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New tantulocarid *Polynyapodella ambrosei* gen. et sp. nov., (Basipodellidae) from the Northeast Water Polynya (Greenland) with emphasis on the phylogeny of its host genus *Cervinia* (Copepoda: Harpacticoida).

Rony HUYS*, Nadja MØBJERG ** and Reinhardt M. KRISTENSEN***
* *Crustacea Research Group, Zoology Department, The Natural History Museum,*
Cromwell Road, London SW7 5BD, U.K. Fax : 44 171 93 89 158 - e-mail : r.huys@nhm.ac.uk
** *August Krogh Institute, University of Copenhagen,*
Universitetsparken 13, DK-2100, Copenhagen Ø, Denmark
*** *Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100, Copenhagen Ø, Denmark*

Abstract: Several life cycle stages of a new genus and species of Tantulocarida are described from the Arctic Northeast Water Polynya (NEW) on the East Greenland shelf. *Polynyapodella ambrosei* gen. et sp. nov. was found to infest a new species of the deepwater harpacticoid genus *Cervinia* (Cerviniidae). The tantulocarid is placed in the family Basipodellidae on account of the male trunk sac formation and appears to be most closely related to *Nipponotantulus heteroxenus* recorded from southern Japan.

The harpacticoid host *Cervinia* sp. shows a close affinity with *Cervinia langi* and *C. philippinensis* sp. nov. (proposed for *C. langi sensu* Itô (1983)). Analysis of the phylogenetic relationships within the genus *Cervinia* revealed that it represents a paraphyletic taxon as it is currently diagnosed. The genus *Pseudocervinia*, previously regarded as a junior subjective synonym of *Cervinia*, is reinstated to accommodate the type-species *P. magna*. *Cervinia tenuiseta* shares a sistergroup relationship with the genus *Expansicervinia* and is assigned to a separate genus *Brotskayaia* gen. nov. The genus *Cervinia* is redefined to include the species of the *synarthra*-group, the type-species *C. bradyi* and *C. pilosa*. *Neocervinia* gen. nov. is proposed to accommodate *C. tenuicauda* and *C. unisetosa*. The taxonomic position of *C. tenuiseta sensu* Por (1969), *C. synarthra sensu* Por (1967) and *C. brevipes* is briefly discussed as well as the taxonomic implications caused by the extreme sexual dimorphism displayed by some species of *Cervinia*.

Résumé : *Un nouveau tantulocaride* Polynyapodella ambrosei *gen. et sp. nov. (Basipodellidae) du Northeast Water Polynya (Groenland) et une analyse de la phylogénie du genre hôte* Cervinia *(Copepoda : Harpacticoida).*
Plusieurs stades du cycle de vie d'un nouveau genre et nouvelle espèce de Tantulocaride sont décrits du Northeast Water Polynya (NEW) (Groenland). *Polynyapodella ambrosei* gen. et sp. nov. infeste une espèce nouvelle du genre *Cervinia* (Cerviniidae), un harpacticoïde des eaux profondes. Ce parasite est placé dans la famille des Basipodellidae en raison de la formation du sac troncal du mâle et il paraît être étroitement apparenté à *Nipponotantulus heteroxenus* signalé du Japon méridional.
L'hôte harpacticoïde *Cervinia* sp. montre une étroite affinité avec *Cervinia langi* et *C. philippinensis* sp. nov. (proposé pour *C. langi sensu* Itô (1983)). L'analyse des relations phylogénétiques dans le genre *Cervinia* a révélé que ce genre représente un taxon paraphylétique, comme cela est couramment admis. Le genre *Pseudocervinia*, précédemment envisagé comme un synonyme de *Cervinia*, est rétabli pour recevoir l'espèce type *P. magna. Cervinia tenuiseta* est le groupe frère du genre *Expansicervinia* et est placé dans un genre à part, *Brotskayaia* gen. nov. Le genre *Cervinia* est redéfini pour inclure les espèces du groupe *synarthra*, l'espèce type *C. bradyi* et *C. pilosa. Neocervinia* gen. nov. est proposé pour recevoir les espèces *C. tenuicauda* et *C. unisetosa.* La position taxonomique de *C. tenuiseta sensu* Por (1969), *C. synarthra sensu* Por (1967) et *C. brevipes* est brièvement discutée ainsi que les implications taxonomiques causées par l'extrême dimorphisme sexuel de certaines espèces de *Cervinia.*

Keywords : Northeast Water Polynya, Tantulocarida, *Polynyapodella* gen. nov., Harpacticoida, *Neocervinia* gen. nov., *Brotskayaia* gen. nov., phylogeny.

Introduction

Polynyas, defined as recurring ice-free areas amid pack or drift ice, are among the most conspicuous oceanographic

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features in polar regions. In the Arctic they are generally regarded as sites of enhanced biological activity and diversity (Struzik, 1989). The Northeast Water (NEW) Polynya on the East Greenland shelf is the largest (ca. 43,000 km^2) and most northern of the Arctic polynyas. It is a summer polynya varying in size and position between years but always located between 77° and 82° N latitude and 5° and 18° W longitude and, at its maximal extent, bounded by the northeast Greenland coast on the west and the shoreward edge of the south flowing East Greenland Current on the east. The NEW Polynya opens annually for the summer in April or May in the northwest corner and closes in September to a small coastal polynya (for overview see Hirche & Deming (1997)).

During an expedition to the NEW Polynya in the summer of 1992 (15 July - 19 August) 26 localities were sampled for meiobenthos between 76° 56' N and 80° 49' N and covering a depth range from 1216 m to 10 m near Henrik Krøyers Holme. Two spadecorers taken at the deepwater station 42 (450 m) contained an extremely diverse hard-bodied meiofauna including nematodes, harpacticoids, kinorhynchs (*Echinoderes* spp., *Pycnophyes* spp.) and tanaids. In addition, several soft-bodied taxa were found such as hydrozoans (*Protohydra* sp.), turbellarians, gnathostomulids, gastrotrichs, nemertines and small polychaetes (*Paranerilla* sp.) (Møbjerg *et al.*, 1995).

During sorting of the meiofauna on board the US Coast Guard vessel *Polar Sea* several life cycle stages of an as yet undescribed tantulocaridan were found attached to harpacticoid copepods (Møbjerg & Kristensen, 1993). The host has been identified as a new species of the deepwater genus *Cervinia* Norman and the tantulocaridan as a new representative of the family Basipodellidae. Descriptions of the various stages of the tantulocarid parasite and morphological notes on the host harpacticoid are provided below.

Material and methods

Meiofauna samples were collected from the US Coast Guard ice-breaker *Polar Sea* using a spadecorer. Brown mud samples from Station 42, located in the southwestern sector of the NEW Polynya at 450 m depth, were obtained on 30 July 1992. The mud samples were treated with Higgins' bubbling technique (Higgins & Kristensen, 1988) and the meiofauna was subsequently bulk-fixed in trialdehyde on board the vessel. The meiofauna of two spadecores SC30 (80° 01.217'N, 15° 57.228'W) and SC32 (80° 01.410'N, 15° 56.851'W) was sorted and examined in detail and resulted in the discovery of 6 copepods infested with various stages of tantulocarids. Both the copepods and the tantulocarids were observed alive using a Zeiss phase contrast miscroscope.

Copepod 1. Copepodid V infested by 2 parthenogenetic ♀♀ (on syncoxa of maxilla and lateral surface of first abdominal somite) and 4 tantulus larvae (on seta V of left caudal ramus, dorsal surface of last abdominal somite, right antennule and basis of antenna); from Stn 42 SC30. One ♀ (maxilla) and 2 larvae (abdominal somite, antennule) fell off when the copepod was embedded and prepared for TEM sectioning. The dislodged larvae were mounted in Epon as Dauer-preparations; one (antennule) is used for the present description and designated as a paratype (reg. no. NHM 1997.1744), the other one is deposited in the Zoological Museum of Copenhagen (ZMUC). Sectioning of the harpacticoid with the remaining 3 stages attached resulted in 64 toluidine blue-borax 1 μm sections and about 6000 ultrasections.

Copepod 2. Adult ♀ infested by 1 parthenogenetic ♀ (on lateral surface of penultimate somite) and 2 tantulus larvae (on P1 and exopodal setae of P4); from Stn 42 SC30. One larva (P4) is used for the present description and designated as a paratype (reg. no. NHM 1997.1745), the other stages have been ultrasectioned and the grids are retained in the personal collection of N.M. & R.M.K. and will be used for TEM.

Copepod 3. Copepodid II infested by a very young ♂ enclosed in the preceding tantulus (on dorsal surface of P1-bearing somite); from Stn 42 SC32; post-fixed in osmiumtetroxide and prepared for SEM. It was dehydrated through graded ethanol, critical point dried with CO_2, mounted on a stub, sputter coated with gold, and examined on a JEOL JSM-840 scanning electron microscope; deposited in ZMUC.

Copepod 4. Copepodid I infested by a young ♂ still enclosed in the preceding tantulus (on P1 exopod); from Stn 42 SC32; used for present description and designated as holotype (reg. no. NHM 1997.1743).

Copepod 5. Copepodid IV infested by a very young ♂ enclosed in the preceding tantulus (on dorsal posterior margin of cephalosome); from Stn 42 SC32; used for present description and designated as paratype (reg. no. 1997.1746).

Copepod 6. Adult ♀ infested by early parthenogenetic ♀ (on lateral surface of genital somite); from Stn 42 SC32; used for present description and designated as paratype (reg. no. NHM 1997.1747).

The holotype ♂ and 3 paratypes (1 larva, 1♀ and 1♂) were cleared in lactic acid and subsequently placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, England) and deposited in the collections of the Zoology Department, The Natural History Museum (NHM), London. All drawings have been prepared using a camera lucida on a Zeiss Axioskop microscope equipped with differential interference contrast.

The descriptive terminology applied to segmentation and setation of body appendages of the harpacticoid host is adopted from Huys & Boxshall (1991). Abbreviations used in the text and figures are: ae, aesthetasc; P1 - P6, first to sixth thoracopods; exp, exopod; enp, endopod; exp(enp)-1 (-2, -3), to denote the proximal (middle, distal) segment of a ramus. Pore signature terminology for the tantulocarid head shield follows Boxshall & Vader (1993).

Phylogenetic relationships between species of *Cervinia* were analysed using the phylogenetic computer package PAUP version 3.1 prepared by D. Swofford, Laboratory of Molecular Systematics, Smithsonian Institution (Swofford, 1993; Swofford & Begle, 1993). The options employed in the analysis were BRANCH AND BOUND, which guarantees to find all most parsimonious trees, and the DELTRAN optimisation, which delays character transformation within the tree.

Systematics

THE TANTULOCARID STAGES

Family BASIPODELLIDAE Boxshall & Lincoln, 1983
Polynyapodella gen. nov.

Diagnosis. - Basipodellidae. Cephalic shield with paired longitudinal lamellae dorsally and laterally, connected by transverse lamellae. Cephalic pore formula as follows: A_{I-IV}, D_{I-IV}, L_{I-V}, V_{I}, M. Cephalic stylet straight. Thoracic tergites 2-6 with well developed pattern of transverse and longitudinal surface lamellae. Thoracopods 1-5 with medial protopodal endite. Thoracopod 1 biramous; endopod without armature; exopod indistinctly 2-segmented, with 1 long terminal seta and 1 short setiform process. Thoracopods 2-5 with endopod bearing 2 setae; exopod 2-segmented, with 3 (thoracopod 2) or 4 well developed setae (thoracopods 2-5). Thoracopod 6 with 2 simple setae. Abdomen with 4 transverse lamellae; dorsal surface with several longitudinal lamellae in distal half and numerous minute surface striations. Caudal rami with long lateral seta; terminal setae spiniform, modified.

Hosts: Harpacticoida (Cerviniidae).

Type and only species. - *Polynyapodella ambrosei* gen. et sp. nov.

Etymology. - The generic name is derived from *polynya*, referring to the habitat of the new genus, and the suffix *podella*, which forms part of the family name Basipodellidae. Gender: feminine.

Polynyapodella ambrosei gen. et sp. nov.

Description

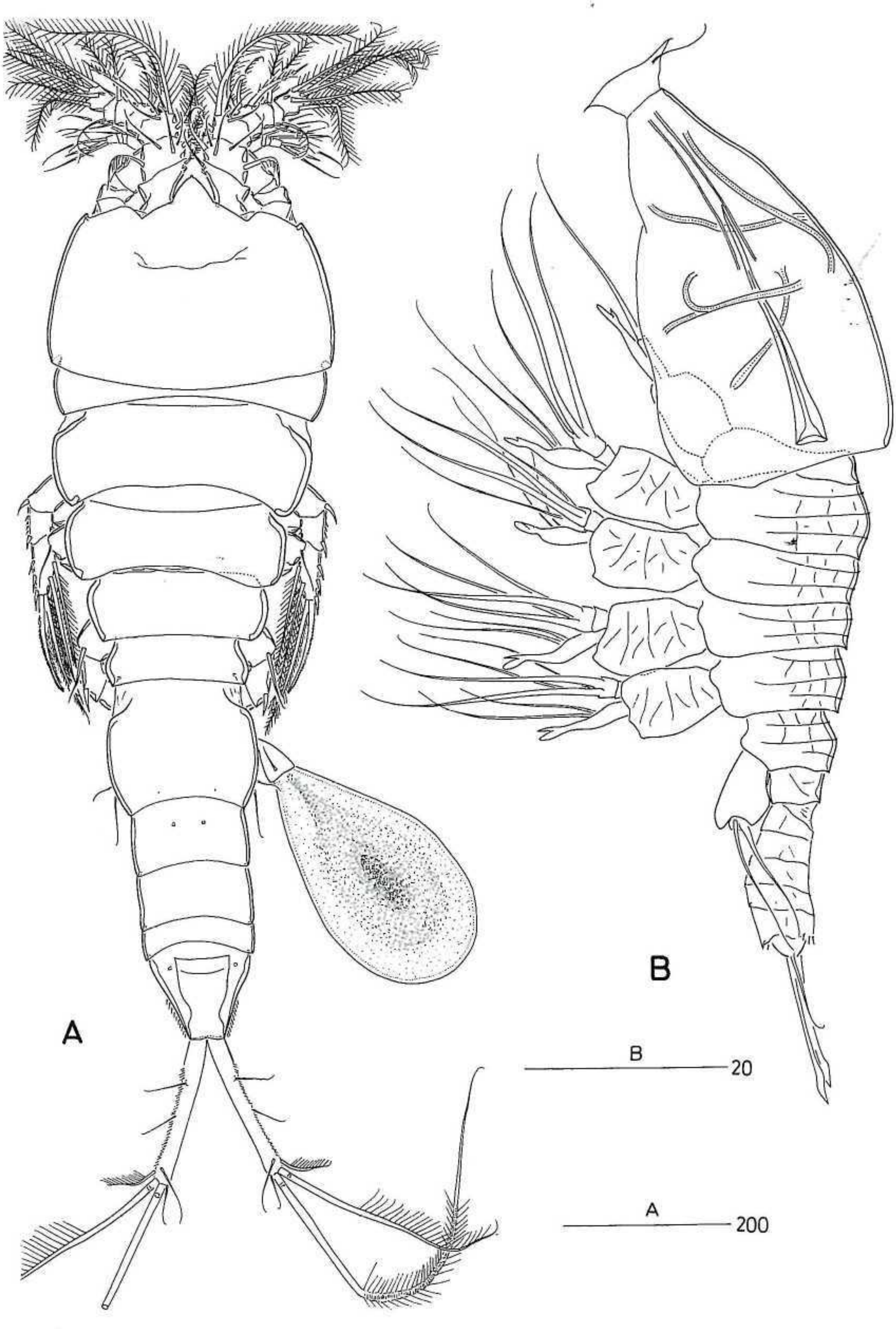
Tantulus larva

Body consisting of cephalon covered by dorsal shield, 6 pedigerous somites and 2-segmented limbless urosome; body length about 120 µm, measured from anterior tip of cephalon to posterior margin of caudal rami (Fig. 1B). Cephalon (Fig. 2A-C) distinctly tapering towards anteriorly located oral disc; dorsal and lateral surfaces ornamented with four pairs of longitudinal epicuticular lamellae extending from posterior end of cephalon to base of oral disc; middorsal longitudinal lamella extending from posterior margin to median M-pores; longitudinal lamellae connected by transverse ones forming anastomotic pattern; ventral surface lacking distinct ornamentation except for striated area at base of oral disc. Cephalic shield about 1.3 times as long as wide (51 µm x 37 µm); posterolateral margins slightly produced and inrolled ventrally. Oral disc about 22 µm in diameter, anteroventrally positioned; partly covered anteriorly by membranous extension of cephalon; paired long filaments present on either side of disc. Cephalon bearing 15 pairs of pores; anterior zone with 4 pairs (A_{I-IV}), posterodorsal zone with 4 pairs (D_{I-IV}), lateral zone with 5 pairs (L_{I-V}); ventral surface with single pair of pores (V_{I}) at about halfway the shield length. Sensilla emerging from pores A_{I}, D_{I} and L_{I}. Median pores (M) arranged asymmetrically, on either side of dorsal midline and posterior to A_{III}. Cephalic stylet 32 µm long, more or less straight; hollow at base. Little internal structure apparent in cephalon; ducts of glandular structures (arranged in pairs) discernible; remnant of internal tubular structure present between base of disc and tip of stylet (Fig. 1B).

Thoracic somites 1 to 6 (Fig. 1B) each provided with well developed tergite and pair of thoracopods. First tergite largely concealed beneath posterior rim of cephalon; lacking surface ornamentation. Tergites 2-6 with distinct surface ornamentation consisting of short longitudinal and transverse ridges (for dorsal view cf. Fig. 4B); posterolateral angles rounded.

Thoracopod 1 (Fig. 3A) with unsegmented protopod bearing medial endite with coupling spine. Endopod well developed, represented by digitiform segment, with proximal half swollen midway and distal half slightly bifid apically ending in spatulate process; outer margin without armature. Exopod indistinctly 2-segmented; segments separated by oblique suture; proximal segment small, drawn out into short setiform process at inner distal corner; distal segment with long terminal seta.

Thoracopods 2 to 5 (Fig. 3B-E) similar, with large unsegmented protopod, subrectangular in shape; medial endite lobate, armed with coupling spine and vestigial seta. Endopod 1-segmented, elongate and slender, with 2 outer setae midway; terminal process flattened, bearing moveable spatulate process. Exopod 2-segmented; proximal segment unarmed; distal segment with 2 long and 1 (thoracopod 2; Fig. 3B) or 2 (thoracopods 3-5; Fig. 3CE) fine setae terminally.


A
B
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20
A
200

Thoracopod 6 (Fig. 3F) uniramous, comprising single, subrectangular protopodal segment; lacking endite, but with 2 coupling spinules along medial inner margin; inner distal corner attenuated; with 2 long setae and short, blunt process; inner seta shorter than outer; none of setae spiniform or distinctly recurved.

Urosome (Fig. 2D-F) consisting of small seventh thoracic somite and large unsegmented abdomen; about 22 µm in length. Seventh thoracic somite tapering anteriorly, with pair of transverse lamellae laterally. Abdomen longer than wide, 18 µm long; with 4 distinct, transverse lamellae dorsally and ventrally, connected by short longitudinal and oblique lamellae laterally (Fig. 2D); ventral surface with short longitudinal lamellae near posterior margin; posterior margin smooth dorsally, with fine spinous processes ventrally. Caudal rami small, each with 1 relatively long lateral seta and 2 spiniform medial setae with sheathed geniculation distally (distal setiform part of setae might be missing).

Male

Male at early stage of development enclosed in reflexed position within expanded trunk sac of preceding tantulus larva (Fig. 4A-B); metamorphosed tantulus about 160 µm in length. Trunk sac expanded dorsally, with major swelling posterior to sixth tergite; additional swelling occurring between posterior rim of cephalon and first thoracic tergite (indicated by small arrowhead in Fig. 4A). Cephalon, rest of thorax including thoracopods, and urosome remaining unchanged from preceding tantulus larva. Metamorphosing male supplied with nutrients via large tissue connection (umbilical cord) containing larval stylet and connecting ventral side of cephalothorax with larval oral disc. Differentiation of tagmosis not discernible yet. Anlagen of 6 pairs of thoracopods, penis and caudal rami present but armature not developed. Aesthetascs not discernible.

Parthenogenetic female

Young stage (Fig. 1A) comprising head and small oval-shaped sac-like trunk; about 370 µm in length. Head covered with dorsal cephalic shield unchanged from attached tantulus larva. Neck area not developed; no eggs discernible.

Sexual female : Unknown

Etymology. - The species is named for Dr. William G. Ambrose Jr. (Bates College, Lewiston, Maine) in recognition of his work on the Northeast Water Polynya.

Discussion

Polynyapodella ambrosei gen. et sp. nov. is placed in the Basipodellidae on account of the male trunk sac formation pattern which involves major swelling posterior to tergite 6 and minor swelling between the cephalic shield and tergite 1 (Huys, 1990a). The Basipodellidae contains six species that exclusively utilize copepods as hosts and are currently accommodated in five genera: *Basipodella* Becker, *Stygotantulus* Boxshall & Huys, *Nipponotantulus* Huys, Ohtsuka & Boxshall, *Hypertantulus* Ohtsuka & Boxshall and *Rimitantulus* Huys & Conroy-Dalton (unpublished). Becker (1975) described *Basipodella harpacticola* from several stages collected in the Peru Trench which were found on three different harpacticoid hosts: *Metahuntemannia magniceps* Becker, *Talpina peruana* (Becker) and a third species of an unidentified family (Schriever in Grygier & Sieg (1988)). *Basipodella atlantica* Boxshall & Lincoln is only known from a parthenogenetic female found on an unidentified tisbid harpacticoid collected at 3000 m depth southwest of the Azores (Boxshall & Lincoln, 1983). *Stygotantulus stocki* Boxshall & Huys was discovered on two unidentified copepods belonging to the Canuellidae and Tisbidimorpha obtained from an anchihaline lava pool on Lanzarote (Boxshall & Huys, 1989). *Nipponotantulus heteroxenus* Huys, Ohtsuka & Boxshall, described from Okinawa (South Japan) was recorded from a wide range of copepods, including calanoids (Pseudocyclopiidae), cyclopoids (Cyclopinidae) and at least five families of harpacticoids (Diosaccidae, Tetragonicipitidae, Paramesochridae, Cylindropsyllidae, Leptopontiidae) (Huys & Ohtsuka, 1993; Huys *et al.*, 1994). *Hypertantulus siphonicola* Ohtsuka & Boxshall was recently described from at least two genera of Asterocheridae (Siphonostomatoida) collected from shallow waters in Western Japan (Ohtsuka & Boxshall, in press). Finally, Huys & Conroy-Dalton recorded the first basipodellid from the hydrothermal vent habitat : *Rimitantulus hirsutus* n. g., n. sp. Huys & Conroy-Dalton (unpublished) was found to infest a new argestid harpacticoid collected from a hydrothermal vent on the Galapagos Rift. The salient morphological features of the six basipodellid genera are summarized in Table 1.

Polynyapodella can be readily distinguished by the presence of only one seta on the exopod of the first thoracopod since all other basipodellid genera possess two well developed setae on this ramus. Within the

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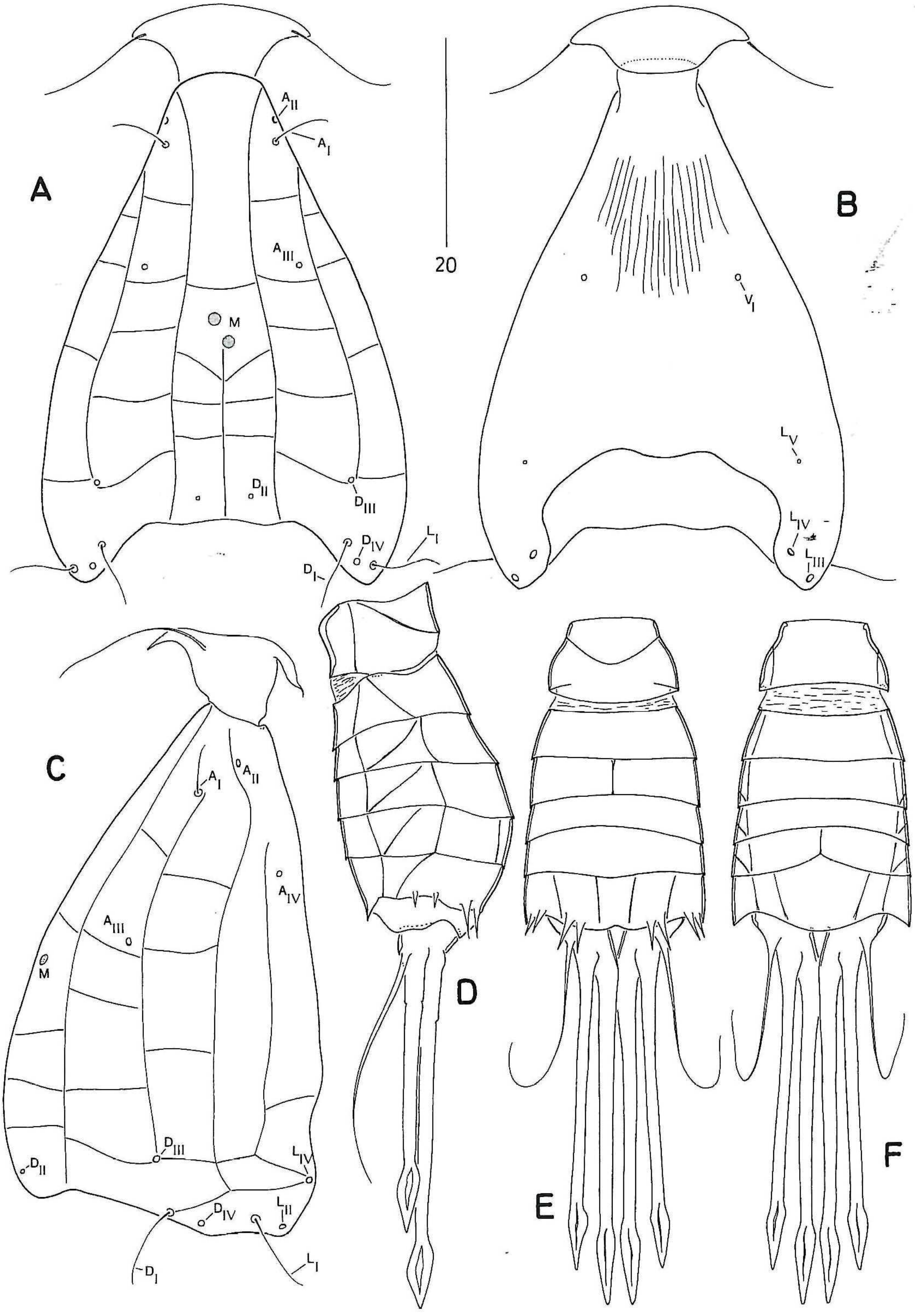
Figure 1. *Cervinia* sp. A, habitus (♀), dorsal with parthenogenetic ♀ tantulocarid attached, *Polynyapodella ambrosei* gen. et sp. nov. (paratype). B, *P. ambrosei*, tantulus larva, lateral. Scales in µm.

Figure 1. *Cervinia* sp. A, habitus (♀), vue dorsale, avec ♀ parthénogénétique de tantulocaride attachée, *Polynyapodella ambrosei* gen. et sp. nov. (paratype) B, *P. ambrosei,* larve tantulus, vue latérale. Échelles en µm.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Tantulocarida only the two genera of the Microdajidae have one exopodal seta on the first thoracopod. The new genus is undoubtedly most closely related to *Nipponotantulus* with which it shares the spiniform modified setae on the caudal rami and the reduced number (3) of exopodal setae on the second thoracopod. In the other basipodellid genera the medial caudal ramus setae are long, slender, clearly setiform and not bifid or distally dilated in lateral aspect. These genera also have 4 setae on the exopod of the second thoracopod. In their redescription of *B. harpacticola* Boxshall & Lincoln (1983) claimed that the second to fifth pairs of thoracopods were similar, each carrying 3 setae on the exopod. Re-examination of Becker's types from the Zoologisches Museum in Kiel revealed that the setation of these thoracopods is indeed identical but that one of the tiny exopodal setae had been overlooked in previous descriptions (Becker, 1975; Boxshall & Lincoln, 1983), the total number of elements on the exopod being four. In addition to the first thoracopod, *Polynyapodella* differs also from *Nipponotantulus* in the presence of four setae on the exopod of the third thoracopod and the form of the inner seta on the sixth thoracopod which is slender and simple, and not recurved and moderately chitinized as in the Japanese genus. The new genus also differs from *Nipponotantulus* by the presence of a well developed medial endite on the first thoracopod and by the longer lateral seta on the caudal ramus. The pattern of integumental lamellae on both the cephalic shield and abdomen is distinctly more complex in *Polynyapodella*, however the generic significance of this character has yet to be revealed.

P. ambrosei displays the ancestral pore pattern on the larval cephalic shield, including the middorsal M-pores and the anteroventral VI-pores. The M-pores, consisting of a pair of asymmetrical pores on either side of the dorsal midline, are of particular interest since they are known only in the Japanese deoterthrid *Itoitantulus misophricola* described by Huys, Ohtsuka & Boxshall (in Huys *et al.*, 1992a). On the basis of the presence of these pores Huys *et al.* (1993) provisionally identified a tantulus larva, containing a sexual female within its expanded trunk sac, as *I. misophricola*. The discovery of the M-pores in the present species (belonging to a different family) suggests that they occur in a wider range of taxa and indicates that the sexual female described by Huys *et al.* (1993) might well belong to another species or possibly even another family, a suspicion supported by the wide depth and geographical distributions of the known records of *I. misophricola* (Huys *et al.*, 1992a, 1993; Ohstuka, 1993). The ventral VI-pores have thus far been reported only in *Amphitantulus harpiniacheres* Boxshall & Vader, a species infesting the common North Sea phoxocephalid amphipod *Harpinia antennaria* Meinert (Boxshall & Vader, 1993).

The presence of six tantulocarids on the same host specimen (Copepod 1) is remarkable but not unique. Huys (1990b) reported 14 individuals of *Coralliotantulus coomansi* Huys on a single specimen of the harpacticoid *Longipedia scotti* Sars. It is likely that these heavy infections are due to chance encounter of the host with swarms of newly released infective larvae which were released en masse near or on the sediment surface (Boxshall & Vader, 1993). The fact that both tantulus larvae and young parthenogenetic females were found on the same host specimen would imply that the latter possibly develop much faster than those larvae which will metamorphose into sexual stages.

Tantulocarids are common in northwest European waters (Boxshall & Lincoln, 1987; Boxshall & Vader, 1993; Boxshall *et al.*, 1989; Greve, 1965, 1988; Grygier & Sieg, 1988; Huys & Boxshall, 1988; Huys *et al.*, 1992b) but this might merely reflect sampling bias (Huys, 1991). Although the presence of tantulocarids at extreme high latitudes had already been demonstrated by Grygier & Sieg (1988), who described *Microdajus aporosus* from a tanaid in the Antarctic Ross Sea at 76°25' S, only one tantulocarid had been reported previously from within the Arctic Circle. Hansen (1913) illustrated a tantulus larva (possibly *Microdajus* sp.) attached to a female *Leptognathia breviremis* (Lilljeborg) (Tanaidacea) which he had collected south of Jan Mayen (69°13'N) during the Danish Ingolf Expedition. The discovery of *P. ambrosei* off northeast Greenland considerably extends the distribution range of the group in the Northern Hemisphere.

IDENTITY OF HARPACTICOID HOST

All infested harpacticoids belong to an as yet undescribed species of the genus *Cervinia* Norman (in Brady (1878)) (Cerviniidae). The only adult (Copepod 6) that we had at our disposal was a partly damaged ♀ which had lost both P3 endopods and was deficient in several other aspects. A brief text description is presented below for future reference.

Cervinia sp.

Body length measured from anterior margin of rostrum to posterior margin of caudal rami 1225 µm (Fig. 1A).

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Figure 2. *Polynyapodella ambrosei*, tantulus larva (holotype). A, cephalon, dorsal; B, same, ventral; C, lateral; D, urosome, lateral; E, urosome, ventral; F, urosome, dorsal.

Figure 2. *Polynyapodella ambrosei*, larve tantulus (holotype). A, céphalon, vue dorsale ; B, vue ventrale ; C, vue latérale ; D, urosome, vue latérale ; E, urosome, vue ventrale ; F, urosome, vue dorsale.

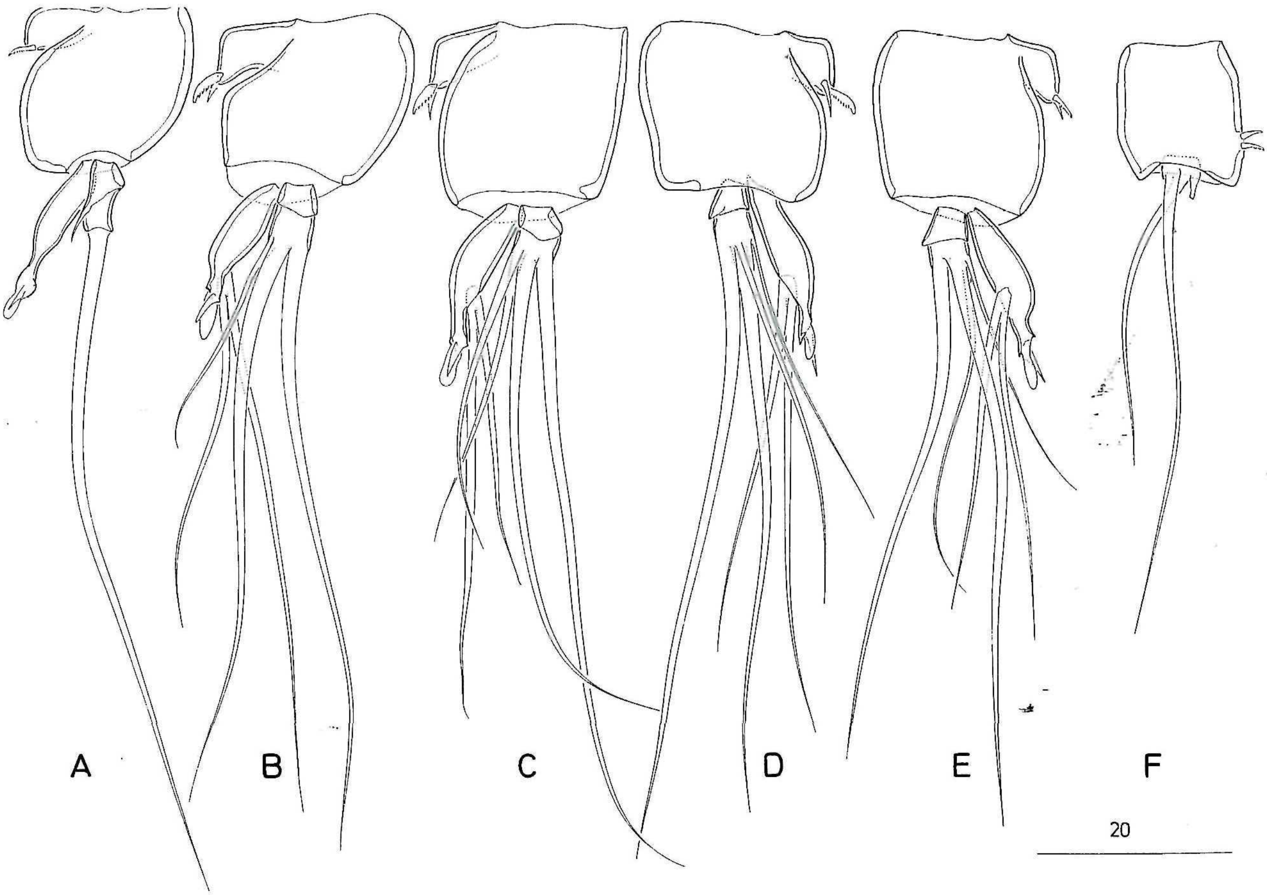

Figure 3. *Polynyapodella ambrosei*, tantulus larva (holotype). A, thoracopod 1; B, thoracopod 2; C, thoracopod 3; D, thoracopod 4; E, thoracopod 5; F, thoracopod 6.

Figure 3. *Polynyapodella ambrosei*, larve tantulus (holotype). A, thoracopode 1 ; B, thoracopode 2 ; C, thoracopode 3 ; D, thoracopode 4 ; E, thoracopode 5 ; F, thoracopode 6.

Antennule 7-segmented; segment 3 with 2 large aesthetascs, distal one fused basally to long seta; segment 7 with tiny aesthetasc sharing common base with strong seta. Armature formula: 1-[1], 2-[6], 3-[11 + (1 + ae) + ae], 4-[3], 5-[2], 6-[2], 7-[6 + (1 + ae)].

Antenna similar to that of *C. langi* Montagna as redescribed by Itô (1983) except for proximal seta of exp-1 being distinctly shorter than its distal seta; armature formula of exopod [2,1,1,3].

Mandible with well developed biramous palp comprising basis, 1-segmented endopod and indistinctly 3-segmented exopod; basis with 3 setae of about equal length and possibly 1 short seta; endopod with 3 spines laterally 5 spines plus 1 seta apically; exopod (Fig. 5A) with 1 short bipinnate spine and 1 very long plumose seta on segment 1, 1 very long plumose seta on segment 2, and 1 well developed plumose seta and 1 minute pinnate seta on vestigial segment 3.

Maxillule. Praecoxal arthrite strong rectangular lobe with 10 spines around distal margin, 2 spines on posterior surface and 2 parallel setae on anterior surface. Coxa with 6 elements on endite; epipodite represented by 1 pinnate

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Figure 4. *Polynyapodella ambrosei* (holotype). A, young ♂ enclosed in trunk sac of preceding tantulus larva, lateral; (arrow heads, see text). B, same, dorsal.

Figure 4. *Polynyapodella ambrosei* (holotype). A, ♂ juvénile à l'intérieur du sac du tronc de la larve tantulus précédente, vue latérale ; (têtes de flèches, voir texte). B, vue dorsale.

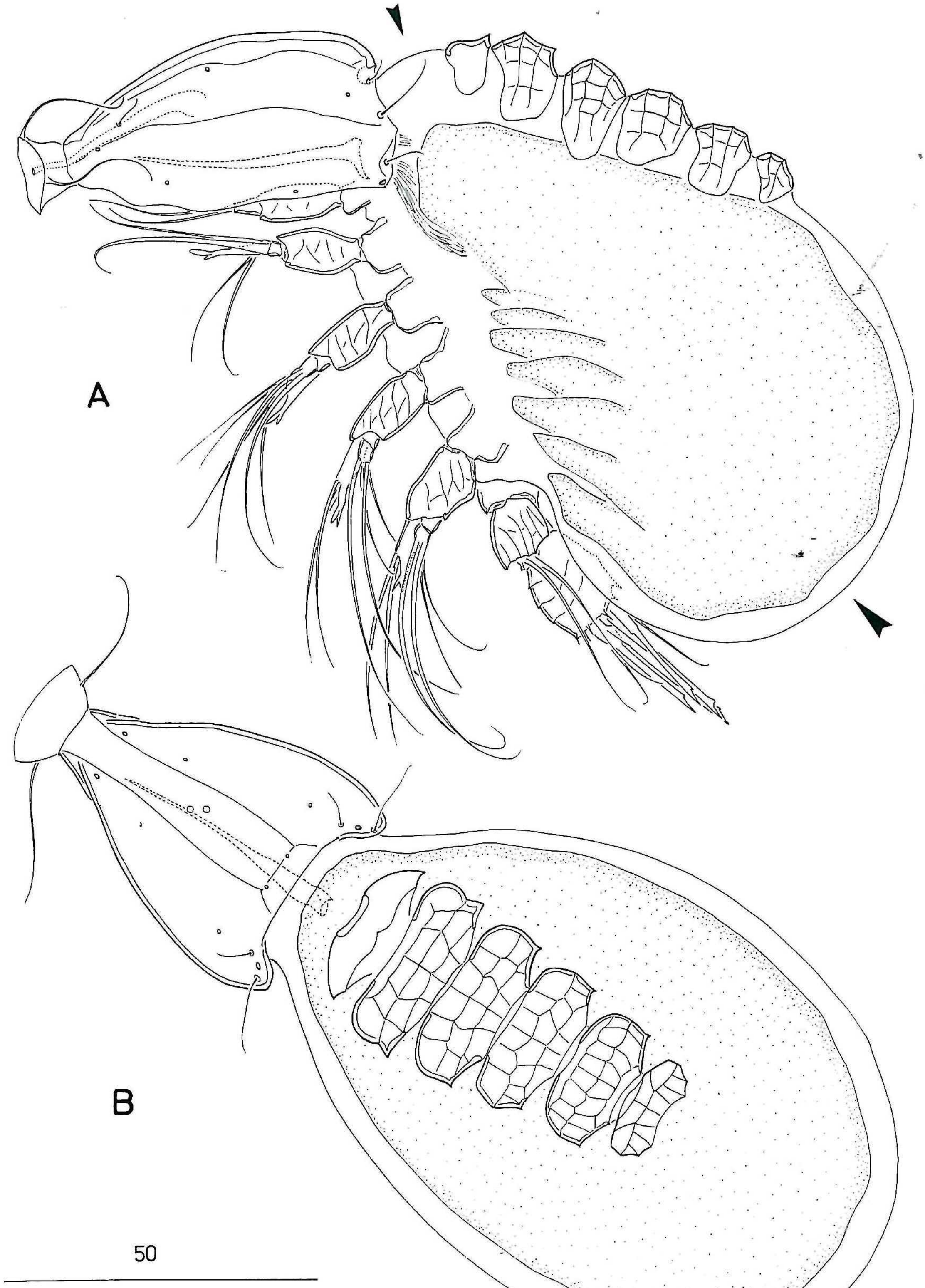
A
B
50

Table 1. Major larval characters of various basipodellid genera.
Tableau 1. Principaux caractères larvaires de différents genres de basipodellidés.

	Number of setae									
	Thoracopod 1		Thoracopod 2		Thoracopod 3		Thoracopods 4-5		Caudal rami	Thoracopod 1
	Exp	Enp	Exp	Enp	Exp	Enp	Exp	Enp	modified setae	exopod
Basipodella	2	0	4	2	4	2	4	2	-	1-segmented
Stygotantulus	2	0	4	2	4	2	4	2	-	1-segmented
Nipponotantulus	2	0	3	2	3	2	4	2	+	2-segmented
Hypertantulus	2	1	4	2	4	2	4	2	-	2-segmented
Rimitantulus	2	0	4	2	5	2	5	2	-	2-segmented
Polynyapodella	1	0	3	2	4	2	4	2	+	2-segmented

seta. Basis and endopod completely fused forming unilobate allobasis bearing total of 13 elements. Exopod a small defined segment with 1 minute and 2 long setae.

Maxilla. Syncoxa with 4 endites (Fig. 5B); distal praecoxal and proximal coxal endite largely incorporated into syncoxa; enditic armature formula [4,2,3,3]. Allobasis drawn out into long curved claw; accessory armature consisting of 2 setae and 1 spine distally and 1 spine plus 1 seta proximally. Endopod 3-segmented; enp-1 with 1 geniculate and 1 long simple seta; enp-2 with 2 geniculate setae; enp-3 with 1 short, 2 long and 1 geniculate setae.

Maxilliped. Syncoxa with 3 endites; proximal endite with 1 large spinulose spine and 1 short pinnate spine; middle endite with 1 large spinulose spine, 1 short spine and 1 seta; distal endite with 2 large spinulose spines. Basis with 1 large spinulose spine and 1 short seta. Endopod 2-segmented; enp-1 with 1 short and 1 long seta along inner margin; enp-2 with 2 bipinnate spines distally, and 1 spine plus 1 seta along outer margin.

Swimming legs with 3-segmented exopods and 3- (P1) or 2-segmented (P2 and P4, ?P3) endopods. P1 inner basal spine plumose, not reaching beyond distal margin of enp-1. Inner element of P1 enp-1 spiniform, pinnate (Fig. 5C). P2 enp-1 (Fig. 5D) with very large spinous process at inner distal corner; inner spine large, curved, pinnate along inner and pectinate along outer margin. P2 enp-2 inner distal corner drawn out into very long spinous process; proximal two inner setae reduced; except for third inner proximal element all other elements spiniform. P2 intercoxal sclerite with paired groups of 4 coarse, long spinules on posterior surface and 2 raised groups of long spinules on anterior surface. P4 endopod (Fig. 5E) with 3 reduced setae long inner margin.

Outer spines of P2-P4 exopodal segments short and stubby. Armature formulae as follows:

	Exopod	Endopod
P1	1.1.123	1.1.221
P2	1.1.223	1.421
P3	1.1.223	?
P4	1.1.223	1.421

P5 (Fig. 5F) 1-segmented; ornamentation consisting of long outer plumose seta, short middle plumose seta and naked inner seta. P6 with 2 long setae apically and short spiniform element along inner margin.

Relationships

The 2-segmented endopods of legs 2-4 clearly relate *Cervinia* sp. to the *synarthra*-group of species which includes *C. synarthra* Sars, *C. pilosa* Lang and *C. langi* Montagna. The first two species can be readily distinguished from the Greenlandic one by the reduced setal formula on the distal endopod segments of legs 2-4. In both species there are only 3 inner elements on the compound distal endopod segment of legs 2 and 4 and comparison with *C. langi* suggests that it is one of the 2 setae derived from the ancestral middle segment which is lost. There is an undeniable, close relationship between *C. langi* and the present species based on the reduced inner setae of the P2 endopod which is unique in the Cerviniidae but common to both. Montagna (1979) described *C. langi* from the Beaufort Sea, however, pointed out that Lang (1936) had already

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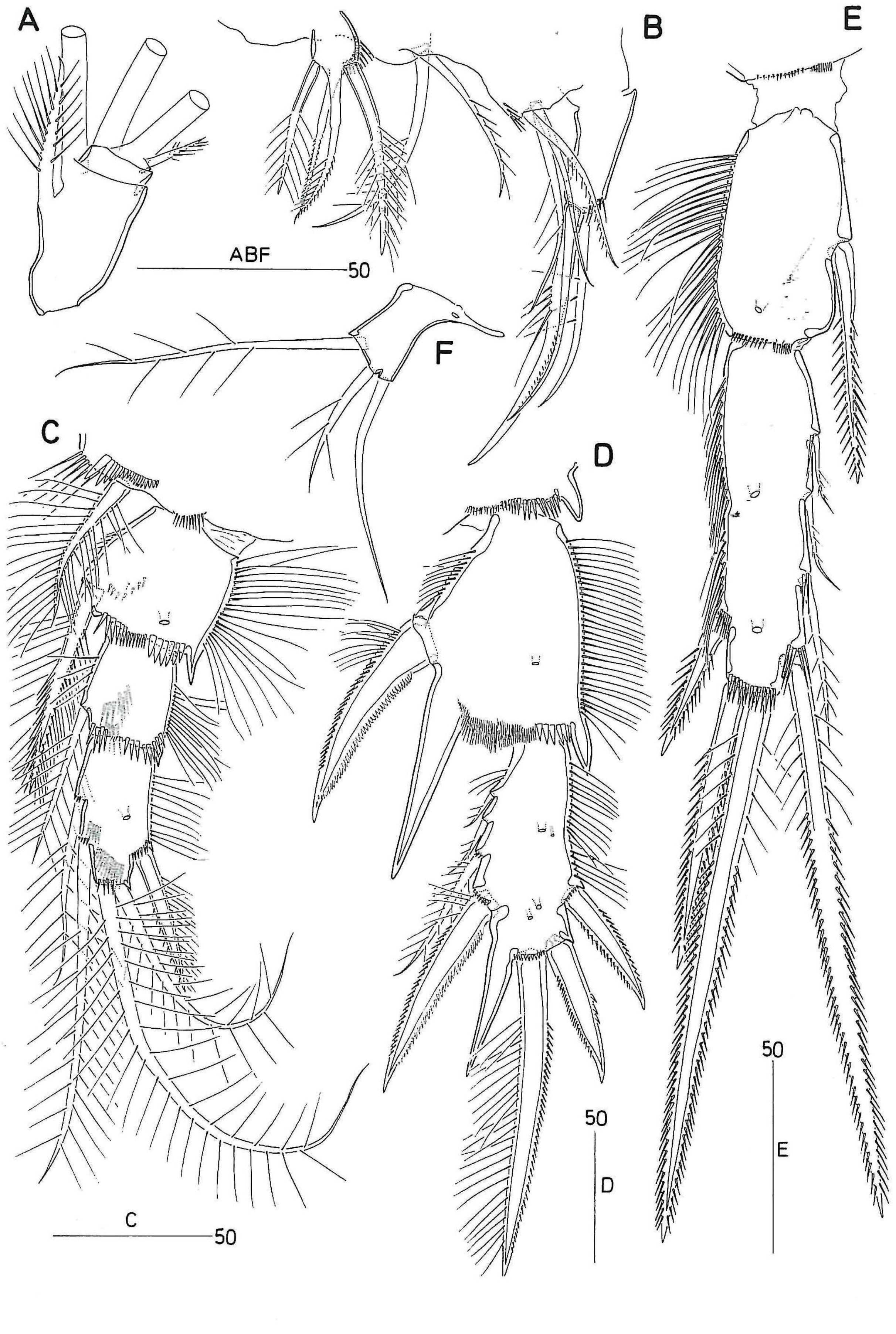
Figure 5. *Cervinia* sp. (♀). A, mandibular exopod; B, endites of maxillary syncoxa; C, P1 endopod, anterior; D, P2 endopod, anterior; E, P4 endopod, anterior; F, P5, anterior.

Figure 5. *Cervinia* sp. (♀). A, exopodite mandibulaire ; B, endites du syncoxa maxillaire ; C, endopodite de P1, vue antérieure ; D, endopodite de P2, vue antérieure ; E, endopodite de P4, vue antérieure ; F, P5, vue antérieure.


A
B
E
ABF
50
F
C
D
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D
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E
C
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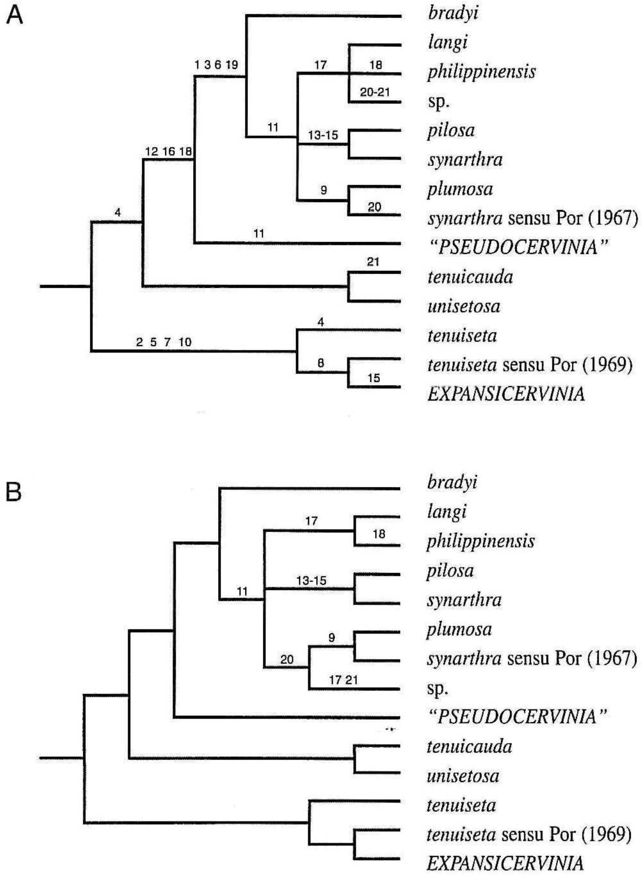

Figure 6. Phylogenetic trees depicting relationships between *Expansicervinia*, *Pseudocervinia* and various *Cervinia* species.

Figure 6. Arbres phylogénétiques montrant les relations entre *Expansicervinia*, *Pseudocervinia*, et différentes espèces de *Cervinia*.

figured this species as an Arctic variant of *C. synarthra*. Lang's illustrations leave little doubt that his specimens, which came from two different localities east of Spitsbergen, belong to two species. *C. langi* can be readily identified (his Figs 5, 6a and 7a) by the reduced setae on the P3-P4 endopods, however, the second species which does not share this character cannot possibly be *C. synarthra* either because of the different setal formula (see his Figs 6b and 7b). Itô (1983) provided an outstanding redescription of *C. langi*, including illustrations of the copepodid IV, yet expressed some doubts about his identification because of certain discrepancies with the original description. Among the many differences found in Itô's (1983) female specimen from off the Philippines should be noted: (1) the absence of a spinous process on the inner distal corner of P2 enp-2, (2) P2 intercoxal sclerite with paired horny structures, (3) P4 endopod much longer and proximal setae of enp-2 less reduced, (4) P5 exopod smaller and middle seta longest, (5) maxilliped with only 1 seta on enp-1. This suite of characters is regarded as sufficient evidence to warrant separate specific status for the Pacific material and we name it *Cervinia philippinensis* sp. n. accordingly, in recognition of the late Dr Itô's outstanding contributions to harpacticoid taxonomy.

The present material differs from both *C. langi* and *C. philippinensis* in (1) the enditic setal formula of the maxillary syncoxa with 4 and 2 setae on the proximal and distal praecoxal endites, respectively; (2) the very large spinous process on P2 enp-2, and (3) the 1-segmented P5 with a total of 3 setae.

Phylogenetic analysis

Of the eleven genera currently regarded as valid in the Cerviniidae (Huys *et al.*, 1996) the type-genus *Cervinia* Norman (in Brady (1878)) is morphologically probably the most diverse in terms of e.g. antennule segmentation, swimming leg setation and segmentation, and P5 structure. Due to the apparent scarcity of males the genus has been the subject of some confusion. Both Por (1967) and Montagna (1979) considered the possibility that some of the species with reduced swimming legs might in fact represent "paedomorphic" variants of *Cervinia bradyi* Norman (in Brady (1878)) which has retained the primitive leg segmentation and armature. Huys *et al.* (1996) remarked that all known males of *Cervinia* exhibit 3-segmented endopods on P1-P4 and that this uniformity could therefore pose problems in the identification of males, even if their matching females clearly differ in swimming leg segmentation. On the basis of this latter character Brotskaya (1963) recognized two groups in the genus, the *bradyi*-group with 3-segmented endopods on P2-P4 and the *synarthra*-group with 2-segmented endopods. Although this subdivision has gained wide acceptance (e.g. Montagna, 1979, 1981; Itô, 1983) the phylogenetic significance and the monophyletic status of these lineages have never been questioned.

In order to assess the relationships of the tantulocaridan host and the monophyly of the genus *Cervinia* a phylogenetic analysis was carried out at the species level. The monotypic genus *Expansicervinia* Montagna, which closely resembles *Cervinia* in various characters (Montagna, 1981), and *Pseudocervinia magna* (Smirnov), which was transferred to *Cervinia* by Montagna (1981), were also included in the analysis.

a. Sexual dimorphism in Cerviniidae

Very few males of *Cervinia* have been recorded thus far (Giesbrecht, 1900; Sars, 1910; Lang, 1948; Por, 1964, 1967; Drzycimski, 1969; Itô, 1983, Huys *et al.*, 1996). Except for one specimen (Itô, 1983) all of them belong to or have been identified as the type-species *C. bradyi* which is the only species in the genus that is known from both sexes. The single male described by Itô (1983) under the name *C. plumosa* differs from the other species of *Cervinia* in a number of interesting characters. The first leg has only 2 outer spines on the distal exopod segment resulting in a 122 setal formula (123 in all other species). This is almost certainly the result of a neotenic event since the setal pattern accords with that of the copepodid IV of other *Cervinia* species (cf. Itô, 1983). The inner basal spine of leg 1 is extremely elongate, extending to the distal margin of enp-2 (short, extending to distal margin of enp-1 in other species). This condition is reminiscent of that found in some species of *Cerviniopsis* Sars and *Pontostratiotes* Brady. A most remarkable feature of *Cervinia plumosa* Itô is the presence of rod-shaped modified spines on all exopod segments and the distal endopod segment of legs 2-4. Itô (1983) remarked that similarly shaped spines are also present on the P2 endopod of *C. tenuicauda* Brotskaya, however Brotskaya's (1963) illustrations can be interpreted differently, when compared with Montagna's (1981) excellent description of the closely related *C. unisetosa*. The mouthparts of *C. plumosa* are generally weakly chitinized and the endites involved in feeding, such as the mandibular gnathobase and the maxillulary arthrite, are reduced. Similar reductions are discernible in the syncoxal endites of the maxilla and the endopod of the maxilliped. There is a clear tendency for males of deep-sea harpacticoids to become non-feeding (Huys, unpublished data) and the reductions observed in the male of *C. plumosa* can be collectively regarded as a first step in the evolution towards fully atrophied mouthparts. It is interesting to note that the antennary and mandibular exopods have retained their full complement of setae. These armature elements are distinctly plumose (cf. name), suggesting that the limbs might still be involved in performing swimming movements, or other functions not related to food manipulation.

From the published literature it would appear that most of these characters are unique in the genus *Cervinia*, suggesting that *C. plumosa* belongs to an independent lineage and therefore be better placed in a genus by itself. Although Itô (1983) recognized a certain affinity between this species and both *C. tenuiseta* Brotskaya and *C. tenuicauda*, their similarity is almost solely based on the extremely elongate caudal rami, a character of high evolutionary plasticity. He also pointed out the striking similarity in the rostrum between *C. plumosa* and the male of *C. bradyi* where it is known to be sexually dimorphic (Giesbrecht, 1900; Sars, 1910).

A second scenario, based on the assumption that the uniqueness of these characters is merely the result of extreme sexual dimorphism, that as yet has remained unrecognized in the genus, is less likely. The evidence in favour of this hypothesis is, however, threefold. First, re-examination of males of *C. bradyi* revealed the presence of rod-shaped spines on the swimming legs on exactly the same segments as in *C. plumosa*, showed the inner basal spine on leg 1 to be of the same relative length and shape as in the latter, and resulted in the discovery of sexual dimorphism in the mandible, maxillule, maxilla and maxilliped. The inner spine of the proximal endopod segment in legs 2-3, which is short and strongly curved in the female of *C. bradyi*, appeared to be long, plumose and distally pinnate in the male as in *C. plumosa*. It should be noted here that Giesbrecht (1900) had already described the atrophied mouthparts of *C. bradyi* in remarkable detail, but that his paper escaped the attention of later workers. The second piece of evidence results from the examination of a deep-sea sample, collected off La Réunion during the French MD32 expedition in 1982 (Stn DS139; 20°46'5 S, 55°38'3E; 1600 m depth), containing males and females in equal proportions. All males in the sample looked very similar to *C. plumosa*, showing identical modifications on the swimming legs, mouthparts and rostrum. The females on the other hand possessed 2-segmented endopods on legs 2-4, and seemed to belong to a species closely related to *C. langi*. Since no other females or males were present in the sample it is conceivable that the specimens represented both sexes of a single species. Finally, the presence of only 2 outer elements on P1 exp-3, which remained as the only unique character of *C. plumosa* was found to be present in a female (NHM reg. no. 1970.5.15.4) from the Gulf of Aqaba, previously identified as *Cervinia synarthra* by Por (1967) [see below]. On the basis of this evidence, it is postulated that the unknown males of the *synarthra*-group probably resemble *C. plumosa* very closely and all display strong sexual dimorphism in the swimming legs (endopod segmentation, rod-shaped spines, inner basal spine of P1), the rostrum and the mouthparts. The rostrum and leg 1 are not sexually dimorphic in *Cervinia magna* Smirnov (Smirnov, 1946; Montagna, 1979, 1981), corroborating Brotskaya's (1963) removal of this species to its own genus *Pseudocervinia*.

b. Doubtful identifications

Itô (1981) pointed out the discrepancies between Brotskaya's (1963) original description of *Cervinia tenuiseta* from the Japan Trench and Por's (1969) subsequent redescription from the Indian Ocean near Madagascar. Significant differences can be found in the setation formula of P1 enp-3, the length of the P2 endopod, the position of the endopodal outer spine in legs 2-4, and the form and shape of the armature elements on the P1 exopod and the first two endopod segments of leg 2. The conspecificity of both sets of specimens is therefore dubious and for that reason *C. tenuiseta sensu* Por (1969) has been scored separately in the phylogenetic analysis below.

Por (1967) mentions the presence of supernumerary setae on the swimming legs of his material of *Cervinia synarthra* from the Gulf of Elat and presents an illustration of leg 2 showing the maximum number of 7 elements on the distal endopod segment. Examination of a single female, deposited by Prof. F.D. Por in The Natural History Museum (reg. no. 1970.5.15.4), resulted in the following swimming leg armature formula (differences with *C. synarthra* are marked in bold):

	Exopod	Endopod
P1	1.1.12**2**	1.1.221
P2	1.1.223	1.**4**21
P3	1.1.223	1.**5**21
P4	1.1.223	1.321

The presence of 2 outer spines on P1 exp-3 is shared with *C. plumosa*, a species only known from the male (Itô, 1983).

Giesbrecht (1900) described the male of *C. bradyi* from the Gulf of Naples, however, there is evidence that at least two other species of *Cervinia* occur in the Mediterranean. Por (1964) recorded both sexes of *C. bradyi* from the Israeli Mediterranean coast and pointed out that the male fifth leg is reduced and only 1-segmented. This character, as well as the smaller body size, were regarded by Por (1964) as possible effects of a more accelerated development due to higher temperatures in the Mediterranean compared with those measured at similar depths in the boreal seas. These characters, in conjunction with the shorter caudal rami and different body ornamentation, rather suggest that Por (1964) was dealing with another species of the *bradyi*-group. Soyer (1970) also recorded *C. bradyi* from the Mediterranean but did not present any morphological details. In his notes on *C. synarthra*, however, he records the presence of supernumerary setae on the swimming legs and particularly on the endopods. Since this character has been misinterpreted as intraspecific variability in earlier studies (Lang, 1936; Por, 1967) it is highly conceivable that Soyer's (1970) identification was erroneous.

Cervinia brevipes Brotskaya is not considered here since its description based on a single damaged female (Brotskaya, 1963) is grossly inadequate and incomplete. Although the segmentation and armature of P2-P4 are entirely unknown, Brotskaya (1963) placed *C. brevipes* in the *bradyi*-group. According to the author the species differs from its congeners in the following combination of characters: the absence of a rostrum, the form of the caudal rami, the shape and the armature of the maxilliped, and the somewhat shortened P1 endopod. Montagna (1981) suggested that *C. brevipes* may not be a *Cervinia*.

c. Character matrix and results

The characters used to construct the character matrix are listed in Table 2. The character matrix (Table 3) contained explicit hypotheses of irreversible character transformation (Camin-Sokal option) for all but one character. This character (18) was released from possible transformation

Table 2. Morphological characters used in the phylogenetic analysis of *Cervinia*. Apomorphic states are referred to in square brackets.
Tableau 2. Caractères morphologiques utilisés dans l'analyse phylogénétique de *Cervinia*. Les caractères apomorphes sont indiqués entre crochets.

1 Body not sexually dimorphic (tergite P1-bearing somite individualized in both sexes) [sexually dimorphic - cyclopiform in ♀, fusiform in ♂; tergite P1-bearing somite completely absorbed in cephalothorax]
2 Rostrum ♀ pointed, anteriorly directed [not developed]
3 Rostrum not sexually dimorphic [strongly developed in ♂]
4 Antennule ♀ 8-segmented [7-segmented due to fusion of segments 3 and 4]
5 Antennulary segment 1 without expanded posterior margin [with knob-like process on posterior margin]
6 P1 inner basal spine not sexually dimorphic [elongated in ♂]
7 P1 exp-3 with normal setae [setae distinctly curly]
8 P1 enp-3 with 2 inner setae [with 1 inner seta]
9 P1 exp-3 with 3 outer spines/setae [with 2 outer spines/setae]
10 P2-P4 without spinous process on inner margin of basis [spinous process present]
11 P2-P4 endopods 3-segmented in ♀ [2-segmented due to fusion of exp-2 and -3]
12 P2-P3 enp-1 inner element setiform, not modified [transformed into curved pinnate spine in both sexes]
13 P2 enp-2 ♀ (as part of compound distal endopod segment) with 2 inner setae [with 1 inner seta]
14 P3 enp-2 ♀ (as part of compound distal endopod segment) with 2 inner setae [with 1 inner seta]
15 P4 enp-2 ♀ (as part of compound distal endopod segment) with 2 inner setae [with 1 inner seta]
16 P2 enp-1 ♀ inner distal corner blunt or forming minute process [with very large spinous process]
17 P2 enp-2 ♀ inner setae (or proximal setae of compound distal segment) normal [strongly reduced]
18 P2 enp-3 ♀ (or enp-2 if endopod 2-segmented) without spinous process between inner terminal and distal inner spine/seta [spinous process present]
19 P2-P4 ♂ exopodal and endopodal spines not rod-shaped [rod-shaped]
20 P5 ♀ with distinct protopod and exopodal segment [P5 1-segmented]
21 P5 ♀ exopod with 3 setae [with 2 setae]

bias by coding it as "unordered". To determine character state polarity, the outgroup concept was used and the closely related but more primitive genus *Cerviniopsis* Sars served as outgroup.

The analysis using the BRANCH AND BOUND algorithm resulted in two most parsimonious trees (Fig. 6) with tree-length 28 and consistency index 0.750. Tree A had a lower f-value (62) and F-ratio (0.0816) than tree B (f-value 68; F-ratio: 0.0889) and is selected here as the best hypothesis. The only difference between both trees is the position of *Cervinia* sp. which forms an unresolved trichotomy with *C. langi* and *C. philippinensis* in tree A but shares a sistergroup relationship with the cluster *plumosa-synarthra sensu* Por (1967) in tree B.

The position of *Expansicervinia* on the trees (Fig. 6) indicates that the genus *Cervinia*, as it is currently defined, represents a paraphyletic group. Montagna (1981) proposed the genus *Expansicervinia* on the basis of the following unique characters: (1) ventral expansion of the second "metasomal segment" (= P2-bearing somite), with an associated broadening of the entire P2 endopod, and (2) the presence of an outer knob-like expansion on the first antennulary segment. He also regarded *E. glacieria* Montagna to be unique in the subfamily Cerviniinae by the presence of the 8-segmented antennule and the absence of a rostrum. Comparison of the various *Cervinia* species shows that the majority of these characters are not restricted to *Expansicervinia.* Although Brotskaya (1963) did not figure *C. tenuiseta* in lateral aspect, her dorsal view of the habitus indicates that the P2-bearing somite is enlarged. This is also apparent from Itô's (1983) description of the fourth copepodid of this species and Por's (1969) dorsal view of his female specimen from the Indian Ocean. The posterior expansion of the first antennulary segment is again not very obvious from Brotskaya's (1963) description (probably due to excessive squashing of the specimen) but both Por (1969) and Itô (1983) leave no doubt about the presence of this modification in *C. tenuiseta.* Brotskaya (1963) described the antennule as 7-segmented but it is clear from Itô's (1983) observations of the fourth copepodid that the tiny fourth segment had been overlooked in the original description. Por (1969), on the other hand, clearly illustrates an 8-segmented antennule. From all descriptions of *C. tenuiseta* it is obvious that a prominent rostrum is absent. In addition, there are several other characters that support a close relationship between *Expansicervinia* and *Cervinia tenuiseta.* The 2-segmented fifth leg with only 2 setae on the exopod, regarded as a diagnostic generic character by Montagna (1981), is also shared by *C. tenuiseta.* The curly setae found on the distal exopod segment of leg 1 in *C. tenuiseta* are, although not mentioned by Montagna (1981), clearly present in *Expansicervinia glacieria.* A conspicuous feature in the latter's description is the presence of a spinous process on the inner distal corner of the bases of P2-P4. This structure is also exhibited by *C. tenuiseta* but appears to be completely absent from the other species currently allocated to *Cervinia.* Finally, although the P2 of *C. tenuiseta* is in no way modified as in *Expansicervinia,* it differs significantly from other species of the Cerviniinae in the extreme elongation of its endopod, which can be regarded as the initial stage leading to the transformed ramus of *E. glacieria.* Taking all these similarities into account, there seems to be a substantial body of evidence supporting a sistergroup relationship between *Expansicervinia* and *Cervinia tenuiseta.* Accordingly, the latter is designated here as the type of a

Table 3. Character data matrix of different Cerviniidae [0 = ancestral (plesiomorphic) state, 1 = derived (apomorphic) state, ? = missing data]. Same characters as in table 2.

Tableau 3. Matrice de caractères chez différents Cerviniidae [0 = état ancestral (plésiomorphe), 1 = état dérivé (apomorphe), ? = données absentes]. Mêmes caractères que dans le tableau 2.

Character	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
bradyi	1	0	1	1	0	1	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0
langi	1	0	1	1	0	1	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0
philippinensis	1	0	1	1	0	1	0	0	0	0	1	1	0	0	0	1	1	0	1	0	0
pilosa	1	0	1	1	0	1	0	0	0	0	1	1	1	1	1	1	0	1	1	0	0
plumosa	1	?	1	?	0	1	?	0	1	0	?	1	0	0	?	?	0	?	1	?	?
sp.	1	0	1	1	0	1	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1
synarthra	1	0	1	1	0	1	0	0	0	0	1	1	1	1	1	1	0	1	1	0	0
synarthra sensu Por (1967)	1	0	1	1	0	1	0	0	1	0	1	1	0	0	0	1	0	1	1	1	0
tenuicauda	?	0	?	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	?	1	1
tenuiseta	?	1	?	1	1	?	1	0	0	1	0	0	0	0	0	0	0	0	?	0	0
tenuiseta sensu Por (1969)	?	1	?	0	1	?	1	1	0	1	0	0	0	0	0	0	0	0	?	0	0
unisetosa	?	0	?	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0
EXPANSICERVINIA	0	1	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0
"PSEUDOCERVINIA"	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0

new genus *Brotskayaia* gen. nov. The primitive position of both genera is evidenced by the 8-segmented antennule in the female, the presence of 3 setae on the proximal endopod segment of the maxilliped, 4 setae on the mandibular basis and 5 elements on the proximal endite of the maxillary syncoxa. We concur with Itô (1983) that Por's (1969) specimens of *C. tenuiseta* are not conspecific with Brotskaya's (1963) type specimen. In the tree depicted in Fig. 6A *C. tenuiseta sensu* Por (1969) occupies an intermediate position because of the presence of only 1 inner seta on the distal endopod segment of leg 1, a character shared with *Expansicervinia*. However, in view of the incomplete description presented by Por (1969) his species is provisionally treated *species inquirenda* in *Brotskayaia* gen. nov.

Montagna (1981) already pointed out the close relationship between *C. unisetosa* and *C. tenuicauda* based on the resemblance displayed in the reduced female fifth legs. Their close affinity and isolated position from the other *Cervinia* species are confirmed by the present phylogenetic analysis (Fig. 6) and both species are consequently referred herein to a new genus *Neocervinia*.

The type species *C. bradyi* shares a sistergroup relationship with a clade represented by an unresolved trichotomy consisting of the *langi*-subgroup, the *synarthra*-subgroup, and the *plumosa*-subgroup (Fig. 6A). This clade is characterized by the 2-segmented condition of the P2-P4 endopods and might eventually deserve separate generic status. However, since within this clade none of the 7 species is known from both sexes, it is preferred to maintain this group together with the type-species in *Cervinia*.

The sistergroup of *Cervinia* is *C. magna* (= "*PSEUDOCERVINIA*" in Fig. 6). The male of *C. magna* differs considerably from the males of *C. bradyi* and *C. plumosa* in the profound sexual dimorphism of the swimming legs and mouthparts, including the peculiar "bottle-opener" modification of the maxillary allobasis and the transformed P4 endopod (Montagna, 1981). On the other hand the male of *C. magna* does not display sexual dimorphism in body shape, rostral development and the form of the exopodal spines on the P2-P4. This combination of characters provides sufficient evidence for the resurrection of *Pseudocervinia* as a distinct genus. In addition, females of both genera can be distinguished by differences in the antennulary aesthetasc pattern, the segmentation of the P1 endopod and the setal formula of the P4 endopod.

Generic diagnoses

Cervinia Norman (in Brady (1878))

Diagnosis. - Cerviniidae. Body shape sexually dimorphic; elongate cyclopiform and tergite of P1-bearing somite free in ♀; fusiform and tergite completely incorporated in cephalothorax in ♂. Rostrum pointed in ♀, strongly developed in ♂. Antennule 7-segmented in ♀, with 2 aesthetascs on segment 3 and 1 aesthetasc on segment 7; 8-segmented in ♂, with large aestethascs on segments 2, 3, 4 and 8; geniculation in ♂ vestigial, located between segments 6 and 7. First antennulary segment of both sexes not distinctly expanded along posterior margin. Mouthparts sexually dimorphic; atrophied in ♂ (particularly maxillule and maxilliped, and to a varying degree antennary exopod, mandible and maxillary endites). P1 inner basal spine usually sexually dimorphic, enlarged in ♂. Setae of P1 exp-3 not curly. P2-P4 without distinct spinous process on inner margin of basis. P2-P4 endopods 2- or 3-segmented in ♀, 3-segmented in ♂. P2-P3 enp-1 inner seta modified into curved pinnate spine. P2 enp-1 ♀ inner distal corner produced into very large spinous process. P2 enp-3 ♀ (or enp-2 if endopod 2-segmented) with spinous process between inner terminal and distal inner seta/spine (except in *C. philippinensis*). P2-P4 ♂ exopodal spines rod-shaped. P1-P4 armature formulae:

	Exopod	Endopod	
		♀	♂
P1	1.1.12[2-3]	1.1.221	
P2	1.1.223	1.2.221 or 1.[3-4]21	1.2.221
P3	1.1.223	1.2.321 or 1.[4-5]21	1.2.321
P4	1.1.223	1.2.221 or 1.[3-4]21	1.2.221

P5 defined at base; in ♀ 2-segmented, comprising protopod and exopod, or 1-segmented, with total of 3-4 setae; in ♂ 2-segmented, comprising unisetose protopod and bisetose exopod. P6 ♂ with 3 setae.

Type species. - *Cervinia bradyi* Norman (in Brady (1878))
Other species. - *C. synarthra* Sars, 1910; *C. pilosa* Lang, 1948; *C. langi* Montagna, 1979; *C. plumosa* Itô, 1983; *C. philippinensis* sp. nov.
Species inquirendae. - *C. synarthra sensu* Por (1967); *Cervinia* sp. [present account]
Species incertae sedis. - *C. brevipes* Brotskaya, 1963

Remark. - The imperfectly described *Cervinia brevipes* is almost certainly based on a copepodid V stage. Evidence for its immature condition is found in the number of body somites and the form of the fifth and sixth legs. The antennule has been described as 8-segmented but the position of the proximalmost posterior seta (derived from ancestral segment XXIV; cf. Huys & Boxshall (1991)) found on segment 5 indicates that the subdivision of the apical segment is based on an erroneous observation and the antennule is actually 7-segmented. Female harpacticoids display a maximum of 9 segments in the antennule with the proximalmost posterior seta arising from the seventh segment, leaving only 2 segments (and thus not 3 as in

Brotskaya's drawing) distal to this reference point. On the basis of the 7-segmented antennule and the long P5 (Brotskaya (1963) presumably figured only the exopod) *C. brevipes* is tentatively placed *species incertae sedis* in *Cervinia.*

Pseudocervinia Brotskaya, 1963

Diagnosis. - Cerviniidae. Body shape not sexually dimorphic; elongate cyclopiform and tergite of P1-bearing somite free in both sexes. Rostrum pointed, not sexually dimorphic. Antennule 7-segmented in ♀, with aesthetasc on segment 3; 8-segmented in ♂, with aestethasc on segment 4 and possibly on segments 6 and 8 (two); geniculation in ♂ vestigial, located between segments 6 and 7. First antennulary segment of both sexes not distinctly expanded along posterior margin. Mouthparts sexually dimorphic; mandibular gnathobase, maxillule and maxilliped atrophied in ♂; ♂ maxilla with allobasal claw modified into "bottle-opener". P1 inner basal spine not sexually dimorphic. Setae of P1 exp-3 not curly. P2-P4 without distinct spinous process on inner margin of basis. P1-P4 endopods 2-segmented in ♀, 3-segmented in ♂. P2-P3 enp-1 inner seta modified into curved pinnate spine. P2 enp-1 ♀ inner distal corner produced into very large spinous process. P2 enp-2 ♀ with spinous process between inner terminal and distal inner seta/spine. P2-P4 exopodal spines not rod-shaped in ♂. Distal and outer elements of P2-P4 endopods spiniform in ♂. P4 enp-3 ♂ very small. P1-P4 armature formulae:

	Exopod	Endopod	
		♀	♂
P1	1.1.123	1.321	1.1.221
P2	1.1.223	1.421	1.2.221
P3	1.1.223	1.421	1.2.321
P4	1.1.223	1.221	1.2.221

P5 defined at base; 2-segmented in both sexes, comprising unisetose protopod and trisetose exopod. P6 ♂ with 3 setae.

Type and only species. - *Cervinia magna* Smirnov, 1946 = *Pseudocervinia magna* (Smirnov, 1946)

Remark. - Montagna (1981) provided the first illustrated description of the male and fifth copepodid of *P. magna.* Although Montagna did not specify the sex of the copepodid stage, it is clear from the setal formula of P3-P4 endopods and the P5 that he was dealing with a male. It is conceivable that the setal formula of the P4 endopod, given in the text as 1.321, is erroneous. The notch present between the long distal spine and the outer seta (his Fig. 4, P4 end.) indicates a missing seta so that the armature formula in reality is 1.421.

Expansicervinia Montagna, 1981

Diagnosis [based on ♀ only]. - Cerviniidae. Tergite of P1-bearing somite free in ♀. P2-bearing somite largest, ventrally expanded. Rostrum not developed. Antennule 8-segmented in ♀, with aesthetasc on segments 3 and 4. First antennulary segment expanded along posterior margin forming knob-like projection. Setae of P1 exp-3 curly. P2 endopod ♀ enlarged, robust, with strong spines on enp-3. P2-P4 with distinct spinous process on inner margin of basis. P1-P4 endopods 3-segmented in ♀. P2-P3 enp-1 inner seta not modified into curved pinnate spine. P2 enp-1 ♀ inner distal corner not produced into very large spinous process. P2 enp-3 ♀ without spinous process between inner terminal and distal inner seta/spine. Outer elements of P3-P4 exp-3 setiform. P1-P4 armature formulae:

	Exopod	Endopod
P1	1.1.123	1.1.121
P2	1.1.222	1.2.221
P3	1.1.222	1.2.221
P4	1.1.222	1.1.121

P5 defined at base; in ♀ 2-segmented, comprising unisetose protopod and minute, bisetose exopod.

Type and only species. - *Expansicervinia glacieria* Montagna, 1981 [by monotypy].

Brotskayaia gen. nov.

Diagnosis [based on ♀ only]. - Cerviniidae. Tergite of P1-bearing somite free in ♀. P2-bearing somite largest, ventrally expanded. Rostrum not developed. Antennule 8-segmented in ♀, with aesthetasc on segment 3 (and possibly 8). First antennulary segment expanded along posterior margin. Setae of P1 exp-3 curly. P2 endopod ♀ longer than exopod and robust, with well developed spines on enp-3. P2-P4 with distinct spinous process on inner margin of basis. P1-P4 endopods 3-segmented in ♀. P2-P3 enp-1 inner seta sometimes not modified into curved pinnate spine. P2 enp-1 ♀ inner distal corner not produced into very large spinous process. P2 enp-3 ♀ without spinous process between inner terminal and distal inner seta/spine. Outer elements of P3-P4 exp-3 spiniform. P1-P4 armature formulae:

	Exopod	Endopod
P1	1.1.123	1.1.221
P2	1.1.223	1.2.221
P3	1.1.223	1.2.321
P4	1.1.223	1.2.221

P5 defined at base; in ♀ 2-segmented, comprising unisetose protopod and bisetose exopod.

Etymology. - The genus is named for the late Dr V.A. Brotskaya in recognition of her contributions to the taxonomy of the Cerviniidae. Gender: feminine.

Type species.- *Cervinia tenuiseta* Brotskaya, 1963 = *Brotskayaia tenuiseta* (Brotskaya, 1963) comb. nov.

Species inquirenda. - *Cervinia tenuiseta* Brotskaya, 1963 *sensu* Por (1969)

Remark. - The allocation of *Cervinia tenuiseta* Brotskaya, 1963 *sensu* Por (1969) to the present genus is tentative. Por's description shows some of the generic diagnostic characters such as the absence of the rostrum, the inner spinous process on the bases of the swimming legs and the setation of leg 5, however, the absence of curly setae on the P1 exopod, the modification of the inner element of P2-P3 enp-1 into a curved spine and the presence of the spinous inner distal corner on P2 enp-1 may indicate that its affinity lies with other genera.

Neocervinia gen. nov.

Diagnosis [based on ♀ only]. - Cerviniidae. Tergite of P1-bearing somite free in ♀. Rostrum well developed in ♀, broad and blunt. Antennule 7-segmented in ♀, with aesthetasc on segment 3. First antennulary segment of both sexes not distinctly expanded along posterior margin. Setae of P1 exp-3 not curly. P2-P4 without distinct spinous process on inner margin of basis. P1-P4 endopods 3-segmented in ♀. P2-P3 enp-1 inner seta not modified into curved pinnate spine. P2 enp-1 ♀ inner distal corner not produced into very large spinous process. P2 enp-2 ♀ without spinous process between inner terminal and distal inner seta/spine. P1-P4 armature formulae:

	Exopod	Endopod
P1	1.1.123	1.1.221
P2	1.1.223	1.2.221
P3	1.1.223	1.2.321
P4	1.1.223	1.2.221

P5 not defined at base; minute and laterally displaced in ♀, with 3 setae.

Etymology. - The generic name is derived from the Greek *neos*, meaning new, young, and refers to the neotenic condition of the female P5.

Type species. - *Cervinia unisetosa* Montagna, 1981 = *Neocervinia unisetosa* (Montagna, 1981) comb. nov.

Other species. - *Cervinia tenuicauda* Brotskaya, 1963 = *Neocervinia tenuicauda* (Brotskaya, 1963) comb. nov.

Remark. - Montagna (1981) named *C. unisetosa* after the unique presence of only 1 seta on the basis of the mandible. The interruption in the cuticle shown between this seta and the articulation with the endopod (his Fig. 2: Md) however, calls for verification as it may well indicate a scar marking the original position of 1 or 2 missing (dislodged?) setae. Brotskaya (1963) figured 3 closely set setae in this position in her description of *C. tenuicauda*.

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