

Arthropod origins

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Abstract. Reconsideration of the position of trilobite-like arthropods leads to an idea of the last shared ancestor of known (eu)arthropods. The ancestry and morphological evolution is traced back from this form to a hypothetical ciliated and pseudosegmented slug-like ancestor. Evolution logically passed through a lobopodian stage. Extant onychophorans, Cambrian xenusians, and perhaps anomalocaridids with their kin (the Dinocaridida) may represent probable offshoots on the way. As such, these groups are highly derived and not ancestral to the arthropods. Results of molecular studies indicate a relationship to moulting worms, which at first could seem to be in conflict with what was just said. However, if this is correct, the arthropod and moulting worm lineages must have diverged when some “coelomate” features such as specific vascular and neural systems were still present. The moulting worms would therefore have lost such characters, either only once or several times.

Key words: arthropod origins, Anomalocaris, Tardigrada, Cambrian arthropods, Cycloneuralia, trilobitomorphs, eye ridge

Introduction

Most of our important information on early arthropods comes from such deposits as the Lower Cambrian Chengjiang beds, the Middle Cambrian Burgess Shale, and the Upper Cambrian Orsten occurrence. Valuable is also information on groups not represented in such well-known sources, for instance, on the oldest merostomes, the Lower Cambrian *Kodymirus* (Chlupáč and Havlíček 1965), *Kockurus* (Chlupáč 1995) and *Eolimulus* (Bergström 1968), and on deviating animals such as *Duslia* (Chlupáč 1988). Additional material made it possible for Chlupáč (1995) to reconstruct the appendages of *Kodymirus*. In the same paper he described *Vladicaris*, which is perhaps the oldest known crustacean – the oldest generally accepted crustaceans come from the Upper Cambrian (for instance, *Bredocaris* Müller & Walossek, 1988). *Vladicaris* was interpreted as a phyllocaridid malacostracan, but it seems to possess too many segments for a malacostracan. It could be a branchiopod crustacean.

Judging only from the morphology, we must confess that the arthropod group is of unknown affinities. This makes it a typical phylum, since “a phylum is a group of organisms of uncertain taxonomic affinities, that is, a problematic taxon” (Bengtson 1986, p. 3). It is true that scientists have been obsessed by the idea that arthropods are closely related to segmented worms, the annelids. There is now evidence from morphological and molecular studies that this cannot be the case (e.g., Eernisse et al. 1992, Eernisse 1998). Focus has therefore shifted to onychophorans and similar worm-like animals with legs and to the extinct Dinocaridida (*Anomalocaris* and its kin; Budd 1996, 1998a, 1999), after the latter were shown to have ventral appendages (Bergström 1986, 1987, Hou et al. 1995, Budd 1996, 1999).

It would help greatly if we could sort out the characteristics of the earliest arthropods. This would tell us what the

immediate ancestors might have looked like, and what they could not have been like. For instance, if the first arthropods were completely primitive in certain respects, they cannot be traced back to animals that are highly derived in these respects.

The problem with sorting out the sequence of events within the Arthropoda is that we have no obvious outgroup to compare with. This, in fact, is a problem also within the Arthropoda. Thus, for example, the trilobite-like arthropods form an interesting array of arthropods with primitive features such as a very low degree of functional tagmosis. Apparently they are a part of a larger group including also the chelicerates (together forming the Arachnomorpha) but for our purposes of comparison these more derived arthropods are not interesting. How are the trilobite-like arthropods (Trilobitomorpha or Lamellipedia) interrelated, and how are they related to other primitive arthropods? Hou and Bergström (1997) suggested that *Marrella* and its kin (the Devonian *Mimetaster* and perhaps the Ordovician *Furca*, see Chlupáč 1999) composed the first branch of lamellipedians. Others (Wills et al. 1998, Edgecombe and Ramsköld 1999) have followed this suggestion, but there may be alternative possibilities. Hou and Bergström (1997, e.g. Fig. 89) also suggested that exopod setae originated once, but immediately diverged into the flat setae characteristic of the lamellipedians and those with round cross section found in other aquatic arthropods. Also this conclusion can be challenged – after all, multiple origins of structures are more typical for evolutionary patterns than the once-and-for-all origination.

Lamellipedian evolution

Leif Størmer (1944, 1959) was the first to realise that the kind of limbs carried by trilobites was characteristic also of many other arthropods. He called them the Trilobitomorpha.

Because of difficulties to see the structures clearly in the fossils, he unfortunately included also arthropods that have turned out not to have this kind of limbs. This is a reason why Størmer's basic result has been neglected in most subsequent studies, and even the truly trilobite-like forms have been distributed irregularly among "non-trilobitoids" in a number of published phylogenetic trees. For instance, Briggs (1990, Fig. 3) had the trilobites, *Naraoia*, *Aglaspis*, *Emeraldella* + *Sidneyia*, and *Marrella* as four lamellipedian groups separated by non-lamellipedians. Also, when trilobite-like limbs have been identified in other arthropods, these have been claimed to be trilobites (*Naraoia*, *Tegopelte*). Bergström (e.g., 1978, 1981) noted that a fundamental characteristic is the presence of flat exopod setae (also known as filaments). In an attempt to get away from the locked situation associated with the concept of trilobitiforms, Hou and Bergström (1997) introduced the term Lamellipedia and illustrated a number of limbs with lamellar setae. Now, after more than a quarter of a century (and half a century after Størmer's first publication on the topic), the existence of this type of limb at last seems to be accep-

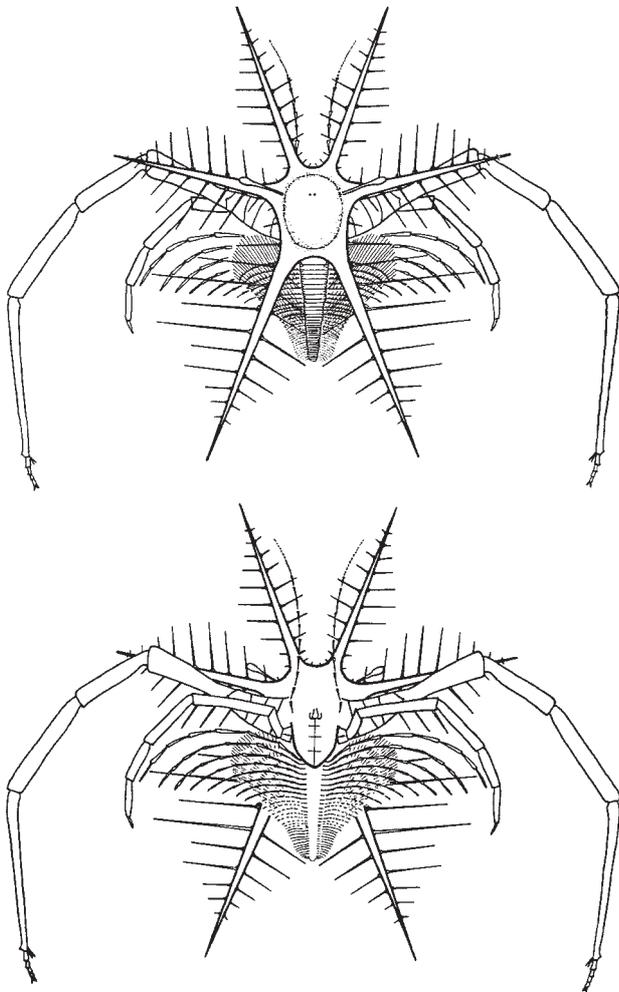


Fig. 1. The Devonian marrellid *Mimetaster hexagonalis* in dorsal and ventral views (from Størmer and Bergström 1976). Marrellids were previously regarded as "primitive" trilobitiforms, but a comparison with Lower Cambrian non-trilobitiform arthropods suggests that their unusual characters are instead signs of a derived state.

ted (e.g., Ramsköld and Edgecombe 1996; Walossek and Müller 1998; Wills et al. 1998, Edgecombe and Ramsköld 1999). This appears necessary for the understanding of the evolution and relationships of early arthropods. Numbers of cladograms not taking the structure of the appendages into account show arachnomorphs, crustaceans and other arthropods disorderly intermixed – even very recently. The lamellipedian structure – much like the amniote egg, the notochord, or the crustacean nauplius larva with its antenna–antenna–mandibula functional formula (Walossek and Müller 1990, 1997) – is not just any character. Its presence appears to be a decisive proof that its owner is a trilobitiform or, in other words, a lamellipedian arachnomorph.

Edgecombe and Ramsköld (1999) made a laborious attempt to come up with new results in the field. In effect, they confirmed the validity of most of the groups identified by Hou and Bergström (1997), although they found that *Retifacies* was (probably) misplaced. Many of their characters (1, 5–8, 10, 13–15, 17, 19, 21, 23, 28) have no bearing on the relationships between groups, since they are characteristic of individual groups or a part of one group. Others are questionable for various reasons. As for character 2, the boundary between head and trunk can hardly be accepted to run through a segment, even if sclerite margins may yield such an impression. Worse still, in most lamellipedians the functional head does not extend behind the antennal segment, and the extent of the cephalic shield covering a number of segments with unspecialised trunk-type appendages is both variable and without deeper interest. Some do not even have so much: with the fusion of tergites in helmetiids, even the cephalon disappears completely as a separate skeletal element (for instance *Skioldia* and *Saperion*, see Hou and Bergström 1997, Figs 64–67). It is also known (Birenheide 1971, Whittington 1971) that even the length of a more inclusive head tagma may differ between closely related forms, such as between *Marrella* with one post-antennal segment with specialised appendages and *Mimetaster* with two similarly equipped post-antennal segments. Thus the argument that the length of a "head shield" (cephalon) in Cambrian groups should have been as stable as are functional heads with specialised appendages in modern groups (Edgecombe and Ramsköld 1999, p. 265) is not relevant – "head" and "cephalon" are not compatible entities. It could also be mentioned that whereas the prosomal tagma is of stable composition in modern arachnids, this unit may carry one, two or three successive tergites. As so often in cladograms, the "character" studied is only a technical word with variable meanings.

Character 3 concerns the curvature of the antenna in a dead animal: what significance can it have? Some specimens have the antennae extending forwards, in others they are curved back to what may be a protective rather than a normal life position. Anyway, state 2 is only found in one of the accepted groups, and state 1 is fairly irregularly distributed in the resulting trees. As to character 11, frontal organs would be difficult to see without distinct sclero-

tisation, so the similarity between two genera is likely to be a chance one. The authors have overlooked that possibly similar organs were reported from *Mimetaster* (Stürmer and Bergström 1976). Character 12, hypostome attachment, is probably without any significance. Even in the best-known group, the trilobites, we have no idea of the state in the oldest representative because there is a variation in many subgroups, including the Early Cambrian olenellids. For 18: trilobites do not have edge-to-edge articulation in the axis, which makes them different from the only other group coded for the same character state. Some trilobites (e.g., lichids) may not have it at all. Character 20, presence of a pygidium: A pygidium is a simple structure likely to have formed several times (for instance, in old xiphosurid chelicerates). Character 22 regards the absence or presence of a pygidium with a median spine and two pairs of lateral spines. This number seems to lack any significance. The number will just grow with the accretion of segments to the pygidium. Thus in the groups supposedly united by two pairs, among the xandarellids *Xandarella* has one pair and *Sinoburius* two pairs of pygidial spines, and among the helmetiids one pair is present in *Rhombicalvaria*, two pairs in *Helmetia* and *Kuamaia lata*, three pairs in *Kuamaia muricata*, and (about) six pairs in *Skioldia*. A similar accretional series is known from Palaeozoic xiphosurids, with the end result being a shield that covers the entire abdomen. For character 29, the matrix has state 0 coded as 1, and 1 as 0. In the treatment of character 26, the authors have reconstructed the exopod of *Emeraldella* with a lateral flap, which would make it unique among trilobitiforms, but code it as terminal.

Characters 4 and 6 both concern the position of the eyes. Only trilobites are said to have dorsal eyes, after an “eye stalk” has been identified in both *Kuamaia lata* (Edgecombe and Ramsköld 1999, Figs 3:2, 5, 6) and *Xandarella spectaculum* (Edgecombe and Ramsköld 1999, p. 271, referring to Hou et al. 1991, Fig. 3B). However, it is clear that these eyes are dorsally positioned, probably looking through the head shield in the former, but through a hole in this shield in the latter. This is not much different from the condition in other arthropods with dorsal eyes: the optical nerve extends upwards through the head to the surface. In such a case it will not extend outside the head as a handle-like eyestalk, attached in both ends. What is seen is therefore the optical nerve extending to a dorsal sessile compound eye, much as we see the eye-ridge extending to the eye in many trilobites (Fig. 2). The authors were lucky to make this mistake. If they had coded these eyes as dorsal, they would have introduced a supposed synapomorphy with trilobites instead of a two-step difference that is more realistic because of parallel evolution (Bergström and Hou 2003). They still have such a mistake in the comparison between *Kuamaia* and *Xandarella*, however.

We do not intend to see what a correction of all mistakes would lead to. Instead, we try a new approach. It is quite possible that the selection of marrellids as an outgroup is incorrect. It is just possible that their different morphology may be a sign of a derived rather than a

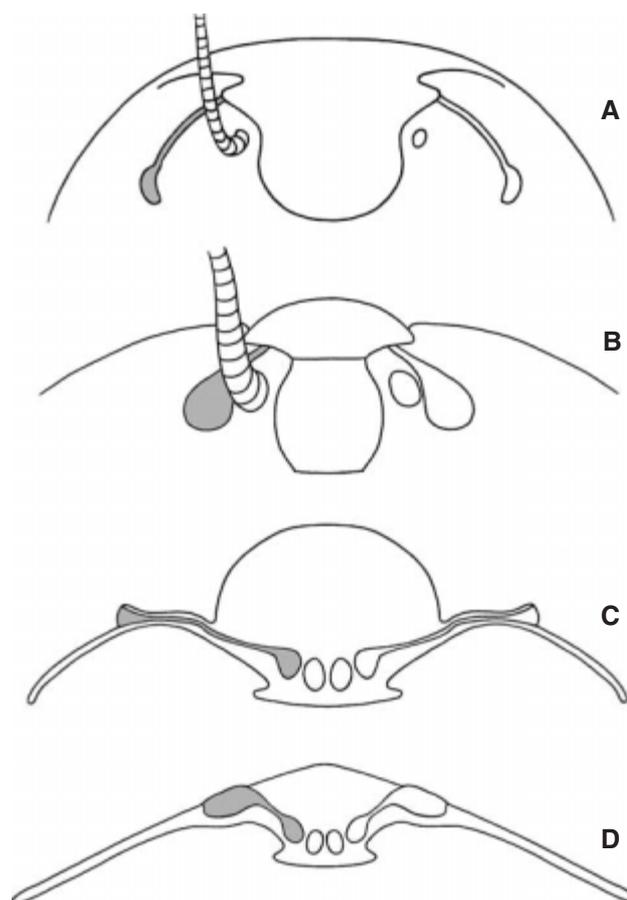


Fig. 2. The optical nerve as it can be reconstructed in trilobitiforms. A and C – the trilobite *Olenoides serratus*; B and D – the helmetiid *Kuamaia lata*. A and B – ventral view; C and D longitudinal view. Shaded: the optical centre of the brain, the optical nerve and the eye. In the trilobite, the eye ridge reveals the course of the optical nerve.

plesiomorphic state. If we try to compare lamellipedians with other arthropods looking plesiomorphic in many characters, fuxianhuids and canadaspidids come to mind as obvious choices for comparison. The lamellipedians coming closest to these in general appearance are not the marrellids but probably the xandarellids (Figs 3, 4), and to some degree also *Sidneyia*. Helmetiids have a structural similarity unseen in other lamellipedians: it is the separation of a rostral part in front of the head shield (or carapace). Since the ocular nerve is seen to emerge from under the rostral shield (Fig. 2; Edgecombe and Ramsköld 1999, Figs 3:2, 5:3) and the antennae originate behind it (Edgecombe and Ramsköld 1999, Fig. 6), it corresponds at least in part to the acron. It is notable that an acron separated from the main part of the head is similarly visible in fuxianhuids and canadaspidids (best seen in *Perspicaris*, see Briggs 1977), as well as in yohoiids.

Whereas most lamellipedians have a hypostome, *Sidneyia* shares the absence with non-lamellipedians. This may give us the starting-point we are looking for. *Sidneyia* lacks segmentation of the exopod and has a true head shield, covering only acron and the antennal segment. Also these character states are acceptable as being possibly plesiomorphic.

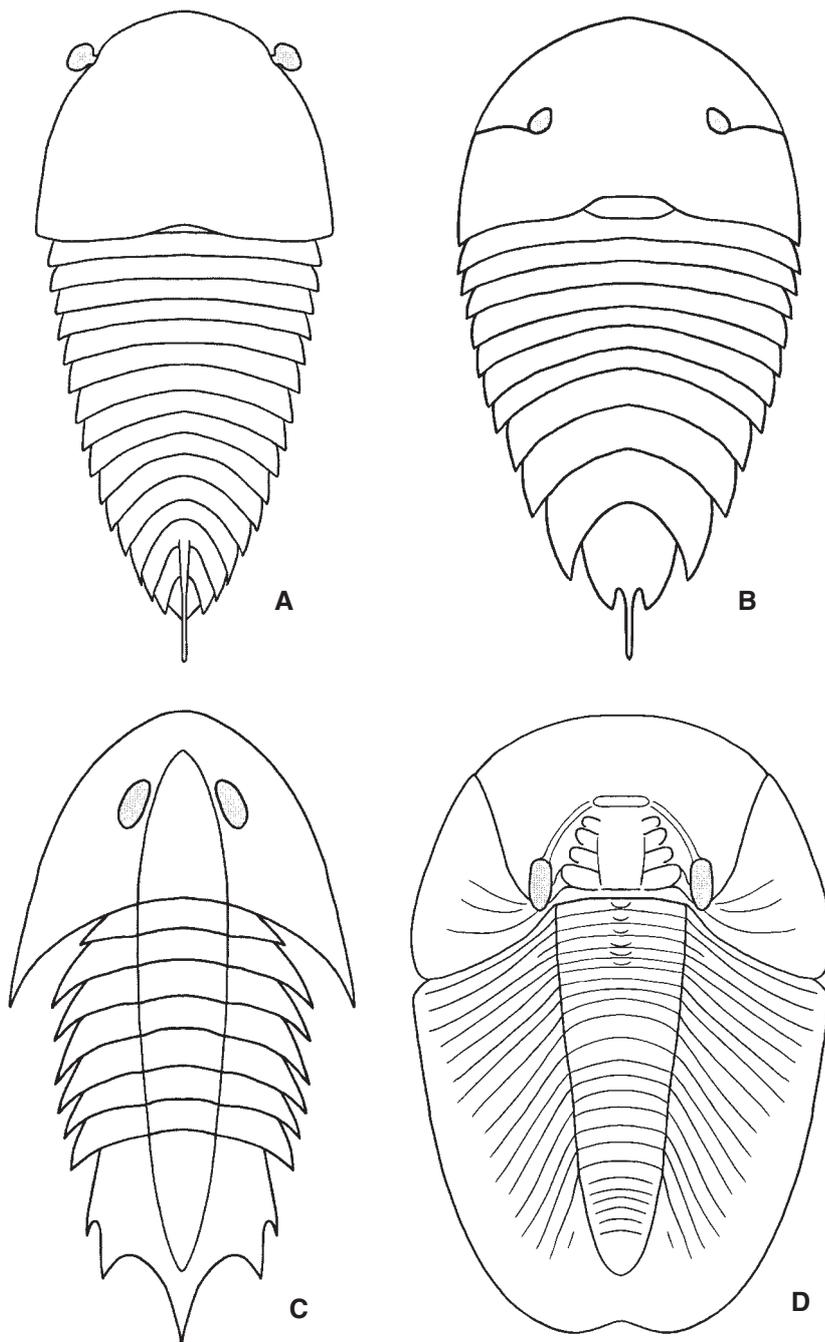


Fig. 3. The diversity among xandarellids as a demonstration of the evolutionary flexibility in early arthropods. A – *Cindarella*; B – *Xandarella*; C – *Sinoburius*; and D – *Phytophilaspis*. *Cindarella* has stalked eyes as a plesiomorphic character, but its long carapace fold is advanced and unique. The others have the eyes retracted along a long fissure (uncertain for *Sinoburius*) and have a cephalic shield rather than a carapace. *Sinoburius* has a very short thorax. In *Phytophilaspis* the post-cephalic body is covered by a single shield, which lacks the terminal spine characteristic to the other members. The eyes are exceptionally far back. The equal length of the thoracic tergites in *Sinoburius* indicates that each may correspond to one leg pair – but proof is lacking. In *Xandarella* the anterior thoracic tergites correspond to just one leg pair, and the posterior tergites to a defined larger number, 12 in the pygidium. *Cindarella* has one leg pair for each tergite anteriorly, but the leg pairs are more closely spaced further back, although without the whole number correspondence seen in *Xandarella*. The condition is unknown in *Phytophilaspis* that, however, demonstrates poor segmental correspondence between axis and pleura.

Rooting lamellipedian arthropods close to fuxianhuids and canadaspidids instead of after the formation of the first exopod setae means reorganisation of the tree. It is now obvious that marrellids must be moved up the tree. Advanced

character states for them must include a tight segmentation of the exopod axis and specialisation of a minimum of one limb behind the antennae. This seems to bring no problems for the tree. *Emeraldella* and *Retifacies* appear to retain a simple exopod blade, similar to that of fuxianhuids and canadaspidids except for the presence of lamellar setae. A number of forms with the exopod divided into proximal and distal blades may form a crown of the tree. Of these, helmetiids differ from the others in the morphology of the distal portion. As a group, they are also easily distinguished on their anterior eyes, separate rostral plate and a roof-like dorsum. Trilobites are characterised by calcification and a horizontal fissure for the eyes in early representatives. Naraoiids are recognised on the strong tendency to fuse the body behind the cephalon. Xandarellids, ultimately, tend to have a characteristic posterior embayment of the cephalic shield resulting in shrinking or bending of the next successive tergites, and most of them have the eye far back at the end of a deep fissure in the shield.

The apparently closely interrelated xandarellids – *Cindarella*, *Xandarella*, *Sinoburius* and *Phytophilaspis* – may be used for a demonstration of the evolutionary flexibility among the early arthropods. Thus, the first tergum is a shield or a carapace, the eye is stalked or sessile, anterior or posterior, the “cephalic” part includes four or six segments, the thorax has 7 to 23 tergites and perhaps 7 to 37 limb pairs, the number of legs corresponding to a tergite can be a whole or a fractionated number, the pygidium has one or two lateral spine pairs, or the thorax and pygidium are fused to a single shield which lacks spines (Fig. 3). *Phytophilaspis* is so strikingly different in superficial characters that its relationships were not realised at first (Ivantsov 1999 – he added to the oddity by introducing a segment-cutting crack as a biological character). This is a part of our great difficulties to understand the Cambrian animals: even a close relationship may be effectively disguised.

Arthropod beginnings

Accepting a rooting of trilobite-like arthropods close to fuxianhuids and canadaspidids, we can begin to figure out

what a shared arthropod ancestor of the two groups would have looked like. The body should have been segmented and fairly long, surrounded laterally by a pleural fold. The dorsum was sclerotised and separated into segmental tergites. There may not have been any tergite covering more than one segment, such as a head shield. The anterior end consisted of a pre-segmental acron carrying a pair of compound eyes. The first segment carried a pair of uniramous antennae. All successive segments carried clumsy paired legs with many short and identical podomeres (leg segments). The proximal part of the leg had a simple exopod blade. It is uncertain if segmentation was well controlled, so that there was only one pair of legs per body segment. The mouth was located behind the antennae, without mouthparts, and without hypostome protection. Older ancestors should be yet simpler.

We suggest that the earliest arthropods were sediment-feeders. The reason for this judgement is that a large proportion, perhaps about one-half, of all the arthropod species in the Lower Cambrian Chengjiang deposit were on an evolutionary level where legs had not yet been transformed into mouthparts. In fossils of these species, but not in others, the gut often contains sediment, occasionally to the degree that it is filled (Hou and Bergström 1997). Sediment feeding thus appears to have gone along with this primary, unspecialised condition.

The Dinocaridida as ancestors?

Collins (1996) included in his class Dinocaridida (misspelt Dinocarida) the anomalocaridids and their kin, including animals such as *Opabinia* and *Kerygmachela*. The Dinocaridida were first believed not to have ventral appendages (see Collins 1996), but we now know that some of them had lobopods, others segmented legs with ring-shaped sclerites and a large lateral flap (Bergström 1986, Budd 1993, 1996, 1999, Chen et al. 1994, Hou et al. 1995). They share several features with arthropods. Bergström (1986, 1987) and Hou et al. (1995) regarded them as not related to arthropods, but being a result of convergent evolution. Chen et al. (1994) regarded them as arthropods. Budd (1993) initially regarded them and arthropods as sister groups. Later on, he advocated that they were immediate arthropod ancestors (Budd 1996, 1998a, 1998b, 1999, 2002), and so did Dewel and Dewel (1998). Wills et al. (1998) ended up with the Dinocaridida and lobopodians–tardigrades–arthropods as sister groups. This places the Dinocaridida fairly far away from arthropods.

Above, we just tried to define the last shared ancestor of arthropods as we know them. An ancestor further back would logically be less specialised in an arthropod direction, although it could have had other types of specialisations. How do the Dinocaridida fit into such a scheme? Budd's schemes (e.g., 1998a, Fig. 11.10) have the Dinocaridida branching off one after another from the line leading to the arthropods. This means that several features are introduced only to be aborted again before the arthropods

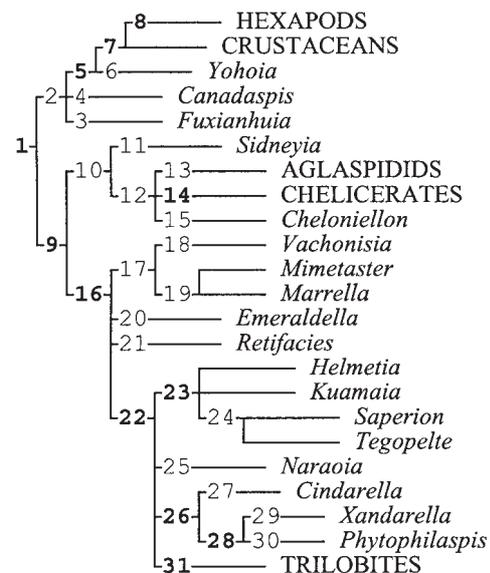


Fig. 4. An attempt to give an outline of arthropod phylogeny, with emphasis on the trilobitomorphs. **Bold numbers** indicate nodes with changes (marked as italics in the following) considered as particularly characteristic. 1 – initial arthropodisation, including the origin of body segments, exoskeleton, limbs, and the specialisation of (1st) antennae; 2 – tail with lateral appendages, acron separate from main “head” tergite; 3 – carapace, telson spine-shaped, segmental disorder between legs and tergites; 4 – carapace; 5 – strong setae, modern legs with long segments; 6 – first appendage chelate; 7 – crustaceans: *medially directed setae, coxa, mandible, nauplius larva, etc.*; 8 – hexapods: *loss of 2nd antenna, three-segmented thorax for locomotion*; 9 – Arachnomorpha: *tergum covers acron, wide pleural fold, exopod with lamellar setae, fewer and longer endopod segments, legs diverging to carry wide body*; 10 – tail with lateral appendages(?), wide ventral cephalic fold(?); 11 – Order Limulavida: *strong xiphosurid type leg attachment, spiny legs*; 12 – dorsal eyes fairly close to axis; 13 – Subclass and Order Aglaspida: *spine-shaped telson, possibly 4 cephalic legs, possibly phosphatic exoskeleton*; 14 – **chelicerates: long prosoma, loss (or remodelling?) of antennae**; 15 – Order Cheloniellida: *five limb pairs of two morphologies added to head, dorsal eyes*; 16 – **Trilobitomorpha (s.s.): hypostome**; 17 – Class Marrellomorpha: *pleural spines lost, exopod shaft multi-segmented, specialised leg pair added to head*; 18 – Order Acercostraca: *dorsum fused to single shield, three leg pairs in head*; 19 – Order Marrellida (= Mimetasterida): *carapace with “horns”, loss of pleural fold*; 20 – Order Emeraldellida: *lanceolate exopod setae, telson spine-shaped, tail with lateral appendages, five post-antennal segments in cephalon*; 21 – Order Retifaciida: *lanceolate exopod setae, three post-antennal segments in cephalon*; 22 – **trilobitomorph crown-groups: exopod end-flap**; 23 – **Subclass Conciliotergera, Order Helmetiida: helmetiid rostral plate, roof-shaped dorsum, initiated fusion of dorsum**, *helmetiid type dorsal eye without opening, lanceolate exopod setae, pygidium, telson spine(?)*; 24 – smooth margin; 25 – Subclass Nectopleura, *naraoiids: large pygidium*; 26 – **Subclass Petalopleura, Order Xandarellida: posterior cephalic embayment**, *small spiny pygidium, terminal tail spine*; 27 – carapace, *supernumerary legs posteriorly with segmental mismatch*; 28 – dorsal eye at end of slit from margin; 29 – *addition of two segments to cephalon*; 30 – *fusion of entire thoracopygidium*; 31 – **Subclass Trilobita: calcified exoskeleton, dorsal eye through horizontal slit**.

could come into being. These “unnecessary” innovations include dorsal “gill” structures, gut diverticulae, a terminal heavily sclerotised grasping appendage, a ring-shaped mouth cone composed of sclerites, gigantism, gnathobases, ventral sclerites, and a fixation in the number of trunk segments (Fig. 7).

We may make an alternative cladogram to check the validity of the cladograms and conclusions presented by Budd (for instance 1998a) and Dewel and Dewel (1998).

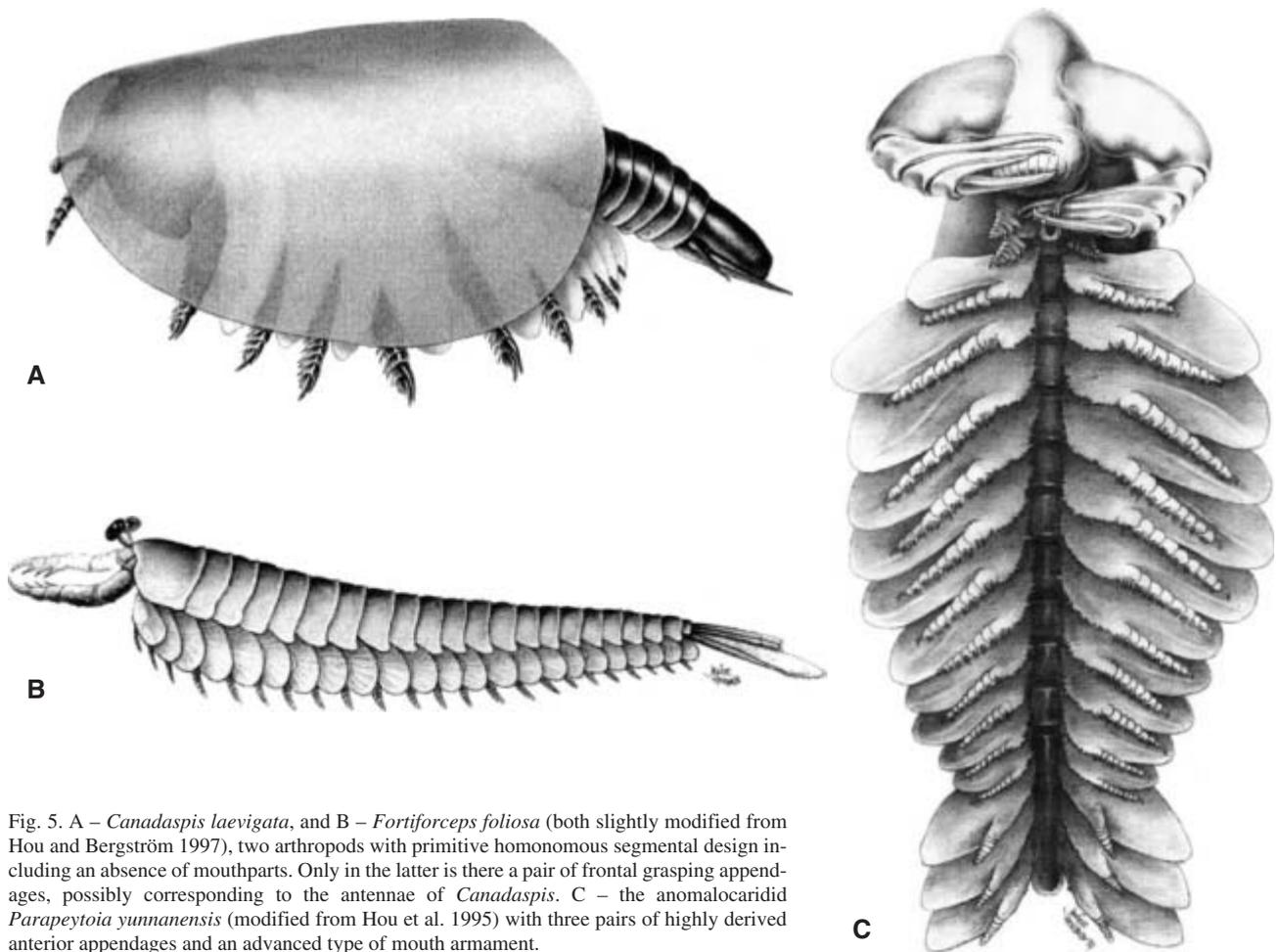


Fig. 5. A – *Canadaspis laevigata*, and B – *Fortiforceps foliosa* (both slightly modified from Hou and Bergström 1997), two arthropods with primitive homonomous segmental design including an absence of mouthparts. Only in the latter is there a pair of frontal grasping appendages, possibly corresponding to the antennae of *Canadaspis*. C – the anomalocaridid *Parapeytoia yunnanensis* (modified from Hou et al. 1995) with three pairs of highly derived anterior appendages and an advanced type of mouth armament.

The latter did not list all their characters. One reason for re-analysing is that some of their characters are not clear to us, another that we recognise some additional characters, and a third that we want to include all genera (except for the poorly known *Pambdelurion*) in order to avoid misleading shortcuts. In making a tree, *Kerygmachela* appears to be an excellent choice for an outgroup: it has lobopodian rather than segmented legs, the grasping appendages are not segmented, and it lacks the “tail fin” of other Dinocaridida. As seen, we agree with Budd (1996) that *Opabinia* and some other Dinocaridida had lobopods, and we recognise (Hou et al. 1995) the legs of *Cucumericrus* as being intermediate between lobopods and the segmented legs present in *Anomalocaris*. With this starting point, the rest of the tree comes into place as a jigsaw puzzle (Fig. 7). Characters are added one by one, virtually without reversals. We do not agree with Wills et al. (1998, Fig. 2.1), who placed *Kerygmachela* outside the Dinocaridida.

Looking for dinocaridid features that may serve as plesiomorphies for arthropods, we find a few. One of them appears to be the low degree of sclerotisation, resulting in usually very poorly preserved fossil remains. At least in some species, the body was covered by a wrinkled skin rather than by skeletal plates (Fig. 6). Another is a possible lack of segmental tergites (although such are somewhat questionably reported). A third is the presence of segmentation. A fourth is the entirely lobopodan legs of *Kerygma-*

chela (Budd 1999) and the apparently only initial segmentation of the walking leg in *Cucumericrus* (Hou et al. 1995). It is possible that also the type of ventral appendages could be accepted as ancestral, given that other features point in the same direction. Basically there is a walking leg medially and a flat flap laterally. The leg is a distal extension of the flap, and not the arthropod-type strong ramus on which the flap is a lateral outgrowth, but this could conceivably be the result of divergent evolution after a split of the lineages. Budd (1996, pp. 8–9, Fig. 8) suggested that the dinocaridid “gills” may be homologous to the “gills” of *Marrella* and similar arthropods. However, the latter are stiff setae situated on the ventral appendages, whereas the former are scales on the dorsal side of many Dinocaridida.

The differences should be hard to cope with for those who want to see the Dinocaridida as arthropod ancestors. As we see, Budd must reverse the evolution in a number of respects (Fig. 7) in order to derive arthropods lacking tagmosis and mouthparts from Dinocaridida having tagmosis and a complicated mouth-cone. All the Dinocaridida have a first pair of appendages, which are strongly specialised for grasping prey (and further specialisation of successive limbs in at least one species). This implies that we have fundamental problems. First, a plesiomorphic feature for arthropod ancestors must be expected to be the presence of a first pair without strong specialisation. Second, the first arthropods apparently were unspecialised sediment-feeders

(see above), and it is most unlikely that their ancestors were specialised carnivores. Third, there should be no mouth armament. Fourth, there should be no sign of tagmosis between the post-antennal limbs.

Thus the Dinocaridida were strongly specialised in a couple of features where specialisation is not acceptable for an arthropod ancestor. At the same time, they are more “primitive” than early arthropods in other respects. Structures were acquired in the following order: mouth armament and specialised limbs for preying > (in some:) transformation of lobopods to segmented legs. In arthropods it was the other way around. Thus, transformation of lobopods to segmented legs > specialised limbs for food catch (in some groups only) > mandibles (in some groups only). Our conclusion, now as previously (Bergström 1986, 1987, Hou et al. 1995), is that the Dinocaridida have acquired some arthropod features independently from arthropods, but not in the same temporal order, and that there is no ancestor-descendant relationship between the two groups.

Tardigrades or xenusians as ancestors

It has been suggested that tardigrades or Cambrian lobopodians, the xenusians, are ancestral to, or have a sister-group relationship to, the arthropods. Commonly the relationship suggested is indirect, with the Dinocaridida being intermediate (for instance, Dewel and Dewel 1998). Wills et al. (1998), as well as Giribet et al. (2001), suggested that tardigrades are the sister group of arthropods, and that this combined group has Cambrian xenusians plus modern onychophorans as the sister group. The tardigrades are very small, which is perhaps the reason why their anatomy is highly derived. For instance, they have a pair of unique mouth styles, which are probably derived from a pair of appendages, and they have a body cavity developing as an enterocoel (typically a deuterostomian character). It has therefore been difficult to make any judgements based on anatomical or morphological data. It is notable, however, that the tardigrade central nervous system is very similar to that of arthropods. The similarities include a brain divided into proto-, deuto- and trito-cerebrum and ventral nerve cords with distinct segmentally arranged ganglia. We will return to the tardigrades below.

Another difficult group is the Cambrian onychophoran-like lobopodians, the so-called xenusians. Opinions vary as to their affinities. From a superficial point of view, they look as if they may have been marine ancestors of modern onychophorans. Their variability is much wider, but this is no argument: we must keep in mind that ecological pressure minimises morphological variation in modern forms. It is much more problematic that the Cambrian forms lack an anterior appendage that may correspond to, and may have resulted in, the antenna of modern onychophorans. Xenusians and onychophorans may just be two or more unrelated groups that have acquired soft lobopod legs (Bergström and Hou 2002). Dinocaridids may be another attempt in the same direction. Still, it is most likely that ar-

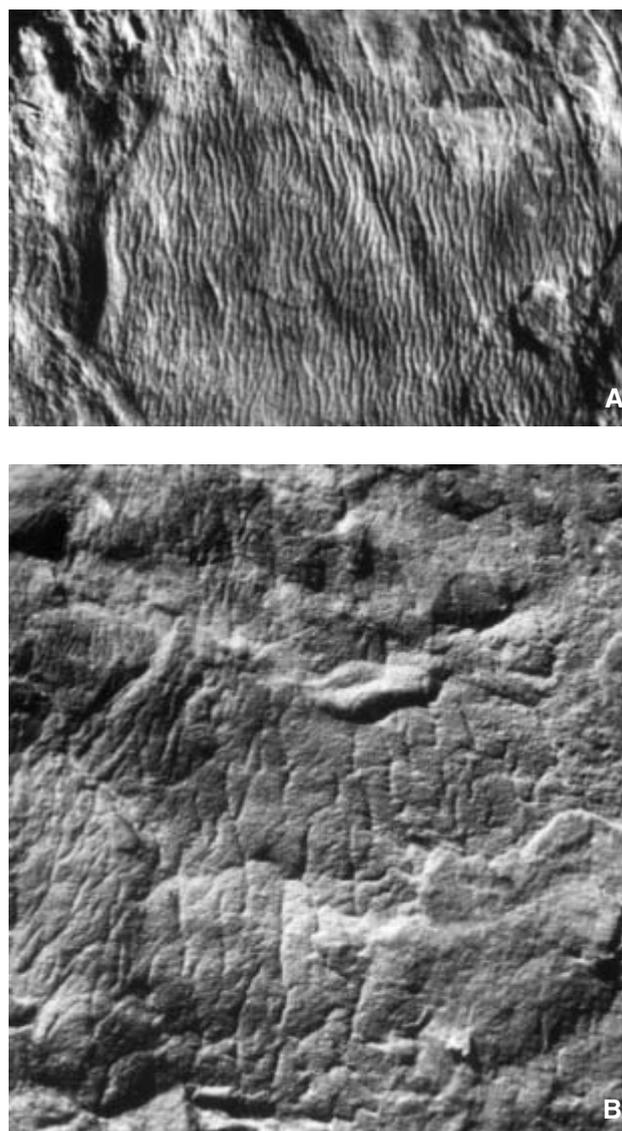


Fig. 6. The anomalocaridids were more or less poorly skeletonized. For instance, *Cucumericrus decoratus* Hou et al., 1995 had a tightly wrinkled skin covering their body, and the legs were of lobopodian, non-segmented type. A – a tight wrinkling with about 8–9 wrinkles in 1 mm. B – a coarser type of wrinkling with about 2 wrinkles per mm. Both illustrations are from the holotype of the species.

thropods passed a lobopodian stage. The endopods of *Fuxianhuia* and *Canadaspis* are remarkably similar to “endopods” in those Dinocaridida that have evolved beyond the lobopodian stage, such as *Anomalocaris* and *Parapeytoia* (compare Hou and Bergström 1997 and Hou et al. 1995).

The tree of animals

In our search for relatives of the arthropods in the animal kingdom we want to have an idea of the phylogenetic tree of the bilaterian animals. A classical bilaterian tree has two main branches, the protostomes and deuterostomes (e.g., Romer 1970, Fig. 10; Nielsen 2001, Figs 9.1, 11.1). The names allude to the idea that the mouth is a different struc-

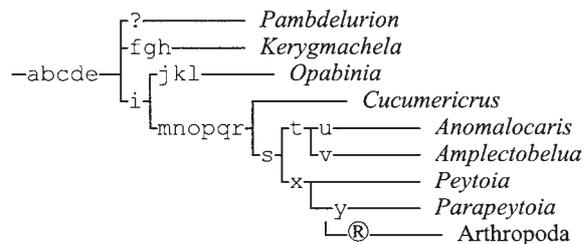


Fig 7. Cladogram illustrating dinocaridid phylogeny and evolution, as we see it. The arthropods are added loosely in the position as a sister group to *Parapeytoia* as suggested by Budd (1998a). This position necessitates a major reversal \textcircled{R} , involving all of the characters b, c, e, i, m, q, r and x. a – lobopodian appendages; b – frontal pair of spiny grasping appendages; c – mouth cone; d – dorsal tergites extending into pleurae; e – sword-shaped scales (“gills”) on pleurae; f – 11 trunk segments; g – segmental ornamented bands alternating with wrinkled zones; h – pair of tail “threads” (possibly a feature of the shared ancestor); i – three last pairs of pleural folds form tail flaps; j – 15 + 3 trunk segments; k – greatly prolonged shared soft cornus to grasping appendages; l – five large dorsal eyes; m – “exopod” flap with striped surface as adaptation to new swimming habits; n – initiated distal segmentation of endopod; o – endites (if not earlier); p – fully segmented grasping appendages; q – loss of dorsal tergites and pleural folds; r – scales moved to dorsum (if not there before); s – complete segmentation of endopod; t – double rows of spines along inside of grasping appendage; u – grasping appendage spines branching; v – grasping appendage has long proximal spines and strong, hooked distal spines; x – grasping appendage with tang on each segment, together forming large shovel; y – all tangs long, also terminal tang.

ture in the two groups. In the protostomes the adult mouth is derived from the embryonal gastropore. In the deuterostomes it is a new structure, it was thought (for instance, Nielsen 2001, p. 370).

However, certain morphological and molecular results have indicated that the concept of Deuterostomia is just a mistake caused by a life upside down in comparison with other animals. Therefore, organs such as the nerve trunk and heart occur on the “wrong” side of the body in vertebrates, the blood circulates in “wrong” direction, and the mouth seemingly forms on the wrong side of the embryo (Geoffroy St. Hilaire 1822, Patten 1912, Romer 1970, Fig. 11 and associated text, and Malakhov 1977 for morphological evidence; Arendt and Nübler-Jung 1994 and 1997, Holley et al. 1995, Hogan 1995 and De Robertis and Sasai 1996 for genetical evidence). Malakhov (1977) realised that deuterostomes are not all alike in this character. He noticed that, while the description may apply to the chordates, the non-chordate deuterostomes are typically protostomian in their embryology and organisation. Ignorant of Malakhov’s result, but starting from the result of Arendt and Nübler-Jung, Bergström (1997) and Bergström et al. (1998) demonstrated that the dividing line goes between the lancelets (Acrania) and the vertebrates, since the former still retain the protostomian habit of living with the main neural chord(s) down. The lancelet is oriented as vertebrates only in our textbooks. In conclusion, the deviating orientation of vertebrates means that the originally dorsal side of the chordate embryo has been compared with the ventral side of the protostomian embryo. No wonder then that the mouth appears to have different origins! Apparently there exist no deuterostomes in the meaning of the term. However, we can still use this misnomer because

hemichordates, echinoderms and chordates seem to form a natural major clade. The new understanding of the so-called deuterostomes is still “controversial” in the usual meaning of this term: it is not generally understood or accepted.

Another “controversial” view is the idea that segmented animals form a distinct clade, the Articulata or Euarticulata/Panarthropoda (see Nielsen 2001, Fig. 14. 2). This view is not supported by molecular data. In phylogenetic studies it now appears to be succeeded by another “controversial” idea, namely that arthropods are closest to those worms called Cycloneuralia by Nielsen (2001, pp. 320–323). All of these lack cilia and have a cuticle. As in other cases of lumping together of phyla, it is difficult to decide to what degree are the similarities a result of their common origin and to what degree are they caused by a convergence in bodily (and associated molecular) evolution.

It is likely that phylogenetic trees involving phyla can be strongly influenced by adaptational modifications. Such modifications include, for instance, two or three pairs of coelom sacs combined with sessility and tentacular ciliary feeding (with upstream-collecting ciliary bands) in adults, segmentation (co-ordinated organ repetition), and the formation of lobopods, perhaps also the formation of a cuticle with associated loss of ciliation.

Molecular evidence

Given the old view that deuterostomes and protostomes are two basal branches of the bilaterian tree, it would be difficult to accept having the former fairly close to arthropods in the tree. On the whole, scientists have (therefore?) avoided publishing tree alternatives with deuterostomes placed among the protostomes. Still some molecular trees produced in traditional ways also place deuterostomes in the proximity of arthropods (Carranza et al. 1997, Lipscomb et al. 1998, Zrzavý et al. 1998).

Eernisse (1998; see also references therein) described the situation regarding the popular 18S rRNA molecule in a revealing way, and we think that it is well worth referring to some of his major results. Thus, although sequences were available from 103 animals, virtually all studies published prior to his analysis included sequences from less than 20 animals (see his references). Eernisse referred to simulation and empirical studies indicating that about 40 sequences are needed for an in-group root node to be determined. Some work indicates that the opposite may be true, but Eernisse’s comparison between results of trees resulting from different numbers of sequences supports the results of the former studies.

In brief, one of his most interesting trees shows arthropods plus tardigrades as a sister group of an association of “moulting worms”, the cycloneuralians. The latter include chaetognaths, nematomorphs and nematodes (occasionally displaced). Just beneath, but so close that it could easily be interpreted as belonging to the previous worm group,

comes a group with the priapulids. All of these, from the arthropods to the cycloneurialian priapulids, are typically non-ciliated animals with a cuticle.

Bergström (1994) suggested two ways to get around the uncertainty resulting from mutational “saturation” hiding the branching order in very old radiations. One of these is to omit molecule positions with too much mutational “noise” inside accepted phyla and lower categories. The acceptable level of noise can be defined. The other is through the use of reconstructed sequences of shared ancestors. Thus, instead of using extremely derived molecules from a modern mouse to find the position of vertebrates, one could use the reconstructed molecule sequences from a Triassic ancestral mammal, or from a Devonian amphibian, or from an Ordovician fish. For molluscs and several other phyla it would be possible to reconstruct a Cambrian archetype molecule. This would greatly diminish the distance to the Cambrian radiation and the amount of mutational saturation. With this procedure, different molecules (cytochrome *c*, globins, 5S rRNA, 28S rRNA, srRNA) gave very similar phyletic trees, typically with molluscs, arthropods and deuterostomes in the top (Bergström 1991, 1994). Unfortunately, the popular 18S rRNA has failed to show a good potential for sorting out the order of branching at the base of the coelomates (Bergström 1991, Fig. 1; cf. Nielsen 2001, Fig. 57.2).

Yet it is possible that some of Eernisse’s (1998, Fig. 5.3) 18S rRNA trees, with deuterostomes and arthropods in high positions, may be good approximations. A much-simplified version of one of them is presented in Fig. 8. What is particularly disturbing with his trees is the lability in the positions of both deuterostomes and cycloneurialian worms. Thus nematodes occur either just below the arthropod–tardigrade group, or in a strikingly different position below the eutrochozoans. In the latter position we also find the gastrotrichs, which may be related to the nematode–nematomorph group. Given this situation, how sure can we be about the position of cycloneurialian worms as a sister group of, or perhaps stem-group of, arthropods?

Wheeler (1998) simultaneously tried to elucidate the position of the arthropods by combining a variety of molecular sequence and morphological data. He excluded the cycloneurialian worms. The groups included are molluscs, annelids, onychophorans, tardigrades, and the main arthropod groups. His result (Wheeler 1998, Fig. 1.5; cf. our Fig. 9) looks promising but we do not know where the cycloneurialians would have appeared had they been included. Eernisse’s cladograms have tardigrades often well inside the arthropod clade. Wheeler placed them distinctly below. It would also have been interesting to know how his addition of 18S rDNA, 28S rDNA and ubiquitin sequences and molecule structure data would have affected a tree based on molecular data alone. After adding morphological data and more sequence data, he instead presents the alternative constellation Crustacea (Hexapoda + Myriapoda). However, we note his statement (Wheeler 1998, p. 14) that almost all molecular work shows three results regarding arthropods: 1) the group Arthropoda is mono-

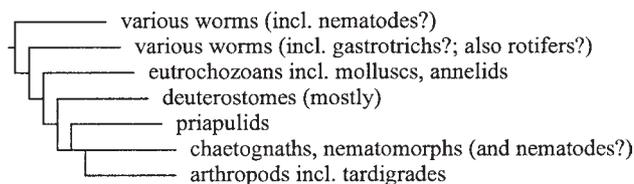


Fig. 8. The crown of Eernisse’s (1998) phylogenetic trees based on 18S rRNA, strongly simplified and summarized.

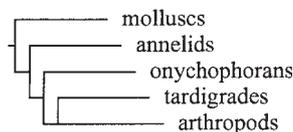


Fig. 9. Wheeler’s (1998) phylogenetic tree (much simplified) based on morphological plus molecular sequence data.

phyletic; 2) the constellation chelicerates + myriapods; 3) the constellation crustaceans + hexapods. Could it be that this result is correct, and that addition of morphological data blurs the result? After all, it is most likely that at least some of the classical characters thought to keep myriapods and hexapods together cannot be synapomorphies. For instance, tracheae must have been formed repeatedly after individual groups invaded land (cf. Haas et al. 2003). The pure molecular result, [(Chelicerata + Myriapoda)(Crustacea + Insecta)], indicates the possibility that myriapods may be derived from lamellipedian arachnomorphs. This would make the Mandibulata diphyletic.

Giribet and Ribera (2000) again attempted to sort up arthropod phylogeny, using 18S and 28S rRNA. Unfortunately, again only cycloneurialian worms were used as outgroups. In five trees out of six, nematomorphs and priapulids are closer to arthropods than are the tardigrades. The authors expressed their frustration as follows: “Despite the molecular analysis neatness, and the methodology used to analyse large data sets, especially of non-conserved molecular data, the phylogenetic conclusions of our study are not very encouraging per se. Those taxa that are difficult to position based on their morphology, for their unusual body plans, present the most unusual sequences as well.” Like other originally promising methods, the molecular methods have proven inefficient when tested. It appears as if in molecules, as well as in morphology, convergent evolution is the rule rather than the exception (Moore and Willmer 1997).

Garey (2003) presented good evidence that the unstable position of nematodes in molecular trees is a result of the use of both slow and fast evolving sequences. If only slow evolving sequences are used, the nematodes definitely end up as being close to the arthropods, with priapulids and kinorhynchids one step further away (Garey 2003, Fig. 3).

Arthropod origins

For long times it was considered as a fact that arthropods were closely related to annelids, because both groups are segmented. Molecular data have recently been used to pro-

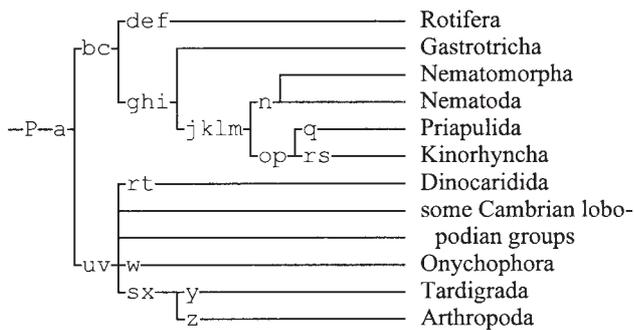


Fig. 10. Evolutionary tree based on the morphological and embryological data. P – plesiomorphic characters: polar bodies apical, spiral (quadrant) egg cleavage, ciliation, with ventral cilia for locomotion, mouth on ventral side for engulfing food from sediment, central nervous system with paired ventral cords and ring around pharynx, blood in vascular system with ventral and dorsal main canals, dorsal canal with heart pumping blood forwards. Apomorphies in selection: a – loss of primary larva; b – first egg cleavage equatorial; c – loss of blood and circulatory system; d – chitinous “mastax”; e – inner epithelial skeleton (“inner cuticle”); f – ciliary feeding apparatus; g – mouth terminal; h – pharynx radial; i – collagenous cuticle; j – loss of locomotory cilia; k – moulting of cuticle; l – armed introvert; m – loss of ciliated sole and creeping; n – loss of circular muscles; o – cuticle chitinous; p – rings of introvert scalids; q – blood filling large body cavity; r – rigid mouth cone; s – segmentation involving exoskeleton and ganglia; t – predatory habits, first appendages grasping; u – chitinous cuticle with moulting and loss of cilia; v – segmentation involving repetition of lobopods; w – mouth armed with modified leg pair; x – full loss of cilia; y – size decrease with loss of organs; z – segmented limb exoskeleton.



Fig. 11. Summary of our present understanding of basal bilaterian relationships. Flatworms are generally understood to constitute the first branch(es). The branching order of the other main groups cannot be sorted out with certainty. Deuterostomes include hemichordates, echinoderms and chordates. Bryozoans cannot easily be placed in any major group. Similarities with entoprocts are occasionally interpreted as a sign of relationship. Lophotrochozoans include annelids, pogonophorans, brachiopods, phoronids, molluscs, nemerteans, sipunculids. Ecdysozoans include lobopods and arthropods, cycloneuralians with gastrotrichs, nematodes, nematomorphs, priapulids, kinorhynchs and loriciferans, and possibly the gnathiferans with gnathostomulids, rotifers and chaetognaths, if these are not a main group of their own. The lobopod–arthropod subgroup must have separated from the rest at an early stage, before important “coelomate” characters were lost.

Some characters: a – bilaterality, ventral mouth leading to blind gut, locomotion by ciliated ventral side; b – anus, circulatory system with dorsal heart pumping blood forwards; c – sessility with ciliary feeding combined with pharyngo-tremation, 3-partite coelom, possibly loss of chitin; d – sessility with ciliary feeding, circulatory system reduced to funiculi; e – typical spiral cleavage; f – reduction of cilia, loss of primary larva.

duce phyletic trees showing that this is not the case. The new alternative, however, is far from crystal clear. Morphological evidence makes a close relationship between rotifers and chaetognaths fairly convincing, but in Fig. 8 they are far apart. Also gastrotrichs, nematodes and nematomorphs are thought to form a natural group, and are similarly widely distributed in the tree, nematodes even flickering from one end to the other. Is it possible that convergent evolution, for instance regarding the development of a cuticle with moulting, with collagen or chitin, and without ci-

lia, causes molecular similarity between, say, arthropods and certain worm groups?

We have to consider again the morphological evidence. In recent years more evidence has been retrieved on the embryology of the tardigrades (Eibye-Jacobsen 1996/97). Perhaps most notably, the styles extending out of the mouth are shown to be claws of a pair of appendages. This evidence is very strongly in favour of a close relationship between tardigrades and true arthropods. The nerves to the styli extend from the tritocerebral part of the brain. These appendages therefore seem to correspond to the post-antennal pair of (eu)arthropods (2nd antennae in crustaceans). It is difficult to imagine that a pair of legs would be moved into the mouth, had the mouth been terminal as suggested in the Ecdysozoa model (Eriksson and Budd 2000). The morphology therefore does not support a derivation from cycloneuralian aschelminths (ecdysozoan worms). It is noteworthy that no single aschelminth has any vascular system (blood is present only in priapulids) at all similar to that typical of most coelomates (arthropods, onychophorans, molluscs, annelids, hemichordates, etc.), with a dorsal heart pumping the blood forwards, and a ventral vessel leading the blood backwards. Only aschelminths (for instance rotiferans, nematodes) deviate from the embryological pattern with polar bodies at the apex: arthropods conform to the pattern found in other non-aschelminths. Aschelminths have a very derived egg cleavage pattern, whereas the least derived pattern in crustaceans starts in a spiralian-type way. Thus true arthropods have retained primitive features lost in aschelminths. This does not prevent arthropods to share an origin with aschelminths, but seems to prevent them having an origin from within the tree. Alternatively, aschelminth characters have evolved several times in parallel.

Onychophorans lack the close similarity with arthropods in, for instance, the nervous system, which has no ventral ganglia and no subdivision of the brain. They cannot be placed among the aschelminths for about the same reasons. If legs were “invented” only once, they would be related to the tardigrade–arthropod group. Furthermore, the various Cambrian groups should be placed in a similar position, but there is nothing to place these groups together. Fig. 10 shows this in outline. Other animal groups are ignored, since we do not seem to have evidence for placing them either inside or outside this diagram. However, as a surprise we find the so-called deuterostomes as the sister group to the Cycloneuralia–Panarthropoda in Eernisse’s trees, and the large array of eutrochozoans one branch further down the tree. The cycloneuralian “moulting worms” have long been considered to be lower on the scale than other “protostomes”, and deuterostomes are usually seen as a much more basal branch not at all related to the arthropod branch. However, this is based on a misunderstanding of the body orientation in chordates (Malakhov 1977), and more precisely in vertebrates (Bergström 1997, Bergström et al. 1998, Nielsen 2001).

Summarizing the evidence for animal relationships, the general result is that we seem to approach an understanding

of how phyla can be collected in large super-phyletic groups (Fig. 11). Of these, the flatworms appear to represent early branches. There is a general disagreement on how to arrange the others, indicating that the factual evidence allows us only to place them as equal branches of a bush. There is strong evidence that lobopodians and arthropods belong to the ecdysozoan branch, but they should have separated before the loss of the characteristic plesiomorphic circulatory system, lacking in all ecdysozoan worms. The compact character of the tree may mean that the “founders” of the four post-flatworm groups were all closely related. Lobopodians and arthropods, representing an early offshoot from ecdysozoans, would therefore also be fairly close to the origins of deuterostomes, bryozoans and lophotrochozoans. This would help explain the extreme difficulties to understand the relationships of arthropods and other animal phyla, whatever method is used.

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