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BEFORE ANIMALS

Despite anecdotal results from the early days of molecular phylogenetics (e.g., Field et al., 1988), all extant animals (Metazoa) unite as a monophyletic group, sharing a common ancestor that evolved from unicellular organisms in the Precambrian (Sebé-Pedrós et al., 2017). The nature and age of this ancestor are a matter of intense debate, one that may not be resolved anytime soon for many reasons. Nonetheless, progress has been made in terms of the genomic complement of such an ancestor by comparing the genomes of metazoans and their closely related unicellular holozoans (choanoflagellates, ichthyosporeans and filastereans) (fig. 1.1) with those of other outgroups (e.g., King et al., 2008; Sebé-Pedrós et al., 2017; Paps and Holland, 2018; Richter et al., 2018) and reconstructing the common repertoire of genes found across metazoans (see Lewis and Dunn, 2018).

This has shown that the addition of novel groups of genes at the node that leads to Metazoa is considerably larger than the novel genes at any nodes surrounding it. Indeed, 25 groups of metazoan-specific genes have been established as essential for this clade (Paps and Holland, 2018), facilitated by the complete genome sequences of four unicellular holozoans (Sebé-Pedrós et al., 2017): two choanoflagellates (*Monosiga brevicollis* and *Salpingoeca rosetta*), a filasterean (*Capsaspora owczarzaki*), and an ichthyosporean (*Creolimax fragrantissima*) (King et al., 2008; Fairclough et al., 2013; Suga et al., 2013; de Mendoza et al., 2015). This data set enables reconstructing the gene content of the unicellular ancestor of animals at an unprecedented level of detail—including the so-called multicellularity genes that have roles in cell–cell recognition, signaling, and adhesion. The study of these genomes resulted in a quite surprising result; although there has been gene innovation at the origin of Metazoa (see Paps and Holland, 2018), the unicellular ancestor of animals already had a rich repertoire of genes that are required for cell adhesion, cell signaling, and transcriptional regulation in modern animals (Sebé-Pedrós et al., 2017).

Another recent study, sampling transcriptomes of nineteen additional choanoflagellates, also suggested that a large number of gene families were gained at the stem of Metazoa (Richter et al., 2018). However, whereas Paps and Holland (2018) estimated that the number of gains was much larger than the number of losses, Richter et al. (2018) found that these numbers are very similar, which has been portrayed as evidence for an “accelerated expansion of gene families” versus an “accelerated churn of gene families” along the metazoan stem (Lewis and Dunn, 2018). Perhaps most important, the new study thoroughly sampling choanoflagellate transcriptomes has provided evidence that hundreds of gene families previously thought to be animal-specific, including Notch, Delta, and homologs of

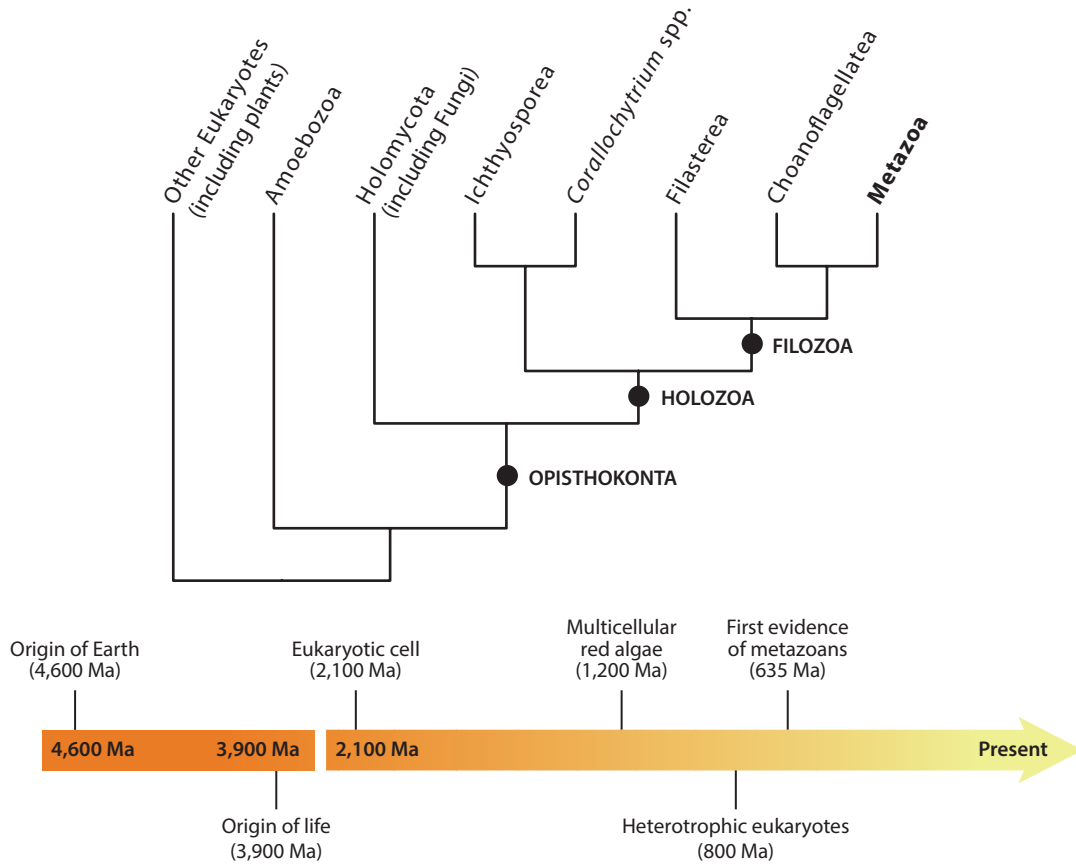


FIGURE 1.1. Top: phylogenetic position of Metazoa among Holozoa and other eukaryotes. Bottom: a timeline of major events leading to the origins of metazoans. Based on Seb -Pedr s et al. (2017).

the animal Toll-like receptor genes, are also found in choanoflagellates (but not in the two highly derived, previously sequenced genomes) and thus predate the choanoflagellate–metazoan divergence. It is anticipated that the early history of the animal gene repertoire will continue to be refined as the genomes of more closely related holozoans are brought into the picture.

The history of the origins of metazoans goes back to Haeckel and Metschnikoff (see a recent historical account in Nielsen, 2012a). Among historical hypotheses, Remane (1963) argued explicitly for a colonial spherical choanoflagellate as an ancestor to Metazoa, instead of the hypothesis of a multinucleated plasmodial cell (e.g., Hadzi, 1953), a hypothesis that at least is supported from a sister group perspective between Choanoflagellatea and Metazoa. However, from a traditional morphological perspective, reconstructing the nature of the oldest metazoan requires optimization of characters on phylogenetic trees. Optimizing characters on a well-resolved phylogeny is especially difficult when few characters are shared between the deepest nodes. Supposing that groups like Ctenophora, Porifera or even

Placozoa were the first offshoots of animal evolution, meaningful character optimization would be reduced to a handful of molecular markers and subcellular structures, something that would not help us in reconstructing the external morphology of an ancestor.

Likewise, such characters are unlikely to be recognized in the fossil record and thus if the last common ancestor of all animals looked like a comb jelly, a sponge, or a placozoan they would be recognized as stem groups of each of those three lineages, but probably not as the so-called Urmetazoan. Only one scenario, that of sponge paraphyly at the base of the animal tree, would provide the necessary power to say something about such an ancestor, as proposed by Nielsen (2008) in his “choanoblastaea” hypothesis. Sponge paraphyly is, however, disfavored in most recent phylogenetic analyses of sponges and metazoans.

Two facts are important for this book. First is the position of Metazoa in the broader tree of life within a clade of Opisthokonta named Holozoa. Holozoa includes, in addition to animals, choanoflagellates, filastereans and ichthyosporideans. Metazoa is well supported in all molecular phylogenetic analyses as sister group of Choanoflagellata (e.g., Torruella et al., 2015) [fig. 1.1]. The resemblance of choanoflagellates to sponge choanocytes is striking and has been used a synapomorphy for the clade containing choanoflagellates and metazoans (= Choanozoa), reinforced in those topologies that suggest sponge paraphyly at the base of animals (Nielsen, 2012a). However, few real comparisons have been made between choanoflagellates and choanocytes until recently (Mah et al., 2014), and these authors indicated that although these cells are similar in some aspects, they differ in others, concluding that homology cannot be taken for granted. Similarities in collar-flagellum systems separated by 600 million years of evolution, whether homologous or convergent, suggest that these form important adaptations for optimizing fluid flow at microscale levels (Mah et al., 2014).

Irrespective of whether or not these two cell types are homologous, animal biologists have much to learn from animals’ closest relatives. The first choanoflagellate genome, for the unicellular species *Monosiga brevicollis*, was thus sequenced to better understand the transition to multicellularity and tissue integration in metazoans. This genome, consisting of approximately 9,200 intron-rich genes, includes genes that encode for cell adhesion and signaling protein domains that were thought to be restricted to metazoans (King et al., 2008), but abundant domain shuffling followed the separation of the choanoflagellate and metazoan lineages. Nonetheless, a series of molecular synapomorphies of metazoans is still supported in the presence of special signaling, adhesion, and transcriptional regulation factors, including Wnt, Frizzled, Hedgehog, EGFR, classical cadherin, HOX, ETS, and POU, or the exclusive metazoan extracellular matrix components such as collagen type IV, nidogen, and perlecan. A list of core animal-specific gene families is given in Richter et al. (2018).

Second is the age of the oldest metazoan fossils, a much more controversial matter (see Sperling and Stockey, 2018, for a recent review). We begin this section by discussing some key paleontological facts and hypotheses in relation to the origin of metazoans.

WHAT IS A METAZOAN?

Defining Metazoa as a term is not trivial, and we now mostly recognize monophyletic groups as they are defined in phylogenies. Metazoa therefore includes any organism that shares a common ancestor with Ctenophora, Porifera, and Bilateria but excludes Choanoflagellata. We do not consider here therefore the plethora of “protozoan” groups that used to be included in some textbooks as “unicellular animals,” for these are not necessarily the closest sister groups of animals. Metazoans are organisms of multicellular organization, as opposed to unicellular or colonial ones, which means that there are special cell–cell junction molecules (Leys and Riesgo, 2012). That said, multicellularity is not exclusive to metazoans, as it occurs in multiple lineages of eukaryotes, even within Opisthokonta (Ruiz-Trillo et al., 2007). This has allowed division of labor, and even the simplest extant metazoans have multiple cell types.

All metazoans are also ingestive heterotrophic, but that is not equivalent to having a mouth, as pinocytosis and phagocytosis are the sole feeding mechanism of sponges and extracellular digestion with endocytosis by the lower epithelium occurs in placozoans. Virtually all other free-living metazoans ingest food through a mouth, with some exceptions of parasitic or symbiotic species. Nevertheless, the ability of metazoans to phagocytize food is unique among the multicellular eukaryotes (Mills and Canfield, 2016). A prevalent hypothesis is that the first metazoans—the common ancestor of all living metazoans—likely subsisted on picoplankton (planktonic microbes 0.2–2 μm in diameter) and dissolved organic matter, as sponges do nowadays and that therefore, through their feeding, helped bridge the strictly microbial food webs of the Proterozoic Eon (2.5–0.541 billion years ago) to the more macroscopic, metazoan-sustaining food webs of the Phanerozoic Eon (the past 541 million years) (Mills and Canfield, 2016). This hypothesis, however, relies upon a similarity between the last common ancestor of modern metazoans and modern sponges. Alternative phylogenetic hypotheses placing ctenophores more basally than sponges have been informally criticized for requiring carnivory to have evolved at the base of the animal tree, but this is not necessarily the case, as extant ctenophores seem to have diversified relatively recently, and there could have been other ecologies earlier in the stem ctenophore lineages. Furthermore, it is difficult to predict the feeding mode of possible extinct stem metazoans, but it is not unlikely that they would have fed on phytoplankton, as many animal larvae do nowadays.

Because multicellular animals must begin as unicellular, metazoan development shares some basic principles in sexual animals. While most nonsexual species tend to have sexual sister species, a few lineages of long-term asexual (mostly parthenogenetic) animals are supposed to exist, for example, bdelloid rotifers (Mark Welch and Meselson, 2000). This phenomenon has, however, recently been disputed, suggesting that bdelloids may have some sort of infrequent or atypical sex, in which segregation occurs without requiring homologous chromosome pairs (Signorovitch et al., 2015). Therefore, the presence of eggs and sperm cells could be considered the typical metazoan condition. After fertilization, metazoan zygotes develop from one of the four cells resulting from meiosis, whereas the other three cells become

polar bodies and often degenerate. Embryogenesis in animals is, however, extremely diverse, and polar bodies can carry information or have specific functions. For example, they are key in fertilization of eggs in parthenogenetic animals, or have a role as extra-embryonic tissue in some parasitic wasps (Schmerler and Wessel, 2011).

Some authors have also attempted to identify metazoan-specific markers, including special glycoproteins such as collagens (a large family of proteins found in the extracellular matrix of metazoans), protein kinase C for cell signaling, or even specific neurotransmitters, but many of these molecules are now known from the genome of *Monosiga brevicollis*, suggesting a premetazoan history of protein domains required for multicellularity (King et al., 2008), and even neurotransmission may have a common origin with the primordial secretion machinery of choanoflagellates (Burkhardt et al., 2011; Hoffmeyer and Burkhardt, 2016). Some recent research may indicate that while fibrillary collagen motifs evolved in the common ancestor of choanoflagellates and metazoans, fibrillary collagen with covalent cross-links between individual fibrils are metazoan synapomorphies (Rodríguez-Pascual and Slatter, 2016). From these, type IV collagen or a type IV-like form (spongulin short chain collagen) is present in the basement membrane of all metazoans (Leys and Riesgo, 2012). TGF- β is also found in all animals but nowhere outside animals, although there are some differences in the complement of genes between sponges and ctenophores with the rest of animals (Pang et al., 2011).

In addition to protein-coding genes, animal *cis*-regulatory complexity (i.e., distinct enhancers and transcription factor binding sites for different genes that regulate their spatial and temporal expression), once thought to be the trademark of complex animals, is now known to be present in sponges (Gaiti et al., 2017; Hinman and Cary, 2017), but this has not been studied in ctenophores or placozoans.

Germ cells play a unique role in gamete production and thus in heredity and evolution. They can be specified either by maternally inherited determinants (preformation) or by inductive signals (epigenesis) (Extavour and Akam, 2003). At the molecular level, metazoans seem to share a germline multipotency program (GMP) with 18 GMP genes present in representatives of sponges, ctenophores, cnidarians, and bilaterians (Fierro-Constaín et al., 2017), showing that some of them evolved in Metazoa. Likewise, while homologizing germ layers across animals may be difficult, the expression of the transcription factor GATA in the sponge inner-cell layer suggests a shared ancestry with the endomesoderm of other metazoans and that the ancestral role of GATA in specifying internalized cells may precede the origin of germ layers (Nakanishi et al., 2014). This may imply that germ layers and gastrulation evolved early in eumetazoan evolution from developmental programs used for the simple patterning of cells in the first multicellular animals (Nakanishi et al., 2014).

■ THE EARLIEST METAZOAN FOSSIL RECORD— THE PRECAMBRIAN

Most of the characters discussed above as likely apomorphies of Metazoa have negligible fossilization potential and, as is often the case, fossils may be assigned to a

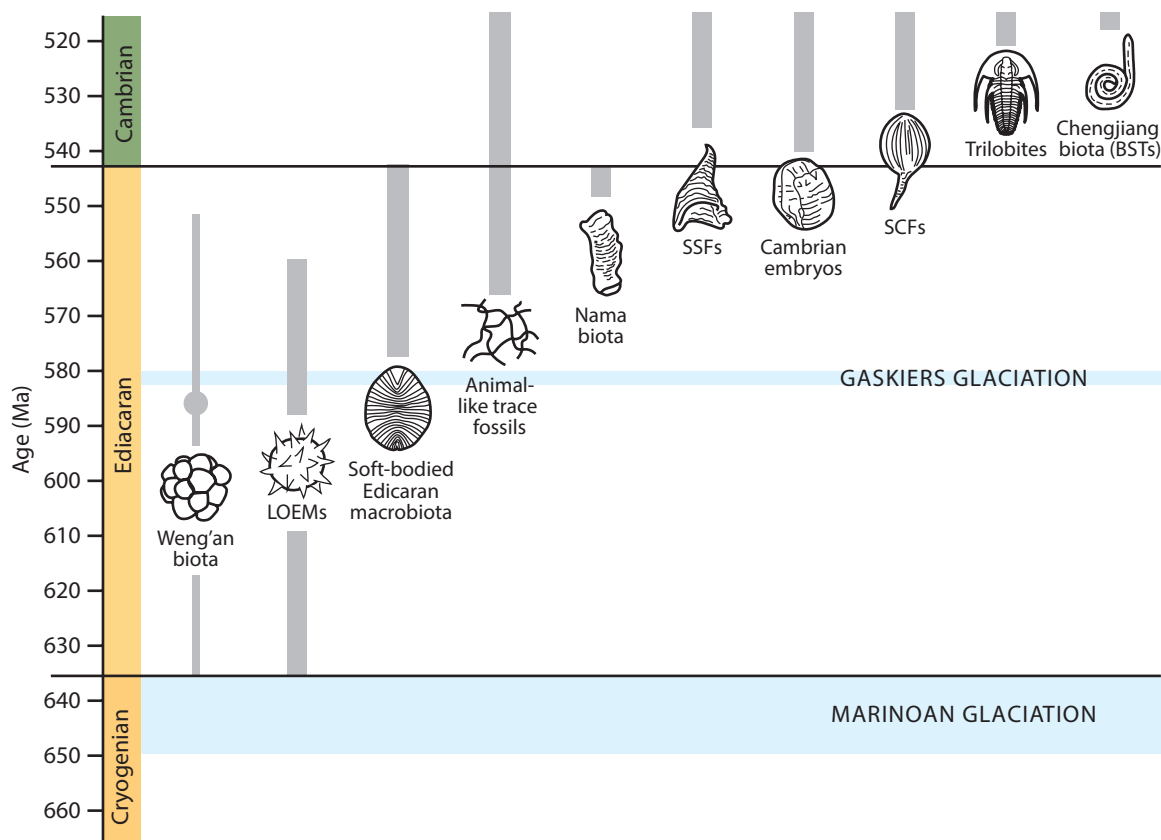


FIGURE 1.2. Temporal occurrence of key Ediacaran and early Cambrian fossil assemblages and preservational styles (based on Cunningham et al., 2017). Abbreviations: BSTs, Burgess Shale-type biotas; LOEMs, Large ornamented Ediacaran microfossils; SCFs, Small carbonaceous fossils; SSFs, Small shelly fossils.

group because they possess diagnostic characters of one or more of its subgroups. A review of metazoan characters proposed by Ax (1996), for example, noted that radial cleavage was the only one with reasonable fossilization potential (Cunningham et al., 2017). This particularly applies to the body fossil record of the earliest metazoans and impedes chances of identifying a stem-group metazoan, very few compelling candidates of which are known from the Proterozoic Eon (the late Precambrian), and these are confined to its latest period, the Ediacaran (635–541 Mya) (fig. 1.2).

Evidence from behavior in the form of trace fossils (=ichnofossils) has generally been regarded as providing the strongest evidence of Metazoa before the Ediacaran–Cambrian boundary (fig. 1.3). Trace fossils from the late Ediacaran (ca. 555 Ma) have the most widespread acceptance as having been made by animals, and some of these traces are generally ascribed to Bilateria (Gaidos et al., 2007; Gehling et al., 2014; Oji et al., 2018), some likely even made by bilaterians with paired appendages (Chen et al., 2018). That said, the situation is less straightforward than it might seem, as locomotory traces that have classically been attributed to Bilateria, such as bilobed trails with a median groove, have been observed to have been made by large

protists (Matz et al., 2008), and other claimed bilaterian traces (Chen et al., 2013) have been attributed to nonanimal behavior, such as by slime molds (Retallack, 2013). Various sources have argued for bilaterian locomotory and feeding traces from earlier sediments, for example >585 Ma (Pecoits et al., 2012). Well-dated locomotory traces from the deep-water Ediacaran deposits in Newfoundland at least indicate that relatively large organisms (trace widths up to 13 mm) were motile by 565 Ma, and the form of the traces is consistent with muscular locomotion as in metazoans (Liu et al., 2010).

The trace fossil record for Ediacaran metazoans is potentially supplemented by biomarkers. At the center of the debate is the discovery of 24-isopropylcholestanes (24-ipc), the hydrocarbon remains of sterols interpreted as having been produced by marine demosponges, derived from rocks as early as 635 Myr old and extending into the Cambrian (Love et al., 2009). This hypothesis was later questioned, as several modern marine algae are also able to produce compositional isomers that are identical to the claimed sponge biomarker (Antcliffe, 2013) and a recent reexamination of the sponge fossil record was unable to unambiguously assign any Precambrian fossil to Porifera (Antcliffe et al., 2014). However, the hypothesis of the sponge biomarker again gained support based on molecular analyses of the origin of the sponge and plant 24-isopropylcholestanes (Gold et al., 2016a), suggesting indeed a gap on the order of 100 Myr for siliceous sponge spicules in the fossil record (Sperling et al., 2010). An additional demosponge-specific biomarker, 26-methylstigmatane (26-mes), has also been identified in Ediacaran sediments (see a summary of demosponge biomarkers in Sperling and Stockey, 2018). However, both 24-ipc and 26-mes have been found to be abundantly biosynthesized

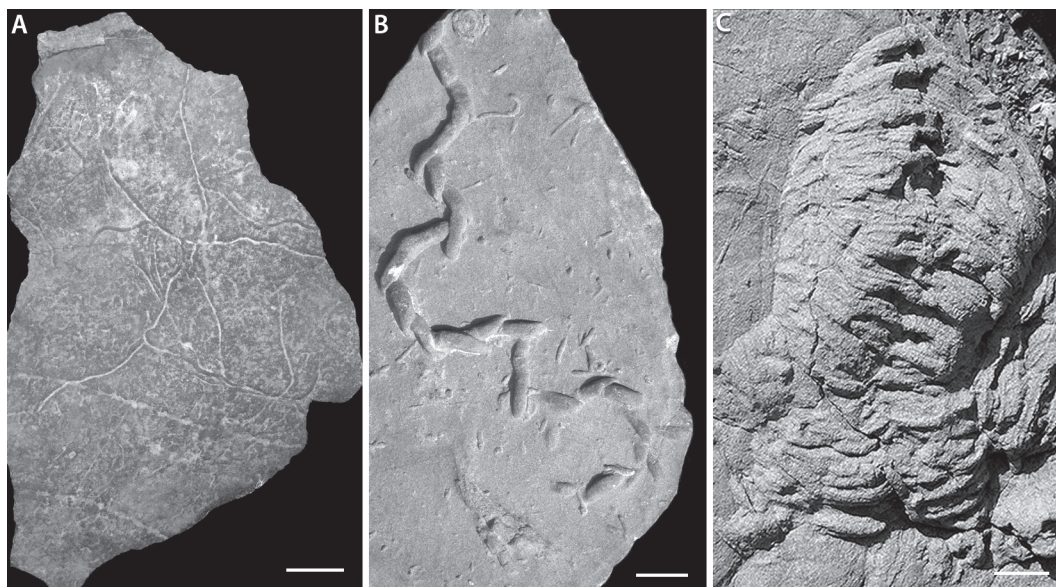


FIGURE 1.3. Metazoan trace fossils from the Ediacaran–Cambrian transition. A, *Helminthoidichnites* from the Ediacaran, scale 2 cm; B, *Treptichmus pedum*, index fossil for the base of the Cambrian, scale 1 cm; C, *Rusophycus burjensis*, a middle Cambrian arthropod resting trace, scale 5 mm. Image credits: B, Sören Jensen; C, Gabriela Mángano.

by unicellular protists in the clade Rhizaria, and the appearance of this group in the fossil record matches the geological appearance of the biomarkers better than does that of sponges (Nettersheim et al., 2019). Irrespective of this debate over demosponges, lipid biomarkers from organic films on Ediacaran dickinsoniid megafossils have been identified as cholesteroloids (Bobrovskiy et al., 2018), discussed below as evidence for total-group Metazoa.

A series of phosphatized and silicified microfossils (Muscente et al., 2015a) from the Doushantuo Formation, South China, known as the Weng'an biota, has yielded an abundance of three-dimensional fossils, including what have been interpreted as metazoan embryos (Chen et al., 2000; Xiao and Knoll, 2000; Chen et al., 2006; Chen et al., 2009b) and small postembryonic stages of metazoans (Xiao et al., 2000; Wang et al., 2008). However, subsequent reexamination or reinterpretation of the Doushantuo specimens has in several cases disputed the proposed evidence for metazoan identities, with many of the putatively biological structures being reinterpreted as geological in origin (reviewed by Crosby and Bailey, 2018). With regards to the putative embryos (fig. 1.4 A), some workers have accepted an identity as embryos but questioned their identification as metazoans, suggesting alternatives such as non-metazoan Holozoa, whereas others have proposed that these fossils are algal or bacterial (Huldtgren et al., 2011; Bengtson et al., 2012; Cunningham et al., 2012; Cunningham et al., 2015).

Another proposed indicator of metazoans in the Ediacaran are acritarchs, known as large ornamented Ediacaran microfossils (fig. 1.4 B, C), some of which have been interpreted as the encysted resting stages of Metazoa (Yin et al., 2007; Cohen et al., 2009). These acritarchs have a temporal range from approximately 635 to 560 Ma, but their precise affinities remain unclear and appear to be phylogenetically varied (Liu et al., 2014b), although some encase embryo-like Doushantuo fossils (Yin et al., 2007).

Perhaps the most fascinating Precambrian biota is the famous Ediacaran megafossils, a series of large (sometimes more than a meter long), soft-bodied, mostly sessile organisms originally described from the Flinders Ranges in Australia (fig. 1.4 G–J) but later extended to be a globally distributed marine biota, now known from all continents but Antarctica (Fedonkin et al., 2007a). Three different assemblages—the Avalon, White Sea Ediacaran, and Nama—are identified, the differences between them reflecting a mix of temporal, biogeographic, and especially environmental/biofacies differences (the Avalon, named for a classic site in Newfoundland, being the oldest and deepest water, and the Nama, first described from Namibia, being the youngest and shallowest). Together they span the interval from ca. 571–542 Mya, and span biofacies from lower-energy inner shelf settings (Avalon-type), wave- and current-agitated shoreface (White Sea Ediacaran) to high-energy distributary systems (Nama) (Grazhdankin, 2014).

Ediacaran organisms like *Dickinsonia*, *Mawsonites*, *Rangea*, and *Charniodiscus*, among others, have been discussed in the context of modern metazoan taxa, especially Cnidaria, but a plethora of other interpretations have been proposed, including that of a protozoan affinity (Seilacher et al., 2003) or being a wholly extinct radiation of nonanimal life, collectively grouped as Vendobionta. *Dickinsonia* (fig. 1.4 J), historically allied to annelids or cnidarians, exemplifies the diversity of current

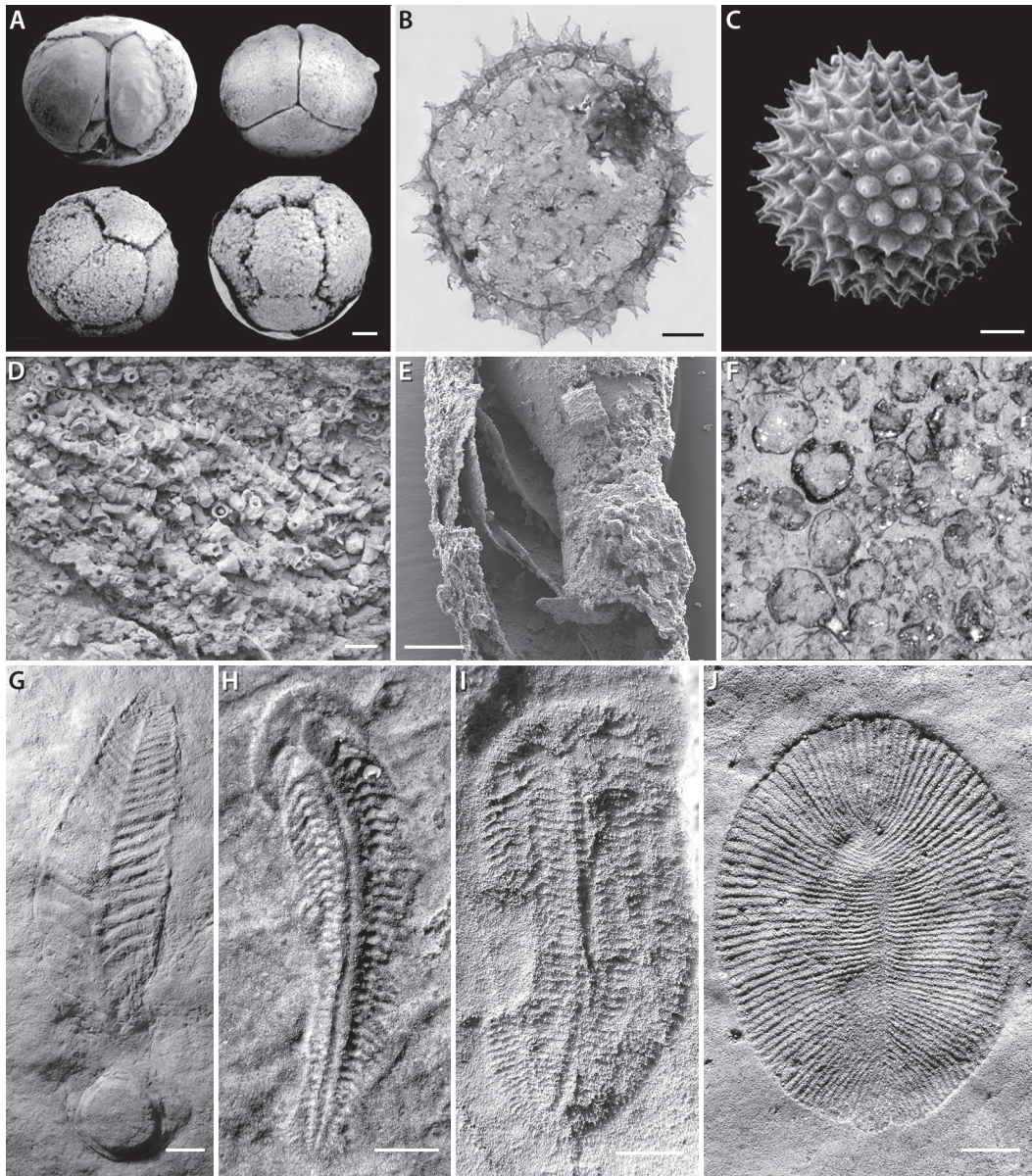


FIGURE 1.4. Fossils from the Ediacaran Period. A, Weng'an microfossils, scale 0.1 mm; B, C, ornamented acritarchs, B, *Ali-coesphaeridium lappaceum*, scale 50 μ m; C, *Meghystrichosphaeridium reticulatum*, scale 50 μ m; D, *Cloudina carinata*, field context, scale 5 mm; E, *Cloudina hartmanae*, SEM, scale 200 μ m; F, *Namacalathus hermanastes*, field context; G–J, South Australian Ediacaran macrofossils; G, *Charniodiscus arboreus*, scale 3 cm; H, *Spriggina floundersi*, scale 5 mm; I, *Marywadea ovata*, scale 5 mm; J, *Dickinsonia costata*, scale 1 cm. Photo credits: A–C, F, Andrew Knoll; D, E, Iván Cortijo; G–J, John Paterson.

opinion on the question of affinities for Ediacaran macrofossils. Its feeding traces (grazing on a microbial mat by absorption across its ventral surface) characteristic of external digestion have been argued to support a placozoan affinity (Spierling and Vinther, 2010). Its inferred mode of growth has alternatively been interpreted

as involving repeated units being added at one pole and compared to terminal addition in metazoans, prompting an assignment to Bilateria (Gold et al., 2015) or instead involving preterminal addition of new units as in Metazoa more generally (Hoekzema et al., 2017; Dunn et al., 2018). *Dickinsonia* is confidently identified as being a mobile organism (Evans et al., 2015), but like the spectrum of Ediacaran macrofossils it lacks any structures that can be convincingly interpreted as a mouth or gut. Cholesteroids as the dominant lipids in *Dickinsonia* and the allied *Andiova* (Bobrovskiy et al., 2018) support an affinity of these organisms with Filozoa, the clade that unites metazoans with Filasterea and Choanoflagellata (see fig. 1.1). This evidence, combined with large size, motility and mode of growth, amplifies the case for such dickinsoniids (and, by association, other Ediacaran megafossils with similar preterminal addition of new units and their subsequent inflation; Dunn et al., 2018) being total-group Metazoa. There is evidence for some frondose Ediacaran-type organisms surviving until the Cambrian (Jensen et al., 1998; Shu et al., 2006; Hoyal Cuthill et al., 2018).

The most widely endorsed body fossil evidence for Ediacaran metazoans comes from its terminal part, in the Nama Group (550–541 Ma) of Namibia and coeval, terminal Ediacaran biotas in Brazil, Russia, China, and other parts of the world. The key fossils are biomineralized and assume quite variable forms. Collectively they represent the earliest experiment in likely animal skeletonization. Such early skeletal fossils include *Cloudina*, a tiny tubular fossil organized as nested calcareous cones (fig. 1.4 D, E), and *Namacalathus*, which has a goblet-shaped calyx with several apertures (fig. 1.4 F), attached to a stalk (see chapters 3 and 44). Both of these as well as the tubular *Corumbella* have been compared to Cnidaria (see chapter 8) as well as other metazoan phyla.

To summarize, early skeletal fossils and a substantial body of indirect evidence suggests a Precambrian origin of Metazoa, in addition to support from nearly all analyses of molecular dating. Indeed, the latter converge on a minimal age for crown-group Metazoa in the Tonian, more than 720 Ma (Sperling and Stockey, 2018). While unambiguous consensus on the animal identity of any of these fossils is yet lacking, biomarkers and developmental modes are consistent with some Ediacaran megafossils being total-group metazoans. In the chapter on Cnidaria (chapter 8), the most likely cases of Ediacaran-age metazoan body fossils are discussed.

THE PRECAMBRIAN-CAMBRIAN BOUNDARY

The dearth of definite metazoans in the Precambrian may of course be the result of multiple factors. Soft-bodied pelagic animals do not fossilize well, and neither do the smallest meiofaunal animals (although Cambrian loriciferans preserved as small carbonaceous fossils provide a fascinating exception; Harvey and Butterfield, 2017). Being small, thin, rare, and of low population density would severely impede the possibility of preservation (Sperling and Stockey, 2018). It is not out of the realm of possibility that some of the earliest animals may have looked like sponge larvae or like many of the microscopic meiofaunal taxa inhabiting water bodies all over the world nowadays.

Most of the animals that today branch out early in the Animal Tree of Life are either pelagic (most ctenophores and jellies, plus several other cnidarians) or, if benthic, are sessile (sponges and many cnidarians). Placozoans, another early animal lineage probably related to cnidarians (Laumer et al., 2018), have been observed swimming but are often collected on glass slides, crawling on surfaces. None of these early animals make burrows or penetrate marine sediments. That said, in contradiction to predictions from molecular dating, there is a sound basis for doubting that animals existed deep into the Proterozoic but failed to be preserved because of deficiencies or preservational biases in the fossil record. Precambrian sediments do in fact preserve fossils in cellular detail (Brasier, 2009), and it is increasingly understood that exceptionally preserved biotas in the late Ediacaran and the Cambrian have similar taphonomy (Daley et al., 2018).

The Ediacaran provides a fossil record in phosphorites, in cherts, as organic fossils, and as compression fossils, yet in striking contrast to the early Cambrian, the abundant and often exquisitely preserved fossil remains from the late Ediacaran are not crown-group animals (Daley et al., 2018). The sequential increase in complexity and diversity of trace fossils across the Ediacaran to middle Cambrian interval (Mángano and Buatois, 2014) is an especially powerful indication that the early Cambrian records key aspects of animal behavior and ecology evolving in real time.

Originally defined by the first appearance of fossil metazoans with mineralized skeletons, such as trilobites, the dating of the Precambrian–Cambrian boundary has changed considerably in the past decades. In the 1970s, with the discovery of small shelly fossils (SSF) below the oldest Cambrian trilobites—a fauna composed of spicules, sclerites, and ossicles of animals plausibly interpreted as sponges, molluscs (including extinct scleritome-bearing groups such as halkieriids), stem-group brachiopods, and so on—the base of the Cambrian was revised. Nowadays it is defined by the first occurrence of the trace fossil *Treptichnus pedum* (fig. 1.3 B), one of the first penetrative burrows, suggesting a metazoan tracemaker able to move between layers of sediments and probably also causing a great deal of bioturbation that oxygenated and mixed the sediment at a depth not previously attained—the so-called agronomic revolution that provides one of the possible ecological explanations for the Cambrian “explosion” of animal life (Brasier, 2009).

The nature of the animal that left the trace fossil *T. pedum* has been a matter of speculation, but it must have been a relatively large (macroscopic) animal based on the size of the burrows. Comparisons with the feeding traces of extant priapulans are consistent with *T. pedum* having been produced by a priapulan-like animal (Vannier et al., 2010), and exceptionally preserved treptichnid traces from the early Cambrian of Sweden closely replicate the morphology of priapulans as well as actualistic observations on burrowing behavior by *Priapululus caudatus* (see Kesidis et al., 2019). *Treptichnus pedum* has also often been associated with the presence of some sort of hydrostatic skeleton, such as a coelomic or a large pseudocoelomic cavity, that allowed the animals to burrow but probably lacked a well-developed cuticle.

Although the presence of a cuticle is quite widespread across animals, a cuticle is in fact difficult to define (Rieger, 1984; Ruppert, 1991b) but may be characterized

as an apical extracellular matrix secreted by and covering the epidermis. Cuticles can be a simple glycocalyx or complex ones consisting of an organic matrix with protein fibers, such as collagen or keratin, or polysaccharides, such as chitin and cellulose. The cuticle can also be mineralized to form spicules or shells. The fossilization potential of different macroscopic coelomate worms can thus be radically different in animals with complex cuticles (e.g., annelids) and those with a simpler ciliated epidermis (e.g., nemerteans), as the latter decay rapidly after death. A bias in sediments that affects fossilization need also be acknowledged. Trace fossils in the earliest Cambrian are often in coarser-grained siliciclastic rocks that typically lack body fossils, particularly nonshelly ones, whereas nonbiomineralized body fossil preservation almost requires a lack of burrowing and disruption/oxygenation of the sediment. This means the two styles of preservation—the traces and the bodies—are almost exclusive of each other.

THE CAMBRIAN EXPLOSION

The term “Cambrian explosion” refers to the relatively sudden appearance of a large number of mostly large-bodied animals during the early Cambrian, including the first records of disparate animal phyla and, ultimately, the rise of metazoan-dominated marine ecosystems. It seems clear now that animal diversification during the Cambrian, giving origin to many animal phyla, was not an explosive radiation per se but that such diversity was made apparent to us through a series of narrow fossilization windows, giving the appearance of a sudden origin of so many animal lineages. Mineralization of course plays a key role in recognizing such diversity (Kouchinsky et al., 2012; Briggs, 2015), given that in several lineages (such as chaetognaths, represented by their organophosphatic grasping spines known as “protoconodonts”), mineralized microfossils precede the first appearance of nonbiomineralized parts of the body. For some of the major groups of animals, the latter coincides with the opening of a taphonomic window known as “Burgess Shale-type preservation” (Gaines, 2014), after the eponymous Burgess Shale in British Columbia, Canada, in which recalcitrant nonbiomineralized tissues are preserved as largely two-dimensional carbonaceous compressions.

This style of preservation is known from the late Proterozoic (Dornbos et al., 2016), exemplified by the Miaohu biota in China, which preserves abundant and diverse macroscopic algae (An et al., 2015), but it is especially characteristic of offshore siliciclastic rocks from a temporal window spanning Cambrian Stage 3 (ca. 518 Ma) to the Early Ordovician (fig. 1.5). For groups like arthropods and priapulans, the skeletal fossil record commences with Burgess Shale-type preservation in the Chengjiang and Qingjiang biotas in China (Hou et al., 2017; Fu et al., 2019) and the nearly synchronous Sirius Passet biota in Greenland (Cambrian Series 2), but the trace fossil record indicates that the lineages extend to or close to the base of the Cambrian.

Other styles of fossil preservation provide vital information about the diversity and ecology of Cambrian animal communities, such as secondarily phosphatized fossils known as Orsten. First and most comprehensively documented from the Guzhangian–Furongian (late Cambrian) of Sweden, Orsten-style preservation is

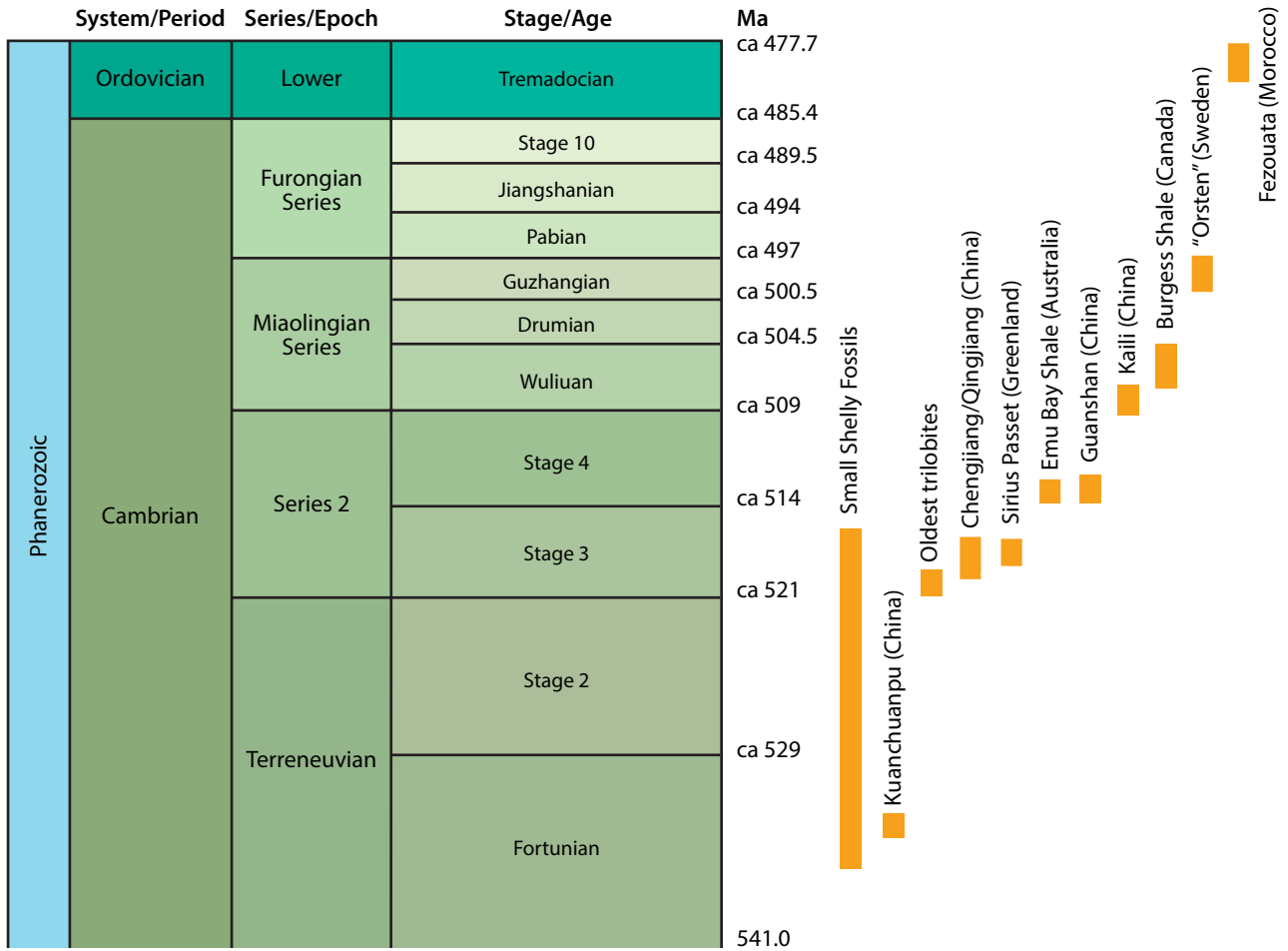


FIGURE 1.5. Temporal occurrence of key Cambrian and earliest Ordovician fossil assemblages relative to the Cambrian time scale (modified from Erwin and Valentine, 2013).

also known from the early Cambrian, permitting embryos, early postembryonic and larval stages to be documented for various groups of animals, including ecdysozoans and cnidarians (Donoghue et al., 2015). Taken together, exceptionally preserved fossil biotas from the Cambrian include a large diversity of animals in extant and extinct lineages. Although it is often said that all major animal phyla except bryozoans appear already in the Cambrian fossil record, this is not true; about half of the currently recognized phyla, including some with numerous species and large sized-animals, like Platyhelminthes and Nemertea, do not have a confirmed Cambrian fossil record.

Many hypotheses have been discussed in the context of the Cambrian explosion of animal life, including a series of intrinsic (genetics, arms race hypothesis) and extrinsic abiotic (changes in ocean circulation patterns, and sea level rise that induced continental flooding and regolith erosion on a vast scale, the Great Unconformity; Peters and Gaines, 2012) and biotic (availability of oxygen and/or food)

factors. For some, the timing of the onset may be constrained by the environment, whereas the duration may be conditioned by developmental innovation (Marshall, 2006). Understanding why this event was unique is often explained by factors ranging from developmental constraints to ecological saturation (Erwin and Valentine, 2013). Conversely, a fundamental distinction between the Cambrian “explosion” and earlier (Ediacaran) events of evolutionary radiation at the base of Metazoa has been questioned, these being seen as part of a longer phase in which animals evolved in response to changes in the Earth’s biogeochemical cycles (Wood et al., 2019). It is inescapable that the Cambrian explosion is in fact a pattern of profound but sequential ecological change that resulted from an interconnected set of biotic and abiotic factors (Smith and Harper, 2013), including carnivory and food availability (Sperling et al., 2013).

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