

# A new harpacticoid copepod family collected from Australian sponges and the status of the subfamily Rhynchothalestrinae Lang

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A new family is proposed for *Hamondia superba* gen. et sp. nov., a shield-shaped harpacticoid collected from washings of sponges from Port Phillip, Australia. It is concluded that the closest relatives of the **Hamondiidae fam. nov.** currently belong to the heterogeneous thalestrid genus *Rhynchothalestris* Sars, 1905 and for that reason the latter is revised. *Rhynchothalestris rufocincta* (Brady, 1880) is redescribed and designated as type species for **Ambunguipes gen. nov.**, comprising also the Indo-Pacific *A. similis* (A. Scott, 1909) which is re-instated. *Ambunguipes vanhoeffeni* (Brady, 1910) is ranked as *species inquirenda* within the genus. Because of its body ornamentation *R. cornuta* Geddes, 1969 is transferred to **Lucayostratiotes gen. nov.** The **Ambunguipedidae fam. nov.**, accommodating *Ambunguipes* and *Lucayostratiotes* are regarded as the sister-group of the Hamondiidae on the basis of the loss of the seta on the first antennular segment, the presence of bifid spinules on the antennary exopod, the presence of a modified seta on the maxillary precoxal endite, the sexual dimorphism of leg 3, the detailed structure of the female genital complex, and the asymmetry of the male P6. The diagnosis of the subfamily Rhynchothalestrinae, encompassing the genera *Rhynchothalestris* and *Peltthestrus* Monard, 1924 is amended, and a redescription of the former's type species *R. helgolandica* (Claus, 1863) is presented. The genus also contains *R. tenuis* Chislenko, 1971 and *R. campbelliensis* Lang, 1934 grad. nov. which is elevated to full species rank. The inadequately described *R. tenuicornis* (Brady, 1910) is ranked as *species inquirenda*. The monotypic genus *Peltthestrus* is regarded as a valid genus. It is suggested that the Rhynchothalestrinae represent an early offshoot in the evolution of the Thalestridae and that the Thalestrinae and the Dactylopusiinae are more closely related to each other than to any other subfamily. *Rhynchothalestris agigensis* Serban, 1959 has no close relationship with either the Rhynchothalestrinae or the Ambunguipedidae and is tentatively considered *incertae sedis* within the Dactylopusiinae. The discovery of *H. superba* and the redescription of *A. rufocincta* have raised the maximum number of antennular segments in male harpacticoids to 14. The terms 'epicopulatory bulb' and 'epicopulatory plate' are coined for peculiar structures of the female genital complex. The development of 'setoid elements' versus addition of novel setae is briefly mentioned.

KEY WORDS:—Copepoda – Harpacticoida – sponges – **Hamondiidae fam. nov.** – **Ambunguipedidae fam. nov.** – Rhynchothalestrinae – **Hamondia gen. nov.** – **Lucayostratiotes gen. nov.** – *Rhynchothalestris* – *Peltthestrus*.

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## INTRODUCTION

In the last few decades, the interest aroused in copepods associated with marine invertebrates has produced an ever increasing volume of literature (Gotto, 1979). Among the main invertebrate phyla of the marine environment, cnidarians, ascidians, echinoderms and molluscs have large numbers of copepod associates (Humes, 1985) whilst copepods associated with sponges are perhaps the least known group (Ho, 1984).

Humes (1985) estimated the number of sponge associated copepods at about 81 but most of these are members of the Poecilostomatoida (e.g. Clausidiidae, Spongiocnizontidae) and particularly Siphonostomatoida (e.g. Asterocheridae, Entomolepidae, Dyspontiidae). Harpacticoid copepods have been less successful in invading the intricate canal systems of the Porifera and often display a rather loose form of association, the nature of which, in some cases, is still uncertain. This is exemplified by the records of A. Scott (1896) who found *Cletodes similis* T. Scott, 1895 (= *Eurycletodes (Oligocletodes) similis* (T. Scott, 1895)), *Laophonte propinqua* T. & A. Scott, 1895 (= *L. serrata* (Claus, 1863)) and *L. intermedia* T. Scott, 1895 (= *Asellopsis intermedia* (T. Scott, 1895)) in washings of sponges from Port Erin, Isle of Man. Similarly, Brian (1928a) reported *Amphiascus tenax* var. *aegaea* Brian, 1927 (= *Robertgurneya similis* (A. Scott, 1896)) between fragments of poriferans off Rhodes. In a later paper (Brian, 1928b), he found a second diosaccid *Amphiascus affinis* Sars, 1906 (= ? *Paramphiascella mediterranea* Lang, 1948) among pieces of sponge collected from Rhodes, Stampalia (= *Astipálaia*) and Piscopi (= *Tílos*). Obviously, this information is only indicative for the habitat where the species are suspected to be found and is no proof for a specific association. This is also illustrated by Pesta's (1959) work in which various harpacticoids are recorded from *Halichondria—Astroides*, *Balanus—Halichondria* and *Euspongia—Tuberella* 'Bestände'.

Pearse (1932) collected and examined the associated fauna found in various sponges at Dry Tortugas, Florida, U.S.A. The copepods were identified to genera by C. B. Wilson. Fragments of a loggerhead sponge *Speciospongia vespara* (Lamarck) Marshall contained 150 harpacticoid copepods, mostly belonging to the Harpacticidae (*Harpacticus* Milne-Edwards), Thalestridae (*Diarthrodes* Thomson; *Thalestris* Claus; *Parathalestris* Brady & Robertson; *Dactylopusia* Norman) and Diosaccidae (*Amphiascus* Sars; *Stenhelia* Boeck). Several specimens of *Metis ignea* Philippi, 1843 (Metidae) were recovered from a reef sponge *Spongia 'officinalis'* L. (= *S. obliqua* Duchassaing & Michelotte). It is apparent that all these copepods are only facultative associates as they are commonly found dwelling on seaweed.

Ho (1984), in describing two new poriferan-associated siphonostomatoids from the Sea of Japan, emphasized the remarkable scarcity of Pacific Ocean records. Vervoort (1964) collected four females of *Microloaophonte spongicola* Vervoort, 1964 (Laophontidae) from sponges at Ifaluk Atoll (Caroline Islands) but this might be a chance association as the second species of the genus *M. trisetosa* Boxshall, 1976 was described from laboratory cultures of the polychaete *Capitellides giardi* Mesnil (cf. Boxshall, 1976). Vervoort's records of *Orthopsyllus dubius* Vervoort, 1964, *Pseudocletopsyllus spiniger* Vervoort, 1964, and *Laophonte dinocerata* Monard, 1926 from sponge washings might be accidental. Most recently Hicks (1986) recovered numerous specimens of a new sponge-associated genus and species of Pacific Peltidiidae. *Alteuthoides kootare* Hicks, 1986 was found in atrial washings of the hexactinellid *Symplectella rowi* Dendy (Rossellidae) taken from off the East Coromandel Coast, Bay of Plenty, New Zealand. In a postscript, the author mentioned finding additional specimens in washings of *Symplectella* sp. collected at Conway Rise, south-east of Kaikoura, New Zealand.

Yeatman (1970) studied the copepod fauna associated with four large sponges (*Halichondria bowerbanki* Burton, *Microciona prolifera* (Ellis & Solander), *Haliclona permollis* (Bowerbank), *Craniella gravida* (Hyatt)) collected from rocks, pilings and bottom sand in Chesapeake Bay, Virginia. Seven harpacticoid species were identified but the gut-contents indicated that they are grazing on algae and scavenging since no sponge cells were recognizable.

Finally, Chislenko (1977) reported on harpacticoid copepods from sponges of Franz Josef Land. A total of 30 species were recovered from *Phakellia cribrosa*. It is clear, however, that a specific association of these species must remain in doubt. The only freshwater find is that of Smirnov (1930) who found *Moraria mrazeki* T. Scott, 1903 in *Spongilla arctica* Annandale, collected in the Russian part of Lappland, but this species is normally free-living.

Several female and male specimens of a sponge-inhabiting harpacticoid collected from Pope's Eye in the entrance to Port Phillip, Victoria, Australia were kindly placed at my disposal by Dr Richard Hamond. Careful examination of both sexes revealed that the species cannot be attributed to any of the currently recognized families.

#### MATERIAL AND METHODS

Before dissection the habitus was drawn in lactophenol and body length measurements were made. Specimens were dissected in lactic acid and the

dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel.

All figures have been prepared using a camera lucida on a Leitz Dialux 20 interference microscope. The terminology is adopted from Lang (1948, 1965) except for (1) the terms *pars incisiva*, *pars molaris* and *lacinia mobilis* which are omitted in the description of the mandibular gnathobase (Mielke, 1984a), (2) the segmental composition of the mandible and maxilliped which are followed according to Boxshall (1985: 341–345). The terminology of Huys (1988a) for the caudal ramus armature is followed.

Both females and males of *Hamondia superba* gen. et sp. nov. and *Rhynchothalestris rufocincta* (Brady, 1880) were examined by scanning electron microscopy (SEM) with a JEOL JSM-840 microscope. Specimens were prepared by dehydration through graded ethanol (20%, 30%, 50%, 70%, 80%, 90%, 96%, 100%), critical-point drying, mounting on stubs and sputter-coating with gold.

Abbreviations used in the text and figures are: A1 = antennula; A2 = antenna; Mx1 = maxillula; P1–P6 = first to sixth legs; exp = exopod; enp = endopod; benp = baseoendopod; exp (or enp) 1 (or 2, 3) to denote the proximal (middle, distal) segment of a ramus. Type specimens are deposited in the collections of the National Museum of Victoria, Melbourne (NMV).

#### SYSTEMATICS

##### *Family Hamondiidae nov.*

##### *Diagnosis*

Body broadly ovoid, dorsoventrally compressed; dorsal surface densely covered with symmetrical pattern of sensillae. Rostrum very reduced, completely incorporated into cephalic shield, with two sensillae. P1-bearing somite fused with cephalosoma. Free prosomites large; those bearing P3 and P4 with pleurotergites strongly expanded posterolaterally. P5-bearing somite visible in dorsal view, but narrow and with undeveloped epimeral plates. Female genital double-somite large, posterolateral margins almost extending to rear edge of urosome; original segmentation marked by dorsolateral suture on either side. Free urosomites small, their combined lengths making up less than 10% of total body length. Pseudoperculum absent. Anal operculum well developed. Caudal rami broader than long, furnished with seven setae.

Antennula slender, with both plumose and smooth setae; with first segment shorter than second, without setae; nine-segmented in female, with aesthetascs on segments IV and IX; 14-segmented and modified in male, with geniculation between segments IX and X and aesthetascs on segments IV and VI. Antenna robust, with allobasis (with abexopodal seta in distal half); endopod one-segmented, bearing strong geniculate spines; exopod three-segmented, segments with two, one and four setae, respectively, exp<sub>3</sub> with bifid spinules. Mandibular gnathobase elongated, with one seta on cutting edge; basis strongly elongated, with three setae; endopod one-segmented, exopod two-segmented. Maxillula with well developed praecoxal arthrite; coxa with cylindrical endite and epipodite represented by one seta; basis with one endite and bearing one-segmented exopod and endopod. Maxillar syncoxa with three endites,

proximal one bilobed (representing fused praecoxal endites), bearing strikingly developed pinnate spine, proximal and distal lobes with two elements each; basis produced into pinnate claw; endopod two-segmented. Maxilliped robust, prehensile; praecoxa well defined; coxa with four setae; basis with two setae; endopod one-segmented and produced into short strong claw bearing four setae.

Swimming legs with well-developed praecoxae, three-segmented rami and extremely wide intercoxal sclerites. P1 adapted for grasping; massive proximal endopodite segment bearing inner seta at one-fifth distance of proximal margin, middle segment asetose, distal segment with two strong claws and minute seta. Proximal segments of rami of P2–P4 with inner seta; outer exopodal spines short and blunt. P5 with separate exopod and baseopod in both sexes; intercoxal sclerite absent; outer basal seta standing on long, non-articulating, cylindrical process; female baseopod leaf-like and having four setae, not joined by an intercoxal sclerite; male baseopods fused medially and bearing three setae each. Female genital complex with separate copulatory pore and having epicopulatory bulb and plate; genital apertures covered by P6 bearing three setae. Male P6 asymmetrical, each plate having two setae.

Sexual dimorphism in antennula, P2 endopod, P3 endopod, both rami of P4, fifth and sixth legs, and in genital segmentation; one spermatophore; one egg-sac.

Marine; associated with sponges.

*Type and only genus*

*Hamondia* gen. nov.

### ***Hamondia* gen. nov.**

*Diagnosis*

As for family.

*Etymology*

The genus is named in honour of my colleague Dr Richard Hamond, in appreciation of his valuable contributions to harpacticoid taxonomy. Gender: feminine.

*Type and only species*

*Hamondia superba* gen. et sp. nov.

### ***Hamondia superba* gen. et sp. nov.**

*Type locality*

Washings from unidentified sponges taken at a depth of 15 to 18 m on a vertical rock face at Pope's Eye, in the entrance to Port Phillip, Victoria; Australia; collected by Mrs J. E. Watson by SCUBA-diving on 30 v 1976.

*Material*

One female (holotype, NMV J17367) dissected and mounted on 12 slides. One male (allotypic paratype, NMV J17368) dissected and mounted on 11 slides. Other paratypes retained in the personal collection of the author are not

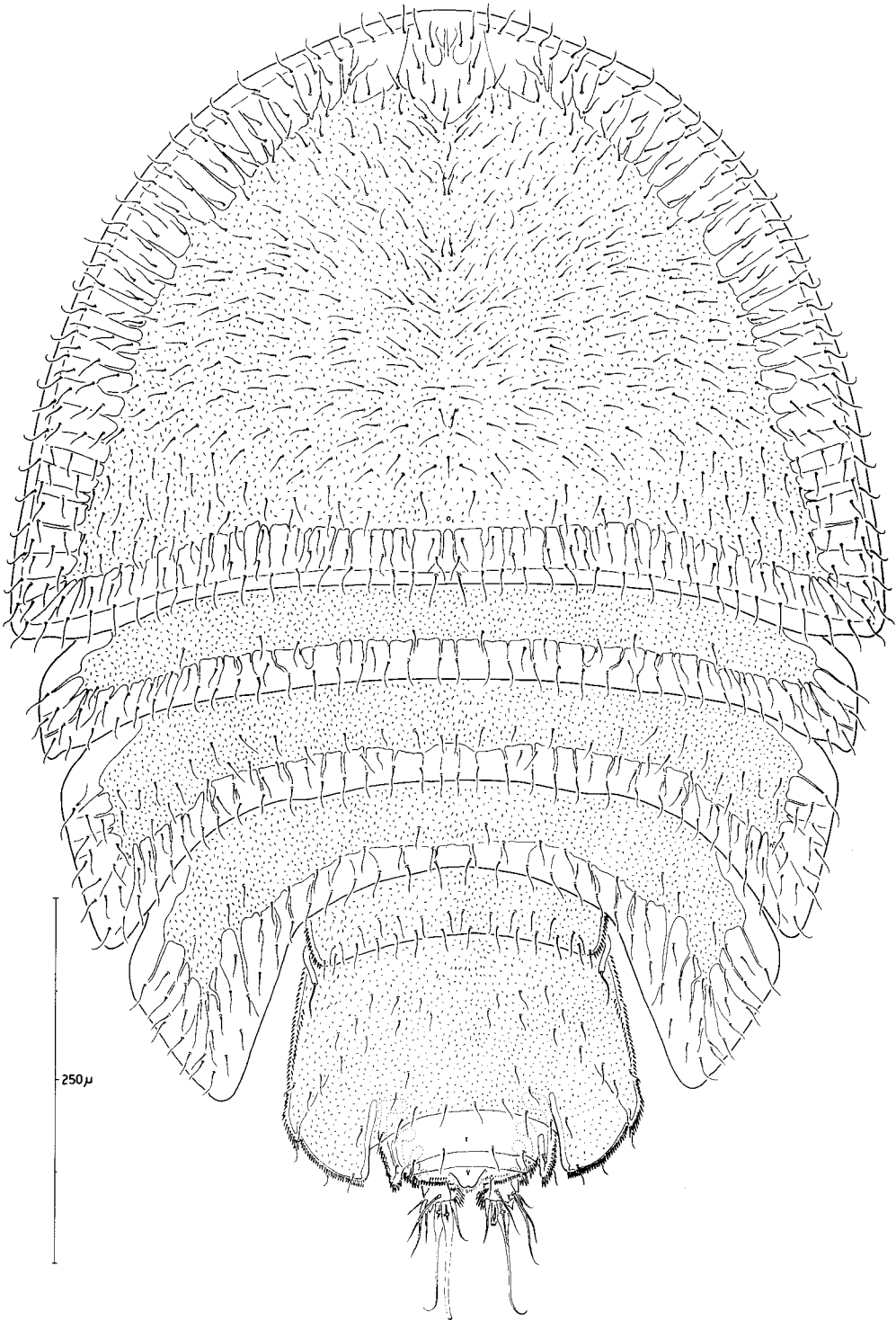


Figure 1. *Hamondia superba* gen. et sp. nov. Female: habitus, dorsal view.

dissected and preserved in alcohol: one female, one ovigerous female and one male copepodid V. One specimen of each sex was sacrificed for SEM.

### *Etymology*

The species name is derived from the Latin *superbus*, and alludes to the remarkable shape of the species.

### *Description*

Female (Figs 1–6, 7A, B, 8A, 9A, 10A, 13–15). Body length 790–805  $\mu\text{m}$  (including caudal rami).

Body broadly ovoid (Figs 1, 13), dorsoventrally compressed, without skeletal patterns (cf. some Peltidiidae). Maximum body width (590  $\mu\text{m}$ ) measured at posterior margin of cephalothorax. Dorsal integument densely covered with minute spinules and symmetrical pattern of sensillae (335 pairs and four medians), ventral surface without sensillae (except rostrals); posterior border of cephalic shield and somites smooth. Rostrum not defined, completely incorporated in cephalic shield; frontal pore and rostral sensillae visible on anterior ventral surface of cephalic shield (Fig. 14A). First pedigerous somite (P1) fused with cephalosome. Somites bearing P2 to P4 large and with dorsal symmetrical pattern of tiny sensillae (P2: 39 pairs; P3: 59 pairs; P4: 43 pairs), none of these somites with ventral sensillae; lateral portions of pleurotergites of P3- and P4-bearing somites strongly developed and protruding posterolaterally; those of P4-bearing somite extending far beyond middle of genital double-somite. Pleural regions of first urosomite undeveloped; tergite visible dorsally, but narrow, lateral margins covered with spinules (Figs 1A, 2B); except for cylindrical process and its basal seta, P5 not visible in dorsal view; dorsal surface showing 14 pairs of sensillae and mid-dorsal pore. Genital double-somite large, nearly as long as wide; lateral and posterolateral margins provided with minute spinules; pleural regions of genital somite weakly developed and marking plane of fusion; original separation also marked dorsally by short dorsolateral suture on either side of midline (Fig. 2B) and ventrally by an internal chitinous ridge on both sides of copulatory pore (Fig. 3B); posterolateral angles of genital double-somite extending to rear edge of following somite; furnished with 13 pairs of delicate sensillae in anterior half and eight pairs in posterior half. Free urosomites combined occupying only 6.5% of total body length (Fig. 1). Antepenultimate and penultimate urosomites also with protruding posterolateral (Figs 2A, 3C) margins which are densely covered with minute spinules; former somite with minute spinules along entire ventral rear margin, with three secretory pores and three pairs of sensillae on dorsal surface and with two pairs of sensillae ventrally; latter somite with midventral spinular row and two dorsolateral secretory pores but no sensillae. Anal somite with well-developed semi-circular anal operculum having bilobed posterior margin; dorsal surface of somite with several oblique rows of spinules, one pair of sensillae (each standing on minute tubercle) and one median pore; ventrally with closely set spinules along rear edge and along both sides of anal slit. Caudal rami (Figs 2A, 3C) shorter than wide, slightly convergent; each with three secretory pores and seven setae (setae I, II, III, V and VII being entirely bare): anterolateral accessory seta (I) well developed and closely set to slightly dorsally displaced anterolateral seta (II); posterolateral seta (III) standing at outer distal corner and separated

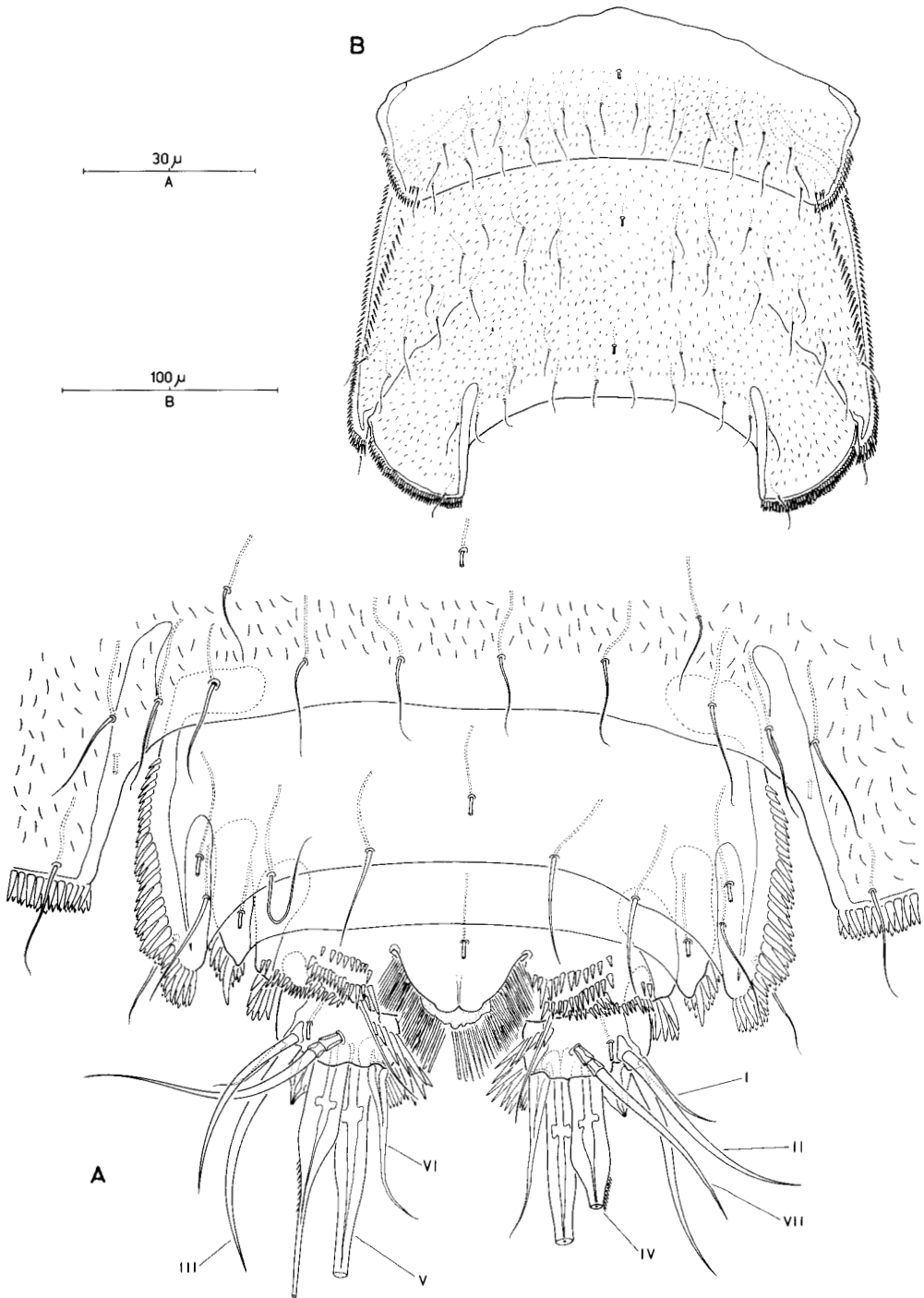


Figure 2. *Hamondia superba* gen. et sp. nov. Female. A, Free urosomites and caudal rami, dorsal view. B, P5-bearing somite and genital double-somite, dorsal view.



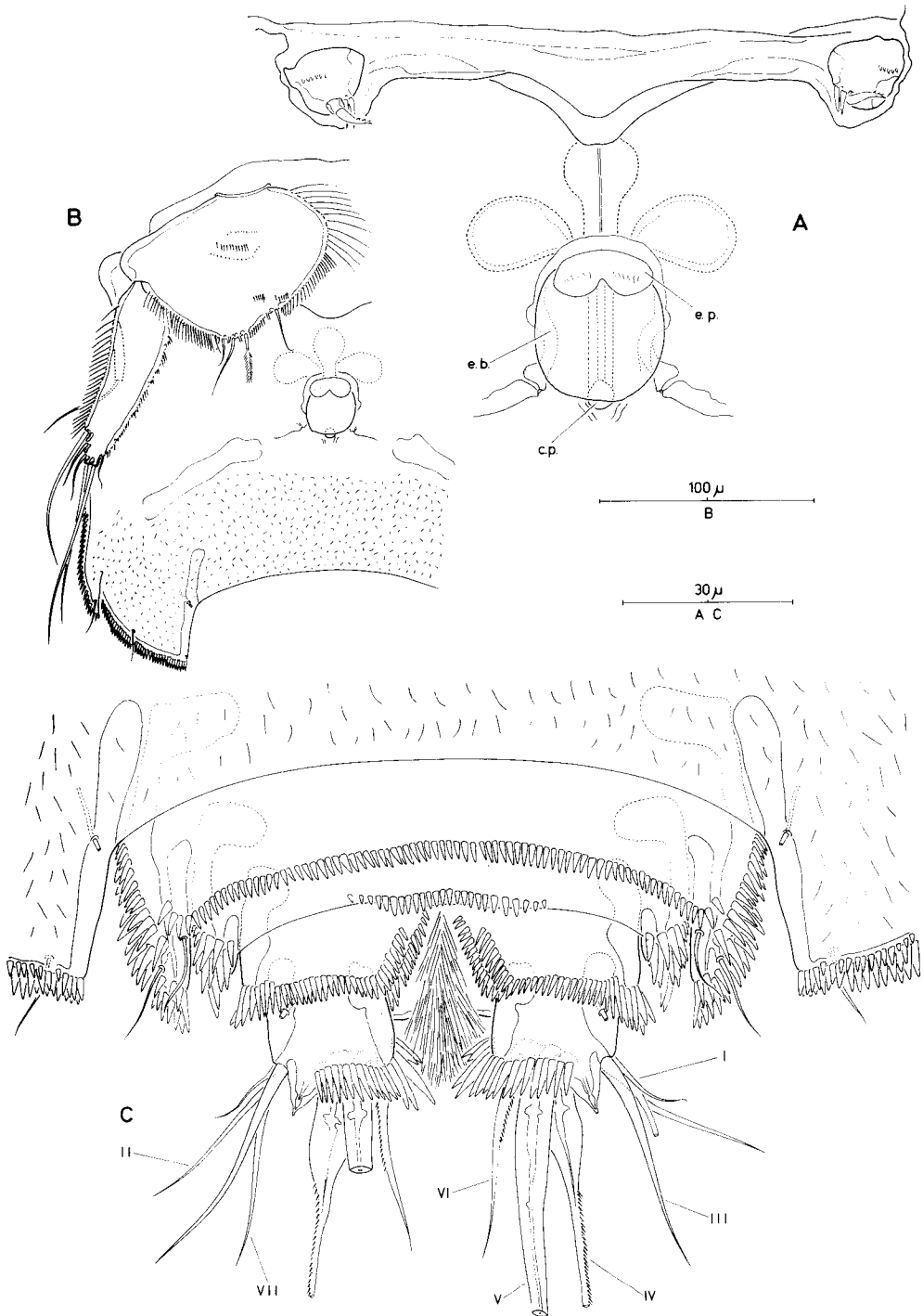


Figure 3. *Hamondia superba* gen. et sp. nov. Female. A, Genital complex (c.p. = copulatory pore; e.b. = epicopulatory bulb; e.p. = epicopulatory plate). B, Genital double-somite and P5, ventral view (right half omitted). C, Free urosomites, ventral view.

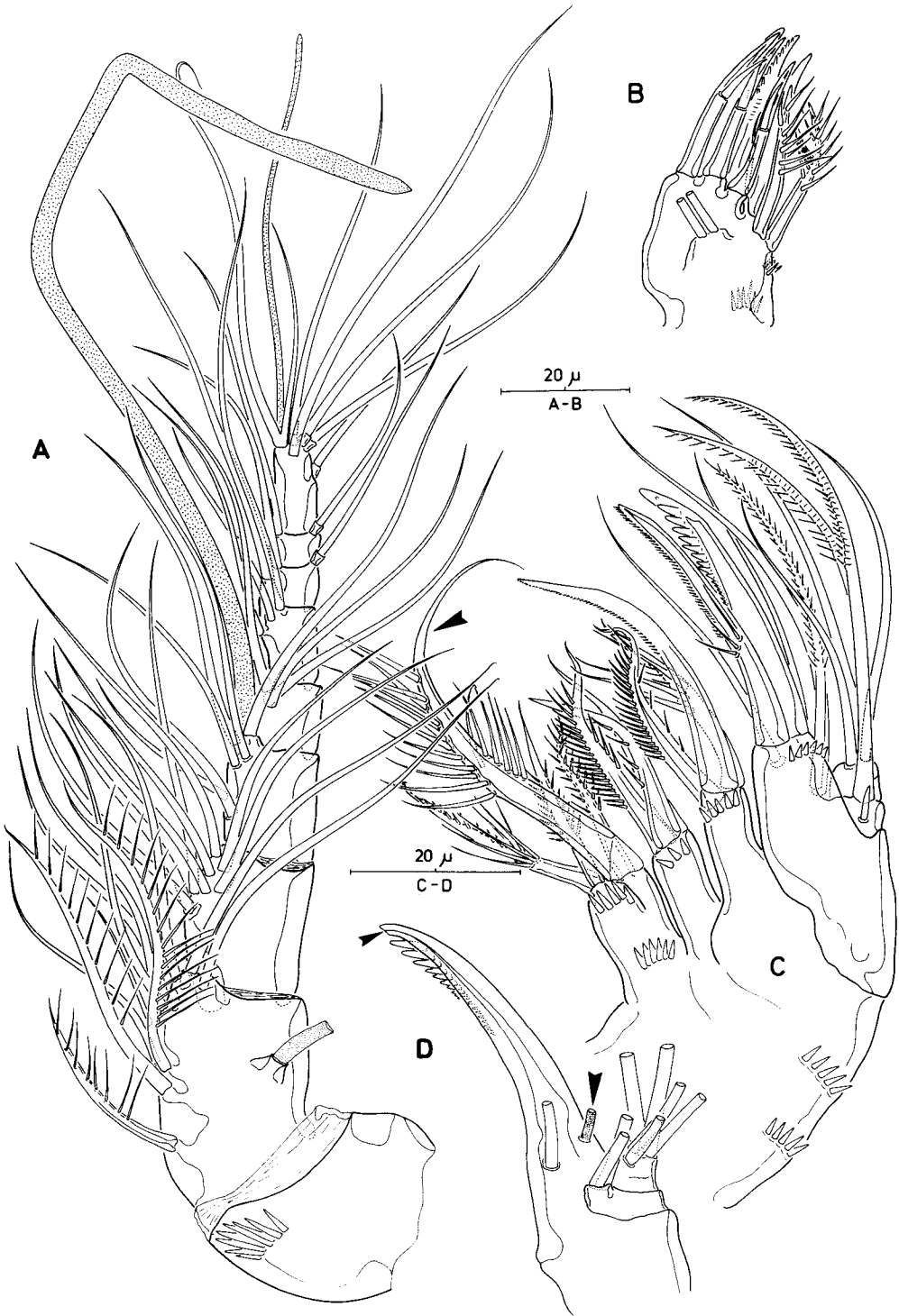


Figure 4. *Hamondia superba* gen. et sp. nov. Female. A, Antennula. B, Praecoxal arthrite of maxillula, anterior view. C, Maxilla (arrow indicating strong pinnate spine on proximal endite). D, Maxilla, basal endite and endopod (arrows indicating tubular pore and minute pore at the tip of the basal claw).

from seta IV by conspicuous pore opening on top of characteristic protuberance; outer terminal seta (IV) with broad base and acutely tapering distally, outer margin spinulose; inner terminal seta (V) strongly developed and more gradually tapering; terminal accessory seta (VI) spinulose along proximal outer margin; dorsal seta VII triarticulated at base; dorsal secretory pore visible between setae II and VII, one located ventrally near outer proximal corner; a spinular row running along inner side of each ramus, starting from dorsal proximal corner and continuing along ventral rear margin.

Antennula (Fig. 4A) slender, nine-segmented, articulating in conspicuous concavity of cephalic shield (Figs 13, 14A); the angle of articulation between segments I and II directs distal segments more ventrally and abaxially; segment I shorter than wide, having spinular row along inner anterior margin and flexible integument (hyaline frill) distally; segment II longest, with three plumose and eight smooth setae along inner margin and conspicuous secretory pore on anterior surface; segment III with eight setae in distal half; segment IV with long, slender aesthetasc and four setae distally and with two setae proximally; segments V and VI with three and four setae, respectively; segments VII and VIII with one outer and one inner seta each; segment IX with five simple setae and two others fused at base with aesthetasc.

Antennae (Fig. 5A) robust; allobases directed adaxially so that endopodal spines are in position ready to grasp (Figs 13, 14A). Distinct vestibulum visible between attachment sites of antennulae and antennae. Coxa well-developed, unarmed. Basis incompletely fused with proximal endopodite segment and forming allobasis (suture is still visible along anterior surface); armed with three spinular rows with pinnate abexopodal seta (of endopodal origin) in distal half. Exopod inserting at about half distance from proximal margin; three-segmented; exopodite segment I longest, with two inner bipinnate setae; segment II shortest, with one bipinnate seta; segment III with one marginal and three apical bipinnate setae and furnished with row of bifid spinules (Fig. 14D). Endopod one-segmented; abexopodal margin armed with tiny spinules, two unipinnate spines and two basally fused setae; distal margin having three pinnate setae (the two outer ones being fused at base), three geniculate spines (becoming stouter and shorter abaxially) and one acutely curved spine; two combs of spinules visible along adexopodal margin (Fig. 14D).

Labrum (Figs 13, 15A). Prominent, trapezoid, distal edge ornamented with densely packed spinules.

Mandible (Fig. 5B). Coxa with strongly elongated gnathobasis having several blunt teeth and a unipinnate spine at cutting edge. Palp well-developed, biramous, with some folded integument at proximal articulation site (Fig. 14B). Basis long and narrow, ornamented with several spinular rows in proximal half and with two pinnate setae and one smooth one along inner margin. Endopod long unisegmented, armed with two marginal and seven apical setae. Exopod two-segmented; proximal segment longest, having one seta at about middle inner edge and another subdistally; segment II square, with four pinnate setae.

Maxillula (Figs 4D, 5C). Praecoxal arthrite squarish; with some spinules on anterior surface; posterior surface with two juxtaposed pinnate setae; inner margin of arthrite with eight strong, ornamented spines and one minute seta. Coxa with spinules along outer margin; epipodite represented by one pinnate seta; endite subcylindrical and having five setae and one pinnate claw. Basis with



Figure 5. *Hamondia superba* gen. et sp. nov. Female. A, Antenna. B, Mandible. C, Maxillula (arrow indicating tubular pore of basal endite).



Figure 6. *Hamondia superba* gen. et sp. nov. Female. A, Maxilliped. B, P1, anterior view. C, Middle and distal endopodite segments of P1, posterior view.

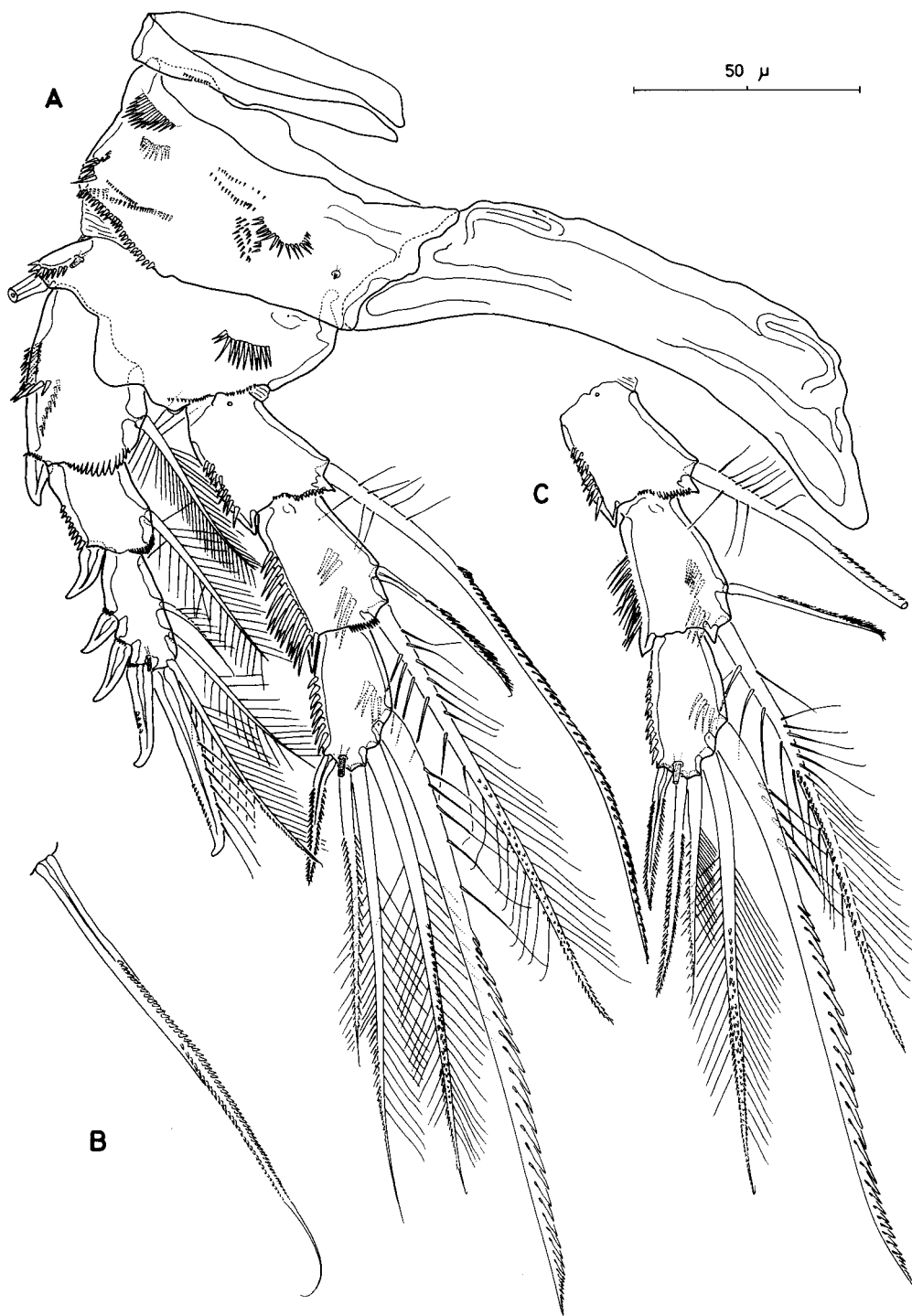


Figure 7. *Hamondia superba* gen. et sp. nov. Female. A, P2 and intercoxal sclerite, anterior view (outer basal seta omitted). B, Outer basal seta of P2. Male. C, Endopod of P2, anterior view.

one endite (derived by fusion of ancestral two endites) bearing tube-pore (arrowed in Fig. 5C) and six setae (one is geniculate). Endopod unisegmented, almost square, with four apical plumose setae. Exopod unisegmented, long and narrow, with four apical plumose setae.

Maxilla (Figs 4C, D). Praecoxa and coxa fused to form syncoxa bearing three endites and with two spinular rows round outer margin; proximal (praecoxal) endite bilobed (derived by fusion of ancestral two endites), proximal lobe with two slender spines, distal lobe with one slender and one extremely developed spine (arrowed in Fig. 4C); middle endite with two spines and one seta; distal endite with two spines and one strong claw. Basis with one secretory pore (arrowed in Fig. 4D), two slender setae, one pinnate spine and one serrate claw (fused with basal endite along posterior surfaces and possessing minute pore at tip). Endopod two-segmented, boundaries not well defined (Fig. 14C); proximal segment broader than long, with short spine and three setae (one geniculate); distal segment square, with four setae (one geniculate).

Maxillipede (Figs 6A, 12C). Robust, directed abaxially (Fig. 13). Praecoxa well defined, with some arthrodial membrane distally. Coxa typically (Fig. 12C) with four slender setae (but sometimes only with three; Fig. 15B) at outer subdistal corner and some patches of spinules at anterior surface. Basis triangular, with areas of flexible integument at articulations with coxa and endopod; ornamented with two setae at about middle inner edge (one on either surface) and showing depression (covered with numerous blunt spinules) near articulation site of endopod. Endopod unisegmented, produced into hook-like claw bearing pinnate seta at posterior surface and three tiny seta-like elements at anterior one.

Swimming legs (Figs 6B, C, 7A, B, 8A, 9A). With three-segmented rami and well-developed intercoxal sclerites. P1 (Figs 6B, C, 13, 15C, D). With well-developed triangular praecoxa, ornamented with some tiny spinules. Coxa with pore near inner margin and with numerous spinules in abaxial half of anterior surface. Basis with several long spinules on both posterior and anterior surfaces and bearing outer unipinnate seta and inner bipinnate spine (standing on anterior surface). Exopod prehensile by means of pivot articulation between segments II and III; proximal segment without inner seta but with outer spine; middle segment longest, with both inner and outer spine (latter implanted at quarter distance from distal margin); distal segment with one tiny seta, three strong claws and one long tripinnate seta. Endopod massive; proximal segment exceeding exopod both in length and in width, inner plumose seta implanted at one-fifth distance from distal margin; no real pivot joint between segments II and III but the well-developed arthrodial membranes between constituent endopodital segments (Fig. 15D) allows a certain degree of flexibility (thus prehensile ability) of distal part of endopod; middle segment asetose; distal segment with one tiny seta and two hook-like claws.

P2-P4 (Figs 7A, B, 8A, 9A). With well-developed U-shaped praecoxae and very broad, unornamented intercoxal sclerites. Endopods either longer (P2-P3) or shorter (P4) than exopods. Anterior surface of coxae with inner tube-pore, of bases with outer tube-pore. Areas of folded membrane present between coxa and basis and between basis and endopod. Basis with either extremely long distally bipinnate spine (P2), or apically unipinnate seta (P3), or naked seta (P4). Exopodal spines short and blunt. Exopodal setae plumose except for inner

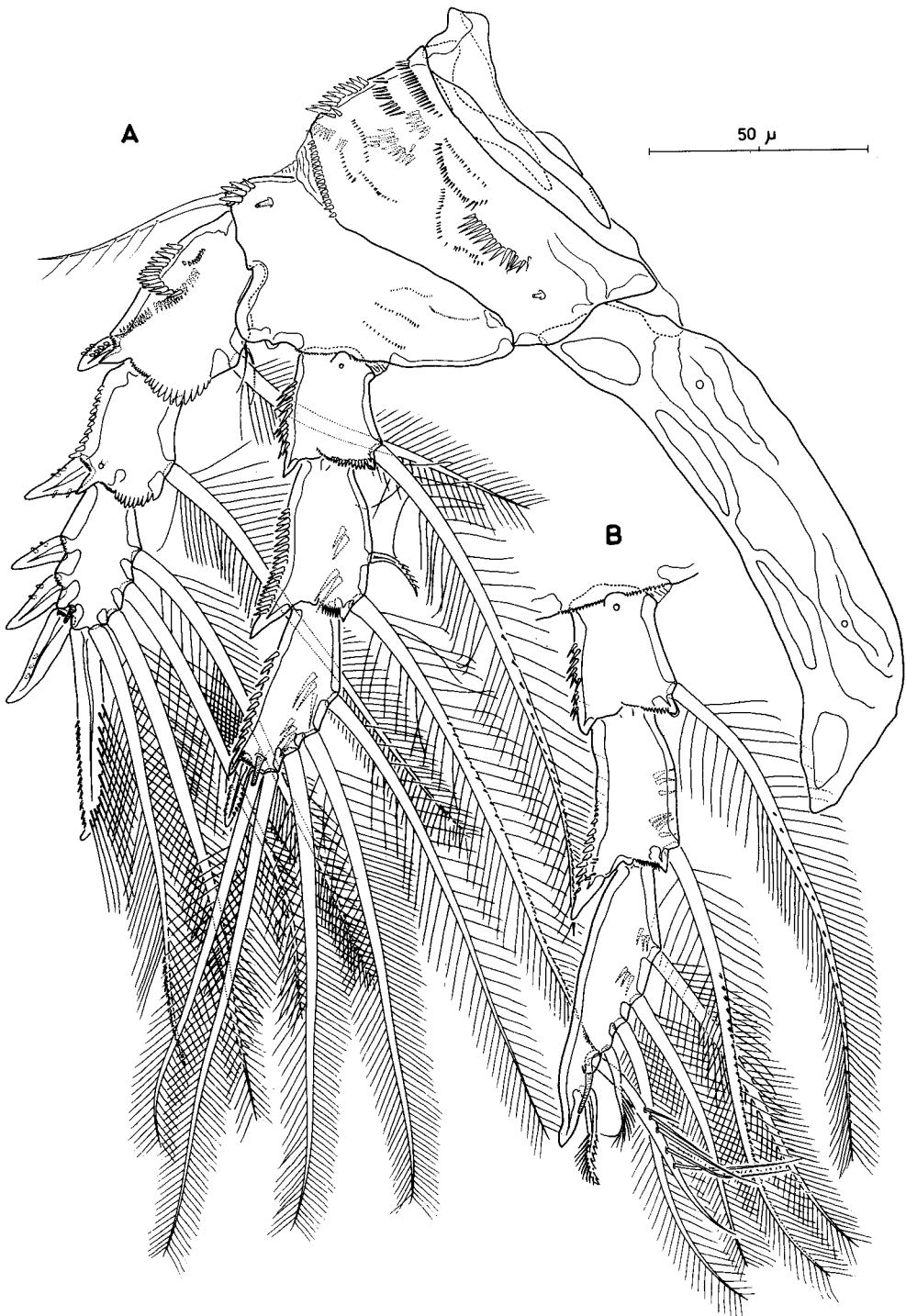


Figure 8. *Hamondia superba* gen. et sp. nov. A, Female. P3 and intercoxal sclerite, anterior view. B, Male. Endopod of P3, anterior view.



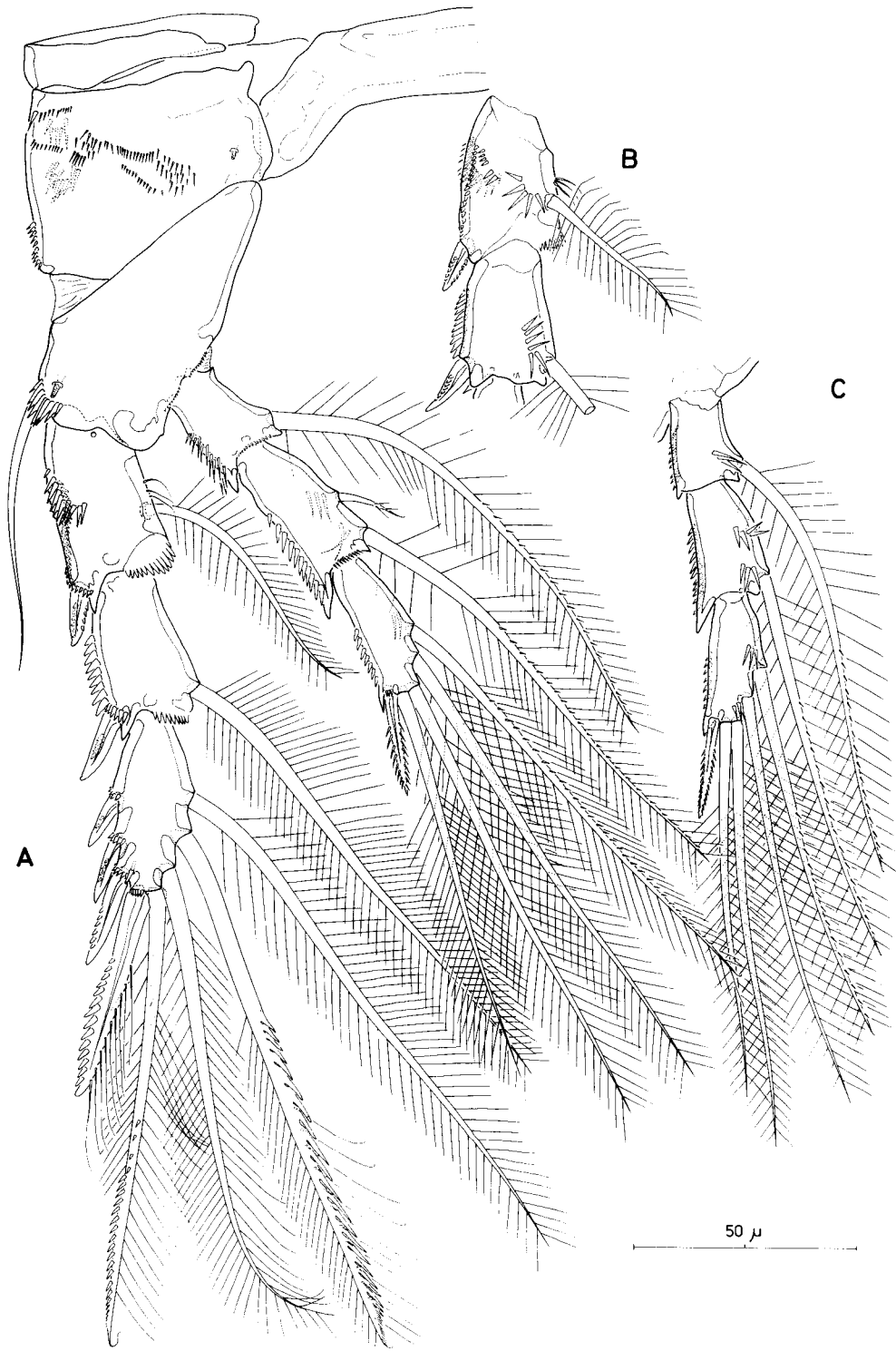


Figure 9. *Hamondia superba* gen. et sp. nov. Female. A, P4 and right half of intercoxal sclerite anterior view. Male. B, Proximal and middle exopodite segments of P4, posterior view. C, Endopod of P4, posterior view.

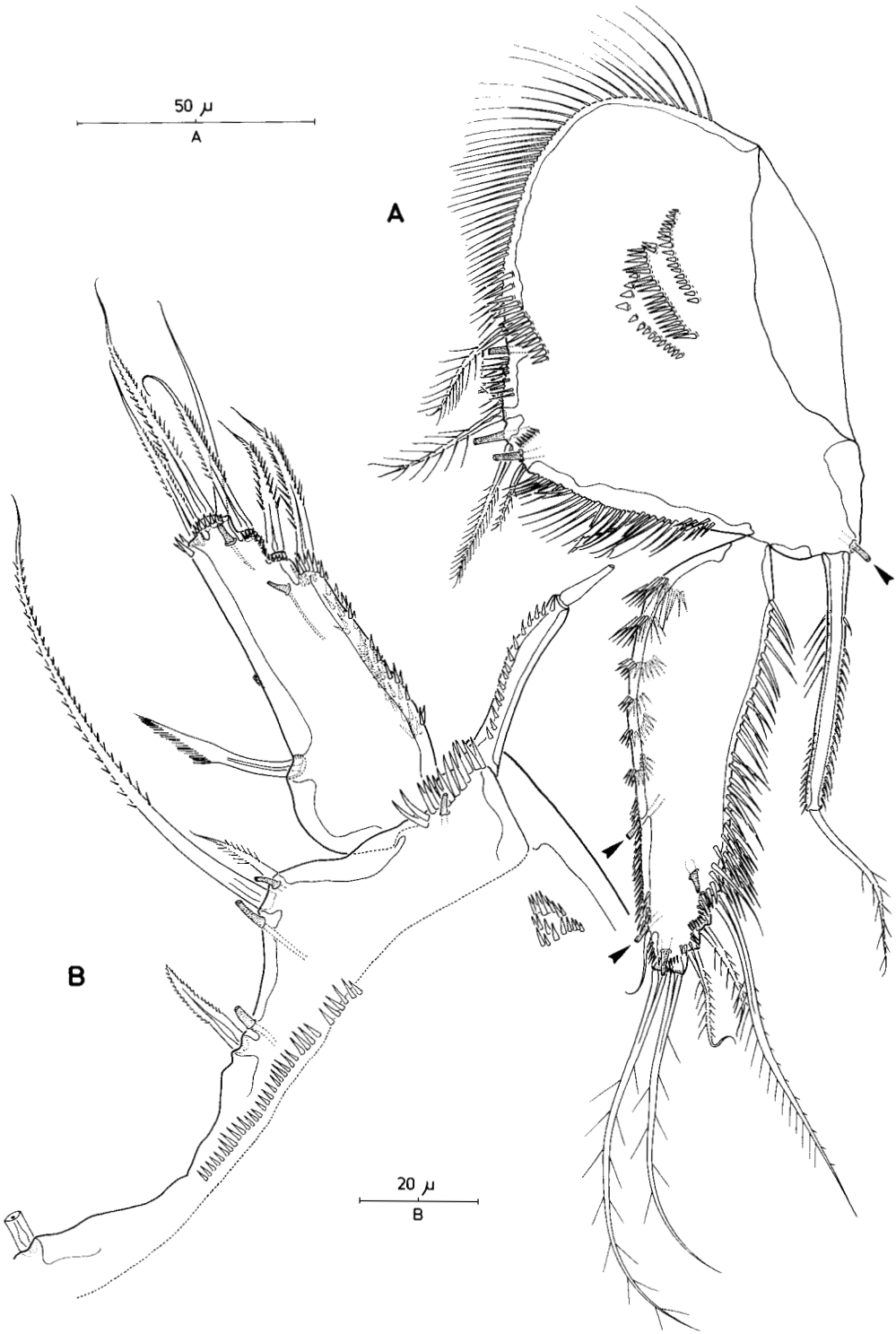


Figure 10. *Hamondia superba* gen. et sp. nov. A, Female. P5, anterior view (arrows indicating tubular pores). B, Male. P5, anterior view.

TABLE 1. Seta and spine formula of *Hamondia superba* gen. et sp. nov.

	Exopod	Endopod
P2	1.1.223	1.2.221
P3	1.1.323	1.2.321
P4	1.1.323	1.2.221

terminal spine pinnate along outer distal margin, and middle inner seta of distal segment of P4 which is serrate. Inner endopodal setae often being tripinnate (P3, P4) or even multipinnate (P2); endopodite-segments of P2 each with one serrate seta. Seta and spine formulae shown in Table 1.

Fifth pair of legs (Figs 3B, 10A). Not fused medially, not joined by intercoxal sclerite; attachment site with supporting somite broad. Baseoendopod leaf-like: inner margin ornamented with long hair-like spinules decreasing in length distally: anterior surface with three central spinular rows; outer margin also with long spinules; distal part having four plumose setae and three secretory pores (each in between two setae); basal seta plumose and standing on very long and narrow, cylindrical process (setophore) which is spinulose along both inner and outer margins and articulating at base; fourth secretory pore (arrowed in Fig. 10A) located proximally of this process. Exopod slender and abaxially directed; attachment site very small; inner margin with several spinular rows, two secretory pores (arrowed in Fig. 10A) and one tiny seta; outer margin with long spinules, one long and two short plumose setae; short distal margin with two slender, plumose setae; all setae implanted in distal fourth of segment; two secretory pores visible at anterior surface.

Genital complex (Fig. 3A, B). Located in anterior half of genital double-somite. P6 represented by subcircular plate having minute spinular row and three tiny setae; genital pores connected by means of a transverse furrow. Seminal receptacles with distinct sclerotized walls, paired. Copulatory pore circular, located in pronounced depression medially and partly covered by median bulb-shaped protuberance (epicopulatory bulb) overlaid in part by conspicuous bilobed operculum (epicopulatory plate); there is no external connection between copulatory pore and the genital apertures; minute pore is visible on either side of copulatory pore.

Male (Figs 7C, 8B, 9B, C, 10B, 11, 12, 16). Body length 745–755  $\mu\text{m}$  (including caudal rami). Habitus as in female, except for free genital somite (Figs 12A, B). Sexual dimorphism in antennula and P2 to P6.

Antennula (Fig. 11). Slender, 14-segmented, modified; geniculation located between segments IX and X; segments distal to geniculation slightly directed anteriorly (Fig. 16C). Segment I asetose, with three spinular rows along the inner margin; segment II short, with secretory pore and one plumose seta; segment III with four plumose and eight naked setae along inner margin; segment IV with two inner processes, the proximal process bearing two setae, distal process bearing short aesthetasc and six setae; segment V very short, with two setae on inner process; segment VI swollen, furnished with five slender seta along inner edge and long aesthetasc accompanied by pinnate seta at distal margin; segment VII very small, with two tiny setae; segment VIII also small,

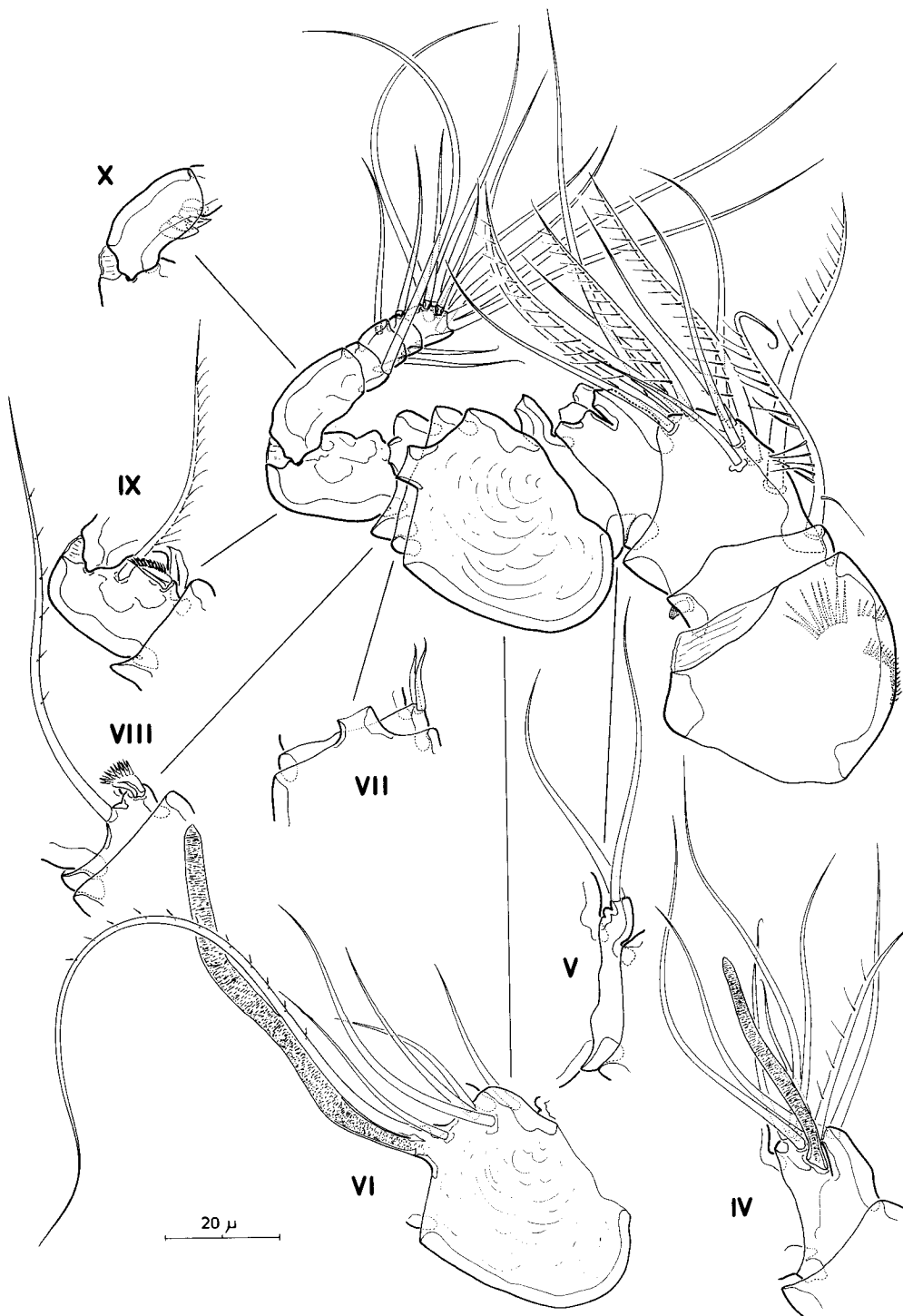


Figure 11. *Hamondia superba* gen. et sp. nov. Male. Antennula (setation of segments IV to X omitted in whole drawing) with its constituent segments.

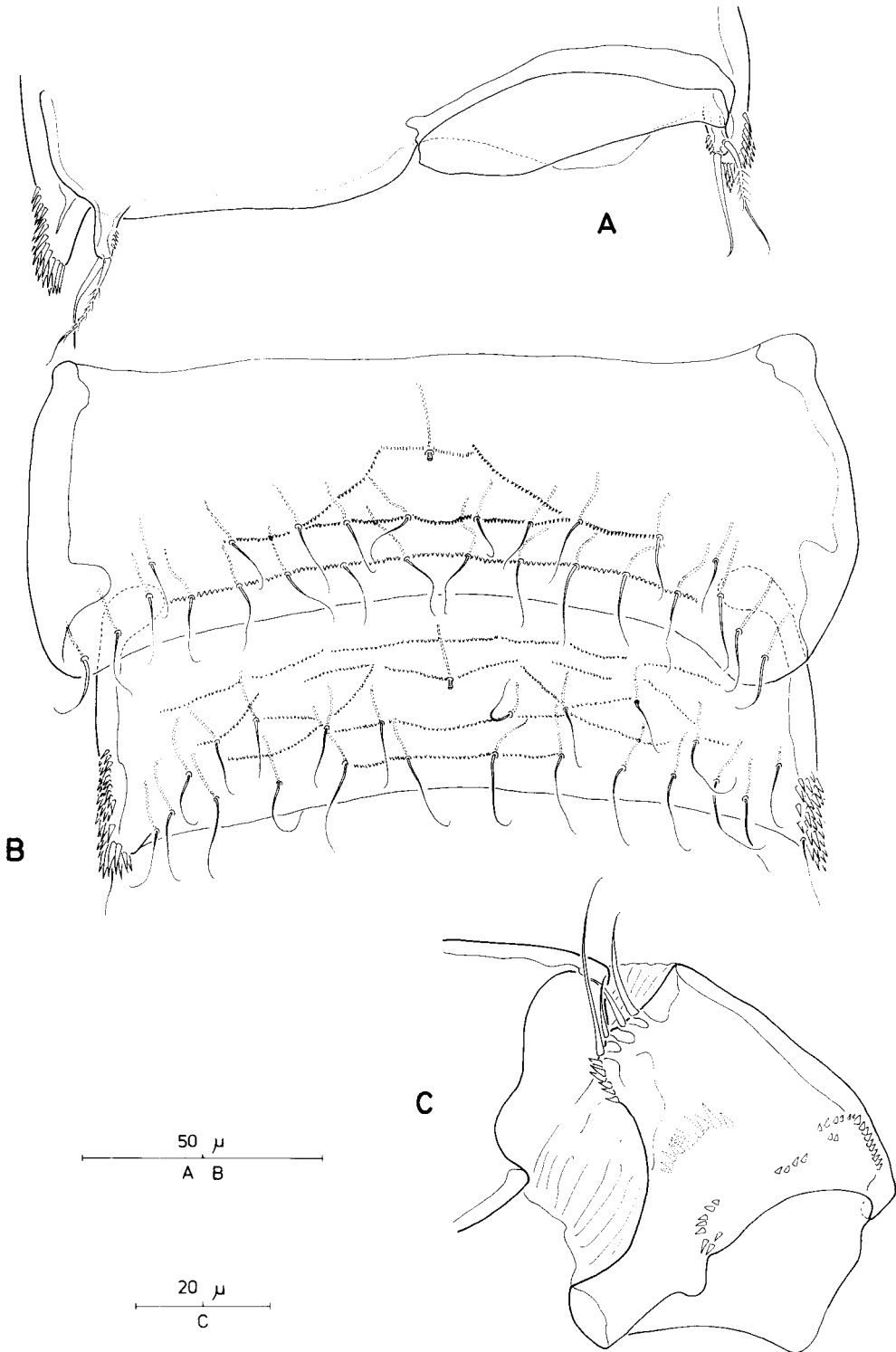


Figure 12. *Hamondia superba* gen. et sp. nov. Male. A, Sixth pair of legs. B, First and second urosomite, dorsal view. C, Coxa of maxillipede.

with one slender seta and one short pinnate spine; segment IX with one modified spine, one slender seta and one short pinnate spine, distal and geniculating with following segment; segment X with three very short, modified spines; segment XI minute, with one inner seta; segments XII and XIII both with one inner and one outer seta; segment XIV with eight setae in total (two confluent at base).

P2 (Fig. 7C). Protopod, exopod and proximal endopodite-segment exactly as in female. Middle segment with outer spinules less long; process at outer distal corner shorter and swollen; inner distal corner also with minute process. Distal segment with apical setae being equal in length and distinctly shorter than in female.

P3 (Figs 8B, 16B). Protopod, exopod and proximal endopodite-segment exactly as in female. Middle segment slightly more slender than in female; outer distal process more pronounced and bearing smaller and less spinules; proximal inner seta missing; distal segment modified, triangular and elongated with blunt tip slightly bending inwards; outer margin without spinules; number of setae same as in female, but all (except seta 6) distinctly shorter; setae I to III well developed, bipinnate, seta IV short and unipinnate; seta V implanted on posterior surface and bearing long pinnules; enlarged tube pore standing on tubercle visible between setae V and VI.

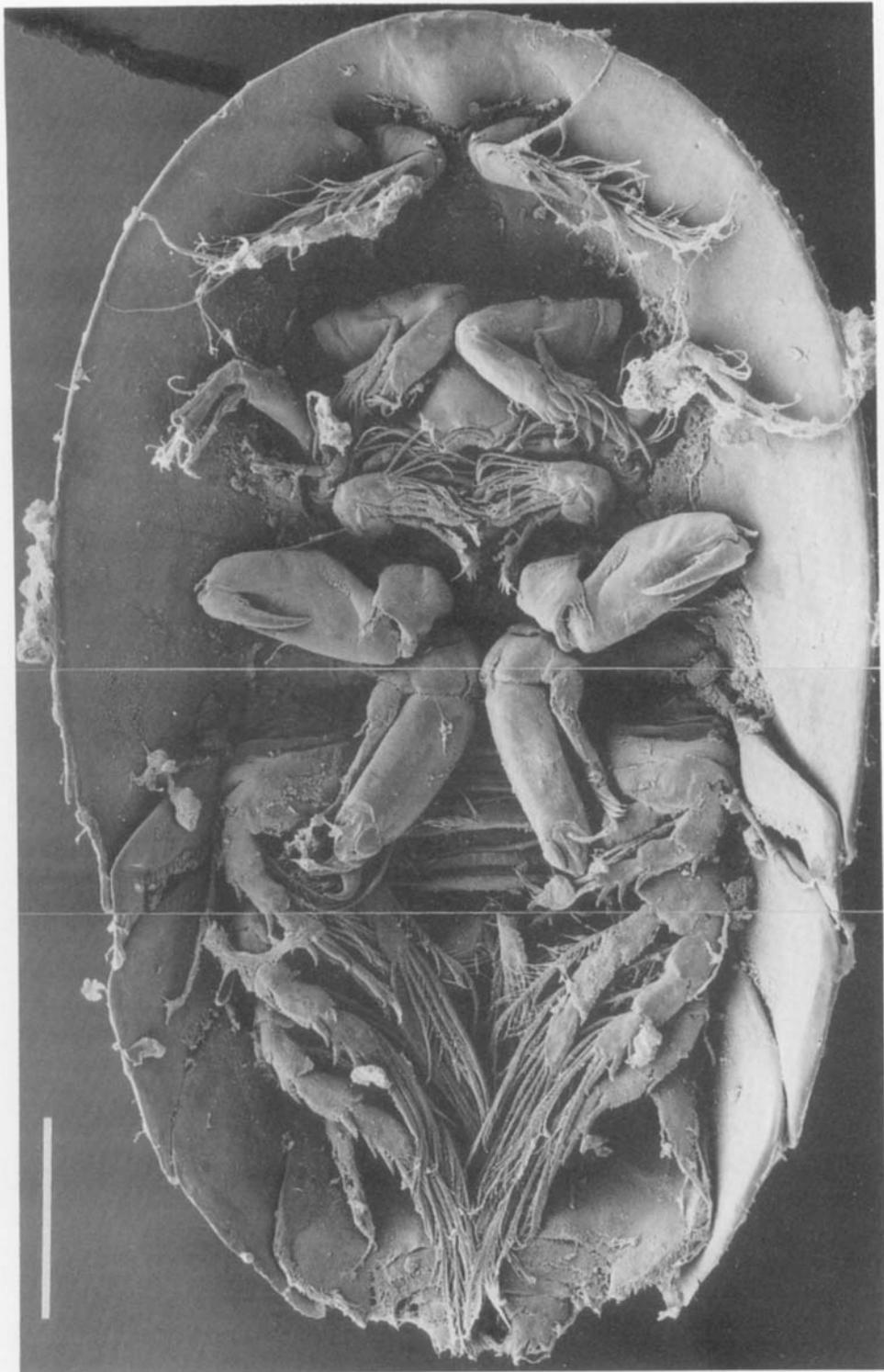
P4 (Fig. 9B, C). Protopod same as female. Proximal and middle exopodite segments (Fig. 9B) and proximal endopodite segment (Fig. 9C) with supplementary spinules on posterior surface, near the implantation of inner seta. Middle endopodite segment with only one seta (proximal inner one missing).

P5-bearing somite (Figs 10B, 12B). Dorsally with 13 pairs of sensillae, one median secretory pore and reticulated pattern of minute spinules; outer margins rounded and smooth; ventral surface with patch of spinules on either side. P5 (Figs 10B, 16A, D) with separate rami; not visible in dorsal aspect. Baseoendopods forming narrow common plate and fused with supporting somite, original articulation still being marked internally; median part bearing transverse row of spinules; basal seta implanted on cylindrical articulating setophore, latter accompanied at base by long spinules and tubular pore; endopodal lobe not pronounced, bearing three setae (middle one being extremely long) and three secretory pores. Exopod one-segmented, narrow, attachment site small; distal outer margin stepped and furnished with three pinnate setae; inner margin almost smooth, with pectinate seta at about quarter distance from proximal margin; apical part with three setae; two secretory pores visible in distal third of anterior surface.

P6-bearing (genital) somite (Fig. 12B). With distal angles slightly produced and spinulose; dorsal surface with 12 pairs of tiny sensillae, one median pore and reticulated pattern of minute spinules. P6 (Figs 12A, 16A) asymmetrical, one member fused with supporting somite, other being narrow plate acting as valve to release spermatophore (dextral and sinistral configurations exist depending on development of either right or left testis); each having outer subcylindrical process bearing two setae.

#### *Variation*

Noticed in, (1) the setation of the maxillipedal coxa (typically with four setae, but sometimes with only three), (2) the outer distal corner of the middle



Scale bar = 100  $\mu$ m.

endopodite-segment P2 of a single male was found to be produced in the same way as in the female, (3) the middle endopodite-segment P3 of a single male had the same setation as in the female, (4) the length of the median spinular row of the male baseoendopods of P5 (compare Figs 10B and 16A).

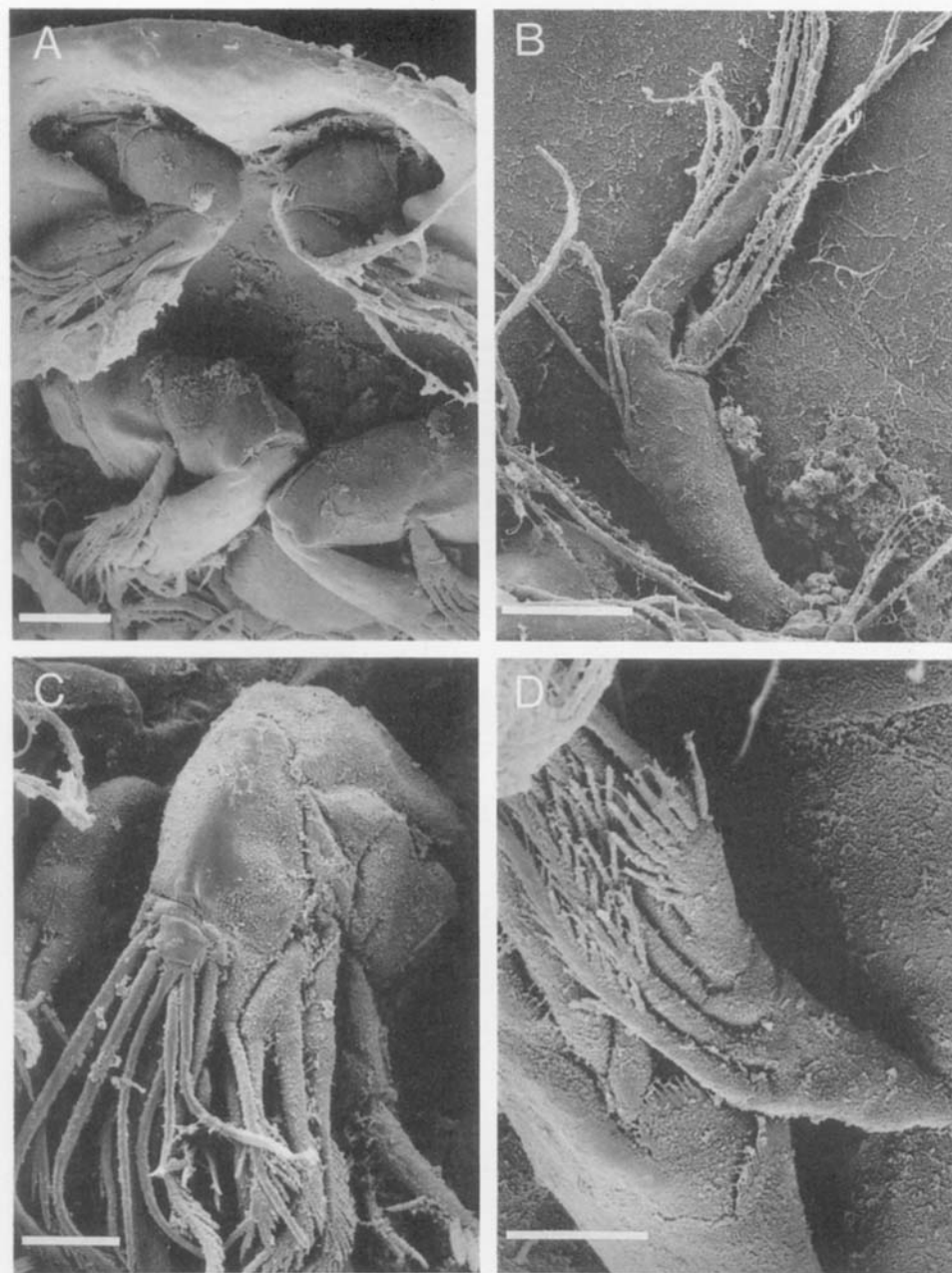
### Discussion

The dorsoventrally flattened body morphology and the presence of potential attachment organs (antenna, maxilliped, P1) of the Hamondiidae are preadaptations for at least a loose association with a host (in this case a sponge). The ovoid, shield-shaped, compressed habitus are reminiscent of other, primarily seaweed-dwelling, harpacticoid families (Porcellidiidae, Peltidiidae) or genera (*Paramenophia* Lang, 1954). However, Porcellidiidae can be easily differentiated from *Hamondia* by, amongst other features, the considerable fusion of the urosome leaving only a narrow P5-bearing somite, a laterally expanded somite bearing the genital apertures, and a minute, medially cleft somite bearing the anus. Moreover, *Porcellidium* Claus, 1860 is characterized by the greatly enlarged fifth pair of legs forming the posterolateral rims of the body and completely enclosing the abdomen. *Paramenophia* differs from *Hamondia* in the presence of sexual dimorphism on leg 1 but not on leg 3, the P5 structure in both sexes, the reductions in the mouthparts (mandible with one-segmented rami; maxillula without epipodite; maxilla with reduced endites and no endopod) and the well-developed rostrum. The Peltidiidae are characterized by the non-prehensile (but sometimes sexually dimorphic; see *Peltidium* Philippi, 1839) endopod of P1, the prehensile maxilla with widely separated endites, the well-developed rostrum (at least in the female), the enlarged female P5 exopods which are visible in dorsal aspect and the absence of an epipodite in the maxillula. The possible relationships of the Hamondiidae will be discussed below.

Until the discovery of the male of *Hamondia superba* the maximum number of antennular segments ever recorded in the Harpacticoida was ten or 11 (depending on the authority). The increase of this number to 14 is due mainly to failure of fusion distal to the geniculation since, in other harpacticoids, the homologues to segments X–XI of *Hamondia* are always fused to form a double segment. A 14-segmented antennula is also found in the males of *Ambunguipes* gen. nov. (= *Rhynchothalestris* Sars, 1905; see below). In most harpacticoids segments XII–XIII also fuse into a double segment, but in a few such as the Neobradyidae (Huys, 1987b) they remain separate. In this context, the retention of the basis number of nine segments in the female is surprising and reinforces its significance in diagnosing the Harpacticoida.

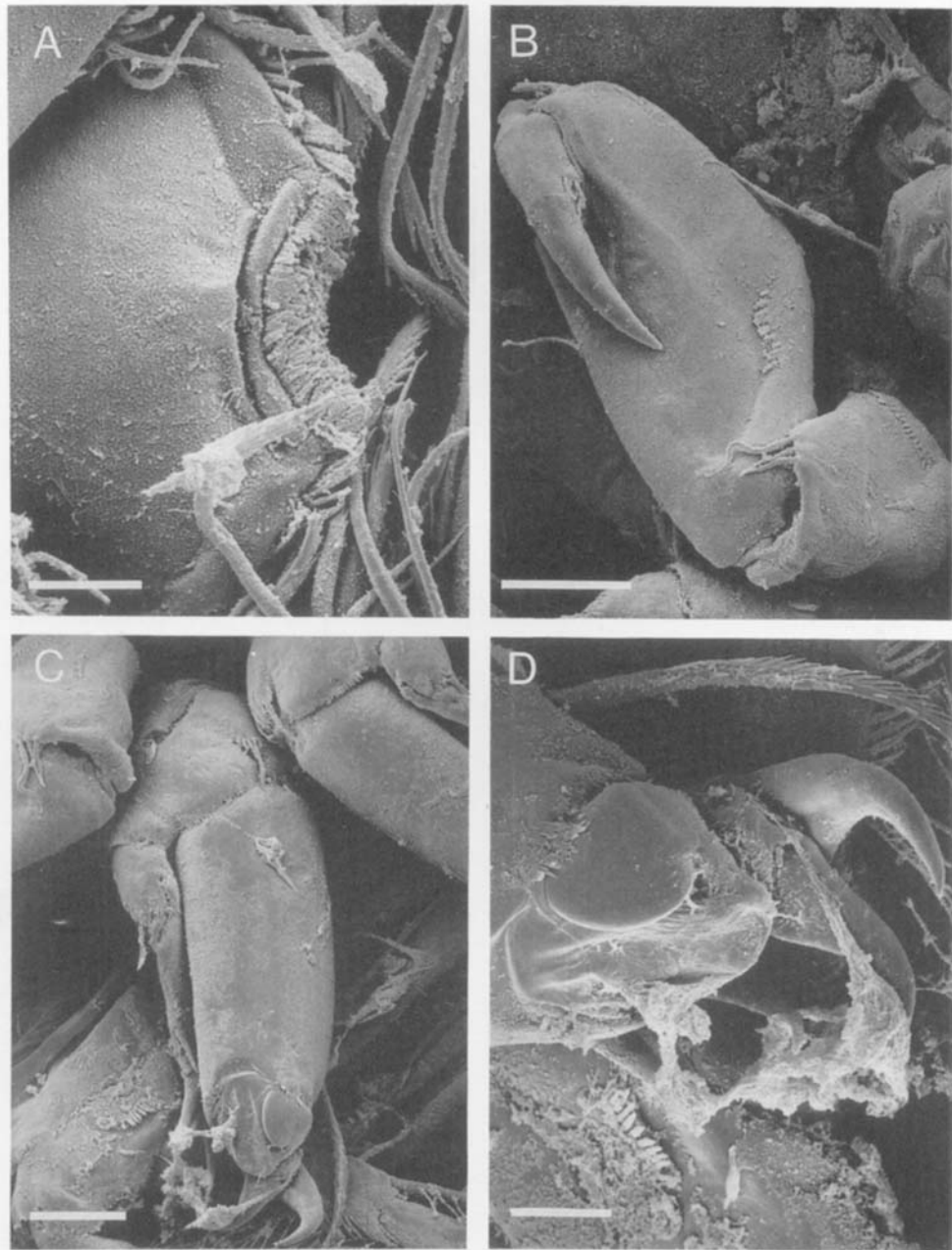
The genital complex of the female is characteristic in having a distinctly swollen, ovoid structure, located medially and ventrally in a pronounced depression of the genital double-somite and overlaying the anterior half of the minute copulatory pore (Fig. 3A, B). This bulb-shaped process is clearly a novel structure for which I introduce the term *epicopulatory bulb*, and is in its turn covered anteriorly by a small medially incised *epicopulatory plate*. These two morphological features are present also in the new genus *Ambunguipes* (Fig. 26A, B), but are definitely absent in the genera of the Thalestrinae, Rhynchothalestrinae and Dactylopusiinae. The functions of these structures are not clear. Fahrenbach (1961) found a small, stout, slightly bilobed cuticular





anterior part of cephalic shield showing implantation of antennula, antennae and rostral sensillae. B, Mandibular palp. C, Maxilla. D, Exopod of antenna. Scale bars: A,B=25  $\mu\text{m}$ ; C,D=10  $\mu\text{m}$ .

eminence just anterior to the copulatory pore of *Diarthrodes cystoecus* Fahrenbach, 1954 which is comparable in all details to the structure found in *Rhynchothalestris helgolandica* (Claus, 1863) (Figs 18A, 22C). Fahrenbach (1961) suggested that this eminence could serve as a surface against which the anterior face of the spermatophore is cemented during copulation.



B, Maxilliped, posterior view. C, Leg 1, anterior view. D, Distal segments of endopod of P1, anterior view. Scale bars: A,D=10  $\mu$ m; B,C=25  $\mu$ m.

#### *Outgroup of Hamondiidae*

Taxa of the Hamondiidae do not show any phylogenetic affinities with the dorsoventrally flattened genera listed above. The shared ovoid depressed body shape is merely a product of parallel evolution. A combination of features such as

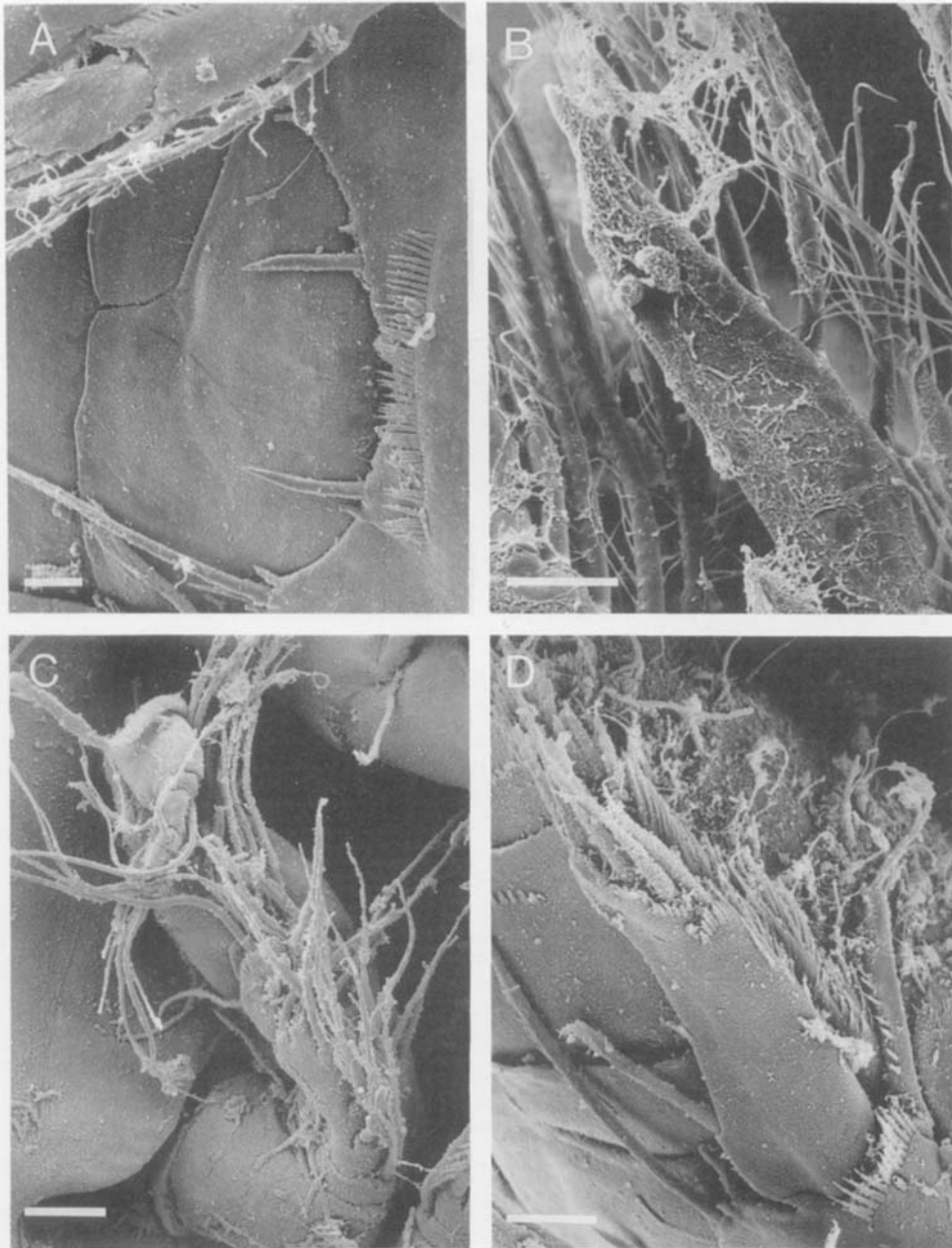


Figure 16. *Hamondia superba* gen. et sp. nov. SEM micrographs. Male. A, Baseoendopods of P5 and sixth pair of legs. B, Distal endopodite segment of P3. C, Antennula. D, Exopod of P5. Scale bars = 10  $\mu$ m.

the nine-segmented female antennule, the three-segmented antennary exopod, the unisetose epipodite of the maxillule, the setation of the maxilliped, the prehensile P1 (both rami) and the presence of three setae on the male baseoendopod of P5 suggest that the hamoniid affinities may lie with some of the 'thalestridimorph' genera. Thalestridae encompasses, according to Lang (1948),

four subfamilies: Thalestrinae, Dactylopusiinae, Rhynchothalestrinae and Pseudotachidiinae. Recently, the Donsiellinae, a former subfamily of the Laophontidae, has also been transferred to the Thalestridae because of well-defined similarities to the Pseudotachidiinae (Hicks, 1988; Huys, 1988b).

Thalestridae constitutes nothing more than a heterogenous assemblage of genera with uncertain relationships to each other, a taxonomic disease expressed in many of the other Langian 'mid-Order' families. This state of affairs led Hicks (1988) to refrain from elevating the Donsiellinae to family status. A complete phylogenetic analysis of the thalestrid genera falls outside the scope of the present account but will be the subject of a forthcoming paper. For the purpose of the present paper attention will be focused only on the Rhynchothalestrinae.

This subfamily, established by Lang (1948), contains the genera *Rhynchothalestris* Sars, 1905 and *Peltthestrus* Monard, 1924, the latter probably having no right of existence (Lang, 1948: 525). Analysis of the former genus revealed that it can easily be subdivided into two species groups which have no clear relationship to each other (Table 2). The first group encompasses the species *R. helgolandica*, *R. helgolandica campbelliensis* Lang, 1934, *R. tenuicornis* (Brady, 1910) and *R. tenuis* Chislenko, 1971. The second group shows an undeniable relationship to the Hamondiidae and comprises *R. rufocincta*, *R. vanhoeffeni* Brady, 1910 and *R. cornuta*, Geddes, 1969. These species share an essential suite of characters with *Hamondia*, not least the homologous sexual dimorphism in the P3 endopod, the absence of a seta on the first antennular segment, the fine structure of the female genital complex, the maxillary praecoxal endite with modified spine, the bifid spinules on the antennal exopod, and the 14-segmented male antennule. Except for the latter character, all others can be considered as unique synapomorphies found neither in any of the

TABLE 2. Salient characters of the two species groups in the genus *Rhynchothalestris sensu* Lang, 1948

<i>R. helgolandica</i> group	<i>R. rufocincta</i> group
Genital double-somite without internal transverse rib	With ventral and lateral internal transverse ribs
Epicopulatory bulb and plate absent	Present
Segment I of antennula with seta	Without seta
Male A1 11-segmented	Male A1 14-segmented
Basis of A2 without abexopodal seta	With seta
Exp of A2 without bifid spinules	With bifid spinules on exp3
Praecoxal endites of Mx1 without modified spine	Distal lobe with modified spine
P1 exp3 with innermost and outermost setae reduced	Innermost and outermost setae well developed
P1 enp 2-segmented; enp2 with 4 elements	3-segmented; enp2 with 1, enp3 with 4 elements
No sexual dimorphism on P3	Present on P3 enp
Female P5 with intercoxal sclerite; exp exceeding twice the size of benp	Intercoxal sclerite absent; exp and benp of about same size
Male P5 benp with 2 setae	Male P5 benp with 3 setae
Male P6 symmetrical; with 2 setae and 1 extremely developed inner spine each	Male P6 asymmetrical; with 3 tiny setae each

remaining *Rhynchothalestris*-species nor in any other thalestridimorph genera. In order to support this interpretation of the above findings, a description of a representative of each group is given below.

### Subfamily Rhynchothalestrinae

In reviewing the thalestrid genera, Lang (1936) placed the genus *Rhynchothalestris* in the Thalestrinae, admitting, however, that it differed from the other members of the subfamily in the nature of the sexual dimorphism. *Peltthestris tripartita* Monard, 1924 could not confidently be placed by Lang (1936) in any of the four subfamilies created by him (at that time the Parastenheliidae were still recognized as a thalestrid subfamily), but at last the genus was relegated with reservations to the Dactylopusiinae. In his monograph, Lang (1948) established the subfamily Rhynchothalestrinae to accommodate both genera but his rather equivocal diagnosis (e.g. male P3 endopod sometimes modified, baseoendopod of male either with two or three setae) already presented some indications that the taxon might not be natural.

#### *Diagnosis* (amended)

Body with prosome distinctly wider than urosome; urosome slightly flattened; prosome with dense sensillary pattern. Rostrum strongly developed, triangular, defined at base, with four pairs of sensillae. P1-bearing somite fused with cephalosome. Free prosomites with well-developed epimeral plates. Urosomites well developed; postgenital ones without posterolateral corners produced into spiniform processes. Female genital double-somite large. Pseudoperculum obsolete, anal operculum well developed. Caudal rami broader than long, with seven setae.

Antennula slender, with both plumose and smooth setae; with well-developed seta on first segment; seven or nine-segmented in female, with aesthetascs on segments IV and IX; at most 11-segmented and modified in male, with geniculation between segments VIII and IX, and aesthetascs on segments IV, VI and XI. Antenna slender, with fully separated basis lacking abexopodal seta; endopod two-segmented, first segment with inner seta, distal segment with long geniculate setae; exopod three-segmented, segments with two, one and four setae, respectively, exp3 without bifid spinules. Mandibular gnathobase strong, with one seta on cutting edge; basis tapering proximally, with three setae; endopod one-segmented, exopod three-segmented. Maxillula with well-developed praecoxal arthrite; coxa with cylindrical endite and epipodite represented by one seta; basis with two endites and bearing one-segmented exo- and endopod. Maxillary syncoxa with three endites; proximal endite bilobed, representing fused praecoxal endites and lacking modified spines, proximal lobe with three, distal lobe with two setae; basis produced into pinnate claw; endopod two-segmented. Maxillipede robust, prehensile; praecoxa fused into syncoxa bearing four setae; basis with two setae; endopod one-segmented and produced into strong claw bearing six setae.

Swimming legs with well-developed praecoxae, three-segmented rami (except endopod P1) and squarish intercoxal sclerites. P1 with both rami adapted for

grasping; exopod with middle segment extremely long, distal segment with three claws and two tiny setae; endopod with very long proximal segment bearing seta midway along inner margin, distal segment with one strong claw, one spine and two minute setae. Proximal segments of rami of P2–P4 with inner seta; outer exopodal spines well developed and bipinnate on segment one or smooth on segments two and three (except distal one). P5 with separate exopod and baseoendopod in both sexes, outer basal seta standing on long, non-articulating, cylindrical setophore, exopods exceeding by far size of endopodal lobes; female baseoendopods bearing five setae and joined by distinct intercoxal sclerite; male baseoendopods fused medially and bearing two setae each. Female genital complex with separate median copulatory pore; epicopulatory bulb and medially incised epicopulatory plate absent; genital apertures covered by P6 bearing three setae. Male P6 symmetrical, medially fused and bearing three setae each, innermost very large and spiniform.

Sexual dimorphism in antennula, P2 endopod, fifth and sixth legs, and in genital segmentation; one spermatophore; one egg-sac.

Marine; predominantly phytal.

*Type genus*

*Rhynchothalestris* Sars, 1905.

*Other genera*

*Pelithestris* Monard, 1924.

*Rhynchothalestris* Sars, 1905

The genus *Rhynchothalestris* was proposed by Sars (1905) to comprise *Thalestris helgolandica* and *Thalestris rufocincta*, but he did not designate the type species. This was also ignored by all subsequent authors until very recently Apostolov & Marinov (1988) quoted *R. helgolandica* as the type of the genus. In the present paper *R. rufocincta* will be removed to a new genus and family (see paragraph IV).

*Diagnosis*

Rhynchothalestrinae. Antennule nine-segmented in female; first segment short, 1.5 times as long as wide. Female genital double-somite with original segmentation marked only by minute suture on either side; no internal chitinous rib visible; about 1.5 times as wide as following urosomite; posterolateral angles only slightly produced.

*Type species*

*Rhynchothalestris helgolandica* (Claus, 1863).

*Other species*

*Rhynchothalestris campbelliensis* Lang, 1934 grad. nov.; *R. tenuis* Chislenko, 1971.

*Species inquirenda*

*Rhynchothalestris tenuicornis* (Brady, 1910).

*Rhynchothalestris helgolandica* (Claus, 1863)*Material examined*

One female and one male; British Museum (Natural History), London: Reg. No. 1911.11.8, 46140–41.

*Description*

Female (Figs 17, 18, 19A, B, 20, 21A, 22A, C, 23B, C). Body length 900  $\mu\text{m}$  (including rostrum and caudal rami). Body stout (Fig. 17A), with clear demarcation between prosome and urosome; urosome compressed dorsoventrally (Fig. 18A, B) much narrower than prosome (Fig. 17A). Maximum body width (390  $\mu\text{m}$ ) measured at posterior margin of cephalothorax. Sensillary pattern well developed. Posterior border of cephalic shield and free prosomites smooth. Rostrum (Fig. 17A, B) strongly developed, triangular, anteriorly directed, defined at base, furnished with four pairs of tiny sensillae and median pore. Cephalothorax distinctly shorter than maximum width; first pedigerous somite (P1) fused with cephalosome. Free prosomites with well-developed pleurotergites; ventrolateral corners slightly protruding posteriorly. P5-bearing somite short. Genital double-somite (Fig. 18A, B) large, posterolateral angles only slightly protruding posteriorly; completely fused; plane of fusion marked ventrally on both sides by minute suture about midway along outer margin (arrowed in Fig. 18E); internal transverse ridges completely absent; two dorsal areas of subintegumental sclerotization visible on both sides of midline (Fig. 17A) but these structures represent only dorsoventrally directed, chitinized bars and do not run around circumference of genital double-somite (see also Chislenko, 1971: 173, fig. 14–2); lateral margin densely spinulose. All urosomites with finely striated hyaline frill (Fig. 18A, B), forming dorsal obsolete pseudopericulum in penultimate somite (Fig. 23B). Anal somite with smooth semi-circular operculum; armed with numerous spinular combs ventrally and laterally, and with long sensilla on either side of anal slit; rear margin spinulose (Fig. 18A, D, 23B). Caudal rami broader than long, almost parallel; furnished each with three secretory pores and seven setae (Figs 18C, D, 23B); largest pore very large, conical, projecting from midventral margin (Fig. 18C); anterolateral accessory seta well developed, spiniform and bipinnate; dorsal seta tri-articulated at base.

Antennula (Fig. 17B). Slender, nine-segmented; segment I as long as segment II, densely spinulose along inner margin and bearing well-developed seta at inner distal corner; segment II with three plumose and nine smooth setae along inner margin, secretory pore missing; segment III with three plumose and five smooth setae in distal half; segment IV with long, slender aesthetasc and five setae; segments V and VI with three and four setae, respectively; segments VII and VIII with one outer and one inner seta each; segment IX with seven setae and slender aesthetasc.

Antenna (Fig. 20A). Slender, coxa well developed, unarmed. Basis with spinules at inner distal corner; abexopodal seta absent. Exopod three-segmented; segment I longest, dilating distally and having two inner bipinnate setae; segment II shortest, with one bipinnate seta; segment III with one marginal and three apical bipinnate setae and furnished with row of (non-bifid) spinules. Endopod two-segmented; segment I with inner seta and spinular comb;

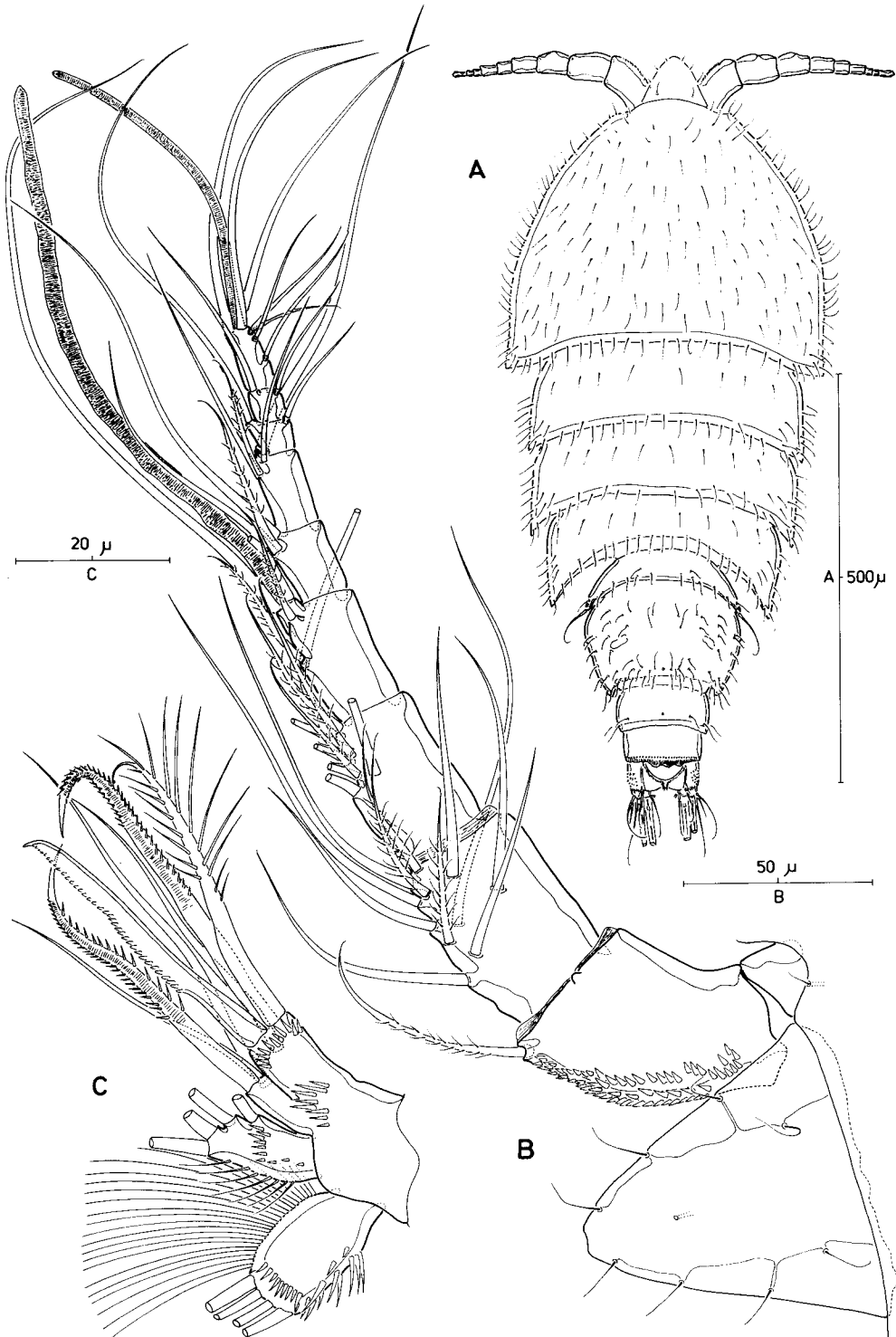


Figure 17. *Rhynchothalestris helgolandica*. Female. A, Habitus, dorsal view. B, Rostrum and antennula. C, Basis and rami of maxillula.



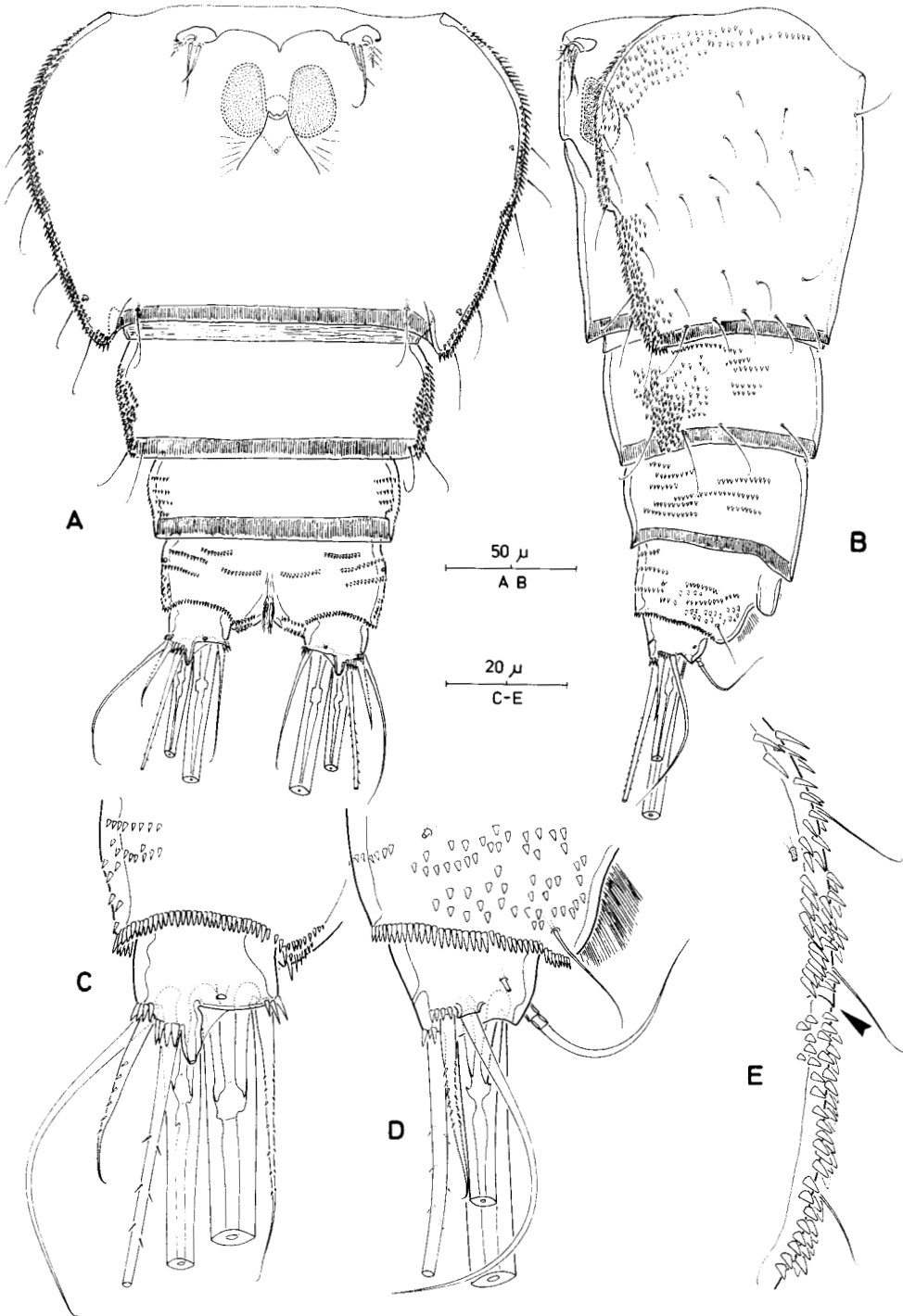


Figure 18. *Rhynchothalestris helgolandica*. Female. A, Urosoma (excluding P5-bearing somite), ventral view. B, Same, lateral view. C, Caudal ramus, ventral view. D, Caudal ramus, lateral view. E, Outer margin of genital double-somite, ventral view (arrow showing only trace of original segmentation).

abexopodal margin of segment II armed with many spinules, two unipinnate spines and two bipinnate setae; distal margin having four geniculate setae, two unipinnate setae (outermost basally fused with outer geniculate seta) and one bipinnate seta medially; two combs of spinules visible along adexopodal margin.

Mandible (not figured but same as Fig. 28A). Coxa with strong gnathobasis having several blunt teeth and bipinnate spine at cutting edge. Palp well developed, biramous. Basis ornamented with numerous spinular rows in proximal half and with three pinnate setae along inner margin. Endopod unisegmented, armed with two marginal and six apical setae. Exopod three-segmented; proximal segment longest, having one seta at about middle inner edge and subdistally; segments two and three minute, with one and three setae, respectively.

Maxillula (Fig. 17C). Praecoxal arthrite squarish; anterior surface with two juxtaposed setae; inner margin of arthrite with nine strong, ornamented spines and one minute seta. Coxa with spinules along outer margin; epipodite represented by one pinnate seta; endite subcylindrical and having six setae. Basis with two endites; proximal endite small, with one geniculate and two simple setae; distal endite with serrate claw and three setae (one bare, one bipinnate, one geniculate). Endopod unisegmented, bearing four plumose setae, outer margin plumose. Exopod unisegmented, with four apical plumose setae, inner margin plumose.

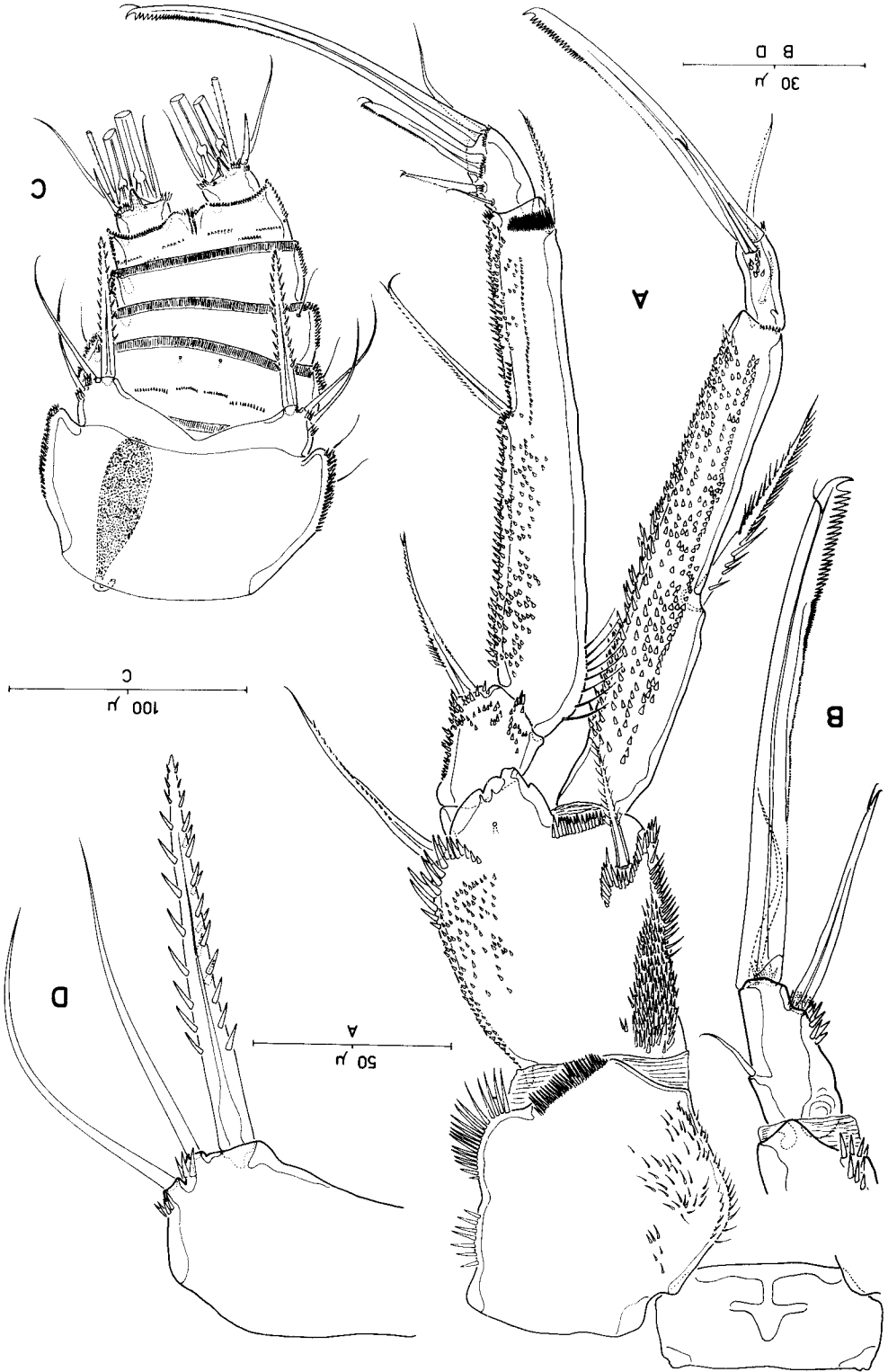
Maxilla (Fig. 20B). Praecoxa and coxa fused to form syncoxa bearing three endites and having long spinules along outer margin; proximal (praecoxal) endite bilobed (derived by fusion of ancestral two endites), proximal lobe with three setae, distal lobe with two setae, none being modified; middle and distal (coxa) endites with three spines each. Basis with two slender setae, two unipinnate curved spines and one serrate claw (fused with basal endite). Endopod two-segmented; proximal segment broader than long, with short spine and three setae (one claw-like); distal segment squarish, with four setae (one geniculate).

Maxillipedes (Fig. 20C). Robust, directed abaxially. Praecoxa and coxa completely fused into syncoxa with spinular ornamentation along both inner and outer margins and with four plumose setae at distal margin. Basis with straight, setulose inner margin, ornamented with minute seta at about midway and slender seta near basis-endopod articulation; convex outer margin with distinct spinular comb. Endopod unisegmented, produced into long, curved claw (reaching to coxa-basis joint and being finely serrated subdistally) bearing three large and three minute setae.

Swimming legs (Figs 19A, B, 21A, 23C). With three-segmented rami (except endopod P1) and well-developed intercoxal sclerites.

P1 (Fig. 19A, B). With rectangular intercoxal sclerite. Praecoxa not observed, presumably completely incorporated in somite wall. Coxa with two combs of spinules along outer margin, minute spinules along inner edge and distinct areas of arthrodistal membrane separated by a median spinular process distally. Basis longer than wide, densely spinulose along both inner and outer margins, and bearing outer unipinnate spine and inner bipinnate seta (standing on anterior surface). Exopod extremely prolonged; prehensile by means of pivot articulation between segments II and III; proximal segment without inner seta but with outer spine; middle segment very long, about six times as long as maximum

Figure 19. *Rhynchohalastria helgolandica*. Female. A, Pl. B, Distal endopodite segment of Pl. Male. C, Urosoma, ventral view. D, Armature of sixth leg.



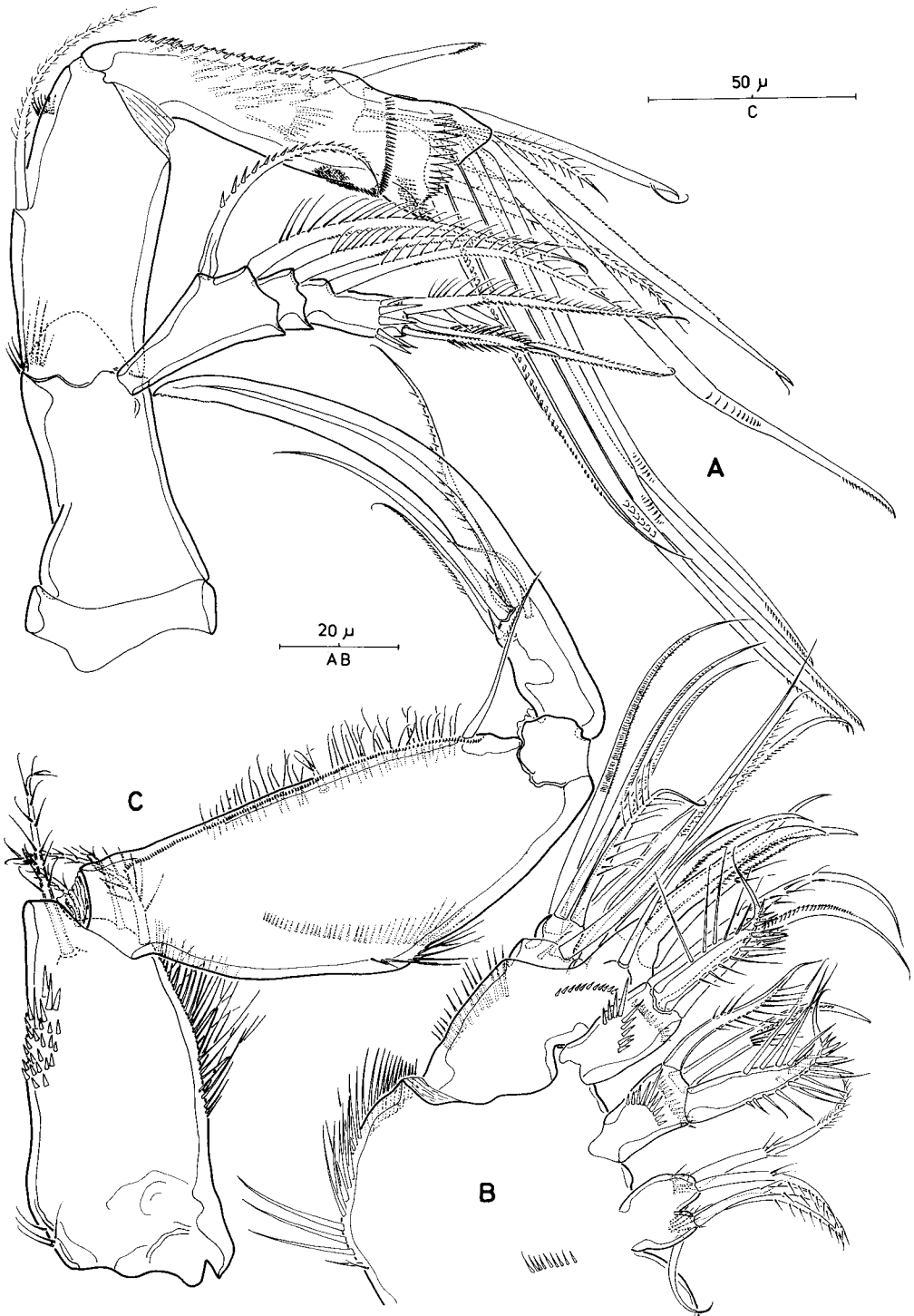


Figure 20. *Rhynchothalestris helgolandica*. Female. A, Antenna. B, Maxilla. C, Maxilliped.

width, with one unipinnate spine implanted slightly distal to middle outer margin, bipinnate seta set near distal inner corner; distal segment with one minute inner seta, one short outer seta and three finely serrated claws, increasing in length adaxially and bearing subapical flagellum. Endopod as long as first two exopodite-segments combined; proximal segment very long, bipinnate spine implanted at about middle inner margin; pivot joint between segments; distal segment with two tiny setae, one acutely curved spine and one long, finely serrated claw.

P2–P4 (Figs 21A, 23C). With well-developed intercoxal sclerites (without spinules along the concave ventral margin). Endopods on slightly shorter than exopods. Basis with plumose seta. Intersegmental hyaline frill of proximal and middle exopodite segments weakly developed, not incised (Fig. 23C). Exopodal spines being strong, markedly bipinnate (proximal segment and distal spine of distal segment) or furnished with flat pinnules (others) (Fig. 23C). Middle endopodite segment with very long process at outer distal corner; inner distal seta of third endopodite segment swollen. Seta and spine formulae are shown in Table 3.

Fifth pair of legs (Fig. 22A). Large, not fused medially; joined by well-developed intercoxal sclerite. Baseoendopod with endopodal lobe tapering distally and not exceeding proximal fourth of exopod; inner margin stepped, ornamented with long spinules, one secretory pore and two pinnate setae; outer margin with short spinules and one bare seta; distal end having two bipinnate setae and one secretory pore; basal seta plumose, standing on long, plumose, non-articulating, cylindrical setophore. Exopod very large, oval, length twice maximum width; partly covered by endopodal lobe; attachment site very small; outer and inner margins densely spinulose and with two secretory pores at anterior surface; furnished with six setae in total.

Genital complex (Figs 18A, 22C). Located in anterior half of genital double-somite. P6 represented by minute plate bearing three short setae, outer plumose; genital apertures probably connected. Seminal receptacles with distinct sclerotized walls, paired. Copulatory pore circular, minute, located in pronounced depression medially but not covered by median epicopulatory bulb. The lateral margins of depression meet each other anteriorly diminutive, medially incised flap discernible; this structure might be homologous with the epicopulatory plate of Hamondiidae and Ambunguipedidae. No external connection between copulatory pore and genital apertures.

Male (Figs 19C, D, 21B, C, 22B, 23A). Body length 720  $\mu\text{m}$  (including rostrum and caudal rami). Habitus as in female, except for separation of genital and first abdominal somites; first abdominal somite also has four ventro-median spinular combs. Sexual dimorphism in antennula and P2, P5 and P6.

TABLE 3. Seta and spine formula of  
*Rhynchothalestris helgolandica*

	Exopod	Endopod
P2	1.1.223	1.2.221
P3	1.1.323	1.2.321
P4	1.1.323	1.2.221

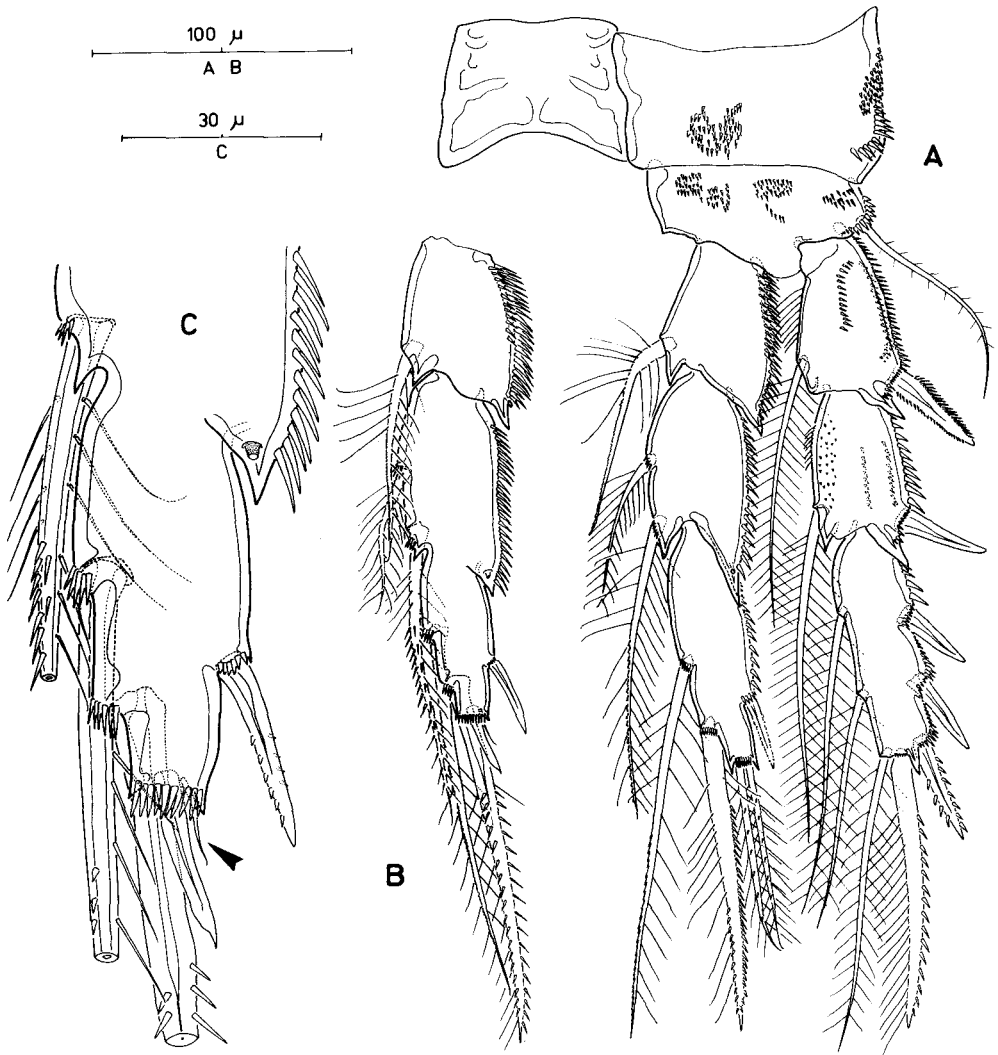
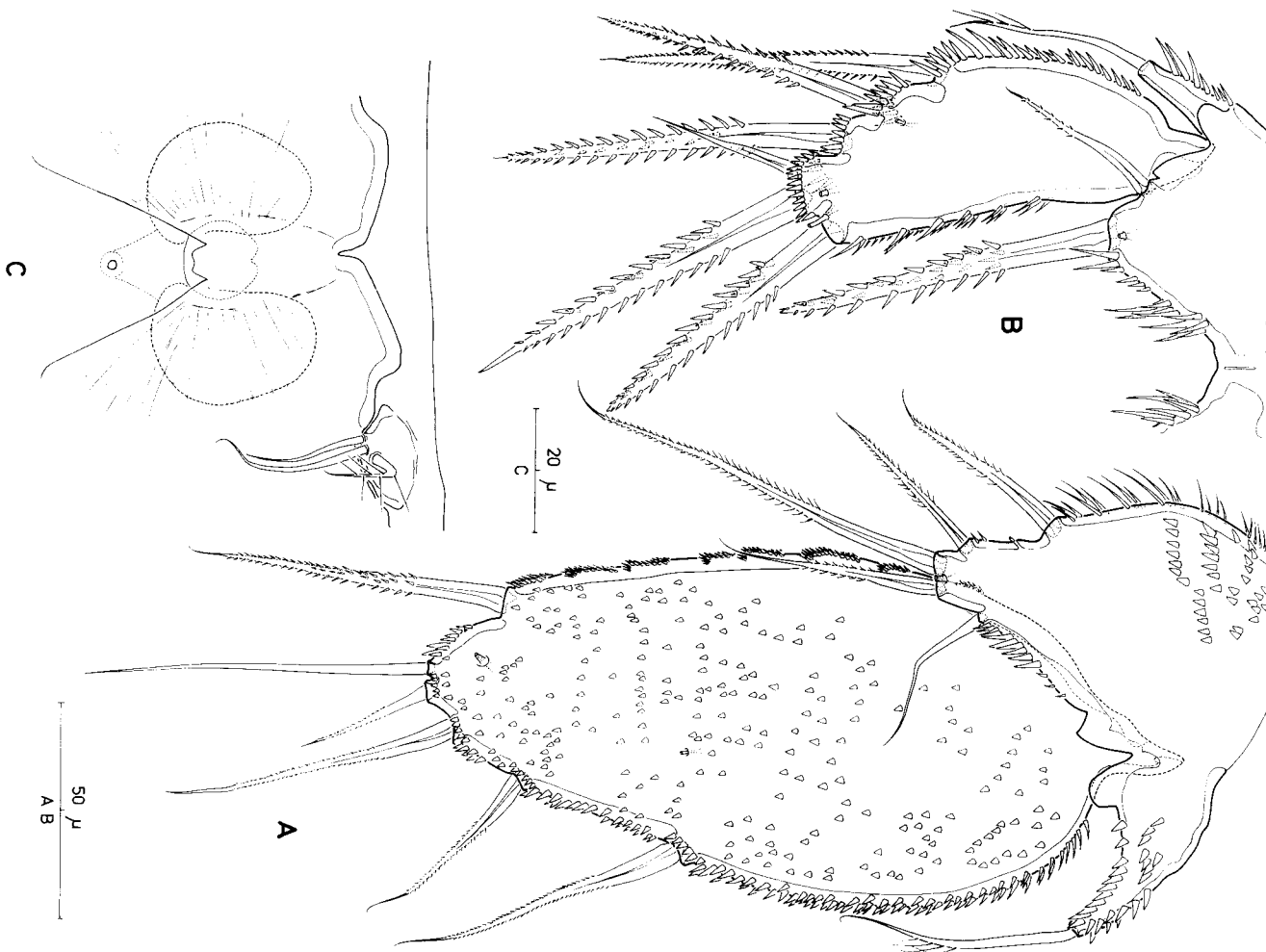


Figure 21. *Rhynchothalestris helgolandica*. Female. A, P2. Male. B, Endopod of P2. C, Distal part of endopod of P2.

Antennula (Fig. 23A). Slender, 11-segmented, modified; geniculation located between segments VIII and IX. Segment I longest, with numerous spinules and plumose along inner margin; segment II short, with plumose seta but without secretory pore; segment III with six plumose and six smooth setae; segment IV articulating with preceding segment by means of large area of folded membrane (and not by ordinary telescoping joint), furnishes with long aesthetasc and six setae; segment V very short, with two setae on inner process; segment VI swollen, armed with six slender setae and two pinnate spines along inner margin, and long aesthetasc standing on short, subcylindrical process and accompanied by long seta; segment VII very small, with one short bipinnate spine and one slender seta; segment VIII with one modified, bifid spine, one slender seta and one short pinnate spine, distal end geniculating with following segment; segment

Figure 99. *Rhynchobolbitis belandiana* Female. A. P5 and intercoxal sclerite. C. Genital complex.



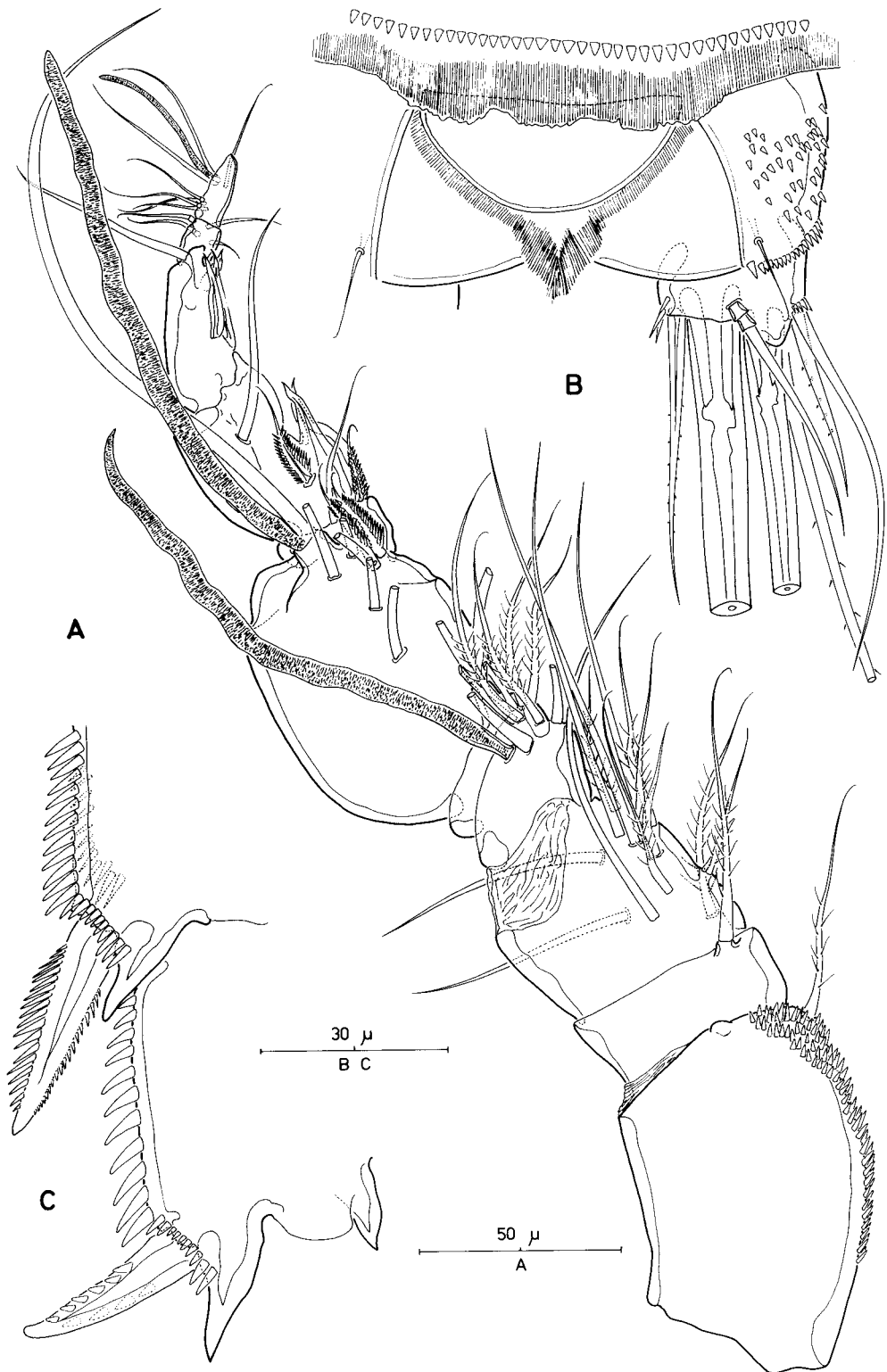


Figure 23. *Rhynchothalestris helgolandica*. Male. A, Antennula. Female. B, Anal somite and right caudal ramus, dorsal view. C, Outer rim of proximal and middle exopodite segment of P2.



IX with three modified, non-articulating spines and one slender seta; segment X minute, with two inner and two outer setae; segment XI thin-walled along outer margin, bearing one short aesthetasc and seven setae in total.

P2 (Fig. 21B, C). Protopod, exopod and proximal endopodite-segment exactly as in female. Middle and distal segments fused with complete retention of female number of setae; setae derived from middle segment not modified. Distal part narrow and much shorter compares to equivalent third segment of females; without distinct processes; outer margin without spinules, outer spine less spinulose than in female; apical setae strongly reduced: outer setule-like, inner short, spiniform and acutely tapering at tip; inner distal setae derived from female middle and distal segments distinctly tripinnate.

P5 (Fig. 22B). With separate rami. Baseoendopods forming common median plate, moderately incised medially; basal seta implanted on long, cylindrical, non-articulating process bearing long spinules along outer margin; endopodal lobe weakly developed, bearing one secretory pore and two armature elements: outer being shortest, setiform, and bipinnate, inner very long (exceeding exopod), spiniform, and multipinnate. Exopod one-segmented, subrectangular, and slightly bent inwards; attachment site small; furnished with one seta, five spines and three secretory pores; outer margin markedly stepped.

P6-bearing (genital) somite (Fig. 19C). With distal angles rounded and spinulose. Sixth pair of legs (Fig. 19C, D) symmetrical; fused medially; each having two outer, bare setae and inner, extremely developed (extending to hind margin of penultimate somite), tripinnate spine.

#### Remarks

This redescription agrees with Chislenko's (1967) drawings of material from the Karelian coast, White Sea. *Rhynchothalestris helgolandica* displays a typical boreo-atlantic distribution with its centre laying in north-western Europe, the only American record thus far being that of Willey (1923) from James Bay, Canada. A closely related antiboreal variety was described by Lang (1934) from Campbell Island, New Zealand. Later, Lang (1948) advanced the idea that *R. helgolandica campbelliensis* might deserve full specific rank but abstained from formally proposing it because of the lack of information on the female P5 exopod. The next reference to this subspecies is that of Pallares (1968) who reports it from Puerto Deseado, Argentina. The concise but well-illustrated redescription corroborates Lang's view. Clear differences, primarily related to the P5 (implantation of exopodal setae; shape of endopodal lobe), are discernible in both sexes and support elevation of Lang's variety to species level.

*Rhynchothalestris tenuis* described from Possjet Bay, Sea of Japan, differs from its relatives in the relatively short endopod of P1, the presence of only one seta on the middle endopod segment of P4 and in the narrower exopod of P5.

Brady's (1910) poorly rendered illustrations of *Amenophia tenuicornis* make reliable identification virtually impossible. Therefore *R. tenuicornis* cannot be treated as anything more than a *species inquirenda*.

#### *Peltthestrus* Monard, 1924

##### Diagnosis

Rhynchothalestrinae. Antennule seven-segmented in female; first segment extremely long, occupying one-third of total antennule length. Female genital

double-somite with original segmentation marked laterally and dorsally by transverse suture and/or internal chitinous rim; about two times as wide as following urosomite; posterolateral angles only distinctly produced posteriorly.

*Type and only species*

*Peltthestrus tripartita* Monard, 1924.

*Remarks*

The validity of *Peltthestrus* was questioned by Lang (1948) who pointed out the striking similarity of its type species with *R. helgolandica*. In view of this, Lang (1948) thought that *P. tripartita* might prove to be a juvenile or a damaged specimen of *R. helgolandica*. Although I admit that *P. tripartita* is urgently in need of re-examination, I cannot entirely concur with Lang's view. Judging from the well-developed genital complex and the urosomal segmentation it is clear that Monard (1924) dealt with an adult female. Some of his statements are either doubtful, if not wrong (antenna with allobasis; P1 exp3 with two claws only; P5 exopod with five setae) or disagree with the drawings (antennary exopod three-segmented). However, the seven-segmented antennule (fusion of segments VI–VIII) with extremely prolonged segment I, and the laterally expanded genital double-somite with complete suture (or internal chitinous rib) dorsally and laterally preclude *Peltthestrus* from being a synonym of *Rhynchothalestris*.

*Discussion*

A character of central importance in the phylogeny of the Thalestridae, but ignored if not overlooked, by Lang (1948) is the sexual dimorphism of the inner basal spine of P1. This novel character is shown by the Thalestrinae and Dactylopusiinae, but not by the Rhynchothalestrinae (the Pseudotachidiinae and Donsiellinae are purposely omitted from the discussion). Otherwise, the Rhynchothalestrinae deviate from the other subfamilies in the presence of only two spines on the baseoendopod of the male leg 5 and in the atypical rostrum with four pairs of sensillae. *Rhynchothalestris* is also unique in having six setal elements on the endopodal claw of the maxilliped; this maximum number is not found in any other thalestrid genera, nor in any other 'oligoarthran' copepods except the Cerviniidae. Finally, the Rhynchothalestrinae differ from the Thalestrinae-Dactylopusiinae grouping in the nature of the sexual dimorphism on leg 2. Representatives of both lineages have five setae or spines on the distal endopod segment of the female P2: two inner setae (nos one and two), two apical setae (nos three and four) and one outer spine (no. 5). In general, the males are characterized by a two-segmented endopod P2 through fusion of segments II and III but the setal modifications are not homologous in the respective lineages. In the Rhynchothalestrinae, modifications occur only in the apical setae, i.e. the outer (no. IV) is extremely reduced and becomes setuliform, the inner (no. III) is also shortened but becomes spiniform; the female shape of the distal segment is more or less retained. The various genera of the Thalestrinae and Dactylopusiinae present a transition series of male modifications in the P2. The most primitive type (Sars, 1905; Lang, 1965; Masunari, 1988) is shared by the thalestrinids *Thalestris*, *Amenophia* Boeck, 1864, *Parathalestris* and *Phyllothalestris* Sars, 1905. In these genera the outer apical seta (no. IV) is strongly developed,

spiniform, and is displaced proximally near the implantation of the outer spine (no. V) which is in its turn strongly developed. The inner apical seta is fairly reduced compared to the female condition. The distal part of the endopod derived from the third segment of the female is distorted, very narrow and ending in an acute point. In a later stage of thalestrid evolution (i.e. within the Dactylopusiinae), the number of armature elements is reduced by fusion of spines IV and V (e.g. *Diarthrodes*, *Dactylopusia* Norman, *Dactylopodopsis* Sars, 1911; see Lang, 1965; Coull, 1973) and subsequent loss of other setae (e.g. *Paradactylopodia* Lang, 1948; see Lang, 1965; Chislenko, 1967).

All these characters suggest that the Rhynchothalestrinae might have diverged early in the evolution of the Thalestridae and that the Thalestrinae and Dactylopusiinae are more closely related to each other than to any other subfamily of the Thalestridae.

### Family **Ambunguipedidae nov.**

This family is established to accommodate all former *Rhynchothalestris* species other than those placed in the presently amended Rhynchothalestrinae.

#### *Diagnosis*

Body almost fusiform; urosome slightly flattened; prosome with dense sensillar pattern. Rostrum strongly developed, triangular, defined at base, with two sensillae. P1-bearing somite fused with cephalosome. Free prosomites with well-developed epimeral plates. Female genital double-somite large; original segmentation marked by internal dorsolateral chitinous stripe on either side. Pseudoperculum and anal operculum well developed. Caudal rami broader than long, with seven setae.

Antennula slender, with both plumose and smooth setae; first segment longer than second, without setae; nine-segmented in female, with aesthetascs on segments IV and XI; 14-segmented and modified in male, with geniculation between segments IX and X, aesthetascs on segments IV, VI and XIV, and cluster of seta-like elements on segment VI. Antenna slender, with fully separated basis bearing abexopodal seta; endopod two-segmented, first segment with inner seta, distal segment with long geniculate setae; exopod three-segmented, segments with two, one and four setae, respectively, exp3 with bifid spinules. Mandibular gnathobase strong, with one seta on cutting edge; basis tapering proximally, with three setae; endopod one-segmented, exopod three-segmented. Maxillula with well-developed praecoxal arthrite; coxa with cylindrical endite and epipodite represented by one seta; basis with one endite and bearing one-segmented exo- and endopod. Maxillar syncoxa with three endites, proximal bilobed (representing fused praecoxal endites) and bearing strikingly developed pinnate spine, both lobes with two elements each; basis produced into pinnate claw; endopod two-segmented. Maxillipede robust, prehensile; praecoxa well defined; coxa with four setae; basis with two setae; endopod one-segmented and produced into long strong claw bearing five setae.

Swimming legs with well-developed praecoxae, three-segmented rami and squarish intercoxal plates. P1 with both rami adapted for grasping; exopod with middle segment extremely long, distal segment with four claws and one well developed inner setae; endopod with very long proximal segment bearing inner

seta at two-thirds distance of proximal margin, middle segment with one inner seta, distal segment with two strong claws and two minute setae. Proximal segments of rami of P2–P4 with inner seta; outer exopodal spines well developed and bipinnate. P5 with separate exopod and baseoendopod in both sexes; intercoxal sclerite absent; outer basal seta not standing on long cylindrical process; exopods and endopodal lobes of about equal size; female baseoendopod with five setae; male baseoendopods fused medially and bearing three setae each. Female genital complex with separate median copulatory pore; epicopulatory bulb and medially incised epicopulatory plate present; genital apertures covered by P6 bearing three setae. Male P6 asymmetrical, each plate having three setae.

Sexual dimorphism in antennula, P2 endopod, P3 endopod, fifth and sixth legs, and in genital segmentation; one spermatophore; one egg-sac.

Marine; predominantly phytal.

*Type genus*

*Ambunguipes* gen. nov.

*Other genera*

*Lucayostratiotes* gen. nov.

***Ambunguipes* gen. nov.**

*Synonymy*

*Rhynchothalestris* (part).

*Diagnosis*

Ambunguipedidae. Urosome slightly flattened dorsoventrally. Cephalothorax accounting for about 40% total body length; without dorso-median process, P2-bearing somite fully exposed. Urosomites well developed. Epimeral plates of thoracic somites and of cephalothorax slightly produced posteriorly. Thoracic somites without paired, dorsal, backwardly directed processes. Lateral processes of genital double-somite and sometimes also of second abdominal somite well developed. Tuft on segment VI of male antennule moderately developed; consisting of about 10–15 setoid elements.

*Etymology*

The generic name is derived from the Latin *ambo*, meaning both, *unguis*, meaning claw and *pes*, meaning leg, and refers to the prehensile ability of both rami in leg 1. Gender: feminine.

*Type species*

*Ambunguipes rufocincta* (Brady, 1880) **comb. nov.**

*Other species*

*Ambunguipes similis* (A. Scott, 1909) **comb. nov.**

*Species inquirendae*

*Abunguipes vanhoeffeni* (Brady, 1910) **comb. nov.**; *A. vanhoeffeni* (Brady, 1910) *sensu* Nicholls, 1944.

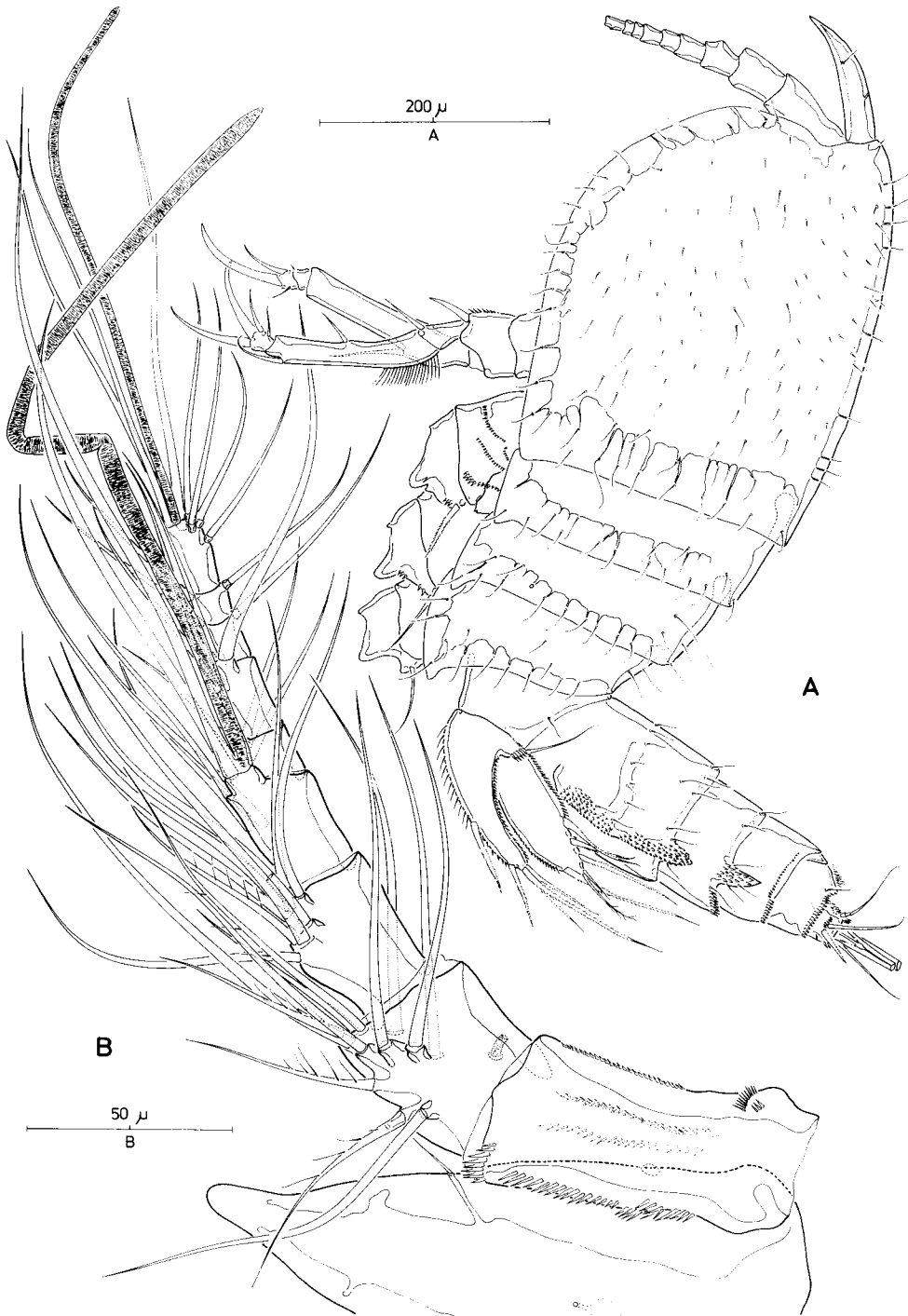


Figure 24. *Ambunguipes rufocincta* **comb. nov.** Female. A, Habitus, lateral view, B, Rostrum and antennula.

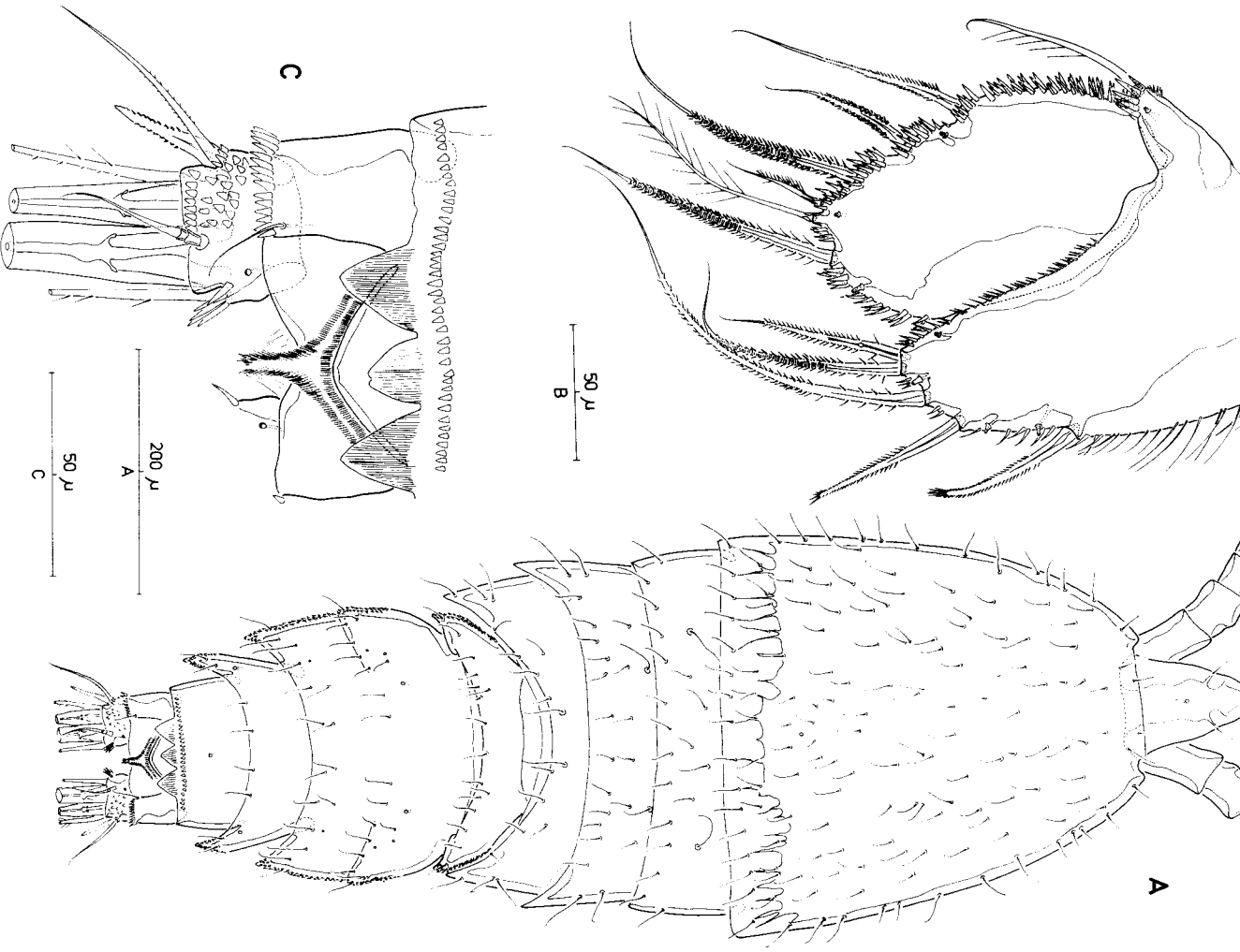
*Ambunguipes rufocincta* (Brady, 1880) **comb. nov.***Material examined*

(i) Nine females and six males from West Runton, Norfolk, in washings of algae (leg. Dr R. Hamond; 29 viii 1988); (ii) five females and three males from Bay of Calvi, Corsica, in washings of *Posidonia oceanica* (L.) Delile taken by SCUBA diving at 4 m depth (leg. C. Heip & L. Thielemans; v 1985); (iii) two females, one male from near the Punta Vico on the north coast of the isle of Ischia in the Gulf of Naples, Italy; from upper leaf region of *Posidonia oceanica* taken by SCUBA diving at 5 m depth (leg. R. Novak, Vienna; Spring 1981).

*Description*

Female (Figs 24–29, 30C, 31, 33B). Body length 940–1020  $\mu\text{m}$  (including rostrum and caudal rami). Body stout (Figs 24A, 25A), with clear demarcation between prosome and urosome; urosome compressed dorsoventrally (Figs 26A, B). Maximum body width (325  $\mu\text{m}$ ) measured at posterior margin of cephalothorax. Sensillar pattern well developed. Posterior border of cephalic shield and free prosomites smooth. Rostrum (Figs 24A, B, 25A) strongly developed, triangular, ventrally deflected, defined at base, furnished with two tiny sensillae and median pore. Cephalothorax distinctly longer than maximum width; first pedigerous somite (P1) fused with cephalosome. Free prosomites with well-developed pleurotergites; ventrolateral corners slightly protruding posteriorly. Urosomites with dorsal surface covered by minute denticles (Fig. 26A). P5-bearing somite short; laterodorsal portions of tergite furnished with minute spinules (Fig. 25A). Genital double-somite (Fig. 26A, B) large, posterolateral angles protruding posteriorly; completely fused and without any external sutures; plane of fusion marked ventrally by internal chitinous ridge on both sides of copulatory pore, and dorsally by analogous dorsolateral ridge on either side of midline; original separation marked laterally by patchy arrangement of spinules of constituent somites (Fig. 26A). First free abdominal somite with posterolateral angles strongly protruding posteriorly and being covered with minute spinules; ventral hind margin armed with spinules (Fig. 26A, B). Penultimate somite with tiny spinules laterally and dorsally along posterior margin and bearing tripartite finely striated pseudopericulum (Fig. 25C). Anal somite with smooth semi-circular operculum; armed with closely set spinules along rear margin and with long sensilla on either side of anal slit (Figs 25C, 26). Caudal rami broader than long, almost parallel; furnished each with four secretory pores and seven setae (Figs 25C, 26); largest pore very large, conical, projecting ventrally from outer distal corner and having cylindrical string of adhesive gelatinous substance (Fig. 26D); anterolateral accessory seta well developed, spiniform and bipinnate; dorsal seta triarticulated at base.

Antennula (Fig. 24B). Slender, nine-segmented; segment I longest, more than twice as long as wide, several longitudinal spinular rows on anterior and posterior surfaces and flexible integument (hyaline frill) distally; segment II with three plumose and nine smooth setae along inner margin and conspicuous secretory pore near outer margin; segment III with eight setae in distal half; segment IV with long, slender aesthetasc and six setae; segments V and VI with three and four setae, respectively; segments VII and VIII with one outer and



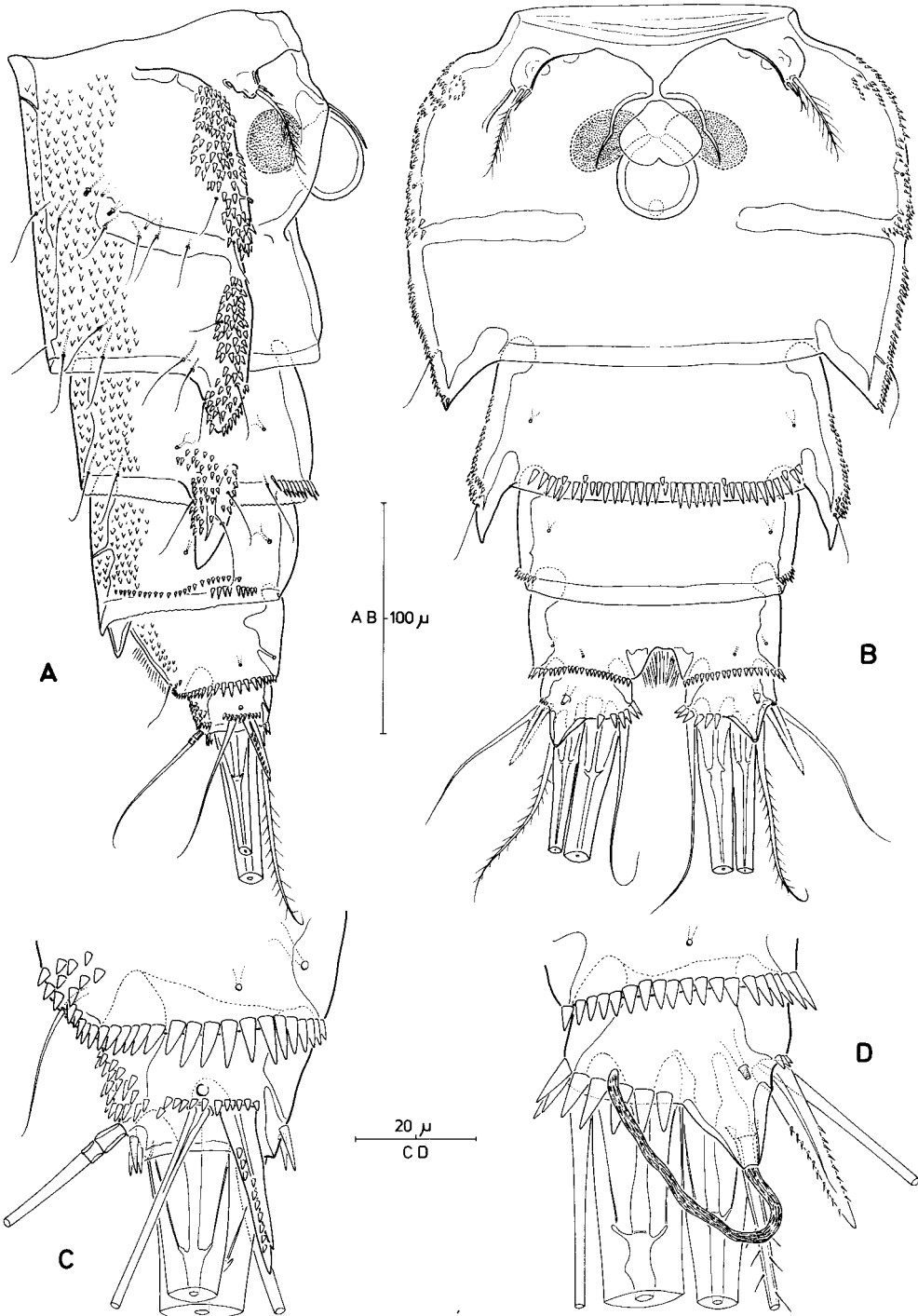


Figure 26. *Ambunguipes rufocincta* **comb. nov.** Female. A, Urosome (excluding P5-bearing somite), lateral view. B, Same, ventral view. C, Caudal ramus, lateral view. D, Caudal ramus, ventral view.



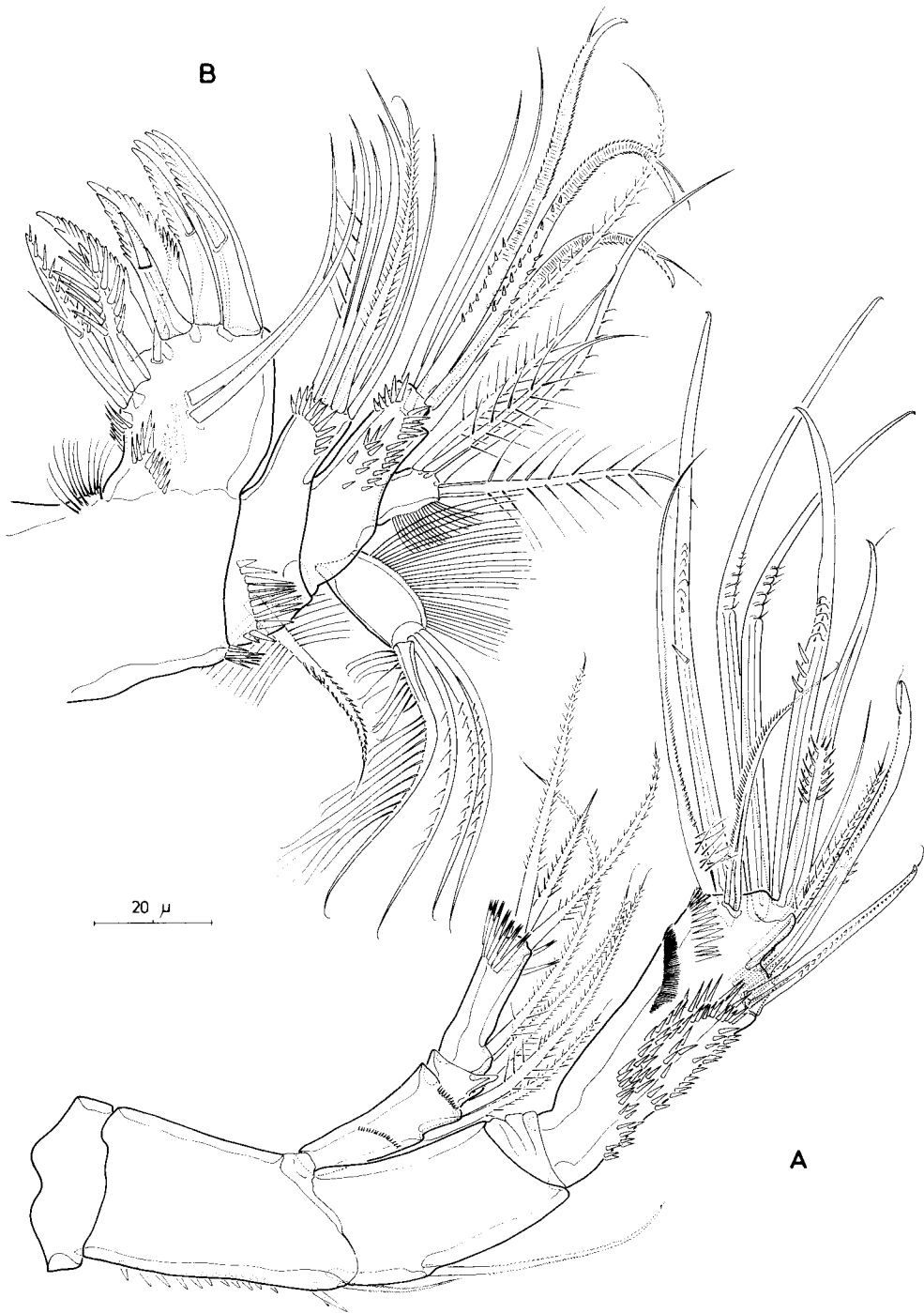


Figure 27. *Ambunguipes rufocincta* **comb. nov.** Female. A, Antenna. B, Maxillula.

one inner seta each; segment IX with five simple setae and two others fused at base with slender aesthetasc.

Antennae (Fig. 27A). Slender; coxa well developed, unarmed. Basis with spinules along inner margin and bearing tiny abexopodal seta. Exopod three-segmented; segment I with two inner bipinnate setae and two rows of diminutive denticles; segment II shortest, with one bipinnate seta and a small process at inner distal corner; segment III with one marginal and three apical bipinnate setae and furnished with row of bifid spinules. Endopod two-segmented; segment I with inner seta; abexopodal margin of segment II with many spinules, two unipinnate spines and two basally fused setae; distal margin with four geniculate setae, two unipinnate setae (outermost being basally fused with outer geniculate seta) and one medially bipinnate spine; two combs of spinules visible along adexopodal margin.

Mandible (Fig. 28A). Coxa with strong gnathobasis having several blunt teeth and bipinnate spine at cutting edge; some long spinules visible near implantation of palp. Palp well developed, biramous. Basis expanding distally, ornamented with numerous spinular rows in proximal half and with three pinnate setae along inner margin. Endopod unisegmented, armed with two marginal and six apical setae. Exopod three-segmented; proximal segment longest, having one seta at about middle inner edge and another subdistally; segments II and III minute, with one and three setae, respectively.

Maxillula (Fig. 27B). Praecoxal arthrite squarish; with some spinules near dorsal margin; anterior surface with two juxtaposed setae; inner margin of arthrite with nine strong, ornamented spines and one minute seta. Coxa with spinules along outer margin; epipodite represented by one pinnate seta; endite subcylindrical and having six setae. Basis with one endite (derived by fusion of the two ancestral endites) bearing six setae (three of which being geniculate). Endopod unisegmented, bearing four plumose setae, outer margin plumose. Exopod unisegmented, long and narrow, with four apical plumose setae, inner margin plumose.

Maxilla (Fig. 33B). Praecoxa and coxa fused and forming syncoxa bearing three endites and with several spinular rows along outer margin; proximal (praecoxal) endite bilobed (derived by fusion of two ancestral praecoxal endites), proximal lobe with two short spines, distal lobe with one short and one extremely developed spine (arrowed in Fig. 33B); middle and distal (coxa) endites with three spines. Basis with two slender setae, one pinnate spine and one serrate claw (fused with the basal endite). Endopod two-segmented, boundaries not well defined (Fig. 14C); proximal segment broader than long, with short spine and three setae (one geniculate); distal segment squarish, with four setae (one geniculate).

Maxillipedes (Fig. 28B). Robust, directed abaxially. Praecoxa well defined, with patch of long spinules. Coxa densely ornamented at both anterior and posterior surfaces and bearing four bipinnate spines near distal margin. Basis triangular; inner margin ornamented with both bipinnate seta and spinular row at either surface; outer margin with some very long spinules. Endopod unisegmented, produced into long claw (almost reaching to coxa-basis joint) bearing two pinnate setae at posterior surface and three tiny setae at anterior one.

Swimming legs (Figs 29, 30B, C, 31). With three-segmented rami and well-developed intercoxal sclerites.

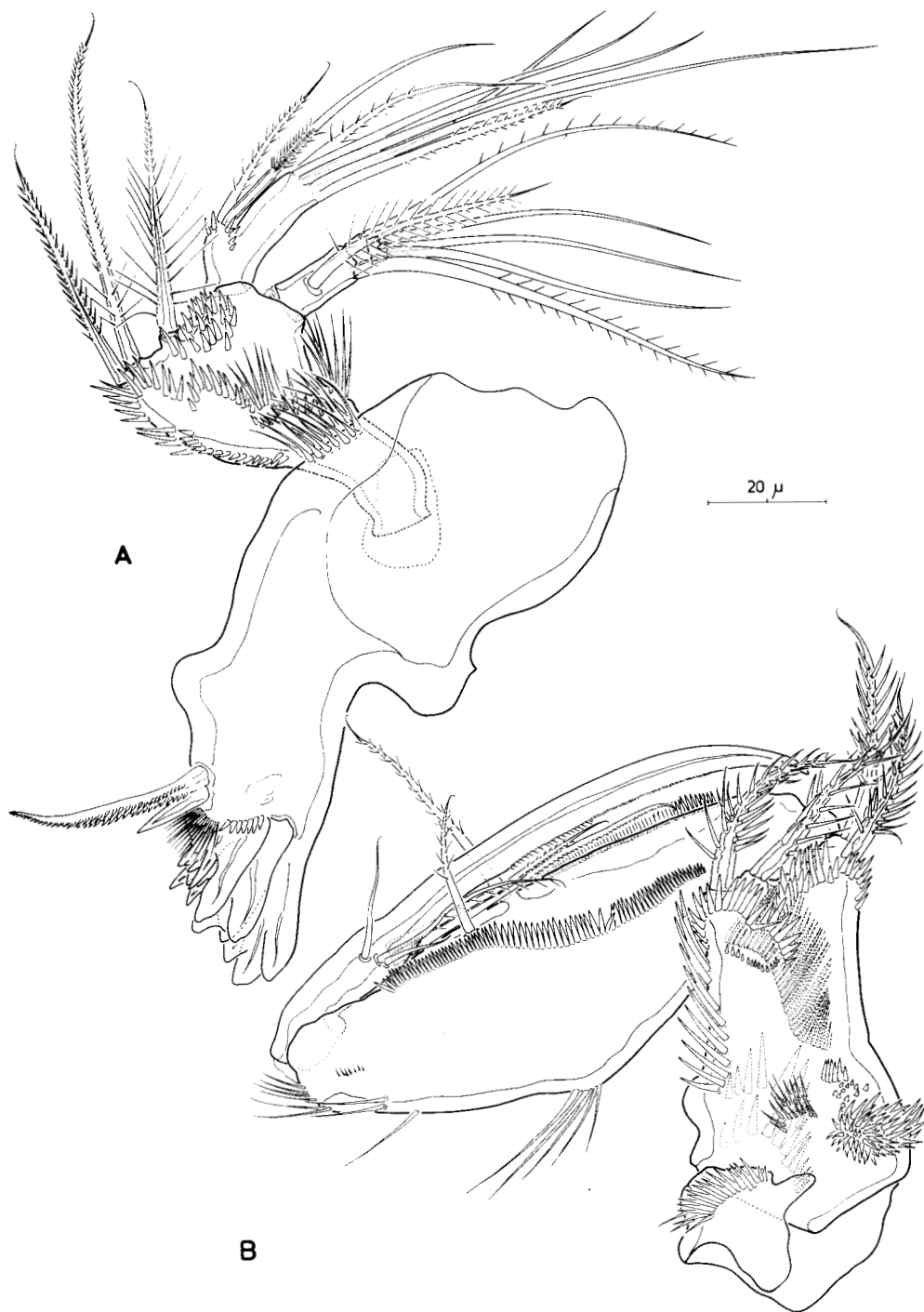


Figure 28. *Ambunguipes rufocincta* **comb. nov.** Female. A, Mandible. B, Maxilliped.

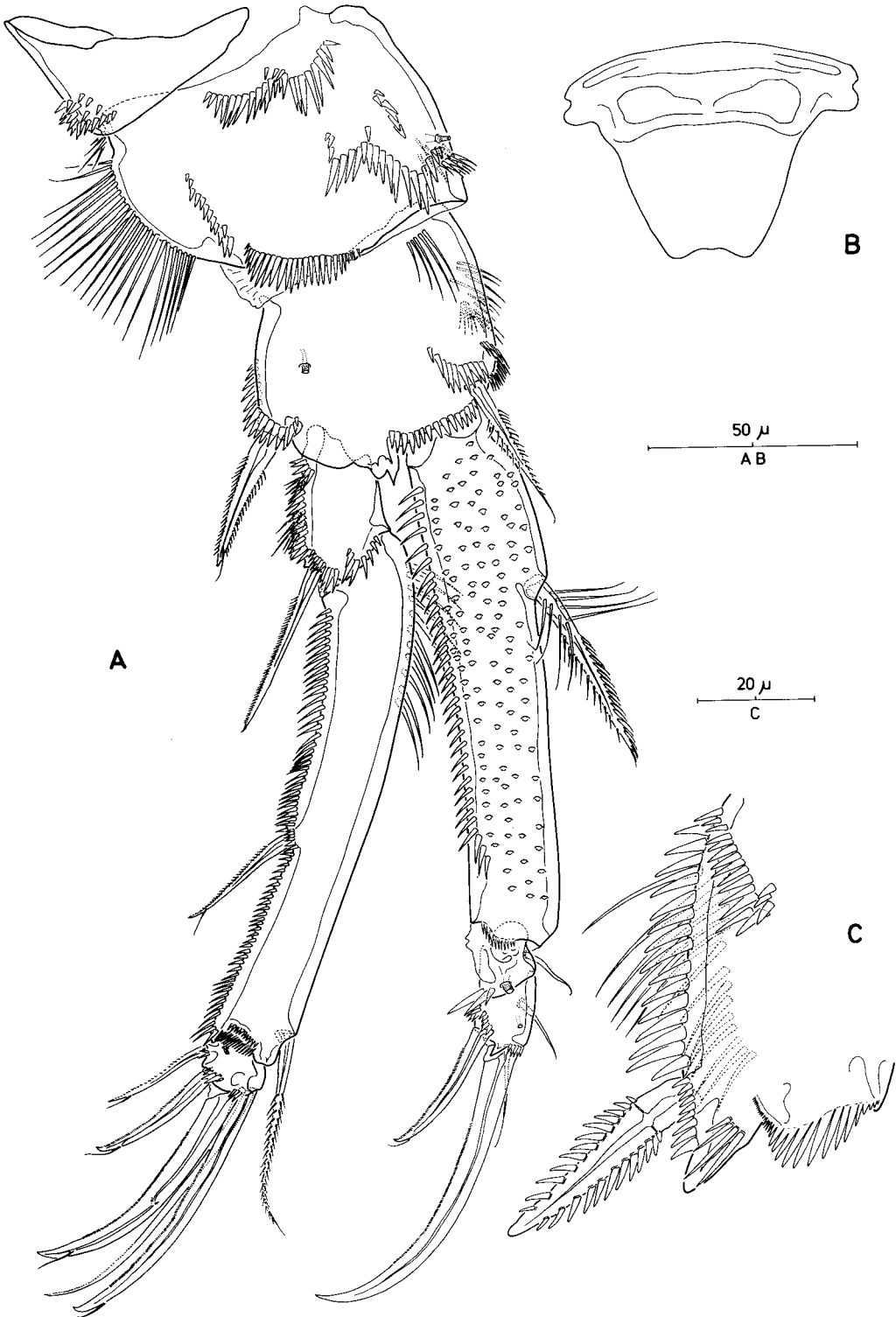


Figure 29. *Ambunguipes rufocincta* **comb nov.** Female. A, P1. B, Intercoxal sclerite of P1. C, Outer rim and spine of proximal exopodite segment of P2.

P1 (Figs 29A, B). With well-developed triangular praecoxa, ornamented with some tiny spinules. Coxa with tubular pore near inner margin and with several combs of spinules at anterior surface. Basis squarish, also with several spinular combs and bearing outer bipinnate spine and inner bipinnate seta (standing on anterior surface). Exopod extremely prolonged; prehensile by means of pivot articulation between segments II and III; proximal segment without inner seta but with outer spine; middle segment very long, about 6.5 times as long as maximum width, with one unipinnate spine implanted at about midway outer margin, and bipinnate seta near distal inner corner; distal segment with five finely serrated claws, increasing in length adaxially and bearing subapical flagellum, and one long inner seta. Endopod long, somewhat shorter than exopod; proximal segment very long, inner spine implanted at two-thirds distance from distal margin; modified pivot joint and well-developed arthrodial membranes between segments II and III; middle segment with tubular pore and tiny seta; distal segment with two tiny setae and two finely serrated claws.

P2–P4 (Figs 29C, 30C, 31). With small praecoxae and well-developed intercoxal sclerites (with spinules along concave ventral margin). Endopods distinctly shorter than exopods. Anterior surface of coxae with inner pore, of bases with outer pore. Basis with either pinnate spine (P2), or plumose seta (P3), or naked seta (P4). Exopodal spines being strong, markedly bipinnate and with distinct breaking plane (Fig. 29C). Exopodal setae plumose except middle inner seta of distal segment of P4 which is serrate. Intersegmental hyaline frill of proximal and distal exopodite segments distinctly incised and well developed. Inner endopodal setae often being tripinnate; endopodite-segments of P2 each with serrate seta. Seta and spine formulae are shown in Table IV.

P5 (Fig. 25B). Not fused medially; attachment site with supporting somite broad; intercoxal sclerite absent. Baseoendopod large; distal margin of endopodal lobe at four-fifths of exopod length; inner margin ornamented with long hair-like spinules decreasing in length distally; outer margin with short spinules; distal part having five bipinnate setae and four secretory pores; basal seta plumose, bi-articulated at base and having secretory pore near implantation. Exopod oval and partly covered by endopodal lobe; attachment site small; outer and inner margins densely spinulose and with one secretory pore each; third secretory pore located near apex; furnished with six setae in total.

Genital complex (Fig. 26A, B). Located in anterior half of genital double-somite. P6 represented by minute flap-like outgrowth of somite having one long outer and two tiny inner setae; genital apertures probably not connected. Seminal receptacles with distinct sclerotized walls, paired. Copulatory pore circular, located in pronounced depression medially and partly covered by median epicopulatory bulb, in its turn overlaid anteriorly by a

TABLE 4. Seta and spine formula of  
*Ambunguiipes rufocincta*

	Exopod	Endopod
P2	1.1.223	1.2.221
P3	1.1.323	1.2.321
P4	1.1.323	1.2.221



Figure 30. *Ambungiipes rufocincta* **comb. nov.** Male. A, Antennula anterior view (aesthetasc, accompanying seta and cluster of seta-like elements omitted). B, Sixth segment of antennula, posterior view, showing cluster of seta-like elements and implantation of aesthetasc and accompanying seta. Female. C, P2.

conspicuous medially incised epicopulatory plate; no external connection between copulatory pore and genital apertures.

Male (Figs 30A, B, 32, 33A, C). Body length 830–855  $\mu\text{m}$  (including rostrum and caudal rami). Habitus as in female, except for separation of genital and first abdominal somites (Fig. 33C) and absence of well-developed, posteriorly directed processes in on all abdominal somites. Posterolateral angles of first three urosomites densely spinulose, of other urosomites naked. First abdominal somite also with ventro-median spinular row. Sexual dimorphism in antennula and P2, P3, P5 and P6.

Antennula (Figs 30A, B). Slender, 14-segmented, modified; geniculation located between segments IX and X. Segment I longest, asetose, with spinules along inner margin; segment II short, with secretory pore and one seta; segment III with three plumose and eight smooth setae; segment IV with two inner processes, proximal bearing two setae, distal bearing long aesthetasc and six setae; segment V very short, with two setae on inner process; segment VI swollen, furnished with four slender seta and cluster of 14 seta-like elements along inner margin, and long aesthetasc accompanied by slender seta at inner distal corner; segment VII very small, with two small bipinnate spines; segment VIII also small, with one slender seta and one short pinnate spine; segment IX with one modified spine, one slender seta and one short pinnate spine, distal end geniculating with following segment; segment X with one thick and two very short modified spines; segment XI minute, with one inner seta; segments XII and XIII both with one inner and one outer seta; segment XIV with seven setae and one slender aesthetasc in total.

P2 (Fig. 32A). Protopod, exopod and proximal endopodite-segment exactly as in female. Middle and distal segments fused with complete retention of female number of setae; setae derived from middle segment not modified; distal part slightly swollen, without distinct processes; inner apical seta of female modified in characteristic stout appendix with bifid apex and distinctly swollen at base; outer seta spiniform and bipinnate instead of slender and tripinnate in female.

P3 (Fig. 32B). Protopod, exopod and proximal endopodite-segment exactly as in female. Middle segment slightly shorter than in female and bearing few spinules at posterior surface; outer distal process slightly more pronounced; distal segment modified, triangular and with bifid tip slightly bending inwards; outer margin without spinules but with two membranous areas; number of setae same as in female; setae I to III well developed, multipinnate; seta IV and V plumose; seta V implanted on posterior surface; tube pore standing on distinct process visible between setae V and VI; outer spine multipinnate in proximal half.

P5 (Fig. 33A). With separate rami; baseopods forming common median plate, deeply incised medially; basal seta bi-articulated and accompanied at base by long spinules and tubular pore; endopodal lobe reaching to distal margin of exopod, bearing three setae (middle one longest) and three secretory pores. Exopod one-segmented, oval, attachment site small; furnished with seven setae and one secretory pore; outer margin stepped and heavily spinulose.

P6-bearing (genital) somite (Fig. 33C). With distal angles slightly produced and spinulose. P6 (Fig. 33C) asymmetrical; one member being fused with supporting somite, other narrow plate acting as valve to release spermatophore (dextral and sinistral configurations exist depending on development of either right or left testis); each with outer subcylindrical process bearing three setae.

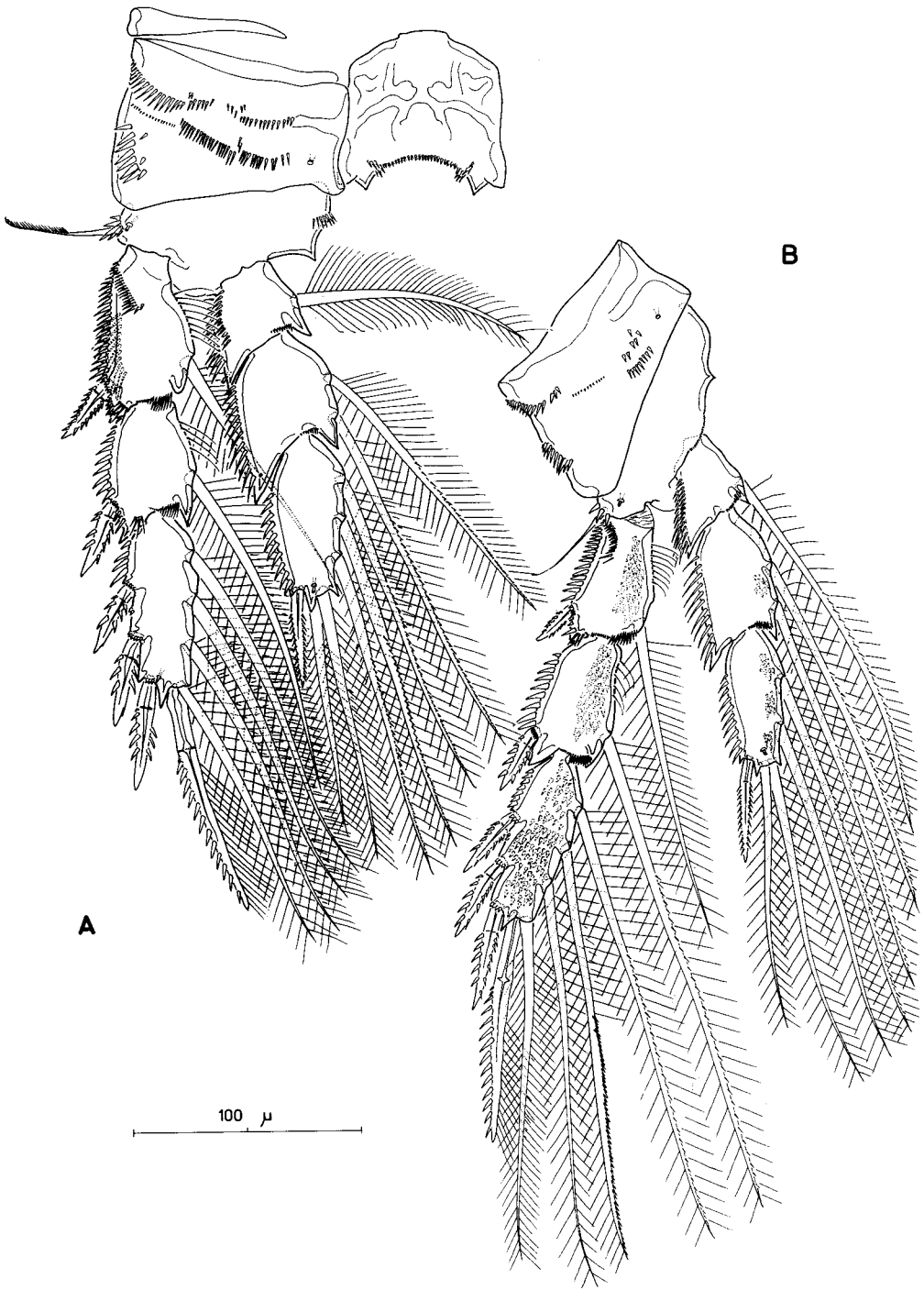


Figure 31. *Ambunguipes rufocincta* **comb. nov.** Female. A, P3. B, P4.



*Remarks*

This species was originally described under The Reverend A. M. Norman's manuscript name *Thalestris rufocincta* in Brady's monograph of the British free and semi-parasitic Copepoda (1880) but it is evident that only the latter deserves the authorship; however, *R. rufocincta* (Norman) still appears occasionally in the literature.

The illustrations of *A. rufocincta* from the Bulgarian coast given by Apostolov & Marinov (1988) agree well with the present redescription (apart from their figure of the supposedly female P5 which is drawn from a male) and proves the validity of Por's (1964) identification. Examination of material from Corsica and Naples (Italy) presented evidence that the species' alleged widespread distribution throughout the Mediterranean (see references in Lang, 1948; Pesta, 1959; Kunz, 1963; Bodin, 1964; Soyer, 1970, 1974) is justified. Judging from Yeatman's (1976) drawings based on Jamaican material and from the North Atlantic records listed in Lang (1948) and Coull (1970, 1971), there is good reason to believe that *A. rufocincta* displays an almost continuous distribution from the Caribbean and Bermuda to the north-eastern Atlantic seaboard between Norway and the Canaries and throughout the Mediterranean and Black Sea basins. Records from outside this area (A. Scott, 1909; Gurney, 1927; Sewell, 1940; Vervoort, 1962) are improbable or must await re-examination.

I cannot accept Lang's (1936, 1948) and other writers' decision to synonymize *R. similis* A. Scott, 1909 with *A. rufocincta*. There is an overall similarity between the single male specimen of *R. rufocincta* obtained by Vervoort (1962) from Nouméa, New Caledonia, the specimens of *R. similis* from Addu Atoll, Maldives (Sewell, 1940) and the males of *R. rufocincta* from Indonesia (A. Scott, 1909). Sewell (1940) had already suspected that the latter were attributed to the wrong species and synonymized them with *R. similis*. Vervoort (1962) also admitted that his specimen approached *R. similis* in most aspects. *Rhynchothalestris similis* is well separated from the type species in the structure of the male P5. In the former the endopodal lobe is weakly developed and reaches only to the implantation of the inner exopodal seta whereas in the latter the endopodal lobe extends to the distal margin of the exopod. This character is remarkably constant in both the North Atlantic-Mediterranean-Pontic and the Indo-Pacific forms and serves to reinstate *A. similis* comb. nov. instead of relegating it to the level of an Indo-Pacific race of *A. rufocincta*. Moreover, *A. similis* differs in the absence of well developed, backwardly produced angles of the first free abdominal somite in the female (Sewell, 1940: fig. 24A).

The Indo-Pacific specimens (all females) of *A. rufocincta* recorded by A. Scott (1909) and Sewell (1940) differ from the European form in the fourth antennular segment being distinctly shorter than the third, the shorter rami of the P5 and the smaller body-size; however, it is difficult to decide on the significance of these characters without having seen the material. Under the circumstances, it is preferable to treat these, as well as Gurney's (1927) find, as doubtful records.

Brady's (1910) description of *R. vanhoeffeni* is grossly inadequate and gives only the barest minimum to allow removal to the genus *Ambunguipes*. The inaccuracies expressed in the drawings and the lack of the male make the description almost useless for comparative purposes. Hence, Sewell's (1940) relegation of *R. vanhoeffeni* to synonymy with *A. rufocincta* is premature and the species in



Figure 32. *Ambunguipes rufocincta* **comb. nov.** Male. A, Endopod of P2. B, Endopod of P3.

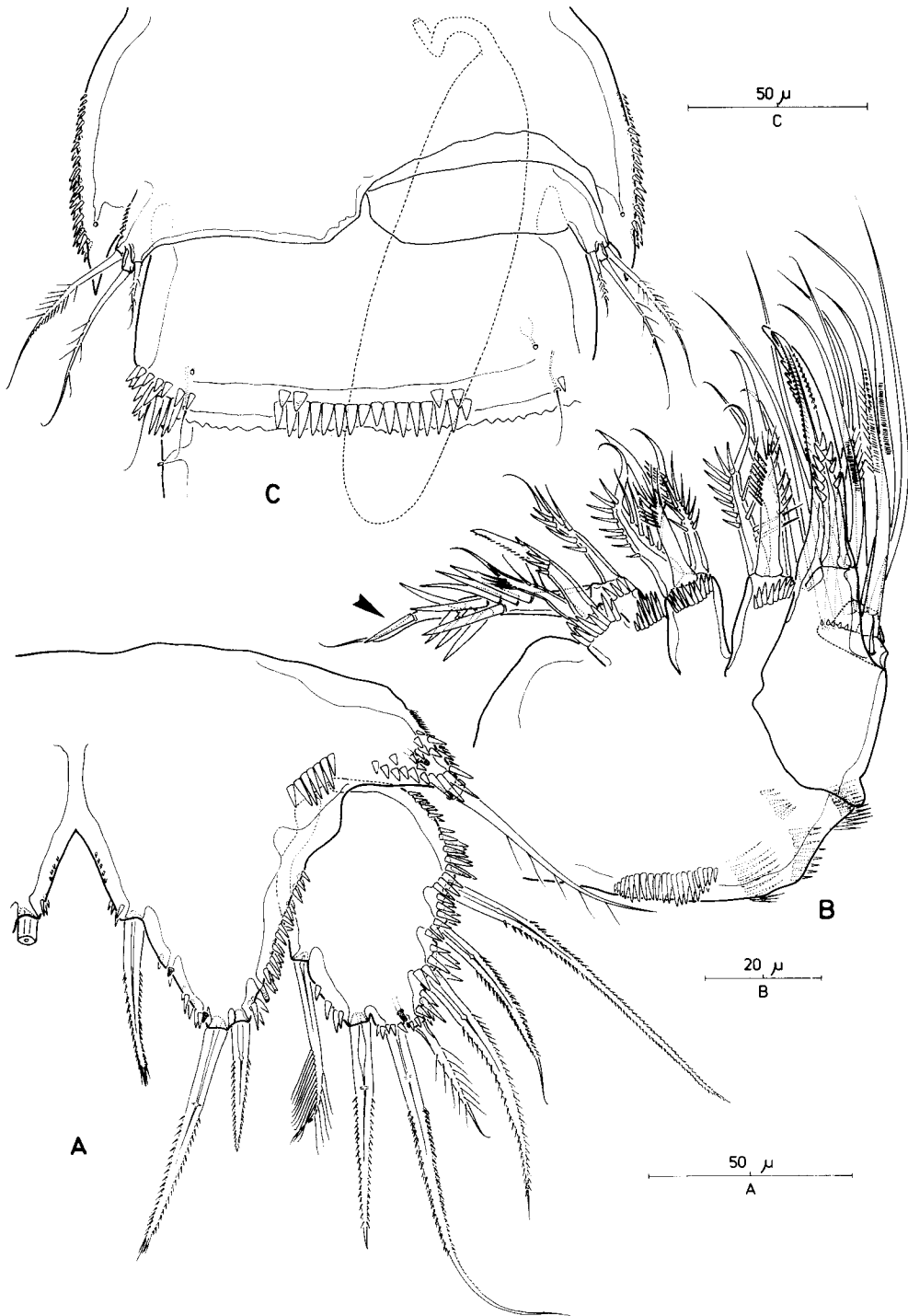


Figure 33. *Ambunguipes rufocincta* **comb. nov.** Male. A, Left P5. C, Genital and first abdominal somites, ventral view. Female. B, Maxilla (modified spine arrowed).

question can at best be ranked as *species inquirenda*. Nicholls (1944) reported finding two females of *R. vanhoeffeni*; however, there is a striking discrepancy in the relative length of the P1 endopod between his Red Sea material and Brady's Cape of Good Hope specimen, probably indicating that they were dealing with different species.

*Rhynchothalestris agigensis* Serban, 1959 is known only from three females collected at Agigea, Rumania (Serban, 1959). Earlier, Chappuis & Serban (1953) had identified this species as *R. rufocincta* despite the profound differences recorded in the antenna, the endopod P1 and the setation of P2–P3. The authors tried to explain this variation by assuming that lower salinity could influence segment numbers, a phenomenon previously observed in *Nitocra* and *Amphiascus*. This hypothesis was refuted later by Serban (1959), who believed that the phreatic habitat might not be the natural one for the species. As a result, he proposed *R. agigensis* as a new species for the Agigean material but this act only complicated the issue rather than elucidating it. Serban's description is very rudimentary and illustrations are lacking altogether; although he announced a detailed description, this has, to my knowledge, never been published. The little information that is given excludes the possibility of referring the species to either the Ambunguipedidae or the Rhynchothalestrinae. The presence of only one inner seta on the middle endopodite segment of P2–P3 is similar to some dactylopusiine genera (*Diarthrodes*, *Dactylopusia*), and the two-segmented condition of the antennary exopod and the P1 endopod is found in the genus *Eudactylopus*. Pending a re-examination of Serban's material, *R. agigensis* can be considered only *incertae sedis* within the Dactylopusiinae.

### ***Lucayostratiotes* gen. nov.**

#### *Synonymy*

*Rhynchothalestris* (part).

#### *Diagnosis*

Ambunguipedidae. Prosome and urosome dorsoventrally compressed. Cephalothorax broad, comprising nearly half total body length. Dorsal part of first free pedigerous somite (P2) largely concealed beneath a strong backwardly directed, median, spiniform extension from posterior margin of cephalothorax. Epimeral plates of thoracic somites bearing P2–P4 and, to lesser extent, of cephalothorax, strongly produced posteriorly; posterolateral angle of P4-bearing somite at least extending to genital complex (in female) or to rear margin of genital somite (in male). First and second free thoracic somites with pairs of dorsolateral, backwardly directed, spiniform processes. Lateral processes of genital double-somite (female) and second abdominal somite weakly developed. Tuft on sixth segment of male antennule strongly developed, consisting of about 40 setoid elements.

#### *Etymology*

The generic name is derived from *Lucayos*, an older name for the Bahamas and from the Greek *stratiotes*, meaning soldier and, alludes to the distinctive armature of the cephalothorax and thoracic somites. Gender: feminine.

*Type and only species*

*Lucayostratiotes cornuta* (Geddes, 1969) **comb. nov.**

*Material examined*

From Dr A. Fosshagen, University of Bergen; Norwegian marine biological investigations in the Bahamas, 1968 (see Brattstrøm, 1968): two females and one male from Little San Salvador, West Bay (station 53-68: 24°34'40"N, 75°57'30"W), sand, *Thalassia* Banks of Solander collected at a depth of 4-7 m with 'Mouse' trap; 26 iii 1968.

*Remarks*

This genus is established to encompass only *R. cornuta* and can be easily differentiated from *Ambunguipes* by the condition of the male antennular tuft and by the unique differentiations of the pleurotergites.

*Discussion*

The antennular tuft, a peculiar structure found in male Ambunguipedidae, is composed of delicate seta-like elements, having the appearance of long and very slender setae. These structures, for which I coin the term *setoid elements*, are planted upon the outer surface of the integument so as to leave a tiny scar when they fall off. Setoid elements are not setal in origin because they do not insert into a hole right through the integument and do not have a central axial core which is almost always visibly hollow. An analogous tuft has been reported recently by Masunari (1988) on the male antennule of *Parathalestris mourei* but here the setoid elements are implanted on a spherical chitinous area on the third segment, whereas the tuft of the Ambunguipedidae originates from the (not homologous) sixth segment. In general, addition of novel setae, not due to character-reversal, is very uncommon among harpacticoid copepods. Some species of *Scottopsyllus* Kunz, 1962 have five inner setae on the basis of leg I (Lang, 1948, 1965; Mielke, 1984b). The presence of novel spines on both rami of the P1 was recorded recently in the cave-dwelling Superornatiremidae (Huys, in press).

Examination of *A. rufocincta* revealed the presence of mucus strings coming out of a distinct pore near the base of the outer terminal seta. These cylindrical strings seem to consist of an adhesive gelatinous substance which is secreted by glands found in the posterior part of the urosome. Analogous mucus strings were first mentioned for *Zausodes sextus* (Lang, 1965) and recently also for *Perissocope biarticulatus* (Watkins, 1987). The latter author observed also similar mucus systems, however less prominent, in other unnamed Pacific coast representatives of the family Harpacticidae. According to Lang (1965) the strings could function as anchors when they are twisted round sediment grains, but recent studies (Chandler & Fleeger, 1984; Williams-Howze, Silverman & Fleeger, 1987; Williams-Howze & Fleeger, 1987) indicate that certain mucus secretions might also be indicative of tube-building capability. Personal observations on live leptastacinid *Cylindropsyllidae* showed that tiny mucus strands, secreted by large glands in the caudal rami, were used in 'mucus-trap feeding'. A similar mechanism of gardening microbiota has already been suggested for meiobenthic nematodes (Riemann & Schrage, 1978; Warwick, 1981). Clearly mucus production in harpacticoids serves for a variety of purposes. In *Ambunguipes*, mucus strings are secreted by a conical pore and a survey of the thalestrid genera

revealed the same pore to be present in exactly the same position although strands were not recorded.

Comparison of the (amended) generic diagnosis reveals that *Rhynchothalestris* and *Ambungiipes* do not show many important characters in common and that the species referred to have been lumped together merely because of their superficial similarity. The few characters that are shared are either the product of convergence or plesiomorphic, and do not favour a close relationship. Amongst the former one can mention the prehensile rami of the P1. Plesiomorphic features are found in the nine-segmented female antennule, the antennary exopod, the setation of the mandible, the setal formulae of P2 to P4, etc., but most of them, if not all, are found in at least some genera of the Thalestrinae, the Dactylopusiinae, and in the Hamondiidae, suggesting that they must have been present also in the ancestor leading to a bigger group of thalestridimorph genera.

Essential differences between Ambungiipedidae and Rhynchothalestrinae are found in the rostrum, the male antennule, the P5 in both sexes, the male P6, the female genital complex, and not the least in the sexual dimorphism of the swimming legs. Rhynchothalestrinae, unlike Ambungiipedidae, lack modifications of the male P3 endopod but both display sexual dimorphism on the preceding leg. However, the strongly modified, bifid, stout spine of the distal part of the P2 endopod, which is typical for the Ambungiipedidae, is missing in *Rhynchothalestris*.

*Ambungiipes* is the only extant thalestridimorph genus thus far known that has retained the abexopodal spine on the antennary basis. It furthermore shares with *Hamondia* the highest number of male antennular segments ever recorded amongst harpacticoids.

The Hamondiidae and the Ambungiipedidae can be considered sister groups on the basis of the following synapomorphies: (i) the loss of the seta on the first antennular segment in both sexes (this seta is present in virtually all other harpacticoid copepods, even in the otherwise reduced interstitial genera; see, e.g. Huys, 1987a, 1988c) and the presence of a characteristic tube-pore on the second segment; (ii) the presence of a uniseriate comb of bifid spinules on the third exopodal segment of the antenna (these morphological minutiae appeared to be absent from all the thalestrid genera I have examined); (iii) the presence of a modified spine on the distal lobe of the praecoxal endite of the maxilla (this spine is much bigger than the others, furnished with numerous spinules and typically directed adaxially); (iv) the sexual dimorphism in the endopod of P3 (the distal segment is transformed in exactly the same way); (v) the detailed structure of the female genital complex with presence of an epicopulatory bulb and medially incised plate; (vi) the asymmetry of the male P6.

Essential differences between the two families are found in (i) the habitus; (ii) the sensillary pattern, (iii) the antennary endopod; (iv) both rami of P1; (v) sexual dimorphism of P2 and P4; (vi) setation of P6.

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