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Phylogeny and adaptive radiation within the Anomopoda: a preliminary exploration

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Abstract

The distinctness of the Anomopoda and the polyphyletic nature of the so-called Cladocera are emphasized.

An attempt is made to reconstruct the ancestral anomopod, which probably lived in Palaeozoic times. This task is facilitated by the availability of detailed information on extant forms, which includes functional as well as purely morphological considerations and enables us to understand the means whereby complex mechanisms were transformed during evolution. Comparative studies on the ecology and habits of extant forms also throw light on the probable way of life of the ancestral anomopod.

Adaptive radiation within the Anomopoda is briefly surveyed and an outline of the suggested phylogeny of the order is indicated.

Introduction

The Anomopoda is a well-defined order of the Branchiopoda, separated by many trenchant characters from the other three orders with which it was for long united in a polyphyletic assemblage under the name Cladocera (Fryer, 1987a, 1987c). Diagnostic features of the order are listed elsewhere (Fryer, 1987c). Differences between the Anomopoda and the superficially similar Ctenopoda, with which it shares certain primitive branchiopod features, but from which it is distinguished in many ways, are discussed in Fryer (1987a). Here it is sufficient to note that a fundamental distinction lies in the nature of the trunk limbs. In the Anomopoda exploitation of diversity within the series of limbs for many different means of collecting and manipulating the food has been an outstanding feature of adaptive radiation. This has been accompanied by related modifications of the carapace, antennae and post-abdomen, in ways that have no parallel in the Ctenopoda, whose trunk limbs are characterised by serial uniformity and display much more restrained modification. These two orders also differ fundamentally in other features, including the nature of the maxillules, the arrangement and details of the ovaries and the means of protecting the resting eggs.

Apart from its implications for Branchiopod evolution as a whole (to be considered elsewhere) recognition of Anomopod distinctness invites examination of affinities within the order, certain aspects of which are explored here. Opinions differ as to the number of families recognised. The Macrothricidae, Chydoridae, Bosminidae and Daphniidae are universally accepted. From the Daphniidae Goulden (1968) split off the Moinidae and this taxon has been widely recognised though it seems not to merit more than sub-familial rank (Fryer, 1991b), and the same applies to the proposed Ilyocryptidae. Likewise Smirnov (1992) allocated what are much the most informative anomopod fossils yet discovered to a new family, the Prochydoridae. These Early Cretaceous animals certainly differ from all modern chydorids in well-defined ways but whether, especially in the absence of information on the nature of the trunk limbs, this justifies familial separation is arguable. Neither of these matters, however, presents difficulties when affinities within the order are considered.

The search for the ancestral anomopod

The Anomopoda is an ancient group. Just how ancient is unknown. As long ago as early Cretaceous times (120–130 m y ago) ephippia were produced that are not only similar to those of modern daphniids but can be assigned to the extant genera *Daphnia*, *Simocephalus* and probably *Moina* (Fryer, 1991; Smirnov, 1992). Others are known of Eocene (Lai & Li, 1987), Oligocene (Heydon, 1862) and (*Moina*) Miocene (Goulden, 1968) age. Daphniid ephippia are the most specialised of all such structures within the Anomopoda and owe their preservation to their robust protective envelopes. The more delicate, more primitive, and often very small ephippia of other families are less likely to be preserved but chydorid ephippia may yet be found in a fossil state. The inference from fossil daphniid ephippia is that they were produced by animals that had other attributes of these genera, but this is unproven. Geographical evidence also indicates that *Daphnia* is an ancient genus (Benzie, 1987). If even extant genera existed so long ago, the order must be much older. If phylogenetic reasoning to be put forward elsewhere is correct, it must have originated earlier than the Devonian.

The claim by Tasch (1963), based on curious logic, that the origin of 'cladocerans' can be restricted to post-Cretaceous, pre-Oligocene times was never convincing and can now be forgotten, as too, incidentally, can his completely untenable, and contradictory, claim that the Haplopoda probably arose in 'the old Pleistocene'. This too is clearly an ancient group.

We recently acquired for the first time information on some features of the morphology of anomopods that flourished in early Cretaceous times (Smirnov, 1992). Whether these are regarded as primitive members of the Chydoridae or as representatives of a distinct family, the Prochydoridae, is unimportant: their significance is that they show that animals with many features of chydorid organisation were abundant some 130 m y ago. These extinct forms also reveal interesting differences from modern chydorids – e.g. they had more antennal setae and some of them apparently had an unconvoluted alimentary canal – and provide valuable information on certain evolutionary trends within the chydorid line and on the time span over which changes of antennal armature may have occurred. In various respects, however, they were already too specialised to throw much light on the nature of the ancestral anomopod.

Reconstruction of the anatomy and way of life of this organism must therefore be based largely on comparative studies of extant forms, particularly within, but also outside, the order. This is a perfectly legitimate approach which, as a result of studies made during recent years, can include functional as well as purely morphological considerations. Indeed without functional knowledge of the mechanisms involved (and there are many), not only is it impossible to understand how one mechanism might have been derived from another, but meaningful comparisons between families are impossible, and it is very difficult to appreciate what the primitive condition may have been. Information on the ecology and habits of extant forms is also extremely helpful. As Patterson (1981) has said, knowledge of the recent biota is the starting-point for all phylogenetic work.

Some attributes can be ascribed to the ancestral anomopod with certainty. For example, when a feature characteristic of, and unique to, the order, such as the nature of the maxillule, or the formation of an ephippium, is shared by all species irrespective of their diverse specialisations, this feature was clearly present in the common ancestor. The only, and less likely, alternative is that it evolved independently several times. This does not mean that certain features have not evolved more than once during the adaptive radiation of the order. Convergence has certainly occurred at times.

The ancestral anomopod: its structure and way of life

The suggested gross morphology of a female of the ancestral anomopod is shown in Figs 1 and 2. Save for a pronounced ventral gape, the trunk was completely enveloped by the carapace. This was derived from a dorsal shield of still earlier ancestors that later folded and extended ventrally on each side to give a functionally bivalved structure while remaining as a single hingeless entity. Its margins were more or less straight and unelaborated but probably bore a few short setae. The carapace was double-walled, the inner wall being very thin, the outer more robust but by no means thick, and scarcely sclerotized. Between the walls was a space, spanned by fibrils, within which blood circulated, and which, anteriorly, housed the tubules of the maxillary glands. The trunk was composed of only six limb-bearing segments and a much abbreviated region posterior to them where it was flexed ventrally and perhaps somewhat anteriorly to form a simple structure, later to become elaborated into the post-abdomen, that terminated in a pair of spines. A pair of sensory setae arose in the region of flexure. The posterior region had some mobility but was not articulated with more anterior parts, nor was it provided with specialised marginal armature though a few spinules were present on the morphologically dorsal surface.

The short head lacked a headshield. The eyes were 'internalised', having sunk beneath the cuticle and were already fused to give a single median structure or were completing the process. An ocellus was present.

The movable antennules were long, slender and of two segments, terminated in a tuft of sensillae, and had a more proximal sensory seta.

The antennae (Fig. 3) were large with a straight protopodite, and bore a four-segmented endopodite and a three segmented exopodite. Fossil evidence produced by Smirnov (1992) shows that in the chydorid lineage there were more setae (up to five) on the basal segment of the exopodite of certain early Cretaceous forms than in modern species that have one or none. As even primitive macrothricids never have more than one long seta or spine on the segment in question, this may have been an experiment in an offshoot of the chydorid lineage, but it remains an open question whether the ancestral anomopod had more exopodite setae than any extant species. Other branchiopod orders that retain locomotory antennae in the adult have more such setae than anomopods, and this is also the case in anostracan nauplii, so the precursor of the Anomopoda may also have had more setae than modern anomopods, but the basic condition suggests that reduction occurred early in their evolution. Only fossils can resolve this question.

The mandibles were of the basic rolling, crushing, branchiopod type and lacked a palp. Already they displayed slight asymmetry, both skeletal-and muscular.

The maxillules (Figs 5 and 6) were similar to those of modern forms, being small and with armature reduced to three spines, which, save for occasional reductions, is a conservative feature in the order and very different from, for example, the arrangement in the Ctenopoda.

It is probable that the maxilla was a simple papilla on which the duct of the maxillary gland terminated and opened. As an alternative hypothesis, the similarity of the inner lobe of trunk limb 1 of certain macrothricids and chydorids to the maxilla, or to the similar lobe borne by this appendage, in the Anostraca and Lipostraca, raises the possibility that it is in fact the maxilla, of which there is otherwise no trace in, for example, the chydorid *Eurycercus* (Fryer, 1968). Even the possibility that what has long been called the first trunk limb is in fact the maxilla needs consideration. There are, for example, beguiling similarities between the first trunk limb of macrothricids and chydorids and the maxilla of such an anostracan as *Branchinecta paludosa* (Fig. in Cannon 1933). If this were the case, trunk limb 2 of anomopods would be the homologue of trunk limb 1 of the lipostracan *Lepidocaris*, to which it bears striking structural, and obviously functional, similarities. However, as Grobben (1879) showed long ago for *Moina* (in which there is no maxilla: only a setose mound), both maxillules and maxillae are evident in the embryo, and the same is true of the macrothricid *Acantholeberis* in which the maxilla is distinct in the embryo (Figs 7and 8) and persists in the adult as a small papilla in addition to the conspicuous inner lobe of trunk limb 1 (Fryer, 1974). Furthermore, Kotov (1995) has shown that the maxilla makes a transitory appearance in the embryo of chydorids, bosminids and daphniids in which there is no trace of this appendage in the adult.

A large median fleshy labrum, with no ventral elaboration, extended posteriorly from the head, covering the mandibles and maxillules ventrally and forming, with the adjacent body wall, a tube bridging the gap between the anterior end of the food groove (see below) and the atrium oris (Figs 5 and 6). Within the labrum were labral glands that discharged entangling secretions.

The mid ventral region of the essentially cylindrical trunk was excavated into a well-marked food groove that extended posteriorly to the level of the fifth pair of trunk limbs.

The trunk limbs lacked joints, nor was there a joint between limb and trunk. Although form was defined by a cuticle, rigidity of the limb was in large measure provided by turgor pressure of the haemocoelic blood system. The trunk limbs already differed among themselves, the last pair being little more than simple flaps. Comparisons of extant species enable a generalised pattern to be determined for each limb and such are shown in Fig. 5. Limbs 3, 4 and 5 bore flap-like exopodites laterally and a swollen epipodite also arose laterally from each limb. A horizontal slice through the mouthparts and trunk limbs is shown in Fig. 6. The proximal portions of the second to fifth pairs of limbs extended as small gnathobases into the median food groove (Fig. 4). This was of great functional significance: remotion (posterior swing) of the limbs result-

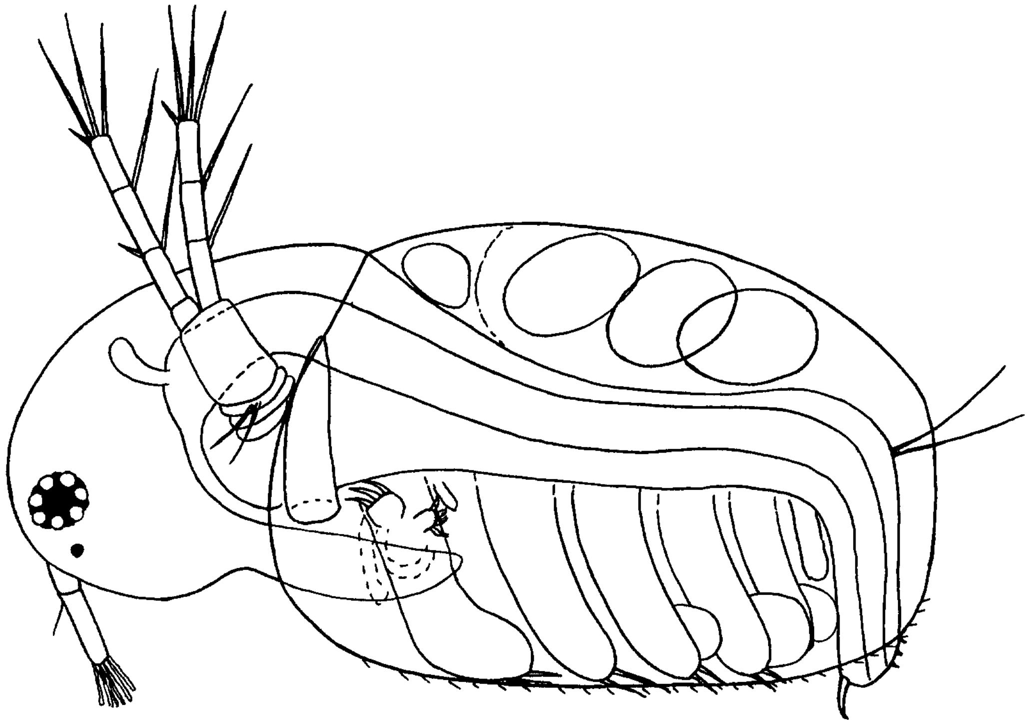


Fig. 1. The ancestral anomopod, lateral. The carapace is shown as if transparent. The trunk limbs are shown as simple outlines only: epipodites are omitted. For details, see Fig. 3.

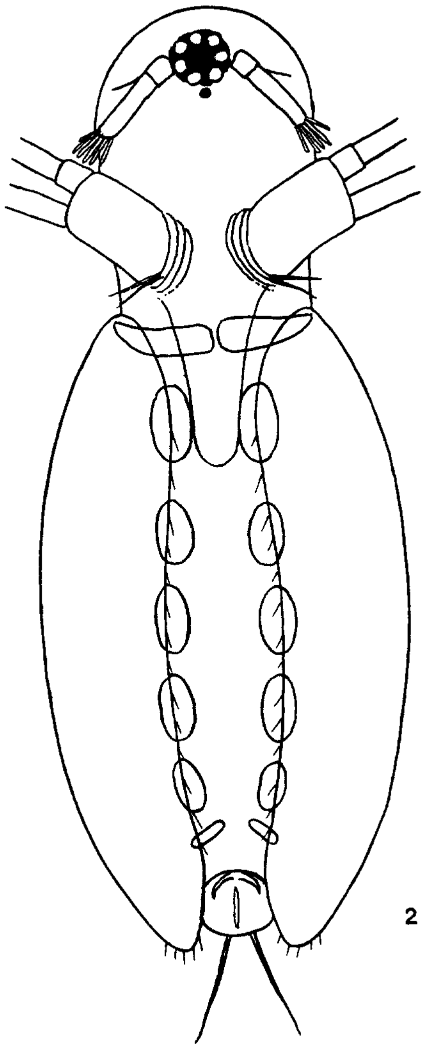
ed in promotion (anterior swing) of the gnathobases which were concerned with the forward movement of food material.

The posteriorly-facing mouth opened into a short, muscular oesophagus that curved dorsally to open into the wider mid-gut which extended into the head. Apart from the necessary sinuosity to curve towards the trunk and, posteriorly, to accommodate the flexure of the proto-postabdomen, the mid gut passed directly from the head along the length of the trunk. There were no convolutions. Anteriorly a pair of simple caeca arose from the mid-gut and extended anteriorly.

From close to its anterior origin the carapace was free from the trunk, leaving a dorsal space which was already used as a receptacle for eggs, both parthenogenetic and sexual. Parthenogenetic eggs were already produced, though precursors of the ancestral anomopod produced only eggs that required fertilization, which probably underwent diapause. This is typical of many primitive extant branchiopods though there have been a few experimental departures, e.g. in species of *Artemia* (Anostraca). All extant Spinicaudata and Laevicaudata except *Cyclestheria* produce only fertilized resting eggs, which they protect beneath the carapace, though not (except in *Cyclestheria*) in a dorsal brood pouch as is the case in the Anomopoda. *Cyclestheria* exemplifies the independent acquisition of the ability to reproduce by parthenogenesis, an ability that was also acquired independently by the Anomopoda and other 'cladoceran' orders. Development of both parthenogenetic and sexual eggs was direct, the nauplius larva having been eliminated from the life cycle.

As in modern anomopods, whether parthenogenetic or sexual eggs were produced was dependent on ecological conditions. Sexual (resting) eggs were produced in small clutches whose number was not fixed, as is still the case in such primitive macrothricids as *Acantholeberis* and *Ophryoxus* and primitive chydorids such as *Eurycercus* and *Saycia.* Little or no modification of the carapace took place for the reception of resting eggs save perhaps for the laying down of a thickened dorsal ridge, but the moulted carapace was used as a container for such eggs and formed a primitive ephippium (or proto-ephippium), a structure diagnostic of the Anomopoda. The thickened dorsal ridge acted as a spring which pulled the valves together when the carapace was moulted and secured the eggs within, offering a measure of protection.

Small secondary sexual differences were apparent. The first trunk limbs played only a minor part



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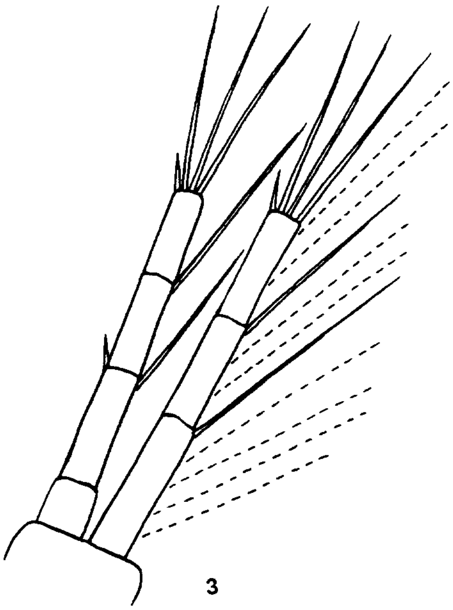

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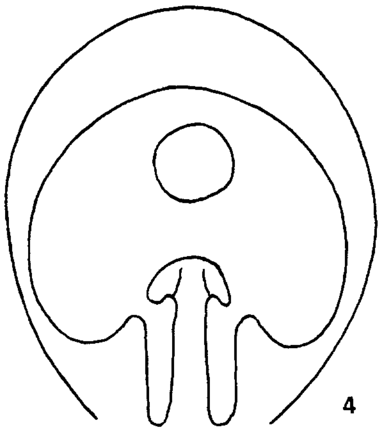

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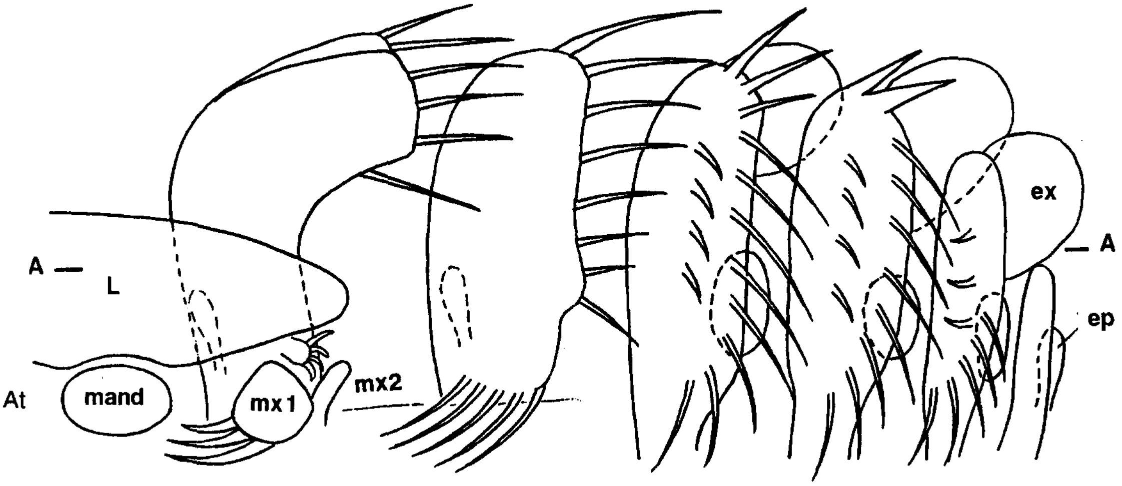
Fig. 2. The ancestral anomopod, ventral. Only the positions of the trunk limbs are indicated. *Fig. 3.* Antenna. Dashed lines on the exopodite indicate the possible presence of additional setae, such as were present in certain Early Cretaceous members of the chydorid line. Whether these are indicative of the ancestral state or of an experiment in that lineage remains unproven. *Fig. 4.* Diagrammatic transverse section through the trunk and a pair of limbs, showing the trunk/limb union and how the gnathobasic spines extend into the food groove and how, when the limbs remote, the gnathobase promotes.

in food collection, were not particularly specialised for other functions, were conveniently located, and acquired simple hooks in the male that helped it to grasp the female. The vasa deferentia opened on the post-abdomen, that resembled that of the female. From such a generalised anomopod it is possible to derive all extant forms including such different animals as *Daphnia, Bosmina, Eurycercus, Pseudochydorus, Graptoleberis, Ilyocryptus* and *Lathonura*, to mention only a few of the many widely divergent genera of all families. That these derivations are based on perfectly feasible morphological transformations, not only of individual appendages but of entire, and complex, mechanical arrangements, gives one confidence that the reconstruction is realistic and that it serves as at least a first approximation of what the ancestral anomopod was like. Furthermore the trends that can be recognised are not based on structure alone: recently acquired knowledge of the functional morphology and ecology of many very different anomopods makes it possible to see how one mechanism could be transformed into or derived from another and to correlate the transforma-



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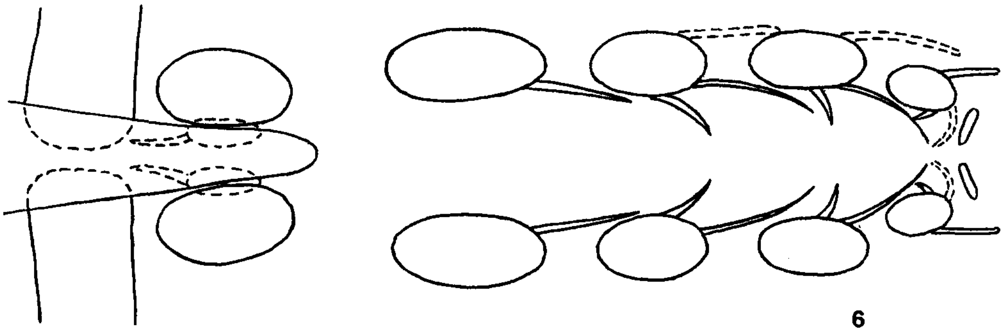

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Fig. 5. The ancestral anomopod. Arrangement of the trunk limbs, medial aspect, with the labrum bisected longitudinally. At = atrium oris; mand = Mandible; mx 1 = Maxillule, mx 2 = Maxilla; ex = exopodite; ep = epipodite; L = labrum. *Fig. 6.* The same. Horizontal slice through the trunk limbs at about the level indicated by A–A in Fig. 5, ventral. The exopodites of trunk limbs 3 and 4, as they appear more ventrally, and a gnathobasic spine of trunk limb 5 as it appears more dorsally, are indicated by dashed lines. Although the sixth trunk limbs are dorsal to the level of the section, their position is indicated, as are the more dorsally lying maxillules (shown by dashed lines) and parts of the mandibles.

tions with shifts in ecology and behaviour. They also make it possible to suggest not only how the ancestral anomopod was constructed but how it worked at the mechanical level – which in these animals is a supremely important level. Only fossil finds can verify or modify these deductions. The sort of transformations that have taken place during the evolution of trunk limb 5, which assumes diverse forms, are shown in Fig. 9 as an example of how continuity was maintained from the ancestral condition. Transitions in limb 4, whether to the basic macrothicid/chydorid type or the daphniid type with its enormous filter – are even easier to envisage.

Habits were essentially benthic. Orientation was horizontal and locomotion was by swimming, usually in short bursts, using the antennae for propulsion. Whenever the antennae ceased to beat the animal sank to the adjacent bottom and there rested on the ventral margins of the carapace. Balance was not very efficient but was facilitated by the gape between the carapace valves and the width of the carapace and was perhaps assisted at times by the outstretched antennae, though these were generally held clear of the bottom and directed somewhat anteriorly and dorsally as well as being extended laterally.

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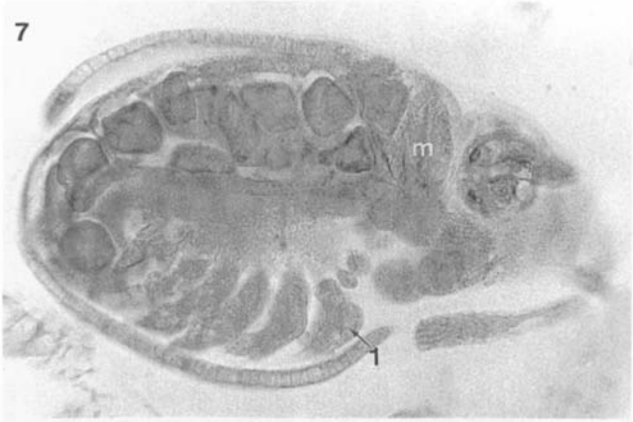

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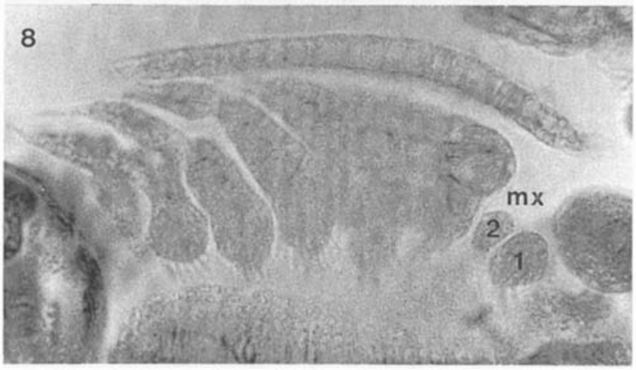

Fig. 7. Median longitudinal section of an embryo of *Acantholeberis curvirostris* showing the presence of a well-defined maxilla between the maxillule and first trunk limb. m = mandible; 1 = trunk limb one. *Fig. 8.* The same, other side, more highly magnified. For ease of comparison Fig. 7 is shown dorsal side uppermost; Fig. 8 ventral side uppermost. mx 1 & 2 = maxillule and maxilla respectively.

In a settled individual the tips of the first three pairs of trunk limbs lay in close proximity to the substratum. Those of the first pair may have been used occasionally for grasping objects, which would assist balance or anchorage, but were not specialised for this. By simple promotion and remotion, assisted by some flexure and extension, the distal spines of each would reach and scratch the substratum and, on remotion, sweep coarse particles posteriorly and dorsally. Further transport of these particles was assisted by suction set up as trunk limb 4 drew away from limb 5, thereby expanding the interlimb space 4/5 towards the end of promotion, to be followed by limb 3 that enlarged interlimb space 3/4, a process that continued as limb 5 began remotion before limb 4. Suction was greatly enhanced by the flap-like exopodites of limbs 3, 4 and 5 which formed a simple pump, later to be modified in different ways in different lineages.

Trunk limb 2 had already acquired a uniseriate row of spines that extended from its tip to more proximal regions. These spines helped to sweep particles dorsally. Particles collected and drawn in by these various means were then trapped in a cage made up of rows of spines, borne on the inner posterior faces of limbs 3, 4 and 5. The rudimentary sixth limb helped to block the posterior end of the cage. Although coarse-meshed, the cage contained the precursors of a filter-feeding device, but true filter-feeding did not occur, and very fine particles could not be retained. The orientation of the cage-forming spines ensured that collected material passed dorsally as well as posteriorly, and, assisted by more anteriorly located spines on the inner faces of limbs 3 and 4, ultimately arrived within the food groove. Passage forward was ensured by the spines of the simple gnathobases of limbs 3, 4 and 5 which swung anteriorly as the limb remoted, as with greater effect did the more elaborately armed gnathobasic region of limb 2 that showed specialisation in this respect from an early stage in evolution, and swept material towards the maxillules which assisted its passage to the mandibles that operated in the basic branchiopod manner.

Adaptive radiation and anomopod phylogeny

Macrothricidae

Of extant anomopods the Macrothricidae retains the most primitive features. I originally thought that the primitive macrothricid was probably a filter feeder, and we now know that true filters, remarkably similar to those of modern branchiopods, had evolved in small arthropods even by early Cambrian times (Butterfield, 1994). The most likely owners of these filters were branchiopod crustaceans. Nevertheless, subsequent studies and comparisons lead me to conclude that several species of the Macrothricidae probably never acquired the ability to filter. In this they differ from non-filter feeding chydorids in which this condition represents a secondary loss. It is much easier to envisage the evolution of the trunk limbs of macrothricids such as *Streblocerus* and *Drepanothrix* from the postulated ancestral condition by reduction and specialisation for grasping and pushing, in minute animals that retained the ancestral benthic habits, and continued to move by means of large antennae, than via the development of filters and their subsequent loss. Likewise it is difficult to see how the substratum-hugging *Lathonura* could have been derived via a filter feeding stage, but its morphological specialisations can be

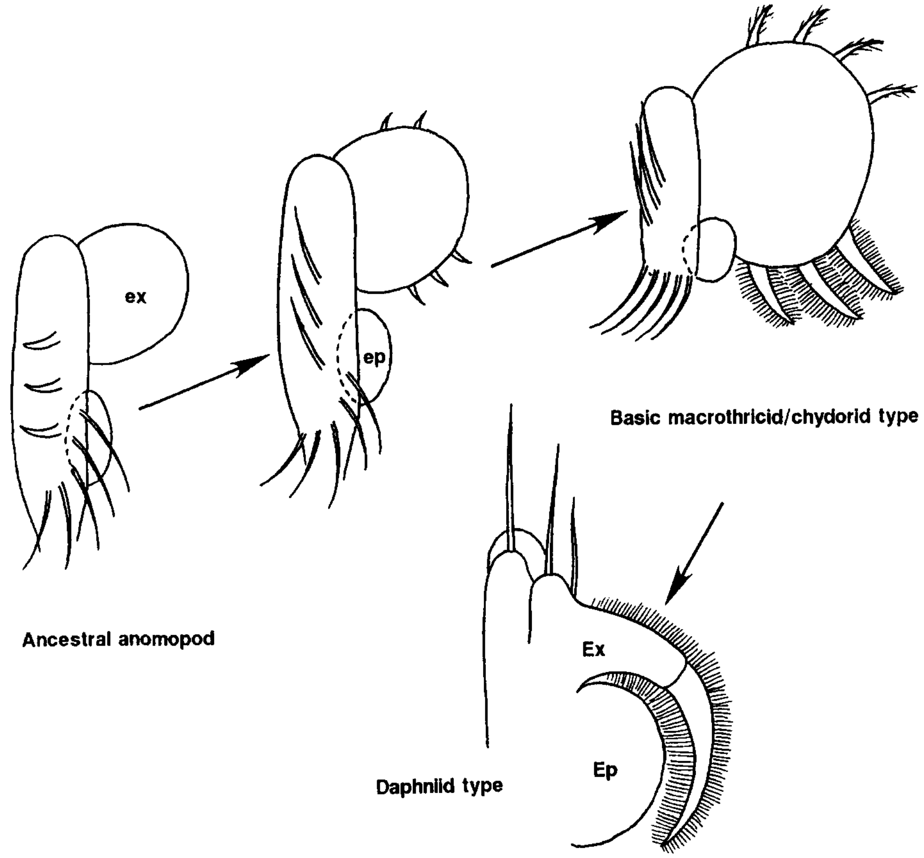

Fig. 9. Transformations of trunk limb 5 from the condition in the ancestral anomopod to that of modern families.

understood if derivation was direct from the condition postulated for the ancestral anomopod.

All macrothricids retain the ancestral association with the bottom or, in a few cases (*Iheringula*, *Macrothrix triserialis*, *Bunops*, *Onchobunops*) with vegetation. Some (*Ilyocryptus*, *Neothrix*) have become specialised burrowers, and others (*Streblocerus*, *Drepanothrix*) readily penetrate flocculent deposits. Most species swim for short distances only but *Ophryoxus* has become a more persistent swimmer, though still over the bottom.

Modifications of the ancestral arrangement of limbs are related to changes in habits, which are reflected in many other morphological features. Primitively the tips of trunk limbs 1 to 3 (and possibly 4) were involved in scratching and sweeping food from the substratum, but limbs 3 and 4 gradually became specialised for dealing with the material so collected and ceased to be involved in food collection. While trunk limb 1 continues to contribute to this process in a few cases (*Acantholeberis*, *Streblocerus*) this role was generally taken over largely or entirely by limb 2, whose armature of spines became more specialised and in many cases developed into a row of scrapers whose form is intimately related to the circumstances in which food is collected. This left the first trunk limbs free to take on other functions, e.g. grasping in *Onchobunops*, or organs of true locomotion, primitive in *Ophryoxus*, more specialised in *Macrothrix triserialis* and *Lathonura*. Limbs 3, 4 and 5 became specialised for handling the material collected by the anterior limbs and were modified in many different ways. Trunk limb 6, originally serving to close the posterior exit from the chamber formed by the trunk limbs, was in most cases eliminated and this role was assumed by limb 5 that, primitively, served a basically similar function to limb 4.

The primitive arrangement of the armature of limbs 3 to 5 was such that it formed a cage that retained collected material. A major, and probably very early, trend was the conversion of the posterior row of spines of these limbs into filter setae, which also called for improved efficiency in the exopodite pump that drew water through the sieve so formed. In several, but not all, cases where filter feeding was adopted, trunk limb 5 ceased to contribute and filtration was concentrated on limbs 3 and 4. In the super-specialised *Ilyocryptus* filtration became so effective that the animal can subsist purely by this process, no scraping by trunk limb 2 being necessary, and that limb has lost its primitive function of food collection (and its armature of scrapers). Trunk limb 1 has also become specialised to provide a screen that excludes the ingress of coarse particles to the filter chamber. These developments went hand in hand with improvements in the gnathobases of the limbs that pass food forward, this being especially the case in trunk limb 2 that came to play a major role in this process.

At the same time, many other changes occurred in different macrothricids. These included diversification of the shape of the carapace, sometimes the development of a headshield, or coiling of the gut, or flexing of the antennae, elaborations of the postabdomen, specialisations of the still primitive ephippium, and other morphological changes, as well as physiological specialisations that led eventually to such abilities as the toleration of strongly acidic conditions (*Acantholeberis*) or of low oxygen levels via the development of haemoglobin (*Ilyocryptus*).

Daphniidae

The daphniid feeding mechanism (Fryer, 1991b) can easily be derived from that of a generalised macrothricid by the expansion of the filtering area of trunk limbs 3 and 4, and improvements in the pumping mechanism, which involves exopodites 3 and 4 and modifications of trunk limb 5 to form a seal. These developments obviate the need to collect particles by scraping and enable them to be obtained entirely from suspension. Furthermore, an extant macrothricid, *Ophryoxus gracilis*, provides a clear indication of the route whereby the Daphniidae arose from the macrothricid stem. *Ophryoxus* is the most persistent swimmer of all the studied macrothricids and its antennae are very similar to those of *Daphnia* (which have an extra exopodite seta). What is more, *Ophryoxus* sometimes swims along vertical objects, its orientation then being the same as that typical of *Daphnia*. It is also a filter feeder (though its feeding mechanism involves scraping) and is one of the macrothricids that has acquired a headshield. It is also, as it happens, the only macrothricid whose alimentary canal has daphniid-like anterior caeca. While not the direct ancestor of modern daphniids, *Ophryoxus* nevertheless throws much light on that ancestry. In essence, if one turns it through 90 ° and changes its feeding mechanism to filtering with trunk limbs 3 and 4, with no preliminary scraping one has a basic daphniid. Such an origin of daphniids explains the large postabdomen, whose derivation is from a structure that served for pushing in their benthic ancestors, but not from one so specialised as to have acquired an articulation.

Adaptive radiation within the Daphniidae has been considerable, but into fewer niches than have been exploited by either the Macrothricidae or Chydoridae. Specialisations include association with the surface film (*Scapholeberis* and *Megafenestra*), filtering while attached to objects (*Simocephalus*), and especially emancipation from the bottom, (*Moina*, *Ceriodaphnia*, *Daphnia*, *Daphniopsis*). Open-water living has led to a truly planktonic lifestyle in at least some members of all the genera that practise it. The exploitation of different size ranges by *Daphnia* and *Ceriodaphnia* has helped to partition resources in what is superficially a uniform habitat. There have also been physiological specialisations, including tolerance of waters of high ionic concentration (especially *Daphniopsis* and several species of *Moina*), and modifications of the reproductive process have been exploited, including obligate parthenogenesis by certain species of *Daphnia*.

Chydoridae

The Chydoridae, with which for the time being I include Smirnov's Prochydoridae, has retained the ancestral association with substrata. Such habits offer the greatest opportunities to the anomopod Bauplan and the Chydoridae has acquired an enormous range of specialisations. Association with bottom deposits or vegetation and the exploitation of scrambling, and especially crawling, of which the family has many specialist exponents, has enabled chydorids to develop thicker carapaces than those of macrothricids – or of daphniids where this trait is incompatible with efficient persistent swimming and has been exploited only to a minor extent in the semi-sedentary *Simocephalus*. Thicker carapaces have in turn facilitated elaboration of their ventral margins which display a wide range of modifications related to association with substrata, some of them exceedingly complex. In the most specialised case, that of *Graptoleberis*, which glides over surfaces like a minute snail, mechanical integration between the structures concerned and the surfaces with which they make contact achieves a level of intricacy that can have few rivals in the animal kingdom.

A thickened cuticle, besides being well-suited to a benthic existence, offers protection against predators, which has been exploited to a striking extent in *Pseudochydorus*, and in a remarkable manner as protection against the nematocysts of *Hydra* by *Anchistropus*. A novel way of obtaining protection, achieved by *Alonopsis elongata* and *Monospilus dispar*, is retention of one or more carapaces after the moult. In the case of the former, an individual seized by a small predator, such as a cyclopoid copepod, can slip out of the old carapace and escape. Remarkable cuticular elaboration, unique to chydorids, has arisen in the so-called honeycombed species of *Chydorus*, of which the most detailed account is given by Frey (1987).

Chydorids have reduced the size of their antennae, which beat rapidly when swimming is necessary, and both rami are reduced to three segments. They have also exploited the basic anomopod trunk limb arrangement in a variety of ways and their feeding mechanisms are diverse. Most are particle feeders, many of which employ filtration, and as many as four pairs of limbs may bear filters. In several genera of different subfamilies, not only are filters borne on limbs 3, 4 and 5, but the gnathobase of limb 2 is filtratory, examples being found in *Eurycercus*, *Alona* and *Chydorus* to mention only three genera. Filtering may, however, be restricted to only two pairs of limbs. For example, in *Alonopsis* filtering is carried out largely by trunk limb 3, with a minor contribution from limb 4. Particles to be filtered are first collected by scrapers borne on trunk limb 2, assisted in some cases (e.g. *Alonopsis elongata*, *Alona affinis*) by distal spines of trunk limb 3.

Some chydorids have abandoned filtration. In the case of *Leydigia*, this is clearly a secondary loss, elements of a filter feeding mechanism being employed. The functional series that leads to the super-specialised *Graptoleberis* also suggests derivation from filter-feeding ancestors, as do certain morphological features, though the mechanism has been drastically modified during the course of its evolutionary history. Morphological considerations also suggest that *Pseudochydorus* (a scavenger) and *Anchistropus* (a parasite of *Hydra*) are derived from filter feeding ancestors. It therefore seems likely that the chydorid line was derived from an ancestral filter feeder.

Of all anomopods the Chydoridae has most fully exploited the potential of the postabdomen whose efficiency in levering, and sometimes its use in ways unknown in other families, has been enhanced by the acquisition of a true articulation between it and the trunk.

Chydorid organisation has permitted the colonisation of habitats inaccessible to other anomopods. Most remarkable has been the exploitation of moisture-holding clumps of bryophytes in wet forests. For life in the thin film of water present in such sites *Bryospilus* has short antennae, no longer used for swimming, of which it is incapable, and is a slow-moving crawler that has lost the compound eye but retains the ocellus (Frey, 1980). Chydorids have also colonised groundwaters, a logical extension of benthic habits. Of the few known species of such habitats *Alona phreatica* has lost the ability to swim and locomotion is restricted to crawling or scrambling (Dumont, 1983). *A. smirnovi* from L. Ohrid also appears to be of interstitial habits, having been found among sand on a beach, and perhaps frequents subterranean springs that debouch there. Its compound eye has lost its pigment (Petkovski & Flössner, 1972). *A. hercegovina* is a true cave-frequenter and has lost the compound eye and the pigment from the ocellus (Brancelj, 1990).

A specialisation of many chydorids (but not of the most primitive) is that they have reduced the clutch and brood size to two, implying a heavier investment per offspring than is usually the case in other anomopods – perhaps exploiting the protection conferred by a more robust carapace? The evolutionary trend in the chydorids has not been towards increased fecundity – and runs counter to theories which claim that to maximise fecundity always has selective advantages – but the implications of the situation remain to be explored (see discussion in Fryer, 1988).

Smirnov's (1992) recent discoveries show that animals similar in many respects to modern chydorids were abundant in Early Cretaceous times. The general arrangement of the headshield, carapace and antennae, both of whose rami had three segments, was remarkably similar to that in modern forms. As to be expected, the mandibles were, like those of modern chydorids, of the typical branchiopod type, and the post-abdomen, of which details are vague, certainly terminated in two spines like those of modern forms. The extra antennal setae, one of the distinguishing features of these animals, may indicate that they tended to swim over bottom deposits rather than scramble or crawl. Conditions in some of these fossils are interpreted by Smirnov as indicating that the gut was not convoluted. If this was so, it represents the retention of an ancestral feature not seen in any extant chydorid. It is, however, difficult to recognise the gut in most of the fossils and it is possible that both the convoluted and non-convoluted condition prevailed in different species. Additional evidence is needed. A coiled gut is a specialisation of extant chydorids. Bottom- or vegetation-frequenting detritus eaters often collect large quantities of low quality food and often much indigestible material, including even inorganic particles. A coiled, and therefore extended, gut is advantageous here, and any increase in density (probably slight) so acquired is no burden and may even be advantageous. Open-water forms, such as daphniids, usually feed on more nutritious material, including living algae, and have less need of a long gut, which would be an inconvenience to animals that have to combat a continuous tendency to sink. They have also developed certain specialisations that improve the efficient utilisation of what is collected (Fryer, 1970). (Macrothricids display both trends. Some retain a primitive condition: others, such as *Drepanothrix dentata*, have a specialised, coiled gut.)

Bosminidae

The Bosminidae arose from a chydorid-like ancestor that, like the Daphniidae, adopted an open-water way of life based on persistent swimming and the filtration of suspended particles. The dichotomy evidently arose before the Chydoridae had lost one antennal segment from the exopodite as the importance of swimming declined. Ancestry is clearly revealed by the trunk limbs. While a statement that bosminids can be regarded as swimming chydorids that have adopted true filtration carried out predominantly by trunk limb 3 is much too crude, it has useful descriptive value and contains a considerable element of truth.

Apart from a pioneer effort by Graf (1930), which established certain points but left some problems unanswered, no real attempt has been made to describe the feeding mechanism of bosminids, of which certain specialisations remain unrecorded. Early statements by Naumann (1921) are incorrect, and while DeMott (1982, 1985) and DeMott and Kerfoot (1982) have produced some useful information, certain functional details have yet to be described. It is, however, clear that an enormous expansion of the filtering surface of trunk limb 3 has been the key to their success as filter feeders. Morphological relics of former scraping by trunk limb 2 in the chydorid manner remain. DeMott and Kerfoot (1982) and DeMott (1985) have emphasised the use of these spines in, as they put it, seizing and manipulating individual algal cells, and regard *Bosmina* as having a 'dual option' feeding mechanism. However, these spines can only manipulate material that has been brought into the filter chamber by currents. They do not collect any material themselves and therefore do not add to the diversity of food collected. *Bosmina* is purely a suspension feeder. That it preferentially retains algal cells rather than bacteria is interesting, but this does not mean that it can collect the former independently of the filtering process. DeMott's demonstration (1982) that it took *Chlamydomonas* and *Aerobacter* from a mixed suspension but hardly removed the latter from a pure offering is explained by the fact that it *had* to take some *Aerobacter* in order to obtain *Chlamydomonas* (which it readily removed from a pure culture), but when offered *Aerobacter* alone, it either let it pass through the filter chamber or, more likely, simply stopped pumping. Respiration-wise, *Bosmina* can probably afford not to pump for long periods. Several benthic macrothricids and chydorids meet their respiratory demands in situations that are often less well oxygenated than those frequented by *Bosmina* without pumping (some have no pump), or by very occasional pumping. Even the actively pumping globular *Chydorus sphaericus* can close up its carapace completely as a defence mechanism and so remain for at least 2 hours while a predatory cyclopoid copepod attempts to gain access.

Possession of delicate cuticle and the lack of association with substrata have granted both daphniids and bosminids freedom to modify external shape to a degree denied to the benthic macrothricids and chydorids. As well as much experimental divergence in form in both families, the adaptive significance of which in many cases remains to be explained, both have been able to exploit cyclomorphosis, which has various ecological advantages.

Phylogeny

Figure 10 shows in a simple manner the suggested phyletic relationships within the Anomopoda. To refine this by including subfamilies (as which the Moininae is here regarded) is best delayed until the taxonomic arrangement has been more precisely analysed. It is, however, already evident that, for example, the Eurycercinae belongs nearer to the base of the chydorid stem than other subfamilies and that what may eventually be defined as the Prochydorinae also belongs near to the base of this lineage so far as it is yet known. As for the early origins of the Anomopoda,

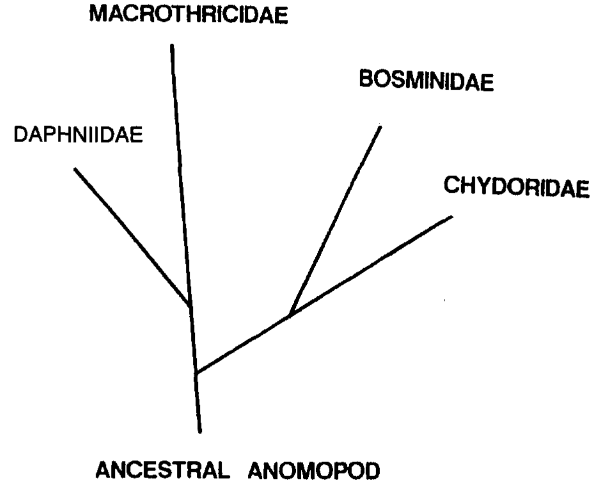

Fig. 10. A suggested phylogeny of the Anomopoda. For comments see text.

these clearly lie far back in time. Discoveries such as the chert-entombed *Lepidocaris* of the Devonian, the phosphatised microcrustaceans of the Cambrian Orsten deposits, and minute fragments, including filters, even in the early Cambrian, give grounds for hope that actual remains of early anomopods or their relatives may yet be found.

Factual information on which much of this analysis is based is presented in Fryer (1963, 1968, 1970, 1972, 1974, 1987b, 1991b).

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