

## ***Bathycamptus eckmani* gen. et spec. nov. (Copepoda, Harpacticoida) with a review of the taxonomic status of certain other deepwater harpacticoids**

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### **Abstract**

*Bathycamptus eckmani* gen. et spec. nov., which is associated with mudballs produced by the cirratulid *Tharyx laticastellus*, is described from bathyal muds in San Diego Trough, off California. *Heteropsyllus minutus* Wells from the Fladen Ground, Scotland is considered to be its closest relative and is placed in the same genus. The genera *Bathycamptus* and *Psammocamptus* Mielke are regarded as sister groups on the basis of the shared sexual dimorphism shown by P3–P4. Relationships with other marine Canthocamptidae are discussed, and a re-evaluation of the genus *Hemimesochra* Sars is made. It is concluded that this genus should encompass only the type species *H. clavularis* Sars. *Leimia dubia* Wells and *H. nympha* Por are transferred to the new genus *Boreolimella*, which is closely related to *Bathycamptus* but not to *Leimia* Willey. The genus *Perucamptus* gen. nov. is established to include *H. rapiens* Becker and shows no clear relationship with the other genera. *H. trisetosa* Coull is assigned to *Carolinicola* gen. nov., which is regarded as being an advanced member of the Paranannopidae. *H. secunda* Wells is recognised as belonging to *Mesopsyllus* Por; whilst *H. nixe* Por is considered the type species of a new genus *Pusillargillus*.

### **Introduction**

In the course of ecological investigations in the bathyal San Diego Trough, a species of harpacticoid copepod was discovered to be strongly associated with the cirratulid polychaete *Tharyx laticastellus* Jumars, 1975 (Thistle & Eckman, 1988). This association is ecologically interesting because it provides an opportunity to study the

processes that underlie community organization in the deep-sea. In particular, *Tharyx* produces and lives in a mud concretion 2–3 cm in diameter and 3–4 cm high (Jumars, 1975). The association of the harpacticoid with these concretions could arise in several ways such as: (1). The worm-concretion combination could provide a refuge from predation; (2). The interaction of the concretion with the near-bottom flow could increase

boundary-skin friction in the vicinity (Eckman & Nowell, 1984) that could stimulate *in situ* bacterial production (Eckman, 1985) and thereby attract the harpacticoid species; or (3). Whatever the distribution of the bacteria on or off the concretions, the latter could provide obstacles behind which the copepod could shelter from the bottom-current, and either feed in sheltered conditions as long as there is risk of it being swept away if exposed, or (whenever the current is not too strong) extend their feeding-area to unsheltered parts of the substrate near its 'home' concretion.

?*Heteropsyllus minutus* from the Fladen Ground in the northern North Sea (Wells, 1965) is recognised below as being the closest relative of the new species. In this area, apart from the Foraminifera, the most abundant group of the macrofauna comprised Polychaeta, represented by nearly 40 species (McIntyre, 1961). It is interesting to note that both *Tharyx multibranchis* and a second unidentified *Tharyx* species are numerically dominant species, and that the substrate closely resembled that on which *B. eckmani* was found, in being mud with a rather unusual greenish tinge.

## Materials and methods

The samples were taken with a Remote Underwater Manipulator (RUM), an unmanned tractor-like vehicle tethered to a surface-support platform (Thiel & Hessler, 1972). RUM used its manipulator arm to take bottom samples, using a modified Ekman grab. The grab measured 20 by 20 cm and was partitioned internally by four 10-by-10 cm subcores. The 0–1 cm layer of each subcore was extruded, sliced off, and fixed in buffered formalin together with the overlying water from the subcore. In the laboratory, each sample was washed on a 0.062-mm aperture sieve, transferred to 80% ethanol, and stained with rose bengal.

Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd Poole England).

All drawings 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 gnathobasis (Mielke, 1984), (2) the segmental composition of the mandible and maxilliped which are followed according to Boxshall (1985: pp. 341–345). The setae of the caudal rami are named and numbered as proposed by Huys (1988).

Both sexes of *Bathycamptus eckmani* gen. et spec. nov. were examined by scanning electron microscopy (SEM) with a JEOL JSM-840 microscope. Specimens were prepared by dehydration through graded ethanol, critical-point dried, mounted on stubs, and sputter-coated with gold.

## Systematics

### *Bathycamptus* gen. nov.

**Diagnosis.** – Body slightly tapering posteriorly. P1-bearing somite fused with cephalothorax. Genital double somite with internal trace of subdivision ventrally and (dorso)laterally. Anal operculum present; anal somite slightly notched in middle of posterior border. Caudal rami elongate, furnished with 6 setae; outer and inner terminal setae well developed, anterolateral accessory seta absent.

Rostrum well developed, fused with cephalothoracic shield. Antennula short, with some pinnate spines; 7-segmented in female, furnished with aesthetasc on 4th and 7th segments; 7- or 8-segmented and haplocerate in male. Antennal exopod small with 2 setae; allobasis with proximal seta. Mandibular basis with 1 seta; endopod 1-segmented with 4 setae; exopod represented by 1 seta. Maxillula with well developed praecoxal arthrite; coxal epipodite absent; exo- and endopod very reduced. Maxillary syncoxa with 2 endites; endopod incorporated into basis. Maxilliped robust, prehensile; syncoxa with 1 seta, basis unarmed, endopod with claw and 1 seta.

Swimming legs with wide intercoxal plates. Leg 1 with both rami 3-segmented; endopod not prehensile or elongate. P2–P4 with 3-segmented exopods and 2-segmented endopods in female; endopod P3 3-segmented in male. Baseoendopod and exopod P5 confluent in both sexes; exo- and endopodal lobes in female with 4 setae; in male with 4 and 2 setae, respectively. Male P6 very reduced, represented by 1 seta. Female copulatory pore circular, conspicuous; genital pores forming a common median slit; P6 represented by 2 setae.

Sexual dimorphism in antennula, endopod P1–P4, fifth and sixth legs and in genital segmentation.

Marine.

Type species: *Bathycamptus eckmani* gen. et spec. nov.

Other species: *B. minutus* (Wells, 1965) comb. nov.

*Etymology.* – The generic name is derived from the Greek *bathys*, meaning deep, and *kamptos* meaning flexible.

*Gender:* masculine.

*Bathycamptus eckmani* gen. et spec. nov.

*Type material:* Holotype female dissected on 6 slides and deposited in the British Museum (Natural History), London under no. 1988: 199. Allotypic paratype is a male dissected on 6 slides (no. 1988: 200). Other paratypes are 2 females and 2 males (spirit preserved) and deposited under nos. 1988: 201–204.

*Type locality:* San Diego Trough, the southernmost basin of the southern California Continental Borderland. The samples were taken in a triangular study site, 500 m on a side centered at 32°35.75' N, 117°29.00' W (Fig. 1). The depth

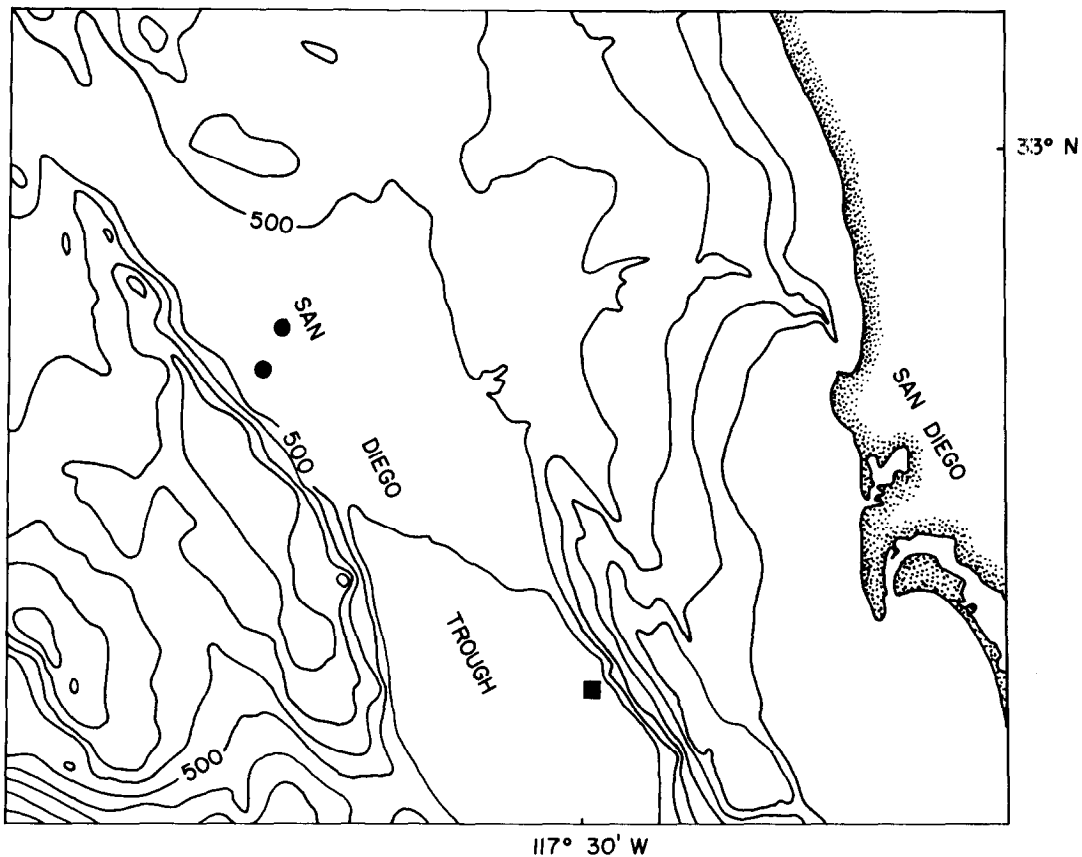


Fig. 1. Chart of San Diego Trough. A square indicates the type locality. The two additional localities are shown as circles. Contours are in fathoms.

varied between 1218 and 1223 m. The bottom-water temperature, salinity and oxygen-concentration are nearly constant at 3.5 °C, 34.53 parts per thousand, and 0.71 ml/l respectively. The sediment is a hemipelagic green mud, 3.0% sand, 52.7% silt, and 44.3% clay by weight.

*Additional material:* five females and six males were found in a second locality further north in San Diego Trough (32°51.02' N, 117°46.97' W; 1035 m depth) and are retained in the personal collection of the first author; the species was also recorded from a third location at 32°52.42' N, 117°45.50' W and a depth of 1050 m.

### *Description:*

#### *Female*

Body length: 298–315  $\mu\text{m}$  ( $\bar{x}$  = 308  $\mu\text{m}$ ;  $n$  = 3) rostrum and caudal rami excluded; 367–380  $\mu\text{m}$  ( $\bar{x}$  = 370  $\mu\text{m}$ ;  $n$  = 4) rostrum and caudal rami included. Body (Figs. 2A, B; 8A) slightly tapering posteriorly and greatest width measured at about midway of the cephalothorax. Nauplius eye not observed; Integument not pitted. First three free thoracic somites and posterior half of cephalothorax provided with very long sensillae dorsally and dorsolaterally. Ventral margin of cephalothoracic shield furnished with long hairs (Fig. 8B). P5-bearing somite, genital double somite and free abdominal somites 1 and 2 with fine spinular rows dorsally and laterally (Figs. 2A, B; 8A). Ventral surface of genital double somite and free abdominal somites with strong spinules posteriorly. Genital double somite with a chitinous internal rib dorsolaterally, laterally and ventrally (Figs. 2B; 5C). Anal somite (Fig. 9B) notched in the middle of its posterior border, furnished with spinules laterally and ventrally. Anal operculum (Fig. 2C) slightly rounded and finely spinulose. Caudal rami (Figs. 2C, D) elongate, about 8 times as long as maximum width, slightly tapering in the middle and posteriorly; furnished with 6 setae: anterolateral accessory seta (I) absent, anterolateral (II) and posterolateral (III) setae slender and bare, outer terminal seta (IV) spinulose and free at base, inner terminal seta (V) strongly developed and spinulose, terminal accessory seta

(VI) small and standing on a minute process, dorsal seta (VII) laterally displaced and triarticulated at base.

Rostrum (Figs. 2A, B, 3B; 8A, B) prominent and pointing downwards, fused with cephalothoracic shield but with a distinct suture at the base, furnished with 2 short sensillae and 1 median pore; minutely bilobed at the apex.

*Antennula* (Fig. 3A) 7-segmented, short; first segment widest, with several spinular rows but without setae; second one with 6 setae and 1 'pineapple-spine' (*sensu* Hamond, 1971); third segment with 2 stout pineapple-spines and 2 slender setae; segment 4 bearing a thick aesthetasc and 2 slender setae; segments 5 and 6 with 1 and 2 bare setae, respectively; distal segment with 1 inner pineapple-spine, 8 setae and 1 short aesthetasc.

*Antenna* (Fig. 3C) with well developed coxa bearing a uniseriate comb of fine spinules at the inner subdistal corner; basis and first endopod segment forming a short allobasis, furnished with a uniseriate comb of long spinules and a minute abexopodal seta in the proximal half; exopod unisegmented with 2 apical setae; endopod 1-segmented, bearing 2 rows of stout spinules and 2 strong pinnate spines along the inner margin, and 5 pinnate spines at the anterior margin.

*Labrum* (Figs. 8B, C) well developed, notched in the middle, lateral margins provided with strong spinules.

*Mandible* (Fig. 3D) small, gnathobase with strong spines and a unipinnate seta; basis spinulose along the inner edge and bearing 1 pinnate spine; endopod 1-segmented and furnished with 1 inner and 3 terminal spines; exopod represented by a short pinnate spine.

*Maxillula* (Fig. 3E). Praecoxa with long setules along the outer edge and with well developed arthrite bearing 2 surface setae and 9 spines along the anterior margin; coxa with setulose outer margin and forming an inner process bearing 2 setae, epipodite absent; basis with setulose inner margin and furnished with 4 terminal and 2 outer setae; endopod a minute segment with 1 seta; exopod represented by 1 bipinnate spine.

*Maxilla* (Figs. 6F, 8D) unsegmented and setu-

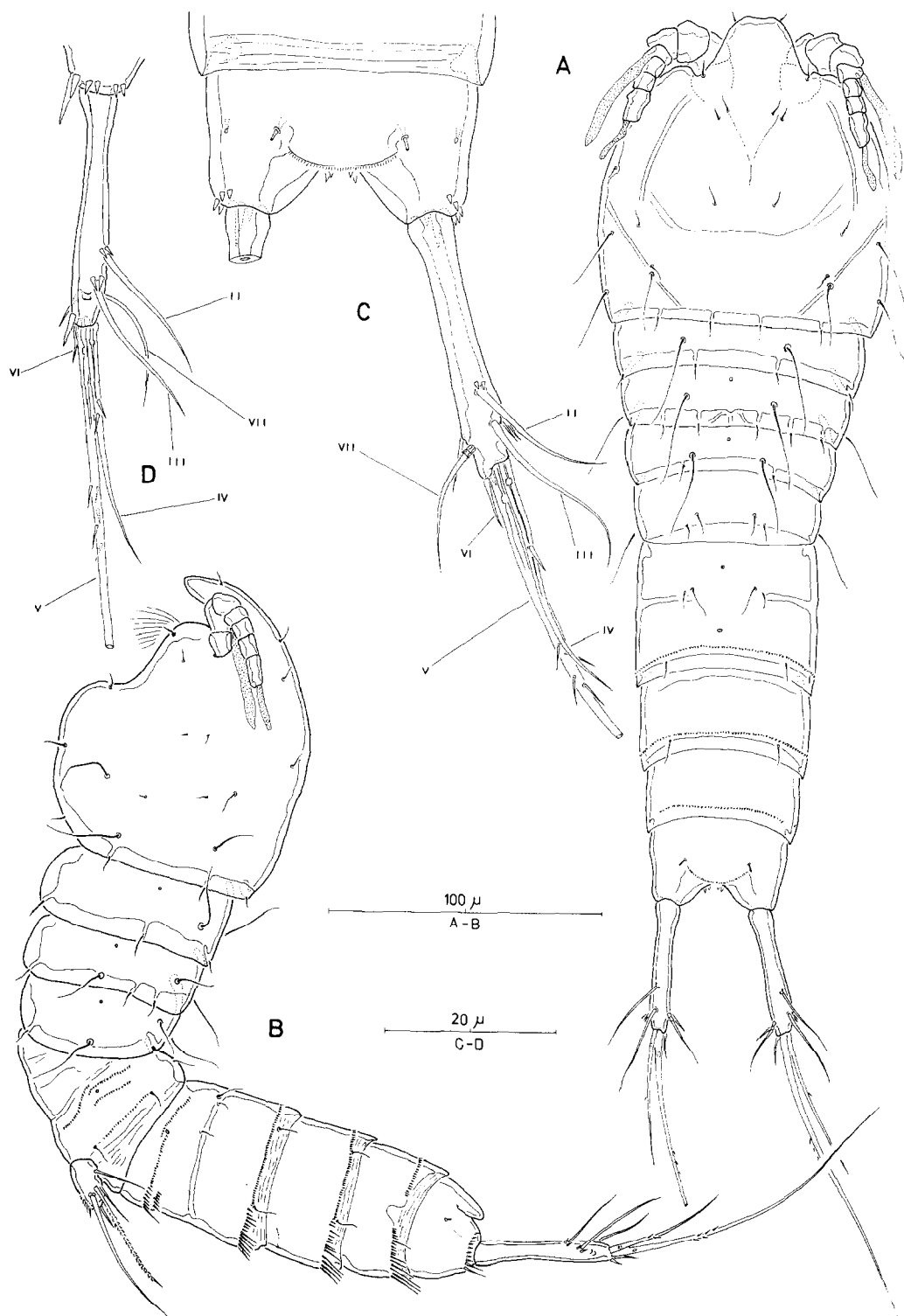


Fig. 2. *Bathycamptus eckmani* gen. et spec. nov. A. female, dorsal view; B. Female, lateral view; C. Anal somite and right caudal ramus, dorsal view; D. Left caudal ramus, outer lateral view.

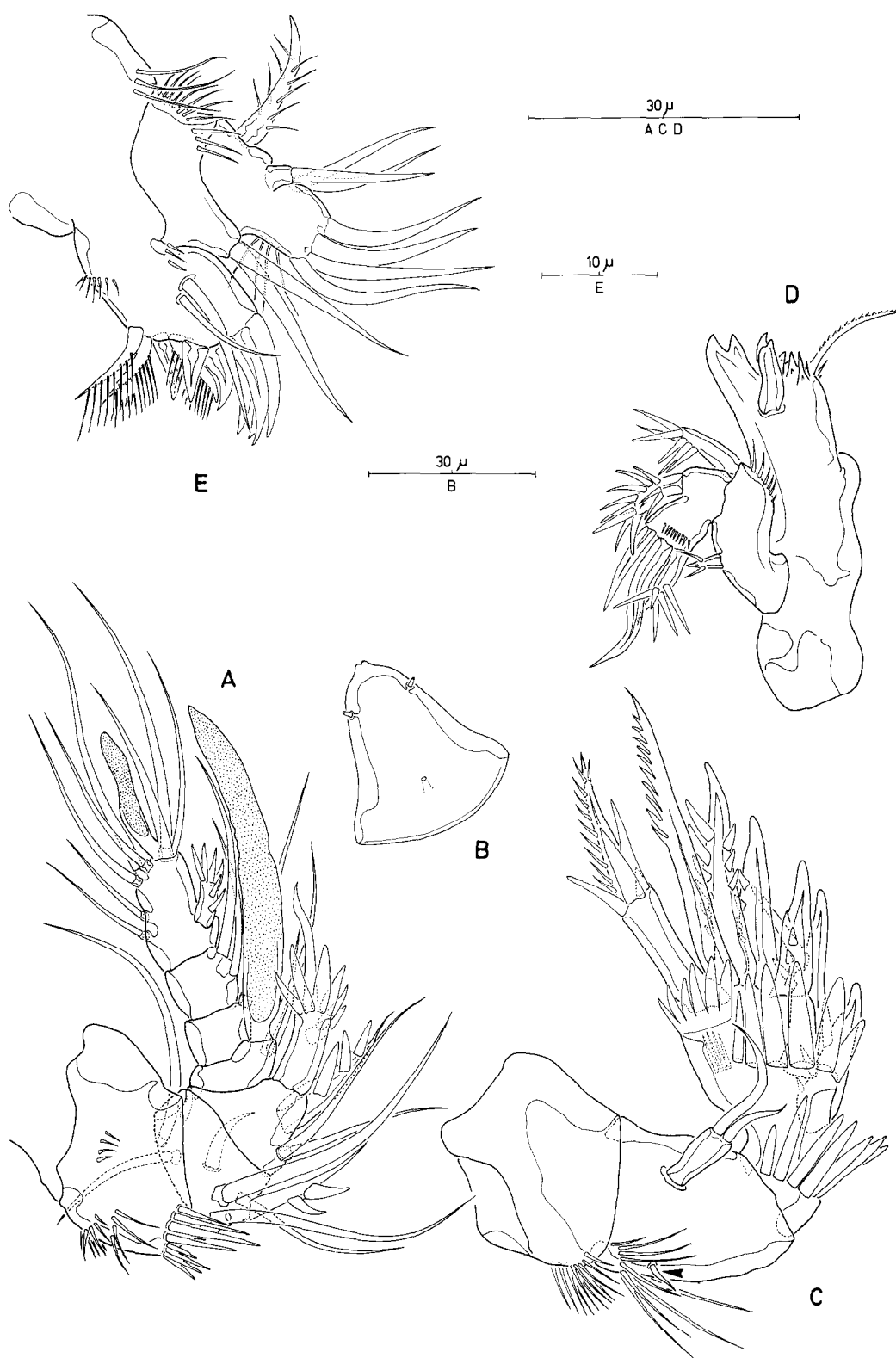


Fig. 3. *Bathycampus eckmani* gen. et spec. nov., female. A. Antennula; B. Rostrum; C. Antenna, arrow indicates minute seta on allobasis; D. Mandible; E. Maxillula.

lose along the outer edge; with 2 endites. Proximal endite produced distally into a rounded lobe from whose proximal flank (and based on its projecting shoulder) there arises a short, stout, and bluntly-pointed spine; the lobe and the spine each have their proximal edges bearing a uniseriate row (extending to the tip) of short broad spinules. Distal endite sub-cylindrical and bearing 3 spines; claw of the basis spinulose along the inner distal half and bearing 5 setae (derived from the basal endite and the endopod) at the base.

*Maxilliped* (Figs. 6G, 8D) short, prehensile; syncoxa with some spinules and a bipinnate seta; basis without spines or setae; but with spinular rows along both the outer and inner margins; endopod represented as proximally swollen claw, spinulose along the inner distal half and furnished with a minute seta at the base.

*Swimming legs* with three-segmented exopods and three- (P1) or two-segmented endopods (P2 to P4). Intercoxal plates well developed, wide and unarmed (Fig. 4B).

*P1* (Fig. 4A) with well developed coxa, spinulose along inner half of distal margin; basis with a slender outer seta, a stout pinnate inner spine, and several spinular rows on the surface. Exopod segments 1 and 2 with strong spinules along the outer and distal margins and with an outer pinnate spine, segment 2 also with a minute inner seta; segment 3 with 1 outer and 2 terminal pinnate spines and 1 inner plumose seta. First endopod segment with a minute inner seta and with strong spinules along the outer and distal margins; segment 2 with an inner pinnate spine and spinules distally; distal segment with a fine inner seta and pinnate spines distally.

*P2* (Fig. 4B). Coxa with spinular rows along the outer margin, basis spinulose along the distal edge and on the anterior surface and bearing some spinules and a short curved spine at the outer edge. Exopod segments 1 and 2 with several spinules and a subdistal bipinnate spine along the outer margin, segment 2 also with an inner plumose seta; segment 3 with 2 outer bipinnate spines, 1 apical and 2 inner plumose slender setae. Endopod segment 1 with a minute inner seta and several spinules along the outer and distal mar-

gins; distal segment with 1 short bipinnate spine, 2 slender plumose setae and 1 distally serrate seta.

*P3* (Fig. 4C). Coxa as in preceding leg; basis with a slender outer seta. Proximal and middle exopod segments as in P2; distal segment with 3 outer pinnate spines, 1 apical and 3 inner terminal setae. Endopod segment 1 with slender spinules along the outer side and 1 minute inner seta; segment 2 with the same arrangement as in P2.

*P4* (Fig. 5B). Basis, coxa and exopod segments 1 and 2 as in P3. Distal exopod segment with 3 outer bipinnate spines and 4 slender setae, one being serrate along the distal end. Endopod segment 1 with smooth inner seta; distal segment with 1 outer bipinnate spine and 3 slender plumose setae.

Seta- and spine formulae:

	exopod	endopod
P1	0.1.121	1.1.111
P2	0.1.212	1.211
P3	0.1.313	1.211
P4	0.1.313	1.211

*P5* (Fig. 5A). Baseoendopod and exopod fused. Exopodal lobe with 2 outer minute setae and 2 inner strong spines of different lengths. Endopodal lobe with 4 strong spines, the outer two being bipinnate, the inner two pectinate along the outer distal margin.

*Genital double somite* (Figs. 2A, B; 5C; 8B; 9C) wider than long. Gonopores fused and forming a common median genital slit. P6 represented by 2 short setae. A set of 3 pores was found posteriorly and on both sides of the genital aperture. Copulatory pore large, located in the center of the genital double somite and slightly widening posteriorly.

#### Male

Body length: 265–280  $\mu\text{m}$  ( $\bar{x}$  = 170  $\mu\text{m}$ ;  $n$  = 3) rostrum and caudal rami excluded; 330–345  $\mu\text{m}$  ( $\bar{x}$  = 340  $\mu\text{m}$ ;  $n$  = 3) rostrum and caudal rami included. Body (Figs. 7A, B; 9A) with ornamentation principally as in female, except for genital segmentation. Sexual dimorphism in the antennula, the endopod of P1–P4, P5 and P6.

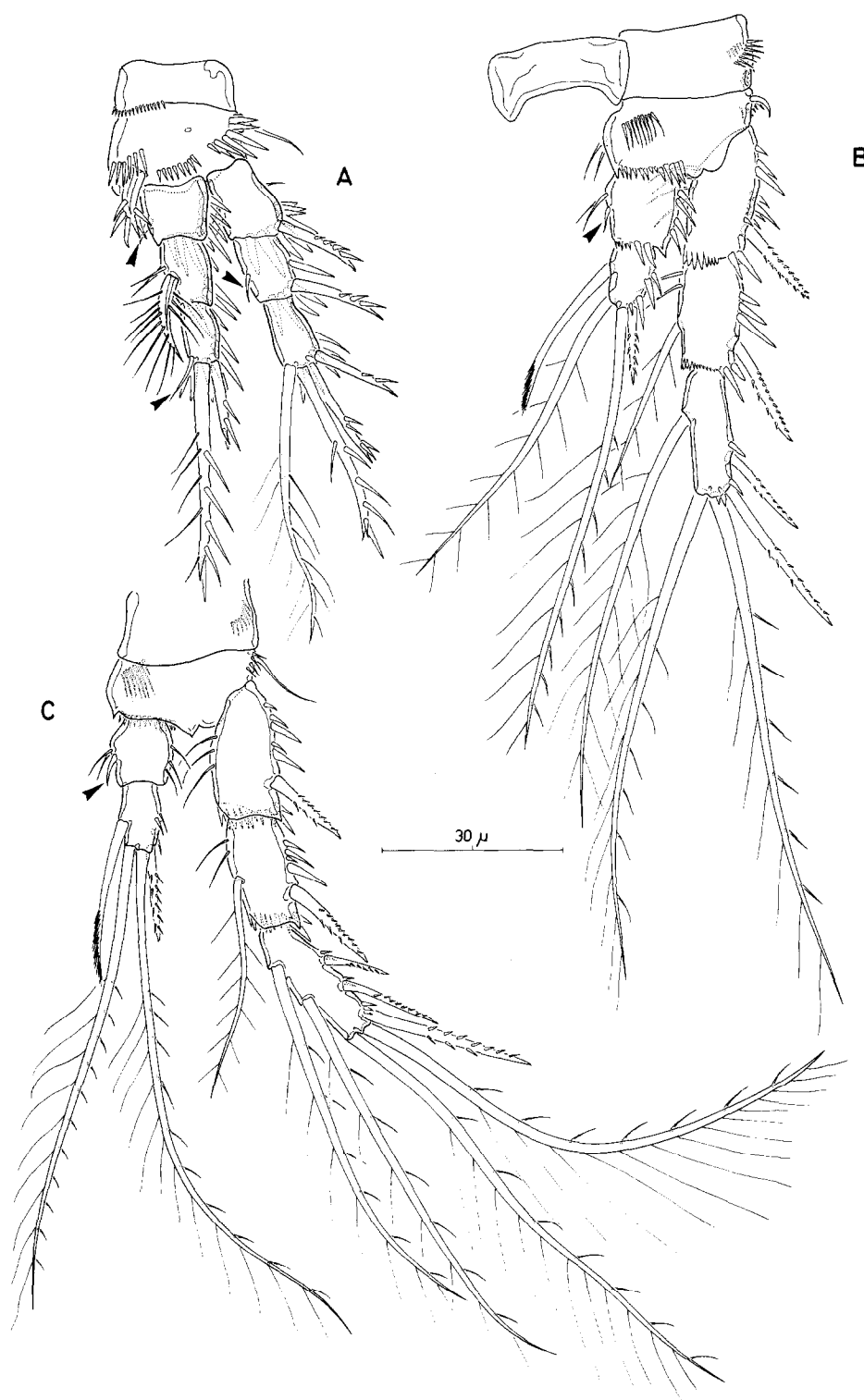


Fig. 4. *Bathycamptus eckmani* gen. et spec. nov., female (arrows indicate minute setae) A. P1; B. P2; C. P3.



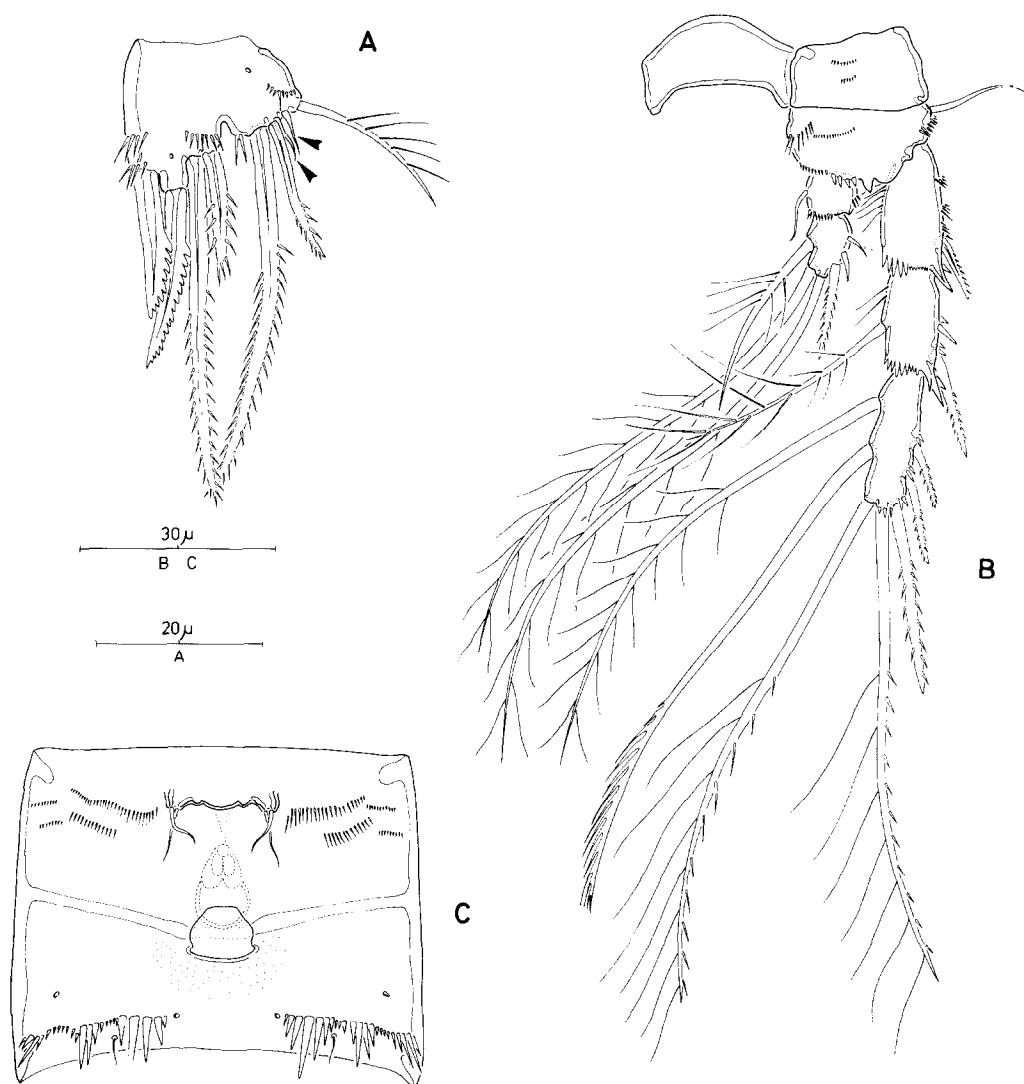


Fig. 5. *Bathycampus eckmani* gen. et spec. nov., female. A. P5 (arrows indicate 2 minute setae); B. P4; C. Genital double-somite, ventral view.

**Antennula** (Figs. 7D, 9A, E) 8-segmented, haplocerate. First segment with spinules along inner margin and inner subdistal corner; segment 2 with 2 stout pineapple-setae and 6 slender smooth setae, the outermost of which is bifid at the tip; third segment with 2 minute setae and 3 slender ones; inner margin of segment 4 furnished with 1 bipinnate spine, 1 smooth spine and 2 minute setae and forming a distinct process, inner subdistal corner forming a sub-cylindrical process furnished with 1 minute seta, 1 slender seta and an extremely long aesthetasc; 5th segment with 2

short setae; segments 6 and 7 forming haplocerate apparatus and furnished with 2 and 3 spherical elements (= modified setae), respectively; segment 6 also with 2 slender setae, segment 7 with 1 distal short seta; distal segment with 9 setae and 1 short aesthetasc.

**P1** (Fig. 6A) as in female, except for the inner seta of the distal endopod segment which is spiniform and bipinnate.

**P2** (Fig. 6B) as in female except for the endopod. Distal endopod segment long and tapering distally; inner margin furnished with 2 slender

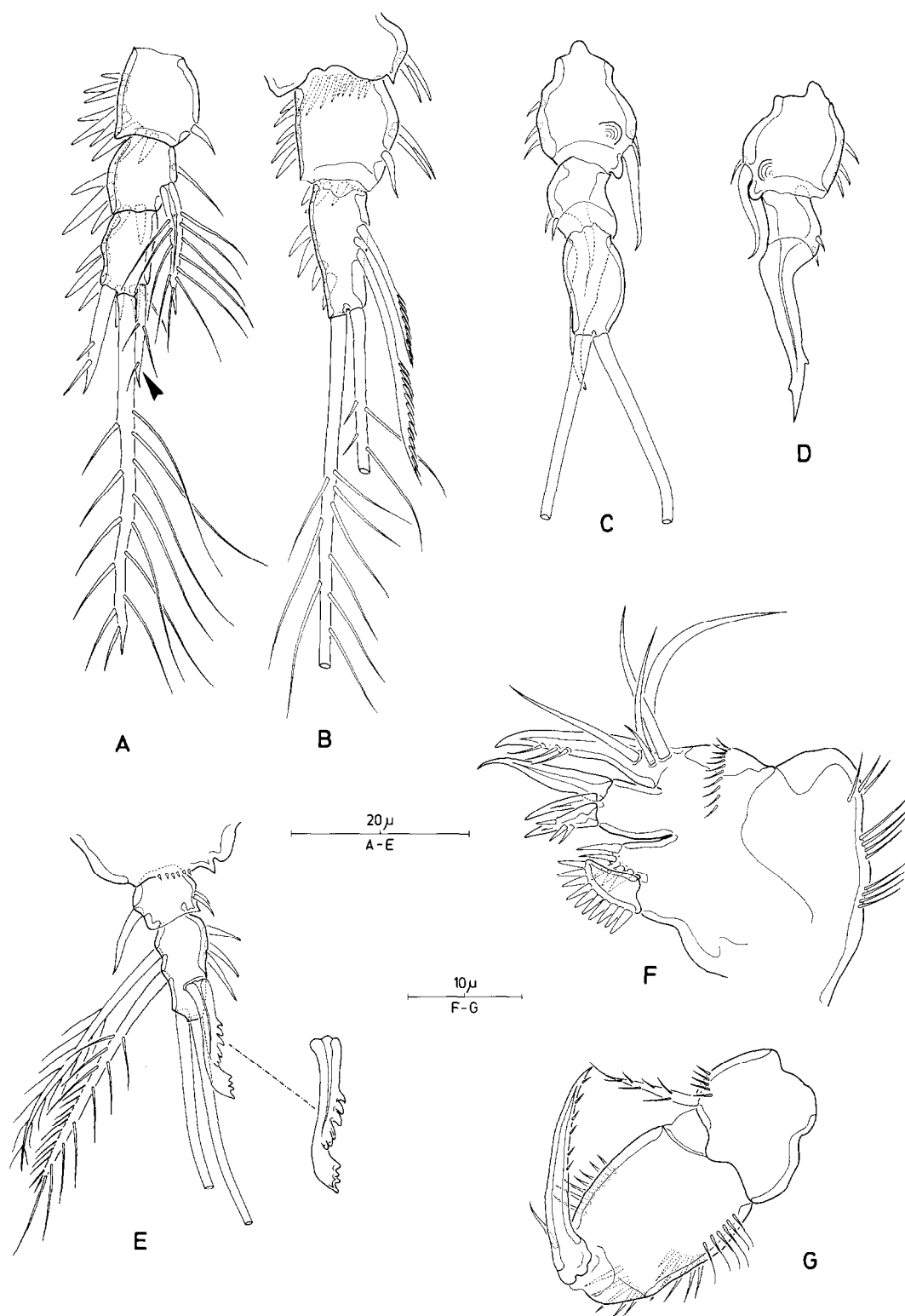


Fig. 6. *Bathycampus eckmani* gen. et spec. nov. A. Endopod P1, male (arrow indicates sexually dimorphic spine); B. Endopod P1, male; C. Endopod P3, male; D. Endopod P3, distal segment omitted, male; E. Endopod P4, male; F. Maxilla; G. Maxilliped.

setae, being serrate along the distal half; outer margin with some strong spinules; distal margin with 2 slender bipinnate setae.

*P3* (Figs. 6C, D) as in female except for the 3-segmented endopod. Proximal endopod segment with a short inner seta and a distinct process on the posterior surface; segment 2 without setae but forming an anterior apophysis extending beyond segment 3, having a small hook on both inner and outer edges; segment 3 with 2 plumose setae distally.

*P4* (Fig. 6E) as in female except for the endopod. Proximal endopod segment wider than long, furnished with a stout inner seta; distal segment with 2 plumose inner setae, 2 distal setae and 1 modified outer spine which is pectinate along the outer margin.

*P5* (Figs. 7B, C; 9D). Fifth pair of legs fused in the middle; baseoendopod and exopod forming a common plate; exopodal lobe with 2 minute outer setae and 3 pinnate spines; endopodal lobe with a short unipinnate outer spine and a long bipinnate inner one.

*P6* (Figs. 7B; 9D) fused with ventrall wall of somite; represented by a minute lobe bearing 1 minute seta.

*Etymology.* – The species is named for Dr. James E. Eckman who was instrumental in its collection.

*Bathycamptus minutus* (Wells, 1965) *comb. nov.*

*Synonymy.* ?*Heteropsyllus minutus* n.sp.

Wells (1965): p. 24–26; Figs. 78–85.

*Type material.* Holotype male deposited as a squash preparation in the British Museum (Natural History), London, no. 1954.3.26.14. Remounted in lactophenol and sealed with glyceel by the first author.

*Type locality.* Fladen Ground (northern North Sea), roughly 100 miles north-east by east of Aberdeen (58°20' N, 00°30' E) and at a depth of 146 m (coll. A. D. McIntyre; 19 January 1962). The sediment is a detritus-rich, greenish-grey mud.

### *Redescription.*

As the holotype was not well preserved, only a brief redescription is given.

### *Male*

Body length 320  $\mu$ m according to Wells (1965, p. 24). Ornamentation of urosome basically as in *B. eckmani*. Caudal rami (Fig. 11B) about 3.3 times as long as wide, slightly tapering distally; inner distal margin furnished with a row of long spinules; rear edge armed with 3 strong spinules; bearing 6 setae (I absent), anterolateral (II) and posterolateral (III) setae slender and dorsally displaced, outer (IV) and inner terminal (V) setae well developed and spinulose along the middle part, terminal accessory seta (VI) short, dorsal seta (VII) bi-articulated at the base.

*Antennula* (Fig. 11C) 7-segmented, haplocerate; first segment with some spinular rows along the inner margin; segment 2 furnished with 6 slender setae (one being bifid at the tip) and 2 unipinnate spines; segment 3 armed with 2 setae and 1 unipinnate spine; inner margin of fourth segment bearing 1 stout spine, 2 setae and a small rounded process, subdistal corner with 2 slender setae and a very long aesthetasc; haplocerate apparatus (segments 5 and 6) as in *B. eckmani*; distal segment with 9 setae and a short aesthetasc.

*Antenna* and other cephalosomic appendages exactly as in *B. eckmani*.

*P1* (Fig. 10A) as in *B. eckmani*. It is not clear whether the inner seta of the distal endopod segment is sexually dimorphic or not.

*P2* (Fig. 10B). Protopod and exopod as in *B. eckmani*. Endopod 2-segmented; proximal segment with a minute inner seta covered by some long spinules; distal segment with an inner seta whose inner edge is minutely pectinate along its distal half, 2 slender plumose setae and 1 unipinnate spine at the apex, and a hook-shaped process and some strong spinules along the outer margin.

*P3* (Fig. 10C). Exopod segments 1 and 2 with a strongly developed thorn at the outer distal corner; distal exopod segment with 2 outer bipinnate spines, 1 apical and 3 inner plumose setae. Endopod 3-segmented; segment 1 with one well-

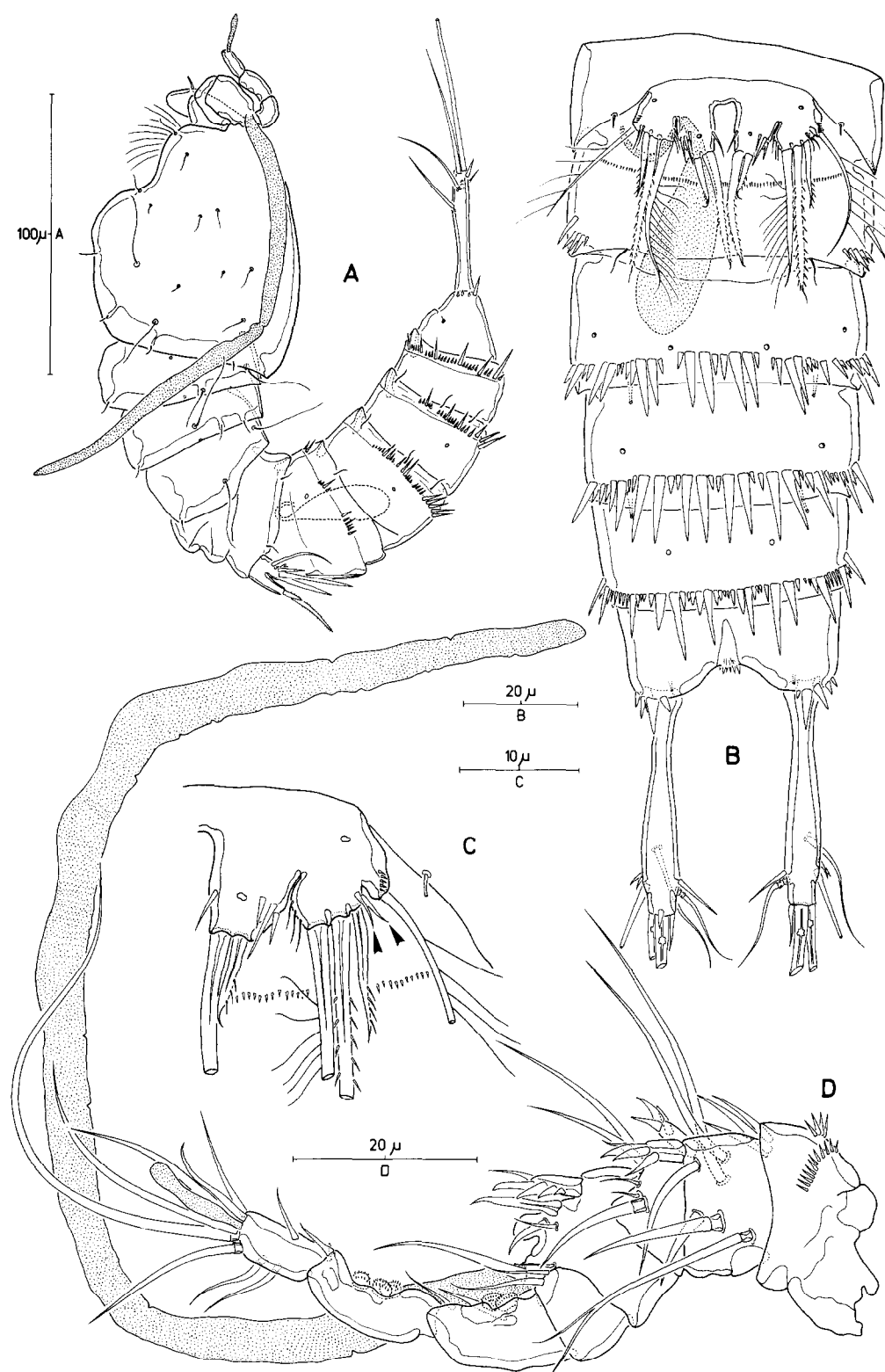


Fig. 7. *Bathycamptus eckmani* gen. et spec. nov., male. A. Habitus, lateral view; B. Urosome, ventral view; C. P5, arrows indicate 2 minute setae; D. Antennula.

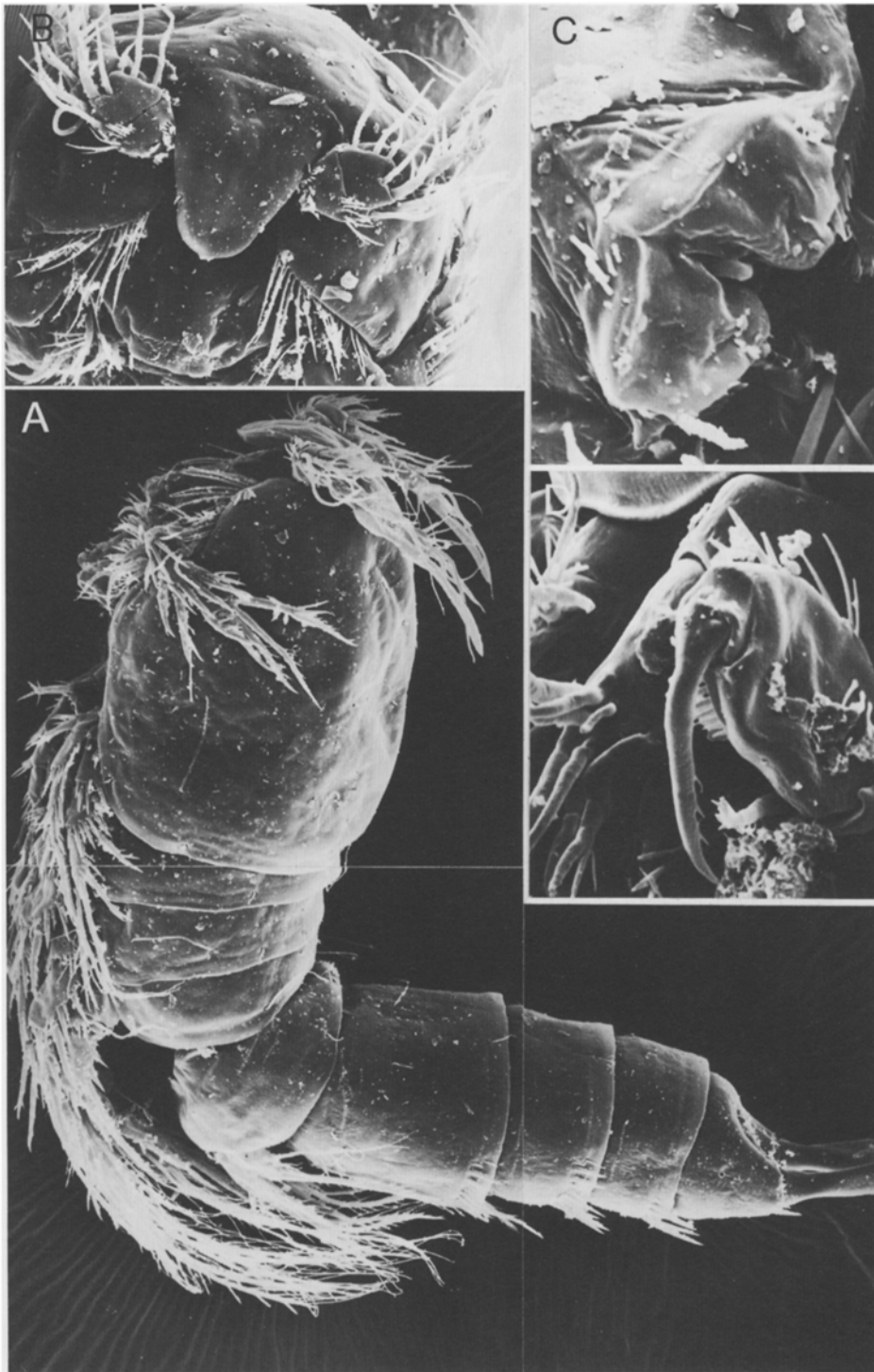


Fig. 8. *Bathycampus eckmani* gen. et spec. nov. (SEM-photography). A. Female, lateral view; B. Anterior view of female cephalothorax showing rostrum and antennulae; C. Labrum; D. Maxilla and maxilliped.

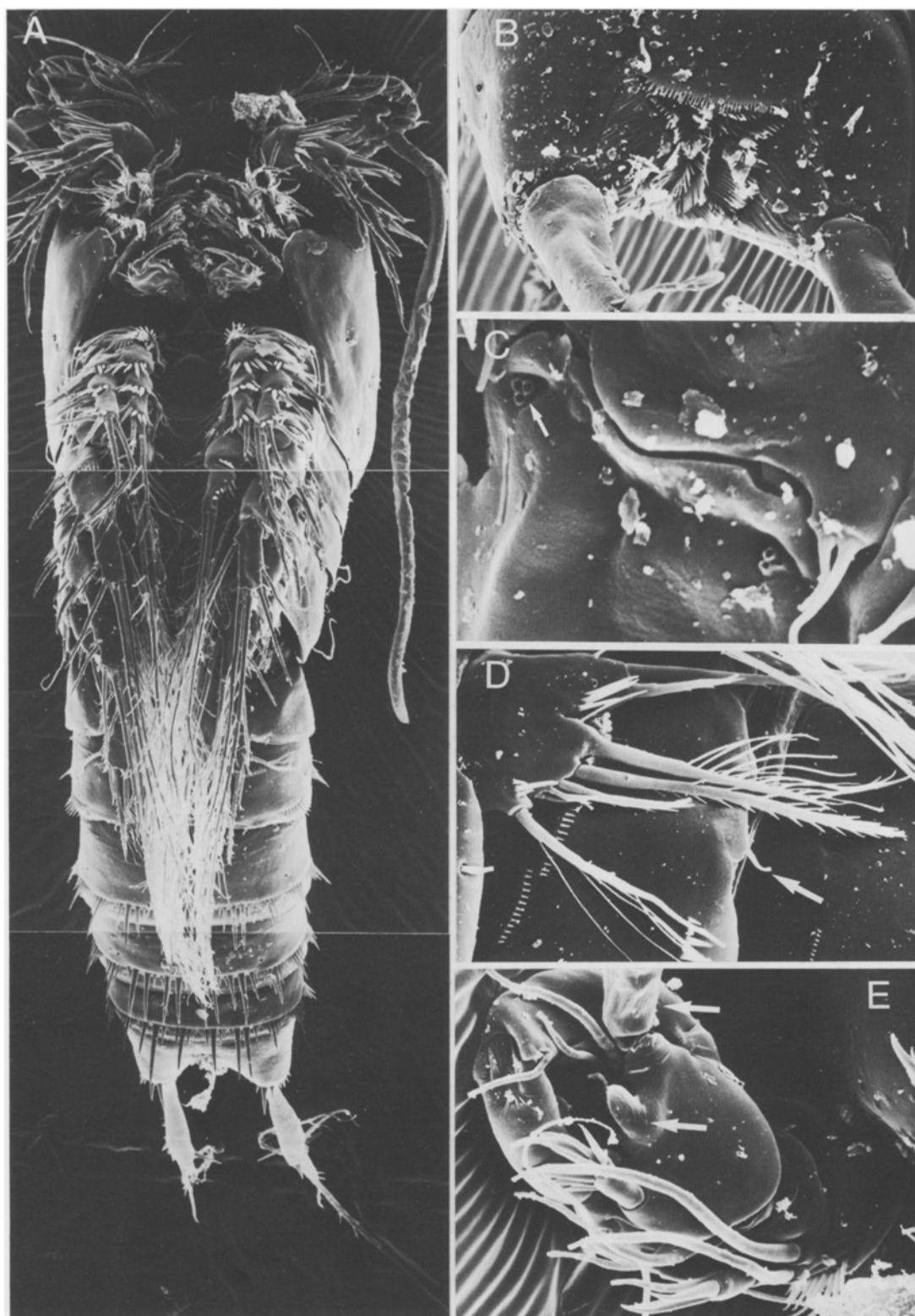


Fig. 9. *Bathycampus eckmani* gen. et spec. nov. (SEM-photography). A. Male, ventral view; B. Posterior view of anal somite; C. Genital apertures and P6 of female, arrow indicates set of 3 pores; D. P5 and P6 (arrowed) of male; E. Distal part of male antennula, arrows indicate process and aesthetasc on segment 4.

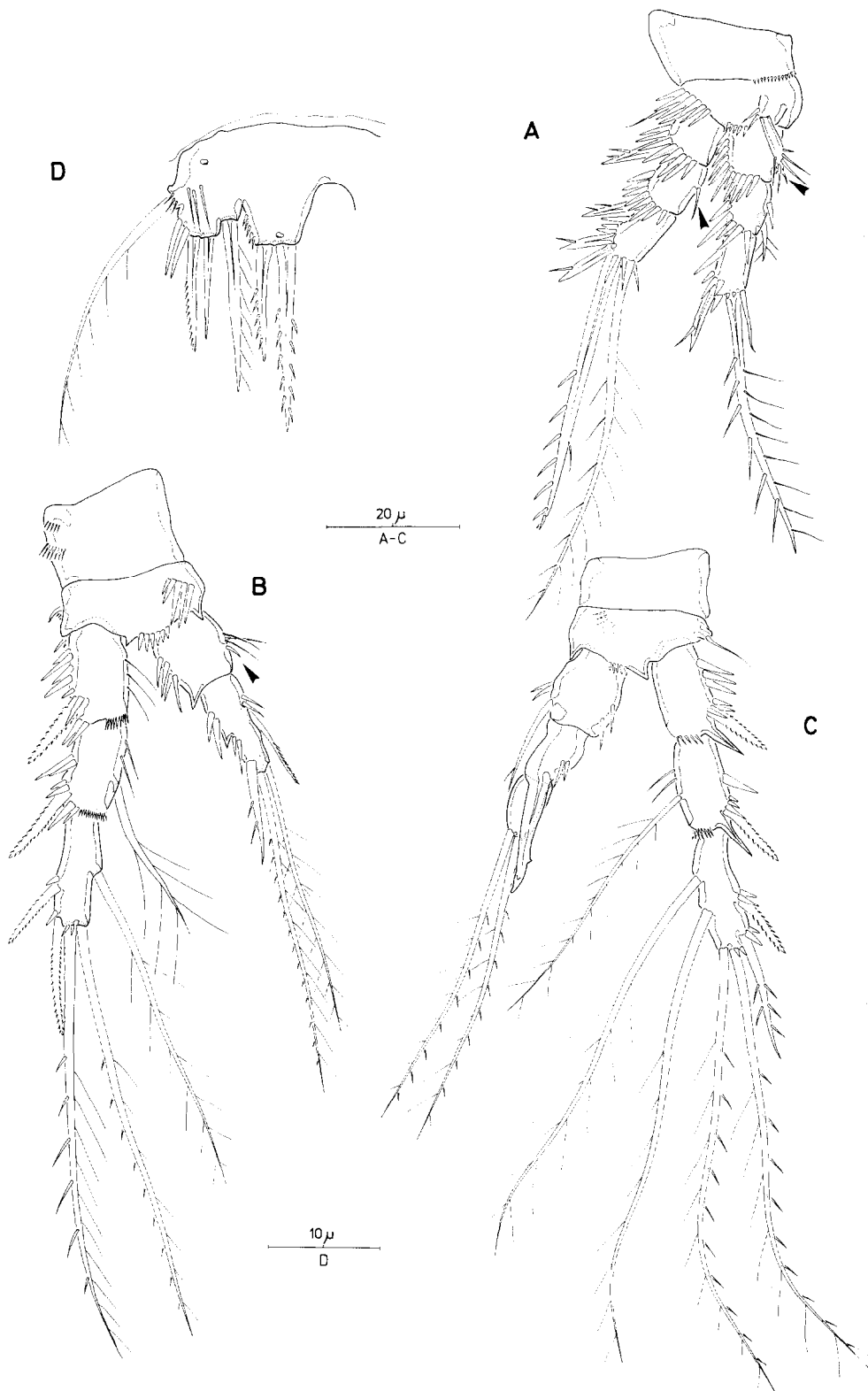


Fig. 10. *Bathycamptus minutus* (Wells, 1965) comb. nov., male (arrows indicate minute setae). A. P1; B. P2; C. P3; D. P5.

developed inner seta; segment 2 bearing a long apophysis anteriorly; segment 3 with 2 plumose setae at the tip.

*P4* (Fig. 11A). Exopod segments 1 and 2 as in preceding leg; segment 3 with 2 outer bipinnate spines, 1 apical and 3 inner plumose setae. Endopod 2-segmented; segment 1 with a long plumose inner seta; segment 2 with 4 plumose setae and a strong modified spine which is pectinate along the distal outer half.

*P5* (Fig. 10D). Fifth pair of legs fused in the middle; baseoendopod and exopod forming a common plate. Endopodal lobe furnished with 2 bipinnate spines; expodal lobe bearing 2 small spiniform outer setae and 3 spines of different lengths.

*P6* fused with ventral wall of somite; represented by a minute lobe bearing 1 minute seta.

#### Female

Unknown.

#### Discussion

*Bathycamptus eckmani* gen. et spec. nov. agrees in many ways with the description of ?*Heteropsyllus minutus* given by Wells (1965) and based on a single male collected in deep mud of the Fladen Ground area, Scotland. This presumed close relationship was corroborated by re-examination of the holotype of ?*H. minutus*, which, in spite of being badly preserved, revealed not only a bisetose exopod on the antenna but also complete agreement in the detailed structure of the other cephalosomic appendages, which were not figured in the original description. Other similarities include the presence of minute inner setae on the proximal endopod segments of P1–P2, the middle exopod segment of P1 and the antennal allobasis (Wells drew only a long spinule; see Fig. 79, p. 25), and the setal arrangement of the male P5. The strongest affinities however, lie in the conspicuous sexual dimorphism in the endopod P2–P4. On the basis of this unique combination of shared characters, we assign Wells' specimen to the genus *Bathycamptus*, thus constituting the second

member of the genus: *B. minutus* (Wells, 1965) comb. nov. The inner seta of the distal endopod segment of leg 1 in male *B. minutus* may also exhibit sexual dimorphism as in the type species; this, however, cannot be confirmed until the adult female is obtained. Distinguishing characters include the number of antennular segments in the male (segments 4 and 5 fused in *B. minutus*), the length: width ratio of the caudal rami, the number of outer spines on the distal exopod segments of P3 and P4, and the configuration of the endopod of the male P2.

Wells (1965) provisionally placed the species in the genus *Heteropsyllus* T. Scott because of the three-segmented nature of the endopod P1, but he retained considerable reservations about its true position. Bodin (1979), in his catalogue, considered ?*H. minutus* a *species incertae sedis* within the genus, whilst Coull (1975) and Coull & Palmer (1980) omitted the species in their respective species-keys. *Heteropsyllus* species typically have short 5-segmented antennulae in the female (with all setae slender and evenly tapering, none of them being of the 'pineapple-type'), 3–4 setae on the antennal exopod and a genital complex quite distinct from that found in *Bathycamptus* (see e.g. Soyer, 1975). Males have a well-developed plate-like P6 with 2 or 3 setae, a subchirocerate antennula with a short aesthetasc, and sexual dimorphism only in the endopod of P3 (*meridionalis*, *confluens*, *major*, *rostratus*, *masculus*), the latter, however, not being comparable to the *Bathycamptus* type (Klie, 1950; Por, 1964a; Bodin, 1970; Soyer, 1975). Some species (*nanus*, *nunni*, *pseudonunni*) have even been reported to lack sexual dimorphism on all the swimming legs (Wells, 1965; Coull, 1975; Coull & Palmer, 1980), a condition quite different from *Bathycamptus*.

The reason why the position of ?*H. minutus* has puzzled Wells (1965) and subsequent workers becomes clear when one considers the weakly defined boundaries of both the Canthocamptidae and the Cletodidae and of their respective genera. The resulting taxonomic chaos is best demonstrated by the reallocation of numerous cletodid genera to the Canthocamptidae (Por, 1986), and the issue is even more complicated at the species



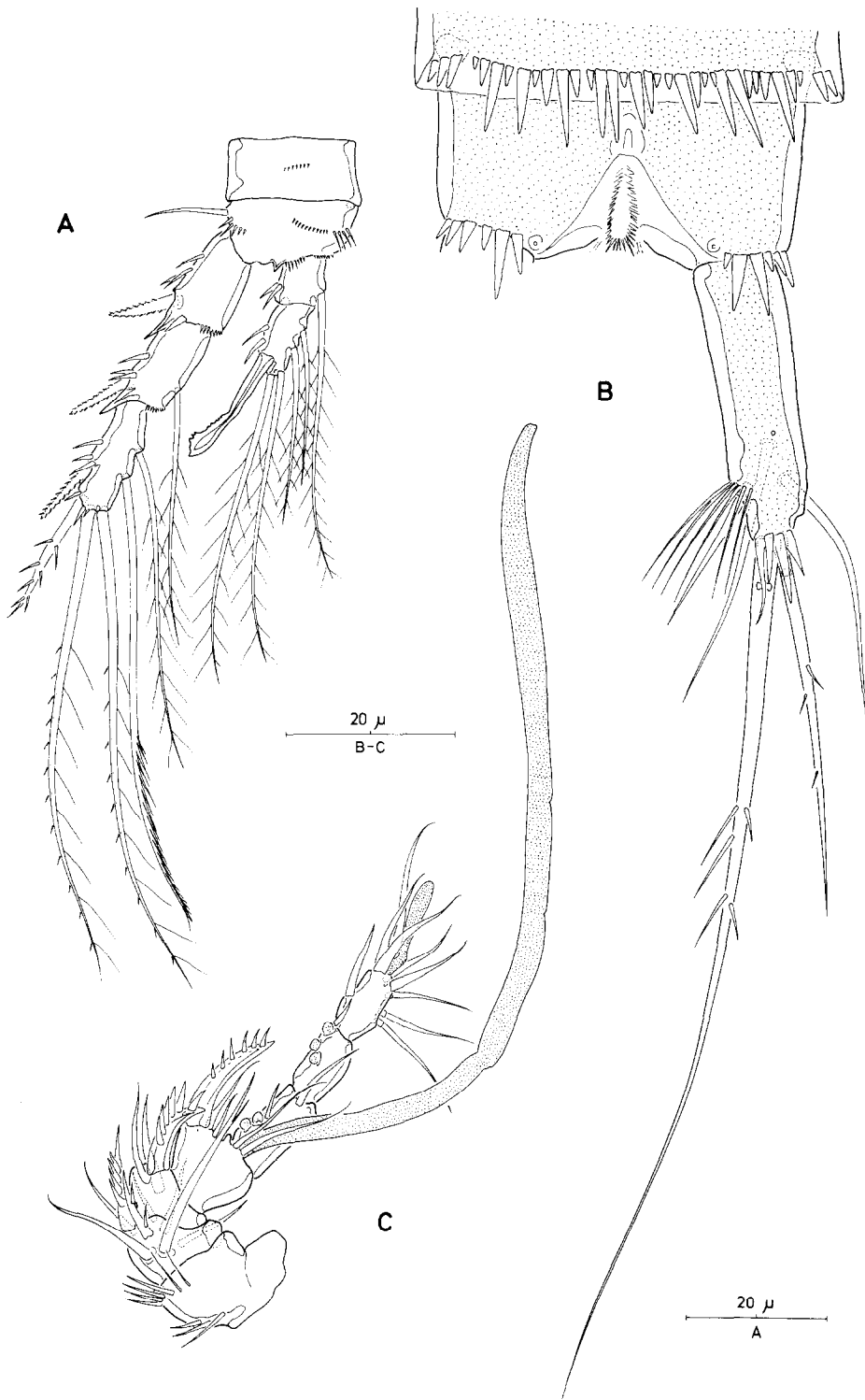


Fig. 11. *Bathycamptus minutus* (Wells, 1965) comb. nov., male. A. P4; B. Anal somite and caudal ramus, ventral view; C. Antennula.

level. For example, the cletodid genus *Hemimesochra* Sars has often been regarded as a missing link between both families (e.g. Por, 1964a), and more recently this idea has even led to the establishment of the new subfamily Hemimesochrinae within the Canthocamptidae (Por, 1986). However, the genus in itself is nothing more than a heterogeneous grouping of weakly related species (see below), linked by a generic diagnosis that had to be altered whenever new species were discovered (Por, 1964a–b; Lang, 1965; Wells, 1965; Coull, 1973; Becker, 1979). We feel that Por's (1986) proposal to dismantle the artificial Cletodidae *sensu* Lang is certainly a step in the right direction, but it is wrong to state that '...the limits of generic variability within the Cletodidae, and the notion of genus itself, have to be taken in a much wider sense than in any other harpacticoid family' (Por, 1968).

Wells (1965) placed ?*H. minutus* in the Cletodidae on the basis of the antennula with its plumose setae on the proximal part, the structure of the maxilliped, and the configuration of P2 to P4. He further excluded the possibility of a canthocamptid relationship, though the combination of the above characters is found in this family as well. Indeed, using the family keys of Lang (1948) and Wells (1976), *Bathycamptus* leads to the Canthocamptidae. Both authors have had to let the family come up several times in each of the keys (a problem inherent in poorly diagnosed taxa). It is clear that *Bathycamptus* shows more affinities to the marine Canthocamptidae than to the typical freshwater genera from which it differs in, amongst other features, the absence of a dorsal nuchal organ, the structure of the genital complex, and the short antennulae. Therefore, the discussion of relationships will be restricted to a particular group of canthocamptid genera (in fact the 'partim' to which *Bathycamptus* keyed out) and to a few others (*ex* Cletodidae) recently allocated to the Canthocamptidae (Por, 1986). These are: *Mesochra* Boeck, *Orthopsyllus* Brady & Robertson, *Itunella* Brady, *Nannomesochra* Gurney, *Pholetiscus* Humes, *Ophirion* Por, *Psammocamptus* Mielke, *Mesopsyllus* Por, *Poria* Lang and *Hemimesochra* (part.).

## Relationships with Langian marine Canthocamptidae

Although the detailed structure of *Orthopsyllus* is well known (Lang, 1965; Wells, 1968; Hamond, 1970), there is neither any agreement as to how many valid species it contains, nor any as to which other genera are its closest relations, although our findings indicate that it has few affinities with *Bathycamptus* and even fewer with any of the genera which have from time to time been assigned either to the Canthocamptidae or the Cletodidae (Sars, 1911, 1920; Lang, 1948). Both genera share a 1-segmented antennal exopod and sexual dimorphism in leg 3, but the resemblance does not go much further. In particular, the dentiform process on the 2nd antennular segment, the subchirocerate nature of the male antennula, the structure of P1 and P5 (in both sexes), the sexual dimorphism in the swimming legs, and the structure of the genital complex in the female are conspicuous characters of *Orthopsyllus* which clearly differentiate it from *Bathycamptus*.

*Nannomesochra* is reminiscent of *Bathycamptus* in the 7-segmented antennula in the female, the antennal allobasis with a 1-segmented bisetose exopod, and in the segmentation of the swimming legs (Lang, 1948; Petkovski & Apostolov, 1974). However, *Nannomesochra* is easily distinguished from the new genus by its lack of a mandibular exopod, the small rostrum, the enlarged proximal endopod segment of P1, the fifth pair of legs with medially fused baseoendopods, and by the short caudal rami which are wider than long. Males exhibit sexual dimorphism only in leg 3, but here the endopod remains 2-segmented (instead of 3-segmented in *Bathycamptus*) with a modified seta on the distal segment (Lang, 1948; Noodt, 1953).

The monotypic genus *Ophirion* resembles *Bathycamptus* in the presence of the broad rostrum, the short antennulae with pinnate setae in the female (but smooth in the male), the detailed morphology of the genital complex, and in the long caudal rami (Por, 1967). Males of both genera exhibit exactly the same modification in the endo-

pod of P3, but those of *Ophirion* lack sexual dimorphism on the other swimming legs. Both sexes share a 6-segmented antennula, which is subchirocerate in the male. In addition to the anal operculum with long spinules, *Ophirion* can be distinguished also on the basis of the 2-segmented endopod of P1, the lack of a mandibular exopod, and the presence of 3 setae on the unisegmented exopod of the antenna.

*Pholetiscus*, living in the branchial chambers of semiterrestrial crabs (*Sesarma*), and originally assigned to the Ameiridae (Humes, 1947; 1956) has only few characters in common with *Bathycamptus*, viz. the 2-segmented nature of the endopods P2–P4 and the similar sexual dimorphism in leg 3. Clear differences are found in the antennula (6–8 segments; no pinnate setae), antenna (1-segmented exopod with 1 seta), mandible (palp represented by 3 setae), P1 (2-segmented; proximal segment elongated), P5, genital complex, and in the configuration of the caudal rami.

The world-wide genus *Mesochra* is clearly in need of a thorough revision (Hamond, 1971), and consequently it is not easy to find well-defined characters common to all species. *Mesochra* females all exhibit the 2-segmented condition in the endopods of P2–P4, whilst the male P3 basically shows the same sexual dimorphism as in *Bathycamptus*, viz. endopod 3-segmented with an apophysis on the 2nd segment and 2 setae on the 3rd segment (these segments can fuse secondarily in, for instance, *M. inconspicua*; Mielke, 1975). This character together with the detailed structure of the male antennula (haplocerate apparatus with spherical modified setae; see e.g. *M. baylyi* Hamond, 1971) clearly relate *Mesochra* to the new genus, yet the antennal exopod with 3–4 setae, the elongated 2- or 3-segmented endopod of P1 with geniculate setae, and the lack of sexual dimorphism in P2 and P4, are clear differences.

*Itunella* and *Psammocamptus* are unusual in that they display sexual dimorphism in at least 2 pairs of swimming legs. Apart from the modified endopod of P3, members of *Itunella* exhibit also sexual dimorphism in P2 and P4 as illustrated in the excellent redescription of *I. muelleri* by Bodin (1973). The distal segment of the 2-segmented

endopod of P4 bears a strong modified spine, which is very similar to that found on the corresponding segment in *Bathycamptus*. In male *Itunella*, the 1-segmented endopod of P2 bears 4 setae instead of 3 in the female (Noodt, 1954; Apostolov, 1973, 1975; Bodin, 1973); in *Bathycamptus*, however, no sex-linked differences could be found in the number of setae in the endopod of P2. In addition to the general appearance, *Itunella* differs considerably in the endopodal segmentation of the swimming legs (P1 2-segmented; P2–P4 1-segmented), the uniramous mandibular palp, the setation of the antennal exopod (4 or 5 setae), the setation and segmentation of the P5 in both sexes, and in the nature of the caudal rami.

The interstitial genus *Psammocamptus*, obtained from the isle of Sylt (Mielke, 1975), is without doubt the closest relative of the new genus. *P. axi* displays exactly the same sexual dimorphism in P3–P4, and it also agrees well in the fine structure of the cephalosomic appendages. Both genera have a similar rostrum, a short antennula with pinnate spines, a robust antenna with a 1-segmented bisetose exopod and an endopod with numerous pinnate spines, and a biramous mandibular palp with the exopod represented by a pinnate spine. Other similarities include the fused rami of the 5th leg in both sexes, the 2-segmented endopods in P2–P4, and the 3-segmented rami of the P1 with the endopod neither being elongated nor bearing geniculate setae. *Psammocamptus* can be distinguished from *Bathycamptus* on the basis of the 6-segmented antennula in the female, the absence of sexual dimorphism in P1–P2, the setation of P1 (distal endopod segment with 2 setae, middle endopod segment without inner spine) and P2–P3 (middle exopod segment without inner seta). Dr. Wolfgang Mielke, University of Göttingen, was so kind as to re-examine the type material of *P. axi* in order to clarify a few minor differences: (1) the allobasis of the antenna bears a rudimentary seta as in *Bathycamptus*, (2) the proximal endopod segment of P1–P4 may have a minute inner seta but this is not clearly discernible, (3) the male endopod of P3 shows a reduced inner seta on the

proximal segment. As a result the generic diagnosis can be altered as follows:

***Psammocamptus* Mielke, 1975**

**Diagnosis.** – P1-bearing somite fused with cephalothorax. Anal operculum present, finely spinulose. Copulatory pore circular, conspicuous. Caudal rami twice as long as wide, furnished with 6 setae; outer and inner terminal setae well developed, anterolateral accessory seta absent.

Rostrum well developed, fused (?) with cephalothoracic shield. Antennula short, with pinnate spines; 6-segmented in female, furnished with aesthetasc on 4th segment; 7-segmented and haplocerate in male. Antennal exopod small with 2 setae; allobasis with minute proximal seta. Mandibular basis with 1 seta; endopod 1-segmented with 4 setae; exopod represented by 1 pinnate spine. Maxillula with well developed praecoxal arthrite; coxal epipodite absent; exopod and endopod represented by 1 and 2 setae, respectively. Maxillary syncoxa with 2 endites; endopod 1-segmented, not incorporated into basis. Maxilliped robust, prehensile; syncoxa with 1 seta, basis unarmed, endopod with claw only.

Leg 1 with both rami 3-segmented; endopod not prehensile or elongate, distal segment with 2 setae. P2–P4 with 3-segmented exopods and 2-segmented endopods in female; proximal endopod segment with inner seta dwarfed; middle exopod segment P2–P3 without inner seta; endopod P3 3-segmented in male. Baseoendopod and exopod P5 confluent in both sexes; exopodal and endopodal lobes in female with 3 and 4 setae; respectively; in male with 4 and 2 setae, respectively.

Sexual dimorphism in antennula, endopod P3–P4, fifth and sixth legs, and in genital segmentation.

Type species: *Psammocamptus axi* Mielke, 1975.

Other species: None.

**An analysis of the genus *Hemimesochra* sensu lato**

The genus *Hemimesochra* encompasses the following species: *H. clavularis* Sars, *H. nixe* Por, *H. nympha* Por, *H. secunda* Wells, *H. dubia* (Wells), *H. trisetosa* Coull and *H. rapiens* Becker. The incorporation of *Mesopsyllus atargatis* and *Hemimesochra derketo* by Por (1964a) was not well grounded (Lang, 1965). Becker (1972) analyzed the phylogenetic relationships within the genus and included ?*Leimia dubia* Wells (see also Becker, 1979).

The seven species can be distributed over the following genera.

***Boreolimella* gen. nov.**

**Diagnosis.** – P1-bearing somite fused with cephalothorax. Condition of anal operculum unknown. Copulatory pore circular, conspicuous. Caudal rami at least 3 times as long as wide, tapering posteriorly; furnished with 6 setae, outer and inner terminal setae well developed, anterolateral accessory seta absent.

Rostrum well developed, fused with the cephalothoracic shield. Antennula short, with pinnate spines; 5- (or 6-) segmented in female with aesthetasc on 3rd (or 4th) segment. Antenna with allobasis; exopod small, of one segment with 2 setae. Mandibular basis with 1 seta; endopod 1-segmented with 4 setae; exopod represented by 1 pinnate spine. Maxillary syncoxa with 2 endites, proximal endite with spinulose process and 1 pinnate claw; endopod incorporated into basis. Maxilliped robust, prehensile; basis not known to be armed.

Leg 1 with the 3-segmented exopod slightly longer than the 2-segmented endopod; neither ramus conspicuously elongated; inner seta of proximal endopod segment long, distal segment with 3 or 4 setae. P2 to P4 with 3-segmented exopods and 2-segmented endopods in female; proximal endopod segment with well-developed inner seta; middle exopod segment with inner seta. Baseoendopod and exopod of P5 confluent

in female; exopodal and endopodal lobes each with 4 setae.

*Male*: Unknown.

*Type species*: *Boreolimella nympha* (Por, 1964) comb. nov.

*Other species*: *B. dubia* (Wells, 1965) comb. nov.

*Etymology*. – The generic name is derived from the Latin *boreos*, meaning north, and *limus* meaning mud. Gender: feminine.

*Remarks*. – *Hemimesochra nympha* Por differs considerably from the type species *H. clavularis* Sars in the presence of (1) an antenna with allobasis and bisetose exopod, (2) strong pinnate spines on the antennula, (3) fused rami of P5, (4) the completely fused genital double somite. In addition to these characters, the robust mandibular palp with the exopod represented by a short stout spine in *nympha* (in contrast to the single slender seta in *clavularis*), the structure of the proximal maxillary endite, the obvious copulatory pore, the long caudal rami tapering posteriorly, the setation of the P5, and the genital double-somite with the ventral internal rib undoubtedly relate *H. nympha* to *Bathycamptus* and *Psammocamptus*. Using Lang's (1948) key, Wells (1965) placed ?*Leimia dubia*, although with hesitation, in the genus *Leimia* Willey on account of the possession of two outer setae on the distal exopod segments P2–P4 and of the fused character of the P5. At the same time, Wells (1965) recognized a certain affinity with *Hemimesochra*, whilst Bodin (1979) regarded the species as being a *Cletodidae incertae sedis*. Becker (1979) decided to allocate *L. dubia* to this genus. In his original thesis, Becker (1972) pointed out the striking similarity between *L. dubia* and *H. nympha*; he also mentioned the discrepancy between Wells' (1965) Fig. 96 and the setal formula of the P1. Clearly, both species have an inner seta on the middle exopod segments of P1, and they should be assigned to a separate genus closely related to *Bathycamptus*. *Boreolimella* gen. nov. can be differentiated from the latter in the 2-segmented endopod of P1, the well-

developed inner seta on the proximal endopod segment of P1 to P4, and the 5 (or 6-) segmented female antennula. Probably the discovery of the male will reveal more differences. There is no close relationship with *Leimia vaga* Willey.

*Perucamptus* gen. nov.

*Diagnosis*. – Body cylindrical, elongated. P1-bearing somite fused with cephalothorax. Abdominal somites without any ornamentation. Anal somite longest, anal operculum smooth. Caudal rami about 3 times as long as wide; furnished with 6 setae, anterolateral accessory seta absent, inner terminal seta strongly developed.

Rostrum well developed, defined at base. Antennula short, without pineapple-setae; 5-segmented in female with aesthetasc on 3rd segment. Antenna strong; allobasis with proximal seta; exopod 1-segmented and trisetose. Mandibular basis with 1 seta; endopod 1-segmented with 4 setae; exopod represented by 1 seta. Maxillula with well developed praecoxal arthritis; endopod and exopod very reduced. Maxillary syncoxa with 2 long endites; endopod incorporated into basis. Maxilliped robust, prehensile; syncoxa with 1 seta, basis unarmed; 1-segmented endopod with claw.

Leg 1 with 3-segmented exopod and 2-segmented endopod; exopod without inner setae; endopod not elongated or prehensile, proximal segment with well developed inner seta. P2 to P4 with 3-segmented exopod, proximal segment without and middle segment with inner seta. Endopods of P2 and P3 2-segmented, proximal segment without inner seta; endopod of P4 absent. P5 rudimentary; basal and exopodal setae laterally displaced; endopodal lobes vestigial, medially located and bisetose.

*Male*: Unknown.

*Type species*: *Perucamptus rapiens* (Becker, 1979). comb. nov.

*Other species*: None.

*Etymology*. – The generic name is derived from the country name *Peru*, referring to the type locality in

the Peru Trench, and from the Greek *kamptos*, meaning flexible. Gender: masculine.

**Remarks.** – There can be no doubt that *Hemimesochra rapiens* has no relationships with either the other species of the genus or with *Bathycamptus*. *Perucamptus* gen. nov. is clearly distinct in general habitus, the loss of the endopod of P4, the vestigial P5, the cylindrical maxillary endites, the absence of pineapple-setae in the antennula, and the smooth abdominal somites and anal operculum. On the basis of this complex suite of characters, it is not even possible to consider *H. rapiens* as an advanced member within the genus as Becker (1972, 1979) supposed. Por (1986) rightly removed the species from the genus *Hemimesochra* and considered it *incertae sedis* within the Canthocamptidae.

***Carolinicola* gen. nov.**

**Diagnosis.** – Body slightly tapering posteriorly; P1-bearing somite fused with cephalothorax. Caudal rami as long as wide, bearing 6 setae; anterolateral accessory seta absent; anterolateral, posterolateral and dorsal setae plumose.

Rostrum broadly rounded, defined at base. Antennula short, with pinnate spines; 5-segmented in female with aesthetascs on 3rd and 5th segments. Antennal exopod 1-segmented with 3 setae; allobasis with strong proximal seta; endopod with pinnate spines. Mandibular palp biramous; basis with 3 setae; endopod with 6 setae; 1-segmented exopod with 4 setae. Maxillula with exo- and endopod incorporated into basis. Maxillary with 2 endites; endopod fused with basis. Maxilliped robust, prehensile; syncoxa with 1 seta, basis unarmed; endopod with pinnate claw (and 1 seta?).

Swimming legs with 3-segmented exopods and 2-segmented endopods. P1 without inner seta on middle exopod segment; endopod not elongated, without geniculate setae on distal segment. P2 to P4 without geniculate setae on distal segment. P2 to P4 without inner seta on proximal exopod segment; proximal endopod segment with well-

developed inner seta. Baseoendopod and exopod forming a common plate; exopodal and endopodal lobes with 4 and 5 setae, respectively.

**Male:** Unknown.

**Type species:** *Carolinicola trisetosa* (Coull, 1973) comb. nov.

**Other species:** None.

**Etymology.** – The generic name is derived from *Carolina*, referring to the type locality in the deep sea off North Carolina, and from the Latin *colere*, meaning to dwell. Gender: feminine.

**Remarks.** – The exact taxonomic position of *Hemimesochra trisetosa* is difficult to decide because of the unknown male. It is nevertheless clear that the species cannot fit well in the generic diagnosis of *Hemimesochra* as defined by Sars (1920) and Lang (1948) because of the mandibular palp with 3 setae on the basis, a well defined exopod with 2 inner and 2 terminal setae and an endopod with both a lateral and an apical group of setae. Such a primitive palp is highly unusual even within the Langian Cletodidae and Canthocamptidae. The antenna of *C. trisetosa*, with an allobasis having a large, proximally inserted, abexopodal seta bearing limp pinnules, differs markedly from that of *H. clavularis* in which the asetose basis is clearly demarcated from the proximal endopod segment, which bears a small seta with short stiff pinnules. The separate status is further also corroborated by the enormous rostrum, the caudal rami with plumose setae and by the short maxilliped with a strong pinnate spine on the syncoxa. All these characters give indication that *H. trisetora* is related to the genera *Paranannopus* Lang and *Cylindronannopus* Coull, which were removed from the Cletodidae and placed rightly in a separate family Paranannopidae by Por (1986). *Carolinicola* gen. nov. can be considered an advanced member of the Paranannopidae because of certain reductions in the cephalic appendages (e.g. the antennal exopod).

*Hemimesochra secunda* is distinct in the possession of a rounded rostrum with a setose apical border. As pointed out by Lang (1965), this character is also found in the monotypic genus

*Mesopsyllus* and allows differentiation of both genera. The 6-segmented antennula with strong pinnate spines, an aesthetasc on the 4th segment and a very long distal segment is also shared by *M. atargatis*. Both species also agree in the nature of the P5, viz. with a small exopod and the outermost seta of the endopodal lobe located near the articulation of the exopod. Furthermore, there is a high similarity in the swimming legs. P3 and P4 have exactly the same setal formula. The inner seta of the proximal endopod segment of P2 is dwarfed in *H. secunda* and for that reason apparently overlooked in the description of *M. atargatis* as Lang (1965) already suspected. The main difference between both species is found in the segmentation of leg 1. In *H. secunda*, the endopod is 2-segmented with 4 setae on the distal segment reflecting the 3-segmented condition (with 1 inner seta on segment 2 and 3 setae on segment 3) exhibited by *M. atargatis*. Both species share a well-developed inner seta on the middle exopod segment of P1. On the basis of these characters, it is clear that *H. secunda* should be transferred to *Mesopsyllus*, thus constituting the second member of the genus, *M. secundus* (Wells, 1965) comb. nov.

According to Por (1960) the antennal exopod is absent in *Mesopsyllus* and the mandibular palp exhibits only an exopod. The latter statement is without doubt wrong as an evolutionary loss of the mandibular endopod is without exception preceded by that of the exopod. Unfortunately neither Por (1960) nor Wells (1965) figured the mandible. The presence of a small bisetose exopod on the antenna in *M. secundus* suggests that it may have been overlooked in the type species.

*Mesopsyllus atargatis* Por is reminiscent of *Bathycampus* in the segmentation of P2–P4, the short antennula with strong pinnate spines, the antenna with allobasis and bisetose exopod, the sexual dimorphism in endopod of P3, and in the long caudal rami. The 6-segmented female antennula, the setulose rostrum, the free rami of the P5 in both sexes, and the absence of sexual dimorphism in P2 and P4 are good differentiating characters and moreover, make it impossible to remove *M. atargatis* to *Hemimesochra* as Por

(1964a) suggested; this view was rightly discounted by Lang (1965).

The generic diagnosis as defined by Lang (1965), can be amended as follows:

### *Mesopsyllus* Por, 1960

**Diagnosis.** – Body slightly tapering posteriorly; P1-bearing somite fused with cephalothorax. Caudal rami at least 2 times as long as wide, bearing 6 setae; anterolateral accessory seta absent; outer and inner terminal setae well developed.

Rostrum rounded, defined at base, anterior border setose. Antennula short, with pinnate spines; 6-segmented in female with aesthetasc on 4th segment; haplocerate in male. Antennal exopod 1-segmented with 2 setae; allobasis without strong proximal seta; endopod with pinnate spines. Mandibular palp uniramous (?); exopod absent (?). Maxillula with exo- and endopod incorporated into basis. Maxilla with 2 endites on syncoxa. Maxilliped robust, prehensile.

Leg 1 with 3-segmented exopod and 3-(or 2-)segmented endopod; with inner seta on middle exopod segment; endopod not elongated, without geniculate setae on distal segment. P2–P4 with 3-segmented exopods and 2-segmented endopods; without inner seta on proximal exopod segment; proximal endopod segment with inner seta, dwarfed in P2. Baseoendopod and exopod not fused; exopodal and endopodal lobes with 4–5 setae in female. Male baseoendopod with 2 setae, exopod with 4 setae. Genital complex unknown.

Sexual dimorphism in antennula, endopod of P3 (middle segment forming apophysis), P5, P6, and in genital segmentation.

**Type species:** *Mesopsyllus atargatis* Por, 1969

**Other species:** *M. secundus* (Wells, 1965) comb. nov.

Of the remaining two species the type species *H. clavularis* stands apart because of the small rostrum which is deflexed and not defined at the base, the antennula with pectinate setae, the antenna with a basis and a trisetose exopod, and

the mandible with 4 setae on the endopod and a vestigial exopod represented by 1 seta. These characters served Lang (1965) to distinguish *Hemimesochra* from *Poria* and *Mesopsyllus*. In *H. nixe*, the rostrum is broad and defined at base, the 5-segmented antennula is furnished with slender non-pectinate setae, the antenna has an allobasis with a bisetose exopod, and the mandibular endopod has 3 setae and the exopod is represented by 2 setae. *H. clavularis* has an inner seta on the first antennal endopod segment, but in *H. nixe* the inner seta on the allobasis is without doubt basal in origin. Sars (1920) described the female P5 of *H. clavularis* with separate baseoendopod and exopod but according to Por (1964a) these are fused; in *H. nixe* the rami are also separate. The latter species differs also in the P1 by the presence of an inner seta on the middle exopod segment and 4 setae on the distal endopod segment (the inner seta indicating a 3-segmented ancestral condition). On the basis of all these differences, it seems appropriate to remove *H. nixe* from *Hemimesochra* and to place it in a new genus that exhibits a sexual dimorphism of the endopod of P3 distinct from that in *Bathycamptus*.

### *Pusillargillus* gen. nov.

**Diagnosis.** – Body slightly tapering posteriorly; P1-bearing somite fused with cephalothorax. Caudal rami as long as wide, bearing 6 setae; anterolateral accessory seta absent; inner terminal seta strongest developed.

Rostrum broadly triangular, defined at base,. Antennula short, without pinnate spines or setae; 5-segmented in female with aesthetasc on 3rd segment; haplocerate in male. Antennal exopod 1-segmented with 2 setae; allobasis with proximal seta. Mandibular palp biramous; basis with 1 seta; endopod with 3 setae; exopod represented by 2 setae. Maxillula with exopod and endopod incorporated into basis. Maxilla with 2 endites, proximal endite with claw; endopod fused with basis. Maxilliped robust, prehensile; syncoxa with 1 seta, basis unarmed; endopod with claw.

Swimming legs with 3-segmented exopods and 2-segmented endopods. P1 with inner seta on middle exopod segment; endopod not elongated, with 4 non-geniculate setae on distal segment. P2 to P4 without an inner seta on the proximal exopod segment; proximal endopod segment with well-developed inner seta. Baseoendopod and exopod of P5 not fused; exopod with 5 setae in both sexes; endopodal lobe with 4 setae in the female, and 2 setae in the male.

Sexual dimorphism in antennula, endopod P3 (2-segmented, distal segment forming into apical apophysis), P5, P6, and in genital segmentation.

**Type species:** *Pusillargillus nixe* (Por, 1964) comb. nov.

**Other species:** None.

**Etymology.** – The generic name is derived from the Latin *pusillus*, meaning very small, and *argilla*, meaning clay. Gender: masculine.

The genus *Poria* was established by Lang (1965) to include *Hemimesochra derketo* Por. Similarities with *Bathycamptus* are found only in the antenna with pinnate spines and bisetose exopod, and in the unmodified P1. However, the three-segmented nature of the endopod of P1 to P3, the big rostrum reaching to the end of the 3rd antennular segment, the short caudal rami, the absence of pinnate spines on the antenna, and the free exopod of the female P5, both clearly differentiate *Poria* from *Pusillargillus*. Because of the similar segmentation and setation of P1 to P4, it is possible that the female specimen described as '*Cletodidae sp. indet.*' by Wells (1965) is closely related to *P. derketo*. Unfortunately the lack of information on the mouthparts and the genital complex in both species (Por, 1964b; Wells, 1965) does not allow a careful comparison which would make possible a correct assessment of their taxonomic position.

### General conclusions

Despite the taxonomic chaos, it is clear that the genera *Bathycamptus* gen. nov., *Psammocamptus* and *Boreolimella* gen. nov. constitute a homo-



genous group of small-sized (less than 0.50 mm) mud-dwelling copepods. These genera are phylogenetically related on the basis of the reduced mandibular palp with the exopod represented by a short pinnate spine, the fusion of the rami in the P5, the conspicuous copulatory pore, the medial fusion of the genital pores and the broad rostrum fused with the cephalosome. *Bathycamptus* gen. nov. and *Psammocamptus* are considered sistergroups because of the shared sexual dimorphism on the endopod of P4 and the long aesthetasc on the male antennula. The sexually dimorphic leg 2 and probably leg 1 are apomorphies for *Bathycamptus* gen. nov., whilst *Psammocamptus* can be defined on the basis of the 6-segmented antennula in the female, the presence of 2 setae on the distal endopod segment of P1 and the loss of the inner seta on the middle exopod segment of P1 to P3 (dwarfed in P4). Because information on the male is at present not available, *Boreolimella* gen. nov. is tentatively regarded as the sistergroup of the *Bathycamptus*-*Psammocamptus* lineage. The 2-segmented endopod of P1 is a clear apomorphy for the genus.

A possible outgroup for these genera might be *Mesopsyllus* because it shares the sexual dimorphism on leg 3, the pinnate spines on the antennula, and the antennal allobasis with bisetose exopod. However, no information is available on either the genital complex or the other cephalosomic appendages, and pending this we can consider it only as a potential relative of the genus-group mentioned above.

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