

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 [Glypheoidea + Astacidea], Sterropoda [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 [Glypheoidea + 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 characters were ordered, while another 15 had step-matrices constructed for them (see Dixon *et al.*, 2003 for details).

We began our study herein with the Dixon *et al.* (2003) analysis as a base. We did find it necessary to alter some of the characters where information was unlikely to be recorded in the fossils. However, for the most part, we selected taxa from the Solnhofen Lagerstätte for our tests to minimize this need. Solnhofen crustaceans are universally noted for their exceptional preservation; in many instances it is almost like having the living animal to

examine (Fig. 1). Some structures are frequently well preserved on the fossils. However, if we deemed a feature for this present study to be one wherein too few specimens would be scored, we omitted that character from the original database. For some of these, the structure is likely to be preserved but not visible because of the orientation of the fossil relative to the bedding plane or because it could be obscured by other body parts. In other cases, the structures are too small or delicate for preservation. Furthermore, we excluded almost all sexually dimorphic characters because of an inability to easily sex most fossils. An exception to this rule exists in regards to *Eryma*[†] (see discussion below). Finally, characters of articulation were often omitted, since it is impossible to ascertain the limits of a fossil's movement. Many characters were excluded for more than one of these reasons, and in total 27 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

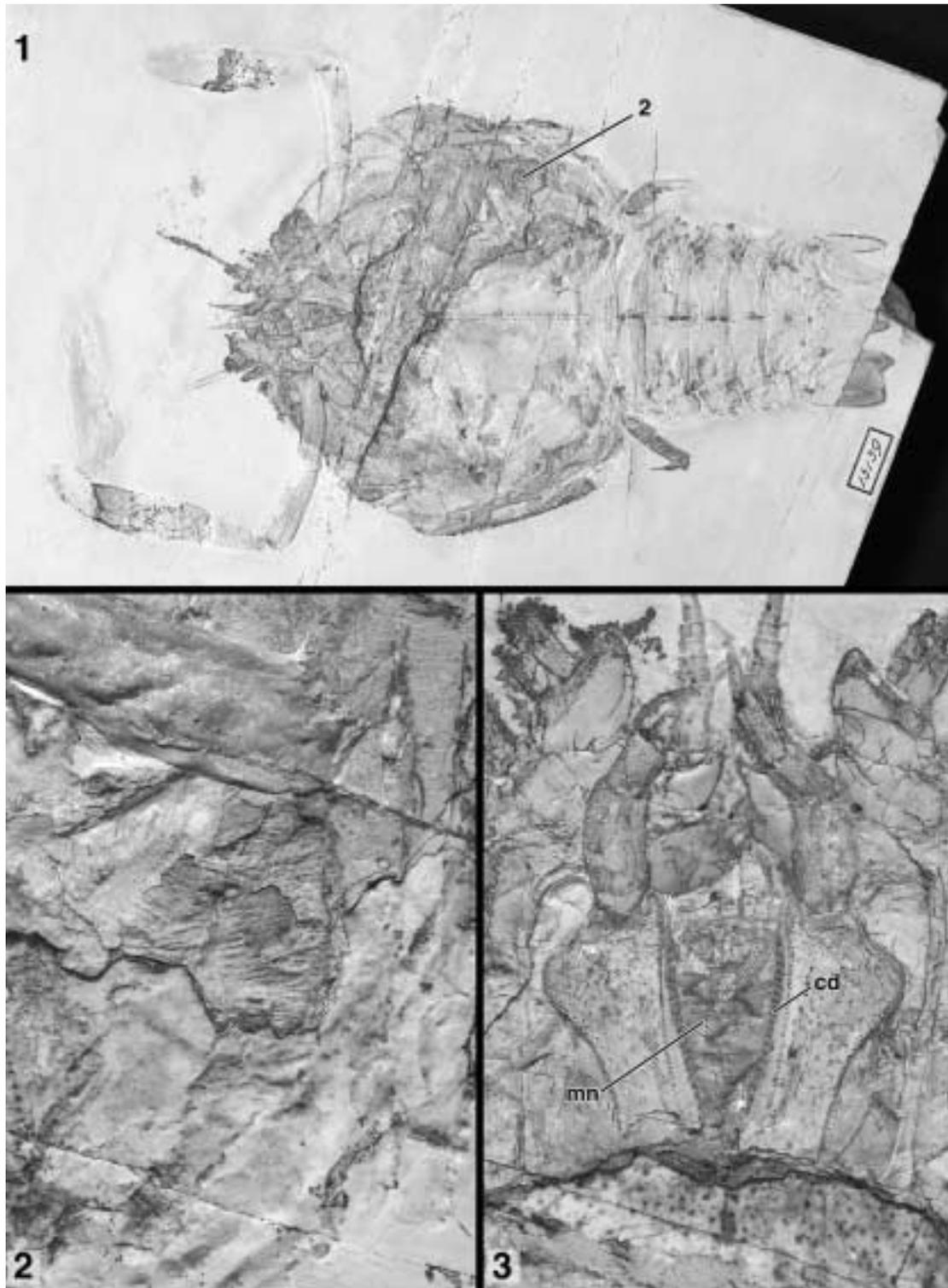


Fig. 1. *Cycleryon propinquus*. 1, Teylers Museum, Haarlem, 13139. 2, close-up of area with arrow in 1, with preservation of gill lamellae. 3, close-up of mouth field displaying crista dentata (cd) and mandibles (mn).

asymmetrical; {2} > [2] 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*[†] 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

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 erymid 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 this strategy 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 madagascarensis*, *Cherax lorentzi*, *Palinurus vulgaris*, *Panulirus guttatus*, *Thenus orientalis*, *Pisidia longicornis*, *Hapalogaster dentatus*, *Lithodes antarcticus*, *Lomis hirta*, *Parapagurus alaminos*, *Raninoides bouvieri*, *Latreilla 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 suerit*[†] (14%), *Glaessnericaris machrochela*[†] (16%), *Mecochirus*[†] (18%), and *Palaeopalaemon newberryi*[†] (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 newberryi* 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 newberryi* 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

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. "O" in the final column indicates an ordered analysis, and "U" indicates an unordered analysis.

	taxa	trees	length	CI	HI	RI	RC	
A	extant taxa only (43)	287	196	0.4235	0.5764	0.7986	0.3382	O
B		15	179	0.4637	0.5363	0.8004	0.3711	U
C	extant taxa + <i>Eryma</i> [†] , <i>Eryon</i> [†] and <i>Glyphea</i> [†] (47)	70	208	0.3990	0.6010	0.7892	0.3149	O
D		523	191	0.4346	0.5654	0.7878	0.3424	U
E	extant taxa + <i>Palaeopalaemon</i> [†] , <i>Glaessnericaris</i> [†] , <i>Mecochirus</i> [†] and <i>Pemphix</i> [†] (46)	834	208	0.3990	0.6010	0.7863	0.3138	O
F		1129	190	0.4368	0.5632	0.7864	0.3435	U
G	all taxa (50)	399	220	0.3773	0.6227	0.7780	0.2935	O
H		296	201	0.4129	0.5871	0.7769	0.3208	U
I	all taxa except <i>Atyoida</i> , <i>Alpheus</i> , <i>Polycheles</i> , <i>C. setimana</i> , <i>U. deltaura</i> , <i>Calcinus</i> and <i>Maja</i> (43)	323	215	0.3860	0.6140	0.7432	0.2869	O
J		111	196	0.4235	0.5765	0.7408	0.3137	U

(*Erymat*[†], *Eryon*[†] and *Glyphea*[†]). 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*, *Polycheles typhlops*, *Callianassa setimana*, *Upogebia deltaura*, *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 Hymenostroaca[†]), 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

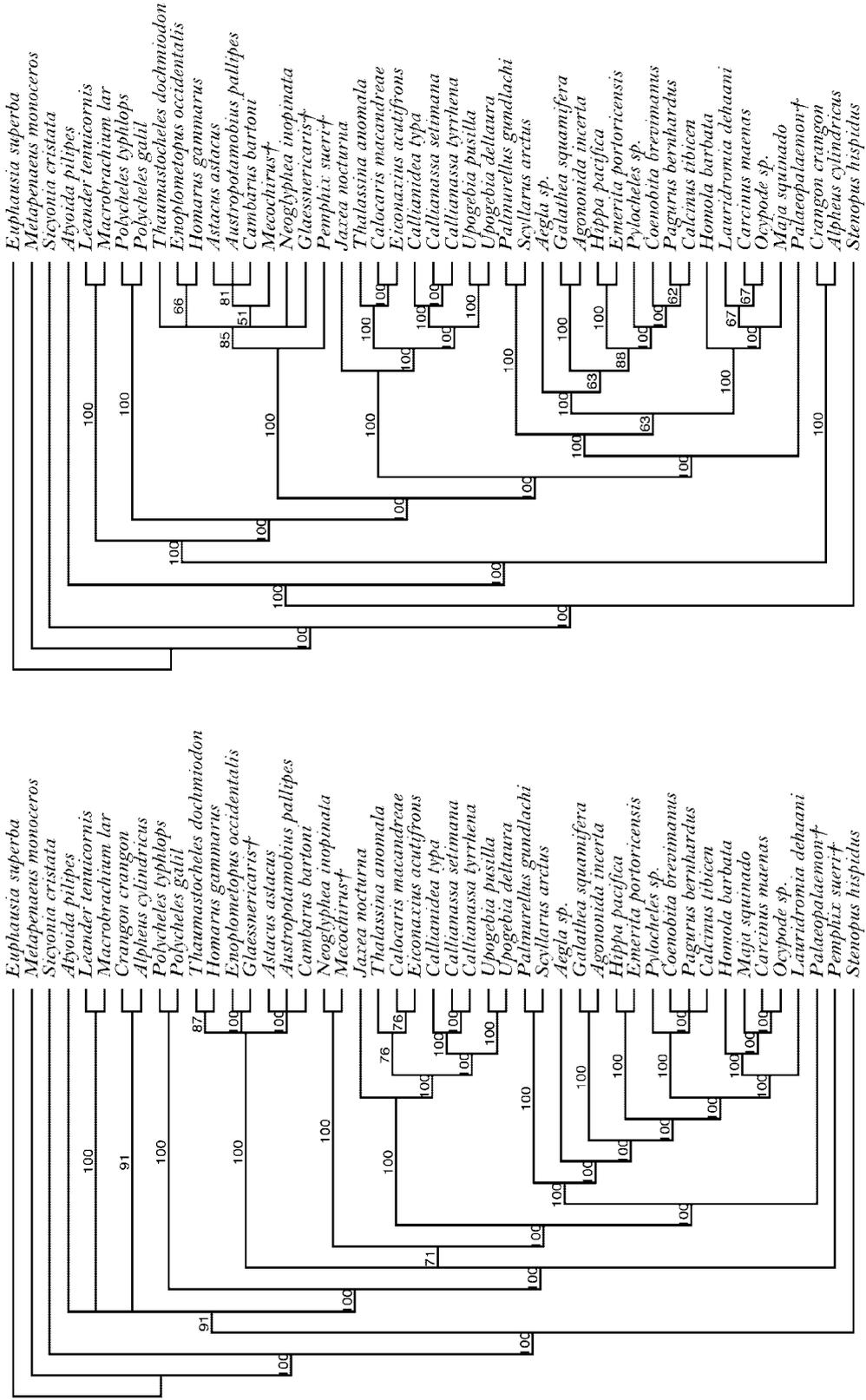


Fig. 4. Addition of fossil taxa to the matrix for which a moderate amount of anatomical information is known. Majority rule consensus trees for analyses E (ordered, left) and F (unordered, right). See text and Table 1 for details.

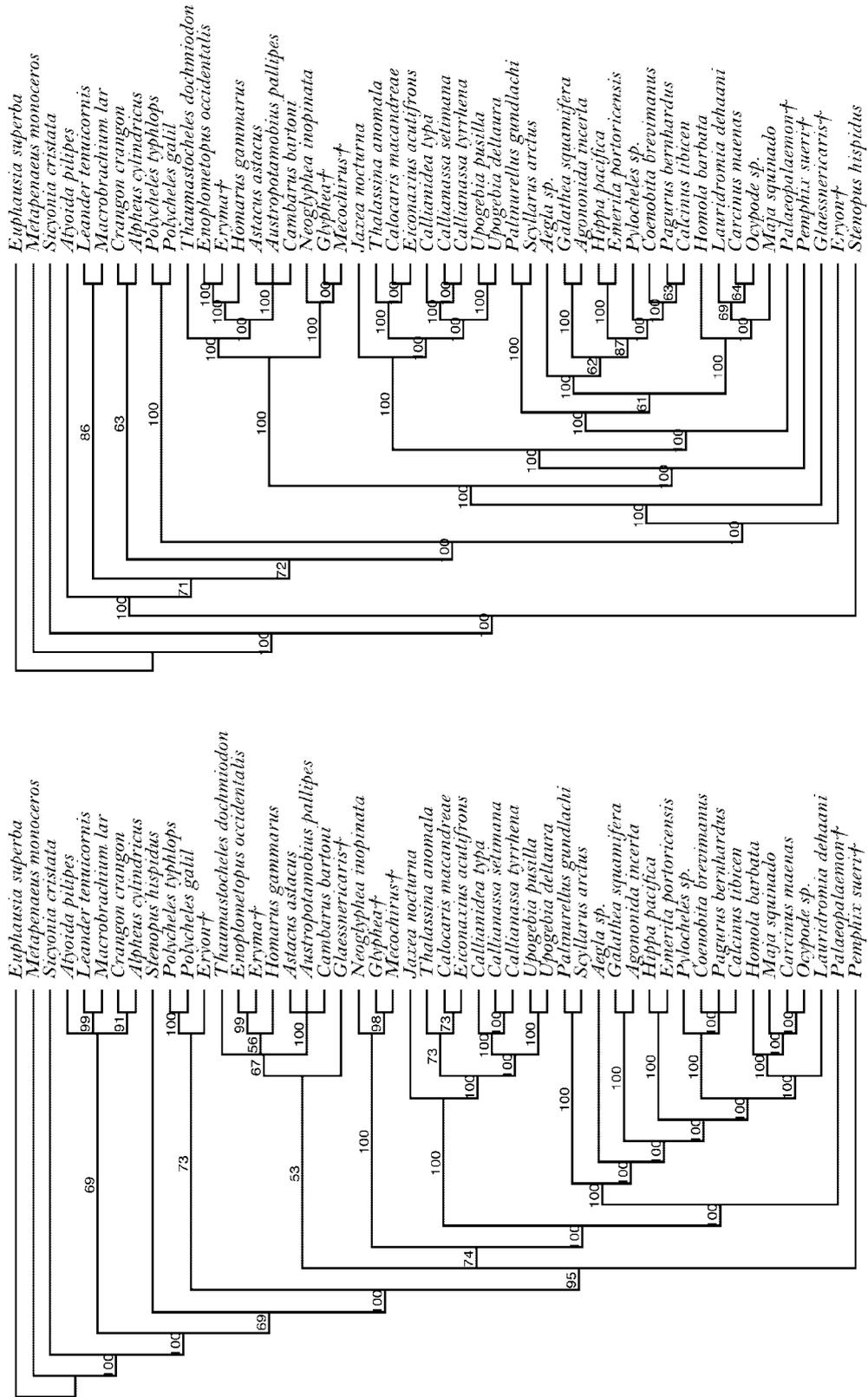


Fig. 5. Addition of all fossil taxa to the matrix. Majority rule consensus trees from analyses G (ordered, left) and H (unordered, right). See text and Table 1 for details.

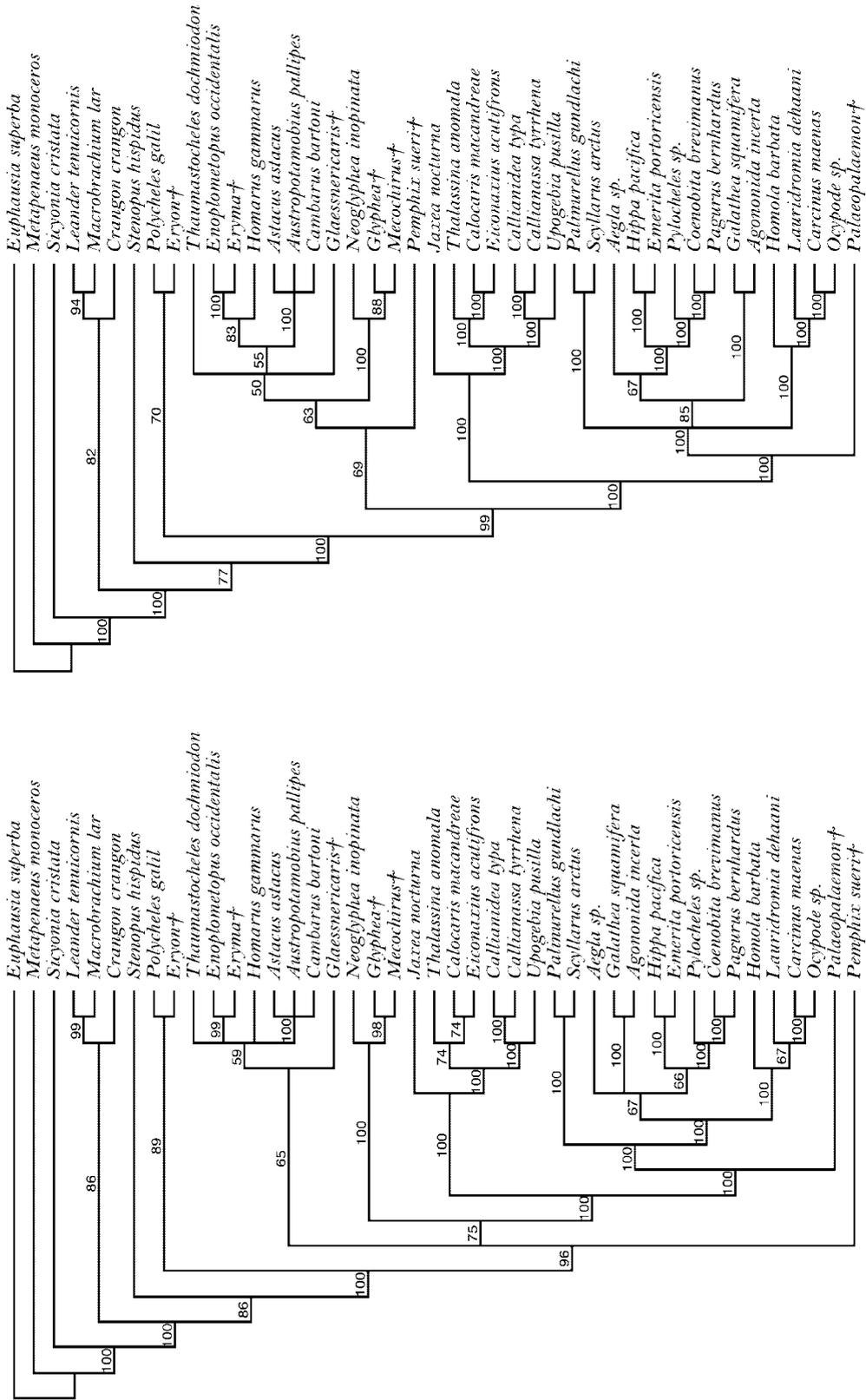


Fig. 6. Addition of all fossil taxa and deletion of a similar number of living taxa. Majority rule consensus trees from analyses I (ordered, left) and J (unordered, right). See text and Table 1 for details.

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 reinstate 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 Eryonidae de Haan, 1841, which along with Polychelidae 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 Polychelida 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 pereopod (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 galil*. 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, Polychelida 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 pereopod (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 Straelen, 1924 and Enoplometopidae de Saint Laurent, 1988 are at least within the same superfamily 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*.

Glypheoidea

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 sueri*[†] relative to the other taxa seemed uncertain. We examined a variety of fossil glypheoids, including *Mecochirus longimanus*, *M. bajori*, *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 glypheoids [*sic*] families" is entirely vindicated.

However, we were unfortunately not able to examine actual specimens of *Pemphix sueri* but rather had to rely on figures and descriptions in the literature. It is hoped that the study of well-preserved material with a specific goal toward filling out the character matrix may lead to a greater understanding of the position of Pemphicidae van Straelen, 1928 within Reptantia.

In contrast to the case of *Pemphix sueri*, we obtained great accuracy of resolution for other glypheoid genera in our study, *Glyphea* and *Mecochirus*. When used together (analyses G-J, Figs. 5 and 6) these consistently emerged as sister taxa of *Neoglyphea inopinata*, as also proved to be the case in the ordered analysis C and E when *Glyphea* and *Mecochirus* were entered separately. The unordered analyses saw glypheoids emerge either as paraphyletic (D, Fig. 3), or as a part of a collapsed clade of Astacida (F, Fig. 4).

***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 "glypheoidean 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 as yet undetected array of mid-Paleozoic fossil decapods are missing and yet to be discovered.

While there are problems that emerge from this

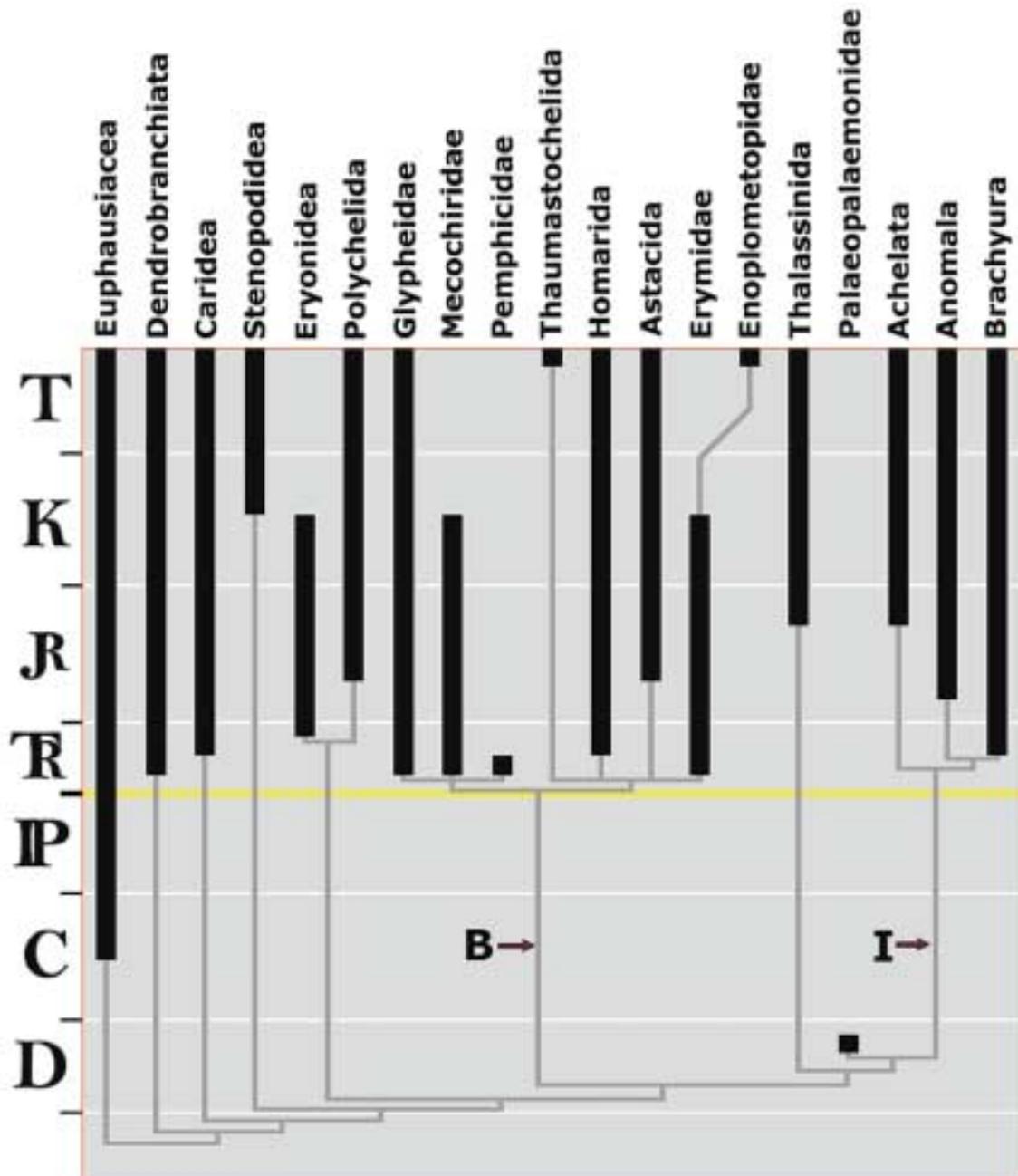


Fig. 7. Inferred cladogram, arranged to reflect stratigraphy. **I** represents the possible location of *Imocaris*[†], and **B** represents the possible location of purported crayfish burrows. Note the abrupt radiation soon after the Permo-Triassic boundary.

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)

Glypheoidea

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 Eupreptantia. Consequently, on the diagram of Figure 7 we have interpreted the burrows of Hasiotis 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†, Thaumastochelidae, 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, this new diagram includes far fewer such ghost ranges. Instead, there is evidence for a great radiation of decapod diversity in the early part of the Triassic. This would fit well with the mass extinction at the end of the Permian, after which few predators and few competitors of the decapods would have survived. It follows that the discovery of fossil decapods from before the Permo-Triassic boundary, 245 million years ago, would be of enormous help if we were to reach a widely accepted view of the phylogeny of the decapods. Such an "ancestor" would be able to confirm or deny countless hypotheses about the development of characters and lineages.

Conclusion

Now that we have a suitably robust data matrix for 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.

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Appendix I - Data Matrix

Character states marked "a" are polymorphic [0 and 1], and the character state marked "b" is polymorphic [1 and 2]. The 44 characters are numbered following Dixon *et al.* (2003) for ease of comparison.

	00000	01111	11222	22233	33334	44444	45556	66666	6677
	25678	90456	89013	67834	56791	23468	90242	34567	8901
<i>Euphausia superba</i>	00000	01000	00001	00000	00000	00000	00000	00000	0000
<i>Metapenaeus monoceros</i>	00000	01000	00011	00000	00010	00000	00000	00000	0000
<i>Sicyonia cristata</i>	00000	01000	00011	00000	00010	00100	00000	10010	0000
<i>Atyoida pilipes</i>	00000	01000	00021	10000	00010	00001	10001	00010	0000
<i>Leander tenuicornis</i>	00000	01011	00221	10000	00010	00001	10001	00010	0000
<i>Macrobrachium lar</i>	00000	01001	00221	10000	00010	00001	10001	00010	0000
<i>Crangon crangon</i>	00000	01000	00121	10000	00000	00001	10001	00010	0000
<i>Alpheus cylindricus</i>	00000	01000	00121	10000	00000	00001	11001	00010	0000
<i>Stenopus hispidus</i>	00000	01100	00311	10000	00010	10001	10000	00010	0000
<i>Polycheles typhlops</i>	- 0000	01001	00111	10000	2a001	11101	10101	00000	0000
<i>Polycheles galil</i>	- 0000	01001	00111	10000	21001	11101	10101	00000	0000
<i>Thaumastocheles dochmiodon</i>	- 0000	01011	10111	31000	01010	20101	11101	00200	0010
<i>Enoplometopus occidentalis</i>	00000	01111	10111	31000	1a010	00101	10101	10110	0011
<i>Homarus gammarus</i>	00000	01111	10111	31000	00010	20101	11101	10110	0010
<i>Astacus astacus</i>	00000	01111	10111	31100	00010	20001	10101	00110	2010
<i>Austropotamobius pallipes</i>	00000	01111	10111	31100	00010	20001	10101	00110	2010
<i>Cambarus bartoni</i>	00000	01111	10111	31100	00010	20001	10101	00110	2010
<i>Neoglyphea inopinata</i>	00000	01110	10101	30000	00010	20101	10101	00100	0010
<i>Jaxea nocturna</i>	10000	01112	10131	30210	0?010	10011	10101	00100	0020
<i>Thalassina anomala</i>	00001	01112	10121	30210	00010	22013	11100	00101	0100
<i>Calocaris macandreae</i>	- 0001	01112	10121	30210	00010	20103	11100	00110	0010
<i>Eiconaxius acutifrons</i>	00000	01112	10121	30210	0?010	20003	11100	10100	0010
<i>Callianidea typa</i>	10000	01112	10120	30010	11000	23013	01-00	00100	0000
<i>Callianassa setimana</i>	10001	01113	10130	30010	11000	23013	01100	00100	0000
<i>Callianassa tyrrehena</i>	10001	01113	10130	30010	11000	20013	01100	00100	0000
<i>Upogebia pusilla</i>	10000	01?12	00131	30210	01010	20013	00100	00100	0000
<i>Upogebia deltaura</i>	10000	01112	00131	30210	01010	20013	00100	00100	0000
<i>Palinurellus gundlachi</i>	01111	12111	12101	32000	0?011	10001	10101	10110	1000
<i>Scyllarus arctus</i>	01111	12012	02101	10000	0?001	00001	10101	10110	1000
<i>Aegla</i> sp.	00211	00112	22131	30002	00011	10013	00111	00200	0000
<i>Galathea squamifera</i>	01111	00112	12131	30002	01012	13011	00111	00300	0000
<i>Agononida incerta</i>	01111	00112	12131	30002	01012	13011	00111	00300	0000
<i>Hippa pacifica</i>	01011	00102	01102	32102	01000	03013	20111	00404	0000
<i>Emerita portoricensis</i>	00011	00?10	01102	22102	0?000	13013	20111	00404	0000

<i>Pylocheles</i> sp.	00110	00112	10131	30004	11101	10013	00110	01202	0000
<i>Coenobita brevimanus</i>	00110	00111	11131	30004	01101	10013	-2 - - -	- 1302	0000
<i>Pagurus bernhardus</i>	01110	00111	21131	30004	01101	10013	-2 - - -	- 1202	0000
<i>Calcinus tibicen</i>	01110	00111	10131	30004	01101	10013	-2 - - -	- 1202	0000
<i>Homola barbata</i>	01111	01113	12131	30001	00001	10012	00120	00103	03-0
<i>Lauridromia dehaani</i>	01111	01113	11131	32103	01002	13013	00120	00103	02-0
<i>Maja squinado</i>	01111	02113	12031	30000	00001	13013	00120	00103	03-0
<i>Carcinus maenas</i>	01111	02113	12131	32005	00002	13013	01120	- 0103	03-0
<i>Ocypode</i> sp.	01?11	02113	02131	30005	00002	13013	01120	00103	03-0
<i>Palaeopalaemon</i> †	???00	0b???	?2131	3?0?0	00010	10111	00100	00400	0000
<i>Glaessnericaris</i> †	00000	01?1?	??111	3?0?0	20010	10?01	00101	00210	0010
<i>Eryon</i> †	00000	00101	10111	30200	20002	00101	10101	00000	0000
<i>Eryma</i> †	00000	01111	10111	31000	11010	20101	10101	10410	0011
<i>Glyphea</i> †	00000	01?11	?0101	3?000	00010	20?13	?0101	10100	1010
<i>Mecochirus</i> †	00000	01???	10101	3?1?0	00010	20?01	10101	101?0	?010
<i>Pemphix sueri</i> †	?0000	011??	?a111	?0000	00010	10001	1010?	10100	0010

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.

Character	status in Dixon <i>et al.</i> (2003)	status in this study
1: orbito-antennularis fossa	step-matrix	excluded: hidden
2: eyestalks	step-matrix	two-state
3: ocular ornamentation	unordered	excluded: rarely preserved
4: antennular chamber	two-state	excluded: hidden
5: first antenna (A1) form	ordered	two-state
6: A1 flagella	ordered	unchanged
7: A1 peduncle	step-matrix	two-state
8: scaphocerite	two-state	unchanged
9: second antenna (A2) size	ordered	two-state
10: A2 basal articles	ordered	unchanged
11: antennal gland opening	ordered	excluded: hidden
12: epistome	ordered	excluded: hidden
13: mandible articulation	two-state	excluded: hidden, articulation
14: mandibular form	step-matrix	two-state
15: third maxilliped (MXP3) dactylus	ordered	unchanged
16: MXP3 overall form	ordered	unchanged
17: MXP3 exopod	unordered	excluded: hidden
18: <i>crista dentata</i>	ordered	unchanged
19: thoracic sternite widths	ordered	unchanged
20: pereopods 1-3 (P1-P3)	step-matrix	unchanged
21: chelae	step-matrix	reduced step-matrix
22: sternite-coxa articulations	ordered	excluded: articulation
23: pereopod dactyli	ordered	unchanged
24: male pereopods	two-state	excluded: sexual dimorphism
25: P1 twist	unordered	excluded: articulation
26: P1 articulations	step-matrix	unchanged
27: P1 ischio-coxal process	unordered	unchanged
28: P1 ischio-meral articulation	unordered	unchanged
29: P1 basis and ischium	two-state	excluded: articulation
30: P2 setal row	two-state	excluded: rarely preserved

31: P3-P5 basis ischium and merus	ordered	excluded: articulation
32: gonopores	ordered	excluded: sexual dimorphism, rarely preserved
33: 7 th thoracic sternite	two-state	unchanged
34: P4 and P5	step-matrix	unchanged
35: P4 chela	ordered	unchanged
36: P5 chela	ordered	unchanged
37: P5 rasp	two-state	unchanged
38: 7 th and 8 th thoracic, and 1 st pleonic segments	ordered	excluded: articulation
39: rostrum	two-state	unchanged
40: carapace calcification	step-matrix	excluded: hidden
41: carapace shape	ordered	unchanged
42: transverse groove	ordered	unchanged
43: carapace margin	unordered	unchanged
44: carapace posterior suture / ridge	two-state	unchanged
45: carapace holding device	step-matrix	excluded: hidden
46: <i>lineae</i>	two-state	unchanged
47: gill morphology	step-matrix	excluded: hidden, rarely preserved
48: first pleonic somite	step-matrix	unchanged
49: lobes overlapping carapace	unordered	unchanged
50: symmetry	step-matrix	reduced, ordered
51: egg fate	two-state	excluded: rarely preserved
52: pleon cross-section	two-state	unchanged
53: pleon sexual dimorphism	unordered	excluded: sexual dimorphism
54: pleonic flexion	ordered	unchanged
55: pleonic calcification	ordered	excluded: hidden
56: pleonic hinges	ordered	excluded: hidden
57: pleopod form	ordered	excluded: rarely preserved
58: female first pleopod	ordered	excluded: sexual dimorphism, rarely preserved
59: combined male gonopod	two-state	excluded: sexual dimorphism, rarely preserved
60: male first pleopod	ordered	excluded: sexual dimorphism, rarely preserved
61: male second pleopod	ordered	excluded: sexual dimorphism, rarely preserved
62: second pleomere pleuron	two-state	unchanged
63: pleonites	two-state	unchanged
64: sixth pleonite transverse furrow	two-state	unchanged
65: telson	step-matrix	unchanged
66: telson spines	ordered	reduced, unordered
67: uropod form	step-matrix	unchanged
68: distal telson cuticle	unordered	unchanged
69: uropods	ordered	unchanged
70: diaereses	ordered	unchanged
71: median plate	not included	two-state

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 pereopods enlarged (66₃), telson spines present (66₁)

Reptantia: pleon dorso-ventrally compressed (52₁)

Polychelida: pereopod 4 chelate (35₂), carapace depressed (41_{1 or 2}), carapace with a posterior suture or

ridge (44₁)

Eureptantia: maxilliped 3 dactylus blunt (15₁), with a crista dentata [also in Eryonidae] (18₁), pereopod 1 enlarged (20₁), carpus-propodus and propodus-dactylus on pereopod 1 with two points of articulation for the joints [also in Eryonidae] (26₃), generally pereopod 4 chelate or subchelate (65_{1 or 2}).

Astacura: typically with a deep transverse groove on carapace (42₂), uropodal exopod with diaeresis (70₁).

Astacidea: pereopod 1 with long ischio-coxal process (70₁), typically telson spines present (66₁).

Astacida: pereopod 1 perpendicular (28₁).

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

Erymida: pereopod 4 semi-chelate (35₁), median plate on carapace (71₁).

Glypheoida: carapace with posterior suture or ridge (44₁).

Pemphicida: pleonites pointed (63₁), uropodal exopod with diaeresis (70₁).

Sterropoda: typically with maxilliped 3 short and pediform or operculiform (16_{2 or 3}), typically pereopod 1 chelate, pereopods 2 and 3 achelate (21₃), typically lineae present (46₁).

Thalassinida: generally with flattened eyestalks (2₁), typically ischio-meral articulation of pereopod 1 curved (28₂), 7th thoracic sternite enlarged and lobate

(33₁), typically transverse groove on carapace deep (42₂), typically 1st pleonic somite short and narrow (48₁).

Eurysternalia (*sensu lato*): thoracic sternites wide (19_{2 or 3}), transverse carapace groove shallow (42₁), often 2nd pleomere pleuron expanded and overlapping the 1st (62₁).

Palaeopalaemonida: carapace with a posterior suture or ridge (44₁).

Eurysternalia (*sensu stricto*): typically antennule flagella with annuli wider than long and flagella similar in length the 2nd peduncular segment (6₁), antennule peduncle z-shaped (7₁), generally scaphocerite absent or if present not articulated (8₁), generally antennule slightly curved (5₁), typically carapace depressed (41_{1 or 2}).

Achelata: antenna enlarged (9₁), basal articles of antenna fused to carapace (10₂), lobes from 1st pleonic pleura overlapping carapace (49₁), pleonites pointed (63₁), telson spines present (66₁), distal telson cuticle softer than proximally (68₁).

Meiura: typically some pattern of reduction and / or dislocation of pereopods 4 and 5 (3₄), typically 1st pleonic somite narrow (48_{2 or 3}), pleonic flexion not macrurous (54_{1 or 2}).