The Cambrian Explosion: How Do We Use the Evidence?

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The Cambrian explosion is an excellent example of a grand idea that has been tempered by the steady collection of data to test hypotheses. Historically, the idea of an "explosion" developed from an apparent lack of bilaterian animal fossils before a certain point in the fossil record, in contrast with a great diversity of life that seemed to appear in the Cambrian period. DNA molecular clock estimates contradict this story, however, with most dates for the divergence of major phyla predating the Cambrian by 100 million to 400 million years. The contradiction might be rectified by corrections to the clock or by discoveries of Precambrian bilaterian fossils. Although many candidates exist, no single environmental or biological explanation for the Cambrian explosion satisfactorily explains the apparent sudden appearance of much of the diversity of bilaterian animal life. Scientists' understanding of this phenomenon has been greatly amplified in recent years by better geological dating and environmental characterization, new fossil discoveries, and by a great expansion of our knowledge of developmental mechanisms and their evolutionary meaning.

Keywords: Cambrian explosion, macroevolution, fossil record, molecular evolution

The term "Cambrian explosion" refers to a hypothesized time when bilaterally symmetrical (bilaterian) animal groups of diverse forms diverged from a common ancestor during the early part of the Cambrian period, a geological period starting about 542 million years ago (Ma). If true, this would surely be one of the most momentous times in animal history, when the stage was set for the evolution of most of the ensuing diversity of animal life, including the extant phyla. We would owe to this time the origin of mollusks, arthropods, and even our own major group, the Chordata. We tend to see the major groups of bilaterians as members of distinct body plans, each belonging to its own phylum. The phyla can be organized into two major groups, the Deuterostomia (echinoderms, chordates, and others) and the Protostomia (annelids, mollusks, and others), whose differences can be diagnosed by both molecular and morphological characters. The protostomes can be subdivided into two major groups, the Ecdysozoa (arthropods, nematodes, and others) and the Lophotrochozoa (annelids, mollusks, nemerteans, brachiopods, and others).

The Cambrian-explosion hypothesis claims that this fantastic animal menagerie diverged from a common ancestor and become a recognizable set of body plans in a mere 20 million years or so. The earliest Cambrian—marked by burrows and small, strange, shelly fossils—culminates in a spectacular array of forms by about 520 Ma. A somewhat softer version of the hypothesis allows for divergence a few million years before the Cambrian, with an explosion of large-bodied organisms in the Early Cambrian.

The history of this idea is as fascinating as the idea itself (see Levinton 2001). By the 1830s and 1840s, a succession of rocks in Wales and England revealed a series of animal forms, with the newest rocks containing forms that strongly resembled living animal species, and the oldest including a series of strata that apparently lacked recognizable animal fossils. Soon thereafter, a great controversy arose between Adam Sedgwick, of Cambridge University, and Roderick Murchison, of the Geological Society of London. Sedgwick proposed the existence of a sequence of rocks in Wales, which he named Cambrian (and where, at first, no fossils were found). The controversy with Murchison was over the exact sequence of rocks from the Paleozoic era. By the 1870s, the idea of a Cambrian, the oldest geological period with animal fossils, was widely accepted.

Charles Darwin recognized the implications of the Cambrian for his ideas on evolution. Although the beginning of animal life appeared to occur in the Cambrian period, Darwin (1859) thought that the fossil record might have failed to record a long preceding time of gradual unfolding of animal life. After all, within the Cambrian, there were well-formed and recognizable brachiopods, trilobites, and other groups that could readily be assigned to major groups of animals. Could these well-formed fossils have sprung from the inchoate, amorphous likely ancestors of animal life with no intermediates? Hardly likely, argued Darwin. He explained:

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> I look at the natural geological record, as a history of the world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines.... On this view, the difficulties above discussed are greatly diminished, or even disappear. (Darwin 1859, pp. 310–311)

If Darwin set the stage for the Cambrian-explosion hypothesis, the cast of zoological characters was elaborated through the momentous discoveries of Charles Walcott, whose great achievements as a Cambrian specialist were matched by his accomplishments in government, leading eventually to his leadership of the US Geological Survey, the Smithsonian Institution, and the Carnegie Institution of Washington (Yochelson 1996). As a geologist, Walcott established the modern framework for the trilobite-based biostratigraphy of the Cambrian period in North America, which arose from many seasons in the montane west and from painstaking work in the laboratory. But he is remembered mainly for the discovery of the Burgess Shale and his description of a menagerie of animal life that could not be imagined to occur in the otherwise much less diverse surrounding Cambrian formations, where few species other than trilobites and brachiopods were preserved. Walcott and his party, which included his wife and children, discovered scores of animal species, many of which were delicate soft-bodied forms, preserved as organic films on the shale surfaces. Considering the remoteness of the site, near Yale, British Columbia, Walcott's personal effort and leadership produced the greatest fossil-collecting achievement in the history of invertebrate paleontology (Gould 1989, Yochelson 1996).

What was so spectacular about Walcott's discovery? Once the fossils he identified (priapulids, annelid worms, crustaceans, and the like) were cataloged, alongside an equally diverse group of fossils later described by paleontologist Harry Whittington (1985) and his colleagues, scientists could say with some confidence that many of the living major groups of animals had appeared by the Middle Cambrian (the age of the Burgess Shale, ca. 505 Ma). Whittington's discoveries expanded the catalog of forms resembling living groups, but it also added a startling array of weird creatures, some of which could not be related easily to any of the known phyla. What could be more spectacular than the formidable predator *Anomalocaris* (figure 1)? And what could be more impenetrable than the classification of genera such as *Opabinia* and *Wiwaxia?* Later discoveries of rocks with similar levels of fossil preservation to that of the Burgess Shale—from sites in Greenland; in Chengjiang, southwestern China; and in other localities—extended the time of origin of these groups to the Early Cambrian and added yet more diversity to this early apparent explosion of animal life, witnessed by the fossil record.

If Darwin established the theater and Walcott and Whittington gave us the cast of characters, it was Preston Cloud who wrote the first draft of the play that has guided all thinking about the Cambrian explosion in recent decades. Like any great playwright, Cloud offered a clear-headed rethinking of a complex situation and focused his audience's thinking on a few great ideas. He had predecessors, but Cloud managed to capture the idea of the Cambrian explosion with the greatest eloquence and geological sophistication.

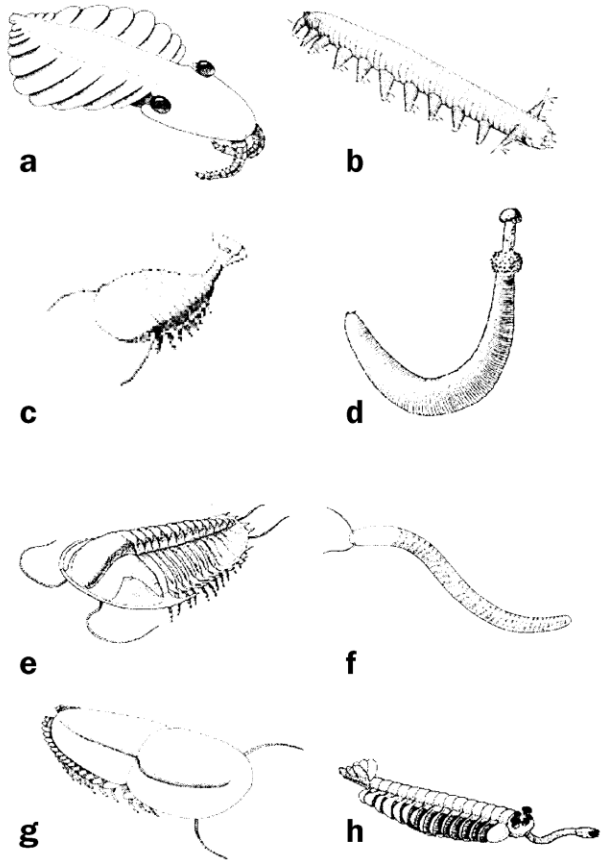

Figure 1. Some animals of the Burgess Shale that are rarely preserved in nearby contemporaneous Middle Cambrian rocks. (a)* Anomalocaris, *systematic status unclear, up to. 0.5 meters long. (b)* Aysheaia, *onychophoran, 1 to 6 centimeters (cm). (c)* Sidneyia, *arthropod, 5 to 13 cm. (d)* Ottoia, *priapulid, 2 to 16 cm. (e)* Naraoia, *two-lobed noncalcified trilobite, 9 to 40 millimeters (mm). (f)* Pikaia, *chordate, 4 cm. (g)* Olenoides, *trilobite, 50 to 85 mm. (h)* Opabinia, *status unknown, 4 to 7 cm. Reprinted from Levinton (2001) with the permission of the Smithsonian Institution.

Cloud was trained as a stratigraphic paleontologist at Yale and later rose as a scientist in the US Geological Survey. Aside from his great leadership and mentoring of a generation of paleontologists, he developed an integrative approach to paleontology, adding skills in paleogeography, carbonate stratigraphy, and carbonate sedimentology. His later career at the University of California, Santa Barbara, widened his interests to astrobiology and the origin of life. His observations

as a paleontologist led him to characterize the Phanerozoic fossil record as a series of evolutionary eruptions, with the Cambrian being the greatest of all (Cloud 1948). But it was Cloud's 1966 Yale lecture that solidified the modern approach to the Cambrian explosion. In the remarkable, long paper that resulted (Cloud 1968), he unified then-innovative studies relating reconstructions of ancient global climate to the Cambrian appearance of animal life. First, and foremost, he insisted that we invest our efforts in the *evidence* for the identity and age of ancient fossils: "Is it surely a fossil or the work of an organism?... And is it surely endemic to rocks whose stratigraphic position is such that they cannot reasonably be included in the Paleozoic?" (Cloud 1968, p. 51). Given the evidence, he concluded, "the appearance of multicellular animal life in the Cambrian may actually have been almost as sudden as the record suggests, an instance of eruptive evolution of the root stock of animal evolution itself" (Cloud 1948, p. 346).

Cloud emphasized the need to find a link between a change in the global environment and the Cambrian evolutionary eruption. His original emphasis on dissolved oxygen, based on evidence from banded iron formations, has not withstood the test of time; but his emphasis on evidence has been a cornerstone of Cambrian studies.

The more recent major paleontological discoveries have intimately related studies of phylogenetic relationships of early bilaterian groups to great refinements of the geological timescale. One must remember that in the 1960s, the error associated with stratigraphic correlation of geological sections and the error produced from radiometric dates produced uncertainties of millions to tens of millions of years in Cambrian and Ordovician time. The most recent geological timescale (Gradstein et al. 2005) shows vast improvement, and the current estimate of the beginning of the Cambrian at 542 Ma is most likely accurate to one million years. The most startling result is the apparent rapid appearance of most of the animal phyla, which can be bracketed within a time frame of approximately 20 million years or less (Bowring et al. 1993).

Evidence on the origin and divergence of bilaterians

The evidence on the origin and divergence of bilaterians falls into four categories: (1) molecular clock data, (2) fossil data on the appearance of bilaterian groups, (3) morphological and phylogenetic study of the fossil record; and (4) genetic evidence.

Molecular clocks. Molecular clocks rest on the presumption of a relationship between the time since two lineages have diverged and the degree of genetic difference between them, based on the idea of integrating evolutionary rate with time. Time can be estimated by taking two sister evolutionary lineages, A and B, and finding dated fossils of each group. Genetic distance is a measure of difference between the number of nucleotides in two DNA sequences or the number of amino acids in two protein sequences. If the fossil record were complete and genetic divergence were at the same constant rate for all genes over the time since the split, this process would be easy. Rates of divergence could be established, and then one might extrapolate the rate to explain the time of divergence for two lineages that are ancient and whose fossil origin dates are unknown. But the fossil record is commonly incomplete, and corrections for genetic divergence must be made for at least the following possible biases: (a) differences in rates of divergence among genes, which make some genes evolve too rapidly to preserve phylogenetic information and others evolve too slowly to give enough sequence change to properly resolve what might have been very rapid splitting events concentrated in a short period; (b) differences in rates of divergence in different lineages on an evolutionary tree; (c) possible differences in rates of genetic divergence over time (e.g., different rates of evolution under certain ecological, environmental, or evolutionary situations); and (d) heterogeneity of rates of change at different parts of a DNA molecule. These biases have led to a number of studies that attempt to correct for rate heterogeneity in different parts of a tree or simply to drop those cases where such heterogeneity exists. Some studies have attempted to incorporate large numbers of genes, which might average out the variation by the law of central tendency.

All major studies consistently produce a date of divergence for the protostomes and deuterostomes considerably before the beginning of the Cambrian (Smith 1999, Levinton 2001). More recent studies have used more genes but have yielded a wide variation of dates (figure 2). Consistently, however, these dates are Precambrian. If all of the major phyla diverged in a very short period of time, we might expect the problems in reconstruction that have been encountered, since closely spaced nodes hundreds of millions of years old would be nearly impossible to resolve (Levinton et al. 2004).

There is still great disagreement over methods and approaches. Earlier studies using few genes (e.g., Wray et al. 1996) have been criticized for including few genes with too much heterogeneity of rates over trees, but the substitute studies by critics have failed to produce dates consistent with the Cambrian and have also failed to produce dates that are highly consistent among genes (e.g., Ayala et al. 1998). Peterson and colleagues (2004) concluded that previous studies had used genes with rates of evolution inappropriate for studying most of the phyla participating in the Cambrian explosion, but their correction still produced dates that preceded the Cambrian by 30 million to 114 million years. Blair and Hedges (2005) reconsidered this most juvenile of Cambrian bilaterian divergence estimates and found that they mostly derived from a selection of fossil calibrations that biases results toward slower rates of divergence, and not toward different rates of molecular divergence between vertebrates and invertebrates, as claimed by Peterson and colleagues. Use of a different fossil calibration led to a corrected range of divergence times, 777 Ma to 851 Ma. With a rapid increase in sequence evolution at the beginning of the radiation, a regular, constant molecular clock might overestimate the divergence time. But

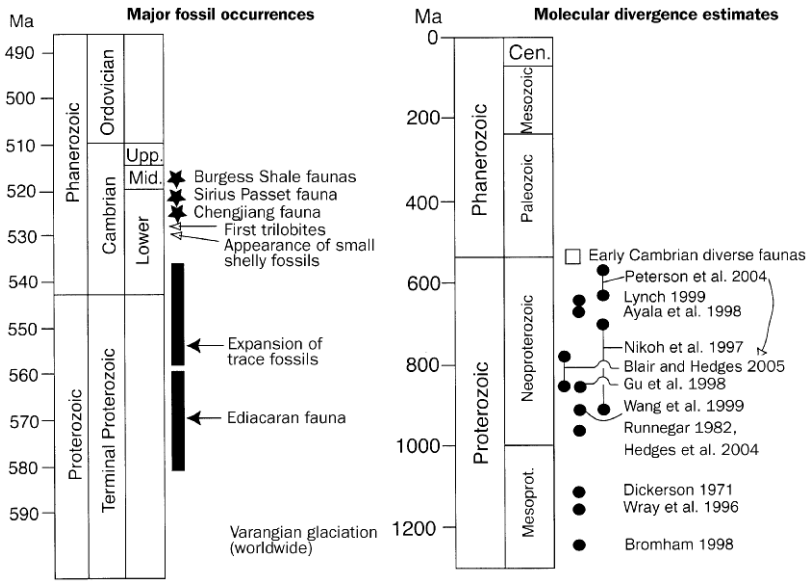

Figure 2. Left: Major fossil occurrences near the beginning of the Cambrian period. Right: Estimates of the divergence time of the protostomes and deuterostomes (i.e., bilaterian animal phyla) derived from various analyses of molecular sequences (Smith 1999, Levinton 2001).

picking the highest rate of sequence evolution would still push the divergence time to no more recently than 586 Ma (Bromham and Hendy 2000). Thus, although the large range of divergence time estimates does not inspire confidence, we must still face the current conclusion that molecular estimates do not square with the fossil occurrence data, which places the great radiation between approximately 540 Ma and 520 Ma. At present, it is likely that the assumptions of the models of molecular evolution may influence the outcomes too strongly to allow any significant confidence in estimates of molecular dates for the divergence of the Bilateria (Welch et al. 2005).

The Cambrian fossil burst. The fossil data support a conclusion at variance with the molecular clock estimates. The bilaterian animal groups seem to appear in the fossil record at or just before the beginning of the Cambrian. In the past 15 years, members of more and more phyla and major bilaterian classes, including vertebrates (Shu et al. 1999), have been found in rocks dating back to the Early Cambrian (Levinton 2001). The literal interpretation of the fossil record would suggest a complete divergence of the bilaterians in about 20 million years or less.

Trace fossils, which are burrows and trails recorded in the sediments, appear in a burst near the base of the Cambrian. Much of this diversity is dominated by burrows that served as shelters from which infaunal animals fed or moved toward the sediment surface (Dzik 2005), but arthropod traces also become prominent in the earliest Cambrian (MacNaughton and Narbonne 1999). The rise of bioturbation at the end of the Late Proterozoic (McIlroy and Logan 1999) may have been responsible for the destruction of microbial mats, which had dominated the sediment surface in the Ediacaran along with some horizontal traces. Deep burrowing, probably a response to surface predators, is not well recorded until the Ordovician and even later.

It is always an open question whether or not the apparent sudden appearance of bilaterians in the Early Cambrian results from a preservation gap. It might well be that rocks inappropriate to preservation dominate the time before the Cambrian. Ediacaran fossils in the latter part of the Proterozoic are abundant, but they are usually found in sand, which would not preserve the delicate structures seen in the organic films discovered in Lower Cambrian finer-grained sediments. With the lack of dissolved oxygen—or perhaps of mineralized skeletons—before the Cambrian, bilaterians might have been quite small in body size, which would reduce the probability of preservation (Levinton 2001). Certainly the special Burgess-Shale type of delicate preservation is lacking in Precambrian rocks younger than 750 Ma to 850 Ma (Butterfield 1995), which leaves a considerable gap in time until the Early Cambrian occurrences.

Morphology and phylogenetics revealed by fossils. Perhaps the strongest evidence to support the Cambrian evolutionary explosion of animal forms is the first clear appearance, in the Early Cambrian, of skeletal fossils representing members of many marine bilaterian animal phyla. (Only the Bryozoa so far elude discovery in the Cambrian, but they are found in the Ordovician.) The impression of an explosion is heightened by a number of fossils with unclear affinities to extant phyla. At first, it was claimed that the Early Cambrian is replete with forms that have no obvious resemblance to extant phyla or even to other ancient groups (Gould 1989). Some species have characters that may place them as ancestral members of extant phyla (Conway Morris and Caron 2007), but controversy exists as to groups such as the halkyerids (Vinther and Nielsen 2005).

A well-known taxonomic bias crept into studies of Cambrian and other early animal fossils. When a strange fossil was found, unclassifiable body parts influenced paleontologists to classify such organisms as members of new classes of extant phyla or even new phyla. Thus, a series of descriptions resulted in 21 named classes of the phylum Echinodermata (Levinton 2001). Ironically, this is precisely the opposite of what Gould (1989) argued was the failing of the great paleontologist Walcott, who supposedly tended to ally the strangest of organisms to conventional groups that had already been described. Gould may have been correct about Walcott, but he missed the rest of the picture. With gay abandon, paleontologists were naming early animal taxa and defining them as members of new phyla or classes. In effect, paleontologists are rewarded with recognition for discovering a new taxon when they assign it to a higher level of classification. (Wouldn't *you* rather discover a new phylum than a new species of an existing

genus?) The trend was accelerated with the second great investigation of the Burgess Shale by Harry Whittington and his colleagues. A weird, spiky, worm-like fossil was whimsically named *Hallucigenia* and thought to be a taxon unrelated to conventional known phyla (Conway Morris 1977). Another fossil, previously thought by Walcott to be an annelid, was redescribed as belonging to a new phylum, perhaps related to mollusks (Conway Morris 1985). This bias forced a notion of an evolutionary lawn, in which numerous unrelated taxa appeared suddenly in the Cambrian (and the Ordovician, in the case of Echinodermata), which fit nicely with Cloud's (1968) concept of the polyphyletic origin of the animal phyla.

Two important breakthroughs changed scientists' conception of a Cambrian explosion as an evolutionary lawn of strange and unrelated shoots: (1) reexamination of the morphology of these "strange" creatures and (2) reconsideration of these disparate taxa as members of an evolutionary tree, which represents the morphological characters of different groups from the point of view of evolutionary relatedness. Many of the supposed oddball echinoderms, for example, were mistakenly classified as advanced, differentiated forms. Instead, they could be assigned to ancestral locations on an echinoderm evolutionary tree. Thus, the evolutionary lawn of echinoderms was transformed into a far more sensible evolutionary tree (Smith 1984). Second, a reexamination of characters began to show that other "oddballs" were not so strange, after all. The supposedly weird *Hallucigenia* was shown to be reconstructed upside down. It was unlikely that this worm sat on spikes, which instead projected upward to protect against predators. More deflating was the discovery that *Hallucigenia* was a mundane member of a larger Cambrian fossil group, the Lobopodia, related to living velvet worms (Ramskøld and Xianguang 1991). The effect was something like being in a dream and seeing a party of weird, colorfully dressed Harry Potter characters, only to wake up and realize that you were looking at your ordinary friends, wearing blue jeans and T-shirts.

The result of this new approach has been very important for comprehending the relationships of early animal life, but we are just at the beginning of an understanding. Researchers are carefully examining the characters of fossils and constructing evolutionary trees, which leads to healthy exchanges of views.

The use of carefully reckoned organismal characters and the construction of phylogenetic relationships have produced some tantalizing results. A major classification of fossil and living representatives of the phylum Arthropoda, based on morphology, has presented a difficult conundrum, perhaps the Achilles heel of the Cambrian-explosion hypothesis. A complete analysis of the evolutionary relationships of the arthropods demonstrates that trilobites are not an ancestral group, but rather are derived (that is, distant from ancestral nodes) in location on the evolutionary tree (Briggs and Fortey 1989). This finding becomes quite intriguing when one realizes that the first appearance of the trilobites not only defines the Early Cambrian appearance of arthropods at the base of the Atdabanian but occurs with the trilobites already deployed into two large-scale biogeographic realms (Fortey et al. 1996). In other words, at the very beginning of known fossil arthropod (and other bona fide bilaterian) preservation, advanced arthropods are already present and bigeographically differentiated.

Moreover, an emerging picture of Early Cambrian arthropods suggests that primitive forms, bearing characters ancestral to many euarthropods (Waloszek and Maas 2005), coexisted with definitive crown-group (meaning that they have characters of derived groups) crustacea, a modern group that dominates the oceans today (Zhang et al. 2007). Arthropods described from southern China, and three-dimensionally preserved Orsten-type fossils from the Lower to the Upper Cambrian, demonstrate a remarkable coexistence of different stages of evolution, from ancestors to derived groups such as crustaceans and their sister group (Siveter et al. 2001, Hou et al. 2004, Waloszek et al. 2007). This remarkable coexistence leads to the inevitable conclusion that, even by the Early Cambrian, arthropods were very diverse and comprised a large number of lineages in diverse evolutionary positions of ancestral and advanced status. This includes a crown-group crustacean of large body size with a sophisticated particle feeding mechanism (Harvey and Butterfield 2007). Could this have happened in a geological "instant"?

There is no surprise in suddenly seeing at the base of the Cambrian a mixture of ancestral and derived forms. Even in our living biota today, we have a surprising range of ancestral forms (sometimes called "living fossils") coexisting with highly derived forms in almost every phylum. But of course the co-occurrence of a panoply of ancestral and derived forms is not evidence that everything happened at once. One cannot escape the conclusion that something is not preserved, or is yet to be found from the fossil record, from before the first occurrence in the Early Cambrian of trilobites and true crustaceans, let alone other bilaterians. I admit that, as Carl Sagan once said, the absence of evidence is not strong evidence of absence. But it does suggest that Cambrian explosionists have some work to do, as do their opponents.

Are there bona fide Precambrian bilaterian fossils? This has been a road littered with difficulty and disappointment. Although Cloud (1968) systematically discredited nearly all described Precambrian bilaterian fossils, he was unable to discredit an annelid-like fossil found in 700-million- to 900-million-year-old rocks in China (Cloud 1986). Some tantalizing fossils that might be bilaterian have been found in the latter part of the Proterozoic, known as the Ediacaran (Fedonkin and Waggoner 1997), and bilaterian-like embryos have been found in the Ediacaran Doushanto Formation in China (Xiao et al. 1998). None of these can easily be placed on a tree of known bilaterian groups. A possible sister group to the trilobites has been described (Fortey et al. 1996). A large menagerie of fossils was found first in south Australia (Glaessner and Wade 1966) and later worldwide in Ediacaran-aged rocks. These fossils appear to belong to the Cnidaria and other groups of uncertain status. A recently discovered trace-

like fossil, claimed to be one billion years old, may belong to a bilateral organism, but not necessarily a bilaterian animal (Bengtson et al. 2007).

Genetic questions. The early origin and conservatism of major functioning parts of the bilaterian genome have been so well documented that they are now textbook truisms. Most intriguing is the constancy of the *Hox* gene complex, whose gene order and action combine to determine anterior-posterior specialization (McGinnis et al. 1984), which is the very essence of being a bilaterian. It has been suggested that the emergence of *Hox* genes allowed the diversification of the Cambrian explosion (Erwin et al. 1997), but this is not likely if all bilaterians shared this specification mechanism. The diversification would have to be caused by genes downstream of *Hox* genes or by other genes entirely such as various transcription factor genes and cell-signalling genes. The two major bilaterian animal groups, the Protostomes and the Deuterostomes, also share genes that are crucial in the development of eyes, circulatory systems, skeletons, and many other systems (table 1; Levinton 2001). These genes suggest the possibility of an ancestral creature deep within the Precambrian that is mobile, with a established genetic mechanisms determining anteroposterior development and the capability of forming eyes, a nervous system, a circulatory system, and a skeleton (the latter owing to the presence of lysiloxidase). In other words, the genetic capability of developing a complex mobile bilaterian creature exists deep within Precambrian time, and the evidence even indicates a radiation of disparate groups that have not yet been found.

The plot thickens. The recent completion of the draft genome of the sea anemone *Nematostella vectensis* (Putnam et al. 2007) suggests a startling genomic complexity in this so-called primitive group, which is the evolutionary sister of the lineage containing all the bilaterians. This anemone demonstrates the presence of vertebrate-like introns and a gene-linkage pattern also quite similar to that of vertebrates. Genes involved with cell adhesion, cell signaling, and synaptic transmission are already present in the anemone, suggesting that the genome was already complex and was modified in various ways in descendants. Surprisingly, stronger similarities are seen between anemones and vertebrates than between anemones and flies, suggesting stronger modifications in the lineages containing the latter. But the presence of genomic complexity, right at the dawn of bilaterian animal life, is inescapable. Even deeper in the evolutionary tree we find *Trichoplax*, which is perhaps the simplest of free-living multicellular metazoans and likely in a sister group of the combined group of Cnidarians and Bilaterians. Its genome is also complex and its genome reveals a large array of transcription factor genes and signaling pathway genes found in more derived bilaterians such as vertebrates, where they are employed to run the many complexities of a cellularly diverse organism (Srivastava et al. 2008). Still, some increases in complexity, such as duplications of *Hox* genes, are apparent in the rise of the bilaterian line (Martinez et al. 1998).

Table 1. Important developmental genes, proteins, or genetically specified systems found in both Protostomes and Deuterostomes, which together constitute the bilaterian animal phyla, or in a presumed common ancestor.

Gene or system	Role in development
Hox genes	Anterior-posterior axis specification
Engrailed	Segmentation specification
Dll	Specifies proximal-distal orientation
Muscle-specific MyoD	Muscle fate
orthodenticles	Cephalization, anterior and regionalized nervous system
Pax-6, ciliary and rhabdomeric eye types	Photoreceptor, eye organizer?
Rhodopsin	Vision
tinman	Sets up circulatory system and heart in *Drosophila* and vertebrates
sog/chd and dpp/Bmp-4	Dorsoventral axis specification
Lysyloxidase protein	Used in cross-linkage of collagen to create skeleton

Source: Levinton 2001.

We can quickly go overboard by accepting the constancy of gene function over such broad sweeps of evolutionary time and taxonomic breadth. Some of the genes thought to be fundamental and constant in the mainstream of development, such as anterior-posterior determination, are employed for a variety of functions. Thus has arisen the concept of a developmental gene tool kit, whose elements may be recruited for many disparate functions in very different cell types. Stages of development, and even fundamental features such as segmentation in different groups, may be accomplished by different genes, which are themselves retained over the history of the bilaterians (Grenier et al. 1997). Many of the genes have been in the metazoans since before the dawn of the bilateria, which makes it difficult to either exclude or confirm the hypothesis that functioning bilateria might have evolved far before the Cambrian.

We therefore cannot exclude the hypothesis that bilaterian animals with complex morphology existed before the Cambrian explosion but somehow were not preserved. We have dealt above with the preservation issue, which is still murky, but we cannot overlook the fact that a treasure trove of Precambrian bilaterian fossils has yet to be found despite much searching.

More exploration into this subject suggests that we still cannot make definitive conclusions about the meaning of action of ancient genes, although some encouraging progress is being made. To make progress, we need (a) a good fossil record, with preserved characters that can be linked to specific genes, and (b) an understanding of the structure and working of the part of the genome that specifies the traits in question. Bottjer and colleagues (2006), for example, have succeeded in linking the traits of Cambrian echinoderms to genes involved in biomineralization in a living sea urchin.

We can illustrate the problem of genome complexity and ancient gene action with the striking universality of the *Pax*-6 gene in protostome and deuterostome Bilateria. One might conclude that *Pax*-6 is a master eye gene, especially after learning that the gene can be transplanted from a mouse or squid into a fly, resulting in the stimulation of ectopic eyes on various inappropriate locations of the fly's body (Tomarev et al. 1997). This finding is peculiar, given the universal belief (before the discovery of *Pax*-6, that is) that eyes evolved independently into the many functional forms we see, sometimes as the result of independent evolutionary convergence of similar and quite detailed structures (e.g., Salvini-Plawen and Mayr 1977).

What explains this apparently incongruous result? Developmental relationships show an association between *Pax*-6 and anterior neural determination. It may well be that this gene was crucial in an ancestral form's detection of light, but inevitably became linked to the instigation of eye development in all subsequent episodes in eye evolution. Thus, *Pax*-6 is an inevitable and stable component of eye development, but is certainly not the determinant of the specific form of the many and independent episodes of evolution that led to eye spots, mirrors, compound eyes, and camera eyes in as many as 60 or so evolutionary events.

Also, invertebrate and vertebrate eyes appeared to have fundamentally different embryological origins, transduction mechanisms, and cellular structure. But the polychaete *Platynereis dumerilii* and other invertebrates have been found to have coexisting vertebrate and invertebrate eye cellular types, which suggests that the common ancestor of vertebrates and invertebrates had both photoreceptor cell types, but that one type has been mainly employed in eyes of each major group (Arendt et al. 2004). Photopigments may have evolved only once with a gene duplication, but photoreceptor cells types have evolved at least twice, and morphologically distinct eyes evolved multiple times.

There is an important lesson here. The genes present for complexity may have been present in ancestral bilaterians, but the genes that determine the detailed structures and functions (circulation, vision, etc.) we associate with bilaterian development are not specified. The devil is in the details...and in the fossils that need to be discovered.

The trigger?

Possible triggers for a Cambrian explosion (table 2) include (a) extrinsic changes in climate, paleogeography, and ocean chemistry; (b) evolutionary adaptive innovations that encouraged diversification; (c) intrinsic mechanisms, usually involving genetic determination of development or other traits; and (d) feedback loops between any of the first three mechanisms, causing a self-propagating explosion.

Abundant data suggest possible extrinsic triggers for a Cambrian explosion. Leading up to the events of about 520 Ma was a period of about 150 million years of continental breakup, followed by collisions that occurred in the Early Cambrian. Strontium isotopic evidence (Nicholas 1996) suggests a major increase in terrestrial weathering, which may reflect increased nutrient inputs during this time. An increase in oxygen around 600 Ma (Canfield et al. 2007) might have allowed the existence of larger-bodied active animals, espe-

Table 2. Some possible causes of the Cambrian explosion.

Cause	Mechanism	One useful reference
External environmental changes		
Oxygenation of the deep ocean	Allows occurrence of larger and calcified animals	Fike et al. 2006
Drop in seawater temperature	Allows oxygen delivery to larger animals	Robert and Chaussidon 2006
Pulses of global warming from methane releases combined with polar wandering	Warming increases nutrient cycling, productivity, and opportunities for increased nutrient flow, supporting more biomass and species	Kirschvink and Raub 2003
Snowball Earth with ice-free refuges, allowing rise of Bilateria	While Earth may periodically have been completely covered by ice, local pockets may have allowed the Precambrian origin of bilaterian groups in the form of larvalike planktonic ancestors	Runnegar 2000
Key organismal/ecological innovations		
Appearance of brain or well-organized nervous system	Allows evolution of complex behavior	Stanley 1992
Appearance of anus, or other manifestations of true directed movement and associated neursensory and other traits	Helps determine anterior-posterior neurosensory evolution, which leads to great diversification	Cavalier-Smith 2006
Appearance of response to light and color	Allows increase of biological interactions, predator recognition, prey crypsis, etc.	Parker 1998
Predation and response of skeletonized fauna	Predators appear, which selects for diverse skeletonized protective mechanisms	Vermeij 1990
Change in primary productivity regime/food	Increased diversity of phytoplankton fossils in the Early Cambrian period might provide diverse trophic inputs into the ocean	Butterfield 1997
Internal developmental/genetic reorganizations		
Looser developmental organization	Allows a diversity of developmental evolutionary directions	Arthur 2000
Appearance of *Hox* genes	Novel genes and arrangement allow great possibilities for diversification	Erwin et al. 1997
Genome or gene duplication	Allows new evolutionary directions for duplicated genes	Lundin 1999

cially those with calcium carbonate skeletons. Finally, the aftermath of a world completely covered by ice, followed by strong global warming (Hoffman et al. 1998), might have included an oxygenated ocean that permitted or even stimulated a radiation of bilaterian animal life. But this episode ended about 600 Ma, many millions of years before the Cambrian. Why the long lag time before the so-called explosion? The issue of response time is probably the single most difficult problem for researchers in macroevolution. There is no theory to tell us how fast a major evolutionary change can occur or how much change should occur, given a predefined set of environmental and biological circumstances.

One of the obvious difficulties here is that we are searching underneath the Cambrian lamppost for the keys to an explosion of animal life. If we searched for a Precambrian time of origin, we might find equally tantalizing explanations. For example, a recent long-term estimate of oceanic temperature shows a drop at about 1200 Ma from likely limiting high temperatures (approximately 70 degrees Celsius [°C]) to temperatures of 30°C, resembling those of our modern ocean (Robert and Chaussidon 2006). This idea is controversial, but it nicely fits some of the Precambrian estimates for the rise of animal life. It might even unify the search for ancient causes with the search for current mechanisms that may limit organismal physiological performance under global warming.

Extrinsic biological factors might also have been instrumental in selection for diverse lifestyles and morphologies. Spectacular predators existed even in the Lower Cambrian, and predators might have stimulated the evolution of diverse morphological, chemical, and behavioral defense mechanisms (Stanley 1976).

Intrinsic factors involve the appearance of a biological innovation whose presence permits a vastly increased potential for diversification. We have discussed above the suggestion that *Hox* genes might have produced a novel developmental mechanism that permitted diversification. The ancient origin of such genes, and even their number, argues against this explanation. Still, given the profound changes occurring at this earlier stage of evolution, major genetic changes might have been focused on one part of the genome involved in major developmental shifts. Perhaps the organization of *Hox* genetic determination differed early in bilaterian evolution, which allowed for profound shifts (Arthur 2000). Gene duplications, even genome duplications, might have characterized Cambrian bilaterians, thus creating a major opportunity for genetic functional divergence (Lundin 1999). Predetermined biases in gene-phenotype organization may also have guided evolutionary direction (West-Eberhard 1989). Unfortunately, there is no reason to exclude a host of other genes and developmental mechanisms.

Many other biological innovations have been related to the Cambrian explosion. For example, the development of a more highly organized nervous system might have permitted a broad range of new behaviors and functional connections among body parts, resulting in a broad range of complex interspecies interactions. Because so many of the groups appearing in the Cambrian had an apparently well-organized nervous system, we can only speculate on the order of cause and effect, since any radiation would have produced an array of species with complex nervous systems. In any event, all bilaterians share the potential for such a complex nervous system, which might be realized by the necessity of ecology. Arguments for other possible intrinsic factors, such as the appearance of iridescent color (Parker 1998), have the opposite drawback, as few groups would have had such features. Could they have precipitated the whole explosion?

A particularly intriguing innovation is the ability of planktonic animal creatures to settle on the bottom and adopt a more complex benthic lifestyle, replete with features common in larger animals, such as skeletons and large-scale circulatory systems. Two different types of planktonic larvae are speculated to be the ancestors of the protostomes and deuterostomes, and the benthic descendants would be the germ of the Cambrian explosion. The limited ability of larval cells to elaborate morphologies might have been changed dramatically by the advent of set-aside cells, which resided in the larva but were used to specify the morphologies characteristic of the larger, more complex benthic adult life stages (Davidson et al. 1995). The latter hypothesis, however, flies in the face of facts: important groups such as arthropods show no strong evidence of such set-aside cells, and other groups have limited evidence for such dramatic changes during metamorphosis from larva to adult (e.g., many annelids). The most ancestral known group of bilaterians, the acoels, lacks the indirect development expected when set-aside cells exist (Ruiz-Trillo et al. 1999).

Feedback loops have been suggested between weathering and the development of early life, and between changes in primary productivity and an explosion of life. The increase in weathering might have been greatly enhanced by the early development of biomineralization, which might have further increased weathering and perhaps nutrient inputs, thus triggering an evolutionary explosion (von Bloh et al. 2003). These events might be linked to a known major turnover in preserved fossil phytoplankton in the Early Cambrian (Butterfield 1997). Phytoplankton would have been consumed by zooplankton, which would have directly provided fecal pellets for export to the bottom, and uneaten phytoplankton would have sunk to the bottom, with both types of plankton providing a trophic stimulus for benthic animals. Although interesting, this connection is entirely speculative and unbounded by any unique data (e.g., the carbon isotope changes mentioned above).

A path for the future?

Will molecular clocks pave the way? At present, molecular evidence points to a Precambrian divergence for the bilaterian animal phyla, but the pointer is rather shaky. We can only hope that better evidence will emerge from the large-scale sequencing under way. At present, it is fair to say that the assumptions behind the methods appear to strongly affect the results, which should heighten skepticism about the power of

molecular clocks to resolve the question of the timing of the divergence of the Bilateria.

Will fossils pave the way? Only new discoveries, combined with sensible analysis of the status of morphological characters, could allow paleontologists to revise the currently robust result that no obvious bilaterian body plans can be found in rocks older than the Cambrian. The sudden appearance of such a complex biota in the Early Cambrian argues that there may be a missing and probably rich ancestral biota earlier than the Cambrian. These fossils, given the likely low oxygen of Precambrian oceans, will be small and unmineralized. Such a discovery will certainly not undermine the clear diversification of a large array of large-bodied forms in the Cambrian. There *was* an explosion of some sort, but its character needs to be better understood. But just one Orsten-like Precambrian discovery might unleash a wealth of Lilliputian morphological diversity that would crack the idea of a Cambrian phylogenetic explosion wide open.

Will gene analysis pave the way? It is painfully apparent that our understanding of the molecular genetic determination of traits is too immature to understand the meaning of the presence or absence of specific gene complexes. We have excellent evidence of the presence of genes that set important developmental processes in motion (e.g., *Hox* genes, *Pax*-6 gene), but we know little of the structure of the downstream genes or of other genes that determine crucial structures of macroevolutionary significance.

Do scientists know enough to understand the pace of body plan evolution? If the fossil record tells us anything, it is that evolution is dominated by radiations of form and genetic structure that are discontinuous in time. Regrettably, we know too little yet to devise an evolutionary model that would predict the pace of evolution on the level of the major body plans of the bilaterian phyla. The few examples discovered so far of molecular underpinnings of extant morphological polymorphism are enticing (e.g., Colosimo et al. 2005), but far too incomplete to allow us to understand the molecular and genetic basis of major morphological transitions, or of the pace of evolution for the major body plans. We also must wonder if analyses of extant variation and change can duplicate the structure of the genome and the genes responsible for the initial fantastic radiation. Equally discouraging is the lack of evidence of definitive geological-climatological events causing evolutionary radiations. We have many potential culprits, but few definitive causes.

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References cited

Arendt D, Tessmar-Raible K, Snyman H, Dorresteijn AW, Wittbrodt J. 2004. Ciliary photoreceptors with a vertebrate-type opsin in an invertebrate brain. Science 306: 869–871.

Arthur W. 2000. The Origin of Animal Body Plans. Cambridge (United Kingdom): Cambridge University Press.

Ayala FJ, Rzhetsky A, Ayala FJ. 1998. Origin of the metazoan phyla: Molecular clocks confirm paleontological estimates. Proceedings of the National Academy of Sciences 95: 606–611.

Bengtson S, Rasmussen B, Krapez B. 2007. The Paleoproterozoic megascopic Stirling biota. Paleobiology 33: 351–381.

Blair JE, Hedges SB. 2005. Molecular clocks do not support the Cambrian explosion. Molecular Biology and Evolution 22: 387–390.

Bottjer DJ, Davidson EH, Peterson KJ, Cameron RA. 2006. Paleogenomics of echinoderms. Science 314: 956–960.

Bowring SA, Grotzinger JP, Isachsen CE, Knoll AH, Pelechaty SM, Kolosov P. 1993. Calibrating rates of Early Cambrian evolution. Science 261: 1293–1298.

Briggs DEG, Fortey RA. 1989. The early radiation and relationships of the major arthropod groups. Science 246: 241–243.

Bromham L. 1998. Combining molecular and palaeontological data to defuse the Cambrian explosion. Geological Society of New Zealand Miscellaneous Publication 97: 7–10.

Bromham LD, Hendy MD. 2000. Can fast early rates reconcile molecular dates with the Cambrian explosion? Proceedings of the Royal Society B 267: 1041–1047.

Butterfield NJ. 1995. Secular distribution of Burgess-Shale type preservation. Lethaia 28: 1–13.

———. 1997. Plankton ecology and the Proterozoic-Phanerozoic transition. Paleobiology 23: 247–262.

Canfield DE, Poulton SW, Narbonne GM. 2007. Late-Neoproterozoic deep-ocean oxygenation and the rise of animal life. Science 315: 92–95.

Cavalier-Smith T. 2006. Cell evolution and Earth history: Stasis and revolution. Philosophical Transactions of the Royal Society B 361: 969–1006.

Cloud P. 1986. Reflections on the beginnings of metazoan evolution. Precambrian Research 31: 405–408.

Cloud PE Jr. 1948. Some problems and patterns of evolution exemplified by fossil invertebrates. Evolution 2: 322–350.

———. 1968. Pre-metazoan evolution and the origins of the Metazoa. Pages 1–72 in Drake ET, ed. Evolution and Environment—A Symposium Presented on the Occasion of the One-hundredth Anniversary of the Foundation of Peabody Museum of Natural History at Yale University. New Haven (CT): Yale University Press.

Colosimo PF, Hosemann KE, Balabhadra S, Villarreal G, Dickson M, Grimwood J, Schmutz J, Myers RM, Schluter D, Kingsley DM. 2005. Widespread parallel evolution in sticklebacks by repeated fixation of Ectodysplasin alleles. Science 307: 1928–1933.

Conway Morris S. 1977. A new metazoan from the Cambrian Burgess Shale, British Columbia. Palaeontology 20: 623–640.

———. 1985. The Middle Cambrian metazoan *Wiwaxia corrugata* (Matthew) from the Burgess Shale and Ogygopsis Shale, British Columbia, Canada. Philosophical Transactions of the Royal Society B 307: 507–582.

Conway Morris S, Caron J-B. 2007. Halwaxiids and the early evolution of the lophotrochozoans. Science 315: 1255–1258.

Darwin C. 1859. On the Origin of Species by Means of Natural Selection. London: John Murray.

Davidson EH, Peterson KJ, Cameron RA. 1995. Origin of bilaterian body plans: Evolution of developmental regulatory mechanisms. Science 270: 1319–1325.

Dickerson RE. 1971. The structure of cytochrome c and the rates of molecular evolution. Journal of Molecular Evolution 1: 26–45.

Dzik J. 2005. Behavioral and anatomical unity of the earliest burrowing animals and the cause of the "Cambrian explosion." Paleobiology 31: 503–521.

Erwin D, Valentine J, Jablonski D. 1997. The origin of animal body plans. American Journal of Science 85: 126–137.

Fedonkin MA, Waggoner BM. 1997. The Late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. Nature 388: 868–871.
Fike DA, Grotzinger JP, Pratt LM, Summons RE. 2006. Oxidation of the Ediacaran ocean. Nature 444: 744–747.
Fortey RA, Briggs DEG, Wills MA. 1996. The Cambrian evolutionary "explosion": Decoupling cladogenesis from morphological disparity. Biological Journal of the Linnaean Society 57: 13–33.
Glaessner MF, Wade M. 1966. The late Precambrian fossils from Ediacara, South Australia. Palaeontology 9: 599–628.
Gould SJ. 1989. Wonderful Life. NewYork: Norton.
Gradstein FM, Ogg JG, Smith AG. 2005. A Geologic Time Scale 2004. Cambridge (United Kingdom): Cambridge University Press.
Grenier JK, Garber TL, Warren R, Whitington PM, Carroll S. 1997. Evolution of the entire arthropod *Hox* gene set predated the origin and radiation of the onychophoran/arthropod clade. Current Biology 7: 547–553.
Gu X. 1998. Early metazoan divergence is about 830 million years ago. Journal of Molecular Evolution 47: 369–371.
Harvey THP, Butterfield NJ. 2007. Sophisticated particle-feeding in a large Early Cambrian crustacean. Nature 452: 868–871.
Hedges SB, Blair JE, Venturi ML, Shoe JL. 2004. A molecular timescale of eukaryotic evolution and the rise of complex multicellular life. BMC Evolutionary Biology 4: 2.
Hoffman PF, Kaufman AJ, Halverson GP, Schrag DP. 1998. A Neoproterozoic snowball Earth. Science 281: 1342–1346.
Hou X-G, Bergstrom J, Xu GH. 2004. The Lower Cambrian crustacean *Pectocaris* from the Chengjian biota, Yunnan, China. Journal of Paleontology 78: 700–708.
Kirschvink JL, Raub TD. 2003. A methane fuse for the Cambrian explosion: Carbon cycles and true polar wander. Comptes Rendus Geoscience 335: 65–78.
Levinton JS. 2001. Genetics, Paleontology, and Macroevolution. New York: Cambridge University Press.
Levinton JS, Dubb L, Wray GA. 2004. Simulations of evolutionary radiations and their application to understanding the probability of a Cambrian explosion. Journal of Paleontology 78: 31–38.
Lundin LG. 1999. Gene duplications in early metazoan evolution. Seminars in Cell and Developmental Biology 10: 523–530.
Lynch M. 1999. The age and relationships of the major animal phyla. Evolution 53: 319–325.
MacNaughton RB, Narbonne GM. 1999. Evolution and ecology of Neoproterozoic-Lower Cambrian trace fossils, NW Canada. Palaios 14: 97–115.
Martinez DE, Bridge D, Masuda-Nakagawa LM, Cartwright P. 1998. Cnidarian homeoboxes and the zootype. Nature 393: 748–749.
McGinnis W, Garber RL, Wirz J, Kuroiwa A, Gehring WJ. 1984. A homologous protein-coding sequence in *Drosophila* homoeotic genes and its conservation in other metazoans. Cell 37: 403–408.
McIlroy D, Logan GA. 1999. The impact of bioturbation on infaunal ecology and evolution during the Proterozoic-Cambrian transition. Palaios 14: 58–72.
Nicholas CJ. 1996. The Sr isotopic evolution of the oceans during the 'Cambrian explosion.' Journal of the Geological Society 153: 243–254.
Nikoh N, et al. 1997. An estimate of divergence time of Parazoa and Eumetazoa and that of Cephalochordata and Vertebrata by aldolase and triose phosphate isomerase clocks. Journal of Molecular Evolution 45: 97–106.
Parker AR. 1998. Colour in Burgess Shale animals and the effect of light on evolution in the Cambrian. Proceedings of the Royal Society B 265: 967–992.
Peterson KJ, Lyons JB, Nowak KS, Takacs CM, Wargo MJ, McPeek MA. 2004. Estimating metazoan divergence times with a molecular clock. Proceedings of the National Academy of Sciences 101: 6536–6541.
Putnam NH, et al. 2007. Sea anemone genome reveals ancestral eumetazoan gene repertoire and genomic organization. Science 317: 86–94.
Ramskøld L, Xianguang H. 1991. New early Cambrian animal and onychophoran affinities of enigmatic metazoans. Nature 351: 225–228.
Robert F, Chaussidon M. 2006. A palaeotemperature curve for the Precambrian oceans based on silicon isotopes in cherts. Nature 443: 972.
Ruiz-Trillo I, Riutort M, Littlewood D. 1999. Acoel flatworms: Earliest extant bilaterian metazoans, not members of platyhelminthes. Science 283: 1919–1923.
Runnegar B. 1982. A molecular-clock date for the origin of the animal phyla. Lethaia 15: 199–205.
———. 2000. Loophole for snowball Earth. Nature 405: 403–404.
Salvini-Plawen LV, Mayr E. 1977. On the evolution of photoreceptors and eyes. Evolutionary Biology 10: 207–263.
Shu D-G, Luo H-L, Conway Morris S, Zhang X-L, Hu S-X, Chen L, Han J, Zhu M. 1999. Lower Cambrian vertebrates from south China. Nature 402: 42–46.
Siveter DJ, Williams J, Waloszek D. 2001. A phosphatocopid crustacean with appendages from the Lower Cambrian. Science 293: 479–480.
Smith AB. 1984. Classification of the Echinodermata. Palaeontology 27: 431–459.
———. 1999. Dating the origin of metazoan body plans. Evolution and Development 1: 138–142.
Srivastava M, et al., 2008. The Trichoplax genome and the nature of placozoans. Nature 454: 955–960.
Stanley SM. 1976. Fossil data and the Precambrian-Cambrian evolutionary transition. American Journal of Science 276: 56–76.
———. 1992. Can neurons explain the Cambrian explosion? Geological Society of America Abstracts with Programs 24: A45.
Tomarev SI, Callaerts P, Kos L, Zinovieva R, Halder G, Gehring W, Piatigorsky J. 1997. Squid *Pax*-6 and eye development. Proceedings of the National Academy of Sciences 94: 2421–2426.
Vermeij GJ. 1990. The origin of skeletons. Palaios 4: 585–589.
Vinther J, Nielsen C. 2005. The Early Cambrian Halkieria is a mollusc. Zoologica Scripta 34: 81–89.
von Bloh W, Bounama C, Frank S. 2003. Cambrian explosion triggered by geosphere-biosphere feedbacks. Geophysical Research Letters 30: CLM6.1–CLM6.5.
Waloszek D, Maas A. 2005. The evolutionary history of crustacean segmentation: A fossil-based perspective. Evolution and Development 7: 515–527.
Waloszek D, Maas A, Chen J, Stein M. 2007. Evolution of cephalic feeding structures and the phylogeny of Arthropoda. Palaeogeography, Palaeoclimatology, Palaeoecology 254: 273–287.
Wang DY-C, Kumar S, Hedges SB. 1999. Divergence time estimates for the early history of animal phyla and the origin of plants, animals and fungi. Proceedings: Biological Sciences 266: 163–171.
Welch JJ, Fontanillas E, Bromham L. 2005. Molecular dates for the "Cambrian Explosion": The influence of prior assumptions. Systematic Biology 54: 672–678.
West-Eberhard MJ. 1989. Phenotypic plasticity and the origins of diversity. Annual Review of Ecology and Systematics 20: 249–278.
Whittington HB. 1985. The Burgess Shale. New Haven (CT): Yale University Press.
Wray GA, Levinton JS, Shapiro LH. 1996. Molecular evidence for deep Precambrian divergences among metazoan phyla. Science 274: 568–573.
Xiao S, Zhang Y, Knoll AH. 1998. Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. Nature 391: 553–558.
Yochelson EL. 1996. Discovery, collection, and description of the Middle Cambrian Burgess Shale Biota by Charles Doolittle Walcott. Proceedings of the American Philosophical Society 140: 469–545.
Zhang X-g, Siveter DJ, Waloszek D, Maas A. 2007. An epipodite-bearing crown-group crustacean from the Lower Cambrian. Nature 449: 595–598.

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