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THE PLACE OF THE HOPLOCARIDA IN THE MALACOSTRACAN PANTHEON

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ABSTRACT

The stomatopod body plan is highly specialized for predation, yet the Superorder Hoplocarida originated from something other than the "lean, mean, killing machine" seen today. The fossil record of the group indicates that it originated early on from a non-raptorial ancestor, with the specialized predatory morphology developing much later. The Recent Hoplocarida have been variously positioned within the Malacostraca, from a Subclass equal in rank to the Eumalacostraca (= Caridoida) to being placed as a Superorder within the Eumalacostraca. Consideration of the early fossil morphology, especially of the form of the carapace, of the position and functioning of the articles in the last three pairs of thoracopods, and of other features, suggests that hoplocarids are early derivatives of a basal eumalacostracan stock that was "shrimp-like" in form. The enhancement of an abdominal respiratory system most likely allowed the development of the anterior thorax into the specialized raptorial system present today.

We want to build a phylogenetic tree that presents the actual evolutionary history of the organisms in it. For phylogeny to be correctly inferred from the wealth of data available, it is necessary to identify informative homologous features that allow us to unite organisms in the tree. . . . Sorting out homology from homoplasy is one of the chief pastimes of phylogeneticists.
—Raff (1996)

The Hoplocarida are best known today as the Order Stomatopoda, the "lean, mean, killing machines" of the shallow marine world. Yet, while it is obvious that the morphology embodied in the modern stomatopods is highly specialized, the origins and affinities of that morphology are not quite as clear (e.g., Schram, 1969, 1974, 1986; Hessler, 1982; Dahl, 1983a; Wheeler, 1998; Wills, 1998). In this paper, the base of the hoplocaridan clade will be examined with a view to establishing its affinities and taxonomic relationships with other malacostracans.

Hoplocarida have historically been difficult to place. Calman (1909) arranged the hoplocaridans along with other groups within the Series Eumalacostraca alongside the Series Phyllocarida. There seems to be no universally accepted position for the group today, however. Modern invertebrate zoology textbooks have taken a variety of approaches:

Ruppert and Barnes (1994) rank the Hoplocarida as a Subclass of the Class Malacostraca, equivalent in rank to the Phyllocarida and Eumalacostraca; Meglitsch and Schram (1991) move the Phyllocarida to a new Class Phyllopoda and rank the Hoplocarida and Eumalacostraca as subclasses of the Malacostraca; and Brusca and Brusca (1990) place the Hoplocarida as a Superorder within the Eumalacostraca, leaving Phyllocarida as a subclass of the Malacostraca, essentially as Calman had done. Among treatments dealing strictly with crustaceans, Bowman and Abele (1982), Schram (1986), and Forest (1994) move the Hoplocarida out of the Eumalacostraca, whereas Kaestner (1970) divides the Malacostraca into six superorders, one of which is the Hoplocarida. In the present paper, we treat the hoplocarids as the sister taxon of the syncarid/eucarid line (Table 1).

From a paleontological as well as neontological perspective, the Hoplocarida is rep-

Table 1.   Conceptual arrangement of the malacostracan orders with stenopodous thoracic limbs (= Eumalacostraca, *sensu lato*), after Watling (1983, 1999) and Schram (1986), with modifications according to the suggestions in this paper. Known geological ranges are given. Taxa marked with a '?' are of uncertain rank. This schema is not to be seen so much as a functional taxonomy but as a heuristic device to focus discussions and stimulate more detailed and comprehensive cladistic analyses in the future. There is much to be gained by setting aside facies concepts and focusing on identifying and rigorously defining monophyletic groups.

Hoplocarida	
Palaeostomatopoda†	(L. Carboniferous–U. Carboniferous)
Stomatopoda	
Archaeostomatopodea†	(M. Mississippian–U. Pennsylvanian)
Unipeltata	(L. Jurassic–Recent)
?Syncarida	
Palaeocaridacea†	(L. Carboniferous–L. Permian)
Anaspidacea	(Triassic–Recent)
Bathynellacea	(Recent)
"Carida"	
Decapoda	(L. Devonian–Recent)
Aeschronectida†	(M. Pennsylvanian)
Belotelsonidea†	(Carboniferous)
Waterstonellidea†	(Carboniferous)
Euphausiacea	(Recent)
Pygocephalomorpha†	(Carboniferous–Permian)
Lophogastrida	(Pennsylvanian–Recent)
Mysida	(?Jurassic–Recent)
Peracarida	
Mictacea	(Recent)
Spaleaogriphacea	(Mississippian–Recent)
Thermosbaenacea	(Recent)
Tanaidacea	(L. Carboniferous–Recent)
Cumacea	(?Pennsylvanian–Recent)
?Amphipoda	(L. Eocene–Recent)
?Isopoda	(M. Pennsylvanian–Recent)

resented by one modern order, the Stomatopoda and the extinct Orders Palaeostomatopoda (Late Devonian through Late Mississippian) and Aeschronectida (see Schram, 1986). The Order Stomatopoda is subdivided into two Suborders, the Unipeltata (Upper Jurassic to Recent) containing fossil taxa as well as the modern stomatopods, and the Archaeostomatopodea (Middle Pennsylvanian to Upper Pennsylvanian) containing only a small group of extinct forms. Recently, Jenner *et al.* (1998) uncovered the possibility that the Palaeostomatopoda might be paraphyletic relative to the monophyletic Stomatopoda.

ARE HOPLOCARIDS EUMALACOSTRACANS?

As a starting point, the early definitions of the Eumalacostraca and the Hoplocarida need to be examined. Schram (1969) noted, after a review of the variously suggested phylogenetic positions, that the "definition of a hoplocarid varied from author to author, depending on the phylogenetic interpretation he adopted" (p. 277).

Calman (1909) gave a brief history of the Malacostraca and then provided definitions of the groups he had proposed five years earlier (Calman, 1904). These include the Series Leptostraca and Eumalacostraca, the latter containing the Divisions Syncarida, Peracarida, Eucarida, and Hoplocarida. Calman's definition of the Eumalacostraca is as follows: "Abdomen of six somites (the number may be reduced by coalescence), the last of which typically bears a pair of appendages, and a telson which never bears moveable furcal rami; no adductor muscle of the carapace; thoracic limbs rarely all similar (Euphausiacea), typically pediform, protopodite of two segments except in Stomatopoda" (Calman, 1909: 148). From the beginning, then, the definition of the Eumalacostraca has exceptions, but seems to be centered around Calman's concept of a "caridoid" facies (Hessler, 1982a).

Phyllocarids differ from the other malacostracans in having polyramous phyllopodous limbs and seven abdominal somites, one of which is without appendages. Exact

definitions for the non-phyllocarid malacostracans have always been troublesome because of the great diversity of body forms encompassed by all the orders, both living and fossil. One solution, derived from the cladistic analysis of Schram (1986), was to move the phyllocarids out of the Malacostraca and unite them with other phyllopodous limb-bearing groups such as the cephalocarids and branchiopodans. This plan generated another suite of criticisms, but it had the advantage of making the Malacostraca more homogeneous.

By 1969, the effective definition of Eumalacostraca had become generalized to include all malacostracans except phyllocarids: "Malacostraca generally of shrimp-like form distinguished from the Phyllocarida by non-bivalve nature of carapace and lack of seventh abdominal somite, telson without unsegmented, movably articulated caudal furca" (Moore, 1969: R332). This definition implicitly assumes that those eumalacostracans without a carapace, e.g., syncarids, amphipods, and isopods, must have lost it secondarily as argued by Calman (1909), Hessler (1982a, 1983), and others. The only synapomorphy in that definition that may have no exceptions is the absence of a seventh abdominal somite, although there is some evidence of the seventh somite having been present (e.g., in lophogastrids and perhaps in cumaceans).

After being unable to find a caridoid link to the hoploid fossil taxa he studied, Schram (1969) suggested that the Eumalacostraca, as conceived at the time, was polyphyletic. This lead him (Schram, 1973, 1981) to move the hoplocarids out of the Eumalacostraca and restrict the definition of the latter to those groups having had a caridoid (*sensu* Calman) ancestor. Bowman and Abele (1982) followed the lead of Schram (1969) and Kunze (1981) in moving the hoplocarids out of the Eumalacostraca.

In the 1983 *Crustacean Issues* volume dealing with crustacean phylogeny, the eumalacostracans received considerable discussion. Of the papers treating this group, Hessler (1983) was unique in keeping the hoplocarids within the Eumalacostraca, albeit distinct from what he terms Caridoida. Dahl (1983a), Kunze (1983), and Watling (1983) delimited the Eumalacostraca so as to exclude the Hoplocarida. In all those papers, no list of synapomorphies was given.

If we focus on hoplocarids and eumalacostracans, Malacostraca *sensu stricto* are united by the following features: "naupliar eye of three cups each with three everse sensory cells, polyramous and stenopodous thoracopods, uropods, and a postcephalic carapace structure that does not envelop the abdomen or thoracic limbs" (Schram, 1986: 528). From there Schram noted that eumalacostracans have a uniarticulate antennal scale and strongly elaborated abdominal musculature to facilitate the caridoid escape reaction, while hoplocarids possess triramous antennules, three-articulate thoracopod protopods, four-articulate thoracopod outer branch, at least in the fossil forms, (if one accepts the view of Claus (1871) that the orientation of the limb rotates during development), and dendrobranchiate-like gills on the pleopods.

The reliance on Calman's caridoid model casts a functional constraint on the eumalacostracans that has necessitated much discussion of loss and reduction in some of the superorders. However, it does not provide a useful starting point for delimiting the differences between the caridoids and the hoploids, nor from the peracarid/brachycarid line, which, as shown by Watling (1999), could be considered a third line of radiation within the Malacostraca. The caridoid facies is a highly developed functional model that reaches its full extent in the modern caridean shrimp and is not always fully present in syncarids (Schram, 1986) and mysids (Watling, 1999). It perhaps would be better to think of the "caridoid facies" as an apomorphic end-point of the phylogeny of the caridoid line rather than as the starting point.

While hoplocarids were considered by Calman, Siewing, and others to be poorly developed, "incomplete," caridoids, Schram (1969) suggested that stomatopods were derived from ancestors, such as the Aeschronectida, that did not show any of the modern carnivorous specializations. On this basis he also proposed that hoplocarids originated separately from the other eumalacostracans, having evolved from a phyllocarid ancestor different from that which gave rise to the caridoid eumalacostracans. Kunze (1981, 1983) extensively analyzed internal and external anatomical features of modern stomatopods, including the functioning of the foregut, and concluded that the "independent origin of the Hoplocarida from an early malacostracan an-

cestral stock is supported" (1983: 185). She viewed the early malacostracan as phyllocarid in design, thus implicitly supporting Schram's contention. Schram's view was strongly refuted by Burnett and Hessler (1973), who proposed a scheme whereby the eumalacostracan ancestor could be derived from a phyllocaridan, which subsequently could give rise to the two separate caridoid and hoploid lineages. Hessler (1983) proposed a sequence wherein the urmalacostracan gave rise to phyllocarids on one hand and eumalacostracans on the other. The hoplocarids were then an early offshoot from a somewhat caridoid-looking eumalacostracan.

The Problem of Stomatopodan Thoracopods 6, 7, and 8

There is a strong difference in the structure of the posterior thoracopod between hoplocarids and caridoids. Hoplocarids are considered to have a 3-articulate protopod, whereas caridoids and all other eumalacostracans have only a coxa and basis. Both groups seem to have exopods on the thoracic legs, at least primitively. In hoplocarids, the exopod is reduced and ultimately lost on all but the last three pairs of thoracopods. Caridoids use the exopod for locomotory purposes, and it is reduced only as the power of the abdominal appendages develop.

Stomatopods are well known for their highly modified thoracic legs, sometimes referred to as maxillipeds (in fact, Hansen (1925) makes the case that only the first of these should be called a maxilliped as the somite to which it belongs is fused to the head). The last three pairs of thoracic legs differ from those of the other malacostracan groups in their possession of three protopodal articles and a reduced number of articles in the putative endopod (inner branch). Calman and subsequent authors refer to the exopod and endopod as inner and outer branches, largely because Claus (1871) raised the possibility that the endopod and exopod reversed position during development. This statement has often been repeated but has never been verified by modern workers; Hansen (1925) strongly disagreed with it. In fact, the orientation of the branches is more anterior-posterior, with the "exopod" posterior to the "endopod." This orientation seems to be present from the earliest larval stages where the rami are visible (Komai and Tung, 1929).

In order to understand more about the posterior thoracopods, we need first to see what can be discerned from the fossil record of the group. For the most part thoracopod preservation in hoplocarid fossils is pretty poor. However, in the aeschronectid, *Kallidecthes richardsoni*, Schram (1969, Fig. 115) illustrates one specimen where all three protopodal articles are preserved. From the third article there is a very clear junction of both inner and outer branches, with the outer branch clearly posterior to the inner, as is seen today. This ancient leg differs from the modern stomatopod thoracopod in two important ways, however (Fig. 1). First, the three protopodal articles are of similar length, whereas in modern stomatopods the middle article is much longer than either of the other two. Second, the inner branch is very long and most likely composed of more than two articles, probably four.

In modern stomatopods, the first protopodal article (precoxa) bears insertions of muscles from the thorax and has a promotor-remotor movement (Table 2). The long second article (coxa) has an abduction-adduction movement and bears proximally the insertion of two large muscles that also originate well inside the body on the thoracic tergites. The third protopodal article moves in the abduction-adduction direction and is capable of complete flexion, forming a "knee" at its junction with the long second protopodal article. It is essentially fixed to the first endopodal article. The junction of the first endopodal article to the third protopodal article is at an angle so that the rolling movement produced results in bending the plane of the leg in a slight promotor-remotor fashion. This range of movement is quite similar to that described for *Anaspides tasmaniae* by Hessler (1982b). The exopod, attached to the posterior margin of the third endopodal article, may comprise two articles, the motion of the whole ramus being anterior-posterior.

Based on these observations, one might ask whether the homologies, so long assumed for the articles of these thoracopods, are incorrect. That is, should the articles of the leg be termed coxa, basis, ischium, merus, and carpus, with the 2-articulate exopod originating from the ischium? Or, has the possible loss of the precoxa in most malacostracans resulted in a shift of the promotion-remotion function to the body-coxa articulation? On the
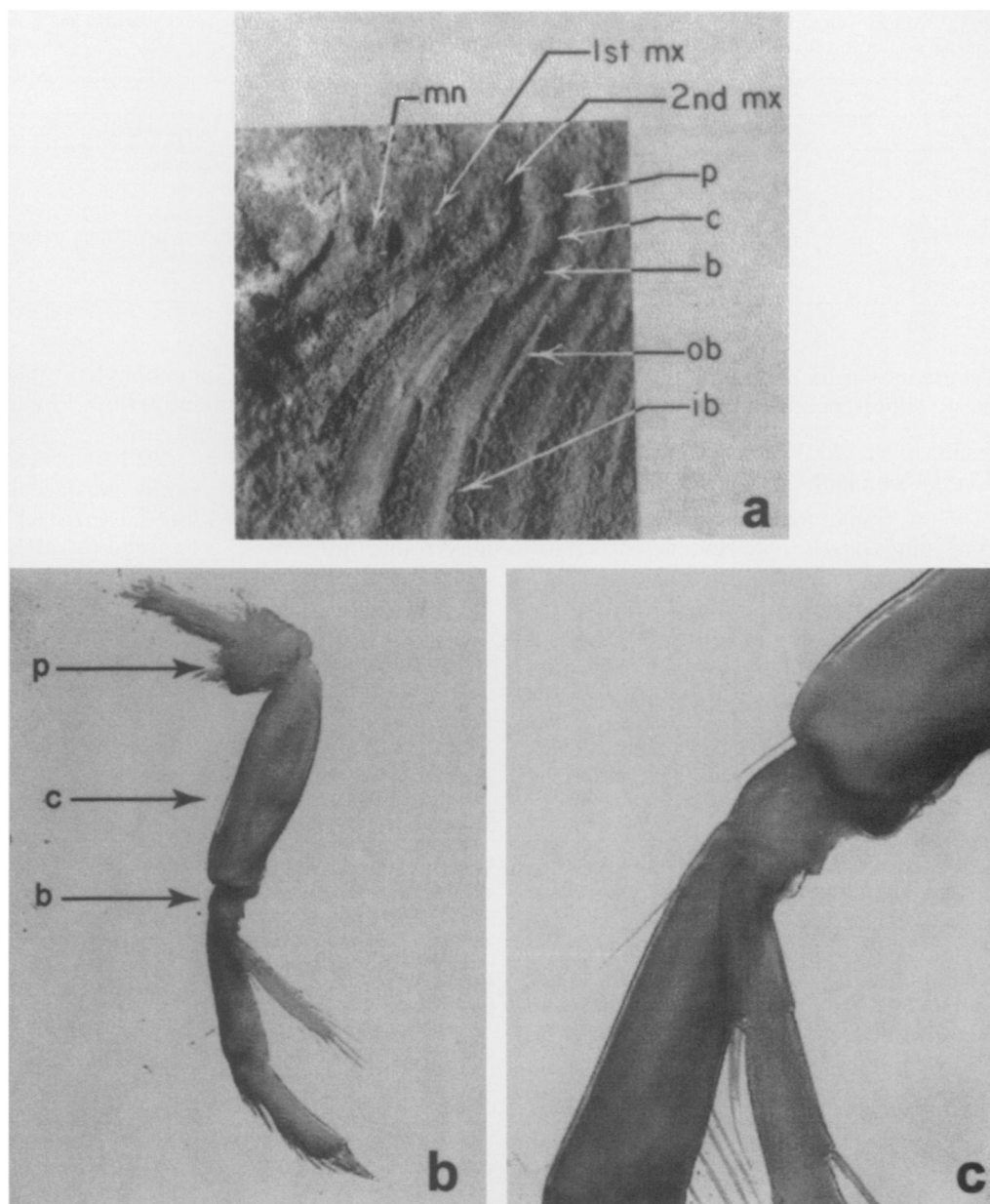
Fig. 1. Details of the hoplocarid thoracopod. a. photograph of the basal portion of the thoracopods of the aeschronectid, *Kallidecthes richardsoni*, clearly showing three-articulate protopod; b. videoprint of thoracopod 7 from an unidentified gonodactylid stomatopod; c. close-up view of the distal part of protopodal article 2, protopodal article 3, and the proximal parts of the endopod and posteriorly located exopod. Note short third protopodal article. mn, mandible; 1st mx, first maxilla; 2nd mx, second maxilla; p, precoxa; c, coxa; b, basis; ob, outer branch; ib, inner branch (a from Schram, 1969).

basis of the comparative data in Table 2, we are more inclined toward the latter alternative. On the other hand, the development of these legs shows relatively weak article boundaries in early larval stages (Komai and Tung, 1929), so the possibility of a shift distally of the articulation of the exopod cannot be entirely discounted. Other alternatives could be advanced here; however, a detailed study of the developmental genetic control of

Table 2. Comparison of thoracopods 6–8 articulation and hinge movement between an anaspid syncarid and a stomatopodan hoplocarid (extension-flexion here is in the transverse plane).

Syncarid		Hoplocarid	
Articulation	Hinge movement	Articulation	Hinge movement
—	—	body-precoxa	promotion-remotion
body-coxa	promotion-remotion	precoxa-coxa	extension-flexion
coxa-basis	extension-flexion	coxa-basis	extension-flexion
basis-ischium	promotion-remotion	basis-ischium	promotion-remotion (rolling motion)
ischium-merus	extension-flexion	ischium-merus	extension-flexion
merus-carpus	extension-flexion	merus-carpus	absent

leg segment formation in stomatopods will begin to supply needed information.

Results of Previous Phylogenetic Analyses Using Computer-Generated Cladograms

"The position of the Hoplocarida" seems to be a heading, or the topic sentence of a paragraph, in nearly all papers treating malacostracan phylogeny (e.g., Dahl, 1983a; Hessler, 1982a; Schram, 1969, 1986; Wills, 1998). Most authors, as already noted above (e.g., Dahl, 1983a; Schram, 1974, etc.), treat the Hoplocarida as a separate subclass of the Malacostraca intermediate between the Phyllocarida and the Eumalacostraca *sensu stricto*. The cladistic analysis of Schram (1986) subsequently removed the phyllocarids to a new Class Phyllopoda, which left the hoplocaridans and eumalacostracans as subclasses of the Class Malacostraca. This move and the subsequent placement of the hoplocarids are supported by the cladistic analyses of Wheeler (1998) and Wills (1998) (Fig. 2), but they used Schram-derived data sets, either directly or with modifications. However, using 18S rDNA, Spears and Abele (1998, 1999) concluded that the Phyllopoda could not be supported as a monophyletic unit and that the Phyllocarida was the sister taxon to a clade containing the hoplocarids, syncarids, and eucarids. Depending on the tree-building method used, the syncarids were either the sister taxon to the eucarids (Fig. 2) or to the hoplocarids, but the hoplocarids, eucarids, and syncarids were consistently grouped in a single clade, supporting a monophyletic clade of the Malacostraca containing both Phyllocarida and Eumalacostraca *sensu lato*.

Schram and Hof (1998) coded 90 characters for both extant and extinct crustaceans and other arthropods. Within the Crustacea, they found most large groupings to reflect what crustacean workers have long thought to be the case (Fig. 2). On the other hand, they expressed surprise that hoplocarids occurred so far up into the eumalacostracan clade, noting that this placement is at odds with the views of most earlier workers on the group. When characters representing primarily soft anatomy were removed, the hoplocarids moved to the base of what could be broadly construed as a malacostracan clade. A tree a few steps longer showed that hoplocarids could still be considered as a sister taxon to Eumalacostraca. Not only does the position of the Hoplocarida seem remarkable, but the other malacostracan groups appear in a variety of topological positions as well.

## Carapace Formation and Its Bearing on Hoplocarid Evolution

The various modes of carapace formation were suggested by Dahl (1991) and reviewed by Watling (1999). While there seem to be five variations in carapace design, the relationships among them are not clearly understood. That is, if a group such as the phyllocarids, for example, is typified by the presence of a dorsal fold extending loosely posteriorly and laterally, whether directly

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Fig. 2. Selection of phylogenetic trees dealing with the position of the Hoplocarida; Schram (1986), compilation of figure 43-1 and 43-2 (B), trees based on morphological data; Spears and Abele (1998), copy of figure 14.4, tree based on maximum parsimony analysis of 232 parsimony-informative characters based on 18S rDNA sequences; Wills (1998), simplified compilation of figure 15.3 (b) and 15.4, strict consensus tree based on the parsimony analysis of morphological data using ordering and weighting techniques; Schram and Hof (1998), edited copy of figure 6.8, 50% majority rule consensus tree based on the parsimony analysis of unordered and unweighted morphological data.
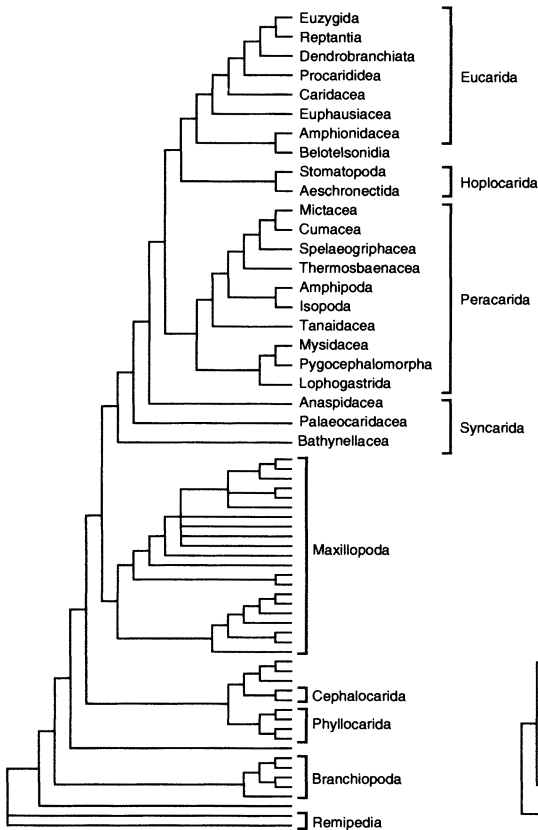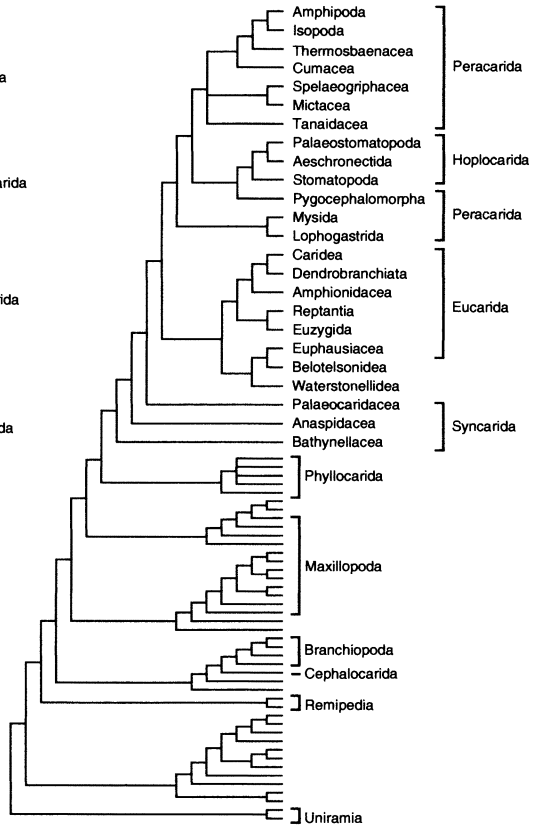
Schram (1986)
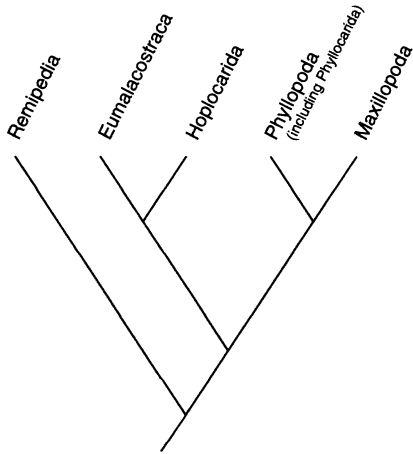
Spears and Abele (1998)
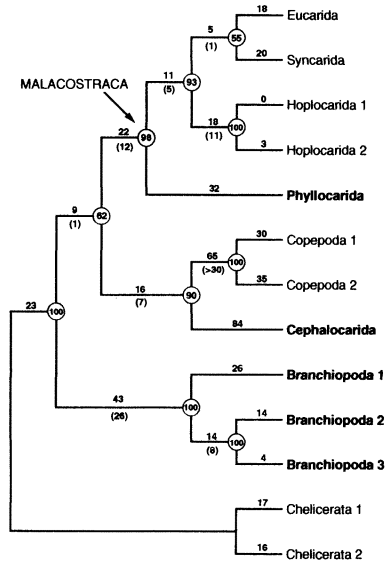
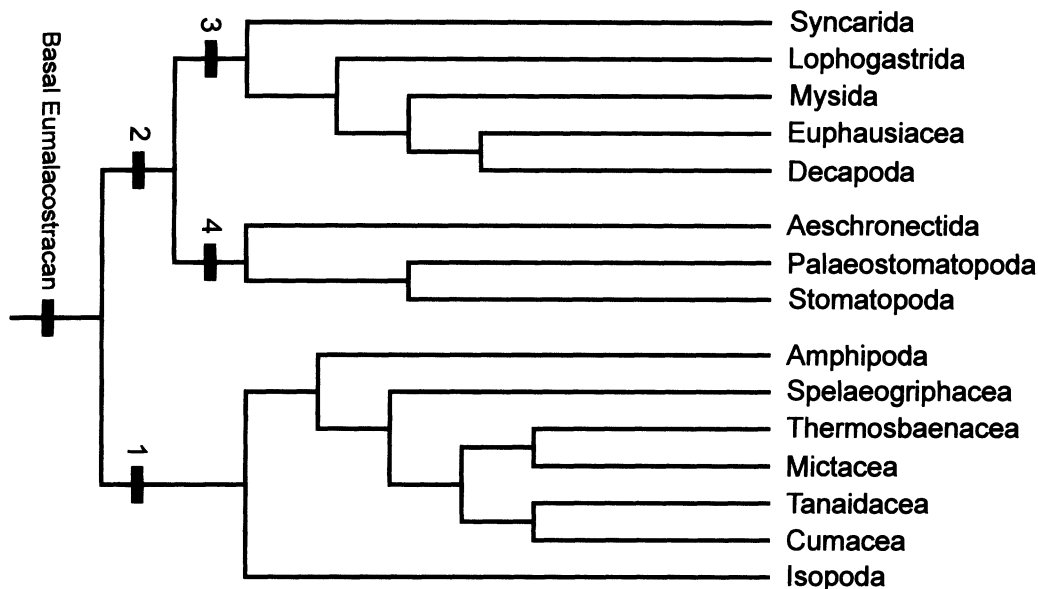## Wills (1998)

Schram and Hof (1998)

Fig. 3. One possible phylogenetic scenario for the Eumalacostraca accommodating morphological information as detailed in the text. Discussion of upper branch arrangements are provided in Watling (1999) for all groups except the Hoplocarida, which is from Jenner et al. (1998). Characters associated with numbered bars, and for the basal eumalacostracan, are given in the text.

from the cephalon as defined by Dahl, or from the posterior margin of the cephalothoracic shield, could that type of carapace be replaced by segmental pleural folds? That particular argument was not considered by Dahl, but he did (Dahl, 1983b) suggest that once a "carapace" encompassed fused thoracic somites (as in the case of segmental pleural folds), it was improbable that that type of carapace could be lost and the individual thoracic somites restored ("Dahl's Rule"). On the other hand, a simple dorsal fold could be long or short, varying with the needs of the animal, and could change with little consequence. Newman and Knight (1984) suggested that the transformation from a dorsal fold emanating from the cephalic shield to a dorsal fold produced from the posterior margin of a progressively posteriorward-developing cephalothoracic shield was a simple and not unexpected development. In contrast to Dahl's assertion, they suggested that the posterior margin of the cephalothoracic shield could be moved more posteriorly or retreat anteriorly with little consequence. There is thus a significant difference between the "fusion" concept of Newman and Knight (1984) and that of Dahl (1991) which needs resolving. Nevertheless, there is still the potential to evalu-

ate the design, if not the origin, of the carapace in several fossil forms.

Several fossil malacostracans are preserved in positions that suggest they possessed a carapace formed by a dorsal fold with branchiostegal flaps (see for example, the phyllocarid, Dithyrocaris rolfei in Schram and Horner, 1978, Pl. 1, Fig. 1; and the palaeostomatopod, Bairdops beargulchensis in Jenner et al., 1998, Pl. IV), whereas others preserved lying sideways sometimes have the carapace in line with the remaining thoracic and abdominal somites and sometimes not (e.g., the archaeostomatopodeans, Tyrannophontes theridion in Factor and Feldmann, 1985, fig. 6; and Gorgonophontes peleron in Schram, 1984). Applying Dahl's Rule, one would predict that the shortened and more firmly attached carapace of the archaeostomatopodeans would be easily derived from the longer and loosely attached carapace seen in the palaeostomatopods. In addition, a small break in the side of the carapace of the Devonian shrimp, Palaeopalaemon newberryi (Pl. 3, Figs. 1–3, in Schram et al., 1978), reveals what could be intact thoracic segments, suggesting that the carapace of this animal consists of a long dorsal fold with lateral branchiostegal flaps. Of course, there are

other explanations for the carapace features seen in these fossils, viz., the possibility of preservation artifacts (Hof and Briggs, 1997) or that the fossils are partially disarticulated shed exoskeletons. Much more needs to be known about the evolutionary development of the carapace and its regulation, perhaps through the discovery of appropriate homeotic gene complexes.

A FUNCTIONAL VIEW OF HOPLOCARID ORIGINS

The fossil record as it is currently known gives significant clues to the development of the Hoplocarida. As Schram has pointed out, the earliest hoplocarids were barely distinguishable from the earliest eucarids. In fact, some of the fossil specimens support the notion that all early carapace-bearing malacostracans (including the Phyllocarida should one choose to include them in this group) had a rather loosely attached carapace consisting of a large dorsal fold with branchiostegal flaps. The issue of the Phyllocarida is a complex one, and for purposes of higher level nomenclature, it will be assumed in this paper that phyllocarids are malacostracans, although the issue can be considered to be unresolved, e.g., see Schram (1986), Spears and Abele (1998), Schram and Hof (1998).

The morphology of the basal eumalacostracan is assumed to have the following features (Fig. 3): a) cephalothoracic shield does not extend beyond first thoracic somite and bears a simple dorsal fold carapace; b) heart with series of lateral arteries in both thorax and abdomen; c) beginning movement of expression of Hox genes posteriorly so that modification of first thoracic limb is begun (see Watling, 1999, for explanation); d) abdominal somites without diagonal muscles; e) 3-articulate thoracopod protopod; and f) first and second antennae biramous.

It seems possible that the basal eumalacostracan developed into two lineages, the true caridoid/hoploid line where the carapace becomes enlarged and confers significant hydrodynamic as well as respiratory advantages, and the peracarid line, which ultimately develops a small carapace for respiratory uses (one of the possibilities of Schram and Hof, 1998; also see Watling, 1999, for details of synapomorphies associated with bar 1 in Fig. 3). Because we are interested here in the derivation of modern stomatopods, we will follow only the large carapace line. This lineage could be characterized by the following synapomorphies (Fig. 3, bar 2): a) carapace developed as a large dorsal fold with branchiostegal flaps (fused at most to the first thoracic somite) covering entire thorax; and b) uropods widened, forming with telson a tail fan.

As suggested by Burnett and Hessler (1973), the divergence of the caridoid and hoploid lineages must have happened soon after the eumalacostracan morphology became established. In fact, evidence from modern circulatory-system design, as well as other features, suggests that the hoploid ground plan was laid before the caridoid body plan became too specialized. Therefore, even though similar in overall body design (e.g., carapace developed as a large dorsal fold covering entire thorax), hoploids differed from caridoids early in their evolution in several important synapomorphic features (Fig. 3, bar 4): a) triflagellate antennule; b) thoracic endopod reduced to four articles; c) ?development of abdominal respiratory system; and d) reduced development of thoracic arterial system concomitant with enhanced abdominal arterial system.

The caridoid synapomorphies, meanwhile, progress in the direction of thoracic specialization for functions such as respiration (Fig. 3, bar 3): a) loss of thoracopod precoxa and transfer of precoxa-body articulation to body-coxa joint; b) development of enhanced thoracic respiratory structures; c) development of thoracic sternal artery; and d) addition of diagonal muscles to the pleonites.

The position of the Syncarida at the base of this lineage is problematic. Modern anaspidacean syncarids possess the sternal artery typical for this entire line, but there is no hint from the fossil record that the earliest syncarids ever possessed a carapace of any kind. However, if the ancestral caridoid carapace comprised a simple dorsal fold, it could have easily been lost (Newman and Knight, 1984). Another possibility, noted by Schram and Hof (1998), is that syncarids are paraphyletic and their true position within these lineages is likely more complicated than we now recognize.

As can be seen (Watling, 1999), the caridoid lineage culminates in the highly specialized decapods where the full range of caridoid features, as delimited by Calman (1909) and Hessler (1983), among others, can be seen. The hoplocarid lineage undergoes a

more extensive modification, culminating in the modern stomatopods. In both cases, there is a continuous change in the carapace from a dorsal fold extending posteriorly and laterally over the thorax to its replacement with the posteriorly developed cephalothoracic shield and fused segmental pleural folds (*sensu* Dahl). In caridoids, the fused pleural folds form a true branchial structure whereas in stomatopods, the fused pleural folds are reduced in number posteriorly and in size laterally, forming a structure with reduced branchial capability and retaining some hydrodynamic advantages while accommodating the raptorial second thoracopod.

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