

**Genetics, Paleontology,
and Macroevolution;
Second Edition**

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A Cambrian Explosion?

All God's critters got a place in the choir
Some sing low, some sing higher,
Some sing out loud on the telephone wires,
And some just clap their hands, or paws, or anything they got now

– Bill Staines, 1979

Introduction

No paleontological challenge rises higher above the landscape of evolutionary biology than the Cambrian Explosion of animal life. If the fossil record is to be taken literally, the Tommotian and Atdabanian stages of the Cambrian encompass the appearance of all but one of the modern bilaterian triploblastic animal phyla (Chen, Dzik, Edgecombe, Ramsköld, and Zhou 1995; Conway Morris 1989). The Manykaian stage presages this eruption with the appearance of a variety of spines and shells of more problematic groups (Bengtson 1977, 1992), and some shelly fossils are found in latest Precambrian rocks, even with evidence of predatory boreholes (Bengtson and Zhao 1992). The metazoan cornucopia pours out brachiopods, arthropods, echinoderms, priapulids, mollusks, onychophorans, and the rest – even chordates – all in rocks representing a breathtaking sprint of less than 10 million years (Bowring et al. 1993; Grotzinger et al. 1995). Only one readily preservable phylum, Bryozoa, still stubbornly refuses to be discovered in the Cambrian, but we can be sure that it is only a matter of time before it will be.

This is the wonderful story told by the rocks, but how sure can we be that what is “writ in stone” is all that reliable? Is it within the range of reason that all of the phyla could have arisen and diverged in so short a time? Is the preservation so good that we can be sure that no echinoderms, arthropods, or mollusks are likely to be discovered in Precambrian rocks? Indeed, what are the stakes behind a refutation of the explosion hypothesis? Is it possible that one can refute the explosion hypothesis without ever discovering a fossil in the Precambrian? These are the subjects of this chapter.

Stanley (1976), in an article brimming with interesting ideas about the Cambrian, articulated the two important questions raised by the apparent sudden appearance of Cambrian fossils:

1. Why do many distantly related skeletal phyla and classes seem to appear almost simultaneously in the fossil record?
2. Why do important skeletal taxa appear at high levels of complexity? (Stanley 1976, p. 209).

These two questions have occupied the attentions of paleontologists for about 150 years, and they show no sign of getting quick answers.

Origins of the Problem

There could be no Cambrian Explosion without the development of the notions of a geological timescale and the realization that there was a beginning to the animal fossil record. Lacking an absolute timescale, geologists could date rocks only by means of their fossils. Such a relative timescale was developed principally during the nineteenth century, when all our familiar period names were coined to denote units of geological time, whose absolute time spans were unknown.

By the 1830s and 1840s, it became clear that rocks of England and Wales contained a succession of fossil faunas that ranged from those that included many living forms to those with completely extinct biotas, connoting great antiquity. The notion of a beginning to the animal fossil record could already be found in William Buckland's 1836 contribution to the famous Bridgewater treatises. Soon a controversy arose over the nature of the oldest Paleozoic rocks. Roderick Murchison, an early officer of the Geological Society of London, named the Silurian system for a characteristic fossil marine fauna found on the Welsh borderland. Adam Sedgwick, the first active occupant of the Woodwardian Chair of Geology at Cambridge University, claimed to find rocks even more ancient in central Wales, which he termed the Cambrian.¹ A debate ensued as to whether such older rocks bore a primordial fauna, distinct from that of the Silurian. The waters were muddied when Murchison later discovered Silurian-type faunas overlying crystalline and presumably abiotic rocks in Sweden, suggesting a beginning of animal life with Silurian-type faunas. But Murchison enlarged his concept of the Silurian to include slightly older faunas, thus excluding the Cambrian and infuriating Sedgwick, whose claim for a distinct biota was co-opted into the Silurian concept. But a pre-Silurian fauna of (what are now recognized as) Cambrian trilobites was found later in Bohemia, in Sweden, and even in Sedgwick's original Welsh Cambrian-age sites, thus vindicating Sedgwick's notion of a Cambrian Period. The Cambrian Period was not officially installed until the 1870s, after intermediate rocks were assigned to the Ordovician Period. Although some of this debate might have involved a competition for priority on names of geological periods, it also established the approximate beginnings of the Paleozoic, below which there were no apparent traces of animal life.

Darwin contemplates the beginning of it all. The controversy between Murchison and Sedgwick established a geological beginning to the record of animal life.

¹ He was aided one season by a Cambridge University student and native to the Welsh borderland, Charles Robert Darwin.

Murchison's error in thinking that fossiliferous rocks overlying crystalline rocks marked the beginning of animal life has reappeared in many subsequent geological controversies. We have frequently mistaken nonpreservational gaps in the geological record for absences of biological activity, which was the core of Darwin's skepticism of the suddenness of the Cambrian explosion. The controversy of a primordial fauna was more or less settled during the writing and revision of *The Origin of Species by Means of Natural Selection*; Darwin used the term *Silurian* in the first edition, but the Cambrian system was mentioned by the issue of the sixth, and last, edition in 1872. In general, Darwin had to grapple with paleontological evidence in all parts of the geological column that faunas had appeared abruptly, with many distantly related new fossil groups springing into being all at once. Darwin was skeptical that evidence for sudden origins would remain the case for long, and he alluded to the many parts of the world where fossils had not been searched for as yet. He also noted a number of exciting discoveries that extended the range of a given group to a point before a previously reckoned abrupt appearance.

Darwin was not so sanguine about the likelihood of future fossil finds before the Cambrian, which appeared to mark the abrupt beginning of animal life. Darwin (1876) saw the beginning as likely to be gradual and long before the Cambrian:

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. For instance, it cannot be doubted that all the Cambrian and Silurian trilobites are descended from some one crustacean, which must have lived long before the Cambrian age, and which probably differed greatly from any known animal. [p. 327]

Darwin noted that many fossils in rocks older than the Silurian had been discovered down to the Lower Cambrian and even perhaps in older Canadian rocks. Darwin (1872) was still able to resort to the possibility that further discoveries might fill in this obvious gap in the record:

I look at the 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. Each word of the slowly changing language, more or less different in the successive chapters, may represent the forms of life, which are entombed in our consecutive formations, and which falsely appear to have been abruptly introduced. On this view the difficulties above discussed are greatly diminished, or even disappear. [p. 331]

Cloud's challenge – the Cambrian was the beginning of it all. Darwin's surmise, that paleontologists would eventually discover Precambrian animal fossils, did not pan out. Further worldwide collecting only heightened the sharpness of the Cambrian beginnings of animal fossils. By the turn of the century, a global Cambrian stratigraphy was sufficiently well developed to present a convincing case for the abrupt Cambrian appearance in the geological column of animal fossils. There were ambiguities, however. Walcott (1899), for example, found Precambrian (Middle Proterozoic) vertical "burrows" in Montana, which he named as two species of *Planolites*. These have been accepted by

some as bona fide metazoan traces (Alpert 1975) but discounted by others (Cloud 1968, Hoffman 1992). But overall, paleontologists could see no strong evidence refuting the idea of a sudden appearance of fossils in the Cambrian. John W. Evans (1912), although noting the possibility of a few Precambrian burrowers, saw the Cambrian appearance as a true evolutionary event and felt that it might have been stimulated by the extensive volcanism recorded in rocks near the base of the Cambrian. He discounted other environmental hypotheses, such as the lack of lime for skeletons, given that there was ample Precambrian limestone. Evans (1912), however, fell in with Darwin as to the suddenness of the event and believed that a late Precambrian episode of exposure was a period during which no fossils were preserved:

It was the gradual advance of the sea over these terrestrial accumulations that marked the coming in of the Cambrian Period, and we need not be surprised that the marine fauna had changed to a very considerable extent in the long interval unrepresented by marine deposits. [p. 344]

The sudden appearance of the Cambrian of many unrelated groups was proof to Evans that a long period of evolution must not have been preserved in the rocks. Given the apparent long range of fossil invertebrate species (ca. 6 million years), the distinguished paleontologist J. Wyatt Durham (1967) also thought that the missing Precambrian record must have been temporally quite extensive.

Evans's article reflected what was to become a pattern in paleontological inference, which involved the search for global-scale climatic changes as the cause of evolutionary eruptions and mass extinctions. Others looked toward biological interactions, such as predation, or the appearance of key innovative adaptations as the magic bullet (Stanley 1973, 1976). Central in the Cambrian debate was the appearance of many distantly related groups with skeletons. On one side was the opinion that the rise of groups with skeletons was a response to the advent of predation (Stanley 1976); alternatively, a global change in geochemistry was thought to stimulate the Cambrian explosion. Calcareous skeletons, for example, were found to be rare in modern dysaerobic environments, which suggested that an increase in oceanic dissolved oxygen might have stimulated the appearance of skeletons (Berkner and Marshall 1965; Rhoads and Morse 1971).

The global changes that might have stimulated the Cambrian rise of animal life were conflated with the question of preservation. If, for example, the rise of predation stimulated the near-simultaneous appearance of distantly related skeletonized phyla, then it might be possible that a long period of Precambrian evolution predated the Cambrian appearance. On the other hand, fossil burrows also increased in abundance and diversity just below the base of the Cambrian, which would weaken the skeleton-predation hypothesis (see Grotzinger et al. 1995; Macnaughton and Narbonne 1999 and references therein). Enter Preston Cloud. It would be incorrect to say that Cloud invented the Cambrian Explosion, but he certainly dealt with the data of the fossil record more directly than did previous workers. In a prescient article in 1948, he pointed out that

The appearance of diversified 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 life itself. [p. 346]

Of particular importance was Cloud's debunking of many so-called Precambrian fossils, mainly identified as burrows and surface trails of macroinvertebrates with hydraulic skeletons (see Fedonkin and Runnegar 1992; Hofmann 1992). Cloud did not see a true Cambrian Explosion as unexpected, as it conformed to his experience in reckoning the rapidity of appearance of many fossil groups, such as the terebratuloid brachiopods, which first appeared as a diverse group in only a few million years in the latest Silurian and early Devonian. Cloud noted that this general aspect of *eruptive evolution*, as he called it, conformed perfectly to George Gaylord Simpson's characterization of the fossil record as punctuated by very short term evolutionary radiations that produced a great deal of morphological diversity (Simpson 1944). As Simpson was the preeminent paleontologist of the twentieth century, it is likely that his conception of evolutionary bursts was coopted, consciously or subconsciously, into the fabric of later ideas on the Cambrian Explosion. Cloud saw the eruptive phase as one of evolutionary plasticity, perhaps enhanced by increased mutation rates and "paedomorphic tendencies."

One must remember that Cloud's characterizations in 1948 came at a time before there was much quantitative appreciation of diversity changes in the fossil record. Mostly, he had to go by individual accounts, usually qualitative and intuitive, of first appearances of fossil groups, leavened by his own extensive experience. It wasn't until a few years later that Norman Newell's classic paper on periodicity in invertebrate evolution appeared, which quantified what was then known of the waxing and waning of fossil groups (Newell 1952). Using compilations at the generic level of better-preserved marine fossils, it was clear that times of diversification and extinction were simultaneous across a wide spectrum of distantly related phyla. This justified Cloud's belief that evolutionary eruptions were widespread and cut across the details of biological specificity. Cloud and Newell could assert that some set of environmental changes, hopefully readable in the rocks, set the pace of evolutionary radiations and extinctions. Newell (1952) thought that submarine diastrophism (readily likened to modern notions of sea-floor spreading and crustal deformation) caused fluctuations in sea level, which in turn caused evolutionary radiations and extinctions.

These ideas lay fallow for a while until Cloud's important 1966 lecture at Yale University on the Precambrian biosphere and Cambrian life (see Cloud 1968). Cloud was a commanding figure, and his interests and geological background made him the perfect person to have the perspective to understand the potential meanings of the dawn of animal life and, for that matter, the origin of life itself. As a graduate student, he arrived at Yale thanks to the encouragement of the great Paleozoic brachiopod expert Charles Schuchert and worked under the direction of Carl O. Dunbar, one of the twentieth century's great invertebrate biostratigraphers. With this background, rocks and fossils were his natural stomping grounds, and he spent many productive years at the United States Geological Survey. But his intellectual development led him toward global theories of evolutionary innovations and eventually to an interest in exobiology. He spent a significant part of his career at the University of California, Santa Barbara, worrying about how extraterrestrial life and the origins of life could be detected and understood. He probably was the most

broadly experienced invertebrate paleontologist we are ever liable to encounter, and the breadth of his work set the stage for a new ecumenism in styles of paleontological inference.

Cloud's theory is simple (Cloud 1968): The Cambrian Explosion was a real diversification, and fairly sudden. It did not matter to him whether it happened in a few million years or a few more. The rocks spoke clearly, however, that the rise of triploblastic metazoans was sudden relative to the broad context of geological time. In cementing this conclusion, Cloud had to deal with a raft of so-called Precambrian body and trace fossils, and he dismissed all of them as sedimentary structures, algae, or other types of misinterpretations.² The sudden appearance of such diverse groups struck Cloud as evidence that the animal kingdom was polyphyletic; given the evidence, he inferred four possible independent rises of invertebrate groups, but he warned that the evidence was insufficient to be sure about details.

With this interpretation, Cloud sought to find a global change that stimulated the rise of so many unrelated groups at an auspicious time such as the Cambrian. He favored the increase of atmospheric oxygen as the trigger of the Cambrian explosion. In rocks younger than about 1.8 billion years, there was evidence of atmospheric oxygen, which was thought to be incompatible with the deposition of more ancient rocks with banded iron formations. Thus, oxygen perhaps began to increase 1,800 million years ago and might have reached a threshold conducive to large body size at the beginning of the Cambrian (Berkner and Marshal 1965). Some of Cloud's argument has foundered. He thought the presence of uraninite to be evidence for anoxia, but uraninite can form in localized environments in an oxic atmosphere. The partial pressure of oxygen might have reached about 1% of the current atmosphere at least 2 billion years ago, which suggests that animals could have lived in profusion, although perhaps not at large body size.

Although the oxygen evolution theory was certainly speculative, Cloud left us with a confrontation. He made us face the rock record as one of facts and left us with a mantra that is being chanted and followed today, to the credit of all paleontologists engaged in the Cambrian debate:

Is it surely a fossil or the work of an organism? Does it represent an authentic metazoan? And is it surely endemic to rocks whose stratigraphic position is such that they cannot reasonably be included in the Paleozoic? For bold though we may be in building hypotheses in context with the framework of knowledge available, that framework itself may be extended beyond known limits only by demonstrable facts. [Cloud 1968, p. 51]

The Early Cambrian Is Established as the Cornucopia of Animal Life

In subsequent decades, the Cambrian was investigated intensively by many paleontologists around the world. By and large, its subdivisions (Figure 8.1) were diagnosed on the basis of successions of fossil faunas, dominated mainly by trilobites, arthropod relatives of unknown affinities, and inarticulate brachiopods. Trilobites,

² Cloud later softened on seeing a deep Precambrian body fossil that he allowed might be a true annelid (Cloud 1986).

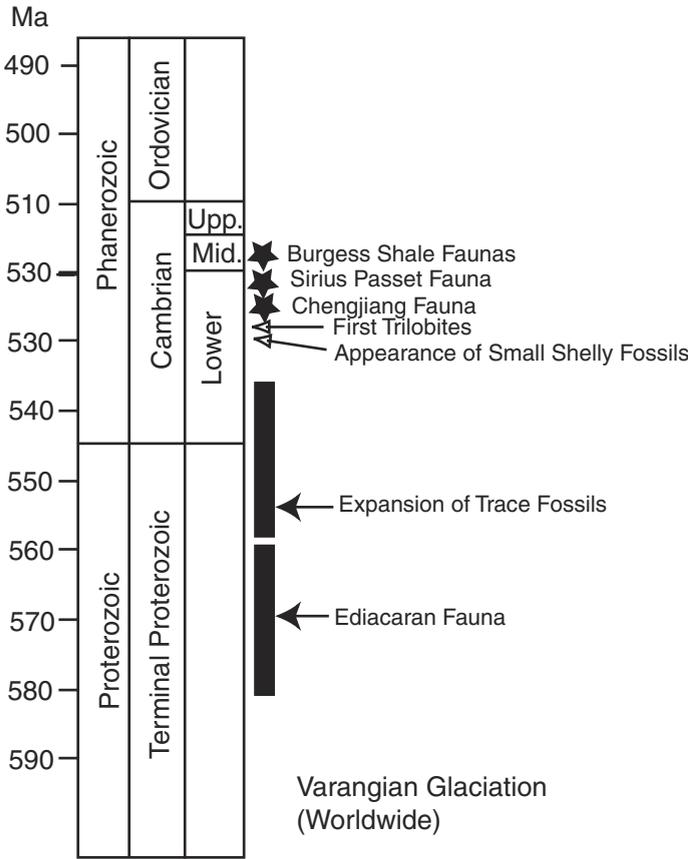


Figure 8.1. The location of the Cambrian in geological time with some important fossil occurrences and events. (After Briggs, Erwin, and Collier 1994).

although diverse, were morphologically simple relative to other arthropods, with very little differentiation among limb pairs. They were therefore taken to be near the ancestral part of the arthropod tree. Inarticulate brachiopods were abundant suspension-feeding epifauna and infauna and could be used, along with trilobites, to designate biostratigraphic zones. Many other groups were also found, including a number of members of the phylum Echinodermata, that could not be safely classified with any of the extant five classes.

Although the more typical Early Paleozoic animal groups appear in one of the earliest stages of the Cambrian, the Atdabanian, it is in the Manykaian and Tommotian stages that we more or less suddenly see the appearance of a large group of enigmatic shelly fossils, along with more familiar forms in the Tommotian. This can be seen, for example, in sections found in Siberia, the place where the “golden spike” has been established to accurately mark the type of Early Cambrian sequences. Nearby volcanic breccias can be dated at 544 million years ago. In the Manykaian, one encounters a variety of plates and spikes of uncertain relation to extant invertebrate groups. Upsection, one encounters beds of small enigmatic cone-shaped fossils known as conularids, among other enigmatic forms. Problematic shelly fossils of this stage are

found worldwide, including eastern Massachusetts, eastern Washington, Siberia, Australia, the Kalmarsund and other areas of southeastern Sweden, and the Welsh borderland. An example is the *Mobergella* fauna (Figure 8.2), found throughout Europe, with representatives in Central Asia and New York, which is dominated by an enigmatic bilateral valved fossil containing radial pits that may be muscle scars (Bengtson 1977; Conway Morris and Chapman 1997). Mobergellan shells appeared to grow by accretion and were composed of primary phosphate. This is the beginning of abundant shelly fossils in the Paleozoic record. Further upsection, in the Tommotian, these give way suddenly to the more typical denizens of the Cambrian, including trilobites and brachiopods. At the very base of the Tommotian, one sees the first appearances of the panoply of the typical Cambrian fauna. At this time, we already encounter biogeographic structure with two major and several distinct minor provinces (Fortey and Owens 1990a; Fortey, Briggs, and Wills 1996).

Radiometric dating has established a new and higher level of confidence on the dating of the Cambrian. Furthermore, the dating gives us a possible story of spectacular evolution. Uranium–lead dates from zircons establish the beginning of the Cambrian at 544 million years ago. Furthermore, the oldest Manykaian stage lasted no less than 10 million years. Finally, the next two stages, where the appearances of the modern phyla are concentrated, lasted no more than 5 million to 10 million years (Bowring et al. 1993). In other words, the Cambrian Explosion of animal phyla, if the fossils tell the whole story, occurred in a geological instant!

I have to take a few sentences to mention the sad question of what it means for an event to occur in a “geological instant.” I would say that it means little. As evolu-

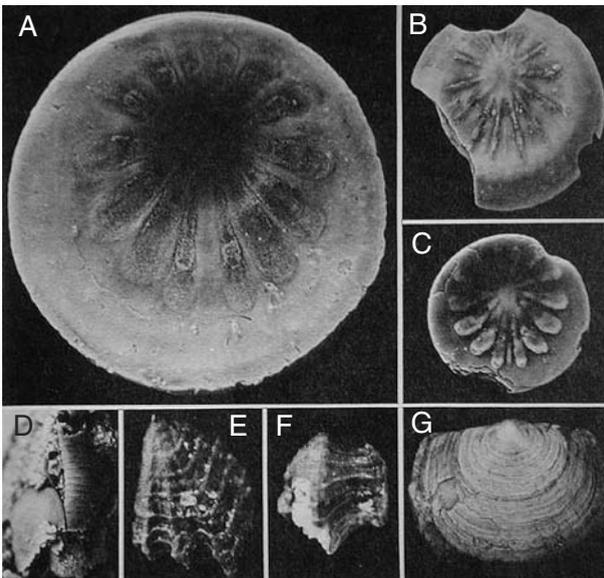


Figure 8.2. Examples of the first shelly fossils of the *Mobergella* fauna, found worldwide. (A–C) Species of *Mobergella*; (D) *Hylolithellus* species; (E–F) *Camenella balthica*; (G) *Micromitra undosa*. (From Bengtson 1977, with permission.)

tionary biologists, we have no theory to set constraints on the rate of evolution or the pace of evolutionary radiations. If all of the animal phyla appeared in 1 million years, would we be surprised? Perhaps, but our conclusion would be emotive, because there is no evolutionary principle we know well that prevents it. Seven days? No, it is not possible. A million years? Who knows?

The Ediacaran Challenge

The only widely accepted serious major challenge to the Cambrian origins story is a fauna first discovered by R. C. Sprigg in the Ediacara Hills, 600 kilometers north of Adelaide, Australia (Glaessner 1984), whose great variety includes a number of apparent coelenterates and perhaps a number of triploblasts. Subsequently, this fauna has been found worldwide, except in Antarctica, dating from approximately 600 million years ago to 620 million years ago to some time in the very early Cambrian. Most of the abundant Ediacaran fossils and burrows are concentrated in rocks of just a few million years before the 544-million-year base of the Cambrian (Grotzinger, Bowring, Saylor, and Kauffman 1995). Fossils that appear to be triploblast animals are in rocks no older than 565 million years (Grotzinger et al. 1995). Ediacaran fossils, at the upper end of their range, have been found commingled with Burgess Shale-like Cambrian fossils (Conway Morris 1993), and deeper water Ediacaran fossils have been found in rocks as young as 510 million years old (Palmer 1995). The Ediacaran-type faunas reach their peak diversity only a few million years before the Cambrian (Grotzinger et al. 1995), as does a rapid increase in the diversity of preserved burrows, which reach a peak just before the start of the Cambrian (Fedonkin and Runnegar 1992).

The Ediacaran fauna, therefore, does not extend the dawn of animal life much further back, but it does present us with a range of enigmatic fossils, few of which can safely be included in the modern cast of animal characters up the section in the Atdabanian. Seilacher (1985) argued that many of the Ediacaran forms represent rather inactive “mattresses” that might have been compartmentalized, which absorbed dissolved organic material from the water by diffusion. The large *Dickinsonia*, classified by Glaessner as a polychaete (Glaessner 1984), actually fits Seilacher’s hypothetical functional description quite well. Some of the Ediacaran animals might therefore be an independent episode in animal evolution, comprising the so-called Vendobionta, a sister group to the entirety of the Animalia (Buss and Seilacher 1994). A detailed character analysis, however, is wanting for this idea, despite its intriguing nature. Certainly, the evidence demonstrating Ediacaran fossils in Cambrian strata (Conway Morris 1993; Palmer 1995; Grotzinger et al. 1995) precludes the hypothesis of the Ediacaran faunas as a Precambrian failed evolutionary experiment.

The question of Ediacaran true animals remains open. Consider the triradiate *Tribrachidium* (Figure 8.3). This disc does not have all of the features we expect of a primordial echinoderm, but trifold symmetry is found in Cambrian stem-group echinoderms. A pentamerous disc, *Arkarua*, with a pentamerous arrangement of grooves on its oral surface, has been found in the Pound Quartzite in the Flinders Ranges of Australia and bears a resemblance to Cambrian edrioasteroids (Gehling

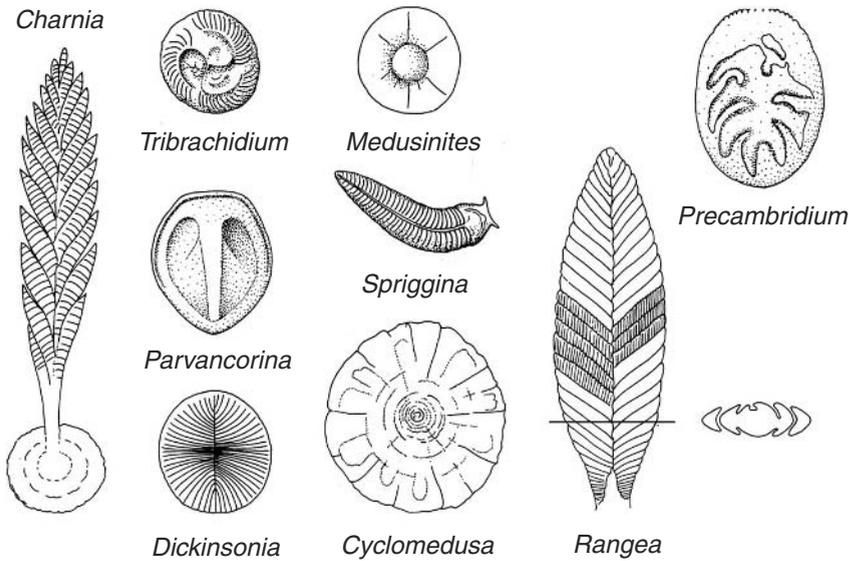


Figure 8.3. Some Ediacaran-age fossils. (After Glaessner 1984.)

1987). The Ediacaran *Parvancorina* somewhat resembles a mature version of the early Cambrian *Naroria*, an unusual arthropod with an exoskeleton composed of two large shields that has been concluded to be the sister group of the trilobites (Fortey et al. 1996). Grotzinger, Watters, Knoll, and Smith (1998) described a small (1-centimeter-wide) goblet-shaped animal of overall hexagonal symmetry, which has proven to be bilaterally symmetrical. It seems likely that more such enigmatic fossils will be discovered, but we are not close in understanding their phylogenetic relationships, or even their functional morphology.

Seilacher devised a classification of Vendian lifestyles for Ediacaran-style animals. They include

1. Mat encrusters
2. Mat scratchers
3. Mat stickers
4. Undermat miners

All of these adaptations depend on the presence of a strong biomat, probably dominated by microbial organisms such as those that construct microbial mats today. The Australian fossil *Radulichnus*, for example, is probably a series of grazing scratches, perhaps generated by grazing by the body fossil *Kimberella*, which has been argued to be an ancestral mollusk (Fedonkin and Waggoner 1997). Mat stickers included tube-making animals that probably stuck in the mat and might have had suspension-feeding tentacles. Undermat miners include a Cambrian fossil *Eochondrites* and a putative 1-billion-year-old fossil that has been found in Mesoproterozoic sandstones in India (Seilacher, Bose, and Pfluger 1998). The exact

date of this locality is in hot dispute. In the Vendian Nama Formation of Namibia, a tubular fossil a few millimeters long has been found and was attached to hard surfaces, suggestive of suspension feeding (Grotzinger et al. 1998). Again, these occurrences are too scattered to tell a phylogenetic tale, but they do give whisperings of a diverse benthic fauna, including bilaterians.

While the phylogenetic links of the Ediacaran fauna are unclear, what is clear is the apparent large body size and the lack of mineral skeletonization of all species described in the fauna. We pay special attention to the lack of skeletons because they are so prominent later in the Cambrian biota. On the one hand it is no special thing to find lots of non-skeletal forms. After all, most of the living invertebrate phyla lack skeletons. The size is another matter. It may be that atmospheric oxygen was now in quantities sufficient to support larger-bodied animals, including the crescendo of animal forms appearing near the base of the Cambrian that have hydrostatic skeletons. The flattened body forms of many of the Ediacaran species might be explained by oxygen that was concentrated enough to allow larger body size but not so abundant as to permit anything more than body forms that relied upon diffusion across a body wall and sluggish life styles, perhaps involving the presence of symbiotic algae. This would be consistent with the great abundance of medusae, which might have been essentially benthic and associated with symbiotic algal forms like zooxanthellae.

Ediacaran preservation is, like the Burgess Shale, of a special nature and preservation problems cloud the potential temporal distribution of Ediacaran faunas. These faunas are preserved in shallow-water sandstones, which were deposited in fairly quiet water. There is no evidence of vertical burrowing until just before the base of the Cambrian, suggesting that the Ediacaran world lacked large animals with hydraulic skeletons. Indeed, it seems likely that the sediment surface was covered with a dense microbial mat, which would have been destroyed with the advent of burrowing animals. Thus, although Ediacaran fossils have now been found in the Lower Cambrian, the potential for preservation of this special microbial mat/sand biota must have radically diminished in the Early Cambrian as larger burrowers appeared.

The Burgess Shale and Charles D. Walcott

I feel a connection to Charles Walcott because my Stony Brook colleague, a descendant of the Boston Brahmin Walcott family, is a blood relation of this great paleontologist. Ben Walcott's wife Roslyn (a geologist) looked up Charles Doolittle Walcott in the Walcott family "stud" book, and he proved to be an "unimportant" member of the family. So it goes with bluebloods, for not only was Walcott one of the greatest paleontologists to walk this earth but also, he distinguished himself as the fourth secretary of the Smithsonian Institution. His upstate New York origins were humble, but his love of fossil collecting led to a position working for the great New York State paleontologist James Hall and eventually to a position in the United States Geological Survey. His wisdom and administrative acumen served him well and he rose to be chief of the Geological Survey, acting assistant secretary of the Smithsonian, and secretary of the Carnegie Institution of Washington, D.C. (Yochelson

1996, 1998). But throughout his career, Walcott remained a dedicated geologist and paleontologist, being especially well remembered for his comprehensive work on the trilobite-based biostratigraphy of the Cambrian in North America and even the discovery of the oldest vertebrate (at the time, and for decades thereafter) in the Ordovician Harding Sandstone. His work was titanic, despite his achievements in government and his position as an advisor to presidents. This will give solace to administrators who often feel written off the face of the academic earth, once they don the mantle of “administrator,” one of the most despised terms among scholars, who often feel a sense of automatic superiority, even though it might just be that they themselves are not suited for positions of leadership.

Of course, Walcott's place in history is identified most with his discovery of the Burgess Shale, surely the greatest invertebrate paleontological find ever. Although the actual discovery story is probably enshrouded in legend (Gould 1989; Yochelson 1996), this much is clear: Walcott and his party, which included his wife and children, found a spectacular fauna of hundreds of animal species, most preserved as carbonaceous films on the bedding planes of the shale with faithfully preserved soft parts, the likes of which had never been seen before in Cambrian fossils. The usual array of trilobites and a few other invertebrates seen in the region (which Walcott was actually collecting) were amplified (Figure 8.4) by beautifully preserved cnidarians, worms, crustacea, priapulids, and a raft of creatures that could not be easily classified by Walcott into existing taxa.

Walcott began the Burgess Shale expeditions with his discovery in the summer of 1909 and continued visiting and collecting from the site until 1924, collecting prodigiously and promptly describing specimens and publishing reports on them. His dedication knew no lapses, even in the face of the shattering news that his wife had died tragically in a train accident. Within the month, he made his way out to his beloved field sites in British Columbia, near the town of Field.

Yochelson (1996) accurately characterized Walcott's efforts, both in field collection and specimen collecting, as among the very most spectacular achievements in paleontology. Remember that this work was done in the waning years of his field career and yet he managed to reach remote sites on horseback, helped with the removal of overburden, and split tons of rock samples, leading a rather small party, which he trained. Whittington (the next great collector of the Burgess Shale) estimated that Walcott had collected a spectacular 60,000 fossils (Whittington 1985); specimens of *Marella*³ alone filled one museum cabinet, 3 feet high (Yochelson 1996). Considering the remoteness of the site and the smallness of the party, let alone the access only by horseback, Walcott's personal effort and leadership produced the greatest collecting achievement in invertebrate paleontological history.

These collections opened a spectacular window onto Middle Cambrian times. Without this fauna, our perception of Cambrian seas would have been restricted at the time to a relatively depauperate fauna of trilobites, brachiopods, and a few other invertebrate species. But the Burgess Shale fossils included a bewildering array of forms, many of which did not fit comfortably into extant groups. In classifying the

³ The most common Burgess Shale fossil.

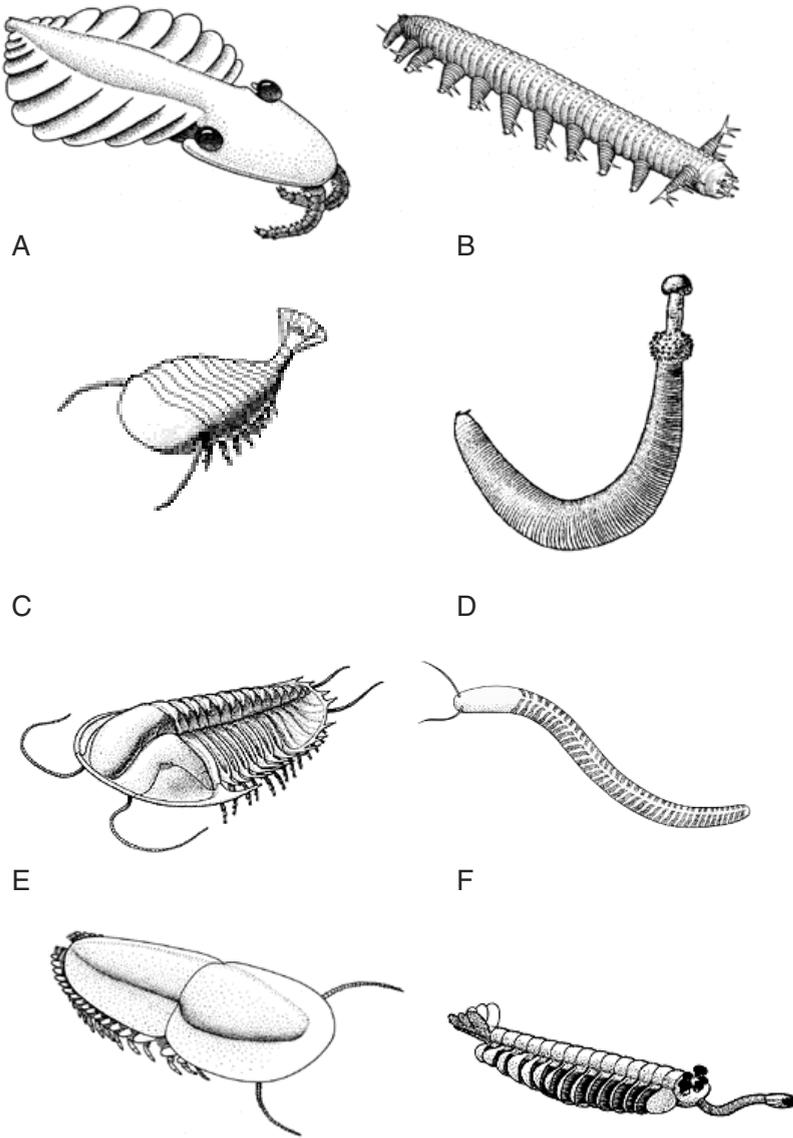


Figure 8.4. Some animals of the Burgess Shale that are mostly soft bodied and not found as well preserved or at all in typical coeval fossil localities. (A) *Anomalocaris*, systematic status unknown; (B) *Aysheaia*, onychophoran; (C) *Sidneyia*, arthropod; (D) *Ottoia*, priapulid; (E) *Naraoia*, two-lobed trilobite; (F) *Pikaia*, chordate; (G) *Olenoides*, trilobite; (H) *Opabinia*, status unknown. (Drawings reprinted with permission of Smithsonian Institution.)

fossils Walcott collected and prepared, it is clear that he lived within the restrictions of systematic practice of the time, largely imposed by the British *Treatise on Zoology*. Contemporary taxonomic practice constrained him to place many arthropods within the extant class Crustacea. But his taxonomic decisions should not be imprinted with any deep philosophical meaning, as Walcott had, only a few years

previously (1894), recognized the Trilobita and Merostomata as classes separate from the Crustacea (Yochelson 1996).

The provenance of the Burgess Shale is of great interest, as it involves a very special preservation that gave us filmlike fossils of soft parts of a large variety of invertebrate fossils. Looming over the shale is a shallow-water dolomite carbonate escarpment (Cathedral Formation), which is a preserved shallow-water complex, perhaps resembling the modern Grand Bahama Bank. Beneath what must have been a submarine carbonate cliff was the Burgess Shale, part of a deeper water and seaward deposit (Stephen Formation) that contains a soft-bodied fauna that has subsequently been found to be widespread in western Canada (Butterfield 1994). The Cambrian submarine escarpment might have been as high as 160 meters (Briggs et al. 1994).

The exquisite preservation of Burgess Shale fossils resulted from downslope turbidity flows, which transported and rapidly buried marine benthos. The Burgess Shale consists of well-layered beds that are coarse at the bottom and decrease in grain size up the bed, which suggests episodic deposition. The fossils themselves are preserved helter-skelter, in many nonlife orientations. All this suggests that the animals did not live where they were deposited and were carried with the downslope currents. These conditions might have been accompanied by bottom-water anoxia, and, therefore, presence of hydrogen sulfide on the bottom, which slowed down aerobic decomposition that normally would have erased the potential for a soft-bodied fossil record. It is also possible that the clay-mineralogical content of the sediment also enhanced the potential for delicate preservation by clay binding with organic molecules and sequestering them from decomposition (Butterfield 1995). The fossils are organic films, covered by aluminosilicates, which might have been the original clay minerals in contact with the organisms that were being fossilized (Butterfield 1990a). The presence of large numbers of burrowing creatures and algae suggests that the Burgess Shale fossils lived in shallow-water muds within the photic zone.

The range of fossils is so large that we do not have the space to describe them here. They are nicely described in several books and papers (Conway Morris 1998; Gould 1989; Whittington 1985; Whittington and Conway Morris 1985) and are introduced and illustrated in excellent photographs in Briggs et al. (1994). One must first remember that fossils typical of the Cambrian – trilobites, brachiopods, and hyoliths – are found in abundance, as they are also found in coeval deposits in the region of Canada and the United States. But the Burgess Shale teaches a sobering lesson about what is normally missing in the fossil record. The soft-bodied fossils comprise the majority of the biota and give us a depressingly clear idea of what is missing from most muddy-bottom fossil deposits. In soft bottoms, we would expect a variety of burrowing and surface grazing invertebrates; these are found in abundance in the Burgess Shale. They include a diversity of the now-depauperate priapulids, an abundant acorn worm-like fossil, a variety of polychaete annelids, the velvet worm *Aysheaia*, and the enigmatic *Wiwaxia*, which must have lived on, and foraged along, the sediment surface. A large fauna of surface-dwelling arthropods was also found, many members of which could not be placed in obvious conventional arthropod cat-

egories (Briggs and Fortey 1989; Whittington and Conway Morris 1985). Especially of interest was the trilobite *Naraoia*, which consisted only of two shields (unlike the normal trilobite three) and lacked a calcified dorsal exoskeleton. Perhaps *Naraoia* is an ancestral trilobite; this might figure importantly in linking the Cambrian trilobites with possible Precambrian forms yet to be discovered (see below).

The Cambrian Diversity Trap

The earliest stages of the Cambrian, the Manykaian and the Tommotian, are distinguished by their peculiar shelly fossil fauna (see discussion in Bengtson 1977, 1992). A diverse array of problematica includes small conelike shells, the conularids, single valves, the so-called *Mobergella* fauna, and even exquisitely preserved embryos and their small hatchlings (Bengtson and Zhao 1997), which are segmented and perhaps juvenile halkyriids. This diversity of weird organisms led Bengtson (1977) to suggest that the Cambrian was a period of evolutionary creativity. Extinction of many groups led to the residual group of phyla that we see in extant faunas. This hypothesis was more or less repeated later by S. J. Gould (1989) as the “Wonderful Life hypothesis,” with the additional suggestion (totally untestable, but fun) that a replay of the “tape of life” would result in a different outcome; our extant fauna might just as well have been dominated by descendants of conularids, for example.

The sense of high Cambrian diversity at high taxonomic levels also infiltrated the field of paleontology through two developments in paleontological analysis during the 1970s and 1980s. Because they were well preserved in some Cambrian and Ordovician rocks, echinoderms were classified into a large number of higher taxa, and eventually there were 21 named taxonomic classes of the phylum Echinodermata, which was quite an increase from the 10 living and extinct classes to be found in Hyman (1955). In the Cambrian, 9 classes were named. After a dip in diversity in the Late Cambrian, probably owing to poor preservation (Smith 1988), the Ordovician experienced a resurgence of echinoderm diversification with 14 recognized classes, with a steady subsequent decline later in the Paleozoic (Sprinkle and Guensburg 1997). This conception of echinoderm evolution only reinforced the idea of early class-level diversity, culminated by culling to the present-day mere 5 extant classes.

Oddly enough, this interpretation of echinoderm evolution happened with no fanfare. The standard treatment in the *Treatise on Invertebrate Paleontology* (Moore and Teichert 1978) described various Cambrian echinoderm fossils that had no obvious affinities to the extant classes. The practice of the time, which was largely based on phenetic association, was to “reward” such differences with a new taxon of high taxonomic level. Thus, the Cambrian and Ordovician came to be populated with a large number of echinoderm forms, some oddballs, of class status. Among these are the celebrated Cambrian carroids, whose morphology was likened to that of chordates (Jefferies, Brown, and Daley 1996), although this hypothesis has been met with widespread skepticism (e.g., Gans and Northcutt 1983; Peterson 1995). These developments produced a group of subphyla or classes with no obvious hierarchical structure.

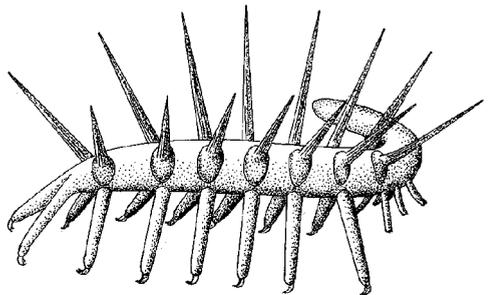
The effect of this class-level approach was to create a series of higher-level taxa with no apparent roots – an “evolutionary lawn,” whose shoots could not be related to each other and whose origins were perhaps polyphyletic.

The next confirmation of early higher taxon richness arose from an extremely important reexamination of the Burgess Shale, supervised by Harry Whittington, who came to occupy the Woodwardian Chair at Cambridge, a worthy successor to Adam Sedgwick. With his students Simon Conway Morris and Derek Briggs, Whittington recollected and restudied the Burgess Shale fauna. In truth, C. D. Walcott had done only a preliminary study on the entire fauna; he did not get to the stage of doing monographic descriptions, including careful morphological study and taxonomic assessment. The new study was much more careful in examining characters of certain taxa that might have had novel taxonomic significance.

The new “Cambridge Campaign” (Conway Morris 1998) moved the Burgess Shale vision of the Cambrian in the direction of the evolutionary lawn concept, previously inspired by the plethora of echinoderm classes. Conway Morris (1977) discovered a distinct new wormlike organism with seven pairs of spines and tentacles. Its consummate weirdness led to its name: *Hallucigenia*. It was portrayed as propped on the bottom by the seven pairs of spines, with tentacles protruding upward (Figure 8.5), which might make sense if the tentacles were armed with poisonous defensive compounds. In any event, its presence suggested that species with no close affinities to extant phyla were to be found in the Burgess Shale. Other taxa only confirmed the impression of the weirdness of Burgess Shale creatures. Walcott first described *Wiwaxia corrugata* as a polychaete annelid, with scales that he likened to the elytra that covered the dorsal surface of scale worms, such as those found in the polychaete family Polynoidae. Conway Morris reexamined *W. corrugata* and published a careful and extensive monograph (1985) that claimed that *Wiwaxia* revealed a new phylum, perhaps related to the mollusks (Figure 8.6). Conway Morris was impressed with the broad ventral surface, which could be likened to the creeping surface of mollusks (like the shell-less aplousophorans), contained a jaw, and lacked the ventral sclerites expected of a polychaete.

These new taxa and their supposedly profound differences were the cornerstone of Gould’s book (1989) *Wonderful Life*, which argued that the weird taxa were part of a menagerie of morphologically disparate phyla that could not be related to extant taxa. Although Gould offered no real morphological or cladistic analysis, he extolled the discoveries and heroic interpretations of Whittington, Briggs, and Conway Morris as

Figure 8.5. The enigmatic fossil *Hallucigenia*, whose oddball status has been reduced to membership in the lobopods, relatives of the extant velvet worms.



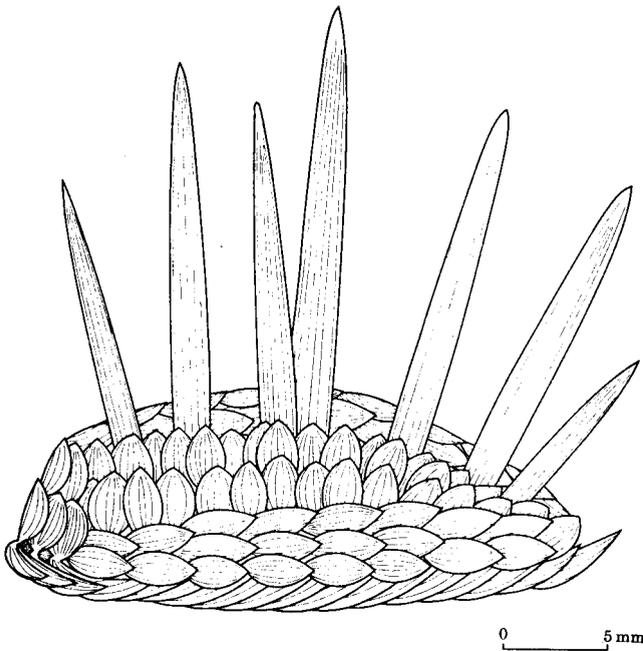


Figure 8.6. Reconstruction of *Wiwaxia corrugata*, a member of a Cambrian invertebrate group with no clear membership in any extant phylum. (From Conway Morris 1985, with permission.)

a reflection of the burst of phylum-level evolution in the Early Cambrian, that was followed by a burst of extinction, leading to the residual of phyla that we know today.

Higher Categories Come First

The next and perhaps most important fact about the Cambrian, won from years of intense collecting, is that all but one of the preservable marine phyla appear in the Cambrian. When I was an undergraduate stratigraphic paleontology student, I had a pile of index cards with fossil ranges, many of which started with Ordovician. No longer true! Cambrian origin applies also to the class level, although the Ordovician has to be added to complete the bulk of the modern story. As discussed in chapter 2, the geological range of the Bivalvia has steadily been extended backward and its lower range now extends to the Early Cambrian. The Bryozoa still stubbornly refuse to be found in the Cambrian, but I suspect that it is a matter of time and collecting luck. What follows from this is an even more interesting fact: Hardly any phyla have their first appearance after the Cambrian. This was stated first by George Gaylord Simpson (1944) as the generality that “higher categories come first.” The meaning of this is clear: So-called higher categories are indicative of basic morphological differences, and the appearance of these differences is concentrated near the beginning of an evolutionary radiation. Cloud (1948) argued similarly that “evolutionary

eruptions” were marked by a high occurrence of variability, perhaps caused by high mutation rates. Some might argue that phyla are hardly hard and fast entities. Earlier splits might be biased in favor of higher-level taxonomic rank. Maybe so, but I think it is fair to say that the basic higher-level status of most invertebrate phyla found in the fossil record existed by the end of the nineteenth century, but our sense of the dictum that phyla come first in the fossil record did not develop until much later. Thus, some notion of fundamental differences – *baupläne*, if you will – arose before we knew that it all began in the Cambrian. This “fact” figures importantly in our conception of the Cambrian as the beginning of it all.

Recapitulation: The Cambrian Catechism

The story told thus far has led to a picture of the Cambrian that involves a novel time of creativity, rapid divergences, production of many phyla that fail to make it to the present day. Here are the talking points:

1. *When?* All modern animal phyla diverged as the fossils indicate, in the second two stages of the Cambrian, or perhaps as far back as the latest Vendian.
2. *Are they all here?* Many phyla erupted in this radiation, but perhaps most did not survive, even beyond the Early Cambrian, to the present day.
3. *Only then?* This creative period was unmatched later; no new phyla appeared, despite subsequent environmental change and major mass extinctions.

Some other points bear mentioning. Although it is true that shelly fossils mark the base of the Cambrian, and the subsequent Tommotian fauna is marked by skeletal phyla such as arthropods and brachiopods, soft-bodied forms clearly also participate in the radiation. Bioturbation is clearly in evidence just below the Cambrian boundary, as is a proliferation of trace fossils (Grotzinger et al. 1995). Furthermore, the Lower Cambrian Burgess Shale–like fossils include a large group of soft-bodied forms. Thus, the radiation may be characterized perhaps as a rise in large-bodied triploblasts, but not as a sudden appearance of mineral skeletonized fossils. We are now finding Vendian calcified tube-dwelling forms in any event (e.g. Grotzinger et al. 1998). In addition, the Cambrian boundary marks an apparent radiation in acanthomorphic acritarchs, a widespread group of spiny planktonic fossils presumably members of the eukaryotic phytoplankton (Butterfield 1997). This radiation may comprise a trophic link to the rise of large numbers of large-size benthic animals, which depend on vertical transport for their food supply, perhaps accelerated by newly arisen zooplankton via fecal pellets (Butterfield 1997; Levinton 1996).

“Oddballs from the Cambrian Start to Get Even”

The witty title of Bengtson’s (1991) article (reproduced in the above heading) aptly describes the fate of the “ain’t that weird!” school of Cambrian paleontology, exemplified by Gould’s 1989 popular book. Indeed, as the book came out, it was already becoming clear that many of the presumed phylogenetic outliers were far more

enmeshed in a more prosaic framework of evolutionary relationships. *Hallucigenia*'s status as a wild and new creature bit the dust just about as Gould's book came to be read. This realization was only part of the many discoveries that evolved from the Late Atdabanian rocks of Chengjiang in southern China, whose fossils had been discovered over 50 years ago but whose significance was not appreciated until restudy in the 1980s (Hou, Ramskøld, and Bergstrom 1991). A large fauna of Early Cambrian fossils strongly resembled those of the Burgess Shale but set back in time the origins of many groups. Most importantly, a fauna of wormlike creatures known as lobopods demonstrated that the velvetworms and allies were diverse in the Cambrian (Ramskøld and Xianguang 1991). The lobopods (Figure 8.7) were distinguished by a series of paired armored plates and the Chinese discoveries made sense of other fossils, such as the Baltic *Xenusion*. *Hallucigenia* was just a member of this clade, and it had been reconstructed upside down to boot! These findings demonstrated that like the priapulids, a presently rare group could have had an earlier time of higher diversity. The lobopods were merely an extinct group on the ancestral part of the tree that included the more derived Onychophora.

The lobopods and allies had a number of characters that clearly allied them with the arthropods but placed them in an ancestral position in the larger arthropod clade. To establish even more perspective, an important contribution by Wills, Briggs, and Fortey (1994) examined all of the arthropods by means of a careful character analysis and demonstrated that the Cambrian arthropods were not a helter-skelter group of taxa with no apparent interrelationships. Rather, they comprised a well-structured clade. There were some interesting surprises. The Trilobitomorpha turned out to be the most derived group of arthropods. This is intriguing, if only because trilobites appear fully formed in the first animal-rich Cambrian deposits, which makes one wonder where all of the ancestral forms were hiding! Previous arthropod bizarre outliers, such as the Burgess Shale *Odaraia*, with enormous eyes and valves, fit safely within the Crustaceanomorpha. And so on. It was a fascinating clade with tremendous diversity, but hardly an evolutionary lawn.

A fairly similar fate awaited the spiny weirdo *Wiwaxia corrugata*. Recall that Walcott had identified this worm as a polychaete, perhaps allied with scale worms. Nicholas Butterfield, who pioneered acid washing as a preparatory technique for the Burgess Shale, was able to discern fine structures in exquisite detail. Butterfield (1990b) found tiny sclerites associated with *Wiwaxia* that resembled the presumed neurochaetae of the Burgess polychaete *Canadia*. This suggests an annelid association for *W. corrugata*. The story is far from settled, however, as *Wiwaxia* has the previously mentioned jaw and ventral surface that appears to ally it with the mollusks and perhaps a group known as the halkyerids. Conway Morris (1985, 1989) argued an affinity of *Wiwaxia* with mollusks but agreed that it is most likely a stem lineage annelid. Conway Morris, however, reserved the halkyerids for a more totipotent position in the history of the animals. The halkyerids can be related to *Wiwaxia* readily because of a similar arrangement of medial, dorsal, and ventral hollow sclerites. *Wiwaxia*'s dorsal sclerites are elongate and all sclerites are unmineralized, but this may be the evolutionary outcome of rather minor character transformations from analogous (perhaps homologous?) characters in the halkyerids

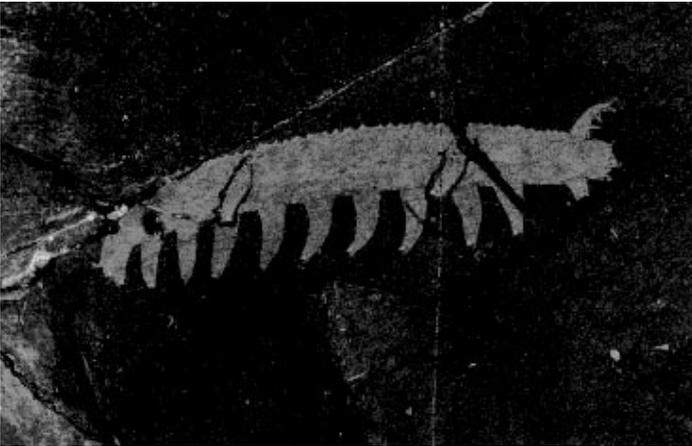
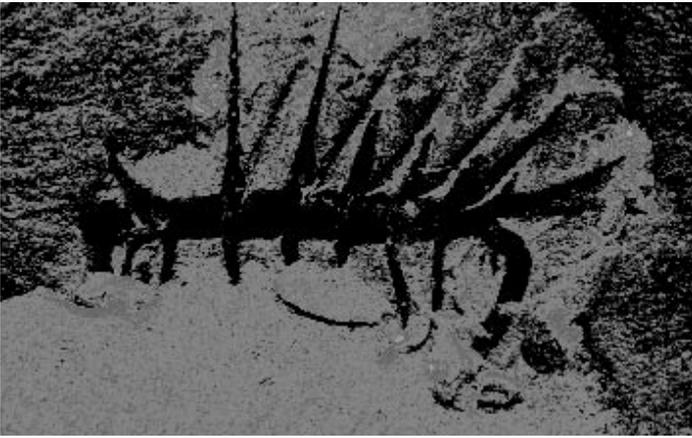


Figure 8.7. Lobopods found in the Cambrian. Top: *Hallucigenia sparsa* from the Middle Cambrian Burgess Shale; middle: *Aysheaia pedunculata*, Burgess Shale; bottom: *Microdictyon sinicum* from the Lower Cambrian Chengjiang Formation, south China. (Top and middle from Briggs et al. 1994, photographed by Chip Clark, with permission from the Smithsonian Institution. Bottom from Conway Morris 1998, with permission.)

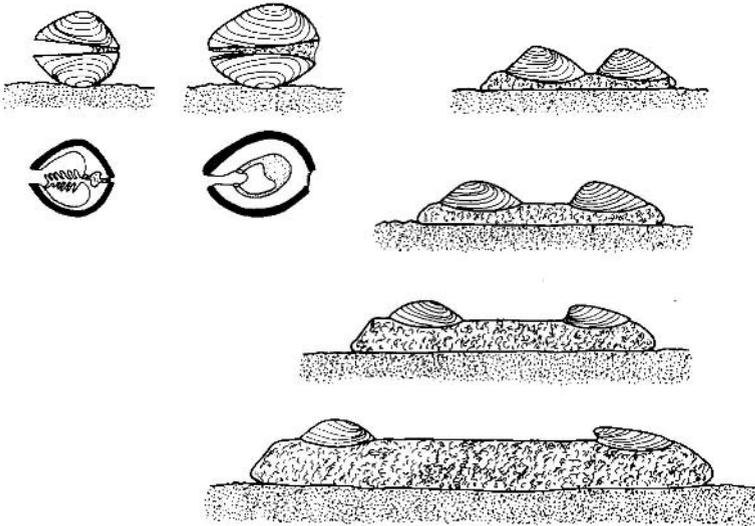
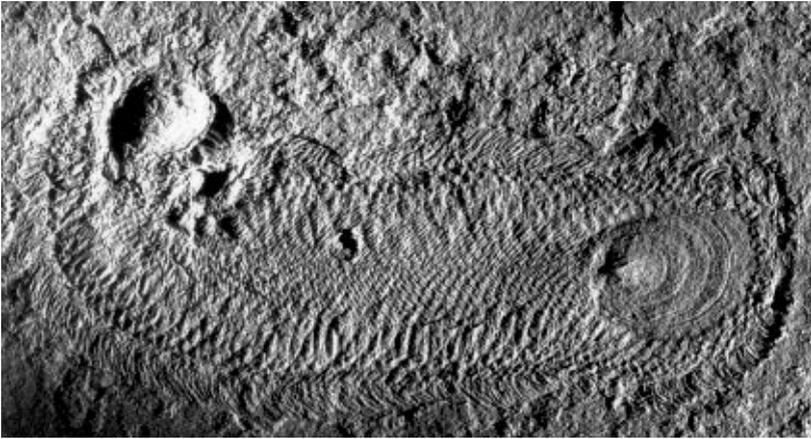


Figure 8.8. Top: a halkyerid from the Sirius Passet site in Greenland; bottom: a set of hypothetical transitions from halkyerids to brachiopods. (From Conway Morris 1998, with permission of Oxford University Press.)

(Figure 8.8). The remarkable halkyerid found in the Greenland Sirius Passet site has an anterior and a posterior dorsal shield, each of which resembles a brachiopod shell. Does this mean that this halkyerid is related to brachiopods? Possibly, and this figure is an interesting, if speculative, evolutionary tree argued by Conway Morris (Figure 8.9). My own intuition simply cannot make the leap from separated “valves” to a brachiopod, but current evidence is too sketchy to exclude many hypotheses.

Finally, we return to the “lawn” of echinoderms. The total of 21 classes, with no apparent cladistic structure, was reexamined by Paul and Smith (1984) and by Smith

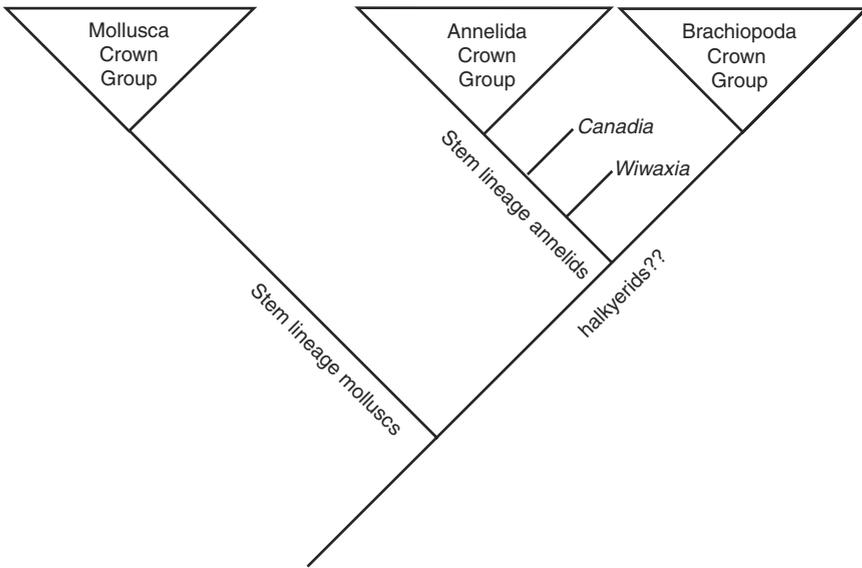


Figure 8.9. Tentative cladogram of three of the protostome animal phyla, emphasizing the position of some stem groups. (Modified from Conway Morris 1998, with permission.)

(1984). Smith (1984) pointed out the lack of information content of older classifications of the Echinodermata, which emphasize the larger subphylum structure with no character analysis. In effect, this approach (e.g., Moore and Teichert 1978) creates the impression of an evolutionary lawn, simply by ignoring the characters that might impart evolutionary structure. As mentioned above, there is a reward for emphasizing difference by recognition of higher-level taxa, which plays into the hands of hypotheses that emphasize the disparity of early Paleozoic fossil groups.

Studies emphasizing character analysis, however, paint a very different picture (Paul and Smith 1984; Smith 1984). For example, both embryological and fossil characters agree in uniting the brittle stars and the asteroid starfish. The eocrinoids can be shown to be a group united more by ancestral character states than by shared derived characters; this makes for confusion, and Smith (1984) demonstrated that they are not a monophyletic group. They are instead probably a hodgepodge of taxa, ancestral to several lines of more derived and monophyletic echinoderm groups. In many cases, ancestral echinoderms have a set of traits that cannot be used to define membership in living or more derived groups. For example, the Cambrian helicoplacoid *Helicoplacus gilberti* is very generalized and its characters allow membership in only the stem group of the entire Echinodermata. Figure 8.10 shows how all of the fossil groups of echinoderms can be assigned to the stem group of one of the crown groups defined by extant forms. Of particular interest is the fossil genus *Camptostroma*, formerly considered to be the only representative of the class Camptostromatoidea. It possesses all of the autapomorphies of crown-group echinoderms but lacks the autapomorphies of either the Pelmatozoa or Eleutherozoa. It therefore defines a three-taxon polytomy (Figure 8.10), defining a group in which the latest ancestor of crown-group echinoderms would be placed (Paul and Smith 1984; Smith 1984).

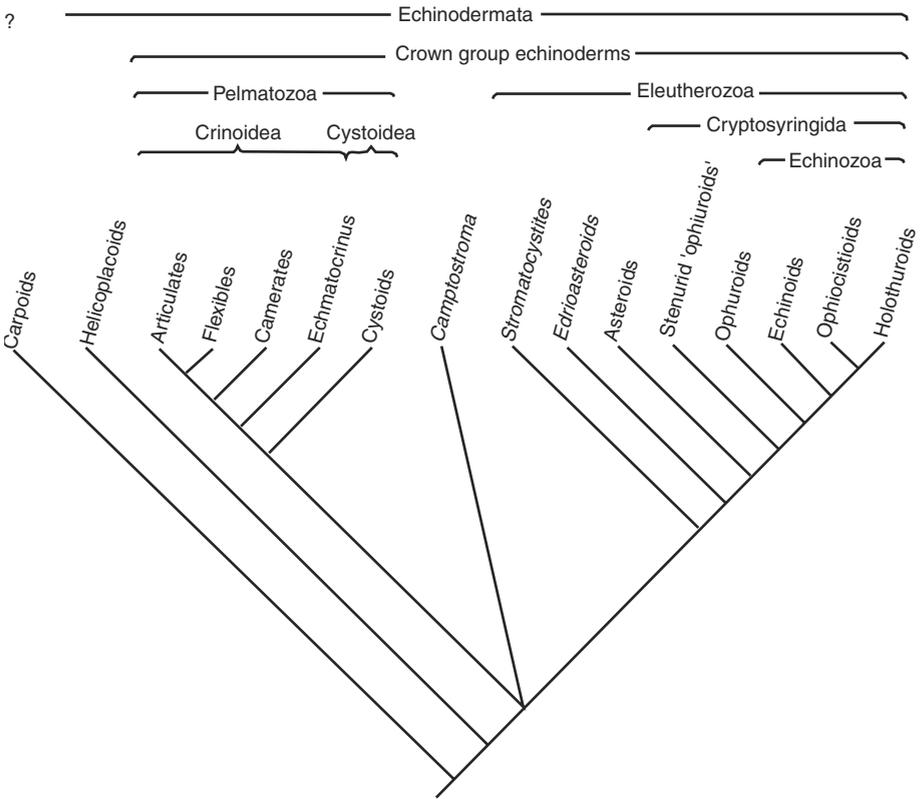


Figure 8.10. Cladogram of the important groups of echinoderms. All fossil groups can be assigned to a stem group of one of the crown groups. (Modified from Smith 1984, with permission of the Palaeontological Association.)

The echinoderm cladogram, based on a careful character analysis, defines a straightforward evolutionary tree, not a lawn, although questions still remain unresolved (Littlewood, Smith, Clough, and Emson 1997). With this analysis, the oddballs continue to become even, kind of like 1960s hippies becoming stockbrokers.

The trend continues. Until the advent of molecular sequence techniques, it was often difficult to establish relationships among apparently distantly related groups; this falsely highlights the multiple weirdo–evolutionary lawn hypothesis. No set of groups has been more victimized by this shortcoming than the “wormy” groups, set into phyla such as the Annelida, Echiura, and Pogonophora. Oddly enough, it was the discovery of the giant vestimentiferan tube worms that set a revision of this story in motion. The vestimentiferans were discovered next to deep-sea hot vents and later near colder water hydrocarbon seeps. They are worms often exceeding 1 meter in length and are the fastest-growing invertebrates in the world (Lutz et al. 1994). At first, they were accorded phylum status, but careful examination of the morphology of early developmental stages showed that they were most likely highly specialized pogonophorans (Jones and Gardiner 1989; Southward 1988). The plot thickened when molecular evidence from several studies characterized pogonophorans as derived annelids and vestimentiferans as members of the Pogonophora (Black et al.

1997; McHugh 1997; Winnepeninckx, Backeljau, and Wachter 1995). The status of the Echiura is still unsure; they may be derived annelids or perhaps a sister group of the annelids. In either event, another lawn has turned into a tree.

The result of this analysis argues strongly against the evolutionary lawn–Cambrian weirdo hypothesis. Indeed, it casts strong doubt on the notion of a Cambrian period of heightened evolutionary creativity of many new phyla and classes, most of which subsequently disappeared. The Cambrian was a time of radiation, no doubt. Indeed, if the fossil appearances are to be believed, the Cambrian explosion is genuine, at least with regard to the appearance of a large number of new groups. But it is hardly the inverted cone of either taxonomic diversity or morphological disparity that has been argued by Gould (1989). Instead, the Cambrian shows a gradual unfolding of groups as they radiated, leading to an eventual radiation of our modern crown groups, often by the later Cambrian or Ordovician. This trend can be seen in echinoderms (Smith 1988), arthropods (Walossek and Müller 1989), and other groups. Gould's point of view is more of an expression of ignorance of the practice of systematics and a mistaken impression of the Cambrian fossil record. Perhaps we should better term this period “wonderful life, writ ordinary”?

Morphological disparity maximized in the Cambrian explosion? The notion of a Cambrian Explosion implies that a period of evolutionary eruption might have produced a peak of morphological difference among taxa, as a presumably ecologically driven radiation expanded taxa into many new ecological roles. The evolutionary lawn metaphor, combined with a proliferation of naming of higher taxa, only reinforces the vision of a Cambrian cornucopia of disparate forms. The argument would be completed by stating that subsequent times experience a winnowing of these major taxa, which results in a reduction of morphological disparity in today's biota. The echinoderm story mentioned above fits well with such a model.

Has disparity peaked in the Cambrian, and has it declined ever since? This was one of Gould's (1989) main arguments. If we fix on groups such as the velvetworms or priapulids, we do get a sense of decline, because these are minor phyla of low present-day morphological diversity. Later evaluations of morphological disparity, however, do not suggest a decline at all. Briggs, Fortey, and Wills (1992) used multivariate techniques to examine disparity in Cambrian and living arthropods and found no difference in level of overall morphological disparity. This result was robust, arising either from phenetic or cladistic analyses. They argue that previous conceptions of high Cambrian disparity related more to artifacts of naming of taxa, rather than by genuine differences in morphological disparity. Problematic taxa were more an artifact of inadequate taxonomy than a result of more disparate Cambrian groups. Recently, Loren Smith and Bruce Lieberman (1999) examined the radiation of olenelloid trilobites to see if morphological change declined with increasing time during the radiation. But transition distances did not decline with rank or age, which suggests that the tempo of morphological evolution did not decline with rank in tree or with advancing time.

Combined with the cladistic reconsiderations of “class proliferation,” these results suggest that the Cambrian might have been the beginning, but it was not a special time of morphological explosion disproportional to those of other times.

So what was special about the Cambrian? Most importantly, it might have been the source of our modern fauna. Given the number of living animal phyla, a relatively small number of species, perhaps all alive in the Early Cambrian, must have given rise to the fauna we observe today. We are no closer now than we were decades ago, however, in understanding whether this small number of lineages was determined by ecological circumstances arising in the Early Cambrian or whether they were survivors of an earlier Precambrian divergence in either the Vendian or much before.

We also are yet to understand whether the sudden appearance of trilobites, brachiopods, and even fishes in the Lower Cambrian was truly the beginning. We can say, however, that the Cambrian was likely a time of steady radiation, which can be seen especially well in trilobites (Smith and Lieberman 1999) and echinoderms (Smith 1988). These Smith Brothers have helped to dispel the idea of a Cambrian cough, which was followed by a precipitous wheeze of diversity.

Gould tears down Walcott: A scientific morality saga. There is a regrettable aspect to this entire story, so get ready here for a diversion. Gould (1989) co-opted Whittington’s hypothesis to develop what he saw as a radically new hypothesis of the nature of evolution. The Cambrian biota was taken to be a diverse series of familiar forms along with many oddballs, whose phylogenetic relationships were distant, reflecting a rapid radiation that resembled a sprouting lawn, whose visible shoots could not be related to each other in the roots below ground. This led to the notion of an inverted cone; the Cambrian had been a wellspring of phylogenetic diversity of groups whose relationships were distant and unfathomable. Thus, the fauna of today is a happenstance group of survivors that might have been completely different if a different chance selection had occurred.

Gould’s book (1989) denigrated Charles D. Walcott’s achievements, to the point of characterizing even his monumental fieldwork as not worthy of extraordinary recognition. This view, to say the least, is not shared by anyone else (see Yochelson 1996), much less the subsequent stars of Burgess Shale inquiries (Conway Morris 1998; Whittington 1985). I have to admit that when I read Gould’s book, this peculiar treatment of Walcott was a shock.

Gould saw Walcott’s identifications of Burgess Shale fossils as a failure to recognize their fundamentally bizarre nature and blamed this failure on the various administrative duties that diverted Walcott from discovering the truth. Walcott’s wartime duties did restrict his time, and he characterized much of his Burgess Shale studies as preliminary, but not many professors with lines of students at the door, meetings to attend, and courses to teach would have been diverted much less or would have achieved nearly as much. Indeed, how many professors do you know who have carried out 60,000 fossils from any locality, even on the side of a freeway? I know a couple, and they are the superstars of the breed. But let’s not get too upset about this, as Gould is eager not so much to tear Walcott down as

to make him a character in a sort of morality play of scholarship. Trapped by your times and distractions, you will fail to see a novel truth.

Gould (1989) also saw Walcott as shackled by the chains of systematic convention; why else did Walcott fail to see that many of his fossils were weird animals, soon to be caged and curated properly in the menagerie of *Wonderful Life*? Well, to put it simply, Walcott did *not* do so badly. Yes, he screwed up the reconstruction of that wonderful predator *Anomalocaris* and shunted off some of its body parts into the wrong phyla. But I assert that you, the reader, would likely have done as badly.⁴ Walcott classified the very enigmatic *Wiwaxia* as a polychaete, resembling a sea mouse. To this day, that hypothesis stands strongly, alongside quite different interpretations (Butterfield 1990b; Conway Morris 1985). *Eldonia* was thought to be a holothurian, and Gould leapt on it as another oddball, but a reanalysis still keeps Walcott's interpretation alive (Yochelson 1996).

Walcott also failed to see that the worm *Aysheaia* was an onychophoran, but so did a contemporary expert (Clark 1915). The person who discovered *Aysheaia*'s velvetworm affinities, G. Evelyn Hutchinson (1931), was, ironically, well tutored in traditional arthropod zoology, having been in classes given by Borradaile at Cambridge and keeping his notebooks for references in his own lectures at Yale University, at least into the 1960s! Indeed, this traditional education allowed him to spot the enormity of Howard Sanders's discovery in the 1950s of specimens of what Sanders was soon to describe as the Cephalocarida, a new subclass of Crustacea.⁵

One can go on like this, but the picture is clear. Walcott identified fossils the way you or I are liable to do: He tried to ally them with groups already identified. He got lots right and correctly recognized that others were unusual and assigned them to new families (although he kept to a standard contemporary higher-level classification, as any field paleontologist would be likely to do). Others he missed, but that is a hazard of identifying an entire fauna with so many species. His was not a formal systematic monograph but a description of a fossil fauna, as Yochelson (1996) aptly pointed out.

As a strong form of poetic justice, Gould's perorations about bizarre unrelated forms came back to haunt him. As discussed above, many of the weirdest fossil species, including the not so aptly named *Hallucigenia*, were later found to be members of a rather clearly related clade, the lobopods, related to the modern velvetworms. Indeed, the work that paved the road to this conclusion (Ramskøld and Xiangang 1991) succeeded because of modern methods of character analysis and cladistic work that had been employed to establish phylogenetic relationships. Such an approach has been absent completely from Gould's analysis or discourse over the years. Personally, I think that is one strong reason why he missed the boat so badly.

⁴ I have a favorite mentor who described eight species of invertebrates, only to be embarrassed by a later worker, who found them articulated as a chiton!

⁵ In my graduate classes in the 1960s, I remember Hutchinson still actively engaged in his discovery of the true affinities of *Aysheaia*.

Precambrian Whisperings of the Rise of Animal Life?

Molecules to the rescue? The relationship of molecular divergence to time has been likened to the ticking of a clock, which might be used to date important moments in evolutionary history such as the divergence of the animals. Unfortunately, as divergence time reaches the level of hundreds of millions of years, several problematic biases creep in. First, not many DNA sequences evolve slowly enough such that given nucleotide sites do not change more than once, which can erase the evolutionary signal. Multiple hits will fog the degree of divergence by allowing the degree of sequence difference with time to reach a plateau where more change does not give more information. Sequence divergence, combined with other processes such as deletions and other rearrangements, also leads to difficulties in aligning sequences of distantly related taxa.

Ever since the idea of a molecular clock has been proposed (Zuckerkanndl and Pauling 1965) we have hoped to be able to estimate times of evolutionary divergence. A random process of substitution is implicit in clock models, which implies that a poisson distribution (variance of substitution rate equals the mean estimated rate) should fit the data (Ohta and Kimura 1971). This model often does not fit the data. As Cutler (2000) notes, there are four typical ways of dealing with this problem:

1. Don't ask, don't tell
2. Shopping for molecules that fit the assumptions
3. Shopping for taxa that fit the assumptions
4. Using models that correct for the usual overdispersion of rates

In order to use many loci in an analysis, investigators are forced to use option one. Any sort of selection to satisfy the random model will greatly reduce the number of molecules or taxa to be employed. For example, the study of Ayala et al. (1998) goes to the extreme of removing about two thirds of the taxa in some cases to achieve a fit. This would call into question the value of ignoring most of the data, for the sake of forcing the small remainder into a particular model. Cutler (2000) strongly recommends option four and devises a test with maximum likelihood as the basis for calculating relative degrees of confidence.

A final and profound problem with using molecular data to date the divergence of the major animal groups is the need to extrapolate from a group of divergences that are calibrated by known fossil data. It is obvious that we cannot use divergence times of the major animal groups themselves, so we must resort to using divergences among fossil groups that are more recent, whose living representatives are also available for DNA sequencing. Given the uneven preservation of the record, we are confined to using milestones in the fossil record of readily fossilizable groups such as vertebrates, mollusks, brachiopods, and echinoderms. In these cases, one could find a number of divergence times for which there is good fossil evidence and hopefully DNA sequences for appropriate genes (e.g., Wray, Levinton, and Shapiro 1996). Furthermore, sequences are uneven in coverage, and the over-the-transom approach often fails to produce sequences for some sister groups that are well documented paleontologically. Very few genes will have enough taxonomic spread to give us a good calibration span-

ning the history of the calibrating data set (e.g., vertebrate divergences). As an alternative, one might use a single calibration date for one well-understood splitting time, reasonably well justified by the fossil record (e.g., tetrapods versus ray-fin fishes-Wang et al. 1999). One might be able to get data for many genes for such a set of taxa. The disadvantage lies in total dependence on one or very few calibrating dates.

First of all, sister taxa must be reckoned, and the earliest occurrence of one of the two taxa is then taken as the time of divergence, even though it is possible that the time might be quite a bit deeper (Smith 1994, Sanderson 1997). This source of error is especially a problem in studies in which one uses only a very few fossil calibration points (e.g., Doolittle et al. 1996; Lynch 1999). It is less a problem when many fossil divergence times are used (e.g. Runnegar 1982), as a regression between time of divergence and sequence difference can be calculated. One does worry, though, about extrapolating such a calibration from a single group such as vertebrates to a larger number of invertebrate phyla.

The first study, using α - and β -hemoglobin amino acid sequences (Runnegar 1982), proved to be a tantalizing challenge to the Cambrian divergence hypothesis, as invertebrate distances suggested a divergence time of 1 billion years ago, based on the overall relationship between calibration points based on vertebrate fossil divergence times and amino acid sequence difference. The study was attacked vehemently by Erwin (1989), a staunch supporter of the Cambrian Explosion hypothesis, who cited the usual problems in using molecular clocks. Most worrisome was the problem of extrapolation, as the vertebrate relationship had to be extrapolated to the much greater invertebrate genetic distances. It was possible, for example, that the rate of sequence evolution might have been different during a highly divergent episode of animal evolution such as that represented by the putative Cambrian Explosion.

In 1996, Wray, Levinton, and Shapiro did a study quite similar to that of Runnegar's pioneering efforts, but they extended the analysis to six additional sequences, including nuclear and mitochondrial sequences. The study also used a large number of taxa for a calibration using vertebrates, to establish a relationship between genetic distance and divergence time (a correction was made for multiple hits, developed by Kimura 1980). The results revealed much scatter (Figure 8.11) but confirmed the deep Precambrian divergence estimate for the divergence time between protostomes and deuterostomes. Estimates of the protostome-deuterostome split (referred to below as the P-D split) hovered around 1.2 billion years ago, although Wray et al. were clear in pointing out that the scatter precluded any conclusion beyond the inference that the divergence of the animal phyla occurred long before the Cambrian explosion hypothesis would allow. Wray and colleagues noted that the greatest problem in making such estimates is the lack of confidence limits of the regression of genetic distance on divergence time in the vertebrate calibration. They used a couple of conservative means of calculating the confidence limits of the P-D split, and yet these error bars still precluded a Cambrian Explosion hypothesis, either the extremist hypothesis (Gould 1995) or the intermediate explosion hypothesis (Valentine, Erwin, and Jablonski 1996).

One alternative hypothesis that cannot be safely ignored is the possibility that molecular evolution accelerated during the Cambrian Explosion. To conform to the

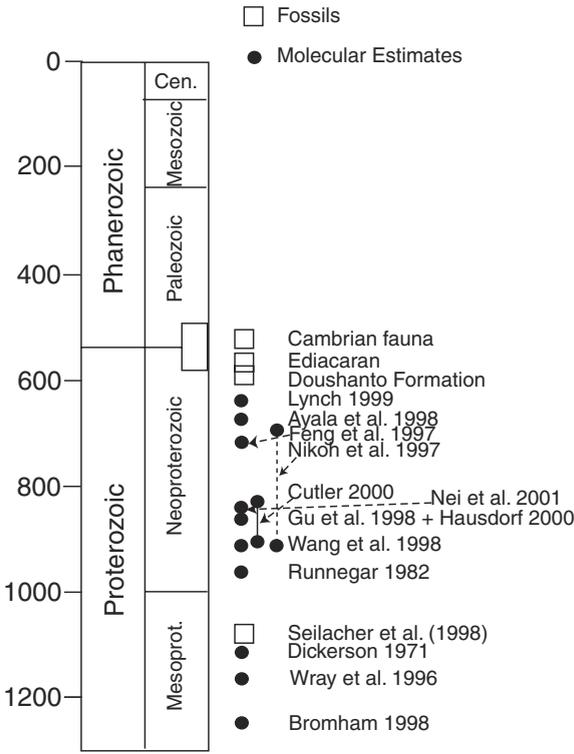


Figure 8.11. Estimates of divergence times of the protostome–deuterostome splits, with some fossil occurrences.

extreme Cambrian Explosion estimate of about 10 million years (Gould 1989; Grotzinger et al. 1995), such an acceleration would have to be by a factor of 65, or by a factor of 10 for the more protracted explosion estimate of about 35 million years (Valentine et al. 1996). Although differences in rates of evolution are well known, this large difference, especially in several genes of unrelated function, including mainly housekeeping genes, would be unprecedented. Even Valentine, Jablonski, and Erwin admitted this. Wray et al.’s data come mainly from amino acid sequences of proteins, and such acceleration would have disastrous functional consequences. Furthermore, Wray et al.’s use of a relative rate test brackets the variation in rates to just a few percent. If one examines the genetic distances in selected genes from nonmetazoan eukaryotes to chordates and compares them with nonmetazoan eukaryotes to protostomes, one finds variation of just a few percent, with no apparent bias in rate difference (Wray et al. 1996). This suggests strongly that there was no such acceleration in molecular substitution rate during a putative Cambrian Explosion.

The problem of early acceleration of substitution rate has recently been studied by Bromham and Hendy (2000), who used multiple calibration dates and a method using empirically determined variation of substitution rates. They found that allowing the substitution rate to be maximal during the basal “interphylum” splits still precludes a Cambrian divergence time for the phyla. As this extreme, the minimum possible divergence time is 586 million years ago.

The Wray et al. study questions the timing of P–D divergence, but what of the explosiveness of it all? The echinoderm–chordate divergence estimate is 172 million years to 224 million years later than the three mean protostome–chordate estimates. Although the exact numbers may be questioned, they suggest that the divergence was protracted and not explosive. Moreover, in six of the seven sequences, we recovered the correct temporal order of the following splits: protostome–deuterostome, echinoderm–chordate, Agnatha–Gnathostomata. Given the wobbly nature of the molecular clock, it seems unlikely that such resolution would be possible if the divergences all occurred within just a few million years, over 500 million years ago.

Since this study, a number of other molecular estimates have all produced Precambrian estimates of the P–D split (Figure 8.11), although most have placed the split closer to 800 million years to 900 million years, as opposed to the 1 billion to 1.2-billion-year estimate of Wray et al. Several of these studies have addressed the problem of rate heterogeneity by dropping cases of significant heterogeneity along different branches of the tree (Bromham, Rambaut, Fortey, Cooper, and Penny 1998; Wang et al. 1999). As an example, Bromham et al. (1998) used a method known as quartets (Rambaut and Bromham 1998) to estimate the time of the P–D divergence. Whole mitochondrial protein-coding sequences as well as 18S rRNA sequences were used. Taxa were grouped into permutations of two pairs of sister taxa. For each pair, genetic distance and divergence time were known, on the basis of fossil data, and those shown to be homogeneous in rate of sequence divergence could be used to estimate the time of splitting of the two sister groups. This approach has the advantage of including many fossil calibrations, as in Wray et al. 1996. A maximum-likelihood approach was used to test and exclude most quartets with significant rate heterogeneity. This approach produces a wide range of estimates, but all are Precambrian and deeper than 680 million years ago. A second recent robust study (Wang et al. 1999) used a more restrictive group of taxa and fossil calibrations but employed a great deal of sequence data to produce an estimate of 942 million years for the arthropod–vertebrate split. Cutler (2000) found a result statistically consistent with Wray, Levinton, and Shapiro (1996) using a Poisson model, but also found that divergence times were inconsistent with this model. Using a model assuming overdispersed divergence rates, he still found a maximum likelihood fit to a Precambrian divergence time for the P–D split, most likely in the confidence range of ca. 824–917 million years. For all seven trees examined, a Cambrian explosion date of 600 million years led to a significantly lower likelihood for the data than the older divergence. Nevertheless, the Cambrian hypothesis (at least of 600 million years divergence time, which Cutler uses for an uncited reason as the base of the Cambrian) still has a good fit, which only further heightens the variability of the data. In sum, the molecular evidence for a Precambrian split between protostomes is overwhelming and consistent. What is not convincing is the exact time; estimates are just too spread out right now to inspire much confidence.

A couple of estimates have placed the P–D split closer to the base of the Cambrian. Ayala et al. (1998) reanalyzed Wray and colleagues' (1996) data and added more, by means of an algorithm that supposedly removes branches of the tree that imply significant heterogeneity in rate. With such an adjustment, they arrived at

an estimate of the P–D divergence of 710 million years ago. This is nearly 200 million years before the Cambrian, but they incorrectly saw this as consistent with the Cambrian Explosion. Regrettably, their results cannot be taken too seriously. The algorithm they used removed as much as two thirds of the taxa originally used by Wray et al. (1996), which violates at least my conception of removing outliers of a distribution. Would chopping two thirds of one's body away be considered a therapeutic amputation? Furthermore, their residual group of taxa used for analysis produces no improvement in the heterogeneity of divergence time estimates among genes, relative to that of Wray et al.

Another estimate employed 10 mitochondrial protein-encoding genes (Lynch 1999). The P–D divergence was found to be 630 million years ago. The use of mitochondrial genomes is potentially an important advance in this field, but Lynch's analysis had the fatal shortcoming of using only two benchmarks, one of which is severely questionable. One was the tetrapod–ray-finned fishes split, which was taken to be 430 million years ago. This is probably close, but the split could have been 100 million years before. The troubling one was the fungi–animal split, taken by fossil evidence to be 1,100 million years ago. It is likely that this date could be wildly inaccurate, especially because eukaryotes appeared about 2,000 million years ago (Knoll 1992). Indeed, the fungi–animal calibration is based on an apparent diversification of eukaryotes at 1,200 million years ago to 1,000 million years ago, not any specific useful information about the fungi–animal split. As Knoll (1992, p. 626) noted, this diversification may demonstrate “diversification within a few easily fossilized groups, rather than among all branches in the crown.” Knoll also noted how poor the fossil record before 1,000 million years ago really is, casting strong doubts on the use of fossils for molecular calibrations. If the fungi–animal split was much deeper in time than 1,100 million years ago, Lynch's estimate would have to be revised deeper in time. At this time, one has to take this result with very little confidence. As Knoll pointed out (p. 623), the split might have been “substantially earlier.” If so, then Lynch's estimate will have to be revised, but only to an earlier time. For example, if the fungi–animal split was 1,500 million years ago, the P–D split would be estimated at 750 million years ago. If the fungi–animal split corresponds more to the time of origin of the appearance of fossil eukaryotes (Knoll 1994a; Knoll and Carroll 1999) at 1,700 million years ago, then the P–D split would be pegged at over 800 million years ago. The molecular estimate of Wang et al. (1999), based on about 50 genes, is 1,500 million years ago to 1,600 million years ago. Unfortunately, Lynch's analysis was not very stable, owing to this problem, but still, taken literally in its current form, it still placed the P–D split about 100 million years before the Cambrian.

There *is* a net trend to all of the analyses. They all refute the estimate that all of the animal divergences occurred at the time of the Early Cambrian. They also refute the estimate of a P–D divergence 30 million years before, as advocated by Valentine and colleagues (1996). They all suggest a deeper time for splitting and a non-explosive spread of divergence times, especially for the bilaterian groups (Wray et al. 1996; Hausdorf 2000). What is discouraging is the tremendous spread of estimates.

Along with time estimates, construction of trees should illuminate our inferences about the divergence of the animal phyla. Unfortunately, not many sequences have

proven useful, because rate of divergence is usually too rapid to be useful for resolution of splits in such deep time. Philippe, Chenuil, and Adoutte (1994) examined 18S rRNA sequences from 15 animal phyla and were not able to resolve triploblasts very well at all. They inferred that the multifurcations found are compatible with a Cambrian Explosion hypothesis and that the explosion must have occurred within 40 million years. Unfortunately, this conclusion is clouded by the strong rate heterogeneity among sites. Abouheif, Zardoya, and Meyer (1998) showed that among-site rate variation was more likely the explanation for the poor resolution of the 18S rRNA phylogeny. Indeed, when they removed some of the more variable sites, much more resolution was found within the deuterostomes, although the protostomes remained unresolved. The combination of a deep split and rate variation probably preclude the use of 18S rRNA as a useful tool for such deep resolution, although generalities such as major groupings within the animals (Aguinaldo et al. 1997) and the monophyly of some phyla can be determined by use of this sequence and others (McHugh 1997). Lynch (1999) noted that the rapid production of mtDNA genomes for many species provide hope for developing accurate phylogenies.

The results of Wray et al. (1996) show that even protein-encoding genes may yield a reasonable phylogeny, which would be a surprise if the major radiations occurred in just a few million years. We can calculate from the data a probability of getting the correct order of appearances (protostome→deuterostome; echinoderm→chordate; agnathan→gnathostome) from the seven sequences (Table 8.1). An assumption of independence of estimates among genes yields a probability of getting the correct order of 0.00016. If rates of the mitochondrial genes are correlated owing to linkage, but the nuclear genes are independent of each other, and of the mitochondrial genes, then the probability of the order found for the different divergences is 0.0348. This latter assumption is overly conservative, because great spans of time would tend to reveal differences related more to difference in substitution rate among the genes, which are considerable.

Given the vagaries of the molecular clock, we would not expect to get a correct order of appearance if the animal phyla diverged in just a few million years, as is suggested by the Early Cambrian fossil record calibrated by radioisotopic estimates. Levinton and others (in preparation) simulated both evolutionary trees and nucleotide sequences and found that it is unlikely that any correct resolution of a tree would be possible under a strict Cambrian Explosion scenario. Indeed, their evidence suggests that the divergence of the animal phyla likely occurred over a protracted period, possibly greater than 100 million years, which fits our molecular results.

If the invertebrates diverged around 1 billion years ago, then they are in good company. At this time, there is evidence for a major radiation of the eukaryotes. The Mesoproterozoic–Neoproterozoic boundary (1,000 million years ago) marks the diversification of the red, green, and chromophytic algae (Knoll 1994a). Molecular phylogenies suggest that this was part of a broader radiation of “higher” eukaryotic phyla. Observed diversity levels for protistan microfossils increased significantly at this time, as did turnover rates. The next period of protistan microfossil diversification was near the base of the Cambrian. Thus, the 1-billion-year mark, or perhaps a few hundred million years before (Cavalier-Smith 1991), might have been the glori-

Table 8.1. Rank Order of Divergence Times for Estimates of Animal Phyla Divergences in Wray et al. (1996)

	ATPase 6	Cytochrome C	COI	COII	Hemoglobin	NADH	18S rRNA
Gene type	Mitochondrial	Nuclear	Mitochondrial	Mitochondrial	Nuclear	Mitochondrial	Nuclear
Protostome–deuterostome	3	3	3	3	3	3	3
Echinoderm–chordate	2	1	2	2	2	2	2
Agnathan–gnathostomata	1	2	1	1	nd	1	nd
Probability	0.167	0.833	0.167	0.167	0.5	0.167	0.5

With 3 divergence times, there are 6 permutations, whereas with 2 estimates, there are just 2 permutations. In the case of cytochrome C, the probability is $1 - [\text{probability of correct sequence of three divergences}]$.

COI = Cytochrome oxidase I; COII = Cytochrome oxidase II; NADH = reduced form of nicotinamide adenine dinucleotide; nd = no data; rRNA = ribosomal RNA.

ous time when all of the divergences of modern eukaryotic groups began, including the animals. This hardly means that groups such as trilobites and brachiopods appeared at this early time fully formed; it means only that the lines leading to these crown groups may be quite ancient.

Morphological and genetic implications of the deep molecular splits. What are the implications of the apparent consistent molecular evidence supporting a Precambrian split, about 800 million years ago to 1,000 million years ago, of the protostome–deuterostome line? Does this mean that we are bound to find a long-overlooked cache of trilobites, brachiopods, and mollusks in billion-year-old rocks? Unlikely! Will we find nautiloids swimming among Precambrian stromatolites? I doubt it. Those who hold the Cambrian as a fount of new large animal phyla, many resembling those of the present, are bound to be vindicated. It is naive to believe that Precambrian splits imply an unpreserved deep Precambrian biota of large-bodied burrowing and epifaunal creatures. For one thing, the lack of vertical burrows much before the upper Vendian precludes this (Budd and Jensen 1998; Grotzinger 1995b; Jensen, Gehling, and Droser 1998)

But it is equally naive to dismiss the evidence for Precambrian divergences as devoid of meaning. Gould (1998) blundered by stating:

In fact, I don't see that it matters one whit ... whether one worm-like species carrying the ancestry of all later animals, or ten similar worm-like species already representing the lineages of ten subsequent phyla, crossed this great divide from an earlier Precambrian history. The Cambrian explosion embodies a claim for a rapid spurt of anatomical innovation within the animal kingdom, not a statement about times of genealogical divergence. [p. 64]

Let's overlook the fact that Gould (e.g., 1989, p. 310) and others *did* believe that the major splits in the history of triploblastic animal life coincided with the appearance of the fossils!

Of course, forms associated with stem groups are liable to look a bit fuzzy with regard to the characters by which we recognize extant crown groups. But rather than emotive statements, we need an assessment of what character appearances might be associated with what phylogenetic divergences and how these associations influence interpretations of morphological evolution.

Take the protostome–deuterostome divergences, for example. We now have convincing evidence that the split occurred substantially before the Cambrian. Conway Morris (1998, pp. 143–144) intuited that it must have occurred with the appearance of small-bodied forms about 750 million years ago, and molecular evidence points to a somewhat deeper time. We can take the synapomorphies of the protostomes and deuterostomes to reconstruct to some degree what the ancestral triploblastic bilaterian must have been like, even if we cannot conjure up its exact appearance. The following list gives us some idea of these features:

1. *Hox* genes – anteroposterior, dorsoventral axis specification
2. *Engrailed*, specifying segmentation
3. *Dll*, specifying distal structures

4. Muscle-specific MYOD – turns on muscle fate
5. Nervous system
6. Cephalization – *orthodenticles* gene, anterior and regionalized nervous system
7. *Pax-6* – photoreceptors, eye organizer?
8. Rhodopsin
9. Gene *tinman* sets up circulatory system – heart in *Drosophila* and vertebrates
10. Dorsoventral axis specification
11. Lysyloxidase protein, needed for cross-linking of collagen→skeleton (Ohno 1996)

These characters give us the following picture: a bilaterian creature with nervous organization, cephalization, the capability of large body size owing to a circulatory system, and the capability of producing a skeleton owing to the presence of lysyloxidase. In other words, even *this* crude an analysis gives us a bilaterian that can take the form of many of the body plans of the modern animal phyla. DeRobertis and Sasai (1996) suggested that the group encompassing a subset of these traits be named the Urbilateria. This gene set is so deep within the history of the bilateria (Figure 8.12) that we clearly need much more information from the fossil record and perhaps the distribution of more diagnostic developmental genes before we can make definitive statements about potential thresholds in animal evolution (Knoll and Carroll 1999).

At the minimum, the implications of this list toss out some current hypotheses. Clearly, organisms bearing much of the modern *Hox* gene arrangement existed in deep Precambrian time; therefore, the presence of *Hox* genes could not have been the cause of the Cambrian Explosion (Erwin, Valentine, and Jablonski 1997). Similarly, the presence of a nervous system likely long predated and therefore cannot be implicated in stimulating the Cambrian Explosion (Stanley 1992).

We need more molecular information to further refine inferences about the features of Precambrian phyla and their body plans. For example, it would be extremely useful to develop molecular estimates of the divergence times among protostome or deuterostome phyla, respectively. For example, Aguinaldo et al. (1997) have identified a subgroup of protostome phyla, including the arthropods, nematodes, onychophorans, priapulids, kinorhynch, and tardigrades, that are unified by the presence of a common molting mechanism, ecdysis (Figure 8.12). If so, we can conclude that ecdysis arose just once. Suppose the divergence date for these phyla proves to be deep within the Precambrian. We can then conclude that this morphological innovation is not related to the Cambrian Explosion. The divergence of the lobopods may be interesting and might have set the stage for a Cambrian radiation, but the crucial character of a molting exoskeleton would not have been the stimulus for the radiation. Similarly, a character such as the presence of a radula might be a crucial synapomorphy for much of the molluscan clade. The timing of divergence of the associated taxa would be crucial in judging whether the rise of this character was influenced by a Cambrian trigger or whether the character was already “in the bank,” waiting to be used at the right moment to help facilitate the divergence of larger-bodied radula-bearing groups in the Cambrian. The discovery of *Kimberella* (Fedonkin and Waggoner 1997) suggests that radulae might have preceded the Cambrian explosion.

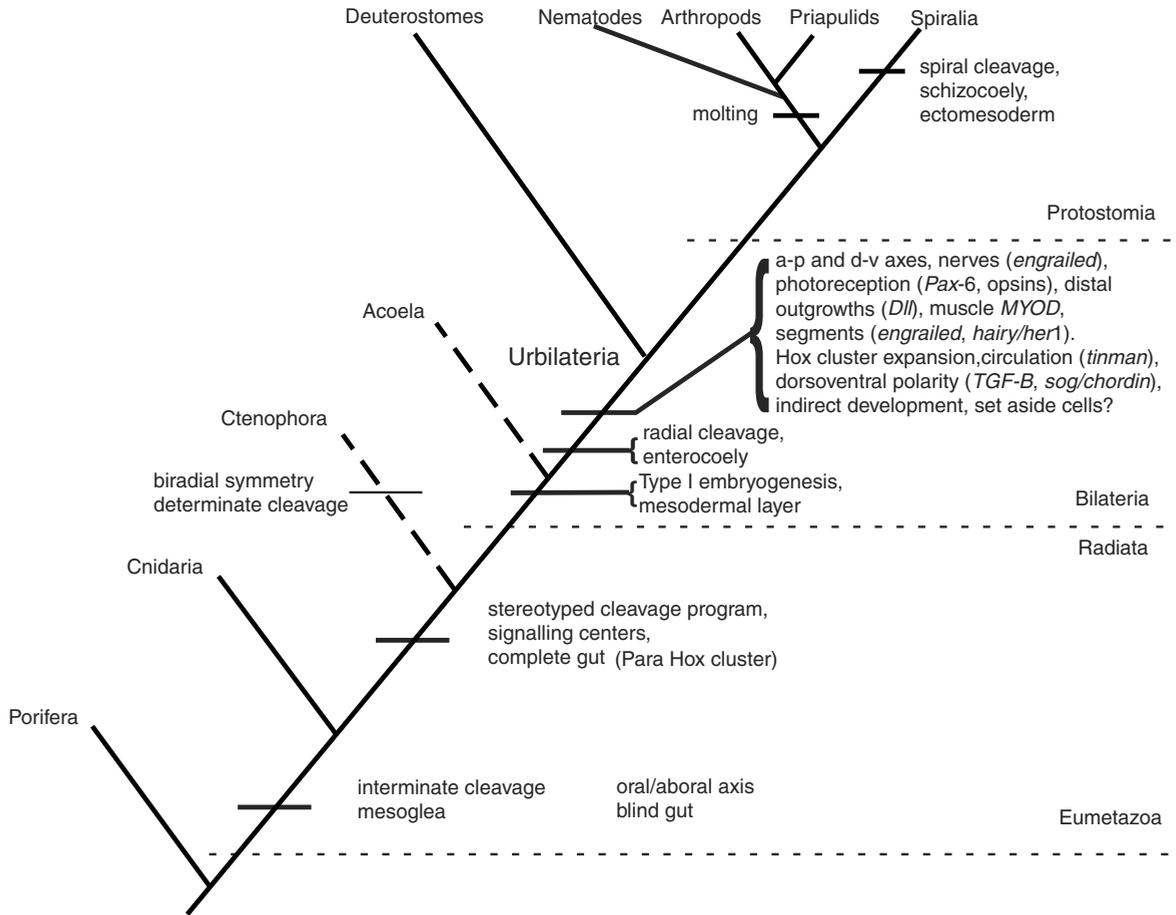


Figure 8.12. Tree depicting major events in the history of animal life. (Modified from Knoll and Carroll 1999, with permission of the American Association for the Advancement of Science.)

Balavoine and Adoutte (1998) pointed out that the support of a division of the protostomes into two monophyletic groups – the molting Ecdysozoa and the Lophotrochozoa – further suggest deep Precambrian origins of major splits within the protostomes. Of greatest interest is the failure of the acoelomate and pseudocoelomate phyla to locate themselves in “primitive” positions on the evolutionary tree (Figure 8.13). The pseudocoelomates do not form a monophyletic group: Rotifers and gastrotrichs are grouped with the lophotrochozoans. Kinorhynchs, priapulids, nematodes, and nematomorphs, however, are grouped with the arthropods in the Ecdysozoa. The acoelomates are found allied with the coelomates. These results make Gould’s above-quoted argument about “ten similar worm-like phyla” rather ironic, as it is obvious that he fell into the trap of believing in a ladder of life, with primitive wormy things coming first, followed by the “higher complex forms.” This is the very mind-set that he so descried in others. As it turns out, the “primitive” wormy forms are often quite derived. As Balavoine and Adoutte pointed out, the traditional organization of life may be upside down, as the forms thought to be coelomless and therefore primitive are widely scattered and allied with derived

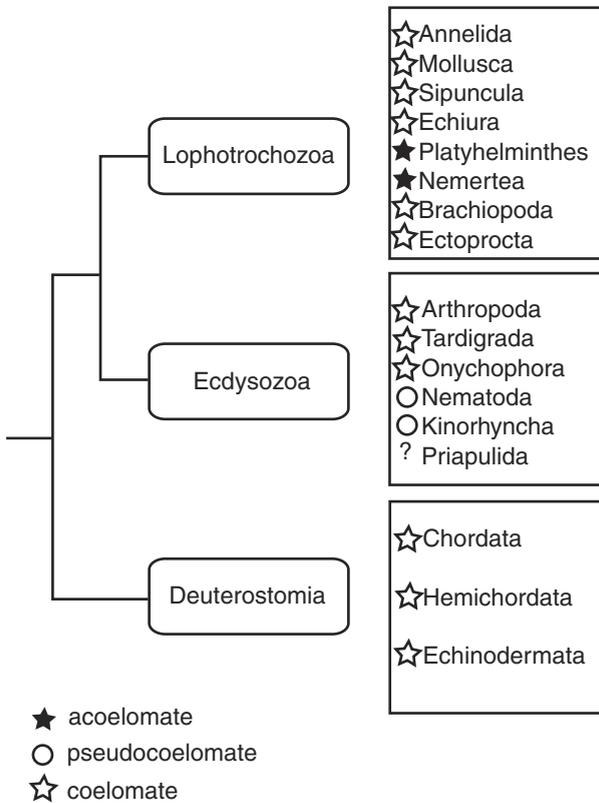


Figure 8.13. Division of triploblastic animals: the Deuterostomia is the sister group of the Lophotrochozoa–Ecdysozoa clade. Note the scattered alliance of acoelomate and pseudocoelomate groups with “higher-grade” animal phyla. (Modified from Balavoine and Adoutte 1998.)

groups. Our new understanding of protostome evolutionary relationships, therefore, opens the possibility that large-bodied coelom-bearing forms or smaller relatives existed in deep Precambrian time.

Precambrian Fossils Reconsidered

Preston Cloud's seminal article convinced us that the Cambrian Explosion might have been much more than an artifact of preservation or just an ecological stimulus that increased body size. Since then, a properly critical eye has been cast on many so-called Precambrian animal fossils, and they have been shown to be sedimentary structures, members of algal groups, or at best unconvincing (Hofmann 1992). And yet, here are the nagging molecular data, asking us to reexamine the situation.

No one doubts the special nature of the Cambrian. Are we likely to find a deep Precambrian and 1-meter-long *Anomalocaris*, "one mean shrimp," as a popular magazine put it? Will we find an *Olenellus* fauna in rocks of a billion years of age? The Cambrian, so beautifully documented by the window Walcott gave us on the Burgess Shale, was clearly a special time when animal life exploded into the wide range of forms that we associate with the modern faunas of today. So what does it mean to find molecular estimates of animal and even within-deuterostome divergences that are so much older? That is the challenge, both to paleontologists and phylogeneticists.

We can imagine three hypotheses that include the possibilities suggested by the molecular data:

1. *Cloudian Cambrian Explosion*: The fossil record as we understand it reflects the divergence of all animal phyla within the Tommotian and Atdabanian stages of the Early Cambrian.
2. *Lost-world hypothesis*: The animal phyla as we know them today (or in the Cambrian) evolved long before the Cambrian, perhaps as far back as 1 billion years ago. Therefore, some day we will find a fossil locality with trilobites and brachiopods, but perhaps in miniaturized form.
3. *Stem-group hypothesis*: The Precambrian molecular divergences exist because there was a deep Precambrian fauna. This fauna, however, is morphologically distinguishable from the Cambrian forms. They have a set of ancestral characters defined by the molecule-dated divergences, along with other apomorphic characters, amounting to a diverse but ancestral fauna.

The molecular data we now have gathered is consistent with the last two hypotheses.

If we take the molecular results seriously, then should paleontologists reconsider their conclusions that true triploblastic metazoans are missing much before the Lower Cambrian? There are several ways to address this.

Are there no fossils? It is not so easy to spin a yarn that connects the Cambrian biota in a continuous chain to our putative point of triploblastic animal origins of 750 million years ago to 1,000 million years ago. A number of fossil finds now suggest that our search image for Precambrian fossils might have misled us.

Taphonomic considerations now suggest that we will not find many instances of Ediacaran-like preservation in the Cambrian, even if the typical Ediacaran animals had lived at the time. Bioturbation would have readily destroyed the special circumstances under which such fossils would have been preserved, as influenced by the presence of microbial mats. In the same manner, we can cast backward and ask the likelihood of Burgess Shale–style preservation before the Cambrian. More recently than the Lower Cambrian, there is a surprising dearth of Burgess Shale–style preservation of organic remains, which are limited perhaps to some lacustrine deposits and perhaps the organic walls of some graptolite-bearing mudstones. Butterfield (1995) argued persuasively that this type of preservation was not unique to the Cambrian but nevertheless cannot be found in older rocks that are younger than the Late Riphean, about 750 million years to 850 million years ago. Thus, there is a broad window of time within which animals might have flourished, but we are bereft of a means to observe them. The style of organic preservation in the Late Riphean is similar to that of the Early Cambrian, so one might argue that here is where Burgess Shale–style fossils should be found, or perhaps even in rocks as old as those from 950 million years ago.

These older rocks have not as yet revealed obvious animal fossils. Sun (1986) reported a series of putative animal fossils from rocks from 900 million years to 700 million years ago in the Huainan District, Anhui, China, and allied them with living annelids. The fossils are black, membranous, carbonaceous remains of various elongate and annulated organisms. It is likely that several of these are algae; they certainly are not reminiscent of annelid segmentation. *Pararenicola* and *Protoarenicola*, however, appear to be worms with elongate, cylindrical, and flexible bodies with annulation and even a differentiated bulbous end (Sun 1986; Sun 1994). Even Cloud (1986) could not dismiss these fossils and declared them to be possible annelids, but ones that required much further study. He dismissed most of Sun's other claimed animal finds as nonanimal, possibly algal, in origin. Also, Butterfield, Knoll, and Swett et al. (1994) failed to find animal remains in rocks from Spitsbergen (Svalbard) of similar age with similar exquisite preservation of organic films.

Other search images, however, have revealed some fascinating new finds. Early diagenetic phosphatization may be a crucial window that will reveal Precambrian animal fossils, for such a form of preservation can retain exquisite three-dimensional detail and is found commonly in Precambrian rocks. Phosphatization can preserve delicate organic structures within days of death (Briggs, Kear, Martill, and Wilby 1993). Bengtson and Zhao (1997) reported a spectacular find of globular Lower Cambrian fossils from Siberia and China that were clearly a developmental series from the egg, through several division cycles, to embryos and hatched juveniles. *Olivoooides* appears to develop into a hatchling that is annulated and conical, with a round cross section (Figure 8.14). It is reminiscent of coronate scyphozoans, although not enough characters are resolved yet for a definitive analysis. The other fossil, *Markuelia*, develops into a worm that is rolled neatly within an embryonic envelope. The worm appears to be segmented, but its affinities otherwise are unknown. The embryos may be halkyerid, but this is not yet confirmed, as no halkyerids have been found preserved with the embryos.

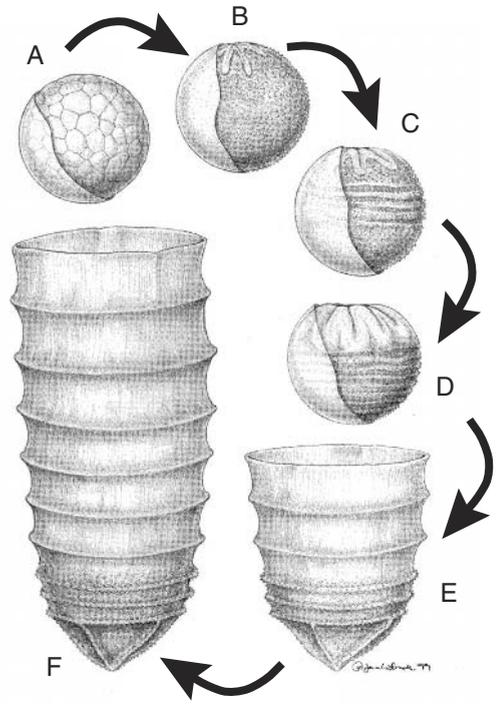


Figure 8.14. A developmental series of *Olivoides* ranging from (A) cleavage embryo to (E) newly hatched and (F) grown specimens. Reprinted from *Embryonic and Post-embryonic Development of the Early Cambrian Cnidarian (Olivoides)* by Yue and Bengtson from *Lethaia*, www.tandf.no/leth, 1999, 32:181–195, by permission of Taylor & Francis. Figure drawn by Pollyanna von Knorring.)

This form of preservation has been pursued in older rocks, and likely cleavage stages of protostome embryos have been found in the Doushantuo Formation (570 million years ago \pm 20 million years) by Xiao et al. (1998). The embryos are all approximately 0.5 millimeter in diameter, with specimens of two, four, eight, and more cells (Figure 8.15). The similar size of all stages strongly suggests an embryo, and the tetrahedral arrangement of cleavage in the four-cell stage suggests a protostome, but possibly a sponge. This exciting development, alas, lacks a corresponding adult, but very little material has been examined thus far. At the least, this is the first direct evidence of bilaterians well before the Cambrian. In the same formation, tiny sponges have been found, including a probable shoe-shaped parenchymella sponge larva (Li, Chen, and Hua 1998). Again, the extension of the range of animals, albeit not bilaterians, has been spread to 50 million to 60 million years before the Cambrian.

These fossils are just tantalizing beginnings. Now that the power of phosphatization as a mode of Precambrian preservation is known, the search will only intensify. This is good, whether or not we extend the range of the protostome and deuterostome Animalia significantly before the Vendian. At least we are looking in a new way.

At the time of this writing, surely the most tantalizing fossil was reported by Seilacher et al. (1998) from the Mesoproterozoic Chorhat Sandstone in India (ca. 1 billion years ago). These appear to be worm trails on weathered bedding planes, interpreted as grazing trails on the sediment surface, beneath a microbial mat. The

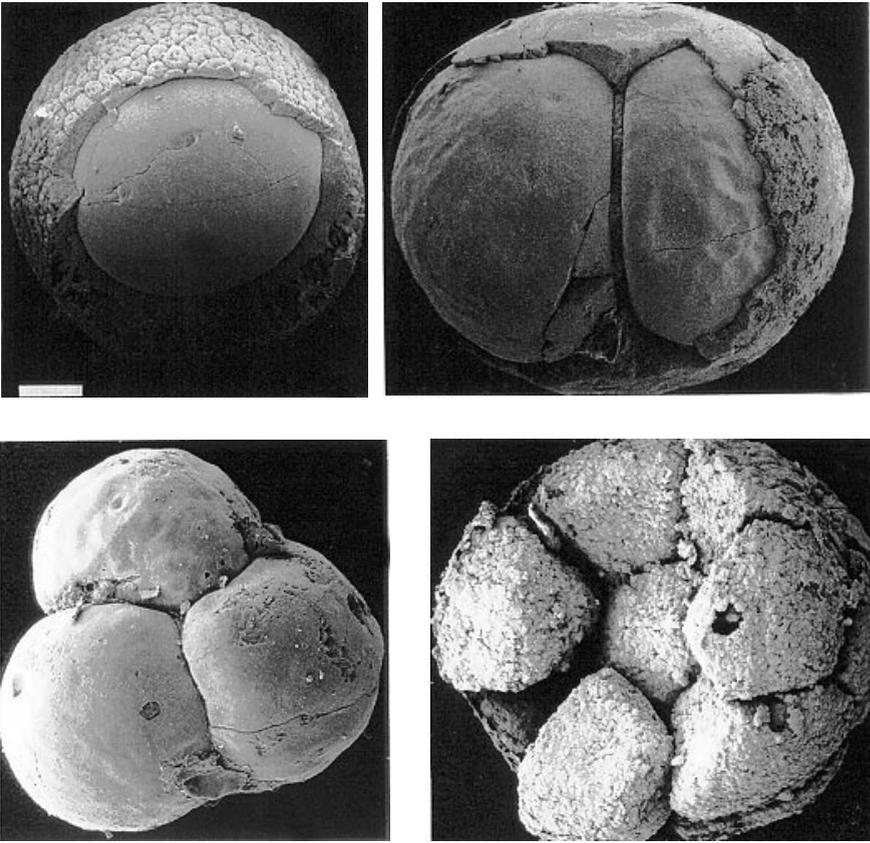


Figure 8.15. Putative fossils of animal embryos from the Doushantuo Formation (570 million years) of China. (Adapted from Xiao, Zhang, and Knoll 1998, with permission from *Nature*.)

shape of the burrows is a bit irregular, but there are ridges of sand on either side of the burrow, suggesting plowing of sediment as the worm moved along. Because the burrows are several centimeters long and a few millimeters wide, we would be dealing with a likely triploblast with a hydraulic skeleton. It may be that such weathered sandstone surfaces bear more examination, but one does wonder why no such burrows have been discovered as yet in rocks between 1 billion years ago and the upper Vendian. Nevertheless, this discovery is very exciting indeed. As of the writing of this chapter, the age of the site is under debate, and even the provenance of the fossil is not generally agreed on.

The recent discoveries should excite paleontologists to start looking intensively for fossils in these previously poorly investigated modes of preservation and to look in other rock and facies types that have been neglected. One must remember that the Burgess Shale was discovered only by accident and relatively recently. It would be unfair to state that there has been a totally inadequate search for Precambrian fossils, but it is equally fair to say that the quest for Precambrian animal life is far from over. The fact that a fish could have been found so recently in well-studied Lower

Cambrian rocks of China (Shu et al. 1999) is an indication that much more will emerge in the coming years.

So Why Not More, Where Are They, and Where Did They Come From?

First, we can consider the possibility that preservation before the Cambrian is inadequate to the task of finding our primordial animal antecedents. Satisfactory explanations in this vein must account for why the fossils have not been found and perhaps where a new search image might produce new fossils. Second, it would be worth a reexamination of some of the Precambrian fossils previously claimed to be triploblasts to see if perhaps they are worth exhuming and subjecting to another necropsy.

Could we find an ancient Precambrian animal fossil at all? A preservational bias hypothesis would argue that some aspect of animal form might preclude its preservation or that the facies appropriate for preservation of the fossils are missing. We discussed above Butterfield's (1995) argument that a large missing time gap in Burgess Shale-like preservation might obscure the rise of the animal phyla between a time of about 750 million years ago and the Cambrian. It is also possible that Precambrian triploblasts were too small to be likely to be preserved as body fossils and that they also left no traces, given that large-bodied creatures with hydraulic skeletons were absent. This hypothesis conforms to notions of the origins of the protostomes and deuterostomes as planktonic larval-like forms, bearing the essences of protostome and deuterostome characters (e.g., Nielsen 1994, 1998). These two groups would have arisen from a radial gastraealike ancestor. Being on the order of a few hundred microns in size at most and soft bodied, such fossils would likely never have been preserved, even if they had an array of morphologies specialized to planktonic and benthic life. I have to admit that the larval-small-size hypothesis is a bit of a cop-out. It safely excludes Precambrian failure of preservation from observational scrutiny. But there it is; it just might be true. It has a venerable history: Ernst Haeckel first conceived of the gastraea as the ancestor of all eumetazoans.

Davidson, Peterson, and Cameron (1995) proposed a developmental constraint that might explain the presence of a diverse but small-body-size Precambrian menagerie. Larvae of many invertebrate species have complete guts and swim and feed in the plankton. Before settlement and metamorphosis, a series of "set-aside" cells develop within the larva that often are the source of the cells that give rise to the entire adult, which develops on metamorphosis. The larval cells by contrast are a developmentally restricted set that, by this hypothesis, cannot give rise to the typical structures we see in large-body-size bilaterians. Thus, the advent of set-aside cells would permit a Cambrian explosion. For this hypothesis to be tenable, one would have to prove that set-aside cells indeed are ubiquitous in indirect developing species (i.e., those with larvae and complete metamorphosis) and that genes specifying spatial organization in adults (i.e., *Hox* genes and others) are not active in larvae. Confirming this, a strong dominance of expression of *Hox* genes has been found in imaginal-type tissue in late-stage larvae of the urchin *Strongylocentrotus purpuratus* (which forms the cells of the adult), but only two of the eight studied

Hox genes show any activity in the early larva (Arenas-Mena, Martinez, Cameron, and Davidson 1998). The lophotrochozoan polychaete *Chaetopterus* sp. apparently does not have *Hox* gene expression in early embryos but expression is found very early in larval development before any trace of segmentation is found. The expression suggests that polychaetes have representative genes of each of the *Hox* cognate groups except *Abd-B* (Irvine et al 1997; Peterson et al. 2000). The expression is localized to the region of teloblasts, but it is not exactly clear that the expression is confined to a true and distinct set-aside cells region. The result is intriguing but awaits further exact study of cell fate.

This hypothesis would require that set-aside cells and the *Hox* body-patterning genes predated the P-D split. It also would require an explanation of arthropods, which do not have indirect larval development. One impediment to this hypothesis is the discovery that the Acoela, once thought to be members of the Platyhelminthes (flatworms), have been reevaluated as the most ancestral bilaterians, on the basis of an 18S rDNA evolutionary tree (Ruiz-Trillo, Riutort, and Littlewood 1999). Although this group superficially resembles other flatworms, a number of embryological features also set it aside from the phylum. It is triploblastic with a spiral cleavage form that is distinct from other spiralian phyla. Most importantly for the Davidson et al. hypothesis, the acoels do not have planktonic larvae, suggesting that there is nothing special about the sudden rise of an adult capable of large body size. Speculation in this direction has only been heightened by the exciting discovery of a strong similarity and perhaps homology between internally fertilized filiform sperm of flatworms, ancestrally positioned annelids, and in the Neomeniomorpha, a group of worm-like aplousobranchs (Buckland-Nicks and Scheltema 1995). These results may further suggest a weakness of the hypothesis that ancestral bilaterians arose from free-spawning organisms with planktotrophic larvae, let alone with set-aside cells. More information is now being developed by Peterson and colleagues on larval versus adult developmental gene expression, especially in basal deuterostomes (e.g., Peterson, Cameron, Tagawa, Satoh, and Davidson 1999; Peterson, Harada, Cameron, and Davidson, 1999b).

The “small and fuzzy” hypothesis seems to include the necessity of the animals having vague morphologies that are unspecialized and bearing no resemblance to the features of the modern animal phyla. As such, some might argue that even if such forms existed, it might be sophistry, therefore, to use the molecular data to deny that there was a Cambrian explosion of animals, in the sense of origin and divergence of the modern animal body plans, in a concentrated period of time. I dealt with this hypothesis above and concluded that the molecular evidence suggests a primordial animal that was equipped to be a typical bilaterally symmetrical organism with a complete nervous system and complete gut. It is entirely reasonable that these forms are members of plesions with a set of ancestral characters and a few more that denote one or more stem groups that became extinct. A good model for such a phylogenetic architecture would be Farrell’s (1998) analysis of the beetles. A more derived set of repeated radiations in the Cretaceous and later was associated with several origins of different angiosperm groups. But this radiation was long preceded by a primitive radiation of pre-angiosperm insect groups associated with

cycads and conifers. Clearly this early group consists of proper beetles, but with primitive features associated with an environment that existed long before the angiosperms, in the same way that small ancestral but well formed animals might have long preceded the Cambrian crown groups.

Consider this additional possibility: The small animals that are not preserved in extant Precambrian outcrops were a reasonably faithful duplicate of modern animal types. A simple possibility might be that all of the animal phyla were represented by interstitial (Boaden 1989) or very small burrowing forms, on the order of 1 millimeter and less in size (requiring the collateral hypothesis that the Cambrian “explosion” was a revolution in size increase and not morphological diversification). Small-animal-body fossils are simply quite rare in the fossil record. We have no good record of harpacticoids or any other copepods, for example, let alone fossils of interstitial polychaetes. Consider a beach on the island of Sylt in the North Sea, studied recently by a consortium of German systematists, who have identified 652 species of animals (Armonies and Reise 2000). With a rarefaction approach, it is believed that a complete recovery would surpass 850 species. It is fair to state that not a single one of these species, no matter how abundant, is likely to be preserved as a fossil. Small body size greatly accelerates the rate of degradation, and the lack of obvious tracks and burrows would exterminate all traces of even a large and diverse fauna. Such is the prospect for recovering Precambrian animal fossils if they are small in body size.

It might be argued that such a “phantom meiofauna” scenario is unlikely, because meiofaunal characteristics are often highly derived, meaning that these groups could not have arisen until more “normal” triploblastic ancestors existed (e.g., with indirect development, which is usually regarded as the ancestral state, relative to lecithotrophic or direct development). Indeed, some characteristics of invertebrates require large body size (Budd and Jensen 1998). But this would be true only if the primordial miniature fauna were confined to interstitial movements among sand grains. If they lived in mud, small body size would be expectable, especially if the food base was scarce and oxygen was in short supply. Such a miniature fauna would also be possible if animals lived in an environment simply not found commonly at the present time. The list of taxa (Table 8.2) includes free-living flatworms and most interestingly nematodes, which are both very abundant in soft sediments. Nematodes may be small, but their free-living representatives are abundant in soft sediments and have a wide diversity of jaw types (Brusca and Brusca 1990).

For example, Seilacher et al. (1998) argued that small metazoans might have lived and foraged at the interface between the sediment surface, but beneath thin algal films or mats. This environment might have disappeared in the Cambrian, during a revolution in body size of burrowing creatures, which would have destroyed previously widespread algal sediment–surface mats. Small annelids (e.g. naids), burrowing a scant 2 millimeters or so below the sediment–water interface, might not have disturbed many bed forms and yet are segmented, much like larger annelids, yet they are triploblastic and have a coelom.

It may be that some shared evolutionary derived characters require some modification of this scenario, at least for some groups. For example, consider the case in which

Table 8.2. Overall Composition of the 652 Animal Species Found on the North Sea Island of Sylt

Faunal Group	Percent of Total Species
Free-living flatworms	32
Nematodes	27
Ciliates	11
Copepods	10
Gastrotrichs	7
Nine other major taxa	13

From Armonies and Reise 1999, with permission.

two closely related phyla or classes share features that require a large body size. It would follow that the common ancestor should be of large body size as well. Small body size would inevitably preclude the development of elaborate gills, large-scale oxygen transporting circulation systems, and so on. It is difficult, for example, to imagine animals smaller than a few millimeters long with a radula although members of the Aplacophora can be less than one mm long. Thus, this trait, if it is the defining synapomorphy of the gastropod–chiton clade, could only have been acquired if body size were of the proportions that would be preservable as fossils. The fossil, however, might be soft-bodied, which would require special circumstances for preservation. It may be that *Kimberella* is just that fossil (Fedonkin and Waggoner 1997).

Perhaps the last breath that can inflate the small-body-size hypothesis comes from some of the known evolutionary relationships of the major phyla, whose sister groups are often unskeletonized and of very small body size (Fortey et al. 1996). For example, the basal sister groups of the rest of the phylum Mollusca are the Aplacophora, especially the Caudofoveata, small wormlike molluscan forms with some peculiar features, such as a possible chitin cuticle. A cladistic analysis of these two groups confirms their basal status (Brusca and Brusca 1990). Similarly, the sister group of the arthropods is the diminutive tartigrades. Maybe one shouldn't get too excited about it, but this at least suggests that the ancestral stocks of some of our known Cambrian dominant phyla could have borne traits that are complex but plesiomorphic.

And Did They Come Only Once?

Cloud (1968) reckoned that the animals arose polyphyletically. This perception would only be heightened by various scenarios that derive the animal phyla from a set of planktonic larval-like forms, which in turn derive from protozoan-like ancestors. If you examine the differences in protostome and deuterostome ciliary beating patterns, you can easily reach the conclusion of a diphyletic origin from several ancestral lines (Nielsen 1994).

One would hope that molecular data would produce a convincing phylogeny that would resolve these problems, but the answer is still voiced without strong conviction. As mentioned above, the antiquity of the splits makes it difficult to find an

ideal set of molecules whose nucleotide divergence rates are homogeneous enough or of the exact rate. In attending a symposium on such problems, I was impressed at how bad any particular analysis was statistically, yet if one flipped through the many studies like a pad of cartoons, some general patterns emerged. At present, they all lean toward monophyly.

Although one of the first major papers analyzing 18S rDNA sequences suggested a diphyletic structure for the animals (Field et al. 1988), other studies convincingly suggest monophyly (Lake 1990; Müller, Müller, Rinkevich, and Gamulin 1995; Schram 1991). Currently evidence supports a P–D split, and a division of the protostomes into the Ecdysozoa (nematodes, arthropods, and other molting animals) and the Lophotrochozoa (annelids, mollusks, lophophorates), with overall support for monophyly of the protostomes and deuterostomes, respectively (Aguinaldo et al. 1997; Balavoine and Adoutte 1998). In any analysis, the strength of these inferences is often muted by poor support for one tree, relative to alternative hypotheses. As mentioned above, the entire P–D line's monophyly is supported by the presence of a large number of genes that are not found outside the protostomes and deuterostomes in some cases, or, in others, not outside those plus the cnidarians and sponges. The cnidarians appear to be connected to a more P–D descendant line by *Hox* genes, some of which probably duplicated (Martinez, Bridge, Masuda-Nakagawa, and Cartwright 1998). The *Hox* genes of cnidarians such as hydroids may prove to serve similar developmental roles of setting of developmental gene cascades (Cartwright, Browsher, and Buss 1999). Finally, *Hox* genes have been found in sponges, and Degnan, Degnan, Andrew, and Morse (1995) argued that this demonstrates the monophyly of the Metazoa. As we approach the "beginning," however, it may be harder and harder to find *Hox* sequences, which might be too different in sequence to encounter easily. Thus, the sponges, cnidarian, and P–D lines may constitute a monophyletic group, but from where did they arise? Alternatively, a set of protozoan groups might all have had *Hox* genes and might have given rise to these three great lines polyphyletically. Admittedly, one might have to resort to arguments of convergence, but *Hox* genes appear already to be used and reused for different functions.

Given the fossils, the bottom line is this: The sponges may be sister group of the cnidarians and perhaps the ctenophores. The connections are dubious thus far. The sponges and cnidarians at one end might form an ancestral group, from which the modern animal groups emerged. On the other end of the timeline, we have the emergence of representatives of many living phyla in the Cambrian and Ordovician. There are tantalizing indications of ancestral forms in many of these phyla, especially among the arthropods and echinoderms. But beyond this, the connections between the ancestors and the living phyla are too sketchy to inspire much confidence about any scenario of origins. All we know is that many appear in the Cambrian "fully formed," as if there is a hidden record. But what is that record?

If the modern phyla arose from small ancestors reminiscent of larvae (Nielsen 1994) and were incapable at first of elaborating large-bodied adults (Peterson, Cameron, and Davidson 1997), then we have no block to placing the divergence of major branches of the animal kingdom before the Cambrian. Indeed, if the P–D line

is a sister group of the Cnidaria, it is fairly easy to imagine small protostomes or deuterostomes with ancestral traits coexisting with cnidarians in an as yet to be found deposit. But if *Hox* genes or other possibly diagnostic traits prove to ally protozoa with these groups, then there are essentially no constraints on origins. Protozoan form is enormous, and it is not hard to imagine multicellular animals of radial and bilateral symmetry arising from them. A planktonic protozoan *Ctenocephrys chattoni* has a surprising resemblance to ctenophores (e.g., Weill 1946, cited in Conway Morris 1998). Although the resemblance could be a simple matter of convergence, it is clear that the search for Precambrian fossils is not enough. More attention should be paid to living protistan forms that may prove to be allied with multicellular animals in surprising ways.

What Was the Cambrian Explosion, and What Did Cause It?

Even if animal life diverged significantly before the Cambrian, we are still left with the question of why large-bodied animals diverged so remarkably in such an apparent short period of time. Two classes of hypotheses can be conjured. First, the *environmental stimulus hypothesis* would argue that the animal groups were a loaded gun that was fired on stimulation by a major facilitating environmental change, such as nutrient enrichment or atmospheric oxygen increase. Second, the *key innovation hypothesis* would argue that the acquisition of a major biological feature, be it a developmental gene or a skeleton, facilitated the sudden divergence of many animal groups. The rise of such a key innovation could have been in response to some biological process such as predation, or it could have simply been in response to the appearance of a mutant that bore a character necessary and sufficient for radiation (e.g., a responsive nervous system).

Environmental stimuli. If we wish to come up with an environmental change that might have triggered the Cambrian Explosion, we of course must provide some target date. But the arguments cited above cast considerable doubt on looking for a major trigger at the beginning of the Tommotian.

The events leading up to the Cambrian suggest major environmental changes that might have had great influence on the rise of the animals. During the time encompassed by the later Vendian, perhaps peaking at 700 million years ago, the continental blocks were in a state of assembly, which might have created an opportunity for strong seasonal fluctuations in climate (Valentine and Moores 1971). This age marks the appearance of glaciers as a major influence of planetary climate. A first glaciation occurred around 750 million years ago. At around 580 million years ago, the widespread occurrence of tillites suggests the presence of worldwide glaciation (Knoll 1994b). The probable occurrence of tillites located near the equator may suggest an earth completely covered by ice. This would entail extremely sluggish water motion and reduced carbon dioxide in the atmosphere, which would further cool the earth into a "snowball" world (Kirschvink 1992). Oxygen levels might also have been severely reduced, which is suggested by the appearance of banded iron formations, which form more readily in a very low oxygen atmosphere. Reduced

oxygen levels might have been accompanied by lower oceanic pH, under the influence of submarine volcanic emissions.

It is possible that the end of glaciation was marked by enhanced oceanic circulation and upwelling. Late Proterozoic and Cambrian rocks are dramatically enriched in phosphorites, which may be a reflection of nutrient input (Cook and Shergold 1984). Carbon 13 (^{13}C) enrichment in 600-million-year-old rocks may reflect a large-scale increase of atmospheric oxygen (Derry, Kaufman, and Jacobsen 1992; Knoll, Hayes, Kaufman, Swett, and Lambert 1986), but a preceding drop in ^{13}C may also reflect a reduction of atmospheric carbon dioxide and a subsequent reduction of greenhouse warming, thus facilitating glaciation (Kaufman, Knoll, and Narbonne 1997). Continental breakup began by 540 million years ago, which might have allowed oceanic currents to dominate and ameliorate climate. The beginning of the Cambrian also coincided with an apparent dramatic rotation of the earth's upper crust and a consequent latitudinal drift of the continents of about 90° . This spectacular change might have caused dramatic climate changes that might have stimulated evolutionary eruptions (Kirschvink, Ripperdan, and Evans 1997).

The beginning of the Cambrian is also marked by dramatic changes in isotopic ratios in sedimentary rocks. ^{13}C enrichments may signify burial of carbon in sediments and increase of oxygen in the ocean and atmosphere (Knoll et al. 1986).

So there is no shortage of environmental change with which to associate an explosion of animal life just before or in Early Cambrian times. We cannot, however, provide a scenario that truly establishes causality. There is no smoking gun, if only because we are not yet sure where to locate the time and scene of the crime.

Innovations. Although intrinsic explanations need not be proposed to the exclusion of environmental stimuli, they depend nevertheless on the fixation in some lineage of a genetic, physiological, or morphological change that is necessary for the radiation of the animal phyla. An environmental connection becomes obvious in cases in which some environmental change is required before a morphological or physiological innovation can produce a functioning animal. Such intrinsic explanations include:

1. *Aerobic metabolism, calcium carbonate, and body size:* Evidence on the oxygen content of the atmosphere suggests an increase approximately 600 million years ago. It is possible that before this time, severe physiological limitations prevented the survival or activity of large active animals. Rhoads and Morse (1971) pointed out that current dysaerobic basins tend to lack animals with robust calcareous skeletons. Calcification, inhibited under conditions of low dissolved oxygen concentrations, might have also been repressed. Thus, the world before the Late Proterozoic might have been one that prevented large-bodied, skeletonized animals from existing. As mentioned above, the evidence from bioturbation suggests strongly that the Cambrian Explosion is not likely just a mineralization event, but it might very well be an event that combined an increase in body size and mineralization. In effect, the increase in atmospheric oxygen, occurring first around 600 million years and then again near the base of the Cambrian (Knoll 1994), might have crossed a threshold that permitted active, large, and often calcified animals.

Unfortunately, current evidence on anaerobiosis does not shed light on this hypothesis. Mangum (1991) argued that many of the current cases known of life under dysaerobic or even temporary anaerobic conditions do not apply to a Cambrian scenario, because the modern mechanisms appeared to be phylogenetically derived modifications of aerobic mechanisms. Thus, aerobic metabolism is ancestral, relative to the low-oxygen lifestyles now known.

It is not easy to disentangle skeletons from large body size. Most importantly, skeletons are support structures, especially as external skeletons in arthropods and as internal skeletons in echinoderms and vertebrates. Also, mineralized structures can be employed for functions other than skeletons, as in the teeth of some chitons (Lowenstam 1981). Although calcified tubes might protect against predators, tubes also allow a polychaete to live in a permanent home that it can ventilate and use as a settling point for detrital food or even perhaps as a microbial garden. Most of these lifestyles are associated with large body size, which might have been the significant change just before or at the beginning of the Cambrian.

2. *Developmental genes*: One of the great advances since the mid-1980s was the discovery of a lingua franca for body patterning that transcends the details of development within individual animal phyla (Akam 1987; Carroll 1996; DeRobertis and Sasai 1996). The so-called *Hox* cluster of genes contains information required for anteroposterior developmental determination. The universality of this information has been thought to be a lynchpin for animal development (Slack and Holland 1993). These rules unite the protostomes and deuterostomes (DeRobertis and Sasai 1996) and apparently represent an increase of complexity over cnidarians, which presumably occupy a more ancestral position in animal phylogeny (Martinez et al. 1998).

The evolution of the protostome–deuterostome *Hox* cluster has been suggested to be the innovation that permitted the later Proterozoic–Cambrian radiation of the animals (Valentine et al. 1996). The latest common ancestor of the protostomes and deuterostomes had six *Hox* clusters, and episodes of gene duplication occurred in deuterostome history. It is not clear, however, that increase in number of *Hox* genes is necessary to increase morphological complexity (Warren, Nagy, Selegue, Gates, and Carroll 1994). Moreover, the *Hox* cluster is just a small part of an upstream–downstream cluster of genetically determined interactions that specify morphology. It is likely that many important parts of development lie outside the *Hox* cluster, which acts more as a set of organizers. It also may be true that natural selection for anteroposterior differentiation (which allows directed sensory perception and locomotion) facilitated the appearance of the *Hox* cluster, and not the reverse.

The molecular data suggests a deep origin for the protostome–deuterostome split. Although a consensus has emerged about the deep Precambrian aspect of this split, one should still reserve judgment about the result, owing to the difficulties in using extrapolation to estimate the time of divergence. Nevertheless, if we accept these results, then the appearance of the sixfold *Hox* cluster could have little to do with the Cambrian Explosion, because it predated it by some 400 million to 600 million years.

3. *Nervous system*: I will use this example as a proxy for a number of other such hypotheses, such as the rise of a muscular system or a complete gut. The development of a fully developed nervous system with ganglia to aid vision and other functions, combined with the presence of a brain to integrate sensory signals, might have been the innovation required to allow the radiation of the bilaterian

triploblasts. Although this hypothesis (Stanley 1992) is attractive, it comes squarely against the molecular data discussed above, which suggests that animals capable of a fully developed nervous system might have been present many hundreds of millions of years before the start of the Cambrian.

4. *Predation or other biotic interactions:* In the Lower Cambrian, we already see a plethora of animal groups with a wide variety of ecological roles. Most noticeable are the large roving predators, including the widespread and seemingly ferocious *Anomalocaris*, which reached lengths of over a meter (Conway Morris and Robison 1988). Although some predators can overwhelm all potential prey, it has long been appreciated that a number of refuges permit predators to escape the attention of prey, especially by nocturnal habits or crypsis. But escape in size is also an effective deterrent against predation, and many invertebrate species can avoid being eaten by virtue of their unmanageable size (Levinton 1995). Thus, a simple Cambrian scenario can be developed where the rise of predation causes rapid natural selection for increased body size. This would presumably happen in many lineages and result in the evolution of increased predator body size, thus promoting an arms race. In space-limiting hard-bottom environments, predation tends to eliminate competitive dominants (Paine 1966) and maintains diversity. It might be that the rise of predation in the Cambrian performed a similar role of promoting diverse biotas of prey (Stanley 1976).

I do not know of a study that attempts to estimate secular changes through the Cambrian in the degree of predation, as measured perhaps by shell repair damage or wounds in trilobite carapaces. It is not unusual to find pieces of trilobite carapaces missing, which might reflect predation attempts. Possibly, other biotic interactions such as competition might also have contributed to increased body size, because larger body size may permit exploitation of larger food items.

Because we do not have an effective accounting of changes in predation through the Cambrian or of the very rise of predation itself in the Cambrian, this hypothesis is untested. Parker (1998) has found evidence for a diffraction grating on external surfaces of several Burgess Shale fossils, which suggests an adaptation to reflect color. This may be related to the rise of predation, but it could just as easily be a sexual recognition signal.

It is very possible that predation might have predated the Cambrian, but we do not have the tools to detect it. The late Precambrian fossil *Cloudina* is the earliest animal known to have produced skeletal remains, in the form of tubes. Bengtson and Zhao (1992) found nearly 3% of tubes from the Shansi province, China, containing rounded holes 40 to 400 micrometers in diameter. A positive correlation between the size of the holes and the width of the bored tubes suggests that the attacking organism was a predator, selecting its prey for size. If true, this would be the oldest case of predation in the fossil record and would support the hypothesis that selection pressures from predation could have been a significant factor in the evolution of animal skeletons around the Precambrian–Cambrian boundary. On the other hand, we may yet find much older tubes with predation holes.

Thomas and Reif (1993) established a scheme of skeletal structures that encompass all skeletonized organisms. As mentioned in chapter 5, such a scheme allows a calculation of the extent of morphospace that is occupied at various points of geological time. Thomas, Shearman, and Stewart (2000) performed such an analysis for Burgess Shale–style faunas and found that the bulk of skeletal morphospace was occupied by Cambrian times. Of 182 possible skeletal ele-

ment pairs, 146 could be found in the Middle Cambrian. Unfortunately, this evolutionary exuberance cannot be used to test the predation hypothesis or other skeleton-related hypotheses. The dominance of single-element rods and metameric exoskeletons is strongly linked to the rise of the sponges and arthropods, respectively. A future phylogenetic analysis of these data may prove illuminating in establishing patterns of taxon-specific and polyphyletic flourishings of specific skeletal designs.

5. *Cropping and bioturbation*: The Ediacaran world appears to be dominated by shallow-water sediments capped by a biomat, perhaps algal. Up to the very top of the Vendian column, we see little evidence of the sort of bioturbation that would vertically disrupt the sediment more than a few millimeters. Then suddenly – by geological standards – the diversity of burrowers and extent of vertical bioturbation increases dramatically. So a chicken-and-egg problem arises immediately. Did the rise of infaunal bioturbators cause the widespread destruction of algal mats, allowing a plethora of new lifestyles and morphologies to arise in the Early Cambrian? Or, alternatively, did the rise of surface-grazing microbial-algal consumers cause the sudden disruption of the mats, allowing bioturbators to penetrate an otherwise impenetrable mat? I can see no evidence at present to allow us to distinguish between the two alternatives. Worse than that, it may be that some more general factor stimulated or permitted the increase of body size at the end of the Precambrian, which would allow the evolution of mat grazers and mat-disrupting burrowers. The Cambrian fossil record does not help us terribly much because the mats and Ediacaran-like preservation disappears, at least in frequency, well before the appearance of the great Early Cambrian diversity in the Tommotian and Atdabanian.
6. *Phytoplankton–zooplankton diversification and vertical transport*: This hypothesis would argue that a sudden change in phytoplankton diversity might have stimulated the diversification of zooplankton. The increase in phytoplankton, registered by an increase in acritarch diversity, might have provided an increased diversity of food supply to suspension feeding benthos, which in turn might stimulate the diversification of other trophic levels. In addition, a diversification of zooplankton, as of yet unregistered in fossils, might accelerate the rain of phytoplankton, via fecal pellets, to the bottom, thus stimulating the evolution of benthos. Although the former hypothesis is a possibility, the latter seems unlikely. Collisions between phytoplankton cells often cause the rapid origin of marine snow, which may sink rapidly to the bottom, even in the deep sea (Christensen and Kannevorf 1986; Riemann 1989; Thiel et al. 1988).

At present, we have no reason to select any one of these as necessary stimuli to the sudden appearance of a diverse animal fauna in the Early Cambrian. Indeed, our problem is that we have too many hypotheses chasing too few data.

The Main Points

1. Most of the preservable and many soft-bodied crown-group animal phyla appear in the second two stages of the Cambrian. These appearances constitute the “Cambrian Explosion.”
2. The Cambrian Explosion might record an evolutionary event, the divergence of the animal phyla, or it might instead merely record an explosion of fossils. Cloud (1968) argued that it was an evolutionary event.

3. Some have argued that the Cambrian Explosion was an evolutionary event, but it might have included a period of several tens of millions of years during the Vendian, when a number of animal groups existed, some perhaps being bilaterian triploblasts.
4. Molecular clock evidence from several studies places the timing of the protostome–deuterostome split much before the Cambrian, with a concentration of dates around 800 million to 1,000 million years ago. This suggests either that the rise of animals is in deep Precambrian time or that some artifact is giving a false molecular timing signal.
5. Molecular developmental evidence suggests that the common ancestor of the protostomes and deuterostomes had a wide variety of features that could specify an animal surprisingly modern in aspect.
6. The Cambrian Explosion was not just an explosion of skeletal types but also an explosion of large-bodied animals, including those with hydraulic skeletons capable of extensive bioturbation.
7. The stimulus for a Cambrian Explosion may lie in an increase of atmospheric oxygen, but changes in climate or even crustal deformation and nutrient input from vulcanism may be implicated.
8. Intrinsic biological factors, such as the rise of *Hox* genes and the rise of a nervous system, are discountable. However, the rise of predation might have stimulated both the sudden increase of body size and the rise to dominance of skeletonized taxa.