

ON THE CLASSIFICATION OF EUMALACOSTRACA

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A B S T R A C T

Traditional views of eumalacostracan phylogeny are not in accord with current understanding of the fossil record. Another approach results from identification of basic morphotypes upon which radiations were built in the course of eumalacostracan history. Random association of characters (absence or varying conditions of the carapace, biramous or uniramous thoracopods, and presence or absence of subthoracic brood pouch of some form) yields an array of 16 morphotypes, of which 10 are recognized in the fossil and Recent record. The resultant "paper animals" combined with an analysis by cladistic methods yield six possible phenograms of eumalacostracan phylogeny. An evolutionary uncertainty principle precludes definitive choice among these patterns to produce a cladogram and taxonomy. However, a taxonomic system is advocated with the subjectivity associated with uncertainty clearly acknowledged.

Perhaps one of the greatest noncontroversies in crustacean evolution has been the phylogeny and interrelationships of the Eumalacostraca. Since Calman (1904, 1909) it has been taken for granted that the higher malacostracans could be classified as discreet superorders which were derived from an ancestral type neatly delineated by a set of characters known as the caridoid facies. However, Calman's synthesis was the result of several decades of debate over how malacostracan groups were related. Boas (1883) visualized a single line arising from the phyllopods and giving off the malacostracan groups at successive levels. Claus (1885) envisioned three branches arising from a "eumalacostracan" stock: leptostracans, stomatopods, and "urschizopods," and this was essentially Grobben's (1892) position as well, except that Grobben had the stomatopods as the earliest offshoot from the "urschizopods." Haeckel (1896) derived his "proschizopods" from the Leptostraca and in turn treated these as an ancestral stock for five lines: mysids, cumaceans, other "peracarids," "eucarids," and stomatopods. Calman's caridoid concept, however, exerted a stabilizing influence on all succeeding speculations on higher malacostracan phylogeny, with the result that subsequent phyletic schemes for these groups have been essentially similar (Giesbrecht, 1913; Grobben, 1919; Balss, 1938; Siewing, 1956, 1963; and Brooks, 1962). Of these, Siewing came to be a focus of a certain school (viz., Fryer, 1964; Hessler, 1969) which essentially holds that all eumalacostracan superorders arose from a central stem. Schram (1969a, b) recently suggested that the Hoplocarida had nothing to do with other Eumalacostraca, but rather had an independent origin separate from the Eumalacostraca *sensu stricto*. This latter position was objected to by Burnett and Hessler (1973) but supported by Reaka (1975), Bowman and Abele (in press), and Kunze (personal communication).

Through all this, the essential stability and supposed interrelationships of the Eumalacostraca *sensu stricto*, viz., syncarids, eocarids, peracarids, pancarids, and eucarids has remained relatively constant. The Eocarida and Syncarida were interpreted as near the base of the eumalacostracan line; and supposedly from somewhere within the eocaridan stock the Eucarida and Peracarida were derived, with the Pancarida seeming to bear some relationships to peracarids (some authors placing them as a separate superorder and others as an order of peracarids). This traditional arrangement of orders is outlined in Fig. 1.

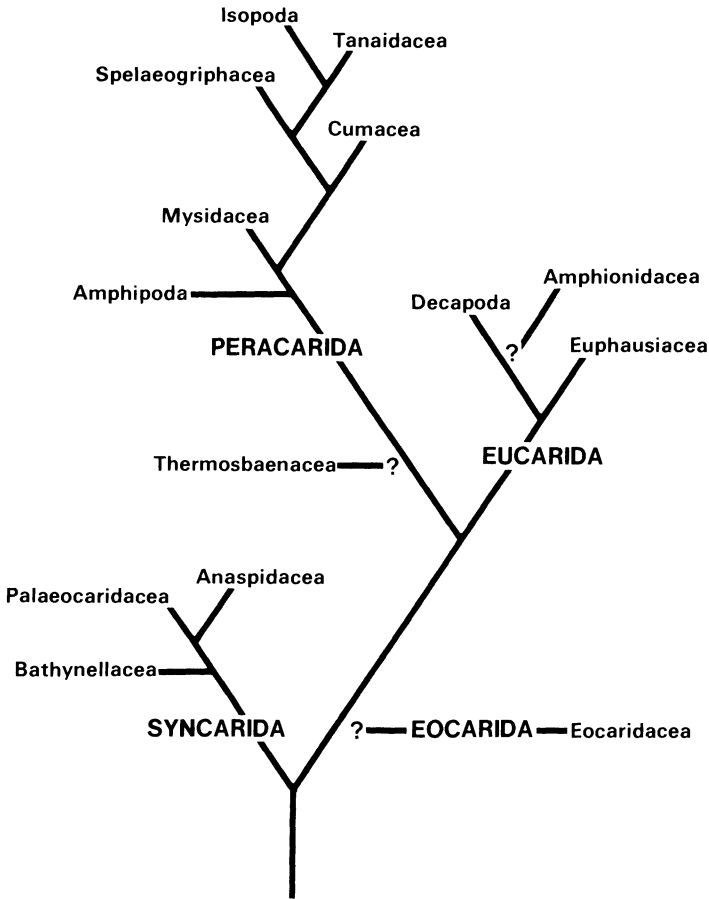


Fig. 1. Traditional phylogenetic tree of the Eumalacostraca.

THE PROBLEM

The caridoid facies of Calman (1909) has taken on a role as a central paradigm in malacostracan and especially eumalacostracan phylogeny, in that all phyletic speculations on the group are referred to that archetype. However, several eminent authorities have challenged the caridoid facies. Tiegs and Manton (1958, p. 295) questioned whether the facies might not be convergent in several groups. Dahl (1963, p. 4) cast doubt on the facies as a primitive pattern for all malacostracans and again (Dahl, 1976, p. 165) questioned whether the caridoid facies were necessary. 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. In addition, the clarity of the Calman superorders has been eroded through time. Peracarids had come to be understood as those forms with an oöstegite brood pouch and a lacinia mobilis. However, laciniae are now known in many groups, e.g., euphausiacean juveniles (Knight, 1978), and, if thermosbaenaceans are to be included within the peracarids, then the consistency of brood pouch features also disappears.

Moreover, our knowledge of the fossil record of the earliest eumalacostracans has significantly improved over the past 15 years to the point that there is in-

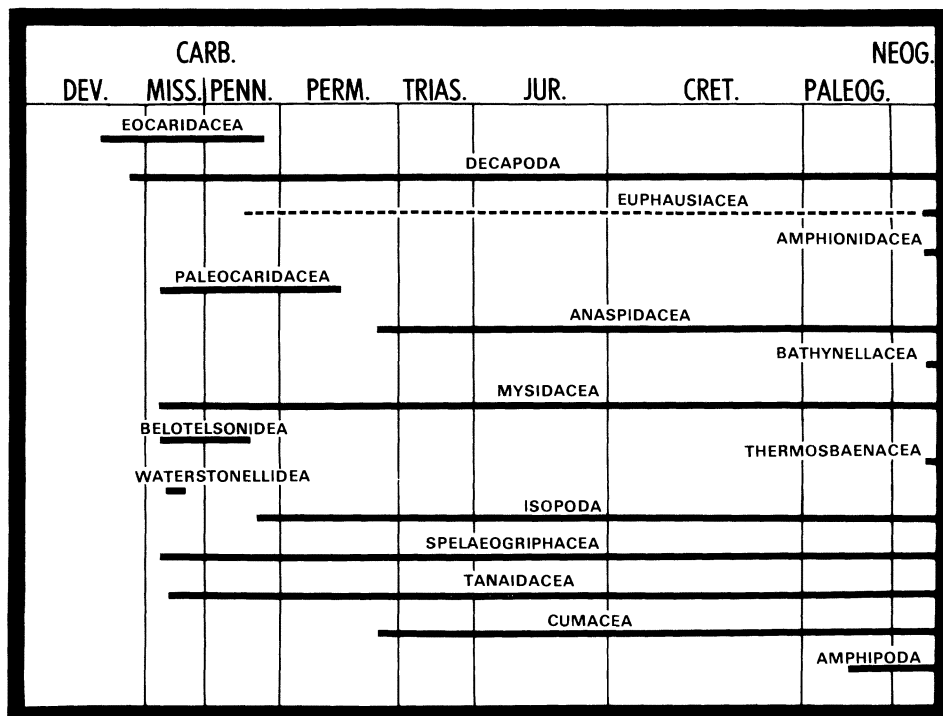


Fig. 2. Stratigraphic ranges of presently recognized orders of Eumalacostraca. The range of Eocaridacea may be shortened as more information becomes available and its constituent taxa are assigned to other orders of Eumalacostraca and possibly even other subclasses of Malacostraca.

creased difficulty in reconciling the fossils with the caridoid facies speculations based largely on living forms. Groups do not appear in the fossil record (Fig. 2) in any way that approaches the sequence of events suggested in Fig. 1. This disparity has already been at least a partial stimulus to attempt a reassessment of the status of some groups. For example, Watling (personal communication) views peracarid relationships utilizing cladistic techniques with essentially three lines: mysidaceans, from which were derived thermosbaenaceans; amphipods; and mancooids, of which isopods are considered the most primitive and cumaceans the most advanced. The picture derived from a consideration of the Late Paleozoic eumalacostracans essentially approaches that of a grass rather than a tree (Fig. 2) with most of the orders with any fossil record arising in a relatively short time interval in the Late Devonian-Early Carboniferous. The fossil record of Eumalacostraca thus would seem to indicate a relatively short interval in which a rather intense deployment of almost all the major types took place. Indeed, such an impression is intensified if one attempts to set aside the preconceptions engendered by the Calman superorder taxonomy of Eumalacostraca and concentrate attention only on the basic morphotypes present.

A SOLUTION

In this regard, it occurred to me in examining the features of eumalacostracan groups that morphologic themes were played out by the interplay of a mosaic of basic characters, whose importance is established by their having been used in

someway by most taxonomists of the Eumalacostraca for the past century. These characters are:

- 1) whether the carapace is either absent, incomplete to some degree, complete and fused to the thorax, or complete and unfused to the thorax,
- 2) whether or not young are brooded in a pouch below the thorax, and
- 3) whether the thoracopods are uniramous or biramous, i.e., whether or not the thoracods are schizopodous.

From a matrix of these characters we can delineate 16 basic morphotypes or "paper animals," and perhaps not too surprisingly affiliate 10 of these morphotypes with known fossil and/or Recent groups. The "paper animals" have the following character states and indicated real equivalents: a) no carapace, lack of brood pouch, schizopodous thoracopods [Syncarida]; b) no carapace, lack of brood pouch, uniramous thoracopods; c) no carapace, brood pouch, schizopods; d) no carapace, brood pouch, uniramous thoracopods [Isopoda and Amphipoda]; e) short carapace, lack of brood pouch, schizopods [Thermosbaenacea]; f) short carapace, lack of brood pouch, uniramous thoracopods; g) short carapace, brood pouch, schizopods [Cumacea, Tanaidacea, and Spelaeogriphacea]; h) short carapace, brood pouch, uniramous thoracopods; i) unfused carapace, lack of brood pouch, schizopods [waterstonellid Eocaridacea]; j) unfused carapace, lack of brood pouch, uniramous thoracopods [belotelsonid Eocaridacea]; k) unfused carapace, brood pouch, schizopods [Mysidacea]; l) unfused carapace, brood pouch, uniramous thoracopods; m) fused carapace, lack of brood pouch, schizopods [Euphausiacea]; n) fused carapace, lack of brood pouch, uniramous thoracopods [Decapoda]; o) fused carapace, brood pouch, schizopods; p) fused carapace, brood pouch, uniramous thoracopods [Amphionidacea]. It is important to realize that I am not suggesting these "paper animals" are archetypal ancestors as such. I am merely shuffling mosaics to delineate an array of morphotypes, i.e., basic structural forms upon which adaptive radiations have been subsequently built. In the process we are able to recognize discrete groups of real animals corresponding to many of these forms which can be clearly defined by a combination of characters (some apomorphic, some plesiomorphic) which are not shared by any other group.

DISCUSSION

It appears that in the origin of Eumalacostraca, there was a rapid and random development of several variant morphotypes. We carcinologists should strive to achieve some kind of cohesive theory of a taxon's evolution that has a consistent approach to all groups within that taxon. The fossil record and morphotypic approach outlined above suggests a more internally consistent alternative for the Eumalacostraca to that of facies theories. If basic constituent features of the Bauplan of eumalacostracan groups went together in a mosaic pattern the entire process can be conceived of as a sort of variant of a child's "Cootie Game." The exact combination of characters which actually appeared and upon which full scale radiations were to be based was the result as much of chance combination as actual selection for particular character suites. In such a stochastic system there is no reason to insist that all possibilities would have been deployed; indeed chance would mitigate against 100% realization of all possible combinations, and in the 16 combination system outlined above only 10 of the variants are recognized to exist. Thus we cannot say that a particular mosaic which we do not yet recognize in the fossil or Recent record (e.g., variant *b* no carapace, no brood pouch,

and uniramous thoracopods) is at any selective disadvantage to any other mosaic combination; we can merely state that either chance mitigated against its development, or that we have not found it yet in the fossil or Recent record.

One might wish to argue with my choice of characters. Other features can be added to augment what I consider these basic three, e.g., presence of maxillipeds, degrees of exopod development, or abdominal specializations. Or some might want to insist on more rigidity in achieving a particular condition; e.g., I do not distinguish here between the subthoracic brood pouch of thoracopod oöstegites in peracarid forms and that of the first pleopods as in amphionidaceans. One could do these; it would complicate the matrix of possible mosaic combinations and thus further reduce the actual number of realized combinations. Consider for example that Savory (1971) recognized 15 characters that are used to define arachnid orders, and mere presence or absence of a particular state of each character would give rise to 32,768 possible arachnid orders, whereas we recognize in the fossil and Recent record something between one to two dozen orders of arachnids. Or, we could define orders of Malacostraca on the basis of appendage variants on some 20 possible somites. If we considered that a particular set of appendages might or might not be specialized from a particular generalized type, we could have 1,048,567 possible basic variants of Malacostraca alone. This would not include orders that one might base on variant specializations we might invent on any segment or series of segments. The point I am making is that the system I have proposed here is *deliberately simple* for conceptual purposes, but the rigid application of the model would in fact more perfectly correspond to what one might expect in the actual realization of probabilities in a time stochastic system.

The point here is to suggest that the identification of phyletic lines is perhaps more important in phylogeny than speculation on cladograms; for trying to determine what is a plesiomorphic or apomorphic character, although a useful exercise, may be irrelevant in a stochastic universe. Raup (1978), Raup *et al.* (1973), Raup and Gould (1974) have begun to move toward a stochastic rather than deterministic theory of evolution. If evolution is stochastic, then a kind of evolutionary uncertainty principle may operate, i.e., either we can delineate lines of evolution (and at best group them in some proximity to each other) but be uncertain as to the proximity of lines; or, we can postulate archetypes to connect lines and be uncertain that any such hypothetical animals ever existed and connected the lines we seek to link.

A further insight into the problem of determining relationships is gained by trying to arrange the morphotypes into a cladogram. Morphotypes and their appropriately associated manifestations from the real world can be associated into a selection of six (permutations of the three basic features) possible phenograms (Fig. 3). The problem then becomes which of these six possibilities might be the one that more closely reflects the supposed true phyletic relationships. The six possible phenograms arise from the fact that there is no way to "slice the pie" of eumalacostracan groups without having convergences. One of the three characters must be used to make the initial branching. When we examine the phenograms we note that certain arrangements seem to be totally spurious; for example, in *A* the distinct isolation of amphionidaceans, or the association of syncarids, thermosbaenaceans, and euphausiaceans; or *B* which is almost a Calman system except for amphionidaceans appearing among peracarids and the various Calman superorders appearing at different levels in the phenogram. On the other hand *C* and *D* seem to offer more or less reasonable arrangements.

How does one *objectively* select from all these. You can pick your favorite,

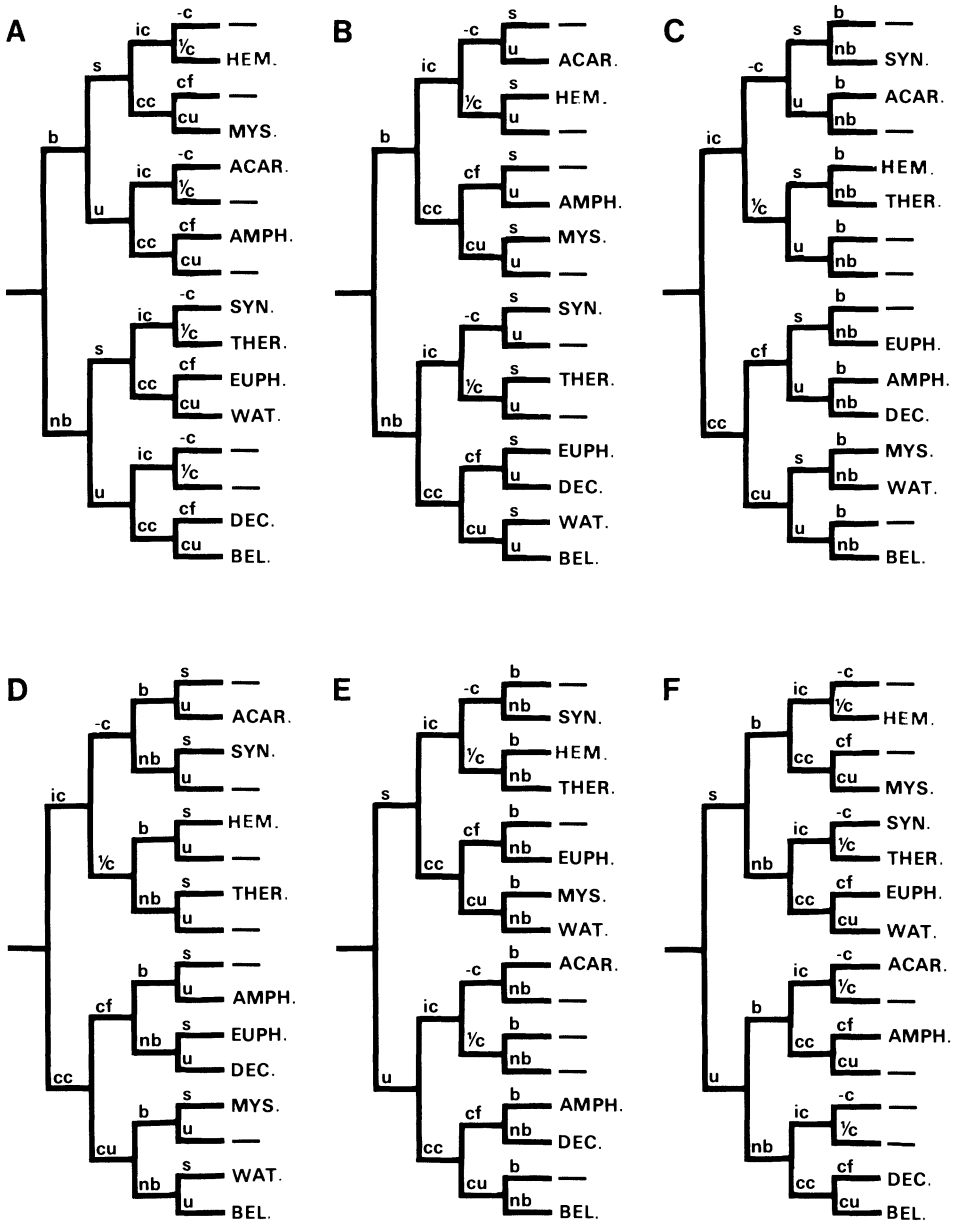


Fig. 3. Phenograms based on alternative arrangements and weightings of the major morphological features used to produce possible eumalacostracan morphotypes. A line indicates lack of existence of a particular "paper animal." Symbols are as follows: (cc) complete carapace, (cf) carapace fused to thorax, (cu) carapace unfused to thorax, (ic) "imperfect" carapace, (-c) no carapace, (1/c) short carapace, (s) schizopodous thoracopods, (u) uniramous thoracopods, (b) subthoracic brood pouch, (nb) no brood pouch.

but the uncertainty principle outlined above would indicate we can never be certain of our choice. For example, *C* and *D* present relationships which most people would recognize and have some "comfort" with. In both cases

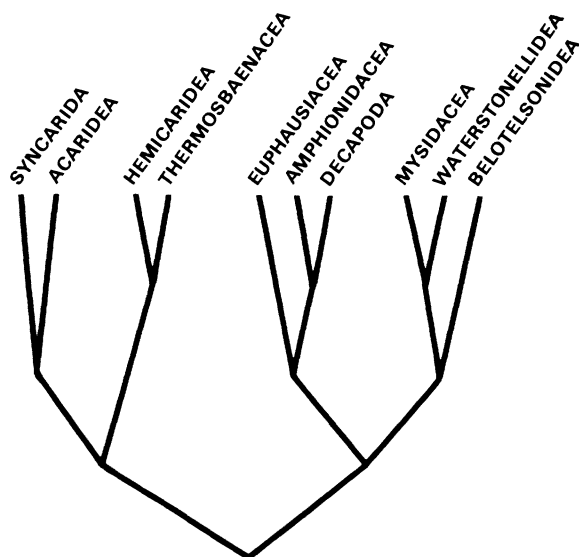


Fig. 4. Cladogram of relationships of eumalacostracan orders derived from phenogram *c* in Fig. 3 and forming a graphic presentation of the taxonomy proposed in the text.

“arthrostracans” and “brachycaridans” stand separate from coherent eucarid and mysid-eocarid clades. On the other hand, *E* also presents groups familiar to us with the “schizopodous caridoids” forming a major clade, “advanced” eucarids affiliated with belotelsonids (another not entirely improbable link), and carapaceless peracarids standing alone again. In all these phenograms we can recognize currently accepted groups, e.g., eucarids, or ones with long historical roots, e.g., arthrostracans and schizopods. The repeated emergence in all phenograms of carapaceless peracarids, however, might be a surprise to many.

However, we must recognize that my perception of “reasonableness” of phenograms *C* and *D* is influenced by the contemporary and historical traditions which most appeal to me. It is not inconceivable that stochastic approaches to evolution theory may be ill-founded, in which case phenograms *A*, *B*, and *F* should perhaps not be so summarily dismissed. At the very least they enter into the uncertainty principle enunciated above. It is a fact of phyletic speculation we must recognize and learn to live with, not unlike the Heisenberg Uncertainty Principle of physics. The fact that *C* and *D* are so similar, despite the respective differences each places on brooding and thoracopods, does indicate a certain stability of this scheme. This combines with the fact that none of the five major links in *C* makes one “uncomfortable,” whereas I find the placing in *D* of amphionids as a sister group to euphausiaceans and decapods would ignore what seems to be a legitimate relationship between amphionids and decapods. If some readers are disturbed by the “subjectivity” of this approach, they must recognize that subjectivity is a necessary adjunct to uncertainty.

CONCLUSION

Strict recognition of the uncertainty principle and the stochastic conceptual approach would require that we recognize just the 10 “orders” of eumalacostracans as discrete lines of evolution and not attempt a further Calman-like grouping

into superorders. However, as evolutionists we seem to prefer clustering our lineages when possible. If this is desired we could then utilize the category *COHORT* to suggest proximity of orders to each other. Erection of extra Hennigian hierarchies such as infraclasses, divisions, and extra superorders to reflect all the branches in any of the phenograms in Fig. 3 is not justified because of the uncertainty involved.

The taxonomy I would propose, with the major basic distinguishing characters (others can be used for detailed definition) for cohorts and orders, is as follows:

Class Malacostraca

Subclass: Phyllocarida Packard, 1879

Subclass: Hoplocarida Calman, 1904

Subclass: Eumalacostraca Grobben, 1892

Cohort: Arthrostraca Burmeister, 1834 (no carapace)

Order: Syncarida Packard, 1885 (schizopodous thoracopods, no brood pouch)

Suborder: Palaeocaridacea Brooks, 1962

Suborder: Anaspidacea Calman, 1904

Suborder: Bathynellacea Chappuis, 1915

Order: Acaridea *nov.* (uniramous thoracopods, oöstegite brood pouch in females)

Suborder: Isopoda Latreille, 1817

Suborder: Amphipoda Latreille, 1816

Cohort: Brachycarida *nov.* (short carapace not completely enveloping thorax)

Order: Hemicaridacea *nov.* (schizopodous thoracopods, oöstegite brood pouch in females)

Suborder: Spelaeogriphacea Gordon, 1957

Suborder: Tanaidacea Dana, 1853

Suborder: Cumacea Kröyer, 1846

Order: Thermosbaenacea Monod, 1927 (schizopodous thoracopods, no brood pouch)

Cohort: Eucarida Calman, 1904 (complete carapace fused to thoracomeres)

Order: Euphausiacea Dana, 1852 (schizopodous thoracopods, no brood pouch)

Order: Decapoda Latreille, 1803 (uniramous thoracopods, no brood pouch)

Order: Amphionidacea Williamson, 1973 (uniramous thoracopods, brood pouch formed by first pleopods in females)

Cohort: Mysoida *nov.* (complete carapace unfused to thorax)

Order: Mysidacea Boas, 1883 (schizopodous thoracopods, oöstegite brood pouch in females)

Suborder: Lophogastrida Boas, 1883

Suborder: Mysida Boas, 1883

Suborder: Pygocephalomorpha Beurlen, 1930

Order: Waterstonellidea *nov.* (schizopodous thoracopods, no brood pouch)

Order: Belotelsonidea *nov.* (uniramous thoracopods, no brood pouch)

Cohort: uncertain

Order: Eocaridacea Brooks, 1962 (Paleozoic families for which no adequate data exists on the nature of the carapace, thoracopods, and possible brood pouch)

[The order Amphionidacea presents something of a problem. Classified for years as a peculiar caridean decapod, *Amphionides reynaudii* was placed in its own order mainly because of the peculiar supposed brood pouch in the females. The adult thoracopods have only a stump for an exopod and are here interpreted as basically uniramous, but in this regard they are somewhat similar to carideans and some peneids (where exopods and exopod stumps are retained as paedomorphic features). Although it would perhaps solve many problems to return amphionids to the carideans, amphionidaceans do not appear to be decapodous, i.e., they have only one pair of maxillipeds. They seem best left as a separate order for now. Eocaridacea is best retained for now as a catchall category for fossil forms with incomplete information about them. Some of these may not even be eumalacostracan, e.g., *Eocaris oervigi*; this Middle Devonian form is possibly an aechronectidan hoplocarid but is known only from one incomplete specimen.]

This taxonomy has the advantage over the traditional scheme of Calman's in that the principal breakdown of groups is based on a consistent assessment of carapace, brood pouch, and thoracopod conditions rather than an inconsistent application of brooding patterns and carapace state. Thus each order is defined by several characters derived from the consideration of basic form.

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