

CRUSTACEAN ISSUES 18



Decapod Crustacean Phylogenetics

edited by

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CRC Press
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CRC Press

Taylor & Francis Group

Boca Raton London New York

CRC Press is an imprint of the
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CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

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Printed in the United States of America on acid-free paper
10 9 8 7 6 5 4 3 2 1

International Standard Book Number-13: 978-1-4200-9258-5 (Hardcover)

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Library of Congress Cataloging-in-Publication Data

Decapod crustacean phylogenetics / editors, Joel W. Martin, Keith A. Crandall, Darryl L. Felder.
p. cm. -- (Crustacean issues)

Includes bibliographical references and index.

ISBN 978-1-4200-9258-5 (hardcover : alk. paper)

1. Decapoda (Crustacea) 2. Phylogeny. I. Martin, Joel W. II. Crandall, Keith A. III. Felder, Darryl L.
IV. Title. V. Series.

QL444.M33D44 2009

595.3'8138--dc22

2009001091

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<http://www.crcpress.com>

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On the Origin of Decapoda

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ABSTRACT

We do not have stem forms in the fossil record for Decapoda, unlike what we have for some groups of crustaceans. Thus, we currently lack a clear understanding concerning the origin of the decapods based on concrete data. Furthermore, several problem areas present themselves: 1) lack of consensus on the sister group to Decapoda, 2) the advanced nature of known Paleozoic decapods, 3) a restricted paleobiogeographic and paleoecologic distribution of these fossils, and 4) possibly incorrect assumptions about what a decapod ancestor should look like. For now the situation seems hopeless, although new data, new lines of evidence, and new perspectives might provide better insight some time in the future.

1 INTRODUCTION

Decapoda stands as one of the most diverse orders of crustaceans in terms of expressed variations on its body plan. That plan includes a carapace fused to the underlying thoracic segments, the first three pairs of thoracopods modified as maxillipeds [and thus their name, “deca”-“poda,” for their five pairs of pereopods], a pleon of six segments, and frequently (but not always) a tail fan including a well-developed telson and uropods. It is a very distinctive and easily recognizable body plan. Yet the origin of the order remains obscure. Indeed, comprehending the origin of any crown group is tied to the recognition and interpretation of its stem forms. In order to offer some promise of success, that task requires preservation of such forms in the fossil record.

It is not an unreasonable hope on our part to expect to find such fossils. For some groups of crustaceans, we do in fact possess sufficient knowledge. An example occurs in the unipeltate stomatopods, the mantis shrimp, a group of crustaceans that also exhibit a highly derived, quite distinctive (one might even say extreme) body plan. Calman (1904) recognized mantis shrimp as so idiosyncratic he erected a separate superorder, Hoplocarida, to accommodate them. Unipeltata, the crown stomatopods, have a modest fossil record that indicates the major superfamilies have Mesozoic origins (Hof 1998; Schram & Müller 2004). However, in recent years sufficient fossils in the Paleozoic have come to light that present a transition series that relates to the crown group Unipeltata (Schram 2007). We effectively now have stem forms that allow us to perceive how Unipeltata evolved.

However, no such array of fossil stem taxa exists as yet that would allow us to probe the earliest evolution of Decapoda. Indeed, what we encounter is a series of problems that obscure the ancient derivations of this important order.

2 PROBLEM ISSUES

I perceive four major areas of concern. These are: 1) no clear consensus about a sister group to Decapoda [and thus no guidance to orient us toward recognizing or interpreting possible stem forms], 2) the rather derived nature of the currently known Paleozoic decapod fossils, 3) a conundrum

concerning the paleobiogeography and paleoecology of Paleozoic malacostracans, and 4) possibly incorrect assumptions concerning an “ancestor” and thus misleading hypotheses about what we might be looking for in a stem form. Let us examine each of these in turn.

2.1 *Sister group to Decapoda*

Ever since the first cladistic analysis of eumalacostracan relationships, the issue of the identity of the sister taxon to Decapoda has presented almost too many options. Schram (1981, 1984) found that his shortest trees had the decapods in a clade with Amphionidacea and Euphausiacea, and these in turn had syncarids as a sister group. However, some of the trees had unresolved polychotomies among the major clades. Many researchers consider that Euphausiacea serves as a sister taxon; Calman (1904) assumed such when he placed Euphausiacea and Decapod together within his superorder Eucarida. Some more recent cladistic analyses indeed recovered such an arrangement, e.g., Wills (1998). However, as in Schram (1984), Amphionidacea appeared as the immediate sister group of Decapoda in the analysis of Richter & Scholtz (2001: fig. 7), but in their analysis Euphausiacea emerges as well-embedded within a group they named Xenommacarida, a clade that contains all the other eumalacostracans.

Hence, while Eucarida often finds expression in the cladograms of eumalacostracan relationships, it is not a particularly robust arrangement. In some ways, the amphionidaceans might serve as a stem form, often emerging from phylogenetic analyses between the decapods and the krill. Amphionidaceans do possess a nicely developed maxilliped, and the second and third thoracopods are miniature versions of the more posterior thoracopods but are widely separated from the maxilliped. However, other aspects of their body habitus isolate Amphionidacea as a unique taxon (see Schram 1986).

Schram & Hof (1998) in some of their cladograms obtained a pattern wherein an array of the Late Paleozoic “eocarids,” e.g., Belotelsonidea (Fig. 1A) and Waterstonellidea (Fig. 1B), emerge in sister status to decapods (sometimes in combination with Euphausiacea). However, perhaps one should first ask just what is an “eocarid.” The group at one time found expression as a formal taxon (Brooks 1962b), but the concept has entailed problems. First, the assemblage is a hodgepodge of often incompletely preserved forms, e.g., lacking complete sets of limbs such as *Eocaris oervigi* Brooks, 1962 (Brooks 1962a: fig. 1C), and *Archangeliphausia spinosa* Dzik, Ivantsov, & Deulin, 2004 (Dzik et al. 2004: fig. 2A). Second, Brooks’ definition of the order is ambiguous [“Length of thorax reduced, caridoid facies” (Brooks 1962b: 271)], and the list of implicit characters implied by “caridoid facies” is composed of plesiomorphic features. Third, some of the taxa placed within the order have proven to be highly specialized in their own right, e.g., Belotelsonidea and Waterstonellidea. Finally, some species once placed in the group have proven to be members of other higher taxa. For example, *Palaeopalaemon newberryi* (see below) was once assigned to the eocarids (Brooks 1962b) but has proven to be a true decapod (Schram et al. 1978). Other eocarid taxa yet might be reassigned to more clearly defined groups; for example, the genus *Eocaris* is probably an aechronectidan hoplocarid, and I suspect that *Archangeliphausia* from the Devonian of northwestern Russia may in fact represent an early eucarid (see below). Hence, the concept of “eocaridacea” is meaningless, a grade rather than a clade, and should not be used.

In regard to the origin of Decapoda, all this is unfortunate. Without a clear consensus on a sister group, we can neither reliably deduce the ground pattern for Decapoda nor derive any well-grounded hypotheses concerning an ancestral form.

2.2 *Paleozoic fossils*

A complicating factor in deducing the origins of the decapods resides in the rather derived state of the known Late Paleozoic decapod fossils. Indeed, the earliest definite decapod, the Late Devonian lobster-like *Palaeopalaemon newberryi* Whitfield, 1880 (Fig. 2), is a species that is clearly a reptant

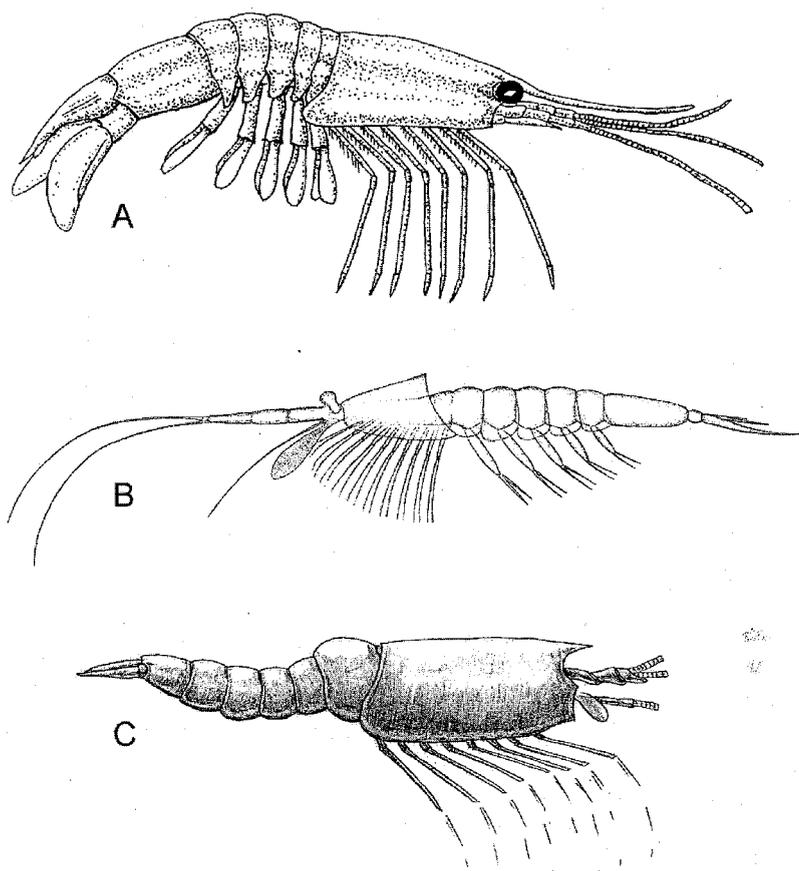


Figure 1. Examples of Late Paleozoic “eocarids.” (A) *Lobetelson mclaughlinae*, a Middle Pennsylvanian belotelsonid (from Schram 2007). (B) *Waterstonella grantonensis*, the Lower Carboniferous waterstonellid (from Briggs & Clarkson 1983). (C) *Eossoidea epiceron*, a Middle Pennsylvanian eumalacostracan of uncertain affinities (from Schram 1974).

(Schram et al. 1978; Hannibal & Feldmann 1984) and that in at least one analysis (Schram & Dixon 2005) emerges high in the decapod tree in a polytomy with Achelata, Anomura, and Brachyura. In any case, it is much too advanced a member of Reptantia to tell us much about decapod origins, let alone be considered an ancestor.

Another intriguing fossil is the Carboniferous genus *Imocaris* Schram & Mapes, 1984 (Fig. 3). Two species are recognized, *I. tuberculata* and *I. colombiensis*. Schram & Mapes (1984) assigned *Imocaris* to Dromiacea, i.e., suggested it belonged among podotreme brachyurans. However, only carapaces are known of this genus, and Racheboef & Villarroel (2003) chose to place *Imocaris* among the pygocephalomorph peracaridans. Resolving the affinities of *Imocaris* is a problem. The pygocephalomorphs bear a single cervical groove on the anterior part of their carapace, and the pattern in *Imocaris* appears more complex, with at least two. In addition, pygocephalomorphs typically bear a long and prominent rostrum, which *Imocaris* lacks. The species of *Imocaris* have a rather ornamented surface, such as one finds in some pygocephalomorphs such as *Teallicaris* and *Pseudoteallicaris*, but ornamentation is a secondary feature and not particularly useful in phylogenetic comparisons. I still prefer a dromiacean assignment for *Imocaris*, but I am willing to consider other

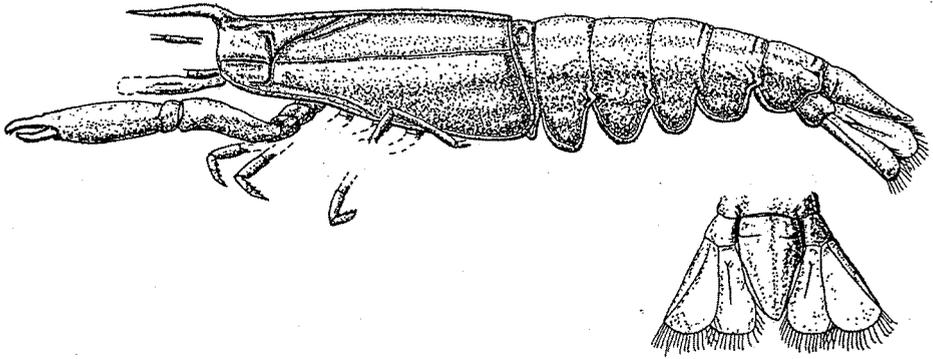


Figure 2. Late Devonian *Palaeopalaemon newberryi*, a reptant lobsteroid (modified from Schram et al. 1978; Hannibal & Feldmann 1985).

affinities for it, even with some group other than decapods or pygocephalomorphs. In any case (dromiacean, pygocephalomorph, or some other taxon), *Imocaris* tells us little about decapod origins.

One other set of fossils to consider consists of certain burrows in the Carboniferous of North America; Hasiotis (1999) believes crayfish made these. His interpretation focused on the markings on the walls of these burrows, which led him to conclude that these resemble similar features made by living crayfish in their burrows. There are no actual body fossils recovered from these tunnels. If these burrows do prove to be those of crayfish, they would again only record the presence of yet another rather derived form of reptantian in the Late Paleozoic.

The fossil record for the other major suborders of decapods essentially begins in the Mesozoic. The earliest members of Dendrobranchiata appear during the Triassic (see Garassino & Teruzzi 1995; Garassino et al. 1996), but a good fossil record for the group does not occur until the Jurassic Solnhofen Limestone (see Glaessner 1969). Fossils of Caridea are scarce; the earliest members apparently occur in the Jurassic, although those fossils are poorly preserved and of uncertain affinities (see Glaessner 1969). Reliably identified caridean fossils, however, do appear in the Cretaceous (Bravi & Garassino 1998a, 1998b; Bravi et al. 1999; Garassino 1997) with at least two families (Palaemonidae and Atyidae) represented there. Finally, Stenopodidea until recently had a problematic fossil record; Schram (1986) tentatively suggested that the Lower Jurassic form *Uncina posidoniae* might bear some relationship to the suborder. Subsequently, an apparent spongicolid, *Jilinocaris chinensis*, was identified from the Cretaceous of northern China (Schram et al. 2000), and a stenopodid, *Phoenice pasinii*, occurs in the Cretaceous of Lebanon (Garassino 2001). All of these Mesozoic decapods are more or less easily recognized members of their suborders and have nothing to tell us about decapod origins.

There are some puzzling Devonian fossils that have been recently recognized and bear consideration. Dzik et al. (2004) described *Archangeliphausia spinosa* from the Early Devonian of northeastern-most Europe (Fig. 4A). The fossils lack any preserved thoracic limbs. Nevertheless, the material suggests that the carapace was fused to the underlying thoracic segments. The fossils are flexed ventrally, but the carapaces do not appear to be lifted off the underlying thoracomeres. Furthermore, the segmental boundaries between the thoracic segments are preserved only ventrolaterally and do not extend to include the dorsal tergites—just what one would expect if the carapace were fused to the thoracomeres. The telson is not of the narrow, elongate, subtriangular form we associate with euphausiaceans and dendrobranchiates, but rather resembles the sub-quadrate form we often see in reptantians. I believe *Archangeliphausia spinosa* might in fact be at least a eucarid,

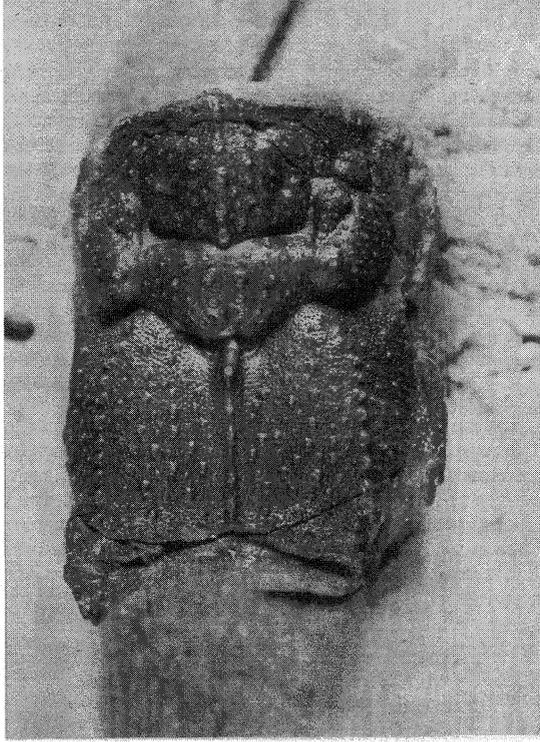


Figure 3. Lower Carboniferous *Imocaris tuberculata*, a probable dromiacean (from Schram & Mapes 1984).

and possibly another example of an advanced reptant decapod. We must wait for the collection of fossils with a full set of thoracic limbs.

Finally, another rather well-preserved, middle Paleozoic eumalacostracan is *Angustidontus seriatus* Cooper, 1936. Several species of *Angustidontus* occur in the Late Devonian and early Carboniferous across North America and Europe, and illustrate the difficulties entailed in studying early malacostracans. Originally, only the remarkable terminal segment of the maxilliped was known, and this was interpreted as a jaw of a fish. Rolfe & Dzik (2006) assembled a more extensive collection from Poland and in combination with previously collected material managed to definitively reconstruct this species as eumalacostracan (Fig. 4B). They compared *Angustidontus seriatus* to *Palaeopalaemon newberryi* and even suggested a possible synonymy of these taxa. However, *P. newberryi* is an entirely different animal, clearly a reptant decapod with the first pereopods bearing chelate claws and the second through fifth pereopods as walking limbs (Fig. 2). In contrast, *A. seriatus* has seven pairs of rather robust pereopods and an elongated specialized maxilliped, a distinctly dissimilar body habitus with its singular pair of maxillipeds. What is *Angustidontus*? If we try for a link with decapods, *A. seriatus* evokes Amphionidacea with the first thoracopods as maxillipeds. *Angustidontus*, however, would seem to be a specialized benthic form rather than a mesopelagic creature like *Amphionides*. An alternative assignment of *Angustidontus* might be within Lophogastrida because *A. seriatus* has rather wide thoracic sternites, not unlike those seen in *Gnathopausia* and the pygocephalomorphs. However, no indication of fossilized oöstegites was noted on any of the fossils studied, structures that are known to occur on pygocephalomorph fossils. The wide thoracic sternites on *A. seriatus* might be akin to such sternites seen in decapods such as Achelata. Thus, whether *Angustidontus* is an early eucarid is not certain.

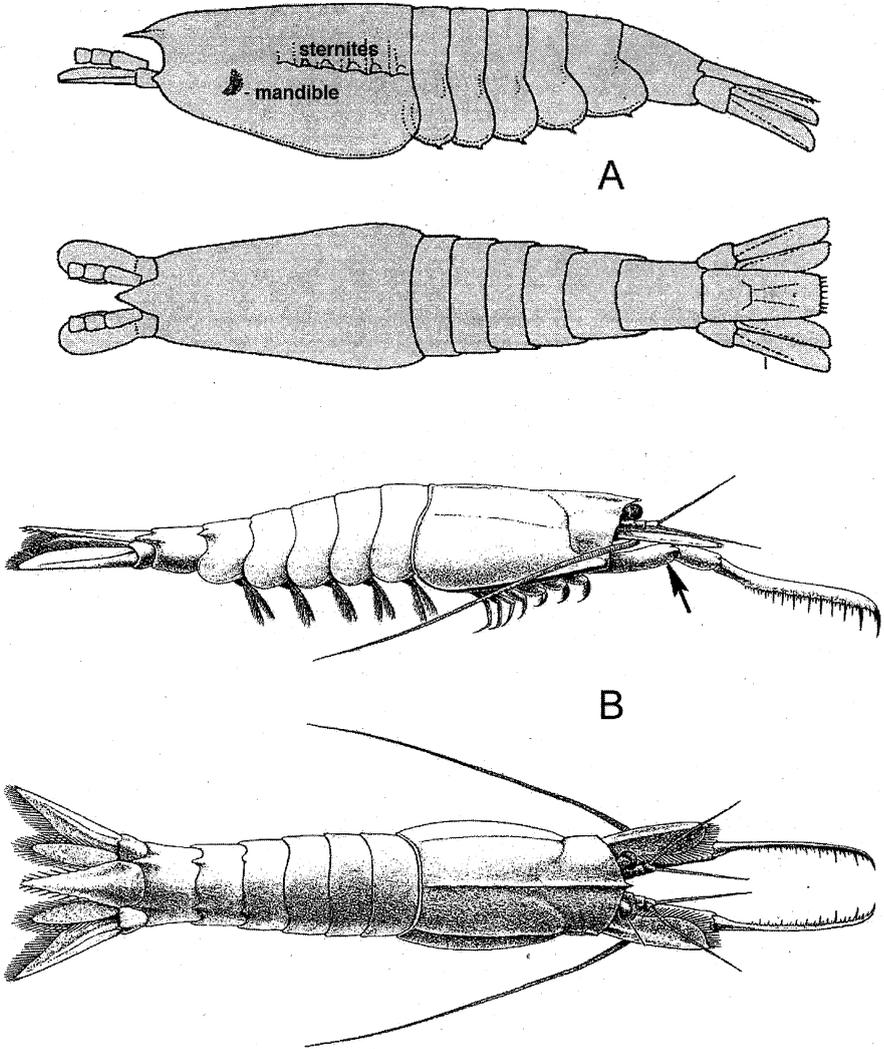


Figure 4. Lateral and dorsal reconstructions of Devonian eumalacostracans of uncertain affinities. (A) *Archangeliphausia spinosa*, a possible eucarid (modified from Dzik et al. 2004). (B) *Angustidontus seriatus*; note the large, specialized maxilliped [arrow] (modified from Rolfe & Dzik 2006).

In summary, while the fossil record of the Paleozoic decapods has interesting fossils, at present they tell us little about the origins of the group. The apparently derived nature of *Palaeopalaemon*, and possibly *Imocaris*, does indicate that there possibly was a long history of the order that extended back in time before the earliest fossils in the Late Devonian. *Angustidontus* and *Archangeliphautia* are intriguing in that they appear to indicate occurrences of at least eucarids, if not clear stem decapods, and hold out a promise of even earlier fossils relevant to decapod origins. How far back? Ordovician? Silurian? Cambrian? We cannot now say.

2.3 Paleobiogeography and paleoecology

One might feel better about this record if we saw an abundance of fossils from a wide array of localities across the world. However, as is the case for eumalacostracans and hoplocaridans as a whole, the Late Paleozoic record of the decapods has been up to now almost completely restricted to the equatorial island continent of Laurentia (Schram 1977). The Late Devonian *Palaeopalaemon newberryi* occurs in several localities across Ohio and Iowa. The Carboniferous *Imocaris tuberculata* was collected from Arkansas. A singular exception to this Laurentian pattern is *I. colombiensis*, which comes from what is now western Colombia on the Paleozoic continent of Gondwana. However, this site is not far paleogeographically from Arkansas during a time in which the continents were beginning to come together to form Pangaea. In a sense, it is the exception that proves the rule, since Schram (1977) postulated that a dispersal of higher malacostracan crustaceans out from Laurentia began with the formation of Pangaea. Nevertheless, compared to other malacostracans in the late Paleozoic, such as the hoplocaridans and peracaridans, the decapods have a paltry record.

Thus, what we have are three species that are decapods (possibly four, counting the elusive crayfish), from a handful of localities—clearly something is missing.

For instance, where were the decapods before the Devonian, assuming there was not a punctuation event in the Devonian or Late Silurian? The early and middle Paleozoic arthropods of the epicontinental seas of the world are not scarce. The diverse record of the trilobites needs no comment, but there was also an abundant array of xiphosurans, eurypterids, and thylacocephalans in those times. The latter two groups were effective predators. It is tempting to speculate that such an assortment of arthropods simply filled in most of the available niches on the epicontinental seas of those times. Thereafter, the late Devonian through Permian record of malacostracans is marked by an abundance of groups such as Hoplocarida, Syncarida, Peracarida (especially Pygocephalomorpha), Belotelsonidea, and Waterstonellidea. Was there too much competition from these diverse forms to allow the decapods to get established on the epicontinental seas of Laurentia? Such a conclusion would seem peculiar, since we live in a time when decapods have so completely dominated their habitats. Was it an instance of first come, first served?

Of course there are lots of places in the early and middle Paleozoic world where decapods might have lived. The decapods could have been denizens of the deep sea; the Panthalassic and Tethys Oceans were extensive. Or, taking a clue from the amphionidaceans, the decapods of that time may have been in the pelagic realm. Or, it is possible that decapods inhabited extremely cryptic habitats on the continents themselves such as interstitial, groundwater, and cave habitats. In regards to this last possibility, we should not overlook that small, cryptic forms were often important in the origin and early evolution of many groups, even phyla such as the mollusks (Mus et al. 2008). Discovery of the right sort of Lagerstätte in the pre-Devonian might provide us some material of significance in this regard.

2.4 Incorrect assumptions concerning “ancestors”

Implicit in all of the above is an assumption that a decapod “ancestor” will essentially be a caridoid with a well-developed pleon of 6 (maybe 7) somites, a carapace fused to the thorax, at least some kind of incipient specialization of the anterior thoracopods towards a maxillipedal condition, and

eggs shed freely into the water column. Such an animal, or series of animals, might yet emerge. We do have fossils of caridoids such as *Archangeliphousia*, *Belotelson*, *Essoidea*, *Lobetelson*, *Waterstonella*, and others, but as mentioned above just what some of these fossils represent is not always clear.

Another deeply embedded assumption about the evolution of Malacostraca is that the 7-segment pleon of the phyllocarids was in some way the precursor of the 6-segment pleon of hoplocaridans and eumalacostracans. However, this supposition seems quite unwarranted. For example, Scholtz (1995) clearly showed in the crayfish *Cherax destructor* that the expression of *engrailed* (a marker for segment boundaries in the arthropod trunk) displays nine, rather than six (or even seven), *engrailed* stripes in the pleon. The ninth stripe is faint and quickly fades to leave eight stripes; the sixth through eighth eventually merge to produce the final 6-segment pleon of the crayfish.

Moreover, this is not a unique pattern. Knopf et al. (2006) recorded in the early development of the amphipod *Orchestia cavimana* eight clearly delineated segmental blocks of cells in the early differentiation of the pleon. In fact, the eighth *Anlage* gives rise to a pair of lateral bulges, and as the seventh and eighth somites are slowly incorporated into the growing sixth pleomere, the bulges continue to grow into distinct lobes that migrate dorsad and mediad to eventually form the so-called bifurcated telson. The adult amphipod pleon clearly begins as a series of eight segmental units.

Finally, in four species of the hermit crab genus *Porcellanopagurus*, a peculiar condition is seen in the urosomal region (cf. McLaughlin 2000). For example, in *P. nihonkaiensis* (Fig. 5), an elongate area of non-sclerotized cuticle separates the tergite of the sixth pleomere and the small telson (Komai & Takeda 2006). This region is clearly not a proximal section of the telson, which retains its characteristic form. From consideration of the larval development of *Porcellanopagurus*, it is obvious that the anus appears initially on the ventral surface of the telson *Anlage* and migrates to a terminal position by the adult stage; hence, this non-sclerotized region has nothing to do with the telson. McLaughlin (personal communication) thinks that this area might somehow be a posterior extension of the sixth pleomere. A similar arrangement is seen in some species of *Solitariopagurus*. Nevertheless, such an extension of a sixth somite posterior to the attachment of the pleopods would be unique. So, what is this? Might this non-sclerotized region be a vestige of additional somites between the sixth pleomere and the telson? The only data that might speak against this as a remnant of such somites are that the area grows in size with growth of an individual. In the examples cited above from *Cherax* and *Orchestia*, the tissues attributed to the putative seventh and eighth somites decrease in size and disappear as the individuals grow. As an alternative hypothesis to consider, I suggest that this tissue does represent remnants of post-sixth somite pleomeres and is worthy of further investigation.

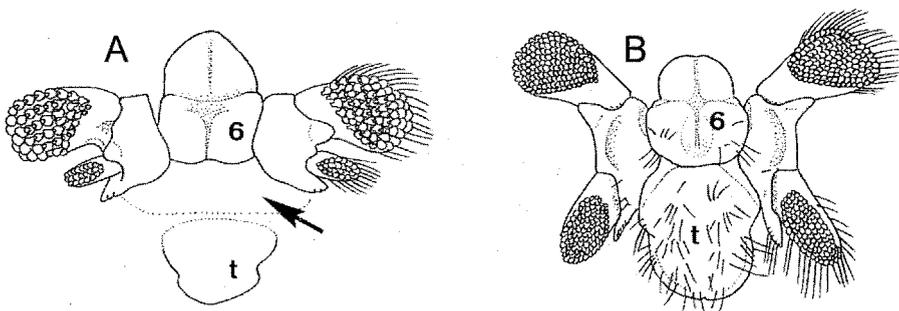


Figure 5. Pleon terminus of pagurid hermit crabs of the genus *Porcellanopagurus* (from Komai & Takeda 2006). (A) *P. nihonkaiensis*; note non-sclerotized region [arrow] between uropod-bearing sixth pleomere [6] and telson [t]. (B) *P. japonicus*, with a more typical anatomy of the urosome.

Just how all this impinges on ground patterns within Eumalacostraca is not clear at this time. However, instead of a 7-to-6 pattern long assumed to be the case, there are now alternative hypotheses to be entertained, viz., 8-to-7-to-6, or even separate scenarios of 8-to-7 and 8-to-6. What is clear is that we should not be surprised to find somewhere in the early or middle Paleozoic fossils of eumalacostracan-like creatures with more than the “expected” number of pleomers.

Another line of evidence that impinges on hypotheses about ancestors arises from a consideration of the central nervous systems of various arthropods. Harzsch (2004) summarizes a series of detailed investigations of brain anatomy. Characteristic patterns of olfactory-globular tracts with chiasmata, olfactory neuropils with glomeruli, and lateral mechano-sensory antenna 1 neuropils suggest a set of synapomorphies shared by Malacostraca and Remipedia. A set of further unique features in regard to the specializations of the protocerebrum and the enervation of the compound eyes draws Hexapoda into this clade. These latter characters would seem to exclude at least the living remipedes, but it is quite possible the fossil enantiopodan remipedes, such as *Tesnusocaris goldichi*, which had very well-developed compound eyes, possessed protocerebral chiasmata as well. Since this complex CNS anatomy could be interpreted as too complicated to be anything other than shared apomorphies, those groups that possess these features might be related. That would mean that the insects, malacostracans, and remipedes form a monophyletic clade, with remipedes and malacostracans as sister groups.

This is a fascinating hypothesis, and it parallels the independent analysis of Schram & Koenemann (2004), which focused on matters of *Bauplan* in crustaceans such as locations of gonopores, *Hox*-gene expression, and numbers and types of trunk segments. They, too, obtained from their cladistic analysis a pattern wherein Remipedia emerged as the sister group to Malacostraca, as well as the core Maxillopoda. In the Schram & Koenemann scenario, we could envision an ancestor with a 16-segment trunk that gave rise to a more derived form bearing an 8-segment thorax and 8-segment pleon, which in turn laid the ground pattern for a line leading to malacostracans.

How all this might bear on the origins of decapods I don't know. On the one hand, the decapods probably emerged after the events suggested above. On the other hand, what comes early has to affect what comes later, and clearly what we had always assumed about caridoid ancestors must be tempered by what we know now. Perhaps we should be willing to consider a non-caridoid ancestor for decapods with weak differentiation between anterior (thorax) and posterior (pleon), a pleon with more than 6 somites, with incipient differentiation of the anterior three thoracopods (putative maxillipeds), and from a cryptic habitat such as groundwater or caves.

3 CONCLUSIONS

It would have been nice to suggest a simple little scenario here for the origin of Decapoda with a sequence of fossils at hand that would fill in the details. Unfortunately, this is not now the case. Even when we have such details, such as that seen in the wide array of Paleozoic pre-mantis shrimp relevant to scenarios about the origins of unipeltate Stomatopoda, the pattern derived is not entirely straightforward. In that example, Schram (2007) could arrange the fossils in a row wherein the increasing specialization and enlargement of the ballistic second maxilliped could be explained. However, the actual cladistic analysis of all the scored characters on these fossils indicated that this expected straight-line pattern had to be tempered by information related to the parallel evolution of the stomatopod pleon, and especially the telson.

One has to take the data as they present themselves. I suspect that while we can hope to see fossils someday that display a series of specializations of the maxillipeds toward a decapod condition, we may have to moderate our expectations. As in the stomatopods, we might have to take into account the evolution of the pleon and its urosome, or even some other aspects of the decapod body plan, to arrive at a complete understanding of the origins of this fascinating group.

ACKNOWLEDGEMENTS

I wish to thank Dr. Pat McLaughlin for showing me the wonders of hermit crab morphology and for reading an early version of the text and making some constructive comments. Prof. Rod Feldmann and Dr. Carrie Schweitzer convinced me that one should express some caution about the possible affinities of *Imocaris*.

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