

Fossils and decapod phylogeny

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Abstract

An expanded series of morphological characters developed for a cladistic analysis of extant decapods has yielded a new hypothesis for the phylogeny of the group. Application of this database to selected fossil genera produces some interesting results and demonstrates the feasibility of treating fossils as full and equal partners in the study of decapod phylogenetic relationships. In addition, it seems clear that rigorous cladistic methods can be used to evaluate the phylogenetic positions of fossils, rather than *ad hoc* speculation.

Introduction

Our understanding of the phylogeny of the decapod crustaceans is a true work in progress. Although the matter was thought settled for many years, Burkenroad (1963, 1981) reopened debate on the subject. Some consensus about the relationships amongst the lower decapods quickly emerged around a paraphyletic arrangement of natantians, but most efforts were based on morphology (see Schram, 2001, for a summary). However, Scholtz & Richter (1995) undertook a new analysis based on examination of morphology that focused on the Reptantia and proposed a new phylogenetic scheme for these forms. They found polychelids to be a sister group to Eureptantia, within which the achelate forms were a sister clade to the Macrochelata. Within the latter, the old Astacidea was broken up to separate the clawed lobsters from a new group, the Fractosternalia. While there was uncertainty concerning the relationship of the fractostern crayfish and the thalassinideans, the Anomala and Brachyura were

closely related as Meiura. The analysis of Scholtz & Richter was based on the manual Method of Hennig, but Schram (2000, 2001) undertook a computer-based cladistic study, which essentially confirmed their results.

Nevertheless, some differences occurred in Schram's tree. *Enoplometopus* emerged separate from the other clawed lobsters; Astacida was separate from all the other fractosternalians; and *Neoglypheia* (the only living member of the Glypheoidea), although previously classified with the achelates, emerged within the higher fractosterns. The consensus values within the paraphyletic "lobsteroids", however, remained low.

A more comprehensive examination of decapod morphology was undertaken with additional taxa and characters by Dixon et al. (in press) and a new arrangement of higher taxa arose (Fig. 1). The fractostern clade disappeared and the characteristic features of that group were suggested to be a manifestation of burrowing life styles. In its place, the old Astacidea (now including the glypheoids, and subsuming *Enoplometopus* back into Homarida) re-emerged alongside a new clade, the Sterropoda. Within the latter group, the Thalassinida occur along with the Eurusternalia, a new grouping of achelates with meirans. The branching arrangements of this new tree remain very stable under various alternative options, and moreover present another positive result. The trees of Scholtz & Richter (1995) and Schram (2001) are unbalanced, presenting essentially a phylogenetic comb of sequentially arranged clades. The Dixon et al. tree is much more balanced, at least with regard to the Reptantia.

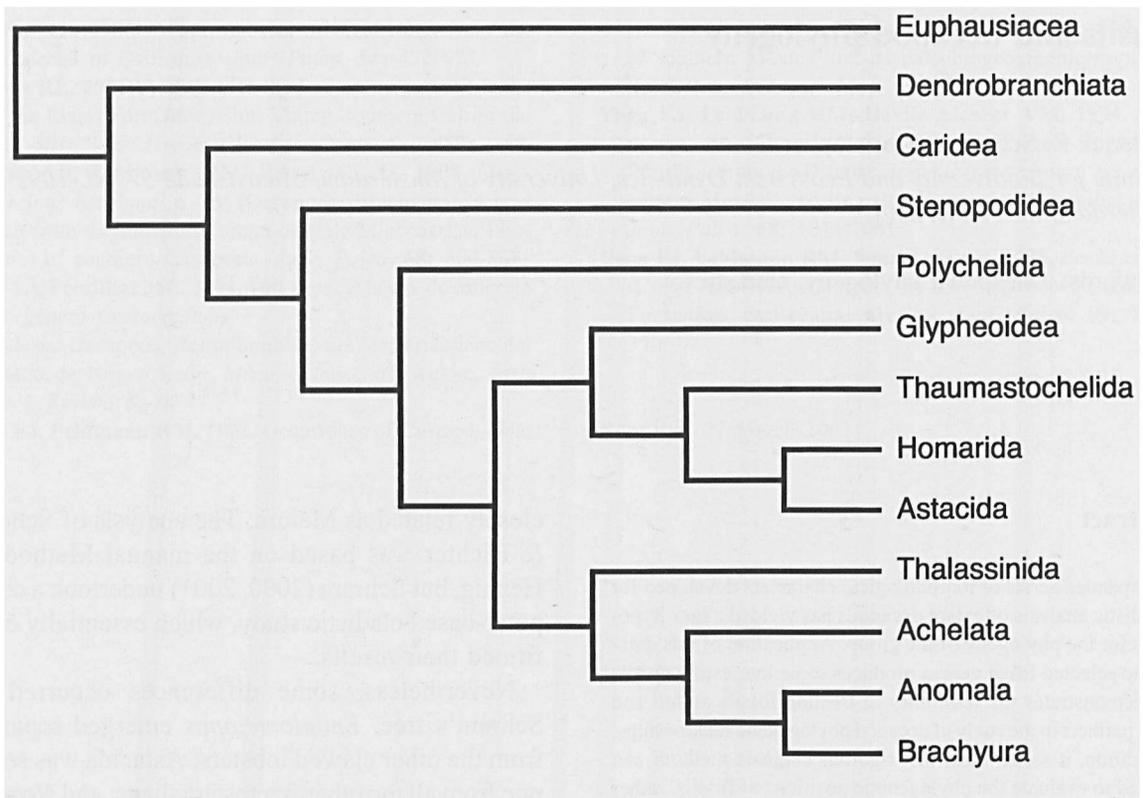


Fig. 1. Simplified cladogram from Dixon et al. (in press) of major relationships within Decapoda.

The Dixon et al. project was undertaken for two reasons. First, we wished to establish a morphological baseline for decapod phylogeny that could be further explored and tested with both the use of molecular sequence data, and additional expansion of the taxon sample. That project continues in collaboration with our colleague Dr Shane Ahyong. Second, we wanted to provide a starting point upon which the phylogenetic position of extinct fossil forms could be assessed. This paper is a progress report of that second project.

The analysis

The data set of Dixon et al. contains 70 characters, of which 52 are multistate. Of these, 60 characters were retained for this study based on the likelihood that they could be found on well-preserved fossils. Interestingly, the reduced database replicated the tree obtained from the full database, confirming the stability of the new tree. In addition,

we examined a selected array of well-preserved reptant forms from the fossil collections of the Teylers Museum (Haarlem). These included the Jurassic Solnhofen genera *Eryma*, *Eryon*, *Glyphea*, and *Mecochirus*, to which we also added scoring for the earliest decapod fossil, the Devonian lobster *Palaeopalaemon newberryi* (cf. Schram et al., 1978). Taxa were added individually and as a whole to the matrix to assess their individual and group effect on the resulting tree.

The results (Fig. 2) confirm the tree of Dixon et al. (in press). Furthermore, the lack of information about some features in the fossils at hand did not result in collapse any of many branching points of the master analysis. The two fossil glypheoid genera we studied grouped with the extant *Neoglyphea* and these together form a sister group to the Astacidea. *Eryma* is placed within the clawed lobsters as the sister taxon to *Enoplometopus*. *Eryon* and the polychelids do not form a monophyletic group as previously thought, but *Eryon* is instead basal to the Euphausiacea. The most surprising result

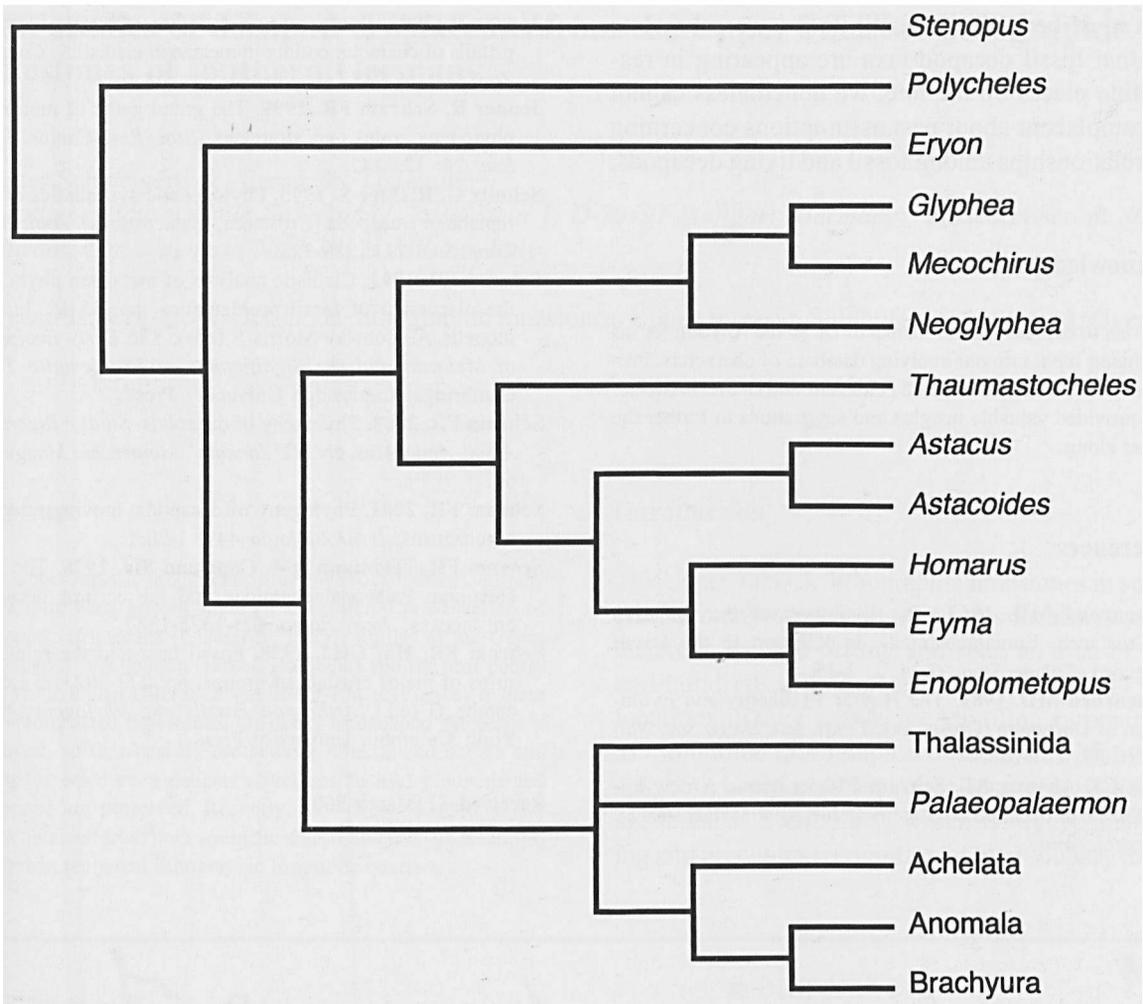


Fig. 2. Cladogram of relationships among genera of fossil and extant reptant decapods

was the placement of *Palaeopalaemon*, the earliest known decapod, high in the tree at an unresolved polytomy with the Thalassinida and the Euruster-nalia.

It seems clear from these preliminary results that the evaluation of fossils directly in connection with modern taxa to obtain a more comprehensive assessment of decapod phylogeny is feasible.

Any phylogenetic tree is only as good as the data that are included in the analysis. The resultant pattern applies only to a specific set of characters that have been scored for a specific array of taxa. Jenner & Schram (1999) demonstrated the need for the most comprehensive analyses possible in regard to both character and taxon sets to obtain accurate

assessments of phylogenetic relationships and Jenner (2002). Inclusion of fossils is thus a necessary component of any phylogenetic studies. Nevertheless, fossils afford distinct problems mainly related to missing data (Schram, 1991; Schram & Hof, 1998). Generally, one cannot overload an analysis with fossils without destabilizing the branching array of a tree. The missing data tends to inject too much uncertainty into the processing of data by the current algorithms. Thus it is encouraging to have a character set for decapod crustaceans that can produce stable trees and provide reasonable assessments concerning the phylogenetic affinities of fossilized forms.

The results obtained here for a selected set of

taxa must be built upon. While it is reassuring to see that fossil decapod taxa are appearing in reasonable places on the tree, we nonetheless cannot be complacent about past assumptions concerning the relationships among fossil and living decapods.

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