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Generic concepts in the Clytemnestridae (Copepoda, Harpacticoida), revision and revival

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SYNOPSIS. The family Clytemnestridae is one of the very few holoplanktonic harpacticoid lineages, typically occurring in the epipelagic zone of all oceans. Its monogeneric status and the cosmopolitan distribution of the only two species, *Clytemnestra scutellata* Dana, 1847 and *C. rostrata* (Brady, 1883), have been universally accepted since 1891. Re-examination of the major expedition collections (*Challenger* 1873–76, Cambridge Suez Canal Expedition 1924, Great Barrier Reef Expedition 1928–29, *Discovery*) in the Natural History Museum proved both perceptions to be false. The generic concepts introduced by Claus (1891*b*) but rejected by subsequent authors are revived, resulting in the recognition of two valid genera *Clytemnestra* Dana, 1847 (syn. *Goniopelte* Claus, 1891*a*) and *Goniopsyllus* Brady, 1883 (syn. *Sapphir* Car, 1890). Genera are separated on the basis of antennulary segmentation, caudal ramus sexual dimorphism and differences in the armature of the antenna, maxillule, maxilla, P1 and P2. Fundamental discrepancies are found in the female genital field and the male gonopores.

Species discrimination prior to this revision was exclusively based on generic characters. Detailed examination of NHM material has quadrupled the number of species in the family. Redescriptions are provided for both *C. scutellata* and *G. rostratus*, and descriptions are given for five new species previously confounded with these type species: *C. farrani* sp. nov., *C. longipes* sp. nov., *C. asetosa* sp. nov., *G. clausi* sp. nov. and *G. brasiliensis* sp. nov.

Goniopelte gracilis Claus, 1891*a* is redescribed and reinstated as a valid species in *Clytemnestra*. It is believed to represent the Atlantic-Mediterranean sister-species of *C. scutellata* which presumably assumes only a restricted eastern Indo-Pacific distribution. Neotypes are designated for *C. scutellata* and *C. gracilis*. Mediterranean and other European records of *G. rostratus* in reality refer to *G. clausi* sp. nov.

C. hendorffi Poppe, 1890 is a junior subjective synonym of *C. scutellata*. The doubtful status of *Sapphir rostratus* Car, 1890, *Clytemnestra tenuis* Lubbock, 1860 and *C. hendorffi* var. *quinquesetosa* Poppe, 1890 is discussed.

The intricate taxonomic history of the family is reviewed, including the nomenclatural confusion surrounding the priority of the family name. The phylogenetic relationships of the Clytemnestridae as well the ontogenetic processes underlying the caudal ramus sexual dimorphism in *Clytemnestra* are discussed. The taxonomic impediment in marine plankton research caused by the failure to recognize pseudo-sibling or cryptic species is highlighted.

INTRODUCTION

The greatest habitat shift performed by copepods was undoubtedly the colonization of the open pelagic environment, covering 71 percent of the Earth's surface and providing a volume of 1347 million cubic kilometres. This habitat was most successfully exploited by the calanoids which can be regarded as the marine planktonic copepods *par excellence* (Huys & Boxshall, 1991), and to a lesser extent by the cyclopoids and poecilostomatoids which can be particularly abundant in small mesh net samples. The evolutionary history of harpacticoid copepods in the marine plankton is less of a success story and is to be viewed as the result of multiple colonization. Only three families are currently considered as exclusively holoplanktonic, the Miraciidae, Euterpinidae and Clytemnestridae, and each of them can be regarded as an evolutionary *cul de sac*. The Miraciidae contains 4 monotypic genera which are typically associated with marine filamentous Cyanobacteria (Huys & Böttger-Schnack, 1994). The Euterpinidae is represented by a single species *Euterpina acutifrons* (Dana, 1847) which is often abundant in shallow neritic waters. The Clytemnestridae currently comprises two cosmopolitan species which are primarily found in the epipelagic zone but frequently penetrate into deeper layers. The Aegisthidae, commonly regarded as typical holoplanktonic forms found in the mesopelagic and bathypelagic zones, has recently been shown to be only a secondary offshoot from a hyperbenthic ancestral stock (Conroy-Dalton & Huys, 1999; Lee & Huys, in press). Other pelagic harpacticoids exhibit an essentially benthic biology by their association with 'planktonic' substrata, such as *Microsetella* spp. which attach themselves to discarded and occupied larvacean houses (Appendicularia) (Ohtsuka *et al.*, 1993), and *Parathalestris croni* (Krøyer, 1846) which is typically associated with floating macroalgal clumps (Ingólfsson & Ólafsson, 1997).

Clytemnestrids have been known since the advent of the pioneering oceanographic expeditions such as the U.S. Explorer Expedition (Dana, 1854) and the Voyage of the H.M.S. *Challenger* (Brady, 1883). They were originally classified as poecilostomatoids until Claus (1891*a*) demonstrated their harpacticoid identity. Virtually all of the taxonomic literature on this family was published in the second half of the 1800s and apart from cursory treatment by Lang (1948), Wells (1970) and Boxshall (1979) no significant contributions have been added since.

MATERIAL AND METHODS

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. Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, England) or transparent nail varnish. All drawings have been prepared using a camera lucida on a Leitz Dialux or Leitz DMR microscope equipped with differential interference contrast.

Clytemnestra gracilis and *Goniopsyllus clausi* were examined with a Philips XL30 scanning electron microscope. Specimens were prepared by dehydration through graded acetone, critical point dried, mounted on stubs and sputter-coated with palladium.

Citations of articles in the International Code of Zoological Nomenclature (ICZN) refer to the fourth edition published in August 1999 and superseding previous editions with effect from 1 January 2000. Type series and other material is deposited in the collections of the Natural History Museum, London (BMNH).

TAXONOMIC HISTORY

The proliferation of generic names in this family at the end of the 19th century marked one of the most virulent episodes in the history of harpacticoid taxonomy. The key players in this debate were the eminent and influential Carl Claus and a cohort of opponents including Wilhelm Giesbrecht, S.A. Poppe and Lazar Car. It is clear that much of the confusion arose from observational errors made by both Dana (1854) and Brady (1883).

Clytemnestra Dana, 1847

Dana introduced the genus *Clytemnestra* in the first part of his 'Conspectus Crustaceorum' which was published in 1847 (for discussion of publication dates see Huys & Böttger-Schnack, 1994) and included the families Cyclopidae and Harpactidae. This paper, completely lacking in illustrations, provided a Latin diagnosis for the genus and its only species *C. scutellata* which was placed in the 'Harpactidae' together with *Harpacticus* Milne Edwards, 1840 and *Setella* Dana, 1846. Although no type locality was designated, the author did mention that the species was found near the Gilbert Islands and east of Tuamotu in the Pacific Ocean and in the South China Sea. In his second volume of the Crustacea of the United States Exploring Expedition (Dana, 1854) a more extensive and illustrated description of *C. scutellata* was given based on specimens from the Tuamotu samples.

Lubbock (1856) added a second species *C. atlantica* which he described on the basis of a single female from an unspecified locality in the Atlantic. The brief original description included illustrations of the habitus and antenna only. Various authors (Poppe, 1891; Giesbrecht, 1892; Lang, 1948) have questioned this identification and referred the species to the genus *Pachos* Stebbing in the Poecilostomatoida. Pesta (1909) considered *C. atlantica* as a synonym of *Pachos punctatum* (Claus). In a later report Lubbock (1860) described *C. tenuis*, again from a single female, collected east of Mauritius. Lubbock himself had some reservations about the sexual maturity of the specimen, and Poppe (1891) considered the species as unrecognizable. Giesbrecht (1892) listed *C. tenuis* as a possible synonym of *C. rostrata*.

Claus (1863) rejected *Clytemnestra* as a valid genus by stating that the illustrations were so inadequate that they were worthless for identification purposes.

Goniopsyllus Brady, 1883

Brady (1883) established this genus for a single specimen found in a tow-net gathering taken off the Argentinean coast during the voyage of the H.M.S. *Challenger*. He regarded *Goniopsyllus rostratus* as most closely related to the harpacticoid genera *Enhydrosoma* Boeck and *Cletodes* Brady despite the marked differences in the mouthparts. In addition, Brady remarked on the similarity in swimming leg morphology with *Peltidium* and recognized a certain affinity with the Sapphirinidae because of the rudimentary structure of the mouthparts. The description of *G. rostratus* is fragmentary and partly inadequate. Brady (1883) failed to observe the mandible.

Sapphir Car, 1890

Car (1890) described both sexes of *Sapphir rostratus* from plankton samples taken off Trieste in the Adriatic. He used and revised Brady's (1878) classification, dividing the free-living copepods in 6 families (Calanidae, Cyclopidae, Harpactidae, Peltididae, Corycaeidae and Sapphirinidae), but was apparently unaware of Brady's (1883) later paper describing the closely related *Goniopsyllus rostratus*. Car (1890) placed *Sapphir* in the Sapphirinidae merely by way of elimination and excluded the genus from the two harpacticoid families known at that time (Harpactidae, Peltididae) by virtue of the absence of (1) geniculate setae on the antennae, (2) a palp on the mandible and maxillule, (3) modifications of the P1, and (4) a foliaceous P5. Allocation to the Sapphirinidae was substantiated by the dorsoventrally depressed body, the 6-segmented antennules which are similar in both sexes (Car did not recognize the sexual dimorphism and male geniculation), the antenna lacking a defined exopod and geniculate setae on the endopod, the reduced mouthparts, the sexually dimorphic maxillipeds and the small P5.

In a short note Dahl (1890) considered *S. rostratus* a junior subjective synonym of *G. rostratus* but gave no justification for this course of action.

Car (1891*a*) admitted that he had overlooked Brady's (1883) *Challenger* report describing *G. rostratus* but maintained the distinction between both genera. His conviction was based on three doubtful observations made by Brady (1883): (1) his statement that all four swimming legs were 'nearly alike' having 3-segmented rami; Brady only figured the P2 which he labelled 'One of the swimming feet', (2) the maxillipeds which were described and figured as 3-segmented, and (3) the 3-segmented fifth legs. Car pointed out that in *Sapphir* the P1 exopod was clearly 1-segmented, and both the maxillipeds and the P5 2-segmented, but did not consider the possibility that this incongruity could be based on observational errors made by Brady. It was largely this failure that initiated the subsequent dispute between Car and Claus.

Goniopelte Claus, 1891*a*

Both sexes of *Goniopelte gracilis* were described in remarkable detail by Claus (1891*a*) on the basis of scanty material (1♀ and 1♂) collected from an unspecified locality in the Eastern Mediterranean. He recognized the male geniculation ('elastischen Cuticularapparat') and the 'accessory' aesthetascs of the antennules, the sexual dimorphism of the caudal rami and the presence of the male P6. Claus also revealed details of the internal anatomy such as the tripartite nauplius eye, the asymmetry of the male genital system and the presence of integumental glands around the rostrum and the pleural areas of the cephalothorax, pedigerous somites and abdomen.

Claus (1891*a*) severely criticized the quality of both Brady's (1883) and Car's (1890) descriptions and like Dahl (1890) professed that *G. rostratus* and *S. rostratus* were not only congeneric but also conspecific. The differentiating characters used by Car (1890, 1891*a*) he regarded as irrelevant to the issue. He presented convincing arguments showing that Brady's holotype of *G. rostratus* could not possibly have been a male. Claus was also the first author to reconsider Dana's *Clytemnestra scutellata*. He placed the species with reservations in the Scutellidiinae ('Scutellidinen'), a subfamily of the Peltidiidae ('Peltididen'), despite similarities in general body shape and maxilliped structure with his new genus and species *Goniopelte gracilis*.

Claus (1891*a*) remarked that the moderate flattening of the body, the reduction of the mandible and maxillule, and the 1-segmented P1 exopod in *G. gracilis* would probably warrant the erection of a third subfamily within the Peltidiidae. An alternative option suggested by Claus was to regard it as a transitionary group between the Peltidiidae and Harpacticidae.

Car's (1891*b*) re-examination of *S. rostratus* did not disclose new information apart from the confirmation of the 4-segmented condition of the antenna. Although his rebuttal was mainly aimed at showing disapproval of Claus' (1891*a*) provocative paper, it contained clear indications of the author's ambivalence about both the conspecificity and familial placement of *S. rostratus*. Car maintained the latter as a valid genus and species but did not exclude potential synonymy with *G. rostratus*. He kept the genus in the Sapphirinidae but pointed out the close relationship between *Sapphir*, *Goniopsyllus* and *Goniopelte* and the possible option of proposing a new family for these three genera. Finally, he disagreed with Claus (1891*a*) on the sexual identity of the holotype of *G. rostratus*, using the unconfirmed presence of an internal spermatophore in Brady's (1883) habitus drawings as the only counterargument.

A breakthrough in unravelling the intricate synonymy was realized by Poppe who had already recognized the identity between *Clytemnestra* and *Goniopsyllus* in 1884 but did not publish his results until 1891. Poppe's (1891) comprehensive paper, which downgraded *Goniopsyllus* and *Sapphir* to junior synonyms of *Clytemnestra*, was based on a wide range of specimens including the holotype of *G. rostratus* and a male of *S. rostratus* from Car's collection. He described a new species, *Clytemnestra hendorffi* from material collected in the Java Sea, the Indian Ocean (south of Madagascar, Western Australian Basin) and the South Atlantic (off Brazil and Argentina). Poppe (1891) also re-examined Thompson's (1888) material of *G. rostratus* from Malta and identified it as *C. hendorffi*. Among the material from the Java Sea he discovered a variety *quinquesetosa* which differed from the typical form in the longer P5 which carried only 5 setae on the exopod, a more stocky abdomen in both sexes and the caudal rami which were relatively wider proximally.

Poppe (1891) synonymised *G. rostratus* and *S. rostratus* and considered the previous distinction between them to be based on erroneous observations of the P5 by both Brady and Car, and the fact that Brady had misidentified the holotype of *S. rostratus* as a male and overlooked the P1 exopod in this species. For some unknown reason he suspected the latter to be 2-segmented in *G. rostratus*. He considered only 3 species as valid, all of which he placed in *Clytemnestra*: *C. scutellata*, *C. hendorffi* and *C. rostrata* (Brady). Poppe further regarded the inadequately described *C. tenuis* as a probable synonym of *C. scutellata* and excluded Lubbock's second species *C. atlantica* from the genus on account of the different body shape and the structure of the antennules.

Poppe (1891) did not accept Car's (1890, 1891*a–b*) placement in the Sapphirinidae and created a new family Pseudo-Peltididae which showed similarities with the Peltidiidae but differed in the morphology of the P1 (exopod not prehensile and 2-segmented (!) according to Poppe's diagnosis), the absence of a well defined antennary exopod and strongly reduced mouthparts.

With Giesbrecht's (1891*a*) claim that *Goniopelte* had already been described under three different generic names the synonymy issue surrounding *Clytemnestra* appeared to have come to a close. Claus (1891*b*), however, continued to defend his genus *Goniopelte* with extraordinary persistence. After re-examination of Poppe's (1891) material, confirming the presence of the male P6, and the vestigial antennary exopod, he acknowledged the conspecificity of *G. gracilis* and *C. hendorffi*. Nevertheless, he adhered to his earlier decision (Claus, 1863) to dismiss *Clytemnestra* as a valid genus. He based this course of action on the rules drawn up by Raphael Blanchard and Maurice Chaper and adopted, in part, at the First International Congress of Zoology (Paris, 1889). They stipulated in § 7 that the valid name should be the oldest one provided that '. . . ce nom etc. aura été clairement et suffisament defini'. Claus (1891*b*) rejected Poppe's (1891) arguments as insufficient for the proposal of a new family and instead created a third subfamily Goniopeltidinae in the Peltididiidae. In this subfamily he recognized two genera, *Goniopsyllus* (syn. *Sapphir*) and *Goniopelte*, which were differentiated on the basis of antennule segmentation, antennary exopod setation and caudal ramus sexual dimorphism.

Claus' (1891*b*) generic concepts were finally rejected by Giesbrecht (1892) who reviewed the intricate synonymy and reinstated *Clytemnestra* as the only valid genus on the basis of the Principle of Priority. Giesbrecht (1891*b*, 1892) recognized only two species, *C. scutellata* and *C. rostrata*, and regarded all other species as subjective synonyms with the possible exception of *C. tenuis*. This course of action was adopted by most subsequent authors such as Lang (1944, 1948) and Boxshall (1979). The rapid accumulation of plankton data during the 20th century fed the conjecture that both species assumed a cosmopolitan distribution. Unfortunately, this presumption made people loose sight of the possible existence of other undescribed species and of the true identitiy of *C. scutellata* and *G. rostratus*.

PRIORITY OF THE FAMILY NAME

Although various authors (Car, 1891*b*; Claus, 1891*a*) had expressed the need to introduce a new family or subfamily for *Goniopsyllus*, *Goniopelte* and *Sapphir* it was finally Poppe (1891) who coined the family name Pseudo-Peltididae for the only included genus *Clytemnestra*. Claus (1891*b*) rejected the family status of Pseudo-Peltididae and established a new subfamily Goniopeltidinae for *Goniopelte* and *Goniopsyllus*. Giesbrecht (1892) did not consider familial assignment which probably misled A. Scott (1909) who did not consult the earlier literature and consequently proposed the new family name Clytemnestridae for the type and only genus *Clytemnestra*. Mori (1929) placed this genus in the Harpacticidae whereas Wilson (1932) referred it to the Tachidiidae for some unknown reason, an inexplicable assignment followed also by Carvalho (1952) and Krishnaswamy (1953).

Most workers (e.g. Sars, 1921; Monard, 1927; Sewell, 1940; Klie, 1943) adopted Clytemnestridae as the valid family name until Lang (1944, 1948) pointed out that Poppe's Pseudo-Peltididae took priority over the latter. Boxshall (1979) remarked that this course of action contravened ICZN Art. 11.7.1.1 since a family-group name must, when first published, be based on the name then valid for a contained genus. Poppe's (1891) family name with its alternative spellings Pseudo-Peltididae (Poppe, 1891), Pseudo-Peltidiidae (Lang, 1944) and Pseudopeltidiidae (Wells, 1976) is therefore unavailable. Boxshall (1979) reinstated Clytemnestridae as the valid name, but unfortunately ignored Claus' (1891*b*) older and validly introduced family-group name Goniopeltidinae. Other authors continued using Pseudopeltidiidae (e.g. Bowman & Abele, 1982).

Were priority to be rigorously enforced, Goniopeltididae should replace its junior synonym Clytemnestridae and hence leave Claus, at best, a pyrrhic victory. However, since the senior synonym Goniopeltidinae has remained unused as a valid name since 1899 (ICZN Art. 13.9.1.1) and the junior synonym Clytemnestridae has been used as the presumed valid name in at least 25 works (Krishnaswamy, 1957; Marques, 1957; Bruce *et al.*, 1963; Kasturirangan, 1963; Cheng *et al.*, 1965; Owre & Foyo, 1967; Fagetti, 1962; Chen *et al.*, 1974; Boxshall, 1979; De Decker, 1984; Citarella, 1986; Hicks, 1988; Huys & Boxshall, 1991; Razouls & Durand, 1991; Campos Hernández & Suárez Morales, 1994; Huys & Böttger-Schnack, 1994; Kazmi & Muniza, 1994; Hirota, 1995; Huys *et al.*, 1996; Razouls, 1996; Bodin, 1997; Chihara & Murano, 1997; Hure & Kršinić, 1998; Reid, 1998; Suárez Morales & Gasca, 1998) published by at least 10 authors in the immediately preceding 50 years (and encompassing a span of not less than 10 years) (ICZN Art. 13.9.1.2.) it is to be considered a forgotten name (*nomen oblitum*). In accordance with Art. 23.9.1. prevailing usage is maintained and the junior name Clytemnestridae is treated as a *nomen protectum*.

SYSTEMATICS

Claus' (1891*b*) generic concepts of *Goniopelte* and *Goniopsyllus* were based on differences in antennule segmentation, antennary exopod setation and caudal ramus sexual dimorphism. Re-examination of material attributed to *C. scutellata* and *C. rostrata* have revealed additional differentiating characters in mouthpart structure, swimming leg setation and female genital field morphology, substantiating Claus' recognition of two distinct genera. Secondly, there is accumulating evidence that both *C. scutellata* and *C. rostrata* represent species complexes, each of which can be justifiably assigned generic rank. It has not been our intention to verify every published record of these species since in most cases the information contained in the numerous marine plankton studies did not permit unambiguous identification. This paper is based almost solely on BMNH collections and serves as a baseline study for future species discrimination in the Clytemnestridae. It is aimed primarily at reviving and elaborating Claus' (1891*b*) original generic concepts, albeit partly under different taxonomic names.

Family **CLYTEMNESTRIDAE** A. Scott, 1909

DIAGNOSIS. Body distinctly tapering posteriorly. Prosome dorsoventrally flattened, urosome slender and cylindrical. First pedigerous somite incorporated in cephalosome forming bell-shaped cephalothorax. Pedigerous somites bearing P2–P4 with posteriorly directed alate projections. Genital and first abdominal somites of ♀ completely fused forming genital double-somite; original segmentation marked by small chitinized internal ribs ventrally or laterally. Anal operculum obsolete; anus terminal.

Sexual dimorphism in antennule, maxilliped, P6, urosomal ornamentation and in genital segmentation; often in rostrum shape, occasionally in caudal ramus. No distinct sexual dimorphism in P1–P5.

Rostrum large, fused to cephalic shield. Antennules slender; 6- or 7-segmented in ♀; haplocer and distinctly or indistinctly 7-segmented in ♂, with geniculation between segments 6 and 7; aesthetascs present on 4th and apical segments in ♀, on 3rd, 5th and apical

segments in ♂; transformed aesthetasc-like setae present on segments 3, 4 and 6(or 7) in ♀, and segments 3, 5 and 7 in ♂. Antenna with separate basis and 2-segmented endopod; basis and proximal endopod segment unarmed; distal endopod segment with 1 lateral and 4–5 apical elements; exopod a minute segment with 1–2 long setae. Mandibles, maxillules and maxillae reduced. Mandible with stylet-like gnathobase, palp represented by 1 short seta. Maxillule a small segment with 1 or 3 elements. Maxilla with 1–2 endites on syncoxa; allobasis with articulating claw and 2 accessory elements. Maxillipeds very large with elongate syncoxa and basis; syncoxa with 1 seta, basis with 1 short seta and 1 pad-like element on palmar margin; endopod represented by sexually dimorphic claw and 5 accessory elements.

P1 with 1-segmented exopod and 3-segmented non-prehensile endopod; basis without inner seta/spine. P2–P4 with transversely elongated basis bearing short outer seta; rami 3-segmented with endopods longer than exopods. Outer spines of exopod segments typically setiform, often with flagellate tip. Armature formula as follows:

	exopod	endopod
P1	[0–1]21	1.1.220
P2	1.1.22[2–3]	1.2.221
P3	1.1.32[2–3]	1.2.321
P4	1.1.32[2–3]	1.2.221

P5 uniramous, comprising basis and 1-segmented exopod; laterally displaced; exopod elongate, with 5–6 setae.

Female genital field positioned anteriorly; genital apertures paired or fused to median slit; closed off by vestigial P6 bearing 1 element; copulatory pore unpaired. P6 ♂ with 1 or 3 elements; closing off median or asymmetrically positioned (sinistral/dextral) genital aperture.

Caudal rami conical or rectangular, short; rear margin between setae III and IV produced into conical process bearing apical pore; setae I–II spiniform and strongly developed (seta I longer than II); setae IV–V fused at base, without fracture planes.

One median egg-sac; spermatophores elongate, with very long recurved neck.

Holoplanktonic, marine.

TYPE GENUS. *Clytemnestra* Dana, 1847

OTHER GENUS. *Goniopsyllus* Brady, 1883

Genus *Clytemnestra* Dana, 1847

Goniopelte Claus, 1891*a* [type species: *G. gracilis* Claus, 1891 – by monotypy]

DIAGNOSIS. Clytemnestridae. Body without dorsal pattern of denticles or spinules on urosomites. Antennule distinctly 7-segmented in both sexes; ♂ segmental homologies: 1–I, 2–(II–VIII), 3–(IX–XIII), 4–(XIV–XVII), 5–(XVIII), 6–(XIX–XX), 7–(XXI–XXVIII); segment 5 in ♂ with large spine. Antenna with 1 lateral and 5 apical elements on distal endopod segment; exopod represented by well defined segment bearing 2 long setae. Maxillule represented by bilobed segment with 1 lateral seta and 2 apical spines. Maxillary syncoxa with 1–2 endites; proximal endite represented by very long seta, sometimes absent; distal endite bearing 3 setae.

P1 with outer seta on basis; exopod with 4 setae. P2 without outer spine on exp–1. P1–P4 armature formula:

	exopod	endopod
P1	121	1.1.220
P2	1.1.22[2–3]	1.2.221
P3	1.1.32[2–3]	1.2.321
P4	1.1.32[2–3]	1.2.221

P5 exopod with 5 or 6 setae in both sexes.

Genital apertures paired in ♀; closed off by paired P6 bearing 1 vestigial element; copulatory pore small, located anteriorly between genital apertures; copulatory duct probably very short and definitely not strongly chitinized.

Male P6 almost symmetrical, fused medially forming membranous operculum closing off single median genital aperture; produced into cylindrical process bearing 3 small setae.

Caudal rami parallel, almost cylindrical; sexually dimorphic with setae IV–V short and pinnate in ♀, long and multiplumose in ♂; additional sexual dimorphism also noted in setae III and VI.

TYPE SPECIES. *Clytemnestra scutellata* Dana, 1847 [by monotypy].

OTHER SPECIES. *C. gracilis* (Claus, 1891*a*) comb. nov., *C. farrani* sp. nov., *C. longipes* sp. nov., *C. asetosa* sp. nov.

SPECIES INQUIRENDAE. *Clytemnestra hendorffi* var. *quinquesetosa* Poppe, 1891

REMARKS. Various authors, including Giesbrecht (1892), Sars (1921), Mori (1937) and Boxshall (1979), have erroneously described the ♀antennule as 8-segmented. From the illustrations of Giesbrecht, Sars and Mori it appears that the basal pedestal has been repeatedly misinterpreted as an additional segment. Although his description contradicts the accompanying illustration, the proportional segment lengths given by Boxshall (1979) for the *C. scutellata* antennule suggest a similar observational error.

Clytemnestra scutellata Dana, 1847

Clytemnestra Hendorffi Poppe, 1891: 132–136, Taf. I.

The form of the maxilliped and the 6-segmented urosome clearly identify Dana's (1854) illustrated specimen as a male. The appendage labelled 'extremity of a maxilliped' (his Fig. 12d) is almost certainly the P5 exopod. We concur with Claus (1863, 1891*a–b*) that the original description of *C. scutellata* does not provide the bare minimum for unequivocal identification. In fact, the synonymy of *Clytemnestra* with *Goniopelte* advocated by Giesbrecht (1891*a*, 1892) is justified solely by the long terminal setae of the caudal rami figured in Dana's (1854) habitus drawing. This sexually dimorphic feature is the only character in Dana's description which both positively identifies his species as a *Clytemnestra* and excludes it from the genus *Goniopsyllus*. If Dana had figured a female specimen even this generic determination would not have been possible.

Since both *Clytemnestra* and *C. scutellata* have now been widely accepted for almost a century, we have retained both names in the interest of stability of nomenclature even though they are virtually unidentifiable on the basis of Dana's description. The original type material no longer exists and the male specimen figured in Dana (1854) is so badly illustrated that we have refrained from designating it as the lectotype. In order to settle the issue a neotype has been designated from BMNH material collected from the Great Barrier Reef by Farran (1936) which forms the basis of the description below.

TYPE LOCALITY. The determination of the type locality presents some difficulty. In his original diagnosis Dana (1847) listed three

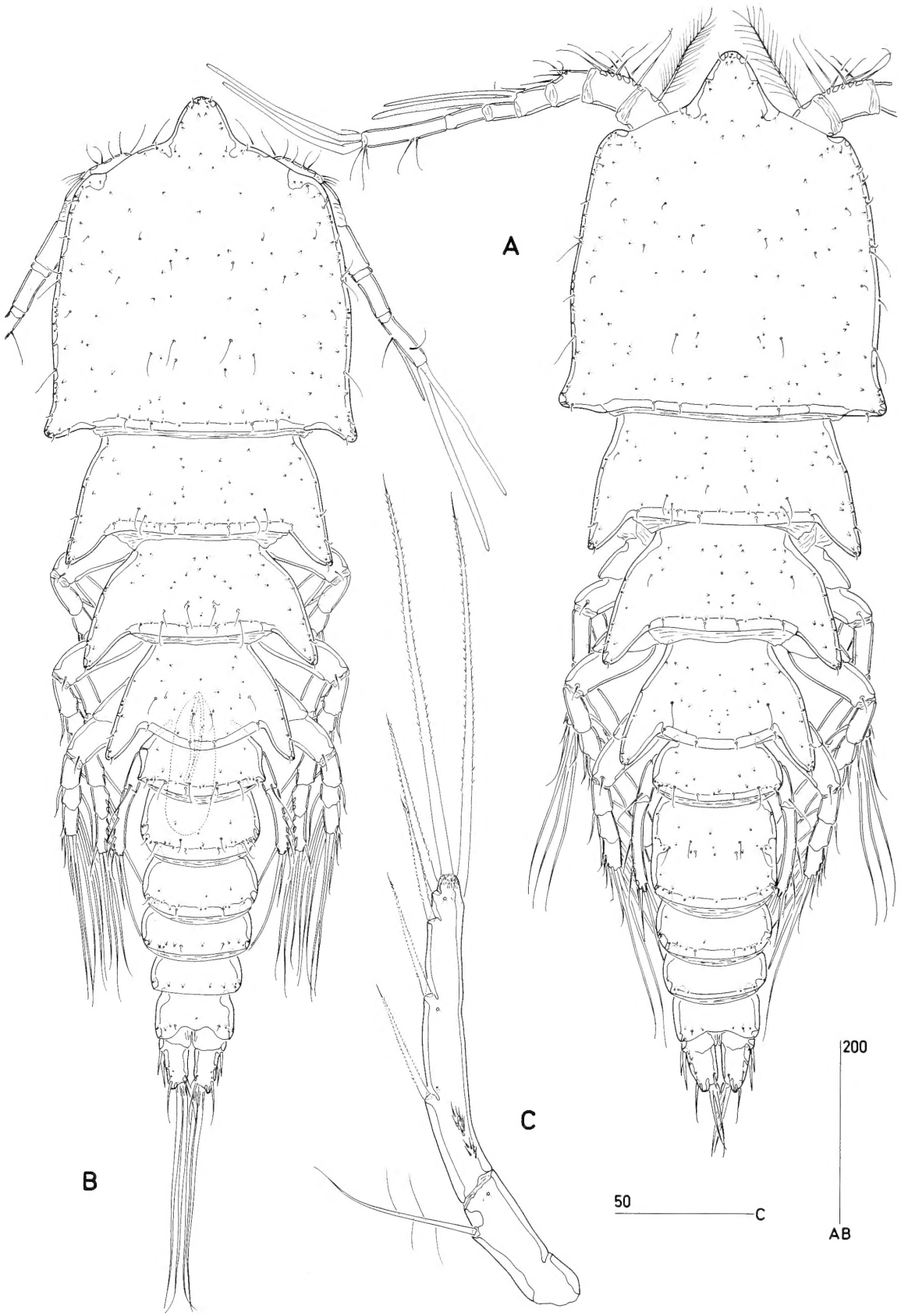

Fig. 1 *Clytemnestra scutellata* Dana, 1847. A, Habitus ♀, dorsal; B, habitus ♂, dorsal; C, P5 ♀, anterior. [A, C based on neotype].

localities, i.e. the South China Sea (300 miles NE of Singapore), near Pitt's Island (Kingsmill Group, Kiribati) and the eastern Pacific Ocean at 18°S 124°W, but he did not designate a type locality. In his illustrated description (Dana, 1854) he mentioned that the description and figures were based on specimens from the eastern Pacific which could arguably be considered as the type locality.

Farran (1936) recorded a total of 11 specimens of *C. scutellata* from 6 different stations sampled during the Great Barrier Reef Expedition in 1928–29. Five specimens were found in serial townettings inside the reef and another six specimens were discovered in deeper waters outside the reef. Examination of Farran's spirit preserved material in the Natural History Museum (BMNH 1948.4.28.121) revealed 3 ♀♀, 5 ♂♂ and 1 damaged ♀ prosome, representing at least 3 different species. According to Farran (1936) the specimens from the reef flat were significantly smaller (0.8–0.9 instead of 1.05–1.20 mm) except for one male which measured 1.15 mm. The small specimens (2 ♀♀, 2 ♂♂) are present amongst the NHM material and represent a new species. The larger male could also be identified and is described below as *C. longipes* sp. nov. Among the remaining material, which must therefore have been collected outside the reef, 1 female and 1 male agreed with (or at least did not contradict) Dana's (1854) description and are here identified as *C. scutellata* primarily on the basis of cephalothorax shape. Moreover, the close size correlation between Dana's male of *C. scutellata* ('1–24th of an inch' = 1058 µm) and the male from the Great Barrier Reef (1064 µm) is striking. The single female specimen is designated here as the neotype, defining Farran's (1936) stations 19, 20 and 28 collectively as the new type locality (ICZN Art. 76.3.) despite previously published statements of the place of origin of Dana's material. All three stations are situated outside the Trinity opening to the reef off Port Douglas at 16°19–20'S, 146°3–7'E (Queensland). The depth ranges from 225 (stn 19) to >600 m (stns 20, 28)

TYPE MATERIAL. Neotype ♀ dissected on 11 slides (BMNH 1999.996); designated from material labelled *Clytemnestra scutellata* (BMNH 1948.4.28.121); collected either on 20 October 1928 (stns 19, 20) or 23 November 1928 (stn 28) during the Great Barrier Reef Expedition 1928–29 (Farran, 1936).

OTHER MATERIAL EXAMINED. One ♂ dissected on 10 slides (BMNH 1948.4.28.121); sampling data as for neotype.

REDESCRIPTION.

FEMALE. Total body length from tip of rostrum to posterior margin of caudal rami: 1121 µm. Maximum width (355 µm) measured at posterior margin of cephalic shield. Posterolateral angles of cephalothorax laterally expanded (Fig. 1A). Somites bearing P2–P4 successively decreasing in width posteriorly and bearing backwardly produced alate processes.

Genital double-somite (Fig. 5A) slightly constricted bilaterally; original segmentation marked by paired transverse chitinous ribs lateroventrally and laterally. Copulatory pore slit-like, located medially between genital apertures; leading to short posteriorly directed, membranous duct connected to bilobate seminal receptacle. Genital apertures located far anteriorly; closed off by small opercula derived from vestigial P6; each with 1 vestigial seta at inner distal corner and anterior tube-pore near base.

Urosomites without dorsal ornamentation (Figs 1A, 4E); penultimate and anal somites with multiple rows of spinules around ventral hind margin (Fig. 5A).

Caudal rami (Fig. 4E) about twice as long as wide, parallel; slightly tapering towards rear margin, with stepped outer margin marking insertion sites of setae I, II and III; produced into conical process bearing terminal pore; posterior third with ventral spinular patch (Fig. 5A). Setae I–II minutely bipinnate, spiniform and strongly developed. Seta III bipinnate. Setae IV–V basally fused; about equally long and only slightly longer than caudal ramus; without fracture planes, multipinnate and spiniform. Seta VI minute, bare; seta VII small, biarticulate at base, bare.

Rostrum (Fig. 1A) triangular with rounded anterior margin, completely fused to cephalothorax; with numerous dorsal surface pores as figured, none on ventral surface; with minute lateral sensillae near apex.

Antennule (Fig. 2A) slender, 7-segmented; segment 7 longest. Plumose setae present on segments 1–4. Segment 1 with small pore near seta and few short spinules along anterior margin. Armature formula: 1-[1 plumose], 2-[9 + 3 plumose], 3-[4 + 3 plumose + 1 transformed], 4-[1 + 1 plumose + (1 transformed + ae)], 5-[1], 6–[3], 7-[8 + acrothek]. Apical acrothek consisting of aesthetasc, long transformed seta and short bare seta. Transformed setae on segments 3, 4 and 7 long and aesthetasc-like, with rounded tip; those on segments 4 and 7 basally fused to aesthetasc. Rudimentary element present at base of acrothek.

Antenna (Fig.3A) 4-segmented, comprising coxa, basis and 2-segmented endopod. Coxa well developed, bare. Basis and proximal endopod segment without ornamentation; unarmed. Exopod inserted in membranous area between basis and endopod; represented by small, well defined segment bearing 2 strong recurved setae apically; exopodal setae multipinnate with long setules in proximal third. Distal endopod segment (Fig. 3A, B) with several surface frills and minute spinules on outer surface and patch of long setules on medial surface; lateral armature consisting of 1 naked seta; distal armature consisting of 5 apical, non-geniculate, bipinnate or multipinnate elements, 2 of which spiniform, recurved and bearing long spinules proximally.

Labrum (Fig. 3C) large, with 6 secretory pores on anterior surface; distal margin spinulose medially and with spinular patch on either lateral lobe.

Mandible (Fig. 3D) reduced. Palp represented by single naked seta. Gnathobase long and narrow, stylet-like; produced into number of cuspidate processes apically and subapically; without dorsal seta(e).

Paragnaths (Fig. 3C) well developed hirsute lobes.

Maxillule (Fig.3E) reduced; represented by small bilobed segment bearing 2 naked apical spines and raised seta along outer margin; posterior surface with distinct pore.

Maxilla (Fig. 3F) 2-segmented, comprising elongate syncoxa and allobasis. Syncoxa with expanded basal portion and 2 endites; exit of maxillary gland large (arrowed in Fig. 3F), partly concealed under lobate extension; proximal endite represented by small cylindrical process bearing very long plumose seta, distal endite cylindrical, with 1 naked and 2 pinnate spines apically. Allobasis with large articulating claw distally, smaller inner pinnate spine and naked seta along outer margin.

Maxilliped (Fig. 4A, B) very large, articulating with well developed pedestal; 3-segmented, comprising syncoxa, basis and endopod. Syncoxa extremely elongate, longer than basis; without ornamentation but with 1 anterior, plumose seta near membranous articulation with basis. Basis elongate; distal third of palmar margin with double spinule row (anterior spinules coarser than posterior ones) and 2 elements located closely to articulation with endopod; proximal element spiniform and bare (arrowed in Fig. 4B), distal element pad-like and spinulose. Endopod represented by short segment bearing short naked claw; accessory armature consisting of 3 anterior and 2 posterior elements.

Swimming legs with wide, narrow intercoxal sclerites and well

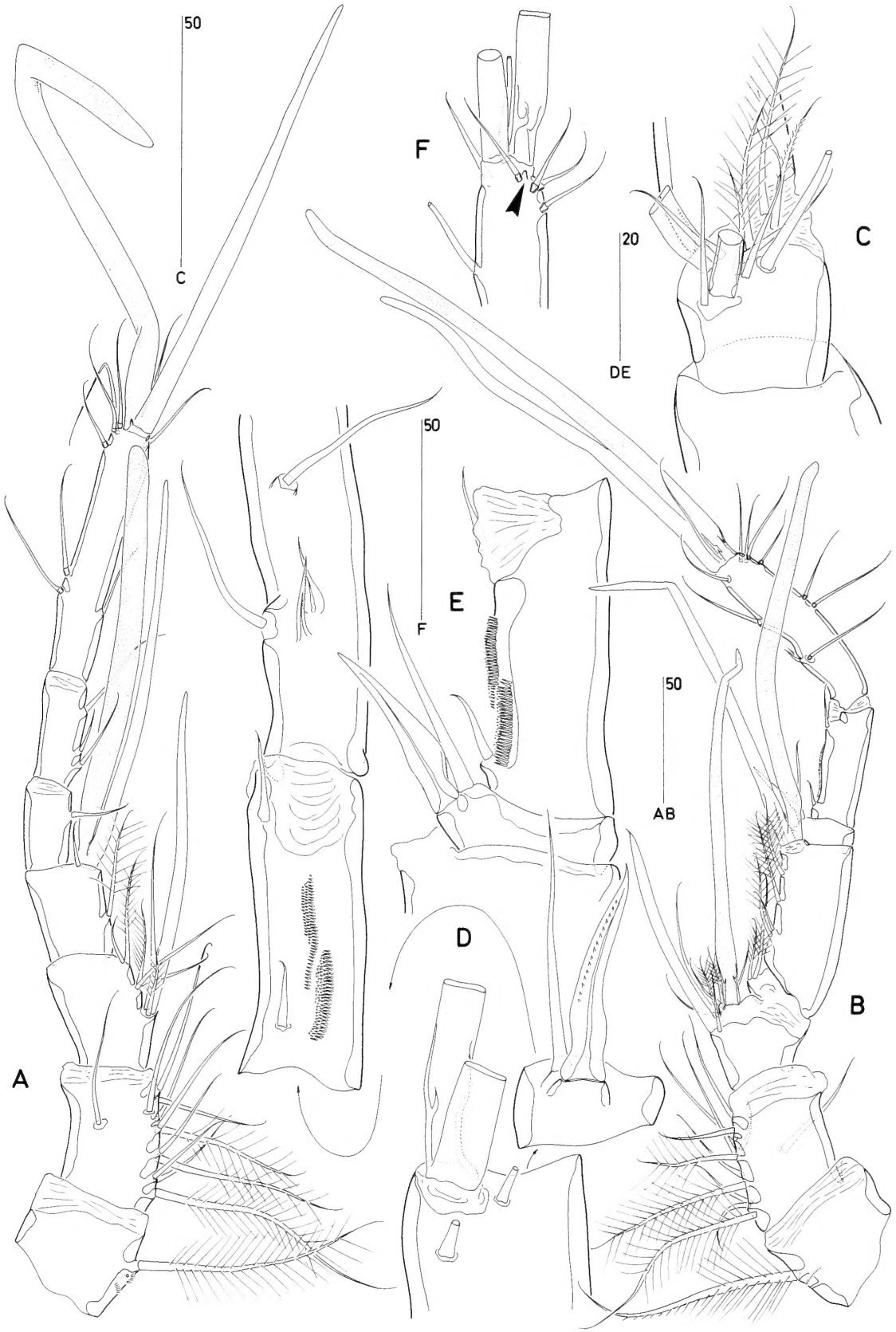

Fig. 2 *Clytemnestra scutellata* Dana, 1847. A, Antennule ♀, dorsal; B, antennule ♂, ventral; C, antennulary segment 3 ♂, anterior; D, antennulary segments 4–7 ♂, anterior [distal portion of segment 7 and proximal portion of segment 4 omitted]; E, antennulary segments 5–6 ♂, ventral; F, antennulary segment 7 ♂, distal portion, dorsal [arrow indicating rudimentary element]. [A based on neotype].

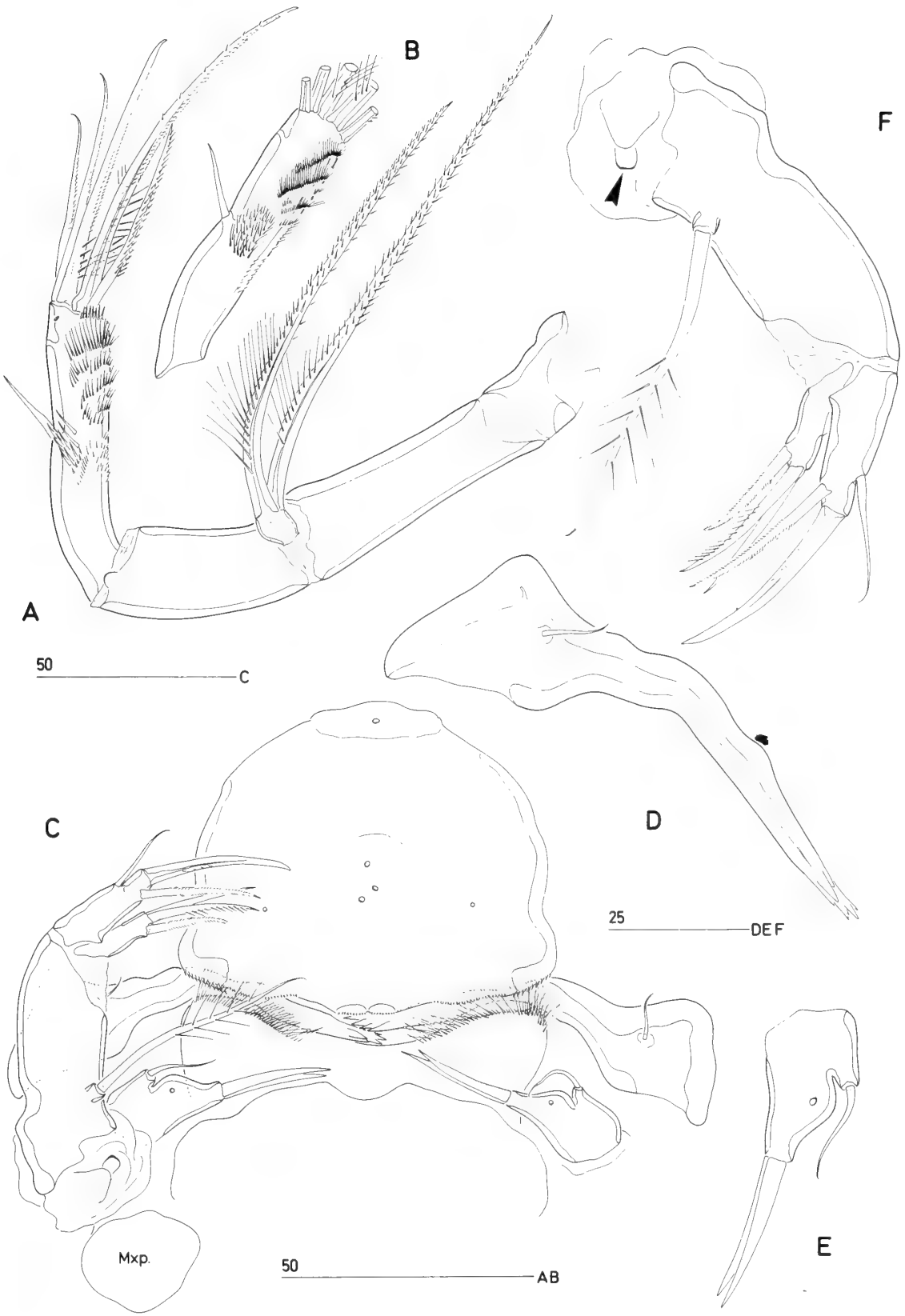

Fig. 3 *Clytemnestra scutellata* Dana, 1847 (♀). A, Antenna, outer; B, distal antennary endopod segment, inner; C, oral area showing position of labrum, paragnaths, mandibles, maxillules and right maxilla [position of maxilliped (Mxp.) indicated], ventral; D, mandible, posterior; E, maxillule, posterior; F, maxilla [exit of maxillary gland arrowed], posterior. [all based on neotype].

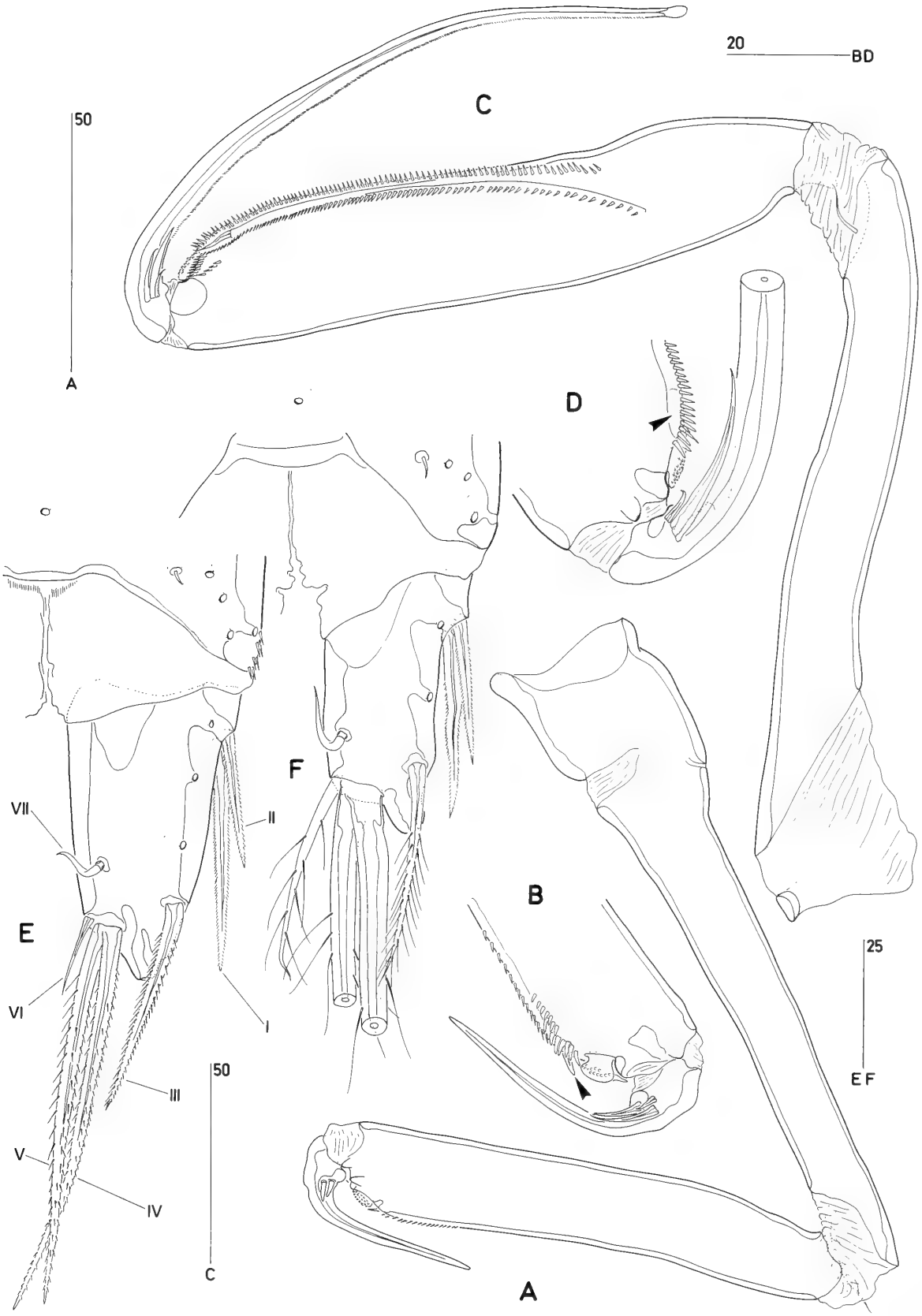

Fig. 4 *Clytemnestra scutellata* Dana, 1847. A, Maxilliped ♀, posterior; B, maxilliped ♀, distal half of basis and endopod, anterior [proximal palmar element arrowed]; C, maxilliped ♂, anterior; D, maxilliped ♂, distal portion of basis and endopod [proximal palmar element arrowed], posterior; E, right caudal ramus ♀, dorsal; F, right caudal ramus ♂, dorsal. [A, B, E based on neotype].

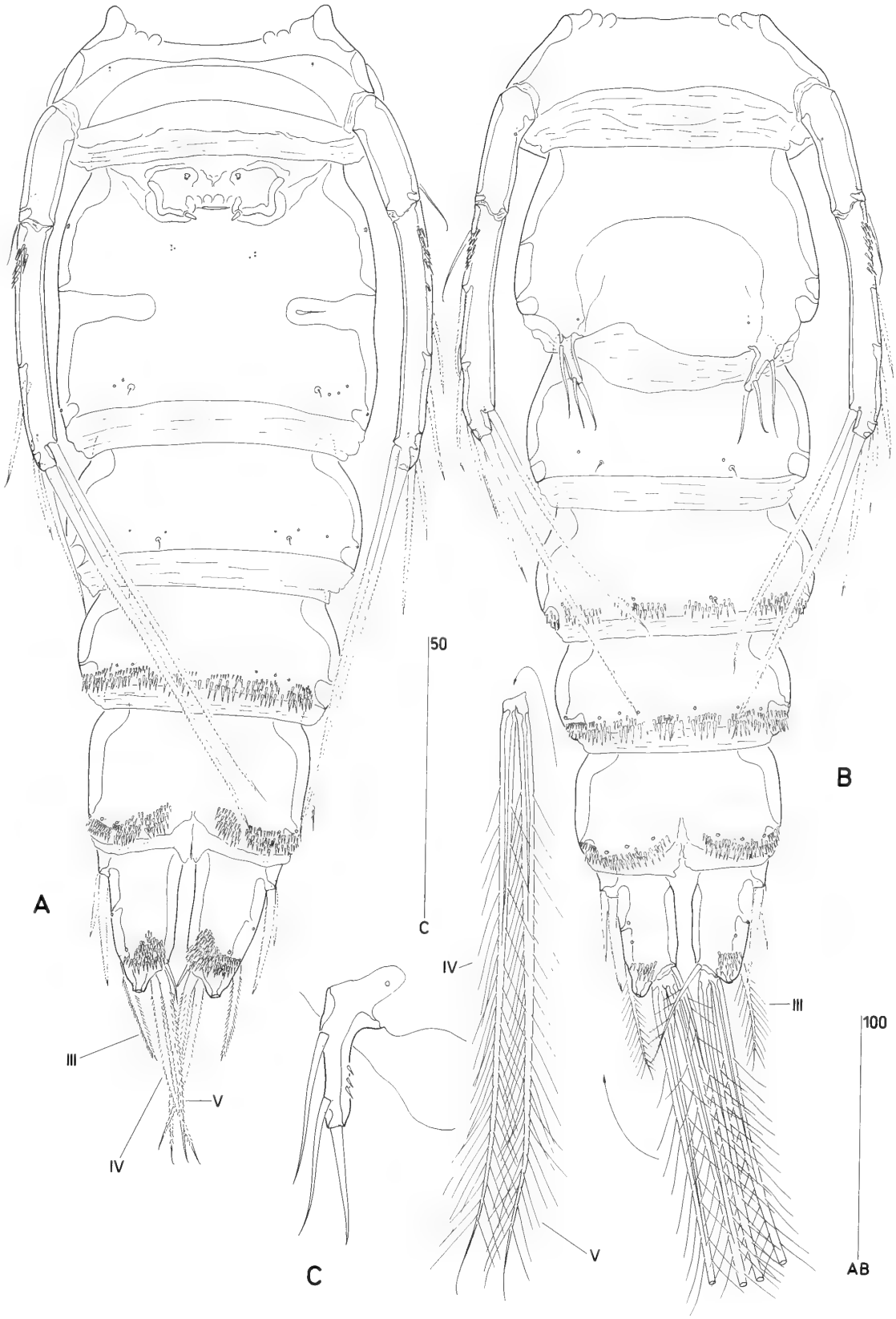

Fig. 5 *Clytemnestra scutellata* Dana, 1847. A, Urosome ♀, ventral; B, urosome ♂, ventral [inset showing setae IV–V at full length]; C, P6 ♂, ventral. [A based on neotype]

developed praecoxa; both without ornamentation. Rami 3-segmented except for P1 exopod.

P1 (Fig. 6A) separated from maxillipeds by large membranous area. Coxa and basis prolonged along dorsoventral axis; without surface ornamentation. Basis with plumose outer spine. Exopod 1-segmented, represented by elongate segment bearing long setules along outer margin; with subapical pore and 1 outer, 2 apical and 1 inner setae. Endopod 3-segmented; segments decreasing in size distally, each with anterior pore; enp-1 and -2 with few setules along outer margin, enp-2 and -3 with posterior spinules; enp-1 with very long inner seta; ornamentation of inner elements typically (multi)pinnate, distal elements of enp-3 plumose.

P2–P4 (Figs 6B; 7A, B) with transversely prolonged basis bearing short outer seta. Endopods distinctly longer than exopods. Exopodal outer spines setiform with flagellate tip. Exopod segments typically with pore near outer distal corner; without ornamentation; exp-2 outer distal corner linguiform. Endopods with long proximal segment, particularly in P2–P3; segments with anterior pore, setules along outer margin and spinules on posterior surface; setal ornamentation typically combination of setular and spinular rows; inner seta of P2–P3 enp-1 short. P1 exp-2 without outer spine. Spine and setal formula of swimming legs as follows:

Exopod	Endopod	
P1	121	1.1.220
P2	1.1.223	1.2.221
P3	1.1.323	1.2.321
P4	1.1.323	1.2.221

P5 (Fig. 1C) uniramous, laterally displaced; 2-segmented; not extending beyond posterior margin of genital double-somite (Fig. 5A). Basis with short outer seta and anterior pore. Exopod about twice as long as basis, slightly curved inwards; outer margin with 4 pinnate setae; inner margin with long plumose seta; apex and inner margin each with 1 long pinnate seta; anterior surface with 3 pores and spinules near apex and in proximal third.

MALE. Total body length from tip of rostrum to posterior margin of caudal rami: 1064 µm. Maximum width (337 µm) measured at posterior margin of cephalic shield. Body (Fig. 1B) with similar projections as in ♀; urosome more slender with genital and first abdominal somites separate (Fig. 5B).

Rostrum (Fig. 1B) more obtuse than in ♀.

Antennule (Fig. 2B) slender, distinctly 7-segmented with ancestral segment XIII completely incorporated into segment 4 (Fig. 2C); haplocer, with geniculation located between segment 6 and 7. Plumose setae present on segments 1–4. Segment 1 with small pore near seta and few tiny spinules along anterior margin. Armature formula: 1-[1 plumose], 2-[8 + 3 plumose], 3-[5 + 3 plumose + 1 pinnate + 1 transformed + ae], 4-[2 + 3 plumose + (1 transformed + ae)], 5- [1 + 1 spine], 6-[2], 7-[9 + 2 modified elements + acrothek]. Apical acrothek consisting of aesthetasc, long transformed seta and short bare seta. Transformed setae on segments 3, 4 and 7 long and aesthetasc-like, with rounded tip; those on segments 4 and 7 basally fused to aesthetasc. Rudimentary element present at base of acrothek (arrowed in Fig. 2F). Segment 6 with 2 patches of spinules on anterior surface (Fig. 2D–E). Segment 7 with 2 fused elements near geniculation (Fig. 2D).

Maxilliped (Fig. 4C) much larger than in ♀, articulating with well developed pedestal; 3-segmented, comprising syncoxa, basis and endopod. Syncoxa extremely elongate but not distinctly longer than basis; without ornamentation but with 1 short anterior seta near membranous articulation with basis. Basis elongate; more swollen than in ♀; middle and distal thirds of palmar margin forming longitudinal furrow bordered by single row of spinules on both anterior and posterior sides; with 2 elements located closely to articulation with endopod; proximal element spiniform and bare (arrowed in Fig. 4D), distal element pad-like and spinulose. Endopod represented by short segment produced into very long naked claw which in reflexed position typically fits in palmar furrow with the apical part closely adpressed onto the anterior surface of the basis; accessory armature consisting of 3 anterior and 2 posterior setae; claw with spatulate apex.

P5 (Fig. 7C) very similar to that of ♀, with identical proportions, pore pattern and setation.

Sixth pair of legs (Fig. 5B) weakly asymmetrical, forming highly membranous midventral area covering single, large median genital aperture; each P6 produced into cylindrical process (Fig. 5C) with 1 apical and 2 outer bare setae; few spinules along inner margin.

Urosomites 4–5 and anal somite with spinules around ventral hind margin (Fig. 5B).

Caudal rami (Fig. 4F) somewhat shorter than in ♀; seta II relatively longer; seta III more slender and with longer pinnules; setae IV–V long (60% of urosome length; Fig. 5B) and plumose; seta VI much longer than in ♀ and sparsely plumose.

Spermatophore with very long, recurved neck.

VARIABILITY. The right distal exopod segment of the male P2 has only 2 outer spines (Fig. 6C).

REMARKS. There are very few published records of *C. scutellata* that can be verified absolutely. There is little doubt that the species described by Poppe (1891) under the name *C. hendorffi* is synonymous with *C. scutellata*. Poppe's detailed description shows similar posterolateral projections on the cephalothorax which are absent in the other species from the Great Barrier Reef. *C. hendorffi* also shows great consistency in body size (♀: 1.09 mm; ♂: 1.07 mm), relative proportions of the caudal rami and P5, and the ventral view of the female urosome demonstrates the absence of spinular patches on the second abdominal somite. The only significant discrepancy is found in the armature of the P2 exopod which Poppe had figured with an outer spine on the proximal segment. The absence of this element is a generic character and we suspect that Poppe had assumed its presence to be the rule in clytemnestrids and had altered his figure accordingly. Poppe's (1891) material came from two localities in the Indian Ocean (West Australian Basin, south of Madagascar), three localities in the southwest Atlantic off the coasts of Brazil and Argentina, and the Karimata Strait in the Java Sea. He also re-identified Thompson's (1888) material of *Goniopsyllus rostratus* from the Maltese Sea as *C. hendorffi*, confirming its presence in the Mediterranean. From a zoogeographical point of view (see below) it appears more conceivable that Thompson had collected the species described by Claus (1891*a*) under the name *Goniopelte gracilis*, the description of which was unknown to Poppe (1891). We have been unable to confirm the presence of *C. scutellata* in the Atlantic or the Mediterranean and therefore suspect that Poppe's records from the southwest Atlantic might have been based on another species, possibly *C. gracilis*. Poppe based his illustrations on specimens from the West Australian Basin, suggesting an Indo-Pacific distribution pattern for *C. scutellata*.

The redescription by Giesbrecht (1892) has long been accepted as the basis for identification of *C. scutellata* even though his material was not from the type locality. However, from our revision it is clear that Giesbrecht had redescribed *Goniopelte gracilis* (see below). Both species are closely related, sharing the posterolateral projections on the cephalothorax and the presence of 3 outer spines on

Fig. 6 *Clytemnestra scutellata* Dana, 1847. A, P1 ♀, anterior; B, P2 ♀, anterior; C, right P2 exp-3 ♂, anterior, aberrant setation. [A, B based on neotype].

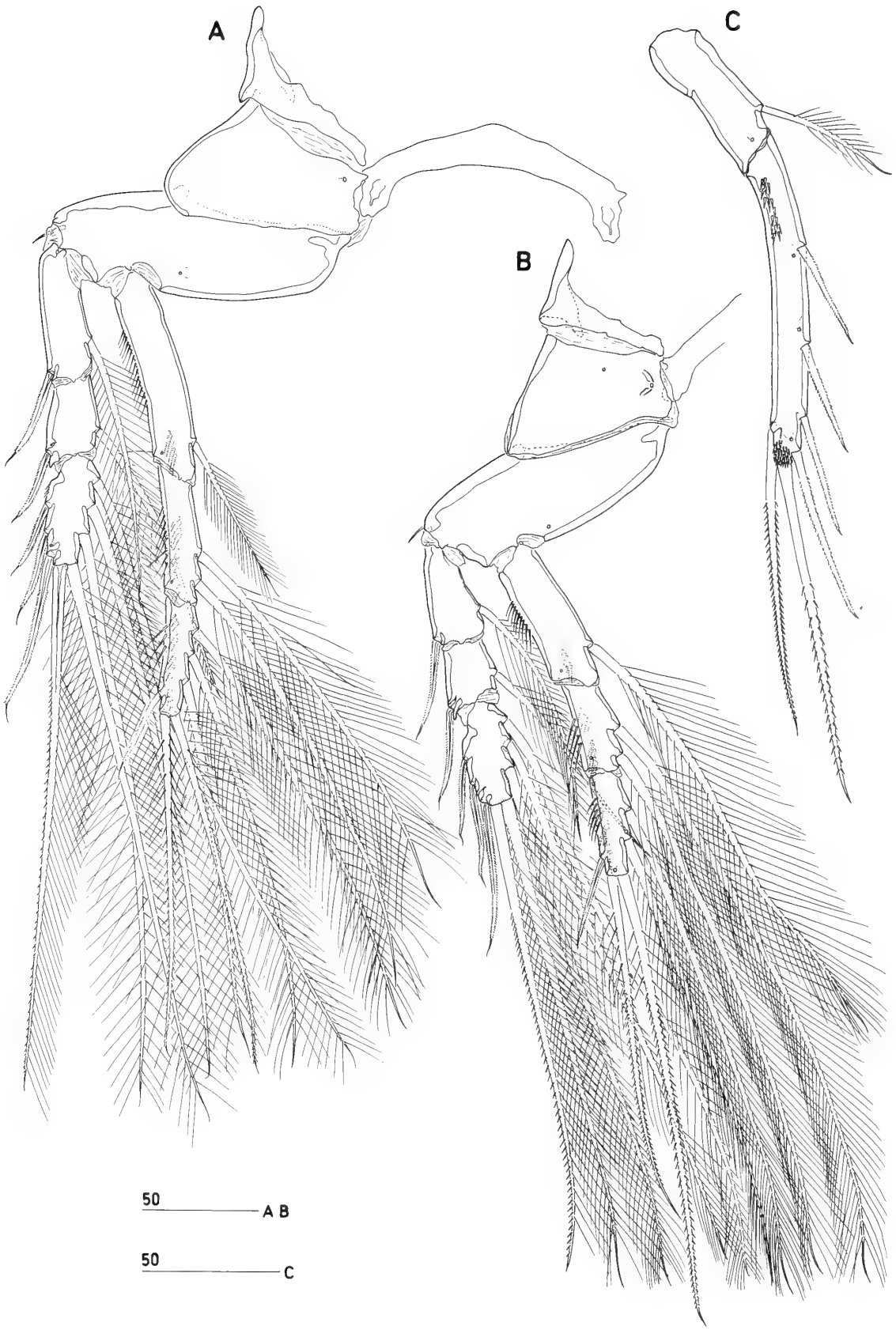

Fig. 7 *Clytemnestra scutellata* Dana, 1847. A, P3 ♀, anterior; B, P4 ♀, anterior; C, P5 ♂, anterior. [A, B based on neotype].

P2–P4 exp-3 and 6 elements on the P5 exopod in both sexes. They can be separated by body size, length of caudal ramus setae IV–V, length of the P5 in both sexes and urosome ornamentation in the female (Table I).

Clytemnestra gracilis (Claus, 1891a) comb. nov.

Goniopelte gracilis Claus, 1891*a*: 1–10; Taf. I–II.
Clytemnestra scutellata Dana, 1847 *sensu* Giesbrecht (1892): 568–572; Taf. 1, fig. 9; Taf. 45, figs. 16–18, 21, 23–24, 27–30, 32, 34–38.
Clytemnestra rostrata (Brady, 1883) *sensu* T. Scott (1894): 106–107; Pl. XII, figs. 47–57; Pl. XIII, figs. 1–3.
Clytemnestra scutellata Dana, 1847 *sensu* Sars (1921): 100–101; Pl. LXVIII.
Clytemnestra scutellata Dana, 1847 *sensu* Vilela (1968): 44; Est. XVII, fig. 1a–c.
Clytemnestra scutellata Dana, 1847 *sensu* Boxshall (1979): 232; Fig. 15A–K.
Clytemnestra scutellata Dana, 1847 *sensu* Huys *et al.* (1996): 301; Fig. 120H.

TYPE LOCALITY. Claus (1891*a*) collected his material from an unspecified locality in the eastern Mediterranean. The neotype designation below redefines the type locality as follows: North-east Atlantic, south-west of Azores, 35°N 33°W, 0–1 m.

TYPE MATERIAL. Claus' (1891*a*) description was based on a single specimen of either sex. Since the type material no longer exists a neotype is designated here to secure stability of nomenclature: adult ♀ in alcohol (BMNH 1999.1024); collected during RRS *Discovery* Cruise 121 (5–26 June 1981), station 10379; 13 June 1981, at night; torpedonet; leg. Institute of Oceanographic Sciences.

OTHER MATERIAL EXAMINED.
(a) from type locality: 11 ♀♀ and 8 ♂♂ in alcohol (1 ♀ and 1 ♂ dissected in half, in separate vials), 1 ♀ dissected on 6 slides (BMNH 1983.53); 2 ♀♀ and 1 ♂ on SEM stub; collection data as for neotype;
(b) Gulf of Guinea, Telegraph Steamer *Buccaneer* (BMNH 1999.1007–1016): 9 ♀♀ (2 damaged) and 1 ♂ (damaged); mislabelled as *Clytemnestra rostrata*; January–February 1886; leg. J. Rattray, det. T. Scott. [body length of 7 ♀♀: 1381–1541 µm, $\bar{x}$ = 1444 µm];
(c) South Adriatic, Croatia: 1 ♀ in alcohol (BMNH 1999.1071); leg. F. Kršinić. [body length: 1309 µm].

DESCRIPTION. (based on *Discovery* material)

FEMALE. Total body length from tip of rostrum to posterior margin of caudal rami: 1330–1562 µm ($\bar{x}$ = 1450 µm; n = 10). Maximum width (382 µm) measured at posterior margin of cephalic shield. Posterolateral angles of cephalothorax slightly expanded (Fig. 8A). General body shape as in type species.

Genital double-somite (Fig. 8B) slightly constricted bilaterally; original segmentation marked by paired transverse chitinous ribs lateroventrally and laterally, joining medially forming continuous but weakly defined rib. Copulatory pore slit-like, located medially between genital apertures (arrowed in Fig. 27B); leading to short posteriorly directed, membranous duct connected to bilobate seminal receptacle. Genital apertures (Fig. 11D) separated by number of rounded swellings (also present in type species: Fig. 5A); closed off by small opercula derived from vestigial P6; each with 1 vestigial seta (coarser than in *C. scutellata*) at inner distal corner and anterior tube-pore near base (arrowed in Fig. 11D).

Urosomites without dorsal ornamentation; penultimate and anal somites with multiple rows or patches of spinules around ventral hind margin and lateroventral patches on second abdominal somite (Fig. 8B).

Caudal rami (Fig. 8B) as in *C. scutellata* but setae IV distinctly shorter than seta V.

Rostrum (Figs 8A; 10C) triangular with rounded anterior margin, completely fused to cephalothorax; with numerous dorsal surface pores; minute lateral sensillae flanking middorsal raised pore.

Antennule 7-segmented, with armature formula as in type species. Antenna, mandible (Fig. 10A), maxillule and maxilla (proximal endite on syncoxa present) as in type species. Palmar elements of maxilliped as in Fig. 10B; proximal element fused to basis and with apical pore; distal element pad-like, forming barbed, linguiform extension posteriorly and bearing double spinule row and tube pore anteriorly.

P2–P4 armature formula:

	exopod	endopod
P2	1.1.223	1.2.221
P3	1.1.323	1.2.321
P4	1.1.323	1.2.221

P5 (Fig. 8B) elongate, extending clearly beyond posterior margin of genital double-somite. Exopod about 2.4 times as long as basis, with 6 setae.

MALE. Total body length from tip of rostrum to posterior margin of caudal rami: 1420–1531 µm ($\bar{x}$ = 1479 µm; n = 8). Body with similar projections as in ♀; urosome more slender with genital and first abdominal somites separate (Fig. 9A).

Antennule with armature as in *C. scutellata*. Maxilliped much larger than in ♀; middle and distal thirds of palmar margin forming longitudinal furrow bordered by single row of spinules on both anterior and posterior sides (Fig. 10D).

P5 (Fig. 9A) very similar to that of ♀, extending to distal margin of first abdominal somite.

Sixth pair of legs (Fig. 9A) weakly asymmetrical, forming highly membranous midventral area covering single, large median genital aperture (Fig. 11A); each P6 produced into cylindrical process (Fig. 11B) with 1 apical and 2 lateral bare setae.

Urosomites 4–5 and anal somite with spinules around ventral hind margin (Fig. 9A).

Caudal rami (Fig. 9A–B) longer and more slender than in ♀; setae I–II bare; setae IV–V long (68% of urosome length; Fig. 9A) and plumose; seta VI longer than in ♀ and sparsely plumose.

VARIABILITY. Some variability was noticed in the caudal ramus length of the *Buccaneer* females, the majority having a slightly longer ramus than in Fig. 8C. In the Adriatic ♀ the spinular patches on the first postgenital somite are wider medially forming an almost continuous zone around the posterior margin.

REMARKS. Claus (1891*b*) himself surmised that *Goniopelte gracilis* was conspecific with *Clytemnestra hendorffi* which in turn became relegated to a junior subjective synonym of *C. scutellata* by Giesbrecht (1892). It is beyond any doubt that Giesbrecht's excellent redescription of *C. scutellata* was based on *C. gracilis*. His illustrations were based on Naples material only, however, it is likely that he included specimens of *C. scutellata* from the Pacific (Giesbrecht, 1891*b*) in his length measurements, possibly accounting for the lower end of his size range (♀: 1.05–1.2 mm; ♂: 1.07–1.3 mm). *C. gracilis* is distinctly larger than *C. scutellata* and can be distinguished from the latter by the slender caudal rami and the longer P5 which extends clearly beyond the posterior margin of the genital double-somite in the female and reaches to the rear margin of

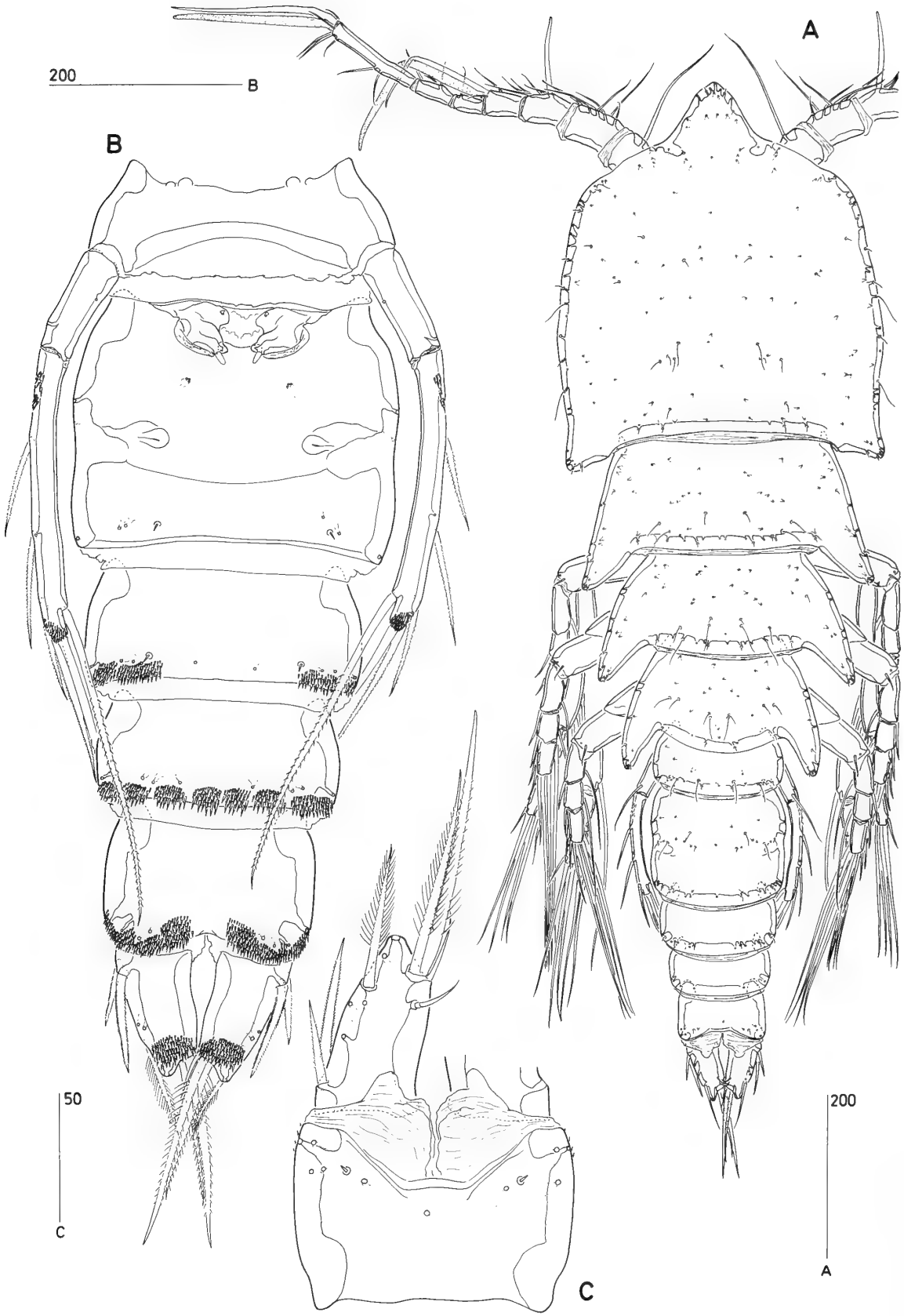

Fig. 8 *Clytemnestra gracilis* (Claus, 1891*a*) comb. nov. (♀) A, Habitus, dorsal; B, urosome, ventral; C, anal somite and right caudal ramus, dorsal.

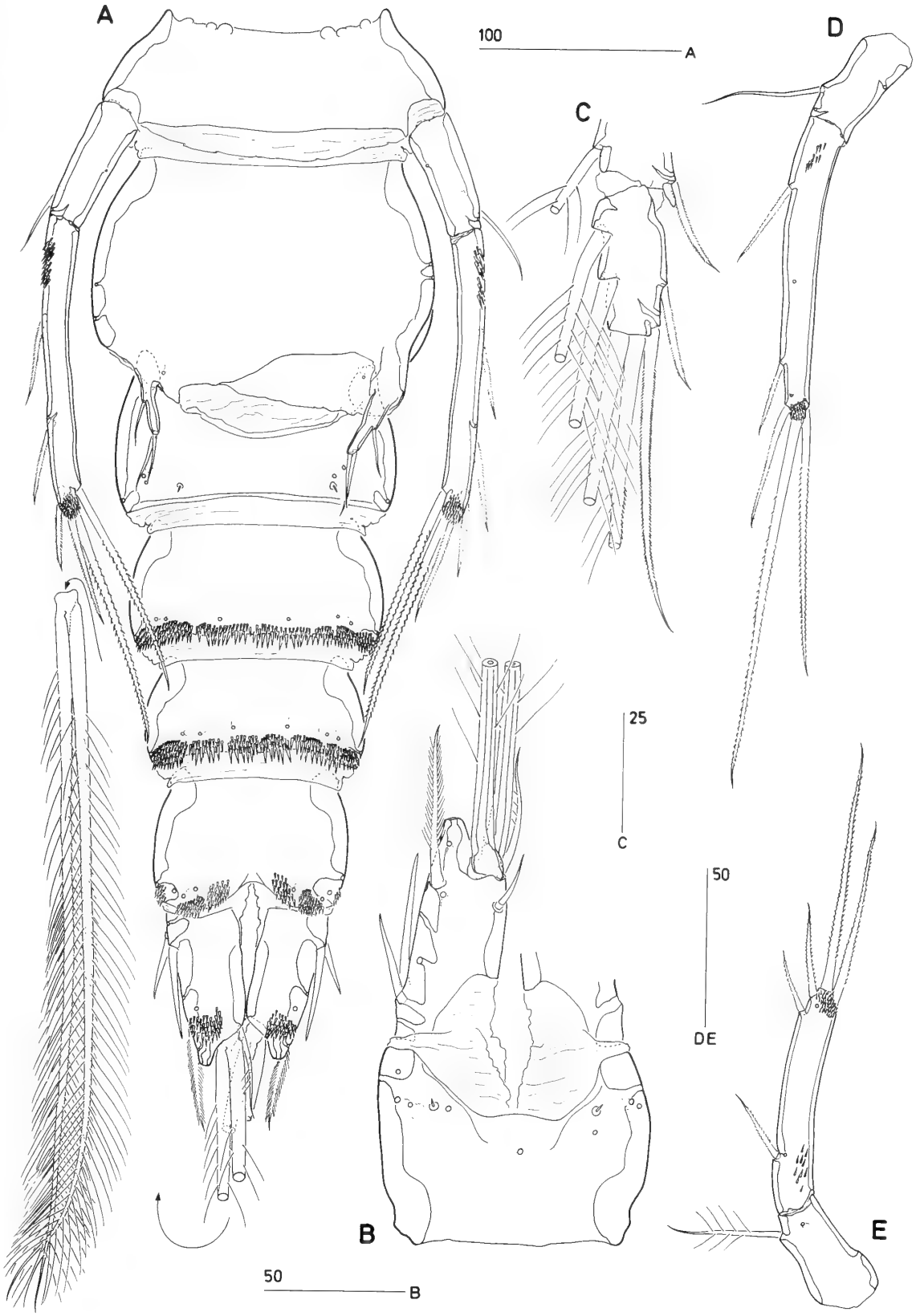

Fig. 9 *Clytemnestra gracilis* (Claus, 1891*a*) comb. nov. (♂) A, Urosome, ventral [inset showing setae IV–V]; B, anal somite and right caudal ramus, dorsal. *Clytemnestra farrani* sp. nov. C, P2 exp-3 ♀, anterior; D, P5 ♀, anterior; E, P5 ♂, anterior.

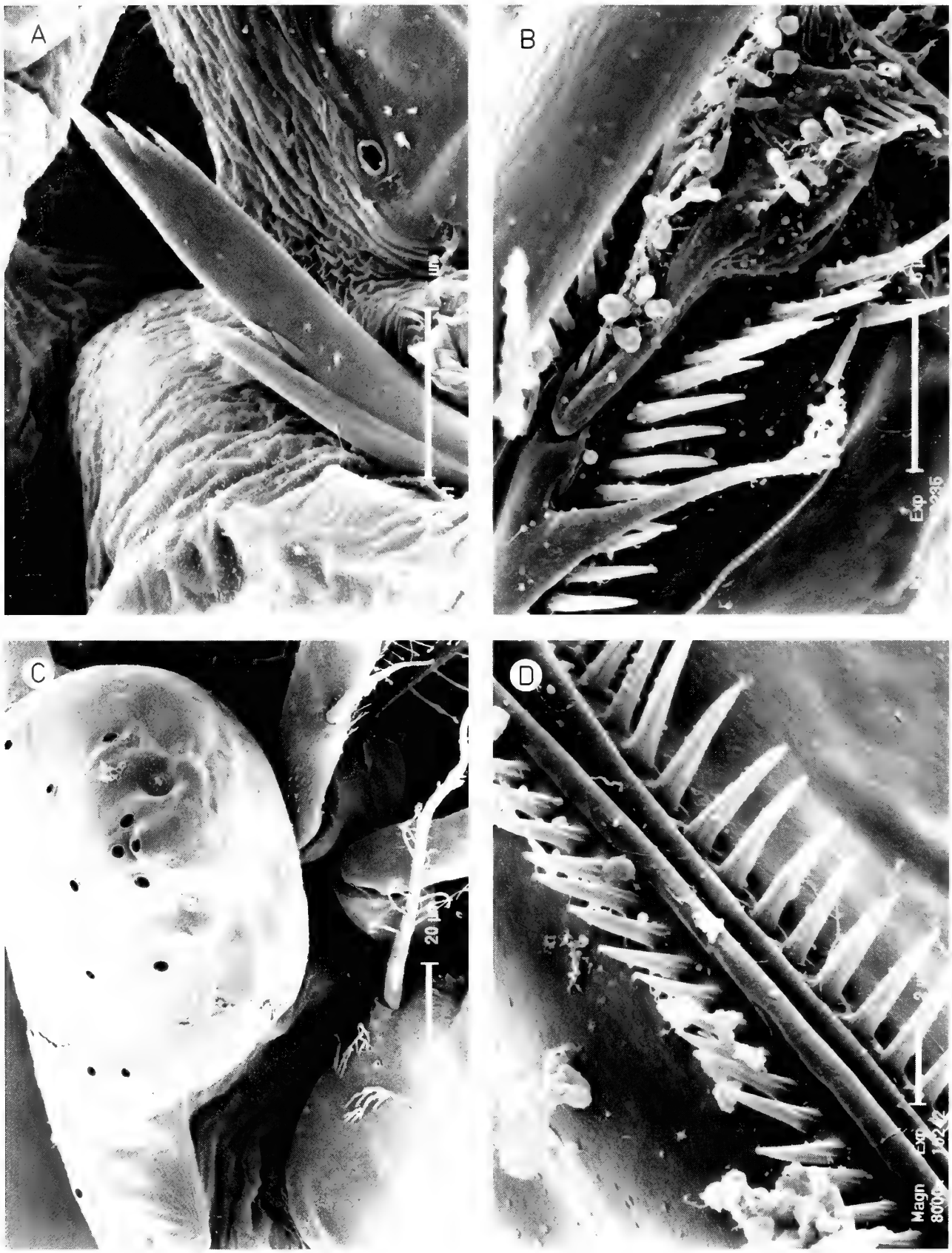

Fig. 10 *Clytemnestra gracilis* (Claus, 1891*a*) comb. nov. SEM photographs. A, Mandibular gnathobase ♀; B, maxilliped ♀, palmar elements; C, rostrum ♀, frontal; D, maxilliped ♂, palmar furrow.

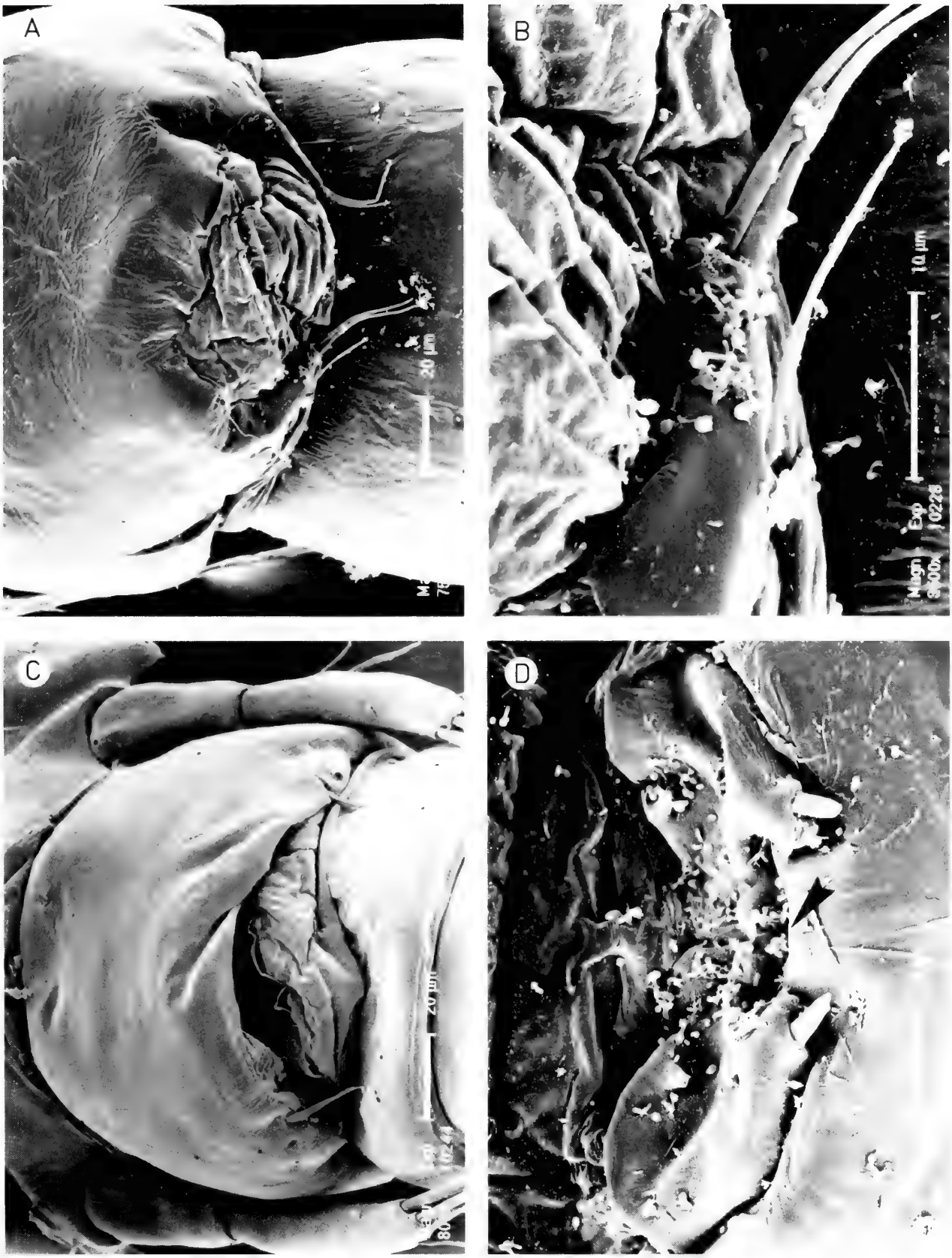

Fig. 11 *Clytemnestra gracilis* (Claus, 1891*a*) comb. nov. SEM photographs. A, Genital aperture and sixth legs ♂; B, P6 ♂; D, genital field ♀[position of copulatory pore arrowed]. *Goniopsyllus clausi* sp. nov. C, Genital aperture and sixth legs ♂.

the first abdominal somite in the male. Females of both species can be differentiated by the ventral ornamentation pattern of the urosome (*C. gracilis* has lateral spinular patches on the first postgenital somite) and the ventral transverse chitinous ridge (marking the original segmentation of the genital double-somite) which is more strongly developed in *C. gracilis*. Giesbrecht (1892) did not illustrate the second abdominal somite in the female, however, stated in the text that spinules were present ventrally around the posterior margin of all three postgenital somites. Caudal ramus seta IV is distinctly shorter than seta V in females of *C. gracilis* (see also Giesbrecht (1892): Taf. 45, Fig. 27; Sars (1921): Plate LXVIII), while both setae are equally long in the female of the type species. Both sexes of *C. gracilis* have a propensity for developing asymmetry in the caudal rami whereby one ramus is markedly narrower than the other (see also Claus (1891*a*): Taf. I, Figs 1–2; Giesbrecht (1892): Taf. 45, Fig. 27).

Despite his own arguments to the contrary, T. Scott (1894) inexplicably identified his clytemnestrid material from the Gulf of Guinea as *C. rostrata*. A. Scott (1909) re-identified the material as *C. scutellata*. Re-examination of the *Buccaneer* material (BMNH 1893.4.22.268–275) has revealed it to be an amalgamate of two species, containing 9 ♀♀ and 1 ♂ of *C. gracilis* and 7 ♀♀ of a smaller *Goniopsyllus* sp. This might explain the discrepancy found between the body length reported by T. Scott (1.25 mm) and our measurements ($\bar{x}$ = 1.44 mm). Since males are usually larger than females (Giesbrecht, 1892) it is doubtful whether Marques' (1973) male specimen (0.99 mm) of *C. scutellata* from São Tomé (Gulf of Guinea) belongs to *C. gracilis*.

The only illustrated record of *C. scutellata* from northern Europe is that by Sars (1921) who found a single female in Oslofjord and described it in great detail. His specimen, 1.24 mm in length, agrees in all aspects with *C. gracilis* and represents a significant range extension for this species. Kasturirangan (1963) reproduced Giesbrecht's (1892) and Sars' (1921) drawings of *C. gracilis* in his identification key to the planktonic copepods of Indian coastal waters, however its presence in the Indo-Pacific has yet to be confirmed.

Vilela (1968) reported two females of *C. scutellata*, measuring 1.24–131 mm, from the Portuguese coast off Lisbon. Her illustrations of the caudal rami and P5 positively identify her material as *C. gracilis*.

Clytemnestra farrani sp. nov.

TYPE LOCALITY. Great Barrier Reef, Queensland, Australia. Farran (1936) recorded a total of 5 specimens (4 belonging to *C. farrani*, 1 to *C. longipes*) from serial townettings (his stations 62, 65, 68) at 3 miles east of the laboratory on Low Island (off Port Douglas); depth 32 m.

ETYMOLOGY. This patronym commemorates the late G.P. Farran for his comprehensive contributions to our knowledge of planktonic copepods.

TYPE MATERIAL. Holotype ♀ dissected on 6 slides (BMNH 1999.998); paratypes are 1 ♀ and 2 ♂♂ in alcohol (BMNH 1999.999–1001). This material was originally registered as *C. scutellata* under reg. no. 1948.4.28.121. Collected during Great Barrier Reef Expedition 1928–29 on either 15 June (stn 62), 10 July (stn 65) or 18 July 1929 (stn 68).

OTHER MATERIAL EXAMINED. From R. Böttger-Schnack: 1 ♀ in alcohol (BMNH 1999.1065); southern Red Sea, *Meteor* cruise 5/5, stn 703 (15°34.8' N, 41°54.9' E); 03 August 1987; multiple opening-closing net, 0.055 mm mesh, vertical hauling, 0–50 m (total water depth 970 m).

DESCRIPTION.

FEMALE. Total body length from tip of rostrum to posterior margin of caudal rami: 927–946 µm ($\bar{x}$ = 937 µm; n = 2). Maximum width (252 µm) measured halfway the cephalic shield length. Posterolateral angles of cephalothorax rounded, not expanded (Fig. 12A). Backwardly produced alate processes of somites bearing P2–P4 distinctly shorter than in *C. scutellata* and *C. gracilis*.

Genital double-somite (Fig. 13A) not constricted bilaterally; original segmentation marked by small, paired, chitinous patches lateroventrally. Genital field as in type species.

Urosomites without dorsal ornamentation; penultimate and anal somites with multiple rows or patches of minute spinules around ventral hind margin and with lateroventral spinular patches on second abdominal somite (Fig. 13A).

Caudal rami (Fig. 13A, C) shorter than in previous species; setae IV slightly shorter than seta V but both setae distinctly shorter than in *C. scutellata* (only slightly longer than ramus and as long as seta III) and minutely pinnate.

Rostrum (Fig. 12A) rounded anteriorly, obtuse.

Antennule 7-segmented, with armature formula as in type species. Antenna, mouthparts (proximal endite on maxillary syncoxa present) and maxillipeds as in type species.

P2 exp-3 with only 2 outer spines (Fig. 9C). P2–P4 armature formula:

	exopod	endopod
P2	1.1.222	1.2.221
P3	1.1.323	1.2.321
P4	1.1.323	1.2.221

P5 (Fig. 9D) extending to posterior margin of genital double-somite. Basis short, exopod about 3 times as long as basis, with 5 setae (3 outer, 1 apical, 1 inner).

MALE. Total body length from tip of rostrum to posterior margin of caudal rami: 939–945 µm ($\bar{x}$ = 942 µm; n = 2). Maximum width (257 µm) measured at posterior margin of cephalic shield. Body (Fig. 12B) with similar projections as in ♀; urosome more slender with genital and first abdominal somites separate (Fig. 13B).

Antennule, antenna, mouthparts and maxilliped with armature as in *C. scutellata*.

P5 (Fig. 9E) distinctly shorter than in ♀, not extending to distal margin of first abdominal somite; exopod 1.9 times as long as basis, apical and inner setae shorter than in ♀.

Sixth pair of legs (Fig. 13B) weakly asymmetrical; each P6 produced into short cylindrical process with 1 outer and 2 apical bare setae.

Urosomites 4–5 and anal somite with spinules around ventral hind margin (Fig. 13B).

Caudal rami (Fig. 13B) stubbier than in ♀; setae I–II bare; setae IV–V very long (95% of urosome length) and plumose; seta VI much longer than in ♀.

REMARKS. *C. farrani* can be readily distinguished from its congeners by the swimming leg setal formula, showing only 2 outer spines on P2 exp-3 but 3 outer spines on P3–P4 exp-3. It is closely related to *C. asetosa* which resembles it in the small size, the absence of posterolateral processes on the cephalothorax and the presence of only 5 setae on the P5 exopod. The number of endites on the syncoxa, the spinulation pattern on the female urosome and the

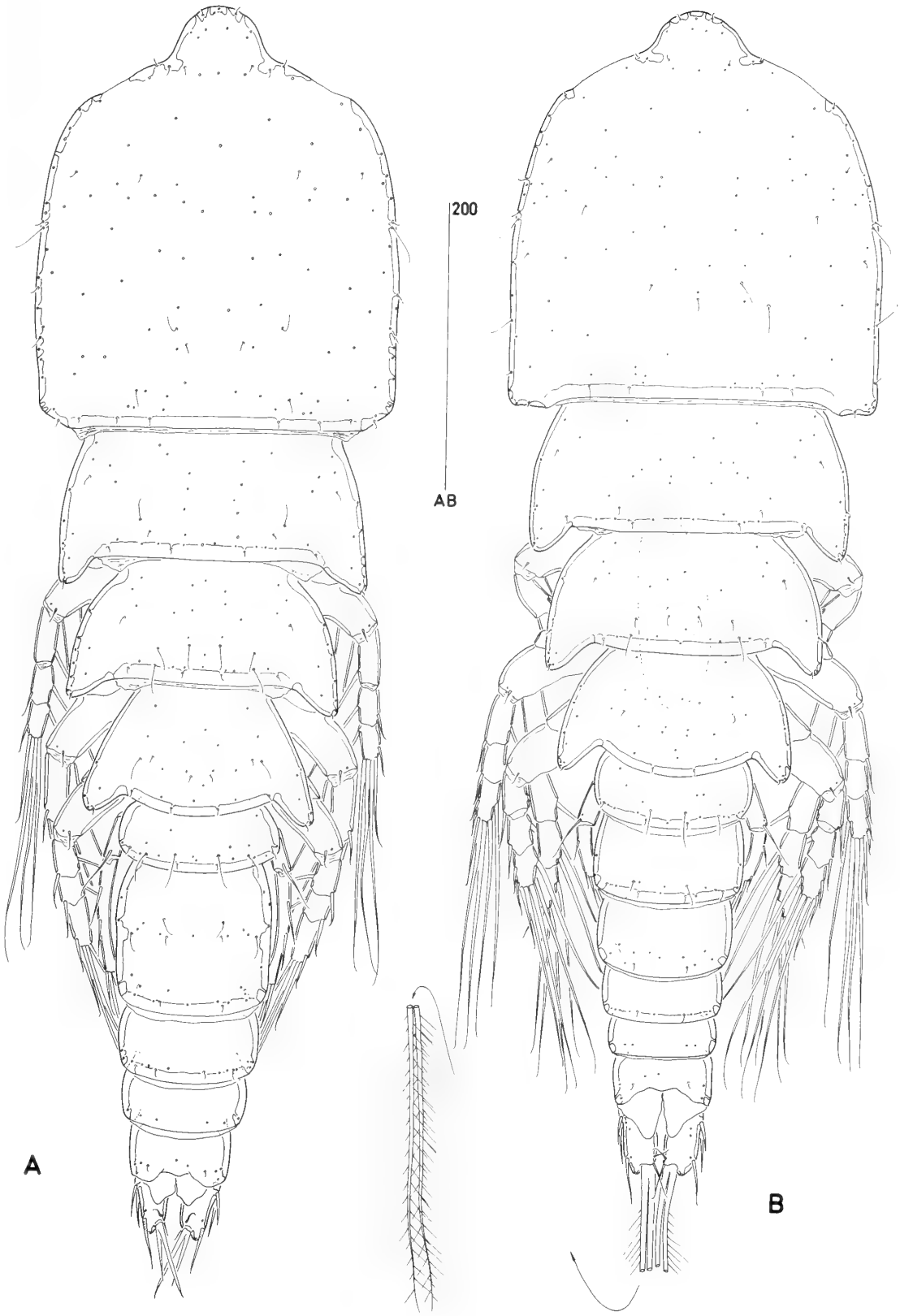

Fig. 12 *Clytemnestra farrani* sp. nov. A, Habitus ♀, dorsal; B, habitus ♂, dorsal [inset showing setae IV–V at full length].

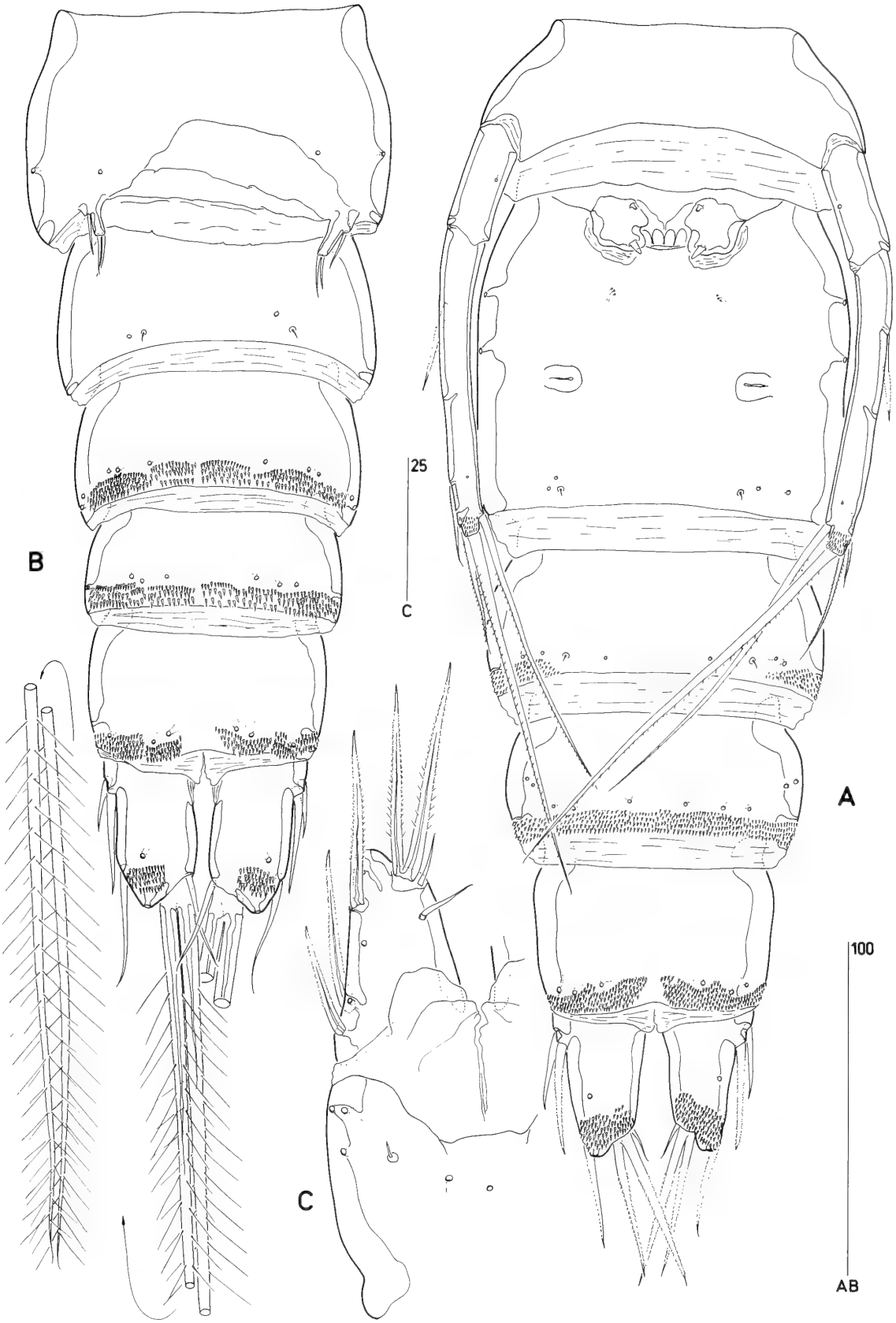

Fig. 13 *Clytemnestra farrani* sp. nov. A, Urosome ♀, ventral; B, urosome ♂ (excluding P5-bearing somite), ventral [inset showing setae IV–V at full length]; C, anal somite and right caudal ramus ♀, dorsal.

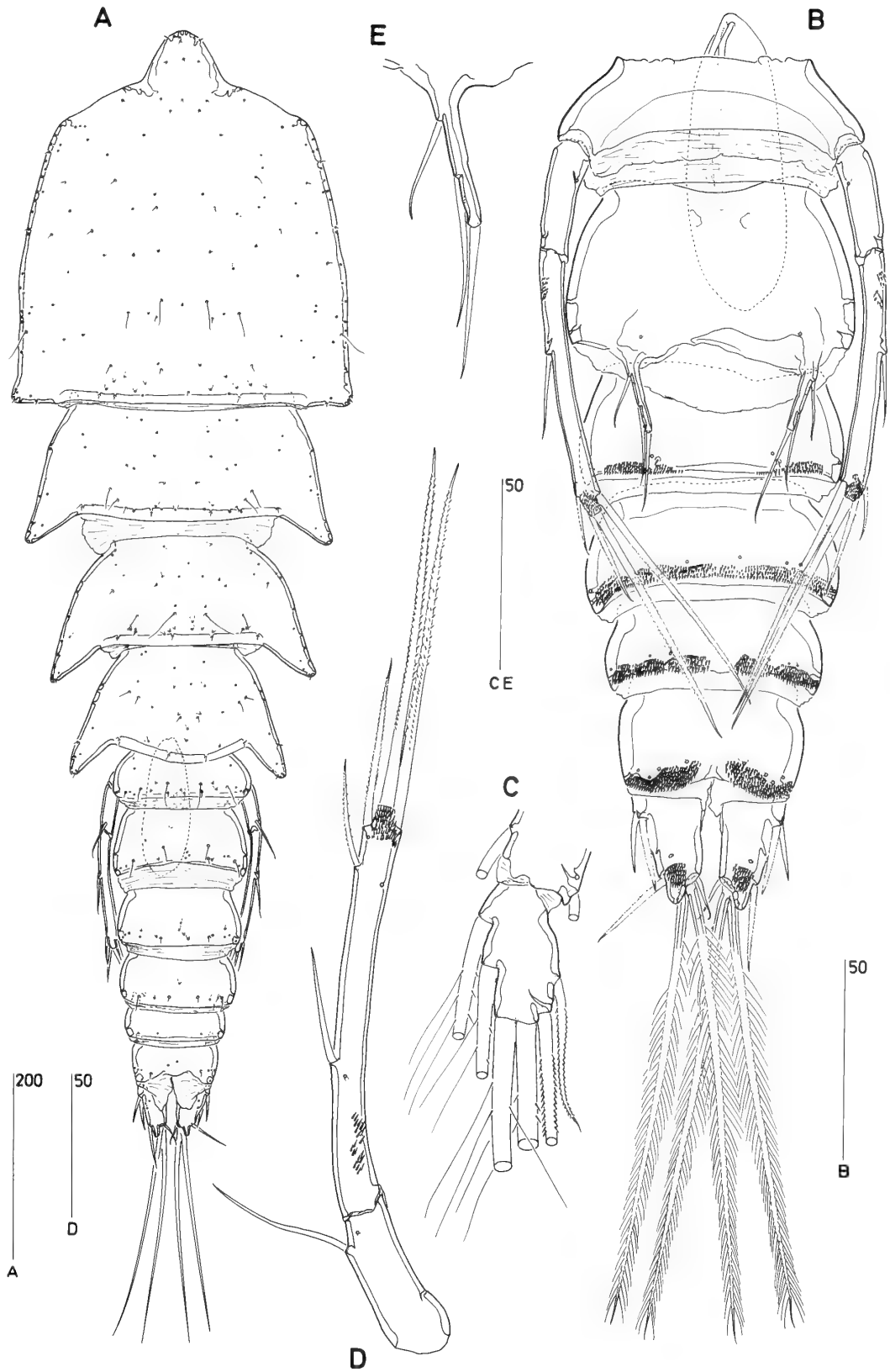

Fig. 14 *Clytemnestra longipes* sp. nov. (♂). A, Habitus, dorsal; B, urosome, ventral; C, P2 exp-3; D, P5, anterior; E, right P6.

relative length of the P5 exopod serve to distinguish both species. *C. farrani* is currently known only from two widely separated localities in the Indo-Pacific, suggesting that it is probably widespread throughout this oceanic basin.

Clytemnestra longipes sp. nov.

TYPE LOCALITY. Great Barrier Reef – see *C. farrani* sp. nov.

ETYMOLOGY. The species name is derived from the Latin *longus* (long) and *pes* (foot), and refers to the very long male P5 and P6.

TYPE MATERIAL. Holotype ♂ in alcohol (BMNH 1999.997). This material was originally registered as *C. scutellata* under BMNH 1948.4.28.121. Collected during Great Barrier Reef Expedition 1928–29 on either 15 June (stn 62), 10 July (stn 65) or 18 July 1929 (stn 68).

DESCRIPTION.

FEMALE. Unknown.

MALE. Total body length from tip of rostrum to posterior margin of caudal rami: 1211 µm. Maximum width (362 µm) measured at posterior margin of cephalic shield. Posterolateral angles of cephalothorax angular, weakly produced (Fig. 14A). Backwardly produced alate processes of somites bearing P2–P4 well developed. Urosome with genital and first abdominal somites separate (Fig. 14B).

Urosomites without dorsal ornamentation; all postgenital somites with multiple rows of minute spinules around ventral rear margin, those on urosomites 3, 5 and 6 arranged in paired patches either side of ventral midline (Fig. 14B).

Caudal rami (Fig. 14B) with bare seta II and minutely pinnate setae I and III; setae IV–V long (54% of urosome length) and plumose.

Rostrum (Fig. 14A) rounded anteriorly, protruding. Antennule, antenna, mouthparts (proximal endite on maxillary syncoxa present) and maxillipeds as in type species.

P2–P4 exp-3 with only 2 outer spines (Fig. 14C). P2–P4 armature formula:

	exopod	endopod
P2	1.1.222	1.2.221
P3	1.1.322	1.2.321
P4	1.1.322	1.2.221

P5 (Fig. 14D) narrow and elongate, extending to distal margin of first abdominal somite (Fig. 14B); exopod 2.7 times as long as basis; with 3 outer seta and 1 long seta at apex and subdistal inner corner.

Sixth pair of legs (Fig. 14E) forming very long cylindrical process with 1 apical and 2 outer bare setae.

REMARKS. The male of this species differs from all known males in (1) the ventral ornamentation pattern of the urosome, displaying spinules on all postgenital somites, and (2) the extreme elongation of the P5 and P6 (the distribution pattern of the 3 elements on the latter indicate that allometric growth must have happened primarily in the apical portion of the cylindrical process). *C. longipes* has the same swimming leg setal formula as *C. asetosa* but, in addition to the characters listed above, differs from the latter in body size and the presence of the proximal endite on the maxillary syncoxa.

Clytemnestra asetosa sp. nov.

TYPE LOCALITY. Suez Canal. Port Taufiq, Bay of Suez (Egypt).

ETYMOLOGY. The species name alludes to the absence of the proximal enditic seta on the maxillary syncoxa.

TYPE MATERIAL. Holotype ♂ dissected on 10 slides (BMNH 1999.1025). Paratypes in alcohol are 3 ♀♀, 2 ♂♂ (1 damaged) and 1 cop. V ♂ (BMNH 1999.1026–1031); collected during the Cambridge Expedition to the Suez Canal, 1924. This material was originally identified as *C. scutellata* by Gurney (1927) and Boxshall (1979).

OTHER MATERIAL EXAMINED. From R. Böttger-Schnack: 3 copepodid II stages in alcohol (BMNH 1999.1066–1068); central Red Sea, *Meteor* cruise 5/5, stn 682 (21°13.9' N, 38°05.7' E); 25 July 1987; multiple opening-closing net, 0.055 mm mesh, vertical hauling, 10–50 m (total water depth 1890 m).

DESCRIPTION.

FEMALE. Total body length from tip of rostrum to posterior margin of caudal rami: 758–830 µm ($\bar{x}$ = 801 µm; n = 3). Maximum width (226 µm) measured halfway down the cephalic shield. Posterolateral angles of cephalothorax rounded, not produced. Backwardly produced alate processes of somites bearing P2–P4 distinctly shorter than in *C. scutellata* and *C. gracilis*. General body shape (Fig. 15A) very similar to that of *C. farrani* (Fig. 12A).

Genital double-somite (Fig. 15B) weakly constricted bilaterally; original segmentation marked by minute, paired chitinous patches ventrally. Genital field as in type species.

Urosomites without dorsal ornamentation; penultimate and anal somites with multiple patches of minute spinules around ventral hind margin (Fig. 15B).

Caudal rami (Fig. 15C) with bare setae I and II; setae IV slightly shorter than seta V, both plumose.

Rostrum (Fig. 15A) rounded anteriorly, not distinctly delimited from cephalic shield.

Antennule (Fig. 16A) 7-segmented, with reduced armature on segments 2 and 3. Armature formula: 1-[1 plumose], 2-[9 + 1 plumose], 3-[3 + 3 plumose + 1 transformed], 4-[1 + 1 plumose + (1 transformed + ae)], 5-[1], 6-[3], 7-[8 + acrothek].

Antenna with weakly defined exopod (Fig. 17G); one seta fused basally to segment.

Mandible (Fig. 16B). Palp represented by minute seta; gnathobase with large lateral tooth (arrowed in Fig. 16C).

Maxillule (Fig. 16D) produced into distal lash (derived from armature element); with 1 lateral seta and 1 apical spine.

Maxilla (Fig. 16E) as in type species except for absence of proximal endite on syncoxa (position in other species arrowed in Fig. 16E). Maxilliped as in *C. scutellata*.

P1 (Fig. 17A) as in *C. scutellata* but setules along inner margin of enp-1 absent. P2–P4 (Fig. 17B–D) with only 2 outer spines on exp-3. P2–P4 armature formula:

	exopod	endopod
P2	1.1.222	1.2.221
P3	1.1.322	1.2.321
P4	1.1.322	1.2.221

P5 (Fig. 17E) nearly extending to posterior margin of genital double-somite. Basis short, exopod about 2.5 times as long as basis, with 5 setae (3 outer, 1 apical, 1 inner).

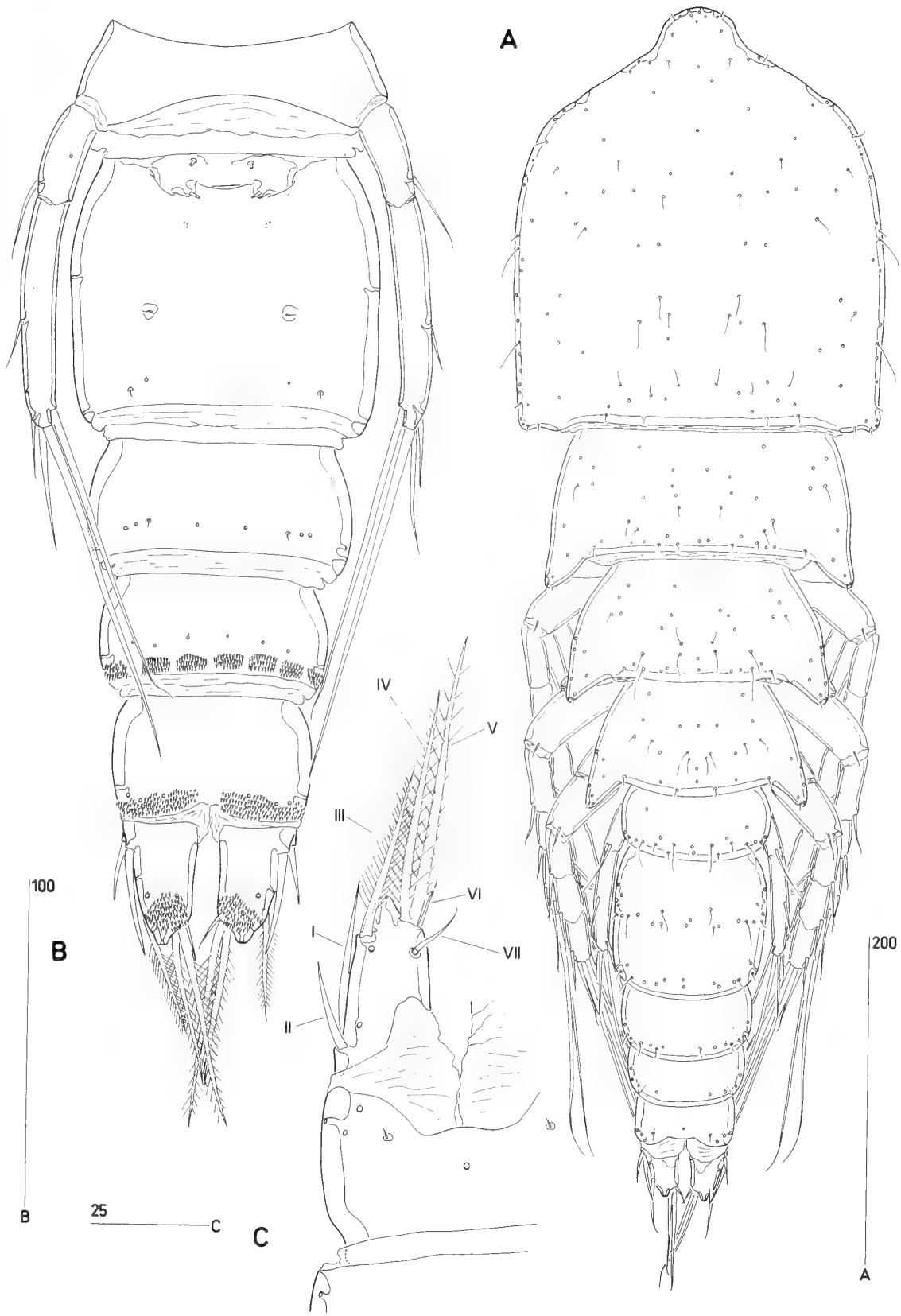

Fig. 15 *Clytemnestra asetosa* sp. nov. (♀). A, Habitus, dorsal; B, urosome, ventral; C, anal somite and right caudal ramus, dorsal.

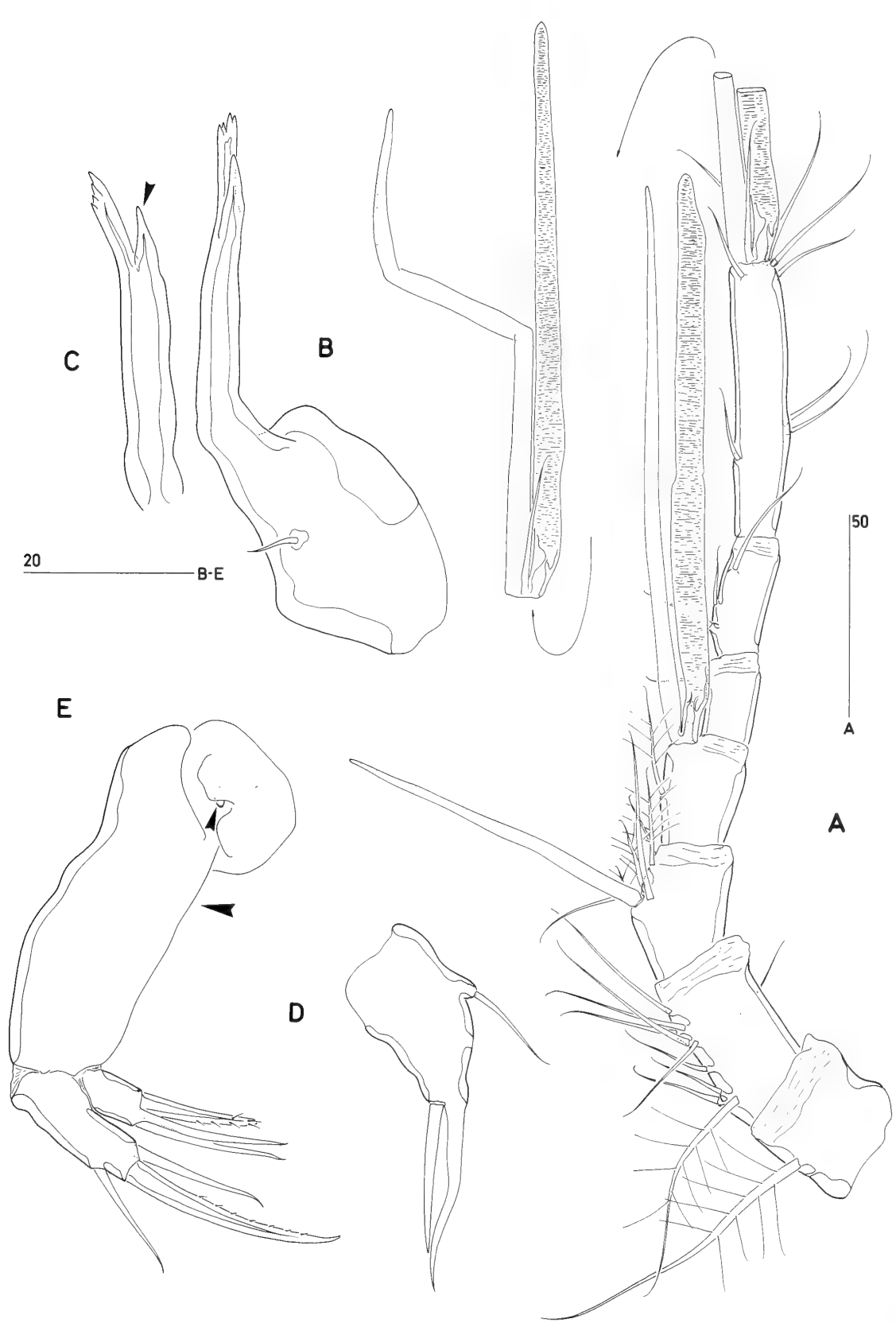

Fig. 16 *Clytemnestra asetosa* sp. nov. (♀). A, antennule, ventral [inset showing acrothek at full length]; B, mandible, posterior; C, mandibular gnathobase, other view [secondary tooth arrowed]; D, maxillule; E, maxilla, posterior [small arrow: exit of maxillary gland; large arrow indicating position of proximal endite in other *Clytemnestra* species].

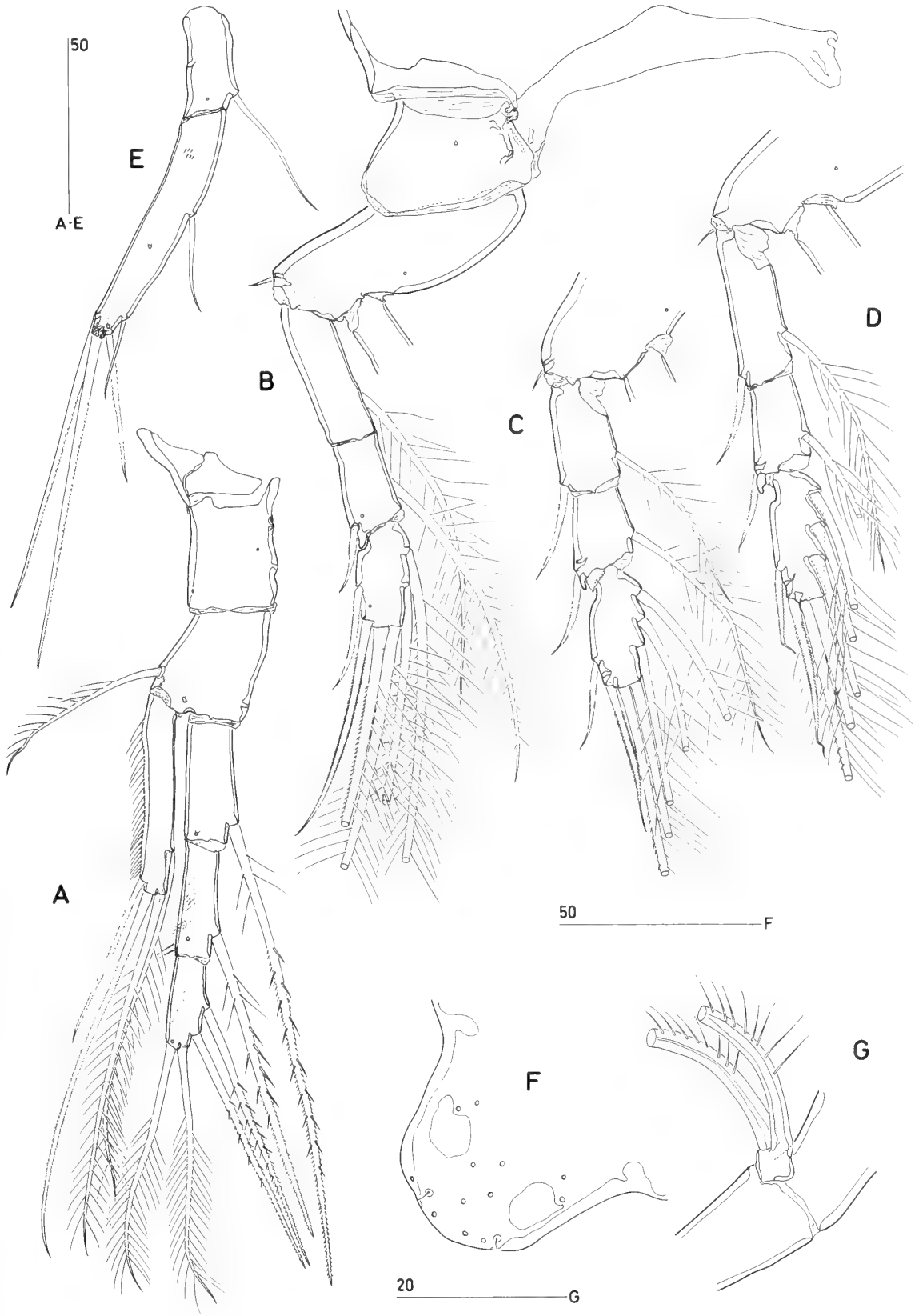

Fig. 17 *Clytemnestra asetosa* sp. nov. (♀). A, P1, anterior; B, P2, intercoxal sclerite, protopod and exopod, anterior; C, P3, distal portion of basis and exopod, anterior; D, P4, distal portion of basis and exopod, anterior; E, P5, anterior; F, rostrum, dorsal; G, antennary exopod.

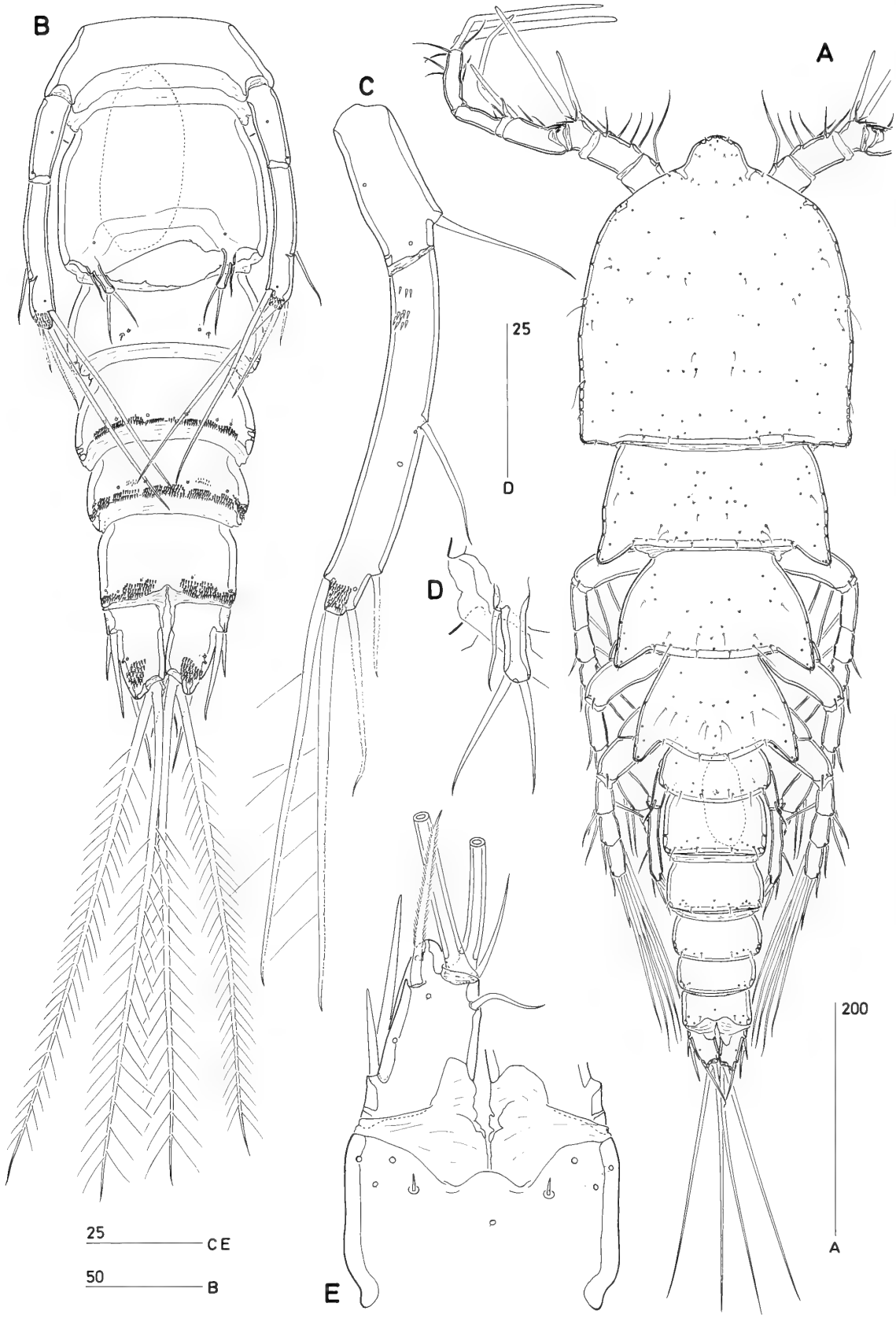

Fig. 18 *Clytemnestra asetosa* sp. nov. (♂). A, Habitus, dorsal; B, urosome, ventral; C, P5, anterior; D, P6; E, anal somite and right caudal ramus, dorsal.

MALE. Total body length from tip of rostrum to posterior margin of caudal rami: 920 µm (n = 1). Maximum width (232 µm) measured at posterior margin of cephalic shield. Body (Fig. 18A) with similar projections as in ♀; urosome more slender with genital and first abdominal somites separate (Fig. 18B).

Antennule, antenna, mouthparts and maxilliped with armature as in *C. scutellata*.

P5 (Fig. 18C) as in ♀, not extending to distal margin of first abdominal somite (Fig. 18B).

Sixth pair of legs (Fig. 18B, D) weakly asymmetrical; each P6 produced into short cylindrical process with 1 outer and 2 apical bare setae.

Urosomites 4–5 and anal somite with spinules around ventral hind margin (Fig. 18B).

Caudal rami (Fig. 18B, E) with bare setae I–II; setae IV–V very long (75% of urosome length) and plumose; seta VI much longer than in ♀.

REMARKS. The early copepodid stages from the central Red Sea were identified on the basis of the absence of the proximal endite of the maxilla and the shape of the cephalothorax. *C. asetosa*, originally identified as *C. scutellata* by Gurney (1927), is the smallest species in the genus. It is similar to *C. farrani* in many respects but differs from it in the armature formula of the antennule, the loss of the proximal endite of the maxilla, the presence of only 2 outer spines on P3–P4 exp-3 and a different spinulation pattern on the female urosome. The species is thus far known only from the Red Sea and the Bay of Suez.

Clytemnestra hendorffi var. *quinquesetosa* Poppe, 1891

Poppe (1891) distinguished this variety on the basis of the following characters: (1) female P5 exopod distinctly longer and bearing 5 setae; (2) urosome of both sexes less slender; (3) caudal rami relatively wider proximally. This variety was collected from two localities in the Java Sea. Most authors have followed Giesbrecht's (1892) decision to discard this variety and regarded it as a synonym of *C. scutellata*. Our revision has revealed that only *C. scutellata* and *C. gracilis* display 6 setae on the P5 exopod and that there are at least three species in the Indo-Pacific which have only 5 setae. As far as we could ascertain from the collections examined P5 setation is never variable within populations and always identical between sexes. Since Poppe (1891) did not provide any figures it is impossible to make any positive statement as to the identity of his material.

Other records

Chen *et al.* (1974) reported *C. scutellata* from the East China Sea (one of the areas where Dana originally recorded the species from). Unfortunately the few illustrations of the habitus and female P5 are of no help in determining the specific identity of their material. Moreover, the extreme body size range (1.0–1.9 mm) strongly suggests the co-occurrence of more than one species in their samples. Cheng *et al.* (1965) also illustrated *C. scutellata* from the East China Sea but their species has only 5 setae on the P5 exopod, lacks posterolateral processes on the cephalothorax and has only 2 outer spines on at least P3 (which was mislabelled as the P2) and P4. Their reported size range (♀♀: 0.86–1.0 mm; ♂♂: 0.80–0.85 mm) strongly suggests that they had identified *C. asetosa* or possibly a related species. Mori's (1929) description of *C. scutellata* from the Sea of Japan is equally brief. Posterolateral projections on the cephalothorax appear to be absent in his material (although they could be obscured by excessive squashing of the figured specimen), indicating that Mori was probably dealing with another species. Mori supplemented his description in 1937.

Kazmi & Muniza (1994) present sketchy figures of what they believe to be *C. scutellata* in their samples from the Arabian Sea. Nothing can be said about the real identity of their material other than that were dealing with a *Clytemnestra*.

The Caribbean records of *C. scutellata* by Owre & Foyo (1967) and Campos Hernández & Suárez Morales (1994) require further investigations. Both descriptions show the unique presence of lateral protrusions halfway down the cephalothorax which may suggest the occurrence of a distinct species in this region. It is impossible to decide from Legaré's (1964) inadequate illustrations whether this modification also occurred in his Venezuelan material. Interestingly, Morales & Vargas (1995) show similar protrusions in a clytemnestrid from the Pacific coast of Costa Rica which they identified as *C. rostratus* but has 7 segments in the antennule.

Genus *Goniopsyllus* Brady, 1883

Sapphir Car, 1890 [type species: *S. rostratus* Car, 1890 – by monotypy]

DIAGNOSIS. Clytemnestridae. Body with dorsal pattern of denticles and spinules on urosomites. Antennule 6-segmented in ♀, indistinctly 7-segmented in ♂ with segments 3–4 incompletely fused; ♂ segmental homologies: 1–I, 2–(II–VIII), 3–(IX–XII), 4–XIII, 5–(XIV–XVII), 6–(XVIII–XX), 7–(XXI–XXVIII). Antenna with 1 lateral and 4 apical elements on distal endopod segment; exopod represented by membranous segment bearing 1 long seta. Maxillule represented by triangular segment with 1 apical spine. Maxillary syncoxa with 1 endite bearing 2 setae.

P1 without outer seta on basis; exopod with 3 setae. P2 with outer spine on exp-1. P1–P4 armature formula:

	exopod	endopod
P1	021	1.1.220
P2	1.1.222	1.2.221
P3	1.1.323	1.2.321
P4	1.1.323	1.2.221

P5 exopod with 5 setae in both sexes.

Genital apertures fused in ♀ forming common medial slit; closed off by paired P6 bearing 1 well developed seta; copulatory pore located medially in large circular depression halfway the length of the genital double-somite; copulatory duct strongly chitinized.

Male P6 asymmetrical, forming membranous opercula closing off single (sinistral or dextral) genital aperture; bearing 1 seta.

Caudal rami convergent, relatively short and conical; not sexually dimorphic.

TYPE SPECIES. *Goniopsyllus rostratus* Brady, 1883 [by monotypy]

OTHER SPECIES. *G. clausi* sp. nov., *G. brasiliensis* sp. nov.

SPECIES INQUIRENDAE. *Goniopsyllus tenuis* (Lubbock, 1860) comb. nov.; *Sapphir rostratus* Car, 1890

Since the type species is only known from the damaged female holotype and no other material was available for study, *G. clausi* sp. nov. is instead selected for the model description.

Goniopsyllus clausi sp. nov.

Clytemnestra rostrata (Brady, 1883) *sensu* Giesbrecht (1892): pp. 568–572; Taf. 45, Figs 22, 31.

Clytemnestra rostrata (Brady, 1883) *sensu* Vilela (1965): p. 21; Est. IX, Fig. 2a–e; (1968): p. 44; Est. XVII, Fig. 2a–c.

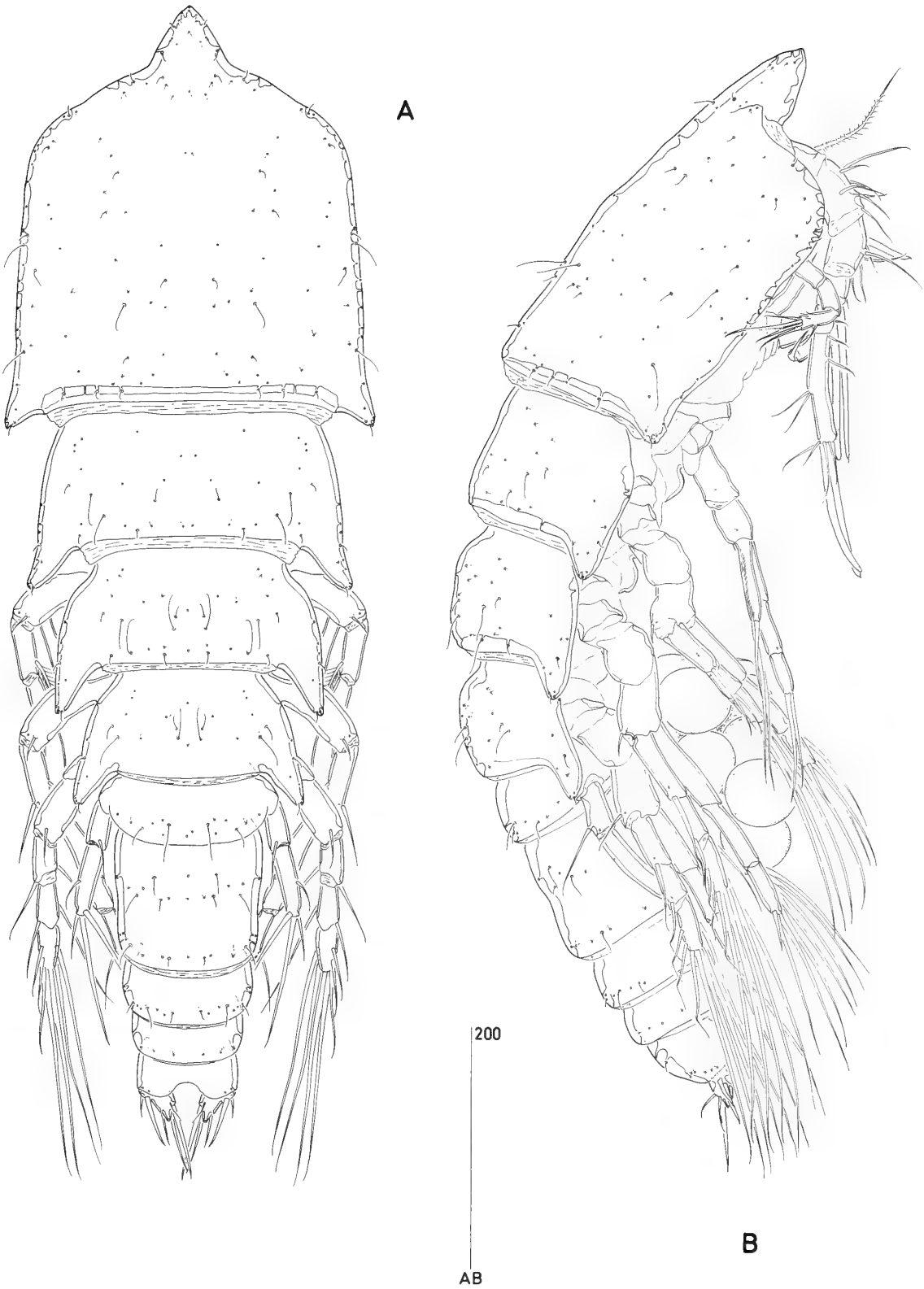

Fig. 19 *Goniopsyllus clausi* sp. nov. A, Habitus ♀, dorsal; B, habitus of ovigerous ♀, lateral.

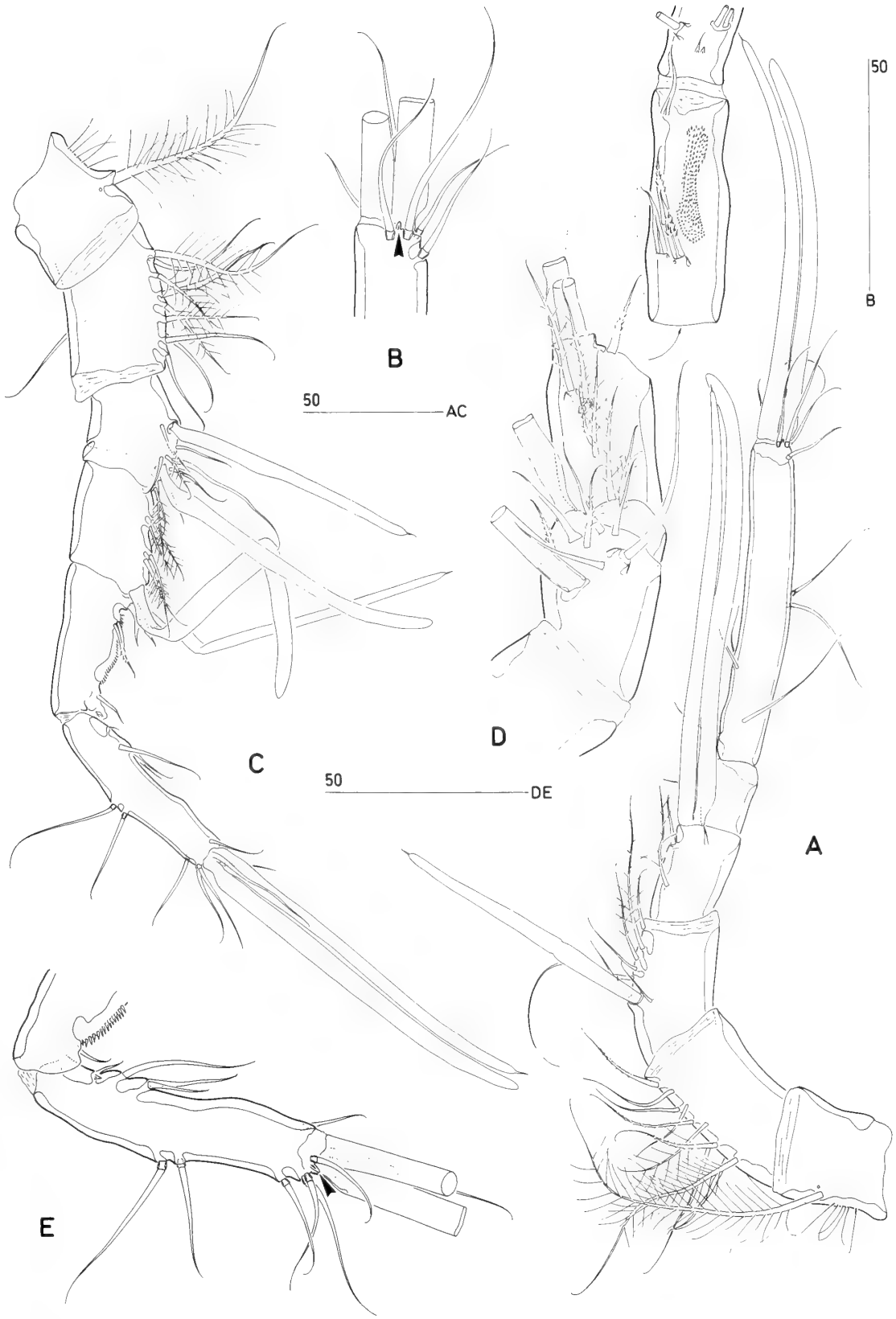

Fig. 20 *Goniopsyllus clausi* sp. nov. A, Antennule ♀, ventral; B, distal portion of antennulary segment 6 of ♀, ventral [rudimentary element arrowed]; C, antennule ♂, ventral; D, antennulary segments 3–6 of ♂, anterior; E, antennulary segment 7 of ♂, ventral [rudimentary element arrowed].

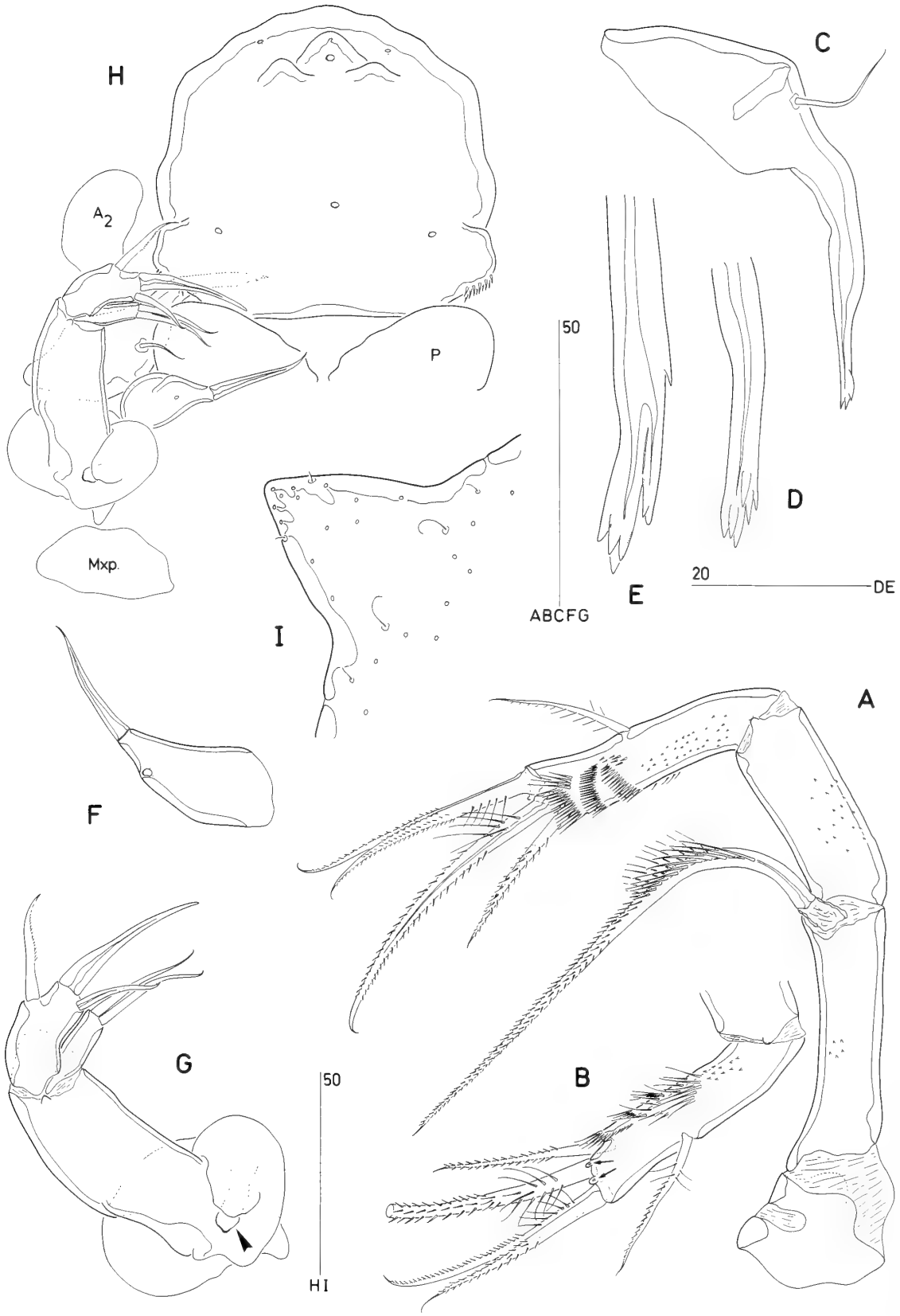

Fig. 21 *Goniopsyllus clausi* sp. nov. A, antenna ♀, outer; B, distal endopod segment of antenna ♀, inner [rudimentary elements arrowed]; C, mandible ♀; D, mandibular gnathobase ♀; E, mandibular gnathobase of ♂ specimen; F, maxillule ♀, posterior; G, maxilla ♀, posterior [exit of maxillary gland arrowed]; H, oral area ♀ showing position of antenna (A_2), labrum, paragnaths (P), mandible, maxillule, maxilla and maxilliped (Mxp.); I, rostrum ♀, dorsal.

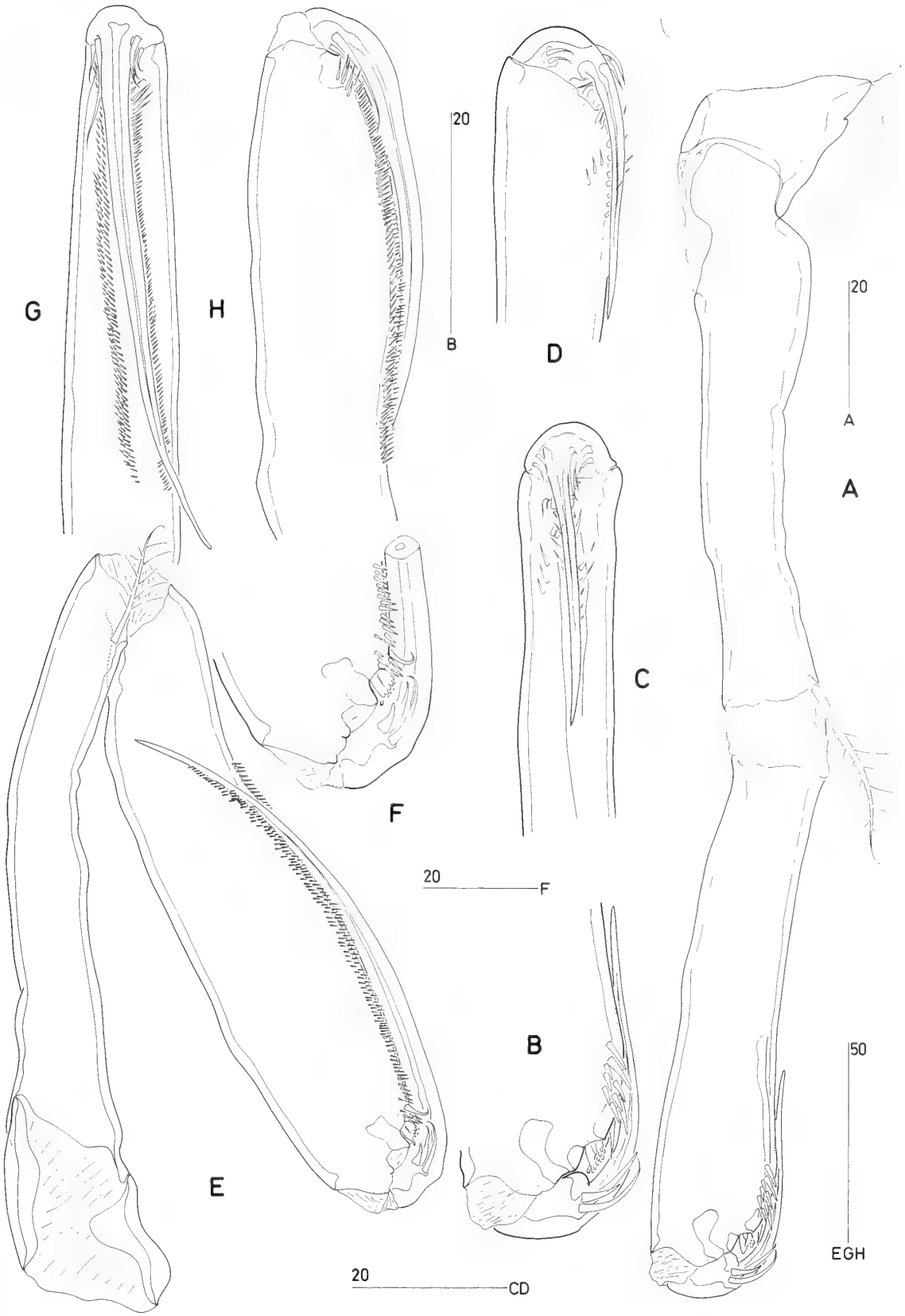

Fig. 22 *Goniopsyllus clausi* sp. nov. A, maxilliped ♀, anterior; B, maxilliped ♀, distal portion of basis and endopod, anterior; C, same, medial; D, same, posterior; E, maxilliped ♂, anterior; F, maxilliped ♂, distal portion and endopod, anterior; G, maxillipedal basis and endopod ♂, medial; H, same, posterior.

Clytemnestra rostrata (Brady, 1883) *sensu* Huys *et al.* (1996): pp. 300–303, Figs 120A–G, 121A–D.

Clytemnestra rostrata (Brady, 1883) *sensu* Boxshall & Huys (1998): p. 782, Fig. 13(a)–(b).

TYPE LOCALITY. Bay of Cadiz, 36°30'N 7°20'W (Spain).

ETYMOLOGY. The species is named in honour of Carl Claus, one of the most prolific 19th century copepodologists, who first called attention to the distinctiveness of the clytemnestrid genera.

TYPE MATERIAL. Holotype ♀ dissected on 10 slides (BMNH 1999.1035). Paratypes are 2 dissected ♂♂ (on 2 and 5 slides, respectively), 2 dissected ♀ (on 1 slide each), and 9 ♀♀ (1 damaged), 1 ♂, 4 copepodids (2 Cop V, 1 Cop IV, 1 Cop III) in alcohol (BMNH 1999.1036–1055). In addition, 2 ♀♀ and 1 ♂ were prepared for SEM. Donated by J.M. Gee, collected by A. Lindley (Plymouth Marine Laboratory), 1984.

OTHER MATERIAL EXAMINED. 4 ♀♀, 2♂♂: Adriatic Sea, Station CJ-008, Pelegrin, Hvar (Croatia), leg. F. Kršinić, *'Bios'*, 23 May 1998 (BMNH 1999.1072–1077).

DESCRIPTION.

FEMALE. Total body length from tip of rostrum to posterior margin of caudal rami: 979–1067 µm ($\bar{x}$ = 1017 µm; n = 8). Maximum width (306 µm) measured at posterior margin of cephalic shield. Posterolateral angles of cephalothorax only weakly expanded laterally but markedly produced posteriorly (Fig. 19A, B). Somites bearing P2–P4 successively decreasing in width posteriorly and bearing backwardly produced alate processes.

Genital double-somite (Figs 23A; 27C) slightly constricted bilaterally; original segmentation marked by two minute chitinous patches ventrally. Copulatory pore (Figs 23C, D; 27A, C) located medially in large circular depression, halfway the length of genital double-somite; leading to anteriorly directed, strongly chitinized duct which at level of P5-bearing somite enters median seminal receptacle. Genital apertures located far anteriorly; closed off by small opercula derived from vestigial P6; each with 1 well developed seta (Figs 23C; 27D).

Urosomites with zone of small denticles around dorsal hind margin (not figured in Fig. 19A, but see Fig. 23B); penultimate and anal somites also with larger spinules around ventral hind margin (Fig. 23A).

Caudal rami short (Figs 23B; 26A), convergent; conical in shape with stepped inner and outer margins marking insertion sites of setae I, II and IV–V; produced into conical process bearing terminal pore; with numerous ventral pores as illustrated in Fig. 26A. Setae I–II bipinnate, spiniform and strongly developed; seta I 1.85 times as long as seta II, extending beyond apex of caudal ramus. Seta III minutely bipinnate. Setae IV–V basally fused, without fracture planes, multipinnate and spiniform; seta V about 2.1 times ramus length. Seta VI minute, bare; seta VII biarticulate at base, bare.

Rostrum (Figs 19A; 21I) triangular and well offset, completely fused to cephalothorax; with numerous dorsal surface pores as figured, none on ventral surface; with minute lateral sensillae near apex.

Antennule (Fig. 20A) slender, 6-segmented; segment 6 very long. Plumose setae present on segments 1–4. Segment 1 with small pore near seta and few long setules along anterior margin. Armature formula: 1-[1 plumose], 2-[6 + 1 plumose + 3 pinnate], 3-[5 + 2 plumose + 1 transformed], 4-[1 + 1 plumose + (1 transformed + ae)], 5-[1], 6-[11 + acrothek]. Apical acrothek consisting of aesthetasc, long transformed seta and short bare seta. Transformed setae on segments 3, 4 and 6 long and aesthetasc-like, with minutely spiniform tip; those on segments 4 and 6 basally fused to aesthetasc. Rudimentary element present at base of acrothek (arrowed in Fig. 20B).

Antenna (Fig. 21A, B) 4-segmented, comprising coxa, basis and 2-segmented endopod. Coxa well developed, bare. Basis and proximal endopod segment with few surface denticles; unarmed. Exopod inserted in membranous area between basis and endopod; represented by small, weakly chitinized segment bearing strong recurved seta apically; exopodal seta multipinnate, spinules in proximal third distinctly longer. Distal endopod segment with 3 surface frills and minute denticles on outer surface and patch of long setules on medial surface; lateral armature consisting of 1 pinnate seta; distal armature consisting of 1 subapical and 3 apical, non-geniculate, bipinnate or multipinnate elements, 2 of which spiniform, recurved and bearing long spinules proximally; distal margin with 2 rudimentary elements on inner surface (arrowed in Fig. 21B).

Labrum (Fig. 21H) large, with 6 secretory pores on anterior surface; distal margin smooth medially and with spinular patch on either lateral lobe.

Mandible (Fig. 21C–E) reduced. Palp represented by single naked seta. Gnathobase long and narrow, stylet-like; produced into number of cuspidate processes apically and subapically; without dorsal seta(e).

Paragnaths (Fig. 21H) well developed lobes without any conspicuous ornamentation.

Maxillule (Fig. 21F) reduced; represented by small triangular segment bearing naked apical seta and raised pore along outer margin.

Maxilla (Fig. 21G, H) 2-segmented, comprising elongate syncoxa and allobasis. Syncoxa with expanded basal portion; exit of maxillary gland large (arrowed in Fig. 21G), partly concealed under lobate extension; coxal endite cylindrical, with 2 naked setae apically. Allobasis with large articulating claw distally, smaller inner spine and unipinnate seta along outer margin.

Maxilliped (Fig. 22A) very large, articulating with well developed pedestal; 3-segmented, comprising syncoxa, basis and endopod. Syncoxa extremely elongate, longer than basis; without ornamentation but with 1 anterior, plumose seta near membranous articulation with basis. Basis elongate; distal third of palmar margin with double spinule row and 2 elements located closely to articulation with endopod (Fig. 22B–D); proximal element spiniform and bare, distal element stubby and spinulose. Endopod represented by short segment bearing naked claw; accessory armature consisting of 3 anterior setae and 2 posterior setae (Fig. 22B–D).

Swimming legs with wide, narrow intercoxal sclerites and well developed praecoxa; both without ornamentation. Rami 3-segmented except for P1 exopod.

P1 (Fig. 23E) separated from maxillipeds by large membranous area. Coxa and basis prolonged along dorsoventral axis; without surface ornamentation. Basis without inner or outer seta (spine). Exopod 1-segmented, represented by elongate segment bearing long setules along outer margin; with subapical pore and 3 setiform elements distally, outer one less than half the length of others. Endopod 3-segmented; segments decreasing in size distally, each with anterior pore and few spinules/setules along outer margin; enp-1 with very long inner seta; ornamentation of inner elements typically (multi)pinnate, distal elements plumose.

P2–P4 (Figs 24A, B; 25B) with transversely prolonged basis bearing short outer seta. Endopods distinctly longer than exopods. Exopodal outer spines setiform with distinct flagellate tip. Exopod segments typically with pore near outer distal corner; without ornamentation. Endopods with long proximal segment, particularly in P2–P3; segments with anterior pore, setules along outer margin and spinules (enp-2 and -3) or setular tuft (enp-1) on posterior surface; setal ornamentation typically combination of setular and

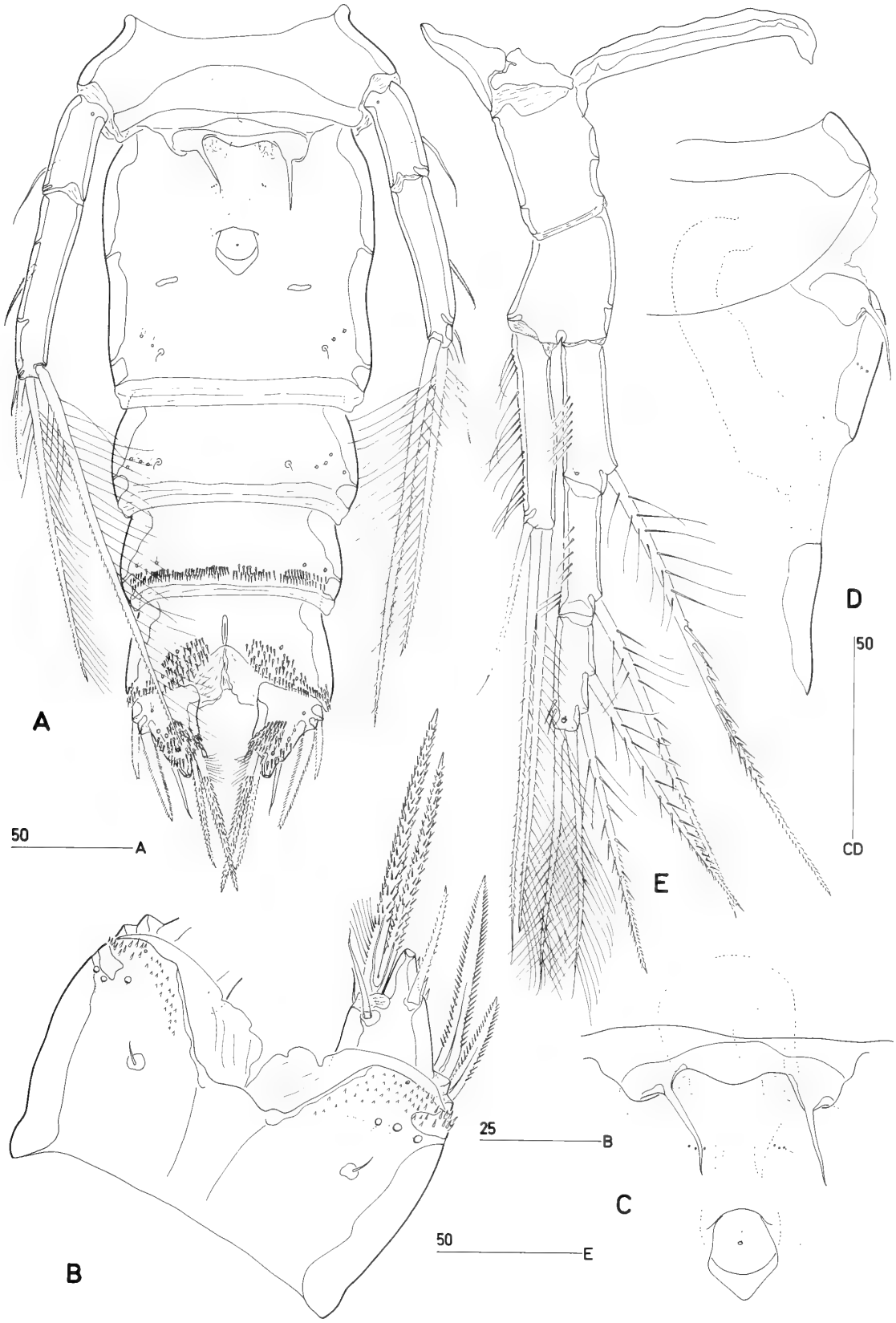

Fig. 23 *Goniopsyllus clausi* sp. nov. (♀). A, Urosome, ventral; B, anal somite and left caudal ramus, dorsal; C, genital field, ventral; D, genital field, lateral; E, P1, anterior.

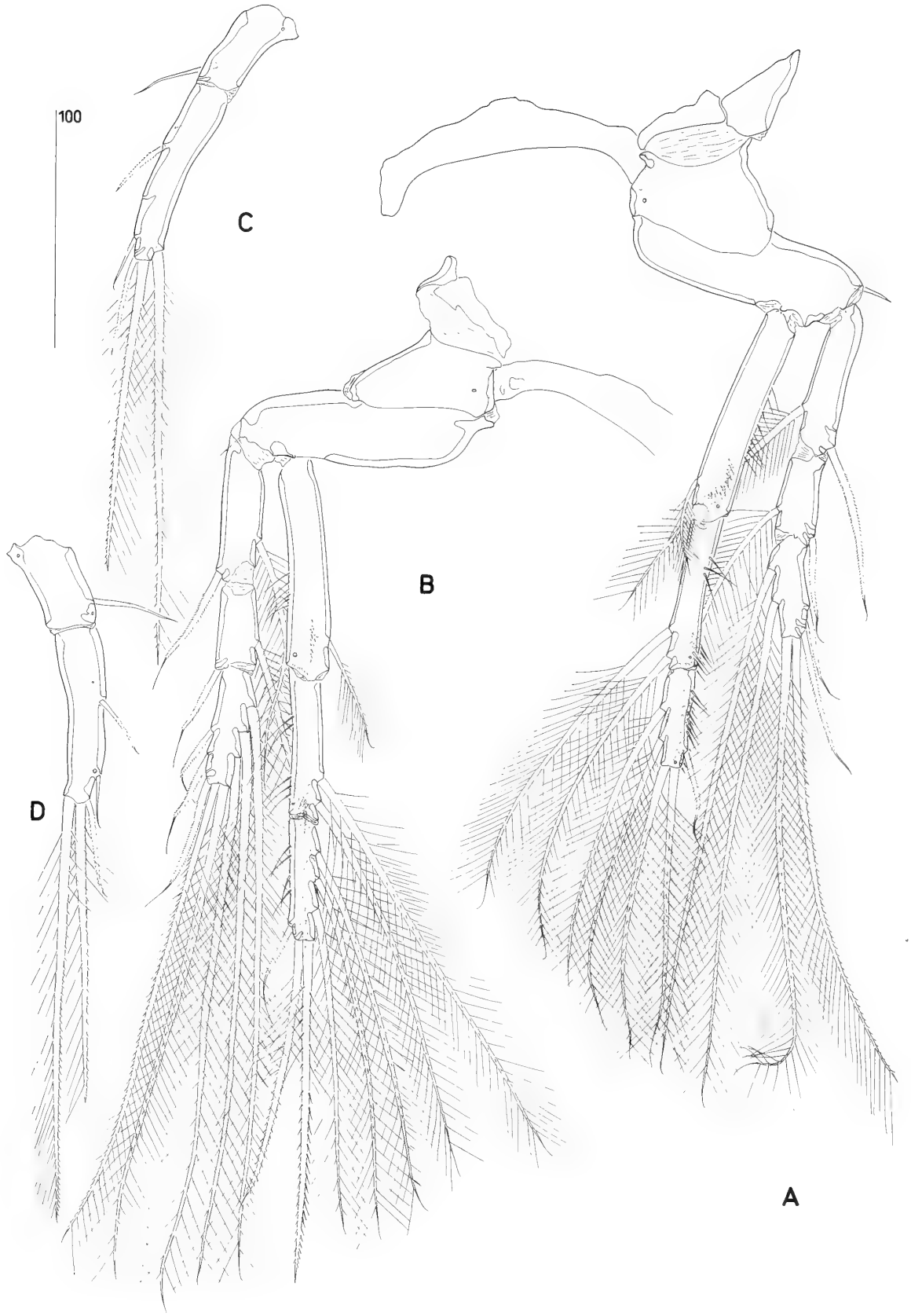

Fig. 24 *Goniopsyllus clausi* sp. nov. (♀). A, P2, anterior; B, P3, anterior; C, P5, anterior; D, aberrant P5, anterior.

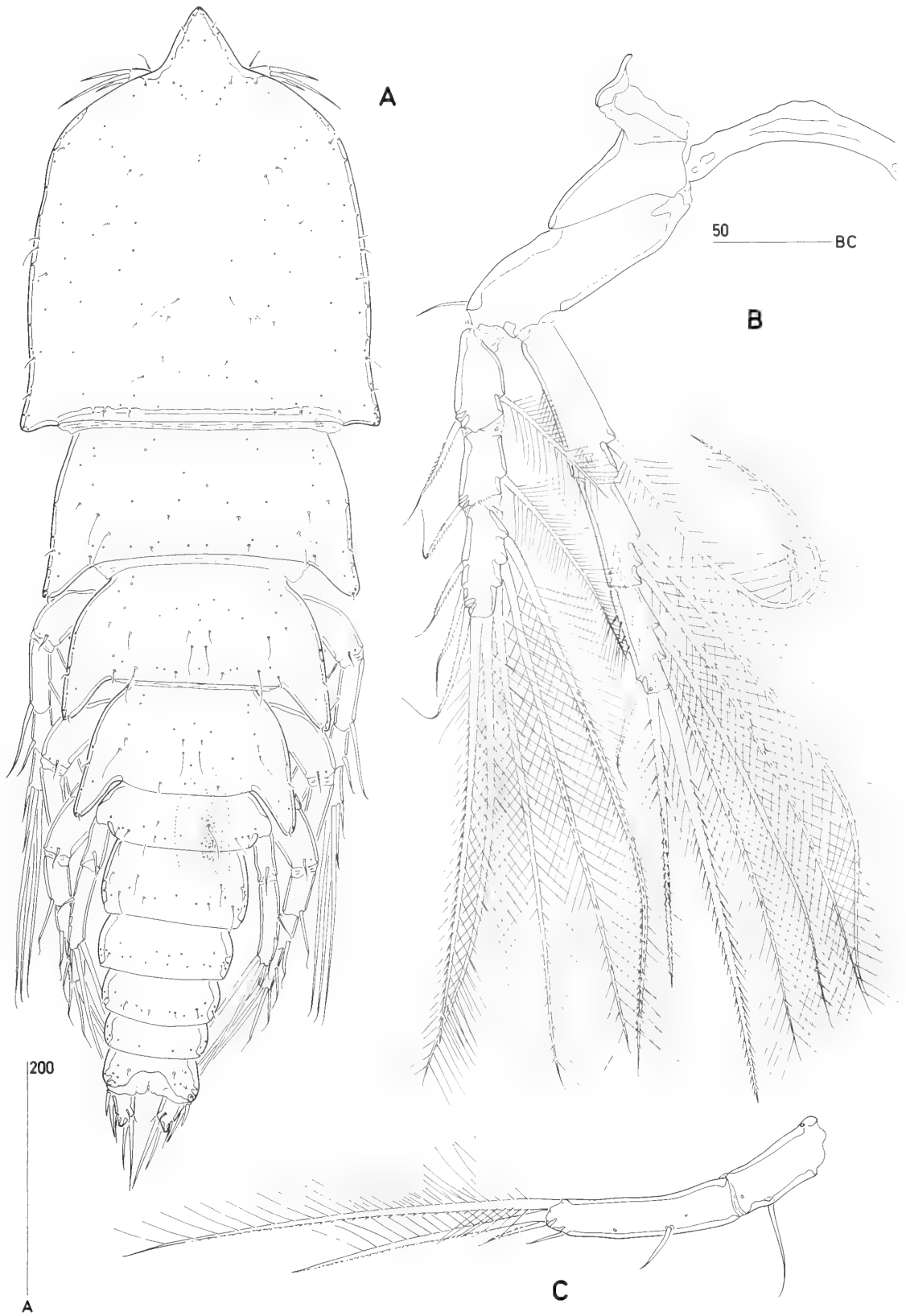

Fig. 25 *Goniopsyllus clausi* sp. nov. A, Habitus ♂, dorsal; B, P4 ♀, anterior; C, P5 ♂, anterior.

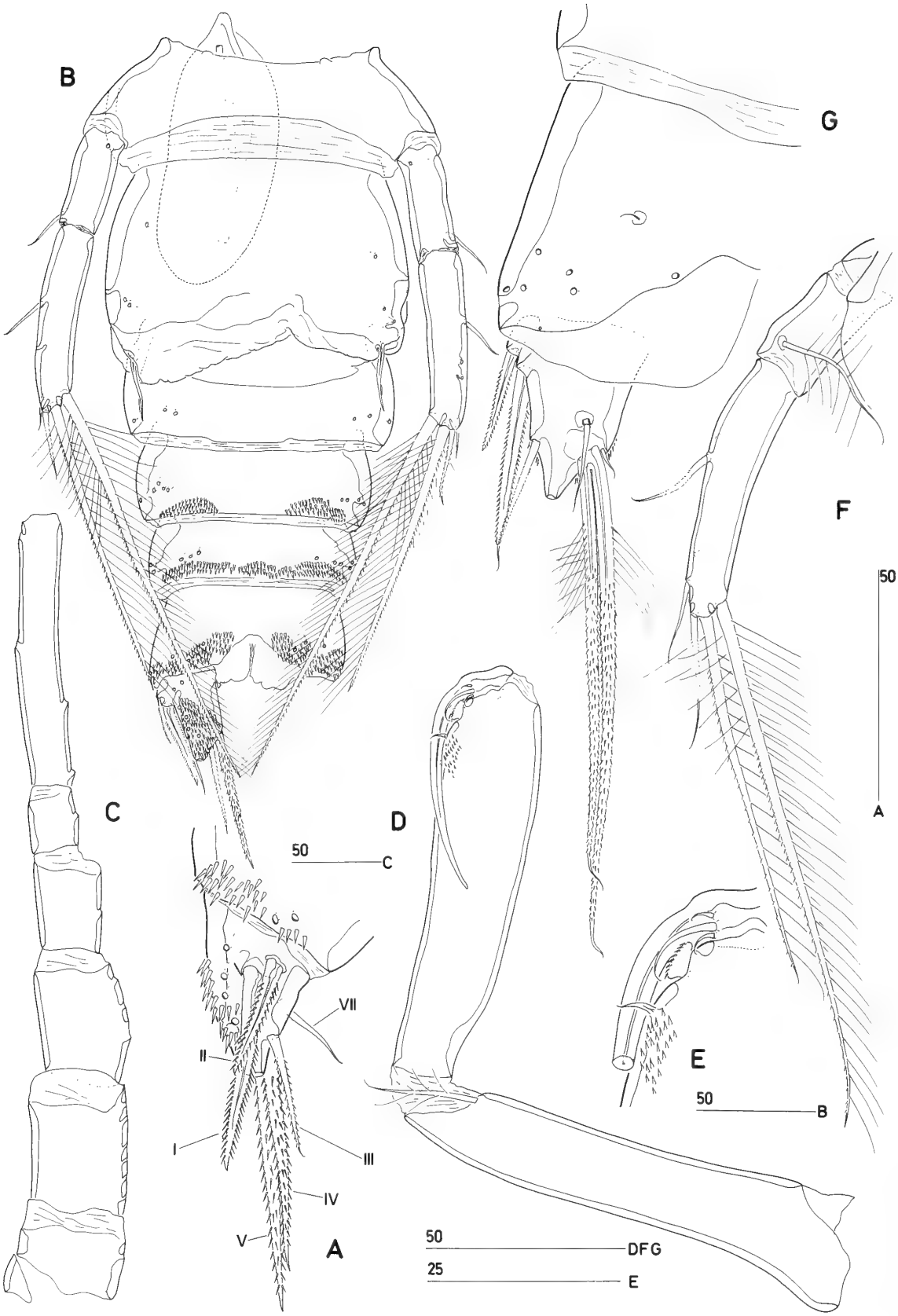

Fig. 26 *Goniopsyllus clausi* sp. nov. A, Caudal ramus ♀, lateral; B, urosome ♂, ventral. *Goniopsyllus rostratus* Brady, 1883 (holotype ♀). C, Antennule (armature omitted); D, maxilliped, anterior; E, maxilliped, distal portion of basis and endopod, anterior; F, P5, posterior; G, anal somite and left caudal ramus, dorsal.

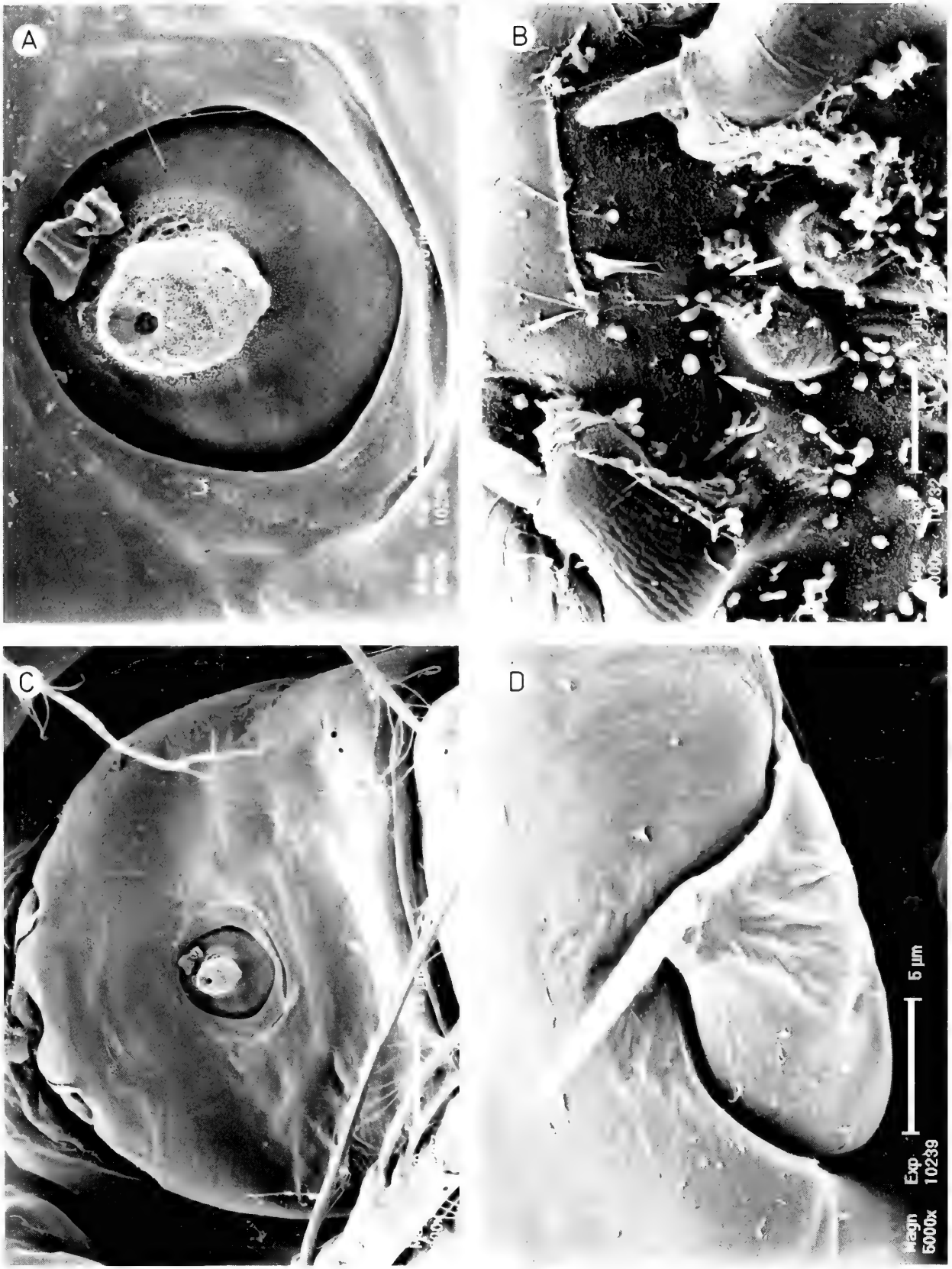

Fig. 27 *Goniopsyllus clausi* sp. nov. (♀). SEM photographs. A, Circular depression surrounding copulatory pore (position obscured by remnant of spermatophore neck); C, genital double-somite; D, genital aperture. *Clytemnestra gracilis* (Claus, 1891*a*) comb. nov. (♀). B, Genital apertures and copulatory pore [arrowed].

spinular rows; inner seta of P2–P3 enp-1 short. Spine and setal formula of swimming legs as for genus.

P5 (Fig. 24C) uniramous, laterally displaced; 2-segmented, comprising basis and 1-segmented exopod; not extending to distal margin of genital double-somite (Fig. 23A). Basis with short outer seta and pore near outer distal corner. Exopod about twice as long as basis, slightly curved inwards; outer margin with 2 pinnate setae and 3 pores; inner margin with long plumose seta; apex with 1 pinnate and 1 plumose seta.

MALE. Total body length from tip of rostrum to posterior margin of caudal rami: 1021 µm (n = 1). Maximum width (304 µm) measured at posterior margin of cephalic shield.

Body (Fig. 25A) with similar projections as in ♀; genital and first abdominal somites separate.

Rostrum (Fig. 25A) more pointed than in ♀.

Antennule (Fig. 20C) slender, indistinctly 7-segmented with segment 4 only demarcated dorsally (Fig. 20D); haplocer, with geniculation located between segment 6 and 7. Plumose setae present on segments 1–5. Segment 1 with small pore near seta and few long setules along anterior margin. Armature formula: 1-[1 plumose], 2-[5 + 5 plumose], 3-[5 + 1 plumose + 1 pinnate + 1 transformed + ae], 4-[2 plumose], 5-[4 plumose + 1 pinnate+ (1 transformed + ae)], 6-[1 + 2 pinnate spines + 1 smooth spine], 7-[10 + 2 vestigial elements + acrothek]. Apical acrothek consisting of aesthetasc, long transformed seta and short bare seta. Transformed setae on segments 3, 5 and 7 long and aesthetasc-like, with minutely spiniform tip; those on segments 5 and 7 basally fused to aesthetasc. Rudimentary element present at base of acrothek (arrowed in Fig. 20E). Segment 6 with continuous patch of spinules on anterior surface (Fig. 20D). Segment 7 with 2 vestigial elements near geniculation.

Maxilliped (Fig. 22E) very large, articulating with well developed pedestal; 3-segmented, comprising syncoxa, basis and endopod. Syncoxa extremely elongate but not longer than basis; without ornamentation but with 1 anterior, plumose seta near membranous articulation with basis. Basis elongate; more swollen than in ♀; middle and distal thirds of palmar margin forming longitudinal furrow bordered by multiple rows of spinules on both anterior and posterior sides; with 2 elements located closely to articulation with endopod; proximal element spiniform and bare, distal element stubby and spinulose. Endopod represented by short segment produced into very long naked claw which in reflexed position typically fits in palmar furrow with the apical part closely adpressed onto the anterior surface of the basis (Fig. 22E, G); accessory armature consisting of 3 anterior setae and 2 posterior setae (Fig. 22F–H).

P5 (Fig. 25C) very similar to that of ♀, with identical proportions and setation but lateral setae of exopod slightly shorter.

Sixth pair of legs (Figs 11C; 26B) asymmetrical, represented by highly membranous non-articulating flaps covering single, large genital aperture (Fig.11C); each lobe with 1 bare seta at outer distal corner.

Urosomites 4–5 and anal somite with spinules around ventral hind margin (Fig. 26B).

Caudal rami (Fig. 26B) slightly more slender than in ♀; conical projection wider and setae I–II relatively shorter.

Spermatophore with very long, recurved neck (Fig. 26B).

VARIABILITY. The left P5 of the holotype ♀ shows slightly different segmental proportions and pore pattern (Figs 23A; 24D).

REMARKS. This species was illustrated by Huys *et al.* (1996) as '*Clytemnestra rostrata*'. Their brief description which was based on material from the Gulf of Cadiz contains some observational errors. The most significant is the setation of the maxillule which was actually based on *C. gracilis*. The armature on the genital field was omitted in their Fig. 120B. The female P5 (their Fig. 121C) also appears shorter but this is to be regarded as the result of excessive squashing during mounting.

The distribution of *G. clausi* is thus far restricted to the Portuguese coast (Vilela, 1965, 1968) and the Mediterranean with confirmed records from the Bay of Cadiz, Naples and the Adriatic. *Sapphir rostratus* has also been recorded from the Adriatic but is probably not synonymous with *G. clausi* (see below). The Naples record refers to Giesbrecht (1892) who found 1 ♂ of '*C. rostrata*' in this area but also attributed Pacific specimens (3 ♀♀, 2 ♂♂) to this species.

Goniopsyllus rostratus Brady, 1883

Clytemnestra rostrata (Brady, 1883) Poppe (1891)

TYPE LOCALITY. South Atlantic, off Argentinean coast; 42°32' S 56°29' W; net at 54 m depth.

MATERIAL EXAMINED. Holotype ♀ dissected on slide (reg. no. C.C.46); collected during Voyage of H.M.S. *Challenger* during the years 1873–1876 (station 318); 11 February 1876. The dissection is imperfect and incomplete (e.g. antenna and P1 are lacking), and the specimen is partly aberrant in the swimming leg setal formula.

REDESCRIPTION.

FEMALE. Genital double-somite (Fig. 28A) relatively short in comparison with other species, not constricted bilaterally; original segmentation marked by two minute chitinous patches ventrally. Copulatory pore (Fig. 28A) located medially in large circular depression, halfway the length of genital double-somite; leading to anteriorly directed, strongly chitinized duct which at level of P5-bearing somite enters median seminal receptacle. Genital apertures located far anteriorly; closed off by small opercula derived from vestigial P6; each with 1 well developed seta.

Urosomites with zone of small denticles around dorsal hind margin; penultimate and anal somites also with larger spinules around ventral hind margin (Fig. 28A).

Caudal rami short (Figs 26G; 28A), convergent; similar in shape to *G. clausi* but proportionally smaller. Setae I–II bipinnate, spiniform and strongly developed; seta I 1.7 times as long as seta II, extending beyond apex of caudal ramus. Seta III minutely bipinnate. Setae IV–V basally fused, without fracture planes, multipinnate and more setiform and distinctly longer than in *G. clausi* (compare Fig. 23B); seta V about 3 times ramus length. Seta VI minute, bare; seta VII biarticulate at base, bare.

Antennule (Fig. 26A) slender, 6-segmented; segment 6 longer than in *G. clausi* (length ratio segment 6 : segment 5 being 6.0 in *G. rostratus*, 5.0 in *G. clausi*). Armature pattern as in *G. clausi*.

Maxilliped (Fig. 26D) with similar armature as in *G. clausi* but with different spinular ornamentation on palmar margin (Fig. 26E).

P2–P4 spine and setal formula of swimming legs as follows (left P3 exp-3 and right P4 exp-3 with aberrant outer spine number):

	Exopod		Endopod
	Right	Left	
P2	1.1.222	1.1.222	1.2.221
P3	1.1.323	1.1.32*2*	1.2.321
P4	1.1.32*2*	1.1.323	1.2.221

P5 (Fig. 26F) 2-segmented, comprising basis and 1-segmented exopod;relative lengths as in *G. clausi*. Exopod outer margin with 2

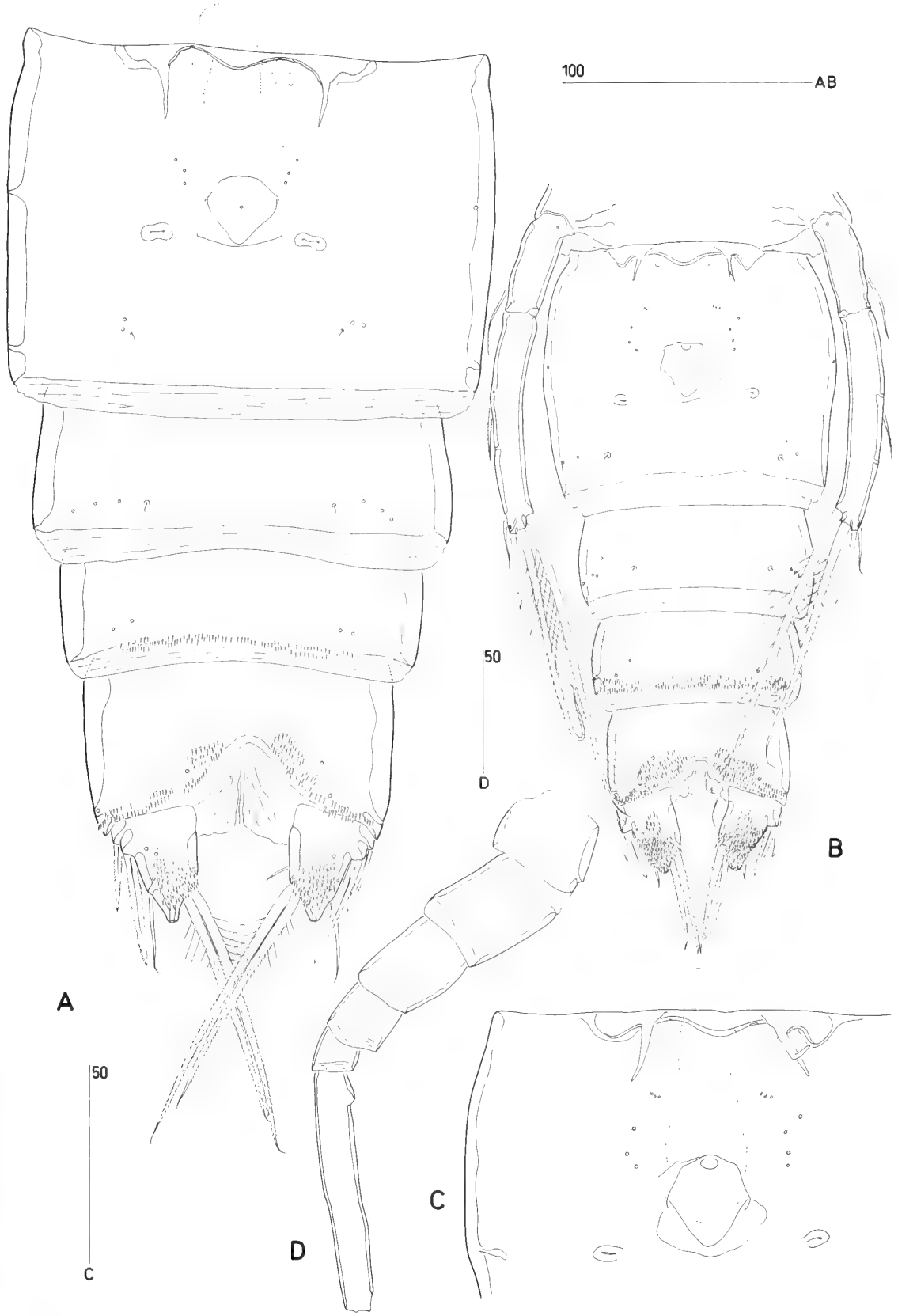

Fig. 28 *Goniopsyllus rostratus* Brady, 1883 (holotype ♀). A, Urosome (excluding P5-bearing somite), ventral [distorted due to excessive squashing]. *Goniopsyllus brasiliensis* sp. nov. (♀). B, Urosome, ventral; C, genital field, ventral; D, antennule (armature omitted).

pinnate setae and 3 pores; inner margin with long plumose seta; apex with 1 pinnate and 1 plumose seta.

MALE. Unknown.

REMARKS. Upon re-examination Boxshall (1979) concluded that the holotype, identified by Brady (1883) as a male, was in reality female. The true sexual identity however, had already been noted by both Poppe (1891) and Claus (1891*a–b*) who based their conclusion on the 5-segmented urosome and the female facies of the antennule and maxilliped. This opinion was also confirmed by Giesbrecht (1892) but not by Car (1891*b*) who continued regarding it as a male on the basis of the internal spermatophore drawn by Brady. The most plausible explanation is that Brady (1883) had misinterpreted the strongly chitinized copulatory duct, a suspicion reinforced by inspection of the holotype.

Giesbrecht (1892: 573) pointed out the discrepancy between the size mentioned in Brady's text and that inferred from his habitus figure reproduced at x80 magnification. According to Brady the holotype is only 0.65 mm long ('1-40th of an inch') but Giesbrecht considered 1.16 mm a more realistic figure. Re-examination of the slides strongly suggests that Brady must have made a morphometric error of at least a factor 2. The urosome (excl. P5-bearing somite) which is mounted intact measures 0.43 mm. Extrapolation by using the urosome/body length ratio found in its congeners *G. clausi* and *G. brasiliensis* (about 0.3) gives an estimated total body length of 1.43 mm. This large size rules out possible conspecificity with *G. brasiliensis* ($\bar{x}$ = 0.96 mm).

Brady (1883) assumed all four swimming legs to be similar, having 3-segmented rami and resembling the leg illustrated in his Fig. 15 (i.e. the P2). His lateral habitus view suggests that the P1 possesses 3-segmented exopods and endopods, however Poppe (1891) suspected that Brady had overlooked the exopod and instead had superimposed both left and right endopods. For some unknown reason he assumed the P1 exopod to be 2-segmented but failed to confirm this against the holotype due to the absence of the P1 on Brady's slide.

G. rostratus can be readily identified from the other South-American species *G. brasiliensis* by the large body size (compare urosomes in Fig. 28A–B drawn at the same scale), the elongate caudal ramus setae IV–V, the long seta I clearly extending beyond the distal margin of the ramus, and additional differences in the ornamentation of the maxilliped (spinule pattern on palmar margin). Brady (1883) also illustrated well developed posterolateral extensions on the cephalothorax which are completely absent in *G. brasiliensis*.

Goniopsyllus brasiliensis sp. nov.

? *Clytemnestra rostrata* (Brady, 1883) *sensu* Ramírez (1966): 291; Lám. II, figs 12–15.

TYPE LOCALITY. Rio Grande do Sul (Brazil); outside opening of Lagôa dos Patos to ocean; 32°11'S 52°7'W.

ETYMOLOGY. The species name refers to the type locality.

TYPE MATERIAL. Holotype ♀ dissected on 8 slides (BMNH 1999.1056). Paratypes are 8 ♀♀ in alcohol (BMNH 1999.1057–1064). Collected by G.A. Boxshall, February 1996, plankton haul.

DESCRIPTION.

FEMALE. Total body length from tip of rostrum to posterior margin of caudal rami: 892–1057 µm ($\bar{x}$ = 958 µm; n = 8). Maximum width (265 µm) measured at posterior margin of cephalic shield. Posterolateral angles of cephalothorax rounded, virtually not expanded laterally (Fig. 29A). Rostrum (Fig. 29A) rounded and less pronounced than in *G. clausi*. Backwardly produced alate processes of somites bearing P2–P4 distinctly shorter and less pointed than in *C. clausi*. Integument generally less chitinized than in *G. clausi*.

Genital double-somite (Fig. 28B) not constricted bilaterally and relatively wider than in *G. clausi*; original segmentation marked by minute, paired, chitinous patches ventrally. Genital field as in *G. clausi* but with additional pores flanking copulatory pore (Fig. 28C).

Urosomites with zone of small denticles around dorsal hind margin (Fig. 29B); penultimate and anal somites also with larger spinules around ventral hind margin (Fig. 28C).

Caudal rami (Figs 28B; 29A–C) short, convergent. Setae I–II bipinnate, spiniform and strongly developed; seta I 1.2 times as long as seta II, not extending beyond apex of caudal ramus. Seta III minutely bipinnate. Setae IV–V basally fused, multipinnate and about as long as in *G. clausi* but seta IV more resilient (compare Fig. 23B); seta V about 1.5 times ramus length. Seta VI extremely small; seta VII biarticulate at base, bare.

Antennule (Fig. 28D) slender, 6-segmented; segment 2 shorter than in *G. clausi* but armature pattern identical.

Mandible and maxillule (Fig. 29D) somewhat more slender than in *G. clausi*.

Maxilliped (Fig. 29E–F) with similar armature as in *G. clausi* but with different spinular ornamentation on palmar margin (Fig. 29F).

P1–P4 with setal formula as for genus.

P5 (Fig. 28B) markedly longer than in *G. clausi*, extending beyond distal margin of genital double-somite.

MALE. Unknown.

REMARKS. Although many South-American authors have recorded specimens that they attribute to *C. rostrata*, there is good reason to believe that in fact often they have mistaken *G. brasiliensis* for this species. In general, with the discovery of *G. brasiliensis* many of the Brazilian records of *G. rostratus* are rendered doubtful (Björnberg, 1963; Björnberg *et al.*, 1981; Campaner, 1985; Carvalho, 1944; Gaudy, 1963; Montú, 1980; Montú & Gloeden, 1986; Montú & Cordeiro, 1988; Santos, 1973; Vega-Perez, 1993). The same applies to Legaré's (1961, 1964) records of *C. rostratus* from Venezuelan coastal waters. The species illustrated by Ramírez (1966) as *C. rostrata* from Mar del Plata in Argentina differs from the one figured in his later paper (Ramírez, 1970) by the complete absence of posterolateral projections on the cephalothorax and is almost certainly conspecific with *G. brasiliensis*. The author described the female antennule as 7-segmented but this clearly contradicts his illustration which shows only 6 segments as in other species of *Goniopsyllus*. The only anomaly remaining is the body size which according to Ramírez (1966) is 1.8 mm for the female and 1.5 mm for the male. Based on his illustrations and the accompanying scale bars the female only measures 0.74 mm and the male 0.77 mm.

It is not clear whether Carvalho's (1952) material of *C. rostrata*, consisting of 5 males from the Bay of Santós (São Paulo State), also belongs to *C. brasiliensis*. His size range (0.50–0.85 mm) precludes possible identity with *C. rostratus* but the illustrations accompanying the brief description are completely worthless and erroneous. The caudal rami are exceptionally long for this genus, the P5 exopod has only 4 elements, and the antennule is 8-segmented. The specimens reported from Guaratuba (Paraná State) in an earlier paper (Carvalho, 1944) are also very small (0.5 mm) and their fragmentary description is equally useless for identification purposes.

Finally, there is no possibility of identifying any specimens from Campos-Hernández & Suárez-Morales' (1994) illustrations of *C. rostrata* from the Gulf of Mexico.

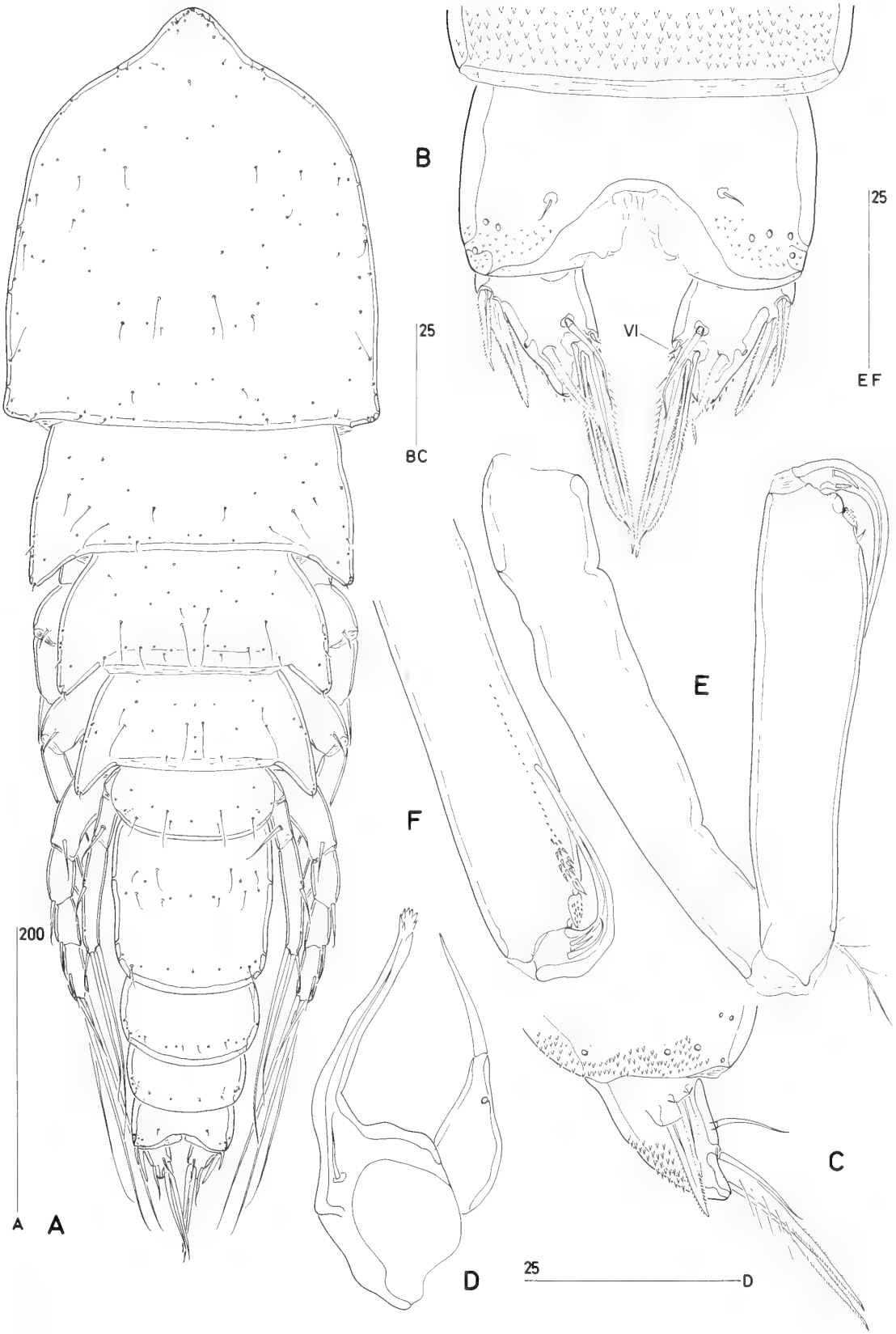

Fig. 29 *Goniopsyllus brasiliensis* sp. nov. (♀). A, Habitus, dorsal; B, anal somite and caudal rami, dorsal; C, caudal ramus, lateral; D, mandible and maxillule; E, maxilliped, posterior; F, maxilliped, distal portion of basis and endopod, anterior.

Goniopsyllus tenuis (Lubbock, 1860) comb. nov.

Clytemnestra tenuis Lubbock, 1860

Lubbock's (1860) description is very incomplete and based on a single specimen. The antennule was figured as 7-segmented but comparison with other clytemnestrid descriptions indicates that the author had erroneously shown the second segment as subdivided into two distinct segments. The segmentation of the distal half of the antennule conforms with the *Goniopsyllus* pattern, justifying its placement in this genus. Giesbrecht (1892) regarded *C. tenuis* as a likely synonym of *G. rostratus* but in the light of the discovery of several closely related species we regard this course of action premature. Conversely, Marques (1973) listed *C. tenuis* in the synonymy of *C. scutellata*. Although Lubbock doubted the sexual maturity of the holotype female this is contradicted by his statements that the specimen was ovigerous and that the second and third abdominal somites had almost completely coalesced (this being in conflict with his illustration of a 6-segmented urosome lacking any trace of a genital double-somite). With the scanty information available it is extremely unlikely that *C. tenuis* will ever be recognized; it is ranked here as *species inquirenda*.

Sapphir rostratus Car, 1890

Conspecificity between *S. rostratus*, described from Trieste (North Adriatic), and *G. clausi*, recorded from the South Adriatic (this paper), seems conceivable on zoogeographical grounds. The relative lengths of the distal antennulary segments in both sexes and the length of caudal ramus seta II, however, do not agree with those of *G. clausi*. It is questionable whether these discrepancies are real or reflect observation bias since Car's (1890) illustrations contain other, more significant errors such as the P5 which is shown with only 3 setae and the P4 which allegedly lacks an outer spine on the distal endopod segment. A final obstacle to conspecificity is the small size of *S. rostratus* which, based on the dorsal view of the male, measures only 0.58 mm. Rather than proposing a new replacement name in anticipation of potential secondary homonymy with the type species, we maintain this species as *species inquirenda* under its current name. If *S. rostratus* and *G. clausi* are conspecific then the former becomes a invalid senior synonym of the latter.

Other records

Monard's (1928) description of '*C. rostrata*' from Banyuls-sur-Mer contains several inconsistencies such as his illustration of the P5 exopod which shows only 4 setae and his statement that the P2–P4 enp-3 setal pattern is 6-5-5, indicating that he has confounded P2 and P3. The author also claims that the male P5 is modified and the female antennule 7-segmented. The small size (0.65 mm) seems to rule out conspecificity with *G. clausi*.

Chen *et al.*'s (1974) record of *G. rostratus* from the East China Sea and Mori's (1937) from Japanese waters are indeterminable on the basis of the few illustrations provided. The short female P5 suggests a species different from *G. rostratus*. Similarly, Marques (1958) did not give convincing evidence for her record from Angola since only the habitus of the male and body length measurements (♀ : 0.4– 0.94 mm; ♂: 1 mm) were provided.

DISCUSSION

Generic concepts and species discrimination

The generic concepts of *Goniopsyllus* and *Clytemnestra* (as *Goniopelte*) introduced by Claus (1891*b*), but dismissed by subsequent authors, are reinstated here. Claus based the distinction on differences in antennule segmentation and setation of the antennary exopod, and on the presence or absence of sexual dimorphism in the caudal rami. *Goniopsyllus* is clearly more advanced than *Clytemnestra*, being illustrated by several reductions in the cephalic appendages, P1 and male P6 which provide additional discrepancies between both genera. In *Goniopsyllus* the number of distal setae on the antennary endopod is reduced (the missing elements being marked by rudiments; arrowed in Fig. 21B), the armature of the maxillule is represented by a single apical element, the distal syncoxal endite of the maxilla bears only 2 elements and the long syncoxal seta representing the proximal endite is lost. The latter character should be used with caution in generic discrimination since convergent loss of the proximal endite has happened in at least one representative of *Clytemnestra* (Fig. 16E). All species of *Goniopsyllus* lack the outer basal seta of P1 and have lost the inner seta of its exopod. The male sixth legs are weakly developed bearing only 1 seta in *Goniopsyllus* (Fig. 11C) but are produced into conspicuous, elongate, trisetose processes in *Clytemnestra* (Fig. 11A–B), resembling the condition found in the Aegisthidae and Cerviniidae.

Although *Clytemnestra* is the more primitive genus, it can be readily identified by the absence of the outer spine on P2 exp-1. As far as we could ascertain this is a unique character in harpacticoids with a 3-segmented P2 exopod. The caudal ramus sexual dimorphism displayed only by *Clytemnestra* requires further ontogenetic study before it can be considered a potential autapomorphy for the genus. The typical caudal ramus condition found in the majority of the Harpacticoida shows normally developed terminal setae IV and V. In the Clytemnestridae this condition is exhibited only by the males of *Clytemnestra* (e.g. Fig. 5B), the atypical female state (Fig. 5A) showing reduced setae. In contrast to swimming leg sexual dimorphism which is nearly always the result of deviations in male ontogeny, secondary sexual characters in the caudal rami are exclusively expressed by the female, and as a rule are not expressed until the final moult. This timing of expression has been demonstrated in various families displaying caudal ramus sexual dimorphism, including the Canuellidae, Cylindropsyllidae and Canthocamptidae. In these families it is intrinsically linked with precopulatory mate guarding where female caudal ramus modification shows substantial congruence with male antennule morphology. Since the atypical condition in female *Clytemnestra* is also found in both sexes of *Goniopsyllus* – and thus unlikely to be the result of transformation at the final moult – a different ontogenetic explanation must apply. This is further corroborated by examination of early copepodids (including Cop V ♂) of *C. asetosa* and *G. clausi* which revealed similarly reduced caudal setae in both species. The male caudal setae in *Clytemnestra* must therefore undergo transformation at the final moult. Hence, it is assumed here that reduction of setae IV–V represents the ancestral state in the family and that elongation evolved only secondarily in male *Clytemnestra*, not being linked to mate guarding but possibly enhancing its capacity during mate location.

Examination of the genital field has revealed significant differences between both genera. In *Goniopsyllus* the copulatory pore is located halfway down the genital double-somite in a large circular depression (Fig. 27A) and connects via a strongly chitinized duct with the anteriorly positioned seminal receptacles (Fig. 23C–D). In *Clytemnestra* the copulatory pore is represented by a posteriorly directed minute slit (arrowed in Fig. 27B), located between the genital apertures far anteriorly on the genital double-somite, and a copulatory duct is hardly differentiated (Fig. 5A). The polarity of copulatory pore displacement is difficult to assess, however, outgroup

Table 1 Diagnostic characters of *Clytemnestra* species [A1 = antennule; GDS = genital double-somite; AS = first adominal somite]. Length measurements are based on material examined in this paper.

	scutellata	*gracilis*	*farrani*	*longipes*	*asetosa*
size ♀(in µm)	1121	1309–1562	927–947	?	758–830
size ♂ (in µm)	1064	1420–1531	939–945	1211	920
cephalothoracic processes	present	present	absent	obsolete	absent
setal number segment 2 A1 ♀	12	12	12	?	10
proximal endite maxilla	present	present	present	present	absent
P2 exp-3 formula	223	223	222	222	222
P3 exp-3 formula	323	323	323	322	322
P4 exp-3 formula	323	323	323	322	322
setal number P5 exopod ♀/♂	6	6	5	5	5
P5 apex ♀ vs GDS posterior margin	coinciding	distad	coinciding	?	proximad
P5 apex ♂ vs AS posterior margin	proximad	coinciding	proximad	coinciding	proximad
spinules 2nd abdominal somite ♀	absent	present	present	?	absent
spinules 1st abdominal somite ♂	absent	absent	absent	present	absent

comparison with the Tegastidae, Peltidiidae and Tisbidae suggests that migration happened anteriorly and the condition in *Clytemnestra* is apomorphic.

Species discrimination in *Clytemnestra* is most easily achieved by comparing primarily cephalothorax shape, swimming leg spine pattern, urosomal ornamentation and setation of the maxillae and antennules (Table I). Conversely, identification of *Goniopsyllus* species is strenuous and largely based on size, maxillipedal ornamentation and proportional lengths of caudal ramus setae. The reported variability in body size and/or P5 setation for both *C. scutellata* and *G. rostratus* (e.g. Boxshall, 1979; Huys *et al.*, 1996) is based on erroneous identifications and observational errors.

Relationships

Prior to Claus' (1891*a*) study the relationships of the Clytemnestridae were believed to lie with the planktonic poecilostomatoid families, in particular the Sapphirinidae (Car, 1890). This concept was partly based on the superficial similarity in dorsoventrally depressed body shape, laterally displaced fifth legs and the failure to recognise the geniculate antennules in the male (Car, 1890). More significantly, this assignment was based also on the strongly reduced mouthparts and the sexual dimorphism displayed by the maxillipeds, two characters regarded as highly diagnostic for the Poecilostomatoida (Huys & Boxshall, 1991).

Sexual dimorphism in the maxillipeds is uncommon in the Harpacticoida. Huys (1988) reviewed the topic, showing that there is clear dimorphism only in the Aegisthidae (as a result of male atrophy), some Tisbidae (e.g. Boxshall, 1979) and deepwater Huntemanniidae (*Metahuntemannia*, *Talpina*). Dahms & Schminke (1993) demonstrated that in *Tisbe bulbisetosa* the male maxilliped is involved in precopulatory mate guarding by holding the female's caudal setae IV and V prior to spermatophore transfer, the antennules playing only an auxiliary role during this process. We speculate that the modified male maxillipeds in clytemnestrids perform a similar function, the elongate endopodal claw probably being involved in holding the female's caudal rami or swimming legs.

Boxshall & Huys (1998) pointed out that the antennulary chemosensory system of *C. rostratus* (= *G. clausi* sp. nov.) is secondarily enhanced in both sexes by transformation of three setae into aesthetasc-like elements. The middle and distal of these elements are fused basally to an aesthetasc. This study has revealed this pattern to be diagnostic for all Clytemnestridae and can be considered an apomorphy for the family. Examination of copepodid stages showed these transformed setae to be present from at least copepodid III onwards. Modification of antennulary elements into putative chemosensors is rare in harpacticoid copepods and has thus far only been recorded in some deep-sea species. Gee & Huys (1991) described a densely opaque, bulbous element on the distal antennulary segment in both sexes of the paranannopid *Leptotachidia iberica* Becker, 1974. The only report of a similar structure is that by Por (1969) who figured a modified bulbiform element on the antennule of *Cerviniopsis obtusirostris* Brotskaya, 1963 (Cerviniidae) which he called the 'Brodskaya organ'.

The complete lack of swimming leg sexual dimorphism impedes an assessment of the relationships of the Clytemnestridae. The 1-segmented P1 exopod is found in several interstitial Paramesochridae, Leptastacidae and Laophontidae, yet it is diagnostic at the family level only in the Rotundiclipeidae and Tegastidae. Lang (1948) recognised a close relationship between the latter, the Peltidiidae and the Clytemnestridae. He based this affinity solely on P1 morphology, including the non-prehensile nature of the endopod and the presence of maximum 5 elements on the distal exopod segment. Within this group of tisbidimorph families he placed the Peltidiidae as the sistergroup of the Clytemnestridae on account of the dorsoventrally flattened body and the reduction of the P5 baseoendopod in the female. The usefulness of Lang's (1948) characters is limited due to their homoplastic nature, however, there are at least two other features which appear to substantiate a close relationship between these three families. First, the aesthetasc pattern on the male antennule (with an additional aesthetasc on ancestral segment XI) is displayed by all three families. Secondly, the modification of the distal palmar element on the maxillipedal basis into a pad-like sensory element (Fig. 10B) is a unique synapomorphy (see Huys *et al.* (1996) for examples in Peltidiidae and Tegastidae). A detailed phylogenetic analysis of the Peltidiidae is nevertheless required before its sistergroup relationship with the Clytemnestridae can be substantiated. Indeed, an alternative evolutionary scenario could be that the latter represent only a specialized terminal branch of the former. Most species of the peltidiid genus *Alteutha* Baird are common members of the coastal plankton, performing pronounced diurnal vertical migrations in the water column. This may well be viewed, either ecologically or evolutionary, as a transitionary step towards the holoplanktonic lifestyle exhibited by the Clytemnestridae.

'Taxonomic Impediment' and Marine Plankton

The present revision has quadrupled the number of species in the family solely by examination of the relatively limited material deposited in the NHM. There is no doubt that this number would

have been significantly higher had the geographic coverage been wider. Indicative of this is the discovery of three species of *Clytemnestra* in a small sample from the Great Barrier Reef. Preliminary examination of material from Brazilian waters (Rio Grande do Sul) revealed a similar sympatry for both *Clytemnestra* and *Goniopsyllus*. Although the discovery of several closely related species in both genera is noteworthy, it is not unexpected nor exceptional for a marine planktonic taxon. For example, recent taxonomic studies have uncovered several important species complexes in the Oncaeidae (Heron, 1977; Heron & Bradford-Grieve, 1995; Böttger-Schnack, 1999). Although this family is morphologically distinctive and arguably the most speciose in the marine plankton, the continuing discovery of pseudo-sibling species and frequent confusion about the validity of rank of its species and morphs tarnish its literature, both taxonomic and ecological. Current research on another planktonic poecilostomatoid genus, *Pachos* Stebbing, resulted in the recognition of several new but previously misidentified species (Huys & Kršinić, in prep.).

The taxonomy of pelagic harpacticoids is plagued by considerable conservatism and inadequate study of morphological features. With the exception of the mesopelagic tisbid genera (Boxshall, 1979) all planktonic harpacticoids were known well before the turn of the century (Krøyer, 1846; Dana, 1847, 1849; Boeck, 1865; Brady, 1883; Giesbrecht, 1891; T. Scott, 1894), yet, their morphological definition and supposedly cosmopolitan breadth of their distribution have hitherto remained unchallenged. The genus *Microsetella* Brady & Robertson currently encompasses only two species, however, one can expect its number of species to increase by an order of magnitude if the many undescribed sibling species are considered (unpubl. data). Similarly, *Euterpina acutifrons* (Dana, 1847) is commonly regarded as a cosmopolitan species but comparison of distant 'populations' suggests that there is no factual justification for this universally accepted view.

In Fleminger & Hulsemann's (1977) scholarly study demonstrating the taxonomic divergence in three sympatrically occurring sibling species of *Calanus* in the North Atlantic, one sentence deserves wide currency: '. . ., the quality of knowledge about circulating oceanic habitats and their entrained ecosystems rests upon the reliability of three interrelated sets of information: systematics of the biota, routine identifications of species, and assessments of their ranges, horizontally and vertically'. Unfortunately, routine identifications in ecological investigations are generally not conducive to the recognition of sibling species and all too often wide geographical distributions have been uncritically accepted as the natural consequence of potentially broad oceanic dispersal. The latter perception is often coloured by underlying assumptions of the lack of isolating physical barriers and global uniformity in the open pelagic environment. Pseudo-sibling species can only be readily distinguished once the appropriate characters are considered. Our study demonstrated that for the last 110 years species discrimination in the Clytemnestridae was based exclusively on generic characters, the current recognition of cryptic species being only an artifact of previous ignorance. Hence, there is considerable doubt involved in collating records of the occurrence of these species from the literature to produce distribution maps. Though *C. scutellata* and *G. rostratus* have universally been regarded as cosmopolitan, this distributional concept is now no longer tenable and the compilation of distribution records must start from scratch. It would be best to consider earlier records primarily as evidence of the occurrence of the respective genera, a useful attribute considering their virtual absence at latitudes above 60° N and 45° S.

Although the geographic location of the collection and/or body size can occasionally be used as indicators of species identity, these approaches are limited in areas of sympatry where often more sophisticated techniques are required. Like *Clytemnestra* in the harpacticoids, *Calanus* is an unusual calanoid genus in that the morphology of the female P5 does not discriminate all of the species (Frost, 1971, 1974). Bucklin *et al.* (1995) showed however, that despite their exceptional morphological similarity, species of *Calanus* are quite distinct genetically. They obtained similar results for the genus *Metridia*, confirming the distinctiveness of *M. lucens* (Boeck, 1865) and *M. pacifica* (Brodsky, 1948). Frost (1989) concluded, based on morphological characters other than size, that there are seven species within *Pseudocalanus*. For some, no absolute morphological criterion could be found to distinguish females, however, their validity was inferred from trends in several morphological characters. Sévigny *et al.* (1989) used patterns of allozyme variation at the GPI (glucose phosphate isomerase) locus to show that Frost's (1989) sibling species were genetically isolated from each other. Their results agreed with McLaren *et al.*'s (1989*a–c*) studies demonstrating differences in genome size and life cycle characteristics among *Pseudocalanus* species. Bucklin *et al.* (1998) showed by DNA sequencing of two mitochondrial genes that the sibling species *P. moultoni* and *P. newmani* can be reliably discriminated. Bucklin *et al.*'s (1996) genetic analysis of DNA sequence variation separated the widespread *Nannocalanus minor* into two genetically distinct types that may represent the previously described *N. m.* forma *major* and *N. m.* forma *minor* which differ primarily in size range and geographic distribution. Finally, McKinnon *et al.* (1992) demonstrated the presence of three sympatric sibling species of *Acartia* using allozyme electrophoresis.

Molecular analysis of marine planktonic copepods is likely to continue to reveal taxonomically-significant genetic partitioning of species populations, including cryptic species. The application of molecular techniques should not however, be an end in itself. Methods used to discriminate sibling species such as protein electrophoresis or discriminant function analysis profit significantly from or even require *a priori* morphological recognition of groups or morphotypes whose distinctiveness can be subsequently tested. In fact, how can one demonstrate the accuracy and resolving power of morphological analysis better than to refer to the thorough revisions by Fleminger (1973) and Fleminger & Hulsemann (1974) who presented most compelling evidence for sibling speciation in marine calanoid copepods long before the deluge of molecular data. Failure to recognize the numerous sibling species inevitably results in bad science and has obvious implications for a large field like marine plankton ecology, crippling our understanding of speciation and resource partitioning in the ocean.

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Basal resolution of laophontid phylogeny and the paraphyly of *Esola* Edwards

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SYNOPSIS. The phylogeny of the Laophontidae, currently the second most speciose family of harpacticoid copepods in the marine environment, is poorly understood. Despite its well established monophyletic status interrelationships within the family have not been re-assessed since Lang's (1948) deceptive phylogenetic hypothesis based on 19 genera (6 being of non-laophontid affinity). Quadrupling of the number of recognized genera in the last 50 years and the persistent failure to recognize the paraphyletic or polyphyletic nature of many of them have severely compromised objective analysis of relationships.

Parsimony analysis employing all informative morphological characters supports a basal dichotomy dividing the family in two clades which are attributed subfamilial status. The Laophontinae, containing 95% of the species, differs from the Esolinae sub fam. nov. in ♀P5 morphology, the loss of the outer spine on the distal endopod segment of P2 and additional losses of armature elements on the maxillipedal syncoxa and P1 endopod which were primitively retained in the Esolinae. Based on P3 endopod

sexual dimorphism *Onychocamptus* Daday and the *Laophonte cornuta*-group invariably form a clade in opposition to all other Laophontinae, implying polyphyly of the type genus.

The Esolinae is a relict group, cosmopolitan in distribution and displaying a complex ecological radiation. Analysis at species level identified *Archilaophonte* Willen as the basal node and *Mourephonte* Jakobi as the terminal branch, and provided strong support for the paraphyly of *Esola* Edwards. Relationships within the Esolinae are largely determined by patterns of transformed integumental pores, sexual dimorphism of P2–P3 and caudal rami, segmentation of ♀ antennule and P1 exopod, and ♀ P5 armature.

The genus *Esola* is redefined to include a crown-group of 8 species, the distribution of which primarily coincides with the circumglobal Tethyan belt. The universally accepted cosmopolitan distribution of the type species *E. longicauda* Edwards is rejected on morphological grounds, resulting in the resurrection of *E. bulbifera* (Norman), the upgrading of *E. longicauda galapagoensis* Mielke and the recognition of four species previously confounded with the type (*E. vervoorti* sp. nov., *E. lobata* sp. nov., *E. canalis* sp. nov.) or based on new collections (*E. profunda* sp. nov.). *Laophonte rhodiaca* Brian is regarded as a likely synonym of *E. bulligera*.

Both *E. hirsuta* (Thompson & A. Scott) and *E. bulligera* (Farran) are allocated to monotypic genera, *Applanola* gen. nov. and *Corbulaseta* gen. nov., respectively. The mediterranean *E. rosei* (Monard) is considered a junior subjective synonym of the northwestern European *C. bulligera*. *E. spelaea* (Chappuis), representing an isolated freshwater incursion in Apulian caves, is transferred to *Troglophonte* gen. nov. and various ambiguities contained in its original description are reviewed. *Bathyesola compacta* gen. et sp. nov. was discovered at 2765 m depth on the North Fiji Ridge, representing the deepest record for the family thus far. *E. typhlops* (Sars) forms an exclusively Atlantic boreo-arctic clade with *E. longiremis* (T. Scott) and *Esola* sp. *sensu* Chislenko (1967). A fourth species, *A. hamondi* from Norfolk, is added to this group which is accorded generic rank (*Archesola* gen. nov.) on the basis of neotenic development of the male P3 endopod.

A generic key to the Esolinae and a review of their ecological radiation are presented.

INTRODUCTION

Laophontids comprise one of the six extant families of the Laophontoidea (Huys & Lee, 1999). They represent by far the most speciose group in this superfamily, currently accommodating 269 valid species and subspecies in 57 genera (Lee & Huys, 1999). Laophontidae are essentially marine, free-living, benthic and restricted to phytal or shallow subtidal and intertidal habitats. Their success in the deep sea is modest and only very few lineages have radiated into freshwater or have entered into associations with invertebrate hosts. The current rate of new species descriptions indicates that only a moderate fraction of their true diversity is known.

Lang's (1948) phylogenetic scheme of the Laophontidae included only 19 genera, six of which being placed in other, existing or new, families since (Hicks, 1988*a*; Huys, 1990*a,b*; Huys & Lee, 1999; Huys & Willems, 1989). Although this re-allocation has significantly refined the taxonomic concept of the family and hence its monophyletic status is no longer a matter of dispute (Huys & Lee, 1999), the relationships between genera are usually not well understood. The justification for creating new genera has traditionally been based on a purely comparative approach, usually by considering a particular combination of characters as unique, rather than on phylogenetic grounds. Some authors (e.g. Noodt, 1958) attempted to unravel the relationships within particular lineages but their kind of analysis was not cladistic and considered only a limited number of characters. Others considered a thorough revision of the type genus *Laophonte* Philippi as a *conditio sine qua non* for a phylogenetic analysis incorporating all genera (Hicks, 1988*b*; Willen, 1996).

The recent discovery of the primitive genus *Archilaophonte* in the Antarctic Weddell Sea (Willen, 1995) has shed some light on the early evolution of the family. Willen (1995) proposed an evolutionary scenario placing *Archilaophonte* and *Esola* as sistertaxa at the base of the laophontid tree. Her analysis did not include the genus *Mourephonte* Jakobi, left the potential paraphyly of *Esola* unchallenged and was based on few characters. In this paper we have first concentrated on the relationships within the genus *Esola* and its affinity to *Mourephonte* and *Archilaophonte*. In order to resolve the basal dichotomy in laophontid evolution we found it necessary to run the analysis at the species level. Re-examination of the majority of these species revealed important new taxonomic information which reinforces the early split of two major lineages in the Laophontidae. In this paper we propose a new hypothesis of basal evolutionary relationships in the Laophontidae which will hopefully provide a solid baseline for future studies addressing the phylogeny of the more advanced crown-group taxa.

MATERIAL AND 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 a Zeiss Axioskop, Leitz Dialux or Leitz DMR microscope equipped with differential interference contrast.

Esola bulbifera, *Applanola hirsuta* and *Archesola typhlops* were examined with a Hitachi S-800 or Philips XL30 scanning electron microscope. Specimens were prepared by dehydration through graded acetone, critical point dried, mounted on stubs and sputter-coated with gold or palladium.

The descriptive terminology is adopted from Huys *et al.* (1996). Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; exp, exopod; enp, endopod; 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, London (BMNH), the Muséum National d'Histoire Naturelle, Paris (MNHNP) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH). Scale bars in figures are indicated in μm.

GENERIC DIAGNOSES AND SPECIES DESCRIPTIONS

Family **LAOPHONTIDAE** T. Scott, 1905

Genus *Esola* Edwards, 1891

Edwards (1891) described *Esola longicauda* from an unknown, shallow coastal locality in the Bahamas. Although the author found the species embedded in mucus inside the body cavity of the

holothurian *Actinopyga agassizii* (Selenka) [as *Mülleria Agassizii*], he considered it to be essentially free-living. He noted the distinctly hirsute appearance and recognized a similarity between *Esola* and *Cleta* Claus, placing the genus in the 'Harpactiden'. Monard (1927) placed the genus in the Laophontidae but erroneously stated in the generic key that the antennule is 5-segmented. Later he professed that *Esola* was really a 'hirsute *Laophonte*', differing from its congeners only by the 1-segmented P1 exopod and its commensal lifestyle with holothurians (Monard, 1935). Nicholls (1941*b*) also regarded the genus as a 'derivative' of *Laophonte*, however maintained the generic name pending a redescription of the type species.

The genus remained monotypic until Lang's (1944, 1948) revision of the Laophontidae which added 8 *Laophonte* species to the genus: *L. hirsuta* Thompson & A. Scott, *L. longiremis* T. Scott, *L. typhlops* Sars, *L. bulligera* Farran, *L. rosei* Monard, *L. spelaea* Chappuis, *L. bulbifera* Norman, and *L. rhodiaca* Brian. Lang (1948) regarded the latter two species as synonyms of *E. longicauda*. He maintained *E. longicauda*, *E. bulligera* and *E. rosei* as distinct species for convenience rather than conviction, believing that future examination might well show all three to be mere forms of the same species. Lang (1944) divided the genus into two groups, the *spelaea*-group, including only *E. spelaea*, and the *longicauda*-group, accommodating all other species.

Nicholls (1941*b*) had adopted a more artificial approach in his revision of the Laophontidae, subdividing the genus *Laophonte* Philippi into five subgenera on the basis of the endopodal setation of the P3, and to a lesser extent also that of P2 and P4. He referred *L. rosei*, *L. bulligera*, *L. bulbifera*, *L. typhlops* and *L. longiremis* to the nominate subgenus *Laophonte*, more specifically to the *typhlops*-group which also included *L. elongata* Boeck, *L. thoracica* Boeck and *L. barbata* Lang. In the subgenus *Mesolaophonte* Nicholls he placed *L. spelaea* which he believed to occupy an isolated position due to the presence of 5 setae on the distal endopod segment of P4. Finally, he regarded both *L. hirsuta* and *L. rhodiaca* as *species inquirendae*, the former because it was inadequately described, the latter because it was only known from the male. This system was heavily criticized by Lang (1948: 1620–1621) in a postscript to his monograph. A similar unnatural division of the genus *Laophonte* had also been proposed by Sewell (1940), using P1 exopod segmentation as the primary divisive character.

With the exception of Vervoort (1964) most authors have uncritically accepted Lang's (1948) decision to consider *E. longicauda* as a variable and cosmopolitan species. Wells & Rao (1987) regard the species as 'highly distinctive pan-temperate/tropical' and express severe doubts about Mielke's (1981) justification for establishing *E. longicauda galapagoensis*. Mielke (1997) hinted at the possibility of *E. longicauda* being a complex of several closely related species and our examination appears to substantiate his conjecture. In this revision we have restricted the genus *Esola* to *E. longicauda* and to those species which have mistakenly been synonymized with the type or were incorrectly described under that name. The major diagnostic characters of these species are tabulated in Table 1. Only *E. bulbifera* will be described in detail below; the descriptions of the other species will be largely confined to the differences with this species.

DIAGNOSIS. Laophontidae. Body cylindrical; posterolateral corners of ♀ genital double-somite and second abdominal somite laterally and backwardly produced. Integument of cephalothorax and body somites with dense pattern of spinules and setules. Rostrum large, partly delimited at base. Four pairs of integumental cup-shaped pores present: anterodorsally on cephalothorax, near ventrolateral margins of cephalic shield, laterally on genital (♂) or genital double-somite (♀) and ventrally on caudal rami. Anal operculum spinulose. Caudal rami modified in ♀, often forming bulbous expansions dorsally, ventrally and medially; rectangular and longer than wide in ♂.

Sexual dimorphism in body shape, antennule, P3 endopod, P5, P6, genital segmentation and caudal rami.

Antennules slender; 6- or incompletely 7-segmented in ♀, subchirocer and 7-segmented in ♂; segment 1 with 2–3 spinous processes along posterior margin; with aesthetasc on segment 4 (♀) or 5 (♂) and as part of apical acrothek on distal segment; segment 5 ♂ swollen, bearing modified spine on anterior outgrowth; proximal aesthetasc fused to 2 setae. Antenna with 4 setae on exopod; allobasis with abexopodal seta. Labrum with overlapping scales distally and dense pattern of spinules proximally. Mandible with short 1- or 2-segmented palp; endopod free or incorporated, represented by 2–3 setae; exopod usually absent, sometimes represented by single seta; basis represented by 1–2 setae. Maxillule with minute, defined exopod. Maxilla with 3 endites on syncoxa; endopod represented by 4 setae. Maxilliped slender; syncoxa with 2 setae; entire palmar margin with spinules; endopodal claw elongate.

P1 with 2-segmented exopod bearing 4–5 setae on exp-2 and elongate endopod; enp-1 without inner seta, enp-2 with minute seta and long, slender claw. P2–P4 with 3-segmented exopods and 2-segmented endopods. P2 basis with very long outer spine. Outer spine of P2–P4 enp-2 very long and setiform. P3 endopod ♂ 3-segmented; enp-2 with inner seta and outer, dentate or smooth, spinous apophysis. Armature formula as follows:

	Exopod	Endopod	
P2	0.1.123	[0–1].221	
P3	0.1.223	[0–1].321	[♂: [0–1].1.220]
P4	0.1.223	[0–1].221	

P5 ♀ with separate rami; exopod elongate, with 6 setae/spines; baseoendopod slightly developed, with 4 setae/spines. P5 ♂ without endopodal lobe; exopod short, with 1 inner, 2 apical and 2 outer elements.

P6 ♀ forming opercula closing off paired genital apertures; with one seta and 2 small processes at outer corner. P6 ♂ asymmetrical; membranous flaps with 2 setae.

TYPE SPECIES. *Esola longicauda* Edwards, 1891 [by monotypy].

OTHER SPECIES. *Esola bulbifera* (Norman, 1911); *E. galapagoensis* Mielke, 1981 grad. nov.; *E. profunda* sp. nov.; *E. canalis* sp. nov.; *E. lobata* sp. nov., *E. vervoorti* sp. nov.

SPECIES INQUIRENDAE. *E. longicauda* Edwards, 1891 *sensu* Noodt (1955); *E. longicauda* Edwards, 1891 var. *sensu* Vervoort (1964); *E. longicauda* Edwards, 1891 *sensu* Wells & Rao (1986); *Esola* spec. *sensu* Mielke (1997).

Esola longicauda Edwards, 1891

TYPE LOCALITY. Unspecified shallow water locality in Bahamas.

TYPE MATERIAL. Edwards (1891) found both sexes but the material is presumably lost.

Lang (1948) pointed out Edwards' observational errors in his description of the P1 such as the presence of 4 setae on the inner margin of the proximal endopod segment and the 1-segmented exopod. Using the insertion site of the endopod as a reference point Lang inferred that Edwards had incorporated the proximal exopod segment into the basis and that the outer basal seta is in reality exopodal.

Although Nicholls (1941*b*) had also questioned the presence of 4 inner setae on the P1 endopod, assuming that they were only long ornamentation elements, he nevertheless used this feature in his generic key. The wide acceptance of Lang's re-interpretation of the P1 exopod, removing the one remaining obstacle to synonymy with *L. bulbifera* and *L. rhodiaca*, made most authors overlook another P1 character, i.e. the presence of only 4 elements on the distal exopod segment. This pattern is also recorded in the subspecies *E. longicauda galapagoensis* described by Mielke (1981) from two islands in the Galápagos and in *Esola* spec., known from a single female collected in North Sulawesi (Mielke, 1997), however, in all other descriptions a consistent number of 5 setae is found.

There has been substantial debate over the supposed variability of the P4 endopod in the various 'populations' of *E. longicauda*. Most authors have dismissed the significance of the absence or presence and relative size of the inner seta on the proximal segment (Table 1). The inner seta is completely absent in Willey's (1935) material of *L. bulbifera* from Bermuda, Sewell's (1940) specimens of *L. bulbifera* from the Nicobar Islands and the Addu Atoll (Maldive Archipelago), Vervoort's (1964) specimens of *E. longicauda* from the Ifaluk Atoll, *E. longicauda galapagoensis* from the Galápagos (Mielke, 1981), Wells & Rao's (1987) single female from Havelock Island (South Andaman), and Mielke's (1997) typical form of *E. longicauda* from Bunaken Island (North Sulawesi). It is represented by a vestigial element in Vervoort's (1964) single male of *E. longicauda* var. from Ifaluk Atoll and Mielke's (1997) single female of *Esola* spec. from North Sulawesi. Finally, it is very well developed in the male of *L. rhodiaca* described from the Aegean Sea (Brian, 1928*a*) and Noodt's (1955) ovigerous female of *E. longicauda* from the Sea of Marmara. The very long seta recorded in this position in *L. bulbifera* by Norman (1911) proved upon re-examination of the holotype to be based on an observational error (see below). Hamond (1969) illustrated a scar which he interpreted as a socket where a seta had probably broken off. It is our contention that these setal differences do not reflect real variability but (in conjunction with other characters) demonstrate that several closely related and frequently sympatric species have been described under the name *E. longicauda*. Unfortunately the condition of the P4 in Edwards' (1891) material is somewhat dubious. On the basis of the [0.1.223] setation pattern of the exopod his Taf. III-Fig. 21 must either be the P3 or the P4 and not the P2 as labelled (BpII!). Edwards is less specific in the accompanying legend which states 'Fuss eines der drei folgenden Segmente'. The presence of only 2 inner setae on the distal endopod segment may indicate that he had figured the P4 in which case the inner seta on the proximal segment is very well developed. Edwards' material differs also in the extremely long and slender claw of the endopod (its length being 83% of that of enp-1) and the elongate caudal rami which are slightly swollen in the female, about 1.7 times as long as wide and have ventrally positioned pores. From the lateral habitus view they appear to be even more slender and elongate in the male. These characters in conjunction with the presence of only 4 setae on P1 exp-2 and the well developed inner seta of P4 enp-1 readily differentiate *E. longicauda* from its congeners. The male is 550 µm long (inferred from the habitus drawing reproduced at ×97 magnification).

Fiers' (1986) single damaged female from Crooked Island (Bahamas) is likely to be the only reliable record of this species. Willey's (1935) record of *Laophonte bulbifera* from Harrington Sound (Bermuda) is zoogeographically closest but his claims that the caudal rami are shortly barrel shaped, being only slightly longer than wide, and that the P4 enp-1 lacks an inner seta cast doubt on his identification. The conspecificity of his smaller female displaying a significant disproportion in size (0.42 mm instead of 0.6 mm) and an atypical 0.022 pattern on the P2 endopod is also highly questionable. Willey (1935) regarded *L. bulbifera* to be close to *L. depressa* T. Scott but gave no justification for this relationship. Alheit & Scheibel (1982) also recorded *E. longicauda* from Harrington Sound but it is unknown whether their identification was based on Willey's or Edwards' description. Finally, Rouch (1962) recorded the species from Pernambuco State in Brazil but gave no evidence to substantiate his identification.

Esola bulbifera (Norman, 1911)

Laophonte bulbifera Norman, 1911
? *Laophonte rhodiaca* Brian 1928*a*
Esola longicauda Edwards, 1891 *sensu* Hamond (1969)
Esola longicauda var. *bulbifera* Norman, 1911 *sensu* Holmes & O'Connor (1990)

TYPE LOCALITY. Lamlash Bay in Firth of Clyde (Scotland).

MATERIAL EXAMINED.
(a) Holotype ♀ dissected on slide (BMNH #396.5); leg. J. Murray & A.M. Norman, July 1888; dredging;
(b) 2 ♀♀ and 1 ♂ collected from West Runton, Norfolk (England), at extreme low water, around and under rocks; leg. R. Hamond, 20 August 1993; 1 ♀ dissected on 13 slides (BMNH 1999.984), 1 ♀ and 1 ♂ preserved in alcohol (BMNH 1999.985–986);
(c) 3 ♀♀ and 1 ♂ collected from Salt Lake (Ardbear Lough), near Clifden, Co. Galway, Ireland; leg. B. O'Connor, July 1980, on *Serpula* reef; det. J.M.C. Holmes; 1 ♂ dissected on 11 slides (BMNH 1999.987), 3 ♀♀ preserved in alcohol (BMNH 1999.988–990).

OTHER MATERIAL. National Museum of Ireland, Dublin: (a) several specimens: Salt Lake, Clifden, Co. Galway; leg. B. O'Connor, July 1980, from *Serpula* reef (in alcohol); (b) 1 ♀: Lough Hyne, Co. Cork; leg. J.M.C. Holmes, 23 September 1987, light trap, 5 m (in alcohol); (c) 1 ♂: Lough Hyne, Co. Cork; leg. J.M.C. Holmes, 08 Augustus 1992 (on slide).

DESCRIPTION.

FEMALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 681 µm (n=5; range: 643–714 µm). Maximum width (181 µm) measured at posterior margin of cephalothorax.

Body (Fig. 1A–B) cylindrical, not dorsoventrally depressed, covered with dense pattern of minute spinules dorsally and laterally. Cephalothorax slightly wider than free somites, posterolateral angles backwardly produced forming lobate extension (Fig. 1B); with paired cup-shaped pores both anterodorsally and anteroventrally on either side of rostrum (arrowed in Fig. 1B), anterodorsal set partly closed off by fringe of setular extensions; with distinct transverse spinule row dorsally about halfway down the cephalothorax length (Fig. 1A). Posterior margin of cephalothorax and all body somites with row of long setules dorsally and laterally. Posterior margin of body somites with minute spinules laterally and ventrally; ventrolateral areas of cephalic shield and pleurotergites of pedigerous somites with longer spinules. Pleurotergite of P5-bearing somite narrowest.

Genital double-somite wide and dorsoventrally flattened; original segmentation marked by bilateral constriction and spinule row arising from transverse surface ridge dorsally and laterally; anterior (= genital) half with large cup-shaped pores laterally, each partly closed off by fringe of setular extensions (Fig. 1C); posterior half with backwardly directed lobate extensions bearing spinular tuft; ventral surface without spinular ornamentation; genital field located near anterior margin (Fig. 1C). Sixth legs forming well developed opercula closing off paired genital apertures; each with outer naked

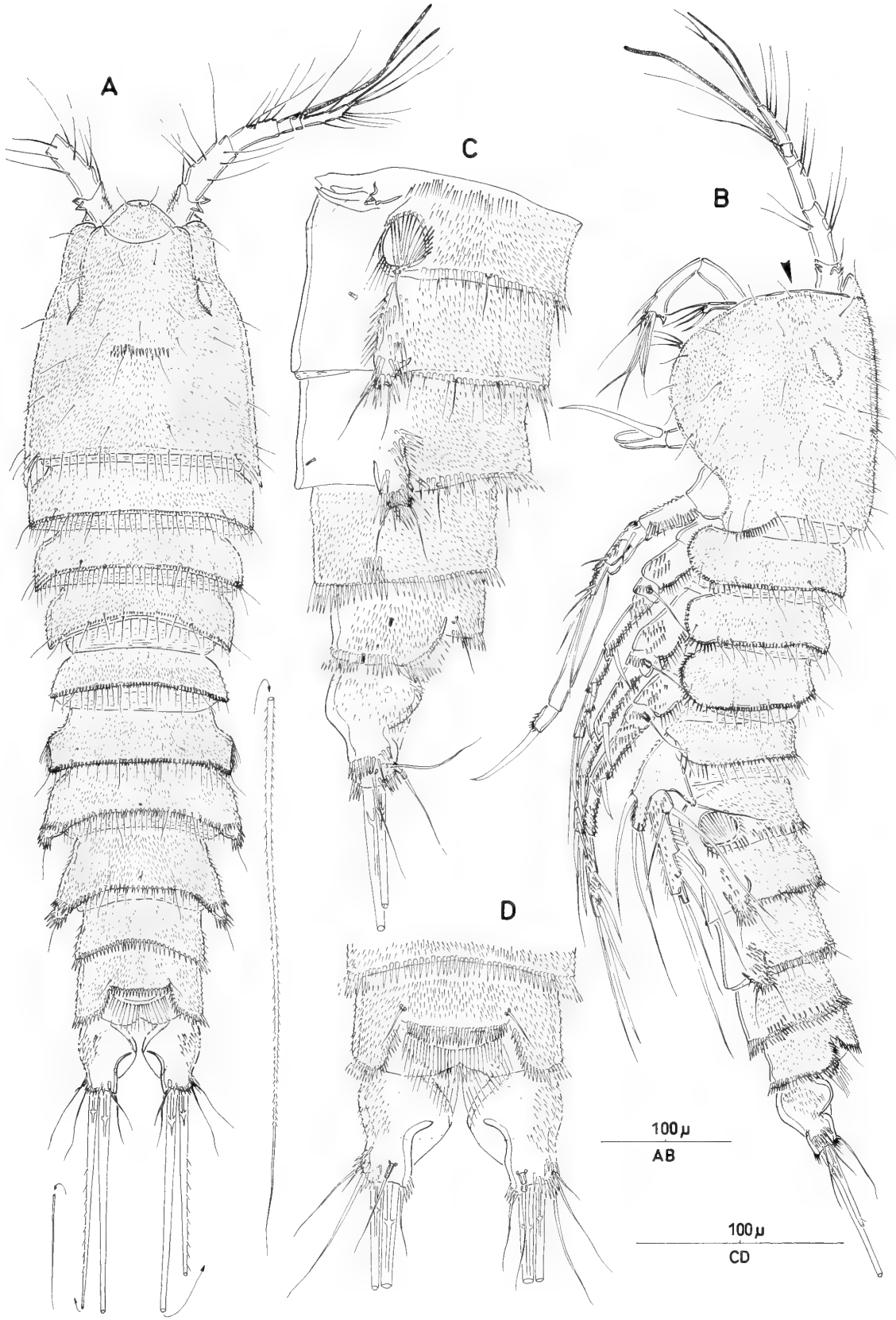

Fig. 1 *Esola bulbifera* (Norman, 1911) (♀). A, Habitus, dorsal; B, habitus, lateral [anteroventral cup-shaped pore arrowed]; C, urosome (excluding P5-bearing somite), lateral; D, anal somite and caudal rami, dorsal.

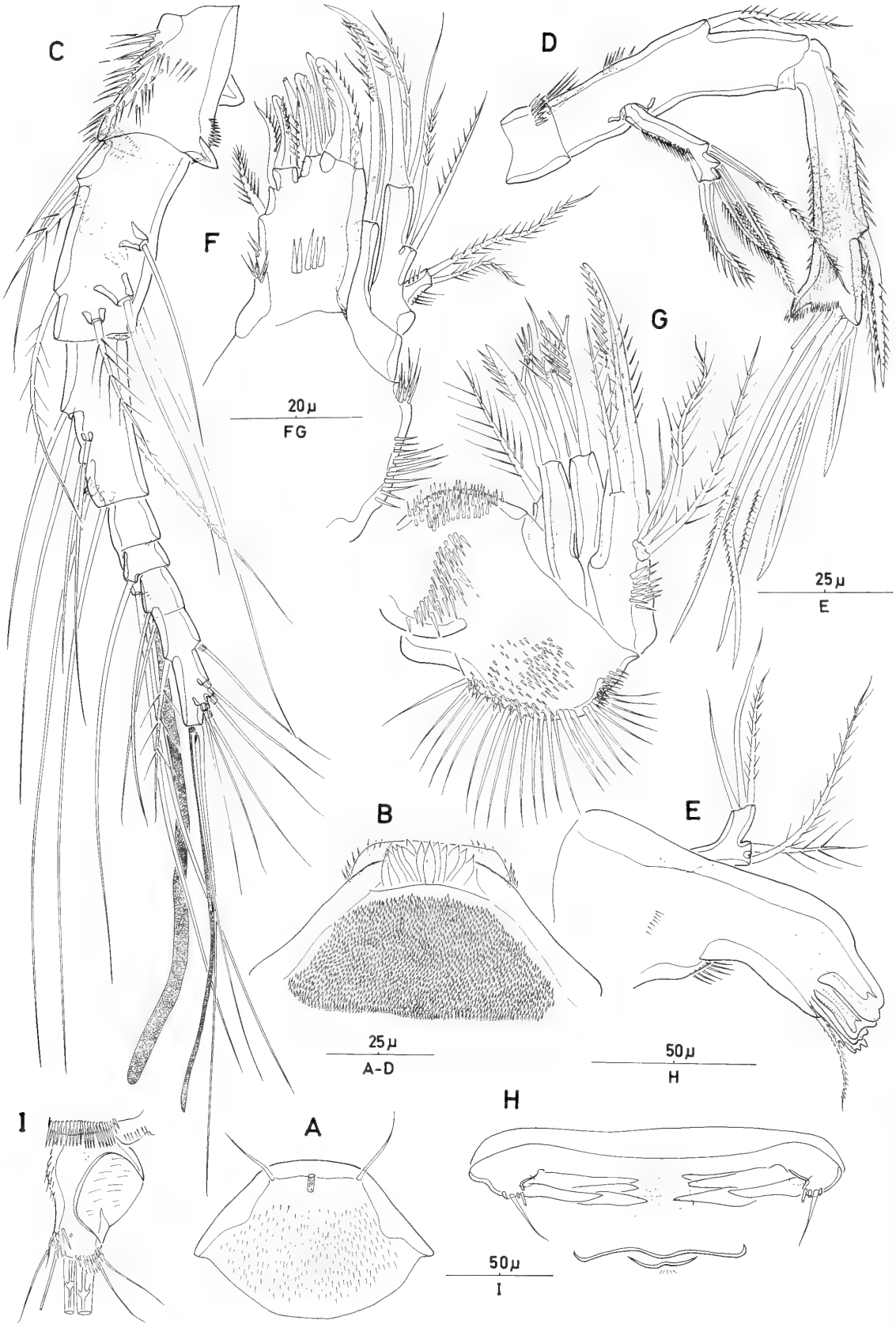

Fig. 2 *Esola bulbifera* (Norman, 1911) (♀). A, Rostrum, dorsal; B, labrum, anterior; C, antennule, dorsal; D, antenna; E, mandible; F, maxillule; G, maxilla; H, genital field; I, right caudal ramus, ventral.

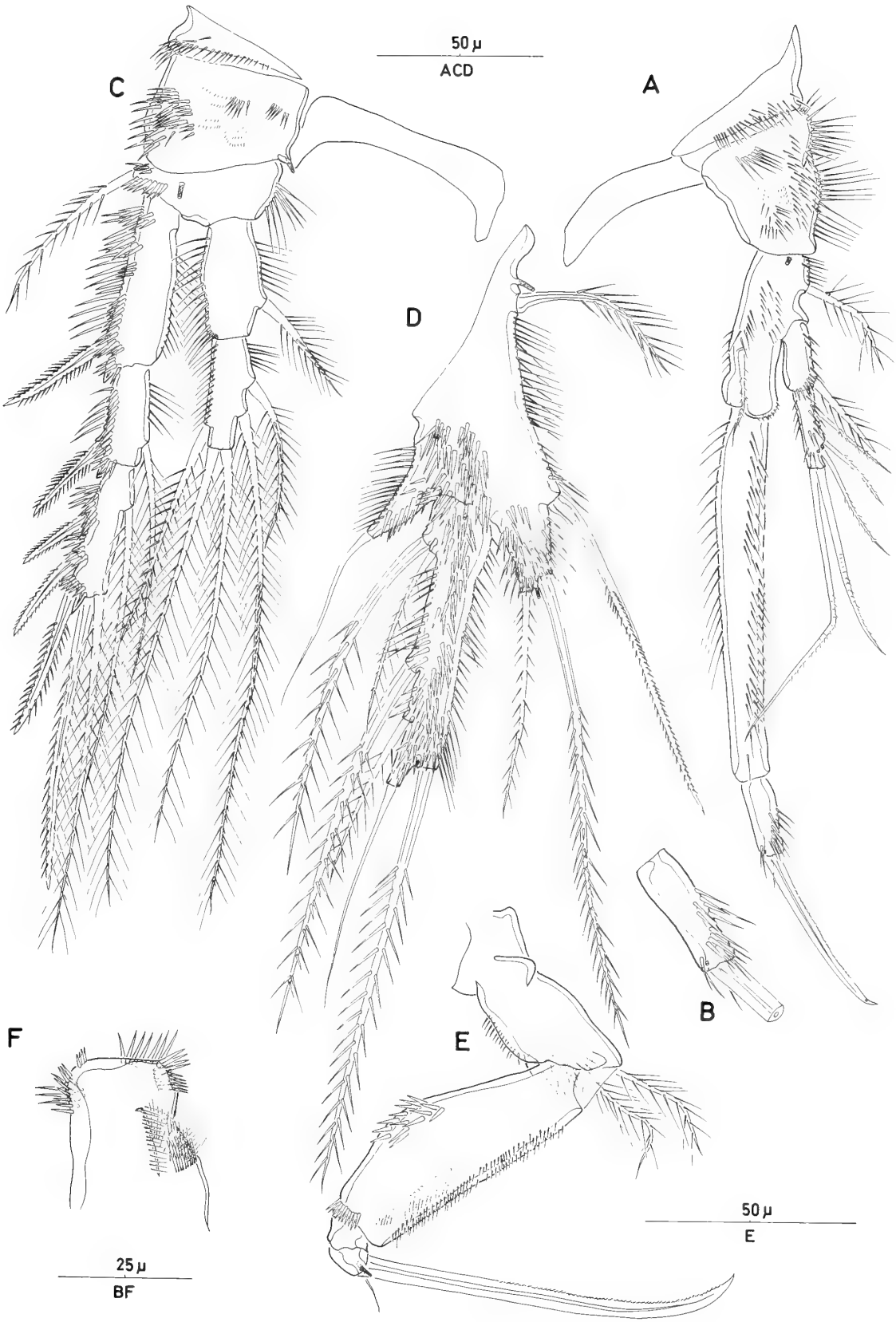

Fig. 3 *Esola bulbifera* (Norman, 1911) (♀). A, P1, anterior; B, P1, distal endopod segment, anterior; C, P2, anterior; D, P5, anterior; E, maxilliped; F, paragnath.

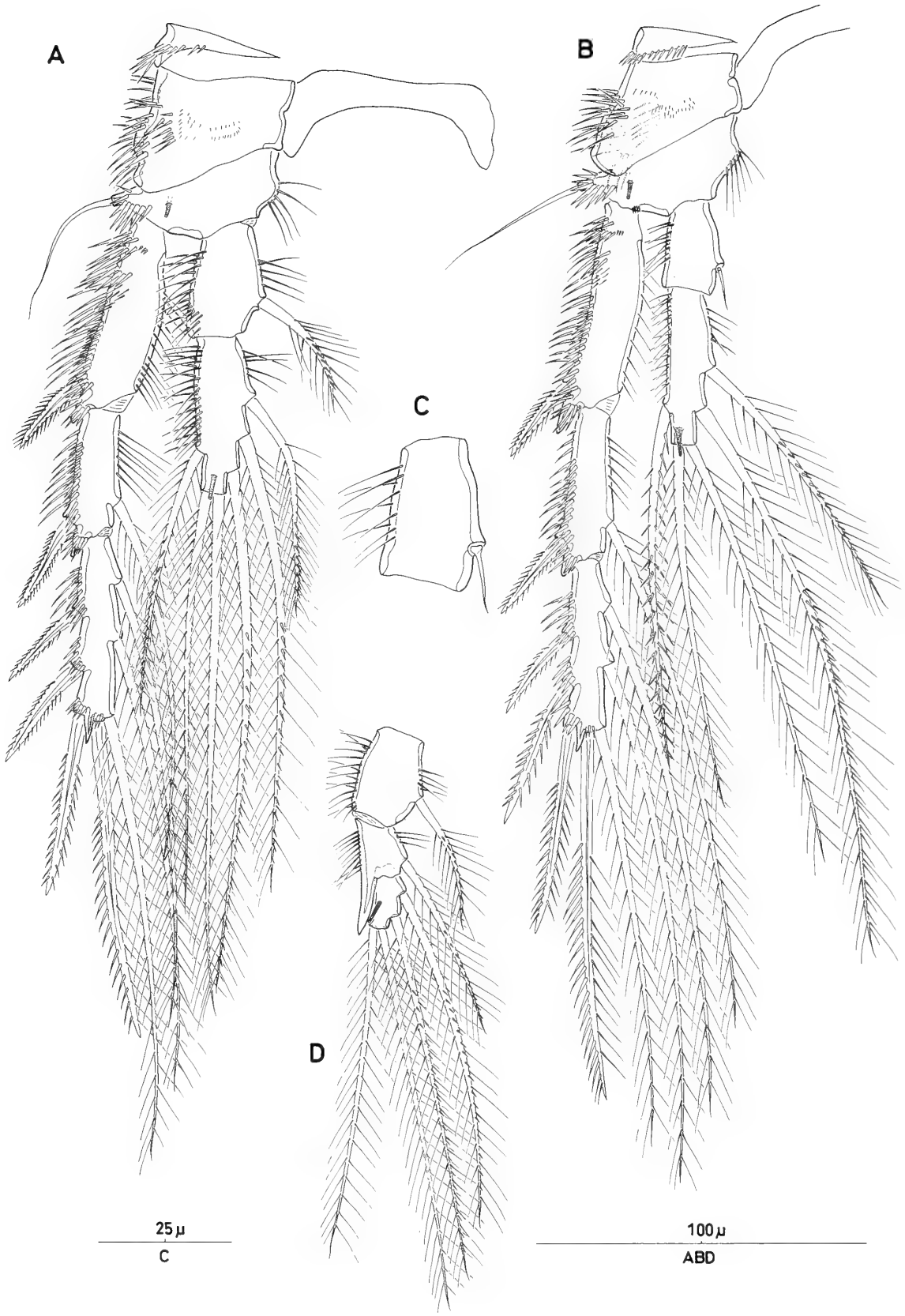

Fig. 4 *Esola bulbifera* (Norman, 1911). A, P3 (♀), anterior; B, P4 (♀), anterior; C, P4 enp-1 (♀), anterior; D, P3 endopod (♂), anterior.

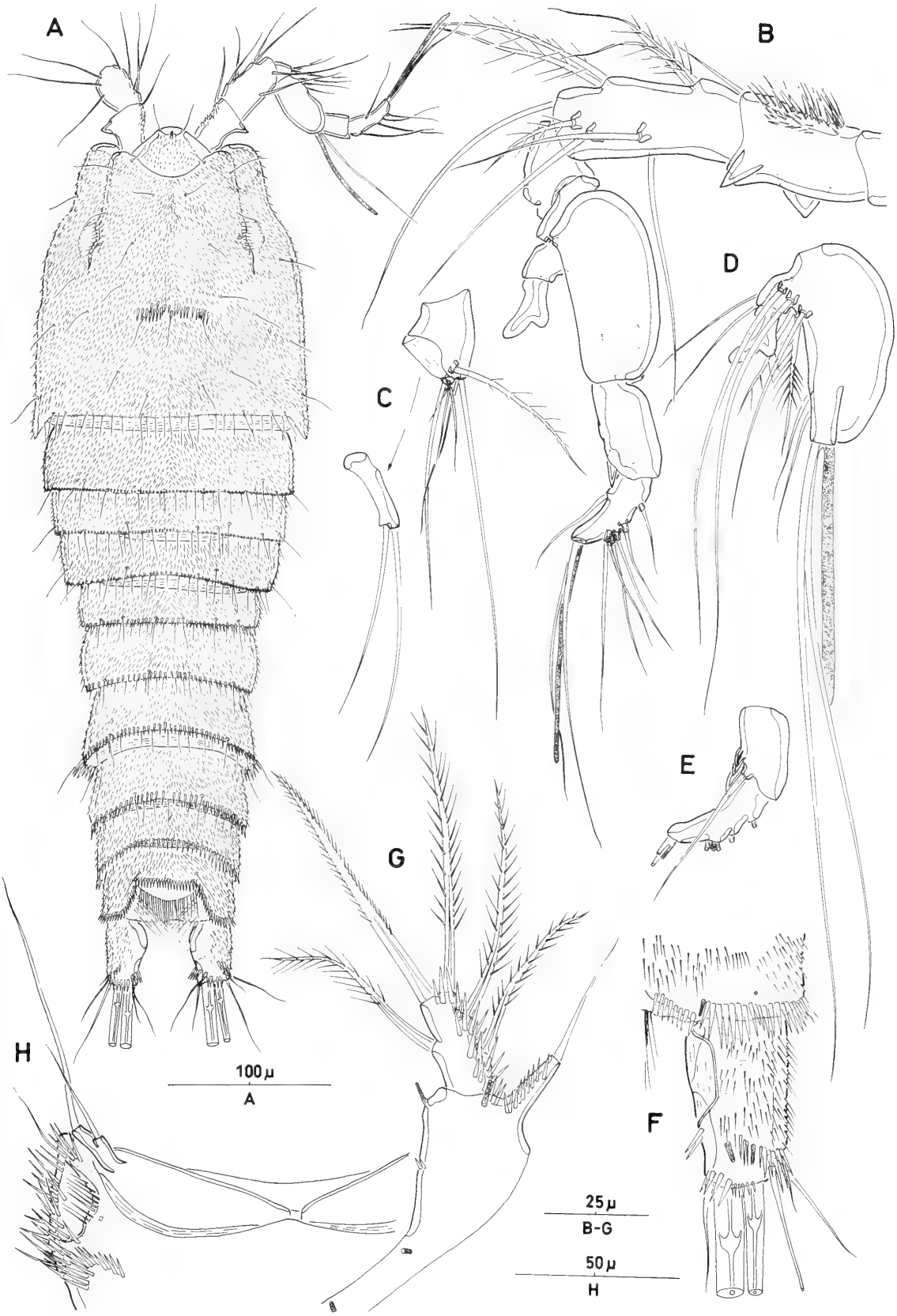

Fig. 5 *Esola bulbifera* (Norman, 1911) (♂). A, Habitus, dorsal; B, antennule, dorsal (armature of segments 3–6 omitted); C, antennulary segments 3–4, ventral; D, antennulary segment 5, ventral; E, antennulary segments 6–7, ventral; F, left caudal ramus, ventral; G, right P5, anterior; H, left P6, anterior.

seta and 2 small processes; with 4 medially directed, spinous processes (Fig. 2H).

First postgenital somite with backwardly produced lateral angles, bearing spinular tuft (Fig. 1C); without ventral ornamentation. Penultimate and anal somites distinctly narrower; ventral posterior border with spinules. Anal somite (Figs. 1D; 31A) with spinulose anal operculum.

Caudal rami (Figs. 1D; 31A) widely separated; slightly longer than widest portion; proximal half distinctly bulbous with major swelling medially, dorsally and ventrally (Fig. 1C); ventral surface with very large semi-circular concavity (Fig. 2I) leading to small tube-pore; dorsolateral surface with minute spinules; seta I small, setae II–III well developed, naked and closely set; setae IV and V pinnate and with fracture planes, seta V 2.5 times as long as seta IV; setae VI–VII naked.

Rostrum (Figs 1A; 2A) large, rounded anteriorly; delimited at base by transverse surface suture; with paired sensillae anteriorly and median tube-pore dorsally.

Antennule (Fig. 2C) slender, incompletely 7-segmented, with 1 minute (obscured by large distal one) and 2 well developed spinous processes on posterior margin of segment 1, no processes on long segment 2. Segment 1 with short spinules posteriorly between processes and large spinular patch around anterior margin. Armature formula: 1-[1], 2-[4 + 4 pinnate], 3-[6], 4-[(2 + ae)], 5-[1], 6-[2], 7-[6 + 1 pinnate + acrothek]. Aesthetasc on segment 4 fused basally to 2 setae. Acrothek consisting of aesthetasc and 2 naked setae; set on apical pedestal. Boundary between segments 6 and 7 only expressed posteriorly.

Antenna (Fig. 2D) with elongate exopod bearing 2 lateral and 2 apical pinnate elements, and a longitudinal row of fine spinules. Allobasis with pinnate abexopodal seta and spinular patch opposite exopod. Endopod with lateral armature consisting of 1 pinnate spine and 2 setae; distal armature consisting of 2 unipinnate spines and 3 geniculate setae (outermost fused basally to small tube-seta).

Labrum (Fig. 2B) with spinules around distal margin; anterior face with dense pattern of fine spinules and distal patch of overlapping scales.

Mandible (Fig. 2E) with short gnathobase and small 1-segmented palp probably representing fused basis and endopod; with 2 lateral (basal) pinnate setae and 3 distal (endopodal) setae (1 pinnate, 2 bare).

Paragnaths highly ornate lobes as in Fig. 3F.

Maxillule (Fig. 2F) with well developed praecoxal arthrite bearing 1 seta on anterior surface and 9 elements around distal margin. Coxal endite with 1 spine and 1 seta, basal endite with 1 spine and 2 setae. Exopod a short segment with 2 distal setae; endopod incorporated into basis, represented by 2 setae.

Maxilla (Fig. 2G). Syncoxa with very long spinules around outer margin and dense surface spinulation as figured; with 3 endites; praecoxal endite small, with 1 plumose seta; middle endite drawn out into pinnate claw, with 2 tube-setae; distal endite with 3 elements. Allobasis produced into strong curved claw; accessory armature consisting of 1 spine and 1 seta; with spinular patch proximal to endopodal setae. Endopod incorporated into allobasis, represented by 2 bare and 2 pinnate setae.

Maxilliped (Fig.3E) slender, with elongate basis and endopodal claw. Syncoxa with 2 plumose setae. Basis with spinular ornamentation as figured; spinules present along entire palmar margin. Endopod represented by very long, minutely pinnate claw bearing 1 accessory seta and tube-pore at base.

P1 (Fig. 3A) with dense ornamentation on praecoxa, coxa and basis. Basis with pinnate seta on anterior surface and along outer margin. Exopod 2-segmented, small compared to endopod; exp-1 not extending to distal margin of basal pedestal, with pinnate outer spine; exp-2 with 3 pinnate outer setae and 2 geniculate setae apically. Endopod slender; enp-1 about 2.5 times as long as basis, with long setules along inner margin and fine spinules along outer margin; enp-2 about 3 times as long as wide, with slender minutely pinnate claw and small accessory seta (Fig. 3B).

P2–P4 (Figs 3C; 4A–B) with 3-segmented exopods and 2-segmented endopods. P2 basis with long, bipinnate outer spine; P3–P4 bases with bare outer seta. P2–P3 enp-1 with multipinnate inner seta; P4-enp-1 (Fig. 4C) with basally swollen, minute seta. Outer spine of P2–P4 enp-2 very long and setiform. Tube-pore present near distal outer corner of P3–P4 enp-2. Armature formula as follows:

	Exopod	Endopod	
P2	0.1.123	1.221	
P3	0.1.223	1.321	[♂: 1.1.220]
P4	0.1.223	1.221	

P5 (Fig. 3D). Endopodal lobe small, extending just beyond insertion sites of proximal outer setae of exopod; with 1 short and 1 long pinnate seta apically, and 2 long widely separated setae along inner margin; tube-pores present near articulation with exopod, between apical setae and proximal to innermost seta. Exopod elongate, produced apically into tubular extension bearing 1 bare seta; inner margin with 1, outer margin with 4 pinnate setae; inner seta distinctly longer than apical one. Both baseoendopod and exopod with elaborate ornamentation pattern as figured.

MALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 512 µm (n=2, range 500–524 µm). Maximum width (168 µm) measured at posterior margin of cephalothorax.

Body (Fig. 5A) more compact and abbreviated than in ♀; covered with similar dense pattern of minute spinules. Pattern of cup-shaped pores as in ♀ except for paired lateral pores present on genital somite. Cephalothorax wider than free somites; body constricted at level of genital somite. None of urosomites with backwardly produced posterolateral corners.

Genital somite with large cup-shaped pores laterally, each partly closed off by fringe of setular extensions (Fig. 5H). Sixth legs represented by well developed opercula, one articulating and closing off left or right genital aperture; each produced into cylindrical process bearing 1 lateral and 1 apical seta.

Antennule (Fig. 5B–E) 7-segmented, subchirocer, with geniculation between segments 5 and 6. Segment 1 with spinules/setules around anterior margin and 2 spinous processes along posterior margin. Segment 2 longest; segment 4 minute, represented by incomplete sclerite. Segment 5 with large proximal process anteriorly, bearing modified bifid spine (Fig. 5D); forming cylindrical process bearing long aesthetasc. Segment 6 with 3 spinous processes along anterior margin. Distal portion of segment 7 elongated, displacing acrothek to position isolated from other armature. Armature formula: 1-[1], 2-[4 + 5 pinnate], 3-[6 + 1 pinnate], 4-[2], 5-[7 + 2 pinnate + 1 bifid spine + (2 + ae)], 6-[1 + 3 processes], 7-[7 + acrothek]. Apical acrothek consisting of aesthetasc and 2 bare setae.

P3 endopod (Fig. 4D) 3-segmented; enp-1 as in ♀; enp-2 with inner seta and short outer apophysis; enp-3 small, with tube-pore, 2 lateral and 2 apical setae.

P5 (Fig. 5G) medially fused, positioned ventrolaterally. Baseoendopod without endopodal lobe; medial margin with 2 spinules and 2 tube-pores; outer basal seta arising from short spinulose pedestal. Exopod free; with 1 apical and 1 inner and 3 outer pinnate setae.

Caudal ramus (Fig. 5F) rectangular, without bulbiform expansions; about 1.6 times as long as wide; with medioventral cup-shaped concavity as in ♀; ventral ornamentation more elaborate than in ♀.

REMARKS. Lang (1948) synonymized *L. bulbifera* with *E. longicauda*, alluding to the congruence in the female P5 baseoendopod between Gurney's (1927) description of *L. bulbifera* and Edwards' (1891) original description of *E. longicauda* (i.e. with 4 setae; Norman (1911) figured only 3), and in the number of processes on the first antennulary segment between the males of *L. rhodiaca* (cf. Brian, 1928*a*) and *E. longicauda* (cf. Edwards, 1891) and the female of *L. bulbifera* (cf. Norman, 1911). He also referred to Willey's (1935) discovery of *L. bulbifera* in Bermuda as additional zoogeographical evidence for this course of action. It is clear however that (1) the morphological grounds for this synonymy only prove generic identity and not conspecificity, (2) Willey's (1935) record is both unreliable and unconfirmed, and (3) Gurney's (1927) records from the Suez Canal in reality refer to another species *E. canalis* sp. nov. (see below).

Our redescription diverges from Norman's illustrations in only two aspects: (1) the presence of 4 setae on the baseoendopod of the ♀ P5, the innermost being overlooked by Norman as already suspected by Lang (1948), and (2) the inner seta of P4 enp-1 which is minute (checked against the holotype) instead of very well developed as figured by Norman. *E. bulbifera* can be differentiated from its congeners on the basis of the following combination of characters: antennule ♀ indistinctly 7-segmented, P1 enp-1 2.5 times as long as basis, P1 enp-2 3 times as long as wide, P2-P4 enp-1 with inner seta (that of P4 minute), outermost seta of ♀ P5 baseoendopod extending to distal margin of exopod, caudal rami ♀ distinctly bulbous.

E. bulbifera is widely distributed around the British Isles with reliable records from Ireland (Farran, 1913, 1915; Holmes & O'Connor, 1990), the west coast of Scotland (Norman, 1911) and Norfolk (Hamond, 1969). Moore's (1973) record of *E. longicauda* from St. Abb's probably also refers to this species. It has not been reported anywhere else in northwest Europe, however, its synonymy with *L. rhodiaca* Brian, first suspected by Nicholls (1941*b*) and later confirmed by Lang (1948), has considerably extended its distribution, including the Mediterranean, Gulf of Suez and Western Australia. Nicholls based his conviction on similarities in the antennule, antennary exopod, P1 and P4 and the modified caudal rami although he admitted that the latter were not bulbous in *L. rhodiaca*. Brian's (1928*a*) original description, based on a single male specimen from Rhodes in the Aegean Sea (Brian, 1928*a–b*), shows very few discrepancies with our material from Ireland and Norfolk. The caudal rami are somewhat longer in the Mediterranean specimen, the inner seta on P4 enp-1 is more developed, the antennule shows an additional segment distal to the geniculation and small proportional length differences can be noted in the antennulary segments and P4 endopod. Lang (1948) had already pointed out that Brian had overlooked one of the outer spines on the P2 exopod. We regard these differences insufficient to warrant the reinstatement of *L. rhodiaca* and tentatively regard it as a junior subjective synonym of *E. bulbifera*. Nicholls' (1945) few illustrations of a male from Port Denison in Western Australia which he attributed to *L. rhodiaca* do not contradict Brian's description. In the absence of information on the swimming legs (except P3 endopod) and the female this geographically widely separated record cannot be verified absolutely.

Monard's (1928) brief description of *L. bulbifera* from the Banyuls area does not contain the level of detail to either confirm or deny his identification. The setae on the P5 baseoendopod were probably not drawn at their full length even though the outermost one appears to be exceptionally short, his spine formula would infer a 123 pattern on P4 exp-3 and the size of his female specimens (0.8 mm) falls outside our recorded range. Monard (1937) recorded the species a second time from Algers but the specimens were apparently distinctly smaller (0.64 mm).

The Croatian records of *L. bulbifera* from Rovinj and Split in the northern Adriatic (Douwe, 1929; Klie, 1941) could not be confirmed. It is conceivable that Vrišer's (1984, 1986) records of *E. longicauda* from the Gulf of Trieste and Petkovski's (1955) record from Montenegro refer to the same species.

Esola galapagoensis Mielke, 1981 grad. nov.

Esola longicauda galapagoensis Mielke, 1981

TYPE LOCALITY. Cabo Douglas, Fernandina (Galápagos).

Wells & Rao (1987) expressed reluctance about the subspecific rank attributed to the Galápagos population of *E. longicauda*. Although Mielke (1981) acknowledged the reported variability and cosmopolitanism of the latter to some extent, he considered the differences exhibited by his material sufficient to warrant the recognition of a distinct subspecies. Mielke diagnosed *E. longicauda galapagoensis* on the basis of the following characters: (1) P1 exp-2 with 4 setae/spines, (2) P1 enp-2 with remarkably short claw, (3) P4 enp-1 without inner seta, and (4) P5 baseoendopod ♀ with strongly reduced outer apical seta. Additional diagnostic features not mentioned by the author include (1) inner seta of P6 ♂ extremely reduced, (2) outer setae of P5 exopod ♂ naked, (3) outer spine of P2–P4 enp-2 remarkably short, and (4) caudal rami very elongate with conspicuous medial swelling in ♀. Based on this suite of characters we feel it justified to upgrade Mielke's form to full species rank as *E. galapagoensis*. The species has thus far been recorded from two localities in the Galápagos archipelago (Mielke, 1981).

Esola canalis sp. nov.

Laophonte bulbifera Norman, 1911 *sensu* Gurney (1927)

TYPE LOCALITY. Suez Canal, Port Taufiq (Egypt).

TYPE MATERIAL. Holotype ♀ dissected on 10 slides (BMNH 1999.993); paratype ♀ in alcohol (BMNH 1999.994); from material originally registered as *Laophonte bulbifera* (BMNH 1928.4.2.116) collected during the Cambridge Expedition to the Suez Canal in 1924; det. R. Gurney.

ETYMOLOGY. The species name refers to the type locality.

DESCRIPTION.

FEMALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 621 µm (n=2; range: 585–658 µm). Maximum width (137 µm) measured at posterior margin of cephalothorax.

Body as in *E. bulbifera*; cephalothorax with paired cup-shaped pores both anterodorsally and anteroventrally on either side of rostrum, and with distinct transverse spinule row dorsally about halfway down the cephalothorax length.

Genital double-somite (Fig. 6A) wide and dorsoventrally flattened; original segmentation marked by bilateral constriction and spinule row arising from transverse surface ridge dorsally and laterally; anterior (= genital) half with large cup-shaped pores laterally; ventral surface without spinular ornamentation. First postgenital somite with backwardly produced lateral angles, bearing spinular tuft (Fig. 6A); without ventral ornamentation. Penultimate and anal somites distinctly narrower; ventral posterior border with spinules (Fig. 6C). Anal somite (Fig. 6B) with spinulose anal operculum; spinules coarser than in *E. bulbifera*.

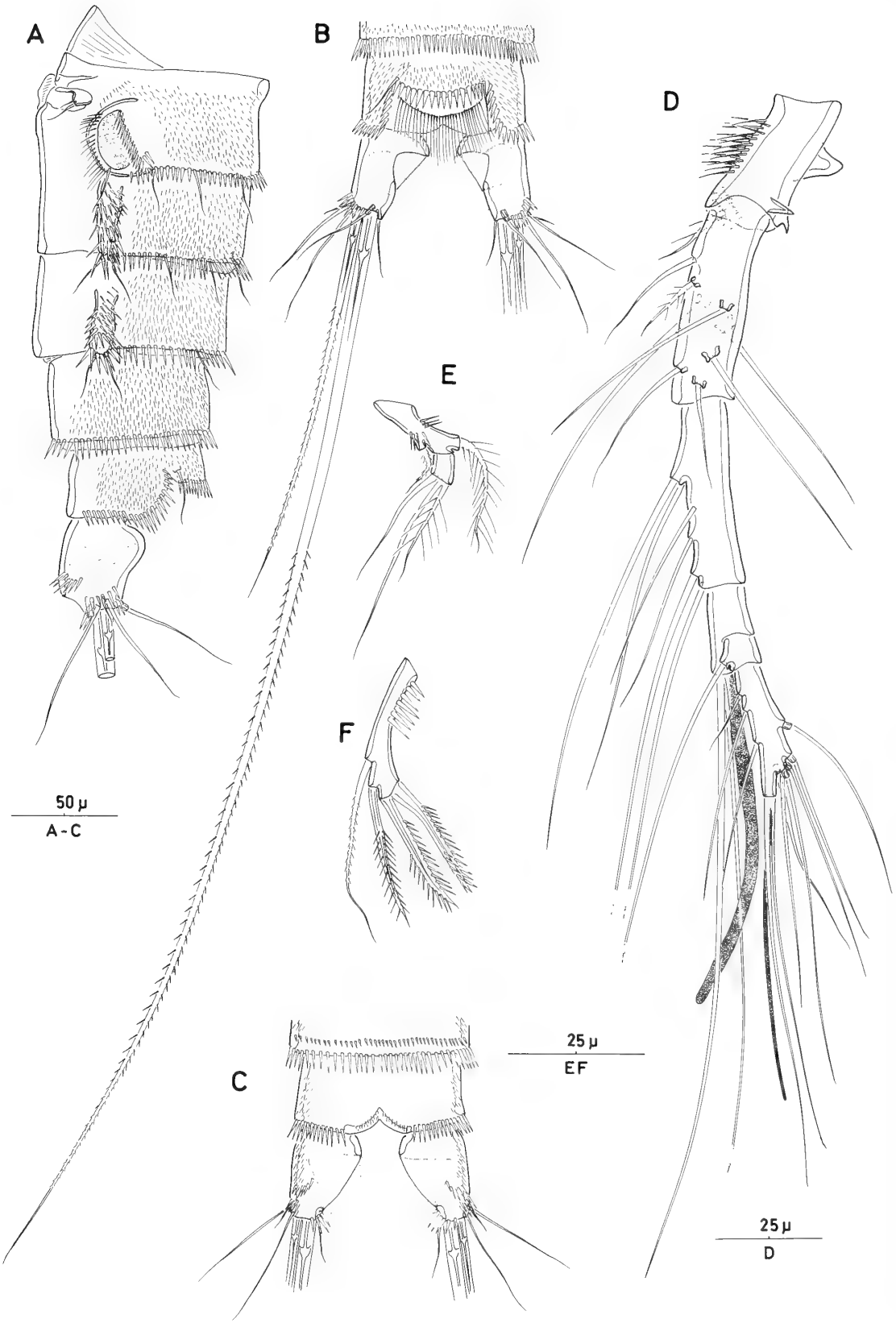

Fig. 6 *Esola canalis* sp. nov. (♀). A, Urosome (excluding P5-bearing somite), lateral; B, anal somite and left caudal ramus, dorsal; C, anal somite and caudal rami, ventral; D, antennule, dorsal; E, mandibular palp; F, antennary exopod.

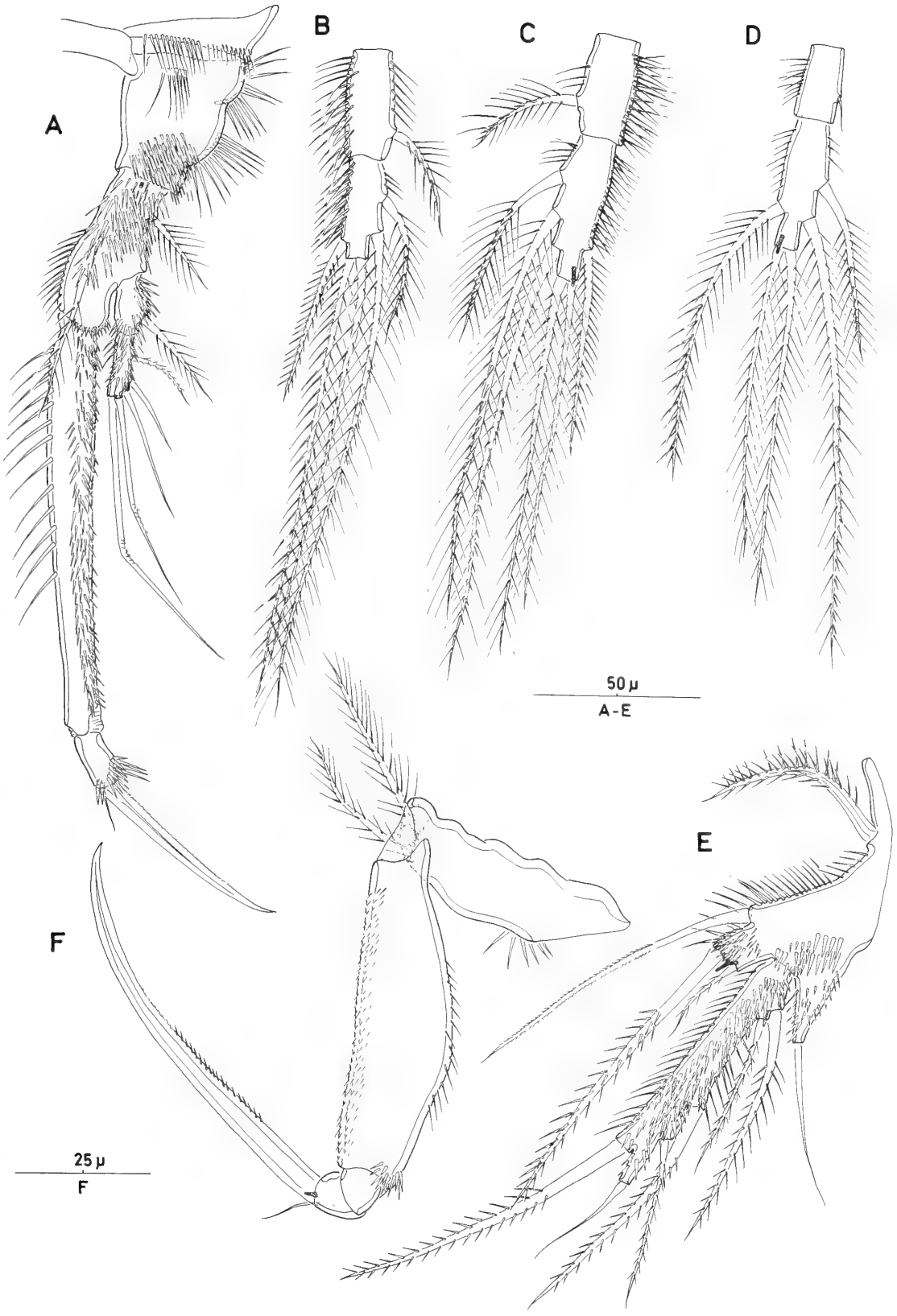

Fig. 7 *Esola canalis* sp. nov. (♀). A, P1, anterior; B, P2 endopod, anterior; C, P3 endopod, anterior; D, P4 endopod, anterior; E, P5, anterior; F, maxilliped.

Table 1. Diagnostic characters of *Esola* species [species A = *Esola* spec. *sensu* Mielke (1997)]. CR = caudal rami, SD = sexual dimorphism.

	longicauda	*bulbifera*	*galapagoensis*	*canalis*	*profunda*	*vervoorti*	*lobata*	species A
♀size (µm)	?	643–714	330–460	585–658	500–529	510	490–530	470
♂ size (µm)	550	500–524	300–360	?	?	389–415	380–450	?
cephalothorax dorsal spinule row	?	present	?	present	present	absent	?	?
mandible – endopod	?	fused, 3 setae	fused, 2 setae	free, 3 setae	free, 3 setae	free, 3 setae	free, 3 setae	free, 2 setae?
– exopod	?	absent	absent	1 seta	absent	absent	absent	absent
– basis	?	2 setae	2 setae	1 seta	2 setae	1 seta	2 setae	2 setae?
P1 exp-2 setal number	4	5	4	5	5	5	5	4
P1 exp-2 outer apical seta SD	?	–	–	?	?	+	–	?
ratio P1 enp-1 : enp-2 claw	0.83	0.50	0.37	0.50	0.55	0.55	0.55	?
P2–P3 enp-1 inner seta	present	present	present	present	present	absent	present	present
P3 enp-2 apophysis ♂	?	smooth	smooth	?	?	dentate	smooth	?
P4 enp-1 inner seta	normal	vestigial	absent	vestigial	absent	absent	absent	vestigial
P5 benp ♀outer apical seta	plumose	plumose	naked	plumose	plumose	plumose	plumose	?
– length*	short	long	vestigial	very short	short	short	~short	?
CR – pore position	ventral	medioventral	ventral	mediodorsal	ventral	medial	ventral	?
– ♀medial swelling	weak	strong	strong	moderate	moderate	moderate	slight	moderate
– ♀length : distal width	3.0	2.3	3.4	3.0	2.5	2.1	3.8	?
– ♂ length : distal width	?	2.5	3.4	?	?	1.7	3.2	?

*: very short = not extending to insertion level of middle outer exopodal seta; short = extending to about insertion level of middle outer exopodal seta; long = extending to about apex of exopod [Note that in *E. lobata* sp. nov. the endopodal lobe is secondarily elongated so that its outer apical seta extends beyond the insertion level of the middle outer exopodal seta despite being short].

Caudal rami (Fig. 6A–C) widely separated; gradually tapering posteriorly and about as long as anal somite; proximal half expanded with major swelling medially and dorsally, and to a lesser extent ventrally (Fig. 6A); large cup-shaped pore located mediodorsally (Fig. 6A) leading to small tube-pore. Armature as in *E. bulbifera*.

Antennule (Fig. 6D) slender, 6-segmented, with 1 large (proximal) and 2 small spinous processes along posterior margin of segment 1. Segment 1 with long spinules around anterior margin. Segments 2 and 3 equally long. Armature formula: 1-[1 pinnate], 2-[7 + 1 pinnate], 3-[6], 4-[(2 + ae)], 5-[1], 6-[9 + acrothek]. Aesthetasc on segment 4 fused basally to 2 setae. Acrothek consisting of aesthetasc and 2 naked setae; set on apical pedestal.

Antennary exopod (Fig. 6F) elongate exopod bearing 2 lateral and 2 apical pinnate elements, and a longitudinal row of coarse spinules proximally.

Labrum with ornamentation as in *E. bulbifera*.

Mandible (Fig. 6E) with small 2-segmented palp; proximal segment with 1 inner (basal) seta and 1 small outer seta representing exopod; endopod a free segment with 3 setae.

Maxilliped (Fig.7F). Basis more slender than in *E. bulbifera* and spinules along outer margin coarser.

P1 (Fig. 7A) similar to that of *E. bulbifera* but basis forming shorter pedestal for endopod, and both exopod (but exp-1 extending to distal margin of basal pedestal) and enp-2 somewhat shorter; exp-2 with 3 outer setae and 2 geniculate setae apically.

P2–P4 (Fig. 7B–D). P2–P3 enp-1 with multipinnate inner seta; P4 enp-1 with vestigial inner seta. Outer spine of P2–P4 enp-2 shorter than in *E. bulbifera*. Armature formula as follows:

	Exopod	Endopod	
P2	0.1.123	1.221	
P3	0.1.223	1.321	[♂: probably 1.1.220]
P4	0.1.223	1.221	

P5 (Fig. 7E). Endopodal lobe small, not extending beyond insertion sites of proximal outer setae of exopod; with 2 apical and 2 widely separated inner setae; outer apical seta very short. Exopod more slender than in *E. bulbifera*; with 1 apical, 1 inner and 4 outer setae; length of inner (ratio to exopod length 1.15 vs 1.5 in *E. bulbifera*) and apical seta (ratio to exopod length 1.25 vs 2.2 in *E. bulbifera*) distinctly shorter.

MALE. Unknown.

REMARKS. Gurney (1927) collected this species from the plankton at Port Taufiq and Le Cap, and in sediment samples from El Ferdane. He attributed his material to *L. bulbifera* but remarked on some differences with Norman's (1911) holotype, such as the discrepancy in body size (0.68 mm instead of 0.80 mm), the P1 endopod which is more slender in the Scottish specimen and the presence of an additional seta (the innermost) on the P5 baseoendopod. We have found these differences to be of no value in discriminating both species. Norman (1911) clearly overlooked the innermost seta (as indicated by the gap along the medial margin in his figure of the baseoendopod). Also, based on a larger sample of *E. bulbifera* we found this species on average to be significantly smaller than Norman's observed size of 0.8 mm, approximating the mean length of *E. canalis* (681 µm vs 621 µm; see also Table I). There is no significant difference in the P1 endopod of both species although the proximal segment appears to be longer in *E. canalis* and the distal segment to be longer in *E. bulbifera*. Gurney (1927) illustrated the P5, caudal rami and the female habitus in lateral view. His illustration of the caudal rami gives a slightly distorted view in that the rami appear to be much longer than in reality. Por & Marcus (1972) recorded *E. longicauda* from four localities in the Suez Canal; it is likely that these records and Por's (1967) previous record from the Gulf of Elat refer to *E. canalis*.

E. canalis is most closely related to *E. bulbifera*. Females of the former can be differentiated by the conical caudal rami, the mediodorsal position of the cup-shaped pores on these rami, and the P5 endopodal lobe which is significantly shorter and has a much smaller outer apical seta. Additional differences can be found in the proportional lengths of the proximal antennulary segments, the slenderness of the maxilliped and the size of particular setae on the P2–P4 endopods and P5 exopod. *E. canalis* is the only species of the genus which has retained a vestige of the mandibular exopod.

Esola lobata sp. nov.

Esola longicauda (Edwards, 1891) *sensu* Mielke (1997)

TYPE LOCALITY. Bunaken Island near Manado, North Sulawesi (Indonesia); sublittoral sand between seagrass and corals.

ETYMOLOGY. The species name refers to the well developed endopodal lobe of the P5 in both sexes.

P2–P4 setal formula:

	Exopod	Endopod	
P2	0.1.123	1.221	
P3	0.1.223	1.321	[♂: 1.1.220]
P4	0.1.223	0.221	

Mielke (1997) provided an excellent description of Sulawesi females and males which he attributed to *E. longicauda*. His illustrations show sufficient differences to warrant separate species status. *E. lobata* is similar to *E. profunda* from the Mediterranean and both *E. vervoorti* and *E. galapagoensis* from the Pacific in the loss of the inner seta on P4 enp-1. The species can, however, be readily distinguished by the long endopodal lobe in the ♀ P5, a well developed bulbous extension on the baseoendopod of the ♂ P5, the elongate caudal rami which are relatively little modified in the female, and the short P1 endopod. Discrepancies are also noted in the female antennule, particularly in the relative lengths of the proximal segments, and the size and precise position of the spinous processes on segment 1. The species is thus far known only from the type locality.

Esola profunda sp. nov.

TYPE LOCALITY. Ligurian Sea (Western Mediterranean; 42°39'12" N, 08°39'30" E), northwest of the Bay of Calvi (Corsica); depth 760 m.

TYPE MATERIAL. 2 ♀♀ from type locality. The bottom sample was taken on 10 June 1986 with a small, modified Reineck box corer (170 cm²) by K. Soetaert. The median grain size of the sediment is 4 µm and the silt-clay amount averages 78.5%. The CPE value is about 0.59 µg/cm² of which 12.6% is represented by chl a. Holotype dissected on 11 slides (BMNH 1999.991), paratype ♀ preserved in alcohol (BMNH 1999.992).

ETYMOLOGY. The species name is derived from the Latin *profundus* (meaning deep) and refers to the bathyal distribution of this species.

DESCRIPTION.

FEMALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 515 µm (n=2; range: 500–529 µm). Maximum width (129 µm) measured at posterior margin of cephalothorax.

Body (Fig. 8A) as in *E. bulbifera* but constrictions between pedigerous somites less defined; cephalothorax with paired cup-shaped pores both anterodorsally and anteroventrally on either side of rostrum, and with distinct transverse spinule row dorsally about halfway down the cephalothorax length.

Urosomites with dense spinulation and irregular pattern of surface ridges laterally and dorsally (Fig. 8B). Genital double-somite (Fig. 8A–B) with large cup-shaped pores laterally in anterior half; ventral surface without spinular ornamentation; posterolateral angles slightly produced. First postgenital somite with backwardly produced lateral angles, bearing spinular tuft; without ventral ornamentation. Penultimate and anal somites distinctly narrower (Fig. 8A); ventral posterior border with spinules (Fig. 8D). Anal somite (Fig. 8C) with spinulose anal operculum.

Caudal rami (Fig. 8C–D) widely separated; with slight swelling medially and virtually no expansion ventrally (Fig. 8B); dorsal surface with 2 chitinous processes in posterior half; large cup-shaped pore located ventrally (Fig. 8D) leading to small tube-pore. Armature as in *E. bulbifera*.

Antennule (Fig. 9A) slender, 6-segmented, with 1 large (proximal) and 2 small spinous processes along posterior margin of segment 1.Segment 1 with long spinules around anterior margin. Segment 2 distinctly longer than segment 3. Armature formula: 1-[1 pinnate], 2-[7 + 1 pinnate], 3-[6], 4-[(2 + ae)], 5-[1], 6-[9 + acrothek]. Aesthetasc on segment 4 fused basally to 2 setae (Fig. 9B). Acrothek consisting of aesthetasc and 2 naked setae; set on apical pedestal.

Antennary exopod (Fig. 9D) elongate exopod bearing 2 lateral and 2 apical pinnate elements; no ornamentation discernible.

Labrum with ornamentation as in *E. bulbifera*.

Mandible (Fig. 9E) with small 2-segmented palp; proximal segment with 2 inner, (basal) setae; endopod a free segment with 3 setae.

Maxillule (Fig.10D) as in *E. bulbifera* but outer apical seta of exopod naked and shorter and distal spine on basis stouter.

P1 (Fig. 8E) similar to that of *E. bulbifera* but both endopodal segments and terminal claw shorter; exp-1 extending to distal margin of basal pedestal; exp-2 with 3 outer setae and 2 geniculate setae apically.

P2–P4 (Figs 9C; 10A–B). Outer basal spine of P2 distinctly shorter and more setiform. P2–P3 enp-1 with multipinnate inner seta; P4 enp-1 inner seta absent. Outer spine of P2–P4 enp-2 shorter than in *E. bulbifera*. Armature formula:

	Exopod	Endopod	
P2	0.1.123	1.221	
P3	0.1.223	1.321	[♂: probably 1.1.220]
P4	0.1.223	0.221	

P5 (Fig. 10C). Endopodal lobe elongate, clearly extending beyond insertion sites of proximal outer setae of exopod; with 2 apical and 2 widely separated inner setae; outer apical seta distinctly shorter. Exopod more slender than in *E. bulbifera*; with 1 apical, 1 inner and 4 outer setae; anterior proximal seta and distalmost outer seta much shorter.

MALE. Unknown.

REMARKS. *E. profunda* is known only from the type locality and represents the deepest record for the genus. It is similar to *E. lobata* in the elongate endopodal lobe of the ♀ P5, the mandibular palp setation, the ventral position of the caudal ramus pores and the absence of the inner seta on P4 enp-1. It differs from this species in the elongate ♀ P5 exopod, caudal ramus shape (presence of dorsal chitinous processes) and the longer P1 enp-2.

Esola vervoorti sp. nov.

Esola longicauda (Edwards, 1891) *sensu* Vervoort (1964)

TYPE LOCALITY. Ifaluk Atoll, Caroline Islands, North Pacific; stn 592 (Vervoort, 1964).

TYPE MATERIAL. National Museum of Natural History, Washington, D.C.: holotype ♀ dissected on 12 slides (NMNH 109702); paratypes are 2 ♂♂ in alcohol (NMNH 288048). Originally labelled *E. longi-cauda*; det. W. Vervoort; 16 October 1953. Two other vials with identical labels contained different species: (a) NMNH 109789: cope-podid V ♀ of *E. longicauda* var. *sensu* Vervoort (1964), from stn 591; (b) NMNH 109790: 1 ♀ and 1 ♂ of *Paralaophonte* sp., from stn 590.

ETYMOLOGY. The species is named in honour of Dr Willem Vervoort (Rijksmuseum van Natuurlijke Historie, Leiden) who first illustrated this species.

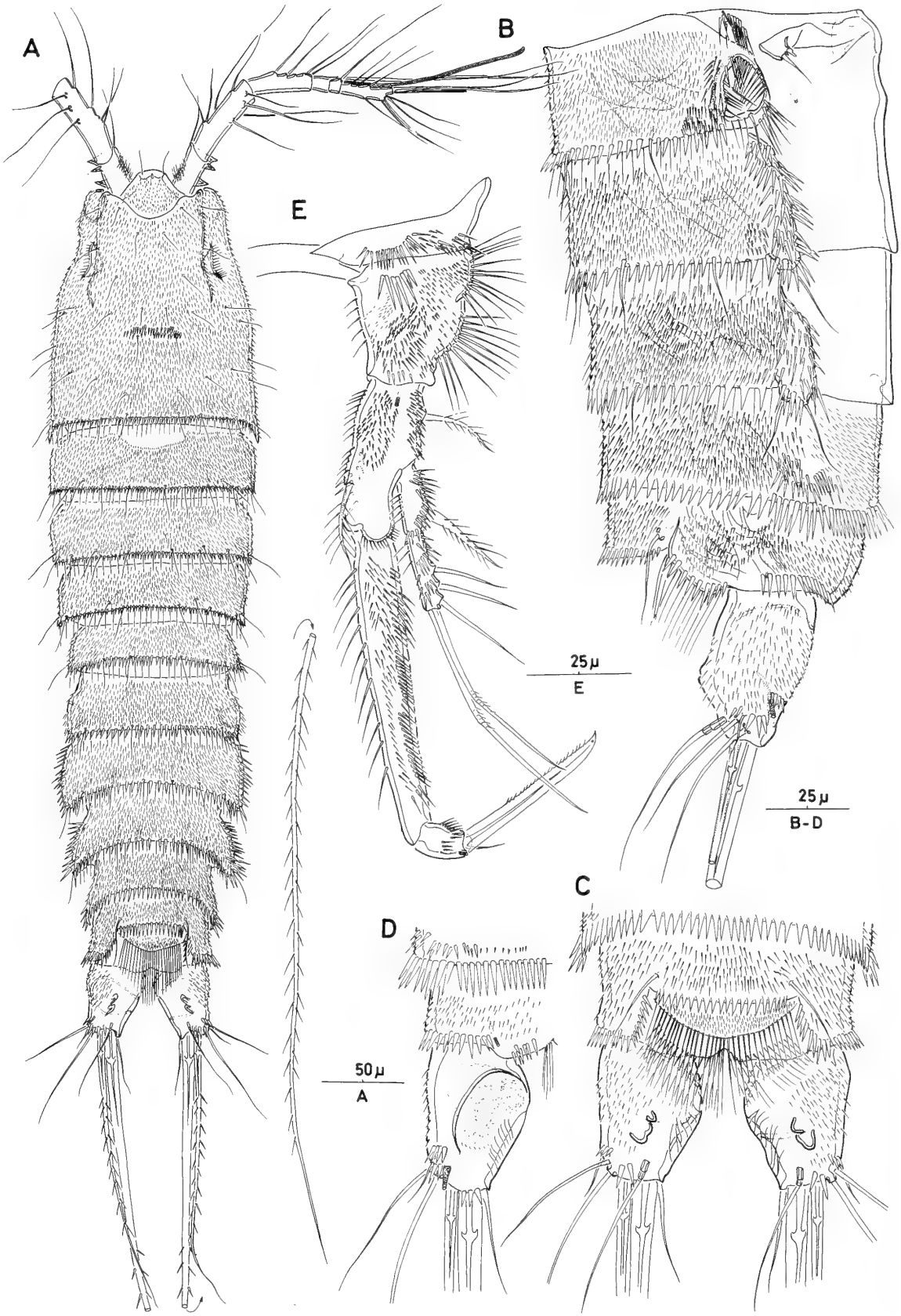

Fig. 8 *Esola profunda* sp. nov. (♀). A, Habitus, dorsal; B, urosome (excluding P5-bearing somite), lateral; C, anal somite and caudal rami, dorsal; D, right caudal ramus, ventral; E, P1, anterior.

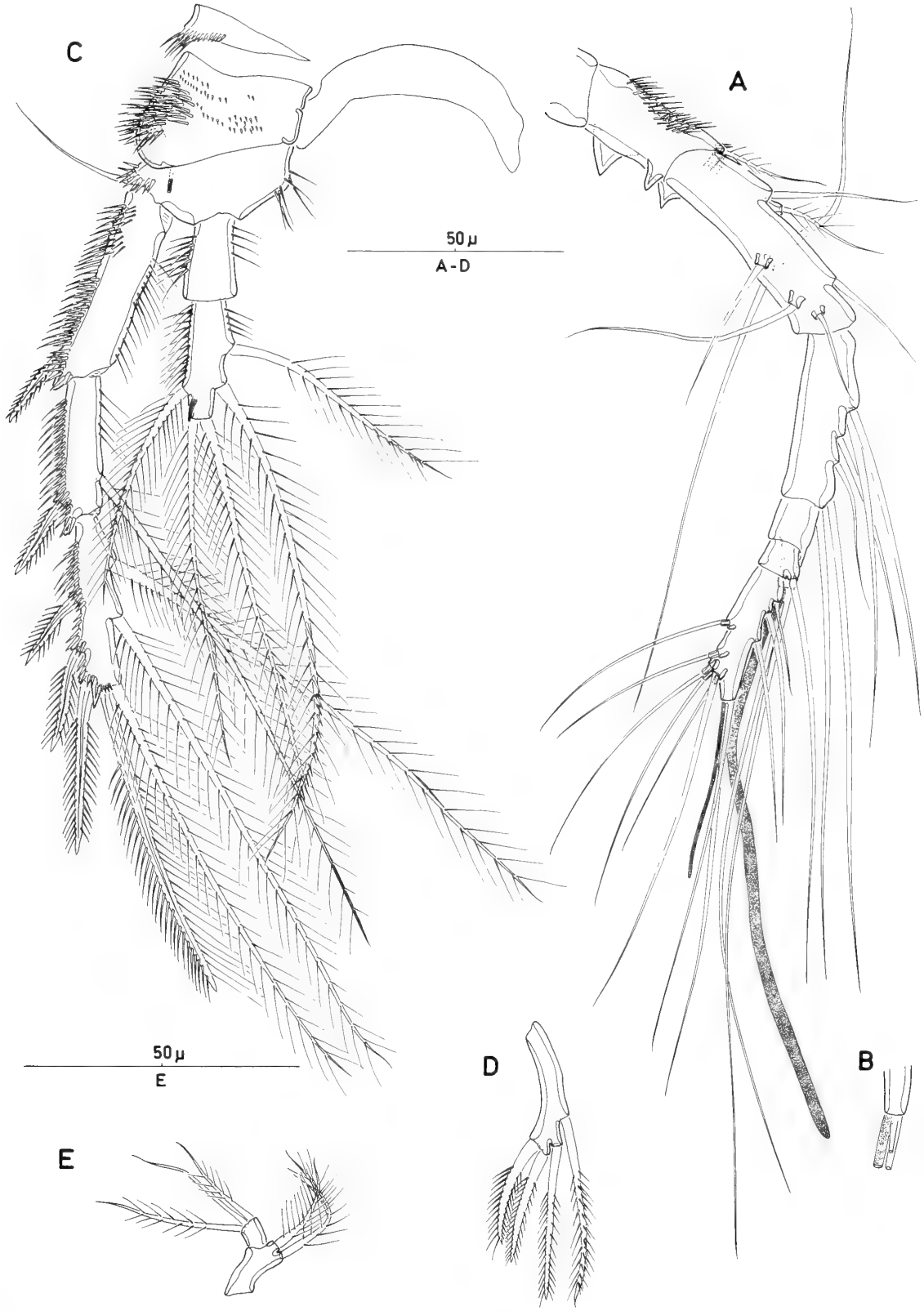

Fig. 9 *Esola profunda* sp. nov. (♀). A, Antennule, dorsal; B, cylindrical outgrowth on antennulary segment 4; C, P4, anterior; D, antennary exopod; E, mandibular palp.

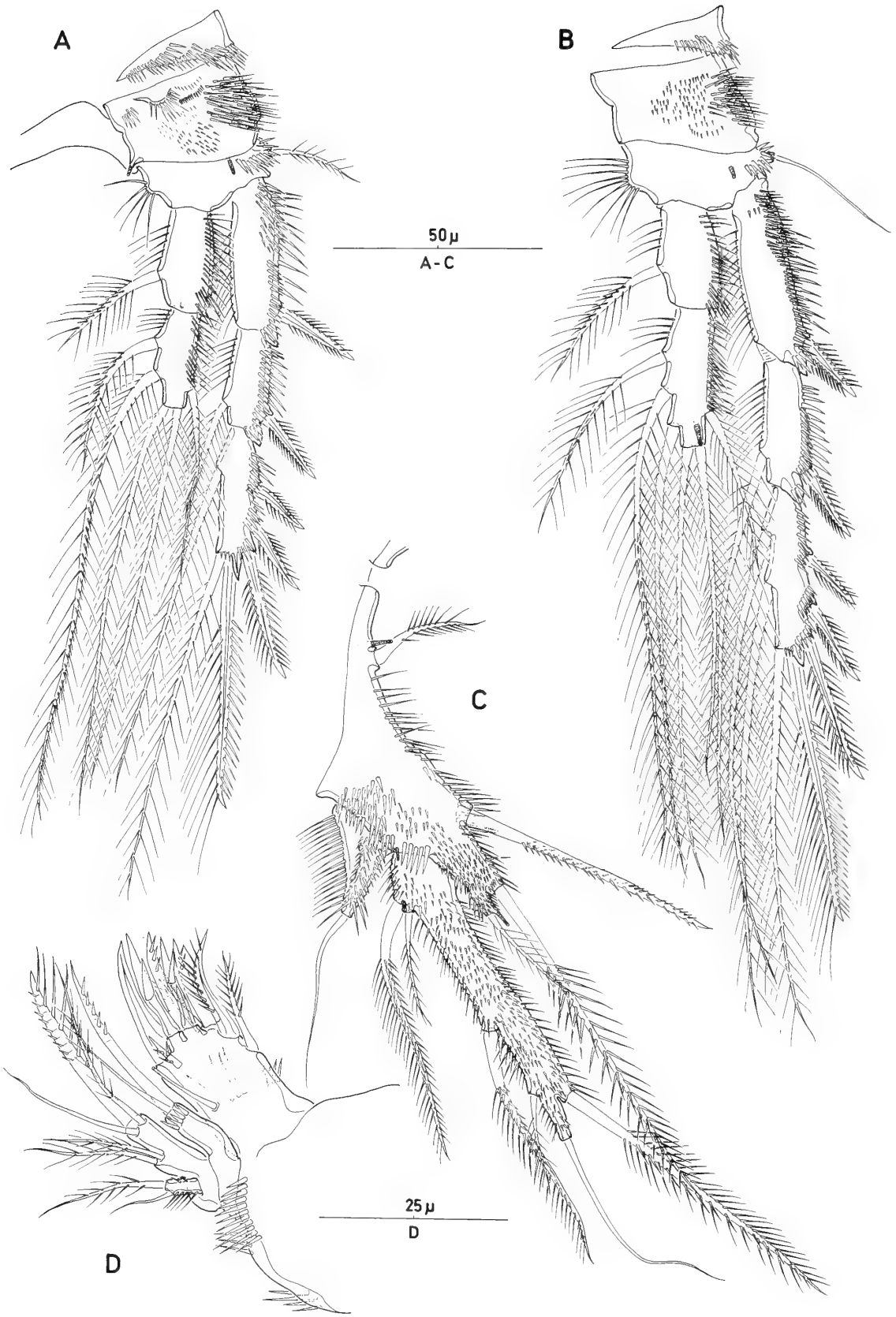

Fig. 10 *Esola profunda* sp. nov. (♀). A, P2, anterior; B, P3, anterior; C, P5, anterior; D, maxillule, anterior.

DESCRIPTION.

FEMALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 510 μm; maximum width 120 μm (Vervoort, 1964).

MALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 401 μm (n=3; range: 389–415 μm). Maximum width (121 μm) measured at posterior margin of cephalothorax.

Body (Fig. 11A) more compact and abbreviated than in ♀; covered with similar dense pattern of minute spinules. Cephalothorax with small cup-shaped pores anterodorsally and anteroventrally on either side of rostrum; wider than free somites; without transverse spinule row dorsally. Urosome distinctly narrower than prosome; none of urosomites with backwardly produced posterolateral corners.

Genital somite with ventrolateral cup-shaped pores (Fig. 11B–C). Sixth legs (Fig. 11B–C) represented by well developed opercula, one articulating and closing off left or right genital aperture; each produced into cylindrical process bearing 1 lateral and 1 apical seta.

Antennule (Fig. 12A–D) 7-segmented, subchirocer, with geniculation between segments 5 and 6. Segment 1 with spinules/setules around anterior margin and 2 spinous processes along posterior margin. Segment 4 minute, represented by incomplete sclerite. Segment 5 longest, with large proximal process anteriorly, bearing modified spine; forming cylindrical process bearing long aesthetasc fused basally to 2 setae (Fig. 12C). Segment 6 with 3 spinous processes along anterior margin. Segment 7 triangular. Armature formula: 1-[1 pinnate], 2-[7 + 2 pinnate], 3-[6], 4-[2], 5-[7 + 2 pinnate + 1 spine + (2 + ae)], 6-[1 + 3 processes], 7-[7 + acrothek]. Apical acrothek consisting of aesthetasc and 2 bare setae.

Mandibular palp (Fig. 11F) small, comprising elongate basis with 1 pinnate seta and free endopod bearing 3 apical setae.

P1 (Fig. 12E) with broader basal pedestal and more robust endopod than in *E. bulbifera*; enp-1 stouter and enp-2 slightly shorter. Exopod small; exp-1 not extending to distal margin of basal pedestal, with stout outer spine; exp-2 with 3 outer setae and 2 apical setae, outer apical seta much shorter than in ♀ and not geniculate.

P2–P4 without inner seta on enp-1 (Fig. 12F–H). P3 endopod (Fig. 12G) 3-segmented; enp-1 as in ♀; enp-2 with inner seta and dentate outer apophysis; enp-3 small, with tube-pore, 2 lateral and 2 apical setae. Armature formula:

	Exopod	Endopod	
P2	0.1.123	0.221	
P3	0.1.223	0.1.220	[♀: 0.321]
P4	0.1.223	0.221	

P5 (Fig. 11E) medially fused, positioned ventrolaterally. Baseoendopod without endopodal lobe; medial margin with 2 tube-pores; outer basal seta arising from short spinulose pedestal. Exopod free; with 1 inner seta and 1 apical plus 3 outer pinnate spines; spines markedly shorter than in *E. bulbifera*.

Caudal ramus (Fig. 11B–D) rectangular, without bulbiform expansions; about 1.7 times as long as wide; with medial cup-shaped concavity as in ♀.

REMARKS. Vervoort (1964) inclined to assign specific status to his material from the Ifaluk Atoll, however, refrained from doing so due to the uncertainty about the widely recorded variability for *E. longicauda*. *E. vervoorti* occupies an isolated position in the genus for a number of reasons: (1) the absence of the inner seta on P2–P4 enp-1, (2) the dentate type of apophysis on the male P3 endopod, (3) absence of transverse spinular row on cephalothorax, (4) reduced mandibular palp, (5) very short ♀ caudal rami, and (6) the sexual dimorphism of the outer apical seta on P1 exp-2. The latter character is unique within the Laophontidae; Vervoort (1964) also illustrated this sexual dimorphism but did not mention it as a feature of high significance.

Esola longicauda Edwards, 1891 *sensu* Noodt (1955)

Noodt (1955) illustrated a single ovigerous female of *E. longicauda* recorded from the Sea of Marmara. His specimen is much larger (0.79 mm) than any other species in the genus (Table I) and like Edwards' (1891) types shows a strongly developed seta on P4 enp-1. It resembles *E. bulbifera* in the bulbiform caudal rami and the incompletely 7-segmented antennule which according to Noodt (1955) displays a partly subdivided apical segment. His statement that the endopodal lobe has only 3 setae is clearly based on an error. Without further information the identity of this specimen cannot be determined.

Esola longicauda Edwards, 1891 var. *sensu* Vervoort (1964)

This variety, known from a single male, differs from Vervoort's (1964) typical specimens of *E. longicauda* (here designated as *E. vervoorti* sp. nov.) in the slender and almost haplocer antennule, the presence of an inner seta on P2–P4 enp-1 and the shorter P4 endopod and P5 exopod. This combination of characters rules out conspecificity with both *E. vervoorti* and *E. lobata*, the only established species from the Western Pacific. It also differs from Mielke's (1997) *Esola* spec. from Sulawesi by the presence of 5 setae on the distal exopod segment of P1. It is conceivable that this variety represents yet another species, however, the discovery of the female is crucial before it can be attributed such status.

Esola longicauda Edwards, 1891 *sensu* Wells & Rao (1986)

Wells & Rao's (1986) record of a single female from Havelock Island (South Andaman) is virtually indeterminable. It is probably conspecific with Sewell's (1940) specimens of *Laophonte bulbifera* recorded from Nankauri Harbour in the Nicobar Islands and Addu Atoll in the Maldive Archipelago. Both share the absence of the inner seta on P4 enp-1 and their antennulary segments have similar proportional lengths.

Esola spec. *sensu* Mielke (1997)

Mielke (1997) provided figures and additional information of a single female which is potentially sympatric with *E. lobata* in North Sulawesi. This form differs from the latter in the size of the processes on the first antennule segment, the shape and setal length of the antennary exopod, mandibular armature, P1 exp-2 setation, presence of a vestigial seta on P4 enp-1 and caudal ramus shape. The presence of only 4 setae on the distal exopod segment of P1 relates it to *E. galapagoensis* and *E. longicauda*, however, differences in the antennules and P4 endopod make conspecificity unlikely.

Genus *Mourephonte* Jakobi, 1953

Moerephonte Jakobi, 1953: *lapsus calami* by Vervoort (1964).

Jakobi (1953) established this genus to accommodate a new species *M. catharinensis* described from the coast of Santa Catarina, Brazil. Vervoort (1964) expressed severe doubts as to the validity of this genus, assuming that the completely reduced P2 endopod and the

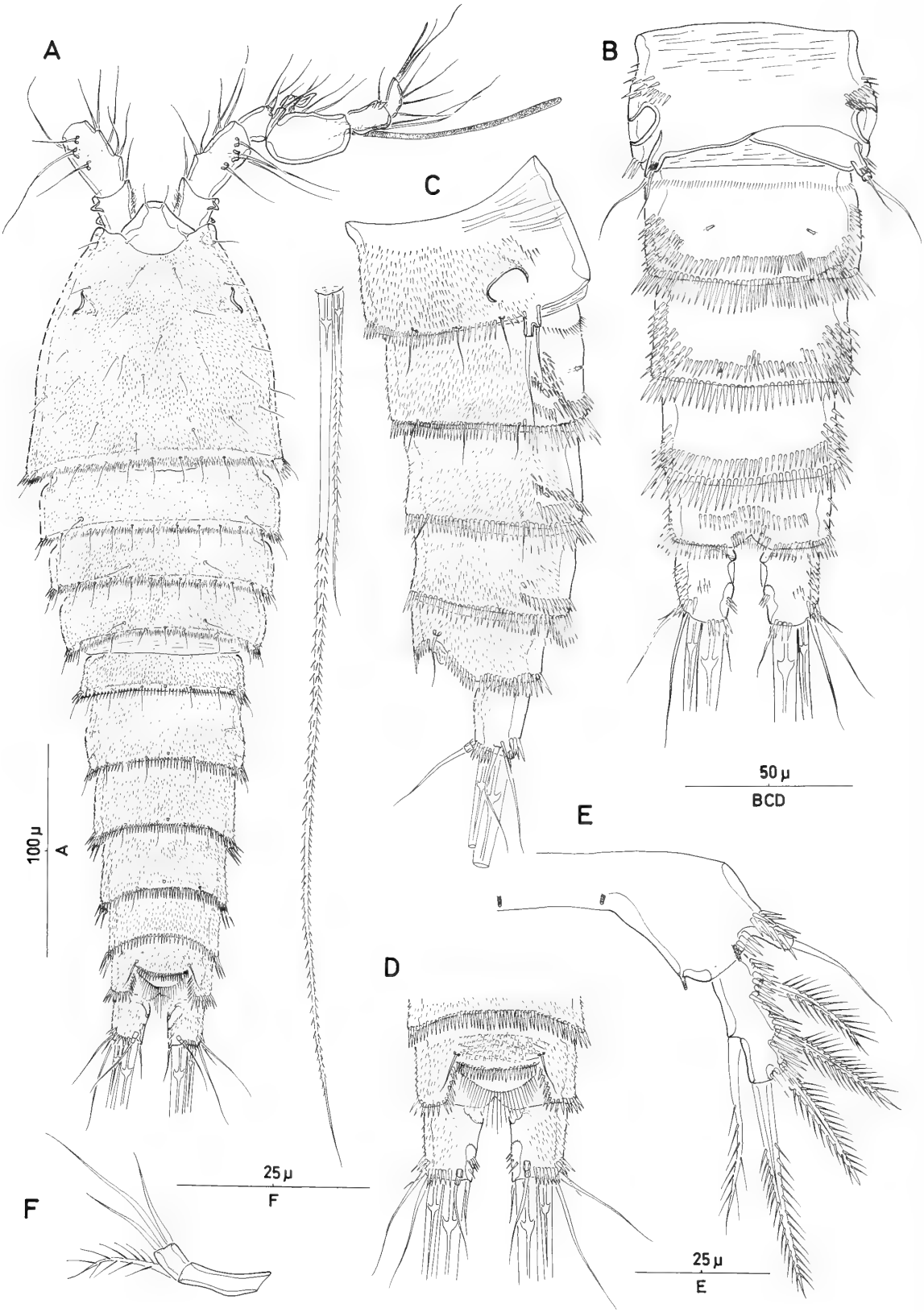

Fig. 11 *Esola vervoorti* sp. nov. (♂). A, Habitus, dorsal; B, urosome (excluding P5-bearing somite), ventral; C, same, lateral; D, anal somite and caudal rami, dorsal; E, left P5, anterior; F, mandibular palp.

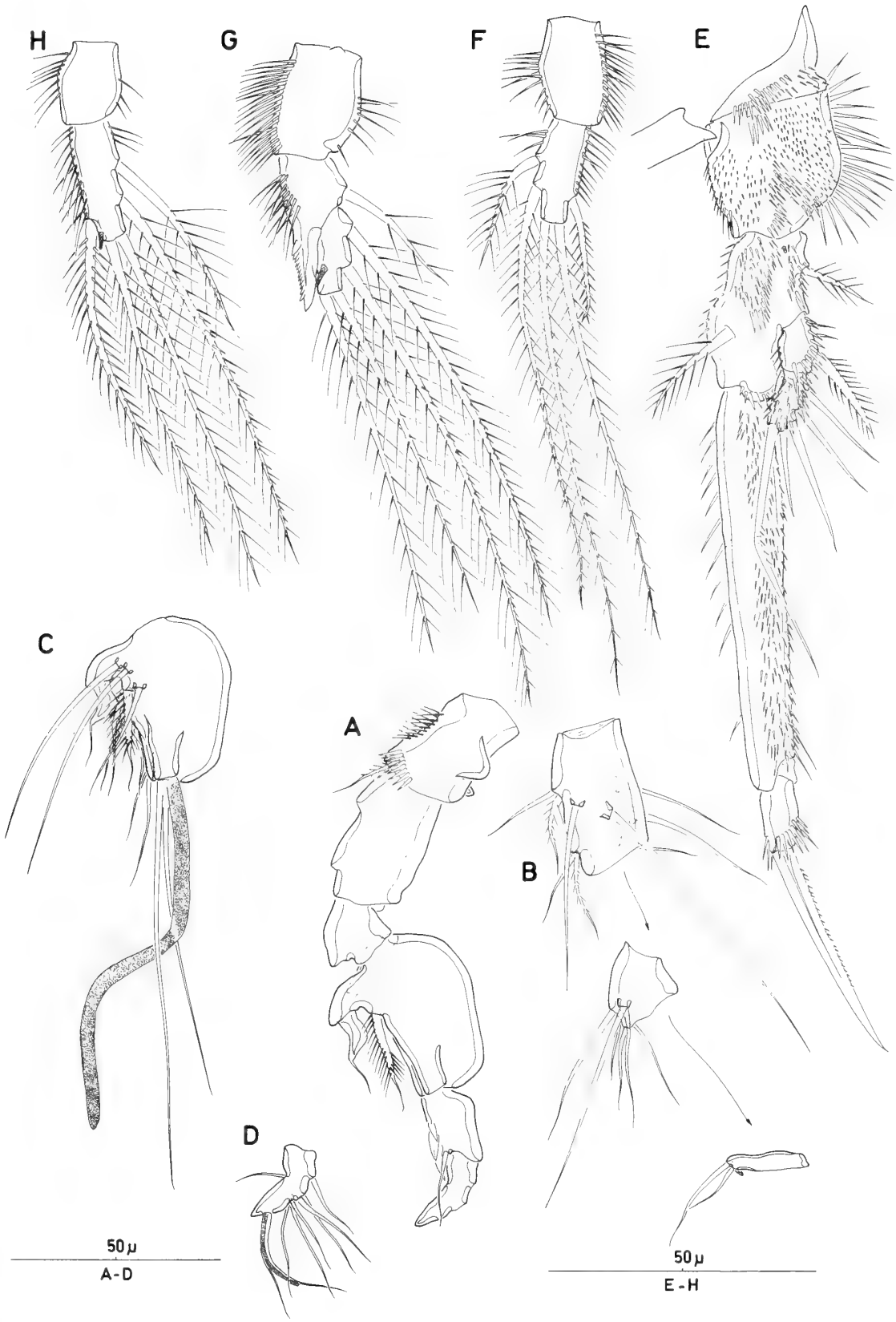

Fig. 12 *Esola vervoorti* sp. nov. (♂). A, Antennule, ventral (armature of segments 2–5 and 7 omitted); B, antennulary segments 2–4; C, antennulary segment 5, ventral; D, antennulary segment 7; E, P1, anterior; F, P2 endopod, anterior; G, P3, exopod, anterior; H, P4, endopod, anterior.

aberrant setal formula most likely resulted from imperfect dissection. In addition, he suspected that *Mourephonte* was a junior subjective synonym of *Esola* and claimed that *M. catharinensis* was probably nothing more than an inadequately illustrated specimen of *Esola longicauda*. Lang (1965) pointed out that Jakobi's species had already been described as *Laophonte longiseta* by Nicholls (1941*a*) and regarded the absence of the P2 endopod and the reduced armature of P2–P4 as sufficient grounds to maintain *Mourephonte* as a distinct genus.

Jakobi's material, consisting of an unspecified number of males collected from the tidal zone at Itapocoroy and Pôrto Belo, is no longer extant, the only specimen available being Nicholls' holotype male of *L. longiseta* deposited in the South Australian Museum, Adelaide. This specimen forms the basis of the redescription given below. The female is as yet unknown.

DIAGNOSIS (based on ♂ only). Laophontidae. Body cylindrical. Integument of cephalothorax and body somites with dense pattern of spinules and setules. Rostrum large, partly delimited at base. Cup-shaped pores present both anterodorsally and anteroventrally on cephalic shield, laterodorsally on caudal rami; absent on genital somite. Anal operculum dentate. Caudal rami rectangular, short.

Sexual dimorphism in antennule, P3 endopod, P5, P6, genital segmentation and caudal rami.

Antennules slender; haplocer and 7-segmented in ♂; segment 1 with 2 small processes along posterior margin; swollen segment 5 with very long aesthetasc (fused basally to 2 setae) but without distinct anterior outgrowth. Antenna with 4 setae on exopod; allobasis with abexopodal seta. Labrum with marginal spinules distally. Mandible with small 1-segmented palp bearing 1 lateral and 3 apical setae. Maxillule without defined exopod, represented by 1 setae. Maxilla with 3 endites on syncoxa; endopod represented by 4 setae. Maxilliped slender; syncoxa with 2 setae; entire palmar margin with spinules; endopodal claw elongate.

P1 very large compared to other legs; with 2-segmented exopod bearing 4–5 setae on exp-2 and elongate endopod; enp-1 without inner seta, enp-2 with minute seta and long, slender claw. P2–P4 with 3-segmented exopods; endopods entirely absent (P2) or 2-segmented (P3–P4). Bases with plumose (P2) or naked (P3–P4) short outer seta. P2–P4 without inner setae on exp-2 and -3. P4 enp-2 with widely separated apical setae. P3 endopod ♂ indistinctly 3-segmented with incomplete surface suture between enp-2 and -3; enp-2 with inner seta and short outer, spinous apophysis. Armature formula as follows:

	Exopod	Endopod
P2	0.0.022	——
P3	0.0.022	1.1.110 [in ♀presumably 1.211]
P4	0.0.022	0.111

P5 ♂ without endopodal lobe; exopod short, with 1 inner, 2 apical and 2 outer setae/spines.

P6 ♀asymmetrical; membranous flaps with 2 setae arising from cylindrical process.

TYPE AND ONLY SPECIES. *Laophonte longiseta* Nicholls, 1941*a* = *Mourephonte longiseta* (Nicholls, 1941*a*)

Mourephonte longiseta (Nicholls, 1941a)

Laophonte longiseta Nicholls, 1941*a*
Mourephonte catharinensis Jakobi, 1953

TYPE LOCALITY. Tidal zone at Itapocoroy and Pôrto Belo, Santa Catarina State, Brazil; holdfasts of *Endocladia* and *Codium*.

MATERIAL EXAMINED. South Australian Museum, Adelaide: Holotype ♂ of *Laophonte longiseta*, dissected on slide Tc 13437 (SAM C5550); Sellick Beach, south of Port Willunga, South Australia; coll. H.M. Hale, 31 January 1937, from a stone in 1.5 m at low tide on south edge of reef. Jakobi's (1953) type material of *M. catharinensis* is lost.

REDESCRIPTION.

FEMALE. Unknown.

MALE. Body length 0.25 (Jakobi, 1953) to 0.30 mm (Nicholls, 1941*a*). Cephalic shield with paired cup-shaped pores both anterodorsally and anteroventrally on either side of rostrum.

Antennule (Fig. 14A–F) 7-segmented, haplocer; geniculation between segments 5 and 6; proximal segments without conspicuous spinous processes but segment 1 with 2 small protuberances; segment 1 with spinular row distally and tiny spinules along anterior margin; segment 2 longest; segment 5 with very long aesthetasc (150 µm). Armature formula: 1-[1], 2-[8 + 1 pinnate], 3-[6], 4-[2], 5-[8 + 1 pinnate + 1 spine + (2 + ae)], 6-[1 + modified seta], 7-[7 + acrothek]. Acrothek consisting of 2 basally fused setae.

Antennary exopod (Fig. 13D) with 2 pinnate setae laterally and 2 pinnate spines distally.

Labrum with marginal spinules distally; without overlapping scales.

Mandibular palp (Fig. 13C)1-segmented, bilobate, rami completely incorporated; with 1 pinnate seta laterally (probably basal in origin) and 3 bare setae distally (representing incorporated endopod). Maxillule and maxilla as in the genus *Esola*.

Maxilliped (Fig. 13B) slender; syncoxa with 3 spinular rows and 2 pinnate setae; basis elongate, with long spinular row on palmar margin and spinular patch on outer margin; endopod represented by tiny setule and very long claw, exceeding length of basis.

P1 (Fig. 13A) large compared to P2–P4; protopodal segments with rows and patches of fine spinules as illustrated; basis with outer spine near joint with coxa and inner pinnate spine on anterior surface. Exopod 2-segmented, exp-1 with pinnate outer spine; exp-2 with 2 spines and 3 geniculate setae. Endopod very long; enp-1 without inner seta; enp-2 with 3 spinular rows, 1 setule and long, denticulate claw.

P2–P4 (Fig. 14G–I) with 3-segmented exopods; endopod 2-segmented (P3–P4) or entirely absent (P2). P3 enp-2 partly subdivided along anterior surface by short transverse suture; apophysis on outer margin short and slightly sigmoid, bare. P4 enp-2 with apical setae widely separated and flanking secretory tube-pore. Armature formula of P2–P4 as for genus.

P5 (Fig. 14J) with baseoendopod fused to somite, endopodal lobe not developed. Exopod rectangular; with 2 outer, 1 apical and 2 inner setae. P6 asymmetrical, produced into cylindrical process at outer corner, bearing long apical and shorter inner seta.

Pleural areas of genital somite without modified pores. Posterior margins of abdominal somites with row of long spinules (Fig. 13F). Anal operculum dentate (Fig. 13E).

Caudal rami (Fig. 13E–F) short, about 1.3 times as long as wide; with 6 setae (seta I absent), seta VII tri-articulate at base and plumose, setae IV and V well developed and fused at base. Inner proximal margin with cup-shaped depression (specialized pore) dorsally, marked by row of tiny spinules set on strongly chitinized margin; cup filled with secretory substance.

REMARKS. Neither Jakobi (1953) nor Nicholls (1941*a*) illustrated cup-shaped pores on the cephalic shield. Vervoort (1964) pointed out that Jakobi had shown an anteriorly directed middorsal spinous

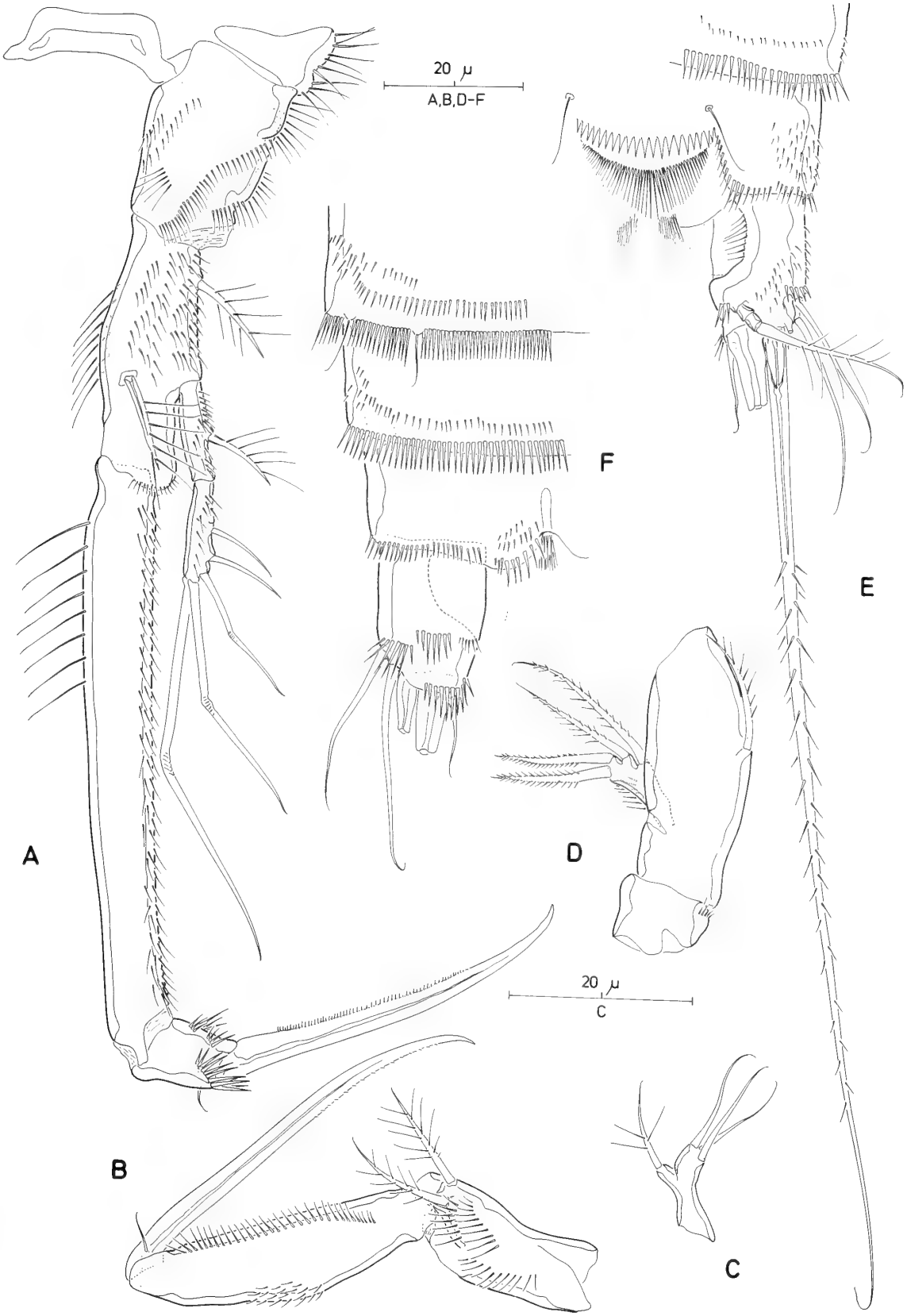

Fig. 13 *Mourephonte longiseta* (Nicholls, 1941*a*) (♂). A, P1, anterior; B, maxilliped; C, mandibular palp; D, coxa, allobasis and exopod of antenna; E, anal somite and right caudal ramus, dorsal; F, posterior urosomites and right caudal ramus, ventral.

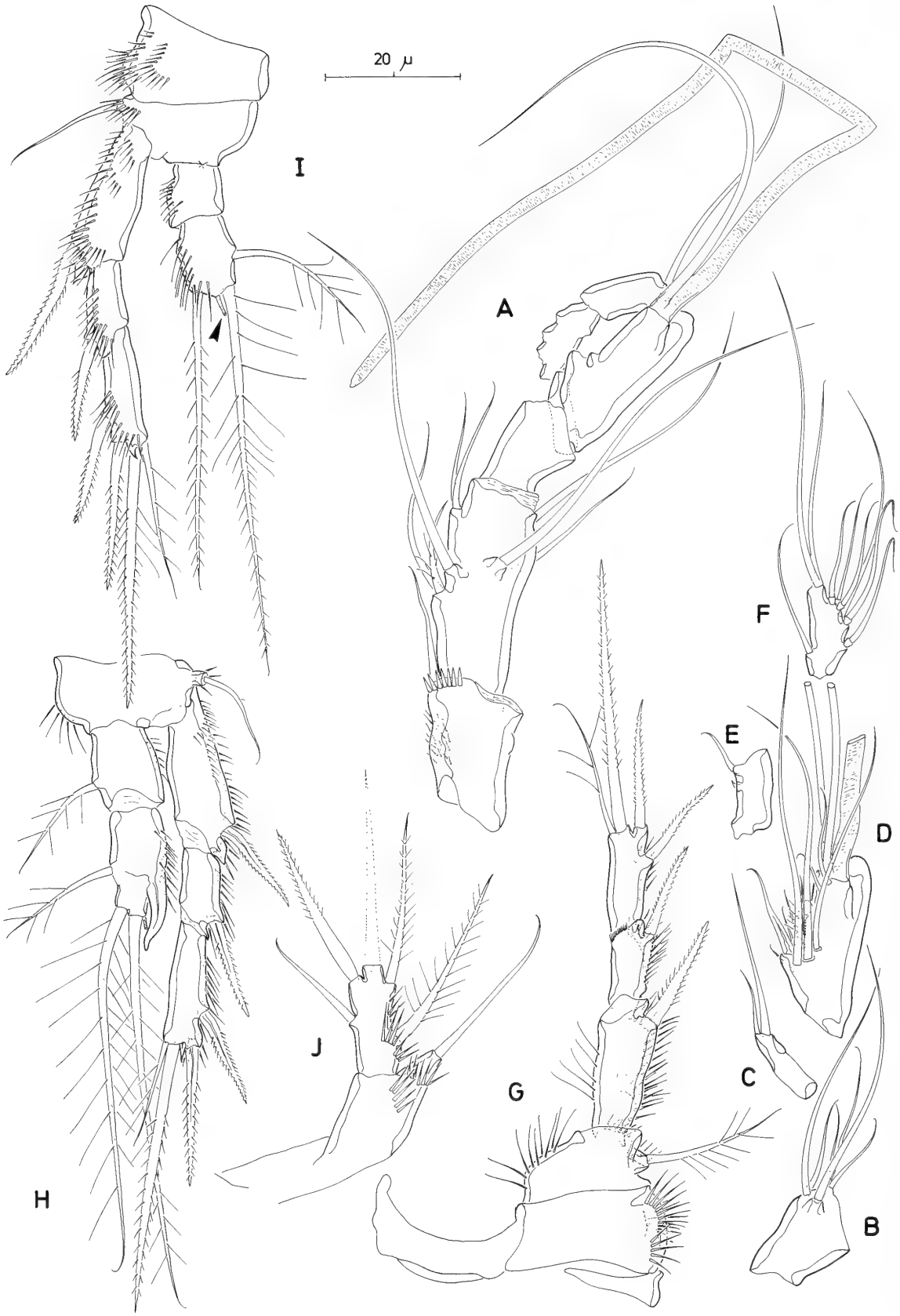

Fig. 14 *Mourephonte longiseta* (Nicholls, 1941*a*) (♂). A, Antennule, ventral (armature of segments 3–7 largely omitted); B–F, antennulary segments 3–7; G, P2, anterior; H, P3, posterior; I, P4, anterior (apical tube-pore arrowed); J, right P5, anterior.

process which was not illustrated in the lateral habitus view, possibly indicating that the author had indeed observed but incorrectly figured the cephalic pores. We have re-examined Nicholls' slide material and found remnants of the cephalic shield, confirming the presence of both anterodorsal and anteroventral pores as in *Esola*. Scrutinous observation failed to reveal any such structures on the genital somite.

With only two records known, *M. longiseta* appears to display a remarkably disjunct distribution. Topotype material from Brazil is required to confirm whether the morphometric discrepancies in Jakobi's description result from imperfect observation or reflect species level differences between the Brazilian and Australian populations.

Genus *Archilaophonte* Willen, 1995

DIAGNOSIS. Laophontidae. Body elongate and slender; cephalothorax slightly wider than rest of body; posterolateral corners of ♀ genital double-somite and second abdominal somites not laterally or backwardly produced. Integument of cephalothorax and body somites with dense pattern of spinules and setules; cup-shaped pores on cephalothorax, genital (double-)somite and caudal rami absent.

Rostrum very large, partly delimited at base. Integumental cup-shaped pores absent. Anal operculum spinulose. Caudal rami very long, cylindrical with posterior halves diverging.

Sexual dimorphism in body shape, antennule, P3 endopod, P5, P6 and in genital segmentation.

Antennules short; 6-segmented in ♀, subchirocer and 7-segmented in ♂;posterior margin of segment 1 with small blunt process, that of segment 2 with distinct spinous process; with aesthetasc on segment 4 (♀) or 5 (♂) and as part of apical acrothek on distal segment; segment 6 of ♂ not particularly modified; proximal aesthetasc fused to 1 seta. Antenna with 4 setae on exopod; allobasis with abexopodal seta. Mandible with biramous palp bearing discrete 1-segmented rami; basis with 1 lateral seta, exopod with 1, endopod with 3 apical setae. Maxillule with seta at base of exopod. Maxilla with 3 endites on syncoxa; endopod represented by 4 setae. Maxilliped moderately slender; with 3 setae on syncoxa; endopodal claw long and slender.

P1 with 2-segmented exopod bearing 5 setae on exp-2 and elongate endopod; enp-1 with inner seta, enp-2 with minute seta and long, slender claw. P2–P4 with 3-segmented exopods and 2-segmented endopods. P2 basis with normally developed outer spine. Outer spine of P4 enp-2 not very long. P3 endopod ♂ 3-segmented; enp-2 with inner seta and very long, slender, sigmoid apophysis. P3 exopod ♂ weakly modified with exp-3 being shorter than in ♀. Armature formula as follows:

	Exopod	Endopod	
P2	0.1.123	1.121	
P3	0.1.223	1.321	[♂: 1.1.220]
P4	0.1.223	1.221	

P5 ♀with separate rami; exopod large and elongate, with 6 setae/spines; baseoendopod well developed, with 5 setae/spines. P5 ♂ with trapezoid endopodal lobe bearing 2 long setae; exopod rectangular, with 1 inner, 1 outer and 2 apical setae/spines.

P6 ♀forming opercula closing off paired genital apertures; with 2 long setae. P6 ♂ asymmetrical; membranous flaps with 1 tiny seta.

TYPE AND ONLY SPECIES. *Archilaophonte maxima* Willen, 1995 [by monotypy].

TYPE LOCALITY. 72°52.3' S, 19°34.7' W, Weddell Sea, Antarctic; 495 m depth.

REMARKS. Willen (1995) described *A. maxima* in great detail; the slight sexual dimorphism illustrated for the P3 exopod was not mentioned in the text. The species is known from two localities in the Weddell Sea.

Genus *Applanola* gen. nov.

DIAGNOSIS. Laophontidae. Body strongly depressed and comparatively short; cephalothorax much wider than rest of body; posterolateral corners of ♀ genital double-somite and second abdominal somites laterally and backwardly produced. Integument of cephalothorax and body somites with dense pattern of spinules and setules. Rostrum very large, partly delimited at base. Four pairs of integumental cup-shaped pores present: anterodorsally on cephalothorax, near ventrolateral margins of cephalic shield, laterally on genital (♂) or genital double-somite (♀) and ventrally on caudal rami. Anal operculum spinulose. Caudal rami short, squarish.

Sexual dimorphism in body shape, antennule, P2–P4 exopods, P3 endopod, P5, P6 and in genital segmentation.

Antennules short; 6-segmented in ♀, subchirocer and 7-segmented in ♂; segments 1–2 without distinct processes; with aesthetasc on segment 4 (♀) or 5 (♂) and as part of apical acrothek on distal segment; segment 6 of ♂ with large bilobate outgrowth dorsally; proximal aesthetasc fused basally to 2 setae. Antenna with 4 setae on exopod; allobasis with abexopodal seta. Labrum with distal patch of long spinules. Mandible with elongate 1-segmented palp with 1 lateral and 3 apical setae. Maxillule with elongate defined exopod. Maxilla with 3 endites on syncoxa; endopod represented by 4 setae. Maxilliped large and robust; with 2 setae on syncoxa; endopodal claw relatively short.

P1 with 2-segmented exopod bearing 5 setae on exp-2 and robust endopod; enp-1 without inner seta, enp-2 with minute seta and short, strongly curved claw. P2–P4 with 3-segmented exopods and 2-segmented endopods. P2 basis with very long outer spine. Outer spine of P4 enp-2 very long. P3 endopod ♂ 3-segmented; enp-2 with inner seta and outer dentate apophysis. P3 exopod ♂ strongly developed with modified outer and distal spines on exp-3; exopods of P2 and P4 similar in size to ♀but with stronger ornamentation on outer spines. Armature formula as follows:

	Exopod	Endopod	
P2	0.1.123	1.220	
P3	0.1.223	1.321	[♂: 1.1.220]
P4	0.1.223	1.221	

P5 ♀ with separate rami; exopod elongate, with 6 setae/spines; baseoendopod slightly developed, with 4 setae/spines. P5 ♂ without endopodal lobe; exopod short, with 1 inner, 2 apical and 2 outer setae/spines.

P6 ♀forming opercula closing off paired genital apertures; with one seta and 2 small processes at outer corner. P6 ♂ asymmetrical; membranous flaps without armature.

TYPE AND ONLY SPECIES. *Laophonte hirsuta* Thompson & A. Scott, 1903 = *Applanola hirsuta* (Thompson & A. Scott, 1903) comb. nov.

ETYMOLOGY. The generic name is derived from the Latin *ad* (to) and *planatus* (flattened), and alludes to the dorsoventrally depressed body. Gender: feminine.

Applanola hirsuta (Thompson & A. Scott, 1903) comb. nov.

Laophonte hirsuta Thompson & A. Scott, 1903
Esola hirsuta (Thompson & A. Scott, 1903): Lang (1948)

Thompson & A. Scott (1903) described *Laophonte hirsuta* from washings of pearl oysters and other unidentified invertebrates dredged in the Gulf of Manaar, Sri Lanka. A. Scott (1909) reported the species from 1595 m in the Banda Sea (Indonesia) but this record is almost certainly the result of contamination by a shallow water sample (Lang, 1948; Lee & Huys, 1999). The unknown male was described by Gurney (1927) from Port Taufiq in the Suez Canal. Por's (1964*b*) records from Haifa Bay and off the coast of Caesarea are likely the result of Lessepsian migration. Both Krishnaswamy (1957) and Krishna Murty (1983) reported the species from the Bay of Bengal. Krishnaswamy collected adults and developmental stages from sponges taken off the Krusadai Islands. Krishna Murty reported some occasional specimens in algal washings from the Visakhapatnam coast. The only other record outside the Indo-Pacific is that by Pesta (1916) from São Tomé in the Gulf of Guinea. Lang (1944, 1948) placed the species in the *longicauda*-group of *Esola*.

TYPE LOCALITY. Muttuvaratu, Sri Lanka; washings of pearl oysters and other dredged invertebrates.

MATERIAL EXAMINED. Cambridge Suez Canal Expedition 1924; Port Taufiq (Egypt): 1 ♀ dissected on 14 slides (BMNH 1999.982), 1 ♂ dissected on 11 slides (BMNH 1999.983); 3 ♀♀ (1 damaged), 2 ♂♂ and 1 copepodid V ♂ in alcohol (BMNH 1928.4.2.111).

REDESCRIPTION.

FEMALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 664 µm (n=3; range: 650–690 µm). Maximum width (281 µm) measured at posterior margin of cephalothorax.

Body very dorsoventrally depressed, covered with dense pattern of minute spinules dorsally (Fig. 30A). Cephalothorax much wider than free somites, posterolateral angles backwardly produced; with paired cup-shaped pores both anterodorsally and anteroventrally on either side of rostrum (arrowed in Fig. 15A–B and 30A–B), anterodorsal set partly closed off by fringe of setular extensions. Posterior margin of cephalothorax and all body somites with row of long spinules dorsally and laterally. Ventrolateral areas of cephalic shield and pleurotergites of first two pedigerous somites with long spinules and setules (Fig. 31B; ventral surface with distinct vent-pore at level of mandibles (Fig. 31B). Pleurotergite of P5-bearing somite wide.

Genital double-somite (Fig. 17A–B) only slightly narrower than pedigerous somites (Fig. 15A); original segmentation marked by bilateral constriction and dorsal transverse spinule row; anterior (= genital) half with large cup-shaped pores laterally (Fig. 29A), each partly closed off by fringe of setular extensions (Fig. 29B–C); posterior half with backwardly directed lobate extensions bearing spinular tuft (Fig. 29A); ventral surface without spinular ornamentation except for spinule row around posterior margin; genital field located near anterior margin. Sixth legs (Fig. 17C) forming well developed opercula closing off paired genital apertures; each with naked seta and 2 small processes at outer corner; inner corner produced into paired, medially directed, spinous processes.

Postgenital somites with spinules around ventral hind margin; second abdominal somite with posteriorly directed lateral angles, bearing spinular tuft; penultimate and anal somites distinctly narrower. Anal somite with paired oblique spinule rows on ventral surface; anal operculum spinulose.

Caudal rami (Fig. 15A, C) widely separated; shorter than wide; inner margin with medial protrusion; ventral surface with 2 spinule rows and large slit-like pore (arrowed in Figs. 15C; 30C) connected with spacious subsurface duct, extending into anal somite; entrance to pore with fine setules (Fig. 30D); dorsal surface with minute spinules; setae I–III all well developed, naked and closely set; setae IV and V pinnate and with fracture planes, seta V twice as long as seta IV; setae VI–VII naked.

Rostrum (Fig. 15A) large, rounded anteriorly; partly delimited at base by transverse surface suture (Fig. 30A); with paired sensillae anteriorly.

Antennule (Figs 15A; 16A) short, 6-segmented, without processes on segments 1–2. Segment 1 with dorsal spinular patch. Armature formula: 1-[1 pinnate], 2-[4 + 4 pinnate], 3-[2 + 2 pinnate], 4-[(2 + ae)], 5-[1], 6-[6 + 3 pinnate + acrothek]. Acrothek consisting of aesthetasc and 2 naked setae; set on apical pedestal.

Antenna (Fig. 16B) with well developed exopod bearing 2 lateral and 2 apical pinnate elements. Allobasis with pinnate abexopodal seta accompanied by setular patch. Endopod with lateral armature consisting of 2 spines and 1 seta; distal armature consisting of 2 unipinnate spines and 3 geniculate setae (outermost shortest and fused basally to setule).

Labrum with elaborate ornamentation around distal margin (Fig. 20E) but without spinules or scales on anterior face (Fig. 29D).

Mandible (Fig. 16C) with elongate gnathobase and long 1-segmented palp (Fig. 31B) probably representing fused basis and endopod; with 1 lateral and 3 distal pinnate setae.

Paragnaths densely hirsute lobes as in Fig. 20D.

Maxillule (Fig. 16D) with well developed praecoxa bearing 1 seta on anterior surface and 8 elements around distal margin. Coxal endite with 2 setae, basal endite with 1 spine and 2 setae. Exopod an elongate segment with 2 distal setae; endopod incorporated into basis, represented by 2 setae.

Maxilla (Fig. 20F). Syncoxa with long coarse spinules around outer margin; with 3 endites; praecoxal endite small and unisetose; middle endite drawn out into pinnate claw, with 2 setae; distal endite with 3 elements. Allobasis produced into strong curved claw; accessory armature consisting of 1 spine and 1 seta. Endopod a minute segment with 4 setae of different lengths.

Maxilliped (Fig. 17D) compact, with relatively short basis and endopodal claw. Syncoxa with 2 pinnate setae. Basis with spinular ornamentation as figured. Endopod represented by unipinnate claw bearing 1 accessory seta and tube-pore at base.

P1 (Fig. 19E) with narrow coxa and basis. Basis with pinnate seta on anterior surface and along outer margin. Exopod 2-segmented, small compared to endopod; exp-1 with pinnate outer seta; exp-2 with 3 distinctly pinnate outer setae and 2 geniculate setae apically. Endopod robust; enp-1 with long setules along inner margin; enp-2 with short, hook-like, naked claw and small accessory seta.

P2–P4 (Figs 17F; 18A, C) with 3-segmented exopods and 2-segmented endopods. P2 basis with very long, multipinnate outer spine; P3–P4 bases with bare outer seta. P2–P4 exp-2 with well developed inner seta. P2–P4 enp-1 small, with inner seta. P2 enp-2 without outer spine; outer spine of P3–P4 enp-2 very long. Tube-pore present near distal outer corner of P3–P4 enp-2. Armature formula as for genus.

P5 (Fig. 17E). Endopodal lobe reduced, not extending beyond proximal outer setae of exopod; with 1 short and 1 long pinnate seta apically, and 2 long widely separated setae along inner margin; anterior face with 2 tube-pores. Exopod elongate, produced apically into tubular extension bearing 1 bare seta; inner margin with 1, outer margin with 4 pinnate setae; inner seta much shorter than apical one. Both baseoendopod and exopod with elaborate ornamentation pattern as figured.

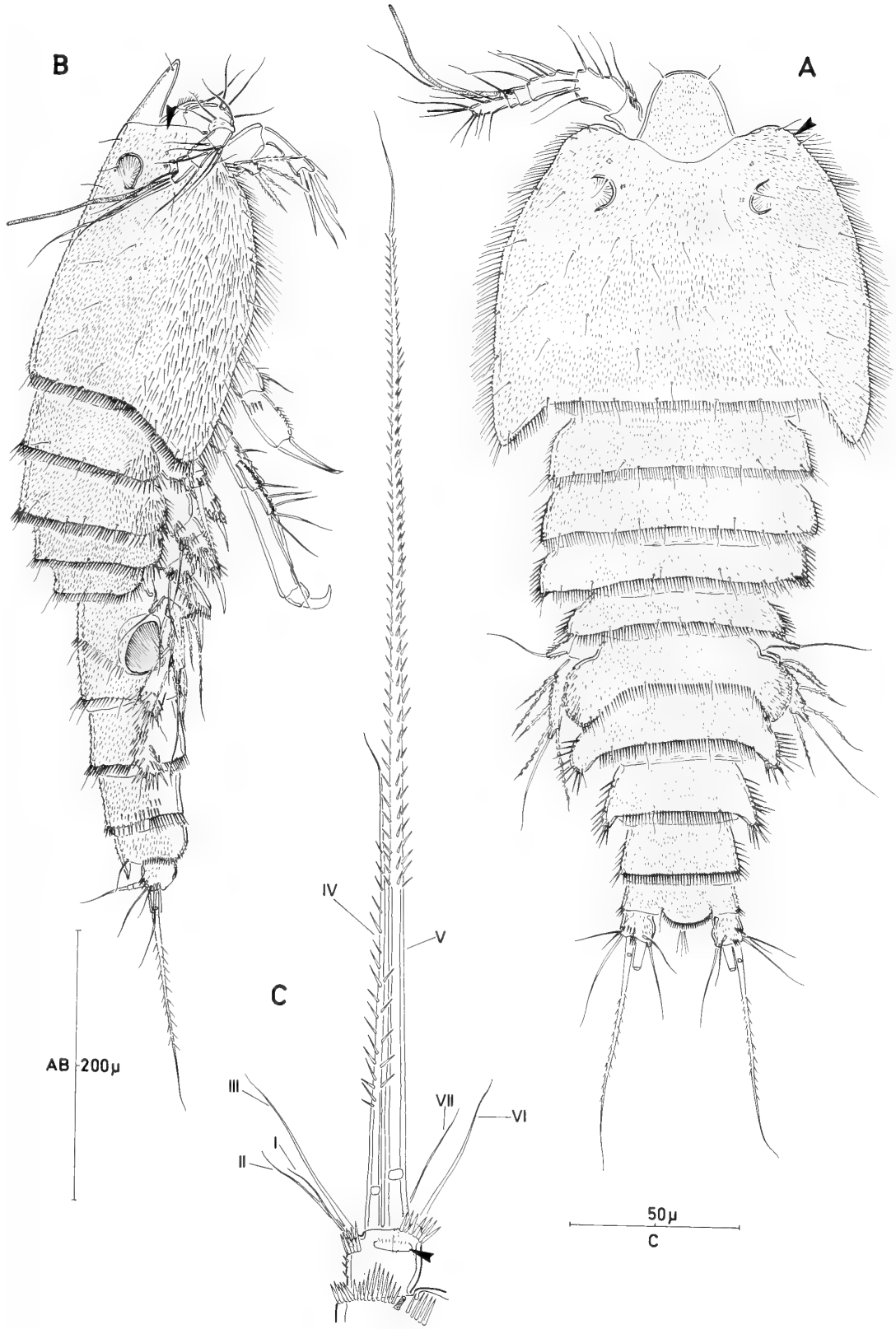

Fig. 15 *Applanola hirsuta* (Thompson & A. Scott, 1903) comb. nov. (♀). A, Habitus, dorsal; B, habitus, lateral; C, left caudal ramus, ventral. [Arrows indicating anteroventral cup-shaped pores in A–B, ventral one in C].

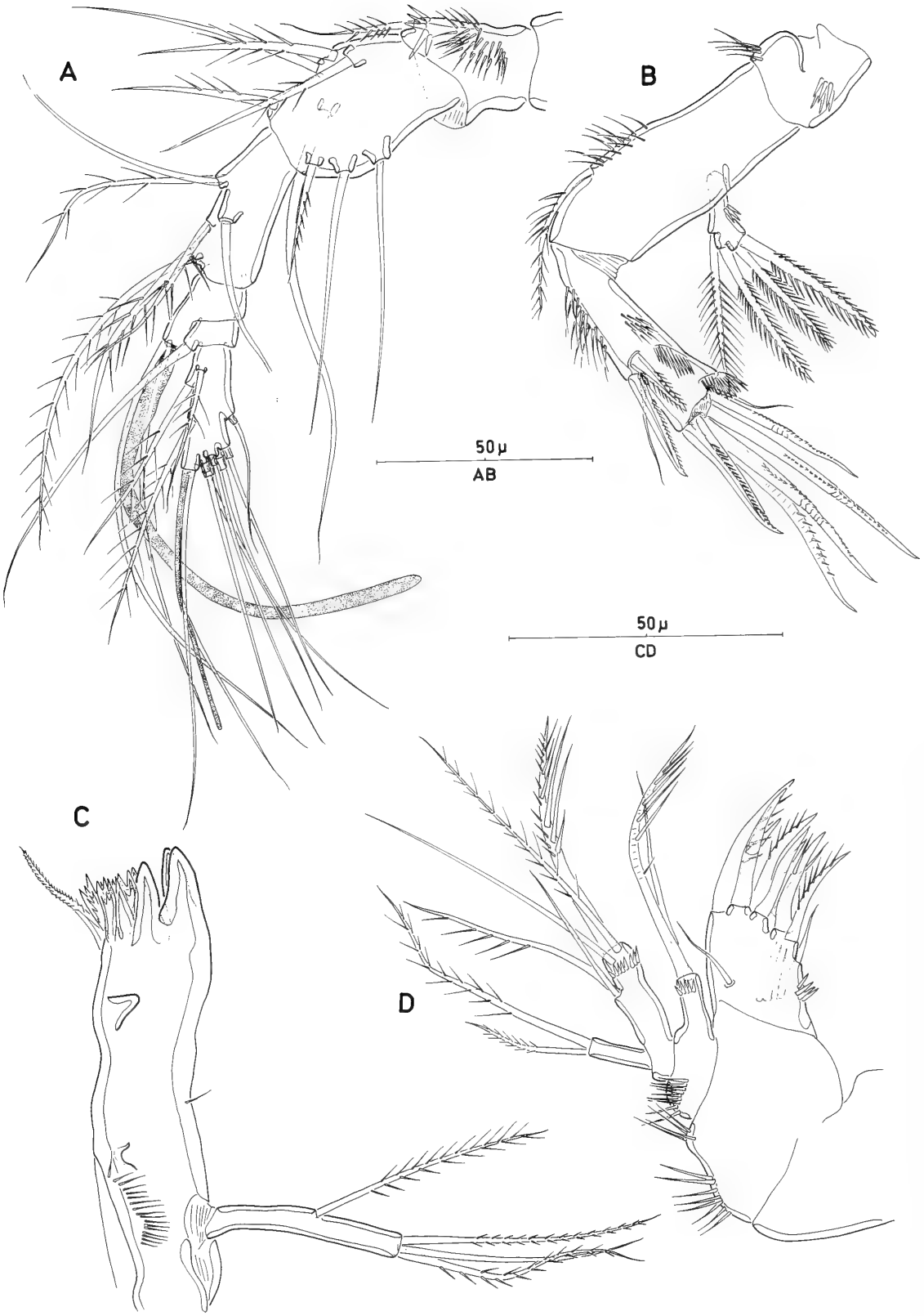

Fig. 16 *Applanola hirsuta* (Thompson & A. Scott, 1903) comb. nov. (♀). A, Antennule, dorsal; B, antenna; C, mandible; D, maxillule.

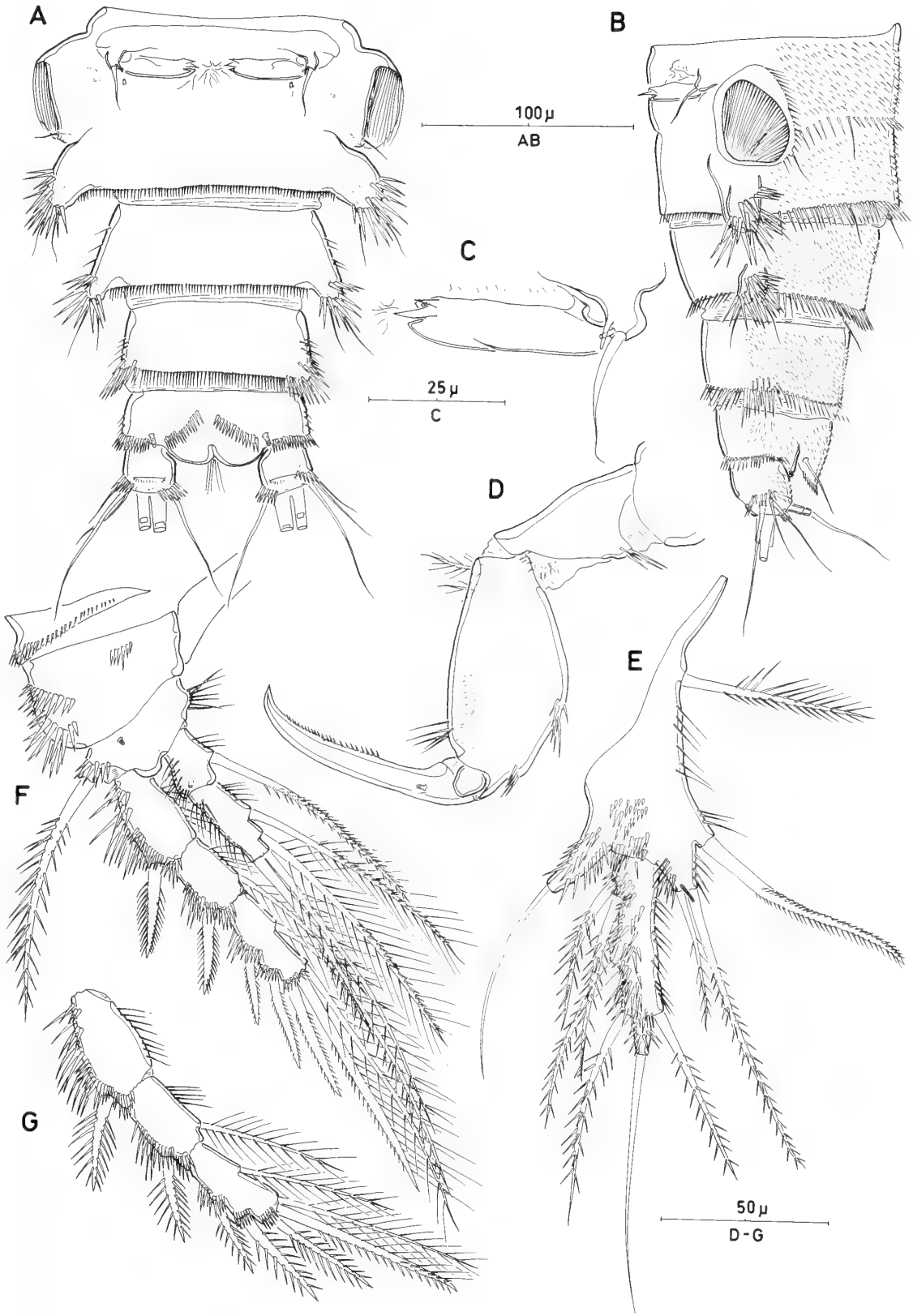

Fig. 17 *Applanola hirsuta* (Thompson & A. Scott, 1903) comb. nov. A, Urosome ♀ (excluding P5-bearing somite), ventral; B, same, lateral; C, left genital aperture ♀, ventral; D, maxilliped; E, P5 ♀, anterior; F, P2 ♀, anterior; G, P2 exopod ♂, anterior.

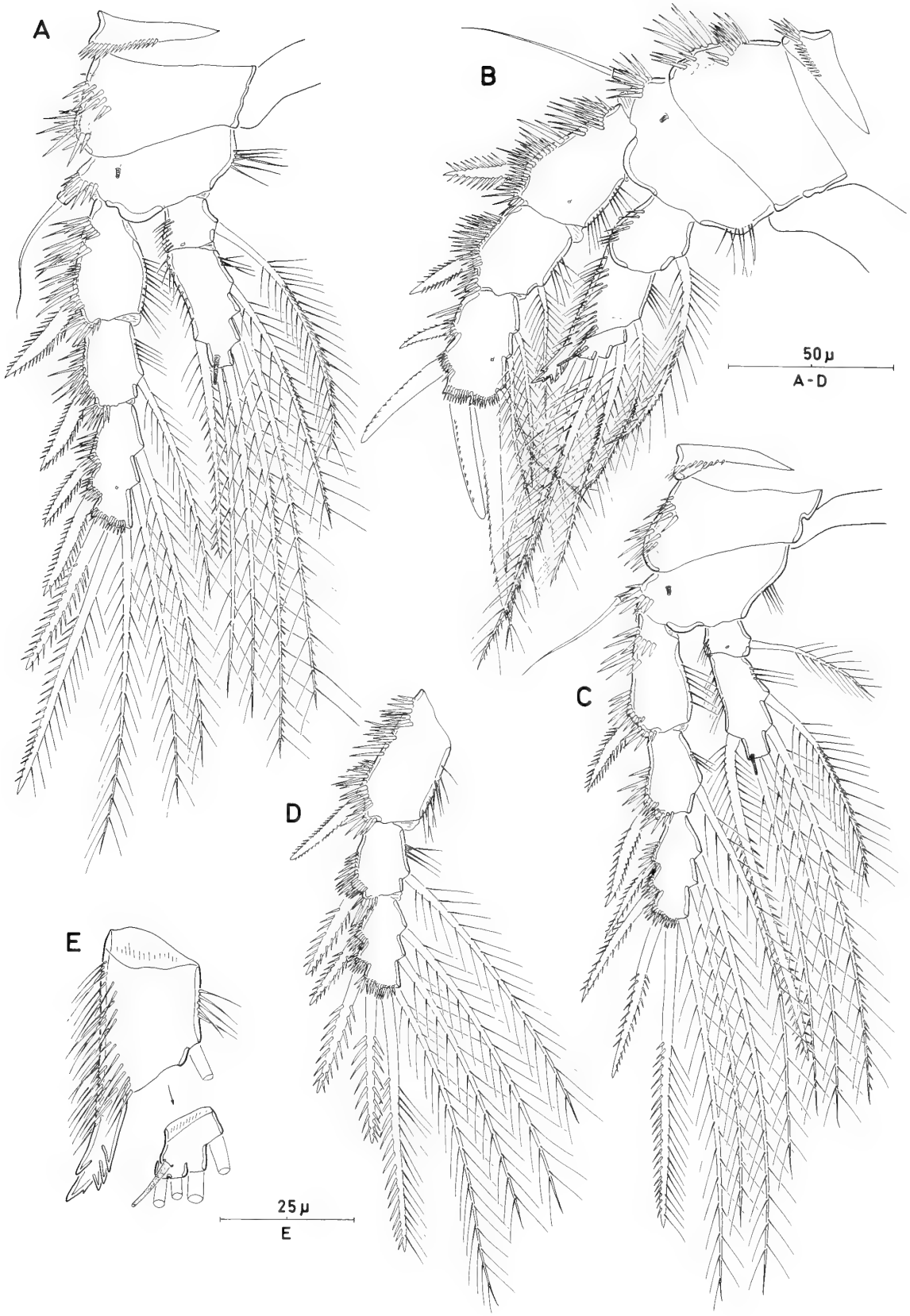

Fig. 18 *Applanola hirsuta* (Thompson & A. Scott, 1903) comb. nov. A, P3 ♀, anterior; B, P3 ♂, anterior; C, P4 ♀, anterior; D, P4 exopod ♂, anterior; E, P3 ♂, disarticulated enp-2 and -3, anterior.

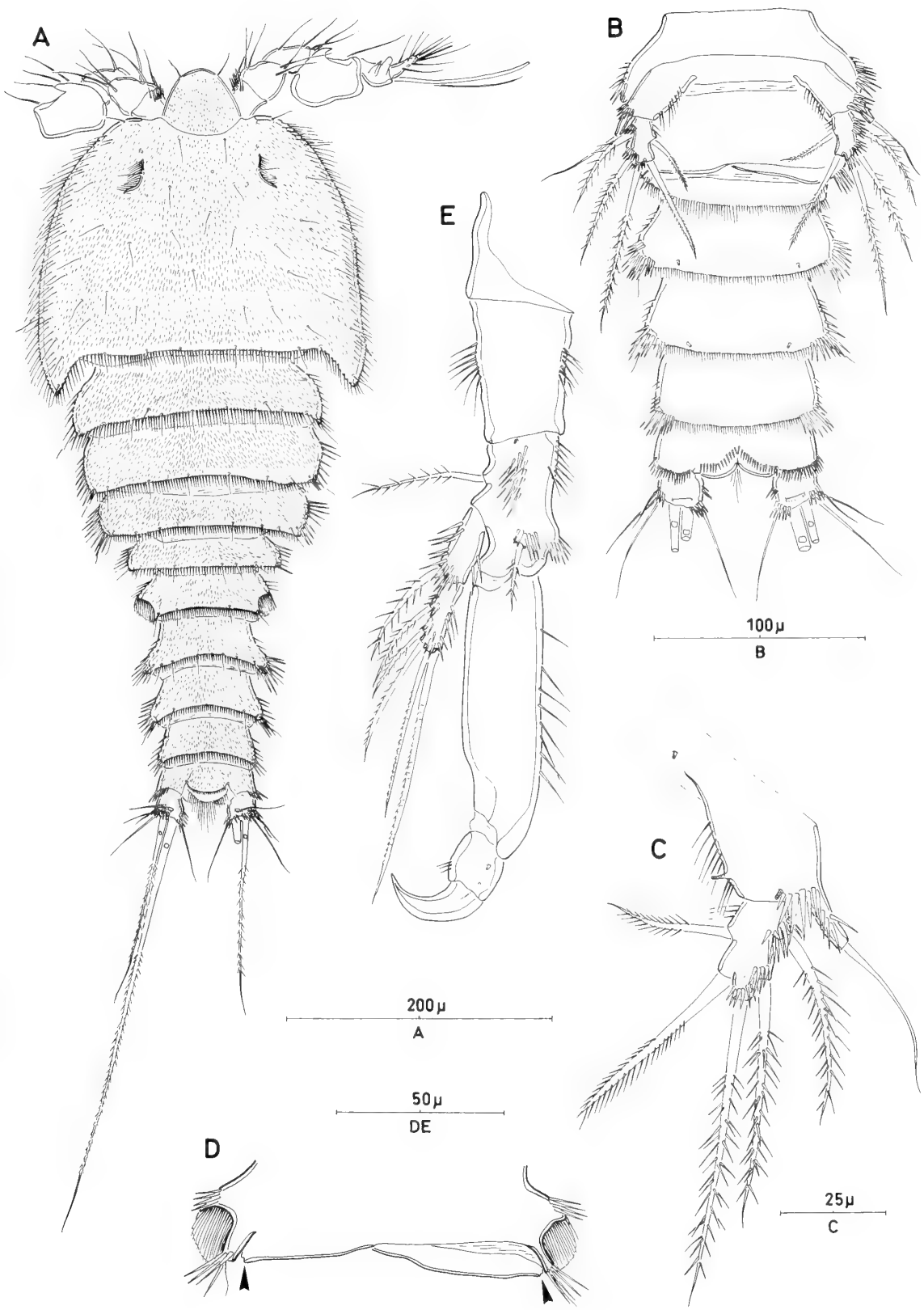

Fig. 19 *Applanola hirsuta* (Thompson & A. Scott, 1903) comb. nov. A, Habitus ♂, dorsal; B, urosome ♂, ventral; C, P5 ♂, anterior; D, genital apertures ♂, ventral [arrows indicating absence of armature]; E, P1, anterior.

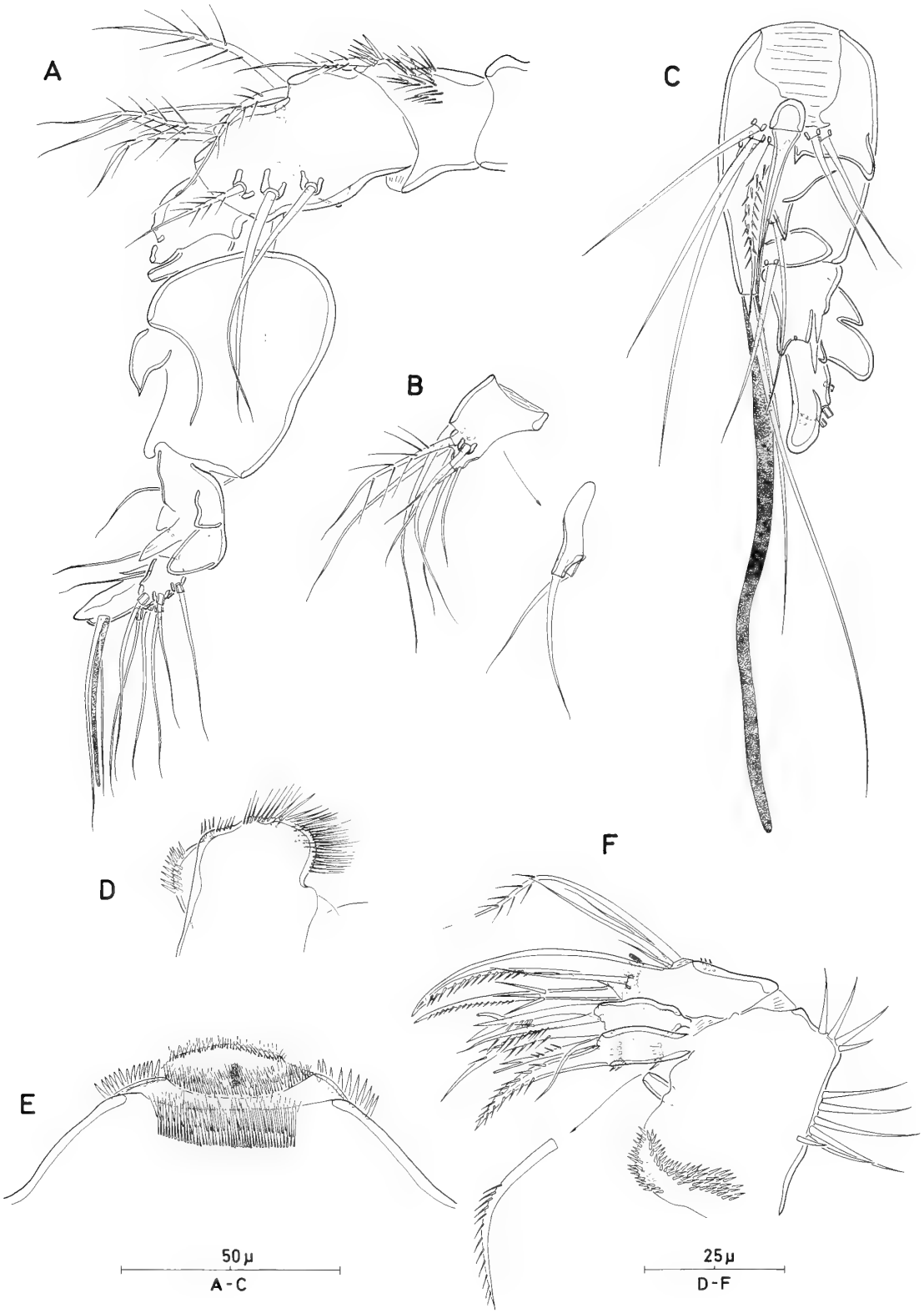

Fig. 20 *Applanola hirsuta* (Thompson & A. Scott, 1903) comb. nov. A, Antennule ♂, dorsal [armature of segments 4–5 omitted]; B, antennulary segments 3–4 of ♂, dorsal; C, antennulary segment 5 of ♂, anterior; D, left paragnath; E, labrum, anterior; F, maxilla.

MALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 581 µm (n=3, range 570–595 µm). Maximum width (248 µm) measured at posterior margin of cephalothorax. Length of ♂ copepodid V: 571 µm.

Body (Fig. 19A) very dorsoventrally depressed, covered with dense pattern of minute spinules as in ♀. Pattern of cup-shaped pores as in ♀ except for paired lateral pores present on genital somite. Cephalothorax much wider than free somites, posterolateral angles backwardly produced. Posterior margin of cephalothorax and all body somites with row of long spinules dorsally and laterally. Pedigerous somites decreasing in width posteriorly. Urosome (Fig. 19B) slender and narrow; pleurotergite of P5-bearing somite narrow; posterolateral corners of all urosomites with spinular tuft and posterior margin with spinules all around.

Genital somite with large cup-shaped pores laterally, each partly closed off by fringe of setular extensions (Fig. 19D); ventral surface without spinular ornamentation except for spinule row around posterior margin. Sixth legs represented by membranous flaps, one articulating and closing off left or right genital aperture; without armature at outer corner.

Antennule (Fig. 20A–C) 7-segmented, subchirocer, with geniculation between segments 5 and 6. Segment 1 with spinules/setules around anterior margin. Segment 2 with minute knob near dorsal posterior margin. Segment 4 minute, represented by incomplete sclerite. Segment 5 with spinous outgrowth on anterior margin, probably interlocking with similar processes on segment 6 (Fig. 20C); forming cylindrical process bearing long aesthetasc. Segment 6 with bilobed outgrowth on ventral surface near posterior margin. Distal portion of segment 7 elongate, displacing acrothek to position isolated from other armature. Armature formula: 1-[1 pinnate], 2-[4 + 5 pinnate], 3-[7 + 1 pinnate], 4-[2], 5-[7 + 1 pinnate + 1 spine + (2 + ae)], 6-[1 + 2 processes], 7-[7 + acrothek]. Apical acrothek consisting of aesthetasc and 2 bare setae.

P2 exopod (Fig. 17G). Outer spines of all segments with much longer pinnules than in ♀.

P3 (Fig. 18B, E). Exopod more robust than in ♀, slightly bent medially; outer spine of exp-1 with longer pinnules than in ♀; middle and distal outer spines and apical spine of exp-3 enlarged, with minute spinules; inner and inner apical setae reduced in length. Endopod 3-segmented; enp-1 larger than in ♀, densely setulose along outer margin; enp-2 with inner seta and short outer apophysis bearing small spinous processes along both inner and outer margin (Fig. 18E); enp-3 small, with long tube-pore and 4 setae.

P4 exopod (Fig. 18D). Proximal segment slightly more robust than in ♀. Outer spines of exp-2 and -3 stubby and somewhat enlarged; spinules typically longer than in ♀.

P5 (Fig. 19C) medially fused (Fig. 19B) positioned ventrolaterally. Baseoendopod without endopodal lobe; medial margin with setules and tube-pore; outer basal seta arising from short spinulose pedestal. Exopod free; with 3 multipinnate (1 apical, 2 outer) and 2 bipinnate (inner) setae, all well developed.

REMARKS. Thompson & A. Scott (1903) illustrated the female P5 with only 3 setae on the baseoendopod, a character included with hesitation by Lang (1948) in the diagnosis of the species. Re-examination revealed that the innermost seta on the endopodal lobe was overlooked. This seta is implanted medially at considerable distance from the others and was also missed by Norman (1911) in his description of *Laophonte bulbifera*. According to Lang's (1948) table XXIV the swimming leg armature formula is constant within the *longicauda*-group, including amongst other patterns the presence of the outer spine on P2 enp-2. One cannot but conclude that Lang (1948) must have overlooked Gurney's (1927) statement that this segment has 2 inner and 2 apical setae. The present redescription has revealed the sexual dimorphism of the exopods of P2 and P4, the presence and pattern of integumental cup-shaped pores, and the detailed morphology of the genital area in both sexes.

Krishnaswamy's (1957) redescription is grossly inadequate and potentially misleading. The ramus labelled 'P2 end ♂' is the male P3 endopod, his illustration of the female P2 is in fact based on the P3 and the real P2 is figured as the P7(!). In view of these inaccuracies the tabulated setal formula and the author's remarks on the generic placement of the species are best ignored. Krishnaswamy's description of the first copepodid is of similarly abominable quality.

Genus *Archesola* gen. nov.

This genus is proposed to include *Esola typhlops* and a number of closely related species. It is difficult to understand why Lang (1965) regarded *Laophonte lamellipes* Nicholls as most closely related to *E. typhlops*. This doubtful statement was based on the similarity in the long caudal rami and the erroneous fact that males of both species show no modifications on the P3 endopod. Noodt (1955) suggested a relationship with the *Laophonte setosa*-group but did not elaborate on this view. Re-examination of Nicholls' (1944) type material (BMNH 1947.10.6.23–27) revealed the true nature of the modified male P2 endopod, confirming close affinity with the genus *Paralaophonte* Lang.

DIAGNOSIS. Laophontidae. Body cylindrical or dorsoventrally depressed; posterolateral corners of ♀ genital double-somite and second abdominal somite laterally but not backwardly produced. Integument of cephalothorax and body somites with irregular pattern of minute surface lamellae. Rostrum large, partly delimited at base by surface furrow. Integumental cup-shaped pores absent on cephalothorax, genital (double-)somite and caudal rami. Anal operculum smooth or bordered with spinules. Caudal rami cylindrical and elongate; not sexually dimorphic.

Sexual dimorphism in antennule, P3 endopod, P5, P6 and in genital segmentation.

Antennules slender; 7-segmented in ♀, haplocer and 7-segmented in ♂; segments 1–2 without spinous processes along posterior margin; with aesthetasc on segment 4 (♀) or 5 (♂) and as part of apical acrothek on distal segment; segment 5 ♂ not swollen, without anterior outgrowth but with very long cylindrical pedestal for aesthetasc; proximal aesthetasc fused to 2 setae. Antenna with 4 setae on exopod; allobasis with abexopodal seta. Labrum with distal spinular ornamentation. Mandible with discrete 1-segmented exopod bearing 1 seta; endopod (3 setae) and basis (2 setae) incompletely fused. Maxillule with minute, defined exopod. Maxilla with 3 endites on syncoxa; endopod represented by 4 setae. Maxilliped slender; syncoxa with 2 setae; palmar margin naked; endopodal claw elongate.

P1 with 3-segmented exopod bearing 4 setae on exp-3 and elongate endopod; enp-1 with inner seta, enp-2 with minute seta and strong claw. P2–P4 with 3-segmented exopods and 2-segmented endopods. P2 basis with long outer spine. Outer spine of P2–P4 enp-2 setiform and very long in P3–P4. P3 endopod ♂ 2-segmented; enp-2 with 3 inner setae and short outer basally fused spine. Armature formula as follows:

Exopod	Endopod		
P2	0.1.123	1.221	
P3	0.1.223	1.321	[♀and ♂]
P4	0.1.223	1.221	

P5 ♀ with separate rami; exopod elongate, with 6 setae/spines; baseoendopod slightly developed, with 5 setae/spines. P5 ♂ without endopodal lobe; exopod short, with 2 outer, 1 apical and 2 inner elements (distal inner spiniform). Outer basal seta arising from long, articulating, cylindrical setophore in both sexes.

P6 ♀ forming opercula closing off paired genital apertures; with 2 small setae at outer corner. P6 ♂ asymmetrical; membranous flaps with 1 apical and 1 lateral seta.

TYPE SPECIES. *Laophonte typhlops* Sars, 1908 = *Archesola typhlops* (Sars, 1908) comb. nov.

OTHER SPECIES. *Laophonte longiremis* T. Scott, 1905 = *A. longiremis* (T. Scott, 1905); *A. hamondi* sp. nov.

SPECIES INQUIRENDAE. *Esola* sp. *sensu* Chislenko (1967); *Esola typhlops pontoica* Por, 1959 = *A. typhlops pontoica* (Por, 1959) comb. nov.

ETYMOLOGY. The Greek prefix *arche* alludes to the primitive position of the genus.

Archesola typhlops (Sars, 1908) comb. nov.

Laophonte typhlops Sars, 1908
Esola typhlops (Sars, 1908) Lang (1948)

TYPE LOCALITY. Flekkerö, south coast of Norway, 36 m depth.

MATERIAL EXAMINED.
(1) West Runton, Norfolk, England: 1 ♂ dissected on 8 slides (BMNH 1999.1079); collected among *Polyclinum* and *Morchellium* under rocks; leg. R. Hamond, September 1971;
(2) Frierfjord/Langesundfjord, Norway: 4 damaged ♀♀ (3 in alcohol: BMNH 1999.1081–1083; 1 dissected on 5 slides: BMNH 1999.1080); 99 m, mud, leg. R. Huys, 1985;
(3) Gullmar Fjord, Sweden: 1 ♀ in alcohol (NMNH 90955); 30 m, sand; leg. K. Lang, 08 July 1942.

REDESCRIPTION.

FEMALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 585 µm (n=4; range: 575–592 µm).

Body cylindrical, not dorsoventrally depressed, covered with dense pattern of minute surface ridges dorsally and laterally. Cephalothorax with almost parallel lateral margins in posterior two-thirds, without paired cup-shaped pores. Posterior margin of cephalothorax and all body somites with row of long setules dorsally and laterally. Posterior margin of urosomites with spinules all around (Fig. 23B); ventrolateral areas of cephalic shield and pleurotergites of pedigerous somites with longer setules. Pleurotergite of P5-bearing somite narrowest.

Genital double-somite (Fig. 23A) wide and dorsoventrally flattened; original segmentation marked by bilateral constriction and transverse surface ridge dorsally; without cup-shaped pores in anterior half; lateral lobes in both anterior and posterior halves with backwardly directed strong spinules; ventral surface without ornamentation except for spinules around hind margin and 2 pairs of medial tube-pores. Genital field located near anterior margin (Fig. 23A); copulatory pore minute. Sixth legs forming well developed opercula closing off paired genital apertures; each with 2 naked setae.

Anal somite (Fig. 23B) with coarse spinules on anal operculum.

Caudal rami (Figs. 23B; 24F; 31C–D) widely separated, cylindrical and slightly tapering posteriorly; without cup-shaped pores; about 4 times as long as wide; setae I–III closely set, I minute, II–III very long and thin; setae IV and V pinnate and with fracture planes, seta IV distinctly longer than caudal ramus; setae VI–VII naked. Vent-pore and small tube-pore present ventrally near insertion sites of setae I–III (Fig. 31C–D).

Rostrum as in ♂ (Fig. 22B); large, trapezoid with straight anterior margin; delimited at base by transverse surface suture; with paired sensillae anteriorly and median tube-pore ventrally.

Antennule (Fig. 22A) slender, 7-segmented; segments 1–2 without processes. Segment 1 with spinules around anterior margin; segment 4 forming large cylindrical pedestal ventrally. Armature formula: 1-[1], 2-[8 + 1 pinnate], 3-[6], 4-[(2 + ae)], 5-[1], 6-[2], 7-[7 + acrothek]. Aesthetasc on segment 4 fused basally to 2 setae. Acrothek consisting of aesthetasc and 2 naked setae; set on small tubercle.

Antenna (Fig. 23C) with elongate exopod bearing 2 lateral and 2 apical pinnate setae, and a longitudinal row of coarse spinules. Coxa with few large spinules, allobasis with pinnate abexopodal seta. Endopod with lateral armature consisting of 1 seta, 1 large and 1 small spine; distal armature consisting of 2 unipinnate spines and 3 geniculate setae (outermost fused basally to small seta).

Labrum as in *A. hirsuta*.

Mandible (Fig. 25A) with short gnathobase and small bilobed palp representing partially fused basis and endopod; with 2 lateral (basal) pinnate setae and 3 distal (endopodal) setae; exopod represented by minute segment bearing 1 apical seta.

Maxillule (Fig. 25B) and maxilla as in *E. bulligera*.

Maxilliped (Fig.23D) slender, with elongate basis and endopodal claw. Syncoxa with 2 pinnate setae. Basis with naked palmar margin and setules around outer margin. Endopod represented by very long, naked claw bearing 1 accessory seta at base.

P1 (Fig. 22F) with sparse ornamentation on coxa and basis. Basis with pinnate seta on anterior surface and along outer margin. Exopod 3-segmented, well developed; exp-1 with long pinnate outer spine; exp-2 with 1 naked outer spine; exp-3 with 2 unipinnate lateral setae and 2 geniculate setae apically. Endopod long and slender; enp-1 with long setules along inner margin and shorter spinules along outer margin, with thin inner seta in distal quarter (arrowed in Fig. 22F); enp-2 about twice as long as wide, with strong minutely pinnate claw and small accessory seta.

P2–P4 as in Sars (1908). P3 enp-2 (Fig. 24B) with setiform outer spine (arrowed). Armature formula typical for genus.

P5 (Fig. 23E). Endopodal lobe well developed, not extending beyond insertion sites of proximal outer setae of exopod; with distinctly stepped inner margin bearing 2 strong spines and 1 long distal seta (extending beyond apex of exopod); apex with 2 setae, outer one about twice length of inner one; tube-pores present near apical setae and proximal to innermost spine; outer basal seta inserting on cylindrical articulating setophore. Exopod narrow and elongate, produced apically into long tubular extension bearing 1 bare seta; inner margin with 1, outer margin with 1 naked and 3 pinnate setae. Both baseoendopod and exopod with elaborate ornamentation pattern as figured.

MALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 475 µm. Sexual dimorphism in antennule, P3 endopod, P5, P6 and genital segmentation.

Antennule (Fig. 22B–E) 7-segmented, haplocer, with geniculation between segments 5 and 6. Segment 1 with spinules/setules around anterior margin; segment 2 longest; segment 4 minute, represented by incomplete sclerite (Fig. 22C). Segment 5 with large process proximally but forming long cylindrical pedestal distally (Fig. 22D). Segment 6 with 3 spinous processes along anterior margin (Fig. 22E). Distal portion of segment 7 elongated, displacing acrothek to position isolated from other armature (Fig. 22E). Armature formula:

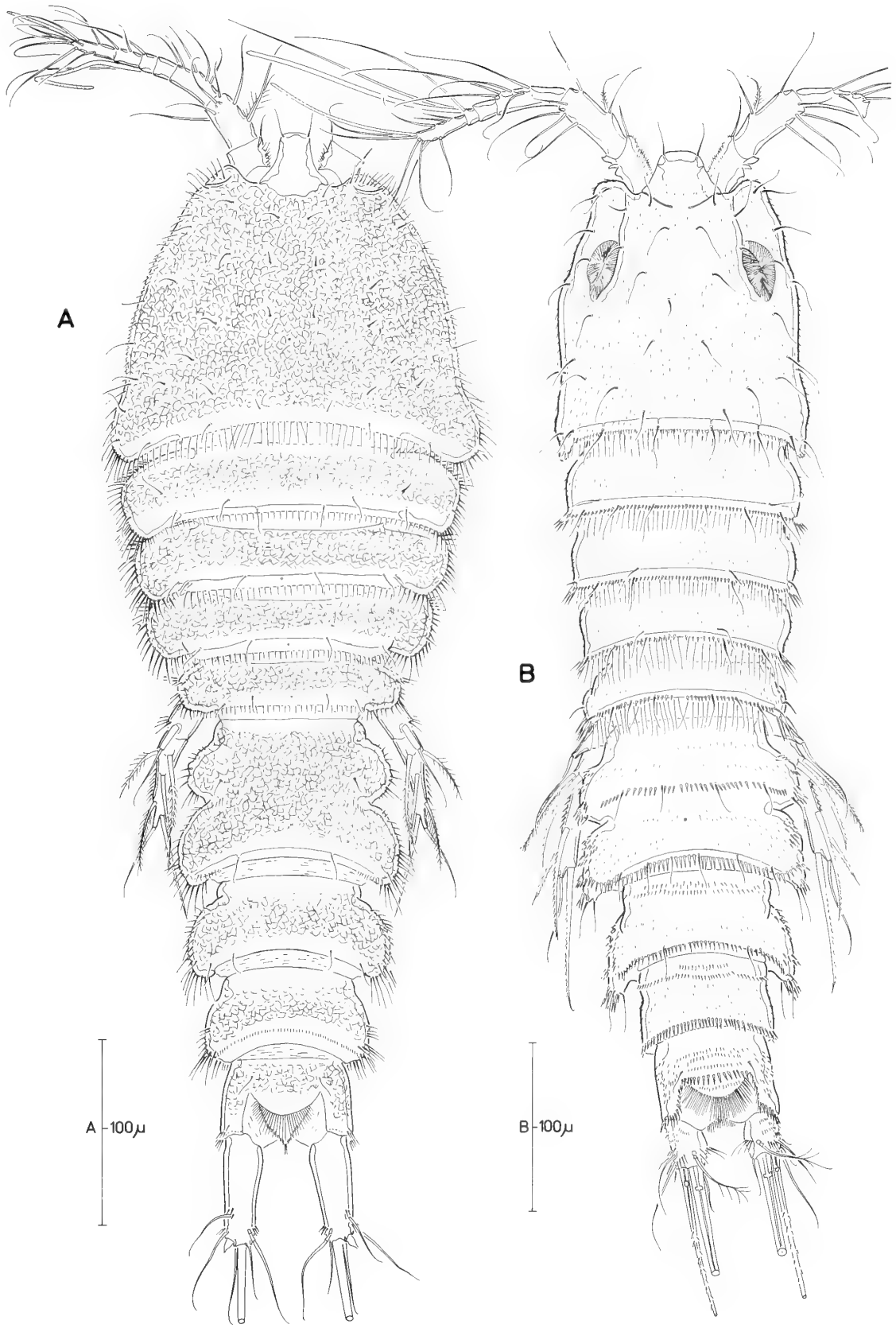

Fig. 21 *Archesola hamondi* gen. et sp. nov. A, Habitus ♀, dorsal. *Corbulaseta bulligera* (Farran, 1913) comb. nov. B, habitus ♀, dorsal.

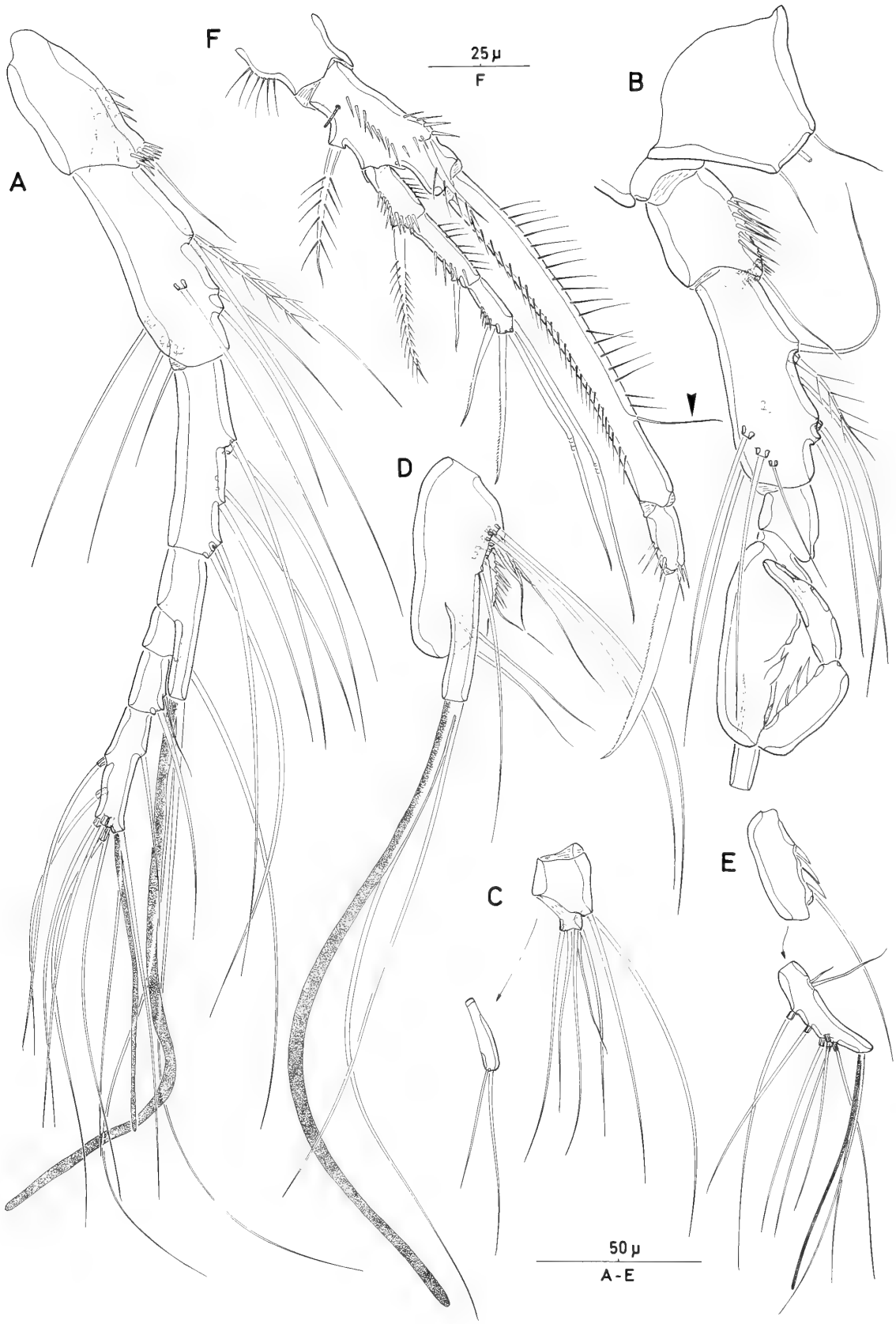

Fig. 22 *Archesola typhlops* (Sars, 1908) comb. nov. A, Antennule ♀, ventral; B, rostrum and antennule ♂, dorsal [armature of segments 3–7 omitted]; C, antennulary segments 3–4 ♂; D, antennulary segment 5 ♂; E, antennulary segments 6–7 ♂; F, P1 ♀, anterior [inner seta on enp-2 arrowed].

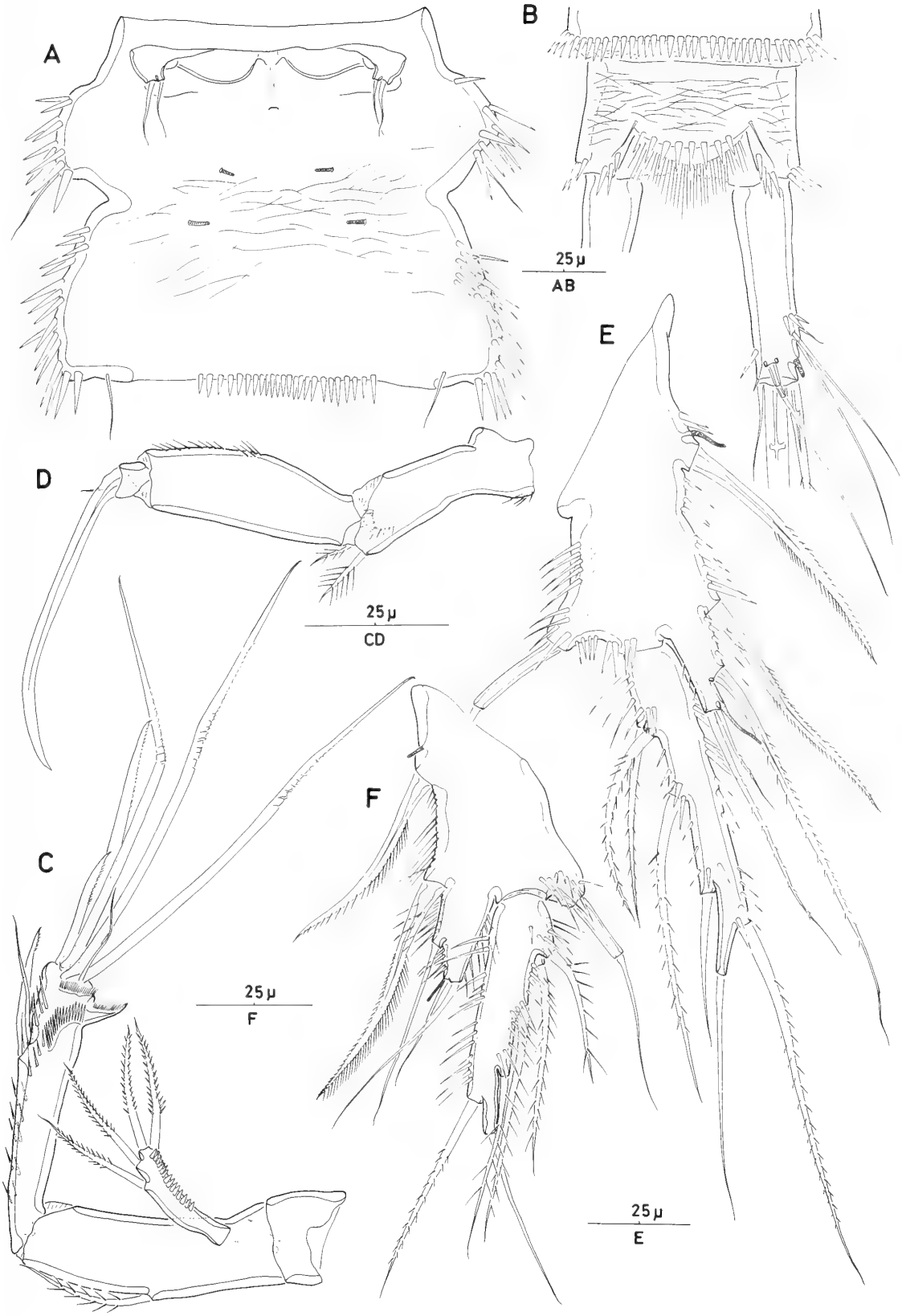

Fig. 23 *Archesola typhlops* (Sars, 1908) comb. nov. (♀). A, Genital double-somite, ventral; B, anal somite and right caudal ramus, dorsal; C, antenna; D, maxilliped; E, P5, anterior. *Archesola hamondi* gen. et sp. nov. F, P5 ♀, anterior.

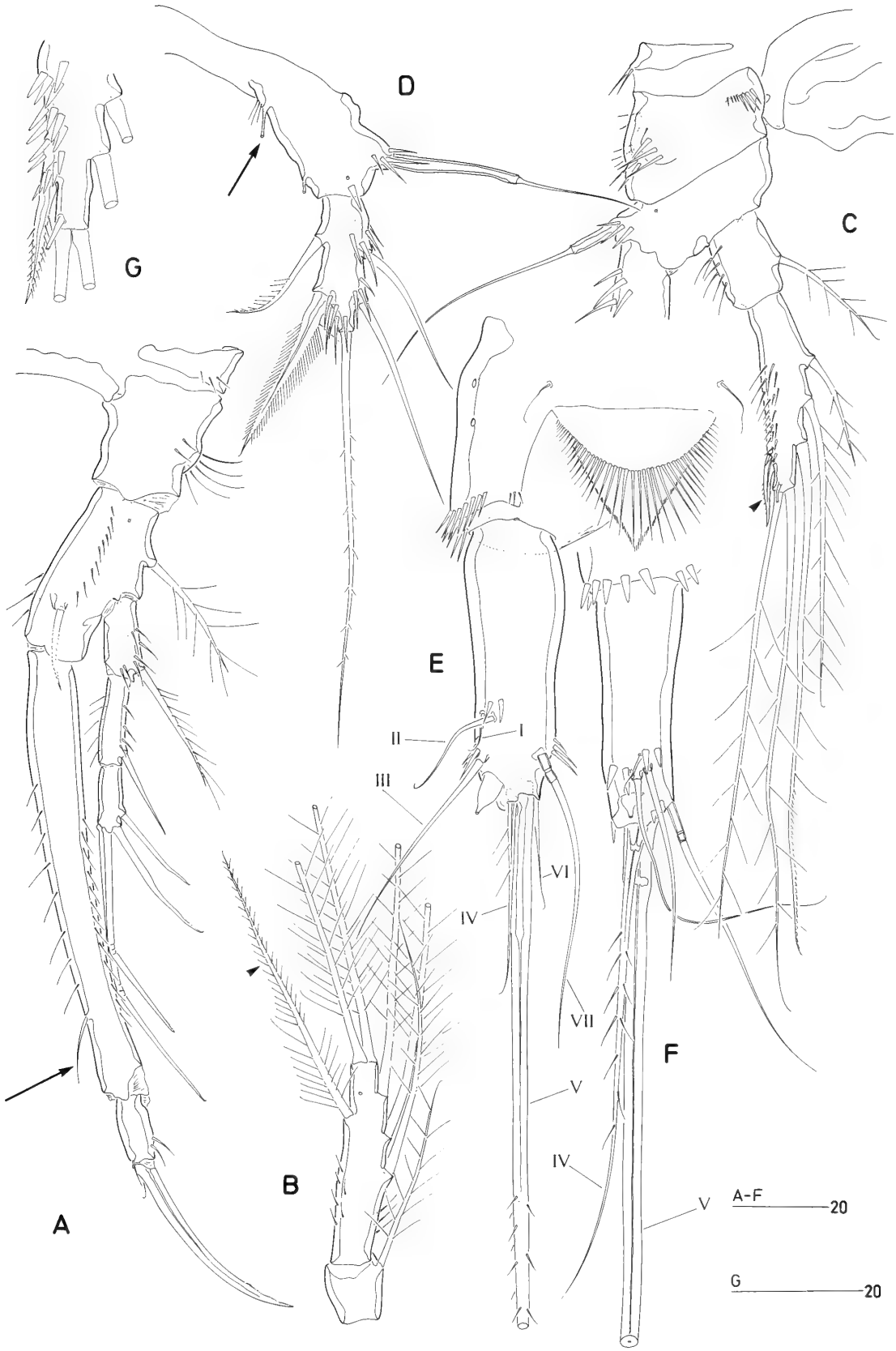

Fig. 24 *Archesola hamondi* gen. et sp. nov. (♀). A, P1, anterior [inner seta on enp-2 arrowed]; E, anal somite and left caudal ramus, dorsal. *Archesola typhlops* (Sars, 1908) comb. nov. B, P3 endopod ♀, anterior [elongate outer spine arrowed]; C, P3 protopod and endopod ♂, anterior [apophysis arrowed]; D, right P5 ♂, anterior [endopodal tube-pore arrowed]; F, left caudal ramus, lateral; G, P3 enp-2 ♂.

1-[1], 2-[8 + 1 pinnate], 3-[7], 4-[2], 5-[8 + 1 pinnate spine + 1 spinous process + (2 + ae)], 6-[1 + 3 processes], 7-[8 + acrothek]. Apical acrothek consisting of aesthetasc and 2 bare setae.

P3 endopod (Fig. 24C, G) 2-segmented; enp-1 as in ♀; enp-2 with 3 inner setae (proximal one being distinctly shorter than in ♀), 2 long apical setae and short pinnate outer spine (fused basally to segment); tube-pore present near outer apical seta.

P5 (Fig. 24D) medially fused, positioned ventrolaterally. Baseoendopod without endopodal lobe or armature; medial margin with few setules and 2 tube-pores (longest arrowed); outer basal seta arising from long, articulating, cylindrical setophore. Exopod free, rectangular; with 1 long pinnate seta apically; inner margin proximal seta and distal bipinnate spine; outer margin with 2 bare setae.

Sixth legs represented by well developed opercula, one articulating and closing off left or right genital aperture; each produced into cylindrical process bearing 1 lateral and 1 apical seta.

REMARKS. Drzycimski (1969) corrected two major errors in Sars' (1908) description. First, he pointed out the presence of the thin inner seta on the proximal endopod segment of P1. Within the Laophontidae this element is further only found in *Archilaophonte maxima*. Secondly, Drzycimski remarked that the inner seta on the baseoendopod of the male P5 is not well developed as in Sars' illustration but greatly reduced. In reality, Drzycimski referred to the short hyaline tube-pore located closely to the exopod whereas in Sars' (1908) illustration it was the longer medial tube-pore (arrowed in Fig. 24D) which was misinterpreted as a genuine seta. One character that has traditionally been used to differentiate *A. typhlops* from *A. longiremis* is the setation of the female P5 exopod. This distinction is invalid since it is based on the erroneously reported absence of the proximal surface seta in Sars' description of *A. typhlops*. The same error also served to distinguish *E. typhlops pontoica* from the type population (Por, 1959, 1964*a*).

Reliable records of *A. typhlops* include Flekkerö (Sars, 1908), Bergen (Drzycimski, 1969) and Frierfjord/Langesundfjord (this account) in Norway, Gullmar Fjord (Lang, 1948) and the Isle of Bonden (Por, 1964*a*) in Sweden, and Norfolk in England (this account). The Scottish records from the River Ythan (Aberdeenshire) by Hockin & Ollason (1981) and Hockin (1982*a–b*, 1984) and that from Newbiggin (Northumberland) by Moore (1973) may be based on *A. longiremis*.

Archesola longiremis (T. Scott, 1905) comb. nov.

Laophonte longiremis T. Scott, 1905
Esola longiremis (T. Scott, 1905) Lang (1948)

TYPE LOCALITY. Granton, Firth of Forth, Scotland; old quarry opening to the sea (T. Scott, 1905, 1906).

TYPE MATERIAL. T. Scott (1905) recorded an unspecified number of females; this material has not been deposited in any of the British museums (London, Newcastle-upon-Tyne, Edinburgh) and is therefore almost certainly lost.

REMARKS. This species is very close to *A. typhlops* and can be differentiated primarily by the shorter caudal rami (only twice as long as wide) and the smaller body size (0.6 mm). Lang (1948) pointed out that T. Scott's (1905) drawing of the P5 showed an aberrant setation on the endopodal lobe (total of 7 setae: 3 inner, 3 apical, 1 outer). The short apical seta is almost certainly the equivalent of the long tube-pore found in this position in *A. typhlops*, however, the presence of the supernumerary outer seta is more difficult to explain since no laophontoidean is known to display more than 5 elements on the endopodal lobe of the female P5 (Huys, 1990*a*; Huys & Lee, 1999). We suspect that this seta is the result of an observational error.

The species has never been figured again since T. Scott (1905) nor has the male been discovered. Wells (1961) illustrated some features of a male specimen from St. Martin's (Isles of Scilly) which he attributed to *E. longiremis*. The P5 shows only 3 setae on the exopod and the endopodal armature is represented by 2 fine setae (one of which likely to be a tube-pore). The P6 bears 2 strong setae but is not drawn out into a cylindrical process as in other species of the genus. These characters in conjunction with his statement that the male antennule is subchirocerate and the endopod 3-segmented clearly exclude the possibility that Wells was dealing with a species of *Archesola* or any other esolinid genus. Wells (1963) also recorded the species from Exmouth (Devon) but this record remains unconfirmed.

The genus *Archesola* consists of a complex of closely related species which can be differentiated primarily by morphometric characters, such as caudal ramus length and P1 exopod: endopod ratio, and various setal length differences on the P5. Coull's (1971) identification of *E. longiremis* from North Carolina suggests an amphi-Atlantic distribution for the genus *Archesola*, however, in view of the relatively subtle differences between congeners, the specific identity of his record remains to be confirmed.

Archesola hamondi sp. nov.

TYPE LOCALITY. 53°10.34'N 00°56.34'E; depth 12–13 m; fine sand with high silt and shell gravel content.

TYPE MATERIAL. This species is only known from the holotype ♀ (leg. R. Hamond; 06 May 1992) which unfortunately was accidentally destroyed before the description could be completed. The brief description below provides sufficient information to warrant the proposal of a new species.

ETYMOLOGY. This patronym is dedicated to Dr Richard Hamond who collected the holotype, in recognition of his significant contributions to laophontid systematics.

DESCRIPTION.

FEMALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 600 µm.

Body (Fig. 21A) dorsoventrally depressed and much wider than in *A. typhlops*; covered with dense pattern of minute surface lamellae dorsally and laterally. Cephalothorax bell-shaped, distinctly widening towards posterior margin; lateral and hind margins fringed with long setules; without paired cup-shaped pores. Setular fringes also present laterally on pedigerous somites and urosomites, sometimes forming tufts locally. Posterior margin of urosomites without distinct ornamentation dorsally except for penultimate somite bearing transverse row of fine spinules.

Genital double-somite (Fig. 21A) wide and dorsoventrally flattened; original segmentation marked by bilateral constriction only; without cup-shaped pores in anterior half; lateral lobes without backwardly directed strong spinules. Genital field as in *A. typhlops*.

Anal somite (Fig. 24E) with distinct setular fringe around anal opening; anal operculum completely bare; posterolateral margins with fine spinules.

Caudal rami (Fig. 24E) cylindrical and slightly swollen in anterior half; distinctly wider than in *A. typhlops*; about 3 times as long as wide. Seta II shorter and seta III posteriorly displaced compared to *A. typhlops*; seta IV reduced, lacking fracture planes, shorter than caudal ramus; seta V well developed, pinnate, without fracture planes; setae VI–VII naked. Large vent-pore present at outer subdistal corner.

Rostrum (Fig. 21A) longer than in *A. typhlops*; trapezoid with straight anterior and concave lateral margins; delimited at base by transverse surface suture; with paired sensillae anteriorly and median tube-pore ventrally.

Antennules to maxillipeds as in *A. typhlops*.

P1 (Fig. 24A) as in *A. typhlops* except for (a) basal pedestal bearing endopod wider, (b) inner seta on enp-1 inserting more distally, and (c) enp-1 about twice the length of exopod (distinctly shorter in type species). P2–P4 as in *A. typhlops*.

P5 (Fig. 23F). Endopodal lobe well developed, well extending beyond insertion sites of proximal outer setae of exopod; with distinctly stepped inner margin bearing 2 strong spines (more closely set than in *A. typhlops*) and 1 bare distal seta (not extending beyond apex of exopod); with 2 apical setae, outer one about 1.5 times length of inner one; tube-pores present near apical setae and proximal to innermost spine; outer basal seta inserting on cylindrical articulating setophore. Exopod elongate but distinctly shorter than in *A. typhlops*, produced apically into short tubular extension bearing 1 bare seta; inner margin with 1, outer margin with 4 pinnate setae. Both baseoendopod and exopod with elaborate ornamentation pattern as figured.

MALE. Unknown.

REMARKS. Differentiation of *A. typhlops* and *A. hamondi* is best achieved by comparison of the general body shape, caudal ramus outline and armature pattern, and ♀ P5 morphology and morphometry

Esola sp. *sensu* Chislenko (1967)

Chislenko illustrated a male which he obtained in *Laminaria saccharina* washings from the White Sea and identified as *Esola* sp. His drawings of the caudal ramus, P3 endopod and P1 leave little doubt that this species belongs to *Archesola* and is obviously close to *A. typhlops* and *A. longiremis*. The caudal ramus L:W ratio appears to be intermediate between the latter two species and the P1 endopod and exopod have slightly different proportions. Chislenko's male (0.35 mm) is smaller than those of *A. typhlops* recorded by Drzycimski (1969) from the Bergen area (0.45 mm) and our single male from West Runton (0.475 mm). The antennary exopod bearing the atypical number of 5 setae is obviously based on an aberrant specimen. His illustration of the P3 endopod lacks the proximal inner seta on the distal segment, its location being indicated by the distinct step in the inner margin. Finally, the small inner seta illustrated on the P5 baseoendopod is probably a tube-pore. The White Sea material identified by Brotskaya (1961) as *E. longiremis* is likely to be conspecific with this species, the true identity of which is as yet uncertain. Consequently, Chislenko's species is tentatively ranked *specues inquirenda* in *Archesola*.

Archesola typhlops pontoica (Por, 1959) comb. nov.

Esola typhlops pontoica Por, 1959

TYPE LOCALITY. Black Sea coast, Rumania.

TYPE MATERIAL. Dr Ileana Negoescu (Museum 'Grigore Antipa', Bucharest) informed us that the syntypes no longer exist.

REMARKS. Por (1959, 1964*b*) established this subspecies for 3 ♀♀ found at 61–69 m depth off the Rumanian coast, however it is doubtful whether his material deserves such status. The author discriminated the Black Sea population on the basis of the presence of 6 setae on the ♀P5 exopod (Sars (1908) erroneously figured only 5), the slightly shorter caudal rami and the incompletely 3-segmented P1 exopod (a feature displayed in only 1 specimen!). The most significant difference, not mentioned by Por, is found in the proportional lengths of the distal antennulary segments (segments 6 and 7 being of equal length). Examination of new material is necessary to resolve the identity of the Rumanian population; *E. typhlops pontoica* is considered here as *subspecies inquirenda*.

Genus *Corbulaseta* gen. nov.

The diagnosis below is based on Vervoort's (1964) redescription of *E. bulligera* and personal observations of Wells' (1970) material from Great Britain Rock, Isles of Scilly, and additional specimens collected from the Belgian North Sea coast by the senior author.

DIAGNOSIS. Laophontidae. Body cylindrical; posterolateral corners of ♀ genital double-somite and second abdominal somite laterally and backwardly produced. Integument of cephalothorax and body somites with dense pattern of spinules and setules. Rostrum large, partly delimited at base by incomplete surface furrow. Cephalothorax with one pair of large, anterodorsal cup-shaped pores; such pores absent on genital (double-)somite and caudal rami. Anal operculum spinulose. Caudal rami rectangular, short; not sexually dimorphic.

Sexual dimorphism in antennule, P3 endopod, P5, P6 and in genital segmentation.

Antennules slender; 6-segmented in ♀, subchirocer and 7-segmented in ♂; segment 1 with 1–2 minute processes along posterior margin; with aesthetasc on segment 4 (♀) or 5 (♂) and as part of apical acrothek on distal segment; segment 5 ♂ swollen, without anterior outgrowth; proximal aesthetasc fused basally to 2 setae. Antenna with 4 setae on exopod; allobasis with abexopodal seta. Labrum with distal spinular ornamentation. Mandible with 1-segmented palp; exopod and endopod represented by small tubercles bearing 1 and 3 setae, respectively; basis represented by 2 apical setae. Maxillule with minute, defined exopod. Maxilla with 3 endites on syncoxa; endopod represented by 3 setae. Maxilliped slender; syncoxa with 2 setae; entire palmar margin with long setules; endopodal claw elongate.

P1 with 2-segmented exopod bearing 5 setae on exp-2 and elongate endopod; enp-1 without inner seta, enp-2 with minute seta and long, slender claw. P2–P4 with 3-segmented exopods and 2-segmented endopods. P2 basis with short outer spine. Outer spine of P2–P4 enp-2 setiform and very long in P3-P4. P4 endopod modified in both sexes; distal inner seta proximally dilated, bearing enlarged spinules which enclose long secretory tube-pore arising from segment. P3 endopod ♂ 3-segmented; enp-2 with inner seta and short outer spinous apophysis. Armature formula as follows:

	Exopod	Endopod	
P2	0.1.123	1.221*	
P3	0.1.223	1.321	[♂: 1.1.220]
P4	0.1.223	0.221	

*: or 1.220 in Vervoort's (1962) ♀ specimen of *E. bulligera* from New Caledonia.

P5 ♀ with separate rami; exopod elongate, with 6 setae/spines; baseoendopod slightly developed, with 4 setae/spines. P5 ♂ without endopodal lobe; exopod short, with 1 inner, 2 apical and 2 outer setae/spines.

P6 ♀ forming opercula closing off paired genital apertures; with 2 small setae at outer corner. P6 ♂ asymmetrical; membranous flaps with 1 long and 1 minute seta.

TYPE AND ONLY SPECIES. *Laophonte bulligera* Farran, 1913 = *Corbulaseta bulligera* (Farran, 1913) comb. nov.

ETYMOLOGY. The generic name is derived from the Latin *corbula* (little basket) and *seta* (bristle) and refers to the modified distal inner seta of P4 enp-2, the proximal setules of which form a trapping basket typically enclosing a secrete bolus.

Corbulaseta bulligera (Farran, 1913) comb. nov.

Laophonte bulligera Farran, 1913
Esola bulligera (Farran, 1913) Lang (1948)
Laophonte rosei Monard, 1926
Laophonte Rosei Monard, 1926: Monard (1928)
Esola rosei (Monard, 1928) Lang (1948)

TYPE LOCALITY. Blacksod Bay, Co. Mayo (Ireland); 1.8–5.4 m depth

MATERIAL EXAMINED. Farran's (1913) type material is lost (J.M.C. Holmes, pers. comm).
(a) Isles of Scilly, Great Britain Rock: 1 ♀ in alcohol (BMNH 1967.10.31.76); coll. University of London Sub-Aqua Expedition 1966; det. J.B.J. Wells;
(b) Belgium, North Sea coast, 51°30"N 2°00"E: 1♀, 1 ♂; 08 April 1986, depth 14.1 m, sandy substrate; leg. R. Huys.

ADDITIONAL OBSERVATIONS.

FEMALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 570–590 µm. Body (Fig. 21B) cylindrical, slightly depressed; covered by irregular pattern of minute surface spinules. Cephalothorax widest, subrectangular; with pair of large cup-shaped pores anterodorsally (Fig. 25C); ventral pores absent; posterior margin and anterior half of ventral margin with setular fringe; posterior half of ventral margin bordered by tiny spinules; posterolateral corner produced forming distinctive lobate extension (Fig. 25C). Prosome gradually tapering posteriorly; all somites with dorsal transverse spinular row and setular fringe around hind margin.

Genital double-somite dorsoventrally depressed; original segmentation marked by bilateral constriction and dorsal transverse spinular row set on surface ridge; ventral surface without conspicuous ornamentation; cup-shaped pores absent. Genital aperture closed off by sixth legs bearing 1 naked seta. Posterolateral corners of second abdominal somite backwardly produced; remaining urosomites distinctly narrower. Ventral posterior margin of penultimate somite with medial fringe of fine setules flanked by strong spinules (decreasing in length ventrolaterally). All urosomites with spinules around dorsal posterior margin. Anal operculum spinulose.

Caudal rami short, slightly longer than wide; all setae arranged in posterior quarter; setae IV and V well developed, pinnate, with fracture planes; no conspicuous pores present.

Rostrum (Fig. 21B) trapezoid, delimited at base by incomplete surface suture; with 2 long sensilla apically and tube-pore ventrally.

Antennule 6-segmented; posterior margin of segment 1 with slight bulbous swelling but no real spinous processes; aesthetasc on segment 4 fused basally to 2 long setae; armature formula: 1-[1], 2-[7 + 1 pinnate], 3-[6], 4-[(2 + ae)], 5-[1], 6-[9 + acrothek]; acrothek consisting of aesthetasc and 2 naked setae. Antennary exopod with strong pinnate outer apical spine and 3 pinnate setae. Labrum with sparse ornamentation resembling condition in *A. hirsuta*. Mandibular palp 1-segmented, with ancestral setation, i.e. 2 basal, 1 exopodal and 3 endopodal setae. Maxillule as in *E. bulbifera*, with endopod represented by 2 setae. Maxilla as in *E. bulbifera*. Maxilliped with 2 setae on syncoxa; palmar margin with long fine spinules; endopodal claw slender and longer than basis, with 1 accessory seta.

P1 as in Farran's (1913) description except for outer spine of exp-1 being longer and pinnate and proximal and middle outer spines of exp-2 distinctly shorter. P2 basis with bipinnate outer spine, P3–P4 bases with smooth outer seta. Outer spine of P3–P4 enp-2 very long and setiform (Fig. 25D).

P4 (Fig. 25D) with 2-segmented endopod; enp-1 short, without inner seta; enp-2 (Fig. 25E–F) highly distinctive: distal inner seta with dilated base bearing comb of long curved setules on both anterior and posterior outer margins; this ornamentation forming trapping basket enclosing large secrete bolus produced by long anterior surface tube-pore located near distal margin of enp-2.

P5 as in original description.

MALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 530 µm. Body more slender than in ♀; none of urosomites with backwardly produced posterolateral corners. Ventral posterior margin of postgenital (except anal) somites with median fringe of fine setules flanked by strong spinules.

Antennule subchirocerate; 7-segmented with geniculation between segments 5 and 6. Segment 1 without distinct processes, segment 5 without anterior outgrowth.

P3 endopod 3-segmented; very similar to that of *E. bulbifera* (Fig. 4D).

P5 without endopodal lobe; medial margin frimged with long spinules and 1 tube-pore; outer basal seta arising from short setophore. Exopod elongate, about 3.5 times as long as wide; with 1 seta and 1 spine along inner margin, apex with 1 long bipinnate seta, outer margin with 2 bipinnate spines.

P6 asymmetrical; each opercular flap with cylindrical extension at outer corner bearing long outer seta and minute inner seta.

REMARKS. Nicholls (1941*b*) pointed out that *Laophonte rosei*, described from Banyuls (Monard, 1926) may well be a junior synonym of *L. bulligera* since the difference between them appears to be based on two doubtful characters. The 'sensory organ' illustrated on the P4 endopod of *L. bulligera* by Farran (1913) was not described for *L. rosei* by Monard (1926) although the latter did illustrate the adjoining modified seta (see also Monard (1928)). Secondly, the different number of setae on the P5 endopodal lobe is based on Monard's failure to observe the seta near the base of the baseoendopod, a portion of which appears to have been lost in *L. rosei*. Lang (1948) also expressed strong reservations about the distinctiveness of *L. rosei* but like Nicholls (1941*b*) and Vervoort (1967) nevertheless maintained it as a valid species. We can see no justification for this distinction and formally relegate *E. rosei* to a junior subjective synonym of *E. bulligera*. Pesta (1959) published an incomplete description of the male (as *E. rosei*) but did not mention the transformed P4 endopod. The discrepancy found in the length of the P1 endopod casts some doubt on his identification.

Pending the re-examination of mediterranean material, the known records suggest an almost continuous boreo-mediterranean distribution pattern with records from Ireland (Farran, 1913, 1915), Isles of Scilly (Wells, 1970), Belgian coast (unpubl.), Banyuls-sur-Mer (Monard, 1926, 1928) and possibly Naples (Pesta, 1959). Por & Marcus (1972) recorded the species also in the Great Bitter Lake and off Port Taufiq in the southern part of the Suez Canal and considered the species an Atlantic (anti-Lessepsian) immigrant. There is no morphological evidence supporting Alheit & Scheibel's (1982) record from Harrington Sound in Bermuda.

The isolated record from New Caledonia by Vervoort (1962) is difficult to interpret, particularly because his single female specimen deviates from European *E. bulligera* in the absence of the outer spine on P2 enp-2. Vervoort (1962) did not remark on this character

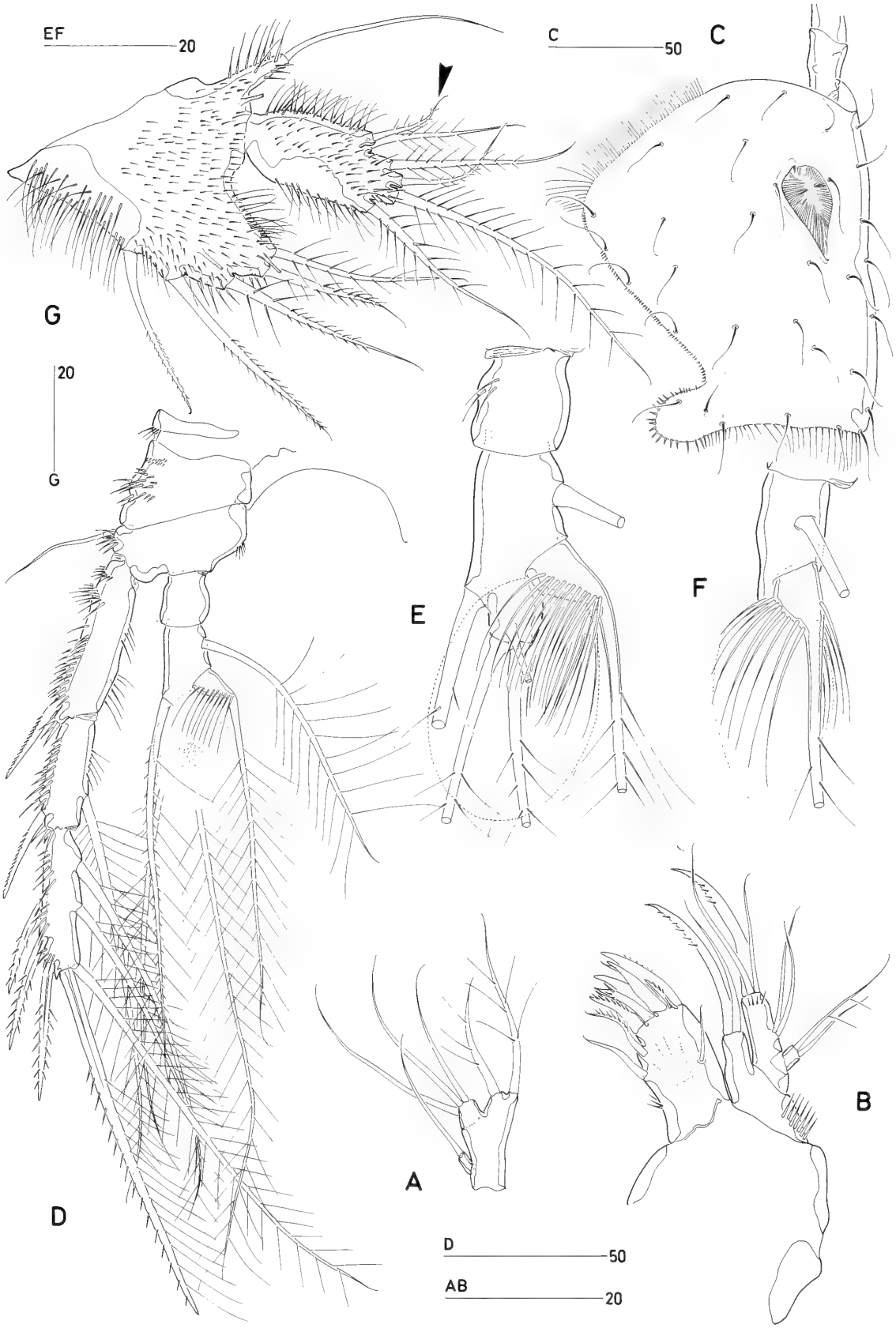

Fig. 25 *Archesola typhlops* (Sars, 1908) comb. nov. A, Mandibular palp; B, maxillule, anterior. *Corbulaseta bulligera* (Farran, 1913) comb. nov. C, cephalothorax, lateral; D, P4 ♀, anterior; E, P4 endopod ♀, anterior; F, P4 enp-2 ♀, medial [contours of secrete bolus stippled in E–F]. *Laophonte parvula* Sars, 1908. G, P5 ♀, anterior [anteriorly displaced outer seta arrowed].

presumably because of the lack of a base for comparison in Farran's (1913) description and illustrations which omitted P2 and P3. The problem is exacerbated by the aberrant left-right asymmetry (1.220 vs 1.320) displayed on the P2 endopods. It is unclear whether the reduced setal formula is real and therefore indicative for the presence of a second species in the western Pacific. There is very little additional evidence pointing in this direction except for the different cephalothorax shape (in lateral aspect: compare Fig. 25C) and some morphometric discrepancies in the caudal rami, which appear to be longer, and in the exopods of P2–P4, which are more abbreviated.

E. bulligera cannot be retained in the genus *Esola* because of the absence of (1) distinct spinous processes on the first antennulary segment, (2) cup-shaped integumental pores on the genital (double-) somite and caudal rami, (3) characteristic labral ornamentation and (4) caudal ramus sexual dimorphism. It is reminiscent of *Bathyesola compacta* (see below) in the presence of only one pair of cup-shapes pores on the cephalothorax but differs from it in the reduced armature on the ♀ P5 exopod and the transformed P4 endopod which is the most significant autapomorphy of *E. bulligera*, justifying its placement in a new genus *Corbulaseta*.

Genus *Bathyesola* gen. nov.

DIAGNOSIS (based on ♀ only). Laophontidae. Body cylindrical; posterolateral corners of ♀ genital double-somite and second abdominal somite laterally and backwardly produced. Integument of cephalothorax and body somites with dense pattern of spinules and setules. Rostrum large, partly delimited at base. Anterolateral pair of small integumental cup-shaped pores present on cephalothorax. Caudal rami not modified in ♀, cylindrical and elongate.

Sexual dimorphism presumably in antennule, P3 endopod, P5, P6, and genital segmentation.

Antennules slender; 7-segmented in ♀; segment 1 without spinous processes along posterior margin; with aesthetasc on segment 4 (fused basally to 2 setae) and as part of apical acrothek on segment 7. Antenna with 4 setae on exopod; allobasis with abexopodal seta. Labrum without overlapping scales distally but with pattern of spinules anteriorly. Mandible with 2-segmented palp; endopod free, with 3 setae; exopod represented by single seta; basis represented by 2 setae. Maxillule with defined exopod. Maxilla with 3 endites on syncoxa; endopod represented by 3 setae. Maxilliped robust; syncoxa with 2 setae; entire palmar margin with spinules; endopodal claw relatively stout.

P1 with large 3-segmented exopod bearing 4 setae on exp-3 and relatively short endopod; enp-1 without inner seta, enp-2 with minute seta and short, curved claw. P2–P4 with 3-segmented exopods and 2-segmented endopods. P2 basis with moderately long outer spine. Inner seta of P2–P4 exp-2 reduced. Outer spine of P2–P4 enp-2 setiform, short in P2–P3, long in P4. Armature formula as follows:

	Exopod	Endopod
P2	0.1.123	1.221
P3	0.1.123	0.321 [♂ presumably 0.1.220]
P4	0.1.123	0.221

P5 ♀ with separate rami; exopod relatively short, with 6 setae/spines; baseoendopod well developed, with 5 setae/spines, apical setae reduced; outer basal seta on short setophore.

P6 ♀ forming opercula closing off paired genital apertures; with 2 small setae.

TYPE AND ONLY SPECIES. *Bathyesola compacta* gen. et sp. nov.

ETYMOLOGY. The generic name refers to the bathyal distribution of the type species.

Bathyesola compacta gen. et sp. nov.

TYPE LOCALITY. 18°50'S, 173°29'W, 'White Lady' site on North Fiji Ridge, west of Fiji; 2765 m depth. Accompanying harpacticoid fauna: several ♀♀ and ♂♂ of *Xylora bathyalis* Hicks, 1988 (Thalestridae: Donsiellinae).

TYPE MATERIAL. Holotype ♀ dissected on 6 slides, deposited in Muséum National d'Histoire Naturelle, Paris under MNHNP Cop-1869; collected during STARMER II expedition, station 14 (Kaiyo 87), dive 19; 14 July 1989; leg. L. Laubier.

ETYMOLOGY. The species name alludes to the compact P1, displaying a short and robust endopod.

DESCRIPTION.

FEMALE. Body length from anterior margin of rostrum to posterior margin of caudal rami 360 µm. Maximum width (105 µm) measured at posterior margin of cephalothorax.

Body (Fig. 26A–B) cylindrical, slightly dorsoventrally depressed, covered with dense pattern of minute spinules dorsally and laterally. Cephalothorax slightly wider than free somites, posterolateral angles backwardly produced forming small lobate extension (Fig. 26B); with pair of small lateral cup-shaped pores. Posterior margin of cephalothorax and all body somites with row of long setules dorsally and laterally. Pleurotergite of P5-bearing somite almost as wide as anterior somites.

Genital double-somite wide and dorsoventrally flattened; with lateral, backwardly produced extensions in posterior (=abdominal) half; original segmentation marked by bilateral constriction and spinule row arising from transverse surface ridge dorsally and laterally; posterior half with backwardly directed lobate extensions bearing spinular tuft; ventral surface without spinular ornamentation; genital field located near anterior margin. Sixth legs forming well developed opercula closing off paired genital apertures; each with 2 small setae.

First postgenital somite with backwardly produced lateral angles, bearing spinular tuft; without ventral ornamentation. Penultimate and anal somites distinctly narrower; ventral posterior border with long spinules. Anal somite with spinulose anal operculum.

Caudal rami (Fig. 26A–B) widely separated; about 4 times as long as average width; maximum width measured at base; dorsal surface with minute spinules; seta I small, setae II–III well developed, naked and closely set; setae IV (naked) and V (pinnate) with fracture planes, seta V 2.8 times as long as seta IV; setae VI–VII naked.

Rostrum (Figs 26A) large, blunt anteriorly; delimited at base by transverse surface suture; with paired sensillae anteriorly and median tube-pore dorsally.

Antennule (Fig. 26A–B) relatively short, distinctly 7-segmented, without spinous processes on segments 1–2. Segment 1 with large spinular patch around anterior margin. Armature formula: 1-[1], 2-[4 + 4 pinnate], 3-[6], 4-[1 + (1 + ae)], 5-[1], 6-[2], 7-[5 + 1 pinnate + acrothek]. Acrothek consisting of aesthetasc and 2 naked setae; set on apical pedestal.

Antenna (Fig. 27A). Coxa with spinules on both inner and outer margins. Exopod short, bearing 2 lateral and 2 apical pinnate elements, and a longitudinal row of fine spinules along outer margin. Allobasis with pinnate abexopodal seta. Endopod with lateral armature consisting of 2 spines and 1 minute seta; distal armature consisting of 2 naked spines and 3 geniculate setae (outermost fused basally to minute seta).

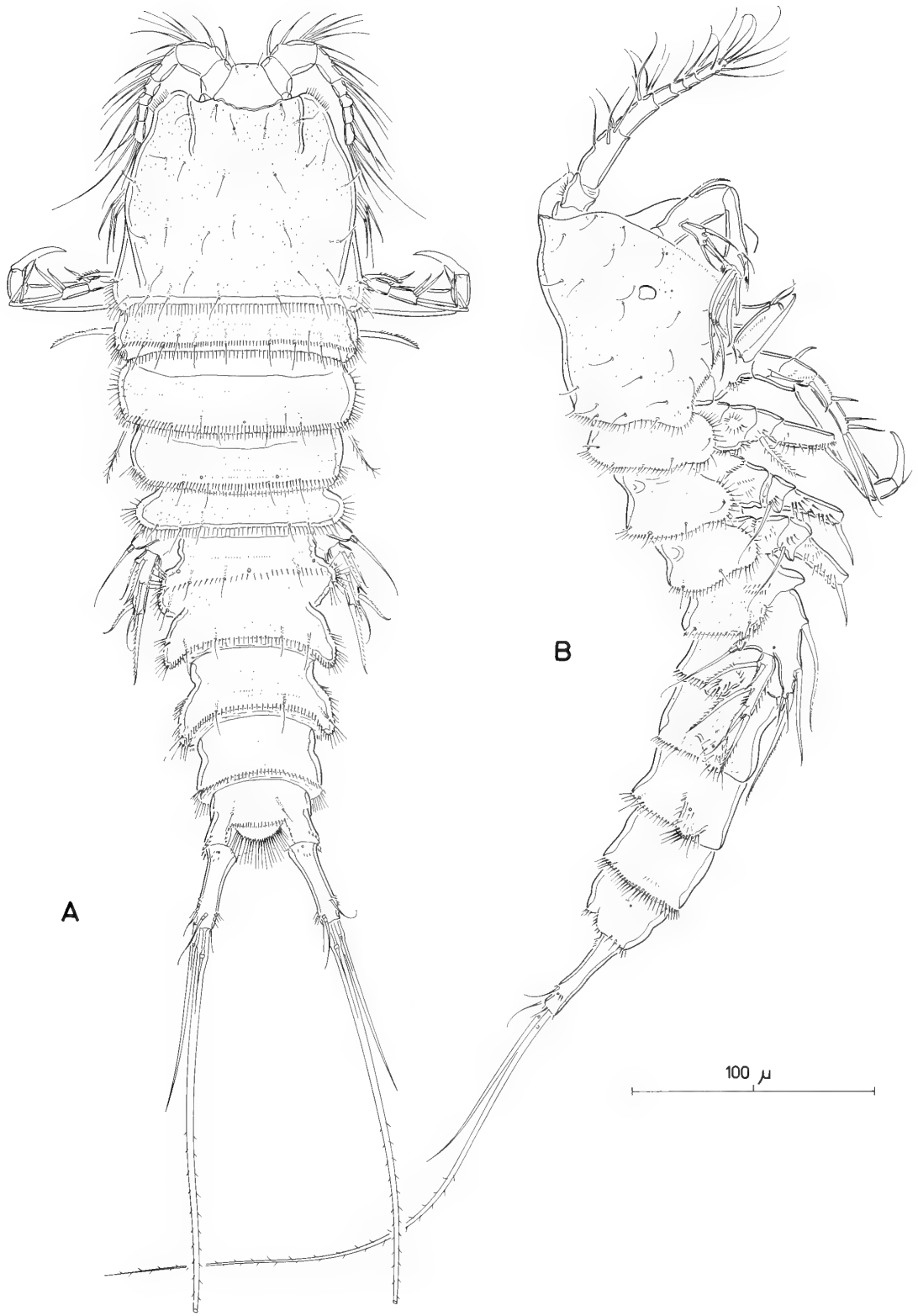

Fig. 26 *Bathyesola compacta* gen. et sp. nov. (♀). A, Habitus, dorsal; B, habitus, lateral.

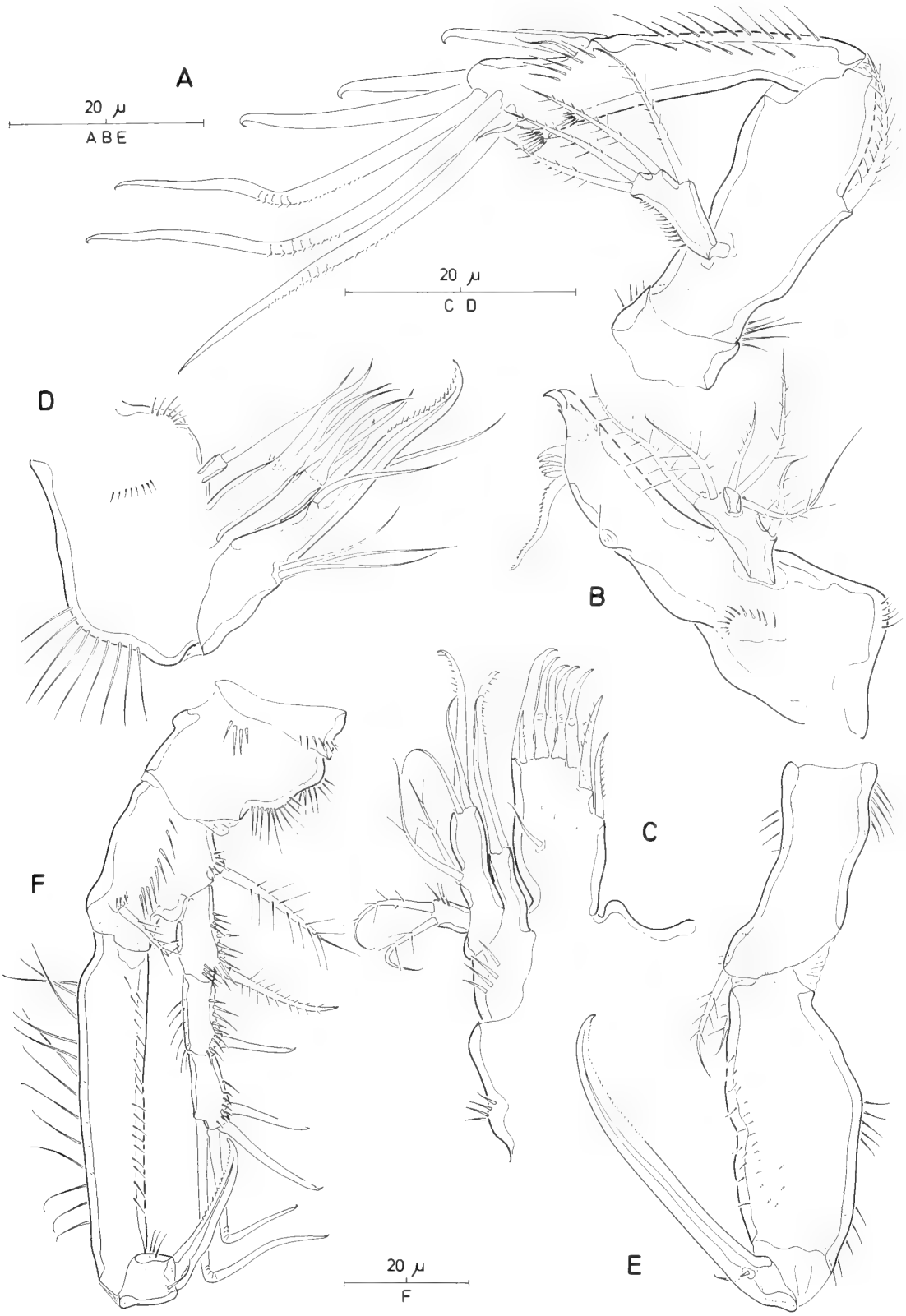

Fig. 27 *Bathyesola compacta* gen. et sp. nov. (♀). A, Antenna; B, mandible; C, maxillule, anterior; D, maxilla; E, maxilliped; F, P1, anterior.

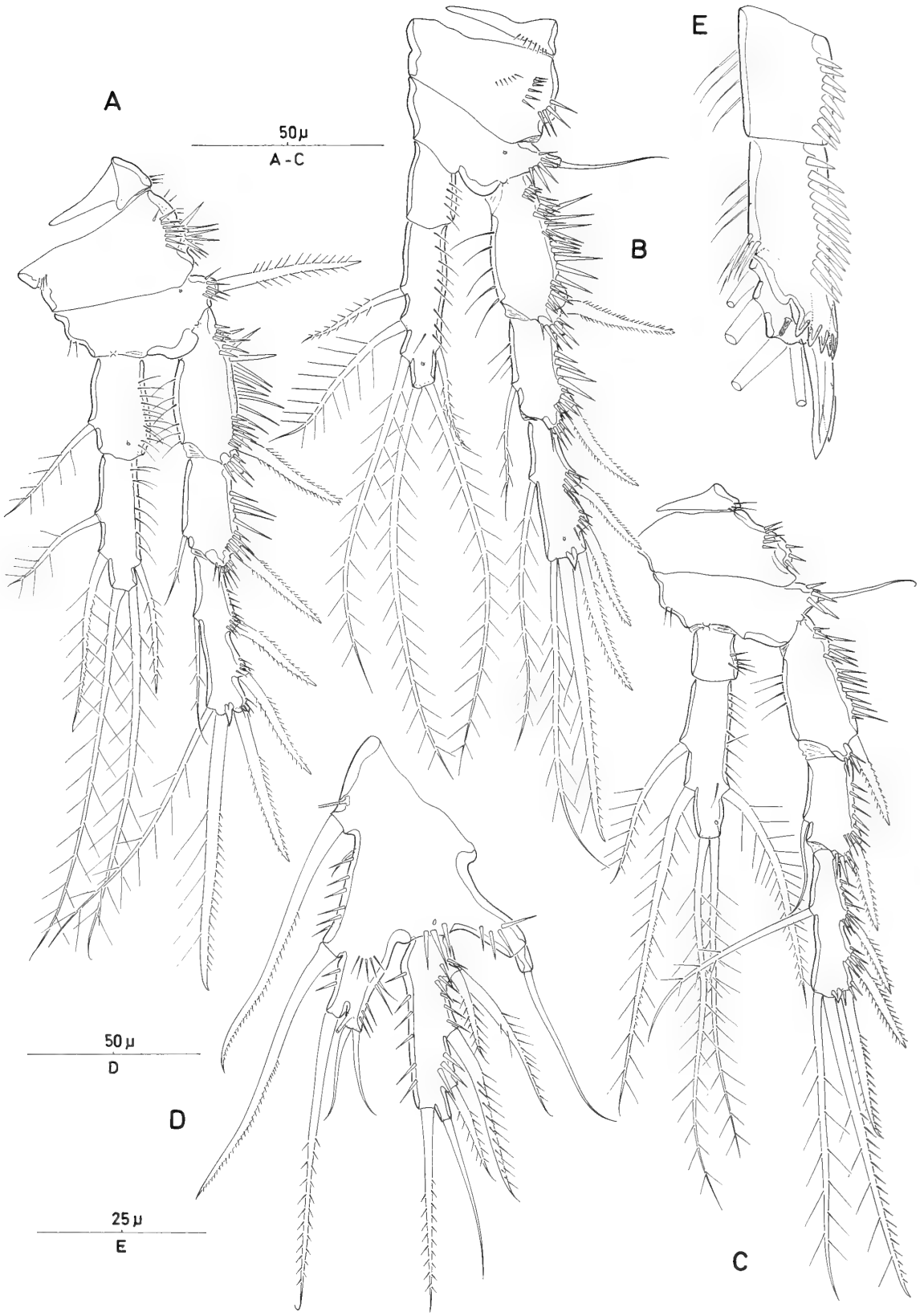

Fig. 28 *Bathyesola compacta* gen. et sp. nov. (♀). A, P2, anterior; B, P3, anterior; C, P4, anterior; D, P5, anterior. *Paralaophonte pilosoma* Vervoort, 1964. E, P3 endopod ♂, anterior.

Labrum with spinular patches on anterior face but no overlapping scales.

Mandible (Fig. 27B) with short gnathobase and small 2-segmented palp representing free endopod and fused basis and exopod; endopod a minute segment with 3 pinnate setae; basal armature represented by 2 lateral pinnate setae, exopod represented by single seta.

Paragnaths highly ornate lobes as in *E. bulbifera*.

Maxillule (Fig. 27C) with elongate arthrite bearing 1 seta on anterior surface and 9 elements around distal margin. Coxal endite with 1 spine and 1 seta, basal endite with 1 spine and 2 setae. Exopod a short segment with 2 distal setae; endopod incorporated into basis, represented by 2 setae.

Maxilla (Fig. 27D). Syncoxa with very long setules around outer margin and few additional spinule rows as figured; with 3 endites; praecoxal endite small, with 1 naked seta; middle endite drawn out into spine, with 2 setae; distal endite with 3 elements. Allobasis produced into strong curved claw; accessory armature consisting of 2 setae. Endopod incorporated into allobasis, represented by 3 bare setae.

Maxilliped (Fig.27E) compact, basis and endopodal claw not particularly elongate. Syncoxa with 2 pinnate setae. Basis with spinular ornamentation as figured; spinules present along entire palmar margin. Endopod represented by stout, minutely pinnate claw bearing 1 accessory seta and tube-pore at base.

P1 (Fig. 27F) with dense ornamentation on praecoxa, coxa and basis. Basis with pinnate seta on anterior surface and along outer margin. Exopod large, 3-segmented; exp-1 with pinnate outer seta; exp-3 with 2 unipinnate outer spines and 2 geniculate setae apically. Endopod robust and relatively short; enp-1 about 2.2 times as long as basis, with long setules along inner margin and fine spinules along outer margin; enp-2 about as long as wide, with short unipinnate claw and small accessory seta.

P2–P4 (Figs 28A–C) with 3-segmented exopods and 2-segmented endopods. P2 basis with long, bipinnate outer spine; P3–P4 bases with bare outer seta. P2 enp-1 with pinnate inner seta, P3–P4 enp-1 unarmed. Inner seta of P2 exp-2 reduced. Outer spine of P2–P4 enp-2 setiform, very long in P4. Pore present near distal outer corner of P3–P4 enp-2. Armature formula as for genus.

P5 (Fig. 28D). Endopodal lobe well developed, extending to halfway down the exopod; with 2 reduced bare setae apically, and 2 long widely separated setae along inner margin; pores present near articulation with exopod, at base of apical setae and proximal to innermost seta. Exopod relatively short, produced apically into short tubular extension bearing 1 bare seta; inner margin with 1, outer margin with 4 pinnate setae; inner seta slightly longer than apical one. Both baseoendopod and exopod with spinulation as figured.

MALE. Unknown.

REMARKS. The discovery of *B. compacta* at 2765 m depth at the North Fiji Ridge represents the deepest record thus far for the family Laophontidae (Lee & Huys, 1999). It displays a mozaic of primitive (7-segmented ♀ antennule; 3-segmented P1 exopod; ♀ P5 endopodal lobe with 5 setae/spines) and advanced characters (P3–P4 enp-1 without inner seta; P3–P4 exp-3 with 1 inner seta) which serves to distinguish the species from other esolinids.

Status of Esola *Spelaea* (Chappuis, 1938)

Lang (1944, 1948) placed *Laophonte spelaea* in the genus *Esola* without giving any explicit reasons. From his generic diagnosis and the phylogenetic scheme presented on p. 1450 (Lang, 1948), one can infer that his course of action was based solely on the presence of an outer spine on the distal endopod segment of P2. Although this character was diagnostic for *Esola* in Lang's sense it is clearly a symplesiomorphy shared by all genera in the *Archilaophonte-Esola* lineage (with the exception of *Mourephonte*) and consequently of no value in inferring relationships. Lang (1944, 1948) subdivided *Esola* into two species groups, diagnosed by the number of setae on the male P5 endopodal lobe and the armature of the P3 in both sexes. His *spelaea*-group included only *E. spelaea* and has until now remained monotypic. It differed from the *longicauda*-group in the presence of 2 setae (rather than 1 or 0) on the ♂ P5 endopodal lobe and a reduced armature on the P3 exopod (exp-3 with only 2 outer spines) and endopod (enp-2 ♀ with only 2 inner setae; endopod ♂ without inner seta on enp-2 and with only 3 setae on enp-3).

Chappuis' (1938) description is very brief and provides illustrations of the male P2–P5 only. Unfortunately the author did not give any information about the position of the setae on the female P5 which could have provided the justification for including *L. spelaea* in the *Archilaophonte-Esola* lineage since in all of its members (1) the proximal seta of the endopodal lobe is medially displaced and (2) the insertion sites of the 2 proximal setae of the exopod are superimposed. Chappuis' statement that there are 4 setae on the baseoendopod and 5 or 6 setae on the exopod can be interpreted in the light of this generalized pattern. His reservation about the correct number of exopodal setae might indicate the close or overlapping position of some of these elements. Secondly, due to its strong medial displacement the proximal endopodal seta has frequently been overlooked or lost during dissection (Thompson & A. Scott, 1903; Norman, 1911; Monard, 1926, 1928; Noodt, 1955), leaving open the possibility of a similar observational error made in Chappuis' (1928) description. The actual number of endopodal setae on the female P5 of *L. spelaea* could therefore be five rather than four. Chappuis'(1928) armature formula of P2 exp-3 tabulated as 222 (i.e. with 2 outer spines) is unlikely to be correct when both P2 and P4 reportedly have 3 outer spines on exp-3. No laophontid described thus far displays a [3-2-3] outer spine pattern for P2–P4 and hence we suspect 123 (as in *B. compacta*) to be the correct formula for P2 exp-3.

Chappuis (1938) described *L. spelaea* from three caves in Apulia, southern Italy (Abisso and La Zinzulusa near Castro, Grotta dei Diavoli near Badisco) and regarded it as a marine relict. The caves exhibit a tidal regime but the salinity approaches that of freshwater ('. . . das Wasser schmeckt aber fast süss') which appears to be confirmed by the presence of the stygobiont mysids *Spelaeomysis bottazzii* Caroli and *Stygiomysis hydruntina* Caroli and the palaemonid *Typhlocaris salentina* Caroli, all of which are endemic to coastal caves and phreatic waters in the Apulia region. Both Pesce (1985) and Rouch (1986) consider the species as a descendant from a marine ancestral stock which successfully colonized subterranean freshwater habitats via littoral karstic systems, possibly during regression periods in the Tertiary ('Regression Model Evolution').

Laophonte spelaea cannot be accommodated in any of the existing laophontid genera. It appears to be related to *Bathyesola* in certain aspects (see above) but differs from it in the presence of an inner seta on P3–P4 enp-1, only 2 inner setae on P3 enp-2 and more primitive setal formula on the P4 exopod. In view of the strong ecological divergence between *B. compacta* and *L. spelaea* we prefer to establish a new genus for the latter. The male P3 endopod in *Troglophonte* gen. nov. does not accord with the pattern found in the other esolinid genera. The absence of an inner seta on the middle segment could be related to the reduced 1.221 pattern in the female but might also indicate a relationship with a large group of other laophontid genera which typically lose the proximal inner seta during male P3 ontogeny.

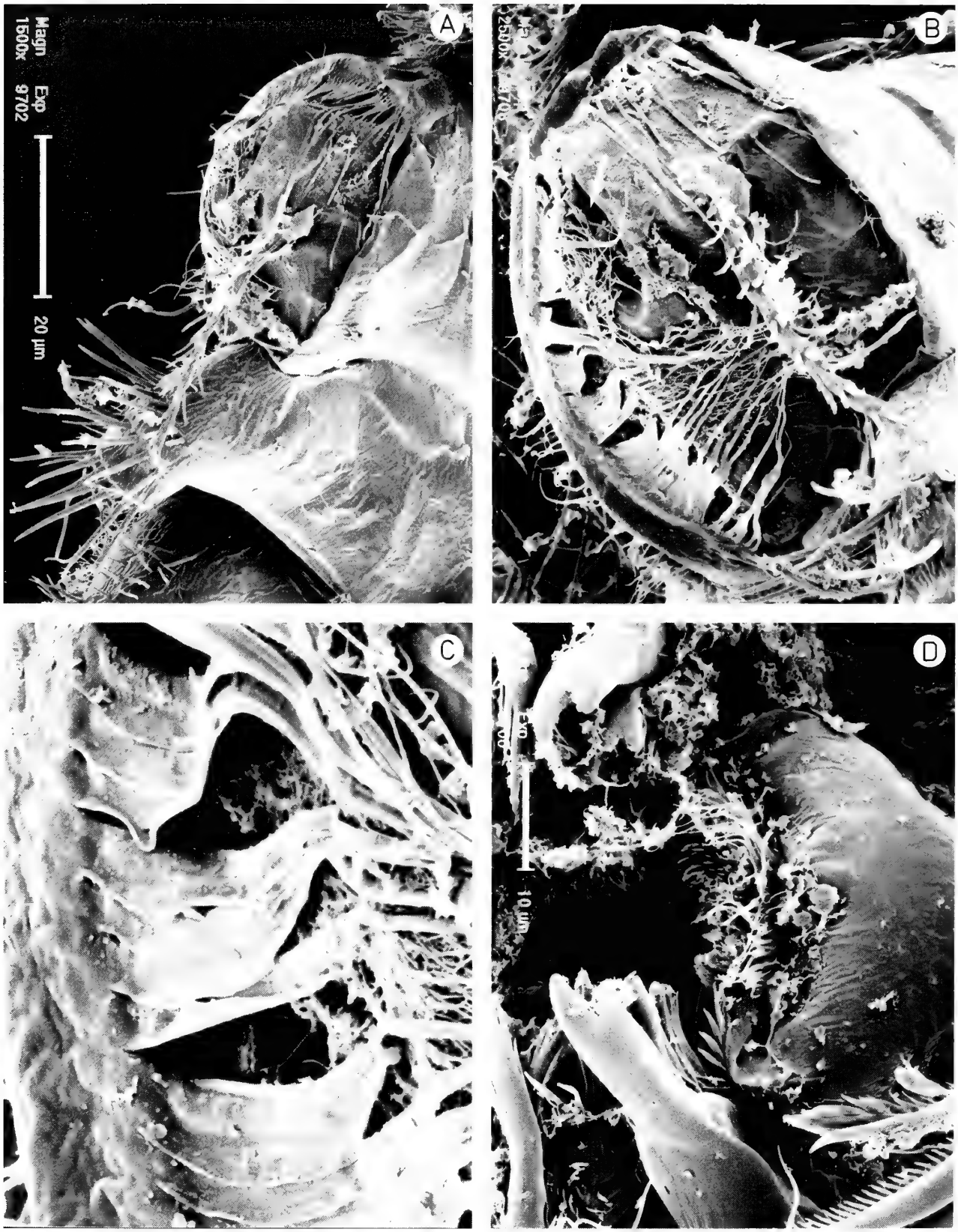

Fig. 29 SEM micrographs. *Applanola hirsuta* (Thompson & A. Scott, 1903) comb. nov. (♀). A, Lateral margin of genital double-somite, ventrolateral; B, lateral cup-shaped pore on genital double-somite [pore exit arrowed]; C, setular extensions bordering dorsal margin of cup-shaped pore; D, labrum and mandibular gnathobases. [Scale bars: 2 µm (C), 10 µm (B, D), 20 µm (A)].

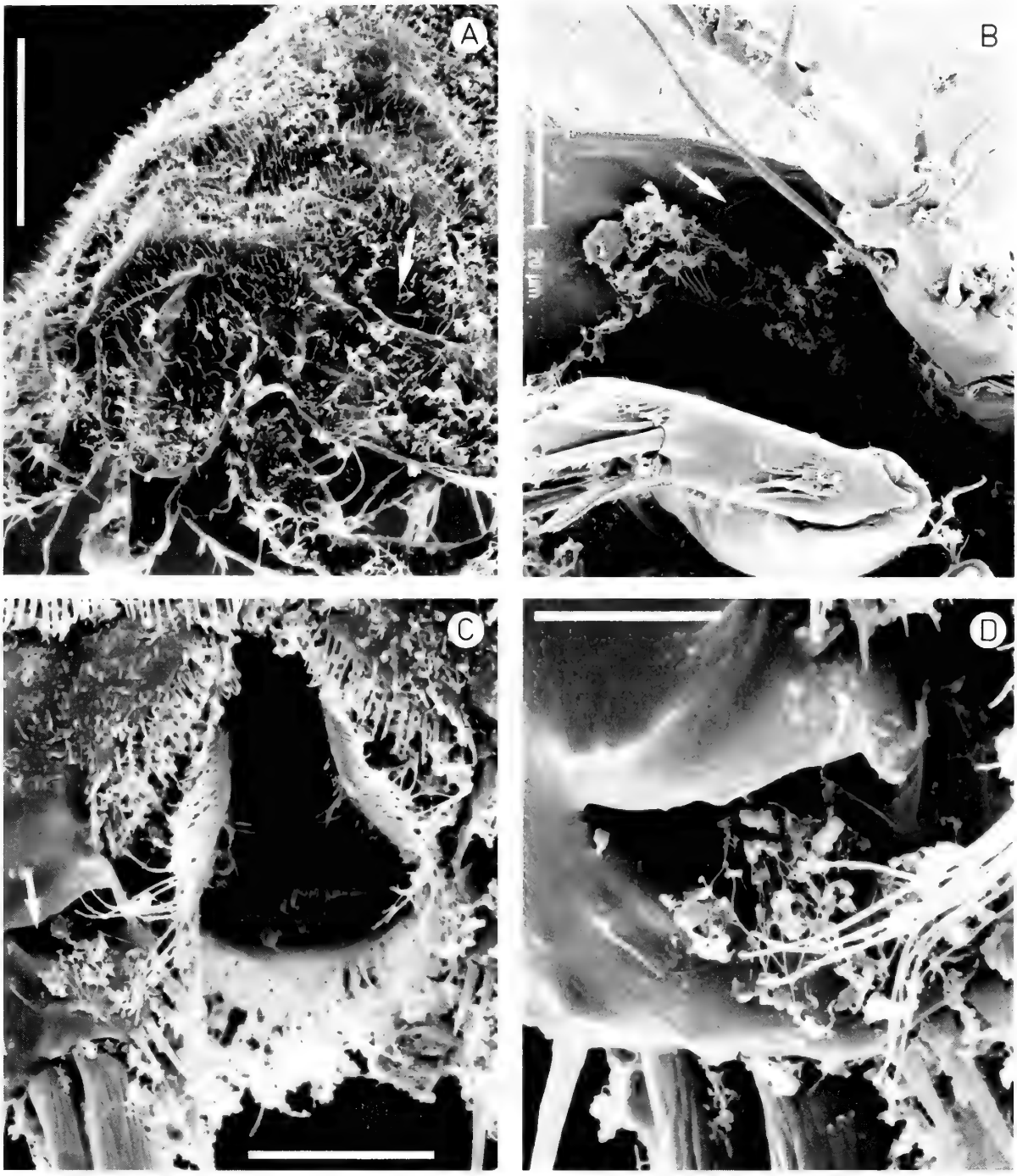

Fig. 30 SEM micrographs. *Applanola hirsuta* (Thompson & A. Scott, 1903) comb. nov. (♀). A, Cephalothorax and rostrum, frontal [anterodorsal pore arrowed]; B, cephalothorax, ventral [anteroventral pore arrowed]; C, anal opening and caudal ramus, ventral [ventral pore arrowed]; D, right caudal ramus, ventral, showing cup-shaped pore. [Scale bars: 6 μm (D), 15 μm (C), 20 μm (B), 60 μm (A)].

Genus *Troglophonte* gen. nov.

DIAGNOSIS. Laophontidae. Body shape unknown but somites not well demarcated. Rostrum short, presumably fused at base. Integumental cup-shaped pores unconfirmed. Anal operculum spinulose. Caudal rami short, squarish.

Sexual dimorphism in antennule, P3 endopod, P5, P6 and in genital segmentation.

Antennules 7-segmented in ♀, segmentation unknown in ♂. Antenna with 4 setae on exopod; allobasis with abexopodal seta. Mouthparts unknown. Maxilliped very slender.

P1 with 3-segmented exopod bearing 4 setae on exp-3 and slender endopod; enp-1 without inner seta, enp-2 with minute seta and slender, strong claw. P2-P4 with 3-segmented exopods and 2-seg

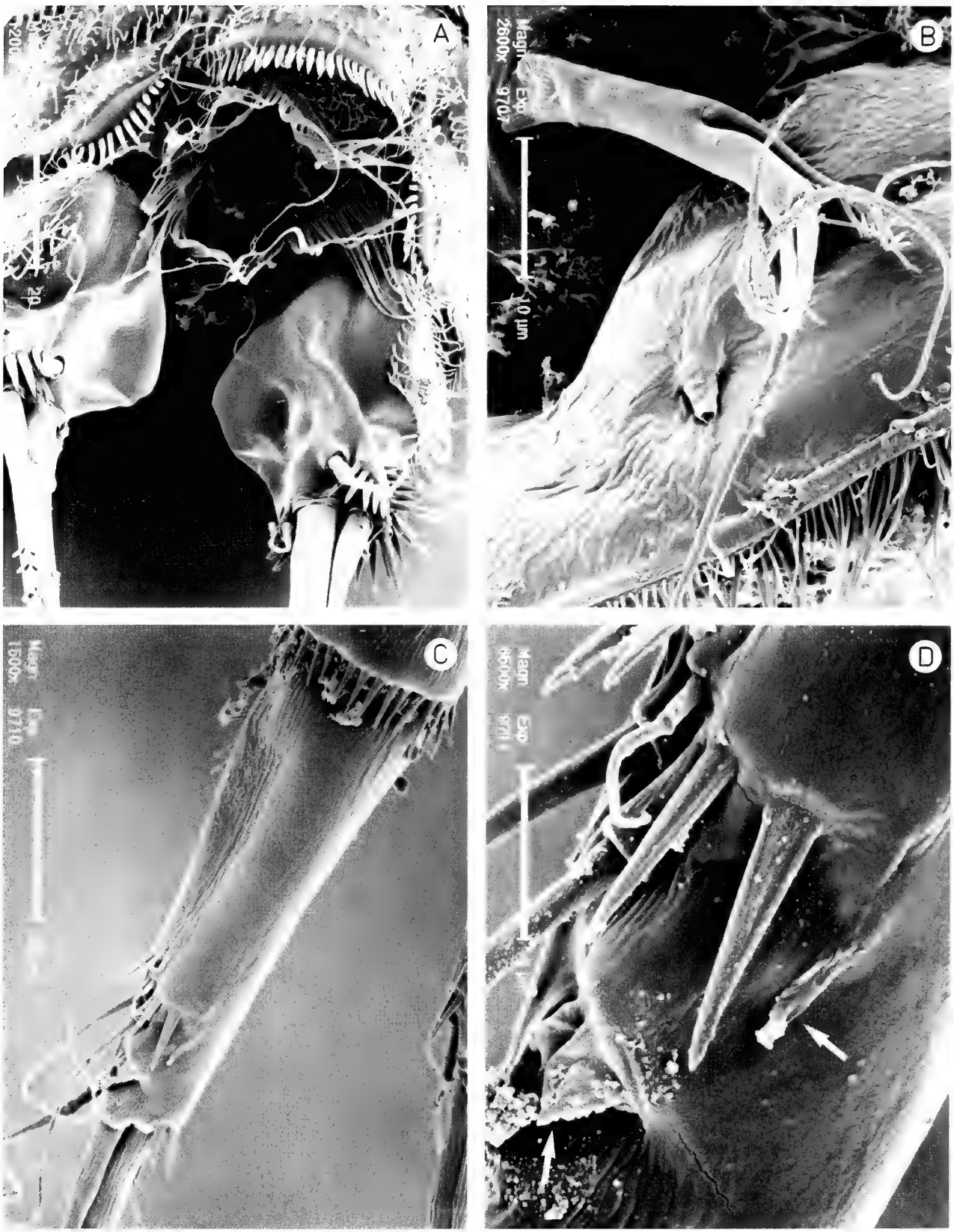

Fig. 31 SEM micrographs. *Esola bulbifera* (Norman, 1911). A, Anal somite and caudal rami, dorsal. *Applanola hirsuta* (Thompson & A. Scott, 1903) comb. nov. B, mandibular palp and inner face of cephalothorax showing vent-pore [arrowed]. *Archesola typhlops* (Sars, 1908) comb. nov. C, caudal ramus, ventral; D, caudal ramus, area around setae I–III showing pores [arrowed]. [Scale bars: 5 µm (D), 10 µm (B), 20 µm (A, C)].

mented endopods. P3 endopod ♂ 3-segmented; enp-2 with outer pinnate apophysis but without inner seta. Armature formula as follows:

	Exopod	Endopod	
P2	0.1.123	1.221	
P3	0.1.123 (or 0.1.222♂)	1.221	[♂: 1.0.120]
P4	0.1.223	1.221	

P5 ♀ with separate rami; exopod elongate, with 5 or 6 setae/spines; baseoendopod slightly developed, with 4 setae/spines. P5 ♂ with trapezoid endopodal lobe; exopod short, with 1 inner, 2 apical and 2 outer setae/spines.

P6 unknown in both sexes.

TYPE AND ONLY SPECIES. *Laophonte spelaea* Chappuis, 1938 = *Troglophonte spelaea* (Chappuis, 1938) comb. nov.

ETYMOLOGY. The generic name is derived from the Greek *trogle*, meaning hole, and refers to the stygobiont life style of the type species. Gender: feminine.

MATERIAL EXAMINED. None. Chappuis' (1938) material no longer exists and the species has not been recorded again since its original description.

PHYLOGENETIC ANALYSIS

Taxa and characters

The analysis was executed at species level in order to test the monophyly of the genus *Esola* and its relationships to both *Mourephonte* and *Archilaophonte*. *Onychocamptus* and the *cornuta*-group of the genus *Laophonte* were also included as separate taxa in the analysis on the basis of their ancestral P3 endopod sexual dimorphism. The highly advanced genus *Folioquinpes* Fiers & Rutledge, although having been positively identified as the sistergroup of *Onychocamptus* (Lee & Huys, 1999), was excluded from the analysis. The residual Laophontidae were replaced by their hypothetical ancestor (Table 4: Other Laophontidae) which was constructed by combining the most plesiomorphic state encountered for each character.

Table 2. Laophontidae with 3 inner setae [3(1-2)(0-1) setation pattern] on P3 enp-2 ♀.

	P2		P3			P4	
	exp	enp	exp	enp ♀	enp ♂	exp	enp
Laophonte Group I	0.1.123	1.220	0.1.223	1.321	1.1.220	0.1.223	1.221
Laophonte adduensis	0.1.122	1.220	0.1.223	1.321	1.1.220	0.1.223	1.221
Laophonte ciliata	0.1.122	1.220	0.1.222	1.321	1.1.220	0.1.222	1.221
Onychocamptus Group I	0.1.123	0.220	0.1.123	0.321	0.1.220	0.1.123	0.111
Onychocamptus besnardi	0.1.123	0.220	0.1.123	0.321	0.1.220	0.1.022	0.111
Onychocamptus anomalus	0.1.123	0.220	0.1.123	0.321	0.1.220	0.1.122	0.111
Onychocamptus taifensis	0.1.123	0.120	0.1.123	0.321	0.1.220	0.1.123	0.111
Onychocamptus krusensterni	0.1.123	0.220	0.1.123	0.321	0.1.220	0.1.122	0.111
Laophonte galapagoensis	0.1.123	0.220	0.1.223	0.321	0.0.220	0.1.223	1.121
Laophonte confusa	0.1.123	0.220	0.1.223	0.321	0.0.220	0.1.223	1.120
Laophonte Group II	0.1.123	0.220	0.1.223	0.321	0.0.220	0.1.223	0.221
Laophonte lignosa	0.1.123	0.220	0.1.223	0.321	0.0.220	0.1.223	0.121
Laophonte setosa	0.1.123	0.220	0.1.223	0.321	0.0.220	0.1.223	0.111
Laophonte elongata	0.1.123	0.220	0.1.223	0.321	0.0.220	0.1.123	0.111
Laophonte Group III	0.1.123	0.220	0.1.123	0.321	0.0.220	0.1.123	0.111
Laophonte nordgaardi	0.1.123	0.120	0.1.123	0.311	0.0.210	0.0.023	0.111
Bathylaophonte spp.	0.1.123	0.220	0.1.223	0.321	0.0.220	0.1.223	0.221
Microlaophonte trisetosa	0.1.122	0.220	0.1.222	0.321	0.220	0.1.222	0.221
Pseudonychocamptus carthyi	0.1.123	0.220	0.1.223	1.321	0.220	0.1.223	1.121
Paralaophonte Group I	0.1.123	0.220	0.1.223	0.321	0.0.220	0.1.223	0.121
Paralaophonte panamensis	0.1.123	0.220	0.1.223	0.321	0.0.220	0.1.222	0.121
Paralaophonte Group II	0.1.123	0.220	0.1.123	0.321	0.0.220	0.1.123	0.121
Paralaophonte tenera	0.1.123	0.220	0.1.123	0.321	0.0.120	0.1.123	0.121
Paralaophonte innae	0.1.123	0.220	0.1.223	0.320	0.320	0.1.223	0.121
Paralaophonte aenigmaticum	0.1.123	0.220	0.1.123	0.320	0.320	0.1.022	0.120
Heterolaophonte campbelliensis	0.1.123	0.220	0.1.223	0.321	0.0.220	0.1.223	0.121
Heterolaophonte Group I	0.1.123	0.220	0.1.123	0.321	0.0.220	0.1.022	0.121
Heterolaophonte Group II	0.1.123	0.220	0.1.123	0.321	0.220	0.1.123	0.121
Heterolaophonte manifera	0.1.123	0.220	0.1.123	0.321	0.220	0.1.122	0.121
Heterolaophonte hamata	0.1.123	0.220	0.1.123	0.321	0.220	0.1.022	0.121
Heterolaophonte minuta	0.1.123	0.220	0.1.123	0.321	0.220	0.0.022	0.121
Paronychocamptus spp.	0.1.123	0.1–220	0.1.223	0.321	0.0.220	0.1.122	0.111
Asellopsis hispida	0.1.123	0.220	0.1.223	0.321	0.0.220	0.1.223	0.111
Asellopsis duboscqui	0.1.122	0.120	0.1.222	0.321	0.0.220	0.1.222	0.111
Folioquinpes chathamensis	0.1.123	0.220	0.1.123	0.321	0.321	0.1.123	0.120

Laophonte: Group I = *cornuta, expansa, plana*; Group II = *inornata, parvula, serrata*; Group III = *adamsiae, thoracica.*
Onychocamptus: Group I = *mohammed, bengalensis, vitiospinulosa*
Paralaophonte: Group I = *asellopsiformis, brevirostris, congenera, dieuzeidei, gurneyi, hyperborea, lacerdai, majae, meinerti, ormieresi, pacifica, pilosoma, royi*; Group II = *karmensis, lunata, spitzbergensis, zimmeri.*
Heterolaophonte: Group I = *discophora, variabilis*; Group II = *murmanica, stromi, uncinata.*

Characters used in the analysis are listed in Table 3. Apomorphic character states are explained inside square brackets using the multistate system. The scores for each character and taxon are compiled in matrix format in Table 4. A question mark indicates missing data, either because the appendage or structure is unknown in that species (certain sexually dimorphic characters could not be scored because only one sex is known) or because it was impossible to score the character accurately due to incompleteness or the lack of detail in the original descriptions. *Esola typhlops pontoica*, *E. longicauda* var. *sensu* Vervoort (1964) and the unnamed forms of *E. longicauda* identified by Noodt (1955) and Wells & Rao (1987) were excluded from the analysis because of their questionable status.

Huys & Boxshall's (1991) study of ordinal copepod phylogeny demonstrated that oligomerization was the dominant trend of evolutionary transformation within the Copepoda. Armature counts used in this analysis were scored according to this overall polarisation mode. Most characters in Table 3 are self-explanatory but additional notes are provided for the following:

Integumental pores (characters 1–4)

The conspicuous cup-shaped integumental pores on the cephalothorax and genital (double-)somite have remained unnoticed in previous descriptions except for Vervoort (1962, 1964) who briefly described the anterodorsal pores in *C. bulligera* and *E. vervoorti* and suspected them to be eyes. Various authors (e.g. Jakobi, 1953; Hamond, 1969; Mielke, 1981, 1997) have unintentionally figured the modified pores on the caudal rami, however, incorrect interpretation of the internal chitinized walls of the ducts as external ridges ('Chitinleiste') made them fail to recognize these structures as true pores. Huys (1990*b*) pointed out that the transformed cup-shaped pores in *Esola* are not serially homologous with the pleural glands of the Adenopleurellidae and consequently cannot serve as a basis for phylogenetic affinity. With the exception of *Archilaophonte* and the *typhlops*-group of *Esola* all other esolinids appear to exhibit a propensity for developing modified secretory pores. The functional correlation between pores of different body-regions is unknown and in view of their positional disparity and structural differences it is unlikely that their expression is controlled by a single gene. We postulate that the cup-shaped pore type evolved from a surface precursor pore by major integumental invagination and secondary development of setular extensions. These marginal extensions either protect the depression or (more likely) maintain the secrete bolus in close contact to the body wall. The degree of invagination is obviously morphologically constrained and this is particularly the case in swimming leg segments which are typically depressed along the antero-posterior body axis. Although the 'trapping basket' seta on the P4 endopod of *C. bulligera* represents a radically divergent modification, it can be viewed as an external analogue of the internal cup-shaped pore which developed in response to this constraint. The tube-pore, which is also found in most other esolinids, is enclosed by the long setules arising from the proximally dilated distal inner seta (Fig. 25E–F) which hold the secrete bolus in position. Since there are no differences in pore pattern between the sexes a possible role in mate recognition is considered unlikely. Huys (1992) demonstrated that in the interstitial Leptastacidae the mucopolysaccharid strands produced by the caudal ramus glands are intimately involved in mucus-trap feeding. We suggest that in esolinids the secretory products discharged by the cup-shaped pores perform a similar role in trophic gardening. It should be noted that the caudal ramus pores located near the insertion sites of setae I–III in *E. typhlops* (Fig. 31C–D) are not homologous to the large slit-like pores found in *Esola* and *Mourephonte*.

Table 3. Characters used in phylogenetic analysis. Apomorphic character states are referred to in square brackets.

1	Paired anterodorsal cup-shaped pores on cephalothorax absent [present]
2	Paired anteroventral cup-shaped pores on cephalothorax absent [present]
3	Paired cup-shaped pores on genital double-somite of ♀ and genital somite of ♂ absent [present]
4	Caudal rami without large pore medially or ventrally [present]
5	Cephalothorax without transverse spinular row dorsally [present]
6	Caudal rami not sexually dimorphic [modified in ♀]
7	Antennule ♀ 7-segmented [6-segmented; failure in separation of segments 6 and 7]
8	Antennule ♂ with 3 segments distal to geniculation [with 2 segments: segments 7 and 8 fused]
9	Aesthetasc of segment 4 in ♀ (and segment 5 in ♂) fused basally to seta [fused to two setae forming trifid compound element]
10	Antennule segment 1 without processes in ♀/♂ [with 3 spinous processes along posterior margin]
11	Antennule segment 2 with large spinous process arising from posterior margin in ♀/♂ [absent]
12	Antennule segment 5 of ♂ without anterior cylindrical process (bearing large spine) [present]
13	Labrum without conspicuous ornamentation on anterior surface [with overlapping scales distally and dense pattern of fine spinules proximally]
14	Maxillulary endopod represented by 3 setae [2 setae, outermost seta lost]
15	Maxillipedal syncoxa with 3 setae [state 1: 2 setae, proximal seta lost; state 2: 1 seta]
16	P1 exopod 3-segmented [2-segmented; exp-2 and -3 fused]
17	P1 exopod 2-segmented, exp-2 with 3 outer spines and 2 apical geniculate setae [exp-2 with 2 outer spines and 2 apical geniculate setae]
18	P1 enp-1 with inner seta [absent]
19	P2 enp-2 with outer spine/seta [absent]
20	P3 endopod ♂ 3-segmented [2-segmented; neotenic development]
21	P3 enp-2 ♂ with inner seta [absent]
22	P5 baseoendopod ♀ with 5 setae [state 1: with 4 setae, middle inner seta lost; state 2: with 3 setae]
23	P5 baseoendopod ♂ with 2 setae [setae absent]
24	P5 basoendopod ♀/♂ without distinct setophore for outer basal seta [basal seta positioned on long cylindrical setophore]
25	P5 exopod ♀ with all outer setae arranged around margin [proximal 2 outer setae displaced with overlapping insertion sites]

Caudal ramus sexual dimorphism (character 6)

Females of *Esola* typically have bulbous caudal rami, displaying a variety of swelling medially, ventrally and/or dorsally. Although the secondary expansion appears to be correlated with the size of the transformed pores, it is decoupled here from character 4 (presence of caudal ramus pores) and scored separately. This is justified by the absence of caudal ramus sexual dimorphism in *A. hirsuta* despite the presence of modified pores in both sexes.

Setal fusion on antennules (character 9)

In most esolinids (except *Archilaophonte*) the proximal aesthetasc (on segment 4 in ♀, segment 5 in ♂) is fused at the base to 2 setae. This trifid compound element is a unique character in the Harpacticoida.

Antennulary processes (characters 10–12)

Within the esolinid grouping a spinous process along the posterior margin of the second antennulary segment (character 11) is present only in *Archilaophonte*. This is not an autapomorphy for the genus but considered a retention of the ancestral state, based on outgroup comparison with the remaining families of the Laophontoidea (Huys, 1990*a*; Huys & Lee, 1999). The presence of auxiliary processes

along the posterior margin of the first segment (character 10) is a unique feature displayed by the species related to *E. longicauda*. There are no equivalent structures known from other Laophontidae and consequently this feature should be regarded an evolutionary novelty for this species-group. In males of the same group the enlarged fifth segment has produced an anterior sub-cylindrical outgrowth bearing a stout modified spine (character 12). Minute outgrowths are found on the first segment of *C. bulligera* but these are not considered important enough to warrant a separate score.

Maxillulary endopod armature (character 14)
The maxillulary endopod typically bears 2 setae along the outer margin of the basis, representing the incorporated endopod. This condition is found in all esolinids while in several other laophontid genera the endopod is represented by a cluster of 3 setae (e.g. *Langia*, *Quinquelaophonte*: Mielke (1997)). A notable exception is *Archilaophonte* in which the outermost third seta is secondarily displaced to a more proximal position, i.e. at the base of the exopod. Consequently, character 14 is scored 0 for *A. maxima* despite the clearly derived positional pattern.

Male P3 endopod segmentation (character 20)
The P3 endopod in the males of *A. typhlops* and *Esola* sp. *sensu* Chislenko (1967) is 2-segmented as in the female. The outer spine forming the apophysis in the males of other esolinids has remained largely unmodified except for reduction in size and basal fusion. This virtual absence of sexual dimorphism is considered the apomorphic state on the basis of ontogenetic evidence. Huys (1990*a*) demonstrated that the typical 3-segmented condition is accomplished at the final moult by secondary subdivision of the distal segment and allometric growth of the spinous apophysis. The atypical pattern in *A. typhlops*, resembling the condition of a copepodid V stage, is interpreted here as the result of neoteny, i.e. the decrease in developmental rate has delayed the segmentation beyond the final moult.

Male P3 endopod armature (character 21)
The modification of the male P3 endopod in esolinids has no effect on the number of armature elements. In particular, the homologue of the outer spine in the female is transformed into a spinous process or apophysis arising from the middle segment in the male (but see character 20), and the proximal inner seta on enp-2 of the 2-segmented endopod in the female is retained on enp-2 of the 3-segmented endopod in the male [typically 1.**1**.22**0** pattern]. The presence of the latter seta in males is a particularly conservative character in primitive laophontids, however, outside the esolinid grouping it is found only in *Onychocamptus* and one species group of the genus *Laophonte*. The fate of this seta during male development can only be traced in Laophontidae displaying the full complement of 3 inner setae in the female enp-2. In these species (Table 2) the endopodal armature pattern is most commonly [0–1.321] but can also be [0.311] in *Laophonte nordgaardi* Sars or [0.320] in some species of *Paralaophonte* Lang. Except for 6 species of *Laophonte* and all species of *Onychocamptus*, the proximal inner seta is consistently lost in the male, resulting in a 0.**0**.220 pattern. The only exceptions with 3 inner setae in the male are those that have lost sexual dimorphism altogether (*Folioquinpes*, *Paralaophonte innae* Chislenko, *P. aenigmaticum* Wells, Hicks & Coull). Vervoort (1964) reported a very long inner seta on the middle segment of *Paralaophonte pilosoma* but re-examination of the holotype (USNM reg. no. 109763) has proven this to be erroneous (Fig. 28E).

The loss of the proximal inner seta in the male is an apomorphy of pivotal importance in laophontid evolution since it unifies nearly 95% of all species. Since many genera have only 0, 1 or 2 inner setae in the female we have assumed that they are descendants from an ancestral stock which displayed the 3-setae condition in the female but lost the proximal one in the male.

Female P5 exopod armature (character 25)
Female esolinids can be readily identified by the setal arrangement around the outer margin of the P5 exopod. The two proximal setae are displaced so that their respective insertion sites have become superimposed on one another. Lang (1948) and Willen (1995) pointed out that a similar displacement also occurs in *Laophonte parvula* Sars (arrowed in Fig. 25G), however, we concur with the latter author that this is the product of convergence.

Results

Analysis was performed with PAUP 3.1.1 (Swofford, 1993) using the exact Branch and Bound algorithm (Hendy & Penny, 1982) that is guaranteed to find all most parsimonious trees (MPTs), with all characters set irreversible up and arbitrary solutions (zero-length branches) suppressed. Analysis of the complete data (Table 4) produced 84 MPTs with tree length 40 and consistency index 0.675. The strict component consensus tree is illustrated in Fig. 32 and has a slightly longer length (42) and lower consistency index (0.643). Relationships within the crown-group *Esola* are poorly resolved, however construction of the majority-rule component consensus tree revealed an additional group (*bulbifera-canalis-profunda*). This boreo-mediterranean majority component appears in 48 (57%) of the trees. *A. longiremis*, *A. hamondi* and *Esola* sp. *sensu* Chislenko (1967) all have different combinations of missing entries, however each is also a potential taxonomic equivalent of *A. typhlops* (Table 4) and can therefore be safely deleted (Wilkinson, 1995). Safe taxonomic reduction of these taxa reduces the number of MPTs to 14 but does not alter tree length or consistency index.

The strict component consensus (Fig. 32) reveals a strongly supported basal dichotomy which divides the Laophontidae into two major clades. In order to reflect the robustness of this dichotomy, subfamilial rank is attributed to the two corresponding lineages. The Esolinae subfam. nov. includes *Archilaophonte*, *Mourephonte* and all species previously assigned to *Esola*. It is supported by male antennulary segmentation (character 8) and the female P5 exopodal setation pattern (character 25).

The primitive position of *Archilaophonte* conjectured by Willen (1995) is confirmed. The genus represents the first offshoot in the evolution of the Esolinae and is tentatively defined by the following suite of autapomorphies: (a) 6-segmented ♀ antennule (segment 6 compound), (b) 2-segmented P1 exopod (fusion exp-2 and -3), (c) P1 enp-2 secondarily elongated P2, (d) P2 enp-2 with only 1 inner seta, (e) P3 enp-2 ♂ with very long sigmoid apophysis, (f) P5 exopod ♂ with 4 setae (loss of proximal inner seta), and (g) extremely elongation of caudal rami. In addition, the maxillulary palp shows a peculiar setal arrangement along the outer margin with 1 seta positioned at the base of the bisetose exopod. Outgroup comparison with the Normanellidae indicates that this seta is of endopodal origin and must therefore have been secondarily displaced to a more proximal position. The basal position of *Archilaophonte* is supported by the presence of (a) a spinous process on the posterior margin of the 2nd antennulary segment, (b) maxillulary endopod represented by 3 setae, (c) 3 setae on the maxillipedal syncoxa, and (d) the well developed ♂ P5 endopodal lobe bearing 2 long setae. The apomorphic alternatives of these characters (Table 3) in conjunction with the formation of a trifid compound element on

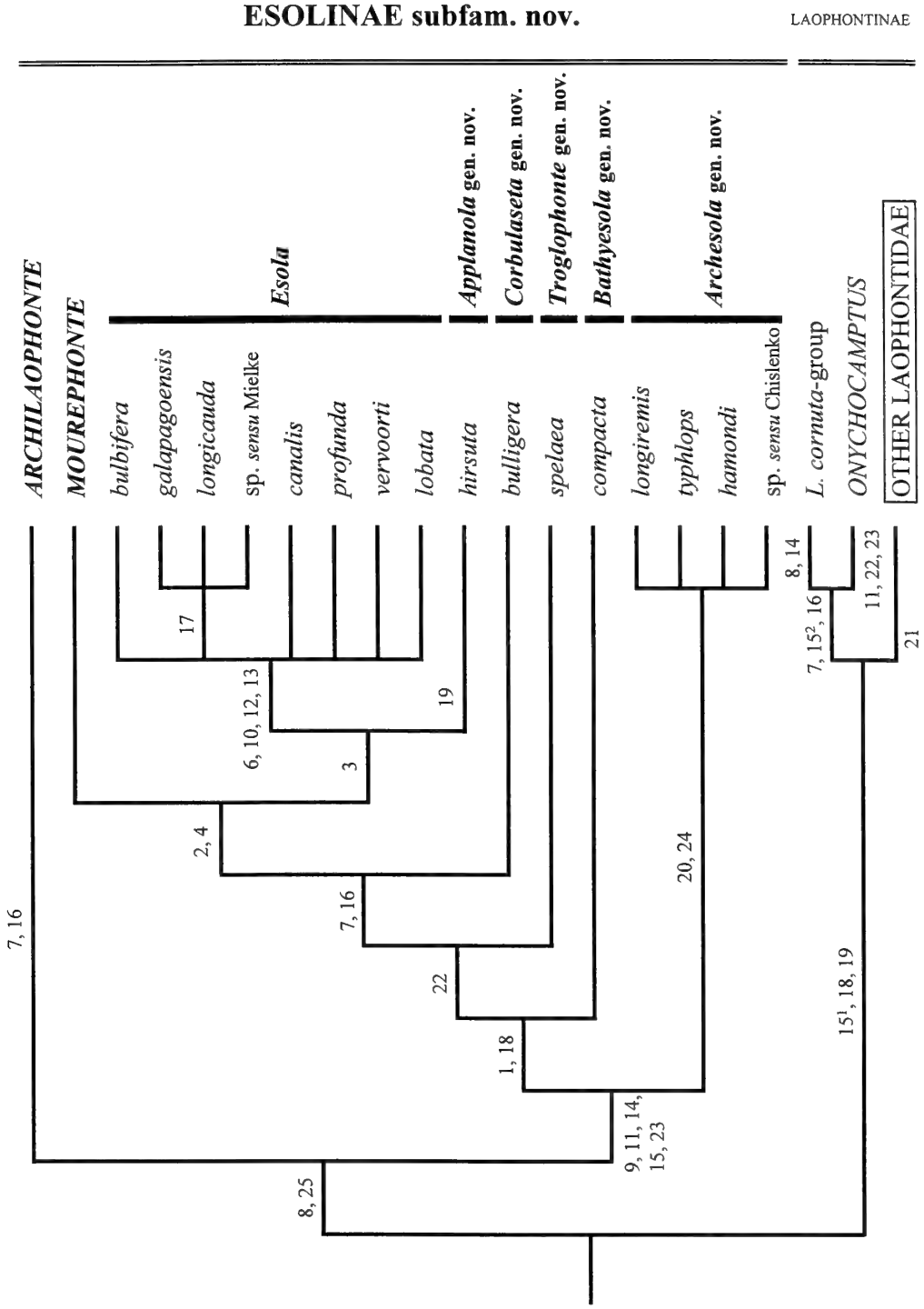

Fig. 32 Strict component consensus tree of 84 MPTs produced by parsimony analysis. Numbers refer to apomorphic character states listed in Table 3 (15^1 and 15^2 denote multistep states).

antennulary segment 4 (or 5 in ♂) provide overwhelming support for the monophyletic status of its sistergroup comprising *Mourephonte* and *'Esola' sensu lato*.

The phylogenetic analysis unequivocally identifies the paraphyly of the genus *Esola* (as originally and pre-cladistically conceived). Three northwestern European species and the unidentifiable *Esola* spec. *sensu* Chislenko (1967) form a basal monophyletic group (*Archesola* gen. nov.) defined by the 2-segmented ♂ P3 endopod and the presence of an articulating basal setophore on the fifth legs of both sexes. The degree of resolution within this clade will undoubtedly increase upon the discovery of the males of *A. hamondi* and *A. longiremis*.

Evolution in the outgroup of *Archesola* is marked by a stepwise addition of modified integumental pores. Initially, only paired anterodorsal (or -lateral) pores were present on the cephalothorax (in *compacta*, *bulligera* and possibly *spelaea*). This condition was

Table 4. States for characters listed in Table 3 [0 = plesiomorphic; 1 = apomorphic; 2 = further derived state]. Characters 14 and 22 are multistep characters.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
ARCHILAOPHONTE	0	0	0	0	0	0	1	1	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0	0	1
MOUREPHONTE	1	1	0	1	?	?	?	1	1	0	1	0	0	1	1	1	0	1	?	0	0	?	1	0	?
bulbifera	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	1	1	0	1
bulligera	1	0	0	0	0	0	1	1	1	0	1	0	0	1	1	1	0	1	0	0	0	1	1	0	1
galapagoensis	?	?	?	1	?	1	1	1	?	1	1	1	?	1	1	1	1	1	0	0	0	1	1	0	1
hirsuta	1	1	1	1	0	0	1	1	1	0	1	0	0	1	1	1	0	1	1	0	0	1	1	0	1
longicauda	1	1	1	1	?	1	1	1	1	1	1	1	1	?	1	1	1	1	0	0	?	1	1	0	1
longiremis	0	0	0	0	?	0	0	?	?	0	1	0	0	?	1	0	0	?	0	?	?	0	?	1	1
spelaea	?	?	0	0	?	0	0	?	?	?	1	?	?	?	?	0	0	?	0	0	1	1	1	0	?
typhlops	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1	1	1
canalis sp. nov.	1	1	1	1	1	1	1	?	1	1	1	?	1	1	1	1	0	1	0	?	?	1	?	0	1
compacta sp. nov.	1	0	0	0	0	0	0	?	1	0	1	?	0	1	1	0	0	1	0	?	?	0	?	0	1
hamondi sp. nov.	0	0	0	0	0	0	0	?	1	0	1	0	0	1	1	0	0	0	0	?	?	0	?	1	1
lobata sp. nov.	?	?	?	1	?	1	1	1	1	1	1	?	?	?	?	1	0	1	0	0	0	1	1	0	1
profunda sp. nov.	1	1	1	1	1	1	1	?	1	1	1	?	1	1	1	1	0	1	0	?	?	1	?	0	1
vervoorti sp. nov.	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	1	1	0	1
spec. *sensu* Chislenko (1967)	?	?	?	0	?	?	?	1	?	0	1	0	?	?	?	0	0	?	0	1	0	?	1	1	?
spec. sensu Mielke (1997)	?	?	?	1	?	1	1	?	1	1	1	?	?	?	?	1	1	1	0	?	?	1	?	0	1
Laophonte cornuta-group	0	0	0	0	0	0	1	1	0	0	0	0	0	1	2	1	0	1	1	0	0	0	0	0	0
Onychocamptus	0	0	0	0	0	0	1	0	0	0	1	0	0	0	2	1	0	1	1	0	0	2	1	0	0
OTHER LAOPHONTIDAE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0

further elaborated in both *Mourephonte* and the residual species of *Esola* by the development of an accessory pair of anteroventral pores on the cephalothorax (character 2) and of ventral or medial pores on the caudal rami (character 4). Finally, the lateral pores on the genital (double-)somite (character 3) evolved not until after the divergence of *Mourephonte*.

The genus *Esola* is redefined here to encompass the terminal polychotomy containing the type species *E. longicauda* and 7 other species (Fig. 32). This strongly supported, cosmopolitan crown-group is characterized by distinctive labral ornamentation, caudal ramus sexual dimorphism, formation of 3 spinous processes on the first antennulary segment and modification of segment 5 in the male antennule *E. hirsuta* is the only species that shares genital cup-shapes pores with this clade, however it is excluded from *Esola* and placed in a monotypic genus *Applanola* on account of the following autapomorphies: (1) dorsoventrally depressed body morphology, (2) elongation of mandibular palp, (3) modification of P1 endopod, (4) exopodal sexual dimorphism of P2–P3, (5) loss of outer spine on P2 enp-2, and (6) strong reduction of the male sixth legs. The sexual dimorphism on the P2–P3 exopod is unique in the Esolinae. Although this character is globally homoplastic within the Laophontidae it can be informative locally (see Lee & Huys, 1999) and should not therefore be routinely ignored in phylogenetic analyses.

The three remaining species, *compacta*, *spelaea* and *bulligera*, are identified as independent lineages splitting off successively between the basal *Archesola* clade and the terminal ((*Mourephonte* + *Esola*) + *Applanola*) clade. *Corbulaseta* gen. nov., accommodating *E. bulligera*, is most closely related to the latter clade because of shared fusions in the female antennule (segments 6–7) and P1 exopod (exp-2 and -3). The modified distal inner seta forming a trapping-basket is a unique autapomorphy for this genus. The position of *Troglophonte* is tentative pending the confirmation of cup-shaped pores on the cephalothorax and of the armature patterns of P2 exopod and P5 in both sexes. The basal position of the genus *Bathyesola* is caused by its retention of the maximum number of setae on the female P5 baseoendopod.

The genus *Mourephonte* is radically divergent from other esolinids. The extreme development of the P1, the complete absence of the P2 endopod, the loss of the inner seta on the P2–P4 exopods and the wide separation of the apical setae on P4 enp-2 form a remarkable combination of autapomorphies which places it on a distinct evolutionary lineage, ruling out possible inclusion in the genus *Esola* under a broader concept.

The residual laophontids, comprising 95% of the known species, are grouped in the subfamily Laophontinae. All 54 genera have lost the inner seta on P1 enp-1 and the outer spine on P2 enp-2, and bear a maximum of 2 setae on the maxillipedal syncoxa (absence of proximal seta). With the exception of the genus *Onychocamptus* and the *Laophonte cornuta*-group all Laophontinae are characterized by the P3 endopod sexual dimorphism involving the loss of the proximal inner seta of enp-2 (character 21). The isolated position of the *cornuta*-group (= *Laophonte* Group I + *adduensis* + *ciliata*: Table 2) testifies to the widely accepted polyphyletic status of the genus *Laophonte* and has major nomenclatural consequences because of its inclusion of the type species *L. cornuta* Philippi. Restriction of the generic concept to the *cornuta*-group will require the other 37 species of *Laophonte* to be re-allocated to other existing or new genera. This is a major task which can only be accomplished by sound phylogenetic analysis involving the remaining laophontinid genera. The sistergroup relationship between the *cornuta*-group and *Onychocamptus* depicted in Fig. 32 is not be taken as absolute since other advanced but closely related genera such as *Folioquinpes* have deliberately been omitted from the outgroup to the Esolinae. Although inclusion of these genera in future analyses may introduce additional basal nodes changing the relative position of *Laophonte* and *Onychocamptus*, we envisage that the latter will consistently show up as an early speciation event predating the evolution of the other Laophontinae.

Subfamilial division

ESOLINAE subfam. nov.

Rostrum delimited at base by surface suture; antennule ♀ 6- or 7-segmented, usually without spinous process on segment 2 but frequently with processes on segment 1; 7-segmented and haplocerate or subchirocerate in ♂, with only 2 segments distal to geniculation;

proximal aesthetasc typically fused to 2 setae (except *Archilaophonte*). Antennary exopod with 4 well developed setae. Mandible typically biramous (except *Applanola* and *Mourephonte*). Maxilla with 3 endites on syncoxa. Maxilliped with 2–3 setae on syncoxa.

P1 with 2- or 3-segmented exopod, retaining full complement of setae (0.0.022 or 0.023); enp-1 occasionally with inner seta. P2 enp-2 with outer spine (except *Applanola*) or entire P2 endopod absent (*Mourephonte*). P3 endopod ♂ retaining proximal inner seta of ♀ enp-2 (except for *Troglophonte* where it is lost in both sexes). Armature formula as follows:

	Exopod	Endopod
P2	0.1.123	0–1.(1–2)2(0–1) or absent
P3	0.1.(1–2)23	0–1.321
P4	0.1.(1–2)23	0–1.221

P5 ♀ with separate rami; exopod elongate, with 6 setae/spines; proximal two setae along outer margin with superimposed insertion sites; baseoendopod trapezoid, slightly developed, with 4–5 setae/spines. P5 ♂ without endopodal lobe (except for *Archilaophonte*, bearing 2 long setae), no endopodal armature; exopod 5 setae/spines.

Typically with cup-shaped transformed pores on cephalothorax, genital (double-)somite, and/or caudal rami.

TYPE GENUS. *Esola* Edwards, 1891

OTHER GENERA. *Mourephonte* Jakobi, 1953; *Archilaophonte* Willen, 1995; *Applanola* gen. nov.; *Archesola* gen. nov.; *Bathyesola* gen. nov.; *Corbulaseta* gen. nov.; *Troglophonte* gen. nov.

Laophontinae T. Scott, 1905

Antennule ♂ with up to 3 segments distal to geniculation; proximal aesthetasc fused to 1 seta. Mandible typically uniramous. Maxilliped with maximum 2 setae on syncoxa. P1 enp-1 without inner seta. P2 enp-2 without outer spine. P3 endopod ♂ typically not retaining proximal inner seta of ♀enp-2 (except for *Laophonte cornuta*-group and *Onychocamptus*).

Proximal outer setae of ♀ P5 exopod with distinctly separated insertion sites.

Cup-shaped transformed pores on cephalothorax, genital (double-) somite, and/or caudal rami never present.

TYPE GENUS. *Laophonte* Philippi, 1840

OTHER GENERA. Fifty-five; see Lang (1948), Bodin (1997), George (1997) and Lee & Huys (1999) for complete list.

KEY TO GENERA OF ESOLINAE

1. P2 endopod absent ..... *Mourephonte* Jakobi, 1953.

   P2 endopod present, 2-segmented ..... 2.

2. Antennulary segment 2 with large spinous process along anterior margin; P2 enp-2 with 1 inner seta; P5 baseoendopod ♂ with 2 long setae ..... *Archilaophonte* Willen, 1995.

   Antennulary segment 2 without spinous process along anterior margin; P2 enp-2 with 2 inner setae; P5 baseoendopod ♂ without setae ..... 3.

3. Antennule ♀6-segmented; P1 exopod 2-segmented; caudal rami with medial or ventral modified pores ..... 4.

   Antennule ♀7-segmented; P1 exopod 3-segmented; caudal rami without such pores ..... 6.

4. Body short, dorsoventrally flattened; P2 enp-2 outer spine absent; P3 exopod ♂ strongly modified ..... *Applanola* gen. nov.

   Body elongate, sub-cylindrical; P2 enp-2 outer spine present; P3 exopod ♂ not modified ..... 5.

5. Antennulary segment 1 with 3 spinous processes along posterior margin; distal inner seta of P4 endopod not transformed; caudal rami ♀ modified, with bulbous swelling dorsally, ventrally and medially ..... *Esola* Edwards, 1891.

   Antennulary segment 1 without distinct spinous processes; distal inner seta of P4 endopod transformed; caudal rami not sexually dimorphic, cylindrical ..... *Corbulaseta* gen. nov.

6. P3–P4 exp-3 with 1 inner seta; P3–P4 enp-1 without inner seta ..... *Bathyesola* gen. nov.

   P3–P4 exp-3 with 2 inner setae *; P3–P4 enp-1 with inner seta ..... 7.

7. P3 enp-2 with 3 inner setae; P3 endopod ♂ 2-segmented; P5 baseoendopod with long articulating setophore in both sexes ..... *Archesola* gen. nov.

   P3 enp-2 with 2 inner setae; P3 endopod ♂ 3-segmented; P5 baseoendopod of both sexes without articulating setophore ..... *Troglophonte* gen. nov.

* Note that Chappuis' (1938) setal formula of P3 exp-3 can also be interpreted as 123, implying the presence of only 1 inner seta.

ECOLOGICAL RADIATION OF ESOLINAE

Although none of the 18 species can be considered as truly cosmopolitan, the subfamily as a whole occurs in all oceanic basins, including the Antarctic Ocean. Superimposing habitat utilization upon the phylogeny presented in Fig. 32 reveals an interesting but complex ecological radiation pattern. Esolinae are essentially shallow water inhabitants, however, the variety of additional habitats exploited by this lineage is startling for its small number of known species. Considered against the background of the overwhelming evolutionary success of their sister-lineage Laophontinae, esolinids can be viewed as relicts of a formerly diverse group.

Lee & Huys (1999) reviewed published deepwater records of Laophontidae and regarded the colonization of the deep sea by this family as remarkably unsuccessful. There is no single lineage containing all deepwater forms, and the three exclusively bathyal genera in the Laophontinae, *Cornylaophonte* Willen, *Weddellaophonte* Willen and *Bathylaophonte* Lee & Huys can be considered as independent colonists of this habitat. Colonization of the deep sea by the Esolinae follows a similarly erratic trend with early attempts by the monotypic genera *Archilaophonte* in the Antarctic and *Bathyesola* in the western Pacific. Within the genus *Esola*, *E. profunda* represents a third, secondary deepwater invasion derived from a shallow water inhabiting ancestral stock (Fig. 32).

According to Pesce (1985) and Rouch (1986) the genus *Troglophonte* is likely to be derived from a marine ancestor stranded during the lowering of sea level during the Tertiary. It is highly endemic to freshwater lenses in several Apulian caves in southern Italy (Chappuis, 1938). These caves are separated from the littoral zone by macroporous karstic rock and exhibit a detectable tidal current which appears insufficient to ensure substantial mixing of the water inside the caves. The strong stratification with freshwater lenses overlying the poorly oxygenated deeper layers has clearly prevented the establishment of a diverse marine benthic fauna. Rather than considering *Troglophonte* a Tethyan relict, its present restricted distribution can also be regarded as a relatively recent landward habitat range extension from a primarily shallow-subtidally residing ancestral stock. Although some Laophontidae are regularly

found in salt-marsh and mudflat habitats within river estuaries (Noodt, 1957; Barnett, 1968; Bodin, 1976) or in brackish lagoons (Heip, 1969; Hamond, 1972), tolerance to oligohalinity may have appeared convergently only twice in the family. Both colonization events presumably occurred early in the evolution of the family (Fig. 32), however their nature is fundamentally different. The evolutionary success of the *Troglophonte* lineage has clearly remained limited, both in dispersal and speciation. It can be considered as a freshwater incursion without further radiation or diversification. The second invasion of low salinity environments is cosmopolitan in scope and probably of Tethyan origin, containing the genera *Onychocamptus* Daday and *Folioquinpes* Fiers & Rutledge (Lee & Huys, 1999).

Little is known about the possible dispersal of Laophontidae in marine caves. Pesta (1959) reported *E. rosei* from a submarine cave near Naples and several unidentified Laophontidae were recorded by Huys (1996) from the anchialine Walsingham Cave on Bermuda. Examination of samples from Caye Chapel Cave in Belize, the type locality of the recently discovered family Novocriniidae (Huys & Iliffe, 1998), resulted in the discovery of a single male belonging to a new genus of Esolinae. The new genus has several characters in common with *Archilaophonte* such as the presence of a spinous process on the second antennulary segment, the displacement of the outermost endopodal seta on the maxillule, the presence of 3 setae on the maxillipedal syncoxa, P1 with 2-segmented exopod and elongate enp-2, P2 enp-2 with only 1 inner seta and presence of a very long apophysis on P3 endopod. Phylogenetic analysis identified the Belize genus unambiguously as the sistergroup of *Archilaophonte*, suggesting the evolution of an independent cavernicolous lineage in the western Atlantic.

The genus *Archesola* is exclusively boreo-arctic in distribution and restricted to the Atlantic basin, with a single known outlier from the Black Sea (Por, 1959). Its southernmost limit based on reliable records is Norfolk (England), however, confirmation of the doubtful records of *A. longiremis* from the south coast of England (Wells, 1961, 1963, 1970) and North Carolina (Coull, 1971) may extend this limit further southward. The genus occurs primarily at higher latitudes, showing limited dispersal in Arctic waters such as the White Sea (Brotskaya, 1961; Chislenko, 1967). It is suggested that the strongly discontinuous, bipolar distribution of the two basal clades, with *Archesola* restricted to northern Europe and *Archilaophonte* to the Antarctic, indicates a wider, perhaps continuous, horizontal zonation of primitive stenothermal esolinids at greater depths. This trend of 'Equatorial Submergence' appears to be supported by the discovery of *Bathyesola* in the deep tropical western Pacific, the first lineage to diverge after *Archesola* (Fig. 32).

A major event in the evolution of the Esolinae was the episode of rapid speciation within the genus *Esola*. This event is revealed as a polychotomy in the cladogram (Fig. 32) although it is clear that the low resolution is partly attributable to the abundance of missing entries for several taxa which are known from one sex only (Table 3). Many of these species are small-sized (Table 1) and adapted to a mesopsammic life-style in shallow subtidal localities and sandy beaches, while others are frequently found associated with algal substrates. Results show that only a fraction of the species is known. Although the genus assumes a cosmopolitan distribution it is predominantly restricted to the circum-tropical belt. This zone coincides with the former Tethyan seaway separating the northern and southern continents, which continued into Palaeogene times with free marine continuity along its length not being interrupted until the beginning of the Neogene. One Pacific-Caribbean subgroup, comprising *E. longicauda*, *E. galapagoensis* and *Esola* sp. (Fig. 32), probably originated from an ancestral stock in the western Pacific. From there, eastward dispersal was greatly influenced by tectonic plate movement, particularly the formation of the Caribbean plate at the beginning of the Oligocene. This was established by decoupling of the eastward protruding tongue of the East Pacific plate, causing the formation of a subduction zone along what is now the western coast of southern Central America, and the subsequent westward motion of North and South America past a nearly stationary Caribbean plate (Malfait & Dinkelman, 1972; Coney, 1982). The entry of the ancestor of *E. longicauda* into the Caribbean must have preceded the closing of the Panama land bridge approximately 3.1–3.5 Ma (Keigwin, 1978).

Applanola displays a more disjunct distribution than its sistergroup *Esola*, provided that Pesta's (1916) record from the Gulf of Guinea is correct. The dorsoventrally depressed body, robust maxillipeds and powerful P1 endopod indicate that *A. hirsuta* may be loosely associated with invertebrate hosts. Thompson & A. Scott (1903) obtained the species from washings of pearl oysters and other dredged invertebrates but did not present any firm evidence for a clear association.

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