

## Cladistic analysis of the calanoid Copepoda

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**Abstract.** Calanoid copepods are extremely successful inhabitants of marine, brackish and freshwater plankton. Morphological data are used to arrive at a first, parsimony-based phylogeny for the calanoid copepods. Each family is represented by at least one exemplar, typically a recognised plesiomorphic species. The Epacteriscidae are sister to all other calanoid copepods – an observation that brings into question the concept of an Epacteriscoidea that includes the Ridgewayiidae. The monophyly of the Augaptiloidea, Centropagoidea, Clausocalanoidea and Pseudocyclopoidea is corroborated. The current analysis suggests there may be two major clades, one containing the Augaptiloidea, Centropagoidea and possibly the Pseudocyclopoidea and Ridgewayiidae and the other including the Megacalanidae, Calanidae/Paracalanidae, Bathypontioidea, Eucalanoidea, Ryocalanoidea, Spinocalanoidea and Clausocalanoidea. The relationships of the Pseudocyclopidae, Boholinidae, and Ridgewayiidae to the Centropagoidea/Augaptiloidea clade received low nodal support. Monophyly of an enlarged Bathypontioidea (including the Fosshageniidae) is proposed. A monophyletic Megacalanoidea is not retrieved. The nature of the inferred ancestral Calanoida is discussed. New evolutionary series are proposed for the female genitalia (including several losses and regaining of seminal receptacles, and independent losses of the genital operculum – once lost it is never regained) and leg I endopod. Paedomorphosis appears to be a dominant process in the evolution of the Calanoida.

### Introduction

Calanoid copepod crustaceans are extremely successful inhabitants of the marine, brackish and freshwater plankton (Huys and Boxshall 1991) and represent an important link in aquatic food webs. They occur at all depths in the water column and comprise 43 families and ~280 genera. The Calanoida have been well defined as an order for more than 100 years (e.g. Giesbrecht 1893; Sars 1901). Within the Calanoida, however, Sars (1901: p. 5) noted that reliable subdivision is difficult to achieve owing to great variation in characters. Giesbrecht (1893) divided the Calanoida into two groups based chiefly on antennule and mouthpart differences: Amphiscandria and Heterarthrandria to which Sars (1902: p. 56) added the Isokerandria.

The Amphiscandria are characterised by both male antennules being alike, without geniculation and with dimorphism between the sexes that includes fusion between some of the antennular segments. Body shape of the male is often very different from that of the female, and male mouthparts are often reduced (Sars 1901). Sars placed the following families in this group: Calanidae (including the now accepted Eucalanidae), Paracalanidae, Pseudocalanidae (including the now accepted Spinocalanidae), Aetideidae, Euchaetidae, Phaennidae, and Scolecitrichidae.

The Heterarthrandria (Sars 1902, 1903) are characterised by the asymmetry of the male antennules, which are prehensile on one side. Mouthparts are equally well developed in both sexes.

In this group, Sars included 14 families (Centropagidae, Diaptomidae, Pseudodiaptomidae, Lucicutiidae, Temoridae, Metridinidae (as Metridiidae), Heterorhabdidae, Arietellidae, Candaciidae, Pontellidae, Parapontellidae, Acartiidae, Tortanidae, and Pseudocyclopidae).

The Isokerandria are characterised by antennules that do not show any sexual dimorphism and mouthparts that are usually similar in both sexes (Sars 1902). Sars placed the following families in this group: Diaixidae, Stephidae, Tharybidae, and Pseudocyclopidae.

Gurney (1931) mentioned two genera that interrupt the integrity of Sars' system: *Platycopia* and *Bathycalanus*. *Platycopia* is now assigned to a separate order (Platycopioidea) being united, along with several other genera by: the female genital somite remaining separate from the first abdominal somite in the adult, exopod segment 1 of legs 2–5 bearing 2 outer border articulated spines, and segments XXVII and XXVIII expressed in the antennule (Fosshagen and Iliffe 1985). *Bathycalanus*, which was then included in the Calanidae (Amphiscandria section), has a geniculate right antennule in males, implying it should be in the Heterarthrandria section. Gurney proposed a different system, based mainly on the structure of the fifth pair of legs in males and females, but this classification was artificial and has never been found useful (Andronov 1974). Although aware of the ambiguities in Sars' (1901) scheme, most workers up until the 1970s adopted Sars' system.

It was not until the work of Andronov (1974) that the nature of a putative calanoid ancestor was considered. He assumed that the ancestral calanoid had all of the putatively primitive characters presently found in Calanoida:

- (1) Pedigerous somite 1 separate from the cephalosome
- (2) Female urosome with 4 free somites (i.e. with a genital double-somite)
- (3) Males and females having similar, well developed mouthparts
- (4) Little differentiation in swimming legs 1–5 in male and females
- (5) The presence of an outer distal seta on the basis of leg 1
- (6) Male and female antennules similar
- (7) Most arthrodial membranes between antennular segments developed.

It is only item 6 that there is some doubt about. It appears that geniculation of male antennules is a basic copepod characteristic if we consider the evidence of symmetrical geniculation that occurs in the platycopioid *Sarsicopia polaris* Martinez Arbizu, 1997 and the presence of right-sided geniculation in the Epacteriscoidea, the calanoid family retaining the most plesiomorphic form.

From this analysis Andronov (1974) chose a set of characters from which his phylogenetic hypothesis was derived:

- (1) Fusion of ancestral segments X and XI of the antennule
- (2) Presence on the male of a geniculate antennule on one side only
- (3) Number of setae on endopod segment 2 of swimming legs 3–4
- (4) Number of setae on endopod segment 3 of swimming legs 3–4
- (5) Number of inner setae on exopod segment 3 of swimming legs 3–4
- (6) Atrophied male mouthparts
- (7) Presence of a seta on the outer border of the basis of leg 1
- (8) Presence of aesthetascs on the geniculate antennule of males
- (9) Location of geniculate antennule – on the right or the left.

Item 8 is the only feature that is questioned here. An investigation of male antennules, carried out as part of this study, revealed that all taxa carry structures that can be interpreted as aesthetascs, although in many families they are not very conspicuous. These characters/states are further evaluated in the discussion.

Andronov (1974) recognised the following superfamilies: Platycopioidea; Pseudocyclopoidea Giesbrecht, 1893; Augaptiloidea Sars, 1905; Centropagoidea Giesbrecht, 1893; Megacalanoidea Sewell, 1947; Bathypontioidea Brodsky, 1950; Eucalanoidea Giesbrecht, 1893; Ryocalanoidea Andronov, 1974; Pseudocalanoidea Sars, 1901. Subsequently, Andronov (1991) changed Augaptiloidea Sars, 1905 to Arietelloidea Sars, 1902; Centropagoidea Giesbrecht, 1893 to Diaptomoidea Baird, 1850; Megacalanoidea Sewell, 1947 to Calanoidea Dana, 1846, ostensibly because of Article 23 (Law of Priority) in the International Code of Zoological Nomenclature (ICZN), whereas Pseudocalanoidea Sars, 1901 was changed to Clausocalanoidea Giesbrecht, 1893 because of the judgement of the Commission that the family name Clausocalanidae should

take precedence over Pseudocalanidae Sars, 1901 (ICZN 1988, Opinion 1503). The superfamilies Epacteriscoidea Fosshagen, 1973 and Spinocalanoidea Vervoort, 1951 were added by Park (1986) and the Ridgewayiidae were removed from the Pseudocyclopoidea and added to the Epacteriscoidea (Fosshagen *et al.* 2001). The Platycopioidea were removed from the Calanoida to a separate order: Platycopioidea Fosshagen (in Fosshagen and Iliffe 1985). Boxshall and Halsey (2004) tentatively accepted the invalidly amended names with some small adjustments. The superfamily Fosshagenioidea (Suárez-Morales and Iliffe 1996) was rejected by Boxshall and Halsey (2004) and the Fosshageniidae was placed within the Diaptomoidea by them.

Ferrari and Ueda (2005) point out that Andronov (1991) was not justified in making the above changes and refer to Article 64 in the International Code of Zoological Nomenclature, in force at the time (ICZN 1985). Article 64 indicates the oldest name does not necessarily have to be chosen for family-group names. Therefore, the superfamily names accepted here are: Augaptiloidea, Bathypontioidea, Megacalanoidea, Clausocalanoidea, Centropagoidea, Epacteriscoidea, Eucalanoidea, Pseudocyclopoidea, Ryocalanoidea, and Spinocalanoidea. More recently, Andronov (2007) has suggested that the Epacteriscoidea should be subsumed into the Pseudocyclopoidea.

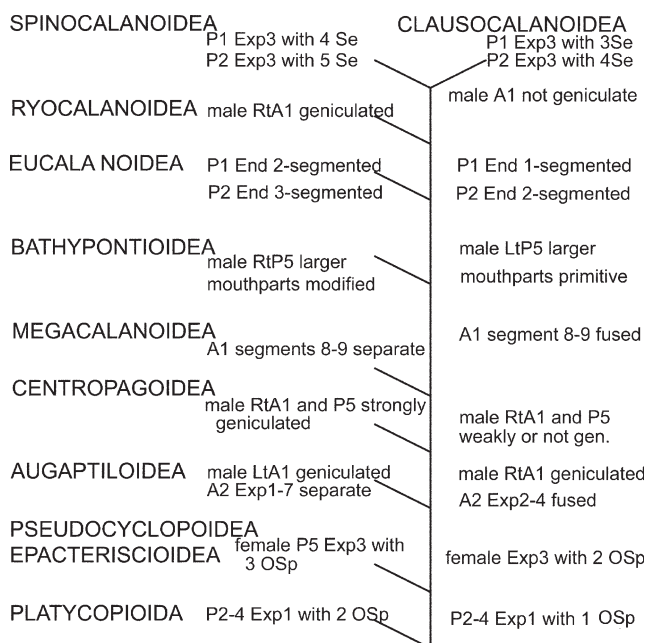
Park (1986) published a phylogenetic hypothesis of the Calanoida but could not determine the position of the Platycopioidea, Pseudocyclopoidea and Epacteriscoidea because of specialisations related to their epibenthic habit. Nevertheless, these superfamilies are illustrated as being 'basal' to the Calanoida. Park considered the Augaptiloidea to have diverged early in the evolution of the Calanoida. After the separation of the Augaptiloidea, the remaining superfamilies were thought to form a monophyletic assemblage (Fig. 1).

Huys and Boxshall (1991) examined broadscale phylogenetic patterns across copepod orders and provided a detailed analysis of homologies among high-level character systems. Herein, we examine the interrelationships within the Order Calanoida based on phylogenetic analysis of morphology, with emphasis on testing superfamily monophyly and relationships among the taxa.

## Materials and methods

### *Ingroup taxa*

All calanoid families (39) for which both the female and male morphology is known, are represented in the ingroup (Table 1). Parkiidae Ferrari & Markhaseva, 1996, Arctokonstantinidae Markhaseva & Kosobokova 2001, Rostrocalanidae Markhaseva, Schulz & Martinez Arbizu, 2009, and Kyphocalanidae Markhaseva & Schulz, 2009 are excluded, being presently known only from females. Also, the Discoidae, a highly reduced member of the Augaptiloidea, is omitted. In most cases, each family was represented by a putatively plesiomorphic species exemplar to represent the stem condition, and where possible, a species that has been well described and/or could be readily verified against specimens. Three families are represented by two terminal taxa each to capture morphological heterogeneity, in the case of the



**Fig. 1.** Phylogeny of the Calanoida (Park 1986) modified from analysis of Andronov (1974). Image reproduced courtesy of the Canadian Museum of Nature, Ottawa, Canada.

Ridgewayiidae, and to test the recent inclusion of additional genera into the Fosshageniidae and Bathypontiidae (Boxshall and Halsey 2004).

#### Outgroup taxon

The outgroup was selected in the context of the current phylogenetic hypotheses concerning copepod orders (Huys and Boxshall 1991). The Platycopioidea is the sister group to all other copepods. The next ordinal clade is the Calanoida which retains the gymnoplean body tagmosis and represents the sister group of the lineages comprising all other remaining copepod orders, characterised by their podoplean body tagmosis. The first offshoot of this podoplean lineage is the Misophrioida.

We agree that an exemplar/s from the sister group to the ingroup is normally the ideal option for outgroup selection. However, the candidate taxa, Platycopioidea and Misophrioida present problems if members of these orders are used as outgroups, resulting in unlikely relationships (e.g. the Lucicutiidae emerges as sister to all other calanoid families thereby breaking up the Augaptiloidea, the monophyly of which has never been challenged). Both orders present a large number of highly derived character states scoreable only as autapomorphies and therefore effectively unavailable to the analysis. These taxa also have insufficient character states in common with the inferred ancestral character set derived from extensive study of character state distributions across the Copepoda (Huys and Boxshall 1991). Additionally, the precise homologies of many of the autapomorphic character states in the Platycopioidea and Misophrioida are difficult to interpret. Therefore an ancestral hypothetical ancestor was scored as outgroup based mainly on Huys and Boxshall (1991).

Most of the Huys and Boxshall (1991) character set was accepted here for the hypothetical calanoid ancestor apart

from: the state of several features of the male geniculate antennule, the postulated number of ancestral antennal exopod segments and resulting setation, the presence of a coxal epipodite on the maxilla and the state of the female genitalia. These characters are evaluated below and where there is insufficient evidence for the ancestral state they are scored 'unknown'.

#### The character set

The character/state set was chosen based on defensible hypotheses of primary homology but we did not include characters that are invariant or otherwise parsimony uninformative. These data are taken mainly from the literature but were checked where inaccuracy was suspected or data were unavailable. Hypotheses of primary homology relating to segmentation and setation employed our current understanding of copepod development. The literature on the development of key calanoid copepod taxa is not extensive; therefore, additional data acquisition may further improve our knowledge of homologies in the future. Our failure to arrive at primary homology hypotheses for many of the mouthpart characters/states is evaluated in the sections below.

Characters (Char.) and their states are listed in Table 2 and the data matrix is given in Table 3. On the figures, specific characters: states are indicated in the form '◀ 3 : 2'.

#### Male dorsal cephalic hump

This organ is a close assemblage of two secretory glands and a receptor that has a very thin cuticle and is probably chemosensory (Nishida 1989). It (Char. 1, Fig. 2) is found only in the families Calanidae, Megacalanidae, and Paracalanidae (now including *Mecynocera* (Bradford-Grieve 2008)) (Table 2). It is assumed to be absent in the hypothetical ancestor (Table 3).

#### Female caudal ramus

The setation of the caudal ramus is analysed according to the interpretation of Huys and Boxshall (1991) in which there are primitively seven setae. The interpretation of the setae on the caudal rami of the Bathypontiidae and Fosshageniidae is problematic. The Bathypontiidae (*Temorites*) have three large terminal setae and a small seta on the distal inner edge. These setae are interpreted as being setae III–VI and that seta VII (Char. 2, Fig. 2) is absent (Sars 1925). Likewise, *Fosshagenia* has three large terminal setae and a small, asymmetrical inner edge seta (posteriorly directed on the left and ventrally directed on the right) (Fosshagen and Iliffe 2004) and are similarly interpreted as being setae III–VI. The location of the point of attachment of seta VII (Char. 3, Fig. 2) is also used in this analysis: it may originate on the dorsal surface towards the mid-line of the copepod (e.g. hypothetical ancestor, Augaptiloidea, Centropagoidea), may originate on the inner border of the caudal ramus (Calanidae, Megacalanidae, Paracalanidae), or may be interpreted as having migrated to the ventral surface in many taxa (e.g. Clausocalanoidea).

#### Female antennule segmentation

Female antennules are analysed according to the interpretation of Huys and Boxshall (1991) in which there are considered to be

**Table 1.** Calanoid copepod taxa used as exemplars in the cladistic analysis of calanoid families

Family	Species	References
Hypothetical calanoid		Huys and Boxshall (1991)
Boholinidae	<i>Boholina crassicephala</i>	Fosshagen and Iliffe (1989)
Pseudocyclopidae	<i>Pseudocyclops ornata</i>	Ohtsuka <i>et al.</i> (1999)
Epacteriscidae	<i>Erebonectes nesioticus</i>	Fosshagen and Iliffe (1985)
Ridgewayiidae	<i>Ridgewayia stygia</i>	Ohtsuka <i>et al.</i> (2000)
Ridgewayiidae	<i>Brattstromia longicaudata</i>	Fosshagen and Iliffe (1991)
Arietellidae	<i>Arietellus plumifer</i>	Ohtsuka <i>et al.</i> (1994)
Augaptilidae	<i>Haloptilus longicornis</i>	Sars (1902)
Heterorhabdidae	<i>Disseta palumboi</i>	Park (2000)
Hyperbionychidae	<i>Hyperbionyx pluto</i>	Ohtsuka <i>et al.</i> (1993a, 1993b)
Lucicutiidae	<i>Lucicutia flavicornis</i>	Personal observation
Metridiidae	<i>Metridia lucens</i>	Personal observation
Nullosetigeridae	<i>Nullosetigera acutiseta</i>	Soh <i>et al.</i> (1999)
Acartiidae	<i>Acartiella faoensis</i>	Personal observation
Candaciidae	<i>Candacia armata</i>	Giesbrecht (1893), Sars (1903)
Centropagidae	<i>Centropages aucklandicus</i>	Personal observation
Diaptomidae	<i>Sinodiaptomus valkanovi</i>	Ueda and Ohtsuka (1998)
Fosshageniidae	<i>Fosshagenia suarezi</i>	Fosshagen and Iliffe (2004)
Fosshageniidae	<i>Temoropia setosa</i>	Schulz (1986)
Parapontellidae	<i>Parapontella brevicornis</i>	Sars (1903)
Pontellidae	<i>Pontella novaezelandiae</i>	Personal observation
Pseudodiaptomidae	<i>Pseudodiaptomus ishigakiensis</i>	Nishida (1985)
Sulcanidae	<i>Sulcanus conflictus</i>	Personal observation, Nicholls (1945)
Temoridae	<i>Temora turbinata</i>	Personal observation
Tortanidae	<i>Tortanus angularis</i>	Ohtsuka (1992)
Calanidae	<i>Calanus australis</i>	Personal observation
Megacalanidae	<i>Megacalanus longicornis</i>	Personal observation
Paracalanidae	<i>Paracalanus c.f. indicus</i>	Personal observation
Bathypontiidae	<i>Temorites elongata</i>	Personal observation
Bathypontiidae	<i>Zenkevitchiella</i> spp.	Brodsky (1955), Grice and Hulsemann (1965, 1967)
Eucalanidae	<i>Eucalanus spinifer</i>	Goetze and Bradford-Grieve (2005)
Ryocalanidae	<i>Ryocalanus</i> spp.	Andronov (1992), Shimode <i>et al.</i> (2000)
Aetideidae	<i>Aetideopsis tumorosa</i>	Personal observation
Clausocalanidae	<i>Clausocalanus brevipes</i>	Personal observation
Diaixidae	<i>Diaixis hibernica</i>	Sars (1902)
Euchaetidae	<i>Euchaeta rimana</i>	Personal observation, Park (1995)
Mesaiokeratidae	<i>Mesaiokeras spitsbergensis</i>	Schulz and Kwasniewski (2004)
Phaennidae	<i>Xanthocalanus longispinus</i>	Personal observation, Bradford-Grieve (2004)
Pseudocyclopiidae	<i>Stygocyclopia balearica</i>	Jaume and Boxshall (1995)
Scolecitrichidae	<i>Pleisioscolecithrix juhlae</i>	Markhaseva and Dahms (2004)
Stephidae	<i>Stephos hastatus</i>	Personal observation, Bradford-Grieve (1999)
Tharybidae	<i>Tharybis inaequalis</i>	Personal observation, Bradford-Grieve (2001)
Spinocalanidae	<i>Spinocalanus longicornis</i>	Damkaer (1975)

28 ancestral segments, the distal pair of which is never expressed in the Calanoida. The antennule develops progressively in copepodite stages from distal to proximal (Hulsemann 1991a; Boxshall and Huys 1998; Ferrari and Benforado 1998) (Fig. 3). The first region to develop in copepodite I (CI) is derived from the terminal segment of the nauplius VI (NVI) antennule, with progressively more segments being added up to CV. At CI the arthrodistal membranes between ancestral segments XXI to XXVII are fully developed in the adult pattern (e.g. Boxshall and Huys 1998). During further development, the proximal three segments of CI subdivide, progressively giving rise to the adult segmentation. Sometimes, several of the arthrodistal membranes that define articulations between proximal segments fail to appear during the development of copepodites. Thus some adult taxa apparently retain aspects of the segmentation of earlier

copepodite stages (e.g. Acartiidae, Sulcanidae, Tortanidae) (e.g. Johnson 1934; Tanimura 1992). The interpretation of the expression of antennular segments (or development of respective arthrodistal membranes) that occurs in two or more taxa is recorded in this analysis (Chars 4–15, Fig. 4). The hypothetical ancestor is assumed to have had all ancestral segments expressed apart from XXVII and XXVIII (Table 3).

#### Male antennule

*Geniculation.* There is evidence (e.g. Epacteriscidae, Boholinidae, Ridgewayiidae, Pseudocyclopidae, Megacalanidae, Augaptiloidea and Centropagoidea) that the ancestral calanoid had asymmetrical antennules with the geniculation between ancestral segments XX and XXI of



**Table 2. Morphological characters/states used for phylogenetic analysis followed by the consistency index and rescaled consistency index (bold)**

1. Male cephalic dorsal hump (absent, present)	0.5	<b>0.25</b>
2. Female caudal ramus seta VII (present, absent)	1	<b>1</b>
3. Female caudal ramus seta VII (dorsal, ventral, inner edge)	0.5	<b>0.43</b>
4. Female A1 ancestral segments I and II (separate, fused)	0.25	<b>0.17</b>
5. Female A1 ancestral segments II and III (separate, fused)	1	<b>1</b>
6. Female A1 ancestral segments III and IV (separate, fused)	0.25	<b>0.16</b>
7. Female A1 ancestral segments IV and V (separate, fused)	0.5	<b>0.25</b>
8. Female A1 ancestral segments V and VI (separate, fused)	0.5	<b>0.25</b>
9. Female A1 ancestral segments VI and VII (separate, fused)	0.25	<b>0.06</b>
10. Female A1 ancestral segments VIII and IX (separate, fused)	0.5	<b>0</b>
11. Female A1 ancestral segments X and XI (separate, fused)	0.14	<b>0.09</b>
12. Female A1 ancestral segments XI and XII (separate, fused)	0.5	<b>0</b>
13. Female A1 ancestral segments XIII and XIV (separate, fused)	0.5	<b>0</b>
14. Female A1 ancestral segments XXIV and XXV (separate, fused)	0.33	<b>0.11</b>
15. Female A1 ancestral segments XXV and XXVI (separate, fused)	0.5	<b>0</b>
16. Male A1 geniculation between XX and XXI (present, absent)	0.5	<b>0.46</b>
17. Male A1 when geniculation between XX and XXI, geniculation on (right, left)	1	<b>1</b>
18. Male A1 ancestral segments XXII and XXIII (separate on both sides, fused on right, fused on left, fused on both sides)	0.38	<b>0.24</b>
19. Male geniculate A1 segment XXI-XXIII setae (absent, present)	1	<b>1</b>
20. Male geniculate A1 supplementary geniculation between ancestral segments XIV and XV (absent, present)	1	<b>1</b>
21. Male geniculate or right A1 ancestral segment I and II (separate, fused)	0.17	<b>0.1</b>
22. Male geniculate or right A1 ancestral segments III and IV (separate, fused)	0.33	<b>0.11</b>
23. Male geniculate or right A1 ancestral segments IV and V (separate, fused)	0.33	<b>0.11</b>
24. Male geniculate or right A1 ancestral segments V and VI (separate, fused)	0.25	<b>0.06</b>
25. Male geniculate or right A1 ancestral segments VI and VII (separate, fused)	0.25	<b>0.06</b>
26. Male geniculate or right A1 ancestral segments IX and X (separate, fused)	0.13	<b>0.02</b>
27. Male geniculate or right A1 ancestral segment X and XI (separate, fused)	0.2	<b>0.16</b>
28. Male geniculate or right A1 ancestral segments XI and XII (separate, fused)	0.14	<b>0.05</b>
29. Male geniculate or right A1 ancestral segments XIII and XIV (separate, fused)	0.2	<b>0.04</b>
30. Male geniculate or right A1 ancestral segments XIV and XV (separate, fused)	0.33	<b>0</b>
31. Male geniculate or right A1 ancestral segments XV and XVI (separate, fused)	0.33	<b>0.11</b>
32. Male geniculate or right A1 ancestral segments XVI and XVII (separate, fused)	0.5	<b>0.25</b>
33. Male geniculate or right A1 ancestral segments XIX and XX (separate, fused)	0.2	<b>0.09</b>
34. Male geniculate or right A1 ancestral segments XXI and XXII (separate, fused)	0.25	<b>0.21</b>
35. Male geniculate or right A1 ancestral segments XXIV and XXV (separate, fused)	0.33	<b>0.3</b>
36. Male geniculate or right A1 ancestral segments XXV and XXVI (separate, fused)	0.33	<b>0.2</b>
37. Female A2 exopod seta 1 (present, absent)	0.5	<b>0.33</b>
38. Female A2 exopod seta 5 (present, absent)	0.5	<b>0</b>
39. Female A2 exopod seta 6 (present, absent)	0.25	<b>0.16</b>
40. Female A2 exopod seta 7 (present, absent)	0.2	<b>0.13</b>
41. Female A2 exopod seta 8 (present, absent)	0.17	<b>0.1</b>
42. Female A2 exopod seta 9 (present, absent)	0.14	<b>0.09</b>
43. Female Mx1 coxal epipodite seta 3 (present, absent)	0.25	<b>0.06</b>
44. Female Mx1 coxal epipodite seta 4 (present, absent)	0.25	<b>0.06</b>
45. Female Mx1 coxal epipodite seta 5 (present, absent)	0.25	<b>0.13</b>
46. Female Mx1 coxal epipodite seta 6 (present, absent)	0.17	<b>0.06</b>
47. Female Mx1 coxal epipodite seta 7 (present, absent)	0.14	<b>0.05</b>
48. Female Mx1 coxal epipodite seta 8 (present, absent)	0.09	<b>0.02</b>
49. Female Mx1 coxal epipodite seta 9 (present, absent)	0.09	<b>0.03</b>
50. Female Mx1 basal exite seta (present, absent)	0.2	<b>0.15</b>
51. Female Mx2 coxal epipodite seta (absent, present)	0.33	<b>0.2</b>
52. Female Mx2 basal endite sensory seta (absent, present)	1	<b>1</b>
53. Female Mx2 endopod sensory setae (absent, present)	1	<b>1</b>
54. Female Mxp endopod and basis short, reduced, syncoxa developed distally (absent, present)	0.5	<b>0.38</b>
55. Female Mxp syncoxal endite 3 sensory setae (absent, present)	0.5	<b>0.25</b>
56. Female Mxp endopod segment 1 seta 1 (present, absent)	1	<b>1</b>
57. Female Mxp endopod segment 1 seta 2 (present, absent)	0.33	<b>0.22</b>
58. Female Mxp endopod segment 2 seta 2 (present, absent)	1	<b>1</b>
59. Female Mxp endopod segment 2 seta 3 (present, absent)	0.33	<b>0.24</b>
60. Female Mxp endopod segment 2 seta 4 (present, absent)	0.14	<b>0.09</b>
61. Female Mxp endopod segment 3 seta 2 (present, absent)	0.5	<b>0.38</b>

(continued next page)

**Table 2.** (continued)

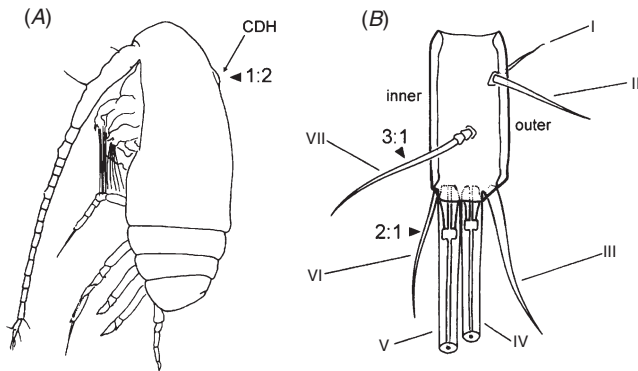
62. Female Mxp endopod segment 3 seta 3 (present, absent)	0.2	<b>0.12</b>
63. Female Mxp endopod segment 3 seta 4 (present, absent)	0.17	<b>0.12</b>
64. Female Mxp endopod segment 4 seta 2 (present, absent)	0.5	<b>0.38</b>
65. Female Mxp endopod segment 4 seta 3 (present, absent)	0.2	<b>0.14</b>
66. Female Mxp endopod segment 5 seta 2 (present, absent)	0.33	<b>0.25</b>
67. Female Mxp endopod segment 5 seta 3 (present, absent)	0.25	<b>0.06</b>
68. Female Mxp endopod segment 5 seta 4 (present, absent)	0.17	<b>0.1</b>
69. Male Mxp outer seta of endopod segments 5 and 6 (not enlarged, enlarged and directed proximally compared with female)	0.5	<b>0.25</b>
70. Male mouthparts (not reduced, reduced)	0.14	<b>0.04</b>
71. Legs 2–4 outer distal exopod spines (articulated, fused to segment)	1	<b>1</b>
72. Leg 1 coxa inner border seta (present, absent)	0.33	<b>0.29</b>
73. Leg 1 basis outer seta (present, absent)	0.1	<b>0.04</b>
74. Leg 1 exopod segment 1 outer edge spine (present, absent)	0.17	<b>0.03</b>
75. Leg 1 exopod segment 1 inner edge seta (present, absent)	0.25	<b>0.2</b>
76. Leg 1 exopod segment 3 inner edge seta 4 (present, absent)	0.5	<b>0.45</b>
77. Leg 1 exopod segment 3 outer edge articulate spine 2 (present, absent)	0.25	<b>0.19</b>
78. Leg 1 endopod segment 1 and 2 (separate, fused)	0.25	<b>0.2</b>
79. Leg 1 endopod segments 2 and 3 (separate, fused)	0.25	<b>0.21</b>
80. Leg 1 endopod segment 2 inner edge setae 2 (present, absent)	0.33	<b>0.17</b>
81. Leg 1 endopod segment 3 outer edge seta (present, absent)	1	<b>1</b>
82. Leg 1 endopod segment 3 inner edge setae 3 (present, absent)	1	<b>1</b>
83. Leg 2 basis outer edge robust setae (present, absent)	0.33	<b>0.11</b>
84. Leg 2 exopod segment 3 inner edge setae 5 (present, absent)	1	<b>1</b>
85. Leg 2 exopod segment 3 outer edge spine 3 (present, absent)	0.17	<b>0.09</b>
86. Leg 2 exopod segment 3 outer edge spine 2 (present, absent)	0.5	<b>0</b>
87. Leg 2 endopod segments 1 and 2 (separate, fused)	0.5	<b>0.44</b>
88. Leg 2 endopod segments 2 and 3 (separate, fused)	1	<b>1</b>
89. Leg 3 basis outer border seta (present, absent)	0.17	<b>0.07</b>
90. Leg 3 exopod segment 3 outer edge spine 3 (present, absent)	0.25	<b>0.13</b>
91. Leg 3 exopod segment 3 outer edge spine 2 (present, absent)	0.5	<b>0</b>
92. Leg 3 exopod segment 3 inner edge seta 5 (present, absent)	1	<b>1</b>
93. Leg 3 endopod segments 1 and 2 (separate, fused)	1	<b>1</b>
94. Leg 3 endopod segment 2 inner border seta 2 (present, absent)	0.33	<b>0.29</b>
95. Leg 3 endopod segment 3 outer edge seta 2 (present, absent)	0.17	<b>0.12</b>
96. Leg 3 endopod segment 3 inner edge seta 3 (present, absent)	0.5	<b>0.46</b>
97. Leg 3 endopod segment 3 inner edge seta 4 (present, absent)	0.14	<b>0.1</b>
98. Leg 4 coxa inner edge seta (present, absent)	0.17	<b>0.03</b>
99. Leg 4 basis outer edge seta (present, absent)	0.14	<b>0.1</b>
100. Leg 4 endopod segments 1 and 2 (separate, fused)	1	<b>1</b>
101. Leg 4 endopod segment 3 outer edge seta 2 (present, absent)	0.17	<b>0.12</b>
102. Leg 4 endopod segment 3 inner edge seta 3 (present, absent)	0.33	<b>0.29</b>
103. Leg 4 endopod segment 3 inner edge seta 2 (present, absent)	1	<b>1</b>
104. Female leg 5 (biramous, uniramous, absent)	0.17	<b>0.09</b>
105. Female leg 5 coxa inner edge seta (present, absent)	0.33	<b>0</b>
106. Female leg 5 endopod segments 2 and 3 (separate, fused)	0.33	<b>0.11</b>
107. Female leg 5 exopod segments 1 and 2 (separate, fused)	0.17	<b>0.11</b>
108. Female leg 5 exopod segment 1 inner border seta (present, absent)	0.33	<b>0.11</b>
109. Female leg 5 exopod segment 3 outer border spine 3 (present, absent)	0.33	<b>0.17</b>
110. Female leg 5 exopod segment 3 inner edge seta 4 (present, absent)	0.25	<b>0.06</b>
111. Female leg 5 exopod segment 2 inner border (seta, non-articulated spine-like process)	1	<b>1</b>
112. Female leg 5 exopod segment 3 insertion on segment 2 (terminal, midway along inner border)	1	<b>1</b>
113. Operculum (completely covers genital atrium, partially covers genital atrium, absent)	0.5	<b>0.38</b>
114. Seminal receptacles and ducts (present, absent)	0.25	<b>0.19</b>
115. Seminal ducts (separate from copulatory canal, seminal duct serves as copulatory duct)	0.5	<b>0.38</b>
116. Nerve axons (not myelinated, myelinated)	1	<b>1</b>

the modified antennule (Char. 16). There is ambiguous evidence concerning the ‘handedness’ of geniculation, the fusion of ancestral segments XXI–XXIII and whether or not there is modification of setae on these segments in the ancestral calanoid.

Calanoid male antennules may be geniculate on the right or left between ancestral segments XX and XXI (Char. 17, Fig. 4), be without geniculation, have supplementary geniculations (e.g. Ohtsuka and Huys 2001), or have other styles of geniculation (Huys and Boxshall 1991). The switch of geniculation from one

Table 3. Data matrix of character state scores. For family exemplars see Table 1

	Characters												
Hypothetical calanoid	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000001	1111111111	1111111111
Boholinidae	1111122111	1111112211	1211112111	1211112111	1111112111	1111112111	1111112111	1111112111	1111112111	1111112111	1111111111	1111121212	1131??
Pseudocyclopididae	1112222221	2112111221	2222211111	1112211111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111211111	1131??
Epacteniscidae	1111111111	1111111221	1211111111	1111211111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111211111	1111??
Ridgewayiidae 1	1112211111	2111111221	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111221211	1212??
Ridgewayiidae 2	1111221111	1111111221	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111221112	1211??
Arietellidae	1112221111	1122212321	2211111111	1111221111	1111112111	1111112111	1111112111	1111112111	1111112111	1111112111	1111111211	11112?2?2??	??311?
Augaptilidae	1112211111	111112321	2211111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	111111222	1111??
Heteronhabitidae	1112211111	111112321	2211111111	1111111111	1111111112	1111111112	1111111112	1111111112	1111111112	1111111112	1111111111	111121221	1112??
Hyperbionychidae	1112211111	111112321	2111111111	1111211212	2222222222	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	1?31??
Lucicutiidae	1112211111	111112321	2211111111	1112211111	1111111112	1111111112	1111111112	1111111112	1111111112	1111111112	1111111111	2111211222	1112??
Metridiidae	1112211111	211112321	2211122112	1112211111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	1?3111
Nullosetigeridae	1112211111	111111221	2211111111	1112211111	1111111112	1111111112	1111111112	1111111112	1111111112	1111111112	1111111111	11112?2?2??	1?31??
Candaciidae	1111221111	111111121	1211111111	1111111111	1111111112	1111111112	1111111112	1111111112	1111111112	1111111112	1111111111	11112?2?2??	??12??
Centropagidae	1111221111	111111121	1211111111	1111111111	1111111112	1111111112	1111111112	1111111112	1111111112	1111111112	1111111111	11112?2?2??	2112??
Diaptomidae	1?2?122111	211111212	1211112121	1211112121	2222111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	1?3?2??
Fosshageniidae 1	1?2?122111	211111212	1211112121	1211112121	2222111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	1?3?2??
Fosshageniidae 2	1111222221	2111211221	1222211111	1122221112	1112122222	2222221211	2222221211	2222221211	2222221211	2222221211	1121121212	211122222?	2112??
Parapontellidae	1111221111	1111111221	1211211121	1112211111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	2112??
Pontellidae	1111221111	1111111221	1211111111	1112211111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	2112??
Pseudodiaptomidae	1111221111	1111111221	1211111111	1112211111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	2112??
Sulcanidae	1111221111	1111111221	1211111111	1112211111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	2112??
Temoridae	1111221111	1111111221	1211111111	1112211111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	2112??
Tortamidae	1112222222	221111221	222222111	1112221222	2222222222	2222222222	2222222222	2222222222	2222222222	2222222222	1121212121	2112?2?2??	2112??
Calanidae	2131221111	211112121	2211111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111211221	111122
Megacalanidae	2131221111	211111121	1211122112	1211122112	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111211221	111122
Paracalanidae	2131221111	111112121	2222221211	1111111111	1111111112	1111111112	1111111112	1111111112	1111111112	1111111112	1111111111	11112?2?2??	??1122
Bathypontidiidae 1	1?2?122111	211111121	1211122111	1112211111	1111111112	1111111112	1111111112	1111111112	1111111112	1111111112	1111111111	11112?2?2??	??1122
Bathypontidiidae 2	1131221111	211111121	1211122111	1111122111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Eucalidae	1121221111	211112121	1211122111	1111122111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Ryocalanidae	1121221111	211112121	1211122111	1111122111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Aetididae	1121221111	211112221	1211122211	1111122211	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Clausocalanidae	1121221111	211112421	2211112221	1111112221	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Diastidae	1121221111	211112221	1211112211	1111112211	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Euchaetidae	1121221111	211112121	1211112211	1111112211	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Mesanoekeratidae	1131221111	211112121	1211112211	1111112211	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Phaenidae	1121221111	211112221	1211112221	1111112221	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Pseudocyclopididae	1122221111	211112221	1211112221	1111112221	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Scolecitrichidae	1121221111	211112221	1211112211	1111112211	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Stephidae	1131221111	211112121	1211112211	1111112211	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Tharybidae	1121221111	211112221	1211112221	1111112221	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122
Spinocalanidae	1131221111	211112221	1211112221	1111112221	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	11112?2?2??	??1122



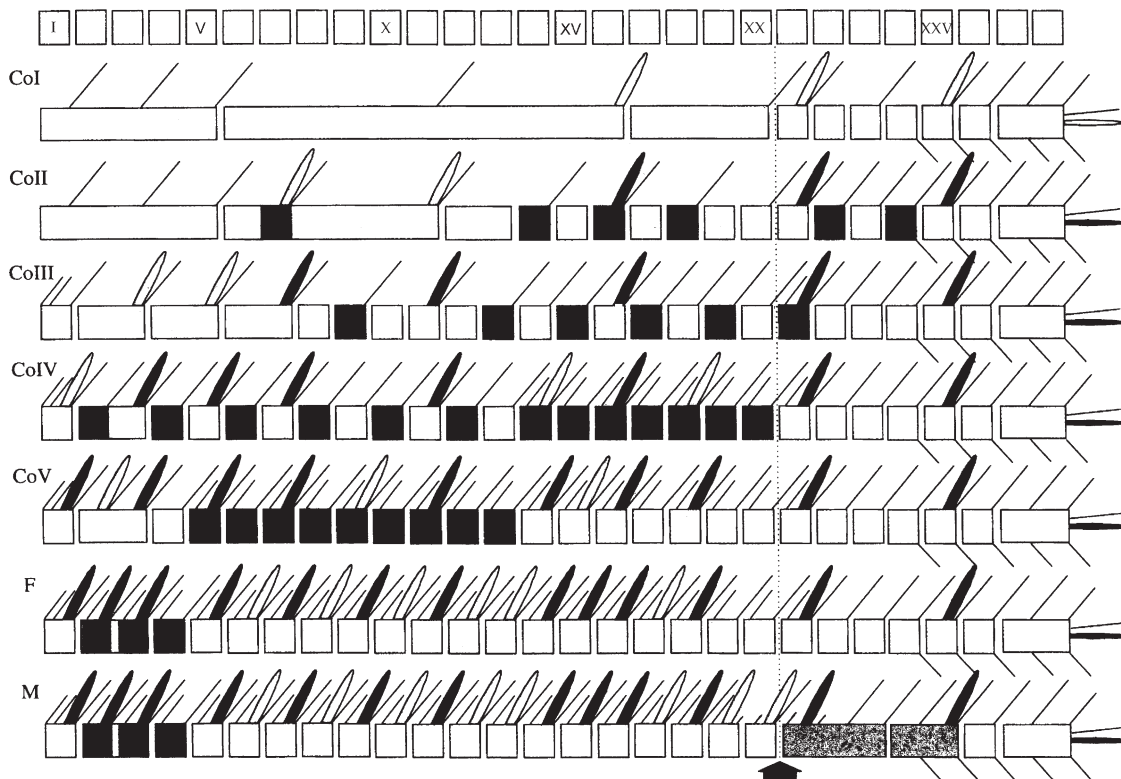
**Fig. 2.** (A) Cephalic dorsal hump on *Paracalanus* c.f. *indicus* (from Bradford-Grieve 1994, with permission); (B) Ancestral caudal ramus in dorsal view indicating setae III and VII (Huys and Boxshall 1991; reproduced with permission from The Ray Society). Triangle indicates selected characters and their state (see Table 2).

side to the other may have come about through a mutation that disrupted the normal right/left asymmetry (e.g. Chang *et al.* 2003). Evidence for the possibility of reversal of geniculation from left to right can be found within some species of *Pleuromamma* (Ferrari 1985). The loss of geniculation is hypothesised to be the failure of the geniculate joint to form between CV and CVI (adult) (e.g. Lawson and Grice 1970; Ferrari and Benforado 1998).

There is contradictory evidence concerning the fusion of segments distal to the geniculation between segments XX and XXI. In the Epacteriscidae (Huys and Boxshall 1991) segments XXI–XXII are separate and segments XXII–XXIII (Char. 18) are fused whereas *Megacalanus longicornis* has none of these segments fused (Bradford-Grieve 1994). The Platycopioida may have segments XXI–XXII fused or separate and XXII–XXIII separate whereas the Misophrioida has segments XXI–XXII fused and segments XXII–XXIII fused or separate. Taken together, the information is ambiguous concerning the likely state of fusion in an ancestral calanoid. Therefore these particular character states (Chars 17–19) are scored ‘unknown’ in the hypothetical ancestor so as not to prejudge the polarity of these states.

Fosshageniidae and Bathypontiidae seem to have a supplementary geniculation between ancestral segments XIV and XV such that the region of articulation is narrowed, possibly allowing a greater range of movement than the normal articulation between antennular segments (Schulz 1986; Ohtsuka and Huys 2001; Fosshagen and Iliffe 2004) (Char. 20). An alternative style of geniculation is found in the Ryocalanidae with the main geniculation being between XXII and XXIII (e.g. Ohtsuka and Huys 2001) – an autapomorphic character state not used in this analysis.

Segments around the XX–XXI geniculation (segments XXIX to XXII) often have elements (modified setae) along the opposed anterior edges that appear to function to assist with gripping



**Fig. 3.** Addition of arthroial membranes during development of the calanoid antennule based on *Epischura massachusettsensis* and *Ridgewayia klausruetzleri* (from Boxshall and Huys 1998; with permission from the Ray Society). CoI–V = coxopods I–V, F = female, M = male, arrow indicates point of geniculation.



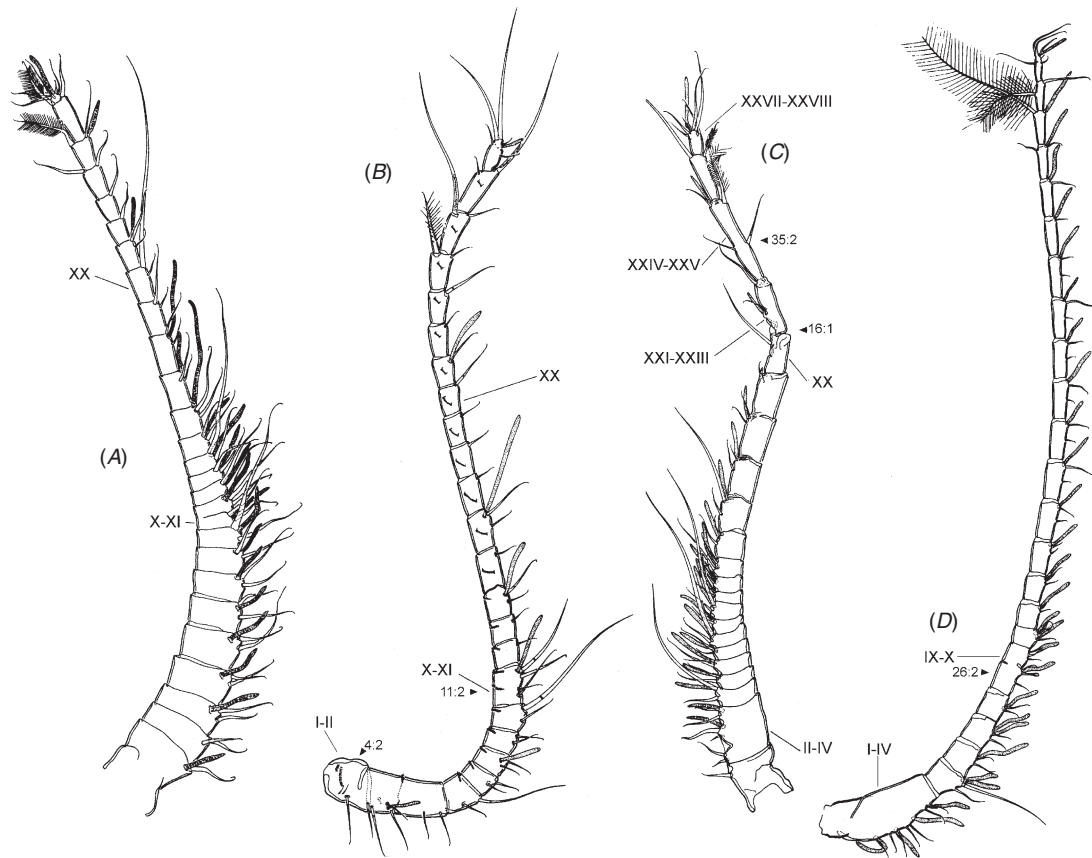


Fig. 4. Some examples of articulation of antennular segments. Female: (A) *Erebonectes nesioticus*; (B) *Stephos lucayensis*. Male: (C) *Enantiosic cavernicola* (right); (D) *Calanus finmarchicus* (right). (From Huys and Boxshall 1991; reproduced with permission from The Ray Society.) Segment numbers in roman numerals. Triangle indicates selected characters and their state (see Table 2).

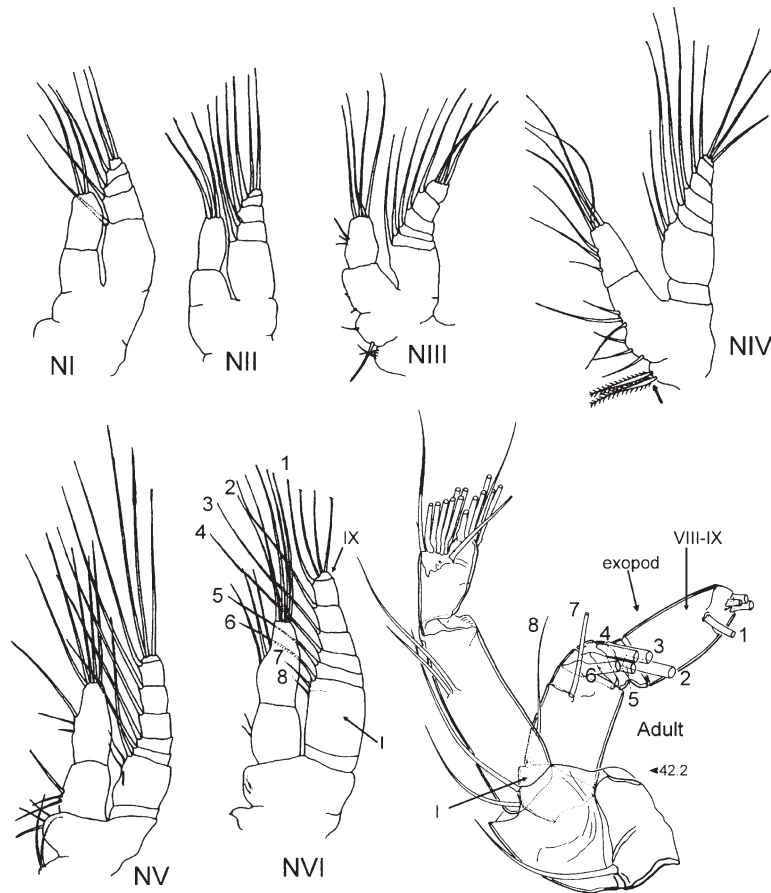
(Char. 19). Any of these segments may have a strong spiniform outgrowth that is either naked or serrated. Ohtsuka and Huys (2001) suggest that the simplest modification of the seta is a sclerotised spiniform process. This process may be articulated to its segment (e.g. *Pseudocyclops*, *Nullosetigera* (Ohtsuka and Huys 2001)), may be fused proximally to its segment (e.g. *Pontella*, *Temora* (Ohtsuka and Huys 2001)), or may be almost fully fused to their segment with only the very distal part free. Nevertheless, these characters vary greatly within one family (e.g. Epacteriscidae (Fosshagen *et al.* 2001)) and the details are deemed not to be phylogenetically useful at the family level. Nevertheless, it is noted that just a few taxa (Fosshageniidae and Bathypontiidae) have no setae (modified or not) on segments XXI–XXIII. The hypothetical ancestor is assumed to have setae on these segments.

**Segmentation.** Compound segments are recorded on the geniculate antennule, whether right or left, since it is assumed that a simple genetic change (see above) was responsible for the handedness of taxa (Chars 21–36, Fig. 4). Thus, the presence of particular compound segments, whether right or left, is considered to be homologous. Boxshall and Huys (1998) noted that compound segments around the geniculation are secondarily fused and, thus, have a different origin from compound segments derived by failure of arthrodial membranes to appear during development.

#### Antenna

During naupliar development of the antennal exopod, setae are added proximally and segmentation begins from the distal to proximal with arthrodial membranes also being added proximally. By naupliar stage VI, the antennal exopod usually has the same complement of setae as the adult although the two terminal segments are usually secondarily fused between nauplius VI and copepodite I (e.g. McKinnon and Arnott 1985; Bradford *et al.* 1988) and bear three terminal setae and one seta from the penultimate segment. The two terminal ancestral segments remain separate in the adult in, for example *Mecynocera* (Paracalanidae), Acartiidae, and *Rhincalanus* (Eucalanidae).

Two groups of families have apparently differing underlying numbers of segments in the antennal exopod. First, in the augaptiloidean families and the Pseudocyclopidae, where adults have 11 exopod setae at most, it appears that the adult has fewer than 10 putative exopod segments because naupliar development does not progress through to a final 12 seta stage, and the proximal seta and segment do not develop (Fig. 5). The evidence for this observation is in the development of the antennal exopod of *Metridia* (Metridiidae) where NVI and the adult have 11 setae (Pinchuk 1997) and *Pseudocyclops umbricatus* NVI where the antennal exopod has 10 setae and copepodite I and the adult has 11 setae with the terminal 3 segments secondarily fused (Costanzo *et al.* 2004). We hypothesise that there is an underlying



**Fig. 5.** Developmental series of an augaptiloidean (*Metridia*) antenna. Naupliar stage I–VI (NI–NVI) (Pinchuk 1997; with permission); adult (*Pleuromamma*) (from Huys and Boxshall 1991; reproduced with permission from The Ray Society). Numbering system for exopod setae used in Table 2 indicated in Arabic numerals. Triangle indicates selected character and its state (see Table 2). Key exopod segment numbers (from proximal to distal) indicated in Roman numerals.

9-segmented state throughout the Augaptiloidea (typified by the Heterorhabdidae (*Disseta*), Metridiidae and Lucicutiidae) and at least the Pseudocyclopidae and probably also the families Epacteriscidae, Ridgewayiidae, and Boholinidae. Only in Pseudocyclopidae do the terminal three rather than terminal two segments secondarily fuse.

In contrast, the remaining families appear to have an underlying 10-segmented condition (Fig. 6). During development an extra segment is added proximally to the exopod. For example, the nauplius VI of *Epischura* (Temoridae) (Humes 1955), *Gladioferens* (Centropagidae) (McKinnon and Arnott 1985), *Paracalanus* (Lawson and Grice 1973), *Neocalanus*, *Calanoides* and *Calanus* (Bradford *et al.* 1988), and the Diaptomidae (Ferrari and Dahms 2007) have 12 setae. The exopod is clearly 10-segmented in adults, with 1 seta each for segments 1–9, and 3 terminal setae with the terminal and penultimate segments secondarily fused (e.g. Centropagidae: Lawson and Grice 1970; Paracalanidae: Lawson and Grice 1973).

In addition, the Misophrioida adults of *Archimisophira discoveryi*, as redescribed by Huys and Boxshall (1991), and *Speleophriopsis balearicus* Jaume and Boxshall, 1996 appear to

have a 9-segmented exopod. The nauplius VI of the harpacticoid *Longipedia* also has an exopod with 11 setae, 3 of these being terminal (Ferrari and Dahms 2007). The CI antennal exopod retains the same number of setae but an additional arthrodistal membrane is added proximally so that each seta represents a segment (note that Ferrari and Dahms (2007) interpret a wrinkle as an additional exopodal segment that does not have a seta). In the adult the terminal two segments are secondarily fused but there is no sign of the proximal segment without a seta (e.g. Huys and Boxshall 1991). Therefore, the ancestral copepod and ancestral calanoid are assumed to have had a 9-segmented antennal exopod with the development of a tenth segment being a derived condition.

Because it is difficult to determine which proximal segments are fused in several families, when setae are absent, we use apparent homologies of the setae as characters. During naupliar development exopod setae develop from distal to proximal (Chars 37–42). The setae are therefore numbered in the order in which they develop, from distal to proximal with the seta relating to the penultimate distal segment being ‘1’ (Figs 5, 6). Setae may be absent for two reasons: various proximal setae fail to

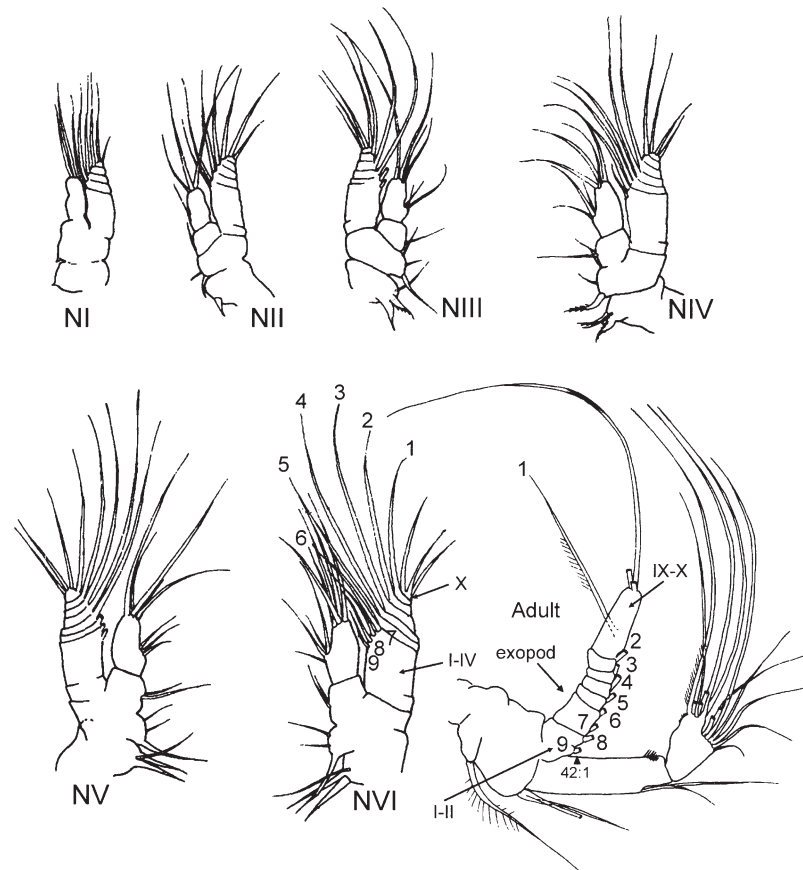


Fig. 6. Developmental series of a megacalanoid (*Neocalanus tonsus*) antenna. Naupliar stages I–VI (NI–NVI) (Bradford *et al.* 1988); adult (*Calanus australis*) (Bradford-Grieve 1994; with permission). Numbering system for exopod setae used in Table 2 indicated in Arabic numerals. Triangle indicates selected character and its state (see Table 2). Key exopod segment numbers (from proximal to distal) indicated in Roman numerals.

develop, or in the case of the proximal-most segment to develop in the Centropagoidea, Megacalanoidea and Clausocalanoidea, the last seta to develop is the 9th seta whereas in the case of the Augaptiloidea and several other families it is the 8th seta which develops last. The presence of seta 9 on the exopod in the hypothetical ancestor is scored 'absent'.

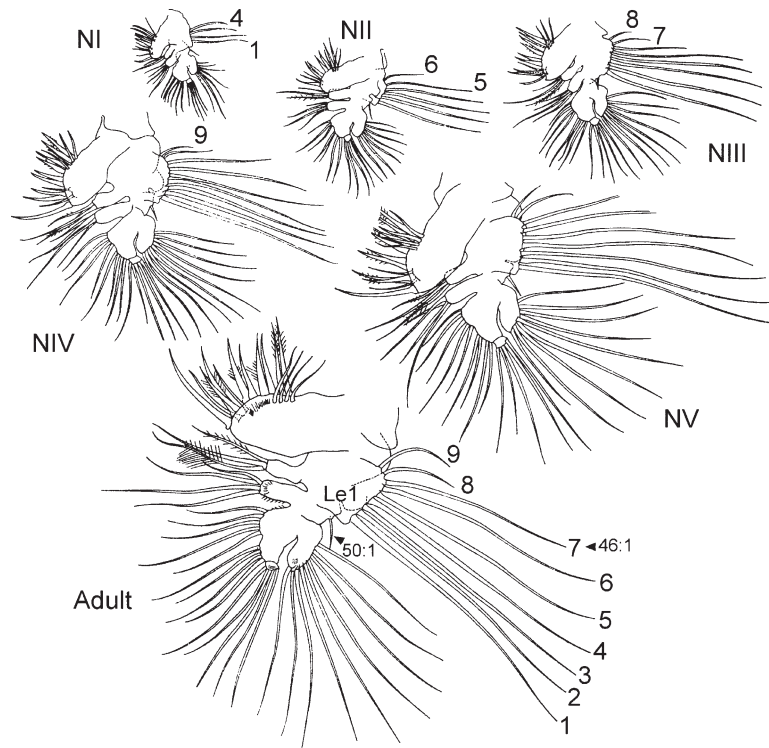
#### Maxillule

The coxal epipodite and the exopod of the maxillule are employed in creating water flow and in swimming, and are least modified by the feeding mode of the copepod. Homologies among setae were investigated using copepodite development. There is no apparent consistent location of setal addition on the exopod; therefore, it was not possible to determine overall homologies. Conversely, the coxal epipodite develops consistently in that setae are always added proximally (with respect to the axis of the whole limb) at each copepodite stage (Lawson and Grice 1970, 1973; Comita and McNett 1976; Bradford *et al.* 1988; Hulsemann 1991b; Ferrari 1995) (Fig. 7). The coxal epipodite usually has 4 setae at CI, a 5th and 6th seta are added proximally at CII, a 7th and 8th seta are added at CIII and a 9th seta is added at CIV. Some taxa have the maximum

number of setae (e.g. Ridgewayiidae, Heterorhabdidae, Metridinidae, Fosshageniidae, Calanidae, Megacalanidae, Clausocalanidae, Stephidae, Spinocalanidae) whereas others have fewer setae (Chars 43–49). In this analysis it is assumed that where there are fewer setae, it is the later, higher numbered setae that have failed to develop. The hypothetical ancestor is assumed to have the maximum number of setae and to have one basal exite seta present (Char. 50), a hypothesis based on the extensive analysis of Calanoida (Huys and Boxshall 1991). Two basal exite setae are present in Platycopioida (Huys and Boxshall 1991) although, unusually, two setae have also been recorded in the calanoid *Speleohvarella gamulini* (Stephidae) (Kršinić 2005).

#### Maxilla

A seta may be present on the outer margin of the coxa of the maxilla, and it has been interpreted as representing a vestige of a coxal epipodite (Huys and Boxshall 1991) (Char. 51, Fig. 8). Among the taxa used in this analysis, such a seta is found only in the Calanidae, Megacalanidae, Paracalanidae, Eucalanidae, Ryocalanidae and some Spinocalanidae. This seta is not found in any of the other copepod orders. Therefore, in this analysis the ancestral calanoid condition is scored 'unknown'.



**Fig. 7.** Developmental series of a centropagoidean (*Centropages typicus*) maxillule. Nauplius I–V (NI–NV) and adult (after Lawson and Grice 1970; with permission). Numbering system for coxal epididite setae used in Table 2 indicated in Arabic numerals. Basal exite indicated with an arrow. Triangle indicates selected characters and their state (see Table 2). Le1 = coxal epididite.

Some setae on the maxilla of some Clausocalanidae are modified into chemosensory structures (Nishida and Ohtsuka 1997) (Fig. 8). Such a modification of setae occurs on the basal endite (Char. 52) and endopod (Char. 53) of the maxilla and is presumed to be absent in the hypothetical ancestor.

#### Maxilliped

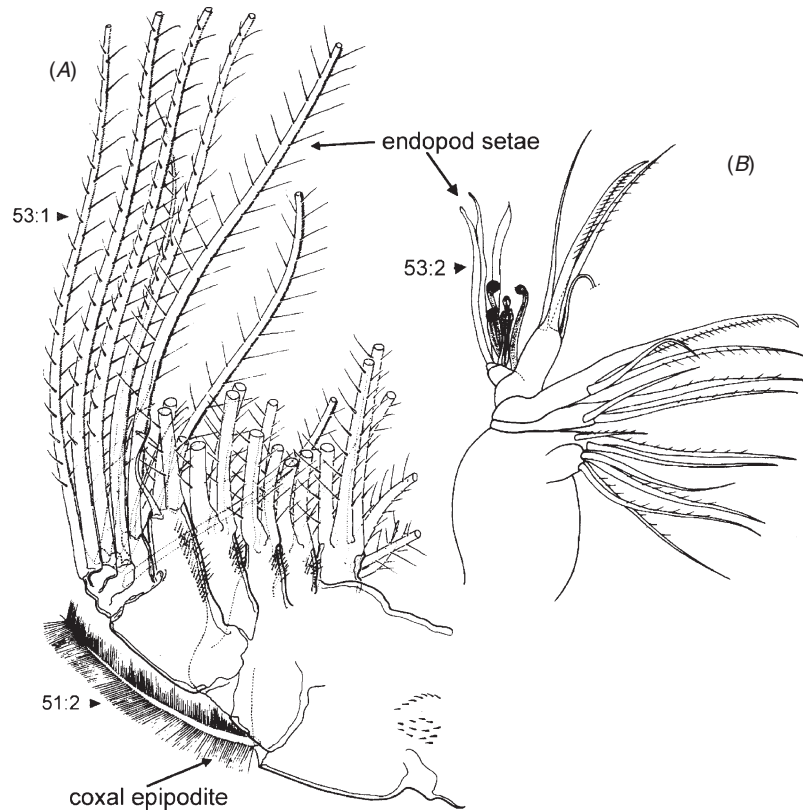
In several families within the Centropagoidea the maxilliped is modified through the atrophy of the endopod and basis, the relative development of the distal part of the syncoxa and its setae, and a generally reduced limb size, as in the Acartiidae, Parapontellidae, Pontellidae, Sulcanidae and Tortanidae (Char. 54, Fig. 9). This aggregate character is included as being present or absent. The state of the maxilliped of *Candacia* is difficult to interpret as it is small relative to the enlarged maxilla and its setation is reduced but the syncoxa is not developed. This character state is scored 'not applicable' since it is autapomorphic and is not homologous with the modified state or the normally-developed state.

Some setae on the maxilliped of some Clausocalanidae are modified into chemosensory structures (Nishida and Ohtsuka 1997). Modified setae are found on syncoxal endites 1–3 of the maxilliped (Char. 55, Fig. 9). It is assumed that the hypothetical ancestor does not have these modified chemosensory setae.

Homologies among the setae on the endopod of the maxilliped (Chars 56–68) can be hypothesised based on the developmental

sequence observed in a few taxa that have been described, and assuming that, where fewer setae occur in the adult, it is the later setae to be added that have failed to develop (Fig. 9). Here, segmental nomenclature of Huys and Boxshall (1991) and the developmental sequence of the segments of Ferrari (1985) is employed. The latest setae to be added are the shorter setae (Lawson and Grice 1970, 1973; Comita and McNett 1976; Ferrari 1985, 1995; Bradford *et al.* 1988; Hulsemann 1991b; Costanzo *et al.* 2004).

The maximum number of setae found on the maxilliped in adults is 2, 4, 4, 3, 3+1, 4 on endopod segments (Ri) 1–6, respectively. Ri1 acquires one seta at CI and a second shorter proximal seta at CII. Ri2 usually acquires one seta at CII, a second proximal seta at CIV, a third proximal seta at CV and fourth proximal shorter seta in the adult. Ri3 usually acquires one seta at CIII, a second proximal seta at CIV, a third proximal seta at CV and a fourth proximal seta in the adult. Ri4 usually acquires one seta at CIV, a second proximal seta at CV and a third proximal seta in the adult. Ri5 usually acquires one inner/anterior seta at CI, one outer/posterior seta at CIII, a second anterior seta located proximally at CIV and a third anterior proximal seta in the adult. Ri6 acquires 3+1 setae at CI. The outer seta on Ri5 of the maxilliped is present in most taxa but is absent in the Augaptiloidea and Bathypontiidae. This seta is also not evident in several Centropagoidea, a state that is associated with the atrophy of the endopod. Thus, this character is scored 'inapplicable' for these taxa.



**Fig. 8.** Maxillae showing position of coxal epipodite and differing states of endopod setae. (A) *Calanus finmarchicus* (after Huys and Boxshall 1991; reproduced with permission from The Ray Society); (B) *Tharybis minor* (after Schulz 1981; with permission). Triangle indicates selected characters and their state (see Table 2).

In some males the outer border setae of segments five and six are directed towards the proximal part of the limb and are extraordinarily developed (Calanidae, Paracalanidae and Eucalanidae) (Char. 69). This type of sexual dimorphism is possibly related to the mode of mate grasping behaviour in these families (see Ohtsuka and Huys 2001). A slightly different type of development of these setae that incorporates the proximally directed state but without extraordinary development has been observed in some Scolecitrichidae (Vyshkvartzeva 2003) but this character state is not used in this analysis.

Male mouthparts may be as well developed as in the female but in several taxa (the Clausocalanoidea and Megacalanoidea) they may be atrophied (e.g. Ohtsuka and Huys 2001) (Char. 70).

#### Swimming legs

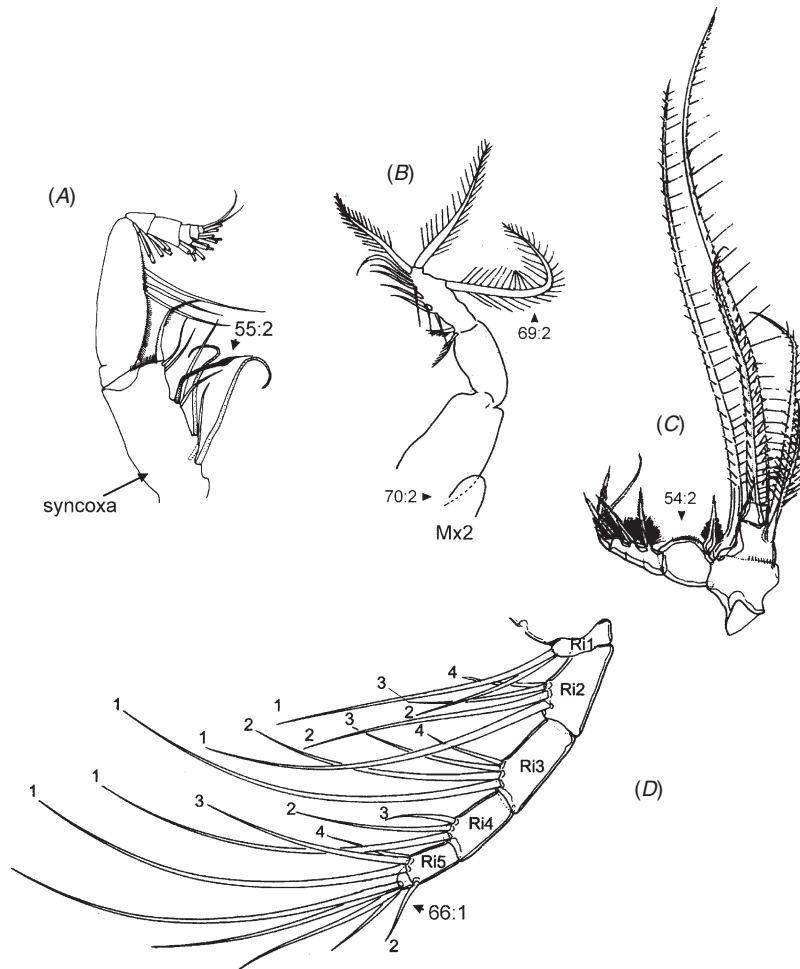
During copepodite development, endopod and exopod articulations provided with arthroal membranes are added from proximal to distal on each ramus (Hulsemann 1991b; Ferrari and Dahms 2007) (Fig. 10). In many families both membranes develop on all legs (e.g. Centropagidae, Calanidae) but in the Clausocalanoidea, Spinocalanidae and Ryocalanidae neither membrane develops in leg 1. In families that have 2-segmented branches this state can be achieved two ways: by failure of the proximal articulation to develop (e.g. Candaciidae, Sulcanidae, Tortanidae) or failure of the

distal articulation to develop (e.g. Clausocalanidae) (Hulsemann 1991b; Ferrari and Dahms 2007) (Fig. 11).

The pattern of segmental expression can usually be deduced from the disposition of the setae. For example, in species with a 2-segmented endopod, if the first segment has 0–1 setae (numbered outer to inner), we can be certain that it is the first segment that is expressed. If the proximal endopod segment has 0–3 or 0–2 setae then we can be sure that segments 1 and 2 are not expressed and that only the arthroal membrane between segments 2 and 3 has developed. The reduction in the number of expressed segments appears to be consistently correlated with the retention of setal configuration in early copepodite stages. For example, the endopod of leg 1 in the CI of *Centropages* and *Neocalanus* (Lawson and Grice 1970; Bradford *et al.* 1988) has 1, 2, 4 setae (outer, terminal, inner). This pattern, minus the outer seta, is found in Clausocalanidae and probably represents the retention of the CI setation (e.g. Hulsemann 1991b).

During copepodite development, when there is more than one seta on an adult segment, setae are always added proximally to the final segment during development or to the segment complex from which the adult state will be formed (Fig. 10). Thus, the setae are numbered sequentially on a segment with the latest seta to develop having the highest number. Character states in adult Calanoida reflect the point at which further development has ceased in particular taxa. On this basis we justify homologising





**Fig. 9.** Maxillipeds showing: (A) the position of sensory seta on syncoxal endite 3 in *Tharybis minor* (after Schulz 1981; with permission); (B) modified male limb in *Paracalanus* (from Bradford-Grieve 1994); (C) modified maxilliped in some Centropagoidea (from Huys and Boxshall 1991; reproduced with permission from The Ray Society); (D) numbering system for setae on endopod segments (from Huys and Boxshall 1991; reproduced with permission from The Ray Society). Triangle indicates selected characters and their state (see Table 2). Ri1–5 = endopod segments 1–5. Mx2 = reduced maxilla.

individual setae/spines across taxa and their states can be coded as present/absent.

In nearly all taxa the outer border spines on the third exopod segment on legs 2–4/5 are robust setae that are articulated with their segments. Exceptions to this are species in the Acartiidae and Sulcanidae (Char. 71) where separate articulated spines are never developed (e.g. Tanimura 1992).

The hypothetical ancestor is assumed to have had a full complement of segments, setae and spines, a hypothesis based on the extensive analysis of Calanoida (Huys and Boxshall 1991).

### Leg 1

The *exopod* of the ancestral calanoid leg 1 is 3-segmented. The arthrodial membrane between segments 1 and 2 appears at CII and that between segments 2 and 3 appears at CV (e.g. Lawson and Grice 1970). The seta on segment 1 inner border usually appears at

CIII but may be absent in Clausocalanoidea (Hulsemann 1991b). On segment 3 a fourth inner proximal seta forms at CV but never appears in a few taxa. The adult configuration of the outer border spines of exopod segment 3 is present at CI and may be either 1 or 2 spines.

The *endopod* of ancestral leg 1 is also 3-segmented. The number of expressed segments and setae appears to be related to whether or not arthrodial membranes develop, whether setal development continues from CI to CIV, on whether there is reduced setation in some taxa at CI, compared with most other taxa, and on the homologies of setae that are assigned at CI (Figs 10, 11).

The expression of segments and presence of specific setae (Fig. 10) are scored where the same state occurs on more than one member of the ingroup (Chars 72–82). In the Paracalanidae it is not possible to tell which of the inner border setae are absent so these characters are scored 'unknown'. Similarly, it is not possible

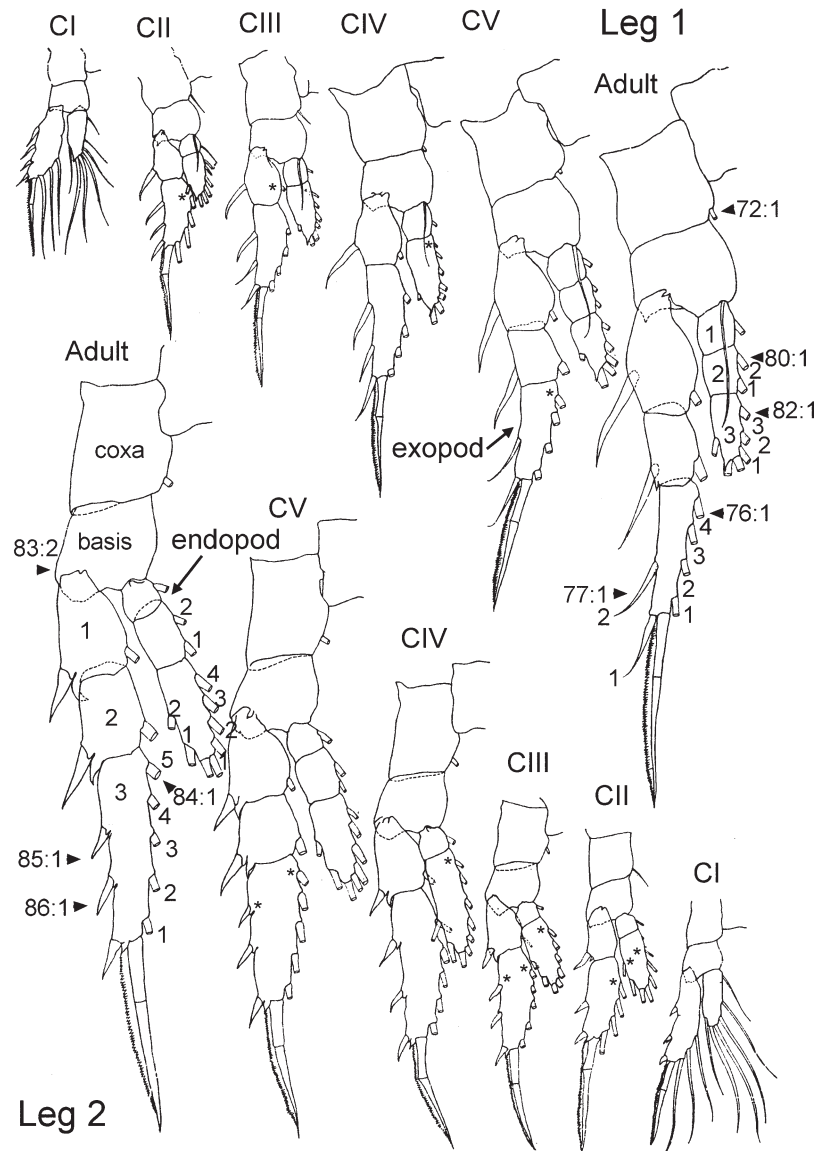


Fig. 10. Development of legs 1 and 2 in *Centropages typicus* (from Lawson and Grice 1970; with permission). \* denotes the added elements. The system of numbering segments and their setae, used in Table 2, is indicated in Arabic numerals. This numbering system is the same for legs 3–5. Triangle indicates selected characters and their state (see Table 2). CI–CV = copepodites I–V.

to tell which of the inner border setae of putative segments 2 and 3 in Fosshageniidae, Bathypontiidae and Eucalanidae are absent so these are also scored 'unknown'.

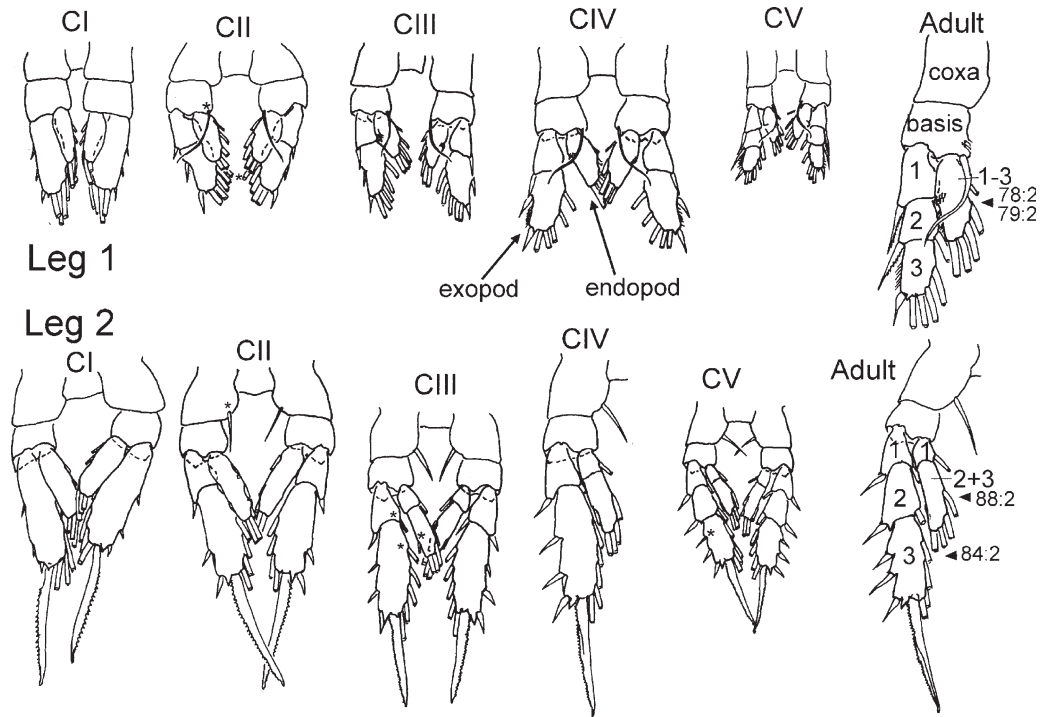
#### Leg 2

The arthrodistal membrane between *exopod* segments 1 and 2 forms at CII and between *exopod* segments 2 and 3 at CV (Lawson and Grice 1970, 1973). On *exopod* segment 3 in most taxa and the hypothetical ancestor a third outer spine is added at CV although in some taxa this addition does not occur. In the hypothetical ancestor, this spine is assumed to be present since the sister orders Platycopioidea and Misophrioida to the Calanoida have this spine (Boxshall and Halsey 2004). Thus the absence of spine 3 in some

of the more plesiomorphic taxa (Epacteriscidae, Boholinidae, Pseudocyclopidae and Ridgewayiidae) is interpreted as being a derived character state.

The Acartiidae has no articulated spines on the outer margin of the *exopod*, resulting from failure of any to appear at CI (Tanimura 1992) (Char. 71). In the Diaptomidae, at CI, only 1 outer spine is present on putative segment 3 and no further spines develop (Reddy and Devi 1985). The adult configuration of inner border setae of *exopod* segment 3 is not complete until CV.

The arthrodistal membrane between *endopod* segments 1 and 2 develops at CII but in the Clausocalanoidea and related taxa this membrane is expressed one stage later (CIII). In Clausocalanoidea the arthrodistal membrane between segments 2 and 3 fails to develop at all (Hulsemann 1991b). In some



**Fig. 11.** Development of legs 1 and 2 in *Drepanopus forcipatus* (from Hulsemann 1991b). \* denotes elements added at that stage. The system of numbering segments and their setae, used in Table 2, is indicated in Arabic numerals. Triangle indicates selected characters and their state (see Table 2). CI–CV = copepodites I–V.

Centropagoidea and a few other taxa a 2-segmented endopod is achieved by the arthrodial membrane between segments 1 and 2 failing to develop.

The expression of segments and presence of specific setae are scored where the same state occurs on more than one member of the ingroup (Chars 83–88) (Figs 10, 11).

#### Leg 3

The arthrodial membrane between *exopod* segments 1 and 2 is usually added at CIII and between segments 2 and 3 at CV (Lawson and Grice 1970, 1973). On *exopod* segment 3 in many taxa a third outer spine is added at CV although in some taxa this addition does not occur. In the Acartiidae, which has no outer articulated spines, this condition results from a failure of any to appear at CII (Tanimura 1992). In the Diaptomidae, at CII only 1 outer spine is present on putative segment 3 and no further spines develop (Reddy and Devi 1985). The adult configuration of the inner border of *exopod* segment 3 is not completed until CV.

The arthrodial membrane develops between *endopod* segments 1 and 2 at CIII, and between segments 2 and 3 at CV (Lawson and Grice 1970, 1973). In some Centropagoidea a 2-segmented endopod is achieved by the arthrodial membrane between segments 1 and 2 failing to develop at CIII. The maximum number of setae that develop on the outer border of *endopod* segment 3 is two, with the second seta appearing at CIII. In Clausocalanoidea and some Centropagoidea this seta fails to appear. The maximum number of setae on the inner border of *endopod* segment 3 is four. The maximum number is found in the Boholinidae, Pseudocyclopidae, Epacteriscidae,

Ridgewayiidae, many Augaptiloidea and Centropagoidea although there are only three or fewer setae in some families. The Clausocalanoidea uniformly have only two setae in this position with no more setae being added during development after CIII (Hulsemann 1991b).

The expression of segments and presence of specific setae are scored where the same state occurs on more than one member of the ingroup (Chars 89–97).

#### Leg 4

The arthrodial membrane between *exopod* segments 1 and 2 is added at CIV and between segments 2 and 3 at CV (Lawson and Grice 1970, 1973). On *exopod* segment 3 in many taxa a third outer spine is added at CV although in some taxa this addition does not occur. In the Acartiidae, which has no outer articulated spines, this condition results from a failure of any to appear at CII (Tanimura 1992). In the Diaptomidae, at CIII only one outer spine is present on putative segment 3 and no further spines develop (Reddy and Devi 1985). The adult configuration of the inner border of *exopod* segment 3 is not complete until CV.

The arthrodial membrane between *endopod* segments 1 and 2 at CIV and between segments 2 and 3 is added at CV (Lawson and Grice 1970, 1973). In some Centropagoidea a 2-segmented endopod is achieved by the arthrodial membrane between segments 1 and 2 failing to develop at CIV. The maximum number of setae that develop on the outer border of *endopod* segment 3 is two with the second seta appearing at CIV. In Clausocalanoidea (Hulsemann 1991b) and some Centropagoidea this seta fails to appear. The maximum number of setae on the

inner border is three and this condition is found in the Boholinidae, Pseudocyclopidae, Epacteriscidae, Ridgewayiidae, many Augaptiloidea and Centropagoidea. There are only two or fewer setae in some families. The Clausocalanoidea uniformly have only two setae with no more setae being added during development after CIV (Hulsemann 1991b).

The expression of segments and presence of specific setae are scored where the same state occurs on more than one member of the ingroup (Chars 98–103).

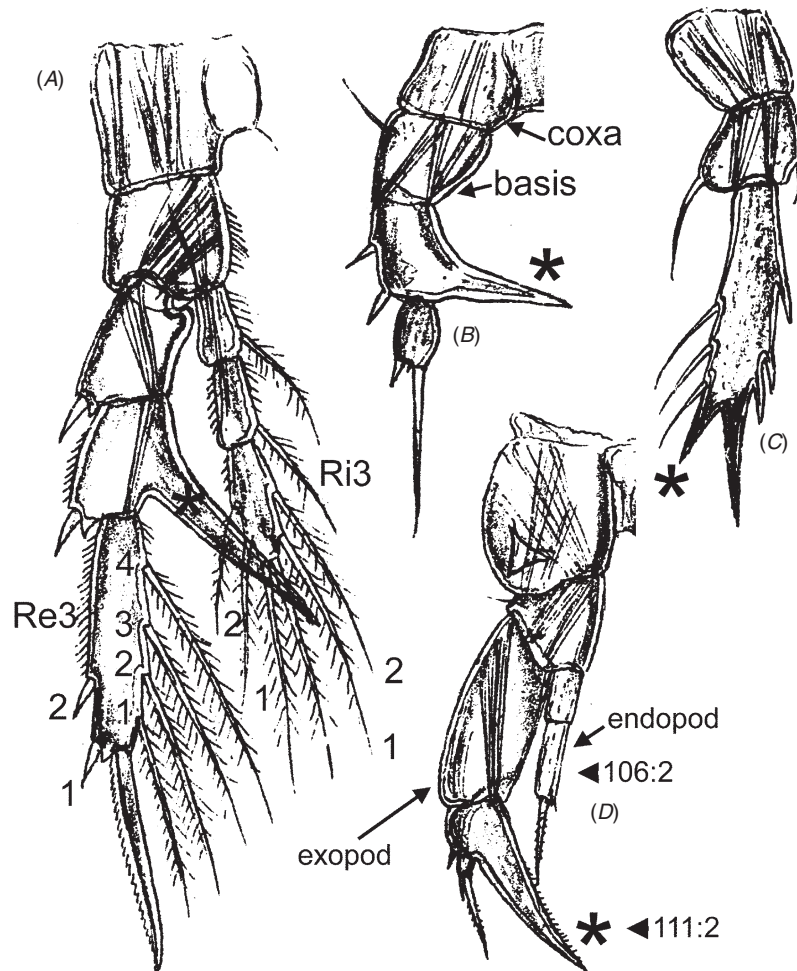
#### Female leg 5

The presence or absence of female leg 5 is recorded as well as whether it is uniramous or biramous (Char. 104). The setae and spine characters are scored in a similar way to the other swimming legs (Chars 105–110) (Fig. 12). A female leg 5 that is similar to the other swimming legs is found in the Boholinidae, Pseudocyclopidae, Epacteriscidae, Ridgewayiidae, Augaptilidae, Heterorhabdidae, Lucicutiidae, Centropagidae,

Calanidae and Megacalanidae. The attenuation of the inner distal corner of exopod segment 2, a synapomorphy for the Centropagoidea, is scored following the analysis of Ferrari and Ueda (2005) (Char. 111). The two ridgewayiid exemplars have a synapomorphic articulation between exopod segments 2 and 3 in leg 5. In this family the articulation occurs at midlength on the inner border of segment 2 (Char. 112). The hypothetical ancestor is assumed to have had the full complement of segments, setae and spines, a hypothesis based on the extensive analysis of Calanoida (Huys and Boxshall 1991), and is without the derived characters found in the Centropagoidea and Ridgewayiidae. For the remaining taxa with very reduced or absent leg 5, characters 105–122 are scored as 'inapplicable'.

#### Female genitalia

Variability in the configuration of the female genitalia has been studied in several families, although not all families and genera are well known. General models of configuration of the genitalia have been partially presented (e.g. Huys and Boxshall



**Fig. 12.** Examples of leg 5 showing the setal numbering system (in part A) and the inner border extension of exopod segment 2 (★) found in the Centropagoidea. (A) *Centropages typicus*; (B) *Eurystemora lacustris*; (C) *Candacia norvegica*; (D) *Diaptomus castor*. After Sars 1902. Ri3 = endopod segment 3, Re3 = exopod segment 3.

1991; Ohtsuka *et al.* 1994; Cuoc *et al.* 1997; Barthélémy *et al.* 1998a; Barthélémy 1999b) and more information, some as yet unpublished, may be found in the thesis of Barthélémy (1999a).

All females have paired oviducts terminating in paired gonopores, closed off by a gonoporal plate (Cuoc *et al.* 1997). The crescent-shaped, closed gonoporal plates and their activating muscles are the most conspicuous parts of the genitalia usually easily observed in all whole females. The position of these two gonopores varies among taxa. They may open directly to the outside environment or be covered completely or partially by an operculum which covers an atrial cavity. The gonopores may be located ventromedially under an operculum (Char. 113) operated by a pair of opercular muscles. A ventromedial genital operculum is present in most families except for Pseudocyclopiidae, Boholinidae, some families of Augaptiloidea and possibly the Bathypontioidea. According to Jaume *et al.* (2008), it is secondarily lost in at least one species of *Stephos*.

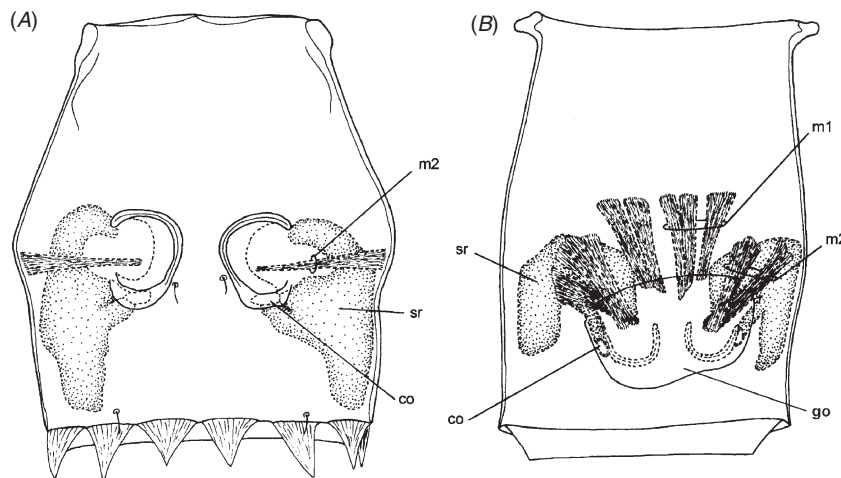
The operculum, if not completely covering the genital atrium, may take various shapes, for example as in the Candaciidae, although in the exemplar used here (*Candacia armata*) the operculum fully covers the genital atrium. In the case of *Sulcanus conflictus* (Barthélémy *et al.* 1998a), the opercular muscles are well developed in spite of the operculum being represented only by an anterior pad. Even though Barthélémy *et al.* (1998a) interpret the operculum as being absent, here, we score it as being incomplete because of the presence of opercular muscles and the imprecise definition of the 'anterior pad'.

When opening directly onto the surface of the urosomite, the gonopores may take a variety of positions both axially and transversely relative to the insertion of the gonoporal plate muscles. Muscles may be inserted dorsally (Acartiidae: Barthélémy 1999b), dorsolaterally (Centropagoidea: Barthélémy *et al.* 1998a; Megacalanoida: Barthélémy 1999a), laterally (*Boholina* (Muna Island, Indonesia) (Fig. 13)), ventrolaterally (*Ridgewayia boxshalli*: Barthélémy *et al.* 1998b), or ventrally (*Pseudocyclops*: Barthélémy 1999a) on the somite. In addition, the position of the gonopores varies

from anterior through to posterior to the insertion of the gonoporal plate muscles. All of these factors appear to govern the direction in which the gonoporal plate hinges relative to the anterior–posterior axis. Our understanding of the factors that combine to govern the position of the hinge is insufficiently developed to allow us to use this character in our analysis.

We do not know if a pair of seminal receptacles (Char. 114) was part of the basic architecture of the female genitalia. Where seminal receptacles occur, they may connect both via a duct that opens to the outside environment through the copulatory pore and via a seminal duct to the oviduct. In some taxa the seminal receptacles are lost along with their ducts and pores. In other taxa there is a variety of configurations of the copulatory pore and seminal duct including the absence of one of these ducts as in the Megacalanoida (Barthélémy 1999a) (Char. 115). The condition in the Clausocalanoida as a whole is not clear. Taxa such as Aetideidae and Clausocalanidae appear to have only one duct serving the seminal receptacles (J. Bradford-Grieve, pers. obs.) whereas Geptner (1968) suggests that there is a seminal duct in the euchaetids he studied. There appear to have been losses of seminal receptacles in most Centropagoidea (Barthélémy 1999b), among some Augaptiloidea (Heterohabdidae and Lucicutiidae) and also in some Calanidae genera (C. Cuoc, Université de Provence, Marseille, pers. comm.).

*The hypothetical calanoid ancestor.* The operculum and its muscles are most likely ancestral, being derived from the 6th legs and their musculature, a condition that is seen in the Cyclopoida (Huys and Boxshall 1991: pp. 323–325) and Misophrioida (Boxshall 1982: p. 173). In the Misophrioida, a sister order to the Calanoida (Ho 1994), the 6th legs are fused in the mid-line (Boxshall 1982) and cover a bilobed genital atrium. This observation, and the occurrence in Epacteriscidae (in *Minnonectes melodactylus* Fig. 13), supports the proposition that the ancestral condition in the Calanoida is to have a single operculum situated ventromedially covering an atrial cavity in which are situated a pair of gonopores. The calanoid ancestor may or may not have had a pair of seminal receptacles that may or



**Fig. 13.** Configuration of the female genital double-somite in: (A) undescribed species of *Boholina* (Muna Island, Indonesia); (B) *Minnonectes melodactylus*. co = copulatory pore; go = genital operculum; m1 = muscles operating the genital operculum; m2 = muscles operating the gonoporal plate; sr = seminal receptacle.



may not have been served by one or a pair of ducts. In view of this uncertainty, the presence of seminal receptacles and the state of their ducts is scored as 'unknown' in the hypothetical ancestor.

In this dataset, although we do not have direct evidence of the character states of all of the specific taxa used here for the main dataset, we derive the likely character states either specifically from the literature on female genitalia or from partial descriptions available in the basic taxonomic literature (Table 1). We have scored character states 'unknown' where there is no specific information.

### Myelination

Davis *et al.* (1999), Lenz *et al.* (2000), Weatherby *et al.* (2000) and Dr Petra Lenz (pers. comm.) showed that the Augaptiloidea (*Pleuromamma xiphias*, *Gaussia princeps*) as well as the Centropagoidea (*Acartia fossae*, *Candacia aethiopica*, *Labidocera pavo*, *L. madurae*, *Epilabidocera longipedata*, *Temora longicornis*, *Centropages* sp.) do not have myelin-like sheaths on the nerve axons. In contrast, species of Megacalanoidea (*Bathycalanus*, *Calanus finmarchicus*, *C. pacificus*, *C. marshallae*, *Undinula vulgaris*, *Neocalanus gracilis*, *Bestiolina similis*), Eucalanoidea (*Eucalanus bungii*), and Clausocalanoidea (*Euchirella* sp., *Pseudocalanus moultoni*, *Euchaeta rimana*, *Paraeuchaeta* sp., *Scolecithrix danae*) have myelinated sheaths surrounding their axons. This revolutionary evolutionary step apparently speeds up the reaction time of the taxa involved. The escape reaction of *Pleuromamma xiphias* which lacks myelination is 6.6 ms in duration compared with that of *Undinula vulgaris* which is 1.5 ms (Lenz *et al.* 2000). The presence or absence of myelination (Char. 116) is used in this dataset, based on the assumption that information on one member of a family is valid for any confamilial exemplars used here. We also assume that the hypothetical ancestor had unmyelinated nerve axons since myelination is not reported to be very common among Crustacea in general (Hartline and Colman 2007). All remaining families are scored 'unknown' until more extensive data are available.

### Analytical methods

A database of 43 taxa including the outgroup and 116 morphological characters (Tables 2 and 3) was initially created using the DELTA software (Dallwitz *et al.* 1993) and output as a nexus file. The majority of characters are binary, although one character has three states and two have four states. Inapplicable characters were coded '?'. Characters were unordered and equally weighted. Since characters are unordered, the scores given for each state (1, 2, 3, etc.) imply nothing about polarity or order.

Phylogenetic analysis under maximum parsimony was conducted in PAUP 4.0b10 (Swofford 2002) (Table 3). Analyses were conducted using the heuristic search (1000 replicates with random input order; branch swapping: tree-bisection-reconnection). Strict consensus and majority-rule consensus trees were computed. Jackknife support on unweighted data was determined in PAUP\* (30% character deletion; 1000 pseudoreplicates). The dataset was then analysed under a single round of successive weighting using the rescaled consistency index (Farris 1969). Character state

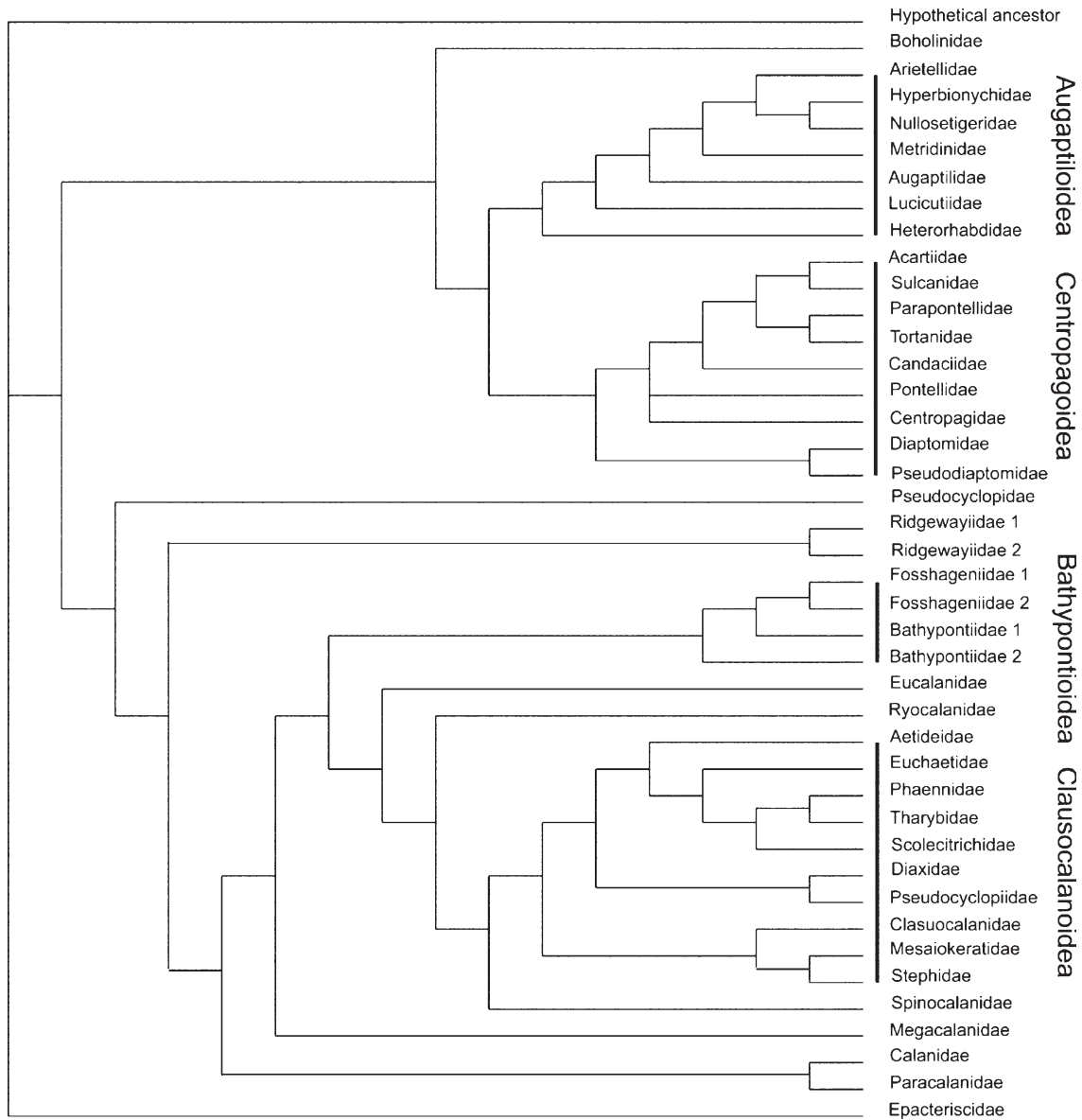
distributions were studied in MacClade 4.0 (Maddison and Maddison 2000).

### Results

The heuristic search retrieved 5 most parsimonious trees of length 426, consistency index 0.28 and retention index 0.67. The strict and 50% majority-rule consensus trees are identical (Fig. 14). In these trees a monophyletic Augaptiloidea, Centropagoidea, and Clausocalanoidea are recovered with moderate to high jackknife support (81, 75 and 93%) (Figs 14, 15). A Bathypontoidea clade (including the Fosshageniidae) was resolved although with 70% jackknife support. A monophyletic Megacalanoidea was not recovered. A clade (8) that contains the Clausocalanoidea, Eucalanidae, Ryocalanidae and Spinocalanidae received strong support (jackknife 98%) and a clade (4) that includes these taxa as well as the Fosshageniidae, Bathypontoidea, Megacalanidae, Calanidae and Paracalanidae received moderate support (jackknife 70%). The relationships among the Boholinidae, Pseudocyclopidae, Ridgewayiidae, and the Augaptiloidea/Centropagoidea clade, evident in the strict and 50% majority-rule consensus trees had less than 50% jackknife support.

As indicated by the rescaled consistency index (*RC*) for each character (Table 2), 62 out of the 116 characters made a small contribution (*RC* < 0.20) to resulting topologies. Among the characters with *RC* > 0.25 are several that are already recognised in the family classification of the Calanoida (e.g. Boxshall and Halsey 2004) and the phylogenies of Andronov (1974) and Park (1986): characters 16, 17, 51, 55, 69, 71, 76, 81, 82, 84, 87, 88, 92–94, 96, 100, 103, 111 and 112 (Table 2). In contrast, it is surprising that some characters, previously thought to be important (the fusion of ancestral segments X and XI on the antennule, atrophy of the male mouthparts, and presence of an outer seta on the leg 1 basis), turn out to be homoplasious in this analysis: characters 11, 27, 70 and 73. Several other characters have not been emphasised in the past as having particular phylogenetic significance. These are: the disposition of seta VII on the caudal rami (Chars 2 and 3), the state of fusion of ancestral segments II and III, IV and V, V and VI on the antennule (Chars 5, 7, 8), the presence of setae on male geniculate antennule ancestral segments XXI–XXIII (Char. 19), the presence of a supplementary geniculation between ancestral segments XIV and XV (Char. 20), the presence or absence of various setae on the endopod segments of the maxilliped (Chars 56, 58, 59, 61, 64, 66), and the presence of an inner border seta on leg 1 coxa (Char. 72).

One round of successive weighting yielded three most parsimonious trees (Fig. 15). The strict and 50% majority-rule consensus of the three trees were identical and differed from the trees derived from unweighted data only in the resolution of a relationship between the Boholinidae and Pseudocyclopidae (Clade 13) and resolution of a clade (21) containing the families Diaixidae, Phaennidae, Tharybidae and Scolecitrichidae. In the weighted analysis the Epacteriscidae is sister to the remaining families in Clade 1 (75% jackknife) (Fig. 15). Clade 1 is united by one unambiguous change: female antennule ancestral segments II and III (Char. 5: fused) (Table 4). Other characters uniting this clade are female antennule ancestral segments III and IV (Char. 6:



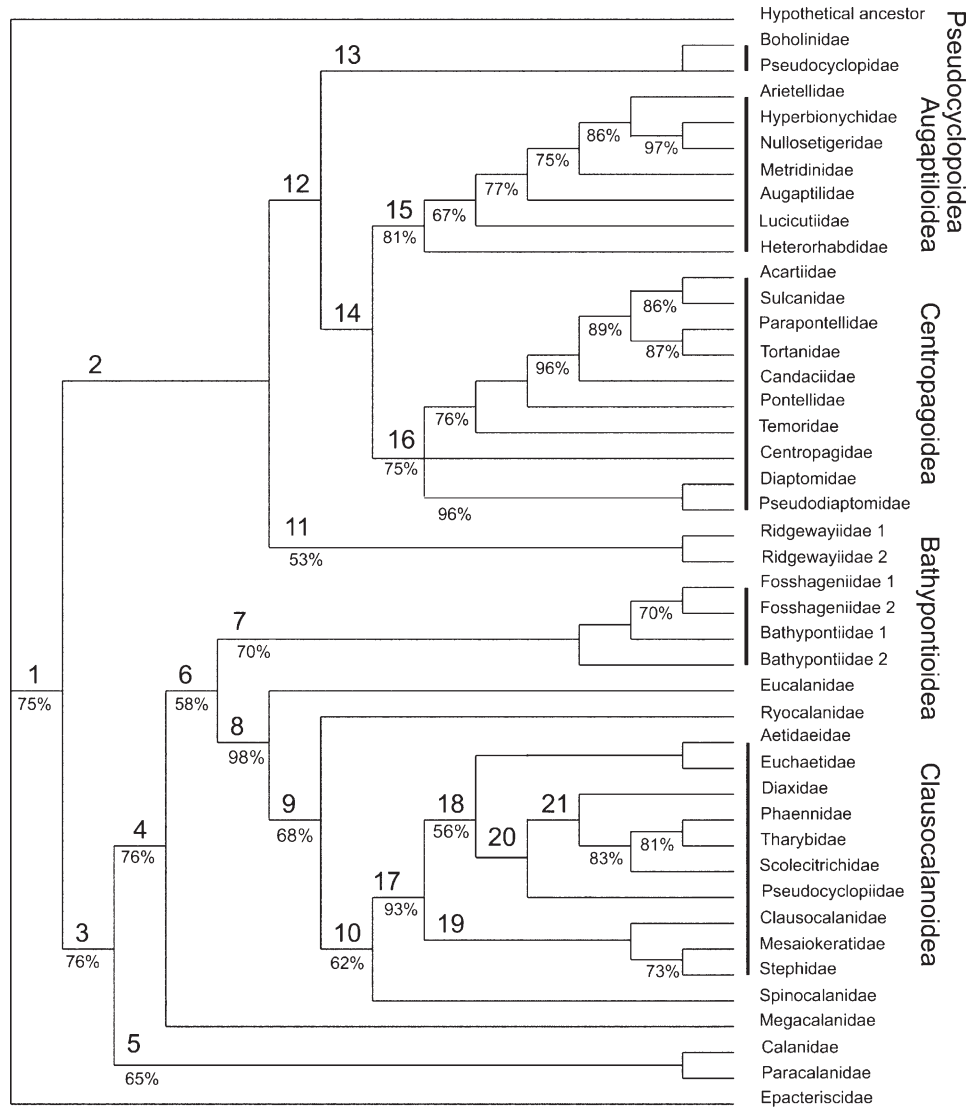
**Fig. 14.** Strict consensus of 66 trees, length 428, consistency index (*CI*) = 0.28, retention index (*RI*) = 0.72. The outgroup is a hypothetical calanoid ancestor. For family exemplars see Table 1.

fused), leg 1 basis outer edge seta (Char. 73: absent) and female leg 5 exopod segment 1 inner border seta (Char. 108: absent). The remaining families are divided into two clades (Clades 2 and 3). Clade 2 is united by only one character, the male geniculate antennule ancestral segments XXI and XXII (Char. 34: fused) and has no jackknife support. Clade 3 (76% jackknife) is united by female caudal ramus seta VII (Char. 3: inner edge), male antennule ancestral segments XXII and XXIII (Char. 18: separate on both sides), female antenna exopod segment proximal seta (9) (Char. 42: present), female maxilla coxal epipodite seta (Char. 51: present) and nerve axons (Char. 116: myelinated).

In Clade 2, the Ridgewayiidae (53% jackknife) (Clade 11) is sister to Clade 12 that contains the Pseudocyclopoidea (Clade 13), the Augaptiloidea (Clade 15) and Centropagoidea (Clade 16)

although the relationships of families Pseudocyclopiidae, Ridgewayiidae and Boholinidae had no jackknife support (Fig. 15). Clade 13 is united by the female genital operculum (Char. 113: absent). Clade 15 (jackknife 81%) is united by three unambiguous changes: male antennules geniculate (Char. 17: left), ancestral segments XXII and XXIII (Char. 18: fused on left) and leg 1 endopod segment 3 inner proximal seta (3) (Char. 82: absent). Other characters uniting this clade are: ancestral segments I and II of female antennules (Char. 4: fused), ancestral segments III and IV of female antennules (Char. 6: separate), ancestral segments I and II of male antennules (Char. 21: fused) and female maxilliped endopod segment 5 outer border seta (2) (Char. 66: absent).

Clade 16 (Centropagoidea) (jackknife 75%) is united by one unambiguous change: female leg 5 exopod segment 2 inner, non-



**Fig. 15.** Strict consensus of three trees after one round of successive weighting. Clade numbers above the line, jackknife support below. Outgroup is a hypothetical calanoid ancestor. For family exemplars see Table 1.

articulated spine-like process (char. 111: present). Other characters uniting this clade are: female antenna exopod proximal seta 9 (Char. 42: present), female maxilliped endopod segment 4 seta 3 (Char. 65: absent), female maxilliped endopod segment 5 seta 4 (Char. 68: absent).

Within Clade 3, Clade 5 (jackknife 65%) is sister to Megacalanidae and Clades 6–21 (Fig. 15). The Megacalanoidea (Andronov 1974) is not recovered as a monophyletic taxon in this analysis (Fig. 15). Clade 7 contains the Bathypontiidae plus Fosshageniidae with 70% jackknife support. Clade 7 is united by one unambiguous change: male geniculate antennule supplementary geniculation between ancestral segments XIV and XV (Char. 20: present). Other characters uniting this clade are: ancestral segments XXII and XXIII of male antennule (Char. 18: fused on right), ancestral segments XXI and XXII of the male geniculate antennule (Char. 34: fused), leg 4 coxa inner

edge seta (Char. 98: absent) and seminal receptacles and ducts (Char. 114: possibly absent). Clade 7 (Bathypontoidea) is sister to Clade 8 which is united by one unambiguous character change: leg 1 endopod segment 3 outer edge seta (Char. 81: absent). Other characters uniting this clade are: leg 1 basis outer seta (Char. 73: present), leg 1 endopod segments 2 and 3 (Char. 79: fused) and female leg 5 exopod segments 1 and 2 (Char. 107: fused).

Clade 17 (Clausocalanoidea) (93% jackknife) is unambiguously united by three characters: legs 2 and 3 exopod segment 3 inner edge seta 5 (Char. 84: absent; Char. 92: absent) and leg 4 endopod segment 3 inner edge seta 2 (Char. 103: absent) (Table 4). Other characters uniting this clade are: leg 1 exopod segment 3 inner edge seta 4 (Char. 76: absent) and legs 3 and 4 endopod segment 3 outer edge seta 2 (Char. 95: absent; Char. 101: absent).

**Table 4. Unambiguous character state changes for one of the three most parsimonious trees after one round of successive weighting (the strict consensus and 50% majority rule consensus trees have the same topology) (Fig. 15)**

Unique character changes at nodes not changing above in the tree are in bold

Clade 1	<b>5: 1→2</b> , 6: 1→2, 73: 1→2, 108: 1→2
Clade 2	34: 1→2
Clade 3	3: 1→3, 18: 2→1, 42: 2→1, 51: 1→2 116: 1→2
Clade 4	27: 1→2, 85: 2→1
Clade 5	16: 1→2, 21: 1→2, 69: 1→2, 70: 1→2, 90: 1→2
Clade 6	73: 2→1, 79: 1→2, <b>81: 1→2</b> , 107: 1→2
Clade 7	18: 1→2, <b>20: 1→2</b> , 34: 1→2, 98: 1→2, 114: 1→2
Clade 8	3: 3→2, 16: 1→2, 72: 1→2, 89: 1→2, 94: 1→2, 96: 1→2, 99: 1→2, 102: 1→2, 104: 1→3
Clade 9	50: 1→2, 75: 1→2, 78: 1→2, <b>88: 1→2</b>
Clade 10	28: 1→2, 51: 2→1, 73: 1→2
Clade 11	22: 2→1, <b>112: 1→2</b>
Clade 12	35: 1→2
Clade 13	113: 1→3
Clade 14	60: 1→2, 85: 2→1, 89: 1→2, 114: 1→2
Clade 15	4: 1→2, 6: 2→1, <b>17: 1→2</b> , <b>18: 2→3</b> , 21: 1→2, 66: 1→2, <b>82: 1→2</b>
Clade 16	42: 2→1, 65: 1→2, 68: 1→2, <b>111: 1→2</b>
Clade 17	76: 1→2, <b>84: 1→2</b> , <b>92: 1→2</b> , 95: 1→2, 101: 1→2, <b>103: 1→2</b>
Clade 18	63: 1→2
Clade 19	104: 3→2
Clade 20	28: 2→1
Clade 21	<b>52: 1→2</b> , <b>53: 1→2</b> , 55: 1→2

## Discussion

The proposed calanoid phylogeny allows us to estimate the state of some uncertain ancestral character states where this was previously unknown, confirms the homoplasy of many characters (e.g. Fig. 16), and reveals possible state distributions for characters that are not well known across all families. Major trends in character state changes can also be traced for the female genitalia, the first leg endopod, as well as the loss of spines, setae and arthroal membranes from mouthparts and swimming legs. Paedomorphosis as a driver of these trends is discussed.

### *Ancestral calanoid*

The outcome of the phylogenetic analysis presented here depends on the polarisation of character states provided by our hypothetical ancestor outgroup. Most character states that can be attributed to a hypothetical ancestral calanoid are well supported by evidence derived from comparative morphology (Huys and Boxshall 1991). A review of up-to-date evidence has changed some notions about ancestral character states. Where changes could be supported by more recent or new evidence (e.g. 9-segment antennal exopod, possession of a ventromedial genital operculum in the female) they were incorporated into the data matrix.

Our results place the Epacteriscidae as the sister taxon to the remaining Calanoida. This topology, along with the distribution of the character states in the Epacteriscidae, the most primitive family (Fosshagen and Iliffe 1985), suggests that the ancestral calanoid probably had segments XXI–XXIII of the male right geniculate antennule with setae although it is equivocal whether segments XXI and XXII were expressed.

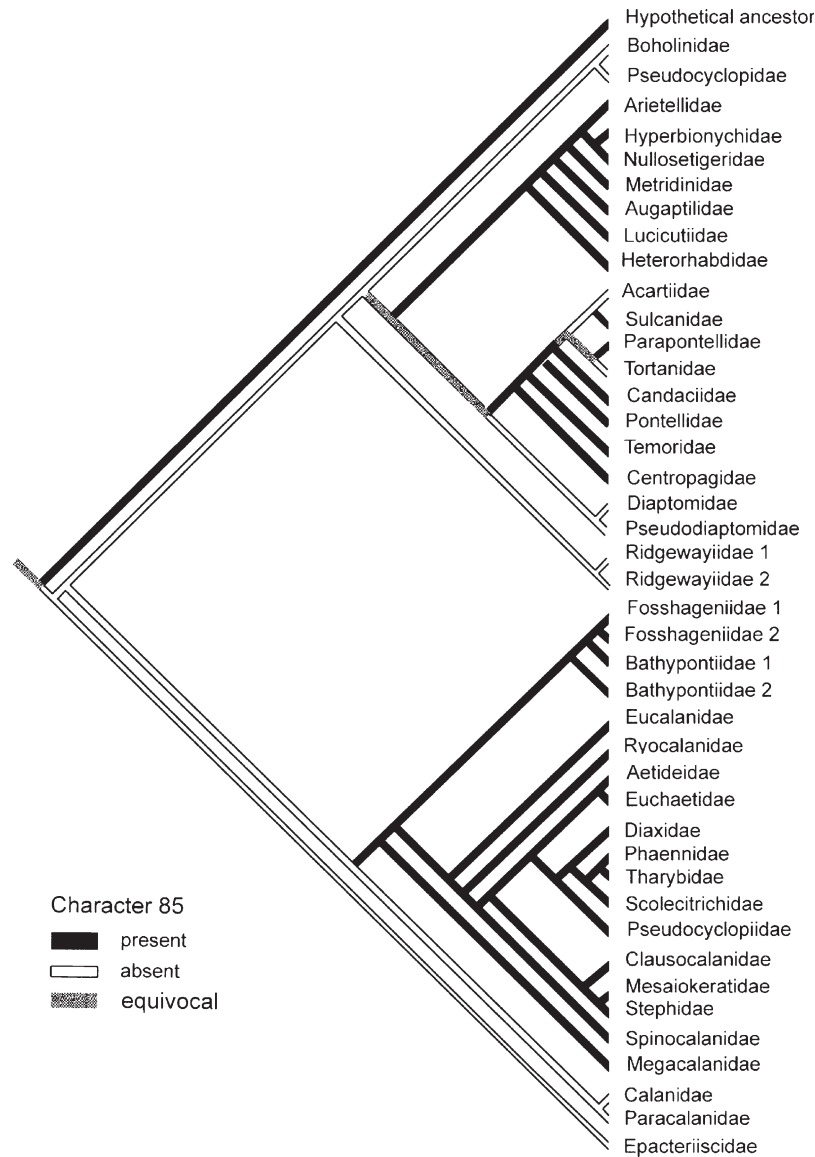
The absence of a coxal epipodite seta on the maxilla in the Platycopioida and Misophrioida suggests that this seta may have

been absent in the ancestral calanoid stem and is a derived character state. Nevertheless, it is possible that the extant representatives of the Platycopioida, basal Calanoida and Misophrioida are derived and do not allow us to accurately trace the evolutionary history of this element.

Based on the overall polarization of character states, the stem calanoid could be inferred to have had seminal receptacles in addition to a single, ventromedial operculum that completely covers a genital atrium. It is equivocal whether the seminal receptacles were served by two ducts (seminal and copulatory) in the ancestor. Nevertheless, we know that the copulatory duct is usually connected to the outside by the copulatory pore (s) located near the gonopores in most taxa with seminal receptacles. In those Arietellidae that have lost a genital operculum, the copulatory pore(s) have often migrated away from the gonopores, interpreted here as a derived condition. A second duct (seminal duct) appears to have connected the seminal receptacles to the oviduct, a condition that is found in *Brattstromia* (Ridgewayiidae), Pseudocyclopidae (Barthélémy 1999a), many Acartiidae (Barthélémy 1999b) as well many Arietellidae (Ohtsuka *et al.* 1994). All these observations require a change in our notion of evolutionary trends (Huys and Boxshall 1991: p. 49) within the Calanoida (Fig. 13) and are discussed in the following section.

### *Characters/states*

Of the nine character states on which Andronov (1974) based his superfamily analysis, only five had a rescaled consistency index of >0.20 in our analysis (Table 5). The remaining four characters states were mostly found consistently in one clade but were also found occasionally in other clades and thus did not contribute strongly to the topology of the trees. For example, character 94 (leg 2 endopod segment 2 inner seta 2: absent) (Fig. 16) was



**Fig. 16.** Distribution of states for character 85: presence of spine 3 (proximal) on the outer border of exopod segment 3 of leg 2. The distribution of character states suggests that the loss of this spine has been reversed several times.

consistently present in Clade 10 but was also present in the Acartiidae and Fosshageniidae. Character 73 (leg 1 basis outer seta: present) was a state inconsistently present in Clade 9 but was also sporadically present elsewhere in Clade 3, and in the Boholinidae and Epacteriiscidae. Also, character 70 (male mouthparts: atrophied) was a state confined to Clade 4 but was not consistently found there. Several other character states relating to the caudal rami, female antennule, male antennule, maxilla, maxilliped, swimming legs and state of the nerve axons (Table 2) contribute strongly to defining the topology of the trees presented here (Fig. 15).

Several mouthpart characters were excluded from this analysis because of the difficulty in assigning homologies based on the few known developmental series. Also, for many families, carnivory

and a benthic habit have apparently produced parallel, but probably not homologous, adaptations of these limbs. It is predicted that these characters might be useful in future analyses of subsets of families once homologies are better understood.

In other cases the lack of information throughout the Calanoida renders characters less useful than they might otherwise have been. For example, the pattern of somite addition to the urosome proceeds by the sequential addition of a somite anterior to the anal somite from CIII to CVI (e.g. Hulsemann 1991a) as in, at least, the Ridgewayiidae, Calanidae, *Rhincalanus* and *Eucalanus* (Eucalanidae) and Clausocalanidae (Geletin 1976; Corkett and McLaren 1979; Bradford *et al.* 1988; Huys and Boxshall 1991; Ferrari 1995).



**Table 5. Evaluation of Andronov's (1974) character set on which superfamilies originally defined**  
 RC = rescaled consistency index; – character not used in the analysis

Characters (from Andronov 1974)	RC	Character # (this dataset)
Fusion of ancestral segments X and XI of the antennule	0.0	12
Presence on the male of a geniculate antennule on one side only	0.46	16
Number of setae on endopod segment 2 of swimming legs 3–4	0.29	94
Number of setae on endopod segment 3 of swimming legs 3–4	1.0	103
Number of inner seta on exopod segment 3 of swimming legs 3–4	1.0	92
Atrophy of mouthparts in the male	0.04	70
Presence of a seta on the outer border of the basis of leg 1	0.04	73
Presence of aesthetes on the geniculate antennule of males	0.0	–
Location of geniculate antennule – on the right or the left	1.0	17

There is usually secondary fusion between urosomites 1 and 2 between CV and CVI in females to form a genital double-somite, except in the Centropagoidea where this fusion occurs one stage earlier (e.g. Ferrari and Ueda 2005). In some taxa, the arthrodistal membrane between some urosomites fails to form, resulting in fewer free urosomites (e.g. in Centropagoidea (apart from the Sulcanidae), Augaptilidae, Metridinidae, Eucalanidae and Paracalanidae). Nevertheless, we are unable to determine homologies among urosomites in adults based on existing information. Within one family the same number of free adult somites is achieved by different developmental paths. In *Rhincalanus*, between CIV and CV, an extra arthrodistal membrane is added in the male and female. Between CV and CVI an extra arthrodistal membrane is added in the male but, in the female, it is likely that the posterior membrane fails to develop and urosomites 1 and 2 fuse so the adult female has 2 free urosomites and an anal somite that is fused to the caudal rami (Geletin 1976). The same superficial segmentation is achieved in the adult female of *Pareucalanus* and *Subeucalanus* by apparently different developmental paths (Geletin 1976). In *Pareucalanus*, secondary fusion of urosomites 1 and 2 occurs at CV and the posterior-most arthrodistal membrane fails to develop at CVI. In *Subeucalanus*, an extra arthrodistal membrane does not form until CIV and already there appears to be a putative genital double-somite judging by its length at CIV. This character could not be used.

Other characters will probably contribute to better resolution of relationships once the distribution of their states throughout families and genera is better known, e.g. myelination of the nerve axons, the morphology of the female genitalia and style of geniculation in the male antennules. These issues are discussed in the following three sections.

#### Myelination

Although the Jackknife support for Clade 6 is weak, support is moderate for clades 3 and 4 suggesting that the Bathypontiidae + Fosshageniidae clade belongs in clade 3 although the exact relationships within this clade are unclear. Knowledge of the state of the nerve axons in these two families could be a significant piece of information to test the position of the Bathypontiidae in Clade 3. The distribution of myelination in families where it is known, and the present topology of the tree (Fig. 15), suggest that myelination might be present in these families.

#### Female genitalia

Contrary to the interpretation of Huys and Boxshall (1991), it is doubtful whether any existing calanoid family has an arrangement of the female genitalia in which each gonopore is separately covered by an operculum. In the 'basal' calanoid family Epacteriscidae (*Minionectes melodactylus*) and the Ridgewayiidae (Clade 11) (Barthélémy *et al.* 1998b, Barthélémy 1999a) there is a single ventromedial, full operculum with paired opercular muscles, whereas in the Pseudocyclopidae and Boholinidae (Clade 13) there is no operculum or opercular muscles, and the gonopores, closed by their gonoporal plate, open directly onto the surface of the genital double somite (Fig. 13) (Ohtsuka *et al.* 1999). Thus, the condition found in the Pseudocyclopidae and Boholinidae appears to be derived.

Female Calanoida have one of the following combinations of character states: an operculum and seminal receptacles; no operculum and seminal receptacles; or an operculum without seminal receptacles. Only in *Acartiella* (Acartiidae) and *Sulcanus* (Sulcanidae) are there no seminal receptacles and largely uncovered gonopores (Barthélémy *et al.* 1998a; Barthélémy 1999b). Thus, we conclude that the Calanoida must have at least a genital operculum and/or seminal receptacles, to ensure that effective fertilisation occurs. It appears that both the operculum and seminal receptacles have been lost independently in various lineages.

The operculum has been lost or reduced in terminal Augaptiloidea (Clade 15), Pseudocyclopidae and Boholinidae (Clade 13) (Fig. 13), in the Acartiidae (Ohtsuka *et al.* 1994; Barthélémy *et al.* 1998a), and in some Clausocalanoidea (Jaume *et al.* 2008). Seminal receptacles have been lost, along with their ducts and pores (Barthélémy 1999a), in several lineages: in Ridgewayiidae (Clade 11) (Barthélémy *et al.* 1998b), in most Centropagoidea (Clade 16) (Barthélémy 1999a), in basal Augaptiloidea in Clade 15 (Augaptilidae, Heterorhabdidae and Lucicutiidae) and some Calanidae genera (C. Cuoc, Université de Provence, Marseille, pers. comm.).

Conversely, seminal receptacles were apparently regained independently in the terminal Augaptiloidean families (Clade 15) (Fig. 15), in *Acartia* in the Acartiidae, and possibly in Clade 5 and the Megacalanidae. The presence of seminal receptacles with only one duct has been recorded in the Megacalanidae, Calanidae and Paracalanidae (Clade 5) (Barthélémy 1999a). The number of ducts leaving the seminal receptacles in the Fosshageniidae,

Bathypontiidae, Ryocalanidae, Spinocalanidae, Eucalanidae and Clausocalanoidea is largely unknown although Geptner (1968) records that there are two ducts in the euchaetids he studied. The possibility that the Euchaetidae have two ducts leaving the seminal receptacle throws into doubt the assumption that the Clausocalanoidea configuration is like that of the 'Megacalanoidea'. Further evidence for the independent formation of seminal receptacles in Clade 5 and Megacalanidae may be the addition of musculature relating to the genital atrium in centropagoidean genera *Candacia*, *Boeckella*, *Osphranticum*, *Anomalocera*, *Labidocera*, *Pontella*, *Eurytemora*, *Heterocope* and *Tortanus* (Barthélémy *et al.* 1998a; Barthélémy 1999a). We could hypothesise an ancestral condition in Clade 3 in common with that in Clade 14. Then, if we assume that the third set of atrial muscles (in addition to the opercular and gonoporal muscles) is homologous with the muscles that operate on the seminal receptacle in *Bathycalanus* and *Megacalanus* (Barthélémy 1999a), it is only a short step from a genital atrium with two large pockets operated by atrial muscles to the restriction of these two pockets as in *Bathycalanus* and *Megacalanus*.

The form of the regained seminal receptacles in *Acartia* differs from the type found in the Augaptiloidea and in Clade 5 and the Megacalanidae. Here the acartiid condition has the copulatory pore located just outside the opening of the gonopore but the fertilisation pore opens into the oviduct some distance from the gonopore (Barthélémy 1999b). In the Augaptiloidea it is the seminal pore that is usually just outside the gonopores whereas the copulatory pore is usually further away (Ohtsuka *et al.* 1994; Cuoc *et al.* 1997).

Based on the proposed phylogeny (Fig. 15), which is not well supported at its base, we propose a transformational series of the female genital double-somite in the Calanoida (Fig. 17). Key transformations from the hypothetical ancestral condition (A), reflected in the Epacteriscidae and *Brattstromia* (Ridgewayiidae) might be to diverge in two ways: B, by losing the medial genital operculum, as in the Pseudocyclopidae and Boholinidae; and C, losing the seminal receptacles and their ducts and gaining atrial musculature as in most Ridgewayiidae, Centropagoidea (except *Acartia*), basal Augaptiloidea and possibly the Bathypontiidae. A second transformation series, based on type C, includes: D, the loss of the genital operculum and regaining of seminal receptacles with two ducts in the 'higher' Augaptiloidea; E, the loss of a genital operculum and regaining of seminal receptacles with two ducts in the crown Centropagoidea genus *Acartia*; and F, retention of the genital operculum and reforming of seminal receptacles with a single duct each as in Megacalanidae, Calanidae, Paracalanidae, Eucalanidae, and possibly the Clausocalanoidea but not Euchaetidae. Confirmation of this series requires a better resolution of the relationships between clades 2 and 3 (Fig. 15).

#### *Geniculation in male antennules*

In the past, geniculation of the male antennule has usually been considered to be homologous through the Calanoida, only changing the side on which the geniculation occurs or this geniculation being lost – presumably because the state of the antennules at copepodite stage V is retained into adulthood (e.g. Sars 1901, 1902, 1903).

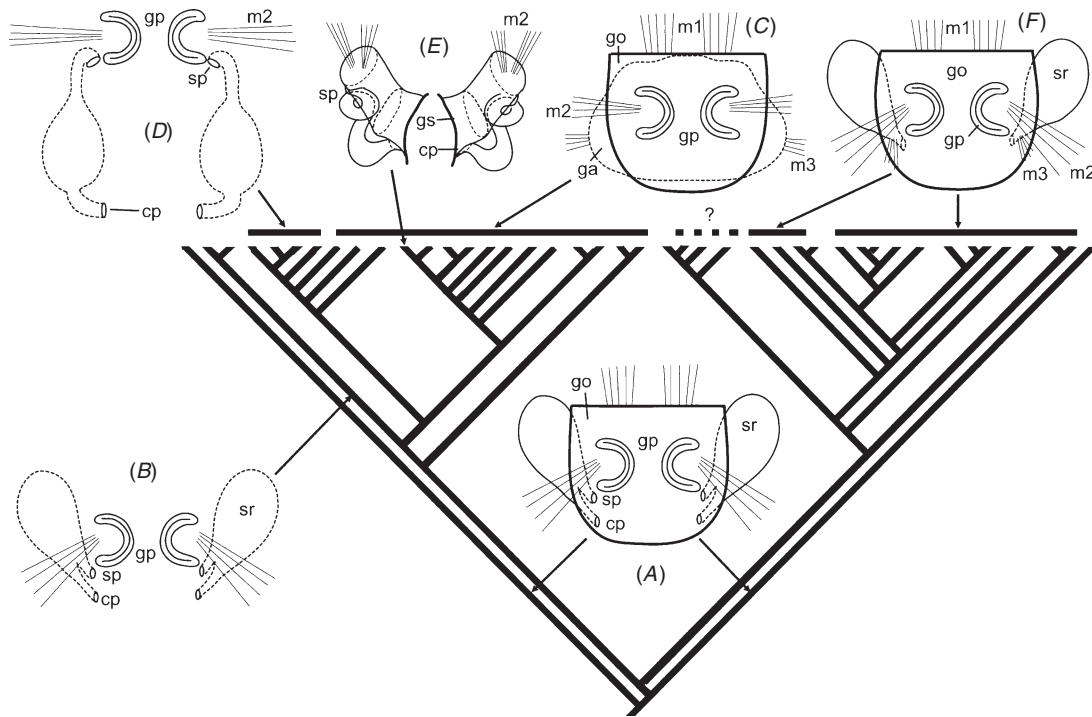
Geniculation between ancestral segments XX and XXI is a consistent feature of the Epacteriscidae, Boholinidae, Pseudocyclopidae, Ridgewayiidae, Megacalanidae, Augaptiloidea, Centropagoidea and Bathypontiidae. Additionally, the Bathypontiidae and Foshageniidae have a supplementary geniculation between ancestral segments XIV and XV and that the Ryocalanidae have a style of geniculation that appears to be unrelated to that which commonly occurs through out the Calanoida (Ohtsuka and Huys 2001; Fosshagen and Iliffe 2004). More recently, a clausocalanoidean species, *Sensiava longiseta* has been shown to have the right antennule different from the left although it is not clear if there is a geniculation at any particular location (Markhaseva and Schulz 2006). Nevertheless, segment XIX on the right bears a large spinous outgrowth and segments XXII and XXIII are fused with a hooked process at mid-length. Thus, the asymmetrical fusion of segments XXII and XXIII, found in many Clausocalanoidea, may be a remnant of this style of asymmetry and not related to the fusion of these segments in other Calanoida. With the discovery of more taxa in the Clausocalanoidea, interpretation of male antennule homologies in Clade 9 (Fig. 15) will probably be refined.

#### *Trends*

Several character states apparently represent the retention of larval characteristics in the adult (paedomorphosis) assuming the polarity provided by the outgroup is correct. Paedomorphosis appears to be widespread and a dominant mode of evolutionary change in the Calanoida. This phenomenon is probably one of the main drivers of the process several workers have referred to as 'oligomerization' – the loss or fusion of serial structures in Copepoda, for example, segments or setae/spines on limbs (e.g. Dogiel 1954; Huys and Boxshall 1991; Monchenko and von Vaupel Klein 1999; Adamowicz *et al.* 2007). This process has been regarded as evolutionarily irreversible (Monchenko and von Vaupel Klein 1999), but Adamowicz *et al.* (2007) note that although the dominant mode of change was loss and reduction, structures may be gained readily as well as lost in the Centropagidae. Our data support both these notions.

The proximal outer border spine on exopod segment 3 of leg 2 (Char. 85) is apparently lost in the Boholinidae, Pseudodiaptomidae, Diaptomidae, Pseudocyclopidae, Ridgewayiidae, Calanidae, Paracalanidae and Epacteriscidae (Fig. 16). This 'loss' has probably occurred through a failure of spine 3 to develop at copepodite stage V on exopod segment 3 of leg 2 (Lawson and Grice 1970). The ancestral state is deduced to have had this spine present (as in the sister Orders Platycopioida and Misophrioida) as well as Clades 4 and 15 and many taxa in Clade 16. This pattern of distribution suggests this character state may be reversible. Thus, the failure of development to proceed through all steps might indicate a mechanism that can be turned on or off during evolution.

Nevertheless, certain losses appear to be irreversible. The failure of an arthrodial membrane to form, separating segments 1 and 2 of the endopod of leg 1, links the Clausocalanoidea together with the Ryocalanidae and Spinocalanidae in Clade 9 (Fig. 15) and the failure of the arthrodial membrane to form between endopod segments 2 and 3 of leg 1 links the Eucalanidae with

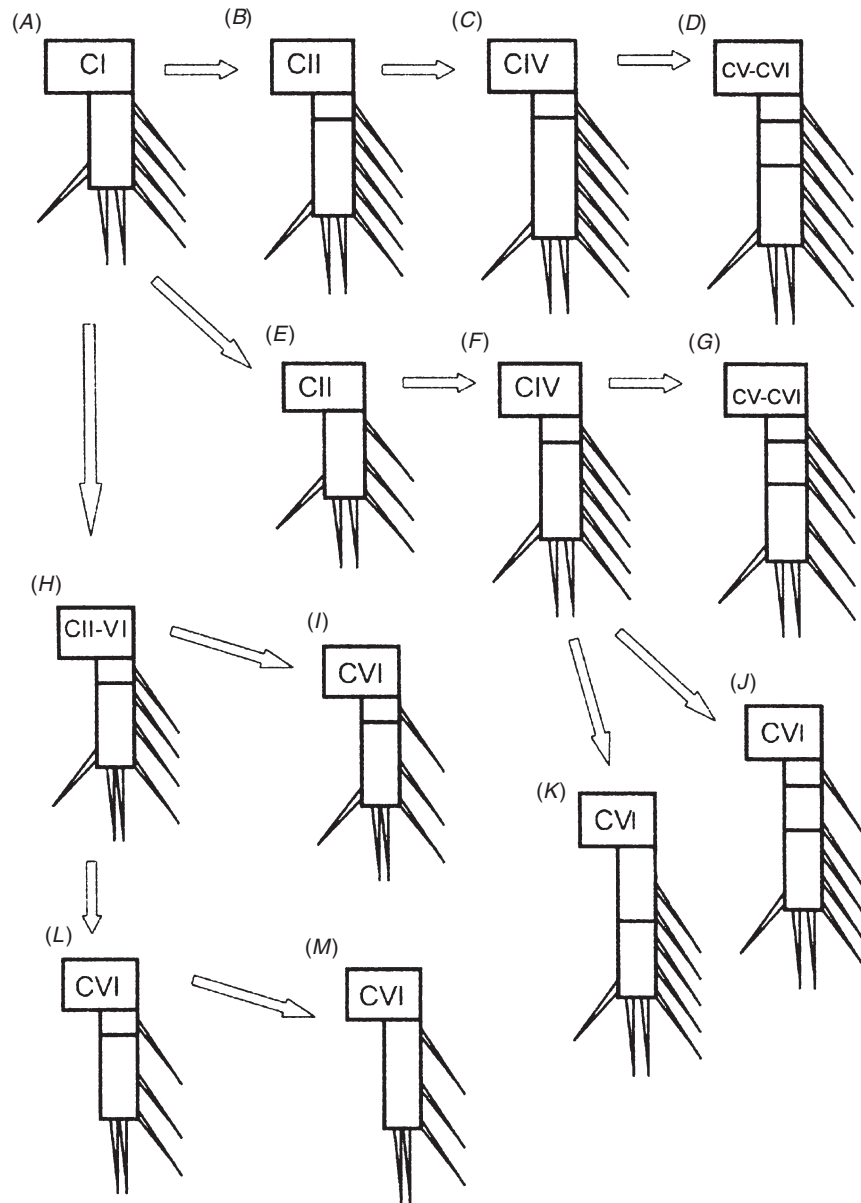


**Fig. 17.** Diagrammatic representation of new hypothesis of evolutionary trends in female genitalia (oviducts and shell ducts omitted). (A) hypothetical ancestor, Ridgewayiidae (*Brattstromia*) and Epacteriscidae; (B) Pseudocyclopidae and Boholinidae; (C) Ridgewayiidae, Centropagoidea (except *Acartia*), Augaptilidae, Lucicutiidae, Heterorhabdidae, and Bathypontioidea?; (D) Augaptiloidea (Arietellidae, Hyperbionychidae, Nullosetigeridae, Metridinidae); (E) Acartiidae (*Acartia*) – not in analysis – no operculum, only integumental fold with genital slit opening to outside; (F) Megacalanidae, Calanidae, Paracalanidae, Eucalanidae, Clausocalanoidea? (not Euchaetidae?). Large arrows indicate directions of transformations, small arrows indicate postulated places on tree (Fig. 16) where each type of configuration probably occurred (information from Cuoc *et al.* 1997; Barthélémy *et al.* 1998b; Barthélémy 1999a, 1999b and original data). cp = copulatory pore; ga = genital atrium; go = genital operculum; gp = gonopore; gs = genital slit; m1 = opercular muscles; m2 = gonoporal plate muscles; m3 = genital atrial muscles; sp = seminal pore; sr = seminal receptacle.

the above-mentioned clade. Therefore, the state that is usually found in copepodite 1 is retained in adults of the Clausocalanoidea and is a form of paedomorphosis. Likewise, a second seta fails to develop on endopod segment 2 of leg 3 and inner seta 5 (proximal) on legs 2 and 3 at CIV and CV, respectively, in the Clausocalanoidea (c.f. Lawson and Grice 1970; Heron and Bowman 1971; Bradford *et al.* 1988).

Aggregate character states of the endopod of the adult leg 1 appear to represent irreversible, paedomorphic evolutionary series (Fig. 18). Most types of adult leg 1 endopod can be derived from the basic developmental series (Fig. 10). The *first type* is where a full suite of setae and arthrodistal membranes develops as in: Pseudocyclopidae, Epacteriscidae, Ridgewayiidae, Candaciidae, Centropagidae, Parapontellidae, Pontellidae, Tortanidae, Calanidae and Megacalanidae (e.g. Lawson and Grice 1970) (Fig. 18A–D). The Boholinidae (Fig. 18B) may be considered to have the same type of development except it has stopped at CII. A *second type* of development may be derived from the first and is found in the Augaptiloidea (Clade 15, Fig. 18E–G). Here, the endopod at CII is the same as at CI in the first type (e.g. Metridinidae: Ferrari 1985; Ferrari and Benforado 1998). The arthrodistal membranes delineating segments 1 and 2 form such that segments 1 and 2

have 1 and 2 setae, respectively. This results in the inner border of segment 3 having only 2 setae. It is assumed that the proximal seta of putative segment 3 has not formed. A *third type* found in the crown Centropagoidea may be derived from the first and is found in the Acartiidae, Diaptomidae and Temoridae (Fig. 18H) which have the setation of the endopod similar to that of CI of the first type but with an arthrodistal membrane delimiting segment 1. The state of the endopod of the Pseudodiaptomidae and Sulcanidae appears to be related. In these two families, the number of setae is similar to CII in the first type but arthrodistal membranes delimit both segments 1 and 2 in Pseudodiaptomidae and only the membrane separating segments 2 and 3 is present in Sulcanidae (Fig. 18K, J). Paracalanid setation at CI through CV (Lawson and Grice 1973) is similar to CI of the first type except there is one less inner border seta (Fig. 18I). An arthrodistal membrane delimiting segment 1 is added in the adult. A *fourth type* may be derived from a CI endopod of the first type but does not have an outer seta and the inner border has only 3 setae. Taxa that retain this configuration on a 1-segmented endopod in the adult are in Clade 9: Clausocalanoidea, Ryocalanidae, Spinocalanidae (e.g. Hulsemann 1991b) (Fig. 18M). This type of configuration is similar in the Fosshageniidae, Bathypontioidea and Eucalanidae in Clade 6 except that the arthrodistal membrane



**Fig. 18.** Evolutionary series of leg 1 endopod segmental and setal character states (CI-CVI) within ingroup taxa. (A-D) Pseudocyclopidae, Epacteriscidae, Ridgewayiidae, Candaciidae, Pontellidae, Centropagidae, Parapontellidae, Tortanidae, Calanidae, and Megacalanidae CI-CVI; (B) Boholinidae CVI; (E-F) Augaptiloidea CII-CVI; (H) Acartiidae, Diaptomidae, and Temoridae CII-CVI; (I) Paracalanidae CVI; (J) Pseudodiaptomidae CVI; (K) Sulcanidae CVI; (L) Fosshageniidae, Bathypontiidae, and Eucalanidae CVI; (M) Clausocalanoidea, Ryocalanidae, and Spinocalanidae CVI.

between segments 1 and 2 has developed (Fig. 18L). Thus all types of adult endopod configuration can be derived from the basic developmental sequence with development apparently halting at a state exhibited by an earlier developmental stage (i.e. a kind of paedomorphosis), or by the loss of some CI setae.

Likewise, other reduction trends are evident. These are the loss of setae on the antennal exopod, maxillular coxal epipodite and maxilliped endopod in crown taxa in clades 7, 13, 15, 16 and 17

(Fig. 15). There is also a tendency for the female leg 5 to migrate from a fully developed, biramous limb to a reduced, biramous form, to uniramous to absent. None of these trends appears to have been reversible, in accord with the notion that the dominant (but not exclusive) mode of evolutionary transformation in copepods is oligomerization (Huys and Boxshall 1991). In most cases such losses probably reflect a paedomorphic origin and, thus paedomorphosis appears to have occurred independently in several characters, lineages and families.



### Phylogeny

The present cladistic analysis recovers several monophyletic lineages within the Calanoida that largely conform to the superfamilies recognised in intuitive classifications (Andronov 1974; Park 1986; Boxshall and Halsey 2004) (Fig. 1). Nevertheless, intuitive methods are not capable of producing hypotheses of phylogenetic relationships that stand up to closer inspection. Here, we have proposed a more detailed calanoid phylogenetic hypothesis than was previously available but acknowledge that more data (including genetic) are required to robustly resolve 'basal' relationships among the families and superfamilies.

In contrast to Andronov (1974) and Park (1986) we hypothesise that the calanoid families other than the Epacteriscidae divide into two major lineages (Clades 2 and 3) (Fig. 15). The possibility (Andronov 2007) that the Pseudocyclopoidea and Epacteriscoidea are monophyletic and synonymous is not supported in this analysis. The relationships among Pseudocyclopoidea, Ridgewayiidae and the Augaptiloidea/Centropagoidea clade are resolved with low jackknife support.

Although the topology of Clade 3 is not strongly supported at its base, the tree suggests that myelination of the nerve axons has arisen only once in the common ancestor of this clade. Nevertheless, we do not know the state of the nerve axons in the Bathypontioidea and this, coupled with incomplete observations of the nature of the female genitalia, means that an important part of the evolutionary picture in Clade 3 is not available.

The topology of the tree presented in Fig. 15 suggests that a derived, underlying 10-segmented condition of the antennal exopod has arisen twice: Clade 3 and Clade 11. Corroboration of this conclusion awaits further testing with genetic data and stronger support for the base of the tree.

An expanded Bathypontioidea clade is present in the analyses with low jackknife support. The form of the leg 1 endopod, the presence of a supplementary geniculation on the male right antennule between ancestral segments XIV and XV (Schulz 1986; Ohtsuka and Huys 2001; Fosshagen and Iliffe 2004), and absence of setae on male geniculate antennule segments XXI–XXIII, link the Bathypontiidae and Fosshageniidae. Thus, the Fosshageniidae which was assigned superfamily status (Suárez-Morales and Iliffe 1996), then moved to the Centropagoidea (Boxshall and Halsey 2004) is probably a bathypontioidean.

Although we have not been able to retrieve a monophyletic Megacalanoida, the families Megacalanidae, Calanidae and Paracalanidae are closely related. We believe that the data we present here are not sufficient to suggest any change to the superfamily names and await genetic data that may solve this problem.

Within superfamilies, it is clear that relationships based on the current dataset, are provisional. It is noted, specifically, that the 'Bradfordian' families (Diaixidae, Phaennidae, Tharybidae and Scolecitrichidae) are linked in Clade 21 (Fig. 15) although the inclusion of the Diaixidae has insignificant jackknife support. A more detailed understanding of relationships among families within superfamilies awaits further detailed morphological and genetic analyses.

Character state change novelties evident in the phylogeny presented here are far out-weighted by reduction in segmentation and losses of setal elements, the majority of which appear to represent pedomorphic changes. Character novelties are: 1 (presence of a dorsal cephalic hump), 17 (side on which male antennular geniculation occurs), 20 (presence of supplementary geniculation between male geniculate antennular segments XIV–XV), 42 (presence of tenth antennal exopod segment), 51 (presence of maxilla coxal epipodite), 52–54 (presence of specialised sensory setae on maxilla and maxilliped), 69 (presence of modified male maxilliped setae on outer endopod), 111 (presence of non-articulated spinous extension of exopod segment 2 of leg 5), 114 (presence of seminal receptacles), and 116 (presence of myelination). These novelties, apart from character 1, are 14% of all unambiguous character state changes in one of the three most parsimonious trees (Table 4). Although character 1 links the families placed by Andronov (1974) in the superfamily Megacalanoida, this superfamily is not recovered in this analysis, therefore character 1 does not appear in the list of unambiguous character state changes in Table 4.

The new scheme of phylogenetic relationships presented here provides a more rigorous morphology-based system than hitherto available. It highlights areas of morphology and comparative anatomy where data are still deficient, but will serve as a working hypothesis which can be tested using newly gathered molecular data.

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### References

- Adamowicz, S. J., Menu-Marque, S., Herbert, P. D. N., and Purvis, A. (2007). Molecular systematics and patterns of morphological evolution in the Centropagidae (Copepoda: Calanoida) of Argentina. *Biological Journal of the Linnean Society. Linnean Society of London* **90**, 279–292. doi:10.1111/j.1095-8312.2007.00723.x
- Andronov, V. N. (1974). Phylogenetic relations of large taxa within the suborder Calanoida (Crustacea, Copepoda). *Zoologicheskij Zhurnal* **53**(7), 1002–1012. [In Russian]
- Andronov, V. N. (1991). On renaming of some taxa in Calanoida (Crustacea). *Zoologicheskij Zhurnal* **70**, 133–134. [In Russian]
- Andronov, V. N. (1992). *Ryocalanus admirabilis* sp. n. (Copepoda, Calanoida, Ryocalanidae) from the central western Atlantic. *Zoologicheskij Zhurnal* **71**(7), 140–144. [In Russian]
- Andronov, V. N. (2007). New genus and species of copepods (Crustacea, Calanoida) from the central-eastern Atlantic and problems of classification of the Superfamilies Pseudocyclopoidea and Epacteriscoidea. *Zoologicheskij Zhurnal* **86**, 671–683. [In Russian]
- Barthélémy, R.-M. (1999a). Biologie de la reproduction des copépodes calanoides: Biodiversité morphofonctionnelle et intérêt phylétique des structures génitales femelles données structurales, ultrastructurales et biochimiques sur les grandes associées. These pour obtenir le grade de Docteur de L'Université de Provence. 95 pp. 41 figs.



- Barthélémy, R.-M. (1999b). Functional morphology and taxonomic relevance of the female genital structures in Acartiidae (Copepoda: Calanoida). *Journal of the Marine Biological Association of the United Kingdom* **79**, 857–870. doi:10.1017/S0025315499001022
- Barthélémy, R.-M., Cuoc, C., Defaye, D., Brunet, M., and Mazza, J. (1998a). Female genital structures in several families of Centropagoidea (Copepoda: Calanoida). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **353**, 721–736. doi:10.1098/rstb.1998.0238
- Barthélémy, R.-M., Ohtsuka, S., and Cuoc, C. (1998b). Description and female genital structures of a new species of the demersal calanoid copepod *Ridgewayia* from southern Japan. *Journal of Natural History, London* **32**, 1303–1318. doi:10.1080/00222939800770651
- Boxshall, G. A. (1982). On the anatomy of the misophrioid copepods, with special reference to *Benthomisophria palliata* Sars. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **297**, 125–181. doi:10.1098/rstb.1982.0036
- Boxshall, G. A., and Halsey, S. H. (2004). An introduction to copepod diversity. (The Ray Society: London.)
- Boxshall, G. A., and Huys, R. (1998). The ontogeny and phylogeny of copepod antennules. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **353**, 765–786. doi:10.1098/rstb.1998.0242
- Bradford, J. M., Ohman, M. O., and Jillett, J. B. (1988). Larval morphology and development of *Neocalanus tonsus*, *Calanoides macrocarinatus*, and *Calanus australis* (Copepoda: Calanoida) in the laboratory. *New Zealand Journal of Marine and Freshwater Research* **22**, 301–320. doi:10.1080/00288330.1988.9516303
- Bradford-Grieve, J. M. (1994). The marine fauna of New Zealand: Pelagic Calanoid Copepoda: Megacalanidae, Calanidae, Paracalanidae, Mecynoceridae, Eucalanidae, Spinocalanidae, Clausocalanidae. *NIWA Biodiversity Memoirs* **102**, 1–160.
- Bradford-Grieve, J. M. (1999). The marine fauna of New Zealand: Pelagic Calanoid Copepoda: Arietellidae, Augaptilidae, Heterorhabdidae, Lucicutiidae, Metridinidae, Phyllopodidae, Centropagidae, Pseudodiaptomidae, Temoridae, Candaciidae, Pontellidae, Sulcanidae, Acartiidae, Tortanidae. *NIWA Biodiversity Memoirs* **111**, 1–268.
- Bradford-Grieve, J. M. (2001). A new species of benthopelagic copepod of the genus *Tharybis* (Calanoida: Tharybidae) from the upper slope, northeastern New Zealand. *New Zealand Journal of Marine and Freshwater Research* **35**, 421–433. doi:10.1080/00288330.2001.9517012
- Bradford-Grieve, J. M. (2004). Two new species of *Xanthocalanus* and the first record of *Brachycalanus* (Copepoda: Calanoida: Phaennidae) from the upper slope, north-eastern New Zealand. *New Zealand Journal of Marine and Freshwater Research* **38**(4), 621–647. doi:10.1080/00288330.2004.9517267
- Bradford-Grieve, J. M. (2008). *Mecynocera clausi* I.C. Thompson, 1988 (Copepoda: Calanoida) is a paracalanid. *Zootaxa* **1852**, 59–64.
- Brodsky, K. A. (1955). The Calanoida of the Kurile-Kamchatka Trench. *Trudy Instituta Okeanologii* **12**, 184–209. [In Russian]
- Chang, S., Johnston, R. J. Jr, and Hobert, O. (2003). A transcriptional regulatory cascade that controls left/right asymmetry in chemosensory neurons of *C. elegans*. *Genes & Development* **17**, 2123–2137. doi:10.1101/gad.1117903
- Comita, G. W., and McNett, S. J. (1976). The postembryonic development instars of *Diaptomus oregonensis* Lilljeborg, 1889 (Copepoda). *Crustaceana* **30**(2), 123–163. doi:10.1163/156854076X00530
- Corkett, C. J., and McLaren, I. A. (1979). The biology of *Pseudocalanus*. *Advances in Marine Biology* **15**, 1–231. doi:10.1016/S0065-2881(08)60404-6
- Costanzo, G., Crescenti, N., and Zagami, G. (2004). Postembryonic development of *Pseudocyclops umbraticus* Giesbrecht, 1893 (Copepoda, Calanoida) from coastal waters of Sicily. *Crustaceana* **77**(1), 49–66. doi:10.1163/156854004323037883
- Cuoc, C., Defaye, D., Brunet, M., Notonier, R., and Mazza, J. (1997). Female genital structures of Metridinidae (Copepoda: Calanoida). *Marine Biology* **129**, 651–665. doi:10.1007/s002270050208
- Dallwitz, M. J., Paine, T. A., and Zurcher, E. J. 1993 onwards. User's guide to the DELTA System: a general system for processing taxonomic descriptions. Edn. 4. 136 pp. (CSIRO Division of Entomology: Canberra.)
- Damkaer, D. M. (1975). Calanoid copepods of the genera *Spinocalanus* and *Mimocalanus* from the central Arctic Ocean, with a review of the Spinocalanidae. *NOAA Technical Report. NMFS Circular* **391**, 1–88.
- Davis, A. D., Weatherby, T. M., Hartline, D. K., and Lenz, P. H. (1999). Myelin-like sheaths in copepod axons. *Nature* **398**, 571. doi:10.1038/19212
- Dogiel, V. A. (1954). Oligomerization of Homologous Organs as One of the Main Pathways of Animal Evolution. Leningrad State University. [Not seen]
- Farris, J. S. (1969). A successive approximations approach to character weighting. *Systematic Zoology* **18**, 374–385. doi:10.2307/2412182
- Ferrari, F. D. (1985). Postnaupliar development of a looking-glass copepod *Pleuromamma xiphias* (Giesbrecht, 1889) with analysis of distribution of sex and asymmetry. *Smithsonian Contributions to Zoology* **420**, i–iii, 1–55.
- Ferrari, F. D. (1995). Six copepodid stages of *Ridgewayia klausruetzleri*, a new species of copepod crustacean (Ridgewayiidae: Calanoida) from the barrier reef in Belize, with comments on appendage development. *Proceedings of the Biological Society of Washington* **108**(2), 180–200.
- Ferrari, F. D., and Benforado, A. (1998). Setation and setal groups on antenna 1 of *Ridgewayia klausruetzleri*, *Pleuromamma xiphias*, and *Pseudocalanus elongatus* (Crustacea: Copepoda: Calanoida) during the copepodid phase of development. *Proceedings of the Biological Society of Washington* **111**(1), 209–221.
- Ferrari, F. D., and Dahms, H.-U. (2007). Post-embryonic development of the Copepoda. *Crustaceana Monographs* **8**, 1–229.
- Ferrari, F. D., and Markhaseva, E. L. (1996). *Parkius karenwishnerae*, a new genus and species of calanoid copepod (Parkiidae, new family) from benthopelagic waters of the eastern tropical Pacific Ocean. *Proceedings of the Biological Society of Washington* **109**(2), 264–285.
- Ferrari, F. D., and Ueda, H. (2005). Development of leg 5 of copepods belonging to the calanoid superfamily Centropagoidea (Crustacea). *Journal of Crustacean Biology* **25**(3), 333–352. doi:10.1651/C2554
- Fosshagen, A., and Iliffe, T. M. (1985). Two new genera of Calanoida and a new Order of Copepoda, Platycopioida, from marine caves on Bermuda. *Sarsia* **70**, 345–358.
- Fosshagen, A., and Iliffe, T. M. (1989). *Boholina*, a new genus (Copepoda: Calanoida) with two new species from an anchialine cave in the Philippines. *Sarsia* **74**, 201–208.
- Fosshagen, A., and Iliffe, T. M. (1991). A new genus of calanoid copepod from an anchialine cave in Belize. *Bulletin of the Plankton Society of Japan* **1991**(Special), 339–346.
- Fosshagen, A., and Iliffe, T. M. (2004). A new species of cave-dwelling calanoid copepod from Grand Bahama. *Sarsia* **89**, 346–354. doi:10.1080/00364820410002613
- Fosshagen, A., Boxshall, G. A., and Iliffe, T. M. (2001). The Epacteriscidae, a cave-dwelling family of calanoid copepods. *Sarsia* **86**, 245–318.
- Geletin, Yu. V. (1976). The ontogenetic abdomen formation in copepods of genera *Eucalanus* and *Rhincalanus* (Calanoida, Eucalanidae) and new systems of these copepods. *Issledovaniya Fauni Morei* **18**, 75–93. [English translation, NIWA, Wellington; original is in Russian]
- Geptner, M. V. (1968). Structure and taxonomic significance of the genital complex in copepods of the family Euchaetidae (Calanoida). *Oceanology* **8**, 543–552.
- Giesbrecht, W. (1893). Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeres. *Fauna und Flora des Golfes von Neapel und der Angrenzenden Meeres, Herausgegeben von der Zoologischen Station zu Neapel* **19**, 1–831.

- Goetze, E., and Bradford-Grieve, J. M. (2005). Description of *Eucalanus spinifer* T. Scott, 1894 (Copepoda: Calanoida), a circumglobal sister species of *E. hyalinus* s.s. (Claus, 1866). *Progress in Oceanography* **65**, 55–87. doi:10.1016/j.pocean.2005.02.015
- Grice, G. D., and Hulsemann, K. (1965). Abundance, vertical distribution and taxonomy of calanoid copepods at selected stations in the northeast Atlantic. *Journal of Zoology* **146**, 213–262. doi:10.1111/j.1469-7998.1965.tb05210.x
- Grice, G. D., and Hulsemann, K. (1967). Bathypelagic calanoid copepods of the western Indian Ocean. *Proceedings of the United States National Museum* **122**(3583), 1–67.
- Gurney, R. (1931). British fresh-water Copepoda 1. pp. 1–238. (Ray Society, London.)
- Hartline, D. K., and Colman, D. R. (2007). Rapid conduction and the evolution of giant axons and myelinated fibers. *Current Biology* **17**(1), R29–R35. doi:10.1016/j.cub.2006.11.042
- Heron, G. A., and Bowman, T. E. (1971). Postnaupliar developmental stages of the copepod crustaceans *Clausocalanus laticeps*, *C. brevipes*, and *Ctenocalanus citer* (Calanoida: Pseudocalanidae). *Antarctic Research Series* **17**, 141–165.
- Ho, J. (1994). Copepod phylogeny: a reconsideration of Huys and Boxshall's 'parsimony versus homology'. *Hydrobiologia* **292/293**, 31–39. doi:10.1007/BF00229920
- Hulsemann, K. (1991a). Tracing homologies in appendages during ontogenetic development of Calanoid copepods. *Bulletin of the Plankton Society of Japan, Special Volume, Proceedings of the Fourth International Conference on Copepoda*, 105–114.
- Hulsemann, K. (1991b). The copepodid stages of *Drepanopus forcipatus* Giesbrecht, with notes on the genus and a comparison with other members of the family Clausocalanidae (Copepoda Calanoida). *Helgolaender Meeresuntersuchungen* **45**, 199–224. doi:10.1007/BF02365642
- Humes, A. G. (1955). The postembryonic developmental stages of the fresh-water calanoid copepod, *Epischura massachusettsensis* Pearse. *Journal of Morphology* **96**, 441–471. doi:10.1002/jmor.1050960303
- Huys, R., and Boxshall, G. A. (1991). Copepod Evolution. (The Ray Society, London.)
- ICZN (1985). International Code of Zoological Nomenclature. Third Edition. (International Trust for Zoological Nomenclature, London.)
- ICZN (1988). Opinion 1503. *Bulletin of Zoological Nomenclature* **45**(3), 228–229.
- Jaume, D., and Boxshall, G. A. (1995). *Stygocyclopia balearica*, a new genus and species of calanoid copepod (Pseudocyclopiidae) from anchihaline caves in the Balearic Islands (Mediterranean). *Sarsia* **80**, 213–222.
- Jaume, D., and Boxshall, G. A. (1996). A new genus and two new species of cave-dwelling copepods from the Balearic Islands (Mediterranean). *Journal of Natural History, London* **30**, 989–1006. doi:10.1080/00222939600770531
- Jaume, D., Boxshall, G. A., and Gràcia, F. (2008). *Stephos* (Copepoda: Stephidae) from Balearic caves (W Mediterranean). *Systematics and Biodiversity* **6**, 503–520. doi:10.1017/S1477200008002764
- Johnson, M. W. (1934). The life history of the copepod *Tortanus discaudatus* (Thompson and Scott). *The Biological Bulletin of Woods Hole* **67**, 182–200. doi:10.2307/1537492
- Kršinić, F. (2005). *Speleohvarella gamulini* gen. et sp. nov., a new copepod (Calanoida, Stephidae) from an anchialine cave in the Adriatic Sea. *Journal of Plankton Research* **27**, 607–615. doi:10.1093/plankt/fbi028
- Lawson, T. H., and Grice, G. D. (1970). The developmental stages of *Centropages typicus* Krøyer (Copepoda, Calanoida). *Crustaceana* **18**(2), 187–208. doi:10.1163/156854070X00806
- Lawson, T. H., and Grice, G. D. (1973). The developmental stages of *Paracalanus crassirostris* Dahl, 1894 (Copepoda, Calanoida). *Crustaceana* **24**(1), 43–56. doi:10.1163/156854073X00056
- Lenz, P. H., Hartline, D. K., and Davis, A. D. (2000). The need for speed. I. Fast reactions and myelinated axons in copepods. *Journal of Comparative Physiology. A, Sensory, Neural, and Behavioral Physiology* **186**, 337–345. doi:10.1007/s003590050434
- Maddison, D. R., and Maddison, W. P. (2000). MacClade 4: Analysis of Phylogeny and Character Evolution. CD-ROM. (Sinauer Associates, Sunderland, Massachusetts.)
- Markhaseva, E. L., and Dahms, H.-U. (2004). *Plesioscolecithrix* (Copepoda, Calanoida, Scolecitrichidae): a new genus, and new species from the high Antarctic Weddell Sea (Southern Ocean). *Sarsia* **89**, 326–337. doi:10.1080/00364820410002596
- Markhaseva, E. L., and Kosobokova, K. N. (2001). *Arctokonstantinus hardingi* (Copepoda, Calanoida, Arctokonstantinidae): new family, new genus, and new species from the bathypelagic Arctic Basin. *Sarsia* **86**, 319–324.
- Markhaseva, E. L., and Schulz, K. (2006). *Sensiaeva longiseta* (Copepoda, Calanoida): a new genus and species from the abyss of the Weddell Sea. *Zootaxa* **1368**, 1–18.
- Markhaseva, E. L., and Schulz, K. (2009). A new family and genus of calanoid copepods (Crustacea) from the abyss of the Atlantic Ocean. *Zootaxa* **2304**, 21–40.
- Markhaseva, E. L., Schulz, K., and Martinez Arbizu, P. (2009). New family of Crustacea (Calanoida) – Rostrocalanidae fam. nov.: making the name available. *Zoosystemica Rossica* **18**, 318–319.
- Martinez Arbizu, P. (1997). *Sarsicopia polaris* gen. et sp. n., the Platycopioida (Copepoda: Crustacea) from the Arctic Ocean, and its phylogenetic significance. *Hydrobiologia* **350**, 35–47. doi:10.1023/A:1003020829836
- McKinnon, A. D., and Arnott, G. H. (1985). The developmental stages of *Gladioferens pectinatus* (Brady, 1899) (Copepoda: Calanoida). *New Zealand Journal of Marine and Freshwater Research* **19**, 21–42. doi:10.1080/00288330.1985.9516072
- Monchenko, V. I., and von Vaupel Klein, J. C. (1999). Oligomerization in Copepoda Cyclopoida as a kind of orthogenetic evolution in the animal kingdom. *Crustaceana* **72**(3), 241–264. doi:10.1163/156854099503320
- Nicholls, A. G. (1945). A new calanoid copepod from Australia. *Annals and Magazine of Natural History* **12**(11), 501–514.
- Nishida, S. (1985). Pelagic copepods from Kabira Bay, Ishigaki Island, Southwestern Japan, with a description of a new species of the genus *Pseudodiaptomus*. *Publications of the Seto Marine Laboratory* **30**, 3125–3144.
- Nishida, S. (1989). Distribution, structure and importance of the cephalic dorsal hump, a new sensory organ in calanoid copepods. *Marine Biology* **101**, 173–185. doi:10.1007/BF00391456
- Nishida, S., and Ohtsuka, S. (1997). Ultrastructure of the mouthpart sensory setae in mesopelagic copepods of the family Scolecitrichidae. *Plankton Biology and Ecology* **44**(1/2), 81–90.
- Ohtsuka, S. (1992). *Tortanus (Acutanus) angularis*, new subgenus and new species (Copepoda: Calanoida), from the Caribbean Sea, with remarks on the subgenera in the genus *Tortanus*. *Proceedings of the Biological Society of Washington* **105**(2), 255–267.
- Ohtsuka, S., and Huys, R. (2001). Sexual dimorphism in calanoid copepods: morphology and function. *Hydrobiologia* **453/454**, 441–466. doi:10.1023/A:1013162605809
- Ohtsuka, S., and Mitsuzumi, C. (1990). A new asymmetrical near-bottom calanoid copepod, *Paramisophria platysoma*, with observations of its integumental organs, behaviour and *in-situ* feeding habit. *Bulletin of the Plankton Society of Japan* **36**, 87–101.
- Ohtsuka, S., Fosshagen, A., and Iliffe, T. M. (1993a). Two new species of *Paramisophria* (Copepoda, Calanoida, Arietellidae) from anchialine caves on the Canary and Galapagos Islands. *Sarsia* **78**, 57–67.
- Ohtsuka, S., Roe, H. S. J., and Boxshall, G. A. (1993b). A new family of Calanoid copepods, the Hyperbionycidae, collected from the deep-sea hyperbenthic community in the northeastern Atlantic. *Sarsia* **78**, 69–82.

- Ohtsuka, S., Boxshall, G. A., and Roe, H. S. J. (1994). Phylogenetic relationships between arietellid genera (Copepoda: Calanoida), with the establishment of three new genera. *Bulletin of the British Museum of Natural History (Zoology)* **60**, 105–172.
- Ohtsuka, S., Fosshagen, A., and Putschakarn, S. (1999). Three new species of the demersal calanoid copepod *Pseudocyclops* from Phuket, Thailand. *Plankton Biology and Ecology* **46**(2), 132–147.
- Ohtsuka, S., Kase, T., and Boxshall, G. A. (2000). A new species of *Ridgewayia* (Copepoda: Calanoida) from a submarine cave in Palau, Western Atlantic. *Species Diversity* **5**, 201–213.
- Park, T. S. (1966). The biology of a calanoid copepod *Epilabidocera amphrites* McMurrich. *Cellule* **66**, 129–251.
- Park, T. S. (1986). Phylogeny of calanoid copepods. *Syllogeus* **58**, 191–196.
- Park, T. (1995). Taxonomy and distribution of the marine calanoid copepod family Euchaetidae. *Bulletin of the Scripps Institution of Oceanography, University of Southern California, San Diego* **29**, 1–203.
- Park, T. (2000). Taxonomy and distribution of the calanoid copepods family Heterorhabdidae. *Bulletin of the Scripps Institution of Oceanography, University of Southern California, San Diego* **31**, 1–269.
- Pinchuk, A. I. (1997). Naupliar development of *Metridia pacifica* (Copepoda: Calanoida) reared in the laboratory. *Journal of Crustacean Biology* **17**(2), 343–351. doi:10.2307/1549283
- Reddy, Y. R., and Devi, C. R. (1985). The complete postembryonic development of *Megadiaptomus hebes* Kiefer, 1936 (Copepoda, Calanoida) reared in the laboratory. *Crustaceana* **48**(1), 40–63. doi:10.1163/156854085X00710
- Sars, G. O. (1901). Copepoda Calanoida. An account of the Crustacea of Norway, with short descriptions and figures of all the species **4**, 1–28.
- Sars, G. O. (1902). Copepoda Calanoida. An account of the Crustacea of Norway, with short descriptions and figures of all the species **4**, 29–144.
- Sars, G. O. (1903). Copepoda Calanoida. An account of the Crustacea of Norway, with short descriptions and figures of all the species **4**, 145–171.
- Sars, G. O. (1924, 1925). Copépodes particulièrement bathypélagiques provenant des campagnes scientifiques du Prince Albert 1er de Monaco. Résultats des Campagnes Scientifiques Accomplis par le Prince Albert 1er de Monaco **69**. Atlas 1924; text 1925.
- Schulz, K. (1981). *Tharybis minor* sp. n. (Copepoda: Calanoida: Tharybidae) aus dem nordwestafrikanischen Auftriebsgebiet mit Anmerkungen zur Gattung *Tharybis* Sars. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* **78**, 169–171.
- Schulz, K. (1986). *Temoropia setosa* n. sp. (Copepoda: Calanoida: Temoridae) aus dem Kanarenstromgebiet (Nordost-Atlantik) mit Anmerkungen zur Gattung *Temoropia* T. Scott. *Mitteilungen aus dem Hamburgischen zoologische Museum und Institut* **83**, 139–146.
- Schulz, K., and Beckmann, W. (1995). New benthopelagic tharybids (Copepoda: Calanoida) from the deep North Atlantic. *Sarsia* **80**, 199–211.
- Schulz, K., and Kwasniewski, S. (2004). New species of benthopelagic calanoid copepods from Kongsfjorden (Spitsbergen, Svalbard Archipelago). *Sarsia* **89**, 143–159. doi:10.1080/00364820410005214
- Shimode, S., Toda, T., and Kikuchi, T. (2000). *Ryocalanus spinifrons*, a new species of Ryocalanidae (Copepoda: Calanoida), from the southwestern part of Sagami Bay, Japan. *Hydrobiologia* **432**, 131–133. doi:10.1023/A:1004090724831
- Soh, H. Y., Ohtsuka, S., Imbayayshi, H., and Suh, H.-L. (1999). A new deep-water calanoid copepod and the phylogeny of the genus *Nullosetigera* nom. nov. in the Nullosetigeridae nom. nov. (pro *Phyllopus*: Phyllopodidae) from Japanese waters. *Journal of Natural History* **33**, 1581–1602. doi:10.1080/002229399299770
- Suárez-Morales, E., and Iliffe, T. M. (1996). New superfamily of Calanoida (Copepoda) from an anchialine cave in the Bahamas. *Journal of Crustacean Biology* **16**, 754–762. doi:10.2307/1549194
- Swofford, D. L. (2002). Phylogenetic Analysis Using Parsimony (\*and other methods) Version 4. Sinauer Associates, Sunderland, Massachusetts. Available at [http://paup.csit.fsu.edu/Command\\_ref\\_v2.pdf](http://paup.csit.fsu.edu/Command_ref_v2.pdf)
- Tanimura, A. (1992). Postembryonic development of *Paralabidocera antarctica* (L.C. Thompson) (Copepoda, Calanoida) from the fast ice near Syowa Station, Antarctica. *Hydrobiologia* **245**, 109–128. doi:10.1007/BF00764771
- Ueda, H., and Ohtsuka, S. (1998). Redescription and taxonomic status of *Sinodiaptomus valkanavi*, a common limnoplanktonic calanoid copepod in Japan, with comparison to the closely related *S. sarsi*. *Hydrobiologia* **379**, 159–168. doi:10.1023/A:1003435701993
- Vyshkvartzeva, N. V. (2003). A new bathypelagic copepod *Pseudoamallothrix paralaminata* sp. n. from the Arctic Basin and arguments for the transfer of *Xanthocalanus soaresmoreirai* Bjornberg, 1975 to the genus *Pseudoamallothrix* (Calanoida: Scolecitrichidae). *Zoosystematica Rossica* **12**(1), 39–47.
- Weatherby, T. M., Davis, A. D., Hartline, D. K., and Lenz, P. H. (2000). The need for speed II. Myelin in calanoid copepods. *Journal of Comparative Physiology. A, Sensory, Neural, and Behavioral Physiology* **186**, 347–357. doi:10.1007/s003590050435
- Yeates, D. K. (1995). Groundplans and exemplars: paths to the tree of life. *Cladistics* **11**, 343–357. doi:10.1111/j.1096-0031.1995.tb00094.x

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