

PRELUDE TO THE CAMBRIAN EXPLOSION

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■ **Abstract** The Prelude began with the origin of Metazoa, perhaps between 720 and 660 million years ago (mya), and ended with the geologically abrupt appearance of crown bilaterian phyla that began between 530 and 520 mya. The origin and early evolution of phyla cannot be tracked by fossils during this interval, but molecular phylogenetics permits reconstruction of their branching topology, whereas molecular developmental evidence supports hypotheses for the evolution of the metzoan genome during the rise of complex bodyplans. A flexible architecture of genetic regulation was in place even before the appearance of crown sponges, permitting increases in gene expression events as bodyplan complexity rose. Neoproterozoic bilaterians were chiefly small-bodied but likely diverse, whereas in the earliest Cambrian, between 543 and approximately 530–520 mya, bodies that were complex by marine invertebrate standards evolved in association with body-size increases.

INTRODUCTION

The Cambrian explosion refers to a period when many living metazoan phyla first appear in the fossil record (reviews in Valentine et al. 1999, Knoll & Carroll 1999, Budd & Jensen 2000) in sediments that date from the middle Lower Cambrian, between 530 and 520 million years ago (mya), and lasting until perhaps 515 mya (see Grotzinger et al. 1995, Landing et al. 1998). During that interval, durable skeletons first became common, and many of the fossils can be assigned to living phyla with some confidence. Also, several localities dating from or immediately after the explosion interval (as Sirius Passet, Greenland and Chengjiang, China) have yielded fossils that were preserved under such exceptional circumstances that many details of their soft-bodied anatomy can be observed. Many of these soft-bodied forms belong to phyla that lack durable skeletons altogether and would not be known from those early times except for the unusually preserved fossil assemblages. It is not inconsistent with what we know of the arrangement of phyla in the tree of life that all living phyla had originated by 515 mya and perhaps earlier, although most of the phyla present in explosion assemblages are represented by extinct subgroups. There are also fossils that cannot be placed within living phyla, but may represent branches with unique bodyplans and histories, and can be thought of as extinct phyla in Linnean terms.

The richness of body design revealed in that relatively narrow slice of geologic time implies a significant evolutionary prehistory. There must have been an interval between the origin of Metazoa and the Cambrian explosion that witnessed the divergence and radiation of the numerous lineages within which many unique bodyplans were assembled. Although the fossil record of Metazoa extends back about 40 million years (Ma) prior to the explosion, it does not contain sequences of fossils that permit us to trace the steps in morphological evolution that led along the divergent branches to the Cambrian forms. Furthermore, we are not sure just when metazoan history began; some workers believe that metazoans had already become quite complex by the time that they first entered the fossil record. The one thing that can be said with confidence is that the biological factors necessary to produce the Cambrian explosion were evolved during late Neoproterozoic and earliest Cambrian times, an interval which forms a Prelude to that remarkable event.

FOSSILS OF THE PRELUDE

Figure 1 depicts a time line of major events registered by fossils during the late Neoproterozoic and Early Cambrian. The earliest known metazoan fossils that are well characterized are found in the Doushantou Formation, Guizhou, China, the age of which can be constrained between 590 and 550 mya (Knoll & Xiao 1999). The fossils are in phosphorites and in some cases have been phosphatized with such fidelity that individual cells can be observed. This assemblage has yielded eggs and blastula-stage embryos (Xiao et al. 1998), tissues with spicule-like structures that have been interpreted as sponges (Li et al. 1998), and small tubular structures that are suggested to be cnidarians (Xiao et al. 2000). There are also algal tissues and cysts encrusted with phosphatic material that have sometimes been mistaken for metazoan remains (Chen et al. 2000, see Xiao et al. 2000). The embryos, while undoubtedly metazoan, do not display the sorts of cleavage patterns or other features that would ally them definitively with either sponges, radiates, or bilaterians.

Other metazoan-like fossils that probably fall within the 590–550 mya interval include body fossils from Newfoundland (see Conway Morris 1988), but most late Neoproterozoic fossils that are putative metazoans are younger, from rocks dating between 550 and 543 mya (the base of the Cambrian; Grotzinger et al. 1995). The richest faunas have been described from rocks of the Russian Platform (the Vendian System; Sokolov 1952, Sokolov & Fedonkin 1984) and from South Australia (Ediacara Member of the Rawnsley Quartzite; see Jenkins et al. 1983), whereas other less diverse late Neoproterozoic faunas are known from about 30 localities and on all continents but Antarctica. Neoproterozoic fossils have been tabulated by Runnegar (1992a,b) and Bengtson (1992).

Figure 2 shows some terminology useful in discussing taxa of the Cambrian explosion and the Prelude; the examples are at the level of the phylum, but the terms are applied to lower taxonomic levels as well. Crown groups are those that include the last common ancestor of living members of a phylum (the crown

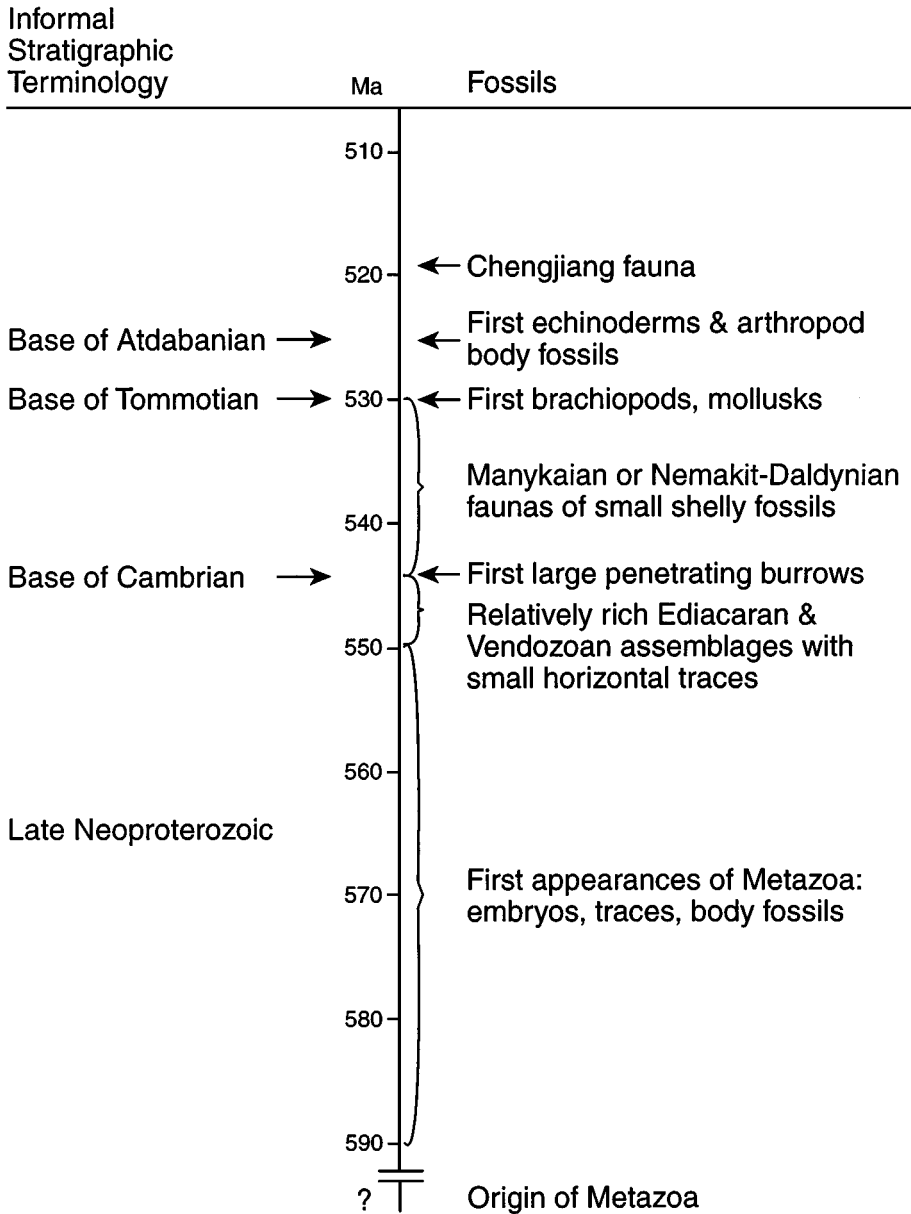


Figure 1 The sequence of appearance of key fossils during Neoproterozoic and Early Cambrian time.

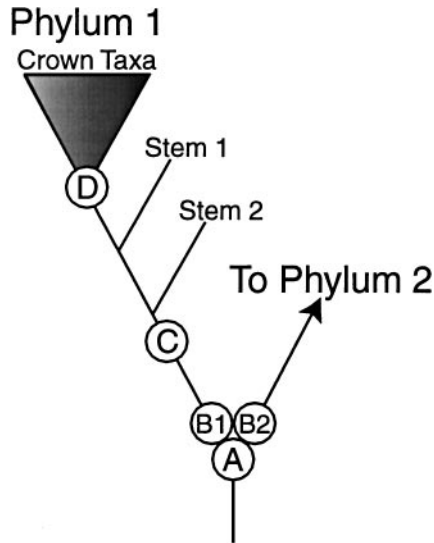


Figure 2 Terminology for ancestors and branches in the phylogenetic tree useful in discussing the early evolution of morphologically based taxa. A, last common ancestor of phyla 1 and 2; B1, B2, founding species of lineages leading to phyla 1 and 2, respectively (note that these species have identical bodyplans); C, stem ancestor of phylum 1; D, crown ancestor of phylum 1; stem taxa of phylum 1 indicated as stem 1 and stem 2.

ancestor), and all its descendants. Stem groups are those that include the first taxon that displayed the characteristic bodyplan of the phylum (the stem ancestor) and all of its descendants except those composing the crown group. In other words, stem groups contain extinct members of a phylum that lie on the branches of the phylogenetic tree that originated earlier than the crown ancestor. The founding species of phylogenetic branches that lead to sister phyla are sister species and have identical bodyplans. The last common ancestor of any two phyla has the bodyplan of neither sister phylum unless one is paraphyletic. The branchpoint between sister phyla is usually inferred from genetic information and is, operationally, a branch on a gene tree. Some of the generally recognized phyla, such as sponges, are certainly paraphyletic (i.e., sponges have descendants that are not sponges).

Except for sponges, the fossils in the Neoproterozoic assemblages cannot be assigned to crown groups of phyla with certainty, and it is not clear that any of them are even stem groups of living phyla, though some may be; an artist's reconstruction of important Prelude members is shown in Figure 3 (Erwin et al. 1997). Of these fossils, the group most likely to have living descendants is composed of radially organized, shallow cone-shaped forms commonly termed medusoids that were likely to have been benthic (*Ediacaria*, *Medusinites*). In some

specimens, several of these medusoid taxa have tentacles preserved around the circumference of what is presumably an oral disk, suggesting that they may be stem cnidarians, possibly sea-anemone-like stem anthozoans (the clade that branches at the base of crown cnidarians; Bridge et al. 1992, 1995; Collins 1998). Other Neoproterozoic forms have fronds or seriated blades (*Charnodiscus*, *Rangia*); some of these broadly resemble pennatulacean cnidarians (sea pens) but are structured somewhat differently (see Conway Morris 1992, Williams 1997) and there is no consensus on their affinities. There are also possible pelagic forms (*Eoporpita*, *Ovatoscutum*). Another group broadly resembles segmented, bilaterally organized animals (*Parvancorina*, *Praecambrium*), but they have not been shown to share derived features with crown phyla. There is an assortment of bag-shaped and flattened forms (*Ernettia*, *Dickensonia*), a triradiate group (e.g., *Tribrachidium*) and a slug-like creature that may be a stem bilaterian (*Kimberella*; see Fedonkin & Waggoner 1997), as well as a number of other, similarly enigmatic fossils. Finally, just before the close of Neoproterozoic time, several sorts of minute mineralized skeletons appeared; they are chiefly conical or tubular.

There is little agreement on how to handle the Neoproterozoic taxa. At one time there was a tendency to “shoehorn” the soft-bodied forms into a living group to which they bore some general resemblance (Glaessner 1984, Gehling 1991). At the other extreme, Seilacher (1989) suggested that those forms may not have been Metazoa, but rather represented a separate branch of multicellular organisms, in effect a kingdom of their own. Several workers have identified morphological groups among the Neoproterozoic fossils and have placed them in phyla of their own within Metazoa (see Pflug 1970; Fedonkin 1983, 1985). Many of the frondose and seriated forms have been placed in an extinct phylum, Vendobionta (Seilacher 1992). All things considered, the Neoproterozoic body fossils appear to be a mixture of stem eumetazoans (Metazoa minus sponges), stem radiates, and possibly stem bilaterians; they are certainly a strange cast of characters, and an unpromising one from which to derive the glaringly rich morphological diversity found during the Cambrian explosion.

One other very important set of Neoproterozoic fossils consists of the trails, burrows, and similar marks left on and within sediments by the activities of animals—the trace fossil assemblages, which appear by at least 570 mya (Jensen et al. 1999). As yet, none of the body fossils mentioned above can be implicated as the originator of any given trace fossil, nor can any specific traces be identified as having been formed by an organism with the bodyplan of any given crown phylum. However, the traces do indicate the sorts of behaviors that the animals of the time were capable of performing, which in turn suggests which structural grades had been evolved. Most of the Prelude traces are horizontal and the sediments were not much churned or bioturbated by animal activity, especially during formation of the earliest trace assemblages, suggesting forms that crept on the sea floor or burrowed only shallowly, near the interface with the water column. The Neoproterozoic traces are quite small, most near 1 mm in width, though a few are as large as 5 mm (Jensen et al. 1999).

The earliest traces appear to be simple meandering grooves, possibly surface trails, but they become more diverse in type and complex in cross section in younger rocks (see Crimes 1989). Some traces display levees at the sides and/or medial ridges that divide the grooves into lobes, and in other cases the traces were originally circular in cross-section, indicating burrows entirely encased within sediment. Surface locomotion in living marine invertebrates with body sizes as small as is indicated by Neoproterozoic traces is usually by mucociliary creeping—a cilia-propelled glide over the substrate on a mucus pad. In some animals, surface tension of the mucus trace will entrain sediment as ridges, with grooves forming where sediment has been displaced into the ridges (Collins et al. 2000). Mucociliary creepers with either radiate or bilaterian bodyplans are capable of making such surface traces, but it is doubtful that burrowing can be accomplished by mucociliary activity alone. Other small marine invertebrates that lack rigid skeletons, and most large ones, use body wall muscles to create peristaltic waves and/or a specialized anterior musculature to probe with an introvert, advancing their bodies over or through substrates and displacing sediment as they go. Many efficient burrowers use these methods. The dearth of burrows that penetrate the sediments to any degree during the Neoproterozoic suggests that fluid skeletal systems required for peristalsis or introvert extension were either absent or relatively inefficient, and remained so until approximately the beginning of Cambrian time.

EARLY CAMBRIAN FOSSIL RECORD

Fossil Metazoa of the Early Cambrian provide the best indication as to what must have been accomplished during the evolutionary Prelude to the Cambrian explosion. The base of the Cambrian is marked by the appearance of larger penetrating burrows. By definition, the boundary is drawn at the earliest appearance of the trace fossil *Trepnichnus pedum* in the Chapel Island Formation, Burin Peninsula, Newfoundland. *T. pedum* is an arcuate horizontal burrow from which branches rise to probe toward the surface. The earliest Cambrian Stage, the Manykaian or Nemakit-Daldyn, began approximately 443 mya and lasted until the explosion, a period that is at least 13 Ma long and may be as long as 23 Ma (Grotzinger et al. 1995, Landing et al. 1998). Lower Cambrian trace fossils are generally larger than those of the Neoproterozoic (the width of many traces comes to be measured in cm rather than mm) and bioturbation tends to increase in intensity and depth during that Epoch (see Droser et al. 1999). Minute skeletons and skeletal elements of metazoans (small shelly fossils; Mathews & Missarzhevsky 1975) become more common during the Manykaian (Figure 1; see Brasier et al. 1996), although none are definitively assigned to crown phyla.

Figure 4 shows the earliest appearances of crown phyla in the fossil record. The explosion itself, beginning at the base of the Tommotian Stage, is marked by shell beds containing small shelly fossils that include crown bilaterian phyla (stem groups of brachiopods and mollusks), probably their earliest known occurrence (see Rozanov & Zhuravlev 1992, Bengtson & Conway Morris 1992). In the

local depositional history. However, there are sections with older rocks that contain small shelly fossil faunas (Brasier et al. 1996), but they lack the diversity of the Siberian Tommotian and its correlatives and are not known to contain crown bilaterian phyla. So while conceding that the term “explosion” is hyperbole, the early Tommotian fossils do usher in a record of bilaterian phyla that by the close of the Atdabanian is consistent with the evolution of stem ancestors of all crown phyla. It is possible that some crown phyla may then have been represented only by ancestral lineages in which the characteristic phylum bodyplans (and therefore the stem ancestor) had not yet evolved. However, the phyla for which this possibility exists tend to be precisely those that are small and soft-bodied with poor fossil records, or that lack fossil records entirely (Figure 4), so to claim them as having evolutionary histories different from the phyla for which better records exist smacks of special pleading. While recognizing that their presence in the Early Cambrian is not confirmed, the absence of those soft-bodied forms is most likely due to nonpreservations.

METAZOAN PHYLOGENY

Major advances in understanding the evolutionary relations among phyla have come from the introduction of techniques of molecular phylogenetics. Most of the information has come from a single molecule, small subunit rRNA (SSU rRNA), which has identified a series of early branches (sponges and radiates) succeeded by the founding of bilaterians and their branching into three major alliances—Deuterostomia, Ecdysozoa, and Lophotrochozoa (Figure 5). Details of the branching topologies within the bilaterian alliances are not yet definitively established, though there is some support for the arrangements suggested in Figure 5. Members of the prebilaterians and of all of the bilaterian alliances occur during the Cambrian explosion. Thus, these records establish a minimum age for the origin of the bodyplans of the phyla involved, most of which are represented by stem forms. The age of the last common ancestors of crown phyla, and of earlier nodes such as those of the protostome/deuterostome and ecdysozoan/lophotrochozoan ancestors, are clearly significantly older than the Cambrian explosion but are not otherwise constrained by metazoan fossil data.

One approach to estimating the age of those ancient nodes is to use the rate of molecular evolution as a “clock.” If rates of molecular change can be calibrated from portions of the fossil record wherein times of divergence are closely constrained, they may then be applied to estimating the age of divergences for which no fossil record is available. Unfortunately, the rates of molecular evolution are not clock-like; different parts of molecules evolve at different rates, molecules within the same lineage vary in their rates of change over time, different molecules evolve at different rates, and homologous molecules in different taxa evolve at different rates. There have been many attempts to cope with such problems, but clock dates estimated for the deep branches of bilaterian clades have varied from 1.5 billion years ago (probably before the protistan ancestors of metazoans had appeared)

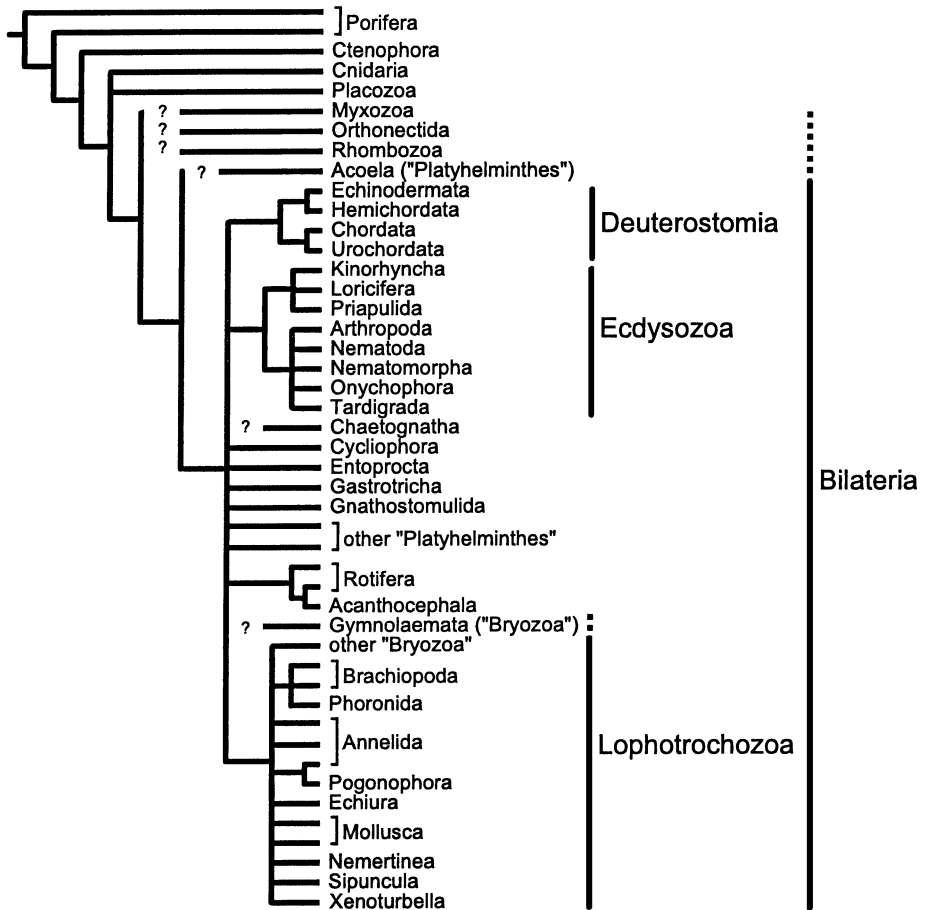


Figure 5 A conservative phylogenetic hypothesis of metazoan phylum-level groups based on SSU rRNA molecular sequence comparisons as reported by various investigators. The lack of resolution within several alliances, such as within Lophotrochozoa, is usually attributed to a radiation of ancestral species in such a narrow time frame that there were few informative changes in the SSU rRNA molecule; this radiation may have occurred late in Neoproterozoic time. From Collins & Valentine 2001.

to between 600 and 700 mya. Molecular clock estimates of the branching points of sister phyla, and therefore of the age of the ancestors of the clades involved, are nearly all significantly older than estimates based on fossils, suggesting either a systematic bias in molecular clock ages or a very long history between the branchpoint and the stem ancestors. It is possible that rates of molecular evolution were particularly high during the evolution of novel bodyplans, even in DNA that does not code directly for the morphological features that are undergoing change,

which might account for some of the disparity between fossils and molecules. For discussions of molecular clock dating see Ayala (1997), Bromham et al. (2000) and references therein. Non-clock methods of dating nodes are now coming into use (see Sanderson 1997, Kishino et al. 2001); applying them to very ancient nodes will be challenging.

MODELS OF METAZOAN EVOLUTION DURING THE PRELUDE

As the fossil data that can be used to interpret the evolution of early metazoan bodyplans before the Tommotian Stage is relatively poor and enigmatic, the appearance of disparate metazoan fossils during the explosion, revealing a rich array of relatively complex animals, comes almost without warning. The contrast between the pre- and postexplosion fossil record raises the questions of what sorts of animals were present; and why were they able to produce stem lineages—bodyplans—of most, if not all, crown phyla.

The Nature of Prelude Faunas

One of the major points established by the trace fossil record is that ambulatory benthic animals of the Neoproterozoic were small-bodied. Reconstructions of early bodyplans must take this observation into account; the presence of bilaterian features whose origins are associated with the requirements of larger body sizes are difficult to account for in Neoproterozoic faunas. It might be postulated that evolution of larger bilaterian body sizes and more complex features occurred among pelagic forms that escaped fossilization, though it is generally conceded that the major design elements of basal branches of marine invertebrate bodyplans, with the possible exception of urochordates and chordates, are adaptive to benthic life. Another possibility is that evolution of larger bilaterians occurred in the deep sea, but then it is necessary to explain why any such organisms did not invade the shallow-water benthos of the platform seas until the Cambrian. On the other hand, the rich variety of benthic bodyplans found during the Cambrian explosion implies a rich variety of ancestral forms in the Neoproterozoic. Thus, metazoan evolution of the platform fauna during the Prelude would seem to be characterized by radiations and significant lineage divergences among small-bodied benthic forms. Crown phyla that are entirely small-bodied are all acoelomate or pseudocoelomate forms with the exception of the bryozoans, which are colonial. The Prelude forms lacked mineralized skeletons and may have had only thin cuticles or lacked cuticles altogether as do some of the small-bodied phyla today; such forms could be fossilized only under quite exceptional circumstances, and it is not surprising that we do not have body fossil records of this minute bilaterian fauna. The vendobionts and their associates fossilize so readily that it is suspected they had sclerotized cuticles (Seilacher 1989) or unusually tough, collagenous mesogloea-like layers (Valentine 1992).

Suggestions for the sequence of evolutionary events during metazoan radiations of the Prelude have been cartooned as three model scenarios (Valentine et al. 1996). The first model envisions a very early origin of the bodyplans of phyla well back in the Neoproterozoic, with the explosion being an artifact of the evolution of durable skeletons. A scenario of early bodyplan evolution is presented by Fortey et al. (1996), based partly on the fossil record of trilobites, which are complex and are already provincially distributed when their body fossils first appear in Atdabanian time. But as emphasized by Budd & Jensen (2000), early fossil evidence of the presence of trilobites is expected under this scenario but has not been found during the Prelude, and indeed large-bodied fossil bilaterians are found during the explosion, and they are accompanied by appropriately large trace fossils, unknown during Neoproterozoic time. The second model envisions a gradual increase in metazoan disparity and complexity throughout the Prelude, with the onset of skeletonization simply revealing the stage that happened to have been reached during the explosion interval. Again, there is no direct fossil evidence for a gradual appearance of morphologically complex bodyplans during Neoproterozoic time, though there is evidence for an increase in the diversity of trace types. The third model envisions few morphological advances during the Prelude, with the major episode of bodyplan evolution beginning just before the explosion, which is thus taken nearly at face value. But the point made by many supporters of the first model, that the disparity of bodyplans found during the explosion implies a fairly lengthy evolutionary history, seems to weigh importantly against any extreme application of model three.

Continuing fossil discoveries, coupled with significant refinement in the dating of late Neoproterozoic and earliest Cambrian horizons, indicate a history of Prelude events at odds with all three cartoon models, yet it involves some elements of each of them. The small body size of the Prelude fauna is an important and well-supported inference. The bodyplans of the explosion taxa include many key features that would not be necessary in the small-bodied forms indicated by trace fossils, such as complicated respiratory systems, extensive blood-vascular systems, coelomic compartments, and rigid, stress-bearing skeletons. There are crown taxa that have some of these features and that are quite small-bodied, but there is evidence that they have been evolutionarily miniaturized from larger ancestors. In fact, the changes in body architecture that are found among minute crown taxa, which have for instance become adapted to meiofaunal life or are parasitic, are quite informative. For example, the minute "archiannelids" are descended from a variety of larger-bodied annelid stocks but are adapted to a common interstitial environment (Fauchald 1975, Bartolomaeus 1994). In some archiannelids the coelomic compartments lack peritoneal linings, and the animals may function essentially as pseudocoelomates, and in even more extreme cases the body becomes functionally acoelomate. Thus, the bodyplans of these forms are reduced to the grades found in small-bodied phyla (see below), and many of them, including some that retain "true" coelomic compartments, employ mucociliary locomotion (Fransen 1980).

Important clues to the bodyplans of the small-bodied trace fossil makers of the Prelude are also found among living ambulatory phyla that are entirely small-bodied. These forms are either acoelomate or pseudocoelomate and lack blood vascular systems; some of them lack cuticles. They have relatively few organs and simple bodies for metazoans, with only approximately 14 to 20 cell morphotypes among free-living forms, and fewer than 10 in some parasitic taxa (see Harrison et al. 1991–99). Such small, soft-bodied animals have very low preservation potentials; six of the nine phyla that lack body fossil records altogether (Figure 4) of this sort and their stem ancestors—that is, ancestors with bodyplans organized like the crown groups—may well have evolved during the Prelude. Certainly, their absence from rocks of the Prelude is not informative as to their times of origin because they don't appear even in Phanerozoic rocks.

The bilaterian fauna of the Neoproterozoic is thus inferred to have consisted chiefly of small-bodied worms, some of which were creepers and some of which were certainly capable of shallow horizontal burrowing. There are among the fossils hints that some larger-bodied bilaterians (lengths measured in a few cm) were present and may have had blood vascular systems such as *Kimberella*, and some may have had seriated muscle and nervous systems such as the “segmented” fossils. Such forms would probably have been moderately complex, but the structural grades of those fossils are not yet well-characterized.

Stem ancestors of many living phyla must have been present during the earliest Cambrian segment of the Prelude interval. Larger body sizes are documented by traces; hence many of the features that accompany body-size increases, such as enlargement of respiratory surfaces, elaboration of circulatory systems, and enhancement of locomotory mechanics, were presumably evolved in some of the lineages during this time. Such features are characteristic of many of the bodyplans found during the explosion interval but are not generally required of the putative bodyplans of the Prelude. For example, stem arthropods probably arose from a moulting pseudocoelomate worm with at least a lightly sclerotized cuticle. A fluid skeletal system was provided by a haemocoel evolving from or on the site of the pseudocoel, encased within the cuticle-bound body wall. Locomotory limbs may have evolved from body-wall protuberances employed as ancillary devices in peristaltic- or introvert-based locomotion (Valentine 1999, Valentine & Collins 2000). Stem annelids may have also evolved from a pseudocoelomate worm, and developed locomotory parapods from body-wall protuberances, but their fluid skeletal system was based on intramesodermal spaces, coelomic compartments involved in the biomechanics of peristaltic and parapodial locomotion.

Thus, the present interpretation of Prelude faunas agrees with the first cartoon model in postulating a lengthy preexplosion evolution of Metazoa, but only at sponge, radiate, and noncoelomate bilaterian grades throughout the Neoproterozoic segment. This interval has a duration of between 14 and 47 Ma recorded by Metazoan fossils, an unfortunately wide window of uncertainty. The second cartoon model specifies a gradual increase in bodyplan complexity, but the picture seems more complicated—a complexity rise is difficult to document during

the Neoproterozoic, but appears to accelerate during the Manykaian, an interval of between 13 and 23 Ma in duration. The third cartoon model, which would place most of the evolutionary action close to the explosion, is not completely wrong, as the Neoproterozoic-Cambrian boundary appears to mark a change in the evolutionary tempo, beginning the introduction of a remarkable array of morphological novelties that eventually included the stem bodyplans of complex living bilaterians.

Although metazoan origins are shrouded, the best interpretation of the fossil record would seem to be one in which Neoproterozoic bilaterians produced trace fossils as they radiated into a wide variety of noncoelomate bodyplans, many of which were vermiform and were similar to, and probably included, stem ancestors of living small-bodied phyla. Near 543 mya, a clear evolutionary trend began toward increased body size in numbers of lineages. This trend entailed the evolution of more complex organs and organ systems to deal with the well-known physiological and biomechanical problems associated with body-size increases. One innovation, adopted in a number of lineages, was the secretion of durable skeletons, some of which were mineralized; thus, the skeletal record of Metazoa came into being. The Cambrian explosion, therefore, represents the culmination of an evolutionary step, or perhaps an evolutionary ramp is a more appropriate image, localized in the Early Cambrian, which produced the bodyplans of complex animals. The bodyplans of those complex invertebrates are estimated to have had in the range of 30 to 40 cell morphotypes, between two to three times more than the average small-bodied phylum, and the early craniate chordates may have had as many as 60 (Harrison 1991–99; see Valentine et al. 1994).

Evolution of Development During the Prelude

Bodyplan evolution is in essence the evolution of development, which involves that part of the genome devoted to the regulation of gene expression. Multicellular organisms express different fractions of their genomes in each of their differentiated cell types. Thus, the origin of multicellularity involves establishment of a system to produce more than one cell type from the same genome and to produce and position appropriate numbers of cells of each type. Key components of this system are the genes whose products help to regulate patterns of expression of other genes within the proliferating cells of a developing organism. Particularly accessible accounts of the general architecture of metazoan gene regulation are by Raff (1996) and Carroll et al. (2001). Although classic microevolutionary processes involving structurally and physiologically important genes are vital to maintenance of populations within their ambient environments, it was chiefly evolution of the patterns of developmental regulation that must have been underway in diverging lineages throughout the Prelude, that generated the morphological diversity found during the Cambrian explosion.

The genetic mechanisms of development involve regulatory DNA sequences that are generally adjacent (in *cis* position) to the transcribed regions of genes.

Transcription is activated or suppressed by means of signals relayed to molecules—transcription factors—that bind to sites (“enhancers”) in the *cis*-regulatory regions. There are sometimes scores of such enhancer sites and a given gene may be expressed at many times or locations during development, each gene expression event being under the aegis of different combinations of signals (see Carroll et al. 2001, Davidson 2001). Clearly, mutations that interfere with the binding of any transcription factor employed at many times and places as a key developmental gene would tend to have highly deleterious effects, and indeed the binding sequences of many regulatory genes are highly conserved right across the metazoan phyla. Most of the important binding motifs, such as the homeobox, are known even in sponges, and many if not all were present in ancestral protistan lineages as well.

The history of Metazoa indicates that increased morphological complexity is commonly favored by selection, and this trend implies an increase in the size or complexity of genetic regulatory systems. There must be two principal ways in which genomes may accommodate selection that results in a complexity increase: One is by adding new genes, which often occurs through gene duplication and then divergence of usage; and the other is by using the same genes more times, which would involve adding enhancer activities (Valentine 2000). In either of these cases, the number of gene expression events can be increased to support increases in morphological complexity.

Sponges possess the earliest extant metazoan bodyplan; all living metazoans have a sponge in their ancestry (see Figure 5). It is quite clear that the basic machinery for regulating multicellular genomes was already in place before the crown ancestor of sponges appeared. Even though their genome is not well known, sponges are known to contain many of the key genes that form the basis of developmental regulation in more derived Metazoa (Müller 1998, Ono et al. 1999, Manual & Le Parco 2000). Some of the mechanisms of gene regulation may have been foreshadowed in colonial predecessors of sponges, perhaps in choanoflagellates or their allies.

Radiates (such as Ctenophora, comb jellies, and Cnidaria, jellyfish and their allies) show features that are lacking in sponges but are common throughout Eumetazoa, such as gastrulation, epithelial tissues, digestive tracts with mouths, and nerve cells. Radiate genomes contain key developmental gene clusters, such as Hox and ParaHox genes (Finnerty & Martindale 1999)—regulatory genes with homeobox binding motifs that pattern the anteroposterior axis and other basic features of bilaterians. Cnidarians also contain numerous genes, expressed around the (presumably anterior) mouth region, that are associated with the organization of anterior structures in Bilateria (Galliot & Miller 2000), suggesting either that aspects of bilaterian patterning evolved from radiate patterning or that both evolved from a common ancestral patterning system. It is possible that such a common ancestral system was found among the vendobionts of the Prelude, whose bodies were built of repetitive parts, some in radiate and some in seriate patterns (Figure 3; see

Valentine 2001). Homologs of many of the other developmental patterning genes found in radiates also pattern the disparate bodyplans found among bilaterians. Some developmental genes have been duplicated many times and are represented by gene families; turnover among duplicates (paralogs) may have been relatively high (Lynch & Conery 2000), making it difficult to find direct gene descendants (orthologs). The morphological features of many bodyplans are quite unique—the water-vascular system of echinoids, the jointed limbs of arthropods, the parapodia of annelids—although, again, key genes mediating bodyplan development are quite similar and are homologous in the broad sense across Metazoa. However, the sizes of key regulatory gene clusters, the presence of regulatory paralogs, and the signaling pathways involved in key regulatory functions vary among higher taxa, indicating the significant changes in *cis*-regulatory “wiring” that accompanied the evolution of developmental gene cascades as novel morphologies evolved. We owe the rich diversity of bodyplans to the combinatorial organization of this regulatory apparatus.

In sum, Metazoa originated from choanoflagellates or their relatives at some unknown time likely to have been before 600 mya, and their appearance marked the evolution of a genome capable of the production and organization of differentiated cell types. This genome was characterized by a *cis*-regulatory architecture of such flexibility that it could evolve so as to mediate the development of bodyplans from sponges and cnidarians to arthropods and vertebrates. By about 570 mya, or perhaps somewhat later, trace fossils appear that suggest the presence of creeping bilaterians. These traces imply that radiates have appeared, and the fauna of the remainder of the Prelude appears to have consisted chiefly of sponges; of moderate-sized to large tissue-grade forms that appear to be at a radiate grade and probably include stem cnidarians; of small-bodied, vermiform, bilaterians that lived on and shallowly within the sediments; and eventually of more complex derivatives of these worms that are likely to have been present by approximately 543 mya and that gave rise to the disparate bilaterian taxa of the Cambrian explosion.

WHY WAS THE PRELUDE SO SHORT? OR SO LONG?

There are a large number of hypotheses as to what features or events might be responsible for the abrupt appearance of crown phyla during the Cambrian explosion. Many of those suggestions involve a trigger, a particular event or situation that produced the explosion as a consequence. Other suggestions involve a fuse, an event or situation that entrained an evolutionary sequence culminating in the explosion. Many of those hypotheses imply that the explosion could have occurred at another time if the trigger or fuse had been activated earlier or later than it was. There are too many of these hypotheses to review here, but a fair sampling can provide some idea of what is thought to have been lacking during the Prelude that prevented the appearance of crown phyla. The arguments in favor of most of

these hypotheses are more extensive than I can do credit to, and the original papers should be consulted for their far richer accounts.

Changes in the Physical Environment

Probably the most pervasive hypothesis about the timing of early metazoan radiations is that oxygen levels were too low before the Cambrian to permit the evolution of active animals, which have relatively high oxygen demands (see Towe 1970). Early champions of this notion scaled the rise of oxygen levels to the minimum requirements of the succession of organisms known as fossils (e.g., Berkner & Marshall 1964), a circular argument that implicated oxygen as a trigger. However, more recent evidence suggests that oxygen levels appropriate for active metazoans were present long before the explosion (Canfield & Teske 1996, Knoll 1996).

There were glaciations during the Neoproterozoic that were undoubtedly extensive; a likely age range for the main glacial periods is from approximately 620 to 590 and perhaps to 575 mya (Harland et al. 1990, Smith 2001), probably preceding the appearance of metazoans in the fossil record. It is argued that the glaciations were so severe that the entire world ocean was frozen over, producing a “snowball Earth” (Kirschvink 1992, Hoffman et al. 1998). The general suggestion offered is that the associated environmental changes paved the way for the metazoan radiation—a fuse hypothesis. However, many lineages of prokaryotes and of protists, and presumably of fungi and metazoans, weathered the glacial times, and so it seems unlikely that the Earth’s surface was completely frozen. The glacial interpretation of some Neoproterozoic deposits is controversial (review in Eerola 2001) and the severity of the glaciations must have depended significantly on planetary geography; a recent paleogeographic reconstruction suggests that the ice cover was indeed not global (Smith 2001).

Brasier (1979, and see Brasier & Lindsay 2001) has pointed out that a transgressive episode was associated with the explosion, which may have been set off by the appearance of novel environments within the newly widespread epicontinental seas. Such an event would certainly be likely to increase species richness and may well be responsible for the appearance of fossil assemblages on and just above pretransgression unconformities, but would not seem particularly conducive to the evolution of novel bodyplans. Transgressions occurred earlier and later, without being associated with the production of bodyplans. Widespread Neoproterozoic deposits (such as the Vendian of the Russian Platform) suggest the presence of heterogeneous marine environments for evolution during the Prelude as well as during the explosion period.

Changes in the Biological Environment

There are a number of ecologically-based hypotheses that speak to the taxonomic richness of the Cambrian explosion, although not necessarily to the origin of bodyplans. These hypotheses imply conditions during the Prelude; the Prelude must have lacked the features that the hypotheses propose to have been important during

the explosion. For example, invasion of the water column by pelagic forms may have had important consequences for the benthic community. Thus, Logan et al. (1995) explored the effects of removal of carbon from the water column by the sinking of faecal pellets during and after the evolution of bilaterian zooplankters. They concluded that the resulting biogeochemical changes on the sea floor could have contributed to the Cambrian radiation. Butterfield (1997, 2001) has noted that acritarchs, a phytoplanktonic group that has left a Neoproterozoic fossil record, were morphologically simple before the Cambrian explosion but became increasingly diversified morphologically in tandem with the benthic radiation (see also Vidal 1997). He interprets those morphological specializations as antipredatory, implying the evolution of a mesoplanktonic tier of zooplankters, and points out that well-known sorts of ecological interactions involving predators and prey, and other interactions as well within the tiers, could have moderated fluctuations in the plankton, stabilizing primary productivity and thereby permitting a diversity rise in both pelagic and benthic communities. In the benthos itself, it is postulated that the appearance of active predators put limits on population sizes, thus freeing resources to permit a Cambrian diversity rise (Stanley 1973). These sorts of ideas suggest just how different the marine biosphere was before the Cambrian explosion, and how much of the feedbacks in interrelations among the evolving lineages must have been part and parcel of the growth of Phanerozoic-style ecosystems.

Changes in the Evolutionary Potential of Metazoa

A further possibility for the length of the Prelude is that it simply reflects factors that regulate the growth rate of complexity in morphology, which in turn implicate growth in the numbers of gene expressions that were selected for their contributions to beneficial morphological change. Once the ancestral metazoan genome had “solved” problems of cell differentiation and positioning along pathways defined by selection for fitter morphologies and true metazoans had appeared, a succession of challenges not unlike those during Phanerozoic time must have been encountered, some of which were successfully met through evolution in some lineages, and some of which must have caused extinctions in others. The character of taxonomic sorting and turnover that went on during, say, a random 100 Ma segment of the Phanerozoic is well known, with incessant low-level background extinctions episodically punctuated by extinction spikes and generally countered by origination events. A reasonable hypothesis would be that a similar pattern was present during the Prelude.

There has apparently been a nearly monotonic rise in the complexity of the most complex organisms throughout the Phanerozoic (Valentine et al. 1994). The pace of this rise can provide some idea of the rate of complexity increase permitted by normative rates of change in those physical environmental factors that interact with evolutionary processes within evolving lineages. The complexity rise seems greater early in the Phanerozoic, but as cell morphotype numbers alone tend to underestimate complexity differences, the overall complexity increase may have

been more nearly linear. At any rate, a complexity increase of roughly 140 cell morphotypes over 500 Ma (say from 60 during the explosion to 200 during the Miocene) works out to an average increase of 0.3 cell morphotype per Ma. If the increase in developmental complexity was similar during the Prelude, backward extrapolation places the origin of Metazoa at approximately 720 mya. Such a date can even be reconciled with some molecular clock dates. However, such a date does place the origin of Metazoa well before the main late Neoproterozoic glaciations. If Neoproterozoic rates of complexity increase were higher than the Phanerozoic average, at least within the chordates (the complexity of which is responsible for adding about 60 Ma to the calculations), the date of origin of Metazoa would be estimated as significantly younger—say, near 660 mya or later. Certainly the rate of increase of complexity in chordates outstripped rates in invertebrate lineages during the Phanerozoic (Valentine et al. 1994).

During the Prelude years, simple, small-bodied grade bilaterians are assumed to have arisen and diversified. How many promising bodyplans may have gone extinct we shall never know. By 543 mya the morphological and physiological bells and whistles that permit the existence of larger bilaterians had been assembled in some lineages, and in some cases were exploited for size increases, doubtless along appropriate fitness pathways. That such an increase would happen at the same time in many phyla without a trigger seems suspiciously fortuitous, but in fact it may not really have been as simultaneous as the explosion metaphor suggests. For example, body sizes of some of the stem taxa, such as Mollusca and Brachiopoda, were quite small during the explosion period, their size increases not occurring until later. There is also a well-defined sequence of appearances of such larger-bodied stem forms as arthropods and echinoderms, which may indicate a sequence of originations that were spread over several million years. Nevertheless, there was apparently a ramping up of both bodyplan disparity and taxonomic richness during the Early Cambrian.

Some of the factors that may have influenced the explosion events have been briefly noted above. They presumably included evolutionary responses within the fauna to those taxa that were emerging with novel bodyplans and occupying new regions of adaptive space, the sorts of adaptive feedbacks that can be imagined as marine ecosystems evolved from Neoproterozoic to Phanerozoic styles. As emphasized by Budd & Jensen (2000), the explosion does not require a radical explanation, at least now that it can be seen how the evolutionary modes involved in the explosion included at their core the evolution of developmental systems and not simply the changes associated with structural gene substitutions. Conditions during the Early Cambrian clearly permitted diversity increases among the explosion taxa, and perhaps the extent of the explosion was influenced by those factors as many workers have suggested. Just how far Neoproterozoic metazoans reached along the trajectory of increasing complexity that culminated in the bodyplans of the explosion fauna, and just how diverse the Prelude faunas were, remain uncertain. Future studies that combine geological and paleontological evidence with molecular tools should take us significantly closer to the answers.

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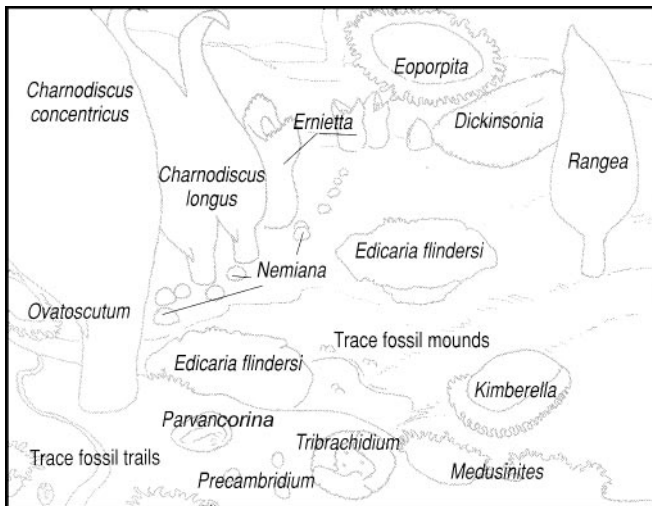


Figure 3 Neoproterozoic organisms visualized as a community on and above a Neoproterozoic sea floor (although these forms have not all been found in the same deposits). From an illustration by David W. Miller in Erwin et al. 1997, © D. W. Miller, by permission.