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A DEFENSE OF THE CARIDOID FACIES; WHEREIN THE EARLY EVOLUTION OF THE EUMALACOSTRACA IS DISCUSSED

'The reports of my death are greatly exaggerated'. S.L.Clemens

ABSTRACT

The caridoid facies is a suite of features that has long been regarded monophyletic and central to eumalacostracan phylogeny. The present defense of this position considers several recent objections to the idea. Much of the caridoid facies is plesiomorphic and cannot be used to argue monophyly. The caridoid apomorphies are found in all eumalacostracans and occur with the first appearance of this taxon in the fossil record. Imperfectly developed abdominal musculature of hoplocarids reflects the early appearance of this taxon in eumalacostracan evolution. Arguments that hoplocarids evolved independently of other eumalacostracans are rejected. The claim that the carapace is polyphyletic is also considered unsubstantiated. In total, the distribution of caridoid features among taxa and in the fossil record strongly suggests the facies evolved once, concurrent with the advent of the Eumalacostraca. The caridoid facies was only part of the cause for eumalacostracan success; the loss of primitive thoracopodan feeding with the appearance of the thoracic stenopodium is likely to have been a more significant event in the genesis of the Eumalacostraca, but the adaptive forces that stimulated the evolution of the two systems may well have intertwined.

1 INTRODUCTION

In the study of malacostracan evolution during the last three-quarters of a century, the concept of the caridoid facies (Calman 1904) has played a dominant role. Its importance was recognized even earlier, for it is embodied in the concept of the Schizopoda (Claus 1885). As seen by its proponents, the caridoid facies is considered a primitive, central morphology from which radiated all the major branches of the Eumalacostraca. This concept and the classification with which it is associated (Hansen 1893, Calman 1904) have had a stabilizing influence on malacostracan systematics from the moment of their inception.

In the last 25 years, however, vociferous discontent with this system has emerged. Some investigators think it probable that the caridoid facies has evolved more than once to serve a pelagic life style (Tiegs & Manton 1958, Dahl 1976). Some regard one of its attri-

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butes, the carapace, to be a product of convergence (Dahl, in press, Watling 1981, Kunze 1981, Schram 1981, 1982). Schram (1981:2), in considering the caridoid facies, points out, '... the difficulty with facies theories built around "archetypes" is that they run the risk of freezing concepts based on the limited understanding and prejudices of the times in which they were originally formulated'.

So far, these attacks have not been answered. Is it possible that these new perceptions are so obviously correct that no adequate answer can be formulated? Is it time to abandon the caridoid facies and the basic Calman classification? I think not. These criticisms seem to be more speculations than substantial falsifications. A central, monophyletic caridoid facies still seems to be the simplest, the most parsimonious interpretation of the facts. This review of the caridoid facies will document why I hold this opinion.

2 NATURE OF THE CARIDOID FACIES

The term 'caridoid facies' was coined by Calman (1904:147) for a series of features shared by the Euphausiacea, Mysidacea, lower Decapoda and 'for the most part also with the Stomatopoda and Leptostraca'. His further consideration in 1909 (p.144) sets the leptostracans aside and includes the Syncarida, which was not mentioned with respect to the caridoid facies in 1904. Calman (1909) diagnosed the facies as follows: (1) carapace enveloping thoracic region; (2) movably stalked eyes; (3) biramous first antenna; (4) scale-like exopod on the second antenna; (5) natatory exopods on the thoracic limbs; (6) elongate, ven-

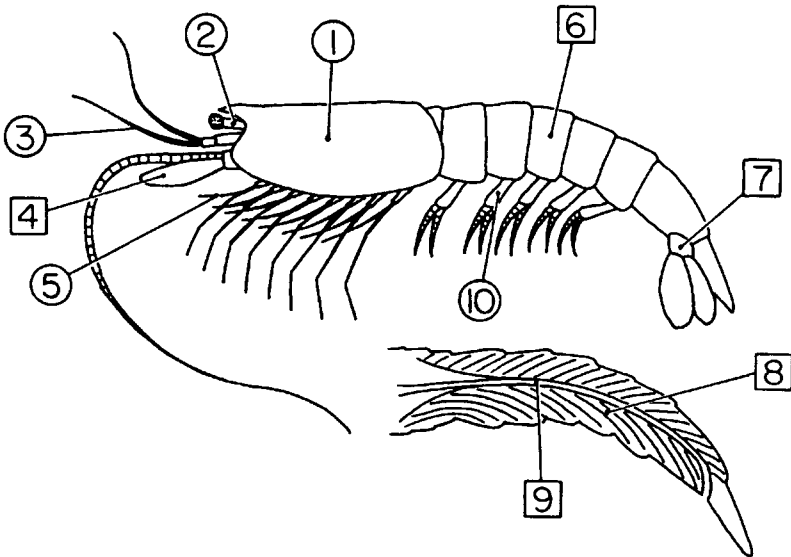


Figure 1. The caridoid facies on a diagrammatic eumalacostracan. Numbers explained in diagnosis on p.146-7. Circled numbers are plesiomorphies; squares indicate caridoid apomorphies.

trally flexible abdomen; (7) tail fan formed by the lamellar rami of the uropods on either side of the telson (Fig.1).

Hessler (1982) extended this list with (8) complex and massive abdominal trunk musculature serving strong ventral flexion; (9) internal organs mainly excluded from the abdomen; (10) pleopods I-V alike, biramous, natatory (Fig.1). These three features are compatible with the general habitus of the caridoid facies which Dahl (1976:165) summarized as 'generally prawn-like and provided with a large carapax'. Hessler also said that the thoracopodal exopods and pleopodal rami are flagelliform, but considering the foliaceous form of these rami in some paleocarid syncarids (Brooks 1969), this seems unduly specific.

The painstaking work of Daniel (1933 and earlier) best documents the necessity of including the nature of the abdominal trunk musculature in the list of features. The same general pattern of complexly intertwining muscles is repeated in the Anaspidacea, Euphausiacea, Mysidacea, and reptantian Decapoda (Daniel 1932). This muscle system is the power source for the caridoid escape reaction, wherein rapid flexion of the abdomen brings the expanded tail fan forward, thus suddenly propelling the animal backward.

Because a large mass of muscle is required, it occupies most of the abdominal cavity. Dahl (1963) noted that the abdomen of caridoids contained a minimum of viscera, even in higher forms where muscles no longer filled the cavity.

Some features attributed to the caridoid facies are actually plesiomorphic to the Eumalacostraca (Fig.1). That is, they are likely to have characterized the urmalacostracan or even the urcrustacean (Hessler & Newman 1975). These include (1) the carapace (to be considered in detail below); (2) movably stalked eyes; (3) biramous first antenna; (10) first five pleopods alike, biramous, natatory. These cannot be caridoid or eumalacostracan apomorphies because they are also found in the Leptostraca and where preserved, other phyllocarids. The natatory thoracopodal exopod (5) is probably also plesiomorphic, since the paddling motion of the exopod is an attribute of the urcrustacean (Hessler & Newman 1975). While these features participate in the caridoid appearance, they cannot be used to argue caridoid monophyly.

The remaining features can. Interestingly, nearly all relate to the caridoid escape reaction. The exceptions are the scale-like antennal exopod, which is used in controlling direction while swimming, and the tail fan, to the extent its initial function was also directional control.

3 THE POSITION OF CONVERGENCE IN PHYLOGENETIC THEORY

A common argument against all or parts of a central, ancestral caridoid facies is, 'How do we know it didn't evolve more than once?' Obviously, the answer is that we don't. However, this is not acceptable cause for rejection of monophyly. There is no case where one can rule out absolutely the possibility of convergence.

Monophyly is unprovable; it can only be falsified (Hessler 1982). For this reason, similarities between taxa occupy a special position in phylogenetic theory. They must be accepted as valid indicators of affinity, i.e. synapomorphies, *until compelling reasons force us* to conclude these properties reflect convergence. If we follow any other path, the decision as to whether a feature should be regarded as convergent becomes a matter of personal preference. We will have thrown away the primary objective tool of phylogenetic methodology — similarity.

Thus, it is convergence which must be proven; only then should we prefer it to monophyletic hypotheses. It is for this reason that none of us should embrace arguments of polyphyly except as a goad to hunt for evidence that will falsify the hypothesis of monophyly. Until such evidence surfaces, monophyly remains the most parsimonious paradigm.

4 MONOPHYLY OF THE CARIDOID APOMORPHIES

It seems simplest to first consider the phylogeny of the caridoid apomorphies (Fig.1). The plesiomorphic portion of the facies will not be discussed except for the carapace, which will be treated subsequently; the monophyly of the other plesiomorphic features (stalked eyes, for example) within the Malacostraca as a whole has never been criticized.

Schram (1981:3) states that the appearance of crustaceans in the fossil record gives 'difficulty in reconciling the fossils with the caridoid speculations based largely on living forms'. Disregarding the danger of using negative evidence in the fossil record, the statement is certainly not correct when applied to the first appearance of the caridoid morphology versus other eumalacostracan morphologies, such as in tanaids or isopods (Table 1). The earliest eumalacostracans that have been identified from Devonian beds, the eocarid *Devonocaris* and the decapod *Palaeopalaemon* (Brooks 1969, Schram 1969a, 1978, 1982) express the full suite of external caridoid apomorphies (internal characters cannot be considered). Thus, if one wishes to use it, the fossil record supports the appearance of the caridoid facies at the base of the eumalacostracan radiation. However, this first appearance should not be given undue weight. The presence of advanced taxa such as tanaids in the Lower Carboniferous testifies to the rapidity of the eumalacostracan radiation, so that the incompleteness of the fossil record could easily mask important chronological details.

It is important to note that Calman specifically included anaspidacean Syncarida among the taxa whose morphology is dominated by the caridoid facies, even though they lack a carapace (Fig.2). This is completely reasonable. Anaspidaceans express the diagnostic fea-

Table 1. First appearance of malacostracans in the fossil record. All taxa have a carapace *except* those in brackets. The first eumalacostracans, appearing in the Devonian have the full suite of caridoid apomorphies except for the Hoplocarida, where the abdominal musculature has not fully achieved the caridoid morphology.

	Peracarids	Other Malacostracans
Cenozoic	[Amphipoda]	Pancarida
Mesozoic		
Permian	Cumacea	
Upper Carboniferous	[Isopoda]	
Lower Carboniferous	Spelaeogriphacea	[Syncarida]
	Tanaidacea	
	Mysidacea	
Devonian		Decapoda
		Eocarida
		Hoplocarida
Silurian		
Ordovician		
Cambrian		Phyllocarida

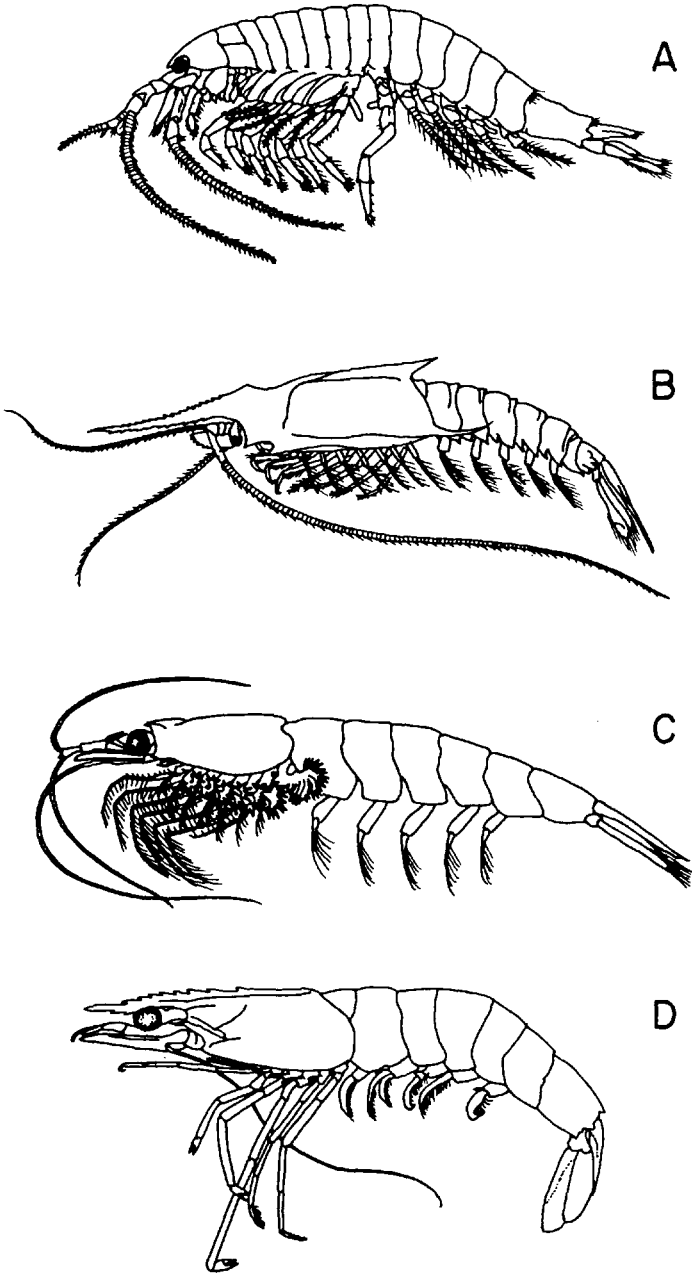


Figure 2. Four major taxa with well-developed caridoid facies. A. anaspidacean syncarid; B. lophogastrid mysidacean; C. euphausiacean; D. peneid decapod. The syncarid deviates in lacking a carapace, the decapod in having vestigial thoracic exopods (after Hessler 1982).

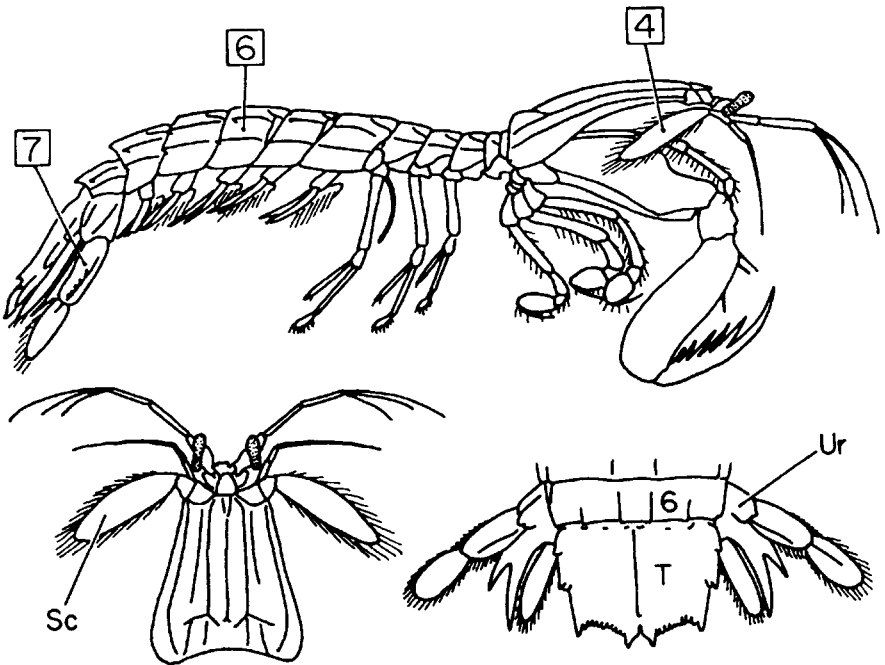


Figure 3. A stomatopod hoplocarid, showing the full external expression of the caridoid apomorphies. Numbers in squares refer to apomorphies listed on p.146-7. (also, see legend, Fig.1). The large protopodal spine separating uropodal exopod and endopod is a stomatopodan apomorphy not seen on early hoplocarids. Symbols: Sc - antennal scale; Ur - uropod; T - telson (after Calman 1909).

tures in every other way, including the escape reaction (Silvey & Wilson 1979, Kunze & Hessler, personal observation). *Anaspides* is caridoid in form even though it is primarily a benthic organism, usually entering the water column only when frightened.

Among the Peracarida, the caridoid apomorphies are fully present in the Mysidacea, and can even be observed in the Mysida, which is specialized in important other ways compared to the Lophogastrida. In the Eucarida, all the caridoid apomorphies can be found in the Euphausiacea and natantian Decapoda.

Thus, all of the caridoid apomorphies occur together on some members of the Syncarida, Peracarida, and Eucarida (Fig.2). This set of features is sufficiently complex that unless contrary evidence were forthcoming, it constitutes a strong synapomorphic suite. In none of the papers criticizing the caridoid facies does such contrary evidence appear. Indeed, Watling's (1981) urmalacostracan incorporates many of these features.

Some divisions do not display the caridoid apomorphies perfectly. The Pancarida is clearly a derived group, as indicated by the absence of an antennal exopod and loss or reduction of pereopods and pleopods. It has a weakly caridoid abdomen as seen from its uropods. The abdominal trunk musculature is modest, but its pattern is basically caridoid, strongly suggesting a caridoid ancestry (Hessler 1964).

The Hoplocarida possess many of the caridoid apomorphies: antennal scale, ventrally

flexible abdomen and a tail fan (Fig.3). Their abdominal trunk musculature is not fully caridoid, but shows all the basic caridoid elements except for the transverse muscles (Hessler 1964). Nor do these abdominal trunk muscles fill the abdomen. Instead some of this space is occupied by the gonads (Dahl 1963). These two deviations from the caridoid facies are what one would expect of the evolving caridoid condition (Hessler, in comments following Dahl 1963, 1964). This interpretation is consistent with the belief that hoplocarids are an early eumalacostracan offshoot of the line leading to the full caridoids (Calman 1909, Siewing 1963, Burnett & Hessler 1973, Hessler 1982) (Fig.4). It is compatible with the early appearance (Devonian) of hoplocarids. In this view, the many remarkable features that characterize the Hoplocarida, including those of the digestive system (Kunze 1981) are apomorphies (Table 2). Contrary to Schram's (1973, fig.9) early claim that the hoplostracan phyllocarids are the independent ancestors of the hoplocarids, current thinking does not relate the two taxa (Rolfe 1981, Schram 1982). Thus, as yet there is no concrete evidence to show that the unique hoplocaridan features did not arise in a eumalacostracan that already had evolved a portion of the caridoid facies. That is, the hoplocaridan apomorphies do not disprove caridoid monophyly.

Kunze (1981: this volume) and Schram (1982 and earlier) strongly oppose this point of view. The reader is advised to consult their papers directly; I cannot do justice to their arguments. Only a few aspects of the debate will be aired here. Schram (1982) rightly criticizes Burnett & Hessler (1973) for neglecting the Aeschronectida when they claimed there is no evidence for the coxal origin of pleopodal gills in hoplocarids. However, these epipodal gills do not demonstrate the independent origin of the hoplocarids, for they are best interpreted as extreme plesiomorphies of the ucrustacean ancestor (Siewing 1963, Hessler 1982); they are moot in the present context.

The hoplocaridan uropod has been described as 'blade like' and the telson 'styloid' (Schram 1969b) but, as seen from Schram's figures, this difference from the caridoid tail fan is not fundamental (see in particular his Figure 131b). Many of the early hoplocarids had an abdomen that looks truly caridoid, and a well-developed antennal scale. The latter is uniquely two-segmented (Hessler 1982), a difference whose importance cannot yet be resolved; reduction of podomere number is a common change in crustacean limb evolution.

Schram (1982) emphasizes the lack of a full caridoid escape reaction in stomatopods. However, this is no more than what one would expect in a precaridoid. Even then, the stomatopod flexure has much of the caridoid behavior; it is similar to that of syncarids, as seen in *Anaspides* (Silvey & Wilson 1979). The stomatopod's erichthus larva utilizes the full caridoid escape reaction and the ventral flexion of the abdomen in adults can be so powerful as to launch a disturbed captive animal backward out of its holding tank (Newman personal communication).

Much of the case for independent origin of hoplocarids is built upon the belief that they achieved six pretelsonic abdominal segments by fusion of two of its anterior somites, rather than posterior ones as in other eumalacostracans (Manton 1928a,b). Depending on the theory, different anterior segments are involved. Komai & Tung (1983) and Siewing (1963) thought details of the circulatory system in *Squilla* bespoke fusion of the first and second abdominal somites. However, Burnett (1973) did not find this condition in *Hemisquilla*. Reaka (1975) saw in the pattern of stomatopod molting sutures evidence that the first abdominal somite had fused to the last thoracic.

Two lines of evidence argue in favor of fusion of the sixth and seventh pretelsonic somites rather than anteriorly (Fig.6). First, Shiino (1942) found ontogenetic evidence of it.

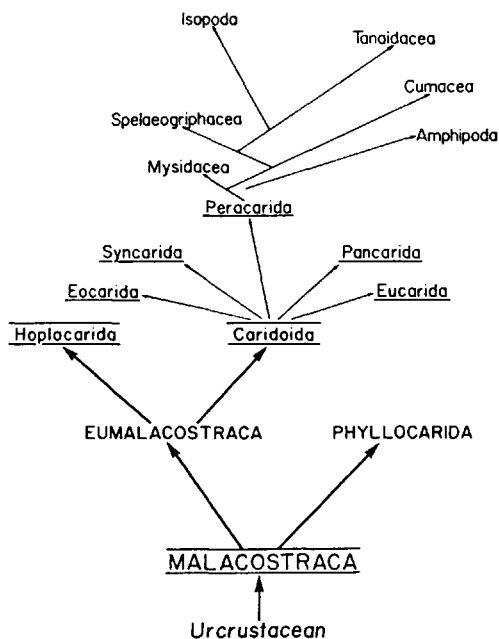


Figure 4. Phylogeny of the Malacostraca. Only in the Peracarida is this carried to order; here, the shortness of the line after its branch point for mysidaceans (lophogastrids) and spelaeogriphaceans reflects their relative lack of major external apomorphies.

Second, the seventh abdominal segment is the only one not known to have an appendage in any phyllocarid. The presence of an appendage on all six pretelsonic abdominal somites in hoplocarids is thus compatible with fusion of the sixth and seventh somites (Hessler 1982). If anterior somites had fused, a limb would have been lost. There is not the slightest evidence such a loss ever took place. These arguments seem more substantial than that of molting sutures, where functional constraints are more likely to dictate pattern than would lingering historical imprint.

Kunze (1981) points out that similarities between phyllocarids and hoplocarids argue against eumalacostracan monophyly. She mentions the cephalic kinesis, cephalic musculature, abdominal viscera and abdominal skeletomusculature. If the last two features are pre-caridoid, as already suggested, her objection is answered. This may also explain the first two features. Grobben (1917) has found remnants of the cephalic kinesis and musculature in decapods.

The discussion here has dwelt on the question of hoplocaridan affinities because if this taxon evolved independently with respect to the other eumalacostracans, then those aspects of the caridoid facies which hoplocarids do possess must have evolved independently as well. The present analysis does not find sufficient substance in the independent origin argument to require us to accept such convergence (Fig.4).

In summary, the fossil record and the distribution of features among taxa are consistent with the hypothesis that the caridoid apomorphies (antennal scale and abdomen) are monophyletic and must occupy a central position in eumalacostracan evolution.

5 THE CARAPACE

The carapace has been the focal point for most of the disagreement with caridoid monophyly. Dahl (1976) questions the necessity of providing the uralacostracan with a carapace. Watling (1981) uses its absence as a starting point. Schram (1981) regards the possibility of its monophyly unknowable. In the present discussion of these criticisms the issue will be limited to the Malacostraca; although the monophyly of the carapace between crustacean classes is also subject of much debate, it is irrelevant in the present context.

The distribution of a carapace among taxa is of paramount importance (Table 1). It is found in all phyllocarids, living and fossil; this taxon is judged more primitive than the Eumalacostraca on the basis of independent criteria (Hessler 1982). Among the Eumalacostraca, it is present in all groups, living and fossil, except the division Syncarida and orders Isopoda and Amphipoda. Malacostracans with a carapace appear in the Cambrian (Rolfe 1969), long before the first appearance of a taxon without one (Carboniferous) (Schram 1969a). Contrary to Dahl's (1976) claim that there is no obvious reason to endow the uralacostracan with a carapace, these lines of evidence lead compellingly to that conclusion.

The arguments against a monophyletic carapace are few. Dahl (1976) sees problems in deriving syncarids, isopods, and amphipods from an ancestor with a carapace. Watling (1981) regards the cumaceans and tanaids as too specialized to be satisfactory intermediates between a caridoid with full carapace and the isopods. Possible other objections are too diffusely expressed to be identified.

One might argue that even if the uralacostracan possessed a carapace, the ancestral eumalacostracan lacked one. This is a major requirement of Watling's hypothesis, which derives this animal from the carapaceless version of the urcrustacean (Hessler & Newman 1975). A difficulty with this scenario is the presence of a carapace on all known phyllocarids, thus making necessary a carapaceless ancestor for which there is absolutely no evidence. Dahl (1976), with Watling's (1981) concurrence, notes the lack of pleura on thoracomeres covered by a carapace. Therefore, the presence of thoracic pleura in amphipods and isopods would imply a carapaceless ancestry. However, these two orders do not have thoracic pleura at all; the lateral outgrowths are epimeral plates of coxae which are broadly attached to the body.

Amphipods and isopods are specialized in many different ways: unstalked, sessile eyes; one of the antennular flagella reduced or absent; highly modified maxilliped; no thoracic exopods; no thoracic epipods (isopods only); little evidence of caridoid abdomen (amphipods only). Therefore, there is no independent reason for regarding their lack of a carapace as primitive. This is not true with syncarids. Anaspidaceans and paleocaridaceans are wonderfully primitive eumalacostracans in many ways. One might well question whether their lack of a carapace is also primitive. However, they are not substantially more primitive than lophogastrid mysids (Fig. 2) or some of the eocarids (whatever they might prove to be), which have a full carapace. In view of the wide distribution of a carapace among malacostracans, it does not make good sense to give more weight to the lack of a carapace in syncarids than the presence of a carapace in lophogastrids.

The various grades of evolution represented by mysidaceans, spelaegriphaceans, cumaceans, and tanaidaceans give adequate clues how the carapace could be lost in isopods (Fig. 5). Unfortunately, such clues are totally missing for syncarids and amphipods. A similar weakness plagues the opposite argument as well; there is no evidence concerning the origins of these taxa.

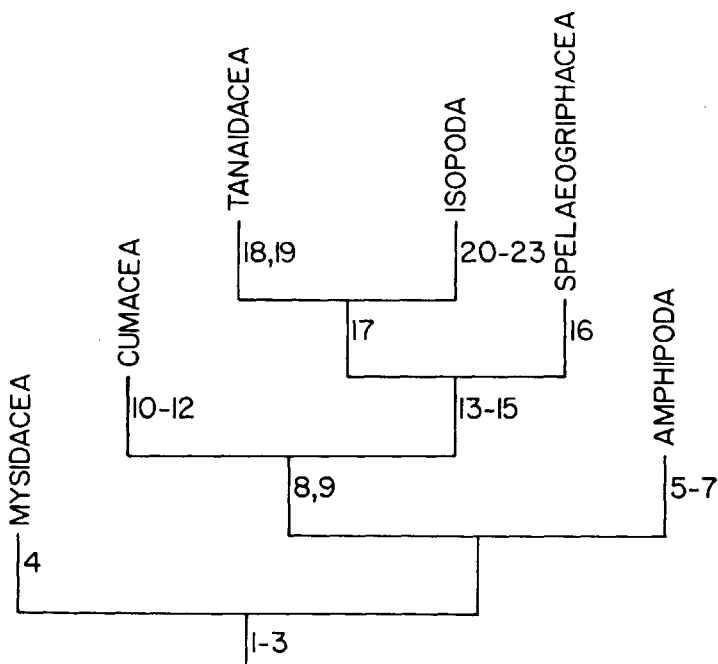


Figure 5. Cladogram of the Peracarida, based on major external features of the thoracic region. The cladogram stems from a presumed ancestor with a full carapace that is not fused to any thoracic segment, thoracopods I-VIII alike, exopods and epipods on all thoracopods, and epipodal respiration. Numbers adjacent to a clade refer to its apomorphies, as listed below. The amphipods could also have been put as a branch from the Mysidacea without loss of parsimony. Apomorphies: (1) thoracomere 1 (T1) fused to cephalon; (2) thoracopod I (T1) a maxilliped; (3) T1 epipod a bailer; (4) T1 epipod non-respiratory; (5) carapace lost; (6) T1-VIII exopods lost; (7) T1 epipod lost; (8) carapace reduced, not covering T4-8 or T5-8; (9) TII-VIII epipod lost; (10) T2-3 or T2-4 fused to cephalon; (11) TII-V are maxillipeds or involved in trophic functions; (12) TII, VIII exopod always lost, TIII-VII sometimes lost; (13) carapace further reduced, not covering T3-8; (14) carapace with respiratory surface; (15) T1 exopod lost; (16) TV-VIII exopods respiratory; (17) TIV-VIII exopod always lost, TII, III exopods vestigial; (18) T2 fused to cephalon; (19) TII involved in nonlocomotory functions; (20) carapace lost; (21) T1 epipod nonrespiratory, nonbailer; (22) TII-TIII exopod lost; (23) pleopods respiratory.

Watling's (1981) phylogeny requires the evolution of a carapace four times in the Malacostraca: (1) Phyllocarida and Hoplocarida, (2) Eucarida, (3) non-isopodan mancooids, and (4) Mysidacea and Pancarida. The more traditional scheme espoused here (Figs. 4, 5) begins with a carapace and requires no independent derivation. It does require reduction and even loss several times: (1) Hoplocarida, (2) Syncarida, (3) Pancarida, (4) Mysida, (5) Amphipoda, and (6) mancooids (Fig. 4). However, it is far easier to envision the multiple reduction or loss of a complex structure than its multiple genesis, as for example in the case of eyes.

Dahl (in press) is concerned with the problem of how animals with many freely articulated thoracomeres, as in the carapaceless isopods or amphipods, could have evolved from an ancestor with thoracomeres fused to the cephalon, as in forms with a carapace like

cumaceans or the Mysida. Even disregarding the possibility that fusion is not necessarily evolutionarily irreversible, the problem is not as serious as indicated. Only in the Peracarida and Pancarida is it of any concern; in eucarids, fusion is always complete, and the carapace is never reduced. For all higher peracarids, the lophogastrid Mysidacea give the model for an ancestor with a carapace, and here, only the first thoracomere is fused (Fig.5). The Spelaeogrifhacea is the most reasonable representative of a generally intermediate condition with respect to isopod evolution (see below). It too has only one fused thoracomere, as do isopods. Tanaids have two, and cumaceans have three to four fused thoracomeres, rarely five to six. The increased degree of fusion shows a general correlation with the number of thoracopods modified as maxillipeds or primarily devoted to food acquisition and non-locomotory functions. In the taxa with one fused thoracomere, there is only a single maxilliped. The greater number of fused somites in cumaceans and tanaids relates to their five and two pairs of trophic limbs, respectively. Since the chelate second thoracopod in tanaids and trophically specialized thoracopods two to five in cumaceans are surely apomorphies of these respective orders, it seems likely that the greater degree of carapace fusion is also apomorphic (Fig.5). Thus, the peracarids give no examples where degree of fusion needed to be reduced during evolution; the degree of fusion in isopods traces smoothly backward to a lophogastrid-like ancestry.

Watling (1981) takes support for a carapaceless origin of the mancoid line (Cumacea, Tanaidacea, Spelaeogrifhacea, Isopoda) from the observation that the more traditional point of view as expressed by Siewing (1963) is inconsistent with the fossil record and cannot explain patterns in the respiratory and circulatory system. His willingness to take literally the order of appearance of peracaridan taxa in the fossil record seems naive, in view of the patchiness of that record.

In the traditional peracaridan phylogeny, the evolution of the respiratory system is not so complicated as Watling suggests. Among peracarids as a whole, only lophogastrid mysidaceans and amphipods rely totally on thoracic epipodal respiration (Fig.5). The primitiveness of this system is documented by its general presence in nonperacarids. Within the Peracarida, the maxillipedal epipod acts as a bailer in mysidaceans, cumaceans, tanaidaceans and spelaeogrifhaceans. In the cumaceans, tanaidaceans and spelaeogrifhaceans it also acts as a gill. Tanaidaceans and spelaeogrifhaceans additionally use the inner surface of the carapace for gas exchange, and spelaeogrifhaceans have branchial exopods. Of these respiratory devices, the nonmaxillipedal ones must be considered apomorphies. Isopods are unique in having pleopodal instead of thoracic epipodal respiration. There is no evidence for regarding the isopodan condition as ancestral; its uniqueness labels it an apomorphy whose origin is totally hidden. It must be emphasized that the respiratory surfaces in isopods are the exopod and endopod, and are therefore in no way related to the epipodal abdominal gills of hoplocarids.

Watling (1981) brings the pancarids into the argument because Siewing placed them among the mancoids, but there is no reason to relate them to the mancoid lineage, or perhaps even to the peracarids (Hessler 1982). Leaving them aside (Fig.4), a simple scheme of respiratory evolution begins with the lophogastrids, fits the three non-isopodan mancoids in the middle, and ends with the unique isopods. Here the maxillipedal epipodal bailer gives a bridge between the Mysidacea and the lower mancoids. One strength of this scheme is that it is concordant with a general reduction of the carapace and disappearance of exopods as well as epipods within the mancoid line; the isopods are most advanced in all respects, as opposed to their condition in Watling's scenario, which makes them primitive in

lacking a carapace, but advanced in lacking thoracopodal exites. This scenario for respiratory evolution is parsimonious in endowing monophyletic origin to all situations.

In regarding the cumacean and tanaidacean carapace, exites and epipodal respiratory system more primitive than in isopods, one need not regard those orders more primitive in all respects. They are obviously uniquely specialized in many ways, but in the characters under consideration here, they reflect a primitive grade of evolution. The Spelaeogriffacea come far closer to what the isopodan ancestor might have been like (Hessler 1982), with a single fused thoracomere, with reduced carapace, thoracic exites, antennal scale and eye lobes, but with large swimming pleopods, uropodal tail fan and abdomen. Here, the abdomen has lost the caridoid flexure, and its musculature is modest.

What about the amphipods? Their presence in the Peracarida is based largely on the presence of a lacinia mobilis and thoracopodal oostegites. They are different from other peracarids in many important ways (Siewing 1963). We now know the lacinia mobilis is not diagnostic of the Peracarida (Dahl & Hessler 1982), leaving thoracic oostegites as the primary unifying feature. The especially great isolation of amphipods among peracarids causes investigators to wonder if they even belong in that division (Watling 1981, Dahl & Hessler 1982, Hessler 1982). Coupled with the complete lack of intermediate forms, living or fossil, to guide us, this phylogenetic distance from other taxa has important implications. If we decide amphipods are not related to other peracarids, there is nothing which compels us to conclude their *immediate* ancestor had a carapace (Dahl 1977); it might have been more like an anaspidean than a lophogastrid (Hessler 1982). However, this does not invalidate any argument that the *ultimate* ancestor had one. The affinities of the Amphipoda are today the most perplexing issue in malacostracan phylogeny.

The purpose of pursuing these circuitous arguments was to search for reasons that require the rejection of the monophyletic carapace. Objections of sufficient substance are not forthcoming. The most parsimonious scenario begins with a carapace which is reduced or even lost in independent lines.

6 EARLY MALACOSTRACAN EVOLUTION

The major conclusion of this inquiry is that the caridoid facies, including a carapace, was present early in eumalacostracan evolution. We know from the Hoplocarida that it was not yet fully developed when the prime diagnostic eumalacostracan apomorphy, six pretelsonic abdominal segments, appeared (Table 2). The complex abdominal trunk musculature that powers the caridoid escape reaction had not achieved its full form, but otherwise the caridoid abdomen was well-developed. At this point, two questions suggest themselves: (1) What was the original purpose of the caridoid abdomen? (2) Is there any functional significance to the loss of the seventh abdominal segment?

The condition of the abdomen in hoplocarids suggests that the caridoid escape reaction may not have been the sole selective advantage to the caridoid abdomen. Here, the uropodal tail fan is highly developed in advance of the perfection of the flexing system. Perhaps originally the tail fan functioned primarily in steering the swimming animal vertically. This is one function of the tail fan today, in hoplocarids and full caridoids. Secondly, it is probably its only function in spelaeogriffaceans and cirrolanid isopods. It would seem to be relatively simple for the caridoid escape reaction to evolve gradually from this beginning.

The loss through fusion of the seventh abdominal segment probably occurred in concert

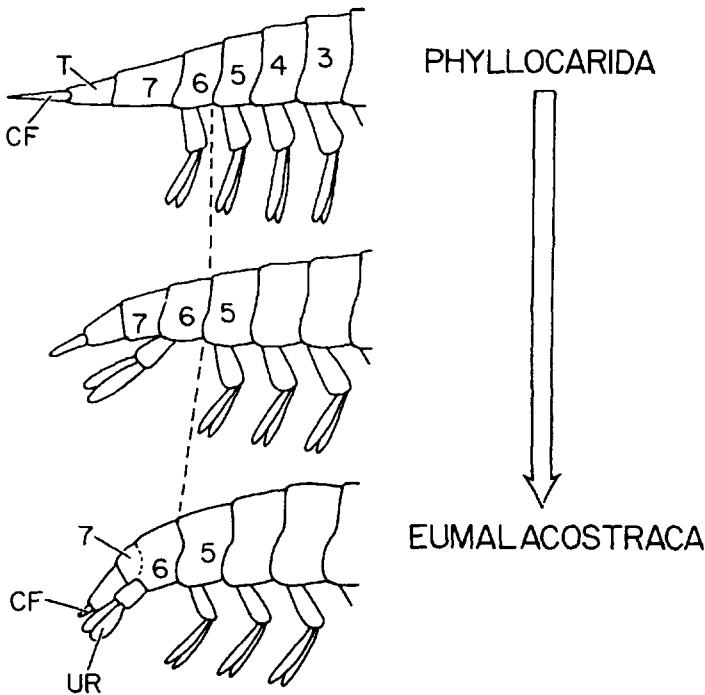


Figure 6. Evolution of the caridoid (eumalacostracan) abdomen from that of a phyllocarid. Symbols: CF – caudal furca; UR – uropod; T – telson; numbers are of abdominal segments.

with the evolution of the tail fan (Fig.6). The uropods are specialized pleopods stemming from the sixth abdominal segment. As already mentioned, no known phyllocarid had a pleopod on the seventh segment. I suggest that the sixth pleopods evolved to uropods because they were the most posterior appendages. Part of their change involved their reorientation to a horizontal, posteriorly directed position. It would seem reasonable that the limbless seventh segment became reduced and fused with the sixth to facilitate the developing tail fan. (According to Manton (1928a,b), fusion allows the uropods to migrate to the posterior end of the seventh segment.) If so, the loss of the seventh segment was not a functionally trivial event, but part of the development of a major eumalacostracan feature.

This hypothesis does not explain why the caudal rami did not play more than a transitory role in tail fan evolution. Nor does it explain why the telson did not fuse at the same time. These do not falsify the hypothesis; they only indicate it is incomplete.

We must consider whether the features of the caridoid facies constitute the driving force for eumalacostracan success. The fossil record leads us to believe most of the major eumalacostracan types were the product of an explosive radiation that occurred in the Devonian-Lower Carboniferous, essentially as soon as the caridoid apomorphies first appeared. Thus, it is reasonable to suspect the caridoid apomorphies played an active role. Functionally, they conferred two capabilities. The antennal scale and tail fan added maneuverability while swimming. The caridoid abdomen provided rapid escape.

Nevertheless, these functions do not seem sufficient to explain so remarkable an evolutionary success. In particular, it does not explain the *reduction* of the caridoid facies in so many of the successful eumalacostracan lines, particularly isopods and amphipods.

The answer lies in another change that evolved at the same time, as far as the fossil record tells us. This was the abandonment of the adult thoracopodan feeding (Table 2), i.e. the primitive system of food acquisition by metachronal activity of the thoracopods, with the food that accumulates along the midline being passed forward to the mouth by proto-

Table 2. External apomorphies of malacostracan taxa through the level of cohort. The features considered here are limited to those relevant to the present discussion. Characters of the urcrustacean model formulated by Hessler & Newman (1975) are regarded as the basic plesiomorphies against which these lists of apomorphies should be judged. The apomorphies and related plesiomorphies of the cohorts Hoplocarida and Caridoida (n.cohort) are the diagnoses of those taxa as seen in their most primitive members.

Class Malacostraca

1. 8 thoracic and 7 pretelsonic abdominal segments
2. Abdominal segments 1-6 with homomorphic, natatory pleopods
3. ♀ gonopore on thoracomere 6; ♂ on thoracomere 8
4. Thoracic endopods with 5 podomeres
5. First antenna biflagellate
6. Carapace (if urcrustacean lacked one)
7. Movable rostrum?
8. Cephalic kinesis?

Subclass Phyllocarida

No meaningful apomorphies, due in part to poor understanding of fossil forms

Subclass Eumalacostraca

1. Second antennal exopod scale-like (for planing)
2. 6th pleopod with fan-like uropod, to help form tail fan
3. Loss of 7th abdominal segment through fusion with 6th
4. Abdomen capable of strong flexion, made possible by coiling of longitudinal trunk muscles
5. Loss of endites on thoracopods 2-8 along with abandonment of primitive thoracopodan feeding
6. Thoracic limb becomes a stenopodium
 - a. protopodal complex small
 - b. endopod large, slender, ambulatory
 - c. epipods purely branchial
 - d. exopods purely natatory

Cohort Hoplocarida

1. Abdomen enlarged
2. First antenna triflagellate
3. Antennal scale 2-segmented? (not known on early fossils)
4. Thoracopods with 3-segmented protopod, 4-segmented endopod
5. Thoracic epipods 6-8 lost? (not known on fossils)

Cohort Caridoida, new cohort

1. Full caridoid abdominal musculature
 2. Pleopodal epipods lost
 3. Cephalic kinesis lost
 4. Movable rostrum lost
 5. Antennal scale 1-segmented
 6. Mandible with row of bristles between incisor and molar processes
-

podal endites (Sanders 1963, Hessler & Newman 1975, Hessler 1982). It was replaced by reliance on the maxillae and the first thoracopod, now a maxilliped (Dahl 1976). This change was either driven by or caused the evolution of the eumalacostracan stenopodium (Hessler 1981). Freedom from the compromises inherent in participation in thoracopodan feeding allowed the epipods to specialize as gills, exopods as swimming organs, and endopods as truly ambulatory structures or anteriorly to be secondarily specialized for new forms of food acquisition or other behavior.

The resulting generalized animal, which must have been like an anaspidacean with a carapace or a lophogastrid that walked, possessed extraordinary evolutionary potential. This was not only a function of the thoracic stenopodium, but also natatory pleopods and the caridoid abdomen. In the major flowering of the Eumalacostraca, different aspects of this generalized form were emphasized in different lineages, as is most vividly revealed in locomotion (Hessler 1981). For example, in the Mysida, thoracic exopods are used for swimming, and the pleopods are reduced or absent; in sergestid decapods, the opposite pertains.

Thus, it would seem that a factor outside of the caridoid facies was the primary key to the eumalacostracan radiation. However, the loss of primitive thoracopodan feeding and the appearance of the stenopodium did appear at the same time as the caridoid apomorphies. The questions remains, was this coincidental, or is there a functional linkage that caused these factors to evolve together?

In concluding, it should be noted that in view of the appearance of most of the caridoid apomorphies and the thoracic stenopodium in the earliest eumalacostracans, the diagnosis of the Eumalacostraca should include this complex of features just as much as it does the presence of six pretelsonic thoracic segments (Table 2). In the past, too much importance has been devoted to abdominal segment count, the apparent trivialness of which is part of the reason why eumalacostracan monophyly has been viewed with such suspicion. An appreciation of the full suite of features that first appeared with the Eumalacostraca, in both the hoplocarids and full caridoids, places the unity of that taxon on much firmer footing.

This does not deny the closer affinity of the full caridoids (Eocarida, Syncarida, Peracarida, Eucarida, and Pancarida) with each other than to the Hoplocarida. This relationship is sufficiently important to justify taxonomic recognition. Therefore, I propose that the full caridoids mentioned above be combined under the name Caridoida, which is a sister group of the Hoplocarida within the Eumalacostraca. The diagnostic differences between these taxa are given as a list of apomorphies in Table 2.

Much speculation has been devoted to the life style of the primitive eumalacostracan. Most commonly, the ureumalacostracan is thought to be primarily, but not exclusively benthic (Manton 1953, Dahl 1976, Watling 1981). For this reason, the observation that the caridoid facies appears best developed in primarily pelagic forms made Dahl (1976) suspicious of its primitiveness. However, this impression is not strictly accurate. While euphausiids, and some lophogastrids and natantian decapods are holopelagic, anaspidaceans, other lophogastrids, mysids and most natantian decapods are benthopelagic, as one would expect in animals outfitted with both ambulatory (thoracic endopods) and natatory (thoracic exopods, pleopods) appendages. The caridoid apomorphies well serve the needs of an animal swimming over the bottom or requiring rapid retreat from some benthic threat. Thus, the combination of the caridoid facies with the primitive thoracic stenopodium is superbly suited for the benthopelagic existence postulated for the eumalacostracan ancestor.

7 SUMMARY

Adherence to the principle that synapomorphy is the fundamental hypothesis of phylogeny frees the systematist from the danger of capricious, subjective utilization of convergence in evolutionary constructs. In the present essay, I have considered the major reasons for dissatisfaction with the caridoid facies as a central, primitive eumalacostracan morphology, to see if they constitute valid falsification of the monophyletic hypothesis. None of them qualified. This is not to say that some day a new perception might not reveal a fatal weakness. Monophyletic schemes can never be free of this possibility.

Until then, the caridoid facies must be regarded as an attribute that appeared with the advent of the Eumalacostraca, at the same time as the appearance of the stenopodium. The details of the origin of the eumalacostracan body plan are almost completely unknown; the fossil record is not helpful, and hoplocarids give only the slightest clue. Once evolved, it was undeniably successful. However, its success should not be equated with static perfection. Rather it lies in having provided a remarkable variety of adaptive opportunities, as testified by the multitude of eumalacostracan taxa today.

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DISCUSSION

SIEG: I have some difficulty with your explanation for the uropods coming from the sixth segment. We have some observations in tanaids, originally made by Claus, where we see the sixth and seventh ganglia in the abdomen in very early stages of development. These ganglia are partially fused, but the nerve for the uropods is coming from the seventh and not the sixth ganglion. Do you have any information that the uropods do in fact develop from the sixth?

HESSLER: The only information I can offer is the work of Manton on *Hemimysis*. This indicated that the limbs migrated to their posterior position from the sixth segment. Your data are very interesting.

SIEG: Could it have evolved twice? In some groups the uropods may have evolved as you've indicated, and in others they may have come from the seventh.

HESSLER: I would say that if both these data sets are incontrovertable, that is the kind of falsification of the scheme presented here I have been talking about.

SIEG: You said that isopods have an epipodite, and that is a common statement in isopod literature. I have looked at some aberrant mysids and done some comparative studies, and I think that what is generally referred to as an epipodite in isopods is an exopodite.

HESSLER: The structure comes off the coxa, which by position makes it an epipod. If you have reasons based on ontogeny that indicate it did not originally come from that spot, then you have good data. If your observations are correct, it would simply make the isopods even more derived as far as I can see.

KUNZE: Do you have any idea as to the functional processes that would have likely led to the loss of the carapace in the course of syncarid evolution, and would these processes have been in operation in amphipods and isopods?

HESSLER: No, I'm sorry, I don't. I cannot explain why syncarids lost their carapace. I feel a little more comfortable with isopods. I feel that in isopods it is the result of gradual progression, as seen in other taxa. However, amphipods again are a problem. I have not the faintest idea where amphipods came from, and therefore, I do not know why they lost the carapace.

WATLING: I will defend myself more readily this afternoon, but I want to offer one quick correction. I do not think I have ever claimed the carapace has evolved four or five times. I think you'll see it's twice.

HESSLER: No, [by having an uralacostracan and urperacaridan which lack a carapace] you derive it separately in the phyllocarids, the mancoids, the mysids, the eucarids, and the hoplocarids [Watling 1981:202, 204].

WATLING: I disagree. But I want to comment on uses of the fossil record, which I think we are all aware has to be used very carefully. Why do you suppose that all the crustaceans that have shown up as fossils, at least since the Devonian, are all large robust forms? Is there some coincidence with that and the fact they do generally have large carapaces? None of the delicate non-carapace forms show up as fossils.

HESSLER: Syncarids have no carapace and they show up as fossils. *Acadiocaris* is a relatively small and delicate animal and it shows up as a fossil.

WATLING: Those things are very rare. The most abundant fossils are all really large, robust, heavily calcified forms.

HESSLER: So?

WATLING: I would suggest that the fossil record is only of limited usefulness in that the only information you can get out of it is the presence of things. You cannot use it to demonstrate the absence.

HESSLER: The only reason I have used the fossil record at all is that two people [Schram 1981:2, 3, Watling 1981:206-208] have said that the fossil record tends to show the caridoid facies is polyphyletic.

NEWMAN: I am interested in this possibility that uropods may have evolved several times. This brings us to crustaceans as a whole, because the same enervation problem exists at the other end of the animal in the head. The second antennae are postoral in their origin and then come to migrate anteriorly. We might be able to follow the same model with the uropods, that is, they may have migrated with their enervation posteriorly. It is just the other end of the animal.

ABELE: I would like to make two comments. One, I do not know what the problem is with the carapace evolving more than once, given the diversity of the carapace and the complete lack of information on its embryological origin, which is only known for a few species. And two, most of the things you've listed are all one thing: the uropods, the flexion, the large musculature in the abdomens. So you have one character, not several.

HESSLER: I agree that all those abdominal characters are very much related.

KUNZE: The antennal scales are rather different between hoplocarids and your caridoids. It has two segments in the hoplocarids, one in the caridoids.

HESSLER: Yes, but who is to say that it is different because it has fewer segments [consider the varying segmentation in decapod pereopods].

WATLING: Another point of contention is the use of the caridoid facies. I would argue

that though mysids, euphausiids, and shrimp-like forms are definitely caridoid in a Calman sense; thermosbaenaceans, cumaceans, tanaids and spelaegriphaceans are not.

HESSLER: Absolutely; they are very derived but lophogastrids are not.

WATLING: Sure, they are an early offshoot of mysids.

HESSLER: There is nothing wrong with evolving a carapace more than once, but I demand that there be evidence that proves it. Until there is such evidence it is most parsimonious to say it evolved only once. That is all I'm saying. I'm waiting for some falsification of my contention.

GRYGIER: Concerning this lack of limbs on the seventh segment, there is at least one pygocephalomorph [the genus *Pygocephalus*] that has two pairs of furca. I am wondering if at least one of those are the rami of the seventh limb.

HESSLER: I don't know what to do with that; Bill Newman also mentioned this to me. It is possible that is the case, but it is also possible that it is more akin to a situation like that seen in euphausiids. which have six spines coming off the telson which can dwindle down to two. We decided those two are spines and not furca, because they are simply two among six.

SCHRAM: I feel compelled to make some comments since I have been an object of attack. Whether you want to call syncarids, pancarids, peracarids, and eucarids Caridoida, as Bob would prefer, or leave the term Eumalacostraca for these as I have suggested is a matter of preference. Our positions are not that far apart. I would point out the apomorphies Bob has used to define the caridoids have different expressions in the hoplocarids, namely, the abdominal musculature and antennal scale. Either these can both be considered apomorphic with regard to some precursor; or as Bob has indicated today for the muscles one is intermediate to the other, that is, one is more primitive and the other advanced. This could indicate separate and coequal groups. These groups are related, since they do have other features that seem to draw them together, but on a much lower level than indicated here.

HESSLER: May I say it seems simpler to keep the term Eumalacostraca for that to which it has always applied, and leave its diagnosis as it always was — a group of animals having lost their seventh segment.

SCHRAM: Until we can sort out what is going on in the phyllocarids and their relationship to these different groups, I prefer to leave it alone. We should simply have three groups in the Malacostraca and not attempt to draw any sister groups because we don't really understand what's going on.

HESSLER: In the traditional view, 'leaving it alone' would mean staying with two groups of Malacostraca.

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There is one radical distinction between different minds . . . that some minds are stronger and apter to mark the differences of things, others to mark their resemblances.

Francis Bacon

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