Palaeogeography, Palaeoclimatology, Palaeoecology 513 (2019) 146–165

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Resolution of the earliest metazoan record: Differential taphonomy of Ediacaran and Paleozoic fossil molds and casts

Breandán Anraoi MacGabhann[a,b,*], James D. Schiffbauer[c,d], James W. Hagadorn[e], Peter Van Roy[f], Edward P. Lynch[a,g], Liam Morrison[a], John Murray[a,h]

[a] Earth and Ocean Sciences, School of Natural Sciences, National University of Ireland Galway, University Road, Galway, H91 TK33, Ireland
[b] Department of Geography, Mary Immaculate College, University of Limerick, South Circular Road, Limerick, V94 VN26, Ireland
[c] Department of Geological Sciences, University of Missouri, 101 Geology Building, Columbia, MO 65211, USA
[d] X-ray Microanalysis Core Facility, University of Missouri, 101 Geology Building, Columbia, MO 65211, USA
[e] Department of Earth Sciences, Denver Museum of Nature & Science, 2001 Colorado Boulevard, Denver, CO 80205, USA
[f] Department of Geology and Soil Science, Ghent University, Krijgslaan 281/S8, B-9000 Ghent, Belgium
[g] Geological Survey of Sweden, Box 670, 751 28 Uppsala, Sweden
[h] Irish Centre for Research in Applied Geosciences (iCRAG), Ireland

ARTICLE INFO

Keywords:
Taphonomy
Eldonid
Biopolymers
Adsorption
Pyritization
Aluminosilicification

ABSTRACT

Much of our knowledge of early metazoan evolution is derived from unmineralized death mask or endorelief mold and cast fossils in Ediacaran clastic sedimentary rocks. This record is often regarded as a unique 'Ediacaran taphonomic window'; however, the prevalence of soft-bodied molds and casts in Paleozoic clastic rocks has been increasing, begging an extension, or modification, to our understanding of this preservational motif. Chief amongst such fossils are eldonids, a non-biomineralized group of stem deuterostomes. Because eldonids are also preserved as compressed or flattened fossils from deposits like the Burgess Shale, Chengjiang and Kaili, they offer a comparative case study for evaluating the taphonomic fidelity of mold/cast-style preservation during this interval. EDS and Raman microspectroscopic analysis of Ordovician and Devonian eldonid molds and casts, and comparison with Burgess Shale eldonids, suggests the mold/cast taphonomic style produces significantly lower fidelity of fossil preservation. We propose that eldonid mold/cast fossils are preserved by the adsorption of reduced iron ions onto tissues composed primarily of high molecular weight (HMW) biopolymers which require enzymatic degradation prior to decay. Nucleation and growth of aluminosilicates and/or sulfides around these adsorbed ions forms a fossilizable surface veneer, preserving a death mask mold. More labile tissues could not be fossilized in this mold and cast style. Ediacaran mold and cast fossils from South Australia, the White Sea region of Russia, Namibia, and Newfoundland exhibit preservational characteristics consistent with this new proposed model. Analysis of their preservational mode suggests that the first metazoans, which would have lacked HMW biopolymeric tissues, could not have been fossilized in this particular style. Thus, understanding the origin and earliest evolution of the Metazoa requires a focus on alternative modes of fossilization.

1. Introduction

The geologically abrupt appearance of most animal groups in the early Cambrian posed a dilemma for Charles Darwin in *On the Origin of Species* (Darwin, 1859), who envisaged a long, cryptic interval of animal evolution prior to the known fossil record. The subsequent recognition of unmineralized animal fossils of Ediacaran age (e.g. Ford, 1958; Glaessner, 1959; Gürich, 1930; Misra, 1969; see also reviews by Fedonkin et al., 2007a; Narbonne, 2005) suggested that Darwin was originally correct; however, questions remain, due principally to incomplete understanding of the processes which facilitate the fossilization of unmineralized organisms. Are all parts of these organisms preserved? Are the ecosystems they originally inhabited faithfully represented? Indeed, with molecular clocks (Erwin et al., 2011) and biomarkers (Gold et al., 2016; Love et al., 2009; Love and Summons, 2015) suggesting that the first metazoans evolved in the Cryogenian (720–635 Ma) or even in the Tonian (1000–720 Ma)—significantly predating the oldest known megascopic fossils of Ediacaran (635–541 Ma) age—do we have a precursor to Darwin's dilemma? Are the oldest known Ediacaran fossil specimens actually fossils of the very

---

[*] Corresponding author at: Department of Geography, Mary Immaculate College, University of Limerick, South Circular Road, Limerick, V94 VN26, Ireland.
E-mail address: breandan.macgabhann@mic.ul.ie (B.A. MacGabhann).

https://doi.org/10.1016/j.palaeo.2018.11.009
Received 30 March 2017; Received in revised form 3 November 2018; Accepted 5 November 2018

first animals, or instead merely the first animals amenable to fossilization? In short: what is the resolution of the earliest metazoan fossil record?

The majority of our knowledge of Neoproterozoic evolution and ecosystem structure is derived from macrofossil molds and casts preserved in Ediacaran clastic sedimentary rocks (Gehling, 1999; Narbonne, 2005): poorly understood organisms preserved in a non-uniformitarian taphonomic window. It has been suggested that this preservational regime effectively closed at the Neoproterozoic-Phanerozoic transition due to the advent of complex ecosystem engineering behaviors that significantly reduced, or removed, the necessary microbial sediment cover (Gehling, 1999; Hagadorn and Bottjer, 1997; Jensen et al., 1998), although this explanation fails to account for the apparent persistence of matgrounds into the Cambrian (Bottjer et al., 2000; Buatois et al., 2014). While such complications could have limited our understanding of this evolutionary story, examination of new and under-documented Phanerozoic examples of Ediacaran-like mold and cast preservation offers the potential to bypass these obstacles.

The main goal of this study is to better understand how non-mineralized organisms can be fossilized as molds and casts in siliciclastic sedimentary rocks. To accomplish this objective, we examined hundreds of fossil molds and casts from the Ordovician of Morocco and the Devonian of New York. Significantly, these fossils are closely related to specimens known from other Phanerozoic Konservat-Lagerstätten, including the Burgess Shale. This dataset allowed us to conduct a large-scale comparison of specimens preserved as molds and casts with similar organisms preserved in other taphonomic styles, including: i) exploration of which parts of organisms are preserved in mold and cast fossils; ii) how faithfully the fossils represent the original organisms; and iii) whether all non-biomineralized organisms are capable of leaving fossils of this style.

2. Background

2.1. Taphonomy of early macroscopic fossils

The range of styles of fossil preservation in the Ediacaran varies considerably, and cannot be universally ascribed to one single taphonomic model (MacGabhann, 2014). Specimens have been described from shales (Dornbos et al., 2016; Xiao et al., 2002; Yuan et al., 2011; Zhu et al., 2008), from coarser clastic siltstones and sandstones (Gehling, 1999; Narbonne, 2005), from volcaniclastic sediments (Hofmann et al., 2008; Liu, 2016; Liu et al., 2015; Narbonne, 2005), and from carbonates (Grazhdankin et al., 2008; Shen et al., 2009; Wood, 2011). Non-biomineralized specimens are known to have been preserved by phosphatization (Han et al., 2017; Schiffbauer et al., 2014a; Xiao and Schiffbauer, 2008; Xiao et al., 1998), pyritization (Cai et al., 2012; Schiffbauer et al., 2014b), carbonaceous compression (Moczydłowska et al., 2015; Xiao et al., 2002), aluminosilicification (Cai et al., 2012), or as molds and casts (Gehling, 1999; Liu, 2016; Narbonne, 2005); biomineralized fossils are also known from the terminal Ediacaran (e.g. Cai et al., 2017; Penny et al., 2014).

Much of the attention to fossils of Ediacaran age has been focused specifically on the subset of unmineralized specimens preserved as molds and casts in siltstones and sandstones. This is often referred to in the literature as 'Ediacara-style' or 'Ediacara-type' preservation (e.g. Butterfield, 2003; Conway Morris and Grazhdankin, 2005; Gehling et al., 2000; MacGabhann, 2014; Tarhan et al., 2016) after the fossiliferous beds of the Ediacara Hills in South Australia. However, Neoproterozoic fossil molds and casts do not all share a single style of preservation. Narbonne (2005) recognized four assemblage variations of mold/cast preservation (Flinders-, Fermeuse-, Conception-, and Nama-styles). Within these Neoproterozoic assemblages, individual fossil molds and casts show subtle but fundamental variations in their style of preservation, depending on where they are preserved with respect to bedding surfaces (MacGabhann, 2014).

2.1.1. Styles of mold/cast preservation in sandstones

Three distinct styles of mold/cast preservation in sandstones are apparent. Termed gravity cast, death mask, and endorelief preservation, these may be distinguished based on the position and orientation of the fossils with respect to bedding plane surfaces. The three styles reflect differences in the mechanisms of preservation.

Gravity cast fossils (MacGabhann, 2007a), also termed 'lower surface preservation' (Liu et al., 2011), exhibit a mold (the part specimen) preserved in negative epirelief on the top surface of a bed, with a corresponding positive hyporelief cast (the counterpart) on the sole of the overlying bed. In this gravity cast taphonomic style, the underlying sediment was able to maintain a mold, despite decay or removal of the organism positioned directly above, until cast by overlying sediment moving downwards under the force of gravity.

Death mask fossils (Gehling, 1999), also termed 'upper surface preservation', are preserved in the opposite orientation, with a negative hyporelief part mold on the bottom surface of the burying bed, and a corresponding positive epirelief counterpart cast on the top surface of the underlying bed. In this particular taphonomic style, the overlying sediment must have maintained a mold, despite decay of the organism beneath, until sediment from the underlying bed moved upwards against the force of gravity to cast the mold.

Endorelief specimens are preserved with both part mold and counterpart cast within event beds (MacGabhann, 2014). These are the product of the formation of a mold inside the sediment horizon. The fossil must have maintained its shape until sediment had moved to fill the space vacated by the decaying organism.

Generally, mold/cast fossils are preserved in one of these three styles. However, combinations are possible. For example, where the lower part of an organism is preserved on a bedding surface in either gravity cast or death mask style. In such situations the upper parts of the fossils are preserved as endorelief casts within the overlying (burying) bed.

2.1.2. Models of sandstone mold/cast preservation

The taphonomy of fossil specimens preserved as molds and casts has been studied from Ediacaran clastic sedimentary rocks for nearly 50 years. It was first investigated by Wade (1968) using material from the Ediacara Member in South Australia. Fossils preserved as negative epirelief gravity casts were referred to as 'non-resistant' forms, and distinguished from 'resistant' forms preserved as negative hyporelief death masks. Wade (1968) suggested that the resistant forms supported the overlying sediment until diagenesis had cemented a mold; but no mechanism was proposed to explain how resistant organisms could have been capable of eluding decay until diagenetic cementation had occurred. This resistance was subsequently ascribed to the presence of a cuticular, non-mineralized, flexible skeleton (Seilacher, 1984) as part of the Vendobionta hypothesis (Seilacher, 1992).

Gehling (1999) offered an alternative hypothesis, proposing that 'death mask' preservation had been facilitated by the presence of ubiquitous seafloor microbial mats in the Ediacaran, rather than by the resistance of the organisms themselves. Gehling (1999) proposed that decay of seafloor microbial mats had proceeded via sulfate reduction, causing the precipitation of early diagenetic iron sulfides (later recrystallizing to pyrite) in the sole of the burying beds. This early precipitation of iron sulfides in bed soles was suggested to have cemented molds of the underlying seafloors (Gehling, 1999), including the upper surface of any organisms present on these seafloors (Fig. 1). Although no pyrite is known from the beds at Ediacara, it was suggested that the iron oxides covering bed surfaces provide a reasonable proxy for the original distribution of pyrite, due to the immobility of oxidized iron.

This taphonomic model has gained widespread acceptance for many Ediacaran localities worldwide. However, specimens preserved as endorelief molds and casts entirely within Ediacaran siliciclastic event beds (Brasier et al., 2013; Dzik, 1999; Elliott et al., 2011; Grazhdankin and Seilacher, 2002; Hall et al., 2013; Meyer et al., 2014; Narbonne,

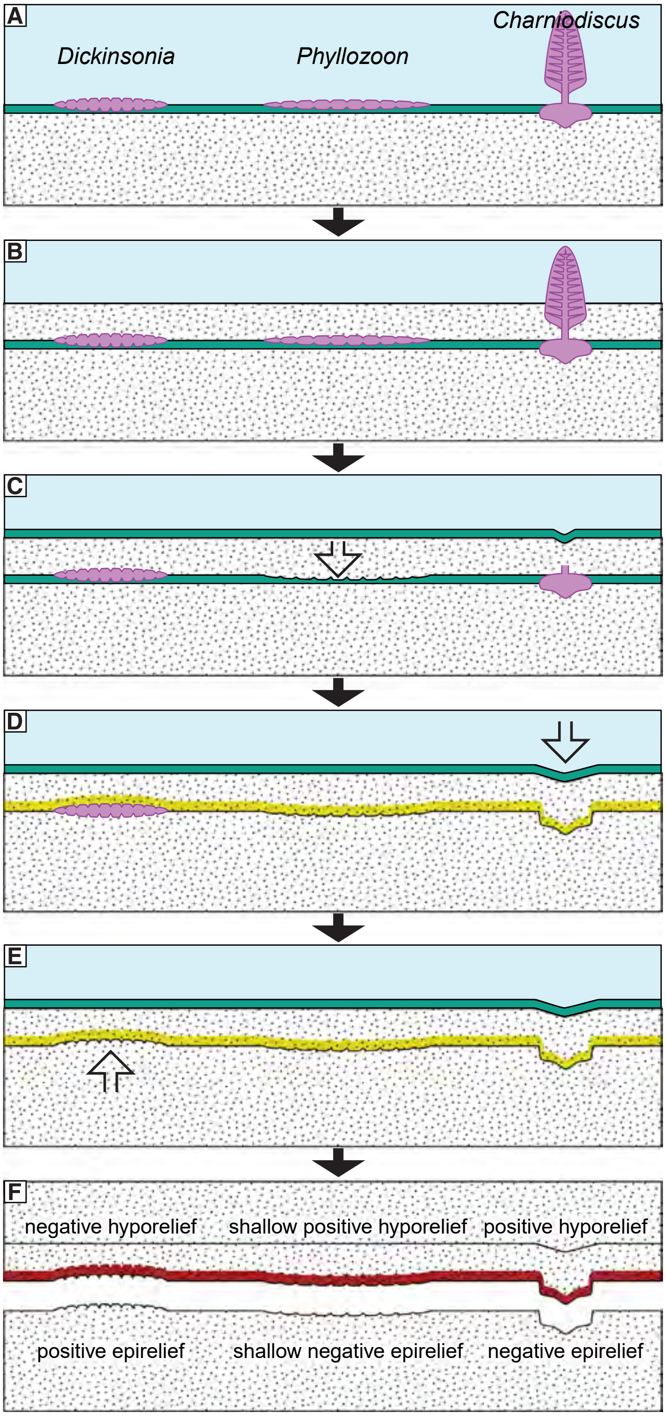


Fig. 1. Gehling (1999) model for the microbial 'death mask' taphonomy of fossils from the Ediacaran of South Australia. A. The living benthic community; shown are *Dickinsonia*, a resistant form; *Phyllozoon*, a non-resistant form; and *Charniodiscus*, a frond with holdfast. B. Burial of the community. C. Decay and compaction of *Phyllozoon*, with sediment moving down to fill the space left by the organic tissues. A new microbial mat forms on the surface of the burying bed, sealing the pore waters from seawater oxygen. D. Decay of the microbial mat by sulfate reduction causes the precipitation of iron sulfides (shown in yellow) in the sole of the burying bed. Decay of *Charniodiscus* holdfast, with sediment moving down to fill the space. E. Sediment moves up from below to fill the space left by the decomposition of *Dickinsonia*. F. Present day. Telodiagenetic oxidation of the pyrite sole veneer to hematite (shown in red), leaving fossils preserved in positive epirelief and both shallow and deep positive hyporelief. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2004, 2005; Vickers-Rich et al., 2013) were not in direct and sustained contact with a microbial mat where they were preserved. This suggests that the taphonomic role of such mats (though not bacterial influence) may not be universal.

Recently, Tarhan et al. (2016) recognized the limitations of the microbial mat-based 'death mask' model and proposed instead that early diagenetic quartz cementation from a silica-saturated ocean was responsible for the cementation of fossil molds and casts at Ediacara. This mode of preservation has been invoked for Proterozoic microfossils (e.g. Newman et al., 2016; Schopf and Oehler, 1976; Xiao et al., 2010), but early quartz cementation produces microcrystalline quartz over a relatively long time—years or more (e.g. Mackenzie and Gees (1971) documented $< 5\,\mu\text{m}$ over three years). Whereas the development of such microcrystalline quartz may be sufficient to stabilize microorganisms on relatively short timescales and in microenvironments, preserving larger organisms through this mode may be problematic. Indeed, organic decay has been shown, even under anoxic conditions, to virtually eliminate invertebrates over a period of twenty-five weeks (Allison, 1988). The timescale for quartz cementation thus greatly exceeds that required for organic decay. While silicification may have aided in the long-term stabilization of fossil molds and casts post-decay, it cannot have been primarily responsible for preservation of such fossils at Ediacara.

2.2. Phanerozoic examples of mold/cast preservation in sandstones

Whereas fossil molds and casts in clastic sediments are common in the Ediacaran, they have generally been regarded as rare in subsequent Phanerozoic strata. Following Gehling's (1999) taphonomic model, this post-Ediacaran scarcity has frequently been linked to the temporal distribution of common seafloor microbial mats. The marked decline in the prevalence of microbial mats across the Neoproterozoic-Phanerozoic transition with the advent of complex ecosystem engineering behaviors has been cited to explain the common restriction of this mold/cast style of fossil preservation to the so-called 'Ediacaran taphonomic window' (Gehling, 1999; Gehling et al., 2005; Jensen et al., 1998; Narbonne, 2005). However, examination of new and under-documented Phanerozoic examples of this preservational style demonstrates that this particular taphonomic window remained at least ajar in the Phanerozoic. A variety of non-mineralized fossils preserved as molds and casts in Phanerozoic siliciclastic sedimentary rocks have previously been described, but have not yet been fully integrated into discussions considering the mechanisms of such preservation.

Amongst these examples are several specimens previously interpreted as porpitid hydrozoans (formerly referred to as 'chondrophorines'). These include ?*Velumbrella bayeri* from the Carboniferous of Kentucky, *Plectodiscus molestus* from the Devonian of New York, and *Plectodiscus circus* from the Carboniferous of Oklahoma (Chamberlain, 1971; Ruedemann, 1916; Yochelson and Mason, 1986) [note: one of the two described specimens of *Plectodiscus circus* along with a number of other putative porpitid hydrozoans (Bell et al., 2001; Caster, 1942; Chamberlain, 1971; Føyn and Glaessner, 1979; Jensen et al., 2002; Narbonne et al., 1991; Stanley and Yancey, 1986) are scratch circles, not body fossils (Jensen et al., 2002)].

A small number of discoidal specimens preserved as molds and casts in siliciclastic rocks have been interpreted as 'medusoids' or 'problematica'. Amongst such examples are isolated specimens described as *Parasolia actiniformis* (Silurian, Canada) and *Patanacta pedina* (Late Ordovician or Early Silurian, Sweden) (Cherns, 1994; Lenz, 1980). These medusoids do not meet some of the criteria set by Young and Hagadorn (2010) for the recognition of fossil medusae. Bona fide medusae have been described preserved as three-dimensional casts/molds in Cambrian sandstones of Wisconsin, New York and Quebec (Hagadorn and Belt, 2008; Hagadorn et al., 2002; Lacelle et al., 2008). A small number of more complex fossils of this kind are also known. These include *Protonympha salicifolia* from the Devonian of New York, and

Priscapennamarina angusta from the Cambrian of China (Conway Morris and Grazhdankin, 2005; Zhang and Babcock, 2001).

Some Phanerozoic examples of fossil molds and casts in sandstones have been previously referred to as ‘Ediacaran survivors’. These are putative fronds from the Cambrian of South Australia and California (Hagadorn et al., 2000; Jensen et al., 1998), and a number of discoid structures (Crimes et al., 1995; Crimes and McIlroy, 1999; Hagadorn et al., 2000) that may represent trace fossils, sedimentary structures, inorganic features, or pseudofossils (Gehling et al., 2000; MacGabhann, 2007a,b; MacGabhann et al., 2007) [note: other reputed ‘survivors’ (Conway Morris, 1993; Shu et al., 2006) are preserved in different taphonomic styles, and some have recently been reinterpreted as early fish (Conway Morris and Caron, 2014)].

Outside of bona fide medusae, perhaps the most significant group of post-Ediacaran organisms which includes specimens preserved as molds and casts in sandstones is the eldonids (Friend, 1995; MacGabhann, 2012). Eldonids are a problematic group of Paleozoic non-biomineralized asymmetrical discoidal organisms, with one convex (dorsal) and one flat (ventral) surface. They are characterized by the presence of a coiled sac, an internal structure which curves counter-clockwise when viewed from above the convex dorsal side. This structure has been interpreted as a peri-alimentary coelom surrounding the alimentary canal. The termination of the sac closest to the center of the organism is interpreted as representing the (proximal) oral opening, with the opposite (distal) termination representing the anus. Both proximal and distal terminations open through an aperture on the ventral side of the organism. Near the oral opening are branched circumoral tentacles interpreted as feeding structures. Internal lobes radiate from the central part of the organism, bifurcating at least once towards the margin, passing underneath the coiled sac. In some specimens, radially-arranged fibers diverge from a central ring, pass underneath the coiled sac, and continue to the margin. Most post-Cambrian eldonids (paropsonemids), generally preserved as molds and casts, exhibit complex ornamentation on the convex surface, consisting of radially arranged ridges, and dissepiments perpendicular to these, congruent with the positions of the internal lobes beneath the surface (MacGabhann, 2012).

Knowledge of the eldonid group remains surprisingly limited, despite the presence of numerous fossils at many significant and well-known Paleozoic localities. Indeed, eldonid specimens are amongst the most common fossils recovered from the Cambrian Chengjiang and Burgess Shale Konservat-Lagerstätten (Friend, 1995; Walcott, 1911; Zhu et al., 2002). The systematic position of the eldonids has also been a matter of considerable disagreement. They are often misinterpreted as porpitid hydrozoans (Fryer and Stanley, 2004), which the presence of internal organs, most especially the coiled sac containing the digestive tract, rules out (Friend, 1995; Hagadorn and Allmon, this issue; MacGabhann, 2012). Some authors have considered them to represent an extinct clade of lophophorates (Dzik, 1991; Dzik et al., 1997), while others have interpreted them as stem-group echinoderms (Friend, 1995). More recently, the eldonids were placed in the unranked stem group Cambroernids, interpreted as basal deuterostomes (Caron et al., 2010).

In the context of the present study, the eldonids are particularly useful as specimens are known preserved in a range of different taphonomic styles. Eldonid taxa with specimens preserved as molds and casts in sandstones include *Eldonia ludwigi* (Cambrian, Russia), *Eomedusa datsenkoi* (Cambrian, Russia), *Discophyllum peltatum* (Ordovician, New York, Morocco, England), *Paropsonema mirabile* (Silurian, Australia), and *Paropsonema cryptophya* (Devonian, New York) (Chapman, 1926; Clarke, 1900; Dzik, 1991; Friend et al., 2002; Fryer and Stanley, 2004; Hall, 1847; MacGabhann, 2012; Popov, 1967; Walcott, 1911). Additionally, *Sinoflabrum antiquum* (Cambrian, China), *Velumbrella czarnockii* (Cambrian, Poland), and *Seputus pomeroii* (Ordovician, Ireland) may also be referable to the eldonids (MacGabhann, 2012; MacGabhann and Murray, 2010; Masiak and Żylińska, 1994; Stasińska, 1960; Zhang and Babcock, 2001). Other eldonid specimens are preserved in different taphonomic styles. For example, *Eldonia ludwigi* from the Cambrian Burgess Shale of Canada and other stratigraphically similar localities, as well as *Eldonia eumorpha* and other eldonids from the Cambrian Chengjiang and Kaili biotas of China, are preserved as aluminosilicate and carbonaceous compressions in shales (Butterfield, 1996; Chen et al., 1995, 1996; Conway Morris, 1990; Conway Morris and Robison, 1988; Durham, 1974; Dzik et al., 1997; Friend, 1995; MacGabhann, 2012; Walcott, 1911; Zhao and Zhu, 1994; Zhu et al., 2002).

Recently, hundreds of non-mineralized specimens preserved as molds and casts in siliciclastics have been discovered in Upper Ordovician strata of the Tafilalt Konservat-Lagerstätte in southeastern Morocco. These fossils were first noted by Samuelsson et al. (2001), with further paleontological and sedimentological description by Van Roy (2006a,b) and MacGabhann (2012). Amongst the non-biomineralized fossils of Tafilalt are abundant specimens of paropsonemid eldonids.

3. Methods

In order to better understand how non-mineralized organisms can be fossilized as molds and casts in siliciclastic sedimentary rocks, we examined 233 fossil eldonid specimens from the Upper Ordovician Tafilalt Lagerstätte in southeastern Morocco, and 20 eldonid specimens from the Upper Devonian Genesee and West Falls Groups of New York (Fig. 2). For comparison, we also examined the type collection of *Eldonia ludwigi* in the Smithsonian Museum of Natural History, as well as 64 additional specimens in the Royal Ontario Museum (specimen prefixes and repositories: F—National Museum of Ireland Natural History; NYSM—New York State Museum, Albany, New York; PRI—Paleontological Research Institute, Ithaca, New York. USNM—Smithsonian Museum of Natural History, Washington, DC). The large number of eldonid mold and cast specimens available for study facilitated careful and systematic investigation of the mineralization involved in their preservation through the use of several destructive analytical techniques. 20 thin-sections were examined from 15 fossil specimens. Three polished thin-sections were examined by Raman microspectroscopy using a Horiba Jobin Yvon LabRam HR confocal Raman instrument with 785 nm laser excitation, and LabSpec 5 software. Nine areas were mapped, with additional point spectra. Polished thin sections and samples of Tafilalt specimens analyzed by environmental scanning electron microscopy (ESEM) were coated with a 20 nm gold-palladium conductive layer in a Cressington 208HR sputter coater, mounted on aluminum sample stages with carbon adhesive, and examined in an FEI Quanta 600F ESEM at high vacuum, with a Bruker QUANTAX 400 energy dispersive X-ray spectrometer (EDS) and Bruker Esprit software. 19 areas were mapped for multiple elements by EDS on 4 thin sections, and 38 areas were mapped on seven specimen surfaces, in addition to backscattered electron (BSE) imaging of all samples. Two uncoated New York specimens were analyzed by EDS on a Zeiss EVO-50 ESEM with an Oxford INCA EDS.

4. Results

The Ordovician Moroccan and Devonian New York eldonid specimens occur as molds and casts, without any evidence for biomineralization, in well-sorted fine-grained (100 μm) to poorly sorted and granular (5 mm) siliciclastic sedimentary rocks, varying in both position and orientation with respect to bedding surfaces. Most fossils occur on bedding plane surfaces, generally as gravity casts in positive hyporelief/negative epirelief (Fig. 2A, E, G, H), with a minority preserved as death mask negative hyporelief molds and positive epirelief casts (Fig. 2D). A significant number of specimens have been found preserved as endorelief casts within event beds (Fig. 2B, C, E, F, I). Some are preserved imbricated or overlapping (Fig. 2A, C, E, G); where this is

Fig. 2. Fossil eldonids from Tafilalt (A–G) and New York (H, I) preserved as molds and casts in siliciclastic sediments. All scale bars 50 mm. A. Three overlapping negative epirelief molds of *Discophyllum peltatum* Hall (F24956). B. Endorelief cast of *D. peltatum* with a conspicuously reddened surface (F25000). C. Two overlapping endorelief casts of *D. peltatum* preserving the coiled sac with negative relief from the surface and with a dark mineral coating (F24907). D. Negative hyporelief mold of *D. peltatum* preserving the coiled sac as a reflective sheen on the dorsal surface (F24989). E. Two overlapping positive hyporelief casts of *D. peltatum*, with the overlapped portion of the upper specimen (arrowed) seen preserved in endorelief in the adjacent (right) image (F24945). F. Endorelief cast of an un-named eldonid with a conspicuously darkened surface (F25230). G. Two overlapping positive hyporelief casts of *D. peltatum*, one of which is folded (F24978). H. Positive hyporelief cast of *Paropsonema cryptophya* Clarke (NYSM 447). I. Positive hyporelief and partial endorelief specimen of *P. cryptophya*, rolled up in a cigar-like shape (NYSM 6817).

seen, both specimens are preserved in areas of intersection. Notably, in the case of overlapping bedding plane specimens, the overlapping portion is preserved within the burying bed (e.g. Fig. 2E), combining gravity cast and endorelief styles of preservation. Other specimens exhibit folding (Fig. 2B, G, I), again combining gravity cast and endorelief preservation, with parts of bedding-plane specimens which are partially folded up from bed surfaces into the overlying enclosing sediment preserved in endorelief (Fig. 2G, I).

The various parts of eldonid anatomy known from Burgess Shale *Eldonia ludwigi*, and other eldonid carbonaceous/aluminosilicate compression fossils, are not all observed in the Moroccan and New York mold/cast specimens. The dorsal surface is commonly preserved, generally exhibiting a surficial ornamentation, and commonly discolored with either reddish (Fig. 2B) or dark gray to black (Fig. 2F) mineral stains, or exhibiting a slightly reflective sheen (Fig. 2A, D, G). Most specimens are preserved with the convex ornamented dorsal surface facing downwards; including those preserved as endorelief casts within event beds. Remarkably, even in specimens preserved in the opposite orientation (e.g. Fig. 2D) and in endorelief, the opposite ventral surface is never seen. For bedding plane surface specimens, the orientation of the dorsal surface correlates with the style of preservation: those with the dorsal surface facing downwards are preserved as gravity casts in positive hyporelief/negative epirelief, and those with the dorsal surface facing upwards are preserved in the opposite orientation as negative hyporelief/positive epirelief death masks.

Some internal structures are also preserved. The coiled sac is present in almost all known specimens, often with negative relief from the fossil dorsal surface (Fig. 2B, C, E, G, H). Frequently, the surface of the coiled sac exhibits either a reflective sheen (Fig. 2D) or a dark mineral coating (Fig. 2C), regardless of any relief. The bifurcating internal lobes are preserved by sediment infill in only three specimens. No other internal structures, including the radial fibers and circumoral tentacles known from other eldonids, are ever observed.

Petrography and Raman microspectroscopy of orthogonally oriented sections of Tafilalt eldonids indicate the presence of a thin veneer, limited to the fossil surfaces. This is composed largely of red-tinted opaque and/or reflective minerals, including hematite, goethite, lepidocrocite, clay minerals, and minor anatase and rutile (Fig. 3). Rare decimicron-sized cubic crystals of hematite and goethite also occur in association with fossil surfaces (Fig. 3).

EDS elemental mapping was conducted on both orthogonal sections and fossil dorsal surfaces of Tafilalt fossils. This shows elevated concentrations of aluminum (Al) and iron (Fe), with corresponding lower amounts of silicon (Si), on fossil dorsal surfaces in comparison to the host sediment (Fig. 4A–C); and further elevated Al and Fe concentrations on the coiled sac as compared to the dorsal surfaces (Fig. 4D). Areas exhibiting surficial blackening represent increased concentrations of manganese (Mn), likely oxides and oxyhydroxides (Figs. 3C, 4C). EDS maps of the coiled sac of an eldonid from New York show an outline of Fe and Al around this organ, with carbon (C) concentrated on the coiled sac (Fig. 4E).

5. Discussion

5.1. Taphonomy of the Tafilalt and New York specimens

The Tafilalt and New York eldonids, like all other known eldonids, were evidently entirely non-biomineralized. This is demonstrated by fossil specimens exhibiting significant plastic deformation (Fig. 2B, G, I), in addition to a lack of any preserved biomineralized structures.

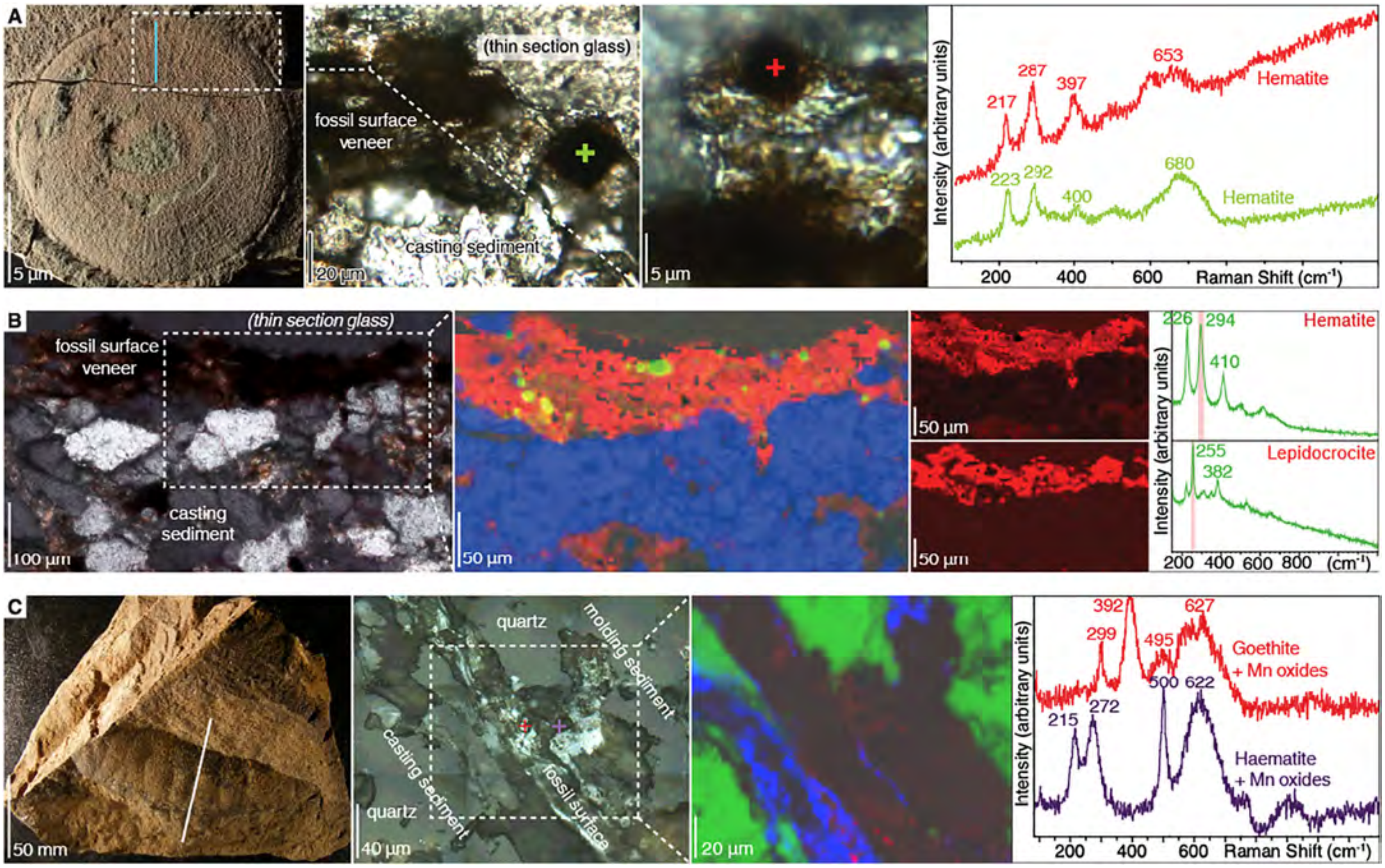


Fig. 3. Raman microspectroscopy of the Tafilalt eldonids. Y-axis in Raman spectra is relative intensity in arbitrary units. A. *D. peltatum* positive hyporelief cast F24995: fossil photograph, showing line of thin section (blue line); thin section photomicrographs in plane polarized light, showing opaque cubic grains in the fossil surface veneer; and Raman point spectra of these cubic opaques, indicating a hematitic composition. B. Same specimen, cross polarized light thin section photomicrograph (same thin section as 3a), showing the fossil surface veneer; Raman multimineral RGB map on the area shown (based on 214–456 cm^{-1} [red] for iron [hydr]oxides, 456–471 cm^{-1} [blue] for quartz, and 633–652 cm^{-1} [green] for anatase); and single mineral maps and Raman spectra for hematite (282–311 cm^{-1}) and lepidocrocite (246–264 cm^{-1}) of the same area. C. Un-named eldonid F25222, preserved in endorelief, with line of thin section indicated; reflected light photomicrograph showing part of the fossil surface in detail, including cubic minerals; Raman multimineral RGB map (based on 215–230 cm^{-1} [red] for hematite, 255–275 cm^{-1} [green] for quartz, and 1075–1095 cm^{-1} [blue] for calcite [late diagenetic cement]) of the area indicated, and Raman point spectra of the indicated cubic grains, suggesting compositions of hematite and goethite with adjacent manganese (hydr)oxides. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

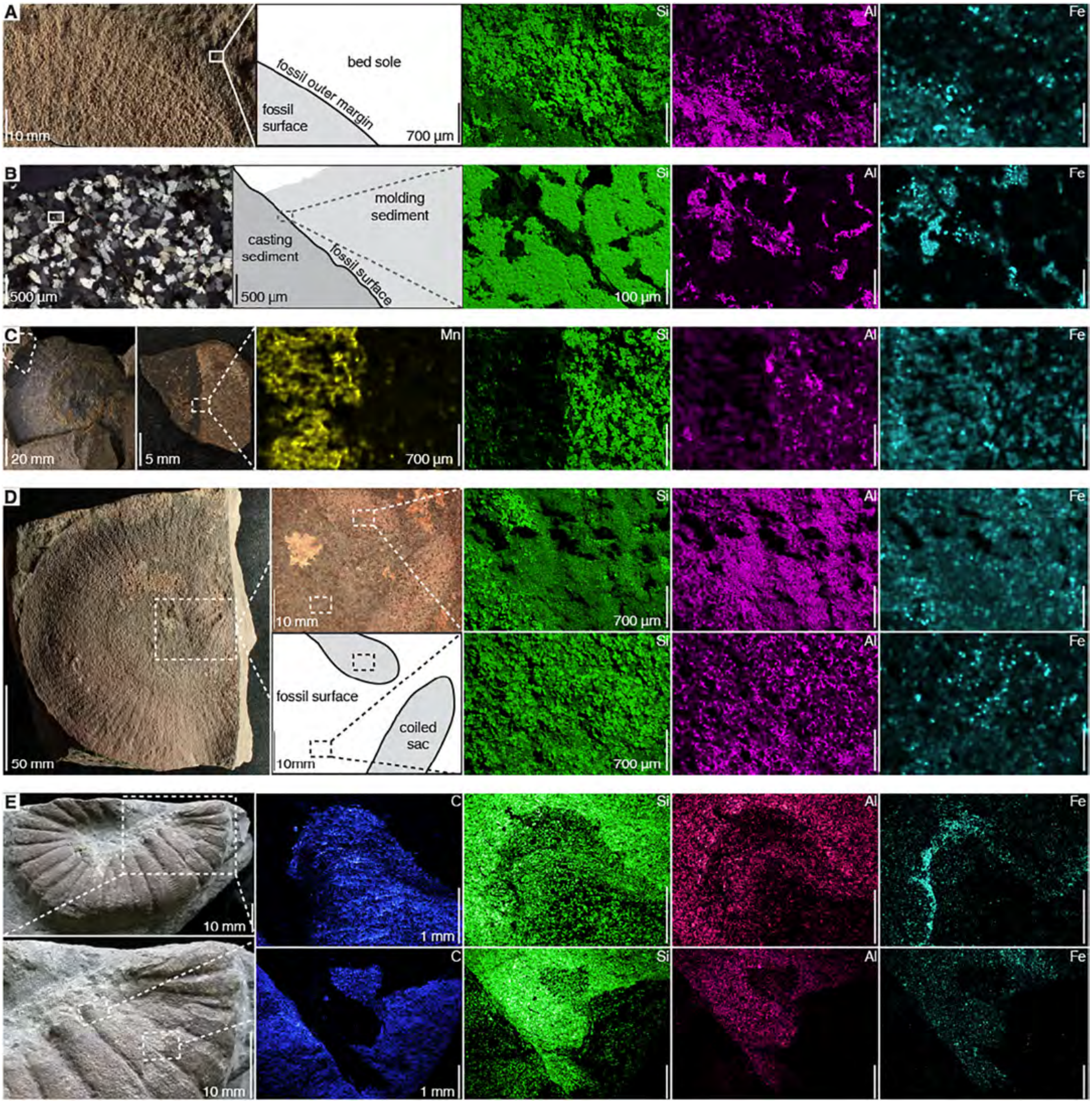


Fig. 4. EDS analysis of eldonid specimens preserved as molds and casts in siliciclastic sediments. A. Specimen from Fig. 3A, B; specimen photograph (magnification of the boxed area in Fig. 3A) with EDS maps of Si, Al, and Fe over the specimen margin (mapped area indicated on the specimen photograph) showing the higher concentration of Al and Fe on the fossil surface, with concomitant reduction in Si. B. EDS maps on a thin section through the specimen from Fig. 3C (cross-polarized light; line of section indicated on Fig. 3C), showing higher concentrations of Al and Fe with lower Si along the fossil surface in endorelief. C. EDS maps on a fragment (shown, with original position on the specimen indicated) of un-named eldonid endorelief mold F25238 over the margin of the fossil, indicating the surficial blackening to be due to the presence of Mn (and higher levels of Fe) on the fossil surface. D. EDS maps on the surface and the coiled sac of *D. peltatum* negative epirelief mold F24981 (mapped areas indicated on specimen photograph and sketch), showing a significantly higher concentration of Al and Fe on the coiled sac. E. An isolated *Paropsonema cryptophya* coiled sac (PRI 42122), with EDS maps on the areas indicated suggesting that the coiled sac wall exhibits carbonaceous preservation, outlined by Fe and Al.

Transport of some fossils is suggested by the imbricated or partially overlapping specimens, and the folded specimen edges (Fig. 2G, I), as well as preservation of fossils within event beds.

There appears to be a consistent bias for the preservation of specific parts of the eldonid anatomy, both for external surfaces and internal organs. Of the fossil surfaces, only the ornamented dorsal surface is ever preserved in the Tafilalt fossils, regardless of the orientation or position of the organisms on or within the substrate. This suggests that the dorsal surface is preferentially preserved in comparison to the opposite ventral surface. The common preservation of the coiled sac is also

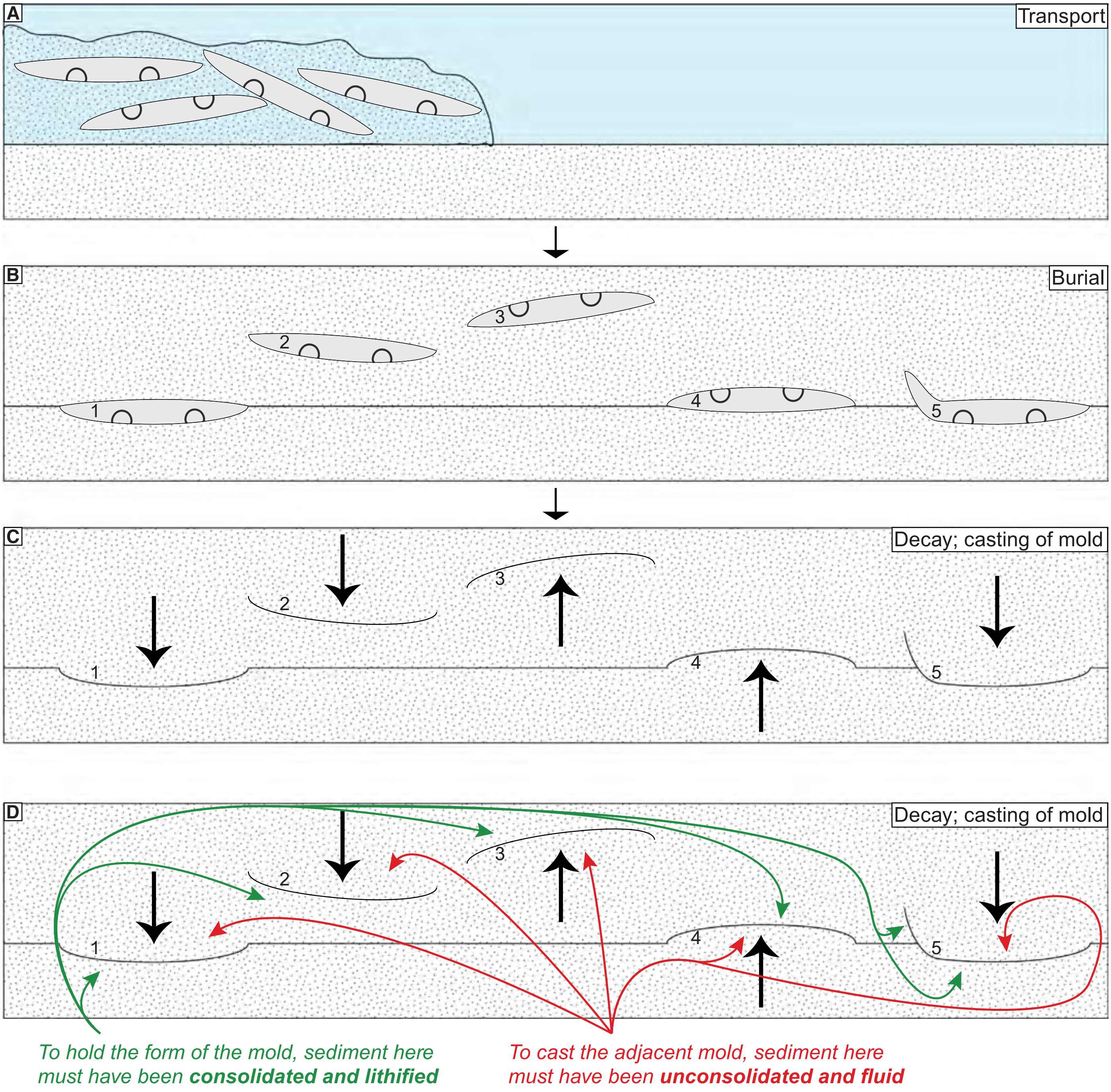


Fig. 5. Rationale why authigenic mineralization must have occurred in all Tafilalt eldonid specimens. A. Specimens transported into the area of preservation. B. Specimens buried, either at the interface between underlying and overlying sediment beds (1, 4), within beds (2, 3), or both (5); and with the presumed dorsal surface facing downwards (1, 2, 5) or upwards (3, 4). C. Decay, and casting of molds of the fossil surfaces by surrounding (enclosing) sediment. Black arrows indicate (compactional) movement of unconsolidated sediment to fill the molds. D. Annotated copy of C. Sediment in both underlying and burying beds must have been unconsolidated and mobile at the time of casting the fossil molds. All molds must therefore have been formed in loose, unconsolidated sediment. Authigenic mineralization must therefore have been required in all specimens, to stabilize the mold in otherwise unconsolidated and unlithified sediment. Because only the ornamented surface and coiled sac are ever mineralized, regardless of the orientation of the fossils, this mineralization must have been limited to these specific structures, rather than indiscriminate mineralization of all organic material, or of inorganic structures such as bedding plane surfaces.

striking given that other internal structures are not preserved, suggesting that specific internal organs may also show similar taphonomic bias.

Contact with bedding plane surfaces was evidently not an essential requirement for fossilization. This is demonstrated by the preservation of the ornamented dorsal surface both on and within beds, and particularly by parts of specimens preserved in endorelief where they are partially folded up in the burying bed. Instead, the surface veneer of iron and manganese oxides/oxyhydroxides and aluminosilicates mantling fossil dorsal surfaces and the coiled sac suggests that authigenic mineralization was involved in the preservation of the eldonid specimens. Moreover, the consistent lack of preservation of the ventral surface, and of internal organs other than the coiled sac, indicates that such authigenic mineralization was likely a requirement to facilitate preservation. Taken together, these observations suggest that the preservation of these specimens must have been reliant on authigenic mineralization of particular organic (morphological) structures, specifically the ornamented dorsal surface and coiled sac, and that preservation did not depend on these features being in contact with either microbial mats or bedding surfaces (Fig. 5).

5.1.1. Decay and authigenic mineralization: the Tafilalt model

The surficial coating by aluminosilicates and Fe and Mn oxides/oxyhydroxides, with a particular concentration on the coiled sac, requires a revised mechanism for the preservation of these (and similarly preserved) fossils. We propose that this Tafilalt-style preservation was facilitated by authigenic mineralization of specific organic structures, which was controlled by their lability or suitability as organic fuel for microbial degradation. This model is broadly similar to previously suggested explanations for partial, anatomically specific pyritization of some Burgess Shale-type fossils (Gabbott et al., 2004; Petrovich, 2001).

Fossilization may have been facilitated by the adsorption of Fe^{2+} ions onto negatively charged functional groups in organic biopolymers of high molecular weight (HMW). Buried large organic particles typically decay anaerobically, even in aerobic environments and coarse-grained porous sediments, due to the high oxygen requirements for aerobic decay, compounded by limitations on oxygen diffusion through sediment pore space (Jørgenson, 1977). As such, decaying carcasses are effectively enclosed in a reducing microenvironment (Allison and Briggs, 1991). If sufficient reactive iron is bioavailable, initial decay of labile tissues will proceed by the reduction of reactive sedimentary ferric Fe^{3+}, producing excess dissolved ferrous Fe^{2+}. Fe^{2+} has a strong affinity for complex HMW organic biopolymers, such as chitin, collagen, cellulose, and peptidoglycan (Beveridge et al., 1983; Doyle et al., 1980; Ferris et al., 1986, 1987, 1988; Fortin et al., 1998; Hawke et al., 1991; Muzzarelli and Tubertini, 1969; Petrovich, 2001; Urrutia and Beveridge, 1993, 1994).

Adsorption of Fe^{2+} ions may promote fossilization both by initially preventing decay, and by facilitating authigenic mineralization. Due to the molecular size of HMW biopolymers, enzymatic degradation to their constituent monomers by exoenzymes is a prerequisite for their decay. Adsorption of Fe^{2+} onto active sites of biopolymers can prevent such enzymatic degradation (Ferris et al., 1988; Petrovich, 2001). Adsorbed ions of Fe^{2+} may also simultaneously provide sites for the nucleation and growth of oxides, aluminosilicates, and other minerals, directly onto organic surfaces (Ferris et al., 1986, 1987, 1988; Fortin et al., 1998; Konhauser, 1997, 1998; Konhauser et al., 1993, 1994; Konhauser and Urrutia, 1999; Schultze-Lam et al., 1996; Ueshima and Tazaki, 2001; Urrutia and Beveridge, 1993, 1994).

Where HMW biopolymers are present as coherent tissues or organs, authigenic minerals formed by direct nucleation on chemically-bound cations may replicate or mold these surfaces. Fossil tissues preserved in this manner could exhibit a combination of preserved organic carbon coated with aluminosilicate clay minerals and perhaps oxides and oxyhydroxides. If decay of labile tissues proceeds further by dissimilatory bacterial reduction of seawater sulfate, then produced sulfide and free sulfur could also react with adsorbed Fe^{2+} ions, forming iron monosulfides. Such iron monosulfides are metastable, and would subsequently recrystallize to pyrite, desorbing Fe^{2+} ions from polymeric tissues, and thus removing the inhibition of enzymatic degradation while mantling the tissues in a veneer of pyrite.

This model, hereafter referred to as the Tafilalt model, would result in fossils preserved with a surface veneer of clay minerals and pyrite (and/or iron oxides and oxyhydroxides such as hematite and goethite, especially where telodiagenetic oxidation has occurred), with organic carbon likely absent in pyritized areas. This authigenic mineralization may form molds of biological structures originally composed of HMW biopolymers, which may be progressively cast by adjacent sediment during late-stage decay (Fig. 6).

5.1.2. Eldonid fossilization

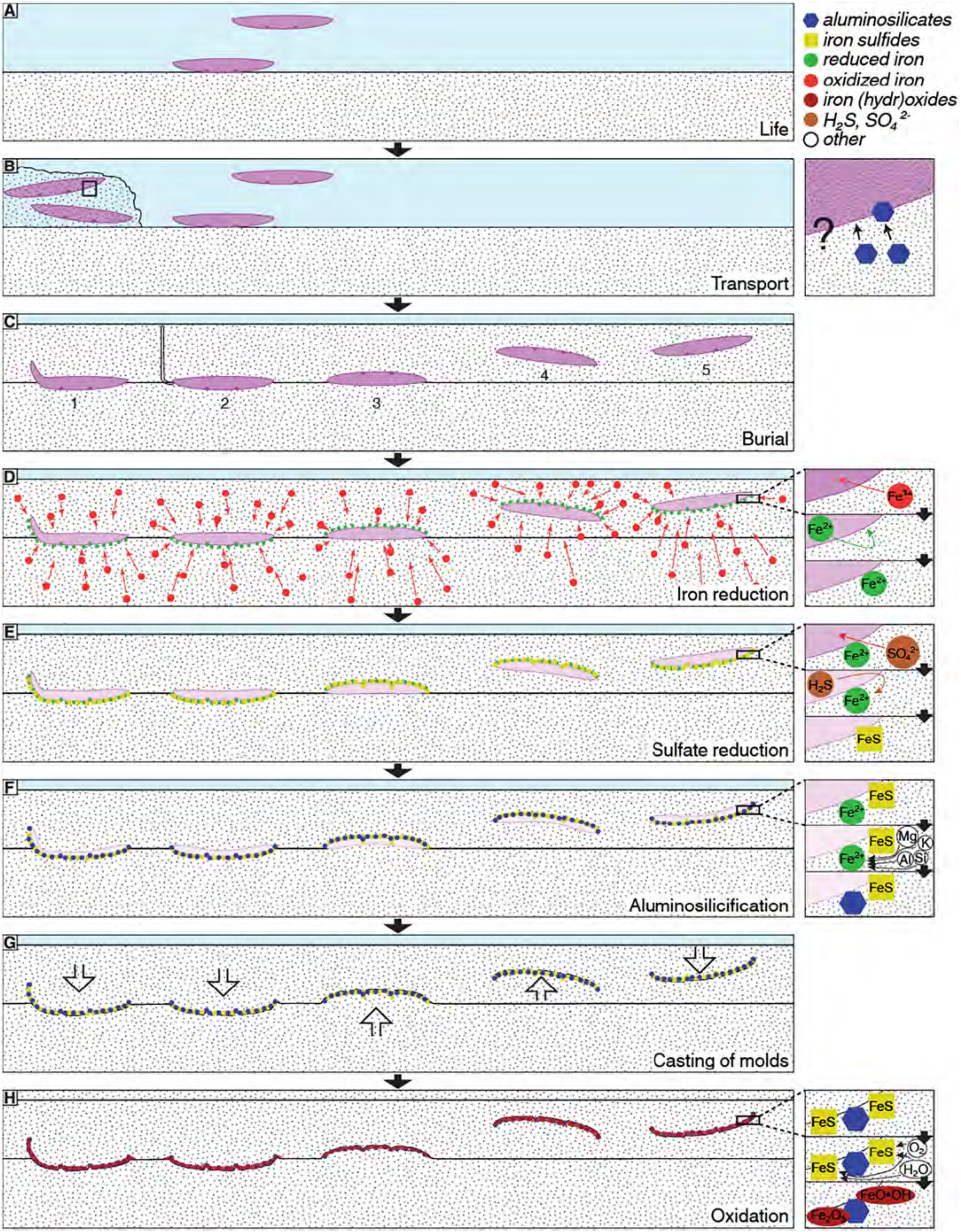
This Tafilalt model is consistent with the observed fossil surface veneers of aluminosilicates and mixed iron oxides and oxyhydroxides, particularly the presence of the cubic iron oxides and oxyhydroxides (likely pseudomorphs after pyrite), in the Ordovician Tafilalt specimens from Morocco. Due to the large size of eldonid organisms, microbial degradation of eldonid tissues not constructed of HMW biopolymers would have quickly used up available pore water oxygen, and would have led to a dominance of anaerobic metabolisms. The presence in the fossil surface veneers of iron minerals suggests decay proceeded principally by means of iron (III) reduction. An excess of dissolved Fe^{2+} would have led to adsorption of reduced iron cations onto tissues composed largely of HMW biopolymers—specifically the dorsal (ornamented) integument and the coiled sac. Enzymatic degradation of the HMW biopolymers in these tissues would have been prevented by the adsorbed cations. The concentration of iron minerals and aluminosilicates in the fossil surface veneers, even inside sandstone beds, and the restriction of these veneers to the dorsal surface and the coiled sac, with no preservation of the ventral surface or any other internal organs, suggests that authigenic aluminosilicates grew around cations adsorbed to the organic tissues of the coiled sac and dorsal integument in particular. Subsequent continuing decay of the more labile tissues—including the ventral surface, and all other internal organs—by means of sulfate reduction would have led to the formation of iron sulfides around Fe^{2+} cations adsorbed to HMW biopolymers of the dorsal integument and coiled sac. The growth of sulfides would have removed adsorbed cations from their positions on these tissues, allowing enzymatic degradation and decay of coiled sac and dorsal integument HMW biopolymeric tissues after the formation of the mineralized fossil surface veneer.

The aluminosilicification of the coiled sac particularly supports this model. Potential alternative hypotheses for aluminosilicification have been proposed in other cases, such as progressive aluminosilicification of organic materials undergoing stepwise maturation during metamorphism (Butterfield et al., 2007; Page et al., 2008). However, these models cannot adequately explain the preferential aluminosilicate replacement of specific internal biological structures or organs and do not apply at sites like Tafilalt which preserve no original organic carbon and have little or no evidence for metamorphism. Manganese oxide/oxyhydroxide coatings on the coiled sac and dorsal surface of certain Tafilalt specimens (Figs. 3C, 4C), which we interpret as late diagenetic due to their texture and their solubility in reducing environments, are also consistent with the Tafilalt model, because such Mn minerals (e.g., pyrolusite) preferentially nucleate on pre-existing iron oxides (Maynard, 2003). It is thus reasonable to infer that pre-Mn mineralization, iron oxides were localized to particular biological surfaces.

Evidence from the Devonian eldonid specimens from New York is also consistent with our taphonomic model. The observations of elevated C and deficient (or absent) Fe on the coiled sac of the analyzed specimen (Fig. 4E) would be expected in our model where sulfate reduction has been limited. In the absence of significant sulfate reduction, little sulfide or free sulfur would be available to react with adsorbed cations. The resultant lack of pyritization would have led to the retention of adsorbed cations on organic surfaces, which thus continue to block enzymatic degradation and thus decay.

5.2. Comparative taphonomy: Tafilalt v Burgess Shale

The presence of eldonids in deposits known for carbonaceous compressions, such as the Burgess Shale, allows for direct comparative preservational analysis with the Tafilalt specimens. Taken together, the same organisms exhibiting two distinct taphonomic modes permits comparison of their corresponding preservational pathways and taphonomic fidelity. Eldonids from the Burgess Shale (Fig. 7) are carbonaceous and aluminosilicate compressions that preserve intricate details of soft-tissue anatomy, including the outer integument and coiled sac as kerogenized organic carbon (Butterfield, 1996), and internal lobes, radial fibers, central ring, and circumoral tentacles replicated in



(caption on next page)

Fig. 6. Simplified and idealized cartoon illustration of Tafilalt eldonid taphonomy. A. Eldonids in life. Coiled sac represented by the dark areas at the dorsal surface. B. Transport. Magnified area shows the potential adsorption of detrital clay minerals to the surfaces of the fossils during transport; these may also adsorb to bacterial exoenzymes (not illustrated). C. The specimens are buried, shown (L–R): 1, with the dorsal side resting on the top surface of the underlying bed, but partially folded up into the sediment. 2, with the dorsal side resting on the top surface of the underlying bed, and evidence for minor scavenging. 3, with the ventral surface resting on the top surface of the underlying bed. 4, entirely within the bed, dorsal side up. 5, entirely within the bed, dorsal side down. D. Decay proceeds first by aerobic decay, then Mn (IV) reduction, then Fe (III) reduction. Reactive iron is reduced and mobilized; Fe^{2+} ions produced adsorb to active sites in complex organic biopolymers constituting the outer integument and coiled sac (shown in the magnified area). Red filled circles represent Fe^{3+}; green filled circles represent Fe^{2+}. Lightening of the color fill of the eldonids represents decay. E. Decay continues by sulfate reduction, with the sulfide produced reacting with adsorbed Fe^{2+} ions to produce iron monosulfides, which subsequently transform to pyrite, in situ on the surfaces of the outer integument and coiled sac (shown in the magnified area). F. Decay continues: clay minerals (represented by blue hexagons) nucleate around adsorbed Fe^{2+} ions on the surfaces of the coiled sac and outer integument, where these have not reacted with sulfide (shown in zoomed area). G. Decay is complete, with sediment having progressively moved to fill the space vacated by the decomposition of the organic tissues. H. Telodiagenetic oxidation of iron sulfides to hematite and goethite or lepidocrocite (represented by dark red filled circles) by reaction with oxygen and water (shown in the magnified area). This is the present-day state of the fossil surface veneer. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

potassium-rich aluminosilicates (Conway Morris, 1990). Burgess Shale specimens also show the eldonid coiled sac to have been a 3-layered structure, with the coiled sac sensu stricto containing an inner coiled tube and surrounded by an outer membrane—further divided into proximal, medial, and distal segments along its length (Fig. 7). Save for the very rare partial preservation of internal lobes by sediment infill in three specimens, none of the Tafilalt or New York eldonids preserve any of these components, nor show any division of the coiled sac, indicating a lower level of taphonomic fidelity than the Burgess Shale.

It appears clear, therefore, that although preservation as molds and casts in siliciclastic sedimentary rocks may preserve internal organs, only certain component parts of an organism can be preserved in this manner. This preservational bias is consistent with the Tafilalt taphonomic model as presented above, which suggests that only coherent tissues composed of HMW organic biopolymers requiring enzymatic breakdown prior to decay could be expected to be preserved by Tafilalt-style molds and casts in siliciclastic sediments. More labile tissues not requiring enzymatic degradation prior to decay, or tissues only partially composed of dispersed biopolymers, are unlikely to be preserved by Tafilalt-style taphonomic mechanisms. Indeed, it is the decay of these labile tissues by bacterially-mediated iron (III) and sulfate reduction which leads to cation adsorption and authigenic mineralization preserving recalcitrant tissues composed of HMW biopolymers.

5.3. Differential taphonomy

Our comparative taphonomic model is useful not only for understanding the taphonomic fidelity of the Tafilalt Lagerstätte itself, but for any fossil specimens preserved in the same manner. Through differential taphonomy (Fig. 8), therefore, we can interpret the taphonomic fidelity of any fossil mold and cast specimens preserved by the Tafilalt processes of iron and sulfate reduction causing early authigenic mineralization via cation adsorption to the surfaces of HMW biopolymers. This approach may be particularly important for certain fossils of Ediacaran age, for which no direct comparative taphonomic evidence is available.

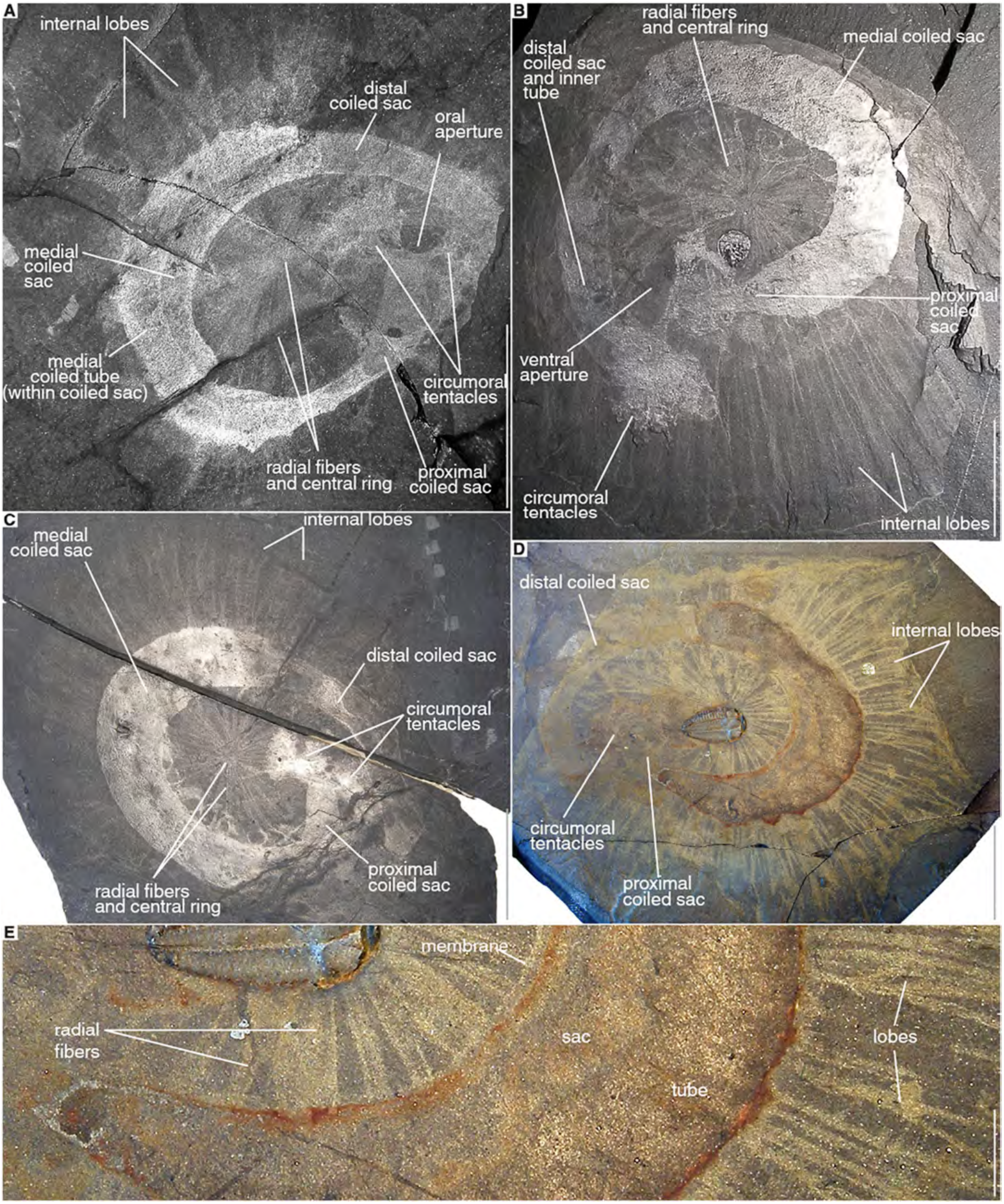
We propose that the Tafilalt taphonomic model complements and augments Gehling's (1999) model hypothesis, while providing a simpler mechanism to explain preservation of Ediacaran death mask and endorelief cast specimens. Gravity casts are specifically excluded from this interpretation, however, because authigenic mineralization is not required to preserve gravity cast fossils such as *Nemiana*, *Ediacaria*, *Aspidella*, or *Epibaion*. Instead, for gravity cast specimens, modification of the substrate is required. For example, owing to the presence of gelatinous microbial mats, the minimal weight of organisms such as *Dickinsonia* would have been insufficient to leave a lasting impression on the substrate (Gehling et al., 2005)—whether prior to or subsequent to burial. Similarly, the paucity of trace fossils in the Ediacara Member is thought to result from the inability of the substrate to record activity which did not modify the microbial mat (Gehling et al., 2005). Gravity cast specimens on microbially bound surfaces must therefore represent modification of a microbially bound substrate—either partially infaunal organisms (such as frond holdfasts) with their surface molded by microbial mats (Laflamme et al., 2011), trace fossils of organisms consuming microbial mats (Fedonkin et al., 2007b; Gehling, 1996; Gehling et al., 2014; Ivantsov, 2011; Seilacher and Hagadorn, 2010), or perhaps degradation of the mat directly beneath a resting organism (McIlroy et al., 2009). In the absence of microbial mats, gravity cast preservation does not require any special conditions, as shown by the Phanerozoic trace fossil record. Early diagenetic mineralization may have occurred with certain gravity cast specimens (particularly those exhibiting fine detail), and available geochemical evidence indicates pyritization and aluminosilicification in specific examples (Laflamme et al., 2011). The Tafilalt model may provide a mechanism for the authigenic mineralization in some of these specimens. However, gravity casts may be preserved without the aid of such authigenic mineralization, and the Tafilalt model therefore is not necessarily required to explain all gravity cast specimens.

Taphonomic evidence for death mask and endorelief cast specimens is available from a number of key Ediacaran localities. Our null hypothesis is that the Tafilalt taphonomic model explains the preservation of Ediacaran death mask and endorelief specimens. Below, we analyze available data from four key localities and compare them to predictions of our model hypothesis.

5.3.1. Dabis Formation, Namibia

Non-mineralized fossils of the Dabis Formation, Kuibis Subgroup, in Namibia, are commonly preserved in endorelief within sandstone and siltstone beds (Dzik, 1999; Elliott et al., 2011; Gehling, 1999; Grazhdankin and Seilacher, 2002; Gürich, 1930, 1933; Hall et al., 2013; Meyer et al., 2014; Narbonne, 2005; Pflug, 1966; Vickers-Rich et al., 2013). Assemblages commonly contain one or more of three particular organisms: *Ernietta plateauensis Pflug* 1966, *Pteridinium simplex* Gürich 1933, and *Rangea schneiderhohni* Gürich 1930. Establishing the degree of transport of these fossils with respect to their original life position has been challenging, with some suggesting infaunal lifestyles (Grazhdankin and Seilacher, 2002, 2005). More recently, specimens of *Pteridinium* (Elliott et al., 2011; Meyer et al., 2014) and *Rangea* (Hall et al., 2013; Vickers-Rich et al., 2013) have been described preserved entirely within large gutter casts and in event beds characterized by scour-and-fill structures.

Fossil surfaces from the Dabis Formation are commonly coated in pyrite or weathering products thereof, such as hematite, goethite, limonite, and jarosite (Dzik, 1999; Gehling, 1999; Vickers-Rich et al., 2013). Specimens of *Pteridinium* preserved within mass flow deposits were molded by pyrite forming on the surfaces of the organisms, and not via association with bedding-plane microbial mats (Meyer et al., 2014). Dzik (1999) and Gehling (1999) suggested that this pyrite was a by-product of the decay by sulfate reduction of the organisms themselves, rather than from the decay of microbial mats. Dzik (1999) further proposed that the preserved parts of *Ernietta* represent only a decay resistant integument, which he suggested to have been constructed of



(caption on next page)

Fig. 7. *Eldonia ludwigi* Walcott (1911) from the Burgess Shale. Scale bars 20 mm for A–D, 5 mm for E. A. *E. ludwigi* (USNM 201692) showing the tripartite lengthwise division of the coiled sac into proximal, medial, and distal portions, with an internal coiled tube. Branched circumoral tentacles surround the oral aperture, while in the inner area, radial fibers extend from a central ring. Internal lobes are also commonly preserved in the outer area of the fossil, often with superimposed radial strands. B. *E. ludwigi* (ROM 95-1119b-1) showing the tripartite lengthwise division of the coiled sac, with the coiled tube visible in the distal portion, and the circumoral tentacles. Radial fibers are also seen diverging from a central ring, and are clearly deflected to allow the proximal and distal terminations of the sac to reach the ventral aperture. The bifurcating internal lobes are also clearly visible in the outer part of the fossil. C. *E ludwigi* (lectotype USNM 57540) showing the proximal, medial, and distal portions of the coiled sac, the circumoral tentacles, the internal lobes, the radial fibers, and the central ring. D. *E. ludwigi* (USNM 188553), with superimposed trilobite, showing the proximal, medial, and distal portions of the coiled sac, with the medial portion clearly surrounded by an outer membrane and containing an internal tube. Circumoral tentacles are also present, and the internal lobes and radial fibers are clear, though the central ring is obscured by the trilobite. E. Magnified view of the specimen in D, showing the coiled sac surrounded by the membrane and containing the tube.

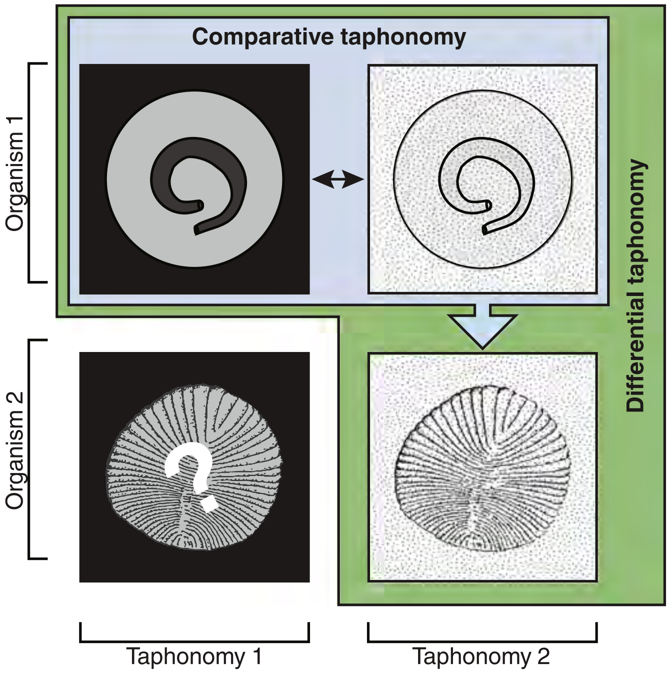


Fig. 8. Differential taphonomy. Comparative taphonomy (blue box), in this instance, is the assessment of similar organisms preserved in two different taphonomic modes. Differential taphonomy, as defined here, is the application of such a comparative analysis to the taphonomy of other organisms, preserved in one of those two taphonomic modes. In this case, we apply a comparative taphonomic analysis of eldonids preserved as molds and casts in siliciclastic sediments, and preserved as Burgess Shale-type compressions in shales, to Ediacaran organisms of unknown affinities, which are also preserved as molds and casts in siliciclastic sediments. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

collagen. This hypothesis was extended to *Pteridinium* by Elliott et al. (2011).

The coating of pyrite (or weathering products thereof) directly on the surfaces of fossils from the Dabis Formation, and the interpretations by Dzik (1999) and Elliott et al. (2011), are entirely consistent with the Tafilalt taphonomic model. Indeed, the presence of pyrite (or oxidation products thereof) largely constrained to the surfaces of *Ernietta*, *Pteridinium*, and *Rangea* from the Dabis Formation suggests the reaction of sulfide with reduced iron ions adsorbed onto their outer integuments. In the absence of such adsorbed ions serving as nucleation foci for iron sulfide mineralization, and if sulfate, organic matter, and reduced/dissolved iron were non-limiting, pyrite would have likely precipitated disseminated throughout beds in the vicinity of decaying *Ernietta*, *Pteridinium*, and *Rangea* specimens. We therefore conclude that the evidence is consistent with the Tafilalt model as a mechanism for the pyritization and preservation of specimens of *Ernietta*, *Pteridinium*, and *Rangea* from the Dabis Formation.

5.3.2. Trepassey Formation, Newfoundland

Rangeomorph specimens from the Trepassey Formation, Conception Group, at Spaniard's Bay in Newfoundland, Canada, are preserved in situ as paleocurrent-oriented molds and casts within the uppermost layers of planar to cross-laminated dark-colored muddy to clean siltstone (Brasier et al., 2013; Narbonne, 2004, 2005). Thin sections through the fossiliferous unit revealed the presence of complex three-dimensional aggregates of pyrite and the iron sulfate bukovskyite resembling portions of rangeomorphs seen in cross-section, precisely at the level of exceptional preservation (Brasier et al., 2013). Microbial mats did not play a role in the taphonomy of these specimens, with hydraulic forces and the fine grain size of the enclosing sediment cited instead as the key factors in their preservation (Brasier et al., 2013). Observations of deformation, deflation, and infilling of the usually inflated rangeomorph frondlets supports the presence of a tough outer membrane, the shape of which was maintained by internal fluid pressure (Brasier et al., 2013). This evidence is consistent with the Tafilalt taphonomic model, with Fe^{2+} adsorption to a tough outer membrane providing a mechanism for iron sulfide mineralization directly on the surfaces of the rangeomorphs following burial.

Elsewhere in the Conception and St. John's Groups in the Ediacaran of Newfoundland, Liu (2016) identified a veneer containing pyrite or iron oxides along fossiliferous bedding plane surfaces in thin section. Because the actual bedding plane surfaces could not be examined in plan view in these cases, it is not known whether these thin sections actually cut fossils, or non-fossiliferous parts of the bedding surfaces. This veneer thus could have been produced by either mineralization of a microbial mat or of macrofossils, and so this evidence is inconclusive in terms of the Tafilalt model. The burial of these surfaces by volcanic ash introduces further variables which may not be accounted for in the Tafilalt model, and we therefore specifically exclude most specimens from the Mistaken Point and Bonavista Konservat-Lagerstätten of Newfoundland (Liu et al., 2015) from our conclusions at this time. Investigation of whether the Tafilalt model does apply to these crucial sites, which include the oldest Ediacaran macroscopic communities (Pu et al., 2016), is thus a clear priority in future research.

5.3.3. Ediacara Member, South Australia

Non-mineralized fossils from the Ediacara Member are preserved as gravity casts, death masks, and rarely in endorelief, in white sandstones with red-stained bedding surfaces (Gehling, 1999; Gehling et al., 2005; Wade, 1968). Lithologically, the strata have generally been described as quartzites with minor feldspar (predominantly orthoclase), aluminosilicates (illite and smectite), and iron oxides (Retallack, 2012; Tarhan et al., 2016; Wade, 1968). Syntaxial quartz cements envelop grains and have been suggested to be early diagenetic (Tarhan et al., 2016; Wade, 1968). The red-staining of bed soles has been ascribed to a hematitic sole veneer, and the presence of hematitic laminae has also been noted within beds, both largely formed by the concentration of pore-filling and grain-coating hematite (Gehling, 1999). Fossil part and counterpart pairs are often separated by a thin coating of limonite, distinct from the hematite sole veneer, and surfaces of endorelief specimens are often similarly coated in hematite. Compelling sedimentological evidence also exists for the former presence of seafloor microbial mats (Gehling, 1999; Tarhan et al., 2015), including filamentous structures interpreted as microbial in origin (Retallack, 2012).

This restriction of iron oxides to sedimentary laminae, fossil surfaces, and bed surfaces reported at Ediacara is akin to that observed at Tafilalt. The limonite fossil surface veneers between Ediacara part and counterpart pairs, and the hematitic fossil surface veneers on specimens preserved in endorelief, are consistent with a concentration of iron sulfides on the surfaces of the fossils, similar to the fossil surface veneer at Tafilalt. Further, such a veneer suggests that an earlier stage of iron reduction caused the adsorption of Fe^{2+} ions to the surfaces of the organisms, providing a source of in situ Fe^{2+} to react with the sulfide produced by bacterial sulfate reduction. The preservation of filamentous microbial structures at Ediacara is also consistent with this taphonomic mechanism; taphonomic experiments have demonstrated that adsorption of Fe^{2+} to the HMW biopolymers which comprise their cell walls significantly enhances the preservation potential of certain bacteria (Beveridge et al., 1983; Ferris et al., 1986, 1987, 1988; Fortin et al., 1997; Konhauser et al., 1993; Schultze-Lam et al., 1996; Urrutia and Beveridge, 1994).

Gehling (1999) and Gehling et al. (2005) proposed that the hematitic sole veneer reflected the primary cementation of the bed sole by disseminated iron sulfides. This latter interpretation is challenged by the observation that hematite occurs concentrated around (present-day) authigenic grains, rather than the original detrital grains. Primary pyrite cementation of the bed sole necessitates that sulfate, organic matter, and dissolved iron are non-limiting. If this is the case, and if mineralization was not specifically localized to organic materials, disseminated iron sulfides should have also precipitated in the pore spaces between detrital grains in the lower part of the burying bed, rather than only being restricted to the bed sole surface. Such interstitial, disseminated pyrite, therefore, should have been overgrown by subsequent syntaxial authigenic quartz, to be preserved as dust rims, or would have prevented the growth of syntaxial authigenic quartz.

We suggest instead that the hematite sole veneer could reflect the mineralization of bacteria in microbial mats by iron sulfides, with redistribution of iron oxides into the overlying bed sole following telodiagenetic oxidation. Our interpretation and model thus modifies and builds on that of Gehling (1999) and Gehling et al. (2005), suggesting that iron sulfide mineralization was localized to organic surfaces of HMW biopolymers in both macro-organisms and microbial mats, rather than bed soles. The available evidence is therefore consistent with the Tafilalt model as a mechanism for the preservation of endorelief and death mask specimens from Ediacara.

5.3.4. Erga and Zimnie Gory Formations, Russia

Non-mineralized fossils from the Erga and Zimnie Gory Formations (formerly placed within the Mezen and Ust'Pinega Formations) of the White Sea region, Russia, are generally preserved as death mask external molds or gravity casts on the soles of sandstone beds; a limited number of fossils are also preserved in endorelief within sandstone beds (Dzik, 2003). Paleoenvironmental evidence exists for the presence of microbial mats, which are visible in cross-section and largely consist of layers of clay minerals (Dzik, 2003; Fedonkin, 1992). Microbial textures are also visible on the bed surfaces, and some filamentous microbial structures are pyritized (Dzik, 2003; Grazhdankin, 2003; Gehling et al., 2005; Steiner and Reitner, 2001), with pyrite $\delta^{34}S$ values indicating a bacterial sulfate reduction origin (Steiner and Reitner, 2001). Of particular significance is the observation that pyrite is largely restricted to death mask external molds, suggesting that the macro-organisms were the most significant source of organic matter for pyrite formation, rather than microbial mats (Dzik, 2003). Further, the localization of pyrite on the specimens is again consistent with iron (III) reduction leading to the adsorption of reduced Fe^{2+} onto the surfaces of the organisms, providing an in situ source of iron (even if dissolved pore water iron is limiting) to react with sulfide produced by sulfate reduction. The pyritization of microbial filaments is also consistent with this process.

In the White Sea deposits, organic preservation sometimes accompanies mold/cast preservation. For example, one frondose White Sea specimen, with a basal attachment disc preserved in negative hyporelief and the stalk and petalodium preserved in endorelief, shows pyritization of parts of the frond surface in addition to carbonaceous preservation with associated potassium aluminosilicates in other areas (Steiner and Reitner, 2001). EDS analysis of part of the frond surface shows that carbonaceous material and associated aluminosilicates are present only where the surface is not pyritized (Steiner and Reitner, 2001). The preservation of carbonaceous material only in areas without pyritization is precisely as predicted by the Tafilalt model, which suggests that carbonaceous preservation (potentially associated with aluminosilicification) should only remain in microenvironments where pyrite did not form. Reaction of adsorbed iron with sulfide would produce pyrite in certain parts of the specimens, removing the decay protection in those specific areas. Curtailment of the sulfate supply would have restricted iron sulfide formation, and left Fe^{2+} ions adsorbed to the organic matter in un-pyritized areas, preventing the necessary ectoenzymatic breakdown prerequisite for decay and facilitating the primary preservation of the organic carbon. Authigenic clay minerals could then have nucleated around the adsorbed ions. The available evidence therefore is consistent with the Tafilalt model as a mechanism for the preservation of death mask and endorelief fossils from the White Sea localities.

5.3.5. Utility of the Tafilalt model for Ediacaran specimens

Taphonomic evidence is not available from all Neoproterozoic fossil localities; however, the available evidence from the Dabis, Trepassey, Erga, and Zimnie Gory Formations and the Ediacara Member appears consistent with the Tafilalt model as a potential mechanism for the preservation of Ediacaran organisms as fossil death masks and endorelief casts. Moreover, none of the published evidence from these localities is sufficient to falsify this proposed hypothesis. The pyritization of microbial mat filaments at the White Sea and Ediacara also supports the Tafilalt model, as this process would have been largely inconsequential to the preservation of the upper surface of the macroscopic organisms positioned directly above the mat. Indeed, because it is the microbial mat that is pyritized, and not the overlying sediment, the preservation of fossils in positive epirelief requires that the microbial mat was mineralized only after the molding of the fossil lying above it. Had the microbial mat been mineralized prior to the completion of decay of the organism it would have prevented sediment from moving upwards to fill the mold, and a void would have resulted in the sediment. Because part molds of negative hyporelief specimens occur, accompanied by positive epirelief counterpart casts, the sediment was clearly capable of moving in this way, evidently prior to mineralization of the microbial mat (Fig. 9). The preservation of fine details may further support the concept of direct authigenesis on the surfaces of the fossils. Molding by precipitation directly onto the surfaces of decaying organisms would facilitate the preservation of morphological details in higher resolution, whereas molding by coarse sediment lithified by disseminated authigenic cements would dramatically lower the fidelity of preservation. Where fine details are preserved on death mask specimens, therefore, direct authigenesis on the upper surface of the organism likely occurred.

Considered together, the similarity in taphonomic evidence between the Paleozoic eldonids and Ediacaran specimens discussed above, lead us to hypothesize that Neoproterozoic specimens preserved as death masks or in endorelief are likely preserved via Tafilalt-like taphonomic processes (Fig. 10). While we would again emphasize the caveat that this model does not necessarily apply to all Neoproterozoic localities and fossil specimens, these findings have recently been echoed from analyses of the terminal Neoproterozoic Gaojiashan Lagerstätte material (Cai et al., 2012; Meyer et al., 2012; Schiffbauer et al., 2014b), in addition to Neoproterozoic Burgess Shale-type microfossil representatives from the Doushantuo and Dengying Formations (Anderson et al., 2011), which are expressed as a combination of carbonaceous, aluminosilicate, and pyritic preservational modes. Indeed,

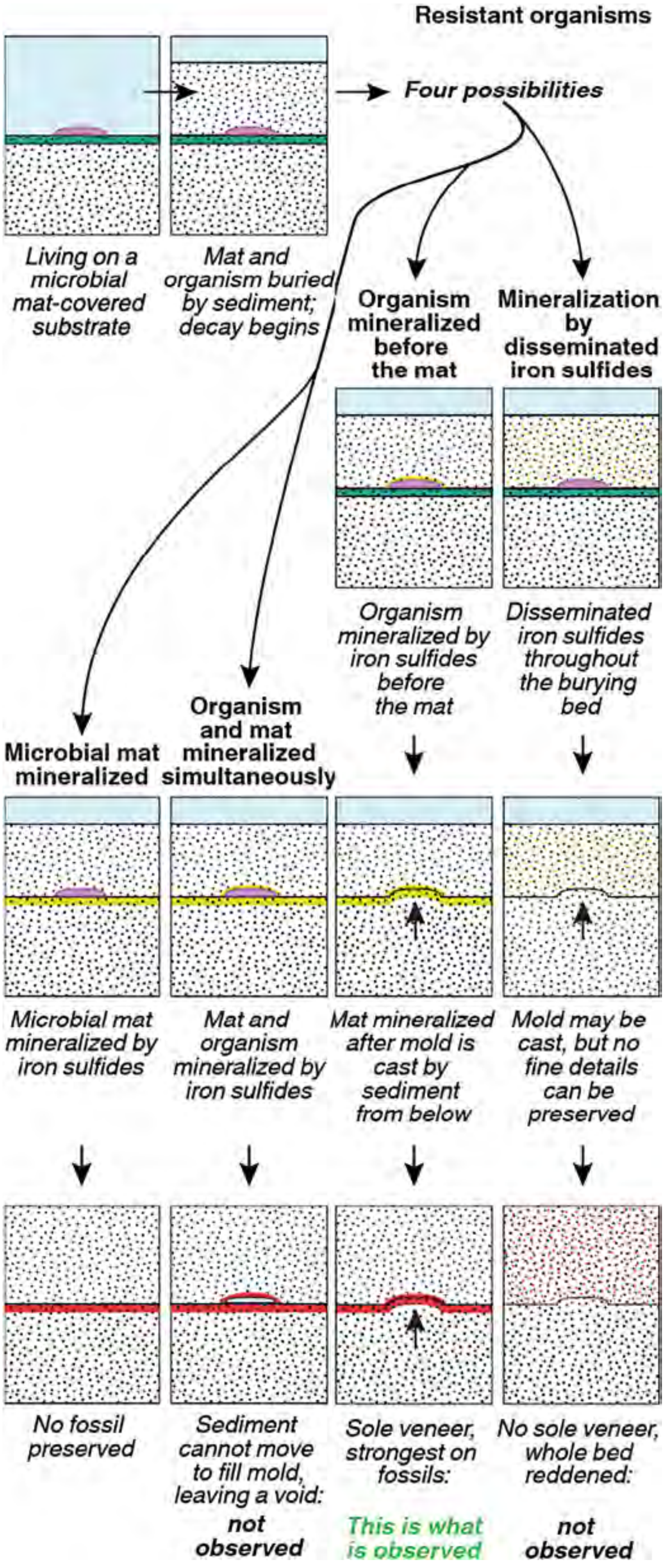


Fig. 9. Locus of authigenic mineralization. Preservation in positive epirelief requires i) mineralization on or above the organism, not just on the mat below, as this could not preserve the upper surface; ii) the sediment below the organism to be fluid after this mineralization, otherwise fossil molds could not be cast; and iii) this mineralization to occur in a concentrated fashion on the surface of the organism, as disseminated mineralization could not preserve fine details.

these three styles of preservation have been proposed by Cai et al. (2012) to represent end-members of a single set of taphonomic processes, further geochemically modeled by Schiffbauer et al. (2014b). We suggest here that the Tafilalt taphonomic model may be at least in part applicable for these styles of preservation, potentially supporting the relevance of the Tafilalt taphonomic mechanism not only to Ediacaran specimens preserved as death mask or endorelief molds and casts in siliciclastics, but also the mixed preservational styles observed in the Gaojiashan and similar Konservat-Lagerstätten.

Additional support for this model is provided by decay experiments conducted by Darroch et al. (2012) and Gibson et al. (2018), which produced a black precipitate, primarily of aluminosilicate-like composition (Al, K, lesser Mg and Fe), around decaying carcasses, with some apparent iron sulfides and even well-defined pyrite reported by the latter authors (Gibson et al., 2018). While Darroch et al. (2012) stated that the presence of iron sulfides supported the Gehling (1999) microbial mat ‘death mask’ model, the precipitate formed (a) around carcasses, not on microbial mats; and (b) formed in control experiments without microbial mats. The lesser extent to which the precipitate formed in control experiments was likely a function of the total organic matter content, reflecting oxidation where there was insufficient organic matter to sustain a reducing environment locally around the decaying carcass. While further work could provide experimental refinement of the Tafilalt model (for example, using larger carcasses, and varying seawater sulfate and sedimentary reactive iron content), the formation of an aluminosilicate precipitate around decaying carcasses is consistent with our proposed new model.

6. Implications

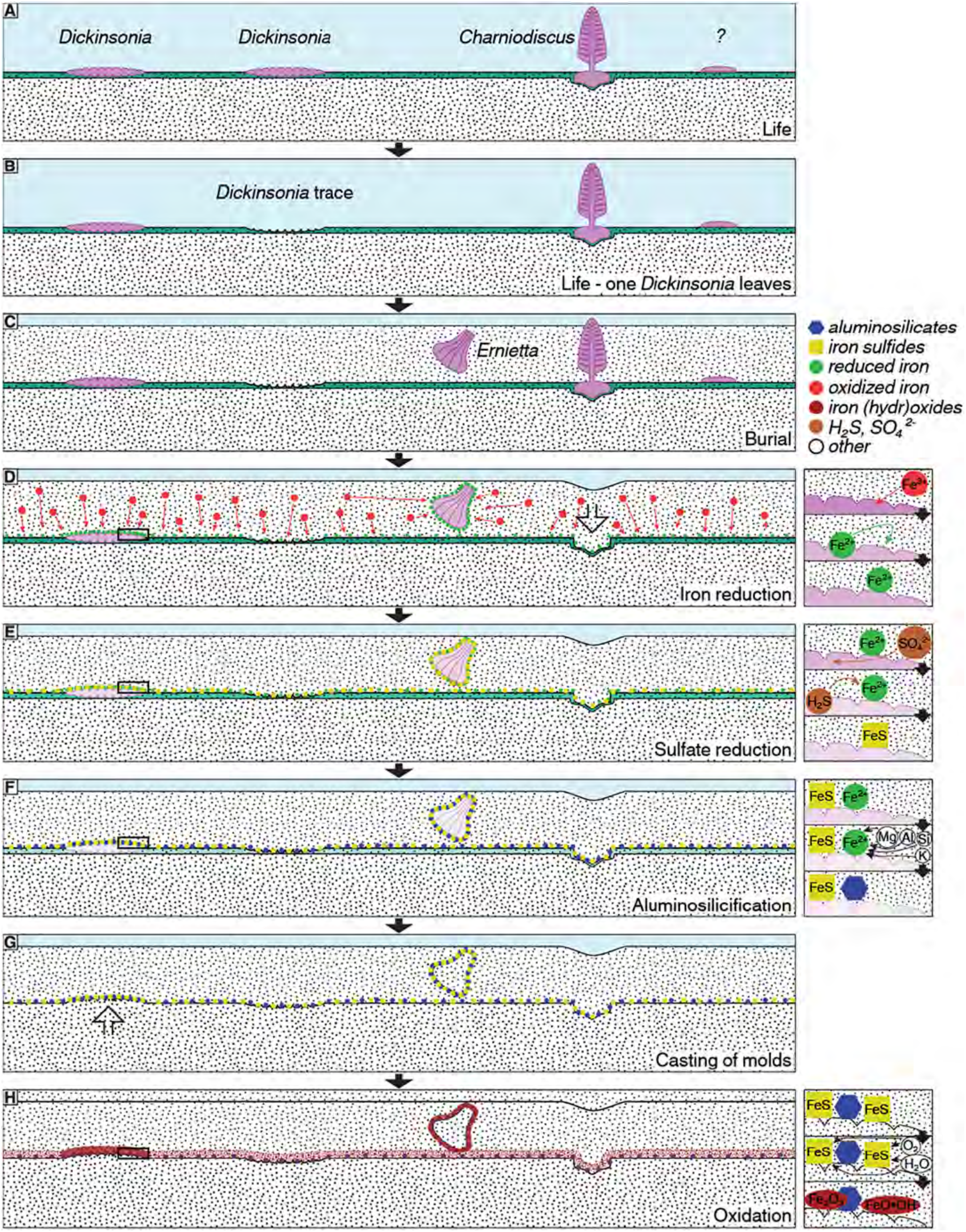
Comparative taphonomy of eldonids from the Burgess Shale and Tafilalt indicates that the Tafilalt specimens have a low taphonomic fidelity. Only discrete tissues composed largely of HMW biopolymers can be preserved in the Tafilalt style; structures or entire organisms lacking such tissues will leave no preserved record in such a setting. The evidence from the Ediacara, Dabis, Trepassey, Erga, and Zimnie Gory units appears to be largely consistent with the Tafilalt model; the low taphonomic fidelity indicated by the comparative taphonomic analysis of Tafilalt-style preservation is thus also applicable through differential taphonomy (Fig. 8) to death mask and endorelief specimens from these localities.

6.1. *Secular distribution of Tafilalt-style preservation*

Our model suggests that the distribution of death mask and endorelief specimens in the Ediacaran was controlled in part by the myriad of sedimentological and geochemical factors on which the Tafilalt taphonomic processes depended, such as pH, Eh, and the availability of sedimentary reactive iron, seawater sulfate, and other ions such as K, Al, Mg, and Si. Both the distribution of fossil assemblages in the Ediacaran, and the decline in the prevalence of this mode of preservation in the Phanerozoic, may reflect changes in these conditions, particularly in terms of seawater chemistry. In addition, secular trends in distal taphonomic factors (or those that facilitate, but do not guarantee, soft-tissue fossil preservation, as opposed to proximal fossil stabilization processes (Cai et al., 2012)) could drastically limit environments in which this taphonomic process might have operated.

6.2. *Fidelity of individual fossil specimens*

Tafilalt-style specimens only represent the parts of the organism composed primarily of HMW organic biopolymers, because these biopolymers require enzymatic degradation prior to decay. Tissues lacking such biopolymers, or with only dispersed biopolymers, would not have been amenable to this style of preservation. As such, previous interpretations that the preservation of such fossils was facilitated by a



(caption on next page)

Fig. 10. Tafilalt taphonomy in the Ediacaran. Idealized cartoon illustration of the taphonomic sequence and processes involved in the preservation of non-mineralized fossils as molds and casts from Ediacaran localities. A. Living benthic community; including *Dickinsonia* (2), *Charniodiscus*, and an unknown non-resistant organism. B. One *Dickinsonia* vacates the area, leaving a 'ghost' imprint. C. Burial by sediment including a specimen of *Ernietta*, which remains entirely within the burying bed. D. Decay is initially aerobic, rapidly followed by Mn (IV) reduction, then Fe (III) reduction. Sediment moves downwards under the force of gravity, filling space vacated by decomposition of the *Charniodiscus* holdfast, the shape of which is maintained by the microbial mat. The unknown non-resistant organism decays completely, leaving no trace. Mobilization of reactive iron by reduction of Fe^{3+} (red circles) is followed by the adsorption of Fe^{2+} ions (green circles) onto complex organic biopolymers in the integuments of *Dickinsonia* and *Ernietta* (inset), and bacterial filaments within the microbial mat. E. Further decay by sulfate reduction produces sulfide, which reacts with adsorbed Fe^{2+} forming iron monosulfides, and subsequently pyrite (yellow squares), in situ on the surfaces of the fossils (shown in the magnified area) and microbial mat bacterial filaments. F. Clay minerals (blue hexagons) nucleate around adsorbed Fe^{2+} ions, where these have not reacted with sulfide (inset). G. Sediment moves upwards against the force of gravity to fill space left by the decomposition of *Dickinsonia*, casting the clay mineral and iron sulfide 'death mask' mold. *Ernietta* is likewise filled with sediment. H. Telodiagenetic oxidation of iron sulfides (inset) produces hematite and iron oxyhydroxides (dark red circles). This is the present-day state of the sole and fossil surface veneers. Note the distinction between the sole and fossil surface veneers. *Dickinsonia* is thus preserved as a positive epirelief cast of a negative hyporelief mold where the organism was present on burial; where it was not, it is preserved as a shallow positive hyporelief cast of a negative epirelief mold. *Charniodiscus* holdfasts are preserved as positive hyporelief casts of negative hyporelief molds. *Ernietta* is preserved in endorelief. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

resistant integument are likely correct (e.g. Seilacher, 1984), but the preservation of the eldonids in a similar manner negates any necessity to invoke non-metazoan grades of organization to explain the nature of this integument. This is consistent with the recent steroid evidence for the metazoan nature of *Dickinsonia* (Bobrovskiy et al., 2018). That said, certain non-metazoan eukaryotes also have the ability to synthesize HMW biopolymers, and a metazoan origin for all mold/cast fossils preserved via the Tafilalt mechanisms should not be taken for granted.

Internal structures may be preserved in this style, either with relief from the surface, or by aluminosilicification or pyritization. As such, it is possible that evidence of internal organs or structures may be present in Ediacaran death mask and endorelief fossils. However, the low taphonomic fidelity—with only HMW biopolymeric tissues preserved, and with the decay of softer tissues required to facilitate preservation of the biopolymeric tissues—suggests that such Ediacaran fossils do not preserve the complete morphology of the original organisms. This limits interpretation of their functional morphologies or autecological life mode strategies.

6.3. Fidelity of fossil assemblages

The Tafilalt model suggests that only organisms with certain tissues composed primarily of HMW organic biopolymers could have had any part of their anatomy preserved as siliciclastic death mask or endorelief molds and casts. Stem- or crown-group representatives of arthropods and mollusks, which use HMW biopolymeric structural tissues, may therefore be represented amongst such specimens. A small number of cnidarians, e.g. coronatid scyphozoans and porpitid hydrozoans, have developed discrete chitinous elements (Ehrlich, 2010), and chitin has been noted in the skeletal framework of the hexactinellid poriferan *Farrea occa* (Ehrlich et al., 2007a) and the demosponges *Aplysina* sp. and *Verongula gigantea* (Ehrlich et al., 2007b). A limited number of cnidarians and poriferans therefore may be preservable in Tafilalt-style. The vast majority of poriferans and cnidarians, however, possess biopolymers primarily as dispersed fibers (Ehrlich, 2010), and would thus have been incapable of Tafilalt-style preservation. These conclusions both support, and are supported by, the interpretation of certain death mask or endorelief Ediacaran specimens as stem- or crown-group mollusks (Fedonkin and Waggoner, 1997) and conulariids (Ivantsov and Fedonkin, 2002), with a notable paucity of poriferan and cnidarian fossils from Ediacaran sediments (Erwin et al., 2011; Sperling et al., 2010). The only death mask or endorelief fossils described as poriferans or cnidarians from the localities under discussion are one hypothesized hexactinellid *Paleophragmodictya* (Gehling and Rigby, 1996), and one possible actinian *Inaria* (Gehling, 1988). *Funisia*, a common fossil interpreted as cnidarian or poriferan grade (Droser and Gehling, 2008), is preserved by sediment infill of a hollow body, not by authigenic mineralization, and so the Tafilalt model does not apply. Only a single species each of Cnidaria and Porifera have thus far been recorded preserved as death masks or endorelief casts, suggesting that this form of preservation does not fully represent the cnidarian and poriferan diversity of the Neoproterozoic. It may be the case that *Paleophragmodictya* and *Inaria* represent rare poriferans and cnidarians with HMW biopolymer structural tissues, however, it is possible they have simply been misplaced taxonomically. Taphonomic limitations of paleoecological studies (e.g. Droser et al., 2006) can now be better constrained where Tafilalt style preservation occurs, because animals which lacked coherent tissues composed primarily of HMW biopolymers may not be represented in fossil assemblages.

6.4. Resolution of the earliest metazoan fossil record

Finally, while the ability to produce HMW biopolymers, such as chitin, is plesiomorphic to the Metazoa (e.g. Ehrlich, 2010), the actuality of construction of coherent tissues primarily composed of HMW biopolymers is not. The dispersed fibers which are the only HMW biopolymers in the vast majority of poriferans and cnidarians would be insufficiently coherent to form a recognizable mold. It is highly plausible, therefore, that the earliest animals could not have been preserved as death mask or endorelief molds and casts in siliciclastics via the Tafilalt model, regardless of the sedimentological and geochemical conditions. Rather, our analyses suggest that Ediacaran specimens preserved as siliciclastic death masks or endorelief casts instead represent only the oldest known fossil organisms which used tissues composed primarily of HMW organic biopolymers. Moreover, because gravity cast fossils require modification of a microbially-bound substrate, they probably reflect particular behavioral or ecological strategies which are likewise not plesiomorphic to the Metazoa. Gravity cast-style preservation may thus be unlikely to have preserved evidence of the earliest animals.

7. Conclusions

The fossil record provides an incomplete picture of evolution, with the Neoproterozoic fossil record arguably even lower in terms of resolution. Similarly, molecular clocks, despite recent advances, can only provide broad estimates for the origins of phyla. However, the 200+ million year gap between even the youngest molecular clock estimates for the origin of the Metazoa (~800 Ma) and the oldest known Tafilalt-style death mask and endorelief cast fossils (~570 Ma) cannot simply be explained by this uncertainty alone, particularly given biomarker evidence for poriferans in the Cryogenian.

Instead, we hypothesize that this gap is a taphonomic artifact in which the paucity of clear-cut Neoproterozoic metazoan fossils stems in part from their lack of tissues composed primarily of HMW biopolymers or their ability to modify microbially bound substrates. Macroscopic metazoans may thus have existed long before the oldest-known Tafilalt-style fossils, with Ediacaran fossil assemblages preserved in Tafilalt-style preserving an incomplete record of some organisms, and no record at all of others.

Our model, which augments and extends the work of generations of paleontologists and taphonomists, suggests that just as Darwin was correct that mineralized fossils did not record the initial stages in the evolution of animal life, fossil molds and casts in clastic sedimentary rocks may similarly have been preceded by a cryptic and perhaps protracted interval of metazoan evolution. The Tafilalt model suggests that siliciclastic molds and casts of Ediacaran organisms, despite how fascinating and inspiring they are, offer little chance of resolving the very first stages of animal life. The most significant leaps in understanding metazoan evolution are already upon us, and they stem from less 'traditional' styles of Neoproterozoic fossilization, such as Burgess Shale-type preservation, carbonaceous preservation, and phosphatization.

Acknowledgments

We thank the two anonymous reviewers and the special issue editors for helping us better contextualize and clarify our observations and interpretations. B.A.M. acknowledges funding from the NUI Thomas Crawford Hayes Trust Fund and IRCSET. J.D.S. is supported by NSF CAREER #1652351 and NSF EAR IF #1636643, and acknowledges the Virginia Tech Institute for Critical Technology and Applied Science Nanoscale Characterization and Fabrication Laboratory for analytical support. J.W.H. thanks D. Bottjer for first introducing him to death, decay and disarticulation, and thanks K. Honda for references, E. Landing (NYSM) and J. Cundiff (Harvard) for collections access, and patrons of the DMNS for supporting analytical work. P.V.R. acknowledges funding provided by the Agency for Innovation through Science and Technology (IWT), IRCSET, The National Geographic Society, Yale University, and the Ghent University Special Research Fund (BOF). Thanks also to R. & V. Reboul, L. Ouzemmou, B. Tahiri, E. Landing, D. Erwin, J.B. Caron, L. Hernick, F. Mannolini, J. Darrell, R. Schmidt, P. Mayer, S. Butts, D.E.G. Briggs, M. Laflamme, S. Xiao, S. Jensen, J.R. Graham, H. Zimmer, D. Cobb, D.A.T. Harper, and C. Swift.

References

Allison, P.A., 1988. The role of anoxia in the decay and mineralisation of proteinaceous macrofossils. Paleobiology 14, 139–154.

Allison, P.A., Briggs, D.E.G., 1991. Taphonomy of nonmineralized tissues. In: Allison, P.A., Briggs, D.E.G. (Eds.), Taphonomy: Releasing the Data Locked in the Fossil Record. Plenum Press, New York, pp. 25–70.

Anderson, E.P., Schiffbauer, J.D., Xiao, S., 2011. Taphonomic study of Ediacaran organic-walled fossils confirms the importance of clay minerals and pyrite in Burgess Shale – type preservation. Geology 39, 643–646.

Bell, C.M., Angseesing, J.P.A., Townsend, M.J., 2001. A chondrophorine (medusoid hydrozoan) from the Lower Cretaceous of Chile. Palaeontology 44, 1011–1023.

Beveridge, T.J., Meloche, J.D., Fyfe, W.S., Murray, R.G.E., 1983. Diagenesis of metals chemically complexed to bacteria: laboratory formation of metal phosphates, sulfides, and organic condensates in artificial sediments. Appl. Environ. Microbiol. 45, 1094–1108.

Bobrovskiy, I., Hope, J.M., Ivantsov, A., Nettersheim, B.J., Hallmann, C., Brocks, J.J., 2018. Ancient steroids establish the Ediacaran fossil *Dickinsonia* as one of the earliest animals. Science 361, 1246–1249. https://doi.org/10.1126/science.aat7228.

Bottjer, D.J., Hagadorn, J.W., Dornbos, S.Q., 2000. The Cambrian Substrate Revolution. GSA Today 10, 1–7.

Brasier, M.D., Liu, A.G., Menon, L., Matthews, J.J., McIlroy, D., Wacey, D., 2013. Explaining the exceptional preservation of Ediacaran rangeomorphs from Spaniard's Bay, Newfoundland: a hydraulic model. Precambrian Res. 231, 122–135.

Buatois, L.A., Narbonne, G.M., Mángano, M.G., Carmona, N.B., Myrow, P., 2014. Ediacaran matground ecology persisted into the earliest Cambrian. Nat. Commun. 5, 3544. https://doi.org/10.1038/ncomms4544.

Butterfield, N.J., 1996. Fossil preservation in the Burgess Shale: reply. Lethaia 29, 109–112.

Butterfield, N.J., 2003. Exceptional fossil preservation and the Cambrian explosion. Integr. Comp. Biol. 43, 166–177.

Butterfield, N.J., Balthasar, U., Wilson, L.A., 2007. Fossil diagenesis in the Burgess Shale. Palaeontology 50, 537–543.

Cai, Y., Schiffbauer, J.D., Hua, H., Xiao, S., 2012. Preservational modes in the Ediacaran Gaojiashan Lagerstätte: pyritization, aluminosilicification, and carbonaceous compression. Palaeogeogr. Palaeoclimatol. Palaeoecol. 326–328, 109–117.

Cai, Y., Cortijo, I., Schiffbauer, J.D., Hua, H., 2017. Taxonomy of the late Ediacaran index fossil *Cloudina* and a new similar taxon from South China. Precambrian Res. 298, 146–156.

Caron, J.B., Conway Morris, S., Shu, D.G., 2010. Tentaculate fossils from the Cambrian of Canada (British Columbia) and China (Yunnan) interpreted as primitive deuterostomes. PLoS One 5, A189–A201.

Caster, K.E., 1942. Two siphonophores from the Paleozoic. Palaeontogr. Am. 3, 56–90.

Chamberlain, C.K., 1971. A "by-the-wind-sailor" (Velellidae) from the Pennsylvanian flysch of Oklahoma. J. Paleontol. 45, 724–728.

Chapman, F., 1926. New or little-known fossils in the National Museum. Part XXX, a Silurian jelly-fish. Proc. Roy. Soc. Victoria 39, 13–17.

Chen, J.Y., Zhu, M.Y., Zhou, G.Q., 1995. The early Cambrian medusiform metazoan *Eldonia* from the Chengjiang Lagerstätte. Acta Palaeontol. Pol. 40, 213–244.

Chen, J.Y., Zhou, G.Q., Zhu, M.Y., Yeh, K.Y., 1996. The Chengjiang Biota: A Unique Window of the Cambrian Explosion. National Museum of Natural Science, Teichuong, Taiwan.

Cherns, L., 1994. A medusoid from the Late Ordovician or Early Silurian of Jamtland, central Sweden. J. Paleontol. 68, 716–721.

Clarke, J.M., 1900. *Paropsonema cryptophya* - a peculiar echinoderm from the Intumescens-zone (Portage beds) of western New York. Bull. N.Y. State Mus. 39, 172–178.

Conway Morris, S., 1990. Burgess shale. In: Briggs, D.E.G., Crowther, P.R. (Eds.), Palaeobiology: A Synthesis. Blackwell, Oxford, pp. 270–274.

Conway Morris, S., 1993. Ediacaran-like fossils in Cambrian Burgess Shale-type faunas of North-America. Palaeontology 36, 593–635.

Conway Morris, S., Caron, J.-B., 2014. A primitive fish from the Cambrian of North America. Nature 512, 419–422.

Conway Morris, S., Grazhdankin, D., 2005. Enigmatic worm-like organisms from the Upper Devonian of New York: an apparent example of Ediacaran-like preservation. Palaeontology 48, 395–410.

Conway Morris, S., Robison, R.A., 1988. More soft-bodied animals and algae from the Middle Cambrian of Utah and British Columbia. Univ. Kans. Paleontol. Contrib. 122, 1–48.

Crimes, T.P., McIlroy, D., 1999. A biota of Ediacaran aspect from lower Cambrian strata on the Digermul Peninsula, Arctic Norway. Geol. Mag. 136, 633–642.

Crimes, T.P., Insole, A., Williams, B.P.J., 1995. A rigid-bodied Ediacaran biota from Upper Cambrian strata in Co Wexford, Eire. Geol. J. 30, 89–109.

Darroch, S.A.F., Laflamme, M., Schiffbauer, J.D., Briggs, D.E.G., 2012. Experimental formation of a microbial death mask. Palaios 27, 293–303. https://doi.org/10.2110/palo.2011.p11-059r.

Darwin, C., 1859. On the Origin of Species by Means of Natural Selection. John Murray, London.

Dornbos, S.Q., Oji, T., Kanayama, A., Gonchigdorj, S., 2016. A new Burgess Shale-type deposit from the Ediacaran of western Mongolia. Sci. Rep. 6, 23438.

Doyle, R.J., Matthews, T.H., Streips, U.N., 1980. Chemical basis for selectivity of metal ions by the *Bacillus subtilis* cell wall. J. Bacteriol. 143, 471–480.

Droser, M.L., Gehling, J.G., 2008. Synchronous aggregate growth in an abundant new Ediacaran tubular organism. Science 319, 1660–1662. https://doi.org/10.1126/science.1152595.

Droser, M.L., Gehling, J.G., Jensen, S., 2006. Assemblage palaeoecology of the Ediacara biota: the unabridged edition? Palaeogeogr. Palaeoclimatol. Palaeoecol. 232, 131–147.

Durham, J.W., 1974. Systematic position of *Eldonia ludwigi* Walcott. J. Paleontol. 48, 750–755.

Dzik, J., 1991. Is fossil evidence consistent with traditional views of the early metazoan phylogeny? In: Simonetta, A.M., Conway Morris, S. (Eds.), The Early Evolution of Metazoa and Significance of Problematic Taxa. Cambridge University Press, Cambridge, pp. 47–56.

Dzik, J., 1999. Organic membranous skeleton of the Precambrian metazoans from Namibia. Geology 27, 519–522.

Dzik, J., 2003. Anatomical information content in the Ediacaran fossils and their possible zoological affinities. Integr. Comp. Biol. 43, 114–126.

Dzik, J., Zhao, Y.L., Zhu, M.Y., 1997. Mode of life of the middle Cambrian eldonioid lophophorate *Rotadiscus*. Palaeontology 40, 385–396.

Ehrlich, H., 2010. Biological Materials of Marine Origin: Invertebrates. Springer Netherlands, Amsterdam.

Ehrlich, H., Krautter, M., Hanke, T., Simon, P., Knieb, C., Heinemann, S., Worch, H., 2007a. First evidence of the presence of chitin in skeletons of marine sponges. Part II. Glass sponges (Hexactinellida: Porifera). J. Exp. Zool. B Mol. Dev. Evol. 308B, 473–483.

Ehrlich, H., Maldonado, M., Spindler, K., Eckert, C., Hanke, T., Born, R., Goebel, C., Simon, P., Heinemann, S., Worch, H., 2007b. First evidence of chitin as a component of the skeletal fibers of marine sponges. Part I. Verongidae (demospongia: Porifera). J. Exp. Zool. B Mol. Dev. Evol. 308B, 347–356.

Elliott, D.A., Vickers-Rich, P., Trusler, P., Hall, M., 2011. New evidence on the taphonomic context of the Ediacaran *Pteridinium*. Acta Palaeontol. Pol. 56, 641–650.

Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D., Peterson, K.J., 2011. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. Science 334, 1091–1097.

Fedonkin, M.A., 1992. Vendian faunas and the early evolution of Metazoa. In: Lipps, J.H., Signor, P.W. (Eds.), Origin and Early Evolution of the Metazoa. Plenum Press, New York, pp. 87–129.

Fedonkin, M.A., Waggoner, B.M., 1997. The late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. Nature 388, 868–871.

Fedonkin, M.A., Gehling, J.G., Grey, K., Narbonne, G.M., Vickers-Rich, P., 2007a. The Rise of Animals: Evolution and Diversification of the Kingdom Animalia. Johns Hopkins University Press, Baltimore.

Fedonkin, M.A., Simonetta, A.M., Ivantsov, A.Y., 2007b. New data on *Kimberella*, the Vendian mollusc-like organism (White Sea region, Russia): palaeoecological and evolutionary implications. In: Vickers-Rich, P., Komarower, P. (Eds.), The Rise and Fall of the Ediacaran Biota. Geological Society of London, Special Publicationspp. 157–179.

Ferris, F.G., Beveridge, T.J., Fyfe, W.S., 1986. Iron-silica crystallite nucleation by bacteria in a geothermal sediment. Nature 320, 609–611.

Ferris, F.G., Fyfe, W.S., Beveridge, T.J., 1987. Bacteria as nucleation sites for authigenic minerals in a metal-contaminated lake sediment. Chem. Geol. 63, 225–232.

Ferris, F.G., Beveridge, T.J., Fyfe, W.S., 1988. Metallic ion binding by *Bacillus subtilis*: implications for the fossilization of microorganisms. Geology 16, 149–152.

Ford, T.D., 1958. Precambrian fossils from Charnwood Forest. Proc. Yorks. Geol. Soc. 31, 211–217.

Fortin, D., Ferris, F.G., Beveridge, T.J., 1997. Surface-mediated mineral development by bacteria. In: Banfield, J.F., Nealson, K.H. (Eds.), Geomicrobiology: Interactions Between Microbes and Minerals, pp. 161–180.

Fortin, D., Ferris, F.G., Scott, S.D., 1998. Formation of Fe-silicates and Fe-oxides on bacterial surfaces in samples collected near hydrothermal vents on the Southern Explorer Ridge in the northeast Pacific Ocean. Am. Mineral. 83, 1399–1408.

Føyn, S., Glaessner, M.F., 1979. *Platysolenites*, other animal fossils, and the Precambrian-Cambrian transition in Norway. Nor. Geol. Tidsskr. 59, 25–46.

Friend, D., 1995. Palaeobiology of Palaeozoic Medusiform Stem Group Echinoderms. Cambridge University, pp. 174.

Friend, D., Zhuravlev, A.Y., Solov'ev, I.A., 2002. Middle Cambrian *Eldonia* from the Siberian Platform. Paleontol. J. 36, 22–26.

Fryer, G., Stanley, G.D., 2004. A Silurian porpitoid hydrozoan from Cumbria, England, and a note on porpitoid relationships. Palaeontology 47, 1109–1119.

Gabbott, S.E., Xian-guang, H., Norry, M.J., Siveter, D.J., 2004. Preservation of early Cambrian animals of the Chengjiang biota. Geology 32, 901–904.

Gehling, J.G., 1988. A cnidarian of actinian-grade from the Ediacaran Pound Subgroup, South-Australia. Alcheringa 12, 299–314.

Gehling, J.G., 1996. Taphonomy of the Terminal Proterozoic Ediacaran Biota, South Australia (PhD thesis). University of California, Los Angeles (222 pp.).

Gehling, J.G., 1999. Microbial mats in terminal Proterozoic siliciclastics; Ediacaran death masks. PALAIOS 14, 40–57.

Gehling, J.G., Rigby, J.K., 1996. Long expected sponges from the Neoproterozoic Ediacara fauna of South Australia. J. Paleontol. 70, 185–195.

Gehling, J.G., Narbonne, G.M., Anderson, M.M., 2000. The first named Ediacaran body fossil, *Aspidella terranovica*. Palaeontology 43, 427–456.

Gehling, J.G., Droser, M.L., Jensen, S., Runnegar, B.N., 2005. Ediacara organisms: relating form to function. In: Briggs, D.E.G. (Ed.), Evolving Form and Function: Fossils and Development. Peabody Museum of Natural History, Yale University, New Haven, pp. 43–66.

Gehling, J.G., Runnegar, B.N., Droser, M.L., 2014. Scratch traces of large Ediacara bilaterian animals. J. Paleontol. 88, 284–298.

Gibson, B.M., Schiffbauer, J.D., Darroch, S.A.F., 2018. Ediacaran-style decay experiments using mollusks and sea anemones. PALAIOS 33, 185–203.

Glaessner, M.F., 1959. Precambrian coelenterata from Australia, Africa and England. Nature 183, 1472–1473.

Gold, D.A., Grabenstatter, J., de Mendoza, A., Riesgo, A., Ruiz-Trillo, I., Summons, R.E., 2016. Sterol and genomic analyses validate the sponge biomarker hypothesis. PNAS 113, 2684–2689.

Grazhdankin, D.V., 2003. Structure and depositional environment of the Vendian Complex in the southeastern White Sea area. Stratigr. Geol. Correl. 11, 313–331.

Grazhdankin, D.V., Seilacher, A., 2002. Underground Vendobionta from Namibia. Palaeontology 45, 57–78.

Grazhdankin, D.V., Seilacher, A., 2005. A re-examination of the Nama-type Vendian organism *Rangea schneiderhoehni*. Geol. Mag. 142, 571–582.

Grazhdankin, D.V., Balthasar, U., Nagovitsin, K.E., Kochnev, B.B., 2008. Carbonate-hosted Avalon-type fossils in arctic Siberia. Geology 36, 803–806.

Gürich, G., 1930. Die bislang altesten Spuren von Organismen in Sudafrika. In: International Geological Congress (XV), Pretoria, Union of South Africa, Die altesten Fossilien Sud-Afrikas. vol. 2. pp. 670–680.

Gürich, G., 1933. Die Kuibis-Fossilien der Nama Formation vom Sudwestafrika. Paläontol. Z. 15, 137–154.

Hagadorn, J.W., and Allmon, W.D. (this issue), Paleobiology of a three-dimensionally preserved paropsonemid from the Devonian of New York: Palaeogeography, Palaeoclimatology, Palaeoecology, https://www.sciencedirect.com/science/article/pii/S0031018218305844

Hagadorn, J.W., Belt, E.S., 2008. Stranded in upstate New York: Cambrian scyphomedusae from the Potsdam Sandstone. PALAIOS 23, 424–441.

Hagadorn, J.W., Bottjer, D.J., 1997. Wrinkle Structures: Microbially Mediated Sedimentary Structures Common in Subtidal Siliciclastic Settings at the Proterozoic-Phanerozoic Transition. Geology 25, 1047–1050. https://doi.org/10.1130/0091-7613(1997)025 < 1047:WSMMSS > 2.3.CO;2.

Hagadorn, J.W., Fedo, C.M., Waggoner, B.M., 2000. Early Cambrian Ediacaran-type fossils from California. J. Paleontol. 74, 731–740.

Hagadorn, J.W., Dott, R.H., Damrow, D., 2002. Stranded on a Late Cambrian shoreline: medusae from central Wisconsin. Geology 30, 147–150.

Hall, J., 1847. Palaeontology of New York. vol. I C. Van Benthuysen, Albany.

Hall, M., Kaufman, A.J., Vickers-Rich, P., Ivantsov, A., Trusler, P., Linnemann, U., Hofmann, M., Elliott, D.A., Cui, H., Fedonkin, M.A., Hoffmann, K.-H., Wilson, S.A., Schneider, G., Smith, J., 2013. Stratigraphy, palaeontology and geochemistry of the late Neoproterozoic Aar Member, southwest Namibia: reflecting environmental controls on Ediacara fossil preservation during the terminal Proterozoic in African Gondwana. Precambrian Res. 238, 214–232.

Han, J., Conway Morris, S., Ou, Q., Shu, D., Huang, H., 2017. Meiofaunal deuterostomes from the basal Cambrian of Shaanxi (China). Nature 542, 228–231.

Hawke, D.J., Sotolongo, S., Millero, F.J., 1991. Uptake of Fe(II) and Mn(II) on chitin as a model organic phase. Mar. Chem. 33, 201–212.

Hofmann, H.J., O'Brien, S.J., King, A.E., 2008. Ediacaran biota on Bonavista Peninsula, Newfoundland, Canada. J. Paleontol. 82, 1–36.

Ivantsov, A., 2011. Feeding traces of proarticulata—the Vendian metazoa. Paleontol. J. 45, 237–248.

Ivantsov, A.Y., Fedonkin, M.A., 2002. Conulariid-like fossil from the Vendian of Russia: a metazoan clade across the Proterozoic/Palaeozoic boundary. Palaeontology 45, 1219–1229.

Jensen, S., Gehling, J.G., Droser, M.L., 1998. Ediacara-type fossils in Cambrian sediments. Nature 393, 567–569.

Jensen, S., Gehling, J.G., Droser, M.L., Grant, S.W.F., 2002. A scratch circle origin for the medusoid fossil *Kullingia*. Lethaia 35, 291–299.

Jørgenson, B.B., 1977. Bacterial sulphate reduction within reduced microniches of oxidized marine sediments. Mar. Biol. 41, 7–17.

Konhauser, K.O., 1997. Bacterial iron biomineralisation in nature. FEMS Microbiol. Rev. 20, 315–326.

Konhauser, K.O., 1998. Diversity of bacterial iron mineralization. Earth-Sci. Rev. 43, 91–121.

Konhauser, K.O., Urrutia, M.M., 1999. Bacterial clay authigenesis: a common biogeochemical process. Chem. Geol. 161, 399–413.

Konhauser, K.O., Fyfe, W.S., Ferris, F.G., Beveridge, T.J., 1993. Metal sorption and mineral precipitation by bacteria in two Amazonian river systems: Rio Solimões and Rio Negro, Brazil. Geology 21, 1103–1106.

Konhauser, K.O., Schultze-Lam, S., Ferris, F.G., Fyfe, W.S., Longstaffe, F.J., Beveridge, T.J., 1994. Mineral precipitation by epilithic biofilms in the Speed River, Ontario, Canada. Appl. Environ. Microbiol. 60, 549–553.

Lacelle, M.A., Hagadorn, J.W., Groulx, P., 2008. The widespread distribution of Cambrian medusae: scyphomedusae strandings in the Potsdam Group of southwestern Quebec. Geol. Soc. Am. Abstr. Programs 40, 369.

Laflamme, M., Schiffbauer, J.D., Narbonne, G.M., Briggs, D.E.G., 2011. Microbial biofilms and the preservation of the Ediacara biota. Lethaia 44, 203–213.

Lenz, A.C., 1980. A planktic problematicum from the Silurian of northern Yukon, Canada. J. Paleontol. 54, 584–587.

Liu, A.G., 2016. Framboidal pyrite shroud confirms the 'death mask' model for moldic preservation of Ediacaran soft-bodied organisms. PALAIOS 31, 259.

Liu, A.G., McIlroy, D., Antcliffe, J.B., Brasier, M.D., 2011. Effaced preservation in the Ediacara biota and its implications for the early macrofossil record. Palaeontology 54, 607–630.

Liu, A.G., Kenchington, C.G., Mitchell, E.G., 2015. Remarkable insights into the paleoecology of the Avalonian Ediacaran macrobiota. Gondwana Res. 27, 1355–1380.

Love, G.D., Summons, R.E., 2015. The molecular record of Cryogenian sponges – a response to Antcliffe (2013). Palaeontology 58, 1131–1136.

Love, G.D., Grosjean, E., Stalvies, C., Fike, D.A., Grotzinger, J.P., Bradley, A.S., Kelly, A.E., Bhatia, M., Meredith, W., Snape, C.E., Bowring, S.A., Condon, D.J., Summons, R.E., 2009. Fossil steroids record the appearance of Demospongiae during the Cryogenian period. Nature 457, 718–722.

MacGabhann, B.A., 2007a. Discoidal fossils of the Ediacaran Biota: a review of current understanding. In: Vickers-Rich, P., Komarower, P. (Eds.), The Rise and Fall of the Ediacaran Biota, pp. 297–313.

MacGabhann, B.A., 2007b. Palaeontology of the Booley Bay Formation, Co. Wexford, Ireland. Department of Earth and Ocean Sciences. National University of Ireland, Galway, Galway, pp. 515.

MacGabhann, B.A., 2012. A Solution to Darwin's Dilemma: Differential Taphonomy of Palaeozoic and Ediacaran Non-Mineralised Discoidal Fossils, Earth and Ocean Sciences. National University of Ireland, Galway, Galway, pp. 657.

MacGabhann, B.A., 2014. There is no such thing as the 'Ediacara Biota'. Geosci. Front. 5, 53–62.

MacGabhann, B.A., Murray, J., 2010. Non-mineralised discoidal fossils from the Ordovician Bardahessiagh Formation, Co. Tyrone, Ireland. Irish J. Earth Sci. 28, 1–12.

MacGabhann, B.A., Murray, J., Nicholas, C., 2007. Ediacaria booleyi: weeded from the Garden of Ediacara? In: Vickers-Rich, P., Komarower, P. (Eds.), The Rise and Fall of the Ediacaran Biota. Geological Society, London, Special Publications, vol. 286. pp. 277–295.

Mackenzie, F.T., Gees, R., 1971. Quartz: synthesis at earth-surface conditions. Science 173, 533–535.

Masiak, M., Żylińska, A., 1994. Burgess Shale-type fossils in Cambrian sandstones of the Holy Cross Mountains. Acta Palaeontol. Pol. 39, 329–340.

Maynard, J.B., 2003. Manganiferous sediments, rocks, and ores. In: Mackenzie, F.T. (Ed.), Treatise on Geochemistry. Sediments, Diagenesis, and Sedimentary Rocks, vol. 7. Pergamon-Elsevier, Oxford, pp. 289–308.

McIlroy, D., Brasier, M.D., Lang, A.S., 2009. Smothering of microbial mats by macrobiota: implications for the Ediacara biota. J. Geol. Soc. Lond. 166, 1117–1121.

Meyer, M., Schiffbauer, J.D., Xiao, S., Cai, Y., Hua, H., 2012. Taphonomy of the upper Ediacaran enigmatic ribbonlike fossil *Shaanxilithes*. PALAIOS 27, 354–372.

Meyer, M., Elliott, D., Schiffbauer, J.D., Hall, M., Hoffman, K.H., Schneider, G., Vickers-Rich, P., Xiao, S., 2014. Taphonomy of the Ediacaran fossil *Pteridinium simplex* preserved three-dimensionally in mass flow deposits, Nama Group, Namibia. J. Paleontol. 88, 240–252.

Misra, S.B., 1969. Late Precambrian (?) fossils from southeastern Newfoundland. Geol. Soc. Am. Bull. 80, 2133–2140.

Moczydłowska, M., Budd, G.E., Agić, H., 2015. Ecdysozoan-like sclerites among Ediacaran microfossils. Geol. Mag. 152, 1145–1148.

Muzzarelli, R.A.A., Tubertini, O., 1969. Chitin and chitosan as chromatographic supports and adsorbents for collection of metal ions from organic and aqueous solutions and sea-water. Talanta 16, 1571–1577.

Narbonne, G.M., 2004. Modular construction of early Ediacaran complex life forms. Science 305, 1141–1144.

Narbonne, G.M., 2005. The Ediacara biota: neoproterozoic origin of animals and their ecosystems. Annu. Rev. Earth Planet. Sci. 33, 421–442.

Narbonne, G.M., Myrow, P., Landing, E., Anderson, M.M., 1991. A chondrophorine (medusoid hydrozoan) from the basal Cambrian (Placentian) of Newfoundland. J. Paleontol. 65, 186–191.

Newman, S.A., Mariotti, G., Pruss, S., Bosak, T., 2016. Insights into cyanobacterial fossilization in Ediacaran siliciclastic environments. Geology 44, 579–582.

Page, A., Gabbott, S.E., Wilby, P.R., Zalasiewicz, J.A., 2008. Ubiquitous Burgess Shale–style "clay templates" in low-grade metamorphic mudrocks. Geology 36, 855–858.

Penny, A.M., Wood, R., Curtis, A., Bowyer, F., Tostevin, R., Hoffman, K.-H., 2014. Ediacaran metazoan reefs from the Nama Group, Namibia. Science 344, 1504–1506.

Petrovich, R., 2001. Mechanisms of fossilization of the soft-bodied and lightly armored faunas of the Burgess Shale and of some other classical localities. Am. J. Sci. 301, 683–726.

Pflug, H.D., 1966. Neue Fossilreste aus den Nama-Schichten in Südwest-Afrika. Paläontol. Z. 40, 14–25.

Popov, Y.N., 1967. New Cambrian scyphozoan. Paleontol. J. 2, 122–123.

Pu, J.P., Bowring, S.A., Ramezani, J., Myrow, P., Raub, T.D., Landing, E., Mills, A., Hodgin, E., Macdonald, F.A., 2016. Dodging snowballs: geochronology of the Gaskiers glaciation and the first appearance of the Ediacaran biota. Geology 44, 955–958.

Retallack, G.J., 2012. Were Ediacaran siliciclastics of South Australia coastal or deep marine? Sedimentology 59, 1208–1236.

Ruedemann, R., 1916. Note on *Paropsonema cryptophya* Clarke and *Discophyllum peltatum* Hall. Bull. N.Y. State Mus. 189, 22–27.

Samuelsson, J., Van Roy, P., Vecoli, M., 2001. Micropalaeontology of a Moroccan Ordovician deposit yielding soft-bodied organisms showing Ediacara-like preservation. Geobios 34, 365–373.

Schiffbauer, J.D., Wallace, A.F., Broce, J., Xiao, S., 2014a. Exceptional fossil conservation through phosphatization. In: The Paleontological Society Papers. vol. 20. pp. 59–82.

Schiffbauer, J.D., Xiao, S., Cai, Y., Wallace, A.F., Hua, H., Hunter, J., Xu, H., Peng, Y., Kaufman, A.J., 2014b. A unifying model for Neoproterozoic–Palaeozoic exceptional fossil preservation through pyritization and carbonaceous compression. Nat. Commun. 5, 5754.

Schopf, J.W., Oehler, D.Z., 1976. How old are the eukaryotes? Science 193, 47–49.

Schultze-Lam, S., Fortin, D., Davis, B.S., Beveridge, T.J., 1996. Mineralization of bacterial surfaces. Chem. Geol. 132, 171–181.

Seilacher, A., 1984. Late Precambrian and Early Cambrian Metazoa: preservational or real extinctions? In: Holland, H.D., Trendall, A.F. (Eds.), Patterns of Change in Earth Evolution. Springer-Verlag, Berlin, pp. 159–168.

Seilacher, A., 1992. Vendobionta and Psammocorallia - lost constructions of Precambrian evolution. J. Geol. Soc. Lond. 149, 607–613.

Seilacher, A., Hagadorn, J.W., 2010. Early molluscan evolution: evidence from the trace fossil record. PALAIOS 25, 565–575.

Shen, B., Xiao, S., Zhou, C.M., Yuan, X.L., 2009. *Yangtziramulus zhangi* new genus and species, a carbonate-hosted macrofossil from the Ediacaran Dengying formation in the Yangtze Gorges area, South China. J. Paleontol. 83, 575–587.

Shu, D.G., Conway Morris, S., Han, J., Li, Y., Zhang, X.L., Hua, H., Zhang, Z.F., Liu, J.N., Guo, J.F., Yao, Y., Yasui, K., 2006. Lower Cambrian vendobionts from China and early diploblast evolution. Science 312, 731–734.

Sperling, E.A., Robinson, J.M., Pisani, D., Peterson, K.J., 2010. Where's the glass? Biomarkers, molecular clocks, and microRNAs suggest a 200-Myr missing Precambrian fossil record of siliceous sponge spicules. Geobiology 8, 24–36.

Stanley, G.D., Yancey, T.E., 1986. A new late Paleozoic chondrophorine (Hydrozoa, Velellidae) by-the-wind sailor from Malaysia. J. Paleontol. 60, 76–83.

Stasińska, A., 1960. *Velumbrella czarnockii* n. gen., n. sp. – méduse du Cambrien inférieur des Monts de Sainte-Croix. Acta Palaeontol. Pol. 5, 337–346.

Steiner, M., Reitner, J., 2001. Evidence of organic structures in Ediacara-type fossils and associated microbial mats. Geology 29, 1119–1122.

Tarhan, L.G., Droser, M.L., Gehling, J.G., 2015. Depositional and preservational environments of the Ediacara Member, Rawnsley Quartzite (South Australia): assessment of paleoenvironmental proxies and the timing of 'ferruginization'. Palaeogeogr. Palaeoclimatol. Palaeoecol. 434, 4–13.

Tarhan, L.G., Hood, A.v.S., Droser, M.L., Gehling, J.G., Briggs, D.E.G., 2016. Exceptional preservation of soft-bodied Ediacara Biota promoted by silica-rich oceans. Geology 44, 951–954.

Ueshima, M., Tazaki, K., 2001. Possible role of microbial polysaccharides in nontronite formation. Clay Clay Miner. 49, 292–299.

Urrutia, M.M., Beveridge, T.J., 1993. Mechanism of silicate binding to the bacterial cell wall in *Bacillus subtilis*. J. Bacteriol. 175, 1936–1945.

Urrutia, M.M., Beveridge, T.J., 1994. Formation of fine-grained metal and silicate precipitates on a bacterial surface (*Bacillus subtilis*). Chem. Geol. 116, 261–280.

Van Roy, P., 2006a. An aglaspidid arthropod from the Upper Ordovician of Morocco with remarks on the affinities and limitations of Aglaspidida. Earth Environ. Sci. Trans. R. Soc. Edinb. 96, 327–350.

Van Roy, P., 2006b. Non-trilobite Arthropods From the Ordovician of Morocco, Department of Geology and Soil Sciences (PhD thesis). University of Ghent, Ghent.

Vickers-Rich, P., Ivantsov, A.Y., Trusler, P.W., Narbonne, G.M., Hall, M., Wilson, S.A., Greentree, C., Fedonkin, M.A., Elliott, D.A., Hoffmann, K.H., Schneider, G.I.C., 2013. Reconstructing *Rangea*: new discoveries from the Ediacaran of Southern Namibia. J. Paleontol. 87, 1–15.

Wade, M., 1968. Preservation of soft-bodied animals in Precambrian sandstones at Ediacara, South Australia. Lethaia 1, 238–267.

Walcott, C.D., 1911. Middle Cambrian holothurians and medusae. In: Smithsonian Miscellaneous Collections. vol. 57. pp. 41–68.

Wood, R.A., 2011. Paleoecology of the earliest skeletal metazoan communities: implications for early biomineralization. Earth-Sci. Rev. 106, 184–190.

Xiao, S., Schiffbauer, J.D., 2008. Microfossil phosphatization and its astrobiological implications. In: Seckbach, J., Walsh, M. (Eds.), From Fossils to Astrobiology: Records of Life on Earth and Search for Extraterrestrial Biosignatures. Springer Netherlands, Dordrecht, pp. 89–117.

Xiao, S.H., Zhang, Y., Knoll, A.H., 1998. Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. Nature 391, 553–558.

Xiao, S., Yuan, X., Steiner, M., Knoll, A.H., 2002. Macroscopic carbonaceous compressions in a terminal Proterozoic shale: a systematic reassessment of the Miaohe biota, South China. J. Paleontol. 76, 347–376.

Xiao, S., Schiffbauer, J.D., McFadden, K.A., Hunter, J., 2010. Petrographic and SIMS pyrite sulfur isotope analyses of Ediacaran chert nodules: Implications for microbial processes in pyrite rim formation, silicification, and exceptional fossil preservation. Earth Planet. Sci. Lett. 297, 481–495.

Yochelson, E.L., Mason, C.E., 1986. A chondrophorine coelenterate from the Borden Formation (Lower Mississippian) of Kentucky. J. Paleontol. 60, 1025–1028.

Young, G.A., Hagadorn, J.W., 2010. The fossil record of cnidarian medusae. Palaeoworld 19, 212–221.

Yuan, X., Chen, Z., Xiao, S., Zhou, C., Hua, H., 2011. An early Ediacaran assemblage of macroscopic and morphologically differentiated eukaryotes. Nature 470, 390–393.

Zhang, W.T., Babcock, L.E., 2001. New extraordinarily preserved enigmatic fossils, possibly with Ediacaran affinities, from the Lower Cambrian of Yunnan, China. Acta Palaeontol. Sin. 40, 201–213.

Zhao, Y.L., Zhu, M.Y., 1994. Medusiform fossils of Kaili Fauna from Taijiang, Guizhou. Acta Palaeontol. Sin. 33, 272–280.

Zhu, M.Y., Zhao, Y.L., Chen, J.Y., 2002. Revision of the Cambrian discoidal animals *Stellostomites eumorphus* and *Pararotadiscus guizhouensis* from South China. Geobios 35, 165–185.

Zhu, M.Y., Gehling, J.G., Xiao, S.H., Zhao, Y.L., Droser, M.L., 2008. Eight-armed Ediacara fossil preserved in contrasting taphonomic windows from China and Australia. Geology 36, 867–870.