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Phylogeny of decapods: moving towards a consensus

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Abstract

Although the recognition of four broad groups within Decapoda – natantians, macrurans, anomurans and brachyurans – has long been a staple of textbooks and even the primary taxonomic literature, a precise resolution of phylogenetic relationships within the order has proved more difficult. Indeed, there have been as many schemes of decapod taxonomy and phylogeny as there were experts who wished to offer an opinion. In this decade, utilization of explicit cladistic methods of analysis and the application of molecular techniques have produced a series of clear hypotheses concerning the relationships within many of the groups of Decapoda. It is apparent that earlier conflicts of opinion can be related in part to the implicit problems of dealing with paraphyletic groups near the base of the tree that are too broadly defined by only general or plesiomorphic features. Comprehensive morphological analyses of both fossil and living forms, with attention being paid to defining synapomorphies, can lead to resolution of old controversies. Molecular techniques hold great promise towards providing further resolution, but currently suffer from insufficiencies of sampling. Nevertheless, where once there was chaos and vexation, there is now some enlightenment. The situation can only improve, but the broad outlines of decapod deep history are already emerging.

Introduction

There have been as many taxonomies and schemes of phylogeny for the Decapoda as there have been experts willing to offer an opinion. Sometimes, experts have been willing to offer more than one opinion. Burkenroad (1963, 1981) held different views at different times, erecting the Pleocyemata in 1963 to contain all abdominal egg-brooders (Table 1) to general acclaim but then abandoning use of the term in 1981 (Table 2), though the clade clearly remained on his cladogram (Fig. 1). Textbooks typically often still employ terms like Natantia and Macrura in classifications, whereas among specialists these terms have fairly well passed out of formal taxonomic use (Tables 1 and 2). Natantians and macrurans are now perceived as stages in the evolution of decapod body plans, and even anomurans are coming to be interpreted in this same light (cf. Burkenroad, 1981; Scholtz & Richter, 1995). Nevertheless, one can still find Anomura employed as a taxon (Table 1), even as a consensus is now emerging that this group is paraphyletic. Only the Brachyura among the old classic suborders is now perceived as a real monophyletic group.

There are many reasons for these disagreements. First, they arise from the differences in perception about the basic nature of taxa that have their roots in phylistic *versus* cladistic approaches to classification and tree building. The old phylistic approaches of evolutionary systematics (Rasnitsyn, 1996) treat primitive groups as a monophylum by uniting them on the basis of plesiomorphic features alone. Macrurous natantians do not form a true monophylum in the cladistic sense since their long-tailed, swimming habitus is essentially a primitive one.

Second, differences can arise from whether or not fossils are included within an analysis. As an example, Schram & Hof (1998) clearly demonstrate what can happen when fossils are included or deleted from an analysis; major shifts of clades can occur. The lesson to be drawn from that exercise is that, while fossils may be frustrating to deal with, often lacking

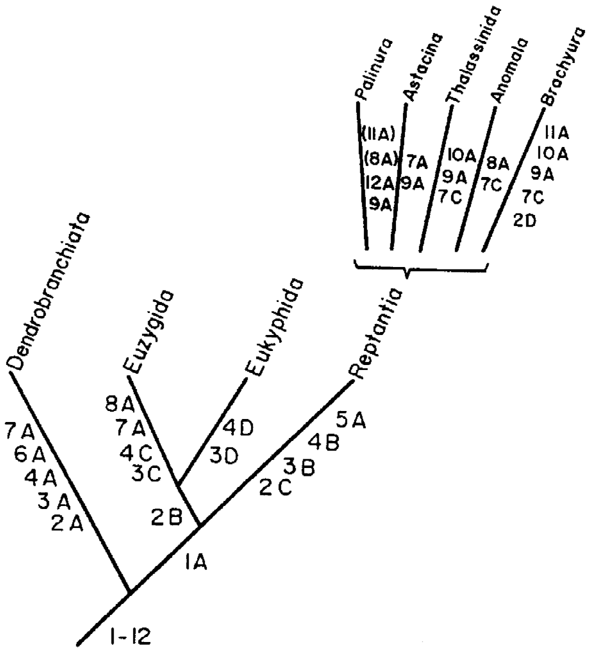

Figure 1. Cladogram of decapod relationships from Burkenroad (1981). Although the clade itself is characterized by a good apomorphy (1A = pleopod brooding of eggs) and is widely accepted among decapod workers, Burkenroad deliberately chose not to recognize the Pleocyemata in this paper. In addition, while Burkenroad believed there were five clearly defined Supersections of Reptantia, his characters could not further define relationships within that Suborder. For details concerning characters, consult Burkenroad (1981).

information we may wish we had, they nonetheless often contain enough information that in fact helps determine the basic structure of phylogenetic trees.

Third, we need to be very careful about how we use characters. This is especially crucial in terms of the use of soft-anatomy features observable only in living forms. For example, information from molecular sequences, developmental genetics, and/or neuroanatomy might seem to indicate apparently robust sister groups (Fig. 2a). However, more inclusive and comprehensive analyses, including larger arrays of characters and/or taxa (Fig. 2b), might actually argue against such groups (see Jenner, 1999; Jenner & Schram, 1999; Schram & Jenner, 2001).

Because of limitations of space, what follows is only a very general overview of some of the issues currently at play in discerning the phylogeny of the Decapoda; and it remains a very personal one at that since it focuses on such matters as have drawn my attention for one reason or another or struck my fancy.

Table 1. Classification of Decapoda from Glaessner (1969)

Order Decapoda Latreille, 1803
Suborder Dendrobranchiata Bate, 1888
Superfamily Penaeoidea de Haan, 1849
Superfamily Sergestoidea Dana, 1852
Suborder Pleocyemata Burkenroad, 1863
Infraorder Caridea Dana, 1852
Infraorder Stenopodidea Huxley, 1879
Infraorder Uncinidea Beurlen, 1930
Infraorder Astacidea Latreille, 1803
Infraorder Palinura Latreille, 1803
Superfamily Glypheoidea Winckler, 1883
Superfamily Eryonoidea de Haan, 1841
Superfamily Palinuroidea Latreille, 1803
Infraorder Anomura H. Milne-Edwards, 1832
Superfamily Thalassinoidea Latreille, 1831
Superfamily Paguroidea Latreille, 1803
Superfamily Galatheoidea Samouelle, 1819
Superfamily Hippoidea Latreille, 1825
Infraorder Brachyura Latreille, 1803
Section Dromiacea de Haan, 1833
Superfamily Dromioidea de Haan, 1847
Superfamily Homoloidea White, 1847
Superfamily Dakoticancroidea Rathbun, 1917
Section Oxystomata H. Milne-Edwards, 1834
Superfamily Dorripoidea de Haan, 1841
Superfamily Calappoidea de Haan, 1833
Superfamily Raninoidea de Haan, 1833
Section Oxyrhycha Latreille, 1803
Section Cancridea Latreille, 1803
Section Brachyrhycha Borradaille, 1907
Superfamily Portunoidea Rafinesque, 1815
Superfamily Xanthoidea Dana, 1851
Superfamily Ocypodoidea Rafinesque, 1815

A more inclusive treatment will have to be presented elsewhere.

Morphology and a natural taxonomy

Of course the 'Holy Grail' of all our work is to arrive at a system of classification that reflects the phylogeny of the Decapoda, and vice-versa. When I accepted the invitation to prepare a contribution of this subject, I naïvely thought that the effort would be a straightforward one and that I could report a complete and acceptable phylogeny of the Decapoda. The issue, naturally, is a lot more complicated than I thought. While

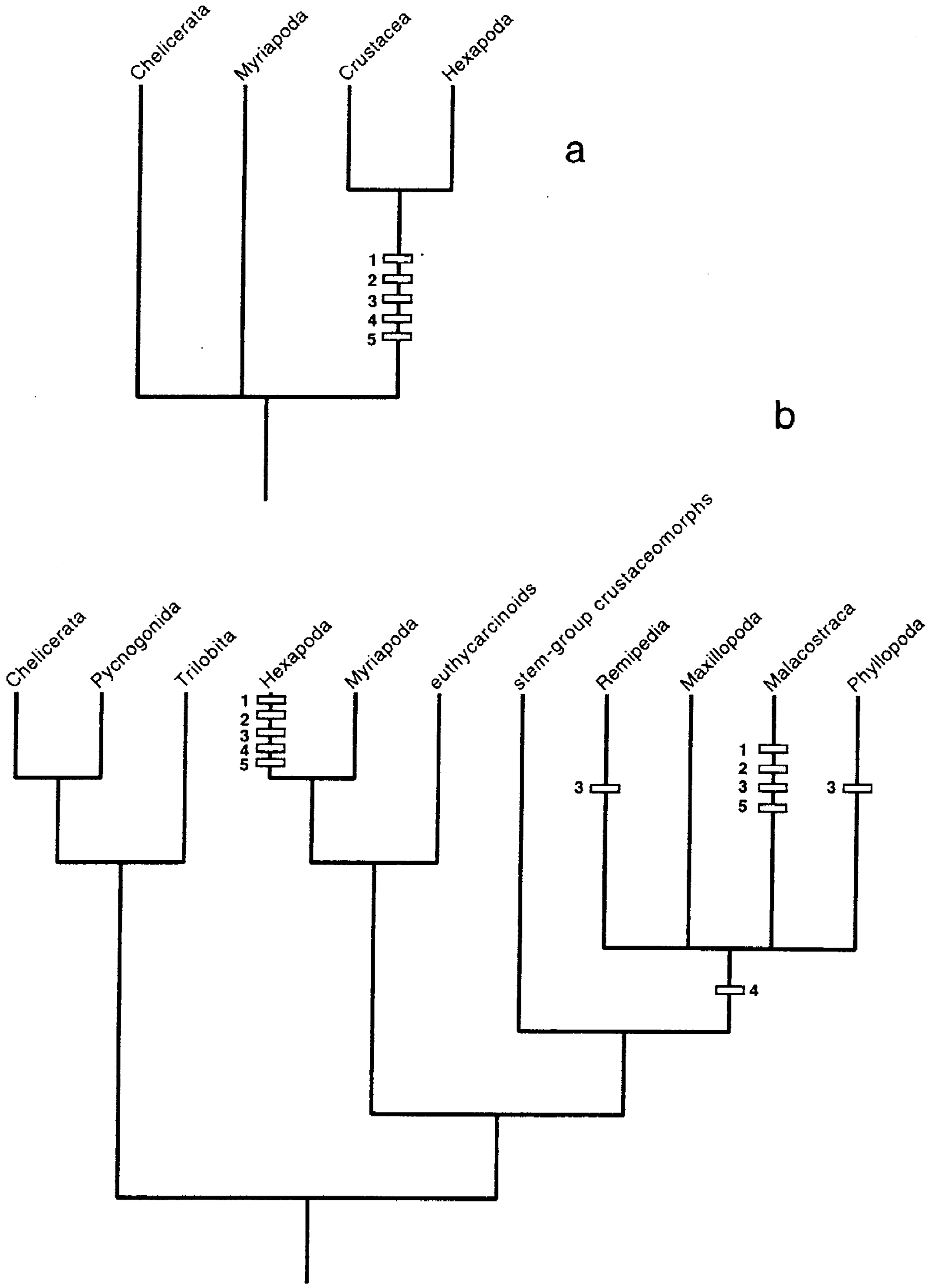

Figure 2. Hypothetical cladograms from Schram & Jenner (2001). (a) A very restricted (pruned) phylogeny of arthropods, and (b) a more comprehensive phylogeny including different crustacean types, pycnogonids and fossil arthropods. Although a particular set of characters may indicate an apparently well-supported clade, addition of other taxa, especially fossil groups, can in fact suggest a distinctly different alternative hypothesis. 1: complex neural chiasmata; 2: pattern of axon growth; 3: distinctive mitochondrial gene order; 4: ommatidia composition in compound eye; 5: neuroblast form. (For details, consult Jenner & Schram, 1999.)

Table 2. Classification of Decapoda modified from Schram (1986)

Order Decapoda Latreille, 1803
Suborder Dendrobranchiata Bate, 1888
Superfamily Penaeoidea de Haan, 1849
Superfamily Sergestoidea Dana, 1852
Suborder Eukyphida Boas, 1880
Infraorder Procarididea Felgenhauer & Abele, 1983
Infraorder Caridea Dana, 1852
Suborder Euzygida Burkenroad, 1981
Infraorder Stenopodidea Huxley, 1879
Infraorder Uncinidea Beurlen, 1930
Suborder Reptantia Boas, 1880
Infraorder Astacidea Latreille, 1803
Infraorder Thalassinidea Latreille, 1831
Infraorder Palinura Latreille, 1803
Infraorder Anomala Boas, 1880
Infraorder Brachyura Latreille, 1803
Section Dromiacea de Haan, 1833
Section Archeobrachyura Guinot, 1877
Section Eubrachyura de St. Laurent, 1980
Subsection Heterotremata Guinot, 1977
Subsection Thoracotremata Guinot, 1977

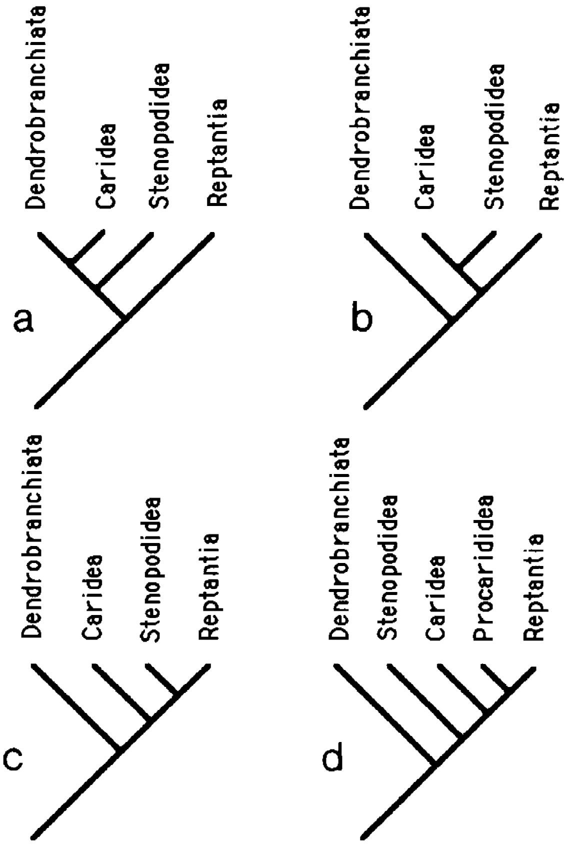

Figure 3. Various hypotheses of relationship among natant decapods. (a) From Borradaile (1907); (b) Burkenroad (1963, 1981); (c) De St. Laurent (1979), Abele & Felgenhauer (1986), Abele (1991); (d) Felgenhauer & Abele (1983). The current consensus favors the tree in (c).

there is a growing consensus about some parts of the decapod family tree, other sectors will take much more work to resolve. However, we are not there yet. For instance, a few years ago, there were several alternative schemes for the relationships of the natantian groups to each other (Fig. 3). Today, one of these is gaining the upper hand (Fig. 3c). Nevertheless, within natant groups, such as the Caridea, work on elucidating phylogenetic relationships is only proceeding very slowly (e.g. see Christoffersen, 1987, 1988, 1989, 1990).

The central core for all this right now remains morphology. There are other important sources of information to be sure, as will be seen below. However, at this time, morphology still forms the only comprehensive database. In this regard, a major step forward occurred with the publication of the overview of Scholtz & Richter (1995). While their treatment focused on the phylogeny of the Reptantia, their inclusion of a wide array of out-group taxa ensured that the basis existed for a more comprehensive analysis. The investigation of Scholtz & Richter (1995) employed the ‘Method of Hennig,’ essentially a paper and pencil approach that relies on the *a priori* recognition of ground patterns. They employed some 63 binary characters to sort 44 in-group taxa and polarised their data set employing 6 out-group species. This resulted in the recognition of 7 monophyletic clades [Polychelida (Achelata (Homarida (Astacida (Thalassinida (Anomala, Brachyura)))))] in an essentially asymmetrical cladogram (Fig. 4). The relationships seemed well supported, except for the position of the Astacida, for which Scholtz & Richter (1995) could not choose between it being a separate clade positioned between the Homarida and the Thalassinida, or a sister group to the latter.

Examination of the character set of Scholtz & Richter (1995) uncovered some duplication of features: e.g. their characters D3 and J3, which both deal with a lack of chelae on pereiopods; or G1 and L5, which both involve the mobility of the last thoracic sternite, the so-called ‘fractostern,’ a most important feature in their matrix. In addition, some binary fea-

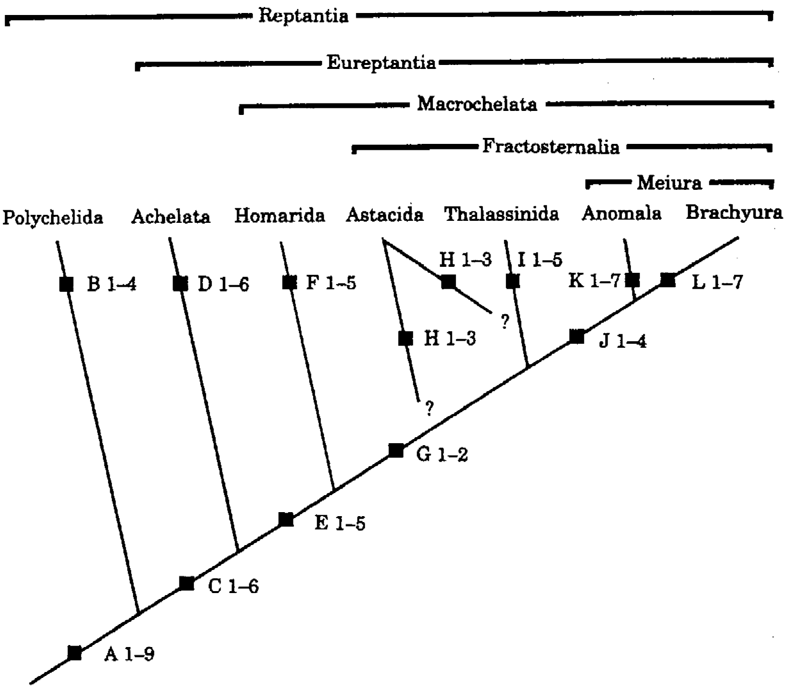

Figure 4. Cladogram of relationships of the Reptantia with suggested names of inclusive clades. For details of apomorphic features consult Scholtz & Richter (1995).

tures that deal with larval types (B4, D6, F4 and H3) result in inappropriate character scorings when employed separately and require a multi-state approach to establish consistency. Even so, a conversion of their raw data into a numerical matrix suitable for a parsimony analysis by PAUP* 4.0 resulted in a duplication of their original result (Fig. 5), with some exceptions. Astacida definitely emerged as a separate clade, sister to all the other Fractosternalia. However, relationships within the Homarida are far from absolutely clear. *Enoplometopus debelius* emerges as a separate clade in a strict consensus tree, something already suspected as a possibility by Scholtz & Richter (1995: 319), while the rest of the Homarida remained unresolved. Only in a 50% majority rule tree (not shown), in which *Thaumastocheles zaleucus* appeared in a separate clade between the Homarida and the Fractosternalia, do the rest of the Homarida occur as a resolved clade. However, a problem arose at this stage in my analysis in that because of the great redundancy in the taxon list, some 32 700 trees resulted before a memory overload occurred. So, while the main clades of Scholtz & Richter (1995) appeared for the most part in the final result, no resolution was possible of course within clades.

To facilitate the use of the database of Scholtz & Richter (1995) with additional taxa, and to allow incorporation of new features, I recast the 63 original characters to eliminate redundancies and inappropriate scorings to yield a base list of 59 features. I then took the features from Burkenroad (1981) and added them to the character list where appropriate to arrive at 65 characters. This allowed the natant out-group taxa of Scholtz & Richter (1995) to be taken into the analysis, with *Euphausia* sp. then serving as a new out-group. The resulting 14 400 trees duplicated the results earlier for the Reptantia alone and also arranged the natantians into a transition series near the base of the tree (Fig. 6).

The next step was to remove the redundancy of the taxon list by removing taxonomic equivalents (Wilkinson, 1995). Representative species were selected for the clades that had consistently appeared up until this point. After that was done, some 18 trees resulted, although the resolution among the basal natantians evident in the previous analysis disappeared (Fig. 7). *Enoplometopus debelius* continued to appear in a separate clade. At this point, though the character set certainly can be refined further, I believe that we have a basic data set that can begin to be employed 'exper-

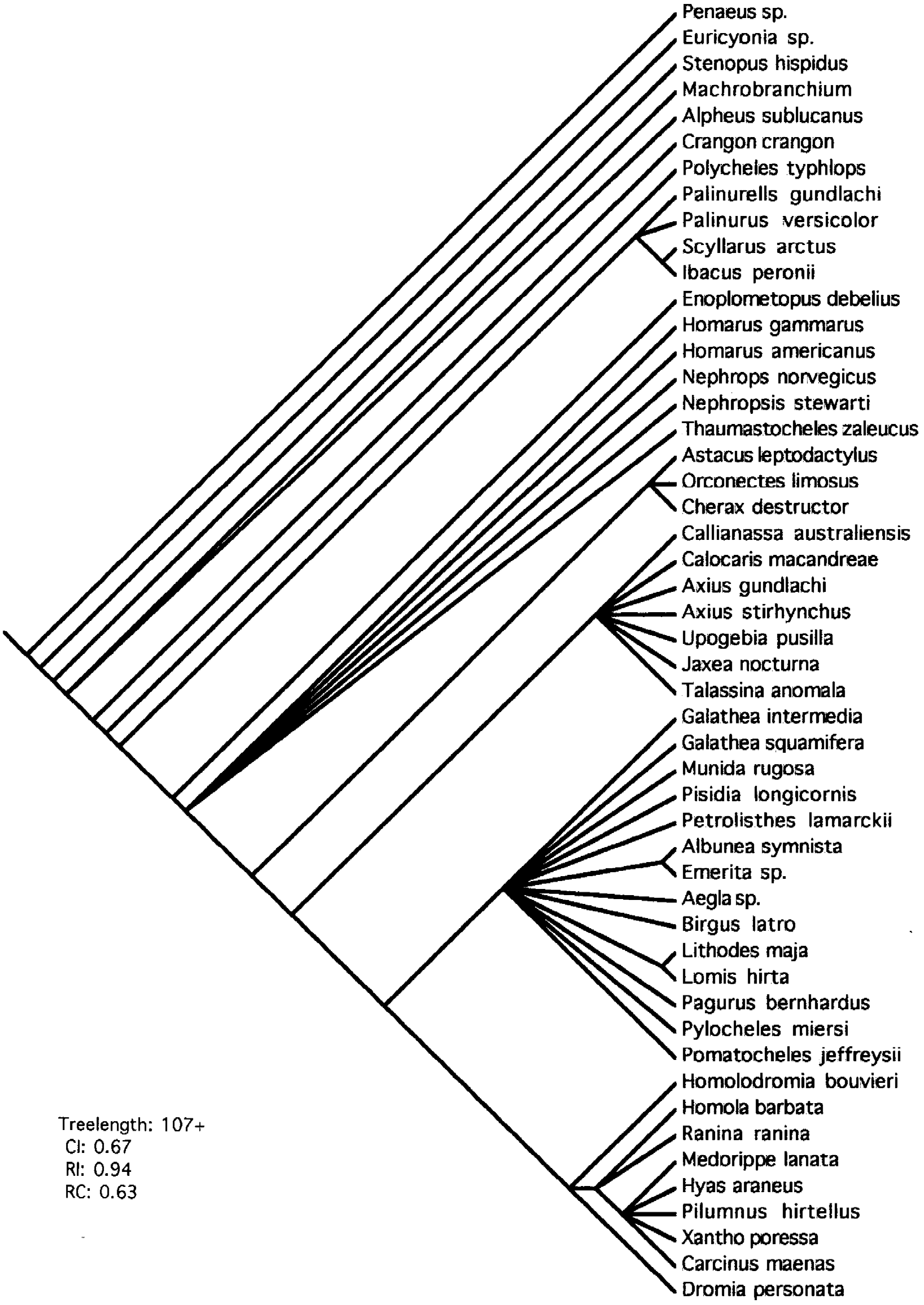

Figure 5. The strict consensus of 32 700 trees of Reptantia that resulted from the analysis with PAUP* 4.0 of a data matrix derived directly from that of Scholtz & Richter (1995). Diagonal format employed to emphasize polychotomies.

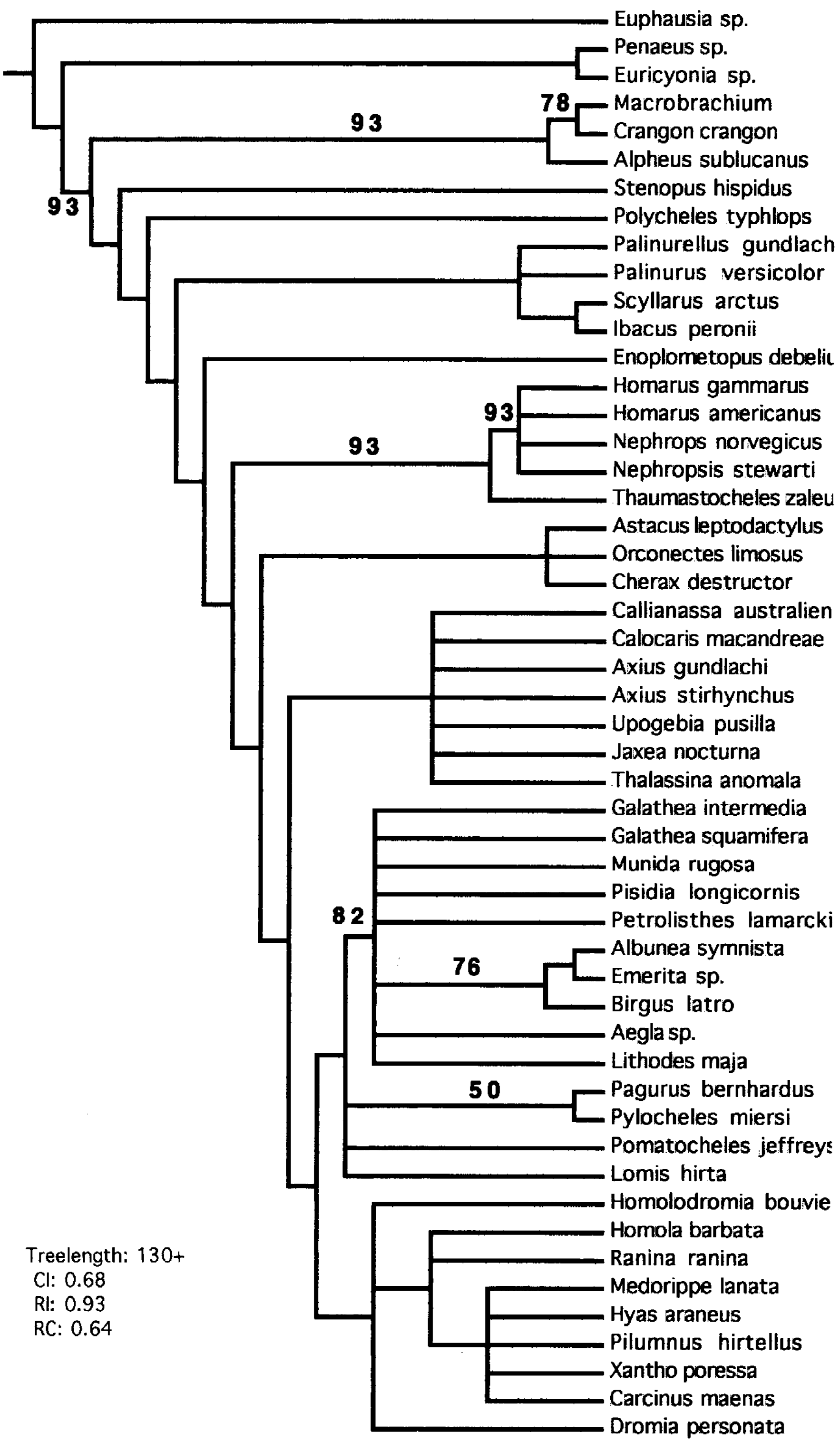

Figure 6. The 50% majority rule tree of 14 400 trees of Decapoda resulting from a reconfigured character set from that used in Figure 5 (see text for details) employing the features derived from Scholtz & Richter (1995) with the addition of characters from Burkenroad (1981). All branches 100% unless otherwise noted.

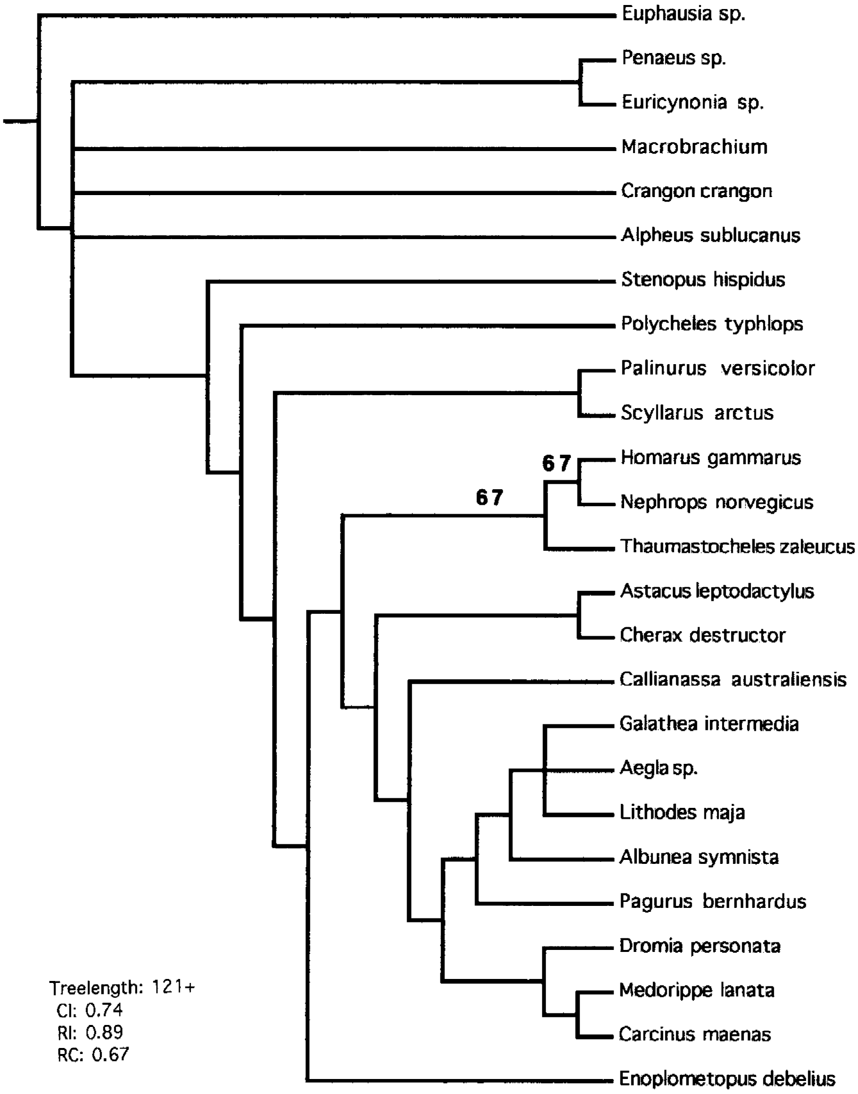

Figure 7. The 50% majority rule tree of 18 trees of Decapoda resulting from a reduced taxon list (same characters used in Fig. 6). All branches 100% unless otherwise noted.

imentally.' Toward that end, I decided to assess the position of taxa, both fossil and living, not included in the original set. As a test, I scored *Neoglyphea inopinata* for the features in my character list. In most classic schemes (Table 1), the Glypheoidea are included within the Palinura, and thus I expected to see *Neoglyphea* emerge fairly low in the tree. However, in this case (Fig. 8), *Neoglyphea* appeared in a polychotomy with higher fractosterns! Scholtz & Richter (1995: 304) suggested as much. Admittedly, my initial scoring of characters was based only on my reading of the excellent description and illustrations of Forest & De Saint Laurent (1981). However, study of the type specimens and related skeletal preparations made by De Saint Laurent in the collections of the Paris Museum confirmed that *Neoglyphea inopinata* in fact possesses the two diagnostic apomorphies of the Fractosternalia, an articulated eighth thoracic sternite or fractostern, and a secula with three sclerites.

Nevertheless, the results of the analysis so far indicate two things. We may agree about the sequence of clades among natantians and that there is a clade Meiura high in the tree. However, the evolutionary events and relationships among the 'macrurans' in the middle of the tree will require a great deal more investigation. The answers may not be easily forthcoming

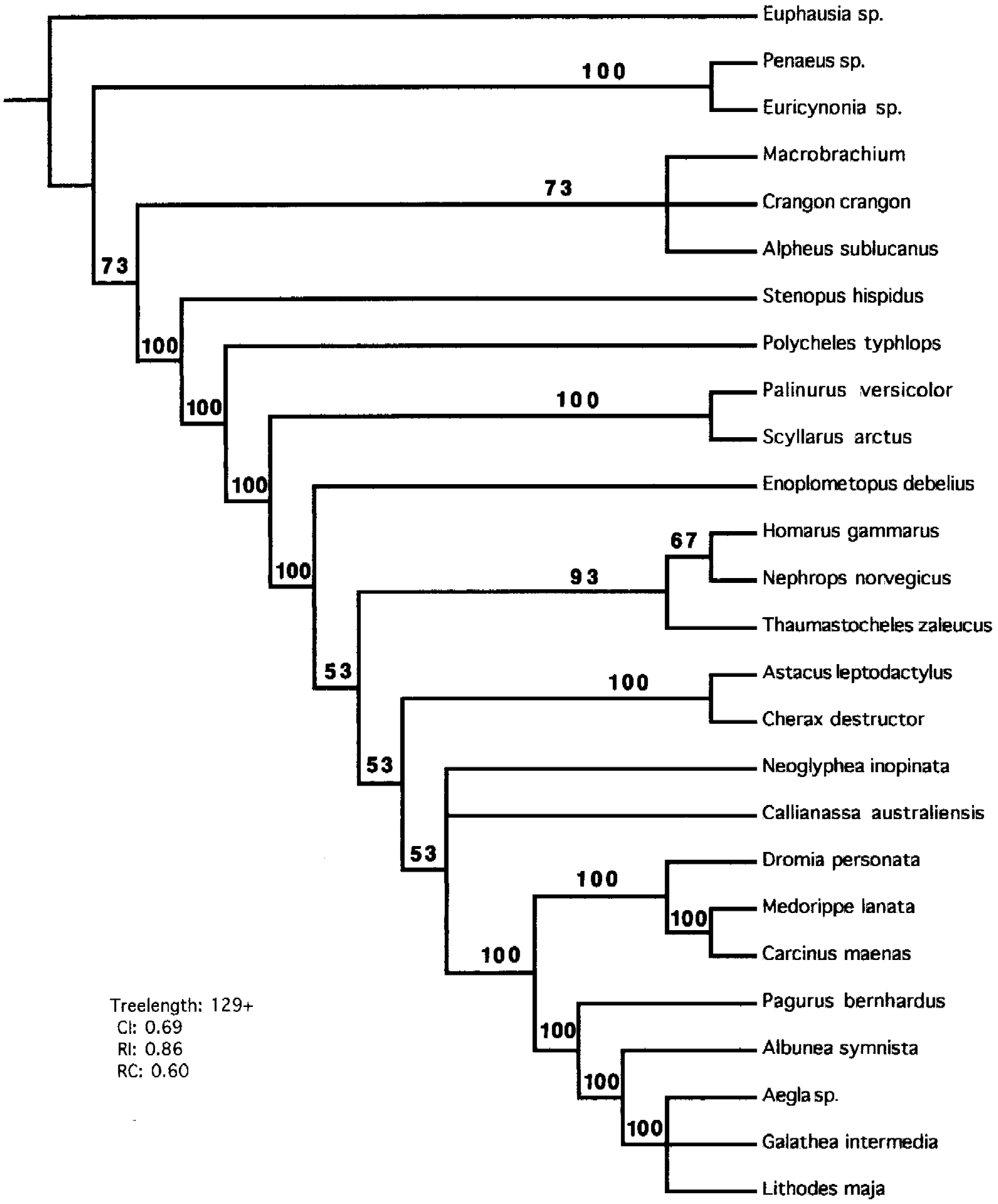

Figure 8. The 50% majority rule tree of 45 trees of Decapoda resulting from the same data set as Fig. 7 except for the addition of *Neoglyphea inopinata*.

either, since an important source of information about biodiversity in this part of the tree will have to be based on fossils. The fossil taxa could be difficult to compare directly with the wealth of information available from examination of living forms. Nevertheless, if we recast the tree of Figure 8 into a stratigraphic context (Fig. 9), we can see that a tremendous number of discoveries in the fossil record of decapods await us.

Anomala: the use of different sources of evidence

The issue of Anomura and Anomala have vexed carcinologists almost since the word 'Go' (for a summary, see McLaughlin & Holthuis, 1985). Nevertheless, a fine example of the wide range of studies that are going on relevant to decapod phylogeny is provided by study of the Anomala. McLaughlin (1983a, b) began to deal with the issue of relationships from a morpho-

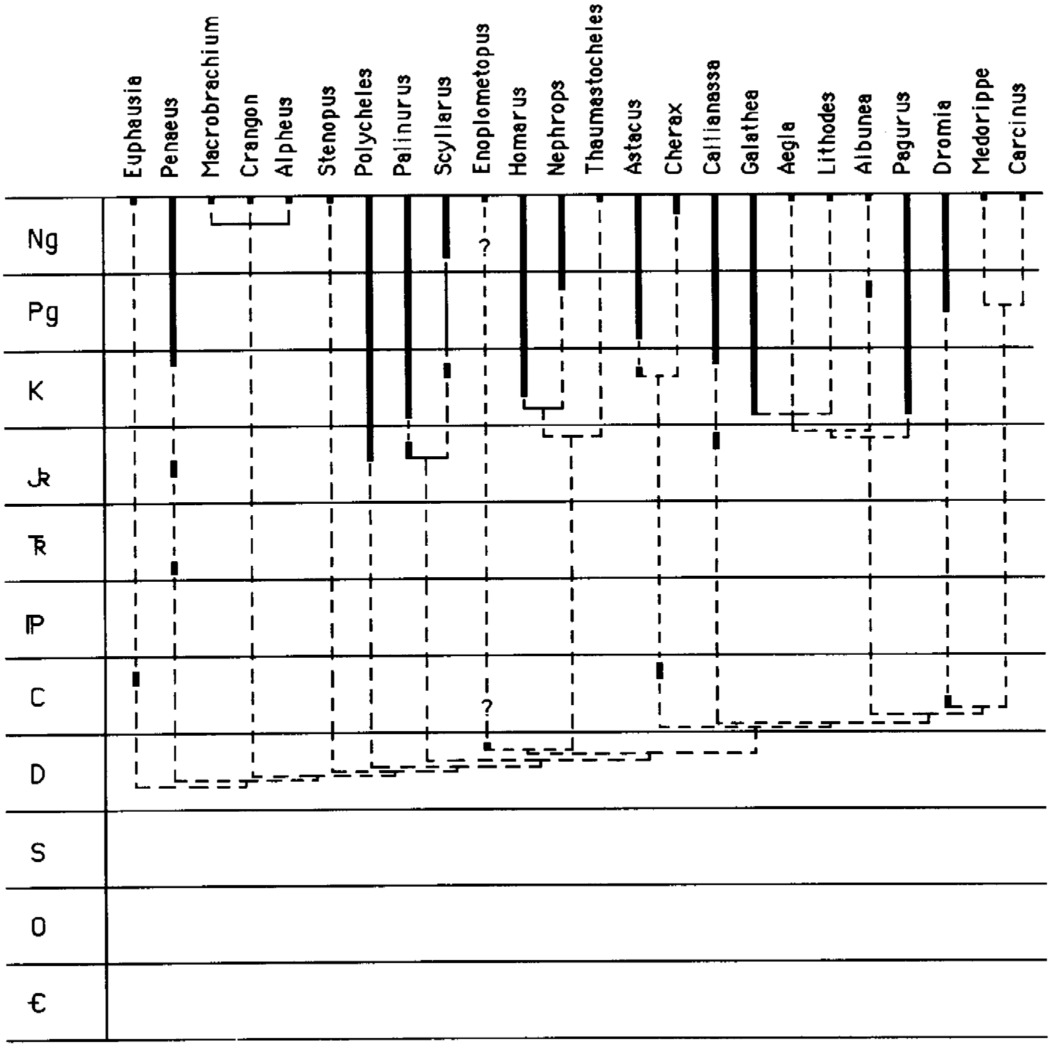

Figure 9. The tree of Fig. 7 rendered into a stratigraphic context. The Carboniferous euphausiacean is linked to certain possible such fossils known from various Coal Age Lagerstatten (see Schram, 1986), and the Carboniferous astacidan is suggested from probable burrows of such (see Hasiotis, 1999). For the sake of convenience, the Devonian 'lobster' genus *Palaeopalaemon* is linked to *Enoplometopus*, although the basis for this must be further explored. The carboniferous dromiacean based on the genus *Imocaris* (see Schram & Mapes, 1984). Note the considerable array of ghost ranges and phantom lineages (dashed lines). Question mark indicates uncertainty about linking *Palaeopalaemon* with the living enoplometopids.

logic perspective in examining the position of *Lomis* and exploring the question of 'what is a hermit crab?' Along these same lines, i.e. focusing on individually important taxa to extrapolate to larger scale issues of phylogeny, Martin & Abele (1986) proposed a family level phylogeny for Anomura that grew out of their study of the genus *Aegla*.

The analysis of Martin & Abele (1986) recognized separate thalassinidean and anomalan clades. However, their study illustrates quite effectively several very important issues of concern. First, they produced a well-resolved phylogeny of 'anomuran' families. However, in doing so, they got out exactly what they put into it. The data were analysed at a family level, and what they achieved was a phylogeny of families. As we will see, analyses by other authors at a genus and species level (e.g. see Richter & Scholtz, 1994) have called into doubt some of the families and superfamilies within the Anomala. One needs to be careful how data are entered into any computer-driven phylogenetic analysis, since it is on the basis of those data that the patterns will be analysed.

Second, Martin & Abele (1986) provide trees derived from both a phenetic UPGMA clustering program and a cladistic parsimony analysis. In doing so, they nicely illustrate the care that needs to be taken with programs that group on the basis of strict similarity, i.e. phenetic analyses, since such approaches fail to sort out relationships among 'primitive' groups, often lumping them into clades near the bases of trees. Thus false signals of monophyly may be indicated, when paraphyly may in fact more accurately describe the relationships.

Third, a phylogenetic analysis can only work with the taxa that are put into the programs. While the Martin & Abele (1986) hypothesis for anomuran phylogeny would appear to emerge as indeed very robust, with lots of congruent characters supporting branches, it is essentially a phylogeny of *only* anomurans rooted to a phylogenetically distant genus *Penaeus*. In these analyses, clades are drawn based on either shared derived features, or degrees of similarity of the taxa given. If more proximal out-groups were utilized, or if additional taxa, in this case brachyurans, were used to effectively sort relationships among an entire potential monophylum, what we could call in the terminology of Scholtz & Richter (1995) the Fractosternalia, it is possible that other hypotheses of relationships could have emerged. Martin & Abele (1986) is a fine study, and I have no argument at all with their results, which are explicitly presented as hypotheses only. However, we all need to keep in mind the nature of the data we put into these analyses, both in terms of the characters as well as the taxa (Jenner & Schram, 1999).

Unless we perform comprehensive cladistic analyses, we cannot be sure that we are in fact dealing with monophyla. Tudge (1997) employed an entirely different source of data towards elucidating relationships of 'anomurans' when he examined ultrastructure of sperm and spermatophore morphology. Although the principal focus was directed at 'anomurans,' a wide array of decapods including astacids, homarids and brachyurans were also analysed. Even though the character set was narrowly cast towards sperm only, the resulting tree structure is interesting (Fig. 10). Thalassinideans emerge as polyphyletic and, while Anomala itself is monophyletic, most families of anomalans are either para- or polyphyletic. The wide range of taxa used, grounded in a rather comprehensive database of characters yields *a* phylogeny and certainly indicates that spermatozoan ultrastructure will be an important source of data in more comprehensive, total evidence approaches to the issues of anomuran phylogeny.

Finally, there are times in which restricted analyses can be useful. Cladistic analyses need not always be directed at producing a phylogeny *per se*. McLaughlin & Lemaitre (1997) were actually only interested in assessing old ideas about the processes and occurrences of carcinization. Their data were collected and analysed at a generic level and might appear to 'demolish' many well-established family and superfamily taxa. However, the authors caution that what they focused on in the analysis were only features directed at assessing degrees of carcinization and not the total array of hard morphological features that might have been employed in a more comprehensive analysis. McLaughlin & Lemaitre (1997) arrived at a fresh understanding of what carcinization actually represented, and in the process they clarified the supposed relationship between lithodids and pagurids.

Brachyura and the use of molecules and sperm

No treatment of decapod phylogeny can escape consideration of molecular issues. However, up until this point, there have been relatively restricted uses of molecular sequence data, although the number of research groups generating and using sequence data is growing. For example, Kim & Abele (1990) and Abele (1991), as part of a larger program to address crustacean phylogeny with 18S rRNA and 18S rDNA data (e.g. see Spears & Abele, 1997), examined the relationships of natant taxa to each other using a limited data set and largely confirmed the results derived from morphology (Abele & Felgenhauer, 1986).

However, one area of study where I believe molecule sequences will be of immense help will be in elucidating the phylogenetic relationships of Brachyura. Ever since the benchmark work of Guinot (1978, 1979), which recognized three groups of brachyurans based on location of male gonopores, the phylogeny of the Brachyura has attracted strong interest. Very quickly after Guinot, De Saint Laurent (1980a, b) elucidated the essentially paraphyletic nature of Guinot's Podotremata while offering a caution against relying too heavily on gonopore locations alone. Subsequently, Spears et al. (1992) using 18S rRNA confirmed the paraphyly of the podotremes (Fig. 11). However, Guinot et al. (1994) in examining sperm structure in Homolidae concluded that a podotreme type sperm could be characterized and thus used

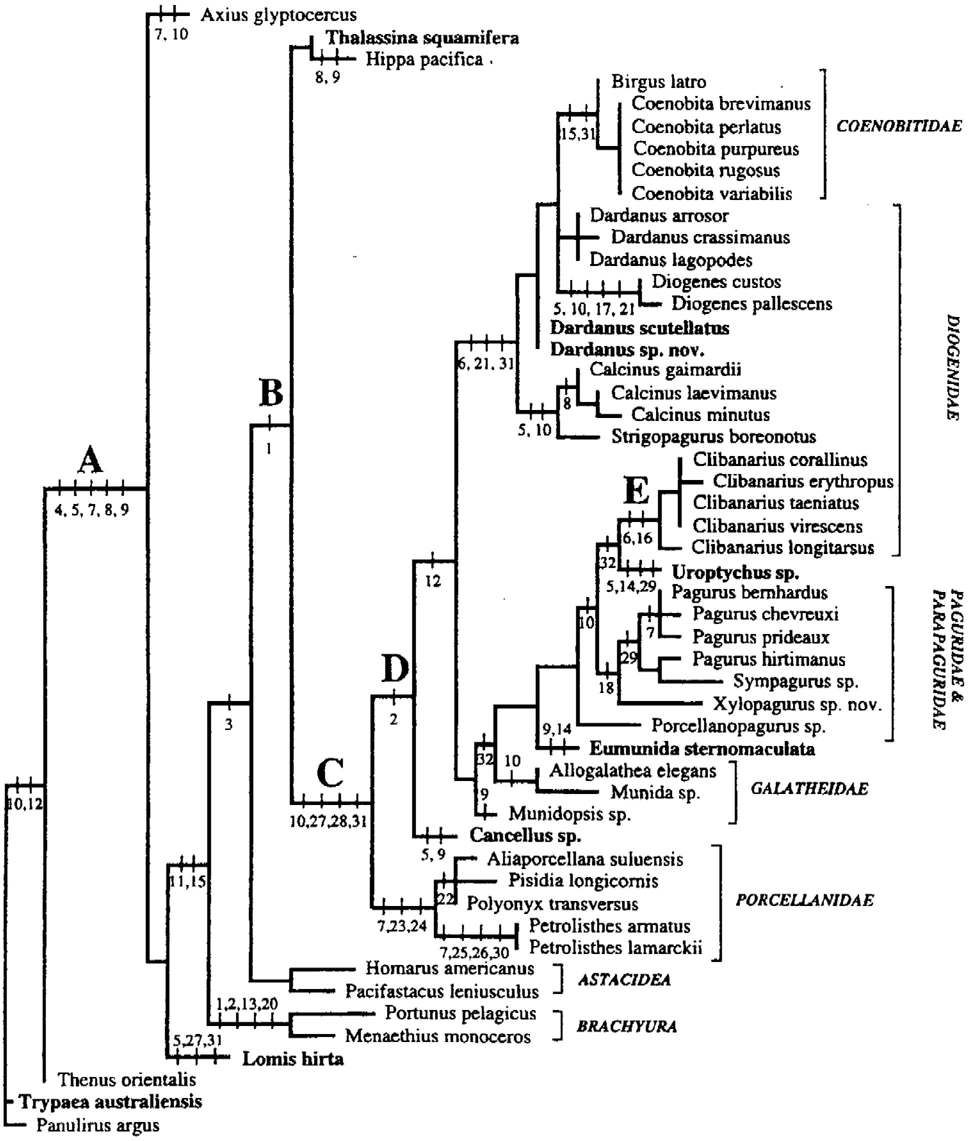

Figure 10. A phylogram for anomurans of a 50% majority rule tree derived from 26 equally parsimonious trees based on analysis of only spermatologic features (see Tudge, 1997 for details). Note the polyphyletic Thalassinida with this data set. Also, while Anomala is monophyletic, the constituent families are mostly para- or polyphyletic.

to justify a monophylum Podotremata. Nevertheless, Guinot et al. (1998) pointed out that, while a dromiacean sperm type could be defined, neither Dromiidae nor Dynomenidae would appear to be monophyletic based on sperm characters alone. Clearly, more comprehensive studies of sperm and molecular sequences of rDNA are needed.

Moreover, within the Heterotremata and Thoracotremata, the situation is far from resolved. The old, classic Sections of the Brachyura from Borradaile (1907) no longer seem very effective. Most authorities these days settle for grouping families within more inclusive superfamilies. However, nested sets of relationships remain obscure. Recently, Schubart et al. (2000) have begun to build a database of 16S rDNA for Eubrachyura with some intriguing results (Fig. 12). While the thoracotremes cluster in a monophyletic clade (with a problematic inclusion of pinnotherids), the heterotremes as a whole would appear to be characterized as more-or-less paraphyletic. This is not a

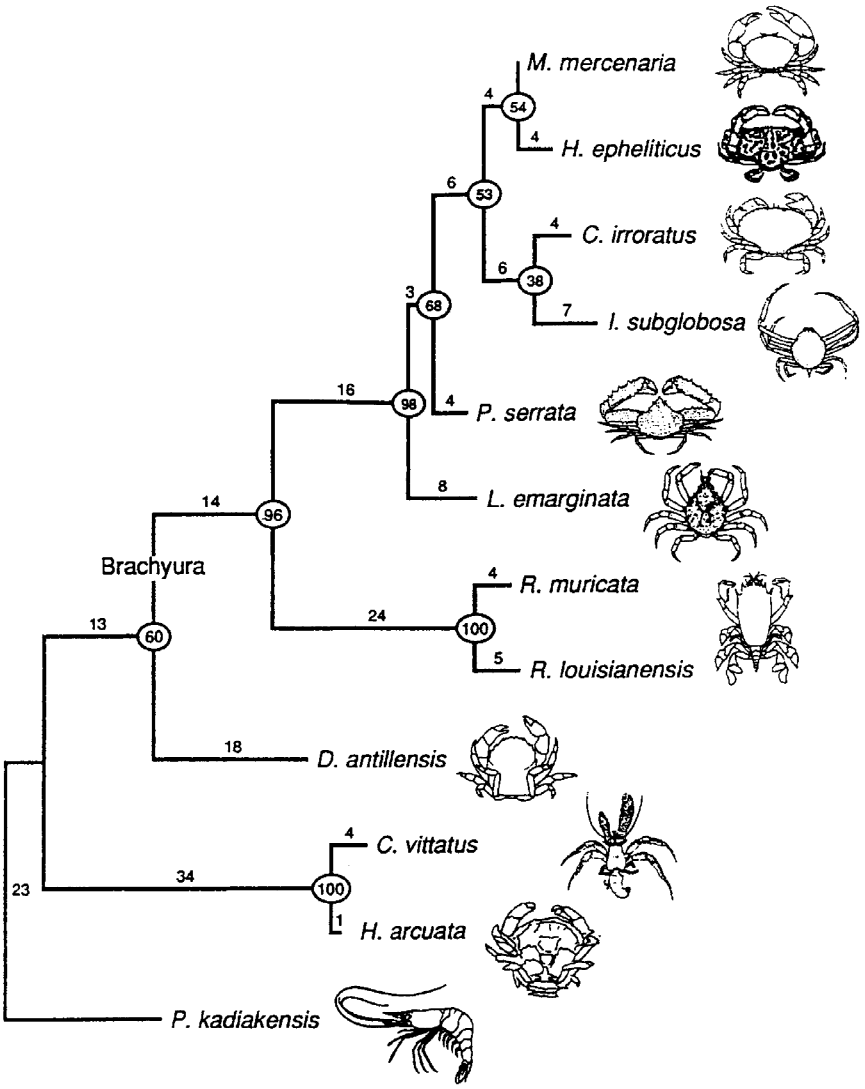

Figure 11. The inferred relationships of Meiura, with the number of steps indicated for each branch, based on analysis of 18S rRNA and confirming the para- or possibly even polyphyletic nature of the podotrematous brachyurans (from Spears et al., 1992). Circled numbers indicate bootstrap values.

complete analysis of all families, although the authors have done additional work (Schubart, pers. com.), and the authors need to include additional relevant outgroups. However, current sequence banks for even 18S rDNA do not contain a full array of brachyurans. Such comprehensive analyses from several molecules will be necessary before we can seek a solution to this problem. In addition, there is no reason to doubt that a more broadly based examination of brachyuran comparative anatomy (cf. Von Sternberg et al., 1997) and larvalogy (in the manner of Rice, 1980, 1983) could make contributions as well towards a final synthesis.

Astacida: a focal point of many problems

Let us return to that array of macrurans in the middle of the decapod tree that will probably continue to give us trouble for some time to come. In particular, I want to focus on the Astacida, the crayfish. An intriguing group, they seem to encapsulate in one taxon a great many problems we will have to come to grips with in our quest for consensus over decapod phylogeny.

First of all, there is a problem with their apparent age (see Fig. 9). The earliest body fossil crayfish are Mesozoic and include the extinct families

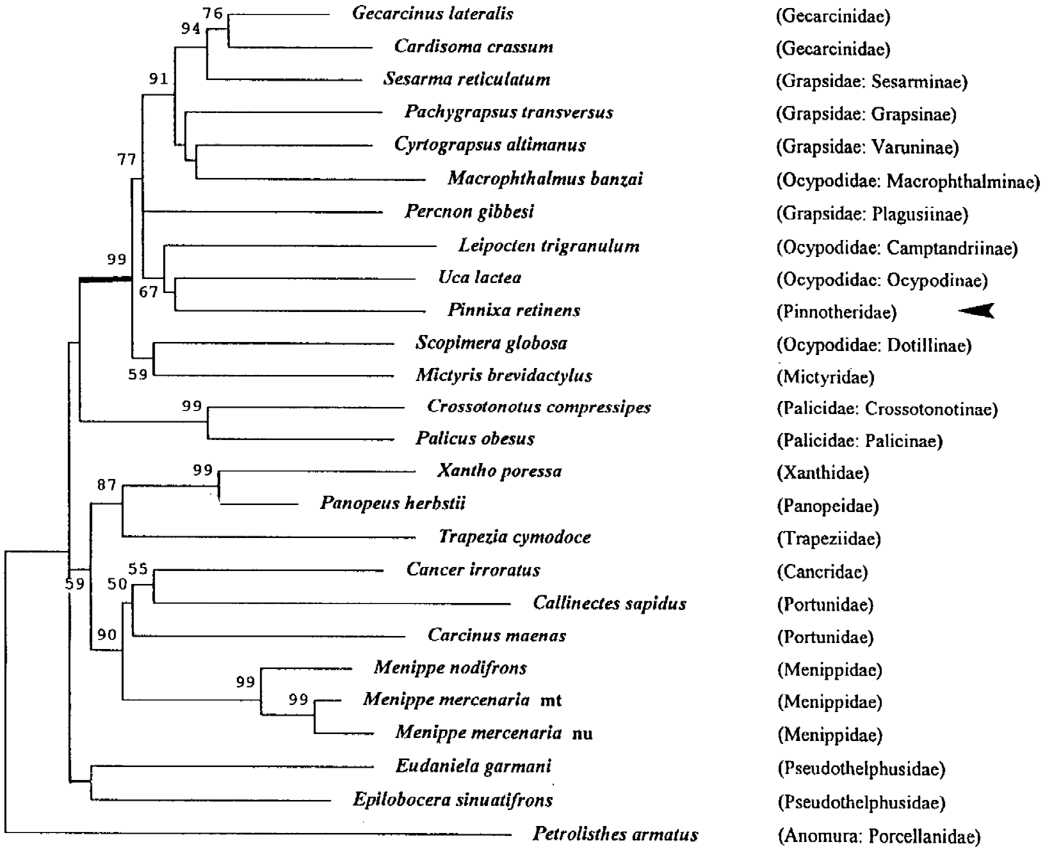

Figure 12. The pattern of relationships among several brachyuran families based on analysis of 16S rDNA (from Schubart et al., 2000). Numbers represent confidence levels from an internal node test. The clade of Thoracotremata marked with heavy black line. While the analysis is not a comprehensive one for all families of Eubrachyura, it is interesting to note the possibility of the paraphyletic nature of Heterotremata (if not polyphyletic, note arrow for heterotrematous pinnotherids).

Protastacidae Albrecht, 1983 from the Jurassic and Cretaceous of Germany, and the Cricoidoscelosidae Taylor et al., 1999, from the Cretaceous of China, both families whose status needs to be critically evaluated. However, the group seems much older than this. Kowalewski et al. (1998) report trace fossils of crayfish burrows from the Triassic, and Hasiotis (1999) even records similar burrows from the Late Pennsylvanian indicating an origin for Astacida probably sometime in the Early Carboniferous. Thus, it would appear that we lack body fossils for more than half of crayfish history, missing information that undoubtedly would lend some insights into the origins and early anatomical evolution of the crayfish.

We might have guessed this was so from consideration of crayfish biogeography alone. The distribution of modern forms (Fig. 13) has always been cited as a classic example of 'disjunct distributions.' Indeed, examination of the pattern based solely on the present day arrangement of the continents makes it difficult to develop logical scenarios to explain the evolution of the group. However, if that same modern distribution is plotted on a paleogeographic map of the Triassic (Fig. 14), the anomalies from the modern geography begin to disappear. One could postulate that the Astacidae were a subtropical to north-temperate family, extending from what is the present northwestern United States across Canada and Greenland into what is today Europe. The Cambaridae appear to have been a tropical to subtropical group in waters across the paleo-equator of Pangaea, connecting perhaps in habitats along the northern coast of the Paleo-Tethys Ocean to what is today eastern Asia. This confirms that the Superfamily Astacoidea is certainly Laurasian in origin (Scholtz, 1995a, 1998, 1999). The Parastacidae are clearly a south-temperate family, occupying freshwater habitats of Gondwanaland. One could in fact use the inferred paleogeographic distri-

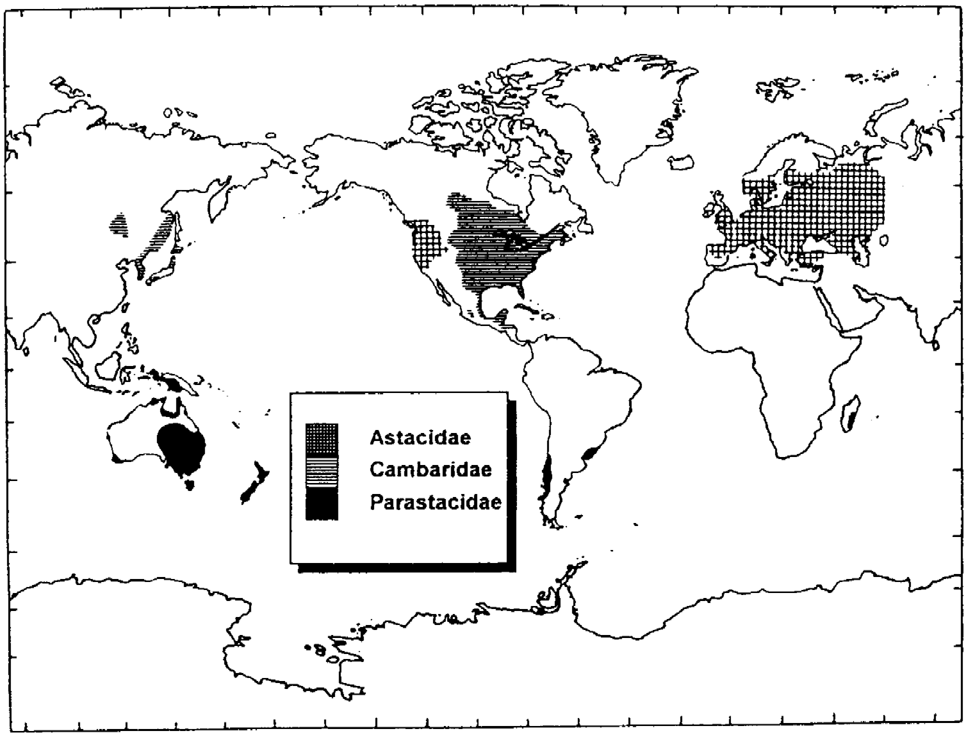

Figure 13. Modern distribution of crayfish families (from Holdich, 1999).

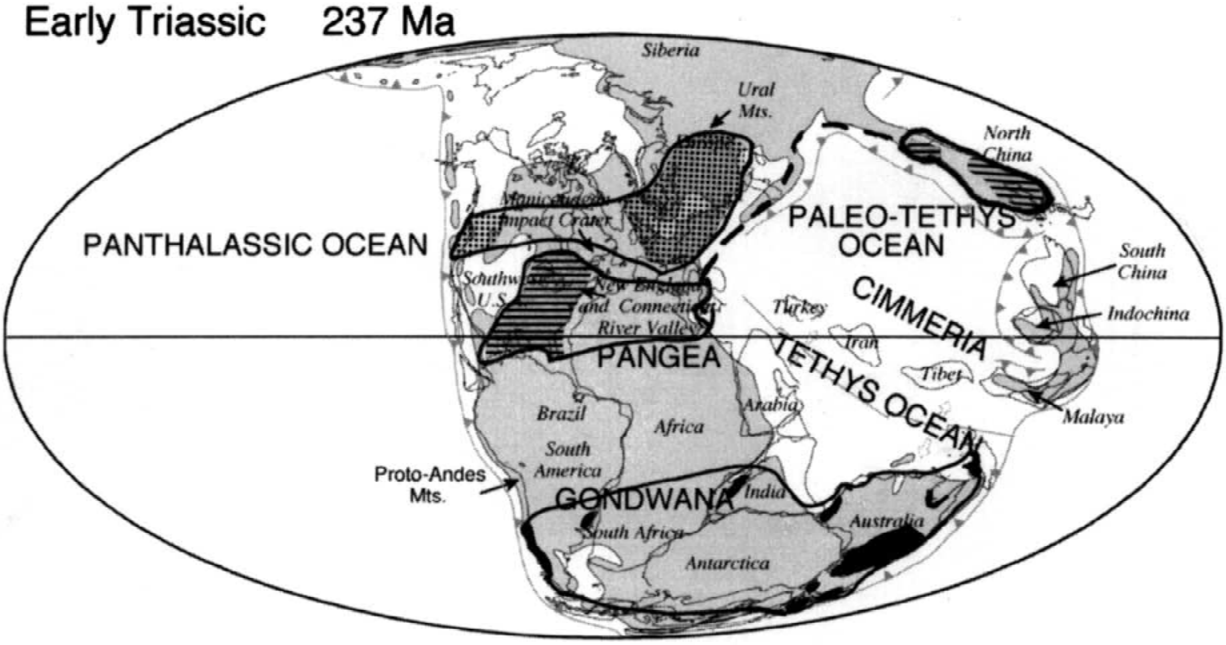

Figure 14. Modern distribution of crayfish families plotted on a paleogeographic map of the Triassic (from Scotese, 1997). Three tracks can be discerned: (1) a subtropical/north-temperate track of Astacidae; (2) a tropical subtropical Cambaridae; (3) south-temperate Parastacidae. Fossil representatives of these families might be expected in the intermediate areas included within the heavy black lines in any time periods since the Early Triassic.

butional tracks to predict areas where explorations for crayfish fossils should be carried out. Given the inferred Triassic distribution, it seems obvious that the origins of the group would have to be sought in pre-Triassic time, as already suggested by Scholtz (1999), giving credence to the claim of Hasiotis (1999) for Carboniferous crayfish burrows. Obviously, we have a great deal more to discover about the history of crayfish.

Despite the work of Scholtz & Richter (1995), the elucidation of relationships within Astacida is still tied to the old idea of Astacidea [= erymids + nephropids + astacids + cambarids + parastacids]. As an example, Tshudy & Babcock (1997) performed a phylogenetic analysis of 'clawed lobsters.' They rooted their tree to *Eryma* as an out-group and recognized two families: the Nephropidae Dana, 1852, which includes the fossil and living marine, clawed lobsters, and a new family, the Chilenophoberidae, an amalgam of Mesozoic 'proto-lobsters.' However, within the Chilenophoberidae they included *Pseudastacus*, a Jurassic genus from Germany. As mentioned above, Albrecht (1983) placed the Protastacidae within the true crayfish. The status of the Protastacidae presents problems. One could question whether these are crayfish. First of all, they are marine taxa. In addition, their carapace groove pattern is really erymid, or clytiopsid, in pattern, and what little can be discerned of the tail fan is not particularly crayfish like. A close reading of Albrecht (1983) reveals that he is an evolutionary systematist and still writes of trends and grades. A rigorous cladistic analysis of his information would more than likely not give the pattern he envisioned. The Tshudy & Babcock (1997) database is more inclusive than the features employed by Albrecht (1983), who focused almost exclusively on a selection of the carapace grooves. Nevertheless, at the very least it is clear that despite our best efforts to produce careful analyses of relationships we still often lack any certain knowledge of what taxa constitute monophyletic groups.

A computer, or a person, given any array of taxa and a selection of characters, can produce on command *a* phylogenetic tree. The question is, does the tree mean anything? One must be very careful. A tree is a tree – a pictorial representation of a matrix of information. It is only as good as the information that goes into the matrix. One must focus on identifying monophyletic groups because not to do so is to run the risk of getting paraphyletic or even polyphyletic groups out of a cladistic analysis conducted without due regard for fundamentals (Jenner & Schram, 1999). Without attention to this crucial issue, we will never be able to sort out the relationships among the macrurous Reptantia.

The origin of Decapoda

The issue of paleogeography emerges again in connection with the origin of Decapoda. That event undoubtedly lies in the deep recesses of the Palaeozoic. The earliest known decapod is *Palaeopalaemon newberryi* in the Upper Devonian of North America (Schram et al., 1978), a macrurous 'lobster' of some kind (Fig. 15). That species is not too far away in time from the fossil species *Imocaris tuberculata* from the Mississippian (Lower Carboniferous) of North America (Schram & Mapes, 1984), which appears to be a dromiacean. The appearance of the Eumalacostraca in the fossil record is abrupt (Schram, 1981a, 1983) – a classic punctuated event. However, a hint as to what could have happened is to be gotten from the paleogeography of contemporaneous trilobites.

When Eldredge was developing his allopatric model of speciation in the Middle Devonian phacopid trilobites (Eldredge 1971, 1972, 1973), he charted the paleogeographic and paleohabitat preferences for his species and subspecies of *Phacops*. His conclusions about allopatric population shifts across the Devonian seas of North America of course ultimately lead to the well-known concept of Punctuated Equilibrium. Eldredge (1974) postulated an allopatric model where changes in anatomy occurred quite rapidly in isolated peripheral populations of his trilobites. The main source of the lineage centered on the shallow marginal seas, whose deposits today stretch across the Middle Atlantic States of America. The peripheral isolates can be collected from the contemporaneous deposits further west, located in the Midwestern States extending from Ohio across to Iowa. These latter deposits represent the deeper water epeiric seas further offshore from that of the shallow water marginal seas to the east (Eldredge & Eldredge, 1972).

Why is this interesting for decapods? *Palaeopalaemon newberryi*, our first decapod, is to be found in these deeper, offshore, epeiric sea deposits of the American Midwest, albeit of the slightly younger Upper Devonian. The obvious working hypothesis is that decapods may be scarce in the latter half of the Palaeozoic because their natural habitat up until that point may have been even deeper water. The few decapod

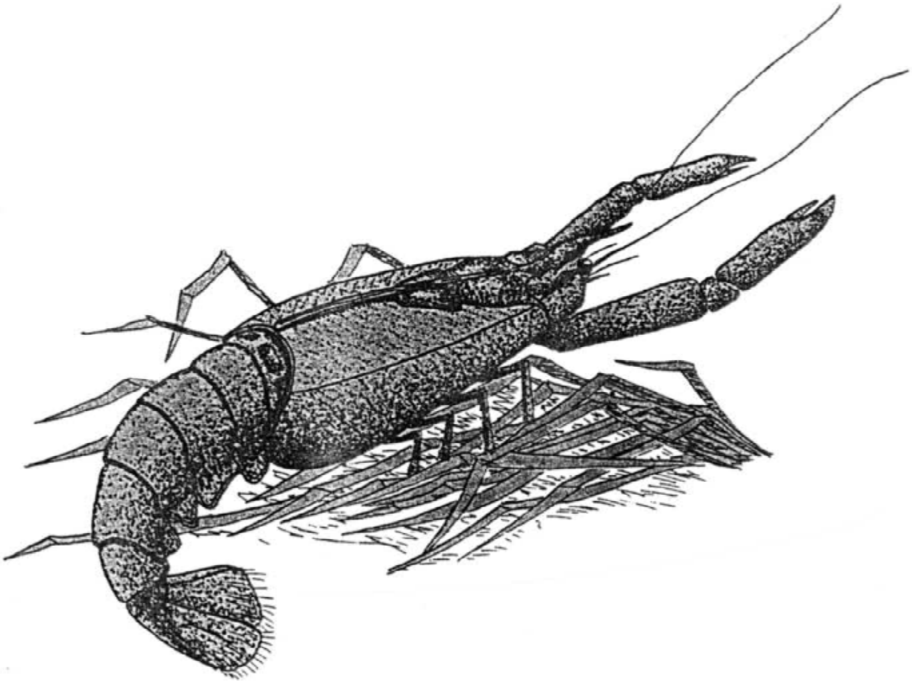

Figure 15. Reconstruction of *Palaeopalaemon newberryi*, the earliest known decapod from the Upper Devonian of North America (from Hannibal & Feldmann, 1985).

species we have in the Palaeozoic – reptantians at that – perhaps are there only because they represent a few pioneer types that ventured up out of the continental shelf and/or slope waters onto the margins of the off-shore, epeiric seas. It is a pattern the reverse of that of the trilobites, which seem to have evolved into the epeiric seas from shallower water.

Probably this model is too simple. Would it also apply to the natant precursors to the Reptantia? What about the origins of other Eumalacostraca? Many of these non-decapod eumalacostracans have a predominantly shallow near-shore, or even fresh water, component (Schram, 1981b) in Carboniferous time. Did these syncaridan, peracaridan and hoplocaridan types also come out of the deep sea? Or did these non-decapod groups have an independent trajectory in shallow, near-shore seas? Again, much needs to be discovered in the Paleozoic fossil record before any consensus can emerge.

Developmental genetics, evolution and phylogeny

Finally, something must be said about the discoveries coming to light from the work of developmental geneticists. This research in regards to crustaceans is just in its infancy. Only a few species relative to the wide morphological diversity of Crustacea as a whole have been studied. Certainly, a great deal more will need to be done in order to get some good insights into the evolutionary history of Decapoda, let alone have any direct significance for consideration of phylogeny. We can summarize a few things here.

Some work has been done on mapping *Hox* gene expression in Malacostraca and relating this to degrees of maxilliped development (Averof & Patel, 1997). However, there have only been limited investigations to date and these studies concern only two of the *Hox* genes, *Ubx* and *abdA*. Nevertheless, what has been seen so far indicates that a concerted effort towards a comprehensive survey and mapping of all *Hox* genes in crustaceans will undoubtedly prove effective towards increasing our understanding of the genetic forces that shaped the evolution of the decapod Bauplan.

More extensive work has been done to elucidate the patterns of expression of *engrailed* (*en*). Aside from basic similarities of *en* expression in the head of crustaceans to the expression seen in insects (Scholtz, 1995b), a peculiar pattern is manifest in decapods. The crayfish *Cherax destructor* displays a total of 9 *en*-

grailed stripes appearing in the course of development in the pleon (Scholtz, 1995c). Whether this represents an autapomorphy for *Cherax* (or even the crayfish), or is the revelation of some underlying primitive pattern for malacostracans is not clear. Furthermore, it appears that the Malacostraca possess a pattern of repeated cell divisions in the ectoderm and mesoderm of the post-naupliar germ band that is unique for arthropods (Scholtz & Dohle, 1996). In connection with this, the malacostracan ground plan seems to include the possession of 19 ectoteloblasts arranged in a ring. Two derived conditions from this ground pattern are recognized. Amphipods have apparently lost the ectoteloblasts altogether, and all crayfish families share the possession of 40 ectoteloblasts (Scholtz, 1993) as a synapomorphy.

These are only tantalizing titbits, but we can only look forward to a considerable amount of undoubtedly important phylogenetic information coming to light in the next several years.

Conclusion

We are nowhere near to approaching a complete consensus on the phylogeny of Decapoda and consequently a universally accepted natural taxonomy of the group. Our understanding of the phylogenetic relationships among the Decapoda has improved in the last 15 years, and at least everyone agrees that we are dealing with a monophyletic group. However, we still are not entirely clear where all the monophyletic groups within the Decapoda sit. While we can have as a working goal the production of a phylogeny for the group as a whole, it would seem efficacious towards this end to concentrate for now on trying to identify the monophyletic groups within the decapods. This can have some immediate benefits in terms of providing a framework for the practical applications of phylogenetic studies in the fields of nature conservation and resource management. The long-term objective will in time emerge of its own accord: a robust, well-supported phylogenetic tree for the order tied to a natural taxonomy of the group.

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