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The role of clay minerals in the preservation of Precambrian organic-walled microfossils

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Abstract

Precambrian organic-walled microfossils (OWMs) are primarily preserved in mudstones and shales that are low in total organic carbon (TOC). Recent work suggests that high TOC may hinder OWM preservation, perhaps because it interferes with chemical interactions involving certain clay minerals that inhibit the decay of microorganisms. To test if clay mineralogy controls OWM preservation, and if TOC moderates the effect of clay minerals, we compared OWM preservational quality (measured by pitting on fossil surfaces and the deterioration of wall margins) to TOC, total clay, and specific clay mineral concentrations in 78 shale samples from 11 lithologic units ranging in age from ca. 1650 to 650 million years ago. We found that the probability of finding well-preserved microfossils positively correlates with total clay concentrations and confirmed that it negatively correlates with TOC concentrations. However, we found no evidence that TOC influences the effect of clay mineral concentrations on OWM preservation, supporting an independent role of both factors on preservation. Within the total clay fraction, well-preserved microfossils are more likely to occur in shales with high illite concentrations and low berthierine/chamosite concentrations; however, the magnitude of their effect on preservation is small. Therefore, there is little evidence that bulk clay chemistry is important in OWM preservation. Instead, we propose that OWM preservation is largely regulated by physical properties that isolate organic remains from microbial degradation such as food scarcity (low TOC) and low sediment permeability (high total clay content): low TOC increases the diffusive distances between potential carbon sources and heterotrophic microbes (or their degradative enzymes), while high clay concentrations reduce sediment pore space, thereby limiting the diffusion of oxidants and degradative enzymes to the sites of decay.

KEYWORDS
clay minerals, mineralogy, organic-walled microfossils, paleontology, Precambrian, preservation

1 | INTRODUCTION

1.1 | Organic-walled microfossils and their preservation in shale

In *On the Origin of Species*, Darwin expressed concern over the "inexplicable" absence of fossils in rocks below Cambrian strata, which he postulated was due to the incompleteness and insufficient sampling of the early rock record (Darwin, 1859). Nearly a century later, microfossils were discovered in Precambrian rocks (Timofeev, 1955; Tyler & Barghoorn, 1954), and the many discoveries that followed have provided a moderately detailed record of life during the Proterozoic Eon (2500–539 million years ago, Ma). Much of this record is composed of organic-walled microfossils (OWMs), which include the organic remains of filamentous and coccus bacteria as well as the complex organic structures of eukaryotic cells and/or cysts (Agić & Cohen, 2021; Javaux et al., 2003). OWMs can be preserved three-dimensionally in phosphorites (e.g., Muscente et al., 2015; Xiao & Knoll, 1999), carbonates (e.g., Cohen et al., 2015), and early diagenetic cherts (e.g., Knoll, 1985; Manning-Berg et al., 2019; Xiao et al., 2010), but over 75% of Proterozoic assemblages containing eukaryotes are preserved as organic compressions in shales (e.g., Butterfield et al., 1994; Cohen & Macdonald, 2015). Fossil-bearing shales are formed in a variety of depositional environments, including nearshore to distal marine (Beghin et al., 2017; Butterfield & Chandler, 1992; Javaux & Knoll, 2017; Miao et al., 2019), as well as lacustrine settings (e.g., Strother and Wellman, 2021). Complex OWMs, interpreted as eukaryotes, first appear ca. 1650 Ma, followed by a plateau in their diversity lasting almost a billion years, and a rise in diversity ca. 800 Ma, although recent work suggests relatively high diversity was reached by ca. 1000 Ma (Agić et al., 2017; Cohen & Macdonald, 2015; Knoll et al., 2006; Loron et al., 2019; Miao et al., 2019; Riedman & Sadler, 2018).

As the overall pattern of early eukaryote evolution is beginning to take shape, the ways in which preservational and sampling biases might have affected this record are also beginning to emerge (Cohen & Macdonald, 2015). OWMs in shale are inherently preserved by processes that retain their original organic structures (though significantly reduced in volume through kerogenization; Butterfield, 1990; Timofeev, 1955; Vandenbroucke & Largeau, 2007). Some OWMs display features that are indicative of their preservational/degradational history (Grey & Willman, 2009; Manning-Berg et al., 2019, 2022); for example, irregular pits and perforations, flattening and folding of the vesicle, and shriveling of vesicle processes can be linked to microbial degradation, compression, and desiccation, respectively (Grey & Willman, 2009). Using similar observations Woltz et al. (2021) created ranked criteria to quantify preservational quality and found that the best-preserved OWM assemblages only occur in shales with low concentrations of total organic carbon (TOC), and that no microfossils were observed in shales with TOC >4.4 wt% (see also Butterfield, 1990). This is of particular importance as TOC varies significantly in time (Sperling & Stockey, 2018), with the lowest median TOC values coinciding with high eukaryotic diversity in the Tonian (1000–720 Ma; Woltz et al., 2021).

One possible explanation for this relationship is that OWMs are preserved through chemical interactions with clay minerals (see Section 1.2), where high levels of disseminated TOC weaken their effect on preservation (Butterfield, 1990, 1995); clay minerals can curb the degradation of organic remains by either binding directly to their surfaces (Orr et al., 1998; Wilson & Butterfield, 2014) or to degradative enzymes, reducing the overall degradative capacity of the environment (Butterfield, 1990; Butterfield et al., 1994). In particular, this hypothesis identified the relative amount of TOC to clay mineral content as a primary factor in organic fossil preservation, since high levels of organic matter can sorb to and saturate reactive clay surfaces (Butterfield, 1990, 1995; Butterfield et al., 1994). Although originally suggested to explain Burgess Shales-type (BST) preservation—the conditions that led to the preservation of soft-bodied animals as organic compressions in early Paleozoic shales—similar conditions might underlie the preservation of certain Proterozoic organic fossil assemblages (Anderson et al., 2011; Butterfield, 1990, 1995; Butterfield et al., 1994; Gaines et al., 2008; Jing et al., 2022; Maloney et al., 2022).

Fossil evidence from both BST assemblages and several Proterozoic assemblages supports the role of clay minerals in organic fossil preservation. Elemental maps of BST fossils show enrichments of Al, K, Si on fossil surfaces, consistent with the presence of clay minerals (e.g, Anderson et al., 2021; Orr et al., 1998), and in situ X-ray diffraction identified the clay mineral kaolinite on BST fossils surfaces more commonly than in their surrounding matrix (Anderson et al., 2021). Similar patterns were documented on organically preserved fossils of the late Proterozoic (e.g., Anderson et al., 2011; though see Wang et al., 2022). Recently, microanalyses from several Tonian assemblages show microfossils directly surrounded by the clay mineral kaolinite (Anderson et al., 2020), and microfossils from the 1000 Ma Torridon Group of Scotland surrounded by an iron-rich clay mineral, possibly berthierine (which can form as an early diagenetic product of kaolinite; Rivard et al., 2013; Wacey et al., 2014). Furthermore, shale containing Cambrian BST fossils can be recognized by the sample's bulk clay mineral assemblage with ~80% accuracy; high concentrations of berthierine (and its diagenetic product, chamosite) and low concentrations of illite greatly increases the probability that a sample contains BST fossils (Anderson et al., 2018).

Here, we ask if Proterozoic OWMs were preserved through interactions with clay minerals, and if TOC interfered with these reactions. We compare the preservational quality of 78 microfossil assemblages from three paleocontinents to the total concentration of clay minerals, the concentration of specific clay minerals, and TOC content. If OWMs are preserved by chemical interactions involving clay minerals, we predict that total clay concentrations as well as particular clay minerals (i.e., kaolinite and/or berthierine) positively correlate with preservational quality, and that high TOC concentrations would reduce the effect of clay mineral content on fossil quality.

1.2 | Physical and chemical effects of clay minerals on organic matter degradation

Clay minerals protect organic matter from degradation through both physical and chemical processes (e.g., Curry et al., 2007; Hedges & Keil, 1995; Keil et al., 1994; Kennedy et al., 2014; Martin et al., 2004; McMahon et al., 2016; Playter et al., 2017; Ransom et al., 1998; Theng, 1974; Wei et al., 2021). The physical effects of clay minerals on organic fossil preservation are derived from their typically small grain size (<2 µm). Clay minerals are an ideal "packing material" to preserve organic fossils (Butterfield, 1990), as their small particles preserve delicate micron-scale structures and significantly reduce sediment permeability, limiting microbial activity (Butterfield, 1990; Mayer et al., 2004; Vidal, 1981). In support, laboratory experiments found that the decay of fish tissues were reduced by burial in small glass beads (with a size range equivalence of silt to very fine sand) compared with burial in larger bead sizes (fine to coarse sand; McCoy et al., 2015). Furthermore, paleontologists have observed that organic-walled microfossils are better preserved in lamina of smaller grain sizes (Peat, 1984), and visible changes in grain size have been used as a tool to identify suitable lithologies for microfossil analysis (Hofmann & Jackson, 1994).

Clay surfaces are also chemically reactive and can bind to various organic compounds dependent upon the mineral composition and structure, ambient pH, availability of cations, and organic loading (e.g, Guenther & Bozelli, 2004; Theng, 1974, 1982; Wei et al., 2021; Yu et al., 2013). Due to their reactive properties (cation exchange capacity) and high surface area, clay minerals can preserve organic remains by either precipitating on or binding to their surfaces (Konhauser et al., 1993; Konhauser & Urrutia, 1999; Martin et al., 2004; Playter et al., 2017), possibly catalyzing polymerization reactions that increase the stability of organic structures (Theng, 1982; Wilson & Butterfield, 2014). Clay minerals can also bind to degradative enzymes, either temporarily or permanently inhibiting their ability to facilitate decay (Leprince & Quiquampoix, 1996; Sinegani et al., 2005; Skujiņš et al., 1974). In support, decay experiments of the polychaete *Nereis* and larvae of the crustacean *Artemia* find that degradation was significantly reduced when buried in kaolinite, compared to burial in calcite, quartz, and other clay minerals (Naimark et al., 2018; Naimark, Kalinina, Shokurov, Boeva, et al., 2016; Wilson & Butterfield, 2014). Kaolinite was also found to decrease the activity of *Pseudoalteromonas luteoviolacea*, an aerobic heterotrophic bacterium (McMahon et al., 2016), and *Desulfovibrio vulgaris*, a sulfate reducing bacterium (Wong et al., 2004), more effectively than other clay minerals and reactive agents.

Given that shales containing BST fossils are significantly enriched in berthierine, the role of kaolinite and/or berthierine in organic fossil preservation may be widespread in the Cambrian (Anderson et al., 2018; Saleh et al., 2019) and might extend to Proterozoic assemblages (Anderson et al., 2020).

2 | MATERIALS AND METHODS

The preservational quality of microfossil assemblages was assessed from 78 Proterozoic shale samples representing 11 lithological units (Figure 1; Table 1; Table S1; see supplementary material for further context). Microfossil preservation was characterized by two indices that numerically describe degradational features using the protocol of Woltz et al. (2021): (i) the density of pitting and perforations on cell/cyst wall surfaces and (ii) the margin quality as measured by the deterioration of the wall margin. Data on preservational quality of microfossil assemblages were either taken from Woltz et al. (2021; $n=34$) where the sample suites overlap or were measured directly in this study ($n=44$). Fifty randomly selected fossils were rated from each sample, except for those samples that had fewer than 50 fossils ($n=19$), wherein all fossils were rated (ranging from 5 to 49 specimens; Table S3). Each fossil was ranked on a scale of 1 to 3 for each index, with a rank of 1 assigned to fossils displaying highly pitted wall surfaces and highly frayed margins, and a rank of 3 assigned to fossils with walls exhibiting almost no pits or perforations and with wall margins intact (Figure S1; Table S2). As indices do not correlate with the level of fragmentation or the relative opacity of the microfossil, they are thought to represent degradational features rather than damage from microfossil extraction or thermal maturation (Figure S2; see supplementary material for further explanation of methods).

Semi-quantitative X-ray diffraction (XRD) was performed on the same sample suite using a PANalytical Empyrean Series 2 powder diffractometer with a Co Kα source and PIXcel-1D detector to obtain bulk mineralogy. XRD was conducted on a portion of each shale sample that was powdered to ~10 µm and randomly oriented on single-crystal silicon substrates. Minerals were identified by diffraction peaks over 5–80° 2θ using the ICDD (the International Centre for Diffraction Data) Powder Diffraction File-4+ database and mineral concentrations (in wt%) were calculated using the reference intensity ratio method (Snyder & Bish, 1989). Abundances of all clay minerals identified in this process were summed to calculate the total fraction of clay minerals within each sample.

To identify clay species, further XRD data were collected over 69–75° 2θ which yields peaks diagnostic of specific clays determined by their 060 or 33–1 reflections (the *hkl* indices of the reflection plane; Środón et al., 2001). To ensure accurate assignment of clay species, slight offsets in peak d-spacing caused by variations in the height of the powdered sample were corrected using the quartz peak at 1.542 Å (present in all samples) for reference. For simplicity, chamosite concentrations (derived from the burial metamorphism of berthierine; Hornibrook & Longstaffe, 1996) were grouped with berthierine concentrations. The relative abundance of clay species within the clay fraction corresponds linearly to the area under each peak in the 69–75° 2θ region (Środón et al., 2001). To estimate the concentration of each clay mineral as a proportion of the total rock sample, relative clay abundances were multiplied by the total clay fraction from the bulk mineralogical analysis. This method was employed by Anderson et al. (2018)

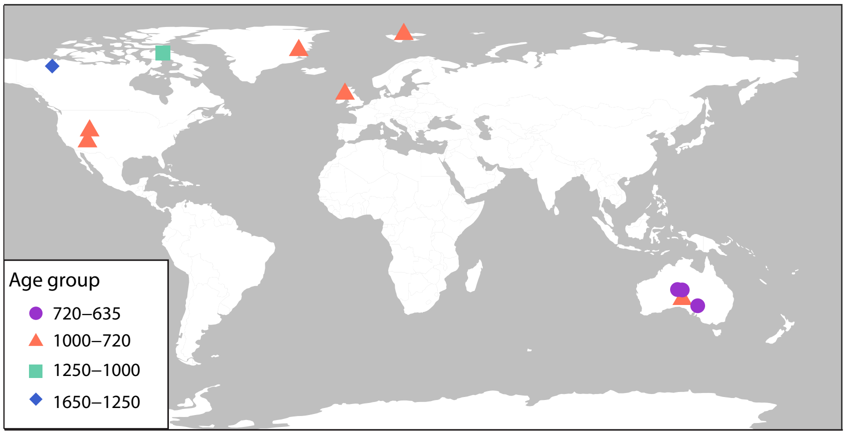


FIGURE 1 Map of locations of deposits with samples studied in this work. Colors and shapes correspond to the ages of the deposits.

TABLE 1 Geologic units, ages, and locations of samples[a].

Geologic unit	Drill-core/ outcrop	Location	Age group (Ma)	Latitude (degrees)	Longitude (degrees)	Samples
Aralka Formation	Wallara-1	Amadeus Basin, Australia	720–635	−24.6153	132.3397	6
Tapley Hill, Umbertana Gp.	SCYW-1A	Adelaide Rift Complex, Australia	720–635	−30.1249	137.1566	1
Areyonga Formation	Wallara-1	Amadeus Basin, Australia	720–635	−24.6153	132.3397	4
	BR05DD01			−24.4557	130.3825	
Uinta Mountain Group	Outcrop	Uinta Mountains, USA	1000–720	40.6333	−110.9533	4
Bedgroup 19, Eleonore Bay	Outcrop	Greenland	1000–720	73.5500	−25.0833	1
Chuar Group	Outcrop	Grand Canyon, USA	1000–720	36.1448	−111.8313	20
Lossit Limestone	Outcrop	Scotland	1000–720	55.6728	−6.1264	1
Alinya Formation	Giles-1	Officer Basin, Australia	1000–720	−28.4317	132.3867	9
Svanbergfjellet Formation	Outcrop	Svalbard, Norway	1000–720	80.1517	18.3350	2
Bylot Supergroup	Outcrop	Baffin Islands, Canada	1250–1000	72.3913	−80.9076	24
Undifferentiated Proterozoic	Mobil Colville Hills E-15	NW Territories, Canada	1650–1250	67.0717	−126.3069	6

[a] See supplementary material (Table S1) for further details.

and incorporates some uncertainty derived from the assessment of total clay content (see Anderson et al., 2018 supplementary material for discussion).

TOC concentrations for the same sample suite were taken from published sources ($n=67$; Woltz et al., 2021 and references therein) or measured in this study ($n=10$; Table S3). Measurements were made by powdering and weighing each sample. Inorganic carbon was removed though acid fumigation using 57% HCl. Dry samples were then wrapped in tin capsules, and total C and N were measured on a Costech 4010 elemental analyzer. Samples run in triplicate yield precision of 0.06 wt% TOC (2σ).

The relationships between microfossil preservation and both total clay and TOC concentrations were examined with multiple logistic regression analyses in R (Version R.4.1.1; R Core Team, 2022; see supplemental material for details on statistical analyses). Total clay and TOC concentrations were used to predict the binary outcome of either the presence of well-preserved microfossils (rank = 3) or the presence of medium to poorly preserved microfossils (rank = 2 and 1). Since individual fossils do not necessarily receive the same preservational rank for index I (density of pitting) and index II (margin quality), separate models were constructed for each index. As the distribution of microfossil preservation differs from sample to sample (Figure S5 and S6), conservative confidence intervals were calculated by applying cluster-robust corrections to standard errors (Pustejovsky, 2022). The significance of each predictor variable (e.g. TOC and total clay concentrations) was determined by a robust-clustering Wald's *z*-test (Pustejovsky, 2022; Zeger & Liang, 1986). The same methods were applied to examine whether concentrations of commonly occurring clay minerals (i.e., illite and berthierine/chamosite) act as predictors of preservation quality.

Interactions between TOC and clay minerals were tested by producing bootstrapped coefficients and 95% confidence intervals. First, TOC and clay concentrations were normalized with respect to their mean and standard deviation (to remove potential effects from differences in scale) and each variable, as well as the product of the variables (i.e. the interaction term), were included as predictor variables of preservational quality. Logistic regression models were run 10^5 times, each time using resampled observations (shale samples) with replacement. The interaction variable is significant if the 95% confidence interval of the coefficient does not include zero (the null hypothesis).

3 | RESULTS

3.1 | Main results

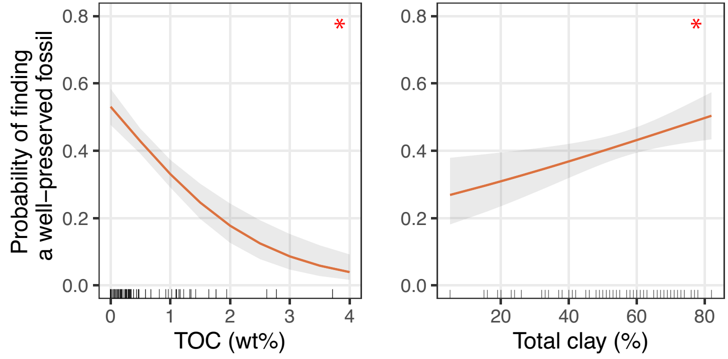
Within the dataset, TOC concentrations vary from 0.05 to 3.77 wt% ($n = 77$; median = 0.30; interquartile range = 0.48) and clay minerals compose between 5% and 82% (by weight) of each rock sample ($n = 78$; median = 56; interquartile range = 18.0; Table S3). The most frequently occurring clay minerals are berthierine (and its diagenetic product, chamosite), celadonite, glauconite, illite, and kaolinite (Figure S3). The concentrations of clay minerals are not highly correlated with each other, however, since illite is the most abundant clay mineral, it is highly correlated with total clay concentrations (Figure S4). High correlation between predictor variables can lead to unreliable model coefficients and *p*-values. These problems are avoided, however, since the effects of total clay and illite concentrations on preservation were tested in separate regression analyses.

Total clay concentrations significantly affect the probability that a microfossil is well-preserved (Figure 2). Over the range of total clay concentrations (from 5% to 82%), the likelihood of finding a well-preserved OWM increases from 0.27 to 0.50 for index I ($p = .0057$) and from 0.42 to 0.64 for index II ($p = .017$). Meanwhile, an increase of TOC concentrations from 0.05% to 3.77 wt% decreases the likelihood of high-quality preservation from 0.53 to 0.04 for index I ($p = 5.1 \times 10^{-10}$) and from 0.66 to 0.09 for index II ($p < 2.7 \times 10^{-7}$).

Within the clay fraction, illite, and berthierine/chamosite concentrations correlate with the probability that a microfossil is well-preserved (Figure 3). Illite concentrations (from 0% to 78%) significantly increase the likelihood of high-quality preservation from 0.32 to 0.51 in index I ($p = .030$) and from 0.43 to 0.67 in index II ($p = .0017$). Berthierine/chamosite concentrations (from 0% to 15%) do not significantly predict preservational quality in index I but significantly decrease the likelihood of a finding well-preserved OWM from 0.60 to 0.38 for index II ($p = .0073$). The clay minerals celadonite, glauconite, and kaolinite are also present but are rare (number of samples present: $n = 5$, $n = 7$, and $n = 13$, respectively); therefore, their effects on preservation are not evaluated. Although multiple statistical analyses can increase the chance of type I (false positive) errors, the main results (presented in Figures 2 and 3) are still consistent with a more conservative (Bonferroni-corrected) significance level (α) of .025 (Sperling et al., 2019).

Finally, models that test for interactive terms between TOC and total clay concentrations—that is, whether the effect of total clay on preservational quality is itself affected by TOC levels—show that the interaction between the two variables is not a significant predictor of preservational quality (Figure 4a). Similarly, interactions between TOC and either illite or bethierine/chamosite are not

(a) Index I: density of pitting



(a) Index II: margin quality

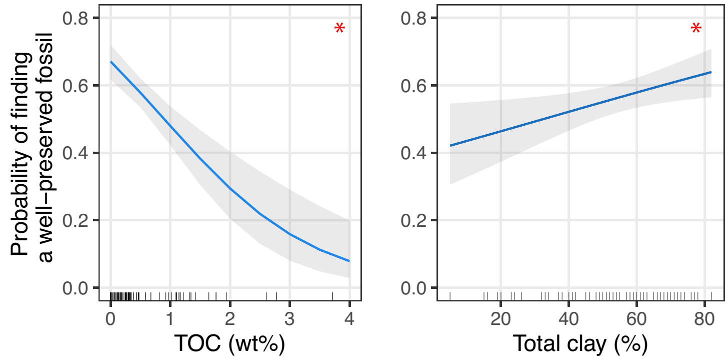


FIGURE 2 Logistic regression models that predict the probability of finding a microfossil that is well-preserved according to (a) index I: density of pitting (orange) and (b) index II: margin quality (blue). Both the total organic carbon (TOC) and the total clay concentrations significantly predict preservational quality, according to the Wald's *z*-test of the coefficients. Relationships that are significant ($p < .05$) are marked with a red asterisk. Gray shaded regions are the 95% confidence intervals calculated from cluster-robust standard errors. Values of each shale sample are marked as black tick marks along each *x*-axis.

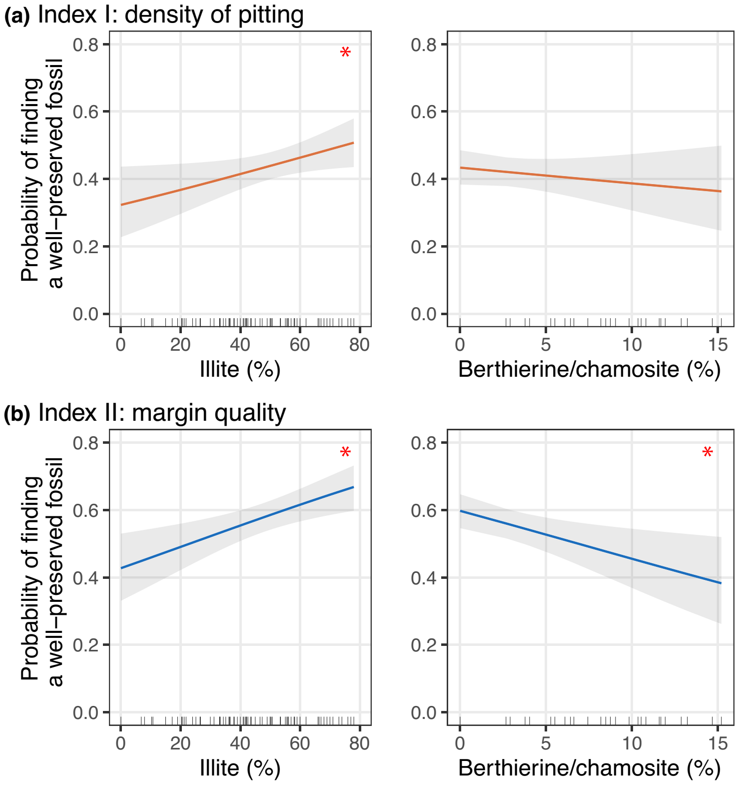


FIGURE 3 Logistic regression models that predict the probability of finding a microfossil that is well-preserved according to (a) index I: density of pitting (orange) and (b) index II: margin quality (blue). Concentrations of illite (in both Index I and II) and berthierine/chamosite (in Index II only) significantly predict preservational quality, according to the Wald's z-test of the coefficients. Relationships that are significant ($p<.05$) are marked with a red asterisk. Gray shaded regions are the 95% confidence intervals calculated from cluster-robust standard errors. Values of each shale sample are marked as black tick marks along each x-axis.

significant predictors of preservation (Figure 4b). These results indicate that the relationship between fossil preservation and total clay, illite, and bertheirine concentrations does not vary as a function of TOC concentration. In other words, the effects of clay on preservational quality are not conditioned on the amount of organic matter in the sample.

3.2 | Uncertainty in mineral abundances

As secondary alteration processes (i.e., diagenetic carbonate addition and hydrothermal alteration) as well as some uncertainty incorporated into clay mineral measurements can affect mineral concentrations, additional regression analyses between clay minerals and preservation quality were conducted. Diagenetic carbonate minerals that form after OWM preservation may alter mineral abundances from their original pre-diagenetic values. However, when the concentration of each clay mineral was calculated as a fraction of the total non-carbonate component of the sample, patterns with preservational quality are similar; illite positively correlates ($p=.023$ and .0026, for index I and II respectively) and berthierine/chamosite negatively correlates ($p=.0041$ for index II) with the likelihood of finding well-preserved OWMs (Figure S7). In addition, some uncertainty comes from the calculation of absolute clay abundances (as a % of the total rock; Anderson et al., 2018); we find that relative concentrations of illite and berthierine/chamosite (as a % of clay fraction) do not significantly predict preservational quality with respect to Index I but remain significant in Index II ($p=.041$ and .0074, respectively; Figure S8).

In addition, lithological units that experienced higher levels of hydrothermal alteration might have undergone a greater degree of clay mineral transformations. Undifferentiated Proterozoic samples from the Colville Hills E-15 drillcore and the lower Bylot Supergroup, Canada are the most thermally mature samples in the dataset (determined by Tmax temperatures from ramped pyrolysis; Fustic et al., 2017; Macauley, 1987; see supplementary material for further detail). To determine the effect these more altered samples might have on the main results, we removed them from the dataset and re-ran the regression analyses (which reduced the number of samples to 46); in this case, berthierine/chamosite concentrations do not significantly predict preservational quality for either index of preservation, and illite concentrations continue to significantly increase the likelihood of finding a well-preserved OWM for index II, margin quality ($p=.020$).

4 | DISCUSSION

4.1 | Mechanisms for OWM preservation

Our results show that high total clay and low TOC concentrations correspond to high preservational quality of OWMs, suggesting that they are (or correlate with) important factors in OWM preservation. Furthermore, we find that these factors are independent—that is, the effects of total clay on preservation are not themselves modulated by TOC concentrations, and vice versa. In addition, we find that illite concentrations positively correlate, and berthierine/chamosite concentrations negatively correlate with preservation quality.

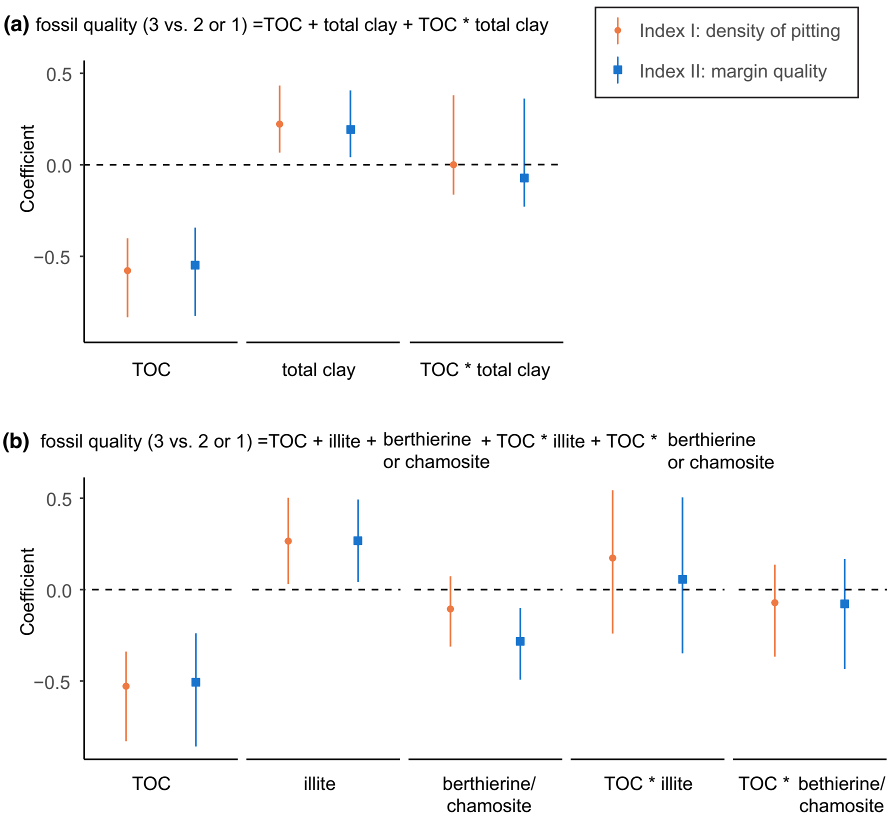
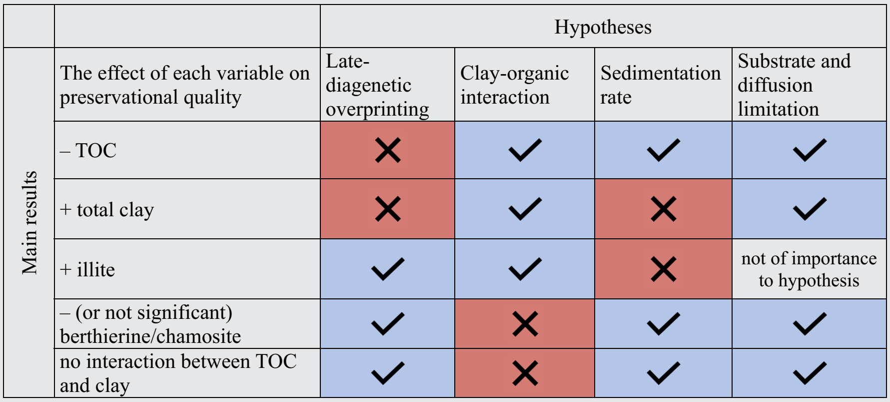


FIGURE 4 Comparison of bootstrapped coefficients with 95% confidence intervals for models that predict preservational quality by pitting (orange circles) and margin quality (blue squares). (a) coefficients of standardized values of TOC, total clay concentrations, and the interaction between TOC and total clay (TOC * total clay). (b) coefficients of standardized values of TOC, illite, berthierine/chamosite, and interactions of TOC*illite and TOC*berthierine/chamosite in models that predict preservational quality. In all cases, the confidence intervals of the interaction terms include zero, and therefore do not have a significant effect on fossil preservational quality.

TABLE 2 Possible processes that explain the main results. Red boxes with x-marks indicate results inconsistent with each hypothesis, and blue boxes with check marks indicate results consistent with each hypothesis. Further explanation of each hypothesis can be found in the discussion.



		Hypotheses			
	The effect of each variable on preservational quality	Late-diagenetic overprinting	Clay-organic interaction	Sedimentation rate	Substrate and diffusion limitation
Main results	– TOC	✗	✓	✓	✓
	+ total clay	✗	✓	✗	✓
	+ illite	✓	✓	✗	not of importance to hypothesis
	– (or not significant) berthierine/chamosite	✓	✗	✓	✓
	no interaction between TOC and clay	✓	✗	✓	✓

However, the role of illite is difficult to decipher given its strong correlation with total clay concentrations, and the effect of berthierine is insignificant in both metrics of preservational quality (Index I and II) when the most thermally mature samples are removed. We examine several possible explanations for these observations (summarized in Table 2).

4.1.1 | Late diagenetic alteration of clay mineralogy

First, it is possible that total clay and/or particular clay mineral concentrations have been secondarily altered so that the correlations between clay concentration and OWM preservation do not reflect primary relationships. In fact, it has been proposed that the clay minerals directly associated with BST fossils were emplaced after fossilization of organic remains during low-grade metamorphism (Becker-Kerber et al., 2022; Butterfield et al., 2007; Gaines et al., 2008; Nielsen et al., 2022; Page et al., 2008). Late-stage diagenetic processes can transform feldspar into chlorite and/or kaolinite, and reactions with late-stage pore fluids can precipitate clay-rich cements (e.g., Baruch et al., 2015; Bjorkum & Gjelsvik, 1988; Rafiei & Kennedy, 2019). The dissolution of Al-rich clays, however, favors clay reprecipitation due to the control of Al on dissolution/precipitation rates (Oelkers et al., 1994; Saldi et al., 2007; Tosca & Wright, 2018). Therefore, we consider these late-stage processes to either conserve a similar clay concentration (via reprecipitation of clay minerals) or secondarily increase the total clay concentration (via mineral transformations and cementation) of a shale after fossilization has occurred. An exception to this may be Mg-rich and Al-poor aluminosilicates, which can either be replaced by smectite or chlorite or dissolve completely (e.g., Jones & Galan, 1988; Tosca et al., 2011; Tosca & Masterson, 2014). However, lithologies high in Mg-clays are rare in the geological record and tend to form in carbonate shelf environments with low siliciclastic input (Tosca et al., 2011; Tosca & Masterson, 2014). Late diagenetic alteration would also negatively impact OWM preservation; although OWMs can survive hydrothermal alteration, their structural integrity is reduced, especially in oxidizing conditions (Schiffbauer et al., 2012). Therefore, it is difficult to explain the observed positive correlation between total clay concentrations and OWM preservational quality through late diagenetic increases in total clay concentrations.

It is also possible that the concentrations of particular clay minerals have been secondarily altered. Many late diagenetic clay alterations favor illite formation from precursor smectite, illite-smectite mixed layer materials, or kaolinite (Bjorkum & Gjelsvik, 1988; Foscolos et al., 1976; Lanson et al., 1998; Pollastro, 1985). These transformations occur at moderate temperatures as low as 90–120°C (Hurst, 1985; Sródón et al., 2009); therefore, it is likely that the original clay compositions of samples in this study have been secondarily altered to some degree. As total clay concentrations strongly correlate with illite (Figure S4), we cannot reject the possibility that particular clay minerals (e.g., berthierine or kaolinite) that were involved in OWM preservation were secondarily transformed to other clay compositions (Butterfield et al., 2007).

4.1.2 | Clay-organic interaction hypothesis

Another possibility is that clay minerals preserve organic remains either by binding directly to their surfaces or to degradative enzymes within the environment. Direct interactions between clay minerals and organic surfaces have been posited to protect organic remains from further degradation (Petrovich, 2001), stabilize and/or restructure organic matter (Anderson et al., 2021; Naimark, Kalinina, Shokurov, Boeva, et al., 2016; Naimark, Kalinina, Shokurov, Markov, & Boeva, 2016; Wilson & Butterfield, 2014), and/or replicate (or in some cases replace) organic structures (Gabbott, 1998; Orr et al., 1998). Other hypotheses suggest that clay minerals suppress the overall degradative capacity of the environment through the adsorption of enzymes onto clay surfaces, which impedes the activity of degradative bacteria, their free enzymes, and unregulated autolytic enzymes released upon death (Butterfield, 1990).

To maximize reactions between clays and both the decaying organic substrate and degradative enzymes/bacteria, it was suggested that concentrations of the total disseminated organic matter in the host sediment (approximated by TOC concentrations) relative to clay concentrations must remain low (Butterfield, 1990; Butterfield et al., 1994). Although experimental evidence is limited, this idea is borne out by the many OWM assemblages occurring in low TOC shales (e.g. Butterfield et al., 1994; Javaux et al., 2010; Woltz et al., 2021).

Furthermore, certain clays are considered to be particularly effective at binding to decaying organics and/or degradative enzymes based on their reactivity and the environmental conditions under which reactivity is maximized. For example, some workers have postulated that the enrichments of kaolinite observed on both OWM surfaces as well as BST fossils are the result of early interactions between the positively charged organic substrate and the negatively charged edge sites of kaolinite minerals under low pH conditions (Anderson et al., 2020, 2021; Orr et al., 1998). Kaolinite has also been shown to reduce the activity of degradative bacteria (McMahon et al., 2016) and bind to enzymes (e.g. chitinase; Skujiņš et al., 1974).

If OWMs are preserved through chemical interactions with clay minerals, then well-preserved microfossil assemblages would occur in shales with high total clay concentrations. Considering the versatile reactions that involve kaolinite (e.g. Skujiņš et al., 1974; Theng, 1974), we would further expect kaolinite or its derivatives (e.g., berthierine and chamosite) to positively correlate with OWM quality. In addition, this hypothesis implies that TOC moderates the effectiveness of clay minerals to interact with organic matter; given the same concentration of a particular clay mineral, its effect on preservation would be significantly reduced in an organic-rich environment compared to an organic-lean setting.

Consistent with this hypothesis, preservational quality of OWM assemblages positively correlates with total clay concentrations. Contrary to predictions, however, berthierine/chamosite concentrations either reduce or do not change the probability that microfossils are well-preserved, and, instead, illite concentrations have a positive effect. Although, as noted previously, it is difficult to distinguish between the effects of total clay and illite (Figure S4), it is possible that illite directly influenced OWM preservation. There is evidence that the surfaces of conodont soft-tissues, chitinozoans, and possibly OWMs from the Ordovician Soom Shale are enriched in illite, suggesting that illite can replace and/or coat organic structures (Gabbott, 1998). Within our dataset, however, it is difficult to discern if illite played a direct role in the initial stabilization and conservation of organic remains, since many alteration pathways can form illite, including some that occur after the fossilization window (see Section 4.1.1). Finally, this mechanism predicts an interaction between TOC and clay concentrations. We have found no evidence for such an interaction in our analysis, although it is possible that interactions occur either at much higher TOC concentrations than are in our dataset, or within a small and chemically distinct fraction of organic matter, which is masked by the bulk measurements of TOC.

4.1.3 | Sedimentation rate hypothesis

A third possibility is that sedimentation rate is driving OWM preservation. Sedimentation rate is generally considered a first-order control on the burial efficiency of organic matter on modern continental shelves (e.g. Hedges & Keil, 1995). Higher sediment input quickly removes organic matter from highly reactive surface sediments and decreases the diffusion of oxidants to deeper sediments. Although the conditions that preserve the original morphology of organic fossils are different from those preserving amorphous organic matter (Wilson & Butterfield, 2014; Woltz et al., 2021), high sedimentation rates would nevertheless increase the preservation potential of organic-walled microfossils through rapid burial and isolation from the degradative surface environment (e.g., Gaines et al., 2012).

Variation in sedimentation rate readily explains the negative correlation between preservational quality and TOC concentrations, as the latter is measured as the percent of the total rock weight. However, the connection between high clay concentrations and high sedimentation rates is less clear, provided that both detrital and authigenic clays contribute to the total clay fraction of shales. Similarly, illite concentrations can also include detrital inputs from physical weathering as well as authigenic transformations of kaolinite and smectite (Bjorkum & Gjelsvik, 1988; Chamley, 1989; Clift et al., 2014; Liu et al., 2008; Pollastro, 1985). However, a particular type of illite (the $2M_1$ polytype) is unambiguously detrital in origin (Weaver, 1958) and its relative abundance compared to the total concentration of illite can be used as a proxy for sedimentation rate (Grathoff & Moore, 1996). Within our data, however, no relationship was found between preservational quality and the relative amount of $2M_1$ illite (Figure S9).

In contrast, the negative relationship between berthierine/chamosite and fossil preservation is generally consistent with sedimentation rate as a driving process for OWM preservation. Berthierine forms by the reaction of kaolinite with reduced iron (Rivard et al., 2013). Provided that seawater was predominantly anoxic and ferruginous during Proterozoic time (Sperling et al., 2015), berthierine formation might not be favored in areas of high sedimentation rate where ion exchange between seawater and sediments would be reduced (Meunier & El Albani, 2007; Taylor & Curtis, 1995).

In all, there is mixed support for the idea that sedimentation rate is driving the observed relationships between OWM preservation, TOC, and clay concentrations. While high sedimentation rates would undoubtedly increase preservation potential, it does not clearly explain all observed patterns in our data. However, variation in sedimentation rate clearly explains TOC concentrations, which have a much larger effect on preservational quality relative to clay concentrations.

4.1.4 | Diffusion and substrate limitation hypothesis

Lastly, it is also possible that physical processes within the sediments limited microbial degradation, thereby promoting OWM preservation. The platy texture and generally small grain size of clay minerals curb microbial activity by reducing the diffusion of oxidants into the sediment and the export of metabolic products out of the sediment, effectively short circuiting many metabolic reactions. As the ability of clay minerals to limit diffusion is based on their grain size and texture, the chemical composition of clays is of no importance to this hypothesis. Others have suggested diffusion reduction as a viable preservation pathway for organic fossil preservation through the early formation of carbonate cements (Gaines et al., 2012). Although we find no evidence that carbonate concentrations significantly correlate with preservational quality ($p=.22$ and $p=.76$ for index I and II, respectively), higher concentrations of clays would have a similar effect with respect to diffusion limitation.

Low concentrations of TOC dispersed within a sediment matrix would further limit the activity of heterotrophic microbes. Degradative bacteria consume organic matter either through enzymes within their cell walls or by exuding free enzymes into the environment to degrade large organic particles into dissolvable components. Models of bacterial foraging in sediment find that the survival of bacteria is directly related to the distance between the bacterial cell and the organic substrate (Rothman & Forney, 2007; Vetter et al., 1998). In clay-rich sediments, the diffusion of enzymes is significantly slowed by the network of platy clay minerals, which increases the travel distance of enzymes to organic matter (i.e. high tortuosity). Enzymes can also become completely halted by small (<4 nm) bottlenecks in the pore space network (Mayer et al., 2004). Therefore, the net energy return from enzymes traveling large diffusive distances would likely be negligible in sediments with low concentrations of organic matter. This idea has been used to explain the persistence of organic matter in oxygenated sediments below marine gyres, which is postulated to evade microbial decay simply by being low enough in concentration (Estes et al., 2019).

In comparison to the clay-organic interactions hypothesis, the diffusion and substrate limitation hypothesis explains the observed patterns with TOC, total clay, and their independence as factors that influence preservation. Although chemical interactions between specific clay minerals and organic matter might still occur at the micron scale in some well-preserved deposits (e.g., Anderson et al., 2020), mechanical occlusion by clays explains the observed patterns at the interlaminar scale and does not require particular clay mineral concentrations or interactions with organic matter. Instead, this hypothesis, which might operate in conjunction with high sedimentation rates, relies on the well-understood mechanical properties that can develop in a wide range of depositional environments. We therefore favor this hypothesis to explain the relationships we find between clays and OWM preservation.

4.2 | Comparison to Burgess Shale-type preservation

It has been hypothesized that the preservation of some Proterozoic OWM assemblages is similar to Burgess Shale-type (BST) preservation (Butterfield, 1995; Butterfield et al., 1994). Even though both OWMs and BST fossils are commonly found in organic-lean shales, the clay mineralogy of these shales differs significantly. BST fossils are preferentially found in shales with low illite concentrations and high berthierine/chamosite concentrations (Anderson et al., 2018), whereas well-preserved OWMs are found in shales with high illite concentrations and average to low berthierine/chamosite concentrations. The magnitude of these relationships also differs. An increase in illite concentration from 0% to 80% of the total shale composition has a large effect on the probability that a sample contains BST fossils, decreasing it from above 0.8 to near zero (Anderson et al., 2018). Conversely, the magnitude of change in the likelihood of finding a well-preserved OWM is much smaller; for example, the probability increases from 0.43 to 0.67 (for index II) over a similar range of illite concentrations (from 0% to 78%).

The distinction between OWM and BST preservational conditions is perhaps not surprising given that the organisms preserved in these settings differ in organic composition and structure. BST fossils include the organic remains of early animals that retain the structures of labile tissues. In contrast to the majority of animal fossils which only retain the mineralized skeletons, BST animal fossils preserve a range of tissue types, including the more resistant outer cuticle as well as labile cellular tissues, which include gut tracts, nerve bundles, and muscle fibers (Saleh et al., 2020). Decay experiments of modern animals document the sequential loss of tissues and provide a relative timeline for the retention of such tissues in BST fossils (Allison & Briggs, 1991; Briggs & Kear, 1993; cf. Parry et al., 2018). At least in BST fossils that preserve the most decay-prone tissues (e.g. guts and muscles), stabilizing processes must occur within days to weeks after deposition (Allison & Briggs, 1991; Briggs, 2003; Briggs & Kear, 1993; Butler et al., 2015). Although normal decay processes must be halted before soft tissue morphology is completely destroyed, many hypotheses of BST preservation suggest that initial decay, possibly by the gut microbiota (e.g., Butler et al., 2015), is actually necessary to establish steep geochemical gradients that enhance mineral precipitation and/or binding onto the organic remains (Anderson et al., 2021; Briggs & Kear, 1993; Gabbott, 1998; Gabbott et al., 2004; Naimark, Kalinina, Shokurov, Boeva, et al., 2016; Naimark, Kalinina, Shokurov, Markov, & Boeva, 2016; Orr et al., 1998; Parry et al., 2018; Petrovich, 2001; Sagemann et al., 1999; Schiffbauer et al., 2014). For mineralization by clays, for example, it has been hypothesized that the initial degradation of organic remains could significantly lower the pH at the site of degradation and perhaps promote the formation of strong bonds with kaolinite (Anderson et al., 2021; Gabbott et al., 2001; Orr et al., 1998).

In contrast, the organic structures that commonly make up Proterozoic OWMs are likely more resistant to degradation than the soft tissues of BST animal fossils. OWMs are considered to be the relatively robust remains of cell walls and cysts of single-celled or simple multi-celled eukaryotes (e.g., protists), as well as bacterial cells and sheaths (Agić & Cohen, 2021). Although maturation of organic matter can secondarily alter their organic chemistry (Briggs & Summons, 2014; de Leeuw et al., 2006; Vandenbroucke & Largeau, 2007), the walls of select Proterozoic OWMs contain structural compounds similar to those found in modern eukaryotes. For example, several OWMs from the Neoproterozoic Centralian Basin of Australia have compositional similarities to dinosporin—a suite of highly resistant biopolymers found in the cysts of dinoflagellates (Arouri et al., 2000; Kokinos et al., 1998; cf. Marshall et al., 2005). Also reported are algaenan-like compounds which in modern chlorophyte, eustigmatophyte, and prasinophyte algae, provide structural support to their cell walls (Arouri et al., 2000; de Leeuw et al., 2006; Derenne et al., 1996; Marshall et al., 2005; though the occurrence of algaenan within these groups might be limited, cf. Kodner et al., 2009). Even though the original composition of OWMs probably differs from modern protists and bacteria, their function and relative resistance to degradation can be reasonably compared (e.g., Bartley, 1996; Graham et al., 2013). For example, several species of chlorophyte algae that underwent chemical hydrolysis as a proxy for microbial degradation, retained recognizable structures of their cell walls that are similar to those observed in Proterozoic OWMs (Graham et al., 2013). In conjunction with microbial degradation, breakdown by the organism's own lytic enzymes (i.e., autolysis) can quickly destroy the intracellular structures of chlorophyte algae; the algaenan-rich cell walls, however, remain intact, although somewhat thinned (Halim et al., 2019). Within dinoflagellates, the recalcitrance of their cysts varies widely among species (Zonneveld et al., 2008) but some particularly resistant taxa are preserved in 10,000-year-old oxygenated sediments and are still identifiable to the species level (Zonneveld et al., 1997). In addition to their resistant composition, the resting stages of various protists, including dinoflagellates and chlorophyte algae, can survive for as many as 100 years in modern sediments and, when returned to favorable laboratory conditions, are able to germinate and reproduce (Ellegaard & Ribeiro, 2018; Kremp et al., 2018; Lundholm et al., 2011). If death occurs after significant burial, the already resistant structures of these cysts are even less likely to be broken down by the lower energy metabolisms that are characteristic of deeper sediments.

In addition to differences in composition and structure of organic remains, there are also significant size differences between OWMs and BST fossils. If BST fossils are preserved through reactions with kaolinite, the relatively large sizes (~1 cm–50 cm) of BST taxa compared to OWMs (~10 μm–250 μm) would provide a sufficient supply of labile organic matter for initial decay resulting in local drawdown of pH, which subsequently may facilitate clay-organic binding (Anderson et al., 2021; Gabbott, 1998; Gabbott et al., 2001; Sagemann et al., 1999). Burial in an otherwise organic-lean environment would further localize mineral-organic reactions to the surfaces of the organic remains (e.g. Raiswell et al., 1993). Not only do OWMs provide less organic matter from early decay but the relative amount of labile vs. resistant organic matter is also much lower. It is, therefore, possible that the initial decay of organic matter sourced from the microorganisms that become OWMs would be insufficient in both quantity and lability to induce the geochemical conditions indicative of BST preservation.

The differences in preservation requirements between BST fossils and OWMs is reflected in the completeness of their fossil records. OWMs are preserved in 3.2 Ga shales to recent sediments (Javaux et al., 2010) and are found in a wide range of environments that span possible lacustrine (Strother & Wellman, 2021; Wacey et al., 2014), deltaic to shallow marine (Beghin et al., 2017), and outer-shelf to basinal settings (Javaux & Knoll, 2017). Conversely, BST preservation is concentrated in early and middle Cambrian strata (Allison & Briggs, 1993; Gaines, 2014; Muscente et al., 2017), outer-shelf environments (>100 km from the shoreline), and in tropical paleolatitudes (Gaines, 2014; Hendricks et al., 2008). This narrow spatiotemporal range likely corresponds to specific environmental, climatic, and/or geographic conditions that arose at this time (e.g., Anderson et al., 2018).

In comparison, small carbonaceous fossils (SCFs)—the disarticulated and most recalcitrant parts of BST animals, including chaetae, cuticles, and scalids—are documented from a wider range of environmental and geographic settings than assemblages of macroscopic BST fossils (Butterfield, 1994; Butterfield & Harvey, 2012). Therefore, the conditions that preserve most Proterozoic OWM assemblages are possibly more comparable to those that preserve SCFs (Slater & Bohlin, 2022). However, little is currently known about the precise conditions that favor SCF preservation.

4.3 | Comparison to exceptionally preserved Proterozoic OWMs

While in general it might be the case that OWMs are preserved by a wider set of circumstances than BST fossils, there is evidence that certain exceptionally preserved assemblages (Lagerstätten) from the Neoproterozoic exhibit BST preservation (Anderson et al., 2020; Butterfield, 1995). Select organic-walled microfossils (5 microfossils in total) from the Lakhanda Group, Russia; Svanbergfjellet Formation, Svalbard, Norway; and Wynniatt Formation, Canada are surrounded by a 0.5–2 μm thick envelope of kaolinite, which is also known to be associated with fossils from the Burgess Shale (Anderson et al., 2020, 2021). Coatings of Fe- and K-rich clay minerals <2 μm thick also surround OWMs from the Torridon Group of Scotland, although this assemblage is also partially phosphatized and might be preserved by different circumstances (Wacey et al., 2014). Since very small concentrations of a particular clay mineral (e.g. kaolinite) would be required to coat microfossil surfaces, the importance of that mineral in preserving OWMs might be unrelated to its total abundance in bulk analyses. Therefore, the differences in mineral patterns between the bulk shale analyses of this study and previous microanalyses might result from differences in the scale of observation.

Apart from differences in scale, however, the contrasting results between the current study and microanalytical studies (Anderson et al., 2020; Wacey et al., 2014) can be largely attributed to the inherent differences between exceptional and non-exceptional preservation. All microfossils in Anderson et al. (2020) are from lithological units that have been previously (and independently) identified as Lagerstattën (Butterfield, 1995). These units preserve delicate fossils with exceptional detail and represent some of the most diverse assemblages known from pre-Ediacaran strata (Butterfield, 1995; Cohen & Macdonald, 2015). The preservation of more delicate taxa (which are absent from most other assemblages), therefore requires a departure from normal depositional conditions (Butterfield, 1995). For example, *Proterocladus*—a multicellular green alga with cell walls tens of nanometers thick—is only known from a few late Mesoproterozoic to Tonian assemblages (Butterfield et al., 1994; Li et al., 2023; Tang et al., 2020). In contrast, most Proterozoic OWM assemblages are composed of frequently occurring and long-ranging taxa (Riedman & Sadler, 2018 and references therein) with relatively more robust walls that range in thickness from 0.5 to 2 μm (Butterfield et al., 1994; Javaux et al., 2004).

It should be noted that the present study includes one lithological unit, the Svanbergfjellet Formation, that is considered a Lagerstätte (Butterfield, 1995). However, exceptionally preserved microfossils of the Svanbergfjellet Formation are highly restricted even within the unit; roughly one third of taxa, including *Proterocladus*, are only known from one shale horizon (sample 86-G-62) out of 400 m of studied stratigraphy (Butterfield et al., 1994). Therefore, the two samples from the Svanbergfjellet included in this study (which do not come from this horizon) are not considered to exhibit exceptional fossil preservation.

Further microscale work on less exceptional deposits is needed to understand the ubiquity of clay-organic interactions in OWM preservation (Anderson et al., 2023). However, since Lagerstätten are exceedingly rare, it is unlikely that the majority of the Proterozoic record is characterized by the same conditions as exceptionally preserved assemblages. Consequently, the units in this study and the weak relationships between fossil quality and sediment mineralogy are probably characteristic of the non-exceptionally preserved OWM assemblages that compose the bulk of the Proterozoic fossil record. Just as Cambrian BST deposits have been ranked into tiers based on their preservational quality (Gaines, 2014; Sperling et al., 2018), it is likely that Proterozoic OWM assemblages can be similarly divided.

4.4 | Preservational biases in the Proterozoic OWM record

Although OWMs are widely preserved throughout the mid to late Proterozoic, trends in their apparent diversity might be affected by changes in the environmental conditions that influence their preservation. If conditions conducive to OWM preservation vary nonrandomly—that is, there are spatial or temporal patterns in their occurrence—then so too might the quality of the fossil record. This, in turn, has the potential to impact current interpretations of early eukaryotic diversity though the Proterozoic.

A large compilation of TOC measurements through the Proterozoic and Phanerozoic found that that average TOC concentrations were anomalously low during the Tonian Period (Sperling & Stockey, 2018), which broadly coincides with a diversification of OWMs (Woltz et al., 2021). Although this diversification might be interpreted as the result of ecological and/or evolutionary changes in early eukaryotes, a shift in the conditions that favor organic fossil preservation might also contribute to this pattern (see Woltz et al., 2021 for further discussion).

There is also some direct evidence that clay concentrations within the sediments may have varied though this time. An increase in total clay concentrations, particularly in chemically derived clays, has been suggested to explain the possible rise in atmospheric oxygen in the late Neoproterozoic (via clay-assisted organic matter burial; Kennedy et al., 2006). However, a more recent study of Archean to Cambrian shales found that total clay concentrations do not correlate with time and exhibit high variability within individual lithologic units (Tosca et al., 2010), although late-stage replacement by clays cannot be ruled out (Rafiei & Kennedy, 2019).

Indirect measures, such as geochemical proxies and models, suggest that clay mineral formation might have been particularly high through much of the Proterozoic. For example, Si isotope ratios in chert through the Paleo- and Mesoproterozoic suggest a greater partitioning of silica into authigenic clays relative to other sinks (Trower & Fischer, 2019), an interpretation consistent with higher predicted rates of authigenic clay production via reverse weathering reactions (Isson & Planavsky, 2018). Si isotopes also suggest less authigenic clay production through the Neoproterozoic, although sparse data coverage through this interval might also contribute to this decline (Trower & Fischer, 2019). In addition to high dissolved silica content, the rates of clay authigenesis strongly increase with pH (e.g. Packter, 1986; Tosca et al., 2011). Anoxic pore waters in Proterozoic marine sediments may have commonly featured elevated pH as a result of enhanced anaerobic respiration of organic matter (Soetaert et al., 2007). In shallow water carbonate-dominated systems, depositional fabrics of calcite (Roest-Ellis et al., 2020; Tosca & Strauss, 2020) and the presence authigenic magnesium-rich clays both suggest that pH commonly exceeded ~8.5 (Tosca et al., 2011).

Together, these observations support the idea that conditions for clay formation were favorable during the Proterozoic as a whole and may have become less favorable towards the Phanerozoic. In light of our results, it is therefore possible that these periods of higher bulk clay concentrations slightly favored OWM preservation, although temporal resolution of clay production estimates through the Proterozoic are low. Mineralogical changes in clay minerals, however, likely had little effect on OWM preservational quality throughout the Proterozoic.

5 | CONCLUSION

Despite the growing body of evidence suggesting that the presence of specific clay minerals in host rocks are major controls on organic fossil preservation, we find limited evidence of their role in the preservation of the majority of Proterozoic OWMs. Although illite positively correlates and berthierine/chamosite negatively correlates with microfossil quality, together they explain relatively little of the total variation in preservation quality. Rather than requiring a specific clay mineral combination, the conservative measures of total clay concentrations and TOC are better predictors of microfossil preservation. These findings indicate that the preservational conditions that form Proterozoic OWMs in shales are significantly different from those of BST preservation. Proterozoic microfossils are preserved in environments where potential carbon sources are scarce (low TOC), and the diffusion of oxidants/degradative enzymes is limited (high total clay content). Therefore, there may be a slight preservational shift through the Proterozoic owing to a changing total clay content, but this remains poorly constrained. Generally, OWMs are preserved in a variety of sediment compositions and depositional environments, giving confidence to interpretations of the spatial and temporal extent of the Proterozoic fossil record.

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CONFLICT OF INTEREST STATEMENT

Authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data as well as the statistical analyses and programming packages we used are available in the supplementary materials.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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