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**Article:**

Schobben, M, Foster, WJ, Sleveland, ARN et al. (2020) A nutrient control on marine anoxia during the end-Permian mass extinction. *Nature Geoscience*, 13. pp. 640-646. ISSN: 1752-0894

<https://doi.org/10.1038/s41561-020-0622-1>

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1 **A nutrient control on marine anoxia during the end-Permian**  
2 **mass extinction**

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6 **Oxygen deprivation and sulfide toxicity is considered a potent kill mechanism during the**  
7 **mass extinction just before the Permian–Triassic boundary (~251.9 million years ago).**  
8 **However, the mechanism that drove vast stretches of the ocean to an anoxic state is**  
9 **unclear. Here, we present paleoredox and phosphorus speciation data for a marine**  
10 **bathymetric transect from Svalbard. This shows that, prior to the extinction, enhanced**  
11 **weathering driven by Siberian Traps volcanism increased the influx of phosphorus, thus**  
12 **enhancing marine primary productivity and oxygen depletion in proximal shelf settings.**  
13 **However, this non-sulfidic state efficiently sequestered phosphorus in the sediment in**  
14 **association with iron minerals, thus restricting the intensity and spatial extent of oxygen-**  
15 **depleted waters. The collapse of vegetation on land immediately prior to the marine**  
16 **extinction changed the relative weathering influx of iron and sulfate. The resulting**  
17 **transition to euxinic (sulfidic) conditions led to enhanced remobilization of bioavailable**  
18 **phosphorus, initiating a feedback that caused the spread of anoxic waters across large**  
19 **portions of the shelf. This reconciles a lag of >0.3 My between the onset of enhanced**  
20 **weathering and the development of widespread, but geographically variable, ocean anoxia,**  
21 **with major implications for extinction selectivity.**

22 The Permian–Triassic (P–Tr) boundary (~251.9 million years ago<sup>1</sup>) record contains  
23 multiple signals suggestive of widespread marine anoxia, a kill mechanism widely implicated in  
24 the end-Permian mass extinction<sup>2–7</sup>. This crisis was the most dramatic turning-point in the  
25 evolution of post-Cambrian life, with a loss of up to 81% of marine species<sup>8</sup>. Mechanisms for the  
26 development of oxygen-depleted oceans on timescales compatible with the duration of the  
27 extinction (~60 ky<sup>1</sup>), include changes in ocean circulation<sup>9</sup>, decreased O<sub>2</sub> solubility under  
28 globally rising temperatures<sup>10</sup>, and enhanced eutrophication<sup>10–13</sup>. In the latter case, recent studies  
29 have postulated that changes in the marine inventory of phosphorus (P)—the ultimate limiting  
30 nutrient for marine productivity on geological timescales<sup>14</sup>—was the main driver for  
31 eutrophication-induced oxygen depletion and ultimately the development of euxinic conditions  
32 in extensive regions of the global ocean<sup>10,11,13</sup>.

33 During Siberian Traps volcanism, an increase in bioavailable phosphorus would be an  
34 expected consequence of increased continental weathering via the dissolution of exposed rock  
35 (driven by CO<sub>2</sub>-induced warming, and SO<sub>2</sub>-induced acid rain), and the disintegration of rock by  
36 an invigorated hydrological cycle<sup>11,12,15,16</sup>. Indeed, a coeval change in both lithium (Li)  
37 concentrations and Li isotope ratios has been interpreted to reflect an increase in weathering<sup>16</sup>.  
38 Subsequently, a change in eruption style to intrusive basalt emplacement has been linked to  
39 halocarbon remobilization and exhalations leading to ozone layer depletion and consequent  
40 terrestrial plant extirpations by UV-B irradiance<sup>17,18</sup>. The effects of this intrusive volcanic phase  
41 on land-plant communities have therefore been related to reduced soil stability<sup>12,15,19</sup>. Combined  
42 with continued greenhouse-induced global warming, and associated changes in the hydrological  
43 cycle, this situation likely led to increased soil erosion and physical weathering, thereby loading  
44 near-shore environments with a higher sediment influx and terrestrial organics<sup>4,7,12,15</sup>

45 Certain aspects of this scenario are problematic, as Siberian Traps activity spans >1 My,  
46 with 2/3 of the volume of lava deposited ~0.3 My before the main extinction pulse<sup>18</sup>.  
47 Furthermore, localized regions of dysoxia/anoxia occur prior to the mass extinction<sup>3,4,6</sup>, but a  
48 major expansion in the areal extent of these conditions occurred at the extinction horizon<sup>5,7</sup>. The  
49 role of these precursor environmental changes in pre-stressed communities is underexplored<sup>20</sup>,  
50 and requires knowledge of the mechanisms that drove the initiation of localized oxygen  
51 depletion and the ensuing expansion of anoxic regions.

52 While an increase in the oceanic influx of bioavailable phosphorus may have occurred in  
53 association with Siberian Traps activity<sup>11,16</sup>, the catalytic effect of local redox conditions on  
54 benthic phosphorus remobilization has often been overlooked in scenarios of eutrophication-  
55 induced marine anoxia. Phosphorus is delivered to sediments in the form of organic matter and  
56 skeletal remains (biogenic apatite), as well as in association with Fe (oxyhydr)oxides and  
57 recalcitrant detrital minerals<sup>21-24</sup>. Organically bound-P ( $P_{org}$ ) may be preferentially released to  
58 sediment porewaters upon microbial remineralisation, resulting in increased  $C_{org}/P_{org}$  ratios in  
59 deposited sediments<sup>21,22</sup>. In addition, the reductive dissolution of Fe (oxyhydr)oxides releases  
60 adsorbed P to solution<sup>21-23</sup>, while biogenic apatite tends to be highly soluble<sup>24</sup>.

61 The dissolved P generated by these processes may undergo 'sink-switching', whereby  
62 dependent on the precise conditions, dissolved P may precipitate as either carbonate-fluorapatite  
63 (CFA)<sup>25</sup> or Fe phosphates (e.g., vivianite)<sup>26</sup>, or may be re-adsorbed to Fe (oxyhydr)oxides where  
64 such minerals persist<sup>23</sup>. However, under sulfidic conditions in particular, a significant proportion  
65 of the dissolved P generated during early diagenesis may be recycled back to the water column,  
66 thus promoting a positive productivity feedback<sup>27</sup>. By contrast, organic-rich oxic, dysoxic and  
67 ferruginous (anoxic Fe(II)-rich) settings are potential loci of high P deposition. These features of

68 phosphorus cycling thus place important constraints on the bio-availability of P, and hence may  
69 ultimately control both the spread of anoxia and the generation of toxic dissolved sulfide<sup>11,27,28</sup>.

70 Previous attempts to reconstruct phosphorus availability<sup>13</sup> across the P–Tr transition have  
71 lacked a precise reconstruction of ocean redox conditions, and detailed consideration of the  
72 phase partitioning of P, which are essential to evaluate the role of the P recycling feedback. To  
73 address this we apply novel sedimentary P records combined with independent redox proxies to a  
74 bathymetric transect across the P–Tr boundary.

## 75 **Geological setting and materials**

76 We investigated the Festningen and Deltadalen sequences (Svalbard; Fig. 1), that were  
77 deposited on a shallow, open-marine shelf at the northern margin of Pangaea, facing the Boreal  
78 Sea and the Panthalassa Ocean beyond (Supplementary Fig. 1 and Sections 1–4). The Kapp  
79 Starostin Formation consists of dark, massive to bedded spiculitic chert (with minor shale) at  
80 Festningen<sup>6,29</sup>, and glauconitic, fine-grained sandstone with chert nodules and beds at Deltadalen,  
81 where the latter is interpreted to be a comparatively more proximal facies<sup>6,30,31</sup>. The Kapp  
82 Starostin Formation is overlain by the shale-dominated Vardebukta Formation at Festningen,  
83 and, the Vikinghøgda Formation at Deltadalen.

84 The end-Permian mass extinction has been defined by a loss of intense bioturbation  
85 dominated by *Zoophycos*<sup>4,6</sup>. However, shallow bioturbation, dominated by small *Planolites*,  
86 persists for ~3 m above the formational contact at Festningen, before disappearing<sup>2</sup>. The P–Tr  
87 boundary is defined by the aid of the  $\delta^{13}\text{C}_{\text{org}}$  record (Fig. 2 and Supplementary Fig. 2) and the  
88 conodont marker species *Hindeodus parvus*<sup>31</sup>.

89

## 90 **Local redox chemistry**

91 We combined iron speciation analyses with redox-sensitive trace element concentrations  
92 (Methods) to differentiate oxic, dysoxic, anoxic ferruginous, and euxinic water column  
93 conditions<sup>32,33</sup>. The Fe speciation method relies on the quantification of operationally-defined Fe  
94 fractions that are considered highly reactive ( $Fe_{HR}$ ) towards dissolved sulfide on early diagenetic  
95 timescales<sup>34,35</sup>. The proportion of  $Fe_{HR}$  relative to total iron ( $Fe_{tot}$ ) has been extensively calibrated  
96 in modern and ancient settings, such that  $Fe_{HR}/Fe_{tot} > 0.38$  suggest an anoxic water column,  
97 values below 0.22 indicate oxic depositional conditions, and values of 0.22–0.38 are considered  
98 equivocal<sup>36</sup>. The extent of pyritisation of  $Fe_{HR}$  is used to differentiate euxinic ( $Fe_{py}/Fe_{HR} > 0.7$ –  
99 0.8) from ferruginous water column conditions ( $Fe_{py}/Fe_{HR} < 0.7$ )<sup>36</sup>.

100 Non-sulfidized  $Fe_{HR}$  has the potential to be converted to less reactive sheet silicate  
101 minerals (termed poorly reactive sheet silicate Fe;  $Fe_{PRS}$ ) during early diagenesis and deeper  
102 burial<sup>35,37,38</sup>. Depletion of  $Fe_{HR}$  by this mechanism is clearly observed in some of the studied  
103 samples, and is marked by the co-occurrence of glauconite at both localities. Glauconite occurs  
104 as fibroradiated precipitates covering quartz grains and shell fragments, suggesting an authigenic  
105 precipitate rather than a late diagenetic replacement product or detrital source, and thus  $Fe_{HR}$   
106 minerals would have been the primary source. To compensate for this transfer of  $Fe_{HR}$  to  
107 glauconite, we apply a correction to samples that show clear enrichment in  $Fe_{PRS}$  over  
108 background values, yielding estimates ( $Fe_{HR}/Fe_{tot}^*$ ,  $Fe_{py}/Fe_{HR}^*$ ) of initial depositional ratios<sup>39</sup>  
109 (Fig. 2, Supplementary Figs. 3 and 6, and Section 7.2).

110 The distinctive geochemical behaviour of molybdenum (Mo), uranium (U) and rhenium  
111 (Re) provides further insight into water column redox conditions. High sediment Mo

112 accumulation tends to occur when water column concentrations of sulfide are high, and likely  
113 relates to the formation of particle-reactive thiomolybdates<sup>33</sup>. By contrast, U may be fixed in the  
114 sediment under anoxic porewater conditions, without the requirement for free H<sub>2</sub>S, and Re may  
115 be sequestered under dysoxic conditions in the water column and sediments, where O<sub>2</sub> penetrates  
116 <1 cm below the sediment–water interface<sup>33,40</sup>. Therefore, high Re/Mo ratios tend to indicate  
117 dysoxic water column conditions<sup>40</sup>, whereas enhanced Mo/U ratios suggest a euxinic water  
118 column<sup>33</sup>.

119 The pre-extinction sandstone of the proximal Deltadalen locality is conspicuous for its  
120 authigenic glauconite content. Glauconite formation is favoured by elevated concentrations of  
121 Fe<sub>HR</sub>, silica and potassium under dysoxic conditions<sup>41,42</sup>. High Re/Mo ratios across this interval  
122 (Fig. 2)<sup>40</sup> coupled with the ichnoassemblage and the impoverished shelly faunal record, which  
123 consists of the inarticulate brachiopod *Lingularia freboldi*<sup>43,44</sup> (Supplementary Figs. 4 and 5; and  
124 Section 7.1), are consistent with prevailing dysoxic seafloor conditions. Thus, the elevated  
125 Fe<sub>HR</sub>/Fe<sub>tot</sub>\* values of the Kapp Starostin Formation (Fig. 2) likely reflect the influx of a high  
126 proportion of Fe (oxyhydr)oxides produced during enhanced weathering<sup>35</sup>, rather than anoxic  
127 water column conditions.

128 Enrichments in Re begin to decrease below the extinction interval at Deltadalen,  
129 coincident with increasing Mo/U ratios (Fig. 2). These high ratios coincide with enhanced  
130 fixation of Fe<sub>HR</sub> as pyrite (Fig. 2), Mo<sub>EF</sub>–U<sub>EF</sub> that approach those observed in modern euxinic  
131 settings (Fig. 3), and the disappearance of burrows (Supplementary Fig. 2), suggesting the  
132 development of dominantly euxinic conditions in the water column in proximal settings at the  
133 extinction boundary and into the Early Triassic<sup>33,36</sup>

134 The sponge spiculite chert of the Kapp Starostin Formation at Festningen (distal) is  
135 marked by  $Fe_{HR}/Fe_{tot}^*$  values in the equivocal zone, as well as low Mo/U and generally low  
136 Re/Mo (Fig. 2). These vast sponge meadows are consistent with a well-oxygenated water  
137 column<sup>30</sup>, whereas infrequent peaks in Re/Mo may indicate occasional dysoxic conditions. A  
138 pronounced peak in non-sulfidized iron, coincident with enrichments in  $Fe_{HR}$ , the precipitation of  
139 glauconite, muted Re/Mo enrichments and bioturbation intensity (Supplementary Fig. 2), occurs  
140 at the extinction horizon in the basal Vardebukta Formation (Fig. 2), suggesting the development  
141 of dysoxic and/or ferruginous conditions in the water column. Enrichments in  $Fe_{HR}$  persist across  
142 the P–Tr boundary at ~5 m above the base of the Vardebukta Formation, with elevated  
143  $Fe_{py}/Fe_{HR}^*$ , moderate enrichments in Mo relative to U (Fig. 2), the cessation of bioturbation  
144 (Supplementary Fig. 2), and  $Mo_{EF}-U_{EF}$  that are comparable to normal oxic marine settings (Fig.  
145 3). Together, this implies the probable development of water column euxinia, but relatively low  
146 levels of Mo drawdown imply either intermittent or weakly sulfidic conditions in this more distal  
147 setting<sup>46</sup>.

148 The spatio-temporal variability in water column redox implies the existence of dysoxic  
149 conditions on the shallow shelf prior to the extinction (Fig. 2). Subsequently, at the extinction  
150 horizon, euxinic conditions developed at the shallowest location (Deltadalen), and dysoxic to  
151 ferruginous conditions expanded into more distal shelf settings (Festningen). This was followed  
152 by the expansion of anoxia across the shelf, with euxinic conditions becoming more widespread  
153 in the post-extinction Early Triassic. The S isotope composition of pyrite provides additional  
154 support for this redox reconstruction. Generally low and quite variable pyrite  $\delta^{34}S$  values ( $-32.7$   
155  $\pm 9.9\%$ ) prior to the extinction horizon at the more distal locality (Fig. 2) are consistent with  
156 microbial sulfate reduction in sediments deposited beneath an oxic water column<sup>47</sup>. By contrast,

157 high  $\delta^{34}\text{S}_{\text{py}}$  where glauconite is prevalent, both in the lower section of the more proximal locality  
158 ( $-16.7 \pm 12.1\text{‰}$ ) and just above the extinction horizon at the more distal locality ( $-16.8 \pm$   
159  $15.1\text{‰}$ ), suggests more complete consumption of sulfate, possibly linked to temporal and spatial  
160 variability in sulfate concentrations across the transect. Particularly in the case of the distal  
161 glauconite-rich horizon, relatively high  $\delta^{34}\text{S}_{\text{py}}$  may be due to significant drawdown of the  
162 continental sulfate flux under euxinic conditions on the more proximal shelf. However, under  
163 euxinic conditions at both sites,  $\delta^{34}\text{S}_{\text{py}}$  values cluster around a narrow range ( $-27.8 \pm 5.4\text{‰}$ ),  
164 which is consistent with the narrow range commonly found in modern and ancient euxinic  
165 settings<sup>47,48</sup>.

166 We use our phosphorus data to test two scenarios that are compatible with redox change  
167 at the extinction horizon. Firstly, the  $\text{Fe}_{\text{HR}}$  flux from the continent may have dropped (Fig. 2)  
168 proportional to the sulfate influx with the switch to deforestation, soil erosion and increased  
169 physical weathering<sup>12,15,16,19</sup>. Alternatively, an increase in organic carbon ( $\text{C}_{\text{org}}$ ) availability (Fig.  
170 4) under eutrophic conditions on the shelf may have increased the production of  $\text{H}_2\text{S}$ , thus  
171 overwhelming the continental supply of  $\text{Fe}_{\text{HR}}$ . Both of these scenarios would initially promote  
172 enhanced production of sulfide on the more proximal continental shelf.

### 173 **Phosphorus recycling and the spread of anoxia**

174 To assess the potential role of phosphorus in driving our proposed redox structure we  
175 quantified different phosphorus-bearing phases (Methods), specifically Fe (oxyhydr)oxide-bound  
176 P ( $\text{P}_{\text{Fe}}$ ), biogenic and authigenic apatite ( $\text{P}_{\text{aut}}$ ), organic-P ( $\text{P}_{\text{org}}$ ), and crystalline detrital phases  
177 ( $\text{P}_{\text{det}}$ )<sup>25</sup>. While detrital P is generally considered unreactive in the water column and during early  
178 diagenesis, the remaining phases comprise a ‘reactive’ P pool ( $\text{P}_{\text{reac}}$ ). However, Fe(III)-rich sheet

179 silicates (e.g. glauconite) can also effectively trap phosphate<sup>49</sup>, which is extracted as part of the  
180  $P_{\text{det}}$  pool (Supplementary Fig. 7 and Section 7.3).

181 Prior to the extinction at Deltadalen (proximal),  $P_{\text{tot}}/\text{Al}$  is considerably enriched relative  
182 to average marine shale (Fig. 4). This suggests an effective drawdown mechanism from a water  
183 column that was rich in phosphate. Furthermore, although preferential release from organic  
184 matter occurred during diagenesis ( $C_{\text{org}}/P_{\text{org}} >$  the molar Redfield ratio of 106/1), low  $C_{\text{org}}/P_{\text{reac}}$   
185 ratios ( $\ll 106/1$ ) combined with high  $P_{\text{tot}}/\text{Al}$ , suggest effective sequestration of P in the  
186 sediment, with no evidence for extensive recycling. To explain these observations we invoke a  
187 high initial weathering influx of phosphate to the proximal shelf associated with initial  
188 emplacement of the Siberian Traps prior to the extinction<sup>18</sup>, which enhanced productivity and  
189  $C_{\text{org}}$  remineralisation in the water column, leading to the development of dysoxic conditions (Fig.  
190 5). However, the extent and intensity of deoxygenation was limited by effective drawdown of P  
191 to the sediments in association with both  $C_{\text{org}}$  and the high weathering influx of Fe  
192 (oxyhydr)oxide minerals, and with long-term retention in CFA and glauconite (Supplementary  
193 Fig. 7).

194 These factors then controlled the geochemistry prior to the extinction at Festningen  
195 (distal), where  $P_{\text{tot}}/\text{Al}$  ratios are close to average shale,  $C_{\text{org}}/P_{\text{org}}$  ratios are elevated relative to the  
196 Redfield ratio, and  $C_{\text{org}}/P_{\text{reac}}$  ratios scatter close to the Redfield ratio (Fig. 4). This suggests that  
197 the high initial weathering influx of P was efficiently sequestered in more proximal settings, thus  
198 limiting the spatial extent of dysoxic conditions. Furthermore, while P was released from organic  
199 matter during microbial respiration ( $C_{\text{org}}/P_{\text{org}} > 106/1$ ), there is little evidence for a high sustained  
200 flux back to the water column ( $C_{\text{org}}/P_{\text{reac}} \approx 106$ ), consistent with the expected behaviour of P in  
201 sediments deposited beneath an oxic water column<sup>27,28</sup>.

202 At the extinction horizon,  $P_{\text{tot}}/\text{Al}$  ratios decrease to average shale values at Deltadalen  
203 (proximal), and both  $C_{\text{org}}/P_{\text{org}}$  and  $C_{\text{org}}/P_{\text{reac}}$  ratios increase considerably to values that exceed the  
204 Redfield ratio (Fig. 4). This suggests that the development of euxinia fuelled efficient release of P  
205 from both  $C_{\text{org}}$  and Fe (oxyhydr)oxides, and a positive productivity feedback was promoted via  
206 enhanced P recycling. The initial driver of euxinia is more difficult to ascertain, but was likely  
207 related to the change to a chemical weathering-limited denudation regime<sup>19</sup> (Fig. 2), thereby  
208 decreasing the land-derived influx of  $\text{Fe}_{\text{HR}}$ . This led to a tipping point whereby a relative excess  
209 of dissolved sulfate over  $\text{Fe}_{\text{HR}}$  promoted the development of euxinia<sup>36</sup>. As discussed above, an  
210 increase in eutrophication driven by an enhanced nutrient influx may also have promoted sulfide  
211 production. However, this seems a less likely explanation for the initial driver of euxinia given  
212 the already high input of P (Fig. 4).

213 In glauconite-rich sediments immediately above the extinction horizon at Festningen  
214 (distal), there is an initial peak in  $P_{\text{tot}}/\text{Al}$  in association with the development of dysoxic and/or  
215 ferruginous conditions. Here, our detailed P speciation analyses suggest that, as with the  
216 glauconite-rich horizon in the proximal locality, P was trapped in the sediment in association  
217 with CFA and glauconite (Supplementary Fig. 7). The high P content of this horizon likely  
218 occurred due to drawdown of P that was recycled under euxinic conditions in more proximal  
219 settings, suggesting the operation of a redox-controlled nutrient shuttle across the shelf. This  
220 nutrient shuttle then drove the development of marine euxinia to its maximum extent in the  
221 aftermath of the mass extinction (Fig. 5), where wind/density-driven water circulation on the  
222 shelf would support upward transport of recycled P, and thus sustained deoxygenation<sup>11</sup>. At  
223 Festningen, however, the development of only weak or intermittent euxinia after the P-Tr

224 boundary restricted the extent of P recycling to the water column ( $C_{\text{org}}/P_{\text{reac}} \approx 106/1$ ; Fig. 4),  
225 which effectively constrained the maximum spatial extent of euxinia.

## 226 **Implications for extinction selectivity**

227 This P-driven biogeochemical cascade is synchronous with independent proxy records for  
228 the global-scale spread of anoxic water masses<sup>5,7</sup>, and it was this that initiated the main marine  
229 extinction pulse. The P-driven control on the extent of initial deoxygenation and subsequent  
230 euxinia promoted life-viable environments in the deep marine realm, thereby shaping the  
231 ecosystems of the surviving biota. Based on the benthos that survived the end-Permian mass  
232 extinction at Deltadalen, a planktotrophic larval stage<sup>50</sup> (Supplementary Section 7.1) and a high-  
233 tolerance to low-oxygen conditions are important traits. These benthic species could rapidly  
234 disperse over large distances, thus increasing the chance of survival in habitable locations.

235 In accordance with theoretical ecological models<sup>51</sup>, environmental deterioration of the  
236 marine realm began before the extinction pulse. The initial development of dysoxic/anoxic water  
237 masses, which were preferentially situated in shallow marine environments in the Boreal  
238 region<sup>20</sup>, may thus be regarded as a prelude to the impending mass extinction. Our redox model  
239 also resolves the apparent conflict between the timing of magmatic activity<sup>18</sup>, enhanced  
240 weathering<sup>16</sup>, and the main extinction pulse. The sum of these changes in marine redox  
241 conditions across large stretches of the shelf, which harboured the majority of the Palaeozoic  
242 biodiversity<sup>2</sup>, appears to have been detrimental to many life forms at the end of the Permian.

243

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365 of Festningen and Deltadalen, respectively.

## 366 **Acknowledgements**

367 MS was funded by a DFG Research Fellowship (SCHO 1689/1–1). SWP acknowledges  
368 support from a Royal Society Wolfson Research Merit Award and a Leverhulme Research  
369 Fellowship. DPGB acknowledges funding from the Natural Environment Research Council  
370 (NE/J01799X/1) as do PBW and RJN (NE/P013724/1). HHS and SP acknowledge support from  
371 the Norwegian Research Council by Centres of Excellence funding to CEED (project number  
372 223272), and Lundin Petroleum, Arctic Drilling AS and Store Norske Spitsbergen Kulkompani  
373 for funding, drilling, and support related to the Deltadalen core.

## 374 **Author contributions**

375 The study was designed by MS, RJN, PBW and SWP. Samples were collected by VZ,  
376 ARNS, HS, SP, PBW, and DPGB. Palaeontological data acquisition was performed by WJF,  
377 MS, PBW, and DPGB. Geochemical analyses were performed by MS, FM and RJN. MS and  
378 SWP interpreted data. MS led the writing of the manuscript with contributions from all co-  
379 authors.

## 380 **Competing interests**

381 The authors declare no competing interests.

## 382 **Figure captions**

383 **Figure 1: Geographical setting of the Festningen section (1) and Deltadalen core (2).** Late  
384 Permian lithofacies of Spitsbergen after ref 29 and Supplementary Section 2; the tentative  
385 location of a northern source area (possibly on the Nordfjorden High) demarcated with a

386 question mark; and the Sørkapp-Hornsund High encircled with a dotted line. The red dots mark  
387 the exact locations of the sites. Base map from GADM database (<https://gadm.org/>)

388

389 **Figure 2: Stratigraphic plot of  $\delta^{13}\text{C}_{\text{org}}$ , Fe speciation, Mo/U, Re/Mo and  $\delta^{34}\text{S}_{\text{py}}$  for the**  
390 **Festningen outcrop and Deltadalen core.** The boundaries (vertical dotted lines) for oxic,  
391 anoxic, ferruginous (Fe(II)-rich) and euxinic ( $\text{H}_2\text{S}$ -rich) water column conditions were calibrated  
392 in modern and ancient aquatic environments (see text for sources). Iron speciation ( $\text{Fe}_{\text{py}}/\text{Fe}_{\text{HR}}^*$ ,  
393  $\text{Fe}_{\text{HR}}/\text{Fe}_{\text{tot}}^*$ ) corrected for excess  $\text{Fe}_{\text{PRS}}$  (excess  $\text{Fe}_{\text{PRS}} = [\text{measured } \text{Fe}_{\text{PRS}}/\text{Fe}_{\text{tot}} - \text{baseline}$   
394  $\text{Fe}_{\text{PRS}}/\text{Fe}_{\text{tot}}] \times \text{Fe}_{\text{tot}}$  if measured  $\text{Fe}_{\text{PRS}}/\text{Fe}_{\text{tot}} > \text{baseline } \text{Fe}_{\text{PRS}}/\text{Fe}_{\text{tot}}$ ) is shown as black circles;  
395 uncorrected values are shown as open circles (See Supplementary Section 7.2). Subscripts of  
396 isotope ratios; org = total organic matter and py = pyrite.  $\text{Fe}_{\text{py}}$  = iron pyrite;  $\text{Fe}_{\text{HR}}$  = highly  
397 reactive iron ( $\text{Fe}_{\text{carb}}$  [iron bound to carbonate] +  $\text{Fe}_{\text{ox}}$  [iron bound to Fe oxy(hydr)oxides] +  
398  $\text{Fe}_{\text{mag}}$  [iron bound as magnetite] +  $\text{Fe}_{\text{py}}$ );  $\text{Fe}_{\text{tot}}$  = total iron;  $\text{Fe}_{\text{PRS}}$  = poorly reactive sheet silicate  
399 iron. Reproducibility for  $\text{Fe}_{\text{py}}$  and  $\text{Fe}_{\text{HR}}$  is better than 5% and 9% relative standard deviations  
400 (RSD), better than 8% RSD for total elemental concentrations, and better than 0.1‰ and 0.9‰  
401 SD for  $\delta^{13}\text{C}_{\text{org}}$  and  $\delta^{34}\text{S}_{\text{py}}$ . Horizontal dashed grey line: extinction event; solid grey line:  
402 Permian–Triassic boundary. Details on lithology and stratigraphy in Supplementary Fig. 2 and  
403 Sections 2 and 3.

404

405 **Figure 3: Crossplots of Mo–U covariation.** Mo and U are given as enrichment factors (EF =  
406  $[\text{element}/\text{Al}]_{\text{sample}}/[\text{element}/\text{Al}]_{\text{AV}}$ , where AV represents average shale<sup>45</sup>) on a  $\log_{10}$ -scale. The  
407 black dashed lines represent seawater (sw) Mo–U mass ratios for modern environments; high

408 (sulfidic Cariaco Basin), moderate (non-sulfidic open marine), and low (restricted, sulfidic Black  
409 Sea)<sup>33</sup>. The panels present the data of: a) Deltadalen, b) Festningen, and c) a conceptual model to  
410 explain the enrichment patterns and changes in sedimentary  $Mo_{EF}$  and  $U_{EF}$  at both sites in  
411 relation to hydrographic and redox conditions<sup>33</sup>, The solid red lines denoted by “particulate  
412 shuttle” show systematics underlain by a fluctuating chemocline, whereas “redox variation”  
413 pertains to the evolution of water mass chemistry. Note, that the red dashed line sketches the  
414 trajectory of the open marine conditions of Deltadalen from dysoxic (low Mo–high U) to euxinic  
415 (high Mo–low U).  $Fe_{py}$  = pyrite iron and  $Fe_{HR}$  = highly reactive iron.

416

417 **Figure 4: Stratigraphic distribution of  $P_{tot}/Al$ ,  $C_{org}$ ,  $C_{org}/P_{org}$ , and  $C_{org}/P_{reac}$  ratios.** The  
418 threshold of  $P_{tot}/Al$  (mass ratio of 0.008; vertical red line) is the average shale reference value<sup>45</sup>,  
419 whereas the C/P molar ratio of 106/1 denotes the Redfield ratio (vertical blue line), and the red  
420 circle represents an outlier ( $P_{tot}/Al > 2.0$ ).  $C_{org}$  = total organic matter;  $P_{org}$  = organic-bound  
421 phosphorus;  $P_{reac}$  = reactive phosphorus ( $P_{org} + P_{aut}$  [apatite P] +  $P_{Fe}$  [Fe (oxyhydr)oxide-bound  
422 P]), and  $P_{tot}$  = total phosphorus. External reproducibility for total P and Al is better than 8%  
423 RSD, better than 10% RSD for  $C_{org}$ , and better than 23% RSD for the different P phases.  
424 Horizontal dashed grey line: extinction event; solid grey line: Permian–Triassic boundary.  
425 Details on lithology and stratigraphy in Supplementary Fig. 2 and Sections 2 and 3.

426

427 **Figure 5: Conceptual model of the development of water column redox conditions.** In the  
428 Late Permian, the inner shelf was dysoxic (demarcated with  $<[O_2]$ ) and large amounts of reactive  
429 P accumulated, whereas the outer shelf harboured a thriving ecosystem (here depicted as crinoids  
430 and molluscs, but which are not representative of the actual fossil assemblages). During the end-

431 Permian mass extinction euxinia (demarcated with [H<sub>2</sub>S]) developed on the inner shelf, whereas  
432 the outer shelf environment became dysoxic/ferruginous (demarcated with [Fe(II)]). Under these  
433 conditions, P was remobilized as dissolved P (demarcated with H<sub>3</sub>PO<sub>4</sub>) from the inner shelf,  
434 invigorating productivity (and thus oxygen depletion), and dissolved P was recycled to the outer  
435 shelf and initially deposited through uptake by Fe (oxyhydr)oxide particles settling on the  
436 seabed. After the extinction, euxinic conditions became more prevalent across the shelf, which  
437 was initiated and maintained by recycling of P. Fe<sub>HR</sub> represents highly reactive iron.

## 438 **Methods**

439 **Organic carbon content and carbon isotopes.** Carbonate was removed by treating the  
440 sample with 2 M HCl. The residues were repeatedly washed with MilliQ water<sup>TM</sup> and dried at  
441 40 °C. The de-carbonated samples were analyzed for total organic carbon (TOC = C<sub>org</sub>) content  
442 and associated carbon isotopic composition using an Elementar Pyrocube elemental analyser  
443 linked to an Isoprime mass spectrometer following a standard protocol. Details regarding the  
444 reproducibility of the carbon isotope measurements and an extended protocol are included in the  
445 Supplementary Section 6.2.

446 **Bulk element content.** Whole rock major- (Fe, P, Al) and minor (Mo, U, Re) elements  
447 were obtained by dissolving ashed samples (550 °C over night) with HNO<sub>3</sub>–HF–HClO<sub>4</sub>  
448 followed by inductively coupled plasma optical emission spectrometry (ICP-OES). The precision  
449 of elemental analysis was monitored by analyzing certified standards, and repeated measurement  
450 yielded RSDs that are better than 8 % for all elements (Supplementary Section 6.1 and Table 1).

451 **Sequential Fe and P extractions.** A standard sequential Fe extraction was followed<sup>32</sup>. A  
452 sodium acetate solution at pH 4.5 for 48 h at 50 °C was used to extract Fe<sub>carb</sub>, followed by a 2 h,

453 room temperature extraction with sodium dithionite solution at pH 4.8 to obtain  $\text{Fe}_{\text{ox}}$ . An  
454 extraction with ammonium oxalate for 6 h at room temperature was then applied to yield  $\text{Fe}_{\text{mag}}$ .  
455 Iron from poorly reactive sheet silicates ( $\text{Fe}_{\text{PRS}}$ ) was dissolved using concentrated, boiling HCl  
456 for 1 min<sup>32</sup>. Iron concentrations in the extraction solutions were measured via atomic absorption  
457 spectrometry (AAS). Phosphorus phases were extracted via a revised SEDEX scheme for ancient  
458 rocks<sup>25,52</sup>.  $\text{P}_{\text{Fe1}}$  (poorly crystalline Fe (oxyhydr)oxides) was extracted with a sodium dithionite  
459 solution (buffered with bicarbonate to pH of 7.6) for 8 h at room temperature;  $\text{P}_{\text{aut}}$  was extracted  
460 with a sodium acetate solution at pH 4 for 6 h at room temperature;  $\text{P}_{\text{det}}$  was extracted with a  
461 10 % HCl solution for 16 h at room temperature;  $\text{P}_{\text{mag}}$  was extracted with an ammonium oxalate  
462 solution for 6 h at room temperature;  $\text{P}_{\text{Fe2}}$  (more crystalline Fe (oxyhydr)oxides) was extracted  
463 with a sodium dithionite solution (buffered with citrate to a pH of 4.8) for 8 h at room  
464 temperature, and, finally the residue was ashed (550 °C for 2 h) and reacted with 10 % HCl  
465 solution for 16 h at room temperature to liberate  $\text{P}_{\text{org}}$ . The sum of  $\text{P}_{\text{Fe1}} + \text{P}_{\text{Fe2}} + \text{P}_{\text{mag}}$  gives  $\text{P}_{\text{Fe}}$ .  
466 The P content of the various extracts was determined either via the molybdate blue method<sup>25</sup> or  
467 ICP-OES (in the case of  $\text{P}_{\text{Fe1}}$ ,  $\text{P}_{\text{Fe2}}$  and  $\text{P}_{\text{mag}}$ ). The precision of the various Fe and P phase  
468 measurements as well as the extended protocols are reported in Supplementary Section 6.1 and  
469 Tables 2 and 3.

470 **Pyrite content and sulfur isotopes.** Pyrite S was measured via the chromium reduction  
471 method<sup>53</sup>. This method liberates  $\text{H}_2\text{S}$ , which is subsequently trapped as silver-sulfide ( $\text{Ag}_2\text{S}$ ).  
472 Pyrite iron was determined stoichiometrically from the weight of the  $\text{Ag}_2\text{S}$  recovered. The  $\text{Ag}_2\text{S}$   
473 was analysed for S isotope composition using an Elementar Pyrocube linked to an Isoprime mass  
474 spectrometer (see Supplementary Section 6.2 for reproducibility of S isotope measurements and  
475 an extended protocol).

476 **Data Availability**

477           The raw and processed geochemical data that support the findings of this study are  
478 available under Zenodo: <https://doi.org/10.5281/zenodo.3878094>

479 **Code Availability**

480           The R Markdown files to reproduce the data analysis as well as generating the  
481 accompanying data figures and the main and supplementary information texts can be found  
482 under Zenodo: <https://doi.org/10.5281/zenodo.3878094>

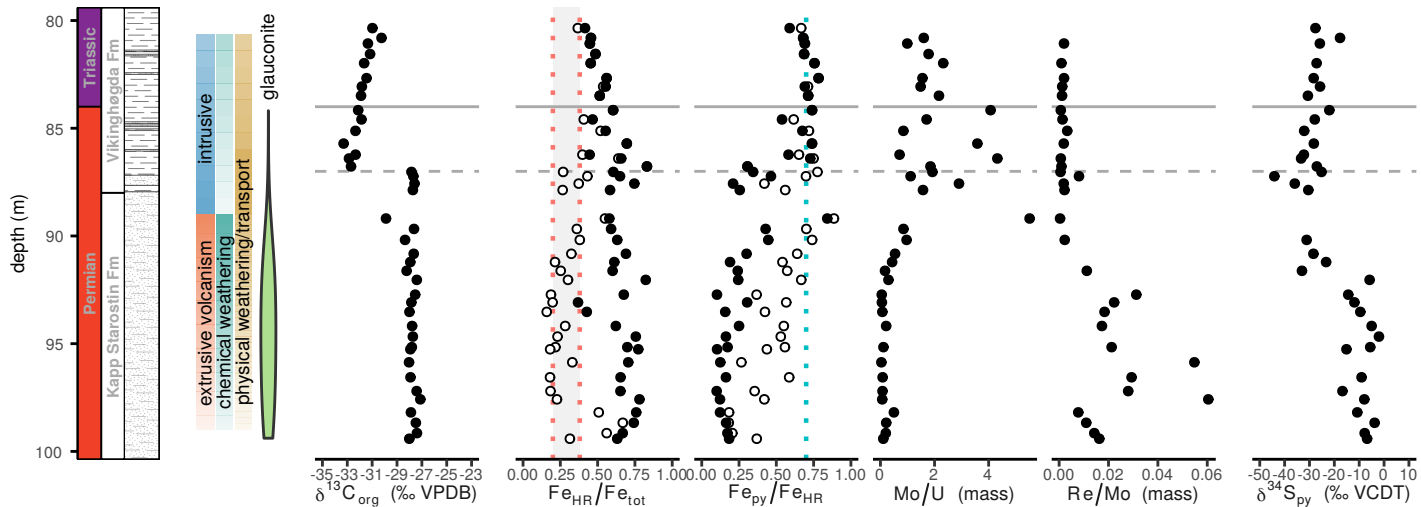
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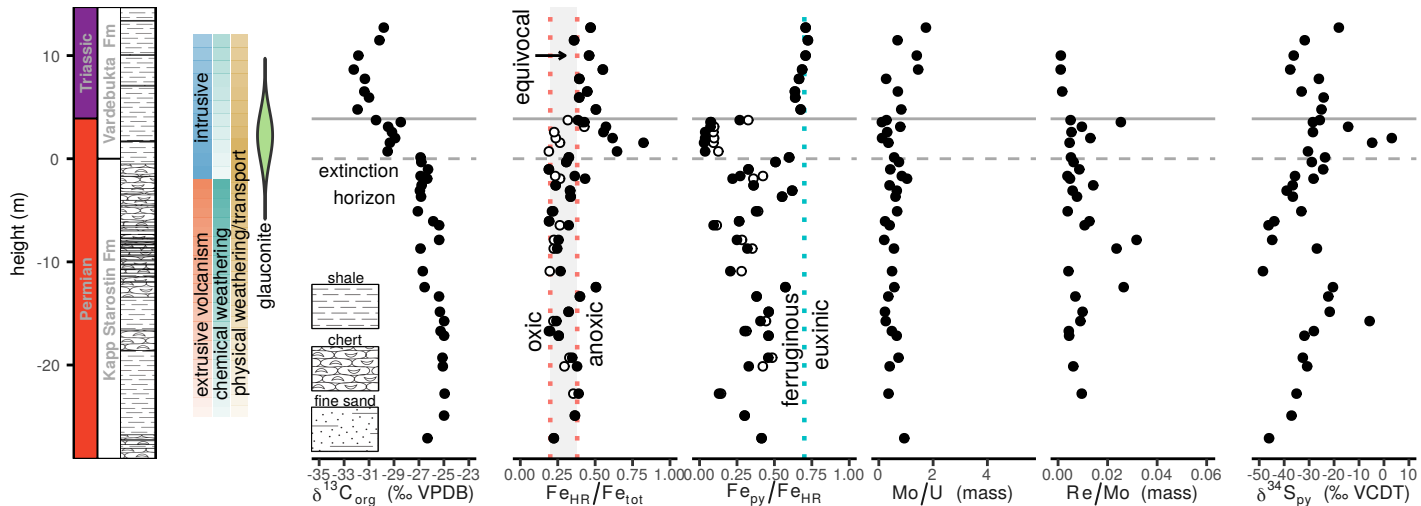
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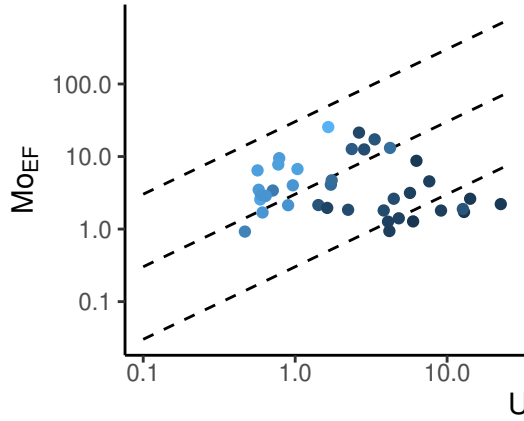
## Deltadalen (proximal)



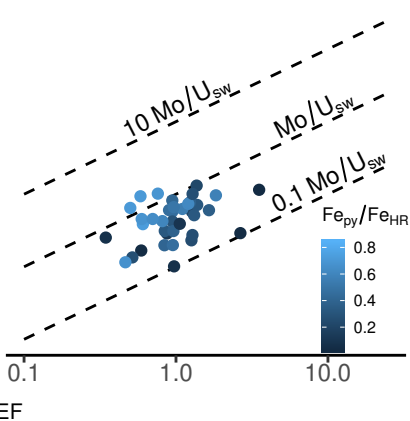
## Festningen (distal)



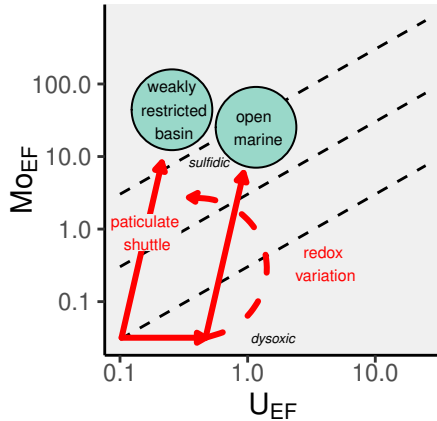
a) Deltadalen (proximal)



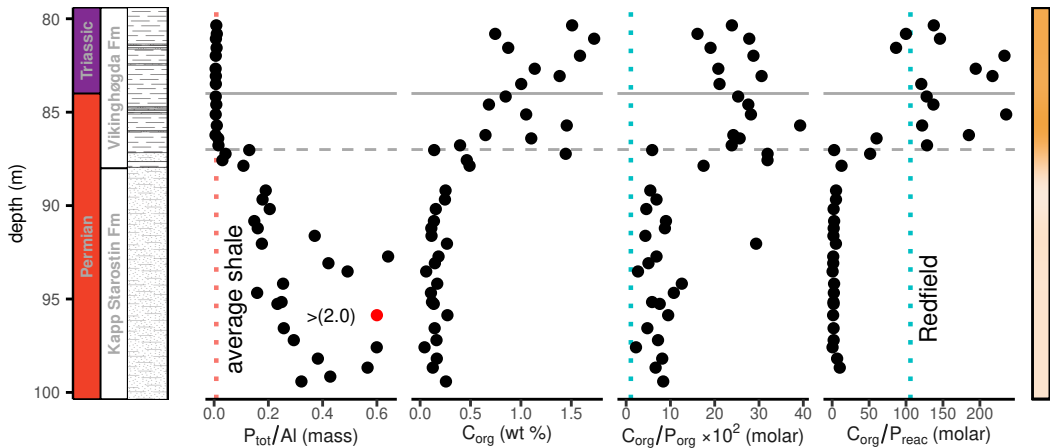
b) Festningen (distal)



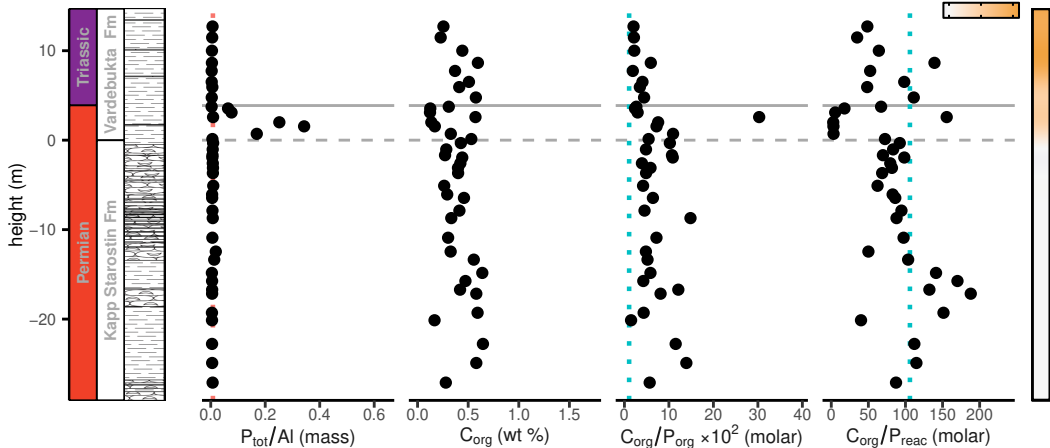
c) Model

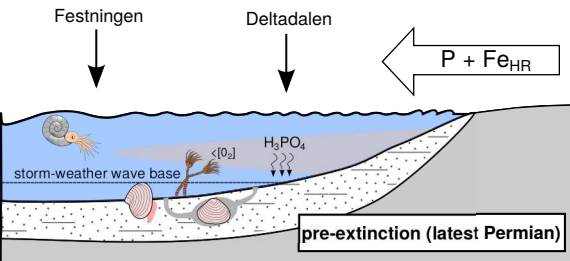
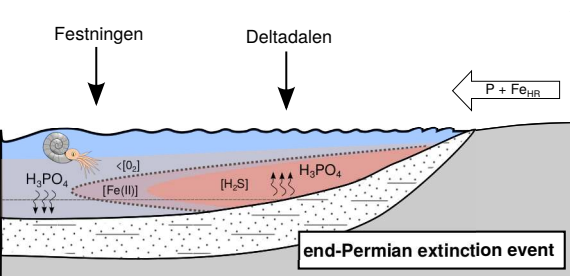
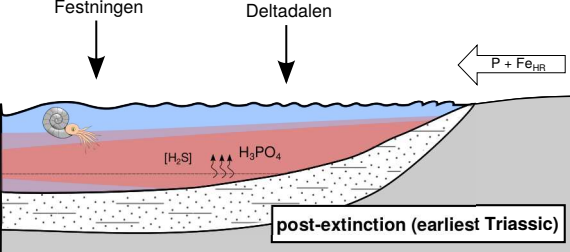


## Deltadalen (proximal)



## Festningen (distal)





continental shelf

Nordfjorden Block