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Two new genera of Laophontidae (Copepoda: Harpacticoida) from the high Antarctic Weddell Sea

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Two new genera of the harpacticoid family Laophontidae from the high Antarctic Weddell Sea are described. At present, both taxa cannot be assigned to any of the known genera or lineages of the family. The Antarctic shows the greatest degree of endemism worldwide in several already investigated taxa and, considering the available records, the Laophontidae appear to be no exception to this rule. The available data on the Laophontidae of the Weddell Sea seem to support a hypothesis of an 'old' antarctic fauna rather than a recolonization by 'phylogenetic younger' taxa after the major climatic changes, which took place in the Antarctic continent and the surrounding waters from the Miocene onwards.

KEYWORDS: Antarctic, Weddell Sea, Copepoda Harpacticoida, Laophontidae, systematics, zoogeography, phylogeny.

Introduction

The Antarctic shows the greatest degree of endemism worldwide. In several taxa (Pisces, Amphipoda, Cumacea, Tanaidacea, Isopoda, etc) more than 80% of the species of this region are found nowhere else (Brandt, 1991). This is due to the particular geological and climatic history of the continent and surrounding waters leading to isolation and extreme living conditions. A number of benthic taxa of the Weddell Sea have already been the subject of ecological, taxonomic and phylogenetic/zoogeographic studies (Holothuria; Gutt, 1988, Tanaidacea; Sieg, 1988; Bivalvia; Hain, 1990; Isopoda; Brandt, 1991). For the Copepoda, a systematic survey of the benthic Harpacticoida has only just begun (Schminke and Dahms, 1989, Dahms, 1992, Dahms and Pottek 1992, etc.), whereas the planktonic copepods are relatively better known. Representatives of two new genera of Laophontidae, described in this paper, were collected during the Ant V expedition of the *Polarstern* in the Weddell Sea in 1986, and are no exception to the rule of high endemism in the Antarctic.

Methods

Holotypes and allotypes were preserved in 5% buffered formalin and subsequently transferred to Zeiss W15 embedding medium. Drawings were made with the aid of a camera lucida on Leitz Diaplan microscopes equipped with a phase contrast 100× objective and with an interference contrast 100× objective respectively. Before dissection, in each case the whole specimen was drawn from the dorsal and lateral side. The dissected parts are mounted on several slides. All specimens are in the collection of the AG Zoomorphologie, C.v.O. Universität Oldenburg. The terminology is adopted from Lang (1948, 1965) except for the segmental composition of mandible, maxilliped and the numbering of the furcal setae, in which cases Huys and Boxshall (1991), have been followed. Abbreviations used in the text: F.R.: furcal rami, Aes: aesthetasc, exp: exopodite, enp: endopodite, "enpl": first segment of endopodite, Md: mandible, Mxl: maxillula, Mx: maxilla, Mxp: maxilliped, P1–P6: swimming legs 1–6.

Systematics

Genus *Cornylaophonte* gen. n.

Since the genus is yet monotypic, its diagnosis concurs with the description of the type species.

Cornylaophonte pleisteri gen. n., sp. n.

[(Figs 1–10)]

Materials. Three males and 2 females collected during AntV/3 from various sites of the Weddell Sea, Antarctic shelf, from sediment bottom, by dredge haul.

Locality. Male holotype: 74°02,4′S, 24°22, 7′W, 31 October 1986, from 350 m depth; female allotype: 72°43,3′S, 19°23, 3′W, 15 October 1986, from 485 m depth.

Etymology. This species is dedicated to Dr Christopher Pleister, chairman of the Oldenburg University Association, for his support of the research activities of the AG Zoomorphologie in the Antarctic.

Description of male

Body length (Rostrum tip to end of F.R.): 0·612 mm. Maximum body width (measured at rear margin of cephalothorax): 0·187 mm. Furcal rami length: 0·050 mm.

Rostrum (Figs 1A, 2) broad triangular, with notch at tip, continuous with cephalothorax, with a pair of tine setules anteriorly.

Body (Figs 1A, 4A) long and slender, tapering posteriorly. Cephalothorax slightly broader than long, regularly covered with tiny setules, additionally with characteristic patches of spinules and cuticular folds. Posterior margin of each somite with setules and spinules. Dorsal surface of somites with spinules. Pleurotergites of somites 1–3 semicirculary produced. Anal operculum spinulose, flanked by two setules.

Furcal rami (Fig. 1A) 2 × as long as broad and spinulose. Furcal setae: I, II and III at outer distal corner, seta I tiny and vestigial, IV and V well-developed, with fused bases, VI stout and pinnate, VII biarticulated, on dorsal surface.

Antennule (Fig. 2) 7-segmented, subchirocer. Segments I and II longest, I with spinules and pointed process, II with large, curved outer process. Segment IV rounded and bulbous. Geniculation between IV and V. Armature: I(1); II(9); III(7); IV(14 + [1 + Aes]); V(0); VI(1); VII(7 + [2 + Aes]).

Antenna (Fig. 9B) allobasis with pinnate, abexopodal seta. Exp unisegmented, with 4 setae. Enp with spinules and 2 subapical frills, bearing subapically 2 spines and 1 long, slender seta; apically 2 spines, one of which twice as long as the other, and 3 long, geniculate setae, outermost of which fused at base with 1 small, slender seta.

Mandible (Fig. 5C). Coxa long and slender, with spinules. Cutting edge from

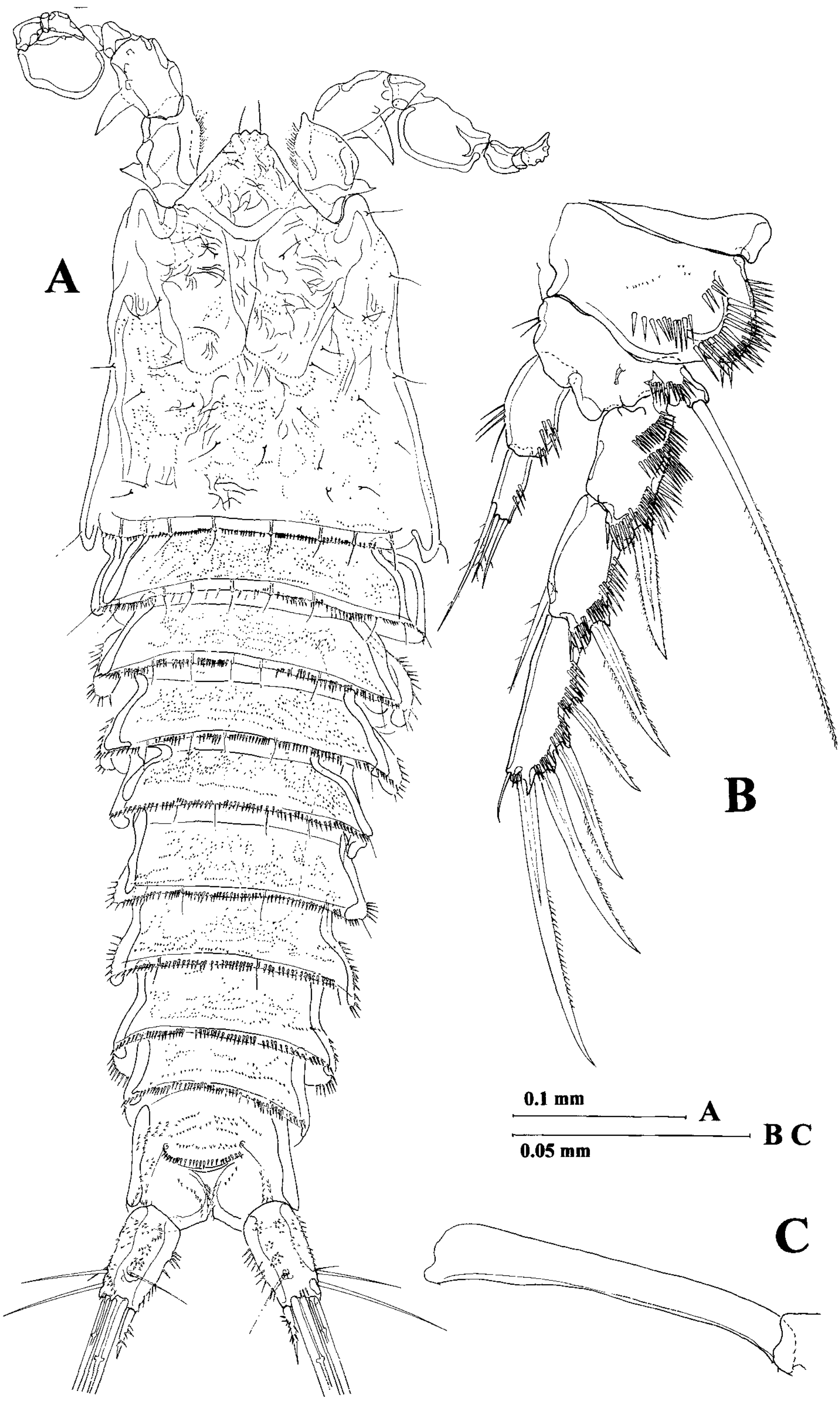

FIG. 1. *Cornylaophonte pleisteri* gen.n, spec.n.: (A) male habitus, dorsal; (B) female P2; (C) intercoxalsclerite of female P2.

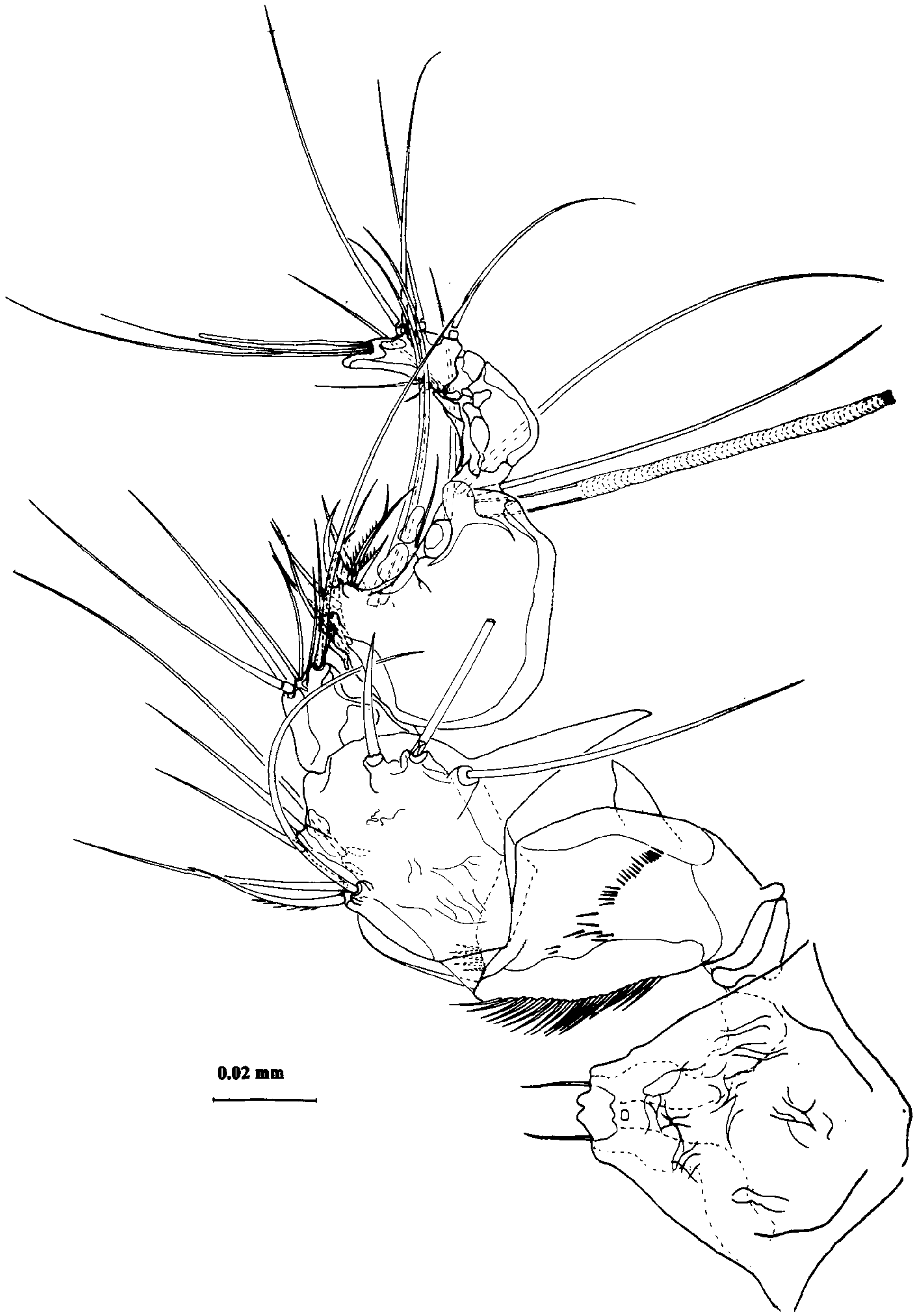

FIG. 2. *Cornylaophonte pleisteri* gen.n., spec.n., male antennule.

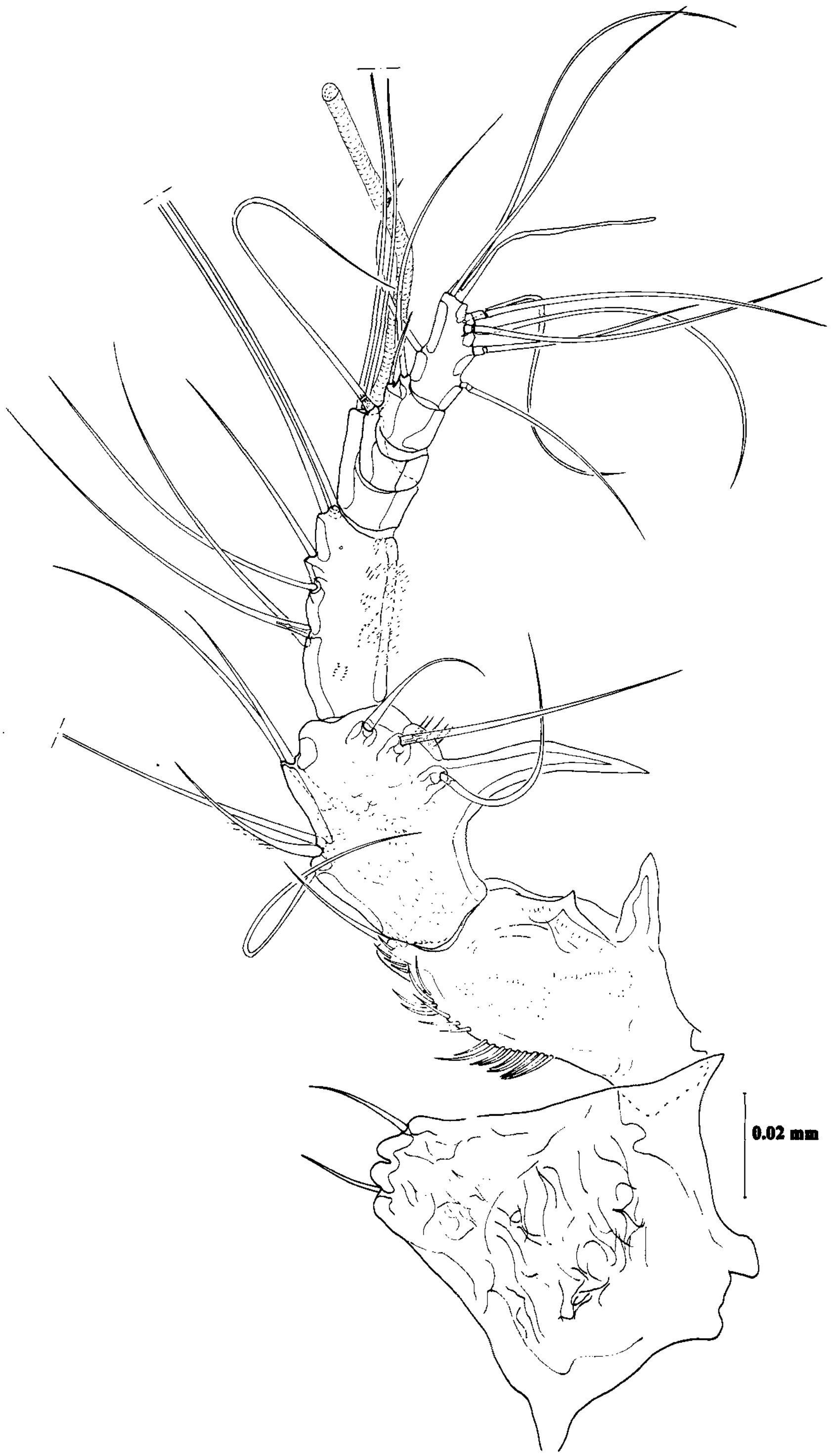

FIG. 3. *Cornylaophonte pleisteri* gen.n., spec.n., female antennule with rostrum.

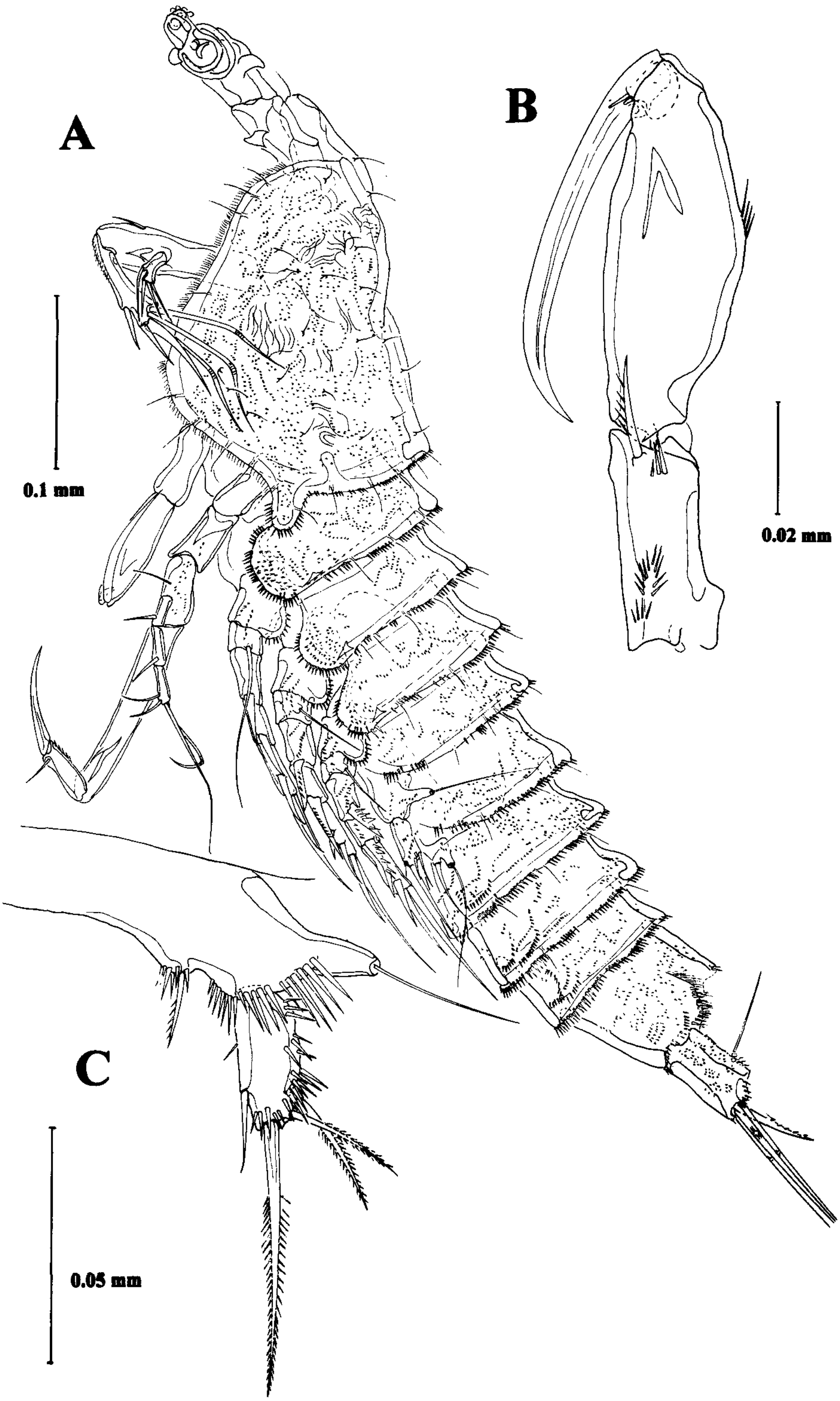

FIG. 4. *Cornylaophonte pleisteri* gen.n., spec.n.: (A) male habitus, lateral; (B) male maxilliped; (C) male P5.

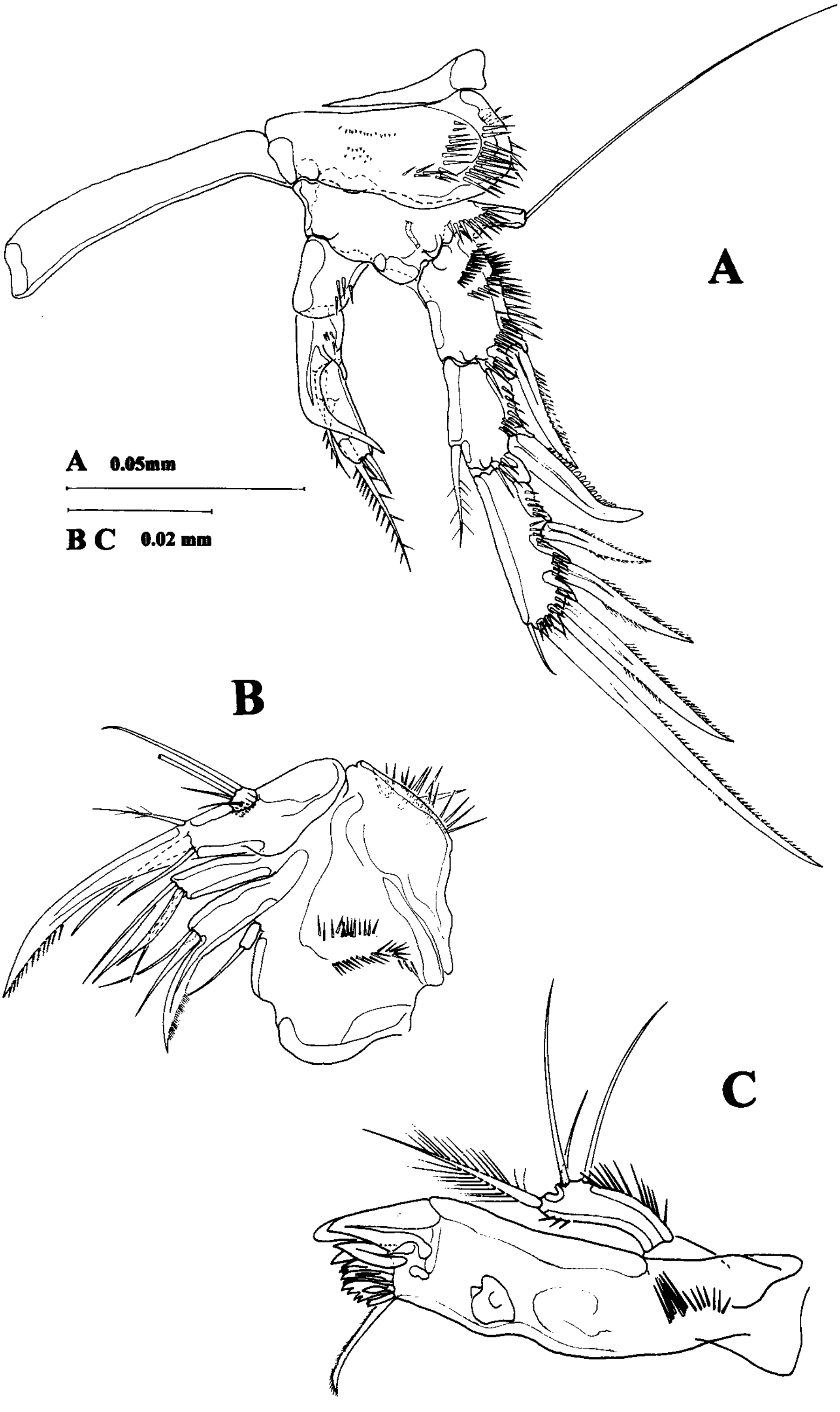

FIG. 5. *Cornylaophonte pleisteri* gen.n., spec.n.: (A) male P3; (B) male maxilla; (C) male mandible.

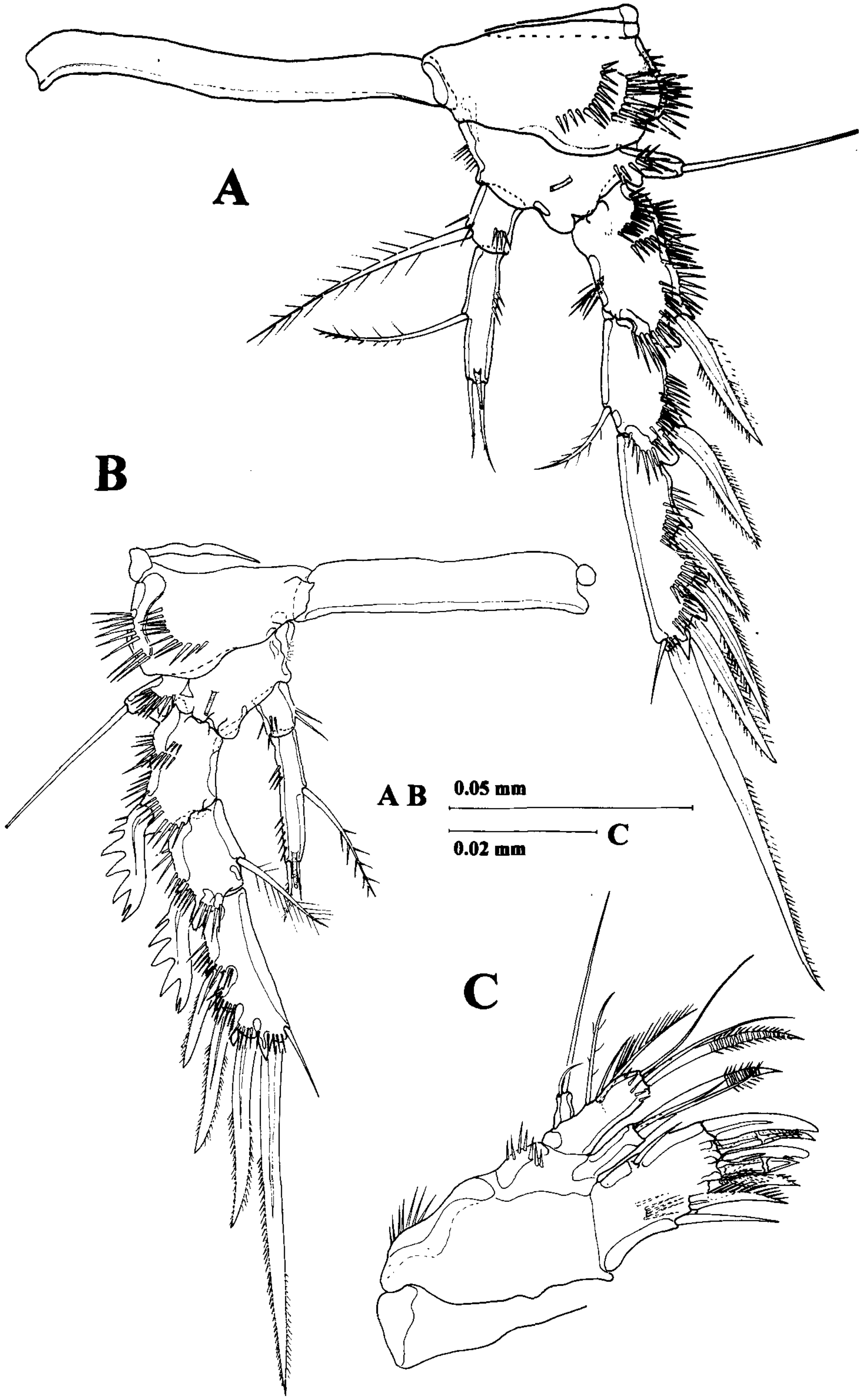

FIG. 6. *Cornylaophonte pleisteri* gen.n., spec.n.: (A) female P4; (B) male P4; (C) male maxillule.

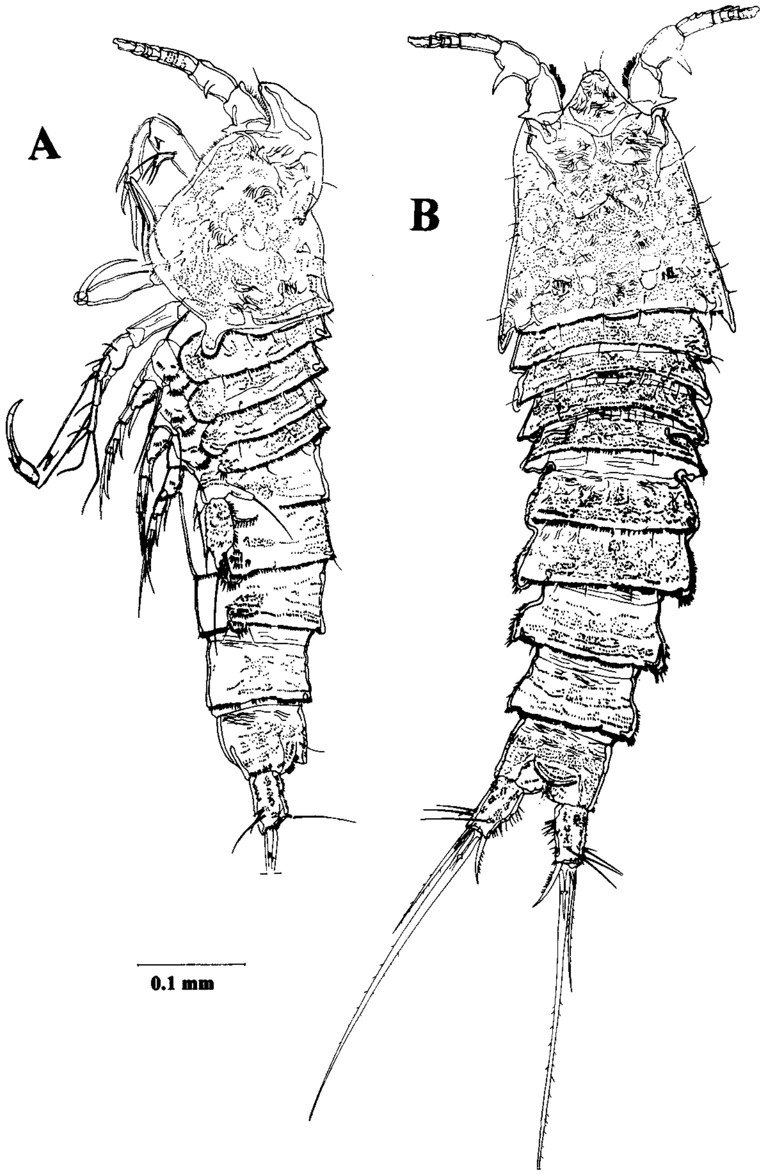

FIG. 7. *Cornylaophonte pleisteri* gen.n., spec.n.: (A) female habitus, lateral; (B) female habitus, dorsal.

distal to proximal corner with two bidentate teeth, several multidentate ones and one long, plumose seta. Palp unisegmented, basis with one strong, plumose seta, enp represented by three setae, exp absent.

Maxillule (Fig. 6C). Arthrite of praecoxa apically with 6 spines, each of them characteristic in shape and ornamentation, with 1 small, obliquely positioned seta and additionally with two setae located at inner and outer margins, respectively. Coxal endite with one claw-like geniculate spine and two setae, basal endite with one claw-like geniculate spine and two setae. Exp cylindrical with two setae, one of which short, enp represented by three setae.

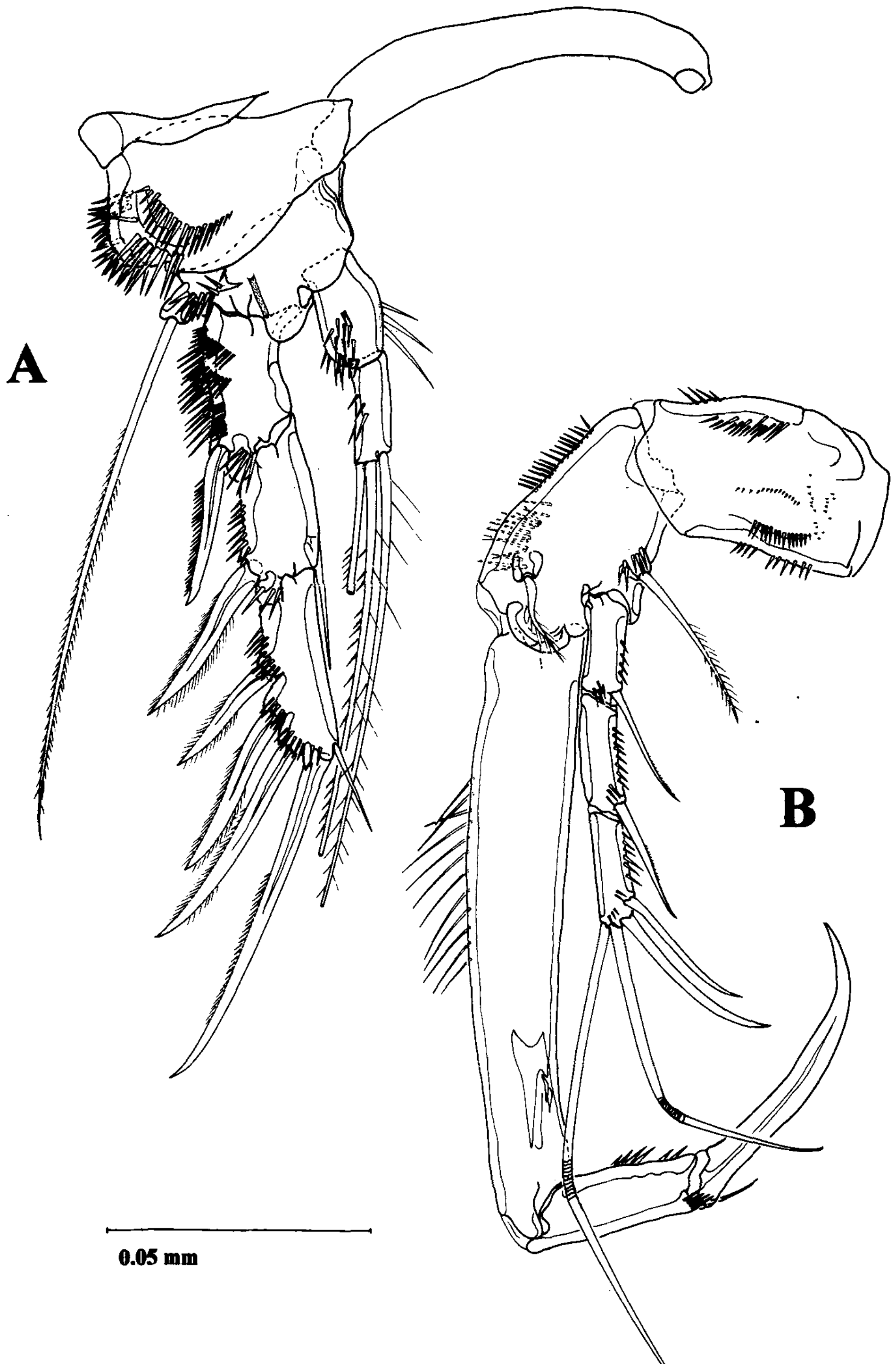

FIG. 8. *Cornylaophonte pleisteri* gen.n., spec.n.: (A) male P2; (B) male P1.

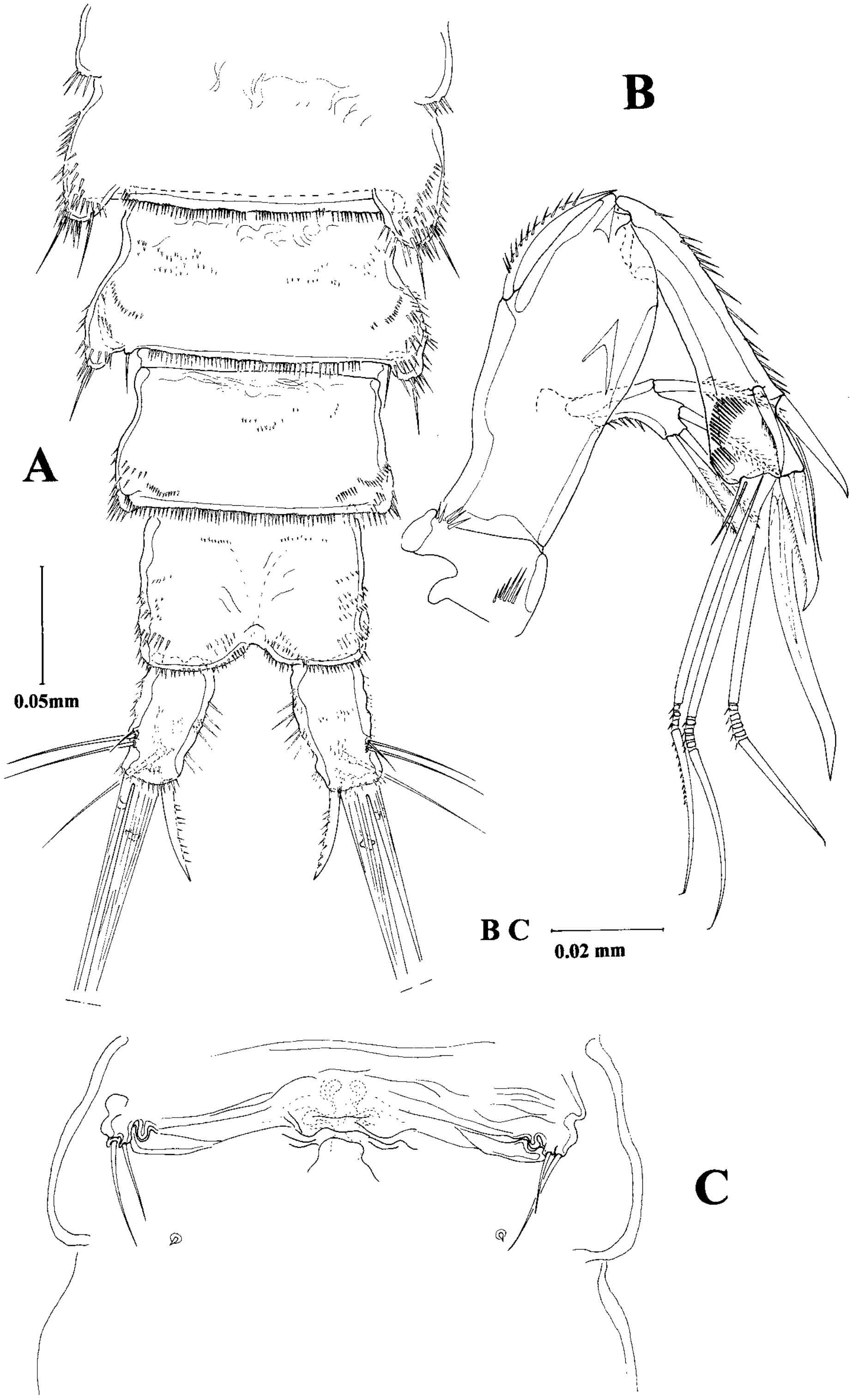

FIG. 9. *Cornylaophonte pleisteri* gen.n., spec.n.: (A) female urosome, ventral; (B) male antenna; (C) female genital field.

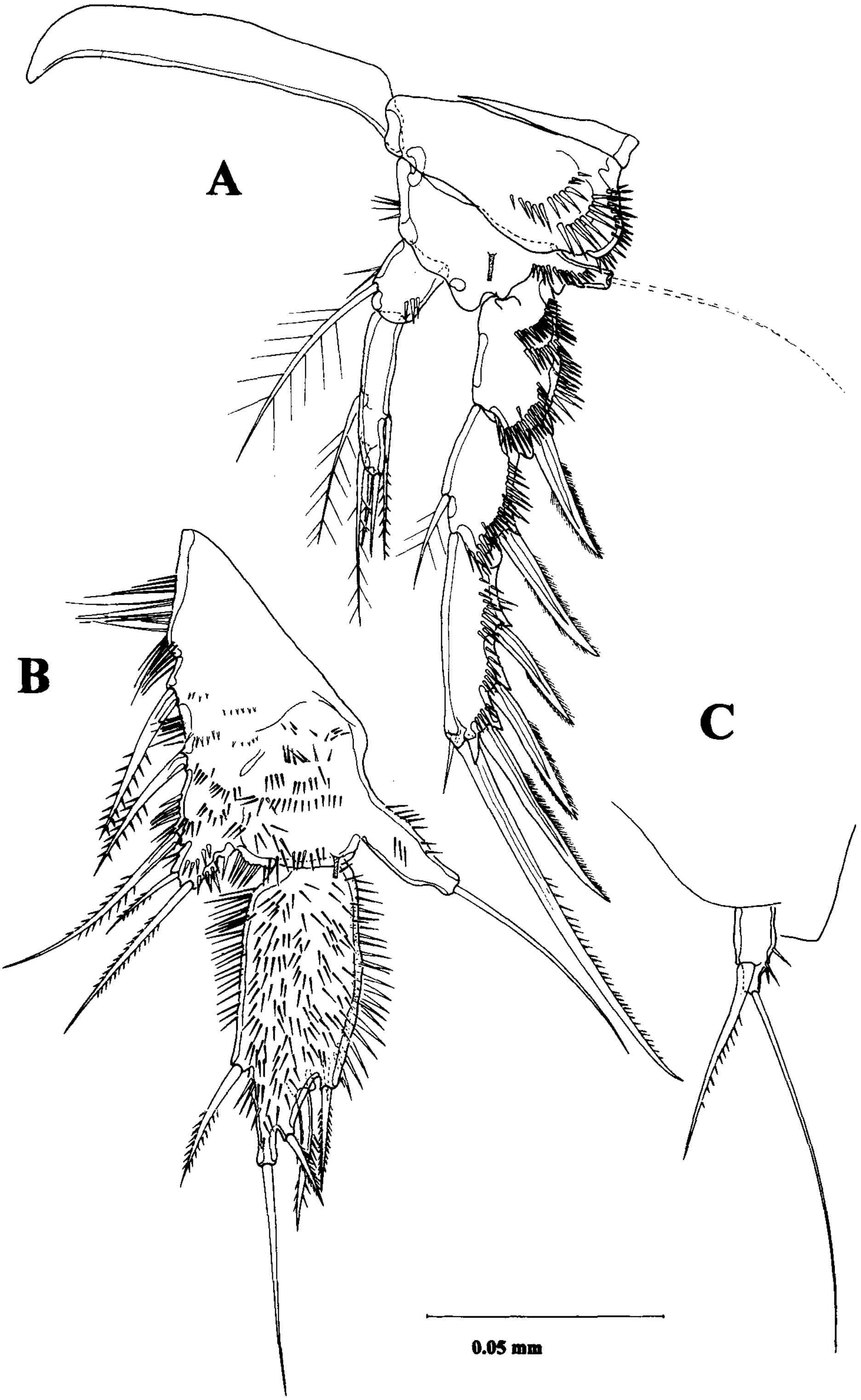

FIG. 10. *Cornylaophonte pleisteri* gen.n., spec.n.: (A) female P3; (B) female P5; (C) male P6.

Maxilla (Fig. 5B). Syncoxa with several spinule rows and three endites. Proximal endite small with one seta. Middle endite ending in a pinnate spine, with two setae. Distal endite with four setae. Basal endite ending in a long claw, accompanied by three setae. Enp not clearly defined, with four setae.

Maxilliped (Fig. 4B) prehensile. Syncoxa with spinules and one apical pinnate seta. Basis asetose, with spinules on outer margin. Enp unisegmented, with one long claw and two tiny seta-like structures proximally.

P1 (Fig. 8B). Coxa and basis longer than broad, with several spinule rows. Basis with a slender, plumose outer seta. Inner basal seta located on anterior surface. Exp 3-segmented, outer margins with spinules. Exp1 and exp2 with slender outer spines, exp3 with two outer spines and two long, geniculate terminal setae. Enp1 much longer and broader than exp, enp2 shorter and terminally with one large anterior claw and one tiny posterior seta.

P2–P4 (Figs 5A, 6B, 8A) expodites and P3enp 3-, P2enp and P4enp 2-segmented. Each leg with small triangular praecoxa without ornamentation. Intercoxal sclerites transversaly extended. Outer basal seta elongate, plumose in P2. Basis with tube pore. Distal segments of expodites without inner and with vestigial inner terminal setae, endopodal segments reduced in size and number of setae. In P3enp3 setae located on posterior surface. P3 and P4 sexualdimorphically modified. P3exp2 with enlarged outer spine being ornamented with rounded spinules, P3enp 3-segmented, with curved apophysis on middle segment, P4exp1 and exp2 with strongly modified outer spines. P4 enp2 with subterminal tube pore.

Setae formulae (according to Sewell, 1949, after Huys and Boxshall, 1991).

	Coxa	Basis	exp	enp
P2	0-0	1-0	I-0; I-1; III,I,1	0; 030
P3	0-0	1-0	I-0; I-1; III,I,1	0; apophysis; 022
P4	0-0	1-0	I-0; I-1; III,I,1	0; 021

P5 (Fig. 4C) pair of legs medially fused. Distal margin of benp with long spinules and long, slender outer seta. Inner lobe reduced, enp represented by one seta. Outer margin of exp spinulose, exp with four setae: innermost bare and small, terminal one long, strong and pinnate, outermost two smaller and pinnate.

P6 (Fig. 10C) consisting of an elongated lobe, anteriorly with one pinnate seta, posteriorly with one long, slender seta.

Description of female

Body length (Rostrum tip to end of F.R.): 0·754 mm. Maximal body width (measured at rear margin of cephalothorax): 0·2 mm. Furcal rami: 0·059 mm.

Body (Figs 7A,B) long and slender, tapering posteriorly. Cephalothorax and somite ornamentation as in male. Somites 5 + 6 fused as genital double somite. Somites 6 + 7 with spinulose ventrolateral expansions. Furcal rami and anal somite as in male.

Antennule (Fig. 3A) 7-segmented, segments I and II as in male. Segments, I, II and III longest, other ones short. Setal ornamentation: (I(1); II(8); III(6); IV(1 + [1 + Aes]); V(1); VI(2); VII(8 + [1 + Aes]).

Antenna, mouthparts and P1 as in male.

P2–P4 (Figs 1B, 6A, 10A) as in male, except for terminal setae of P2enp2 much shorter, P3 and P4exps not modified, P3 and P4enp1 with inner setae, P3enp 2-segmented, without apophysis but with five setae on enp2.

Setal formulae (according to Sewell, 1949, after Huys and Boxshall, 1991).

	Coxa	Basis	exp	enp
P2	0-0	I-0	I-0; I-1; III;I,1	0-0; 0,2,1
P3	0-0	I-0	I-0; I-1; III,I,1	0-1; 1,2,2
P4	0-0	I-0	I-0; I-1; III,I,1	0-1; 0,2,1

P5 (Fig. 10B) totally covered with spinules. Benp of almost triangular shape, with one long outer seta. Inner lobe concave, with five pinnate setae one of which short. Exp slightly elongated, with five setae distally. Second outer seta inserting on posterior surface.

Genus *Weddellaophonte* gen.n.

Since the genus is monotypic, its diagnosis concurs with the description of the species.

Weddellaophonte anyae gen.n., sp.n

[(Figs 11–18)]

Material. One male and 1 female collected from the Weddell Sea during AntV/3 expedition.

Locality. Female holotype: 70°30,4′S, 008°02,5′W, 12.10.1986, from 281 m depth, sediment bottom, by dredge haul; male allotype: 72°51,4′S, 019°41,4′W, 8.11.1986, from 710 m depth, sediment bottom.

Etymology. This species is dedicated to Ms Anya Abshagen, Münster, Germany.

Description of female

Body length (Rostrum tip to F.R.): 0·493 mm. Maximal body width (measured at rear margin of cephalothorax): 0·146 mm. Furcal rami: 0·037 mm.

Rostrum (Figs 11C, 15B) broad triangular, rounded at tip, apically with two setules, continuous with cephalothorax.

Body (Figs 11A,C) cylindrical, only slightly tapering posteriorly, slightly flattened. Cephalothorax almost as broad as long, dorsally covered with setules and net-like arranged cuticular folds. Posterior margin of each somite with spinules and/or setules. Dorsal surface of somites with spinules and cuticular folds. Pleurotergites of somites 1–3 semicircularly produced. Somites 5 and 6 fused as genital double somite. Somites 6–8 with ventrolateral, spinulose expansions (Figs 11A,C, 14B). Anal operculum (Fig. 11C) flanked by two setules. Furcal rami spinulose, 2 × as long as broad; setae: I, II, and III at outer distal corner, I tiny and vestigial; IV and V well-developed, fused at base, IV smaller; V long and pinnate; VII biarticulated, on dorsal surface (Fig. 11C and 14B).

Antennule (Fig. 15B) 6-segmented, segment I spinulose, with small rounded projection on outer margin; segment II without any process. Setal ornamentation: I(1); II(8); III(6); IV(1 + [1 + Aes]); V(1); VI(9 + [1 + Aes]).

Antenna (Fig. 14C), Md (Fig. 12B), Mx, P1 (Fig. 13A) as in *Cornylaophonte*, except Md exp represented by one seta, Mx enp and distal syncoxal endite with three setae respectively.

Mxl (Fig. 12C). Arthrite of praecoxa with six terminal spines, each of characteristic shape and ornamentation, with one small obliquely positioned seta being armed with long spinules, additionally with two naked setae located on upper and lower margin,

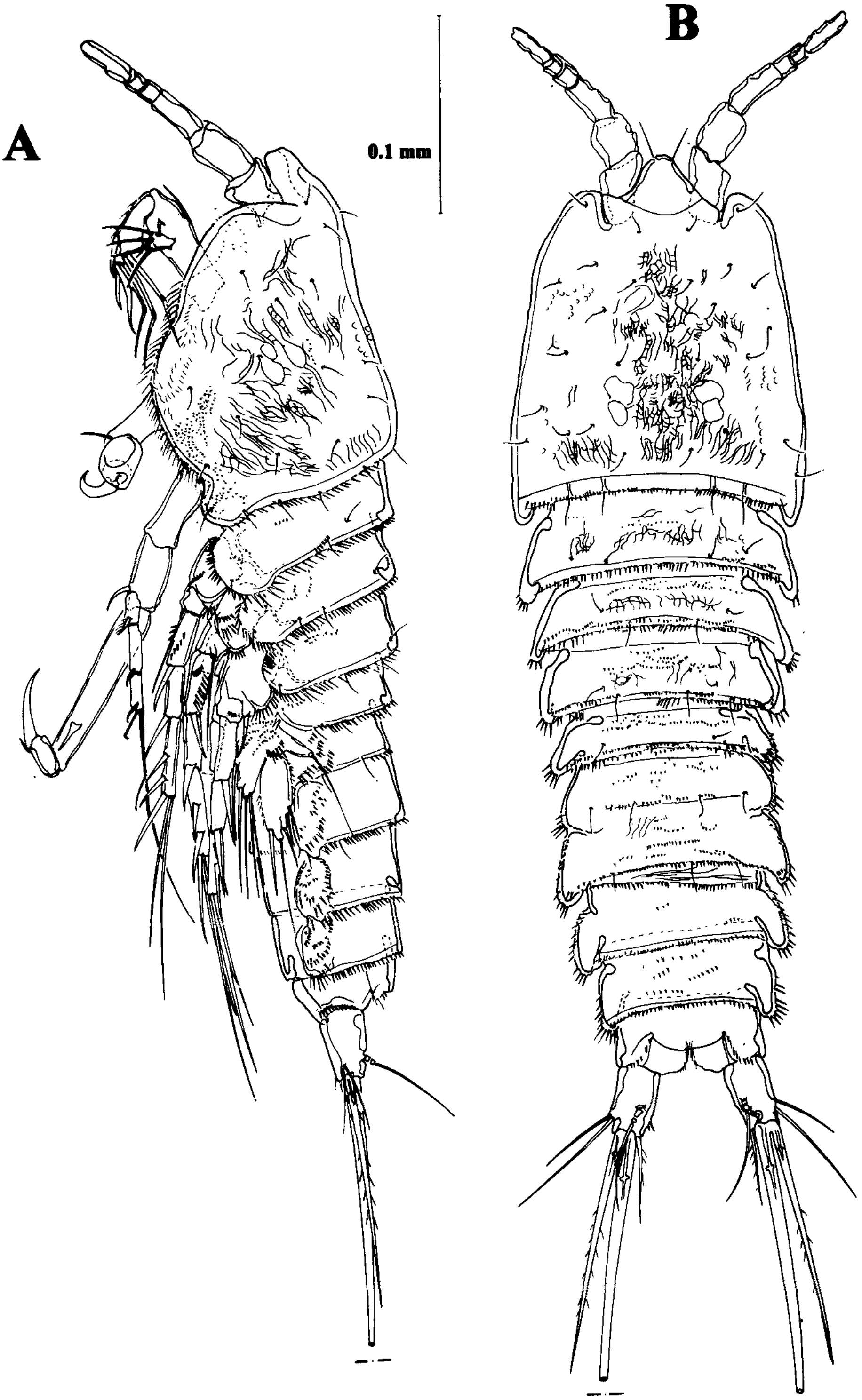

FIG. 11. *Weddellaophonte anyae* gen.n., spec.n.: (A) female habitus, lateral ; (B) female habitus, dorsal.

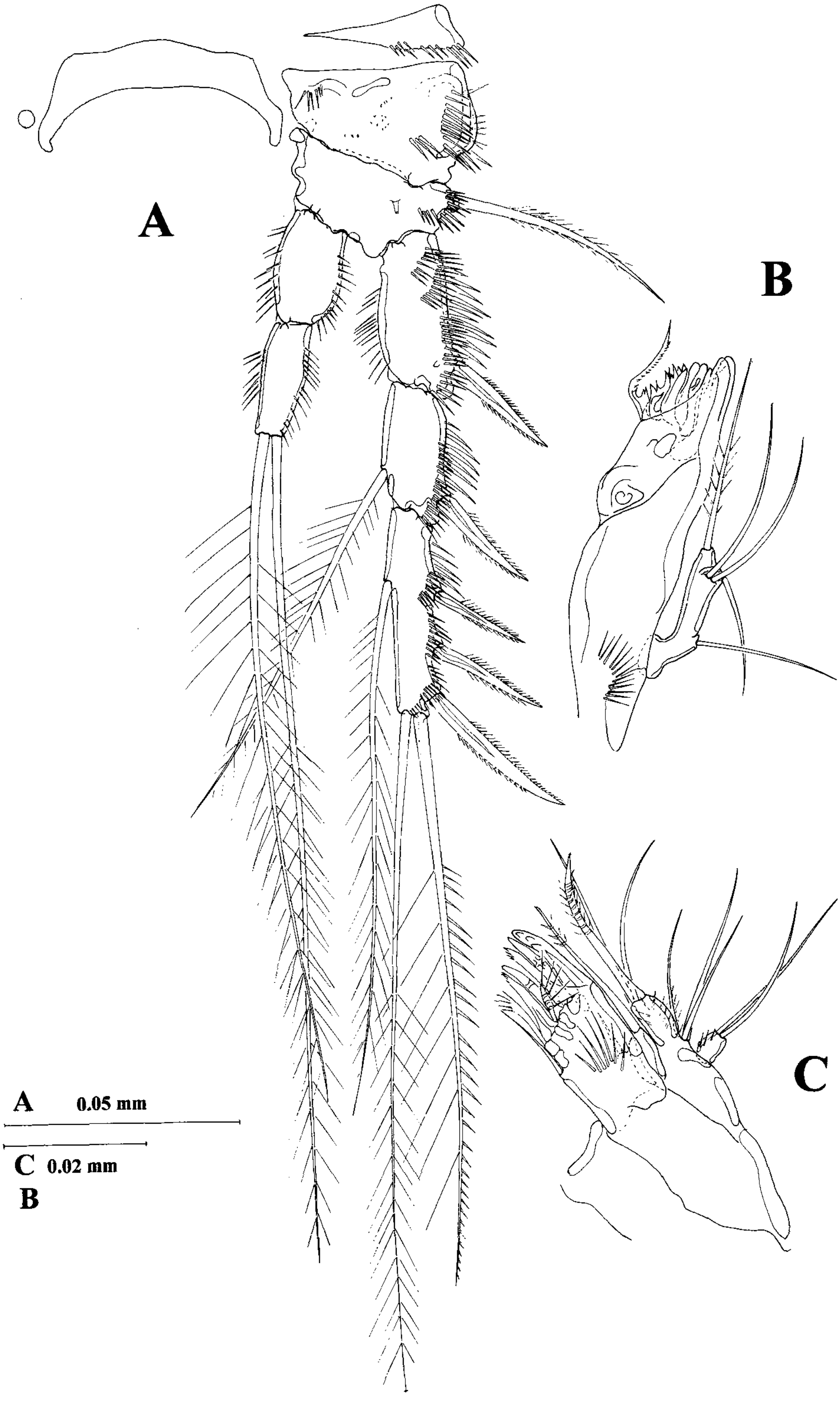

FIG. 12. *Weddellaophonte anyae* gen.n., spec.n.: (A) female P2; (B) female mandible; (C) female maxillule.

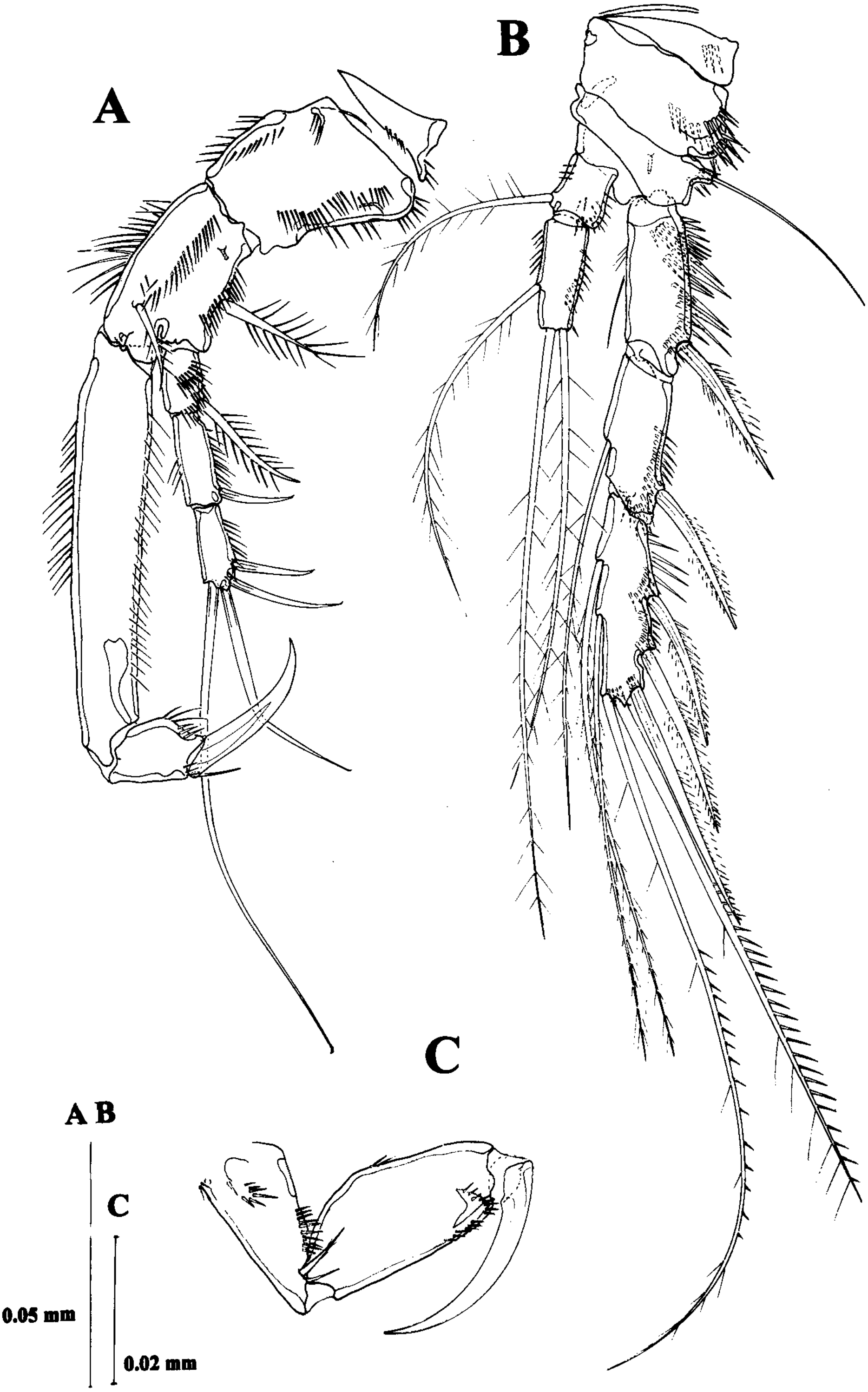

FIG. 13. *Weddellaophonte anyae* gen.n., spec.n.: (A) female P1; (B) female P4; (C) female maxilliped.

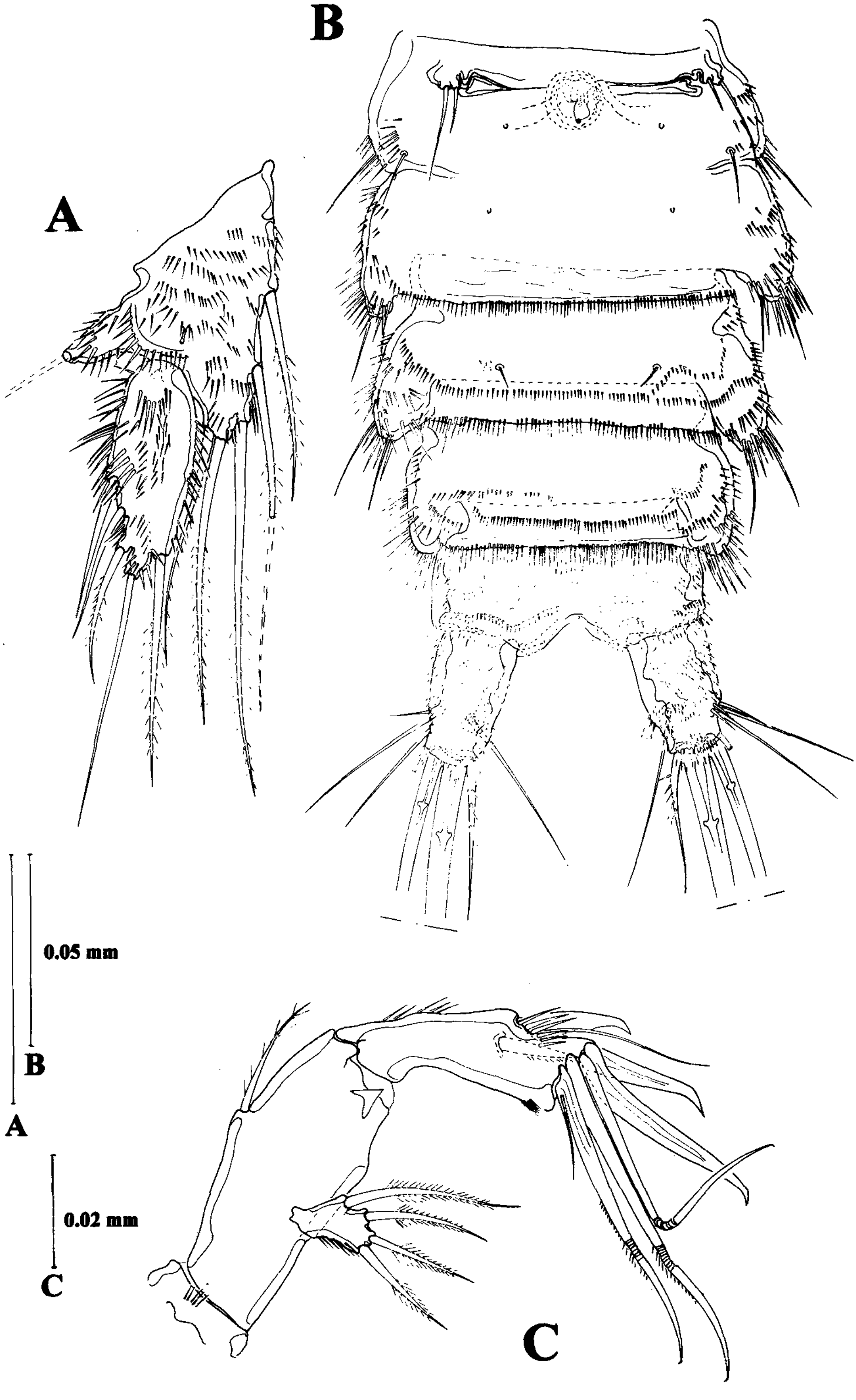

FIG. 14. *Weddellaophonte anyae* gen.n., spec.n.: (A) female P5; (B) female urosome and genital field, ventral; (C) female antenna.

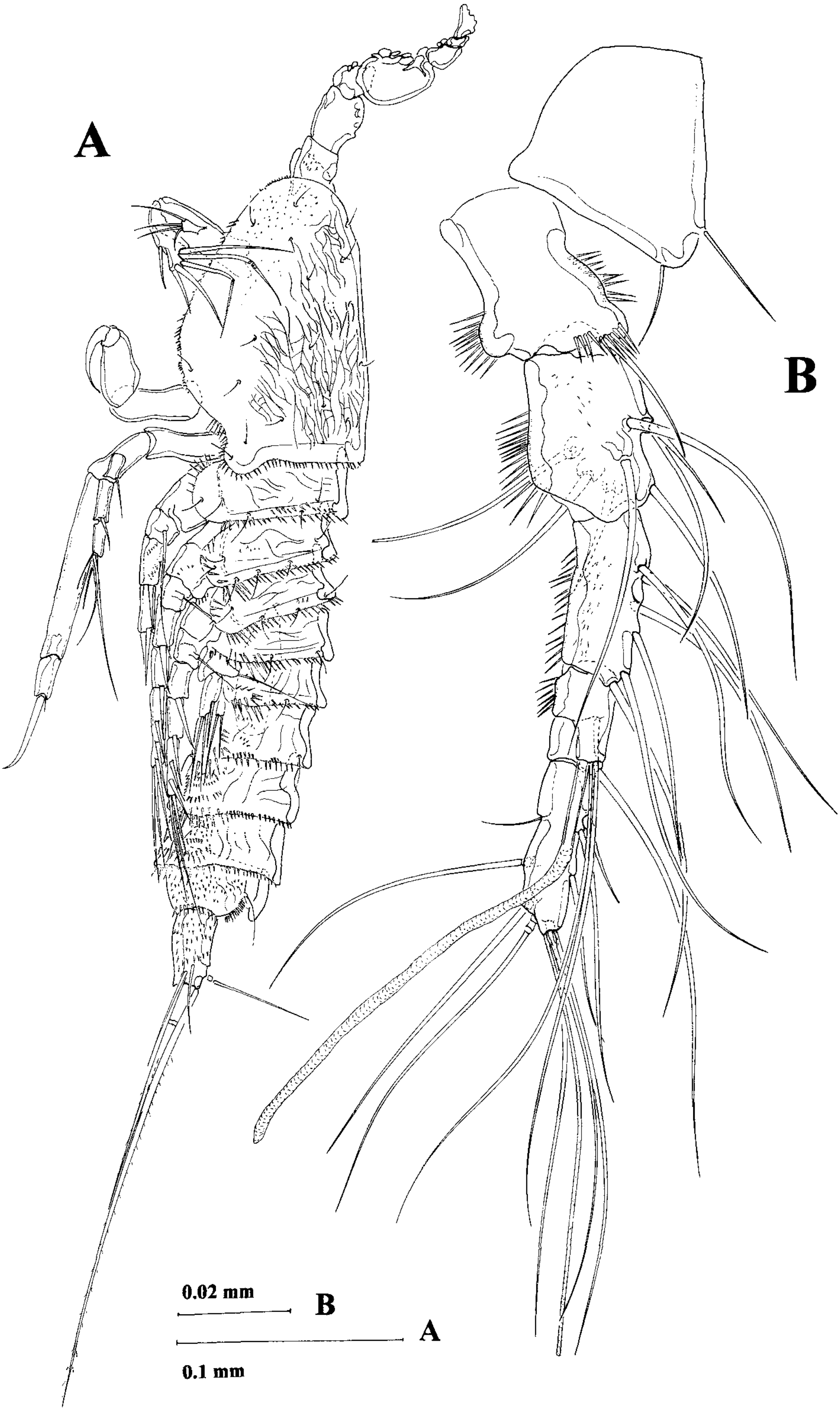

FIG. 15. *Weddellaophonte anyae* gen.n., spec.n.: (A) male habitus, lateral; (B) female antennule and rostrum.

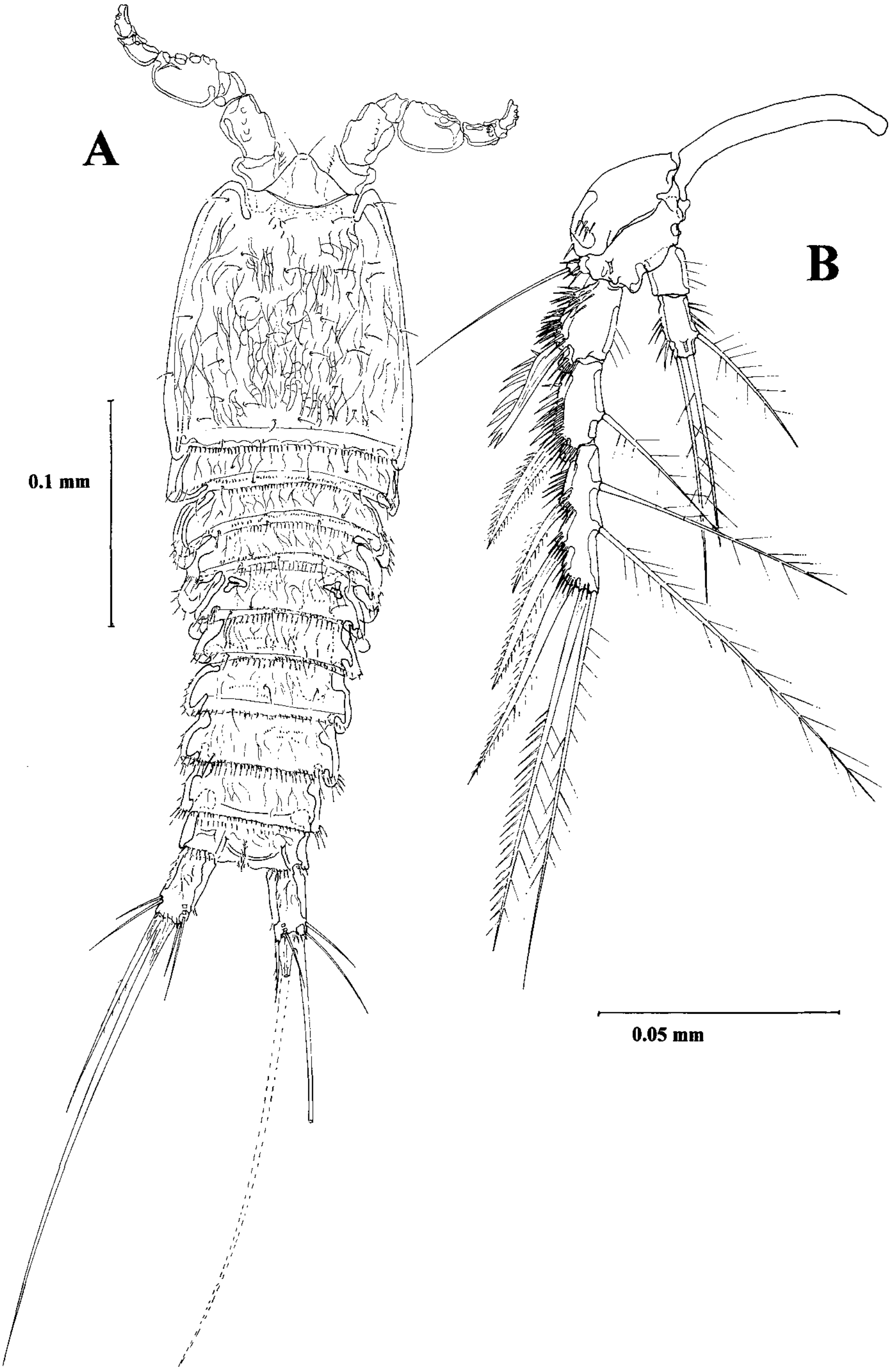

FIG. 16. *Weddellaophonte anyae* gen.n., spec.n.: (A) male habitus, dorsal; (B) male P4.

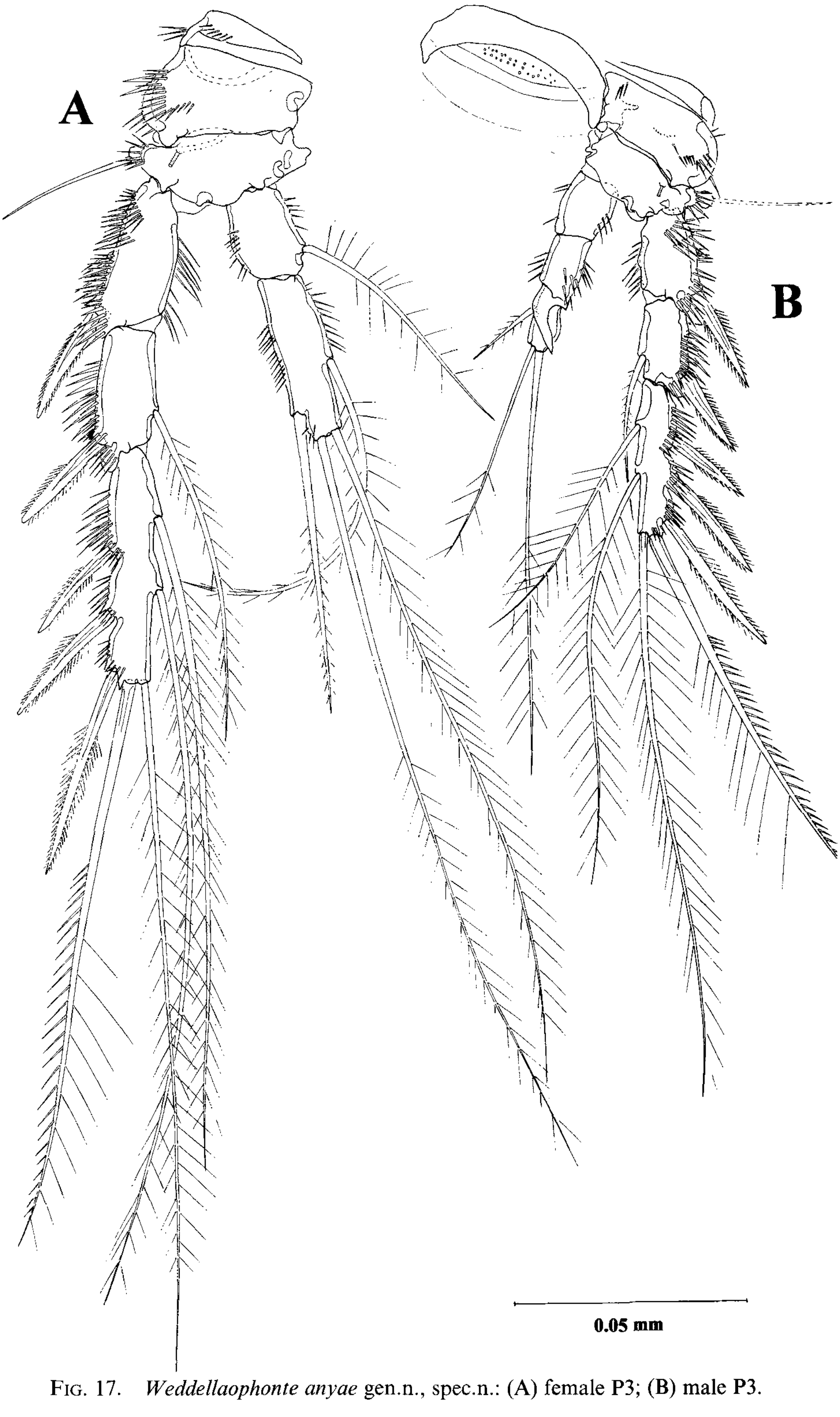

FIG. 17. *Weddellaophonte anyae* gen.n., spec.n.: (A) female P3; (B) male P3.

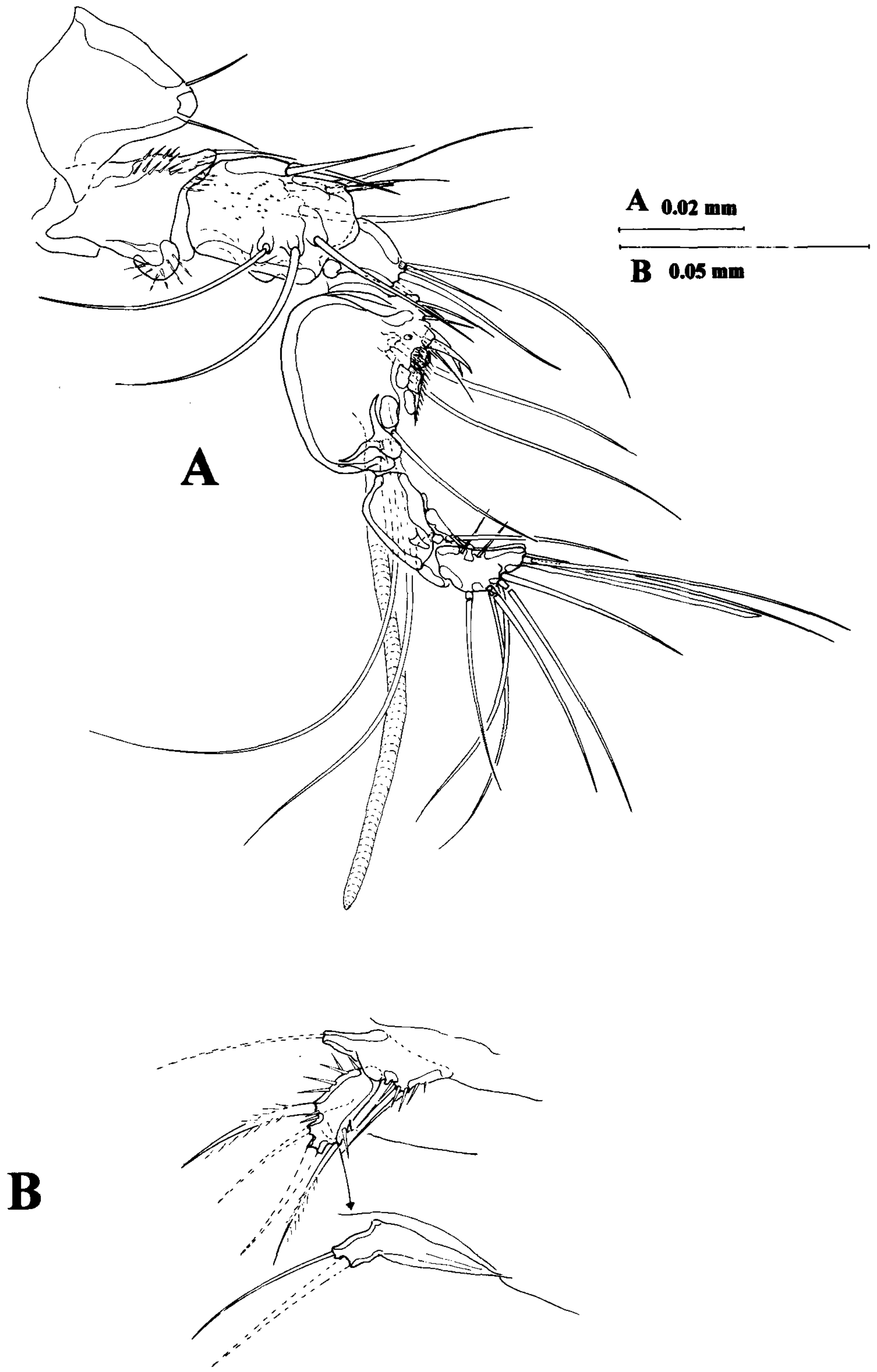

FIG. 18. *Weddellaophonte anyae* gen.n., spec.n.: (A) male antennule; (B) male P5 and P6.

the former being shifted towards anterior surface. Coxal endite with 1 seta only. Basal endite with one geniculate and two naked setae. Endopodite represented by three setae, exopodite cylindrical, with two long terminal setae.

Mxp (Fig. 13C) prehensile, all parts comparatively strong and stout. Syncoxa with spinules and two apical setae. Basis broad, asetose and with spinules. Enp represented by small sclerite, with strong, curved claw.

P2–P4 (Figs 12A, 13B, 17A) exopodites 3-, endopodites 2-segmented, endopodites much shorter than exopodites, intercoxal sclerites not extended. Each leg with triangularly shaped praecoxa. Outer margin of coxae slightly rounded. Basis with large tube pore and spinules at base of outer setae. Outer setae slender, pinnate in P2. Exps with spinules on outer margin and anterior surface. Outer spines pinnate, terminal and endopodal setae developed as swimming setae.

Spine and setal formulae as follows (according to Sewell, 1949, after Huys and Boxshall, 1991):

	Coxa	Basis	exp	enp
P2	0-0	I-0	I-0; I-1; III,I,2	0-0; 020
P3	0-0	I-0	I-0; I-1; III,I,3	0-1; 121
P4	0-0	I-0	I-0; I-1; III,I,3	0-1; 021

P5 (Fig. 14A) covered with long spinules. Benp forming almost an acute triangle, bearing one long, slender outer seta. Inner lobe slightly produced, with three inner and two terminal pinnate setae. Exp long, with three outer, one terminal and one inner seta.

Description of male

Body length: 0·35 mm. Maximal body width: 0·11 mm. Furcal rami: 0·037 mm.

Body (Figs 15A, 16A) shorter than in female, somites 5 and 6 separate, somites 6–8 without lateral spinulose expansions.

Antennule (Fig. 18A) subchirocer, 7-segmented. Segments I and II as in female. Segment IV bulbous, geniculation between IV and V. Armature: I(1); II(9); III(4); IV(10 + [1 + Aes]); V(0); VI(1); VII(7 + [1 + Aes]).

Antenna, mouthparts and P1 as in female.

P2–P4 (Figs 17B, 16B) as in female, except for P3- and P4enp1 without inner setae, P3enp 3-segmented, with apophysis and P4exp1 with modified outer spine.

P5 (Fig. 18C) benp defined? inner lobe slightly produced, with two setae. Exp elongated, with four strong setae.

P6 (Fig. 18B) consisting of small lobe with two setae.

Discussion

Phylogenetic aspects

Cornylaophonte exhibits a mixture of highly derived (e.g. the shape of the swimming legs, sexual dimorphism), and surprisingly primitive characters (e.g. four setae on the Mx enp and distal syncoxal endite respectively, presence of inner setae on P3 and P4enp, female benp setation, etc). A striking peculiarity is the modification of the outer spines of P4exp in the male (Fig. 6B). Similar modifications of the homologous spines occur in *Paralaophonte quaterspinata* (Brian, 1917), *Maiquilaophonte uachi* Mielke, 1985, *Laophonte farrani* Roe, 1958, *Klieonychocamptus ponticus* (Serban and Plesa, 1957) and *Heterolaophonte tenuispina* (Lang, 1934). All these species belong to different lineages within the

Laophontidae. *Paralaophonte quaterspinata*, *H. tenuispina* and *K. ponticus* are true members of their respective genera and not closely related to *Cornylaophonte*. The occurrence of this peculiar spine modification in the male P4 within different lineages of the Laophontidae can be regarded as a true case of parallelism or homoilogy, for it is yet unknown from other harpacticoids.

A further modification of the male P4exp is found in *Laophonte farrani*, where also the terminal spines are transformed. The outer spines of exp1 and 2 are described as 'antler-like' (Roe, 1958), while in *Cornylaophonte* their shape is jagged and serrate. There is no sexual dimorphism in the male P3exp in *L. farrani*. The setal reduction apparently followed a pattern different from that in *Cornylaophonte*: P2enp is smaller than enp1, with only 1 seta, all inner setae of the endopodites are lost (while retained in the female of *Cornylaophonte*), P3enp2 setation without reduction, P4enp quite small (in *Cornylaophonte* as long as in other swimming legs) with the setae located terminally. Other derived characters of *L. farrani* are the 5-segmented female antennule and the loss of the process on its second segment. All these characters indicate a different direction of evolutionary development for both species, despite of superficial similarities.

Another question is the relationship between *Cornylaophonte* and *Maiquilaophonte uachi* Mielke, 1985. There are several similarities: comparatively reduced setation in swimming leg exopodites and Md palp and again the modified spine on male P4exp1. However, *Maiquilaophonte* shows a lot of unique derived characters, such as the short and modified furcal setae, sexual dimorphism in segmentation of P4exp, 1-segmented and asetose P2enp. A closer look at the setal reduction reveals different patterns: *Cornylaophonte* retains the 2-segmented nature of the swimming-leg endopodites and shows instead just a shortening of terminal setae in P3, P4 and female P2, while in *Maiquilaophonte* the P2 and P4 enp are reduced to a single lobe, becoming asetose in P2 and being armed with well-developed (though reduced in number) strong setae in P4. Additional features separating *Cornylaophonte* and *Maiquilaophonte* are the different shape of the modified spine in the male P4 and shape and setation of the female P5, as well as the absence of sexual dimorphism in the male P3exp in *Maiquilaophonte*. Therefore, a close phylogenetic relationship between both genera/species appears to be rather unlikely.

The loss of the inner setae in exp3 and the reduction of the inner terminal setae in the exopodites of the swimming legs is a very common phenomenon within the Laophontidae and has developed several times independently, e.g. numerous species of the polyphyletic genus *Laophonte* (*L. danversae* Hamond, 1969, *L. foxi* Harding, 1956, *L. hirsutus* Pallares, 1979, etc), *Arenolaophonte* Lang, 1965, *Stygolaophonte* Lang, 1965 and *Apolaophonte* Wells and Rao, 1987, etc. However, different male morphology and differently derived characters indicate convergent evolution of this feature.

Parallel evolution of the swimming legs can also be recognized in the species of *Platychelipus* Sars, 1908, which are supposed to be unable to swim and which live in the intertidal muds, being specialized for crawling on the surface sediments (Barnett, 1966). The loss of the inner terminal exopodal setae, the stout outer spines and the slight bandy-legged appearance apart from sexual dimorphism—enables the animal to move by using legs and antennules to lever the body through the substratum (Barnett, 1966). In *Cornylaophonte* the degree of these adaptations takes in a kind of intermediate position between *Platychelipus littoralis* (Brady, 1880) and *P. laophontoides* Sars, 1908. The extended intercoxal sclerites, the solid appearance of the exopodites, with a trend to reduce the endopodites, suggest a similar life style for *Cornylaophonte*.

Unique characters of *Cornylaophonte* within the Laophontidae are the modification of the outer spine in the male P3exp2, the shortened and posteriorly located setae on P3enp2 in both sexes and the elongate basal setae, especially in P2. The new genus cannot be related to any of the known laophontid genera or lineages so far.

The assessment of the systematic position of *Weddellaophonte anyae* is even more difficult. Quite primitive characters like (within the family) complete setation of the swimming-leg exopodites, only slightly reduced setation of the endopodites (excl. P3 male), primitive male P3enp and lack of sexual dimorphism in the male exopodites, except for the modified spine on male P4exp1, are of no help in identifying relationships. Derived characters of the genus are the 6-segmented female antennule without a process on the second segment, the loss of inner setae on both segments of P2enp, of 2 inner setae on P3enp2 and of one inner and one outer seta on P4enp2, as well as the slightly flattened habitus.

There are indications of a closer relationship with *Cornylaophonte*: comparable shape of the female P5 (benp triangular, exp slender, longer than broad, its setation located terminally), whole P5 covered with spinules, setation of P3 and P4 in both genera sexually dimorphic: inner setae of enp1 in both limbs present in the female and absent in the male [This kind of sexual dimorphic setation however, also exists in some species of *Laophonte* (*L. confusa*, *L. depressa*, *L. galapagoensis*, *L. lignosa* in P4), *Paronychocamptus* (*P. exiguus, P. connexus* in P3), *Amerolaophontina* in P4 and the genus *Pseudonychocamptus* (in both P3 and P4?)], the similarly modified spine in the male P4exp1 (though in *Weddellaophonte* not as pronounced as in *Cornylaophonte*), loss of inner and outer seta in P4enp2, P2enp setation restricted terminally.

On the other hand there are also differences. In *Weddellaophonte* the terminal and inner setae of both rami of the swimming legs have fully maintained the character of long swimming-setae, the female genital field is quite different. [However, Fiers (1991) showed a considerable inter-specific variability of the shape of the genital field in the genus *Galapalaophonte*]. *Cornylaophonte* is far more derived and specialized in many aspects than *Weddellaophonte*. As long as there is no thorough revision of the taxa (particularly the genus *Laophonte*) at the base of the Laophontidae the position of *Weddellaophonte* must remain open.

Zoogeographic remarks

Table 1 shows the distribution of Laophontidae in the Antarctic and surrounding regions as known from the literature and evidenced by the present paper. The subantarctic (incl. South America, New Zealand, Southern Australia, subantarctic islands) fauna is dominated by the genera *Heterolaophonte* Lang, 1944 (and the related genera *Quinquelaophonte* Hicks, Wells and Coull, 1982, *Mictyricola* Nicholls, 1957) and *Paralaophonte* Lang, 1944, in terms of numbers of species. Representatives of both taxa could be expected to occur also in the high Antarctic. However, no single specimen of a *Heterolaophonte*-related taxon has been recorded in the Weddell Sea material so far, whereas two new species of *Paralaophonte* have been found, belonging to a new species-group. These new species will be described and discussed in detail elsewhere.

Hicks (1977) showed that the harpacticoid faunas of New Zealand and South America are more similar to each other than those of New Zealand and Australia, or New Zealand and South Africa. This is confirmed by the data available for the

Table 1. Hitherto known species of Laophontidae of the gondwanian continents.

South America/Falkland Islands/Tristan da Cunha

Species	Record
Endemic/only recorded from antiboreal region	
Loureirophonte catharinesis Jakobi, 1953	Brazil/south coast (Jakobi, 1953)
L. paranaensis Jakobi, 1953	Brazil/south coast (Jakobi, 1953)
Mourephonte longiseta (Nicholls, 1941)	Brazil/south coast (Jakobi, 1953)
Paralaophonte lacerdai Jakobi, 1953	Brazil/south coast (Jakobi, 1953) Argentina/Punta Canteras (Rouch, 1962)
Paralaophonte gracilipes (Brady, 1910)	Falkland Island (Lang, 1936) Argentina/Ria Deseado (Pallares, 1968)
Paralaophonte meinerti (Brady, 1899)	Argentina/Ria Deseado (Pallares, 1968) Tristan da Cunha (Wiborg, 1964)
Klieonychocamptoides itoi Mielke, 1985	Chile (Mielke, 1985)
Heterolaophonte campbelliensis (Lang, 1934)	Tierra del Fuego (Lang, 1936) Argentina/Ria Deseado (Pallares, 1968)
Heterolaophonte insignis (T. Scott, 1914)	Falkland Islands (T. Scott, 1914)
Heterolaophonte pauciseta (Lang, 1936)	Argentina/Ria Deseado (Pallares, 1968)
Heterolaophonte tenuispina (Lang, 1934)	Argentina/Ria Deseado (Pallares, 1968)
Galapalaophonte chilensis Fiers, 1991	Chile (Fiers, 1991)
Paronychocamptus connexus Pallares, 1979	Tierra del Fuego (Pallares, 1979)
Chilaophonte maiquillahuensis Mielke, 1985	Chile (Mielke 1985)
Chilaophonte concepcionensis Mielke 1985	Chile (Mielke 1985)
Afrolaophonte chilensis Mielke, 1985	Chile (Mielke 1985)
Maiquilaophonte uachi Mielke, 1985	Chile (Mielke 1985)
Laophonte hirsutus Pallares, 1979	Tierra del Fuego (Pallares, 1979)
Phycolaophonte insularis Pallares, 1975c	Tierra del Fuego (Pallares, 1975c) Chile (Mielke 1985)
More widespread distribution/cosmopolitan	
Esola longicauda Edwards, 1891	Brazil/Recife (Rouch, 1962)
Laophonte elongata barbata Lang, 1934	Argentina/Ria Deseado (Pallares, 1970)
Laophonte dinocerata Monard, 1926	Tierra del Fuego (Pallares, 1975)
Onychocamptus mohammed (Blanchard and Richard, 1891)	Brazil/Recife (Chappuis, 1936)
Laophonte cornuta Philippi, 1840	Tristan da Cunha (Wiborg, 1964) Argentina, Ria Deseado (Pallares, 1968)
Scotia arc	
Endemic	
Heterolaophonte australis (T. Scott, 1912)	South Orkney Islands (T. Scott, 1912)
Heterolaophonte exigua (T. Scott, 1912)	South Orkney Islands (T. Scott, 1912)
H. rottenburgi (T. Scott, 1912)	South Orkney Islands (T. Scott, 1912)
Laophonte wiltoni (T. Scott, 1912)	South Orkney Islands (T. Scott, 1912)
Heterolaophonte pauciseta (Lang, 1936)	South Georgia (Lang, 1936)
Kerguelen	
Endemic/only recorded from antiboreal region	
Paralaophonte gracilipes (Brady, 1910)	(Brady, 1910)
Laophonte euxiniphila Soyer, 1977	(Soyer, 1977)
Laophonte varians Brady, 1910	(Brady, 1910)
Cosmopolitan	
Laophonte cornuta Phillipi, 1840	(Brady, 1910)

Table 1. Continued

South Africa

Endemic

Wellsiphontina distincta (Wells, 1967)	Mozambique (Wells, 1967)
Afrolaophonte brevipes (Chappuis, 1954)	Madagascar (Chappuis, 1954)
Psammolaophonte spinicauda Wells, 1967	Mozambique (Wells, 1967)
Tapholeon ornatus Wells, 1967	Mozambique (Wells, 1967)
T. uniarticulatus Wells, 1967	Mozambique (Wells, 1967)
Laophonte spinifer Kunz, 1965	South Africa/East London (Kunz, 1975)

More widespread distribution/cosmopolitan

Folioquinpes chathamensis (Sars, 1905)	Capetown (Rühe, 1914)
Laophonte cornuta Phillipi, 1840	Mozambique (Wells, 1967)
Laophonte inornata A. Scott, 1902	Mozambique (Wells, 1967)
Paralaophonte brevirostris (Claus, 1863)	Mozambique (Wells, 1967)
P. congenera (Sars, 1908)	Mozambique (Wells, 1967)
P. tenera (Sars, 1920)	Mozambique (Wells, 1967)
Quinquelaophonte quinquespinosa (Sewell, 1924)	Mozambique (Wells, 1967)
Laophonte elongata barbata Lang, 1934	South Africa/East London (Kunz, 1975)

Australia

Endemic/only recorded from antiboreal region

Laophonte adduensis Sewell, 1940	West-Australia/Port Denison (Nicholls, 1945)
Mictyricola typica Nicholls, 1957	Australia/Tansmania (Nicholls, 1957)
M. proxima Nicholls, 1957	Australia/Tansmania (Nicholls, 1957)
Quinquelaophonte wellsi (Hamond 1973)	Southeast-Australia (Hamond, 1973)
Mourephonte longiseta (Nicholls 1941)	West-Australia/Port Denison (Nicholls, 1941)

More widespread distribution/cosmopolitan

Paralaophonte congenera (Sars, 1908)	West-Australia/Port Denison (Nicholls, 1945)
Laophonte cornuta Philippi, 1840	Tasmania (Lang, 1934)
Onychocamptus bengalensis (Sewell 1934)	Southeast-Australia (Hamond, 1973)
Quinquelaophonte quinquespinosa (Sewell, 1924)	Southeast-Australia (Hamond, 1973)
Esola longicauda Edwards, 1891	West-Australia/Port Denison (Nicholls, 1945)
Echinolaophonte armiger (Gurney, 1927)	West-Australia (Nicholls 1945)

New Zealand/Campbell Island/Stewart Island/Chatham Islands

Endemic/only recorded from antiboreal region

Paralaophonte aenigmaticum Wells, Hicks and Coull, 1982	New Zealand (Wells, Hicks and Coull, 1982)
Laophonte lignosa Hicks, 1988	New Zealand (Hicks 1988)
Quinquelaophonte candelabrum Hicks, Wells and Coull, 1982	New Zealand (Wells, Hicks and Coull, 1982)
Heterolaophonte campbelliensis (Lang, 1934)	Campbell Island (Lang, 1934)
H. tenuispina (Land, 1934)	Campbell Island (Lang, 1934)
Coullia spec. A & B	New Zealand (Hicks 1977)
Paronychocamptus exiguus (Sars, 1905)	Chatham Islands (Sars, 1905)
Paralaophonte meinerti (Brady, 1899)	Campbell Island (Lang, 1934) New Zealand (Hicks) 1977 New Zealand (Brady 1899)

Table 1. Continued

More widespread distribution/cosmopolitan

Laophonte cornuta Philippi, 1840	New Zealand (Brady, 1899) Campbell- and Stewart Islands (Lang, 1934)
L. cornuta var. *nigrocincta*	New Zealand (Hicks, 1977)
L. elongata barbata Land, 1934	Stewart Island (Lang, 1934)
L. cf. *inornata*	New Zealand (Hicks, 1977)
Folioquinpes chathamensis (Sars, 1905)	Chatham Island (Sars, 1905)
Quinquelaophonte longifurcata (Lang, 1965)	New Zealand (Hicks, 1977)
Harrietella simulans (T. Scott, 1894)	New Zealand (Hicks, 1989)
Laophonte cf. *sima* Gurney, 1927	New Zealand (Hicks, 1977)

Antarctic

Endemic

Laophonte glacialis Brady, 1910	East Antarctic/Gauss-Station (Brady, 1910)
Archilaophonte maxima Willen, 1995	Weddell Sea (Willen, 1995)
Cornylaophonte pleisteri gen.n., spec.n	Weddell Sea, present paper
Weddellaophonte anyae gen.n., spec.n	Weddell Sea, present paper
Paralaophonte spec. 1	Weddell Sea, Willen, unpubl.
spec. 2	Weddell Sea, Willen, unpubl.

Laophontidae (Table 1). Whereas New Zealand and South America have 3 laophontid species in common (not counting the cosmopolitan and widespread species) New Zealand and Australia have none. Hicks (and also Wells, 1986) rejects the view that long distance transoceanic dispersal of harpacticoids by rafting on algae and other floating objects may have been important for the present day distribution. He found continental drift to be the most plausible explanation for the present day distribution patterns, assuming connections between New Zealand and South America via West Antarctica and between Australia and South African via East Antarctica.

The question of the origin and age of the Antarctic fauna has been the subject of several investigations. During the Miocene the glaciation of the Antarctic continent is supposed to have resulted not only in the extinction of most of the terrestrial fauna and flora, but also the marine fauna has been affected through a drop in the water temperatures. Only cold stenotherm species could have survived these climatic changes (Brandt, 1991). In his phylogenetic analysis of the Tanaidacea, Sieg (1988) found the recent tanaidacean taxa of the Antarctic mainly to be 'phylogenetically young'. He postulated an almost entire extinction of the Antarctic species during the maximal phase of glaciation, and recolonization by younger deep-sea and partly more primitive Magellanian taxa. He also interpreted the data available for other macrofaunal crustaceans as pointing in the same direction, thus denying the existence of primitive or relict species in the Antarctic. In contrast, Brandt (1991) shows deep-sea submergence for several isopodan families. The Serolidae and Arcturidae, for example, are represented by more primitive genera in the Antarctic, with high species diversity and endemism, indicating an Antarctic/gondwanian origin. The author therefore assumes that several benthic taxa have survived the glaciation in biological refuges.

The present data on meiofaunal harpacticoids also do not fit Sieg's hypothesis

(1988). The Antarctic Laophontidae recorded thus far—except for *Cornylaophonte*—are undoubtedly 'phylogenetically old'. *Archilaophonte maxima* Willen, 1995, the most primitive laophontid species known so far, appears to be a relict, being restricted to the Antarctic, while its sister taxon *Esola* Edwards, 1891, has a worldwide distribution. *Weddellaophonte anyae* also shows mainly primitive features. The present data speak more in favour of an old Antarctic (at least Weddell Sea) laophontid fauna, having survived and adapted to the climatic changes. No cosmopolitan or more widespread species, otherwise present in all or several gondwanian continents (e.g. like *Laophonte cornuta*, Table 1), have been detected in the Weddell Sea samples, suggesting the possibility, that they have not been able to colonize the high Antarctic. In other harpacticoid taxa the situation may be different. *Laophontodes whitsoni* T. Scott, 1912 (Ancorabolidae) for example, first recorded from the South Orkney Islands and later from Tierra del Fuego (Pallares, 1975a), has also been found in the Weddell Sea (redescription by George, 1993, unpublished). Therefore each taxon needs to be investigated separately. The derived *Cornylaophonte* could either have developed *in situ*—maybe from a common ancestral stock with *Weddellaophonte*—or migrated from elsewhere. Deep-sea emergence, for example, cannot be excluded, as long as there are no data from the adjacent deep sea regions.

The laophontid species of the isles of the Scotia-Arc (except for *Laophonte wiltoni* T. Scott, 1912) have all been assigned to the genus *Heterolaophonte* by Lang (1948). Since the descriptions of T. Scott (1912) are over 80 years old and incomplete (the males of all species, which are important for exact determination, being still unknown), the generic status of *Heterolaophonte exigua*, *H. rottenburgi* and *H. australis* remains doubtful. The occurrence of a process on the second segment of the female antennule, as in *H. rottenburgi*, is not known from any other *Heterolaophonte* species. These taxonomic uncertainties show that no more than a few preliminary statements can be made with respect to the zoogeography of Antarctic Harpacticoida.

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