The Multiple Origins of Complex Multicellularity

Andrew H. Knoll

Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138; email: aknoll@oeb.harvard.edu

Annu. Rev. Earth Planet. Sci. 2011. 39:217–39

The *Annual Review of Earth and Planetary Sciences* is online at earth.annualreviews.org

This article's doi:
10.1146/annurev.earth.031208.100209

0084-6597/11/0530-0217$20.00

Keywords

Metazoa, embryophytes, evolution, fossil, diffusion, bulk transport

Abstract

Simple multicellularity has evolved numerous times within the Eukarya, but complex multicellular organisms belong to only six clades: animals, embryophytic land plants, florideophyte red algae, laminarialean brown algae, and two groups of fungi. Phylogeny and genomics suggest a generalized trajectory for the evolution of complex multicellularity, beginning with the co-optation of existing genes for adhesion. Molecular channels to facilitate cell-cell transfer of nutrients and signaling molecules appear to be critical, as this trait occurs in all complex multicellular organisms but few others. Proliferation of gene families for transcription factors and cell signals accompany the key functional innovation of complex multicellular clades: differentiated cells and tissues for the bulk transport of oxygen, nutrients, and molecular signals that enable organisms to circumvent the physical limitations of diffusion. The fossil records of animals and plants document key stages of this trajectory.

INTRODUCTION

Complex multicellular organisms dominate the space in which we live. Plants, animals, and macroscopic fungi pattern terrestrial landscapes, whereas animals and seaweeds animate the sea. Complex multicellularity arose relatively late in the history of life, entering the fossil record during the Ediacaran Period, more than three billion years after microbial life began to diversify. But what do scientists actually mean by complex multicellularity? How are complex multicellular organisms distinguished structurally, functionally, and genetically from simple multicellular life? And how do these distinguishing features help us to interpret the early fossil records of complex organisms?

These are the questions that motivate this review. Fortunately, as complex multicellularity has arisen independently within several eukaryotic clades, we can approach key issues from a comparative standpoint, integrating phylogeny, genetics, and the fossil record. What commonalities unite complex multicellular organisms, and which appear to be clade specific?

SIMPLE VERSUS COMPLEX MULTICELLULARITY

Simple multicellular organisms include filaments, clusters, balls, or sheets of cells that arise via mitotic division from a single progenitor; differentiation of somatic and reproductive cells is common, but more complex patterns of differentiation are not. Although simple multicellular eukaryotes have diverse origins, most share several properties. Adhesive molecules (or, as in some filamentous diatoms, simple interlocking of wall protuberances) connect the products of successive cell divisions to form a coherent and reproducible morphology. However, communication between cells and the transfer of resources from one cell to another is commonly limited. The multicellular state is both functional and persistent in these organisms, and it appears to confer selective advantage in deterring protistan predators (e.g., Boraas et al. 1998), maintaining position on a substrate or within the water column, or directing fluid flow to facilitate feeding. Key to the explicitly biophysical perspective adopted here is that essentially every cell in simple multicellular organisms lies in direct contact with the external environment, at least during phases of the life cycle characterized by nutrient acquisition and active metabolism (Knoll & Hewitt 2011).

Complex multicellular organisms show not only evidence of cell-cell adhesion but also intercellular communication and, commonly, tissue differentiation mediated by networks of regulatory genes. Programmed cell death occurs in a number of these groups, but unprogrammed cell or tissue loss can be lethal—perhaps more so in metazoans than in other groups with persistent stem cells. Notably, complex multicellular organisms display a three-dimensional organization in which only some cells are in direct contact with the environment. This organization is critically important for organismic function because it introduces transport problems for oxygen, nutrients, and signaling molecules that are required by internal as well as external cells (Schlichting 2003, Beaumont 2009, Knoll & Hewitt 2011). As discussed below, complex multicellular organisms have evolved structures that circumvent the limitations of diffusion, including both molecular conduits for cell-cell communication and tissues that facilitate bulk transport. Indeed, the circumvention of diffusion can be considered a physiological key to the evolutionary success of complex multicellular life (Knoll & Hewitt 2011).

In a recent review of eukaryotic diversity, Adl et al. (2007) recognized 119 major clades, with the possibility of more high-level diversity among poorly characterized (largely unicellular) taxa not included in their analysis. Of these, 83 contain only unicells, whereas 36 include species that are characterized by simple multicellularity, the product of at least 22 independent origins. *Volvox carteri*, a simple multicellular green alga, provides a genetic hint to the relative ease by which simple multicellularity can evolve (Grosberg & Strathmann 2007); its genome differs only in minor ways from that of its close unicellular relative *Chlamydomonas reinhardtii* (Prochnik et al.

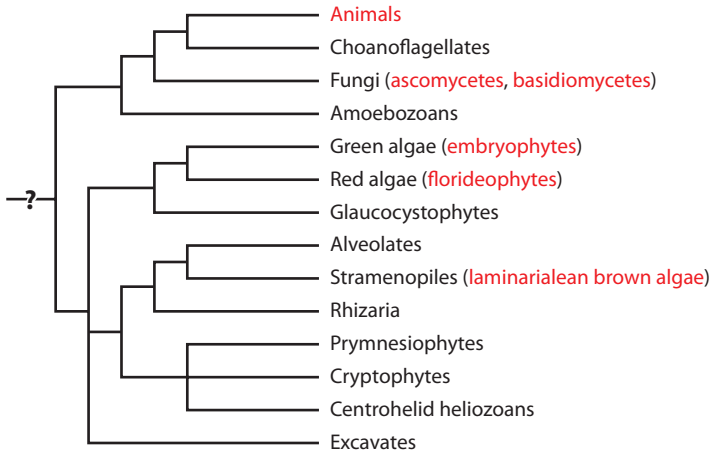

Figure 1

Eukaryotic phylogeny, showing the positions of complex multicellular organisms (*red*).

2010). In contrast, the genomes of mosses and flowering plants encode three to four times as many protein domains as *V. carteri* and *C. reinhardtii* (Prochnik et al. 2010).

Genomic differences suggest that the evolutionary hurdle to complex multicellularity is relatively high, and phylogeny corroborates this view. Complex multicellularity has evolved only six times: within the animals, embryophytic land plants, florideophyte red algae, laminarialean brown algae, basidiomycete fungi, and ascomycete fungi (**Figure 1**). [An additional origin within the fungi is possible, depending on the phylogenetic position of the complex genus *Neolecta* (Schoch et al. 2009).] All but the animals have known sister groups characterized by simple multicellular organization.

REQUIREMENTS FOR COMPLEX MULTICELLULARITY

The Eukaryotic Cell as the Substrate for Complex Multicellularity

Simple multicellularity exists within the Bacteria. Many cyanobacteria, for example, form filaments containing dozens if not hundreds of cells, and some differentiate multiple cell types (e.g., Rossetti et al. 2010). A few myxobacteria even aggregate to form macroscopic fruiting bodies with differentiated cells (Velicer & Vos 2009). Despite this, complex multicellularity, as defined here, occurs only in the Eukarya. What features of eukaryotic cells provide the evolutionary substrate for complex multicellularity, and what features, in particular, unite clades containing complex multicellular organisms and separate them from other eukaryotes?

A fundamental feature of eukaryotes is the dynamic cytoskeletal and membrane system that governs morphological patterning in cells. This system enables eukaryotes to package signaling molecules in endosomes, tiny vacuoles that bud from surface membranes, and transport them through the cell by means of molecular motors at rates much faster than would be possible by diffusion alone (Scita & di Fiore 2010). As a result, eukaryotic cells can change shape or physiology in response to molecular signals, permitting processes such as phagocytosis, amoeboid locomotion, and permanent cell differentiation (Fletcher & Mullins 2010). Together, the dynamic cytoskeleton and membrane system of eukaryotic cells open up possibilities of size, structure, function, and development not available to prokaryotic organisms.

Cell differentiation is widespread among eukaryotes and is not limited to multicellular clades—many unicellular protists differentiate distinct cell morphologies in the course of their life cycles. Commonly, for example, environmental stress (e.g., nutrient deprivation, hypoxia) induces spore formation in eukaryotic unicells. Increasing research indicates that this cell differentiation is induced by reactive oxygen species formed in response to environmental cues (Aguirre et al. 2005). Protists can also undergo programmed cell death in response to environmental stress (Bidle & Falkowski 2004, Deponte 2008, Nedelcu 2009). Thus, two processes critical to the development of complex multicellular organisms—cell differentiation and programmed cell death—originated in unicellular eukaryotes early in the evolutionary history of the domain.

The genomic architecture of eukaryotic cells may also facilitate accumulation of the regulatory genes central to cell differentiation and development. In Bacteria and Archaea, rates of cell division are limited by the speed of DNA replication, at least for replication times beyond those required to complete other processes involved in binary fission. As this involves replication of a single circular chromosome from one or a very few initiation sites, advantage accrues to streamlined genomes. Because eukaryotic genomes replicate from a potentially large number of initiation sites in multiple chromosomes, the accumulation of genes for signaling molecules, transcription factors, and regulatory RNA carries no comparably large burden. Indeed, in complex multicellular organisms, replication speed is divorced from reproductive success. In a new and different line of reasoning, Lane & Martin (2010) have recently proposed that bacterial genome size is also limited by bioenergetics, a constraint lifted in eukaryotes by mitochondria.

Finally, it has been proposed that simple multicellularity may be linked to eukaryotic cell architectures in which the same microtubules are used for locomotion and mitosis (Margulis 1981, Buss 1987). Nascent multicellularity provides a solution: two daughter cells adhere to one another; one remains totipotent, whereas the other differentiates terminally into a locomotory cell. Complex multicellularity, however, requires something more.

Complex Multicellularity Requires Adhesion, Communication, and a Developmental Program

A fundamental feature of complex multicellular organisms is the molecular adhesion that governs formation of a distinctive and reproducible multicellular morphology. In animals, cell adhesion is mediated by a battery of proteins, including those that give rise to epithelia (tightly controlled sheets of oriented cells that underpin tissue function) (Cereijido et al. 2004). Plants, in contrast, use pectins and, perhaps, hemicelluloses to mediate cell-cell adhesion (Roberts & Gonzalez-Carranza 2007, Ordaz-Ortiz et al. 2009).

All cells have transmembrane receptors that mediate signals from the environment. Complex multicellular organisms, however, have an additional path for cell-cell communication in the form of microscopic passageways across cell walls and membranes. These passageways facilitate electrical, metabolic, and signal communication between cells and do so in spatially specific, or targeted, ways. In plants and complex brown algae, these ultrastructural connectors are plasmodesmata, ER-linked strands of cytoplasm that link adjacent cells through minute holes in cell walls (Lucas et al. 2009). Similarly, cells in florideophyte red algae are joined by protein-plugged pores called pit connections (Pueschel 1990), and pores of varying complexity bridge the walls between cells in ascomycete and basidiomycete fungi (e.g., Markham 1994). Communication between adjacent animal cells is enabled by gap junctions, proteinaceous channels that mediate transport of ions and molecules across cell membranes (Elias & Kriegstein 2008). Of course, intercellular signals underpin multicellular development, as signaling molecules generated in one cell can inhibit or facilitate gene expression in others.

Indeed, the development of complex multicellular organisms requires a genetic program in which well-defined molecular signaling networks interact in time and space. Signaling by reactive oxygen species, already introduced in association with life-cycle differentiation among protists, finds use in both plant (Foyer & Noctor 2005) and animal (Fisher & Burggren 2007) development. And the regulatory genetic networks that govern animal development (Davidson 2006) also find counterparts in plants, which employ similar regulatory logic but use largely unrelated gene families (Meyerowitz 2002).

Circumventing Diffusion

Early in the past century, Krogh (1919; see also Runnegar 1991) noted that where oxygen is supplied to tissues by diffusion alone, size is limited by ambient pO_2. At present-day oxygen levels, diffusion-limited organisms should attain cell or tissue thicknesses of, at most, a few millimeters. Obviously, many organisms are larger than this, suggesting that they have cellular or multicellular mechanisms to transport oxygen. Animals illustrate distinct ways by which larger size can be achieved in the face of diffusional limitation. Porifera, or sponges, are highly porous organisms in which most cells lie in direct contact with circulating waters; the material between inner and outer surface layers, called mesohyl, is largely acellular. Coordinated flagellar movement facilitates water flow across cell surfaces, as does the structure of internal canals and, in some sponges, contraction of epithelia-like cell sheets that line the body (Leys et al. 2009). Cnidaria, the phylum that includes sea anemones, corals, and jellyfish, also grow large by elaborating thin sheets of metabolically active tissues; commonly, the thicker parts of cnidarians are metabolically inert, for example, the mesogloea, or "jelly," of jellyfish. In most bilaterian animals, however, well-developed respiratory and circulatory systems facilitate gas exchange and the transport of oxygen through the body. This bulk transport of oxygen, nutrients, and hormones underpins the functional biology, and therefore the extraordinary diversity, of bilaterian animals. There are perhaps 20,000 species of sponges and cnidarians, but up to 10 million bilaterian species.

Plants have also evolved tissues for bulk transport; the xylem of vascular plants transports water upward through the stem, whereas phloem sustains long-distance transport of nutrients and molecular signals (Evert & Eichhorn 2006). The complex functionality that results from these tissues has major consequences for diversity—the close algal relatives of land plants have a few to a few thousand species, whereas embryophytes (vascular plants, mosses, and their relatives) may have as many as half a million. Laminarialean brown algae, the largest of all primary producers in the sea, also differentiate specialized cells, called trumpet hyphae, to transport photosynthate though distances as long as 10 m or more (Buggeln 1983).

Chicken and Egg, or Positive Feedback?

Theorists have paid much attention to the origins of simple multicellular organisms (Buss 1987, Pfeiffer & Bonhoeffer 2003, Michod 2007, Willensdorfer 2009). Much less attention has been given to the evolution of complex multicellularity, although this is clearly where key questions of diversity and ecological success lie. It has been proposed that (relatively) large size is a prerequisite for complex multicellular organization, but it would also appear that large organisms with three-dimensional tissues require differentiated structures for the transport of oxygen, nutrients, and molecular signals. Like many chicken and egg problems, this one is best addressed in terms of positive feedbacks (Knoll & Hewitt 2011). An increase in the size of a three-dimensional multicellular eukaryote will necessarily increase surface-to-interior gradients of oxygen and nutrients. Given the importance in protists of nutrient deprivation and hypoxia as signals for cell differentiation,

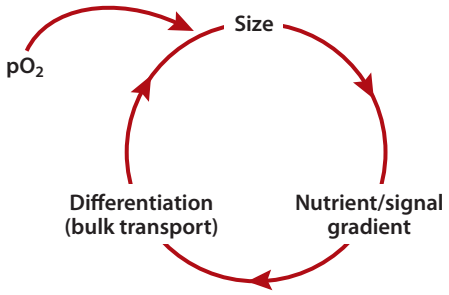

Figure 2

Diagram illustrating how increasing oxygen availability could potentiate a positive feedback cycle involving size, nutrient/signaling gradients, and cell differentiation (including cell and tissue differentiation that facilitates bulk transport), leading to complex multicellularity.

these gradients may induce differentiation of interior cells. And when cell differentiation includes products that facilitate intercellular communication and transport, larger size is made possible. Repeated passage through such a feedback loop could give rise to complex multicellular organisms (**Figure 2**).

Beaumont (2009) has proposed that bulk transport in animals originated when early, gastrula-like metazoans evolved the physiological capacity to pump molecules into a fluid-filled space lined by epithelium. This innovation allowed external feeding cells to transfer nutrients and signals not just to physically adjacent cells but to a much larger cell population in contact with the fluid. Further increases in size were made possible by more highly specified circulatory systems and the evolution of molecules to bind and transport oxygen (Fisher & Burggren 2007).

How might such a feedback loop be activated? A simple way would be to increase pO_2. Increasing ambient oxygen would increase the permissible size of a diffusion-limited multicellular organism, and this, in turn, would allow a given exterior-interior oxygen gradient to be maintained while steepening gradients in nutrient concentration and signaling molecules generated at the surface. Moreover, increasing oxygen should increase oxidative stress, altering the chemical landscape of reactive oxygen species capable of inducing cell differentiation (Lesser 2006). Thus, for both biophysical and developmental reasons, one might predict that increasing oxygen in the atmosphere and oceans should promote increasing complexity of multicellular organisms (e.g., Blackstone 2000). Oxygen may not have jump-started all complex multicellular clades, but as discussed below, at least five independent lines of evidence tie increasing oxygen levels to the Ediacaran radiations of animals and complex red algae.

LAYING THE GROUNDWORK: NEOPROTEROZOIC PROTISTAN EVOLUTION

If complex multicellularity requires the cellular and genetic architecture provided by eukaryotic cells, then the earliest fossils of plants and animals must rest on a prior history of protistan evolution. Molecular clocks uniformly suggest that metazoans began to diversify long before animals first entered the fossil record. Some indicate an improbably long metazoan prehistory, longer than the animal fossil record (e.g., Blair et al. 2005), but even those in closest accord with paleontology indicate that sponges began to diverge at least 800–750 Ma (Peterson et al. 2008, Lartillot et al. 2009, Sperling et al. 2010b). The date of 800 Ma appears repeatedly in molecular estimates of eukaryotic diversification. For example, Berney & Pawlowski (2006) propose that although

eukaryotes as a whole originated earlier, animals, fungi, red algae, green algae, and a large clade made up of rhizarians, stramenopiles, and alveolates all began to diversify 800 ± 100 Ma. Lücking et al. (2009) and Zimmer et al. (2007) favor similar timescales for fungal and green algal divergences, respectively.

In fact, eukaryotic fossils show a marked increase in diversity ca. 800 Ma (Knoll et al. 2006). More than a dozen taxa of distinctive and easily fossilizable tests ascribed to lobose amoebae and other protists occur widely in ca. 800–740 Ma rocks but not, as far as we know, earlier (Porter et al. 2003). At least two dozen morphospecies of microscopic scales that armored early protists occur abundantly in carbonate rocks radiometrically constrained to be 811.5 ± 0.25–716.47 ± 0.24 Ma (Allison & Hilgert 1986, MacDonald et al. 2010). Diverse organic-walled protists, including simple multicellular organisms, have been recorded widely in cherts and shales from this interval (Butterfield et al. 1994; Butterfield 2004, 2005a,b). In addition, steranes, which are molecular fossils derived from sterols synthesized by eukaryotes, first occur in abundance at approximately 750–800 Ma (Brocks 2009).

Numerous Neoproterozoic fossils have been compared with extant protists, including siphonocladalean green algae (Butterfield et al. 1994), amoebozoans (Porter et al. 2003), euglyphid rhizarians (Porter et al. 2003), and stramenopile algae (Xiao et al. 1998, Butterfield 2004). Some of these attributions may be correct (e.g., *Cladophora*-like green algae and *Arcella*-like amoebozoans), but much younger molecular clock estimates for other clades suggest that many Neoproterozoic fossils are better regarded as extinct stem-group members of their respective clades (Berney & Pawlowski 2006, Cavalier-Smith 2006, Silberfeld et al. 2010). If so, however, characters such as scale formation, test synthesis, and coenocytic organization evolved earlier than might be implied by their distribution in extant taxa.

Both microfossils and simple macrofossils of eukaryotic origin occur in rocks 1800–1400 Ma (Javaux et al. 2004, Knoll et al. 2006), but their relationships to extant clades are uncertain, and they may well represent stem-group eukaryotes. Putative fossils of macroscopic multicellular organisms have also been described from 2100 Ma rocks in Gabon (El Albani et al. 2010), but whether these record true multicellularity or colonies, eukaryotes or bacteria, or even fossils as opposed to abiotic structures remains to be seen. The oldest fossil population assigned to a crown group eukaryotic clade is *Bangiomorpha*, simple multicellular fossils with differentiated holdfasts and reproductive cells, preserved in silicified lagoonal carbonates from Arctic Canada (Butterfield 2000). Published radiometric constraints define only a broad depositional window—1267 ± 2–723 ± 3 Ma—however, sequence stratigraphy and an unpublished Pb-Pb date of 1198 ± 24 Ma suggest that *Bangiomorpha*'s true age lies near the lower age constraint. If so, this would suggest that major branches of the eukaryotic tree began to diverge earlier than 1000 Ma (i.e., crown group eukaryotes existed), but that little recognizable diversity accrued within these branches for several hundred million years.

Why should diversification within eukaryotic clades postdate the origin of the domain by so long? The answer remains uncertain, but recent geochemical data point in a promising direction. For much of the Proterozoic Eon, moderately oxic surface waters in the world's oceans were underlain by an oxygen minimum zone that was commonly both anoxic and enriched in sulfide (Anbar & Knoll 2002). At approximately 800 Ma (perhaps a bit earlier, but not much later), sulfidic water masses began to recede, replaced by subsurface waters that were anoxic but ferruginous (Canfield et al. 2008, Johnston et al. 2010). Sulfide is generally toxic to eukaryotes; thus, decay of euxinic water masses in Neoproterozoic oceans may have removed a barrier to the spread of eukaryotic cells (Martin et al. 2003, Johnston et al. 2010). This, of course, leaves open the possibility that some eukaryotic clades diversified earlier in nonmarine environments less well sampled by the sedimentary record.

Regardless of systematic relationships, Proterozoic fossils confirm the phylogenetic inference that simple multicellularity evolved early and often within the Eukarya (Knoll et al. 2006, Butterfield 2009). The basic features of eukaryotic biology that underpin multicellular organization were emplaced well before the Ediacaran Period, and, more to the point, so were at least some of the adhesion and signaling domains critical for complex multicellularity.

THE EARLY EVOLUTION OF ANIMALS

Comparative Biology

In the age of molecular phylogeny, many aspects of animal phylogeny have become clear, although uncertainty remains about some critical points (**Figure 3**). On the key question of animal relationships to other eukaryotes, molecular data confirm what many biologists have thought since the late nineteenth century: The single-celled choanoflagellates are sister to the metazoans (Carr et al. 2008). Most molecular data also confirm that sponges diverged from the base of the animal tree. Whether sponges comprise a monophyletic sister group to all other animals (**Figure 3**) or a paraphyletic group from which other animals emerged is still debated (Phillipe et al. 2009, Sperling et al. 2009). The monophyly of bilaterian animals, however, is strongly supported. Three additional clades are key to discussions of early animal evolution: the Cnidaria, Ctenophora, and Placozoa. The phylogenetic position of the ctenophores remains uncertain (e.g., Marshall & Valentine 2010), but leaving them aside, genomic data support the placement of cnidarians as sister to bilaterian animals and placozoans as sister to the Cnidaria plus Bilateria (termed Eumetazoa; Srivastava et al. 2010).

An increasing number of genomes enables us to begin trimming the animal tree with genes that govern adhesion, communication, and development (**Figure 3**). For example, genomic research

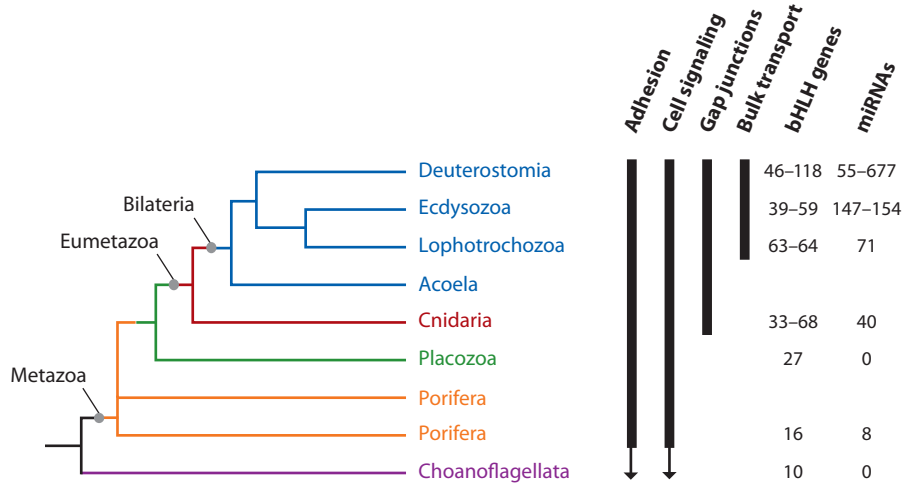

Figure 3

Metazoan phylogeny (after Marshall & Valentine 2010), showing the phylogenetic distribution of key molecular, cellular, and physiological characters that collectively underpin complex multicellularity in animals (Nichols et al. 2006, Shalchian-Tabrizi et al. 2008, Sebè-Pedrós et al. 2010, Srivastava et al. 2010). bHLH gene numbers exemplify the increasing diversity of transcription factors from choanoflagellates to bilaterians (Degnan et al. 2009); microRNA (miRNA) diversity shows a similar pattern of increase along the path to bilaterians (Technau 2009).

shows that the key families of animal adhesion genes occur in sponges and so must have evolved early in animal evolution (Nichols et al. 2006, Srivastava et al. 2010). Indeed, basic components of these systems occur in choanoflagellates (King et al. 2008) and even deeper in the eukaryotic tree. Components of the integrin adhesion complex have been identified in *Ministeria vibrans*, part of the sister clade to animals plus choanoflagellates (Shalchian-Tabrizi et al. 2008), and, more recently, in apusozoans (Sebè-Pedrós et al. 2010), unicellular eukaryotes thought to be a sister group to fungi, animals, and their unicellular sisters. The function of these proteins in unicellular organisms is not known, but their phylogenetic distribution suggests that the multicomponent integrin complex was assembled through time, coming together in essentially modern form in the immediate ancestors of animals and their closest relatives (Sebè-Pedrós et al. 2010).

Similar to adhesion molecules, signaling proteins that mediate cell-cell communication have deep phylogenetic roots. For example, tyrosine kinases, key components of cell-cell signaling in animals, have been identified in choanoflagellates, where they are more diverse than in metazoans (Manning et al. 2008). Only 4 of the 128 tyrosine kinase genes found in the choanoflagellate *Monosiga brevicollis* have orthologs in animals, but these (and their receptors) show evidence of marked diversification between the last common ancestor of animals and choanoflagellates and the divergence of sponges. The six other signaling families key to metazoan development have not been found in choanoflagellates but do occur in sponges (Nichols et al. 2006, Srivastava et al. 2010); some of their constituent protein domains have been identified in *Ministeria* and other groups closely related to animals plus choanoflagellates (Shalchian-Tabrizi et al. 2008).

To cite another example, the Notch pathway contains numerous proteins that interact to effect signaling in animals. Gazave et al. (2009) tracked 22 of its constituent genes across 35 sequenced eukaryotes. Only four of these genes are restricted to bilaterians, and only nine occur exclusively in metazoans, but these include the Notch ligand and receptor, key components of the signaling mechanism. The Notch protein appears to be found only in metazoans, but its three constituent domains all occur individually in earlier diverging eukaryotes. Gazave et al. (2010, p. 3) state the case succinctly, "... while the Notch pathway is a metazoan synapomorphy, it has been assembled through the co-option of premetazoan proteins, and their integration with novel metazoan-specific molecules acquired by various evolutionary mechanisms."

Major transcription factors employed in metazoan development similarly show a pattern of early appearance and later diversification. ANTP, Pax, and other gene classes have been found in sponges, but with only a few genes per class; these gene families show more diversity in eumetazoans, as do microRNAs, which are known to play important roles in animal development (**Figure 3**; Grimson et al. 2008, Wheeler et al. 2009). In general, as stressed by Degnan et al. (2009), the molecules that guide animal development include core elements inherited from protistan ancestors, new gene families, complex adhesion and signaling pathways established in the ancestors of sponges, and further expanded gene families that evolved in the immediate ancestors of eumetazoans. How is the evolutionary pattern reflected in early metazoan fossils?

The Fossil Record of Early Metazoans

Phylogenetic inference might predict that the earliest animal record should be dominated by sponges, but this does not appear to be the case. Porifera make up a limited proportion of Ediacaran macrofossils (Gehling & Rigby 1996), although a possible sponge occurs locally in the oldest (579–565 Ma) Ediacaran assemblages (Sperling et al. 2010a). In part, the apparent dearth of sponges may be taphonomic. Mineralized spicules are rare or absent from Ediacaran rocks, and unmineralized sponges do not preserve well in rocks of any age [but see Sperling et al. (2009), who argue for an early origin of siliceous spicules]. Alternatively, early sponges may have been tiny, epithelia-clad

organisms, more comparable to the larvae of living sponges (Degnan et al. 2005) than to adults. Fossil steranes interpreted as products of demosponge biosynthesis occur in relative abundance in Ediacaran strata and have been reported from rocks more than 635 Ma (Love et al. 2009). Other reports of pre-Ediacaran sponges rest on unusual textures in earlier carbonate rocks (Neuweiler et al. 2009, Maloof et al. 2010); these fabrics fall short of compelling demonstration, but show that there is much to be gained from a systematic exploration of 700–800 Ma carbonates.

Much more abundant and diverse are modular macrofossils grouped together as vendobionts by Seilacher (1992). There is no reason to view vendobionts as monophyletic, although they include several monophyletic groups, including rangeomorphs and dickinsonids (e.g., Narbonne 2004). Some of these were originally interpreted as sea-pen-like colonial cnidarians anchored to the Ediacaran seafloor, but the Ediacaran fossils tend to lack morphological features consistent with a cnidarian interpretation (Narbonne 2004, Antcliffe & Brasier 2007, Laflamme & Narbonne 2008, Xiao & Laflamme 2009), including oral openings and tentacles. An alternative interpretation holds that vendobiont fossils accurately capture their main morphological features—if oral openings, tentacles, and other attributes are missing, it is because they were never present. It is hard to envision vendobiont development in the absence of epithelia, but their anatomy may not have been much more complicated (Laflamme et al. 2009, Sperling & Vinther 2010). Leaving phylogeny aside, then, a focus on function suggests that vendobiont-type organisms may have been modular structures with units made of upper and lower epithelia that lined a fluid-filled or mesogloea-like interior. Feeding is hypothesized to have been by phagocytosis and/or absorption of dissolved organic molecules. In short, many complex Ediacaran macrofossils appear to share more features with placozoans than they do early sponges or cnidarians (Sperling & Vinther 2010).

Care is advisable when pursuing the placozoan comparison. *Trichplax adhaerens*, the sole placozoan described to date, has neither basal lamina nor extracellular matrix (Schierwater 2005); thus, it lacks key features of the epithelia found in eumetazoans. The likely presence of epithelia in Ediacaran taxa suggests that many of these fossils are best viewed not strictly as giant placozoans, but rather as stem-group eumetazoans (see also Buss & Seilacher 1994, Sperling & Vinther 2010)—simply organized absorption feeders whose closest functional and anatomical counterpart among living animals is the diminutive (relict?) *Trichoplax*.

If so, this suggests a different explanation for the dearth of sponges and cnidarians in Ediacaran rocks—perhaps placozoan-grade organisms were among the first macroscopic metazoans to spread across the shallow seafloor, with preservable sponges and cnidarians gaining ecological prominence later. The oldest Ediacaran macrofossil assemblages, well dated at 579–565 Ma, are dominated by rangeomorph taxa (**Figure 4**; Bamforth & Narbonne 2009, Narbonne 2004, Narbonne et al. 2009).

Ediacaran rocks of broadly comparable age in China contain beautifully preserved microfossils interpreted as metazoan eggs and embryos (**Figure 4**; Xiao & Knoll 2000). These fossils lack the distinguishing features of sponge and most eumetazoan embryogenesis and so have been interpreted as stem-group metazoans (Hagadorn et al. 2006). However, the Chinese fossils have much in common with interpreted eggs and embryos of *Trichoplax* (Grell 1972, Srivastava et al. 2008), thus paralleling and perhaps corroborating interpretations of vendiobiont-type macrofossils.

Microfossils also shed light on early metazoan life cycles. Large (commonly >200 μm), highly ornamented microfossils in earlier Ediacaran successions have been interpreted as the egg or diapause cysts of animals with an inducible resting stage in their life cycle (**Figure 4**; Cohen et al. 2009). By convention, organic-walled microfossils with spiny projections have been interpreted as algae; however, the combination of size, morphology, wall ultrastructure, and internal contents of these fossils rule out algae known to make resting cysts. Animal cysts, however, match the fossil populations in all criteria. Cohen et al. (2009) suggested that episodic anoxia on earlier Ediacaran

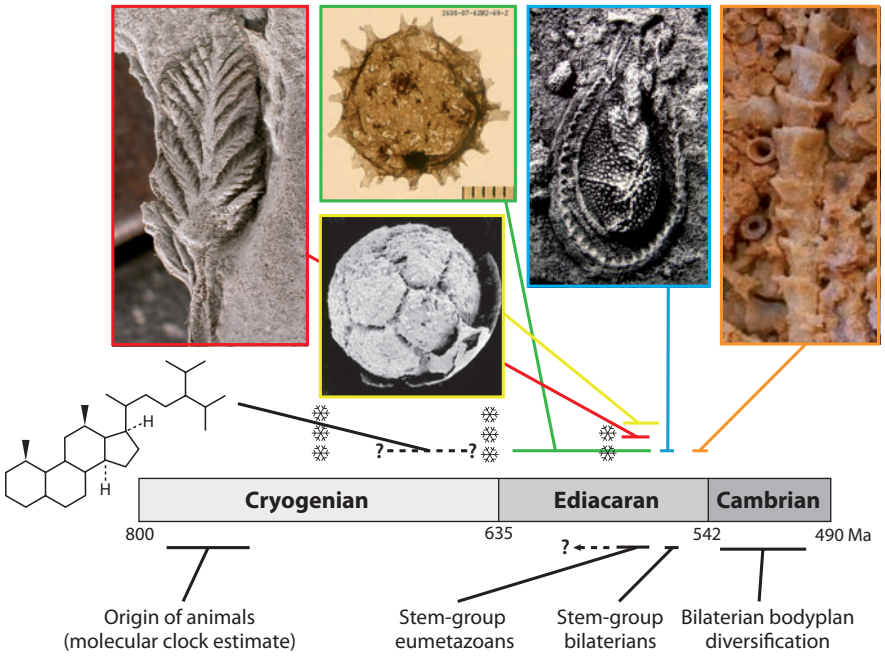

Figure 4

The geologic record of early animal evolution. Fossils, from left to right, include the structure of 24-isopropyl-cholestane, a molecular fossil attributed to demosponges (courtesy of Roger Summons); a rangeomorph vendobiont from 579–565 Ma deposits in Newfoundland (courtesy of Guy Narbonne); an organic cyst, interpreted as the egg or diapause cyst of an early animal, from <560 Ma shales in Russia; early cleavage stage embryo from 580–560 Ma phosphorite in China; *Kimberella*, the earliest known bilaterian, from 560–555 Ma rocks in Russia (courtesy of M.A. Fedonkin); and *Cloudina*, an early skeleton-forming animal, possibly related to the Cnidaria, from <549 Ma beds in Spain (courtesy of Sören Jensen and Iván Cortijo). Snowflake patterns indicate widespread glaciations.

seafloors would have favored early animals able to form resting cysts, and this view is supported by geochemical analyses that indicate a shift from variable but commonly anoxic seafloors to more stable, oxic conditions at the stratigraphic level where the cysts largely disappear (D.T. Johnston, T. Goldberg, S.W. Poulton, V.N. Sergeev, V. Podkovyrov, N.G. Vorob'eva, A. Bekker & A.H. Knoll, unpublished manuscript). Yin et al. (2007) found early cleavage stage embryos in at least one morphospecies of these microfossils, linking the organic cysts to phosphatized embryos. Thus, at least some of the sponge- and placozoan-like animals of early Ediacaran shelf communities appear to have maintained life cycles that facilitated persistence on variably oxic seafloors.

If this emerging picture of older Ediacaran metazoans is correct, the genetic leap from choanoflagellates to animals had already taken place by 579–565 Ma, resulting in macroscopic sponges, placozoan-like forms, and basal eumetazoans with diverse genes for cell-cell adhesion and signaling molecules (**Figure 4**). Functionally, these earliest Ediacaran animals gained nutrition by adsorption and phagocytosis and were still broadly limited by diffusion.

Short (<17.5 mm) trace fossils indicate additional diversity in rocks a bit younger than 565 Ma (Liu et al. 2010). It is difficult to exclude large coenocytic protists as the makers of these traces, but Liu et al. (2010) note their similarity to sea anemone trails produced experimentally. Thus, divergence of the main eumetazoan clades may have begun by this time. By 560–555 Ma, divergence was certainly underway; rocks of this age contain both fossils (Fedonkin 2007) and trace fossils

(Jensen et al. 2006) of motile macroscopic bilaterians in low diversity. The best known example, *Kimberella* (Fedonkin 2007), shares many features with mollusks, although in toto its preserved characters suggest a stem-group bilaterian. Functionally, these animals must have had coordinated muscles capable of sustained locomotion, a digestive system for processing food captured using a radula-like oral apparatus, and a circulatory system that freed *Kimberella* from diffusional constraints (**Figure 4**). Slightly younger (ca. 549 Ma) rocks contain evidence of template-directed carbonate biomineralization, perhaps in part by cnidarians (**Figure 4**; Grant 1990, Grotzinger et al. 2000).

Thus, by the last 10–15 million years of the Ediacaran Period, the principal genetic and functional prerequisites for bilaterian diversification appear to have been in place. Only in Cambrian rocks, however, do fossils record the diversification of bilaterians, cnidarians, and sponges that herald the modern marine fauna. During the long interval traditionally regarded as early Cambrian (32 million years, from 542 to 510 Ma), recognizable bilaterian bodyplans took shape. Most of these, however, still belong to stem-group members of animal phyla or classes; only during the subsequent Ordovician Period did marine faunas come to be dominated by crown group bivalves, gastropods, echinoderms, and other bilaterian clades that populate the present-day ocean (Budd & Jensen 2000).

As noted above, geochemistry suggests that the Ediacaran Period was a time of environmental as well as biological transition. As early as 1992, Derry et al. modeled rates of organic carbon burial, based on carbon and strontium isotopes, and concluded that the interval 580–560 Ma was a time of unusually high organic carbon burial and, hence, a probable time of increasing pO_2. Data from sulfur isotopes also support the hypothesis that atmospheric oxygen levels increased 580–560 Ma (Canfield & Teske 1996, Fike et al. 2006), and more recently, the abundance (Scott et al. 2008) and isotopic composition (Dahl et al. 2010) of molybdenum have been employed as proxies for marine redox state, further corroborating the view that oxygen-rich water masses expanded at this time. Independently, the iron chemistry of marine mudstones indicates widespread ventilation of deep ocean basins beginning at approximately 580 Ma (Canfield et al. 2007, Shen et al. 2008) and increased stability of oxic shelf environments by 560 Ma (D.T. Johnston, T. Goldberg, S.W. Poulton, V.N. Sergeev, V. Podkovyrov, N.G. Vorob'eva, A. Bekker & A.H. Knoll, unpublished manuscript). Water masses that washed the late Ediacaran seafloor were richer in oxygen and more predictably oxic than those of previous eras. Thus, consistent with the feedback model outlined above, the genetic innovations that underpin complex multicellularity in animals passed through an environmental gate mediated by oxygen.

THE EARLY EVOLUTION OF COMPLEX MUTLICELLULARITY IN PLANTS

Land plants provide a second instance of complex multicellularity that can be approached through the integration of fossils, phylogeny, and genetics. Plant evolution involves both an environmental shift (from water to land) and the intercalation of a new multicellular generation (the diploid sporophyte), complicating comparisons to early animals. Nonetheless, the grand themes of adhesion, communication, development, and the circumvention of diffusion are apparent, suggesting important commonalities in independent origins of complex multicellularity.

Comparative Biology

Green algal phylogeny traces a clear evolutionary path from unicells to complex multicellularity (**Figure 5**). Molecular phylogenies show that greens first diversified as flagellated unicells (the

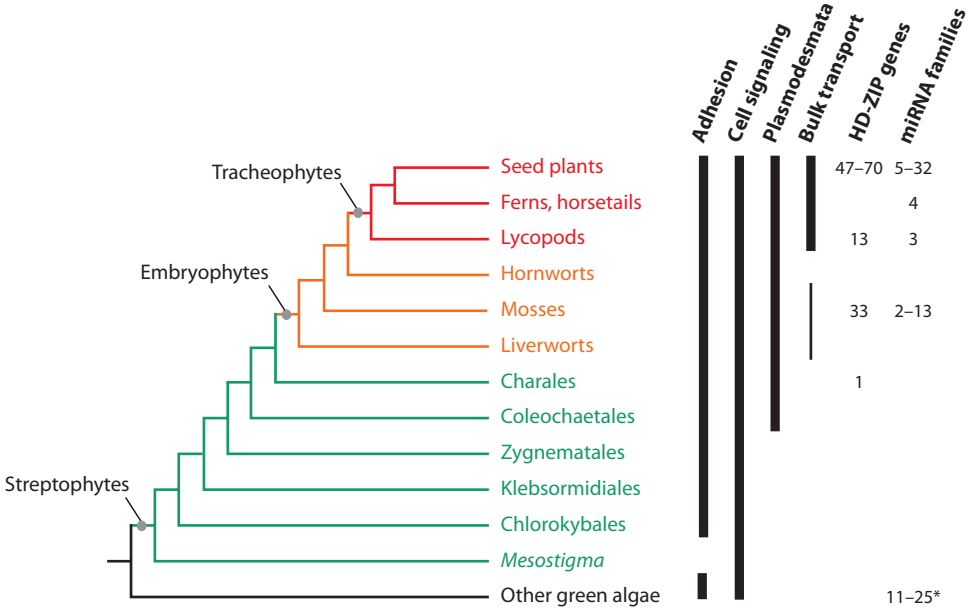

Figure 5

Streptophyte and embryophyte phylogeny (after Lewis & McCourt 2004, Qiu et al. 2006) showing the phylogenetic distribution of key molecular, cellular, and physiological characters that collectively underpin complex multicellularity in vascular plants (Cook et al. 1997, Raven 1997, Floyd & Bowman 2007, Eder & Lütz-Meindl 2010). HD-ZIP (homeodomain/leucine zipper) gene numbers exemplify the increasing diversity of transcription factors from green algae to seed plants (Mukherjee et al. 2009); microRNA (miRNA) family diversity shows a similar pattern of increase along the same phylogenetic path (Willmann & Poethig 2007). Asterisk: The miRNA molecules reported for nonstreptophyte green algae come from *Chlamydomonas reinhardtii*, *Ostreococcus tauri*, *Ostreococcus lucimarinus*, and *Volvox carteri*; none of these miRNAs have homologs in embryophytic land plants (Zhao et al. 2007).

paraphyletic prasinophytes) from which two distinct lines of evolution emerged. Simple multicellularity evolved numerous times within the chlorophyte lineage (this is where to find macroscopic green seaweeds as well as the much studied *Volvox*). Embryophytes, however, fall on the other great branch of greens, the streptophytes (Lewis & McCourt 2004).

The freshwater flagellate *Mesostigma viride* lies at the base of the streptophyte branch. Ninety percent of its genes bear close similarity to those in other streptophytes, including *BIP2*-like and *KNOX*-family homeobox genes, both implicated in moss and vascular plant development (Nedelcu et al. 2006, Simon et al. 2006). Similar to the adhesion genes of choanoflagellates, the function of these genes in *M. viride* remains unknown.

More derived streptophytes are multicellular, ranging from the simple soil alga *Chlorokybus* (up to 4 cells); through the (in part) filamentous Zygnematales; to *Coleochaete* and the Charales, multicellular algae characterized by apical growth. The Charales are sister to the embryophytes (Lewis & McCourt 2004).

Much research has focused on the relationships of vascular plants (the Tracheophyta) with three clades traditionally grouped as bryophytes: liverworts, hornworts, and mosses. Whereas streptophyte algae develop multicellular structures only in the gametophytic phase of their life cycles, embryophytes have multicellular gametophytes and sporophytes (Niklas & Kutschera 2010). Vascular plants have a conspicuous, long-lived sporophyte and a variably small gametophyte. In

contrast, the conspicuous generation of bryophytes is the gametophyte. In liverworts and mosses, the sporophyte is an unbranched axis nutritionally dependent on its parent gametophyte; in hornworts, however, the sporophyte is persistently photosynthetic. Multigene phylogenies favor hornworts as sister to the tracheophytes (Qiu et al. 2006). Within vascular plants, the lycopods are sister to the ferns (including horsetails) plus seed plants (**Figure 5**).

Tracing the evolution of adhesion and signaling mechanisms is more difficult in streptophytes than it is among animals and their relatives, in part because fewer key organisms have been sequenced and in part because key molecular processes remain incompletely known. Complete genomes exist for several flowering plants (notably *Arabidopsis thaliana* and cereals), but the genome of the moss *Physcomitrella patens* has also been published, and that of the lycopod *Selaginella moellendorffii* soon will be (Rensing et al. 2008). Genomes exist, as well, for a prasinophyte, a unicellular chlorophyte, and a simple multicellular chlorophyte. Continuing research will undoubtedly target key streptophyte taxa.

At our current state of knowledge, the evolutionary trajectory to complex multicellularity in plants appears to share many features with that leading to animals (**Figure 5**). Some genes, including those critical to adhesion, long predate the divergence of vascular plants (e.g., Eder & Lütz-Meindl 2010). Plasmodesmata, however, are restricted to the embryophytes and their closest algal sisters (Cook et al. 1997, Raven 1997), again linking the capacity for complex multicellularity to ultrastructural conduits between cells.

Signaling molecules and transcription factors also show parallels to animal evolution. Whereas plant development involves gene families largely distinct from those used by animals, tracheophytes do employ receptor-like kinase signaling (de Smet et al. 2009), homeotic genes that code for transcription factors, and microRNAs, perhaps reflecting a molecular toolkit broadly available for co-optation in multicellular patterning. As in animals, some transcription factors predate the origin of embryophytes, including Class HD-Zip III, MIKC-class MADS-box, and ARP2 genes, whereas others appear to have originated along the road from charalean algae to embryophytes (Floyd & Bowman 2007). Many of these families have continued to diversify during the course of vascular plant evolution (Tanabe et al. 2005, Floyd & Bowman 2007, Mukherjee et al. 2009). Similarly, microRNAs have diversified through time (Willmann & Poethig 2007, Axtell & Bowman 2008). As streptophyte algae have no multicellular sporophyte and derived vascular plants have organs not found in earlier diverging plants, the functional roles of regulatory genes have evolved along with their diversity. In short, the sequential evolution of structural and physiological features permitting photosynthetic life on land was paralleled by the evolution of molecules and ultrastructural features to promote adhesion, communication, and development. With the evolution of vascular tissues that facilitated bulk transport, tracheophytes covered the continents in green.

The Fossil Record of Early Land Plants

A good place to begin discussion of early land plants is the Rhynie Chert, paleobotany's answer to the Burgess Shale. Cherts deposited some 400 Ma along the margins of a siliceous hot spring (Rice et al. 2002) preserve a unique record of early embryophyte anatomy and diversity. *Asteroxylon mackiei* (Kidston & Lang 1920) bears the closest resemblance to extant vascular plants, its branching sporophyte vascularized by unambiguous tracheids and covered by helically arranged leaf-like emergences. Many morphological characters mark *A. mackiei* as a stem-group lycopod, indicating that crown-group tracheophytes existed 400 Ma. *Rhynia gwynne-vaughani* was also a vascular plant, but with naked photosynthetic axes, terminal sporangia, and only a thin strand of vascular tissue (**Figure 6**; Kidston & Lang 1917); it is commonly interpreted as a stem-group tracheophyte. *Aglaophyton major* has broadly similar sporophyte morphology, but no true vascular tissue (Edwards

1986), suggesting that it was a stem-group tracheophyte that diverged before interacting processes of tissue differentiation and programmed cell death gave rise to tracheids.

The Rhynie assemblage is doubly remarkable because it preserves gametophytes as well as sporophytes (Remy et al. 1993). The gametophytes are axial in organization, suggesting that developmental programs in the two multicellular generations were not as distinct early on as they are today—perhaps not surprising insofar as the first multicellular sporophytes of necessity employed genes previously expressed in gametophyte development.

Thus, the Rhynie Chert indicates that a moderate diversity of land plants, with morphologies that document several key stages of early tracheophyte evolution, coexisted in terrestrial communities 400 Ma. The succeeding 45 million years of the Devonian Period would witness the evolution of roots, leaves, secondary tissues, and the seed habit, most arising independently in two or more lineages (Boyce 2010). Only toward the end of the Paleozoic, however, would vascular floras come to be dominated by crown-group ferns (leptosporangiate and marattoid) and seed plants.

What came before Rhynie? Stem-group lycopods in upper Silurian rocks (**Figure 6**; Kotyk et al. 2002) extend crown-group tracheophytes back to approximately 420 Ma, and slightly older rocks preserve tiny (millimeter scale) branched axes with terminal sporangia (**Figure 6**). Some of these axes have a vascular strand and so appear to be stem-group tracheophytes (Edwards 2003). Others, however, have no vascular tissue and, in some cases, may have been nonphotosynthetic (Boyce 2008). By approximately 425 Ma, the genetic features that differentiate vascular plants from other embryophytes had begun to accumulate, and the capacity for bulk transport had been established.

Tracing the record backward from this point is challenging, because bryophyte-grade organisms do not preserve well. Charalean algae occur at Rhynie (Kelman et al. 2004) but extend only a

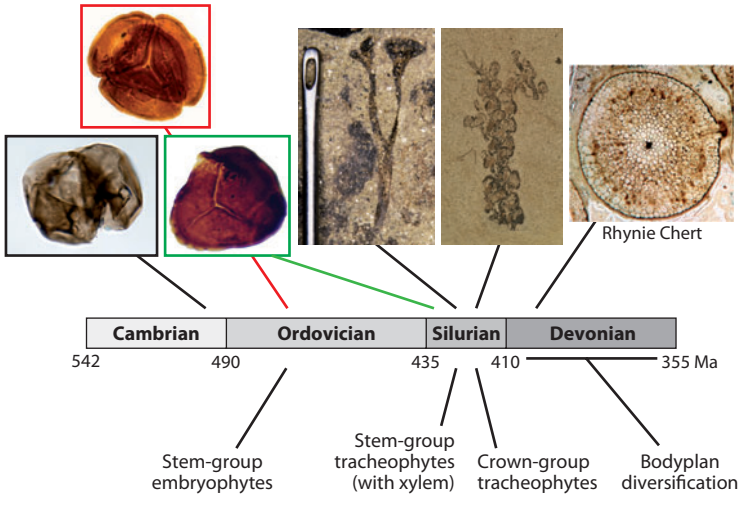

Figure 6

The geologic record of early plant evolution. Fossils, from left to right, include a dyad of a possible early stem-group embryophyte from ca. 500 Ma rocks in the Grand Canyon (courtesy of Paul Strother); Ordovician spore tetrad (courtesy of Charles Wellman); Silurian trilete spore (courtesy of Charles Wellman); *Cooksonia*, the earliest branching sporophytes (copyright Natural History Museum, London, used by permission); cf. *Bathurstia*, a stem-group lycopod from ca. 420 Ma rocks in Canada (courtesy of James Basinger); and a cross section of anatomically preserved *Rhynia*, from the Rhynie Chert, Scotland (courtesy of Hans Steur).

few million years deeper into the past (Feist et al. 2005). What the record does preserve are organic microfossils that illuminate aspects of the earliest embryophyte flora. Principal among these are trilete spores—sporopollenin-impregnated structures that bear a distinctive triradial mark on one face, a consequence of meiotic division to form four tetrahedrally arranged spores. Trilete spores (**Figure 6**) are a synapomorphy of the Embryophyta, so their occurrence in rocks as old as Late Ordovician (450 Ma; Gensel 2008) sets a minimum date for the divergence of embryophytes from charophyte algae.

Persistent cell tetrads, arranged tetrahedrally (**Figure 6**), extend backward to the Early Ordovician (perhaps 470 Ma); some are enclosed by an outer envelope (Wellman & Gray 2000). Liverworts produce obligate spore tetrads, providing a reasonable basis for microfossil interpretation (Wellman & Gray 2000). The enveloped tetrads may record an additional stage of embryophyte origins. A number of green algae, including the Charales, form resting cells by enclosing zygotes in a sporopollenin-impregnated wall. Given that the evolution of desiccation resistance in spores (possibly by redeployment of genes earlier expressed in zygote protection) should logically precede its loss in zygotes, the enveloped tetrads could represent a semi-emergent streptophyte with desiccation-resistant spores but not yet a multicellular sporophyte. Enigmatic dyads in upper Cambrian (500–490 Ma) rocks have been interpreted as still earlier intermediates in the conquest of land—spores formed during meiosporogenesis similar to that of extant *Coleochaete*, but rendered desiccation resistant by sporopollenin (**Figure 6**; Taylor & Strother 2009).

Other microfossils in Ordovician and Silurian rocks include tubes and cuticle-like fragments likely to be the disaggregated remains of bryophyte-grade organisms (Kroken et al. 1996, Graham et al. 2004, Gensel 2008). In sum, organic microfossils tell us that the genetic and morphological gap between streptophyte algae and embryophytes was bridged at least 470 Ma.

BROADER COMPARISONS AND CONCLUSIONS

Phylogeny and fossils suggest that there is no clear line of demarcation between simple and complex multicellular organisms, but comparison of plants and animals suggests a common trajectory along which complex organisms able to circumvent the limitations of diffusion have evolved. In both plants and animals, the path began with adhesion—forming simple (but functional) multicellular structures from a single progenitor cell. In animals, at least, cell-cell adhesion was achieved initially by the co-optation of proteins evolved for other purposes, with increasing diversity and complexity of adhesion complexes accompanying greater morphological complexity.

The next step appears to be key: the evolution of ultrastructural bridges between cells, facilitating the spatially specific transport of nutrients and signaling molecules. This innovation occurs in all clades with complex multicellularity but few others. Continuing co-optation and de novo evolution of signaling molecules and transcription factors led to more complex bodyplans, including those able to move oxygen, nutrients, and molecular signals via bulk transport. With the evolution of bulk transport, new functional capabilities become possible, seeding the diversity and ecological prominence seen today in plants and animals: bilaterians comprise at least 99% of all animal species, whereas vascular plants make up at least 90% of all species in the streptophyte/embryophyte clade.

Less information is available for the other clades of complex multicellular organisms. For fungi, we have good phylogenies (e.g., Schoch et al. 2009), molecular clocks (Lücking et al. 2009), and a wealth of genomic data; although, with the exception of the cup fungus *Coprinopsis cinerea* (Stajich et al. 2010), genomes focus on yeasts and other simple species. Fungi also have a good fossil record, but one weighted strongly toward microorganisms (Taylor & Krings 2010)—an exception is *Prototaxites*, an interpreted fungus with cells differentiated for bulk transfer that must have been

among the largest organisms in early Devonian landscapes (Boyce et al. 2007). Much remains to be learned about morphogenesis in complex fungi, but once again, protein kinases appear to play key roles in cell signaling (Stajich et al. 2010, Kosti et al. 2010). Complex fungi make up 80–90% of described fungal diversity.

For red algae, we have some phylogenies but limited data on developmental genetics. As noted above, fossils suggest that simple multicellular reds existed relatively early in the history of eukaryotes, but the oldest red algae with complex three-dimensional growth are probable stem-group florideophytes in approximately 580–560 Ma rocks (Xiao et al. 2004). These were part of a broader Ediacaran diversification of macroscopic seaweeds known mostly from compressions and probably including both red and green algae (Xiao et al. 2002). Complex red algae differentiate distinct interior and exterior tissues, although the differentiation of cells for bulk transfer is limited, perhaps because oxygen and nutrients can be supplied by water within the interstices of porous pseudoparenchymatous tissues. Despite this limited capacity for bulk transport, complex (florideophyte) species outnumber simple multicellular reds by 20 to 1.

For brown algae, we have good phylogenies and molecular clocks (Silberfeld et al. 2010), but only one genome and a limited understanding of developmental genetics (Cock et al. 2010). Browns display varying degrees of morphological complexity, but only the laminarialean seaweeds have tissues that facilitate transport within the thallus. Molecular clocks suggest that kelps diversified only within the past 30 million years (Silberfeld et al. 2010); nonetheless, these largest of algae are major contributors to the photosynthetic biomass of the oceans. In general, our patchy knowledge of these additional examples of complex multicellularity suggests evolutionary trajectories broadly consistent with those established for plants and animals, providing a hypothesis to be tested in ongoing studies.

One final point. Accepting molecular clock estimates of 750–800 Ma for the origin of animals, it took 280–340 million years to go from the first sponge-like metazoans to faunas dominated by crown-group members of the classes that populate modern oceans—roughly 40% of the evolutionary history of the kingdom. In plants, the comparable path from proto-embryophytes to floras dominated by crown-group seed plants, leptosporangiate ferns, and marattioid ferns took approximately 190 million years, again some 40% of embryophyte history. Such protracted early evolution does not lessen interest in events such as the Cambrian explosion and its Devonian counterpart in plants, but rather emphasizes that the great intervals of bodyplan diversification should be viewed as single large steps in long evolutionary histories. The beautiful blooms of complex multicellularity had long stems.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

I thank D. Hewitt, E. Sperling, G. Giribet, E. Kramer, C. Simpson, and B. Seah for illuminating discussions, and E. Sperling, N. King, and E. Kramer for helpful comments on the manuscript. I also thank G. Narbonne, M.A. Fedonkin, S. Jensen, I. Cortijo, P.K. Strother, C. Wellman, P. Kenrick (and the Natural History Museum, London), J.F. Basinger, and H. Steur for images used in **Figures 4** and **6**. Research leading to this review was supported, in part, by the NASA Astrobiology Institute.

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Annual Review
of Earth and
Planetary Sciences
Volume 39, 2011

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