Introduction

ಆ Life arose on Earth more than three and a half billion years ago (3.5 gigayears, or Ga, ago; 1 Ga = 1 billion years) with the evolution of the first living cells. Soon (geologically speaking), three major, single-celled evolutionary lineages became established: the Eubacteria ("true" bacteria), the Archaea, and the stem Eukaryota (the lineage that now includes plants, animals, and fungi). The cells of each of these domains are very different from one another: Eubacteria and Archaea have their DNA dispersed throughout the cell, whereas in Eukaryota the DNA is enclosed within a membrane-bound nucleus. These single-celled forms diversified broadly, inventing a wide array of biochemical specializations. Although the lineage that gave rise to eukaryotes seems to be as ancient as the Eubacteria and Archaea, the earliest eukaryotic cells now recognized in the fossil record date to about 1.8 Ga, and it seems unlikely that they evolved much before 2 Ga. The cell lineages that gave rise to the Eukaryota are unknown. These early organisms were able to transfer genetic material between lineages, so the phylogenetic histories of their genes—their family trees—do not branch in a tree-like manner but instead involve many cross-links, greatly complicating the reconstruction of their phylogenies (Rivera and Lake 2004). Lateral gene transfers occur in animals as well, but at much lower frequencies and chiefly among early lineages.

The evolutionary changes since the origin of life have been accompanied by extensive changes in environmental conditions, some caused by purely physical and chemical processes and others by interactions of organisms with the atmosphere, oceans, and crustal materials. For example, the initial rise of oxygen in the oceans and atmosphere about 2.4 Ga was caused by the evolution of oxygenic photosynthesis that probably became important about 2.7 Ga. This process entrained a complex series of oxidation reactions with elements such as iron and uranium, and it eventually led to the spread of low levels of free oxygen. The evolutionary history of life has been sensitive to such changes.

The earliest fossil eukaryotic cells arose through the acquisition of symbionts by a host cell (Embley and Martin 2006; Margulis 1970). Organelles such

as mitochondria and the chloroplasts began as small cells that lived within a host cell symbiotically—for mutual benefits—and that became incorporated as obligate endosymbionts. They eventually evolved into cellular structures, organelles that function within eukaryotic cells much like organs function in animal bodies. Not all organelles arose from symbiosis; some simply evolved to function within their present clades. All organisms that are large, complex, or multicellular or that have a diversity of structures are eukaryotes; evidently, the structure of the eukaryotic genome is an advantage in achieving a certain kind of multicellularity. It may be that the evolution of the traits that permitted the eukaryote host cell to acquire symbionts as permanent organelles, making the host's cells multicellular in a sense, underlay the ability of eukaryotes to eventually form bodies composed of many differentiated cell types (Awramik and Valentine 1985).

Today, some two dozen major eukaryotic groups have bodies composed of more than one cell, but few have progressed beyond the stage of an association of essentially identical cell types (Buss 1987; Knoll 2011). Eukaryotes include protistan colonies and various algae that have many cells, but there is no evidence that any of these groups has ever achieved the developmental control required to produce more complex morphologic patterns. Multicellular algae and fungi have only a few cell types, whereas other eukaryotic lineages are multicellular but exhibit none of the hierarchical structure of differentiation seen in plants and animals. At least eight different groups of these multicellular eukaryotes arose well before animals finally evolved sometime more than 750 million years ago (Ma). Complex multicellularity involves a hierarchical structure of differentiated cell types, tissues, organs, and the regionally differentiated structures found in animals and vascular land plants. As we will see in chapter 3, there is good evidence that the environmental settings of mid-Proterozoic time would have inhibited the evolutionary success of those groups even if they had appeared.

Multicellularity is a generative evolutionary innovation in the sense that it provides the basis for two additional important evolutionary steps: greater body size and increased division of labor among differentiated body parts. Greater size quite literally changes the nature of the world experienced by organisms. Most single cells in the sea live in a world in which their motion is dominated by the viscosity of the water rather than by the inertia of their bodies (as expressed by the Reynolds number[1]). Body size is a multiplier of inertia, and most multicellular organisms are large enough that they cross the boundary into a world where inertial forces become important. At such larger sizes, most organisms evolved new ways of locomotion and feeding, facilitated by the specialization of cells, tissues, organs, and differentiated body parts. Such division of labor is evident even in sponges, the earliest metazoan group, but becomes far more pronounced in more complex animals.

Choanoflagellates, a unicellular group that feeds on bacteria and other minute food items, are the closest living relatives of animals. The earliest animals likely fed in a similar manner, but evolved larger, multicellular feeding chambers and were able to capture more food, to support their increased body masses, from larger volumes of water. From this fairly unpromising beginning arose all the rich diversity of the animal kingdom. Humanity owes a special debt to sponges.

Some 120 million to 170 million years after the origin of sponges, the scrappy fossil record improved with a bang, geologically speaking. Following a prelude of a diverse suite of enigmatic, soft-bodied organisms beginning about 579 Ma, a great variety and abundance of animal fossils appear in deposits dating from a geologically brief interval between about 530 to 520 Ma, early in the Cambrian period. During this time, nearly all the major living animal groups (phyla) that have skeletons first appeared as fossils (at least one appeared earlier). Surprisingly, a number of those localities have yielded fossils that preserve details of complex organs at the tissue level, such as eyes, guts, and appendages. In addition, several groups that were entirely soft-bodied and thus could be preserved only under unusual circumstances also first appear in those faunas. Because many of those fossils represent complex groups such as vertebrates (the subgroup of the phylum Chordata to which humans belong) and arthropods, it seems likely that all or nearly all the major phylum-level groups of living animals, including many small soft-bodied groups that we do not actually find as fossils, had appeared by the end of the early Cambrian. This geologically abrupt and spectacular record of early animal life is called the Cambrian explosion. The explosion tells us a great deal about ecological and evolutionary history and, even more importantly, about the many processes involved in evolutionary change.

Although the earliest, preexplosion history of animals is not well recorded by fossils, it can be pieced together from a fragmentary fossil record and from knowledge of the morphologies and genomes of animals whose body plans evolved during that remote period, especially living sponges, cnidarians, and primitive bilaterian groups. The rest is history, one that can be reconstructed from the fossil record, the comparative study of living metazoans, the record of evolution preserved in the genomes of living groups, and the study of the ecological and evolutionary processes that shaped the living fauna.

The reality of the Cambrian explosion has been questioned by a number of scientists. One line of argument has been that because the fossil record is incomplete, the absence of earlier animal fossils is not evidence that such forms were not present in earlier faunas. Therefore, it has been argued that the explosion is more apparent than real and simply reflects unusual conditions of fossil preservation. Another frequent criticism is that because evolution is assumed to proceed by rather gradual change and not by jumps, the rapid

appearance of such a diverse, novel fauna could not have arisen in such a short period of time as the explosion interval, almost a geological instant. Arguing from negative evidence is clearly dangerous.

Because unusual claims require unusual evidence, such concerns are entirely legitimate. The unique Cambrian fossil assemblages were revealed in large part due to studies of the Burgess Shale fauna discovered in 1909 by paleontologist Charles Walcott (fig. 1.1) but finally brought to full light by Harry Whittington and his colleagues beginning in the 1970s. Even older, spectacular Cambrian faunas from China were discovered in 1984 by Hou Xian-guang. The evolutionary history behind these assemblages was not well understood, however. A long, hidden history of animal evolution seemed possible. Taken at face value, the geologically abrupt appearance of Cambrian faunas with exceptional preservation suggested the possibility that they represented a singular burst of evolution, but the processes and mechanisms were elusive.

Although there is truth to some of the objections, they have not diminished the magnitude or importance of the explosion. A long history of metazoan evolution did precede the Cambrian, perhaps by 200 million years or more. This long history was unknown when the explosion faunas were first described but is being gradually revealed by comparative studies of the rates of molecular sequence divergence (so-called molecular clocks), by studies of molecular fossils or biomarkers and by a growing knowledge of the fossil record. The only animals present during most of the preexplosion interval were sponges and architecturally simple organisms built of sheets of tissues. A few tens of millions of years before the explosion, however, small organisms that had body plans designed for locomotion on the seafloor—bilaterian-grade forms—evolved. Their evolution may have been enabled by an increase in oxygen levels that permitted an expansion in metabolic activities, although oxygen levels were still quite low by modern standards (1–10% of present atmospheric levels). A continuing increase in oxygen levels may have permitted the evolution of larger-bodied architectures that arose from varied members of the chiefly worm-like bilaterian fauna. Solutions to some of the biomechanical problems posed by those larger bodies commonly involved the evolution of either tough organic or even mineralized skeletons. It was this round of metazoan evolution that produced the fossils of the Cambrian explosion. Thus, explosion fossils did have a metazoan ancestry stretching back well before the Cambrian into the Neoproterozoic, but the earlier faunas did not consist of numerous, large, complicated body plans.

Several lines of evidence are consistent with the reality of the Cambrian explosion. First, metazoan fossils are not the only fossil groups to suggest an unusual period of evolutionary activity during the early and middle Cambrian. The rise in fossil metazoan diversity is closely tracked by an increased

Figure 1.1 Paleontologist Charles Walcott, the fourth secretary of the Smithsonian Institution, discovered the Burgess Shale Fauna in August of 1909. Walcott is shown with three other men excavating the quarry, in British Columbia, Canada. Walcott is in the center of the picture with hand on hip. Photograph courtesy of the Smithsonian Institution Archives.

diversity of organic-walled microfossils known as acritarchs as well as by an increase in the diversity and complexity of trace fossils—the signs of animal activity such as trails or burrows. Each of those fossil types is subject to unique preservational requirements; thus, they represent independent metrics of diversity change. The similarity in their patterns suggests a general expansion of biodiversity, not just among early animals but among many other groups as

well. Finally, many of the changes in preservation are a consequence of the biotic innovations (Butterfield 2003). For example, a revolutionary change in the sedimentary environment   from microbially stabilized sediments during the Ediacaran to biologically churned sediments as larger, more active animals appeared—occurred during the early Cambrian. Thus, the quality of fossil preservation in some settings may actually have declined from the Ediacaran into the Cambrian, the opposite of what has sometimes been claimed, yet we find a rich and widespread explosion of fauna.

The Cambrian explosion is also correlated with changes in the amount of oxygen in the oceans, with the construction of animal-dominated marine ecosystems, and with the expansion of the developmental processes—leading from egg to adult—that underpin the ability of animal genomes to generate the morphologies of more complex animals. These three elements—changes in the physical environment, the establishment of new ecological relationships, and the evolution of developmental systems—form the changes that are most critical for understanding the explosion. A central theme of this book is the exploration of the contributions of each of these elements and particularly of the interactions between them. Many accounts of the explosion focus on only one, or sometimes two, parts of this triad as the primary driver for this extraordinary episode of evolutionary innovation. In our view, the early diversification of animals was not simply a response to a changing environment or to the acquisition of a particular new adaptation or to the invention of new types of development, but to interactions among all three.

The subtitle of this book, *The Construction of Animal Biodiversity*, captures a second theme: the importance of building the networks that mediate the interactions. Networks exist between the physical environment and the biota to affect geochemical cycles, between various species to construct marine ecosystems, and among genes and cells within diversifying animal lineages as the developmental process evolved. Each of these theaters of evolutionary change involved the formation of new interaction networks, and in many ways the Cambrian explosion is dominated by the issue of network dynamics. Take just one example that we will explore later in more detail: the oxygenation of the oceans. Precambrian oceans were largely anoxic, with unhealthy doses of sulfur and iron. Their conversion to the well-oxygenated oceans of today set the stage for the diversification of marine animals. The oxygen originally was generated by algal photosynthesis, but it is only a necessary precondition. What we need to know is how the change worked. Although many purely geological and geochemical scenarios have been proposed, there is also evidence of a significant role for the activity of animals. For example, it is possible that the action of sponges and their allies in sequestering carbon in the sediments

may have been critical in the oxygen buildup in ocean waters in the late Neoproterozoic (Sperling, Pisani, and Peterson 2007). If this hypothesis is correct, it exemplifies the contributions of the animals in the building of an environment that permitted their own diversification through the development of ecological interaction networks.

Increased genetic and developmental interactions were also critical to the formation of new animal body plans. By the time a branch of advanced sponges gave rise to more complex animals, their genomes comprised genes whose products could interact with regulatory elements in a coordinated network. Network interactions were critical to the spatial and temporal patterning of gene expression, to the formation of new cell types, and to the generation of a hierarchical morphology of tissues and organs. The evolving lineages could begin to adapt to different regions within the rich mosaic of conditions they encountered across the environmental landscape, diverging and specializing to diversify into an array of body forms.

A third theme of this book is the tension between the nature of explanations for major evolutionary transitions in general and that of the Cambrian explosion in particular. In each of the three trajectories of change explored in this book—of the physical environment, of ecological interactions, and of the growth of developmental interactions—some workers have favored explanations that are consistent with how processes work today. Others, though, interpret the evidence to suggest that the world of the Ediacaran and Cambrian operated in very different ways or at least produced very different effects than what similar changes would produce in the modern world. For example, some geochemists have suggested that the carbon cycle involved in the late Ediacaran operated in very different ways from today and that only by reconstructing the ancient dynamic of the carbon cycle can we understand the increase in oxygen levels of the time. Geologists describe such settings as "nonanalog conditions." Much warmer or colder climates, more extensive continental seas, and widespread ocean anoxia are examples of such conditions. Having recognized the occurrence of nonanalog conditions, the challenge becomes to understand whether the processes that produced them also differ from those operating in the modern world.

As geologists, we view this tension as a debate over the extent to which uniformitarian explanations can be applied to understand the Cambrian explosion. Uniformitarianism is often described as the concept, most forcefully advocated by Charles Lyell in his *Principles of Geology,* that "the present is the key to the past" (Lyell 1830). Lyell argued that study of geological processes operating today provides the most scientific approach to understanding past geological events. Uniformitarianism has two components. Methodological

uniformitarianism is simply the uncontroversial assumption that scientific laws are invariant through time and space. This concept is so fundamental to all sciences that it generally goes unremarked. Lyell, though, also made a further claim about substantive uniformitarianism: that the rates and processes of geological change have been invariant through time (Gould 1965). Few of Lyell's contemporaries agreed with him (Rudwick 2008). Today, geologists recognize that the rates of geological processes have varied considerably through the history of Earth and that many processes have operated in the past that may not be readily studied today.

Whether uniformitarian explanations can be appropriately applied to understanding events of the Ediacaran and Cambrian will arise in several chapters of this book. Although it has not usually been framed this way, we will see that debates over the nature of the geochemical evidence, the processes involved in the construction of Ediacaran and Cambrian ecological assemblages, and the processes of change in developmental evolution in early metazoans all involve differences of opinion as to whether a uniformitarian approach is appropriate (Erwin 2011).

The nature of appropriate explanations is particularly evident in the final theme of the book: the implications that the Cambrian explosion has for understanding evolution and, in particular, for the dichotomy between microevolution and macroevolution. If our theoretical notions do not explain the fossil patterns or are contradicted by them, the theory is either incorrect or is applicable only to special cases. Stephen Jay Gould employed the animals of the Burgess Shale and the early Cambrian radiation in his book *Wonderful Life* (Gould 1989) to advance his own view of evolutionary change. Gould argued persuasively for the importance of contingency—dependence on preceding events—in the history of life. Many other evolutionary biologists have also addressed issues raised by these events. One important concern has been whether the microevolutionary patterns commonly studied in modern organisms by evolutionary biologists are sufficient to understand and explain the events of the Cambrian or whether evolutionary theory needs to be expanded to include a more diverse set of macroevolutionary processes. We strongly hold to the latter position.

In general, microevolution treats changes within populations and species, underpinned by the natural selection of genetic variation that arises through mutation or recombination within the genome. These genetic changes arise within individuals but are promulgated over time within populations and species, depending on the advantage, disadvantage, or neutrality of the changes with respect to the relative reproductive success of the individuals that carry them; in other words, they are scrutinized by selection. Sometimes, this evo-

lutionary mode is characterized as evolution by change in gene frequency. Microevolutionary change often produces new species when different populations of a species are isolated genetically, or nearly so, such that each pursues a separate pathway of genetic change and they become distinct species; in animals, it usually means that they can no longer exchange genes. Macroevolution, by contrast, involves the study of what happens in evolution beyond the mechanisms of the formation of species. Some species, for example, are founders of major clades that encompass millions of species that occupy a wide range of ecological occupations, whereas other species are merely found in minor branches of life's tree with rather similar ecologies or simply become extinct without issue (other patterns are not uncommon). Each of the species with those very different evolutionary outcomes arose through microevolutionary processes, yet there is obviously more to be said about their evolution, which forms the topic of macroevolution. Some macroevolutionary studies focus on the waxing and waning of clades through space and time and on the causes of their relative abilities to expand, to resist extinction, to deploy ecologically, and to generally prosper or not. Other studies focus on the rise of evolutionary novelties within some branches that produce novel body plans and, in some cases, many "subplans," as in the Arthropoda. In yet other branches, some rich in species and some not, only a single, narrow range of body plan morphology occurs, as in the priapulids (see chap. 4). Clearly, the results of all speciation events are not equal. These two macroevolutionary areas—relative richness and relative novelty—are clearly related, with differences in body plans being responsible for some differences in branching patterns in the tree of life. The change from studying microevolution to macroevolution involves a hierarchical step (Erwin 2000; Jablonski 2007) that is important because it moves the focus of interest from processes that affect individuals within species to those that affect species within higher-order groups. Thus, the move from micro to macro forms a discontinuity. Novel features arise within lineages, just as do changes leading to speciations, but the subsequent behavior of the groups with respect to evolutionary rates, diversifications, extinctions, and ecological and geographic ranges must be studied among lineages. It is in work o the origin of novelties that explanations for the Cambrian explosion are now emerging. Since the 1990s, there has been a revolution in our understanding of the mechanisms governing the development of animals and how these mechanisms evolve.

Here, then, is a perfect scientific challenge: to unravel events of basic importance to our understanding of the history of life and of the processes that underlay it, set in oceans of the remote past and obscured by far more than half a billion years of subsequent evolution of both the environment and

the biota. With a fragmentary and often mysterious fossil record, combined with such information as can be gleaned from the rock sequences in which the fossils are preserved, the Cambrian explosion was a major transition in the history of life, and it plays a critical role in evaluating our theories and understanding of the processes of evolution. What could be more appealing?

NOTE

1. The Reynolds number can be expressed as Re $= lU/v$, where l represents the size of the organism as a function of some linear dimension, U is the velocity of a fluid medium relative to the organism, and v is the kinematic viscosity of the fluid (the ratio of dynamic viscosity to density). See S. Vogel (1994) for a most readable account of the Reynolds number and its consequences.