

Partial re-assessment of the family structure of the Clausocalanoidea (Copepoda: Calanoida) using morphological data

JANET M. BRADFORD-GRIEVE^{1*} and GEOFFREY A. BOXSHALL²

¹National Institute of Water and Atmospheric Research, Private Bag 14901, Kilbirnie, Wellington 6241, New Zealand

²Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK

Received 17 June 2018; revised 28 September 2018; accepted for publication 18 October 2018

A cladistic analysis of the non-‘Bradfordian’ genera was used to improve the classification of the superfamily Clausocalanoidea. The prevalence of homoplasy among the morphological characters used interfered with tree inference and our assessment of support for the topologies produced. Characters previously thought to have phylogenetic significance appear to be homoplasious (e.g. the presence of large spinules on the coxa of leg 4). Other characters, not previously thought to have phylogenetic significance, contributed to the fundamental topology of the trees even though incompletely congruent. These female characters are the setation of: antennular ancestral segments I, XIII, XV, XXI and XXIII; mandible basis and endopod segment 1; maxillule exopod; the maxilla praecoxal endite 1; and segmentation of the leg 1 exopod and leg 2 endopod. Our phylogenetic hypothesis of the non-‘Bradfordian’ Clausocalanoidea, using ‘Bradfordian’ taxa as the outgroup, gives some confidence in three clades: Aetideidae Giesbrecht, 1893, Clausocalanidae Giesbrecht, 1893 and Pseudocyclopiidae G. O. Sars, 1902, a conclusion requiring corroboration with genetic data. The Euchaetidae are always nested within the Aetideidae, and the Stephidae are paraphyletic and nested within the Clausocalanidae. The Mesaiokeratidae is a terminal branch within a clade composed of genera currently grouped as the Stephidae.

ADDITIONAL KEYWORDS: anchialine – benthopelagic – pelagic – phylogeny.

INTRODUCTION

The copepod superfamily Clausocalanoidea currently comprises 13 families, several of which are abundant and diverse members of the epipelagic (e.g. Clausocalanidae) and mesopelagic (e.g. Aetideidae) zooplankton communities of the global ocean. Seven of these clausocalanoidean families (Diaixidae, Kyphocalanidae, Parkiidae, Phaennidae, Rostrocalanidae, Scolecitrichidae and Tharybidae) are referred to as ‘Bradfordian’ because they share the possession of characteristic vermiform and brush-like sensory elements on the modified maxilla (Bradford, 1973; Markhaseva *et al.*, 2014). The Bradfordian families are monophyletic and terminal among the Clausocalanoidea (Blanco-Bercial *et al.*, 2011; Bradford-Grieve *et al.*, 2010, 2014; Laakmann *et al.*, 2018). The remaining six families (Aetideidae,

Clausocalanidae, Euchaetidae, Mesaiokeratidae, Pseudocyclopiidae and Stephidae) are non-‘Bradfordian’ and retain unmodified setal elements on the maxilla. The family structure within the non-‘Bradfordian’ genera of Clausocalanoidea (Andronov, 1974, as Pseudocalanoidea) and the phylogenetic relationships among and within families are becoming increasingly unclear as new benthopelagic taxa are added. For example, *Peniculoides* Markhaseva & Renz, 2015 shares morphological features with both the Clausocalanidae and the Aetideidae (Markhaseva & Renz, 2015). It was previously suggested that the Aetideidae might be paraphyletic (von Vaupel Klein, 1984: 56), a question supported by Boxshall & Halsey (2004: 120), who recommend ‘a full revision of the aetideid-euchaetid complex’. Furthermore, *Pseudotharybis* Scott, 1909 and *Valdiviella* Steuer, 1904 have been interpreted as occupying an intermediate position between the Euchaetidae (two genera) and

*Corresponding author. E-mail: janet.grieve@niwa.co.nz

Aetideidae (29 genera) (e.g. [Boxshall & Halsey, 2004: 57](#), and references therein).

Within the remaining non-‘Bradfordian’ Clausocalanoidea there are several families that contain a limited number of genera. The Pseudocyclopiidae contains five benthopelagic genera: *Frigocalanus* Schulz, 1996, *Paracyclopia* Fosshagen in Fosshagen & Iliffe, 1985, *Pseudocyclopia* Scott, 1892, *Stygocyclopia* Jaume & Boxshall, 1995 and *Thompsonopia* Jaume, Fosshagen & Iliffe, 1999. The Clausocalanidae contains six pelagic genera: *Clausocalanus* Giesbrecht, 1888, *Ctenocalanus* Giesbrecht, 1888, *Drepanopus* Brady, 1883, *Microcalanus* Sars, 1903, *Pseudocalanus* Boeck, 1872, *Spicipes* Grice & Hulsemann, 1965 and a benthopelagic genus: *Peniculoides*; note that *Spicipes* has been provisionally placed in the Clausocalanidae ([Boxshall & Halsey, 2004: 92](#)), and *Farrania* Sars, 1920 has been reassigned to the Aetideidae ([Markhaseva & Renz, 2015](#)). The Mesaiokeratidae contains one benthopelagic genus: *Mesaiokeras* Matthews, 1961, and the Stephidae contains four benthopelagic genera: *Miostephos* Bowman, 1976, *Parastephos* Sars, 1902, *Speleohvarella* Kršinic, 2005 and *Stephos* Scott, 1892. [Schulz \(1996\)](#) noted the similarity between *Frigocalanus* (currently in the Pseudocyclopiidae) and the Mesaiokeratidae, and [Boxshall & Halsey \(2004\)](#) noted the similarity of Mesaiokeratidae (one genus) to the Stephidae. Also, they noted that *Pseudocyclopia minor* Scott, 1892 cannot be placed within the two genera created by splitting the type genus ([Jaume et al., 1999](#)). Within the Clausocalanidae, *Clausocalanus* and *Ctenocalanus* are similar because they are linked by the possession of posterodistal spines on the basis of swimming legs 2 and 3 and by the absence of an inner border coxal seta on leg 4, whereas the remaining genera in this family do not exhibit these features (e.g. [Bradford-Grieve, 1994](#)). Also, *Spicipes* and *Microcalanus* have four setae on the leg 1 endopod compared with five setae in the remaining clausocalanid genera. The Pseudocyclopiidae have five setae on the endopod of leg 1 except for *Paracyclopia*, which has four setae ([Boxshall & Halsey, 2004](#)). Furthermore, the Clausocalanoidea, according to [Sars \(1902\)](#) when he defined the Isokerandria, contain taxa across the ‘Bradfordian’–non-‘Bradfordian’ divide that are characterized by antennules that show little sexual dimorphism and by female and male mouthparts that are usually similar (Stephidae, Tharybidae, Pseudocyclopiidae and *Diaixis*).

All these observations suggest that the current system of classification of the Clausocalanoidea does not reflect the distribution of the various plesiomorphic and specialized features found within this superfamily.

To make the initial task of re-evaluating the family structure in the Clausocalanoidea manageable, the

‘Bradfordian’ families have been omitted from the present analysis. The evidence in support of this course of action comes from a phylogeny of ‘Bradfordian’ genera ([Laakmann et al., 2018](#)) which placed the ‘Bradfordian’ families as a monophyletic group sister to the non-‘Bradfordian’ families within the Clausocalanoidea. A similar result was obtained in a morphology-based analysis ([Bradford-Grieve et al., 2010](#)) using single plesiomorphic exemplars. Together, these analyses show that the Clausocalanoidea represent a derived lineage that is sister to the Spinocalanoidea and Ryocalanidae, both lying within a larger clade also containing the Megacalanidae, Bathypontioidea and Eucalanoidea.

Here, we present a cladistic analysis of the non-‘Bradfordian’ genera of the Clausocalanoidea based on morphology. The aims are to find all the likely phylogenetically informative characters/states and to test the monophyly of existing families and whether, in the case of the monogeneric Mesaiokeratidae and the Euchaetidae, they represent terminal branches more properly belonging within other, possibly paraphyletic, families.

MATERIAL AND METHODS

DATA

The data used in the analysis of genera in the Clausocalanoidea are derived from among the best species descriptions in the literature ([Table 1](#)). Where character states vary within a genus these descriptions were augmented by data from the most plesiomorphic species in each genus (based on generally accepted notions of character polarity), e.g. *Bradyidius* Giesbrecht, 1897, *Chiridiella* Sars, 1907, *Euchirella* Giesbrecht, 1888, *Gaetanus* Giesbrecht, 1888, *Paracomantenna* Campaner, 1978, *Prolutamator* Markhaseva & Schulz, 2008, *Pseudochirella* Sars, 1920 and *Pseudotharybis* Scott, 1909. Original observations were made of the following: *Sursamucro spinatus* [Bradford, 1969b](#) (holotype re-examined J.M.B.-G.), *Farrania frigida* (Wolfenden, 1911) (J.M.B.-G.) and *Azygokeras columbiae* Koeller & Littlepage, 1976 (paratype re-examined J.M.B.-G.). The female antennule setation was augmented by additional observations of *Pseudeuchaeta brevicauda* Sars, 1905, *Chirundina streetsii* Giesbrecht, 1895, *Undeuchaeta major* Giesbrecht, 1888, *Euchaeta rimana* Bradford, 1974, *Paraeuchaeta exigua* (Wolfenden, 1911), *Valdiviella insignis* Farran, 1908 and *Aetideopsis tumorosa* Bradford, 1969a from the National Institute of Water and Atmospheric Research (NIWA) invertebrate collection (J.M.B.-G.). *Microcalanus pusillus* Sars,

Table 1. Calanoid copepod taxa considered as exemplars in the cladistic analysis of non-'Bradfordian' genera of the Clausocalanoidea

Genus/species	Reference	Additional information	Habitat
Diaxiidae G.O. Sars, 1902			
<i>Neoscoleithrix japonica</i>	Ohtsuka <i>et al.</i> , 2003		Benthopelagic 337–340 m
<i>Thoxancalanus spinatus</i>	Markhaseva <i>et al.</i> , 2014		Benthopelagic 5148 m
Clausocalanidae Giesbrecht, 1893			
<i>Clausocalanus brevipes</i>	Bradford-Grieve, 1994	Giesbrecht, 1892/93; Frost & Fleminger, 1968 Giesbrecht, 1892/93	Epipelagic
<i>Ctenocalanus citer</i>	Heron & Bowman, 1971		Epipelagic
<i>Drepanopus forcipatus</i>	Hulsemann, 1991		Epipelagic
<i>Microcalanus pusillus</i>	Sars, 1903	G.A.B., pers. obs.	Pelagic > 275 m
<i>Peniculoides secundus</i>	Markhaseva & Renz, 2015		Benthopelagic 4000 m
<i>Pseudocalanus acuspes</i>	Markhaseva <i>et al.</i> , 2012		Epipelagic
<i>Spicipes nanseni</i>	Grice & Hulsemann, 1965		Bathypelagic 1900–3000 m
Mesaiokeratidae Matthews, 1961			
<i>Mesatokeras spitsbergensis</i>	Schulz & Kwasiński, 2004		Benthopelagic 20–800 m
Pseudocyclopiidae G.O. Sars, 1902			
<i>Frigocalanus rauscheri</i>	Schulz, 1996		Benthopelagic sublittoral
<i>Paracyclopia naessi</i>	Fosshagen & Iliffe, 1985	G.A.B., pers. obs.	Marine cave
<i>Pseudocyclopia crassicornis</i>	G.A.B., pers. obs.	T. Scott, 1892	Benthopelagic ~40 m
<i>Stygocyclopia balearica</i>	Jaume & Boxshall, 1995		Marine cave
<i>Thompsonopia mediterranea</i>	Jaume <i>et al.</i> , 1999	Ohtsuka, 1992	Marine cave
Aetideidae Giesbrecht, 1893			
<i>Aetideopsis rostrata</i>	Markhaseva, 1996	Bradford, 1969a; Park, 1978; Shih & Maclellan, 1981; McKinnon <i>et al.</i> , 2011	Benthopelagic to pelagic < 500 m
<i>Aetideus acutus</i>	Park, 1974	Park, 1968, 1978	Epiplanktonic
<i>Azygokeras columbiae</i>	Koeller & Littlepage, 1976	J.M.B.-G., pers. obs.	Benthopelagic 650 m
<i>Batheuchaeta anomala</i>	Markhaseva, 1981, 1986		Abyssopelagic
<i>Bradyetes pacificus</i>	Ohtsuka <i>et al.</i> , 2005	Markhaseva & Schulz, 2006	Benthopelagic 600 m
<i>Bradydium capax</i>	Bradford-Grieve, 2003	Markhaseva, 1996	Benthopelagic 300–450 m
<i>Chiridiella kuniae</i>	Markhaseva, 1996	Sars, 1924/25; Grice, 1969; Deevey, 1974; Markhaseva, 1996	Bathy- to abyssopelagic
<i>Chiridius gracilis</i>	Park, 1978; Markhaseva, 1996		Mesopelagic 500–1000 m
<i>Chirundina streetsii</i>	Tanaka, 1957	Markhaseva, 1996	Epi- to mesopelagic
<i>Chirundinella magna</i>	Wolfenden, 1911; Tanaka, 1957, 1969	Markhaseva, 1996	Meso- to bathypelagic
<i>Comantenna recurvata</i>	Grice & Hulsemann, 1970; Alvarez, 1986		Benthopelagic 1100–1800 m
<i>Crassantenna comosa</i>	Bradford, 1969b; Markhaseva <i>et al.</i> , 2017		Benthopelagic 1383–5399 m

Table 1. Continued

Genus/species	Reference	Additional information	Habitat
<i>Euchirella rostrata</i>	Markhaseva, 1996	Giesbrecht, 1892/93; Bradford & Jillett, 1980; von Vaupel Klein, 1984	Epi- to mesopelagic
<i>Farrania frigida</i>	Vervoort, 1951	Tanaka, 1956; J.M.B.-G., pers. obs.	Meso- to bathypelagic
<i>Gaetanus minutus</i>	Park, 1967 as <i>columbicae</i>	Park, 1973; Markhaseva, 1996	Meso- to bathypelagic
<i>Jaschnovita brevis</i>	Markhaseva, 1980, 1996	Markhaseva, 1980	Benthopelagic or under ice
<i>Lutamator paradiseus</i>	Ohtsuka <i>et al.</i> , 2005	Alvarez, 1984	Benthopelagic 600 m
<i>Mesocomantenna spinosa</i>	Alvarez, 1986		Benthopelagic 340 m
<i>Paivella inaciae</i>	Vervoort, 1965		Epipelagic
<i>Parabradidius angelikae</i>	Schulz & Markhaseva, 2000	Bradford, 1969b	Benthopelagic 1983 m
<i>Paracomantenna goi</i>	Ohtsuka <i>et al.</i> , 2005	Markhaseva & Schnack-Schiel, 2003	Benthopelagic 135–537 m
<i>Prolutamator hadalis</i>	Markhaseva & Schulz, 2008		Benthopelagic 5000 m
<i>Pseudeuchaeta arctica</i>	Markhaseva, 1986, 1996	Markhaseva & Schnack-Schiel, 2003; Markhaseva & Schulz, 2006; Markhaseva <i>et al.</i> , 2017	Benthopelagic 3300–3500 m
<i>Pseudochirella obesa</i>	Roe, 1975; von Vaupel Klein & Rijkerkerk, 1996, 1997	Park, 1978; Markhaseva, 1996	Mesopelagic
<i>Pseudotharybis polaris</i>	Markhaseva & Schulz, 2008	Bradford, 1969b	Benthopelagic 3500 m
<i>Senecella siberica</i>	Vyshkvartzeva, 1994	Juday, 1925	Brackish, shallow waters
<i>Sursamucro spinatus</i>	Bradford, 1969b	Holotype re-examined, J.M.B.-G.	Benthopelagic 1000–2000 m
<i>Undeuchaeta incisa</i>	Park, 1978	von Vaupel Klein, 1984	Meso- to bathypelagic
<i>Valdiviella insignis</i>	Sars, 1925; Park, 1978	Zvereva, 1975	Meso- to bathypelagic
<i>Pterochirella</i> male, female unknown		Schulz, 1990	Benthopelagic? 1318 m
Euchaetidae			
<i>Euchaeta marina</i>	Park, 1995		Epipelagic
<i>Paraeuchaeta norvegica</i>	Park, 1995		Epi- to mesopelagic
Stephidae G.O. Sars, 1902			
<i>Miostephos cubrobex</i>	Bowman, 1976	G.A.B., pers. obs.	Anchialine pool
<i>Parastephos occatum</i>	Damkaer, 1971		Benthopelagic 160 m
<i>Speleohvarella gamulini</i>	Kršinić, 2005		Marine cave
<i>Stephos vivesi</i>	Jaume <i>et al.</i> , 2008		Marine cave

Species were chosen based on well-described species, augmented in some cases by more plesiomorphic species. Where original or subsequent descriptions were not sufficient, additional specimens were examined for this work (indicated as, e.g. G.A.B., pers. obs.); see section on Data.

1903 (from Aalesund, Norway, collected by G. O. Sars, in Norman collection British Museum of Natural History (BMNH) Reg. Nos. 1911-11.8.37519–37538), *Pseudocyclopia crassicornis* Scott T., 1892 (from Firth of Forth, Scotland, Norman collection BMNH Reg. No. 1911.11.8.38037–38042), *Paracyclops naessi* Fosshagen & Iliffe, 1985 and *Miostephos leamingtonensis* Yeatman, 1980/*cubrobex* Bowman, 1976 were also re-examined (G.A.B.). The proximal setation of the antenna exopod of *Clausocalanus arcuicornis* (Dana, 1849) (Zoological Institute, Russian Academy of Sciences, 1/40817) was re-examined by Dr Elena Markhaseva, Institute of Zoology, Russian Academy of Sciences, St Petersburg, who has also shared other aspects of her work on the Clausocalanoidea (see Acknowledgements).

The challenge during this work was to add to the relatively small number of characters that have been used in the taxonomy of the Clausocalanoidea and that have been described consistently in the literature. We investigate which characters/states are homologous and likely to contain a phylogenetic signal.

CHARACTER ANALYSIS

Female representatives of most Clausocalanoidea genera are represented in the ingroup of an analysis of relationships among these genera (Table 1) except for *Spicipes*, which was omitted because too many characters have not been described. Male characters were analysed (Table 2) but not included in the cladistic analysis because males of six genera are unknown and a further six genera have incomplete data (Supporting Information, Appendix S1).

Outgroup taxa

The outgroup taxa were chosen in the context of the current phylogenetic hypothesis of Bradford-Grieve *et al.* (2010, 2014) and Laakmann *et al.* (2018), where the Clausocalanoidea represent a derived lineage that is sister to the Spinocalanoidea and Ryocalanoidea. Here, we use two Bradfordian genera as the outgroup to polarize character states among non-‘Bradfordian’ Clausocalanoidea. We have chosen *Neoscolecithrix* Canu, 1896 and *Thoxancalanus* Markhaseva *et al.*, 2014 as relatively plesiomorphic Bradfordian genera placed in the Diaixidae by Markhaseva *et al.* (2014).

The character set

The character set was chosen based on hypotheses of primary homology. These data were mainly taken from the literature, but taxa were additionally checked where there was a question about a character state and type or voucher specimens were available.

Hypotheses of primary homology relating to segmentation and setation are based upon our current understanding of copepod development (see Bradford-Grieve *et al.*, 2010 and references therein). Where we failed to arrive at a hypothesis of primary homology for individual mouthpart characters/states, this failure is evaluated in the sections below.

Characters (char.) and their states are listed in Table 2, and the data matrix is given in the Supporting Information (Appendix S1). In the figures, selected specific characters and states separated by a colon are indicated in the form ‘character 1: state 2’ or ‘◀ 1:2’. Developmental stages are denoted as follows: copepodid stages I–V (CI–V) and naupliar stages (NI–VI).

Female anterior body: A setulose lobe (supralabrum) on the anteroventral surface, anterior to the mouth (Fig. 1A), is a synapomorphy of the Euchaetidae (char. 1).

The copepod ‘rostrum’ has been defined as a median extension of the anterior margin of the dorsal cephalosome that carries the rostral sensory complex (Huys & Boxshall, 1991: 358), which includes a median pore and a pair of sensilla (Fig. 1A–C) and often a pair of rostral filaments. Hosfeld (1995/96) makes it clear that a pair of rostral filaments as in, for example, *Calanus* Leach, 1816, are a part of the complex, which is not found in *Euchaeta* Philippi, 1843 or *Chiridius* Giesbrecht, 1893 (Elofsson, 1971: 300). Hosfeld (1995/96) showed that the rostral sensory complex also includes the sensory pore X-organ (SPX-organ) (Elofsson, 1971; Hosfeld, 1995/96). Elofsson (1971) demonstrated the gross morphology of the organ, which includes a pair of nerves that emanate from the anterior portion of the brain and run each side of the naupliar eye towards the anterior of the animal. When studied with the electron microscope, the paired organ consists of three morphologically separate units combined within each nerve. The first unit is made up of a pair of heavily myelinated dendrites that continue on into two small anterior sensilla. The second unit consists of dendrites whose cilia are split in a distinct arrangement surrounded by a specialized glial cell. Hosfeld (1995/96: 187) and Elofsson (1971: 307) both confirmed that it is unit 3 which runs into the paired rostral filaments (Fig. 1C). These filaments have a porous cuticle in genera such as *Calanus* but were not present in *Euchaeta* or *Chiridius*. Little is known about these structures in other Calanoida. The following characters are likely to be related to the SPX-organ, the study of which could result in a deeper understanding of the evolution of the rostral area.

Hosfeld (1995/96) postulated that a bifurcate rostral margin with paired rostral filaments is the plesiomorphic state, and an unpaired rostral

Table 2. Morphological characters/states used for phylogenetic analysis, using *Neoscolecithrix* and *Thoxancalanus* as the outgroup, followed by the consistency index and rescaled consistency index

Character (states)	CI	RC
1. Supralabrum (1. Absent; 2. Present)	1.00	1.00
2. Female rostral filaments (1. Present; 2. Absent)	0.20	0.12
3. Female anterior head margin (1. Bifurcate; 2. Single extension; 3. Not produced)	0.15	0.08
4. Female seta II of caudal ramus (1. Present; 2. Absent or minute)	0.25	0.17
5. Female caudal ramus seta VII (1. Small; 2. Highly developed as appendicular seta)	1.00	1.00
6. Female caudal ramus seta VII insertion (1. Symmetrical; 2. Asymmetrical)	1.00	1.00
7. Female caudal rami seta VII inserted on (1. Inner border; 2. Ventral surface)	0.50	0.42
8. Female A1 ancestral segment I number non-aesthetasc setae (1. Three setae; 2. Two setae; 3. One seta)	1.00	1.00
9. Female A1 ancestral segment XXIII distal seta extends (1. Short of end of A1; 2. Well beyond end of A1)	0.50	0.46
10. Female antennule ancestral segments I and II (1. Separate; 2. Fused)	0.25	0.06
11. Female A1 ancestral segment 12 with (1. Two setae; 2. One seta; 3. Zero setae)	0.40	0.33
12. Female A1 ancestral segment 13 with (1. Two setae; 2. One seta; 3. Zero setae)	0.25	0.21
13. Female A1 ancestral segment 15 with (1. Two setae; 2. One seta; 3. Zero setae)	1.00	1.00
14. Female A1 ancestral segment 16 with (1. Two setae; 2. One seta)	0.25	0.13
15. Female A1 ancestral segment 17 with (1. Two setae; 2. One seta)	0.17	0.12
16. Female A1 ancestral segment 18 with (1. Two setae; 2. One seta)	0.25	0.18
17. Female A1 ancestral segment 19 with (1. Two setae; 2. One seta)	0.20	0.15
18. Female A1 ancestral segment 20 with (1. Two setae; 2. One seta)	0.25	0.17
19. Female A1 ancestral segment 21 with (1. Two setae; 2. One seta)	1.00	1.00
20. Female A2 basis and endopod segment 1 (1. Separate; 2. Fused)	0.50	0.25
21. Female A2 exopod segment 1 and 2 (1. Separate; 2. Fused)	0.50	0.44
22. Female A2 exopod segments 4 and 5 (1. Separate; 2. Fused)	1.17	0.11
23. Female A2 exopod segment 1 seta (1. Present; 2. Absent)	0.09	0.04
24. Female A2 exopod segment 2 seta (1. Present; 2. Absent)	0.13	0.07
25. Female A2 exopod segment 3 seta (1. Present; 2. Absent)	0.17	0.06
26. Female A2 exopod segment 4 seta (1. Present; 2. Absent)	0.33	0.00
27. Female A2 exopod segment 9 seta (1. Present; 2. Absent)	0.11	0.04
28. Female Mn basis seta 4 (1. Present; 2. Absent)	0.50	0.45
29. Female Mn basis seta 3 (1. Present; 2. Absent)	0.11	0.07
30. Female Mn basis seta 2 (1. Present; 2. Absent)	0.25	0.16
31. Female Mn basis seta 1 (1. Present; 2. Absent)	0.50	0.00
32. Female Mn endopod segment 1 seta 4 (1. Present; 2. Absent)	0.50	0.44
33. Female Mn endopod segment 1 seta 3 (1. Present; 2. Absent)	0.20	0.14
34. Female Mn endopod segment 1 seta 2 (1. Present; 2. Absent)	0.17	0.11
35. Female Mx1 coxal endite seta 5 (1. Present; 2. Absent)	0.11	0.05
36. Female Mx1 coxal endite seta 4 (1. Present; 2. Absent)	0.17	0.13
37. Female Mx1 coxal endite seta 3 (1. Present; 2. Absent)	0.33	0.20
38. Female Mx1 coxal endite seta 2 (1. Present; 2. Absent)	1.00	1.00
39. Female Mx1 basal endite 2 seta 5 (1. Present; 2. Absent)	0.17	0.05
40. Female Mx1 basal endite 2 seta 4 (1. Present; 2. Absent)	0.20	0.07
41. Female Mx1 arthrodistal membrane between basis and endopod segment 1 (1. Present; 2. absent)	0.10	0.03
42. Female Mx1 arthrodistal membrane between endopod segment 2 and 3 (1. Present; 2. Absent)	0.09	0.04
43. Female Mx1 exopod seta 11 (1. Present; 2. Absent)	0.17	0.12
44. Female Mx1 exopod seta 10 (1. Present; 2. Absent)	0.33	0.24
45. Female Mx1 exopod seta 9 (1. Present; 2. Absent)	0.33	0.24
46. Female Mx1 exopod seta 8 (1. Present; 2. Absent)	1.00	1.00
47. Female Mx1 exopod seta 7 (1. Present; 2. Absent)	1.00	1.00
48. Female Mx1 coxal epipodite seta 9 (1. Present; 2. Absent)	0.09	0.03
49. Female Mx1 coxal epipodite seta 8 (1. Present; 2. Absent)	0.14	0.05

Table 2. *Continued*

Character (states)	CI	RC
50. Female Mx1 coxal epipodite seta 7 (1. Present; 2. Absent)	0.17	0.05
51. Female Mx1 coxal epipodite seta 6 (1. Present; 2. Absent)	0.33	0.11
52. Female Mx1 coxal epipodite seta 5 (1. Present; 2. Absent)	0.50	0.25
53. Female Mx1 coxal epipodite seta 4 (1. Present; 2. Absent)	0.50	0.25
54. Female Mx2 praecoxal endite 1 seta 5 (1. Present; 2. Absent)	0.33	0.28
55. Female Mx2 praecoxal endite 1 seta 4 (1. Present; 2. Absent)	1.00	1.00
56. Female Mx2 basal endite seta 4 (1. Present unmodified; 2. Present, modified; 3. Absent)	0.50	0.43
57. Female Mx2 endopod seta 1 (1. Untransformed; 2. Transformed)	1.00	1.00
58. Female Mx2 endopod seta 2 (1. Untransformed; 2. Transformed; 3. Absent)	1.00	1.00
59. Female Mx2 endopod seta 3 (1. Untransformed; 2. Transformed; 3. Absent)	1.00	1.00
60. Female Mx2 endopod seta 4 (1. Untransformed; 2. Transformed)	1.00	1.00
61. Female Mx2 endopod seta 5 (1. Untransformed; 2. Transformed)	1.00	1.00
62. Female Mx2 endopod seta 6 (1. Untransformed; 2. Transformed; 3. Absent)	0.67	0.44
63. Female Mx2 endopod seta 7 (1. Untransformed; 2. Transformed; 3. Absent)	0.17	0.06
64. Female Mx2 endopod seta 8 (1. Untransformed; 2. Transformed; 3. Absent)	0.22	0.09
65. Female Mx2 endopod seta 9 (1. Untransformed; 2. Transformed; 3. Absent)	0.33	0.11
66. Female Mxp syncoxal endite 3 seta 3 (1. Present; 2. Absent)	0.50	0.25
67. Female Mxp syncoxal endite 4 seta 4 (1. Present; 2. Absent)	0.50	0.43
68. Female Mxp syncoxa terminal sensory appendage (1. Absent; 2. Present)	0.50	0.40
69. Female Mxp endopod segment 2 seta 4 (1. Present; 2. Absent)	0.20	0.00
70. Female Mxp endopod segment 3 seta 4 (1. Present; 2. Absent)	0.17	0.05
71. Female P1 basis outer border seta (1. Present; 2. Absent)	0.14	0.09
72. Female P1 basis inner border seta (1. Present; 2. Absent)	0.50	0.38
73. Female P1 exopod segment 1 outer edge spine (1. Present; 2. Absent)	0.14	0.06
74. Female P1 endopod with (1. Five setae; 2. Four setae)	1.00	1.00
75. Female P1 arthrodistal membrane between exopod segments 1 and 2 (1. Present; 2. Absent or partial)	1.00	1.00
76. Female P2 arthrodistal membrane between endopod segments 1 and 2 (1. Present; 2. Absent)	1.00	1.00
77. Female P2–P3 basis distoposterior border spinous extensions (1. Absent; 2. Present)	1.00	1.00
78. Female P4 coxa inner seta (1. Present; 2. Absent)	1.00	1.00
79. Female P4 coxa inner proximal border large spines (1. Present; 2. Absent)	0.50	0.25
80. Female P5 (1. Present; 2. Absent)	0.13	0.08
81. Male A1 ancestral segments I and II (1. Separate; 2. Fused)	0.20	0.10
82. Male geniculate or right A1 ancestral segments XI and XII (1. Separate; 2. Fused)	0.11	0.04
83. Male A1 ancestral segments XXII and XXIII (1. Fused on one side; 2. Fused on both sides; 3. Separate on both sides)	0.15	0.05
84. Male mouthparts (1. Same as female; 2. Inner parts atrophied)	0.20	0.13
85. Male right P5 (1. Biramous; 2. Uniramous; 3. Absent)	0.33	0.26
86. Male right P5 basis swollen relative to coxa (1. Absent; 2. Present)	0.25	0.19
87. Male left P5 (1. Biramous; 2. Uniramous; 3. Absent)	0.20	0.16
88. Male left leg 5 exopod segment 3 opposed to extension of segment 2 (1. Absent; 2. Present)	0.08	0.04
89. Male left P5 exopod segment 2 serrated lamella (1. Absent; 2. Present)	1.00	1.00

Male characters (81–89) were omitted from the analysis.

Abbreviations: A1, antennule; A2, antenna; CI, consistency index; Mn, mandible; Mx1, maxillule; Mx2, maxilla; Mxp, maxilliped; P1–P5, legs 1–5; Pd5, pedigerous somite 5; RC, rescaled consistency index.

margin with paired filaments represents a derived state (Fig. 1D). In the Clausocalanoidea, a further modification seems to be loss of paired rostral filaments (Fig. 1E), with unit 3 of the anterior nerve presumably ending in the cuticle (Elofsson, 1971). We note, from a re-examination, that *Farrania* does not have an anterior head rostral extension (unlike the

description by Vervoort, 1951) nor does it have rostral filaments.

In our data set, we included the nature of the frontal margin of the head, which may or may not have rostral filaments (char. 2) and may or may not extend into bifurcate points (Fig. 1E), into a single structure (pointed or rounded), or not be produced (char. 3).

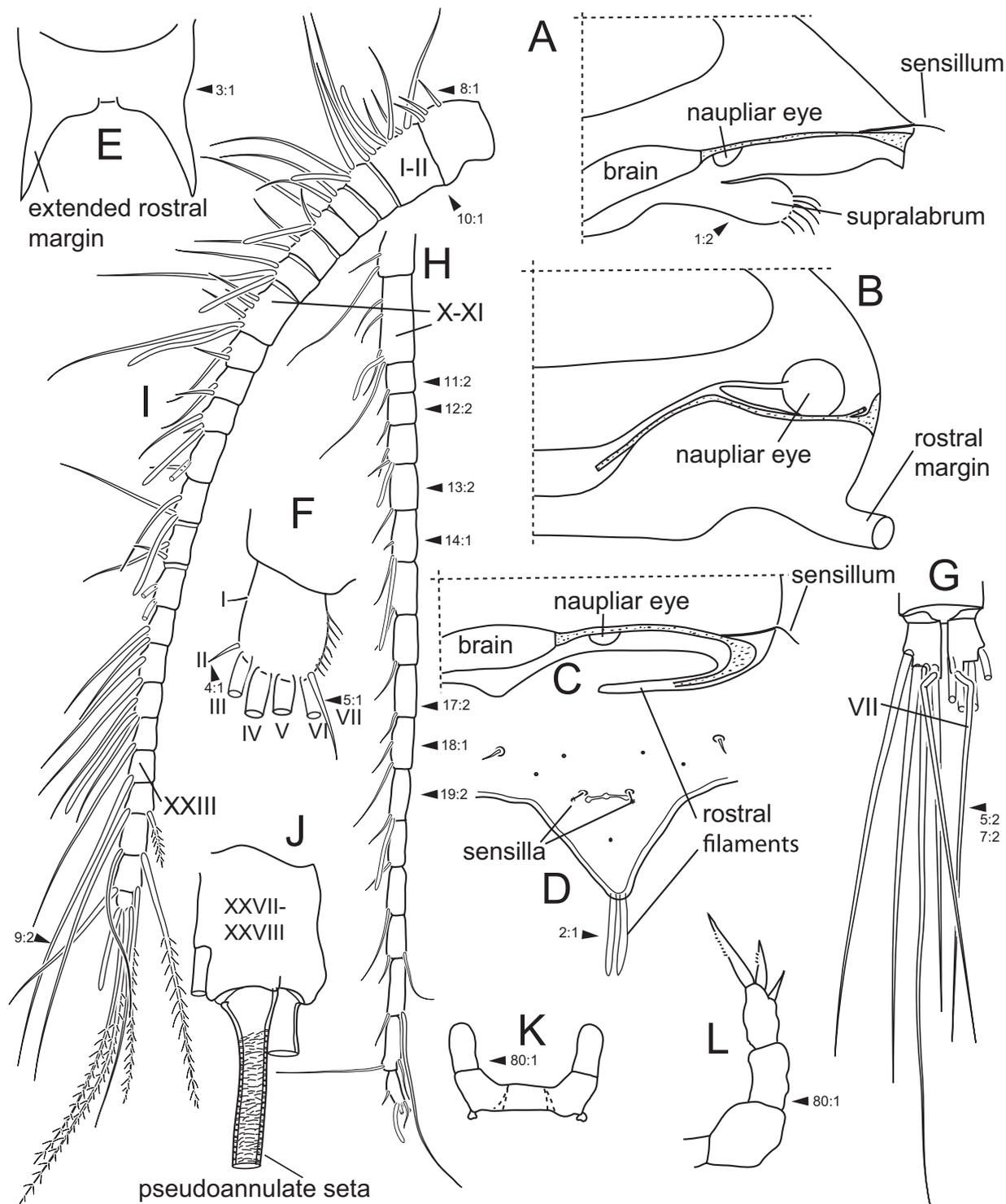


Figure 1. Illustrations of character location and selected states for characters in Table 2. Female: schematic longitudinal cross-section of head region of: A, *Euchaeta*; B, *Chiridius*; C, *Calanus*; stippled region represents sensory pore X-organ in the sense of Elofsson (1971). Frontal margin of head: D, *Stygocyclops*; E, *Aetideus*. Caudal rami: F, schematic, ventral view; G, Euchaetidae, ventral view. Antennule: H, *Drepanopus*; I, *Bradyidius*. J, *Sursamucro* pseudoannulate seta, dorso-terminally on right antennular segment XXVIII. Leg 5: K, *Paracomantenna*; L, *Pseudotharybis*. (Figures modified and redrawn from: Elofsson, 1971; Bradford, 1971; Hulsemann, 1991; Park, 1995; Jaume *et al.*, 2001; Bradford-Grieve, 2003; Markhaseva & Schnack-Schiel, 2003; Ohtsuka *et al.*, 2005; Markhaseva & Schulz, 2008; Bradford-Grieve *et al.*, 2017). Character and states are indicated; for example, '◄ 1:2'.

Female caudal rami: The setation of the caudal rami in copepods was analysed by Huys & Boxshall (1991), who noted the presence of seven setae, primitively. Seta I is usually absent in most clausocalanoidean taxa apart from a few plesiomorphic aetideids, pseudocyclopiids and one outgroup member (*Neoscolecithrix*). Setae II–VII are present in most Clausocalanoidea. Seta II is apparently absent in *Mesocomantenna* Alvarez, 1986, *Mesaiokeras*, *Clausocalanus*, *Ctenocalanus* Giesbrecht, 1888, *Microcalanus*, *Paivella* Vervoort, 1965 and the Stephidae (char. 4). Seta VII is usually short but is elongated and strongly developed in the Euchaetidae (Fig. 1G) (char. 5). Seta VII may be inserted symmetrically on each caudal ramus or asymmetrically as in *Mesaiokeras* and *Speleohvarella* (char. 6). Seta VII is inserted on the inner border in *Microcalanus*, *Pseudocyclopia*, some *Thompsonopia*, most Stephidae and *Mesaiokeras* (char. 7), but the remaining genera have this seta inserted on the ventral surface (Fig. 1G), although the plesiomorphic position of insertion of this seta is on the dorsal surface (Huys & Boxshall, 1991: 28). We noted that *Farrania* has seta VII inserted on the ventral surface, a fact not mentioned by Vervoort (1951).

Female antennule: Uttieri *et al.* (2008) characterized the antennular setae of *Clausocalanus furcatus* (Brady, 1883). There were aesthetascs and simple setae with a smooth external surface and a tapering tip (two serrulate setae were on both segments I and XXVII–XXVIII) on most segments, but pseudoannulate setae are not mentioned. A few modified, possibly bimodal mechano-chemoreceptive, setae were found on segments V, IX, X–XI, XVI, XII, XVII, XX and XXIII.

In the non-‘Bradfordian’ clausocalanoidean genera, there are two distribution patterns for the longest, non-aesthetasc setae: the first set of taxa have the longest setae typically on ancestral segments V, IX, XI, XVI, XX, XXIII and XXVII–XXVIII (Frost & Fleminger, 1968: 111), with the remaining setae being short and straight along the other segments of the limb (Clausocalanidae and the more derived Aetideidae) (Fig. 1H). In planktonic Aetideidae, these setae are moderately long, being two to three times the length of a segment, but in the Euchaetidae these setae are extremely developed, being up to nine times the length of their segment, and are arranged in three planes with a specialized basal articulation that allows rotation of each seta to streamline the antennule during escape movements (Yen & Nicoll, 1990; Boxshall *et al.*, 1997).

In contrast, a second set of taxa have setae that are consistently longer, often conspicuously pseudoannulate and curved (Weatherby *et al.*, 1994) (Fig. 1I) (*Bradyetes* Farran, 1905, *Comantenna* Wilson, 1924, *Crassantenna* Bradford, 1969, *Farrania*, *Lutamator* Bradford, 1969, *Mesocomantenna*,

Parabradyidius Schulz & Markhaseva, 2000, *Paracomantenna*, *Prolutamator*, *Pseudeuchaeta*, *Sursamucro* Bradford, 1969 and *Pseudotharybis*). Pseudoannulate setae are textured in scanning electron microscope photographs of *Pleuromamma* (Weatherby *et al.*, 1994: 676, fig. 4d), and the cuticle appears to be unevenly thickened in *Sursamucro* using a light microscope (Fig. 1J). The nature and function of the pseudoannulation is not known. Nevertheless, Petra Lenz, University of Hawaii (pers. com.) speculates that these setae might be strengthened in some fashion to allow bending and may be serviced by bend-sensitive neurons, as proposed by Garm *et al.* (2004) for setae on some of the mouthparts of the spiny lobster *Panulirus argus* (Latreille, 1804). We note that the pseudoannulate type of seta is conspicuous in benthopelagic Clausocalanoidea. Such setae are also present in *Mesaiokeras* (Schulz & Kwasniewski, 2004) but are not as long as in the Aetideidae. To represent the elongate, pseudoannulate type of setation, the length of the distal seta on ancestral segment XXIII in relationship to the end of the antennule (char. 9) was recorded. That is, this seta extends either short of, or well beyond, the end of the antennule. Note that the pseudoannulate seta on segment XXIII of *Farrania* extends well beyond the end of the antennule, not as illustrated by Vervoort (1951).

Ancestral segment 1 primitively has three setae (Boxshall & Huys, 1998). The distal seta is always present and well developed, but one or both proximal setae may be absent. It is assumed that where there are two setae it is the same two that are present. The number of setae (one, two or three) on ancestral segment I was recorded (char. 8).

In some genera of Pseudocyclopiidae and Stephidae, ancestral segments I and II are partly fused, without a fully formed arthrodistal membrane between them. This characteristic in the Pseudocyclopiidae is associated with very short antennules. Whether ancestral segments I and II are separate or fused was noted (char. 10).

There is a dichotomy in the number of female non-aesthetasc setae on the antennule (Markhaseva & Renz, 2015) between the Clausocalanidae + Pseudocyclopiidae + Stephidae + Mesaiokeratidae and the Aetideidae + Euchaetidae (Supporting Information, Appendix S2). That is, there tends to be one seta on most of ancestral segments XII, XIII, XV, XVII, XVIII, XIX and XXI in the Clausocalanidae, Stephidae, Pseudocyclopiidae and Mesaiokeratidae (Fig. 1H). The Aetideidae tend to have two setae on these segments, and the Euchaetidae has one seta on segments XII, XIII, XVII, XIX and two setae on XV, XVIII and XXI (Fig. 1I). ‘Bradfordian’ genera tend to have one seta on at least segments XII, XIII, XV and XXI and usually, but not always, on segments

XVII and XIX. Further examination of specimens of *Farrania frigida* (as *Drepanopus*) confirm Vervoort's (1951) observations, although we further note that an aesthetasc is found on each of ancestral segments III, VII, XI, XIV, XVII, XXI and XXVIII and that most setae along the whole antennule are conspicuously pseudoannulate (note that this genus is not known to have a benthopelagic habit; see Table 1). The number of non-aesthetasc setae on segments XII, XIII, XV, XVI, XVII, XVIII, XX and XXI is recorded (char. 11–19) in our data set. Preliminary analyses suggested that the distribution of aesthetascs does not contain phylogenetic information at the family level; therefore, these characters were omitted from the final analysis.

Female antenna: The antenna is analysed following the interpretation of Huys & Boxshall (1991) (Fig. 2A–D). In most taxa, the basis and endopod have a fully formed arthrodistal membrane between them, apart from three pseudocyclopiid genera (*Pseudocyclopia*, *Paracyclopia* and *Thompsonopia*) (char. 20) (Fig. 2C). Exopod segments I and II and IV and V may be fused or separate (char. 21, 22). Ancestral exopod segments I, II, III, IV and IX were investigated to determine whether (Fig. 2B) they bear one seta each (char. 23–27). Among the exemplars used, several taxa have a full suite of exopod setae, or only the proximal seta is absent, enabling the interpretation of which proximal ancestral segments are fused. Nevertheless, it was discovered that some taxa (*Clausocalanus*, *Pseudocalanus*, *Ctenocalanus*, *Azygokeras* Koeller & Littlepage, 1976 and *Bradyidius*) have the arthrodistal membrane between exopod segments I and II not evenly formed such that it was possible to interpret their state as either fused or separate (e.g. Fig. 2D'–D''). In some genera, it was clear that segments I and II are fused [*Bradyetes* (Markhaseva & Schulz, 2006), *Lutamator* (Bradford, 1969b; Alvarez, 1984), *Crassantenna* (Bradford, 1969b), *Pseudeuchaeta* (Markhaseva & Schulz, 2006), *Prolutamator* (Markhaseva & Schulz, 2006), *Sursamucro* (Bradford, 1969b), *Senecella* Juday, 1923 (Vyshkvartzeva, 1994), *Jaschnovia* Markhaseva, 1980 (Markhaseva, 1980)]. *Lutamator hurleyi* Bradford, 1969b was re-examined, and it was confirmed that setae of exopod segments 1 and 9 were absent. A second group of taxa was interpreted as having ancestral segments I and II separate (char. 21) (Fig. 2A) [*Aetideus* Brady, 1883, *Azygokeras*, *Ctenocalanus*, *Drepanopus* (cf. Hulsemann, 1991), *Farrania*, *Microcalanus*, *Mesaiokeras*, *Parabrydium*, *Peniculoides*, *Paracyclopia*, *Pseudocyclopia*, *Stygocyclopia*, *Bradyidius*, *Chirundina*, *Paivella*, *Pseudochirella*, *Miostephos*, *Parastephos*, *Speleohvarella*, *Pseudocalanus* and *Stephos*]. There are some genera within the Clausocalanoidea with more

than one proximal seta missing. In these cases, it was impossible to be certain which arthrodistal membrane has failed to develop; therefore, these were scored as 'unknown'.

Female mandible: Plesiomorphically, the mandibular palp has four setae on the basis and on endopod segment 1 (Huys & Boxshall, 1991: 20) (Fig. 2E). It is difficult to determine individual setal homologies for these segments because during development the full suite of setae is present at CI (Hulsemann, 1991), and in *Clausocalanus* nauplii there are four setae on the basis at naupliar stages NIV and NV (Björnberg, 1972). We assumed, initially, that the same total number of setae are homologous across clausocalanoidean genera. The characters used are presence or absence of setae 1–4 on the basis (char. 28–31) and setae 2–4 on endopod segment 1 (char. 32–34) (Fig. 2E).

Female maxillule: The maxillule, in the plesiomorphic state, is orientated such that the main axis of the limb almost passes through the endopod, and the praecoxal arthrite is directed into the animal's midline and has a conservative number of setae as analysed by Giesbrecht (1892/93) (Fig. 2F). In the Euchaetidae, the endopod is twisted through ~90° towards the animal's midline and overlaps the praecoxal arthrite, and the coxal and first basal endites are reduced or may be even absent, a characteristic that appears to be related to a carnivorous habit (Yen, 1985). In some aetideid taxa (e.g. *Pseudochirella obesa* Sars, 1920) the endopod also lies at ~90° to the main axis (von Vaupel Klein & Rijerkerk, 1997), and in *Euchirella messinensis* (Claus, 1863) the endopod lies at ~45° to the main axis (von Vaupel Klein, 1982), apparently related to an omnivorous habit (Sano *et al.*, (2013, 2015). The angle at which the endopod lies to the main axis of the limb was difficult to measure objectively and interpret; therefore, it was omitted from the final analysis.

Initially, we hypothesized that the reduced number of setae observed in the adult stage of many Clausocalanoidea maxillules represents the retention of larval states of development (by failure to add setae following the typical ancestral developmental sequence), and therefore it might be reasonable to assume that similar numbers of setae are strictly homologous. For example, it was noted that during development of Clausocalanidae (Heron & Bowman, 1971) CI and CII have three setae on basal endite 2, CIII and CIV have four setae, and CV and CVI have five setae. Of note were *Peniculoides*, *Pseudocyclopia*, *Paracyclopia*, *Thompsonopia*, *Stygocyclopia*, *Euchaeta*, *Paraechaeta* and *Spicipes*, all of which have only two setae on the coxal endite. The presence or absence of setae 2–5 on the coxal endite and setae 5 and 4 on basal endite 2 was noted (char. 35–40) (Fig. 2F).

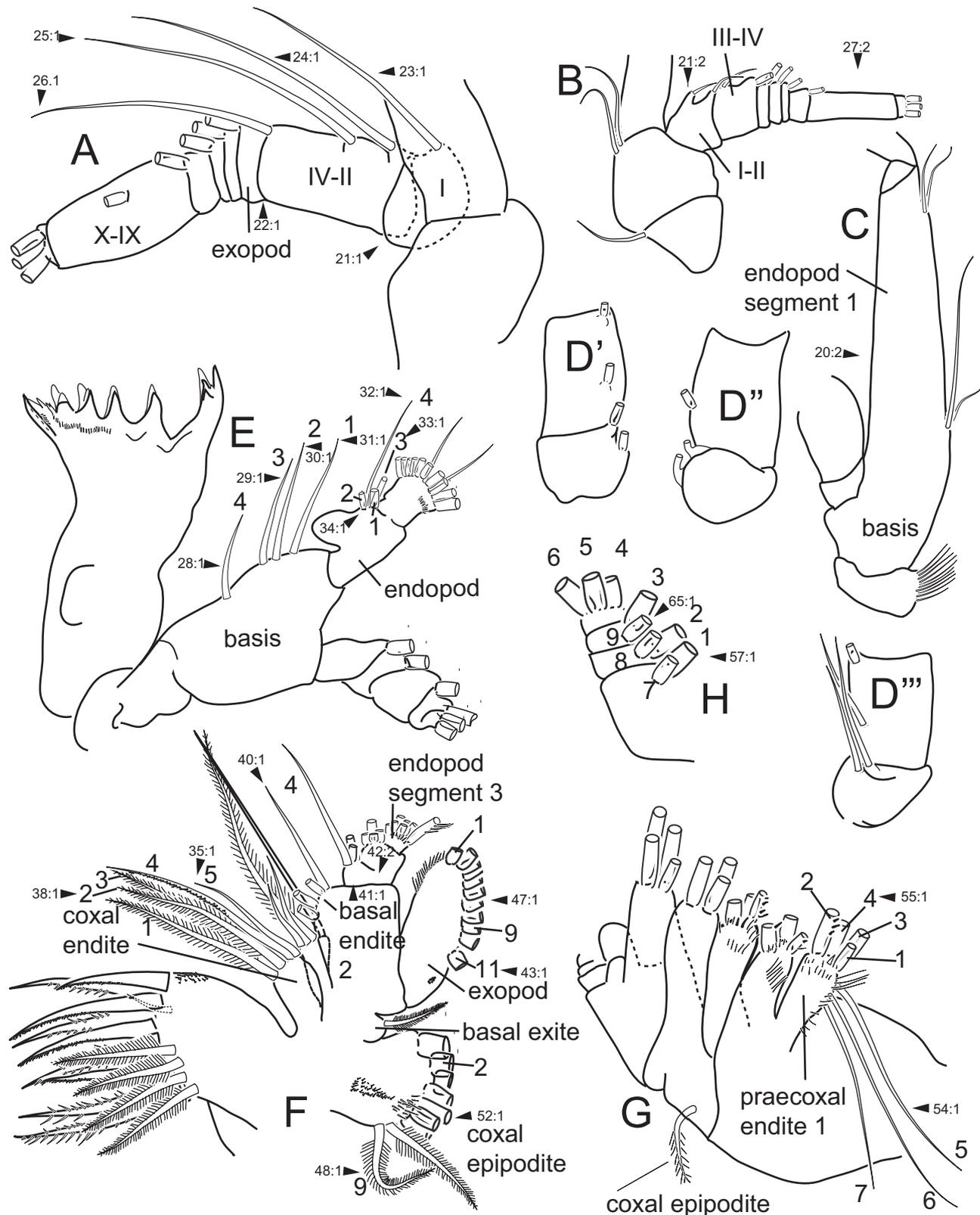


Figure 2. Illustrations of character location and selected states for characters in Table 2. Female: A, antenna exopod of *Megacalanus*; B, antenna exopod of *Bradyetes*; C, antenna basis and endopod of *Thompsonopia*; D–D”, three different views

The development of the maxillule endopod seems to express features of larval segmentation as observed in the Clausocalanidae (Heron & Bowman, 1971). It is very difficult to establish homologies among variable numbers of setae on each endopod segment throughout the Clausocalanoidea; therefore, these character states are not used. The presence or absence of an arthrodial membrane between the basis and endopod segment 1 and between endopod segments 2 and 3 were scored (char. 41, 42) (Fig. 2F). On the exopod, it was assumed that similar numbers of setae are homologous with taxon. It was noted that most genera have 11 or ten setae, with the fewest (fewer than nine) being found in *Peniculoides*, *Frigocalanus*, *Pseudocyclopia*, *Paracyclopia*, *Thompsonopia*, *Stygocyclopia*, *Mesaiokeras* and *Spicipes*. The presence or absence of setae 7–11 on the exopod (char. 43–47) was noted. The coxal epipodite appears to develop by the addition of setae proximally (see Bradford-Grieve *et al.*, 2010 and references therein). Therefore, we considered setae to be homologous, counting from the distal part of the epipodite. The presence or absence of setae 4–9 on the coxal epipodite (char. 48–53) was noted.

Female maxilla: The calanoid maxilla plesiomorphically has ten setae on the first praecoxal endite, four setae on the basal endite and 13 setae on a four-segmented endopod (Huys & Boxshall, 1991), but the maximum number of setae on the maxilla of Clausocalanoidea are five, four and nine setae, respectively.

As pointed out by Markhaseva & Renz (2015), the setation of praecoxal endite 1 is useful in separating the Clausocalanidae and Aetideidae. Praecoxal endite 1 has a maximum number of setae in the spinocalanid *Monacilla*: two medioterminal, two outer terminal and three proximal setae, plus an additional small attenuation (Fig. 2G). The Aetideidae and Euchaetidae have three terminal setae, with seta 4 (distomedial terminal seta) missing. A small number of taxa have from four to six setae. The presence or absence of setae 5 and 4 on praecoxal endite 1 (char. 54, 55) was recorded.

The maximum number of setae (four) on the basal endite of the ingroup is found in most Stephidae, Mesaiokeratidae and Clausocalanidae, but three in the Aetideidae and Euchaetidae. In the case of the outgroup taxa, the fourth seta is modified into a chemosensory structure (Ohtsuka *et al.*, 2003; Markhaseva *et al.*,

2014). The presence, absence or modification of seta 4 of the basal endite was recorded (char. 56).

The calanoid maxilla endopod has a maximal number of 11 setae on segments 1–4, as in *Megacalanus* (Bradford-Grieve *et al.*, 2017: 46), which are arranged as four, two, two and three, respectively. In the Clausocalanoidea there can be four separate endopod segments or the first segment may be fused to form an allobasis plus three separate segments. The maximum number of setae recorded in the Clausocalanoidea is nine. These are located on segments 1–4 as follows: two, two, two and three, respectively, in, for example, *Pseudochirella obesa* (von Vaupel Klein, 1998), *Euchirella messinensis* (von Vaupel Klein, 1982: 32) or *Lophothrix frontalis* (J.M.B.-G., pers. obs.). These setae are numbered from proximal to distal on the outer surface (from one to six) and from seven to nine from proximal to distal on the inner surface (Fig. 2H). In many taxa, the number of setae is reduced to six, and they are distributed one, one, one and three. In this case, it is assumed that it is the inner setae (7–9) that have been lost, especially given that, where setae 7–9 are present, they are often reduced in size (e.g. *Pseudochirella obesa*). The total number of well-developed endopod setae is most frequently six across the non-‘Bradfordian’ members of the superfamily, but a number of taxa retain additional rudimentary setae (e.g. one seta: *Aetideus* and *Lutamator*; two setae: *Euchirella*, *Chiridius*, *Bradyidius*, *Bradyetes*, *Parabradyidius*, *Prolutamator*, *Senecella*, *Pseudotharybis* and *Thompsonopia*; and three setae: *Aetideopsis*, *Paracomantenna* and *Pseudochirella*).

Where there are fewer than six setae it is interpreted that *Peniculoides* has setae 2, 3, 8 and 9 missing, and *Speleohvarella* and *Mesaiokeras* have setae 6–9 missing. The ‘Bradfordian’ families stand apart because most of the eight or nine setae found on the maxilla endopod are modified into chemosensory setae (Nishida & Ohtsuka, 1997). Therefore, the unmodified presence, absence or modification of setae 1–9 were recorded (char. 57–65).

Female maxilliped: Plesiomorphically, the maximum number of setae on the syncoxal endites is one, two, four and four (Fig. 3A) (Huys & Boxshall, 1991: 27). In the Clausocalanoidea, syncoxal endite 3 usually has only three setae (except *Mesaiokeras*, *Paracyclopia* and *Pseudocyclopia*, which have two setae), and endite 4 has three setae (except in *Bradyetes*, *Comantenna*,

of antenna exopod segments 1–4 of *Clausocalanus*, which illustrates the difficulty in deciding whether segments 1 and 2 are fused or separate (drawn by E. L. Markhaseva); E, mandible of *Megacalanus*; F, maxillule of *Megacalanus*; G, maxilla of *Monacilla*; H, schematic diagram of maxilla endopod with setae numbered: endopod segment 1 fused to form allobasis in this example. (Figures modified and redrawn from: Schulz, 1989; Markhaseva, 1996; Jaume *et al.*, 1999; Markhaseva & Schulz, 2006; Bradford-Grieve *et al.*, 2017). Character and states are indicated; for example, ‘◀ 1:2’.

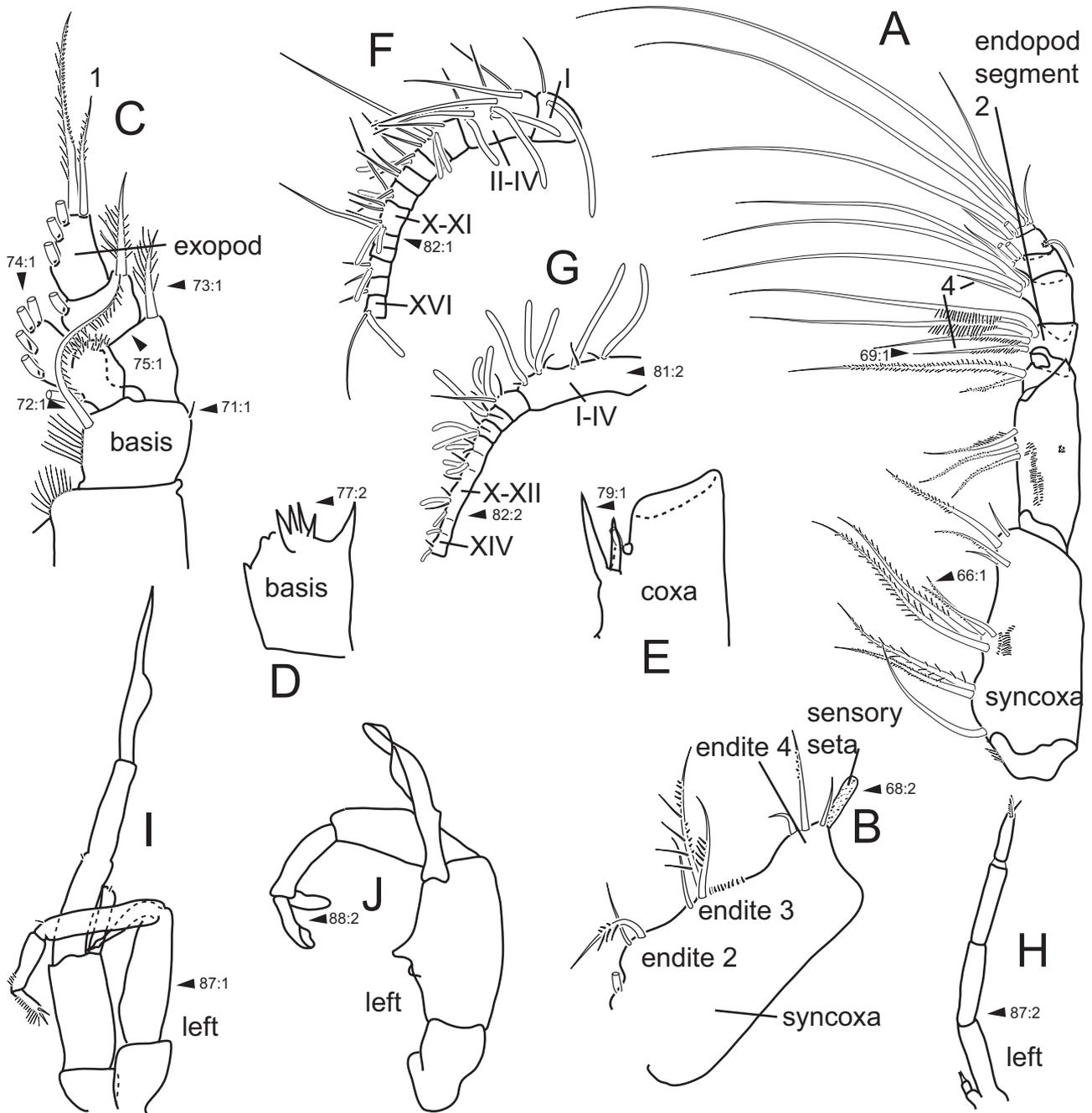


Figure 3. Illustrations of character location and selected states for characters in Table 2. Female: A, maxilliped of *Megacalanus*; B, syncoxa of maxilliped of *Paracomantenna*; C, leg 1 of *Paracomantenna*; D, basis of leg 3 of *Ctenocalanus*; E, coxa of leg 4 of *Euchirella*. Male: F, proximal antennule segments of *Mesaiokeras*; G, proximal antennule segments of *Clausocalanus*. Male leg 5: H, *Clausocalanus*; I, *Aetideopsis*; J, *Batheuchaeta* (left). (Figures modified and redrawn from: Bradford, 1969a; Bradford-Grieve, 1994; Markhaseva, 1996; Markhaseva & Schnack-Schiel, 2003; Bradford-Grieve *et al.*, 2017). Character and states are indicated, for example, '◀ 1:2'.

Crassantenna, *Lutamator*, *Mesocomantenna*, *Paracomantenna* and *Pseudeuchaeta*, which have four setae). Here, it is assumed, as a first approximation, that where there are fewer than the maximum number of setae, the lesser numbers of setae are

homologous among genera. Here, the presence or absence of seta 3 on syncoxal endite 3, and of seta 4 on endite 4 were recorded (char. 66, 67) (Fig. 3B). In some Aetideidae (*Bradyetes*, *Comantenna*, *Mesocomantenna*, *Paracomantenna*, *Pseudeuchaeta* and *Crassantenna*)

one of the setae on syncoxal endite 4 is modified into a sensory structure (char. 68) (Fig. 3B). The maximum number of setae on endopod segments 2–5 is four, four, three and three plus one, respectively. Endopod segments acquire setae during development in an order which is revealed by their length, i.e. the shorter setae were the most recently added (see Hulsemann, 1991). It is assumed that it is the later setae to be added that have failed to develop. The presence or absence of seta 4 on endopod segments 2 and 3 (Fig. 3A) was recorded (char. 69, 70).

Female legs: Legs 1–4 in the Clausocalanoidea have three-segmented exopods, whereas endopods are one-, two-, three- and three-segmented, respectively, with the arthroial membrane between segments 1, 2 and 3 having failed to develop in leg 1 and between segments 2 and 3 in leg 2. The female leg 1 basis in the Clausocalanoidea may or may not have an outer border reduced seta (char. 71), and the mediodistal seta may sometimes be absent (char. 72) (Fig. 3C). Leg 1 exopod segment 1 outer spine may or may not be present (char. 73). Leg 1 endopod usually bears five setae in most genera in this analysis, although *Microcalanus* and *Paracyclops* have only four setae (char. 74). The arthroial membrane between exopod segments 1 and 2 of leg 1 and between segments 1–2 of leg 2 may or may not be present (char. 75, 76). The presence of spine-like extensions on the distoposterior border of the basis of legs 2 and 3 (Fig. 3D) of *Ctenocalanus* and *Clausocalanus* was recorded (char. 77). The coxa of leg 4 usually bears an inner border seta (char. 78) except in *Clausocalanus* and *Ctenocalanus*. The inner border, proximal to this seta, is usually ornamented with very fine setules apart from in *Euchirella*, *Gaetanus*, *Valdiviella*, *Euchaeta*, *Paraechaeta*, *Parabradidius*, *Chirundina*, *Pseudochirella*, *Undeuchaeta*, Stephidae and Pseudocyclopiidae. Of these listed genera, *Gaetanus*, *Pseudochirella* and *Euchirella* all have large, well-defined spinules (char. 79) (von Vaupel Klein, 1998) proximal to the inner border seta (Fig. 3E); smaller strong spinules are also present in *Undeuchaeta*, *Aetideus* and *Paivella* (Bradford, 1980; Markhaseva, 1996). Typically, the lack of an ornamentation of fine setules is correlated with the presence of heavy spinules, suggesting that strong spinules are modified fine setules. Nevertheless, *Paivella* has two rows of small spinules in addition to fine setules.

Female Clausocalanoidea are either without leg 5 or have simple fifth legs (Fig. 1K, L) composed of a fused basal part comprising the fused coxae and the intercoxal sclerite, a globular basis and a terminal segment that is a featureless rudiment (*Sursamucro*) or, more usually, a cylindrical segment with one to three spine-like extensions, which may be fused to,

or variously articulated with, the segment (Fig. 1K, L) (*Pseudotharybis*, *Parabradidius*, *Stygocyclops*, *Frigocalanus*, *Thompsonopia*, *Paracyclops*, *Pseudocyclops*, *Mesaiokeras*, *Spicipes*, *Farrania* and *Clausocalanus*). In addition to these forms, *Ctenocalanus* and some *Comantenna* do not have a third segment. *Comantenna* has a multi-segmented exopod and rudimentary endopod. The presence or absence of fifth legs was coded (char. 80). *Farrania* may or may not have a fifth leg in the female (Tanaka, 1956). Although it is tempting to assume that the presence of a fifth leg is the plesiomorphic state, the presence of fifth legs on females of some apparently non-basal Aetideidae (e.g. *Comantenna*, *Paracomantenna*, *Parabradidius*, *Sursamucro* and *Pseudotharybis*) suggests that in some genera this is a homoplasious feature and possibly not homologous across the Aetideidae, Clausocalanidae, Pseudocyclopiidae, Stephidae and Mesaiokeratidae.

Male antennules and mouthparts: A group of clausocalanoidean families were placed in the no-longer-accepted grouping, the Isokerandria, by Sars (1902: 56). This group was based on the nature of the male antennules and mouthparts and the general body shape, i.e. the proximal segments of the male and female antennules and the general body shape do not differ appreciably, and male mouthparts are usually identical to those of the female. Sars (1902: 57) noted that genera in this grouping are benthopelagic. Markhaseva & Renz (2015) noted that Clausocalanidae males have ancestral segments I and II of the antennule fused (Fig. 3G), whereas these segments in the Aetideidae are separate. We also noted that segments I and II are fused in both males and females of *Stygocyclops*, *Pseudocyclops* and *Stephos*, whereas in *Frigocalanus* and *Mesaiokeras* the female and male antennules have segments I and II separate (Fig. 3F).

The right antennule in the genus *Azygokeras* is adapted for grasping but is not in the form of a geniculation between ancestral segments XX and XXI (Boxshall, 1985: 320; Ohtsuka & Huys, 2001; Bradford-Grieve *et al.*, 2017: 13). That is, from segments XIX to XXIV in *Azygokeras* there are separate flexor muscles capable of bending each joint relative to its neighbour (J.M.B.-G., unpublished data). This type of grasping antennule is an autapomorphy and so is not included in our data set. Male antennules may or may not have ancestral segments I and II (char. 81) and ancestral segments XI and XII fused (char. 82). Ancestral segments XXII and XXIII may be separate on both sides, fused on one side or fused on both sides (char. 83), and male mouthparts may have the inner parts too reduced to be functional or developed in a similar manner to the female (char. 84).

Male leg 5: In members of the Clausocalanoidea, leg 5 may be biramous or uniramous or sometimes absent on one side and is often very slender (Fig. 3H–J). The number of rami on the right leg 5 (char. 85) was recorded, in addition to whether or not the right basis is swollen, as in some aetideid genera and the Euchaetidae (char. 86). The number of rami on the left leg 5 (char. 87) was recorded. The presence of an extension of the left exopod segment 2, which opposes exopod segment 3 (char. 88), was recorded, in addition to the presence or absence of a serrated lamella on left exopod segment 2, which is a unique character for the Euchaetidae (char. 89). In the final analysis, the male characters were omitted because there were six genera for which males have not been described, plus six where the existing descriptions were incomplete.

ANALYTICAL METHODS

A database of 50 taxa including the outgroup (Table 1) and 89 morphological characters was initially created using the DELTA software (Dallwitz *et al.*, 1993) and output as a nexus file (Supporting Information, Appendix S3). Most characters are binary, although 12 characters have three states. Inapplicable characters were coded '?'. Characters were unordered and equally weighted. Given that characters are unordered, the scores given for each state (1, 2 or 3) imply nothing about polarity.

Phylogenetic analysis under maximum parsimony was conducted in PAUP v.4.0a163 (Swofford, 2002). Analyses were conducted using the heuristic search (1000 replicates with random input order; branching swapping: tree bisection–reconnection). Strict consensus and majority rule consensus trees were computed. Jackknife support for each node using unweighted data was determined in PAUP (30% characters deletion; 500 pseudoreplicates). The data set was finally analysed under a single round of successive weighting using the rescaled consistency index (Farris, 1969). Character state distribution was studied in MacClade v.4.0 (Maddison & Maddison, 2000).

RESULTS

CLADISTIC ANALYSIS

Using *Neoscolecithrix* and *Thoxancalanus* as the outgroup, the heuristic search retrieved 394 most parsimonious trees of length 330, consistency index 0.273 and retention index 0.659. In the strict consensus tree, the Aetideidae were grouped together, but there were many unresolved relationships (Fig. 4A). The 50% majority rule consensus tree (Fig. 4B) had more resolved relationships, and Pseudocyclopiidae genera

+ *Peniculoides* were grouped together, as were the Clausocalanidae + Stephidae + Mesaiokeratidae. The Pseudocyclopiidae + *Peniculoides* were sister to all other genera.

In the 50% majority rule consensus tree (Fig. 4B) there were only two basal monophyletic clades with high jackknife support (98 and 93%, respectively). Clade A contained all the non-‘Bradfordian’ taxa and clade B the Aetideidae + Euchaetidae + Clausocalanidae + Stephidae + Mesaiokeratidae. Six terminal clades had strong to medium jackknife support (*Comantenna* + *Mesocomantenna*, *Jaschnovia* + *Senecella*, *Euchaeta* + *Paraeuchaeta*, *Clausocalanus* + *Ctenocalanus*, *Peniculoides* + *Frigocalanus* and *Paracyclopia* + *Pseudocyclopia* + *Stygocyclopia* + *Thompsonopia*). Many intermediate clades had < 50% jackknife support (Fig. 4B). In the jackknife analysis, if random selection of characters does not include the few characters most consistent with the cladogram, the topology will not be well supported. This result reflects the high homoplasy among the characters used in this analysis (more than half the characters) and is indicated by the low values for the rescaled consistency index (RC) (Table 2).

As indicated by the RC index for each character (Table 2), 39 out of 80 female characters made no or a small contribution (RC < 0.20) to the resulting topologies. Among the characters with RC > 0.20, some have been recognized historically in the family classification of the Clausocalanoidea (see Boxshall & Halsey, 2004). For example, in the ingroup, all setae of the maxilla endopod are untransformed compared with most of these setae being transformed into chemosensory elements in the outgroup (char. 57–65); the Euchaetidae has been defined by the presence of a supralabrum and highly developed caudal seta VII (char. 1 and 5, respectively); some Pseudocyclopiidae have the basis and endopod segment 1 of the antenna fused (char. 20); and Aetideidae and Euchaetidae have only three setae on praecoxal endite 1 of the maxilla (char. 54, 55). Other characters that have high RC values have not been widely recognized as having phylogenetic significance; the quantitative distribution of non-aesthetasc setae on certain antennular segments, for example. Thus, these analyses indicated that the presence of two setae on ancestral segment XXI is a synapomorphy for the clade containing the Aetideidae + Euchaetidae (char. 19) (e.g. Fig. 5E).

One round of successive reweighting (to reduce the influence of homoplasious character states on tree topologies) yielded a single most parsimonious tree. The strict and 50% majority rule consensus trees were identical. The 50% majority rule consensus tree is illustrated (Fig. 6) and differed in some respects from the trees derived from unweighted data (Fig. 4). In the reweighted analysis, all the relationships amongst

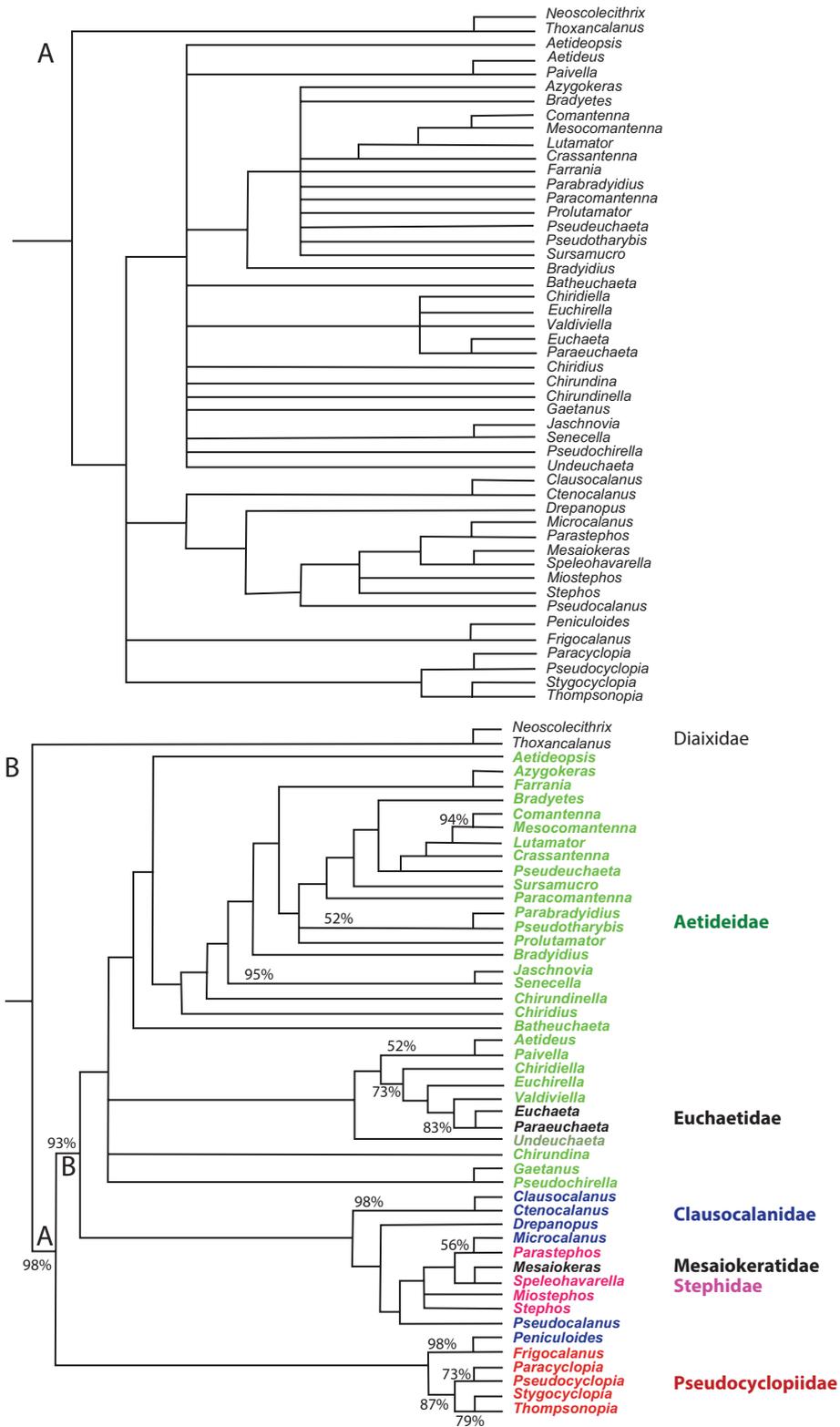


Figure 4. Strict consensus (A) and 50% majority rule consensus (B) of 394 most parsimonious trees of length 330, consistency index (CI) 0.273 and retention index (RI) 0.659. Clade numbers 1 and 2 are indicated, as is the jackknife support. The outgroup is *Neoscolecithrix* and *Thoxancalanus*. Current family groupings of genera are indicated in colour. For species exemplars, see [Table 1](#).

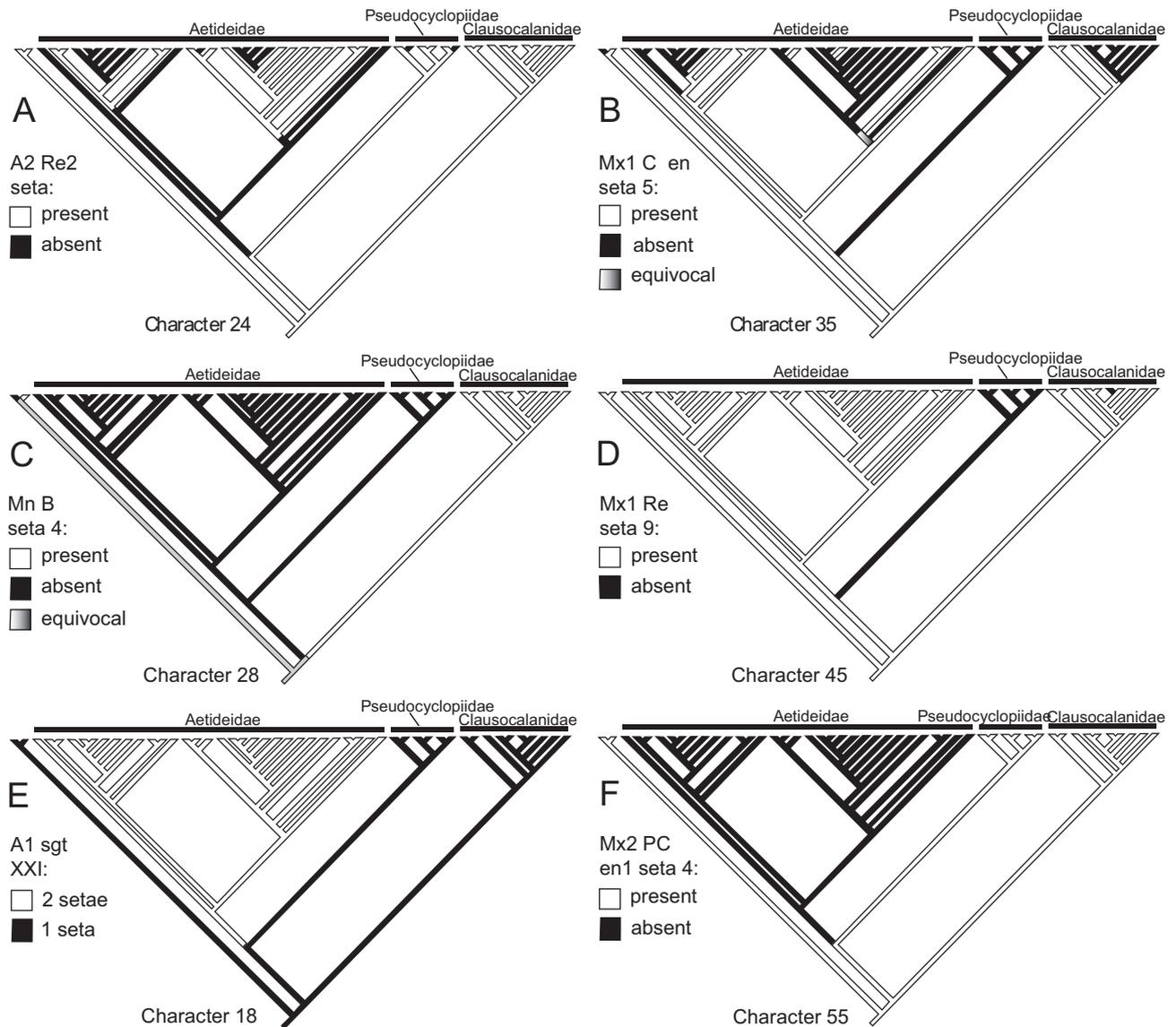


Figure 5. Distribution of unambiguous character state changes for six characters. A, B, homoplasious characters; C, for clade 1 (Clausocalanidae *s.l.*); D, for clade 4 (Pseudocyclopiidae); E, F, for clade 3 (Aetideidae) and clades 1 and 4. For genus labels, see [Figure 4](#). For character list, see [Table 2](#).

the genera were resolved. The clade containing Clausocalanidae, Stephidae and Mesaiokeratidae was the same as that derived from the unweighted data except that this clade was sister to all other genera in the reweighted tree. In the reweighted analysis, the clade containing the Aetideidae and Euchaetidae had the relationships of some genera differently resolved; nevertheless, *Aetideopsis* was sister to all other Aetideidae using both unweighted and reweighted data.

In the final tree, after one round of successive reweighting, clade 1 (Clausocalanidae + Stephidae + Mesaiokeratidae) ([Fig. 6](#)) was united by two character

states: seta 4 of the mandibular endopod segment 1 (char. 32: present) and seta 11 of the maxillule exopod (char. 43: present) ([Tables 2](#) and [3](#)). Clade 2 was united by one character: seta 5 of the maxilla praecoxal endite 1 (char. 54: absent). Clade 2 divided into clades 3 and 4 ([Fig. 6](#)). Clade 3 (Aetideidae + Euchaetidae) was united unambiguously by two character state changes that did not change above in the clade: the number of non-aesthetasc setae on antennule ancestral segment XXI (char. 21: two setae) and the maxilla praecoxal endite 1, seta 4 (char. 55: absent). Seven other characters united this clade ([Tables 2](#) and [3](#)), amongst which were: rostral filaments (char. 2:

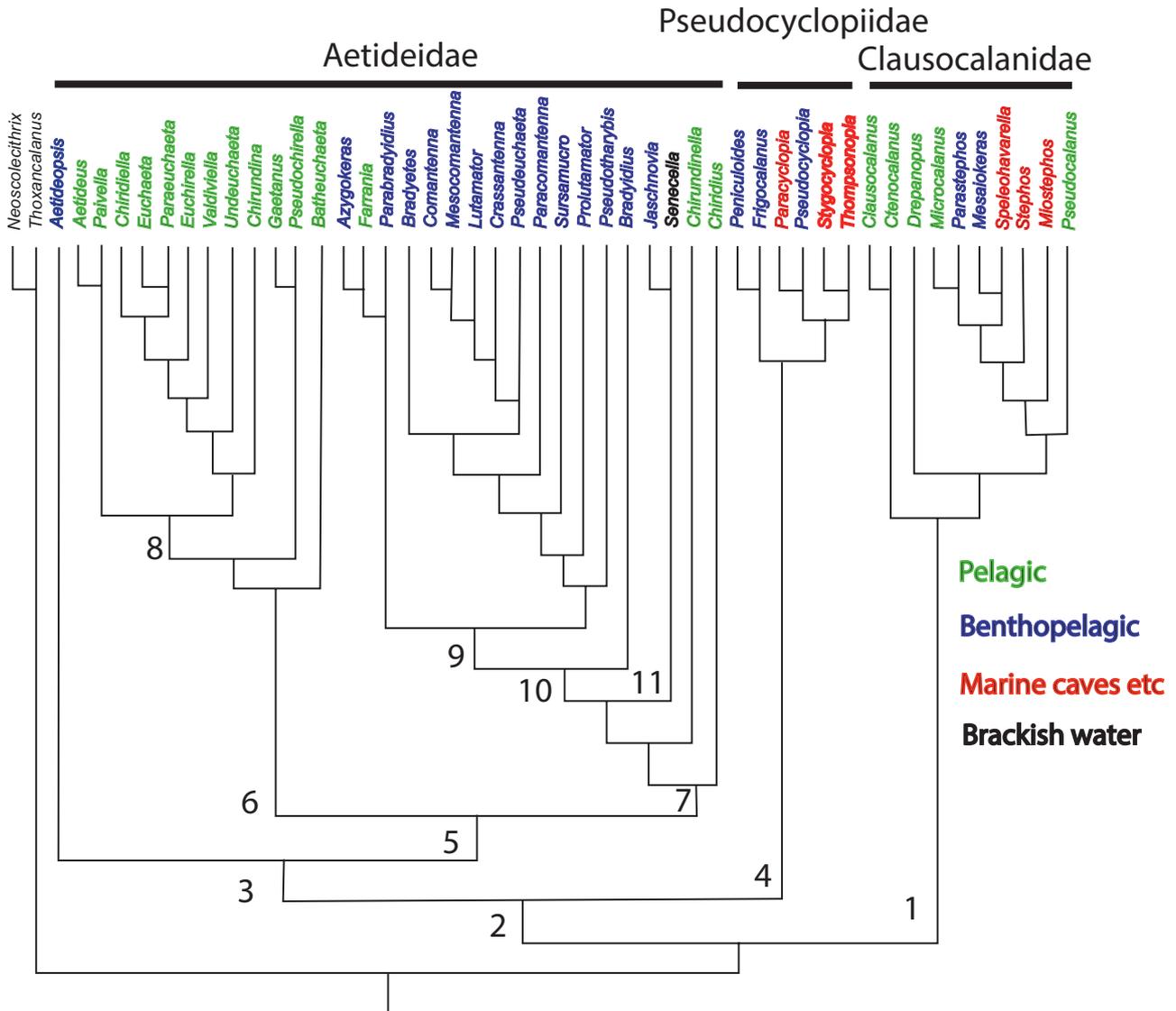


Figure 6. The 50% majority rule consensus of the single final maximum parsimony tree after one round of successive reweighting. Clade number is to the left of the line. Outgroup is *Neoscolecithrix* and *Thoxancalanus*. Family groups are indicated. For species exemplars, see [Table 1](#).

absent), and setae on ancestral segment XIII of antennule (char. 12: two setae). In clade 3, *Aetideopsis* was sister to all the remaining Aetideidae (clade 5). Clade 4 (Pseudocyclopiidae + *Peniculoides*) was united by four character states: maxillule coxal endite setae 4 and 5 (char. 35 and 36: absent) and maxillule exopod setae 9 and 10 (char. 44 and 45: absent). Clade 5 was united unambiguously by one character state change that did not change above in the clade: the number of non-aesthetasc setae on antennular ancestral segment XV (char. 13: two setae). The other character uniting this clade was the number of non-aesthetasc setae on antennular ancestral segment XVII (char. 15: two setae). Clade 5 divided into clades 6 and 7. Clade 6

was united by one character state change: seta 11 on the exopod of the maxilla (char. 43: present). Clade 7 was united by two character state changes: setae 7 and 8 on the endopod of the maxilla (char. 63 and 64: untransformed). Clade 8 was united unambiguously by one character state change that did not change above in the clade: leg 2 arthrodistal membrane between endopod segments 1 and 2 (char. 76: absent). Clade 9 was united unambiguously by one character state change that did not change above in the clade: number of non-aesthetasc setae on antennular segment I (char. 8: one seta). Two other character states united this clade ([Table 3](#)). Clade 10 was united by two character states: distal seta of antennular segment XXIII

Table 3. Unambiguous character state changes for the single most parsimonious tree after one round of successive reweighting (Fig. 6)

Clade 1	32: 2→1, 43: 2→1
Clade 2	54: 1→2
Clade 3	2: 1→2, 12: 2→1, 19: 2→1 , 22: 2→1, 24: 1→2, 29: 1→2, 55: 1→2 , 56: 1→3, 80: 1→2
Clade 4	35: 1→2, 36: 2→1, 44: 1→2, 45: 1→2
Clade 5	13: 2→1 , 15: 2→1
Clade 6	43: 2→1
Clade 7	63: 3→1, 64: 3→1
Clade 8	76: 1→2
Clade 9	8: 1→3 , 43: 2→1, 80: 2→1
Clade 10	9: 1→2, 29: 2→1
Clade 11	21: 1→2, 27: 1→2, 48: 1→2, 73: 1→2

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

(char. 9: extends well beyond end of antennule) and seta 3 of mandibular basis (clade 29: absent). Clade 11 (*Jaschnovia* + *Senecella*) was united by four character state changes: antennal exopod segments 1 and 2 (char. 21: fused), seta of antennal exopod segment 9 (char. 27: absent), seta 9 of maxillule coxal epipodite (char. 48: absent) and leg 1 exopod segment 1 outer border spine (char. 73: absent).

DISCUSSION

DATA/CHARACTERS

The most noteworthy characterization of the present data set is the prevalence of homoplasy and low level of congruence of individual character states. An explanation for these characteristics might lie in a lack of well-supported hypotheses of homology, which has resulted in otherwise potentially apomorphic character states behaving as homoplasious states.

Typical examples of a homoplasious distribution of character states are to be found among the presence or absence of individual setae on the exopod segments of the female antenna (char. 23–25) and on the maxillule: coxal endite, basal endite 2, exopod and coxal epipodite (char. 35–38, 39–40 and 43–53; e.g. Fig. 5A, B). There is a possibility that we have made an incorrect analysis of which setae are homologous, but equally, these character states might be genuinely homoplasious, having been lost several times independently in addition to apparently undergoing reversals back to the ancestral (plesiomorphic) state.

One character, previously thought to be a synapomorphy indicating relatedness, appears to be homoplasious: character 79 (female leg 4 coxa inner

proximal border large spinules: present) currently defines the Euchirellinae. This character fails to unite any clade identified here unambiguously. Nevertheless, we note that *Aetideus*, *Paivella* and *Undeuchaeta*, which have small, strong spinules on the coxa of leg 4, are also recovered in the same clade as *Gaetanus*, *Pseudochirella* and *Euchirella* (Fig. 6).

Fifteen female characters out of 77 were important in the overall structure of the trees (Table 2; examples shown in Fig. 5). These include the following characters: 8 (number of setae on antennule segment 1), 9 (length seta on antennule segment XXIII), 12 (number of setae on antennule segment XIII), 13 (number of setae on antennule segment XV), 19 (number of setae on antennule segment XXI), 21 (antenna exopod segment 1 and 2 separate), 22 (antenna exopod segment 4 and 5 separate), 28 (mandible basis seta 4 absent), 32 (mandible endopod segment 1 seta 4 absent), 44 (maxillule exopod seta 10 absent), 45 (maxillule exopod seta 9 absent), 54 (maxilla praecoxal endite 1 seta 5 absent), 55 (maxilla praecoxal endite 1 seta 4 absent), 56 (maxilla basal endite seta 4 absent), 75 (leg 1 arthrodial membrane between exopod segments 1 and 2), and 76 (leg 2 arthrodial membrane between endopod segments 1 and 2) (Table 2). Of these characters, 8, 13, 19 and 55 are almost congruent and help to define clades 3, 5 and 9 (Table 3). Characters 12, 22, 32, 44, 45, 54 and 76 help to define clades 1, 3, 4 and 8. Most of the above 14 characters have not been used before in diagnoses of Clausocalanoidea or as indicators of phylogenetic relationships.

Male characters were not included in our analysis because descriptions of five genera did not contain complete data, and the males of seven other genera are currently unknown. In general, most male characters have rather low rescaled consistency indices (RC) (Table 2). Character 89 (presence of a serrated lamella on the exopod segment 2 of the male fifth legs) is a synapomorphy of *Euchaeta* and *Paraeuchaeta* (RC = 1), and char. 85 (right leg 5 is uniramous) is found mostly in clades 1 and 4 (RC = 0.26).

IMPACT OF HOMOPLASY ON PHYLOGENETIC RECONSTRUCTION

The widespread prevalence of homoplasy has implications for our cladistic analysis. First, it means we have a reduced number of characters/states that support nodes in our trees and second, Brandley *et al.* (2009) and Chemisquy & Prevosti (2013) showed how elevated levels of homoplasy can interfere with accurate tree inference in a manner that is related to clade size. This is apparently because greater homoplasy increases the number of random or near-random trees obtained during the resampling of data sets (during the calculation of branch support), increasing the

chance that medium-sized clades will be contradicted, thus lowering branch support (Chemisquy & Prevosti, 2013: 269).

PHYLOGENY AND TAXONOMY

We accept that monophyletic groups and lineages are the fundamental basis of taxonomy and evolution (e.g. Cantino & de Queiroz, 2010). Therefore, the provisional phylogeny of the non-‘Bradfordian’ Clausocalanoidea suggests that the family structure may need future adjustment because the monophyly of some existing families appears to be in doubt. We have some confidence in the conclusions concerning the deep branching topology of our hypothetical phylogeny because Goloboff *et al.* (2008) showed that down-weighting characters according to their homoplasy increases jackknife frequencies and produces results that are more stable. Therefore, we attach significance to the phylogeny produced after one round of successive reweighting (Fig. 6). Clade 1, which contains genera from the Clausocalanidae, Stephidae and the genus *Mesaiokeras*, suggests that the Clausocalanidae, as currently configured, is paraphyletic. The Pseudocyclopiidae (clade 4) may be monophyletic, although it has several character states in common with the Clausocalanidae (usually one seta on antennule ancestral segments XIII, XV, XVII and XXI; four setae on praecoxal endite 1 of maxilla and usually four setae on the basal endite; e.g. Fig. 5E, F). Also, the highly modified genus, *Peniculoides*, currently assigned provisionally to the Clausocalanidae, is sister to *Frigocalanus* in the present analysis. The Aetideidae (clade 3) appears to be paraphyletic as currently configured because *Euchaeta* and *Paraeuchaeta*, currently in the Euchaetidae, nests within clade 6. There is a possibility that the Aetideidae could be divided further in the future, but there is no jackknife support for such a move based on the present data (Fig. 4B).

These results are viewed here as hypotheses that can be evaluated further using, for example, genetic data. Our hypothesis, based on present evidence, is that non-‘Bradfordian’ Clausocalanoidea may be composed of three families. Aetideidae *s.l.* is chosen as the name for clade 3 because it contains the type genus, *Aetideus* (Boeck, 1872), and contains the most genera in comparison with the Euchaetidae, a family name that was published simultaneously [also the Aetideidae (clade 3) takes page precedence over the Euchaetidae in Giesbrecht, 1892/93]. Clausocalanidae takes precedence for clade 1 because it is the oldest available name; there are currently no morphological data to support Stephidae as a stand-alone monophyletic taxon, and the monogeneric *Mesaiokeratidae* is recovered as a terminal branch

within this clade. Pseudocyclopiidae plus *Peniculoides* may remain as a monophyletic family, although it does not have clear synapomorphies, the nearest being eight or fewer setae on the exopod of the maxillule, a character held in common with *Mesaiokeras* in clade 1 (Fig. 5D).

Historical taxonomic enterprise relating to the Aetideidae *s.l.* and Clausocalanidae *s.l.* was originally undertaken mostly on pelagic genera (e.g. Giesbrecht, 1892/93; Sars, 1903, 1924/5). Therefore, families were created that grouped genera together that appeared to be related at that time. Increasingly, as benthopelagic taxa and taxa from anchialine environments were discovered, these genera did not fit neatly into existing families, and the creation of new families has left some taxa stranded in ‘dustbin’ families. For example, the Clausocalanidae, as presently understood, cannot be defined unambiguously as a monophyletic entity.

We note that Andronov’s (2014: 155) revision of the Calanoidea considered a superfamily Clausocalanoidea to contain the Spinocalanidae, Ryocalanidae and an enlarged Clausocalanidae. The Clausocalanidae was composed of the Clausocalaninae, which included the current Clausocalanidae, *Mesaiokeratidae* and Stephidae; the Aetideinae, which included the present Aetideidae and Pseudocyclopiidae; the Euchaetinae; and Scolecitrichinae, which incorporated all ‘Bradfordian’ genera. It is probably a matter of opinion as to whether it is appropriate to lower the rank of current families, but we find no evidence that the Pseudocyclopiidae are closely related to the Aetideidae. Andronov (2014: 95) appears to have based his conclusion on the insertion of seta VII on the ventral surface of the caudal rami in Pseudocyclopiidae but did not consider the setation of praecoxal endite 1 of the maxilla. Also, it appears that seta VII may be on the ventral surface or the inner border in the Pseudocyclopiidae: e.g. seta VII is on the inner border in *Paracyclopia naessi*, *Pseudocyclopia crassicornis* and *Thompsonopia stephoides*.

Our analyses support the hypothesis that at least the taxa Euchaetidae and Stephidae should probably not be recognized as stand-alone monophyletic entities. The two genera currently comprising the former are always nested within the Aetideidae, and the latter is itself paraphyletic and nested within the Clausocalanidae. The *Mesaiokeratidae* is a terminal branch within a subclade composed of the genera currently grouped as the Stephidae. Therefore, we provisionally diagnose the non-‘Bradfordian’ Clausocalanoidea families here, as follows.

Aetideidae s.l. (Aetideidae + Euchaetidae): Clausocalanoidea without modified setae on maxilla and maxilliped: rostral filaments absent; antennule ancestral segment XXI with two non-aesthetasc seta, ancestral segment XV usually with two setae (one seta

in *Aetideopsis*); mandibular basis with three or fewer setae; maxilla praecoxal endite 1 with three setae, basal endite with three setae; female leg 5 usually absent or vestigial.

Clausocalanidae s.l. (*Clausocalanidae* + *Stephidae* + *Mesaiokeratidae*): Clausocalanoidea without modified setae on maxilla and maxilliped: rostral filaments absent or present; four setae in the mandibular basis; antennule ancestral segment XXI with one non-aesthetasc seta, ancestral segment XV usually with one seta; maxilla praecoxal endite 1 with four or more setae; female leg 5 usually present (except *Microcalanus* and *Pseudocalanus*).

Pseudocyclopiidae (*Pseudocyclopiidae* + *Peniculoides*): Clausocalanoidea without modified setae on maxilla and maxilliped: rostral filaments usually present; maxillule exopod with eight or fewer setae; antennule ancestral segment XXI with one non-aesthetasc seta, ancestral segment XV usually with one seta (no seta in *Paracyclopia*); mandibular basis with three or fewer setae; maxilla praecoxal endite 1 with four or more setae; female leg 5 present.

HABITAT

In this phylogenetic study, genera from similar habitats are often grouped together; some groups of genera are planktonic, whereas other groupings relate to benthopelagic or anchialine habitats, and another to brackish water (Table 1; Fig. 6). For example, the basal taxa of clade 1 (*Clausocalanus*, *Ctenocalanus*, *Drepanopus* and *Pseudocalanus*) are pelagic, whereas the remaining taxa (*Stephidae* and *Mesaiokeras*) are either shallow benthopelagic or inhabitants of anchialine caves. Also, taxa in clade 4 (*Pseudocyclopiidae*) are either benthopelagic or inhabitants of marine caves. In the non-planktonic genera of clades 1 and 4, male mouthparts are the same as those of the female, i.e. functional. The presence of feeding males with functional mouthparts suggests there is an advantage to these males of being longer lived and available for mating at any time, in contrast to many planktonic genera (Ohtsuka & Huys, 2001: 463), which have short-lived males without functional mouthparts. Strong seasonality or another mechanism synchronizes maturation, ensuring that males and females are present together in the breeding season.

Clade 6, composed of the genera *Aetideus* to *Batheuchaeta* (Fig. 6), have epi- to bathypelagic habits (Table 1). Clade 10, composed of the genera *Azygokeras* to *Bradyidius* (Fig. 6), consists of benthopelagic forms (apart from *Farrania*) (e.g. Markhaseva, 1996; Schulz & Markhaseva, 2000; Markhaseva & Schulz, 2008). Nevertheless, there is no evidence for feeding males

within any groups in this clade. This suggests that even in the deep sea there is a synchronization mechanism for the maturation of short-lived males, which appear in the population at the same time as females mature. Clade 10 is united by char. 9 (long pseudoannulate seta on ancestral antennular segment XXIII). This seta is representative of what may be bend-sensitive setae along the whole antennule and may be associated with a need to search the seafloor for prey.

It appears that most of the aetideid genera may be carnivores, omnivores or scavengers based on mouthpart morphology in the original descriptions. Mouthpart indicators of possible feeding mode may include the rotation of the endopod of the maxillule to lie at 45–90° to the main axis of this limb. *Euchaeta* and *Paraeuchaeta* are extreme examples of adaptation to carnivory, with very modified maxillules, maxillae and maxillipeds (e.g. Yen, 1985; Park, 1995). The maxillipeds of most Aetideidae are usually not extremely enlarged and are probably indicative of omnivory (Sano *et al.*, 2013), but a group of genera (*Bradyetes*, *Pseudeuchaeta*, *Comantenna* and *Mesocomantenna*) have a sensory structure distally on the maxilliped syncoxa, suggesting that these genera might be scavengers (e.g. Nishida & Ohtsuka, 1997).

Finally, a strongly supported clade 11 (Fig. 4B) contained *Senecella* and *Jaschnovia* (Fig. 4B) from brackish waters and shallow benthopelagic (or under-ice) habitats, respectively (Markhaseva, 1996) (Table 1). This clade appears to be composed of genera occupying marginal habitats and is united by character state changes for characters 21, 23, 48 and 73 (Tables 1 and 3).

The habitats of the above groupings of genera suggest that invasions of certain habitats have driven the evolution of clausocalanoidean copepods. Among these habitats, an oxygenated benthic boundary layer may have been important in the evolution of many aetideid, clausocalanid and ‘Bradfordian’ genera. This radiation of genera may have occurred after the end-Permian extinction event, when many niches were unoccupied (e.g. Bradford-Grieve, 2004). Nevertheless, we do not currently understand why there is so much homoplasy and lack of congruent character states that would allow the further subdivision of these taxa into monophyletic groups. The repeated colonization of these benthopelagic habitats by different lineages within the Clausocalanoidea might be part of the explanation for the elevated levels of homoplasy revealed in this analysis.

CONCLUSIONS

Our phylogenetic hypothesis of the non-‘Bradfordian’ Clausocalanoidea, based on a cladistic analysis using ‘Bradfordian’ exemplars as the outgroup,

gives some confidence in three clades: Aetideidae Giesbrecht, 1893, Pseudocyclopiidae G.O. Sars, 1902 and Clausocalanidae Giesbrecht, 1893, a conclusion that needs corroboration using genetic data. Based on previous evidence, the group of non-‘Bradfordian’ clausocalanoidean families is sister to the ‘Bradfordian’ families. There are currently no morphological data to support families Euchaetidae and Stephidae as stand-alone monophyletic taxa, and the monogeneric Mesaiokeratidae is nested within the Stephidae. The prevalence of homoplasy among characters used in our cladistic analyses interfered with tree inference and our assessment of support for the topologies produced.

Our analyses suggest that characters previously thought to have phylogenetic significance proved to be homoplasious (e.g. char. 79), whereas other characters not previously thought to have phylogenetic significance contributed to the fundamental topology of the trees. These informative female characters include the antennule setation of ancestral segments I, XV, XXI and XXIII; setation of the mandible basis and endopod segment 1; setation of the maxillule exopod; setation of the maxilla praecoxal endite 1; and segmentation of leg 1 exopod and leg 2 endopod. Although incompletely congruent, these characters define major clades 1–4.

ACKNOWLEDGEMENTS

We gratefully acknowledge the help of Dr Elena Markhaseva of the Zoological Institute, Russian Academy of Sciences, St Petersburg, who shared her previous work and data on the Clausocalanoidea. She pointed out the significance of the non-aesthetasc antennular setation to higher level taxonomy, and the reduced number of setae on the maxilla first praecoxal endite of the Aetideidae, and provided new information about selected clausocalanoid species. J.M.B.-G. acknowledges the general support of the National Institute of Water and Atmospheric Research, New Zealand.

CONFLICT OF INTEREST

Both authors have no conflict of interest to declare.

REFERENCES

- Alvarez MPJ. 1984.** Two bottom living Copepoda Calanoida Aetideidae – *Bradyidius plinoi* and *Lutamator elegans*, n. sp. collected in Brazilian waters. *Boletim de Zoologia, Universidade de São Paulo* **8**: 93–106.
- Alvarez MPJ. 1986.** New calanoid copepods (Aetideidae) of the genera *Comantenna*, *Mesocomantenna*, new genus, and *Paracomantenna* off the Brazilian coast. *Journal of Crustacean Biology* **6**: 858–877.
- Andronov VN. 1974.** Phylogenetic relations of large taxa within the suborder Calanoida (Crustacea, Copepoda). *Zoologicheskyy Zhurnal* **53**: 1002–1012. [In Russian.]
- Andronov VN. 2014.** *Revision of systematics and phylogeny of copepod order Calanoida*. Kalingrad: R.A.S. Institute of Oceanology P.P. Shirshov, Atlantic Section, 204. [In Russian.]
- Björnberg TKS. 1972.** Developmental stages of some tropical and subtropical planktonic marine copepods. *Studies on the Fauna of Curacao and other Caribbean Islands* **40**: 1–185.
- Blanco-Bercial L, Bradford-Grieve J, Bucklin A. 2011.** Molecular phylogeny of the Calanoida (Crustacea: Copepoda). *Molecular Phylogenetics and Evolution* **59**: 103–113.
- Boeck A. 1872.** Nye Slaegter og Arter af Saltvands-Copepoder. *Forhandlinger i Videnskabs-selskabet i Kristiania* **1872**: 35–60.
- Bowman TE. 1976.** *Miostephos cubrobex*, a new genus and species of copepod from an anchialine pool in Cuba (Calanoida: Stephidae). *Proceedings of the Biological Society of Washington* **89**: 185–190.
- Boxshall GA. 1985.** The comparative anatomy of two copepods, a predatory calanoid and particle feeding mormonilloid. *Philosophical Transactions of the Royal Society of London* **B311**: 303–377.
- Boxshall GA, Halsey SH. 2004.** *An introduction to copepod diversity*. London: The Ray Society.
- Boxshall GA, Huys R. 1998.** The ontogeny and phylogeny of copepod antennules. *Philosophical Transactions of the Royal Society B: Biological Sciences* **353**: 765–786.
- Boxshall GA, Yen J, Strickler JR. 1997.** Functional significance of the sexual dimorphism in the cephalic appendages of *Euchaeta rimana* Bradford. *Bulletin of Marine Science* **61**: 387–398.
- Bradford J. 1969a.** New species of *Aetideopsis* Sars and *Bradyidius* Giesbrecht (Copepoda: Calanoida) from the Southern Hemisphere. *New Zealand Journal of Marine and Freshwater Research* **3**: 73–97.
- Bradford J. 1969b.** New genera and species of benthic calanoid copepods from the New Zealand slope. *New Zealand Journal of Marine and Freshwater Research* **3**: 473–505.
- Bradford JM. 1971.** *Aetideus* and *Euaetideus* (Copepoda: Calanoida) from the Pacific and Atlantic Oceans. *New Zealand Journal of Marine and Freshwater Research* **5**: 12–40.
- Bradford JM. 1973.** Revision of some family and generic definitions in the Phaennidae and Scolecithricidae (Copepoda: Calanoida). *New Zealand Journal of Marine and Freshwater Research* **7**: 133–152.
- Bradford JM. 1974.** *Euchaeta marina* (Prestandrea) (Copepoda: Calanoida) and two closely related species from the Pacific. *Pacific Science* **28**: 159–169.
- Bradford JM, Jillett JB. 1980.** The marine fauna of New Zealand: pelagic calanoid copepods: family: Aetideidae. *Memoir of the New Zealand Oceanographic Institute* **86**: 1–102.

- Bradford-Grieve JM. 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 JM. 2003.** A new species of benthopelagic calanoid copepod of the genus *Bradyidius* Giesbecht, 1897 (Calanoida: Aetideidae) from New Zealand. *New Zealand Journal of Marine and Freshwater Research* **37**: 95–103.
- Bradford-Grieve JM. 2004.** Deep-sea benthopelagic calanoid copepods and their colonization of the near-bottom environment. *Zoological Studies* **43**: 276–291.
- Bradford-Grieve JM, Blanco-Bercial L, Boxshall GA. 2017.** Revision of family Megacalanidae (Copepoda: Calanoida). *Zootaxa* **4229**: 183.
- Bradford-Grieve JM, Boxshall GA, Ahyong ST, Ohtsuka S. 2010.** Cladistic analysis of the calanoid Copepoda. *Invertebrate Systematics* **24**: 291–321.
- Bradford-Grieve JM, Boxshall GA, Blanco-Bercial L. 2014.** Revision of basal calanoid copepod families with a description of a new species and genus of Pseudocyclopidae. *Zoological Journal of the Linnean Society* **171**: 507–533.
- Brady GS. 1883.** Report on the Copepoda collected by the H.M.S. Challenger during the years 1873–76. *Reports on the Scientific Results of the Voyage of H.M.S. Challenger*. *Zoology* **8**: 1–142, plates 1–55.
- Brandley MC, Warren DL, Leaché AD, McGuire JA. 2009.** Homoplasy and clade support. *Systematic Biology* **58**: 184–198.
- Campaner AF. 1978.** On some new planktonobenthic Aetideidae and Phaennidae (Copepoda, Calanoida) from the Brazilian continental shelf. 1. Aetideidae. *Ciência e Cultura* **30**: 863–876.
- Cantino PD, de Queiroz K. 2010.** *PhyloCode. International Code of Phylogenetic Nomenclature. Version 4c.* Committee on Phylogenetic Nomenclature. Available at: <http://ohio.edu/phylocode>. Accessed 27 November 2018.
- Canu E. 1896.** Copépodes. In: Koehler R, ed. *Résultats scientifiques de la campagne du “Caudan” dans le Golfe de Gascogne*. Paris, Masson et Cie. p. 421–438.
- Chemisquy MA, Prevosti FJ. 2013.** Evaluating the clade size effect in alternative measures of branch support. *Journal of Zoological Systematics and Evolutionary Research* **51**: 260–273.
- Claus C. 1863.** *Die freilebenden Copepoden mit besonderer Berücksichtigung der Fauna Deutschlands, der Nordsee und des Mittelmeeres*. Germany: Verlag von Wilhelm Engelmann, Leipzig: 1–130, plates 1–37.
- Dallwitz MJ, Paine TA, Zurcher EJ. 1993.** *User's guide to the DELTA system: a general system for processing taxonomic descriptions, 4 edn.* Canberra: CSIRO Division of Entomology, 136.
- Damkaer DM. 1971.** *Parastephos occatum*, a new species of hyperbenthic copepod (Calanoida: Stephidae) from the inland marine waters of Washington State. *Proceedings of the Biological Society of Washington* **83**: 505–514.
- Dana JD. 1849.** Conspectus crustaceorum, quae in orbis terrarum circumnavigatione, Corolo Wilkes, e classe Reipublicae foederatae duce, lexit et descripsit Jacobus D. Dana. *American Journal of Science* **8**: 276–285, 424–428.
- Deevey GB. 1974.** *Chiridiella* Sars (Copepoda: Calanoida): descriptions of nine species, six new, from the Sargasso Sea. *Bulletin of Marine Science* **24**: 439–472.
- Elofsson R. 1971.** The ultrastructure of a chemoreceptor organ in the head of copepod crustaceans. *Acta Zoologica, Stockholm* **52**: 299–315.
- Farran GP. 1905.** Report on the Copepoda of the Atlantic slope off counties Mayo and Galway. *Scientific Investigations of the Fisheries Branch, Ireland 1902–1903*. Dublin: Department of Agriculture and Technical Instruction for Ireland, appendix 2, 3–52, plates 3–13.
- Farran GP. 1908.** Second report on the Copepoda of the Irish Atlantic slope. *Scientific Investigations of the Fisheries Branch, Ireland 1906*. Dublin: Department of Agriculture and Technical Instruction for Ireland, 1–104, plates 1–11.
- Farris JS. 1969.** A successive approximations approach to character weighting. *Systematic Zoology* **18**: 374–385.
- Fosshagen A, Iliffe TM. 1985.** Two new genera of Calanoida and a new order of Copepoda, Platycopioidea, from marine caves. *Sarsia* **70**: 345–358.
- Frost B, Fleminger A. 1968.** A revision of the genus *Clausocalanus* (Copepoda: Calanoida) with remarks on distribution patterns in diagnostic characters. *Bulletin of the Scripps Institution of Oceanography, University of Californian, San Diego* **12**: 1–99, 67 pls.
- Garm A, Derby CD, Høeg JT. 2004.** Mechanosensory neurons with bend- and osmo-sensitivity in mouthpart setae from the spiny lobster *Panulirus argus*. *Biological Bulletin* **207**: 195–208.
- Giesbrecht W. 1888.** Elenco dei Copepodi pelagici raccolti dal Tenete di bascello Gaetano Chierchia durante il viaggio della R. Corvetta “Vettor Pisani” negli anni 1882–1885 e dal Tenente di vascello Francesao Orsini nel Mar Rosso, nel 1884. *Atti della Accademia Nazionale dei Lincei, Classe di scienze fisiche, matematiche e naturali* **42**: 284–287, 330–338.
- Giesbrecht W. 1892/93.** 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.
- Giesbrecht W. 1895.** Die pelagischen Copepoden. In: Report of the dredging operations off the west coast of central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried out by the U.S. Fish Commission steamer “Albatross” during 1891. *Bulletin of the Museum of Comparative Zoology at Harvard* **25**: 243–263.
- Giesbrecht W. 1897.** Notizen zur Systematik der Copepoden. *Zoologischer Anzeiger* **20**: 253–255.
- Giesbrecht W, Schmeil O. 1898.** Copepoda I. Gymnoplea. *Tierreich* **6**: 1–169.
- Goloboff PA, Carpenter JM, Arias JS, Esquivel DRM. 2008.** Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics* **24**: 758–773.
- Grice GD. 1969.** Calanoid copepods from the Caribbean Sea and Gulf of Mexico. 1. New species and new records from midwater trawl samples. *Bulletin of Marine Science* **19**: 446–455.

- Grice GD, Hulsemann K. 1965.** Abundance, vertical distribution and taxonomy of calanoid copepods at selected stations in the northeast Atlantic. *Journal of Zoology* **146**: 213–262.
- Grice GD, Hulsemann K. 1970.** New species of bottom-living calanoid copepods collected in deep water by the DSRV Alvin. *Bulletin of the Museum of Comparative Zoology, Harvard* **139**: 185–227.
- Heron GA, Bowman TE. 1971.** Postnaupliar developmental stages of the copepod crustaceans *Clausocalanus laticeps*, *C. brevipes*, and *Ctenocalanus citer* (Calanoida: Pseudocalanidae). *Antarctic Research Series* **17**: 141–165.
- Hosfeld B. 1995/96.** The relationship between the rostrum and the Organ of Bellonci in Copepods: an ultrastructural study of the rostrum of *Canuella perplexa*. *Zoologischer Anzeiger* **234**: 175–190.
- Hulsemann K. 1991.** The copepodid stages of *Drepanopus forcipatus* Giesbrecht, with notes on the genus and a comparison with other members of the family Clausocalanidae (Copepoda Calanoida). *Helgoländer Meeresuntersuchungen* **45**: 199–224.
- Huys R, Boxshall GA. 1991.** *Copepod evolution*. London: The Ray Society.
- Jaume D, Boxshall GA. 1995.** *Stygocyclopiopsis balearica*, a new genus and species of calanoid copepod (Pseudocyclopiidae) from anchialine caves in the Balearic Islands (Mediterranean). *Sarsia* **80**: 213–222.
- Jaume D, Boxshall GA, Gràcia F. 2008.** *Stephos* (Copepoda: Calanoida: Stephidae) from Balearic caves (W Mediterranean). *Systematics and Biodiversity* **6**: 503–520.
- Jaume D, Boxshall GA, Humphreys WF. 2001.** New stygobiont copepods (Calanoida; Misophrioida) from Bunderia sinkhole, an anchialine cenote in north-western Australia. *Zoological Journal of the Linnean Society* **133**: 1–24.
- Jaume D, Fosshagen A, Iliffe TM. 1999.** New cave-dwelling pseudocyclopiids (Copepoda, Calanoida, Pseudocyclopiidae) from the Balearic, Canary, and Philippine archipelagos. *Sarsia* **84**: 391–417.
- Juday C. 1923.** An interesting copepod from the finger lakes, New York. *Science, New York* **58**: 205.
- Juday C. 1925.** *Senecella calanoides*, a recently described freshwater copepod. *Proceedings of the US National Museum* **66**: 1–6.
- Koeller PA, Littlepage JL. 1976.** *Azygokeras columbiae*, a new genus and species of marine epibenthic copepod (Calanoida: Aetideidae) from British Columbia. *Journal of the Fisheries Board of Canada* **33**: 1547–1552.
- 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.
- Laakmann S, Markhaseva EL, Renz J. 2018.** Do molecular phylogenies unravel the relationship among the evolutionary young “Bradfordian” families (Copepoda; Calanoida)? *Molecular Phylogenetics and Evolution* **130**: 330–345.
- Latreille PA. 1804.** *Histoire naturelle générale et particulière des crustacés et des insectes. Ouvrage faisant suite aux oeuvres de Leclerc de Buffon et partie du cours complet d'histoire naturelle rédigé par C.S. Sonnini, Vol. 7*. Paris: Dufart.
- Leach WE. 1816.** Annulosa. In: *Encyclopedia Britannica, supplement to the fourth, fifth and sixth editions*. **1**, 401–453, plates 20–26.
- Maddison DR, Maddison WP. 2000.** *MacClade 4: analysis of phylogeny and character evolution*. CD-ROM. Sunderland: Sinauer Associates.
- Markhaseva EL. 1980.** Kalanidy roda *Jaschnovia*, nom. n. (*Derjuginia* Jaschnov, nom. Praeocc.) (Calanoida, Aetideidae). *Issledovaniya Fauny Morei* **25**: 63–67. [In Russian.]
- Markhaseva EL. 1981.** Novye vidy *Batheuchaeta* (Calanoida, Aetideidae) iz Kurilo-Kamchatskogo zheloba i pereodisanie *B. lamellata*. *Zoologicheskii Zhurnal* **60**: 1151–1159. [In Russian.]
- Markhaseva EL. 1986.** Revision of the genus *Batheuchaeta* (Calanoida, Aetideidae). *Zoologicheskii Zhurnal* **65**: 837–850. [In Russian.]
- Markhaseva EL. 1996.** *Calanoid copepods of the family Aetideidae of the world ocean*. St Petersburg: Russian Academy of Sciences, Zoological Institute.
- Markhaseva EL, Abramova AA, Mingazov ND. 2012.** *Pseudocalanus acuspes* (Crustacea: Copepoda) from the White Sea. *Proceedings of the Zoological Institute, RAS* **316**: 57–70.
- Markhaseva EL, Bradford-Grieve JM, Renz J. 2017.** New records of the rare benthopelagic genera *Comantenna* Wilson, 1924 and *Crassantenna* Cole, Green, Howcroft et Rawlings, 1972 (Copepoda: Calanoida: Aetideidae) from the North Pacific abyss. *Arthropoda Selecta* **26**: 25–34.
- Markhaseva EL, Laakmann S, Renz J. 2014.** An interim synopsis of the Bradfordian families with a description of *Thoxancalanus spinatus* (Copepoda: Calanoida), a new diaixid genus and species from the deep Atlantic. *Marine Biodiversity* **44**: 63–88.
- Markhaseva EL, Mohrbeck I, Renz J. 2017.** Description of *Pseudeuchaeta vulgaris* n. sp. (Copepoda: Calanoida), a new aetideid species from the deep Pacific Ocean with notes on the biogeography of benthopelagic aetideid calanoids. *Marine Biodiversity* **47**: 289–297.
- Markhaseva EL, Renz J. 2015.** A new genus *Peniculoides* (Copepoda, Calanoida) from deep waters of the North Atlantic with notes on Clausocalanidae definition. *Crustaceana* **88**: 1031–1047.
- Markhaseva EL, Schnack-Schiel SB. 2003.** New and rare calanoid copepod from the Great Meteor Seamount, North Eastern Atlantic. *Ophelia* **57**: 107–123.
- Markhaseva EL, Schulz K. 2006.** New benthopelagic aetideids (Crustacea: Copepoda: Calanoida) from deep Antarctic waters. *Invertebrate Zoology* **3**: 137–155.
- Markhaseva EL, Schulz K. 2008.** Two new species of *Prolutamator* gen. nov. and a new species of *Pseudotharybis* (Copepoda: Calanoida: Aetideidae) from deep waters of the South Atlantic and Antarctic. *Mitteilungen au dem Hamburgischen Zoologischen Museum und Institut* **105**: 31–51.
- Matthews JBL. 1961.** A new species of copepod (Calanoida) from western Norway. *Sarsia* **4**: 33–38.
- McKinnon AD, Corley J, Duggan S. 2011.** Two new species of *Aetideopsis* (Copepoda, Aetideidae) from the eastern Indian Ocean. *Crustaceana* **84**: 831–848.

- Nishida S, Ohtsuka S. 1997.** Ultrastructure of the mouthpart sensory setae in mesopelagic copepods of the family Scolecitrichidae. *Plankton Biology and Ecology* **44**: 81–90.
- Ohtsuka S. 1992.** Calanoid copepods collected from the near-bottom in Tanabe Bay on the Pacific Coast of Middle Honshu, Japan. IV. Pseudocyclopiidae. *Publications of the Seto Marine Biological Laboratory* **35**: 295–301.
- Ohtsuka S, Boxshall GA, Fosshagen A. 2003.** A new species of *Neoscolecithrix* (Crustacea; Copepoda; Calanoida) from off Okinawa, southwestern Japan, with comments on the generic position in the superfamily Clausocalanoidea. *Bulletin of the National Science Museum, Tokyo* **29**: 53–63.
- Ohtsuka S, Boxshall GA, Shimomura M. 2005.** Three new species of deep-sea hyperbenthic aetideid copepods (Crustacea) collected from Nansei Islands, southwestern Japan. In: Hasegawa K, Shinohara G, Takeda M, eds. *Deep-sea fauna and pollutants in Nansei Islands, Vol. 29*. Tokyo: National Science Museum Monographs, 225–247.
- Ohtsuka S, Huys R. 2001.** Sexual dimorphism in calanoid copepods: morphology and function. *Hydrobiologia* **453/454**: 441–466.
- Park TS. 1967.** Two new species of calanoid copepods from the Strait of Georgia, British Columbia, Canada. *Journal of the Fisheries Board of Canada* **24**: 231–242.
- Park TS. 1968.** Calanoid copepods from the central North Pacific Ocean. *Fishery Bulletin* **66**: 527–572.
- Park TS. 1973.** Redescription of *Gaetanus intermedius* Campbell (Calanoida: Copepoda) from the type locality. *Journal of the Fisheries Board of Canada* **30**: 1597–1600.
- Park TS. 1974.** Calanoid copepods of the genus *Aetideus* from the Gulf of Mexico. *Fishery Bulletin* **72**: 215–221.
- Park TS. 1978.** Calanoid copepods (Aetideidae and Euchaetidae) from Antarctic and Subantarctic waters. *Antarctic Research Series* **27**: 91–290.
- Park TS. 1995.** Taxonomy and distribution of the marine calanoid copepod family Euchaetidae. *Bulletin of the Scripps Institution of Oceanography, University of California, San Diego* **29**: 1–203.
- Philippi A. 1843.** Fernere Beobachtungen über die Copepoden des Mittelmeeres. *Archiv für Naturgeschichte* **9**: 54–71.
- Roe HSJ. 1975.** Some new and rare species of calanoid copepods from the northeastern Atlantic. *Bulletin of the British Museum of Natural History, Zoology* **28**: 295–372.
- Sano M, Maki K, Nishibe Y, Nagata T, Nishida S. 2013.** Feeding habits of mesopelagic copepods in Sagami Bay: insights from integrative analysis. *Progress in Oceanography* **110**: 11–26.
- Sano M, Nishibe Y, Tanaka Y, Nishida S. 2015.** Temporally sustained dietary niche partitioning in two mesopelagic copepod species and their mouthpart morphology. *Marine Ecology Progress Series* **518**: 51–67.
- Sars GO. 1902.** Copepoda Calanoida. *An account of the Crustacea of Norway, with short descriptions and figures of all the species* **4**: 29–144, pls. 17–96.
- Sars GO. 1903.** Copepoda Calanoida. *An account of the Crustacea of Norway, with short descriptions and figures of all the species* **4**: 145–171, pls. 97–102, suppl. pls. 1–6.
- Sars GO. 1905.** List préliminaire des Calanoides recueillis pendant les campagnes de S.A.S. le Prince Albert de Monaco, avec diagnoses des genres et des espèces nouvelles (1^{re} partie). *Bulletin du Musée Océanographique de Monaco* **26**: 1–22.
- Sars GO. 1907.** Notes supplémentaires sur les Calanoides de la Princess-Alice. (Corrections et additions). *Bulletin du Institut Océanographique de Monaco* **101**: 1–27.
- Sars GO. 1920.** Calanoides recueillis pendant les campagnes de S.A.S. le Prince Albert de Monaco (Nouveau supplément). *Bulletin du Institut Océanographique de Monaco* **377**: 1–20.
- Sars GO. 1924/25.** Copépodes particulièrement bathypélagiques provenant des campagnes scientifiques de Prince Albert 1^{er} de Monaco. *Résultats des Campagnes Scientifiques accomplies par le Prince Albert I, Monaco* **69**: pls 1–27 (1924), 1–408 (1925).
- Schulz K. 1990.** *Pterochirella tuerkayi*, new genus, new species, an unusual calanoid copepod from the deep Gulf of Aden (Indian Ocean). *Mitteilungen au dem Hamburgischen Zoologischen Museum und Institut* **87**: 181–189.
- Schulz K. 1996.** *Frigocalanus rauscherti*, a new genus of hyperbenthic copepod (Calanoida: Clausocalanoidea) from the sublittoral of King George Island (Antarctica). *Mitteilungen au dem Hamburgischen Zoologischen Museum und Institut* **93**: 73–82.
- Schulz K, Kwasniewski S. 2004.** New species of benthopelagic calanoid copepods from Kongsfjordem (Spitsbergen, Svalbard Archipelago). *Sarsia* **89**: 143–159.
- Schulz K, Markhaseva EL. 2000.** *Parabradysidius angelikae*, a new genus and species of benthopelagic copepod (Calanoida: Aetideidae) from the deep Weddell Sea (Antarctica). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* **97**: 77–89.
- Scott A. 1909.** The Copepoda of the Siboga expedition. Part 1. Free-swimming, littoral and semi-parasitic Copepoda. *Siboga Expeditie* **29a**: 1–323, plates 1–69.
- Scott T. 1892.** Additions to the fauna of the Firth of Forth. Part IV. *Annual Report of the Fishery Board for Scotland* **10**: 244–272, plates 7–13.
- Shih C-T, Maclellan DM. 1981.** *Aetideopsis albatrossae*, new species (Crustacean; Copepoda) from east of Mindoro, the Philippines. *Journal of Crustacean Biology* **1**: 567–572.
- Steuer A. 1904.** Copepoden der Valdivia-expedition. *Zoologischer Anzeiger* **27**: 593–598.
- Swofford DL. 2002.** *Phylogenetic analysis using parsimony (*and other methods) version 4*. Sunderland: Sinauer Associates.
- Tanaka O. 1956.** The pelagic copepods of the Izu region, middle Japan. Systematic account II. Families Paracalanidae and Pseudocalanidae. *Publications of the Seto Marine Biological Laboratory* **5**: 367–406.
- Tanaka O. 1957.** The pelagic copepods of the Izu region, middle Japan. Systematic account IV. Families Aetideidae (Part 2). *Publications of the Seto Marine Biological Laboratory* **6**: 169–207.
- Tanaka O. 1969.** Some calanoid copepods collected by the U.S. steamer Albatross from the Pacific Ocean. *Publications of the Seto Marine Biological Laboratory* **17**: 253–278.

- Uttieri M, Brown ER, Boxshall GA, Mazzocchi G. 2008.** Morphology of antennular sensors in *Clausocalanus furcatus* (Copepoda: Calanoida). *Journal of the Marine Biological Association of the United Kingdom* **88**: 535–541.
- von Vaupel Klein JC. 1982.** A taxonomic review of the genus *Euchirella* Giesbrecht, 1888 (Copepoda, Calanoida). II. The type species, *Euchirella messinensis* (Claus, 1863). A. The female of f. typica. *Zoologische Verhandelingen, Leiden* **198**: 1–131.
- von Vaupel Klein JC. 1984.** A primer of a phylogenetic approach to the taxonomy of the genus *Euchirella* (Copepoda, Calanoida). *Crustaceana Supplement* **9**: 1–194.
- von Vaupel Klein JC. 1998.** Interpretation of character phylogenies in calanoid copepods by implementing Dollo's law. *Journal of Crustacean Biology* **18**: 153–160.
- von Vaupel Klein JC, Rijerkerk CDM. 1997.** A detailed redescription of the *Pseudochirella obesa* female (Copepoda, Calanoida). II. antennae and mouthparts. *Crustaceana* **70**: 394–417.
- Vervoort W. 1951.** Plankton copepods from the Atlantic sector of the Antarctic. *Verhandlingen der Koninklijke Nederlandse Akademie van Wetenschappen, afd. Natuurkunde, Section 2* **47**: 1–156.
- Vervoort W. 1965.** Pelagic Copepoda, Part II. *Atlantide Report* **8**: 9–216.
- Vyshkvartzeva NV. 1994.** *Senecella siberica* n. sp. and the position of the genus *Senecella* Calanoida classification. *Hydrobiologia* **292**: 113–121.
- Weatherby TM, Wong KK, Lenz PH. 1994.** Fine structure of the distal sensory setae on the first antennae of *Pleuromamma xiphias* Giesbrecht (Copepoda). *Journal of Crustacean Biology* **14**: 670–685.
- Wheeler EH. 1970.** Atlantic deep-sea calanoid Copepoda. *Smithsonian Contributions to Zoology* **55**: 1–31.
- Wilson CB. 1924.** New North American parasitic copepods, new hosts and notes on copepod nomenclature. *Proceedings of the United States Natural History Museum* **64**: 1–22.
- Wolfenden RN. 1911.** Die marinen Copepoden der Deutschen Südpolar Expedition 1901–1902. II. Die pelagischen Copepoden der Westwinddrift und des südlichen Eismeers met Beschreibung mehrerer neuer Arten aus dem Atlantischen Ozean. *Deutsche Südpolar-Expedition* **12**: 181–230, pls 22–41.
- Yeatman HC. 1980.** *Miostephos laemingtonensis*, a new species of copepod from Bermuda. *Journal of the Tennessee Academy of Science* **51**: 22–21.
- Yen J. 1985.** Selective predation by the carnivorous marine copepod *Euchaeta elongata*: laboratory measurements of predation rates verified by field observations of temporal and spatial patterns. *Limnology and Oceanography* **30**: 577–597.
- Yen J, Nicoll NT. 1990.** Setal array on the first antennae of a carnivorous marine copepod, *Euchaeta norvegica*. *Journal of Crustacean Biology* **10**: 218–224.
- Zvereva ZhA. 1975.** *Valdiviella brodskyi* sp. n. (Copepoda, Calanoida) iz Tikhogo Okeana i sravnii genital'nykh polei vidov etogo roda. *Zoologicheskii Zhurnal* **54**: 1890–1894. [In Russian.]

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Data matrix of character state scores.

Appendix S2. Female antennule segmental fusions, seta and aesthetasc distributions.

Appendix S3. Clausocalanoidea_part.nex