



Relationships within Eumalacostracan Crustacea

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Abstract. A cladistic analysis was performed on 20 constituent higher taxa within the Eumalacostraca based on 31 characters of external anatomy. Variants of the most parsimonious scheme are presented, and the effects of tolerating different levels of uncertainty are evaluated. It is concluded that: 1) while the basic outline of Calman's (1904) taxonomy of Eumalacostraca might be utilized, the arrangement within peracarids postulated by Siewing (1956) cannot be maintained; 2) the *Baupläne* approach of Schram (1981) has some merit and some of the controversial higher taxonomic groupings of eumalacostracan "orders" originally indicated by that method are vindicated; 3) the idea that the carapace is a derived feature within eumalacostracans, advanced by Dahl (1983), can be maintained only if a high level of homoplasy is tolerated; 4) the concept of a taxon Mysidacea seems best abandoned.

INTRODUCTION

The basic modern classification of eumalacostracan crustaceans was outlined by Calman (1904, 1909) with little reference at that time to what the details of phyletic relationships between and within groups might have been. However, it was Siewing (1951, 1956) who presented a phylogenetic tree for eumalacostracans widely subscribed to by subsequent authorities (e.g., Fryer 1964, Hessler 1969).

Recently, however, the Calman/Siewing scheme for Eumalacostraca *sensu stricto* has been questioned. Schram (1981) recognized basic structural plans within the Eumalacostraca, but the methodology he employed was limited by the number of characters that could be handled essentially by pencil and paper. However, the method was helpful in three respects. First, it illustrated a variable range of possible dendrograms. Each variant dendrogram was constrained by which characters received initial emphasis and, thus, demonstrated the basic range of uncertainty that must be implicit in any phylogenetic analysis. Second, the analysis suggested certain "supraordinal" relationships which were a bit unexpected, especially within the peracarid groups. For example, isopods and amphipods were united; and cumaceans, tanaids, and spelaeogriphaceans were allied to each other with some suggestion of more distant possible links of these to thermosbaenaceans. Third, the method also produced a number of "paper" *Baupläne* which were not occupied or had yet to be discovered. Implicit in these hypothetical morphotypes was the idea that if the method had any merit at all, some of those "empty" *Baupläne* might eventually be found.

Watling (1981, 1983) questioned the unity of the superorder Peracarida as a natural taxon. He produced two different cladograms for the peracarids. His stated purpose (in Schram, 1983:347) was to search for ". . . *Baupläne* that include the fine structure . . .," and he believed that ". . . the first step in the analysis is to look at all these structures for pattern . . ." In this respect Watling (1983) performed a useful function by focusing attention on characters that had largely been overlooked by previous workers such as mandible function, maxilliped form, and patterns of arterial circulation.

Dahl (1983) formally proposed a concept that had been implicit in several of his earlier papers, viz., that the lack of a carapace is a primitive feature, that the evolution of the carapace had occurred independently several times, and that Calman's caridoid

facies was a set of convergent phenomena. Dahl presented some interesting observations on comparative carapace development related to these ideas. Watling (especially 1983) acknowledged his indebtedness to Dahl's concept of the carapace as a derived feature.

Finally, Hessler (1983) produced a "defense" of the caridoid facies in which he attempted cladistic analysis of the Siewing scheme for peracarids in a more formal manner than had ever been presented before. Hessler's study, however, produced a scheme in which the Siewing arrangement of taxa could be retained only by tolerating a great deal of convergence (10 of his 23 characters are convergent in whole or part to one or more of the others).

Thus, several items bear on the problem of eumalacostracan relationships and demand some sort of a resolution. First, is the need to assess relationships among eumalacostracans by the use of as many characters as possible, and use these characters across-the-board for all taxa, fossil and Recent. Second, a test is demanded both for Dahl's concept of the carapace as a derived feature, as well as some of the "strange" higher groupings suggested by Schram (1981). And third, it is necessary to arrive at a scheme which will group the taxa in question strictly by their shared derived character states with the fewest number of convergences possible.

METHOD

One way to analyze large numbers of characters and taxa so as to achieve the most parsimonious arrangement, based solely on shared derived characters, is to use one of the various versions available for the Wagner 78 program. For this analysis, I decided to "break up" certain large and diverse traditional eumalacostracan taxa and treat their components as separate units to test both the viability of such taxa and the "reasonableness" of the characters used. To this end the suborders of Mysidacea (Mysida, Lophogastrida, and Pygocephalomorpha) and of Decapoda as outlined by Burkenroad (1981) (Dendrobranchiata, Eukyphida, Euzygida, and Reptantia) were evaluated as separate entities. The choice of taxa for the decapods was somewhat arbitrary since, for example, Felgenhauer and Abele (1983) break the Eukyphida into two groups coequal with the others, Procarididea and Caridea.

The 31 characters used for this analysis were selected by repeated trial and error (as is standard in any computer-generated cladistic treatment of such data), rejecting potentially useful characters which had low consistency indexes (i.e., high homoplasy values). The ultimate aim of these initial assessments of potentially useful characters was to yield the most parsimonious and congruent cladogram possible. Only characters that could be assessed for all groups relatively unambiguously were used. For example, I did not use the lacinia mobilis because I do not feel its homology has been demonstrated. As has been shown recently (Dahl and Hessler, 1982), this character is not only present in several groups, but is developed differently in these taxa. How can one compare the massive laciniae of lophogastrids with the rather delicate ones in other peracarids? Or, how are larval laciniae to be judged in comparison to those of adults? More needs to be known about the development and functional morphology of laciniae before they can be adequately assessed in a phylogenetic analysis. Other characters were not used because, while they serve to characterize specific taxa, they are quite homoplastic and are known to occur convergently in widely separated groups. For example, the use of the presence of second or third maxillipedes was avoided in the final analysis since it only served to confirm groupings achieved more effectively by singularly derived features. The characters eventually settled upon are given in Table 1, the numbers indicated corresponding to those used in the cladograms.

The program was run using several different outgroups, Hoplocarida, Leptostracan Phyllocarida, and a hypothetical ancestor arbitrarily designated primitive for all 31 characters. No differences in any of the resultant eumalacostracan cladograms were noted. Among other parameters, the program also calculated total lengths of trees (i.e., the total number of incidences of derived characters in the cladogram) and the total homoplasy value (i.e., a measure of the total array of convergences and character

TABLE 1. Opposing list of character states used in the analysis of relationships within Eumalacostraca. Numbers correspond to those used in cladograms.

Primitive	Derived
1. Non-caridoid musculature	caridoid musculature
2. No zoeal larvae	zoeae
3. Carapace not fused to all thoracomeres	carapace fused to all thoracomeres
4. No petasma	petasma
5. First thoracomere free of head	first thoracomere fused to head
6. Maxillipede with epipodite	maxillipede without epipodite
7. No brood pouch formed by first pleopod	brood pouch between first pleopod and venter of thorax
8. No scaphognathite	scaphognathite on maxilla
9. First thoracopod unmodified	maxillipedes with lamellate protopod, coxal/basal endites directed mediad
10. Maxillipede endopod robust	maxillipede endopod flagelliform
11. Eggs not brooded on pleopods	eggs brooded on pleopods
12. No caridean lobe	caridean lobe on maxillipede
13. Biramous thoracopods	uniramous thoracopods
14. All pleopods present	pleopods lost or reduced
15. First thoracopod unmodified	maxillipedes with tendency to form gnathobasic endites, endopod pediform
16. Pereiopodal epipodite gills	no pereiopodal epipodite gills
17. First thoracopod unmodified	maxillipedes with basal endites lobate and directed distad
18. No marsupium	oöstegite marsupium
19. Thoracic endopods non-filtratory	thoracic endopods filtratory
20. No male cones	male cones
21. Thoracic coxae unmodified	thoracic coxal plates
22. Eyes stalked or lobed	eyes sessile
23. One pair of uropods	more than one pair of uropods
24. Pleopods non-respiratory	pleopods respiratory
25. Carapace not short	carapace short
26. Eggs not brooded under carapace	eggs brooded under carapace
27. Maxillipedal epipodite if present simple	epipodite specialized as cup- or spoon-like respiratory organ
28. Rostrum simple	pseudorostrum and maxillipedal siphons
29. Thoracic exopods non-respiratory	thoracic exopods respiratory
30. Maxillipedal epipodite as a single segment	epipodite with tendency to form as 2-3 segments
31. Carapace	carapace absent
<i>Character reversal used in analysis portrayed in Figure 3</i>	
31. No carapace	carapace

reversals in the cladogram). These factors proved useful in qualitatively comparing different cladograms.

RESULTS

The computer program generated several variant cladograms. That variant which was most parsimonious and yielded the fewest number of convergences and character reversals is given in Figure 1. In the series of cladograms summarized in Figures 1-3, previous outgroup analysis indicated that the presence of a carapace should be treated as primitive because it is present in all hoplocaridans and phyllocaridans. As can be seen, the program produced (Fig. 1) an unresolved polychotomy with four branches at the base of the Eumalacostraca: eucarids, belotelsonids, syncarids, and waterstonellid/peracarids. A variant of this scheme (Fig. 2) yields an unresolved polychotomy of five branches. Although the latter cladogram has the same number of convergences as the former, it is somewhat shorter than that of Figure 1. A convergence in the secondary reevolution of pereiopodal epipodite gills between Mysida and Amphipoda is traded off for a convergence in the primary loss of pereiopodal epipodite gills in Watersto-

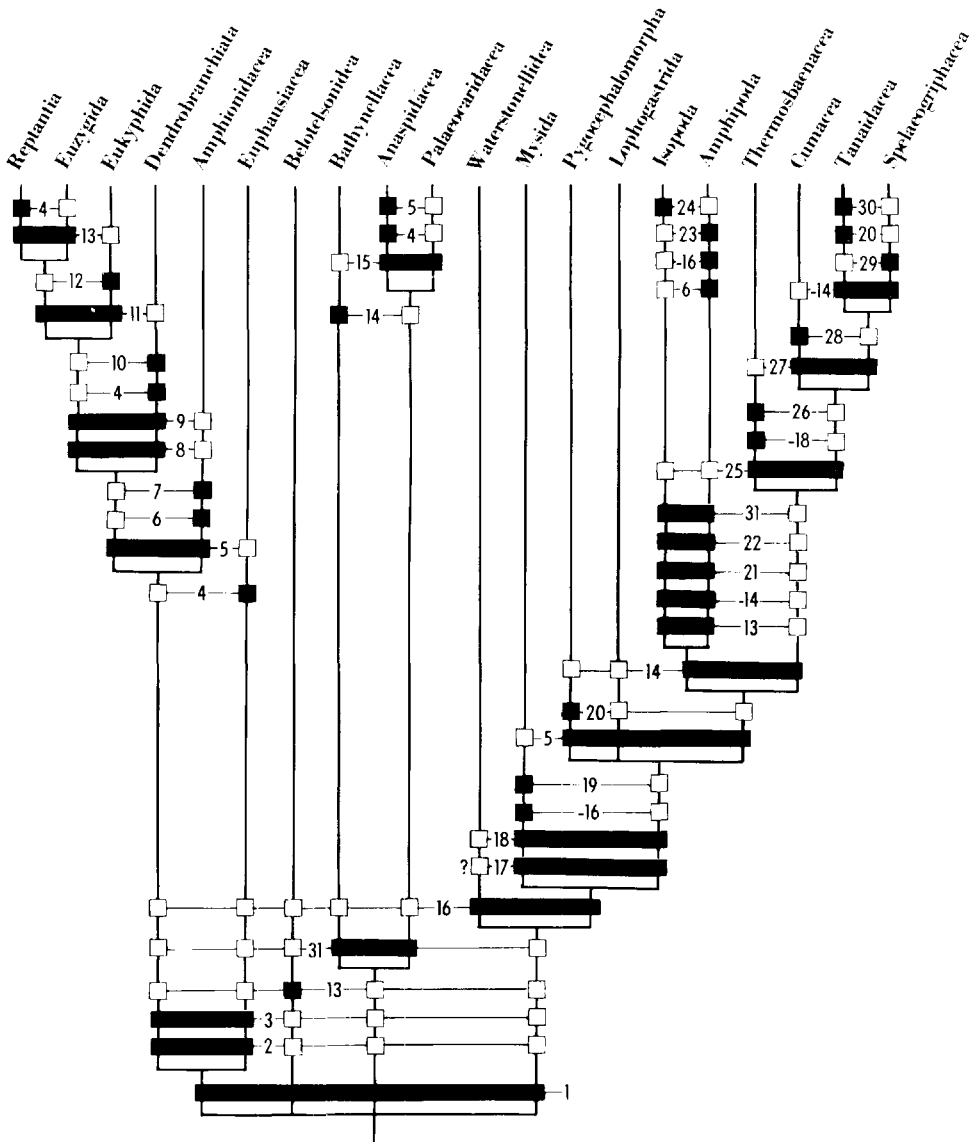


FIGURE 1. Cladistic relationships of component taxa of the Eumalacostraca, the presence of a carapace considered primitive. This is the shortest cladogram with the lowest homoplasy value, the base of the cladogram with an unresolved quadrotomy between eucarids, belotelsonids, syncarids, and waterstonellids/peracarids. □ primitive, ■ derived.

nellidea and the "peracarid" line above Mysida. Wagner 78 is designed to produce the best resolved cladogram possible from the data given and, thus, the preferred version is that seen in Fig. 1. If on the other hand we wish to tolerate a slightly greater degree of uncertainty (Schram, 1983), then we may choose the variant of Fig. 2 in which peracarids can be recognized as a distinct lineage. The relationships indicated in Figure 1, however, are not without considerable biological interest. The thrust of the early evolution of the waterstonellid/peracarid line was towards increasing specialization of thoracopods. First the primitive respiratory epipodites were lost, then oöstegites and maxillipedes were evolved, and finally some further specializations occurred in specific lineages such as filtratory endopods in mysidans (Attramadal, *pers. comm.*), and further maxillipedal and ambulatory modifications in pygocephalomorphs (Schram, 1974).

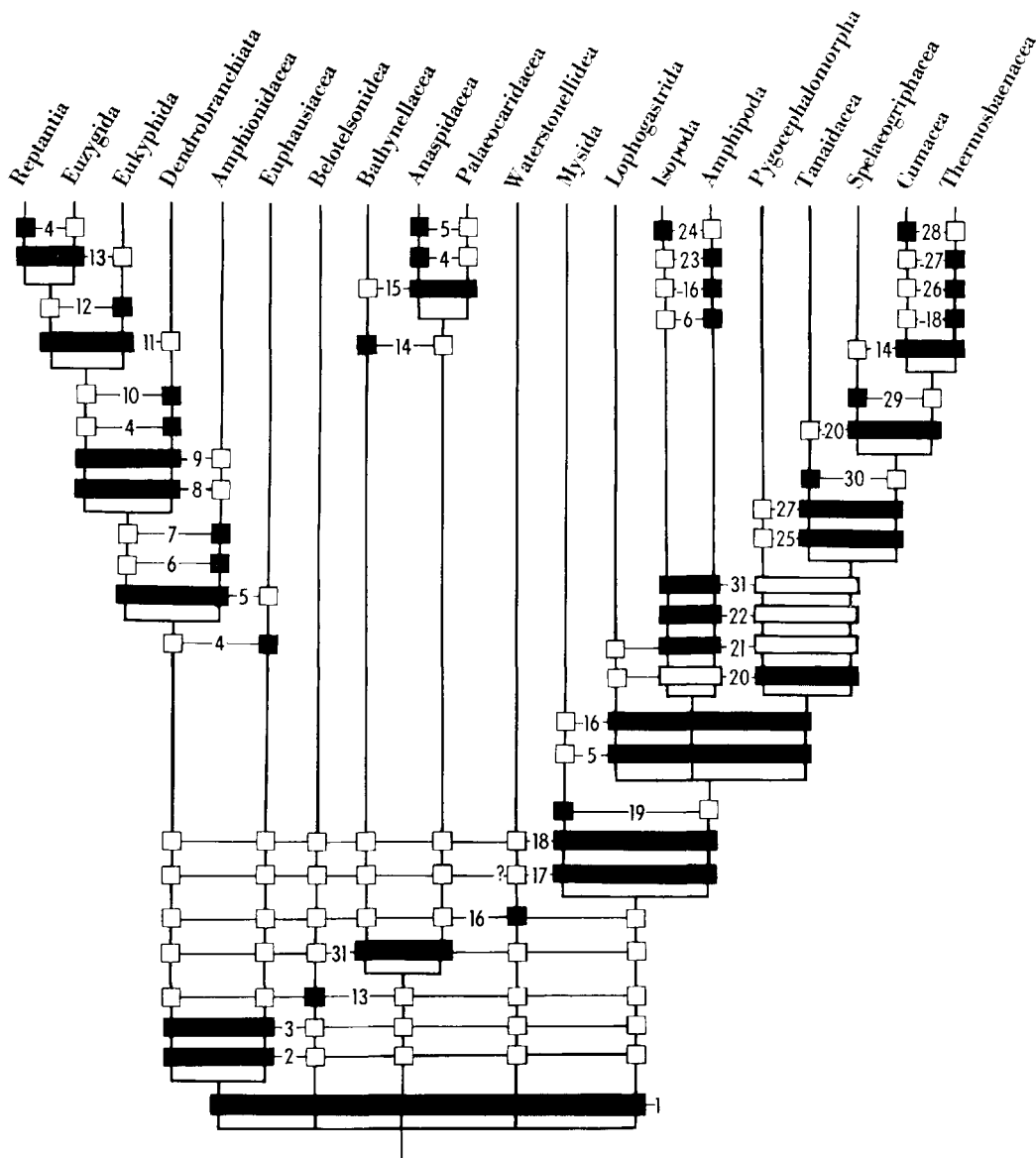


FIGURE 2. Cladistic relationships of component taxa of the Eumalacostraca, the presence of a carapace considered primitive. A variant cladogram from that of Fig. 1 exhibiting (1) unresolved quintichotomy at the base that allows a separation of waterstonellids and peracarids (which would shorten the tree, not involve any change in the number of convergences over that of Fig. 1, but would inject a higher level of uncertainty into the cladogram) and (2) an association of pygocephalomorphs as a sister group of the brachycaridans (which would not involve a lengthening of the cladogram but would inject one extra character reversal over that seen in Fig. 1). □ primitive, ■ derived.

Several interesting points emerge from these analyses. Many of the more-or-less controversial higher taxa (Cohorts and Orders) of Schram (1981), emerge, viz., Hemica-ridea (Cumacea, Tanaidacea, and Spelaeogriphacea), Brachycarida (Hemica-ridea and Thermosbaenacea), Eucarida (Euphausiacea, Amphionidacea, and Decapoda), and Acaridea (Isopoda and Amphipoda). The latter also seems to bear some relationship to a yet unnamed new order being proposed by T. Bowman, R. Hessler, and H. Sanders which, interestingly, seems to fill one of the "unoccupied" *Baupläne* of Schram (1981). On the other hand, some taxa derived from Schram (1981) do not seem viable: e.g.,

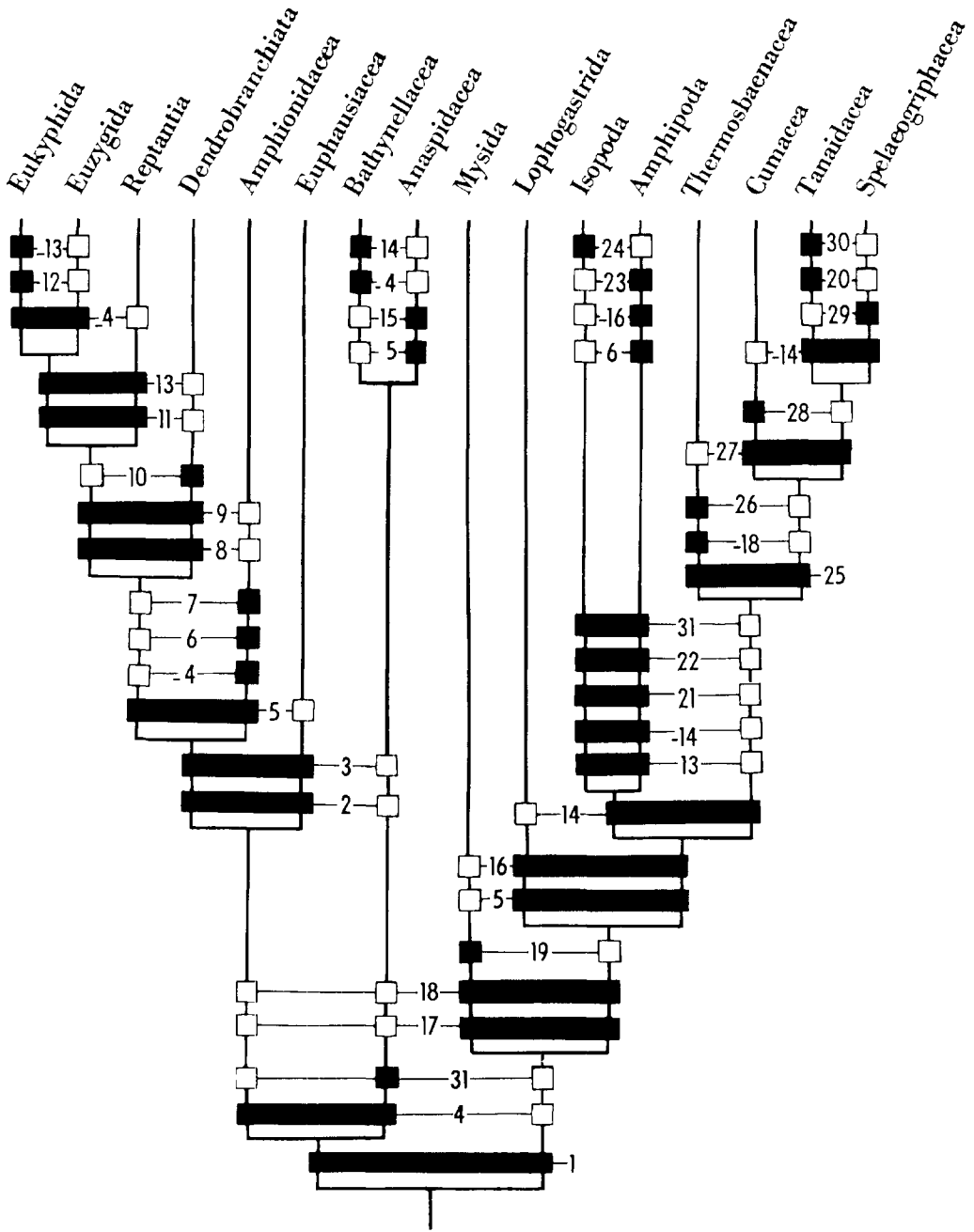


FIGURE 3. Cladogram based on the same character data as that used in cladograms of Figure 1, but analyzing only living groups and excluding the 4 extinct taxa, Palaeocaridacea, Belotelsonidea, Waterstonellidea, and Pygocephalomorpha. □ primitive, ■ derived.

Arthrostraca in the sense of Haeckel (1896), Giesbrecht (1913), or Grobben (1919) which unites all carapaceless syncarid and acaridean forms; or Mysoida (Belotelsonidea, Mysidacea, and Waterstonellidea), which seems invalid as a cladistic or taxonomic unit.

I decided to test the effect on the overall scheme of relationships when the fossil taxa were excluded from consideration (Fig. 3). Little change was noted except to ally

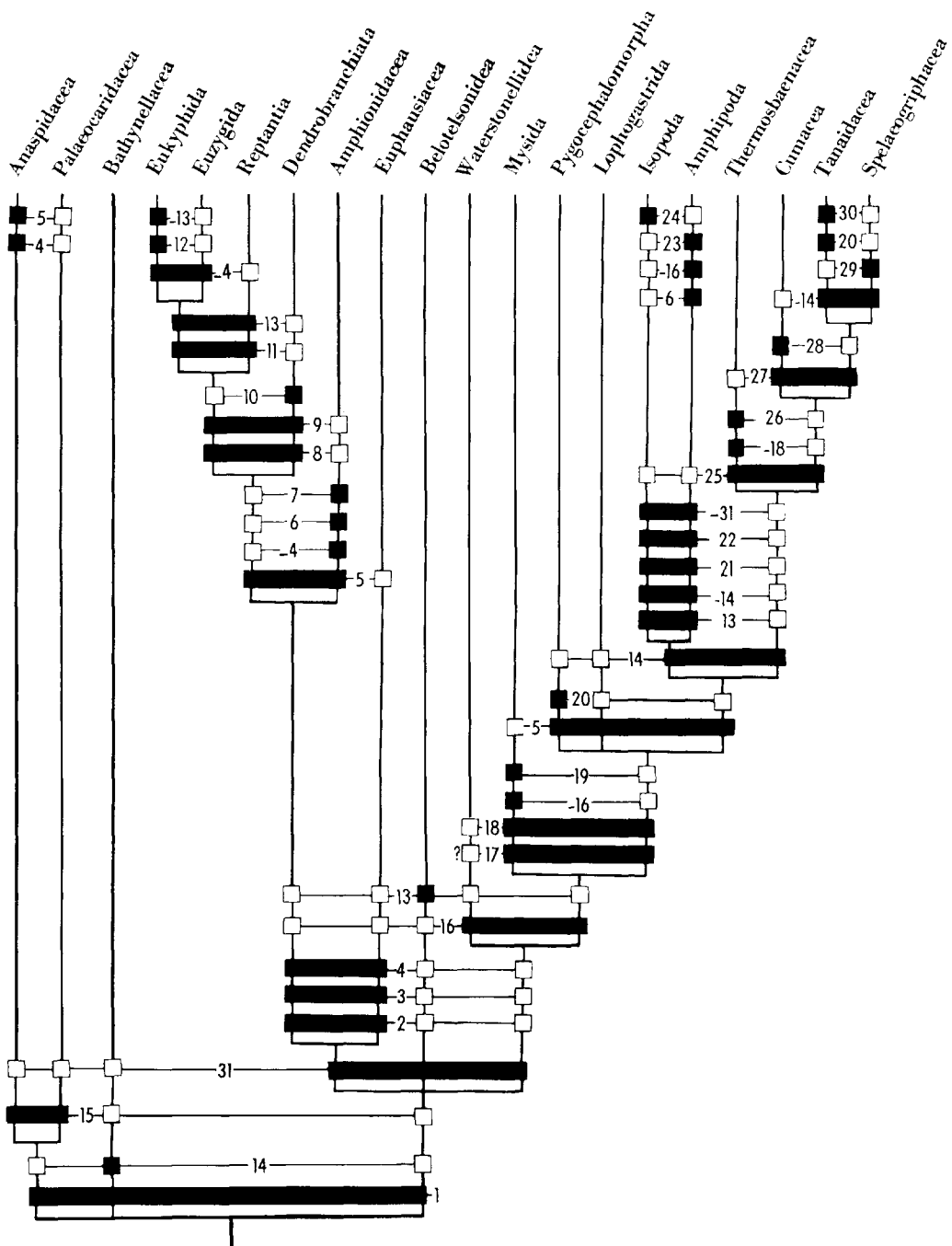


FIGURE 4. Cladogram with all taxa and character data the same as in Fig. 1, except the scoring of character 31 is reversed and the presence of a carapace is treated as a derived feature, as favored by Dahl (1983). □ primitive, ■ derived.

syncarids and eucarids as sister groups. Some slight modifications occurred in the arrangement of higher eucarids, but otherwise the basic relationships of the taxa of Fig. 1 are preserved. The total homoplasy value (a measure of the amount of convergence) is somewhat higher (388 vs. 372) in the non-fossil scheme than in that which includes the extinct groups, although the total length of both trees is not that much different, 44 without fossils as opposed to 46 with extinct groups included.

I also tested the contention of Dahl (1983) that the carapace is a derived feature, the lack of a carapace being viewed as primitive (Fig. 4). This test resulted in a somewhat longer cladogram than those in Figure 1 (47 vs. 46), but one which has a dramatically higher total homoplasy value (510 vs. 372). Similar results were obtained when the data based on Dahl's concept were run without extinct taxa. It would seem, therefore, that the suggestion by Dahl that the carapaceless state is the primitive one for eumalacostracans engenders a more complicated and less parsimonious array of relationships. Note, however, that the relationships within peracarids persist, including that of breaking apart Mysidacea.

DISCUSSION

Characters difficult to use

Certain characters were deliberately not used here though they have found widespread employment in the taxonomy and phylogenetic discussions of Eumalacostraca by various authors.

In eucarids, although the structure of maxillipedes was used (lamellate appendages with endites directed mediad), the number of them was not (three maxillipedes and thus the name decapod). The anatomical and functional state of thoracopods in higher eucarids is actually more varied than one would be led to believe from the automatic connotation engendered by the term "decapod." In several instances, e.g., many Dendrobranchiata, the so-called third maxillipede is actually more "pediform" in structure and function than "maxillipediform." Also, certain "pereopods" actually have little locomotory function but are utilized in food acquisition and processing as well as defense. For example, in euzygids (=stenopodids) the fourth and fifth thoracopods are chelipedes and directed anteriorly towards the mouth field resulting in a hexapodous condition instead of a decapodous one in these animals. In astacideans the characteristic great chelipedes of the fourth thoracopods serve in food procurement and defense, making the animal functionally octopodous. So while there are good maxillary and maxillipedal features which can serve to delineate a taxon Decapoda, ironically true decapody is not a particularly good character to assist in such delineation.

Another feature taken for granted in discussion of eumalacostracan evolution is the fusion of the first thoracomere to the cephalon. Bathynellacea, of course, do not have this fusion. The Carboniferous genera *Belotelson* and *Waterstonella* apparently had free first thoracomeres as well, as they lacked maxillipedes altogether. Hence, it is imperative to resolve whether or not all living forms with a carapace do or do not fuse the first thoracomere to the head. For example, euphausiaceans lack a maxillipede, have the carapace fused to the thoracomeres, but have all thoracomeres associated together separate from the maxillary segment. Examination of mysidaceans revealed a variable state of affairs. Lophogastridans, with their well-developed maxillipedes, closely associate the first thoracomere with the cephalon and separate it from the second and following thoracomeres. However, in the mysidan *Neomysis americana* there is a separation of the maxillary from the thoracic segments, with all eight sets of thoracopods closely associated and separated by a distinct skeletal bar from the more anterior mouthparts. So in mysidans the first thoracomere is clearly not fused to the cephalon, although there is a tendency to develop maxillipedes. This feature serves to break apart the taxon Mysidacea, making Mysida a sister group to all other peracarids.

I also excluded three characters which have been asserted as distinctly peracaridan, including the lacinia mobilis mentioned above. The presence of a manca stage is frequently cited as a characteristic of peracarids. Generally workers used this feature as if they were dealing with a manca larva. Mancas, however, are not to be equated with the zoea, cypris, or other larval types which have considerable cladistic merit (see for example character 2). A "manca" is a stage of development which can have various forms of expression (Newman 1983). Amphipods are generally said to lack a manca, yet some hyperiids are freed from the female in a virtual manca state (Laval 1980). Some adults express a permanent manca condition, e.g., the genus *Thermosbaena*.

Manca stages also occur outside the peracarids, e.g., bathynellaceans hatch in an extreme “mancoïd” condition lacking several of the posterior thoracopods and in the adults of some forms the last thoracopod can be missing or greatly atrophied. The presence or absence of a manca may be better understood in terms of constraints placed on development by egg size (e.g., Steele and Steele 1975). Characters of marsupial and maxillipedal form alone can be used to delineate peracarids more securely; and while the presence of a manca stage may assist in this delineation, it is not as unambiguous as one would suppose.

The same observation can be made of the monocondylic coxa/basis articulation recently noted by Hessler (1982). This character might appear to be a useful congruent feature towards establishing a concept of Peracarida. However, it has a variety of expression difficult at this time to evaluate. For example, the monocondyle variously arises from positions that are either lateral (tanaïds), purely posterior (*Spelaeogriphus*), or postero-lateral (all other peracarids). Nor do all thoracopods have this joint. In tanaïds the third through fifth limbs have a dicondylic joint whereas only the sixth through eighth have the distinct monocondyle. Completely aberrant condyle, muscle, and/or joint arrangements are seen in amphipods and mysidaceans. These latter two groups also display different degrees of expression of these features throughout the whole thoracopodal limb series. Although coxal/basal structure seems to second peracarid monophyly, problems with variety of expression and assessment of polarities between these variations preclude its use here.

Characters rejected for use

Two suites of traditional characters were completely rejected, viz., those of gut structure and embryo flexion which have played so prominent a role in the work of Siewing, and which resulted in the diametric separation of isopods and amphipods. The more that is discovered about gut morphology, the more it seems that the digestive system is too plastic to yield any useful data for phylogenetic analysis. Kunze (1981, and *personal communication*) has noted that the anatomy of the stomach of isopods is closely tied to feeding habits. Ide (1892) and Naylor (1955) provided details of gut structure in *Idotea* identical to that supposedly characteristic of amphipods, including an anteriorly directed mid-dorsal caecum in *I. tricuspidata*. Carol Diebel (*pers. comm.*) is finding that stomach structure among hyperiid amphipods is so diverse as to be uncharacterizable because of adaptations to particular feeding strategies.

The other character rejected here, but given great weight by Siewing, is whether the developing embryo is flexed ventrally or dorsally within the egg membranes. First, few studies within and between groups of peracarids have been performed to determine the distribution of these states. Second, one of these flexures must be primitive and the other advanced. As such, only one of them can be used to characterize one of the groups which possesses it, but they are not both derived characters. It might appear that the dorsal flexure is derived, but insufficient data exist from within and without peracarids in order to assess polarity. And third, flexure in embryos seems better understood in terms of the mechanics of a particular developmental sequence rather than in terms of phyletic trends. Note that in forms with a ventral flexure, there is typically a very distinct egg-nauplius stage in early development, the development of the teloblasts lags behind that of the primary part of the head. The development of a caudal papilla and a caudal furrow which lead to ventral flexure is thus possibly related to the rapid development of the naupliar region. In contrast, in animals with a dorsal flexure, the appearance of the naupliar Anlagen lags. In such forms the teloblasts not only appear early in the sequence of events around the blastopore, they initiate their divisions early such that the naupliar and anterior metanaupliar somites appear virtually simultaneously. It would appear that because of the slower head development the proliferation of body somites is allowed to occur along the entire ventral and posterior surfaces of the egg without the appearance of a caudal furrow or papilla to produce ventral flexure. Clearly the “phylogenetic power” of the apparent differences of flexure between isopods and amphipods has been somewhat overextended.

Variant cladograms

Two variants in the cladograms were produced by the program frequently enough to require some comment here. One is a variation in the higher decapods seen in Figures 1 and 3. In one (Fig. 1), somewhat more parsimonious, eukyphids are placed as a sister group to euzygids and reptants. In the other (Fig. 3), reptants are a sister group of euzygids and eukyphids. The former is a more traditional arrangement, but the latter is all the more startling in light of the pregnant comment of Felgenhauer and Abele (1983) that it was their belief that the origins of the so-called "natant" groups of decapods "... are to be found among those groups traditionally considered reptants."

Indeed the entire issue of relationships within the decapods is under intense study right now. Burkenroad (1981), using branchial and ontogenetic characters not employed in this analysis, essentially obtained an arrangement of taxa like that seen in Figure 3. However, Felgenhauer (*personal communication*) is examining various features of external and internal anatomy of natant forms in an attempt to arrive at an assessment of cladistic relationships within decapods. For these reasons, it may be wise to avoid use of terms like Decapoda and/or Pleocyemata for the time being, and rather treat the taxa within Eucarida as one long transition series.

Another notable variant is seen in the higher peracarids between Figs. 1 and 2. The scheme in Fig. 2 is slightly less parsimonious, but if one can tolerate the additional character reversal it entails, then the arrangement is a sequence of events which is of considerable biological interest. The isopod/amphipod line seems to represent one in which the thrust of the radiation is toward varied exploitation of food resources because of the great plasticity in gut structures. The brachycaridan line, especially when the pygocephalomorphs are associated with it, seems to be a line which represents exploitation of reproductive strategies. Both pygocephalomorphs and tanaids have cones on the males. The supposed seminal receptacles mentioned by Brooks (1962) on pygocephalomorphs bear little actual resemblance to such structures. These structures are more likely large genital cones on the eighth thoracic sternites of males. The brachycaridan line is generally characterized by respiratory specializations of the maxillipedes and thoracopods. It is also a transition series in which carapace, pleopods, and the oöstegite brood pouch are reduced or lost, culminating in the condition seen in the thermosbaenaceans. Insofar as the component taxa are currently understood, this line also exploits reproductive and unusual sexual strategies that maximize the number of offspring from any one generation (e.g., see Sieg 1983, for tanaidaceans, or Corey 1981, for cumaceans).

CONCLUSIONS

Several conclusions can be drawn concerning the analyses made here:

1) At least in part, the taxonomic scheme for the Eumalacostraca suggested by the identification of *Baupläne* within the group (Schram 1981) is supported, especially in regards to peracarid types. The idea of a taxon Arthrostraca is not favored, but the reassociation of isopods with amphipods in the sense of the old taxon Edriophthalma, and the linking of short carapace forms, does have some merit.

2) If some degree of uncertainty is accepted, then the relationships within Peracarida postulated by Siewing (1951, 1956) can be subscribed to, but only if considerable multiple convergences can be tolerated within a distinctly unparsimonious scheme.

3) The concept of the carapace as a derived feature in the sense of Dahl (1983) is acceptable only by tolerating a great many more convergences than occur when the presence of a carapace is viewed as primitive.

4) The concept of a formal taxon Mysidacea seems best abandoned. The three subtaxa traditionally placed within it (Lophogastrida, Mysida, and Pygocephalomorpha) are distinct from each other regardless of whether the presence of a carapace is considered primitive or derived.

What taxonomy of Eumalacostraca should be derived from all this? The eucarids are destined for some kind of realignment, especially of the higher taxa. The phylo-

genetic integrity of the brachycaridans is stable enough, whether or not pygocephalomorphs are closely associated with them. The resolution of relationships within the edriophthalman branch must await the description and evaluation of the new order of Bowman, Hessler, and Sanders, as well as a reevaluation of relationships within isopods and amphipods using a careful analysis of character states in all subgroups therein. In regards to the latter, we may resurrect the old taxon Laemodipoda, wherein caprellids and cyamids are separated as sister groups off by themselves. Such a study is currently under way.

It is my intent here to point out two things. First, there is merit in carefully reflecting on what are the constituent structural plans expressed within any particular taxon, alert to the fact that any particular *Bauplan* may or may not be developed, or may or may not be the basis of an extensive radiation. Second, regardless of the ongoing philosophical and in large part tautological debate on taxonomic theory, we must make some organized careful evaluations of characters and what their condition and polarity might be throughout *all* members of a group. These are problems which have been all too often neglected in the history of crustacean studies, but are not unique to the study of these arthropods.

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