Life on the Edge: The Cambrian Marine Realm and Oxygenation

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Abstract

The beginning of the Phanerozoic saw two biological events that set the stage for all life that is to come: (*a*) the Cambrian Explosion (the appearance of most marine invertebrate phyla) and (*b*) the Great Ordovician Biodiversification Event (GOBE), the subsequent substantial accumulation of marine biodiversity. Here, we examine the current state of understanding of marine environments and ecosystems from the late Ediacaran through the Early Ordovician which spans this biologically important interval. Through a compilation and review of the existing geochemical, sedimentological, and fossil records, we argue that this interval was one of sustained low and variable marine oxygen levels that both led to animal extinction and fostered biodiversification events throughout the Cambrian and Early Ordovician. In this way, marine ecosystems of the Cambrian and Early Ordovician existed on the edge—with enough oxygen to sustain them but with the perennial risk of environmental stressors that could overwhelm them.

- We review the current research on geochemistry and paleontology of the Cambrian and Early Ordovician periods.
- Low and oscillating oxygen levels in the marine realm promoted diversification and evolutionary innovation but also drove several extinction events.
- Taphonomic modes and marine authigenic pathways that were abundant in the Cambrian were supported by oceans that were persistently less oxygenated than today's oceans.

1. INTRODUCTION

The interval of time from the later Ediacaran into the Ordovician is one of the most critical intervals in evolutionary history of life on our planet. The skeletal marine phyla appear for the first time (Sperling et al. 2013, Wood et al. 2019, Zhuravlev et al. 2022), and ecological interactions become a driver of evolution (Hsieh et al. 2022). Following the initial late Ediacaran diversifications and subsequent Cambrian Explosion of animal life from ~538 to 522 million years ago (Maloof et al. 2010, Nelson et al. 2022), biodiversity levels stagnated for the next ~40 million years until the Great Ordovician Biodiversification Event (GOBE), where familial diversity increased dramatically (Servais et al. 2023, Stigall et al. 2020). The early initial radiation of organisms in the Ediacaran (Tarhan 2018, Wood et al. 2019) is firmly established in the Cambrian, with new organisms shaping the seafloors and pelagic realms in terms of both the ecosystems in these environments and their physical and chemical state. On the seafloor, bed penetrative trace fossils—most famously *Treptichnus pedum*—show that organisms were capable of disrupting the fabric of the sediment (e.g., Gehling et al. 2001). This change in bioturbation is linked to the expansion of the bilaterian body plan (Droser et al. 2002, Dzik 2005), much like the changes in morphological disparity also happening (Marshall 2006). During the Cambrian Explosion, the appearance of armor (Murdock 2020), sensory organs (Hsieh et al. 2022), and mobility (Wood et al. 2019), all with likely roots in the Ediacaran, reflected a fundamental change in animal ecology. In addition, the first reefs inhabited by animals appeared, built in part by archaeocyath sponges (e.g., Zhuravlev et al. 2022) and creating a locus for skeletal carbonate production.

Following these transformative evolutionary innovations, an early Cambrian extinction event occurred near the end of Cambrian Stage 4 (Pruss et al. 2019b, Zhuravlev & Wood 1996) that notably removed the archaeocyath sponges and robust calcifying animals from reefs for ~40 million years (Pruss et al. 2010). What followed was an interval of high turnover rates exemplified by the trilobite biomere events (Taylor 2006)—extinction events of shallow shelf fauna immediately followed by rapid diversifications that lasted from the middle and later Cambrian (Wuliuan to Stage 10) and into the Early Ordovician (Tremadocian) (**Figure 1**). Recent work on the end Cambrian Stage 4 post-extinction interval also reveals a burgeoning prevalence of other sponges in later Cambrian microbial reefs, in spite of the loss of the archaeocyaths (Lee & Riding 2018). Even so, with the disappearance of the first animal reefs at

the end of the early Cambrian, there is an interval of arguably low diversity (Harper et al. 2019) and low abundance of skeletonizing animals (Pruss et al. 2010). The drivers of this later Cambrian–Early Ordovician plateau of diversity are poorly understood, and the marine biosphere was likely influenced by multiple causal factors and feedbacks (both physical and biological) operating across a range of spatiotemporal scales that ultimately gave way to the Middle Ordovician biodiversification event (e.g., Stigall et al. 2020).
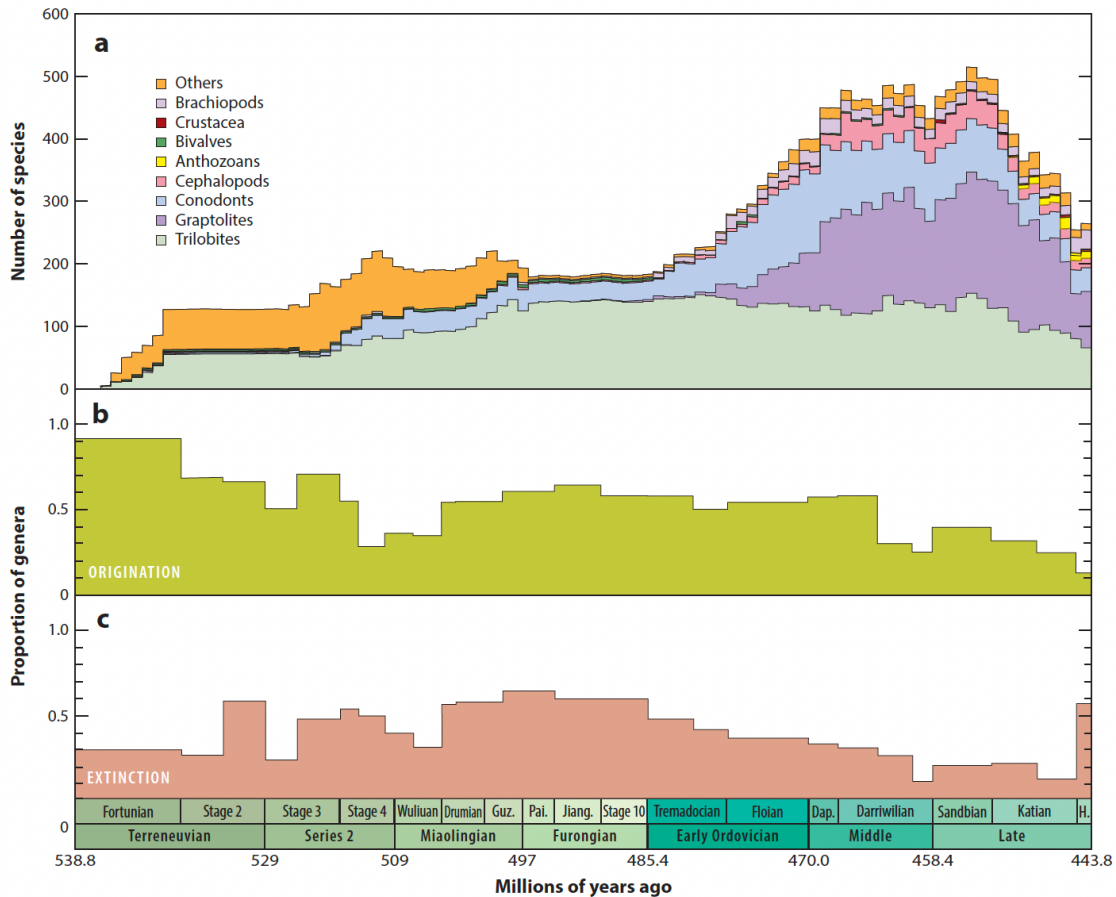

Figure 1 Marine species-level diversity and genus-level origination and extinction rates through the Cambrian and Middle Ordovician. Species diversity data are from the analyses of Fan et al. (2020); genus-level origination and extinction rates are based on the analysis of Bambach et al. (2004). Abbreviations: Dap., Dapingian; Guz., Guzhangian; H., Hirnantian; Jiang., Jiangshanian; Pai., Paibian. Note that the ages of all stage boundaries have been rounded to the nearest millions of years.

As a backdrop to these critical evolutionary changes in the oceans, there is now a voluminous body of research that indicates that the later Ediacaran through the Cambrian and Early

Ordovician oceans were not as well oxygenated when compared to those later in the Phanerozoic (e.g., Dahl et al. 2014; Gill et al. 2011; Guilbaud et al. 2018; Hammarlund et al. 2018; LeRoy et al. 2021; Li et al. 2017; Lu et al. 2018; Pruss et al. 2019a; Sperling et al. 2013, 2015). In addition, the redox state of the oceans during this interval appears to have been highly variable with transient episodes of increased deoxygenation (Dahl et al. 2014, 2017, 2019; Gill et al. 2011; He et al. 2019; Zhang et al. 2023; Zhao et al. 2023). These lower oxygen and unstable redox conditions in the oceans appear to have had a profound influence on the trajectory of the evolution and ecology of marine ecosystems (Dahl et al. 2019; Gill et al. 2011; He et al. 2019; Ivantsov et al. 2005; Pruss et al. 2010; Sperling et al. 2013, 2015; Wood et al. 2019). The redox state of Cambrian oceans likely also had an important effect on marine authigenesis (minerals precipitated from porewaters during early diagenesis) (Pruss et al. 2019a, Wang et al. 2023) and the taphonomic pathways that resulted in the Cambrian fossil record (Anderson et al. 2018, Gaines 2014).

Here, we discuss the role that sustained low marine oxygenation had on the evolutionary trajectory of life in the Cambrian by both fostering diversification in ecosystems and leading to elevated rates of extinction. The Cambrian interval is situated amid a prolonged interval of these marine conditions that originate in the Ediacaran and extend into the Early Ordovician; we focus here mainly on the Cambrian specifically because the evolutionary events of the Cambrian, reviewed below, separate it from both the preceding and following intervals of time. Together, the mounting geochemical evidence, rates of extinction, fossil skeletal abundance, and style of fossil preservation throughout the Cambrian point to a shallow seafloor that was dynamically and unevenly oxygenated with deeper basinal environments that were generally anoxic but with periodic intervals of oxygenation. We argue that less oxygenated oceans affected the Cambrian fossil record because low oxygen and oscillating redox conditions play a key role in the formation of authigenic minerals, important in both the occurrences of small shelly fossils (SSFs) and contributing to the unusual abundance of fossil lagerstätten in the Cambrian.

Understanding this dynamic world and the interplay between biology and environments helps us better know the landscape that gave rise to the appearance of animal phyla in the Cambrian and the subsequent biological radiations of the Ordovician. Future work on this critical interval of early animal evolution may benefit from biological, geochemical, and taphonomical work that seeks to better and more finely constrain absolute oxygen levels and biogeochemical feedbacks

that operated during this time.

2. CAMBRIAN EVOLUTION OF MARINE ECOSYSTEMS

The Cambrian Explosion has been reviewed extensively in the literature, in terms of both diversity and ecological changes to the marine realm (Bowyer et al. 2022, Conway Morris 2000, Erwin & Valentine 2013, Marshall 2006). Of note is the more recent debate about whether the early Cambrian contains a truly unique macroevolutionary event, or if it is simply a continuation of biological innovation that had its roots in the Ediacaran and earlier (Cai et al. 2019, Darroch et al. 2021, Wood et al. 2019). Others have suggested it was part of a longer, single diversification event that includes the GOBE (Servais et al. 2023). Regardless, the early Cambrian interval is marked by the appearance of members of many recognizable phyla (Butterfield 2003, Daley et al. 2018, Lee et al. 2013, Paterson et al. 2019), including some of the earliest predators on the seafloor.

A potentially unifying feature of the emergence of these ecosystems was an adaptation to low oxygen conditions (Sperling et al. 2021). While some oxygen is required for all animal metabolisms (Tostevin et al. 2016), and higher oxygen levels might spur ecological interactions (Sperling et al. 2013), the appearance of animals in the Cambrian is consistent with a pattern of the most hypoxic-tolerant animals appearing first and those with higher oxygen needs appearing later. Some have argued that shallow water oxygenation exerted a direct control on the timing and tempo of marine diversification in the Cambrian (He et al. 2019) and the Ordovician (Edwards et al. 2017). It is clear that, while some oxygen is necessary for the diversity and complexity of Cambrian and Ordovician ecosystems, the oxygen demands of these organisms were likely lower (Mills et al. 2014, Sperling & Stockey 2018, Sperling et al. 2013), and these ecosystems evolved and thrived in an overall lower oxygen world (Sperling et al. 2015).

With the increases in marine diversity seen during the Cambrian Explosion, there was a transition from arguably simpler Ediacaran ecosystems to more complex ones, though this transition was likely dynamic (Bowyer et al. 2022, Cribb et al. 2023, Darroch et al. 2021, Droser et al. 2017, Erwin & Valentine 2013, Nelson et al. 2022, Topper et al. 2022). These ecological shifts are ultimately reflected in a variety of morphological changes in organisms, including the development of both predatory and antipredatory features. Further ecological development in the early Cambrian included the expansion of bed penetrative bioturbation, which marks the

beginnings of the exploration of the infaunal realm ([Bottjer et al. 2000](#), [Crimes & Anderson 1985](#), [Mángano & Buatois 2017](#), [Tarhan & Droser 2014](#)), and the development of more complex ecosystems, notably the appearance of animal (archaeocyathan)-containing reefs ([Rowland & Gangloff 1988](#)).

2.1. Predators and Prey

One fundamental change that occurred in earnest during the Cambrian was the establishment and expansion of predator-prey dynamics among many different groups of organisms. The development of predation might be best reflected in the radiation of diverse skeletal elements and in a group of early Cambrian fossils appropriately named SSFs (e.g., [Porter 2004](#), [Skovsted & Peel 2007](#)). These morphological innovations signal the preponderance of predator-prey interactions in Cambrian seas ([Bicknell et al. 2022](#), [Pates & Bicknell 2019](#), [Sperling et al. 2013](#)), made possible by the appearance of sensory organs ([Marshall 2006](#), [Paterson et al. 2020](#), [Hsieh et al. 2022](#)) and greater mobility ([Erwin & Valentine 2013](#), [Wood et al. 2019](#)).

Predators ranged from the famous *Anomalocaris* (e.g., [Paterson et al. 2011](#)) to shell drilling organisms ([Conway Morris & Bengtson 1994](#)). There is debate about how much escalation happened as a result of these new predation pressures, but the expansion of shell-making points to an evolutionary advantage for added protection ([Vermeij 1989](#)). Recently, trilobite cannibalism has been documented in the Emu Bay Shale of southern Australia, with extensive wounds documented on trilobite fossils and co-occurring shelly coprolites cited as evidence ([Bicknell et al. 2022](#)). Further, the genetic capacity for skeleton-making predates their expansion in the Cambrian ([Marshall 2006](#)), which points to biological interaction as perhaps one of the most important drivers for the morphological expression of predator-prey dynamics that manifest in Cambrian fossils. [**AU: This reference is not in the Lit. Cited. Please add there or remove from here.**]). Taken as a whole, these evolutionary and ecological advances demonstrate the beginning of the Cambrian way of doing business in a new eat-or-be-eaten world.

2.2. Infaunalization

In addition to appearance and diversification of skeletal taxa, the Cambrian is noted as the moment the worm turned ([Droser et al. 1999](#)) with the advent of bed destructive bioturbation occurring substantially for the first time. In this way, the sedimentary record was itself

influenced by evolutionary innovation; complex modes of infaunalization had appeared in the Cambrian (Tarhan 2018, Tarhan & Droser 2014). Some studies point to specific instances of substantial bioturbation as harkening a new evolutionary moment (Mángano & Buatois 2017, Seilacher & Pflüger 1994) with large-scale implications on the biogeochemistry of the oceans (Boyle et al. 2018, van de Velde et al. 2018 [**AU: This reference is not in the Lit. Cited. Please add there or remove from here.**][added]). Other authors point to the subtlety of the Cambrian trace fossil revolution, with an emphasis on environmental heterogeneity and a delayed onset of deep and substantial sediment mixing (Tarhan 2018, Tarhan & Droser 2014, Tarhan et al. 2023) and more modest implications for its influence on marine biogeochemistry (Cribb et al. 2023, Tarhan 2018, Tarhan & Droser 2014). Even with a later establishment of a mixed layer, the evolutionary significance of Cambrian bioturbators is unequivocal. Diverse organisms, represented by diverse behaviors, are exploiting the infaunal realm for the first time (Seilacher & Pflüger 1994). This revolution in trace making illustrates that the Cambrian explosion is not simply, or only, a skeletal evolutionary event (Crimes & Anderson 1985).

2.3. Reefs and Skeletons
Another Cambrian ecosystem that reflects the increase in abundance of skeletal animals (Li & Droser 1997) is the appearance and expansion of archaeocyathan reefs, which fostered an increase in abundance of animals both within and around the reefs (Zhuravlev et al. 2022). Cambrian reef ecosystems function in some ways like those of the later Ediacaran—they serve as a locus for attached skeletal taxa (Grotzinger et al. 2005), and though they appear to be ecologically more simple, they behave in some ways like modern reef ecosystems (Rowland & Gangloff 1988). The early Cambrian extinction (Zhuravlev & Wood 1996) resulted in a disappearance of animal reef ecosystems (Pruss et al. 2019b, Zhuravlev & Wood 1996), replaced by microbial buildups (Adachi et al. 2014) that, while similar to their Neoproterozoic counterparts in many ways, are more influenced by animals and macroalgae. Sponge/microbial reefs are also noted from this interval of time (Lee & Riding 2018, Lee et al. 2015), but skeletal abundance in these settings declined during the archaeocyath extinction and remained low (Pruss et al. 2010) and framework reefs did not fully reemerge until the Ordovician.

After the extinction of archaeocyaths in middle and later Cambrian time, microbial reefs are thought to flourish again in the absence of metazoan reef builders/dwellers (Adachi et al. 2014, Lee et al. 2015). Further investigation of middle and later Cambrian microbial buildups revealed

the prevalence of sponges in these structures, often siliceous lithistid and occasionally anthaspidellid sponges. This replacement of archaeocyaths with lithistid sponges has caused some authors to posit that lithistid sponges might have been well adapted to the low oxygen conditions of this middle and later Cambrian greenhouse world (Lee & Riding 2018). In some cases, lithistid sponges may have locally formed framework reefs but certainly persisted through much of this time period in a consortium with microbes. The oxygen influence on lithistid sponges is also revealed by the small size of these sponges, perhaps as a way to manage oxygen stress (Lee & Riding 2018). Finally, the mineralogy of lithistid sponges is much different than the archaeocyaths of the early Cambrian and the subsequent reef builders of the Early and Middle Ordovician. Lithistid sponges make siliceous skeletons, and these skeletons may have fared better in the Cambrian than their calcareous counterparts, due to a variety of environmental factors, including adaptations to low oxygen settings (e.g., Lee & Riding 2018).

In the middle and later Cambrian, the abundance of skeletal animals outside of the microbial reefs was also low (Pruss et al. 2010), as compared to most earlier archaeocyathan reef settings (Pruss et al. 2019b) and to environments later in the Ordovician (Pruss et al. 2010, Stigall et al. 2020). The organisms contributing to the majority of skeletal carbonate during this time were trilobites and echinoderms. Furthermore, repeated trilobite biomere extinction events during this interval point to repeated, if not sustained, environmental stress (Taylor 2006).

In the Early Ordovician, the lithistids are joined by *Calathium*, tabulate corals, stromatoporoids, and pulchrilaminids, which transformed reef-building (Kröger et al. 2017) by adding thick carbonate skeletons to reef frameworks. In all these ways, the lower oxygen condition of the Cambrian paved the way for a second phase of metazoans contributing to reefs in the middle and later Cambrian (Lee & Riding 2018) **[**AU: This reference is not in the Lit. Cited. Please add there or remove from here.**]**), and the subsequent amelioration of these environmental conditions may have led to the next phase of metazoan carbonate framework reef-building during the GOBE (Kröger et al. 2017).

3. MARINE OXYGENATION IN THE CAMBRIAN

It was long thought that the last step toward modern levels of the oxygenation of the oceans and atmosphere occurred during the Ediacaran leading to evolution of the first animals (as reviewed in Knoll & Carroll 1999). In fact, the appearance of animals with their metabolic demand for at

least some oxygen was taken as evidence for a late Proterozoic rise in oxygen (e.g., Berkner & Marshall 1965, Nursall 1959). What is now clear is that multiple lines of evidence support the notion that the early Paleozoic atmosphere and oceans were less oxygenated than those later in the Phanerozoic and were likely more similar to those of the preceding Ediacaran (Gill et al. 2011; Lu et al. 2018; Sperling et al. 2015, 2021; Wei et al. 2021). To see a discussion of factors that may have contributed to maintaining low oxygen conditions in oceans of the Cambrian and Early Ordovician, see the sidebar titled What Caused Cambrian and Early Ordovician Oceans to Be Less Oxygenated?**[**AU: Edit OK?**][YES]

WHAT CAUSED CAMBRIAN AND EARLY ORDOVICIAN OCEANS TO BE LESS OXYGENATED?

Several environmental factors likely contributed to less oxygenated Cambrian and Early Ordovician oceans. Atmospheric oxygen was well below modern levels [less than 10% of the modern (Krause et al. 2018, Lenton et al. 2018)], and that would have translated into lower dissolved oxygen concentrations in shallow and deeper marine waters. The warmer climate present through most of the Cambrian [evidenced by sea surface temperatures derived from oxygen isotopes and clumped isotope proxy data (Goldberg et al. 2021, Hearing et al. 2018, Trotter et al. 2008)] would have led to lower oxygen solubility in shallow marine waters in contact with the atmosphere. The warmer climate was likely linked to higher atmospheric pCO_2 (e.g., Lenton et al. 2018) potentially caused by elevated continental arc volcanism (McKenzie et al. 2014). The higher pCO_2 and warm climate would have also fostered higher rates of continental weathering, which is supported by radiogenic values of the marine strontium isotope record throughout the Cambrian (e.g., Montañez et al. 1996) that later declined in the Ordovician (e.g., Edwards et al. 2015, Shields et al. 2003). This weathering would have enhanced phosphorus delivery to the ocean, primary productivity, and eutrophication in areas of the oceans.

Some of the first evidence that suggested the oceans were less oxygenated in the Cambrian and Early Ordovician came in the form of the stratigraphic distribution of organic-rich black shale facies. Compilations of facies in sedimentary sequences show that the Cambrian along with two other intervals of the early Paleozoic (specifically portions of the Ordovician and Silurian) contain an abundance of organic-rich facies (e.g., Berry & Wilde 1978). While organic-rich sediments can accumulate under lower oxygen conditions, they can also accumulate under a variety of water column redox conditions, making this evidence less conclusive. Subsequently, a large body of geochemical data has been brought to bear on the question of Cambrian and Early Ordovician marine chemistry and oxygenation, and we summarize this here (see **Figure 2**).
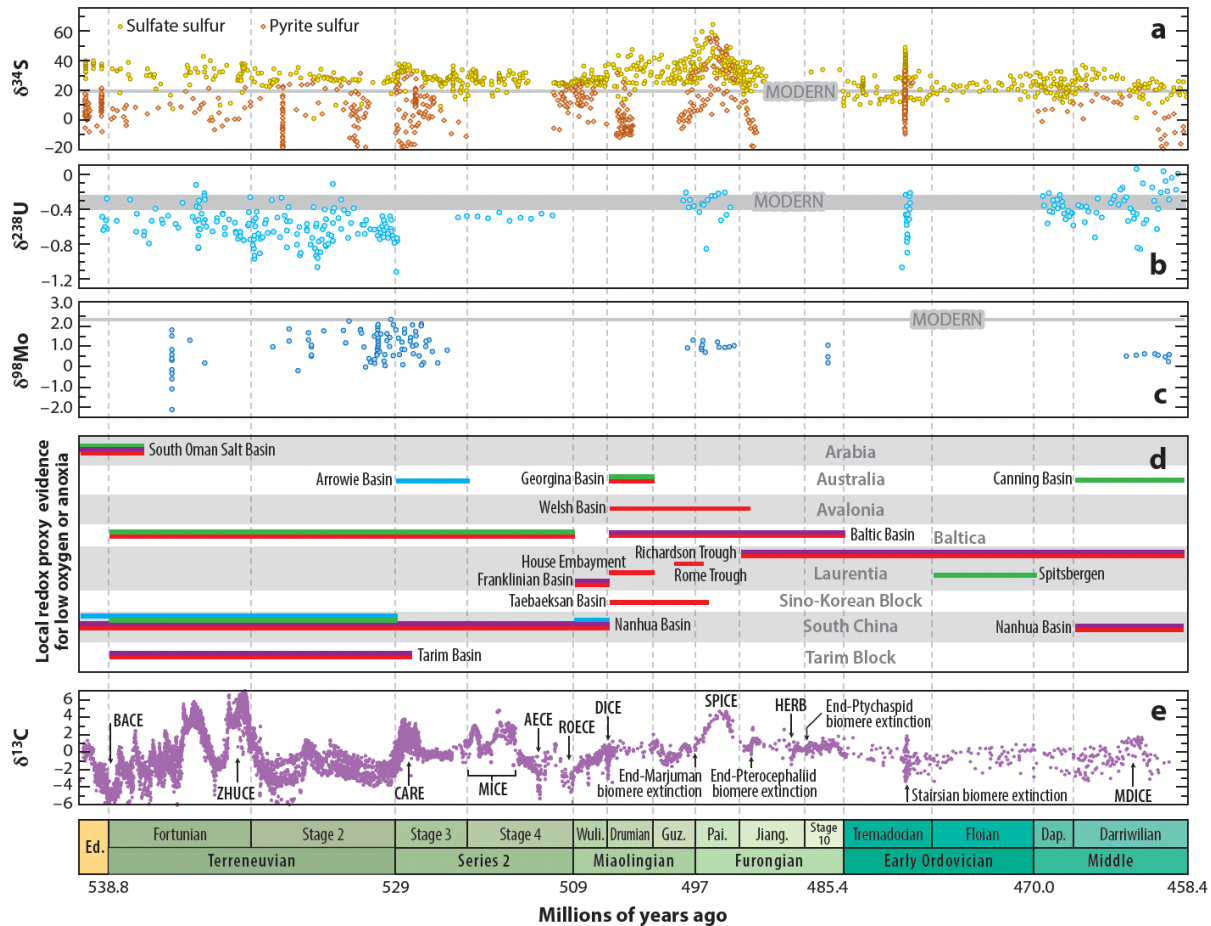
Figure 2 Summary of geochemical proxy data from the latest Ediacaran through Middle Ordovician. References for all geochemical data are provided in the **Supplemental Table**. (*a*) Sedimentary sulfur isotope (δ^{34}S) data. The horizontal gray line on the sulfur isotope plot is the modern data sulfur isotope composition of marine sulfate (+21‰), and sulfate sulfur isotope data that fall above this field suggest higher rates of pyrite burial and therefore less oxygenated oceans. (*b*) Uranium isotope (δ^{238}U) data from carbonate rocks. The horizontal gray box indicates the uranium isotope composition of modern carbonates, and data that fall below this field suggest less oxygenated oceans as compared to modern. (*c*) Molybdenum isotope (δ^{98}Mo) data from shales deposited under euxinic conditions (most likely to potentially capture seawater) as determined by iron speciation analyses. The horizontal gray line indicates the modern marine isotope composition of seawater (+2.3‰), and data below this line suggest less oxygenated oceans as compared to modern. (*d*) Bar graphs indicating basins with sedimentary successions where local redox proxy data point to lower than modern oxygenation and/or anoxia in the water column. The types of data are indicated by the color of the bars: Trace metals concentrations are purple, iron speciation analyses are red, organic biomarkers are green, and cerium anomalies are blue. Note that occurrences of local geochemical redox indicators are binned roughly by geologic stage and do not necessarily point to the continuous availability of data and occurrence of low oxygen conditions or anoxia during the stage. (*e*) Carbon isotope data indicated as black circles. Recognized carbon isotope excursions are indicated on the plot. Abbreviations: AECE, Archaeocyathid Extinction Carbon isotope Excursion; BACE, BAse of the Cambrian Excursion; CARE, Cambrian Arthropod Radiation isotope Excursion; Dap., Dapingian; DICE, Drumian Carbon Isotope Excursion; Ed., Ediacaran; Guz., Guzhangian; HERB,

HEllnmaria-Red Tops Boundary; Jiang., Jiangshanian; MDICE, Middle Darriwilian Carbon Isotope Excursion; MICE, Mingxinsi Carbon Isotope Excursion; Pai., Paibian; ROECE, Redlichiid and Olenellid Extinction Carbon isotope Excursion; SPICE, Steptoean Positive Carbon Isotope Excursion; Wuli., Wuliuan; ZHUCE, ZHUjiaqing Carbon isotope Excursion. Note that the ages of all stage boundaries have been rounded to the nearest millions of years.

Global-scale marine redox proxies, such as sulfur, molybdenum, and uranium isotopes (δ^{34}S, δ^{98}Mo, and δ^{238}U, respectively) broadly suggest less oxygenated conditions in the oceans during portions of the Cambrian and Early Ordovician (**Figure 2***b–d*; **Supplemental Table**). These proxies can be used to track cycles of these elements and the processes that discriminate between their different isotopes. Importantly, all these elements have burial fluxes out of the ocean that are tied to changes in the areal extent of deposition under anoxic water columns and/or sediments with reducing porewaters. While all these proxy data have caveats to their interpretation (i.e., the potential for local processes and later alteration by diagenesis influencing the preserved signals), as a whole, they paint a clear picture of less oxygenated oceans during the Cambrian and Early Ordovician.

Cambrian and Early Ordovician marine sulfate sulfur isotope compositions are higher and more geographically variable than the modern ocean and those seen later in the Phanerozoic, which suggests higher burial fluxes of sedimentary pyrite and lower marine sulfate concentrations (Dahl et al. 2019, Gill et al. 2011, He et al. 2019, Wotte et al. 2012) (**Figure 2***a*; **Supplemental Table**). The formation and burial of pyrite is the end product of microbial sulfate reduction (MSR), which occurs in anoxic water columns or within sedimentary porewaters and utilizes sulfate to produce hydrogen sulfide. This sulfide can react with iron to produce sedimentary pyrite, which can be buried in sediments with anoxic porewaters or under anoxic water columns. MSR also preferentially produces sulfide depleted in ^{34}S; therefore, elevated burial rates of pyrite can lead to residual marine sulfate reservoirs being enriched in δ^{34}S.

Rapid changes, a million years or possibly less, in the isotope composition of marine sulfate also characterize much of the Cambrian and Early Ordovician (Dahl et al. 2017; Edwards et al. 2018; Gill et al. 2007, 2011; He et al. 2019; Saltzman et al. 2015; Zhang et al. 2023). This suggests a smaller marine sulfate reservoir as compared to the modern (Algeo et al. 2015; Gill et al. 2007, 2011), which is also supported by fluid inclusion data from Cambrian marine halites (Brennan et al. 2004) and the regional heterogeneity found in the δ^{34}S of marine sulfate (Gill et al. 2007, 2011). The small marine sulfate reservoir would be expected in oceans with higher

burial rates of pyrite ([Gill et al. 2007](#)). Additionally, the $\delta^{34}S$ of sedimentary pyrite is elevated throughout the Cambrian and Early Ordovician as compared to modern and other Phanerozoic sedimentary pyrites (e.g., [Edwards et al. 2015](#), [Gill et al. 2011](#), [LeRoy & Gill 2019](#), [LeRoy et al. 2021](#), [Wotte et al. 2012](#)) (**Figure 2a**). This likely reflects the elevated $\delta^{34}S$ of parent seawater sulfate but also the product of hydrogen sulfide in sedimentary porewaters more commonly displaying closed system isotopic behavior: less overall isotopic offset between the $\delta^{34}S$ of seawater sulfate and MSR-produced hydrogen sulfide caused when more of the available sulfate is consumed by MSR. More common ^{34}S-enriched pyrites are also consistent with sulfate-poor Cambrian and Early Ordovician oceans, which would have promoted more frequent quantitative conversion of sulfate to sulfide in sedimentary porewaters (i.e., [LeRoy et al. 2021](#)).

Uranium isotope data from Cambrian and Early Ordovician marine carbonates also point to more prevalent marine anoxia (reviewed in [Wei et al. 2021](#)) (**Figure 2b**). While the U isotope composition of carbonates is offset from seawater, it can be leveraged to track the relative proportions of oxic and anoxic U removal from seawater (as reviewed in [Lau et al. 2019](#)). The reduction and burial of U into reducing sediments, often adhering to organic matter, is the largest sink of U in the oceans today, preferentially removes the heavier uranium isotopes, and carries the largest U isotope fractionation: up to 1‰ relative to other oceanic U sinks (~0.03‰). Carbonates from the Terreneuvian and Series 2 (e.g., [Dahl et al. 2017](#), [2019](#); [Wei et al. 2018](#), [2021](#)) and intervals of Furongian (e.g., [Dahl et al. 2014](#)) predominately have $\delta^{238}U$ that is less than that from modern carbonates, implying larger areas of oxygen-deficient deposition within the oceans. Rapid variations in this record also imply highly dynamic changes in marine redox during intervals of the Cambrian ([Dahl et al. 2014](#), [Wei et al. 2018](#)), which are discussed later.

Molybdenum isotopes from Cambrian and Early Ordovician shales also suggest lower marine oxygenation (reviewed in [Dahl et al. 2017](#) and [Wei et al. 2021](#)) (**Figure 2c**). Processes that remove molybdenum from seawater carry isotopic fractionations that are controlled by redox conditions in the depositional environment. In brief, the more oxidized sinks of molybdenum, such as iron and manganese oxides, sediments with hydrogen sulfide confined to the porewaters preferentially remove the lighter molybdenum isotopes (as reviewed in [Kendall et al. 2017](#)). Sediments deposited under euxinic conditions (anoxic and sulfide-containing water columns) show smaller isotopic offsets from seawater and under particular conditions (euxinic settings with high levels of sulfide) can record seawater $\delta^{98}Mo$. Note that this record is more temporally

limited than that of sulfur and uranium isotopes given the lithofacies requirement (euxinic black shales) needed for potentially capturing the seawater δ^{98}Mo signature. High marine δ^{98}Mo signatures in shales can be taken as evidence of a greater predominance of the sink of molybdenum and thus more oxygenated oceans or the lesser extent of marine euxinia. The low δ^{98}Mo of euxinic Cambrian and Early Ordovician shales can therefore be taken as evidence of less oxygenated oceans ([Wei et al. 2021](#)) (**Figure 2b**).

While the systematics of the S, U, and molybdenum isotope proxies can be useful for tracking the global-scale changes in the area of reducing deposition within the oceans, they do not specifically identify the particular areas in the oceans that were deposited under these redox conditions. Voluminous local redox proxy data such as iron speciation (e.g., [Guilbaud et al. 2018](#), [LeRoy et al. 2021](#), [Sperling et al. 2015](#)), redox-sensitive metal enrichments (e.g., [Gill et al. 2021](#), [Pruss et al. 2019a](#), [Zhao et al. 2023](#)), cerium anomalies (e.g., [Wei et al. 2018](#)), iodine contents (e.g., [Edwards et al. 2018](#), [Lu et al. 2018](#)), and organic biomarkers (e.g., [Pagès et al. 2016](#)) from the majority of sedimentary basins point to relatively persistent deeper water anoxia throughout the Cambrian and Early Ordovician (summarized in **Figure 2d**; references provided in the **Supplemental Materials**).

The majority of these local proxy studies document deeper waters that were predominantly ferruginous (anoxic and with excess iron compared to H_2S), with less common intervals of euxinia (anoxic with excess H_2S relative to iron) ([Guilbaud et al. 2018](#), [LeRoy et al. 2021](#), [Sperling et al. 2015](#)). Such conditions are also thought to characterize Ediacaran oceans (e.g., [Sperling et al. 2015](#)). Further, some data from proximal to distal depositional transects have been used to advocate for an oxygen minimum zone (OMZ)-like, anoxic wedge model: shallow oxygenated waters underlying euxinic waters in the more proximal position, followed by ferruginous conditions in more deep and distal portions of the basins ([Guilbaud et al. 2018](#), [Wei et al. 2021](#)). In this model, the area of euxinia within the wedge expands and contracts with changes in the local primary productivity and/or the supply of sulfate from weathering on land or open ocean. However, it should be noted that the local redox proxy record contains major geographical and temporal biases. For example, the Terreneuvian and Series 2 are much more densely sampled, and the overwhelming majority of these samples derive from successions in the Nanhua Basin of South China. However, these data, when viewed in conjunction with global-scale proxies, point to oxygen deficiency being a common feature of the deeper portions of

Cambrian and Early Ordovician oceans.

This persistent deeper ocean anoxia would have left shallow water environments more vulnerable to episodes of deoxygenation, and in fact, many studies also indicate the dynamic nature of marine redox conditions in Cambrian and Early Ordovician oceans. Frequently changes in marine redox coincide with linked perturbations in the carbon cycle expressed as carbon isotope excursions in the sedimentary record; transient expansions of anoxic conditions in the oceans have been suggested to occur in concert with changes in the carbon cycle (**Figure 2***e*) in the Terreneuvian (e.g., Wei et al. 2018), just after the Stage 2–3 boundary (Dahl et al. 2017, He et al. 2019), in the Drumian and Paibian (Gill et al. 2011, Zhang et al. 2023), and in the Tremadocian (Edwards et al. 2018, Saltzman et al. 2015).

Among these intervals, the Steptoean Positive Carbon Isotope Excursion (SPICE) is the best-studied example. The SPICE is large (+4 to +5‰), with positive carbon excursion recorded marine carbonates and organic matter found in Paibian-age strata on multiple paleocontinents (e.g., Saltzman et al. 2000). In concert with the SPICE, there is a parallel positive sulfur isotope excursion in marine sulfate (Gill et al. 2007, 2011; Zhang et al. 2023) and sedimentary pyrite (Gill et al. 2011, LeRoy & Gill 2019, LeRoy et al. 2021) and a parallel negative molybdenum isotope excursion (Gill et al. 2021) and a negative uranium isotope excursion that occurs with the rising limb of the SPICE (Dahl et al. 2014). These combined geochemical signals have been linked to an expansion of the areal extent of seafloor anoxia driving enhanced burial of organic matter, pyrite, and redox-sensitive trace metals within the oceans (Dahl et al. 2014, Gill et al. 2011, LeRoy & Gill 2019, Zhang et al. 2023). In support of this scenario, there are some locations that record enrichments of redox-sensitive trace metals during the SPICE as compared to the succeeding **[**AU: Is this what was meant?**]**and preceding stratigraphic intervals (LeRoy & Gill 2019, Pruss et al. 2019a, Zhang et al. 2023), which point to the local expansion of reducing conditions. Further, the alum shale from Baltoscandia records persistently anoxic (ferruginous and euxinic) conditions and shows depletions in the trace metal enrichments in the interval that contains the SPICE that have been suggested to reflect depletion in the marine reservoirs of these elements during the expansion of anoxic conditions (Gill et al. 2011, 2021; Zhao et al. 2023).

The initiation of the SPICE also appears to be temporally coupled with one of the biomere extinction events (the end-Marjuman) recognized on several paleocontinents (e.g., Saltzman et

al. 2000, Zhang et al. 2023) and suggests that the expansion of anoxia may be one of the drivers of this event. Later, in the wake of expanded ocean anoxia during the SPICE, there is evidence for a net rise in marine oxygenation linked to enhanced organic carbon and pyrite burial that occurred across the event (Saltzman et al. 2011, Zhang et al. 2023, Zhao et al. 2023). This potential oxygenation event has been invoked as a driver of the radiation of plankton that occurred after the SPICE (Servais et al. 2016). Subsequent studies of the Stairsian biomere extinction that occurs in the Early Ordovician have documented similar geochemical changes across that event (Edwards et al. 2018, Saltzman et al. 2015) and suggest a role for expanding deoxygenation in the oceans for the other biomere extinctions. All these connections highlight the links between changes in marine oxygenation and life during the Cambrian and underscore the need to conduct similar studies to explore these records across other Cambrian extinction events, such as the early Cambrian archaeocyath extinction and later biomere events.

4. MARINE AUTHIGENESIS AND FOSSIL PRESERVATION IN THE CAMBRIAN

The more reducing Cambrian and Early Ordovician oceans likely had an influence on marine authigenesis and biogeochemical cycles, and, in turn, the taphonomic pathways preserving fossils. Here we define marine authigenesis as the formation of minerals within the sediment during early marine diagenesis. As noted earlier, several lines of evidence point to Cambrian and Early Ordovician oceans that were sulfate poor and likely maintained by less oxygenated marine waters. These conditions permit different pathways for iron during diagenesis in marine sediments and allowed for the more frequent authigenic formation of iron minerals other than pyrite, such as glauconite, vivanite, berthierine, and chamosite (Anderson et al. 2018). Moreover, similar to Neoproterozoic oceans, reducing and anoxic ferruginous water columns and porewaters would have also led to phosphorous cycling that was different from later Phanerozoic oceans (Reinhard et al. 2017). Both these factors likely had a hand in some of the unique aspects of the Cambrian and Early Ordovician sedimentary and fossil record, which we discuss below.

4.1. Small Shelly Fossil Preservation in the Cambrian

SSFs, carbonate-secreted (and later replaced or molded) skeletons, and skeletal elements are a feature of Cambrian deposits globally (Brasier 1990, 1992; Dzik 1994) (**Figure 3a**). In fact, SSFs have long been considered a Cambrian phenomenon, with far more occurrences in the

Cambrian than after it ([Porter 2004](#)). What unites SSFs is that these skeletons and skeletal elements were replaced or molded by minerals during fossilization, most commonly by apatite ([Creveling et al. 2014](#), [Porter 2004](#)) but also glauconite and iron oxides. A long-standing question has been whether the decline of SSFs was reflective of their true decline, an actual decrease in the abundance, or changes in the conditions that led to their preservation.
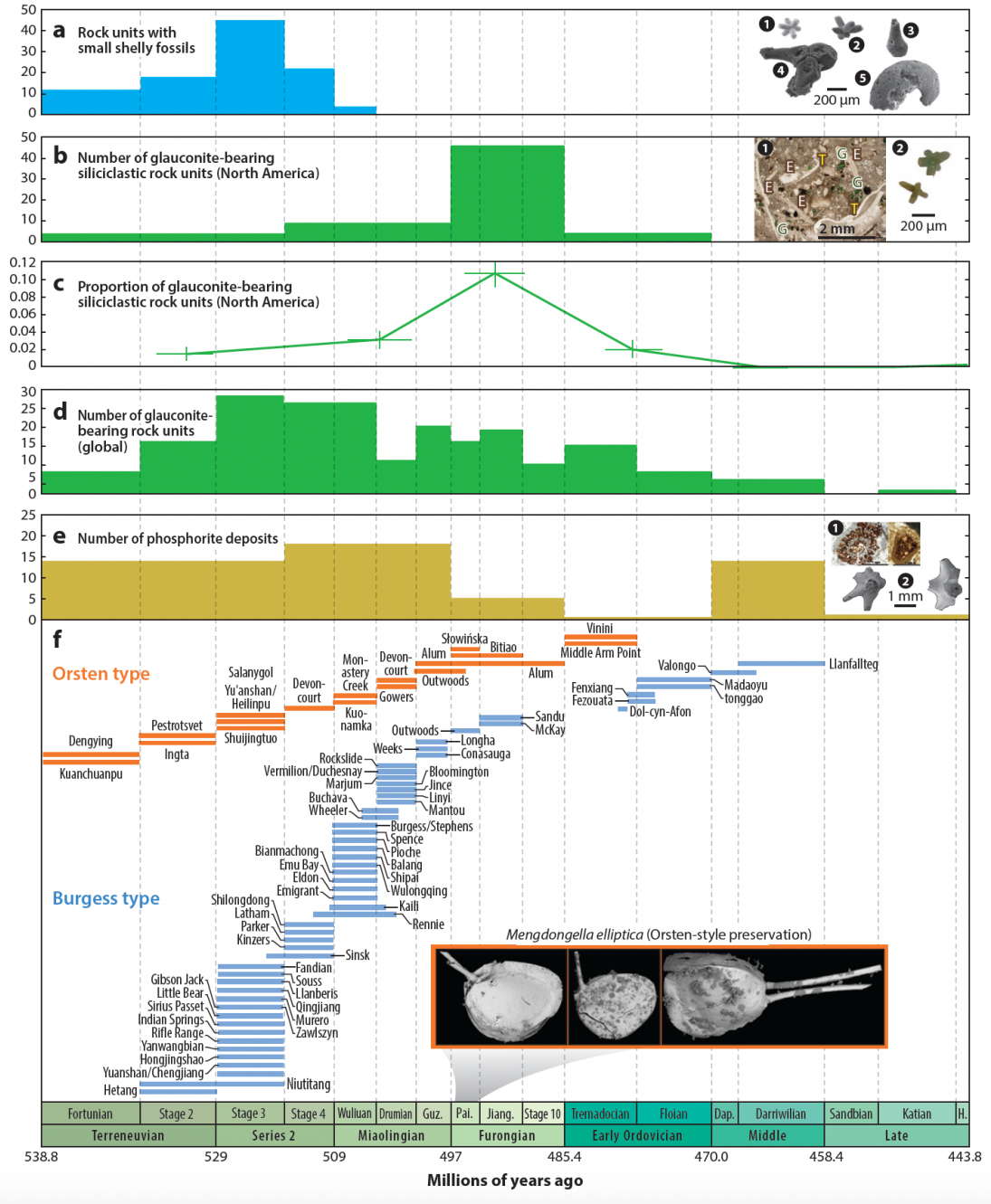
Figure 3 Temporal distribution of small shelly fossils (SSFs), glauconite, phosphate deposits, and lagerstätten. (*a*) Examples of SSFs from the Harkless Formation: 1 and 2 are sponge spicules, 3 and 4 are chancelloriid sclerites, and 5 is a primitive mollusk. Panel *a* modified from Pruss et al. (2019b). (*b*) Examples of glauconite: 1 shows glauconite in a thin section (G), with echinoderm debris (E), and trilobite fragments (T); 2 shows glauconitic molds of sponge spicules from the same unit in panel *a*. (*c*) Proportion of glauconite-bearing siliciclastic rocks from North America (data from Peters & Gaines 2012). (*d*) Global compilation of glauconite-bearing rocks (references are in the **Supplemental Materials**). (*e*) Examples of phosphatized fossils: 1 shows apatite infilling archaeocyath fossil interiors,

and 2 shows phosphatized chancelloriids, both from the lower Cambrian Salaagol Formation, Mongolia. Panel *e* modified from Pruss et al. (2019c). Temporal distribution of phosphorite deposits is from Planavsky (2014). (*f*) Global compilation of fossil lagerstätten (data sources can be found in the **Supplemental Materials**). Photo images courtesy of Zhang H & Xiao S (2017). Abbreviations: Dap., Dapingian; Guz., Guzhangian; H., Hirnantian; Jiang., Jiangshanian; Pai., Paibian. Note that the ages of all stage boundaries have been rounded to the nearest millions of years.

The conditions that led to apatite's role as a replacement (or moldic) mineral have also been investigated in ancient settings. For example, Creveling et al. (2014) used independent redox proxies to argue that low oxygen conditions must have persisted during the early diagenetic formation of apatitic SSFs. Glauconite also molds or replaces skeletons (Brasier 1990, Porter 2004), and subsequent work suggests this preservation mode may be more widespread in the sedimentary record than previously thought (Dzik 1994; Pruss et al. 2018, 2019b). In addition to the porewater conditions that led to fossilization, the size of these fossils likely also played a role in their preservation. Limestones from the Thorntonia Formation well known for their SSF components (Cambrian Series 2, Stage 4) also contain larger fossils whose mineralogy was neomorphosed but not replaced like the SSFs (Creveling et al. 2014). The size, and therefore volume, of fossils may have influenced the redox gradients that existed within the fossils (Pruss et al. 2018), perhaps fostering microenvironments that led to their replacement by phosphate and iron-bearing minerals. This has also been observed in fossils from other time intervals, such as the Early Triassic (Pruss et al. 2018), so size appears to matter, in the case of SSFs, because of the redox gradients that can then be established across them during early diagenesis.

Clarifying the link between paleoenvironment and fossilization is important to understand what closed the taphonomic window that fostered these styles of preservation in the later early and middle Cambrian globally (Porter 2004) (see **Figure 3**). The occurrence of phosphatized and/or glauconitized fossils at other intervals in the Paleozoic (Dattilo et al. 2019, Dzik 1994) and Mesozoic (Maxwell et al. 2021, Pruss et al. 2018) suggests that recurring environmental factors led to these styles of preservation. In this case, the small size of skeletal material (and organismal volume) coupled with early oscillating porewater redox conditions must be critical factors in these modes of preservation and to marine authigenesis of the Cambrian more broadly.

The occurrence of glauconite in Cambrian time is not limited to the preserving mineral of SSFs. Glauconite green sands and pellet deposits are well known from the Cambrian (e.g., Brasier 1980, Chafetz & Reid 2000) (**Figure 3*b*–*d***) with glauconite showing a peak in abundance

in Macrostrat analyses as well ([Peters & Gaines 2012](#)) (**Figure 3***b*,*c*). Glauconite is a redox-sensitive mineral with its initial growth happening under anoxic conditions and its subsequent growth and oxidation of Fe(II) to Fe(III) occurring in the presence of transient oxygen (e.g., [O'Brien et al. 1990](#)). Its widespread distribution across the globe during Cambrian time has been noted, occurring both in siliciclastic sediments and carbonates, but no mechanism for its occurrence has been offered as explanation. If viewed through the lens of redox, the unusual abundance of Cambrian sedimentary glauconite ([Peters & Gaines 2012](#)) must represent porewater redox oscillations occurring near the sediment/water interface. As such, abundant glauconite formation through authigenesis in Cambrian seas requires low oxygen conditions persisting at or near the seafloor ([O'Brien et al. 1990](#)) through much of Cambrian time.

Phosphogenesis of Cambrian fossils has also been globally noted, as the vast majority of SSFs are phosphatized ([Porter 2004](#)), and it plays a significant role in Orsten-style preservation, which involves the phosphatization of delicate features such as embryos and muscle tissue ([Maas et al. 2006](#)). The unusual abundance of phosphatic fossils in Cambrian deposits has begged for an explanation for the origin of the phosphate ([Creveling et al. 2014](#)). [Creveling et al. (2014)](#) argue that while the soft tissue of decaying organisms might have supplied some phosphorus to the phosphatic minerals molding and replacing the Cambrian skeletons, local ferruginous conditions allowing phosphorus to adhere to iron minerals serve as another, arguably more substantial source of phosphorus to shallow marine sediments. The allochthonous deposition of small fossils away from their more oxic setting during life to deeper, less oxic conditions can also lead to phosphatization through the reduction of iron oxides and subsequent release of adsorbed phosphorous that was on their surfaces ([Creveling et al. 2014](#)), again linking the role of redox to authigenic mineral formation in many Cambrian environments. In Orsten-style preservation, soft tissues are preserved through phosphatization before substantial decay, as has been invoked for other preservation windows. Outside of phosphate as a fossilizing authigenic mineral, large phosphorite deposits also have an unusual abundance in the Cambrian ([Cook & Shergold 1984](#)) (**Figure 3***e*), and at least some of these formed under anoxic/oxic fluctuating conditions ([Shields & Stille 2001](#), [Zhang et al. 2022](#)). The establishment of oxygen variability across environments as a result of a redox stratified ocean has also been implicated in widespread phosphorite deposition ([Fan et al. 2016](#)). Both as a local authigenic mineral active during fossilization of Cambrian organisms and in large deposits, the unusual abundance of

phosphate in Cambrian oceans is linked to a world dominated by low levels of oxygen and its heterogeneity across environments.

4.2. Redox and Lagerstätten of the Cambrian

The widespread occurrence of Cambrian lagerstätten has revealed a large diversity of organisms, particularly arthropods, that appeared and radiated during Cambrian time (Allison & Briggs 1993, Erwin et al. 2011) (**Figure 3***f*). While much attention has been appropriately paid to the fossils themselves and what they mean in the evolutionary history of life, there is also a story embedded in the very occurrences and abundance of fossil lagerstätten in the Cambrian. The name lagerstätten is given to those fossil occurrences considered out of the ordinary, or exceptional, often with preserved soft parts or lightly mineralized hard parts that are typically unlikely to be preserved in the rock record. Yet, the Cambrian has more global occurrences of fossil lagerstätten than any other time period (e.g., Allison & Briggs 1993), such as the Burgess Shale, Chengjiang Formation, Weeks Formation, and many others. While many of these occur in the early Cambrian, such as the newly discovered Fandian biota (Du et al. 2020), lagerstätten are found throughout the Cambrian, including the famous Orsten-style deposits of the Series 2 and later Cambrian (Maas et al. 2006).

While the literature and discussions of Cambrian lagerstätten are voluminous, here we focus on those occurrences whose mechanistic underpinnings are entwined with oxygen levels (**Figure 3***f*; **Supplemental Table**). Among these are Orsten-style preservation, which is characterized by phosphatization of fossils in carbonate nodules preserved in shale and that often preserve arthropods (Maas et al. 2006), and Burgess-style preservation, which is characterized by the preservation of soft tissues, including cuticle, preserved as carbonaceous remains with some occasional mineralization of gut contents and limbs (Gaines 2014). The distribution of these two styles of lagerstätten deposits in the Cambrian is shown in **Figure 3**. Orsten-style deposits extend throughout the Cambrian, with a slight increase during the middle and later Cambrian. Burgess-type deposits undergo an expansion during the middle Cambrian, with a peak in the Miaolingian, and a decrease into the Furongian. Many of these preservational windows, even with their differences, potentially rely on shared characteristics (Butterfield 2003), begging the questions, what does the prevalence and distribution of lagerstätten during Cambrian time reveal about environmental conditions during this interval and does this unique aspect of the Cambrian also point to life on the edge?

Phosphatization of fossils occurs throughout geologic time, and the prevalence of phosphatization increases in later Ediacaran time. Orsten-type preservation persists throughout the Cambrian (**Figure 3F**). This type of preservation is characterized by the preservation of small fossils (100 μm to 2 mm), particularly those with cuticles, in limestone nodules in dysoxic shales (Maas et al. 2006). Although not completely isolated to the Cambrian, its occurrence, including its eponymous occurrence in Sweden, is prevalent during Cambrian time. In both observational (Maas et al. 2006) and experimental work (Briggs & Wilby 1996, Briggs et al. 1993), the phosphatization of these fossils is linked to organic matter decay, low oxygen, and authigenic mineral precipitation. The source of the phosphorus remains debated in these (Maas et al. 2006) and for SSF-style preservation (Creveling et al. 2014), but the relationship between a low oxygen (micro)environment and the preservation of soft parts in this way is clear.

Burgess Shale–type preservation is arguably the most famous preservation style of the Cambrian (Conway Morris 1992) and refers to the style of preservation first recognized in fossils of the Burgess Shale, a unit initially studied by Charles Doolittle Walcott. In the past >100 years, Burgess Shale–type preservation has been discovered in numerous Cambrian deposits worldwide (Butterfield 1995, Gaines 2014). The literature on Burgess Shale–style preservation is voluminous, describing the fossils preserved and mechanisms of preservation and examining its distribution in time. The environmental implications of widespread Burgess Shale–type preservation in the Cambrian might reveal connections between fossilization and the marine realm. Burgess Shale deposits occur from the second half of the Terreneuvian into the Darwinian Stage of the Ordovician, with a peak in abundance at the base of the Miaolingian (**Figure 3f**). Most mechanisms rely on inhibition of microbial degradation in a fast burial environment (Gaines 2014). Pyrite precipitation (Briggs 2003) and authigenic clay formation (Anderson et al. 2018, Orr et al. 1998) likely also play a role in their preservation, the latter of which has been shown to inhibit bacterial decay (e.g., Newman et al. 2017). The authigenic formation of many of the minerals associated with Burgess Shale–style preservation [including glauconite (see Section 4.1)] can be understood through the evolutionary and environmental lens of the Cambrian: Low oxygen conditions, limited scavenging, reduced bioturbation (Tarhan & Droser 2014), porewaters in Cambrian shelf environments that were regularly dysoxic or anoxic (Allison & Brett 1995), and oscillating and variable redox conditions of these settings promoted authigenic clay and other mineral formation that replaced soft body parts of Cambrian organisms (Newman

et al. 2019). The widespread occurrence of Burgess Shale–style preservation and its subsequent decline after the Cambrian point to changing environmental/taphonomic conditions in the Ordovician and later in the Phanerozoic (Butterfield 1995, Gaines 2014), likely related to a more ventilated ocean floor and more sediment mixing by animals.

5. LOW OXYGEN ENVIRONMENTS AND THEIR CONSEQUENCES FOR CAMBRIAN LIFE

Low and variable oxygen conditions in the oceans have been simultaneously argued as a cause for diversification and innovation (e.g., Nursall 1959, Wood & Erwin 2018) and as a factor that inhibited biodiversity (Sperling et al. 2013). Further, the oxygen requirements for early metazoans were likely low (Cole et al. 2020). Given the mounting evidence for a prevalence of low and variable shallow marine oxygen levels throughout the Cambrian, if not much of the early Paleozoic, what consequences might this have had on biology?

Wood & Erwin (2018) argue that low oxygen conditions are found to correspond with innovations among soft-bodied organisms, essentially creating stock for later diversification events when higher oxygen conditions appeared. This assertion relies on the notion that oxygen gradients over short distances can lead to isolation of organisms and enhanced speciation. Wood & Erwin (2018) argue that there is an innovation phase during which small nonskeletal taxa acquire morphological diversity. As oxygen rises and/or stabilizes, these morphological traits can be expressed in skeletal organisms, possibly of larger size. This argues for an oscillation between low oxygen and oxygen-rich conditions, where the low oxygen phase favors innovations that are later expressed when less stressful environmental conditions allow. In this way, low oxygen conditions are still viewed as inhibitors to most skeletal taxa, but without the persistence of low oxygen, the evolutionary history of life might be shaped differently (Knoll & Sperling 2014, Wei et al. 2018).

Although there is mounting evidence that low oxygen conditions fostered innovation in a variety of ways early in the evolutionary history of eukaryotic life (Hammarlund et al. 2018, Knoll & Sperling 2014, Wood & Erwin 2018), low oxygen also served as a stressor for Cambrian ecosystems. Saltzman et al. (2015) provide environmental constraints on the repeated biomere extinction events in the later Cambrian and Early Ordovician (reviewed in Taylor 2006). As noted above, various geochemical evidence supports the notion that low oxygen waters

occasionally impinged on the shelf (e.g., Edwards et al. 2018, Gill et al. 2011, Saltzman et al. 2015), resulting in the rapid turnover of trilobite species and the recolonization of nearshore environments by trilobites living in offshore environments in potentially lower levels of oxygenation. These extinctions were then followed by a rapid diversification of nearshore trilobites (e.g., Taylor 2006). In this way, intervals with varying extents of marine anoxia are responsible for animal turnover, extinction, and diversification within the later Cambrian and Early Ordovician.

The demise of archaeocyathan reefs has also been linked to persistent low oxygen conditions (Zhuravlev & Wood 1996). In the later early Cambrian, the Hawke Bay regression represents a major sea level change recorded in parts of Laurentia and Scandinavia. In other parts of the world, a major transgression follows this regression and is termed the Sinsk event. During this event, there is extensive loss of diversity that had been established in early Cambrian time, including the disappearance of archaeocyathan reefs (e.g., Zhuravlev & Wood 1996). The Sinsk event itself is marked by facies reflecting low oxygen conditions such as laminated black shales that occur across the Siberian Platform, as well as South Australia, on the Yangtze Platform, and in some sections in Iran, Kazakhstan, and Mongolia. The coeval disappearance of prolific reef communities with widespread evidence for anoxia links the two events. However, the mechanisms for extinction remain elusive—for example, it may be that the persistence of low oxygen conditions of the shelf smothered the reefs (Zhuravlev & Wood 1996), perhaps linked to Kalkarindji eruptions (Glass & Phillips 2006). Others argue that the extinction of archaeocyaths reflects a redox-modulated change in the saturation state of the oceans not unlike extinction mechanisms at the end of the Permian (Knoll et al. 2007), perhaps also related to the Kalkarindji eruption, with a large input of CO_2 (Knoll & Fischer 2011) into a warm and stagnant ocean/atmosphere system that reduced the ability for animals to calcify (Pruss et al. 2010). In either scenario, persistent low oxygen conditions likely played a role in the extinction of these first animal reefs, and future studies of this event are needed to better constrain this role.

Other ecological innovations of the Cambrian must have also been shaped by low oxygen conditions. For example, although penetration of the seafloor is underway by Cambrian time, the intensity of it varies across environments. For example, when bioturbation has been measured in environments across time from the lower Cambrian through the Lower Ordovician, some the most intense areas of bioturbation are those that occurred earliest in the sequence, but also

closest to shore, suggesting that higher oxygen levels in shallow marine settings could have fostered more intense bioturbation than those that are temporally later in time but more offshore (Tarhan et al. 2023). Certainly, nutrient levels, salinity, and substrate availability among other factors may have influenced the distribution of bioturbators during Cambrian time, but the prevalence of intense (high ichnofabric indices) nearshore bioturbation from around the world suggests some relief from oxygen stress in these settings that permitted metabolically demanding infaunalization in oceans with low overall oxygen levels (Tarhan et al. 2023). Predator-prey dynamics may also be influenced by low oxygen levels. Studies of modern OMZs suggest that the distribution of carnivorous taxa is controlled by oxygen, with the lowest oxygen settings having lower proportions of these organisms and higher oxygen settings linked to more complex food webs (Sperling et al. 2013). Further, the metabolic demands of carnivory—something that is critical in the arms race model of the Cambrian Explosion—require baseline oxygen levels that might not have been present for much of the Proterozoic (Sperling et al. 2013). These studies suggest that even as ecological complexity is increasing in the Cambrian, there is a strong fingerprint of oxygen levels on the distribution and abundances of organisms across environments, with oxygen providing a bridge between environment and ecology.

Some Cambrian ecosystems, such as those from deep water successions of Avalonia and Baltica, seem adapted and resilient to low oxygen levels. Morphological features of organisms from some ecosystems suggest that they were adapted to low oxygen conditions, such as trilobites interpreted as chemoautotrophic symbionts (Fortey 2000) and, more broadly, entire ecosystems that are thought to have lived under dysaerobic conditions, with low diversity and high dominance of stress-tolerant detritovores and scavengers (Ivantsov et al. 2005). In contrast, vulnerable organisms such as reef dwellers fared quite poorly in the face of low oxygen water masses impinging on the shelf (Zhuravlev & Wood 1996). While the overall low biomass and low metabolic demand of most Cambrian organisms made them well suited to a lower oxygenated marine realm (Ivantsov et al. 2005), stressors still overwhelmed local ecosystems throughout the Cambrian, leading to high turnover (Bambach et al. 2004).

6. CONCLUSIONS AND FUTURE DIRECTIONS

There is some emerging consensus around the role played by changing ocean oxygenation across the Cambrian in the evolutionary and ecological diversification of animal ecosystems. Cambrian

organisms reflect the most diverse ecosystems to have existed on the planet up to that point, yet there is a delicate balance between evolutionary innovation and extinction that sets up a unique Cambrian dynamic characterized by high turnover rates (e.g., Bambach et al. 2004).

In this way, the ecosystems of the Cambrian seem to be both a manifestation of and a response to sustained environmental stress, likely overall lower and variable oxygenation across environments. This is exemplified in the case of the trilobite biomere extinctions in which nearshore taxa are replaced by low diversity groups living offshore in less oxygenated settings that subsequently colonized shelf environments (Taylor 2006). The case has also been made that higher oxygen levels lead to greater instances of carnivory among polycheate taxa in modern OMZ settings (Sperling et al. 2013), which again points to variable oxygen levels as a driver of innovation, applicable to the Cambrian. Even the fossils themselves reflect low oxygen conditions—the unusual abundance of lagerstätten and SSFs that provide such rich ecological information on the Cambrian might not exist at all if not for the low and oscillating oxygen levels that fostered their preservation.

In summary, oscillating and variable spatial concentrations of oxygen across marine environments may have simultaneously played a role in the early expansion of metazoans during Cambrian time and created occasional stresses that overcame these early ecosystems. Anoxic events succeeded in periodically wiping out accumulated diversity, particularly skeletal groups, and essentially resetting the evolutionary clock. Perhaps the complicated relationship between innovation, extinction, and oxygen explains much of the pattern we see through the Cambrian and into the Early Ordovician—and even the fossil record itself. Oscillating redox allowed for particular types of mineral authigenesis that led to unique taphonomic pathways, resulting in both an explosion of SSF-style preservation and an abundance of soft-bodied lagerstätten fostered by authigenic mineral formation. Stabilization of environments, and a more even distribution of shallow water oxygen levels, in Middle Ordovician time may have allowed for the expansion into yet-unexplored morphological variability (Wood & Erwin 2018) in the vast radiation of skeletal and other organisms during the GOBE (Servais et al. 2010, Stigall et al. 2020).

Moving forward, to better draw linkages between life, the fossil record, and the environment during this critical interval in Earth history, we advocate future work focusing on the following: developing better constraints on the environmental conditions necessary for certain pathways of

marine authigenesis and fossil preservation; refining and developing proxies that can better quantify levels of oxygen relevant to animal life; performing experimental work on taphonomy that could help constrain absolute oxygen levels and biogeochemical feedbacks; and further exploration of the Cambrian and Early Ordovician primary rock record, particularly high-resolution studies of the end Stage 4 extinction and the interval that follows, which has received relatively less attention.

DISCLOSURE STATEMENT

[**AU: Please insert your Disclosure of Potential Bias statement, covering all authors, here. If you have nothing to disclose, please confirm that the statement below may be published in your review. Fill out and return the forms sent with your galleys, as manuscripts CANNOT be sent for proof layout until these forms are received.**] The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review. [This statement is correct.]

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