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Archilaophonte maxima gen.n., spec.n., a new taxon of the Laophontidae (Copepoda, Harpacticoida) from the high Antarctic (Weddell Sea)

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Abstract

Male and female of a new genus and species of the family Laophontidae, *Archilaophonte maxima*, are described. The specimen was found in the high Antarctic (Weddell Sea) and appears to be the most primitive genus up to now within the superfamily Laophontoidea as defined by Huys (1990). Based on its setation of legs and mouth parts, however, it can be placed unequivocally into the family Laophontidae. *Archilaophonte maxima* gen. n. shows close affinities to the laophontid genus *Esola* Edwards, 1891. Both genera form a monophyletic group which is interpreted here as the first and most primitive offshoot in the evolution of the Laophontidae. The synapomorphies of the former lineage are the shape of the protopodite of the P1 and shape and setation of the female P5.

Introduction

An investigation of meiobenthos samples from the Weddell Sea collected during three expeditions of the Polarstern has produced a few new laophontid species, one of which will be described here.

Up to now the only laophontid species to be recorded from the high Antarctic is *Laophonte glacialis* Brady, 1910, which was collected at Gauss-Station (East- Antarctica) during the 'Deutsche Südpolar-Expedition' 1901–1903. Unfortunately Brady's description does not show sufficient detail to place the species unambiguously into one of the genera of the Laophontidae (Lang, 1948).

In subantarctic regions (Magellan-region, Kerguelen, Campbell-Island), South Georgia and South-Orkney-Islands the Laophontidae are mainly represented by several species of the genera *Heterolaophonte* Lang, 1944, *Laophonte* Phillipi, 1840, and *Paralaophonte* Lang, 1944. Two new species of the latter genus have also been found in the material from the Weddell Sea and will be described in a subsequent paper.

Materials and methods

3 females and 2 males collected during Ant V/3 expedition from various sites of the Weddell Sea, Antarctic shelf.

Locality of female holotype: 72° 52.3′, 019° 34.7′W, 20.10.1986, from 495 m depth.

Locality of male allotype: 72° 52.4′S, 019° 31.2′W, 3.11.1986, from 430 m depth.

The holotype has been preserved in 5% buffered formaldehyde and later transferred into Zeiss W15 embedding medium. Drawings were made with the aid of a camera lucida on a Leitz Diaplan microscope equipped with a phase contrast $100 times$ objective. Before dissection, the whole specimen was drawn from the dorsal and lateral side. The dissected parts are mounted on 6 slides. All specimen are in the author's collection.

The terminology is adopted from Lang (1948, 1965) except for the segmental composition of mandible and maxilliped which are followed according to Huys & Boxshall (1991). The setae of the caudal rami are also numbered according to Huys & Boxshall (1991). Abbreviations used in the text: C.R.: caudal rami, Aes: aesthetasc, exp: exopodite, enp: endopodite, 'enp1': first segment of endopodite, P1–P6: swimming legs 1–6.

Description of female

Body length	0.984 mm (incl. C.R.)
Caudal rami	0.194 mm
Maximum body width	0.197 mm (measured at rear margin of cephalothorax)

Rostrum (Fig. 1) slightly longer than broad and rounded at tip, continuous with cephalothorax, with a pair of tiny setules anteriorly.

Body (Figs. 1, 7) long and slender, tapering posteriorly. Cephalothorax almost square in shape. Whole surface of somites covered with regularly spaced minute spinules. Dorsal surface of cephalothorax also regularly ornamented with setules. A pore opens dorsally in the middle of posterior margin of every somite (incl. cephalothorax, excl. anal somite and penultimate somite). Posterior margin of each segment (excl. anal somite) with spinules interspersed with several setules. Pleurotergites of thoracic somites (bearing P2–P4) semicircular, produced ventrally and partly fringed with spinules. Genital and first abdominal somite fused to form genital double somite. Genital complex with large copulatory pore and large, tube-shaped copulatory duct; P6 consisting of 2 long, slender setae and 2 spinule rows on each side. Free abdominal somites with slight, spinulose ventrolateral expansions.

Anal somite with spinulose anal operculum flanked by 2 setules arising from small knobs. Base of caudal rami partly surrounded by spinular row. The 'glandular modifications' described by several authors and summarized by Huys (1990) at the inner margin of the caudal rami, the genital double somite and the cephalic shield of *Esola longicauda* (Edwards, 1891) could not be observed in *Archilaophonte* gen.n..

Caudal rami (Figs 1, 6) app. 8 times longer than broad; elongate, all setae located near posterior end; setae I and II subterminal at outer margin, the latter arising from a small process. IV, V and VI terminal: IV well developed, shorter than V which is longest, VI small and bare. VII situated in midline of dorsal surface near posterior end, biarticulated at the base and slightly plumose. Surface ornamentation consisting of tiny spinules; several rows of stronger spinules running along dorsal midline.

Antennule (Fig. 2) six-segmented, outwardly directed, majority of setae long and slender. First segment covered with tiny spinules as well as 2 rows of stronger ones and with 1 slightly pinnate seta at distal inner corner. Second segment with a well developed outer spinous process and with 9 setae, 8 of which arising from a small knob; one seta midway along anterior margin short and pinnate, the other setae longer and slender, at least 2 of them slightly plumose. Third segment longest, with 6 setae arising in pairs along anterior margin. Fourth and fifth segment comparatively short. Fourth segment with 1 seta and 1 long aesthetasc sharing a common base with another seta, both arising from a protrusion at inner distal corner; protrusion longer than half of the fifth segment. Fifth segment smallest with 1 long, slender seta at the anterior distal edge. Sixth segment long, with 11 setae and 1 aesthetasc, the latter confluent at base with one of distal setae. Outer margin with 2 articulated setae arising from small knob, inner margin with 3 comparatively short setae. Distal margin besides aesthetasc and its accompanying seta with 4 articulated setae and 1 additional seta on a knob more proximally.

Armature formula: I-1, II-9, III-6, IV-2 + Aes, V-1, VI-11 + Aes.

Antenna (Fig. 3) Coxa with spinule row. Allobasis slightly constricted, covered with spinules proximally. Abexopodal margin with irregular row of spinules and pinnate seta. Exp 1-segmented with four pinnate setae, one of which quite short. Enp with several spinule rows and two lateral spines, one of which slightly pinnate at tip; apical armature consisting of 6 elements: 2 spiniform setae and 3 long, slender and geniculate setae, the outermost of which pinnate and fused basically with a very small and short seta. Subapically 2 prominent chitinous membranes fringed with a frill.

Mandible (Fig. 3) Coxa basally with comb of longer spinules and row of spinules at outer margin. Cutting edge from ventral to dorsal corner 2 uni- or bidentate teeth, with 2 tri- or multidentale ones, 2 terminally indented elements and a slender, plumose seta. Palp: both enp and exp well defined. Enp with 3 setae, exp with 1 seta; basis with strong, plumose seta.

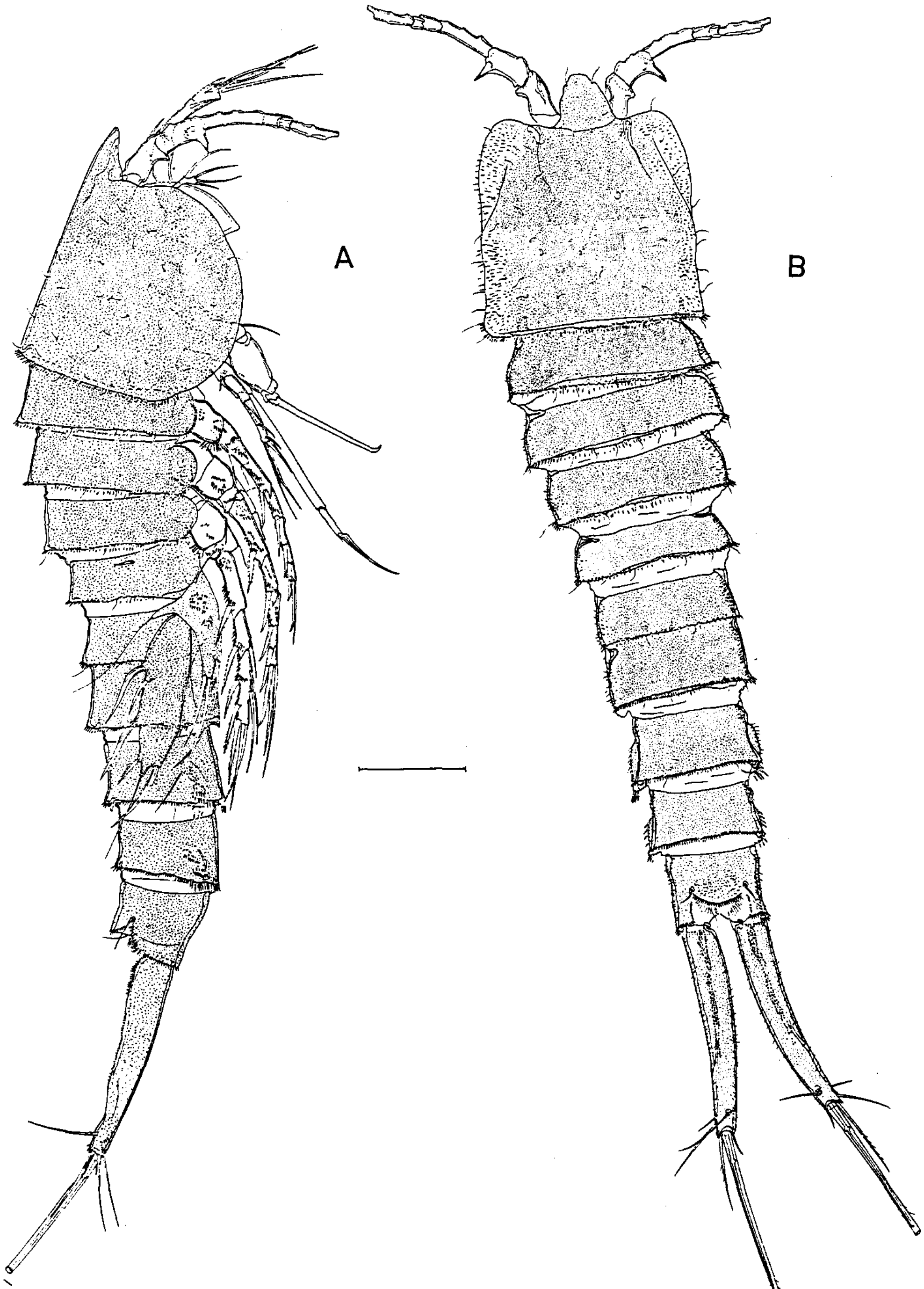

Fig. 1. Archilaophonte maxima gen.n., sp.n.; female habitus, A, lateral view, B, dorsal view. Scale bar = 0.1 mm.

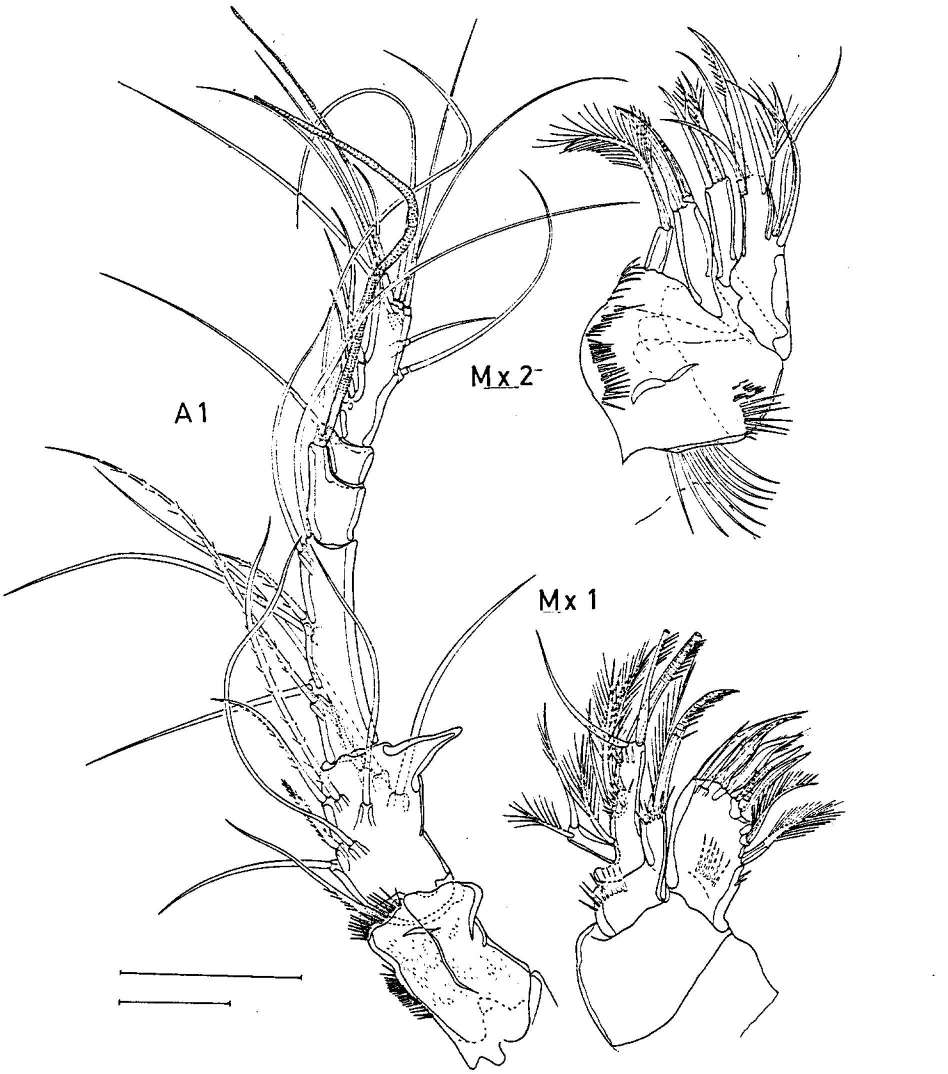

Fig. 2. *Archilaophonte maxima* gen.n., sp.n.; female antennule, maxilla and maxillula. Scale bars = above 0.05 mm (A1), below 0.02 mm (Mx, Mxl).

Maxillule (Fig. 2) Arthrite of praecoxa apically with 7 elements, from outside to inside with 1 bare and slender seta, 3 claw-like spines of which one is slightly plumose at tip, and with 2 slender spines, anterior of which there is a short oblique seta; also with slender bare seta on small knob inserting subapically near outer margin; inner margin with 2 strong, plumose setae; anterior surface proximally with row of longer spinules. Coxal endite with 1 strong, spinulose claw, 1 plumose seta, and a spinule row distally. Endite of basis carrying 3 setae, one of which geniculate and pinnate. Enp not defined, consisting of 3 setae, 2 of which plumose. Exp cylindrical with 2 plumose setae, one of which quite short; an additional seta inserts at or near base of exp.

Maxilla (Fig. 2) Syncoxa with several rows and patches of more or less long spinules and 3 endites. Proximal endite smallest, with long, plumose seta; middle endite with claw-like spine and spiniform, geniculate seta; distal endite with 3 setae, outermost of which plumose subapically. Endite of basis strong, claw-like and pinnate near tip, accompanied by 4 setae. enp fully incorporated in basis represented by 4 setae, one of which short.

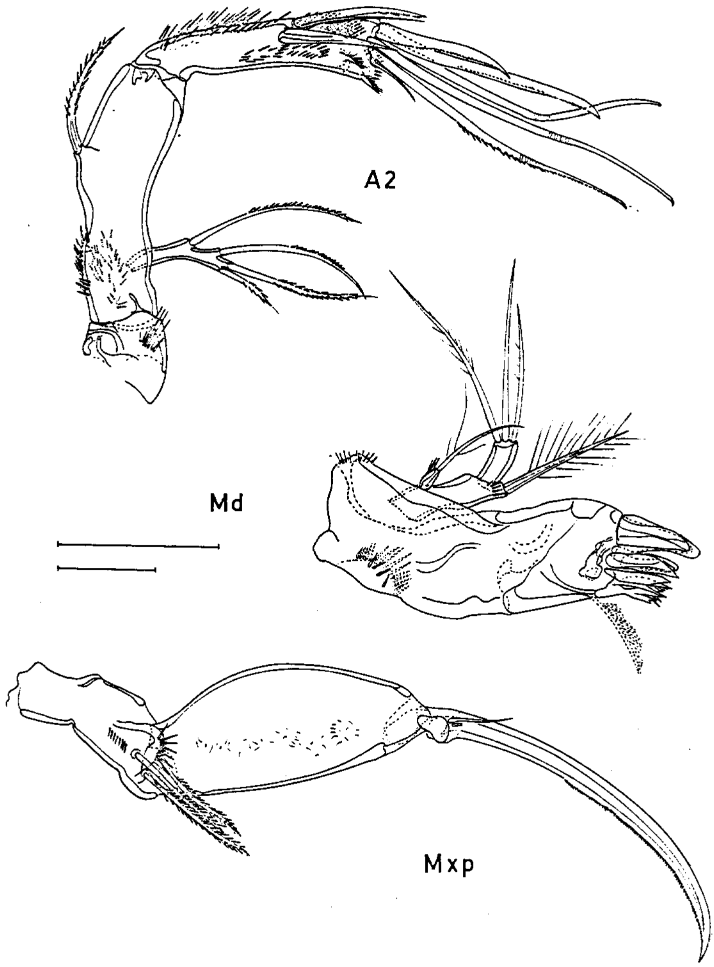

Fig. 3. Archilaophonte maxima gen.n., sp.n.; female antenna, mandible and maxilliped. Scale bars = above 0.05 mm (A2, Mxp), below 0.02 mm (Md).

Maxilliped (Fig. 3) prehensile. Syncoxa with spinulose lump distally, bearing 3 plumose setae. Basis long and swollen, with few tiny spinules along longitudinal axis. Enp small, unisegmented, carrying a very long, curved and slightly denticulate claw, 1 very small seta and a tiny tubercle.

P1 (Fig. 4) praecoxa small, triangular, with spinule row distally. Coxa with 2 spinule rows along outer margin and on anterior surface. Inner margin of basis with spinules, inner basal seta inserted on cylindrical process located on anterior surface; this surface also ornamented with at least 2 rows of spinules; outer margin of basis with plumose seta. Exp displaced; inserting slightly distal of outer basal seta; 2-segmented, outer margins of segments with several spinule rows, exp1 with 1 long, pinnate seta, exp2 with 3 unilaterally pinnate setae and 2 terminal long, pinnate and geniculate ones. Exp extending to first third of enp1. Enp1 long and slender, spinules along lateral margins and on anterior surface; inner margin with 1 slender, bare seta at about halfway. Enp2 small, with spinules along outer margin and distally with 2 terminal elements: posteriorly 1 tiny seta and anteriorly 1 long, slender, serrate claw.

P2–P4 (Figs 4, 5) exp 3-segmented, enp 2-segmented. Praecoxa triangular, with spinules along

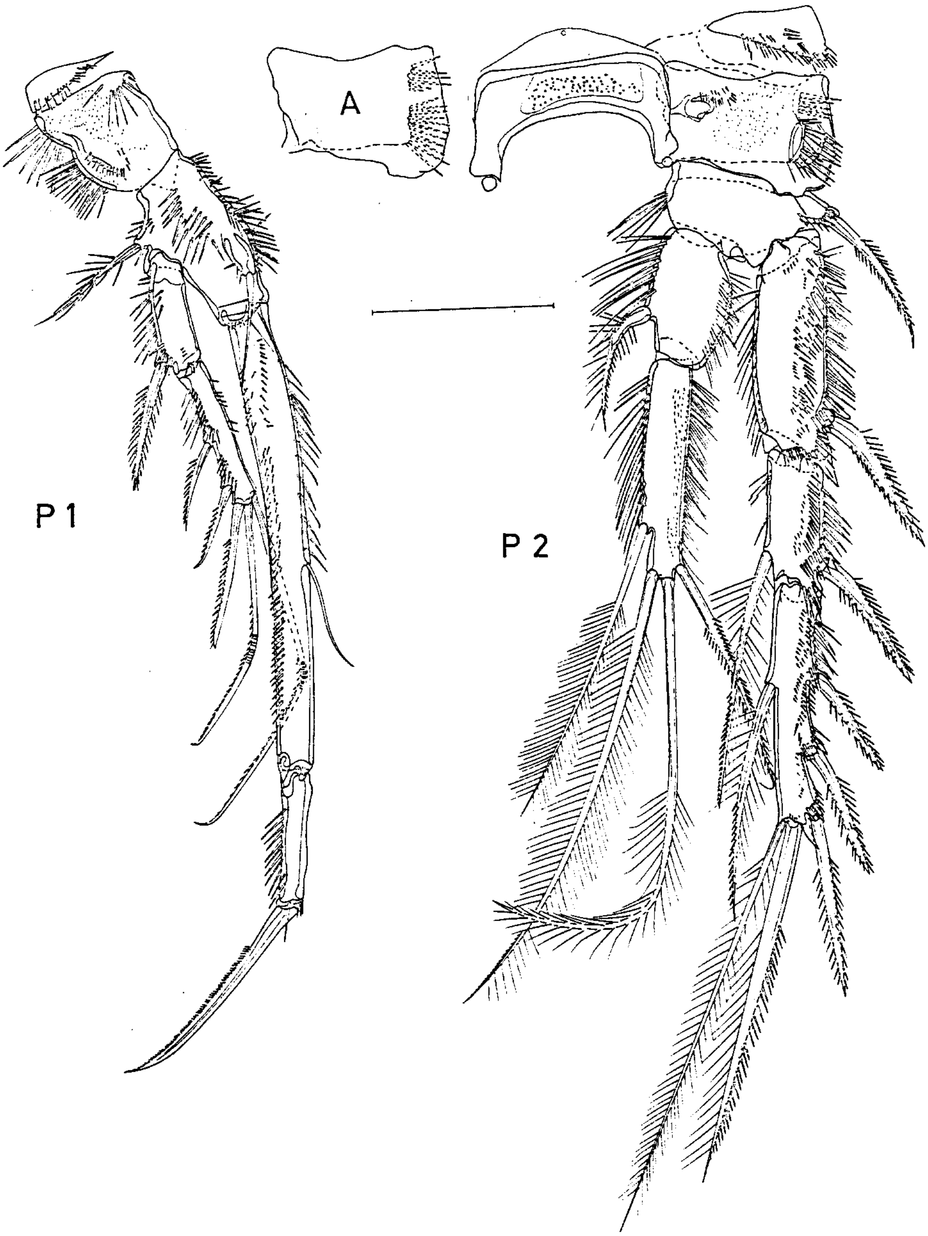

Fig. 4. *Archilaophonte maxima* gen.n., sp.n.; female P1 and P2, A, posterior side of P2 coxa. Scale bar = 0.05 mm.

distal margin. Coxae rectangular, with 2 spinular rows laterally on anterior surface and 1 (P4) or 2 (P2, P3) on posterior surface, respectively. Basis with long spinules along inner margin, with 1 seta on a process and a spinular row at its base on outer margin, seta short and pinnate (P2) or long and slender (P3, P4) respectively. Exp segments with several rows of spinules of different size along outer margins, distal margins of segments with a set of smaller spinules. Outer distal corner of all segments produced into a tooth. Exp1 and exp2 with 1, exp3 with 3 outer bipinnate setae, terminally with one long, strong outer seta being pinnate on outer and plumose on inner side, and 1 long, slender plumose seta. Inner margin of exp1 without seta. Exp2 with 1, exp3 with 1 (P2) seta or 2 (P3, P4) setae which are plumose and pinnate in distal half. Enp1 of P3, P4 short, enp2 elongate. Enp1 of all legs with plumose curved inner seta. Inner and outer margins of enp1 with delicate spinules (P3, P4) or with long and slender spinules along inner margin (P2). Enp2 quite long, inner margin with slender spinules, outer with very delicate ones, surface with small denticles in outer half. Enp2 of each leg with outer bipinnate seta, 2 long, plumose terminal setae, as well as 1 (P2), 2 (P4) and 3 (P3) plumose inner setae, respectively, which except for P2 are pinnate in distal portion.

Setae formulae (after Sewell 1949):

Coxa	Basis	Exp	Enp
P2 0–0	1–0	I-0; I-1; III,I,2	0–1; 1,2,1
P3 0–0	1–0	I-0; I-1; III,I,3	0–1; 1,2,3
P4 0–0	1–0	I-0; I-1; III,I,3	0–1; 1,2,2

P5 (Fig. 6) whole surface covered like body-somites with small spinules. Benp slender and nearly triangular, with long spinules along margins and a patch of stronger ones on proximal surface. Outer margin with 1 long bare and slender seta arising from a long protuberance. Inner margin with 1 curved plumose seta proximally and 2 pinnate setae distally, the distalmost being longest, and, with 2 pinnate setae apically, innermost of which long and strong, outermost shorter. Exp drawn out and narrow, fringed with spinules along inner margin and partly along outer margin. Proximal half with 2 setae, one pinnate, short and situated anteriorly to the other seta which is strong, multipinnate and curved downwards. More distally another multipinnate, curved seta. Terminally 3 setae: outermost plumose and short, middle one long, bare and slender, arising from a protuberance and innermost strong and multipinnate.

Description of male

Body length: 0.834 mm Caudal rami: 0.2 mm maximum body width: 0.25 mm

Body (Fig. 7) ornamentation and habitus as in female except for genital and first abdominal somites fully separated.

Antennule (Fig. 8) 7-segmented, sexualdimorphically modified, geniculation between fifth and sixth segment. Second segment with spinous outer process. Fourth segment swollen and slightly elongated. Armature formula: I-1; II-9; III-8; IV-2; V-2 strong and pinnate + 8 + 1 + Aes; VI-1; VII-9 + 1 + Aes.

Mouthparts and swimming legs as in female, except for P3 (Fig. 8) having a 3- segmented endopod and a very long inner apophysis on the middle segment.

P5 (Fig. 8) pair of legs medially fused, inner lobe of benp quite well developed with 2 long setae. Exp long and slender with 4 setae.

P6 (Fig. 8) vestigial, located on ventral surface, consisting of 1 small seta.

Discussion

Archilaophonte maxima gen.n., sp.n. shares a number of characters with *Esola* Edwards, 1891.

Nevertheless, the new species differs in a suite of characters explained below from all other Laophontidae. However, it can be placed without doubt in the family because of the following synapomorphies defined by Huys (1990):

- mandibular palp with 3 setae on the enp, 1 seta on the exp and 1 basal seta.
- P1 with inner seta of basis displaced to anterior surface, enp2 bearing an anterior claw and a posterior tiny seta.
- maxillule lacking a second basal endite and the two juxtaposed setae on the posterior surface of the praecoxal arthrite.

Characters shared by Esola and Archilaophonte maxima gen.n., sp.n.

1.Structure of P5 (Fig. 6)

Shape and setation of the female P5 are very distinctive in *Archilaophonte* gen.n. and *Esola*. The benp is almost triangular in shape and slender. The exp is also slender and elongated, extending far beyond the benp and bearing proximally on the outer margin 2 setae that are almost superimposed. The upper seta inserts on the posterior face at least in *Archilaophonte* gen.n.. Whether it also inserts there in *Esola* is not clear, but at least both setae are always present and superimposed as in *Archilaophonte* (on the drawings of other authors it is impossible to distinguish the insertion point of this seta). However, in the description of *Esola typhlops* and *E. rosei* made by Sars (1908) and Monard (1926) respectively, one of these setae seems to be missing.

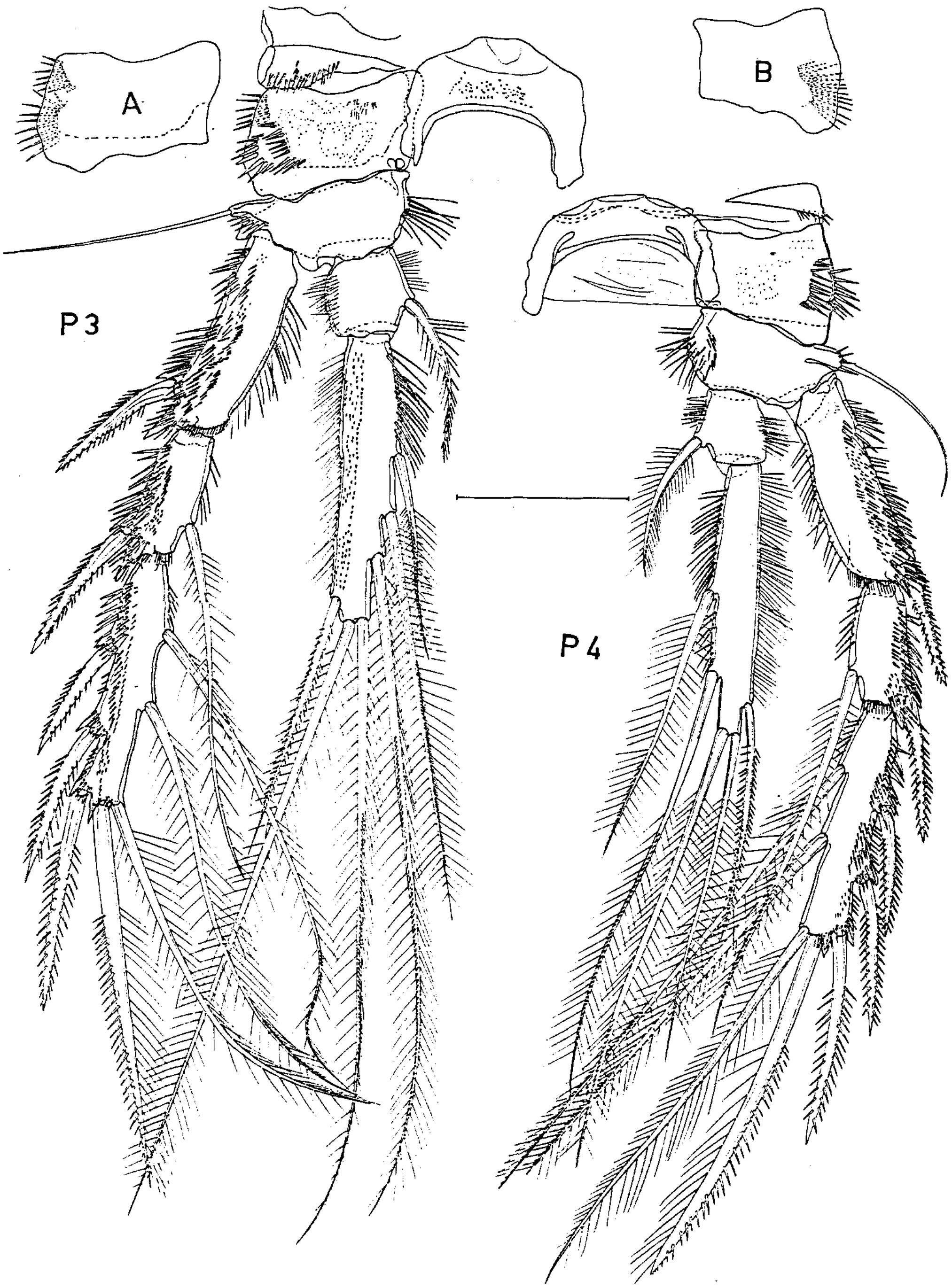

Fig. 5. Archilaophonte maxima gen.n., sp.n.; female P3 and P4, A,B, posterior side of P3 and P4 coxa respectively. Scale bar = 0.05 mm.

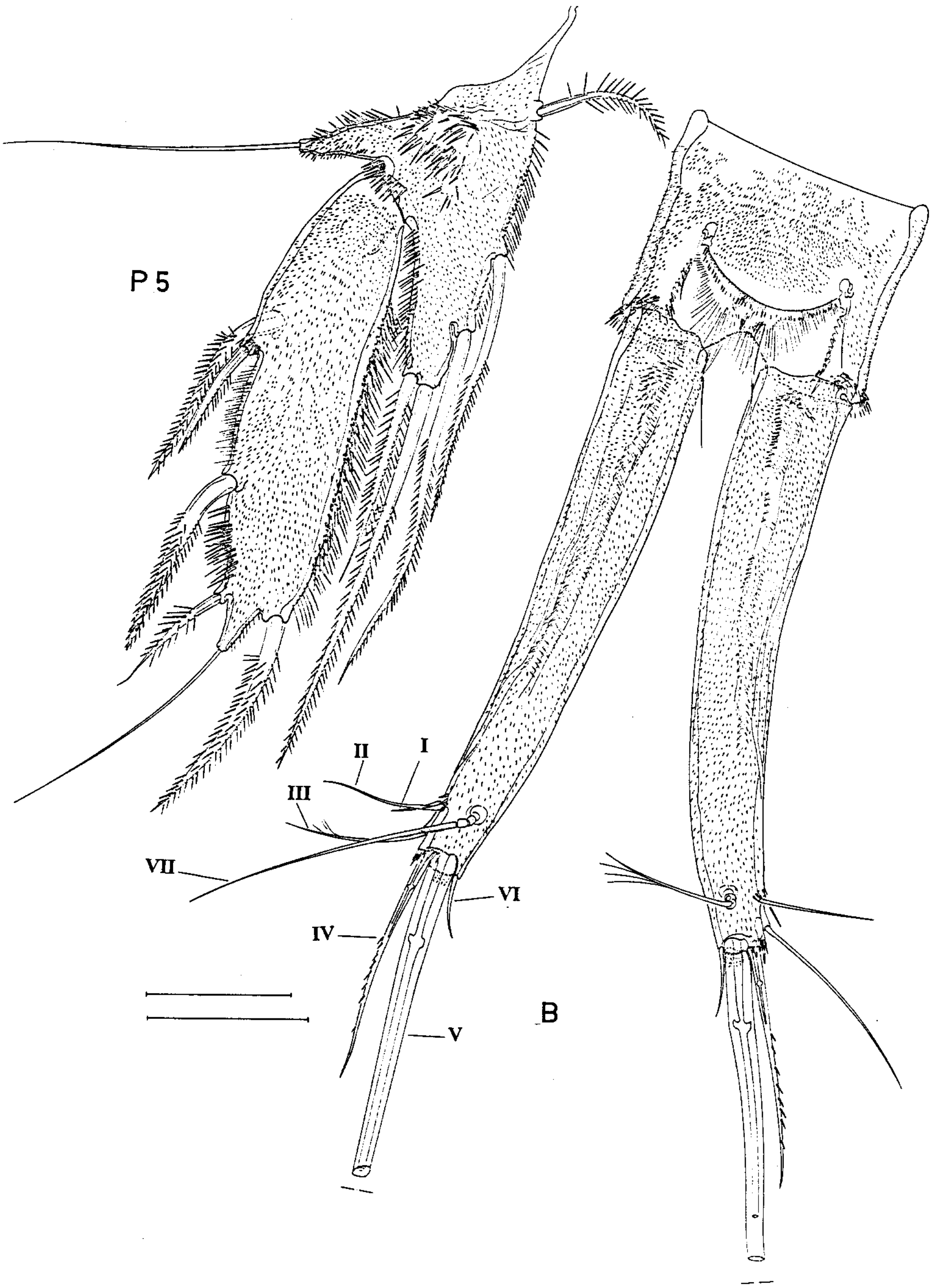

Fig. 6. Archilaophonte maxima gen.n., sp.n.; female P5, B, caudal rami. Scale bars = 0.05 mm, above P5, below C.R.

Probably they have been overlooked, as had also been presumed by Lang (1948). The occurrence of 2 similar setae in *Laophonte parvula* Sars, 1908 is probably convergent because the shape of both rami is very different from that in *Archilaophonte gen.n./Esola*. A triangular shape of benp and an elongated exp also occur in other species of the genus *Laophonte* (*L. elongata* Boeck, 1872, *L. depressa* T. Scott, 1894) but not as pronounced as in *Archilaophonte gen.n./Esola* and without the characteristic setae.

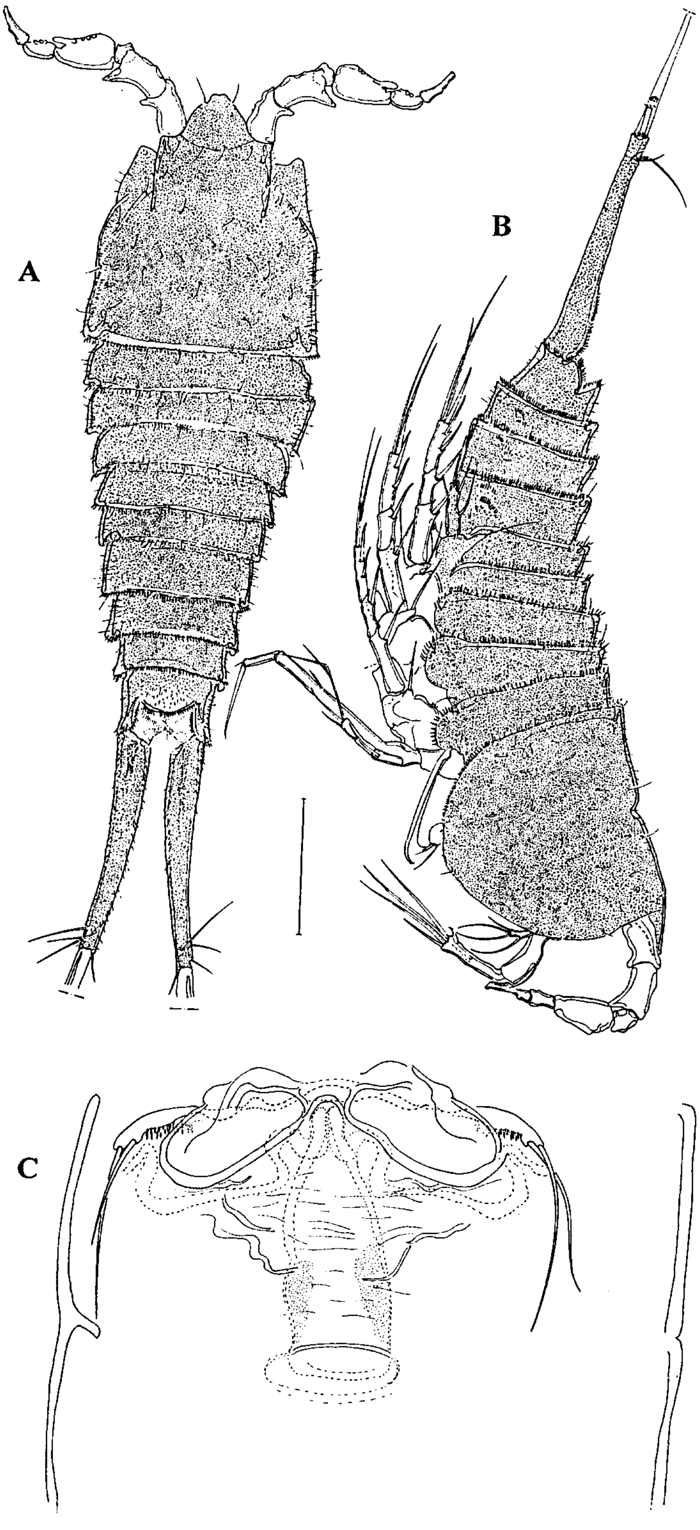

Fig. 7. Archilaophonte maxima gen.n., spec.n.; male habitus, A, dorsal view, B, lateral view, C, female genital field. Scale bar = 0.05 mm

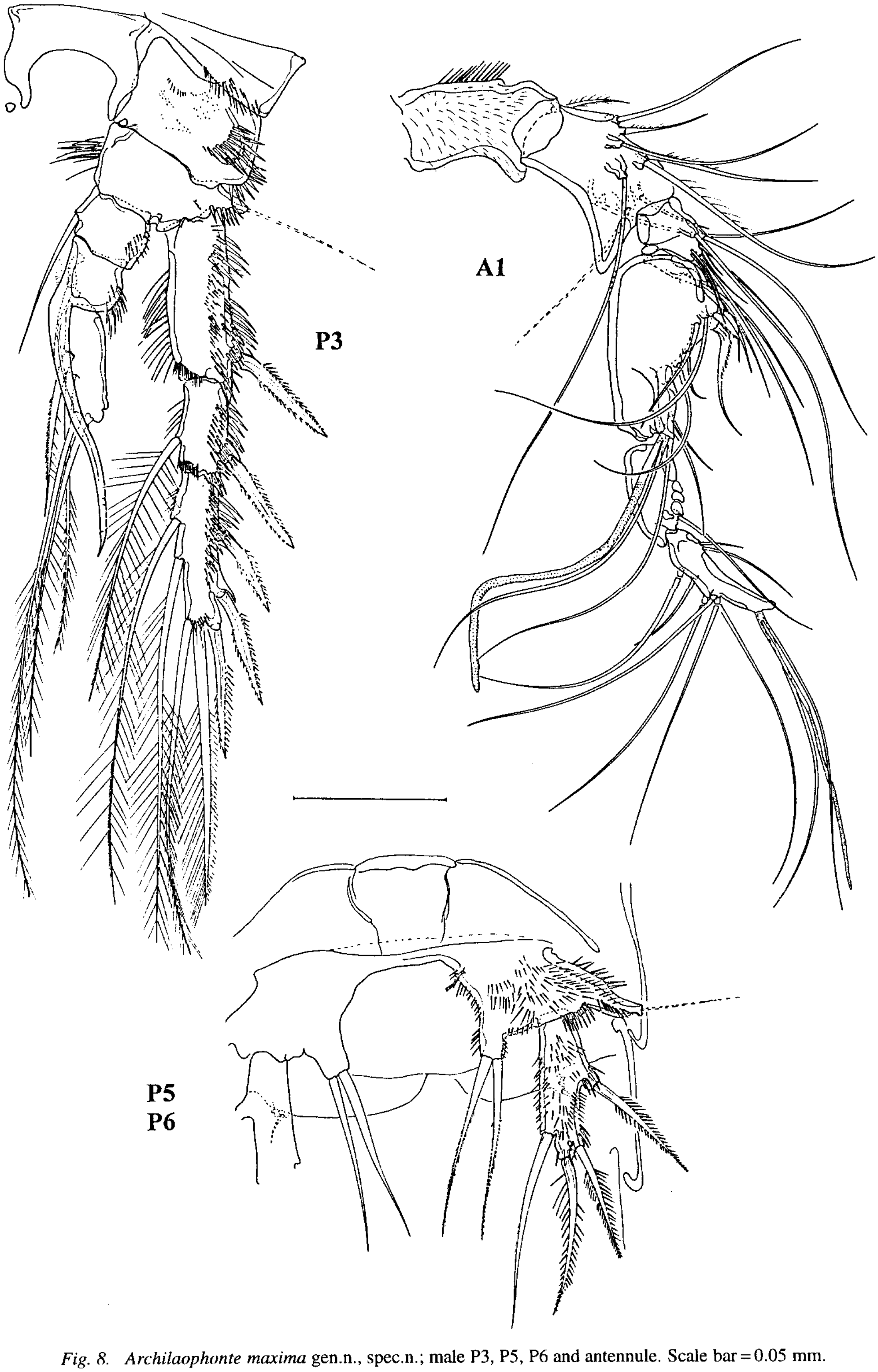

Fig. 8. Archilaophonte maxima gen.n., spec.n.; male P3, P5, P6 and antennule. Scale bar = 0.05 mm.

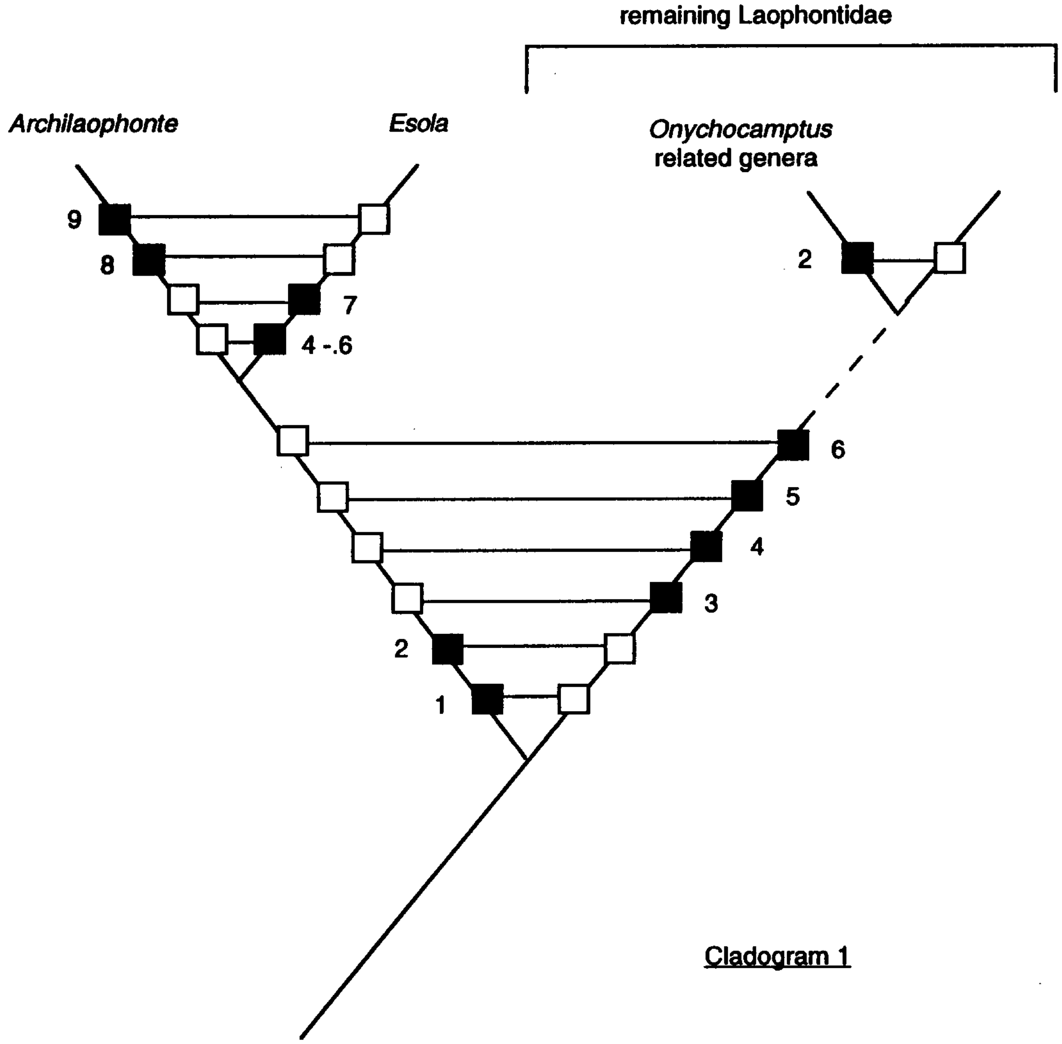

Fig. 9. Cladogram 1. The numbering of characters is the same as in the text.

The peculiar characteristics of the female P5 can therefore be considered as a synapomorphy for *Archilaophonte gen.n./Esola.*

2. Shape of P1 protopodite (Fig. 4)

In *Archilaophonte maxima* gen.n., sp.n. and *Esola* the basis of the P1 is slender and elongated, whereas the insertion-point of the exp has been shifted proxima towards the basal seta. In *Archilaophonte* gen.n. this character is more pronounced than in *Esola.*

In the other Laophontidae a similar structure of the P1 protopodite is found in the genera being related to *Onychocamptus* (Daday, 1903) such as *Klieonychocamptus* Noodt, 1958, *Klieonychocamptoides* Noodt, 1958 and *Folioquinpes* Fiers & Rutledge, 1990.

The genus *Onychocamptus* is characterized by short female antennulae (not more than 5 segments), only 3 setae on female P5 benp, 2 on male P5 exp and a 2-segmented P1 exp. *Onychocamptus* and the *Klieonychocamptus/Klieonychocamptoides*-line share a common ancestor but followed different evolutionary directions (Noodt, 1958). The *Klieonychocamptus*-line is highly specialized by — among other characters — reduced setation of the swimming-legs and a vermiform body-shape. *Folioquinpes* is also related to *Onychocamptus* for exhibiting a 4-segmented antennule and a similar setation of the P5 in both male and female (Fiers & Rutledge, 1990). Therefore the *Ony-*

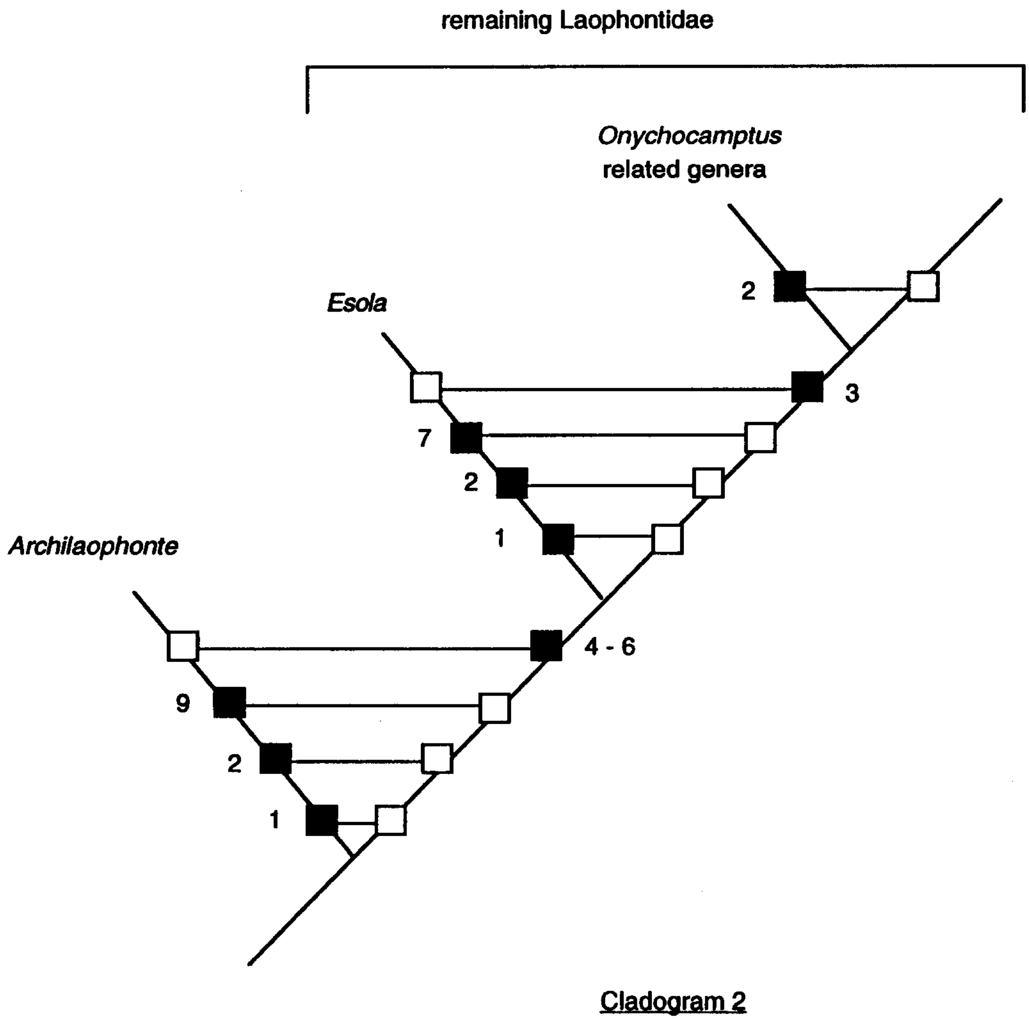

Fig. 10. Cladogram 2. The numbering of characters is the same as in the text.

chocamptus related genera are showing mainly derived characters, indicating an evolutionary stage already far from the basis of the Laophontidae. The very different form of the female P5 also makes a close relationship of this group with *Archilaophonte gen.n./Esola* rather unlikely.

Thus the special shape of the P1 is regarded here also as an synapomorphy for *Archilaophonte gen.n./Esola*, although having been developed independently at least twice within the Laophontidae.

3. P2 enp outer seta (Fig. 4)
Contrary to all other Laophontidae both *Archilaophonte* gen.n. and *Esola* retained the outer seta on P2 enp2. As a plesiomorphic character this does not indicate close affinity.

Characters separating Archilaophonte gen.n. from the rest of the Laophontidae incl. Esola

4. Md exp (Fig. 3)
The exp of the Md palp is well defined in *Archilaophonte* gen.n. while in the other Laophontidae and in most of the other Laophontoidea it is represented only by a seta. Therefore the identification of the Md palp setae as being endopodal, exopodal or basal in origin, can now unequivocally be done in the Laophontidae, confirming the descriptions of previous authors.

Within the Laophontoidea the loss of the Md exp must have occurred independently in the Laophontidae, since in *Laophontopsis borealis* (Huys & Willems, 1989), belonging to the sistergroup of the Laophontidae (Huys, 1990), the exp is developed as a small process without being demarcated from the basis.

5. Mxp syncoxa setation (Fig. 3)
Archilaophonte gen.n. bears 3 setae on the syncoxa of the Mxp while 2 setae is the highest number in the other Laophontidae. The presence of 3 setae represents the ancestral state within the Laophontoidea.

6. P1 enp (Fig. 4)
Archilaophonte gen.n. retains the inner seta on the enp1 of P1 while it is lost in the other Laophontidae. Some genera of the Orthopsyllidae and all Laophontopsidae also still possess this seta (Huys, 1990). However, the nature of the armature of the distal enp segment clearly shows that *Archilaophonte* gen.n. already belongs to the laophontid branch within the Laophontoidea.

Characters separating Esola and Archilaophonte gen.n.

7. Spinous outer process on antennule (Fig. 2)
Archilaophonte gen.n. has retained the spinous outer process on the second segment of the antennule while in all species of *Esola* it is completely lost.

8. Caudal rami (Figs 1, 6)
The caudal rami of *Archilaophonte* are app. 8 times longer than broad, in *Esola* at most 4 times. The extreme length of the caudal rami is interpreted here as a derived condition of the 'normal' form of caudal rami. In addition, *Archilaophonte* gen.n. is with a body length of nearly 1 mm much larger than the *Esola*-species (average body length = 0.5 mm). However, these characters are of no great value to clear up the relationships between *Archilaophonte* gen.n. and the remaining Laophontidae, since in the latter there are several species — not related to each other — reaching these dimensions in body length and caudal rami-ratio (e.g. *Platychelipus littoralis* Brady, 1880; *Pseudolaophonte spinosa* (I.C. Thompson, 1983); *Laophonte longistylata* Willey, 1935).

9. P6 of male (Fig. 8)
The ancestral form of the male P6 within the Laophontidae — also in *Esola* — includes a small lateral lobe with 1 strong inner and 1 long, slender outer seta. In *Archilaophonte* gen.n. one of these setae is lost — probably the outer one — and the remaining seta is small and vestigial.

Characters 4–6
Phylogenetic relationships

An analysis of the phylogenetic relationships between *Archilaophonte* gen.n., *Esola* and the other Laophontidae using the above discussed characters leads to 2 possible cladograms depicted in Figs. 9 and 10. The states of characters being apomorphic or plesiomorphic have been deduced from a comparison with the hypothetical ancestor of the superfamily Laophontoidea as reconstructed by Huys (1990). Moreover Huys & Boxshall (1991) are followed in the assumption that evolution within the Copepoda proceeded primarily by oligomerization and loss of setation.

Cladogram 1 (Fig. 9)

In cladogram 1 *Archilaophonte* and *Esola* together are interpreted as the relatively plesiomorphic sistergroup of the rest of the Laophontidae. The former taxon is defined by the synapomorphies 1 and 2 while the other Laophontidae exhibit the derived state of the characters 4–6. Thus the special shape of protopodite P1 (Character 2) has developed only twice independentely within the Laophontidae. According to this interpretation it must be assumed that the apomorphic states of characters 4–6 have evolved twice, in *Esola* as a branch of the group *Archilaophonte/Esola* and in the rest of the Laophontidae.

Cladogram 2 (Fig. 10)

Cladogram 2 shows the taxon *Archilaophonte* as the relatively plesiomorphic sistergroup of the remaining Laophontidae including *Esola*. In this case the characters 1 and 2 are only weak synapomorphies for *Archilaophonte* because they would have evolved a second time (character 1) and a third time (character 2) independently in *Esola* and the *Onychocamptus* related genera respectively. *Esola* shares characters 4–6 — which on this assumption evolved only once — with the remaining Laophontidae.

Both cladograms require the same number of steps for the evolution of the genus *Esola*, and both also include parallel evolution of characters. In cladogram 1 characters 4–6 and 2 evolved twice while in cladogram 2 characters 1 and 2 evolved twice (1) or even three times (2).

Nevertheless cladogram 1 is preferred here because the peculiar P5 (character 1) is such a unique and specialized feature that it appears less likely to have evolved separately in *Archilaophonte* gen.n. and *Esola* than parallel reducting characters 4–6.

Archilaophonte gen.n. up to now is the relatively most 'plesiomorphic genus' within the Laophontidae considering the setation of legs and mouth parts.

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References

Brady, G. S., 1990. Die marinen Copepoden der deutschen Südpolar-Expedition, 1901–1903. I. Über die Copepoden der Stämme Harpacticoida, Cyclopoida, Notodelphyoida und Caligoida. Deutsche Südpolar Expedition 1901– 1903 /Berlin 11: 497–593.

Fiers, F. & P. Rutledge, 1990. Harpacticoid copepods associated with *Spartina alterniflora* culms from the marshes of Cocodrie, Lousiana (Crustacea, Copepoda). Bull. Inst. Sci. nat. Belg., Biologie 60: 105–125.

Huys, R., 1990. A new family of harpacticoid copepods and an analysis of the phylogenetic relationships within the Laophontoidea T. Scott. Bijdr. Dierk. 60: 79–120.

Huys, R. & G. Boxshall, 1991. Copepod Evolution. Ray Society, London: 1–468.

Huys, R. & K. A. Willems, 1989. *Laophontopsis* Sars and the taxonomic concept of the Normanellinae (Copepoda: Harpacticoida): a revision. Bijdr. Dierk. 59: 203–208.

Lang, K., 1944. Monographie der Harpacticiden (Vorläufige Mitteilung). Uppsala: 1–39. (19-ii-1944).

Lang, K., 1948. Monographie der Harpacticiden I und II. Reprint Otto Koeltz Science Publ., Koenigstein, West Germany: 1682 Seiten.

Mielke, W., 1981. Interstitielle Fauna von Galapagos. XXVIII. Laophontinae (Laophontidae), Ancorabolidae (Harpacticoida). Mikrofauna Meeresboden 84: 1–106.

Monard, A., 1926. Description de quelque espèces nouvelles d'Harpacticides marins de la région de Banyuls. Revue suisse Zool. 33: 619– 628.

Noodt, W., 1958. Die Copepoda Harpacticoidea des Brandungsstrandes von Teneriffa (Kanarische Inseln). Abh. ma.-nat. Kl. Akad. Wiss. Mainz 2: 53–116.

Por, F., 1959. Harpacticoide noi (Crustacea, Copepoda) din milurile Marii Negre. Stud. Cercet. Biol. (Biol. anim.) 4: 347–368.

Sars, G. O., 1908. Copepoda Harpacticoida. Laophontidae (continued). An account of the Crustacea of Norway (Bergen Museum, Bergen) 5: 257–276.