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MALACOSTRACAN PHYLOGENY AND EVOLUTION

ABSTRACT

Malacostracan ancestors were benthic-epibenthic. Evolution of ambulatory stenopodia probably preceded specialization of natatory pleopods. This division of labor was the prerequisite for the evolution of trunk tagmosis. It is concluded that the ancestral malacostracan was probably more of a pre-eumalacostracan than a phyllocarid type, and that the phyllocarids constitute an early branch adapted for benthic life. The same is the case with the hoplocarids, here regarded as a separate subclass with eumalacostracan rather than phyllocarid affinities, although that question remains open. The systematic concept Eumalacostraca is here reserved for the subclass comprising the three caridoid superorders, Syncarida, Eucarida and Peracarida. The central caridoid apomorphy, proving the unity of caridoids, is the jumping escape reflex system, manifested in various aspects of caridoid morphology. The morphological evidence indicates that the Syncarida are close to a caridoid stem-group, and that the Eumalacostraca *sensu stricto* were derived from pre-syncarid ancestors. Advanced hemipelagic-pelagic caridoids probably evolved independently within the Eucarida and Peracarida.

1 INTRODUCTION

The differentiation of the major crustacean taxa must have taken place very early, probably at least partly in the Precambrian (cf. Bergström 1980). From the Cambrian we have proof of the presence of branchiopods (Simonetta & Delle Cave 1980, Briggs 1976), ostracods (Müller 1979, 1981), and cephalocarids or forms resembling them (Müller 1981). It has also been more or less generally accepted that phyllocarid malacostracans were represented in the Cambrian faunas. However, a critical review of modern redescriptions of the best-preserved taxa, *Perspicaris* (Briggs 1977), *Canadaspis* (Briggs 1978) and *Plenocaris* (Whittington 1974), has shown that the morphology at these taxa in various respects is incompatible with the universally accepted definition of the Malacostraca (Dahl, in press 2). These findings make the malacostracan nature of less well-defined taxa, such as *Hymenocaris* and others, still more doubtful. Pending the discovery of new evidence, it would appear we have no proof that Malacostraca existed in the Cambrian even if that may well have been the case. The earliest unequivocal Malacostraca are, as demonstrated by Rolfe (1962) for *Ceratiocaris*, the Archaeostraca, known from the Ordovician onwards.

2 GENERAL REMARKS ON THE MALACOSTRACA

The Malacostraca constitute a well-defined taxon, the main diagnostic features being the strictly uniform tagmosis and the presence of paired appendages on all segments except, in the Phyllocarida, the seventh abdominal segment.

It deserves recalling in this context that while the cephalon is well-defined, even if thoracic segments may become secondarily incorporated, the terms thorax and abdomen, when applied for example to the branchiopods, are used much less strictly than in the case of the Malacostraca (Dahl 1963) and that the segmental composition of these tagmata varies from group to group. The Malacostraca stand out as a very isolated crustacean taxon, and we have no definite indication of a close relationship to any of the others. The similarities with the Cephalocarida, although providing possible indications concerning evolutionary trends within the Crustacea (Sanders 1963, Hessler 1964, 1982, Anderson 1973), are rather symplesiomorphies than anything else.

I wish to call attention here to two organ complexes which underline the high degree of malacostracan isolation, mainly because their importance has been neglected or misunderstood. These organ complexes are the frontal eyes (sensu Elofsson 1966c) and the compound eyes. With respect to the frontal eye complex Elofsson (1965, 1966a,b,c) demonstrated the presence of four distinct patterns, one of which is found within the Malacostraca, the other three in the non-malacostracan groups. The frontal eyes of the Malacostraca differ from those of the other taxa in having everse receptor cells resembling those of the compound eye retina.

The differences between malacostracan and non-malacostracan compound eyes are even greater and more fundamental (Elofsson & Dahl 1970). Neither type could be derived from the other without a complete breakdown and rebuilding of the whole neuronal connection pattern in the lamina ganglionaris in the medulla externa-medulla interna region. Hessler & Newman (1975) failed to see the essential problem, and referred it to the separation of the medulla externa from the medulla interna, only partial in *Nebalia,* which is a point of minor importance. Paulus (1978) in an attempt to explain away existing differences between compound eyes by means of sweeping generalizations and deliberate over-simplifications, sought to minimize this piece of adverse evidence by means of a phrase concerning ontogenetical processes, which could not have been less relevant.

In 1963 at the Harvard Conference on Crustacea it was stated that we have no evidence enabling us to derive any crustacean taxon at what is now regarded as the class level from another such taxon (Dahl 1963). This, unfortunately, is still the case, the only possible exception being the taxa forming the core of the Maxillipoda (Hessler 1982). In the case of the Malacostraca from conchostracan ancestors, as proposed by Lauterbach (1975) appears very unlikely on account of various fundamental differences (Dahl 1976, Hessler 1982) not least in the structure of the protocerebral sense organs.

On the other hand, there exists a considerable degree of agreement concerning fundamental traits of the morphology of the ur-crustacean as an animal with numerous appendage-bearing segments and a subterminal mouth, with an atrium oris opening posteriad behind a labrum and receiving food from behind by means of a ventral transport mechanism (Calman 1909, Dahl 1956, Hessler & Newman 1975, Lauterbach 1980, Hessler 1982). We do not know whether the early Malacostraca, like the Cephalocarida, had two modes of feeding, or only a cephalic filter feeding mechanism (Cannon & Manton 1927, Manton 1930, Attramadal 1981). Both methods use appendages behind the mouth (Sanders 1963, Dahl 1956, 176, Hessler 1982). This question will be discussed below in section 5.

It is important that the Malacostraca, in contrast to all other more or less multi-segmented Crustacea, have retained a full set of appendages; and that a crucial event in the fixation of the malacostracan functional model system was the establishment of a rigid tagmosis with a thorax of eight segments and an abdomen bearing six pairs of appendages (Calman 1909, Lauterbach 1975, 1980, Dahl 1976, and in press 2). It was in fact only due to the organization with a specialized locomotory pleon and a thorax with appendages free to differentiate in a great variety of directions that a foundation could be laid for the singular evolutionary success of the Malacostraca. This was denied non-malacostracan groups such as Copepoda and Cirripedia which have a short abdomen devoid of limbs and a limited number of thoracic segments, possibly as a result of neotenic evolution (Gurney 1942, Hessler 1982). It would appear that a limited number of thoracic appendages is not a sufficient basis for large scale evolutionary flexibility.

Another important point was the fixation of the gonopores on the sixth (female) and eighth (male) thoracic segments. The position of the female gonopore was a prerequisite for the participation of the thoracopods in brood care, an arrangement peculiar to certain malacostracan taxa (Phyllocarida and Peracarida) and with bearings upon the evolution of these taxa.

3 EARLY MALACOSTRACAN ADAPTATIONS

The ancestral malacostracans were certainly benthic-epibenthic, a conclusion that appears now to be widely accepted. Manton (1953) showed that an adaptation of the anterior trunk-limbs for walking is advantageous for arthropods in the process of adapting ambulatory habits. She concluded that in the case of the Malacostraca tagmatization took place at a stage when benthic locomotion was predominant, pleopod adaptation for swimming came later in connection with an increasing tendency to move above the bottom. A tagmatization so profoundly influencing the total structural plan would probably not have occurred if predominantly natatory habits had preceded ambulatory ones. These conclusions gain strength from the retention of ambulatory thoracic endopods in all pelagic eumalacostracans.

If this argument holds, and it appears to have a sound foundation in observed facts and less of a need for hypothetical intermediary forms than possible alternatives, it would imply that the stenopodium is a very old attribute, i.e. an adaptation to ambulatory habits in ancestral malacostracans.

There also exists ontogenetic evidence that bears upon the evolution of the malacostracan structural plan which has been largely overlooked in the current discussion of malacostracan evolution and phylogeny. As pointed out by Anderson (1973) the ontogeny of the postnaupliar segments and their appendages in primitive malacostracans follows a pattern in principle identical with that found in the Cephalocarida (Sanders 1963) with a serial formation of segments and later of appendages in an anteroposterior direction. This has been demonstrated for Leptostraca (Manton 1934). Syncarida (Hickman 1937) and for Peracarida (Manton 1928) in mysids, in amphipods (Weygoldt 1958), in tanaids (Scolle 1963), and in isopods (Strömberg 1965, 1967, 1971). In these taxa no evidence of embryonization of larvae later than the nauplius has been found (Anderson 1973). Only in the Eucarida and, probably, the Hoplocarida 'did an evolution of post-naupliar larval specializations precede the embryonization of larval stages in association with increased yolk' (Anderson 1973). In view of this ontogenetic retention of embryonized larval specializations in the Eucarida Anderson concluded 'that the malacostracan ancestors of the Leptostraca, Syncarida, and Peracarida did not have larval stages other than the nauplius'.

4 SYNCARIDA, EUCARIDA, AND PERACARIDA

4.1 *The caridoid concept*

The caridoid facies (see Hessler, this volume, fig.1) constitutes an important manifestation of eumalacostracan morphology, considered as ancestral among the eumalacostracans by many authors including Calman (1909), Siewing (1963), and Hessler (1982). In a previous paper, however, (Dahl, in press 1), I noted the need for a fresh evaluation of the caridoid morphological type with respect to its significance in eumalacostracan evolution and phylogeny. This will be one of the main subjects of the present chapter.

Calman (1909) listed the characteristics of the caridoid facies in its most advanced form. Hessler (1982) amended this list to comprise the following features: (1) a carapace enclosing the thorax, (2) movable stalked eyes, (3) biramous antennules, (4) exopod of the antenna scale-like, (5) all thoracopods with flagelliform exopods, (6) abdomen well-developed with complex and massive musculature, designed for flexing the tail fan, (7) uropods and telson together forming a tail fan, (8) pleopods 1-5 alike with two flagelliform rami, (9) internal organs mainly excluded from the abdomen. These various features will be discussed in some detail below.

Advanced caridoids, possessing all the features listed by Hessler (1982) are found among the Peracarida (order Mysidacea) and the Eucarida (orders Decapoda and Euphausiacea). The third eucarid order, the Amphionidacea, although caridoid, is too imperfectly known to be included in this discussion. Hessler (1982) after defining the caridoid facies, added the following important sentence, which deserves being quoted in full: 'The close adherence to caridoid morphology of the benthic *Anaspides* demonstrates that a 'shrimplike' habitus *sensu stricto* (as in euphausiids and peneids) is not a necessary quality of the caridoid facies *in its most meaningful sense*'. (The last italics are mine.) Hessler then went on to say that my own reluctance to accept 'the unity of caridoids' (Dahl 1976, and in press 1) might be due to my using a too restrictive concept. However, as early as at the Harvard conference on Crustacea in 1963 (Dahl 1963) I discussed the caridoid concept in its widest possible sense calling attention also to caridoid parallels in non-malacostracan crustaceans. I have found no reason to abandon this broad concept, which I share with Hessler. It is just when seen in this very broad perspective that the question of the unity of the caridoids becomes particularly interesting. Various aspects of this question will be dealt with below.

Looking somewhat more closely upon the caridoid features listed by Hessler, one finds that they are not all of the same diagnostic significance. Hessler (1982) pointed out that in his opinion the large carapace (1) the stalked eyes, (2), and the biramous antennule (3) were to be regarded as malacostracan plesiomorphies rather than diagnostic caridoid features. This is undoubtedly so with (2) and (3), while (1), the question of the carapace/cephalothorax, will be discussed in more detail in section 4.3. In addition to the remarks made by Hessler (1982), it may be added that the biramous pleopod (8) is also a malacostracan plesiomorphy and that the exclusion of the viscera from the abdomen (9) is a direct effect of the strong development of the abdominal musculature (6). Concerning (4), the antennal scale, (6), the abdominal musculature, and (7), the tail fan, some further remarks are necessary. The antennal scale is, in its typical form, a unique caridoid feature, present in all eucarid and peracarid caridoids and in paleocaridacean and anaspidacean syncarids. Its function has not been understood, and tentative suggestions have been made concerning aid in swimming (Calman 1909) and stabilizing effects (Tattersall & Tattersall 1951). Recently, however, Mr Y.Attramadal (in preparation) has found experimentally in mysids that it plays an important part in giving effect to the caridoid escape reflex. This explains why it is lacking in fast-swimming isopods and amphipods which have uniramous antennae and do not jump. Within the Peracarida it is found only in the caridoid Mysidacea and, in a very vestigial form, in *Spelaeogriphus.*

It should be noted in this context that the generally ellipsoid expansion of the second, not the first, article of the stomatopod antennae is said to have a definite rudder function (Balss 1938). It is thus probably not homologous with the caridoid antennal scale.

It then becomes evident that in caridoids the strong abdominal musculature, the antennal scale, and the tail fan as well as the appropriate receptors of external stimuli and the co-ordinating nervous mechanisms are all components of one single integrated functional system, designed to produce the jumping escape reaction. This system constitutes, in fact, in its entirety the only truly diagnostic feature of the caridoid facies. As such it is of the greatest importance for the understanding of the interrelationships of the advanced eumalacostracan superorders, to which we shall revert in section 4.4.

However, before leaving the morphological aspects of the caridoid facies, something should be said about the carapace. The carapace is certainly not a diagnostic feature of the caridoids, for it is lacking in the syncarids and present in various non-caridoid peracarid orders. However, in the form in which it is present in euphausiids, natantian decapods, lophogastrids, and certain mysids it can be said to be at least characteristic of the most advanced exponents of the caridoid facies.

The advanced caridoid has a very large carapace/cephalothorax provided with a rostrum. This rostrum is long and laterally compressed in most natantian decapods and some euphausiids and lophogastrids (*Gnathophausia*), short but still laterally compressed in certain natantians (e.g. Pasiphaeidae), most euphausiids, and certain lophogastrids. The wide distribution of the carapace and rostrum in the most advanced caridoids, indicates they possess advantageous hydrodynamic properties; however, such have never been properly investigated. In the case of the euphausiids this argument gains strength from the fact that the carapace is not directly involved in the respiration/ventilation system (see section 4.2). Therefore, it is difficult to imagine any function other than a hydrodynamic one. The lateral compression suggests a function of cleaving the water like the bow of a ship. In this context, it is suggestive that certain caridoid members of the taxa in question which have become partly benthic have no or only a small rostrum (e.g. the caridean genera *Crangon* and *Pontophilus*) or a horizontally flattened rostral plate (e.g. the lophogastrid genus *Lophogaster*).

4.2 *Manifestations of functional systems*

Although the basic structural plan of the Eumalacostraca can be readily recognized in all its members, variations within the frame of this plan are nevertheless considerable. The molding forces, which call forth morphological adaptations, have both exogenous and endogenous components. The exogenous forces are clearly connected with the habitat and mode of life: pelagic, epibenthic, benthic, fossorial, tubicolous. The endogenous forces are based upon the requirements of the various functional systems in forming their external manifestations. The habitus always reflects both these kinds of influence, but their relative importance is not always immediately evident. Thus in the advanced caridoids discussed in the previous section the effects of exogenous forces shaping the taxa into a pattern suitable for a pelagic or hemipelagic life tend to obscure deep-lying differences between the same taxa. The present section will deal with external expressions of functional systems which are at least partly due to the effect of endogenous forces.

The functional systems exerting the greatest influence upon the structural patterns of the three superorders under discussion are those involved in respiration and ventilation, locomotion, alimentation, and reproduction. Some remarks on ontogenetic patterns will also be included.

The primary respiratory organs are the thoracic epipods. Originally, there appear to have been at least two on each thoracopod (this is the number still found in the syncarids), while there appears to be three epipods in the Decapoda (Calman 1909). Not more than one epi-

Table 1. Respiratory organs of caridoids

Taxon	Thoracic epipod			Ventilation	Accessory respiratory organs
	Morphology	Exposure	Occurrence, Series		
Syncarida					
(Anaspides) *(Bathynella)*	Simple	Exposed	P1-P7 T1-T6	Autochthonous + thoracic exopods and pleopods 1-2	Thoracic exopods
Eucarida					
Euphausiacea	Complex	Exposed	T1-T8	Thoracic exopods	–
Decapoda *(Peneus)*	Complex	Enclosed by branchiostegal folds	P1-P7 P2-P7 P3-P7	Maxillary exopod (= scaphognathite)	Inner wall of branchiostegal folds
Peracarida					
Proximal, epipod series partly oöstegites in female, lost in male					
Lophogastrida	Complex	Enclosed by branchiostegal folds	P2-P7	P1 (mxp) epipod plus thoracic exopods	–
Mysida *(Boreomysis)*	Lost except on P1, non-respiratory	”	–	P1 (mxp) epipod	Inner wall of branchiostegal and carapace folds
Tanaidacea *(Apseudes)*	Lost except on P1, complex	”	P1	P1 (mxp) epipod	”
Cumacea *(Diastylis)*	Lost except on P1, complex	”	P1	P1 (mxp) epipod	?
Amphipoda	Simple	Exposed	P2-P6(P7)	Pleopods	?
Isopoda	Lost	–	–	–	Pleopods

pod is retained in the Peracarida, but there are good reasons to presume that in the female the proximal epipod on certain thoracic legs has been transformed into an oöstegite, the whole proximal epipod series having been lost in the male (Claus 1885, Calman 1909, Siewing 1956, Dahl 1977). In *Gammarus pulex* L. transmission electron microscope examination revealed a close similarity in the general structural patterns of epipod and oöstegite, the main difference consisting in the much richer vascularization of the epipod (Dahl, unpublished). Also the mutual positions of oöstegite and epipod in *Gammarus* are identical with those of the two epipods in *Anaspides* (Dahl 1977). It seems safe to conclude that the oöstegite in the *Gammarus* female, and by inference those of other Peracarida, are transformed epipods of the proximal series.

In decapods and certain peracarids the inner wall of the carapace may serve as a respiratory organ, and the same is the case with the thoracic exopods of the syncarids. This may also apply to certain pleopods. The simplest respiratory system is found in the Anaspidacea where the two flat and uncomplicated epipods, present on all thoracopods except the last one, are ventilated, partly by means of autochthonous vibration, partly by the beating of the thoracopod exopods and the two anterior pleopods. Only the amphipods have a system built on the same principle but with a more sophisticated ventilatory system (Dahl 1977). Exposed respiratory epipods are also found in the Euphausiacea; however, there the epipods themselves are highly complicated. One series of epipods has been lost, possibly in connection with the proliferation of the other series. Ventilation is provided by the thoracic exopods which are exclusively ventilatory and do not take part in locomotion (Mauchline 1980).

In comparison, all other taxa show further complications. The actual situation encountered in those taxa where conditions are reasonably well-known are summarized in Table 1, where the progressive degrees of complication in comparison with the simple syncarid system have been noted. These various degrees of complication must not, however, be understood directly to represent evolutionary lines. Evolutionary implications are there, but they will be discussed in a later connection.

Some further brief comments may be of interest. It is obvious that the enclosure of gills into branchiostegal chambers leads to a demand for specialized ventilatory mechanisms and that the answer is different in the Decapoda and the Peracarida. It is also obvious that an evolution away from simple and generalized epipod respiration has proceeded much farther in peracarids than in eucarids. In this respect the Isopoda with their exclusive reliance upon pleopod respiration stand apart from all other Peracarida.

Concerning locomotory adaptations Manton (1953) concluded that ambulatory habits in malacostracans preceded natatory ones (see section 3), and that this was a basic reason for tagmatization. In the Malacostraca in general, including the Leptostraca and apparently also the Archaeostraca, tagmatization is complete as far as locomotion is concerned, with a complete segregation between thoracopod and pleopod activity.

The Syncarida, however, constitute a remarkable exception (Manton 1930). In the Anaspidacea, and also in some Palaeocaridacea (e.g. *Squillites*), the endopods of pleopods 1-5 are reduced. The exopod is used both for walking and for swimming. When walking the pleopods 'move in a series with the thoracic endopodites' (Manton 1930). The thoracic exopods in *Anaspides* are constantly in motion, swinging antero-posteriorly and 'when stationary the first one or two pairs of pleopods beat gently in series with the thoracic exopodites' (Manton 1930). When swimming the thoracic exopods and the pleopods also beat metachronally in series, although more rapidly. In *Paranaspides* Manton did not find the same degree of co-ordination, but occasionally the thoracic and pleopod exopods beat in series.

The fact that 'both in swimming and walking *Anaspides* uses the thorax and abdomen as a single functional region' appeared to Manton to indicate a persistence of a functional continuity taken over from early Malacostraca before a functional tagmatization was complete. Manton also considered the alternative possibility that it might be a result of the 'crawling habits' of *Anaspides.* Nothing similar, however, is known to occur in any other malacostracan with comparable habits. Therefore the first alternative proposed by Manton appears more likely.

Some comments should be made upon the fact that the co-ordination of the pleopodal exopod is with the thoracic endopods when walking, and with the thoracic exopods when ventilating and swimming. This, however, is only logical for in all Malacostraca a locomotory pleopod always acts as one single unit. Therefore one has to expect that either type of co-ordination with the thoracopods should be with the whole pleopod. The loss of the endopod in the Anaspidacea and certain Palaeocaridacea may be connected with the participation of the pleopods in walking, for a biramous pleopod acting as a whole may cause difficulties, especially on rough ground.

Whereas the recent freshwater anaspidids have a reduced pleopod endopod the situation was more diversified in the Carboniferous Palaeocaridacea living in fresh water, brackish water, and marine habitats (Brooks 1962c, Schram & Schram 1974, Schram 1981a). The genera *Acanthotelson* and *Palaeocaris* had biramous pleopods with laminate rami, while *Praeanaspides* had biramous annulate pleopods, and *Squillites* possessed a uniramous annulate pleopod with the endopod being reduced. It should be noted here that among the peracarids multiarticulate pleopodal rami are only found in Mysidacea and Amphipoda. In the Eucarida and other Peracarida they are uni- or biarticulate.

There is a trend towards reduction of pleopods in interstitial eumalacostracans and also in some other peracarid taxa, viz. the Thermosbaenacea and females of Mysida and Cumacea. In these cases natatory functions are performed by the thoracopod exopods. On the other hand there exists an opposite trend, certainly evolved independently, towards more or less complete reduction of thoracopodal exopods and an emphasis on pleopod swimming in natatory decapods, amphipods, and isopods. Outwardly thorax-abdomen tagmosis is much less evident in the Syncarida than in the Peracarida and Eucarida.

In comparison with the functional systems dealt with above, alternative alimentary adaptations exert a profound influence upon the topography of the cephalon (Dahl 1956) but less so on the general structural plan. There exists very striking differences in the cephalon between malacostracans which use a maxillary filtering mechanism and convey the filtered food into the atrium oris from behind, and those where the emphasis lies upon mandibular browsing. In the former, found in its most typical form in mysids, the cephalon is opisthognathous and the opening of the atrium oris is directed posteriad. In the latter, found, for example, in most isopods and in talitrid amphipods, the cephalon is prognathous and the atrium oris opens obliquely anteriad. Every intergradation occurs and the connection with the feeding method is generally quite clear. A prognathous condition, which has certainly evolved independently in isopods and talitrids, leads to a 'tipping over' of the anterior part of the cephalon. The tip of the labrum becomes the anterior end of the body, the antennules become more or less dorsal and the compound eyes lie behind them. These topographical relationships are different from the normal crustacean plan, and recall the situation found in many insects and myriapods. The incorporation of one or more of the anterior thoracopods into the alimentary apparatus appears to have taken place repeatedly and at least partly independently.

In the reproductive system, taken in its widest sense, the formation of a marsupium, apparently by transformation of certain female epipods into oöstegites distinguishes the Peracarida from the other two superorders. This feature forms a somewhat tenous link between the various peracaridan orders (Fryer 1964, Dahl & Hessler 1982), since the question of whether the formation of oöstegites has taken place more than once remains open.

Transformation of pleopods into male copulatory organs occurs among Syncarida and Eucarida but never in the Peracarida.

There exists no ontogenetic pattern common to all the three superorders. The marine Eucarida have normally a more or less complicated ontogeny with series of free-swimming larval stages, the Peracarida a direct lecitotrophic one. The Syncarida also have direct development. Within the Eucarida the patterns of larval development are similar enough to leave no doubt about the comparatively close relationship between euphausiids and decapods. Nevertheless, the euphausiid larvae are easily recognized and in their development, in contrast to that of the Decapoda, there is no well-marked metamorphosis (Gurney 1942). Within the Decapoda only the Dendrobranchiata hatch as nauplii, but throughout the order there exists an embryonic nauplius stage. The embryos of the Syncarida and the Peracarida, despite their direct development, pass through a distinct nauplius stage but show little indication of a previous existence of later specialized larval stages (Anderson 1973).

Thus a nauplius stage, though actually only hatching in euphausiids and peneids, is recognizable in the ontogeny of all three superorders. Free-swimming larval stages constitute a means of early ontogenetic exploitation of pelagic resources. The acquisition of different types of larval development in eucarids (and also in hoplocarids) appears to be apomorphic and may have evolved independently in euphausiids and decapods.

4.3 *The carapace/cephalothorax*

The genetic potential for forming dorsal and lateral folds or shields in the cephalic-thoracic regions appears to be inherent in the basic crustacean organization. Traditionally a structure of this kind is referred to as a carapace. It is not certain that the general application of this term is correct but that it is a matter for future research. In the present connection the problems possibly involved need not be considered, for the carapace/cephalothorax of the Malacostraca always appears to be formed in the same manner. Within the nine classes of Crustacea now recognized carapace structures in the widest sense are found in five, viz. the Branchiopoda, Ostracoda, Cirripedia, Branchiura, and Malacostraca; but are typically lacking in the Cephalocarida, Copepoda, Mystacocarida, and Remipedia. Out of the first-mentioned five classes two, the Branchiopoda and the Malacostraca, include taxa at the ordinal or higher levels which do not possess a carapace.

This in no way contradicts the statement made above concerning a probable basic potential for carapace formation. However, a structure such as the carapace, generally voluminous and demanding for its formation and maintenance a very considerable expenditure of energy, is not just there. If present, it will have a function. In all carapace-bearing Malacostraca one or more such functions can be recognized.

In the Malacostraca a free carapace fold is comparatively rare. More often the dorsum of the thorax, or part of it, is covered by a vaulted, unsegmented shield, continuous with the cephalon and referred to as the cephalothorax. The free carapace fold, when present, forms a posterior continuation of this shield. In the three superorders now under consideration a well-developed carapace/cephalothorax occurs in all members of the Eucarida, in the order Mysidacea of the Peracarida, and not at all in the Syncarida. Of the six remaining peracaridan orders, four have some kind of carapace/cephalothorax, viz. the Tanaidacea, Cumacea, Spelaeogriphacea, and Thermosbaenacea, while the Isopoda and Amphipoda have none. However, especially in many amphipods, the dorsum of thoracic and abdominal segments form folds which may project posteriad over the adjoining segment. Similar structures are found in abdominal segments of decapod larvae. It seems not improbable that the formation of such structures is related to that of other dorsal folds.

According to the classical concept the carapace is a fold growing out from the maxillary segment, and if segments behind the maxillary segment are included in a cephalothorax this is supposed to be due to a fusion of the carapace fold to the dorsal integument. This is the view still taken by Hessler in his latest very important paper on the evolution of Crustacea, and it plays a considerable part in his derivation of the Eumalacostraca from advanced caridoid ancestors (Hessler 1982). In a paper now in press (Dahl, in press 1) and quoted by Hessler (1982) I tried to point out the difficulties confronting the classical carapace concept in the malacostracan context, but without throwing any doubt upon the general potential for carapace formation mentioned above. Some further comments upon this problem appear to be necessary.

It has in fact been known for a very long time that the malacostracan carapace/cephalothorax is not basically an outgrowth from the maxillary segment. This was shown by Manton in *Nebalia* as early as 1934 (see Manton 1934, Figs.3, 4, 5, 7 and 8). The carapace in *Nebalia* begins to form as lateral folds on either side of the body. These folds extend backwards to include the third thoracic segment and then curve dorsad so that a continuous fold is formed. By the dorsal fold growing in from behind it is, figuratively speaking, lifted up from the dorsum. This 'lifting' by means of a fold formation proceeds forwards so that the third and second segments become disengaged. It is not known whether this is effected during one single molt. The formation of the anterior part of the free carapace fold actually then proceeds from behind forwards instead of the other way round as demanded by the classical theory. Simultaneously, the posterior portion of the fold continues to grow posteriad, to cover the back and sides of the thorax.

In all other Malacostraca for which observations are available the carapace/cephalothorax formation follows the same general patterns as in *Nebalia*, although a large free carapace fold is formed only in the Mysidacea and the hoplocarid larvae. In the Mysidacea the free carapace fold is attached to the second to fourth thoracic segment. Otherwise the process of formation is essentially the same as in *Nebalia*. This is definitely the case in *Praunus* (Dahl, unpublished, see also Manton 1928 on *Hemimysis*, fig.15).

In *Meganyctiphanes* (Euphausiacea) I have studied the formation of the cephalothorax from the first calypotopis through furcilia stages up to the adult. Branchiostegal folds are formed on the lateral sides of the whole thoracic area growing backwards at the same rate as differentiation proceeds. Dorsad of the fold a vaulted cephalothoracic shield is formed, very thin in the early stages. At the posterior margin of the thorax it is continuous with the abdominal integument. In this area a slight folding of the posterior margin is indicated. In *Euphausia* this fold is more distinct and produced (Gurney 1942), but in principle there is no difference between the two genera.

In decapods, information on cephalothorax formation in the peneid genus *Gennadas* is found in Gurney (1942). In the protozoea no thoracic segment is included in the cephalothorax and the border between the maxillary segment and the thorax is actually indicated by a small fold (Gurney 1942, Fig.52) which can be interpreted as a carapace fold. However, from the molt of the third protozoea to the first zoea the whole thorax has been incorporated into the cephalothorax. In some other peneid genera the process includes more steps (Gurney 1942). It is obvious, however, that it proceeds along the same lines as in other malacostracans, i.e. by means of progressive branchiostegal fold formation and the production of a continuous cephalothoracic shield. The continuity of the dorsal thoracic integument with the abdominal integument could be verified by the writer in larvae of the natantians *Crangon* and *Leander.* Evidence of branchiostegal fold formation in the crab *Pilumnus* is found in Anderson (1973, fig.124).

The larvae of the Hoplocarida may constitute an exception from the general rule concerning cephalothorax formation in the malacostracans, for they have a large carapace fold attached to the maxillary segment (Calman 1909). Details concerning the mode of formation of this carapace are not available. If it grows out from the maxillary segment it would mean another indication of the isolated position of the Hoplocarida within the malacostracans.

According to Schram (1979) the pelagic Carboniferous genus *Waterstonella* had a large and thin carapace, enveloping the thorax and the proximal parts of the thoracopods and not attached to any of the thoracic segments. *Waterstonella* was provisionally placed among the Eocarida, i.e. 'unassignable schizopodous caridoids' (Schram 1979). For obvious reasons, it is impossible to evaluate its significance in the present context, for it is the mode of formation of the carapace rather than the final product which is of primary relevance to the present discussion.

The second fundamental aspect of the classical carapace theory is the postulate that in those malacostracans which possess a more or less complete cephalothorax this has been formed by a complete or partial fusion of a free maxillary segment carapace fold to the dorsum of the thorax (see above). As far as can be seen from the literature this has been assumed an axiom and no one seems to have produced any evidence to support it. In order therefore to verify or falsify this fusion hypothesis I have examined histologically a large number of malacostracans, where possible both larvae and adults, of the orders Decapoda, Euphausiacea, and Mysidacea (including the genera *Lophogaster* and *Eucopia*) together with a few species of Cumacea and Tanaidacea, all from the very extensive collections of sectioned Crustacea of the Department of Zoology in the University of Lund. If a carapace fold grew out from the maxillary segment and at some ontogenetic stage become fused to the dorsum it should, in the crudest case, show up as the two superficial layers of a three-layered dorsal integument. There should at the very least exist some indication that at some ontogenetic stage such a fusion had taken place. No such indication was found in any of the species investigated by me. Nor was any such indication to be expected for, as shown above, the cephalothoracic shield, in all cases where its development could be traced, is formed in a different manner.

When the branchiostegal folds grow outward, dorsal segmental borders between cephalon and thorax or between thoracic segments are not formed in the areas involved in the process. The simple dorsal integument comes to form a continuous dorsal and lateral shield, often more or less heavily calcified. In the Eucarida, it is always continuous with the abdominal integument, in the Cumacea and Tanaidacea with the segmented thoracic integument directly behind the shield. Apart from the sometimes heavy calcification referred to above, there is nothing which distinguishes the integument of the cephalothoracic area from that of adjacent areas of cephalon or body. Thus, it would simply be an act of realism to accept the fallacy of the hypothesis of the fusion of a free carapace fold to the thoracic dorsum as part of the formation of a cephalothoracic shield.

In summary, it can be stated that carapace/cephalothorax formation in *Nebalia* and those Eumalacostraca which have been examined starts with the formation of branchiostegal folds and leads to the formation of a histologically simple dorsal and lateral cephalothoracic shield from the posterior margin of which a free carapace fold in some cases grows out. The hoplocarid larvae may constitute an exception which merits further research. The normal process in the Malacostraca differs from that found in the Notostraca where a free carapace fold grows out from the posterior margin of the maxillary segment (Dahl, in press 1). It is the application of this process in the Notostraca to all Crustacea which has produced confusion, and has led to erroneous conclusions. A closer study of the formation of mantle folds in cirripeds, shell valves in ostracods, and the dorsal shield in the Branchiura might lead to clarification of the carapace concept in regard to all Crustacea.

4.4 *Evolution and interrelationships of the caridoid superorders*

Morphologically and ecologically the fully developed caridoid facies can be seen as a functional system adapted to marine pelagic existence, including the transition between pelagic and benthic habits.

More or less perfected caridoids, partly belonging to recent taxa, partly of uncertain relationships, were present in the Carboniferous and Devonian (Brooks 1962b, Schram et al 1978). These and other records, particularly in papers by Schram (1969, 1970, 1974a,b, 1978, 1979, 1981) indicate a Devonian radiation of the Eumalacostraca, including caridoid types. At least some of these genera had a strong caridoid abdomen, a tail fan and antennal scales, indicating the possibility, even the probability, that they possessed the caridoid escape reaction. This applies to the Devonian genera *Devonocaris* (Brooks 1962b) and *Palaeopalaemon* (Schram et al. 1978), and to the Carboniferous genera *Belotelson* and probably *Peachocaris* (Schram 1974). At least some of the more heavily-built Carboniferous pygocephalomorphs, now considered to be peracarids related to the lophogastrids, also had the combination of antennal scales and a well-developed tail fan, among them *Tealliocaris* and *Pygocephalus* (Schram 1979). The evolution of the caridoid escape reaction indicates an adaptation to predation by agile predators; and the coincidence in time between taxa with the external attributes associated with this escape reflex and the Devonian radiation of marine crossopterygians may be more than a coincidence.

The synapomorphies connected with the escape reflex alone provide evidence that the three caridoid superorders are more closely related to each other than any of them are to the Hoplocarida or the Phyllocarida. As recorded by Hessler (1982) and above (section 4.1), it is among the mysidaceans, euphausiids, and natant decapods that we find the habitus typical of advanced caridoids. In some of them, notably the lophogastrids, euphausiids, and peneids, we find a large number of plesiomorphies retained. It is perhaps not surprising therefore that Calman (1909) and Siewing (1963) in their figures of the 'ur-malacostracan' presented a caridoid of a plesiomorphic type and that this interpretation found a wide acceptance. Their habitual similarity notwithstanding, these advanced caridoids are, however, unmistakably representative of their respective orders: Euphausiacea, Decapoda, and Mysidacea.

The crucial question is whether the advanced caridoid facies was inherited from the ancestral eumalacostracan! If so, the non-caridoid taxa within the three superorders (and also the Hoplocarida) have evolved as a result of the disintegration of an ancestral caridoid pattern. This is the line taken by Hessler (1982, this volume). An alternative is that the final perfection of the advanced caridoid form proceeded independently within the Eucarida and the Peracarida.

It is implicit in the hypothesis of the advanced caridoid ancestor that the evolution of the caridoid superorders took place under pelagic or semipelagic conditions. The absence of a carapace in the Syncarida is then merely an instance of the disintegration mentioned above, and a logical consequence of the stand taken by Hessler (1982). It appears, however, that the significance of the Syncarida has been underrated in discussions of malacostracan phylogeny and evolution. The syncarids are the only eumalacostracans in which the tagmosis is less advanced morphologically *and* functionally than in the other members of the subclass. In the Palaeocaridacea and the Bathynellacea, the first thoracic segment is not incorporated into the cephalon. Furthermore, the Syncarida are the only Malacostraca which do not have a complete functional thorax-abdomen tagmosis. Instead the two tagmata, as stated above, are co-ordinated 'as a single functional region' both in swimming, walking, and ventilation of epipodal branchiae (Manton 1930).

The respiratory system of the Anaspidacea, with its double rows of simple epipods ventilated by thoracic exopod and pleopod beating, is the least complicated one found in any eumalacostracan taxon. Ventilation by non-locomotory thoracic exopods occurs only in two other plesiomorphic taxa, the lophogastrids and the euphausiids, but in the former group it is supplementary to the beating of maxillipedal epipods. The euphausiids are the only caridoids, besides the syncarids, which have exposed respiratory epipods, in all others they are enclosed in branchiostegal folds and have apomorphic ventilatory mechanisms (scaphognathites or specialized maxillipedal epipods). Even in the euphausiids one series of respiratory epipods has disappeared and those of the remaining series have become enlarged and complicated.

With respect to sensory systems Hanström (1934, 1937, 1947) found that the optic ganglia and the optic nerve in the compound eye of *Anaspides, Paranaspides,* and *Micraspides* are less complex than those of decapods and stomatopods, and that the protocerebral associative centers and the deutocerebrum are less complicated. Elofsson & Dahl (1970) demonstrated the transformations in the topographical relationships of the optic ganglia during malacostracan ontogeny. In the embryos the medulla externa length axis forms a 90° angle with those of lamina ganglionaris (which is the case also in adult branchiopods) and the medulla interna. Later a 90° rotation of the medulla externa takes place so that all three length axes become parallel. In the Anaspidacea, however, there is only a partial rotation. A recent control of the conditions in *Anaspides* and *Paranaspides* showed that the angle between the length axes of lamina and medulla externa in the adults was 45 to 60°. Also, in the Euphausiacea the embryonic topographical relationships are partly retained. There, however, the arrangement of the perikarya of the lamina ganglionaris and medulla externa have become arranged in a manner which is unique among the Malacostraca and certainly apomorphic.

The anatomy of the jumping reflex system in regards the tail fan and the antennal plate are well-developed not only in the Anaspidacea but also in those Palaeocaridacea where the state of preservation permits comparisons (Brooks 1962c, Schram 1979). Concerning the trunk musculature, the abdominal part of which supplies the motor element in the caridoid reflex system, it has been shown that the most primitive caridoid type is to be found in the Syncarida (*Paranaspides*) which lack specialized caridoid elaborations (Dahl 1931a,b, 1932, 1933) and therefore should form the basis of comparisons between advanced peracarid and eucarid caridoids (Hessler 1964).

Finally, as shown by Anderson (1973) there are no indications of larval stages later than the nauplius in Phyllocarida, Syncarida, and Peracarida. This indicates that pelagic larvae are apomorphic in Eucarids.

As is apparent from this survey, the Anaspidacea and, as far as we can judge, the Palaeocaridacea in system after system are found to be more primitive than any other caridoids, and with respect to the thorax-abdomen functional tagmosis even more primitive than the phyllocarids.

When Hessler (1982) writes that 'Anaspidaceans are no more primitive than . . . *Waterstonella* and the euphausiaceans, whose first thoracopod is also unmodified as a maxilliped', this does not reveal a full recognition of salient facts concerning the Syncarida. Moreover, the statement is hardly adequate, for as indicated above the euphausiids with their complete tagmosis, their strict division of labor between thoracopods and pleopods, their more derived respiratory system, their more complex musculature (Daniel 1929), and their pelagic larvae are certainly less primitive than the Syncarida. Concerning *Waterstonella* we simply have not enough information to make a qualified statement concerning its degree of primitivity.

Siewing (1956, 1963) on the basis of a comprehensive comparative anatomical investigation concluded that the Peracarida and the Eucarida were derived from ancestors of the Syncarida. Daniel (1933) drew the same conclusions from his musculature studies. Fryer (1964) on the other hand saw the evolution of the three superorders as a radiation from common ancestors among pygocephalomorphs and eocarids; however, this presumed common foundation has since been undermined. The pygocephalomorphs are now regarded as probable mysidaceans; and the eocarids, as originally understood, have been shown to include a conglomerate of species belonging to established taxa or which are too imperfectly known to permit conclusions concerning their true affinities (Schram 1979). The account of the functional systems given above and in sections 4.1 and 4.2 strongly supports the conclusions drawn by Siewing & Daniel that the caridoid superorders were derived from pre-syncarid ancestors.

The caridoid escape reaction with all its morphological attributes is unique and constitutes a set of interdependent synapomorphies clearly illustrating the genetic relationship between the three superorders containing caridoid forms. In comparison cephalic and/or thoracic shields and valves, 'carapaces' in a sense so wide that a single relevant definition is difficult to formulate, fulfill a variety of functions separately elaborated within the taxa possessing them. Where carapaces can serve no functions, they are not formed (section 4.3). Within the three superorders a fully developed 'caridoid' carapace/cephalothorax is found only in the Eucarida and the order Mysidacea. In all of these, except the Euphausiacea, and also in some peracarid orders with a less developed carapace/cephalothorax it is always involved in the respiratory system, which, as pointed out above, includes apomorphic adaptations not present in the Syncarida. In all advanced caridoids it is also highly probable that the carapace/cephalothorax fulfils hydrodynamic functions. Finally, in benthic decapods calcification of the exoskeleton and particularly of the cephalothorax provides protection against predation. Consdering the presence of a cephalothorax in the euphausiids, where it has no respiratory function, one might speculate that the possible order of which these three functions evolved was (1) hydrodynamic, (2) respiratory, (3) protective. It is almost certain that the sequence 2-3 is correct. The sequence 1-2 is more doubtful, however, for in the non-caridoid peracarid orders the function of the cephalothorax as a respiratory system appears to be the only one, and we have no means to tell whether this is a secondary or a primary situation.

It was presumed by Hessler (1982) that fully caridoid ancestors of the Syncarida later lost their carapace. There exists no evidence, however, that syncarids were anything but benthic-epibenthic, and secondarily interstitial and subterranean. If so, a hydrodynamically advantageous carapace/cephalothorax was hardly required. The plesiomorphic arrangement of the respiratory epipods on the thoracic legs (which were used by Hessler to exemplify an unmodified stenopodium) and the ventilatory system connected with them do not require a carapace, and if they had ever been included in a branchiostegal respiratory system they would most probably have been modified and had a different ventilatory system. Only if we accept a carapace/cephalothorax, even without a function, as a malacostracan prerequisite (section 4.3) do we have a reason to presume its existence in a syncarid ancestor. The general plesiomorphic nature of the syncarid organization, however, does not support such a presumption.

If on the other hand the advanced caridoid facies was independently perfected within the Eucarida and the Mysidacea, then it is less difficult to see how a carapace/cephalothorax with the respiratory apomorphies connected with it came to be superimposed upon the different basic epibenthic organizational patterns of eucarids and peracarids.

Presuming then that all three caridoid superorders were derived from pre-syncarid ancestors we have to consider the mutual relationships between the three taxa. The Syncarida have generally been considered to be more closely related to the Eucarida than to the Peracarida. Synapomorphies shared with the former group are antennular statocysts, receptaculum seminis in the female, and sexual dimorphism in the pleopods (Calman 1909). Further evidence along the same lines was recently produced by Schminke (1978) who demonstrated remarkable similarities between peneid larvae and bathynellacean syncarids, and by Hessler (in press) who showed that the coxal-body articulation was similar in syncarids and eucarids. In both these cases symplesiomorphies are probably involved.

It appears probable that the peracarids deviated earlier than the Eucarida from common pre-syncarid ancestors. It is not certain that the formation of oöstegites was a unique event. However, presuming this was the case, evolution of peracarids from pre-syncarid ancestors may have proceeded along separate benthic, epibenthic, and hemiphelagic-pelagic lines. A detailed discussion of peracarid evolution and interrelationships falls outside the scope of the present chapter. Moreover, these questions are under consideration by others. Consequently, only a few remarks will be made here on the two carapace-less orders. The amphipods with their undifferentiated epipods and the curvature of their embryos appear to share syncarid symplesiomorphies. Moreover, their respiratory-ventilatory system, like that of the syncarids, provides no evidence of having ever been enclosed by branchiostegal folds. The last can also be said about isopods, which are certainly not closely related to amphipods (Siewing 1951). Isopods have always been considered to be derived from mysids by a series of reductions. The argumentation has always appeared to be a circular one in that, being (axiomatically) derived from mysids, isopods show a reduction of mysid features. No tangible supporting evidence has been produced for this proposition. It appears that, like the amphipods, the isopods represent a separate line which had neither a caridoid habitus nor a caridoid respiratory and ventilatory system. A derivation of more advanced caridoids from pre-syncarid ancestors removes the difficulties involved in deriving amphipods and isopods from advanced caridoids.

Looking upon the advanced caridoids we find, as already noted above, that some of them, notably lophogastrids, euphausiids, and peneids, have features plesiomorphic within their respective taxa or within the Eumalacostraca in general. It appears most likely that these undoubtedly ancient forms independently and at different times deviated from the main current of epibenthic hemipelagic evolution in order, figuratively speaking, to go up into pelagic habitats in order to exploit its resources. The marine and above all the open ocean pelagic system is one of the most stable of habitats, even the most dramatic changes in the history of the earth having been buffered by its enormous water masses. Once adapted to it a taxon stands a good chance of long survival with comparatively little change.

In summary, it appears most probable that the caridoid orders Syncarida, Eucarida, and Peracarida evolved from pre-syncarid ancestors without a carapace/cephalothorax but otherwise of an incipient caridoid type with a caridoid escape reflex. Perfection of the advanced caridoid facies adapted to a hemipelagic-pelagic life and with a well-developed carapace/cephalothorax took place independently within the Eucarida and Peracarida, in the latter only in the order Mysidacea.

The writer is in full agreement with Hessler (1982, and this volume) about the unity of the caridoids, but finds the explanation of their origin given above the more plausible one. A derivation of syncarids from advanced caridoids by means of a disintegration of caridoid features appears improbable: (1) because of the profound primitive nature of the syncarids, and (2) because it would demand a derivation of eumalacostracans from hemipelagic-pelagic ancestors, which, for reasons given in sections 3 and 4, appears unlikely.

5 MALACOSTRACAN ANCESTORS

Because of their long fossil record and primitive features in their structural plan, the Phyllocarida have been more or less universally regarded as ancestors of the Eumalacostraca. Calman (1909), however, interpreted them as an early branch of the main malacostracan evolutionary line, and Manton (1953) appears to have favored a similar interpretation. Dahl (1976, and in press) found it difficult to derive a eumalacostracan functional model from a phyllocarid ancestor. Rolfe (1981) indicated that Dahl (1976) had paid too little attention to the Archaeostraca, and this criticism is partly justified even if information on archaeostracan functional systems is poor.

The phyllocarids retain many plesiomorphic features, but that is the case also in other taxa and particularly so in the syncarids. Indeed, with respect to the imperfect thoracoabdominal tagmosis, the recent Anaspidacea are more plesiomorphic than the Phyllocarida, and the Palaeocaridacea and the Bathynellacea share with the Leptostraca a cephalon in which no thoracic segments have become incorporated. Some syncarid taxa also possess furca. In other respects, such as the retention of the seventh abdominal segment, the Phyllocarida are more plesiomorphic. [It should be noted that the statements by Siewing (1956, 1969) about the presence of a seventh segment in the palaeocaridacean genus *Uronectes* (= *Gampsonyx*) is erroneous. Unfortunately, Brooks (1962c) in his graphic reconstruction of *Uronectes* drew seven well-developed abdominal segments. It is to be surmised that this is a mistake.]

Feeding in the Leptostraca takes place by means of ventral food transport effected by thoracopod beating, and by final sorting and ingestion with the aid of maxillulae and maxillae. The presence of numerous juvenile stages in certain Archaeostraca does not in itself provide arguments in favour of a different mode of feeding, although differences in the size of particles handled by various size classes appear likely. The big mandibles found in certain large Archaeostraca (Rolfe 1969, 1981) could possibly be used for picking food items directly from the bottom. However, even if such feeding took place it would not be a cephalic filter feeding of the type referred to above, and we have no evidence that such a possible mode of feeding replaced the ventral feeding transport. The large mandibles are more likely to have been an adaptation to large food particles, e.g. shelled animals, transported by the ventral mechanism of a large archaeostracan. Archaeostracan general morphology makes it likely that in a way similar to that found in the Leptostraca they plowed in mud and used a similar feeding mechanism. The sediment gut filling found in certain Archaeostraca might point that way, even if Rolfe (1981) is of the opposite opinion. The living Crustacea best suited for a functional comparison, i.e. the Notostraca, plow in mud in a way comparable to that employed by the recent Phyllocarida and use a morphologically different but functionally similar ventral food transport mechanism. They have very strong mandibles, are mainly carnivorous (Lundblad 1920) and ingest considerable quantities of sediment from which they obtain prey organisms which are crushed by their strong mandibles. An investigation of gut contents in sectioned specimens of two species of *Triops* (Dahl, unpublished) revealed the presence of crushed remains of ostracods and probably other arthropods, organic debris, and inorganic particles including large sandgrains. It is, however, by no means surprising that the intestine of non-filtering carnivores sometimes contain sediment. I have frequently seen this in raptorial amphipods where the histological methods employed made it clear that the sediment was often contained in the intestines of prey animals.

Manton (1953), as discussed in more detail in section 3.2, maintained that the evolution of a stenopodium with an ambulatory endopod was a prerequisite for the formation of a malacostracan thoraco-abdominal tagmosis and a division of labor between thoracopods and pleopods. It was maintained by Sanders (1963) and Hessler & Newman (1975) that cephalocarids were related and perhaps ancestral to malacostracan ancestors. Powerful beating of cephalocarid legs produces locomotion (Sanders 1963) but they are not ambulatory. If a cephalocarid ventral food filtering and transport mechanism had been retained in malacostracan ancestors the origin of a functional demand for tagmatization is difficult to understand. Malacostracan stenopodia are not suited for ventral food filtration and transport and the beating of pleopods would interfere with a filtration current system.

Phyllocarida have efficient natatory pleopods, but they are inactive when the ventral feeding mechanism is in function. Phyllocarid thoracopods, insofar as we understand them and in any case in the Leptostraca, are non-ambulatory. This might imply that phyllocarid ancestors in the course of a specialization for benthic life either completely or partly lost the locomotory function of the thoracopods and became secondarily adapted for thoracopod filtering and food transport. This might explain the vicariating thoracopod and pleopod function mentioned above.

The argument that ventral food transport is secondary gains force from the fact that the phyllocarid trunk limb, like malacostracan stenopodia in general, is devoid of enditic structures. In those taxa where ventral food transport is primary, the Branchiopoda and the Cephalocarida, a variety of enditic structures and their armature play important parts in the transport mechanism. The Leptostraca for the same purpose are restricted to the use of the setal armature of the smooth medial borders of the thoracopods (Cannon 1927).

And it is worth noting that the leptostracan limb, particularly that of the genus *Paranebalia* (generally considered most plesiomorphic), has more in common with a primitive stenopodium than with a cephalocarid limb.

An aspect which has not been discussed in the present context is the phyllocarid brood care and its role in the functional system. As pointed out above (section 2) the position of the female malacostracan gonopore on the medial side of the base of the sixth thoracopod facilitates the brood care prevalent in some of the taxa. In decapods it allows the female to cement fertilized eggs to the pleopods by bending the abdomen below the thorax. In phyllocarids and peracarids the thoracopods become directly involved in the process by forming brood chambers. In the Leptostraca the whole series of thoracopods of the ovigerous female grow long setae on the distal part of the endopod, and thus form a large brood chamber covering the whole ventral side of the thorax. This has far-reaching functional consequences, as observed by Claus (1888) in his studies of living *Nebalia*. Claus found that in ovigerous females the thoracopod movement which produces the feeding current and the transport of food was reduced to small swinging movements, barely sufficient to ventilate the respiratory surfaces and the eggs in the brood chamber, while food intake was more or less completely suspended. Checking this observation on sectioned ovigerous *Nebalia* females I found very little matter in the intestine.

Although this type of brood care works well enough in the mud-living Leptostraca, it affords no sound basis for evolutionary radiation, adding, as it does, one more function to impede thoracopod differentiation. Peracarids have overcome this problem by means of the transformation of the proximal epipods of some thoracopods into an oöstegite. Together these oöstegites form a brood chamber which leaves the endopods free for other tasks.

Nothing definite is known about brood care in the Archaeostraca. Figures of *Nahecaris* (Broili 1928) show rounded thoracopod tips, possibly with setae. In *Ceratiocaris* Rolfe (1962) recorded the presence of very slender distal parts of thoracopod endopods. In both genera thoracopod structure would appear to be compatible with a brood care function similar to that found in the Leptostraca. Rolfe (1981), however, referred to a possible occurrence of pelagic larvae in other archaeostracan species and, if confirmed, that might open fresh alternatives.

As far as we know, the structure and function of the phyllocarid abdomen tends to bear out the isolated position of the taxon. Both in the Leptostraca and the Archaeostraca (cf. figures of *Nahecaris* in Broili, 1928 and of *Ceratiocaris* in Rolfe 1969 and 1981) there exists a tendency to reduction of the posterior pleopods, whereas the four (in *Ceratiocaris* possibly the five) anterior pairs form a series more or less distinctly decreasing in length and volume posteriad. This arrangement may be involved in mechanical aspects of pleopod swinging. It does not form a good starting point for the evolution of a pleon of the eumalacostracan type. Rolfe (1981) realized the problems inherent in the structure of the phyllocarid abdomen and indicated that possible phyllocarid ancestors of the Malacostraca may have to be found among still undiscovered Phyllocarida with a full set of pleopods.

Despite the plesiomorphies retained by the Phyllocarida, the balance seems to be at least slightly in favor of their being derived from benthic-epibenthic ancestors of a basically eumalacostracan type rather than being themselves ancestral to the eumalacostracans.

6 THE POSITION OF THE HOPLOCARIDA

It is obvious that the hoplocarids stand well apart from the rather close-knit assemblage of caridoid superorders. The evidence, i.e. the roomy abdomen, indicates a separation at a stage when advanced natatory habits had not yet been adopted by eumalacostracan ancestors. Later some Hoplocarida, notably the genus *Kallidecthes,* within the extinct order Aeschronectida appears to have been natatory, but the general morphology of the Hoplocarida including the extinct forms indicates a predominantly benthic mode of life throughout the history of the taxon.

Recent discussions of hoplocarid-eumalacostracan affinities largely center around a derivation of the hoplocarids from caridoid ancestors (Hessler 1982, and this volume), and quite logically so considering the hypothesis maintained by Hessler (1964, 1975, and 1982) and others that the ancestral eumalacostracan was a more or less advanced caridoid. But if, as maintained in section 4, the caridoids were more probably derived from ancestors of a pre-syncarid type, a separate hoplocarid derivation from benthic-epibenthic pre-caridoid ancestors becomes more plausible.

The most important apomorphies within the hoplocarid structural plan are the folding raptorial thoracopods, well-developed in the Carboniferous palaeostomatopods (Schram 1969b), the highly diagnostic proventriculus (Kunze 1981), and the specific larval types. The diagnostic value of other features discussed in this context (cf. Siewing 1956, Burnett 1973, Burnett & Hessler 1973, Hessler 1982) appears more doubtful (see Kunze, this volume). The fossil record of the hoplocarids extends to the Devonian, and the considerable degree of differentiation then attained indicates a comparatively long previous history at the hoplocarid level.

A direct derivation of the hoplocarids from phyllocarids instead of from eumalacostracans was advocated by Schram (1969c, 1973) and Kunze (1981) and to some extent supported by Rolfe (1981). Even if the sum of the evidence hitherto presented can hardly be said to be convincing the possibility cannot be written off. On the other hand, the close and well-substantiated relationships between the three caridoid superorders and the distance between each one of them and the hoplocarids makes a subclass Eumalacostraca comprising these four superorders of equal rank somewhat incongruous. Recognizing the value of existing apomorphies, the above-mentioned incongruity, and the still doubtful relationships between the Hoplocarida and other malacostracans it appears justified at least provisionally to remove the superorder Hoplocarida from the subclass Eumalacostraca and to elevate it to subclass rank.

7 THE HIGHER SYSTEMATICS OF THE MALACOSTRACA

In recent years, the debate about malacostracan phylogeny and evolution has gained impetus at least partly because new arguments have been introduced and concepts of long standing questioned. This has led to some divergences of opinion concerning the interpretation of malacostracan relationships.

Schram (1981b) recognizing the difficulties involved, tried to eliminate confusion and apparent contradictions by means of an analysis of the Malacostraca based on a random association of characters, deliberately reducing the demand of phylogenetic coherence. For obvious reasons the malacostracan system resulting from this approach differs considerably from a natural system also in those aspects where we have fairly definite information about actual affinities. Even if some aspects of malacostracan systematics remain obscure, the approach chosen by Schram appears over-pessimistic. The situation is not quite so bad.

Rolfe (1981) pointed out that a Hennigian analysis of malacostracan systematics has never been performed. It is doubtful, however, whether such an analysis would fulfil a purpose. The history of malacostracan evolution is certainly much longer than its fossil record, which starts at least in the Ordovician for the phyllocarids and in the Devonian for the hoplocaridans and eumalacostracans. But this certainly tells far less than enough about the actual age of the taxon Malacostraca. The absence of cephalocarids from the Cambrian to the Recent (Müller 1981) and of phyllocarids from the Permian to the Recent (Rolfe 1969) shows how erratic this record may be (Brooks 1969, Bergström 1980). Dealing with taxa, the early history of which is so obscure, will unavoidably lead to problems in discerning what is plesiomorphic and what is apomorphic within the respective units. When the necessary choice has been made in this respect, however, the logical rigidity (which is the strength of the cladistic method) makes the final result a foregone conclusion, irrespective of whether it is correct or not (see Schram, this volume). However suitable for low-level taxonomic analysis, where fundamentals are secure, the Hennigian method is hardly meaningful in a situation where the possibility of discerning basic facts is in doubt, for it does not in itself recognize controversy. This is probably the reason why it has not been applied in the present context.

The present survey is based on a review of comparative morphology of functional systems, their presumed origins, and integrations and segregations. It need hardly be pointed out that progressive integration or segregation, where discernible, gives important indications with respect to apomorphies. It appears as if the present approach has been fruitful, especially in the case of the caridoid superorders where the sum effects on the structural plans of the caridoid escape reaction, in conjunction with the respiratory, ventilatory and locomotory systems, has led to what may be an improved understanding of the taxa and their interrelationships. It has also introduced some new arguments into the discussion of the early evolution of the Malacostraca, and appears to have shed some new light upon the relative merits of the hypotheses of a phyllocarid versus a eumalacostracan type of ancestor.

It is concluded that the malacostracan ancestor was possibly of an incipient eumalacostracan rather than of a phyllocarid type, and that the phyllocarids, mainly as a result of progressive benthic adaptation of an ancestor of the former type, came to represent the earliest known lateral branch in malacostracan evolution. The hoplocarids are also presumed to be an early benthic side branch stemming from a basically eumalacostracan parentage. The caridoid superorders constitute the typical Eumalacostraca and are certainly closely related. They share in the caridoid escape reaction and its comprehensive synapomorphic system.

The general primitive nature of the Syncarida, including also the muscular part of the caridoid reflex system, led to the conclusion that syncarids and their ancestors rather than advanced caridoids were the parents of the unique caridoid constellation of superorders. This would imply that a final perfection of the caridoid facies in its most advanced form took place independently in eucarids and mysidacean peracarids. It may also explain why the orders Amphipoda and Isopoda among the Peracarida appear never to have had a carapace. The widespread opinion that the Eucarida are more closely related to the syncarids than the Peracarida gains further support.

The higher classification of the Malacostraca with one single deviation from that of Calman (1909) appears as follows. All definitions are as formulated by Calman (1909) with the exception of the reference to the Stomatopoda in the diagnosis of the Eumalacostraca, which should be deleted.

- Class Malacostraca
  - Subclass Phyllocarida
  - Subclass Hoplocarida
  - Subclass Eumalacostraca
    - Superorder Syncarida
    - Superorder Eucarida
    - Superorder Peracarida

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REFERENCES

Anderson, D.T. 1973. *Embryology and phylogeny in annelids and arthropods.* Oxford: Pergamon Press.

Attramadal, Y.G. 1981. On a non-existent ventral filtration current in *Hemimysis lamornae* (Couch) and *Praunus flexuosus* (Müller) (Crustacea: Mysidacea). *Sarsia* 66:283-286.

Balss, H. 1938. Stomatopoda. In: *Bronns Klassen u.Ordn.d. Tierreichs. V.1,* 6(2):1-173. Leipzig: Fisher Verlag.

Bergström, J. 1980. Morphology and systematics of early arthropods. *Abh. naturwiss. Ver. Hamburg (NF)* 23:7-42.

Briggs, D.E.G. 1976. The arthropod *Branchiocaris* n.gen., Middle Cambrian, Burgess Shale, British Columbia. *Bull. Geol. Surv. Canada* 264:1-29.

Briggs, D.E.G. 1977. Bivalved arthropods from the Cambrian Burgess Shale of British Columbia. *Palaeontol.* 20:595-621.

Briggs, D.E.G. 1978. The morphology, mode of life, and affinities of *Canadaspis perfecta* (Crustacea: Phyllocarida), Middle Cambrian, Burgess Shale, British Columbia. *Phil. Trans. Roy. Soc. London* (B)281:439-487.

Broili, F. 1928. Beobachtungen an *Nahecaris. Sitz.-ber. Bayer. Akad. Wiss. math.-naturw.* 1928:1-19.

Brooks, H.K. 1962a. On the fossil Anaspidacea, with a revision of the classification of the Syncarida. *Crustaceana* 4:229-242.

Brooks, H.K. 1952b. Devonian Eumalacostraca. *Ark. Zool.* (2)15:307-315.

Brooks, H.K. 1962c. The Paleozoic Eumalacostraca of North America. *Bull. Amer. Paleontol.* 44:160-338.

Brooks, H.K. 1969. Syncarida. In: R.C.Moore (ed.), *Treatise on Invertebrate Paleontology. Part R. Arthropoda 4:* R345-359. Lawrence: Geol. Soc. Am. & Univ. Kansas Press.

Burnett, B.R. 1973. Notes on the lateral arteries of two stomatopods. *Crustaceana* 23:303-305.

Burnett, B.R. & R.R.Hessler 1973. Thoracic epipodites in the Stomatopoda (Crustacea): a phylogenetic consideration. *J. Zool. Lond.* 169:381-392.

Calman, W.T. 1909. Crustacea. In: Sir Ray Lankester (ed.), *A treatise on Zoology Vol.7.* London: Adam & Charles Black.

Cannon, H.G. 1927. On the feeding mechanism of *Nebalia bipes. Trans. Roy. Soc. Edinb.* 55:355-369.

Cannon, H.G. & S.M.Manton 1927. On the feeding mechanism of a mysid crustacean, *Hemimysis lamornae. Trans. Roy. Soc. Edinb.* 55:219-253.

Claus, C. 1885. Neue Beiträge zur Morphologie der Crustaceen. *Arb. zool. Inst. Wien* 6:1-108.

Claus, C. 1888. Ueber den Organismus der Nebaliiden und die systematische Stellung der Leptostraken. *Arb. Zool. Inst. Wien* 8:1-147.

Dahl, E. 1956. On the differentiation of the topography of the Crustacean head. *Acta Zool.* 37:123-192.

Dahl, E. 1963. Main evolutionary lines among Recent Crustacea. In: H.B.Whittington & W.D.I.Rolfe (eds), *Phylogeny and Evolution of Crustacea:* 1-14. Cambridge: Mus. Comp. Zool.

Dahl, E. 1976. Structural plants as functional models exemplified by the Crustacea Malacostraca. *Zool. Scr.* 5:163-166.

Dahl, E. 1977. The amphipod functional model and its bearing upon systematics and phylogeny. *Zool. Scr.* 6:221-228.

Dahl, E. (in press). Alternatives in malacostracan evolution. *Rec. Aust. Mus.*

Dahl, E. (in press). The subclass Phyllocarida (Crustacea) and the status of some early fossils. *Vidensk. Medd. Dansk. Naturh. Foren.*

Dahl, E. & R.R.Hessler 1982. The crustacean lacinia mobilis: a reconsideration of its origin, function and phylogenetic implications. *Zool. J. Linn. Soc.* 74:133-146.

Daniel, R.J. 1929. The abdominal musculature system of *Meganyctiphanes norvegica* (M.Sars). *Proc. Trans. Liverpool Biol. Soc.* 43:149-180.

Daniel, R.J. 1931a. The abdominal muscular systems of *Paranaspides lacustris* (Smith). *Proc. Trans. Liverpool Biol. Soc.* 46:26-45.

Daniel, R.J. 1931b. Comparative study of the abdominal musculature in Malacostraca. Part I. The main ventral muscles of the typical abdominal segments. *Proc. Trans. Liverpool Biol. Soc.* 45:57-71.

Daniel, R.J. 1932. Comparative study of the abdominal musculature in Malacostraca. Part II. The superficial and main ventral muscles, dorsal muscles and lateral muscles, and their continuations into the thorax. *Proc. Trans. Liverpool Biol. Soc.* 46:46-107.

Daniel, R.J. 1933. Comparative study of the abdominal musculature in Malacostraca. Part III. The abdominal muscular systems of *Lophogaster typicus* M.Sars and *Gnathophausia Zoëa* Suhm, and their relationships with the musculatures of other Malacostraca. *Proc. Trans. Liverpool Biol. Soc.* 47:71-133.

Elofsson, R. 1965. The nauplius eye and frontal organs in Malacostraca (Crustacea). *Sarsia* 19:1-54.

Elofsson, R. 1966a. The nauplius eye and frontal organs of the non-Malacostraca (Crustacea). *Sarsia* 25: 1-128.

Elofsson, R. 1966b. Notes on the development of the nauplius eye and frontal organs of decapod crustaceans. *Acta Univ. Lund. II, 1966* 27:1-23.

Elofsson, R. 1966c. The nauplius eye and frontal organs in Crustacea morphology, ontogeny and fine structure. *Diss. inaug. Lund:* 1-12.

Elofsson, R. & E.Dahl 1970. The optic neuropiles and chiasmata of Crustacea. *Z. Zellforsch.* 107:343-360.

Fryer, G. 1964. Studies on the functional morphology and feeding mechanism of *Monodella argentarii* Stella (Crustacea: Thermosbaenacea). *Trans. Roy. Soc. Edinb.* 66:49-90.

Gurney, R. 1942. *Larvae of Decapod Crustacea.* London: Ray Soc.

Hanström, B. 1934. Neue Untersuchungen über Sinnesorgane und Nervensystem der Crustaceen. IV. *Ark. Zool.* 26A(24):1-66.

Hanström, B. 1937. Neue Untersuchungen über Sinnesorgane und Nervensystem der Crustaceen. *V.K. Fysiogr. Sällsk. i Lund Förh.* 5(16):1-14.

Hanström, B. 1947. The brain, the sense organs, and the incretory organs of the head of the Crustacea Malacostraca. *Acta Univ. Lund.* (2), 43(9):1-45.

Hessler, R.R. 1964. The Cephalocarida comparative skeletomusculature. *Mem. Conn. Acad. Arts Sci.* 16:1-97.

Hessler, R.R. 1982. Evolution within the Crustacea. In: L.G.Abele (ed.), *Biology of the Crustacea, vol.1:* 149-185. New York: Academic Press.

Hessler, R.R. 1982. The structural morphology of walking mechanisms in malacostracan crustaceans. *Phil. Trans. Roy. Soc. London.* (B)296:245-298.

Hessler, R.R. & W.A.Newman 1975. A trilobitomorph origin for the Crustacea. *Fossils and Strata* 4:437-459.

Hickman, V.V. 1937. The embryology of the syncarid crustacean, *Anaspides tasmaniae. Pap. Proc. Roy. Soc. Tasmania* 1936:1-35.

Kunze, J.C. 1981. The functional morphology of stomatopod Crustacea. *Phil. Trans. Roy. Soc. London* (B)292:255-328.

Lauterbach, K.-E. 1975. Ueber die Herkunft der Malacostraca (Crustacea). *Zool. Anz.* 194:165-179.

Lauterbach, K.-E. 1980. Schlüsselereignisse in der Evolution des Grundplans der Mandibulata (Arthropoda). *Abh. naturwiss. Ver. Hamburg (NF)* 23:105-161.

Lundblad, O. 1920. Vergleichenede Studien über die Nahrungsaufnahme einiger schwedischen Phyllopoden. *Ark. Zool.* 13(1):1-32.

Manton, S.M. 1928. On the embryology of a mysid crustacean, *Hemimysis lamornae. Phil. Trans. Roy. Soc. London* (B)438:363-463.

Manton, S.M. 1930. Notes on the habits and feeding mechanisms of *Anaspides* and *Paranaspides* (Crustacea, Syncarida). *Proc. Zool. Soc. London* 1930:791-800.

Manton, S.M. 1934. On the embryology of the Crustacean *Nebalia* bipes. *Phil. Trans. Roy. Soc. London* (B)498:163-204.

Manton, S.M. 1953. Locomotory habits and the evolution of the larger arthropodan groups. *Symp. Soc. Exp. Biol. VII Evolution:*339-376.

Mauchline, U. 1980. The biology of mysids and euphausiids. *Mar. Biol.* 18:1-677.

Müller, K.J. 1979. Phosphatocopine ostracodes with preserved appendages from the Upper Cambrian of Sweden. *Lethaia* 12:1-27.

Müller, K.J. 1981. Arthropods with phosphatized soft parts from the Upper Cambrian 'Orsten' of Sweden. *US Geol. Surv. Open-File Report* 81-743:147-151.

Paulus, H.F. 1978. Eye structure and the monophyly of the Arthropoda. In: A.P.Gupta (ed.), *Arthropod phylogeny:*299-383. New York: Van Nostrand Reinhold.

Rolfe, W.D.I. 1962. Grosser morphology of the Scottish Silurian phyllocarid crustacean *Ceratiocaris papilio* Salter in Murchison. *J. Palaeontol.* 36:912-932.

Rolfe, W.D.I. 1969. Phyllocarida. In: R.C.Moore (ed.), *Treatise on Invertebrate Paleontology. Part R. Arthropoda 4:*R296-331. Lawrence: Geol. Soc. Am. & Univ. Kansas Press.

Rolfe, W.D.I. 1981. Phyllocarida and the origin of the Malacostraca. *Geobios* 14:17-24.

Sanders, H.L. 1963. The Cephalocarida. Functional morphology, larval development, comparative external anatomy. *Mem. Conn. Acad. Arts Sci.* 15:1-80.

Schminke, H.K. 1981. Adaptation of Bathynellacea to life in the interstitial ('Zoea Theory'). *Int. Rev. ges. Hydrobiol.* 66:575-637.

Scholl, G. 1963. Embryologische Untersuchungen an Tanaidaceen (*Heterotanais oerstedi* 'Kröyer)). *Zool. Jb. Anat.* 80:500-554.

Schram, F.R. 1969a. Some Middle Pennsylvanian Hoplocarida (Crustacea) and their phylogenetic significance. *Fieldiana Geol.* 12:235-289.

Schram, F.R. 1969b. Polyphyly in the Eumalacostraca? *Crustaceana* 16:243-350.

Schram, F.R. 1970. Isopod from the Pennsylvanian of Illinois. *Science* 169:854-855.

Schram, F.R. 1973. On some phyllocarids and the origin of the Hoplocarida. *Fieldiana Geol.* 26:77-93.

Schram, F.R. 1974a. The Mazon Creek caridoid Crustacea. *Fieldiana Geol.* 30:9-65.

Schram, F.R. 1974b. Palaeozoic Peracarida of North America. *Fieldiana Geol.* 33:95-124.

Schram, F.R. 1979. British Carboniferous Malacostraca. *Fieldiana Geol.* 40:1-129.

Schram, F.R. 1981a. Late Paleozoic crustacean communities. *J. Palaeontol.* 55:126-137.

Schram, F.R. 1981b. On the classification of Eumalacostraca. *J. Crust. Biol.* 1:1-10.

Schram, F.R., R.M.Feldmann & M.J.Copeland 1978. The late Devonian Palaeopalaemonidae and the earliest decapod crustaceans. *J. Palaeontol.* 52:1375-1387.

Schram, J.M. & F.R.Schram 1974. *Squillites spinosus* Scott 1938 (Syncarida, Malacostraca) from the Mississippian Heath Shale of Central Montana. *J. Palaeontol.* 48:95-104.

Siewing, R. 1956. Untersuchungen zur Morphologie der Malacostraca (Crustacea). *Zool. Jb. Anat.* 75: 39-176.

Siewing, R. 1963. Studies in malacostracan morphology: results and problems. In: H.B.Whittington & W.D.I.Rolfe (eds), *Phylogeny and evolution in Crustacea:*85-103. Cambridge: Mus. Comp. Zool.

Simonetta, A. & R.Delle Cave 1980. The phylogeny of the Palaeozoic arthropods. *Boll. Zool.* 47(suppl.): 1-19.

Strömberg, J.-O. 1965. On the embryology of the isopod *Idothea. Ark. Zool.* (2)17:421-473.

Strömberg, J.-O. 1967. Segmentation and organogenesis in *Limnoria lignorum* (Rathke) (Isopoda). *Ark. Zool.* (2)20:91-139.

Strömberg, J.-O. 1971. Contribution to the embryology of bopyrid isopods. *Sarsia* 47:1-46.
Tattersall, W.M. & O.S.Tattersall 1951. *The British Mysidacea.* London: Roy. Soc.
Weygoldt, P. Die Embryonalentwicklung des Amphipoden *Gammarus pulex pulex* (L.). *Zool. Jb. Anat.* 77:51-110.
Whittington, H.B. 1974. *Yohoia* Walcott and *Plenocaris* n.gen., arthropods from the Burgess Shale, Middle Cambrian, British Columbia. *Bull. Geol. Surv. Canada* 231:1-21.