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Title:

Phylogeny within the Chondracanthidae (Poecilostomatoida, Copepoda)

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Running title:
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Abstract

Østergaard, P., Boxshall, G. A. & Quicke, D. L. J. (2002). Phylogeny within the Chondracanthidae (Poecilostomatoida, Copepoda). — *Zoologica Scripta*, *00*, 000-000.

The existing systematics of the Chondracanthidae is based predominantly on female characters and divides them into two subfamilies; Chondracanthinae and Lernentominae. Phylogenetic analyses using maximum parsimony were performed using 186 male and female characters. Different trees were generated when male and female characters were analysed separately. Differential weighting showed that the female characters were dominant but not to a great extent and subsequent analyses were run with both partitions combined. Different trees were generated depending on the character setting (unordered, ordered and irreversible-up). Interestingly, a basal backbone comprising the same nine ingroup taxa was present in all the trees, although the sequence of those taxa could differ. Constraining the two subfamilies to be monophyletic caused tree length to be increased and the Templeton and Kishino-Hasegawa tests showed the constrained tree to be significantly different from the unconstrained. The two subfamilies are considered invalid and Lernentominae Oakley, 1927 is formally synonymised with Chondracanthinae Milne Edwards, 1840. The validity of the Pharodidae was tested similarly. *Pharodes tortugensis*, representing the family Pharodidae was always recovered nested deep within Chondracanthidae. The Pharodidae Illg, 1948 is therefore synonymised with the Chondracanthidae Milne Edwards, 1840.

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Introduction

The Chondracanthidae Milne Edwards, 1840 is a family of highly modified parasitic copepods found on many taxa of marine fish. Though, very little is known about their biology and about their effects on the host (Kabata 1970). The females have undergone profound morphological transformation, but the males also show adaptations to this mode of life. In the most recent revision of the family (Ho 1970) two subfamilies were recognised: the main difference between them being the relative position of the neck separating the head from the trunk. The larger of the two subfamilies, the Chondracanthinae Milne Edwards, 1840, is characterised by having a post-oral neck whereas Lernentominae Oakley, 1927 is characterised by a pre-oral neck. At the time of Ho's (1970) revision only 30 genera of Chondracanthidae were known. Since then a further 13 new genera have been added so the Chondracanthinae currently comprises 39 genera and the Lernentominae four.

Kabata (1991) discussed the taxonomic criteria used to distinguish between genera within the Chondracanthidae and found that double standards exist. He pointed out that if the same criteria used to group all species together in *Chondracanthus* Delaroche, 1811 were applied to the subfamily Lernentominae, then all four lernentomine genera would be placed in a single genus. Ho (1991) attempted to reclassify *Chondracanthus* but the results of his cladistic analysis were inconclusive. The type genus *Chondracanthus* remains heterogeneous and its classification remains problematic. A species-level revision of the genus is required.

The genera *Acanthochondria* Oakley, 1927 and *Chondracanthus* are the most species rich with 44 and 38 described species respectively, but more than half of the recognised genera are currently monotypic. Ho (1970) expressed concern as to whether all these monotypic genera were justifiable or whether the family was overly split. Ho also found the classification within the family unstable since most genera were defined solely on adult female characters with much emphasis on body shape and on the number, shape and distribution of body processes. This problem is compounded by evidence that the shape of the body, and the size and number of body processes can change with maturity in some species (Ho 1970; Kabata 1979), and can even be affected by fixation.

Routine identification of the chondracanthids is based on the large females and most genera are defined primarily on the basis of female characters, but as Ho (1970) remarked, use of male characters is equally valid. Hogans & Sulak (1992) subsequently found that males provided useful characters at species level.

Reduction in number of expressed segments of the body and/or the appendages, and of setation elements on the limbs, referred to as oligomerization, has been identified as the dominant evolutionary trend in copepods (Boxshall *et al.* 1984). It is often associated with adaptation to parasitism as a mode of life as in the family Chondracanthidae, some members of which display a great reduction in appendage armature as well as loss of body segments in the females. The prevalence of reduction characters is problematic for phylogenetic reconstruction. Reduction characters (also called negative gain characters, see Mikkelsen (1998) for definition) are likely to show homoplasy and are often omitted from analyses (Sanderson & Donoghue 1996; Mikkelsen 1998). However, Sanderson & Donoghue (1996) have shown that homoplasy can be found in cladograms with high level of confidence and they do not recommend that these reduction characters are automatically deleted from the analyses. Almost all of the characters in the present analysis are reduction characters and this may be common for parasitic taxa: Excluding them would leave virtually no data.

The problem with reduction characters could be overcome and the phylogeny strengthened by taking larval morphology into consideration. Izawa (1987) tried to accumulate all the works on poecilostome copepod larvae, but the knowledge is still too sparse to make any useful contributions to the present analysis.

The family Pharodidae Illg, 1948 was also included in the analysis. This small family comprises only six species, all of which belong in the genus *Pharodes* Wilson, 1935, which was included as a subfamily within the Chondracanthidae until Ho (1971) redescribed *Pharodes tortugensis* Wilson, 1935 and concluded that this genus should be in a family of its own. Ho (1971) raised Pharodinae to family level transferring all six species. Despite sharing several characters with the Chondracanthidae (modified antenna, legs, and genito-abdomen with pair of modified caudal rami), *Pharodes* exhibits two major differences: The female has a midventrally placed abdomen and the male attaches directly to the fish host (rather than to the female as in typical chondracanthids), both of which Ho (1971) regarded as fundamental and sufficient justification for this separation.

The aims of this paper are to explore phylogenetic relationships within the Chondracanthidae and to examine character change using parsimony analysis, firstly to construct cladograms, and secondly to determine what reliable phylogenetic information is present in those cladograms. The analysis is used to discuss the biased use of female characters in the present taxonomy and to test support for the existing subfamily classification as well as shed light on the position of the Pharodidae.

Materials and methods

Taxa

Thirty-nine of the 43 currently known genera are included in the analysis. *Humphreysia* Leigh-Sharpe, 1934; *Markevitchielinus* Titar, 1975; and *Scheherazade* Leigh-Sharpe, 1934 were excluded because males are unknown for these monotypic genera. *Immanthe* Leigh-Sharpe, 1934 was excluded because insufficient information on the genus could be obtained. In most cases the type-species is used to represent each genus but in the following cases the type-species descriptions were inadequate and an alternative species were chosen to represent the genus in the analysis: *Heterochondria pilla* Ho, 1970 was used instead of *Heterochondria longicephala* (Yü & Wu, 1932); *Jusheyhoea ryukyuensis* Ho, 1994 instead of *Jusheyhoea macrura* Villalba & Fernandez, 1985 (except for the antennule which is undescribed for *J. ryukyuensis*); *Medisicaste penetrans* Heller, 1865 instead of *Medisicaste triglarum* Krøyer, 1863; *Praecidochondria setoensis* Izawa, 1975 instead of *Praecidochondria galatheae* Kabata, 1968; *Prochondracanthus platycephali* Ho, 1975 instead of *Prochondracanthus haliichthydis* Yamaguti, 1939; and *Protochondracanthus trilobatus* (Pillai, 1964) instead of *Protochondracanthus alatus* (Heller, 1868). For *Pseudacanthocanthopsis apogonis* Yamaguti & Yamasu, 1959 most character states used in the data matrix were taken from Izawa's (1975) redescription of the type species but in the case of the female maxillule, maxilla and maxilliped and male maxillule information for *P. rohdeii* Ho & Dojiri, 1976 was used. Villalba and Fernandez's (1985) description of the antennule in female *Juanettia continentalis* Villalba & Fernandez, 1985 has been used in the matrix because Ho (1970) was unable to give a full description of that structure in *J. cornifera* Wilson, 1921. *Pharodes tortugensis* Wilson, 1935 represents the only genus of the Pharodidae.

Material

The phylogenetic analysis was based on morphological characters only. Data were retrieved from published accounts (cf. Ho, 1970; Østergaard & Boxshall in prep.) and from direct observation of specimens. The following material was studied: *Acanthochondria cornuta* (Müller, 1776) (BMNH 1951.11.24.2), *Acanthochondrites annulatus* (Olsson, 1868) (BMNH 1976.1225-1228), *Andreina synapturae* Brian, 1939 (MT I-1938.24058-24064), *Apodochondria medusae* Ho & Dojiri, 1988 (SAM C4158-4159), *Auchenochondria lobosa* Dojiri & Perkins, 1979 (USNM 171429), *Bactrochondria papilla* Ho, Kim & Kumar, 2000 (Donated by Dr. Il-Hoi Kim, Kangreung National University, Kareung, South Korea – donated material deposited in BMNH 2001.7059-7062), *Berea ancoralis* (Bere, 1936) (USNM 69845 & 79088), *Blias prionoti* Krøyer, 1863 (BMNH 1979.672-680), *Brachiochondria pinguis* Shiino, 1957 (University of Mie, Japan, S-302), *Brachiochondrites longicollis* Markewitsch, 1940 (Pacific Biological Station, Nanaimo, B.C., Canada), *Ceratochondria brevicollis* (Krøyer, 1863) (NHMW 19537), *Chelonichondria okamurai* Ho, 1994 (USNM 266514)**,** *Chondracanthodes deflexus* Wilson, 1932 (BMNH 1994.3204-3209), *Chondracanthus zei* Delaroche, 1811 (BMNH 1975.327-330), *Diocus gobinus* (Müller, 1776) (ZMUC), *Heterochondria petila* Ho *et al.*, 2000 (USNM 285486), *Lagochondria nana* Ho & Dojiri, 1988 (SAM C4160-4161), *Lernentoma asellina* (Linnaeus, 1758) (BMNH 1975.667-677), *Mecaderochondria pilgrimi* Ho & Dojiri, 1987 (NMNZ Cr. 4639-4640), *Medesicaste triglarum* Krøyer, 1863 (IRSNB I.G. 16.808), *Neobrachiochondria qudrata* Kabata, 1969 (SAM C3373-3374)**,** *Pharodes tortugensis* Wilson, 1935 (USNM 59767, 69783), *Prochondracanthus haliichthydis* Yamaguti, 1939 (NMNZ Cr3457), *Protochondracanthus alatus* (Heller, 1868) (Donated by Dr. Il-Hoi Kim, Kangreung National University, Kangreung, South Korea – donated material deposited in BMNH 2001.7063-7065), *Pseudacanthocanthopsis apogonis* Yamaguti &

Yamasu, 1959 (University of Mie, Japan, K-149), *Pseudacanthocanthopsis rohdei* Ho & Dojiri, 1976 (USNM 168011), *Pseudoblias lyrifera* Heegaard, 1962 (BMNH 1984.75), *Pseudochondracanthus diceraus* Wilson, 1908 (USNM 60544), *Pseudodiocus scorpaenus* Ho, 1972 (USNM 134665 & 134672), *Pterochondria alatalongicollis* Heegaard, 1940 (BMNH 1984.72), *Rhynchochondria longa* Ho, 1967 (USNM113614), *Rohdea cryptopoda* Kabata, 1992 (BMNH 1991. 282-286), *Strabax monstrosus* von Nordmann, 1864 (BMNH 1982.226). Depositories for specimens are abbreviated as follows: BMNH, The Natural History Museum (London, UK); MT, Africa Museum (Tervuren, Belgium); NHMW, Naturhistorisches Museum Wien (Vienna, Austria); NMNZ, Museum of New Zealand, Te Papa Tongarewa (Wellington, New Zealand); IRSNB, Royal Belgian Institute of Natural Sciences (Brussels, Belgium); SAM, South Australian Museum (Adelaide, Australia); USNM, National Museum of Natural History, Smithsonian Institution (Washington DC, USA); ZMUC, Zoological Museum, University of Copenhagen (Copenhagen, Denmark).

Character description and character states

A total of 186 morphological informative characters was used (86 female and 100 male). The characters are grouped according to the region of the body. A score of "0" is assigned to the putative plesiomorphic state and is based on outgroup comparison (using Taenicanthidae Wilson, 1911 and Bomolochidae Claus, 1875 as outgroup); "1" is given to the apomorphic state and "2", "3" etc. to successively more derived states. Terminology of copepod anatomy follows Huys & Boxshall (1991). A data matrix was constructed (Appendix A) using the characters and character states given below.

Female characters

Body. The female body (Fig. 1A-B) comprises four main regions. 1) Head region consisting of cephalosome or cephalothorax comprising cephalosome fused with first pedigerous somite. 2) The neck, which can vary in length from inconspicuous to very long (length exceeding that of rest of body). In Lernentominae the neck is formed by postantennal constriction of the cephalon (= pre-oral neck). In Chondracanthinae the neck is post-oral and can be formed in five ways: by elongation of the interpodal region between cephalosome and first pedigerous somite (as in *Brachiochondria* Shiino, 1957), by elongation of first pedigerous somite (as in *Chondracanthus* Delaroche, 1811 (Fig. 1A)), by elongation of interpodal region between first and second pedigerous somites (as in *Rhynchochondria* Ho, 1967), by elongation of both first and second pedigerous somites (as in *Mecaderochondria pilgrimi* Ho & Dojiri, 1987 (Fig. 1B)) or by elongation of second pediger only (as in *Pseudodiocus* Ho, 1972). 3) The trunk comprises first, second or third to fifth pedigerous somites and 4) genitoabdomen which comprises genital and abdominal somites. The first three body regions often carry conspicuous processes and the following characters largely adopt the definitions given by Kabata (1979). The expression of various processes and lobes in the head and body region is considered derived, and are some of the only positive gain characters in this character list.

Head region.

1. Anterolateral processes/lobes (e.g. Kabata 1979: Text fig. 34G): 0 = absent; 1 = present.
2. Posterolateral processes/lobes (e.g. Kabata 1979: Text fig. 34K): 0 = absent; 1 = present.
3. Dorsolateral processes/lobes (e.g. Dojiri & Perkins 1979: fig. 3): 0 = absent; 1 = present.
4. Dorsomedial process/lobe (e.g. Kabata 1979: Text fig. 34D): 0 = absent; 1 = present.
5. Posterodorsal processes/lobes (e.g. Kabata 1979: Text fig. 34N, S): 0 = absent; 1 = present.
6. Median processes/lobes in postoral region (e.g. Kabata 1979: Text fig. 34Q): 0 = absent; 1 = present.
7. Processes/lobes anterolateral to oral region (e.g. Kabata 1979: Text fig. 34L): 0 = absent; 1 = present.

Trunk region.

8. Processes/lobes on the trunk: 0 = processes/lobes absent; 1 = posterolateral

processes/lobes only present (e.g. Kabata 1979: Text fig. 41K, j); 2 = as 1 but with at least one other pair of lateral processes/lobes present (e.g. Kabata 1979: Text fig. 41K, g-h); 3 = posterolateral processes/lobes absent but at least one pair of lateral processes present.

9. Number of lateral processes/lobes excluding posterolateral processes (e.g. Kabata 1979: Text fig. 41K, g-h) (if processes/lobes are present, i.e. character 8 scores 2 or 3): 0 = absent; 1 = one pair present, 2 = two pairs present, 3 = three or more pairs present.
10. Posteromedian process/lobe (e.g. Kabata 1979: Text fig. 41K, d) (if processes/lobes are present, i.e. character 8 scores 2 or 3): 0 = absent; 1 = present.
11. Dorsal processes/lobes in dorsomedian line from neck to genital area (e.g. Kabata 1979: Text fig. 41K, a-c) (if processes/lobes are present, i.e. character 8 scores 2 or 3): 0 = absent; 1 = 1 present, 2 = 2 or more present.
12. Dorsolateral processes/lobes (e.g. Kabata 1979: Text fig. 41K, e-f) (if processes/lobes are present, i.e. character 8 scores 2 or 3): 0 = absent; 1 = 1 pair present; 2 = 2 or more pairs present.

Neck region.

13. Trunk separated from head by neck: 0 = absent; 1 = indistinct; 2 = short (neck < trunk); 3 = medium (neck = trunk); 4 = long (neck > trunk).
14. Position of neck relative to mouth: 0 = post-oral; 1 = pre-oral.
15. Segments included in neck: 0 = interpodal region between cephalosome and first pediger; 1 = first pediger only; 2 = interpodal region between first and second pediger; 3 = first and second pedigers; 4 = second pediger only.

Antennule. The poecilostomatoid antennule is uniramous with a maximum of seven segments where three of the segments lie distal to the ancestral XX and XXI articulation (Boxshall & Huys 1998). (Segmental homologies are based on the scheme proposed by Huys & Boxshall (1991) for their hypothetical ancestral copepod). A maximum of six segments (the XVII and XVIII articulation is not expressed) is observed in primitive Chondracanthidae (e.g. male *Auchenochondria* Dojiri & Perkins, 1979 and female *Rhynchochondria* Ho, 1967) (Fig. 2A). The number of segments, setae and aesthetascs is constant distal to the XX and XXI articulation but shows a greater variety on the proximal part of the antennule, in accord with the scheme of antennulary development described by Boxshall & Huys (1998). Non-expression of articulations and setation is considered derived and in many of the transformed Chondracanthidae the entire antennule is indistinctly segmented. The transformed female being most modified with a swollen and fleshy antennule where most of the setae are lost apart from the terminal eight which are usually present. The division in character 21 is arbitrary. If the antennule is absent then characters 16-21 are scored "-" for inapplicable.

16. Articulation between segments V and VI: 0 = expressed; 1 = partly expressed or not expressed.
17. Articulation between segments XIII and XIV: 0 = expressed; 1 = partly expressed or not expressed.
18. Articulation between segments XX and XXI: 0 = expressed; 1 = partly expressed or not expressed.
19. Articulation between segments XXIV and XXV: 0 = expressed; 1 = partly expressed or not expressed.
20. Articulation between segments XXV and XXVI: 0 = expressed; 1 = partly expressed or not expressed.
21. Setal number on proximal part (segments I-XX): 0 = more than or equal to 20; 1 = 10-19; 2 = 5-9; 3 = less than or equal to 4.

Antenna. The poecilostomatoid antenna is uniramous (the exopod is absent) and modified into a grasping organ used for attachment to the host (Fig. 2B). It comprises a coxobasis (fused coxa and basis) with three-segmented endopod; coxobasis bearing one seta; first endopodal segment one seta; second endopodal segment four setae; and third endopodal segment seven setae (Huys & Boxshall 1991). The atrophied tip (previously known as the accessory antennule; see Ho 1984) found in many Chondracanthidae is homologous with the third endopodal segment. Loss of the atrophied tip is considered derived. First and second endopodal segments are commonly fused and one of the setae, probably from second endopodal segment, is often modified into a massive claw. All other setae are reduced or absent. In a few females the claw is developed into a specialised structure at the expense of most or all the segments and setae (e.g. *Berea*

Yamaguti, 1963; *Blias* Krøyer, 1863 and *Diocus* Krøyer, 1863).

22. Seta on coxobasis: 0 = present; 1 = absent.
23. Atrophied tip (third endopodal segment): 0 = defined; 1 = absent.
24. Number of setae/elements on atrophied tip (third endopodal segment) (when defined): 0 = seven setae/elements; 1 = six; 2 = five; 3 = four; 4 = three; 5 = two; 6 = one; 7 = zero.
25. Claw or other elements on second endopodal segment: 0 = not developed; 1 = developed; 2 = developed into a specialised structure.
26. Number of setae/elements (incl. claw) on first and second endopodal segments: 0 = five setae/elements; 1 = four; 2 = three; 3 = two; 4 = one; 5 = zero.

Maxillule and maxilliped. The oral appendages in Chondracanthidae are unique (e.g. the mandible), however most are relatively uniform and difficult to use as characters at the generic level. Some others vary so much within each genus that no meaningful generalisation can be made. Only the maxillule and maxilliped are used in this analysis.

The bilobed poecilostomatoid maxillule comprises an outer palp and an inner praecoxal endite with five and three setae respectively (Huys & Boxshall 1991). The chondracanthid maxillule is reduced and unilobate with a maximum of four elements, the homology of which is difficult to establish.

The poecilostomatoid maxilliped is four-segmented comprising syncoxa with two setae; basis with two setae; two-segmented endopodal segment with two setae on proximal segment and four setae on apical segment (Huys & Boxshall 1991). Male *Auchenochondria* Dojiri & Perkins, 1979 is the only member of the Chondracanthidae that has a four-segmented maxilliped: the syncoxa is unarmed; the basis has patches of spinules or denticles; the proximal endopodal segment is unarmed; and the apical endopodal segment is developed into a claw armed with up to two small teeth or hooklets. All other genera of Chondracanthidae have a three-segmented maxilliped; the articulation between the two endopodal segments being absent.

27. Number of elements on maxillule: 0 = four or more elements; 1 = three; 2 = two; 3 = one; 4 = zero.
28. Basis of maxilliped: 0 = armed with setae; 1 = patch(es) of denticles/spinules; 2 = unarmed.

29. Terminal segment (= claw) of maxilliped: 0 = armed; 1 = unarmed.

Swimming legs. A wide range of variation is seen in Chondracanthid swimming legs (Fig. 3A-D). Segmental and setal homologies are identified by reference to the larval descriptions of Izawa (1986), Ho & Kim (1990) and Kim & Ho (1992) and by reference to the rules of development of legs in copepods identified by Ferrari (1993). The poecilostomatoid swimming legs 1-4 are biramous with three-segmented rami (Huys & Boxshall 1991).

In Chondracanthidae the primitive condition in swimming legs 1-3 of both females and males is biramous with two-segmented rami in e.g. *Juanettia* Wilson, 1921, *Rhynchochondria* Ho, 1967 and *Apodochondria* Ho & Dojiri, 1988. Swimming leg 4, if present, is uniramous with two-segmented exopod in the male and only a protopod with outer basal seta in the female.

The poecilostomatoid swimming leg 5 is uniramous with one-segmented exopod (Huys & Boxshall 1991). If present, swimming leg 5 is represented by a small lobe with a few setae in the Chondracanthidae. Swimming leg 6 in Chondracanthidae is usually present with a few setae on the genital opercula as in most copepods.

The legs of greatest interest in this analysis are swimming legs 1-4. Specialisation of these legs occurs by fusion of segments (Fig. 1B), loss of armature and/or transformation into lobe-like structures (Fig. 1C-D). These lobe-like legs resemble body-processes but are distinguished by their possession of muscles and the presence of the outer basal seta on the protopod (Ho 1970). The most derived condition is loss of all legs.

First pair of swimming legs. If the first pair of swimming legs is absent (character 30 scores 2) then all the following characters (31-54) are scored “-” for inapplicable.

30. Leg 1: 0 = biramous; 1 = unilobed; 2 = absent.
31. Inner coxal seta: 0 = present, 1 = absent.
32. Outer basal seta: 0 = present; 1 = absent.
33. Articulation between coxa and basis: 0 = expressed; 1 = not expressed.
34. Outer seta/spine on first exopodal segment: 0 = present; 1 = absent.
35. Proximal outer spine on terminal exopodal segment (originating from second

exopodal segment): 0 = present; 1 = absent.

36. Middle outer spine on terminal exopodal segment: 0 = present; 1 = absent.
37. Distal outer spine on terminal exopodal segment: 0 = present; 1 = absent.
38. First inner seta on terminal exopodal segment: 0 = present; 1 = absent.
39. Second inner seta on terminal exopodal segment: 0 = present; 1 = absent.
40. Third inner seta on terminal exopodal segment: 0 = present; 1 = absent.
41. Fourth inner seta on terminal exopodal segment: 0 = present; 1 = absent.
42. Fifth inner seta on terminal exopodal segment: 0 = present; 1 = absent.
43. Articulation between proximal and terminal exopodal segments (one- or two-segmented rami): 0 = expressed; 1 = not expressed.
44. Inner seta on first endopodal segment: 0 = present; 1 = absent.
45. Outer spine on terminal endopodal segment: 0 = present; 1 = absent.
46. First seta on terminal endopodal segment: 0 = present; 1 = absent.
47. Second seta on terminal endopodal segment: 0 = present; 1 = absent.
48. Third seta on terminal endopodal segment: 0 = present; 1 = absent.
49. Fourth seta on terminal endopodal segment: 0 = present; 1 = absent.
50. Fifth seta on terminal endopodal segment: 0 = present; 1 = absent.
51. Sixth seta on terminal endopodal segment (seta originating from second endopodal segment): 0 = present; 1 = absent.
52. Articulation between first and terminal endopodal segments (one- or two-segmented rami): 0 = expressed; 1 = not expressed.
53. Articulation between first endopodal segment and basis: 0 = expressed; 1 = not expressed.
54. Articulation between first exopodal segment and basis: 0 = expressed; 1 = not expressed.

Second pair of swimming legs. If the second pair of swimming legs is absent (character 55 scores 2) then all the following characters (56-78) are scored “-” for inapplicable.

55. Leg 2: 0 = biramous; 1 = unilobed; 2 = absent.
56. Inner coxal seta: 0 = present, 1 = absent.
57. Articulation between coxa and basis: 0 = expressed; 1 = not expressed.
58. Outer seta/spine on first exopodal segment: 0 = present; 1 = absent.

59. Proximal outer spine on terminal exopodal segment: 0 = present; 1 = absent.
60. Middle outer spine on terminal exopodal segment: 0 = present; 1 = absent.
61. Distal outer spine on terminal exopodal segment: 0 = present; 1 = absent.
62. First inner seta on terminal exopodal segment: 0 = present; 1 = absent.
63. Second inner seta on terminal exopodal segment: 0 = present; 1 = absent.
64. Third inner seta on terminal exopodal segment: 0 = present; 1 = absent.
65. Fourth inner seta on terminal exopodal segment: 0 = present; 1 = absent.
66. Fifth inner seta on terminal exopodal segment: 0 = present; 1 = absent.
67. Sixth inner seta on terminal exopodal segment (seta originating from second exopodal segment): 0 = present; 1 = absent.
68. Articulation between first and terminal exopodal segments (one- or two-segmented rami): 0 = expressed; 1 = not expressed.
69. Inner seta on first endopodal segment: 0 = present; 1 = absent.
70. First outer spine on terminal endopodal segment: 0 = present; 1 = absent.
71. Second outer spine on terminal endopodal segment: 0 = present; 1 = absent.
72. First inner seta on terminal endopodal segment: 0 = present; 1 = absent.
73. Second inner seta on terminal endopodal segment: 0 = present; 1 = absent.
74. Third inner seta on terminal endopodal segment: 0 = present; 1 = absent.
75. Fourth inner seta on terminal endopodal segment (seta originating from second endopodal segment): 0 = present; 1 = absent.
76. Articulation between first and terminal endopodal segments (one- or two-segmented): 0 = expressed; 1 = not expressed.
77. Articulation between first endopodal segment and basis: 0 = expressed; 1 = not expressed.
78. Articulation between first exopodal segment and basis: 0 = expressed; 1 = not expressed.

Third pair of swimming legs. If the third pair of swimming legs is absent (character 79 scores 2) then all the following characters (80-85) are scored “-” for inapplicable.

79. Leg 3: 0 = biramous; 1 = unilobed; 2 = absent.
80. Inner coxal seta: 0 = present, 1 = absent.
81. Fourth inner seta on terminal exopodal segment: 0 = present, 1 = absent.

82. Fifth inner seta on terminal exopodal segment: 0 = present, 1 = absent.
83. Inner seta on first endopodal segment: 0 = present, 1 = absent.
84. First seta on terminal endopodal segment: 0 = present, 1 = absent.
85. Second seta on terminal endopodal segment: 0 = present, 1 = absent.

Fourth pair of swimming legs.

86. Leg 4: 0 = biramous; 1 = lobate; 2 = absent.

Male characters

Body. The body of the male (Fig. 1C) is smaller and not as modified as the female body. It is cyclopiform and primitively retains well-defined segmentation with a cephalothorax (fused cephalosome and first pedigerous somite), free second to fifth pedigerous segments, a genital somite and a four-segmented abdomen. The cephalothorax is often swollen and globose which makes the rest of the body looks like a “tail” which is often ventrally flexed (Ho 1970). In derived forms the segmentation is indistinct or completely lost.

87. Body segmentation: 0 = distinct; 1 = indistinct or absent.
88. Cephalosome and first pedigerous segment: 0 = not fused; 1 = fused.
89. First and second pedigerous segments: 0 = not fused; 1 = fused.
90. Second and third pedigerous segments: 0 = not fused; 1 = fused.
91. Third and fourth pedigerous segments: 0 = not fused; 1 = fused.
92. Fourth and fifth pedigerous segments: 0 = not fused; 1 = fused.
93. Fifth and sixth pedigerous segments: 0 = not fused; 1 = fused.

Antennule. See comments under female antennule. The adult male is usually less modified in its structure with a more slender and cylindrical antennule usually armed with more elements than the female. The division in character 100 is arbitrary. If the antennule is absent (character 94 scores 1) then all the following characters (95-100) are scored “-” for inapplicable.

94. Antennule: 0 = present; 1 = absent.
95. Articulation between segments V and VI: 0 = expressed; 1 = partly expressed or

not expressed.

96. Articulation between segments XIII and XIV: 0 = expressed; 1 = partly expressed or not expressed.
97. Articulation between segments XX and XXI: 0 = expressed; 1 = partly expressed or not expressed.
98. Articulation between segments XXIV and XXV: 0 = expressed; 1 = partly expressed or not expressed.
99. Articulation between segments XXV and XXVI: 0 = expressed; 1 = partly expressed or not expressed.
100. Setal number on proximal part (segments I-XX): 0 = greater than or equal to 20; 1 = 10-19; 2 = 5-9; 3 = less than or equal to 4.

Antenna. See comments under female antenna.

101. Seta on coxobasis: 0 = present; 1 = absent.
102. Atrophied tip (third endopodal segment): 0 = defined; 1 = absent.
103. Number of setae/elements on atrophied tip (third endopodal segment) (when defined): 0 = seven setae/elements; 1 = six; 2 = five; 3 = four; 4 = three; 5 = two; 6 = one; 7 = zero.
104. Number of setae/elements (incl.claw) on First and Second endopodal segments: 0 = five setae/elements; 1 = four; 2 = three; 3 = two; 4 = one; 5 = zero.

Maxillule and maxilliped. See comments under female maxillule and maxilliped. The male appendages are similar apart from the usual sexual dimorphism.

105. Number of elements on maxillule: 0 = four or more elements; 1 = three; 2 = two; 3 = one; 4 = zero.
106. Maxilliped four-segmented: 0 = yes; 1 = no.
107. Basis of maxilliped: 0 = armed with setae and patch(es) of denticles; 1 = patch(es) of denticles/spinules; 2 = unarmed.
108. Terminal segment (= claw) of maxilliped: 0 = armed; 1 = unarmed.

Swimming legs. See comments under female swimming legs.

First pair of swimming legs. If the first pair of swimming legs is absent (character 109 scores 2) then all the following characters (110-135) are scored “-” for inapplicable.

109. Leg 1: 0 = biramous; 1 = unilobed; 2 = absent.
110. Intercoxal sclerite: 0 = present; 1 = absent.
111. Inner coxal seta: 0 = present; 1 = absent.
112. Outer basal seta: 0 = present; 1 = absent.
113. Articulation between coxa and basis: 0 = expressed; 1 = not expressed.
114. Outer seta/spine on first exopodal segment: 0 = present; 1 = absent.
115. Proximal outer spine on terminal exopodal segment: 0 = present; 1 = absent.
116. Middle outer spine on terminal exopodal segment: 0 = present; 1 = absent.
117. Distal outer spine on terminal exopodal segment: 0 = present; 1 = absent.
118. First inner seta on terminal exopodal segment: 0 = present; 1 = absent.
119. Second inner seta on terminal exopodal segment: 0 = present; 1 = absent.
120. Third inner seta on terminal exopodal segment: 0 = present; 1 = absent.
121. Fourth inner seta on terminal exopodal segment: 0 = present; 1 = absent.
122. Fifth inner seta on terminal exopodal segment: 0 = present; 1 = absent.
123. Sixth inner seta on terminal exopodal segment (seta originating from second exopodal segment): 0 = present; 1 = absent.
124. Articulation between first and terminal exopodal segments (one- or two-segmented rami): 0 = expressed; 1 = not expressed.
125. Inner seta on first endopodal segment: 0 = present; 1 = absent.
126. Outer spine on terminal endopodal segment: 0 = present; 1 = absent.
127. First seta on terminal endopodal segment: 0 = present; 1 = absent.
128. Second seta on terminal endopodal segment: 0 = present; 1 = absent.
129. Third seta on terminal endopodal segment: 0 = present; 1 = absent.
130. Fourth seta on terminal endopodal segment: 0 = present; 1 = absent.
131. Fifth seta on terminal endopodal segment: 0 = present; 1 = absent.
132. Sixth seta on terminal endopodal segment (seta originating from second endopodal segment): 0 = present; 1 = absent.
133. Articulation between first endopodal segment and terminal endopodal segments (one- or two-segmented rami): 0 = expressed; 1 = not expressed.
134. Articulation between first endopodal segment and basis: 0 = expressed; 1 = not

expressed.

135. Articulation between first exopodal segment and basis: 0 = expressed; 1 = not expressed.

Second pair of swimming legs. If the second pair of swimming legs is absent (character 136 scores 2) then all the following characters (137-162) are scored “-” for inapplicable.

136. Leg 2: 0 = biramous; 1 = unilobed; 2 = absent.
137. Intercoxal sclerite: 0 = present; 1 = absent.
138. Inner coxal seta: 0 = present; 1 = absent.
139. Outer basal seta: 0 = present; 1 = absent.
140. Articulation between coxa and basis: 0 = expressed; 1 = not expressed.
141. Outer seta/spine on first exopodal segment: 0 = present; 1 = absent.
142. Proximal outer spine on terminal exopodal segment: 0 = present; 1 = absent.
143. Middle outer spine on terminal exopodal segment: 0 = present; 1 = absent.
144. Distal outer spine on terminal exopodal segment: 0 = present; 1 = absent.
145. First inner seta on terminal exopodal segment: 0 = present; 1 = absent.
146. Second inner seta on terminal exopodal segment: 0 = present; 1 = absent.
147. Third inner seta on terminal exopodal segment: 0 = present; 1 = absent.
148. Fourth inner seta on terminal exopodal segment: 0 = present; 1 = absent.
149. Fifth inner seta on terminal exopodal segment: 0 = present; 1 = absent.
150. Sixth inner seta on terminal exopodal segment (seta originating from second exopodal segment): 0 = present; 1 = absent.
151. Articulation between first and terminal exopodal segments (one-or two-segmented rami): 0 = expressed; 1 = not expressed.
152. Inner seta on first endopodal segment: 0 = present; 1 = absent.
153. First outer spine on terminal endopodal segment: 0 = present; 1 = absent.
154. Second outer spine on terminal endopodal segment: 0 = present; 1 = absent.
155. Third outer spine on terminal endopodal segment: 0 = present; 1 = absent.
156. First inner seta on terminal endopodal segment: 0 = present; 1 = absent.
157. Second inner seta on terminal endopodal segment: 0 = present; 1 = absent.
158. Third inner seta on terminal endopodal segment: 0 = present; 1 = absent.
159. Fourth inner seta on terminal endopodal segment (seta originating from second

endopodal segment): 0 = present; 1 = absent.

160. Articulation between first and terminal endopodal segments (one- or two-segmented rami): (0 = expressed; 1 = not expressed.
161. Articulation between first endopodal segment and basis: 0 = expressed; 1 = not expressed.
162. Articulation between first exopodal segment and basis: 0 = expressed; 1 = not expressed.

Third pair of swimming legs. If the third pair of swimming legs is absent (character 163 scores 2) then all the following characters (164-184) are scored “-” for inapplicable.

163. Leg 3: 0 = biramous; 1 = unilobed; 2 = absent.
164. Intercoxal sclerite: 0 = present; 1 = absent.
165. Inner coxal seta: 0 = present; 1 = absent.
166. Articulation between coxa and basis: 0 = expressed; 1 = not expressed.
167. Outer seta/spine on first exopodal segment: 0 = present; 1 = absent.
168. Proximal outer spine on terminal exopodal segment: 0 = present; 1 = absent.
169. Distal outer spine on terminal exopodal segment: 0 = present, 1 = absent.
170. Second inner seta on terminal exopodal segment: 0 = present, 1 = absent.
171. Third inner seta on terminal exopodal segment: 0 = present, 1 = absent.
172. Fourth inner seta on terminal exopodal segment: 0 = present, 1 = absent.
173. Fifth inner seta on terminal exopodal segment: 0 = present, 1 = absent.
174. Sixth inner seta on terminal exopodal segment (seta originating from second exopodal segment): 0 = present, 1 = absent.
175. Articulation between first and terminal exopodal segments (one-segmented): 0 = expressed; 1 = not expressed.
176. Inner seta on first endopodal segment: 0 = present, 1 = absent.
177. Outer spine on terminal endopodal segment: 0 = present; 1 = absent.
178. First inner seta on terminal endopodal segment: 0 = present, 1 = absent.
179. Second inner seta on terminal endopodal segment: 0 = present, 1 = absent.
180. Third inner seta on terminal endopodal segment: 0 = present, 1 = absent.
181. Fourth inner seta on terminal endopodal segment: 0 = present, 1 = absent.
182. Articulation between first and terminal endopodal segments (one- or two-

segmented rami): 0 = expressed; 1 = not expressed.

183. Articulation between first endopodal segment and basis: 0 = expressed; 1 = not expressed.
184. Articulation between first exopodal segment and basis: 0 = expressed; 1 = not expressed.

Fourth pair of swimming legs. If the fourth pair of swimming legs is absent (character 185 scores 2) then character 186 is scored "-" for inapplicable.

185. Leg 4: 0 = biramous; 1 = uniramous; 2 = lobate; 3 = absent.
186. Proximal outer spine on terminal exopodal segment: 0 = present, 1 = absent.

Cladistic analysis

The Taenicanthidae Wilson, 1911 and Bomolochidae Claus, 1875 are closely related families of parasitic copepods within the order Poecilostomatoida (Dojiri & Cressey 1987) and are used as outgroups (cf. Maddison *et al.* 1984; Nixon & Carpenter 1993). Members of both families are relatively less modified for a parasitic mode of life than chondracanthids and they more closely resemble free-living poecilostomatoids such as the Oncaeidae Giesbrecht, 1892 and Sapphirinidae Thorell, 1859. *Bomolochus soleae* Claus, 1864 has been used for the analysis and *Taeniacanthus lagocephali* Pearse, 1952 has been used instead of the type-species, *T. carchariae* Sumpf, 1871, because the latter is insufficiently well characterised. Other potential outgroups were considered: Shiinoidae Cressey, 1975; Telsidae Ho, 1967 and Tuccidae Vervoort, 1962. These were not included in the analysis for different reasons e.g. only the female was known for Tuccidae, whereas the mode of attachment to the host was fundamentally different in Telsidae, and Shiinoidae has an extremely different antenna.

Some crustacean researchers do not accept character reversibility and run their phylogenetic analyses with all characters set as irreversible-up (e.g. Huys & Boxshall 1991; Böttger-Schnack & Huys 1998). This kind of *a priori* speculation about character evolution in copepods is controversial and has never been demonstrated as a valid method. Therefore we carried out analyses with characters set as unordered, ordered, and irreversible-up. Characters 1-15 and 25 were kept unordered even in ordered and irreversible analyses because they were the only positive gain characters (addition characters) in the whole data set and no *a priori* assumptions on character development were imposed. All phylogenetic analyses were performed using PAUP*, version Paup4.0b8 (Swofford 1999).

In addition to whether characters were treated as unordered, ordered or irreversible, separate analyses were performed on only male characters (Analysis set 1), only female characters (Analysis set 2) and on male and female data combined (Analysis set 3). The nine combinations are: **Analysis 1**: **MU** with male characters 87-186 set unordered; **MO** with male characters 87-186 set ordered; and **MI** with male characters 87-186 set irreversible-up. **Analysis 2**: **FU** with female characters 1-86 set unordered; **FO** with female characters 16-24 and 26-86 set ordered, characters 1-15 and 25 set unordered; and **FI** with female characters 16-24 and 26-86 set irreversible-up, characters 1-15 and 25 set unordered. **Analysis 3**: **MFU** with all characters 1-186 set unordered; **MFO** with characters 16-24 and 26-186 set ordered, characters 1-15 and 25 set unordered; and **MFI** with characters 16-24 and 26-186 set irreversible-up, characters 1-15 and 25 set unordered.

Separate male and female analyses (Analyses 1 and 2)

Most parsimonious trees (MPTs) were found using heuristic search (HS) with random addition sequences (RAS) followed by tree bisection-reconnection (TBR) branch swapping on 10,000 replicates (MulTrees was in effect and only one tree in each replicate was saved) for each of the three different character settings (unordered, ordered and irreversible-up). This strategy (see Quicke *et al.* 2000) allows searching in a wide area of tree space and maximises chances of finding multiple islands of equally parsimonious trees (Maddison 1991; Goloboff 1999). Thereafter, all trees from the different islands were used as starting trees for further TBR searches with maxtrees effectively unlimited. All resulting trees were compared to see if they differed, or whether the same island has been hit by random. Finally, when multiple MPTs were obtained, strict consensus trees and agreement subtrees were calculated.

Support for individual branches was assessed by bootstrapping (Felsenstein 1985). The bootstrap analyses were run with 1000 replicates of 50 random additions and holding only one tree at each replicate. This was a faster method of running bootstrap, but because the analysis may have given less optimal cladograms, the values obtained were an underestimate of the real support, thus they were conservative (cf. Gauthier *et al.* 2000).

The two partitions, male and female, were compared using the Incongruence Length Difference (ILD) test to assess the significance of incongruence between them (Farris *et al.* 1994). The test was run with 500 replicates of 100 random additions. Tests were done to determine whether noise was a significant factor by randomly shuffling (using the shuffle function in MacClade 3.0 (Maddison & Maddison 1992)) first one partition and testing it against the other using ILD and then vice versa (Dolphin *et al.* 2000).

The potential dominance of one partition over the other was tested by giving different weights to the individual partitions (Fig. 4). HS was run as above with both partitions simultaneously, giving weight to male characters of 1.0, 1.25, 1.5, 2 and 5× those of females and vice versa. A strict consensus tree for each weighted analysis was calculated. The strict consensus trees from the HS with sexes unequally weighted were compared with the strict consensus tree from the HS with both sexes equally weighted using the agreement subtrees method implemented in PAUP. If the number of taxa in the resultant agreement subtree was high the non-weighted sex was dominant, because despite being suppressed it still managed to get some signal through. The strength of dominance could therefore be assessed by examining how the number of taxa in the subtrees was affected by differential weighting of male and female characters.

Male and female simultaneously (Analysis 3)

The initial tree searching and bootstrapping were carried out as outlined above for single sex analyses. MPTs were found for three different character settings; unordered, ordered and irreversible-up. Bootstrap support was assessed for each of the three analyses.

To test the validity of the subfamilies, Chondracanthinae and Lernentominae, additional analyses were performed a) with the two subfamilies set as two separate monophyletic groups and b) with Lernentominae only as monophyletic, allowing

Chondracanthinae to be paraphyletic. Tree searching was carried out as outlined above for each character setting (unordered, ordered and irreversible-up) with the different constraints. The MPTs resulting from these analyses were compared with the MPTs from MFU, MFO and MFI respectively using both Kishino-Hasegawa and Templeton (non-parametric) tests both tools implemented in PAUP.

To test the validity of the family Pharodidae constrained analyses as outlined above were carried out with Pharodidae set as a separate monophyletic group. Statistical support was assessed using the Kishino-Hasegawa and Templeton tests.

Results

Male versus female characters

Phylogenetic analyses of the two partitions, male and female, each with characters set unordered, ordered and irreversible-up, gave six different sets of trees whose strict consensuses are shown in Fig. 5A-F. Common to all trees except FI (Fig. 5F) was a strongly supported basal backbone (bootstrap values higher than 70%) and a relatively less resolved terminal clade with no or little internal bootstrap support. A backbone of nine ingroup taxa (*Auchenochondria* Dojiri & Perkins, 1979; *Juanettia* Wilson, 1921; *Prochondracanthus* Yamaguti, 1939; *Rhynchochondria* Ho, 1967; *Hoia* Avdeev & Kazatchenko, 1985; *Pseudacanthocanthopsis* Yamaguti & Yamasu, 1959; *Cryptochondria* Izawa, 1971; *Lagochondria* Ho & Dojiri, 1988 and *Apodochondria* Ho & Dojiri, 1988) was always the same in all six trees, but their detailed arrangement differed slightly from tree to tree.

The agreement subtree for MU+MO+MI showed which taxa were recovered in the same relative positions on all MPTs in Analysis 1 (Fig. 6A). In this case, only 19 of the 42 ingroup taxa were positioned similarly and only 15 of 42 taxa were positioned similarly in the agreement subtree when comparing FU+FO+FI from Analysis 2 (Fig. 6B).

When comparing male with female it was clear that there was some similarity in the backbone of the two partitions. Six out of the twelve taxa in the agreement subtree for MU+FU (Fig. 7A), and five out of twelve taxa in the agreement subtrees for MO+FO (Fig. 7B) and MI+FI (Fig. 7C) all belonged to the basal backbone taxa observed in the strict consensus trees of the two partitions (cf. Fig. 5).

The ILD test showed the two data partitions (male versus female) were significantly incongruent, regardless of whether the test was run with characters unordered, ordered or irreversible-up ($p < 0.002$). We do not know how much is due to noise, because when we ran shuffled tests (Dolphin *et al*. 2000) they gave exactly the same p-values, which were always the limit of the search and we were not able to find the actual p-value within a reasonable computing time.

Differential weighting of male and female characters showed that female characters were dominant compared to male characters. This dominance was clear because, despite giving a higher weight to male characters (male = 1.25), the resultant tree was an exact duplicate of the tree where all characters were of equal weight (= MFU) (Table 1). When repeated for female characters (female = 1.25) the resultant trees had only 27 taxa in exactly the same position as in the MFU tree (Table 1). This indicated that even though the female characters were dominant and had been given a higher weight, male characters still influenced the topology of the tree. However, female dominance was not that pronounced, as indicated by the reduction in the number of taxa found when even higher weight were given to male characters (male = 1.5, 2 or 5) (Table 1).

Unordered versus ordered

Different trees were generated when characters were set as unordered, ordered or irreversible-up while running simultaneous phylogenetic analyses of male and female partitions (Fig. 8A-C). A backbone comprising the same nine ingroup taxa as in Analyses 1 and 2, was present in all three strict consensus trees. The sequence of taxa in the backbone was also more or less the same for all three trees.

Despite strong similarities in the basal part of the tree, the top of the trees from the three analyses were very different. An agreement subtree of all MFU+MFO+MFI trees showed that only 14 out of 42 taxa (Fig. 8D) was placed similarly for all three character settings, and eight of these were from the backbone.

Support for existing subfamilies

The four genera (*Brachiochondrites* Markewitsch, 1940; *Chelonichondria* Ho, 1994; *Jusheyhoea* Villalba & Fernandez, 1985 and *Lernentoma* de Blainville, 1822) currently placed in the subfamily Lernentominae did not cluster together in any of the unconstrained trees (Figs. 5 & 8). When a monophyly constraint for the two subfamilies was imposed, tree lengths increased by 17.5% for MFU, 17.7% for MFO and 15.0% for MFI. The Kishino-Hasegawa and Templeton tests both showed that the trees were significantly different (P<0.0001).

Validity of Pharodidae

Pharodes was located at the top of the MFU (Fig. 8A) and MFO (Fig. 8B) trees and in the middle of the MFI tree closer to the basal backbone (Fig. 8C). In both MFU and MFI *Pharodes* showed a close affinity with *Praecidochondria* Kabata, 1968, but the characters defining their closest common nodes were different in the two analyses. In MFU the characters shared included presence of atrophied tip on antenna in female (character 23), one element on female maxillule (character 27) and female leg 2 absent (character 55). In MFI the characters shared included one element on female maxillule (character 27), terminal segment on male maxilliped unarmed (character 108) and reduced leg 1 and 2 in male (characters 109 and 136).

When a monophyly constraint for Pharodidae was imposed, tree lengths increased by 15.0% for MFU, 16.0% for MFO and 14.6% for MFI. Kishino-Hasegawa and Templeton both showed that the trees were significantly different (P<0.0001).

Discussion

Incongruence between male and female character partitions

The method of calculating agreement subtrees is very useful when looking for a subset of taxa among a set of MPTs or several combined sets of MPTs whose relationships are of special interest. If the number of taxa present on an agreement subtree was close to the number of taxa included in the analysis then all the MPTs in the subset were very similar. If not, then the MPTs were very different which indicated that the two sets of MPTs (i.e. the result of the two analyses) were not telling the same phylogenetic story.

The agreement subtrees found in the present analysis clearly showed that the male and female data sets were very different. This result was also supported by the ILD test which showed a significant incongruence between male and female data sets (i.e. they do not tell the same phylogenetic story).

The two data sets were also tested for relative dominance and, as indicated by the outcome of differential weighting, the female character set was found to be dominant. However, this dominance was not excessive as the number of taxa on the agreement subtree soon decreased when female influence was outweighted. Even though male characters are not dominant, this result supports Kabata & Gusev (1966), Ho (1970) and Hogans & Sulak (1992) when they suggest that male characters be regarded as equally important to female characters for assessing Chondracanthid relationships. Therefore the two partitions were run simultaneously.

Unordered versus ordered

There is no consensus on how the characters should be treated when studying the phylogeny of copepods. The assumption that character reversals are rare has been used to justify running phylogenetic analyses with all characters set as irreversible, in order to suppress character reversals at the expense of introducing extra convergence (e.g. Huys & Boxshall 1991; Böttger-Schnack & Huys 1998). In order not to impose such assumptions other copepod phylogenetic analyses have been undertaken with all characters set as unordered (e.g. Dojiri & Deets 1988; Ho 1994). The results obtained here have suggested that it makes a difference (i.e. MFI trees were a lot longer than e.g. MFU trees), and that it is better to apply as few *a priori* constraints as possible.

It is not only within copepods that no consensus has been reached. Discussions on the use of characters as unordered or ordered (e.g. irreversible) are common (e.g. Pimentel & Riggens 1987; Hauser & Presch 1991; Wilkinson 1992; Kim 1993;

Mikkelsen 1998). As ordering characters requires a hypothesis concerning evolutionary assumptions, unordered coding of characters has widest support. However, a general agreement is to perform both analyses together (Hauser & Presch 1991; Wilkinson 1992; Mikkelsen 1998) and sometimes both show the same result.

Support for existing subfamilies

At present the family Chondracanthidae comprises two subfamilies. This division is not supported by any of the present analysis. The Lernentominae is defined on the possession of a pre-oral neck but, a survey of neck development in chondracanthids reveals five different patterns of neck formation previously grouped together as a post-oral neck. Long necks originated several times (e.g. in *Auchenochondria* Dojiri & Perkins, 1979; *Strabax* von Nordmann, 1864; *Mecaderochondria* Ho & Dojiri, 1987; *Pterochondria* Ho, 1973 and *Medesicaste* Krøyer, 1863) (Fig. 8), and there is no justification in subjectively treating the development of a pre-oral neck as a unique event. Statistical comparison (using both the Kishino-Hasegawa and Templeton tests) of MPTs and those constrained to recover subfamilies as monophyletic all showed significant difference, we therefore formally synonymize Lernentominae Oakley, 1927 with Chondracanthinae Milne Edwards, 1840.

Validity of Pharodidae

Statistical comparison (Kishino-Hasegawa and Templeton tests) of MPTs and those constrained to recover Pharodidae as monophyletic all showed significant difference indicating that Pharodidae is not truly monophyletic. The following arguments also support this result.

A dorsal protrusion (Ho 1971) here interpreted as an expanded posteromedian process was observed in *Pharodes*. Similar expansion of this process has also been observed in *Jusheyhoea*, *Cryptochondria* and some *Chondracanthus* species, however, the extent to which it is expanded in *Pharodes* is unique.

A close relationship between the *Praecidochondria* and *Pharodes* was indicated by the present analysis. Ho (1971) noted that the female maxilliped, maxilla and mandible were different in Pharodidae, however, *Praecidochondria* shows similar trends in those limbs. The maxillipeds of both *Pharodes* and *Praecidochondria* are unarmed pointed processes. The terminal segment of the maxilla in *Pharodes* is unarmed, as it in *Praecidochondria*. The mandible in *Pharodes* is a blade with a few spinules, in *Praecidochondria* it is a blade with teeth, but unlike most other chondracanthids, the blade is only armed on one edge as in *Pharodes*.

Another character, a midventrally placed abdomen observed in Pharodidae was one of the fundamental differences justifying its split from Chondracanthidae (Ho 1971). Interestingly, a comparable structure has been found within the chondracanthid *Praecidochondria* (Ho 1970). Since this character was not included in the analysis (it is an autapomorphy) and has not been observed in any of the outgroup taxa our following argument finds strong support and *Pharodes* is therefore transferred here back into the family Chondracanthidae and the diagnosis of the family Chondracanthidae will be amended accordingly (Østergaard & Boxshall in prep). Pharodidae Illg, 1948 is therefore a junior subjective synonym of Chondracanthidae Milne Edwards, 1840.

Acknowledgements

We would like to thank the following people and institutions for arranging loans or donations of the material used in this study: P. Dworschak (Naturhistorisches Museum Wien, Austria); F. Fiers (Royal Belgian Institute of Natural Sciences, Brussels, Belgium); K. Izawa (University of Mie, Japan); Z. Kabata (Pacific Biological Station, Nanaimo, B.C., Canada); I. Kim (Kangreung National University, Kangreung, South Korea); Jørgen Olesen (Zoological Museum, University of Copenhagen, Denmark); D. Van den Spiegel (Africa Museum, Tervuren, Belgium); C. Walter (National Museum of Natural History, Smithsonian Institution, Washington DC, USA); R. Webber (Museum of New Zealand, Te Papa Tongarewa, Wellington, New Zealand); and W. Zeidler (South Australian Museum, Adelaide, Australia).

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Fig. 1 A—C. Line drawings. —A. Ventral view of female *Chondracanthus zei* Delaroche 1811 with egg sacs removed. —B. Ventral view of female *Mecaderochondria pilgrimi* Ho & Dojiri 1987 with one egg sac removed. Note the male attached to the female genital area. —C. Lateral view of male *M. pilgrimi*. Symbols: P1 and P2 or asterisks, swimming legs 1 and 2. Scales: 2 mm in A, B; 0.1 mm in C. [Original drawings from Kabata (1979) (A), and from Ho & Dojiri (1987) (B-C), with permission of authors].

Fig. 2 A—B. Schematic drawings. —A. Unisex antennule showing the maximum of six segments observed in Chondracanthidae. Elements are shown as setae (thin line), aesthetascs (thick line). —B. Chondracanthid antenna with first and second endopodal segments fused and forming a claw (c) with up to 4 setae: atrophied tip (a) is present with up to 7 setae. The coxobasis (b) bears one seta.

Fig. 3 A—D. Schematics of unisex swimming legs. —A. Most plesiomorphic state, with 2-segmented rami and maximal setation. —B. Intermediate reduced, biramous stage with some setal elements retained. —C. Most reduced biramous state, with no segmentation expressed and only the outer basal seta remaining. —D. Unilobate leg with no trace of rami and only an outer basal seta retained. Elements are shown as setae (thin line), outer basal seta (thick line) or spine (triangles). Unexpressed articulations (dotted line).

Fig. 4 Flow chart showing the procedure for differential weighting.

Fig. 5 A—F. Results of phylogenetic analysis of the two partitions (M and F). Each tree is strict consensus of all MPTs with characters treated as unordered (U), ordered (O) or irreversible up (I). Numbers above branches show bootstrap values >70%. —A. MU: 270 trees (3 islands; 162, 54, and 54 trees respectively), length 251, CI = 0.47, HI =

0.53, RI = 0.82. —B. MO: 63 trees (2 islands; 36 and 27 trees respectively), length 264, CI = 0.45, HI = 0.55, RI = 0.82. —C. MI: 156 trees (2 islands; 78 trees each), length 333, CI = 0.35, HI = 0.65, RI = 0.91. —D. FU: 8004 trees (8 islands; 3682, 1632, 1355, 822, 354, 102, 54, and 3 trees respectively), length 273, CI = 0.41, HI = 0.59, RI = 0.75 . —E. FO: 1889 trees (7 islands; 702, 504, 286, 239, 104, 28, and 26 trees respectively), length 300, CI = 0.39, HI = 0.61, RI = 0.73. —F. FI: 112 trees (1 island), length 351, CI = 0.34, HI = 0.66, RI = 0.88.

Fig. 6 A—B. Analysis of the two partitions. Trees are agreement subtrees. —A. MU, MO and MI pooled: 19 taxa of the original 42 occur in the same positions on all MPTs. —B. FU, FO and FI pooled: 15 taxa occur in the same positions on all MPTs.

Fig. 7 A—C. Analysis of the two partitions. Trees are agreement subtrees. —A. MU and FU pooled: 12 taxa occur in the same positions on all MPTs. —B. MO and FO pooled: 12 taxa occur in the same positions on all MPTs. —C. MI and FI pooled: 12 taxa occur in the same positions on all MPTs.

Fig. 8 A—D. Results of simultaneous analysis of male and female partitions. Trees are strict consensus of all MPTs with characters treated differently. Numbers above branches show bootstrap values >70%. —A. MFU: 1 tree (1 island), length 595, CI = 0.39, HI = 0.61, RI = 0.73. 42% of all character changes take place in basal backbone. —B. MFO: 60 trees (2 islands; 30 trees each), length 638, CI = 0.37, HI = 0.63, RI = 0.73. 42% of all character changes take place in basal backbone. —C. MFI: 2 trees (1 island), length 782, CI = 0.30, HI = 0.70, RI = 0.87. 36% of all character changes take place in basal backbone. —D. MFU, MFO and MFI pooled: 15 out of 42 taxa occur in the same positions on all MPTs. Taxa belonging to the subfamily Lernentominae are indicated by black circle, and taxa with a long post-oral neck an open circle. The position of *Pharodes* is indicated arrowed.

Table 1. Numbers of taxa remaining in agreement subtree between trees with male or female character partitions weighted pooled with the trees from MFU (where all characters were of equal weight). The maximum score is 42 (i.e. total number of taxa included in the analysis).

Differential weighting of character partitions							
Male characters weighted high				Female characters weighted high			
5:1	2:1	1.5:1	1.25:1	1.25:1	1.5:1	2:1	5:1
27	29	36	42	27	26	21	17

Figure 1

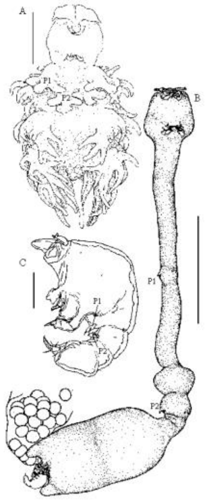


Figure 2

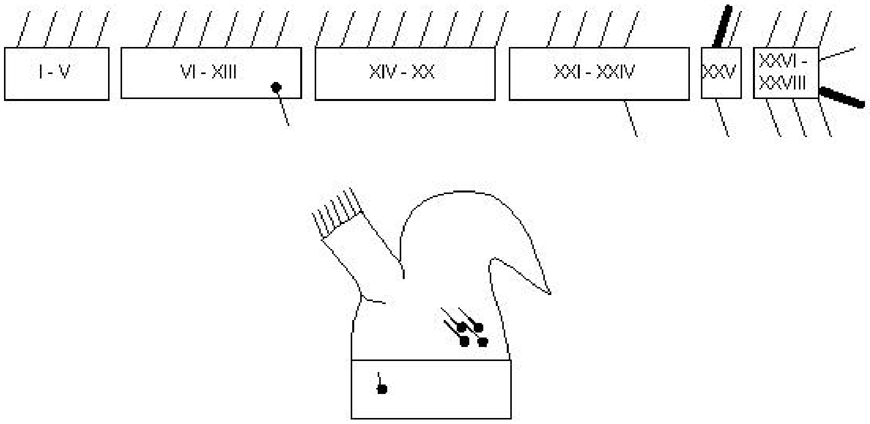


Figure 3

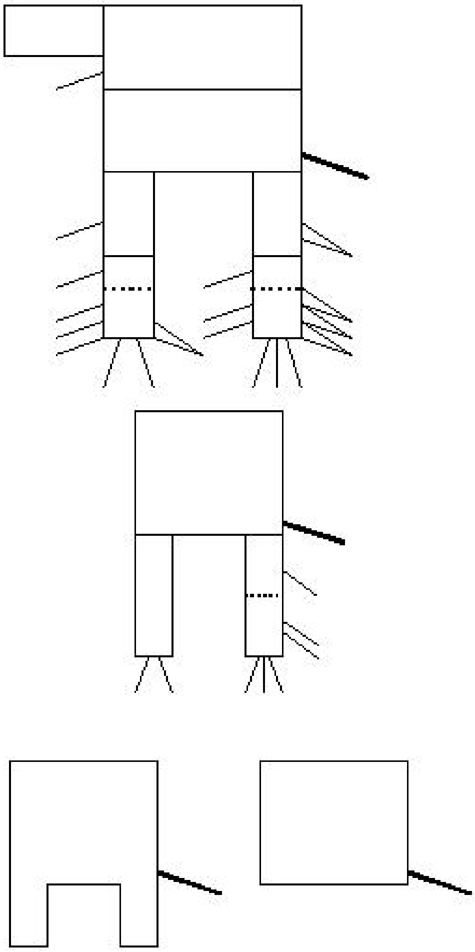


Figure 4

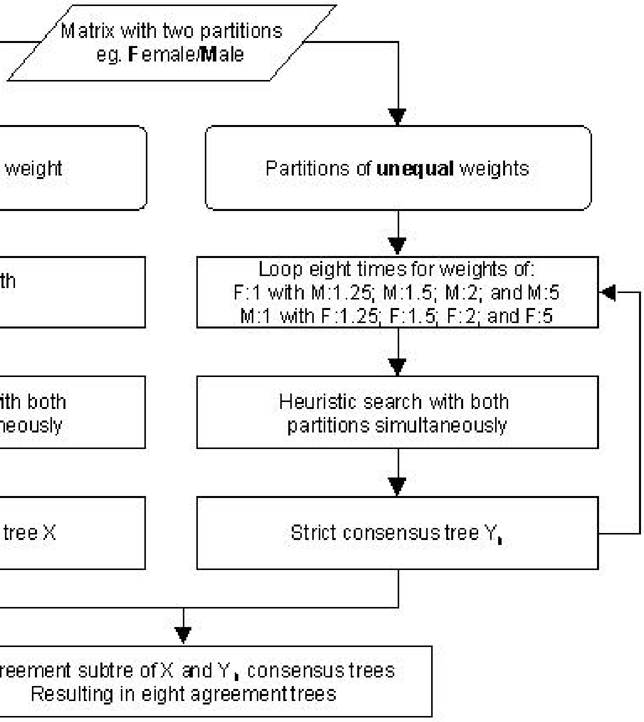

Matrix with two partitions
eg. **F**emale/**M**ale
Partitions of **equal** weight
Partitions of **unequal** weights
Base tree with
F:1, M:1
Loop eight times for weights of:
F:1 with M:1.25; M:1.5; M:2; and M:5
M:1 with F:1.25; F:1.5; F:2; and F:5
Heuristic search with both
partitions simultaneously
Heuristic search with both
partitions simultaneously
Strict consensus tree X
Strict consensus tree Y_i
Agreement subtre of X and Y_i consensus trees
Resulting in eight agreement trees

Figure 5

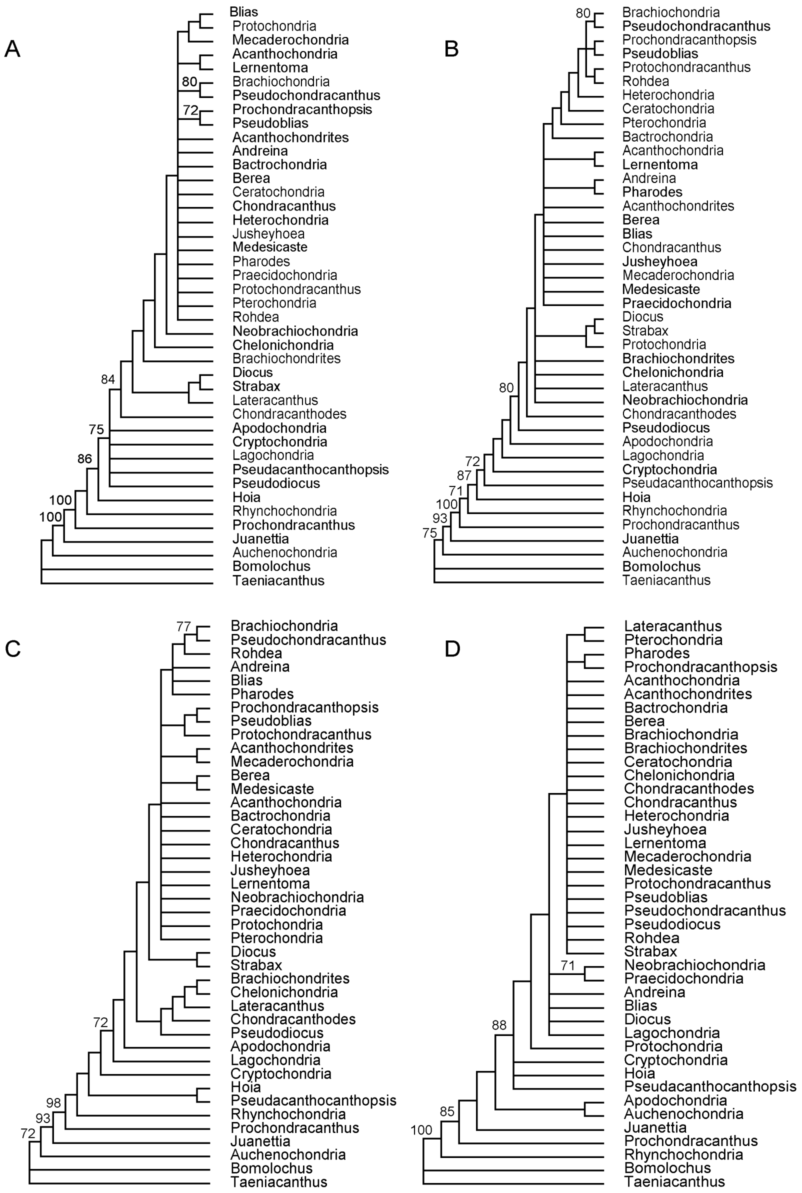

A
Blias
Protochondria
Mecaderochondria
Acanthochondria
Lernentoma
80
Brachiochondria
Pseudochondracanthus
72
Prochondracanthopsis
Pseudoblias
Acanthochondrites
Andreina
Bactrochondria
Berea
Ceratochondria
Chondracanthus
Heterochondria
Jusheyhoea
Medesicaste
Pharodes
Praecidochondria
Protochondracanthus
Pterochondria
Rohdea
Neobrachiochondria
Chelonichondria
Brachiochondrites
84
Diocus
Strabax
Lateracanthus
Chondracanthodes
75
Apodochondria
Cryptochondria
86
Lagochondria
Pseudacanthocanthopsis
Pseudodiocus
100
Hoia
100
Rhynchochondria
Prochondracanthus
Juanettia
Auchenochondria
Bomolochus
Taeniacanthus
B
80
Brachiochondria
Pseudochondracanthus
Prochondracanthopsis
Pseudoblias
Protochondracanthus
Rohdea
Heterochondria
Ceratochondria
Pterochondria
Bactrochondria
Acanthochondria
Lernentoma
Andreina
Pharodes
Acanthochondrites
Berea
Blias
Chondracanthus
Jusheyhoea
Mecaderochondria
Medesicaste
Praecidochondria
Diocus
Strabax
Protochondria
Brachiochondrites
Chelonichondria
80
Lateracanthus
Neobrachiochondria
Chondracanthodes
Pseudodiocus
Apodochondria
Lagochondria
72
Cryptochondria
87
Pseudacanthocanthopsis
71
Hoia
100
Rhynchochondria
93
Prochondracanthus
75
Juanettia
Auchenochondria
Bomolochus
Taeniacanthus
C
77
Brachiochondria
Pseudochondracanthus
Rohdea
Andreina
Blias
Pharodes
Prochondracanthopsis
Pseudoblias
Protochondracanthus
Acanthochondrites
Mecaderochondria
Berea
Medesicaste
Acanthochondria
Bactrochondria
Ceratochondria
Chondracanthus
Heterochondria
Jusheyhoea
Lernentoma
Neobrachiochondria
Praecidochondria
Protochondria
Pterochondria
Diocus
Strabax
Brachiochondrites
Chelonichondria
Lateracanthus
Chondracanthodes
72
Pseudodiocus
Apodochondria
Lagochondria
Cryptochondria
Hoia
98
Pseudacanthocanthopsis
93
Rhynchochondria
72
Prochondracanthus
Juanettia
Auchenochondria
Bomolochus
Taeniacanthus
D
Lateracanthus
Pterochondria
Pharodes
Prochondracanthopsis
Acanthochondria
Acanthochondrites
Bactrochondria
Berea
Brachiochondria
Brachiochondrites
Ceratochondria
Chelonichondria
Chondracanthodes
Chondracanthus
Heterochondria
Jusheyhoea
Lernentoma
Mecaderochondria
Medesicaste
Protochondracanthus
Pseudoblias
Pseudochondracanthus
Pseudodiocus
Rohdea
Strabax
71
Neobrachiochondria
Praecidochondria
Andreina
Blias
Diocus
88
Lagochondria
Protochondria
Cryptochondria
Hoia
Pseudacanthocanthopsis
85
Apodochondria
Auchenochondria
100
Juanettia
Prochondracanthus
Rhynchochondria
Bomolochus
Taeniacanthus

Figure 5, continued

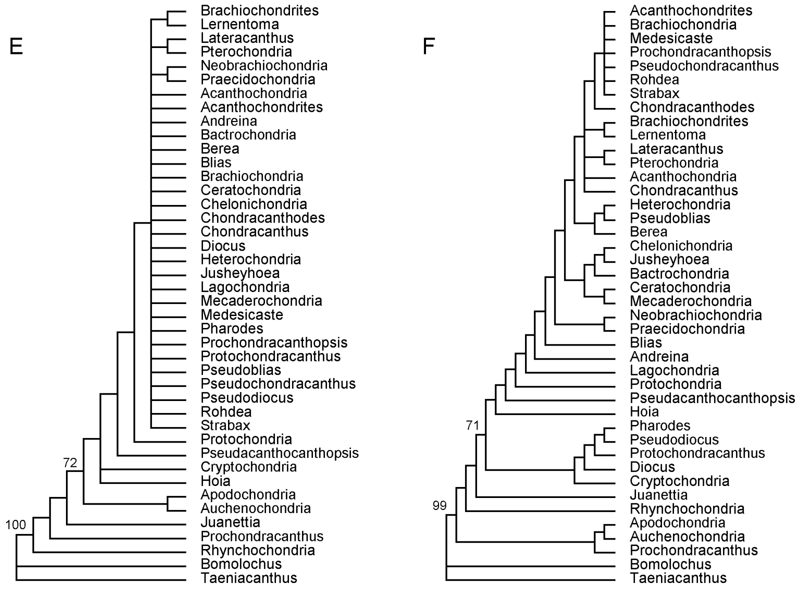
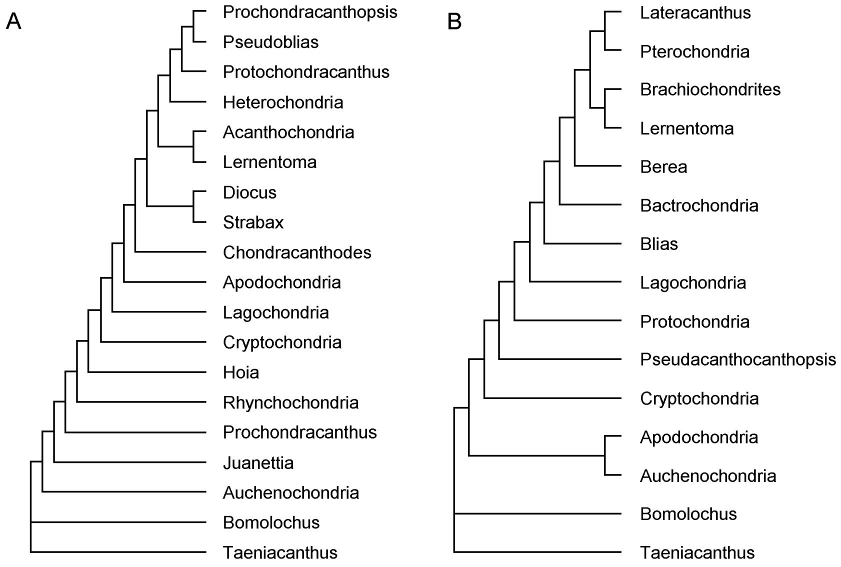


Figure 6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Pseudoblias
Protochondracanthus
Heterochondria
Acanthochondria
Lernentoma
Diocus
Strabax
Chondracanthodes
Apodochondria
Lagochondria
Cryptochondria
Hoia
Rhynchochondria
Prochondracanthus
Juanettia
Auchenochondria
Bomolochus
Taeniacanthus
B
Lateracanthus
Pterochondria
Brachiochondrites
Lernentoma
Berea
Bactrochondria
Blias
Lagochondria
Protochondria
Pseudacanthocanthopsis
Cryptochondria
Apodochondria
Auchenochondria
Bomolochus
Taeniacanthus

Figure 7

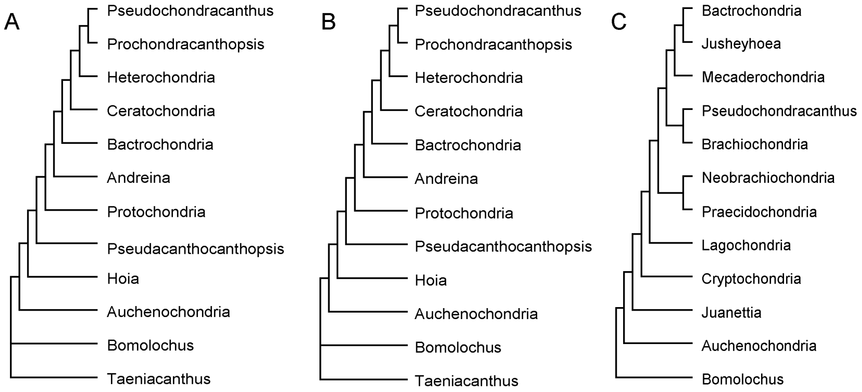
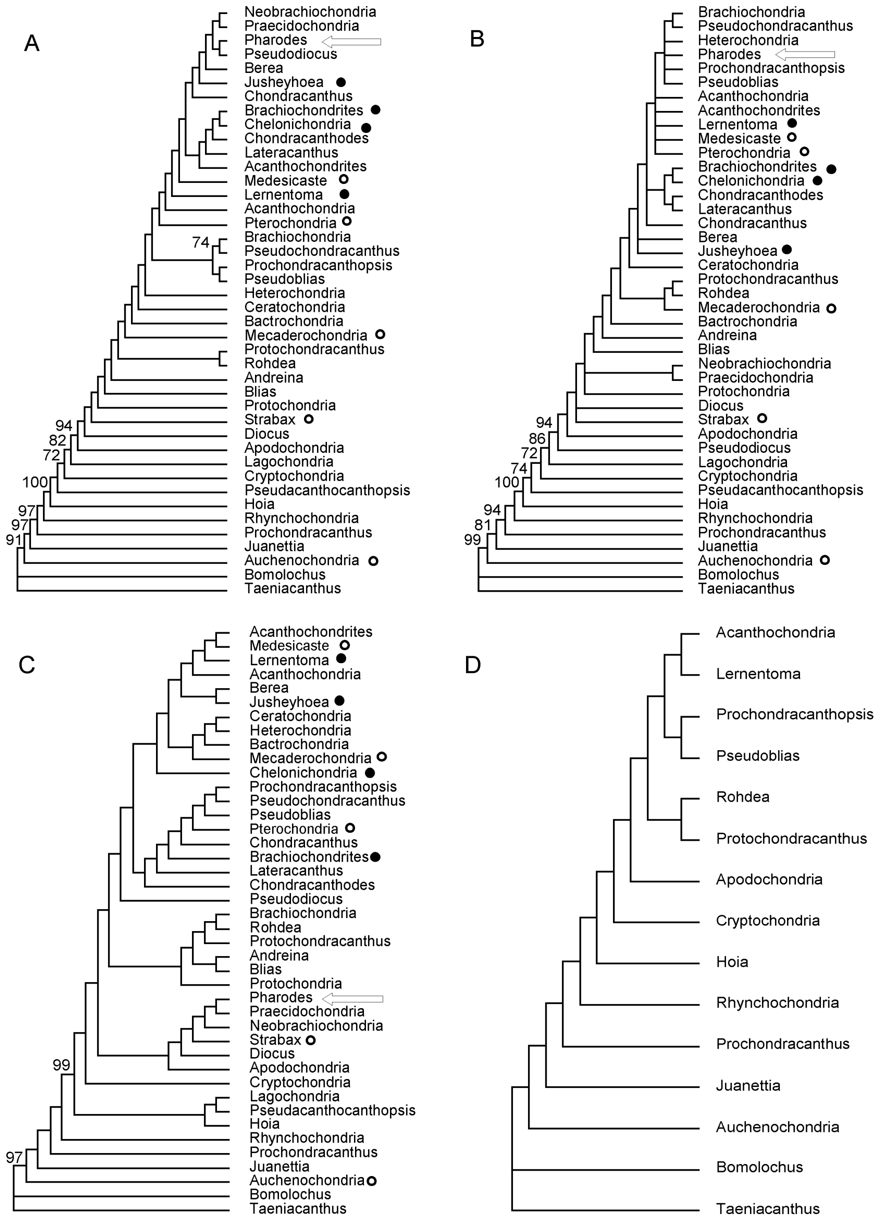

A
Pseudochondracanthus
Prochondracanthopsis
Heterochondria
Ceratochondria
Bactrochondria
Andreina
Protochondria
Pseudacanthocanthopsis
Hoia
Auchenochondria
Bomolochus
Taeniacanthus
B
Pseudochondracanthus
Prochondracanthopsis
Heterochondria
Ceratochondria
Bactrochondria
Andreina
Protochondria
Pseudacanthocanthopsis
Hoia
Auchenochondria
Bomolochus
Taeniacanthus
C
Bactrochondria
Jusheyhoea
Mecaderochondria
Pseudochondracanthus
Brachiochondria
Neobrachiochondria
Praecidochondria
Lagochondria
Cryptochondria
Juanettia
Auchenochondria
Bomolochus

Figure 8


A
Neobrachiochondria
Praecidochondria
Pharodes
Pseudodiocus
Berea
Jusheyhoea ●
Chondracanthus
Brachiochondrites ●
Chelonichondria ●
Chondracanthodes
Lateracanthus
Acanthochondrites
Medesicaste ○
Lernentoma ●
Acanthochondria
Pterochondria ○
74
Brachiochondria
Pseudochondracanthus
Prochondracanthopsis
Pseudoblias
Heterochondria
Ceratochondria
Bactrochondria
Mecaderochondria ○
Protochondracanthus
Rohdea
Andreina
Blias
Protochondria
Strabax ○
94
Diocus
82
Apodochondria
72
Lagochondria
Cryptochondria
100
Pseudacanthocanthopsis
Hoia
97
Rhynchochondria
97
Prochondracanthus
91
Juanettia
Auchenochondria ○
Bomolochus
Taeniacanthus
B
Brachiochondria
Pseudochondracanthus
Heterochondria
Pharodes
Prochondracanthopsis
Pseudoblias
Acanthochondria
Acanthochondrites
Lernentoma ●
Medesicaste ○
Pterochondria ○
Brachiochondrites ●
Chelonichondria ●
Chondracanthodes
Lateracanthus
Chondracanthus
Berea
Jusheyhoea ●
Ceratochondria
Protochondracanthus
Rohdea
Mecaderochondria ○
Bactrochondria
Andreina
Blias
Neobrachiochondria
Praecidochondria
Protochondria
Diocus
Strabax ○
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Apodochondria
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Pseudodiocus
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Lagochondria
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Cryptochondria
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Pseudacanthocanthopsis
Hoia
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Rhynchochondria
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Prochondracanthus
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Juanettia
Auchenochondria ○
Bomolochus
Taeniacanthus
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Lernentoma ●
Acanthochondria
Berea
Jusheyhoea ●
Ceratochondria
Heterochondria
Bactrochondria
Mecaderochondria ○
Chelonichondria ●
Prochondracanthopsis
Pseudochondracanthus
Pseudoblias
Pterochondria ○
Chondracanthus
Brachiochondrites●
Lateracanthus
Chondracanthodes
Pseudodiocus
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Rohdea
Protochondracanthus
Andreina
Blias
Protochondria
Pharodes
Praecidochondria
Neobrachiochondria
Strabax ○
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Cryptochondria
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Pseudacanthocanthopsis
Hoia
Rhynchochondria
Prochondracanthus
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Auchenochondria○
Bomolochus
Taeniacanthus
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Acanthochondria
Lernentoma
Prochondracanthopsis
Pseudoblias
Rohdea
Protochondracanthus
Apodochondria
Cryptochondria
Hoia
Rhynchochondria
Prochondracanthus
Juanettia
Auchenochondria
Bomolochus
Taeniacanthus

Appendix A

Character state distributions in Chondracanthidae, Pharodidae and two outgroup taxa. Refer to text for character list and character descriptions. Character states are scored 0-7 and missing/unknown states are denoted “?”. Inapplicable data are scored “-”, which is also used in the outgroup when the ingroup states are not present in the outgroup. Key: A = 1&2, B = 3&4, C = 0&4, D = 2&4, E = 2&3.

	Characters						
		1	2	3	4	5	6
Taxa	123456789	0123456789	0123456789	0123456789	0123456789	0123456789	01234
Acanthochondria	00000001-	---2031111	1311-14110	0101111111	1111111111	1111101111	11111
Acanthochondrites	00000001-	---2011111	1311-14210	1101111111	1111111111	1111111111	11111
Andreina	00000000-	---10-1111	131??1?210	0101000000	0111100001	1111101101	10001
Apodochondria	111111022	00010-1100	0100714200	2---------	----------	-----2----	-----
Auchenochondria	111100020	0013021000	0100314210	0101000000	0000000000	0000001100	00000
Bactrochondria	10000000-	---2011111	1311-14111	0101010000	1111111111	1111101101	10001
Berea	10000000-	---2011111	1311-2-110	0101111000	1111111111	1111101111	11001
Blias	00000000-	---2011111	1311-2-210	0101010000	011111?001	1111101101	10000
Brachiochondria	00001000-	---2001111	1311-14411	2---------	----------	-----2----	-----
Brachiochondrites	000000021	00041-1111	1311-13211	0101111111	1111111111	1111101111	11111
Ceratochondria	000000020	0102011111	131??1?211	0101010000	1111111111	1111101111	11001
Chelonichondria	000000022	01041-11?1	1311-14111	0101?11000	1111111111	1111101101	1000?
Chondracanthodes	000000022	1102011111	1311-14210	0101111111	1111111111	1111101111	11111
Chondracanthus	000000023	1222011111	1311-14110	0101111111	1111111111	1111101111	11111
Cryptochondria	110000021	10020D0000	0211-14?10	0100000000	0110100001	1100001101	10001
Diocus	000010022	0002021100	0211-2-121	0101010000	0110111001	1111101101	00000
Heterochondria	00000000-	---2031111	1311-14211	1101111?00	1111111111	1111111111	11001
Hoia	110000022	0002021111	1110014111	0101000000	0110000000	1100001101	10001
Juanettia	010001122	0012021100	0300014110	0000000000	0000000000	010002----	-----
Jusheyhoea	000000023	11041-1111	1311-14111	0101111100	1111111111	1111101111	11001
Lagochondria	10000001-	---2011111	1200214110	0100010000	0111100001	1111101101	10000
Lateracanthus	01000001-	---2031111	1301-13210	0101111111	1111111111	1111101111	11111
Lernentoma	100000022	00031-1111	1311-14210	0101111111	1111111111	1111101111	11111
Mecaderochondria	00000001-	---4031111	1311-14210	0?0101?000	1111111111	111110?111	10001
Medesicaste	000000021	0004031111	1311-14210	0111111111	1111111111	111112----	-----
Neobrachiochondria	110000021	0001021111	1310214110	0111111000	1111110001	111112----	-----
Praecidochondria	100000121	00020D1111	1310414310	0101011000	1111111001	111112----	-----
Prochondracanthopsis	11000000-	---2031111	1311-14321	1111111111	1111111111	1111111111	11111
Prochondracanthus	01000000-	---2021100	0100413110	0000000000	0000000000	0100000001	00000
Protochondracanthus	010000021	0001001111	1211-1B210	0101010000	0111111111	111102----	-----
Protochondria	000000030	1002031111	1300014110	0101000000	0111110001	1110001101	10000
Pseudacanthocanthopsis	10000001-	---2041111	1310314110	0101010000	0110100001	1100001101	00000
Pseudoblias	00000000-	---1031111	1311-14210	0101111???	1111111111	1111101111	1???1
Pseudochondracanthus	10000001-	---2011111	1311-14211	01011111?1	1111111111	111112----	-----
Pseudodiocus	110010023	1102041000	13????221	0101010000	1111111111	111112----	-----
Pterochondria	01001001-	---4031111	1301-14211	0101111111	1111111111	1111101111	11111
Rhynchochondria	010001022	0002020000	0100214010	0000000000	0000000000	0100000001	00000
Rohdea	000000020	10020?1111	1311-14210	2---------	----------	-----2----	-----
Strabax	110010021	100403----	--11-14?--	2---------	----------	-----2----	-----
EXTRA							
Pharodes	100000031	1101001100	0310?14320	11011111?1	1111111111	111112----	-----
OUTGROUP							
Bomolochus	00000000-	---0--0100	0000000000	0000000000	0000000000	0000000000	00000
Taeniacanthus	00000000-	---0--0000	0000000000	0000000000	0000000000	0000001000	00000

Appendix A *Continued*

	Characters						
					1	1	1
	6	7	8	9	0	1	2
Taxa	56789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789
Acanthochondria	11111	1111111112	------2110	0001011111	301-2A1100	1101111100	1111111111
Acanthochondrites	11111	1111111112	------2110	0001011111	3006321101	1101111100	1111111111
Andreina	11111	0001111112	------2000	0001011111	3106B21111	1101111100	1111111111
Apodochondria	-----	---------2	------2010	0001000000	1002221200	1101011000	1111011110
Auchenochondria	00000	0000010001	1111111000	0000000000	1003C20100	0100000000	0000000000
Bactrochondria	11111	1111111112	------2110	0011011111	311-321111	1101111100	1111111111
Berea	11111	1111111112	------2110	0001011111	3006421110	1101111100	1111111110
Blias	11111	1001111112	------2100	0001011111	3105421101	1101?1?000	1111111111
Brachiochondria	-----	---------2	------2211	11111-----	-106441112	----------	----------
Brachiochondrites	11111	1111111112	------2211	1111011011	3005411110	1101010000	0111111110
Ceratochondria	11111	11?1111112	------2110	0001011111	311-421111	11?11111?1	1111111111
Chelonichondria	11111	1111111112	------21?0	0001011111	3105411110	1101010000	1111111111
Chondracanthodes	11111	1111111112	------2110	0001011111	3004311100	1101010000	1111111111
Chondracanthus	11111	1111111112	------2110	0001011111	3104411110	1101111100	1111111111
Cryptochondria	11101	0001110002	------2000	0000010000	2104421100	1000000000	0111011000
Diocus	11101	0001111112	------2110	0001011000	2001321100	1101010000	1111111100
Heterochondria	11111	1111111112	------2110	0111011111	311-421101	11?11111?1	1111111111
Hoia	11100	0001110002	------2000	0000011111	1002211110	0100000000	0011000000
Juanettia	-----	---------2	------2000	0000001000	1000211100	0000000000	0001000000
Jusheyhoea	11111	1111111112	------2110	0001011111	3005321110	1101111100	1111111111
Lagochondria	11110	0001111112	------2000	0001011111	1003311200	0101000000	0111011000
Lateracanthus	11111	1111111112	------2010	0001011??1	3004321100	1101010000	1111111110
Lernentoma	11111	1111111112	------2100	0001011111	301-321100	1101111100	1111111111
Mecaderochondria	11111	1111111112	------2110	0011011111	3005221101	1101111?00	1111111111
Medesicaste	-----	---------2	------2110	0001011111	3006421100	1101111100	1111111111
Neobrachiochondria	-----	---------2	------2???	??????????	?102411100	1101111000	1111111111
Praecidochondria	-----	---------2	------2110	00?1011111	2102411111	1101111100	1111111111
Prochondracanthopsis	11111	1111111112	------2???	????0?????	3?1-421211	1111111111	1111111111
Prochondracanthus	00100	0000000000	0111111010	0000011000	1002211100	1000000000	0001000000
Protochondracanthus	-----	---------2	------2211	1111011111	311-B11101	1101111100	1111111111
rotochondria	11111	?001111002	------2000	0001011011	30012?1101	1101011000	1111111111
Pseudacanthocanthopsis	11100	0001110002	------2000	0000011000	1003411210	0000000000	0011010000
Pseudoblias	11111	1111111112	------2211	1111011111	311-421111	1111111101	1111111111
Pseudochondracanthus	-----	---------2	------2211	11111-----	-11-421112	----------	----------
Pseudodiocus	-----	---------2	------2100	0001011000	1004211210	11????????	???1??????
Pterochondria	11111	1111111112	------2110	0001011111	311-421110	1101111111	1111111111
Rhynchochondria	00000	0000000000	0000002000	0000010000	1002301100	1000000000	0001000000
Rohdea	-----	---------2	------2211	1111011000	3105421101	1101111100	1111111111
Strabax	-----	---------2	------2110	0001001000	10014E1111	1101010000	1111111111
EXTRA							
Pharodes	-----	---------2	------2010	0001011000	3106431?11	11011111?1	1111111111
OUTGROUP							
Bomolochus	00000	0000000000	0000000010	0000001000	1000-00000	??00000000	0000000000
Taeniacanthus	00000	0000000000	1000000010	0001000000	0000-00000	0000000000	0000000000

Appendix A *Continued*

	Characters					
	1	1	1	1	1	1
	3	4	5	6	7	8
Taxa	0123456789	0123456789	0123456789	0123456789	0123456789	0123456
Acanthochondria	1111110110	1111100111	1111111111	1112------	----------	-----3-
Acanthochondrites	1111111110	1111100111	1111111111	1112------	----------	-----3-
Andreina	1111111110	1111101111	1111111111	1112------	----------	-----3-
Apodochondria	1111000110	1011000011	1111100111	1001111111	?111111111	111113-
Auchenochondria	0000000010	0000000000	0000000000	0000010000	0000000000	0000010
Bactrochondria	1111111110	1111100111	1111111111	1112------	----------	-----3-
Berea	1111110110	1111100111	1111111111	1112------	----------	-----3-
Blias	1111111110	1111100111	1111111111	1112------	----------	-----3-
Brachiochondria	------2---	----------	----------	---2------	----------	-----3-
Brachiochondrites	1111110110	1011000111	1111111111	1112------	----------	-----3-
Ceratochondria	1111112---	----------	----------	---2------	----------	-----3-
Chelonichondria	1111110110	1011000?11	1111111111	1112------	----------	-----3-
Chondracanthodes	1111000110	1?11000111	1111111111	1002------	----------	-----3-
Chondracanthus	1111110110	1111101111	1111111111	1112------	----------	-----3-
Cryptochondria	1111000100	0010000001	1110000111	1001111111	?111111111	111113-
Diocus	1111110110	1111100111	1111111111	1111111111	1111111111	111113-
Heterochondria	1111112---	----------	----------	---2------	----------	-----3-
Hoia	0010000010	0010000001	1000000011	0002------	----------	-----3-
Juanettia	0010000000	0010000000	0000000000	0000000010	0000000100	0000011
Jusheyhoea	1111110110	1111100111	1111111111	1112------	----------	-----3-
Lagochondria	1111000010	1010000001	1111000111	1002------	----------	-----3-
Lateracanthus	1111110110	1011000011	111111?111	1112------	----------	-----3-
Lernentoma	1111110110	1111100111	1111111111	1112------	----------	-----3-
Mecaderochondria	1111111110	11111?0111	1111111111	1112------	----------	-----3-
Medesicaste	1111110110	1111100111	1111111111	1112------	----------	-----3-
Neobrachiochondria	1111110110	1111000111	1111111111	1112------	----------	-----3-
Praecidochondria	1111111111	1111111111	1111111111	1112------	----------	-----3-
Prochondracanthopsis	1111111111	1111111111	1111111111	1112------	----------	-----3-
Prochondracanthus	0010000100	0010000001	1000000001	0000110010	0000111110	1110021
Protochondracanthus	1111112---	----------	----------	---2------	----------	-----3-
Protochondria	1111111110	1111000111	1111111111	1112------	----------	-----3-
Pseudacanthocanthopsis	1110000010	0010000001	1010000111	0002------	----------	-----3-
Pseudoblias	1111111111	1111111111	1111111111	1112------	----------	-----3-
Pseudochondracanthus	------2---	----------	----------	---2------	----------	-----3-
Pseudodiocus	??????011?	?????????1	1???????11	???2------	----------	-----3-
Pterochondria	1111110110	1111100111	1111111111	1112------	----------	-----3-
Rhynchochondria	0010000100	0010000000	0000000001	0000111010	0011101101	111113-
Rohdea	1111111110	1111100111	1111111111	1112------	----------	-----3-
Strabax	1111111110	1111000111	1111111111	1111111111	?111111111	111113-
EXTRA						
Pharodes	1111111110	11111?1111	1111111111	1111111111	1111111111	111113-
OUTGROUP						
Bomolochus	0000000?00	0000000000	0000000000	0000000000	0000000000	0000000
Taeniacanthus	0000000010	0000000000	0000000000	0000010000	0000000000	0000000