Life in Changing Fluids: A Critical Appraisal of Swimming Animals Before the Cambrian

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Synopsis

Molecular and fossil data place the initial diversification of animals in the Neoproterozoic, though there remains too much enough uncertainty to produce an exact chronology. This is unfortunate, as the Neoproterozoic represents a period of intense climate change, including multiple global glaciation events as well changes to ocean chemistry and oxygen content. Several authors have suggested that the coevolution of animals and their environment was tightly coupled, but such hypotheses rest on the presence of swimming (pelagic) species. In this paper, I review the evidence for pelagic animals during the Neoproterozoic. I conclude that there are very few groups of planktotrophic swimming animals that were likely to have existed at this time, with the possible exception of medusozoan cnidarians (jellyfish). Ultimately, hypotheses connecting Earth and animal evolution in the Neoproterozoic need to be tested with more geochemical work, fossil discoveries, and refinement of molecular clocks targeted on the relevant groups.

Introduction

Research over the last few decades paints a picture of animal origins that began on the ocean floor. While millimeter-scale acritarchs and phytoplankton drifted across the open oceans, the fossil record suggests multicellular life proliferated on the seabed, where simple forms competed to colonize, crawl, and chew their way through thick microbial mats (Droser et al. 2017; but see Meyer et al. [2018] for a discussion of possible preservational biases). At some point animals left their benthic competitors behind, leveraging muscle-powered swimming to take to the open ocean. Significant attention has been given to the origin of animal life, but this paper is concerned with evolution of these swimming, or pelagic, animals (although as we will see, these two origins might be one and the same). I will start with the evidence for animals originating in the Neoproterozoic (~1000 to 541 million years ago [Mya]), and explain why this is such an interesting geological window for their diversification. After making some important distinctions about pelagic animal types, I will then go through the evolutionary tree, trying to determine what we can infer about Neoproterozoic animals given the paucity of their fossil record. Despite the lack of direct evidence, molecular clocks and phylogenetic inference suggest that jellyfish and marine invertebrate larva were likely present in the late Neoproterozoic. The movement of these animals through the Neoproterozoic oceans had the potential to shape early ocean chemistry, paving the way for modern ocean cycles and the radiation of animal life in the Cambrian.

The evidence for and significance of Neoproterozoic animals

Fossil and molecular data are converging upon a unified picture of early animal evolution. For many decades, the paradigm has been a “Cambrian explosion” model, where all major groups of animals originated in a geologically brief window around 541 Mya. While there remains compelling evidence that animal phyla experienced an evolutionary...
radiation in the Cambrian (Briggs 2015), molecular clock studies consistently support an older, Neoproterozoic date for their origin (Erwin et al. 2011; Parfrey et al. 2011; dos Reis et al. 2015; Gold et al. 2015; Sharpe et al. 2015; Dohrmann and Wörheide 2017). There remains a significant degree of uncertainty in these molecular clocks, as we are still learning the ways in which they are sensitive to taxonomic/gene sampling, the mathematical model(s) of evolution being applied, and the fossil calibrations that are included (dos Reis et al. 2015; De Baets et al. 2016; Cunningham et al. 2017). But given the diversity of techniques and datasets used in these studies, the general consensus is striking. New discoveries in the fossil record similarly move animal origins deeper in time. Geochemical “biomarkers” suggest that sea sponges were present ~650 Mya (Love et al. 2009; Gold et al. 2016a), and recent discoveries of additional biomarkers suggest they might be even older (Brocks et al. 2016). Trace fossils demonstrate that animals were moving across the seabed ~560 Mya (Jensen et al. 2006), and burrowing into the seafloor ~550 Mya (Seilacher and Pflüger 1994; Parry et al. 2017). Finally, complex bilaterian animals such as Kimberella are known from ~550 Mya (Fedonkin and Waggoner 1997).

Collectively, these fossils provide an upper limit to the age and diversification of the oldest animal groups (Fig. 1, Top). If we want to understand the ecological and geological conditions that coincide with the initial diversification of animals, we must turn our attention to the Neoproterozoic.

The Neoproterozoic was a time of great environmental upheaval, which likely had profound impacts on the evolution of animals. Geochemical data suggest that oceans were highly euxinic at the start of the Neoproterozoic, with the water column not being fully oxygenated until the late Ediacaran (Fig. 1; Johnston et al. 2010). This was followed by an intermediate period where the ocean was highly stratified. Opposing trends from different geographic regions suggest that these stratified oceans were heterogeneous, shifting betweenoxic and anoxic conditions (Fike et al. 2006; Frei et al. 2009; Johnston et al. 2010; Sahoo et al. 2012). Adding to this environmental chaos was at least three major glaciation events, the Sturtian (~717–643 Mya), Marinoan (~650–635 Mya), and Gaskiers (~579 Mya) glaciations (Canfield et al. 2007; Rooney et al. 2014). It is hard to imagine such profound changes in ocean chemistry and climate did not impact the evolution of animals. Cold, poorly-oxygenated waters might have hindered the development of complex animals (Canfield et al. 2007; Chen et al. 2015; Tostevin et al. 2016).

Alternatively, shifting oxic conditions could have provided an impetus to evolve pelagic life stages, which could escape from poisonous shifts in local environments. In addition to the impact that the ocean might have had on animals, it is equally intriguing to consider the impact animals may have had on the ocean. Small, planktonic animals drifting along ocean currents could have played a critical role in capturing photosynthetically-produced organic matter and developing the ocean’s “biological pump” (Turner 2015). Additionally, many pelagic animals move up and down the water column based on a daily cycle (diel vertical migration), and play a significant role in ocean mixing (Katija and Dabiri 2009; Dabiri 2010).

Several recent papers hypothesize feedback loops between animal evolution and the Neoproterozoic environment (Butterfield 2009, 2011, 2018; Lenton et al. 2014): implicit in many of these proposals is the presence of diverse, pelagic animal species. Such proposals run counter to a direct reading of the fossil record, which suggests that pelagic animals radiated in the Cambrian–Ordovician (Nützel and Fryda 2003; Vinther et al. 2014; Servais et al. 2016) and again in the Silurian–Devonian (Klug et al. 2010, 2017). Understanding whether pelagic animals existed in the Neoproterozoic is critical to assessing hypotheses about Earth–life interactions at this important time.

Although there is no strong evidence for pelagic animals in the Neoproterozoic fossil record, we should be able to deduce whether pelagic forms existed based on molecular clock data combined with phylogenetic inference. But as this review will demonstrate, the issue is not straightforward. It cuts across contemporary debates about the earliest-branching animal lineages, as well as century-old arguments regarding the complexity of the first bilaterians and the homology of certain larval forms. It is also the case that not all pelagic animals are comparable; the ecological role of microscopic larvae passively drifting across ocean currents is distinct from large jellyfish moving through the water in search of prey. Subsequently, some important distinctions need to be made:

1. Plankton versus nekton: Firstly, it is important to distinguish between animals that are passively moved by ocean currents (the plankton), and those that actively swim through the water column (the nekton). These two ecological modes are not mutually exclusive; copepods, jellyfish, and salps largely function as plankton, but many species are capable of active swimming and participate in diel vertical migration.
(Wiebe et al. 1979; Lampert 1989; Klug et al. 2010). Animals that are microscopic and use cilia-powered locomotion are less likely to play an important role in ocean mixing than those that are macroscopic and use muscle-powered locomotion.

(2) Larvae versus adults: A second complication is that most marine invertebrates demonstrate complex life cycles, and it is common for them to have benthic adult stages with pelagic larval stages. Some scientists have hypothesized that this pelago-benthic lifecycle is ancestral, meaning pelagic larvae are as old as animals (Jagersten 1972; Nielsen 2012). However, many larval forms are short lived and/or poor swimmers, and are therefore unlikely to make major contributions to plankton ecology.

(3) Lecithotrophy versus planktotrophy: A third consideration is the type of larvae that various animals produce. Larvae can be broadly divided into non-feeding forms that get their energy from a yolk (lecithotrophy) and those that feed on other organisms (planktotrophy). Only planktotrophic larvae can play a major role in sequestering carbon and organic material from the ocean’s surface. Planktotrophic larvae can also survive in the water column for much longer than lecithotrophic larvae, and subsequently travel greater distances on ocean currents. This not only has profound evolutionary implications for benthic animals (Jablonski and Lutz 1983), but the presence of planktotrophic larvae in Neoproterozoic oceans would also suggest a complex food web had developed by this time.

(4) Crown versus stem groups: In phylogenetics, organisms are (ideally) grouped together based on the presence of a shared last common ancestor. That last common ancestor and all of its descendants, living and extinct, represent the crown members of a group. For example, the “arthropods” are a group of animals that can be defined as those species that share a common ancestor with horseshoe crabs and insects. These “crown” members need to be distinguished from extinct “stem” members of the group, which

![Diagram](https://example.com/diagram.png)
evolved prior to the last common ancestor (Budd and Jensen 2000; Budd and Jackson 2016). Members of the stem group often have some traits of the crown group, but not all of them. The stem/crown distinction is critical for this discussion, because most of the animals that existed in the Neoproterozoic were probably stem members of major crown groups. As an example, molecular clocks support the idea that crown-group arthropods originated around the Cambrian, but the lineage leading to arthropods (the stem) extended back into the Neoproterozoic (Lee et al. 2013). Crown arthropods all have rigid exoskeletons and jointed appendages, but there is no evidence for animals with such traits in the Neoproterozoic fossil record. The easiest explanation for this discrepancy is that Neoproterozoic stem arthropods lacked such traits. In short, just because living members of a group are all pelagic does not mean that the stem members of that group were also pelagic.

These distinctions are critical for assessing the types of pelagic animals that might have existed in the Neoproterozoic, and what sort of ecological roles they might have played. At each stage of animal evolution, we have to consider what the last common ancestor of the crown group looked like, when it evolved, and what can we infer about the stem members of that lineage. Ultimately, the goal of this paper is to use this phylogenetic approach to determine what evidence, if any, exists for pelagic animals in the Neoproterozoic.

**Were the first animals pelagic? Porifera and Ctenophora**

Right out the gate we are met with a hurdle, caused by ongoing uncertainty about the evolutionary relationships between the earliest animals. There are currently two phyla fighting for the position of earliest-branching animal lineage: the sea sponges (phylum Porifera) and the comb jellies (phylum Ctenophora) (Fig. 2). The last decade has seen a flurry of papers using molecular data to support one hypothesis over the other (Dunn et al. 2008; Philippe et al. 2009; Pick et al. 2010; Borowiec et al. 2015; Whelan et al. 2015, 2017; Feuda et al. 2017; Simion et al. 2017). In the ongoing debate, there have been challenges to the idea that the first animals were sponge-like (e.g., sponge choanocytes are not homologous to choanoflagellates) or ctenophore-like (e.g., the nervous system of ctenophores arose independently from other animals) (Dunn et al. 2015; Moroz 2015). While arguments on both sides have merit, the last common ancestor must have looked like something. In truth both sponges and ctenophores contain a mosaic of ancestral and derived traits, and disentangling which characters are ancestral will be a complicated effort, regardless of which lineage evolved first (King and Rokas 2017). Unfortunately, disentangling these traits is critical to understanding when pelagic forms evolved in the animals.

Sponges are sessile (immobile) filter-feeders that lack the nervous and muscular systems found in other major animal groups. Most sponges produce ciliated, lecithotrophic larvae, which undergo metamorphosis within 24 h of their release (Pechenik 2010). While such larvae appear too short-lived to make meaningful contributions to Neoproterozoic oceans, sea sponges have traits that could have made them robust competitors on the ocean floor. Many sponge species can grow and reproduce under extremely cold temperatures, low oxygen concentrations, and can subsist on a diet of dissolved organic matter (De Goeij et al. 2013; Mills et al. 2014; Sperling et al. 2015). Early sponges could have had an ecology similar to the rangeomorphs, frond-like benthic organisms that represent the oldest large eukaryotes in the Neoproterozoic fossil record (Narbonne 2004; Ghisalberti et al. 2014). Indeed, putative (albeit inconclusive) sponge fossils have been recovered alongside these rangeomorphs (Sperling et al. 2011; Zhang and Cui 2016; Butterfield 2018; Rytkönen 2018), suggesting that sponges might have diversified while competing with rangeomorphs for organic matter.

In contrast to sponges, the ctenophores are active (albeit weak) swimmers that prey on zooplankton. Ctenophores swim using rows of cilia, but they also have musculature that controls their mouth, digestive system, and tentacles. Several unusual features about this clade make it difficult to infer what ancient ctenophores looked like. Firstly, the living ctenophores are only represented by ~150 species (Pechenik 2010), and they are closely related. So although the stem ctenophore lineage extends back to the origin of animals, the last common ancestor of living ctenophores is quite young; the most recent molecular clocks suggest they originated between 456 and 261 Mya (Whelan et al. 2017). Secondly, putative fossil ctenophores from the Cambrian are quite different from living forms, and include a variety of benthic and armored species (Ou et al. 2015). It is quite possible that ctenophore morphology as seen today is highly derived, and swimming ctenophores could have developed in the Cambrian from sessile organisms like *Stromatoveris* (Shu et al. 2006). There is good reason to be skeptical about using living
ctenophores as models of the first animals, regardless of their evolutionary position.

Can anything be inferred about the earliest animals given our uncertainty regarding the base of the animal tree? Perhaps the most compelling evidence comes from the geochemical record, where certain Neoproterozoic rocks are dominated by unusual lipid compounds such as 24-isopropylcholestane (Love et al. 2009) and crysotane (Brocks et al. 2016). These compounds are rare in nature, but produced in abundance by certain sea sponges living today. Genetic studies of biomarker biosynthesis suggest that sponges were the only organisms capable of generating 24-isopropylcholestane in the Neoproterozoic (Gold et al. 2016a, 2017); cryostane has yet to be analyzed with similar methods. Importantly, it is thought that these exotic lipids evolved in sponges as a chemical defense against microbes and predators, since sponges have no physical means to escape predation. So despite ongoing uncertainty about the exact interpretation of these geochemical compounds (Gold et al. 2016b), 24-isopropylcholestane offers a strong indicator of sessile, sponge-grade (i.e., sponge or stem-sponge) animals in the Neoproterozoic. This helps bring the fossil record and molecular clocks into congruence, but does little to inform us of when the first ecologically-important pelagic animals evolved.

**Jellyfish oceans: the Cnidaria**

The Cnidaria is a diverse animal clade that encompasses sea anemones, corals, hydroids, and jellyfish. Phylogenetic analyses consistently place cnidarians between the sponges and bilaterians (Fig. 2) making them one of the earliest-branching animal lineages. The cnidarians can be subdivided into two major clades: the Anthozoa (sea anemones and corals) and Medusozoa (hydroids and jellyfish). The parasitic and secondarily-simplified myxozoans are also part of the Medusozoa (Jiménez-Guri et al. 2007), but for the purposes of this paper I use the term to
refer to the three major clades: Hydrozoa, Scyphozoa, and Cubozoa. Both anthozoa and medusozoa have a ciliated larval form called the planula. The ancestral planula was probably lecithotrophic, although some anthozoa have evolved planktotrophic larva, presumably as a way to increase larval dispersal (Collins 2002). In anthozoa, the adult or polyp stage is generally sessile and benthic; medusozoa often have a polyp stage as well as an additional adult stage called the medusa (Fig. 2). The medusa generally exhibits muscle-powered swimming, and is what people commonly think of when they envision a jellyfish. The morphology and development of medusae is highly variable, but gene expression analyses (Kraus et al. 2015) and ancestral state reconstruction (Kayal et al. 2017) suggest that the medusa life stage was present in the last common ancestor of crown-group Medusozoa. There are no well-supported medusa fossils in the Neoproterozoic, but fossils of the major living medusozoan clades exist in the middle Cambrian, ~505 Mya (Cartwright et al. 2007) with probable crown-group medusae ~521 Mya (Han et al. 2016). Similar to sponges, cnidarian larva likely played minimal ecological roles in the Neoproterozoic, but medusae may have been active swimmers and predators at this time.

The morphology of the first cnidarians is a debate that goes back over a century (Brooks 1866). Prior to the era of phylogenetics, many scientists preferred the hypothesis that the first cnidarians were medusozoa (Hyman 1940). However, molecular data strongly suggest that anthozoans and medusozoa are sister groups (Fig. 2; Zapata et al. 2015). The derived structure of medusozoan mitochondrial DNA (Bridge et al. 1992), cladistics analyses (Marques and Collins 2005), and ancestral state reconstruction of life history characters (Kayal et al. 2017) all suggest that the medusa life stage is derived. However, the polyp and medusa stages are both unique to Cnidaria, and given the sister-group relationship of the two clades, the gain of the medusa life stage in Medusozoa is not significantly less parsimonious than the loss of the medusa life stage in Anthozoa.

Fortunately, knowing the life cycle of the original cnidarian is not necessary to make inferences about pelagic cnidarians in the Neoproterozoic. Phylogenetic inference dictates that planula larvae must have evolved by the origin of crown-group Cnidaria, which molecular clocks consistently place in the Neoproterozoic (Fig. 1). Many molecular clock analyses have not sufficiently sampled medusozoa to get a crown-group date, but those that have support the hypothesis that they also diversified in the Neoproterozoic (Park et al. 2012; Dohrmann and Wörheide 2017). The divergence of crown-group Medusozoa in the Neoproterozoic provides the first line of evidence that animals capable of muscle-powered swimming had evolved by this time. Since all cnidarians are carnivores, the presence of medusozoa in Neoproterozoic oceans also implies the existence of other animal groups; what those animals might have been like requires an analysis of the final major animal clade—the Bilateria.

**Prelude to the Cambrian: Bilateria**

Bilateria make up ~99% of all living animal species, and they dominate the animal contribution to the modern ocean, ranging from crustacean larvae and pteropod molluscs in the plankton to fish, whales, and squid in the nekton. Most bilaterians can be subdivided into three “superphyla” (Fig. 2): the Deuterostoma (echinoderms, vertebrates), Lophotrochozoa (annelid worms, flatworms, molluscs), and Ecdysozoa (arthropods, nematode worms). The Xenacoelomorpha represents a fourth minor clade of small, ciliated worms, and is probably a sister group to the rest of the Bilateria (Cannon et al. 2016). Molecular clocks are broadly consistent with the hypothesis that most bilaterian phyla originated at or around the Neoproterozoic/Cambrian boundary, with their ancestors diverging in the Neoproterozoic. Thus the ecology of bilaterians in the Neoproterozoic is largely contingent on what stem members of the various phyla and superphyla looked like.

Once again, the morphology of the first bilaterians runs into a long and unresolved scientific debate. The Xenacoelomorpha are small, benthic, ciliated worms, with the last common ancestor likely exhibiting direct development from a lecithotrophic embryo (Nakano et al. 2013). If Xenacoelomorpha are taken as a good proxy for the earliest bilaterians, then the last common ancestor would have lacked a larval stage or a benthic-pelagic life cycle. Moving higher up the phylogenetic tree (node “Nephrozoa” in Fig. 2), the picture becomes more ambiguous. Many nephrozoan animals have a pelagic larval stage, and debates tend to focus on whether the last common ancestor was pelagic and larval-like, benthic, and adult-like, or featured a dual lifecycle with both stages (Nielsen 2008, 2012; Raff 2008). In other words, are the larva of bilaterian animals shared from a last common ancestor?

Some paleontologists have attempted to answer this question using the fossil record. Animal larvae
are generally associated with larger-bodied animals (Olive 1985), and Ediacaran fossils of benthic animals the size of Haootia, Kimberella, and (controversially) Dickinsonia could indicate the presence of larvae (Fedonkin and Waggoner 1997; Liu et al. 2014; Gold et al. 2015). Similarly, putative animal embryos from the Neoproterozoic Doushantuo Formation (~570 Mya) are on the larger end of the size spectrum (Xiao and Knoll 2000), which is often an indicator of lecithotrophic larva. These arguments are difficult to test. Several studies have looked at the anatomy of Cambrian molluscs and brachiopods to determine whether their larvae were ancestrally lecithotrophic and planktotrophic; unfortunately these studies offer conflicting results, and have come under heavy scrutiny (Freeman and Lundelius 1999, 2005, 2007; Nützel et al. 2006; Runnegar 2007). There is a lot of potential in these paleontological analyses, but the current interpretations are far from conclusive.

Part of the difficulty in homologizing bilaterian larvae is the vast variety of larval forms; a sampling is illustrated in Fig. 2, although it fails to do justice to their diversity. Many attempts have been made to unify these larvae into homologous forms based in biology. For example, molluscs, annelids, entoprocts, and some nemerteans are thought to share a “trochophore”-type larva, defined by a homologous ring of cilia called the prototroch (Rouse 1999; Maslakova et al. 2004a, 2004b). Similarly, echinoderm and hemichordate deuterostomes likely share a “dipleurula”-type larva from their last common ancestor (Byrne et al. 2007; Cannon et al. 2014). The real debate is whether distantly related larval forms like the trochophore and dipleurula also share a common ancestor. This has proven hard to determine based on physical traits; larvae are morphologically simple and very similar in size and ecology, meaning convergent evolution is likely to be rampant. More recently, gene expression data have been used to argue that the larvae of bilaterians are homologous to each other and even to cnidian planula (Marlow et al. 2014). But candidate genes sometimes give inconsistent results, and similarities in gene expression could represent convergent cooption of particular cell types and/or developmental patterning process in various larval groups (Raff 2008). Even if the last common ancestor had a larval stage, there is disagreement about whether that larva could feed (Signor and Vermeij 1994; Peterson 2005). Many animal groups exhibit multiple shifts between lecithotrophic and planktotrophic larva, sometimes over rapid evolutionary timescales (McHugh and Rouse 1998; Rouse 2000; Raff 2008).

The diversity and plasticity of animal larvae should give us pause before concluding that they are all homologous, and impedes confidence that any Neoproterozoic bilaterians were active swimmers.

**Conclusion: missing records and long fuses**

While there is a growing consensus that animals evolved and diversified in the Neoproterozoic, uncertainty about the relationships between certain animal groups and larval forms severely limits our ability to infer what these early animals looked like. I have attempted to summarize this uncertainty in Fig. 2, with a conservative view on the homology of larval forms. Based on these results, I think it is likely that lecithotrophic larvae existed in the Neoproterozoic, and it is quite possible that planktotrophic larvae were present as well. Unfortunately, it does not appear that the latter can be said with confidence, given the rapid ability of larva to evolve back and forth between the two strategies. This is an important caveat, as hypotheses that suggest zooplankton helped drive changes in Neoproterozoic ocean chemistry require larvae that are feeding and sequestering organic matter.

Besides looking for new discoveries in the fossil record, what can be done to resolve this uncertainty? Firstly, refinement of the molecular clock is needed. While some of the variables affecting molecular clocks need continued evaluation (e.g., models of evolution, substitution rates, calibrations), an obvious way forward involves better taxon sampling. Even the most recent molecular clocks only have a few representatives of early-branching animal lineages, and many of them are missing major clades entirely. Well-sampled trees with cnidarians and sponges would allow for greater fossil calibration, and more reliable date estimations for crown groups. Once these clocks are established, ancestral state reconstruction could be used to better understand the gain and loss of pelagic life stages across the animals. Such work has recently been done in arthropods, and suggests that larval metamorphosis could have evolved in this group in the Neoproterozoic (Wolfe 2017). Broadening this approach across the entire animal tree would provide a major step forward in this problem.

A second area of focus involves the medusozoan jellyfish (the one group of muscle-powered animals that almost certainly swam in the Neoproterozoic) and their role in ocean chemistry. Besides their above-mentioned role in ocean mixing, jellyfish are planktonic predators that concentrate and transport...
nutrients through their environment. Jellyfish are known to release carbon-rich dissolved organic matter that is readily taken up by bacterioplankton, and population explosions (or blooms) of jellyfish are associated with shifts in ocean bacterial communities (Condon et al. 2011). Jellyfish also recycle large amounts of phosphorous and nitrogen, and depending on the species can either provide a source of these nutrients for phytoplankton, or else compete with them for it (Pitt et al. 2009). Studying the growth and metabolism of jellyfish under Neoproterozoic-like oceanic conditions could elucidate their contribution to ancient nutrient cycling. Through this combination of experimental and genetic approaches, the significance of swimming animals in the Neoproterozoic will be clarified.

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**References**


