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

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CONTENTS

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

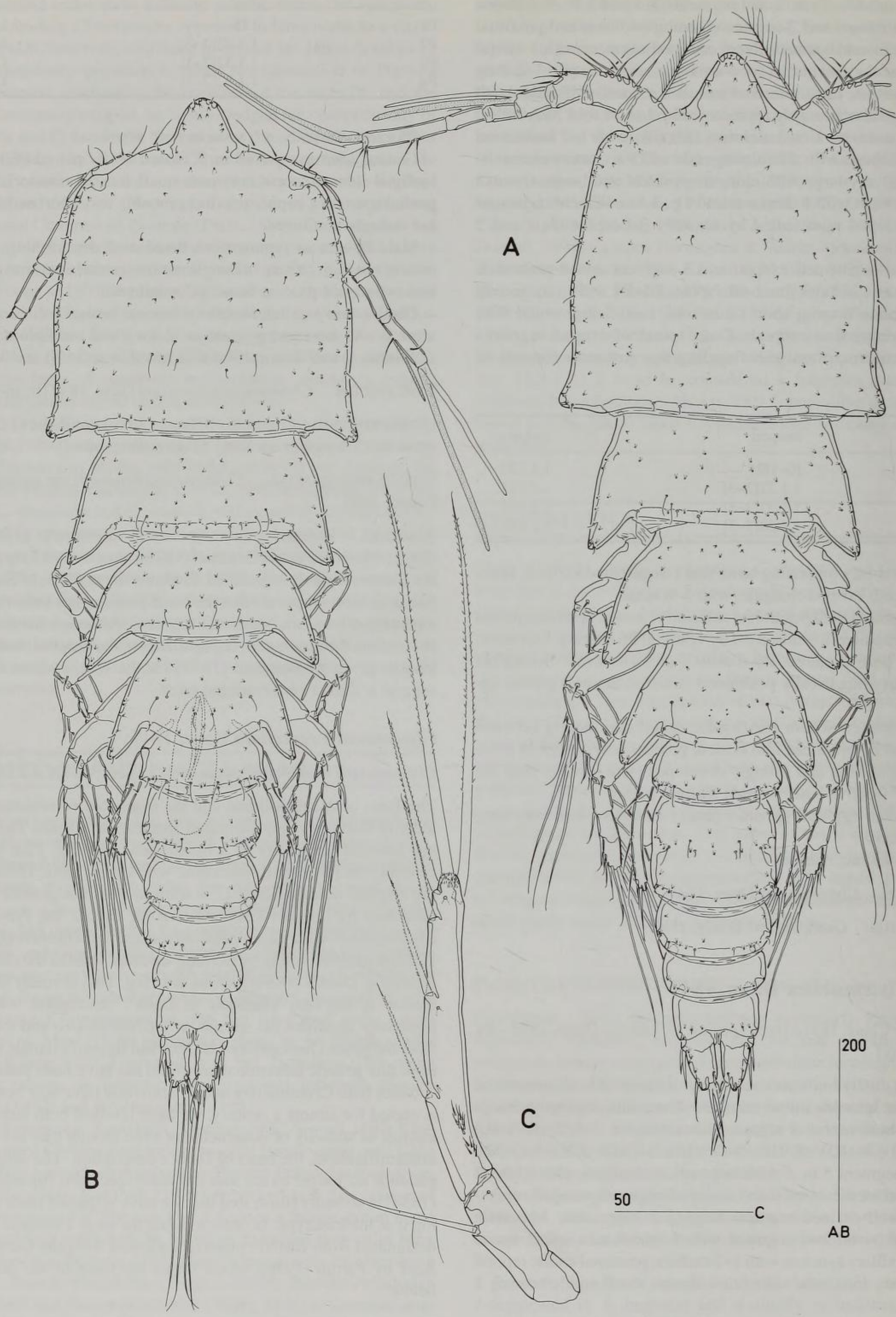


Fig. 1 *Clytemnestra scutellata* Dana, 1847. A, Habitus ♀, dorsal; B, habitus ♂, dorsal; C, P5 ♀, anterior. [A, C based on neotype].

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

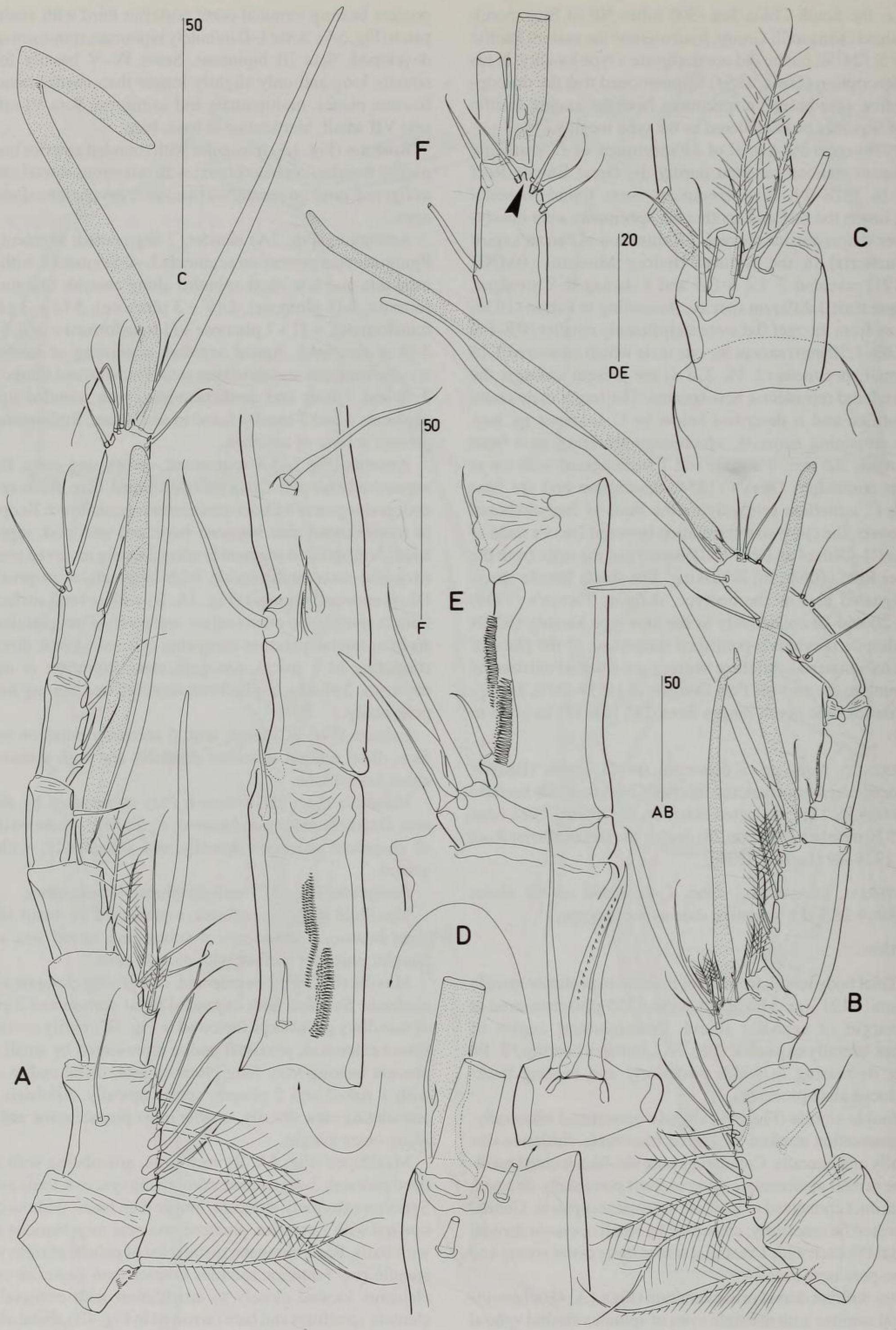


Fig. 2 *Clytemnestra scutellata* Dana, 1847. A, Antennule ♀, dorsal; B, antennule ♂, ventral; C, antennulary segment 3 ♂, anterior; D, antennulary segments 4–7 ♂, anterior [distal portion of segment 7 and proximal portion of segment 4 omitted]; E, antennulary segments 5–6 ♂, ventral; F, antennulary segment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

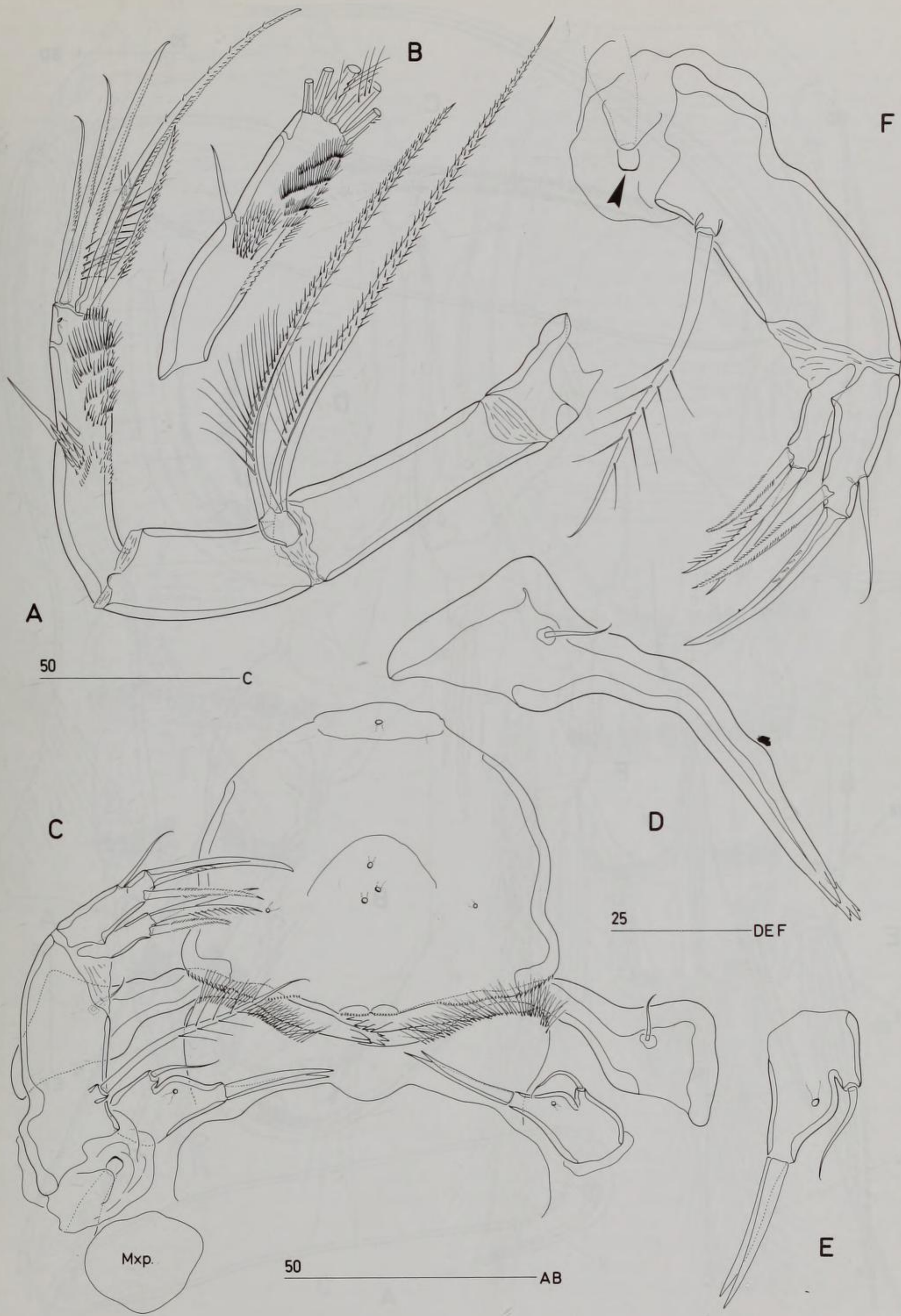


Fig. 3 *Clytemnestra scutellata* Dana, 1847 (♀). A, Antenna, outer; B, distal antennary endopod segment, inner; C, oral area showing position of labrum, paragnaths, mandibles, maxillules and right maxilla [position of maxilliped (Mxp.) indicated], ventral; D, mandible, posterior; E, maxillule, posterior;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

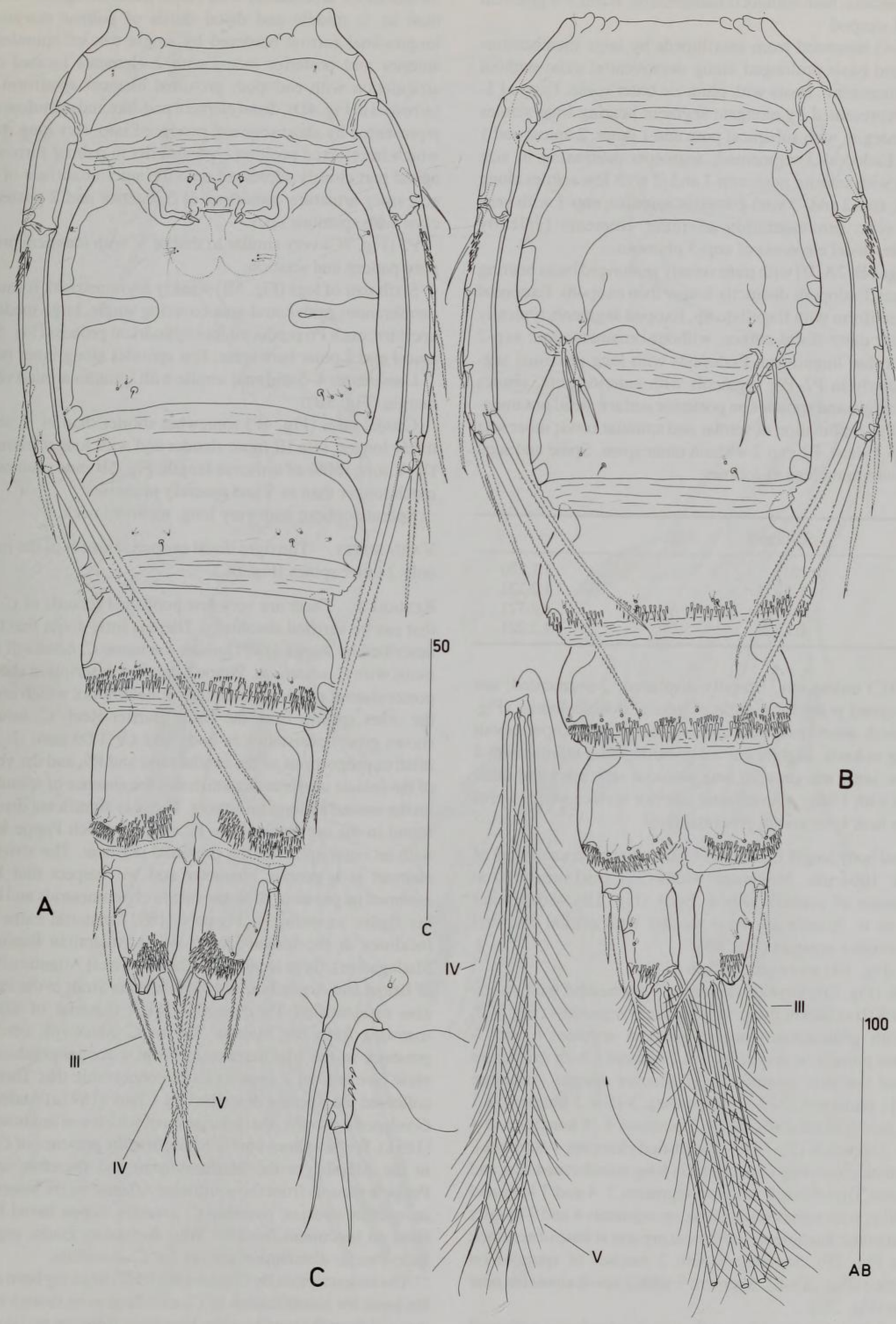


Fig. 5 *Clytemnestra scutellata* Dana, 1847. A, Urosome ♀, ventral; B, urosome ♂, ventral [inset showing setae IV–V at full length]; C, P6 ♂, ventral. [A based on neotype]

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].

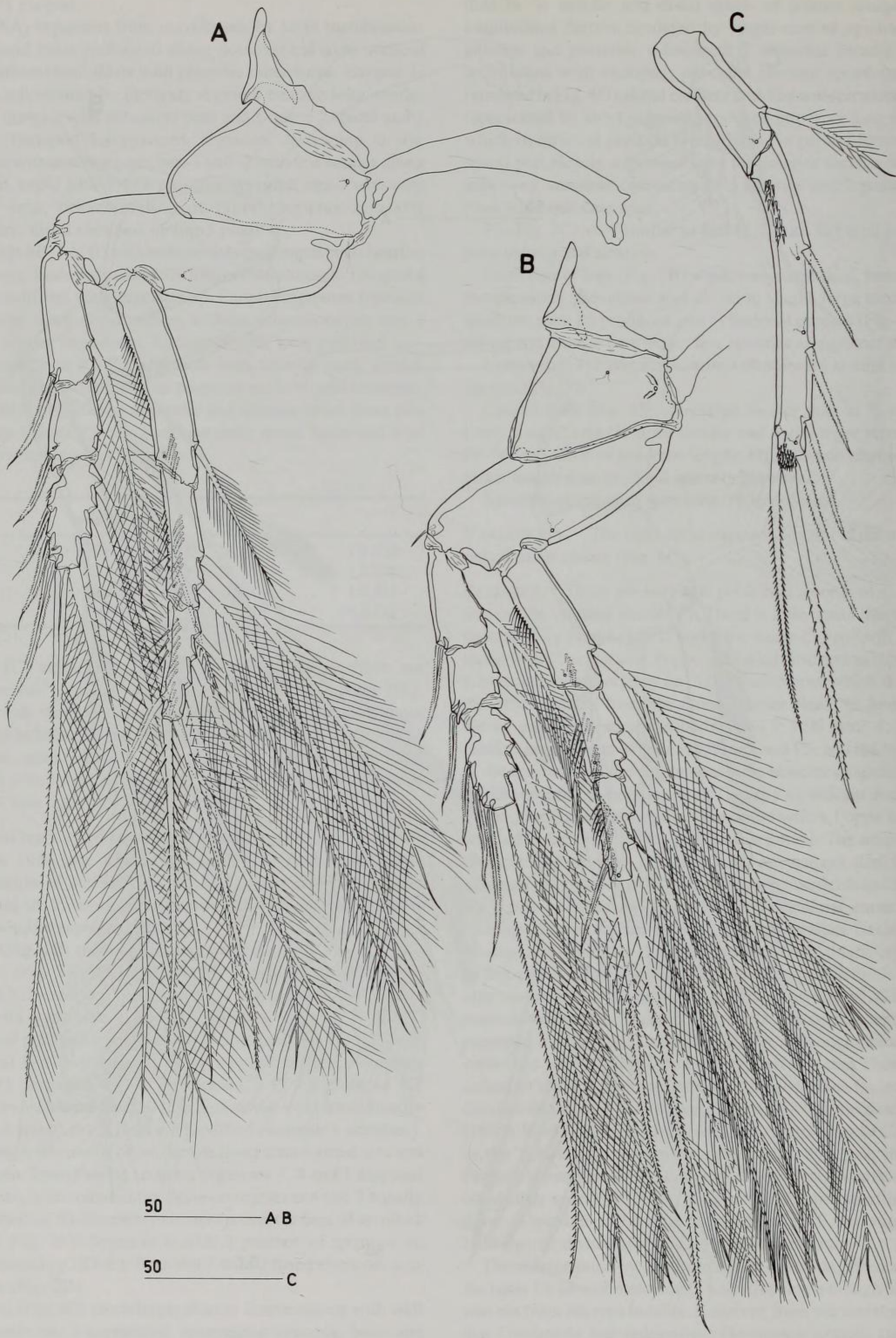


Fig. 7 *Clytemnestra scutellata* Dana, 1847. A, P3 ♀, anterior; B, P4 ♀, anterior; C, P5 ♂, anterior. [A, B based on neotype].

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

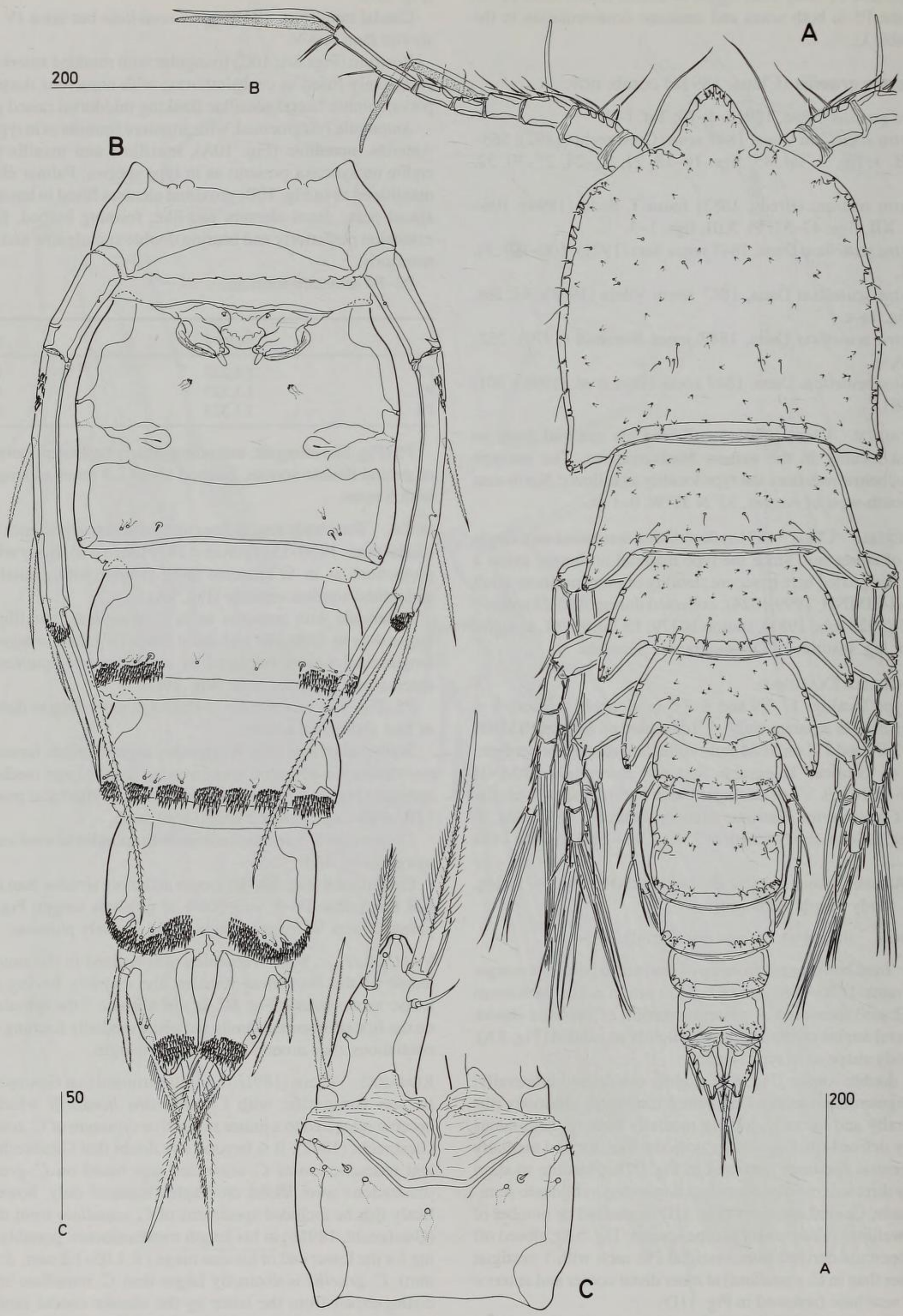


Fig. 8 *Clytemnestra gracilis* (Claus, 1891*a*) comb. nov. (♀) A, Habitus, dorsal; B, urosome, ventral; C, anal somite and right caudal ramus, dorsal.

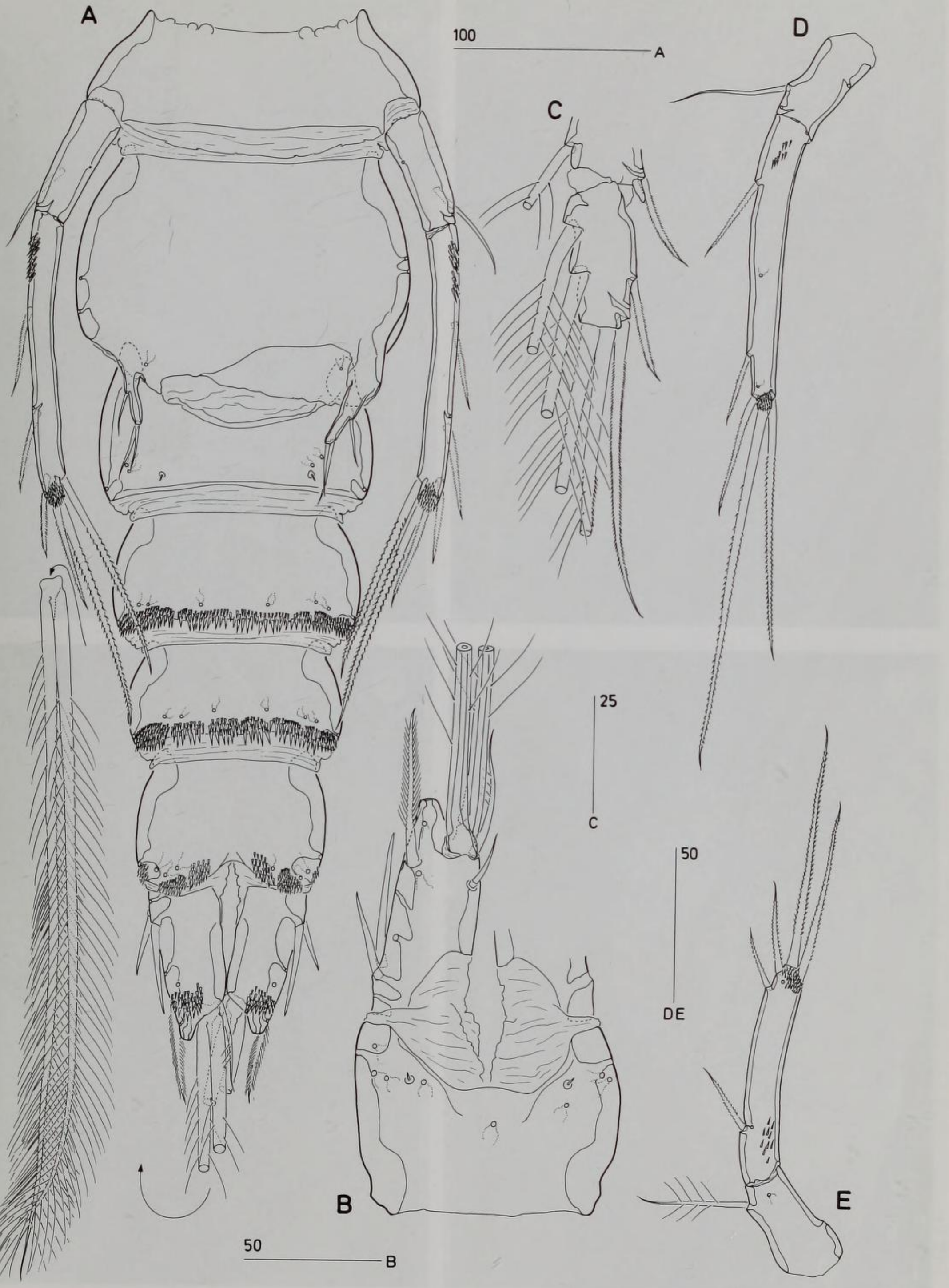
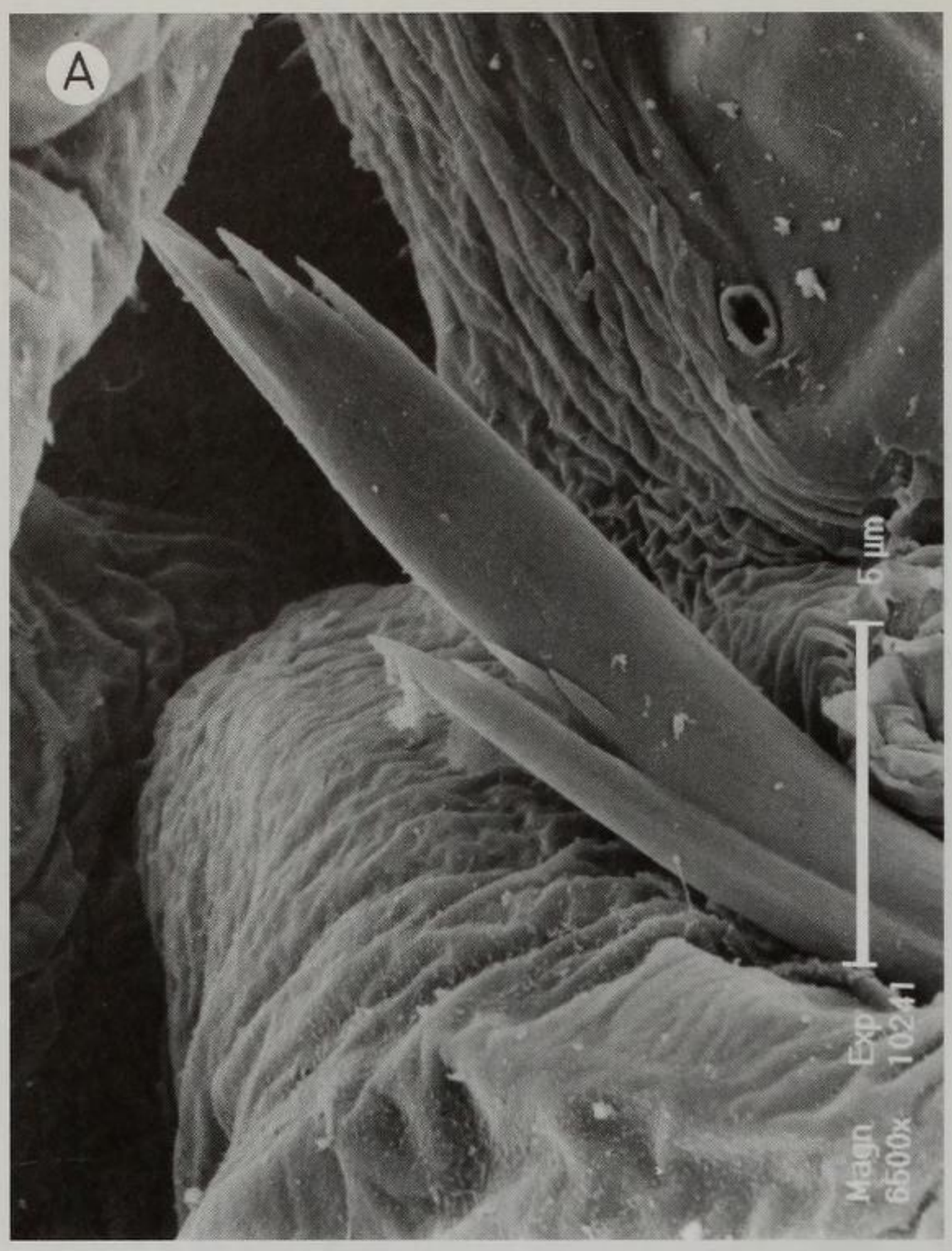
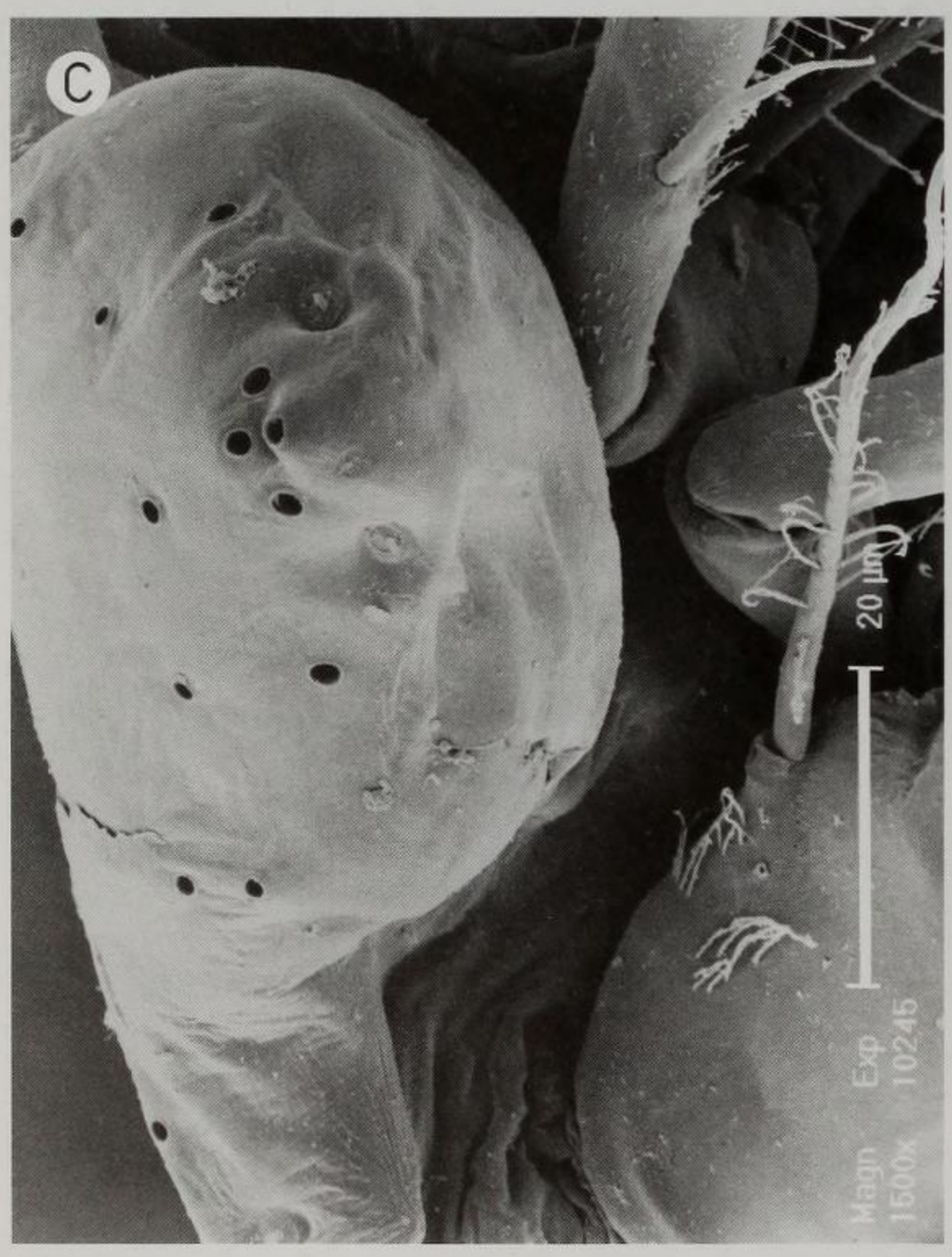


Fig. 9 *Clytemnestra gracilis* (Claus, 1891*a*) comb. nov. (♂) A, Urosome, ventral [inset showing setae IV–V]; B, anal somite and right caudal ramus, dorsal. *Clytemnestra farrani* sp. nov. C, P2 exp-3 ♀, anterior; D, P5 ♀, anterior; E, P5 ♂, anterior.





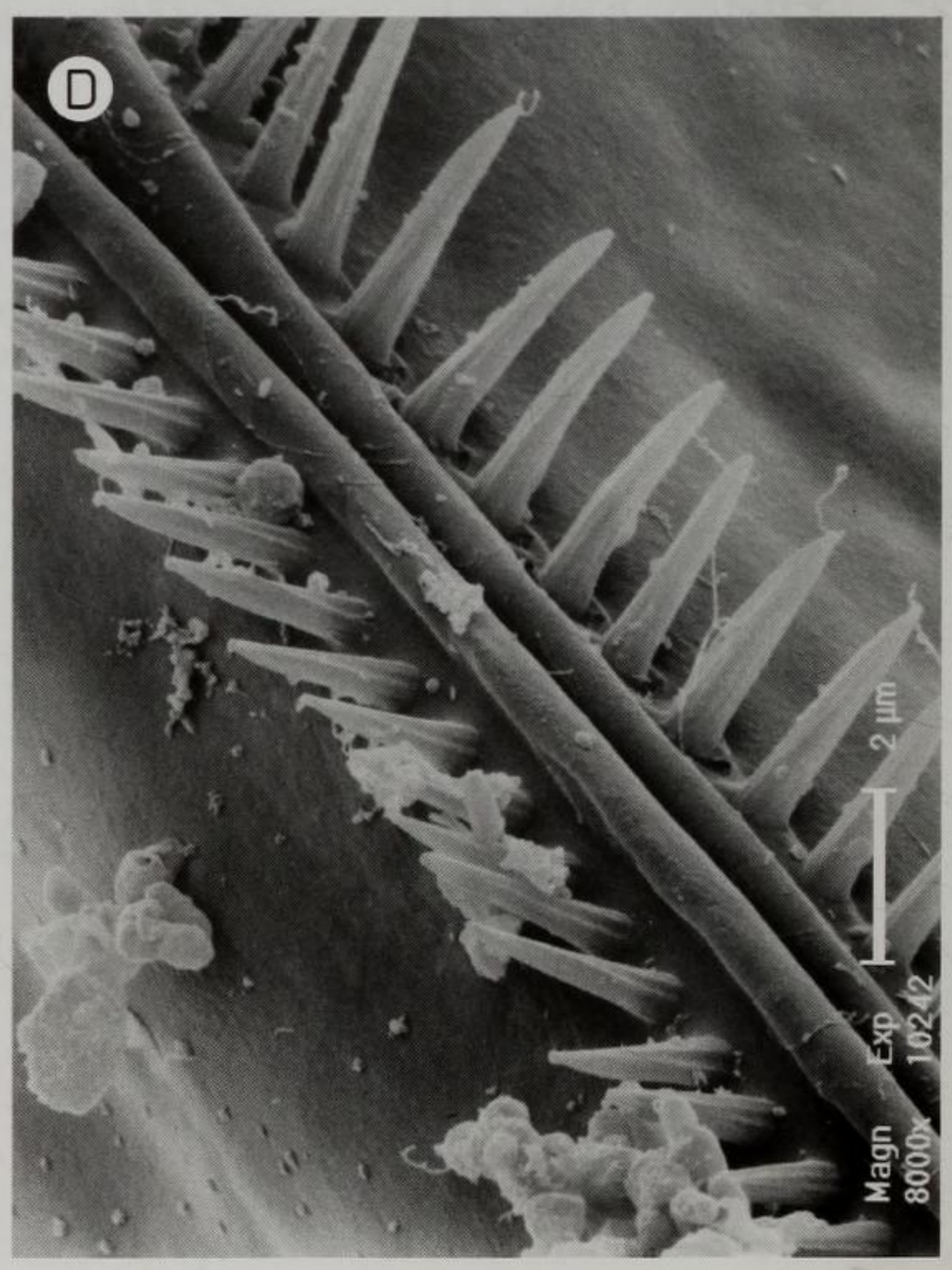
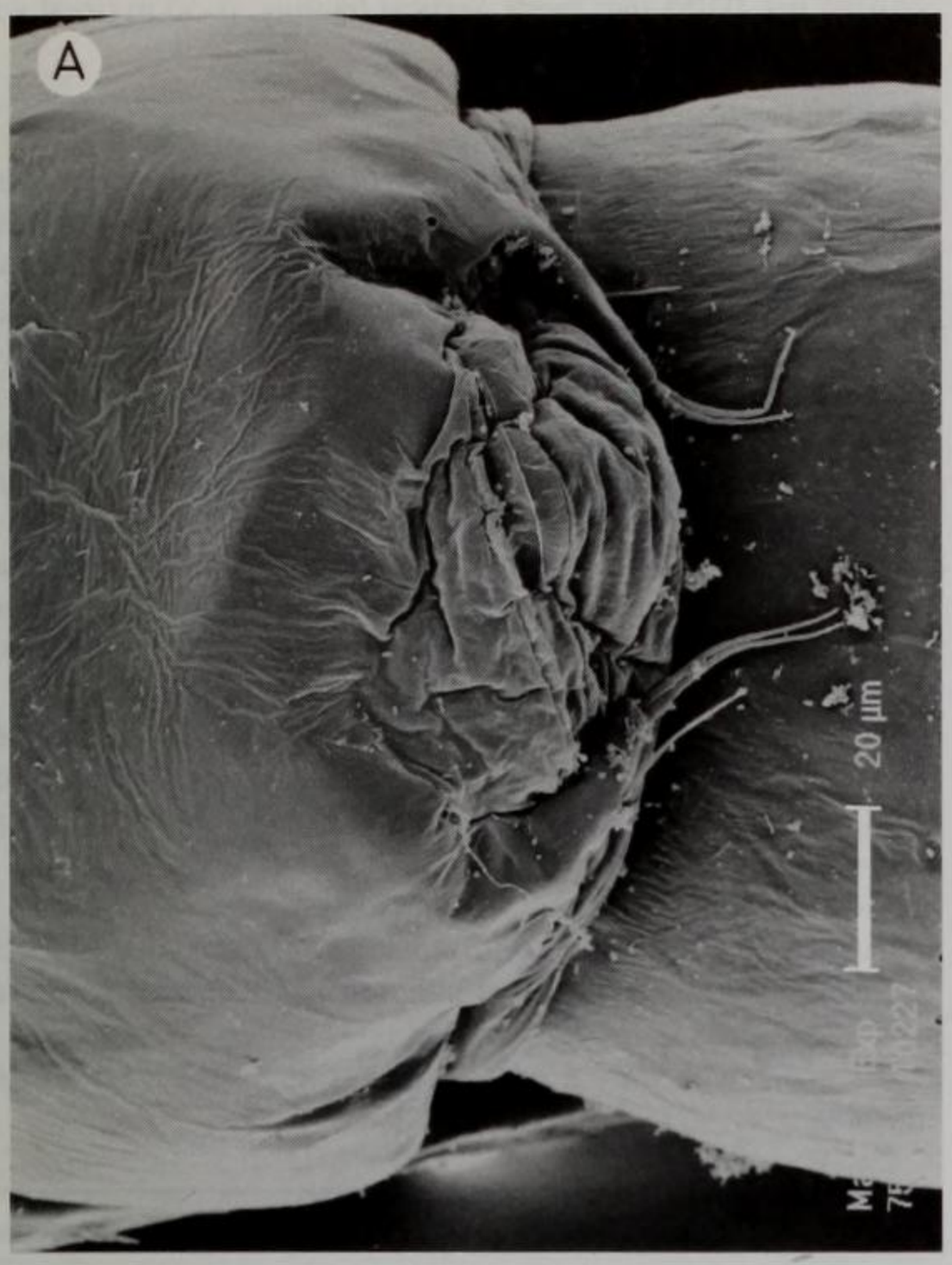
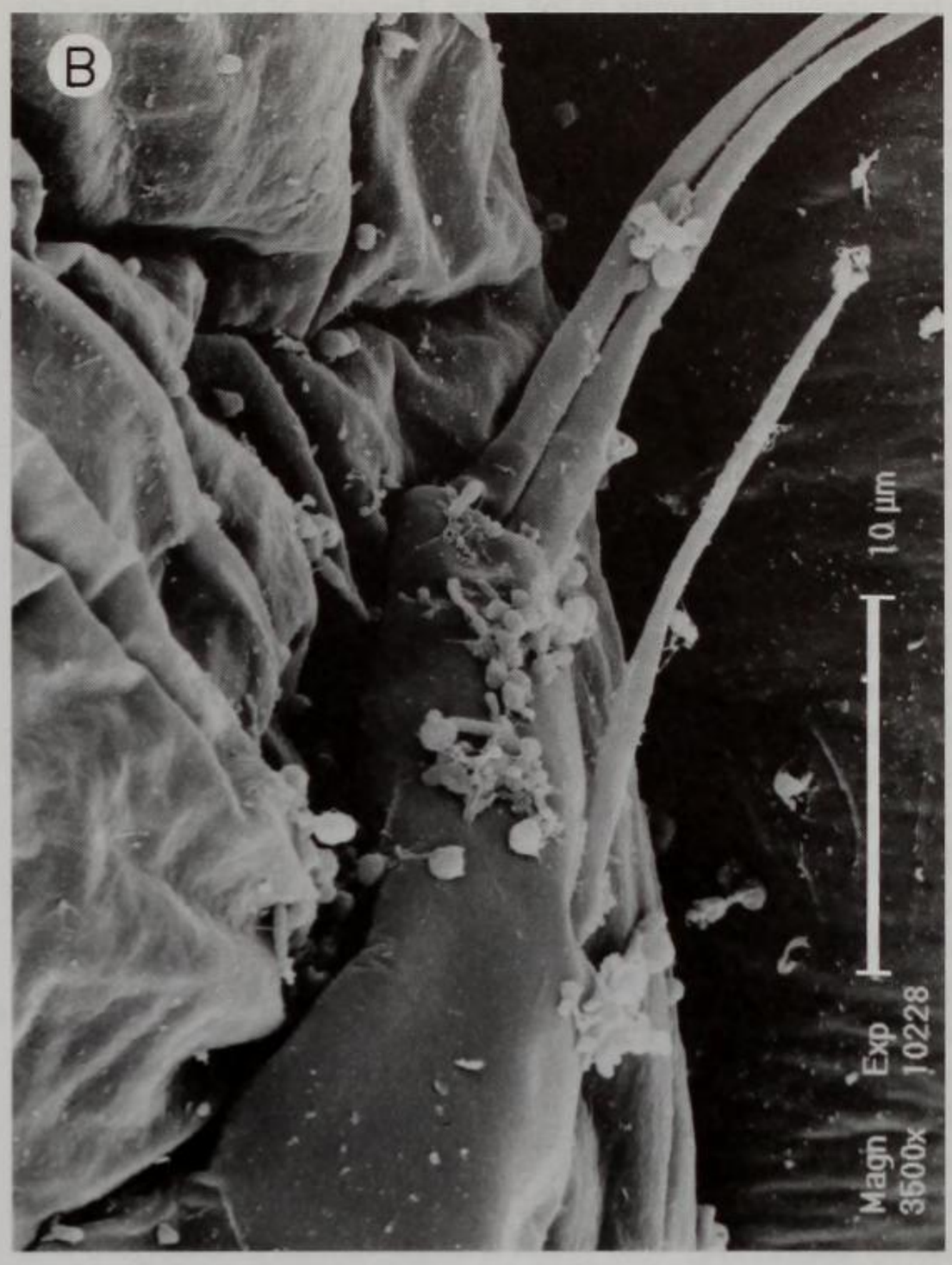


Fig. 10 *Clytemnestra gracilis* (Claus, 1891*a*) comb. nov. SEM photographs. A, Mandibular gnathobase ♀; B, maxilliped ♀, palmar elements; C, rostrum ♀, frontal; D, maxilliped ♂, palmar furrow.





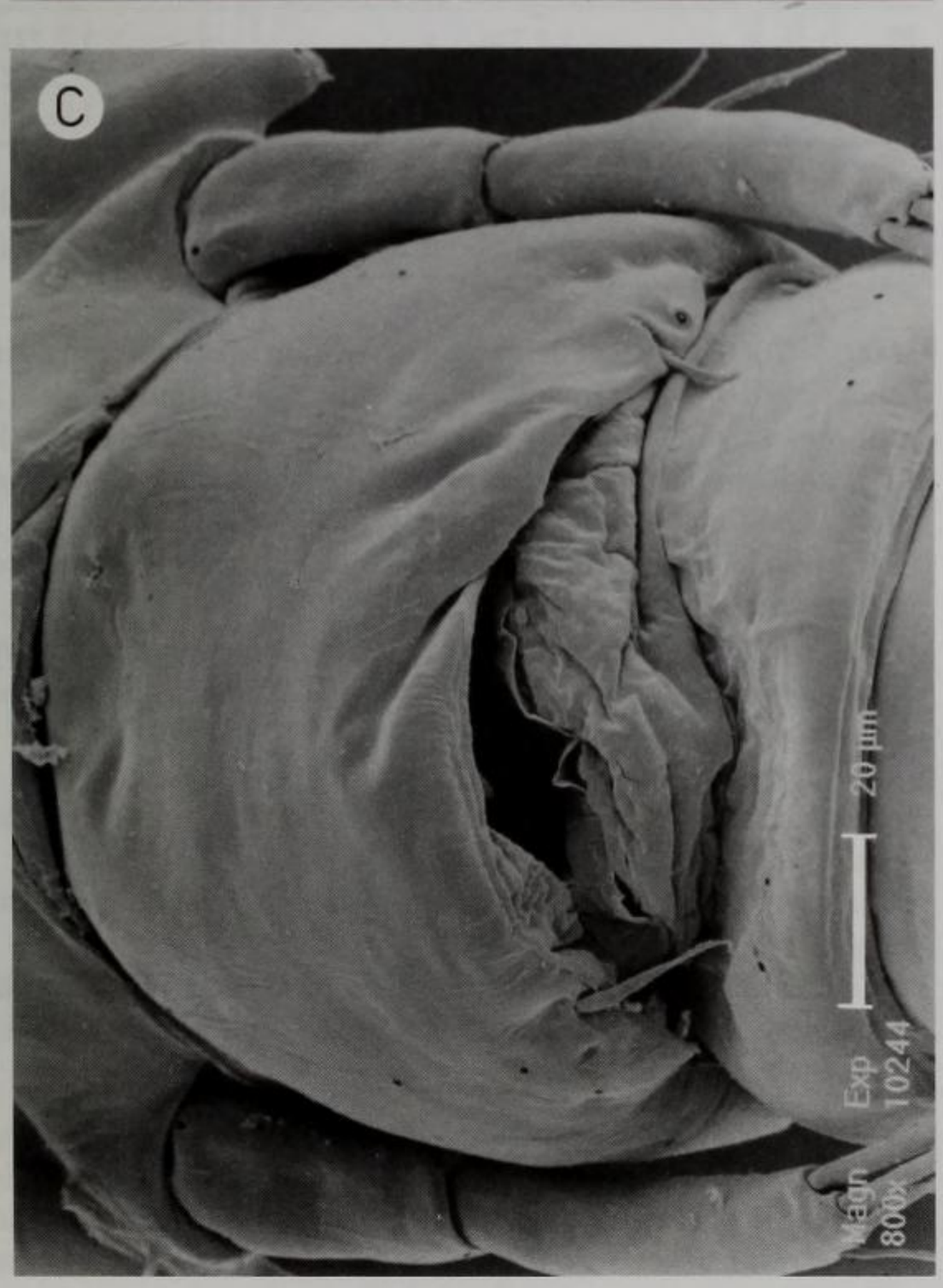


Fig. 11 *Clytemnestra gracilis* (Claus, 1891*a*) comb. nov. SEM photographs. A, Genital aperture and sixth legs ♂; B, P6 ♂; D, genital field ♀[position of copulatory pore arrowed]. *Goniopsyllus clausi* sp. nov. C, Genital aperture and sixth legs ♂.

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

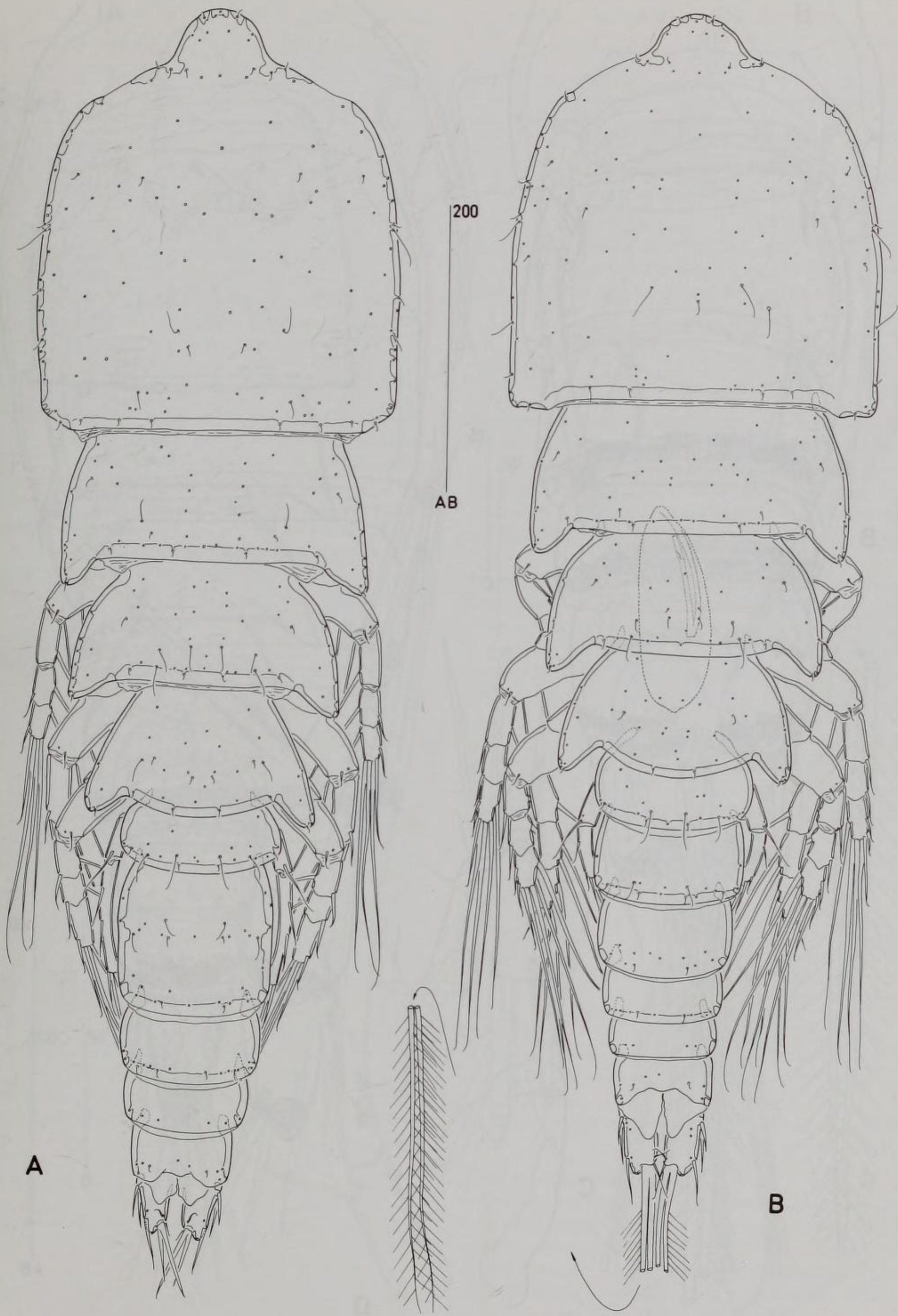


Fig. 12 *Clytemnestra farrani* sp. nov. A, Habitus ♀, dorsal; B, habitus ♂, dorsal [inset showing setae IV–V at full length].

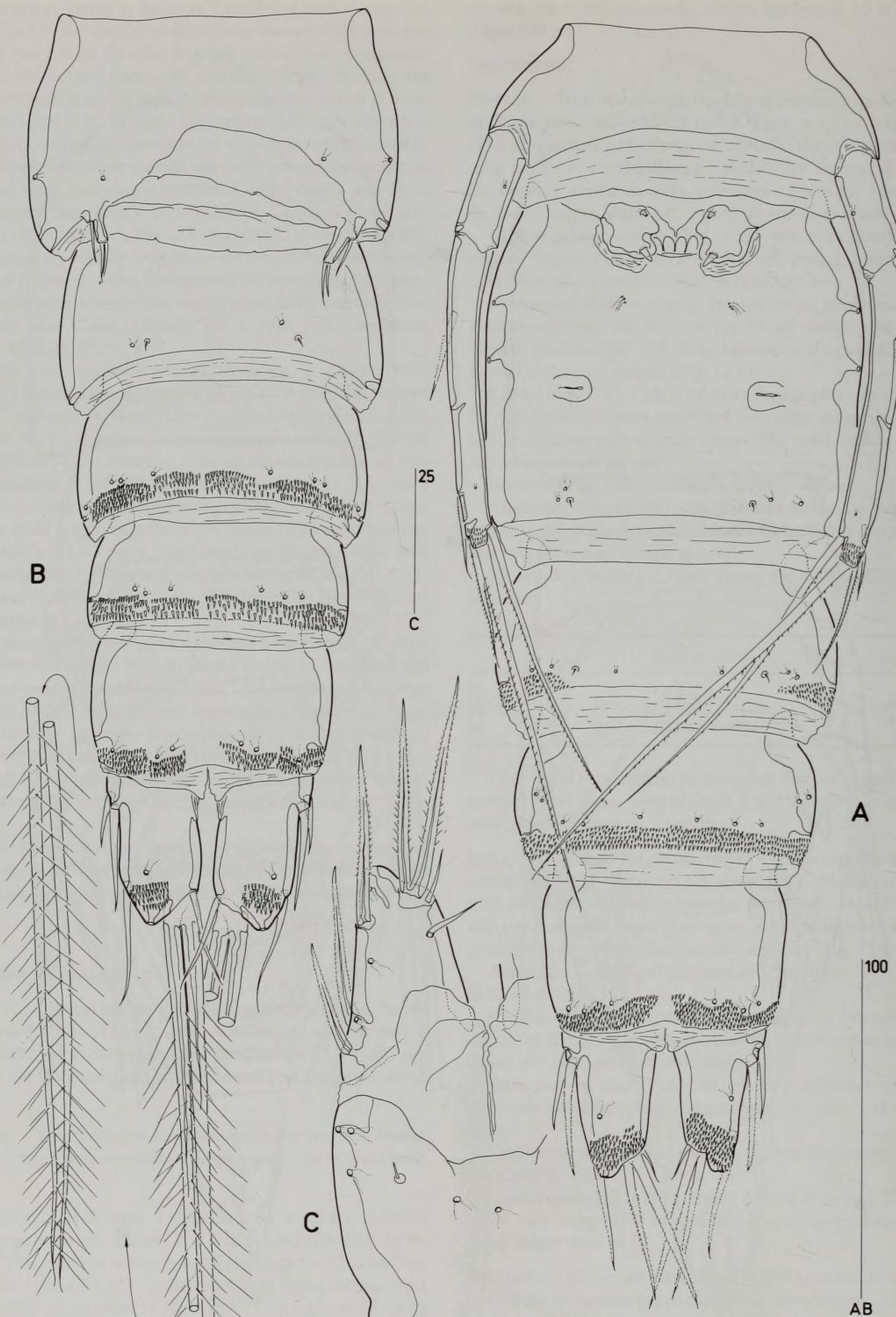


Fig. 13 *Clytemnestra farrani* sp. nov. A, Urosome ♀, ventral; B, urosome ♂ (excluding P5-bearing somite), ventral [inset showing setae IV–V at full length]; C, anal somite and right caudal ramus ♀, dorsal.

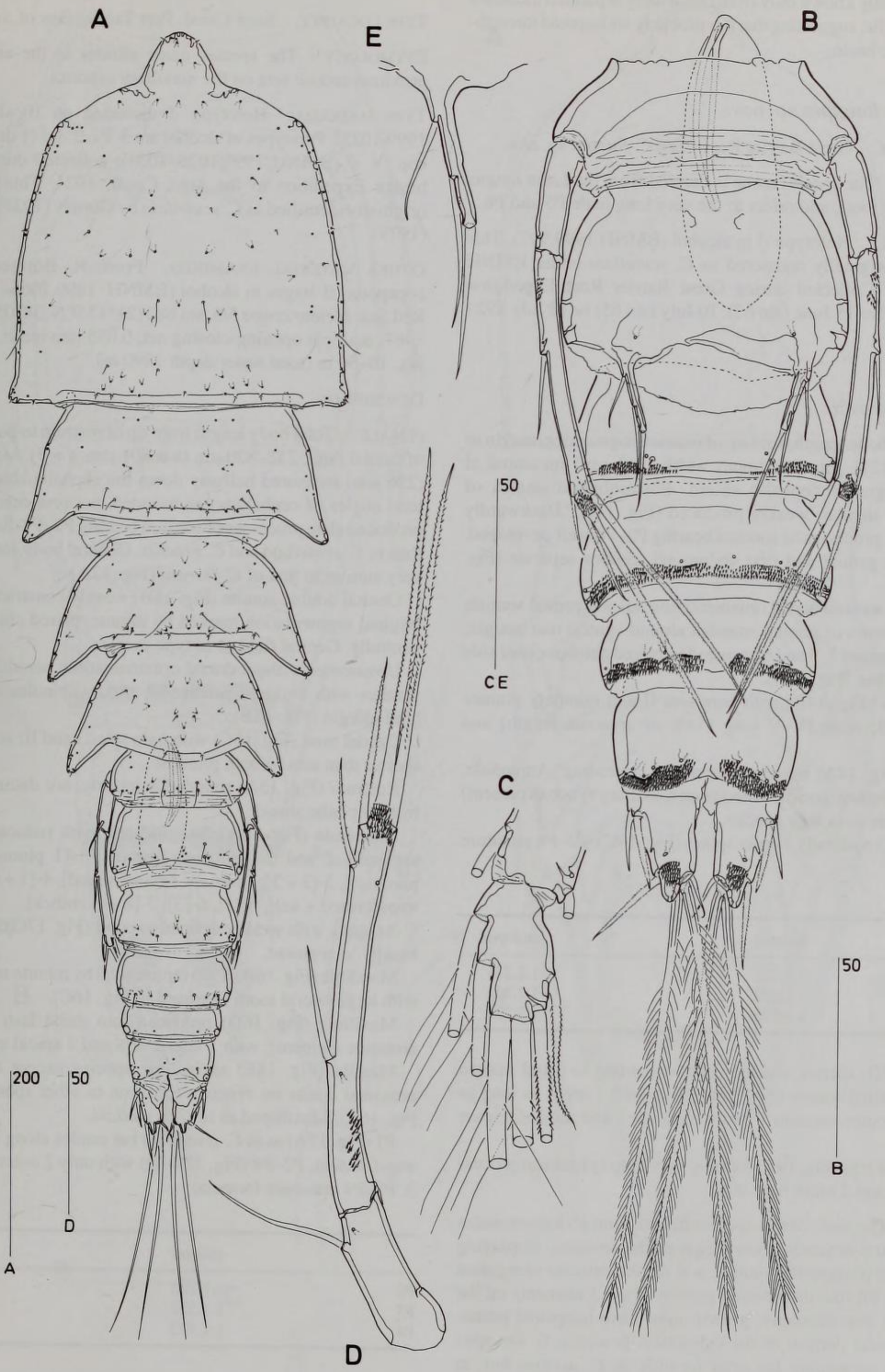


Fig. 14 *Clytemnestra longipes* sp. nov. (♂). A, Habitus, dorsal; B, urosome, ventral; C, P2 exp-3; D, P5, anterior; E, right P6.

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).

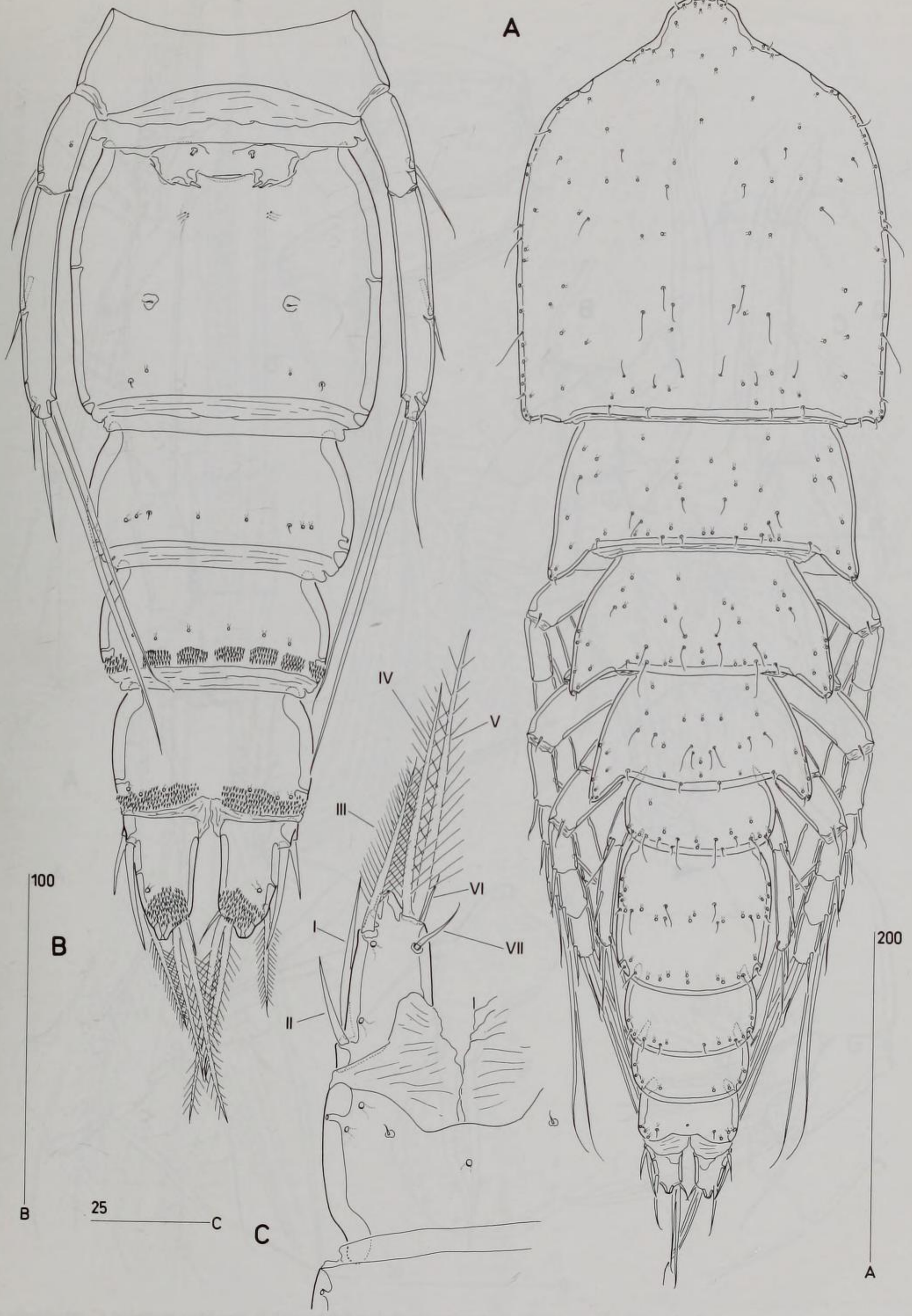


Fig. 15 *Clytemnestra asetosa* sp. nov. (♀). A, Habitus, dorsal; B, urosome, ventral; C, anal somite and right caudal ramus, dorsal.

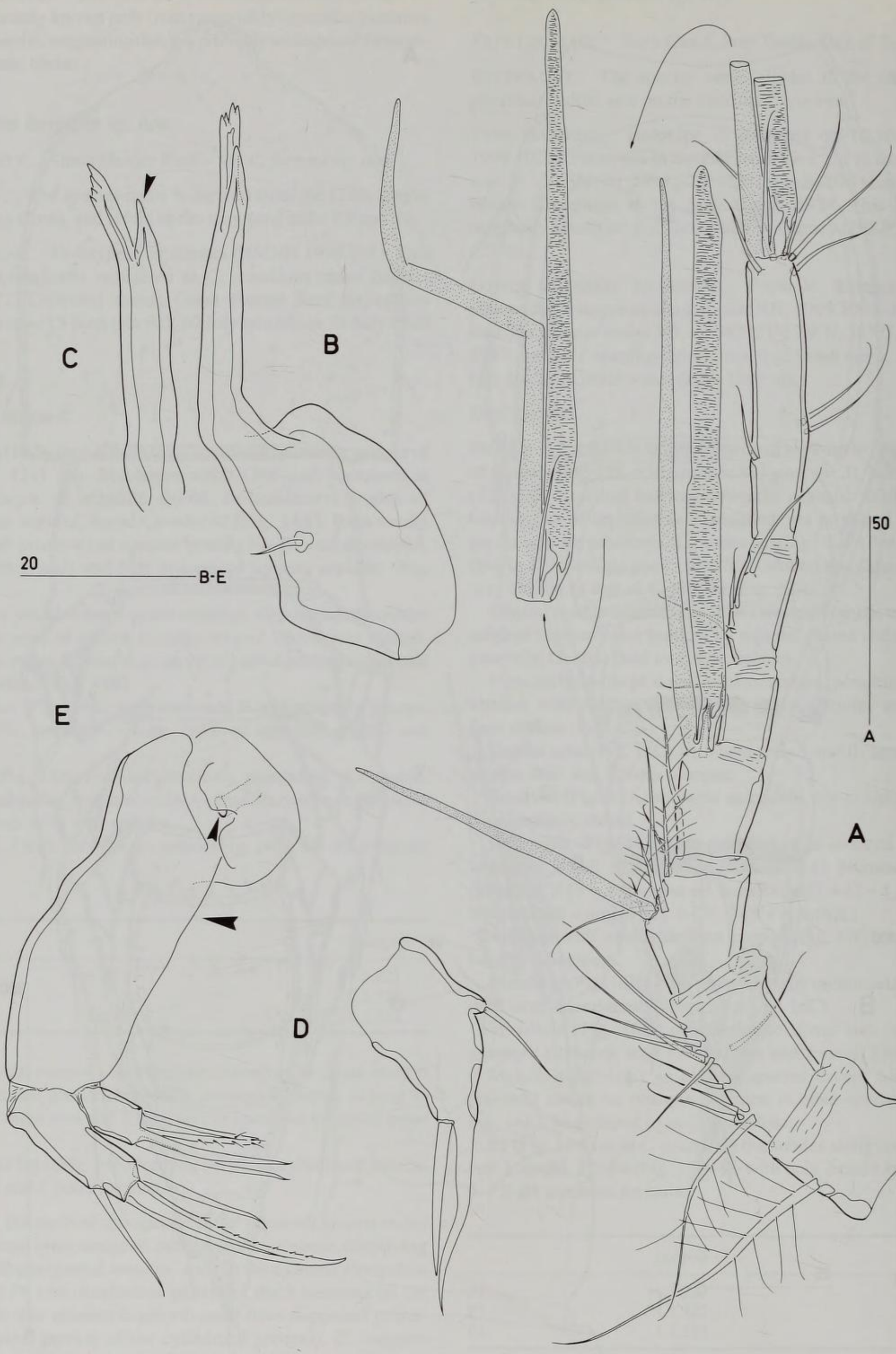


Fig. 16 *Clytemnestra asetosa* sp. nov. (♀). A, antennule, ventral [inset showing acrothek at full length]; B, mandible, posterior; C, mandibular gnathobase, other view [secondary tooth arrowed]; D, maxillule; E, maxilla, posterior [small arrow: exit of maxillary gland; large arrow indicating position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

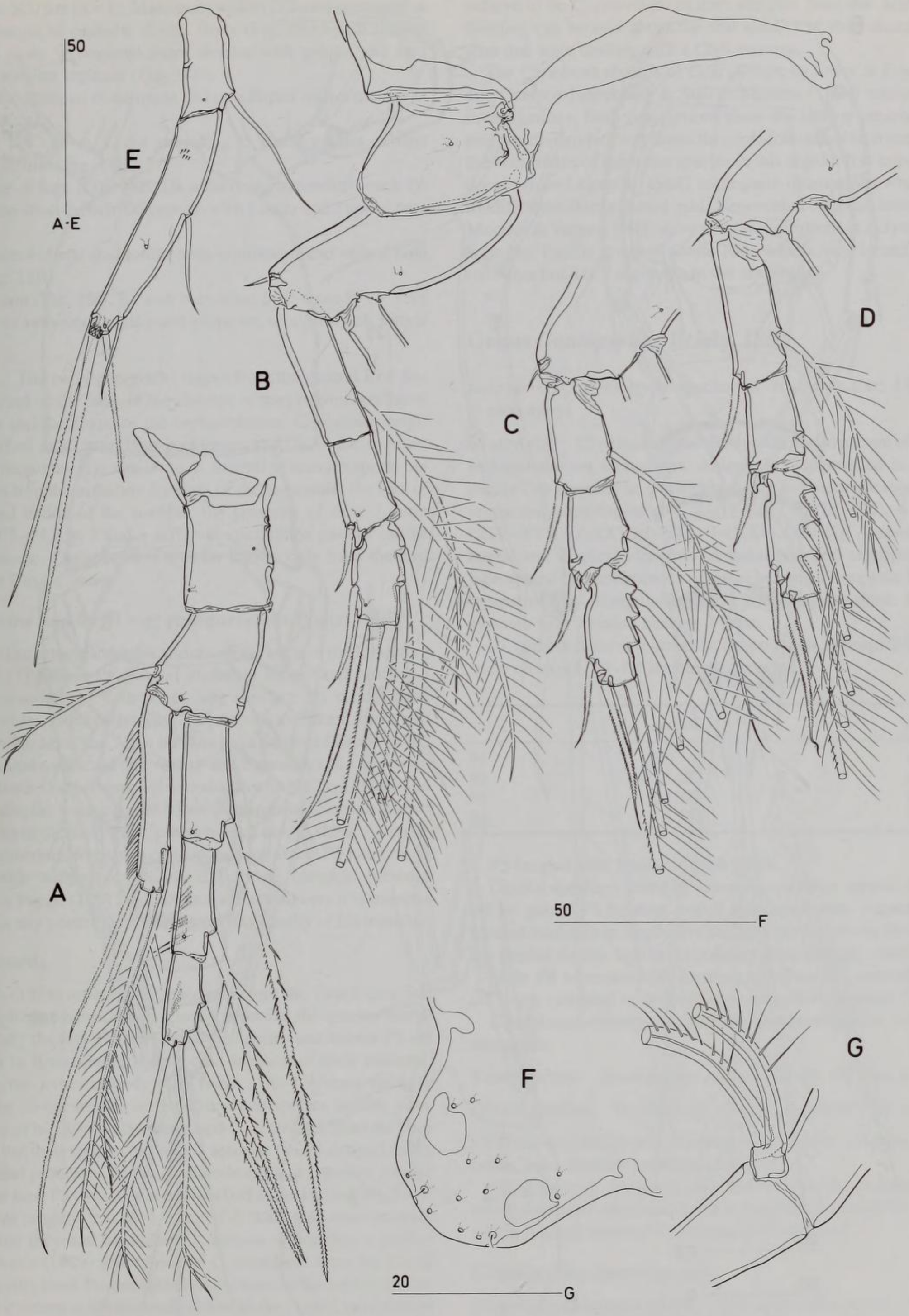


Fig. 17 *Clytemnestra asetosa* sp. nov. (♀). A, P1, anterior; B, P2, intercoxal sclerite, protopod and exopod, anterior; C, P3, distal portion of basis and exopod, anterior; D, P4, distal portion of basis and exopod, anterior; E, P5, anterior; F, rostrum, dorsal; G, antennary exopod.

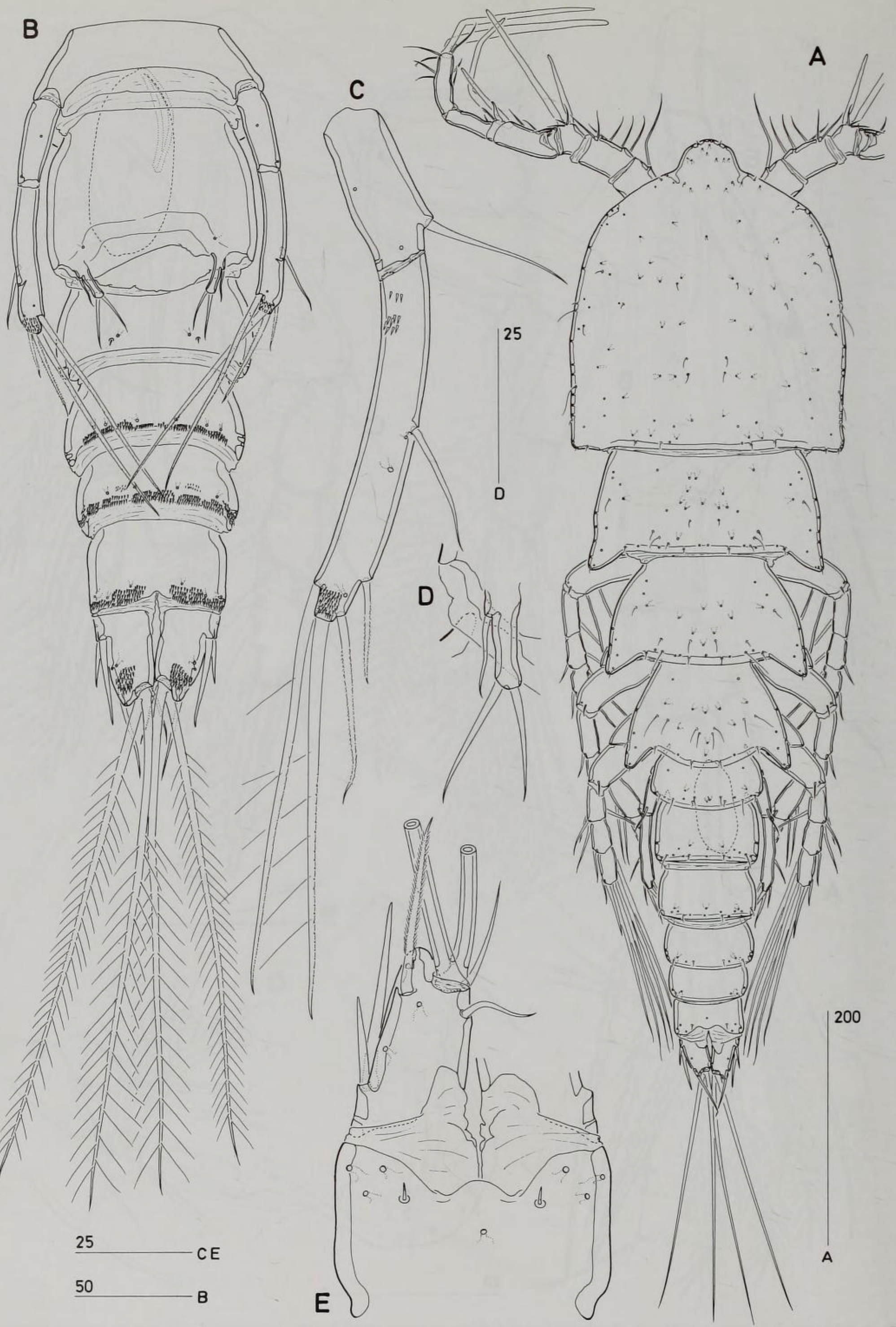


Fig. 18 *Clytemnestra asetosa* sp. nov. (♂). A, Habitus, dorsal; B, urosome, ventral; C, P5, anterior; D, P6; E, anal somite and right caudal ramus, dorsal.

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.

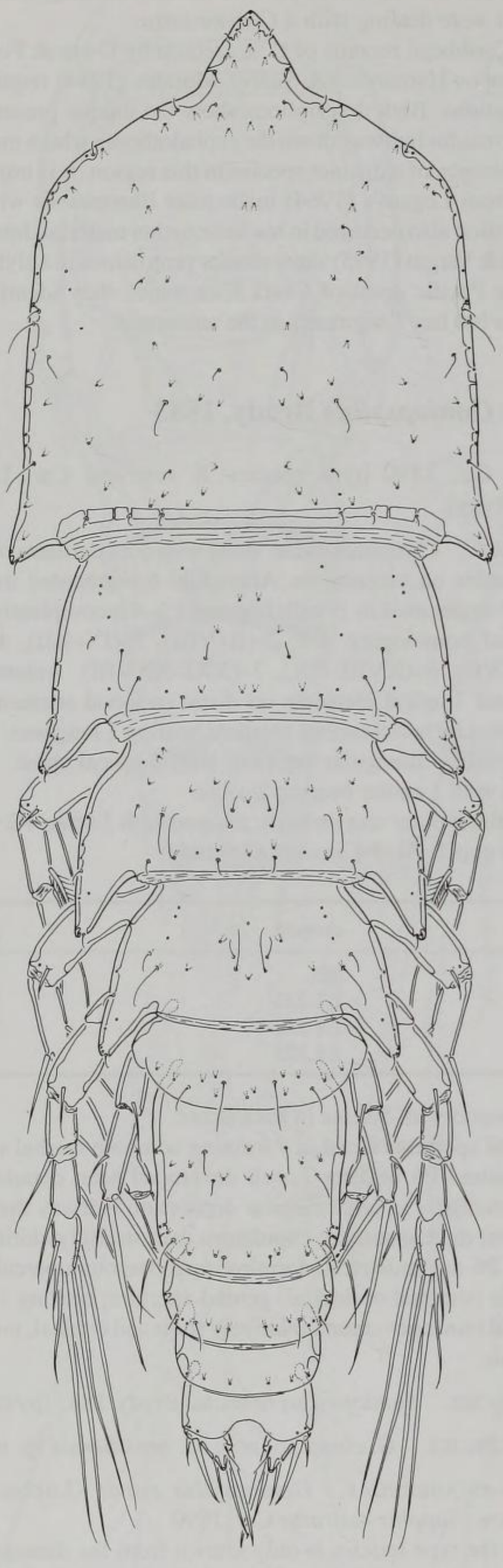
SPECIES INQUIRENDAE. *Goniopsyllus tenuis* (Lubbock, 1860) comb. nov.; *Sapphir rostratus* Car, 1890

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.



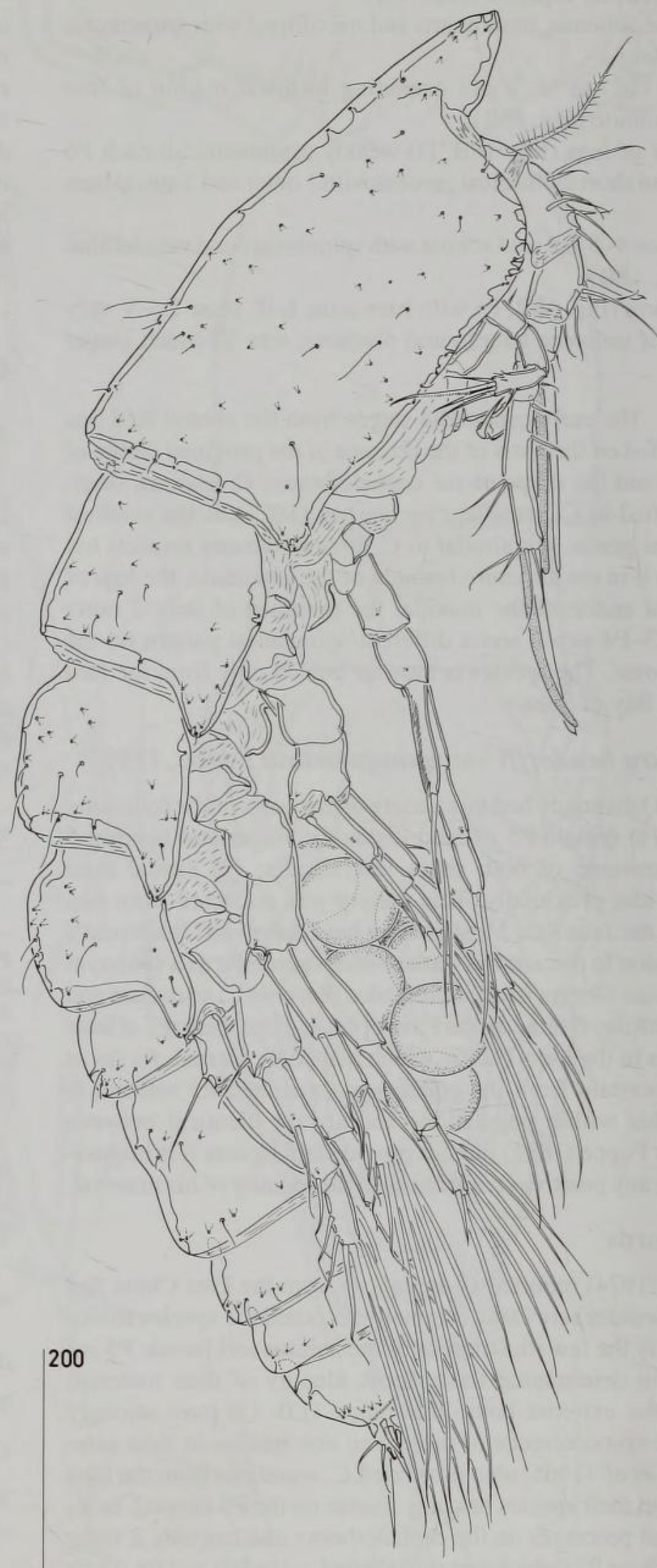


Fig. 19 *Goniopsyllus clausi* sp. nov. A, Habitus ♀, dorsal; B, habitus of ovigerous ♀, lateral.

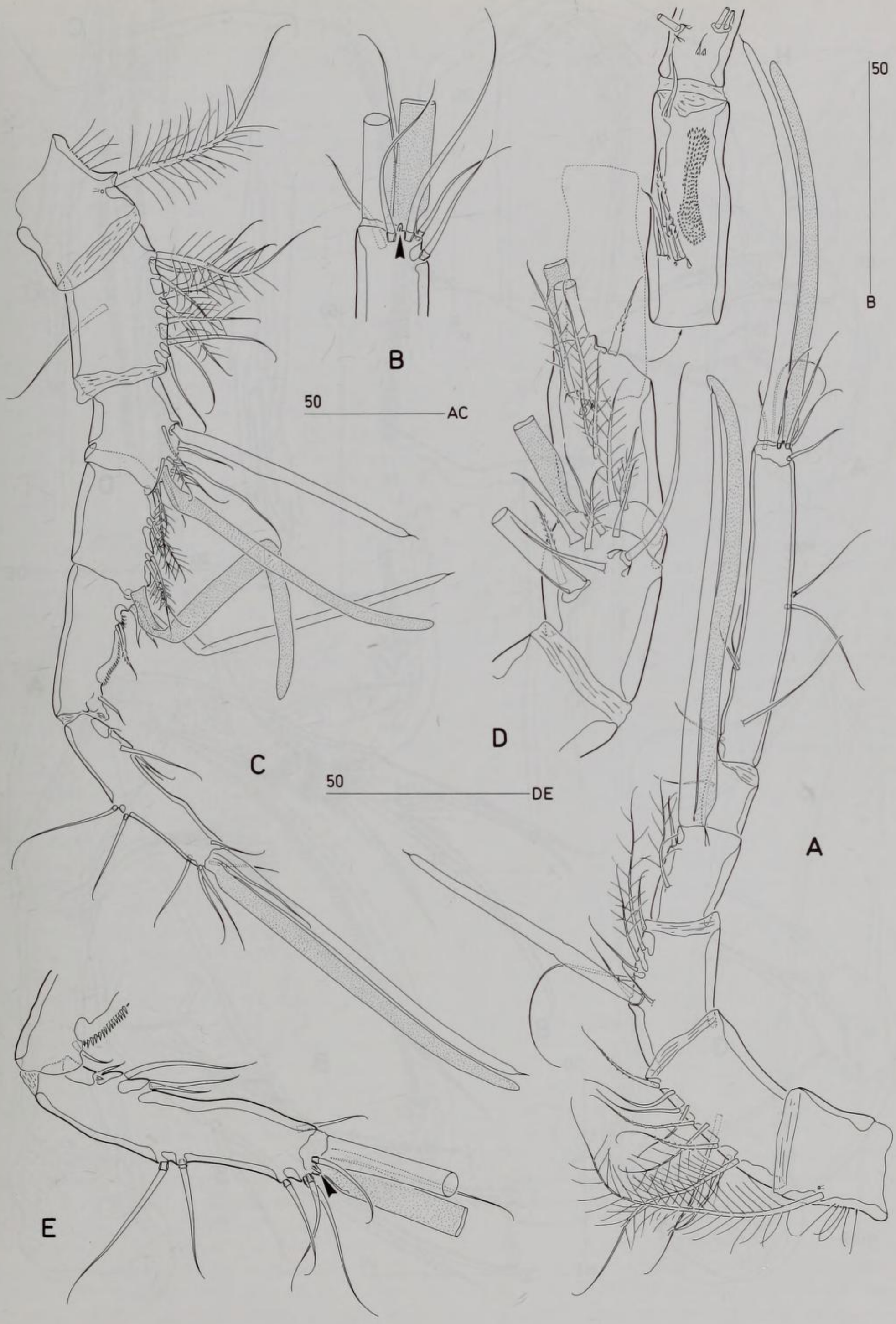
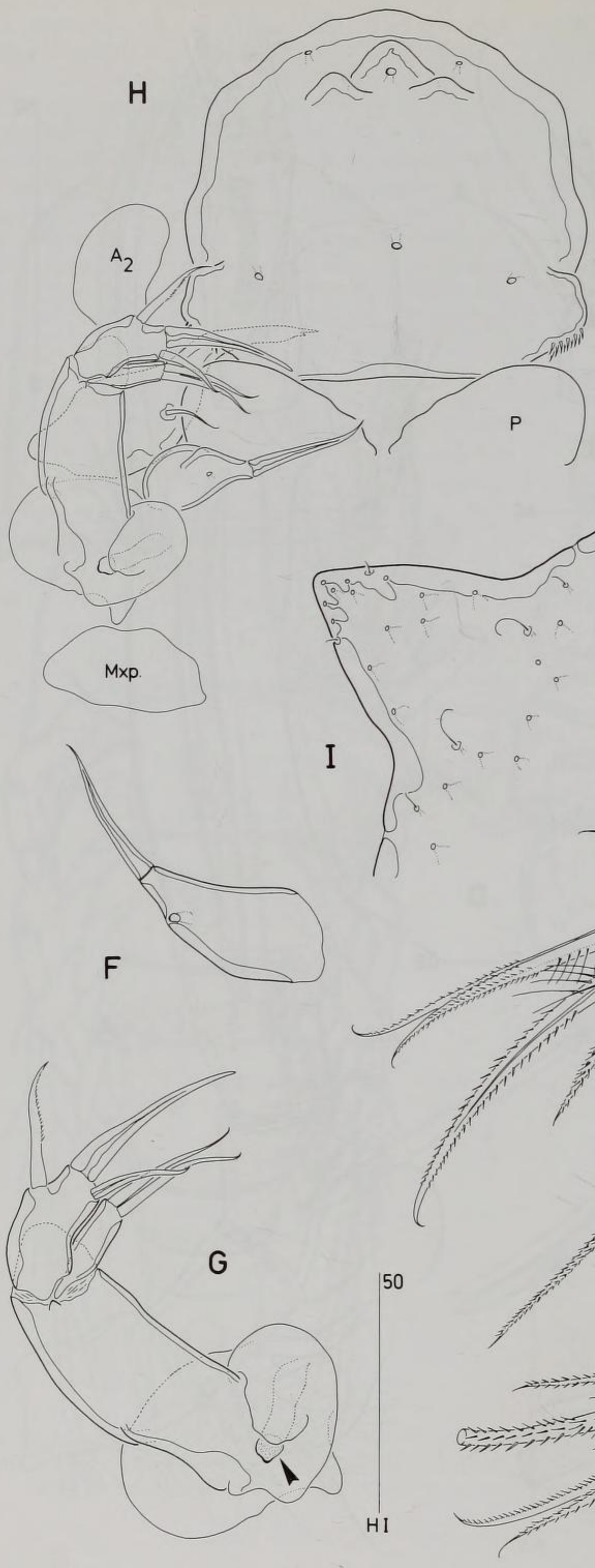


Fig. 20 *Goniopsyllus clausi* sp. nov. A, Antennule ♀, ventral; B, distal portion of antennulary segment 6 of ♀, ventral [rudimentary element arrowed]; C, antennule ♂, ventral; D, antennulary segments 3–6 of ♂, anterior; E, antennulary segment 7 of ♂, ventral [rudimentary element arrowed].



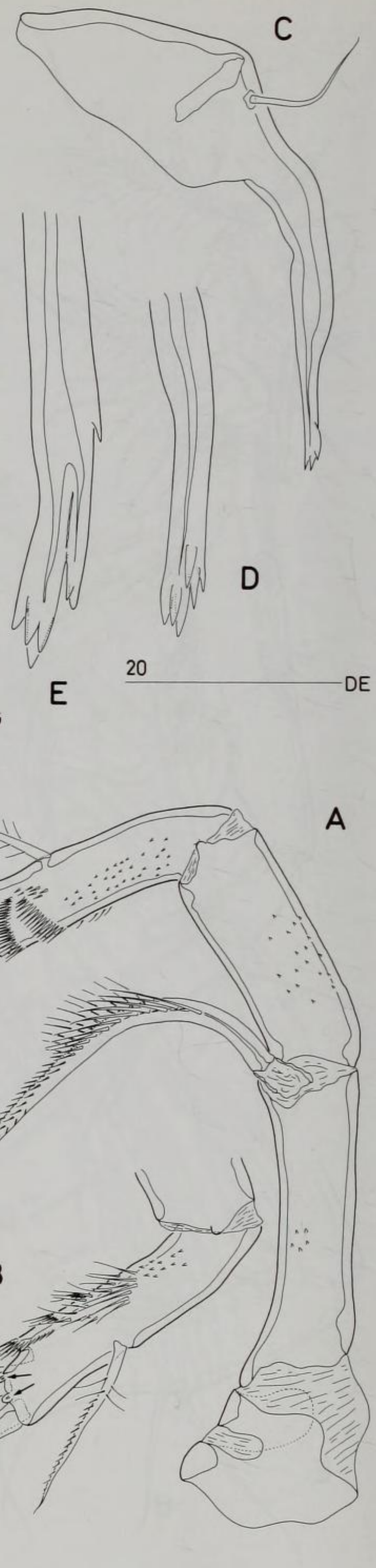


Fig. 21 *Goniopsyllus clausi* sp. nov. A, antenna ♀, outer; B, distal endopod segment of antenna ♀, inner [rudimentary elements arrowed]; C, mandible ♀; D, mandibular gnathobase ♀; E, mandibular gnathobase of ♂ specimen; F, maxillule ♀, posterior; G, maxilla ♀, posterior [exit of maxillary gland arrowed];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

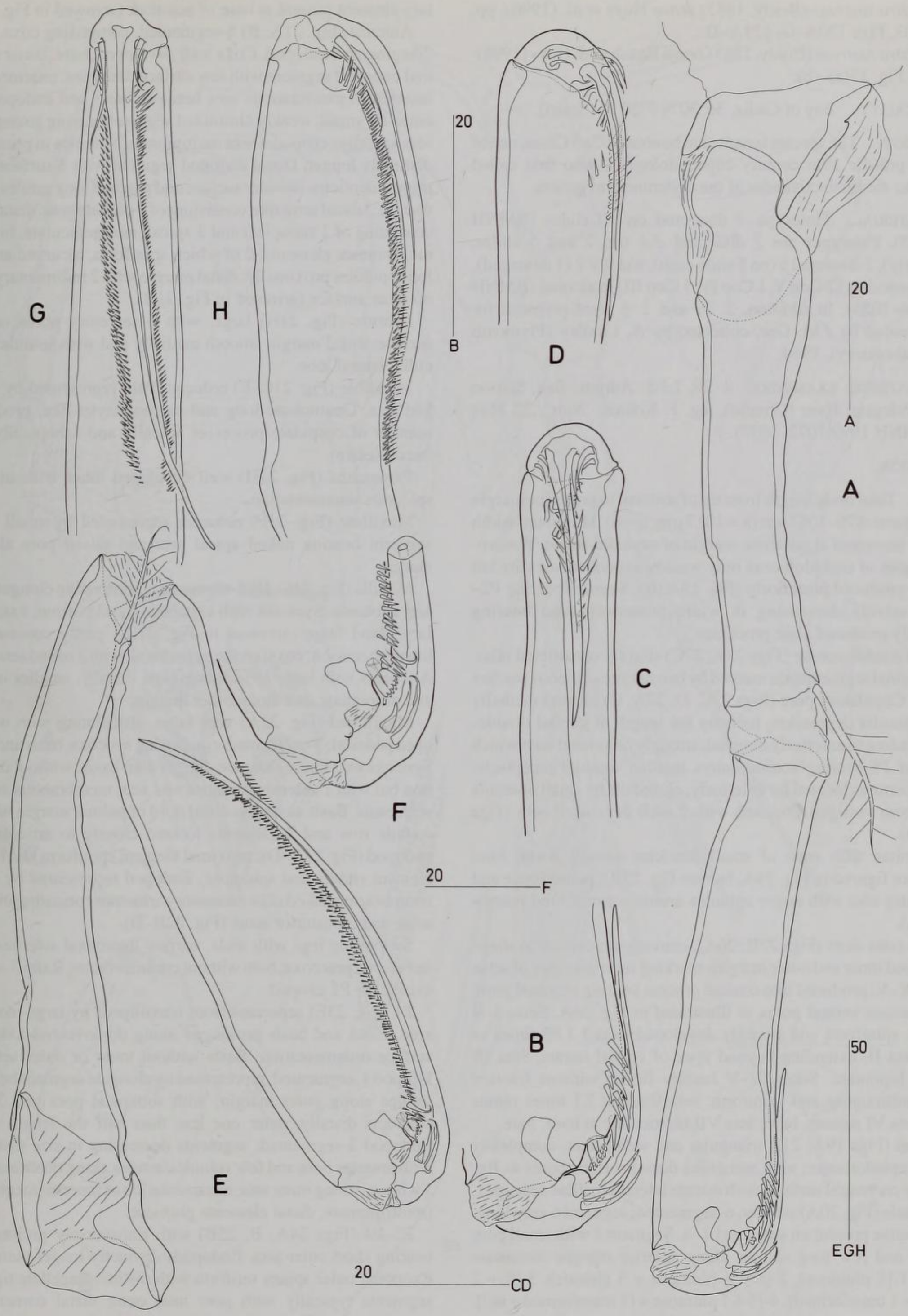


Fig. 22 *Goniopsyllus clausi* sp. nov. A, maxilliped ♀, anterior; B, maxilliped ♀, distal portion of basis and endopod, anterior; C, same, medial; D, same, posterior; E, maxilliped ♂, anterior; F, maxilliped ♂, distal portion and endopod, anterior; G, maxillipedal basis and endopod ♂, medial; H, same,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

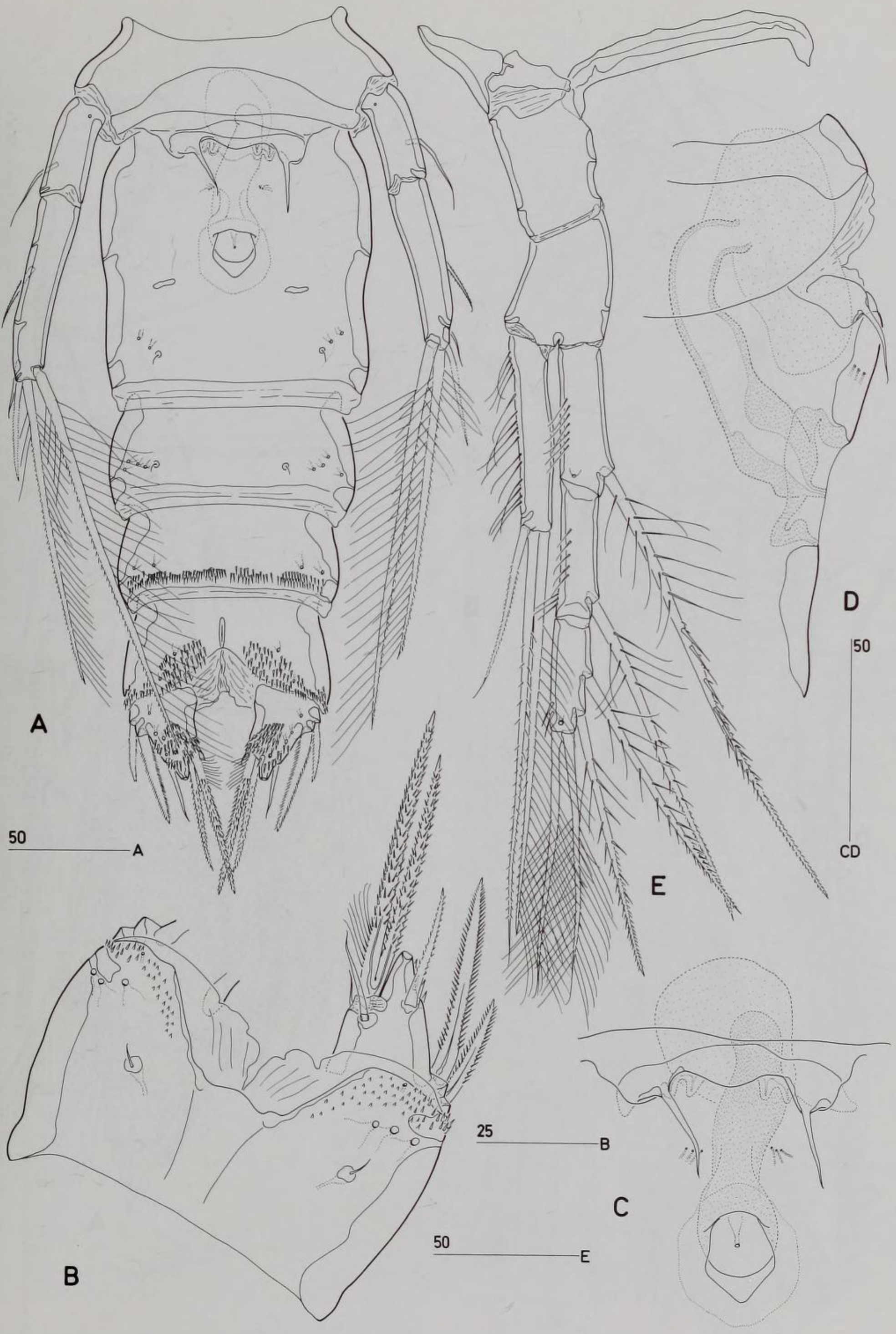


Fig. 23 *Goniopsyllus clausi* sp. nov. (♀). A, Urosome, ventral; B, anal somite and left caudal ramus, dorsal; C, genital field, ventral; D, genital field, lateral; E, P1, anterior.

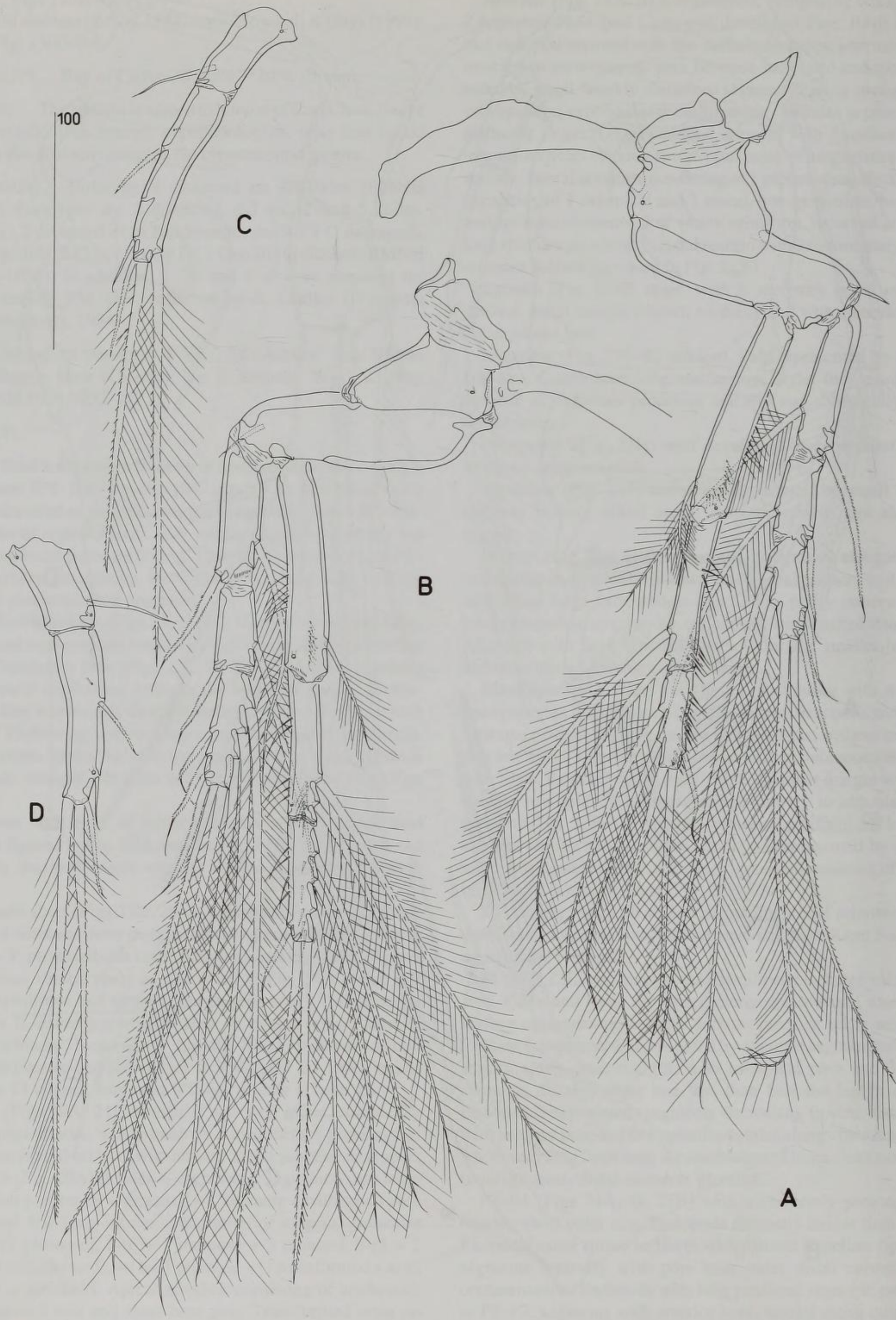


Fig. 24 *Goniopsyllus clausi* sp. nov. (♀). A, P2, anterior; B, P3, anterior; C, P5, anterior; D, aberrant P5, anterior.

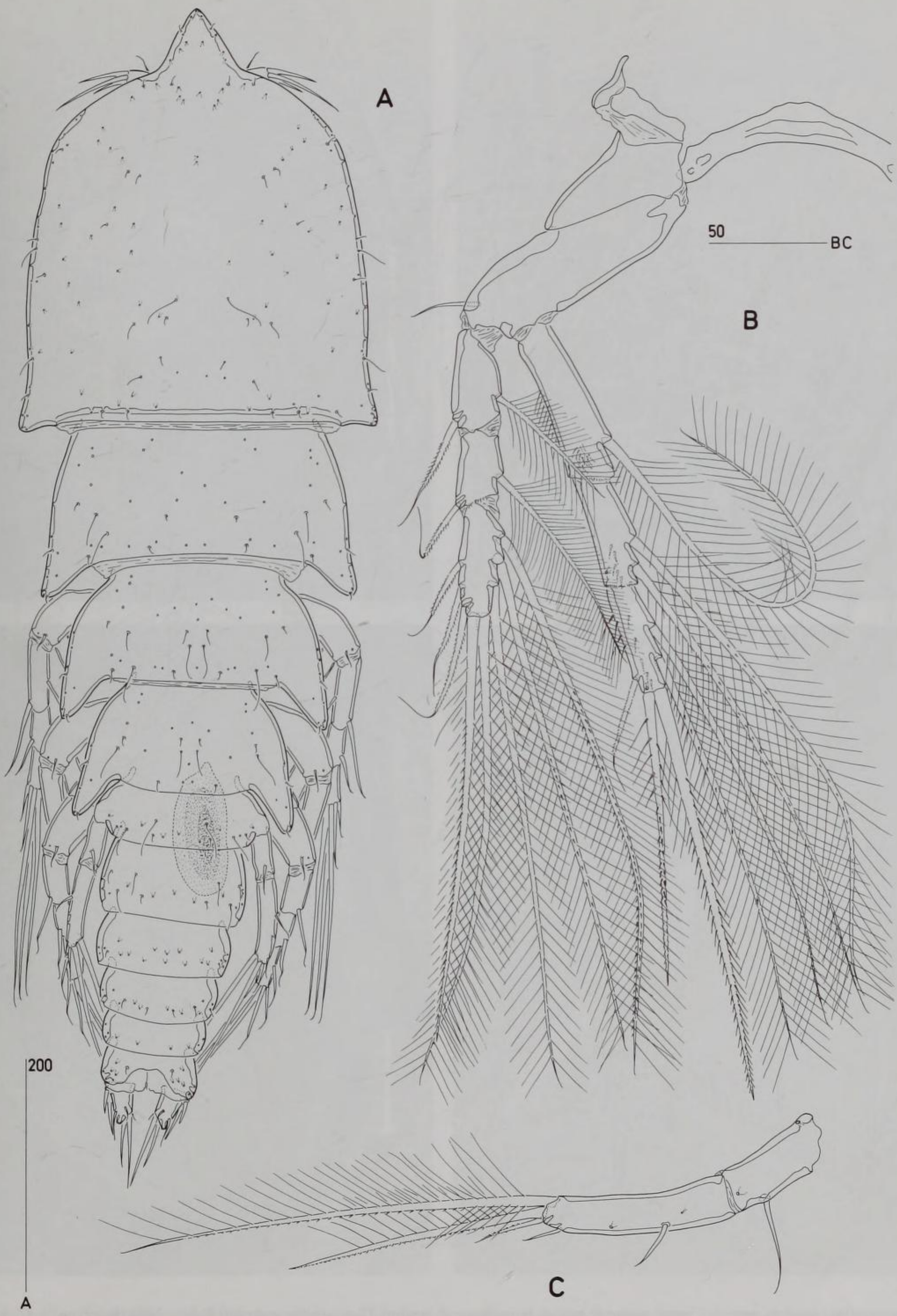


Fig. 25 *Goniopsyllus clausi* sp. nov. A, Habitus ♂, dorsal; B, P4 ♀, anterior; C, P5 ♂, anterior.

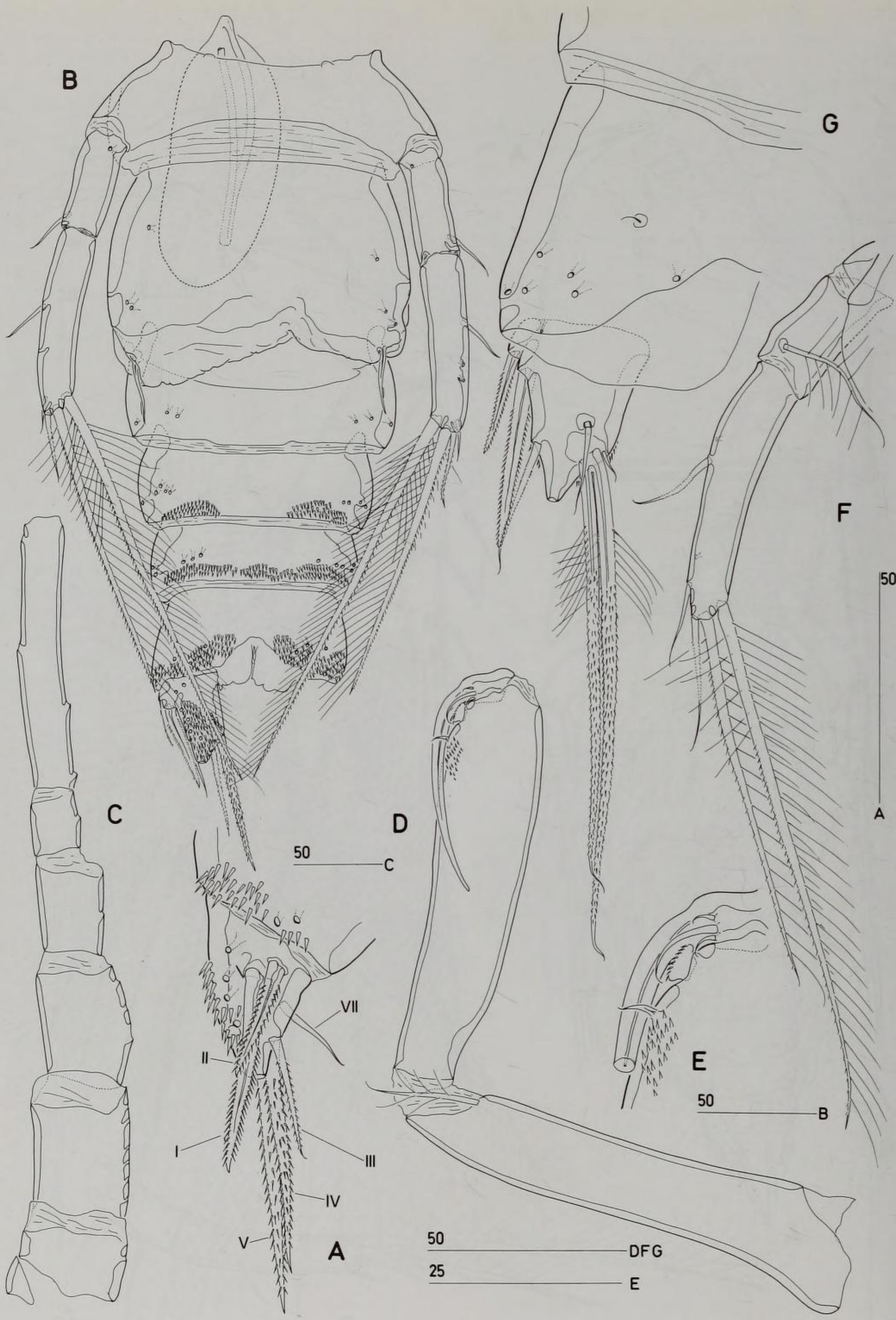
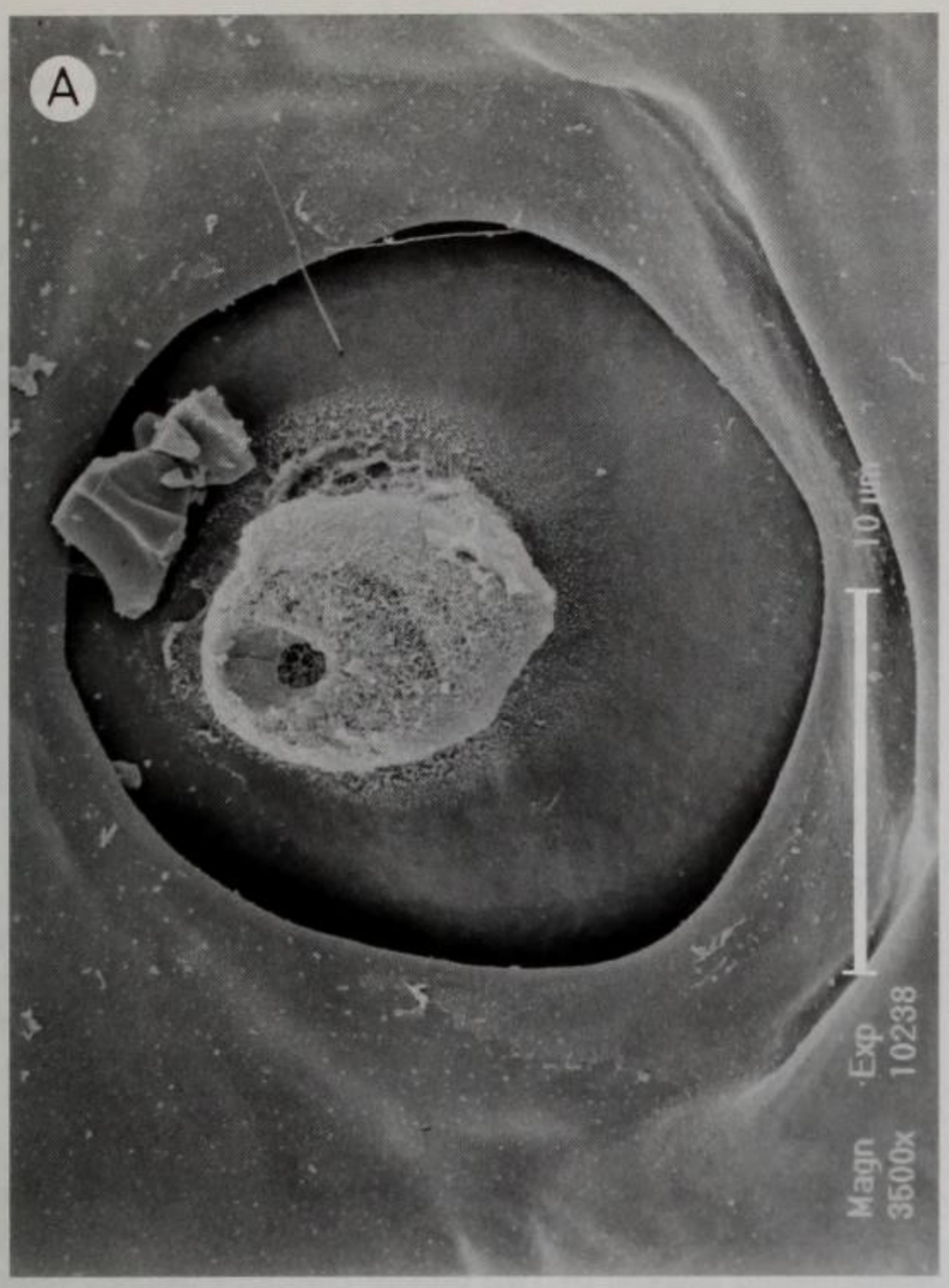
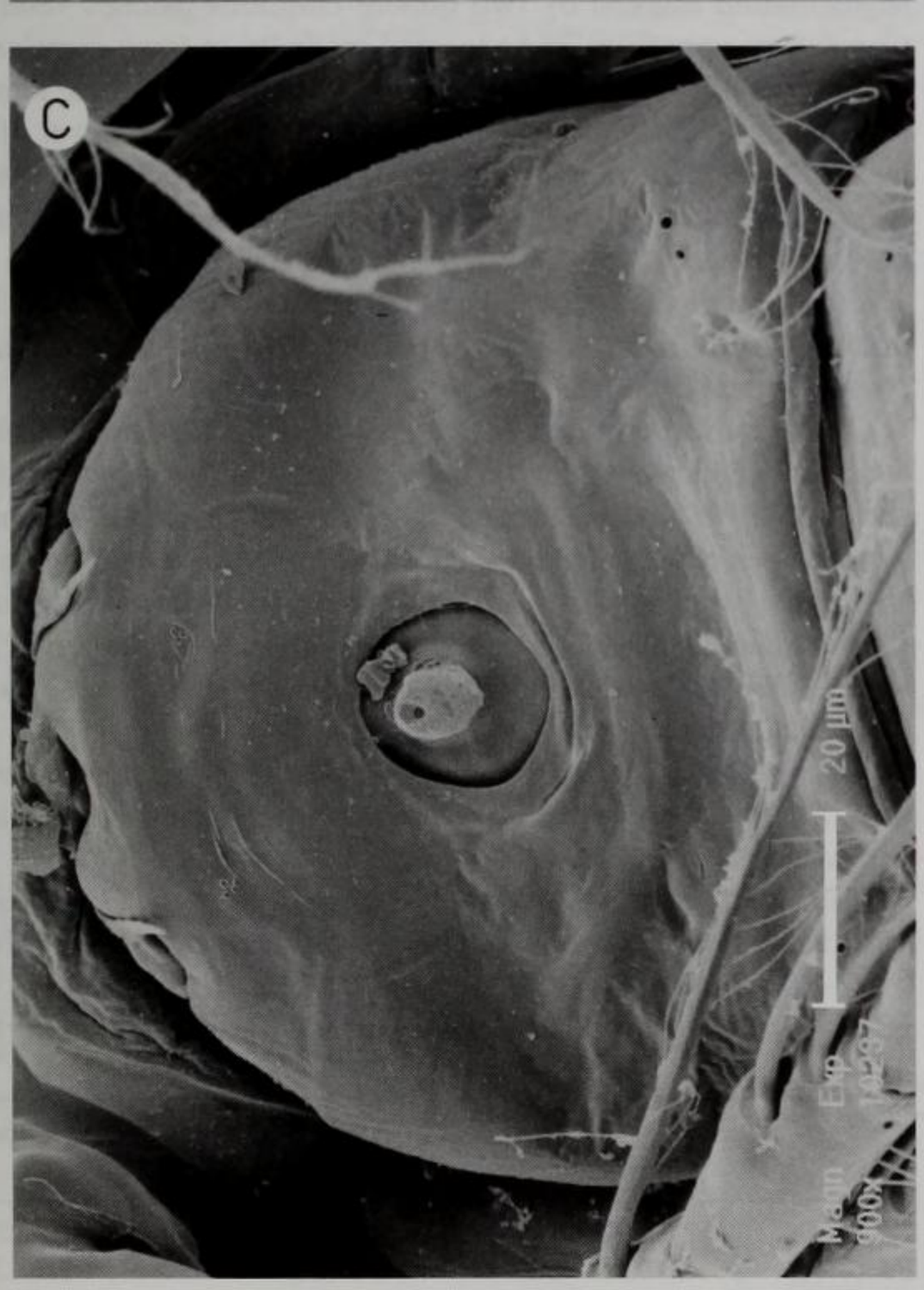


Fig. 26 *Goniopsyllus clausi* sp. nov. A, Caudal ramus ♀, lateral; B, urosome ♂, ventral. *Goniopsyllus rostratus* Brady, 1883 (holotype ♀). C, Antennule (armature omitted); D, maxilliped, anterior; E, maxilliped, distal portion of basis and endopod, anterior; F, P5, posterior; G, anal somite and left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





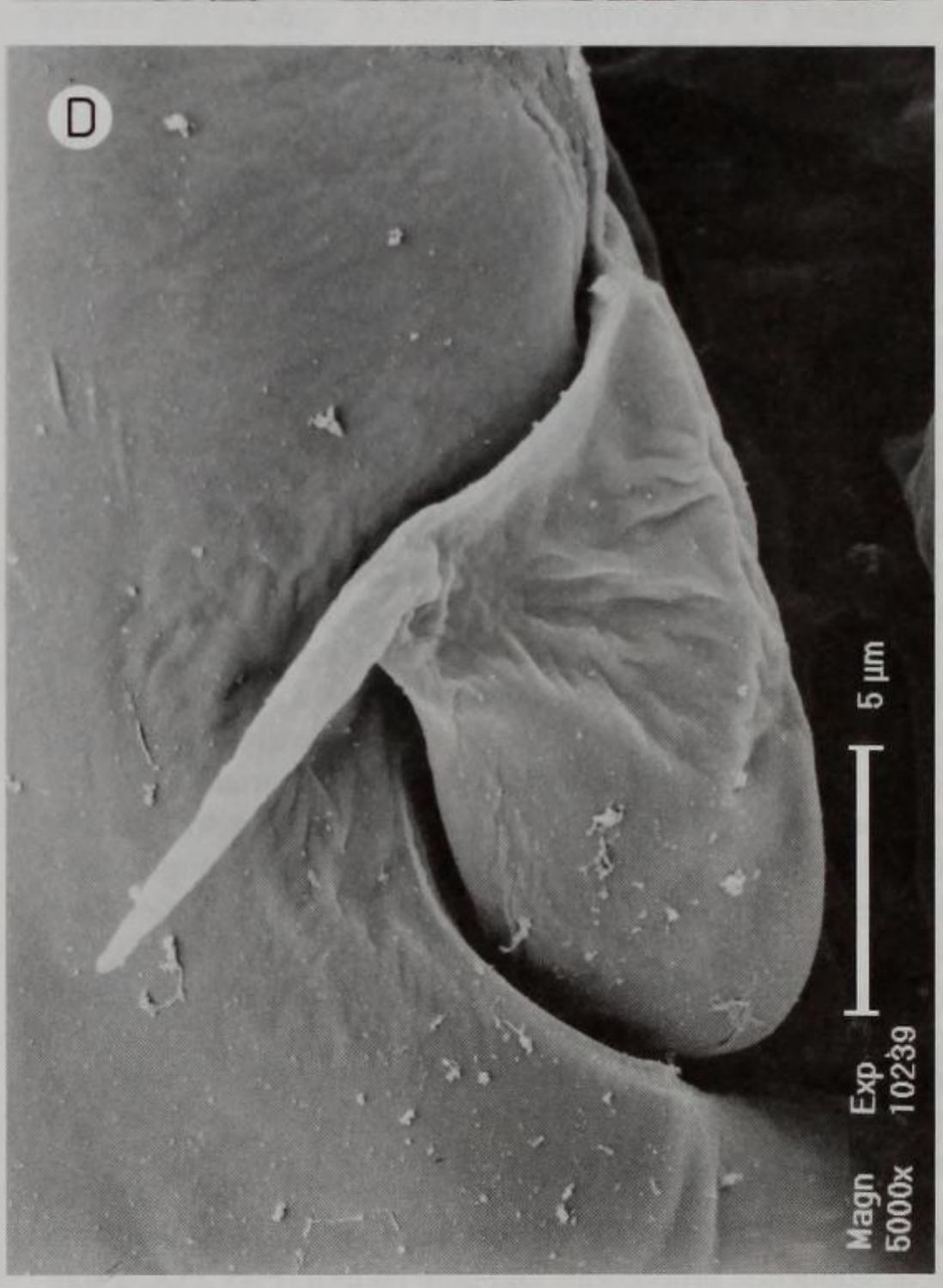


Fig. 27 *Goniopsyllus clausi* sp. nov. (♀). SEM photographs. A, Circular depression surrounding copulatory pore (position obscured by remnant of spermatophore neck); C, genital double-somite; D, genital aperture. *Clytemnestra gracilis* (Claus, 1891*a*) comb. nov. (♀). B, Genital apertures and copulatory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

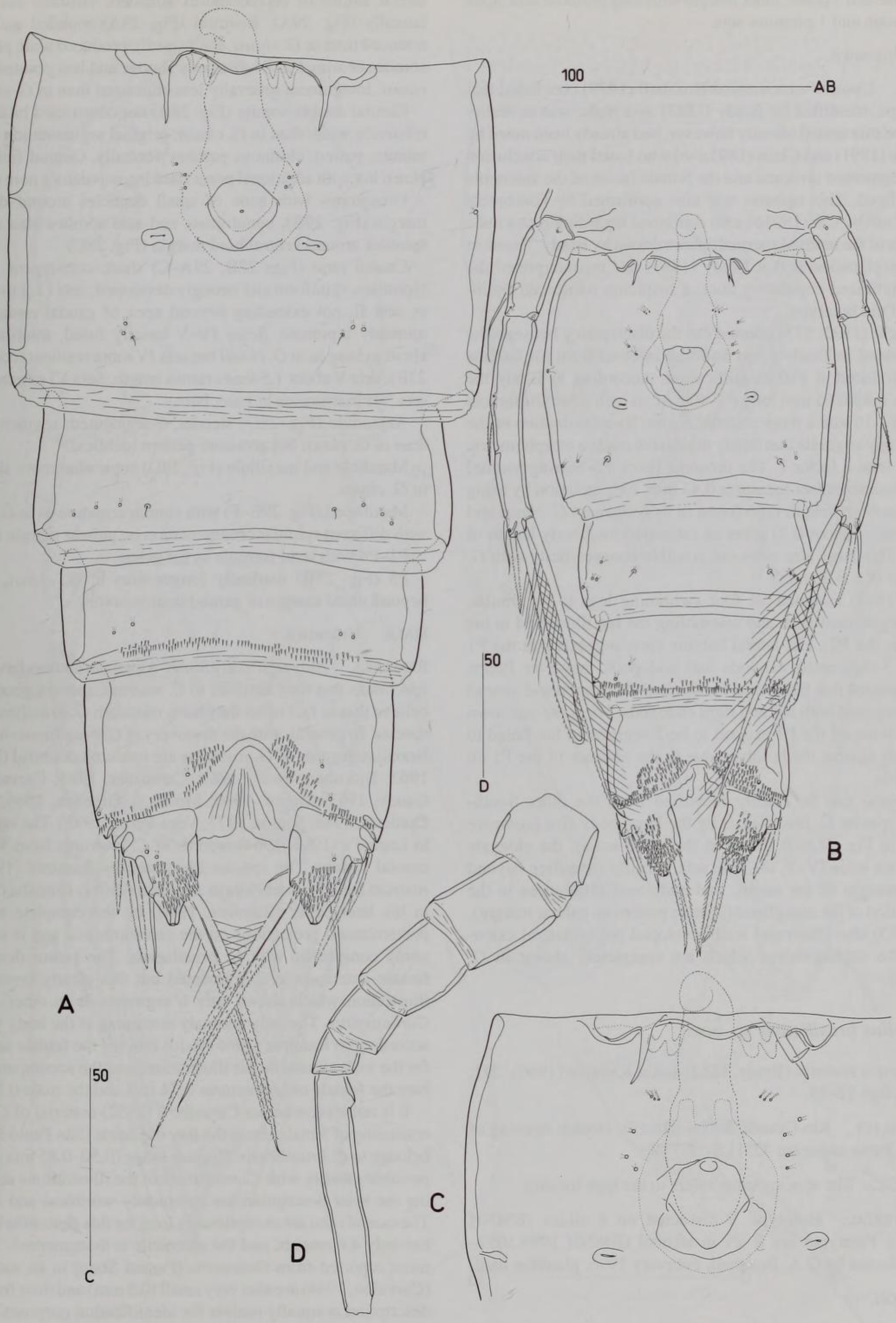


Fig. 28 *Goniopsyllus rostratus* Brady, 1883 (holotype ♀). A, Urosome (excluding P5-bearing somite), ventral [distorted due to excessive squashing]. *Goniopsyllus brasiliensis* sp. nov. (♀). B, Urosome, ventral; C, genital field, ventral; D, antennule (armature omitted).

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.

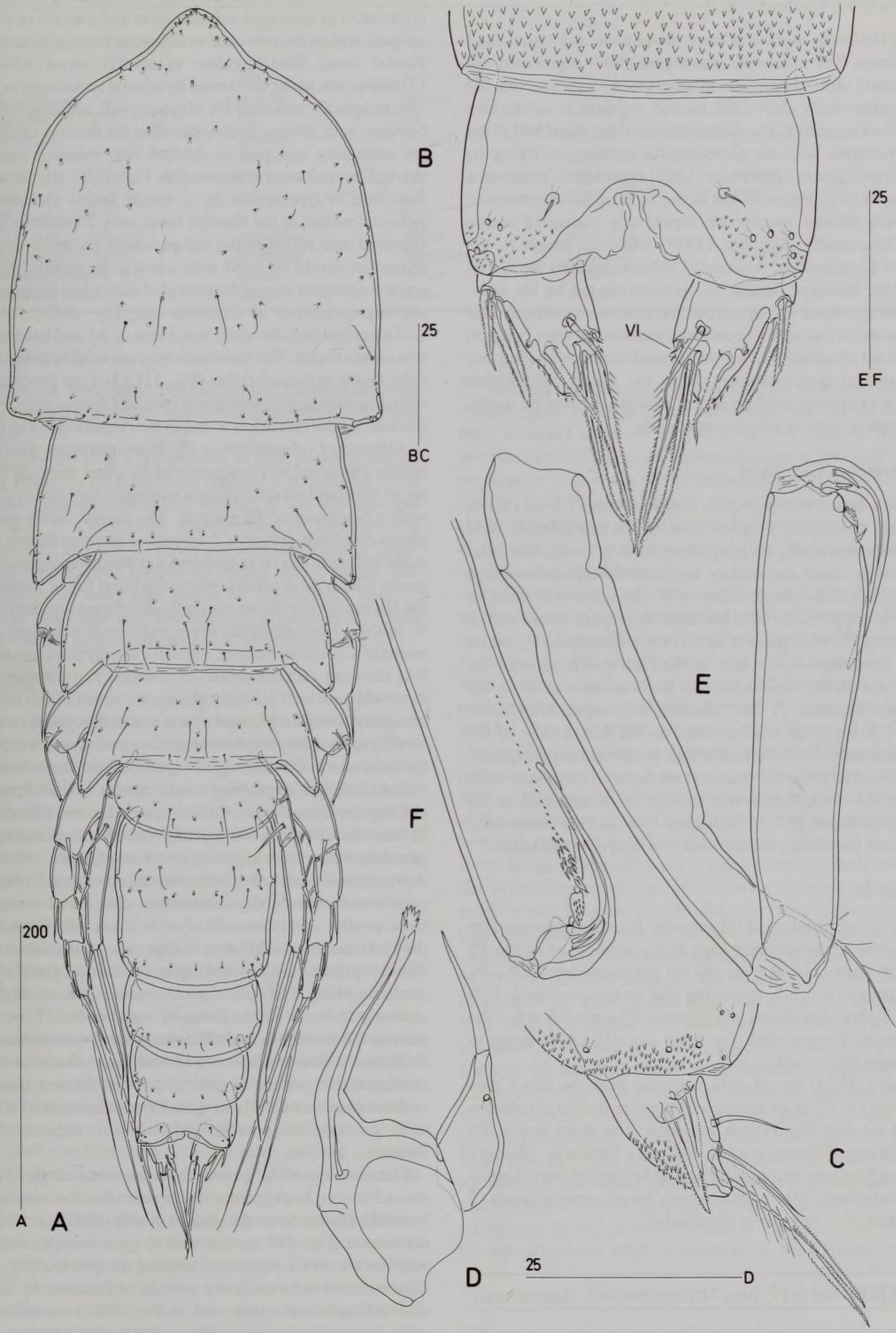


Fig. 29 *Goniopsyllus brasiliensis* sp. nov. (♀). A, Habitus, dorsal; B, anal somite and caudal rami, dorsal; C, caudal ramus, lateral; D, mandible and maxillule; E, maxilliped, posterior; F, maxilliped, distal portion of basis and endopod, anterior.

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 Peltididiidae 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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