

CRUSTACEAN ISSUES 18



# Decapod Crustacean Phylogenetics

edited by

**Joel W. Martin, Keith A. Crandall, and Darryl L. Felder**



**CRC Press**  
Taylor & Francis Group

# Decapod Crustacean Phylogenetics

Edited by

**Joel W. Martin**

Natural History Museum of L. A. County  
Los Angeles, California, U. S. A.

**Keith A. Crandall**

Brigham Young University  
Provo, Utah, U. S. A.

**Darryl L. Felder**

University of Louisiana  
Lafayette, Louisiana, U. S. A.



**CRC Press**

Taylor & Francis Group

Boca Raton London New York

---

CRC Press is an imprint of the  
Taylor & Francis Group, an **informa** business

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

© 2009 by Taylor & Francis Group, LLC  
CRC Press is an imprint of Taylor & Francis Group, an Informa business

No claim to original U.S. Government works  
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)

This book contains information obtained from authentic and highly regarded sources. Reasonable efforts have been made to publish reliable data and information, but the author and publisher cannot assume responsibility for the validity of all materials or the consequences of their use. The authors and publishers have attempted to trace the copyright holders of all material reproduced in this publication and apologize to copyright holders if permission to publish in this form has not been obtained. If any copyright material has not been acknowledged please write and let us know so we may rectify in any future reprint.

Except as permitted under U.S. Copyright Law, no part of this book may be reprinted, reproduced, transmitted, or utilized in any form by any electronic, mechanical, or other means, now known or hereafter invented, including photocopying, microfilming, and recording, or in any information storage or retrieval system, without written permission from the publishers.

For permission to photocopy or use material electronically from this work, please access [www.copyright.com](http://www.copyright.com) (<http://www.copyright.com/>) or contact the Copyright Clearance Center, Inc. (CCC), 222 Rosewood Drive, Danvers, MA 01923, 978-750-8400. CCC is a not-for-profit organization that provides licenses and registration for a variety of users. For organizations that have been granted a photocopy license by the CCC, a separate system of payment has been arranged.

**Trademark Notice:** Product or corporate names may be trademarks or registered trademarks, and are used only for identification and explanation without intent to infringe.

---

**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

---

Visit the Taylor & Francis Web site at  
<http://www.taylorandfrancis.com>

and the CRC Press Web site at  
<http://www.crcpress.com>

# Contents

Preface	ix
JOEL W. MARTIN, KEITH A. CRANDALL & DARRYL L. FELDER	
I <i>Overviews of Decapod Phylogeny</i>	
On the Origin of Decapoda	3
FREDERICK R. SCHRAM	
Decapod Phylogenetics and Molecular Evolution	15
ALICIA TOON, MAEGAN FINLEY, JEFFREY STAPLES & KEITH A. CRANDALL	
Development, Genes, and Decapod Evolution	31
GERHARD SCHOLTZ, ARKHAT ABZHANOV, FREDERIKE ALWES, CATERINA BIFFIS & JULIA PINT	
Mitochondrial DNA and Decapod Phylogenies: The Importance of Pseudogenes and Primer Optimization	47
CHRISTOPH D. SCHUBART	
Phylogenetic Inference Using Molecular Data	67
FERRAN PALERO & KEITH A. CRANDALL	
Decapod Phylogeny: What Can Protein-Coding Genes Tell Us?	89
K.H. CHU, L.M. TSANG, K.Y. MA, T.Y. CHAN & P.K.L. NG	
Spermatozoal Morphology and Its Bearing on Decapod Phylogeny	101
CHRISTOPHER TUDGE	
The Evolution of Mating Systems in Decapod Crustaceans	121
AKIRA ASAKURA	
A Shrimp’s Eye View of Evolution: How Useful Are Visual Characters in Decapod Phylogenetics?	183
MEGAN L. PORTER & THOMAS W. CRONIN	
Crustacean Parasites as Phylogenetic Indicators in Decapod Evolution	197
CHRISTOPHER B. BOYKO & JASON D. WILLIAMS	
The Bearing of Larval Morphology on Brachyuran Phylogeny	221
PAUL F. CLARK	

## II *Advances in Our Knowledge of Shrimp-Like Decapods*

- Evolution and Radiation of Shrimp-Like Decapods: An Overview 245  
CHARLES H.J.M. FRANSEN & SAMMY DE GRAVE
- A Preliminary Phylogenetic Analysis of the Dendrobranchiata Based on Morphological Characters 261  
CAROLINA TAVARES, CRISTIANA SEREJO & JOEL W. MARTIN
- Phylogeny of the Infraorder Caridea Based on Mitochondrial and Nuclear Genes (Crustacea: Decapoda) 281  
HEATHER D. BRACKEN, SAMMY DE GRAVE & DARRYL L. FELDER

## III *Advances in Our Knowledge of the Thalassinidea and Lobster-Like Groups*

- Molecular Phylogeny of the Thalassinidea Based on Nuclear and Mitochondrial Genes 309  
RAFAEL ROBLES, CHRISTOPHER C. TUDGE, PETER C. DWORSCHAK, GARY C.B. POORE & DARRYL L. FELDER
- Molecular Phylogeny of the Family Callinassidae Based on Preliminary Analyses of Two Mitochondrial Genes 327  
DARRYL L. FELDER & RAFAEL ROBLES
- The Timing of the Diversification of the Freshwater Crayfishes 343  
JESSE BREINHOLT, MARCOS PÉREZ-LOSADA & KEITH A. CRANDALL
- Phylogeny of Marine Clawed Lobster Families Nephropidae Dana, 1852, and Thaumastochelidae Bate, 1888, Based on Mitochondrial Genes 357  
DALE TSHUDY, RAFAEL ROBLES, TIN-YAM CHAN, KA CHAI HO, KA HOU CHU, SHANE T. AHYONG & DARRYL L. FELDER
- The Polychelidan Lobsters: Phylogeny and Systematics (Polychelida: Polychelidae) 369  
SHANE T. AHYONG

## IV *Advances in Our Knowledge of the Anomura*

- Anomuran Phylogeny: New Insights from Molecular Data 399  
SHANE T. AHYONG, KAREEN E. SCHNABEL & ELIZABETH W. MAAS

## V *Advances in Our Knowledge of the Brachyura*

- Is the Brachyura Podotremata a Monophyletic Group? 417  
GERHARD SCHOLTZ & COLIN L. MCLAY

Assessing the Contribution of Molecular and Larval Morphological Characters in a Combined Phylogenetic Analysis of the Superfamily Majoidea	437
KRISTIN M. HULTGREN, GUILLERMO GUERAO, FERNANDO P.L. MARQUES & FERRAN P. PALERO	
Molecular Genetic Re-Examination of Subfamilies and Polyphyly in the Family Pinnotheridae (Crustacea: Decapoda)	457
EMMA PALACIOS-THEIL, JOSÉ A. CUESTA, ERNESTO CAMPOS & DARRYL L. FELDER	
Evolutionary Origin of the Gall Crabs (Family Cryptochiridae) Based on 16S rDNA Sequence Data	475
REGINA WETZER, JOEL W. MARTIN & SARAH L. BOYCE	
Systematics, Evolution, and Biogeography of Freshwater Crabs	491
NEIL CUMBERLIDGE & PETER K.L. NG	
Phylogeny and Biogeography of Asian Freshwater Crabs of the Family Gecarcinucidae (Brachyura: Potamoidea)	509
SEBASTIAN KLAUS, DIRK BRANDIS, PETER K.L. NG, DARREN C.J. YEO & CHRISTOPH D. SCHUBART	
A Proposal for a New Classification of Portunoidea and Cancroidea (Brachyura: Heterotremata) Based on Two Independent Molecular Phylogenies	533
CHRISTOPH D. SCHUBART & SILKE REUSCHEL	
Molecular Phylogeny of Western Atlantic Representatives of the Genus <i>Hexapanopeus</i> (Decapoda: Brachyura: Panopeidae)	551
BRENT P. THOMA, CHRISTOPH D. SCHUBART & DARRYL L. FELDER	
Molecular Phylogeny of the Genus <i>Cronius</i> Stimpson, 1860, with Reassignment of <i>C. tumidulus</i> and Several American Species of <i>Portunus</i> to the Genus <i>Achelous</i> De Haan, 1833 (Brachyura: Portunidae)	567
FERNANDO L. MANTELATTO, RAFAEL ROBLES, CHRISTOPH D. SCHUBART & DARRYL L. FELDER	
Index	581
Color Insert	

# On the Origin of Decapoda

FREDERICK R. SCHRAM

*Burke Museum, University of Washington, Seattle, U.S.A. Contact address: PO Box 1567, Langley WA 98260, U.S.A.*

## 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.

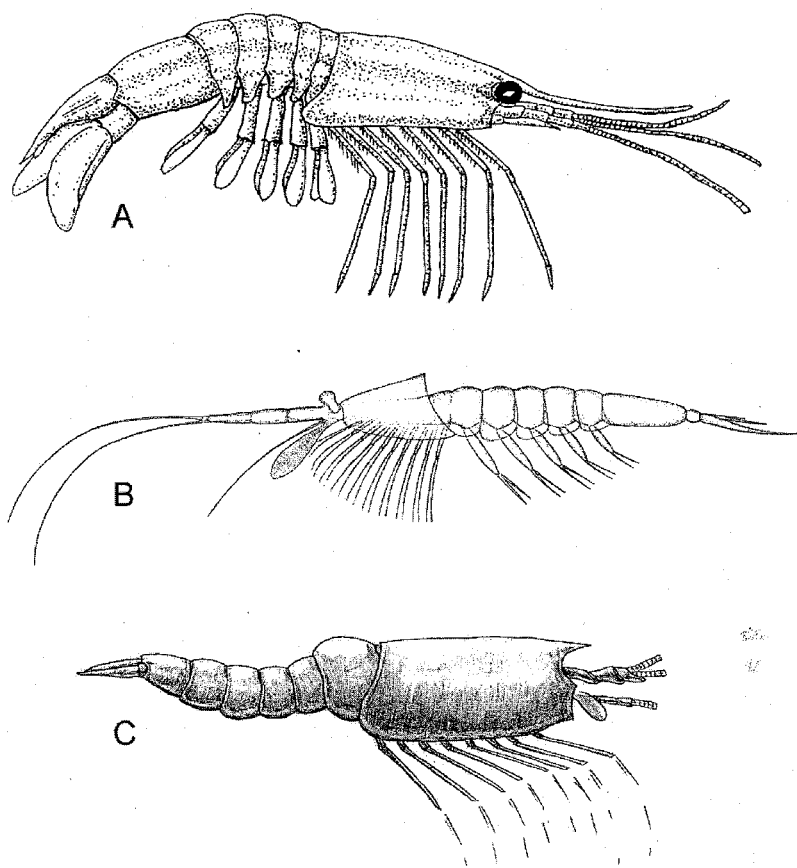
Hence, while Eucarida often finds expression in the cladograms of eumalacostracan relationships, it is not a particularly robust arrangement. In some ways, the amphionidaceans might serve as a stem form, often emerging from phylogenetic analyses between the decapods and the krill. Amphionidaceans do 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

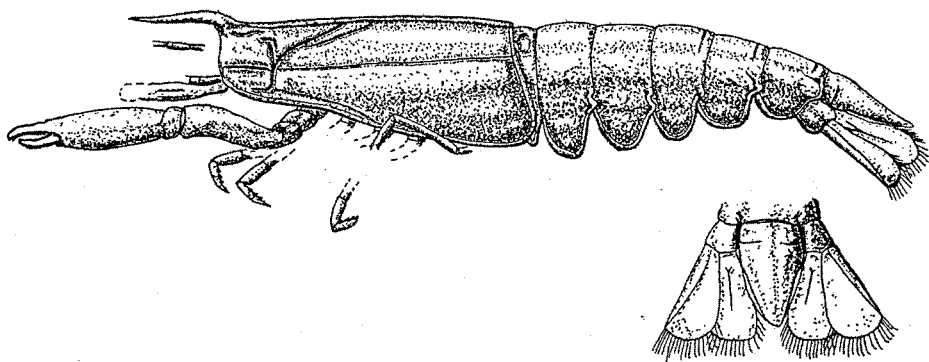
A complicating factor in deducing the origins of the decapods resides in the rather derived state of the known Late Paleozoic decapod fossils. Indeed, the earliest definite decapod, the Late Devonian lobster-like *Palaeopalaemon newberryi* Whitfield, 1880 (Fig. 2), is a species that is clearly a reptant



**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) *Esoidea 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 *Tealliocaris* and *Pseudotealliocaris*, 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



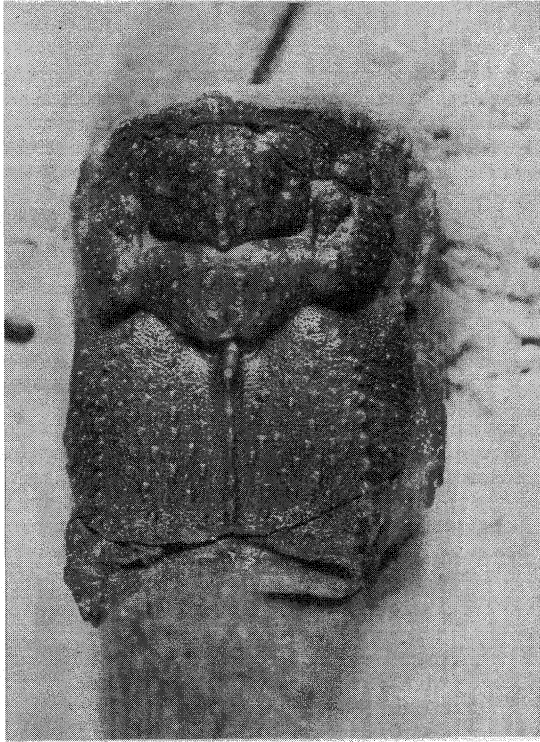
**Figure 2.** Late Devonian *Palaeopalaemon newberryi*, a reptant lobsteroid (modified from Schram et al. 1978; Hannibal & Feldmann 1985).

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, *Phoenixe 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.

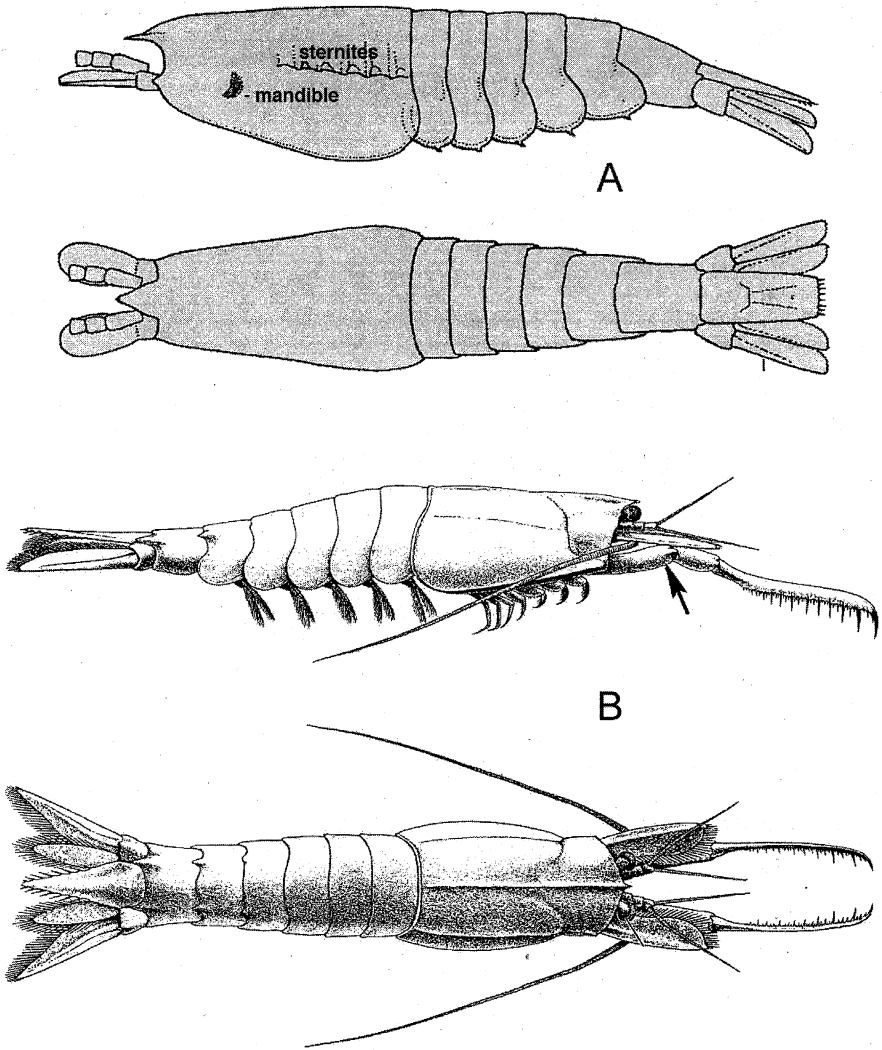
There are some puzzling Devonian fossils that have been recently recognized and bear consideration. Dzik et al. (2004) described *Archangeliphausia spinosa* from the Early Devonian of northeastern-most Europe (Fig. 4A). The fossils lack any preserved thoracic limbs. Nevertheless, the material suggests 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 *Gnathophausia* 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 *Archangeliphausia* 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”

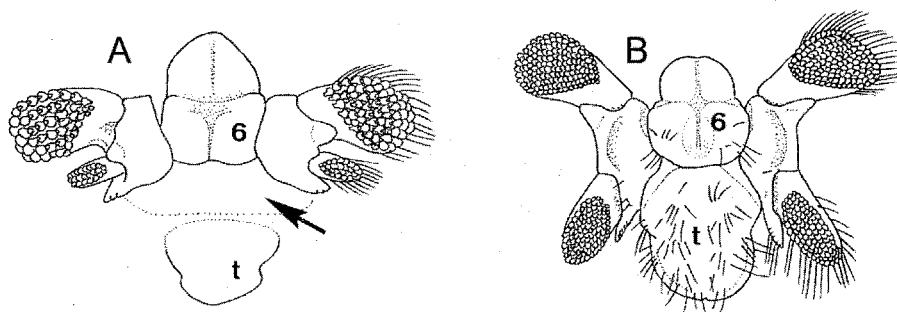
Implicit in all of the above is an assumption that a decapod “ancestor” will essentially be a caridoid with a well-developed pleon of 6 (maybe 7) somites, a carapace fused to the thorax, at least some kind of incipient specialization of the anterior thoracopods towards a maxillipedal condition, and

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 *Archangeliphausia*, *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*.

## REFERENCES

- Bravi, S. & Garassino, A. 1998a. Plattenkalk of the Lower Cretaceous (Albian) of Petina, in the Alburni Mounts (Campania, S Italy) and its decapod crustacean assemblage. *Atti Soc. It. Sci. Nat. Museo Civ. Stor. Nat., Milano* 138: 89–118.
- Bravi, S. & Garassino, A. 1998b. New biostratigraphic and palaeoecologic observations on the Plattenkalk of the Lower Cretaceous (Albian) of Pietraroja (Benevento, S Italy), and its decapod crustaceans assemblage. *Atti Soc. It. Sci. Nat. Museo Civ. Stor. Nat., Milano* 138: 119–171.
- Bravi, S., Coppa, M.G., Garassino, A. & Patricelli, R. 1999. *Palaemon vesolensis* n. sp. (Crustacea: Decapoda) from the Plattenkalk of Vesole Mount (Salerno, Southern Italy). *Atti Soc. It. Sci. Nat. Museo Civ. Stor. Nat., Milano* 140: 141–169.
- Briggs, D.E.G. & Clarkson, E.N.K. 1983. The Lower Carboniferous Granton ‘shrimp bed’, Edinburgh. *Spec. Pap. Palaeontol.* 30: 161–177.
- Brooks, H.K. 1962a. Devonian Eumalacostraca. *Arkiv för Zool.* 2: 307–317.
- Brooks, H.K. 1962b. The Paleozoic Eumalacostraca of North America. *Bull. Amer. Paleol.* 44: 163–338.
- Calman, W.D. 1904. On the classification of the Crustacea Malacostraca. *Ann. Mag. Nat. Hist.* (7) 13: 144–158.
- Cooper, C.L. 1936. Actinopterygian jaws from the Mississippian black shales of the Mississippi Valley. *J. Paleol.* 10: 92–94.
- Dzik, J., Ivantsov, A. Yu. & Deulin, Yu. V. 2004. Oldest shrimp and associated phyllocarid from the Lower Devonian of northern Russia. *Zool. J. Linn. Soc. Lond.* 1142: 83–90.
- Garassino, A. 1997. The macruran decapod crustaceans of the Lower Cretaceous (Lower Barremian) of Los Hoyas (Cuenca, Spain). *Atti Soc. It. Sci. Nat. Museo Civ. Stor. Nat., Milano* 137: 101–126.
- Garassino, A. 2001. New decapod crustaceans from the Cenomanian (Upper Cretaceous) of Lebanon. *Atti Soc. It. Sci. Nat. Museo Civ. Stor. Nat., Milano* 141: 237–250.
- Garassino, A. & Teruzzi, G. 1995. Studies on Permo–Trias of Madagascar. 3. The decapod crustaceans of the Ambilobé region (NW Madagascar). *Atti Soc. It. Sci. Nat. Museo Civ. Stor. Nat., Milano* 134: 85–113.
- Garassino, A., Teruzzi, G. & dalla Vecchia, F.M. 1996. The macruran decapod crustaceans of the Dolomia di Forni (Norian, Upper Triassic) of Carnia (Undine, NE Italy). *Atti Soc. It. Sci. Nat. Museo Civ. Stor. Nat., Milano* 136: 15–60.
- Glaessner, M.F. 1969. Decapoda. In: Moore, R.C. (ed.), *Treatise on Invertebrate Paleontology, Part R, Arthropod 4, Volume 2*. Univ. of Kansas and Gel. Soc. America Lawrence.
- Hannibal, J. & Feldmann, R.M. 1985. Newberryi’s lobster—the earliest decapod. *Explorer* 27: 10–12.
- Harzsch, S. 2004. The tritocerebrum of Euarthropoda: a “non-drosophilocentric” perspective. *Evol. Devo.* 6: 303–309.
- Hasiotis, S.T., 1999. The origin and evolution of freshwater crayfish based on crayfish body and trace fossils. *Freshwater Crayfish* 12: 49–70.
- Hof, C.H.J. 1998. Fossil stomatopods (Crustacea: Malacostraca) and their phylogenetic impact. *J. Nat. Hist.* 32: 1567–1576.

- Knopf, F., Koenemann, S., Schram, F.R. & Wolff, C. 2006. The urosome of the Pan- and Peracarida. *Contrib. Zool.* 75: 1–21.
- Komai, T. & Takeda, M. 2006. A review of the pagurid hermit crab (Decapoda: Anomura: Paguroidea) fauna of the Sagami Sea, central Japan. *Mem. Natn. Sci. Mus., Tokyo* 41: 71–144.
- McLaughlin, P.A. 2000. Crustacea Decapoda: *Porcellanopagurus* Filhol and *Solitariopagurus* Türkay (Paguridae), from the New Caledonian area, Vanuatu and the Marquesas: new records, new species. *Mem. Mus. Nat. Hist. Nat.* 184: 389–414.
- Mus, M.M., Palacios, T. & Jensen, S. 2008. Size of the earliest mollusks: did small helcionellids groom to become large adults? *Geology* 36: 175–178.
- Racheboef, P. R. & Villarroel, C. 2003. *Imocaris colombiensis* n. sp. (Crustacea: Decapoda) from the Pysylvanian of Colombia. *N. Jb. Geol. Paläont. Mh.* 2003: 577–590.
- Richter, S. & Scholtz, G. 2001. Phylogenetic analysis of the Malacostraca (Crustacea). *J. Zool. Syst. Evol. Res.* 39: 113–136.
- Rolfe, W.D.I. & Dzik, J. 2006. *Angustidontus*, a Late Devonian pelagic predatory crustacean. *Trans. Roy. Soc. Edin., Earth Sci.* 97: 75–96.
- Scholtz, G. 1995. Expression of the engrailed gene reveals nine putative segment-anlagen in the embryonic pleon of the freshwater crayfish *Cherax destructor* (Crustacea, Malacostraca, Decapoda). *Biol. Bull.* 188: 157–165.
- Schram, F.R. 1974. Mazon Creek caridoid Crustacea. *Fieldiana: Geol.* 30: 9–65.
- Schram, F.R. 1977. Paleozoogeography of Late Paleozoic and Triassic Malacostraca. *Syst. Zool.* 26: 367–379.
- Schram, F.R. 1981. On the classification of the Eumalacostraca. *J. Crust. Biol.* 1: 1–10.
- Schram, F.R. 1984. Relationships within eumalacostracan crustaceans. *Trans. S.D. Soc. Nat. Hist.* 20: 301–312.
- Schram, F.R. 1986. *Crustacea*. Oxford Univ. Press, London.
- Schram, F.R. 2007. Paleozoic proto-mantis shrimp revisited. *J. Paleo.* 81: 895–916.
- Schram, F.R. & Dixon, C.J. 2005. Decapod phylogeny: addition of fossil evidence to a robust morphological cladistic analysis. *Bull. Mizunami Fossil Mus.* 31: 1–19.
- Schram, F.R. & Hof, C.H.J. 1998. Fossils and the interrelationships of major crustacean groups. In: Edgecomb, G. D. (ed.), *Arthropod Fossils and Phylogeny*. Columbia Univ. Press, New York.
- Schram, F.R. & Koenemann, S. 2004. Developmental genetics and arthropod evolution: On body regions of Crustacea. In: Scholte, G. (ed.), *Crustacean Issues 15, Evolutionary Developmental Biology of Crustacea*: 75–92. Lisse, Balkema.
- Schram, F.R. & Mapes, R.H. 1984. *Imocaris tuberculata* n. gen., n. sp. (Crustacea: Decapoda) from the Upper Mississippian Imo formation, Arkansas. *Trans. San Diego Soc. Nat. Hist.* 20: 165–168.
- Schram, F.R. & Müller, H-G. 2004. *Catalog and Bibliography of the Fossil and Recent Stomatopoda*. Backhuys Publ., Leiden.
- Schram, F.R., Feldmann, R.M. & Copeland, M.J. 1978. The Late Devonian Palaeopalaemonidae Brooks, 1962, and the earliest decapod crustaceans. *J. Paleo.* 52: 1375–1387.
- Schram, F.R., Shen, Y-B., Vonk, R. & Taylor, R.S. 2000. The first fossil stenopodidean. *Crustaceana* 73: 235–242.
- Whitfield, R.P. 1880. Notice of new forms of fossil crustaceans from the Upper Devonian rocks of Ohio, with descriptions of new genera and species. *Amer. J. Sci.* 3: 33–42.
- Wills, M. 1998. A phylogeny of the recent and fossil Crustacea derived from morphological characters. In: Fortey, R. A. & Thomas, R. H. (eds.), *Arthropod Relationships. Syst. Assoc. Spec. Vol. Series* 55: 189–209.