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ALTERNATIVES IN MALACOSTRACAN EVOLUTION

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SUMMARY

The Malacostraca appear to have been derived from epibenthic ancestors with many caridoid features. Despite their very long palaeontological record the Phyllocarida differ in so many respects from the basic eumalacostracan morphological and functional plan that they are regarded as unlikely ancestors and more probably an early diverging branch.

The general morphology of the malacostracan cephalothorax and carapace is discussed and it is shown that the concept of a maxillary segment carapace common to all Crustacea is not valid. The malacostracan dorsal shield is produced by a fusion of terga and a free carapace fold is sometimes formed at its posterior margin.

Some functional systems of the various caridoid Malacostraca are discussed. Attention is drawn to the unsolved problem of secondary segmentation after the alleged loss of a cephalothorax, e.g. in the Syncarida.

The unsatisfactory status of the diagnosis of the superorder Peracarida is pointed out and a revision recommended.

Introduction

Since Calman (1909) presented his views on the 'caridoid facies' and the 'generalised malacostracan' the position of a crustacean of this general type as ancestral to the Malacostraca has remained practically unchallenged, accepted also by more recent revisors (Siewing, 1956, 1963; Fryer, 1964). Nevertheless certain observations, old and new, are not easy to reconcile with this traditional concept of the ancestral caridoid.

Similarly, the higher systematics of the Malacostraca proposed by Calman (l.c.) has remained unshaken and as far as its fundamentals are concerned is likely to remain so. Recently, however, the position of the Hoplocarida within the framework of this system has been questioned by Schram (1969). The current definition of the Peracarida, too, appears more and more unsatisfactory (Dahl and Hessler, 1982).

The aim of the present paper is to focus attention on a number of areas within which a fresh evaluation of current interpretations appears desirable.

Diagnostic features of the Malacostraca

Malacostracans have stalked eyes with a unique neuronal pattern, biramous antennules, tagmatisation of the postcephalic body, fixed number of segments, fixed position of gonopores, respiratory thoracopod epipods, and natatory pleopods. These characteristics are shared by less derived members of all four eumalacostracan superorders and by the leptostracans. The position of the Malacostraca as a natural taxon is secure.

The Eumalacostraca are further defined by the presence of ambulatory endopods and natatory exopods on the thoracopods, as well as by fan-shaped uropods.

Many of the traits enumerated above are more or less typically caridoid. There can be little doubt that Crustacea with these basic morphological traits were originally epibenthic swimmers and walkers.

Cephalothorax and carapace in the Malacostraca

The presence of a cephalothoracic shield is a prominent feature of the typical caridoid. This shield is often referred to as the 'carapace' but this is not wholly correct.

The carapace, by definition, is a fold growing out from the posterior border of the maxillary segment. It is to be found in its typical form in the Notostraca. In *Triops* it starts growing in connection with metamorphosis towards a benthic mode of life. It grows backwards more rapidly than the body itself and soon covers most of it. However, the carapace is not attached to the maxillary segment in all non-malacostracans. In the Cladocera one, two, or, in *Leptodora,* more segments are fused to the head, and the carapace fold is attached to the last of these segments. Similar conditions appear to prevail in ostracods.

In the Malacostraca the formation of branchiostegal folds always precedes possible carapace formation. Lateral folds grow out from the cephalon and thorax of the embryo (Manton, 1934; further instances in Anderson, 1973). The folds grow out laterad and ventrad, and in the peracarids, where they are always short, sometimes also posteriad beyond their point of attachment to the body wall.

These folds form the branchiostegal chambers. Generally within these chambers segment borders disappear and the segments fuse to become integrated into the cephalothorax. In the Leptostraca, however, where the large folds envelop not only the body but also the thoracopods, lateral segment borders are retained. Dorsad to the folds the tergal parts fuse and thus complete the cephalothorax.

Sometimes, in the Leptostraca, certain Peracarida, and larvae of stomatopods and penaeid decapods, there are not only lateral branchiostegal folds but also continuous with them a transversal dorsal fold projecting posteriad over a varying number of segments. This dorsal part of the fold is attached to the posterior margin of the dorsal shield formed by the fused terga. Consequently the position of this attachment varies from group to group—in the Mysidacea, where a variable number of segments are included in the dorsal shield, even from genus to genus. Considering what has been stated above concerning carapace attachment in the non-Malacostracan groups, this structure can also be regarded as a carapace.

In decapods the fused dorsal shield comprises the entire thorax, in the peracarids a varying but lower number of segments, in *Nebalia* only the first thoracic segment. No adult malacostracan has a carapace attached to the maxillary segment, not even the Leptostraca, although this is stated in practically every text-book. Only stomatopod larvae are reported to have a carapace fold attached to the maxillary segment (Calman, 1909).

It is also frequently stated that in malacostracans with a dorsal shield this shield is formed by the fusion of the maxillary segment carapace to the dorsum.

This is not so. A histological investigation of representatives of leptostracans, mysids, euphausians, and decapods at various stages of their development has nowhere revealed any sign of integumental folding in the dorsal shield region. As already stated the dorsal shield is formed by a fusion of the segments involved and this gives as its result a simple and continuous dorsal body integument.

The alleged omnipresent maxillary carapace has profoundly influenced the discussion of malacostracan derivation and evolution but can and should now be relegated to history. What remains is a tendency among the Malacostraca to form thoracic shields and folds fulfilling various important functions. In the Malacostraca they are generally part of the respiratory system, and their high degree of development in pelagic forms indicates little-investigated hydrodynamic functions.

Phyllocarida and Eumalacostraca

Mainly owing to their antiquity the Phyllocarida have often been supposed to be ancestral to the Eumalacostraca. However, the phyllocarid functional pattern with non-locomotory respiratory and filtering thoracopods, absence of an independent cephalic feeding mechanism, and, throughout the known record, an abdomen of a very special type, differs very much from any known eumalacostracan pattern and indicates differentiation in a diverging direction. Preliminary observations on the Devonian *Nahecaris* from an investigation carried out together with Professor Stürmer and Dr Bergström give a wealth of new data but no promise of information on the origin of the Eumalacostraca.

Following Calman (1909) I regard the Phyllocarida as an early diverging branch of the Malacostraca, and with Burnett and Hessler (1973) I do not find a separate phyllocaridan derivation of the Hoplocarida probable. In this connection I wish to stress the importance of the new results published by Schram (1978, 1979) which indicate that eumalacostracan radiation took place much earlier than generally presumed.

Eumalacostracan caridoids

Typical caridoid forms are found among eucarids and peracarids and as larvae in the Hoplocarida. Also the anaspidacean syncarids, although lacking a branchiostegal cephalothorax, have a general resemblance to caridoids (Calman, l.c.; Manton, 1930). Between the various caridoid types, however, differences exist which are probably of evolutionary significance.

Eucarida

The eucaridan cephalothorax comprises the whole or nearly the whole thorax. In the Euphausiacea locomotion is effected by pleopod and exopod swimming, partly integrated with respiratory ventilation. The respiratory epipods lie outside the non-respiratory branchiostegal chambers. The function of the cephalothoracic shield is unknown but probably hydrodynamic. In caridoid decapods swimming is effected by the pleopods and respiration by highly developed epipods enclosed in branchiostegal chambers and ventilated by the maxillary scaphognathite. Thus segregation between locomotion and respiratory ventilation is complete.

Peracarida

The cephalothorax is short, comprising at most 4 segments (certain Cumacea), generally fewer. A free carapace fold sometimes occurs. The Lophogastrida are unique within the group in possessing a full set of thoracic epipods. The function of their exceptionally large carapace seems to be the enclosing of these epipods within the branchiostegal chambers so that ventilation by means of the maxilliped epipod may become effective. Swimming in the lophogastrids is effected by pleopods and exopods. A branchiostegal respiratory system is found also in Mysidacea (s.s.), Cumacea, Tanaidacea, Spelaeogriphacea, and Thermosbaenacea. In connection with a more benthic life the pleopods tend to become reduced, especially in the females. Natatory exopods are found in the epibenthic—pelagic mysids. Of thoracopod epipods only the ventilatory and respiratory maxilliped endopod is retained, supplemented by a respiratory branchiostegal wall and sometimes by respiratory exopods. However, there are strong reasons to presume that in the peracarids it is the proximal epipod of certain female thoracopods that has been transformed into an oostegite.

The divergent functional and morphological patterns of isopods and amphipods will be discussed in the next section.

Syncarids

In the paleocaridacean syncarids all eight thoracic segments were free (Brooks, 1969). Also the Anaspidacea appear to be in many respects very primitive. Manton (1930) noted the surprisingly high degree of locomotory integration between thorax and abdomen, which she tentatively interpreted as a sign of incomplete tagmatisation. In any case it is unique within the Malacostraca. Respiration is effected by means of double pairs of epipods, ventilated by autochonous vibration and exopod beating. At least some exopods are also respiratory.

The peracarid concept

Within the Peracarida all the orders except the Isopoda and Amphipoda represent a natural group centred around a functional model which recurs in easily recognisable forms within the various orders, and the main characteristics of which were described in the previous section.

The lophogastrids, probably representing a separate order, stand a little apart from the other members of this group. Their internal morphology is characterised by many primitive traits (Siewing, 1956), and they have a very peculiar type of mandible (Dahl and Hessler, 1982), thoracic epipod respiration, pleopod and exopod swimming, remnants of a seventh abdominal segment, and a telson with what appears to be remnants of a furca. Probably they were at a very early stage adapted for a pelagic mode of life, and within the peracarid assemblage they may possibly link up more closely with the pygocephalomorphs than with the more derived orders.

Mysids are generally supposed to have descended from lophogastrids, but morphologically they are not very close to them, and the tendency to reduction of pleopods points to a more benthic mode of life, although they are in many respects less modified in this direction than the other orders.

The isopods have traditionally been considered to form the terminal link in an evolutionary chain going from mysids via tanaids. This, however, demands the loss in isopods of the peracarid respiratory system and its replacement by pleopod respiration, the retention of natatory pleopods, and, in connection with the loss of the branchiostegal cephalothorax, the establishment of a secondary segmentation.

The amphipods have the thoracopod epipod respiration, which is probably plesiomorphic in malacostracans, and lack a maxilliped epipod. They have developed a unique ventilation system, integrated with pleopod swimming, and they have a subtagmatisation of the abdomen without counterpart among the Malacostraca. A derivation from the characteristic peracarid model discussed above offers difficulties. The thoracic respiratory epipods remain in what must be considered to be their original position—identical with that found in the Anaspidacea—and have not been displaced ventrally as suggested by Grindley and Hessler (1971). Considering this and the absence of a maxilliped epipod it is very difficult to see any functional reason for the existence of a peracarid type cephalothorax-carapace and its subsequent disappearance. Hessler (in press) in his comprehensive investigation of the walking mechanisms of the Eumalacostraca found a general peracarid pattern in the hinge structures. But in this respect also those of the amphipods stand somewhat apart and permit different interpretations. The current definition of the Peracarida appears far from satisfactory and a revision of the higher systematics of the group appears desirable. It is not impossible that such a revision may lead to a subdivision or even a splitting of the superorder.

The direction of eumalacostracan evolution

What one is tempted to call the most perfect manifestations of the caridoid facies as we see them in decapods, euphausians, and certain peracarids display a high degree of outward conformity. However, if we look into the functional systems involved in and partly responsible for the establishment of these manifestations we find that they are by no means uniform. If derived from a basic caridoid stock they must have diverged fairly early. The best argument for the existence of such a basic caridoid stock appears to be provided by the Euphausiacea, retaining basic modes of locomotion and respiration and having a cephalothorax without recognised functional differentiation.

This, however, leaves the Syncarida unexplained. As pointed out above they appear to be plesiomorphic with respect to segmentation, locomotion, respiration, respiratory ventilation, and, possibly, tagmatisation. At the same time recent results presented by Schminke (1978) indicate a close relationship between syncarids and penaeid decapods. Theoretically it is not very difficult to visualise the evolutionary steps by which the various caridoid types could have been derived from a syncarid-type ancestor. Reversing the process appears a good deal more difficult and once more forces us to solve the problem of the loss of a cephalothorax and the establishment of a secondary segmentation. In connection with the Syncarida such processes have repeatedly been referred to (among others by Manton, 1930; Siewing 1958, 1963; Hessler and Grindley 1973). With respect to amphipods Bousfield (1978) also considered a derivation from carapace-bearing ancestors as the most likely alternative, and this confronts us with the same problem. Siewing (1958) expressed the opinion that the establishment of a secondary segmentation is a much more difficult problem than the loss of segmentation, but nobody has really seriously faced it. Yet this is what we have to do if the concept of the caridoid ancestor shall be either vindicated or rejected and if, on the whole, we wish to understand the course of malacostracan evolution.

Conclusions

In concluding this brief review it appears to the writer—who has to some extent deliberately acted the part of the *advocatus diaboli*—that, although many problems concerning crustacean relationships have found solutions, we have during a long time tended to bypass or sweepingly explain away some of the most crucial problems inherent in the study of malacostracan evolution.

Attention has been drawn to some of the alternatives with which we have to deal. Many of the problems have become apparent during an attempt to think in terms not only of comparative anatomy, but also of functional systems and the integration and segregation of such systems. This seems to be a tool useful not only in the identification but also in the solution of problems.

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