

The fossil record and the early evolution of the Metazoa

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The appearance of the multicellular animals, or Metazoa, in the fossil record about 600 million years ago marks a revolution in the history of life. Molecular biology is continuing to increase our understanding of metazoan evolution, yet information from fossils is still an important component in deciphering metazoan phylogeny, and data on rapidly radiating animal groups place early metazoan evolution in a new perspective.

WOULD you like a game of 'Metazoan Phylogeny'? The prospect is daunting. The board encompasses the entire Earth: the only game ever attempted has already taken almost a billion years and shows no signs of a conclusion. The number of players varies (around 35 at the last count), and the strategic implications of such rules as may exist have not been fully worked out. Ideas about metazoan phylogeny are legion and often contradictory¹⁻⁴. A few principles are widely, but not universally, accepted, but no coherent phylogeny for the roughly 35 metazoan phyla exists. Speculation has been based mostly on anatomy, both adult and larval; meanwhile ultrastructural studies, immunology and biochemistry have added to the debate, and sometimes the confusion. Now, the picture has changed for ever. The true outlines of metazoan phylogeny seem to be emerging. This is due to advances in molecular biology, most notably data from ribosomal RNA⁵⁻⁸.

If the broad outline of metazoan phylogeny is now becoming clear, then surely all we need to do is commiserate with the authors of innumerable failed schemes constructed over the past century and promptly move on to more interesting problems. This would be a mistake, for three reasons.

First, the power of molecular phylogeny is not unlimited. If diversification is rapid, then the precise order of branching is very difficult to resolve^{8,9}. At present, unresolved branchings (polychotomies) persist, especially in triploblastic protostomes⁶.

Second, the new schemes of metazoan phylogeny tell us nothing about the actual anatomical and functional transitions between related phyla. For instance, molecular evidence¹⁰ suggests a close alliance between molluscs and annelids, but it is hard to imagine how an animal like the most primitive known annelid (an archiannelid?) was transformed into a primitive mollusc (a chiton?). The morphological gaps that, by definition, separate phyla, remain inviolate. We remain uninformed both about the now-extinct intermediates and the evolutionary processes that would have been responsible for the diversification of early multicellular animals into what we now perceive as distinct phyla, each with its own body plan.

Third, the new view of metazoan phylogeny requires a radical review of existing data, especially about ultrastructure, functional anatomy and biomineralization. Convergent evolution is likely to have been rampant.

If these problems can be solved, we would have an enhanced understanding of the constraints that guide evolutionary processes, the role of intrinsic and extrinsic factors in diversification, and a new appreciation of metazoan diversity: in short, the rules of the game.

My purpose here is to review how the fossil record of early metazoans might be integrated with the new phylogeny. Three types of fossil deposit yield relevant information: Ediacaran-type assemblages of soft-bodied animals from the latest Precambrian (Vendian), typified by the Ediacara fauna of South Australia; the earliest assemblages of animals with hard parts, from the Lower Cambrian; and the distinctive faunas from the Lower

and Middle Cambrian, exemplified by the Burgess Shale of western Canada (Fig. 1). All these deposits have attracted wide attention because of the apparent abundance of novel body plans. These so-called 'bizarre' fossils may help to unravel the basic structure of metazoan evolution (Fig. 2).

Pre-Ediacaran metazoans?

When did metazoans appear? The objective fossil record starts with the first Ediacaran assemblages (~560-600 million years (Myr) ago), but some evidence suggests that metazoans were already in existence as early as ~800-1000 Myr ago. Several lines of evidence indicate that metazoans originated at around that time, such as a decline in the diversity of stromatolites, possibly indicative of grazing and burrowing of the microbial-mat communities by metazoans¹¹. Other explanations for stromatolite decline, however, are also plausible. These include changes in ocean chemistry¹² or the microbial mats adapting to the evolution and arrival of a wide range of new types of protistan¹³. Second, trace fossils, including what may be metazoan faecal pellets¹⁴, are found in rocks of this age. But protists can produce structures similar to metazoan faecal pellets¹⁵, and no systematic survey for pre-Ediacaran traces, including bioturbation fabrics^{16,17} and geochemical anomalies around possible burrows^{18,19}, has been undertaken. Third, evidence from molecular biology^{20,21} indicates that the major lineages of Metazoa were distinct at least 700 Myr ago (suggestive of even earlier origins), but this too is disputed²².

Molecular evidence indicates a major diversification of eukaryotes⁸ perhaps ~1,000 Myr ago^{13,23}. Were metazoans part of that evolutionary event? Millimetres in size, perhaps interstitial in sediments, their inability to fossilize or leave obvious traces could explain their absence from Proterozoic rocks. The reconciliation of this idea with what is known of subsequent evolutionary events remains problematic (Fig. 1). If triploblasts (metazoans with three germ layers) occur in Ediacaran assemblages, then perhaps they too had an extended history in parallel with early diploblasts (two-layered animals such as modern coelenterates). Why the first, albeit hypothetical, metazoans never grew beyond a few millimetres in size is not understood. A persistently low concentration of atmospheric oxygen is one possible explanation, but alternatives include the late acquisition of collagen (not unconnected with the oxygen-concentration idea²⁴).

Ediacaran metazoans

The soft-bodied Ediacaran animals occupied a wide range of Vendian (Latest Proterozoic) marine environments and are now known from all over the world. Many of the fossils are generally interpreted as coelenterates, and some segmented forms as arthropods, annelids or other triploblasts. Nevertheless, Ediacaran fossils may not be representative of all Vendian metazoans. A newly described assemblage²⁵ from black shales in the Doushantuo Formation (Yangtze Gorges) in China

includes tubular fossils that might have been occupied by metazoans. The presence of fossils of seaweeds from the same deposits suggests that the remains of soft-bodied animals, not just their traces, will be found there in the future.

Molecular evidence is also consistent with the early appearance of coelenterates (cnidarians and ctenophores)⁶, but probably not independently of other metazoans²⁶. Only sponges⁸ and the microscopic placozoans may have branched off earlier. The chance of placozoans fossilizing is minuscule, but the apparent absence of Precambrian sponges is puzzling. Siliceous spicules of demosponges occur in strata in Iran²⁷ that may be of Ediacaran age, and claims for Precambrian sponge spicules²⁸ need re-examination, especially as protistan biomineralization²⁹, possibly of silica, is known from the preceding Riphean Period (Fig. 1)³⁰.

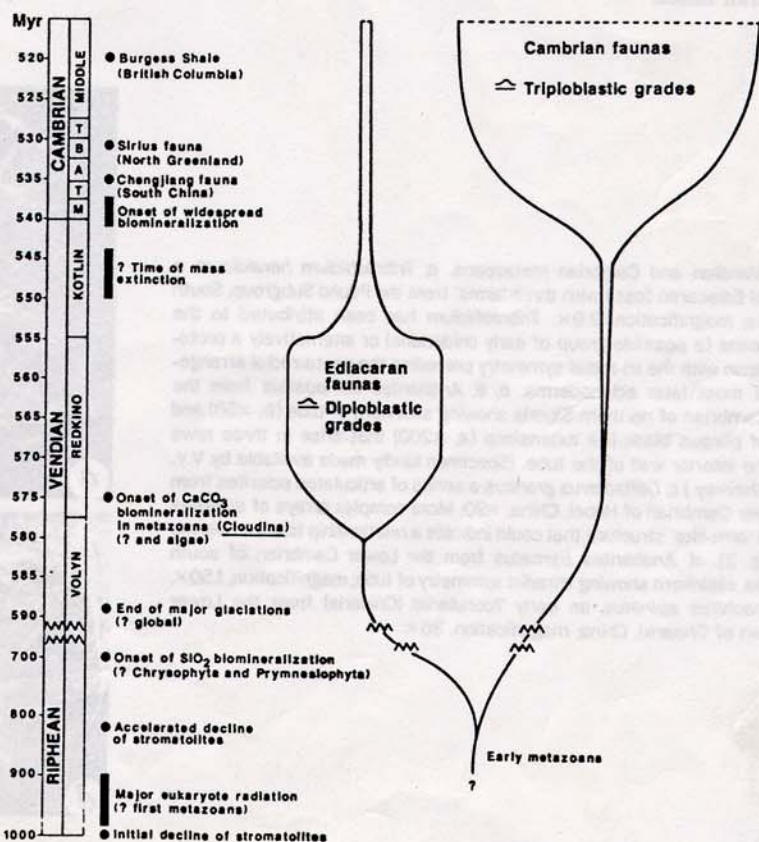
The primitive position of coelenterates⁴⁻⁸ accords well with the domination of the Vendian radiation by diploblastic animals. This supposition³¹ has been overshadowed by the 'Vendobionta' hypothesis^{32,33}, in which Ediacaran animals are thought to constitute an extinct clade of multicellular eukaryotes, neither diploblast nor triploblast, with a unique construction of tough cuticle and mattress-like body, and possibly the absence of alimentary tract, musculature and nervous tissue. This concept is open to debate, in that at least some Ediacaran fossils can be compared with known metazoans^{31,34}. *Inaria*, for example, may be an actinian coral³⁵, and the fivefold arrangement of putative feeding grooves in the minute epibenthic *Arkurua* suggests an affinity with echinoderms³⁶. Other organisms show evidence for muscular activity³⁴ and so presumably a nervous system, as well as the inferred presence of a circulatory system. An analogue of Ediacaran organization may be found in the modern deep-water scleractinian coral *Leptoseris fragilis*: instead of tentacles, it uses its ciliated surface as a food-gathering organ, and has an internal canal-like gastrovascular system that communicates with the exterior through pores³⁷. So is the Vendobionta concept completely redundant? Not necessarily, because the Proterozoic may

have witnessed the achievement of the multicellular grade of organization several times, and in quite unrelated lineages.

As for coelenterates, though, several arguments suggest that all four extant cnidarian classes can be recognized in early metazoan assemblages. Anthozoans are represented by penatulacean-like fossils³⁸ such as the Ediacaran *Charniodiscus*. Relatives in the Burgess Shale show what may be zooids³⁹. Actinians may have occupied bowl-like fossils such as the Vendian *Beltanelliformis*^{40,41} and the Cambrian *Berguaria*⁴². Biomineralization of cnidarians produced a variety of primitive coral-like fossils⁴³. *Kimberella* may be a cubozoan³⁸, represented today by the venomous box-jellies, whereas forms such as *Ovatoscutum*³⁸ may represent the floats of hydrozoans, as in the present-day Portuguese man-of-war. Jellyfish-like Ediacaran forms have been compared with 'true' jellyfish, or scyphozoans, but there the evidence is more tenuous.

Probably related to the scyphozoans are the enigmatic conulariids, with ribbed phosphatic tests and a characteristic tetradial symmetry. The Lower Cambrian carinacitiids (Fig. 3f) and hexagulaconulariids⁴⁴ are probably conulariids, and the Ediacaran *Conomedusites*⁴⁵ may also belong in this group. The xianguangiids⁴⁶, from the Burgess Shale-type fauna at Chengjiang in China (Fig. 1), are interpreted as anthozoan-like cnidarians on account of a basal disc, polyp-like body with possible septal impressions, and a distal crown of tentacles. The tentacles, however, are unique in bearing closely spaced pinules, a feature overlooked in the original description⁴⁶. One group of Ediacaran medusiforms is characterized by tri-radial symmetry. Cambrian descendants of these so-called trilobozaans (such as *Albuares* and *Tribrachidium*; Fig. 3a) may be represented by the anabaritids^{47,48}; their calcareous tubes are tri-radial (Fig. 3d), as defined by internal keels (Fig. 3b, e). Rare branching in anabaritid tubes⁴⁹ is consistent with a cnidarian grade. Cnidarians may also be represented by the tube-like byroniids⁴⁸, the possibly tentacle-bearing *Cambrorhytium*⁵⁰, the paiutiids with septate tubes⁵¹, and conceivably the tubular

FIG. 1 The geological framework of early metazoan evolution and related biological events. The geochronological scale takes the Precambrian-Cambrian boundary at ~540 Myr ago¹¹² and the Ediacaran faunas as ~580-560 Myr ago. The stratigraphic divisions of the Vendian and Lower Cambrian (M, Manykay; T, Tommotian; A, Atdabanian; B, Botomian; T, Toyonian) follow the Russian and Siberian standards. Metazoans are hypothesized to have arisen as part of a major eukaryotic radiation, ~800-1,000 Myr ago^{13,23}. Tangible fossil evidence includes the Ediacaran radiations of mostly cnidarian grade, but also stem protostomes and possible deuterostomes. The 'Cambrian explosion' is largely a triploblastic radiation, but diploblasts and triploblasts may have diverged substantially before Ediacaran times.



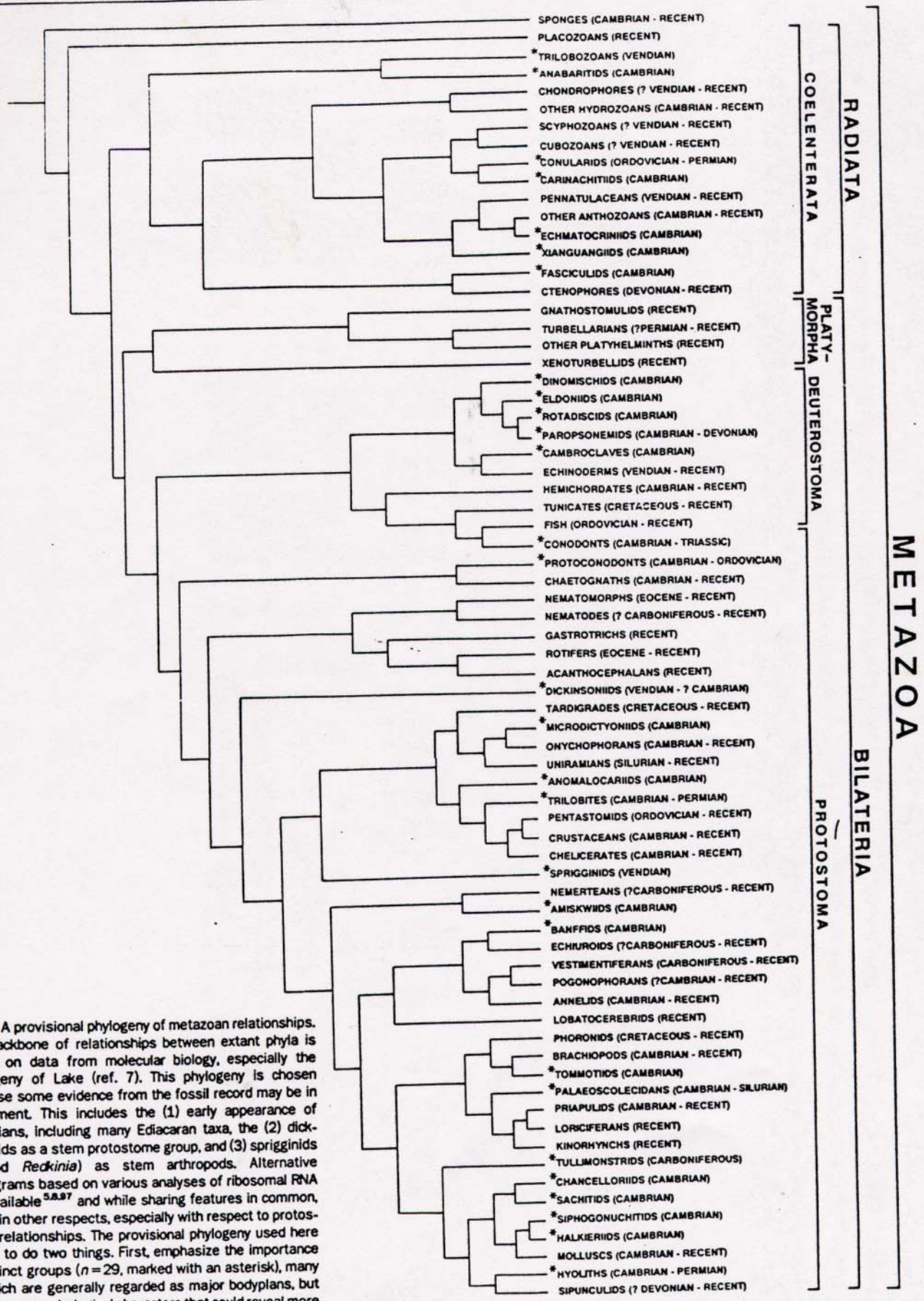


FIG. 2 A provisional phylogeny of metazoan relationships. The backbone of relationships between extant phyla is based on data from molecular biology, especially the phylogeny of Lake (ref. 7). This phylogeny is chosen because some evidence from the fossil record may be in agreement. This includes the (1) early appearance of cnidarians, including many Ediacaran taxa, the (2) dickinsoniids as a stem protostome group, and (3) sprigginids (? and *Redkinia*) as stem arthropods. Alternative cladograms based on various analyses of ribosomal RNA are available^{5,8,97} and while sharing features in common, differ in other respects, especially with respect to protostome relationships. The provisional phylogeny used here seeks to do two things. First, emphasize the importance of extinct groups ($n=29$, marked with an asterisk), many of which are generally regarded as major bodyplans, but may have morphological characters that could reveal more clearly relationships between disparate extant phyla. Second, this cladogram is an exercise in inference because many of the extinct groups remain poorly documented; the text offers justification for many of the placements. Note that the levels of branching are arbitrary and no precise metric is

applied to distance between the nodes. A number of clades are still too poorly known to be included. These include mobergellids, rhombocorniculids, nectocariids, cribricyathids, radiocyathids, escumasiids, myoscolexids, coleoliids, agmatans, typhloesids and ainktozoonids.

cloudinids. The last constitute an important Vendian group⁵², and are among the first metazoans to have acquired hard parts. Another candidate is the Burgess Shale *Echmatocrinus*, currently interpreted not as a cnidarian at all, but as an echinoderm, the earliest crinoid⁵³: the supposed tube feet are very large and could instead be anthozoan-like tentacles. In contrast, *Echmatocrinus* had plated structures on its polyp and tentacles but, unlike the co-occurring eocrinoids⁵³, the plates appear not to show a stereom structure.

The sister group of the Cnidaria is the Ctenophora, the comb-jellies. A pelagic habit and a delicate, gelatinous body account for their poor fossil record. *Fasciculus*⁵⁴, from the Burgess Shales and adjacent localities, is an early ctenophore, but differs from extant and Devonian ctenophores⁵⁵ in the number of comb-rows.

Triploblasts inherit the Earth

If Ediacaran assemblages are dominated by coelenterates, the ensuing Cambrian radiations are largely the irruption of triploblastic phyla. There are essentially two kinds of coelomate triploblastic metazoans: the protostomes and the deuterostomes. Protostomes, such as annelids and arthropods, are usually regarded as having spiral, determinate embryonic cleavage, and the embryonic blastopore is situated at the rear, at or near the site of the future mouth. Deuterostomes, in contrast (principally echinoderms and chordates) generally have radial, indeterminate cleavage, and the blastopore is associated with the position of the adult anus⁴.

Fossil evidence for the 'Cambrian explosion'⁵⁶⁻⁵⁹ is evident from the widespread rise of animal skeletons^{48,49}, the major diversification of trace fossils⁶⁰ and the Burgess Shale-type faunas⁶¹. But it would be unwise to draw too strong a line between Ediacaran and Cambrian faunas. The Ediacaran *Dickinsonia* may be a stem-group protostome: it is segmented, bilaterally symmetrical and has a clear anteroposterior axis^{31,34}. Other Ediacaran taxa could also be protostomes. *Spriggina* (Fig. 4e) could be a stem arthropod, and *Redkinia*⁵⁹ could represent mandible-like jaws: and if *Arkurua*³⁶ is interpreted as an echinoderm, the deuterostome lineage is also present in Ediacaran times.

Triploblastic diversification was rapid on a geological time-scale^{6,8}, and resolution of the branching order is consequently difficult. Refined stratigraphy, including recent advances in chemo- and magnetostratigraphy⁶², may resolve some orders of appearance on a global scale. As far as fossils go, though, local taphonomic bias in favour of the preservation of either articulated scale-like armour⁶³, phosphatized skeletal fragments^{48,49} or soft parts⁶¹ leads to a sporadic and incomplete record.

The 'Cambrian explosion' is a real evolutionary event, but its origins are obscure. At least 20 hypotheses have been proposed, and although arguments linking diversification to oxygen levels, predation, faunal provinciality and ocean chemistry all attract support, it is the case that 'The emergence of Metazoa remains the salient mystery in the history of life' (p. 17, ref. 58).

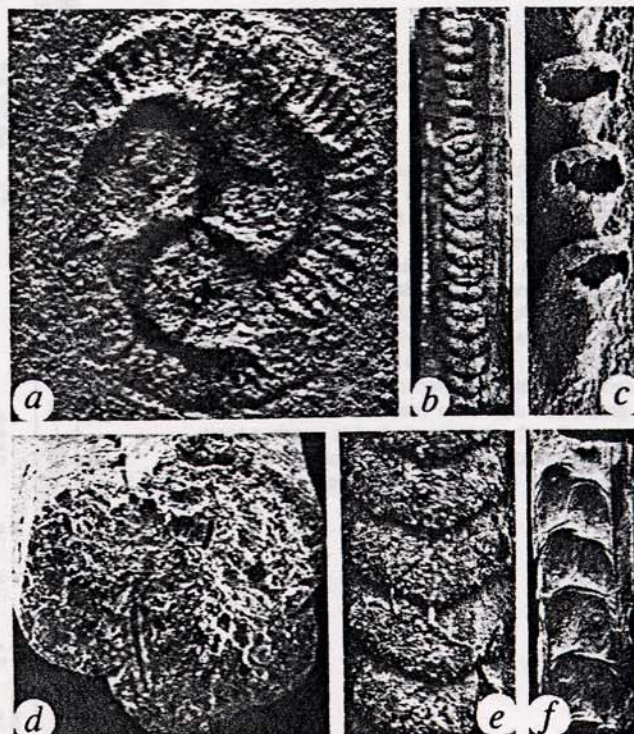
Deuterostome radiations

Molecular data⁶⁻⁸ suggest a profound evolutionary gulf between deuterostomes and protostomes. Among the Cambrian deuterostomes, the echinoderms have a good fossil record, and the inter-relationships between many of the supposedly disparate classes are becoming clearer⁶⁴. If the characteristically echinoderm skeleton of calcareous 'stereom' was acquired before the equally distinctive water-vascular system, then the aberrant cornutes (which have the first, but not the second) are a very early branch of echinoderms. The chordate-like features of cornutes, which have been proposed to indicate a close relationship with chordates⁶⁵, arose by convergence. The most primitive echinoderm with a water-vascular system appears to have been *Helicoplacus*, notable in having three rather than five ambulacra⁶⁴. These observations need to be reconciled with the pentaradial arrangement in the Ediacaran *Arkurua*³⁶, and also suggest an alternative assignment for trilobozoans (Fig. 3a). The cambroclaves may be allied to echinoderms, albeit more tentatively, because of their arm-like arrays^{66,67} of articulated sclerites (Fig. 3c). These structures seem to suggest a sessile, echinoderm-like form rather than the creeping, slug-like habit previously suggested for these animals⁶⁷.

Chordates appear with *Pikaia* from the Burgess Shale⁶¹. This creature superficially resembled the modern amphioxus and had



FIG. 3 Vendian and Cambrian metazoans. a, *Tribrachidium heraldicum*, a discoidal Ediacaran fossil with three 'arms' from the Pound Subgroup, South Australia; magnification, 2.9x. *Tribrachidium* has been attributed to the trilobozoans (a possible group of early cnidarians) or alternatively a protoechinoderm with the tri-radial symmetry preceding the penta-radial arrangement of most later echinoderms. b, e, *Anabarites compositus* from the Lower Cambrian of northern Siberia showing steinkern of tube (b; x50) and detail of porous blade-like extensions (e, x200) that arise in three rows along the interior wall of the tube. (Specimen kindly made available by V.V. Missarzhevskiy.) c, *Deltaclavus graneus*, a series of articulated sclerites from the Lower Cambrian of Hubei, China, x90. More complex arrays of sclerites have an 'arm-like' structure that could indicate a relationship to echinoderms (see Fig. 2). d, *Anabarites trymatius* from the Lower Cambrian of south Australia, steinkern showing triradial symmetry of tube; magnification, 150x. f, *Carinachites spinatus*, an early ?cnulariid (Cnidaria) from the Lower Cambrian of Shaanxi, China; magnification, 36x.



a bilobed head and pair of tentacles, as well as myotomes and a notochord which, unlike the amphioxus, appears not to have extended to the anterior. Gill slits may have been present, but are hard to identify with certainty in the compressed material available. Apart from conodonts⁶⁸, unequivocal evidence for fish does not occur until the Ordovician⁶⁹. In particular, the fossil *Anatolepis*, which first occurs in the Upper Cambrian and has been interpreted as the dermal scales of a heterostracan fish⁷⁰, is more likely to have belonged to an arthropod⁷¹.

The record of hemichordates is moderately good^{72,73}; the organic tubes of rhabdopleurid pterobranchs have a fair preservation potential, and the Burgess Shale '*Ottoia*' *tenuis* may be an enteropneust similar to the extant acorn-worm *Balanoglossus* (unpublished observations by S.C.M.).

The nature of the deuterostome ancestor is speculative. The eldoniids⁷⁴, a group of medusiform animals each with a prominent coiled gut (Fig. 4a) may repay consideration in this regard. They could represent a group of pre-echinoderm deuterostomes, as neither stereom nor a true water-vascular system appears to be present. Groups that may be related to the eldoniids include rotadiscids⁷⁵, paropsonemids⁷⁶ and *Velumbrella*⁷⁷.

Protostome radiations

Platyhelminthes appear to be the most primitive triploblasts but, apart from possible trace fossils⁷⁸, their fossil record is almost non-existent. Again, fossils have little to say about the aschelminthes (nematodes, rotifers and others) which may, in any case, be a polyphyletic grade. The nematodes and the related nematomorphs may be relatively primitive, but the present proximity of groups such as the rotifers and the related acanthocephalans⁷⁹ could require revision.

The branching pattern of the remaining protostomes is just as contentious. Lake⁷ upset established orthodoxy by arguing that the arthropods are paraphyletic, arising before annelids and molluscs. In contrast, R.A. Raff (personal communication) regards arthropods as the sister group of molluscs-annelids-brachiopods-pogonophorans, the latter assemblage arising as an unresolved polychotomy.

Arthropods and pre-arthropods. The fossil record of Cambrian arthropods is moderately good, and even the riot of supposedly disparate forms from the Burgess Shales seem to fall into a phylogenetically coherent scheme. The available cladograms⁸⁰ are as yet tentative, but as information about arthropods from the Burgess Shale-like Chengjiang⁸¹ and the Sirius Passet fauna from northern Greenland becomes available, cladistic analyses should improve.

More important is the nature of the pre-arthropod stocks. Apart from *Spriggina* (and possibly *Redkinia*), the anomalocariids⁸² currently attract much interest. They are very diverse, but they all have prominent lobate appendages, a well developed head with eyes, and sometimes a tail-fan. Undescribed material from localities adjacent to the Burgess Shale (D. Collins, personal communication) and the Sirius Passet fauna will help to make sense of this intriguing group. Anomalocariids may achieve importance, not as a supposedly unique clade of extinct animals, but as a group close to the ancestry of modern arthropods.

The onychophorans, represented today by *Peripatus* of southern tropical forests and its relatives, is now known to have enjoyed considerable success in the Cambrian. These early, marine forms included the hitherto enigmatic *Hallucigenia*⁸³, as well as *Microdictyon*⁸⁴, which before its discovery in the Chengjiang fauna (Fig. 1) was known only from dispersed phosphatic sclerites. The Chengjiang fauna has yielded several other onychophores^{85,86}, and other examples include *Xenusion* from Scandinavia⁸⁷. *Facivermis*⁸⁸ is peculiar because the anterior region bears five pairs of lobopod-like appendages, whereas the rest of the body is smooth. Sclerotization of such an animal, with jointed limbs replacing lobopods, could lead to an animal similar to phosphatized Ordovician fossils from Öland⁸⁹, regar-

ded as primitive pentastomids (still extant as parasitic animals whose postulated position in the crustaceans⁹⁰ has been recently confirmed by molecular evidence⁹¹). There is insufficient information to resolve the phylogenetic relationships between anomalocariids, onychophores and arthropods exactly, but the first group may be a glimpse of what early arthropod-like protostomes were really like. Recent molecular analysis of extant onychophorans supports their place in the arthropods, but questions their primitive status⁹².

Annelids, molluscs and relatives. Further protostome diversification led to a plexus of annelids, molluscs and near relatives. If the scheme of Lake⁷ is followed, then the annelids arose next. In the Burgess Shale there is an undescribed worm (Fig. 4b) with prominent lateral extensions that may be close to the basal annelid stock. The first definitive record of the annelids is as polychaetes⁹³, which are diverse in the Burgess Shale: their absence from the Chengjiang fauna may not be significant because they are present in the slightly younger Sirius Passet fauna. There is general agreement that pogonophorans are related to annelids⁹⁴. The elongate, organic-walled tubes of sabelliditids, abundant in the Vendian and lower Cambrian, may have housed pogonophorans. There are, however, differences in wall ultrastructure between these and modern pogonophoran tubes^{95,96}.

Molecular data suggest that the nemerteans, traditionally placed close to the platyhelminths, are coelomate protostomes, perhaps related to the annelids⁹⁷, but with a distinctive coelom (rhyngocoel surrounding the proboscis). The nemertean fossil record is very meagre, but amiskwiids⁹⁸ (represented by *Amiskwia* from the Burgess Shale) may represent an early stage of their divergence. Molecular evidence likewise places the brachiopods close to the annelids, and the chaetae in both groups are similar⁹⁹. Understanding of the initial radiation of brachiopods is improving, especially with the description of supposedly enigmatic groups^{48,58}. But pitfalls remain; for example, a putative brachiopod-like shell from the lower Cambrian of Irkutsk¹⁰⁰ could be a percussion fracture formed when the drill core was broken open, a telling illustration of the difficulties sometimes incurred in interpreting problematic fossils. Tommotiids, only known from dispersed phosphatic sclerites, have been reconstructed as slug-like animals¹⁰¹. Some sclerites, however, recall brachiopods, and comparison of shell ultrastructure¹⁰² supports the possibility that tommotiids and brachiopods are related⁵⁶.

A relationship between annelids and brachiopods may be difficult to reconcile with data from haemerythrin sequences that indicate a close relationship between priapulids and the inarticulate brachiopod *Lingula*¹⁰³. Nevertheless, current evidence suggests that priapulids (and the closely related kinorhynch and loriciferans, both without a fossil record), are part of the coelomate protostome radiation. Whether Cambrian priapulids^{50,104} will throw light on early protostome relationships is difficult to judge. Fossils called palaeoscolecidans, known to bear phosphatic sclerites¹⁰⁵, may be of interest here: specimens from the Sirius Passet fauna display what look like spiny snouts similar to those that distinguish priapulids, suggestive of a close relationship. Conversely, rows of phosphatic sclerites similar to those of palaeoscolecidans have been found in a Burgess Shale priapulid¹⁰⁴ (Fig. 4d). Of potential significance also is the Chengjiang priapulid *Cricocosmia*¹⁰⁶, which has two rows of convex shell-like sclerites on its trunk.

Molluscs may have evolved from a flatworm-like ancestor independently of the annelids⁴, but molecular evidence¹⁰ supports the possibility of an annelid link. The fossil record is silent on this transition, but the earlier stages of mollusc evolution are becoming clear. Cardinal evidence comes from the halkieriids⁶³ (Fig. 4c), which had an articulated armour of sclerites together with prominent anterior and posterior shells. A number of mollusc-like shells are known from the Cambrian and it is likely that some derive from halkieriid or related scleritomes.

*Triplicatella*⁴⁸, from South Australia and possibly southern Siberia¹⁰⁷, very probably comes from the scleritome of the halkieriid. *Thambetolepis*. Prominent folds on the shell margin of *Triplicatella* may mark sites of exhalent and inhalent water currents⁴⁸, perhaps connected with gills similar to molluscan ctenidia.

In turn, similarity of sclerite structure suggests a link between halkieriids and the Coeloscleritophora⁴⁸, a diverse Cambrian group that includes siphonoguchitids, sachtitids and chancelloriids. The first of these probably had a scleritome similar to halkieriids, with at least one shell and two types of sclerite¹⁰⁸. Chancelloriid sclerite structure does not support their earlier assignment to sponges, but overall body shape is consistent with a sessile habit. Chancelloriid sclerites were evidently embedded in a resistant cuticle (Hou Xiangang, personal communication). Sachtitids may be intermediate in form between chancelloriids and halkieriids⁴⁸.

Trace fossils

Even if no soft-bodied fossils had been preserved in the Cambrian, their adaptive radiations would be evident from the record of trace fossils^{58,60}. Although some traces, such as scratch marks, can be attributed to arthropods (or perhaps the related anomalocariids), in general tying traces to their makers is difficult. Trace fossils have consequently played little part in discussions of metazoan phylogeny, but they may nevertheless contribute useful information. Although many kinds of trace fossil are known from a long geological time span, some are confined to the Cambrian and could record extinct body plans, as well as details of early metazoan activities such as locomotion and feeding. For example, the giant trace *Climactichnites* from the Upper Cambrian of North America is believed to have been constructed by an otherwise unknown Metazoan of novel appearance¹⁰⁹.

Phyla and the role of problematic taxa

Schemes of metazoan phylogeny based on molecular evidence but which have been broadened to include information from fossils have been presented before^{110,111}. I have taken it a stage further with the inclusion of many groups usually seen as problematic, linking them with more familiar body plans. But this is not meant to belittle the magnitude of the adaptive radiations that took place in the Vendian and Cambrian periods. Within a period of about 20 Myr (taking the Ediacaran faunas as ~560 Myr old and the base of the Cambrian as ~540 Myr old¹¹²), the oceans changed from habitats housing a rich but effectively microscopic biota¹³, to one teeming with macroscopic animals engaged in a wide range of ecologies and presumably showing a degree of behavioural sophistication. Is it realistic to talk of a multiplicity of body plans in the Cambrian, far exceeding that of the present day¹¹³? At the other extreme, the argument that extant phyla maintain their identity back to the Cambrian¹¹⁴ offers no more than a tautology. Such phyla so persist because the only way they can be recognized is by reference to themselves. Consider the potential disagreements that surround the interpretation of various Cambrian fossils: are the pseudo-brachiopods⁴⁸ 'truly' brachiopods? Are the anomalocariids⁸² 'really' arthropods? Are hyoliths or stenotheocoids 'actually' molluscs? Definitions of major groups are less secure than sometimes imagined.

I argue that the supposed problematic taxa, now in imminent danger of elevation to a classic status as evolutionary enigmas¹¹³, hold the key to understanding many aspects of early metazoan evolution. This view contrasts with that of a 'pool' of generalized coelomate ancestors from which at least the main phyla of protostomes were derived^{114,115}. In such models the problematic taxa are further and separate derivatives, useful for documenting the range of metazoan morphospace but irrelevant for establishing relationships at the base of metazoan evolution.

Conclusion

Future advances will depend largely on molecular biologists and palaeontologists, although no data-source should be neglected¹¹⁶. The former need to tackle new gene sequences and extend the database. It is necessary also to enlarge our understanding of developmental mechanisms, and there is growing interest in the widespread occurrence of at least some regulatory genes in disparate phyla^{117,118}. What is equally important to know, however, is how these genes have either been co-opted or have changed their function, not only among metazoan phyla but in their protistan ancestors.

What can palaeontologists contribute? The discovery of Cambrian faunas similar to that of the Burgess Shale is likely⁶¹. Further preparation of collections of calcareous and phosphatic shelly Cambrian fossils may well produce dividends, and such disarticulated remains that are etched out of the rock should be held up against articulated scleritomes, either actual or hypothesized. The diversification of trace fossils still lacks a biological context, and there is an urgent need to test whether at least some Ediacaran fossils could be assigned to the Vendobionta, rather than to Metazoa¹⁰.

And yet, at the heart of the matter, a coherent explanation for the origin and scope of the early metazoan radiations is still missing⁵⁸. Family trees based on molecular data can be festooned

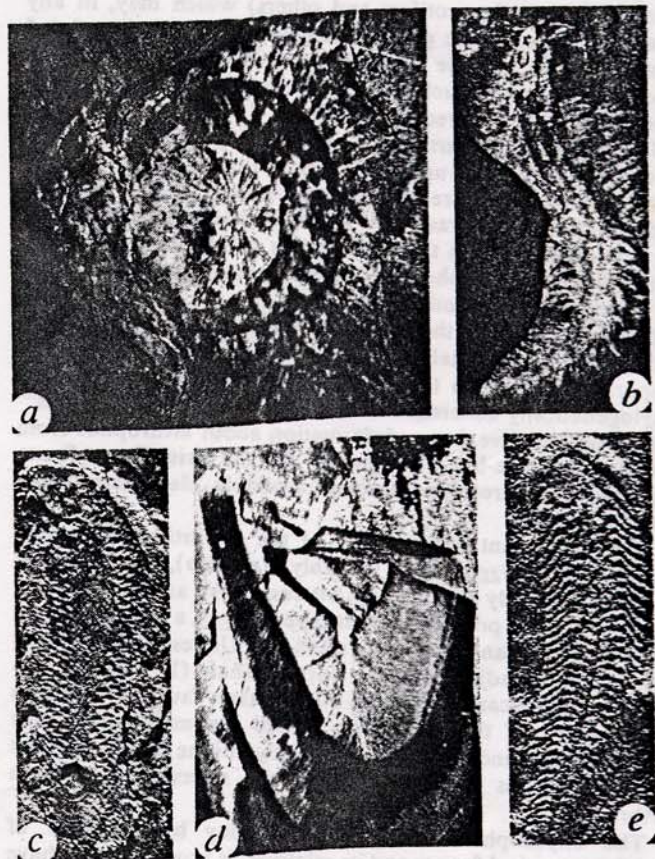


FIG. 4 Burgess Shale-type fossils (a-d) and a possible stem arthropod (e). a, *Eldonia ludwigi*, an early Ambulostome that may show features of pre-echinoderms; magnification, 1.1 \times . Specimen from Middle Cambrian (Burgess Shale), British Columbia. b, Unidentified worm from Middle Cambrian (Burgess Shale), British Columbia, possibly representing an early annelid; 3.2 \times . c, Articulated halkieriid from the Lower Cambrian (Buen Formation) of the Sirius Passet fauna, north Greenland; 1.5 \times . Halkieriids appear to represent a very early stage of mollusc evolution. d, The priapulid worm *Louisella pedunculata* from the Middle Cambrian (Burgess Shale), British Columbia; 0.85 \times . The trunk bears rows of sclerites, closely similar in arrangement to those of palaeoscolecidans. e, *Spriggina frundersi*, with segmented body and cephalic shield, a possible member of the arthropod stem group from the Vendian Pound Subgroup, south Australia; 2.3 \times .

with fossils but this is perhaps rather premature. Instead, we should be asking how the diversity of body plans so evident in the Vendian and Cambrian affected the shape of things to come. Evolutionary innovations such as nerve tracts, seriation, mesoderm, spacious body cavities and circulatory systems, all implied by the fossils already available, must have had profound phylogenetic consequences. Again, the causes of this diversification still remain a mystery, although changes in the concentration of atmospheric oxygen¹¹⁹, trophic resources, and ecological response, especially to predation, may have all played a part. Certainly the acquisition of hard parts as a deterrent to

predators is a compelling hypothesis¹²⁰. Increasing evidence for major changes in the environment during the Vendian and Cambrian¹²¹ also require further assessment. The once stagnant field of metazoan phylogeny is being rejuvenated by new discoveries that promise to call a wide range of scientific disciplines. 'Metazoan Phylogeny' is exciting to play, and we may, at last, be on the verge of working out some of the rules of the game. □

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