



## ***Bathylaophonte* gen. nov. from deep-sea hydrothermal vents and the polyphyly of *Paronychocamptus* (Copepoda: Harpacticoida)**

Wonchoel LEE and Rony HUYS

*Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*

**Abstract:** Two new species of laophontid harpacticoids are described from deep-sea hydrothermal vents near the Azores in the Atlantic and north of Easter Island in the Pacific. Both species are placed in a new genus *Bathylaophonte* on account of the complex dorsal reticulation pattern on the cephalothorax and free body somites, the distinctive sexual dimorphism on both rami of P2-P4, and the relatively primitive setal formula of the swimming legs. The northwest European *Laophonte faroensis*, currently considered as *species incerta* in the family (Lang, 1948), is removed from its doubtful status and transferred to *Bathylaophonte*.

The genus *Paronychocamptus* is identified as a polyphyletic taxon, comprising five lineages. Under the revised concept the genus is exclusively boreal, including only two European species, *P. curticaudatus* and *P. nanus*, and two North American species, *P. huntsmani* and *P. wilsoni*. The other species *P. exiguus*, *P. leuke*, *P. proprius*, *P. connexus* and *P. anomalus* are reallocated to *Onychocamptus* Daday and three new genera. *Paronychocamptus* is tentatively regarded as the most likely sistergroup of *Bathylaophonte*.

The brackish water species *P. anomalus* from Andhra Pradesh (India) is transferred to the genus *Onychocamptus*. *O. besnardi* from Brazil and *O. vitiospinulosa* from China are removed from the synonymy of *O. mohammed* and reinstated as valid species. The primitive position of the genus and its relationship with *Folioquinpes* are discussed.

*P. proprius* from California, is placed in a new genus *Psammoplatypus* together with *Klieonychocamptus discipes* which occupied an isolated position in the genus *Klieonychocamptus*. *Psammoplatypus* is placed in the genus group comprising *Coullia*, *Phycolaophonte*, *Hemilaophonte* and *Robustunguis*.

The *exiguus*-group of *Paronychocamptus*, including *P. exiguus* from the Chatham Islands and *P. connexus* from Tierra del Fuego, is upgraded to generic level as *Heteronychocamptus* gen. nov. It is considered as most closely related to *Pilifera*, *Pseudonychocamptus* and *Weddellaophonte* on the basis of the sexually dimorphic setation of P3-P4 enp-1.

There is an undeniable relationship between *P. leuke* and the species described by Griga (1963) as *Laophonte brevifurca*. Both species (the latter renamed *P. grigae* sp. nov.) are placed in a new genus *Pontophonte* which is most closely related to the newly defined *nordgaardi*-group of *Laophonte*.

Species keys are given for *Paronychocamptus*, *Onychocamptus* and *Bathylaophonte* gen. nov. The radiation of the family Laophontidae into deepwater habitats is reviewed. Re-examination of previous reports of 8-segmented antennules in female Laophontidae has proven these to be incorrect.

**Résumé :** Deux nouvelles espèces d'Harpacticoïdes Laophontidae sont décrites de sources hydrothermales situées près des Açores, dans l'Atlantique, et au nord de l'Île de Pâques, dans le Pacifique. Ces deux espèces sont placées dans un genre nouveau, *Bathylaophonte*, en raison d'un modèle complexe de réticulation dorsale sur le céphalothorax et sur les somites libres, d'un dimorphisme sexuel distinct sur les deux rames des P2-P4, et de la formule sétale relativement primitive des pattes natatoires. L'espèce de l'Europe du N-W, *Laophonte faroensis*, considérée jusqu'ici comme *species incerta* dans cette famille (Lang, 1948), perd son statut incertain et est transférée dans le genre *Bathylaophonte*.

Le genre *Paronychocamptus* est considéré comme un taxon polyphylétique comprenant cinq ramifications. Ainsi révisé, le genre est exclusivement boréal, ne comprenant plus que deux espèces européennes, *P. curticaudatus* et *P. nanus*, et deux espèces nord-américaines, *P. huntsmani* et *P. wilsoni*. Les autres espèces, *P. exiguus*, *P. leuke*, *P. proprius*, *P. connexus* et *P. anomalus*, sont redistribuées dans le genre *Onychocamptus* et trois nouveaux genres. *Paronychocamptus* est provisoirement considéré comme le taxon le plus proche de *Bathylaophonte*.

L'espèce d'eau saumâtre *P. anomalus*, de l'Andhra Pradesh (Inde), est transférée dans le genre *Onychocamptus*. La synonymie de *O. besnardi*, du Brésil, et *O. vitiospinulosa*, de Chine, avec *O. mohammed* est supprimée et ces espèces sont restaurées comme espèces valides. La position primitive du genre et ses affinités avec *Folioquinpes* sont discutées.

*P. proprius*, de Californie, est placée dans un nouveau genre, *Psammoplatus*, conjointement avec *Klieonychocamptus discipes* qui occupait une position isolée dans le genre *Klieonychocamptus*. *Psammoplatus* est situé dans le groupe de genres comprenant *Coullia*, *Phycolaophonte*, *Hemilaophonte* et *Robustunguipes*.

Le groupe *exiguus* du genre *Paronychocamptus*, qui comprend *P. exiguus*, des îles Chatham, et *P. connexus*, de la Terre de Feu, est élevé au niveau de genre sous le nom de *Heteronychocamptus* gen. nov. Ce genre est considéré comme très proche de *Pilifera*, *Pseudonychocamptus* et *Weddellaophonte* en raison du dimorphisme sexuel noté dans la chétotaxie des enp-1 P3-P4.

Il existe une similitude indéniable entre *P. leuke* et l'espèce décrite par Griga (1963) sous le nom de *Laophonte brevifurca*. Les deux espèces (la seconde étant renommée *P. grigae* sp. nov.) sont placées dans un nouveau genre, *Pontophonte*, qui est très proche du groupe *nordgaardi* nouvellement défini dans le genre *Laophonte*.

Des clés sont données pour les espèces des genres *Paronychocamptus*, *Onychocamptus* et *Bathylaophonte* gen. nov. La pénétration de la famille des Laophontidae dans les biotopes profonds est révisée. Un réexamen des signalements d'antennules à 8 articles chez les femelles de Laophontidae a montré que cela n'était pas exact.

**Keywords :** Taxonomy, Copepoda, *Bathylaophonte* gen. nov., *Pontophonte* gen. nov., *Heteronychocamptus* gen. nov., *Paronychocamptus*, *Onychocamptus*, hydrothermal vents.

## Introduction

Copepoda commonly occur at deep-sea hydrothermal vents and cold seeps, and Siphonostomatoida in particular can be extraordinarily abundant (Humes & Segonzac, 1998). In contrast to hydrothermal vents, which harbour a diverse endemic copepod fauna, very few species have been described from cold seeps. Harpacticoid copepods have rarely been reported from either deep-sea hydrothermal vents or cold seeps (Humes & Segonzac, 1998), and their taxonomic study has only recently begun. Huys & Conroy-Dalton (1997) reported *Argestoides prehensilis* which is a host of a new tantulocarid from hydrothermal vents at the Galapagos Rift. Since Lee & Yoo (1998) reported *Neocervinia itoi* from the hyperbenthos of the Hatsushima cold-seep site in Sagami Bay, a number of other harpacticoid copepods, belonging to the Aegisthidae and Normanellidae, have been described from the hydrothermal vents and cold seeps in the western Pacific (Lee & Huys, 1999, in press).

The Laophontidae currently encompass 53 genera (Lang, 1948; Bodin, 1997; George, 1997), the majority of which inhabit the intertidal zone or shallow subtidal localities. Exceptions include species associated with invertebrate hosts such as holothurians and decapods (*Namakosiramia* Ho & Perkins, *Mictyricola* Nicholls, *Robustunguis* Fiers, etc.), few brackish-water or freshwater inhabiting species such as *Onychocamptus mohammed* (Blanchard & Richard) and some recently reported genera from the Antarctic deep waters (*Archilaophonte* Willen, *Cornylaophonte* Willen and *Weddellaophonte* Willen; Willen, 1995, 1996). Laophontidae are as yet unknown from deep-sea hydrothermal vents and cold seeps and have rarely been reported from bathyal habitats in general. Recently, harpacticoids were collected during various French cruises (IFREMER) using the submersible *Nautile*, operating from the N/O *Nadir* (cf. Humes & Segonzac, 1998). Among them, two unusual laophontids were found, the description and phylogenetic position of which form the subject of the present paper.

## Material and methods

The copepods reported in this study were collected during several French cruises (1991-1995), using the submersible *Nautille*, operating from the *N/O Nadir* (IFREMER). They were extracted from the invertebrates living in the hydrothermal fluids by means of a slurp gun or were sorted from washings of polychaetes, vestimentiferans, bivalves, or shrimps (Humes & Segonzac, 1998). The harpacticoid copepods described here were taken during the DIVA 1 (Diving In Vents at the Azores: 22 May 1994; 37°50.46' N, 31°31.35' W) and DIVA 2 (7 June 1994, 37°17.48' N, 32°16.87' W) campaigns conducted in the Atlantic south-west of the Azores, and the NAUDUR campaign (NAUtile Dorsale Ultra Rapide: 8 December 1993; 17°25.79' S, 113°12.33' W) north of Easter Island in the South Pacific Ocean. Additional information on sampling dates and localities is given by Humes & Segonzac (1998).

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

The descriptive terminology is adopted from Huys et al. (1996). Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; exp, exopod; enp, endopod; P1-P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus. Type series are deposited in the collections of the Muséum National d'Histoire Naturelle in Paris (MNHN) and The Natural History Museum, London (NHM). Scale bars in figures are indicated in  $\mu\text{m}$ .

## Systematics

Family Laophontidae T. Scott, 1904

Genus *Bathylaophonte* gen. nov.

Diagnosis. Laophontidae. Body elongate, sub-cylindrical; with distinct reticulation and tiny spinules. Cephalothorax and body somites with smooth posterior margin. Genital double-somite with transverse surface ridge dorsally and laterally, indicating original segmentation. Genital field with small copulatory pore located in median depression. Anal operculum well developed. Sexual dimorphism in antennule, P2-P4 (both rami), P5, P6, and in genital segmentation.

Rostrum bell-shaped, not defined at base. Antennule with small process on segment 2; 7-segmented in ♀, 8-segmented and subchirocer in ♂; aesthetascs on segments 4 and 7 in ♀, and 5 and 8 in ♂; apical acrothek consisting of minute aesthetasc and 2 setae. Antennary exopod well developed,

with 4 setae. Mandibular palp small, rami fused to basis forming small peduncles; basis, exopod, and endopod with 1,1, 3 setae, respectively. Maxillule with 1 seta and 1 spine on coxa; basis with 2 setae and 1 spine; endopod represented by 3 setae; exopod with 2 setae. Maxillary syncoxa with 3 endites, formula [1, 3, 3]; endopod represented by 3 setae. Maxilliped with 2 setae on syncoxa; endopodal claw long and sparsely pinnate, bearing 1 short seta at base.

Swimming legs P1-P4 with 3-segmented exopods and 2-segmented endopods (except ♂ P3 endopod 3-segmented). P3 enp-2 in ♂ produced into conspicuous apophysis (homologous with outer spine of enp-2 in ♀). Exopodal segments of P2 - P4 elongate and more strongly developed in ♂; outer spines stronger than in ♀; setae and spines of endopod, and inner setae of exopod shorter in ♂ than in ♀. Exopods of P2-P4 in ♂ somewhat bent toward endopod. Swimming leg setal formulae:

	Exopod	Endopod
P2	0.1.123	0.220
P3	0.1.223	0.321 [0.0.220 in ♂]
P4	0.1.223	0.221 [0.121 in ♂ of <i>B. pacifica</i> ]

P5 with separate exopod and baseoendopod. Exopod elongate or ovoid, with 5 setae in ♀, 4 setae in ♂. Endopodal lobe well developed in ♀, subrectangular, with 4 setae; rudimentary with 1 seta and medially fused in ♂.

P6 forming well developed operculum with 2 small setae in ♀; asymmetrical in ♂ (with dextral or sinistral configuration), with outer distal corner produced into cylindrical process bearing 2 well developed elements.

Caudal ramus longer than wide, with 7 setae; seta V longest.

Type species. - *Bathylaophonte azorica* gen. et sp. nov.

Other species. - *Laophonte faröensis* T. Scott, 1903 = *B. faroensis* (T. Scott, 1903) comb. nov.; *B. pacifica* sp. nov.

Etymology. - The generic name refers to the primarily bathyal zonation of its species. Gender: feminine.

*Bathylaophonte azorica* gen. et sp. nov.

Type locality. - Atlantic, south-west of Azores (37°50.46' N, 31°31.35' W), DIVA 1, DV 14-4, depth 845 m.

Material. - (a) From type locality: holotype ♀ dissected on 12 slides (MNHN-Cp 1769); paratypes are 1 ♀ dissected on 13 slides (MNHN-Cp 1770), 1 ♂ dissected on 11 slides (MNHN-Cp 1771), 5 ♀♀ and 1 ♂ in 70% alcohol (MNHN-Cp 1772), and 3 ♀♀ and 1 ♂ in 70% alcohol (NHM reg. no. 1999.160-163); all collected 22 May 1994;

(b) Atlantic, south-west of Azores (37°17.48' N, 32°16.87' W), DIVA 2, PL 05, depth 1715 m - paratypes: 1 ♀ and 1 ♂ in 70% alcohol (MNHN-Cp 1773); collected 7 June 1994.

#### Female

Total body length 619 - 851 µm (n=10;  $\bar{x}$  = 699 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 185 µm. Urosome gradually tapering posteriorly (Fig. 1A).

Cephalothorax with smooth posterior margin; pleural areas well developed and rounded with lobate posterolateral angles; entire surface covered with distinct reticulation, and tiny spinules [partially indicated by small points] as illustrated in Fig. 2A; sensillae and few pores present as illustrated in Figs. 1A-B, and 2A. Rostrum bell-shaped (Figs. 2A, 3A), with bifid apex; completely fused to cephalosome; with pair of sensillae near apex; dorsal surface with distinct reticulation and minute spinules (Fig. 3A).

Pedigerous somites covered with reticulation and minute spinules. All prosomites without defined hyaline frills; hind margin smooth. Each pedigerous somite with 1 row of spinules near posterior margin. Body not markedly constricted between individual somites.

Urosome (Figs 1A-B; 2B) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites with surface ornamentation consisting of reticulation and small spinules dorsally and laterally; ventral surface wrinkled (genital double-somite), or reticulated; ventral hind margin with large spinules laterally and small spinules medially. Hyaline frills of urosomites not distinct.

Genital double-somite (Figs. 1A-B, 2B, D) with transverse, surface ridge dorsally and laterally, indicating original segmentation; completely fused ventrally. Genital field (Fig. 2D) with small copulatory pore located in median depression; copulatory pore containing bulbous tube-like extension; gonopores fused medially forming single genital slit covered on both sides by opercula derived from sixth legs; P6 with small protuberance bearing 2 bare setae; outer seta set on small peduncle (Fig. 2D).

Anal somite (Fig. 2C) with well developed operculum bearing row of spinules and flanked by pair of sensillae.

Caudal rami (Fig. 2B-C) long, cylindrical, 3.8 times longer than wide; each ramus with 7 setae: seta I bare, shortest; setae II and III bare; setae IV and V fused basally, with predesigned fracture planes (seta IV unipinnate; seta V tripinnate, longest, and longer than urosome); seta VI bare and small; seta VII tri-articulate at base. Each ramus with spinules on outer dorsal surface; additional spinular ornamentation present along inner and outer margins and

around ventral hind margin; large tube pore present near ventral hind margin.

Antennule (Fig. 3A) 7-segmented; with well developed sclerite around base of segment 1; irregular reticulation present on all segments. Segment 1 covered with long spinules. Segment 2 largest; with small blunt process on dorsal surface and several spinular rows around posterior margin. Segment 3 with spinular rows around posterior margin. Segment 4 with aesthetasc fused basally to seta and set on distinct pedestal. Armature formula: 1-[1], 2-[7 + 1 pinnate], 3-[6], 4-[1 + (1 + ae)], 5-[1], 6-[2], 7-[7 + acrothek]. Apical acrothek consisting of small aesthetasc fused basally to 2 bare setae.

Antenna (Fig. 3E) 3-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa small, with 2 rows of spinules. Allobasis elongate; without distinct surface sutures marking original segmentation; with 1 abexopodal pinnate seta in distal half. Exopod small, 4 times longer than width, with 4 well developed pinnate setae (2 laterally, 2 apically); spinules along lateral margin posteriorly. Endopod shorter than allobasis; lateral armature arising in distal half, consisting of 1 small bare seta flanked by 2 strong pinnate spines; apical armature consisting of 2 pinnate spines, and 3 geniculate setae (1 geniculate seta fused basally to short seta). Endopod with 2 rows of long spinules laterally and 2 transverse hyaline frills subapically.

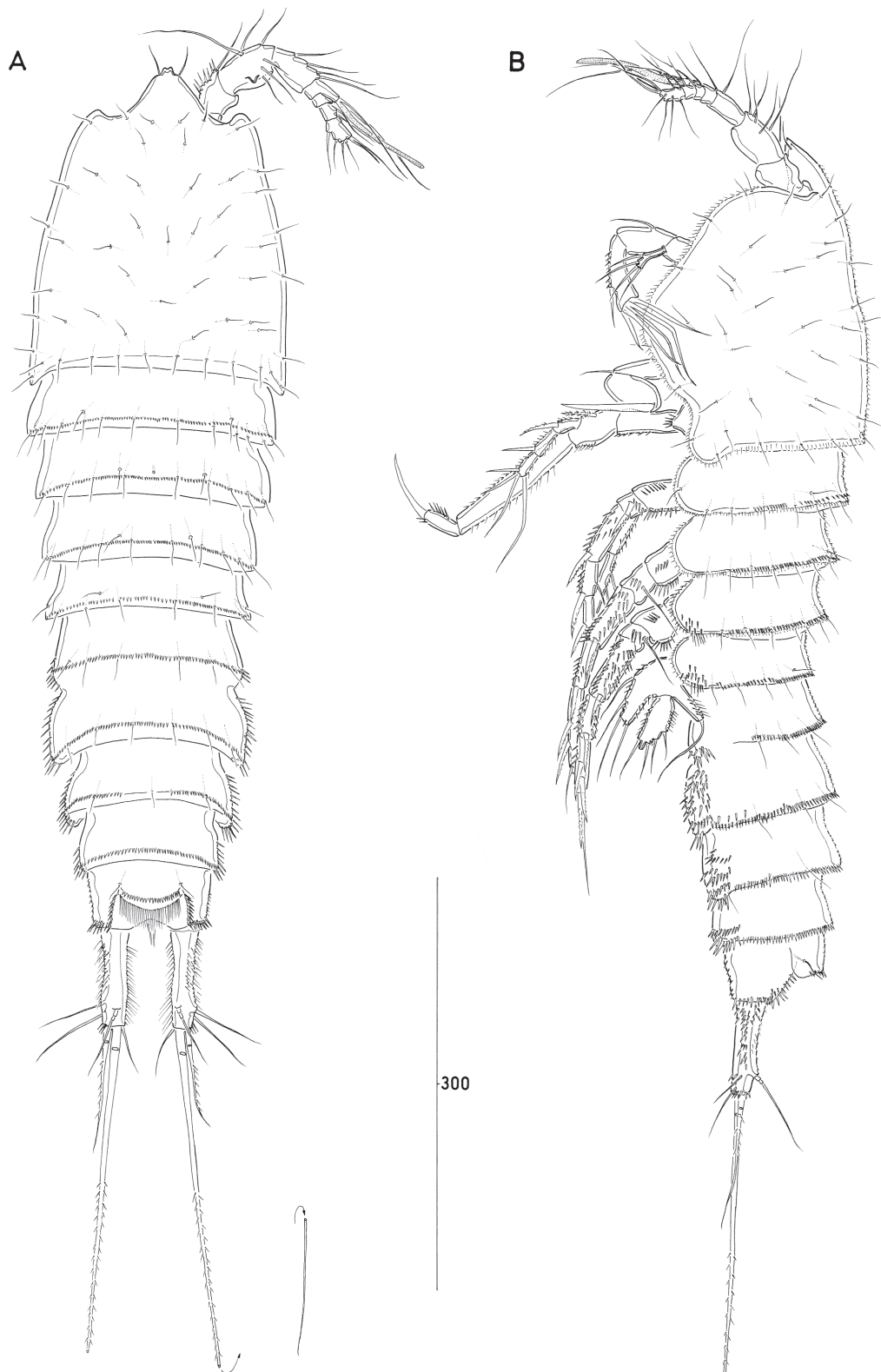
Labrum with spinular ornamentation and pores as in Fig. 7C.

Mandible (Fig. 3C) with well developed gnathobase bearing several multicuspitate teeth around distal margin and 1 pinnate spine at dorsal corner; with several rows of spinules on surface. Palp small, endopod and exopod fused to basis, represented by small peduncles bearing 3 plumose and 1 pinnate seta(e), respectively. Basal armature represented by 1 plumose seta.

Paragnaths (Fig. 4A) strongly developed lobes with medially directed hair-like setules, separated by medial lobe covered with dense pattern of short setules.

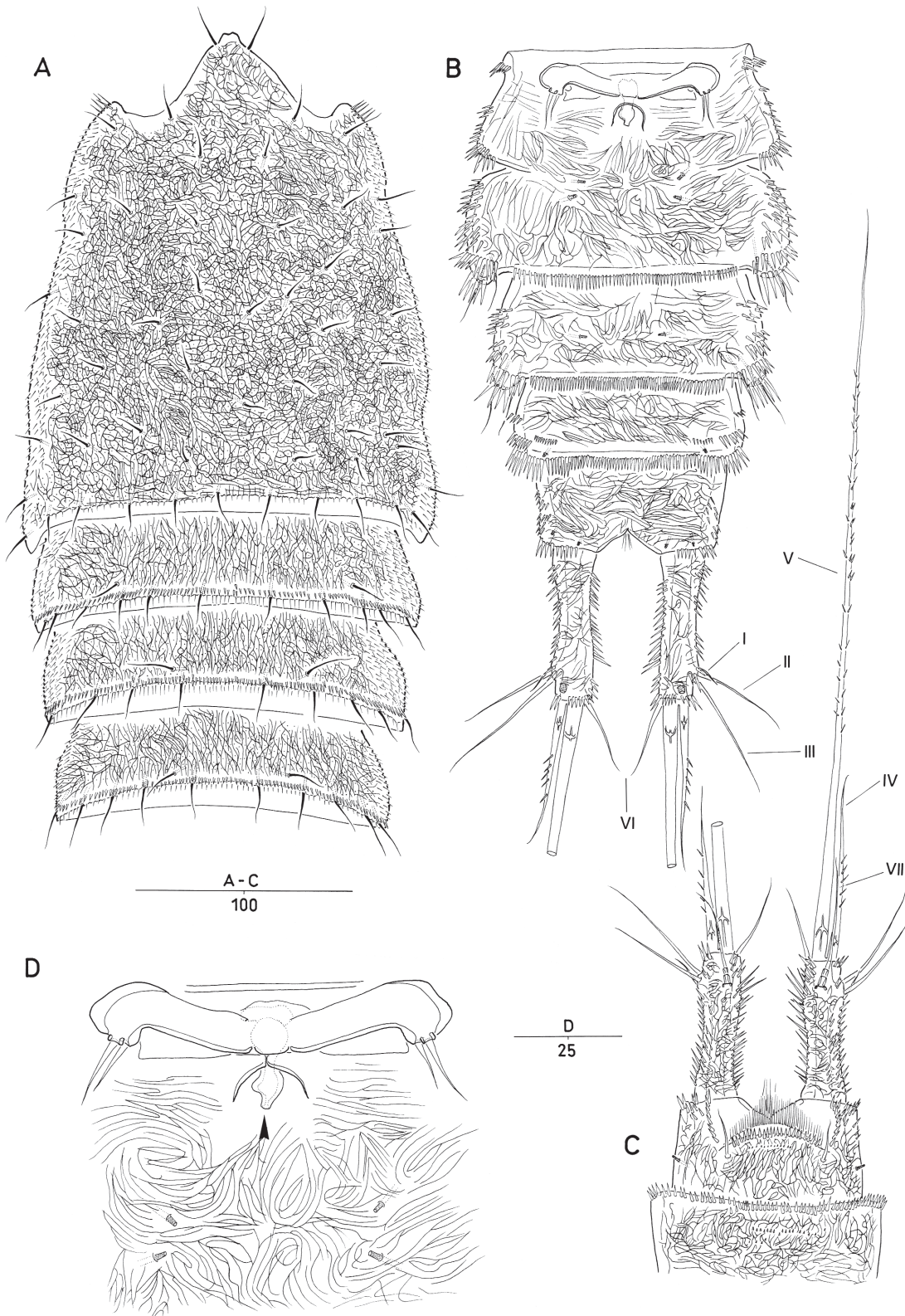
Maxillule (Fig. 4B). Praecoxa with few long spinules around outer margin; arthrite strongly developed, with 1 naked seta, and 1 row of spinules on anterior surface and 8 spines/setae around distal margin; 1 row of long spinules on posterior surface, and 1 row of small spinules on inner margin of arthrite. Coxa with cylindrical endite bearing 1 naked seta and 1 curved, pinnate spine; with spinular row on anterior surface, and several long spinules around outer margin. Basis with cylindrical endite bearing 2 naked setae, and 1 curved, pinnate spine; with several spinules around inner distal margin and base of endopod. Endopod nearly incorporated in basis, forming small peduncle with 3 plumose setae; exopod 1-segmented, with 2 plumose setae and several rows of spinules laterally and posteriorly.





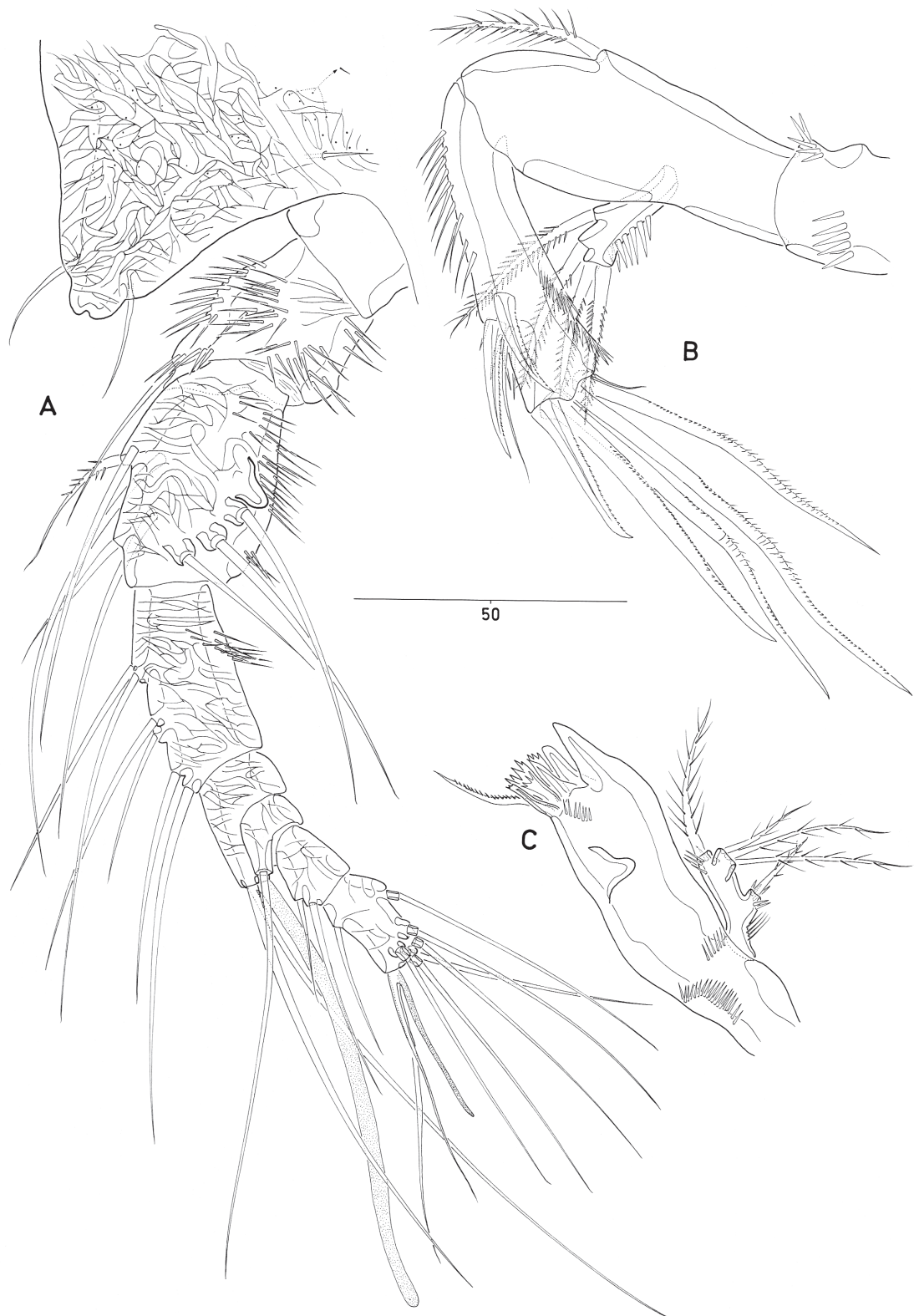
**Figure 1.** *Bathylaophonte azorica* gen. et sp. nov. (♀). A, habitus, dorsal; B, habitus, lateral.

**Figure 1.** *Bathylaophonte azorica* gen. et sp. nov. (♀). A, habitus, vue dorsale ; B, habitus, vue latérale.



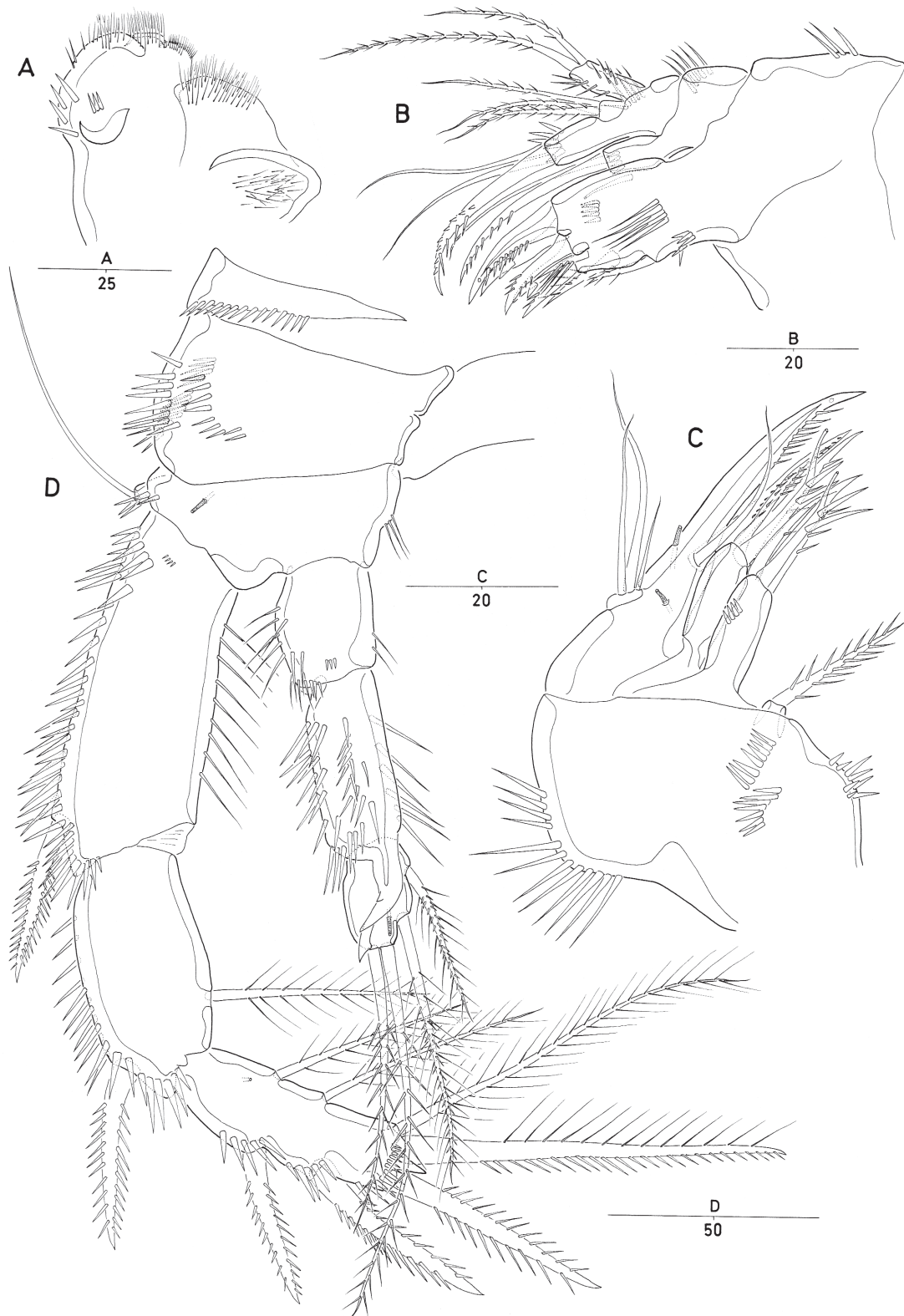
**Figure 2.** *Bathylaophonte azorica* gen. et sp. nov. (♀). A, prosome, dorsal; B, urosome, ventral [excluding P5-bearing somite]; C, anal somite and caudal rami, dorsal; D, genital field [copulatory pore arrowed].

**Figure 2.** *Bathylaophonte azorica* gen. et sp. nov. (♀). A, prosome, vue dorsale ; B, urosome, vue ventrale [sauf le somite portant P5] ; C, somite anal et rame caudale, vue dorsale ; D, aire génitale [la flèche indique l'orifice copulateur].



**Figure 3.** *Bathylaophonte azorica* gen. et sp. nov. (♀). A, rostrum and antennule, dorsal; B, antenna; C, mandible.

**Figure 3.** *Bathylaophonte azorica* gen. et sp. nov. (♀). A, rostre et antennule, vue dorsale; B, antenne; C, mandibule.



**Figure 4.** *Bathylaophonte azorica* gen. et sp. nov. (♀). A, paragnath; B, maxillule; C, maxilla; D, P3 (♂), anterior.

**Figure 4.** *Bathylaophonte azorica* gen. et sp. nov. (♀). A, paragnathe ; B, maxillule ; C, maxille ; D, P3 (♂), vue antérieure.



Maxilla (Fig. 4C). Syncoxa with 3 endites; with 1 row of long spinules along outer margin, 2 rows of spinules on posterior surface, and several spinules along inner margin; praecoxal endite small and cylindrical, with 1 strong pinnate seta; both coxal endites with 1 strong pinnate spine, 1 pinnate seta with subapical tubular extension, and 1 small pinnate seta; proximal coxal endite with 1 row of spinules posteriorly. Allobasis drawn out into strong, slightly curved, distally pinnate claw; accessory armature consisting of 1 pinnate spine on anterior surface, 1 naked seta on posterior surface, and 2 tube pores. Endopod represented by 3 naked setae.

Maxilliped (Fig. 5C) with 2 plumose setae and several patches of spinules on syncoxa. Basis with 2 rows of spinules along outer margin and 1 longitudinal setular row along palmar margin. Endopod drawn out into long, minutely pinnate claw; accessory armature consisting of 1 short naked seta anteriorly, and 1 tube pore posteriorly.

Swimming legs P1-P4 (Figs 5A-B; 6A-B) with wide intercoxal sclerites and well developed praecoxae. Coxae and bases with anterior rows of surface spinules as figured. Exopods 3-segmented, endopods 2-segmented.

P1 (Fig. 5A). Coxa large; with several spinular rows and patches as figured. Basis with 1 strong, bipinnate spine on distal pedestal, long setules along inner margin and 1 stout bipinnate spine and few spinules along outer margin; 1 anterior tube pore present near articulation with coxa. Exp-1 with 1 stout bipinnate spine; exp-2 with 1 naked outer spine; exp-3 with 1 naked spine, 1 unipinnate spine and 2 geniculate setae. Enp-1 1.8 times as long as exopod, with long spinules along inner margin, and short spinules along outer margin; enp-2 with 1 strong denticulate claw, and 1 small naked seta.

P2-P4 (Figs 5B; 6A-B). Coxae and bases with spinular rows along outer margin and anterior surface; basis with 1 tube pore on anterior surface; outer margin of basis with bipinnate spine (P2) or naked seta (P3-P4); all segments with pattern of spinules as figured; inner margins of exopod and endopod segments with long setules or spinules; tube pore present near distal margin of enp-1 in P2 and enp-2 in P3-P4. P2 enp-2 1.4 times longer than enp-1; endopod reaching to distal margin of exp-2; exp-3 longest. P3 enp-2 3 times longer than enp-1; endopod reaching to proximal third of exp-3; exp-3 longer than exp-1. P4 enp-2 3.3 times longer than enp-1; endopod reaching to about middle of exp-3; exp-3 shorter than exp-1. Exp-3 of P3 and P4 with 1 tube pore. Spine and setal formulae as in generic diagnosis.

Fifth pair of legs (Fig. 7D) with separate exopod and baseoendopod, each with pattern of spinules and covered with distinct surface reticulation as figured. Baseoendopod forming long, outer setophore bearing basal seta and row of spinules; with 3 tube-pores. Endopodal lobe extending to middle of exopod, with 1 apical and 3 lateral bipinnate

setae. Exopod elongate, about twice longer than wide; with 1 naked terminal seta, 1 bipinnate inner seta, and 3 short, pinnate setae along outer margin; terminal seta arising from distinct cylindrical process.

#### Male

Body length 619 - 727  $\mu\text{m}$  (n=4;  $\bar{x}$ 667  $\mu\text{m}$ ; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at P2-bearing somite: 231  $\mu\text{m}$ . Urosome distinctly narrower than prosome (Fig. 7A).

Prosome (Fig. 7A) 4-segmented, comprising cephalothorax and 3 free pedigerous somites. Cephalothorax with smooth posterior margin; pleural areas well developed and rounded, with lobate posterolateral angles; whole surface covered with distinct reticulation and tiny spinules as in ♀. Rostrum bell-shaped (Fig. 8A), with weakly bifid apex; completely fused to cephalosome; with pair of sensillae near apex; dorsal surface with distinct reticulation and minute spinules as in ♀.

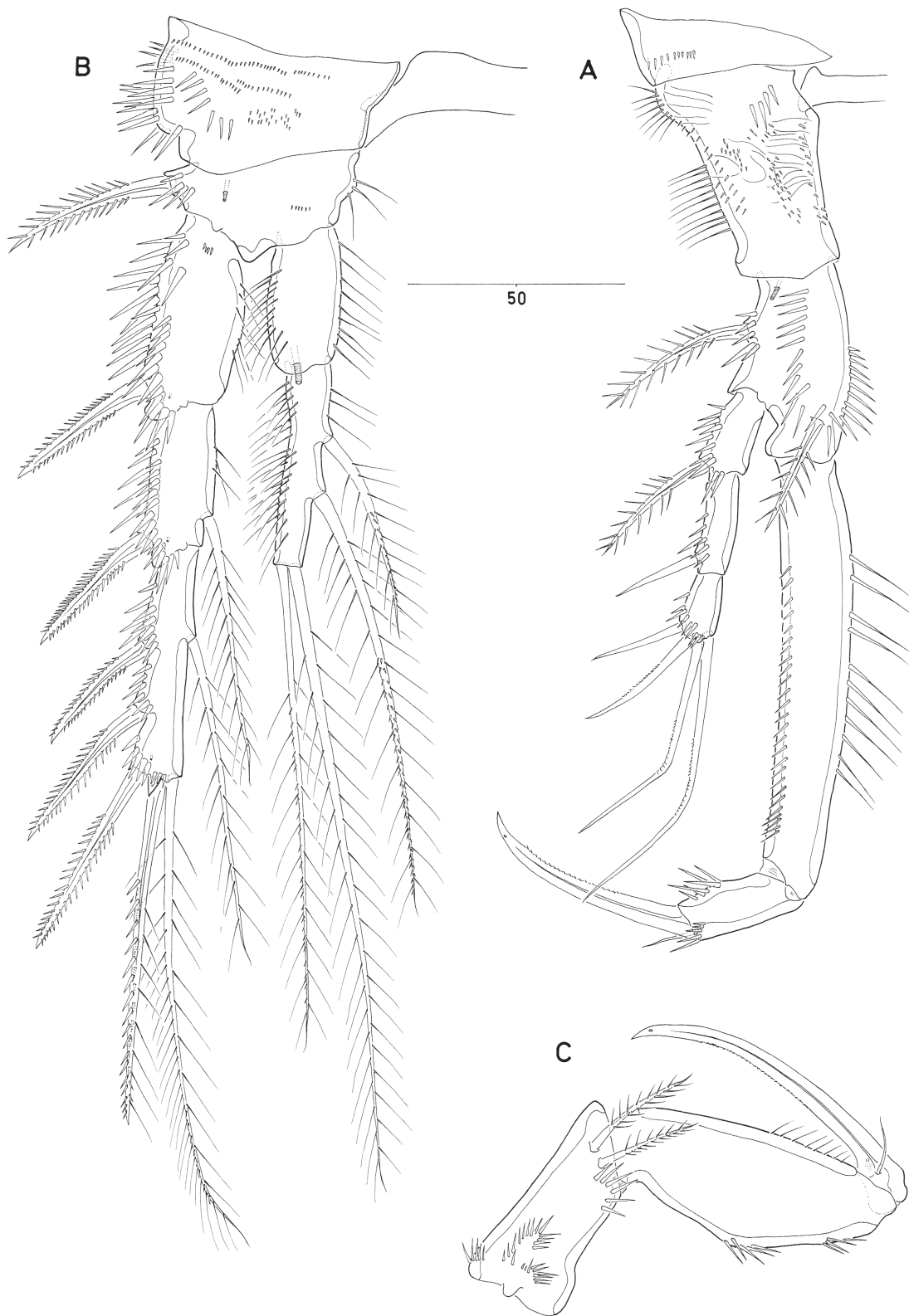
Pedigerous somites covered with reticulation and minute spinules; somites bearing P2-P4 distinctly wider than in ♀. All prosomites without defined hyaline frills; hind margin smooth. Each pedigerous somite with 1 row of spinules near posterior margin. Body not markedly constricted between individual somites.

Urosome (Fig. 7A) 6-segmented, comprising P5-bearing somite, genital somite and 4 abdominal somites. All urosomites with surface ornamentation consisting of reticulation and small spinules dorsally and laterally; ventral surface reticulated; ventral hind margin with large spinules laterally and minute spinules medially. Hyaline frills of urosomites not distinct.

Antennule (Fig. 8A-D) 8-segmented; subchirocer with geniculation between segments 5 and 6. Segment 1 with several rows of long spinules along whole surface. Segment 2 with small knob on dorsal surface. Segment 4 represented by small sclerite along anterior margin (inserted in Fig. 8B). Segment 5 swollen. Segment 8 triangular. Segmental homologies: 1-I, 2-(II-VIII), 3-(IX-XII), 4-XIII, 5-(XIV-XX), 6-(XXI-XXII), 7-XXIII, 8-(XXIV-XXVIII). Armature formula: 1-[1], 2-[1 pinnate + 8], 3-[7], 4-[2], 5-[7 + 2 pinnate + 2 modified + 2 spinous processes + (1 + ae)], 6-[6 spinous processes], 7-[1], 8-[8 + acrothek]. Apical acrothek consisting of minute aesthetasc and 2 naked setae.

P2-P4 (Figs 4D; 9A-B). Intercoxal sclerites and protopods as in ♀, with surface ornamentation as figured. Exopodal segments more strongly developed than in ♀.

P2 (Fig. 9A). Exopod strongly developed with segments larger and more robust than in ♀; slightly bent inwards to endopod; exp-1 elongate, about as long as exp-3. Endopod relatively shorter than in ♀; not reaching to distal margin of exp-2; enp-2 shorter than in ♀, subequal to enp-1; distal inner seta and both apical setae markedly shorter than in ♀.

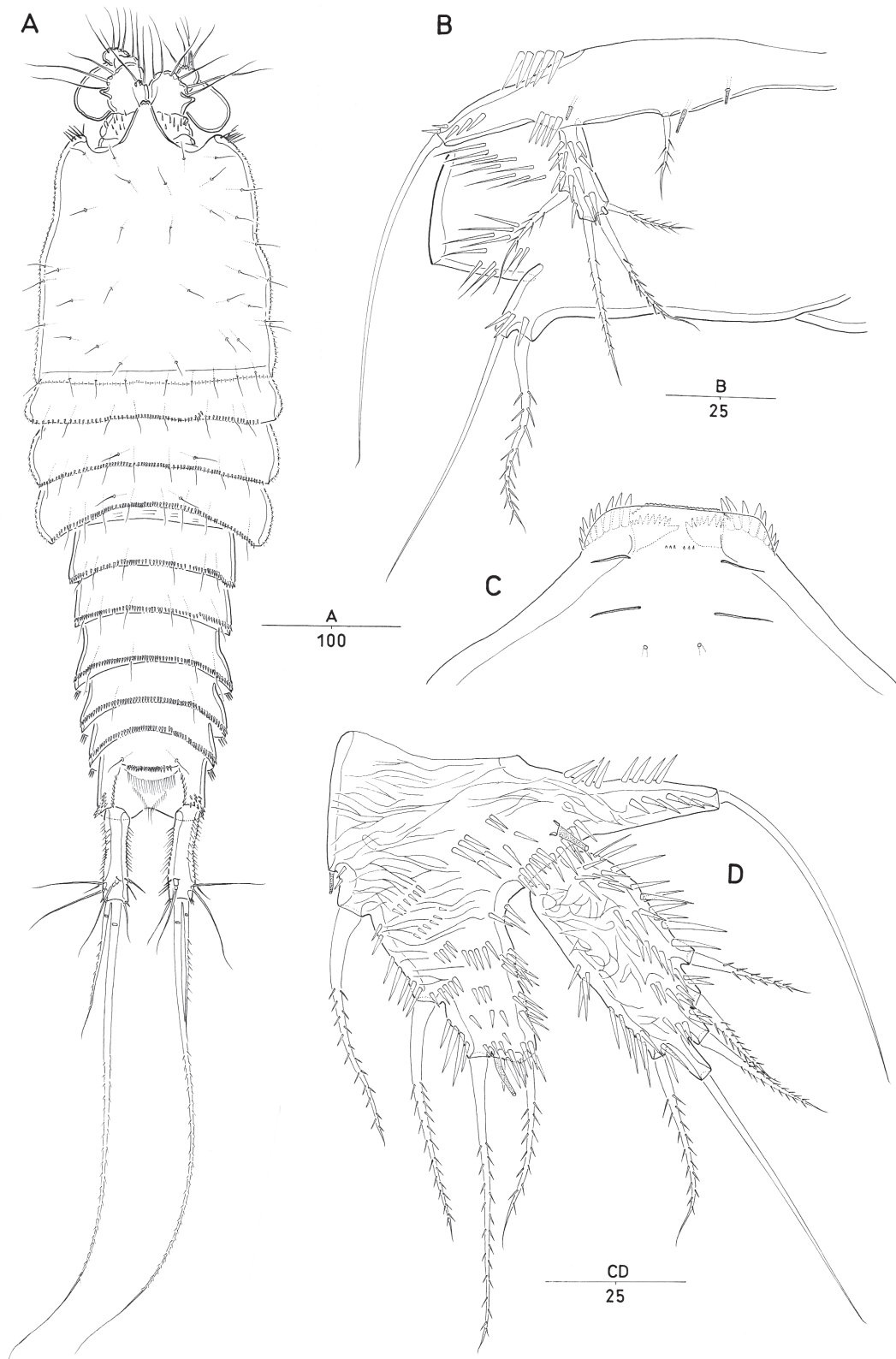


**Figure 5.** *Bathylaophonte azorica* gen. et sp. nov. (♀). A, P1, anterior; B, P2, anterior; C, maxilliped.

**Figure 5.** *Bathylaophonte azorica* gen. et sp. nov. (♀). A, P1, vue antérieure ; B, P2, vue antérieure ; C, maxillipède.



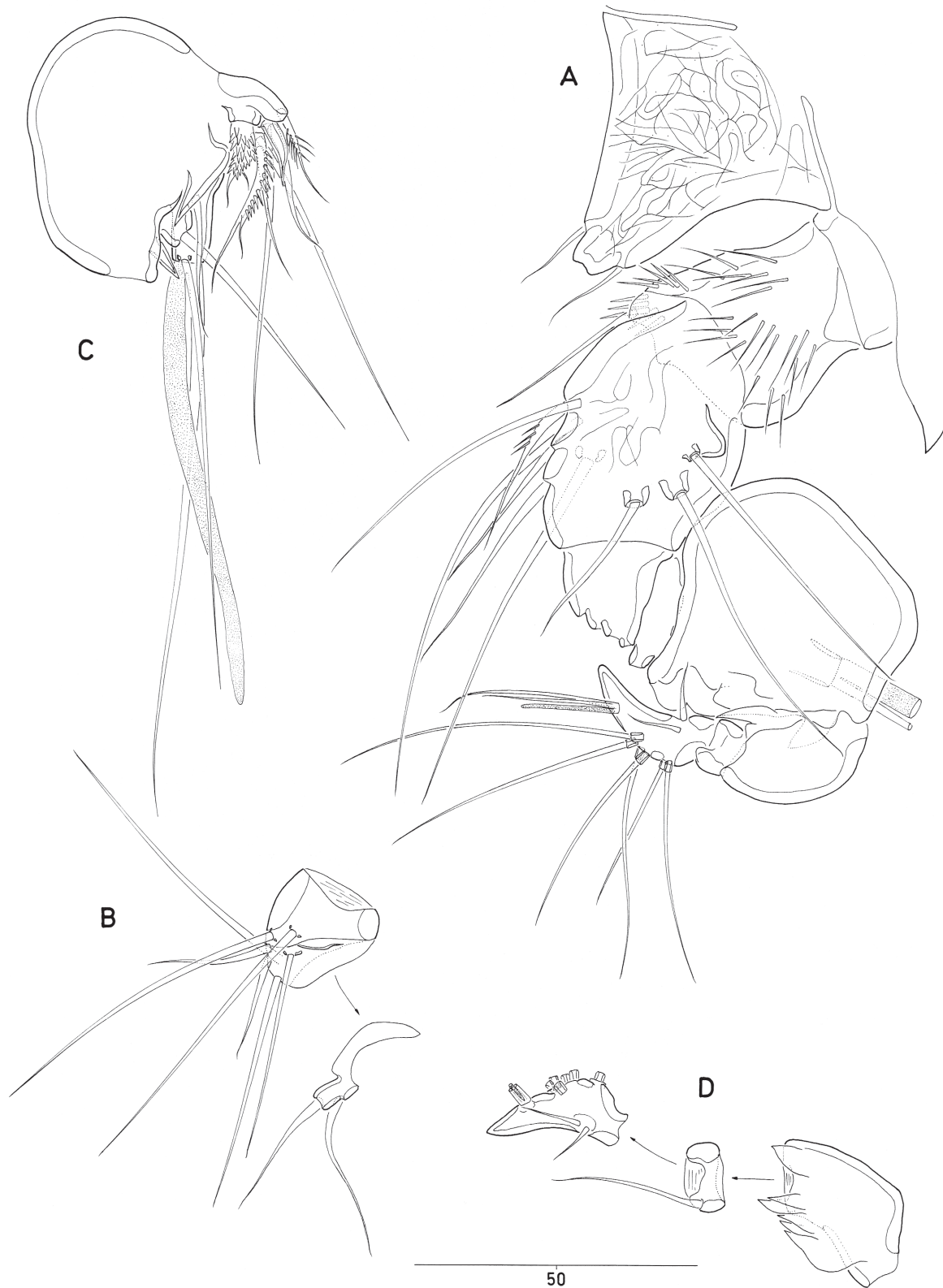
**Figure 6.** *Bathylaophonte azorica* gen. et sp. nov. (♀). A, P3, anterior; B, P4, anterior.  
**Figure 6.** *Bathylaophonte azorica* gen. et sp. nov. (♀). A, P3, vue antérieure ; B, P4, vue antérieure.



**Figure 7.** *Bathylaophonte azorica* gen. et sp. nov. (♂). A, habitus, dorsal; B, P5 and P6; C, labrum (♀); D, P5 (♀), anterior.

**Figure 7.** *Bathylaophonte azorica* gen. et sp. nov. (♂). A, habitus, vue dorsale ; B, P5 et P6 ; C, labre (♀) ; D, P5 (♀), vue antérieure.





**Figure 8.** *Bathylaophonte azorica* gen. et sp. nov. ( $\delta$ ). A, rostrum and antennule [armature omitted in segments 3-7]; B, antennular segments 3 - 4 disarticulated; C, 5th antennular segment; D, antennular segments 6-8 [disarticulated].  
**Figure 8.** *Bathylaophonte azorica* gen. et sp. nov. ( $\delta$ ). A, rostre et antennule [armature des articles 3-7 omise] ; B, articles antennulaires 3 - 4 [détachés] ; C, article antennulaire 5 ; D, articles antennulaires 6 - 8 [détachés].



**Figure 9.** *Bathylaophonte azorica* gen. et sp. nov. ( $\delta$ ). A, P2, anterior; B, P4, anterior.

**Figure 9.** *Bathylaophonte azorica* gen. et sp. nov. ( $\delta$ ). A, P2, vue antérieure ; B, P4, vue antérieure.

P3 (Fig. 4D). Exopod very robust and distinctly bent inwards; exp-1 longer than other segments; outer and distal spines of exp-3 enlarged with coarse spinules; inner setae of exp-2 and -3 shorter than in ♀. Endopod 3-segmented, modified, not reaching to distal margin of exp-2; enp-2 distally produced into short, barbed apophysis (homologous with outer spine of enp-2 in ♀); enp-3 with only 2 inner and 2 apical setae, all being shorter than their homologues in the ♀.

P4 (Fig. 9B). Exopod strongly modified; exp-1 very elongate, longer than endopod with middle and distal segments distinctly bent inwards; outer spines of exp-2 and -3 and distal spine of exp-3 enlarged and with coarser spinules; inner setae of exp-3 much shorter than in ♀. Endopod relatively shorter than in ♀; distal inner and both apical setae reduced in size.

Fifth pair of legs (Fig. 7B) fused medially; defined at base. Baseoendopod with large setophore bearing outer basal seta, and obsolete endopodal lobe represented by 1 pinnate seta; with 2 tube-pores along medial margin, and 1 tube-pore near articulation with exopod; few coarse spinules near articulation with exopod. Exopod about 3 times as long as maximum width; with 1 inner, 1 outer and 2 pinnate setae; several large spinules on anterior surface.

Sixth pair of legs (Fig. 7B) asymmetrical; represented on both sides by small plate (fused to ventral wall of supporting somite along one side; articulating at base and covering gonopore along other side); outer distal corner produced into cylindrical process bearing few spinules, 1 bipinnate inner and 1 naked outer seta.

Etymology.- The species name refers to the type locality, i.e. south-west of the Azores.

Notes. *B. azorica* can be readily distinguished from its congeners by the slender, elongate P1 endopod. The first endopod segment of P1 is 1.8 times longer than the exopod, while in the other species it is less than 1.5 times (1.3 in *B. azorica*, 1.15 in *B. faroensis*). The distal endopod segment is also distinctly longer than in its congeners. *B. azorica* is more slender in general appearance due to the lack of marked constrictions between the individual body somites which are clearly pronounced in both *B. pacifica* and *B. faroensis* (see below). The most distinctive feature in males of *B. azorica* is the modified P4 exopod which has a remarkably long proximal segment, being much longer than the middle and distal exopod segments combined. In the other members of the genus this segment, although being elongate, is clearly shorter than the other exopod segments combined. The apophysis on the middle endopod segment of the male P3 resembles that of *B. faroensis*, however the segment it arises from is much longer than in this species. The elongated shape of the ♀ P5 exopod is similar to that of *B. faroensis*, however, in the latter all setae insert in the

distal half of the exopod whereas in *B. azorica* the proximalmost outer seta is clearly located in the proximal half. Finally, the male P6 shows minor ornamental differences; it has 1 bare and 1 bipinnate seta, while in the other species both setae are clearly bipinnate.

*Bathylaophonte pacifica* sp. nov.

Type locality. - South-East Pacific, north of Easter Island (17°25.79' S, 113°12.33' W), NAUDUR, Stn ND 03-6-1B, depth 2572 m.

Material. - Holotype ♂ dissected on 10 slides (MNHN-Cp 1774); paratypes are 1 ♀ dissected on 12 slides (NHM reg. no. 1999.164) and 2 copepodids (1 CIV ♀ and 1 CV ♀: MNHN-Cp 1775) preserved in 70% alcohol; all from type locality; collected 8 December 1993.

Female

Damaged during observation. Total body length 810 µm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at P2-bearing somite: 229 µm. Urosome narrower than prosome (Fig. 11A). Body more dorsoventrally depressed than in *B. azorica*. Body markedly constricted between individual somites.

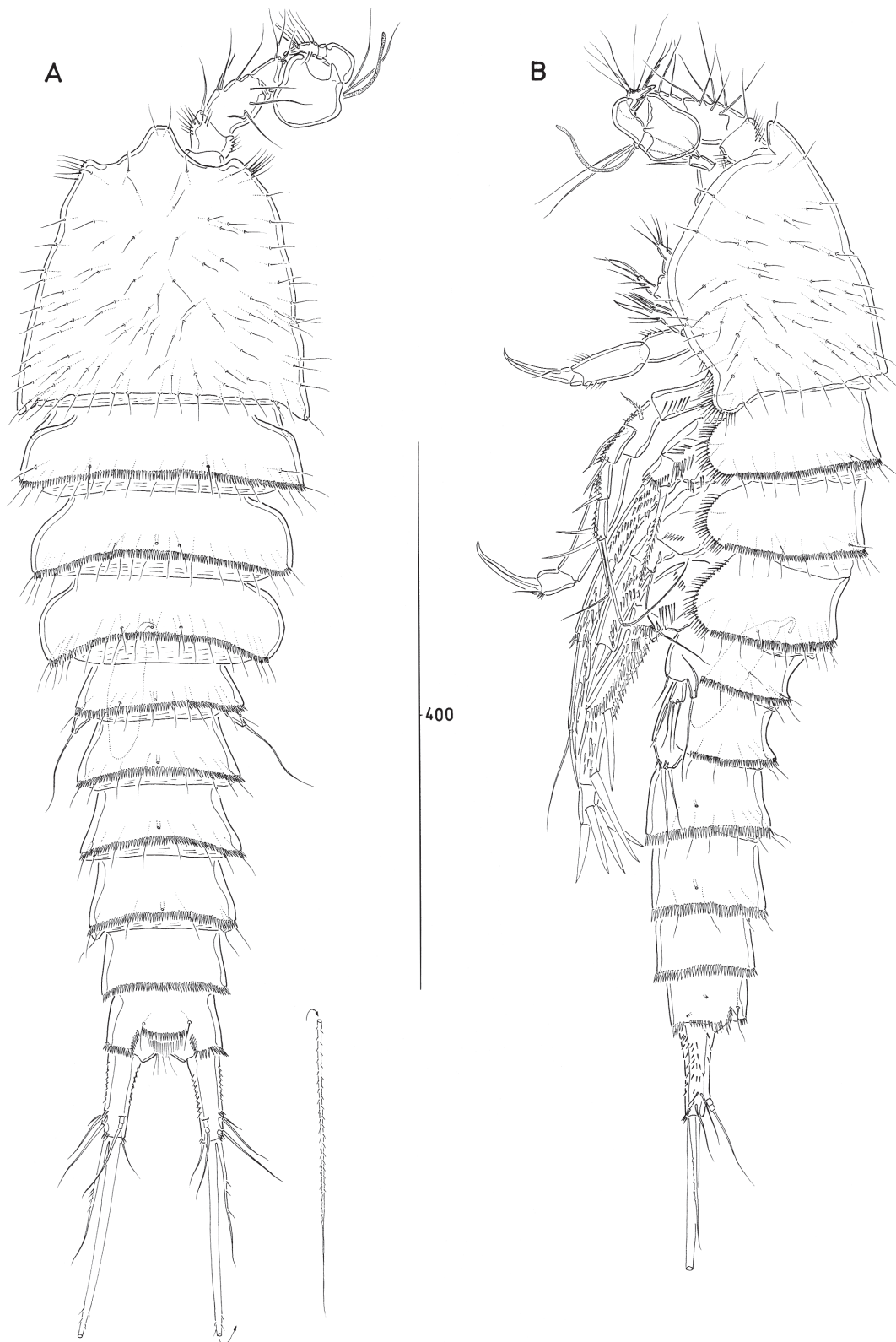
Cephalothorax with smooth posterior margin; pleural areas well developed and rounded with lobate posterolateral angles; entire surface covered with distinct reticulation and tiny spinules as in *B. azorica* (i.e. Fig. 2A); sensillae present as illustrated in Fig. 11A and more numerous than in *B. azorica*. Rostrum bell-shaped (Fig. 11A), with blunt apex; completely fused to cephalosome; with pair of sensillae near apex; dorsal surface with distinct reticulation and minute spinules as in *B. azorica*.

Pedigerous somites covered with reticulation and minute spinules. All prosomites without defined hyaline frills; hind margin smooth. Each pedigerous somite with 1 row of spinules near posterior margin; spinules longer than in *B. azorica*.

Urosome (Fig. 11A) 5-segmented; all urosomites with surface ornamentation consisting of reticulation and small spinules dorsally and laterally; ventral surface wrinkled (genital double-somite), or reticulated; ventral hind margin with large spinules laterally and minute spinules medially. Hyaline frills of urosomites not distinct. Genital double-somite as in *B. azorica* but bilateral constriction marking original segmentation more pronounced. P6 with small protuberance bearing 2 bare setae; outer seta set on small peduncle.

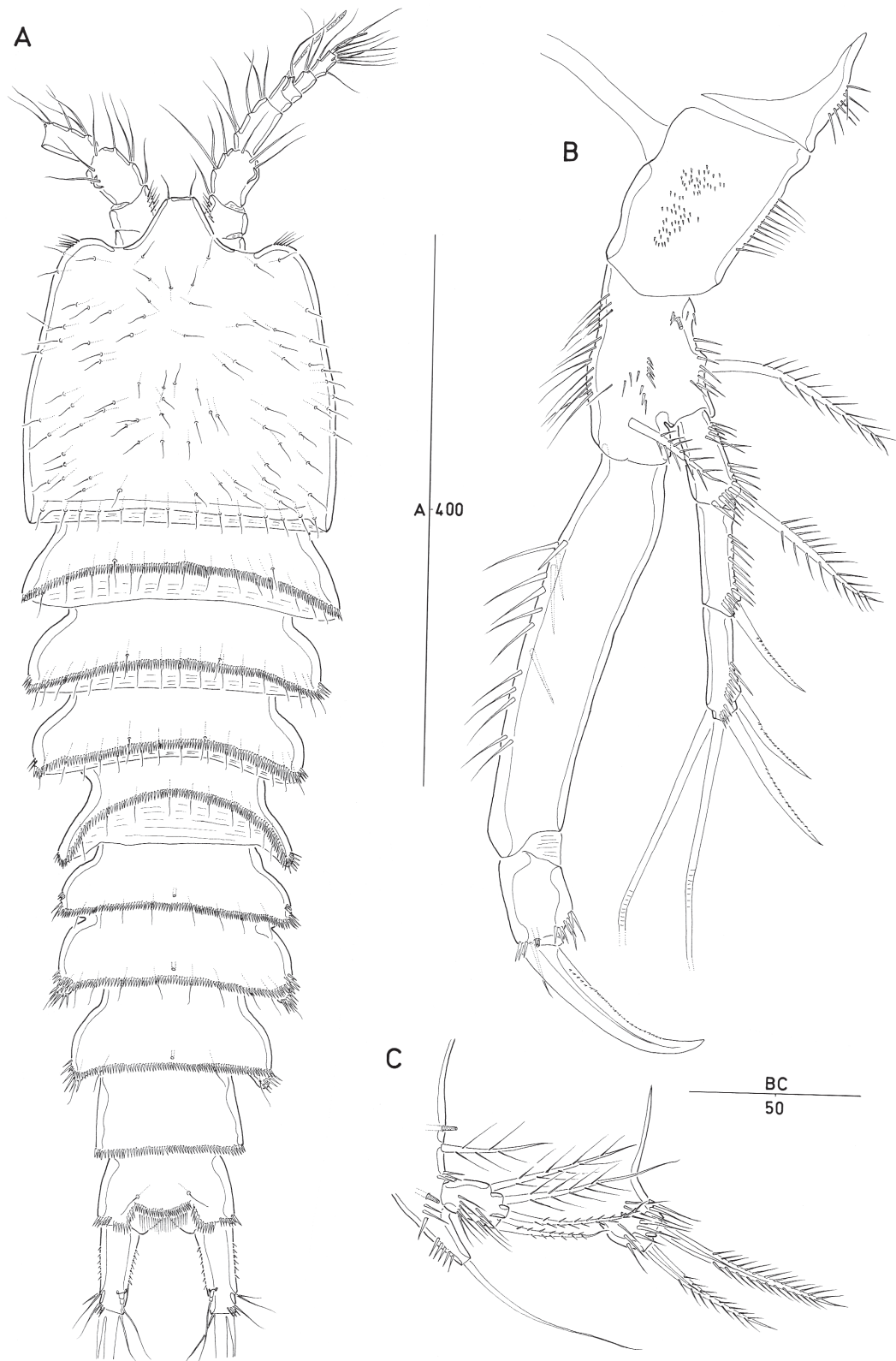
Anal somite (Fig. 11A) with well developed operculum bearing spinule row and flanked by pair of sensillae.

Caudal rami (Fig. 11A) cylindrical, about 3 times longer than wide; each ramus with 7 setae: form and arrangement



**Figure 10.** *Bathylaophonte pacifica* gen. et sp. nov. (♂). A, habitus, dorsal; B, habitus, lateral.

**Figure 10.** *Bathylaophonte pacifica* gen. et sp. nov. (♂). A, habitus, vue dorsale ; B, habitus, vue latérale.



**Figure 11.** *Bathylaophonte pacifica* gen. et sp. nov. (♀). A, habitus, dorsal; B, Pl, anterior; C, P5 and P6 (♂).

**Figure 11.** *Bathylaophonte pacifica* gen. et sp. nov. (♀). A, habitus, vue dorsale ; B, Pl, vue antérieure ; C, P5 et P6 (♂).

as in *B. azorica*. Each ramus with tiny spinules on outer dorsal surface; additional spinular ornamentation present along inner and outer margins and around ventral hind margin; large tube pore present on outer ventral hind margin.

Antennule 7-segmented, armature formula and ornamentation same as in *B. azorica*. Antenna, mandible, maxillule, maxilla, and maxilliped as in *B. azorica*.

Swimming legs P1-P4 (Figs 11B, 12A, 13A, and 14A) with wide intercoxal sclerites and well developed praecoxae. Coxae and bases with anterior rows of surface spinules as figured. Exopods 3-segmented, endopods 2-segmented.

P1 (Fig. 11B). Coxa large with row of spinules along outer margin and spinular patch on anterior surface. Basis with strong, bipinnate spine on distal pedestal, long setules along inner margin and 1 stout bipinnate spine and few spinules along outer margin; 1 tube pore present near articulation with coxa. Exp-1 with 1 long bipinnate spine; exp-2 with 1 unipinnate outer spine; exp-3 with 2 unipinnate spines and 2 geniculate setae. Enp-1 1.3 times as long as exopod, with long spinules along inner margin, and without spinules along outer margin; enp-2 with 1 strong, denticulate claw, 1 small naked seta, and 1 small tube pore.

P2-P4 (Figs 12A, 13A, and 14A). Coxae and bases with spinular rows along outer margin and on anterior surface; basis with 1 tube pore on anterior surface; outer margin of basis with long bipinnate spine (P2) or naked seta (P3-P4); all segments with pattern of spinules as figured; anterior tube pore present near distal margin of enp-1 in P2 and enp-2 in P3-P4. P2 (Fig. 12A) [right P2 with aberrant exp-3 and enp-2 figured, left one lost during preparation]; outer basal spine much longer than in *B. azorica*; enp-2 slightly longer than enp-1; endopod extending beyond middle of exp-3; exp-3 as long as exp-1. P3 (Fig. 13A) enp-2 twice longer than enp-1; endopod extending to distal margin of exp-2; exp-3 slightly longer than exp-1. P4 (Fig. 14A) endopod reaching to middle of exp-2, with long spinules on anterior surface of both segments; enp-2 2.3 times longer than enp-1; exp-3 shorter than exp-1, with expanded outer margin. Spine and setal formulae as in generic diagnosis (except for aberrant P2 enp-2; see notes below).

Fifth pair of legs (Fig. 14B) with separate exopod and baseoendopod, each densely covered with spinules as figured. Baseoendopod forming outer setophore bearing basal seta and row of spinules; with 2 tube-pores. Endopodal lobe extending beyond middle of exopod, with 1 apical and 3 lateral bipinnate setae. Exopod ovoid, about 1.5 times longer than wide; all 5 setae bipinnate, closely set in distal region and arising from very small cylindrical processes.

#### Male

More slender than ♀. Body length 745 µm (measured from

anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 215 µm. Urosome distinctly narrower than prosome (Fig. 10A). Body constricted between individual somites.

Prosome (Fig. 10A-B) and rostrum covered with distinct reticulation and tiny spinules as in ♀.

Urosome (Fig. 10A-B) 6-segmented; all urosomites with surface ornamentation consisting of reticulation and small spinules dorsally and laterally; ventral surface reticulated; ventral hind margin with large spinules laterally and minute spinules medially. Hyaline frills of urosomites not distinct.

Antennule 8-segmented, segmental homologies and armature formula as in *B. azorica*.

P2 - P4 (Figs 12B, 13B, and 14C). Intercoxal sclerites and protopods as in ♀ with surface ornamentation as figured. Exopodal segments more strongly developed than in ♀.

P2 (Fig. 12B). Exopod distinctly longer than in ♀, not bent towards endopod; all segments elongate, exp-1 slightly longer than exp-3. Endopod not reaching to distal margin of exp-2; segmental proportions as in ♀; all setae of enp-2 shorter than in ♀.

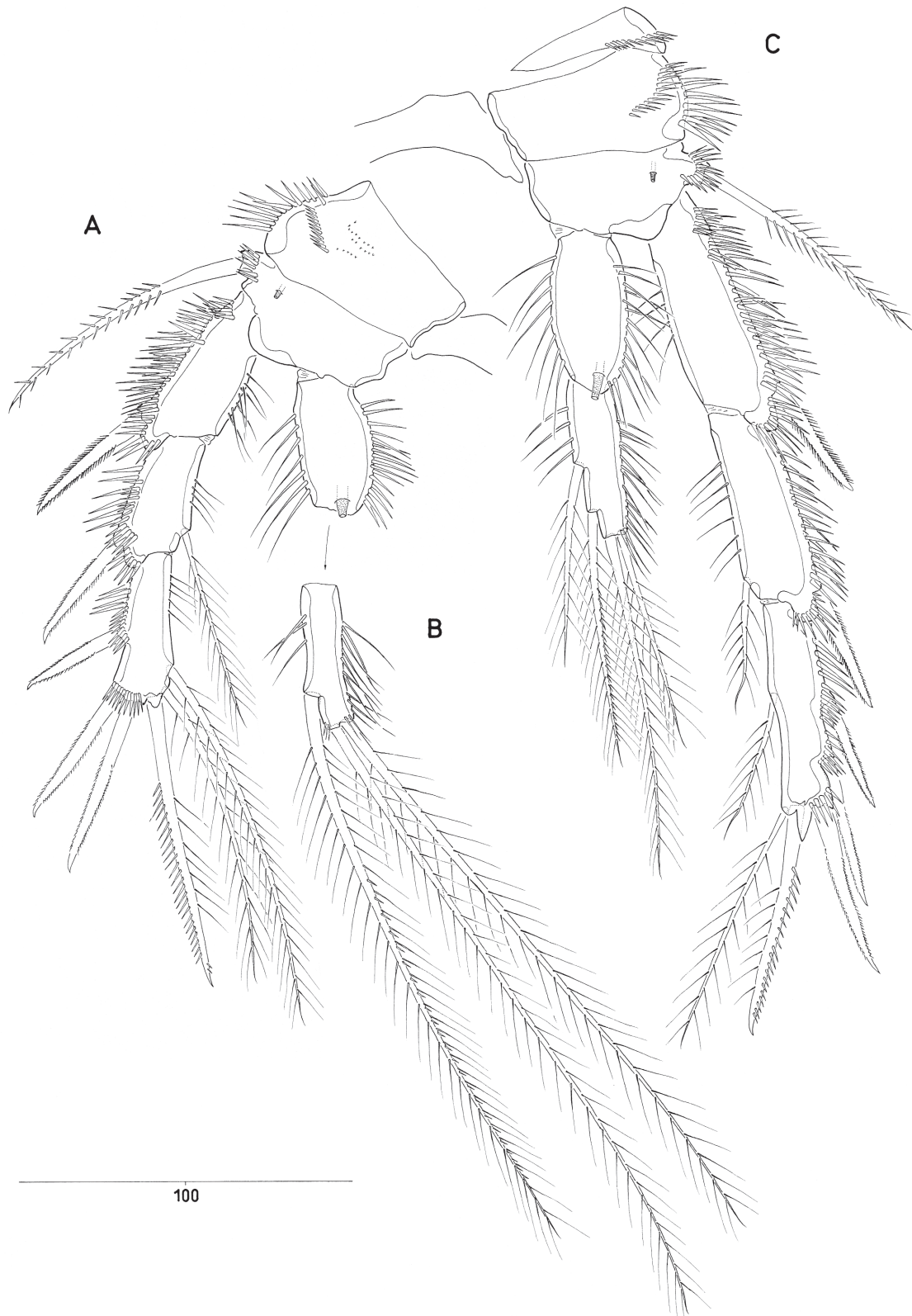
P3 (Fig. 13B). Exopod very robust, not bent inwards; exp-1 longer than other segments; outer spines of exp-3 enlarged but with same ornamentation as in ♀; distal spine of exp-3 much shorter than in ♀, unipinnate. Setae of exp-2 and -3 reduced in size. Endopod 3-segmented, modified; enp-2 produced into conspicuous sigmoid apophysis (homologous with outer spine of enp-2 of ♀); enp-3 with only 2 inner and 2 apical setae, all being shorter than their homologues in the ♀.

P4 (Fig. 14C). Exopod strongly developed and markedly bent inwards; exp-1 and -2 more elongate than in ♀; exp-3 with distal margin forming spinous process separating outer spines from distal one; all spines of exp-3 distinctly enlarged but distal spine shorter than in ♀; inner setae of exp-2 and -3 reduced in length. Endopod shorter than exp-1, enp-2 slightly wider than in ♀; with spinular ornamentation as in ♀; all elements of enp-2 shorter than in ♀.

Fifth pair of legs (Fig. 11C) fused medially; defined at base. Baseoendopod with short setophore bearing outer basal seta and few spinules, and obsolete endopodal lobe represented by 1 pinnate seta; with 1 tube-pore along inner margin and 1 tube-pore near articulation with exopod. Exopod ovoid, about 1.5 times as long as maximum width; with 1 outer bipinnate, 1 apical bipinnate and 2 plumose inner setae; several large setules on anterior surface.

Sixth pair of legs (Fig. 11C) asymmetrical; represented on both sides by small plate (fused to ventral wall of supporting somite along one side; articulating at base and covering gonopore along other side); outer distal corner produced into cylindrical process bearing long spinules and 2 strong bipinnate setae.





**Figure 12.** *Bathylaophonte pacifica* gen. et sp. nov. A, P2 protopod, exopod and enp-1, anterior (♀); B, P2 enp-2 [aberrant], posterior (♀); C, P2, anterior (♂).

**Figure 12.** *Bathylaophonte pacifica* gen. et sp. nov. A, P2 protopodite, exopodite et enp-1, vue antérieure (♀) ; B, P2 enp-2 [anormal], vue postérieure (♀) ; C, P2, vue antérieure (♂).



**Figure 13.** *Bathylaophonte pacifica* gen. et sp. nov. A, P3, anterior (♀); B, P3, anterior (♂).

**Figure 13.** *Bathylaophonte pacifica* gen. et sp. nov. A, P3, vue antérieure (♀); B, P3, vue antérieure (♂).





**Figure 14.** *Bathylaophonte pacifica* gen. et sp. nov. (♀). A, P4, anterior [damaged]; B, P5, anterior [damaged]; C, P4, anterior (♂).

**Figure 14.** *Bathylaophonte pacifica* gen. et sp. nov. (♀). A, P4, vue antérieure ; B, P5, vue antérieure [endommagé] ; C, P4 vue antérieure (♂).

**Etymology.**- The species name refers to the type locality in the Pacific Ocean.

**Notes.** *B. pacifica* is easily distinguishable without dissection by its depressed body shape and pronounced intersomitic constrictions. It is similar to *B. faroensis* in many characters (see below), however, differences in the female P4-P5 and male P3-P4 in conjunction with the wide vertical and horizontal separation of both type localities justify its establishment as a new species. The right P2 in the adult ♀ paratype (Fig. 12A) shows an aberrant armature pattern on the distal exopod and endopod segments. On the distal exopod segment virtually all elements are displaced towards the apical margin. More significant is the atypical armature of the distal endopod segment which bears only 3 setae. Although the left P2 was lost during dissection of the only female available, we assume that the normal setal number on this segment is four. This has been confirmed by examination of the female copepodid stages IV and V as well as the male holotype (Fig. 12B). The adult male of *B. pacifica* bears only 4 setae on the distal endopod segment of P4 (Fig. 14C) compared to 5 setae in the female and in both sexes of the other species. This sexual dimorphism results from the loss of one of the inner setae expressed in the female (Fig. 14A). Since there is no evidence that this is an aberrant feature for the holotype male it has to be regarded as diagnostic for *B. pacifica* (see key to species).

The species can also be differentiated by the ovoid P5 exopod in the female, the long outer basal spine on the P2 and the shape of P4 exp-3 in the female. The sensillar pattern on the cephalothorax and pedigerous somites of *B. pacifica* is also much more elaborate than in *B. azorica*.

*Bathylaophonte faroensis* (T. Scott, 1903) comb. nov.

*Laophonte faroensis* T. Scott, 1903: 4-6, Pl. 1 figs. 9-14, Pl. 2 figs. 1-8.

**Type locality.** - Faroe Channel, depth 159 m.

**Material.** - The original type material is almost certainly lost.

**Note.** - T. Scott (1903) reported *Laophonte faroensis* from a piece of water-logged and partly decayed wood perforated by the boring mollusc *Xylophaga dorsalis* and dredged from about 87 fathoms (159 m) in the Faroe channel. This species

has not been recorded again and attempts to trace the original type material failed. Lang (1948) suspected that T. Scott (1903) had figured leg 3 (his Pl. 2, fig. 4) instead of leg 4 and on the basis of this assumption hinted at a relationship with the *karmensis*-group of the genus *Pseudonycho-camptus* Lang. The uncertainty about the swimming leg setal formula made Lang to relegate *L. faroensis* as *species incerta* in the family. Sewell (1940) used antennule segmentation and P5 armature to divide the genus *Laophonte* Philippi and placed *L. faroensis* in a group containing *L. baltica* Klie, *L. congenera* Sars (= *Paralaophonte*), *L. curticaudata* Boeck (= *Paronycho-camptus*), *L. inornata* A. Scott and *L. meinerti* Brady (= *Paralaophonte*). In his revision of the Laophontidae, Nicholls (1941) considered *L. faroensis* as *species inquirenda* in *Laophonte*, possibly in the *sensu stricto* group, on account of the elongate antennule, the well developed antennary exopod and the rather elongate fifth legs.

T. Scott's (1903) description is remarkably accurate by contemporary early 1900s standards, showing important details such as the presence of the praecoxal endite on the maxilla, the spinulation on the proximal antennule segments and male P4 endopod and the setal ornamentation of the male P6. The setal formula and sexual dimorphism of the swimming legs, the antennule segmentation, the facies of the P1, and the shape and armature of the fifth pair of legs in both sexes unequivocally identify *L. faroensis* as a member of *Bathylaophonte*. Within this genus it clearly occupies an intermediate position between *B. azorica* and *B. pacifica*. With the former it shares the elongate P5, the shape of the apophysis on the male P3 endopod and the setation pattern of the male P4 endopod. Remarkable similarities with *B. pacifica* include the robust P1 endopod, the degree of modification of the male P3-P4 exopods, the setal ornamentation of the male P6 and the sexually dimorphic spinulation of the P4 endopod. *B. faroensis* can be readily distinguished from its Pacific congener by (1) P1 enp-1 being wider and shorter, (2) P3 enp-2 ♂ with differently shaped apophysis, (3) P4 enp-2 ♀ being distinctly longer, (4) P4 exp-3 ♀ not being expanded, (5) P4 enp-2 ♂ with 5 setae/spines (i.e. with 2 inner setae), (6) different P5 exopod shape in ♀ (elongate vs ovoid).

#### Key to species

1. P1 enp-1 1.8 times longer than exopod; P4 exp-1 ♂ longer than exp-2 and -3 combined ..... *B. azorica* sp. nov.  
 P1 enp-1 at most 1.5 times longer than exopod; P4 exp-1 ♂ shorter than exp-2 and -3 combined ..... 2.
2. P5 exopod ♀ ovoid; P4 enp-2 with 4 setae/spines in ♂ ..... *B. pacifica* sp. nov.  
 P5 exopod ♀ elongate; P4 enp-2 with 5 setae/spines in ♂ ..... *B. faroensis* (T. Scott, 1903) comb. nov.

## Discussion

Members of *Bathylaophonte* exhibit a complex surface reticulation and small spinules over the entire dorsal body surface which is reminiscent of the ornamentation pattern described for two other deepwater laophontid genera, *Cornylaophonte* and *Weddellaophonte* (Willen, 1996). Although integumental reticulation seems to be widespread in deep-sea harpacticoids such as Cerviniidae (Itô, 1982, 1983) and Aegisthidae (Lee & Huys, in press a), it is at present very difficult to speculate about its functional significance.

Reductions in swimming leg armature are extremely common in the Laophontidae and a growing body of evidence suggests that similar reductions may have arisen independently numerous times as a result of change in life style such as the adaptation to the interstitial environment. One ramus, which is particularly subjected to such reduction, is the P4 endopod which has retained its ancestral complement of 5 elements on the distal segment in only a minority of the Laophontidae. Apart from the genera of the *Esola*-lineage this [221] pattern is further only found in several species of *Laophonte sensu lato*, and in the genera *Microlaophonte* Vervoort and *Bathylaophonte* (Table 1). None of these genera shares a direct relationship with *Bathylaophonte* which is considered here as a primitive offshoot of a separate lineage and which probably diverged early in the evolution of the non-esolid Laophontidae. The primitiveness of *Bathylaophonte* is also indicated by the

**Table 1.** Swimming leg setal formulae of all Laophontidae with [221] pattern on P4 enp-2.

**Tableau 1.** Formules sétiales des pattes natatoires des Laophontidae présentant la formule [221] à l'enp-2 des P4.

	P2		P3		P4	
<i>Esola typhlops</i> <sup>1</sup>	0.1.123	1.221	0.1.223	1.321	0.1.223	1.221
<i>Esola hirsuta</i>	0.1.123	1.220	0.1.223	1.321	0.1.223	1.221
<i>Esola spelaea</i>	0.1.123	1.221	0.1.222	1.221	0.1.223	1.221
<i>Esola bulligera</i>	0.1.123	1.221	0.1.223	1.321	0.1.223	0.221
<i>Archilaophonte</i>	0.1.123	1.121	0.1.223	1.321	0.1.223	1.221
<i>Laophonte cornuta</i> <sup>2</sup>	0.1.123	1.220	0.1.223	1.321	0.1.223	1.221
<i>BATHYLAOPHONTE</i>	0.1.123	0.220	0.1.223	0.321	0.1.223	0.221
<i>Laophonte</i> spp. <sup>3</sup>	0.1.123	0.220	0.1.223	0.321	0.1.223	0.221
<i>Laophonte adduensis</i>	0.1.122	1.220	0.1.223	1.321	0.1.223	1.221
<i>Laophonte ciliata</i>	0.1.122	1.220	0.1.223	1.321	0.1.222	1.221
<i>Microlaophonte trisetosa</i>	0.1.122	0.220	0.1.222	0.321	0.1.222	0.221
<i>Microlaophonte spongiicola</i>	0.1.122	0.120	0.1.222	0.220	0.1.222	0.221
<i>Laophonte wiltoni</i> <sup>4</sup>	0.1.023	0.120	?	?	0.1.023	0.221

<sup>1</sup> and related species *E. longiremis* (T. Scott), *E. longicauda* Edwards

<sup>2</sup> and related species *L. expansa* Fiers, *L. plana* Fiers

<sup>3</sup> *L. serrata* (Claus), *L. dominicalis* Monard, *L. inornata* A. Scott, *L. parvula* Sars

<sup>4</sup> Lang (1948) suspected that T. Scott (1912) had figured P3 instead of P4.

7-segmented antennule in the female, the well developed antennary exopod, the mandibular palp showing vestigial rami and the retention of the ancestral setation on the exopods of P2-P4 and on P3 enp-2 [321].

Huys (1990) postulated that the presence of a spinous process on the second antennular segment in Laophontidae was a plesiomorphic condition inherited from the common laophontoidean stock and that this process was secondarily reduced or lost in several lineages independently. The condition in *Bathylaophonte* where the spinous process is represented by a small knob-like protuberance can be interpreted as a transitional state towards total loss. Due to their small size and frequent unsatisfactory orientation and mounting of antennules, similar rudimentary processes in other genera may have been overlooked in previous descriptions.

*Bathylaophonte* displays a unique sexual dimorphism on the swimming legs. The exopods of P2 - P4 are elongated in the ♂, the exopods of P3 - P4 having stronger external spines and shorter inner setae than in the ♀. Exopodal modifications of the swimming legs are common in the Laophontidae and particularly well expressed in the genera *Heterolaophonte* Lang, *Platyhelipus* Brady, *Paralaophonte* Lang and *Paronychocamptus* Lang. The latter genus is reviewed in more detail below since some of its species show noteworthy similarities with *Bathylaophonte*.

### Polyphyletic status of *Paronychocamptus*

Lang (1944) first proposed the genus *Paronychocamptus* in a short introductory paper announcing the publication of his 1948 monograph. He subdivided the genus into the *curticaudatus*-group and the *exiguus*-group for which he designated *Laophonte curticaudata* and *Laophonte exigua* Sars, 1905 as the respective type species. Since the author did not designate a type for the genus itself Lang's (1944) generic name cannot be validated as an available name (ICZN Art.13(b)). In his monograph Lang (1948) presented a more comprehensive account of the genus with diagnoses of all the species, maintaining the subdivision in two groups and formally designating *L. curticaudata* as the type species. In the *curticaudatus*-group he further included *Paronychocamptus nanus* (Sars, 1908), *P. huntsmani* (Willey, 1923) and *P. capillatus* (Wilson, 1932), all formerly described in the genus *Laophonte*. The *exiguus*-group contained only *P. exiguus* (Sars, 1905).

Four species have been added since: *P. leuke* Por, 1959 from the Rumanian Black Sea coast, *P. proprius* Lang, 1965 from California, *P. connexus* Pallares, 1979 from Tierra del Fuego and *P. anomalus* Ranga Reddy, 1984 from India.

Lang (1948) split *Laophonte capillata*, Wilson, 1932 into two different species, placing the female of Wilson's (1932) description into the genus *Paronychocamptus* with the specific name *capillatus*, and the male into the genus

*Heterolaophonte* as a new species *H. noncapillata*. Coull (1976) re-examined the original type material and pointed out that Wilson (1932) had designated the male and not the female as the type of *L. capillata*. Hence, the correct name for *L. capillata* is *Heterolaophonte capillata*, rendering *H. noncapillata* Lang, 1948 a junior subjective synonym of the latter. Coull (1976) placed *H. capillata* in the *quinespinosa*-group which was upgraded to generic level as *Quinquelaophonte* by Wells et al. (1982). He further confirmed Lang's (1948) placement of the female of *L. capillata* in *Paronychocamptus* and renamed it *P. wilsoni*.

Lang (1965) transferred *P. leuke* to *Laophonte* without giving any explicit reasons other than that it differs fundamentally in the sexual dimorphism of the swimming legs. He also expressed doubts about his own placement of *P. proprius* in *Paronychocamptus* and for some unknown reason left *P. capillata* out of his key to species.

Upon re-examination of the descriptions of all nine species it became obvious that the genus *Paronychocamptus* represents a polyphyletic taxon, containing representatives of five lineages. We have re-allocated the species as summarized in Table 2. In its amended definition the genus includes only *P. curticaudatus*, *P. nanus*, *P. huntsmani* and *P. wilsoni*. This is a well defined group of exclusively boreal species characterized by a 0.111 formula on P4 enp-2, only 4 setae on the ♀ P5 baseopod and a primitive P3 exopod with 7 setae/spines on the distal segment (Table 3).

#### Diagnosis

Laophontidae. Body sub-cylindrical, slightly depressed.

Rostrum small. Caudal rami cylindrical, setae IV and V well developed. Antennule 6- or 7-segmented in ♀, with aesthetasc on segment 4 and as part of acrothek on apical segment; without process on segment 2. Antennary exopod well developed with 4 setae or vestigial and bisetose. Maxilliped with 1 seta on syncoxa. P1 exopod 2- or 3-segmented; exp-1 with normal outer spine; exopod armature formula [0.0.022 or 0.023]. P2-P4 with 3-segmented exopods and 2-segmented endopods; setal formula as follows:

	exopod	endopod
P2	0.1.123	0.120 or 0.220 [ $\delta$ : always 0.120]
P3	0.1.223	0.321 [ $\delta$ : 0.0.220]
P4	0.1.122	0.111

P2 endopod with elongate segments in  $\delta$ ; enp-2  $\delta$  with 1 inner seta. P3 endopod  $\delta$  3-segmented; enp-2 without inner seta but with short spinous apophysis. Exopods of P2 and P4 moderately, of P3 strongly sexually dimorphic; segments and outer spines more strongly developed; inner distal seta of exp-3 not modified into short spine but inner setae of  $\delta$  P3-P4 exp-3 often spiniform.

P5 ♀ endopodal lobe with 4 setae, located around distal and inner margin; exopod with 5 setae. P5  $\delta$  exopod with 3-4 setae; endopodal lobe absent or represented by 1 seta.

P6  $\delta$  with 2 well developed setae.

One egg-sac.

Predominantly marine and brackish water.

**Table 2.** Re-allocation of species formerly placed in the genus *Paronychocamptus* (marked in bold).

**Tableau 2.** Réaffectation des espèces (en gras) préalablement placées dans le genre *Paronychocamptus*.

Genus	Other species included	
<i>Paronychocamptus</i> Lang, 1948	<b><i>curticaudatus</i></b> <b><i>nanus</i></b> <b><i>huntsmani</i></b> <b><i>wilsoni</i></b>	
<i>Onychocamptus</i> Daday, 1903	<b><i>anomalus</i></b>	<i>O. mohammed</i> (Blanchard & Richard, 1891) <i>O. bengalensis</i> (Sewell, 1934) <i>O. besnardi</i> Jakobi, 1954 <i>O. vittospinulosa</i> (Shen & Tai, 1963) <i>O. taifensis</i> Kikuchi, Dai & Itô, 1993 <i>O. krusensterni</i> Schizas & Shirley, 1994
<i>Heteronychocamptus</i> gen. nov.	<b><i>exiguus</i></b> <b><i>connexus</i></b>	
<i>Psammoplatypus</i> gen. nov.	<b><i>proprius</i></b>	<i>Klieonychocamptus discipes</i> Noodt, 1958
<i>Pontophonte</i> gen. nov.	<b><i>leuke</i></b>	<i>Laophonte brevifurca</i> Sars, 1908 sensu Griga (1963)

**Table 3.** Species previously allocated to *Paronychocamptus*. Antennule (♀) segmentation and setal formula of P2-P5 (e = exopod; b = baseoendopod).

**Tableau 3.** Espèces préalablement placées dans le genre *Paronychocamptus*. Segmentation de l'antennule (♀) et chétotaxie des P2-P5 (e = exopodite ; b = baséoendopodite).

species		P2		P3		P4		P3 enp ♂		P5♀		P5♂		A1 ♀
		e	b	e	b	e	b	e	b	e	b	e	b	
<i>curticaudatus</i>	♀/♂	0.1.123	0.120	0.1.223	0.321	0.1.122	0.111	0.0.220	5	4	4	1	7	
<i>nanus</i>	♀	0.1.123	0.220	0.1.223	0.321	0.1.122	0.111		5	4			6	
	♂	—	0.120	—	—	—	—	0.0.220			3	0		
<i>huntsmani</i>	♀/♂	unknown	unknown	0.1.223	0.321*	0.1.122	0.111	0.0.220	5	4	4	0	6	
<i>wilsoni</i>	♀	0.1.123	0.220	0.1.223	0.321	0.1.122	0.111		5	4			6	
	♂	—	0.120	—	—	—	—	0.0.220			4	0		
<i>exiguus</i>	♀	0.1.123	1.120	0.1.123	1.221	0.1.122	1.121		4	5			7	
	♂	—	—	—	0.0.220	—	0.121	0.0.220			4	0		
<i>connexus</i>	♀	0.1.123	0.120	0.1.123	1.221	0.1.123	1.121		5	5			7	
	♂	—	0.(1-2)20	—	0.0.220	—	0.121	0.0.220			4	0		
<i>proprius</i>	♂	0.0.023	0.120	0.1.023	0.0.020	0.1.023	0.(1-2)20	0.0.020			4	2		
<i>anomalus</i>	♀/♂	0.1.123	0.220	0.1.123	0.321	0.1.122	0.111	0.1.220	4	3	3	0	5	
<i>leuke</i>	♀/♂	0.1.123	0.220	0.1.123	0.221	0.1.123	0.111	0.0.220	5	4	5	2	7	

\*: by comparison with ♂ P3 (Willey, 1923: Fig. 18)

Key to species

1. P1 exopod 2-segmented; P5 exopod ♂ with 3 setae ..... *P. nanus* (Sars, 1908).  
 P1 exopod 3-segmented; P5 exopod ♂ with 4 setae ..... 2.
2. Antennule ♀ 7-segmented; P2 enp-2 ♀ with 1 inner seta; P5 baseoendopod ♂ with 1 seta ..... *P. curticaudatus* (Boeck, 1865).  
 Antennule ♀ 6-segmented; P2 enp-2 ♀ with 2 inner setae; P5 baseoendopod ♂ without setae ..... 3.
3. Antennary exopod small, with 2 setae; caudal ramus slightly longer than wide ..... *P. wilsoni* Coull, 1976.  
 Antennary exopod well developed, with 4 setae; caudal ramus about 3 times longer than wide ..... *P. huntsmani* (Willey, 1923).

Redefinition of *Onychocamptus* Daday, 1903

The genus *Onychocamptus* has a complicated taxonomic history, having served at times as a repository for various unrelated species. The gradual subdivision of the genus has significantly refined its boundaries, and following the establishment of the genera *Echinolaophonte* Nicholls, *Klieonychocamptus* Noodt and *Folioquinpes* Fiers & Rutledge only 6 species are currently included in the genus (Nicholls, 1941; Noodt, 1958; Lang, 1965; Fiers & Rutledge, 1990). Fiers (1998) unequivocally demonstrated that *O. talipes* (Wilson, 1932) is a junior subjective synonym of *O. mohammed*.

Ranga Reddy (1984) recognized the similarity between *Paronychocamptus anomalus* and the genus *Onychocamptus* in the ♀ 5-segmented antennule, the

presence of sensillar tubercles (socles) on the body somites, the strongly developed seta V of the caudal ramus and the trisetose baseoendopod of the ♀ leg 5. Despite these diagnostic characters the author preferred to place the species in *Paronychocamptus*, a decision which was not based on similarities with the latter but on differences with *Onychocamptus*, i.e. the reduced antennary exopod, the presence of only 2 outer spines on P4 exp-3 and of 4 setae on the P5 exopod in both sexes. Re-examination of the paratypes of *P. anomalus* (NHM reg. no. 1982.274) revealed that the antennary exopod is indeed rudimentary but bears only 1 seta instead of 2 as Ranga Reddy (1984) claimed. We could also confirm the presence of 4 setae on the ♀ P5 exopod, however failed to do so for the ♂ P5. The innermost spiniform element illustrated by Ranga Reddy is one of the

three spinules found around the inner margin, the exopod therefore bearing only 3 setae. The unusual [0.1.122] formula of the P4 exopod has since been found in another species, *O. krusensterni*, described from a lagoon in northwestern Alaska (Schizas & Shirley, 1994). A similar reduction of the P2 endopod was recently recorded in *O. taifensis* by Kikuchi et al. (1993) showing that the swimming leg armature is not constant within the genus *Onychocamptus* (Table 4). Two additional characters, the 2-segmented P1 exopod (with a large pinnate outer spine on exp-1) and the ♂ P3 endopod (retaining the inner seta on enp-2) provide further evidence for the placement of *P. anomalus* in *Onychocamptus*. The few similarities with *P. nanus* outlined by Ranga Reddy (1984) are regarded here as a product of convergence. *O. anomalus* comb. nov., known only from the brackish water Lake Kolleru in Andhra Pradesh (India), occupies an isolated position in *Onychocamptus* because of the primitive P5 and the reduced antennary exopod.

Lang (1965) regarded *O. besnardi* (from Paraná and Santa Catarina, Brazil) as a forma of *O. mohammed*. Jakobi's (1954) description is fragmentary in many aspects but shows two important differences with the latter: (1) P4 exp-3 with only 2 outer spines (as in *O. anomalus* and *O. krusensterni*) and without inner seta, (2) much shorter caudal rami. Jakobi also lists 0.221 for the ♀ P3 endopodal formula but does not figure this leg. However, comparison with his illustration of the ♂ P3, showing a 0.1.220 formula, suggests that this is an error and that the female has 3 inner setae on the distal endopod segment as in other members of the genus. Although *O. mohammed* has been recorded from other localities in Brazil (Chappuis, 1936; Schubart, 1938; Por, 1984; Por et al., 1984) we prefer to maintain

*O. besnardi* as a distinct species pending the collection of topotype material.

Shen & Tai (1963) described *Laophonte vitiospinulosa* from the delta of the Pearl River in South China and pointed out differences in the female P5, shape of genital double-somite and caudal ramus length with *O. mohammed*, which they had redescribed (as *L. mohammed*) in an earlier paper on the freshwater copepods of the Wu-Li Lake (Shen & Tai, 1962). Lang (1965) regarded *L. vitiospinulosa* as a subspecies of *O. mohammed* but Dussart & Defaye (1990) did not follow this relegation and continued to consider it as a distinct species. In view of the presence of other *Onychocamptus* species in the Chinese-Korean region (Kikuchi et al., 1993; Song & Chang, 1995) we consider Lang's (1965) decision premature and have included *O. vitiospinulosa* in the species key below. A more complete redescription of both sexes of *O. vitiospinulosa* was given by Shen (1979).

The genus *Onychocamptus* belongs to an ancient lineage which probably diverged very early on from the marine laophontid stemgroup and subsequently radiated in brackish water and lacustrine environments. It successfully colonized all continents including Australia (Hamond, 1973a) and New Zealand (Lewis, 1984). Although the genus is advanced in many aspects such as the armature of the P4 endopod, the P5 in both sexes and the 5-segmented ♀ antennules, the retention of the ancestral pattern on the ♂ P3 endopod unequivocally indicates its early origin. The majority of the Laophontidae with a 0-1.321 pattern on the ♀ P3 endopod have a 0-1.0.220 formula in the male, resulting from (a) the modification of the outer spine into an apophysis on enp-2, and (b) the loss of the proximal inner seta. In *Onychocamptus* the latter seta is retained in the male

**Table 4.** Species of *Onychocamptus* (upper) and *Folioquinpes* (lower). Armature formula for antennary exopod, P2-P4 (♀) and P5 of both sexes.

**Tableau 4.** Espèces des genres *Onychocamptus* (en haut) et *Folioquinpes* (en bas). Formule de l'armature de l'exopodite des antennes, des P2-P4 (♀) et des P5 (pour les deux sexes).

	A2	P2		P3		P4		P5♀		P5♂
		exp	enp	exp	enp	exp	enp	exp	enp	exp
<i>mohammed</i> (Blanchard & Richard, 1891)	4	0.1.123	0.220	0.1.123	0.321	0.1.123	0.111	3	3	2
<i>bengalensis</i> (Sewell, 1934)	4	0.1.123	0.220	0.1.123	0.321	0.1.123	0.111	3	3	2
<i>besnardi</i> Jakobi, 1954	4	0.1.123	0.220	0.1.123	0.321*	0.1.022	0.111	3	3	2
<i>vitiospinulosa</i> (Shen & Tai, 1963)	4	0.1.123	0.220	0.1.123	0.321	0.1.123	0.111	3	2	2
<i>anomalus</i> (Ranga Reddy, 1984) comb. n.	1	0.1.123	0.220	0.1.123	0.321	0.1.122	0.111	4	3	3
<i>taifensis</i> Kikuchi, Dai & Itô, 1993	4	0.1.123	0.120	0.1.123	0.321	0.1.123	0.111	3	3	2
<i>krusensterni</i> Schizas & Shirley, 1994	4	0.1.123	0.220	0.1.123	0.321	0.1.122	0.111	3	3	2
<i>chathamensis</i> (Sars, 1905)	4	0.1.123	0.220	0.1.123	0.321	0.1.123	0.111	3-4	3	3
<i>mangalis</i> Fiers & Rutledge, 1990	4	0.1.123	0.220	0.0-1.123	0.221	0.0.123	0.111	4	2	2

\* corrected (see text).

and located on the middle endopod segment. This ancestral pattern is very rare in the family and further only found in the *Archilaophonte-Esola* lineage (Huys & Lee, in prep.) and the *cornuta*-group of the genus *Laophonte*, including *L. cornuta* Philippi, *L. adduensis* Sewell, *L. ciliata* Noodt, *L. expansa* Fiers and *L. plana* Fiers. The genus *Onychocamptus* has often been affiliated with *Paronychocamptus* and *Klieonychocamptus* because of the sexual dimorphism of the P3-P4 exopods. There is no doubt that exopodal sexual dimorphism, in particular the enlargement and modification of armature elements, has evolved several times independently in the evolution of the Laophontidae. The key to understanding this multiple origin lies in the scrutinous comparison and hence homology of female and male elements. In *Onychocamptus* the inner distal seta of P3-P4 exp-3 is well developed in the female but modified into a strong spine in the male. This is a marked difference with other genera such as *Heterolaophonte* and *Paronychocamptus* where the inner distal seta is usually reduced in the male.

Fiers & Rutledge (1990) transferred *O. chathamensis* to a new genus *Folioquinpes* but did not discuss the relationships of this genus. Assessment of the phylogenetic position of *Folioquinpes* is hampered by the complete lack of swimming leg sexual dimorphism which is probably the result of heterochrony. However, the presence of sensillar tubercles on the body somites, the morphology of leg 1 (large pinnate seta on exp-1; exopod 2-segmented), the swimming leg setal formula (Table 4), the short ♀ antennules (with at most vestigial process on segment 2), the armature of the ♀ P5 and the reduced ♂ P5 provide sufficient evidence for a sistergroup relationship with *Onychocamptus*. Incidentally, both *Folioquinpes* species typically inhabit brackish water habitats and saline lakes (Sars, 1905; R  he, 1914; Sewell, 1924; Fiers & Rutledge, 1990).

*Diagnosis*

Laophontidae. Body sub-cylindrical, slightly depressed. Posterior margin of cephalothorax and body somites (except penultimate and anal somites) with sensillar tubercles (socles). Rostrum small. Caudal rami cylindrical, seta V strongly developed, seta IV reduced. Antennule 5-segmented in ♀, with aesthetasc on segment 3 and as part of acrothek on segment 5; without process on segment 2. Antennary exopod well developed with 4 setae or vestigial and unisetose. Maxilliped with 1 seta on syncoxa. P1 exopod 2-segmented; exp-1 with long pinnate outer spine; exp-2 with 5 elements. P2-P4 with 3-segmented exopods and 2-segmented endopods; setal formula as follows:

	exopod	endopod
P2	0.1.123	0.[1-2]20
P3	0.1.123	0.321 [♂: 0.1.220]
P4	0.1.[0-1]2[2-3]	0.111

P3 endopod ♂ 3-segmented; enp-2 with inner seta and short spinous apophysis. P3-P4 exopods sexually dimorphic; segments and outer spines more strongly developed; inner distal seta of exp-3 modified into short spine. Slight sexual dimorphism often also in P2 exopod.

P5 ♀ endopodal lobe with 2-3 setae, located around inner margin; exopod with 3-4 setae, fused or vaguely defined at base. P5 ♂ exopod small, with 2-3 setae; endopodal lobe absent, no armature.

P6 ♂ with 2 well developed setae.

One egg-sac.

Predominantly in brackish and freshwater.

Type species: *Onychocamptus heteropus* Daday, 1903 = *Laophonte Mohammed* Blanchard & Richard, 1891 = *Onychocamptus mohammed* (Blanchard & Richard, 1891) [by monotypy; Daday (1903)]

Key to species

1. P4 exp-3 with 2 outer spines..... 2.  
    P4 exp-3 with 3 outer spines..... 4.
2. Antennary exopod reduced, with 1 seta; P5 exopod with 4 setae in ♀ and 3 setae in ♂ ..... *anomalus* (Ranga Reddy, 1984) comb. nov.  
    Antennary exopod well developed, with 4 setae; P5 exopod with 3 setae in ♀ and 2 setae in ♂ ..... 3.
3. P4 exp-3 with inner seta; caudal rami about three times as long as wide ..... *krusensterni* Schizas & Shirley, 1994  
    P4 exp-3 without inner seta; caudal rami about twice as long as wide ..... *besnardi* Jakobi, 1954
4. P2 enp-2 with 1 inner seta ..... *taifensis* Kikuchi, Dai & It  , 1993  
    P2 enp-2 with 2 inner setae ..... 5.
5. P5 ♀ with fused exopod and baseoendopod forming bilobate plate ..... *bengalensis* (Sewell, 1934)  
    P5 ♀ with exopod and baseoendopod not fused ..... 6.
6. P5 baseoendopod ♀ with 3 setae ..... *mohammed* (Blanchard & Richard, 1891)  
    P5 baseoendopod ♀ with 2 setae ..... *vitiospinulosa* (Shen & Tai, 1963)

*Psammoplatypus* gen. nov.

Lang (1965: 486) pointed out some unusual characters in the male of *Paronychocamptus proprius*, in particular the robust P2 exopod, the peculiar modification of the P3 endopod and the presence of 2 setae on the endopodal lobe of leg 5. In the absence of the female he considered the generic placement of this species as provisional. In the same paper Lang (1965: 446) remarked on the great diversity in the secondary sexual characters within the genus *Klieonychocamptus* as diagnosed by Noodt (1958), and suspected that the taxon was artificial, an opinion recently reiterated by Wells & Rao (1987). Although there are a number of similarities between some of the species, it is clear that Noodt (1958) blurred the generic boundaries considerably by including *K. discipes* into the genus. This species differs from its supposed congeners in the presence of an inner seta on P3-P4 exp-2 and a P2 endopod which is markedly reduced in size, being smaller than that of P3 and P4. The female has a characteristically flattened P4 exopod (cf. name) and 5 setae on the P5 baseoendopod (instead of 3 or 4 in the other species). Males differ in the 3-segmented P3 endopod (instead of 2-segmented) and the presence of 2 setae on the P5 baseoendopod (instead of 1). Comparison of the swimming legs of *K. discipes* and *P. proprius* reveals remarkable similarity and rises the strong suspicion that Lang (1965) has mislabelled P2 and P4 in the latter species. The leg labeled as P4 is undoubtedly the P2 as evidenced by the very small endopod and the slight modification of the exopod. Conversely, his P2 is in reality the P4, showing the typical modification of the exopod as found in the P3. This pattern in which the P2 exopod shows a slight modification and the P3-P4 exopods are transformed in a more profound but similar way is widespread in the Laophontidae. The configuration implied by Lang's (1965) interpretation however, is not displayed in any other member of the family.

*K. discipes* and *P. proprius* display a striking similarity in the male morphology, including the 3-segmented P3 endopod with well developed apophysis on enp-2, the exopodal sexual dimorphism, and the setation of leg 5 with 2 setae on the baseoendopod and 4 on the exopod, the inner one being clearly shorter than the others. The resemblance between both species is also reflected in the amended setal formula (Table 5). It should be noted that both Noodt (1958) and Lang (1965) ignored the reduced seta at the inner corner of P2-P4 exp-3 in their swimming leg setal formulae. Noodt (1958) also illustrated what appears to be a small inner seta on P2 enp-2 in the male of *K. discipes*, but not in the female. This minute seta was also found by Lang in the male of *P. proprius*, however, without knowledge of the female it is difficult to decide whether this is a genuine sexually dimorphic feature. In spite of the differences in P1 exopod

segmentation, P3 endopodal setation and caudal ramus morphology we propose a new genus *Psammoplatypus* to accommodate both species. The discovery of the unknown female of *P. proprius* will be crucial in either confirming or rejecting this course of action.

## Diagnosis

Laophontidae. Body sub-cylindrical, slightly depressed. Body covered with minute spinules. Rostrum bell-shaped, small. Caudal rami cylindrical, setae IV and V well developed. Antennule 6-segmented in ♀, with aesthetasc on segment 4 and as part of acrothek on segment 6; without (♀) or with small (♂) spinous process on segment 2. Antennary exopod well developed with 4 setae. Maxilliped with 1 seta on syncoxa. P1 exopod 2- or 3-segmented; exp-1 with short outer seta; distal exopod segment with 4 (if 3-segmented) or 5 elements (if 2-segmented). P2-P4 with 3-segmented exopods and 2-segmented endopods; P2 endopod much smaller than in P3; P4 exopod ♀ flattened; with setal formula as follows:

	exopod	endopod
P2	0.0.023	0.020 [♂: 0.120]
P3	0.1.023	0.121 [♂: 0.0.(0-1)20]
P4	0.1.023	0.121 [♂: 0.(1-2)2(0-1)]

P3 endopod ♂ 3-segmented; enp-2 without inner seta but with well developed curved apophysis. P3-P4 exopods sexually dimorphic; segments and outer spines more strongly developed; inner distal seta of exp-3 rudimentary. Slight sexual dimorphism also in P2 exopod.

P5 ♀ endopodal lobe with 5 setae, located around inner margin; exopod elongate-oval, with 4 setae. P5 ♂ exopod longer than wide, with 4 setae; endopodal lobe weakly developed, with 2 setae.

P6 ♂ with 2 well developed setae.

One egg-sac.

Sandy beaches.

Type species. - *Klieonychocamptus discipes* Noodt, 1958 = *Psammoplatypus discipes* (Noodt, 1958) comb. nov.

Other species. - *Paronychocamptus proprius* Lang, 1965 = *Psammoplatypus proprius* (Lang, 1965) comb. nov.

Etymology. - The generic name is derived from the Greek *psammos*, sand, *platys*, flat and *pous*, foot, and refers to the flattened P4 exopod of this sandy beach inhabiting genus. Gender: masculine.

Notes. The reduced P2 endopod, being distinctly smaller than the endopods of P3 and P4, is a character of pivotal phylogenetic significance. Fiers (1992a-b) used it as a synapomorphy to link the genera *Hemilaophonte*



**Table 5.** Comparison between *Paronychocamptus proprius* Lang, 1965 and species of *Klieonychocamptus* Noodt (e = exopod, b = baseoendopod).

**Tableau 5.** Comparaison entre *Paronychocamptus proprius* Lang, 1965 et les espèces du genre *Klieonychocamptus* Noodt (e = exopodite, b = baséoendopodite).

species		P2		P3		P4		P3 enp ♂		P5 ♀		P5 ♂	
		e	b	e	b	e	b	e	b	e	b	e	b
<i>P. proprius</i>	♂ (Lang, 1965)	0.1.023	0.(1-2)20	0.1.023	0.0.020	0.0.023	0.120	0.0.020	—	4	2		
	♂ (revised)	0.0.023	0.120	—	—	0.1.023	0.(1-2)20						
<i>Klieonychocamptus</i>													
	<i>kliei</i>	0.0.023	0.120	0.0.023	0.121	0.0.023	0.121	0.120	4	3	3	1	
	<i>confluens</i>	0.0.023	0.120	0.0.023	0.121	0.0.023	0.121	0.120	4	3	3	1	
	<i>ponticus</i>	0.0.022	0.120	0.0.022	0.121	0.0.022	0.12(0-1)	0.120	4	3	3	0	
<i>discipes</i>	♀	0.0.023	0.020	0.1.023	0.121	0.1.023	0.121		4	5			
	♂		0.120		0.0.120			0.0.120			4	2	

Jakubisiak, *Coullia* Hamond, *Phycolaophonte* Pallares and *Robustunguis* Fiers. Males of these genera also share the 2-segmented P3 endopod, typically bearing a slightly curved apical or subapical apophysis on the distal segment which is closely associated with the 2 terminal setae. No males have been described for the genus *Coullia* but Fiers (1992a) confirmed this character in some as yet undescribed species of this genus. Members of this genus-group typically have 6 setae on the P5 exopod in the female and 5 in the male (unknown in *Coullia*) (Table 6). The close relationship of *Psammoplatypus* gen. nov. to this lineage is demonstrated by the reduced P2 endopod, the absence of inner setae on P2-P4 exp-3, the sexual dimorphism on the P2-P4 exopods involving the reduction of the inner distal seta of exp-3 and the elongate-oval P5 exopod of the female.

Additional similarity is revealed in the 6-segmented ♀ antennule and the absence of distinct processes on the first two segments of this appendage. The male P5 baseoendopod is remarkably constant, bearing the ancestral number of 2 setae in all genera.

*Psammoplatypus* is regarded as the most primitive genus in this lineage. Evidence for this ancestral position is found in the swimming leg armature and the 3-segmented condition of the male P3 endopod (Table 6). The inner seta of P3-P4 exp-3 is retained in both sexes of *Psammoplatypus* but is absent in the other genera with the exception of the male of *Phycolaophonte insularis* Pallares which has an inner seta on P3 exp-2 (Pallares, 1975). Mielke (1985), who figured only the endopods in his partial but excellent redescription, gave no evidence to contradict this

**Table 6.** Genera related to *Psammoplatypus* gen. nov. Antennule ♀ segmentation and armature of P2-P5 of both sexes. A = absent; e = exopod; b = baseoendopod.

**Tableau 6.** Genres apparentés à *Psammoplatypus* gen. nov. Segmentation des antennules (♀) et armature des P2-P5 chez les deux sexes. A = absent ; e = exopodite ; b = baséoendopodite.

		A1 ♀		P2		P3		P4		P5 ♀		P5 ♂	
		e	b	e	b	e	b	e	b	e	b	e	b
<i>Psammoplatypus</i> gen. nov.	♀	6	0.0.023	0.020	0.1.023	0.121	0.1.023	0.121	4	5			
	♂	-	0.0.023	0.120	0.1.023	0.0.(0-1)20	0.1.023	0.(1-2)2(0-1)			4	2	
<i>Phycolaophonte</i> Pallares	♀	6	0.0.023	0.020	0.0.023	0.021	0.0.023	0.021	6	5			
	♂	-	0.1.023	0.020	0.1.023	0.020	0.0.022	0.021			5	2	
<i>Coullia</i> Hamond <sup>1</sup>	♀	6-7?	0.0.023	0.020 or A	0.0.023	0.02(0-1)	0.0.022	0.020	6	3-5	?	?	
<i>Hemilaophonte</i> Jakubisiak	♀/♂	6	0.0.023	0.020	0.0.023	0.020	0.022	0.020	6	4	5	2	
<i>Robustunguis</i> Fiers <sup>2</sup>	♀	6	0.0.022	010	0.0.022	020	0.0.022	020	6	4			
	♂	-	0.1.022	0.010	0.0.022	020	0.0.022	0.021			5	2	

<sup>1</sup> Based on *Coullia heteropus* Hamond, *C. clysmiae* (Por & Marcus) and *C. platychelipusoides* (Noodt). Both Hamond (1973b) and Noodt (1958) overlooked the tiny inner distal seta on P2-P4 exp-3. The 7-segmented condition of the ♀ antennule of *C. platychelipusoides* requires confirmation.

<sup>2</sup> Based on the most primitive species *R. unguatus* Fiers.

observation. The primitive position of *Psammoplatypus* is reinforced by the retention of the inner seta on P4 enp-2 which is lost in all other genera.

Autapomorphies for the new genus include the reduced armature (4 setae) on the P5 exopod in both sexes and the flattened P4 exopod in the female. Both species of *Psammoplatypus* typically inhabit sandy beaches and are thus far known only from their respective type localities. *Hemilaophonte*, *Phycolaophonte*, *Coullia* and *Robustunguis* all have a robust P1 endopod and/or claw which is related to their close association with decapods (Fiers, 1992a-b) and *Macrocystis* algae (Pallares, 1975).

*Pontophonte* gen. nov.

Por (1959, 1964b) placed *P. leuke* in *Paronychocamptus* but Lang (1965) transferred this Black Sea species to the genus *Laophonte* for no apparent reason. There is a remarkable similarity between *P. leuke* and another species from the Black Sea described by Griga (1963) under the name *Laophonte brevifurca*. The latter shows some important differences with Sars' (1920) original description of *L. brevifurca* which was based on a single female recorded outside Oslofjord. The Norwegian specimen can be distinguished from the Ukrainian material by the presence of only 1 inner seta on P2 enp-2 (instead of 0.220) and the reduced [0.111] armature on the P3 endopod (instead of 0.221). Additional differences can be found in the relative proportions of the endopodal segments of P2-P4 and of various setal elements but these discrepancies are of minor significance. Females of Griga's (1963) species differ from *P. leuke* only in the 6-segmented antennule which was described (but not figured) as 7-segmented by Por (1959, 1964b). Both species can be most easily distinguished on the basis of male characters although some of these should be used with caution. For example, the male P5 of *L. brevifurca* sensu Griga (1963) shows 3 long setae on the baseoendopod but it is unlikely that this is the normal condition since the maximum setal number displayed in the families of the Laophontoidea is two (Huys, 1990; Huys & Lee, 1999). Similarly, Por (1959) figures 5 setae on the male P5 exopod but only 4 are illustrated by Griga (1963). From the relative lengths of the setae it seems possible that Griga (1963) overlooked the small seta situated between the two long inner ones of *P. leuke*. The male P3 exopod is only slightly modified in the Ukrainian species but is much more robust in *P. leuke* and shows the typical blunt spines on the distal segment. The P3 endopod has retained two inner setae on the distal segment in the latter but only 1 in Griga's species although this difference would require confirmation.

Both Black Sea species are accommodated in a new genus *Pontophonte*. The Ukrainian material is designated here as a distinct species *P. grigae* sp. nov. in recognition of

Dr R.E. Griga's contributions to the taxonomy of Black Sea harpacticoids.

Diagnosis

Laophontidae. Body sub-cylindrical, slightly depressed. Posterior margin of cephalothorax and body somites (except penultimate and anal somites) without sensillar tubercles (socles). Rostrum prominent, rounded anteriorly. Caudal rami cylindrical, slightly longer than wide, setae IV and V strongly developed. Antennule 6- or 7-segmented in ♀, with aesthetasc on segment 4 and as part of acrothek on apical segment; without distinct process on segment 2. Antennary exopod well developed, with 4 setae. Syncoxal armature of maxilliped unconfirmed. P1 exopod 3-segmented; exp-1 outer spine not elongate. P2-P4 with 3-segmented exopods and 2-segmented endopods; setal formula as follows:

	exopod	endopod
P2	0.1.123	0.220
P3	0.1.123	0.221 (♂: 0.0.[1-2]20)
P4	0.1.123	0.111

P3 endopod ♂ 3-segmented; enp-2 without inner seta but with sigmoid, barbed, spinous apophysis. P3 (and sometimes P4) exopod sexually dimorphic; segments and outer spines more strongly developed; inner distal seta of exp-3 not modified.

P5 ♀ endopodal lobe with 4 setae, apical setae widely spaced; exopod defined at base, not elongate, with 5 setae. P5 ♂ exopod small, wider than long, with 5 setae; endopodal lobe slightly protruding, with 2 well developed setae.

P6 ♂ unconfirmed.

Thus far only in coastal Black Sea waters.

Type species: *Paronychocamptus leuke* Por, 1959 = *Pontophonte leuke* (Por, 1959) comb. nov.

Other species: *P. grigae* sp. nov. [= *Laophonte brevifurca* Sars, 1920 sensu Griga (1963)]

Etymology. The genus name refers to its distribution in the Pontic Basin.

Notes. *Pontophonte* gen. nov. has a number of characters in common with both *Bathylaophonte* gen. nov. and the genus *Paronychocamptus* as redefined in this paper (Tables 3, 7). All three genera have the same setal formula on the female leg 5, i.e. 5 setae on the exopod and 4 on the baseoendopod. The homology of the setae on the latter can be deduced by using the distal tube pore as a reference point. The position of the pore between the two apical setae indicates that the 4-setae condition arose from the ancestral 5-setae state by the loss of the outer element. The two distal setae on the endopodal lobe are typically spaced out. This displacement

is particularly well expressed in *P. leuke*, *P. nanus* and both species of *Bathylaophonte*. All three genera also have primitively a 7-segmented female antennule without a distinct process on segment 2.

Although *Bathylaophonte*, *Paronychocamptus* and *Pontophonte* appear to form a coherent group, the individual relationships between the genera remain partly unresolved. *Bathylaophonte* is clearly the most primitive genus within the lineage, displaying 2 inner setae on P4 exp-3 and a [221] pattern on P4 enp-2. All other species within this genus group have a [111] pattern but this state does not necessarily imply monophyly since it is known to have evolved convergently in other genera such as *Onychocamptus* and *Asellopsis* Brady & Robertson. *Paronychocamptus* and *Bathylaophonte* have retained a more ancestral armature pattern on the P3 ([223] on exp-3 and [321] on enp-2 instead of [123] and [221] in *Pontophonte*) and share the well developed sexual dimorphism on the exopods of P2-P4, and the reduced armature on both rami of the male P5 (4 on exopod, endopodal lobe vestigial with at most 1 seta). These two synapomorphies favour a sistergroup relationship between *Bathylaophonte* and *Paronychocamptus*. In such a scenario the autapomorphies for the latter are the reduced setal formula on the P4 exopod (0.1.122), P4 endopod (0.111) and the sexual dimorphism on P2 endopod (segments elongate and enp-2 with only 1 inner seta in ♂). *Bathylaophonte* is then defined by the peculiar exopodal sexual dimorphism, the body reticulation, and the characteristic apophysis of the male P3 endopod. The latter character may also indicate an alternative scenario of sistergroup relationship between *Bathylaophonte* and

*Pontophonte*. Por (1964b) describes the apophysis in *P. leuke* as “a tooth-like prominence which has a basal incision and curved shape” and Griga (1963) illustrates a clearly sigmoid apophysis in *P. grigae*. The significance of apophysis morphology is, however, outweighed by exopodal sexual dimorphism and male P5 morphology, making this evolutionary scenario less likely.

The closest known relatives of *Pontophonte* are currently accommodated in the *denticornis*-group of the genus *Laophonte* which according to Lang (1948, 1965) encompasses *L. denticornis* T. Scott, *L. nordgaardi* Sars, *L. brevifurca* Sars, *L. baltica* Klie, *L. recticaudata* Willey and *L. adriatica* Petkovski. Within this heterogeneous assemblage a core group of three species (*L. nordgaardi*, *L. brevifurca*, *L. baltica*) can be identified which all lack a spinous process on the second antennular segment, have a similarly reduced swimming leg setal formula, 4 setae on the female P5 baseoendopod, 5 setae on the male P5 exopod and 1 seta on its endopodal lobe (Table 7). To this group should be added *L. arenicola* Nicholls which was described from a single male discovered in the St. Lawrence River, Canada. Lang (1965) considered the position of the latter as undeterminable since Nicholls (1942) had not figured the exopods of the swimming legs. Nicholls (1942) does, however, mention in the text that the setal formula for the exopods is [0.1.123], corroborating its close relationship with *L. nordgaardi*. The only differences between these two species are found in the segmentation of the P1 exopod, the setal formula of the P4 exopod (Table 7) and the presence of an additional seta on the endopodal lobe of the male P5. The minute size of this element suggests that Sars (1908) had

**Table 7.** Comparison between species of *Bathylaophonte* gen. nov., *Pontophonte* gen. nov. and species of the *Laophonte nordgaardi*-group (e = exopod; b = baseoendopod).

**Tableau 7.** Comparaison entre les espèces de *Bathylaophonte* gen. nov., *Pontophonte* gen. nov. et les espèces du groupe *Laophonte nordgaardi* (e = exopodite ; b = baséoendopodite).

	A1 ♀ P2		P3		P4		P3 enp ♂		P5 ♀		P5 ♂	
	e	b	e	b	e	b	e	b	e	b	e	b
<i>Bathylaophonte</i> spp.	7	0.1.123	0.220	0.1.223	0.321	0.1.223	0.221	0.0.220	5	4	4	1
<i>P. leuke</i>	7	0.1.123	0.220	0.1.123	0.221	0.1.123	0.111	0.0.220	5	4	5	2
<i>P. grigae</i> sp. nov.	6	0.1.123	0.220	0.1.123	0.221	0.1.123	0.111	0.0.120	5	4	5 <sup>1</sup>	2 <sup>2</sup>
<i>L. arenicola</i> [♂ only]	?	0.1.123	0.120	0.1.123	0.221 <sup>3</sup>	0.1.123	0.111	0.0.120	?	?	5	1
<i>L. nordgaardi</i>	6	0.1.123	0.120	0.1.123	0.221	0.0.023	0.111	0.0.120	4	4	5	1
<i>L. brevifurca</i>	6	0.1.123	0.120	0.1.123	0.111	0.1.123	0.111	?	5	4	?	?
<i>L. baltica</i>	7	0.1.023	0.120	0.1.023	0.111	0.1.023	0.111	0.0.110	5	4	5	1
<i>L. baltica</i> f. <i>baltica</i>	7	0.1.023	0.010	0.1.023	0.111	0.1.023	0.111	0.0.110	5	4	5	1

<sup>1</sup> Griga (1963) figured only 4 setae but probably overlooked the short middle one

<sup>2</sup> Griga (1963) figured an aberrant specimen with 3 long setae

<sup>3</sup> by inference from the ♂ P3 endopod

figured the tube pore which is frequently found in this position (Fig. 7B).

Of the other species allocated to the *denticornis*-group by Lang (1948) *L. recticaudata* should be placed in the *setosa*-group and *L. denticornis* possibly in its own genus. Fiers (1986) had already pointed out that *L. adriatica* belongs to *Lipomelum* Fiers. The four remaining species are here referred to as the *nordgaardi*-group (Table 7) and regarded as the terminal branch of the *Bathylaophonte-Paronychocamptus-Pontophonte* lineage. We have refrained from attributing generic status to this group since only two species are known from both sexes and the setal formulae of P2-P4 indicate the possible presence of two lineages within this species complex. Each species is known from very few specimens only and the true extent of swimming leg variability is largely unknown. Drzycimski's (1993) recent recognition of a new form of *L. baltica* in the Southern Baltic is probably the result of underrating such variability (Table 7).

#### *Heteronychocamptus* gen. nov.

This genus is established to accommodate the *exiguus*-group of *Paronychocamptus*. Pallares (1979) did not assign *P. connexus* to any group but it is clear from her excellent description that it is very closely related to *P. exiguus*. The female antennules of both species have been described as 8-segmented, however, there is evidence that both Sars (1905) and Pallares (1979) made a mistake in their observations. In the description of *P. connexus* the aesthetasc is drawn on the fifth segment which is a condition unknown in any female harpacticoid. The presence of the remarkably straight suture subdividing the third and fourth segments is difficult to explain but has probably resulted

from some kind of damage caused to the specimen. In Sars' (1905) description of *P. exiguus* the aesthetasc arises from the fourth segment but the apical segment is suspiciously minute. We suspect that the boundary separating segments 7 and 8 is unreal and that the antennule is 7-segmented as in *P. connexus*. There are very few reports of 8-segmented female antennules within the Laophontidae (Huys, 1990). Three species of *Paralaophonte* have been described with 8 segments, *P. gurneyi* (Lang, 1934), *P. octavia* (Monard, 1935) and *P. lamellipes* (Nicholls, 1944). The type material of *P. octavia* is no longer extant but we have re-examined types of the other species (NHM reg. nos. 1928.4.2.122 and 1947.10.6.23-27, respectively) and could confirm that the female antennule is clearly 7-segmented in both. This strongly suggests that the ancestral condition in the Laophontoidea was not 8-segmented as initially postulated by Huys (1990) but only 7-segmented.

The new genus differs from *Paronychocamptus* in the P4 endopod which is more primitive (enp-2 with 2 distal setae instead of 1), the P3 exopod which is more reduced (exp-3 with only 1 inner seta instead of 2) and the ♀ P5 baseoendopod which bears 5 instead of 4 setae (Table 3). *Heteronychocamptus* gen. nov. can also be differentiated by the sexually dimorphic setation of P3-P4 enp-1. In both *H. connexus* and *H. exiguus* the females possess an inner seta on this segment which is absent in the males. A similar kind of sexual dimorphism was recently also found in the two Antarctic genera *Cornylaophonte* and *Weddellaophonte* (Willen, 1996) and had been reported before for the genera *Pilifera* Noodt (Noodt, 1952) and *Pseudonychocamptus* Lang (e.g. Lang, 1965; Ceccherelli, 1988) although in the latter the extreme reduction of the male P4 endopod has obscured this character (Table 8). In female *Laophonte danversae* Hamond the inner seta is absent on P3 enp-1 but

**Table 8.** Comparison between genera and species with sexually dimorphic setation on P3-P4 enp-1 (e = exopod; b = baseoendopod).

**Tableau 8.** Comparasion entre les genres et les espèces présentant un dimorphisme sexuel dans la chétotaxie de l'enp-1 des P3-P4. (e = exopodite; b = baséoendopodite).

		A1 ♀	P2		P3		P4		P5 ♀		
									e	b	
<i>Heteronychocamptus</i>	♀	7	0.1.123	[0-1].120	0.1.123	1.221	0.1.12[2-3]	1.121	4-5	5	
	♂		0.1.123	[0-1].120	0.1.123	0.0.220	0.1.12[2-3]	0.121	4	0	
<i>Pilifera</i>	♀	7	0.1.123	0.120	0.1.123	1.121	0.1.122	1.121	5	5	
	♂		0.1.123	0.120	0.0.122	0.020	0.0.022	0.020	4	2	
<i>Pseudonychocamptus</i>											
	<i>carthyi</i>	♀	7	0.1.123	0.220	0.1.223	1.321	0.1.223	1.121	6	5
	others	♀	7	0.1.123	0.220	0.1.123	1.[1-2]21	0.1.123	1.121	5-6	5
<i>Weddellaophonte</i>	♂		0.1.123	0.120	0.1.123	0.[0-2]20	0.1.123	020	3-4	2	
	♀	6	0.1.123	0.020	0.1.223	1.121	0.1.223	1.120	5	5	
<i>Laophonte danversae</i>	♂		0.1.123	0.020	0.1.223	0.0.120	0.1.223	0.120	4	2	
	♀	7	0.1.023	0.120	0.1.023	0.121	0.0.222	1.021	6	5	
	♂		0.1.023	0.120	0.1.023	0.020	0.0.022	0.021	5	2	

present on P4 enp-1 (Hamond, 1969), whereas in the male the latter is missing on both P3 and P4 enp-1 (Hicks, 1982). In view of the obviously close similarity between *Pilifera gracilis* (T. Scott) and *L. danversae* this sexual dimorphism is considered as a vestige of the ancestral pattern displayed in *Heteronychocamptus*, *Weddellaophonte* and *Pilifera* (Table 8). This pattern is a robust synapomorphy linking *Pseudonychocamptus*, *Weddellaophonte*, *Pilifera* and *Heteronychocamptus* in a monophyletic group (PWPH). Within this lineage *Pseudonychocamptus* and *Pilifera* are considered sistergroups on the basis of the sexually dimorphic P4 endopod, characterized by a profound setal reduction on the distal segment in the male. *Pseudonychocamptus carthyi* Hamond displays the most primitive swimming leg armature (Table 8) and probably occupies a position close to the ancestor of the PWPH-lineage. The discovery of the male is necessary to confirm its current generic placement.

#### Diagnosis

Laophontidae. Body sub-cylindrical. Rostrum small. Caudal rami cylindrical, short; setae IV-V well developed. Antennule 7-segmented in ♀, with aesthetasc on segment 4 and as part of acrothek on segment 7; without process on segment 2. Antennary exopod well developed with 4 setae. Maxilliped with 2 setae on syncoxa. P1 exopod 3-segmented; exp-1 with short outer spine. P2-P4 with 3-segmented exopods and 2-segmented endopods; setal formula as follows:

	exopod	endopod
P2	0.1.123	[0-1].120
P3	0.1.123	1.221 [♂: 0.0.220]
P4	0.1.12[2-3]	1.121 [♂: 0.121]

P3 endopod ♂ 3-segmented; enp-2 without inner seta and well developed spinous apophysis. P2-P4 exopods sexually dimorphic; segments and outer spines more strongly developed; P2 endopodal segments distinctly elongate in ♂; P3-P4 enp-1 without inner seta in ♂.

P5 ♀ endopodal lobe with 5 setae; exopod ovoid, with 4-5 setae. P5 ♂ exopod small, with 4 setae; endopodal lobe absent, no armature.

P6 ♂ with 2 well developed setae.

One egg-sac.

Brackish water or marine.

Type species: *Paronychocamptus connexus* Pallares, 1979 = *Heteronychocamptus connexus* (Pallares, 1979) comb. nov.

Other species: *Laophonte exigua* Sars, 1905 = *H. exiguus* (Sars, 1905) comb. nov.

Etymology. The genus name is derived from the Greek *heteros*, meaning other, and alludes to the sexually dimorphic setation on P3-P4 enp-1.

#### Radiation of Laophontidae into deepwater habitats

The discovery of *B. pacifica* at 2572 m depth in the southeastern Pacific represents a significant depth range extension for the family Laophontidae, the deepest record prior to this paper being that of *Weddellaophonte anyae* from 710 m in the Antarctic Weddell Sea (Willen, 1996). The few qualitative studies on the deep sea Harpacticoida (e.g. Bodin, 1968; Becker, 1972; Schriever, 1986) all indicate an overall dominance of the families Cerviniidae, Paranannopidae, Argestidae, Huntmanniidae and Cletodidae and suggest that Laophontidae are virtually non-existent in bathyal communities.

Many of the early deepwater records (e.g. *Laophonte thoracica*, *L. longicaudata*, *Paralaophonte brevirostris*) refer to Lang's (1948) extensive work in the Gullmar Fjord. In terms of depth, however, these records are rather modest and do not extend beyond the 120 m isobath. Table 9 lists all literature records of Laophontidae collected in the bathyal zone, i.e. between 200 and 4000 m depth. As Lang (1948) had pointed out before A. Scott's (1909) records of

**Table 9.** Bathyal records of Laophontidae (doubtful records indicated by \*).

**Tableau 9.** Signalisations bathyales de Laophontidae (\* indique les signalisations incertaines).

Species	Depth	Locality	Reference
<i>Laophonte longicauda</i>	200 m	Skagerak, Sweden	Por (1964a)
<i>Laophonte cornuta</i>	300 m	Bergen, Norway	Drzycimski (1969)
<i>Laophonte glacialis</i>	385 m	Posadowsky Bay, Antarctic	Brady (1910)
<i>Laophonte thoracica</i>	450 m	Bergen, Norway	Drzycimski (1969)
<i>Cornylaophonte pleisteri</i>	350-485 m	Weddell Sea, Antarctic	Willen (1996)
<i>Archilaophonte maxima</i>	430-495 m	Weddell Sea, Antarctic	Willen (1995)
<i>Laophonte elongata</i>	512 m	Bergen, Norway	Drzycimski (1969)
<i>Weddellaophonte anyae</i>	281-710 m	Weddell Sea, Antarctic	Willen (1996)
<i>Esola hirsuta</i> *	1595 m	Banda Sea, Indonesia	A. Scott (1909)
<i>Laophonte cornuta</i> *	1595 m	Banda Sea, Indonesia	A. Scott (1909)
<i>Bathylaophonte azorica</i>	845-1725 m	SE of Azores	this paper
<i>Bathylaophonte pacifica</i>	2572 m	N of Easter Island, SE Pacific	this paper

*Laophonte cornuta* and *Esola hirsuta* from great depth in the Banda Sea are extremely doubtful. A. Scott (1909) identified both species from the same two samples, one taken at 13 m depth and one at 1595 m depth. Since they were the only species found at these localities it is highly conceivable that the extremely wide vertical separation of both records resulted from sample contamination. The majority of deepwater records refer to high latitude localities, both in the Northern and Southern Hemispheres. Various species of *Laophonte sensu lato* which are normally encountered at moderate depths appear to be capable of penetration into the deeper layers of fjords (Lang, 1948; Por, 1964a; Drzycimski, 1969). The discovery of *B. azorica* and *B. pacifica* represent the first records from deep subtropical waters. Although *Bathylaophonte* is clearly a deepwater genus, the record of *B. faroensis* from 159 m in the Faro Channel indicates that the genus is not restricted to the bathyal zone proper. Its association with hydrothermal vent fields is likely to be coincidental.

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