Decapod phylogeny: addition of fossil evidence to a robust morphological cladistic data set

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Abstract

Incorporating fossils into schemes for the phylogenetic relationships of decapod crustaceans has been difficult because of the generally incomplete nature of the fossil record. Now a fairly robust data matrix of characters and taxa relevant to the phylogeny of decapods has been derived from consideration of living forms. We chose several taxa from the fossil record to test whether the robustness of the matrix can withstand insertion of fossils with various degrees of incomplete information. The essential structure of the original tree survives, and reasonable hypotheses about the affinities of selected fossils emerge. Sometimes we detected singular positions on our trees that indicate a high certainty about where certain taxa fit, while under other conditions there are alternative positions to choose from. Definitive answers are not to be expected. Rather, what is important is the demonstration of the usefulness of a method that can entertain and specifically document multiple alternative hypotheses.

Key words: Decapoda, phylogeny, cladistics

Introduction

Taxonomies of Decapoda have typically been constructed either with almost no regard to the fossil record, or, in a few cases, with an extreme focus towards the fossil record. As a result, two very different schools of classification emerged. The first approach, and more widely used, grew out of the system of H. Milne Edwards (1834) with the decapods divided into Natantia and Reptantia, and Reptantia further divided into the traditional groups Astacura, Palinura, Anomura, and Brachyura. The second approach, championed by Beurlen and Glaessner (1930), is much less familiar in its terminology, employing such neologisms as Nectochelida [Stenopodidea + Dendrobranchiata], Gastralida [Polychelida + Achelata + Brachyura + some Anomala], and Anomocarida [Thalassinida + Paguridea + Caridea]. The difference between the two systems is striking.

Nevertheless, by the 1990s the classification of the decapods, having been essentially stagnant for some time, was re-invigorated by Scholtz and Richter (1995), who for the first time used the concepts of phylogenetic systematics (Hennig, 1966) to elucidate the relationships among Reptantia. Scholtz and Richter uncovered some interesting clades, viz., groups they termed Fractosternalia [Astacida + Thalassinida + Anomala + Brachyura], and Meiura [Anomala + Brachyura]. Schram (2001) later computerized their analysis, allowing a more objective view of similar data.

Subsequently, Dixon et al. (2003) in striving to expand the data set of both Scholtz and Richter and also that of Schram increased the taxonomic sampling and improved on the coding of characters to arrive at an unexpectedly different phylogenetic tree, and their analyses suggested a new classification for Decapoda. Fractosternalia were subsumed within Eureptantia as a whole, while three new clades were recognized: Astacura [Glypheoida + Astacidea], Sterroparda [Thalassinida + Eurysternalia], and Eurysternalia [Achelata + Meiura].

While the differences between these most recent efforts to sort out the phylogenetic relationships of Decapoda are noteworthy, they all agree in major ways. A paraphyletic series of natantians leads to a monophyletic Reptantia. This latter is composed of two sister groups: the polychelids, and the eureptantians. The long established taxon Palinura [Glypheoida + Achelata + Eryonoidea] is not a monophyletic group. Anomala is the sister taxon to Brachyura, which together form Meiura, and consequently Anomura [Thalassinida + Anomala] is paraphyletic. If the
result of this work was to challenge the traditional groups of Milne Edwards (1834), defined in terms of extant taxa, then the fossil-based taxa fared no better. No support could be found at all for any of the idiosyncratic groups proposed by Beurlen and Glaessner (1930).

Systematists working with the decapods of course would like a single, stable, useful, widely accepted, (ideally true) classification that can be used for extinct and extant forms alike - the holy grail of carcinology. The only way to achieve this would be to include both extinct and extant taxa in the process of building the tree and the resultant classification.

However, Schram and Hof (1998) found that the addition of fossil crustaceans to a sizeable matrix consisting of both external and internal characters could destabilize the resultant cladograms causing a loss of resolution, a shift in the location of whole clades, and an increase in the number of trees to excessive levels. Yet, fossils contain useful information relevant to determining phylogenetic relationships, and somehow the two sources of data, that from the fossils and that from the modern fauna, must come together to provide a comprehensive picture of the tree of life. The cladogram that emerged from the data matrix developed by Dixon et al. (2003) seemed to be robust and relatively impervious to changes in taxa or character codings, and therefore promised a basis upon which to experiment with the addition of fossil taxa. More importantly, the Dixon et al. (2003) data matrix also provides an opportunity to discover how successful the combination of fossil and recent evidence can be, and thereby lend insights into methodological issues that could be of assistance in clarifying the phylogeny of other groups as well.

Methods

The study of Dixon et al. (2003) utilized a data matrix with 60 taxa and some 70 characters. Wherever appropriate, they combined characters into multi-state features to minimize dependence between characters such that 52 of them were multi-state and 18 were binary. Both unordered and ordered analyses were run, and of the latter 30 them were multi-state and 18 were binary. Both unordered but are effectively both ordered and unordered. It makes no difference whether a two-state character is ordered characters then had too few states to be ordered. Some 70 characters. Wherever appropriate, they combined characters into multi-state features to minimize dependence between characters such that 52 of them were multi-state and 18 were binary. Both unordered and ordered analyses were run, and of the latter 30 characters were removed from the original list of 70. Appendix II provides details of these characters omitted from the Dixon et al. (2003) database and the reasons for their deletion.

Similarly, a number of character states of features in the original matrix were combined or removed because they would not be visible on many fossils. In addition, some characters were uninformative given the reduced number of taxa we employed, and so some states were combined, especially where homology had been shown by the phylogeny of Dixon et al. (2003). As a result, some step-matrices used in the ordered analysis of the living taxa were altered or abandoned, and some previously ordered characters then had too few states to be ordered. It makes no difference whether a two-state character is ordered or unordered; such characters are considered unordered but are effectively both ordered and unordered. These changes are given below. As in Dixon et al. (2003), characters that were ordered in the ordered analysis are marked with an asterisk (*), and characters with step-matrices in the ordered analysis are marked with an obelisk (*). Taxa marked with an obelisk are extinct. Character states as found in Dixon et al. (2003) are given in curly brackets { }, and new character states are given in square brackets [ ].

Char. 2, eyestalks: {0 & 1} > [0] cylindrical; {2 and 3} > [1] flattened; step-matrix removed.

Char. 5, first antenna (A1): {0 & 1} > [0] straight; {2} > [1] strongly curved; not ordered.

Char. 7, A1 peduncle: {0 & 1} > [0] straight; {2 and 3} > [1] Z-shaped; step-matrix removed.

Char. 9, second antenna (A2): {0} slender; {1 and 2} > [1] enlarged; not ordered.

Char. 14, mandibles: {0, 1 & 2} > [0] no molar process, flat; {3} > [1] rounded; step-matrix removed.

Char. 21, chelae: state {4} abandoned, but step-matrix otherwise unchanged.

Char. 50, symmetry: {0} > [0] asymmetrical; {1} > [1] chelae
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asymmetrical: \( \{2\} > \{1\} \) chelae and pleon asymmetrical; states \( \{3\} \) and \( \{4\} \) abandoned; ordered in ordered analysis, instead of step-matrix.

Char. 66, telson spines: \( \{0\} > \{0\} \) absent; \( \{1, 2 & 3\} > \{1\} \) present; not ordered.

The remaining thirty-six characters were not altered from those used in Dixon et al. (2003). Only one new character was added to the analysis. Character 71 concerns the presence [1] or absence [0] of a median plate on the carapace. The median plate is found in specimens of Erymidae (of which the genus Eryma\(^a\) is included in this study), and also, we believe, in members of the extant Enoplometopidae. In Enoplometopus, a series of carinae adorns the frontal section of the carapace, and immediately lateral to these carinae we observed a faint line of thinner exoskeleton. These lineae on either side of the carapace

Fig. 1. Cyderyon propinquus. 1, Teylers Museum, Haarlem, 13139. 2, close-up of area with arrow in 1, with preservation of gill lamellae. 3, close-up of mouth field displaying crista dentata (cd) and mandibles (mn).
meet at the center-line immediately behind the posterior extensions of the carinae. We suggest that these lines are homologous with the boundary of an eyrid median plate, albeit a somewhat enlarged version. Only one enoplometopid (Enoplometopus occidentalis) is included in the study, so this character is uninformative in analyses that excluded Eryma. All other characters are informative in all analyses.

Since the stability of any tree depends broadly on the ratio between the number of characters and the number of taxa, several taxa used in the original analysis were removed. These taxa were mostly from areas of the tree where there had been no doubt as to phylogenetic position, or where the positions of taxa were known to be misleading as a result of homoplasy. It was hoped that the removal of some taxa would result in as few trees as possible without compromising the legitimacy of the results. The omitted taxa were: Procaris ascensionis, Nephropsis stewarti, Cambaroides bartoni, Astacoides madagascarenis, Cherax lorentzi, Palinurus vulgaris, Panulirus guttatus, Thenus orientalis, Pisidia longicornis, Hapalogaster dentatus, Lithodes antarcticus, Lomis hirta, Parapagurus alaminos, Raninoides bouvieri, Latrelia elegans, and Chiromantes haematocheir.

The additional seven fossil taxa we studied (with the proportion of missing data for them in the matrix) were: Eryon (0%), Eryma (0%), Glyphea (11%), Pemphix sueri (14%), Glaessnericaris machrochela (16%), Mecochirus (18%), and Palaeopalaemon newberry (20%). We used specimens of Eryma, Eryon (Cycleryon), Glyphea and Mecochirus from the Solnhofen lithographic limestone collections of the Teylers Museum, Haarlem. As noted, the preservation of Solnhofen fossils is remarkable, due to the fineness of the sediment and the rapidity with which the animals (and any potential consumers thereof) were killed (Barthel et al., 1990), and details of even soft structures are often visible. Data concerning the other taxa such as Glaessnericaris machrochela and Palaeopalaemon newberry were taken from literature (Glaessner, 1969; Schram et al., 1978; Garassino and Teruzzi, 1993; Garassino, 1996), with the addition of some information derived from unpublished photographs of Palaeopalaemon newberry from a research archive (FRS).

The resulting data matrix comprised 44 characters (13 orderable, 7 with step-matrices, 19 with only two states each, 5 multi-state but not orderable) and up to 53 taxa (see Appendix I for complete matrix of included taxa and character states). As with the study by Dixon et al. (2003), both ordered and unordered analyses were run, with all characters unordered in the unordered analyses, but with some ordered, and some referring to step-matrices in the ordered analyses. Character states are as in Dixon et al. (2003) except where otherwise mentioned above. Analyses were carried out with a heuristic search in PAUP* 4.0b10 (Swofford, 2002). Characters were optimized and trees examined with MacClade 4.03 PPC (Maddison and Maddison, 2001).

**Results**

The objective of our study was to compare and assess the effect on the emergent trees of the addition of information derived from the selected fossil decapods. Our analyses were first carried out without inclusion of any fossil taxa (Fig. 2, analyses A and B, Table 1). This was done to provide a background against which to test the effects of adding fossil taxa as well as to compare the results of the altered data set with the original results of Dixon et al. (2003). The fossil taxa were then added in two groups chosen on the basis of the amount of missing data. We performed the second set of analyses (Fig. 3, analyses C and D, Table 1 - one ordered, and one unordered) with the inclusion of the three most completely known taxa, i.e., those with the least amount of missing data.

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Table 1. The analyses undertaken, labeled A to J. Bracketed numbers after taxa names are the numbers of taxa included in each analysis. CI = consistency index, HI = homoplasy index, RI = retention index and RC = rescaled consistency index. A 0 in the final column indicates an ordered analysis, and U indicates an unordered analysis.
A third set of analyses (Fig. 4, analyses E and F, Table 1 - one ordered, and one unordered) then occurred when the four most incompletely known taxa, i.e., those with the most missing data (Palaeopalaemon, Glaessnericaris, Mecochirus and Pemphix), were added to the base matrix. A fourth set of analyses included all the taxa (Fig. 5, analyses G and H, Table 1 - one ordered, and one unordered). The final set of analyses (Fig. 6, analyses I and J, Table 1 - one ordered, and one unordered) included all the fossil taxa and all of the extant taxa except for the deletion of Atyoida pilipes, Alpheus cylindricus, Polychelis typhlos, Callianassa setimana, Upogebia deltata, Calcinus tibicen and Maja squinado. In this final analysis, the number of extant taxa removed is the equal to the number of fossil taxa added.

In order to more adequately study the potential affinities of Palaeopalaemon newberryi in particular, we combined the results of analyses E, F, G, H, I, and J, and we eliminated duplicate trees along with any taxa not present in all of those analyses. This resulted in 281 trees, in every one of which Palaeopalaemon occupies the same position, basal to Eurysternalia (sensu stricto). Majority-rule consensus trees are given in Figures 2-6, along with the results of the analyses in Table 1.

There is a decrease in the values for consistency (CI), retention (RI) and rescaled consistency indices (RC) as the number of fossil taxa is increased, and a concomitant increase in the value for homoplasy index (HI) and tree length. Each of these measures shows that trees that include fossil taxa are somewhat less reliable than those without. Trees resulting from the ordered analyses are, as expected, longer than those from the equivalent unordered analyses, by around eighteen steps in each case. Values for CI, HI, and RC are always better in the unordered analyses than their ordered counterparts, while values for RI are almost identical for each pair.

### Discussion

#### Methodological Issues

As noted above, Schram and Hof (1998) found that the addition of fossil taxa to their analyses introduced variation to the number and the topology of the trees recovered by a parsimony analysis. They attributed this to the vraagteken effect (from the Dutch and Flemish word for question mark ?), whereby groups shift about the tree, sometimes dramatically, and strange groupings of taxa occur. Because of all the uncertainty attached to lack of knowledge about character states in fossils, current cladistic algorithms cannot handle the ambiguity and thus frequently a great many possible sister taxa arrangements are equally parsimonious. The fossil taxa in the analysis of Schram and Hof displayed levels of missing data from 29% (in the case of Bredocaris) to 91% (in the case of the phyllocarid Hymenostraca), with an average of 52%.

In our analysis herein, curiously, the taxa with the most uncertainties did not destabilize the tree any more than the more completely understood fossils. Indeed, analysis F, wherein 4 incompletely known fossil taxa were analyzed in an unordered analysis, resulted in somewhat shorter (by one step - 190 vs. 191) and slightly more robust (higher CI, lower HI, higher RC) trees than analysis D, wherein only 3 fairly well-understood fossil taxa were analyzed in an unordered analysis. Aside from this perhaps anomalous example, the vraagteken effect does seem to prevail in our analysis. Analyses I and J have the same number of taxa as analyses A and B, but result in trees with 9.6% more steps with noticeably worse scores for CI, HI, RI and RC. However, another explanation for this might better suffice here, one related to a systematic bias. The extant taxa that were deleted in the analyses seen in I and J were those that added little information to the analyses because of their redundancy with taxa retained. This stands in contrast to the fossil taxa that replaced the deleted living forms since they were so chosen because they could provide new phylogenetic information, thus by definition requiring further steps in trees that involve them.

The number of good, independent characters available always limits any morphological analyses. This also constrains the number of taxa that can be included. Our study shows, however, that with certain reservations data from fossils can be included and provide new insights into the evolutionary past without causing a total collapse of clades. The amount of missing data must be kept to a minimum, e.g., the maximum amount of missing data in this study being 20% (Palaeopalaemon), compared to the minimum of missing data of 29% seen in Schram and Hof (1998). Clearly the stability of the analyses here is a reflection of the underlying robustness of the original analyses of Dixon et al. (2003).

Nevertheless, the most effective strategy to determine phylogenetic position of a fossil species would be to construct a robust data matrix of extant forms, with as comprehensive a character set as possible, and then add only one taxon to determine its position. One would then replace these fossil taxa with others until a position is known for each. This would overcome the problem of too many fossil taxa in an analysis and the associated vraagteken effect, but one would have to assume that the initial analysis is well founded. It would therefore only be useful in groups with diverse extant representatives. However, the assumption that the starting tree is correct must be justifiable. If the addition of fossil evidence is
Fig. 2. The base analyses run with altered living taxon and character sets to compare to the results of Dixon et al. (2003). Majority rule consensus trees from Analyses A (ordered, left) & B (unordered, right). See text and Table 1 for details.
Fig. 3. Addition of fossil taxa to the matrix for which the maximum amount of information is known. Majority rule consensus trees from analyses C (ordered, left) and D (unordered, right). See text and Table 1 for details.
Fig. 4. Addition of fossil taxa to the matrix for which a moderate amount of anatomical information is known. Majority rule consensus trees for analyses E (ordered, left) and F (unordered, right). See text and Table 1 for details.
Fig. 5. Addition of all fossil taxa to the matrix. Majority rule consensus trees from analyses G (ordered, left) and H (unordered, right). See text and Table 1 for details.
Fig. 6. Addition of all fossil taxa and deletion of a similar number of living taxa. Majority rule consensus trees from analyses I (ordered, left) and J (unordered, right). See text and Table 1 for details.
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...enough to destabilize the original tree, then that tree cannot have been stable enough to begin with. This only confirms that good, robust data sets must be established.

It might be tempting to replace several taxa with a single hypothetical ancestor, but this should be avoided as it assumes that none of the fossils will be found to belong within extant groups. As the case of Enoplometopus and Eryma shows, this assumption can, and will on occasion, be false. The only hope for enlarged matrices is an increase in the number of useful characters, which in turn requires careful study. The recognition of previously unused, phylogenetically informative characters, e.g., the ischio-coxal process of astacideans (Dixon et al., 2003), or the degree of attachment of the epistome to anterior carapace margin in glypheoids and astacideans (Ahyong and Schram, 2002), shows that careful comparative morphological study can still be fruitful even in a group as well studied as the order Decapoda.

Decapod Tree Topology

The first noticeable difference resulting from the modified data set is the loss of resolution apparent in the cladograms (Figs. 2-6) compared with that seen in Dixon et al. (2003). While few of the important relationships are altered, the consensus values are considerably lower. Those relationships that have changed are among the more poorly supported in the analyses of Dixon et al. (2003), such as the branching pattern among the natant decapods (Dendrobranchiata, Caridea, Stenopodidea), and the relationships within Anomala. This loss of resolution is not surprising given the reduction in information content following the reduction of the data set, in terms of both taxa and characters. When informative characters are removed, no reduction in the number of taxa is likely to reinstates a clade. However, a reduced data set, even with fewer taxa, is generally more poorly resolved. In this respect, the analysis of Dixon et al. (2003) is the more robust.

Our attentions herein focused on relationships within Reptantia. Let us consider the positions of the major fossil taxa in turn whose positions we wanted to test with these current analyses.

Eryon

The eryonids represent one of the most distinctive body plans among the macrurous reptants. Eryon and several related genera occupy the family Eryoniidae de Haan, 1841, which along with Polycheleidae Wood-Mason, 1874 and some other families were placed by Glaessner (1969) within the infraorder Palinura. We examined for this study material attributed to Eryon arctiformis and Cycleryon propinquus.

The cladistic analyses of Scholtz and Richter (1995), Schram (2001), and Dixon et al. (2003) all agree that Polycheleida form a sister group to Eureptantia. Hence, determining the phylogenetic affinities of the eryonids is of interest. Schram and Ahyong (2002) noted the presence of undisclosed eureptantian features in Eryon; indeed the possession of a crista dentata on the third maxillipeds (Fig. 1-3) (char. 18) and the double hinge between carpus and propodus of the first pereiopod (char. 28) would argue in favor of eureptantian affinities. In such a scenario, the similarities between Eryon and Polycheles, such as the body shape (char. 41), unusual number of chelae (chars. 35 and 36) and so on, are due to symplesiomorphies alone. Two of our unordered analyses display this pattern. However, in 4 of our analyses, Eryon emerged as a sister taxon to Polycheles gailii. In this instance, some of the primitive features of Polycheles are interpreted as character reversals. The polychelids in this scenario would, for instance, possibly have lost the crista dentata, rather than never having had it (although an alternative hypothesis is that the crista dentata evolved independently in both eryonids and the Eureptantia). Note, however, that even so, Polycheles remains the sister group to all the other Reptantia.

One particular specimen (Fig. 1) of Cycleryon propinquus (Teylers Museum specimen number 13139) showed truly exceptional preservation, with the gills clearly visible through the carapace (Fig. 1-2). This does not mean that the omission here of the original character 47, gill morphology, from the analysis was mistaken since few other fossils would have been scored for this feature, and thus to have included it would only have increased the vraagteken effect. It is, nevertheless, a relief to discover that the gills are clearly trichobranchiate, as was predicted by previous analyses (Scholtz and Richter, 1995; Schram, 2001; Dixon et al., 2003), and it increases the expectation that other delicate structures may be discovered on other specimens, filling in the gaps in our knowledge of fossil anatomy. If just one fossil specimen was found with an unexpected gill morphology, such as a dendrobranchiate gill on a reptantian, we would have to re-appraise our views of the evolution of such a character.

Eryma

We examined a diverse array of species attributed to Eryma, in particular E. modestiformis and E. fuciformis. Among Homarida, the genera Enoplometopus and Eryma inevitably emerge as sister taxa in our analyses. Each genus is currently placed in its own family and / or superfamily separate from Nephropidae (see Glaessner, 1969; and Martin and Davis, 2001). Although our results might have been skewed by the inclusion of a controversial feature (char. 71 - median carapace plate) that unites the two taxa, it is not only the presence of a median plate that
brings Enoplometopus and Eryma together. Some specimens of Eryma exhibit a chelate fourth pereiopod (char. 35), while others do not. Although this feature could be indicative of inter-specific differences, we interpreted it as a sexual dimorphism, i.e., a further character shared exclusively between Eryma and Enoplometopus. Furthermore, there are no characters that argue against a close relationship between these two groups, i.e., in favor of some other relationship. Few characters are operant within the whole of Astacidea, and so for us to find two characters that support this relationship might be interpreted as good evidence.

The fossil record of the erymids extends from the Permo-Triassic to the late Cretaceous (? Paleocene) (Glaessner, 1969), whereas enoplometopids are known only from the Recent fauna. On the basis of this information and the phylogenetic results, we suspect that Erymidae van Straalen, 1924 and Enoplometopidae de Saint Laurent, 1988 are at least within the same superfamly clade, if not within the same family. A more detailed study concentrating on the relationships within Astacidea is needed before conclusions can be firmly drawn.

Glaessnericaris machrochela

Glaessnericaris machrochela Garassino and Teruzzi, 1993 was included in a total of six of our analyses to try to assess the status of the family Platychelidae Glaessner, 1969. In one of these (analysis H), it was found to be a sister group to the entire Eureptantia, but in the remaining five analyses it appeared either within, or as a sister group to, Astacidea. However, the paucity of useful characters within Astacidea prevents us from making judgments about relationships of Glaessnericaris machrochela with certainty. We can only reiterate the need for further study of well-preserved material of this family. The phylogenetic position of Glaessnericaris appears less certain than that of Eryma.

Glyphea
dea

One of the areas highlighted by Dixon et al. (2003) for further research was the issue of the monophyly or otherwise of the Glypheoidea. In particular, the position of Pemphix suerii relative to the other taxa seemed uncertain. We examined a variety of fossil glypheoids, including Mecochirus longimanus, M. bajeri, Glyphea tenuis, G. pseudoscyllaris, as well as Pemphix sueri. The results of our studies confirm that Pemphix does not appear to form a monophyletic group with the other glypheoid families. The close relationship between Glypheidae and Mecochiridae seems certain, although it is beyond the scope of this study to determine whether each is truly monophyletic, or to discover the characters defining each. The position of Pemphix, however, is less easy to ascertain. In some of our analyses it is basal to Astacidea, and in others, it is basal to Sterropoda. The warning given by Schram and Ahyong (2002) that we should not automatically assume the placement of the ... other glypheoid families is entirely vindicated.

Palaeopalaemon newberryi

Perhaps the most surprising result of this study is the indicated position of Palaeopalaemon newberryi. As a denizen of the Late Devonian period, over 360 million years ago, this species is the earliest decapod crustacean known. This date was taken originally as evidence for a basal position for Palaeopalaemon among the reptants, i.e., it was assumed to be relatively primitive. Schram et al. (1978) placed Palaeopalaemon within Pleocyemata, or egg-brooding decapod and suggested affinities with both glypheoid families palinurans (Achelata) and astacideans. At the time, there was no evidence to suggest that Achelata might be an advanced group, as proposed later by Dixon et al. (2003), and hence the position Schram et al. (1978) suggested is a fairly basal one. Schram (2001) speculated that Palaeopalaemon might even have some affinities with the enoplometopids. In our study here, by contrast, Palaeopalaemon newberryi appears high in the tree, in a stable and unchanging position as a sister taxon to Eurysternalia. This relationship is supported by, amongst other things, the statement that in Palaeopalaemon, the thorax appears to have wide sternites (Schram et al., 1978) (char. 19). The presence of lineae (char. 46) also ensures that Palaeopalaemon belongs within Sterropoda, as does its monochelate condition (char. 21).

Such a cladistic position along with its incongruously old age suggests a scenario in which Palaeopalaemon would be an ancestor to modern Eurysternalia. There are several problems with such an idea, however, chiefly with regard to the morphology of the urosome. The telson of
Palaeopalaemon is not the broad, snub-ended shape found in the achelates and most anomalans, but instead is of a longer, more pointed form, much reminiscent of the telson of a shrimp or prawn. This might be explained away with reference to the hippoids, whose telsons are also apparently natant-like but which are distinguished by their convexity, as also appears to be the case in Palaeopalaemon. The uropods of Palaeopalaemon are even more troublesome; they resemble those of natantians perfectly, except for perhaps an increased degree of calcification, and are most unlike the uropods expected of a eurysternalian.

Beyond consideration of the morphology of the urosome, the reassignment of Palaeopalaemon to a position high in the decapod tree injects serious complications concerning the timing of decapod history. If this genus is rather derived in form, then all the major branching events in the evolution of Reptantia, as well as lower Decapoda, have to have occurred prior to the Late Devonian (Fig. 7). While this is not impossible, it is only fair to point out that at present there is no indication that this was the case. To maintain this interpretation would then require that we assume, in fact, that an extensive and an as yet undetected array of mid-Paleozoic fossil decapods are missing and yet to be discovered.

While there are problems that emerge from this
analysis concerning the placement of Palaeopalaemon, nevertheless, it does seem possible that the phylogenetic position of Palaeopalaemon newberryi has been singularly misjudged. Whatever the true position of Palaeopalaemon, some characters will need to be reconsidered with this taxon in mind. For instance, either the broad sternum is homoplastic, or the tail-fan morphology is. There is clearly much still to be learnt from further detailed study of Palaeopalaemon, and it is not impossible that new insights into the morphology of this species could significantly shift the position yet again to a position lower in the tree.

**Suggested Relationships**

The general, higher classification given below includes our current best assessments about decapod relationships that result from the analyses discussed above. We adapt the sequence for lower decapods evident from earlier morphological and molecular work, and as outlined in Dixon et al. (2003). The reptants remain a monophyletic group. The position of Glaessnericaris was considered too uncertain to be included, although it seems to be an astacidean. Names of taxa have been altered to fit a general pattern of -ida endings, which for now we prefer to leave devoid of the Linnaean ranks that so often rankle. This is not meant as a definitive classification, merely a guide to the relationships that emerged herein. In several instances trichotomies in the trees are evident where relationships are not certain enough. Eurysternalia appears twice, once with [Eurysternalia - sensu lato], and once without Palaeopalaemon [Eurysternalia - sensu stricto]. Apomorphies for the main groups are provided in Appendix III.

**DECAPODA**

**DENDROBRANCHIATA**

**PLEOCYEMATA**

Caridea

unnamed clade

Stenopodidea

Reptantia

Polychelida

Polychelidae

Eryonidae

Eureptantia

Astacura

Astacidea

Astacida

Homarida

Erymida (possibly including Enoplometopidae)

Glyphheoidea

Pemphicida

Sterropoda

Thalassinida

Eurysternalia (sensu lato)

Palaeopalaemonida

Eurysternalia (sensu stricto)

Achelata

Meiura

Anomala

Brachyura

Our analyses can be re-cast in a stratigraphic context, in order to gauge the extents of ghost ranges and phantom lineages. The stratigraphic diagram of Schram (2001: Fig. 9) included a great deal of relevant information, but was based on a different model of decapod evolution (the fractostern theory of Scholtz and Richter, 1995). Figure 7, herein, may be considered an update of that diagram. Only first and last appearances in the fossil record are considered; gaps in the fossil record within a single lineage are ignored. The first fossil stenopid (Schram et al., 2000) extends back a reptant sister-group, and several taxonomic judgments have been changed. Schram (2001) suggested a link of Palaeopalaemon with the modern Enoplometopus (this study has shown that the two probably are not related) and also accepted suggestions that certain Carboniferous burrows are similar to those of modern freshwater crayfish.

Schram and Mapes (1984) and Schram (2001) considered that the genus Imocaris was probably a dromiacean crab. Imocaris tuberculata Schram and Mapes, 1984 is known only from a single well-preserved carapace. Subsequently, a second species, Imocaris colombiensis Racheboef and Villarroel, 2003 has been described, again from a single carapace, in connection with an assessment of the affinities of Imocaris, and they suggested several possible alternative taxonomic relationships for the genus but concluded it was probably a pygocephalomorph. While we cannot easily accept that possibility, neither can we reject it out of hand. Clearly, we must await discovery and description of parts of Imocaris other than just the carapace. For the time being, we leave the assignment uncertain within Decapoda but indicate its place in the Carboniferous.

The issue of the time of crayfish origins has been a problem. Schram (2001) in considering the present and fossil distributions of the astacids concluded that on the basis of paleobiogeography the origins of the group must lay at least in Triassic times. Hasiotis (1999) mentioned what he believes are probably crayfish burrows in the Carboniferous of North America. However, we see no reason to believe that such burrows must have been created by a freshwater crayfish. Since no comparative studies are readily available to establish the differences between the burrows of different decapod taxa, we cannot assume that the thalassinideans, the nephropids, some extinct group, or ancestors to one or other extant group
could not have made these burrows. Furthermore, Dixon et al. (2003) speculated that burrowing might be the primitive condition within Eureptantia. Consequently, on the diagram of Figure 7 we have interpreted the burrows of Hasios as ancestral astacideans rather than extend the range of Astacida directly, although these burrows might equally be interpreted as ancestral thalassinideans.

If the freshwater crayfish had diverged from other astacideans by the Carboniferous, then there would be considerable ghost ranges for both the crayfish and the true lobsters (Nephropidae, Erymidae, Thaumastocheilidae, and Enoplometopidae). The monophyly of the freshwater crayfish, though previously doubted, is now universally accepted (see Dixon et al., 2003, for a discussion of the characters supporting this view). If there was a single origin for the crayfish and they cannot survive in salt water, then they must have diverged before the continents they now inhabit had separated.

The three families of crayfish live nowadays in Europe and western North America (Astacidae), east Asia and eastern North America (Cambaridae), and South America, South Africa, Madagascar and Australasia (Parastacidae). The last time in which these continents were conjoined was in the Triassic, before Fenno-Scandia (Eurasia) separated from Greenland (North America) with the opening of the Atlantic Ocean (Scotese, 1997).

As is usual for such diagrams, the shortest possible ranges are shown; it is always possible for groups to be considerably older than is depicted, but we have no reason to assume so. Similarly, although the monophyly of Astacidea including all three glypheoid families is not quite convincing, this interpretation gives the shortest ghost ranges, and so that arrangement is depicted.

The diagram differs from that of Schram (2001) quite clearly in its overall form. While the unbalanced tree of Schram resulted in lengthy ghost ranges for most groups, stretching from the Devonian or Carboniferous periods, the advent of characters and lineages.

Conclusion

Now that we have a suitably robust data matrix for the decapod crustaceans, fossil taxa can be added without nullifying or collapsing the results of cladistic analyses based initially on living forms. The numbers of fossil taxa must, however, be limited, and the amount of missing data kept low. There can be no substitute now for careful study of extant and extinct taxa to discover informative characters for phylogenetic analysis. Moreover, the day is at hand when ad hoc explanations about the phylogenetic affinities of individual fossil groups can no longer be tolerated. It is clear that ad hoc methods must yield to more explicit procedures that can produce multiple alternative hypotheses that in turn can form the basis for determining future lines of research.

Acknowledgements

We wish to express our thanks to Bert Sliggers, Conservator of the Paleontologic and Mineralogic Cabinet, Teylers Museum, Haarlem, for allowing us access to the extensive collection of Solnhofen materials housed in that institution. Additional thanks go to Prof. Agnes Rage, Institute of Paleontology, National Museum of Natural History, Paris, for her assistance with examining the Solnhofen fossils there.

References


Racheboef, P. R. and C. Villarroel (2003), Imocaris colombiensis from the
Appendix I - Data Matrix

Character states marked \( \bullet \) are polymorphic \([0 \text{ and } 1]\), and the character state marked \( \bullet \) is polymorphic \([1 \text{ and } 2]\). The 44 characters are numbered following Dixon et al. (2003) for ease of comparison.

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Appendix II - Characters

List of the characters used in Dixon et al. (2003) and in this study. Changes made to the characters are highlighted in bold in the right-hand column, along with the reason(s) for exclusion (where applicable). These may be hidden if the structure is covered by other body parts or is obscured by the flattening of the fossil, rarely preserved if the structure is too delicate to be preserved frequently, articulation if the characters refers to articulations, or sexual dimorphism if the structure is excluded for being sexually dimorphic.

<table>
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<th>status in this study</th>
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Appendix III - Apomorphies

The effective apomorphies for the suprafamilial groups of Pleocyemata outlined in the Discussion are provided here. Features below are numbered as in the data matrix of Appendix I, subscripts indicate the specific character state. Only those characters that we used in this study (see Appendix II) with the highest consistency values are provided. The other features that are too homoplastic are not given. If the character below is unqualified, it is a robust apomorphy; typically means that with a very few exceptions the feature prevails in that clade; generally means that the feature prevails in well over half the constituent taxa of the clade; often means the feature occurs in just under half the taxa although it is still believed to be characteristic. For further defining apomorphies of these groups derived from the original set of 70 characters, consult the discussion in Dixon et al. (2003).

**Caridea:** telson spines present (661)

**Stenopodidea:** 3rd pereiopods enlarged (661), telson spines present (661)

**Reptantia:** pleon dorso-ventrally compressed (521)

**Polychelida:** pereiopod 4 chelate (351), carapace depressed (411, 412), carapace with a posterior suture or ridge

<table>
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</table>
Decapod phylogeny: addition of fossil evidence to a robust morphological cladistic data set

*Eureptantia*: maxilliped 3 dactylus blunt (15), with a crista dentata [also in Eryonidae] (18), pereiopod 1 enlarged (20), carpus-propodus and propodus-dactylus on pereiopod 1 with two points of articulation for the joints [also in Eryonidae] (26), generally pereiopod 4 chelate or subchelate (65w, 2).

**Astacura**: typically with a deep transverse groove on carapace (42), uropodal exopod with diaeresis (70).

**Astacidea**: pereiopod 1 with long ischio-coxal process (70), typically telson spines present (66).

**Astacida**: pereiopod 1 perpendicular (28).

**Homarida**: none that are robustly diagnostic in this study.

**Erymida**: pereiopod 4 semi-chelate (35), median plate on carapace (71).

**Glypheoida**: carapace with posterior suture or ridge (44).

**Pemphicida**: pleonites pointed (63), uropodal exopod with diaeresis (70).

**Sterroidea**: typically with maxilliped 3 short and pediform or operculiform (16w), typically pereiopod 1 chelate, pereiopods 2 and 3 achelate (21), typically lineae present (46).

**Thalassinida**: generally with flattened eyestalks (2), typically ischio-merial articulation of pereiopod 1 curved (28), 7th thoracic sternite enlarged and lobate (33), typically transverse groove on carapace deep (42), typically 1st pleonic somite short and narrow (48).

**Eurysternalia (sensu lato)**: thoracic sternites wide (19w, 2), transverse carapace groove shallow (42), often 2nd pleomere pleuron expanded and overlapping the 1st (62).

**Palaeopalaemonida**: carapace with a posterior suture or ridge (44).

**Eurysternalia (sensu stricto)**: typically antennule flagella with annuli wider than long and flagella similar in length the 2nd peduncular segment (6w), antennule peduncle z-shaped (7), generally scaphocerite absent or if present not articulated (8), generally antennule slightly curved (5), typically carapace depressed (41w).

**Achelata**: antenna enlarged (9), basal articles of antenna fused to carapace (10), lobes from 1st pleonic pleura overlapping carapace (49), pleonites pointed (63), telson spines present (66), distal telson cuticle softer than proximally (68).

**Meiura**: typically some pattern of reduction and / or dislocation of pereiopods 4 and 5 (3), typically 1st pleonic somite narrow (48w), pleonic flexion not macrurous (54w).