somewhat triangular (Fig. 11C), bifid at apex; completely defined at the base; with pair of tiny sensillae and a midventral tube-pore near the apex; dorsal surface areolated as in cephalosome.

Pedigerous somites covered with minute spinules; posterior margin crenate.

Urosome (Figs 8A-B; 9A) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites with surface ornamentation consisting of small spinules dorsally and ventrally. Hyaline frills of urosomites not developed but hind margin distinctly serrate dorsally. Hind margin of urosomites 3-4 with large spinules ventrolaterally and fine or minute spinules ventrally; ventral surface partially wrinkled proximally.

Genital double-somite with transverse, serrate surface ridge dorsally and laterally (Fig. 8A-B), indicating original segmentation; completely fused ventrally (Fig. 9A); whole ventral surface with minute surface ridges; posterolateral angles with large spinules ventrally. Genital field with large copulatory pore located in median depression; gonopores fused medially forming single genital slit covered on both sides by opercula derived from sixth legs; P6 with small protuberance bearing 1 sparsely plumose outer seta and 1 bare inner seta (Fig. 9D).

Anal somite (Fig. 9A-B) with finely serrate, well developed operculum flanked by row of spinous processes overlying anterior margin of caudal rami; median ventral surface wrinkled without denticles; ventral posterior margin with fringe of setular extensions (anal frill).

Caudal rami (Figs 8C; 9A-B) cylindrical, about twice as long as wide; each ramus with 7 setae; seta I bare, shortest (Fig. 9B); setae II and III bare; setae IV and V fused basally (Fig. 9A), without internal fracture planes (seta IV unipinnate; seta V bipinnate, longest, and subequal to combined length of urosomites); seta VI bare and small; seta VII tri-articulate at base. Each ramus with minute spinules on dorsal and ventral surface; few additional spinules present around bases of setae II, III and VII.

Antennule (Fig. 10A-B) 5-segmented, segment 3 longest; with well developed sclerite around base of segment 1. Armature formula: 1-[1 pinnate], 2-[1 + 8 pinnate], 3-[4 + 5 pinnate + (1 + ae)], 4-[1 + 2 pinnate], 5-[5 + 2 pinnate + acrothek]. Apical acrothek consisting of small aesthetasc fused basally to 1 slender seta and 1 strong pinnate spine. Segment 1 with 2 spinular rows around anterior margin. Segment 3 with aesthetasc fused basally to seta and set on distinct pedestal. Anterior elements on segments 4 and 5 setiform and not coarsely pinnate.

Antenna (Fig. 10C) 3-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa small, with 1 row of spinules. Basis and proximal endopod segment fused forming elongate allobasis with transverse surface sutures marking original segmentation; with 1 abexopodal seta in distal half (insertion site arrowed in Fig. 10C). Exopod small, 4.5 times longer than width with 2 bipinnate setae laterally, and 2 bipinnate setae apically (lost during dissection but insertion sites arrowed in Fig. 10C). Endopod subequal to allobasis; lateral armature consisting of 2 short pinnate spines; apical armature consisting of 2 pinnate spines, 2 geniculate setae, and 1 strong pinnate spine (fused basally to short seta). Allobasis with small spinules on abexopodal lateral surface. Endopod with row of long spinules laterally and 1 transverse hyaline frill subapically.

Labrum with elaborate spinular ornamentation and pores as in Fig. 11D.

Mandible (Fig. 10F) with well developed gnathobase bearing several multicuspidate teeth around distal margin and 1 small pinnate spine at dorsal corner. Palp small, biramous. Basis with 2 bipinnate setae; with minute spinules on median surface, and around base of endopod. Exopod 1-segmented, longer than endopod, with 1 pinnate seta apically and row of setules laterally. Endopod 1-segmented, with 3 pinnate setae apically, and 1 pinnate seta laterally.

Paragnaths (Fig. 11D) strongly developed lobes with medially directed hair-like setules.

Maxillule (Fig. 10D). Praecoxa with few long spinules around outer distal margin; arthritis strongly developed, with 2 naked setae on anterior surface and 9 spines/setae around distal margin. Coxa with cylindrical endite bearing 1 naked seta and 1 curved, pinnate spine. Basis with 2 endites (distal with 2 pinnate setae, proximal with 2 pinnate setae, and 1 curved, pinnate spine). Endopod incorporated in basis, represented by 3 pinnate setae; exopod 1-segmented, with 2 pinnate setae.

Maxilla (Fig. 10E) with 3 endites on syncoxa; praecoxal endite small and cylindrical, with 1 strong, pinnate seta; proximal coxal endite with 1 row of spinules posteriorly, 1 strong spine fused to endite, 1 pinnate seta with subapical tubular extension, and 1 naked seta; distal coxal endite with 2 pinnate setae armed with subapical tubular extension, and 1 sparsely pinnate seta. Allobasis drawn out into strong, slightly curved, weakly serrate claw; accessory armature consisting of 1 spine and 1 naked seta on anterior surface, and 1 naked seta on posterior surface; short tube-pore along outer margin; endopod represented by 3 plumose setae.

Maxilliped (Fig. 10G) with 2 pinnate setae and several patches of spinules on syncoxa. Basis with 2 rows of spinules on outer distal region and 1 longitudinal spinular row along palmar margin. Endopod a minute segment drawn out into long, naked claw; accessory armature consisting of long naked seta and minute outer seta.

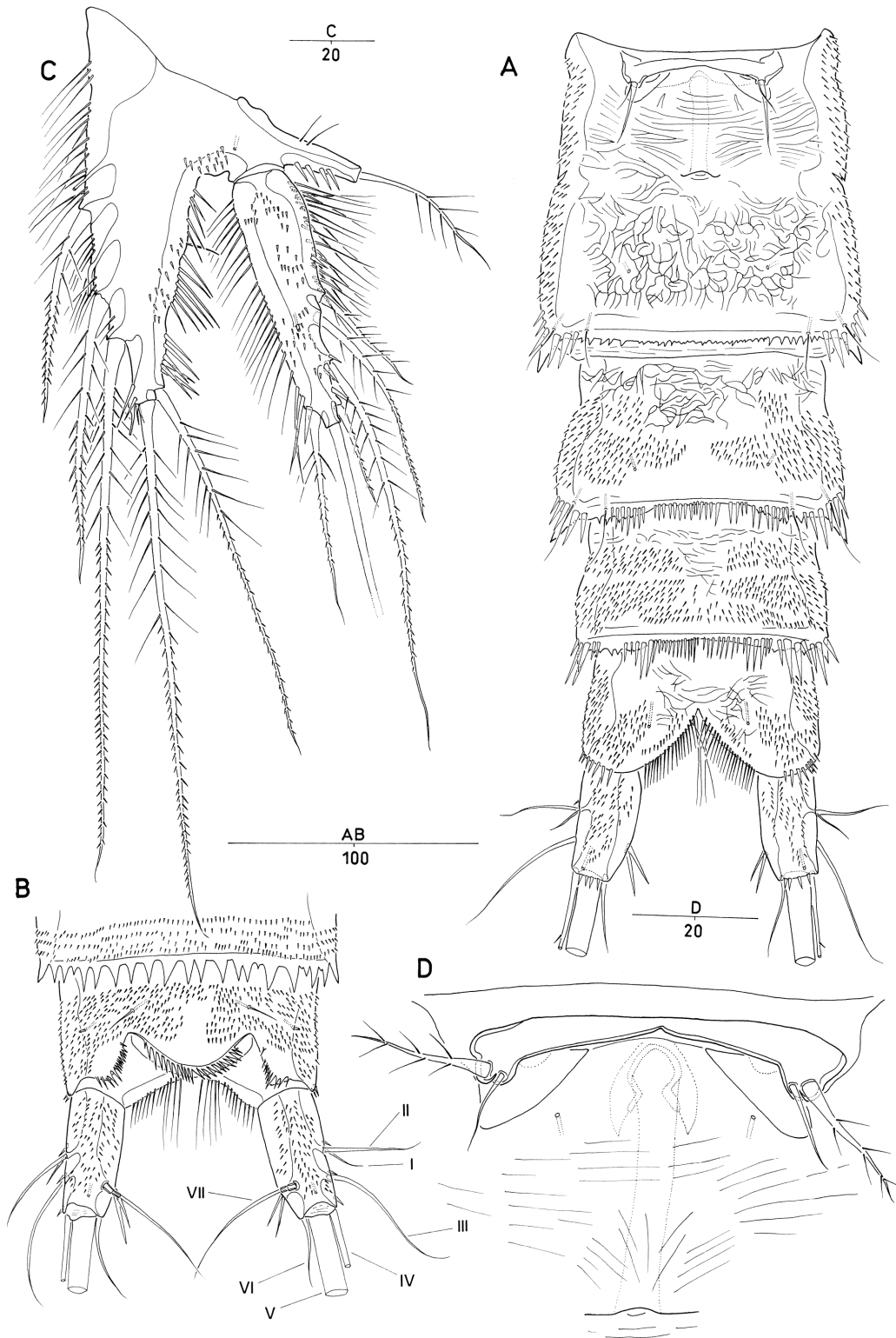


Figure 9. *Normanella bifida* sp. nov. (♀). A, urosome [excluding P5-bearing somite], ventral; B, anal somite and caudal rami, dorsal; C, P5, anterior; D, genital field.

Figure 9. *Normanella bifida* sp. nov. (♀). A, urosome [sauf le somite portant P5], vue ventrale ; B, somite anal et rames caudales, vue dorsale ; C, P5, vue antérieure ; D, aire génitale.

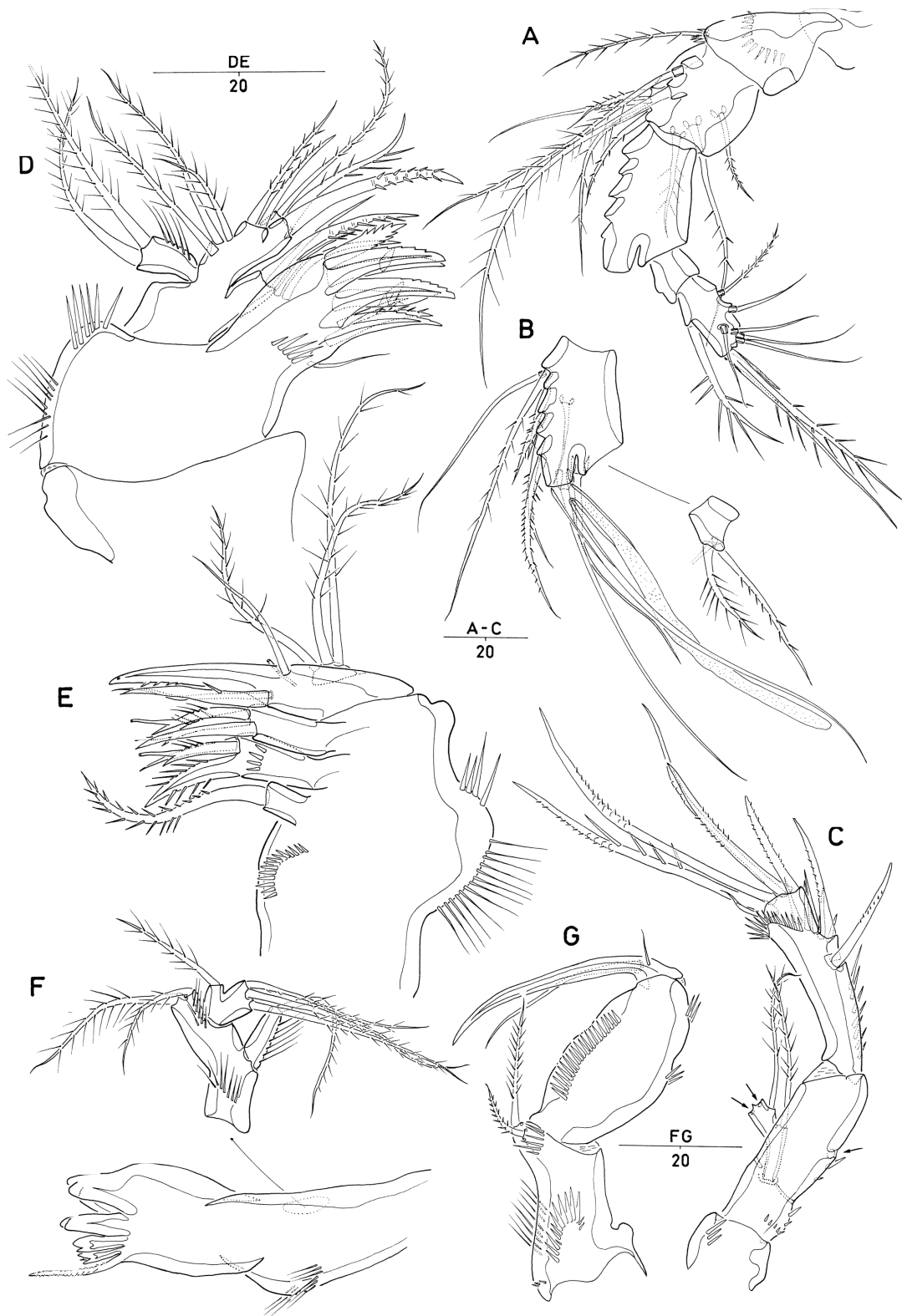


Figure 10. *Normanella bifida* sp. nov. (♀). A, antennule [armature of segments 3-4 omitted]; B, antennular segments 3-4; C, antenna [missing setae arrowed]; D, maxillule, posterior; E, maxilla; F, mandible [with palp disarticulated]; G, maxilliped.

Figure 10. *Normanella bifida* sp. nov. (♀). A, antennule [armature des articles 3-4 omise]; B, articles antennulaires 3-4; C, antenne [les flèches indiquent les soies manquantes]; D, maxillule, vue postérieure; E, maxille; F, mandibule [avec palpe détaché]; G, maxillipède.

Swimming legs P1-P4 (Figs 11A-B; 12A-C) with wide intercoxal sclerites and well developed praecoxae. Coxae and bases with anterior rows of surface spinules as figured. Exopods 3-segmented, endopods 2-segmented.

P1 (Fig. 11A) with large coxa; with long spinules along outer margin and row of spinules on anterior surface. Basis with strong, bipinnate spine and long setules along inner margin and with 1 bipinnate spine and few spinules along outer margin. Exp-1 with 1 long, bipinnate spine (1.5 times as long as outer spine of exp-2); exp-2 with 1 bipinnate, outer spine and 1 short, plumose inner seta; exp-3 with 3 pinnate spines and 2 geniculate setae; endopod 2.1 times as long as exopod, enp-1 with 1 long, plumose inner seta, enp-2 with 1 slender, denticulate claw, 1 geniculate seta, and 1 small plumose seta.

P2-P4 (Figs 11B; 12A-C). Coxa and basis with secretory pores at anterior surface and spinular rows along outer margin; basis with bipinnate spine (P2) or plumose seta (P3-P4); exp-1 and -2 with coarse frill at inner distal corner; all segments with pattern of spinules as figured; inner margins of exopod and endopod segments with long setules. P2 enp-2 long and narrow; 2.2 times longer than enp-1; 6 times longer than wide; endopod reaching to middle of exp-3. P3 enp-2 2.4 times longer than enp-1; 4 times longer than wide; endopod reaching to distal margin of exp-2; inner distal corner of enp-2 produced into short tubular extension (Fig. 12C). P4 enp-2 twice longer than enp-1; 3 times longer than wide; endopod reaching to subdistal margin of exp-2; inner distal corner of enp-2 produced into long tubular extension. Spine and setal formula as in Table 2.

Fifth pair of legs (Fig. 9C) not fused to supporting somite; rami separate. Baseoendopod forming short, outer setophore bearing plumose, basal seta and row of spinules; with 3 tube-pores along inner margin and 1 pore near boundary with exopod; endopodal lobe elongate and narrow but not extending to distal margin of exopod, with 3 bipinnate setae laterally and 2 bipinnate setae apically; rows of spinules along outer margin, and long setules along inner margin. Exopod elongate, distinctly tapering distally; with 1 terminal seta, 1 bipinnate inner seta, and 2 short, unipinnate setae, plus 2 bipinnate setae along outer margin; terminal seta arising from small cylindrical process; 1 tube-pore at anterior surface; long setules along inner margin, short spinules anteriorly, and dense long setules along proximal outer margin.

Male

Unknown.

Etymology.- The species name is derived from the Latin *bis*, meaning twice, and *findere*, meaning to split, and refers to the bifid rostrum.

Notes. - *N. bifida* can be readily distinguished from its congeners by the dorsal H-shaped pattern on the cephalic shield and the bifid rostrum. The presence of only 2 inner setae on P2 enp-2 is shared by certain other members of the *mucronata*-lineage such as *N. reducta*, *N. mucronata* sensu Griga (1963) and *N. mucronata* sensu Marinov (1977), however this species group has also lost a seta on P4 enp-2. (Table 2). A similar reduction in P2 endopod is also exhibited by both species of *Sagamiella* gen. nov. but females of this genus can be differentiated from *N. bifida* by the 6-segmented antennule and the trisetose antennary exopod. Since *N. bifida* does not share a close relationship with the second cold seep species (placed in *Sagamiella* gen. nov.; see below), this deep-sea habitat must have been colonized at least twice by Normanellidae.

(c) The *minuta*-lineage

This lineage groups the majority of species and will eventually be split up in several secondary groupings with the discovery of additional new species. One such group could comprise *N. tenuifurca* and *N. paratenuifurca*, which are characterised by the presence of long caudal rami and the loss of the internal fracture plane on seta IV. *N. incerta*, *N. porosa* and *N. obscura* all have an elongate endopodal and also seem to form a natural group. Many species in this lineage are known from females only.

Normanella minuta (Boeck, 1873)

Mesochra minuta Boeck, 1873

Type locality. - Oslofjord, Norway.

Material. - The Natural History Museum, London: (a) 1 ♀ and 1 ♂ dissected on 8 and 5 slides, respectively; 7 ♀♀, 13 ♂♂ and 1 copepodid in alcohol; among algae at extreme LWST at West Runton, Norfolk, England; coll. R. Hamond, 20 August 1993; reg. nos. 1996.647-656; (b) 1 damaged ♀ (in alcohol) collected from washings of a brittle star (*Amphipholis* sp.); Scotland (locality not identified); coll. G. Smaldon; reg. no. 1976.1096.

Female

Total body length 495 - 550 µm (n=6; \bar{x} = 533 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 147 µm. Urosome slightly narrower than prosome (Fig. 13A).

Cephalothorax with crenulate posterior margin; pleural areas well developed, rounded; posterolateral angles minutely crenate; ornamentation consisting of sensillae as illustrated in Fig. 13A-B; few weakly defined surface lamellae present dorsally and laterally but no areolation discernible. Cephalothorax without minute denticles as

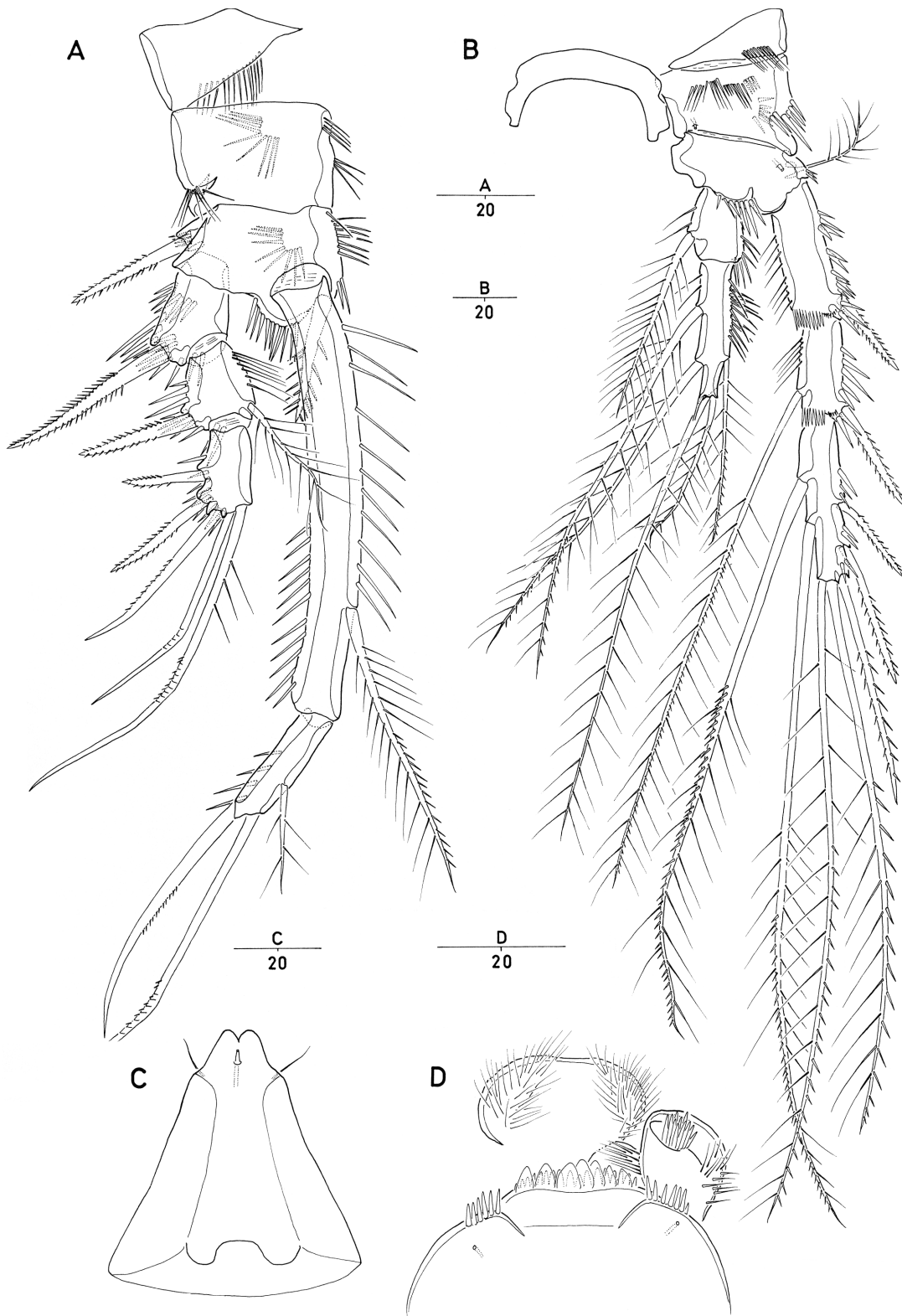


Figure 11. *Normanella bifida* sp. nov. (♀). A, P1, posterior; B, P3, anterior; C, rostrum, ventral; D, oral area, ventral.

Figure 11. *Normanella bifida* sp. nov. (♀). A, P1, vue postérieure; B, P3, vue antérieure; C, rostre, vue ventrale; D, région orale, vue ventrale.

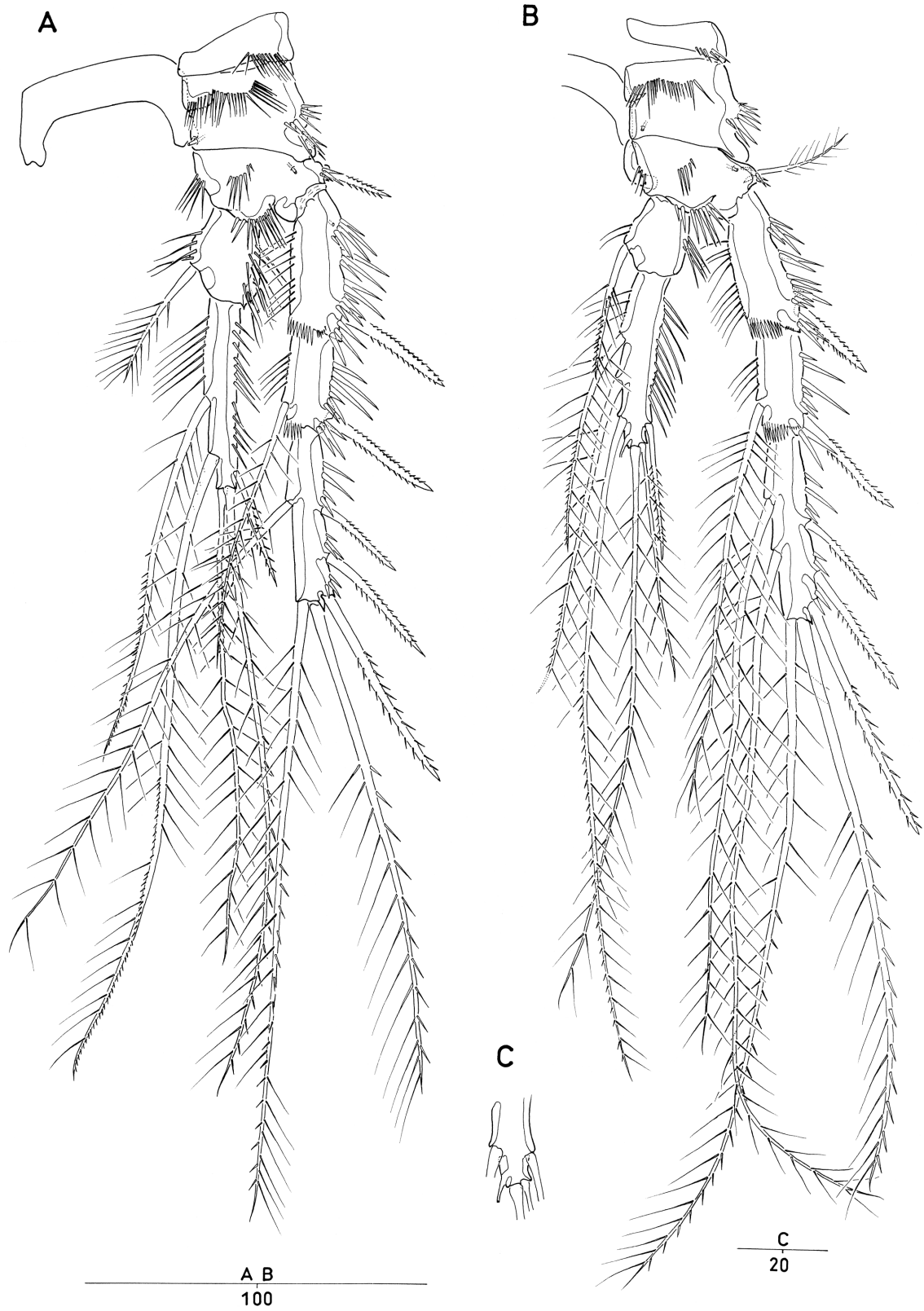


Figure 12. *Normanella bifida* sp. nov. (♀). A, P2, anterior; B, P4, anterior; C, distal area of P4 enp-2, anterior.
Figure 12. *Normanella bifida* sp. nov. (♀). A, P2, vue antérieure ; B, P4, vue antérieure ; C, région distale de P4 enp-2, vue antérieure.

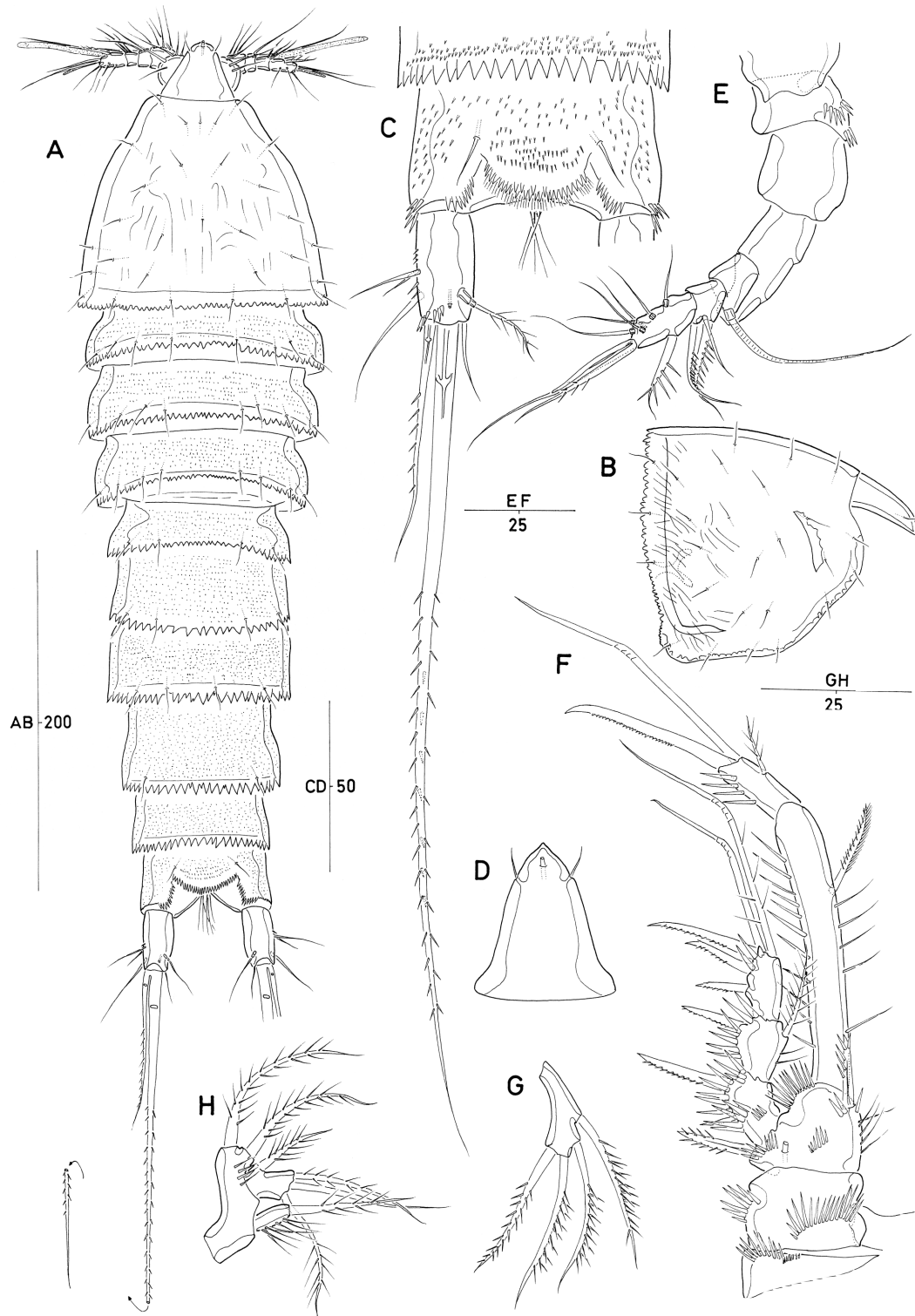


Figure 13. *Normanella minuta* (Boeck, 1873) (♀). A, Habitus, dorsal; B, cephalothorax and rostrum, lateral; C, anal somite and left caudal ramus, dorsal; D, rostrum, dorsal; E, antennule [armature of segment 1-3 omitted]; F, P1, anterior; G, antennary exopod; H, mandibular palp.

Figure 13. *Normanella minuta* (Boeck, 1873). A, habitus, vue dorsale ; B, cephalothorax et rostre, vue latérale ; C, somite anal et rame caudale gauche, vue dorsale ; D, rostre, vue dorsale ; E, antennule [armature des articles antennulaires 1-3 omise] ; F, P1, vue antérieure ; G, exopodite de l'antenne ; H, palpe mandibulaire.

found on free body somites. Rostrum triangular (Fig. 13D), with almost straight lateral margins and pointed anterior margin; with pair of tiny sensillae and a middorsal tube-pore near the apex; dorsal and ventral surface smooth, without denticles.

Pedigerous somites covered with minute spinules. All prosomites without defined hyaline frills; hind margin serrulate.

Urosome (Figs 13A; 14A) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites with surface ornamentation consisting of small spinules dorsally and laterally; hind margin distinctly serrate dorsally and laterally. Ventral hind margin of urosomites 2-4 with setular extensions; covered with large spinules laterally and fine spinules medially.

Genital double-somite (Fig. 14A) with original segmentation indicated by transverse, serrate surface ridge dorsally and dorsolaterally and short surface suture ventrolaterally; completely fused ventrally. Genital field with small copulatory pore located in median depression; gonopores fused medially forming single genital slit covered on both sides by opercula derived from sixth legs; P6 with small protuberance bearing 1 long outer seta and 1 inner seta (Fig. 14A).

Anal somite (Figs 13C; 14A) with well developed, serrulate anal operculum flanked by row of spinous processes; anal opening with fringe of long setular extensions, bordered by spinules ventrally.

Caudal rami (Figs 13C; 14A) relatively short, about twice as long as maximum width; each ramus with 3 tube-pores and 7 setae; seta I bare and shortest, closely set to bare seta II; seta III bare, positioned ventrolaterally; setae IV and V fused basally, bipinnate (seta V longest, about as long as urosomites (excl. caudal rami) combined; with internal fracture plane and slightly swollen at base); seta VI bare and small; seta VII tri-articulate at base. Each ramus with minute spinules, dorsally and ventrally; additional spinular ornamentation present along outer margins and around ventral hind margin.

Antennule (Fig. 13E) 6-segmented, segment 3 longest. Armature formula: 1-[1 pinnate], 2-[3 + 5 pinnate], 3-[3 + 5 pinnate + (1 + ae)], 4-[1], 5-[1 + 2 pinnate], 6-[7 + 1 pinnate + acrothek]. Apical acrothek consisting of small aesthetasc fused basally to 1 short slender seta and 1 pinnate seta. Segment 1 with 2 spinular rows around anterior margin. Segment 3 with aesthetasc fused basally to seta and set on distinct pedestal. Anterior elements on segments 5 and 6 clearly setiform and less coarsely pinnate than in *N. dubia*.

Antennary exopod (Fig. 13G) with 2 lateral and 2 apical bipinnate setae.

Mandibular palp (Fig. 13H) as in *N. dubia*.

P1 (Fig. 13F) with large coxa; with long spinules along outer margin and on anterior surface. Basis with stout,

bipinnate spine and few long setules along inner margin and with 1 stout bipinnate spine and few spinules along outer margin. Exp-1 with 1 long, bipinnate spine (distinctly longer than other exopodal spines); exp-2 with 1 bipinnate, outer spine and 1 plumose, inner seta (not extending beyond exp-3 distal margin); exp-3 with 3 bipinnate spines and 2 geniculate setae. Endopod 1.9 times as long as exopod, enp-1 with 1 short, bipinnate inner seta, enp-2 with 1 slender, denticulate curved claw and 1 geniculate seta apically, and 1 small plumose seta along inner margin.

P2-P4 with spine and setal formula as in *N. dubia* (Table 2). P2-P3 endopods with slender enp-2 (Fig. 14C; 30J). P2 enp-1 with tube-pore at distal outer corner.

P5 (Fig. 14B). Baseoendopod forming short, outer setophore bearing basal seta and row of spinules; with pore near boundary with exopod. Endopodal lobe short, extending to level of insertion of 2nd outer seta of exopod, with 3 bipinnate setae laterally and 2 bipinnate setae apically; rows of long spinules along outer margin, and long setules plus 3 tube-pores along inner margin. Exopod relatively elongate, distinctly tapering distally and with stepped outer margin; with 1 naked terminal seta, 1 bipinnate inner seta, and 4 pinnate setae of different length along outer margin; terminal seta arising from small cylindrical process; outer margin with numerous short spinules and long setules; inner margin with long setules.

Male

More slender than female. Body length 437 - 460 μm (n=12; \bar{x} = 446 μm ; measured from anterior margin of rostrum to posterior margin of caudal rami).

Antennule 7-segmented, with armature as in other members of the family.

P2 endopod (Fig. 30I) with modified enp-2; inner distal seta shortened by 2/3 in comparison to ♀ and bipinnate instead of plumose; outer distal seta extremely reduced, bare, about 1/4 the length of inner distal seta and slightly shorter than outer spine; outer spine shorter than in ♀.

P3 endopod (Fig. 14D-E). Enp-1 inner seta shorter than in ♀, extending to about insertion level of middle inner seta of enp-2. Enp-2 outer margin with short mucroniform process being homologous with outer spine of enp-2 of ♀; both apical setae strongly reduced with outer one much shorter than inner one, set on small lobe; inner setae not modified.

Fifth pair of legs (Fig. 14F) fused medially; defined at base. Baseoendopod with short setophore bearing outer basal seta, and weakly developed endopodal lobe with 2 bipinnate setae apically; with tube-pores near boundary with exopod and medial of innermost endopodal seta. Exopod about 2.5 times as long as maximum width; with 1 bipinnate inner seta, 1 bipinnate apical seta, and 1 bipinnate distal and

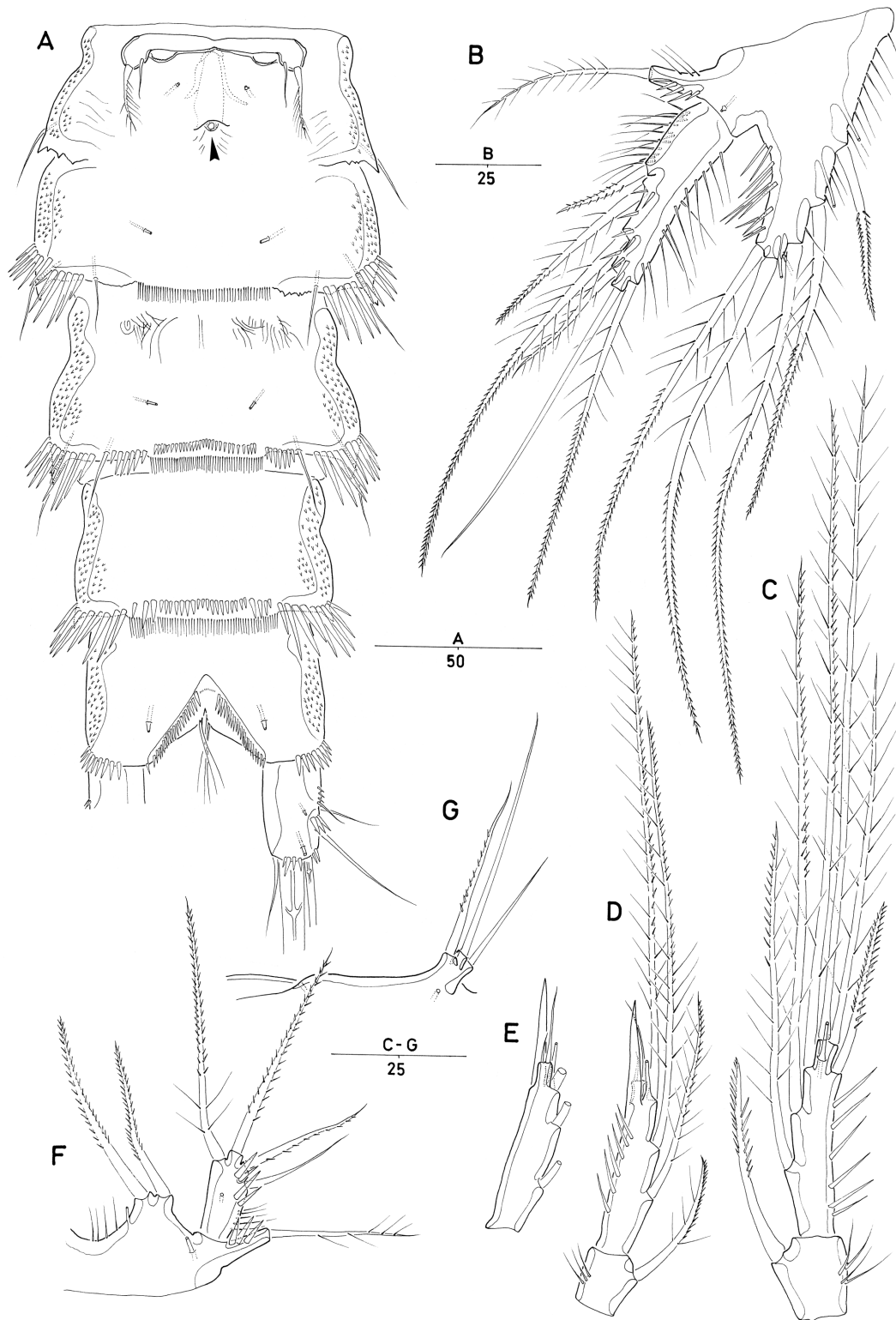


Figure 14. *Normanella minuta* (Boeck, 1873). A, urosome ♀ [excluding P5-bearing somite], ventral; B, P5 ♀, anterior; C, P3 endopod ♀, anterior; D, P3 endopod ♂, anterior; E, P3 enp-2 ♂, posterior; F, P5 ♂, anterior; G, P6 ♂.

Figure 14. *Normanella minuta* (Boeck, 1873). A, urosome ♀ [sauf le somite portant P5], vue ventrale ; B, P5 ♀, vue antérieure ; C, endopodite de P3 ♀, vue antérieure ; D, endopodite de P3 ♂, vue antérieure ; E, P3 enp-2 P3 ♂, vue postérieure ; F, P5 ♂, vue antérieure ; G, P6 ♂.

1 bare proximal seta along outer margin; with few long setules on posterior surface.

Sixth pair of legs (Fig. 14G) asymmetrical; represented on both sides by a small plate (fused to ventral wall of supporting somite along one side; articulating at base and covering gonopore along other side); outer distal corner produced into cylindrical process bearing 1 pinnate and 2 naked setae.

Notes. - *N. minuta* was the first species of the genus to be described. Boeck (1873) described it from 4 specimens collected in Oslofjord, however, it was Sars' (1909) redescription which formed the reference for subsequent identification. In view of the sympatric occurrence of several species in Norwegian waters it is almost inexplicable how Sars (1909) succeeded to identify his material with Boeck's fragmentary description of *Mesochra minuta*, which is entirely lacking in illustrations and provides information only about antennule segmentation, form and armature of P5, and caudal ramus shape. Sars (1909) described the antennule as 5-segmented but Boeck indicated that it was 6-segmented although he did not explicitly mention the number of segments. Boeck states that the third and fourth segments are fused and that the three distal ones are very short. This comparative statement clearly refers to Boeck's (1865) earlier generic diagnosis of *Mesochra* which was largely based on *M. lilljeborgi* Boeck, 1865, a species displaying a 7-segmented antennule. Klie (1950) also pointed out that the vast majority of his specimens of *N. minuta* from Helgoland possessed 6 segments in the antennule, and we found this condition also to be present in all female specimens from Norfolk. Roe (1958, 1960; E and SE Ireland - might be *N. dubia*: cf. Holmes & O'Connor (1990)), Wells (1964; S Wales) and Hamond (1969; Norfolk) only recorded specimens that had 6 clearly defined segments. This accumulating evidence strongly suggests that Sars (1909), who had only few specimens at hand, figured an aberrant individual in which the third and fourth segments had failed to separate.

N. minuta and *N. dubia* are the only NW European species which lack surface areolation on the cephalic shield and possess a 6-segmented antennule. Other characters should be taken into consideration to differentiate these species such as the form of the rostrum, P5 and caudal rami. Males of *N. minuta* differ from other known males in the strong setal reductions on the P2 endopod (Fig. 30A-C; E, I, G).

Bodin (1972) attributed with reservations an adult male from La Rochelle to *N. minuta*. The specimen differs from Sars' (1909) and our description in the shorter caudal rami (L:W ratio 1.8) and the elongate P5 exopod. Bodin described the anal operculum as smooth, however, re-examination of the original slide proved it to be weakly serrate (Bodin, pers. commn). The differences in the

endopods of both P2 (outer distal seta longer than outer spine) and P3 (enp-2 relatively truncate) also indicate that Bodin's male belongs to another species different from *N. minuta*. Pending the discovery of the female and a more complete description we include *N. minuta* (?) sensu Bodin (1972) as *species inquirenda* in the genus (Table 1). Bodin (pers. commn) confirmed that his later record of *N. minuta* from the Pertuis Charentais (Bodin, 1977) also refers to this species.

Arlt (1983) recorded *N. mucronata* and *N. cf. minuta* from the Kattegat, the latter material consisting of one female which differs from *N. minuta* in the fifth leg. The latter appears to have unusually short endopodal and exopodal lobes and supernumerary elements on the exopod. Comparison with Bodin's (1968) immature female of *N. aberrans* shows that Arlt (1983) was dealing with a copepodid V stage, possibly belonging to *N. mucronata*.

As for many other species in their monographs both Griga (1969) and Apostolov & Marinov (1988) used Sars' (1909) illustrations for their Black Sea form of *N. minuta* without presenting evidence for this conspecificity. Apostolov (1969) recorded the species from Mitschurin along the Bulgarian coast but did not provide illustrations to substantiate his identification. The only other Black Sea records are those of Griga (1961, 1963, 1964) from various localities along the Ukrainian coast. Unfortunately Griga's (1961) poor illustrations are of no help in elucidating the identity of her material so that there is at present no reason to assume that *N. minuta* occurs in the Black Sea basin. Similarly, the records from the Western Mediterranean by Monard (1935a: Tunisia), Bodin (1964: Marseille) and Soyer (1971: Banyuls-sur-Mer) were not accompanied by morphological data and remain questionable pending the discovery of material from this region.

The presumed amphiatlantic distribution pattern of *N. minuta* suggested by the records of Willey (1930), Coull (1971), Pallares (1975) and Coffin (1981) is fallacious. Coffin's *N. minuta* from the Gulf of Maine is only a name in a species list and hence indeterminable. The same can be said for Coull's (1971) record from the North Carolina continental shelf. Willey's (1930) specimens from Bermuda are distinctly smaller than the NW European populations and appear to lack the ventral spinule rows on the abdominal somites. Furthermore, Willey's illustration of the male P2 endopod shows the outer distal seta to be distinctly longer than the outer spine whereas in *N. minuta* this seta is extremely reduced and barely as long as the outer spine. Although there is little possibility of identifying any specimens from Willey's incomplete description, these differences raise grave doubts as to whether the author was observing *N. minuta*. The Bermudian form of *N. minuta* is therefore regarded as *species inquirenda* in the *minuta*-lineage (Table 1).

Pallares & Hall (1974a-b) and Pallares (1975) reported finding *N. minuta* in the Ria Deseado, Argentina and the latter presented a brief but well illustrated description. Pallares' material is clearly very similar to *N. minuta* as shown by, for example, the rostrum, caudal ramus and male P5. There are however a number of differences which suggest that the South American specimens represent a sibling species which we name *N. pallaresae* sp. nov.: (a) size: the Argentinean material is much larger (♀: 650 - 710 µm; ♂: 430 - 500 µm); (b) the ♀ antennule is 5-segmented; (c) the endopodal lobe of ♀ P5 is less slender; (d) the cephalic shield is areolated.

The published (reliable and probable) records indicate that *N. minuta* is quite common throughout NW Europe. As Lang (1936) pointed out the majority of these records have to remain unconfirmed since morphological evidence for the identification is frequently lacking and *N. minuta* is known to co-occur with other morphologically similar congeners such as *N. similis*:

Norway: Oslofjord (Boeck, 1873), south and west coast (Sars, 1909), Trondhjem Fjord (Sars, 1909), Bergen (Drzycimski, 1969). Sweden: Gullmar Fjord (Lang, 1936; 1948); Mitskären (Por, 1964b). Germany: Helgoland (Klie, 1950). Ireland: Dublin Bay (Roe, 1958), Lough Ine (Roe, 1960; Holmes, 1985). Scotland: Aberdeenshire (Hockin, 1982; Hockin & Ollason, 1981), Loch Torridon (Wells, 1965), Borders (Moore, 1973; Hicks, 1980). England: Norfolk (Hamond, 1969), Southern Celtic Sea (Gee, unpublished), Durham and Northumberland (Moore, 1973), North Yorkshire (Hicks, 1980). Wales: Pembrokeshire (Wells, 1964), Menai Strait (Geddes, 1972). Isle of Man (Moore, 1979). France: Roscoff (Monard, 1935b).

Normanella tenuifurca Sars, 1909

Type locality. - Bukken, southwest coast of Norway; about 30 m depth.

Material. - The Natural History Museum, London: 4 ♀♀ (3 ♀♀ in alcohol, 1 ♀ dissected on 7 slides) and 1 ♂ (dissected on 6 slides); Frierfjord/Langesundfjord, Norway, 99 m deep mud, coll. R. Huys, 1985; reg. nos 1998.2147-2151.

Female

Total body length 492 - 547 µm (n=4; \bar{x} = 514 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 120 µm. Urosome slightly narrower than prosome (Fig. 15A).

Cephalothorax with crenulate posterior margin; pleural areas well developed, rounded; posterolateral angles weakly serrulate (Fig. 15B); ornamentation consisting of sensillae as illustrated in Fig. 15A-B; paired longitudinal surface

lamellae present dorsally; areolation present dorsally and laterally but pattern scattered. Cephalothorax without minute denticles as found on free body somites. Rostrum triangular (Fig. 15D), with almost straight lateral margins and obtuse apex; with pair of tiny sensillae and a middorsal tube-pore near the apex; dorsal and ventral surface smooth, without denticles.

Pedigerous somites covered with minute spinules. All prosomites without defined hyaline frills; hind margin serrulate.

Urosome (Figs 15A; 16A) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites with surface ornamentation consisting of small spinules dorsally and laterally; hind margin distinctly serrate dorsally and laterally. Ventral hind margin of urosomites 2-4 with setular extensions medially and large spinules laterally; those of urosomites 3-4 also with fine spinules medially.

Genital double-somite (Figs 15A; 16A) with original segmentation indicated by transverse, serrate surface ridge dorsally and dorsolaterally and short surface suture ventrolaterally; completely fused ventrally. Genital field with small copulatory pore located in median depression; gonopores fused medially forming single genital slit covered on both sides by opercula derived from sixth legs; P6 with small protuberance bearing bipinnate outer seta and shorter bare inner seta (Fig. 16A).

Anal somite (Figs 15C; 16A) with well developed, serrulate anal operculum flanked by row of spinous processes; anal opening with fringe of long setular extensions, bordered by fine spinules ventrally.

Caudal rami (Figs 15C; 16A) long, about 4.6 times as long as maximum width; each ramus with 3 tube-pores and 7 setae; seta I bare and shortest, closely set to bare seta II; seta III bare, positioned ventrolaterally; setae IV and V fused basally, bipinnate (seta IV without fracture plane; seta V longest, about as long as urosomites (excl. caudal rami) combined; with internal fracture plane); seta VI bare and small; seta VII tri-articulate at base. Surface spinules lacking; few spinules present along proximal outer margin and around ventral hind margin.

Antennule (Fig. 15D) 5-segmented; segment 3 longest, with incomplete transverse suture along posterior margin. Armature formula as in *N. dubia* but anterior elements on segments 4 and 5 clearly setiform and less coarsely pinnate.

Antennary exopod with 2 lateral and 2 apical bipinnate setae. Mandibular palp as in *N. dubia*.

P1 as described by Sars (1909).

P2-P4 with spine and setal formula as in *N. dubia* (Table 2). P2-P3 endopods with slender enp-2 (Fig. 16B; 30F). P2 enp-1 with tube-pore at distal outer corner.

P5 (Fig. 15E). Baseopod forming short, outer setophore bearing basal seta and row of spinules; with pore

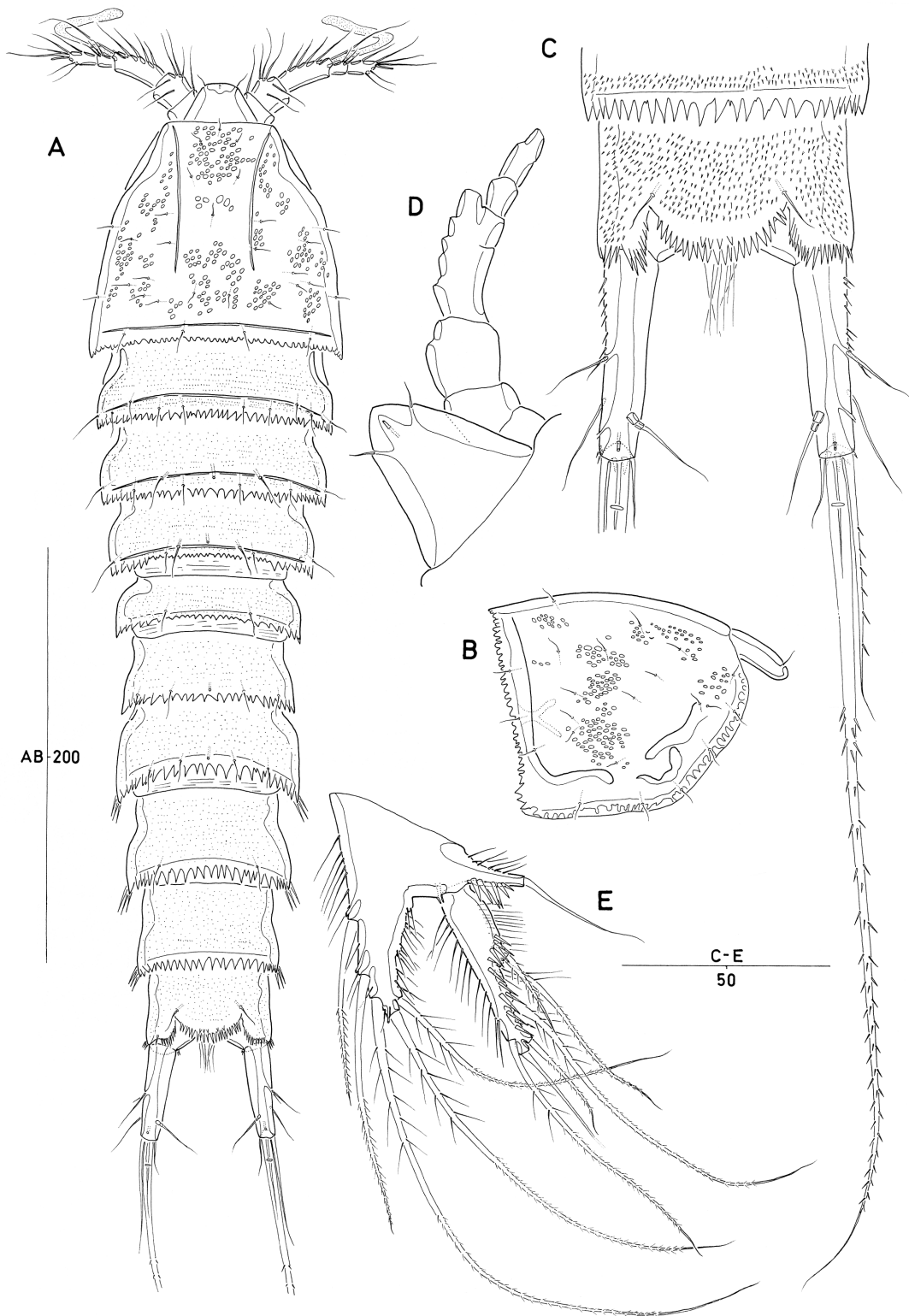


Figure 15. *Normanella tenuifurca* Sars, 1909. (♀). A, habitus, dorsal; B, cephalothorax and rostrum, lateral; C, anal somite and caudal rami, dorsal; D, rostrum and right antennule [armature omitted], dorsal; E, P5, anterior.

Figure 15. *Normanella tenuifurca* Sars, 1909. (♀). A, habitus, vue dorsale; B, cephalothorax et rostre, vue latérale; C, somite anal et rames caudales, vue dorsale; D, rostre et antennule droite [armature omise], vue dorsale; E, P5, vue antérieure.

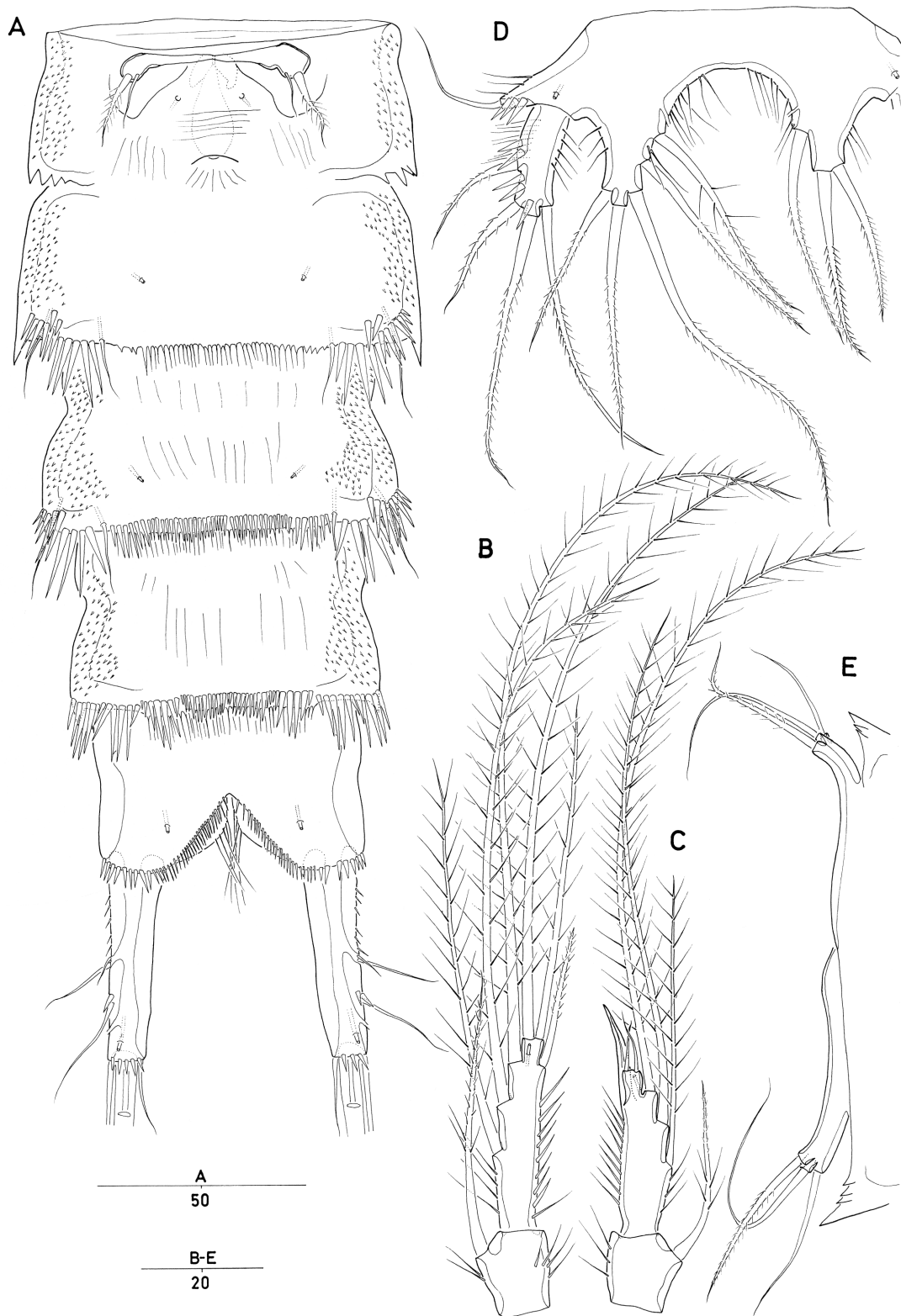


Figure 16. *Normanella tenuifurca* Sars, 1909. A, urosome ♀ [excluding P5-bearing somite], ventral; B, P3 endopod ♀, anterior; C, P3 endopod ♂, posterior; D, P5 ♂, anterior; E, P6 ♂.

Figure 16. *Normanella tenuifurca* Sars, 1909. A, urosome ♀ [sauf le somite portant P5], vue ventrale ; B, endopodite de P3 ♀, vue antérieure ; C, endopodite de P3 ♂, vue postérieure ; D, P5 ♂, vue antérieure ; E, P6 ♂.

near boundary with exopod. Endopodal lobe slender, slightly curved outwards; extending to just beyond level of insertion of 2nd outer seta of exopod; with 3 bipinnate setae laterally and 2 bipinnate setae apically; long setules along outer margin, and long setules plus 3 tube-pores along inner margin. Exopod elongate, distinctly tapering to slender distal portion; with 1 naked terminal seta, 1 bipinnate inner seta, and 4 pinnate setae of different length along outer margin; terminal seta arising from small cylindrical process; outer margin with numerous short spinules and long setules; inner margin with long setules.

Male

More slender than female. Body length 475 µm (measured from anterior margin of rostrum to posterior margin of caudal rami).

Antennule 7-segmented, with armature as in other members of the family.

P2 endopod (Fig. 30E) with modified enp-2; inner distal seta shortened, only half the length of that in ♀ and bipinnate instead of plumose; outer distal seta reduced, sparsely pinnate, about half the length of inner distal seta but distinctly longer than outer spine; outer spine slightly shorter than in ♀.

P3 endopod (Fig. 16C). Enp-1 inner seta shorter than in ♀, extending to about insertion level of inner distal seta of enp-2. Enp-2 outer margin with short mucroniform process being homologous with outer spine of enp-2 of ♀; both apical setae strongly reduced, equally long and set on small lobe; inner setae not modified.

Fifth pair of legs (Fig. 16D) fused medially; defined at base. Baseopod with short setophore bearing outer basal seta; tube-pores present near boundary with exopod and medial of innermost endopodal seta. Endopodal lobes well developed, with aberrant setation showing 5 setae on right side and 3 setae on left side. Exopod about 2.7 times as long as maximum width; with 1 bipinnate inner seta, 1 bipinnate apical seta, and 2 bipinnate setae along outer margin; with few long setules on posterior surface and along inner margin.

Sixth pair of legs (Fig. 16E) asymmetrical; represented on both sides by a small plate (fused to ventral wall of supporting somite along one side; articulating at base and covering gonopore along other side); outer distal corner produced into cylindrical process bearing 1 pinnate and 2 naked setae.

Notes. - Sars (1909) differentiated this species from *N. minuta* on the basis of the distinctive shape of the rostrum and the elongate caudal rami. We found additional differences in the cephalic shield, antennule ♀ and P2 endopod ♂. Monard (1935b) described the male from Roscoff, however, based on the size of the endopodal lobe

of the P5, we are inclined to believe that he was dealing with another species, possibly *N. paratenuifurca* sp. nov. (see below). *N. tenuifurca* appears to assume a NW European distribution with one outlier in the Mediterranean (Soyer, 1971), however it is conceivable that other, as yet unknown, species with elongate caudal rami have been identified as *N. tenuifurca* and some of the records below should be taken with caution: Norway: Bukken (Sars, 1909), Bergen (Drzycimski, 1969); Sweden: Gullmar Fjord (Lang, 1948); Wales: Pembrokeshire (Crothers, 1966); England: River Exe (Wells, 1963), Whitstable (El-Maghraby & Perkins, 1956); France: Brittany (Monard, 1935b; Bodin & Le Guellec, 1992), La Rochelle (Bodin, 1977).

Normanella incerta Lang, 1934

Type locality. - Perseverance Harbour, Campbell Island, 40 m depth.

Note. - This species is known from a single female specimen only and has not been recorded again since, except for Bodin & Le Guellec (1992) who reported it from North Brittany. It is conceivable that the latter record refers to *N. obscura* sp. nov. which shows a superficial resemblance in the P5 and caudal rami. Lang (1934) pointed out the similarity in rostrum shape between *N. tenuifurca* and *N. incerta*.

Normanella serrata Por, 1959

This species was originally described from the Romanian Black Sea coast (Por, 1959) based on material collected in various localities between 28 and 56 m depth. The original description in Romanian was later translated (without figures) in Por (1964a). According to Por the species displays gross morphometric variability in body size (♀: 0.48 - 0.60 mm), P5 exopod ♀ (L:W ratio 3.0 - 5.2) and caudal ramus (L:W ratio 2.0 - 3.7 in ♀♀; 4.8 in 1 ♂!). We find it hard to believe that such wide range of variability can be exhibited by a single species since our observations of all other species point to the opposite trend, suggesting that an amalgamate of species must have been represented in Por's material. Por suggested a relationship with *N. semitica* and *N. quarta* on the basis of the 6-segmented antennule in the ♀, however the elongate caudal rami and ♀ P5 exopod also led him to recognise a certain affinity with *N. tenuifurca* and to a lesser extent, *N. minuta*. The author found additional evidence for the former relationship in the serrulate posterior border of the body somites, a character referred to by Lang (1948) as «juvenile» in both *N. semitica* and *N. quarta*. It is obvious that Por (1959) placed too much importance on this feature since a denticulate or serr(ul)ate border is diagnostic for all Normanellidae. Other Black Sea records of the species include those of Marinov (1974, 1978).

The next illustrated reference to *N. serrata* is that by Božić (1964) who reported a single female from La Réunion, Indian Ocean. This specimen differed from the Black Sea material by its smaller size (0.4 mm), the shorter caudal rami (only twice as long as wide), the wide anal operculum and different relative proportions of the P5 exopod and baseoendopod. Božić (1964) also remarked on the long caudal ramus setae which had not been figured at their full length by Por (1959). The antennule was interpreted as 6-segmented although the boundary between segments 3 and 4 is incomplete. Božić maintained that the P2-P4 displayed the same setal formula as in *N. minuta*, however his drawing of the P3 endopod does not show an inner seta on the proximal segment; this must be based on an error. The author provisionally identified his specimen as *N. serrata*, considering the differences in the caudal rami as part of the wide variability already reported for this species (Por, 1959). The suite of differences outlined above in conjunction with the widely disjunct distribution of both records raise serious doubts about their conspecificity and hence we prefer to consider Božić's (1964) form as *species inquirenda* in the *minuta*-lineage.

Marinov & Apostolov (1985) reported finding 5 ♀♀ in the eastern Atlantic off the Spanish Sahara and ascribed them with reservations to *N. serrata*. They recorded differences with Por's (1959) description in the length of the P5 endopodal lobe, the shape of the P5 exopod and the caudal ramus which is distinctly shorter but has longer terminal setae. The authors do not mention the segmentation of the antennule nor do they present any information about the rostrum. They point out the similarity in size between their material and Božić's (1964) specimen from La Réunion and further maintain that the P5 is also similar. Although there appears to be a resemblance in the caudal ramus between the latter and the Spanish Sahara material, the P5 is in our opinion clearly different. Most significant is the shape of the exopod which has a distinct step in the outer margin, forming a kind of socket for the 2 closely set proximal setae. This condition is identical to the P5 described herein for *N. sarsi* (Fig. 21E) and there is little doubt that both species are very closely related (if not conspecific). The only marked difference that can be detected is the size of the endopodal lobe of the P5 which is shorter than the exopod in Marinov & Apostolov's females but slightly longer in *N. sarsi*.

The record of *N. serrata* from the U.S. Virgin Islands (Hartzband & Hummon, 1974) is indeterminable and probably false.

Normanella porosa Noodt, 1964

Type locality. - Egypt: Red Sea off Ghardaqa; coralline sand; 2-4 m depth.

Note. - Noodt (1964) established this species on a number of dubious grounds: (1) shape of the rostrum: there is no doubt that the rostrum is clearly foreshortened in Noodt's illustration and does not represent the true shape; (2) P1 exp-2 without inner seta: Noodt referred to the similar absence of this seta in *N. dubia* and *N. mucronata* var. *quinquesetosa* but these accounts have proven erroneous; (3) presence of additional little seta on P5 baseoendopod: it is clear that Noodt was referring to the tube-pore which is found in a similar position in other congeners; (4) presence of only 1 well developed terminal seta on the caudal ramus (i.e. seta V): the full complement of setae (except seta I) is shown in Noodt's drawing and the relative difference in length between setae IV and V is quite similar to that found in the majority of *Normanella* species. Finally, Noodt (1964) also overlooked the small inner seta on P1 exp-2 (no reference is made to this absence).

N. porosa is undoubtedly very close to *N. obscura* from England. Unfortunately, both species are known from females only and detailed information on the sexual dimorphism would have facilitated differentiation. Pending a redescription of *N. porosa*, they can be separated on the basis of the areolated pattern on the cephalic shield which is much more developed in the latter, and the P5 which has a more slender endopodal lobe and a flask-shaped exopod in *N. obscura*.

Normanella paratenuifurca sp. nov.

Type locality. - Off Norfolk coast, 53°10.34' N, 00°56.34' E; 12-13 m depth; fine sand with high content of dark grey silt and finely-ground shell-fragments.

Material. - The Natural History Museum, London: holotype ♀ (dissected on 9 slides; reg. no. 1998.2116) and paratypes (9 ♀♀ in alcohol; 1 ♂ dissected on 6 slides; reg. nos 1998.2117-2126); originally labelled as *Normanella tenuifurca*; coll. R. Hamond, 06 May 1992.

Female

Total body length 520 - 603 µm (n=10; \bar{x} = 569 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Body more slender than in *N. tenuifurca*. Largest width measured at posterior margin of cephalic shield: 125 µm. Urosome narrower than prosome (Fig. 17A).

Cephalothorax with serrulate posterior margin; pleural areas well developed, rounded; posterolateral angles minutely crenate; ornamentation consisting of sensillae as illustrated in Fig. 17A-B; paired longitudinal surface lamellae present dorsally; areolated pattern present dorsally and laterally and different from that of *N. tenuifurca* in lateral aspect. Cephalothorax without minute denticles as found on free body somites. Rostrum triangular (Fig. 18B),

with almost straight lateral margins and pointed anterior margin; with pair of tiny sensillae and both midventral and middorsal tube-pore near the apex; dorsal surface striated, without denticles.

Pedigerous somites covered with minute spinules. All prosomites without defined hyaline frills; hind margin serrulate.

Urosome (Figs 17A; 18A) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites with surface ornamentation consisting of small spinules dorsally and laterally; ventral surface with irregular pattern of fine lamellae; hind margin distinctly serrate dorsally and laterally. Ventral hind margin of urosomites 2-4 with setular extensions medially and large spinules laterally; those of urosomites 3-4 also with fine spinules medially.

Genital double-somite (Figs 17A; 18A) with original segmentation indicated by transverse, serrate surface ridge dorsally and dorsolaterally and short surface suture ventrolaterally; completely fused ventrally. Genital field with small copulatory pore located in median depression; gonopores fused medially forming single genital slit covered on both sides by opercula derived from sixth legs; P6 with small protuberance bearing 1 bipinnate outer seta and 1 bare inner seta which is much smaller than in *N. tenuifurca* (Fig. 18A).

Anal somite (Figs 17C; 18A) with well developed, deeply serrate anal operculum flanked by row of spinous processes; anal opening with fringe of long setular extensions, bordered by fine spinules ventrally.

Caudal rami (Figs 17C; 18A) long, just over 3 times as long as maximum width; each ramus with 2 tube-pores and 7 setae; seta I bare and shortest, closely set to bare seta II; seta III bare, positioned ventrolaterally; setae IV and V fused basally, bipinnate (seta IV without fracture plane; seta V longest, about as long as urosomites (excl. caudal rami) combined; with internal fracture plane); seta VI bare and small; seta VII tri-articulate at base. Each ramus with minute spinules, dorsally and ventrally; sparse additional spinular ornamentation present along outer margin (around base of setae I-II), inner margin (near base of seta VII) and around ventral hind margin.

Antennule (Fig. 18B) 5-segmented, segment 3 longest (without vestigial suture as in *N. tenuifurca*). Armature formula as in *N. dubia* but anterior elements on segments 4 and 5 clearly setiform and less coarsely pinnate.

Antennary exopod with 2 lateral and 2 apical bipinnate setae. Mandibular palp (Fig. 18C) as in *N. dubia*.

P1 as in *N. tenuifurca*. P2-P4 with spine and setal formula as in *N. dubia* (Table 2). P2-P3 endopods with slender enp-2 (Fig. 17D; 30D).

P5 (Fig. 17E). Baseoendopod forming short, outer setophore bearing basal seta and row of spinules; with pore

near boundary with exopod. Endopodal lobe short, extending to level of insertion of 2nd outer seta of exopod, with 3 bipinnate setae laterally and 2 bipinnate setae apically; rows of long spinules and spinules along outer margin, and long setules plus 2 tube-pores along inner margin. Exopod relatively elongate, tapering distally but more gradually than in *N. tenuifurca*; with 1 naked terminal seta, 1 bipinnate inner seta, and 4 pinnate setae of different length along outer margin; terminal seta arising from small cylindrical process; outer margin with numerous short spinules and long setules; inner margin with long setules.

Male

More slender than female. Body length 495 µm (measured from anterior margin of rostrum to posterior margin of caudal rami).

Antennule 7-segmented, with armature as in other members of the family.

P2 endopod (Fig. 30C) with modified enp-2 as in *N. tenuifurca* but inner distal seta comparatively shorter.

P3 endopod (Fig. 18F). Enp-2 outer margin with long mucroniform process (longer than in *N. tenuifurca*), being homologous with outer spine of enp-2 of ♀; both apical setae strongly reduced with outer one shorter than inner one, set on small lobe; inner setae not modified.

Fifth pair of legs (Fig. 18D) fused medially; defined at base. Baseoendopod with short setophore bearing outer basal seta, and weakly developed endopodal lobe with 2 bipinnate setae apically; tube-pore present near boundary with exopod and medial of innermost endopodal seta. Exopod about 2.3 times as long as maximum width; with 1 bipinnate inner seta, 1 bipinnate apical seta, and 2 bipinnate setae along outer margin; with few long setules on posterior surface.

Sixth pair of legs (Fig. 18E) asymmetrical; represented on both sides by a small plate (fused to ventral wall of supporting somite along one side; articulating at base and covering gonopore along other side); outer distal corner produced into cylindrical process bearing 1 pinnate and 2 naked setae.

Etymology. - The Greek suffix *para-*, meaning by the side of, near, alludes to the close resemblance with *N. tenuifurca*.

Notes. - *N. paratenuifurca* sp. nov. has thus far been recorded only from Norfolk but we suspect that several of the British records of *N. tenuifurca* as well as the Roscoff male illustrated by Monard (1935b) also pertain to this species. Females of both species can be separated on the basis of the rostrum, antennule, caudal ramus length and shape of P5 exopod. The length of the mucroniform process on P3 enp-2 and the shape of the P5 endopodal lobe serve to distinguish males.

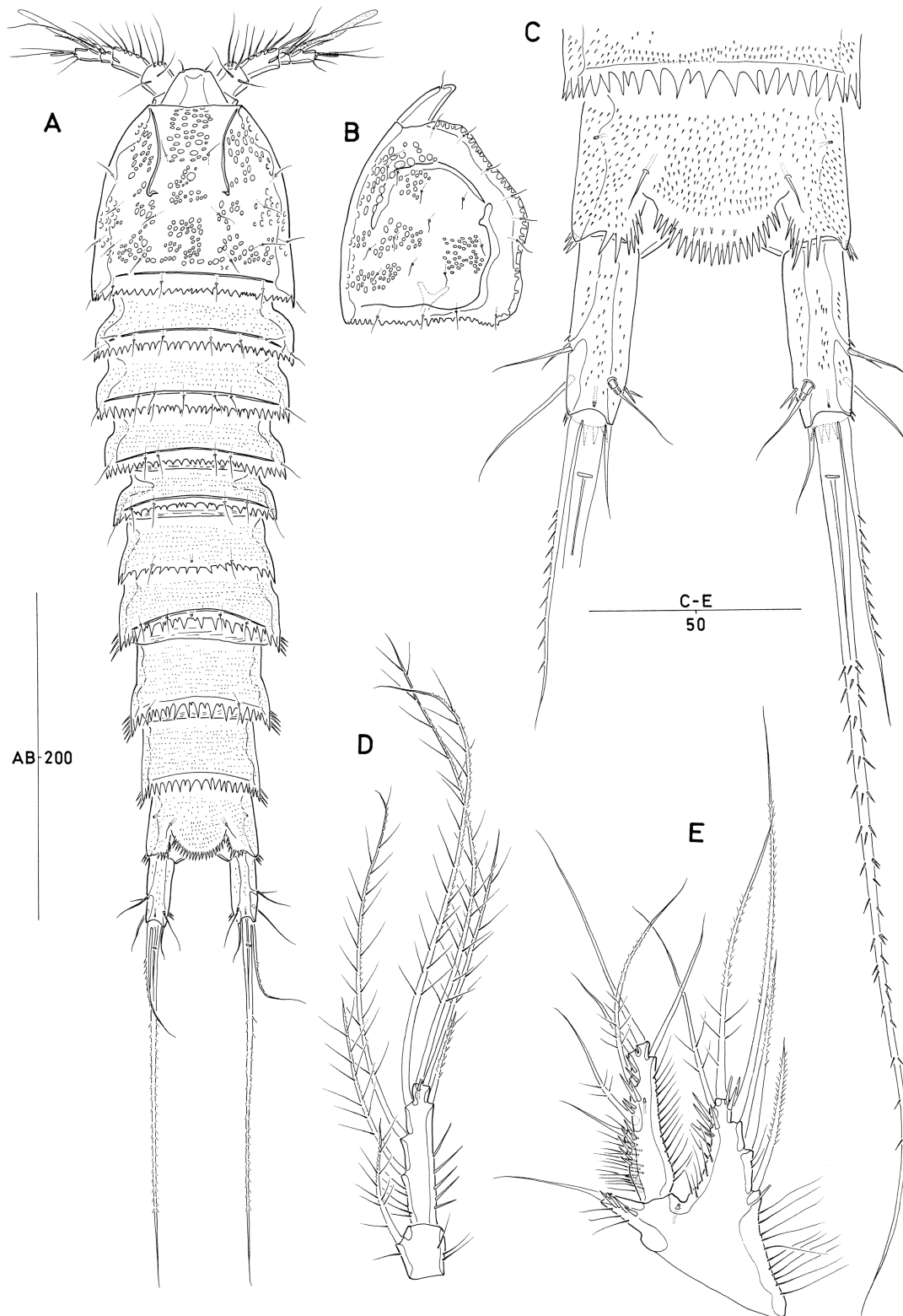


Figure 17. *Normanella paratenuifurca* sp. nov. (♀). A, habitus, dorsal; B, cephalothorax and rostrum, lateral; C, anal somite and caudal rami, dorsal; D, P3 endopod, anterior; E, P5, anterior.

Figure 17. *Normanella paratenuifurca* sp. nov. (♀). A, habitus, vue dorsale ; B, cephalothorax et rostre, vue latérale ; C, somite anal et rames caudales, vue dorsale ; D, endopodite de P3, vue antérieure ; E, P5, vue antérieure.

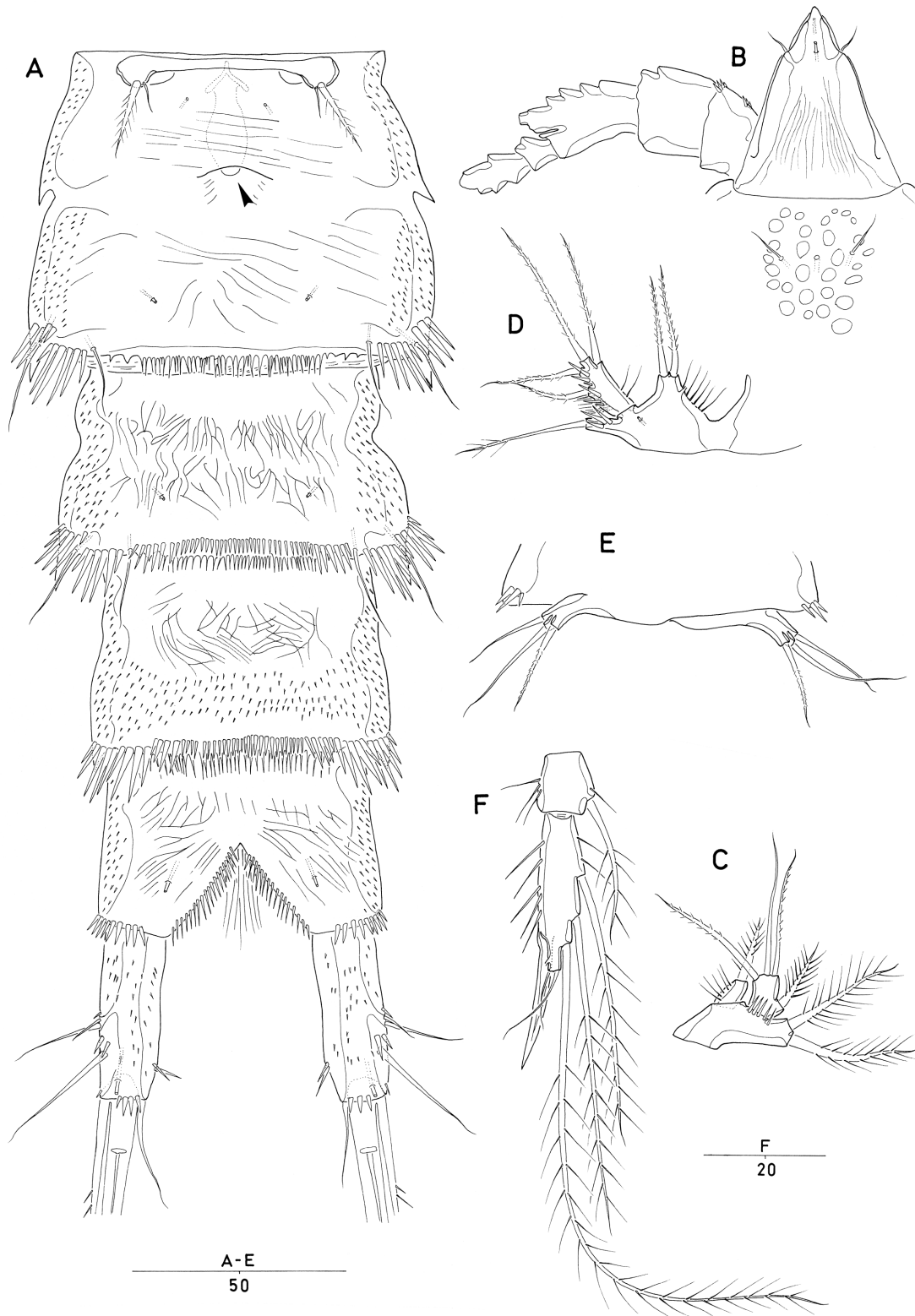


Figure 18. *Normanella paratenuifurca* sp. nov. A, urosome ♀ [excluding P5-bearing somite], ventral; B, rostrum and left antennule ♀ [armature omitted], dorsal; C, mandibular palp ♀; D, P5 ♂, anterior; E, P6 ♂; F, P3 endopod ♂, posterior.

Figure 18. *Normanella paratenuifurca* sp. nov. A, urosome ♀ [sauf le somite portant P5], vue ventrale ; B, rostre et antennule gauche ♀ [armature omise], vue dorsale ; C, palpe mandibulaire ♀ ; P5 ♀, vue antérieure; E, P6 ♂ ; F, endopodite de P3 ♂, vue postérieure.

Normanella obscura sp. nov.

Type locality. - Eddystone Lighthouse, off Devon coast, England.

Material. - The Natural History Museum, London: (a) holotype ♀ (dissected on 8 slides; reg. no. 1998.2493); paratypes are 1 ♀ dissected on 8 slides (reg. no. 1998.2494), 5 ♀♀ in alcohol (reg. nos 1998.2495-2499); originally labelled as *Normanella dubia*; coll. Norman & T. Scott, 31 August 1903; (b) 1 damaged ♀ (in alcohol; reg. no. 1998.2500); Exmouth; originally labelled as *Normanella dubia* var.; coll. Norman & T. Scott, 09 June 1884.

Female

Total body length 490 - 595 µm (n=5; x = 552 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 117 µm. Urosome slightly narrower than prosome (Fig. 19A).

Cephalothorax with crenulate posterior margin; pleural areas well developed, rounded; posterolateral angles minutely crenulate; ornamentation consisting of sensillae as illustrated in Fig. 19A-B; paired longitudinal surface lamellae present dorsally; areolated pattern weakly developed, consisting of scattered areolated patches dorsally and laterally. Cephalothorax without minute denticles as found on free body somites. Rostrum triangular (Fig. 19E), with almost straight lateral margins and pointed apex; with pair of tiny sensillae and both midventral and middorsal tube-pore near the apex; dorsal surface finely striated, ventral surface smooth, without denticles.

Pedigerous somites covered with minute spinules. All prosomites without defined hyaline frills; hind margin serrulate.

Urosome (Figs 19A; 20A) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites with surface ornamentation consisting of small spinules dorsally and laterally; hind margin distinctly serrate dorsally and laterally. Ventral hind margin of urosomites 2-4 with setular extensions medially and large spinules laterally; those of urosomites 3-4 also with fine spinules medially.

Genital double-somite (Fig. 19A; 20A) with original segmentation indicated by transverse, serrate surface ridge dorsally and dorsolaterally and short surface suture ventrolaterally; completely fused ventrally. Genital field with small copulatory pore located in median depression; gonopores fused medially forming single genital slit covered on both sides by opercula derived from sixth legs; P6 with small protuberance bearing pinnate outer seta and minute, naked inner seta (Fig. 20A).

Anal somite (Figs 19C; 20A) with well developed, serrate anal operculum flanked by row of spinous processes;

anal opening with fringe of long setular extensions, bordered by spinules ventrally.

Caudal rami (Figs 19C; 20A) relatively short, about 1.9 times as long as maximum width; each ramus with 2 tube-pores and 7 setae; seta I bare and shortest, closely set to bare seta II; seta III bare, positioned ventrolaterally; setae IV and V fused basally, bipinnate (seta IV with fracture plane; seta V longest, slightly longer than urosomites (excl. caudal rami) combined; with internal fracture plane); seta VI bare and small; seta VII tri-articulate at base. Each ramus with minute spinules, dorsally and ventrally; sparse additional spinular ornamentation present along inner and outer margins and around ventral hind margin.

Antennule (Fig. 19D) 5-segmented, segment 3 longest. Armature formula as in *N. dubia* but anterior elements on segments 4 and 5 clearly setiform and less coarsely pinnate.

Antennary exopod and mandibular palp as in *N. dubia*.

P1 (Fig. 19F) with large coxa; with long spinules along outer margin and on anterior surface. Basis with stout, bipinnate spine and few long setules along inner margin and with 1 stout bipinnate spine and few spinules along outer margin. Exp-1 with 1 long, bipinnate spine (distinctly longer than other exopodal spines); exp-2 with 1 bipinnate, outer spine and 1 plumose, inner seta (extending to exp-3 distal margin); exp-3 with 3 bipinnate spines and 2 geniculate setae. Endopod 2.2 times as long as exopod, enp-1 with 1 short, bipinnate inner seta, enp-2 with 1 slender, denticulate curved claw and 1 geniculate seta apically, and 1 small plumose seta along inner margin.

P2-P4 with spine and setal formula as in *N. dubia* (Table 2). P2-P3 endopods as in Fig. 20B-C; P2 enp-1 with tube-pore at distal outer corner.

P5 (Fig. 19G). Baseoendopod forming short, outer setophore bearing basal seta and row of spinules; with pore near boundary with exopod. Endopodal lobe long and very slender, extending to just beyond apex of exopod; with 3 bipinnate setae laterally and 2 bipinnate setae apically; rows of long setules along outer margin, and long setules plus 3 tube-pores along inner margin. Exopod flask-shaped, distinctly tapering distally; with 1 naked terminal seta, 1 bipinnate inner seta, and 4 pinnate setae of different length along outer margin; terminal seta arising from small cylindrical process; outer margin with few short spinules and numerous long setules; inner margin with long setules.

Male

Unknown.

Etymology. - The species name is derived from the Latin *obscurus*, meaning covered, obscure, and refers to its discovery among the NHM material that was registered as *N. dubia*.

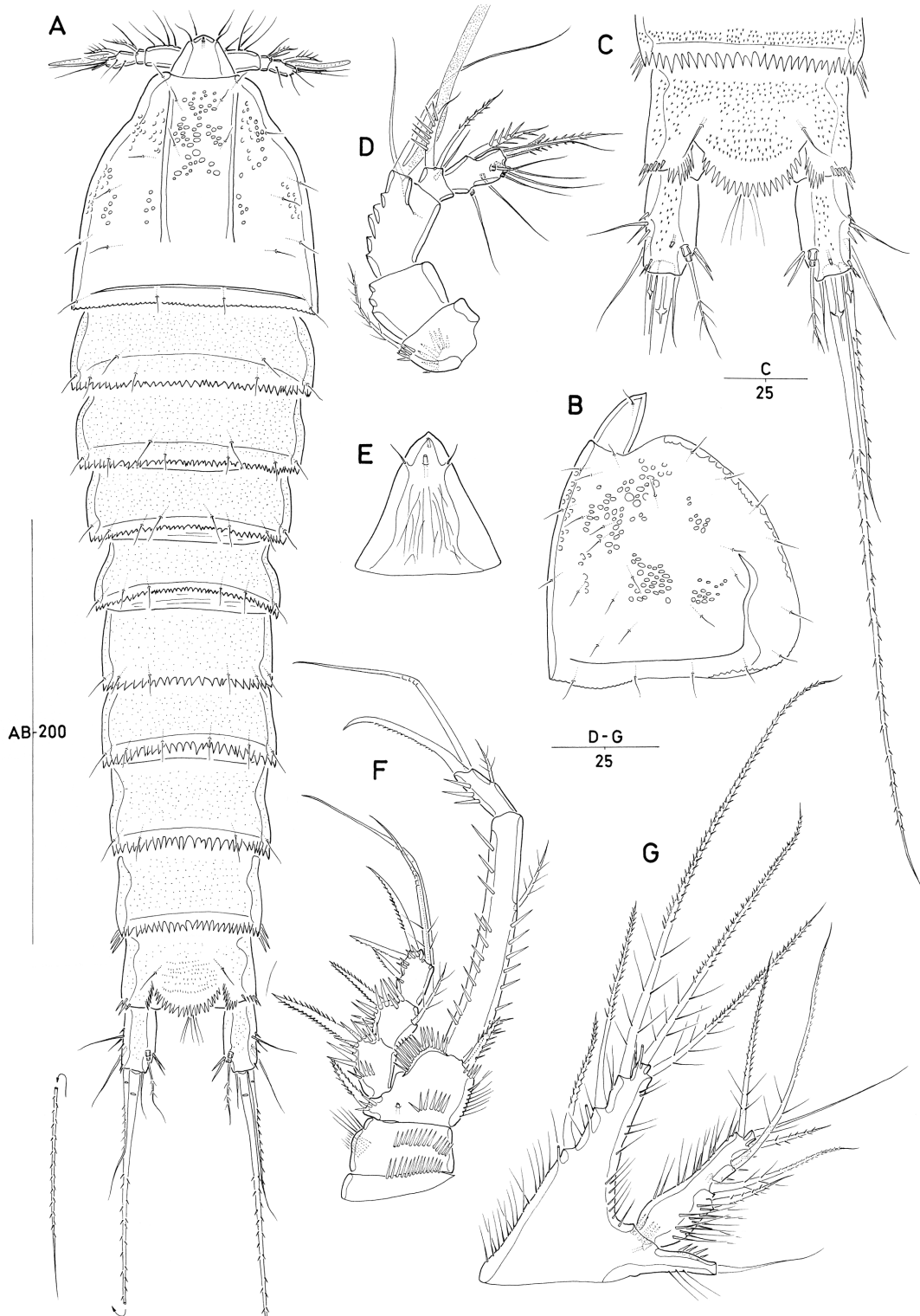


Figure 19. *Normanella obscura* sp. nov. (♀). A, habitus, dorsal; B, cephalothorax and rostrum, lateral; C, anal somite and caudal rami, dorsal; D, antennule, ventral [armature of segment 2-3 omitted]; E, rostrum, dorsal; F, P1, anterior; G, P5, anterior.

Figure 19. *Normanella obscura* sp. nov. A, habitus, vue dorsale ; B, cephalothorax et rostre, vue latérale ; C, somite anal et rames caudales, vue dorsale ; D, antennule, vue ventrale [armature des articles antennulaires 2-3 omise] ; E, rostre, vue dorsale ; F, P1, vue antérieure ; G, P5, vue antérieure.

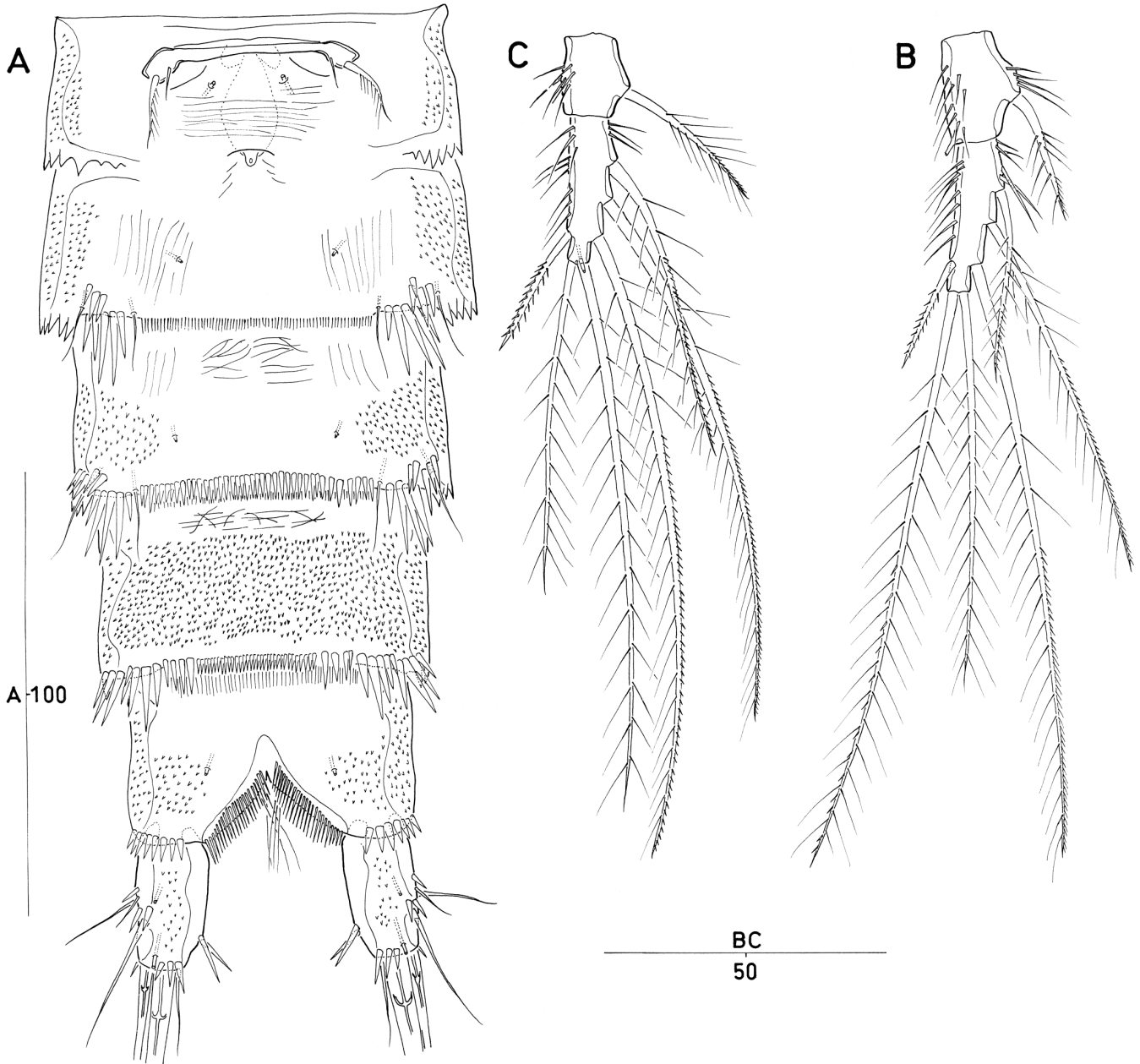


Figure 20. *Normanella obscura* sp. nov. (♀). A, urosome [excluding P5-bearing somite], ventral; B, P2 endopod, anterior; C, P3 endopod, anterior.

Figure 20. *Normanella obscura* sp. nov. (♀). A, urosome ♀ [sauf le somite portant P5], vue ventrale ; B, endopodite de P2, vue antérieure ; C, endopodite de P3, vue antérieure.

Note. - The species is most closely related to the Red Sea species *N. porosa* (see above). Bodin & Le Guellec's (1992) record of *N. incerta* from North Brittany may be based on *N. obscura*.

(d) The *sarsi*-lineage.

This lineage comprises *N. sarsi* sp. nov. and possibly a second species from off the Spanish Sahara, erroneously identified as *N. serrata* by Marinov & Apostolov (1985). Both species can be readily identified by the ♀ P5 exopod which shows a distinct notch on the outer margin, marking the transition between the broad proximal half and the slender distal half, and coinciding with the insertion site of 2 closely set proximal setae.

Normanella sarsi sp. nov.

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

Material. - The Natural History Museum, London: Holotype ♀ dissected on 7 slides (reg. no. 1998.2465); paratypes are 26 ♀♀ in alcohol (reg. nos 1998.2467-2492) and 1 ♂ dissected on 6 slides (reg. no. 1998.2466); coll. R. Huys, 1985.

Female

Total body length 563 - 627 µm (n=10; \bar{x} = 595 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 140 µm. Urosome slightly narrower than prosome (Fig. 21A).

Cephalothorax with weakly crenulate posterior margin; pleural areas well developed, rounded; posterolateral angles minutely crenate; ornamentation consisting of sensillae as illustrated in Fig. 21A; paired longitudinal lamellae present dorsally and laterally; areolated pattern discernible laterally and dorsally. Cephalothorax without minute denticles as found on free body somites. Rostrum triangular (Fig. 21C), with straight lateral margins and rounded anterior margin provided with apical protrusion; with pair of tiny sensillae and a middorsal tube-pore near the apex; dorsal and ventral surface smooth, without denticles.

Pedigerous somites covered with minute spinules. All prosomites without defined hyaline frills; hind margin serrulate.

Urosome (Figs 21A; 22A) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites with surface ornamentation consisting of small spinules dorsally and laterally; hind margin distinctly serrate dorsally and laterally. Ventral hind margin of urosomites 2-4 with setular extension medially and large spinules laterally; those of urosomites 3-4 also with fine or minute spinules medially.

Genital double-somite (Figs 21A; 22A) with original segmentation indicated by transverse, serrate surface ridge dorsally and dorsolaterally and short surface suture ventrolaterally; completely fused ventrally. Genital field with small copulatory pore located in median depression; gonopores fused medially forming single genital slit covered on both sides by opercula derived from sixth legs; P6 with small protuberance bearing 1 pinnate outer seta and 1 smaller naked, inner seta (Fig. 22A).

Anal somite (Figs 21B; 22A) with well developed, deeply serrate anal operculum flanked by row of spinous processes; anal opening with fringe of long setular extensions, bordered by spinules ventrally.

Caudal rami (Figs 21B; 22A) moderately long, about 2.4 times as long as maximum width; each ramus 7 setae; seta I bare and shortest, closely set to bare seta II; seta III bare, positioned ventrolaterally; setae IV and V fused basally, bipinnate (seta IV with fracture plane; seta V longest, longer than urosomites 3-5 and caudal rami combined; with internal fracture plane and slender at base; seta VI bare and small; seta VII tri-articulate at base. Each ramus with minute spinules, dorsally and ventrally; sparse additional spinular ornamentation present around bases of setae I and VII and ventral hind margin.

Antennule (Fig. 21C) 5-segmented, segment 3 longest. Armature formula as in *N. dubia* but anterior elements on segments 4 and 5 clearly setiform and less coarsely pinnate.

Antennary exopod and mandibular palp as in *N. dubia*.

P1 (Fig. 21D) with large coxa; with few short spinules along outer margin and long spinules on anterior surface. Basis with stout, bipinnate spine and few long setules along inner margin and with 1 stout bipinnate spine and few spinules along outer margin. Exp-1 with 1 long, bipinnate spine (distinctly longer than other exopodal spines); exp-2 with 1 bipinnate, outer spine and 1 plumose, inner seta (not extending to exp-3 distal margin); exp-3 with 3 bipinnate spines and 2 geniculate setae. Endopod twice as long as exopod, enp-1 with 1 short, bipinnate inner seta, enp-2 with 1 slender, denticulate curved claw and 1 geniculate seta apically, and 1 small plumose seta along inner margin.

P2-P4 with spine and setal formula as in *N. dubia* (Table 2). P2-P3 endopods with slender enp-2 (Figs 22B; 30H). P2 enp-1 with tube-pore at distal outer corner.

P5 (Fig. 21E). Baseopod forming short, outer setophore bearing basal seta and row of spinules; with pore near boundary with exopod. Endopodal lobe long, extending beyond apex of exopod, with 3 bipinnate setae laterally and 2 bipinnate setae apically; rows of fine spinules along outer margin, and long setules plus 3 tube-pores along inner margin. Exopod relatively compact, with distinct step halfway forming socket for 2 closely set setae; distal half much narrower; with 1 naked terminal seta, 1 bipinnate inner seta, and 1 naked plus 3 pinnate setae of different

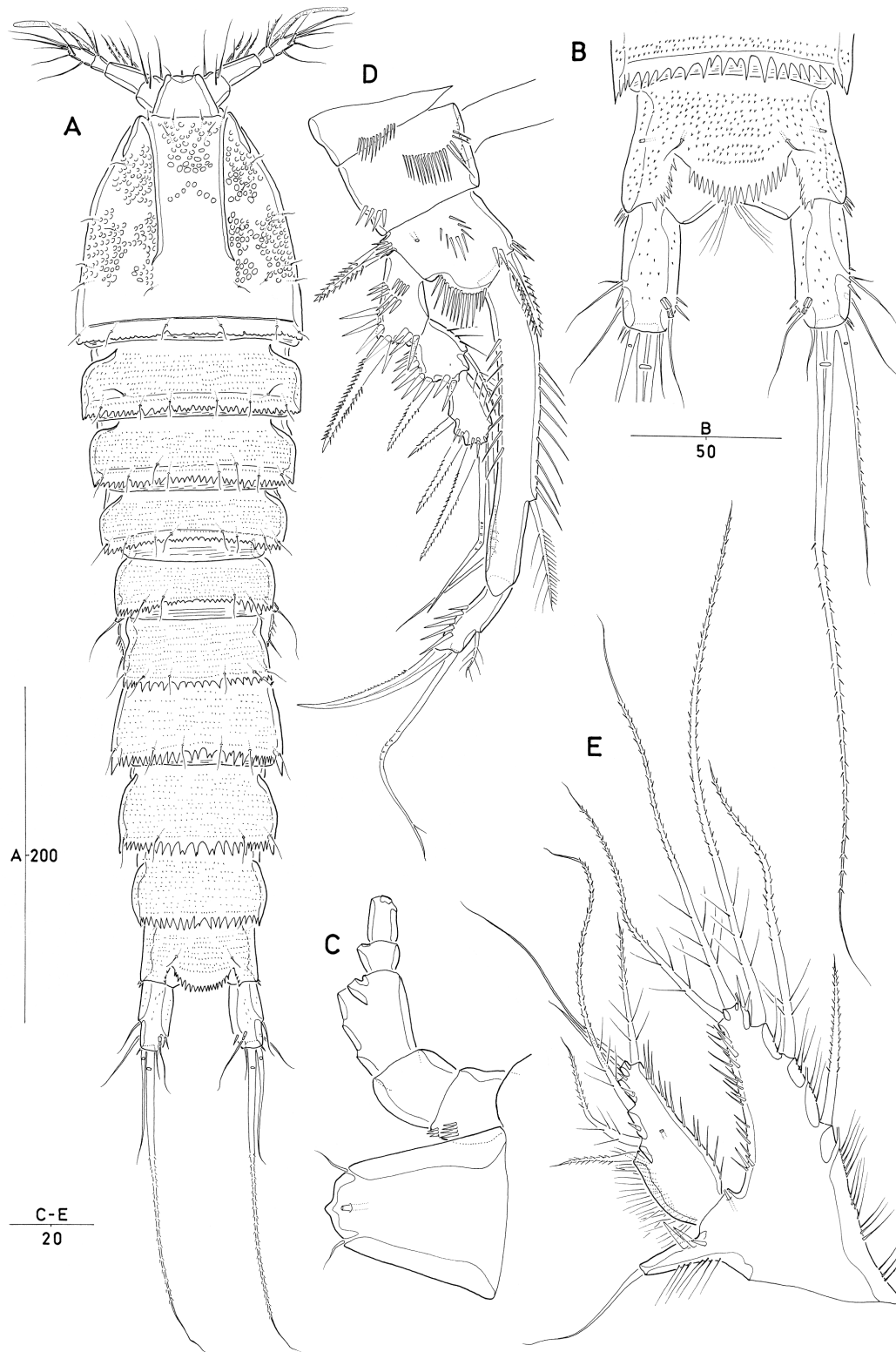


Figure 21. *Normanella sarsi* sp. nov. (♀). A, habitus, dorsal; B, anal somite and caudal rami, dorsal; C, rostrum and right antennule [armature omitted], dorsal; D, P1, anterior; E, P5, anterior.

Figure 21. *Normanella sarsi* sp. nov. (♀). A, habitus, vue dorsale ; B, somite anal et rames caudales, vue dorsale ; C, rostre et antennule droite [armature omise], vue dorsale ; D, P1, vue antérieure ; E, P5, vue antérieure.

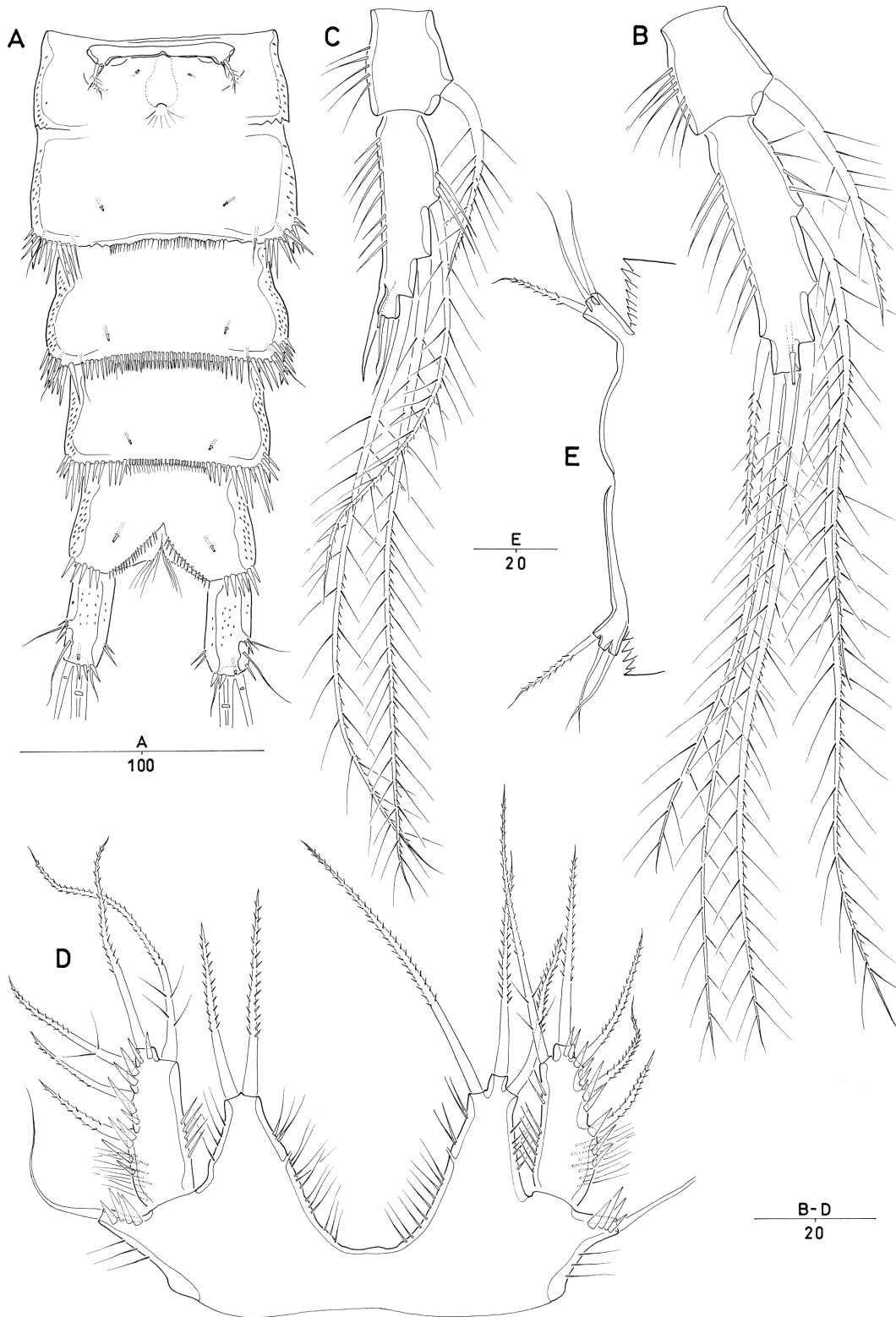


Figure 22. *Normanella sarsi* sp. nov. A, urosome ♀ [excluding P5-bearing somite], ventral; B, P3 endopod ♀, anterior; C, P3 endopod ♂, posterior; D, P5 ♂, anterior; E, P6 ♂.

Figure 22. *Normanella sarsi* sp. nov. A, urosome ♀ [sauf le somite portant P5], vue ventrale; B, endopodite de P3 ♀, vue antérieure; C, endopodite de P3 ♂, vue postérieure; D, P5 ♂, vue antérieure; E, P6 ♂.

length along outer margin; terminal seta arising from minute cylindrical process; outer margin with few spinules and numerous long setules; inner margin with long spinules.

Male

More slender than female. Body length unknown (only specimen dissected).

Antennule 7-segmented, with armature as in other members of the family.

P2 endopod (Fig. 30G) with modified enp-2; inner distal seta shortened, only half as long as equivalent in ♀ and bipinnate instead of plumose; outer distal seta extremely reduced, bare, about half the length of inner distal seta and only slightly longer than outer spine; outer spine slightly longer than in ♀.

P3 endopod (Fig. 22C). Enp-1 inner seta slightly shorter than in ♀. Enp-2 outer margin with short mucroniform process being homologous with outer spine of enp-2 of ♀; both apical setae strongly reduced with outer one slightly shorter than inner one, set on small lobe; inner setae not modified.

Fifth pair of legs (Fig. 22D) fused medially; defined at base. Baseoendopod with short setophore bearing outer basal seta, and well developed endopodal lobe with 2 bipinnate setae apically on left side and 3 bipinnate setae on right side; with tube-pore medial of innermost endopodal seta. Exopod about 2.7 times as long as maximum width; with 1 bipinnate inner seta, 1 bipinnate apical seta, and 3 bipinnate setae along outer margin; with long setules on posterior surface proximally and several coarse spinules anteriorly.

Sixth pair of legs (Fig. 22E) asymmetrical; represented on both sides by a small plate (fused to ventral wall of supporting somite along one side; articulating at base and covering gonopore along other side); outer distal corner produced into cylindrical process bearing 1 pinnate and 2 naked setae.

Etymology. - The species is named after Georg Ossian Sars who made the first significant contribution to the taxonomy of the genus *Normanella*.

Notes. - The presence of 5 setae on the male P5 exopod is unique within the genus which otherwise has 4 setae. The malformation of the endopodal lobe on one side raises the suspicion that the supernumerary outer seta is also teratological. Unfortunately only a single male was present in our material and the closely related *N. serrata* sensu Marinov & Apostolov (1985) is known exclusively of females. An alternative interpretation could be that the ancestral pentasetose condition has been retained only in the *sarsi*-lineage. Evidence in favour of this hypothesis is the apparent symmetry of the exopods lacking any sign of aberration, and the fact that this ancestral condition is still

found in the Orthopsyllidae, Laophontopsidae and a number of genera belonging to the Laophontidae such as *Esola* Edwards and *Paralaophonte* Lang.

The status of *N. serrata* sensu Marinov & Apostolov (1985) has already been discussed above.

(e) The *bolini*-lineage.

Only two species belong to this lineage, *N. similis* from N Europe and *N. bolini* from California. Both share a characteristic ♀ P5 consisting of a short, oval exopod and a broadly triangular endopodal lobe. Other diagnostic characters include the short caudal rami with reduced setae IV-V, the triangular rostrum with obtuse apex, and 5-segmented ♀ antennule. The cephalic shield is areolated in at least *N. bolini*.

Normanella similis Lang, 1936

Type locality. - Öresund, NW of Hven, Sweden; 22 m depth; mud.

Note. - With the exception of Klie (1950) who found 1 ♀ in the Kieler Bucht, all other records are Scandinavian: Sweden: Öresund (Lang, 1936), Gullmar Fjord (Lang, 1944); Denmark: Skagen (Lang, 1948). Lang (1936) believed that many early records of *N. minuta* actually refer to *N. similis*.

Normanella bolini Lang, 1965

Type locality. - California: Monterey Bay, off Hopkins Marine Station; tidal pools.

Note. - Lang (1965) suggested a relationship with *N. incerta* but did not provide evidence for this statement. *N. bolini* can be differentiated from *N. similis* by the much shorter caudal rami and by the longer P5 endopodal lobe in the female and the longer P5 endopodal setae in the male.

Key to species

As with previous keys (Lang, 1948, 1965) it has proven impossible to construct a key which is entirely applicable to both sexes. Due to the lack of males for several species the last six couplets (11-16) are essentially based on female characters. It is vital that any identification made with the key should be checked against the relevant descriptions. *N. serrata* is left out of the key since we suspect that it is based on an amalgamate of species (see above). Two species of the *dubia*-lineage, *N. quarta* and *N. semitica* are indeterminable at present and are also excluded. Whilst constructing this key we have assumed that cephalic surface areolation is present in *N. serrata* sensu Božić (1964) and *N. similis*.

1. P2 enp-2 with 2 inner setae 2.
P2 enp-2 with 3 inner setae 3.
2. P4 enp-2 with 4 setae/spines (outer spine absent) *reducta* Noodt, 1955.
P4 enp-2 with 5 setae/spines (outer spine present) *bifida* sp. nov.
3. P4 enp-2 with 4 setae/spines (outer spine absent) *mucronata* sensu Marinov (1978).
P4 enp-2 with 5 setae/spines (outer spine present) 4.
4. Caudal ramus with strongly developed, proximally dilated seta V, lacking internal fracture plane.
Rostrum distinctly pointed 5.
Caudal ramus with normally developed or reduced seta V, always with internal fracture plane.
Rostrum of different shape 6.
5. Rostrum with short apical portion, distance between sensillae and apex about 18% of rostrum length.
Caudal ramus seta V distinctly lanceolate in proximal half and with flagellate distal third. Middle and distal outer setae of P5 exopod ♀ clearly separated; distance between insertion site of middle outer seta and apex about 1/4 of outer margin length *confluens* Lang, 1965.
Rostrum with long apical portion, distance between sensillae and apex at least 1/4 of rostrum length. Caudal ramus seta V gradually tapering distally. Middle and distal outer setae of P5 exopod ♀ closely set; distance between insertion site of middle outer seta and apex about 1/8 of outer margin length *mucronata* Sars, 1909.
6. Caudal ramus at least 3 times as long as maximum width 7.
Caudal ramus shorter 8.
7. Caudal ramus shorter than 4 times maximum width *paratenuifurca* sp. nov.
Caudal ramus longer than 4 times maximum width *tenuifurca* Sars, 1909
8. Cephalic shield without surface areolation 9.
Cephalic shield with surface areolation 10.
9. Rostrum with straight lateral margins. Caudal ramus about twice as long as wide; setae IV -V well developed. P2 enp-2 ♂ outer apical seta minute, shorter than outer spine *minuta* (Boeck, 1873).
Rostrum with distinctly concave lateral margins. Caudal ramus shorter than twice the width; setae IV -V reduced. P2 enp-2 ♂ outer apical seta small, longer than outer spine *dubia* Brady & Robertson in Brady (1880).
10. Caudal ramus slightly longer than wide *bolini* Lang, 1965.
Caudal ramus at least twice as long as maximum width 11.
11. P5 endopodal lobe ♀ distinctly shorter than exopod 12.
P5 endopodal lobe ♀ extending to or beyond distal margin of exopod 14.
12. Antennule ♀ 6-segmented *serrata* sensu Božić (1964).
Antennule ♀ 5-segmented 13.
13. Rostrum with pointed apex. P5 exopod ♀ elongate (greatest width measured proximally) *pallaresae* sp. nov.
Rostrum with blunt apex. P5 exopod ♀ oval (greatest width measured at about halfway) *similis* Lang, 1936.
14. P5 exopod ♀ with clear step halfway outer margin (Fig. 21E); P5 exopod ♂ with 5 (?) setae *sarsi* sp. nov.
P5 exopod ♀ without clear step halfway outer margin; P5 exopod ♂ with 4 setae 15.
15. P5 exopod ♀ flask-shaped, with proximal swelling along inner margin *obscura* sp. nov.
P5 exopod ♀ not flask-shaped, with straight inner margin 16.
16. Caudal ramus 2.5 times as long as wide. P5 exopod ♀ slender, 4.3 times as long as basal width *N. incerta* Lang, 1934.
Caudal ramus twice as long as wide. P5 exopod ♀ shorter, 3.5 times as long as basal width *N. porosa* Noodt, 1964.

Genus *Sagamiella* gen. nov.

This genus is exclusively abyssal in distribution. It is established to accommodate *Normanella aberrans*, originally described from a single male and a copepodid V stage collected at 1200 m depth in the Gulf of Biscay

(Bodin, 1968), and a second new species discovered in the cold seeps of Sagami Bay.

Diagnosis.

Normanellinae. Antennule ♀ 6-segmented. Antennary exopod with 3 setae. Mandible with endopod fused to basis;

basis with 1 seta. Maxillule with 1 basal endite. Maxilla with allobasis accompanied by 1 seta and 1 spine. P6 ♂ with 2 setae. Swimming leg setal formulae:

	Exopod	Endopod
P2	0.1.123	1.221
P3	0.1.223	1.321
P4	0.1.223	1.221

Type species. - *Sagamiella latirostrata* gen. et sp. nov.

Other species. - *Normanella aberrans* Bodin, 1968 = *Sagamiella aberrans* (Bodin, 1968) comb. nov.

Etymology. - The generic name is derived from the type locality, Sagami Bay. Gender: feminine.

Sagamiella latirostrata gen. et sp. nov.

Type locality. - Japan, Sagami Bay, Stn DT1-3, depth 830.5m.

Material. - Holotype ♀ dissected on 13 slides (NHM reg. no. 1998.2127); 22-23 February 1992. Paratypes are (a) 1 ♂ dissected on 9 slides (NHM reg. no. 1998.2128), from Sagami Bay, Dive 514, depth 1100 m, 5 November 1990, (b) 1 ♀ in alcohol (NHM reg. no. 1998.2114), from Sagami Bay, Stn DT2-2, depth 941.6 m, 22-23 February 1992, and (c) 1 ♂ in alcohol (NHM reg. no. 1998.2115), from Sagami Bay, Dive 452, depth 1160 m, 23 October 1989.

Female

Total body length 651 - 685 µm (n=2; x = 668 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 173 µm. Urosome slightly narrower than prosome (Fig. 23A).

Cephalothorax with crenulate posterior margin and 4 pairs of weakly developed longitudinal ridges dorsally and laterally (Fig. 23A-B); pleural areas well developed, rounded; posterolateral angles minutely crenate; ornamentation consisting of sensillae and few pores as illustrated in Fig. 23A-B and irregular pattern of weakly defined circular and linear surface structures present dorsally and laterally. Cephalothorax without minute denticles as found on free body somites. Rostrum bell-shaped (Fig. 24E), with almost straight lateral margins and rounded anterior margin; completely defined at the base; with pair of tiny sensillae and a midventral tube-pore near the apex; dorsal and ventral surface smooth, without denticles.

Pedigerous somites covered with minute spinules. All prosomites without defined hyaline frills; hind margin denticulate.

Urosome (Figs 23A-B; 24B) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites with dense surface ornamentation consisting of small spinules dorsally and laterally; also present ventrally on urosomites 3-4 (Fig. 24B). Hyaline frills of urosomites not developed but hind margin distinctly serrate dorsally and laterally. Ventral hind margin of urosomites 2-4 with large spinules laterally and fine or minute spinules medially.

Genital double-somite (Figs 23A; 24B) with original segmentation indicated by transverse, serrate surface ridge dorsally and dorsolaterally and surface suture laterally and ventrolaterally; completely fused ventrally. Genital field with small copulatory pore (arrowed in Fig. 24B) located in median depression; gonopores fused medially forming single genital slit covered on both sides by opercula derived from sixth legs; P6 with small protuberance bearing 1 long outer seta and 1 inner seta (Fig. 24B).

Anal somite (Fig. 24A-B) with well developed, serrate anal operculum flanked by row of spinous processes overlying anterior margin of caudal rami; midventral surface without ornamentation; anal opening with fringe of long setular extensions, bordered by spinules ventrally.

Caudal rami (Figs 23C; 24A-C) short, ovoid, 1.6 times longer than maximum width; tube-pore (arrowed in Fig. 24C) present on subdistal ventral surface; each ramus with 7 setae; seta I bare and shortest, closely set to bare seta II; seta III bare, positioned ventrolaterally; setae IV and V fused basally, bipinnate (seta V longest, about as long as last 3 urosomites and caudal rami combined; with internal fracture plane); seta VI bare and small; seta VII tri-articulate at base. Each ramus with minute spinules, dorsally and ventrally; additional spinular ornamentation present along inner and outer margins and around ventral hind margin.

Antennule (Fig. 28A-B) 6-segmented, segment 3 longest (measured along anterior margin); with well developed sclerite around base of segment 1. Armature formula: 1-[1 pinnate], 2-[3 + 5 pinnate], 3-[3 + 5 pinnate + (1 + ae)], 4-[1], 5-[2 pinnate], 6-[7 + 1 pinnate spine + acrothek]. Apical acrothek consisting of small aesthetasc fused basally to 1 short slender seta and 1 strong pinnate seta. Segment 1 with 2 spinular rows around anterior margin. Missing setae on segment 2 indicated by arrows in Fig. 28A. Segment 3 with aesthetasc fused basally to seta and set on distinct pedestal. Anterior elements on segments 5 and 6 more setiform and less coarsely pinnate than in *Normanella*.

Antenna (Fig. 28C-D) 3-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa small, with 1 row of spinules. Basis and proximal endopod segment fused forming elongate allobasis with incomplete transverse surface suture marking original segmentation; with 1 abexopodal seta in distal half. Exopod small, 3 times longer than width but distinctly tapering proximally; with 1 pinnate

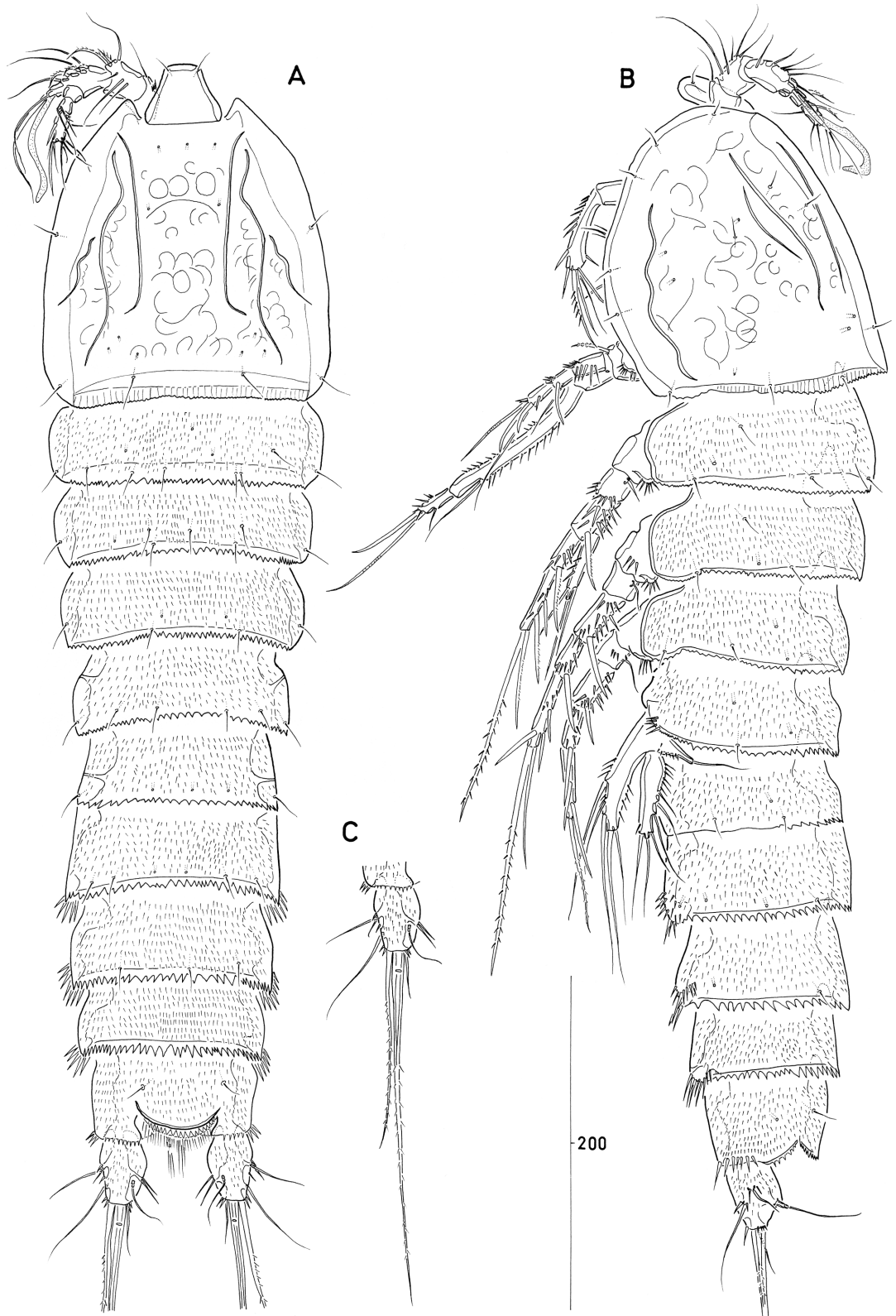


Figure 23. *Sagamiella latirostrata* gen. et sp. nov. (♀). A, habitus, dorsal; B, habitus, lateral; C, left caudal ramus, dorsal.
Figure 23. *Sagamiella latirostrata* gen. et sp. nov. (♀). A, habitus, vue dorsale ; B, habitus, vue latérale ; C, rame caudale gauche, vue dorsale.

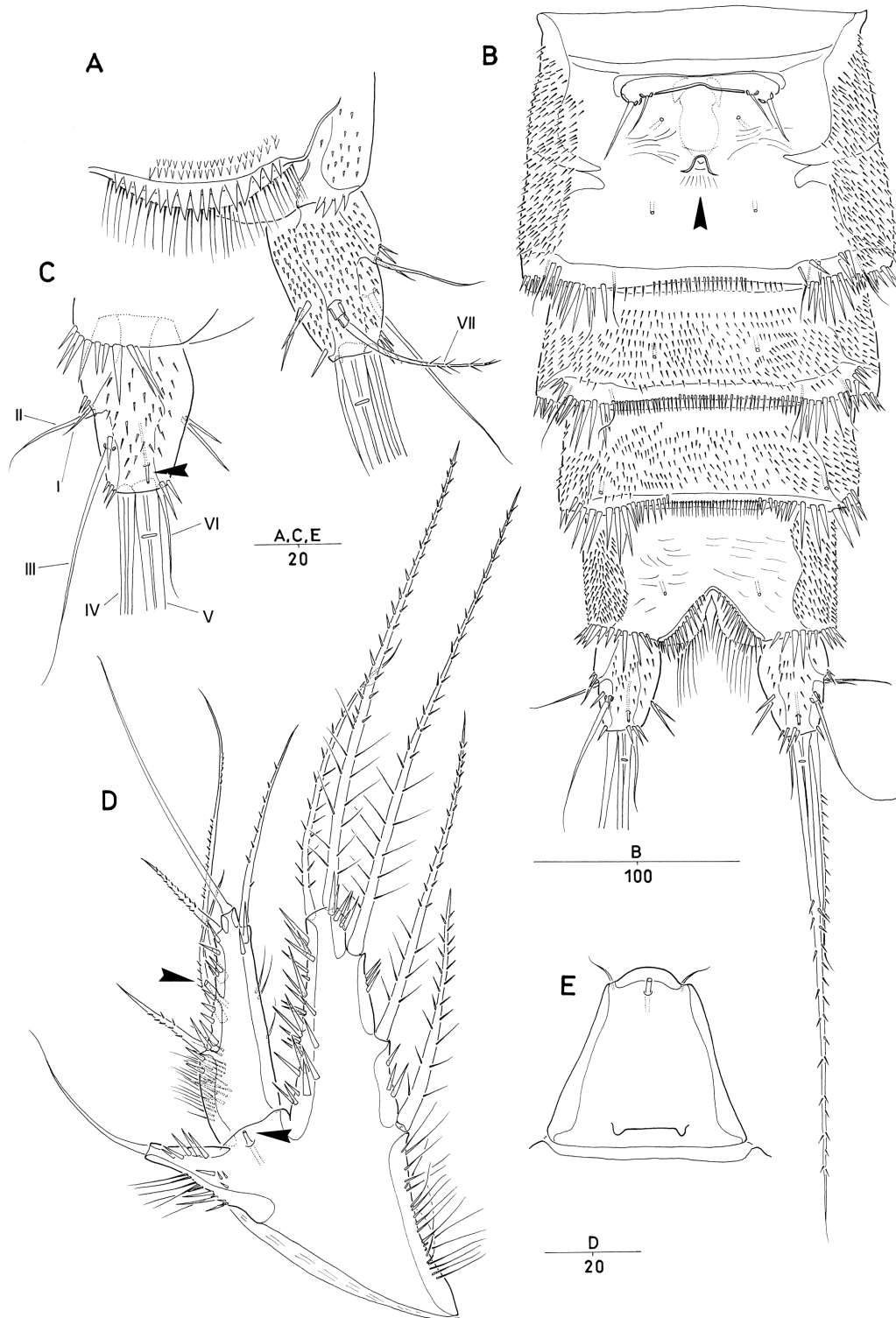


Figure 24. *Sagamiella latirostrata* gen. et sp. nov. (♀). A, anal somite and right caudal ramus, dorsal; B, urosome [excluding P5-bearing somite], ventral [copulatory pore arrowed]; C, right caudal ramus, ventral [tube-pore arrowed]; D, P5, anterior [tube-pores arrowed]; E, rostrum, ventral.

Figure 24. *Sagamiella latirostrata* gen. et sp. nov. (♀). A, somite anal et rame caudale droite, vue dorsale ; B, urosome [sauf le somite portant P5], vue ventrale [la flèche indique l'orifice copulateur] ; C, rame caudale droite, vue ventrale [la flèche indique le pore tubulaire] ; D, P5, vue antérieure [les flèches indiquent les pores tubulaires] ; E, rostre, vue ventrale.

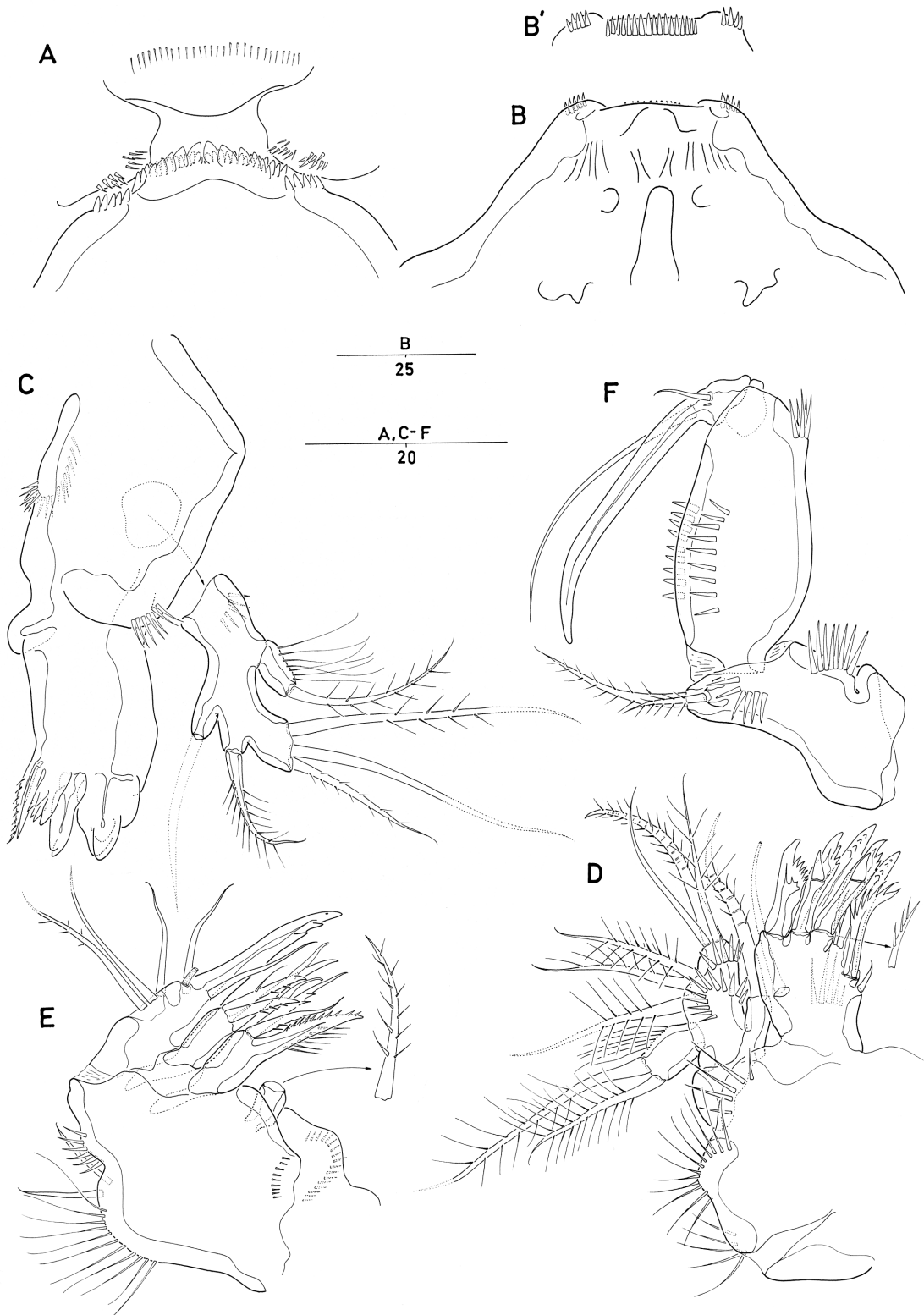


Figure 25. *Sagamiella latirostrata* gen. et sp. nov. (♀). A, oral area, ventral; B, labrum, anterior; B', distal area of labrum, posterior; C, mandible [with disarticulated palp]; D, maxillule, posterior; E, maxilla; F, maxilliped.

Figure 25. *Sagamiella latirostrata* gen. et sp. nov. (♀). A, région orale, vue ventrale ; B, labre, vue antérieure ; B', région distale du labre, vue postérieure ; C, mandibule [avec palpe détaché] ; D, maxillule, vue postérieure ; E, maxille ; F, maxillipède.

seta laterally, and 2 pinnate setae apically. Endopod (twisted in Fig. 28C due to imperfect mounting) subequal to allobasis; ornamentation and armature essentially as in *N. dubia*; outermost geniculate seta fused basally to short seta (Fig. 28D).

Labrum with elaborate spinular ornamentation around distal margin as illustrated in Fig. 25A-B.

Mandible (Fig. 25C) with well developed gnathobase bearing large multicuspidate teeth around distal margin and 1 small unipinnate spine at dorsal corner. Palp small, biramous but only exopod discrete. Basis with 1 plumose seta; with minute spinules proximally. Exopod 1-segmented, small, with 1 plumose seta apically and row of long setules laterally. Endopod fused to basis, with 1 naked and 2 pinnate setae apically, and 1 pinnate seta laterally.

Paragnaths (Fig. 25A) strongly developed lobes with medially directed spinules, separated by medial lobe (not figured) covered with dense pattern of short setules.

Maxillule (Fig. 25D). Praecoxa with 3 spinule rows around outer margin; arthrite rectangular, with 1 naked seta on anterior surface and 8 spines/setae around distal margin (innermost very small). Coxa with cylindrical endite bearing curved, pinnate spine. Basis with 1 naked and 1 plumose seta, and 1 curved, bipinnate spine; with 2 rows of spinules on anterior surface. Endopod incorporated in basis, represented by 3 plumose setae. Exopod 1-segmented, with 2 plumose setae.

Maxilla (Fig. 25E) with 3 endites on syncoxa; praecoxal endite small and cylindrical, with 1 strong, pinnate seta; proximal coxal endite with 1 strong spine fused to endite and 2 pinnate setae; distal coxal endite with 1 naked seta, and 2 pinnate spines with subapical tubular extension. Allobasis drawn out into strong, slightly curved, sparsely denticulate claw; accessory armature consisting of 1 naked seta on anterior surface, and 1 naked seta plus short tube-pore along outer margin; endopod represented by 1 pinnate and 2 naked setae.

Maxilliped (Fig. 25F) with 2 pinnate setae and several patches of spinules on syncoxa. Basis with 1 row of spinules along outer distal margin and 2 longitudinal spinule rows along palmar margin. Endopod drawn out into long, slender claw; accessory armature consisting of long naked seta and short seta accompanied by minute element.

Swimming legs P1-P4 (Figs 26A-B; 27A-C) with intercoxal sclerites and well developed praecoxae. Coxae and bases with anterior rows of surface spinules as figured. Exopod 3-segmented, endopod 2-segmented.

P1 (Fig. 26A) with large coxa; with long spinules along outer margin and on anterior surface. Basis with slender, bipinnate spine but no long setules along inner margin and with 1 bipinnate spine and few spinules along outer margin. Exp-1 with 1 long, bipinnate spine (distinctly longer than other exopodal spines); exp-2 with 1 bipinnate, outer spine

and 1 plumose, inner seta (extending beyond exp-3 distal margin); exp-3 with 3 bipinnate spines and 2 geniculate setae. Endopod 2.2 times as long as exopod, enp-1 with 1 long, plumose inner seta, enp-2 with 1 slender, denticulate curved claw and 1 geniculate seta apically, and 1 small plumose seta along inner margin.

P2-P4 (Figs 26B; 27A-C). Coxae and bases with secretory pores on anterior surface and spinular rows along outer margin; basis with bipinnate spine (P2) or naked seta (P3-P4). Exopodal and distal endopodal segments generally more slender than in *Normanella*; spines of exp-3 also more slender (those of P4 almost setiform) and only sparsely pinnate; exp-1 and -2 with finely incised frill at inner distal corner; all segments with pattern of spinules as figured; inner margins of exopodal and endopodal segments with long setules or spinules except for P2 enp-1. P2 enp-2 1.7 times longer than enp-1; endopod extending just beyond distal margin of exp-2. P3 enp-2 2.1 times longer than enp-1; endopod extending beyond distal margin of exp-2. P4 enp-2 short, 1.6 times longer than enp-1; endopod extending almost to distal margin of exp-2; inner distal corner of enp-2 produced into long tubular extension (arrowed in Fig. 27C). Spine and setal formula as in Table 2.

Fifth pair of legs (Fig. 24D) not fused to supporting somite; rami separate. Baseoendopod forming short, outer setophore bearing basal seta and row of spinules; with tube-pore (arrowed in Fig. 24D) near boundary with exopod. Endopodal lobe almost extending to distal margin of exopod, with 3 bipinnate setae laterally and 2 bipinnate setae apically; rows of long spinules along outer margin, and long setules along proximal inner margin. Exopod elongate, distinctly tapering distally; with 1 naked terminal seta, 1 bipinnate inner seta, and 4 pinnate setae of different length along outer margin; terminal seta arising from small cylindrical process; outer margin with 1 secretory pore (arrowed in Fig. 24D) and numerous short spinules and long setules; inner margin with few setules or spinules.

Male

More slender than female. Body length 509 - 524 μm ($n=2$; $x = 517 \mu\text{m}$; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 120 μm . Body gradually tapering posteriorly (Fig. 29A).

Prosome (Fig. 29A) 4-segmented, comprising cephalothorax and 3 free pedigerous somites. Rostrum distinct at base; distinctly wider than in ♀. Cephalothorax with denticulate posterior margin and 3 pairs of longitudinal ridges; additional surface ornamentation consisting of sensillae and minute (mostly circular) lamellae as figured. All body somites covered dorsally with minute spinules and with denticulate hind margin.

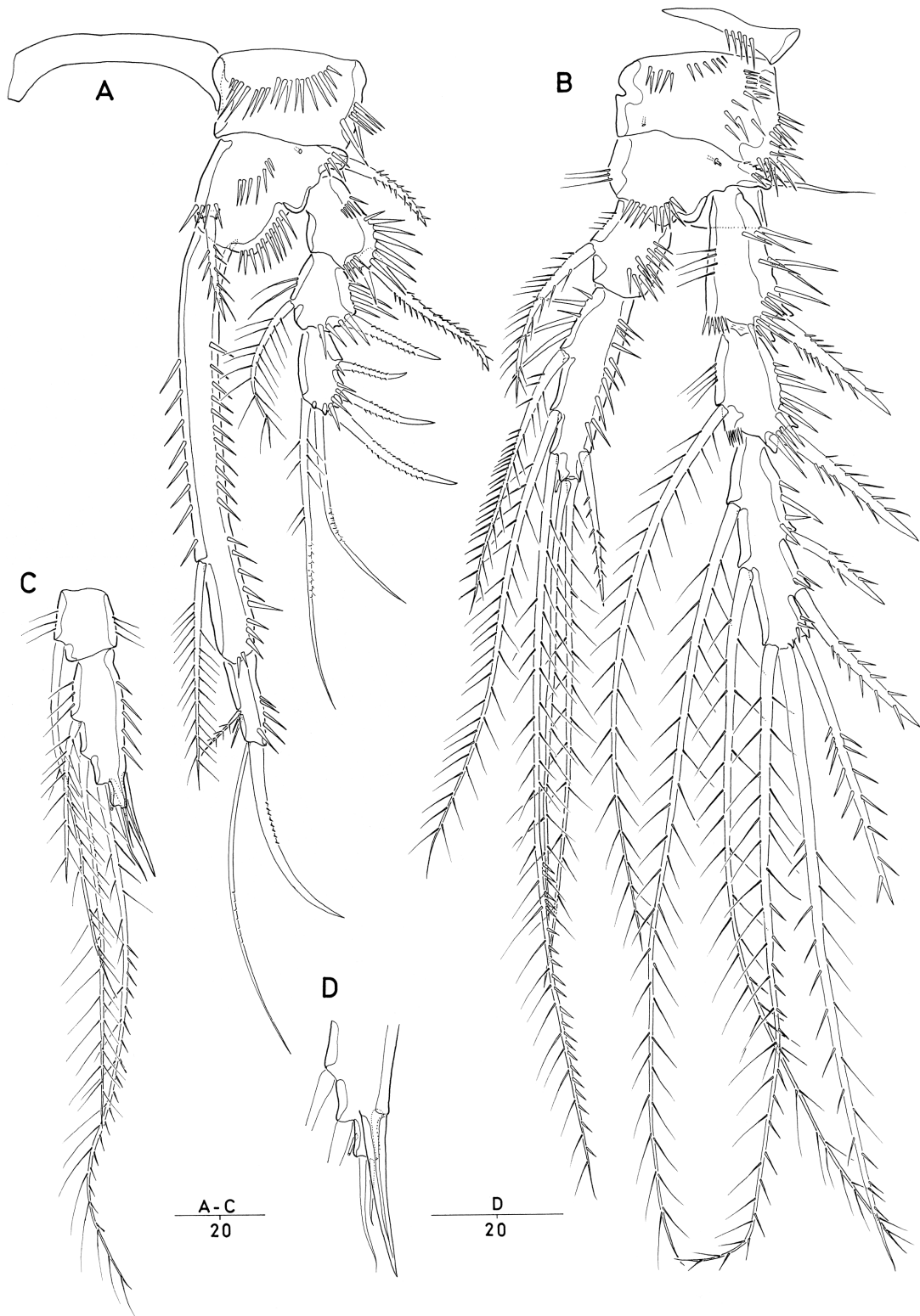


Figure 26. *Sagamiella latirostrata* gen. et sp. nov. A, P1 ♀, anterior; B, P3 ♀, anterior; C, P3 endopod ♂, posterior; D, distal area of P3 enp-2 ♂, anterior.

Figure 26. *Sagamiella latirostrata* gen. et sp. nov. A, P1 ♀, vue antérieure; B, P3 ♀, vue antérieure; C, endopodite de P3 ♂, vue postérieure; D, région distale de P3 enp-2 ♂, vue antérieure.

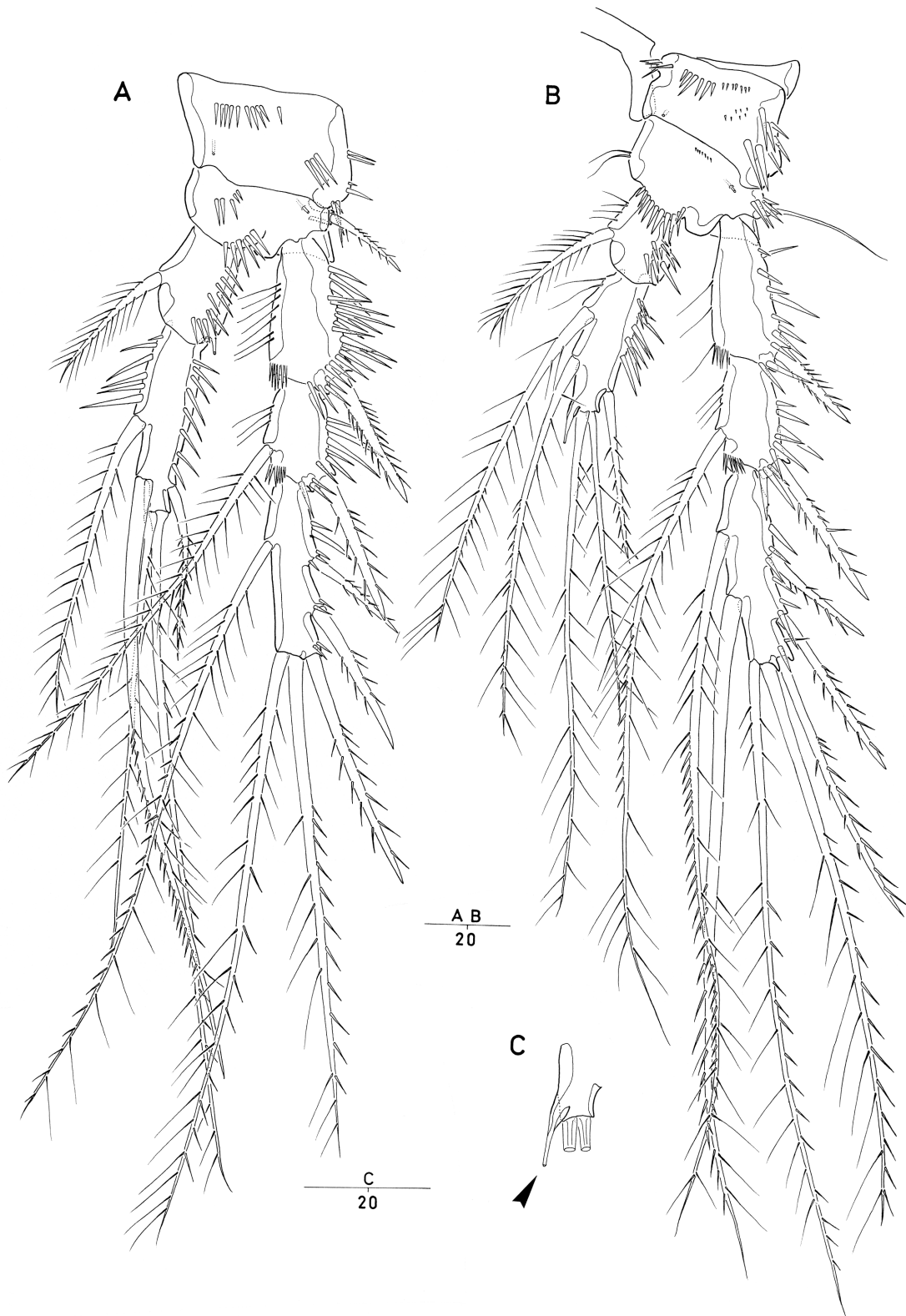


Figure 27. *Sagamiella latirostrata* gen. et sp. nov. (♀). A, P2, anterior; B, P4, anterior; C, distal area of P4 enp-2, anterior.

Figure 27. *Sagamiella latirostrata* gen. et sp. nov. (♀). A, P2, vue antérieure ; B, P4, vue antérieure ; C, région distale de P4 enp-2, vue antérieure.

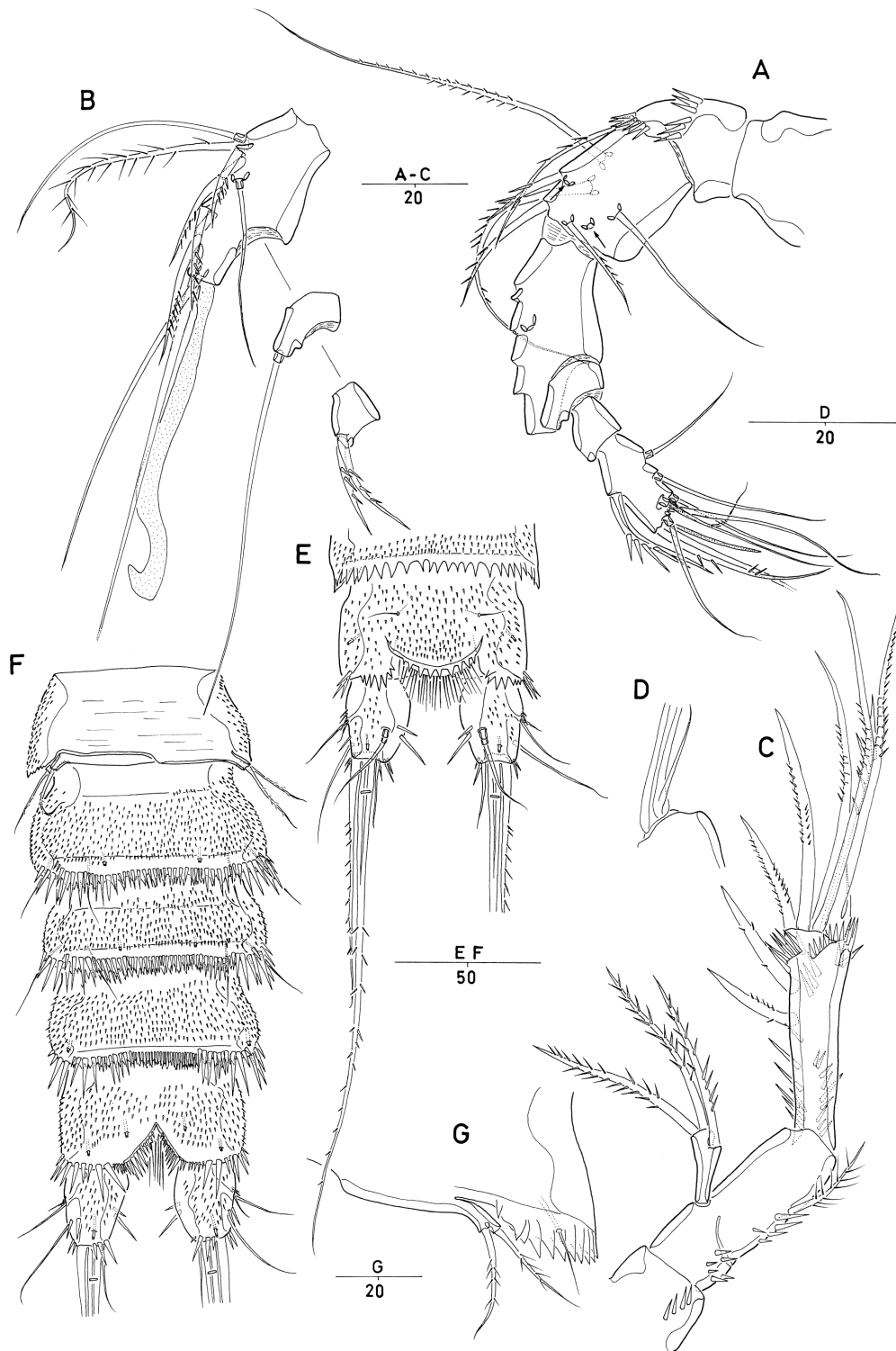


Figure 28. *Sagamiella latirostrata* gen. et sp. nov. A, antennule ♀ [armature of segments 3-5 omitted; arrows indicating missing setae on segment 2]; B, antennular segments 3-5 ♀; C, antenna ♀; D, base of bifid seta on antennary endopod ♀; E, anal somite and caudal rami ♂, dorsal; F, urosome ♂ [excluding P5-bearing somite], ventral; G, P6 ♂.

Figure 28. *Sagamiella latirostrata* gen. et sp. nov. A, antennule ♀ [armature des articles antennulaires 3-5 omise ; des flèches indiquent les soies manquantes de l'article 2]; B, articles antennulaires 3-5 ♀; C, antenne ♀; D, base de la soie bifide de l'endopodite de l'antenne ♀; E, somite anal et rames caudales ♂, vue dorsale; F, urosome ♂ [sauf le somite portant P5], vue ventrale; G, P6 ♂.

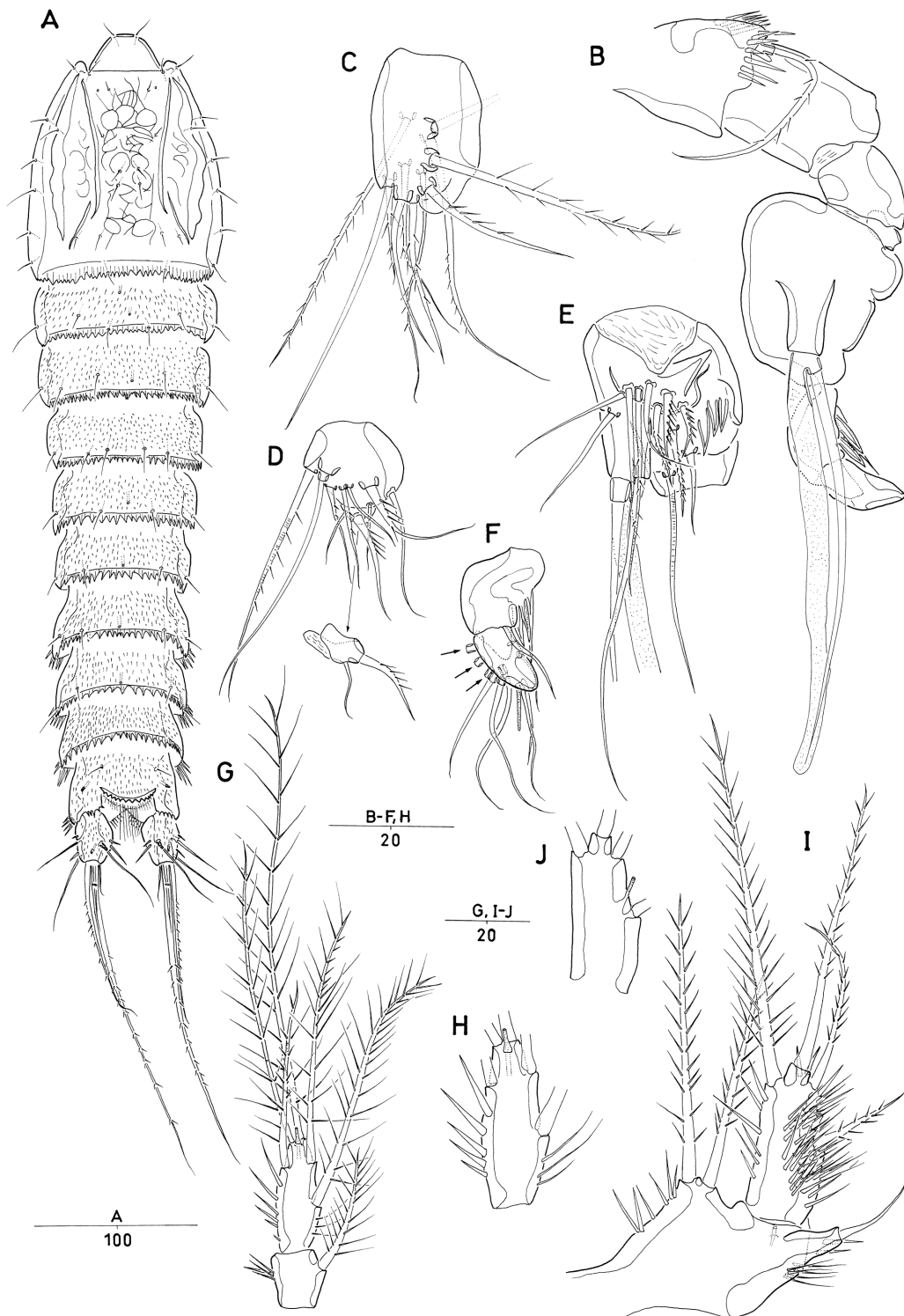


Figure 29. *Sagamiella latirostrata* gen. et sp. nov. (δ). A, habitus, dorsal; B, antennule [armature of segments 2-7 omitted]; C, 2nd antennular segment; D, 3rd and 4th antennular segments; E, 5th antennular segment; F, 6th and 7th antennular segments [missing setae on segment 7 arrowed]; G, P4 endopod; H, P4 enp-2; I, P5, posterior; J, P5 exopod [ornamentation omitted].

Figure 29. *Sagamiella latirostrata* gen. et sp. nov. (δ). A, habitus, vue dorsale; B, antennule [armature des articles 2-7 omise]; C, article antennulaire 2; D, articles antennulaires 3-4; E, article antennulaire 5; F, articles antennulaires 6-7 [les flèches indiquent les soies manquantes de l'article 7]; G, endopodite de P4; H, P4 enp-2; I, P5, vue postérieure; J, exopodite de P5 [ornementation omise].

Urosome (Fig. 28E-F) 6-segmented, comprising P5-bearing somite, genital somite and 4 abdominal somites. Postgenital somites numerous minute spinules on ventral surface; each with transverse spinule row overlapping denticulate ventral posterior margin. Anal somite and caudal rami as in ♀.

Antennule (Figs 29B-F) 7-segmented; subchirocer with geniculation between segments 5 and 6. Segment 1 with 2 rows of spinules along anterior margin. Segment 4 represented by small U-shaped sclerite (cf. insert in Fig. 29D). Segment 5 largest, swollen. Segment 6 forming dorsal outgrowth covering anterior part of segment 7. Segment 7 subtriangular. Segmental homologies: 1-I, 2-(II-VIII), 3-(IX-XII), 4-XIII, 5-(XIV-XX), 6-(XXI-XXIII), 7-(XXIV-XXVIII). Armature formula: 1-[1 pinnate], 2-[2 + 9 pinnate], 3-[4 + 4 pinnate], 4-[1 + 1 pinnate], 5-[7 + 5 pinnate + 3 spinous processes + (1 + ae)], 6-[1 + 3 spinous processes], 7-[7 + acrothek]. Apical acrothek consisting of minute aesthetasc and 2 naked setae.

P2 endopod (Fig. 30A) with modified enp-2; inner distal seta shortened, only half as long as equivalent in ♀ and bipinnate instead of plumose; outer distal seta reduced, shorter than inner distal seta and only slightly longer than outer spine; outer spine slightly longer than in ♀.

P3 endopod (Fig. 26C) 2-segmented; modified. Enp-1 with fewer spinules along outer margin; inner seta much longer than in ♀, extending beyond distal margin of enp-2. Enp-2 slightly shorter than in ♀; outer margin with short mucroniform process (Fig. 26D) being homologous with outer spine of enp-2 of ♀; both apical setae strongly reduced and set on small lobe; inner setae not modified.

P4 endopod (Fig. 29G-H) 2-segmented; slightly modified. Enp-1 and -2 slightly narrower than in ♀; anterior tube-pore of enp-2 reduced and displaced to position in between both apical setae.

Fifth pair of legs (Figs 29I-J) fused medially; defined at base. Baseoendopod with short setophore bearing outer basal seta, and weakly developed endopodal lobe with 2 pinnate spines apically; with anterior tube-pore near boundary with exopod. Exopod about 2.3 times as long as maximum width; with 1 bipinnate inner seta, 1 bipinnate apical seta, and 2 bipinnate setae plus tube-pore (Fig. 29J) along outer margin; with dense patch of long setules on posterior surface.

Sixth pair of legs (Fig. 28F-G) asymmetrical; represented on both sides by a small plate (fused to ventral wall of supporting somite along one side; articulating at base and covering gonopore along other side); outer distal corner produced into cylindrical process bearing 2 bipinnate setae.

Etymology. - The species name is derived from the Latin *latus*, meaning broad, and *rostrum*, meaning beak, and refers to the wide rostrum of the male.

Notes. - *S. latirostrata* can easily be distinguished from *S. aberrans* by the shorter caudal rami which are almost ovoid in shape. Bodin (1968) failed to describe the mouthparts of *S. aberrans*, however, our dissection of *S. latirostrata* has shown that there are no fundamental differences with those of *Normanella*. The antennule of *S. aberrans* is 5-segmented at the copepodid V stage but we suspect it to become 6-segmented at the final moult as in the adult of *S. latirostrata*. There is some uncertainty about the homology of the mandibular palp in *Sagamiella* caused by the secondary fusion of the endopod to the basis. On the basis of the location of the two lateral setae it is assumed here that the endopod has retained its full complement of setae and the basis has lost one seta. This interpretation has been followed in the diagnoses of the genus and the family. The alternative possibility could be that the basis has retained both its setae and the lateral endopodal seta was lost.

Concluding remarks

Our study of the Normanellidae of NW Europe is indicative of the grossly underestimated species diversity of this family. Although this is partly reflected in the many false records based on misidentifications, it is obvious that only a small fraction of the actual number of species has been discovered. With the discovery of several new species in NW Europe, for example, many of the records of the earlier described species in this region are rendered doubtful, particularly in areas where species occur sympatrically. We believe that even in this intensively investigated area new species are likely to be discovered in the near future. For example, in the Bay of Morlaix (Pierre Noire) and around south Belle-Île island (southern Brittany), Bodin (pers. comm) recorded specimens of the *mucronata*-lineage which displayed a [1.321] formula on the P2 endopod and a [1.220] formula on the P4 endopod, agreeing in this respect with *N. mucronata* sensu Marinov (1977). Several unnamed species are known to occur along the Atlantic coast of the U.S.A. (Coffin, 1981; Coull & Dudley, 1985) and with the exception of one unidentified (Kask et al., 1983) and three isolated records (Red Sea, Campbell Island, Monterey Bay) no shallow water Normanellidae have been recorded from the entire Indo-Pacific. The family has been recorded from all continents and occurs in a wide variety of habitats ranging from cold seeps and abyssal muds to shallow subtidal sandy substrates and intertidal rockpools.

Contrary to earlier reports, the material that we have examined was remarkably constant in all features. The only noteworthy exception is the male P5 which in a number of species showed supernumerary setae - often in asymmetrical numbers - on the endopodal lobe. This kind of

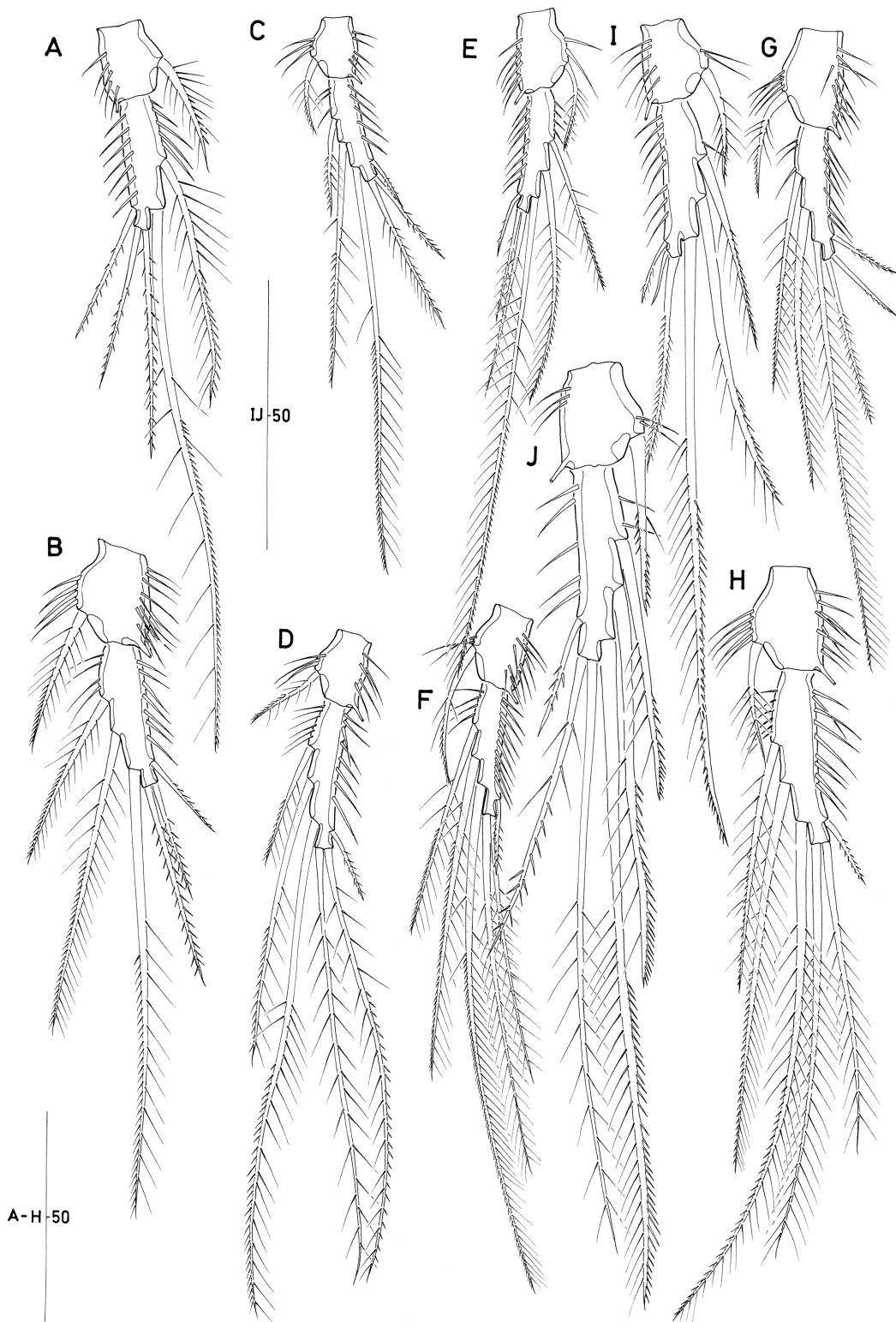


Figure 30. P2 endopod ♀. D, *N. paratenuifurca*; F, *N. tenuifurca*; J, *N. minuta*; H, *N. sarsi*. P2 endopod ♂. A, *S. latirostrata*; B, *N. dubia*; C, *N. paratenuifurca*; E, *N. tenuifurca*; G, *N. sarsi*; I, *N. minuta*.

Figure 30. Endopodite de P2 ♀. D, *N. paratenuifurca* ; F, *N. tenuifurca* ; J, *N. minuta* ; H, *N. sarsi*. Endopodite de P2 ♂. A, *S. latirostrata* ; B, *N. dubia* ; C, *N. paratenuifurca* ; E, *N. tenuifurca* ; G, *N. sarsi* ; I, *N. minuta*.

aberration appears to be quite common in the Normanellidae. Huys & Iliffe (1998) recently argued that the setation of the endopodal lobe in the male harpacticoid P5 is under inhibitory control. Lifting of the gene repression can therefore result in the re-appearance of setae which otherwise develop only in the female.

The family is remarkably conservative in mouthpart structure, swimming leg sexual dimorphism and even overall setation patterns. This morphological uniformity is the root cause for the many misidentifications that have happened in the past. We recommend that future descriptions and identifications pay particular attention to (a) shape of the rostrum, (b) surface texture of the cephalic shield, (c) the shape of the exopod and endopodal lobe of the P5 in both sexes, (d) the shape of the caudal ramus, (e) the form and length of caudal ramus setae IV and V, (f) the P2 endopod in the δ .

Our study has revealed that the mucroniform process on the distal endopod segment of the male P3 represents the positional homologue of the outer spine on the same segment in the female. This homology is identical to that of the families of the Laophontoidea (Huys, 1990) and provides robust evidence for a sistergroup relationship (Huys & Lee, 1999). In the P3 endopod of male Normanellidae none of the 3 inner setae is transformed, however, both apical setae are strongly reduced and represented by two setule-like elements which constitutes an autapomorphy for the family.

The sexual dimorphism on the P2 endopod (Fig. 30) was first remarked upon by Willey (1930) but remained unnoticed in later descriptions. We regard its presence to be diagnostic for the Normanellidae and consider it a further autapomorphy for this family.

Key to genera

- Antennary exopod with 3 setae; δ P6 with 2 setae
 *Sagamiella* gen. nov.
 Antennary exopod with 4 setae; δ P6 with 3 setae
 *Normanella* Brady, 1880.

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References

- Apostolov A.M. 1969.** Harpacticoiden (Crustacea Copepoda) von der bulgarischen Küste. *Zoologischer Anzeiger*, **183** (3-4): 260-267.
- Apostolov A.M. & Marinov T.M. 1988.** Copepoda Harpacticoida (morski kharpaktikoidi). [Copepoda, Harpacticoida (marine harpacticoids)]. *Fauna Bolgarii* [Fauna Bulgarica], **18**: 1-384. [In Bulgarian].
- Arlt G. 1983.** Taxonomy and ecology of some harpacticoids (Crustacea, Copepoda) in the Baltic Sea and Kattegat. *Zoologische Jahrbücher für Systematik*, **110**: 45-85.
- Bodin P. 1964.** Recherches sur la systématique et la distribution des Copépodes Harpacticoides des substrats meubles des environs de Marseille. *Recueil des Travaux de la Station marine d'Endoume, Marseille*, **51** (= Bulletin 35): 107-183.
- Bodin P. 1968.** Copépodes Harpacticoides des étages bathyal et abyssal du golfe de Gascogne. *Mémoires du Muséum national d'Histoire naturelle, Paris, n. sér., (A)* **55** (1): 1-107.
- Bodin P. 1972.** Copépodes Harpacticoides marins des environs de la Rochelle. III. Espèces de la zone intertidale de Fouras-Nord. *Téthys*, **3**(4): 841-864.
- Bodin P. 1977.** Les peuplements de Copépodes Harpacticoides (Crustacea) des sédiments meubles de la zone intertidale des côtes Charentaises (Atlantique). *Mémoires du Muséum national d'Histoire naturelle, Paris, (A)* **104**: 1-120 and index on pages 1-31.
- Bodin P. 1984.** Densité de la meiofaune et peuplements de Copépodes Harpacticoides en baie de Douarnenez (Finistère). *Annales de l'Institut océanographique, Monaco*, **60**(1): 5-17.
- Bodin P. 1997.** Catalogue of the new marine harpacticoid copepods. *Studiedocumenten van het K.B.I.N.*, **89**: 1-304.
- Bodin P. & Le Guellec C. 1992.** Meiobenthos of the Bay of Saint-Brieuc (North Brittany, France). II: Harpacticoid copepod diversity and species assemblages. *Oceanologica Acta*, **15**(6): 673-686.
- Bodiou J.-Y. 1976.** Copépodes Harpacticoides (Crustacea) des sables fins infralittoraux de Banyuls-sur-Mer. I. Description de la communauté. *Vie et Milieu, (B)* **25**(2): 313-330.
- Bodiou J.-Y. 1982.** Copépodes Harpacticoides (Crustacea) des sables fins infralittoraux de Banyuls-sur-Mer. II. Variations saisonnières qualitatives du peuplement. *Vie et Milieu*, **30**(3-4): 269-274.
- Boeck A. 1865.** Oversigt over de ved Norges Kyster jagttagne Copepoder henhørende til Calanidernes, Cyclopidernes og Harpacticidernes Familier. *Forhandlinger i Videnskabselskabet i Kristiania*, **1864**: 226-282.
- Boeck A. 1873.** Nye Slaegter og Arter af Saltvands-Copepoder. *Forhandlinger i Videnskabselskabet i Kristiania*, **1872**: 35-60.

- Bossanyi J. & Bull H.O. 1971.** The marine fauna of the Cullercoats district. 5. Arthropoda. 33. Crustacea: Copepoda. *Reports of the Dove marine Laboratory*, (3)17: 1-59.
- Božić B. 1964.** Copépodes Harpacticoides et Cyclopoïdes de la Réunion. II. Plage St. Pierre. *Bulletin du Muséum national d'Histoire naturelle, Paris*, (2) 36(4): 481-499.
- Brady G.S. 1880.** A Monograph of the Free and Semi-parasitic Copepoda of the British Islands, 2. The Ray Society: London. 182 pp.
- Brady G.S. & Robertson D. 1876.** Report on dredgings off the coast of Durham and North-Yorkshire in 1874. *Reports of the British Association for the Advancement of Science*, 45: 185-199.
- Chamroux S., Boucher G. & Bodin P. 1977.** Étude expérimentale d'un écosystème sableux. II. Évolution des populations de bactéries et de méiofaune. In: O. Kinne & H.-P. Bulnheim, eds., Ecosystem research. International Helgoland Symposium 1976. *Helgoländer wissenschaftlichen Meeresuntersuchungen*, 30(1-4): 163-177.
- Coffin W.L. 1981.** A list of harpacticoid copepods from northern New England, U.S.A. *Vie et Milieu*, (AB)28-29(4): 589-595.
- Coull B.C. 1971.** Meiobenthic Harpacticoida (Crustacea, Copepoda) from the North Carolina continental shelf. *Cahiers de Biologie marine*, 12(2): 195-237.
- Coull B.C. & Dudley B.W. 1985.** Dynamics of meiobenthic copepod populations: a long term study (1973-1983). *Marine Ecology Progress Series*, 24(3): 219-229.
- Crothers J.H. (ed.) 1966.** *Dale Fort Marine Fauna (second edition)*. Field Studies Council: London. xxiv + 169 pp.
- Dinet A., Nodot C., Vitiello P. & Vivier M.-H. 1982.** Impact d'un effluent thermique sur une communauté de Copépodes Harpacticoides benthiques. *Téthys*, 10(4): 355-363.
- Drzycimski I. 1969.** Harpacticoida (Copepoda) wód morskich okolic Bergen (Zachodnie Wybrzeże Norwegii) i ich ekologia. Harpacticoida (Copepoda) of sea waters in Bergen region (West Coast of Norway) and their ecology. *Wyzsza Szkoła Rolnicza w Szczecinie*, 17: 1-72. [In Polish with English and Russian summaries].
- El-Maghraby A.M. & Perkins E.J. 1956.** Additions to the marine fauna of Whitstable. *Annals and Magazine of Natural History*, (12)9 : 481-496.
- Geddes D.C. 1972.** The Copepoda Harpacticoida of Anglesey and the North Wales coast. *The Naturalist, Hull*, 921 : 61-76.
- Griga R.E. 1961.** Harpacticoida raiona Sevastopolya. [Harpacticoids of the Sebastopol region.]. *Trudy Sevastopol'skoi Biologicheskoi Stantsii*, 14 : 109-125. [In Russian].
- Griga R.E. 1963.** Harpacticoida donnykh biotsenozov yuzhnogo berega Kryma i Kaukaza. [Harpacticoids of the benthonic biocenoses in the southern coast of the Crimea and Caucasus.]. *Trudy Sevastopol'skoi Biologicheskoi Stantsii*, 16 : 159-172. [In Russian].
- Griga R.E. 1964.** Copepoda donnykh biotsenozov Chernogo morya raiona evpatorii. *Trudy Sevastopol'skoi Biologicheskoi Stantsii*, 15 : 101-117. [In Russian].
- Griga R.E. 1969.** Otryad Garpacticoida-Harpacticoida G.O. Sars. In: F.D. Mordukhai-Boltovskoi, Klass Rakoobraznye-Crustacea. *Opredeliteli Fauny Chernogo i Azovskogo Morei*, 2: 56-113. [In Russian].
- Hamond R. 1969.** The Laophontidae (Copepoda, Harpacticoida) of the shore at West Runton, Norfolk, England. *Crustaceana*, 16(1): 1-14.
- Hartzband D.J. & Hummon W.D. 1973.** Sub-community structure in subtidal meiobenthic Harpacticoida. *Oecologia*, 14(1-2): 37-51.
- Hashimoto J., Ohta S., Tanaka T., Hotta H., Matsuzawa S. & Sakai H. 1989.** Deep-sea communities dominated by the giant clam, *Calyptogena soyoeae*, along the slope foot of Hatsushima Island, Sagami Bay, central Japan. *Palaeogeography, Palaeoclimatology and Palaeoecology*, 71: 179-192.
- Hicks G.R.F. 1980.** Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. *Journal of experimental marine Biology and Ecology*, 44(2-3): 157-192.
- Hockin D.C. 1982.** The harpacticoid copepod fauna of the River Ythan and its estuary, Aberdeenshire, Scotland. *Journal of the marine biological Association of the United Kingdom*, 62(3): 729-736.
- Hockin D.C. & Ollason J.C. 1981.** The colonization of artificially isolated volumes of intertidal estuarine sand by harpacticoid copepods. *Journal of experimental marine Biology and Ecology*, 53(1) : 9-29.
- Holmes J.M.C. 1985.** Crustacean records from Lough Ine, Co. Cork; part III. *Bulletin of the Irish biogeographical Society*, 8: 19-25.
- Holmes J.M.C. & O'Connor J.P. 1990.** A provisional list of the Harpacticoida (Crustacea: Copepoda) of Ireland. *Bulletin of the Irish biogeographical Society*, 13: 44-130.
- Huys R. 1990.** A new family of harpacticoid copepods and an analysis of the phylogenetic relationships within the Laophontoidea T. Scott. *Bijdragen tot de Dierkunde*, 60(2): 79-120.
- Huys R., Gee J.M., Moore C.G. & Hamond R. 1996.** *Marine and brackish water harpacticoid copepods. Part 1.* Synopses of the British Fauna (New Series), No. 51: i-viii, 1-352.
- Huys R. & Iliffe T.M. 1998.** Novocriiniidae, a new family of harpacticoid copepods from anchihaline caves in Belize. *Zoologica Scripta*, 27 : 1-15.
- Huys R. & Lee. W. 1999.** On the relationships of the Normanellidae and the recognition of Cletopsyllidae grad. nov. (Copepoda, Harpacticoida). *Zoologischer Anzeiger*, 237: 267-290.
- Huys R. & Willems K.A. 1989.** *Laophontopsis* Sars and the taxonomic concept of the Normanellinae (Copepoda: Harpacticoida): a revision. *Bijdragen tot de Dierkunde*, 59: 203-227.
- Kask B.A., Sibert J.R. & Windecker B. 1983.** A checklist of marine and brackish water harpacticoid copepods from the Nanaimo Estuary, southwestern British Columbia. *Syesis*, 15: 25-38.
- Klie W. 1950.** Harpacticoida (Cop.) aus dem Bereich von Helgoland und der Kieler Bucht. (Fortsetzung). *Kieler Meeresforschungen*, 7: 76-128.
- Lang K. 1934.** Marine Harpacticiden von der Campbell-Insel und einigen anderen südlichen Inseln. *Acta Universitatis Lundensis*, n. ser., Avd. 2, 30(14) (= *Kungliga Fysiografiska Sällskapets i Lund. Handlingar*, n. ser. 45(14)): 1-56.

- Lang K. 1936.** Undersökningar över Öresund. Untersuchungen aus dem Öresund. XX. Harpacticiden aus dem Öresund. *Acta Universitatis Lundensis*, n. ser., Avd. 2, **31**(8): 1-52.
- Lang K. 1944.** *Monographie der Harpacticiden (Vorläufige Mitteilung)*. Uppsala: Almqvist & Wiksells Boktryckeri Ab. 39 pp.
- Lang K. 1948.** *Monographie der Harpacticiden*. Håkan Ohlsson: Lund. 1682 pp.
- Lang K. 1965.** Copepoda Harpacticoida from the Californian Pacific coast. *Kungliga Svenska Vetenskapsakademiens Handlingar*, (4)**10**(2) : 1-560.
- Lee W. & Huys R. (in press).** New Aegisthidae (Copepoda: Harpacticoida) from western Pacific cold seeps and hydrothermal vents. *Zoological Journal of the Linnean Society*, in press.
- Lee W. & Yoo K.-I. 1998.** A new species of *Neocervinia* (Copepoda: Harpacticoida: Cerviniidae) from the hyperbenthos of the Hatsushima cold-seep site in Sagami Bay, Japan. *Hydrobiologia*, **377**: 165-175.
- Marcotte B.M. & Coull B.C. 1975.** Pollution, diversity and meiobenthic communities in the North Adriatic (Bay of Piran, Yugoslavia). *Vie et Milieu*, (B)**24**(2): 281-300.
- Marinov T.M. 1971.** Kharpatikoidi ot b'lgarskoto kraibrezhnie na Chernomore. [Harpacticoids of the Bulgarian Black Sea coast.]. *Izvestiya na Institutata Okeanografiya i Ribno Stopanstvo. Varna*, **11** : 43-87. [In Bulgarian with English and Russian summaries].
- Marinov T.M. 1974.** Dop'nenie k'm izuchavaneto na kharpatikoidnata fauna ot b'lgarskoto Chernomorsko kraibrezhie. [Supplement to the study of the harpacticoid fauna from the Bulgarian Black Sea coast.]. *Izvestiya na Institutata Okeanografiya i Ribno Stopanstvo. Varna*, **13**: 77-92. [In Bulgarian with English and Russian summaries].
- Marinov T.M. 1977.** Kharpatikoidi ot tsentralnata chast na iztochnoto kraibrezhie na Atlanticheskiya okean. [Harpacticoida from the eastern Central Atlantic coast.]. *Izvestiya na Institutata Okeanografiya i Ribno Stopanstvo. Varna*, **15**: 83-98. [In Bulgarian with English and Russian summaries].
- Marinov T.M. 1978.** Kachestven s'tav i kolichestveno razpredelenie na meiobentosa ot B'lgarskiya uchast'k na Chernomore. 1. Qualitative composition and quantitative distribution of the meiobenthos of the Bulgarian Black Sea waters. *Izvestiya na Institutata Okeanografiya i Ribno Stopanstvo. Varna*, **16**: 35-49. [In Bulgarian with Russian and English summaries].
- Marinov T.M. & Apostolov A.M. 1981.** Contribution à l'étude des Copépodes Harpacticoides de la mer Adriatique (côte Yougoslave). 2. Sur le méiobenthos du cap Piran. *Acta zoologica bulgarica*, **18**: 23-30.
- Marinov T.M. & Apostolov A.M. 1985.** Copépodos Harpacticoides de l'Océan Atlantique. 1. Espèces des côtes du Sahara espagnol. *Cahiers de Biologie marine*, **26**(2): 165-180.
- Monard A. 1928.** Les Harpacticoides marins de Banyuls. *Archives de Zoologie expérimentale et générale*, **67**: 259-443.
- Monard A. 1935a.** Les Harpacticoides marins de la région de Salammbô. *Bulletin de la Station océanographique de Salammbô*, **34**: 1-94.
- Monard A. 1935b.** Étude sur la faune des Harpacticoides marins de Roscoff. *Travaux de la Station biologique de Roscoff*, **13** : 5-88.
- Monard A. 1937.** Les Harpacticoides marins de la région d'Alger et de Castiglione. *Bulletin de la Station d'Aquiculture et de Pêche de Castiglione*, **1935**(2): 9-93.
- Moore C.G. 1979.** Analysis of the associations of meiobenthic Copepoda of the Irish Sea. *Journal of the marine biological Association of the United Kingdom*, **59**(4): 831-849.
- Moore P.G. 1973.** The kelp fauna of northeast Britain II. Multivariate classification: turbidity as an ecological factor. *Journal of experimental marine Biology and Ecology*, **13**: 127-164.
- Nicholls A.G. 1945.** Marine Copepoda from Western Australia. III. Littoral harpacticoids from Port Denison. *Journal of the Royal Society of Western Australia*, **29**: 1-16.
- Nodot C. 1978.** Cycles biologiques de quelques espèces de Copépodes Harpacticoides psammiques. *Téthys*, **8**(3): 241-248.
- Noodt W. 1955.** Marmara denizi Harpacticoid'leri (Crust. Cop.). Marine Harpacticoiden (Crust. Cop.) aus dem Marmara Meer. *Istanbul Üniversitesi Fen Fakültesi Mecmuası*, (B)**20**(1-2): 49-94.
- Noodt W. 1964.** Copepoda Harpacticoida aus dem Litoral des Roten Meeres. *Kieler Meeresforschungen*, **20**, Sonderheft: 128-154.
- Norman A.M. & Brady G.S. 1909.** The Crustacea of Northumberland and Durham. *Transactions of the Natural History Society of Northumberland, Durham and Newcastle-upon-Tyne*, n.ser. **3** : 252-417.
- Norman A.M. & Scott T. 1906.** *The Crustacea of Devon and Cornwall*. London: William Wesley and Son. i-xv + 232 pp.
- Pallares R.E. 1975.** Copépodos marinos de la Ría Deseado (Santa Cruz, Argentina). Contribución sistemático-ecológica. IV. Conclusión. *Physis*, (A)**34**(89): 213-227.
- Pallares R.E. & Hall M.-A. 1974a.** Analisis bioestadístico-ecológico de la fauna de Copépodos asociados a los bosques de *Macrocystis pyrifera*. *Physis*, (A)**33**(86): 275-319.
- Pallares R.E. & Hall M.-A. 1974b.** Analisis bioestadístico-ecológico de la fauna de Copépodos asociados a los bosques de *Macrocystis pyrifera*, conclusión. *Physis*, (A)**33**(87): 409-432.
- Por F. 1959.** Harpacticode noi (Crustacea, Copepoda) din mîlurile Mării Negre. [Harpacticoides nouveaux (Crustacés, Copépodes) des vases de la mer Noire]. *Studii si Cercetari de Biologie, Seria Biologie animala*, **4**(11): 347-368.
- Por F.D. 1964a.** A study of Levantine and Pontic Harpacticoida (Crustacea, Copepoda). *Zoologische Verhandlungen, Leiden*, **64**: 1-128.
- Por F.D. 1964b.** Les Harpacticoides (Crustacea, Copepoda) des fonds meubles du Skagerak. *Cahiers de Biologie marine*, **5**: 233-270.
- Por F.D. 1965.** Harpacticoida (Crustacea, Copepoda) from muddy bottoms near Bergen. *Sarsia*, **21**: 1-16.
- Roe K.M. 1958.** The littoral harpacticoids of the Dalkey (Co. Dublin) area with descriptions of six new species. *Proceedings of the Royal Irish Academy*, (B)**59**(12): 221-255.
- Roe K.M. 1960.** Some harpacticoids from Lough Ine, with descriptions of two new species. *Proceedings of the Royal Irish Academy*, (B)**60**(8): 277-289.
- Rouch R. 1962.** Harpacticoides (Crustacés Copépodes) d'Amérique du Sud. *Biologie de l'Amérique Australe*, **1**: 237-280.

- Sars G.O. 1909.** Copepoda Harpacticoida. Parts XXV & XXVI. Laophontidae (concluded), Cletodidae (part). *An Account of the Crustacea of Norway, with short descriptions and figures of all the species*, 5: 277-304.
- Sars G.O. 1911.** Copepoda Harpacticoida. Parts XXXIII & XXXIV. Supplement (continued). *An Account of the Crustacea of Norway, with short descriptions and figures of all the species*, 5: 397-420.
- Scott T. 1894.** Additions to the fauna of the Firth of Forth. *Report of the Fishery Board for Scotland*, 12(3): 231-271.
- Scott T. 1897.** The marine fishes and invertebrates of Loch Fyne. *Report of the Fishery Board for Scotland*, 15(3): 107-174.
- Scott T. 1904.** Copepoda. In: Plankton tables. Scotland. *Bulletin des Résultats acquis pendant les Courses périodiques. Publié par le Bureau du Conseil permanent international pour l'Exploration de la Mer*, 1903-1904(D): 38-47, 108-109, 140-142, 186-199.
- Scott T. 1906.** A catalogue of the land, fresh-water and marine Crustacea found in the basin of the River Forth and its estuary. Copepoda. *Proceedings of the Royal Physical Society of Edinburgh*, 16: 296-375.
- Scott T. 1907.** Copepoda. In: Plankton tables. Scotland. *Bulletin trimestriel des Résultats acquis pendant les Croisières périodiques. Conseil permanent international pour l'Exploration de la Mer*, 1905-1906(D): 20-23, 56-57, 78-79, 122-122b.
- Soyer J. 1971.** Bionomie benthique du plateau continental de la côte catalane française. III. Les peuplements de Copépodes Harpacticoides (Crustacea). *Vie et Milieu*, (B)21(2): 337-511.
- Terazaki M. 1991.** Study on deep-sea plankton. *Proceedings. Advances in Marine Technology Conferences*, 4: 25-31. [In Japanese].
- Thompson I.C. 1893.** Revised report on the Copepoda of Liverpool Bay. *Proceedings and Transactions of the Liverpool Biological Society*, 7: 175-230.
- Toda T., Kikuchi T., Hashimoto J. & Terazaki M. 1995.** A survey of deep-sea benthopelagic organisms by a multiple plankton sampler attached to the deep tow system. In: Snidvongs A, Utoomprukporn W, Hungspreugs M (eds). *Proceedings of the NRCT-JSPS Joint Seminar on Marine Science, December 2-3, 1993, Songkhla, Thailand*. Bangkok: Department of Marine Science, Chulalongkorn University: 171-178.
- Wells J.B.J. 1963.** Copepoda from the littoral region of the estuary of the River Exe (Devon, England). *Crustaceana*, 5(1): 10-26.
- Wells J.B.J. 1964.** Some additions to the Dale Fort marine fauna. *Proceedings of the zoological Society of London*, 142: 453-458.
- Wells J.B.J. 1965.** Copepoda (Crustacea) from the meiobenthos of some Scottish marine sub-littoral muds. *Proceedings of the Royal Society of Edinburgh*, (B)69(1): 1-33.
- Wells J.B.J. 1970.** The marine flora and fauna of the Isles of Scilly. Crustacea: Copepoda: Harpacticoida. *Journal of natural History*, 4: 255-268.
- Willey A. 1930.** Harpacticoid Copepoda from Bermuda. Part I. *Annals and Magazine of Natural History*, (10) 6: 81-114.