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Morphology and Systematics of early Arthropods*

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With 14 figures

Inhalt

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Abstract: The systematics and evolution of arthropods are discussed, particularly on the basis of the morphology of various Palaeozoic groups. Uniramians are considered as a distinct phylum. Fragmentary Cambrian arthropods may represent marine, well sclerotized myriapod-like uniramians. The Middle Cambrian *Aysheaia* lacks jaws and antennae and is not a representative of the Onychophora. Arachnomorphs and crustaceans must have had a similar origin in animals with branched limbs and less dependence on crawling than the uniramians. As similar basic adaptations logically should give a parallel evolution of morphological characters it is hard to tell whether the similarities between arachnomorphs and crustaceans are due to phylogenetic relationship or to adaptational parallelism. The terms Schizoramia and Biantennata appear useful for separate arachnomorph and crustacean phyla. If crustaceans prove to belong together with the arachnomorphs they may be included in the Schizoramia. A characteristic feature of undoubted aquatic arachnomorphs is the flattened lamellar spines of an outer limb branch. Important features for recognozing fossil crustaceans are the crustacean-type carapace and the uropods (including the furcal rami), the latter found in almost all extant crustaceans. Various crustacean groups were represented already in the Cambrian. Many arthropods cannot be placed in any particular group. In cases this is apparently due to poor knowledge of the morphology, whereas in other cases, like the Middle Cambrian *Opabinia*, there may be representatives of groups approaching an arthropod level independently.

A. Introduction

Recent arthropods fall into a number of well defined groups like the hexapods, crustaceans and arachnomorphs. As distinguishing characters are present in the exoskeleton, it would be supposed that most fossil arthropods would also be easily classifiable into large and easily recognized groups. It would also be suspected that extinct groups would elucidate the phylogeny of the arthropods. However, this is only partially the case. There is a lot of mainly Palaeozoic "trilobitomorphs" and other odd arthropods which have been notoriously difficult to place systematically and which tend to confuse rather than elucidate the phylogenetic picture. The isolated position of many of these arthropods indicates that only a small fraction of the Early Palaeozoic phyletic lineages are known. An understanding of the difficult fossil groups and of the early phylogeny of the arthropods needs more data for comparative anatomy and also new types of considerations.

B. Basic division of the Arthropoda

The segmented body and articulated appendages, the exoskeleton and other widely spread structures such as the compound eyes, malpighian tubules, tracheae and mandibles have long been thought of as proof that the arthropods constitute a phylogenetically homogeneous group. The only problem was thought to be the pararthropods, protarthropods, lobopods or what they have been called, the small groups with characters somewhat intermediate between those of annelids and arthropods. However, TIEGS & MANTON (1958) and recently MANTON (1972) from a study of functional aspects suggested that arthropods can not be derived from a single common arthropod ancestor. The onychophoran - myriapod - hexapod assemblage form one unit, particularly characterized morphologically by uniramous appendages and whole-limb jaws. This assemblage was called the Uniramia. Other arthropod groups have originally branched appendages with the ability to form gnathobasic jaws. These are the arachnomorphs and the crustaceans. I have been urged to replace the cumbersome term Arachnomorpha with something lighter, and my suggestion is Schizoramia (BERGSTRÖM 1976), which matches Uniramia. The Schizoramia could be construed to include both arachnomorphs and crustaceans, if these groups are considered as belonging together, or the crustaceans may be contained in a separate phylum Biantennata (a term suggested to me by Professor ERIK DAHL, Lund. This term is superior to Diantennata as *bi-* means *two-*, but *dis-* has the meaning *in parts, separate*.)

ANDERSON (1973: 454-471) presents strong embryological support for the unity of the Uniramia and for its relationship with the Annelida. The Crustacea form a fairly uniform group with embryological characteristics which place them well apart from the Uniramia - Annelida. The chelicerate schizoramians are embryologically unique, but a relationship with annelids or crustaceans can not be excluded from an embryological point of view. Several basic morphological adaptations tend to unite the Crustacea and the Arachnomorpha (HESSLER & NEWMAN 1975), and a common origin seems possible. On the other hand a parallel or convergent evolution can not be entirely excluded as there obviously are immense potentialities in the animal kingdom to acquire repeatedly identical or almost identical solutions to adaptational evolutionary problems. MANTON (1964: 100) stated that the differences in function between merostome and crustacean gnathobases must mean that the gnathobases were independently acquired as a parallel evolution. There is no need to see this as a definite argument against an arachnomorph - crustacean affinity as defended by HESSLER & NEWMAN (1975: 454). Indeed, the probable absence of gnathobases in *Mimetaster* may indicate that gnathobases were acquired at a comparatively late stage in the evolution of the schizoramians (STÜRMER & BERGSTRÖM 1976).

In principle it would certainly be possible to derive uniramous articulates from schizoramous forms. However, it is impossible to derive simple lobopodial animals like tardigrades and *Aysheaia* with a primarily terminal mouth and without jaws or antennae from schizoramous trilobitomorphs or crustaceans with corresponding features apomorphically changed. A separate origin of some uniramous (lobopod) forms thus is unescapable. It appears simpler to derive all the Uniramia from this inescapable group (or from a similar origin) than to derive some of them from schizoramians. A particular difficulty with an intercalation of schizoramians between annelids and uniramians is that the two latter groups have (plesiomorphically ?) similar embryology, whereas the known embryological development in schizoramians appear to be apomorphically strongly drifted (ANDERSON 1973). The differences may be due to discontinuous morphological steps in the evolution of embryology and not necessarily to so different origins as postulated by ANDERSON (see FRYER 1976 for discussion and examples of steps). There is no compelling reason to see structures such as compound eyes, antennae and jaws as homologous throughout the Arthropoda, not even if they are situated in corresponding segments. The evolution of these structures is only logical, as well as the anterior position. Cases of convergent evolution are so common among animals that we should be very careful. It may be instructive to hint at the well known evolution of brachiopods, where for instance a calcareous shell developed independently at least four times, a skeletal support for the lophophores at least three times, cementation to the substrate at least four times, and formation of caeca for storage purposes in the shell at least six times, just to mention a few examples (RUDWICK 1970). An example of striking convergent evolution among arthropods is found among the malacostracans, where most groups have a carapace, stalked eyes and thorax segments distinctly shorter than the abdominal segments. Independently in three groups, however, there has been a reduction of the carapace and the eye stalks and a lengthening of the thoracic segments. These groups are the Isopoda, Amphipoda and Syncarida. Among the Syncarida only the Koonungidae have finished the trend, whereas various intermediate stages are found in the Anaspididae and among fossil representatives. Without taking function into consideration it would seem almost impossible that such a combination of characters would result from convergent evolution. Thus it should come as no surprise if vital basic needs had caused the formation of widely spread organs such as antennae and jaws not once but several times. The Onychophora form one proof that at least jaws actually have been formed more than once, and the step from accepting this twofold formation to a possibility of a threefold or manyfold development is really very small.

The pantopods and linguatulids are definitely advanced arthropod groups, but far-reaching specialization and simplification makes it difficult to place them without question in any of the main arthropod groups. The tardigrades take quite another position. The lack of true chitin and of any kind of specialized limbs in the head, particularly in connection with the terminal position of the mouth, indicate that they are on a truly pre-arthropod or at the most initial arthropod evolutionary level. It is possible that they are in some way related to the uniramian group, but this is by no means proven.

C. Basic morphology and habits in uniramians and schizoramians

MANTON (1972) characterized the initial uniramians as "ancestral multilegged, soft bodied arthropods with lobopodial limbs, manipulating food (incipient biting) by the tips of future jaws, contrasting with the Chelicerata and Crustacea, each of which possess a different type of sclerotized gnathobasic jaw and different type of biramous limb". Modern uniramian groups are all terrestrial and go back to the Silurian (Myriapoda) and Devonian (Hexapoda). The primary groups must have been aquatic, and the almost total lack of knowledge of those groups is very frustrating. Anyhow, MANTON's description is reasonable. The animal as described was clearly not adapted to swimming habits but must have crawled on the bottom. The presence of lobopodial limbs suggests that the animal was not a burrower. The body was probably more or less cylindrical and worm-like.

MANTON (1973: 114, 117) believed, that uniramians left water in a soft-bodied state and that the whole-limb mandibles are an effect of land life. Another alternative, which seems more plausible to me, is the following. In arthropods with branched and more or less flattened limbs food could easily be collected behind and transported forwards to the mouth along the ventral side. This possibility was not present in an aquatic arthropod with unbranched and more or less cylindrical limbs. The food therefore had to be picked up directly from the substrate into the mouth already in aquatic uniramians. This could be done by direct mud-suction or particle selection from the mouth. A more sophisticated method would be to use at least one pair of limbs to reach the subsurface. A kind of grasping appendages on this organizational level was present in Cambrian *Aysheaia* (Fig. 13). It appears reasonable to suppose that limbs used in this way may be transformed into jaws, with the tip of the limb still being used for the handling of the food. The lack in the mandible of musculature associated with a segmentation as found in more posterior limbs may be the due to a transformation into jaws on an pre-segmental stage. The simple musculature of the mandibles in myriapods and insects therefore may have no bearing on the question of whether the jaws are whole-limb structures or not.

In contrast to the uniramians, schizoramians und crustaceans include well known aquatic groups, both living and extinct, from which ancestral characteristics may be extrapolated. HESSLER & NEWMAN (1975) extrapolated an ancestral crustacean, which is close to schizoramian conditions and makes comparison between schizoramians and crustaceans easy. The ancestral schizoramians and crustaceans, regardless of whether they were arthropodized several times or only once, appear to have had branched appendages. It is probably not correct to call the type of branching just bifid (HESSLER & NEWMAN 1975: 455), but the exact pattern is not known and is not essential to this discussion. There was probably a large labrum. The comparatively large surface of the limbs would have made swimming habits possible. The swimming may have been close to the bottom. In moving forwards, currents around the limbs and eddy currents at the edge of the labrum could not be avoided, and the ancestral schizoramians and crustaceans therefore presumably were suspension-feeders or possibly mud-eaters. This means that the food was collected behind the mouth and transported forwards to the mouth, with opened backward. The food was probably sucked in initially without the aid of gnathobases, if the absence of gnathobases in *Mimetaster* actually is a primitive feature. The branched limbs were highly adaptable, and with growing size the original mode of life could be easily modified.

The ancestral uniramians, schizoramians and biantennates were probably present well back in the pre-Cambrian. This is indicated not only by the presence of highly developed arthropod groups in the Early Cambrian but also by the diversity in the chemical composition of the exoskeleton of various groups. The sclerotization and in particular the incrustation with inorganic compounds must have occurred independently in different groups.

I. Uniramians

Living uniramians belong to three well defined groups, the Onychophora, Myriapoda and Hexapoda. Several fossil groups may be discussed with more or less reason in connection with the uniramians. These include the marine *Anomalocaris* and *Xenusion*, both (with some reservation for *Xenusion*) from the Cambrian, further the probably limnic Euthycarcinida from the Carboniferous and Triassic, and the possibly amphibious Arthropleurida from the Early Devonian and Late Carboniferous (Fig. 1).

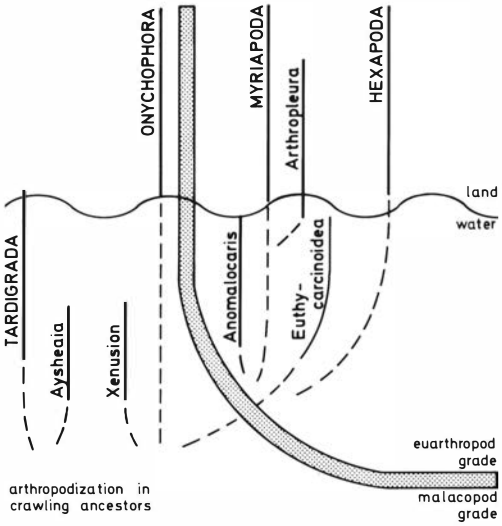

Fig. 1: Possible evolutionary relationship between some uniramous groups, including tardigrads, the similar Middle Cambrian *Aysheaia*, and the Uniramia. The boundary between the malacopod and euarthropod grades is the demarcation between groups without and those with integumental sclerotization.

1. *Xenusion*

The single specimen of *Xenusion auerswaldae* POMPECKJ, 1927 (a second specimen unfortunately was lost), is preserved in a quartzitic sandstone thought to be of Early Cambrian age (JAEGER & MARTINSSON 1967). The anterior end of the body is not preserved, which makes any discussion on its phylogenetic position hazardous. However, the general habitus is that of an onychophoran and there are no distinguishable sclerites, although the relief and cracked midline indicates that the integument may have been fairly tough.

2. *Anomalocaris*

Species of *Anomalocaris* may be sorted in two groups (Fig. 2). In one, including *A. canadensis* WHITEAVES, 1892, *A. cranbrookensis* RESSER, 1929, *A. pennsylvanica* RESSER, 1929, and others, perhaps also the large *A. gigantea* WALCOTT, 1912, the "body" is a segmented and typically curved structure with spines on the concave side. In some cases it can be seen that there are two spines on a segment.

ROLFE (in MOORE 1969: R 323 and Fig. 149:2) considered this type as possibly the body of the crustacean *Tuzoia*. However, the structures have no particular similarity to the body of any arthropod, and in particular the stout and stiff ventral(?) spines can not readily be accepted as limbs. It is also remarkable that all forms lack a head. In alternative explanation is that these anomalocarids represent the uniramian limbs of large arthropods. In this case the overall shape including the spines is comparable to the leg of *Arthropleura*. Also the legs of *Xenusion* have ventrally directed short spines.

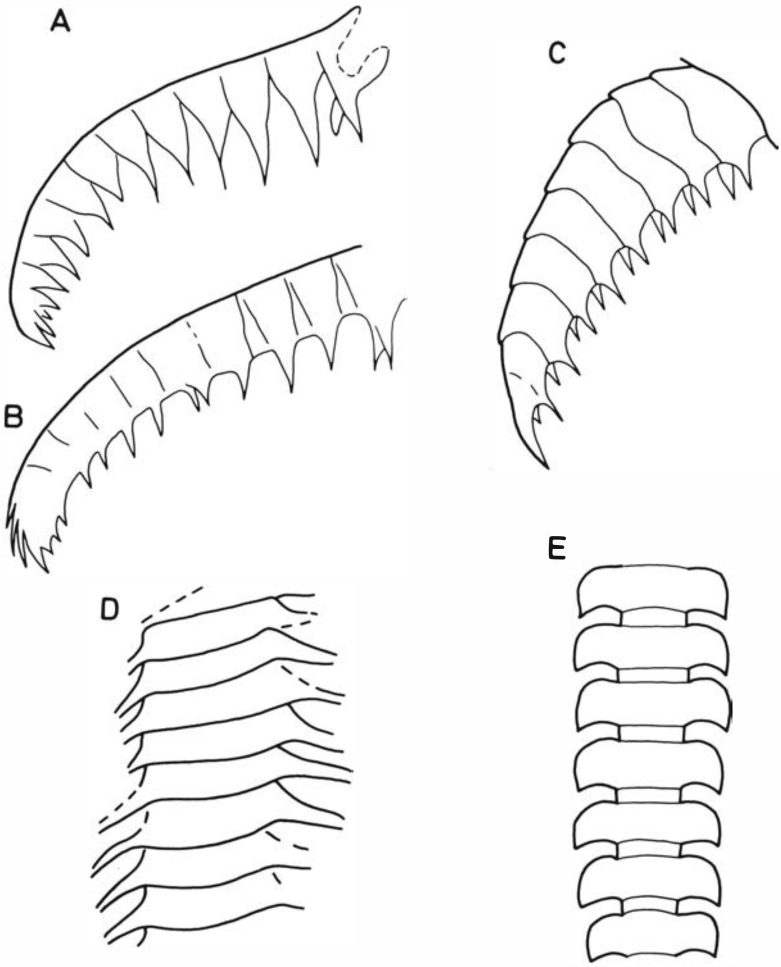

Fig. 2: A and B, leg-like remains from the Cambrian, compared with a leg of a Carboniferous myriopod, C. A, *Anomalocaris cranbrookensis*; B, *A. canadensis*; C, *Arthropleura*. D, supposed part of body of Cambrian "myriapod", *Anomalocaris lineata*, and C, part of extant myriapod *Polydesmus* for comparison. A from RESSER, B from Treatise on Invertebrate Paleontology, courtesy of the Geological Society of America and University of Kansas, C from ROLFE & INGHAM, D from RESSER & HOWELL.

While the first group of *Anomalocaris* species is asymmetric, the second group, represented by *A. lineata* RESSER & HOWELL, 1938, is probably symmetric and provided with one row of spines on each side, each sclerite carrying one spine on each side. Whereas in the first group the sclerites taper toward the concave, spiniferous side, they are of strictly even width between the spine bases in *A. lineata*. Also different from the first group the whole body is of even width at least for the length of nine or ten segments. The bilateral symmetry and even width indicates a body of myriapod appearance, and the spines may be compared to the pleura of *Arthropleura* and many myriapods. *Anomalocaris lineata* therefore may represent an at least exteriorly myriapod-like early uniramian group.

3. Euthycarcinoidea

The strange euthycarcinoids have been regarded as copepods, branchiopods, or as an independent group of crustaceans and as trilobitoids, merostomoids or possibly merostomes (RIEK 1964, 1968; MOORE in MOORE 1969: R196-199; SCHRAM 1971; these authors provide older references). All these suggestions indicate that the euthycarcinoids would have branched appendages. However, careful examination of the Triassic *Euthycarcinus* (GALL & GRAUVOGEL 1964) and *Synaustrus* (RIEK 1968) and the Late Carboniferous *Kottixerxes* (SCHRAM 1971) revealed multiarticulated uniramous legs, with a basal outgrowth in *Euthycarcinus* that was interpreted as an epipod. This interpretation seems to be doubtful. Each podomere is provided with a long seta in *Euthycarcinus* and a shorter seta or spine in *Kottixerxes*. I had the opportunity to study *Synaustrus* during a stay in Sydney in 1976. In this animal no setae are discernible, possibly due to poor preservation. The mouth-parts appear to be whole-limb jaws in *Euthycarcinus*. They are not clearly visible in the other forms. Two pairs of antennae have been reported in all three forms, but the evidence is very slight. In the holotype of *Synaustrus*, e. g., there is an anterior transverse convexity that was interpreted as the proximal part of the second antenna (RIEK 1964, Pl. 35, fig. 1). Actually, the convexity appears to be the doublure of an anterior head sclerite, which was not fused to the main head sclerite. A similar anterior head sclerite is indicated in *Euthycarcinus* (GALL & GRAUVOGEL 1964, Pl. 2, Fig. 1; Pl. 3, in particular Figs 1, 4; Pl. 5, Figs 1, 3), and *Kottixerxes* (SCHRAM 1971, particularly Fig. 3). In addition there appears to be a short but wide labral plate. In this animal at least there is a wide lateral doublure of the posterior head sclerite. The abdomen is divided in a preabdomen with legs and a postabdomen without legs but with a tail spine. Each of the preabdominal tergites covers one, two or three segments. There are no uropods, a character found in all crustaceans except the reduced myodocopid ostracodes and some adult crabs (BOWMAN 1971). The various characters are difficult to evaluate, particularly as some of them are not very safely known. The subdivision of the head tagma, the absence of uropods, the probable absence of a second antenna and the uniramian character of the appendages makes a crustacean affiliation entirely unlikely. In particular there is no similarity whatsoever between the limbs of euthycarcinids and branchiopods. Merostomes differ in having chelicerae and lacking antennae. All definite trilobitoids and merostomoids have branched "trilobite appendages" with lamellar spines and lack real jaws (although not gnathobasic processes). The general outline and the tail spine have been regarded as trilobitomorph characters. However, the outline depends for instance on the general mode of life, and a tail spine or plate is found in almost all major arthropod groups. Schizoramian affinities are therefore unlikely. The uniramian legs are indicative of uniramian affinities, if not secondarily achieved. The basal outgrowths in *Euthycarcinus* may be comparable with the peculiar B-, K- and rosette plates in the arthropleurid myriapods. The whole-limb jaws, if correctly interpreted, distinctly indicate uniramian conditions. Double and triple segments are found in the Myriapoda only and may hint at some kind of similarity, although compound segments must have been independently developed in euthycarcinoids. In balance, euthycarcinoids seem to show important similarities only with the uniramian groups and probably represent a distinct uniramian group comparable in rank with the Myriapoda and Hexapoda.

4. Arthropleurids

ROLFE & INGHAM (1967) restudied the large Carboniferous *Arthropleura* and stated that the presumed bifid legs are actually uniramous (Fig. 2 c). *Arthropleura* therefore is decidedly myriapod-like. STØRMER regarded the Early Devonian *Eoarthropleura devonica* STØRMER, 1976, definitely as a myriapod, representing the order Arthropleurida WATERLOT, 1934. The arthropleurids may have been herbivorous or possibly omnivorous, and their association with swamp deposits may indicate that they were more or less amphibious (STØRMER 1976: 113).

II. Arachnomorphs

Living arachnomorphs are the mostly terrestrial chelicerates, which have lost the branched nature of their appendages. An attempt to map the phylogeny presents different problems (Figs 3, 9). We know that the terrestrial forms must be far removed morphologically and ontogenetically from aquatic ancestors. The only extant primarily aquatic group is the Xiphosura with only a few living species. The xiphosurids and the extinct eurypterids do not represent aquatic ancestral groups for most terrestrial arachnids, and there must have been a number of unknown aquatic groups leading to the arachnids, which are first known from the Devonian (I do not consider scorpions as true arachnids as they are morphologically close only to eurypterids and apparently became adapted to a life on land later than typical arachnids). The chelicerates may also include the Cambrian and Ordovician aglaspidids with schizoramous(?) appendages. The general habitus of these and the construction of their appendages appear to prove a relationship to the trilobites and to various other trilobitomorph groups. Most of these are poorly known, commonly only from one or few species. As these are preserved due to extraordinary sedimentological circumstances part of their appendage morphology is commonly known, but we are often left with interesting hints and are unable really to see critical details. The striking diversity among arthropods classified as trilobitomorphs therefore presents large difficulties. STØRMER (1944: 133) mentioned the trilobitan appendage as one distinguishing character. He (STØRMER 1944: 119) considered the proximal (precoxal) position of the trilobite outer appendage branch an important character, distinct from the more distal position of the outer branch in crustaceans. Much stress has been laid on this dif-

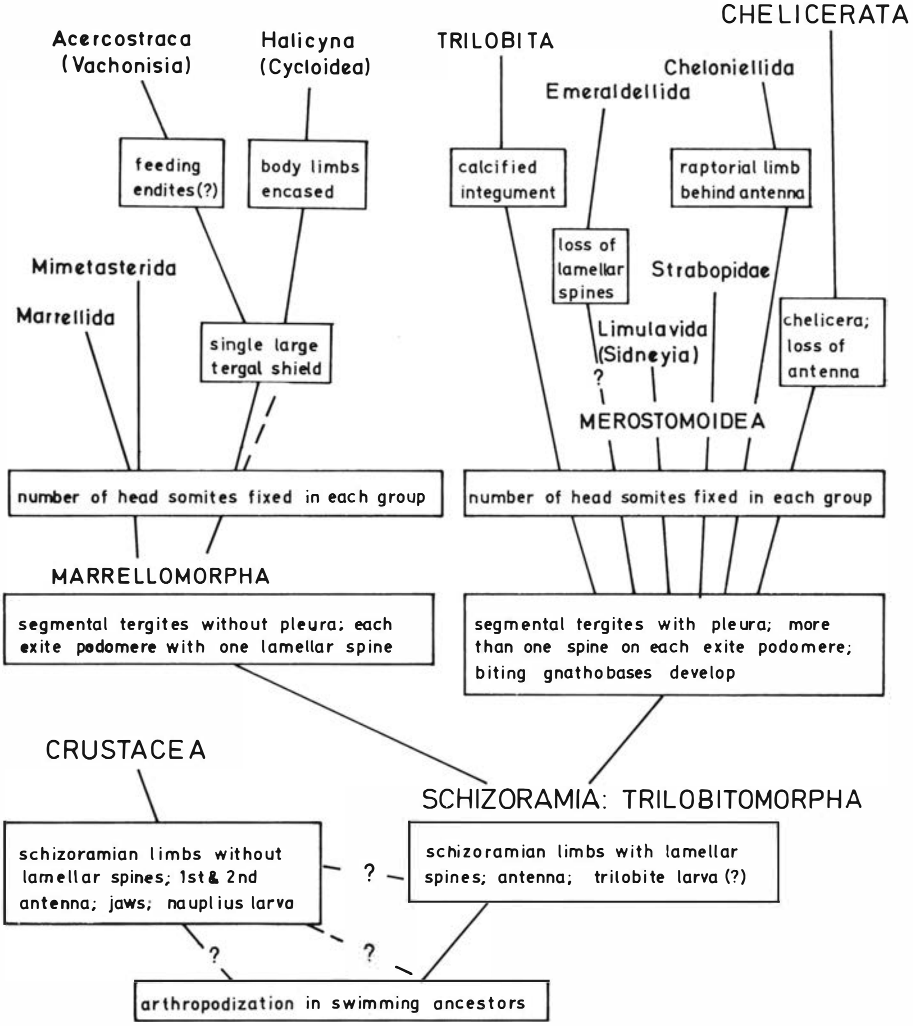

Fig. 3: Suggested evolutionary relationships of schizoramous groups, the Schizoramia (Arachnomorpha) and the Biantennata (Crustacea). The similarities between these two groups may be due to a common origin in the pre-Cambrian or to parallel evolution. Among the uncertainties is the position and composition of the so called Emeraldellida.

ference by various authors. New evidence from trilobites (STÜRMER & BERGSTRÖM 1973; CISNE 1975; WHITTINGTON 1975) throws doubt on the validity of the observation of a precoxa in trilobites, and in addition the morphology in crustaceans appears to be less rigid than previously thought (HESSLER & NEWMAN 1975). However, the trilobitan appendage has an additional quality which appears to be distinctly unique among arthropods and therefore useful as an identification guide. It is the shape of the structures attached to the outer ramus and known as gill-blades, filaments or lamellar spines (Fig. 4). These are typically flattened and may have a thickened border, and they are "distinctly different from common setae" (STØRMER 1944: 119, 1933, 1939: 263). Due to the lack of suitable material STØRMER knew the details of these structures only in trilobites and xiphosurids, and in the latter case they are so modified that there may be some doubt that they represent the same structures. However, new material und new methods seem to verify STØRMER's basic idea of a distinct trilobitan appendage, characterized by the lamellar spines, as a typical feature of aquatic arachnomorphs.

1. Trilobites

Trilobites constitute the largest and best known group of the trilobitomorphs, and it is practical to begin the discussion of schizoramians with them. Trilobites invariably have a calcified exoskeleton. However, the calcification is limited to the dorsal side, the doublure and the labral plate, whereas most of the ventral side including the appendages was not calcified. The exoskeleton, like that of ostracodes but unlike that of most other arthropods, is commonly very well preserved, and the trilobites therefore are comparatively over-represented as fossils. In many Cambrian deposits they strongly dominate the preserved faunas, but the evolution already in Cambrian times in at least two or three lineages of an enrollment ability (BERGSTRÖM 1973 a), apparently for protection, indicate the presence of powerful enemies, virtually unknown in the fossil record.

There is one pair of uniramous multijointed antennae originating at the sides of the labrum. The dorsal morphology commonly would seem to indicate the presence of four pairs of postantennal cephalic appendages, but actual evidence has revealed the existence of only three pairs in *Phacops* (STÜRMER & BERGSTRÖM 1973), *Triarthrus* (CISNE 1975), *Olenoides* (WHITTINGTON 1975), and "*Asteropyge*" (STÜRMER & BERGSTRÖM, unpublished evidence). However, there is a general tendency in aquatic arachnomorphs for the anterior cephalic or prosomal appendages to become smaller than the posterior ones, and a secondary reduction of numbers in the above four genera cannot be excluded at present. The appendages of the thorax and pygidium are similar to those of the cephalon. The pygidial appendages may be more or less reduced in some groups, e. g. illaenids and agnostids, as indicated by the dorsal morphology (size and position of muscle scars). The last pair of appendages are developed as uniramous cerci in *Olenoides*, but not in other well known genera. All appendages except antennae and cerci are biramous. The inner ramus or telopodite may be considered to be a walking leg in most trilobites. However, in the olenid *Triarthrus* the telopodites are kept straight and held in a lateral direction, consequently aligned with the outer branches. Thus, the feet are not directed towards any possible substratum. The aligned telopod-outer branch unit may have been used as an oar in swimming. Lightening of the exoskeleton including strong shortening of the pleura is in accordance with a swimming mode of life. Swimming habits are also likely for ecological reasons in the Late Cambrian Olenid Sea in Norden, dominated by olenids and agnostids. The outer ramus or exite is of variable construction (Fig. 4). In *Ceraurus* (STØRMER 1939) and possibly also in *Phacops* (STÜRMER & BERGSTRÖM 1973) the lamellar spines are confined to a distal podomere of the exite shaft and they are ventrally (anteroventrally) directed. The

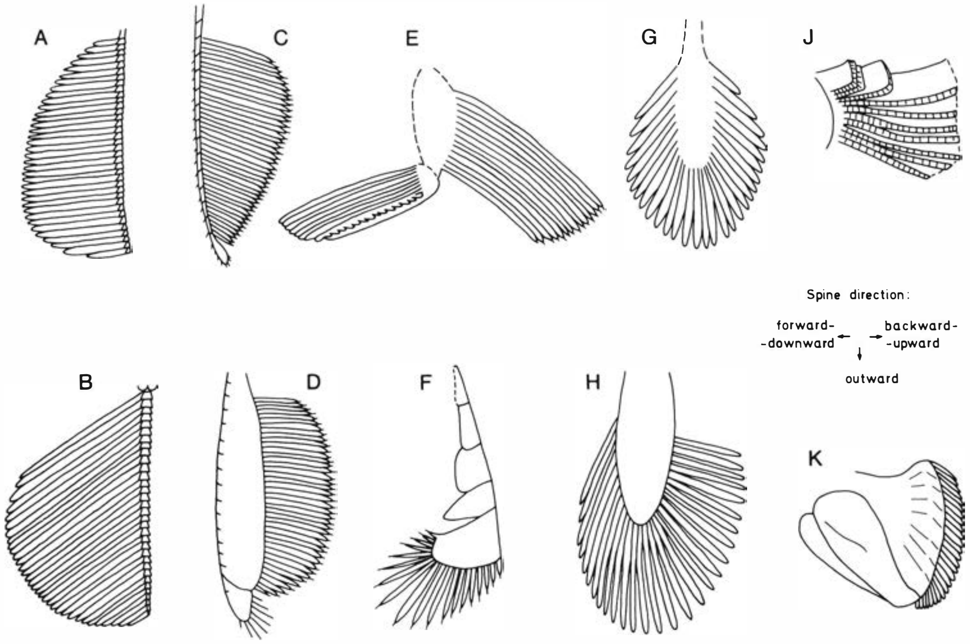

Fig. 4: Diagram to show the distribution and variable arrangement of lamellae in the outer appendage branch of various schizoramians. In trilobitomorphs and aglaspidid chelicerates (A to J) the lamellae form strong needle-shaped lamellar spines, mostly with a thickened border. In xiphosurid chelicerates (K) they are transformed into broad lamellar gills. In marrellomorphs (A and B) there is one row of ventrally directed spines, each extending from a distinct podomere. Trilobitomorphs and merostomoids (C - H) have ventrally and/or dorsally directed spines, at least as a rule belonging to larger podomeres. The arrangement in the merostomoids (G, H) is not yet well known in detail.

shaft of the outer branch has but a few podomores. In *Olenoides* (WHITTINGTON 1975) the distal shaft podomere is devoid of lamellar spines, whereas the very long and flattened paenultimate podomere carries posterodorsally directed lamellar spines. In *Triarthrus* (WALCOTT 1921, Pl. 95: 20, 22, 23; STØRMER 1939: 206-208) the outer branch shaft is slender and multiarticulate, each podomere carrying a few lamellar spines on the posterior side. The exite shaft in *Triarthrus* ends with a distal spoon-shaped element devoid of lamellar spines. In *Cryptolithus* (RAYMOND 1920, Pl. 7: 4-5; BERGSTRÖM 1973 b: 197 and Fig. 4) the ventral view presents evidence for a set of comparatively short and distally placed lamellar spines, which may be described as pendant. The most distal element (of the shaft ?) is rake-like. The dorsal view shows evidence of longer and posterodorsally directed lamellar spines, which are more proximally based and extend more laterally than the distal set of spines. The shaft has not been observed, but it is likely that the distal ventrally directed and the proximal posterodorsally directed spines sets belong to different podomeres. Although the position and orientation of the lamellar spines differ, they are remarkably similar in the various only distantly interrelated trilobites. They may be described as flattened or lamellar and of even width throughout the impressive length (Fig. 5). The margin is thickened at least in *Ceraurus* (STØRMER 1939, Figs 11, 14), *Olenoides* (WHITTINGTON 1975, Pl. 22: 4), *Triarthrus* (STØRMER 1939: 208), *Cryptolithus* (RAYMOND 1920, Pl. 7: 2-5) and *Calymene* (WALCOTT 1921, Pl. 97: 10). The surface of the lamellar spines may carry setae, of which one or a few at the distal end may be stronger than the others. The spines are aligned in a single line and turn the flattened and grooved sides against each other.

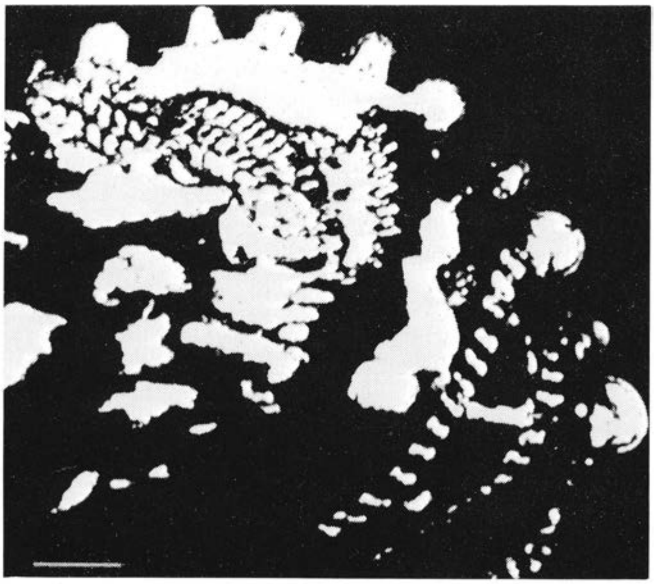

Fig. 5: Longitudinal section through trilobite *Ceraurus* to show serial arrangement of lamellar spines and their thickened borders. Figured by WALCOTT 1881, Pl. 3, Fig. 4 (section 24). White bar is 1 mm.

In some trilobites the medial side of the basis is notably spinous throughout the body (*Olenoides*, Whittington 1975; *Triarthrus*, CISNE 1975) or only in the cephalon (*Phacops*, STÜRMER & BERGSTRÖM 1973). This morphology indicates an active treatment of the food along the midline, and in *Phacops* probably real crushing. In forms like *Olenoides, Phacops* and *Cryptolithus* the strong and more or less curved telopodites carry strong ventral spines, indicating raptorial habits, i. e. feeding on large prey (SEILACHER 1962, STÜRMER & BERGSTRÖM 1973: 118-119). Probable trilobite hunting burrows have also been described (BERGSTRÖM 1973 a: 54 and Pl. 5: 10; OSGOOD & DRENNEN 1975: 330 and Pl. 1: 1). There is no similar indication for *Triarthrus*, and in *Onnia* (related to *Cryptolithus*) the intestine has been found stuffed with mud (BEYRICH 1846, Pl. 4: 1 c; BARRANDE 1852, Pl. 30: 38-39). The mode of feeding therefore probably varied quite a lot between different trilobites. The presence of the lamellar spines in various morphologically quite different trilobites indicates that they were functionally important. However, the quite different orientation in different trilobites also indicates that the spines were subject to functional modifications. Previously they were commonly regarded as gills, but, if true at all, a breathing function was certainly not the only function. There is distinct evidence from trace fossils that some trilobites had very strong spines used for reworking the bottom sediments (Fig. 6). On the other hand it seems very probable that the telopodite and the outer branch in *Triarthrus* were used together as a laterally directed oar unit to propel the animal in swimming. The characteristic cross section of the lamellar spines (Fig. 5) probably made them stiff in one direction and somewhat flexible in a perpendicular direction, and the functional significance of this

Fig. 6: Trilobitomorph (supposed trilobite) trace fossil *Cruziana rugosa* from the Lower Ordovician of Bell Island, Newfoundland. The specimen is a cast of the original burrow, and the ridges therefore represent the scratches made by the strong lamellar spines of the outer appendage branches. Note the serial arrangement of the scratches, comparable to the serial arrangement of the spines (Fig. 5). An estimate based on the depth and areal extent of each set indicates that a large trilobite of the type making this trail was able to shovel away more than 1000 mm³ of sediment with a single stroke of a single appendage. The strength of the lamellar spines apparently was greatly enhanced by the shape of the cross section (Fig. 5). The example only illustrates one of the ways the lamellar spines were exploited in early schizoramians - burrowing was definitely impossible in certain types. Scale in cm. Reprinted with permission from the Canadian Journal of Earth Sciences, National Research Council, Ottawa.

property is unknown. The spines are large enough to permit blood to circulate, which would make them possible gills (Dr. SIDNIE M. MANTON, personal communication). On the other hand their apparent toughness and good preservation, fully comparable to that of the walking legs, may indicate that the gill function was instead concentrated to the ventral side of the pleural region, where the integument appears to have been softer. A pleural gill position would agree with the gill position in eurypterids. BERGSTRÖM (1969: 410-411) suggested that the posterodorsally directed lamellar spines may have served to protect the soft ventral side and in particular to supply the gills with circulating water.

2. Merostomoids

Some groups show similarities with the trilobites in the presence of one pair of antennae, schizoramian postantennal appendages optimally with lamellar spines, and a dorsal exoskeleton more or less reminding of that in trilobites and merostomes. The characters are so variable that the different groups may equal the trilobites in rank, but the poor knowledge may merit the use of a single unit for the moment. With this definition, the merostomoids may provisionally include the following forms: *Sidneyia, Helmetia, Cheloniellon,* and the strabopids (*Paleomerus, Strabops, Neostrabops*). The strabopids are known only from the casts of their dorsal exoskeleton, which may have been calcareous, and are included only because of the general habitual similarity to the others. *Sidneyia* (WALCOTT 1911, SIMONETTA 1963, Pl. 1o: 139705) and *Helmetia* (STØRMER 1944, Fig. 17: 7, 8; SIMONETTA & DELLE CAVE 1975, Pl. 2: 2, 16: 1) have easily recognizeable lamellar spines, although the cross section is unknown (Fig. 4). Also in *Cheloniellon* there are strong lamellar spines (STÜRMER & BERGSTRÖM 1978).

SIMONETTA (1963: 104-105) regards *Sidneyia inexpectans* to have been a formidable predator, ecologically replacing the eurypterids. This suggestion is supported by the presence of coarse and spinous telopodites with strongly serrated gnathobases and, occasionally, agnostids and inarticulate brachiopods in the intestine (WALCOTT 1911, SIMONETTA 1963; Dr. DAVID BRUTON, information presented at the trilobite meeting in Oslo in 1973). As the massive *Sidneyia* no doubt was benthic, it is probable that the eaten agnostids were also benthic.

My own observations on the type specimen of *Helmetia expansa* indicate that the oval plate in front of the head shield is a turned-over labral plate. Fairly close to the anterior margin of the head shield is a pair of rounded structures, which appear to be sessile eyes. Behind the eyes three pairs (possibly more) of faint markings probably indicate the appendage bases. No traces of telopodites could be seen. The stout body construction may indicate carnivorous habits.

While most other supposed merostomoids are Cambrian (*Neostrabops* is Late Ordovician), *Cheloniellon calmani* from the Hunsrück Shale is of Devonian age. Although it is much too late to be a chelicerate ancestor, it shows a mixture of trilobitomorph and chelicerate characters likely to have been present in a chelicerate forebearer. There is a pair of uniramous antennae as in other trilobitomorphs, and in addition there is a pair of uniramous appendages placed behind the antennae but in front of the mouth. These appendages have a spiniferous side, and the distal part could possibly be folded in on the proximal part to grasp a prey between the spiniferous podomeres. The position in front of the mouth and the function appear to make these appendages closely comparable to the chelicerae of chelicerates, and if the antennae were lacking *Cheloniellon* would probably be classified as a chelicerate. The four succeeding pairs of appendages have strong serrated gnathobases, and as normal in trilobitomorphs and aquatic chelicerates the posterior pairs are stronger than the anterior ones. The morphology and considerable size certainly made the benthic *Cheloniellon* a powerful carnivore (STÜRMER & BERGSTRÖM 1978).

3. Marrellomorphs

Some fossil arthropods agree with trilobites and merostomoids in having one pair of antennae and schizoramian appendages with lamellar spines but differ appreciably in the development of the cephalic appendages and the dorsal exoskeleton. Gnathobases are not developed, as far as known, and there are either no free segmental tergites at all, or there are segmental tergites devoid of pleura. In trilobites and merostomes, as far as known, with certainty each podomere of the outer branch carries more than one lamellar spine, whereas in the marrellomorphs there seems to be always one spine pro podomere (Fig. 4). The exite shaft is filiform.

The central members of this group are *Marrella splendens* WALCOTT, 1912, from the Cambrian Burgess Shale and *Mimetaster hexagonalis* (GÜRICH 1931) from the Devonian Hunsrück Shale (Fig. 7). The most notable difference between the two forms is the presence of only one postantennal appendage in the head of *Marrella* (WHITTINGTON 1971) but of two similar head appendages in *Mimetaster* (STÜRMER & BERGSTRÖM 1976). There is a very large labrum, but gnathobasic gnathal processes are missing. The most anterior appendages are long, especially in *Mimetaster*. The lamellar spines are best known in *Mimetaster*, where they have the same flattened shape with thickened borders as in trilobites. There is a large dorsal head shield with two pairs of spines in *Marrella* and three pairs in *Mimetaster*. The body, devoid of pleura (epimeres), is covered by simple crescent-shaped segmental sclerites. Both animals were benthic. Their mode of feeding is not clearly understood although it seems reasonable to suggest that they may have been deposit feeders.

Although habitually quite different from *Marrella* and *Mimetaster*, the Devonian *Vachonisia rogeri* (LEHMANN 1955) shares the type of appendages (STÜRMER & BERGSTRÖM 1976) (Fig. 8). The detailed morphology of the exite spines is not known. The presence of two pairs of strong enditic processes(?) directed toward a point where the mouth appears to have been located indicates large-particle feeding, and the strong curved telepodites of the body indicate possible carnivorous or raptorial habits. The overall organization shows some analogies with limulids, with a large vaulted shield, three large pairs of walking legs in the head, and the appendages of the body protected in a ventral concavity of the shield. The number of body appendage pairs is around 80, an impressively large figure.

The cycloids from the Early Carboniferous to the Late Triassic, known from marine and limnic deposits, have presented large dif-

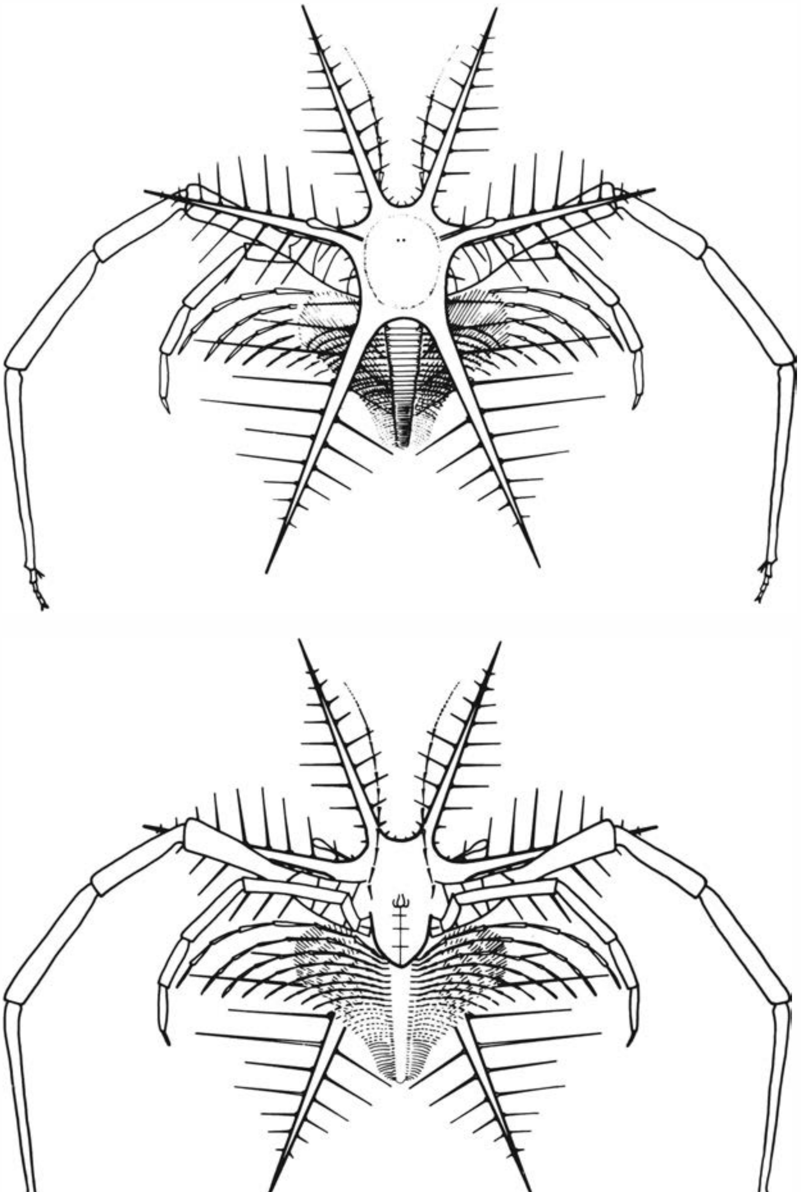

Fig. 7: Reconstruction of dorsal and ventral aspects of Devonian marrellomorph *Mimetaster*. After STÜRMER & BERGSTRÖM (1976).

ficulties at classification attempts. At present they tend to be classified as questionable crustaceans (GALL & GRAUVOGEL 1967; GLAESSNER in MOORE 1969: R568, 629; HESSLER in MOORE 1969: R205, did not accept them as branchiuran relatives). The body is covered by a large shield and a rostral plate. There seems to be one pair of uniramous, multiarticulated antennae. There are five pairs of strong walking legs, each apparently with a filiform outer branch. In the rear part of the body there is on each side a series of some 75 lamellae ("lamelle branchiale") well covered in a groove with a narrow opening (GALL & GRAUVOGEL 1967). The entire organization is indeed entirely different from that in crustaceans. On the other hand there are similarities with the marrellomorphs, particularly with *Vachonisia*. Cycloids may be visualized as being derived from a *Vachonisia*-like animal through the change of the body appendages into plates and the encasing of these plates in almost closed furrows. The plates are regarded as gill lamellae, and this explanation appears likely. The outer branch of the walking legs is easily derived from a marrellomorph outer branch through the loss or transformation of the lamellar spines. GALL & GRAUVOGEL (1967: 10) state that the cycloids were benthic.

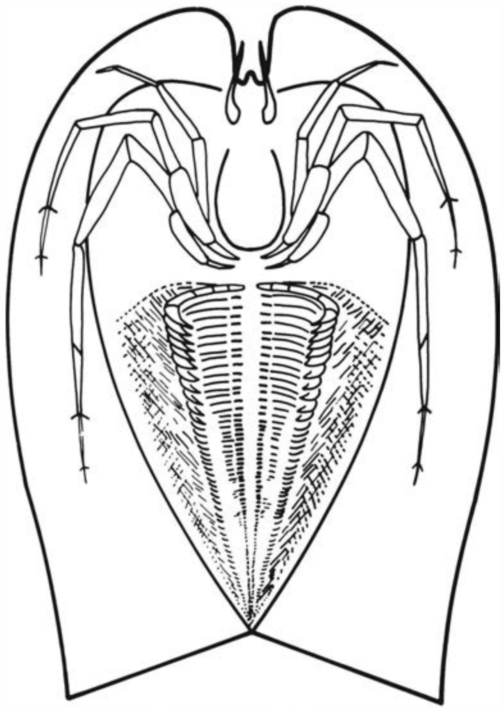

Fig. 8: Reconstruction of ventral aspect of Devonian supposed marrellomorph *Vachonisio*. After STÜRMER & BERGSTRÖM (1976).

The marrellomorphs may represent a primitive stage in the evolution of the arachnomorphs (Fig. 3). The organization of the dorsal exoskeleton is not stabilized, as shown by the variation in the number of distinct tergites from one to over 30. The exact one lamellar spine to podomere correspondence may also be a primitive feature, although it may just as well be advanced. The absence of pleura in the segmental tergites of *Marrella* and *Mimetaster* is possibly a primitive (plesiomorphic) feature. The absence of gnathobasic processes appears primitive; at least phylogenetically gnathobasic processes must have come into existence only after the original development of limbs. Gnathobasic processes also may have been secondarily aborted in the ancestors of *Mimetaster*, but it is difficult to see the functional explanation for such a reduction. The variation in the number of cephalic appendages does not have the same important taxonomic implication as in extant arthropods, but is only to be expected in early groups. The stalked eyes in *Mimetaster* and the cycloid *Halicyne* are exceptional among arachnomorphs but this feature is not considered systematically important. The plausible loss or at least transformation of the exite lamellar spines in the walking legs of *Halicyne* yields valuable information about the evolutionary plasticity also of a feature considered most characteristic of the trilobitomorphs. Trilobites, merostomoids and chelicerates may have evolved from a marrellomorph-like origin.

4. Aglaspidids

The aglaspidids have a merostome-like habitus but a phosphatic integument. The appendages are similar in head and body. RAASCH (1939) reported 6 pairs of appendages in the head, but BRIGGS et al. (1979) found only 4 or 5 pairs and thought that the first pair represented antennae. The stout and parallel-sided habitus is not in accordance with that opinion, and the matter remains unsettled. The legs are poorly preserved, and outer branches are not seen. However, REPINA & OKUNEVA (1969) described lamellae reminiscent of trilobitomorph outer branch lamellae in *Khankaspis bazhanovi* (Fig. 4), which has aglaspidid habitus and phosphatic integument.

With the fragmentary knowledge in mind, the conclusion by BRIGGS et al. (1979) that aglaspidids are certainly not chelicerates is not warranted. It may be correct, but as stressed repeatedly, the composition of the head varied and must have varied considerably within early arthropod groups. Even within the Merostomata there is a variation from 6 to 7 pairs of prosomal appendages. Limb pairs in the trunk of extant pycnogonids number from 5 to 9.

The section on the aglaspidids was rewritten in proof.

5. Merostomata

Xiphosurids, eurypterids and scorpions may represent a natural group of chelicerates. At least in xiphosurids the prosoma contains seven segments, i. e. one segment more than in arachnids and more than in aglaspidids as well (BERGSTRÖM 1975). The merostomes, including early scorpions, are basically aquatic carnivores. There is invariably a tail spine. The appendages are strongly modified as compared with aglaspidids and trilobitomorphs. The prosomal appendages have lost the outer branch (except possibly for a functionally important remnant in xiphosurids), and the last pair of walking legs are reduced to chilaria except in the Devonian *Weinbergina* (Fig. 10; BERGSTRÖM 1975). The opisthosomal appendages apparently have reduced the walking branch, and the axis of the outer

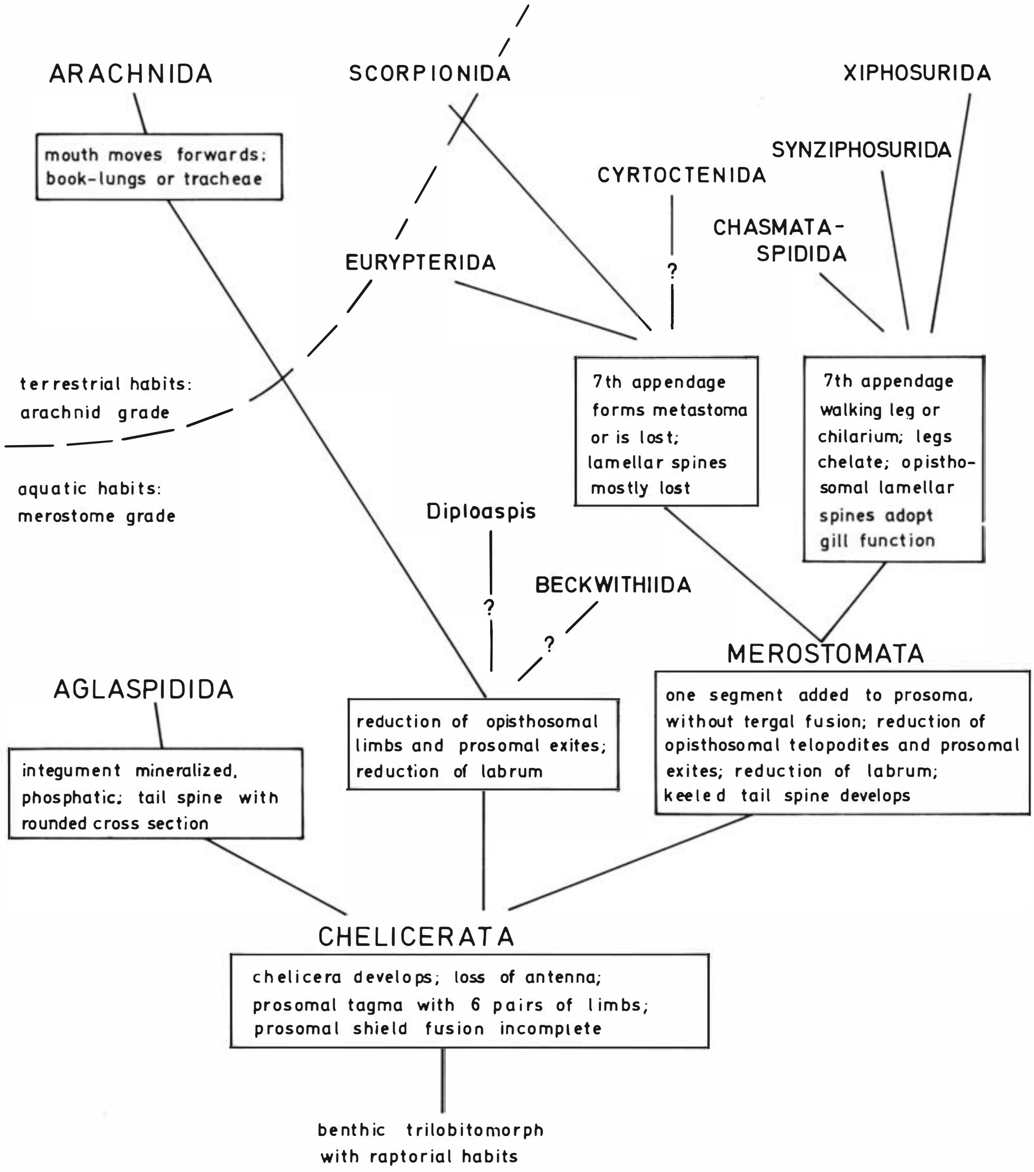

Fig. 9: Suggested evolutionary relationships of chelicerate groups. Although not indicated in the diagram, it is possible or probable that the groups covered by the term Arachnida became land dwellers through more than one change-over from aquatic habitats. All the earliest scorpions were aquatic, and some eurypterids appear to have been amphibious or terrestrial (STØRMER 1976). This emphasizes the impossibility to use a terrestrial or aquatic habitat or the associated adaptations as a basis for classification. The chelicerate nature of the Aglaspidida is questionable.

branch is transformed to a broad plate. In xiphosurans the dorsal side of the plate carries a series of flat branchial lamellae with rounded outline (Fig. 4). The position strongly indicates homology with the lamellar spines in trilobites (STØRMER 1944: 70), and the existence of a marginal thickening in the branchial lamellae provides a distinct morphological similarity with the lamellar spines. The vastly enlarged surface in the branchial lamellae in comparison with the lamellar spines is probably an adaptation to the branchial function. In eurypterids the gills are on the ventral body surface, where they are protected by the flattened opisthosomal appendages (WILLS 1965; WATERSTON 1975), and the lamellar spines are completely lost. In scorpions, the pectines may represent a pair of opisthosomal outer branches with modified lamellar spines. This organ seems to have some sensory function in discerning particular characteristics of the ground.

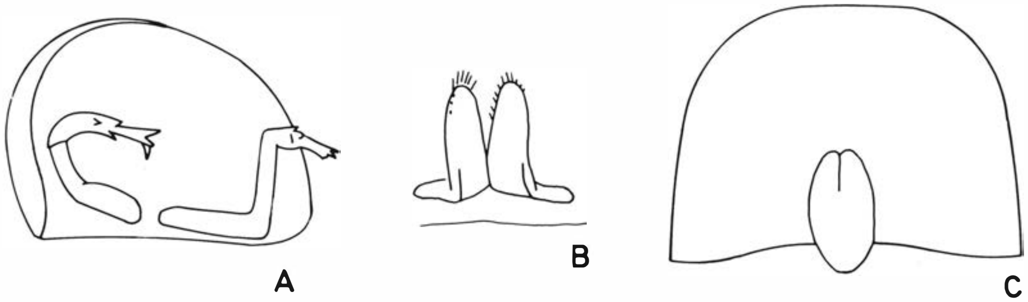

Fig. 10: The sixth post-cheliceral appendages in various Merostomata. A, the Devonian xiphosuran *Weinbergina*, with the last prosomal appendages apparently developed as typical prosomal legs. B, extant xiphosuran *Limulus* with only gnathobases (chilaria) remaining of the last prosomal limbs. C, probable fused last limb pair, forming the metastoma, in the Silurion eurypterid *Baltoeurypterus*. The anterior margin of the metastoma commonly had the denticulated morphology typical of the more anterior gnathobases. A after LEHMANN, B and C after HOLM (redrawn).

The groups treated above as merostomes apparently do not contain the origin of terrestrial chelicerates other than the scorpions (Fig. 9). However, the terrestrial arachnids, first known from the Early Devonian (e. g. STØRMER 1970), must also have aquatic forebearers representing the merostome grade in arachnid evolution. These merostome-like chelicerates should have only six pairs of prosomal appendages and there should be no tail spine of the type found in true merostomes. Unfortunately the number of appendages is of no practical aid for the moment. Studying the single specimen of the Middle Cambrian *Beckwithia typa* RESSER, 1931, I found traces of black-coloured "chitinous" integument, proving that the type of integument is quite different from that in the aglaspidids, where it is mineralized and glossy. As *Beckwithia* is apparently no xiphosuran or eurypterid, it must represent a parallel radiation of aquatic chelicerates. The size of this radiation is unknown, and it cannot at present be stated whether *Beckwithia* is an arachnid on merostome level of evolution or not. The presence of a pygidial shield in *Beckwithia* would seem to rule it out as a direct ancestor of any known chelicerate.

Another interesting merostome grade chelicerate was described from the Lower Devonian by STØRMER (1972) as *Diploaspis casteri*. The hind end of the body lacks a spine and has the generalized appearance that would be expected in aquatic arachnid ancestors. The large anterior opisthosomal shield is a specialization that rules out *Diploaspis* itself as a direct ancestor but it may likely belong to a group from which terrestrial archnids evolved. There is a possibility that *Diploaspis* was amphibious (STØRMER 1976). The presence of swimmerets is an adaptional feature in this animal and has no deeper phylogenetic implication. The absence of paired eyes is by no means proven. Experience from the synziphosurids shows how misleading the absence of direct observation of eyes may be (ELDREDGE 1974, BERGSTRÖM 1975).

III. Crustaceans and probable crustaceans

Despite the modern success and diversity of crustaceans, their fossil history is poorly known. Only the malacostracans are generally considered to be represented by reliable fossil material, the hymenostracan *Hymenocaris*, in the Cambrian. Malacostracan Archaeostraca occur first in the Ordovician and Eumalacostraca in the Devonian. Ostracodes are known from the Ordovician and possibly from the Cambrian, cirripeds from the Silurian or possibly from the Early Cambrian (the phosphatic tommotiids, see BISCHOFF 1976; opinions vary widely), conchostracans from the Devonian or possibly from the Early Cambrian (the lepidittids, see KOBAYASHI 1972), anostracans and lipostracans from the Devonian, notostracans from the Carboniferous, and cladocerans and copepods from the Tertiary. Other groups are unknown as fossils. Even the earliest members of each group are so advanced as to add no information about the relationships between the groups and still less between crustaceans and schizoramians. It is apparent that the history of the individual groups must extend further back in time. Early crustaceans would be expected to occur in the Middle Cambrian Burgess Shale, and several of the arthropods occurring there have been considered as crustaceans from time to time. However, STØRMER (1944) claimed that some of them had trilobite limbs and included them in his trilobitomorph subclass Pseudocrustacea but later changed to exclude them from the Trilobitomorpha (STØRMER in MOORE 1959). Considering the general similarity between trilobitomorph and crustacean limbs and the absence of trilobitomorph lamellar spines in the "pseudocrustaceans", I do not believe that these can be contained within the Trilobitomorpha.

Odaraia alata WALCOTT, 1912 and *Branchiocaris pretiosa* RESSER, 1929 have a notostracan-like appearance with a large carapace and a body with numerous short segments and numerous pairs of blade-like appendages (RESSER 1929, Pl. 4, Figs 1-2; SIMONETTA & DELLE CAVE 1975, BRIGGS 1976, Text Fig. 2, Pls 2-6). Unfortunately the preparation of specimens (BRIGGS 1976) has not revealed the outline of the appendages but only the existence of flat surfaces within them, and the nature of the "proximal element" of the appendages is also in doubt. Other figures (SIMONETTA & DELLE CAVE 1975, Pl. 54, Fig. 2 A-B and photographs kindly provided by Dr. SIMONETTA) reveal a strong convexity and jointing of the "proximal element", and it seems quite possible that these elements in reality are endopods. BRIGGS further revealed the presence of two anterior pairs of appendages which may be considered as first and second antennae, even if the detailed morphology is not well known. The bivalved character of the carapace has been used as an argument to exclude these forms from the Notostraca (RESSER 1929). I do not personally believe that this character is very important, as for instance both bivalved and entire carapaces occur within the Malacostraca. On the other hand the possible endopod ("proximal element") would seem to be on a cephalocarid stage of development, that is on a stage that branchiopods logically would have passed early in their evolution (SANDERS 1957, 1963). The rear part of the body lacks a telson (BRIGGS 1976: 9, ".. the anus, which occupies most of the posterior margin of the telson .."; also text Fig. 2; see definition of telson in SHAROV 1966, BOWMAN 1971), but carries large uropods (furca). The terminal tergite is considerably larger than the ones just in front. In these characters *Branchiocaris* is closely comparable to conchostracan and cladoceran branchiopods (Fig. 12; for the rear end of the body cf. BOWMAN 1971, Figs 5-8). *Branchiocaris* has a large body extending outside the carapace valves, and the possible large endopods indicate that it may be intermediate between a more generalized crustacean and branchiopods. However, the bivalved character of the carapace, the lack of known eyes and the morphology of the rear end of the body makes it plausible that *Branchiocaris* is close to the Conchostraca and Cladocera. It may be included in the Branchiopoda Diplostraca as a representative of an early group, for which the order Pseudonotostraca RAYMOND, 1935 is an available name.

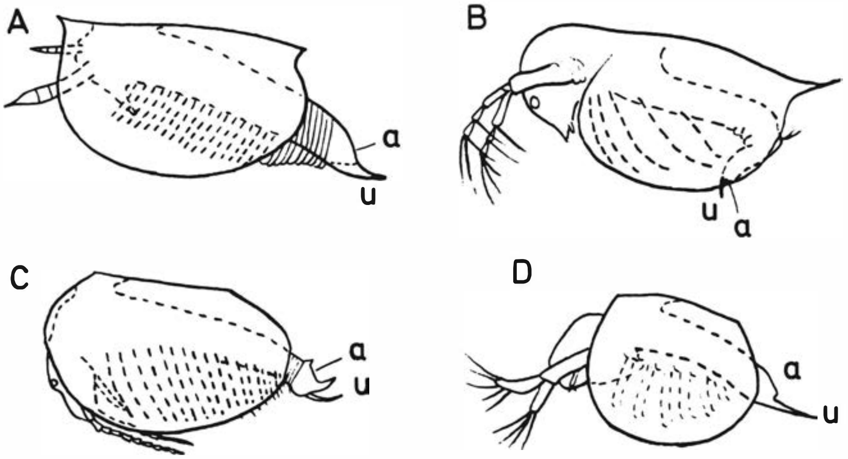

Fig. 11: A, the Middle Cambrian *Branchiocaris*, compared with B, *Daphnia* (Cladocera), C, *Cyzicus* (Conchostraca), and D, larva of *Limnadia* (Conchostraca). Note the great similarities in the presence of a large terminal unit with anal opening (a) and uropods (u) and therefore a true segment (a telson is missing). Redrawn, A from BRIGGS, B from KÜKENTHAL, C from CALMAN, D from SARS.

The appendages of *Odaraia alata* are not well enough known to show if this species belongs in the same or another branchiopod group. There appears to be stalked compound eyes (SIMONETTA & DELLE CAVE

1975, Pl. 52, Figs 3-7; photographs kindly provided by Dr. SIMONETTA), a feature known only from anostracans among living branchiopods. However, experience from the malacostracans demonstrates that eye stalks are not useful as a systematic character beyond and in cases not even within the order level.

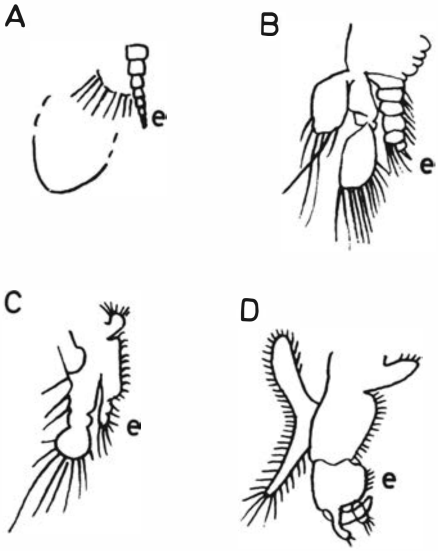

Fig. 12: A, appendage of the Middle Cambrian *Branchiocaris*, compared with appendages of B, cephalocarid (*Hutchinsoniella*), C, cladoceran, and D, conchostracan. e, endopod. B from SANDERS, C and D after LANG & HESCHELER.

Canadaspis perfecta (WALCOTT, 1912), *Plenocaris plena* (WALCOTT, 1912) and *Waptia fieldensis* WALCOTT, 1912, all from the Middle Cambrian Burgess Shale, have a more or less typical malacostracan habitus. They have a carapace of crustacean appearance. At least most of the abdomen lacks pleura and appendages apart from uropods (developed as furca in *Canadaspis*, see valuable discussion on the nature of the telson and furca in SHAROV 1966 and BOWMAN 1971). *Canadaspis* has branched appendages with a walking branch and an outer foliaceous part (ROLFE in MOORE 1969: R324 and Fig. 149: 4b). There are pedunculate eyes, a small rostrum and furca-like spines. The general morphology and all known details fit only a crustacean, and as the limb morphology with a walking branch is alien to phyllopods *Canadaspis* should be a malacostracan. *Plenocaris* was recently treated by WHITTINGTON (1974). The limbs are poorly known. *Plenocaris* has rostrum and uropods but no telson (WHITTINGTON's report of a telson is based on the common misinterpretation). *Waptia* is generally similar to *Plenocaris*. It has peduncular eyes and jointed uropods and shortened segments under the carapace as in malacostracans. There is no telson. As in the other forms the limbs are poorly known in detail, and the absence of a second antenna in reconstructions does not mean that a second antenna was definitely missing.

Canadaspis, Plenocaris and *Waptia* are better known than most Cambrian and later phyllocarids, which tend to be readily accepted as malacostracans. It would be illogical to exclude the Burgess Shale forms from the Malacostraca just because they are not still better known and despite the fact that all known features fit reasonably well with the Malacostraca and definitely with the Crustacea. The Archaeostraca and Eumalacostraca represent two end lines of malacostracans, neither of which could have been derived from the other (e. g. because the uropods are apomorphically reduced to simple styli in the archaeostracans but are primitively jointed and branched in many eumalacostracans). There must have been an early radiation with perhaps much morphological variation within the basic stock before archaeostracans and eumalacostracans became finally crystallized as distinct groups. For instance there may have been some variation in the number of segments in the body tagmata. The fact that the above mentioned arthropods do not fit exactly into the archaeostracan or eumalacostracan pattern therefore does not permit the conclusion that they are no malacostracans. On the contrary the variation found among them is only to be expected in early malacostracans.

IV. Some problematic groups

1. Late pre-Cambrian forms

Three pre-Cambrian fossils have recently been supposed to be possible arthropod remains. These are *Praecambridium sigillum* GLAESSNER & WADE, 1966 and *Parvancorina minchami* GLAESSNER, 1958 from the Pound Quartzite of South Australia and *Vendia sokolovi* KELLER, 1969 from Valdai Series of Russia. *Vendia* was described as non-symmetrical, but GLAESSNER & WADE (1971) indicated that asymmetry in this form and the similar *Praecambridium* was casual and caused by deformation. The "ribs" in the oval bodies would then be symmetrically arranged and reminiscent of segments in a polymerous animal. Having rejected *Praecambridium* from annelids because of the lack of visible parapodia, GLAESSNER & WADE (1971: 74) are left with the alternative that it is some kind of arthropod, presumably a primitive one. However, I have seen a photograph of a well preserved specimen of *Vendia sokolovi* which does not appear to be in any way distorted and, in addition, cannot be brought into a symmetric shape by angular distortion from its present shape. I am therefore convinced that there is a lack of genuine bilateral symmetry in *Vendia*, which in all probability means that this form is not an arthropod. I agree with GLAESSNER & WADE (1971: 75) that *Vendia* and *Praecambridium* appear to be related, which would mean that also the latter cannot be an arthropod.

Like the other two forms, *Parvancorina* is preserved as oval imprints of what may be a dorsal surface of an animal. There is a prominent median ridge without subdivisions but with a pair of anterior extensions, and in the lateral fields there are faint wrinkles which have been thought to represent some kind of appendages. The median ridge is not quite straight, which may indicate some mobility and flexibility of the structure in the living animal. The oval shield may have been some kind of carapace with the other parts of the body preserved imprinted in it. It is not possible for the moment to judge whether *Parvancorina* is an arthropod or not.

2. *Opabinia*

Opabinia regalis WALCOTT, 1912, is a particularly crucial animal. While in most other cases additional information may solve the question of the systematic position, the additional knowledge gained through the restudy of *Opabinia* by WHITTINGTON (1975 a) made the interpretation more difficult than might have been expected. The appendages are entirely unlike anything seen in other arthropods, composed as they seem to be of one flat and one folded plate. There is an unpaired frontal appendage somewhat reminding habitually of the second antennae in some anostracans but probably quite different in detail. Five dorsal structures in the head appear to represent one unpaired and four paired compound eyes. The body is cylindrical, without pleura (if the supposed appendages are not considered as pleura). There is no particular similarity even in the ground plan either to uniramians or to schizoramous arthropods, and it is possible that *Opabinia* represents a separate line of segmented animals that reached the arthropod level of organization independently.

3. *Aysheaia*

The remarkably well preserved *Aysheaia pedunculata* WALCOTT, 1911, from the Burgess Shale is generally regarded as an aquatic onychophoran (e. g. MOORE 1959: 18). DELLE CAVE & SIMONETTA (1975) noted that the so called antennae are post-oral and more comparable to legs, although they show some specialization. After Dr. SIMONETTA informed me about the observations in 1973, I had the opportunity to visit the United States National Museum in Washington, D. C., in 1974, where I had a look at the specimens of *Aysheaia pedunculata*. I noticed that the first appendages tended to be extended on opposite sides of the body, even in specimens laterally compressed and with the walking legs of both sides lying compressed on one side (WALCOTT 1931, Pl. 11: 1; DELLE CAVE & SIMONETTA 1975, Figs 3, 12, 13A?). This indicates that the first appendage was strictly laterally directed while the legs were ventro-lateral (Fig. 13). In addition, the first appendage has an anterior row of strong and long spines (WALCOTT 1931, Pl. 11: 1; DELLE CAVE & SIMONETTA 1975, Fig. 2A), indicating that the appendage may have been used for grasping the food, probably consisting of prey. Whereas there are constantly four tubercle body rings on each pair of legs, there are about eight (the faintness makes counting somewhat difficult) between the grasping limb and the first leg, indicating perhaps the presence of a limbless body segment in this region. The mouth is terminal, without jaws. The pharynx appears to have been evertible (DELLE CAVE & SIMONETTA 1975).

The terminal mouth, the lack of antennae, jaws and slime papillae, and the presence of grasping appendages and probably of a limbless segment make *Aysheaia* profoundly different from onychophorans, although the importance of the lack of antennae ist dependent on whether the onychophoran antenna is homologous with the myriapod - hexapod antenna or with the preantenna. On the other hand, *Aysheaia* shows similarities to the Tardigrada in the presence of a terminal mouth without jaws, many-clawed feet and a terminal position of the last pair of appendages. These characters are not found together in any other arthropods. In addition, both groups lack antennae, a feature which may be primitive in these groups but advanced in other arthropods (like the chelicerates) where it is met with. Tardigrades are much smaller and have fewer body segments than *Aysheaia*, but this may well be related to the particular mode of

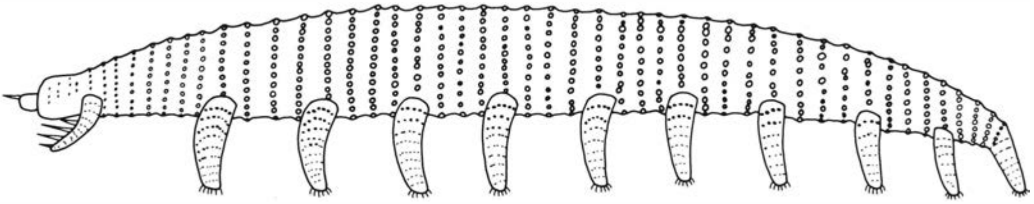

Fig. 13: New reconstruction of Middle Cambrian *Aysheaia*. Note the terminal position of the mouth and last appendages and the multiple claws, features reminiscent of the Tardigrada. Antennae are missing, and the only appendages of the head are a pair of laterally directed limbs with very strong spines on the anterior side, probably used for catching prey. There are four rings of nodes on the body for each appendage pair except between the spiniferous limbs where there are about eight rings, suggesting the presence of a limb-less segment.

life. The similarities and possible relationship between *Aysheaia* and tardigrades have been repeatedly pointed out, e. g. by TIEGS & MANTON (1958: 322), WILMOTH (1967: 237). DELLE CAVE & SIMONETTA (1975: 75-76), and SIMONETTA (1976: 114-115, 121). *Aysheaia* (and tardigrades) still may be on the uniramian line of evolution, but if so obviously further apart from the extant groups than formerly thought (Fig. 1). Added in proof: A redescription by WHITTINGTON (1978) conforms with the above description and strengthens the conclusions.

4. Isopygous forms with short thorax

A few early arthropods, including *Mollisonia symmetrica* WALCOTT, 1912, and *Thelxiope paleothalassia* SIMONETTA & DELLE CAVE, 1975, from the Middle Cambrian Burgess Shale and an Early Ordovician (Tremadocian) form from Australia, being studied by Mr. Ian STEWART, National Museum of Victoria, Melbourne, have large cephalic and pygidial shields separated by six to seven thoracic tergites (Fig. 14). No appendages are known. The Australian form appears to have a wide cephalic doublure, leaving only a fairly narrow space in the middle. Nothing similar is known from any trilobitomorph, instead the head shield may perhaps be compared with the head capsule of myriapods. *Thelxiope* and *Mollisonia* have a general appearance and pleural facets indicating that they may have been able to enroll sphaeroidally, and specimens of the former also show initiated bending of the body (Fig. 14; SIMONETTA & DELLE CAVE 1975, Pl. 22, Figs 4, 5). There is no reason to regard these forms as trilobitomorphs as they are not similar to trilobitomorphs in any particular respect. There is a possibility that they may be uniramians, but this suggestion can hardly be substantiated at present. Available suprageneric names are the order Mollisoniida SIMONETTA & DELLE CAVE, 1975 and the family Mollisoniidae SIMONETTA & DELLE CAVE, 1975 (both names corrected herein).

5. Some Burgess arthropods

A number of Burgess Shale arthropods have a general merostomoid habitus without, as far as known, having the lamellar spines of the "trilobitan appendage". These are the "emeraldellids", the genera *Emeraldella* WALCOTT, 1912, *Emeraldoides* SIMONETTA, 1964, *Molaria* WALCOTT, 1912 and *Habelia* WALCOTT, 1912. At least in some of these genera there is one pair of uniramous antennae, and the postantennal appendages are branched, with an inner walking branch and an outer setiferous plate-like branch (SIMONETTA 1964). A proximal part of the outer branch or possibly a second outer branch may carry dorsally directed setae(?) (SIMONETTA 1970, Pl. 2: 1 c, which is an *Emeraldella brooki* according to Dr. David BRUTON, formal talk presented at the Trilobite meeting in Oslo 1973). It may be that the main lobe compares with the distal exite lobe in such a trilobite as *Olenoides*, where there are also setae and no lamellar spines. It is possible that the lamellar spines were originally present but were lost or transformed into the short proximal setae(?) referred to above. The emeraldellids or some of them may therefore constitute a group of trilobitomorphs. However, there may be other possibilities as well.

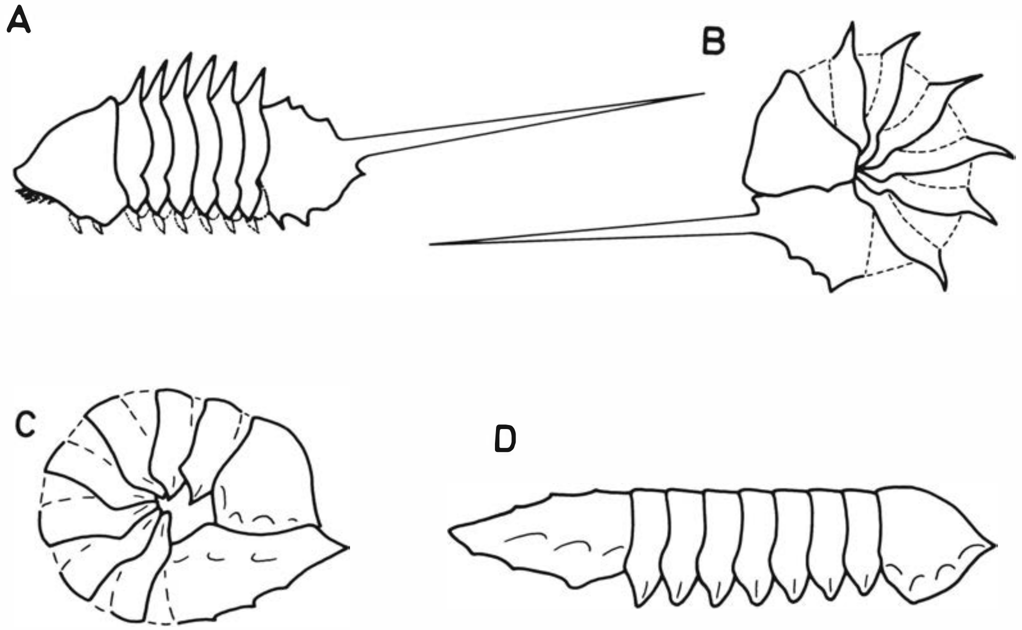

Fig. 14: A, B, *Thelxiope paleothalassia*, and C, D, *Mollisonia symmetrica* from the Middle Cambrian Burgess Shale. B and C show the forms may fit in enrollment. A, D after SIMONETTA & DELLE CAVE.

Another questionable form is *Burgessia bella* WALCOTT, 1912, which was most recently redescribed by HUGHES (1975). Also this species has one pair of uniramous antennae and a series of postantennal branched appendages. The latter consist of an inner walking branch and an outer setiferous plate (or a filiform branch in the most anterior appendage pairs). There are no lamellar spines. There is a large carapace of crustacean type except for the inclusion of a pair of large digestive diverticula. Despite the carapace it is quite difficult to accept this form as a true crustacean, and it may represent an unknown group of arthropods.

Structures at least strikingly similar to lamellar spines are found in the Burgess Shale arthropod *Actaeus armatus* SIMONETTA, 1970 (SIMONETTA 1970, Pl. 9: 3 and p. 43). Unfortunately the possible walking branch is poorly known. See also below.

6. Arthropods with "great appendage"

Some arthropods from the Middle Cambrian Burgess Shale are known to have one pair of large branched anterior appendages. These are *Yohoia tenuis* WALCOTT, 1912, *Leanchoilia superlata* WALCOTT, 1912, *L.? protogonia* SIMONETTA, 1970, "*L.*" *amphiction* SIMONETTA, 1970, and *Actaeus armatus* SIMONETTA, 1970. *Yohoia*, recently treated by SIMONETTA (1970), SIMONETTA & DELLE CAVE (1975) and WHITTINGTON (1974), is probably the best known of them. The anus is situated just in front of the terminal plate-like element, which therefore is to be considered as a post-segmental telson. There appears to be limbs on all segments except for the last three or so, meaning that there are no uropods (furca). At least many of the appendages have flattened setiferous lobes. A walking branch is known with certainty only from the anterior region. The "great appendage" has an "elbow" in the middle and a set of four movable(?) terminal spines. There is no sign of any uniramous antenna. WHITTINGTON (1974) desbribed a "median frontal lobe" and a "lateral area of cephalon". The former reminds of the rostrum in leptostracan and archaeostracan malacostracans. The "lateral area" is drawn too small in the reconstructions (WHITTINGTON 1974, text Figs 2, 5), and to me it looks more like a stalked compound eye than an appendage, even in the absence of reflecting matter (WHITTINGTON 1974, p. 8 and Pl. 2 Fig. 2, Pl. 7 Figs 1, 2, Pl. 11, Fig. 5, Pl. 10 (XII), Fig. 4). Actually one specimen appears to have light reflecting "lateral areas" (USNM 179017; WHITTINGTON 1974, Pl. 9, Figs 1, 2).

Apart from the "great appendage" there is no evidence of branching in the appendages of the other arthropods listed above. The structure is too poorly known to form the basis of a serious discussion. According to the reconstruction of *Actaeus* (SIMONETTA 1970, Pl. 31, Fig. 3) there is a distal set of spines on the "great appendage", approximately as in *Yohoia*. In addition there is a pair of apparently uniramous antennae, of which I cannot see any evidence in the published photographs (SIMONETTA 1970, Pl. 30, Figs 4 a, b). There is a pointed telson(?), but no uropods.

The "great appendage" of the species referred to *Leanchoilia* by SIMONETTA has distally two spines and one long flagella(?) in addition to two more proximally positioned long branches according to reconstructions (SIMONETTA & DELLE CAVE 1975, Pl. 1, Figs 1, 2, 6). Apart possibly from *L. amphiction*, there is a styliform telson with marginal spines.

There is a remote similarity between the "great appendage" and the crustacean second antenna in the mode of branching, but there is in no way any proof of homology. *Yohoia* is habitually very malacostracan-like, with possible rostrum and stalked compound eyes in addition to a shrimp-like bend of the body (WHITTINGTON 1974, Pl. 1, Figs 1-4 in particular) which is not shown in any reconstructions. However, the crucial structure of the "great appendage", the poor knowledge of the other appendages and the absence of uropods (present as uropods or a "furca" in all vagile crustaceans except for some ostracodes and crabs) make it impossible at present to refer the "great appendage" arthropods to any particular group. It is not even sure that they belong together.

D. Conclusion

Many arthropods remain to be discussed in an attempt to sort up the large phyletic lines in the Palaeozoic, but for a meaningful discussion much more data on their morphology is needed.

1. On morphological grounds, the arthropods are divisible into two main groups: the uniramous forms characterized by unbranched legs, and the schizoramous forms with branched appendages. The Cambrian *Opabinia* may represent a third main type.

2. The uniramians probably originated from a benthic crawling annelid-like worm with anteriorly or antero-ventrally directed mouth, feeding on mud or large particles, which were ingested directly or handled by the tips of anteriorly situated appendages.

3. Soft-skinned, malacopod-grade uniramous arthropods may include the Cambrian *Xenusion* in addition to the extant Onychophora and perhaps some other groups. The Cambrian *Aysheaia* is found to differ profoundly from onychophorans in the probable presence of only one pair of specialized limbs, the post-oral spiniferous raptorial appendages, and possible absence of limbs in the next segment, as compared to three pairs (antennae, jaws, oral papillae) in onychophorans. *Aysheaia* may be closer to tardigrades, and its possible relationship with the uniramians must be fairly remote.

4. Arthropod-grade uniramians are probably represented already in the Cambrian by the aquatic myriapod-like *Anomalocaris*, of which one species may be based on part of the body, others on isolated appendages. The Devonian to Carboniferous arthropleurids are myriapods with possibly amphibious life habits. Basic myriapod habits may not have changed too much in connection with a change-over to land life, and this change-over is not necessarily connected with a switch from malacopod to arthropod grade characteristics. Euthycarcinoids may represent a group of uniramians distinct from myriapods and hexapods and known from Late Carboniferous and Triassic limnic deposits. They may have been primarily aquatic.

5. The schizoramous arthropods probably originated from more or less swimming polymerous animals with branched protrusions for locomotion. Food was collected either from the sediment surface or from suspension with the aid of postoral appendages and brought forward to the posteriorly directed mouth.

6. The arachnomorphs (Schizoramia) form one apparently natural schi-

zoramous group, the crustaceans (Biantennata) another. The general similarity may be due to a common origin or to a similar mode of evolution from pre-arthropod animals. The fossil forms do not permit a direct linking of crustaceans to the early trilobitomorphs. On the contrary, already Cambrian crustaceans are more or less typical members of still living main groups, and common crustacean ancestors must be pre-Cambrian. Similarly schizoramians (arachnomorphs) are split up on various groups already in the Cambrian, and no truly ancestral groups are known.

7. The most distinctive morphological character in schizoramians may be the lamellar spines of the outer branches. It has been identified in trilobites, *Sidneyia, Helmetia, Cheloniellon*, marrellomorphs, and aglaspidids, and in a modified form in xiphosurids and possibly in scorpions.

8. Among the trilobitomorphs (antennate Schizoramia), the marrellomorphs may be primitive in lacking gnathobases and segmental pleura (epimeres). They also appear to differ from trilobites and merostomoids in having exite lamellar spines arranged in only one row (as compared to a primitive set of one ventral and one dorsal row in the latter), with only one spine pro podomere.

9. Chelicerates are morphologically linked to the trilobitomorphs through the presence of intermediate forms such as the merostomoid *Cheloniellon*, with preoral chelicera-like appendages in addition to the antennae, and the aglaspidids. The latter had a phosphatic integument, one pair of preoral appendages (chelicerae or antennae?), and a long series of possibly schizoramous limbs, of which 3 or 4 pairs belonged to the head. Arachnids have 6 pairs of prosomal limbs. The Merostomata (taken to include scorpions, eurypterids and xiphosurids) apparently added one segment to the prosoma. As previously defined, the Merostomata constituted an evolutionary grade.

10. Many Cambrian arthropods of crustacean habitus have been considered as pseudocrustacean trilobitomorphs because of a supposed trilobitomorph character of the appendages. However, the cardinal characteristic of the trilobitomorphs, the lamellar spines, does not occur in the "pseudocrustaceans" as far as known, and it is not possible to tell whether the appendage branching is of trilobite or crustacean type. The general crustacean habitus in addition to crustacean type of carapace, rostrum, stalked eyes, tagmosis, presence or absence of telson, presence of uropods including "furcal rami", and arrangement of appendages along the body in different types therefore provide strong arguments for a crustacean affiliation of the "pseudocrustaceans". Some appear to be branchiopods, others may be regarded as malacostracans. It is important to remember that both eumalacostracans, leptostracans and archaeostracans are phyletic end-lines and that early malacostracan radiation must have included more variation than is evident from the surviving groups.

11. If the Uniramia MANTON, 1971, are considered to constitute a separate phylum, the consequence is that also the schizoramous arthropods must be raised to phylum level. Despite some similarities, arachnomorphs and crustaceans cannot at present be definitely connected and may be regarded as distinct phyla. Suitable names are Schizoramia BERGSTRÖM, 1976 for the arachnomorphs and Biantennata new phylum for the crustaceans.

E. Acknowledgements

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Addendum

WHITTINGTON (1977) recently redescribed the Middle Cambrian Burgess Shale arthropod *Naraoia* and considered it to be a trilobite of the order Nectaspida (recte: Nectaspidida). *Naraoia* was formerly regarded as a non-trilobite trilobitomorph, differing from trilobites for instance in the presence of only two large tergites, in the absence of exoskeletal mineralization, and possibly in the presence of a pair of eyes situated at the margins of the axial lobe (and not laterally as in trilobites). An additional difference was thought to be found in the terminal spine thought to be present in *Naraoia* and now not recognized by WHITTINGTON. This reclassification may have considerable impact on the ideas on trilobitomorph evolution and systematics and is therefore discussed here.

The characters in *Naraoia* which have been used for an association with trilobites are the following (WHITTINGTON 1977: 439-440): 1. There is a raised axial lobe. This is actually a common feature in trilobites, although not found in all trilobites. It is also found in other arthropods, as for instance in the trilobitomorph *Cheloniellon*. 2. There is one pair of antennae followed by a series of similar biramous appendages. This is a general and primitive (plesiomorphic) feature in the trilobitomorphs, and cannot therefore be used as evidence for relationship with any particular subgroup (in contrast to apomorphic features). 3. There are alimentary diverticula which ramify in the pleural area of the head. This is said to be the case also in trilobites (and obviously is so at least in some groups, like the agnostids), although the trilobite hinted at (*Papyriaspis*) has an anastomosing pattern quite different from the not anastomosing patterns in *Naraoia*. As it is also found backwards to the pygidium the anastomosing pattern more likely shows the course of a vascular system (BERGSTRÖM 1973 a: 5-6). In addition, STÜRMER & BERGSTRÖM (1973) have shown the presence of a single pair of alimentary diverticula not in the pleural lobes but in the axial lobe of the trilobite *Phacops*. Finally, alimentary diverticula with a similar arrangement are also found in other groups, as for instance *Burgessia*, xiphosurids and arachnids. 4. The limbs are biramous and somewhat similar to those of the trilobite *Olenoides*. Again, this is a feature which is fairly similar throughout the Trilobitomorpha and may be present in *Khankaspis* (Aglaspidida). 5. There are four pairs of limbs in the head. This is true for a least some more or less advanced trilobites, but the glabellar morphology of certain trilobites hints at the possibility of a secondary reduction of the first pair of postantennal limbs in those trilobites where the limbs are known. Therefore it cannot be stated with full confidence that the original numbers are identical. Moreover, various groups of trilobitomorphs and chelicerates have included from one to some 7 pairs of postantennal limbs in the head tagma, obviously not by adding one pair at a time but through primary division of the body into two functional tagmata. Within some groups the number may vary (the probably closely related *Marrella* and *Mimetaster* have one and two postantennal pairs, respectively), whereas an identical number is quite likely to be met with in different groups, more likely the more groups there are. An exact correspondence in this particular respect therefore cannot be considered proof of relationship.

WHITTINGTON (1977: 421) is of the opinion that a pair of reflective spots found close to the anterior end of the stomach are muscle attachments rather than eyes, in particular because they are not elevated. No other case of reflective muscle attachments is reported. They have formerly been regarded as eyes, and there is no reason why sessile eyes in a thin unmineralized exoskeleton would have to be elevated over the surroundings. In their position and outline, these spots conform with the eyes of *Cheloniellon*, whereas the position is different in trilobites.

The similarities with trilobites therefore are on the same level as the similarities with other trilobitomorphs. The number of podomeres, the unique dorsal arrangement of the exoskeleton, the lack of mineralization, the lack of protruding pleurally positioned eyes, eye ridges, and facial ecdysial sutures would seem to place *Naraoia* well separated from the trilobites. The position of the naraoiids as a group of their own among trilobitomorphs is therefore as justified as for marrellids, trilobites and cheloniellids, to mention a few examples. They would seem to be somewhat intermediate between the Marellomorpha on the one hand and the Trilobita-Merostomoidea on the other.

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