

1 **Nannofossil imprints across the Paleocene-Eocene Thermal Maximum**

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9

10 ABSTRACT

11 **The Paleocene-Eocene Thermal Maximum (PETM; ~56 million years ago) geological**
12 **interval records a marked decline in calcium carbonate (CaCO₃) in seafloor sediments,**
13 **potentially reflecting an episode of deep- and possibly shallow-water ocean acidification.**
14 **However, because CaCO₃ is susceptible to post-burial dissolution, it remains uncertain to what**
15 **extent this process has influenced the PETM geological record. Here we test for evidence of post-**
16 **burial dissolution by searching for imprint fossils of nanoplankton preserved on organic**
17 **matter. We studied a PETM succession from the South Dover Bridge (SDB) core, Maryland,**
18 **USA, comparing our imprint record with previously published data from traditionally sampled**
19 **CaCO₃-preserved nanoplankton body fossils. Abundant imprints through intervals devoid of**
20 **CaCO₃ would signify that post-burial dissolution removed much of the CaCO₃ from the rock**
21 **record. Imprints were recorded from most samples but were rare and of low diversity. Body**
22 **fossils are substantially more numerous and diverse, capturing a more complete record of the**
23 **living nanoplankton communities through the PETM. The SDB succession records a**
24 **dissolution zone/low carbonate interval at the onset of the PETM, through which nanoplankton**
25 **body fossils are rare. No nanoplankton imprints were found from this interval, suggesting that**
26 **the rarity of body fossils is unlikely to have been the result of post-burial dissolution. Instead, our**
27 **findings suggest that declines in CaCO₃ through the PETM of SDB were the result of: (i) biotic**
28 **responses to changes that were happening during this event, and/or (ii) CaCO₃ dissolution that**
29 **occurred before lithification (i.e., in the water column or at the seafloor).**

30

31 INTRODUCTION

32 **The Paleocene–Eocene Thermal Maximum (PETM; ~56 million years ago) was a geologically**
33 **rapid global warming event, lasting ~200 thousand years, throughout which global temperatures**
34 **increased by ~5–8 °C (McInerney & Wing 2011 and references therein). The event was likely caused**
35 **by a massive injection of isotopically light carbon into the ocean–atmosphere system over several**
36 **thousands of years (McInerney & Wing 2011; Turner 2018), although the carbon sources and ultimate**

37 trigger of the PETM are still debated (e.g., McInerney & Wing 2011; Kender et al., 2021). In the
38 geological record, marine PETM successions are generally characterized by major declines in calcium
39 carbonate (CaCO_3) (Zachos et al., 2005) alongside marked changes in micro- and nanno-fossil
40 assemblages, including benthic foraminiferal extinctions (Thomas 1989, 2003, 2007), calcareous
41 nannoplankton species turnover (Gibbs et al., 2006) and reduced nannoplankton calcification rates
42 (O’Dea et al., 2014). Together with boron-based proxy evidence (Penman et al., 2014; Babila et al.,
43 2018, 2022), such signals are commonly associated with deep-, and possibly shallow-water, ocean
44 acidification (OA) (Zachos et al., 2005; Kump et al., 2009; Gibbs et al., 2010; Bralower et al., 2018;
45 Babila et al., 2022), and/or other environmental changes, such as elevated sea surface temperatures
46 (Aze et al., 2014). However, the extent to which post-burial CaCO_3 dissolution – also termed chemical
47 erosion (Bralower et al., 2014) – has affected these records is difficult to determine, and where severe
48 dissolution has likely taken place, its timing generally remains unclear.

49 Imprint fossils of nannoplankton preserved on organic matter provide a tool to test the degree
50 and timing of CaCO_3 dissolution throughout intervals where CaCO_3 preservation is poor (Slater et al.,
51 2022). Although other approaches have been applied to PETM strata to understand the impact of
52 dissolution, such as foraminiferal fragmentation and dissolution of nannofossil rims and central areas
53 (Bralower et al., 2014), these methods rely on the preservation of CaCO_3 and are not necessarily
54 indicative of the timing of dissolution. For example, dissolution of nannofossil liths could occur at any
55 point after their formation; in the water column, at the seafloor, or after deposition and lithification.
56 Nannofossil imprints, however, can be preserved in sediments devoid of CaCO_3 , and where this is the
57 case, they can reveal that CaCO_3 has been removed from the rock record after deposition (Slater et al.,
58 2022).

59 Here we searched for nannofossil imprints through a PETM succession from the South Dover
60 Bridge (SDB) core, southern Maryland, USA [38°44’49.34”N, 76°00’25.09”W] (Fig. 1; drilled by the
61 U.S. Geological Survey), with the aim to determine the timing of potential CaCO_3 dissolution. The
62 SDB section was chosen because it represents a relatively shallow water marine environment (~120–
63 150 meters depth) (Self-Trail et al., 2012; Robinson and Spivey 2019) that preserves organic matter

64 (Alemán González et al., 2012; Edwards 2012), required for imprint preservation (Batten 1985; Slater
65 et al., 2022). Furthermore, the succession appears to record a spectrum of dissolution conditions
66 through the PETM interval, from little to no dissolution below and above the CIE, to pervasive
67 dissolution at the base of the carbon isotope excursion (CIE). The calcareous nannoplankton ‘body’
68 fossils (i.e., the calcite fossil remains of nannoplankton cell wall coverings) from this succession have
69 previously been studied in detail, with diverse and abundant assemblages spanning the PETM
70 described by Self-Trail (2011), Alemán González et al. (2012) and Self-Trail et al., (2012). A notable
71 ~2-m-thick dissolution zone has been recognized near the base of the CIE, through which
72 nannoplankton body fossils are extremely sparse (Self-Trail 2011; Self-Trail et al., 2012). Bralower et
73 al. (2018) described a low carbonate interval (LCI) – representing a slightly amended version of the
74 dissolution zone – from several PETM sections across Maryland and New Jersey, including the SDB
75 core. Bralower et al. (2018) discussed numerous possible causes for the LCI, hypothesizing that this
76 was likely due to shoaling of the lysocline and calcite compensation depth (CCD), but that
77 eutrophication and microbial activity potentially exacerbated the impact of acidification. Further
78 proxy-based reconstructions of seawater pH from the SDB core have inferred that OA started prior to
79 the main CIE, during a pre-onset excursion (Babila et al., 2022). Indeed, these studies point to
80 relatively shallow-water OA. However, rich and abundant nannofossil imprints preserved within the
81 sediments low in CaCO₃ could reveal that CaCO₃ was removed by diagenetic dissolution, rather than
82 *in situ* water column OA or changes to the CCD or lysocline depth that affected seafloor carbonate.
83 Such results would not necessarily discount that changes to seawater chemistry influenced CaCO₃
84 PETM records, but could provide an indication of the extent of diagenetic CaCO₃ dissolution.

85 Post-drilling dissolution of carbonate is common in organic-rich sediments of the Atlantic
86 Coastal Plain, likely due to pyrite oxidation, thus sampling for body fossils needs to occur as soon as
87 possible after coring (Self-Trail & Seefelt 2005; Self-Trail 2011). This is likely why the sediments of
88 the Marlboro Clay in the SDB core record abundant body fossils, whereas their outcrop counterparts
89 are generally barren or yield very sparse nannofossils (Bybell & Gibson 1991; Bybell & Gibson 1994;
90 Gibson & Bybell 1994; Self-Trail 2011). As the SDB core was recovered in 2007, it is probable that at

91 least some post-drilling dissolution of CaCO₃ has taken place; a secondary goal of this study was
92 therefore to examine the nannofossil assemblages using an approach that may be immune to the
93 modifying effects of diagenetic and post-drilling dissolution, by studying their imprints.

94

95 **METHODS**

96 We examined 12 samples spanning the PETM of SDB (Fig. 2). Rock samples were dissolved in
97 HCl and HF and resultant residues were sieved at 5 µm to isolate organic matter. Processing was
98 conducted at Global Geolab Limited, Canada. Final residues were studied using light microscopy
99 (LM) with an Olympus BX53 and scanning electron microscopy (SEM) using an ESEM FEI Quanta
100 FEG 650 scanning electron microscope at the Swedish Museum of Natural History.

101 For LM, residues were strewn across cover slips and mounted onto glass slides with epoxy
102 resin. To assess the composition of organic matter, palynofacies analysis was conducted, where a
103 minimum of 300 organic particles were counted per sample (see Table S1 for palynofacies categories).

104 For SEM, residues were strewn across SEM stubs, dried and gold coated. Organic matter on
105 SEM stubs was observed in systematic traverses for 2 hours per sample at ×10,000 magnification,
106 followed by 30 minutes at ×5,000 magnification, through which all potential imprints were
107 photographed; followed by 30 minutes at ×5,000 magnification to search for well-preserved
108 specimens. Unprocessed rock material from two samples (PJ-SDB13-003 and PJ-SDB13-004) was
109 also examined for imprints and body fossils. For this approach, freshly cleaved rock was mounted onto
110 SEM stubs, gold coated and examined for 2 hours per sample at ×10,000 magnification.

111

112 **RESULTS**

113 **Nannofossil Imprints**

114 We found imprints in nine of the 12 investigated samples (Fig. 2; Table S1). Including
115 indeterminate coccoliths, eight taxa were recorded (Fig. 2). Preservation was variable, with a mixture
116 of well-preserved (Fig. 2B, C) and poorly preserved (Fig. 2G) specimens.

117

118 **Nannofossil Imprints vs. Body Fossils**

119 Imprint assemblages were considerably less rich than previously sampled body fossils,
120 demonstrating that body fossils capture a more complete record of nannoplankton through the PETM
121 of SDB (Fig. 3). Previous studies have shown that body fossils are extremely sparse through the
122 dissolution zone/LCI (Fig. 3; Self-Trail 2011; Self-Trail et al., 2012; Bralower et al., 2018).
123 Observations of rock surfaces and organic residues from the sample taken from the dissolution
124 zone/LCI here (PJ-SDB13-003), reveal similar findings; one taxon, either *Braarudosphaera* sp. or
125 *Micrantholithus* sp. (a more definitive identification was difficult since only a side-view was visible),
126 was recorded on rock surfaces (Figure S1), and no imprints were found in organic residues. For
127 sample PJ-SDB13-004, which yielded the richest imprint assemblage, body fossils on rock surfaces
128 were common and well-preserved (Figure S1).

129

130 **Organic Matter**

131 Palynofacies assemblages were co-dominated by phytoclasts, amorphous organic matter (AOM)
132 and marine palynomorphs. The dinoflagellate, *Apectodinium*, was present through the PETM,
133 recording the acme interval associated with this event (Bujak and Brinkhuis 1998; Crouch et al.,
134 2001). Amorphous organic matter increases in relative abundance around the onset of the CIE, within
135 the dissolution zone/LCI, reflecting a relative increase in organic matter deposition, and a
136 corresponding decline in CaCO₃ preservation, associated with the PETM (Zachos et al., 2005;
137 Schneider-Mor & Bowen 2013).

138

139 **DISCUSSION**

140 The rarity of nannofossil imprints across the PETM suggests that the taphonomic conditions
141 required for their preservation were sub-optimal compared to body fossils (Fig. 3; Self-Trail 2011;
142 Self-Trail et al., 2012). Imprints were only recorded from strata that also yielded body fossils (Fig. 3)
143 and none were found on unprocessed rock surfaces. Hence, rather than representing ‘ghost’

144 nannofossils – imprints found in rocks that are barren of body fossils (Slater et al., 2022) – imprints
145 here are likely the molds of body fossils that were dissolved during acid digestion in the laboratory.

146 Although only one sample was examined from the dissolution zone/LCI here, both the absence
147 of imprints and rarity of body fossils suggests that: (i) nannoplankton production declined through the
148 early stages of the PETM; and/or (ii) dissolution of CaCO_3 occurred before lithification, in the water
149 column, at the seafloor, or during the earliest stages of diagenesis. If dissolution occurred after
150 lithification, we would expect to find imprints, as overburden would have likely facilitated their
151 formation. At this stage, our data alone cannot discount interpretations (i) or (ii), but previously
152 studied nannoplankton counts with taxon-specific Sr/Ca data from other localities support the
153 hypothesis that the decrease in CaCO_3 through the PETM was primarily driven by an increase in
154 seafloor dissolution, rather than a decrease in production in surface waters (Gibbs et al., 2010). The
155 scarcity of imprints suggests that the timing of potential CaCO_3 dissolution was unlikely to have been
156 post-lithification and our findings therefore support the hypothesis that shelf acidification linked to
157 shoaling of the lysocline and CCD contributed to the decline in CaCO_3 preservation at the onset of the
158 PETM in the SDB region (Bralower et al., 2018).

159 Nannofossil imprint assemblages from Mesozoic oceanic anoxic events (OAEs), and especially
160 the Toarcian-OAE, are generally richer, more numerous and better preserved than those documented
161 here (Slater et al., 2022). In addition to variations in seawater chemistry, these discrepancies likely
162 also relate to the amount and type of organic matter – and in particular the quantity of AOM, since this
163 is a good substrate for imprinting (Slater et al., 2022) – preserved through these different events and
164 localities. Given that organic matter appears necessary for imprinting, the rarity of imprints through
165 the PETM compared to the OAEs is likely a product of the lower relative abundances of AOM and the
166 generally lower total organic carbon values (Bralower et al., 2018) compared to the OAEs (e.g.,
167 McArthur et al. 2008). Furthermore, the preservation of AOM as larger fragments through the OAEs
168 (Slater et al., 2022) appears to be important, because imprints are less distinct on the smaller, highly
169 fragmented pieces that are typical of the PETM of SDB. Although imprints are apparently most
170 common on AOM compared to other types of organic matter, they can also preserve on dinoflagellates

171 (Downie 1956), prasinophyte algae, and pollen (Slater et al., 2022). The lack of imprints on the
172 dinoflagellate *Apectodinium*, which is abundant through the PETM of SDB, suggests that the surface
173 of this cyst was a poor substrate for imprinting.

174 Comparisons of imprint and body nannofossil records through the Mesozoic OAEs revealed
175 marked differences in abundance and diversity patterns between these fossil records. In numerous
176 OAE samples, imprint assemblages were substantially more diverse than body fossil records, and in
177 many cases, rich imprint records were found in samples barren of body fossils (Slater et al., 2022).
178 This is not the case for the PETM of SDB. Although the sampling resolution of imprints here is lower
179 than body fossil records (Self-Trail 2011; Self-Trail et al., 2012), the pattern of lower imprint richness
180 through the studied succession is consistent. More generally, the abundance of body fossils and the
181 scarcity of imprints throughout most of the PETM of SDB indicates that post-burial CaCO_3 dissolution
182 was less pervasive compared to the OAE records. These observations bolster confidence that
183 traditionally-sampled body fossil records (Self-Trail 2011; Self-Trail et al., 2012) have not been
184 extensively modified by post-burial dissolution and thus provide a relatively good representative
185 signal of the buried CaCO_3 in the Atlantic Coastal Plain region.

186

187 **CONCLUSIONS**

188 Imprint fossils of nanoplankton represent a relatively novel tool with which to test the extent
189 and timing of CaCO_3 dissolution through geological intervals where CaCO_3 preservation is poor. In
190 the case of the PETM, the scarcity of these fossils through intervals of low CaCO_3 preservation
191 suggests that any dissolution to have happened took place before lithification, in the water column or
192 at the seafloor, supporting hypotheses of seafloor and/or potentially shallower-water CaCO_3
193 dissolution. Future studies testing for the presence and abundance of nannofossil imprints through the
194 PETM at higher-resolution, and in deep-water successions elsewhere, will potentially shed more light
195 on the timing of dissolution through this important geological interval.

196

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204

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322

323 **FIGURE CAPTIONS**

324

325 **Figure 1. Location of the South Dover Bridge (SDB) core, Southern Maryland, USA. Modified**
326 **from Self-Trail (2011).**

327

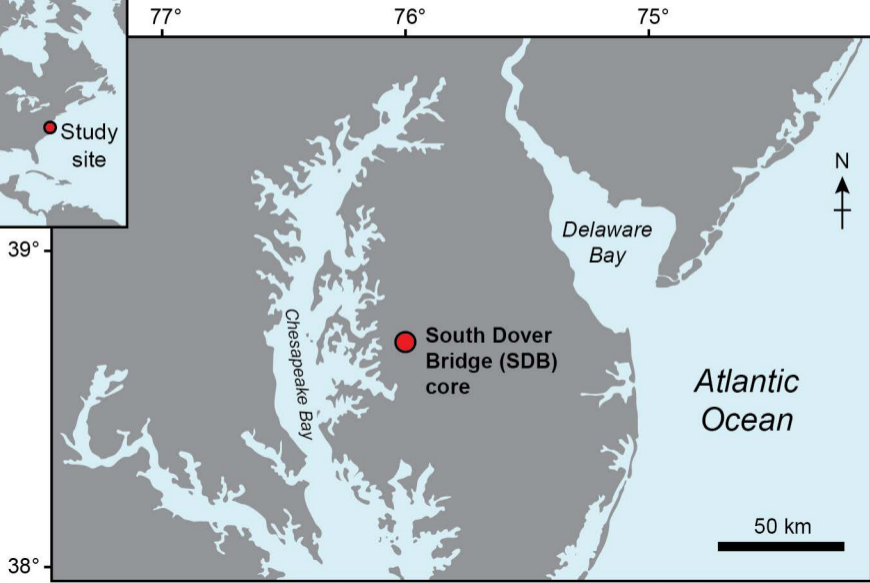
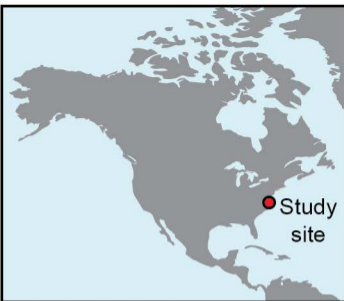
328 **Figure 2. Selected nannofossil imprints on organic matter. A, imprints on AOM, sample PJ-**
329 **SDB13-004. B, small *Toweius*, enlarged image of A. C, small *Coccolithus*, enlarged image of A. D,**
330 **indeterminate very small coccoliths, sample PJ-SDB13-002. E, indeterminate very small**
331 **coccoliths, enlarged image of D. F, indeterminate very small coccoliths, sample PJ-SDB13-004.**
332 **G, indeterminate coccoliths, PJ-SDB13-005. H, *Neochiastozygus* sp., sample PJ-SDB13-005. I,**
333 **small *Calcidiscus*, sample PJ-SDB13-004. J, small *Toweius*, PJ-SDB13-004. K, *Discoaster***
334 ***multiradiatus*, sample PJ-SDB13-006. L, *Umbilicosphaera bramlettei*, sample PJ-SDB13-008. Red**
335 **images are inverted. Arrows indicate nannofossil imprints.**

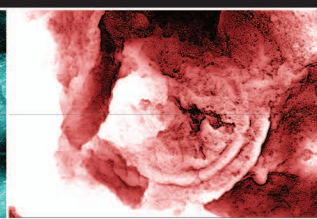
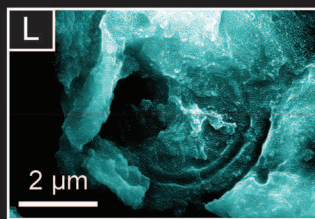
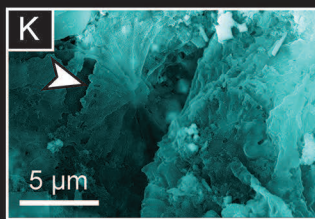
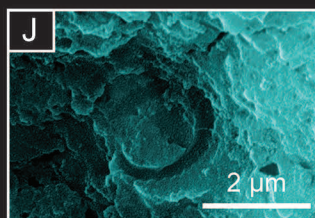
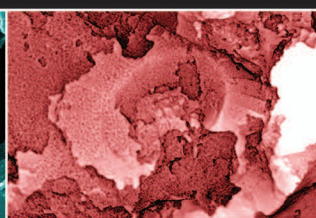
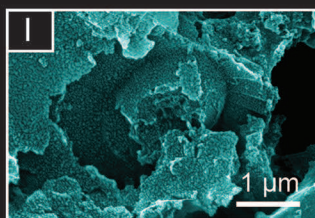
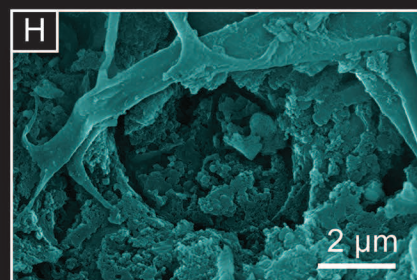
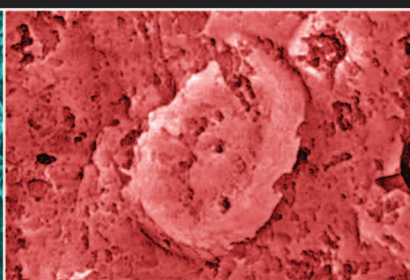
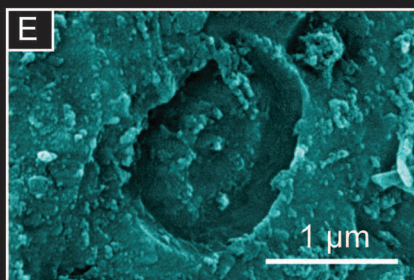
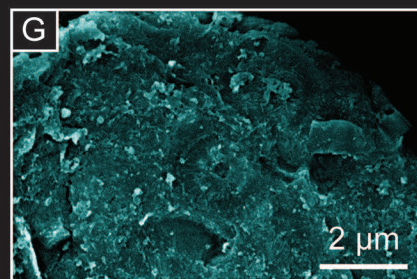
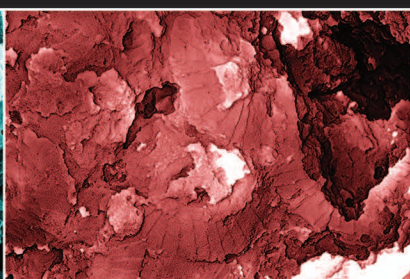
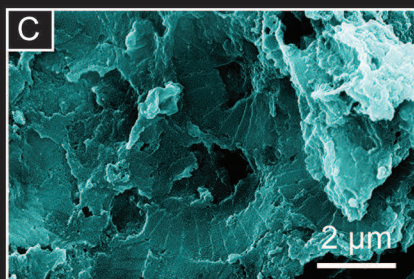
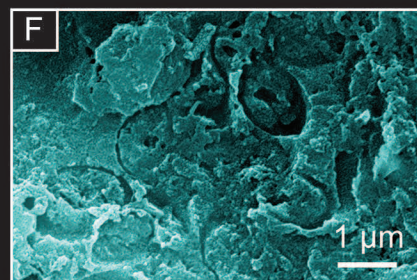
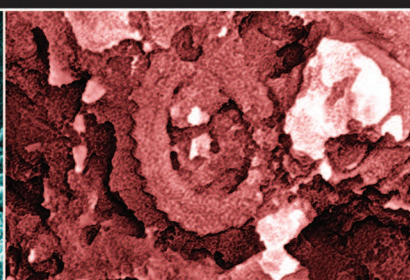
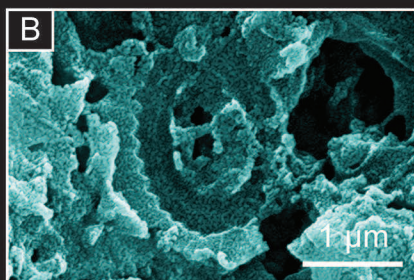
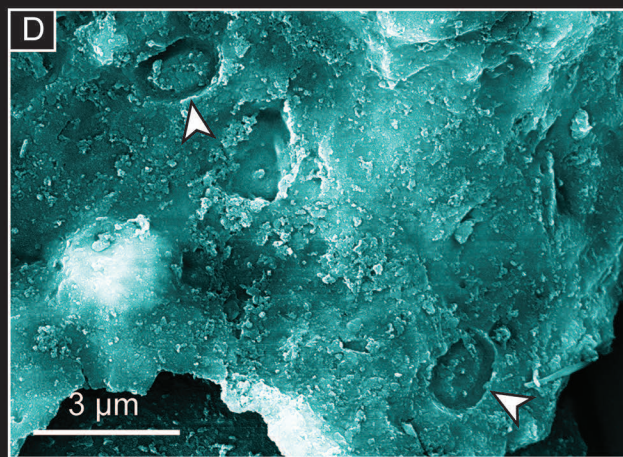
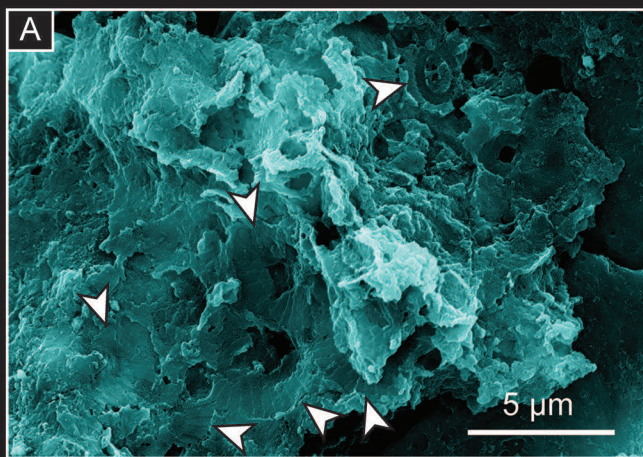
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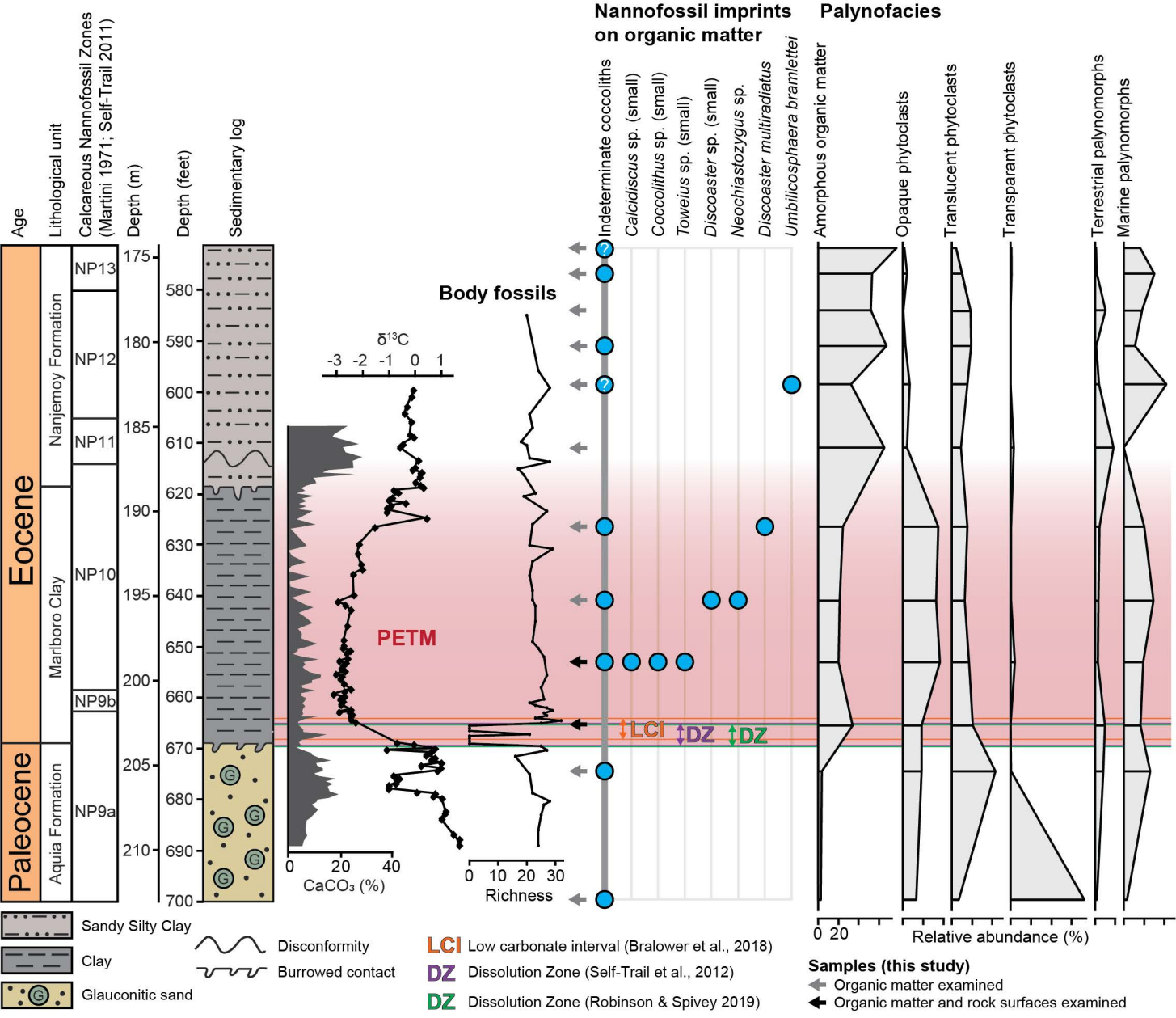
337 **Figure 3. Sedimentary log, carbon isotope, nannofossil imprint, nannoplankton body fossil, and**
338 **palynofacies data through the PETM of SDB. Organic matter categories comprising <1% of the**
339 **total count are excluded here. See Table S1 for sample details and raw data. Richness values for**
340 **body fossils based on counts of 400 specimens (from Self-Trail et al., 2012). CaCO₃ (%) content**
341 **data is from Doubrawa et al., (2022). Bulk carbon isotope data is from Self-Trail (2011).**

342

343 **Figure S1. Scanning electron micrographs of selected nannoplankton body fossils on rock**
344 **surfaces. A, B, Side view of *Braarudosphaera* sp. or *Micrantholithus* sp., sample PJ-SDB13-003.**
345 **C, *Blackites* sp., sample PJ-SDB13-004. D, E, *Coccolithus pelagicus*, sample PJ-SDB13-004. F,**
346 ***Neochiastozygus dentatus*, sample PJ-SDB13-004. G, *Toweius eminens* (left), sample PJ-SDB13-**
347 **004. H, I, *Toweius pertusus*, sample PJ-SDB13-004.**







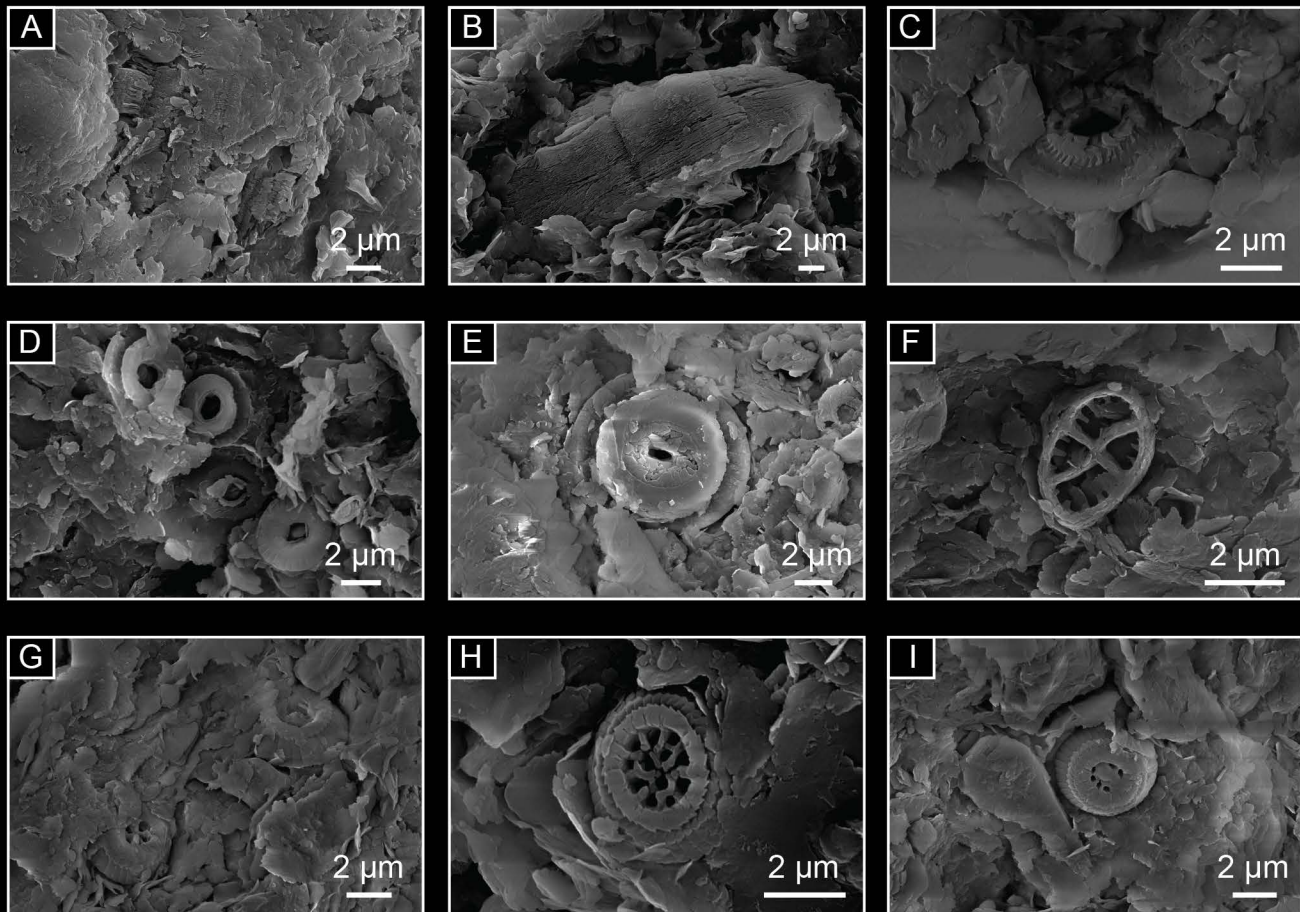


Figure S1. Scanning electron micrographs of selected nannoplankton body fossils on rock surfaces. A, B, Side view of *Braarudosphaera* sp. or *Micrantholithus* sp., sample PJ-SDB13-003. C, *Blackites* sp., sample PJ-SDB13-004. D, E, *Coccolithus pelagicus*, sample PJ-SDB13-004. F, *Neochiastozygus dentatus*, sample PJ-SDB13-004. G, *Toweius eminens* (left), sample PJ-SDB13-004. H, I, *Toweius pertusus*, sample PJ-SDB13-004.