# Response of siliceous marine organisms to Permian-Triassic climate crisis based on new findings from central Spitsbergen, Svalbard

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#### Abstract

Siliceous marine ecosystems play a critical role in climate regulation and the severe impact of the Permian-Triassic mass extinction on silica-secreting animals may have contributed to a sustained greenhouse climate during the Early Triassic, via decreased export of organic carbon burial and increased reverse weathering rates. Yet, our understanding of siliceous marine organisms during this critical interval is poor, and whilst radiolarians experienced the strongest diversity loss in their evolutionary history and perhaps also the greatest population decline of silica-secreting organisms, only a small number of Griesbachian localites that record siliceous organisms are known. Here, we report newly discovered latest Changhsingian to early Griesbachian (Clarkina meishanensis - Hindeodus parvus Zone) radiolarians and siliceous sponge spicules from Svalbard. This fauna documents the survival of a low-diversity radiolarian assemblage alongside stem-group hexactinellid sponges. This is, therefore, the first described account of post-extinction silica-secreting organisms from the Permian/Triassic boundary, a shallow marine shelf environment, and a mid-northern palaeolatitudinal setting. Our new data suggest that latitudinal diversity gradients for silica-secreting organisms following the mass extinction were significantly altered, and that silica productivity was restricted to high latitude and deep water thermal refugia. This also suggests that the export of organic carbon to the deep ocean and reverse weathering rates were not as severely impacted at non-equatorial latitudes.

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- 3 findings from central Spitsbergen, Svalbard
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- 20 Key Points:
- We document the first occurrence of siliceous sponge spicules and radiolarians (biogenic silica) from a mid-northern paleolatitude following the mass extinction event
- Holdover radiolarian species show poleward range shifts
- The ecological composition and the restriction to shallow water oxygenated facies
   suggests a shallow mid-latitude refuge for siliceous marine organisms
- This result has potential to further shape our understanding of changes to marine
   dissolved silica levels and in turn rates of reverse weathering, with implications for our
   understanding of Permian-Triassic carbon cycle dynamics.

#### 29 Abstract

Siliceous marine ecosystems play a critical role on the Earth's climate system through its 30 influence on organic carbon burial and rates of marine authigenic clay formation (i.e. reverse 31 weathering). The ecological demise of silicifying organisms associated with the Permian-Triassic 32 mass extinction is postulated to have elevated rates of marine authigenic clay formation, 33 resulting in a prolonged greenhouse climate during the Early Triassic. Yet, our understanding of 34 35 the response of siliceous marine organisms during this critical interval is poor. Whilst radiolarians experienced the strongest diversity loss in their evolutionary history and perhaps also the 36 37 greatest population decline of silica-secreting organisms during this event, only a small number 38 of Griesbachian (post-extinction) localities that record siliceous organisms are known. Here, we 39 report newly discovered latest Changhsingian to early Griesbachian (Clarkina meishanensis -40 Hindeodus parvus Zone) radiolarians and siliceous sponge spicules from Svalbard. This fauna documents the survival of a low-diversity radiolarian assemblage alongside stem-group 41 hexactinellid sponges making this the first described account of post-extinction silica-secreting 42 43 organisms from the Permian/Triassic boundary in a shallow marine shelf environment and a midnorthern palaeolatitudinal setting. Our findings indicate that latitudinal diversity gradients for 44 45 silica-secreting organisms following the mass extinction were significantly altered, and that silica 46 productivity was restricted to high latitude and deep water thermal refugia. This result has potential to further shape our understanding of changes to marine porewater and seawater 47 dissolved silica levels and in turn rates of reverse weathering, with implications for our 48 49 understanding of carbon cycle dynamics during this interval. This also suggests that the export of 50 organic carbon to the deep ocean was not as severely impacted at non-equatorial latitudes.

#### 51 1 Introduction

52 The Permian-Triassic mass extinction was the most catastrophic extinction event of the 53 Phanerozoic, resulting in major changes in marine ecosystem diversity, ecosystem functioning 54 and the biosphere's evolutionary pathway (Muscente et al., 2018). The mass extinction was notably catastrophic for biosiliceous productivity, resulting in a biodiversity crisis for silica-55 56 secreting organisms (Liu et al., 2013; De Wever et al., 2006) and the Early Triassic chert gap, a five-million-year interval of global low chert occurrence in the global rock record (Isozaki, 1997; 57 58 Racki, 1999; Beauchamp and Grasby, 2012; Isson et al., 2022; Yang et al., 2022). Notably, the 59 Early Triassic chert gap directly deviates from observations of increased chert burial following other Phanerozoic hyperthermals (e.g., PETM; Triassic-Jurassic) as a result of increased silicate 60 weathering rates (Kump, 2018; Ritterbush et al., 2014; Ritterbush 2019; Isson et al., 2020). 61

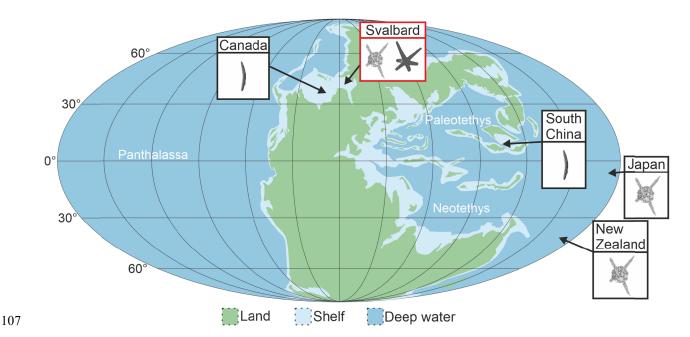
It is traditionally viewed that following a carbon-injection event, an increase in atmospheric  $pCO_2$ 62 would foster an increase in silicate weathering and in turn carbon burial through the deposition 63 of carbonate and chert, which would act to reduce  $pCO_2$  levels to pre-injection conditions on the 64 ~10<sup>5</sup> year timescale (Urey, 1952, Walker et al., 1981, Berner et al., 1983; Isson et al., 2020). The 65 Permian-Triassic hyperthermal deviates from this framework of climate regulation. Here, climate 66 67 recovery was slow, with temperatures remaining elevated for millions of years in the aftermath of the mass extinction. This has led to the view of a fundamentally altered climate system in the 68 wake of the Permian-Triassic mass extinction, in which silicate weathering was ineffective at 69

drawing down  $pCO_2$  and lowering temperatures (Kump, 2018; Isson et al., 2022). It is postulated 70 that volcanic carbon release may have been substantially large enough to 'exhaust' the supply of 71 72 silicate minerals available for weathering at Earth's surface (Kump, 2018). Recent work has also 73 called upon the widespread loss of marine silicifying organisms, and resulting increase in marine dissolved silica concentration, as a catalyst for increased CO<sub>2</sub> release via marine authigenic clay 74 75 formation (Isson et al., 2022). Marine authigenic clay formation consumes alkalinity and dissolved cations initially released via the process of silicate weathering, and in turn acts to re-76 liberate the  $CO_2$  initially captured as dissolved carbon (HCO<sub>3</sub>). Overall, marine authigenic clay 77 78 formation acts to recycle carbon within the ocean-atmosphere system, variation in the extent of this process can drive changes in atmospheric  $pCO_2$  levels and global climate (Isson & Planavsky, 79 2018). In this view, the demise of silicifying ecosystems (and the Early Triassic chert gap) are 80 81 directly responsible for the anomalous Triassic warm period (Isson et al., 2022).

Estimates of changes in marine dissolved silica concentration used in global carbon-silica cycle models are reliant on direct observations of biogenic silica burial in the global rock record (Isson, et al., 2022). Therefore, finding new Permian/Triassic successions that record siliceous organisms and documenting the extent of biogenic silica productivity in different environments is essential in understanding the evolution of silica-secreting organisms, their refugia during climate crises, and impact on changes to global climate.

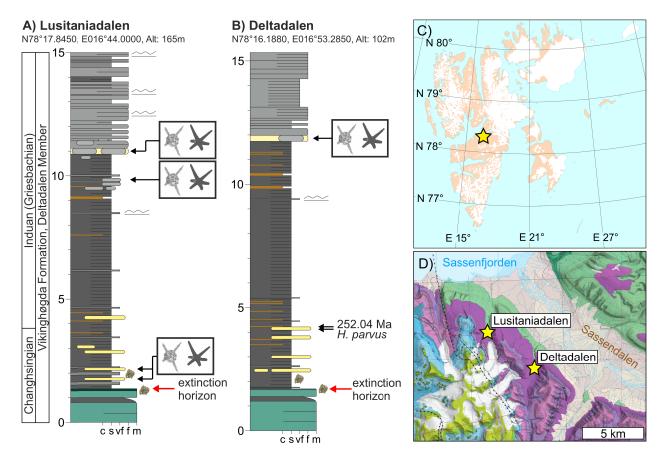
88 Siliceous sponges and radiolarians, both of which evolved in the latest Precambrian, were the 89 predominant silicifying organisms during the Permian-Triassic. Globally, radiolarians, along with 90 acritarchs, were the primary fossil record of plankton biodiversity through the Permian-Triassic 91 transition and suffered from the most severe extinction in their evolutionary history (De Wever et al., 2006; O'Dogherty et al., 2010). Many aspects of this extinction, and the subsequent 92 93 radiation are poorly known due to the paucity of material in the earliest Triassic (O'Dogherty et 94 al., 2010). Furthermore, post-extinction (Griesbachian) radiolarians have only been identified in two regions in the world, New Zealand (Takemura et al., 2002; Hori et al., 2011) and Japan (Sano 95 et al., 2010) (Fig. 1). Siliceous sponges show a similar trend, where they thrived during the 96 Permian, depositing large quantities of biogenic chert across large areas of shelf and slope 97 98 settings (Beauchamp and Baud, 2002), and then virtually vanish following the extinction event. Only a single morphology and rare occurrence of undescribed smooth siliceous monaxone 99 sponge spicules have been reported from the Griesbachian in South China (Liu et al., 2013) and 100 Canada (Grasby and Beauchamp, 2009) (Fig. 1), but in both cases it is possible that these post-101 extinction sponge spicules were reworked from pre-extinction sediments (Beauchamp, pers. 102 comm). This lack of known localities with silica skeletal remains from the Griesbachian, and even 103 the subsequent Dienerian and Smithian, suggests that the absence of biogenic chert deposits 104 105 carries a genuine biological (productivity) signal.

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**Figure 1**. Paleogeographic map for the Permian/Triassic boundary showing the records of radiolarians and siliceous sponges in the Griesbachian, Early Triassic. Svalbard (45°N), this study; Canada (40°N) (Grasby and Beauchamp, 2009); South China (8°N), (Liu et al. 2013); Japan (6°S) (Sano et al. 2012); and New Zealand (36°S), (Takemura et al. 2002). Base map after Blakey (2012).

Here we report new finds of radiolarians and sponge spicules in the Vikinghøgda Formation at Lusitaniadalen and Deltadalen, Svalbard (Fig. 2). These findings represent the first described post-extinction (Changhsingian-Griesbachian) record of siliceous sponges and radiolarians from both the Boreal Realm and a shallow depositional setting, with implications for improving our understanding of the distribution of post-extinction silica-secreting organisms, and refugia during global warming events.



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Figure 2. Stratigraphic succession at Lusitaniadalen and Deltadalen, Svalbard. A) Radiolarians and 120 sponges recorded at 1.8, 9.8 and 11.0 m into the Vikinghøgda Formation at Lusitaniadalen 121 (78.2986, 16.7331) and B) 12.0 m into the Vikinghøgda Formation at Deltadalen (78.2698, 122 16.8881), Svalbard. The samples that yielded siliceous fossils are shown by the avatars. Position 123 124 of the Permian/Triassic boundary and the U/Pb date comes from Zuchuat et al. (2020). C) Inset of Svalbard. D) Geological map of Sassendalen. Geological map after 125 map https://geokart.npolar.no/geologi/GeoSvalbard. 126

## 127 **2** Materials and Methods

#### 128 2.1 Geological Setting

The Vikinghøgda Formation can be traced across central and eastern Svalbard and records 129 deposition through the latest Permian and entire Early Triassic in a mid-paleolatitude (~45°N, 130 Hounslow et al., 2008), siliciclastic, open-marine, shelf setting (Mørk et al., 1999). Both 131 Lusitaniadalen (78.2986, 16.7331) and Deltadalen (78.2698, 16.8881), record the Permian-132 Triassic transition and have been stratigraphically-constrained through magnetostratigraphy, U-133 Pb geochronology and biostratigraphy. The radiolarians and sponges from these sections are, 134 therefore, well-constrained as belonging to the latest Changhsingian to early Griesbachian 135 Clarkina meishanensis - Hindeodus parvus Conodont Zones (Mørk et al., 1999; Zuchuat et al., 136 137 2020) (Fig. 2). The concretions come from interbeds of siltstones and very fine sandstones, 138 where the heterolithic beds are bioturbated by shallow burrowing *Skolithos* and *Arenicolites* and 139 both record ripple structures and a diverse fauna, which indicate deposition in an oxygenated, shallow, marine setting (Foster et al., 2017; 2022). 140

## 141 2.2. Materials and sample processing

142 Samples were collected every 50 cm throughout the succession from all the lithologies. Each sample was then disaggregated using 10% hydrogen peroxide with the solution changed every 143 48 h. In addition, samples were collected from each concretionary horizon. The samples from 144 the concretionary horizons were mechanically disaggregated into 1-2 cm-sized blocks, and the 145 pieces that did not have fossils on their surfaces were disaggregated with the buffered formic 146 acid technique (Jeppsson and Anehus, 1995). To maximize yield, the residue was collected at c. 147 12 hour intervals, washed thoroughly with tap water to remove any excess solution and to avoid 148 crystal growth, and dried. The fossils were then picked using standard microfossil picking 149 techniques and mounted onto stubs for imaging using a scanning electron microscope. The 150 specimens are housed in the University of Oslo, Natural History Museum. 151

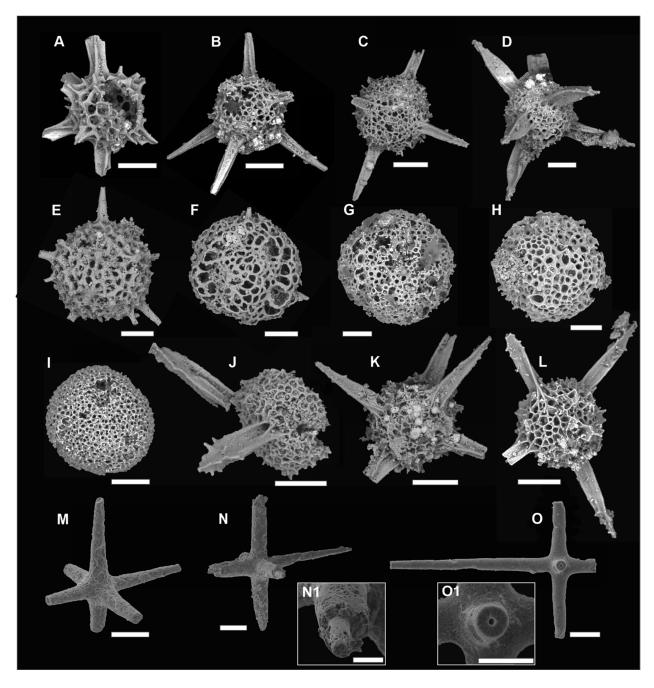
152 2.3. Analyzing species diversity

To assess the differences in species richness between the samples from Svalbard and between 153 the different radiolarian localities for the Griesbachian, a sample-size-based rarefaction using 154 absolute abundance data was done for the samples from Svalbard and a coverage-based 155 156 rarefaction curve using incidence data was done for all of the Griesbachian radiolarian samples 157 using the data from Sano et al., (2010; 2012), Hori et al., (2011), and Takemura et al., (2002). Estimates of the asymptote species richness for the samples from Svalbard was done using the 158 Chao 1 richness index (Chao et al., 2009). The rarefaction curves and Chao index were computed 159 using the iNEXT package (Hsieh et al., 2014) in R. 160

#### 161 3 Results

Sponge spicules and radiolarians were discovered in the concretionary horizons of the 162 Vikinghøgda Formation indicated in Figure 2. The fauna identified from the Vikinghøgda 163 164 Formation are not considered to have been reworked from the underlying pre-extinction, spiculitic Kapp Starostin Formation for the following reasons: (1) the Kapp Starostin Formation 165 and the Vikinghøgda Formation in central Spitsbergen record stark lithological differences and 166 167 lithological features of the Kapp Starostin Formation are not recorded in association with the siliceous fossils (e.g., glauconitic sand), (2) the fossils are well-preserved with delicate thin 168 skeletal elements that would have been destroyed if reworked, (3) abrasion on some specimens 169 170 is interpreted as a consequence of the disaggregation methods, (4) the Vikinghødga Formation 171 does not record significant bioturbation that could have reworked the fossils into younger strata, and (5) the silicified fauna is dominated by Mesozoic taxa. 172

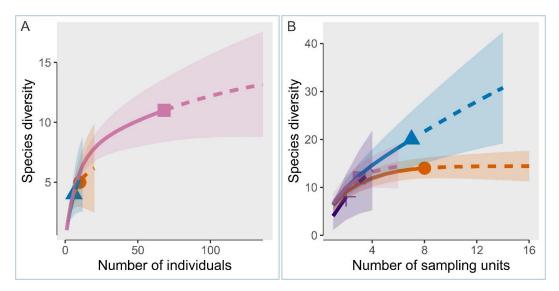
The identified fauna includes 238 radiolarians, of which 87 could be identified to the genus-level 173 and 61 to the species-level. Ten distinct species were identified (Fig. 3) and only four were 174 Permian holdovers (Entactinia itsukaichisensis, Hegleria mammilla, Hegleria sp., Grandetortura 175 nipponica). Five species are recorded from the Griesbachian for the first time, including one new 176 species (Entactinia n.sp.). Three of those were previously known from the Early Triassic but 177 178 represent range extensions back to the *H. parvus* Zone. In addition to no signs of reworking, these Triassic species support that the radiolarian assemblage does not represent a reworked 179 Permian fauna. One species is recorded in the Triassic for the first time (Grandetortura 180 nipponica), which records one of the last occurrences of the order Latentifistularia that 181 subsequently the Pelsonian al., 2000). 182 went extinct in (Feng et



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Figure 3. Radiolarians and sponge spicules from the Griesbachian (Hindeodus parvus Conodont 184 Zone) of central Svalbard. A) Entactinia itsukaichisensis (Sashida and Tonishi 1985), 1JB1.1. B) 185 Entactinia nikorni (Sashida and Igo 1992), 1JB2.1. C) Entactinia cf. chiakensis (Sashida and Igo 186 1992), JB4.19. D) Entactinia n. sp., 1JB2.4. E) Polyentactinia cf. phattalungensis Sashida and Igo 187 1992, JB5.19. F) Grandetortura nipponica Sashida and Tonishi 1991, 2JB8.4. G) Hegleria 188 mammilla (Sheng and Wang 1985), 1Rad2.6. H) Hegleria sp., 1RAD3.7. I) Gen et sp. indet., 189 1Rad4.3. J) Thaisphaera? igoi Kamata 1999, 2JB9.10. K) Thaisphaera? igoi Kamata 1999, 2JA5.5. 190 191 L) Thaisphaera? igoi Kamata 1999, 1Rad3.6. M-O) Hexactinellida sponge spicules, N1 and O1 192 close-up views of the axial canal. scale bar = 100  $\mu$ m, except N1 and O1 where scale bar = 30 $\mu$ m.

The observed species richness of the samples from Svalbard is highly dependent on sample size 193 194 and a sample-based rarefaction curve for the three samples from Svalbard (Fig. 4) suggest that 195 the asymptote for species richness from these assemblages has not yet been reached and that the samples are likely more species-rich than observed. Comparisons of species richness 196 between Svalbard and other Griesbachian radiolarian localities could only be made using a 197 198 coverage-based rarefaction which suggest that the asymptote for species richness has not yet 199 been reached for any Griesbachian locality (Fig. S2B) and the samples from Svalbard are not significantly different from the species richness of the other localities. 200



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203 Figure 4. Rarefied species richness curves (solid line segment) and extrapolation (dotted line segments) sampling curves with 95% confidence intervals (shaded areas) for the Griesbachian 204 Radiolarians. A) Sample-size-based rarefaction for the samples from Svalbard (this study), from 205 11.8 m into the Vikinghøgda Formation at Deltadalen (pink square), 9.8 m (orange circle), and 206 11.0 m (blue triangle) at Lusitaniadalen. B) Coverage-based rarefaction curve for the 207 Griesbachian radiolarians collected from Arrow Rocks (orange circle) and Waiheke Island, New 208 209 Zealand (purple cross); Mino Terrane, Japan (blue triangle); and the Vikinghøgda Formation in 210 Svalbard (pink square). Data: Svalbard = This Study, Mino terrane, Japan = Sano et al. (2010; 211 2012), Waiheke Island, New Zealand = Hori et al., (2011), Arrow Rocks, New Zealand = Takemura 212 et al., (2002).

The fauna also includes abundant siliceous sponge spicules that can be confidently described as oxyhexactin, which are siliceous spicules with six unbranched rays perpendicular to one another that taper to a point (Boury-Esnault and Rutzler, 1997). The lack of any other siliceous spicule morphology suggests both a low diversity and that the spicules belong to a stem-hexactinellid, representing a Permian holdover. In addition, a thin section from the first concretionary horizon above the mass extinction event at Lusitaniadalen, also records radiolarians and oxyhexactin spicules in four thin sub-beds (up to 2 cm). 220 The radiolarian and sponge fossils are also interpreted to represent para-autochthonous 221 assemblages. This is because the fossils are reported from the base of the Vikinghøgda 222 Formation which is characterized by silty mudstone and deposition in a low-energy environment (Mørk et al., 1999). In addition, the composition of the radiolarians represent a typical shallow 223 224 water assemblage (see Discussion). The fossils are, therefore, likely to have undergone some 225 spatial-averaging but their exquisite preservation also suggests that they were rapidly buried. Notably, the silicified fossils from the base of the Vikinghøgda Formation with 3D preservation 226 are restricted to concretionary beds (see also Foster et al., 2017), whilst macrofossils in the 227 228 surrounding silts and muds are typically flattened moulds. The radiolarians and sponge spicules 229 found here also record exquisite 3D preservation and have only been observed within 230 concretionary beds. This suggests that the fossils were preserved within the concretions during 231 early diagenetic stage that prevented the siliceous fossils from undergoing diagenetic dissolution or partial-dissolution, as observed in the underlying Kapp Starostin Formation. 232

## 233 4 Discussion

Numerous post-extinction refugia have been suggested from various paleogeographic locations 234 235 and depositional settings (Beatty et al., 2008; Twitchett et al., 2004; Godbold et al., 2017) and in particular shallow marine settings in the Boreal realm (Wignall et al., 1998; Beatty et al., 2008). 236 237 Our new data highlight that the fossil record from Svalbard is exceptional in not only recording 238 diverse and complex marine ecosystems (Foster et al., 2017), but also recording faunal groups 239 currently unknown from coeval shallow marine settings, including radiolarians (this study), hexactinellid sponges (this study), large bivalves (Foster & Buchwald, pers. obvs.), red algae 240 (Wignall et al., 1998) and bryozoans (Nakrem and Mørk, 1991). In addition, the only other 241 242 reports of Griesbachian siliceous sponge spicules come from South China and Canada (Grasby and Beauchamp, 2009, Liu et al., 2013). Sponge spicules are reported as occurring in Wadi 243 244 Maqam (Oman) during the Griesbachian in a review by Isson et al. (2022), but this occurrence could not be verified. The absence of these groups recorded in Svalbard from intensely studied 245 shallow marine successions from the Tethys and Panthalassa oceans suggests that their absence 246 247 in these equatorial settings represents a biological signal and more habitable conditions for siliceous and calcareous organisms in the Boreal Realm during the Permian-Triassic climate crisis. 248

One explanation for the absence of siliceous marine organisms from low-latitude, shallow marine 249 250 localities could be thermal stress associated with the mass extinction. Species track their thermal niches through range shifts resulting in latitudinal diversity gradients in marine species (including 251 primary planktic production) becoming significantly altered; with an equatorial depression in 252 diversity and increased diversity towards temperate latitudes (Yasuhara et al., 2020; Chaudhary 253 et al., 2021). Consistent with this observation, the altered latitudinal diversity gradient during the 254 255 Griesbachian implies a relatively greater ecological impact in the tropics (Foster and Twitchett, 2014; Song et al., 2020). However, mid- to high-latitude regions are hypothesized to have higher 256 turnovers in faunal composition, owing to the combination of local extinctions, extirpations and 257 poleward range extensions of low-latitude taxa (Reddin et al., 2022). The range extensions and 258 dominance of many Triassic fossil species and genera to the Griesbachian belonging to new, 259

post-extinction orders because of new data from Svalbard (this study, see also Foster et al. 2017)
 also suggests high extinction and origination rates in this region.

The Permian holdover radiolarians Hegleria mammilla, Entactinia itsukaichisensis, and 262 Grandetortura nipponica recorded in this study all show poleward latitudinal range extensions 263 out of the tropics across the mass extinction event. In addition, laboratory cultures show that 264 265 subtropical radiolarians can only survive for a few days when exposed to high temperature stress 266 (Andersson et al., 1989), and the overall low-diversity recorded in Svalbard could be attributed to thermal stress even at higher latitudes. This is in line with predictions of climate warming, 267 oxygen loss and metabolic theory, and the observation that the toll of the extinction event for 268 marine genera was greater in higher latitudes than in the tropics (Penn et al., 2018). Taken 269 together, the impact of climate change would have been detrimental to higher latitude 270 ecophysiotypes, yet the mid- to high-latitude Boreal Ocean setting of Svalbard must still have 271 had substantially lower sea-surface temperatures and higher rates of primary productivity 272 compared to the tropics. Moreover, a strong increase in primary productivity is recorded in the 273 274 latest Changhsingian and early Griesbachian at Lusitaniadalen by enhanced input of chlorophyllderived biomarkers (Buchwald, pers. obvs.). With radiolarian abundance being linked to 275 276 chlorophyll concentrations (Lampitt et al., 2009), food availability was likely increased for the radiolarian assemblage, which possibly contributed to the relatively high radiolarian abundance 277 278 in this setting.

279 An alternative adaptation to thermal stress is to track a thermal niche through migrating down the water column to cooler waters. Our radiolarian assemblage is dominated by entactinarians, 280 two latentifistularians and a single spumellarian, which, consistent with the facies interpretation 281 282 (Foster et al., 2017), is indicative of a shallow water assemblage (Xiao et al., 2017). This also supports the interpretation that the radiolarians represent a para-autochthonous assemblage. 283 284 For the silica-secreting organisms in Svalbard, however, the water column migration of taxa would not have been possible as the deeper water facies are inferred to have been anoxic, or 285 euxinic, for most parts of the Griesbachian (Nabbefeld et al., 2010; Zuchuat et al., 2020). 286 287 Siliceous organisms in Svalbard were, therefore, restricted to shallow marine settings and only groups that could tolerate the associated environmental stressors in this setting would survive. 288 289 The restriction of diverse marine fossil assemblages to shallow marine ecosystems was also 290 demonstrated with the distribution of trace fossils in NW Pangaea (Beatty et al., 2008). The virtual absence of the Albaillellaria and Latentifistularia from the Svalbard samples also suggests 291 292 that these orders were unable to respond to expanding oxygen minimum zones by migrating into 293 shallower settings. It is therefore clear that consistent with recent studies (e.g., Penn et al., 2018) the combined effects widespread anoxia and high sea surface temperatures played a key role in 294 limiting the diversity and abundance of silica-secreting organisms and primary production. 295

The low species richness of siliceous organisms in Svalbard could be related to the shallow depositional setting rather than a consequence of the climate crisis. Modern hexactinellids for example generally inhabit deep-water habitats (greatest diversity at 300-600 m depths) and only a few populations inhabit shallow settings (Leys et al., 2007). The distribution of sponges during Permian was, however, more widespread with sponges being abundant in very shallow, inner

ramp settings, which also lead to the development of glass ramps along the NW Pangaea 301 302 coastline (Gates et al., 2004) and extensive chert deposition in shallow basins on the South China 303 block (Liu et al., 2013). In addition, radiolarians are recorded as occupying water depths from 100s to 1000s of meters deep with a distinct ecological zonation in the Permian (Xiao et al., 304 2017). This may also explain why the oceanic settings of Japan and New Zealand both record a 305 306 greater diversity of radiolarians in the Griesbachian, which includes latentifistularians, albaillellarians, spumellarians, entactinarians and nassellarians (see Table S1), i.e. these 307 assemblages will have much larger spatial averaging of habitats. Alternatively, the shallow 308 309 epicontinental setting of the Barents Sea - Svalbard area compared to the open oceanic settings of Panthalassa may explain the paucity of both pre- and post-extinction radiolarians 310 assemblages. The low species richness of radiolarians and hexactinellids from Svalbard does not, 311 312 therefore, negate the mid-latitudinal setting as a refuge for shallow water forms.

The preferential survival of siliceous organisms in mid-latitude and deep-water habitats supports 313 the view that thermal stress drove the collapse of silica productivity during the climate crisis and 314 provides a further constraint on the extent of biogenic silica burial decline following the end-315 Permian mass extinction. This restriction of biogenic silica productivity has key implications for 316 317 the regulation of Earth's climate during the Griesbachian. Directly, radiolarians are major exporters of organic carbon to the deep ocean (Lampitt and Johns, 2009), and the widespread 318 decline in large-scale silica-production would have limited the oceans ability to sequester carbon 319 320 dioxide from the atmosphere. Further, the widespread loss of silicifying organisms potentially increased marine dissolved silica concentration and marine authigenic clay formation, trapping 321 the Earth in a prolonged hyperthermal state (Isson et al., 2022). The findings of siliceous 322 organisms and thin siliceous beds in Svalbard (this study) and potentially also Canada (Grasby 323 and Beauchamp, 2009) suggests a poleward expansion of silica productivity. 324

325 Observations of radiolarians and sponge spicules here suggest a poleward expansion of silica productivity and spatially varied changes in biogenic silica burial following Permian-Triassic 326 extinction event. This has potentially critical implications for our understanding of both global 327 marine dissolved silica levels and also local porewater conditions (the locus of marine clay 328 formation). For instance, biogenic silica fixation and in turn local scale depletion of seawater 329 330 dissolved silica could have been most intense at mid-latitude and deep-sea environments 331 (distinct to the modern day and Permian systems). Relatively elevated biogenic silica deposition in these restricted environments may further alter porewater dissolved silica levels. Overall, this 332 shift in the locus of biogenic silica production and deposition has potential to influence the global 333 distribution and rates of marine clay formation and in turn atmospheric  $pCO_2$  levels. 334

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#### 343 Open Research

All of the data used in this study is available in the supplementary files and the specimens have

345 been accessioned at the natural History Museum, University of Oslo.

#### 346 References

Anderson, O.R., Bennett, P., & Bryan, M. (1989), Experimental and observational studies of radiolarian physiological
ecology: 3. Effects of temperature, salinity and light intensity on the growth and survival of *Spongaster tetras*maintained in laboratory culture. *Marine Micropaleontology*, *14*, 275-282. https://doi.org/10.1016/S03778398(96)00011-4

Beatty, T.W., Zonneveld, J.P., & Henderson, C.M. (2008), Anomalously diverse Early Triassic ichnofossil assemblages
in northwest Pangea: a case for a shallow-marine habitable zone: *Geology*, *36*, 771-774.
https://doi.org/10.1130/G24952A.1

Beauchamp, B., & Baud, A. (2002), Growth and demise of Permian biogenic chert along northwest Pangea: evidence
for end-Permian collapse of thermohaline circulation: *Palaeogeography, Palaeoclimatology, Palaeoecology, 184*, 3763. https://doi.org/10.1016/S0031-0182(02)00245-6

Berner, R. A., Lasaga, A. C. & Garrels, R. M. Carbonate-silicate geochemical cycle and its effect on atmospheric
carbon dioxide over the past 100 million years. *Am. J. Sci.; (United States)* 283:7, Medium: X; Size: Pages: 641-683
2016-2004-2026 (1983). https://doi.org:10.2475/ajs.283.7.641

Boury-Esnault, N., & Rützler. (1997), Thesaurus of sponge morphology. *Smithsonian Contributions to Zoology*, 596, 65 p. https://doi.org/10.5479/si.00810282.596

Chao, A., Colwell, R. K., Lin, C. W., & Gotelli, N. J. (2009). Sufficient sampling for asymptotic minimum species richness estimators. *Ecology*, 90, 1125-1133, https://doi.org/10.1890/07-2147.1

Chaudhary, C., Richardson, A.J., Schoeman, D.S., & Costello, M.J. (2021), Global warming is causing a more
pronounced dip in marine species richness around the equator. *PNAS*, *118*, e2015094118.
https://doi.org/10.1073/pnas.201509411

De Wever, P., O'Dogherty, L., & Gorican, S. (2007), The plankton turnover at the Permo-Triassic boundary, emphasis
on radiolarians, in Baumgartner P.O., Aitchison J.C., Wever P., Jackett S-J., eds., *Radiolaria*: Birkhäuser, Basel, 49-62,
https://doi.org/10.1007/978-3-7643-8344-2\_4

Jeppsson, L., & Anehus, R. (1995), A buffered formic acid technique for conodont extraction: *Journal of Paleontology, 69*, 790-794. https://doi.org/10.1017/S0022336000035319

Feng, Q., Yang, F., Zhang, Z., Zhang, N., Gao, Y & Wang, Z. (2000). Radiolarian evolution during the Permian and Triassic transition in South and Southwest China. In: H. Yin., J.M. Dickens., G.R. Shi & J. Tonmg (eds). Persian-Triassic

Biological and South an

Foster, W.J., & Twitchett, R.J. (2014), Functional diversity of marine ecosystems after the Late Permian mass extinction event. *Nature Geoscience*, 7, 233-238. https://doi.org/10.1038/ngeo2079

Foster, W.J., Danise, S., & Twitchett, R.J. (2017), A silicified Early Triassic marine assemblage from Svalbard. *Journal* of *Systematic Palaeontology*, *15*, 851-877. https://doi.org/10.1080/14772019.2016.1245680

Foster, W.J., Hirtz, J.A., Farrell, C., Reistroffer, M., Twitchett, R.J., Martindale, R.C. (2022). Bioindicators of severe ocean acidification are absent from the end-Permian mass extinction. *Scientific Reports* 12, 1202.

- Gates, L., James, N.P., & Beauchamp, B. (2004). A glass ramp: shallow-water Permian spiculitic chert sedimentation,
   Sverdrup Basin, Arctic Canada. *Sedimentary Geology*, *168*, 125-147.
- Godbold, A., Schoepfer, S., Shen, S-Z., & Henderson, C.M. (2017), Precarious ephemeral refugia during the earliest
   Triassic. *Geology*, 45, 607-610. https://doi.org/10.1130/G38793.1
- Grasby, S.E., & Beauchamp, B. (2009), Latest Permian to Early Triassic basin-to-shelf anoxia in the Sverdrup Basin,
   Arctic Canada. *Chemical Geology 264*, 232-246.
- 387 Hori, R.S., Yamakita, S., Ikehara, M., Kodama, K., Aita, Y., Sakai, T., Takemura, A., Kamata, Y., Suzuki, N., Takahashi, S., 388 Spörli, B., & Grant-Mackie, J.A. (2011), Early Triassic (Induan) Radiolaria and carbon-isotope ratios of a deep-sea 389 sequence from Waiheke Island, North Island, New Zealand. Palaeoworld, 20, 166-178. 390 https://doi.org/10.1016/j.palwor.2011.02.001
- Hounslow, M.W., Peters, C., Mørk, A., Weitschat, W., & Vigran, J.O. (2008), Biomagnetostratigraphy of the
  Vikinghøgda Formation, Svalbard (Arctic Norway), and the geomagnetic polarity timescale for the Lower Triassic. *Geological Society of America Bulletin, 120*, p. 1305-1325. https://doi.org/10.1130/B26103.1
- Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity
  (Hill numbers). *Methods in Ecology and Evolution*, 7, 1451-1456, https://doi.org/10.1111/2041-210X.12613
- Isozaki, Y. (1997), Permo-Triassic boundary superanoxia and stratified superocean: records from lost deep sea.
   *Science*, 276, 235-238. https://doi.org/10.1126/science.276.5310.235
- Isson, T. T. & Planavsky, N. J. Reverse weathering as a long-term stabilizer of marine pH and planetary climate.
   *Nature* 560, 471-475 (2018). <u>https://doi.org:10.1038/s41586-018-0408-4</u>
- Isson, T.T., Zhang, S., Lau, K.V., Rauzi, S., Tosca, N.J., Penman, D.E., & Planavsky, N.J. (2022), Marine siliceous
  ecosystem decline led to sustained anomalous Early Triassic warmth. *Nature Communications, 13,* 3509.
  https://doi.org/10.1038/s41467-022-31128-3
- 403 Jeppsson, L., & Anehus, R. (1995), A buffered formic acid technique for conodont extraction. *Journal of* 404 *Paleontology*, 69, 790-794, https://doi.org/10.1017/S0022336000035319
- 405 Kump, L. R. Prolonged Late Permian–Early Triassic hyperthermal: failure of climate regulation? *Philosophical* 406 *Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **376**, 20170078 (2018)
- Lampitt, R.S., Salter, I., and Johns, D. (2009), Radiolaria: Major exporters of organic carbon to the deep ocean: *Global Biogeochemical Cycles, 23*, GB1010. https://doi.org/10.1029/2008GB003221
- Leys, S.P., & Lauzon, N.R. (1998), Hexactinellid sponge ecology: growth rates and seasonality in deep water sponges. *Journal of Experimental Marine Biology and Ecology, 230*, 111-129. https://doi.org/10.1016/S0022-0981(98)00088-4
- Liu, G., Feng, Q., Shen, J.U.N., Yu, J., He, W., & Algeo, T.J. (2013), Decline of siliceous sponges and spicule
  miniaturization induced by marine productivity collapse and expanding anoxia during the Permian-Triassic crisis in
  South China. *PALAIOS*, *28*, 664-679. https://doi.org/10.2110/palo.2013.p13-035r
- 415 South China. ( ALAIOS, 20, 004-075. https://doi.org/10.2110/pai0.2015.p15-0551
- 414 Mørk, A., Elvebakk, G., Forsberg, A.W., Hounslow, M.W., Nakrem, H.A., Vigran, J.O., & Weitschat, W. (1999), The 415 type section of the Vikinghøgda Formation: a new Lower Triassic unit in central and eastern Svalbard. *Polar* 416 *Pacagrep*, 18, 51, 82 https://doi.org/10.2400/polar.v181.6558
- 416 *Research, 18*, 51-82. https://doi.org/10.3402/polar.v18i1.6558
- Muscente, A.D., Prabhu, A., Zhong, H., Eleish, A., Meyer, M.B., Fox, P., Hazen, R.M. & Knoll, A.H. (2018). Quantifying
  ecological impacts of mass extinctions with network analysis of fossil communities. *Proceedings of the National Academy of Sciences, 115*, 5217-5222. https://doi.org/10.1073/pnas.1719976115
- 420 Nabbefeld, B., Grice, K., Twitchett, R.J., Summons, R.E., Hays, L., Böttcher, M.E., & Asif, M. (2010), An integrated
- 421 biomarker, isotopic and palaeoenvironmental study through the Late Permian event at Lusitaniadalen, Spitsbergen.
- 422 EPSL, 291, 84-96. https://doi.org/10.1016/j.epsl.2009.12.053

- 423 Nakrem, H. A., & Mørk, A. (1991), New Early Triassic Bryozoa (Trepostomata) from Spitsbergen, with some remarks 424 investigated horizons. Geoloaical 129-140. on the stratigraphy of the Magazine, 128, 425 https://doi.org/10.1017/S001675680001832X
- 426 O'Dogherty, L., Carter, E.S., Goričan, Š., & Dumitrica, P. (2010), Triassic radiolarian biostratigraphy. *Geological* 427 *Society, London, Special Publications, 334*, 163-200. https://doi.org/10.1144/SP334.8
- Penn, J.L., Deutsch, C., Payne, J.L., & Sperling, E.A. (2018), Temperature-dependent hypoxia explains biogeography
  and severity of end-Permian marine mass extinction: *Science*, *362*, eaat1327.
  https://doi.org/10.1126/science.aat1327
- Racki, G. (1999), Silica-secreting biota and mass extinctions: survival patterns and processes: Palaeogeography,
  Palaeoclimatology, Palaeoecology, 154, 107-132. https://doi.org/10.1016/S0031-0182(99)00089-9
- Reddin, C.J., Aberhan, M., Raja, N.B., & Kocsis, Á.T. (2022), Global warming generates predictable extinctions of
  warm-and cold-water marine benthic invertebrates via thermal habitat loss. *Global Change Biology, 28*, 5793-5807.
  https://doi.org/10.1111/gcb.16333
- Ritterbush, K. A., Bottjer, D. J., Corsetti, F. A. & Rosas, S. New evidence on the role of siliceous sponges in ecology
  and sedimentary facies development in Eastern Panthalassa following the Triassic–Jurassic mass extinction. *Palaios*29, 652-668 (2014).
- 439Ritterbush, K. Sponge meadows and glass ramps: state shifts and regime change. Palaeogeography,440Palaeoclimatology, Palaeoecology 513, 116-131 (2019)
- Sano, H., Kuwahara, K., Yao, A., & Agematsu, S. (2010), Panthalassan seamount-associated Permian-Triassic
  boundary siliceous rocks, Mino terrane, central Japan. *Paleontological Research*, 14, 293-314.
  https://doi.org/10.2517/1342-8144-14.4.293
- Sano, H., Kuwahara, K., Yao, A., & Agematsu, S. (2012), Stratigraphy and age of the Permian-Triassic boundary
  siliceous rocks of the Mino terrane in the Mt. Funabuseyama area, central Japan. *Paleontological Research*, *16*, 124https://doi.org/10.2517/1342-8144-16.2.124
- 447 Song, H., Huang, S., Jia, E., Dai, X., Wignall, P.B., & Dunhill, A.M. (2020), Flat latitudinal diversity gradient caused by 448 the Permian–Triassic mass extinction. *PNAS, 117*, 17578-17583, https://doi.org/10.1073/pnas.1918953117
- Takemura, A., Aita, Y., Hori, R.S., Higuchi, Y., Spörli, K.B., Campbell, H.J., Kodama, K., & Sakai, T. (2002), Triassic
  radiolarians from the ocean-floor sequence of the Waipapa Terrane at Arrow Rocks, Northland, New Zealand. New
  Zealand Journal of Geology and Geophysics, 45, 289-296. https://doi.org/10.1080/00288306.2002.9514974
- Twitchett, R.J., Krystyn, L., Baud, A., Wheeley, J.R., & Richoz, S. (2004), Rapid marine recovery after the end-Permian mass-extinction event in the absence of marine anoxia. *Geology*, *32*, 805-808. https://doi.org/10.1130/G20585.1
- Urey, H. C. On the early chemical history of the earth and the origin of life. *Proceedings of the National Academy of Sciences* 38, 351-363 (1952).
- 456 Walker, J. C., Hays, P. & Kasting, J. F. A negative feedback mechanism for the long-term stabilization of Earth's 457 surface temperature. *Journal of Geophysical Research: Oceans* **86**, 9776-9782 (1981).
- Wignall, P.B., Morante, R., & Newton, R. (1998), The Permo-Triassic transition in Spitsbergen: δ13Corg
  chemostratigraphy, Fe and S geochemistry, facies, fauna and trace fossils. *Geological Magazine*, 135, 47-62.
  https://doi.org/10.1017/S0016756897008121
- 461Xiao, Y., Suzuki, N., & He, W. (2017), Water depths of the latest Permian (Changhsingian) radiolarians estimated462fromcorrespondenceanalysis.Earth-ScienceReviews,173,141-158.463https://doi.org/10.1016/j.earscirev.2017.08.012
- Yang, F., Sun, Y. D., Frings, P. J., Luo, L., Wang, L. N., Huang, Y. F., Wang T., Müller, J. & Xie, S. C. (2022). Collapse of
  Late Permian chert factories in the equatorial Tethys and the nature of the Early Triassic chert gap. *Earth and Planetary Science Letters*, 600, 117861.

- 467 Yasuhara, M., Wei, C. L., Kucera, M., Costello, M.J., Tittensor, D.P., Kiessling, W., Bonebrake, T.C., Tabor, C.R., Feng,
- 468 C.R., Baslega, A., Kretschmer, K., Kusumoto, B., & Kubota, Y. (2020), Past and future decline of tropical pelagic
- 469 biodiversity. *PNAS, 117*. 12891-12896. https://doi.org/10.1073/pnas.1916923117
- 470 Zuchuat, V., Sleveland, A.R.N., Twitchett, R.J., Svensen, H.H., Turner, H., Augland, L. E., Jones, M.T., Hammer, Ø.,
- 471 Hauksson, B.T., Haflidson, H., Midtkandal, I., & Planke, S. (2020), A new high-resolution stratigraphic and
- 472 palaeoenvironmental record spanning the End-Permian Mass Extinction and its aftermath in central Spitsbergen,
- 473 Svalbard. Palaeogeography, Palaeoclimatology, Palaeoecology, 554, 109732.
- 474 https://doi.org/10.1016/j.palaeo.2020.109732