Article


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The Fossil Record of the Cambrian “Explosion”: Resolving the Tree of Life[1]

Keith B. Miller

The Cambrian “explosion” has been the focus of extensive scientific study, discussion, and debate for decades. It has also received considerable attention by evolution critics as posing challenges to evolution.

In the last number of years, fossil discoveries from around the world, and particularly in China, have enabled the reconstruction of many of the deep branches within the invertebrate animal tree of life. Fossils representing “sister groups” and “stem groups” for living phyla have been recognized within the latest Precambrian (Neoproterozoic) and Cambrian. Important transitional steps between living phyla and their common ancestors are preserved. These include the rise of mollusks from their common ancestor with the annelids, the evolution of arthropods from lobopods and priapulid worms, the likely evolution of brachiopods from tommotiids, and the rise of chordates and echinoderms from early deuterostomes.

With continued new discoveries, the early evolutionary record of the animal phyla is becoming ever better resolved. The tree of life as a model for the diversification of life over time remains robust, and strongly supported by the Neoproterozoic and Cambrian fossil record.

The most fundamental claim of biological evolution is that all living organisms represent the outer tips of a diversifying, upward-branching tree of life. The “Tree of Life” is an extremely powerful metaphor that captures the essence of evolution. Like the branches of a tree, as we trace individual lines of descent (lineages) back into the past (down the tree), they converge with other lineages toward their common ancestors. Similarly, these ancient lineages themselves converge with others back in time. Thus, all organisms, both living and extinct, are ultimately connected by an unbroken chain of descent with modification to a common ancestral trunk among single-celled organisms in the distant past.

This tree metaphor applies as much to the emergence of the first representatives of the major groups of living invertebrates (such as snails, crabs, or sea urchins) as it does to the first appearance and diversification of dinosaurs, birds, or mammals. This early diversification of invertebrates apparently occurred around the time of the Precambrian/Cambrian boundary over a time interval of a few tens of millions of years. This period of rapid evolutionary diversification has been called the “Cambrian Explosion.”

The Cambrian explosion has been the focus of extensive scientific study, discussion, and debate for decades, and is increasingly receiving attention in the popular media. It has also received considerable recent attention by evolution

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critics as posing challenges to evolution. These critics argue that the expected transitions between major invertebrate groups (phyla) are absent, and that the suddenness of their appearance in the fossil record demonstrates that evolutionary explanations are not viable.

What are some of the arguments of the evolution critics? John Morris of the Institute for Creation Research writes,

> If evolution is correct, the first life was quite simple, evolving more complexity over time. Yet the Cambrian Explosion of Life has revealed life's complexity from the start, giving evolution a black eye. The vast array of complex life that appears in the lowest (or oldest) stratigraphic layer of rock, with no apparent ancestors, goes hard against evolutionary dogma. Evolution's desperate attempt to fill this gap with more simple ancestral fossils has added more injury ... Think of the magnitude of this problem from an evolutionary perspective. Many and varied forms of complex multi-celled life suddenly sprang into existence without any trace of less complex predecessors. There are numerous single-celled forms at lower stratigraphic levels, but these offer scant help in solving the mystery. Not one basic type or phyla [sic] of marine invertebrate is supported by an ancestral line between single-celled life and the participants in the Cambrian Explosion, nor are the basic phyla related to one another. How did evolution ever get started?[2]

Intelligent design advocate Stephen Meyer and others have written:

> To say that the fauna of the Cambrian period appeared in a geologically sudden manner also implies the absence of clear transitional intermediates connecting the complex Cambrian animals with those simpler living forms found in lower strata. Indeed, in almost all cases, the body plans and structures present in Cambrian period animals have no clear morphological antecedents in earlier strata.[3]

And

> A third feature of the Cambrian explosion (as well as the subsequent fossil record) bears mentioning. The major body plans that arise in the Cambrian period exhibit considerable morphological isolation from one another (or "disparity") and then subsequent "stasis." Though all Cambrian and subsequent animals fall clearly within one of a limited number of basic body plans, each of these body plans exhibits clear morphological differences (and thus disparity) from the others. The animal body plans (as represented in the fossil record) do not grade imperceptibly one into another, either at a specific time in geological history or over the course of geological history. Instead, the body plans of the animals characterizing the separate phyla maintain their distinctive morphological and organizational features and thus their isolation from one another, over time.[4]

Are these critiques warranted? To what extent is the Cambrian explosion really problematic for the evolutionary picture of an unbroken tree of life extending back to the earliest life on Earth?

Defining the Cambrian "Explosion"

The relative rapidity of the diversification of invertebrates during the Cambrian "explosion" is set against the backdrop of the earth's geologic and biologic history. Geologic time is unfamiliar to most people, and its shear vastness is difficult to grasp.

Two lines of evidence impact our understanding of the duration of the animal diversification that led to the appearance of the major groups of living invertebrates. The first is the dating of critical levels within the geological timeline such as the Precambrian-Cambrian boundary and various important fossil-bearing horizons. The second is the time of appearance of the first widely recognized fossil representatives of the major living groups (phyla) of invertebrate animals. The latter is in considerable flux as new fossil discoveries are made.

Originally, the base of the Cambrian had been set at the earliest appearance of organisms with mineralized skeletons—particularly trilobites. However, a diverse collection of tiny mineralized plates, tubes, and scales was discovered to lie below the earliest trilobites.[5] This interval of "small shelly fossils" was designated the Tommotian. Because of the presence of even earlier tiny mineralized tubes and simple burrows, there was no internationally accepted definition for the boundary until 1994. At that time, the base of the Cambrian was placed at the first appearance of a particular collection of small fossil burrows characterized by *Treptichnus pedum*.[6]

Until the early 1990s, the age of the Precambrian-Cambrian boundary was not tightly constrained, and was estimated to be about 575 million years ago. However, in 1993, new radiometric dates from close to the accepted Precambrian-Cambrian boundary revealed that it was significantly younger—about 544 million years.[7] A more precise date of 542 ± 0.3 million years has recently been formally accepted by the International Commission on Stratigraphy. The basis for this date was the discovery that a sharp worldwide fall (or negative spike) in the abundance of the isotope carbon-13 was coincident with the Cambrian boundary as previously defined. In Oman, this isotopic marker also coincides with a volcanic ash layer that yielded the 542-million-year date using uranium/lead radiometric methods.[8] This horizon also marks the last occurrence of several fossils characteristic of the underlying late Precambrian Ediacaran Period.[9] Such extinction events are commonly used to subdivide the geologic time scale.

The earliest diverse fossil invertebrate communities of the Cambrian are represented by the Chengjiang, in China. These deposits are dated at 525–520 million years. The famous Burgess Shale is considerably younger, dating at about 505 million years, and the end of the Cambrian Period is set at 490 million years. The Cambrian Period thus lasted for 52 million years, and the Early Cambrian alone was an extended period of time lasting 32 million years.[10] To put this in perspective, the time elapsed from the extinction of the dinosaurs at the end of the Cretaceous to the present has been 65 million years. The Cambrian was a very long period of time (see fig. 1).

If the Cambrian "explosion" is understood to comprise the time from the base of the Cambrian to the Chengjiang fossil beds, then this period of diversification in animal body plans appears to have lasted about 20 million years. However, not all living animal phyla with a fossil record first appear within this time window. The colonial skeleton-bearing bryozoans, for example, are not known from the fossil record until near the end of the Cambrian around 491 million years ago.[11] In addition, most of the Early Cambrian fossils recognized as related to modern phyla are actually intermediates or stem groups (see discussion below). Furthermore, recent refined dating of first appearances of the Early Cambrian stem groups has indicated that even the "explosive" start of the Cambrian diversification was more gradual and episodic than previous thought.[12]

Defining the Cambrian "explosion" is not as straightforward as it might seem. Although there was clearly a major burst of evolutionary innovation and diversification in the first 20 million years or so of the Cambrian, this was preceded by an extended period of about 40 million years during which metazoans arose and attained critical levels of anatomical complexity. Significantly, several living invertebrate phyla have a fossil record that extends into the late Neoproterozoic before the Cambrian. Sponges have been recognized as early as 580 million years, cnidarians (the group including jellyfish and anemones) are present among the Ediacaran animals at around 555 million years, and the stem groups for some other phyla were also likely part of the Ediacaran communities. The Ediacaran saw the appearance of organisms with the fundamental features that would characterize the later Cambrian organisms (such as three tissue layers, and bilaterally symmetric bodies with a mouth and anus), as well as the first representatives of modern phyla. The base of the Cambrian is not marked by a sharp dramatic appearance of living phyla without Precambrian roots. It is a subjectively defined point in a continuum.

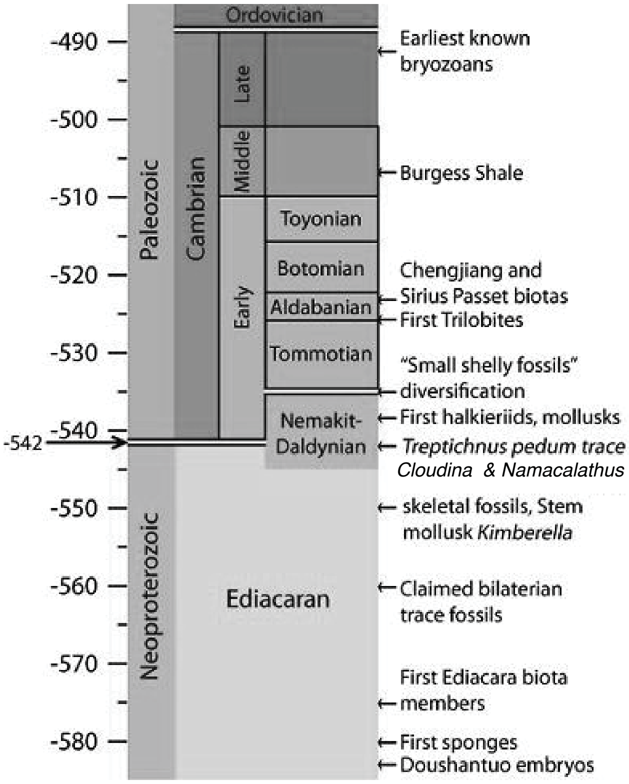

Figure 1. Timeline showing the interval from the late Neoproterozoic (Ediacaran) through the Cambrian. Marked on the timeline are the positions in time of some of the more important fossil localities, and the time of first appearances of selected metazoan groups.

Drawing Trees and Assigning Names

The procedure of classifying organisms is called taxonomy, and the general name for individual groups is "taxa." The first question that needs to be addressed is "What is a phylum?" A phylum is often identified as a group of organisms sharing a basic "body plan" or a group united by a common organization of the body. However, phyla can be understood fundamentally, like all other taxonomic categories, as groupings of taxa that are more closely related to each other than to any other group.

The most widely accepted method for grouping organisms today is called cladistics.[13] In cladistics, all taxonomic groups are monophyletic, that is, all of the members of the group are descended from a common ancestor that is the founding member of that taxon. A branch of the tree of life whose members all share the same ancestor is called a "clade"—thus the term "cladistics." A taxon or taxonomic group that is the closest relative of another group, and that shares the same common ancestor, is called a "sister taxon" or "sister group." The early representatives of two sister groups commonly resemble each other more than the descendant relatives resemble the ancestors of their clade. As a result, placing these organisms into their correct monophyletic groups can be very difficult. Thus, primitive organisms within a given phylum may bear close similarities to those from another closely related sister phylum. In fact, the assignment of a given organism or fossil specimen to a phylum can be just as problematic as assignments to lower-ranked taxa such as classes, orders, families, and so forth.[14] This fact alone indicates that biological diversity is more a continuum than a collection of discrete groups.

Further complicating the assignment of fossil organisms to phyla is that the anatomical characteristics that are used to define living phyla did not appear simultaneously, but were added over time. This has resulted in the distinction between "crown groups" and "stem groups" in the scientific literature[15] (fig. 2). This terminology can be applied to any level of the taxonomic hierarchy. A crown group phylum is composed of all the living organisms assigned to that phylum, plus all the extinct organisms that were descended from the common ancestor of those living organisms. The stem group is composed of extinct organisms more closely related to one particular living phylum than to any other, but that were not descended from the common ancestor of the living representatives of that phylum. Stem groups typically do not possess all of the defining characters of the crown group of that phylum. It turns out that the organisms appearing in the Early Cambrian are, with few exceptions, not crown groups but stem groups. That is, the complete suite of characters defining the living phyla had not yet appeared. Many crown groups do not appear in the fossil record until well after the Cambrian.[16]

The existence of stem groups provides a way to understand how the basic body plan of a living invertebrate could have been built up in steps. The major invertebrate groups are often portrayed by evolution critics as possessing anatomies that are both irreducible in organization and separated from other groups by unbridgeable gaps. However, the identification of stem and sister groups explicitly recognizes the existence of fossil taxa that possess transitional morphologies between recognized modern taxonomic groups (including phyla).

Some critics of evolution make much of the "top-down" versus the "bottom-up" pattern of appearance of higher taxa. That is, phylum-level diversity reaches its peak in the fossil record before class-level diversity, and the class-level diversity before that of orders, and so forth. These critics interpret this apparent "top-down" pattern as contrary to expectations from evolutionary theory. For example, Stephen Meyer and others have argued:

> Instead of showing a gradual bottom-up origin of the basic body plans, where smaller-scale diversification or speciation precedes the advent of large-scale morphological disparity, disparity precedes diversity. Indeed, the fossil record shows a "top-down" pattern in which morphological disparity between many separate body plans emerges suddenly and prior to the occurrence of species-level (or higher) diversification on those basic themes.[17]

However, this pattern is an artifact, being generated by the way in which species are assigned to higher taxa. The classification system is hierarchical with species being grouped into ever larger and more inclusive categories. When this classification hierarchy is applied to a diversifying evolutionary tree, a "top-down" pattern will automatically result. Consider species belonging to a single evolving line of descent given genus-level status. This genus is then grouped with other closely related lines of descent into a family. The common ancestors of these genera are by definition included within that family. Those ancestors must logically be older than any of the other species within the family. Thus the family-level taxon would appear in the fossil record before most of the genera included within it. Another way of looking at this is the fact that the first appearance of any higher taxon will be the same as the first appearance of the oldest lower taxon within the group. For example, a phylum must be as old as the oldest class it contains. Most phyla contain multiple classes, which in turn include multiple orders, and so forth. Thus, each higher taxon will appear as early as the first of the included lower taxa. The "top-down" pattern of taxa appearance is therefore entirely consistent with a branching tree of life.

There is one last bias in our reconstruction of the past that is generated by the process of assigning organisms to a particular phylum. Because phyla are defined by particular anatomical character traits, they cannot be recognized in the fossil record until after those specific characters evolve. However, the splitting of the branch of the tree of life to which

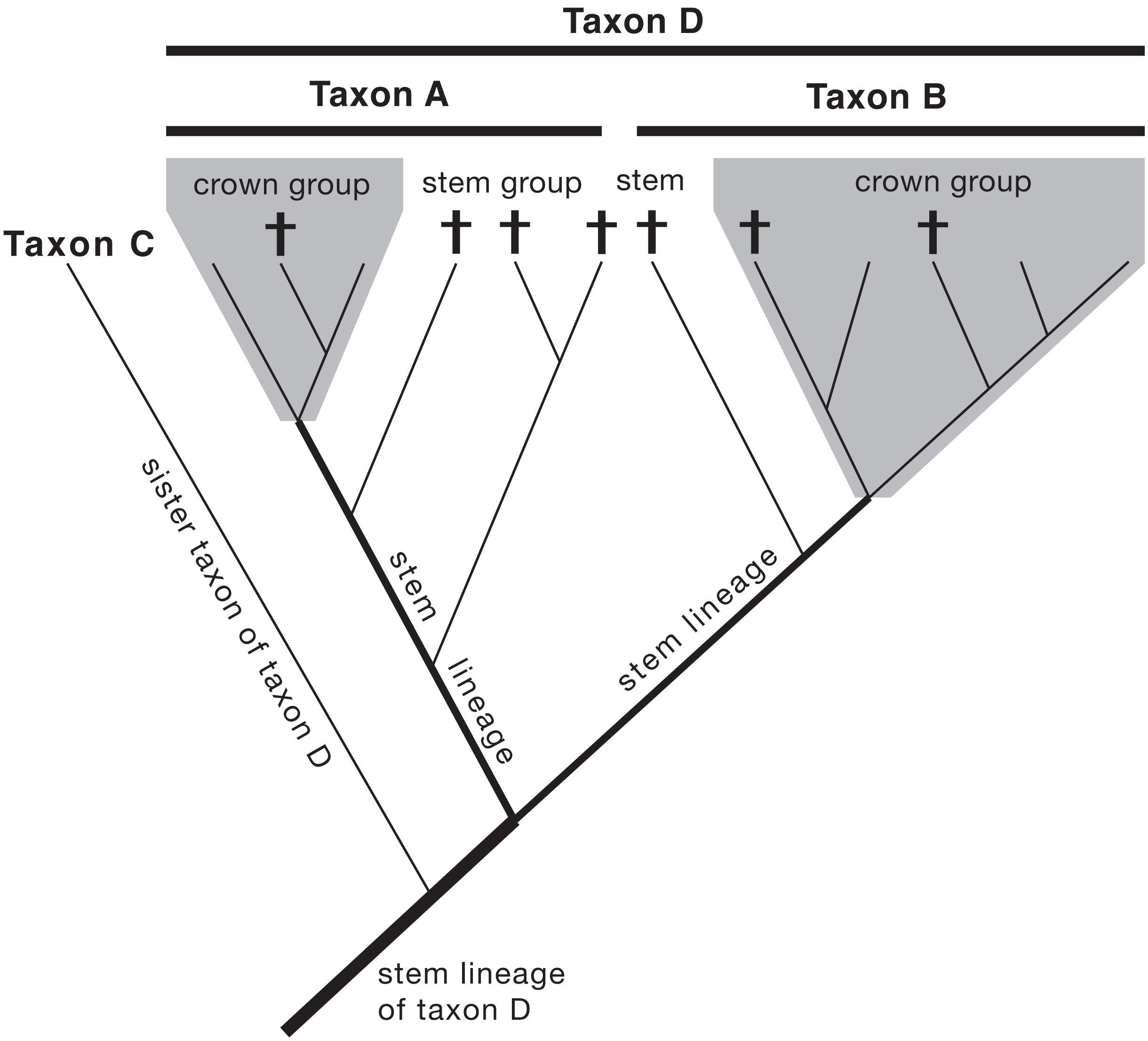

Figure 2. Diagram illustrating the difference between stem and crown groups. The crown group includes the living organisms that possess the characters used to define a modern taxonomic group, and all of the extinct fossil organisms that were descended from the last common ancestor of all members of the crown group. The extinct fossil organisms of the stem group possess some, but not all, of the characters diagnostic of the crown group, and are more closely related to the crown group than any other organisms. A sister group includes those organisms that are more closely related to the total group (crown and stem group) than to any other group of organisms. In this diagram, taxon A and taxon B are sister groups, and taxon C is a sister group to the more inclusive taxon D. (This diagram was modified from the Palaeos website, http://www.palaeos.org/Crown_group.)

a phylum belongs may have occurred many millions of years previous to the evolution of those characters. The characters that we use to define a phylum very likely do not correspond to the characters that actually marked the initial separation of that evolutionary lineage from its closest relative. The actual first appearance of a fossil assignable to a particular phylum thus would likely occur after significant anatomical evolution has occurred along that particular branch of the tree. Branching points in the tree of life will always be older than the named taxa.[18]

The Completeness of the Fossil Record

There are two opposite errors which need to be countered about the fossil record: (1) that it is so incomplete as to be of no value in interpreting patterns and trends in the history of life, and (2) that it is so good that we should expect a relatively complete record of the details of evolutionary transitions within all or most lineages.

What then is the quality of the fossil record? It can be confidently stated that only a very small fraction of the species that once lived on Earth have been preserved in the rock record and subsequently discovered and described by science.[19]

There is an entire field of scientific research referred to as "taphonomy"—literally, "the study of death." Taphonomic research includes investigating those processes active from the time of death of an organism until its final burial by sediment. These processes include decomposition, scavenging, mechanical destruction, transportation, and chemical dissolution and alteration. The ways in which the remains of organisms are subsequently mechanically and chemically altered after burial are also examined—including the various processes of fossilization. Burial and "fossilization" of an organism's remains in no way guarantees its ultimate preservation as a fossil. Processes such as dissolution and recrystallization can remove all record of fossils from the rock. What we collect as fossils are thus the "lucky" organisms that have avoided the wide spectrum of destructive pre- and post-depositional processes arrayed against them.

Soft-bodied organisms and organisms with non-mineralized skeletons have very little chance of preservation under most environmental conditions. Until the Cambrian, nearly all organisms were soft bodied, and even today the majority of species in marine communities are soft bodied. The discovery of new soft-bodied fossil localities is always met with great enthusiasm. These localities typically turn up new species with unusual morphologies, and new higher taxa can be erected on the basis of a few specimens! Such localities are also erratically and widely spaced geographically and in geologic time.

Even those organisms with preservable hard parts are unlikely to be preserved under "normal" conditions. Studies of the fate of clam shells in shallow coastal waters reveal that shells are rapidly destroyed by scavenging, boring, chemical dissolution, and breakage. Environments with high sedimentation rates, or those with occasional rapid sedimentation during major storm events, tend to favor the incorporation of shells into the sedimentary record, and their ultimate preservation as fossils.[20]

The potential for fossil preservation varies dramatically from environment to environment. Preservation is enhanced under conditions that limit destructive physical and biological processes. Thus marine and fresh water environments with low oxygen levels, high salinities, or relatively high rates of sediment deposition favor preservation. Similarly, in some environments biochemical conditions can favor the early mineralization of skeletons and even soft tissues by a variety of compounds (e.g., carbonate, silica, pyrite, phosphate). The likelihood of preservation is thus highly variable. As a result, the fossil record is biased toward sampling the biota of certain types of environments, and against sampling the biota of others.

In addition to these preservational biases, the erosion, deformation, and metamorphism of originally fossiliferous sedimentary rock have eliminated significant portions of the fossil record over geologic time. Furthermore, much of the fossil-bearing sedimentary record is hidden in the subsurface, or located in poorly accessible or little studied geographic areas. For these reasons, of those once-living species actually preserved in the fossil record, only a small portion have been discovered and described by science. However, there is also the promise, and reality, of continued new and important discovery as new sedimentary units are examined, and new techniques are applied. The rapidity with which new fossil discoveries are being made within Neoproterozoic and Cambrian strata is actually quite remarkable.[21]

The forces arrayed against fossil preservation also guarantee that the earliest fossils known for a given animal group will always date to some time after that group first evolved. The fossil record always provides only minimum ages for the first appearance of organisms.

Because of the biases of the fossil record, the most abundant and geographically widespread species of hardpart-bearing organisms would tend to be best represented. Also, short-lived species that belonged to rapidly evolving lines of descent are less likely to be preserved than long-lived stable species. Because evolutionary change is probably most rapid within small isolated populations, a detailed species-by-species record of such evolutionary transitions is unlikely to be preserved. Furthermore, capturing such evolutionary events in the fossil record requires the fortuitous sampling of the particular geographic locality where the changes occurred.

Using the model of a branching tree of life, the expectation is for the preservation of isolated branches on an originally very bushy evolutionary tree. A few of these branches (lines of descent) would be fairly complete, while most are reconstructed with only fragmentary evidence. As a result, the large-scale patterns of evolutionary history can generally be better discerned than species-by-species transitions. Evolutionary trends over longer periods of time and across greater anatomical transitions can be followed by reconstructing the sequences in which anatomical features were acquired within an evolving branch of the tree of life.

The Precambrian Fossil Record

A very important concern is what organisms existed before the Cambrian "explosion." Were there Precambrian precursors, or did the Cambrian "explosion" really happen in a biological vacuum? Many critics of evolution claim that the Precambrian is devoid of fossils that could represent body plans ancestral to those of the Cambrian invertebrates.

The words of Darwin are often cited as evidence of the seriousness of the problem for evolution.

> There is another and allied difficulty, which is much more serious. I allude to the manner in which species belonging to several of the main divisions of the animal kingdom suddenly appear in the lowest known fossiliferous rocks. Most of the arguments which have convinced me that all the existing species of the same group are descended from a single progenitor, apply with equal force to the earliest known species.[22]

When Darwin published his model of descent with modification by means of natural selection, knowledge of the fossil record was in its infancy. In particular, the Precambrian and Early Cambrian fossil record was virtually unknown. Even the fossils of the now famous Burgess Shale and similar units were as yet undiscovered. After nearly a century and a half of paleontological work, the situation has changed dramatically. In keeping with evolutionary expectations, fossils are now known from the late Precambrian and early Cambrian that record several dramatic transitions in the history of life.

The presence of Late Precambrian animals was recognized in the 1950s and became widely publicized by the early 1970s. These are the famous Ediacaran fossils named for fossil-rich beds in the Ediacara Hills of South Australia and now recognized at sites throughout the world. These organisms are typically preserved as impressions in sandstones and siltstones. Associated with these fossils are trails and simple burrows of organisms that show a limited increase in complexity and diversity toward the Cambrian.

The record of life actually extends far beyond the Ediacaran fossils (~575–542 My) into the deep geologic past. Fossils of algae, protists, and bacteria are present throughout much of the Precambrian. The earliest convincing fossils of bacteria are recognized in rocks 3.5 billion years old, and chemical signatures point to the presence of life even earlier. Finely layered mounds (called stromatolites) produced by the activity of mat-building bacteria and algae appear at about this time and become relatively abundant by around 2.7 billion years ago. Evidence of eukaryotic algae, possessing membrane-bounded nuclei and internal organelles, dates to about 1500 million years ago, or earlier if chemical evidence is accepted. Multicellularity had appeared by 1000 million years ago in the form of diverse and relatively advanced seaweeds.[23] The earliest fossils of metazoans (multi-celled animals) may be represented by simple disk-shaped fossils found in rocks 610–600 million years old.[24]

The earliest unambiguous indication of the rise of metazoan life is preserved in the spectacular phosphorite deposits of the Doushantuo Formation of China dating to at least 580 million years ago. Phosphate can preserve organisms and tissues in such great detail that individual cells can often be recognized. Where environmental conditions are ideal for this type of preservation, extraordinary fossil deposits may result. In the case of the Doushantuo, phosphatization has preserved not only a variety of algal remains, but also the cellular tissues and spicules of sponges.[25] These sponges appear to belong to the class Demospongia. However, even more spectacular within the Doushantuo phosphorites is the preservation of metazoan eggs and early embryos. These embryos are of uncertain affinities, but they may represent stem cnidarians (the phylum including "jellyfish," anemones, and corals) or even bilaterians (animals with bilateral symmetry).[26] Recently described millimeter-sized phosphatic tubes with internal chambers and apical budding also suggest a cnidarian affinity.[27]

The Ediacaran biota provide the next window into the rise of metazoans. These fossil-bearing units span from about 575 million years to the base of the Cambrian (an interval of ~33 million years), and are found in south Australia, Namibia, the White Sea coast of Russia, and Newfoundland. The enigmatic soft-bodied organisms were preserved as impressions, or molds, on the surfaces of sandstone and siltstone layers. These sediment layers accumulated in shallow-marine environments where the seafloor was covered by firm microbial algal mats. The microbial mats covering the seafloor appear to have been important in determining the lifestyles of the Ediacaran organisms, as well as their unique mode of preservation.[28]

Most soft-bodied impressions of the Ediacaran can roughly be placed into three general groups—disks; fronds; and flat-bodied, bilaterally-symmetric forms. The biological affinity of these fossils is very difficult to determine and highly debated.[29] Disks are the earliest appearing, and most common, Ediacaran fossils. A few disk-shaped fossils are fossil impressions of sponges. One such form appears to be a sponge that might be assignable to the modern class of Hexactinellida.[30]

Many disk-shaped impressions have often been identified as medusoids ("jellyfish") but many appear to have been attached to the bottom, and none bear clear structures that would place them in a living group. Some do clearly possess tentacles around their margins, suggesting a stem or sister group relationship to the cnidarians. Furthermore, recent descriptions of very small phosphatized fossils that predate the Cambrian by 25 million years or more have demonstrated the presence of cnidarians that might even be stem anthozoans (the cnidarian class that includes anemones and corals).[31]

The frond-shaped forms include organisms that were attached to the bottom by a stalk, and others that appear to have been free lying. These fossils have also been assigned by some workers to a group of modern cnidarians (the "sea pens") or to ctenophores. However, like the disks, the fronds are fairly diverse and some may be unrelated to living phyla.[32] Others, although likely not able to be placed into a living cnidarian group, may be stem cnidarians, or even stem anthozoans. The discovery of better preserved fronds in the Cambrian that closely resemble some of the Ediacaran fossils would seem to support this interpretation.[33]

The bilaterally symmetric forms of the Ediacaran are the most diverse and most enigmatic fossils of the late Precambrian. Some of these fossils may represent early experiments on the pathway to the living phyla.[34] For example, *Dickinsonia* and the similar *Yorgia* are fairly large flat highly segmented forms that some workers have interpreted as annelids or stem annelids, while others have seen resemblances to other worm phyla or even chordates. These organisms do appear to have been able to move about the bottom as seen by associated crawling and resting traces. Even if not members of a living phylum, these organisms appear to at least be mobile bilateral metazoans (or bilaterians).

Another bilateral form that has been the subject of much recent attention is the 555-million-year-old mollusk-like *Kimberella* (see fig. 3). This organism appears to have lacked several features characteristic of modern mollusks and thus has been interpreted as a stem mollusk.[35] Scratch marks found associated with *Kimberella* indicate that it had some form of feeding structure (though probably not a true mollusk radula) that enabled it to graze the abundant algal mats.

An important, but less attention-getting, component of the Ediacaran fossil record is the presence of trace fossils such as trails, burrows, and feeding traces.

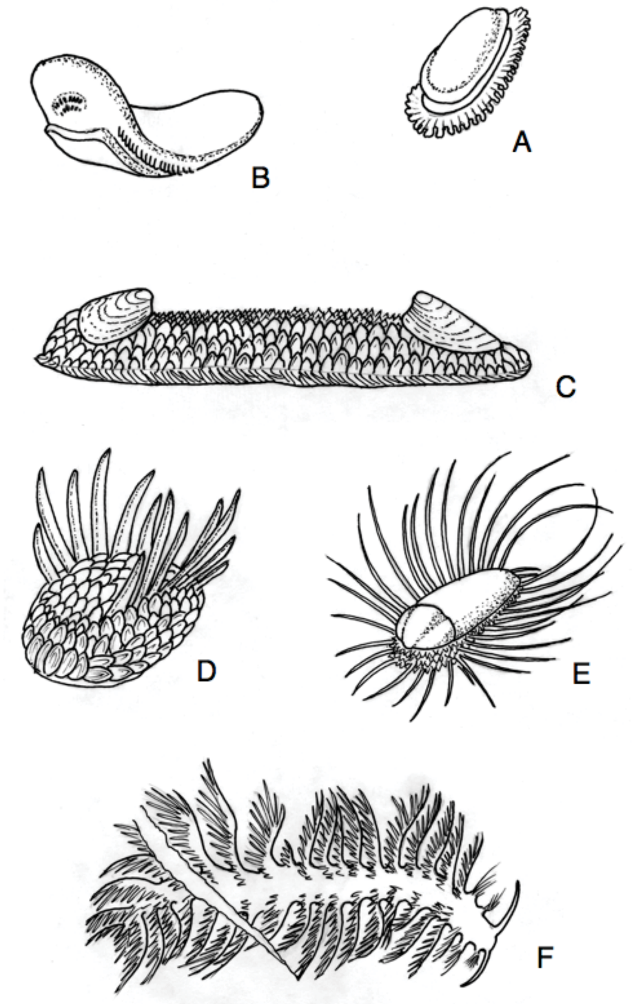

Figure 3. Examples of stem mollusks and annelids, and of halwaxiids, a possible sister group of the annelids, include (A) the probable stem mollusk *Kimberella* from the Ediacaran; (B) the Cambrian stem mollusk *Odontogriphus*; (C) the early Cambrian halwaxiid *Halkieria* with mineralized sclerites covering the body, and anterior and posterior mollusk-like shells; (D) the early Cambrian halwaxiid *Wiwaxia* covered in unmineralized chitinous sclerites similar to the setae of annelids, and possessing long ribbed spines; (E) the recently described middle Cambrian halwaxiid *Orthozanclus* with slender unmineralized chitinous spines and a single anterior mollusk-like shell; and (F) the middle Cambrian stem annelid *Canadia* with rigid setae extending from lateral outgrowths of the body. (A is modified from reconstruction by M. A. Fedonkin and B. M. Waggoner, "The Late Precambrian Fossil *Kimberella* Is a Mollusc-like Bilaterian Organism," *Nature* 388 [1997]: 868–71. B is redrawn from reconstruction in J. B. Caron, A. Scheltema, C. Schander, and D. Rudkin, "A Soft-Bodied Mollusc with Radula from the Middle Cambrian Burgess Shale," *Nature* 442 [2006]: 159–63. C is based on the illustration in Susannah Porter's website http://www.geol.ucsb.edu/faculty/porter/Early_Animals.html by Jennifer Osborne. D is based on the illustration at the website of the Burgess Shale Geoscience Foundation http://www.burgess-shale.bc.ca/discover-burgess-shale/ancient-creatures/wiwaxia. E is redrawn from S. Conway Morris and J. B. Caron, "Halwaxiids and the Early Evolution of the Lophotrochozoans," *Science* 315 [2007]: 1255–8. F is drawn based on specimen shown at the Royal Ontario Museum website, http://burgess-shale.rom.on.ca/en/fossil-gallery/list-species.php.)

Except in the few cases mentioned above, there are no body fossils preserved of the organisms that made these traces. These traces tend to be small unbranched sediment-filled burrows that run horizontally along the sediment surface or under the microbial algal mats. Somewhat more complex burrows appear toward the base of the Cambrian, including irregularly branching burrows and shallow vertical burrows.[36] These traces are important because they point to the existence of small worm-like organisms that were probably feeding on and in the algal mats that covered extensive areas of the seafloor. The biological identity of these burrowing organisms is unknown, although they were clearly bilaterian.

There is one more set of fossils that are known from the late Ediacaran (550–543 million years) that reveal yet another aspect of the metazoan diversity before the Cambrian. These fossils include tiny calcified or phosphatized tubes, cones, and goblet-shaped structures that record the presence of animals capable of producing mineralized skeletons. They are commonly embedded within algal buildups that formed reef-like structures, and are locally quite abundant.[37] These algal-metazoan reefs foreshadow the later algal reefs of the Cambrian. The very peculiar cm-sized goblet-shaped *Namacalathus* (found as calcified fossils) lived attached to the algal mounds by stalks. Although the preserved shape of these fossils is consistent with that of cnidarians, their biology is uncertain. The tiny partitioned and budded tubes of *Sinocyclocyclicus* bear a strong resemblance to the skeletons of some primitive corals.[38] The cone-in-cone structures of *Cloudina*, and the more tubular *Sinotubulites* could have been produced by various types of worms such as serpulids. However, as with the trace fossils, the identity of the actual tube formers remains unknown. A significant observation of the *Cloudina* fossils is that many of them are perforated by borings. These borings provide the first clear evidence of predation before the Cambrian.

It is clear from the above discussion of the latest Precambrian, that the Cambrian "explosion" did not occur in a biological vacuum. Although many of the fossil specimens are enigmatic and difficult to classify, they nonetheless show significant biological diversity. Furthermore, at least a few living phyla had already appeared by the beginning of the Cambrian, and other forms likely represented sister groups or stem groups related to later-evolving phyla.

The Cambrian Record of Evolutionary Transitions

One of the most important features of the Cambrian “explosion” was the rapid diversification of organisms with shells, plates, and various other types of hard parts. A wide variety of soft-bodied organisms are also known from the Cambrian. Although some fossils can be assigned to living phyla, there are also specimens that appear to represent stem groups or intermediates between modern phyla, as well as specimens of unknown relationship. Representatives of several living classes and other lower taxonomic categories also appear in the Cambrian. A few deposits with exceptionally good preservation of fossils, such as the Burgess Shale in Canada, contribute to the wide range of taxa known from the Cambrian. Such deposits with exceptional preservation are known as Konservat-Lagerstätten (from the German “conservation deposits”). Similar deposits have since been found around the world in the Early to Middle Cambrian, notably the Early Cambrian Chengjiang fauna of China. Additionally, trace fossils become much more varied, complex, and abundant in the Cambrian, suggesting a newly widened range of animal activity.

As stated earlier, the first appearance of the burrow *Treptichnus pedum* defines the base of the Cambrian. The organisms forming those burrows were likely priapulid worms, a worm phylum that is well represented among the Chengjiang and Burgess fossils.[39] Significantly, the early Cambrian is marked by a significant increase in the diversity of burrows associated with the onset of vertical mixing of the sediment by organisms, and the destruction and loss of the algal mat-grounds that characterized the Ediacaran. This “substrate revolution” from stable firm ocean floors to soft, muddy, turbid ones, had a major impact on the bottom-dwelling organisms of the Cambrian.[40] Organisms responded by becoming more mobile, and by moving below the sediment surface and into the overlying water column.

Some of the very first fossils to appear near the base of the Cambrian are tiny skeletal plates, spines, tubes, and cap-shaped shells that have been called the “small shelly fossils.”[41] Among these are the spicules of different groups of sponges and the shells of the earliest known “crown group” mollusks and brachiopods. However, the biological identities of many of these tiny skeletal elements were completely unknown until fairly recently. Well-preserved complete fossils in the Chengjiang, and other fossil lagerstätten around the world, have revealed that many of these small shelly fossils were actually the spines and “armoring” of larger metazoans. More detailed analysis of other fossils has revealed that they may represent the stem groups of living phyla rather than evolutionary dead ends.

The discovery of complete specimens from later in the early Cambrian has revealed that a variety of scales, plates, and spines found among the “small shelly fossils” actually fit together and overlapped to cover the bodies of slug-like organisms.[42] These organisms are the halkieriids and wiwaxiids (fig. 3). The halkieriids bore conical mollusk-like shells as well as calcareous structures similar to the chitinous bristles typical of polychaete annelid worms. The slightly younger *Wiwaxia* was covered in scale-like and spine-like structures even closer to those of the polychaetes, and also possessed a radula diagnostic of mollusks. These various unusual organisms bear resemblances to both mollusks and polychaete annelid worms, which are closely related phyla.[43] Thus these organisms would appear to be positioned somewhere on the evolutionary tree near the branching point of the mollusks with the annelids. Stem group polychaete annelid worms also appear in the early Cambrian.[44]

The first likely “crown group” mollusks appear in the earliest Cambrian as part of the small shellys. While recognizable as mollusks, many of these fossils belong either to sister groups or to stem groups of living classes. Cap-shaped fossils called helcionelloids are interpreted as monoplacophoran-like crown group mollusks. There is good fossil evidence of the transition from these primitive cap-shaped helcionelloids to the first bivalves by way of the extinct group of rostroconchs. The hinged valves of clams appear to have evolved by the lateral compression of cap-shaped shells and then the thinning and loss of shell material along the hinge line.[45] There are also likely fossil transitions from coiled helcionelloids to the first gastropods.

Another important group of organisms represented by small plates in the early Cambrian are the lobopods. Lobopodians, until very recently an enigmatic group of strange fossils, were “caterpillar-like” organisms with fleshy lobed limbs and mineralized plates or spines running along their backs. They are similar to the living Onychophora, or velvet worms, but are considered a distinct group.[46] The oldest known lobopodian bears certain similarities to a distinctive group of worms called the palaeoscolecid priapulids that also bore small plates or tubercles along their bodies.[47] Lobopods may have been derived from these worms that also have an early Cambrian fossil record. Furthermore, the lobopods have become recognized as the critical link in reconstructing the assembly of the arthropod body plan. They have anatomical features in common with the arthropods, particularly with peculiar Cambrian stem arthropods such as *Opabinia* and *Anomalocaris* that are preserved in the younger Chengjiang and Burgess fossil beds. These later organisms possessed lobopod limbs but also had gill flaps along their bodies and jointed feeding appendages. Intermediates between lobopodians and the early stem group arthropods have also been discovered that possessed gills.[48] Of even greater interest is the evidence available from the extraordinary preservation of muscle tissue in a few of these transitional organisms. These specimens suggest a progression of steps in the transformation of internal anatomy from lobopodians to true arthropods.[49]

The tommotiids, a group of tiny roughly conical-shaped shells composed of calcium phosphate, have been, until recently, one of the most enigmatic of the small shelly fossils. However, new discoveries of articulated specimens have shown that pairs of symmetrical skeletal elements fit together to form an open cone that was attached to the seafloor at the base. An opening at the base indicates the presence of a muscular attachment structure likely similar to the pedicle of brachiopods. The paired shells also have features similar to the tiny paterinids, crown group brachipods with calcium phosphate shells that also appear in the early Cambrian.[50] These fossils therefore appear to represent stem brachiopods that were themselves derived from armored tubular filter feeders attached to the seafloor (fig. 4).

The living phoronid worms are a phylum closely related to the brachiopods. Like the brachiopods, they are filter-feeders using a ring of ciliated tentacles called a lophophore. However, unlike brachiopods, they are not enclosed within paired shells but construct chitinous tubes. The recent description of an early Cambrian unmineralized, “soft-shelled” lingulid brachiopod strongly suggests that phoronids evolved from crown-group brachiopods by the loss of a mineralized shell.[51] This transitional form also provides evidence for the transformation of the musculature from that typical of shelled brachiopods to the longitudinal arrangement of phoronids. These “soft-shelled” brachiopods are likely stem-phoronids.

Following the appearance of the small shelly fossils, the diverse metazoan fossil communities of the Chengjiang in China are dated at around 525– 520 million years, 20 million years after the beginning of the Cambrian. The exceptional preservation in these fossil beds is similar to that of the Burgess Shale deposits that are dated around 515–505 million years.

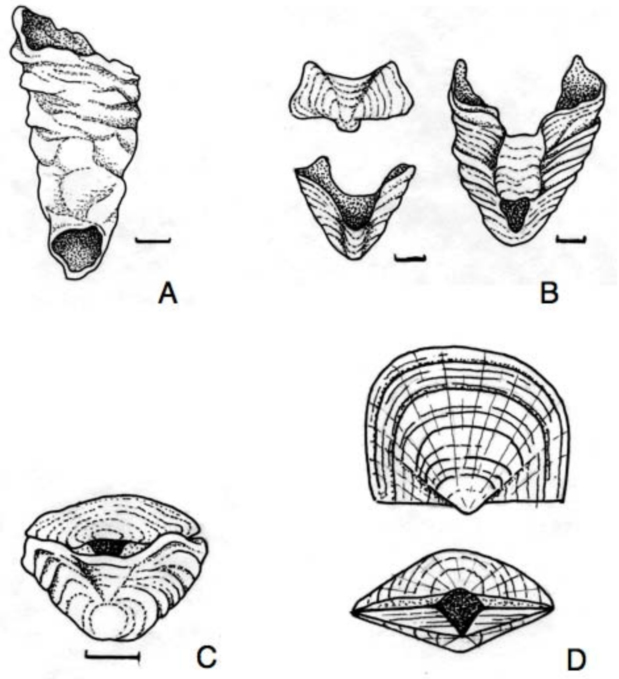

Figure 4. These fossils illustrate the transition from tommotiids to brachiopods: (A) the conical phosphatic shell of the tommotiid *Eccentrotheca* with an opening at the apex (scale bar 0.5mm); (B) the tommotiid and stem brachiopod *Paterimitra* with a conical shell of articulated phosphatic sclerites, a “pedicle tube” for attachment, and an upper valve (scale bar 0.2mm); (C) the bivalved *Micrina*, the most brachiopod-like tommotid yet known (scale bar 0.5m); and (D) the early Cambrian crown group brachiopod *Psiloria* (shell about 1 cm across). (A is drawn from an image in C. B. Skovsted, G. A. Brock, J. R. Paterson, L. E. Holmer, and G. E. Budd, “The Scleritome of *Eccentrotheca* from the Lower Cambrian of South Australia: Lophophorate Affinities and Implications for Tommotiid Phylogeny,” *Geology* 36 [2008]: 171–4. B is drawn from an illustration in C. B. Skovsted, L. E. Holmer, C. M. Larsson, A. E. S. Högström, G. A. Brock, T. P. Topper, U. Balthasar, S. P. Stolk, and J. R. Paterson, “The Scleritome of *Paterimitra*: An Early Cambrian Stem Group Brachiopod from South Australia,” *Proceedings of the Royal Society B* 276 [2009]: 1651–6. C is drawn from L. E. Holmer, C. B. Skovsted, G. A. Brock, J. L. Valentine, and J. R. Paterson, “The Early Cambrian Tommotiid *Micrina*, A Sessile Bivalved Stem Group Brachiopod,” *Biology Letters* 4 [2008]: 724–8. D is drawn from an illustration at the website http://www.museumwales.ac.uk/en/1625/.)

These extraordinary fossil sites give us our best views into the composition of marine biological communities from these times, preserving both soft-bodied organisms and those with mineralized skeletons.[52] These beds contain abundant and diverse sponges and cnidarians, as well as priapulid worms, annelid worms, lobopods, stem mollusks such as *Wiwaxia*, and brachiopods. However, probably the most dramatic characteristic of the Chengjiang- and Burgess Shale-type deposits is the abundance and diversity of arthropods.

Arthropods comprise 50% or more of all of the fossil specimens collected from these beds. These fossils include stem arthropods such as the anomalocarids, trilobites which came to dominate the Paleozoic, and some species that appear to be crustaceans and chelicerates. However, most of the fossils belong to primitive stem groups that likely represent evolutionary dead ends after the appearance of true arthropods but before the rise of most living arthropod groups. In the Burgess Shale, one such primitive species (*Marrella*) alone comprises a third of all fossil specimens. These fossils show unusual arrangements, and types, of appendages.

The chordates (that include vertebrates), hemichordates (that include the living "acorn worms"), and echinoderms (that include the living starfish and echinoids) are all deuterostomes and have the same pattern of early embryo development. Although the modern representatives of these phyla appear extremely different, they are actually closely related branches on the tree of life, and are understood to have evolved from a common ancestor. Some rare, but very significant, specimens in the Chengjiang seem to be stem chordates and stem echinoderms, as well as specimens that have been interpreted as organisms close to the common ancestors of chordates and echinoderms. These rather simple Cambrian organisms possess the anatomical characteristics that would be expected in organisms that had acquired some, but not all, of the distinctive features of chordates or echinoderms.

A newly described group of primitive soft-bodied deuterostomes, called vetulocystids, bears similarities to some of the bizarre early echinoderms. These organisms rested on the bottom and possessed echinoderm-like respiratory openings and two ribbed cones that likely represented the mouth and anus. Unlike all living echinoderms, however, they lacked any calcite skeletal plates.[53] They may represent organisms that belonged to a sister group ancestral to the first stem-group echinoderms. The most primitive echinoderms were characterized by flattened, nearly bilaterally symmetrical forms. The earliest stage of echinoderm evolution is represented by *Ctenoimbricata* from the early middle Cambrian. These flattened stem echinoderms were completely covered on their lower side by calcite plates, but were largely uncalcified on their upper (dorsal) sides.[54] The ctenocystoids and cinctans were similar stem echinoderms that show increasing coverage of their dorsal sides by interlocking calcite plates (fig. 5).

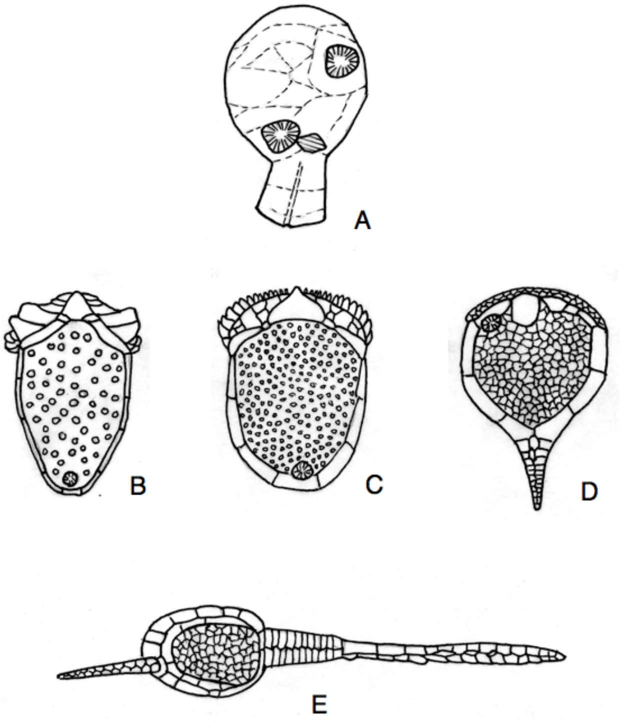

Figure 5. Stem echinoderms and the early evolution of the Echinodermata as illustrated by (A) the soft-bodied ventulocystid *Ventulocystis*, a primitive deuterostome, possibly a sister group to the stem echinoderms; (B) *Ctenoimbricata* is the most primitive known stem echinoderm with only scattered calcified elements on the dorsal side; (C) the ctenocystid *Courtessolea*, a slightly more derived stem echinoderm; (D) the cinctan *Sotocinctus*, a stem echinoderm with a body completely covered by calcite plates and a "tail" appendage; and (E) the stem group solute *Syringocrinus* with a "tail" and feeding arm appendage. (A is drawn from an illustration in D-G. Shu, S. Conway Morris, J. Han, Z-F. Zhang, and J-N. Liu, "Ancestral Echinoderms from the Chengjiang Deposits of China," *Nature* 430 [2002]: 422–8. B, C, and D are redrawn from S. Zamora, I. A. Rahman, and A. B. Smith, "Plated Cambrian Bilaterians Reveal the Earliest Stages of Echinoderm Evolution," *PLoS ONE* 7, no. 6 [2012], e38296. doi:10.1371. E is redrawn from the Palaeos website http://palaeos.com/metazoa/deuterostomia/homalozoa/soluta.html.)

Another very primitive stem group of deuterostomes, called ventulicolians, has also recently been described that might represent the anatomy of organisms near the base of the deuterostome evolutionary branch that were ancestral to both the chordates and echinoderms. These soft-bodied organisms possessed segmentation and oval structures interpreted as gill slits, and a terminal mouth.[55] The most primitive group of chordates are the urochordates, or tunicates, that have a sack-like adult body that filters seawater through pharyngeal slits. In their tadpole-like larval form, they possess stiff notochords (a structure diagnostic of chordates) that is lost in the adult form. A likely tunicate has been described from the Chengjiang.[56] Another group of primitive chordates are the cephalochordates (represented today by the lancelets) that possess a notochord as adults, pharyngeal slits, and muscles arranged in parallel bundles. Some fossils have been interpreted as stem cephalochordates.[57] Lastly, and of particular interest, is a fossil that may be a stem vertebrate.[58] *Myllokunmingia*, in addition to a notochord, gill pouches and muscle bundles, also appears to have had some structures characteristic of vertebrates. These vertebrate features include a cavity surrounding the heart, a dorsal fin, and cartilage around the head and as a series of elements along the notochord. The Chengjiang thus includes fossil specimens that occupy several significant transitional stages from primitive deuterostomes to stem echinoderms and stem chordates (fig. 6).

Conclusions

Given our current, and continually growing, knowledge of the deep past, it is increasingly clear that the rise of multicellular animals is not an impenetrable mystery. While there is much that is not known, and some that will never be known, there is also much that has been discovered, and much excitement for what will yet be learned. New discoveries and analyses are continually adding to our knowledge of evolutionary transitions in the latest Precambrian and Cambrian.

The Cambrian "explosion" was a time of great evolutionary significance, as it established the anatomical templates for much of the diversification to come. It was also extraordinary in that it was a time of accelerated evolutionary change for marine organisms across the animal kingdom. However, despite its relative rapidity, the time during which the rise of modern animal phyla occurred was still a lengthy interval, with the Early Cambrian alone lasting 32 million years. Furthermore, critical evolutionary innovations were established in the 40 million years of the Ediacaran preceding the Cambrian.

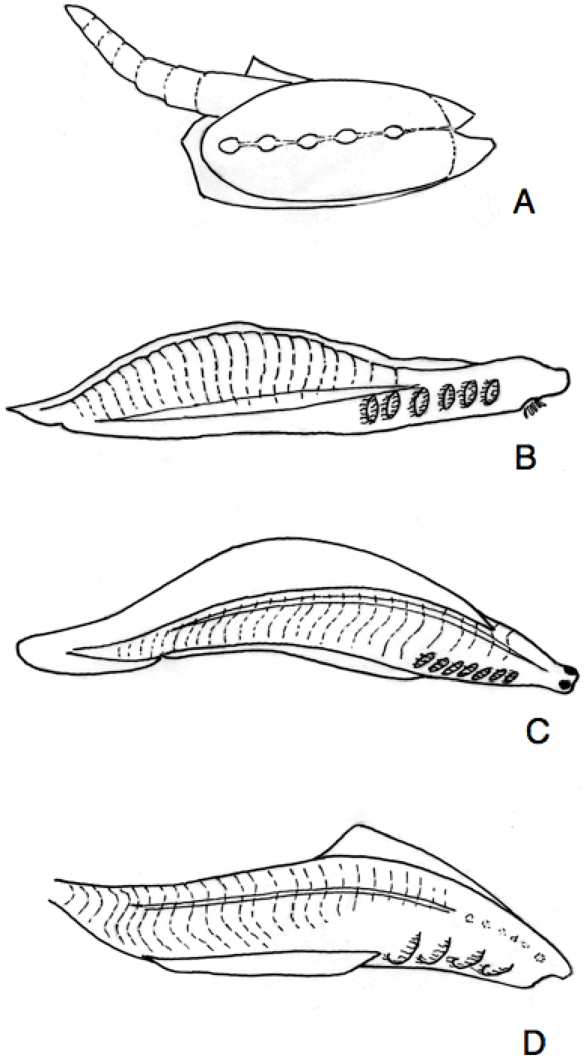

Figure 6. The evolution of chordates from primitive deuterostomes as illustrated by (A) the vetulicolian *Vetulicola* interpreted as a stem deuterostome with some features suggestive of chordates; (B) the lancelet-like stem chordate *Haikouella* (about 3cm long); (C) *Haikouichthys*, another likely stem chordate (about 2.5cm long); and (D) *Myllokunmingia*, is a possible stem vertebrate (about 3cm long). (A is drawn from an illustration in D-G. Shu, S. Conway Morris, J. Han, L. Chen, X-L. Zhang, Z-F. Zhang, H-Q. Liu, Y. Li, and J-N. Liu, "Primitive Deuterstomes from the Chengjiang Lagerstätte (Lower Cambrian, China)," *Nature* 414 [2001]: 419–24. B is redrawn from J-Y. Chen, D-Y. Huang, and C-W. Li, "An Early Cambrian Craniate-Like Chordate," *Nature* 402 [1999]: 518–22. C is modified from a reconstruction in X-G. Zhang and X-G. Hou, "Evidence for a Single Median Fin-Fold and Tail in the Lower Cambrian Vertebrate, *Haikouichthys ercaicunensis*," *Journal of Evolutionary Biology* 17, no. 5 [2004]: 1162–6. D is drawn from an illustration in D-G. Shu, H-L. Luo, S. Conway Morris, X-L. Zhang, S-X. Hu, L. Chen, J. Han, M. Zhu, Y. Li, and L-Z. Chen, "Lower Cambrian Vertebrates from South China," *Nature* 402 [1999]: 42–6.)

The animals of the Cambrian did not appear in all their modern complexity out of a void, but rather they provide pointers to their common ancestry. Despite the claims of evolution skeptics, the fossil record provides multiple examples of organisms displaying transitional anatomies. As we have seen, these fossil organisms were largely representative of stem groups that possessed some, but not all, of the diagnostic features that define the major groups of living organisms. The anatomical characters that define the body plans of the major living animal phyla can be seen to have been acquired piecemeal during the early evolution of the metazoans. Just as with all other taxonomic groups (e.g., classes, orders, families, genera, species), the divisions between phyla break down as we move closer to their times of origin from common ancestors. While the picture is incomplete, recent spectacular fossil discoveries strongly support the conclusion that the major branches of the animal tree of life are joined to a common metazoan trunk. The tree of life continues to stand tall. ∽

Acknowledgments

I would like to thank the editors at BioLogos for initially encouraging me to write a blog series on the Cambrian explosion. Those essays formed the foundation for this article. I also greatly appreciate the very thorough and constructive comments by an anonymous *PSCF* reviewer. Any errors of fact or interpretation are mine alone.

Notes

[1] Some material in this article appeared earlier in the six-part blog series "The Cambrian 'Explosion,' Transitional Forms, and the Tree of Life" on The BioLogos Forum, December 2010 to March 2011, http://biologos.org/.

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[14] See the discussion in J. W. Valentine, "The Nature of Phyla," in *On the Origin of Phyla* (Chicago, IL: University of Chicago Press, 2004), 7–39. Also see K. B. Miller, "Common Descent, Transitional Forms, and the Fossil Record," in *Perspectives on an Evolving Creation*, ed. K. B. Miller (Grand Rapids, MI: Wm. B. Eerdmans, 2003), 152–81.

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[18] See the discussion in J. W. Valentine, "The Nature of Phyla," in *On the Origin of Phyla*, 7–39.

[19] A more expanded discussion of this topic can be found in K. B. Miller, "Common Descent, Transitional Forms, and the Fossil Record," 152–81.

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