AN ALTERNATIVE PHYLOGENY OF PERACARID CRUSTACEANS

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ABSTRACT

In order to properly understand the origins of the Order Amphipoda, their phylogenetic position within the Superorder Peracarida must first be established. A hypothetical ancestral peracarid is derived from Dahl's hypothetical ancestral eumalacostracan, which was proposed as lacking a carapace. The independent derivation of a carapace for special needs on at least two occasions is thus a central feature of a new phylogenetic arrangement for the peracaridan orders. This phylogeny is based on an analysis of 29 character states using Hennigian methods. Two lineages are immediately apparent: 1, a heterogeneous line containing the Amphipoda, Mysidacea, and Thermosbaenacea; and 2, a homogeneous "mancoid" line leading from the Isopoda through the Spelaeogriphacea and Tanaidacea to the Cumacea. The mancoid line as proposed is inverted relative to earlier phylogenetic schemes; however, this new arrangement is more in accord with the known fossil record. It is suggested that future examinations of the phylogeny of peracarid orders be based on a scheme for the Superorder, thus enabling plesiomorphic features of individual orders to be properly defined. Lastly, the polyphyletic nature of the Peracarida is discussed and it is suggested that at least three independent lines of "peracaridan" radiation might have arisen from a pre-Carboniferous syncarid-like ancestral eumalacostracan.

This study began as an inquiry into the origins and distribution of the malacostracan Order Amphipoda. The group is represented by more than 7,000 described species, of which at least 70% are marine (Barnard, personal communication). Of use to the following discussion, pertinent facts about amphipods include: a) they are found in nearly all environments from fresh and brackish waters to the deep sea, from the poles to the tropics; b) most amphipod families are very widespread, being represented in the shallow seas surrounding all continents; c) embryos are carried in a brood pouch and have direct development, thus excluding a dispersive planktonic larval stage; and d) fossils are rare, the oldest being Upper Eocene and looking very much like a modern gammaridean. In addition, because of the supposed young age of the group and its high species richness, amphipods have been often characterized (Bousfield, 1973) as "explosive" speciators. Barnard (personal communication), however, has in press papers hypothesizing a late Paleozoic presence of modern kinds of amphipods in Pangaean freshwaters.

To properly place amphipodan origins it is first necessary to discuss their phylogenetic position within the Superorder Peracarida. The latter is one of five superorders within the Class Malacostraca which includes such diverse organisms as the crabs, krill, and stomatopods, along with a host of interesting lesser-known forms. All adult malacostracans have the following features in common: a) the head bears five pairs of appendages (antennules, antennae, mandibles, maxillules, and maxillae); b) the body is composed of well-differentiated thoracic and abdominal parts; c) the thorax consists of eight somites; d) the abdomen consists of six (rarely seven) somites and telson; e) the male genital aperture is located on the eighth thoracic somite whereas the female genital aperture is on the sixth thoracic somite; f) the pereopod endopod is developed into the walking leg; and g) the digestive tract is distinctive in that the posterior part of the foregut is differentiated into anterior chewing and posterior filtering parts.

THE MALACOSTRACAN FRAMEWORK FOR PERACARIDAN EVOLUTION

Until only a few years ago, the generally accepted ancestral malacostracan was of the form proposed by Calman (1909). This animal was regarded as being shrimplike and possessed the following features, referred to as the "caridoid facies": a) a carapace which covered the thoracic region; b) movable, paired eyestalks; c) biramous antennules; d) a flattened, scalelike exopod on the antennae; e) generally elongate, ventrally flexed abdomen; f) tail fan composed of uropods and telson; and, g) swimming exopodites on the thoracic limbs. While some of these features may indeed be primitive attributes (b, c, and d), many are essentially structures common to some members of each superorder. Tiegs and Manton (1958) noted that these features are most fully developed in pelagic filter-feeders and further suggested "the caridoid facies has been perfected convergently in relation to habit" (p. 295). The poor development of caridoid features in benthic crawlers or burrowers would suggest, according to Calman's scheme, a bentho-pelagic swimming origin for the malacostracans in general, and through the Mysidacea for the peracarids in particular. The bentho-pelagic caridoid facies has been used by Bousfield (1978) to suggest that a pelagic terminal male is a plesiomorphic feature of the Amphipoda. The problems associated with this model will be dealt with later.

Utilizing a functional-morphological approach, a nonswimming benthic malacostracan ancestor has been proposed by Dahl (1976), the structure of which he derived from the hypothetical Urcrustacean of Hessler and Newman (1975). The latter authors suggested that this original crustacean, which they also argued probably evolved from a trilobitomorph ancestor, had the following features: a) the cephalon possessed five pairs of appendages (antennules, antennae, mandibles, maxillules, maxillae); b) in the juvenile there was a cephalic feeding mechanism, augmented or replaced in the adult by a thoracopod filtering system; c) the trunk consisted of many serially homologous somites, most of which possessed a pair of multiramous limbs; d) the metachronal beating of the thoracopods would allow food to be carried anteriorly by the endites to the mouth as well as propel the animal through, or over, the sediment; e) a carapace fold may or may not have been present; f) the compound eyes were stalked; and g) the first free-living stage was a nauplius larva. Among Recent crustaceans this form is most closely approximated by the Cephalocarida.

The evolution from this Urcrustacean to a eumalacostracan was outlined by Dahl (1976) as consisting of two main steps: 1) a functional subdivision of the trunk appendages into non-natatory thoracopods and natatory pleopods; and 2) the loss of thoracopod filter-feeding leading to the development of the thoracopods as ambulatory legs. Dahl argued that this evolution must have occurred in benthic-epibenthic habitats, and that the presence of eight walking legs would offer a ground plan for almost unlimited diversification. Further, he noted Lauterbach (1974) had found that pleura were always absent on thoracic somites covered by the carapace. Since both amphipods and isopods have pleura on all thoracic somites, he suggested "there exists no obvious reason why a primitive epibenthic eumalacostracan with a basic functional pattern of the type outlined above should have a caridoid habitus of the types proposed by Calman (1909) or Siewing (1963), i.e., that it should have been generally prawn-like and provided with a large carapace" (Dahl, 1976: 165).

From these beginnings, and utilizing common features of fossil and Recent forms, we can infer an ancestral eumalacostracan which possessed the following features: a) a functional subdivision of the body into a head, consisting of six

fused somites (including the embryonic preantennulary somite), a thorax of eight somites, the most anterior of which was functionally associated with feeding, and an abdomen of seven somites; b) a carapace was probably absent but the head shield was strongly developed and could easily support the growth of a carapace; c) antennules and antennae were biramous, the antennal exopod being reduced to a scale; d) the remaining thoracic legs were similar but with endopod more strongly developed for ambulatory purposes; e) five pairs of pleopods modified as natatory structures; and f) the sixth pair of pleopods modified as uropods. It is possible, with a minimum of alterations, to derive from this ancestor the stem forms leading to the modern eumalacostracan superorders, but for the purposes of this paper only the Peracarida will be dealt with further.

Phylogeny of the Peracarida

The Peracarida are a rather heterogeneous group of malacostracans united by their common possession of the following features: a) first thoracomere incorporated into the head; b) mandible of the rolling type with crushing molar, biting incisor, lacinia mobilis, and mouthwardly directed seta row (Manton, 1977); c) teloblastic development of most postnaupliar somites (Anderson, 1973); d) eggs, and often the young, carried in a brood pouch which, with the exception of the Order Thermosbaenacea, consists of medially directed outgrowths (termed oostegites) of some or all of thoracopods 2 to 7. Superimposing these features on the ancestral eumalacostracan model delimited above, and utilizing characters considered to be primitive within the Malacostraca generally (Calman, 1909, Hessler and Newman, 1975), the following additional plesiomorphic character states for the hypothetical ancestral peracaridan can be obtained: e) body cylindrical, pleura present but not extending strongly ventrally; f) carapace absent; g) antennule with two long, subequal flagella; h) antennae biramous, with scalelike exopod; i) thoracopod 1 (maxilliped) pediform, without strong endites; j) thoracopod 1 with unspecialized epipod and exopod; k) pereopods pediform with unspecialized exopod; l) pereopods with coxae small and freely articulating with the body; m) five pairs of pleopods; n) uropods and telson flattened, forming tail fan; o) telson not fused to last abdominal somite; p) eyes stalked; q) 19 ectoteloblasts in embryo (Dohle, 1976); r) embryo hatches as a miniature adult presumably without all appendages, but with significant embryonization which, in crustaceans, is characteristic of brooded young (Anderson, 1973). In many respects this model of an ancestral peracaridan looks much like an anaspidacean, which Kaestner (1970) and Schram (in press) suggest may be closest to the ancestral eumalacostracan.

The phylogenetic sequence derived below (Fig. 1) for the orders of the Peracarida is based on information from many sources. What is known morphologically of fossil forms comes from the work of Schram (1970, 1974), of the Spelaeogriphacea from Gordon (1957), and Thermosbaenacea from Fryer (1965), Stock (1976) and references therein. The other orders of Peracarida are wellknown to students of Crustacea and references for their anatomy can be found in Kaestner (1970). The argumentation scheme used in Fig. 1 follows methods outlined by Hennig (1966).

In the following account the character states used to derive the phylogenetic sequence are numbered sequentially in the text and in Fig. 1. Unless otherwise noted, statements made regarding various characters will apply to the most primitive representative of a given order.

Amphipods, mysids, and thermosbaenaceans share the following derived characters not attained by other peracarids: *1*, embryo hatches with all appendages present at least as rudiments (plesiomorphic condition in mancoid line, which
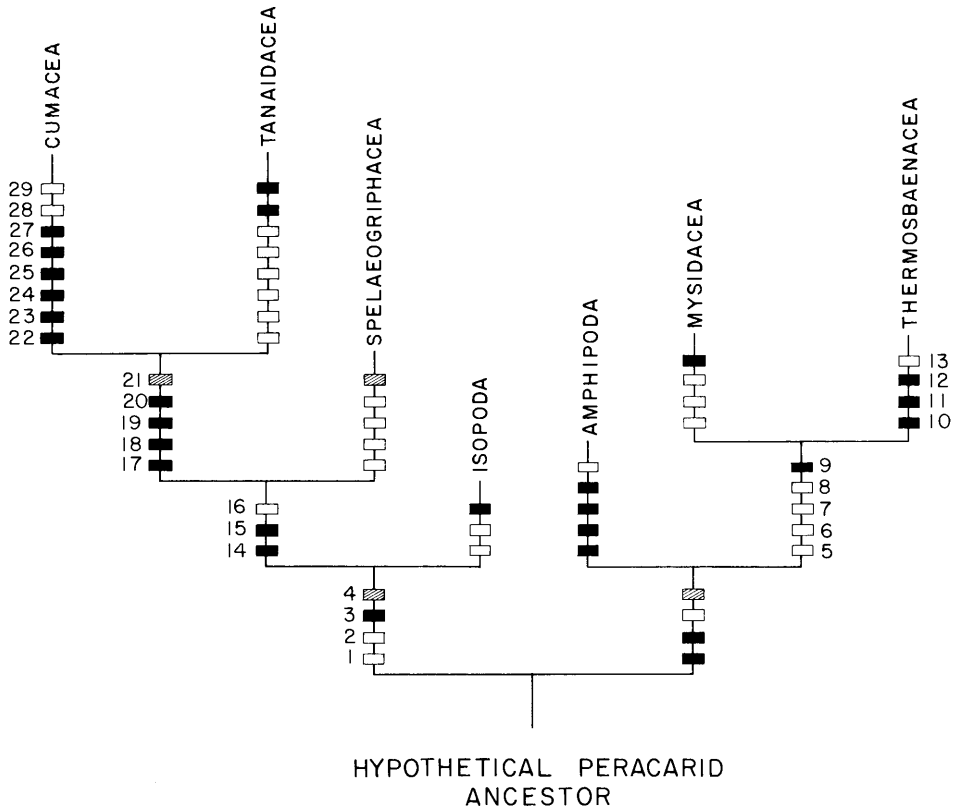
Fig. 1.   Phylogenetic scheme for the Orders of the Superorder Peracarida. Numbers refer to characters discussed in the text. Open boxes indicate plesiomorphic states, closed boxes indicate apomorphic states, and cross-hatched boxes derived states which are different for each line.

includes isopods, cumaceans, tanaidaceans, and possibly spelaeogriphaceans [the larvae of this group have not yet been observed] is the manca larva, which does not possess the last pair of appendages); *2*, foregut with pyloric funnel of the gastric mill and a pyloric bristle chamber (plesiomorphic condition in mancoids is a simple, unelaborated foregut). Amphipods, mysids, and thermosbaenaceans share the following plesiomorphic character not retained by the mancoids: *3*, multicellular midgut epithelium (synapomorphic state in mancoids is the syncytial midgut). Divergent apomorphic characters are, *4*, maxillary glands of mancoids and antennal glands of amphipods, mysids, and thermosbaenaceans. These are referred to as divergent apomorphic characters because in many larval crustaceans both nephridial sets are present, one of which is lost in subsequent development.

Mysids and thermosbaenaceans share the following plesiomorphic characters not retained by amphipods: *5*, abdominal part of body nearly cylindrical, without strong ventral extension of pleura (derived condition is extensive ventrally directed pleura on first three abdominal somites in amphipods); *6*, antennule strongly biramous (derived condition of amphipods is strong reduction or absence of one flagellar ramus); *7*, uropods and telson flattened, more or less forming a tail fan (derived condition in amphipods is cylindrical uropods situated ventral to the

narrow telson); 8, all pereopods with the same neutral orientation (derived condition in amphipods is the tagmosis of the pereopods into three groups, two of 2 pereopods each of which is anteriorly directed and the last group, 3 pereopods which are posteriorly directed).

The single plesiomorphic character retained by amphipods but not by mysids and thermosbaenaceans is, 9, the absence of a carapace. In mysids the carapace extends backward over the entire thorax and laterally to the pereopodal coxae forming an extensive respiratory surface in the Suborder Mysida but not in the more primitive Suborder Lophogastrida which have epipodal gills. Thermosbaenaceans possess a very short carapace in males and subadult females, covering only two thoracic somites. Fryer (1965) noted that in *Monodella* (Thermosbaenacea) it was unlikely that the inner surface of the carapace was important for respiration since no current passed over it. In mature female thermosbaenaceans the carapace is extended posteriorly over 3–6 thoracic somites, forming a brood chamber.

The Amphipoda have diverged considerably and possess many characters derived independently of the other Peracarida. Dahl (1977) discussed the functional significance of the amphipodan body and noted that several derived characters could be attributed to the ventral concentration of external functions such as respiration. The independently attained apomorphic features of amphipods include the following: (a) eyes sessile; (b) thoracopod 1 (maxilliped) shortened, with strong coxal and basal endites, endopod of reduced importance, exopod and epipod absent; (c) pereopods lacking exopods, epipods located on the inside of the leg and functioning as gills; and (d) abdomen subdivided into pleosome and urosome of three somites each with concomitant modification of "pleopods" 4 and 5 into "uropods".

Relative to the thermosbaenaceans, mysids have the following plesiomorphic features: 10, biramous antenna (vs. uniramous in thermosbaenaceans); 11, thoracopod 1 lacking endites, at least in Lophogastrida (vs. presence of coxal and basal endites); 12, possession of thoracopod oostegites (vs. loss of oostegites in favor of brooding eggs dorsally under the carapace). Thermosbaenaceans retain the following plesiomorphic character which is modified in mysids: 13, thoracic exopods are unspecialized, flattened lobes (vs. being elongate, annulate natatory structures). Mysids are bentho-pelagic forms whose apomorphic features correspond primarily to the development and elaboration of the carapace and the adoption of a strong swimming habit. On the other hand, thermosbaenaceans are known so far only from interstitial or hypogean fresh and brackish waters, and derived features such as loss of eyes and an antennal ramus are undoubtedly correlated with this habitat. Stock (1976), reviewing the geographical distribution of the known species, suggested that marine thermosbaenaceans are yet to be discovered.

The evolution of the mancoid peracarids is marked by the same divergence of body form seen in the amphipod, mysid, and thermosbaenacean line. Isopods have retained the following plesiomorphic characters relative to spelaeogriphaceans, tanaids, and cumaceans: 14, a carapace has not been developed (vs. various degrees of development of the carapace); 15, uropods and telson form a tail fan (vs. cylindrical or elongate uropods and variously modified telsons). In contrast, spelaeogriphaceans, tanaids, and cumaceans have retained the following plesiomorphic character: 16, first thoracopod with epipod (which is absent in isopods). Isopods possess derived or independently acquired characters of their own, which include: (a) sessile eyes; (b) strong abdominal pleura in some suborders; (c) antennule with one ramus reduced or absent; (d) thoracopod 1 with

large basal endite and reduced endopod; (e) pereopods without exopods; (f) pleopods large, flattened, specialized for respiration; and (g) telson fused to last abdominal somite.

Spelaeogriphaceans are further segregated from cumaceans and tanaids on the basis of the following plesiomorphic characters: *17,* carapace covers only one thoracic somite (vs. covering at least two thoracic somites); *18,* thoracopod 1 endopod elongate (vs. shortened and highly modified); *19,* thoracopod 2 pediform (vs. thoracopod 2 modified either as chela [in tanaids] or maxilliped [in cumaceans]); *20,* uropods flattened (vs. uropods cylindrical). Cumaceans and tanaids possess the following synapomorphic feature not found in spelaeogriphaceans: *21,* maxillule with elongate palp, usually directed backwards into branchial cavity (vs. apomorphic maxillule palp reduced to setalike article). Independently acquired apomorphic features seen in spelaeogriphaceans include: (a) "ventilatory" exopods on thoracopods 2–4; (b) mandible with palp reduced to a single article; and (c) thoracopods subdivided into a group of three anteriorly-directed pairs and four posteriorly-directed pairs.

Tanaids and cumaceans have diverged considerably, most of the morphological differences between the two being a consequence of the enlarged carapace and rapid-burrowing habit in cumaceans. The tanaids possess the following plesiomorphic features relative to cumaceans: *22,* carapace covers two thoracic somites (vs. covering 3-6 thoracic somites); *23,* antennule biramous, both rami elongate (vs. both rami much reduced); *24,* antenna biramous (vs. uniramous); *25,* thoracopod 3 pediform (vs. reduced endopod of thoracopod 3 modified as maxilliped); *26,* five pairs of pleopods in both sexes (vs. two pairs of pleopods in the female of a single cumacean species; all other known females are without pleopods); *27,* mandible with palp (vs. mandible without palp). In contrast, cumaceans have the following primitive features relative to tanaids: *28,* exopods on as many as four pairs of thoracopods (vs. exopods on only two pairs of thoracopods); *29,* abdomen without pleura (vs. abdomen with pleura).

DISCUSSION

The generally accepted scheme of peracarid phylogeny (Fig. 2) is the one originally proposed by Siewing (1963) and later modified by Fryer (1965). According to this scheme, amphipods represent one branch from the mysidacean stem while the other leads from the carapace-bearing cumaceans through the thermosbaenaceans, spelaeogriphaceans, and tanaidaceans to the carapace-less isopods. There is a clearly implied trend toward reduction of the carapace. Taking only the cumacean to isopod branch of Siewing's phylogenetic scheme, the following difficulties are encountered. Cumaceans possess three pairs of specialized thoracic appendages associated with their longer carapace in contrast to the single pair of modified thoracic legs (maxillipeds) associated with the shorter carapace in spelaeogriphaceans, thermosbaenaceans, and tanaids. Cumaceans thus must have diverged very early while the ancestral form for the rest of the line retained primitively simple thoracic appendages under the carapace. As the carapace became reduced only the anterior-most thoracic appendage was modified to serve both feeding and respiratory functions. Arguments against this proposed phylogeny come from fossil as well as recent evidence. First, the fossil record of the Peracarida as documented by Schram (1974, 1977) indicates that spelaeogriphaceans, tanaids, and isopods were present during the Carboniferous whereas there is no evidence of cumaceans until the Permian. While it has to be admitted that the fossil record is extremely spotty, it should also be pointed out that many
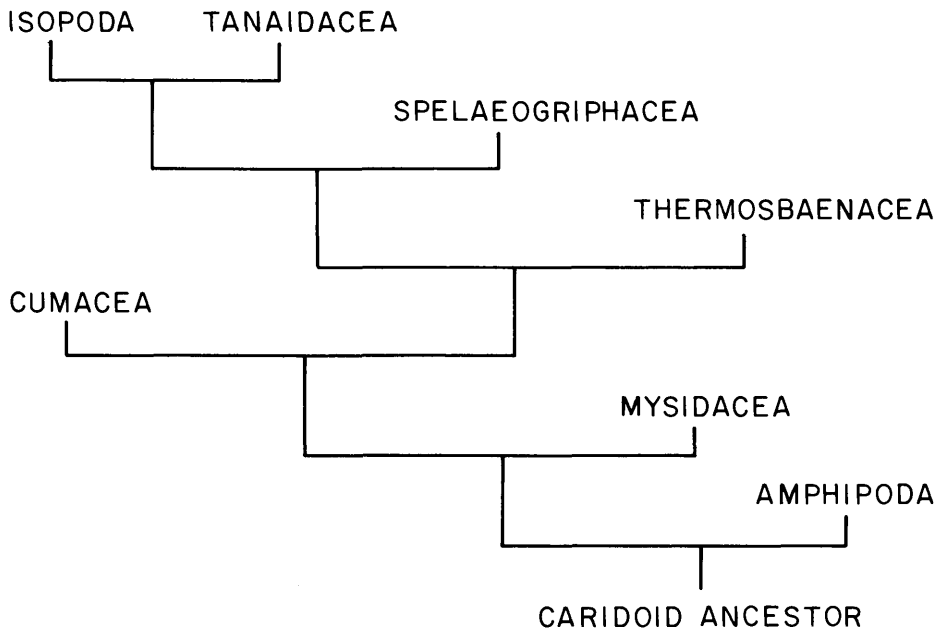
SIEWING SCHEME:

Fig. 2.   Phylogeny of the Peracarida according to the scheme of Siewing (1963) as modified by Fryer (1965).

cumacean carapaces are heavily calcified and thus are more likely to be preserved than are the lightly calcified spelaeogriphaceans. Additionally, according to this scheme, isopods are the last group to evolve and show the greatest divergence from the other orders in the line, yet they are clearly known from the Middle Pennsylvanian. Such a strong divergence would mean that all peracarid forms had been developed at least by the Devonian. There is currently no evidence for this (Schram, 1977).

Second, by Siewing's scheme, there is an implied gradual change in respiratory mechanisms coupled with the reduction and eventual loss of the carapace. Cumaceans, having diverged early, would necessarily have independently developed a complex respiratory structure involving the use of the carapace as a branchial chamber and parts of anterior thoracic appendages as gills. Thermosbaenaceans presumably represent the ancestral condition where exopods were retained as respiratory structures. Spelaeogriphaceans and tanaids developed again a maxillipedal respiratory structure and carapace branchial chamber which, however, was not as elaborate as that seen in cumaceans. At the end of this evolutionary line, in the isopods there was a change again, this time to pleopods as respiratory structures. If one also examines the structure of the heart and the distribution of ostia and lateral arteries, Siewing's scheme seems to have the most highly modified forms earlier in the sequence. For example, cumaceans have a shortened heart, one pair of ostia and three or four pairs of lateral arteries, whereas the isopods have an elongate heart located in the posterior part of the body, two pairs of ostia and five pairs of lateral arteries.

The major differences between the scheme presented here and that of Siewing (1963) are as follows: the Thermosbaenacea have been removed from the "mancoid" line, and the "mancoid" line is inverted, with the isopods considered to be the oldest while the highly derived cumaceans are the most recently evolved forms. The thermosbaenaceans are a good example of how the carapace can be acquired and independently modified for a special need; in this case, the development of a dorsal brood space. There is no evidence to suggest that the underside of the thermosbaenacean carapace is used for respiration even though a "branchial" epipod occurs on the maxilliped (Fryer 1965). In fact, a modified maxillulary palp, associated with respiratory carapaces in tanaids and cumaceans, is not found in thermosbaenaceans. It should also be noted that the thermosbaenacean genus *Halosbaena,* described by Stock (1976) from the Caribbean, possesses many highly adapted appendages together with a carapace which is much longer (covering thoracic pedigerous somite 6) than previously seen in this order. It is thus reasonable to suggest, on the basis of the scheme presented above, that the ancestors of the mysids, predating the highly specialized pygocephalomorphs, also had a short carapace. That the development of a long, versus a short, carapace was an important innovation can clearly be seen in the diversity of modern mysids.

The scheme presented in this paper is fully compatible with the known fossil record and the inferred ages of nonfossilized groups as outlined for malacostracans in general by Schram (1977) and for thermosbaenaceans by Stock (1976). By the present scheme, the Amphipoda must be considered to be at least as old as the mysids, suggesting that their broad geographic distribution is due more to the earth's changing morphology than it is to their limited dispersal capabilities.

The evolution of the "mancoid" line as presented here proposes another, independent trend in the evolution of the carapace toward a respiratory function. In this case beginning with spelaeogriphaceans there is a gradual development of the carapace into a true branchial cavity with concomitant modification of associated thoracic appendages. This sequence reaches its peak with the cumaceans where the three anterior-most pairs of thoracic appendages are housed under the carapace and are variously modified. Concurrently a gradual reduction in the circulatory system is also seen. In isopods, though the heart has moved posteriorly, it has remained elongate, has two pairs of ostia and bears five pairs of lateral arteries. In spelaeogriphaceans the heart extends the length of the thorax, but the number of ostia and lateral arteries is unknown (personal observation of living specimens). The number of lateral arteries is reduced in tanaids and, in cumaceans, the heart is shortened and there is only a single pair of ostia.

Bousfield (1978) recently proposed a non-Hennigian, speculative phylogeny of the Order Amphipoda. His scheme used as a basis the supposed primitiveness of the carapace-bearing Mysidacea and Cumacea. Because these forms show extreme sexual dimorphism and have pelagic, terminal males, Bousfield reasoned that similar morphological features ought to represent the primitive condition in the Amphipoda. Such features included: elongate antennae with elaborate sensory structures, large and heavily pigmented eyes, powerfully developed pleopods and tail fan, but no sexual dimorphism in gnathopods (modified pereopods 1 and 2). There are several difficulties with using cumaceans and mysids as representing the plesiomorphic condition for amphipods. First, extreme sexual dimorphism appears to be a secondary modification in both groups. The Lophogastrida, acknowledged to be the most primitive of the mysids (on the basis of appendage morphology as well as clear relationship to fossil forms such as the Pygocephalomorpha) exhibits only the normal minor sexual dimorphism of peracarids (e.g., presence of penial lobes in males, brood plates in females). Băcescu (1972)

has recently discovered a deep-sea cumacean with two pairs of pleopods in the female, suggesting that in this group also, females and males were quite similar early in their history. Since it has also been shown above that a carapace-bearing bentho-pelagic organism is not a good representative of the hypothetical peracarid ancestor, Bousfield's scheme does not appear to be well-founded and should be dismissed as mere speculation.

Of the other peracarids, only the phylogeny of the Isopoda has been dealt with in any detail, again using speculative rather than Hennigian methods. Schram (1974) derived a series of archetypal character states from an examination of fossil and Recent morphologies. On the basis of fossil history Schram stated that phreatoicids stood closest to the ancestral isopod with flabelliferans being an early derivative. Hessler, Wilson, and Thistle (1979) stated that flabelliferans are the most primitive isopods but present no evidence in support of their statement. Schultz (1979) presented a phylogenetic scheme for the entire order. He suggested that *Protallocoxa* and the flabelliferan family Plakarthriidae were the most primitive living isopods since they both possessed free coxae on pereonite 1. Additionally, *Protallocoxa* possesses an occipital groove indicating that the head and first thoracic somite are incompletely fused. This may be additional evidence for the relative primitiveness of the isopods within the mancoid line as presented above.

In summary, a testable hypothesis for the origin and phylogeny of the Peracarida has been presented. This hypothesis is based on the notion that early malacostracans were not carapace-bearing bentho-pelagic forms but rather were carapace-less benthic crawlers. The form of the phylogenetic scheme will need to be tested and refined as more information on the developmental history and functional morphology of the various orders becomes available; this is especially true for the spelaeogriphaceans. Phylogenetic schemes for individual orders must be founded in an acceptable scheme for the Peracarida if they are to have any credibility. Lastly, the unity of the Peracarida must be questioned. Traditionally, the Superorder has been defined on the basis of two features: the common possession of oostegites in the female, and the lacinia mobilis on the mandible. Thermosbaenaceans do not and apparently never have possessed oostegites. The lacinia mobilis is undoubtedly a specialized feature, probably derived from several of the distalmost setae in the mouthwardly directed setal row between the molar and incisor. Such a feature has recently been seen in juvenile euphausiaceans and may occur in several other groups. In the present paper, the form of the mandible, teloblastic development of most postnaupliar somites, and the incorporation of the first thoracomere into the head are also offered as definitive features of the Peracarida. However, none of these are distinctive in themselves. The question must therefore be posed: are the Peracarida monophyletic? The mancoid line presents a strongly unified group but it shows few affinities with the Amphipoda, Mysidacea, and Thermosbaenacea. Within the latter line, the Amphipoda are different in most respects from the mysids and thermosbaenaceans. Three separate "peracarid" lines may therefore be indicated, each arising independently from a pre-Carboniferous syncarid-like ancestral eumalacostracan. A revised classification of the peracaridan forms might then be: Superorder Mancoida, containing the Orders Isopoda, Spelaeogriphacea, Tanaidacea, and Cumacea; Superorder Amphipoda; Superorder Pancarida, erected earlier by Siewing for the Thermosbaenacea; and the Mysidacea would be removed to the old Schizopoda together with the Euphausiacea as recently suggested by Land (1980) on the basis of eye structure. Thus, whether the Peracarida should be retained or should be split into component Superorders requires further study and will be dealt with in a future paper.

ACKNOWLEDGEMENTS

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