

# Peracarida: monophyly, relationships and evolutionary success

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## Abstract

Although the monophyly of the Peracarida has from time to time been questioned, this seems now to be no longer in doubt, Mysida excepted. A phylogenetic analysis of relationships between the orders based on parsimonious analysis of 92 morphological characters (Syncarida as outgroups) has discovered that: (1) Mysida and Lophogastrida are sister taxa and the most basal clade; (2) Isopoda and Amphipoda are sister taxa and derived; (3) Cumacea and Tanaidacea belong in the same clade as these two; (4) Spelaeogriphacea (*Spelaeogriphus*, *Potiicoara* and *Mangkurtu*) are a monophyletic taxon; (5) Mictacea (*Mictocaris*, *Hirsutia* and *Thetispelecaris*) are monophyletic and related to Spelaeogriphacea; (6) Thermosbaenacea are sister taxon to Spelaeogriphacea and Mictacea or more basal to a larger clade including these two orders; and (7) the hypothesis proposing an alternative ordinal structure, Cosinzenaceae and Bochsaceae (for Spelaeogriphacea and Mictacea) is not supported. *Acadiocaris* and *Liaoningogriphus* are supposed fossil spelaeogriphaceans but in fact display few of the characters defining that order. Previous attempts at elucidating peracarid relationships that were not based on a parsimonious treatment of characters produced widely divergent results, none similar to that proposed here. Others using smaller character suites treated parsimoniously are in many ways congruent with that proposed here. Two recent studies based on molecular data found that Mysida are more related to decapods or euphausiids and not to Lophogastrida, a result at odds with the morphological consensus. Spears et al.'s finding that Spelaeogriphacea and Amphipoda are sister taxa has no morphological support. The morphological cladogram relating peracarid orders suggests a succession of evolutionary events correlated with behavioral and ecological changes. Mysida and Lophogastrida are epibenthic swimming crustaceans with a carapace that survive by swarming. Other epibenthic orders with short carapaces (Thermosbaenacea, Spelaeogriphacea and Mictacea) are represented today by few species in relictual freshwater or deep-sea habitats. Only the cryptic, benthic Cumacea and Tanaidacea (with short carapace) and Isopoda and Amphipoda (lacking a carapace) are now hyperdiverse and superabundant in marine environments.

## Introduction

Peracarids are crustaceans that usually brood their young in a marsupium formed by branches of the thoracic limbs. Some, isopods and amphipods, include dozens of families and are among the most common of all marine crustaceans. Representatives of these orders are found in fresh water and on land. Tanaidaceans and cumaceans are likewise predominantly marine but are slightly less diverse. Spelaeogriphaceans, mictaceans and thermosbaenaceans on the other hand are rare (with few species) and confined to unusual habitats, caves, fresh water or the deep sea. Mysids and lophogastrids differ from these benthic taxa in being demersal or pelagic, and rarely non-marine.

The relationships between the orders of Peracarida have long attracted interest and controversy. Even which orders to include or exclude has been debated. The debate has attracted the interest of many experienced crustacean biologists and has been summarised in greater or lesser detail before (e.g. Pires, 1987; Wagner, 1994; Schram and Hof, 1998; Hessler and Watling, 1999; Richter and Scholtz, 2001). Much of the uncertainty that has hindered wide acceptance of a common view has revolved around character interpretation, notably homologies in the carapace. Early contributions to the debate did not rely on what is now accepted as a standard methodology, parsimonious cladistic analysis of shared homologous characters, and some recent opinions do not depend on this methodology either. Approaches to the problem are various but have not been critically assessed in the light of modern methods. The need to re-examine peracarid relationships has also been stimulated by the disturbing findings from molecular genetics (Jarman *et al.*, 2000; Spears *et al.*, in press) that suggested that the composition of Peracarida was not as popularly accepted but, instead, more like views held in the nineteenth century. Morphological evidence has not to date provided a widely accepted phylogeny against which molecular evidence could be tested.

Many authors have come to the problem of peracarid phylogeny from the bottom-up, as part of exploration of the Malacostraca, Crustacea or Arthropoda as a whole. My interest was sparked from the top-down, an investigation of the relationships between four living species of Spelaeogriphacea to each other and to two supposed spelaeogriphacean fossil taxa (Poore and Humphreys, 1998, 2003). The search for an outgroup for these was not satisfied by the contradictory views in the literature. The relationship between the species in three Gondwanan continents and two fossil taxa in Laurasian continents invites investigation of their phylogeny, in particular how this might explain their biogeography.

The monophyly of most peracarid orders has not been disputed. Intermediate forms have not been reported even among fossil taxa (but see discussion on spelaeogriphaceans below). Amphipoda, Isopoda, Tanaidacea and Cumacea are each well defined by numerous unique autapomorphies. The same is true for Thermosbaenacea but they have switched from Peracarida (Monod, 1927) to their own separate superorder, Pancarida (Taramelli, 1954; Bowman and Abele, 1982) and back again (Wagner, 1994; Martin and Davis, 2001). Mysida and Lophogastrida (Richter, 2003) have always been thought of as monophyletic but whether they are two orders or one order, Mysidacea, has been debated. This has become an issue as Mysida has been shown from molecular evidence to be distant from Lophogastrida and other peracarids (Jarman *et al.*, 2000; Spears *et al.*, in press). The monophyly of Spelaeogriphacea, comprising three extant and two fossil genera (Poore and Humphreys, 1998; Shen *et al.*, 1998; Poore and Humphreys, 2003), and Mictacea, of two families and three genera (Bowman *et al.*, 1985), is not universally accepted. Gutu and Iliffe (1998) and Gutu (1998) pointed out significant differences between the two mictacean families, Mictocarididae and Hirsutiidae, and proposed new ordinal names for Hirsutiidae alone (Bochusacea) and Mictocarididae plus Spelaeogriphidae (Cosinzenaceae).

This paper offers a critique and tests of competing hypotheses. It attempts once again to hypothesise relationships between peracarid orders. Relationships between the extant and fossil spelaeogriphacean genera, mictacean genera and the monophyletic peracarid orders are investigated. Three eucarid taxa, Order Euphausiacea and the suborders Caridea and Dendrobranchiata of Order Decapoda, are included because of their supposed affinities with mysids and lophogastrids. The data are morphological characters, essentially a compilation of those used previously but with additions.

## Materials and Methods

### Taxa chosen

Phylogenetic (cladistic) methods were used to generate cladograms as hypotheses of the relationships of peracarid taxa.

Characterisation of orders of undisputed monophyly was based on their hypothetical ground-pattern. Data was gathered directly from specimens in the extensive collections of Museum Victoria and complimented with generalities in the literature. Nouvel *et al.* (1999) and Tattersall and Tattersall (1951) were the principal sources for Mysida and Lophogastrida. Bacescu and Petrescu (1999) reviewed Cumacea, Gutu and Sieg (1999) Tanaidacea, Roman and Dalens (1999) Isopoda, Bellan-Santini (1999) Amphipoda and Wagner (1994) Thermosbaenacea. Views on the most plesiomorphic isopod have changed significantly recently and a phreatoicid-like or asellote-like ground pattern is chosen (Wägele, 1989; Brusca and Wilson, 1991; Brandt and Poore, 2003). Other orders appear more uniform and the the ground pattern less contentious.

All spelaeogriphacean genera were included: three extant (monotypic except in one case) and the two supposed fossil species. Except for the Australian species, information relied on literature: *Spelaeogriphus lepidops* (Gordon, 1957, 1960), *Potiicoara brasiliensis* (Pires, 1987), and *Mangkurtu mityula* and *M. kutjarra* (Poore and Humphreys, 1998, 2003). Information on fossil species of purported spelaeogriphaceans came from published works: *Acadiocaris novascotica* (Copeland, 1957) in Carboniferous marine sediments in Canada (Copeland, 1957; Schram, 1974) and *Liaoningogriphus quadripartitus* in lacustrine deposits of Jurassic age in China (Shen *et al.*, 1998; Shen *et al.*, 1999).

Five species in three genera comprise the Mictacea: *Mictocaris halope* (Bowman and Iliffe, 1985), *Hirsutia bathyalis* and *H. sandersetalia* (Sanders *et al.*, 1985; Just and Poore, 1988), and *Thetispelecaris remex* and *T. yurikago* (Gutu and Iliffe, 1998; Gutu, 2001; Ohtsuka *et al.*, 2002). Characterisation of the three genera relied on this literature and the one specimen of *H. sandersetalia* in Museum Victoria.

Scoring of the three eucaridan taxa, Euphausiacea, Caridea and Dendrobranchiata, was based on McLaughlin (1980) supplemented by personal observations of specimens in Museum Victoria.

Outgroups were chosen from Syncarida, a generalised member of Anaspidacea (close to *Anaspides*) and Bathynellacea (*Parabathynella*) (Schminke, 1973; Coineau, 1996). These were chosen using the argument that neither possesses any form of carapace or associated scaphognathite branchial ventilation as seen in the ingroups (amphipods and isopods excepted).

### Characters

The phylogenetic analyses of Watling (1981, 1983, 1999), Pires (1987), Wagner (1994), Schram and Hof (1998), Shen *et al.* (1998) and Richter and Scholtz (2001) were reviewed as were the order, family and genus diagnoses of Bowman and Iliffe (1985, for *Mictocaris*), Sanders *et al.* (1985, for *Hirsutia*), Just and Poore (1988, for *Hirsutia*), Gutu and Iliffe (1998, for *Thetispelecaris*) and Ohtsuka *et al.* (2002, also for *Thetispelecaris*), Poore and Humphreys (1998, for *Mangkurtu*), Shen *et al.* (1998, 1999, for *Liaoningogriphus*) and Schram (1976 for *Acadiocaris*). Some characters were expressed in different ways by different authors and care was taken to avoid replication. Several characters, especially those used by Shen *et al.* (1998) were found to be difficult to categorise (proportions of tagmata, shape etc.) and were omitted. Because an early objective was to discover relationships within Spelaeogriphacea several characters were added that applied only to their genera. The character list was supplemented and checked for accuracy and general applicability by reference to specimens of many species in the collections of Museum Victoria.



A database of the distribution among taxa of 92 potentially synapomorphic characters was assembled using the software DELTA (Dallwitz *et al.*, 1999) (Table I). Many of the characters have been discussed before at length, particularly by Watling (1981, 1983, 1999), Dahl (1991), Schram and Hof (1998), and Richter and Scholtz (2001) who all gave primary sources for more detailed anatomical studies. Most of the characters are self-explanatory with reference to the literature. The carapace has always been controversial in Peracarida but I follow Watling's (1999) analysis based on Dahl's interpretation. I treat the ocular lobe as homologous in the absence of evidence to the contrary and its presence or absence in Amphipoda ambiguous (Schram, 1986). The form of the mandible and its incisor was described by Watling (1983) who differentiated the amphipod-isopod "transverse-biting" type from the "rolling, dual-purpose" type in all other taxa. His view was contradicted in discussion of his paper (Watling, 1983: 226–227). The character was excluded; inclusion only reinforced the resulting cladogram. The structure of the mandibular lacinia mobilis was elucidated by Richter *et al.* (2002) although lacinia mobilis or spine row precursors would seem to be a plesiomorphic condition in Eumalacostraca (Dahl and Hessler, 1982). In fact, it matters little if the left and right peracarid lacinias are uniquely and differently derived as new structures as convincingly detailed by Richter *et al.* (2002) or, less likely, modifications of an existing one. Peracarids are scored differently from other taxa for this character. For the homology of maxilla 2, I follow Wagner (1994) recognising a coxal endite bearing a long mesial row of plumose setae, three basal endites of which the first is poorly differentiated from the coxal endite and bears terminal setae and the second and third are overlapping plates with oblique distal rows of long complex microdentate setae. Maxilla 2 may have a palp (endopod) reduced to a single seta in Hirsutiidae, and an exopod. Thoracopods 1–8 are alternatively called a maxilliped and pereopods 1–7 as in literature dealing with most of these groups. While I agree with Gutu and Iliffe (1998) that thoracopod 2 of hirsutiids is smaller than the one following it is not a maxilliped in the sense this term is used in Cumacea or Decapoda. Only informative characters are included in Table I and the data matrix (Table II).

#### Cladistic analysis

A data matrix (nexus file) was generated for input into the phylogenetic program PAUP\* 4.0b10 (beta-test version for Windows, 2001) (Swofford, 1998). All characters were unordered and treated as having equal weight in the first analysis (Table I). Taxa scored with more than one state for a character were treated as polymorphic rather than uncertain (MSTAXA=POLYMORPH)

An heuristic search (hsearch) was initiated, a treespace search using tree bisection and reconnection (TBR), characters optimised using accelerated transformation (ACCTRANS) and with randomised addition of taxa (addseq=random); 1000 replications were completed setting branch swapping options to save no more than three trees with length greater than or equal to the shortest tree found in each replicate (nchuck=3 chuckscore=1 nreps=1000 randomise=trees). Branches of these were then swapped for a second search, retaining all minimum-length trees (hsearch start=current nchuck=0 chuckscore=0).

If needed, improved resolution was sought by the "reweight" option in PAUP whereby characters are reweighted to constant weight based on the initial rescaled consistency indices (RI). This was achieved in two "reweight" runs, each using the heuristic protocol described above. A strict consensus tree was calculated if necessary. An Adams tree, the preferred consensus method suggested by Kearney (2002) for analyses with considerable missing data, was calculated when fossils were included. Only selected cladograms are figured (Fig. 1).



The number of taxa in the full data-set was 20, 18 in the ingroup, two in the outgroup. Four reduced data-sets were also assembled, modified as follows:

- (1) two fossil genera excluded (18 taxa, 92 characters);
- (2) 47 characters unknown for the two fossils excluded (20 taxa, 45 characters);
- (3) three spelaegriphacean and three mictacean genera replaced with just those two orders, some characters scored as variable to take into account different states in extant genera, and fossils excluded (14 taxa, 73 characters)
- (4) 45 characters (mostly losses of limb branches or articles or significant changes in form) made irreversible and one ordered (14 taxa, 73 characters; see Table I).

Character transformations were found using PAUP's "apolist" option. Stability of the reweighted trees was assessed using bootstrap (Felsenstein, 1985). Bootstrap was implemented in PAUP based on 1000 pseudoreplicates. A tree space search used 5 random-addition sequence iterations with 10 trees saved per iteration. Trees were drawn using TreeView 1.6.5 (© Roderic D.M. Page 2001) and edited in Adobe Illustrator©.

**Table I:** Characters and character states used in cladistic analysis of Peracarida. States are labelled 1, 2 etc. Weights applied in the weighted analysis of all taxa and all characters are appended to each line, followed by (I) for characters treated as irreversible in the last analysis. Character 5 was ordered for the last analysis. Autapomorphies (characters uninformative in this analysis) are not included.

1	Cervical groove: 1, absent. 2, present (at least in part). 0.43
2.	Cephalothoracic shield (thoracomeres): 1, first only. 2, involves 2 or more. 0.33 (I)
3.	Dorsal fold: 1, absent. 2, present. 0.11 (I)
4.	Cephalic pleural fold: 1, absent. 2, present. 0.16 (I)
5.	Segmental pleural folds (branchiostegal folds): 1, absent. 2, thoracomere 1 only. 3, thoracomeres 2–6. 4, thoracomeres 1–8. 0.62 (I)
6.	Branchiostegal flaps: 1, absent. 2, present. 1.00 (I)
7.	Pleonite musculature: 1, not capable of caridoid escape response. 2, with diagonal muscles crossing pleonite boundaries enabling caridoid reverse escape response. 1.00 (I)
8.	Eye optics: 1, apposition (no clear zone between crystalline cone and rhabdom). 2, superposition (clear zone formed by reticular cells and/or distal pigment cells separating cone and rhabdom). 0.37
9.	Ommatidia, crystalline cone: 1, tetrapartite. 2, bipartite. 1.00
10.	Ocular lobe: 1, present. 2, absent. 0.06 (I)
11.	Naupliar eye of adult: 1, present. 2, absent. 1.00
12.	Antenna 1, outer ramus: 1, multiarticulate (more than 20 articles). 2, with fewer than 10 articles. 0.16 (I)
13.	Antenna 1, inner ramus: 1, multiarticulate (more than 20 articles). 2, rarely more than 6 articles. 0.20 (I)
14.	Antennal gland: 1, present. 2, absent. 0.12
15.	Antenna 1 statocyst: 1, absent. 2, present. 0.11
16.	Antenna 2 peduncle article 3: 1, about third as long as article 4 (or more). 2, very much shorter than article 4. 3, fused to article 4(?). 1.00
17.	Antenna 2 outer ramus: 1, present. 2, absent. 0.06 (I)
18.	Antenna 2 outer ramus: 1, linear. 2, scale-like (scaphocerite). 0.25 (I)
19.	Antenna 2 scale (scaphocerite): 1, as long or longer than peduncle articles 3+4. 2, half length of peduncle articles 3+4. 0.33
20.	Labrum: 1, without posterior tooth. 2, with posterior tooth. 1.00 (I)

21. Mandibular incisor: 1, stout, tooth-like. 2, thin, blade-like. 0.23 (I)
22. Mandible, lacinia mobilis (broad on right, narrower spine on left): 1, absent. 2, present. 1.00 (I)
23. Mandibular spine row and lacinia mobilis: 1, short and compact, incisor and molar closely-set. 2, long, incisor and molar widely-spaced. 0.43 (I)
24. mandibular palp: 1, with lateral setae on articles 2 and 3. 2, with distal setae on article 3 only. 0.25
25. Labium: 1, with apices rounded, without long seta; mesial faces smooth. 2, with acute apices, each bearing long seta; mesial faces bearing tooth plus 2 denticulate setae. 1.00
26. Maxilla 1: 1, with palp (endopod). 2, without palp (endopod). 0.15 (I)
27. Maxilla 1 palp (endopod): 1, distally produced. 2, reflexed. 0.25 (I)
28. Maxilla 1 proximal endite: 1, with row of long marginal setae. 2, with 3-4 short pappose setae. 3, with 2 apical pappose setae. 4, with 4-5 spiniform setae. 5, with few distal simple setae. 1.00
29. Maxilla 1 distal endite: 1, without distolateral row of denticulate setae or teeth. 2, with distolateral row of denticulate setae (longer and distinct from distal spiniform setae). 1.00
30. Maxilla 1 distal endite: 1, without lateral pappose setae (usually pair of facial long pappose setae instead). 2, with single distolateral or facial pappose seta. 1.00
31. Maxillary gland: 1, present. 2, absent. 0.10
32. Maxilla 2 basal endites: 1, longer than wide. 2, about as wide as long. 0.33 (I)
33. Maxilla 2 basal endites 2 and 3: 1, with simple, setulate or pectinate setae along distal margin. 2, each with mesial row of long setae with claw-shaped ends (pectinate setae distally). 1.00
34. Maxilla 2 endopod (palp): 1, present. 2, absent. 0.20 (I)
35. Maxilla 2 palp: 1, articular. 2, reduced to long external seta at base of outer lobe. 1.00
36. Maxilla 2 exopod: 1, present. 2, absent. 0.22 (I)
37. Maxilla 2 exopod: 1, simply lamelliform. 2, produced proximally (posteriorly into branchial chamber as scaphognathite). 1.00 (I)
38. Thoracopods 1-3: 1, undifferentiated from posterior thoracopods. 2, first differentiated as maxilliped with well developed basal endite. 3, at least two (often three) differentiated as diverse maxillipeds from posterior thoracopods. 4, all three differentiated as similar maxillipeds from posterior thoracopods. 0.36
39. Thoracopod 2 (pereopod 1): 1, ambulatory or not enclosing mouthparts as follows, ischium-merus articulation linear. 2, enclosing mouthparts, ischium-merus articulation angled anteriorly; basis more elongate than that of pereopod 2. 1.00
40. Thoracopod 1 (maxilliped) basal endite: 1, with setae variously structured. 2, with c. 8 short distomesial robust setae, lateral simple setae. 1.00
41. Thoracopod 1 (maxillipedal) palp article 5: 1, aligned with article 4. 2, at right angles to article 4. 1.00
42. Thoracopod 1 (maxillipedal) palp articles 2 and 3: 1, not mesially expanded, with few mesial setae. 2, mesial expanded, with mesial row of plumose setae. 1.00
43. Thoracopod 1 (maxillipedal) exopod: 1, present. 2, absent. 0.43 (I)
44. Thoracopod 1 (maxillipedal) exopod: 1, linear. 2, with expanded basal section. 1.00

45. Thoracopod 1 (maxillipedal) epipod: 1, present. 2, absent. 0.10
46. Thoracopod 1 (maxillipedal) epipod: 1, short, linear (or in Isopoda not expanded into branchial cavity). 2, expanded into branchial cavity. 0.11
47. Thoracopod thorax-coxa articulation: 1, thorax and coxa articulating on transverse hinge. 2, thorax and coxa articulating in anteroposterior axis. 3, coxa immobilised. 1.00
48. Thoracopod coxa-basis articulation: 1, dicondylic along anteroposterior axis. 2, monocondylic. 1.00
49. Thoracopods, intrabasal articulation: 1, absent. 2, present. 1.00 (I)
50. Pereopods: 1, with few short setae on articles. 2, with row of long setae on all articles. 1.00
51. Pereopodal unguis: 1, short, curved. 2, long, setiform. 1.00
52. Thoracopod 2 (pereopod 1) exopod: 1, present. 2, absent. 0.06 (I)
53. Thoracopods 3-4 (pereopods 2-3) exopods: 1, present. 2, absent. 1.00 (I)
54. Thoracopod 3-4 (pereopods 2-3) exopods: 1, of at least 3-4 articles. 2, of 2 articles. 0.08 (I)
55. Thoracopods 5 and 6 (pereopods 4 and 5) exopod: 1, present. 2, absent. 1.00 (I)
56. Thoracopod 5 (pereopod 4) exopod of female: 1, of 2 (or more) articles. 2, of 1 article. 0.10 (I)
57. Thoracopod 6 (pereopod 5) exopod: 1, of at least 2-4 articles. 2, of 1 article. 0.10 (I)
58. Thoracopod 7 (pereopod 6) exopod: 1, present. 2, absent. 0.33 (I)
59. Thoracopod 7 (pereopod 6) exopod: 1, of at least 2-4 articles. 2, of 1 article. 0.16 (I)
60. Thoracopod 8 (pereopod 7) exopod: 1, present. 2, absent. 0.25 (I)
61. Thoracopod 5-7 (pereopods 4-6) basis, pedunculate setae: 1, absent. 2, 2-3 present. 0.33
62. Thoracopodal epipods (oostegites excluded): 1, absent. 2, present. 0.42 (I)
63. Thoracopodal epipods: 1, one or two, linear. 2, two or three (complex branchiae). 3, one coxal gill. 0.33 (I)
64. Oostegites: 1, absent. 2, present. 0.40 (I)
65. Oostegites: 1, with marginal setae. 2, without marginal setae. 0.10
66. Oostegite on thoracopod 2 (pereopod 1): 1, present. 2, absent. 0.25 (I)
67. Oostegite on thoracopod 7 (pereopod 6): 1, present. 2, absent. 0.16 (I)
68. Pleopods 1-5: 1, well developed, biramous. 2, small, uniramous (or further reduced). 0.16 (I)
69. Pleopodal sexual dimorphism: 1, pleopods in males reduced or absent, at least posteriorly. 2, pleopods 1 and 2 forming petasma in male. 3, pleopods undifferentiated. 4, pleopod 2 of male differentiated. 0.08
70. Male pleopod 2: 1, undifferentiated. 2, endopod single non-setose article, exopod of 2 articles. 0.00
71. Pleopodal exopods: 1, annulate. 2, of 2 articles. 3, of 1 article. 4, obsolete. 0.35
72. Uropodal rami: 1, flattened (most setae on lateral margins). 2, styliform (most setae on upper margin). 0.08
73. Uropodal endopod: 1, of 1 article. 2, of 2 articles. 3, of 3 or more articles. 0.50 (I)



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- 74. Uropodal exopod: 1, of 1–2 articles. 2, of at least 5 articles. 0.25 (I)
  - 75. Uropodal exopodal proximal article: 1, longer than distal article. 2, shorter than distal . 0.00
  - 76. Telson: 1, not fused to pleonite 6. 2, fused to pleonite 6. 0.00
  - 77. Embryo flexion: 1, ventral. 2, dorsal. 0.37
  - 78. Yolk in posterior part of embryo: 1, none. 2, present. 1.00
  - Development of appendages: 1, advanced development of anterior head
  - 79. appendages. 2, continuous anteroposterior decrease in degree of appendage formation . 1.00
  - 80. Manca stage (juvenile lacking p7): 1, absent. 2, present. 0.23
  - 81. Dorsal frontal organ: 1, absent. 2, present. 0.25
  - 82. Ventral frontal organ: 1, absent. 2, present. 1.00
  - 83. Foregut shape: 1, anterior section of similar dimension to posterior. 2, anterior section enlarged. 0.33
  - 84. Foregut, dorsolateral and midventral ridges: 1, with setae. 2, with teeth or ossicles. 0.37
  - 85. Foregut, fine filter channels: 1, 1 or 2. 2, numerous. 0.33
  - 86. Foregut, superomedianum: 1, absent. 2, present. 1.00
  - 87. Foregut, entoderm plates: 1, unpaired. 2, paired. 1.00
  - 88. Foregut, dorsal caeca: 1, absent. 2, present. 0.25
  - 89. arterial system: 1, arteries arising only from anterior and posterior ends of heart. 2, several segmental arteries arising from heart. 1.00
  - 90. Arteria subneuralis: 1, absent. 2, present. 0.20
  - 91. Spermatophore: 1, present. 2, absent. 0.33
  - 92. Sperm, cross-striated perforatorium: 1, absent. 2, present. 0.33
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## Results

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### Overall pattern

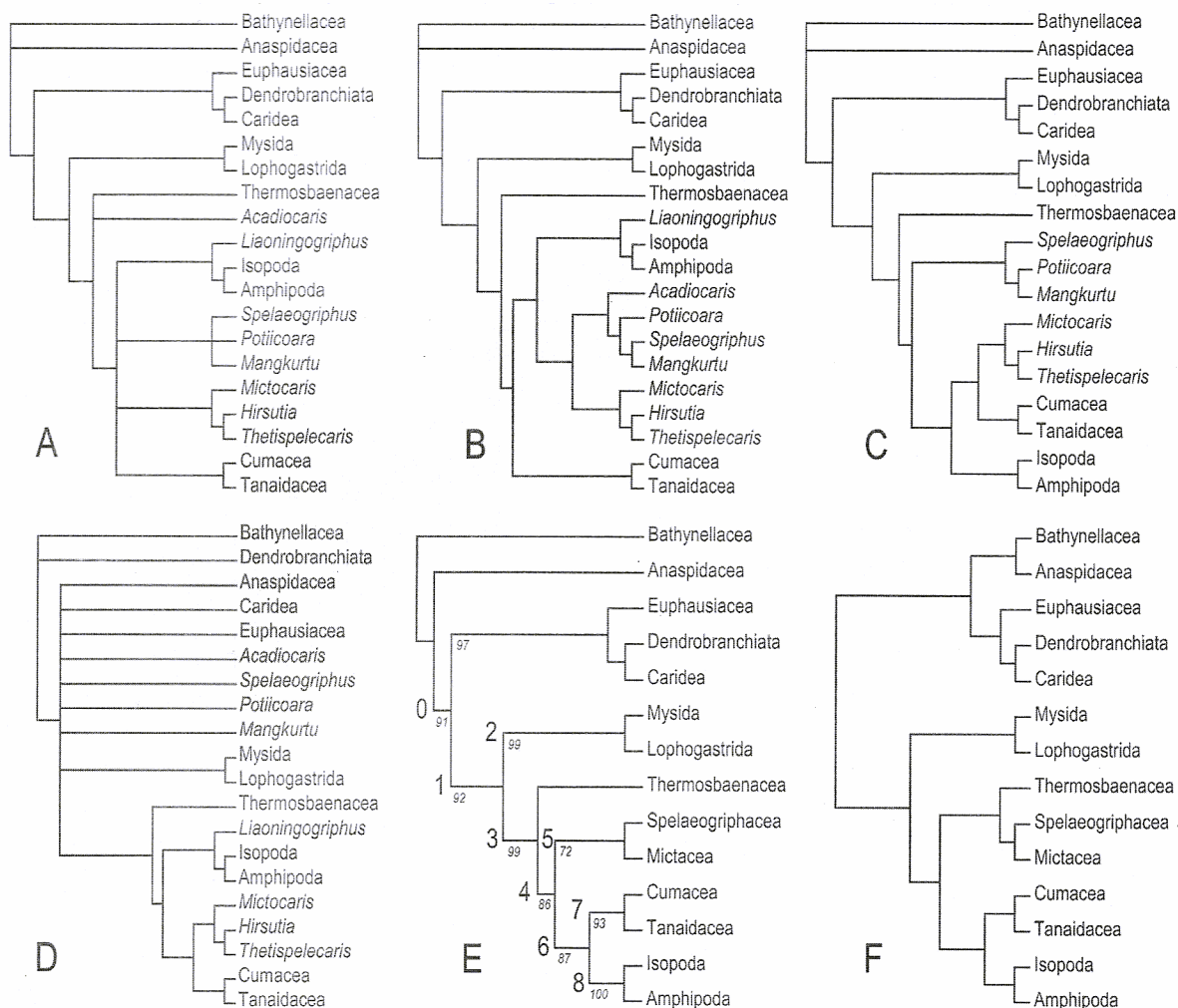
The first analysis of the full data-set using unweighted characters discovered 19 most-parsimonious trees of length 222 steps, consistency index (CI) 0.54, and retention index (RI) 0.69. In the strict consensus tree, there exists a peracarid clade that includes the sister-taxa Mysida and Lophogastrida, Mictacea are monophyletic, Cumacea and Tanaidacea are sister-taxa as are Isopoda and Amphipoda. The Adams tree (which accommodates missing data) aligns *Liaoningogriphus* with Isopoda + Amphipoda (Fig 1A).

Reweightings of characters decreased the weights of 60 of the 92 characters. Three of these were given zero weight so effectively excluded from the analysis. A single most-parsimonious tree was found in which Mysida and Lophogastrida were found to be the most basal peracarids, Thermosbaenacea next, Cumacea plus Tanaidacea next, Isopoda + Amphipoda + *Liaoningogriphus* next, then the sister taxa Spelaeogriphacea + Mictacea (Fig. 1B; CI=0.74, RI=0.86). In view of the result that only one of the two fossil "spelaeogriphaceans" aligned with extant members of this order, the matrix was run again without fossils. Effectively the same result was obtained; two trees were found differing only in the relative position of the outgroups (Fig. 1C; length = 218, CI=0.55, RI=0.69).

Table II: Data matrix of 20 taxa and 92 characters used in full analysis. — is inapplicable, ? is unknown. Fractions denote alternative states.

character	1234567891	1234567892	1234567893	1234567894	1234567895	1234567896	1234567897	1234567898	1234567899	12
Bathynellacea	21111121?2	?2221111-1	211212-511	111112-11-	--112-1111	1112122121	1211---23-	42111121?11	??1?22211	2?
Anaspidae	2111112221	11122111-1	1111111111	111112-211	1111111111	1111111111	1211---12-	1111111111	2111121211	21
Dendrobranchiata	2221412211	111211211	1111111111	211111231-	--12121111	1112122121	1221---12-	3111111111	2222221212	11
Caridea	2212412211	111211211	1111111111	211111231-	--12121111	1111111111	1221---141	3111111111	2222221212	11
Euphausiacea	2122412221	111111211	1111111111	211111111-	--11121111	1212122111	1221---12-	3111111111	1222221212	11
Mysida	2122222221	2111211212	121112-111	211111111/31-	--11122121	1211111111	121211111¼1	1111111211	1122122212	½2
Lophogastrida	2122222221	2111111212	1211112111	111111111-	--112-2121	1111111111	122211111¼1	1111111?11	111222?212	2?
Thermosbaenacea	1122211?1	?1121?2--1	2221111111	2211111211	1111123211	1112111111	11-1---23-	211111121½	??11122211	2?
<i>Laoninogriphus</i>	112221?2?2	?11?2?1211	?2221111111	?2221111111	?2221111111	122-2--2-2	?1-?2?21?2	211111?2?2	?2221112221	??
<i>Acadiocaris</i>	212221?2?2	?11?2?2--1	?2221111111	?2221111111	?2221111111	?2221111111	?1-?2?21?2	311111?2?2	?2221112221	??
<i>Spelaeogriphus</i>	2122211?1	?11?21221	222?12-212	?222-2-212	222-123211	1112121122	11-2?12141	311111?2?2	?2221112221	??
<i>Potticoara</i>	2122211?1	?11?21211	222112-312	?222-2-212	212-113211	1112122122	11-2?12142	311121?2?2	?2221112221	??
<i>Mangkurta</i>	2122211?1	?112121211	222112-212	?22112-212	222-113211	1112122121	21-2212142	3111112?22	?2221112221	??
<i>Mictocaris</i>	1112211?1	?222?11221	222112-311	?11112-211	112-2-3211	11121112-2	21-2212241	4221212?22	?2221112221	??
<i>Hirsutia</i>	1112211?2	?22?111221	222222-421	?11122-221	112-2-3212	2211111112	21-212124?	4222-1?2?2	?2221112221	??
<i>Thetispelecaris</i>	1112211?2	?222111221	222222-421	?11122-221	112-2-3212	2111111112	21-21212?2	4222-1?2?2	?2221112221	??
Cumacea	12123111?2	2222112--1	122?112111	1112-1141-	--11123211	1211111112	11-221211-	22311½2222	111112?121	22
Tanaidacea	121231112½	21211111-1	1221112111	1112-2-211	112-123211	1111111111	11-221211-	2232-22222	1111122121	21
Isopoda	1111111122	2112112--1	121112-111	1112-2-211	112-113211	122-2--2-2	11-2½111¼1	2211122222	1111112122	22
Amphipoda	111111112½	2111112--1	1211111111	2112-2-211	112-2-3211	122-2--2-2	1232½2213-	122111122½	1111112221	22

*Nauplius*



**Figure 1:** Cladograms of relationships of peracarid taxa. A, Adams consensus tree of all taxa, based on 92 unweighted characters. B, Single tree of all taxa, based on 92 weighted characters. C, Single tree of all extant taxa, based on 92 weighted characters. D, Strict consensus tree of all taxa with 47 characters not informative for fossils excluded. E, Single tree of 14 orders, based on 73 unweighted characters (clades 0–8 and associated bootstrap values are labelled). F, Single tree of 14 orders, based on 73 irreversible weighted characters.

With fossil taxa included and 47 characters not informative for fossils excluded, the number of trees discovered was 460 (length=114, CI=0.50, RI=0.66), reduced to 16 following reweighting to constant weight (CI=0.71, RI=0.86). Without character reweighting neither fossil taxon could be placed in any extant order. After reweighting, *Liaoningogrhipus* was sister taxon to Amphipoda + Isopoda (Fig. 1D) and other peracarid orders were arranged much as before. No conclusion could be drawn about the affinities of *Acadiocaris*.

The monophyly of extant members of Spelaeogrhipacea and Mictacea permitted these to be scored as single orders, taking into account variation across genera. Analysis of the reduced data matrix of 14 taxa and 73 informative characters resulted in a single tree (Fig. 1E; length=214, CI=0.57, RI=0.64). The basic structure is similar to Figs 1B and C but Mictacea appear more related to Spelaeogrhipacea than to Cumacea + Tanaidacea. All cladograms have high bootstrap values.

The analysis was also constrained by making some characters (45 of the 74 in the orders-only matrix) irreversible. As anticipated, longer trees were obtained, 233 vs 214. Relationships of major groups were much as before in the strict consensus of four shortest trees (CI=0.58, RI=0.63) and a single tree was found after reweighting with Thermosbaenacea belonging to the Mictacea + Spelaeogrhipacea clade (Fig. 1F, CI=0.71, RI=0.84). Significantly, Peracarida remain monophyletic.



## Character changes

Character changes at each node (Table III) are discussed first with reference to Fig. 1E. Autapomorphies of each taxon are not discussed.

The Eucarida + Peracarida, clade 0 (Fig. 1E), share 11 synapomorphies that distinguished it from syncarids: dorsal and cephalic pleural folds [character 3]; branchiostegal folds on thoracomere 1 [5]; antennal gland [14]; scaphocerite [18]; no maxillary gland [31]; maxilla 2 exopod present [36]; maxillipedal expanded into branchial cavity [46]; two or three thoracopodal epipods developed as complex branchiae [63]; dorsolateral and midventral ridges of foregut with teeth or ossicles [84]; and presence of an arteria subneuralis [90].

The data matrix was not expanded to explore relationships between eucaridan taxa and their synapomorphies are not explored here.

Changes taking place at clade 1 (Peracarida) are loss of adult naupliar eye [11], lacinia mobilis [22], thoracopods with thorax and coxa articulating in anteroposterior axis [47], oostegites [65], pleopod 2 of male differentiated [69], yolk in posterior part of embryo [78], paired entoderm plates in the foregut [87], and sperm with cross-striated perforatorium [92]. Some of these are reversed later.

Mysida + Lophogastrida (clade 2) share branchiostegal flaps [6], a labrum with a posterior tooth [20], thoracopods with intrabasal articulation [49] and thoracopodal 3–4 (pereopods 2–3) exopods of at least 3–4 articles [54]. Mysida, as well as their autapomorphies have an antenna 1 statocyst [15], no exopod on thoracopod 2 (pereopod 1) [52], possess thoracopodal epipods [63], and have a foregut with an enlarged anterior section [83]. Lophogastrida have a maxillary gland [31], no maxillipedal epipod [45] and a foregut with numerous fine filter channels [85] as well as numerous autapomorphies.

**Table III:** Synapomorphies of the nodes labelled on Fig. 1E, the cladogram of peracarid orders (and autapomorphies of terminal taxa). Character numbers are not annotated when the state changed from 1 to 2, -1 indicates a reversal from state 2 to 1, and changes from and to other states are indicated by >. Autapomorphies of the decapod taxa are not indicated.

node-0	3 4 5 14 <sup>-1</sup> 18 31 36 <sup>-1</sup> 46 63 84 90
node-1	11 22 47 64 69 <sup>2&gt;4</sup> 78 87 92
node-2	6 20 27 49 54 <sup>-1</sup>
Mysida	15 26 52 63 <sup>-1</sup> 83
Lophogastrida	31 <sup>-1</sup> 45 85
node-3	1 <sup>-1</sup> 7 <sup>-1</sup> 8 <sup>-1</sup> 14 17 19 21 23 38 47 <sup>2&gt;3</sup> 48 63 <sup>-1</sup> 63 <sup>2&gt;3</sup> 65 67 71 80 84 <sup>-1</sup> 90 <sup>-1</sup>
Thermosbaenacea	3264 <sup>-1</sup> 68 69 <sup>4&gt;3</sup>
node-4	3 <sup>-1</sup> 31 <sup>-1</sup> 36 43 60 77 79 88 <sup>-1</sup> 89
node-5	17 <sup>-1</sup> 26 28 3 61 71 <sup>2&gt;3</sup> 75
Spelaeogriffacea	1 3 16 30 32 33 40 41 56 57 59
Mictacea	12 13 45 68 71 <sup>3&gt;4</sup> 73
node-6	5 <sup>-1</sup> 10 18 <sup>-1</sup> 21 <sup>-1</sup> 34 52 54 <sup>-1</sup> 72 76
node-7	2 5 3 13 27 69 <sup>4&gt;1</sup> 73 <sup>3</sup>
Cumacea	12 36 <sup>-1</sup> 38 <sup>2&gt;4</sup> 43 <sup>-1</sup>
Tanaidacea	14 <sup>-1</sup> 17 <sup>-1</sup> 52 <sup>-1</sup> 60 <sup>-1</sup> 74 92 <sup>-1</sup>
node-8	4 <sup>-1</sup> 23 <sup>-1</sup> 46 <sup>-1</sup> 53 55 56 58 86 <sup>-1</sup>
Isopoda	26 67 <sup>-1</sup> 90
Amphipoda	14 <sup>-1</sup> 31 45 62 66 69 <sup>4&gt;3</sup> 71 <sup>-1</sup> 73 76 <sup>-1</sup> 77 <sup>-1</sup> 88

Nineteen character changes define clade 3, peracarids beyond Mysida + Lophogastrida. The most important are: loss of caridoid escape response [7]; apposition eye optics [8]; loss of antennal gland [14]; long mandibular spine row and lacinia mobilis, widely-spaced incisor and molar [23]; first thoracopod differentiated as a maxilliped with well developed basal endite [38]; thoracopodal coxa immobilised and monocondylic coxa-basis articulation [47, 48]; no thoracopodal epipods (oostegites excluded) [62]: oostegites without marginal setae [65]; no oostegite on thoracopod 7 [67]; pleopodal exopods of two articles [71]; a manca stage [80]; dorsolateral and midventral ridges of foregut with setae [84]; and a heart without arteria subneuralis [90]. Others are changes or losses that are later reversed: loss of the outer ramus of antenna 2 [17]; and thin, blade-like mandibular incisor [21].

Thermosbaenacea, most importantly, are characterised by replacement of the oostegites [64] by brooding under the dorsal carapace fold, and reduction of pleopods [68, 69].

The synapomorphies of clade 4 are absence of a dorsal fold [3], absence of a maxillary gland [31], presence of maxilla 2 exopod [36], absence of maxillipedal and pereopod 7 exopods [43, 60], dorsal flexing of the embryo [77], absence of foregut dorsal caeca [88] and several segmental arteries arising from the heart [89].

Spelaeogriphacea and Mictacea (clade 5) share: presence of an outer ramus on antenna 2 [17]; no maxilla 1 palp [26]; the proximal endite of maxilla 1 with two unique apical pappose setae [28]; special pedunculate setae on the bases of pereopods 4–6 [61]; uniarticulate pleopodal exopods [71]; and the proximal article of the uropodal exopod shorter than the distal [75].

Spelaeogriphacea possess a cervical groove [1] and a dorsal fold [3]. Autapomorphies are: short article 3 of antenna 2 [16]; a single distolateral or facial pappose seta on the distal endite of maxilla 1 [30]; maxilla 2 basal endites about as wide as long, each with a mesial row of long setae with claw-shaped ends (pectinate setae distally) [32, 33]; maxillipedal basal endite with c. 8 short distomesial robust setae, lateral simple setae [40]; pereopodal exopods of one article [56, 57, 59]. Mictacean autapomorphies are: short rami on antenna 1 [12, 13]; no maxilliped epipod [45]; reduced pleopods [68, 71]; and a uropodal endopod of two articles [73].

Clade 6 includes the four speciose marine orders of peracarids. Its synapomorphies are: loss of branchiostegal folds [5], ocular lobe [10], scaphocerite [18], maxilla 2 endopod [34], pereopod 1 exopod [52] and articles from pereopod 2–3 exopod [54]; styliform uropods [72]; and potentially fused telson and pleonite 6 [76].

In Cumacea + Tanaidacea (clade 7): the cephalothoracic shield and branchiostegal folds extend to at least thoracomere 2 [2, 5]; the inner ramus of antenna 1 is short [13]; maxilla 1 palp is reflexed [27]; pleopods in males are reduced or absent, at least posteriorly [69]; and the uropod endopod is of three or more articles [73]. Cumacea share, on top of unique autapomorphies: a short outer ramus on antenna 1 [12]; a maxilla 2 and maxilliped exopod [36, 43]; and three maxillipeds differentiated from posterior thoracopods [38]. Tanaidacea, on the other hand share: no antennal gland [14]; no outer ramus on antenna 2 [17]; no exopod on pereopods 1 and 7 [52, 60]; multiarticulate uropodal exopod [74]; and no cross-striated perforatorium on the sperm [92].

Amphipoda + Isopoda (clade 8) have several characters states in common, some reversals to the condition seen in syncarids: loss of cephalic pleural fold [4]; a short and compact mandible with incisor and molar closely-set [23]; reduced or absent maxillipedal epipod [46]; no pereopodal exopods [53, 55, 58]; and no superomedianum in the foregut [86]. Besides their unique synapomorphies, Isopoda share: no maxilla 1 palp [26]; primitively an oostegite on pereopod 6 [67]; and a heart with an arteria subneuralis [90]. Amphipoda too share several states in addition to the unique three-uropod pleon: antennal gland [14]; no maxillary gland [31]; no maxillipedal epipod [45]; thoracopodal epipodal gills [62]; no oostegite on pereopod 1 [66]; pleopods with annulate rami and not sexually differentiated [69, 71]; uropod (3) sometimes of two articles [73]; the telson not fused to pleonite 6 [76]; ventral embryo flexion [77]; and the foregut with dorsal caeca [88].

Spelaeogriphacea can be defined by several synapomorphies (see above) but their diagnosis relies on characters seen only in extant taxa. In Fig. 1B, *Acadiocaris* joins the three extant genera but the cervical groove and the dorsal fold are the only shared characters visible in the fossil. *Liaoningogriphus* also displays these two character states but the absence of thoracopodal exopods excludes the genus from Spelaeogriphacea.

*Potiicoara* and *Mangkurtu* were shown to be most related pair of spelaeogriphacean genera in Fig. 1C with 73% bootstrap support. Notably, these two genera share long antenna 2 scale [19] and modified male pleopod 2 [70]. Each of the other two pairs of spelaeogriphacean species shares one or two character states and the relationship was different when the fossil was included.

Autapomorphies of Hirsutiidae (synapomorphies of *Hirsutia* + *Thetispelecaris* in Figs 1A, 1B, 1C) are: mandibular palp with distal setae on article 3 only [24]; labium with acute apices [25]; maxilla 1 proximal endite with 4 or 5 spiniform setae [28]; maxilla 1 distal endite with distolateral row of denticulate setae [29]; maxilla 2 palp reduced to a long external seta at the base of its outer lobe [35]; pereopod 1 enclosing mouthparts [39]; pereopods with row of long setae on all articles [50]; pereopodal unguis long, setiform [51]; oostegites with marginal setae [65]; oostegite absent from thoracopod 2 [66] but present on thoracopod 7 [67]; and uropodal exopod of at least 5 articles [74].

Autapomorphies of Mictacea (synapomorphies of Hirsutiidae + *Mictocaris* in Figs 1A, 1B, 1C) are: thin, blade-like mandibular incisor [21]; maxilla 1 proximal endite with 2 apical pappose setae [28]; maxilla 2 endopod present [34]; maxillipedal epipod absent [45]; pereopods 4–6 bases with pedunculate setae [61]; pleopods 1–5 small, without exopods [68, 71]; and uropodal exopodal proximal article shorter than distal article [75].

Character transitions calculated in this way by PAUP on parsimonious criteria often include many reversals that could be avoided in a longer tree. The tree constructed with 45 irreversible characters explores this possibility. The major conflict between this and other trees is in the relationships of Thermosbaenacea, Spelaeogriphacea and Mictacea: in Fig. 1F they are members of a single clade. Synapomorphies of this clade are: a cephalic pleural fold [4]; scaphocerite [18]; thin, blade-like mandibular incisor and widely-spaced incisor and molar [21, 23]; and a single distolateral or facial pappose seta on the distal endite of maxilla 1 [30].

## Discussion

### Overall patterns

The results of the cladistic analyses were susceptible to the numbers of included taxa and characters and any conclusion must be a compromise between all the parsimonious cladograms. The cladograms differed depending on whether fossils were included or not, whether two small orders were treated as multiple species or single orders, and whether or not characters were treated as irreversible. In general, the numbers of possible trees found on parsimony criteria were small, only a single tree resulted in each case after characters were reweighted, and bootstrap values were high. It can be concluded that:

- Peracarida include Mysida, Lophogastrida and Thermosbaenacea
- Mysida and Lophogastrida are sister taxa and the first offshoot of the Peracarida
- Isopoda and Amphipoda are sister taxa, both remote from the root of the Peracarida
- Cumacea and Tanaidacea are sister taxa, both remote from the root of the Peracarida and probably most related to Isopoda + Amphipoda
- Spelaeogriphacea and Mictacea are each monophyletic and possible sister taxa
- Thermosbaenacea could be either the most basal peracarids after mysidaceans or sister taxon to Spelaeogriphacea and Mictacea



### Spelaeogriphacea and the placement of fossils

It can be concluded that the extant Spelaeogriphacea are certainly monophyletic. It is probable that *Acadiocaris* is also a spelaeogriphacean but it is less certain that *Liaoningogriphus* is; on the basis of characters visible in fossils its placement in any order is impossible to justify. While the Spelaeogriphacea can be diagnosed with numerous autapomorphies, only two of these, the incomplete cervical groove and the dorsal carapace fold, are preserved in the fossils. The ocular lobe and antennal scale, spelaeogriphacean autapomorphies, have not been reported in either fossil. No character for which it was possible to score *Acadiocaris* sets it apart from extant Spelaeogriphacea or aligns it with another extant taxon. Schram (1974) included this taxon with this order on the basis of "second antennal peduncle with four segments" (probably the plesiomorphic condition), "carapace covering but not fused to second thoracomere, natatory pleopods, and the nature of the telson and uropods" (states not exclusive to this taxon and probably plesiomorphic).

On the other hand, *Liaoningogriphus* was never included within Spelaeogriphacea in these analyses. It differs principally in the absence of pereopodal exopods, an ocular lobe and an antennal scale, characters which place it with Isopoda and Amphipoda. While exopods may not have been preserved in the fossil, their absence and absence of other features from all well preserved limbs of all specimens suggests this is real. If the genus is a spelaeogriphacean it is highly derived. One highly characteristic feature, the right-angled maxillipedal palp seen in extant spelaeogriphaceans is also seen in *Liaoningogriphus* but is unknown in the other fossil. Shen *et al.* (1998) listed no characters shared when they placed *L. quadripartitus* in this order. They found four genera of Spelaeogriphacea (*Mangkurtu* not included) paraphyletic, the clade supporting them also including Tanaidacea and Cumacea. Their analysis included none of the antennal, mouthpart, pereopodal and pleopodal characters which so clearly unite the extant genera in my data set.

If *Liaoningogriphus* is not a spelaeogriphacean, what is it? The options within extant orders are limited. The sister relationship with Isopoda and Amphipoda, principally on the strength of the absence of pereopodal exopods, ocular lobe and scaphocerite, seems improbable but these are the only peracarid orders with this combination. Possession of flat uropods makes amphipod and isopod affinities improbable. The presence of well developed pleopods prevents it being a thermosbaenacean. Absence of fragile limb elements from fossils is weak evidence for excluding the taxon from the clade supporting Spelaeogriphacea.

### Spelaeogriphacea, Mictacea and alternative orders

Relationships between the spelaeogriphacean genera remain ambiguous. Gutu's (1998) proposal for subfamilies for each of the two species, *Spelaeogriphus lepidops* and *Potiicoara brasiliensis*, has no cladistic support. Shen *et al.* (1998) also attempted a phylogenetic analysis of extant and fossil spelaeogriphacean taxa. They limited themselves to characters that were present in the fossil taxa. They included in their analysis the peracaridans, *Mictocaris balope* (Order Mictacea), and one species each of orders Thermosbaenacea, Cumacea and Tanaidacea. They found the "spelaeogriphacean" taxa intermediate between Mictacea and Thermosbaenacea at the root and Cumacea and Tanaidacea at the apex of their tree. The small number of characters was clearly a limitation.

The Hirsutiidae (*Hirsutia* + *Thetispelecaris*) and Mictacea (Hirsutiidae + *Mictocaris*) are well supported and their relationships are unambiguous. However, no autapomorphy of Mictacea is unique and universal and none of those said by Bowman *et al.* (1985) would today fit these criteria (see too Richter and Scholtz, 2001). The carapace is the same as in Spelaeogriphacea and perhaps Tanaidacea, the antennal scale is as seen in Spelaeogriphacea, Thermosbaenacea, Mysida, Lophogastrida and Eucarida, maxilla 1 palp is absent as in Spelaeogriphacea and Isopoda,

and pleopods are uniramous as in *Thermosbaenacea*. The absence of the maxillipedal epipod is paralleled in *Amphipoda*. Bowman *et al.* (1985) noted similarity to *Spelaeogriphacea* and *Thermosbaenacea*, not least in the characters listed above, and interpreted *Mictacea* as occupying “an intermediate position by displaying many features of ... [Calman’s] caridoid facies in reduced form ...” I agree but go further by finding *Mictacea* sister group of *Spelaeogriphacea*.

Gutu’s (1998) alternate proposal to join the *Mictocarididae* and *Spelaeogriphidae* in a new order, *Cosinzenaeceae*, is not sustained. He listed 28 characters shared by the two families but with one exception are probable plesiomorphies shared with *Thermosbaenacea*; many are shared with most other peracaridans. Examples are fused head and pereonite 1, eyelobes, 3-articled mandibular palp, seven pereonites, six pleonites, wide biramous uropods and free telson. The exception is a manca stage in these two families but this occurs in four other orders and may well be plesiomorphic within the *Peracarida*. Characters defining Gutu and Iliffe’s (1998) *Bochusacea* (= *Hirsutiidae*) are autapomorphies so shed no light on relationships. My matrix contains no synapomorphies of *Mictocarididae* and *Spelaeogriphidae* that would support *Cosinzenaeceae*; *Bochusacea* is unnecessary by default.

### Competing pre-parsimony hypotheses on peracarid relationships

Before comparing these results with earlier views, it is illuminating to review opinions hitherto held, to examine the evidence offered in support and the manner in which it was treated. Many of the competing hypotheses have been reviewed uncritically by Hessler and Watling (1999) who had themselves contributed significant ideas independently over the previous two decades. Several of the authors cited below also reviewed prior contributions.

Calman (1904) introduced the “division” *Peracarida* to include the five orders then known, *Mysidacea*, *Cumacea*, *Tanaidacea*, *Isopoda* and *Amphipoda*. He acknowledged that his classification was based on well developed ideas elucidated by Hansen (1893a; 1893b). The brood-pouch formed by oostegites (modified coxal epipods) and a mandibular lacinia mobilis were the critical characters distinguishing *Peracarida* from other divisions of *Malacostraca*: *Syncarida*, *Eucarida* and *Hoplocarida*. Calman recognised precursors of these characters in some eucaridans. *Euphausiaceans* carry eggs in a basket formed by the pereopods. Larval *euphausiidaceans* and some other taxa have mandibular spines that appear to be an elementary lacinia mobilis or spine row. Calman (1904) hypothesised that the ancestral malacostracan was an animal displaying what he called the caridoid “facies”. Such an animal has a thoracic carapace, moveable eyestalks, an antennal scaphocerite (plate-like exopod), thoracic exopods, elongate abdomen and a tail-fan (flat uropods plus telson). He did not discuss relationships between the peracarid orders. Calman (1909) reiterated this classification and, despite arguments about the relationships between the peracarid orders and whether or not *Thermosbaenacea* and *Mysidacea* should be included, is the standard used almost universally today (e.g. Martin and Davis, 2001).

Siewing (1963 and earlier papers) believed that the ancestral malacostracan has the caridoid facies and that the *Syncarida* branched off from the main malacostracan stem earlier than *Peracarida* and *Eucarida*. Siewing was the first to spell out a modern methodology for reconstruction of relationships within *Crustacea*, and *Peracarida* in particular. He wrote of homologies and shared characters but was as influenced as earlier authors by unique differences. Thus, he supported the *Pancarida* as a division for *thermosbaenaceans* separate from peracarids because of their “uncommon breeding habit”. Siewing expressed his view of relationships of peracarid taxa as a “phylogenetic tree” and also figured shared homologous characters in a Venn diagram (Fig. 2A). Curiously, a parsimonious analysis of the 15 characters (13 informative) and five taxa does not result in the tree that he deduced. On this criterion, *Tanaidacea* are closer to *Cumacea* than to *Isopoda*. Sieg (1983) largely accepted Siewing’s phylogeny and added the *Spelaeogriphacea* as sister group of *Tanaidacea* + *Isopoda* as Siewing had intimated in his Fig. 42.



Schram (1981) approached the Eumalacostraca from a combined probabilistic-cladistic approach but without parsimony to derive another very different classification. He discussed the carapace, brooding and thoracopods briefly and admitted to a high degree of subjectivity in proposing a classification without Peracarida as such.

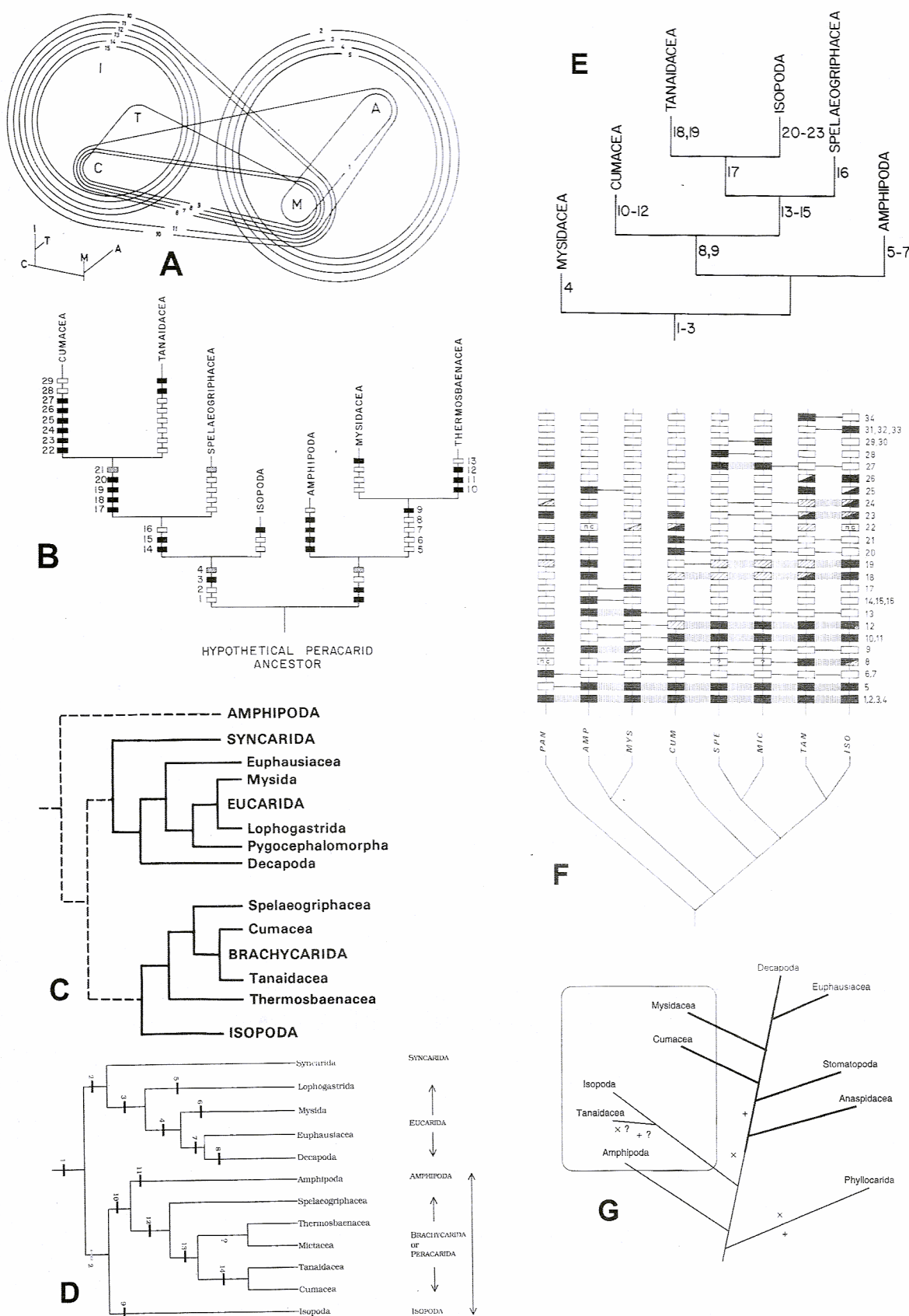
Also in 1981, Watling offered the first of his peracarid phylogenies and criticised that of Siewing as modified by Fryer (1965) to include the Thermosbaenacea. Watling did not believe that the caridoid facies was primitive and based his "phylogenetic scheme" on ten synapomorphies and another 19 numbered autapomorphies (and others unnumbered) to define the clades supporting seven orders. Although Watling's methodology was "Hennigian" in the sense that he constructed clades based on shared characters, he made an a priori decision to divide the peracarids into "mancoïd" and non-mancoïd lines and then selected synapomorphies at will for each of the other four clades required (Fig. 2B). He listed several characters as "independently derived" autapomorphies of amphipods, isopods and spelaeogriphaceans without discussing whether they, rather than others, were homoplasious.

Watling (1983) acknowledged that his 1981 scheme was "incomplete and in need of further revision". He hypothesised an alternative phylogeny and classification of Eumalacostraca that did not include a peracarid clade (Fig. 2C). In the prelude to this, he reviewed the carapace, eyes, mandible, maxilliped, blood system and developmental patterns, features that he believed were "relatively conservative". His view of the carapace was influenced by the opinion of Dahl (1983a), expanded by Dahl (1991), that the malacostracan carapace was a novel phenomenon not homologous with that of other crustaceans. On the basis of these body systems alone, Watling recognised five superorders: Amphipoda, Isopoda and Syncarida as conventionally understood, plus "Eucarida" and "Brachycarida". Each superorder was diagnosed in terms of at most nine characters, some with the same state in more than one superorder. Except in a brief discussion, Watling did not justify how he decided on the relationships of orders within superorders. His scheme is notable for the isolation of Amphipoda (from all other eumalacostracans) and Isopoda (from all other peracarids). The justification in both cases seems to be the possession of unique autapomorphies: an elaborate blood system and unique maxillipedal epipod in Isopoda; and reduced blood system, three pairs of uropods, fused maxillipedal coxa "and a host of other features" in Amphipoda. The shared characters of the two taxa (no carapace, "rolling" mandible, sessile eyes, apposition optics) were treated as convergences.

Watling (1999) carried his arguments about the value of examining major structural features further and reduced the carapace, foregut morphology and oostegites to comparable homologies. In a new cladogram (Fig. 2D), he restated his support for the five superorders proposed in 1983 but was more explicit about relationships between them and altered relationships between the orders within Brachycarida and Eucarida. He did not justify the choice of clades or the characters defining them.

The character analyses by Siewing (1963), Schram (1981) and Watling (1983; 1999) have greatly illuminated appreciation of peracarid evolution and much is intuitively good sense. The most terminal clades of some of their hypothesised phylogenies are also believable but the absence of a stated methodology that deals with potential homoplasies leaves the cladograms subject to criticism. In the 1983 paper, Watling was vague when drawing relationships at the base of the cladogram between Eucarida, Brachycarida and Amphipoda, but was more certain in the 1999 paper. Watling (1999) nominated suites of synapomorphic characters for each clade of his cladogram; possible homoplasies or reversals were not discussed. Other arrangements could equally have been chosen and (according to my cladistic analyses using the same data suites) are more probable on the parsimony criterion.





**Figure 2:** Published cladograms illustrating relationships of peracarid taxa that use non-parsimonious criteria. A, diagram of 15 shared characters and resulting tree (taxa displayed by initial letter: Amphipoda, Isopoda, Mysidacea, Cumacea, Tanaidacea) (Siewing, 1963: fig. 39). B, Cladogram of Watling (1981: Fig. 1). C, Cladogram and proposed higher taxa of Watling (1983: Fig. 4). D, Cladogram and proposed higher taxa of Watling (1999: Fig. 1). E, cladogram of Hessler (1983: Fig. 5). F, cladogram and character distribution of Pires (1987: Fig. 23). G, cladogram of Mayrat and de Saint Laurent (1996: Fig. 342) (x = appearance of eyestalks, + = appearance of carapace).

Dahl's and Watling's rejection of Calman's caridoid facies, supported by Schram (1982), was criticised by Sieg (1983) and by Hessler (1982; 1983). Hessler in particular argued convincingly for the caridoid facies and the carapace in particular being plesiomorphic malacostracan features. To test whether the choice of Syncarida as an outgroup, lacking a carapace, influences the outcome of my treatment, an analysis was performed without carapace characters 1–6. Before reweighting of characters, the position of Mysida + Lophogastrida was ambivalent, affinities with eucaridans and other peracarids being equally probable. After reweighting, a single tree identical to Fig. 1E was obtained. Debates about the monophyly or otherwise of the carapace and homology of non-malacostracan and malacostracan carapaces are largely irrelevant.

Hessler's alternative peracarid phylogeny (1983: fig. 5) did not include Thermosbaenacea and relied on only six synapomorphies to define the clades (Fig. 2E). In essence, these reduce to only three multistate characters: extent of carapace and thoracopodal epipods and exopods.

Pires (1987) also tackled the issue of peracarid phylogeny assuming that the Pancarida (Thermosbaenacea) were a sister taxon to seven other orders. Pires (1987) applied an outgroup analysis and Hennigian methodology but did not adopt parsimony as a criterion for selecting synapomorphies. Of 34 ordered 2- or 3-state characters defined, only 14 are informative (the rest are said to be autapomorphies). The cladogram of relationships that she presented (Fig. 2F) is not the most parsimonious treatment of her data.

As part of a study of the eumalacostracan heart, Nylund *et al.* (1987) proposed that the unique location of the heart and membrane systems of the heart myofibres of Isopoda justified them being sister taxon to all other malacostracans. They used other characters (citing Watling, 1983) to place the other peracarid, syncarid and eucaridan orders.

In an hypothesis most divergent from any before or since, Mayrat and de Saint Laurent (1996) hypothesised a polyphyletic Peracarida. They noted the similarity of mysidaceans to euphausiids. They doubted the homology of the brood-pouch and believed the lacinia mobilis to be a retained larval character of no defining value. In their view, the most basal peracarid orders did not possess a carapace, which they also believed was not a homologous structure (Fig. 2G). They indicated the appearance of eyestalks and the carapace that they believed took place more than once in their tree. While discounting the homology of all the characters they discussed, they substituted none in their place.

#### Parsimony-based hypotheses on peracarid relationships

Schram (1986: Fig. 43-3) proposed a tree of peracarid orders as part of a parsimony-based cladogram of eumalacostracan orders (Fig. 3A). He recognised Mysida and Lophogastrida as early derivatives, Isopoda, Amphipoda and Mictacea as next most derived, and Thermosbaenacea, Cumacea, Tanaidacea and Spelaeogriphacea next. Eleven characters contributed to his synapomorphies.

Wagner (1994) was the first to carry out an explicit phylogenetic analysis of the Peracarida alone based on a criterion of parsimony (Fig. 3B). He chose a crustacean with a caridoid facies as a hypothetical outgroup, 39 ordered informative characters and nine peracarid orders. He presented a fully resolved 50% majority-rule tree (of three trees) that can also be derived by automatic reweighting of his characters. Wagner's characters were informed by the character discussion of authors such as Watling (1983; 1999), Schram (1984) and Pires (1987). Wagner presented his cladogram as a preliminary to a discussion of relationships within Thermosbaenacea but did not discuss his results.

Schram and Hof (1998) elucidated phylogenies of peracarid orders as part of a wider study of interrelationships of major fossil and extant crustacean groups. Of the 90 characters

used by them, 39 are informative about relationships between eight peracarid and three decapod orders with Anaspidacea as an outgroup. A reanalysis of this limited suite of their data was more resolved than they were able to discover but the major clades were as they stated (Fig. 3C). When Schram and Hof included fossil taxa in their treatment, the relationships between peracarid orders was resolved in 50% of trees but this relationship is not the same as mine with a more limited data suite.

As part of a phylogenetic analysis of Recent and fossil Crustacea based on morphological characters, Wills (1998) found Peracarida to be supported, Mysida and Lophogastrida sister taxa and basal, Isopoda and Amphipoda to be sister taxa and terminal, and other orders including Thermosbaenacea ranged intermediately. The number of characters contributing to resolution of the peracarid clade was 40. When treated alone these resolve relationships only after reweighting (Fig. 3D) but with a slightly different result. Many of Wills' characters relied on the number of articles in limbs, variable for some taxa.

Wheeler (1998) used 552 morphological characters (assembled from Schram's papers, W. Wheeler, pers. comm.) to investigate the relationships of 90 arthropod lineages, among them nine peracarid orders. Mysida and Lophogastrida were again found to be basal, Mictacea and Spelaeogriphacea distinct from the rest, and Amphipoda and Isopoda next in sequence (Fig. 3E).

In the most recent phylogenetic analysis of malacostracan relationships (Richter and Scholtz, 2001), characters were drawn from many sources and discussed in detail. A consensus cladogram failed to find more than four monophyletic clades of peracarids: Thermosbaenacea; Lophogastrida + Mysida; Amphipoda; and Cumacea + Tanaidacea + Isopoda + Mictacea + Spelaeogriphacea. The authors choose one of the individual trees as their preferred tree of relationships and this was confirmed by me as parsimonious after reweighting their data (Fig. 3F). Seventy-three characters of the 93 used by them are informative for peracarids alone. They believed that the monophyly of the Peracarida was "comparatively well supported." Thermosbaenacea were found to be the most plesiomorphic peracarid clade (reviving the possibility of the Pancarida) but synapomorphies of the sister taxon were few: 19 ectoteleblasts variable in number, arranged in a row, being the most significant. Richter and Scholtz (2001) found no support for a sister relationship of Amphipoda and Isopoda.

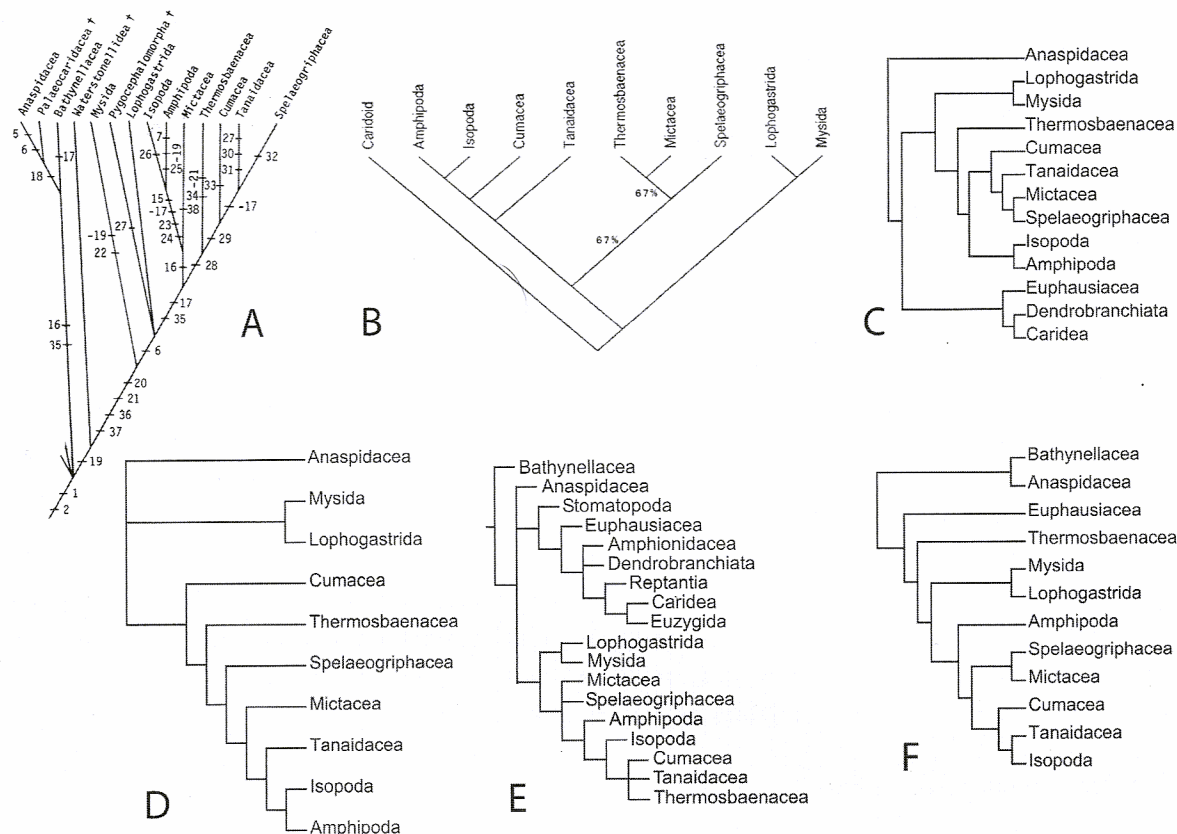
#### General conclusions on morphological evidence

Prior to Schram's (1986) treatment, analyses of peracarid relationships were either based on limited data suites, or used data that did not support the arguments advanced, or proposed no explicit criterion (such as parsimony) to choose between the many possible evolutionary scenarios, or combined all or some of these limitations. Classifications of other taxa proposed in the past and suffering from these criticisms have not always proved to be wrong when tested with more data or modern analytical methods. For example, the peracarid orders are much as conceived by nineteenth century biologists. But relationships within orders are not as originally conceived, for example in Amphipoda (Myers and Lowry, 2003) and Isopoda (Brandt and Poore, 2003). The critique above shows that in spite of the valuable contributions to understanding of characters, there was little agreement about relationships until Schram's and Wagner's analyses. Prior cladograms are hypotheses that have not withstood more rigorous testing. Mayrat and de Saint Laurent's later (1996) tree falls into the same class.

Beginning with Schram (1986) and Wagner (1994) and continuing with Schram and Hof (1998), Wills (1998), Richter and Scholtz (2001) and to a lesser extent Wheeler (1998), there is remarkable consistency in the cladograms (Fig. 3). My own confirms the general pattern. Part of the explanation for this is that all are drawing on similar suites of characters although the number of characters ranges from around 40 in the studies from the 1990s to more than 70 in



Richter and Scholtz's and mine. And all rely on parsimony as a criterion to select among trees. In summary, several recent cladistic analyses using a variety of morphological characters and different suites of taxa have greater consensus than is first apparent. The view that Lophogastrida and Mysida occupy a basal position is universal in these works and are sister taxa in all except Schram's (1986) tree. Most tests found strong support for a relationship between Spelaeogriphacea and Mictacea and usually with Thermosbaenacea too. The three are usually paraphyletic but under some scenarios could be a monophyletic clade. Most analyses found that Amphipoda and Isopoda are sister taxa and only one that they not related. The relationship between these two orders may have been obscured in the past by the belief that isopods display a tail fan reminiscent of a caridoid (e.g., Wägele, 1994). As has been convincingly demonstrated, the primitive isopod does not have a tailfan (Schram, 1974; Brusca and Wilson, 1991).



**Figure 3:** Published cladograms illustrating relationships of peracarid taxa that use parsimonious criteria. A, section of cladogram of Schram (1986: Fig. 43-3). B, 50% majority-rule tree cladogram of Wagner (1994: Fig. 489). C, parsimony cladogram calculated from limited data set of Schram and Hof (1998). D, parsimony cladogram calculated from limited data set of Wills (1998). E, eumalacostracan section of cladogram of Wheeler (1998: Fig. 8.3). F, part of cladogram of Richter and Scholtz (2001: Fig. 7 redrawn).

Richter and Scholtz differed most significantly from these conclusions, placing Thermosbaenacea basal and Amphipoda and Isopoda remote from each other. Cumacea and Tanaidacea are usually placed close together, on one clade or paraphyletically, only Wills (1998) finding them remote. My and Wagner's analyses placed them on a clade with Isopoda + Amphipoda; while most others agree they are similar, they align them differently.

My view is that the Peracarida arose from a shrimp-like malacostracan crustacean displaying a caridoid facies. The ancestor of the mysidacean orders was an early offshoot retaining many of these features but one that adopted oostegal brooding. Thermosbaenacea, Spelaeogriphacea and Mictacea branched off from the same ancestor (but in which order is uncertain) after significant shortening of the carapace (with only the first order adopting a unique carapace

brood-chamber). The terminal clade of four orders lost pleonal musculature and developed styliiform uropods. While Cumacea and Tanaidacea retained some form of carapace, the Amphipoda and Isopoda lost it completely along with pereopodal exopods.

This hypothesis makes explicit the view hinted at by Calman (1909: 181): "... the connection of the Mysidacea, through the Cumacea and Tanaidacea, with the Amphipoda and Isopoda is shown ... by the many connecting characters which link together the individual orders." This "classical view of evolution of the peracaridan orders" was expounded by Hessler (1982: 177), listing reduction of the carapace, immobilisation and loss of eyestalk, loss of antennal scale, changes in respiratory patterns related to reduction and loss of thoracopodal exites and epipods, incorporation of coxae into the body, and reduction of the abdomen, including reduction of the uropods and pleopods. He and a coauthor had briefly put the same view earlier (Grindley and Hessler, 1971), using evolution of the respiratory mechanism as an argument. The views of Dahl (1976; 1983a; 1983b) and Watling (1981) that the absence of a carapace is plesiomorphic and the peracarid ancestor is syncarid-like are not supported by several parsimonious analyses.

### The appeal of autapomorphies

Taxa with numerous or obvious autapomorphies attract undue attention and are often diverted early in classification and placed at higher taxonomic rank than they deserve. The birds (flying dinosaurs) are a classic example. In Crustacea, the amphipod suborder Caprellidea is simply a highly derived branch of corophiid Gammaridea (Myers and Lowry, 2003). The isopod suborders Gnathiidea, Anthuridea and Epicaridea are highly derived members of the Subfamily Cymothooidea (Brandt and Poore, 2003). The same phenomenon has persisted and distracted investigation of the Peracarida. Thermosbaenacea were placed in their own order, Pancarida, on the basis of a unique brooding method (Siewing, 1963 among others) while many characters shared with certain peracarid orders were overlooked. The carapace brooding could have arisen at any time along the malacostracan clade (or even within a monophyletic peracaridan lineage with loss of oostegal brooding) and in itself is not informative about relationships; other thermosbaenacean characters are.

Several authors (Fryer, 1965; Dahl, 1977; Watling, 1981; Hessler, 1983; Watling, 1983; Mayrat and de Saint Laurent, 1996) remarked on the many unique characteristics of Amphipoda (e.g., three pairs of uropods, simple non-foliaceous epipodal gills, maxillipedal structure, coxal plates). While these authors were correct to point out the special features of Amphipoda, none of these characters, all autapomorphies, is helpful in assessing relationships. Amphipods share diverse characters with cumaceans, tanaids and isopods: loss of branchiostegal folds, ocular lobe, scaphocerite, maxilla 2 endopod and pereopodal exopods plus a change to styliiform uropods. The complete absence of any carapace features places amphipods closest to isopods. Siewing (1963) elucidated at length the characters that isopods and amphipods shared but believed that because they are reductions they are therefore likely to be convergences. Evidence, tested by cladistic analyses (Wagner, 1994; Schram and Hof, 1998; Wills, 1998), supports Schram's (1986) contrary view that amphipods and isopods are closely related. I am not as "bothered" as Schram and Hof predicted (p. 270) by their and others' discovery of "the persistent linkage of isopods and amphipods" and agree with them that this "must give some pause to arguments against their alignment into the Edriophthalmata" (p. 292).

Isopoda have suffered the same treatment on the basis of an unusual heart, most notably by Watling (1983) and Nylund *et al.* (1987) who placed isopods in positions distinct from other peracarids, ignoring the potential synapomorphies they share with other taxa, amphipods in particular.

## Molecular studies

The number of molecular studies of Peracarida is surprisingly few. Jarman *et al.* (2000) used 28S rDNA to explore the relationships of the Euphausiacea and in doing so concluded that Mysida were closer to euphausiids and Anaspidacea than to Lophogastrida. The latter were more closely related to Isopoda, Tanaidacea and Cumacea. Amphipoda and Decapoda sat on another clade.

Babbitt and Patel (2005) used 18S (~1800 bp) and 28S (~350 bp) RNA in an investigation of Crustacea-Hexapoda relationships but discussed malacostracan relationships in the process. Different analytical methods gave different results and only a majority-rule Bayesian treatment of 34 malacostracan taxa was able to group two mysid taxa, two amphipods and six isopods into three monophyletic clades. In other analyses, amphipods and isopods appeared polyphyletic. However, in this cladogram, neither Peracarida nor Decapoda was found to be monophyletic and traditional views of these taxa and of Pleocyemata were not supported. They found mysids belonging to a clade containing a stomatopod, euphausiaceans, a syncarid, *Stenopus*, *Pennaeus*, lobsters, anomurans, crabs and a cumacean. Sister to this clade was another of carids, amphipods and isopods. Except for the outlying position of Mysida (no lophogastrid was included), their cladogram is impossible to reconcile with any classification based on morphology.

Spears *et al.* (in press) used full-length nuclear SSU rDNA to explicitly explore the relationships between all peracarid orders. While there was some discrepancy between various analytical methods, they were able to confirm the monophyly of Peracarida only by excluding Mysida. They found two major clades of peracarids, one comprising Lophogastrida and Spelaeogriphacea + Amphipoda, and the other, Isopoda + Cumacea + Tanaidacea. The relationships of Thermosbaenacea and Mictacea were undecided.

From a morphological point of view, some of these findings can be accepted. That Mysida could be the sister taxon of decapods rather than of peracarids is in line with their intermediate position on the morphological consensus trees but not with their similarity to Lophogastrida. The number of morphological characters shared by the two orders is considerable. More characters, foreguts, midguts and hepatopancreas are similar (De Jong-Moreau *et al.*, 2000; De Jong-Moreau and Casanova, 2001). Even some molecular data suggest that Lophogastrida and Mysida differ from all other peracarid orders except Isopoda in the absence of long branches (expansion segments) on the nSSU rDNA gene (Spears *et al.*, in press). They do in fact have a molecular feature in common, albeit plesiomorphic. Attainment of long branches in non-mysidacean peracarids and subsequent loss in isopods is a possible scenario.

The molecular affinity of Amphipoda with Spelaeogriphacea is surprising. A scan of the 93 morphological characters (Table II) reveals not a single one shared by these taxa and *not* shared by all or most non-mysidacean peracarids. A Cumacea + Isopoda + Tanaidacea clade suggested by the some of Spears *et al.*'s results has morphological support but their finding that the Mictacea, Spelaeogriphacea and Thermosbaenacea are only remotely related is less credible.

A significant discrepancy between the molecular and morphological evidence remains, or parsimony must be sacrificed to reach agreement.

## Evolutionary and ecological implications for the Peracarida

*Nauplius* While debate on peracarid relationships has been intense, little thought has been put into an evolutionary or ecological interpretation. In spite of using an outgroup without a carapace, results of most recent analyses support the hypothesis that the most plesiomorphic peracarids possess one and evolution has taken a path from an ancestor with the caridoid facies to groups



without.

Mysidaceans (Lophogastrida and Mysida) have a well developed carapace not unlike that in caridean shrimps. They are pelagic or benthopelagic and mysids in particular abundant in marine environments. Swimming with the aid of large thoracopodal exopods, walking, and swarming behaviour are ideally combined with the caridoid reverse escape reaction in mysids which live close to the bottom. This behaviour enables them to avoid predation by fishes (e.g. Flynn and Ritz, 1999).

Unlike mysidaceans, thermosbaenaceans, spelaeogrphaceans and mictaceans have a short carapace, weak thoracopodal exopods and (except for *Hirsutia*) flat uropods. All are weakly swimming, epibenthic forms of soft sediments (Fryer, 1965; Grindley and Hessler, 1971; Bowman and Iliffe, 1985) whose evolutionary success has been limited. They are found today only in caves, anchialine water, hypogean environments or in the deep sea. A marine fossil spelaeogrphacean, *Acadiocaris novascotica*, is known. The three groups comprise little over 40 species (Thermosbaenacea, 34 species; Spelaeogrphacea, four species; Mictacea, five species). Their experiment with a shortened carapace and this way of life has not been rewarding except in marginal environments. Small free-living but weakly swimming, non-swarming crustaceans would seem easy targets for predatory fish in diverse marine environments. The biology of the deep-sea *Hirsutia* spp. is unknown but parallels could be drawn with more successful tanaidaceans.

In the terminal peracarid clade, cumaceans to amphipods, the carapace is compacted and eventually lost. The uropods are styliform, pereopods more ambulatory, and no musculature exists for the caridoid escape. All orders comprise predominantly species buried in soft sediments or hiding in complex habitats such as reefs or algal turfs. None can swim except briefly for feeding or reproduction. Tube construction is widespread. These taxa dominate all marine benthic environments where densities can be as high as for any other invertebrate taxon. Likewise, species diversity on a local scale (thousands of species per square metre of sea floor) and taxon-wide (thousands or tens of thousands of species per order) are higher than for other crustaceans. Amphipods and isopods, which have moved furthest from the caridoid facies, are among the most successful of any marine invertebrate group. While they are still prey to many fishes, their more cryptic behaviour has protected them from the fate of their more mobile cousins.

This scenario is an elaboration of a similar one advanced many years ago (Schram, 1974). Schram proposed that the radiation of the Peracarida took place in the Permo-Triassic, the period when the first recognisable peracarid fossils appeared (Schram, 1986). In his view, the dominant Palaeozoic peracarids were the Pygocephalomorpha (fossil mysidaceans) which were epibenthic. At the end of the Permian, primitive peracarids occupied refugia or went extinct and were replaced by advanced peracarids adapted to benthic strategies. Schram excluded amphipods from this scheme.

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