

## Special Paper for 100th Anniversary

# Extinctions, Morphological Gaps, Major Transitions, Stem Groups, and the Origin of Major Clades, with a Focus on Early Animals



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**Abstract:** Systematic extinctions can leave major morphological gaps between living crown-group clades. Such morphological gaps would be perceived, from a neontological point of view, as major evolutionary transitions. In order to fill these morphological gaps and to map the evolutionary steps toward major evolutionary transitions, we need to integrate extinct stem-group taxa in phylogenetic studies. However, the recognition of stem group has not been widely adopted in the study of early animal fossils, despite that all fossils are stem groups at one level or another. Part of the difficulty is that stem groups may not have all features that collectively diagnose the respective crown group, and they can have unique (autapomorphic) features, making them tantalizingly similar to and frustratingly different from the crown group (e.g., stem-group eukaryotes can be prokaryotic and stem-group animals can be protistan). The need to embrace stem groups and to implement the PhyloCode, in order to achieve phylogenetic clarity and to offer key paleontological insights into the origin and early animal evolution, is illustrated in debates on several controversial Ediacaran and Cambrian fossils.

**Key words:** metazoan, Ediacaran, Cambrian, evolutionary radiation, stem group, crown group

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## 1 Introduction

Although fossils as remains of extinct organisms has been known for a long time, Charles Darwin was among the first to have appreciated the importance role of extinction in shaping the evolutionary history of life. This is evident in the only diagram in his book “On the Origin of Species by Means of Natural Selection” (Darwin, 1859), where extinct species are included in a tree-of-life diagram. In 1837, shortly after he came back from the Beagle voyage, Darwin sketched a famous diagram (Fig. 1) in a notebook, which was archived in the Cambridge University library but went missing for over 20 years until it was anonymously returned to the library in March, 2022. Next to the sketch is Darwin’s handwriting: “Case must be that one generation then should be as many living as now. To do this & to have many species in same genus (as is) requires extinction. Thus between A & B immense gap of relation. C & B the finest gradation, B & D rather greater distinction. Thus genera would be formed, bearing relation to ancient types.” What Darwin was trying to show is that systematic extinctions create morphological gaps. As shown in Figure 2, without extinction, speciation would eventually lead to more or less random and even occupation of a morphospace, with unoccupied morphospace being theoretically impossible (McGhee, 2015) or phylogenetically unattainable (e.g., three-legged animals; Thomson, 2019). With extinctions, however, it is possible to wipe out lineages with unique genetic

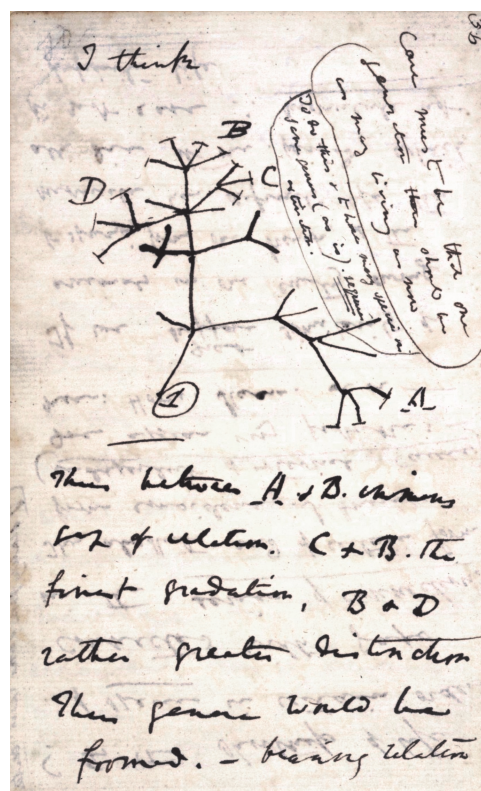


Fig. 1. The tree-of-life diagram in Darwin’s 1837 notebook. From <http://darwin-online.org.uk/>.

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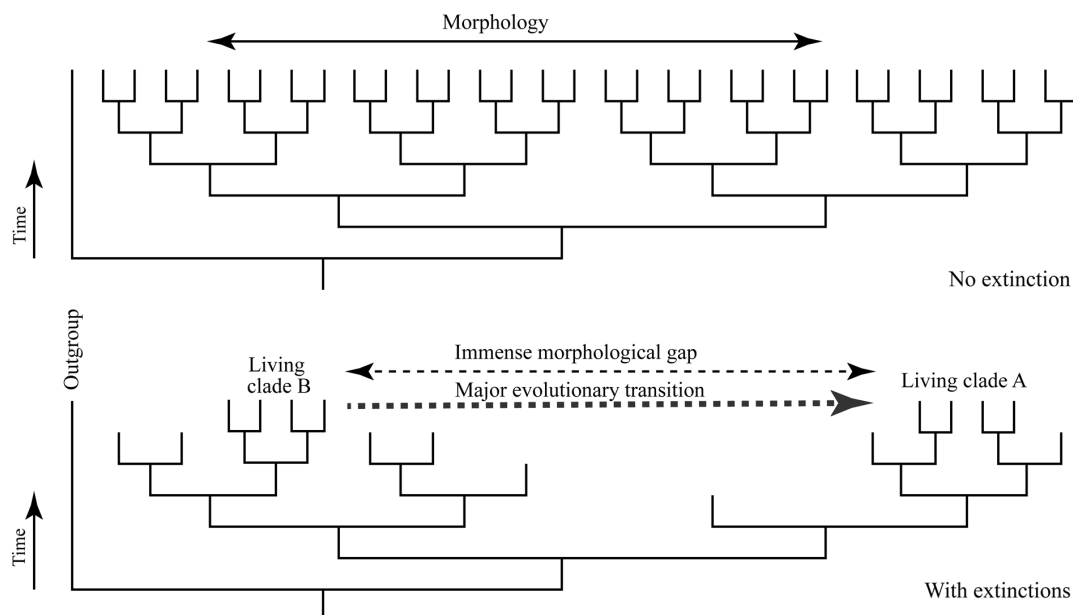


Fig. 2. Phylogenetic trees illustrating that systematic extinctions can potentially lead to immense morphological gaps among surviving clades. Such gaps can be perceived as major evolutionary transitions from a neontological point of view.

possibilities to occupy certain parts of the morphospace, leaving large morphological gaps or unoccupied morphospace. In other words, three-legged animals may have been genetically possible (e.g., *Tribrachidium*), but they were annihilated in their evolutionary cradle. Real examples in the fossil record include the complete elimination of morphospace that used to be occupied by rudist bivalves, stromatoporoids, archaeocyathans, and many others. Thus, systematic extinction would lead to large morphological gaps (i.e., immense gaps in Darwin's words) among the survivors.

These immense gaps can then be perceived as major evolutionary transitions from a neontological point of view. But, in a sense, they are “artifacts” of systematic extinctions that have wiped out many taxa with transitional features, leaving large morphological gaps among the surviving clades. From a neontological point of view, such gaps are insurmountable through microevolutionary changes, and are often thought to represent major innovations achieved through rapid saltational evolution. Hopeful monsters (Goldschmidt, 1940), quantum evolution (Simpson, 1944), and punctuated equilibrium (Eldredge and Gould, 1972) are all along this line of thinking, although they represent different magnitudes of saltational evolution. Saltational evolution is likely feasible and it may have played an important role in the origin of key innovations and the evolution of major clades (Theissen, 2006; Katsnelson et al., 2019). However, from a paleontological point of view, gradual evolution should be the null hypothesis. This is because gradual evolution predicts the presence of transitional features that can be tested against the fossil record, whereas saltational evolution predicts the lack of transitional features and thus paleontological data are irrelevant.

Extinctions, therefore, can in principle account for

major gaps between living clades. Such gaps can be significant, can mask the stepwise assembly of a series of morphological features, and can be perceived as major evolutionary transitions. There are numerous examples, including the morphological gaps between living whales and terrestrial artiodactyls (the evolution of marine mammals), between living birds and crocodylians (the origin of feathered wings and powered flight), between living tetrapods and lungfishes (the origin of vertebrate limbs), between living jawed vertebrates and cyclostomes (the origin of jaws), between living arthropods and tardigrades (the origin of jointed appendages), between living metazoans and their protistan relatives (the origin of animal multicellularity and many other metazoan features), between living angiosperms and acrogymnosperms (the origin of flowers), and between living eukaryotes and prokaryotes (the origin of nuclei, mitochondria, and many other features). So, what would these extinct lineages look like? Importantly, because the features that diagnose a living clade need to be amalgamated in a step-by-step fashion, it is logical to predict that the extinct forms would be transitional in morphological features, and they would likely have some but not all of the features that collectively diagnose the living clade (e.g., characters a1–a4 in Fig. 3); in other words, they may have some but not all of the synapomorphies of the living clade. Similarly, features may be lost along the stem leading to the living clade (e.g., character a0 in Fig. 3) such that, if only these features were used for phylogenetic analysis, we could incorrectly place some of the fossils in the phylogenetic tree; for example, as shown in Fig. 3, the presence of character a0 in fossils 1–5 and in living clade B vs. the absence of character a0 in living clade A would persuade the phylogenetic alignment of fossils 1–5 with the living clade B. Additionally, extinct lineages may evolve unique

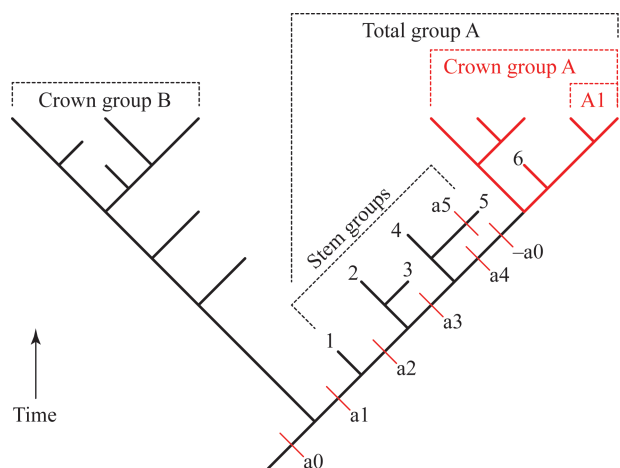


Fig. 3. Phylogenetic tree illustrates the concept of stem group, crown group, and total group.

Note that stem groups (species 1–5 in the diagram) to the crown group A are extinct lineages that have some but not all of the characters (a1–a4) that collectively diagnose the crown group A, can have characters (a5) that are not present in the crown group A, and can have characters (a0) that are absent from the crown group A but present in the crown group B. Also note that all extinct lineages are stem groups at one level or another; for example, fossil species 1–5 are stem groups to the crown group A, whereas fossil species 6 is a member of the crown group A but a stem group to the crown group A1.

features or autapomorphies that are not present in the living clade (e.g., character a5 in Fig. 3). Consequently, extinct lineages can appear tantalizingly familiar, but in the same time frustratingly alien, when compared with their most closely related living clade. Sometimes, they can also be deceptively similar to other living clades, particularly if not all morphological characters are preserved or available for study.

The perplexing nature of extinct lineages can be illustrated by two examples (Figs. 4–5). The extant sister group of living tetrapods is the Dipnoi or lungfishes (Amemiya et al., 2013). From a neontological point of view, there is an “immense gap” between lungfishes and tetrapods. Among many features that distinguish tetrapods and lungfishes are the presence of limbs, a distinct neck, and a shoulder girdle separated from the head in tetrapods. There is a rich fossil record that documents transitional anatomy from lobe-finned fishes to limbed tetrapods (Daeschler et al., 2006; Clack, 2012; Schneider and Shubin, 2013). These fossils chronicle the “progressive” evolution toward tetrapod limbs in many extinct tetrapodomorphs. However, some of them were aquatic fish-like vertebrates and did not have fully functional limbs for a terrestrial lifestyle, and they are aptly called “finned tetrapods” (Lu et al., 2012). Additionally, many of these fossils have more than five digits to their limbs (Coates and Clack, 1990), a condition known as polydactyly, which is the topic of Stephen Jay Gould’s well-known essay “Eight (or Fewer) Little Piggies” (Gould, 1991). The condition of polydactyly is in sharp contrast to the five-digit ancestral archetype of all living tetrapods (Fig. 4). As another example, the numerous fossils leading to the clade of living gnathostomes (jawed vertebrates) are

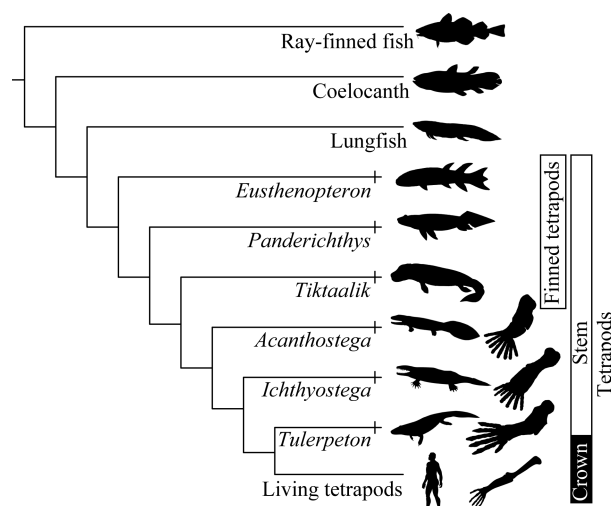


Fig. 4. Simplified phylogenetic tree of fossil and living tetrapods, highlighting the concept of stem and crown groups. Crosses denote extinct lineages. “Finned tetrapods” (Lu et al., 2012) are fish-like stem-group tetrapods.

Note the polydactyly condition among stem-group tetrapods such as *Acanthostega*, *Ichthyostega*, and *Tulerpeton*. Animal thumbnails of *Eusthenopteron*, *Tiktaalik*, and *Panderichthys*, as well as limb thumbnails, were redrawn from diagrams in wikipedia.org under a Creative Commons license. All other animal thumbnails from phylopic.org under a Creative Commons license; *Tulerpeton* artwork by Dmitry Bogdanov (vectorized by T. Michael Keesey).

morphologically diverse, and some of them (e.g., the “ostracoderms”) do not have jaws (Fig. 5). These examples echo the statement that, from a neontological perspective, fossils can appear familiar and alien at the same time. From a paleontological perspective, however, this is exactly what should be expected for fossils with transitional anatomies as well as features that are not represented in living groups.

## 2 Stem Group, Crown Group, and Total Group

How to accommodate fossils in phylogenetic frameworks, which are often (at least initially) construed on the basis of living taxa? Here, the concepts of crown group, stem group, and total group are useful (Fig. 3) (Jefferies, 1979; Budd and Jensen, 2000; Xiao, 2004; Donoghue, 2005). A crown group is the minimum clade that includes all living members of a clade and their last common ancestor. In other words, it is the least inclusive group that contains all living members of a clade, and it is diagnosed by a set of synapomorphies or uniquely evolved, shared, derived characters. Relative to the crown group, a stem group refers to extinct lineages that lie outside a crown group but are more closely related to the crown group than to any other living group. Stem lineages often form a paraphyletic group and they possess a subset of synapomorphies that diagnose the respective crown group. A total group is the sum of the crown group and its stem-group lineages. Stem groups have the following features:

(a) All stem groups are extinct or fossils and only fossils can be stem groups.

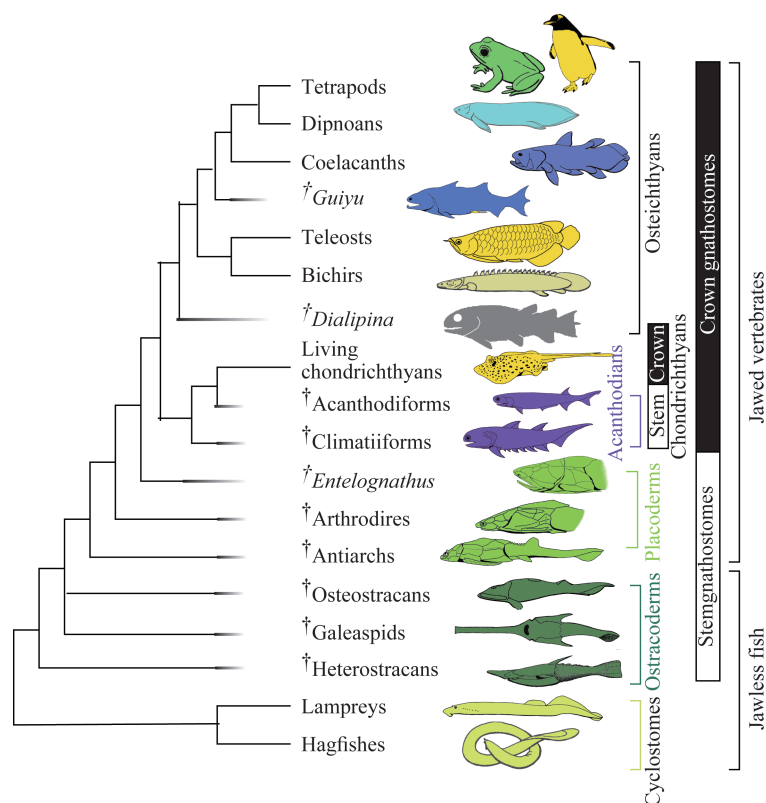


Fig. 5. Simplified phylogenetic tree of fossil and living gnathostomes, highlighting the concept of stem and crown groups.

Crosses denote extinct lineages. Note the stem-group gnathostomes (e.g., ostracoderms) can be jawless. Also note that acanthodians are crown-group gnathostomes but stem-group chondrichthyans. Modified from Gai et al. (2017), with permission from the authors.

(b) All fossils are stem groups at one level or another (Fig. 3).

(c) Stem groups do not need to have all synapomorphies diagnosing the respective crown group, but need to have at least one such feature (Fig. 3).

(d) Stem groups can have their own autapomorphies and can have plesiomorphies that are lost in the respective crown group but present in its living sister clade (Fig. 3).

In the framework of stem groups, it is easy to understand that fossils with transitional features are tantalizingly familiar and surprisingly alien from a neontological perspective. From a paleontological point of view, however, it is not surprising that many stem-group tetrapods have polydactylous limbs and fish-like bodies (Fig. 4); indeed, had lungfishes gone extinct, they would be stem-group tetrapods by definition. Similarly, it is not surprising that ostracoderms, like cyclostomes, lack jaws although they are stem-group gnathostomes (Fig. 5), and that stem-group birds (e.g., pterosaurs, ornithischians, sauropods, and extinct theropods) can have poorly developed feathers or no feathers at all. Relevant to the early evolution of life, it is important to point out that stem-group eukaryotes can be prokaryotic (Fig. 6), insofar as nucleus may not be the first eukaryote feature to evolve and organisms lacking a nucleus are prokaryotic. Likewise, stem-group animals can be multicellular organisms or unicellular protists (Fig. 7).

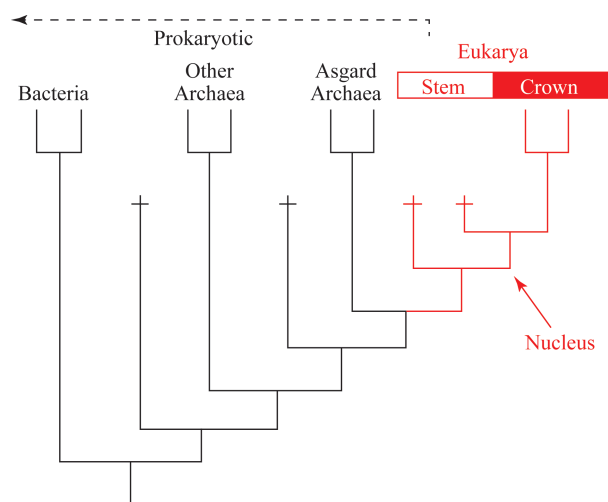


Fig. 6. Simplified tree of life, showing that stem-group eukaryotes do not necessarily have nuclei and can thus be prokaryotic in nature, if nucleus was not the first feature to appear after the divergence of Eukarya from Asgardarchaeota (or Asgard). Crosses denote extinct lineages.

### 3 Early Animal Fossils

The origin of animals is considered a major evolutionary transition (Maynard Smith and Szathmary,

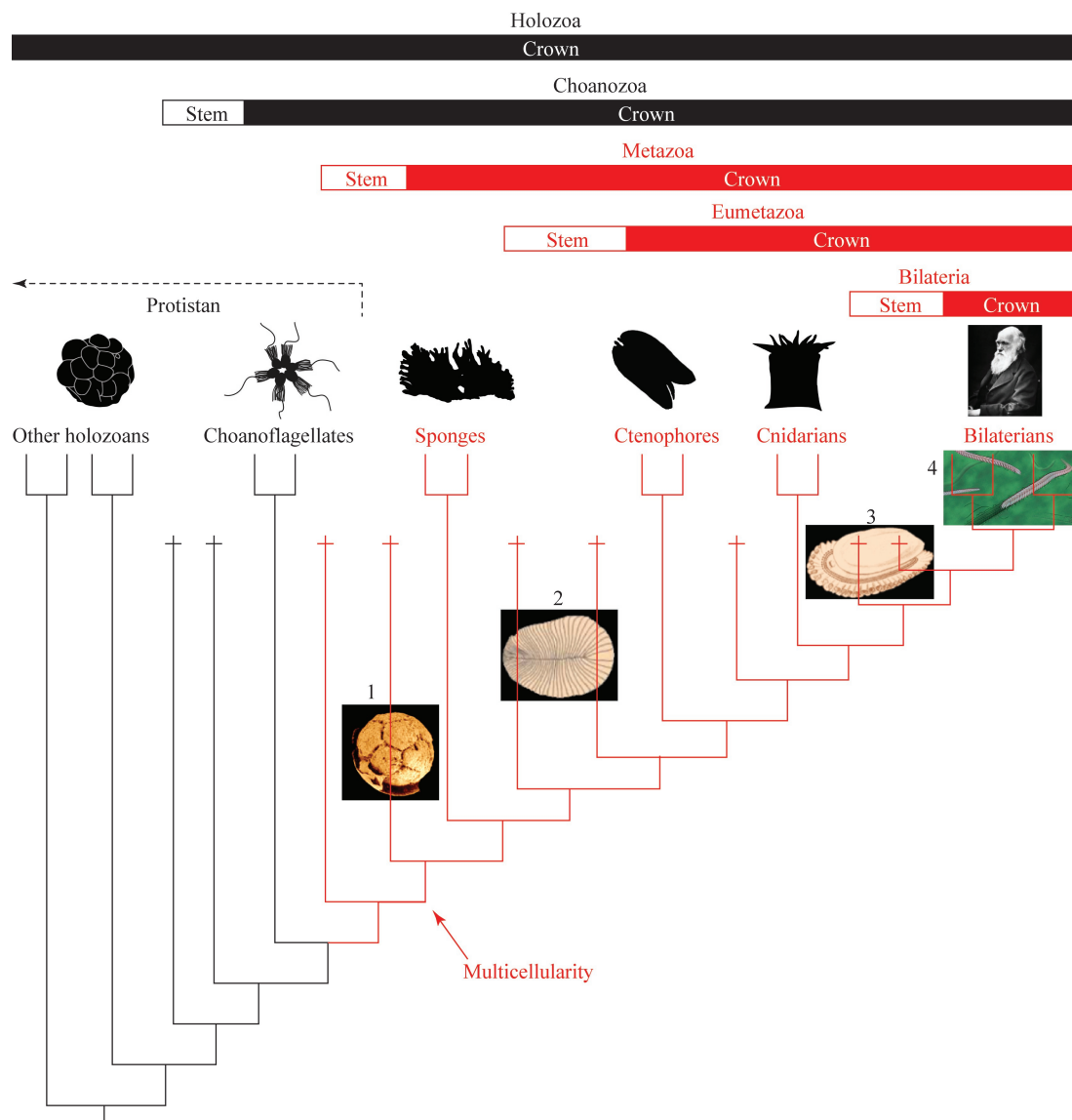


Fig. 7. Simplified phylogenetic tree of holozoans, showing that stem-group animals can be unicellular protists, if multicellularity was not the first feature to appear after the divergence of the Metazoa from the Choanoflagellata.

The Ediacaran fossil *Megasphaera* (1) may represent a stem-group animal (Hagadorn et al., 2006), *Dickinsonia* (2) a stem-group eumetazoan (Evans et al., 2017) or a total-group bilaterian (Gold et al., 2015), *Kimberella* (3) a total-group or even crown-group bilaterian (Martin et al., 2000), and *Yilingia* (4) a crown-group bilaterian (Chen et al., 2019). Crosses denote extinct lineages.

1997). This evolutionary event epitomizes the independent origins of multicellularity (Cavalier-Smith, 2017), as well as the rise of complex genetic regulations and the diversification of animal body plans (Erwin, 2020). There is consensus that all living animals form a monophyletic group that is characterized by complex multicellularity with differentiated cell types, tissue differentiation, embryogenesis, cell adhesion through cell-cell and cell-matrix junctions, germ sequestration, apoptosis, and an immune system. If ctenophores turn out to be the earliest-branching animal phylum and the living sister group to all other living animals (Dunn et al., 2008), then additional animal synapomorphies can be added to the list, including epithelium, axial polarization, body regionalization, and various developmental gene expression patterns. These

features place an immense gap between living metazoans and other holozoans, including the choanoflagellates, which are the living sister group to the metazoans. As these features need to be assembled through evolution in a step-by-step fashion before the origin of the crown-group metazoans, there must be a series of extinct stem-group metazoans in the fossil record. However, the interpretation of these fossils can be challenging because they lack the entire suite of features that diagnose living metazoans.

The embryo-like fossil *Megasphaera* from the Ediacaran Doushantuo Formation at Weng'an in South China (Xiao et al., 1998; Xiao and Knoll, 2000) serves as an example to illustrate the important points. *Megasphaera* has been proposed as a stem-group metazoan (Hagadorn et al., 2006), although this fossil has

also been interpreted as a holozoan (Hultgren et al., 2011), an unspecified protist (Zhang and Zhang, 2022), or a sulfur-oxidizing bacterium (Bailey et al., 2007). Most paleontologists now agree that the bacterium interpretation is less likely because *Megasphaera* does not have any uniquely bacterial features; instead it has a complex ornamented envelope (Xiao et al., 2007), multicellular developmental stages with differentiated cells (Chen et al., 2014), and putative nuclei (Hagadorn et al., 2006; Schiffbauer et al., 2012; Yin et al., 2017), — features only found in eukaryotes. The protist interpretation is not phylogenetically informative because protists do not form a monophyletic group, and also because the grade of protist organization is compatible with the stem-group animal interpretation (i.e., stem-group animals can be protists; Fig. 7). Instead, the developmental complexity of *Megasphaera* and related fossils gravitates toward a stem-group or total-group metazoan interpretation (Hagadorn et al., 2006; Chen et al., 2014; Yin et al., 2022). Future research to test *Megasphaera* as a stem-group animal should rely more on positive evidence (i.e., features that *Megasphaera* shares with its interpretive models) and less on negative evidence (i.e., features that are absent from *Megasphaera* but present in its interpretive models), because a stem-group representative would certainly lack some of features that diagnose the respective crown group. The same can be said of the holozoan and protist interpretations, except that in the protist interpretation, a specific protistan clade should be proposed as an interpretive model and the possibility of protistan stem-group animals should be considered.

The stem group concept also provides a framework for the interpretation of other early animal fossils as well. Of importance are members of the Ediacara biota (Narbonne, 2005; Xiao and Laflamme, 2009; Droser et al., 2017). Ediacara-type fossils represent soft-bodied macroorganisms that are typically preserved as casts and molds. Early attempts to classify them in living animal phyla (Glaessner, 1984) have been criticized because of their differences from crown-group animal clades. Subsequently, many Ediacara fossils were placed in the phylum Vendozoa or Vendobionta, united by a unique quilt-like body construction and considered as a clade distantly related to animals (Seilacher, 1992) or a sister group to the eumetazoans (Buss and Seilacher, 1994). Recent analyses, however, indicate that the Ediacara biota is phylogenetically diverse and represents a sample of marine biodiversity in the Ediacaran Period (Runnegar, 1995; Xiao and Laflamme, 2009). In other words, the Ediacara biota is an artificial grouping united by its cast-and-mold preservation and the macroscopic and soft-bodied nature of its members. As shown in Fig. 7, the Ediacara biota likely includes stem-group animals (Xiao and Laflamme, 2009), stem-group eumetazoans (Evans et al., 2017; Dunn et al., 2019), stem-group bilaterians (Gold et al., 2015), total-group bilaterians (Chen et al., 2019), and even macroalgae (Xiao et al., 2020). In this light, the Ediacara biota can help fill the immense gaps among major animal groups.

The early Cambrian fossil *Yunnanozoon* serves as another example. This genus has been variously

interpreted as a stem-group vertebrate (Tian et al., 2022), a chordate (Chen et al., 1995), a hemichordate (Shu et al., 1996), or a stem-group deuterostome (Shu et al., 2003). While the interpretation and homology of key features in *Yunnanozoon* remain open to debate (Cong et al., 2015), it is important to point out that, as a stem-group representative, *Yunnanozoon* does not need to have all features that diagnose the respective crown-group. For example, it is perfectly acceptable that, as a stem group vertebrate, *Yunnanozoon* may not have vertebrae, a braincase, eyes, and other features found in crown-group vertebrates (Tian et al., 2022). The real debate should be focused on whether *Yunnanozoon* has at least one of the many features that collectively diagnose crown-group vertebrates, and if so, how *Yunnanozoon* and related fossils (e.g., *Haikouichthys*, *Mylokunmingia*) can help fill the gap between vertebrates and non-vertebrates, thus providing insights into a major evolutionary transition.

#### 4 Prospect

The narrative above highlights the indispensable role of stem-group fossils in filling immense morphological gaps and in understanding major evolutionary transitions, but it also raises a key problem for traditional taxonomic nomenclatures. If stem-group eukaryotes can be prokaryotic and stem-group animals can be protistan, how do we maintain nomenclature clarity, considering that eukaryotes vs. prokaryotes and animals vs. protists are traditionally perceived as antithetic and mutually exclusive groupings? In a sense, this is a semantic issue, which critically depends on how animals and eukaryotes are diagnosed. Following the widely accepted diagnoses (e.g., eukaryotes have nuclei and animals are characterized by the combination of multicellularity, cell differentiation, heterotrophy, embryogenesis, etc.), then stem-group eukaryotes can be prokaryotes and stem-group animals can be protists, as long as the diagnostic feature(s) are not the first to appear since the divergence of the eukaryotes and animals from their respective living sister clades. However, the nomenclatural ambiguity goes away if eukaryotes and animals are phylogenetically defined as stem-based clades following the PhyloCode (<http://phylonames.org/code/>). The PhyloCode is a solution to mitigate the potential nomenclature confusion when stem groups are introduced in phylogenetic discussion. PhyloCode is strictly based on clades (or monophyletic groups), which can be defined in three different ways (Fig. 8).

(a) A node-based clade includes the last common ancestor of two taxa, and all descendants of this ancestor (for example, the crown-group Metazoa can be defined as the last common ancestor of *Homo sapiens* and *Hallucigenia sparsa*, plus all descendants of this ancestor; the so-defined Metazoa would be equivalent to crown-group animals).

(b) A branch-based or stem-based clade includes the first ancestor of a taxon which is not also an ancestor of another taxon, and all descendants of this ancestor (for example, the Metazoa can be defined as the first ancestor of *Homo sapiens* which is not an ancestor of

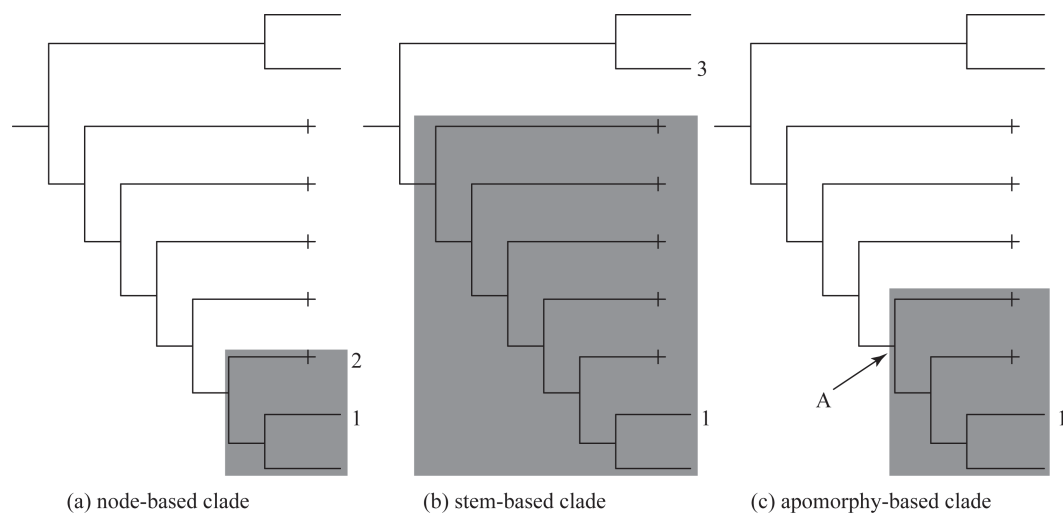


Fig. 8. Simplified diagram showing a node-based clade (a, the last common ancestor of species 1 and 2, and all descendants of this ancestor), a stem-based clade (b, the first ancestor of species 1 that is not also an ancestor of species 3, and all descendants of this ancestor), and an apomorphy-based clade (c, the first ancestor of species 1 to possess the apomorphy A, and all descendants of this ancestor). Crosses denote extinct lineages.

choanoflagellates, plus all descendants of this ancestor; the so-defined Metazoa would be equivalent to total-group animals).

(c) An apomorphy-based clade includes the first ancestor of a taxon to possess a particular character present in and inherited by this taxon, and all descendants of this ancestor (for example, the Eukarya can be defined as the first ancestor of *Homo sapiens* to possess a nucleus in its cell, plus all descendants of this ancestor).

Following the PhyloCode means that many new clades and names will be introduced. This is a necessary step toward phylogenetic and nomenclature clarity. Only when the clades are precisely defined, can they be used as a phylogenetic framework to orient stem groups. And only when stem group fossils are placed in a precisely defined phylogenetic framework, can they be used to reconstruct the sequence of character acquisition and to fill morphological gaps between living clades.

The successful implementation of the PhyloCode requires a sound phylogenetic tree, but the phylogenetic interpretation of fossils, particularly early animal fossils, is often controversial, highlighting the challenges in adopting the PhyloCode in paleontological studies. However, as each phylogenetic tree is a hypothesis that is subjected to refinement, revision, and rejection, so are PhyloCode-based clades. Vertebrate paleontologists are better positioned to embrace the PhyloCode, partly because vertebrate fossils are character-rich and hence phylogenetically better resolved than early animal fossils. The fossil record of early animals (particularly those in the Ediacaran Period), on the other hand, suffers incomplete preservation because they largely lack hard skeletons. Thus, it is a challenging task to resolve their phylogenetic relationships based on their simple morphologies that requires exceptional conditions for preservation, can be altered by taphonomic processes, and are subject to convergent evolution. As challenging as it is, however, interrogating the fossil record is rewarding as it provides

the only direct evidence for evolution. With continuing exploration of exceptionally preserved fossil assemblages and broader adoption of the stem-group concept, it is hopeful that we will be able to fill the immense morphological gaps envisioned by Darwin, to chart the evolutionary path toward crown-group animals, and to better understand the major evolutionary transition from protists to animals.

## 5 Conclusions

Although Darwin recognized the importance of fossils in the study of evolution, incorporating the fossil record in phylogenetic and evolutionary studies is not straightforward and full of challenges. This is because phylogenetic and evolutionary frameworks are typically established on the basis of living organisms; thus, from a neontological point of view, fossils can be both incomplete (because they do not have all features that collectively diagnose their respective living clades) and alien (because they can have features that are not found in living clades). Despite these challenges, fossils are indispensable in the study of evolution, particularly in the study of major evolutionary transitions, which are characterized by major morphological gaps between living clades but can result from pervasive extinction of taxa. These extinct taxa are best understood in a phylogenetic framework that incorporates stem groups. Stem-group fossils provide the direct evidence for us to fill morphological gaps, to retrace evolutionary steps, and to understand major evolutionary transitions. Embracing the stem-group concept and practicing PhyloCode nomenclature is a necessary step toward clarifying the evolutionary significance of early animal fossils.

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