

A Phylogenetic Analysis of the Isopod Family Janiridae (Crustacea)

George D. F. Wilson

Australian Museum, PO Box A285, Sydney South,
NSW 2000, Australia.

Abstract

A phylogeny of the isopod family Janiridae and genera from presumptive outgroups, Acanthaspidiidae, Joeropsididae and Microparasellidae is estimated. Characters were gathered from the published literature, and assembled into a data matrix for cladistic analysis. The data, when evaluated with heuristic search algorithms, yielded eight most-parsimonious trees, none of which supported the monophyly of the Janiridae. To evaluate the impact of homoplasy, characters with a rescaled consistency less than 0.1 were deleted, resulting in four somewhat different trees that were non-monophyletic for the janirids. With the smaller data set, trees supporting janirid monophyly were 10 steps longer. A permutation tail probability test found substantially more hierarchical information in the janirid data set than in randomised data. Internal topologies of the shortest trees were evaluated as hypotheses for new family-level groups, although new family-level classifications cannot be proposed at this time owing to insufficient evidence. The Janiridae therefore cannot be considered monophyletic.

Introduction

The asellote isopod family Janiridae is a large taxon consisting of many shallow-water marine species, with scattered representatives in the deep sea and in fresh water. A companion review of the Janiridae now restricts the family to 20 genera and approximately 164 species (Wilson and Wägele 1994). An estimate of the relationships of the Janiridae and related taxa is essential for understanding the phylogeny of the Janiroidea, a superfamily that currently includes 22 families. The Janiridae have been portrayed in past literature as 'archetypical' janiroideans (Hessler *et al.* 1979), where plesiomorphic similarities with other major groups of Asellota were emphasised. Two explicit branching diagrams of phylogenetic descent (Kussakin 1973, 1979; Fresi *et al.* 1980) place the Janiridae either as an internal node or branching from the centre of a janiroidean polytomy. These concepts assert, therefore, that the Janiridae is paraphyletic, with polyphyly as a real possibility. Wilson (1987) presented a simple cladistic estimate of the relationships for the Asellota, in which the Janiridae are not the earliest derived family of the Janiroidea. This phylogeny, based on a well-corroborated cladogram, was more parsimonious than the cladograms derived from the trees of Kussakin (1973) and Fresi *et al.* (1980). The janiroidean part of the phylogeny, which was divided into three superfamilial groups, was shown to have a high probability on the basis of bootstrap confidence limits (Wilson 1987). More recently, another janiroidean phylogeny argued for a basal dichotomy between a 'munnoidean' group of families (Dendrotridae, Haplomunnidae, Munnidae, Paramunnidae and Pleurocopidae) and the remaining families, of which the janirids are portrayed as a paraphyletic basal taxon (Wägele 1989). This latter non-cladistic phylogeny, however, ignores several characters that were

Nevertheless, a consistent result of all these phylogenies is that some taxa in the Janiridae are derived early in the evolution of the Janiroidea. This paper, therefore, attempts to understand the relationships of the 20 janirid genera and related taxa. Character data were obtained from Wilson and Wägele (1994), and analysed cladistically. Although a clear resolution of janirid classification is not achieved, the phylogenetic estimates presented here provide useful hypotheses for future research and highlight the remaining difficulties.

A Definition of the Janiroidea and Hypothetical Ancestral States

Wilson (1987) discussed the rationale for removing the 'Janiridae' as the earliest-derived member of the Janiroidea. Two groups of taxa, the Munnidae-Santiidae (Wolff 1989) and the Paramunnidae (now including the Abyssianiridae: Just 1990) may be derived earlier. The janirids (and the other members of the Janiroidea) have an advanced dorsolateral position of the spermathecal pore (Wilson 1986, 1991), and a first pereopod that grasps between the carpus and propodus, rather than the more primitive configuration between the propodus and dactylus (Wilson 1987). An independent analysis using all janiroidean families (Wilson 1985, 1987) agrees with this arrangement, although these analyses showed low overall consistency. The hypothetical ancestral states for the janirids were identified using states found in these outgroups in order of increasing evolutionary proximity: Stenetriidae, Pseudojaniridae, Munnidae-Santiidae and Paramunnidae. In some instances, the latter two groups show derived states with respect to the Janiridae, such as the absence of the accessory seta or third claw on the pereopodal dactyli. These instances are interpreted as either reversions in the janirids or convergence in the earlier derived families to states found within the 'Janiridae'.

A definition of the Janiroidea is provided as a phylogenetic hypothesis for future work. Past definitions have relied heavily on plesiomorphic characters to define the superfamily, such as the general *Asellus*-like appearance of the body. The current definition, which adds to the concept introduced by Harrison (1987), avoids this problem by using only synapomorphies of the Janiroidea.

Superfamily Janiroidea Sars, 1897

Isopoda Asellota with the following characteristics. Pereopod I carpus elongate, not small and triangular, partially or wholly participating in opposition to propodus and dactylus. Female pleopod II covering pleopodal cavity. Female spermathecal duct ('cuticular organ') either adjacent to oopore or separate and situated anterodorsally on pereonite 5, without coupling apparatus around external opening. Male penes (penile papillae) on posterior margin of sternum of pereonite 7, forming cone or tapering adjacent penes. Male pleopods I fused into single elongate unit with medial sperm channel along line of fusion, with distal tip having dorsal opening of sperm channel and stylet guides. Dorsolateral section of male pleopod I with locking ridges allowing pleopods I and II to function as single unit. Male pleopod II endopod proximal article with exopod coupling ridge. Male pleopod II distal article of endopod forming elongate sharp stylet of varying lengths with ventromedial opening of sperm tube; sperm tube extending to stylet tip. Male pleopod II exopod fused into single article with blunt, anteriorly directed hook on dorsomedial part of distal tip. In male, pleopods I and II forming operculum to pleopodal cavity, or (rarely) pleopod III forming operculum with pleopods I-II being smaller. In female, pleopod II forming operculum to pleopodal cavity.

Although Kussakin (1969) was the first to use the superfamily name in its correct form, the first use of the family-group name, albeit misspelled, was Sars (1897). Brusca and Wilson (1991) provide a well-corroborated cladistic analysis arguing for the early derivation of the Asellota among all isopods. The above definition serves to distinguish the Janiroidea from the other asellotan superfamilies (characters discussed in Wilson 1987), including Aselloidea, Gnathostenetroidoidea, Stenetrioidoidea, Pseudojaniroidea and Protojaniroidea. The last

Character Analysis

Despite the rearrangements of species in each janirid genus (Wilson and Wägele 1994), a genus may not be a monophyletic unit. Therefore, the character-state data below was derived primarily from the type species of each genus. Species other than the type of the genus were used only where the genus was clearly monomorphic. The data scored for *Janiralata*, for example, do not show the entire range of features in this polymorphic genus, but primarily uses those features found in *J. davisii*. This scoring principle was applied throughout.

The ancestral janirid has the general characters listed above with the spermathecal duct (originally called the 'cuticular organ'; see Wilson 1991) in an anterodorsal position, and the carpus of pereopod I is elongate. The following paragraphs discuss other character states found in the janirid taxa, with an attempt to identify those that might be plesiomorphic or ancestral. These states may also apply to the ancestor of the 'higher Janiroidea' *sensu* Wilson (1987). In addition, variation in these characters is noted, and apomorphies used in the analysis appear as parenthetical numbers. An explicit list of these characters and their states is given below, and their distribution among the taxa is given in the data matrix of Table 1 as well as in the text.

Body Form

As mentioned above, a flattened, well-articulated 'Asellus-like' body form is the dominant habitus for the Asellota. Because this form appears throughout the Asellota, it may be ancestral. Some janirids are quite narrow, usually—but not always—associated with the interstitial habit. Two independent body forms can be recognised in this group: an advanced interstitial form where the body is worm-like and pleonite 1 is elongate (¹²), seen only in *Angeliera* and *Microcharon*; and a slender 'Ectias-like' body form in which the body is narrower than a typical *Janira* but not highly modified (¹¹, seen in *Caecianiropsis*, *Ectias*, *Mackinia*, *Microjaera*, *Microparasellus*, *Paracharon*). The important changes that must take place in the basic janirid body form suggests that these apomorphies may not be reversible and their multiple appearance indicates probable convergence. The asellotan plesiomorphic state for free pleonites is 3 (Just and Poore 1992), of which often only 1 remains. In this analysis, two somites are the plesiomorphic state for the Janiroidea, as observed in *Iathrippa*, at least on the ventral side. Because the pleonite reduction occurs several times to various degrees, this character is not used in the analysis. Several janirid genera have bodies that broaden posteriorly, resulting in the pleotelson and/or pereonites 6–7 being distinctly broader than the anterior pereonites (2 found in *Caecijaera*, *Hawaiianira*, *Heterias*, *Iais*, *Jaera*, *Janthura* and *Mackinia*). This feature does not appear in the generally broad outgroups like the Pseudojaniridae and Santiidae, where they are broadest at pereonites 4 or 5, so the ancestral state is scored 0.

Lateral Tergite Form

Tergal projections called 'lappets', often with protruding pereopodal coxae, are found on many Janiroidea (e.g. Acanthaspidiidae, Mesosignidae, Janirellidae). However, some janirids have laterally truncate or rounded tergites with the coxae generally not visible in dorsal view. Lappets do not appear in the potential outgroups, indicating that lappets (³²) are an apomorphy of some subset of the Janiroidea (in the janirid genera *Iathrippa*, *Janiralata*, *Janthura*). Within the janirids, some genera have rudimentary lappets (³¹) that are apparent by the presence of tergal lateral margins that are concave and have coxae visible in dorsal view (*Janira*, *Janaira*, *Janiropsis*, *Carpas* and *Iathrippa*, *Heterias*, *Fritzianira*, *Iais*, *Microjanira*, *Neojaera*). This feature may be subject to reduction and reversion, judging from its apparently scattered appearance in higher Janiroidea (Wilson 1985). The rotation of the insertions of the coxae to a dorsolateral position (³³) is a synapomorphy of *Angeliera*, *Microcharon* and *Paracharon*. The ancestral state is scored undefined (?).

antennae removed (e.g. Wilson 1989) are invaluable for defining characters such as this. In the 'Janiridae', the rostrum may be thin, as in *Iathrippa* and some species of *Janira* and *Janiralata* (4¹), broad (or the frontal margin will be broad), as in *Austrofilius*, *Caecianiropsis*, *Iais*, *Jaera*, *Joeropsis*, *Microjaera* and *Microjanira* (4²), or absent (4⁰), as in many janiroideans. A frontal cephalic projection (rostrum) between the antennulae appears to be an ancestral character of the Janiroidea, because it appears in the Stenetrioidea and the Pseudojaniroidea (Wilson 1987). Because several of the immediate outgroups (Munnidae, Santiidae) lack a rostrum, the ancestral state is scored as undefined. Transitions between the narrow and the broad rostral types are treated as independent events because no *a priori* information indicates a developmental connection between the two forms.

Cephalic Spines

Elongate spines on the lateral margins of the cephalon is an apomorphy (5¹) found in some species of *Janiralata* and the Acanthaspidiidae. Because of the variation observed in the former taxon, the relationships between the two taxa are not especially strong on the basis of this character. Once *Janiralata* is redefined to a smaller set of taxa, this feature may gain more significance. Another set of genera (*Caecijaera*, *Hawaianira*, *Jaera*, *Janiralata*, *Janthura*, *Joeropsis*, *Neojaera*) have broad heads and a flattened lateral margin with a clear separation between the eyes and the lateral margins (5²).

Head Form

A synapomorphy of *Angeliera*, *Microcharon* and *Paracharon* is a head that is longer than broad, often broadening anteriorly (6). All 'janirids' and potential outgroups have a much broader head, even taxa known to be interstitial.

Antennular Basal Article

A more or less elongate antennular article 1 is found in the outgroups, while some janirids (*Caecijaera*, *Hawaianira*, *Microjanira*, *Neojaera*) have a broad article that has a distinct medial lobe (7). The first article is not highly modified, as in the Munnopsididae (Wilson 1989), so the character should be interpreted as reversible.

Flagellar Articles

The antennula and antenna are seen to vary considerably among the janirids, although they are generally long and with many flagellar articles in the outgroups. The variation in flagellar articles has been gap coded. For the antennula, the flagellar character states are divided into groups of greater than 12 (8⁰), between 12 and 5 (8¹), and less than 5 (8²). Practically all taxa in this latter category have only 2 or 3 flagellar articles. In the antenna, the character states are greater than 12 articles, and less than 12 (9). In cases where the count lies on the dividing point, the count for the type of the genus is chosen. The antennal flagellum of some janirids (*Caecijaera*, *Ectias*, *Janaira*, *Janiralata*, *Microjaera*) has enlarged basal articles (10¹), which sometimes become swollen and conjoint (10²) as in *Austrofilius*, *Hawaianira* and *Joeropsis*. The primitive state for the flagellar articles is articles that are longer than wide.

Antennal Basal Articles

A derived condition where the antennal articles 5 and 6 are approximately the same length as the basal 4 articles (11) is found in *Angeliera*, *Caecijaera*, *Microcharon* and *Microparasellus*. Articles 5 and 6 being elongate is the primitive condition. Elongation of the antennal third article (12) is a synapomorphy of the microparasellids *Angeliera*, *Microcharon*, *Microparasellus* and *Paracharon*. This feature is also found in the Paramunnidae, although differences in the structure between the two families indicates that this similarity is non-homologous. The antennular third article in all other 'janirid' taxa may be more robust than the other basal articles, but it is never elongate, that is, much longer than

Jaera, *Joeropsis*, *Microparasellus*) of the antennal scale is somewhat useful for differentiating subsets of janirid taxa.

Mandibular Characters

The mandible is a complex feature of isopodan anatomy, so knowledge of its three-dimensional structure could be highly useful. It is usually drawn, however, in only one or two simple views. The following features of the mandible should be unambiguously illustrated: incisor process, spine row, molar process with close-up of the tritulative surface, dorsal articular condyle (practically always omitted), and shape of the posterior margin (often omitted). Janirid literature allowed only the preliminary use of one mandibular feature, the shape of the molar process. The ancestral form is a process that is robust, distally truncate, with a tritulative surface having spines and setae on the posterior edge. Alternative states that were common in the janirids were a reduced, rounded molar process and a pointed, spine-like process. Unfortunately, when used in preliminary runs this character was highly homoplastic, as defined above. The microparasellids, however, are defined by a reduced, rounded and setose molar process (14), a feature also seen in *Protocharon* and *Microjaera*.

Maxilliped

The ancestral maxilliped is a broad structure with an endite that is longer than wide, and a palp that is as wide as or wider than the endite. A narrow maxillipedal palp (15) is found in *Angeliera*, *Austrofilius*, *Hawaianira*, *Iais*, *Joeropsis*, *Neojaera* and *Protocharon*. Variability in the shape of the epipod and distal setation of the endite prevented the use of these features in this analysis. Elongation of the distal articles of the palp appears to be a recurrent theme in the janirids and related families, but was variable within genera and lacked a clear pattern of descent. A possibly useful feature that was illustrated in all taxa was the form of palp article 3: primitively rectangular or tapering distally (16, found in *Caecianiropsis*, *Carpas*, *Hawaianira*, *Heterias*, *Iais*, *Ianiropsis*, *Jaera*, *Janthura*, *Mackinia*, *Microcharon* and *Microjanira*).

Pereopod I

Wilson (1987) established that the carpus of pereopod I did not participate in grasping in the distant ancestors of the Janiroidea, although the proximal ancestors had an enlarged carpus that could grasp. Within the 'Higher Janiroidea' *sensu* Wilson (1985, 1987), the transformation of the grasping pereopod is complete, with grasping occurring between the carpus and propodus, and the dactylus becoming short and decidedly less flexible. Within the janirids, two distinct types of first pereopods are seen, a carpus being either slender or elongate, more robust and oval (17, found in *Carpas*, *Ectias*, *Ianiropsis*, *Iathrippa*, *Janaira*, *Janira* and *Janiralata*). The ancestry of these states is not apparent. The carpus of *Acanthaspidia* has a single row of robust spine-like sensory setae (18⁰), which are typically thick walled and unequally bifid, with a small subapical sensilla. Alternative derived states seen in the janirids are two rows of setae (18¹, found in *Carpas*, *Ianiropsis*, *Iathrippa*, *Janaira*, *Janira* and *Janiralata*; see Wägele 1989, fig. 38a), and few to no setae (18², in the remaining taxa) on the carpus. The propodus of pereopod I appears either with a few spine-like setae or none (19). The ancestral state of this latter character is not apparent because both states appear in the outgroups.

Pereopodal Claws

Much discussion appears in the literature concerning the number of claws on pereopods II through VII (i.e. Wolff 1962; Menzies 1962). Throughout the janirids, one finds a variety of 2- and 3-clawed states and often authors have been inaccurate in describing a particular genus (e.g. the incorrect report of 2 claws in *Janira*: Moreira and Pires 1977). A review of the Janiridae (Wilson and Wägele 1994) establishes the number of claws for each genus. Wilson (1987) reported that the ancestors of the Janiroidea had three claws, although the

claw (e.g. Wägele 1989, fig. 38b; also found in the genera *Janiralata* and *Paracharon*). Most janirids either have three well-developed claws (20^2 , seen in *Angeliera*, *Carpas*, *Ectias*, *Iais*, *Ianiropsis*, *Iathrippa*, *Jaera*, *Janaira*, *Janira* and *Joeropsis*) or they have only two with the accessory seta or claw missing (20^1 , in the remaining genera). Both states are apomorphic at the janiroidean level and either may develop independently. Alternatively, the absent third claw state may be derived from an enlarged third claw state. The distal two claws can be described as having one dorsal and one ventral from the viewpoint of an outstretched limb. The janiroidean outgroups have both claws approximately the same size, while the ventral claw is smaller in some janirids (21 , found in *Angeliera*, *Caecijaera*, *Heterias*, *Janthura*, *Mackinia*, *Microchiron*, *Microjanira*, *Microparasellus*, *Neojaera* and *Protochiron*).

Male Pleopods

The male pleopod I contains a useful complex of characters for studying the descent of the janirids. The variability in some groups and the unevenness of the descriptions, however, made the interpretation of the male pleopod difficult. Therefore, pleopod I characters are not used in this analysis. The endopod of pleopod II is generally illustrated well enough to use here. The ancestral janiroidean endopod proximal article is approximately the width of the maximum width of the distal article (the stylet or appendix masculina), and the latter is generally curved but never greatly longer than the sympod of pleopod II. An enlarged, decidedly rounded endopodal proximal article (23) is characteristic of *Austrofilius*, *Caecianiropsis*, *Caecijaera*, *Ectias*, *Heterias*, *Janthura* and *Neojaera*. Some janirids (*Austrofilius*, *Caecianiropsis*, *Neojaera*) have a stylet that is distinctly longer than the sympod, with its distal part being thin and coiled (24^2), and others (*Caecijaera*, *Ectias*, *Heterias*, *Jaera*, *Janthura*, *Microjaera*) have an elongate and curving but not distally coiled stylet (24^1). *Angeliera* and *Microchiron* have penes on the coxae, which is a primitive feature in the Asellota (Just and Poore 1992). The derivation of this feature in these two taxa, however, could be an apomorphy owing to the movement of the coxae dorsally, thus favouring a reversion to this primitive state. If the insemination of the female returned to a direct penial interaction (primitive), then the male pleopods might also degenerate, which is the case in these genera. These two taxa are scored with a plesiomorphic state and the remaining janirids are scored as derived (22), although the analysis might force a reversion in this feature.

Pleopod III

Pleopods III–V are all potentially useful, although only pleopod III is described well enough to be used here. The primitive pleopod III, observed in males of *Jaera* and *Iathrippa*, is opercular and covers pleopods IV and V (Wilson 1987). The endopod is broad and has three large plumose setae distally; the exopod is broad, laterally rounded, much longer and wider than the endopod, distinctly segmented into two parts, with no plumose setae distally. In most janiroideans, however, pleopods I and II are opercular, relieving the third pleopod of this function. As a result, pleopod III varies considerably over the entire superfamily. Within the janirids, several states were observed. The pleopod III endopod was observed to either have more than three plumose setae (25^1 , found in *Caecijaera* and *Hawaiianira*) or have no seta or one seta (25^2 , found in *Angeliera*, *Heterias*, *Iais*, *Jaera*, *Mackinia*, *Microchiron*, *Microjaera*, *Microparasellus* and *Protochiron*). The exopod apomorphies include gaining distal plumose setae (26 , found in *Ectias*, *Heterias* and *Janiralata*), fusing the endopod into a single unit (27 , found in *Angeliera*, *Carpas*, *Janaira*, *Janira*, *Microjaera*, *Microjanira* and *Protochiron*), width either reducing to the same as the endopod (28^1 , in *Janthura*) or narrower [28^2 , found in *Angeliera*, *Austrofilius*, *Caecianiropsis*, *Caecijaera*, *Carpas*, *Ectias*, *Hawaiianira*, *Iais*, *Iathrippa* (also state 0 in males), *Jaera* (also state 0 in males), *Janaira*, *Janira*, *Janiralata*, *Joeropsis*, *Microchiron*, *Microjaera*, *Microjanira*, *Microparasellus*, *Neojaera*, *Parachiron* and *Protochiron*] and exopod length

Uropods

The primitive uropod is a distinctly biramous structure approximately as long as the pleotelson, with subequal, distally positioned rami that are longer than the sympod. Examples of such uropods are seen in the Pleurocopidae, the Santiidae or the Pseudo-janiridae. Apomorphies observed in the janirids include a short uropod distinctly shorter than the pleotelson but otherwise unmodified (30¹, found in *Austrofilius*, *Ectias*, *Iais*, *Microjaera*), a uropod with squat articles shorter than a short, squat protopod (30², found in *Caecijaera*, *Hawaiianira*, *Jaera*, *Joeropsis*, *Microparasellus*, *Neojaera*), a thin protopod that is subequal to the rami (30³, found in *Heterias*, *Mackinia*, *Microjanira*, *Protocharon*), and a uropod with an elongate, robust protopod that is longer than the rami (30⁴, found in *Angeliera*, *Microcharon*, *Paracharon*). Other apomorphies include a uropodal exopod that is distinctly subapical and projects laterally (31, found in *Angeliera*, *Microcharon*, *Mackinia*, *Paracharon*, *Protocharon*), and an exopod that is reduced (32¹, found in *Caecianiropsis*, *Microjaera*) or absent (32², found only in *Microparasellus*).

List of Characters

Unless stated otherwise, the ancestral state for each character is assumed to be 0.

1. Body 'Asellus-like' or broad, width unmodified (0), or body slender and pleonite 1 near width of pereonites but not elongate (1), or body slender and pleonite 1 elongated as well as near width of pereonites (2).

2. Body widest at pereonites 4-5 (0), or body widest at pereonites 6-7 and/or pleotelson (1).

3. Tergites of pereonites 2 and 3 laterally rounded or linear (0), laterally concave with the coxa protruding between them (1), laterally with distinct lappets (2), or coxae inserting dorsolaterally. Ancestral state '?'.

4. Rostrum absent (0), or rostrum present and narrow (1), or frontal area broad with large separation between antennulae (2). Ancestral state '?'.

5. Cephalon lateral margin not elaborate (0), or with large lateral spines (1).

6. Head wider than long (0), or head longer than wide (1).

7. Antennular article 1 length greater than width (0), or article 1 enlarged laterally with distinct medial lobe and width near length or wider (1).

8. Antennular flagellar articles number greater than 12 (0), between 5 and 12 (1), or less than 5 (2). Ancestral state '?'.

9. Antennal flagellar articles number greater than 12 (0), or less than 12 (1). Ancestral state '?'.

10. Antennal flagellum proximal articles separate and longer than wide (0), articles wider than long so that basal articles near width of article 6 (1), or conjoint and swollen (2).

11. Antennal articles 5 and 6 longer than basal articles 1-4 (0), or articles 1-6 similar in length (1).

12. Antennular basal articles all same length (0) or article 3 enlarged compared with articles 1 and 2 (1).

13. Antennular article 3 with scale (0), or scale tiny (1), or scale absent (2).

14. Mandibular molar process either truncate or spine-like (0), or distally rounded with several setae (1).

15. Maxillipedal palp broader than endite (0), or narrower than endite (1). Ancestral state '?'.

16. Maxillipedal palp article 3 subrectangular and broad (0), or distally tapering (1). Ancestral state '?'.

17. Pereopod I carpus slender (0), or elongate, oval, or otherwise enlarged (1). Ancestral state '?'.

19. Pereopod I propodus with at least a few spine-like setae (0), or without spine-like setae (1). Ancestral state '?'.
20. Dactylus of walking legs with subdistal accessory seta (0), or with only 2 distal claws (1), or accessory seta enlarged into third claw (2).
21. Dactylus of walking legs with ventral claw near same size as dorsal claw (0), or distinctly smaller (1).
22. Penes on coxae of pereopods VII (0), or posteromedially on sternite of pereonite 7 (1).
23. Male pleopod II: proximal article of endopod near maximum width of distal article (stylet) (0), or enlarged, decidedly rounded, and thicker than stylet (1).
24. Male pleopod II stylet (appendix masculina) shorter or near length of sympod (0), or stylet elongate and curving, but not distally thin and coiled (1), or stylet longer than sympod and distal part thin and coiled (2).
25. Pleopod III endopod with 3 (0), many (1), or no (2) plumose setae.
26. Pleopod III exopod without plumose setae (0), or with 2 or more plumose setae (1).
27. Pleopod III exopod with 2 free articles (0), or articles fused (1).
28. Pleopod III exopod wider than endopod (0), same size as endopod (1), or more slender than endopod (2).
29. Pleopod III exopod longer than endopod (0), or same length as or shorter than endopod (1).
30. Uropods not modified, length near that of pleotelson (0), or uropod reduced, distinctly shorter than pleotelson (1), or uropod with squat rami and sympod (2), or uropod elongate with thin subequal sympod and rami (3), or uropod with elongate robust sympod longer than rami (4).
31. Uropodal exopod apical (0), or subapical, distinctly projecting laterally (1).
32. Uropodal exopod only somewhat shorter than endopod (0), or exopod tiny or rudimentary (1), or exopod absent (2).

Taxa Included in Phylogenetic Analysis

Representatives of three separate families [Joeropsididae (*Joeropsis*), Acanthaspidiidae (*Acanthaspidia*), and Microparasellidae (*Angeliera*, *Microcharon*, *Microparasellus*, *Paracharon*)] have been included as potential outgroup taxa. As will be seen below, however, they are not strictly outgroups unless one redefines the 'Janiridae' as several separate monophyletic taxa. For the 'Janiridae', the following genera were used: *Austrofilus*, *Caecianiropsis*, *Caecijaera*, *Carpas*, *Ectias*, *Hawaiianira*, *Heterias*, *Iais*, *Ianiropsis*, *Iathrippa*, *Jaera*, *Janaira*, *Janira*, *Janiralata*, *Janthura*, *Mackinia*, *Microjaera*, *Microjanira*, *Neojaera* and *Protocharon*. Because important differences (such as the antennal scale and dorsally visible coxae) define the subgenera of *Heterias*, *H. (Heterias)* and *H. (Fritzianira)* were included separately. Therefore, a total of 28 taxa were included in the analysis.

Analytical Methods

An earlier evaluation of janirid relationships (discussed in Wägele 1989) was assisted by two computer program packages: PHYLIP versions 3.0–3.2 ('PHYLogenetic Inference Package'; Felsenstein 1985) and PAUP version 2.4 ('Phylogenetic Analysis Using Parsimony'; Swofford 1985, 1990). Initial analyses were used to evaluate potentially useful characters on the basis of literature survey. Characters containing as many steps as taxa having the apomorphic state (low retention index; see Farris 1989) were deleted from the data set. PAUP version 2.4 was used to check the results of the analyses, using several data sets derived from the PHYLIP MIX data file. More recently (September 1992), a study of these data was undertaken using PAUP 3.0s (Swofford 1990) on a Macintosh computer. Analyses were tested using unordered characters or with some characters set to either ordered or irreversible (see character analysis). The trees were Lundberg-rooted using ancestral states derived from a study of earlier-derived outgroups (Wilson 1987). Taxa with more than 1 state of a character were treated as polymorphic

nection) were used because the number of taxa precluded the use of exhaustive or branch and bound methods. Characters were optimised using delayed transformation (see Swofford 1990; Swofford and Olsen 1990). To test the hypothesis that the Janiridae are monophyletic, a topological constraint forced the presumed janirid genera into a single monophyletic group, thus excluding genera belonging to the Acanthaspidiidae, Joeropsididae and Microparasellidae. The unordered character data were then reanalysed in PAUP with the topological restraint to obtain tree length and other indices for comparison with the most parsimonious solutions. The data were also analysed with HENNIG86 (Farris 1989), version 1.5, primarily as a means of employing the permutation tail probability (PTP) test of Faith and Cranston (1991; see also Archie 1989; Faith 1991; Faith and Cranston 1992; Bryant 1992). To use HENNIG86, all polymorphic characters (e.g. '{0,1}') were changed to '?'. A HENNIG86 analysis of the original data with characters non-additive was compared with the results from PAUP (multistate taxa considered scored uncertainty). The original data were reformatted to a PHYLIP format and then the PHYLIP tool SEQBOOT (version 3.4; Felsenstein 1992) randomly permuted each original character among taxa for 100 new data sets. The 100 data sets were edited to a multiple-analysis HENNIG86 file format. Because the HENNIG86 implicit enumeration ('ie') had an extremely long run time, each permuted data set was analysed with the procedures 'mh*' plus 'bb*' with all characters non-additive. The results were input into a spreadsheet program and sorted to evaluate the distribution of tree lengths. Using these randomly permuted data sets, the PTP value (defined as the estimate of the proportion of times that a tree can be found as short or shorter than the original trees: Faith and Cranston 1991), was considered significant if the proportion was less than 5% of the analyses.

Results of Phylogenetic Analysis

Using the data in Table 1, PAUP's heuristic search algorithm (MULPARS, Tree-bisection-reconnection) with 10 iterations of randomised taxon input found 8 nearly identical trees (see Fig. 1 for one of the trees with character changes marked) with an unrooted length of 141 steps (multistate taxa interpreted as polymorphic). These trees differ only in the relative positions of *Janira*, *Carpas* and *Ianiropsis*, and all 8 trees are surprisingly well resolved. The consistency index, however, was low [consistency index (CI)=0.411; retention index (RI)=0.587; rescaled consistency index (RC)=0.241], indicating that many characters had multiple derivations or reversals. Considering the superficial nature of many characters (forced by a lack of information in the literature), this is not surprising. These trees, therefore, are hypotheses for future analysis of the genera of the Janiridae. HENNIG86 and PAUP gave identical results (length 132, CI=0.37, RI=0.59, RC=0.22) when multistate taxa were interpreted as uncertainty. The shorter tree lengths result because the terminal character changes in multistate taxa are not counted. The tree topologies between the two PAUP methods are identical.

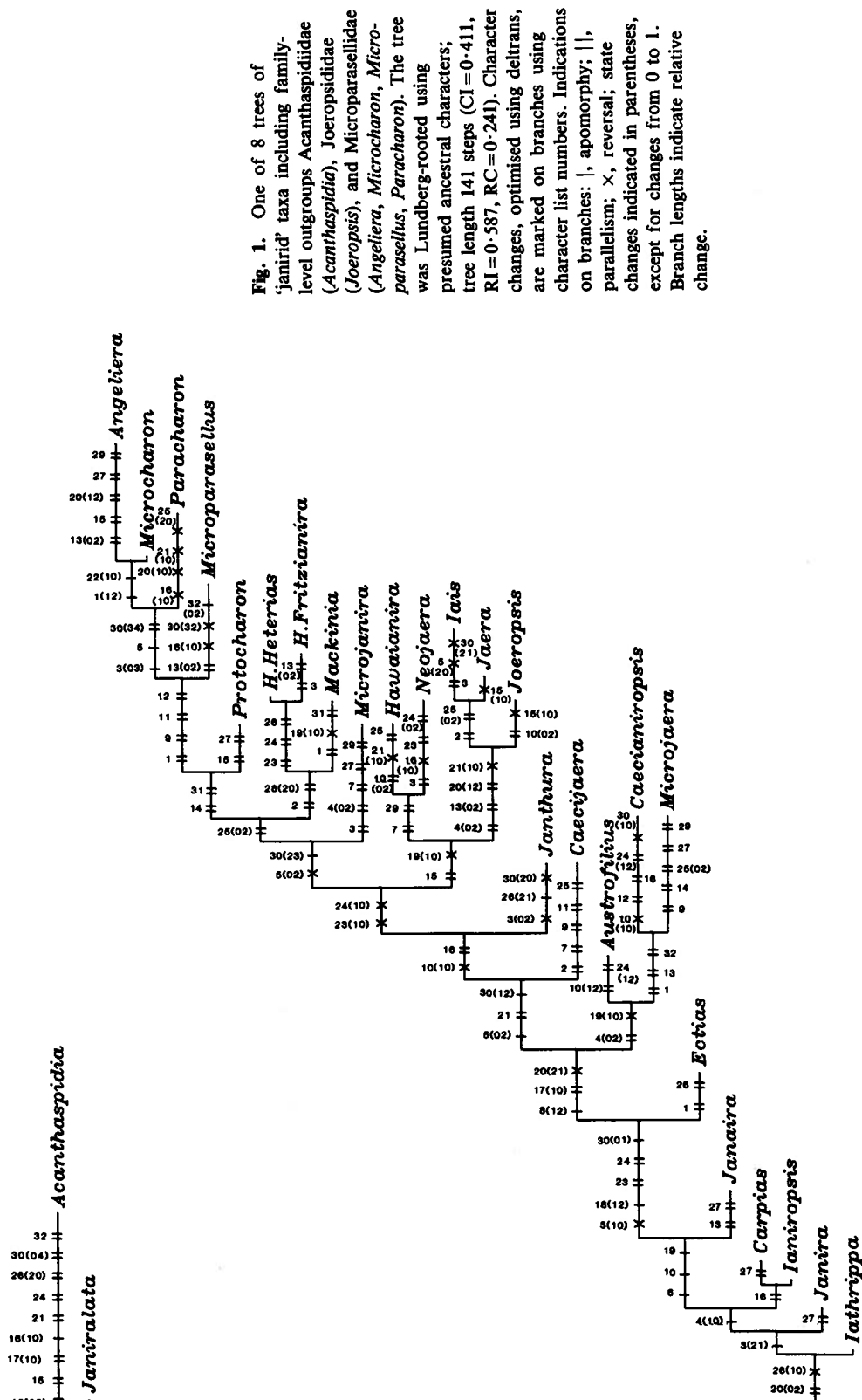
One might argue that the homoplasy of some characters swamps the analysis and the signal of 'janirid' relationships is lost. To test this possibility, the most homoplastic characters, defined as having a rescaled consistency less than 0.1, were excluded from the analysis. These excluded characters were Nos 10, 15, 16, 27 and 29, most of which had a RC=0. Removing these data from the analysis caused the results to be much better resolved: only 4 trees were found (length=108 steps; CI=0.481; RI=0.665; RC=0.320). One of the 4 trees with character changes marked is shown in Fig. 2. Again the trees differed by the relative positions of *Janira*, *Carpas* and *Ianiropsis*, while the position of *Janthura* and *Caecijaera* are changed (see Fig. 3A, B).

Regardless of how one might root the tree (see unrooted trees in Figs 4, 5), the 'outgroups' cannot be segregated from the janirid taxa. To determine how much less parsimonious a 'janirid'-constrained tree might be, a constraint was used that retained only trees with Janiridae monophyletic (i.e. excluding these genera: *Acanthaspidia*, *Angeliera*, *Joeropsis*, *Microcharon*, *Microparasellus*, *Paracharon*). The analysis used the revised data set excluding the homoplastic characters. In all, 22 'janirid'-constrained trees were found with a length of 118 (CI=0.441, RI=0.605, RC=0.267), 10 steps longer than the unconstrained analysis. The consensus tree of the 22 topologically constrained trees (compare consensus trees shown in Fig. 3) is also much less well resolved. The 10-step difference between the unconstrained and the constrained analysis is a substantial parsimony gulf to

Table 1. Character data for janirid taxa used in phylogenetic analysis

'{...}' signifies instances where a taxon was scored with more than one character state. Character 33 is a dummy character that provides a fake synapomorphy of the Janiridae; taxa scored plesiomorphic are conjectural outgroups for the Janiridae

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33			
	Character																																			
Ancestral states	0	0	?	?	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Acanthaspidia</i>	0	0	2	1	1	0	0	0	0	2	0	{0,1}	0	0	1	0	0	0	0	{0,1}	1	1	0	1	0	1	0	0	0	0	4	0	1	0		
<i>Angellera</i>	2	0	3	0	0	1	0	2	1	0	1	1	2	1	1	?	0	2	1	2	1	0	0	0	2	0	1	2	1	4	1	0	0	1		
<i>Austrofilus</i>	0	0	0	2	0	0	0	2	0	2	0	0	0	0	0	0	0	0	2	0	1	0	1	1	2	0	0	0	2	0	1	0	0	1		
<i>Caecianiropsis</i>	1	0	0	2	0	0	0	2	0	0	0	1	1	0	0	1	0	2	0	1	0	1	1	2	0	0	0	2	0	0	0	1	1	1		
<i>Caecijaera</i>	0	1	0	0	2	0	1	2	1	1	1	0	0	0	0	0	2	1	1	1	1	1	1	1	1	0	0	2	0	2	0	0	1	1		
<i>Carpas</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	2	0	1	0	0	0	0	0	1	2	0	0	0	0	1		
<i>Ecitas</i>	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	2	1	2	0	1	1	0	1	0	1	0	2	0	1	0	0	1		
<i>Hawaiianira</i>	0	0	0	0	2	0	1	2	0	2	0	0	0	0	1	1	0	2	0	1	0	1	0	0	1	0	1	0	2	1	2	0	0	1		
<i>H. Heterias</i>	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	2	1	1	1	1	1	1	2	1	0	0	0	3	0	0	1			
<i>H. Fritzanira</i>	0	1	1	0	0	0	0	2	0	0	0	2	0	0	0	1	0	2	1	1	1	1	1	1	2	1	0	0	0	3	0	0	1	1		
<i>Isais</i>	0	1	1	2	0	0	0	2	0	0	0	2	0	1	1	0	2	0	2	0	2	0	1	0	0	2	0	2	0	1	0	0	1	0	1	
<i>Janiropsis</i>	0	0	1	0	0	0	0	{0,1}	0	0	0	0	0	0	0	0	1	1	1	0	2	0	1	0	0	0	0	0	2	0	0	0	0	1	0	
<i>Iathrippa</i>	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	1	0	0	0	0	0	2	0	0	0	0	1	0	
<i>Jaera</i>	0	1	0	2	2	0	0	2	0	0	0	2	0	0	0	1	0	2	0	2	0	1	0	{0,1}	2	0	0	{0,2}	0	2	0	0	1	1	0	
<i>Janaira</i>	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	2	0	1	0	0	0	0	0	1	2	0	0	0	0	1	0	
<i>Janira</i>	0	0	1	{0,1}	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	1	0	0	0	0	1	2	0	0	0	0	1	0	
<i>Janiralata</i>	0	0	2	{0,1}{1,2}	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	2	0	0	0	0	1	
<i>Janthura</i>	0	0	2	0	2	0	0	2	0	0	0	0	0	0	0	0	1	0	2	1	1	1	1	1	0	0	0	1	2	0	0	0	0	1	0	
<i>Joeropsis</i>	0	0	0	2	2	0	0	2	0	2	0	2	0	0	1	0	0	2	0	2	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
<i>Mackinia</i>	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	2	0	1	1	1	0	0	0	0	0	2	0	0	3	1	0	1	0	
<i>Microcharon</i>	2	0	3	0	0	1	0	2	1	0	1	1	0	1	0	1	0	2	1	1	1	0	0	0	2	0	0	2	0	4	1	0	0	0	0	
<i>Microjaera</i>	1	0	0	2	0	0	0	2	1	1	0	0	1	1	0	0	0	2	0	1	0	1	?	1	2	0	1	2	1	1	0	1	0	1	1	
<i>Microjanira</i>	0	0	1	2	0	0	1	2	?	0	0	0	0	0	0	1	0	2	1	1	1	1	0	0	0	0	0	1	2	1	3	0	0	1	0	
<i>Microparasellus</i>	1	0	0	0	0	0	0	2	1	0	1	2	1	0	0	0	0	2	1	1	1	1	1	0	0	2	0	0	2	0	2	?	2	0	1	0
<i>Neojaera</i>	0	0	1	0	2	0	1	2	0	0	0	0	0	0	1	0	0	2	0	1	1	1	1	1	2	0	0	0	2	1	2	0	0	1	0	
<i>Paracharon</i>	1	0	3	0	0	1	0	2	1	0	?	1	0	1	0	0	0	2	1	0	0	1	0	0	0	0	0	0	2	0	4	1	0	0	1	
<i>Protocharon</i>	0	0	0	0	0	0	0	2	?	?	?	?	?	1	1	?	?	?	?	?	1	1	1	0	0	2	0	1	2	0	3	1	0	1	0	



found in the 'janirid'-constrained analysis (Fig. 3C). The length of these trees would then be 123, with a parsimony difference of 15 steps! Similar, but less parsimonious, results are found if the homoplastic characters are included in the analysis. Therefore the monophyly of the Janiridae cannot be justified using parsimony.

Do these data have significant cladistic structure or are the data no better than that achieved by randomly permuting characters? That is, do the data have a hierarchical

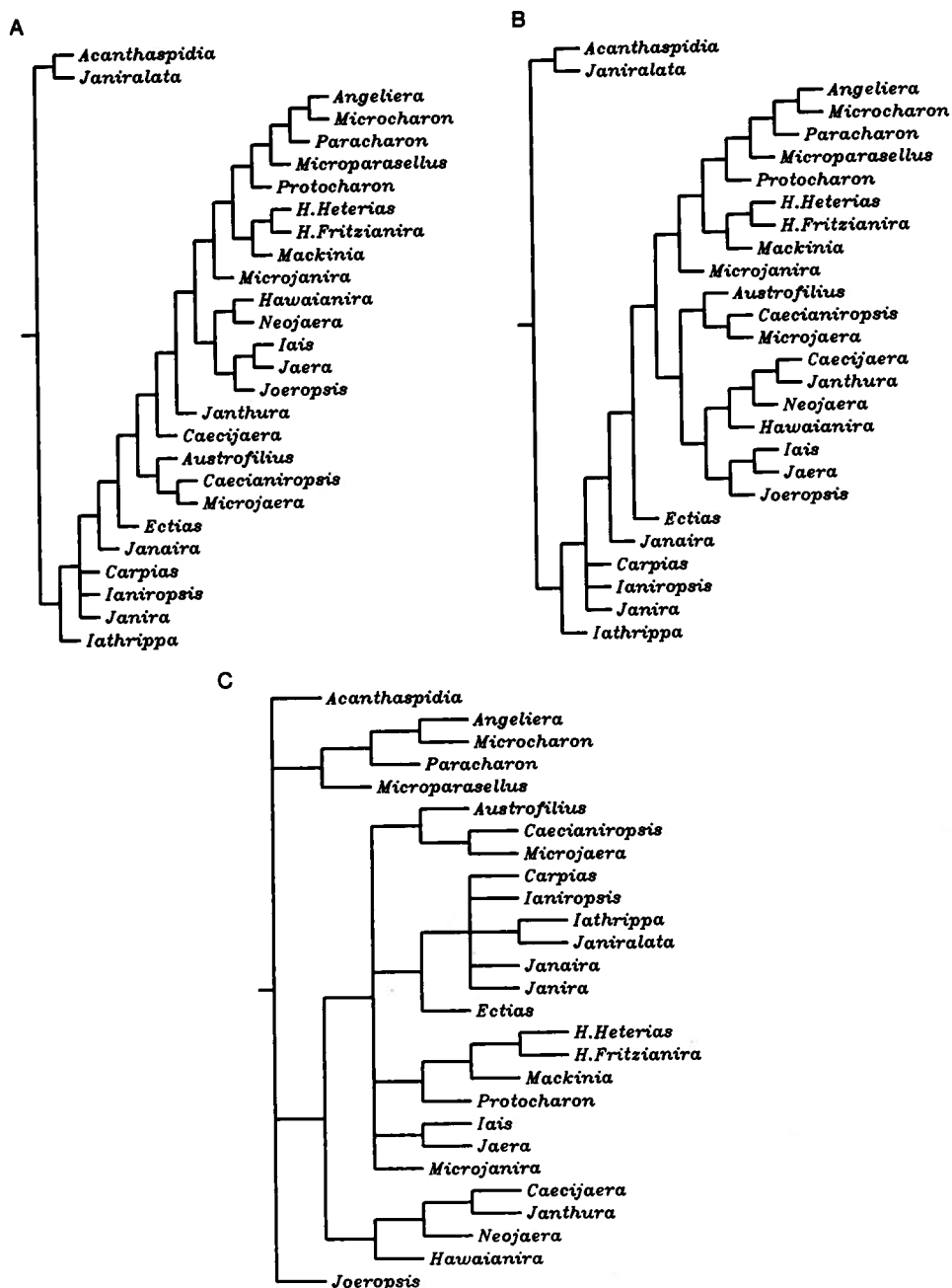


Fig. 3. Consensus trees. A, strict consensus of 8 trees using all data in Table 1 (1 tree shown in Fig. 1). B, strict consensus of 4 trees using data in Table 1 except characters 10, 15, 16, 27 and 29. C, strict consensus of 4 trees using the same data as used in

structure that results in a correlated placement of the characters on the trees? If the data have cladistic correlation among characters, one would expect much shorter tree lengths than when the characters are placed in the data set at random. The method of Faith and Cranston (1991), implemented in SEQBOOT (PHYLIP version 3.4; Felsenstein 1992) was used to generate 100 data sets with characters permuted among taxa randomly. A HENNIG86 analysis of these 100 randomly permuted data sets found no tree lengths that came near the results of the actual data (Fig. 6: PTP < 0.01). Therefore, the actual data do have significant cladistic structure despite the high level of homoplasy among all characters. The relationships of janirid taxa may be portrayed by the phylogenetic estimates derived from these data.

Discussion

At first sight, these results do not suggest a better janirid classification. Nevertheless, several useful hypotheses are offered by the trees. By using hypothetical ancestral states and Lundberg rooting, the ancestral node was placed near *Janiralata*, suggesting that a revision of this genus alone may go far in establishing the relationships of the whole suite of genera that appear near the ancestral node. The group *Mackinia* + *Heterias* appears consistently as a sister group of Microparasellidae + *Protocharon*. *Iais* clusters with *Jaera*, as suggested by Veuille (1979). *Jaera* traditionally has been considered a janirid but this genus is not closely related to the basal janirids (*Janiralata*, *Janira*, *Janaira*, *Carpas*, *Ianiropsis*, *Iathrippa*). While the basal janirids have relatively unmodified uropods and antennulae, the species of

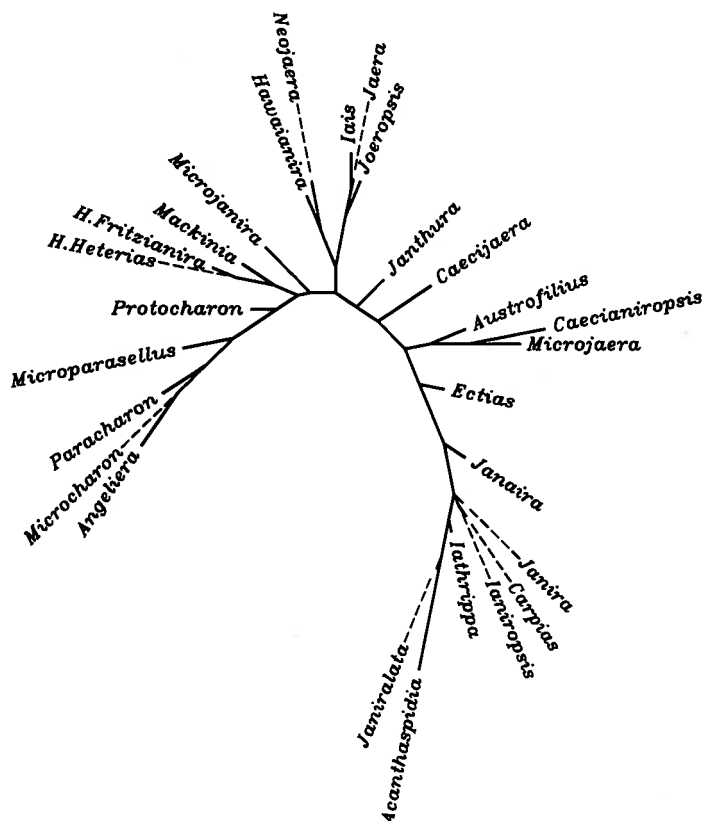


Fig. 4. Tree of 'janirid' taxa and outgroups, all characters in Table 1 used, same tree as Fig. 1 but unrooted. Branch lengths are proportional to the

Jaera and *Iais* have distinctly reduced uropods and antennulae. The family name Jaeridae Stebbing, 1905 is available for the group *Jaera*+*Iais*, although better evidence may be required to re-establish this family. The sister group relationship of *Iais*+*Jaera* with *Joeropsis* is especially interesting, and may provide a useful hypothesis for new classifications for these cosmopolitan taxa.

Most importantly, the tree shows that none of the presumed janirid outgroup families cluster separately from the remaining genera. *Acanthaspidia* always appears near the hypothetical ancestral node of the trees, and perhaps is a candidate for the sister-group to the remaining genera derived later than the basal janirids. On the other hand, acanthaspidiids have derived characters relative to *Janira*, *Janiralata* and the basal janirid genera that must be reconciled. *Joeropsis* and the microparasellids are highly derived in many features, and, as discussed above, might have sister taxa within the janirids. Therefore, the Janiridae *sensu lato* of Wolff (1962) and other authors is at the least paraphyletic, and is highly likely to be polyphyletic. Unfortunately, no simple solution can be offered for the classification of this group because the phylogenetic analysis does not warrant it. A larger data set including more families of janiroideans will be necessary to define family-level taxa from the janirids.

The unrooted trees in Figs 4 and 5 suggest several lines of research. For example, if new data on the Janiroidea were uncovered that allowed placement of the root near *Ectias*,

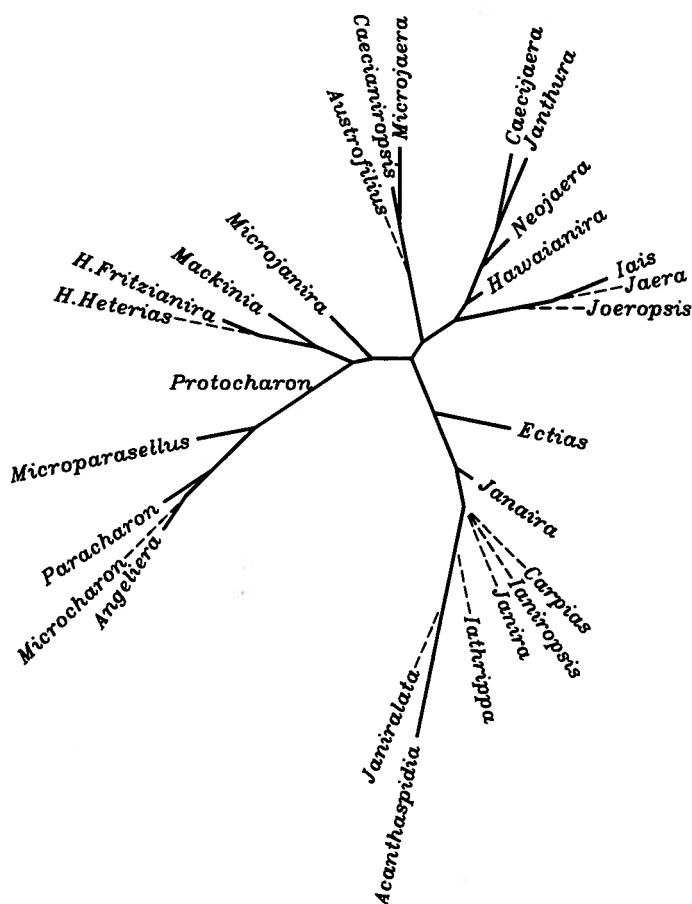


Fig. 5. Tree of 'janirid' taxa and outgroups, homoplasous characters

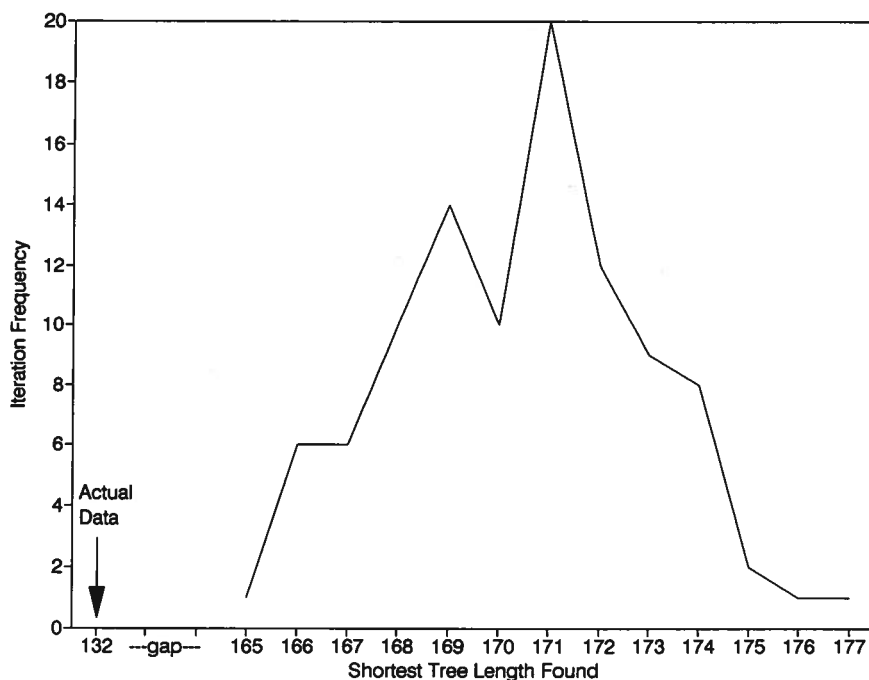


Fig. 6. Frequency of tree lengths resulting from 100 iterations of HENNIG86 analyses using characters randomly permuted among taxa. Tree length obtained from analysis of unrandomised real data indicated by arrow.

then the 'basal janirids' become rather more monophyletic. In both trees, midpoint rooting (i.e. rooted at the point of greatest phylogenetic change) occurs on the longest branch between *Ectias* and the more-derived janirids. The flagellar articles of the antennula may be a key character because a change from a multiarticulate condition to a 2–4-articled condition (the 'less than 5 articles' character state) divides the tree into two major groups: the basal janirids and more-derived taxa near the midpoint root. If the basal division were made near the change in this character, the problem of paraphyly in the janirid classification would be considerably reduced. The lack of a well-resolved phylogeny for asellotan families prevents establishing a better result for the Janiridae.

Moreover, as alluded to above, detailed morphological studies are required on many genera. Each genus dealt with in this paper should be re-illustrated and described with the goal of resolving its classification. If readers of this paper find a new species of 'janirid' and wish to prepare a description, they are strongly encouraged to get the type of the genus and to prepare fully comparative descriptions of their species and the type of the genus, as well as possibly related species. Unfortunately, most recent papers on janirids have not been of this sort.

Conclusions

The Janiridae are not defined or reclassified because the data allow monophyly only under a broad taxonomic definition that includes acanthaspidiids, microparasellids, joeropsids, and probably many other janiroidean families. Using such a broad concept, other higher janiroidean families would have janirid ancestors, rendering this family paraphyletic. If Joeropsididae, Microparasellidae and Acanthaspidiidae are recognised as separate families then new janirid-group families must be defined rather finely to avoid paraphyly—an asset for providing a clear understanding of janiroidean relationships. Most apomorphies are

should be natural, monophyletic, and defined as objectively as possible. The current taxonomy of the Janiridae falls well short of this desirable goal although the amendments proposed in Wilson and Wägele (1994) leave the genera more homogeneous internally. The Janiridae *sensu lato* has no synapomorphies, so its status must remain undefined.

Acknowledgments

J.-W. Wägele participated in a character study and cladistic analysis conducted in 1987 that resulted in preliminary cladograms (see Wägele 1989). I am grateful for financial support provided by the National Science Foundation, grants BSR 86 04573 and BSR 88 18448, and by Australian Research Council Grant No. A19131795. Useful reviews of this manuscript were provided by G. C. B. Poore, and by two anonymous reviewers of an earlier version of this paper. E. L. Ho prepared several of the cladograms for publication.

References

- Archie, J. W. (1989). A randomisation test for phylogenetic information in systematic data. *Systematic Zoology* 38, 219–52.
- Bryant, H. N. (1992). The role of permutational probability tests in phylogenetic systematics. *Systematic Biology* 41, 258–63.
- Brusca, R. C., and Wilson, G. D. F. (1991). A phylogenetic analysis of the Isopoda with some classificatory recommendations. *Memoirs of the Queensland Museum* 31, 143–204.
- Faith, D. P. (1991). Cladistic permutation tests for monophyly and nonmonophyly. *Systematic Zoology* 40, 366–75.
- Faith, D. P., and Cranston, P. S. (1991). Could a cladogram this short have arisen by chance alone?: on permutation tests for cladistic structure. *Cladistics* 7, 1–28.
- Faith, D. P., and Cranston, P. S. (1992). Probability, parsimony and Popper. *Systematic Biology* 41, 252–7.
- Farris, J. S. (1989). The retention index and the rescaled consistency index. *Cladistics* 5, 417–19.
- Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39, 783–91.
- Felsenstein, J. (1992). PHYLIP (Version 3.4), Phylogenetic Inference Package. Seattle: University of Washington. Distributed by Author.
- Fresi, E., Idato, E., and Scipione, M. B. (1980). The Gnathostenetroidae and the evolution of primitive asellote isopods. *Monitore Zoologico Italiano* 14, 119–36.
- Harrison, K. (1987). Deep-sea asellote isopods of the north-east Atlantic: the family Thambematidae. *Zoologica Scripta* 16, 51–72.
- Hessler, R. R., Wilson, G., and Thistle, D. (1979). The deep-sea isopods: a biogeographic and phylogenetic overview. *Sarsia* 64, 67–76.
- Just, J. (1990). Abyssianiridae, a synonym of Paramunnidae (Crustacea: Isopoda: Asellota), with two new species of *Abyssianira* from south-eastern Australia. *Memoirs of the Museum of Victoria* 50, 403–15.
- Just, J., and Poore, G. C. B. (1992). Vermectiidae, a new primitive asellote isopod family with important phylogenetic implications. *Journal of Crustacean Biology* 12, 125–44.
- Kussakin, O. G. (1973). Peculiarities of the geographical and vertical distribution of marine isopods and the problem of deep sea fauna origin. *Marine Biology* 23, 19–34.
- Kussakin, O. G. (1979). Marine and brackish water likefooted Crustacea (Isopoda) of the cold and temperate waters of the Northern Hemisphere. I. Suborder Flabellifera. *Akademia Nauk, Leningrad*, 472 pp. [In Russian.]
- Menzies, R. J. (1962). The isopods of abyssal depths in the Atlantic Ocean. *Vema Research Series* 1, 79–206.
- Moreira, P. S., and Pires, A. M. S. (1977). *Janaira gracilis*, a new genus and species of janirid isopod from Brazil. *Crustaceana* 33, 23–32.
- Sars, G. O. (1897). 'Isopoda. Part V, VI. Idotheidae, Arcturidae, Asellidae, Ianiridae, Munnidae.' In Series 'An Account of the Crustacea of Norway with Short Descriptions and Figures of All the Species', vol. 2. (Bergen Museum: Bergen, Norway.) (Plates XXXIII–XLIX.)
- Swofford, D. L. (1985). PAUP (version 2.4), phylogenetic analysis using parsimony. Champaign: Illinois Natural History Survey. Distributed by author.

- Swofford, D. L. (1990). PAUP (version 3.0 for the Macintosh), phylogenetic analysis using parsimony. Champaign: Illinois Natural History Survey. Distributed by author.
- Swofford, D. L., and Olsen, G. J. (1990). Phylogeny reconstruction. In 'Molecular Systematics'. (Eds D. M. Hillis and C. Moritz.) pp. 411-501. (Sinauer Associates Inc.: Sunderland, Massachusetts.)
- Veuille, M. (1979). L'évolution du genre *Jaera* Leach (Isopodes, Aselotes) et ses rapports avec l'histoire de la Méditerranée. *Bijdragen tot de Dierkunde* 49, 195-218.
- Wägele, J.-W. (1989). Evolution und phylogenetisches System der Isopoda. Stand der Forschung und neue Erkenntnisse. *Zoologica* 140, 1-262.
- Wilson, G. (1985). The systematic position of the ilyarachnoid Eurycopidae (Crustacea, Isopoda, Asellota). Doctoral dissertation, University of California, Scripps Institution of Oceanography. 403 pp.
- Wilson, G. D. F. (1986). Evolution of the female cuticular organ in the Asellota (Crustacea, Isopoda). *Journal of Morphology* 190, 297-305.
- Wilson, G. D. F. (1987). The road to the Janiroidea: comparative morphology and evolution of the asellote isopod crustaceans. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 25, 257-80.
- Wilson, G. D. F. (1989). A systematic revision of the deep-sea subfamily Lipomerinae of the isopod crustacean family Munnopsidae. *Bulletin of the Scripps Institution of Oceanography* 27, 1-138.
- Wilson, G. D. F. (1991). Functional morphology and evolution of isopod genitalia. In 'Crustacean Sexual Biology'. (Eds R. Bauer and J. Martin.) pp. 228-45. (University of Columbia Press: New York.)
- Wilson, G. D. F., and Wägele, J.-W. (1994). Review of the family Janiridae (Crustacea: Isopoda: Asellota). *Invertebrate Taxonomy* 8, 683-747.
- Wolff, T. (1962). The systematics and biology of bathyal and abyssal Isopoda Asellota. *Galathea Report* 6, 1-320.
- Wolff, T. (1989). The genera of Santiidae Kussakin, 1988, with the description of a new genus and species (Crustacea, Isopoda, Asellota). *Steenstrupia* 15, 177-91.