





Review

Fossilisation processes and our reading of animal antiquity

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Estimates for animal antiquity exhibit a significant disconnect between those from molecular clocks, which indicate crown animals evolved ~800 million years ago (Ma), and those from the fossil record, which extends only ~574 Ma. Taphonomy is often held culpable: early animals were too small/soft/fragile to fossilise, or the circumstances that preserve them were uncommon in the early Neoproterozoic. We assess this idea by comparing Neoproterozoic fossilisation processes with those of the Cambrian and its abundant animal fossils. Cambrian Burgess Shale-type (BST) preservation captures animals in mudstones showing a narrow range of mineralogies; yet, fossiliferous Neoproterozoic mudstones rarely share the same mineralogy. Animal fossils are absent where BST preservation occurs in deposits ≥ 789 Ma, suggesting a soft maximum constraint on animal antiquity.

The origin of animals: a disconnect in the evidence

The probability of fossilisation has long been recognised as a significant factor in our reading of early animal evolution and the antiquity of **Metazoa** (see [Glossary](#)). Charles Darwin was troubled by the sudden appearance of animal life in basal **Cambrian** strata and was unable to explain the lack of animals in **Precambrian** rocks: ‘It is indisputable that before the lowest [Cambrian] stratum was deposited, long periods elapsed ... and ... the world swarmed with living creatures. To the question why we do not find records of these vast primordial periods, I can give no satisfactory answer’ [1]. Since Darwin, the scarcity of Precambrian animal fossils has often been attributed to **taphonomic** factors: early animals were too small or fragile to fossilise [2], preservation was not favoured until animals evolved biomineralised skeletons [3], or palaeontologists have searched in the wrong settings [4].

The importance of taphonomic factors gains support in molecular estimates that extend the timing of animal origins into the **Neoproterozoic** Era (Figure 1). Almost all recent molecular clocks predict that the last common ancestor of extant animals inhabited seas of at least **Cryogenian** age [720–635 million years ago (Ma)] or even older (e.g., 800 Ma, during the **Tonian** Period) [5–8], but no *bona fide* animal body fossils are known from strata of this age [9]. A diversity of nonbiomineralised organisms has been recovered from Proterozoic successions [10], but most are interpreted as microbes (e.g., bacteria, protists) [9,11]. The macroscopic **Ediacara Biota** provides the oldest compelling candidates for early soft-bodied animal fossils. *Dickinsonia* has been interpreted as an animal (possibly even a **eumetazoan** [12]) based on behavioural [13], developmental [12], and geochemical [14] evidence, and metazoan affinities have been proposed for other Ediacara Biota fossils with varying degrees of support (e.g., *Kimberella* [15] and frondose forms [12]). The oldest candidate Ediacara Biota animal fossils are from the Drook Formation (Newfoundland, Canada), 574.17 ± 0.66 Ma [16,17]. Older records of animals (mostly microscopic cyst and embryo-like fossils)

Highlights

The last common ancestor of animals is thought to have been small and soft-bodied and therefore would have required special conditions for its preservation.

Limited availability of these conditions in the Neoproterozoic could explain the discrepancy between molecular clock predictions for the timing of animal origins and the fossil record of animals.

We assess the availability of these conditions, particularly those of Burgess Shale-type, which are known to preserve animals with tissues of varied composition.

Burgess Shale-type conditions are rarely associated with Neoproterozoic fossil biotas, but in the few assemblages with these conditions, dated to 789 million years ago or older, no animals have been identified, suggesting they had not evolved by this time.

This provides a soft maximum age constraint on crown group animals of 789 million years ago.

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have been proposed [18–20], but alternative interpretations are possible [9,21], and even the biological origin of some is questioned [9,22].

How can the disparity in estimates of animal origins based on molecular clocks and fossils be reconciled? The fossil record might fail to capture the first animals because (i) Neoproterozoic environments were unsuitable for their fossilisation, (ii) animals lived in areas not sampled by the Neoproterozoic fossil record, (iii) they were too small/soft/fragile or rare to be preserved, or (iv) early animal fossils were not recognisable because they did not preserve distinguishing features. Alternatively, molecular estimates may exaggerate the antiquity of animal evolution [23]. Here, we incorporate geochemical and mineralogical data to address a fundamental question: To what extent did the conditions that facilitated the exceptional preservation of early animals in the Cambrian prevail during the Neoproterozoic? We highlight how future research could lead to a better understanding of the availability of favourable fossilisation conditions in space and time, and how such conditions might promote the preservation of different animal groups.

Burgess Shale-type preservation – the preeminent mode of fossilisation for early animals

The first animals presumably lacked biomineralised shells or skeletons and required exceptional conditions for fossilisation [24] (Box 1). Exceptional preservation is relatively common in Cambrian **mudstone** deposits (>50 sites) via **Burgess Shale-type (BST) preservation** [25]. Much of our understanding of Cambrian animal diversity, disparity, and ecology relies on fossils preserved in this way. For example, the iconic Burgess Shale Formation in British Columbia, Canada, preserves not only the usual Cambrian shelly fauna but also a diverse assemblage of entirely soft-bodied animals [26]. BST preservation conserves a spectrum of animal tissues, which can be characterised as biomineralised, **sclerotised**, **cuticularised** (but not sclerotised), and cellular [27], and even nervous tissue has been documented [28]. Moreover, the BST record is not confined to macroscopic organisms: a plethora of microscopic animals, including arthropods and loriciferans, has been recovered as **small carbonaceous fossils** (SCFs) [29,30]. All the major groups (phyla) of modern animals are represented in Cambrian deposits with BST preservation apart from Entoprocta, Nermertea (ribbon worms), Nematoda (round worms), Platyhelminthes (flatworms), Rotifera (wheel animals), and possibly Bryozoa (moss animals) [6,31].

Much of the known Proterozoic fossil record (early eukaryotes, bacteria), i.e., ~75% of described fossil assemblages, is recorded in fine-grained mudstones [10]. The **lithological** similarity between Neoproterozoic and Cambrian mudstones that preserve soft-bodied organisms prompts us to ask whether the same fossilisation processes were at play in each. Are organic fossils in Neoproterozoic mudstones the result of BST preservation? Given that BST conditions preserve small, soft, and fragile animals in the Cambrian, a lack of widely accepted animal fossils in Neoproterozoic successions, even if BST preservation occurred, would suggest a real absence of animals at that time.

An assortment of environmental factors are involved in BST preservation including limited oxidant supply (both oxygen and sulfate), sediment (e.g., clay) that minimises porosity/permeability and provides an antibacterial burial environment, **authigenic** mineralisation that replicates soft tissues in geologically long-lived minerals (Al- and Fe-rich clays, as well as phosphate and pyrite), **polymerisation** that enhances the decay resistance of organic remains, and early cementation (e.g., authigenic carbonate) forming sedimentary seals that stop oxidants diffusing to the carcass [25]. Clay minerals are a key component of both sediment composition and authigenic mineralisation in BST preservation [32–35] and are a factor in soft-tissue fossilisation more generally [36]; experiments show that carcasses undergo markedly less decay when clay minerals are present

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[37]. Geological evidence [38–40] (Figure 2A,B) has been used to test the role of clays in BST preservation, but has so far focussed on the Al- and Fe-rich clays **kaolinite** and **berthierine** (berthierine can form during early **diagenesis** via the transformation of structurally analogous kaolinite in the presence of pore-water Fe^{2+} [41]), which have been shown to have antibacterial properties [42].

Motivated by evidence of a role for clays, we focus here on the occurrence of BST preservation in Neoproterozoic strata as a potential source of the first animals. We track two distinct but complementary factors affecting preservation: (i) clay enrichment within the host sediment and (ii) clays bonded directly to fossils (Box 2).

Sedimentary clay enrichment

Until recently, data on the mineralogical composition of deposits with BST preservation were limited to a small number of biotas, e.g., Burgess Shale, Chengjiang (China) [38]. This was remedied by an analysis of the mineralogy of fossiliferous Cambrian mudstones globally (19 sites), using X-ray diffraction to compare those hosting BST fossils with those preserving only biomineralised remains (e.g., trilobites/brachiopods) [38] (Figure 2B). It found that mineralogy can predict the occurrence of BST preservation in fossiliferous Cambrian mudstones with an accuracy >80% [38]. Deposits preserving BST fossils are characterised by a restricted mineralogy enriched in the antibacterial [42] clay berthierine; samples comprising >20% berthierine yield BST fossils in >90% of cases [38]. Preservation falls significantly, however, with increased illite content: samples with >50% illite have <30% chance of yielding BST fossils [38]. The Fezouata Shale (Morocco), an **Ordovician** deposit with BST preservation, is also berthierine-rich [39].

The distribution of clay minerals in Neoproterozoic mudstones is poorly known [43,44] (Figure 2C–E). However, a recent study of Neoproterozoic mudstones that host **organic-walled microfossils** shows that specific clays such as berthierine have a limited (perhaps even negative) impact on preservation quality [45]. Nonetheless, the probability that well-preserved microfossils are present in Neoproterozoic mudstones increases with the content of clays of any kind: the chance of finding well-preserved microfossils (indicated by the survival of details of the cell-wall margin) is >50% in the presence of clay concentrations >40% [45].

The contrast between the specific mineralogy of Cambrian deposits with BST preservation and the varied mineralogies of Neoproterozoic deposits that yield organic-walled microfossils [45] may reflect the less exacting conditions required to preserve cell walls in the latter [46]. Organic-walled microfossils are thought to represent a variety of microscopic eukaryotes and bacteria, organisms that have resistant cell walls of **aliphatic** composition similar to dinosporin, sporopollenin, or algaenan today [47,48], or protective bacterial sheaths composed of carbohydrate fibrils and proteins [49]. In contrast, early animals were composed of a variety of labile proteins, carbohydrates, and lipids, which require rapid stabilisation to be fossilised [50], as well as more decay-resistant sclerotised and cuticularised tissues [27].

In summary, the available evidence suggests that the mineralogical composition of fossiliferous Neoproterozoic sediments facilitated the preservation of resistant biopolymers such as those in organic-walled microfossils, but rarely reached the threshold (e.g., presence of particular mineral phases such as berthierine) for the preservation of labile animal tissues via BST preservation.

Clay-organic matter bonding

Heterogeneities in the chemical composition of anatomical features in Burgess Shale fossils were first documented using energy dispersive X-ray spectroscopy (EDS) and attributed to the

Glossary

Acanthomorphic: bearing spines.

Aliphatic: organic compounds in which the carbon atoms form open chains.

Authigenic: precipitated where it is found.

Berthierine: iron-rich, aluminous, clay mineral belonging to the kaolinite-serpentine group (Fe^{2+} , Fe^{3+} , $\text{Al}_3(\text{Si,Al})_2\text{O}_5(\text{OH})_4$).

Bilateria: clade of crown animals characterised by bilateral symmetry.

Burgess Shale-type preservation: style of exceptional preservation of fossil soft tissues characterised by carbonaceous remains preserved in fully marine, fine-grained, siliciclastic rocks.

Cambrian: geological period from 539 Ma to 485 Ma.

Chert: hard, fine-grained sedimentary rock composed of silica (SiO_2).

Cryogenian: geological period from 720 Ma to 635 Ma.

Cuticularised: body with a unsclerotised cuticle (i.e., noncellular outer body surface that is composed of collagen or cross-linked polysaccharides).

Diagenesis: physical and chemical changes of sedimentary materials that occur after initial deposition and before rock metamorphism.

Ediacara Biota: assemblage of macroscopic fossils with complex morphologies known from the later part of the Ediacaran Period worldwide. Iconic sites include those in South Australia and Newfoundland (Canada). The assemblage includes the oldest definitive animal fossils.

Ediacaran: geological period from 635 Ma to 539 Ma.

Eumetazoa: clade of animals comprising all crown animals except sponges.

Kaolinite: aluminium-rich clay $\text{Al}_2\text{Si}_2\text{O}_5(\text{OH})_4$.

Lithology: referring to types of rock as defined by their general physical characteristics.

Metazoa: clade defining all crown animals and their last common ancestor.

Mudstone: fine-grained sedimentary rock made predominantly of clay. It is a common repository of exceptionally preserved fossils in the Neoproterozoic and Cambrian.

Neoproterozoic: geological era from 1000 Ma to 539 Ma.

Ordovician: geological period from 485 Ma to 444 Ma.

influence of differing reactivity of tissues on the precipitation or physical attachment and binding of clays during decay [34]. The role of direct clay-organic bonds in BST preservation is controversial, however, and the association of clay films with BST fossils has also been explained as a result of low-grade thermal maturation which occurred later in their history [51,52] or as an indication that metal iron adsorption (e.g., Fe^{2+}) was the agent inhibiting decay [35]. Analysis of fossils from the Burgess Shale Formation using the new method of *in situ* selected-area X-ray diffraction to map the distribution of minerals rather than elements, however, showed that kaolinite bonded to decaying carcasses at a very early stage [40].

Microanalytical study of direct clay-microfossil associations from three of the most biodiverse Neoproterozoic mudstones, the ~1000-million-year-old Lakhanda Group (Siberia, Russia), and the ~800-million-year-old Svanbergfjellet (Svalbard, Norway) and Wynnatt (Nunavut, Canada) formations, suggests that the role of BST preservation promoted by clays was as important in some Neoproterozoic as in Cambrian settings [53]. These three deposits preserve multicellular and filamentous microorganisms, as well as forms with complex spines/processes that appear to be more fragile than typical spheroidal organic-walled forms common in Neoproterozoic assemblages [11,33]. Elemental (EDS) and mineralogical mapping (synchrotron-based infrared microspectroscopy) revealed enrichments of kaolinite immediately adjacent to cell walls and forming protective haloes around the fossils [53].

Similarities in the distribution of clays in fossils from these three Neoproterozoic deposits and those from the Burgess Shale suggest that, in both cases, clays attached to or precipitated on decaying tissues, and that conditions conducive to BST preservation were available in both time periods. The diversity of fossil organisms and biopolymers preserved in this way shows no phylogenetic bias. Burgess Shale fossils representing stem taxa from a variety of groups (*Canadia* – annelid, *Marrella* and *Opabinia* – euarthropods, *Ottoia* – priapulid, *Pikaia* – chordate) are associated with kaolinite [40]. Tonian microfossils associated with kaolinite include a chlorophyte, other undetermined eukaryotes, and probable cyanobacteria [53], organisms composed of a variety of biopolymers [27,46–48]. However, no metazoan fossils have been reported from these Neoproterozoic deposits [29].

Integrating fossilisation knowledge to infer animal antiquity

Available data on associations between fossils and clays suggest that Neoproterozoic shales containing diverse organic-walled microfossils were rarely similar in chemical composition to those preserving Cambrian animals via BST preservation. This suggests that fossiliferous Neoproterozoic deposits were less likely to preserve animals. However, geochemical data indicate that some Tonian fossil deposits (Lakhanda Group, Wynnatt Formation, Svanbergfjellet Formation) do share aspects of BST preservation, specifically bonding of clay to fossil organic matter. Nonetheless, animal fossils are absent in these deposits [29], even though conditions are favourable for their preservation [53]. These data support the view that animals had not evolved by the mid-Tonian, contrary to some molecular clock estimates [29,53]. Thus, taphonomic evidence argues for a maximum constraint of 788.72 ± 0.29 Ma on crown animal antiquity (the youngest estimated age of the Svanbergfjellet Formation, which is the youngest Tonian deposit investigated in detail [54]; Figure 1). A constraint of 833 Ma, based on the age of the Bitter Springs Formation (central Australia), which is predominantly **cherty** limestone, was used in some molecular studies [7]. However, we do not know whether the Bitter Springs Formation was favourable for early animal fossilisation.

Other explanations for the absence of animal fossils in the Tonian Period would violate this new maximum constraint: (i) early animals were extremely rare and the Neoproterozoic fossil record

Organic-walled microfossils:

microscopic fossils from the Precambrian that have soft (nonbiomineralised) organic walls.

Phosphatisation: replication of organism soft tissues in the phosphate minerals.

Polymerisation: process of reacting monomer molecules together in a chemical reaction to form polymer chains. These polymer chains are more resistant to decay.

Precambrian: informal interval of geological time from the formation of the Earth ~4600 Ma to 539 Ma.

Pyritisation: replication of organism soft tissues in the mineral pyrite.

Sclerotised: organically strengthened.

Siliceous: made of silica (SiO_2).

Small carbonaceous fossils: exceptionally preserved microscopic fossils of early animals in whole or parts.

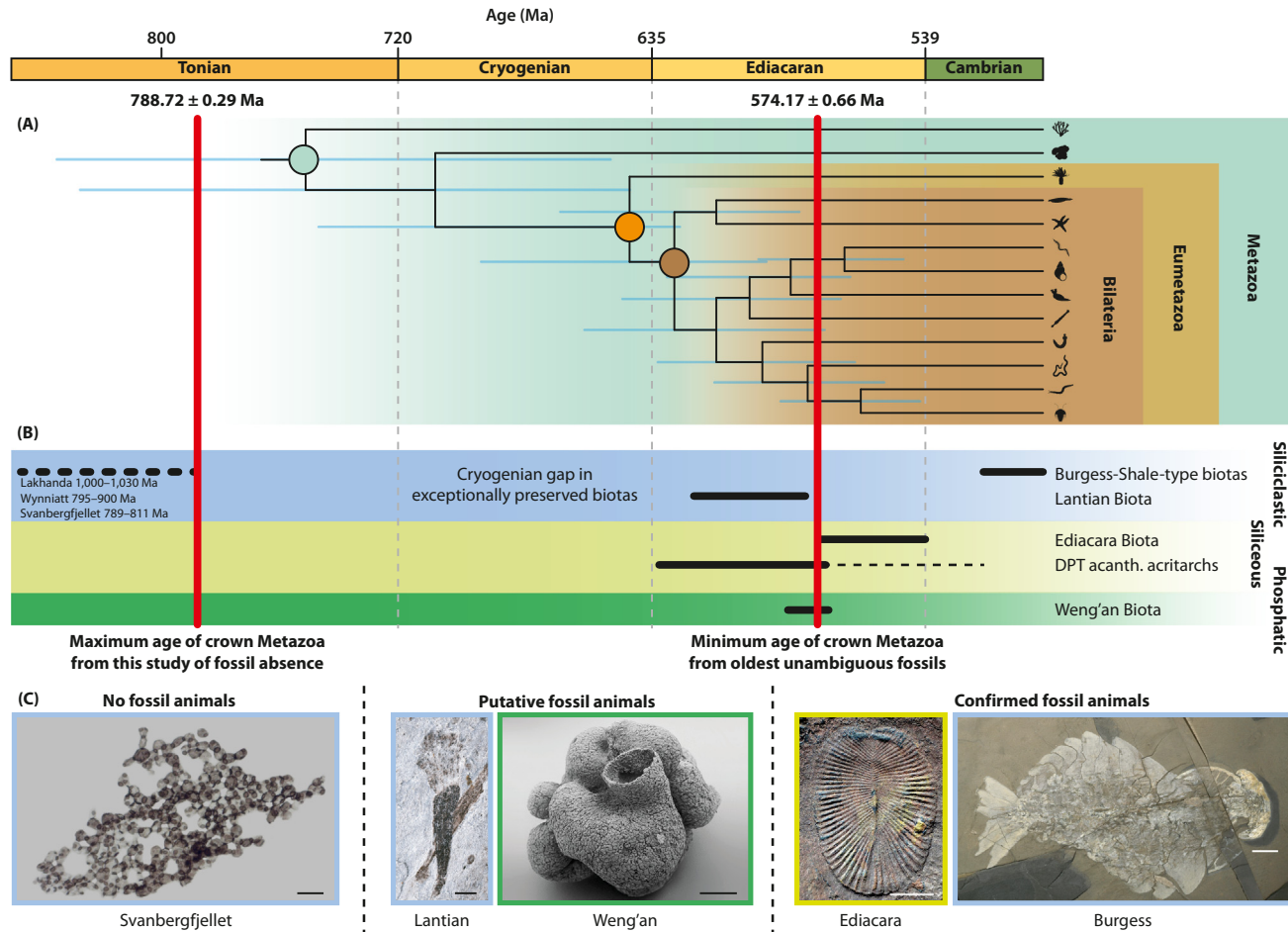
Soft maximum: maximum age constraint used in a Bayesian molecular clock to denote the youngest evidence of true evolutionary absence of a clade. It incorporates uncertainty as a probability that the constraint is violated, typically 1–10%.

Taphonomy: the study of fossilisation processes. Taphonomic factors refer to those that affect the potential for fossilisation.

Terreneuvian: oldest geological series of the Cambrian Period from 539 to ~521 Ma.

Tonian: geological period from 1000 Ma to 720 Ma.

Total organic carbon: total amount of organic carbon in a rock that is used as a proxy for organic matter, whether fossil related or disseminated, expressed as a percent of weight (wt%).



Trends in Ecology & Evolution

Figure 1. Overview of the temporal disconnect between molecular clocks and fossils in the reading of animal antiquity. (A) Animal molecular clock analysis [5,9] that argues for a Tonian last common ancestor. Major groups of animals are highlighted in colour (i.e., Metazoa in sea green, Eumetazoa in tan, and Bilateria in brown) and key nodes by corresponding circles (i.e., last common ancestors of Metazoa, Eumetazoa, and Bilateria). (B) Key fossil assemblages (DPT acanth. = Doushantuo Pertatataka-type acanthomorphic) from different preservation settings. (A, B) Red lines indicate maximum and minimum ages for the origin of crown animals. (C) Representative fossils. Left to right: *Palaeastrum*, a non-metazoan multicellular eukaryote from the Tonian Svanbergfjellet Formation, Norway, scale = 50 μ m (courtesy S. Mughal); *Lantianella*, a possible cnidarian-grade metazoan from the Ediacaran Lantian Formation, China, scale = 5 mm [61]; *Eocyathospongia*, a possible sponge of the Weng'an Biota from the Ediacaran Doushantuo Formation, China, scale = 200 μ m [81]; *Dickinsonia*, an early animal of the Ediacara Biota from the Ediacaran Rawnsley Quartzite Formation, Australia, scale = 10 mm [58]; and *Anomalocaris*, a stem group arthropod from the Cambrian Burgess Shale Formation, Canada, scale = 20 mm (courtesy: Royal Ontario Museum, Canada).

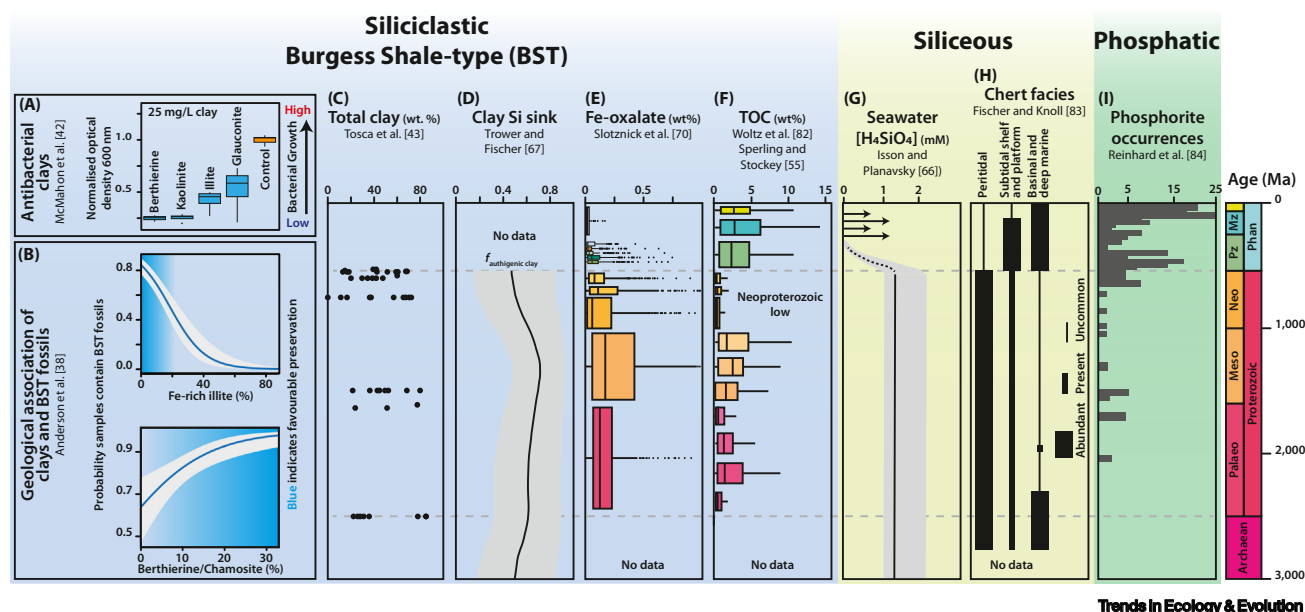
simply does not sample them or they have not yet been found [55], (ii) early animals were present but not recognisable as such because of uncertainty regarding their distinguishing morphological features [56] (Box 1), (iii) BST preservation does not capture all animal groups [6] or sample all environments where early animals may have lived [25], and (iv) we have not sufficiently investigated other rock types, e.g., sandstones such as those that preserve the Ediacara Biota [57,58] (Box 3).

A response to these caveats is the application of ‘soft-maxima’ to molecular clocks using Bayesian methods. Soft-maxima are based on maximum age constraints from the fossil record combined with probabilities that those constraints are violated in order to account for uncertainty in the evidence for evolutionary absence [59]. The taphonomic insights discussed here provide a strong basis for refining the choice of soft-maxima and probability of violation (commonly 1%–

Box 1. Fossilisable features of early animals

Documenting and interpreting the fossil record of the earliest animals requires an understanding of their likely morphology and the organic components used in their construction, as well as a consideration of the conditions required to preserve them in the fossil record via Burgess Shale-type (BST) preservation or other means. Ancestral state reconstruction shows that almost all ancestors of major animal groups and the last common ancestor of animals were entirely soft-bodied and nonbiomineralised [24,56]. The exception is sponges: phylogenetic analysis reconstructs the skeleton of their last common ancestor as siliceous but with some uncertainty as the relationships among sponge classes are not well supported [24] and their fossil record includes a variety of mineralised, weakly mineralised, and entirely nonbiomineralised forms [85]. Even if ancestral sponges lacked biomineralised parts, however, they could be represented via BST preservation. Phylogenomic data show that the last common ancestor of opisthokonts (which include animals and fungi) already had a complex array of synthases of chitin [86], a relatively decay-resistant organic compound. The Cambrian sponge *Vauxia*, which had an entirely organic skeleton likely composed of chitin, occurs in the Burgess Shale [87].

Phylogenetic relationships among basal animals are controversial. There is debate, for example, as to whether sponges or ctenophores (comb-jellies) are sister to all other animal phyla [88]. These alternatives make different predictions about the construction of the first animals and the susceptibility of their organic components to decay. Whereas some traits of the last common ancestor of animals can be predicted regardless of the sponge/ctenophore controversy (e.g., obligate and clonal multicellularity, spermatogenesis, epithelia, cells with a single apical flagellum) [56,88], the presence of others depends on which taxon is considered basal. Ctenophores, in contrast to sponges, are gelatinous animals with distinctive combs of cilia. Despite their gelatinous nature, however, ctenophores are known from Cambrian BST deposits, and some may have had a sclerotised integument [89]. Thus, BST preservation has the potential to record the first animals regardless of whether they shared more traits with sponges or ctenophores.



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Figure 2. Geochemical factors that influence exceptional preservation across geological time. (A) Antibacterial properties of clays. The growth of the heterotrophic bacterium *Pseudoalteromonas* is suppressed in the presence of clays at 25 mg/L clay compared with a control medium [42]. (B) Geological association of clays and BST fossils. The probability of a Cambrian mudstone with fossils of BST preservation as a function of the clay minerals Fe-rich illite and berthierine [38]. (C–I) Geochemical factors leading to BST (siliciclastic) preservation, **siliceous** preservation, and phosphatic preservation tracked across geological time (Palaeo = Palaeoproterozoic, Meso = Mesoproterozoic, Neo = Neoproterozoic, Pz = Palaeozoic, Mz = Mesozoic). (C) Total clay content from X-ray diffraction (dots) of Archaean/Palaeoproterozoic, Mesoproterozoic, and Neoproterozoic mudstone samples [43]. (D) Authigenic clay sink as fraction f of the total Si sink (black line = median, grey shaded area is between the 10th and 90th percentiles), modelled on the basis of Si isotopes (simplest model) – note inverse modelling can yield non-unique solutions [67]. (E) Fe-oxalate (possible proxy for Fe-bearing clays) as wt% in Fe-speciation shown as box and whisker plots (horizontal bars are median values, boxes are interquartile range, outliers above 1% not shown) [70]. (F) **Total organic carbon** (TOC) shown in box-and-whisker plots (horizontal bars are median values, boxes are interquartile range) [55,82]. (G) Modelled seawater silica concentration through time, with arrows denoting possible variation in dissolved silica associated with the ecological success of siliceous organisms [66]. (H) Facies of chert deposition through time [83]. (I) Occurrences of phosphorites through time [84].

Box 2. How do clays promote Burgess Shale-type preservation?

Clays may impact Burgess Shale-type (BST) preservation either through a role in the host sediment or through direct clay-organic chemical interactions. In the host sediment, they have been posited to interfere with microbial decay [32], with recent work focussing on the clays kaolinite and berthierine. These clays have antibacterial properties, likely due to their constituent Al^{3+} and Fe^{2+} , although the precise mechanisms by which they (and other clays) interfere with microbial activity remain to be determined. Experiments have shown that both kaolinite and berthierine inhibit the growth of *Pseudalteromonas* (Figure 2A), a heterotrophic bacterium involved in the decay of marine animals today, and kaolinite also suppresses the growth of sulfate-reducing bacteria, autotrophic methanogens, and a heterotrophic soil bacterium [42]. Kaolinite and berthierine also deactivate autolytic enzymes important to the decay process [32]. Limiting the growth of decay bacteria and the effect of their enzymes inhibits decay, providing a causal link between the clay mineralogy of the host sediment and exceptional preservation.

Clays have been implicated in Cambrian BST preservation also through direct chemical bonding within individual carcasses. These chemical reactions promote the transformation of reactive organic compounds to more recalcitrant counterparts by fostering polymerisation [90], deactivating functional groups through adsorption [91], and stabilising pre-existing polymer cross-linkages [92]. Whether clays precipitated *de novo* or pre-existing clays attached to carcasses remains to be determined: experimental studies suggest that both attachment [93] and precipitation [94] of clays on organic tissues are viable. So far, geochemical analysis of fossils has suggested kaolinite may be the dominant clay involved in this process [34,40,53]. Kaolinite may be suited to interactions with decaying organic matter, given the acidity and area of its edge sites (10%–20% of its entire surface area) where organic binding would occur [95]. However, whether kaolinite is uniquely suited to such interactions is unclear; existing experimental and observational data on the role of clays in BST preservation have not yet elucidated the molecular scale mechanisms underpinning exceptional preservation.

10% [59]) and will lead to greater confidence in the ages used to calibrate molecular clocks. In the case of the origin of animals, the probability that the ~789 Ma constraint is violated by the clock will be reduced if future investigations of fossiliferous deposits ≥ 789 Ma with fossil-clay associations reveal no animals. Likewise, if the abundance of Neoproterozoic mudstones reaching the threshold weight percentage for minerals required for BST preservation were known, and none of them preserve animal fossils, those data could be included in the Bayesian clock model, increasing confidence in the maximum constraint.

Box 3. Other preservation windows for early animals

Burgess Shale-type (BST) preservation is not the only route to the fossilisation of early animals. Most Ediacara Biota fossils, for example, are preserved in sandstones, where various factors may contribute to their preservation, e.g., microbes and minerals [57], rheology [96]. Recently, silicification has been considered a major agent [58]. Early diagenetic silica, which stabilises the sediment surrounding the decaying carcass to mould 3D morphology, is somewhat dependent on seawater silica concentrations [58]. These have varied markedly over geological time (Figure 2G) and were much higher during the Proterozoic before silica was sequestered in skeletons [66,67]. Marine silica concentrations may not have differed, however, between the early Neoproterozoic and Ediacaran, such that conditions favoured Ediacara-style preservation long before Ediacara Biota fossils appeared, implying that the appearance of those organisms marks a real evolutionary event [58]. Thermodynamics and kinetics also identify nearshore peritidal environments as a locus for Proterozoic silica precipitation (Figure 2H) [83]; animals in other settings are thus unlikely to be captured by this taphonomic mechanism.

Replication in authigenic minerals other than clays provides a further mechanism to preserve early animals [50]. For example, animal affinities have been argued for a number of Ediacaran taxa preserved in phosphatic sediments (e.g., *Megasphaera*, *Eocyathospongia* from the Doushantuo Formation [China] [18,19,21,81], although alternative interpretations have been offered [9,21]), soft-bodied animals have been reported replicated in phosphate from the Cambrian [97], and pyrite is responsible for the preservation of some tissues in early animal fossils [98]. **Phosphatisation** occurs in shallow subtidal settings near the suboxic/anoxic boundary in sediments underlying oxic bottom waters [99]. The complex dynamics between phosphatisation and redox place constraints on the animals able to live and die where phosphatisation is favoured [99]. Nevertheless, phosphatisation represents a potential target for early animal fossils as phosphate-rich deposits are common through the Ediacaran and Cambrian [84] (Figure 2I). Pyrite formation requires sources of iron, organic carbon, and sulfate [50]. Marine iron [69] and sulfate [100] levels varied throughout the Neoproterozoic and temporal biases in the occurrence of pyritisation should be explored to see whether this mechanism of fossilisation was favoured at specific times through the Neoproterozoic-Cambrian interval.

Future research to refine animal antiquity

Comparing the role of clays in the preservation of Cambrian and Neoproterozoic soft-bodied fossil assemblages highlights the value of taphonomic data in substantiating the absence of animals. We have presented a new maximum constraint on animals of ~789 Ma (Tonian), while unambiguous fossils from the Ediacara Biota place a minimum constraint at ~574 Ma (**Ediacaran**).

Filling the late Tonian–Ediacaran gap in BST preservation

Clearly a priority is determining whether mudstones that lie in age between the two constraints and preserve organic fossils, but no convincing animals, exhibit BST preservation. Only a handful of fossiliferous Cryogenian deposits are known, but abundant organic-walled microfossils as well as macroscopic soft-bodied fossils have been recovered from late Tonian and especially early Ediacaran mudstones [10]. Chief among them is the Lantian Biota of China [60], which includes fossils of putative animals, including cnidarians [60,61]. The evidence for the animal nature of these fossils is based on broad morphological similarities (e.g., conical body with tentacle-like structures), but other possible affinities (e.g., macroalgae) cannot be ruled out [9,61]. If the rocks hosting the Lantian Biota share the same mineralogical/geochemical conditions as those leading to BST preservation of soft-bodied animals, but lack such fossils, this would provide evidence for a younger soft maximum age of 602 ± 7 Ma for Metazoa [17,62]. If they do not share these precise conditions, they may not have had the taphonomic capacity to preserve early animals. **Pyritisation** plays a role in the preservation of some Lantian fossils [63], but it is not known whether BST preservation is also important. For example, little is known about the influence of clay minerals on the initial degradation of the organisms preserved in the Lantian Biota [64]. Other Ediacaran macroscopic fossils preserved in mudstones are associated with clay films, but these were formed after fossilisation [65] or their precise mineral composition is uncertain because they were identified only on the basis of elemental composition [36].

Further research to understand bias in the early fossil record

Significant work also remains to be done to determine the influence of preservation bias on the early animal fossil record. Such research includes documenting the temporal and geographic/environmental distribution of clay assemblages conducive to BST preservation, recording how ubiquitous this mode of fossilisation is among different animal groups, and understanding the chemical mechanics involved and the factors controlling it across Neoproterozoic–Cambrian time. There are also other preservation windows for the fossilisation of soft-bodied early animals, e.g., Ediacara-style and phosphatisation. Box 3 provides a discussion of current data on these additional windows.

Temporal distribution of BST clays

An important area of future work is to determine the distribution of sediment clay mineralogy conducive to BST preservation in Neoproterozoic strata more broadly (i.e., beyond the fossiliferous mudstones studied so far [45]). The limited mineralogical data available (Figure 2C,D) suggest that clay concentrations increased throughout the Proterozoic [44,66,67], but with high variability within individual units [43]. Kaolinite formation may have been enhanced by Neoproterozoic–Cambrian climatic shifts (e.g., Snowball Earth) and associated fluctuations in continental weathering [68], whereas Fe^{2+} -rich anoxic Neoproterozoic–Cambrian seawaters [69] may have enhanced the production of berthierine [42]. Fe-speciation data (Figure 2E) may indicate that Proterozoic Fe-silicate formation exceeded that in modern marine environments [70]. Enhanced microbial iron reduction or secular changes in seawater chemistry may have increased pore-water alkalinity, encouraging the formation of authigenic clays in Neoproterozoic–Cambrian marine sediments [71,72]. These factors suggest that Neoproterozoic–Cambrian marine chemistry favoured BST preservation of early animals at that time, but more data are required for confirmation.

Spatial/environmental distribution of BST clays

Another area that merits investigation is the distribution of Neoproterozoic clays by environment. If kaolinite were the most important clay in BST preservation, that might imply a geographic bias in favour of settings that promote its formation [73], such as sedimentary source terrains featuring high drainage and low pH, conditions similar to those common in today's tropics. Cambrian BST preservation reflects this bias, almost always occurring in tropical palaeolatitudes [74] as does Tonian BST preservation (e.g., Svanbergfjellet Formation) [75]. In contrast, deposits with Proterozoic organic-walled microfossils, not all of which require BST preservation, are found globally [10,45]. The earliest animals may have evolved in deeper, cooler waters characterised by greater temperature stability [76], perhaps away from the tropics – if so, the BST fossil record is less likely to capture them. New geochemical databases, such as the *Sedimentary Geochemistry and Palaeoenvironments Project* [77], offer the prospect of significant advances in our understanding of how mineral assemblages conducive to BST preservation are distributed in time and space.

Prevalence of direct clay-organic interactions

The prevalence of clay-organic interactions remains to be determined. The direct association of organic-walled microfossils and clay has yet to be investigated in Neoproterozoic deposits beyond the three Tonian examples discussed here [53]. The presence of more fragile fossils in these three deposits than found in most of this age [11,33] may indicate that BST preservation was unusual in Neoproterozoic rocks. Elemental enrichments indicative of clays (Al and Fe) occur in intimate association with other Neoproterozoic fossils, but their precise host minerals are difficult to constrain [36]. Future research is needed on deposits that yield robust spheroidal organic-walled microfossils alone, e.g., Chuar Group, USA [78], or Neoproterozoic macroalgal fossils [79] to determine whether they also rely on clay associations for preservation. Such recalcitrant organic materials are relatively common in the fossil record (e.g., dinoflagellates, graptolites, pollen) and may not require exceptional conditions for preservation [46].

Chemistry underpinning the influence of clays on BST preservation

Further research is needed on the fundamental chemical mechanics of how clays influence BST preservation. How are clay-organic interactions influenced by the chemical composition of the degrading organic matter, the metabolic pathways of degraders, and the chemistry and redox of the pore waters? Research has so far focussed on the role of kaolinite and berthierine [42]. Additional experiments are necessary to determine which other mineral species are important.

Other BST factors

We have focussed on the importance of clays in BST preservation, but other factors have also been invoked. How important are they? Can they be tracked across geological time and space as additional indicators of the temporal/spatial extent of BST preservation? Sealing of beds with carbonate cements was an important factor for BST preservation in some settings, such as Chengjiang [72], but was not ubiquitous [80]. Some samples from deposits enriched in kaolinite/berthierine nonetheless lack soft-bodied fossils [38]. Detailed microstratigraphy in combination with geochemical analyses will yield important insights [39,72]. Cambrian BST deposits preserve fossils with a variety of tissue types, but not all tissues are preserved in every case [27]. Detailed study of individual deposits might reveal site-specific conditions that increase the likelihood of preserving specific tissues and consequently representatives of particular animal groups, constraining the probability of obtaining fossil evidence to calibrate molecular clocks. The preservation of nervous tissue, for example, which may be critical to phylogenetic interpretations, is unusual [28].

Concluding remarks

The antiquity of animals remains one of the most fundamental yet elusive questions in biology. Although the fossil record and molecular clocks often yield conflicting estimates for the origin of animals, a clearer understanding of fossilisation conditions (see [Outstanding questions](#)), particularly of BST preservation, may hold the key to reconciling these disparate data. Integration of soft maximum bounds constrained by taphonomic data into molecular clocks offers the prospect of a more robust chronology for early animal evolution.

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Declaration of interests

The authors have no interests to declare.

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Outstanding questions

How do early animals get preserved?

How do different clays affect microbial metabolisms and, thus, rate of decay?

What are the mechanisms that underpin clay-organic interactions in Burgess Shale-type (BST) preservation?

How do the dominant degrader metabolism, clay mineral type, pore-water chemistry (e.g., redox, pH), organic biopolymer type, and the morphology and ecology of an organism affect clay-organic interactions?

Are organic-walled microfossils always preserved in direct association with clay minerals, and does this vary by geological formation or the phylogenetic affinity of the fossil?

Do individual animal clades or tissue types require different conditions for their preservation?

What are factors leading to the preservation of early animals in other settings, e.g., Ediacara-style preservation?

What is the extent of favourable fossilisation conditions in time and space?

What is the distribution of clay minerals favourable to BST preservation through geological time and palaeogeographic space?

What is the distribution of other geochemical indicators of BST preservation (e.g., total organic carbon) through geological time and paleogeographic space?

Why is there a dearth of BST preservation in Ediacaran and **Terreneuvian** rocks relative to the rest of the Cambrian and Lower Ordovician?

Were the same conditions responsible for preservation of the Ediacaran Lantian Biota as for the Cambrian BST biotas?

When did animals evolve?

Are there younger late Tonian, Cryogenian, or early Ediacaran

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examples of BST preservation that do not yield early animals and could therefore provide younger soft maximum ages on animals?

What is the availability of specific conditions for the preservation of particular animal clades and tissues? Can we use this to determine soft maximum bounds on their evolution?

How can taphonomic data be better incorporated statistically into molecular clocks as probabilistic evidence of absence?

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