



2 evaluation of biomarker paleothermometry and dinoflagellate cyst 3 paleoecology at Ocean Drilling Program Site 1172 4 Peter K. Bijl^{1*}, Joost Frieling^{1,2}, Marlow J. Cramwinckel^{1,3}, Christine Boschman¹, Appy 5 Sluijs¹, Francien Peterse¹ 6 7 8 ¹Department of Earth Sciences, Utrecht University, Utrecht, the Netherlands. 9 ²now at: Department of earth Sciences, University of Oxford, South Parks Road OX1 10 3AN, UK 11 ³now at: School of Ocean and Earth Science, National Oceanography Centre 12 Southampton, University of Southampton, Southampton, UK 13 14 * corresponding author. email: p.k.bijl@uu.nl 15 16 **Abstract** Sea surface temperature (SST) reconstructions based on isoprenoid glycerol dialkyl 17 18 glycerol tetraether (isoGDGT) distributions from the Eocene southwest (sw) Pacific 19 Ocean are unequivocally warmer than can be reconciled with state-of-the-art fully 20 coupled climate models. However, the SST signal preserved in sedimentary archives 21 can be affected by contributions of additional isoGDGT sources. Methods now exist to 22 identify and possibly correct for overprinting effects on the isoGDGT distribution in 23 marine sediments. We here use the current proxy insights to assess the reliability of 24 the isoGDGT-based SST signal in 69 newly analysed and 242 re-analysed sediments 25 ODP Site 1172 (East Tasman Plateau, Australia) following state-of-the-art 26 chromatographic techniques, in context of paleo-environmental and 27 paleoclimatologic reconstructions based on dinoflagellate cysts. The resulting ~130 28 kyr-resolution Maastrichtian-Oligocene TEX₈₆-based SST record confirms previous 29 conclusions of anomalous warmth in the early Eocene sw Pacific and remarkably cool 30 conditions during the mid-Paleocene. Dinocyst diversity and assemblages show a 31 strong response to the local SST evolution, supporting the robustness of the TEX₈₆ 32 record.

Maastrichtian-Rupelian paleoclimates in the southwest Pacific - a critical





Soil-derived branched GDGTs stored in the same sediments are used to reconstruct 33 34 mean annual air temperature (MAAT) of the nearby land using the MBT'_{5me} proxy. 35 MAAT is consistently lower than SST during the early Eocene, independent of the 36 calibration chosen. General trends in SST and MAAT are similar, except for: 1) an 37 enigmatic absence of MAAT rise during the Paleocene-Eocene Thermal Maximum and 38 Middle Eocene Climatic Optimum, and 2) a subdued middle-late Eocene MAAT 39 cooling relative to SST. Both dinocysts and GDGT signals suggest a mid-shelf 40 depositional environment with strong river-runoff during the Paleocene-early 41 Eocene, progressively becoming more marine thereafter. This trend reflects gradual 42 drying and more pronounced wet/dry seasons in the northward drifting Australian 43 hinterland, which may also explain the subdued middle Eocene MAAT cooling relative 44 to that of SST. The overall correlation between dinocyst assemblages, marine 45 biodiversity and SST changes suggests that temperature exerted a strong influence on 46 the surface-water ecosystem, probably in part through sea level changes caused by 47 steric effects. Finally, we find support for a potential temperature control on 48 compositional changes of branched glycerol monoalkyl glycerol tetraethers 49 (brGMGTs) in marine sediments. It is encouraging that a critical evaluation of the 50 GDGT signals confirms the vast majority of the generated data is reliable. However, this also implies the high TEX86-based SSTs for the Eocene sw Pacific, and the 51 52 systematic offset between absolute TEX86-based SST and MBT'5me-based MAAT 53 estimates remain unexplained.





1. Introduction

56 1.1 The Paleogene Southwest Pacific Ocean 57 Reconstructions of deep-sea (Westerhold et al., 2020) and sea surface 58 temperature (Bijl et al., 2009; 2013a; Cramwinckel et al., 2018; Frieling et al., 2014; 59 Hollis et al., 2014; 2019; Inglis et al., 2015; 2020; O'Brien et al., 2017; Evans et al., 60 2018; O'Connor et al., 2019; Sluijs et al., 2020) have revealed overall cool climate in 61 the Maastrichtian and Paleocene, long-term warming towards the early Eocene 62 Climatic Optimum (EECO; 53.4 – 49.2 Ma), and subsequent cooling during the middle 63 and late Eocene (48.6 - 33.6 Ma). The EECO stands out as particularly warm, with ice-64 free polar regions (Bijl et al., 2013a; Hines et al., 2017; Pross et al., 2012; Frieling et 65 al., 2014). Certain southern high-latitude regions retain warm-temperate conditions into the late Eocene (Bijl et al., 2009; Houben et al., 2019) and, despite ample 66 67 evidence for pronounced Antarctic glacial expansion across the Eocene-Oligocene 68 transition (Salamy and Zachos, 1999; Bohaty et al., 2012), even into the early 69 Oligocene (Hartman et al., 2018; Passchier et al., 2013; 2017; O'Brien et al., 2020). 70 Variations in atmospheric CO₂ concentrations (Beerling and Royer, 2011; Anagnostou 71 et al., 2016; Foster et al., 2017) are likely the primary driver of these multi-million-72 year climatic trends (Cramwinckel et al., 2018). While equatorial proxy-based sea 73 surface temperatures (SSTs) and deep-sea temperatures, assumed to reflect high-74 latitude SSTs, show good correspondence with numerical model simulations under 75 Eocene boundary conditions and with varying CO₂ forcing (Cramwinckel et al., 2018), 76 proxy-based SST reconstructions of the southwest (sw) Pacific remain warmer than 77 those from model simulations (Bijl et al., 2009; Cramwinckel et al., 2018; Hollis et al., 78 2012; Lunt et al., 2021), despite proposed zonal heterogeneity (Douglas et al., 2014). 79 Specifically, numerical models are currently unable to simulate a paleoclimate in 80 which the annual SST difference between the equatorial Atlantic Ocean (Cramwinckel 81 et al. 2018) and the sw Pacific Ocean (Bijl et al., 2013a; Hollis et al., 2012) is as small 82 as the proxy data suggests. Without this model-data mismatch resolved, it remains 83 unclear to what extent numerical models properly simulate polar amplification of 84 Paleogene climates and if the current proxies properly reflect high latitude 85 temperatures under greenhouse conditions (Lunt et al., 2012).





86 Proxy evidence for warmth in the Eocene sw Pacific region derives from a 87 suite of organic and calcite-based proxies. In terms of the latter, oxygen isotope ratios 88 $(\delta^{18}O)$ and trace element ratios (Mg/Ca) from well-preserved planktonic foraminifera 89 indicate warm temperatures from Eocene sections in New Zealand (Creech et al., 90 2010; Hines et al., 2017; Hollis et al., 2009; 2012). These proxies require assumptions regarding seawater chemistry (Mg/Ca, δ^{18} O seawater, pH) that carry significant 91 92 uncertainty (e.g., Kozdon et al., 2020, Evans et al. 2018). The application of clumped 93 isotope paleothermometry has great potential to partially alleviate such concerns, as 94 evident from work on Seymour Island (Douglas et al., 2014). Pollen-based vegetation 95 reconstructions from New Zealand, the Tasman region and Wilkes Land (Carpenter et 96 al., 2012; Contreras et al., 2013; 2014; Huurdeman et al., 2020; Pross et al., 2012), 97 however, confirm warm conditions, and arguably deliver the best constraints on 98 winter temperatures. This is because of fundamental physiological restrictions in 99 their individual tolerances (e.g., Reichgelt et al., 2018), whereas mean annual air 100 temperature (MAAT) reconstructions from pollen assemblages are complicated 101 because MAAT exerts much less control on the standing vegetation than seasonal 102 temperature and hydrological extremes. Reconstructions of the warm Eocene 103 primarily relied on organic geochemical proxies, notably TEX₈₆ (Bijl et al., 2009; 104 2013a; Cramwinckel et al., 2018; 2020; Crouch et al., 2020; Hollis et al., 2009; 2012; 105 Sluijs et al., 2006; 2009; 2011). These absolute SST estimates for the sw Pacific are 106 closer to those from the equatorial Atlantic as they are to the deep-sea (Cramwinckel 107 et al., 2018), which is surprising given that the South Pacific was presumably the 108 dominant region of deep-water formation during the Eocene (Huber and Thomas, 109 2010; Thomas et al., 2003; 2014). 110 111 1.2 GDGT paleothermometry 112 TEX₈₆ utilizes the correspondence of higher abundances of cyclopentane rings 113 in sedimentary archaeal membrane lipids termed isoprenoid glycerol dialkyl glycerol tetraethers (isoGDGTs) with higher SST of the overlying surface water (Schouten et 114 115 al., 2002). This relation is attributed to a viscoelastic adaptation of the membrane of

pelagic Thaumarcheota, the dominant source organisms of isoGDGTs, to temperature

(Schouten et al., 2002; 2013). For some periods in geological deep time, including the

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118 Paleocene and Eocene, TEX₈₆ calibrations based on GDGTs in core top sediments need 119 to be extrapolated above the modern SST range ($\sim 30^{\circ}$ C) to estimate SST. The 120 linearity of the relation at and beyond the high-end of the core-top calibration is 121 poorly known, leading to very high uncertainty in SST estimates at the warm end of 122 the calibration (Hollis et al., 2019). However, as the absolute TEX₈₆ values of many 123 Eocene sediments exceed those observed for modern core-tops, even the most 124 conservative calibrations yield SSTs >30°C in the warmest intervals. Increasingly, 125 such temperatures are corroborated by estimates from other SST proxies (e.g., Zachos 126 et al, 2006; Frieling et al., 2017; Evans et al., 2018). 127 Along with calibration uncertainties, a number of confounding factors have 128 been identified since first publication of the isoGDGT-based SST records from the sw 129 Pacific (Hollis et al., 2009; 2012; Bijl et al., 2009; 2013), relating to a suite of pre-, syn-130 , and post-depositional processes that might alter the pelagic isoGDGT signal in 131 marine sediments. IsoGDGT contributions from methanogenic (Blaga et al., 2009) and 132 methanotrophic (Weijers et al., 2011; Zhang et al., 2011) archaea, deep-dwelling 133 archaea (Taylor et al., 2013) and terrestrial sources (Hopmans et al., 2004; Weijers et 134 al., 2006) to the sedimentary isoGDGT pool have been determined. These factors can 135 be recognized in GDGT distributions, leading to better interpretation of TEX₈₆-based 136 SST reconstructions. However, the influence of growth phase (Elling et al., 2014), and 137 environmental ammonium and oxygen concentrations (Qin et al., 2015; Hurley et al., 138 2016) on sedimentary isoGDGT distributions are as yet poorly constrained. 139 Branched GDGTs (brGDGTs) produced by soil bacteria provide 140 reconstructions of mean annual air temperature (MAAT) using the MBT'_{5me} index (De 141 Jonge et al., 2014a; Naafs et al., 2019; Peterse et al., 2012; Weijers et al., 2007; Dearing 142 Crampton-Flood et al., 2020). Based on brGDGTs supplied to marine sediments, the 143 MAAT evolution of Australian-New Zealand continents followed the trends in deep-144 and surface ocean temperature remarkably well, but with much lower absolute 145 values than SST (Bijl et al., 2013a; Pancost et al., 2013). Albeit to a lesser extent than 146 SST, southern high-latitude MAAT reconstructions remain warmer than model 147 simulations (Huber and Caballero, 2011) as well, even when simulations replicate 148 equatorial surface and global deep ocean temperatures (Cramwinckel et al., 2018). 149 With improved analytical techniques (Hopmans et al., 2016), brGDGT isomers with a





150 methylation on the 5- or the 6-position of the alkyl chain can now be separated and 151 quantified (De Jonge et al., 2013). With this separation, the pH co-dependence of the 152 brGDGT signal can be removed, isolating the temperature relation (De Jonge et al., 153 2014a; Naafs et al., 2017a). The separation of brGDGT isomers also allows to 154 recognize and correct for potential contributions of aquatic brGDGTs to the soil-155 derived brGDGT signal stored in marine sediments that complicate the use of 156 brGDGTs as continental paleothermometer in continental margin sediments (De 157 Jonge et al., 2014b; 2015; Dearing Crampton-Flood et al., 2018; Peterse et al., 2009; 158 Sinninghe Damsté, 2016; Tierney and Russell, 2009; Zell et al., 2013). 159 Lipids from a related biomarker family, the branched glycerol monoalkyl 160 glycerol tetraethers (brGMGTs), were identified in the marine realm in core-top 161 sediments (Liu et al., 2012), oxygen minimum zones (Xie et al. 2014), and later in peat 162 (Naafs et al 2018a) and East African lake sediments (Baxter et al 2019), the latter 163 identifying 7 individual brGMGTs. The brGMGTs contain a covalent bond connecting 164 the two alkyl chains. The abundance of brGMGTs relative to that of brGDGTs, as well 165 as the relative distribution of brGMGT isomers seems to vary with temperature in 166 some degree (Baxter et al., 2019; Naafs et al., 2018a; Tang et al., 2021), although this 167 is thus far only based on empirical relationships. The exact sources of these 168 compounds, and consistency of such signals in various terrestrial, lacustrine and 169 marine realms, are as yet not fully understood. The degree of methylation of a specific 170 subset of brGMGT compounds (Naafs et al., 2018a, Sluijs et al. 2020) is however 171 similar to those in brGDGTs for which membrane stability regulation is proposed as 172 underlying mechanism (Weijers et al., 2007). Paleogene marine sediments from the 173 Arctic Ocean do contain abundant brGMGTs (Sluijs et al., 2020), and these seem to be 174 produced in the marine system with a strong oxygen minimum zone, and substantial 175 terrestrial input. While the degree of methylation of acyclic brGMGTs (HMBTacyclic) 176 does show similar trends to TEX₈₆ in the Paleogene Arctic record, brGMGTI, which 177 was tentatively calibrated to temperature using a suite of tropical lakes (Baxter et al., 178 2019) does not (Sluijs et al., 2020). The response of brGMGTs to environmental and 179 climatic changes, as well as their sourcing in the marine realm, is clearly diverse, 180 complex and, as yet, poorly understood.

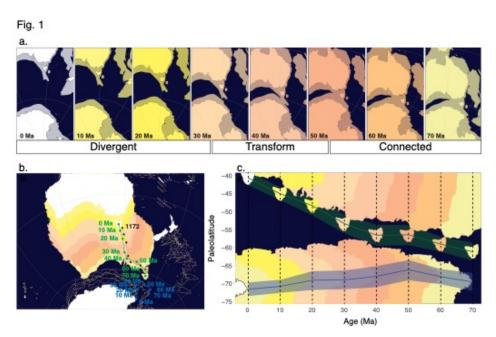




183 From the new insights about the GDGT-based proxies, it is clear that assessing 184 the reliability of previously published GDGT-based temperature reconstructions 185 requires a revisit and a detailed constraints on past environmental, climatological and 186 depositional conditions. Moreover, the presence and proxy potential of brGMGTs the 187 early Paleogene sw Pacific has not yet been assessed. To this end, we have revisited a 188 sedimentary record from the sw Pacific Ocean: ODP Site 1172 on the East Tasman 189 Plateau (ETP), which contains an almost complete succession of late Cretaceous to 190 early Oligocene sediments (Bijl et al., 2013b; 2014; Brinkhuis et al., 2003; 191 Schellenberg et al., 2004; Stickley et al., 2004a). We have newly analysed isoGDGTs, 192 brGDGTs, and brGMGTs from the Maastrichtian and Paleocene section of the record, 193 and re-analysed previously published sample sets using the chromatography method 194 with improved compound separation (Hopmans et al., 2016). We critically evaluate 195 the biomarker results using established indicators for pre-, syn- or post-depositional 196 overprint of the primary sea surface and air temperature signals. In addition, we use 197 dinoflagellate cyst assemblages and terrestrial palynomorph abundance as recorders 198 of paleoenvironmental change on the continental shelf, for constraints on 199 depositional, environmental and hydrological changes, in order to aid interpretations 200 of the GDGT indices. We also evaluate the nature, source and possible temperature 201 affinity of the brGMGTs in our record. After this critical (re-)evaluation, we interpret 202 the Maastrichtian to early Oligocene sea surface and air temperature, and 203 paleoenvironmental evolution of the sw Pacific region.

1.3 Revisiting GDGTs, and investigating GMGTs at Site 1172





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Figure 1. Absolute plate tectonic changes around Tasmania during the Maastrichtian to recent. a. TG opening in 8 time slices, from 70 Ma to present. Relative tectonic motion between Australia and Antarctica is limited until about 53 Ma, transfer until 34 Ma and divergent from 34 Ma onwards. b. Like a, but on an orthographic projection (compiled with Gplates, using paleomagnetic reference frame (Torsvik et al., 2012) from Seton et al. (2012)). Green and blue lines and dots represent the pathways of Tasmania and Cape Adare, respectively, black dashed line and dots represent the paleo-position of Site 1172. c. The absolute paleolatitude of Cape Adare, Antarctica (blue line, blue shading = uncertainty), as indicative of the plate tectonic motion around the pathway of the Tasman Current, and of Tasmania (green line, green shading = uncertainty), as indicative of the plate tectonic motion of the source area of the terrestrial organic matter, in 10 Myr time steps from 70-0 Ma. obtained from paleolatitude.org (Van Hinsbergen et al., 2015). Plate contours represent paleolatitude of present-day shorelines, for orientation (obtained from Gplates). Note that in visualizations b and c, submerged continental crust is not shown, but does limit TG opening.

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2. Material

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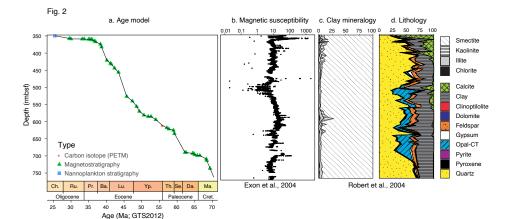
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2.1 Site locality and tectonic evolution

Since the Cenomanian, the continental complex including Australia, Tasmania, ETP and the South Tasman Rise (STR) tectonically moved as one continental plate (Müller et al., 2000) - here referred to as Australia. True polar wander, although relatively poorly constrained, has caused absolute plate motions relative to the spin axis of the Earth (Torsvik et al., 2012; Van Hinsbergen et al., 2015). On a paleomagnetic reference frame, Antarctica and Australia rotated northwestward by 3° of latitude and over 3° longitude between 70 and 50 Ma (Fig. 1), with only little transform displacement between them. From 50 Ma onwards, the tectonic drift orientation of Antarctica shifted slightly more southwards than that of Australia, causing left transform motion between notably west of Cape Adare and west Tasmania (Fig. 1; Williams et al., 2019). Although this divergence effectively opened the Tasmanian Gateway (TG) to surface flow of the Antarctic Counter Current close to the early-middle Eocene boundary (Bijl et al., 2013a), probably through subsidence of the Antarctic continental margin and STR, rapid northward movement of Australia and southward movement of East Antarctica did not start before about 40 Ma (Fig. 1; Cande and Stock, 2004; Seton et al., 2012). Yet, a connection between Australian and Antarctic continental blocks persisted until 34Ma when transform motion between STR and Wilkes Land changed into spreading and ocean crust formation (Cande and Stock, 2004; Seton et al., 2012).







246	Figure 2. a. Age tie points used to construct the age model for ODP Site 1172, based on
247	carbon isotope (Bijl et al., 2010; Sluijs et al., 2011), magnetostratigraphic (Bijl et al.,
248	2010; Houben et al., 2019; Stickley et al., 2004a), and nannofossil (Houben et al.,
249	2019) age constraints. b. Shipboard magnetic susceptibility from Exon et al. (2001). c.
250	Shore-based clay mineralogy and d. smear slide-based lithological observations from
251	Robert (2004).
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254	2.2 Lithology
255	A 760 meter thick sediment sequence was recovered at ODP Site 1172, on the
256	western part of the ETP, east of Tasmania, Australia (Exon et al., 2001). We studied
257	the interval from 760 meters below sea floor (mbsf) to about 350 mbsf in a composite
258	(Röhl et al., 2004a) of Hole A and D. The carbonate ooze from 350 mbsf upwards did
259	not yield any GDGTs. The studied succession consists broadly of green-grey silty
260	claystones from 760 to \sim 505 mbsf, grading into dark grey to black silty claystones
261	from 636 – 625 mbsf, then a return of the greenish grey silty claystones, which is
262	interrupted by a more lithified unit at 610 mbsf (Exon et al., 2001; Röhl et al., 2004a,
263	b; Schellenberg et al., 2004; Sluijs et al., 2011). The silty claystones turn gradually and
264	cyclically lighter from 570 mbsf upwards until $\sim\!361$ mbsf, with gradually more
265	calcium carbonate and diatoms preserved (Röhl et al., 2004a). The clay mineralogy is
266	dominated by smectite but contains progressively more kaolinite above ${\sim}500~\text{mbsf}$
267	(Fig. 2; Exon et al., 2001; Robert, 2004). Grey silty claystones give way to a green
268	glauconitic horizon between 360.1 and 357.3 mbfs (Exon et al., 2001). Above this
269	greensand, carbonate oozes continue further upwards. The record is quasi-
270	continuously bioturbated by zoophycos (Exon et al., 2001). We follow the depth
271	corrections published in (Sluijs et al., 2011) for Cores 12R-31R, based on the
272	correlation of core-log and downhole log magnetic susceptibility.
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274	2.3 Age model
275	For age tie points (Table S1; Fig. 2), we use the identification of the PETM
276	(Sluijs et al., 2011) and Middle Eocene Climatic Optimum (MECO; Bijl et al., 2010) and
277	robust biostratigraphical constraints from the Eocene–Oligocene Boundary interval





278 (Houben et al., 2019; Sluijs et al., 2003). In the intervals in between, the age model 279 relies on magnetostratigraphy, which in some intervals suffers from a strong normal 280 overprint (Dallanave et al., 2016), calibrated using nannofossil- diatom- and dinocyst 281 biostratigraphy (Bijl et al., 2013b; Stickley et al., 2004). Despite the overprint, there 282 does seem to be a paleomagnetic signal preserved in the inclination data (Fuller and 283 Touchard, 2004), and biostratigraphic constraints are broadly consistent with nearby 284 sites (Bijl et al., 2013b; Dallanave et al., 2016). 285 The nature of the sediments and depositional setting (see below) implies that 286 small hiatuses may exist between the age tie points (Röhl et al., 2004a). Indeed, 287 hiatuses were already identified across the Cretaceous-Paleogene Boundary 288 (Schellenberg et al., 2004), in the mid-Paleocene (Bijl et al., 2013b; Hollis et al., 2014), 289 early Eocene (Bijl et al., 2013b) and in the middle Eocene (Röhl et al., 2004a), 290 corresponding to increases in magnetic susceptibility (Fig. 2). The section across the 291 Eocene-Oligocene transition is strongly condensed (Houben et al., 2019; Stickley et 292 al., 2004a, b). 293 294 2.4 Depositional setting 295 From the lithology (Robert, 2004) and palynological content (Brinkhuis et al., 296 2003), the Maastrichtian-Eocene part of the record was interpreted to represent a 297 shallow-marine, mid-continental shelf depositional setting, with gradual deepening in 298 the middle Eocene based on an increase in calcium carbonate content (Fig. 2; Röhl et 299 al., 2004a). The late Eocene greensands have been initially interpreted as evidencing 300 strong deepening and current inception as a result of widening of the TG (Stickley et 301 al., 2004b). Later studies have related the greensands to invigorated ocean circulation 302 and winnowing (Houben et al., 2019), and not necessarily deepening of the site. 303 Volcanic activity of the Balleny plume in the late Eocene (Hill and Moore, 2001) might 304 have played a profound role in the bathymetric changes of the ETP, in addition to the 305 tectonic stresses that act on diverging plates in the TG area. 306 The regional tectonic evolution has implications for interpreting the marine 307 and terrestrial temperature record at this site, because it influenced regional 308 oceanography and climatic conditions in the hinterland catchment area. Field data

and model simulations indicate that with a closed TG, the Tasman Current, a strong





310 western boundary current of the proto-Ross gyre, bathed the plateau with Antarctic-311 derived surface waters (Bijl et al., 2011; 2013b; Huber et al., 2004; Sijp et al., 2014; 312 2016). Palynological evidence confirms that the Proto-Ross Gyre influence persisted 313 at the ETP until the late Eocene (Bijl et al., 2011; Warnaar et al., 2009). This means 314 that despite northward tectonic drift, the same strong western boundary current 315 bathed the site during the Maastrichtian to early Eocene (Sijp et al., 2016), with 316 perhaps some intermittent influence of East Australian Current waters from the north 317 (Bijl et al., 2010; Cramwinckel et al., 2020). This ended when the proto-Leeuwin 318 Current started to flow through the progressively widening TG (Fig. 1), bringing the 319 ETP under the influence of more northerly sourced surface waters (Houben et al., 320 2019; Stickley et al., 2004b). 321 The source area for the terrestrial organic matter (OM) and detrital input was 322 likely Tasmania. Persistent terrigenous input (Brinkhuis et al., 2003) arguably 323 requires a large terrestrial catchment area, and the ETP seems too small (~50,000 324 km²) to have had vast areas above sea level. Moreover, Paleocene-Eocene terrestrial 325 palynomorph assemblages contain common Permian-Triassic elements (Contreras et 326 al., 2014); the Permian-Triassic upper Parmeener group contains thick terrestrial 327 (coal) deposits and comprises the surface lithology of most of eastern Tasmania 328 today. Although that same formation might be present in the ETP subsurface as well, 329 it was probably covered with sediment throughout the Cenozoic (Hill and Moore, 330 2001). Rivers flowing from southeast Australia drained into the Gippsland and Bass 331 Basins, and that terrigenous material is unlikely to have reached the ETP. Seismic 332 information from the East Tasman Saddle, connecting the Tasmanian Margin to the 333 ETP, does not suggest there was a deep basin in between (Hill and Exon, 2004). 334 Therefore, Tasmanian-sourced detrital material could reach the ETP. The ETP was 335 close enough to the Antarctic margin during the Maastrichtian-early Eocene to have 336 received perhaps a minor component of Antarctic-sourced terrestrial OM input, in 337 addition to the dominant Tasmanian source. The regional palynology (Macphail, 338 2000; 2002; Carpenter et al., 2012; Pross et al., 2012; Contreras et al., 2013; 2014; 339 Truswell, 1997), the abundance of peatlands (Holdgate et al., 2009), and the felsic 340 lithology (Moore, Betts, and Hall, 2013) suggests the hinterland catchment contained 341 acidic, wet soils and peats.





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343	2.5 Samples
344	For this study, we used lipid extracts that have been analysed for GDGTs
345	previously (Bijl et al., 2009; Hollis et al., 2014; Houben et al., 2019; Sluijs et al., 2011).
346	We augmented these with 69 new extracts of sediments from the Maastrichtian and
347	the Paleocene, to extend and improve the temporal resolution of the record.
348	Unfortunately, not all archived samples from the PETM interval (Sluijs et al., 2011)
349	could be located, and the interval was reanalysed in a lower resolution (6 samples
350	over the PETM interval). For the remaining PETM, we used the published peak areas
351	(Sluijs et al., 2011) to calculate TEX $_{86}$, which is warranted given the new analytical
352	technique does not affect isoGDGT peak area ratios (Hopmans et al., 2016). For
353	palynology, we collated and revisited data presented in (Bijl et al., 2010; 2013b;
354	Brinkhuis et al., 2003; Houben et al., 2019; Sluijs et al., 2011) and generated higher-
355	resolution data for the Maastrichtian and Paleocene.
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357	3. Methods
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359	3.1 Organic geochemistry
360	3.1.1 Extraction, column separation and analysis
361	Earlier work (Bijl et al., 2009; 2010; 2013a; Houben et al., 2019; Sluijs et al.,
362	2011) presented in detail the extraction, $Al_2O_x column separation$ and filtering
363	techniques used for the samples. We followed the same procedures for the processing
364	of the new samples. We reanalysed all available polar fractions using the double
365	column UHPLC-MS approach as described in (Hopmans et al., 2016). In short,
366	processing involved extraction with a Dionex accelerated solvent extractor using
367	dichloromethane:methanol (DCM:MeOH) 9:1 (v/v), column separation of the total
368	lipid extract using solvent mixtures hexane:DCM 9:1 (v/v), hexane:DCM 1:1 (v/v) and
369	DCM:MeOH 1:1 (v/v) for apolar, ketone and polar fractions, respectively. Polar
370	fractions were filtered using a 0.45 μm polytetrafluorethylene filter, and analysed
371	using an Agilent 1260 Infinity series HPLC system coupled to an Agilent 6130 single-
372	quadrupole mass spectrometer.
373	3.1.2 Data analysis: indices, overprints





Since the discovery of isoGDGTs as proxy for SST (see Schouten et al. (2013) for a review), several non-SST effects have been identified that may affect the distribution of isoGDGTs in the sediment. Several indices have been developed to identify most of the known sources of overprints (Table 1). Next to signalling SST-unrelated influences on the isoGDGT pool, these indices also provide information on the prevailing marine and paleoenvironmental and depositional conditions.

Table 1: Indices from iso- and brGDGTs and brGMGTs. For the chemical structure of these components see Fig. 3.

Index name	Equation	Proxy for	Cut-off value	Source
TEX ₈₆	GDGT2 + GDGT3 + Cren'	Sea surface		(Schouten et
I EA86	$\overline{GDGT1 + GDGT2 + GDGT3 + Cren'}$	temperature	-	al., 2002)
BIT index	IIIa + IIIa' + IIa + IIa' + Ia	Terrestrial input	>0.4? Site-	(Hopmans
DIT IIIuex	$\overline{Cren + IIIa + IIIa' + IIa + IIa' + Ia}$	Terrestrial input	dependent	et al., 2004)
	0/(0)	Non-thermal		(O'Brien et
fcren'	%Cren` %Cren` + %Cren	contribution of	0.25	al., 2017)
	7007011 77007011	crenarchaeol isomer		
		Contribution by		(Zhang et
Methane	GDGT1 + GDGT2 + GDGT3	methane-	.02	al., 2011)
Index	$\overline{GDGT1 + GDGT2 + GDGT3 + Cren + Cren'}$	metabolising	>0.3	
		archaea		
		Contribution by		(Weijers et
AOM ratio	io GDGT2/Cren	anaeropbic methane	>0.2	al., 2011)
		oxydizers		
GDGT2/3		Contribution by		(Taylor et
ratio	GDGT2/GDGT3	deep-dwelling	>5	al., 2013)
Tallo		archaea		
Methano-		Contribution by		(Blaga et al.,
genesis	GDGT0/Cren	methanogenic	>2.0	2009)
genesis		archaea		
Ring index	0*%GDGT0 + 1*%GDGT1 + 2*%GDGT2 +	Non-pelagic GDGT	ΔRI >0.3*	(Zhang et
(RI)	3*%GDGT3 + 4*%Cren + 4*%Cren'	composition	ΔKI >0.3	al., 2016)
MBT'5me	IIIa + IIIb + IIIc	Mean annual air		(De Jonge et
IVID 1 5me	$\overline{IIIa + IIIb + IIIc + IIa + IIb + IIc + Ia}$	temperature	-	al., 2014a)
CBT'	IIIb + IIb' + IIc' + Ia'	(soil-)pH	_	(De Jonge et
CDI	IIIa + IIa + Ia	(3011-Jh11		al., 2014a)
#rings _{tetra}	$\frac{Ib + 2 * Ic}{Ia + Ib + Ic}$		>0.7	





#rings _{penta}	IIb + IIb' + 2 * IIc + 2 * IIc'		_	(Sinninghe
B-penta	IIa + IIa' + IIb + IIb' + IIc + IIc'			Damsté,
#rings _{penta5}	$\frac{IIb + 2 * IIc}{IIa + IIb + IIc}$	Marine in situ brGDGT production	-	2016)
#rings _{penta6}	$\frac{IIb' + 2 * IIc'}{IIa' + IIb' + IIc'}$		-	
IR	IIa' + IIb' + IIc' + Ia'		Depends on	(De Jonge et
II.	$\overline{IIa + IIa' + IIb + IIb' + IIc + IIc' + Ia + Ia'}$	River in situ brGDGT	soil value	al., 2014b)
IRhexa	<u>Ia'</u>	production		(Sinninghe
	$\overline{Ia + Ia'}$		-	Damsté,
IR _{penta}	$\frac{IIa' + IIb' + IIc'}{IIa + IIa' + IIb + IIb' + IIc + IIc'}$			2016)
brGMGTI	H1020c + H1034a + H1034c		In lakes	(Baxter et
bramari	H1020b + H1020c + H1034a + H1034b + H		III lakes	al., 2019)
%brGMGT,	$\frac{[brGMGT]}{[brGMGT] + [brGDGT]} \times 100$			(Baxter et al.,
%brGMGT _a	$\frac{[brGMGT] + [brGDGT]}{[brGMGT]} \times 100}{\frac{[brGMGT]}{[Ia + IIa + IIIa + brGMGT]} \times 100}$	Temperature,	In peats,	2019)
,0212122			lakes	(Naafs et al.,
cyclic				2018a)
HMBT _{acyclic} ,	H1020a + H1020b + H1	oxygenation?	In neate	(Naafs et al.,
all	$\overline{H1020a + H1020b + H1020c + H1034a + H1020c}$		In peats	2018a)
			In Arctic	Sluijs et al.,
имрт	H1020 <i>c</i>		Ocean	2020, sensu
HMBT _{acyclic}	$\overline{H1020c + 1034b + H1048}$			Naafs et al.,
			sediments	2018a)

* Cutoff depends on TEX₈₆ value. Δ RI = RI_{TEX} – RI, where RI_{TEX} = -0.77*TEX₈₆ + 3.32*TEX₈₆^2 + 1.59

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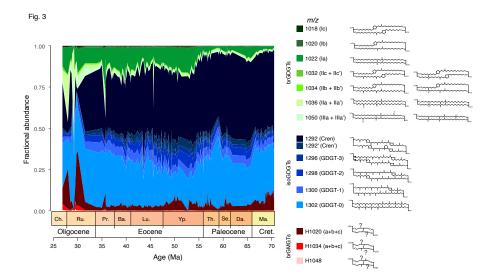






Figure 3. Fractional abundances of the various branched (green) and isoprenoidal (blue) GDGTs, and branched GMGTs (red) at ODP Site 1172.

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All of the ratios that signal biases express the influence of this bias relative to modern "normal" or idealized compositions. The abundance of overprinted components is divided over either a total sum of overprinted and non-overprinted components (closed sum; e.g., methane index, IR) or over only the non-overprinted (ratio; GDGT2/3 ratio, AOM ratio). The complication is that a change in index value can be caused by changes in the denominator or numerator. This is particularly evident in the interpretation of the branched and isoprenoid tetraether (BIT) index. It was proposed that the closed sum ratio between brGDGTs, which were thought to derive exclusively from soils, and the isoGDGT crenarchaeol, which was thought to be produced exclusively by marine archaea, could be an indicator for the relative contribution of soil organic matter (OM) into marine sediments (Hopmans et al., 2004). However, it was subsequently shown that crenarchaeol, but critically also other isoGDGTs are produced on land (Weijers et al. (2006), and that a large contribution of soil-OM to marine sediments can cause a bias in TEX₈₆. Weijers et al. (2006) used an end-member model to calculate the potential bias in TEX₈₆-based SST reconstructions in the Congo Fan and this shows significant bias (>2°C) for BIT above 0.3. However, it is rather arbitrary to assign a cut-off for BIT based on the magnitude of the SST bias alone, as this bias depends primarily on the difference between the isoGDGT composition of the soil and marine endmembers. As a consequence, there is no uniform cut-off value for BIT index above which TEX₈₆ should be discarded. Secondly, because the BIT index is a closed sum, the index is equally affected by increased production of crenarchaeol as it is by the input of brGDGTs. Although this could be verified with absolute concentrations of GDGTs, these are not always presented. Third, brGDGTs are produced in situ in the marine realm (Dearing Crampton-Flood et al., 2019; Peterse et al., 2009; Sinninghe Damsté, 2016). The corollary of this is that the cut-off value for BIT to infer an overprint in the isoGDGTbased SST signal should be assumed to differ per environmental setting, and perhaps

also through time if the setting changes majorly (e.g., Sluijs et al., 2020). As a result,





418 cut-offs were set higher (e.g., 0.4; Bijl et al., 2013a) when no relationship between 419 TEX₈₆ and BIT index values was detected. This approach is also not without 420 complications, because the abundance and composition of isoGDGTs (including 421 crenarchaeol) in soil material varies (Weijers et al., 2006; De Jonge et al., 2015; De 422 Jonge et al., 2016; Naafs et al., 2019; Sluijs et al., 2020). This in turn implies that in 423 samples with high BIT (Weijers et al., 2006), the terrestrially-derived isoGDGT 424 contribution will not be uniform, and might become impossible to detect in a TEX86-425 BIT index cross plot. In some paleo-environmental settings that evidently lack high 426 input of soil-OM, BIT index values are high (Leutert et al., 2020). For reasons given 427 above, this could either mean very low crenarchaeol production in the marine realm, 428 or in situ production of brGDGTs. These two scenarios make for a completely 429 different paleoenvironmental interpretation, and fail to indicate whether the 430 brGDGTs can be used to reconstruct MAAT of the hinterland or whether isoGDGTs 431 can be used for reliable paleothermometry. For that, it is important to assess the 432 sources of brGDGTs, as brGDGTs produced in rivers (De Jonge et al., 2014b; Zell et al., 433 2013) or the (coastal) marine environment (Dearing Crampton-Flood et al., 2019; 434 Peterse et al., 2009; Sinninghe Damsté, 2016) may contribute and thereby bias the 435 initial soil-derived brGDGT signal, affecting the reliability of MAAT reconstructions. 436 Fortunately, production of brGDGTs in the marine realm can be recognized based on 437 the weighed number of rings of the tetramethylated brGDGTs, quantified in the 438 #rings_{tetra}, where values >0.7 indicate a purely marine source of the brGDGTs 439 (Sinninghe Damsté, 2016). Similarly, brGDGTs that are produced in rivers are 440 characterized by a relatively high abundance of the 6-methyl brGDGTs relative to the 441 5-methyl brGDGTs, expressed as the Isomerization Ratio (IR; De Jonge et al., 2014b). 442 For the other overprinting indices, cut-off values may not be as uniformly 443 applicable to all depositional settings either. Leutert et al. (2020) showed that 444 modern samples exceeding cut-off values for the GDGT2/3 ratio and methanogenesis 445 index do not have anomalous TEX₈₆ index values in the modern core-top dataset 446 based on the Ring index. This suggests that the TEX₈₆ index value is not equally 447 influenced by non-thermal contributions in all depositional settings. As a result, 448 evaluating non-thermal contributions on TEX₈₆ index values should consider the 449 depositional and environmental setting along with the cut-off values.





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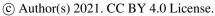
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3.1.3 Calibrations for TEX₈₆ and MBT'_{5me}

An extensive number of calibrations has been proposed to convert TEX₈₆ index values to sea surface temperatures. At the heart of the calibration discussion is the uncertainty whether the TEX₈₆-to-SST relationship continues in a linear way beyond the modern SST range, or in an exponential way (Hollis et al. 2019). The answer to that is beyond the scope of this paper, and we refer to (Cramwinckel et al., 2018; Hollis et al., 2019; O'Brien et al., 2017; Tierney et al., 2017) for detailed discussions, specifically about using TEX₈₆ in regions with SSTs warmer than modern. Following recent recommendations (Hollis et al. 2019), we here apply several calibrations to convert our TEX₈₆ values to SSTs. We apply an exponential calibration (Kim et al., 2010) for which we acknowledge that this calibration suffers from a regression dilution bias (Tierney and Tingley, 2015), and two linear calibrations; one on the warm part (>15°C) of the core-top dataset (O'Brien et al., 2017) and one using Bayesian statistics (BAYSPAR; Tierney and Tingley, 2015) to convert our TEX₈₆ values to SSTs. BAYSPAR produces a linear calibration based on a subset of the core top data with similar GDGT assemblages as the measured TEX₈₆, with a user-defined tolerance. The larger the subset of core tops (i.e., when the number of identified core-top analogues to the sample TEX86 values is large), the closer the Bayesian calibration will approach a global linear regression. For MAAT reconstructions, we use the Deming regression of the soil-specific calibration of Naafs et al. (2017b; MAAT_{soil}) and the Bayesian BayMBT₀ of Dearing Crampton-Flood et al. (2020). The latter follows the approach of BAYSPAR, but then for MBT'_{5me}. We will compare the calibrations for both proxies to middle Eocene UK'37-based SSTs (from Bijl et al., 2010, but using BAYSPLINE calibration of Tierney and Tingley, 2018) and Paleocene-early Eocene sporomorph-based MAAT estimates (Contreras et al., 2014) from the same site.

Table 2. Calibration equations for TEX₈₆ and MAAT

Calibration	Equation	Туре	Proxy for	Source
SST _{exp}	68.4 * log10(TEX ₈₆) + 38.6	Exponential	Mean annual SST (0-	(Kim et al., 2010)
(TEX ₈₆ H)		(regression	20m)	
		dilution)		







SST _{lin}	58.8 * TEX ₈₆ - 11.18	Linear	Mean annual SST (0-	(O'Brien et al., 2017)
			20m)	
BAYSPAR	Prior mean = 20, prior std	Bayesian	Mean annual SST (0-	(Tierney and Tingley,
	= 10, search tolerance =	linear	20m)	2015)
	0.15			
MAATsoil	40.01 * MBT' _{5me} -15.25	Linear,	Mean annual air	(Naafs et al., 2017b)
		Deming	temperature (for days	
		regression	above freezing)	
BayMBT ₀	Prior mean = 20, prior std	Bayesian	Mean annual air	(Dearing Crampton-
	= 15	linear	temperature	Flood et al., 2020)

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3.1.4 R-script for data analysis and evaluation

To facilitate systematic calculation of GDGT ratios, data analysis, visualization, and evaluation, we constructed a set of R markdowns (https://github.com/bijlpeter83/RGDGT.git) that can be applied to any time- or depth series of isoGDGT, brGDGT and/or brGMGT data. The R script loads peak areas of GDGTs/GMGTs from Microsoft excel spreadsheets, calculates and plots fractional abundances, overprinting indices and paleotemperature time or depth series.

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3.2 Palynology

3.2.1 Sample processing

Palynological sample processing techniques were published in the original papers describing these datasets (Bijl et al., 2010; 2013b; Brinkhuis et al., 2003; Houben et al., 2019; Sluijs et al., 2011). We followed the same procedure for the new Maastrichtian-Paleocene samples. The different publications do indicate differences in the employed sieve mesh sizes (10 or 15 μ m) but given all counted dinocysts are larger than 15 μ m, this has not led to differences in the dinocyst results.

3.2.2 Taxonomy

We used the taxonomic framework cited in Williams et al., (2017) in our counts down to the species level, with one exception. For the Wetzelielloidae subfamily, we follow Bijl et al. (2017), for reasons stated therein. We also follow the supra-generic classification based on Fensome et al. (1993); genera described post-1993 were added into that classification accordingly.

3.2.3 Ecological affinities of dinocyst ecogroups





In this paper, we present our results plotted in eco-groups and complexes, which groups dinocyst species with similar ecologic affinities based on modern (for extant taxa) and empirical (for extant and extinct taxa) data (Frieling and Sluijs, 2018; Sluijs et al., 2005). The species of which the ecologic affinity was not assessed previously were included into larger groups based on shared morphological characteristics; primarily tabulation, archaeopyle and cyst- and process shapes. For example, the "Apectodinium complex" is equated to "Wetzellioids" following Frieling et al. (2014; see Table S2 for taxonomic grouping). We directly compare dinocyst- and terrestrial palynomorph indices with GDGT-based indices (following the approach of Frieling and Sluijs, 2018) to arrive at multi-proxy reconstructions of SST, river runoff and distance to shore (Table 3). For this, we resampled and binned GDGT-based indices to the sample resolution of the dinocyst data.

Table 3. Environmental parameters, and their corresponding GDGT indices and dinocyst eco-groups, based on Sluijs et al. (2005), Frieling and Sluijs (2018) and Sluijs and Brinkhuis (2009).

Environmental	GDGT index	Dinocyst eco-group
parameter		
Sea surface	TEX ₈₆	%Thermophiles (Wetzellioideae,
temperature		Hafniasphaera spp., Florentinia reichartii,
		Polysphaeridium spp, Homotryblium spp.,
		Heteraulacacysta spp., Eocladopyxis spp.,
		Dinopterygium spp.)
Runoff, fresh water,	IR, BIT	%Senegalinium cpx, %Phthanoperidinium
salinity		spp., %Terrestrial palynomorphs
Distance to shore	BIT,	%Open marine (Apectodinium spp.,
	#ringstetra	Impagidinium spp., Operculodinium spp.,
		Spiniferites spp.), %Glaphyrocysta cpx.,
		%Epicystal Goniodomids
		(Polysphaeridium spp, Homotryblium spp.,
		Heteraulacacysta spp., Eocladopyxis spp.,





Dinopterygium spp.), %Terrestrial palynomorphs

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3.2.4 Diversity and variability indices

To gain insight into the diversity and variability of the dinocyst assemblage through time, we employ several indices (Table 4), and compare their results at species and ecogroup level. We note that diversity in dinocyst taxonomy is complicated since dinocysts are dominantly produced during the hypnozygotic phase of the dinoflagellate life cycle following sexual reproduction. Only $\sim 15\%$ of modern dinoflagellates features this cyst stage (Fensome et al., 1993), which leaves a large proportion of the biological group unrepresented in the fossil record, including for example coral and foraminifer symbionts, but also more closely related freeswimming taxa. Dinocyst diversity can therefore only be used as an indicator for dinocyst-producing dinoflagellates. As a further complication, taxonomic divisions of cysts, although strongly related to dinoflagellate morphology and taxonomy, is fully based on the morphology of dinocysts. Even modern dinoflagellate-dinocyst relationships are often not unambiguous. Some dinoflagellate species produce various cyst morphologies (Rochon et al., 2008) that represent multiple cyst genera or species. Some of these cyst morphological variations are the result of ecology (Mertens et al., 2011). This complicates comparing cyst datasets on the species level and affects assessing biological diversity based on cysts. On the genus level, taxonomic division of cysts is in most cases based on plate tabulation, which is the morphologic feature that has the closest relationship to dinoflagellate biological diversity (Fensome et al., 1993). However, ecologic or biogeographic affinities have been established for some dinocysts on a species level (e.g., Frieling and Sluijs, 2018), which does suggest subtle morphological features may have biologic and ecologic significance. The eco-groups we use here are the result of extensive reviews of empirical data. These groups combine dinocyst genera and species with fundamentally similar plate tabulations, and thus probably group cysts of closely affiliated biological dinoflagellate species, and, as such also ecologic affinities. For our





diversity calculations we use both the ungrouped data on species level and the diversity in dinocyst ecogroups.

As the simplest approximation of biological diversity, the richness R in terms of dinocyst taxa was summed. Furthermore, several diversity measures were calculated using the R package Vegan (Oksanen et al., 2015). Of these, Fisher's alpha (α) is based on the count data, whereas the Shannon index (H') and Simpson index (D) derive from the relative abundance data. Finally, we employed the Σ cv metric (Gibbs et al., 2012), which we here dub the "Gibbs index", and which provides a measure for assemblage variability. Together, these metrics can give insight into changing stability and diversity of these regional dinocyst assemblages over the Maastrichtian to early Oligocene.

Table 4. Diversity and variability indices for (fossil) assemblages. In the Shannon and Simpson indices, p_i represents the proportional abundance of the i^{th} taxon of the total amount of taxa R. The Gibbs index summates the coefficients of variation (SD/mean) of all taxa (i to R) over a certain rolling window $t_1 \rightarrow t_2$. In Fisher's alpha, the α parameter is estimated from the dataset in which S is the expected number of species with an abundance of n. x represents a nuisance parameter estimated from the dataset, generally between 0.9 and 1. While the Gibbs index is calculated over a rolling window, the other indices are calculated per sample.

Index	Equation	Source
Shannon index (H')	$H' = \sum_{i=1}^{R} p_i * \ln p_i$	(Shannon, 1948)
Simpson index (D)	$D = \sum_{i=1}^{R} p_i^2$	(Simpson, 1949)
Gibbs index (Σcv)	$\Sigma cv = \sum_{i=1}^{R} \left(\frac{SD_{i,t_1 \to t_2}}{mean_{i,t_1 \to t_2}} \right)$	(Gibbs et al., 2012)
Fisher's alpha (α)	$S_n = \frac{\alpha x^n}{n}$	(Fisher et al., 1943)

3.3 Comparison of GDGT and dinocyst assemblage data





Both dinocyst ecogroups and GDGT indices bear information on SST, runoff (~salinity), nutrients and marine primary productivity, and relative distance to shore (Table 4). As dinocyst and GDGT analyses were performed on partly separate datasets, the highest resolution dataset (dinocysts) was linearly resampled to the depth intervals of the GDGT data to facilitate inter-comparison.

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4. Results

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4.1 GDGTs

The resulting dataset has an average temporal resolution of ~ 130 kyrs for the time interval between 70 and 30 Ma. IsoGDGTs dominate the pool of GDGTs (particularly GDGT-0 and crenarchaeol), with a gradual increasing relative abundance of brGDGTs (particularly Ia) throughout the record (Fig. 3). BrGMGTs are in low (<10%) relative abundance, except in the Oligocene, where they account for up to 30% of the total GDGT/GMGT pool.

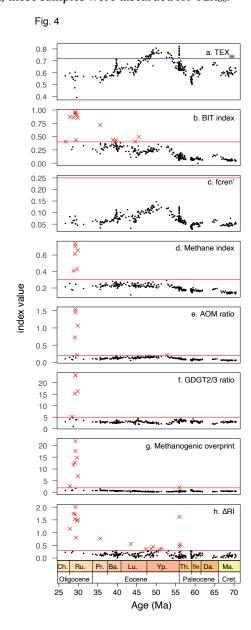
4.1.1 Isoprenoidal GDGTs

Before the TEX₈₆ index results (Fig. 4a) can be interpreted in terms of SST, we assess whether the isoGDGTs are primarily derived from the sea surface, or have received contributions from non-pelagic sources. Across the Ypresian, the BIT index (Fig. 4b) increases from values around 0.1 in the underlying sediments to values at times exceeding 0.4. Most EECO and middle Eocene values, however, have BIT index values between 0.2 and 0.35. The remaining sediments have BIT index values of around 0.3, with the exception of some upper Eocene and Oligocene sediments that occasionally have values around 0.75. There is no correlation between TEX₈₆ and BIT in our entire dataset (p=0.15). None of the samples have fcren' (Fig. 4c) values above the cut-off of 0.25, suggesting no non-temperature related contribution of the crenachaeol isomer to the isoGDGTs. In fact, the consistent trend in (fcren') and the TEX₈₆ index (Fig. 4) (and TEX₈₆^L, not shown) demonstrates the temperature sensitivity of cren' and confirms that discarding it from the index as was done for the cold-temperature index TEX₈₆^L (Kim et al., 2010) is not justified here. With the exception of 6 samples in the Oligocene, all samples have methane index values below the conservative cut-off value of 0.3 (Fig. 4d), although in the early and middle





Eocene, methane index values do approach the cut-off. AOM ratio values suggest an overprint from anaerobic methane oxidisers in one sample in the early Eocene that also has a high BIT index, and 5 samples from the Oligocene where isoGDGTs supposedly received a contribution of anaerobic methane oxidisers (Fig. 4e). As a result, these samples were discarded for TEX_{86} .







608 Table 1. Red line indicates the cut-off value, red crosses indicate samples exceed the 609 cutoff a. TEX₈₆ (Schouten et al., 2002), with blue line indicating the maximum modern 610 core-top value (~0.72). b. BIT index (Hopmans et al., 2004). c. fcren' (O'Brien et al., 611 2017), no samples discarded; d. Methane index (Zhang et al., 2011), ndiscarded = 6. e. 612 AOM ratio (Weijers et al., 2011), n_{discarded} = 6. f. GDGT2/3 (Taylor et al., 2013), 613 conservative cut-off of 5, n_{discarded} = 4, one sample retained for absence of anomalous 614 Ring index values (see text). g. Methanogenesis (Blaga et al., 2009), cut-off of 2.0, 615 $n_{discarded} = 8$. h. $\Delta RI n_{discarded} = 18$. 616 617 618 619 Values signalling a deeper water column overprint (GDGT2/3 ratio) fall below 620 5 for most of the data (Fig. 4f), which was expected given the depositional setting on a 621 continental shelf. A total of 5 samples has water GDGT2/3 values exceeding 5, 4 of 622 which also had other indications of overprinted isoGDGT signals. We discard eight 623 TEX₈₆ datapoints because GDGT-0/crenarchaeol ratios are over 2 (Fig. 4g). One of 624 these is from the PETM, with a value just above the cut-off. The others represent 625 Oligocene samples. 626 In total, 18 samples fall outside the range of RI values that characterize 627 modern pelagic-derived isoGDGT compositions (\Delta RI > 0.3; Fig. 4h, or 95% confidence 628 interval; Fig. 5). Nine of these 18 come from the interval >43 Ma and have no other 629 indications of overprints. These samples fall just outside the 95% confidence interval 630 limits (Fig. 5) and do follow the overall RI/TEX86 trend, but we here discard them to 631 be conservative. The other 9 samples with too high ΔRI come from the late Eocene-632 Oligocene and have BIT index values over 0.4. Two of these samples have no other 633 overprint indication, the other 7 have multiple other overprints. One sample has RI 634 values above the range of modern samples (with no other overprinting indications), 635 the others have too low RI values. Eight samples with normal RI values do have 636 overprints based on the other indices: BIT index values slightly over 0.4 (6 samples), 637 GDGT2/3 ratio values over 5 (1 sample), and AOM ratio over 0.2 (1 sample). 638 Following Leutert et al. (2020) we retained the samples with normal RI values and

Figure 4. TEX₈₆ index and overprinting indices. For the equations of these indices see





high BIT or GDGT2/3 ratio values. After considering all these potential biases, and retaining those with normal isoGDGT distributions, we discard a total of 19 samples.

Most discarded samples are from the Oligocene and meet multiple overprint criteria.

Fig.5

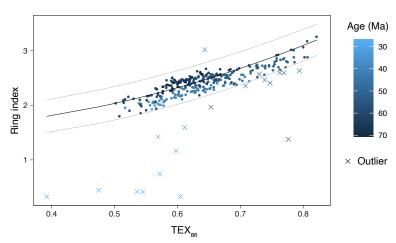


Figure 5. Ring index (RI) versus TEX_{86} . Dots indicate RI/ TEX_{86} values for samples that are retained, crosses indicate samples that are discarded (see Fig. 4). Color of all datapoints indicates age of the sample, from Maastrichtian (dark blue) to Oligocene (light blue). Black and grey curves represent the RI/ TEX_{86} relationship of modern core top samples, and 95% confidence interval, respectively.

4.1.2 Branched GDGTs

Before brGDGT distributions can be interpreted in terms of air temperature, we assess whether they are primarily derived from soils, or have received contributions from river-, or marine in situ production. The relative abundance of tetra-, penta- and hexamethylated brGDGTs in the samples from 1172 deviates from that in modern and Paleogene soils and peats (Fig. 6): it has either comparatively less tetra-, less penta-, or more hexamethylated brGDGTs, and the data split into 2 clusters. The largest cluster follows the distribution observed in modern soils and peats with an offset (Fig. 6). This generally indicates brGDGT contributions from sources other than soils. The smaller second cluster, containing exclusively mid-to-late Paleocene samples, is indeed close to that of modern continental shelf sediments





(Svalbard and Berau delta; Dearing Crampton-Flood et al., 2019; Sinninghe Damsté, 2016) for which in situ brGDGT production substantially exceeds soil contributions. This would generally suggest that the smaller cluster, and perhaps also the larger cluster of samples, have contributions from marine in-situ brGDGT production. However, unlike those modern marine sediments, our entire record does not show elevated #rings_{tetra} values that are associated to marine *in situ*-produced brGDGTs (Fig. 7). The low #rings_{tetra} values on our record (<0.3) suggest brGDGTs have a terrestrial source.

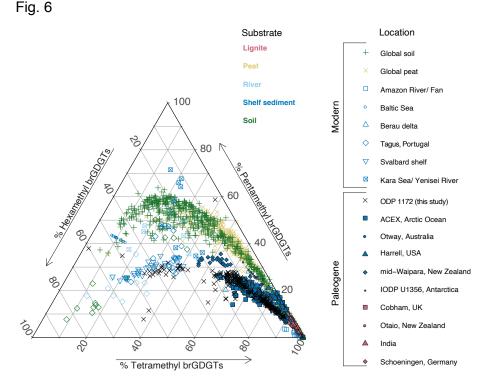


Figure 6. Ternary diagram showing fractional abundance of tetra-, penta- and hexamethylated brGDGTs from modern soils (Dearing Crampton-Flood et al., 2020), peats (Naafs et al., 2017b), rivers (Tagus River, Portugal (Warden et al., 2016) and Yenisei River (De Jonge et al., 2015)) and marine sediments (Kara Sea (De Jonge et al., 2015), Svalbard (Dearing Crampton-Flood et al., 2019), Berau delta (Sinninghe Damsté, 2016), Portugal (Warden et al., 2016), Baltic Sea (Warden et al., 2018), and





Amazon Fan (Zell et al., 2014)), Paleogene lignites (Cobham, Schoeningen, India and
Otaio (Naafs et al., 2018b)) and Paleogene marine sediments (Arctic Ocean, IODP
Arctic Coring Expedition ACEX (Willard et al., 2019), Otway Basin, Australia
(Huurdeman et al., 2020), Gulf of Mexico coastal plain, Harrel core (Sluijs et al., 2014),
New Zealand (Pancost et al., 2013) and Antarctic Margin IODP Site U1356 (Bijl et al.,
2013a)). Data from ODP Site 1172 in black crosses.

Fig.7

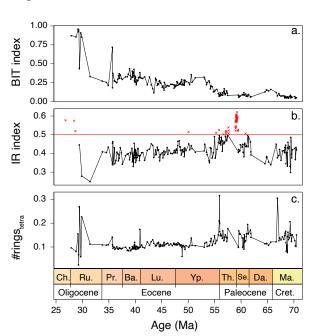
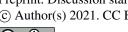


Figure 7. a. BIT index, b. IR (with cut-off value of the Australian soil IR of 0.5 and discarded MAAT samples in red crosses) and c. $\#rings_{tetra}$ from Site 1172.

In the modern soil- and peat brGDGT dataset $\#rings_{penta}$ and $\#rings_{tetra}$ are below 0.7 and follow a coherent 1:1 correlation (Fig. 8a). Values >0.7 suggest brGDGTs cannot come purely from soils (Sinninghe Damsté 2016). All samples from 1172 are below 0.7 for both these indices, which suggests a terrestrial origin is likely, and a strong contribution by marine in situ produced brGDGT is unlikely. We do note that while $\#rings_{tetra}$ is below 0.3, $\#rings_{penta}$ ranges up to 0.6. This diverts from the





694 1:1 line but brings the brGDGT dataset from Site 1172 within the area of other 695 Paleogene marine brGDGT datasets (Fig. 8a). This is consistent with the relative 696 abundances of tetra-, penta- and hexamethylated brGDGTs plotted in the ternary 697 diagram, where all Paleogene data plotted offset to that in modern soils. #ringstetra 698 and #rings_{penta} for the 5- (Fig. 8b) and 6-methyl brGDGTs (Fig. 8c) separately shows 699 that the diversion of the 1172 data from modern soils and peats is primarily caused 700 by a larger degree of cyclisation of the 6-methyl brGDGTs, suggesting an influence by 701 river brGDGT production. 702 The samples within the Paleocene cluster do have relatively high IR. The IR in 703 our record averages ~0.4, but is elevated between 62 Ma and 54 Ma, with peak values 704 in the mid-Paleocene up to 0.6 (Fig. 7). Although based on only two datapoints, 705 modern southeast Australian soils have IR values of maximum 0.5 (De Jonge et al., 706 2014a). Hence, any values exceeding that of the corresponding hinterland soils could 707 indicate a contribution by non-soil sources (be it marine or river in situ production; 708 De Jonge et al., 2014a). Given that #rings indices values argue against a large 709 contribution from marine in-situ production, we suggest that river-produced 710 brGDGTs contribute to the GDGT pool in the Paleocene samples with high IR. 711 Therefore, for MBT'_{5me} calculation, we eliminate all brGDGT samples in our record that have IR values above that of Australian soils. The IR $_{\text{penta}}$ and IR $_{\text{hexa}}$ are well within 712 713 the range of the modern soil and peat data (Fig. 8d) and settings affected by marine or 714 river in situ production (Svalbard, Kara / Yenisei), and plot far away from lignite 715 deposits. 716



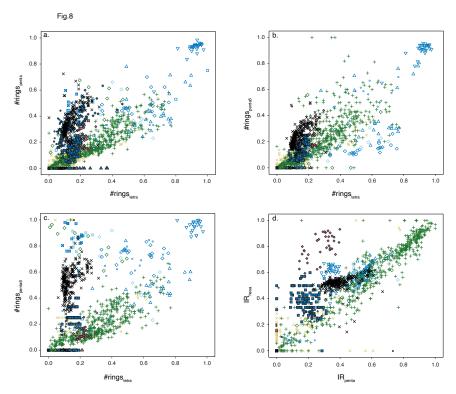


Figure 8. Crossplots of various brGDGT indices. a. #rings_{tetra} vs. #rings_{penta}, #rings_{tetra} vs. #rings_{penta}, #rings_{tetra} vs. #rings_{penta}, IR_{penta} vs. IR_{hexa}. For color and symbol legend see Figure 6.

The consistent offset in brGDGT composition in Paleogene marine sediments

relative to modern soils can potentially be explained by non-soil contributions even though many (most) indices suggest soil-dominated sourcing. Notably, not only Paleogene marine sediments from Site 1172 are offset from present-day soils, but this extends to other sites as well, including Paleogene lignites that are not influenced by marine contributions. We thus argue that there may be an additional evolutionary- or bacterial community factor that is at least in part responsible for the observed offset brGDGT distributions during the Paleogene, and argue that, with some exceptions

where indices do suggest non-soil contributions, Paleogene marine sediments contain a dominant soil-derived brGDGT signal in spite of their offset composition.

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734	4.2 SST and MAAT reconstructions
735	4.2.1 SST
736	By removing all samples with potential overprint from the record we can now
737	assess the trends in TEX86-based SST (Fig. 9a). Reconstructed SSTs differ to up to 4 $^{\circ}$ C
738	between the exponential SST_{exp} and the linear SST_{lin} calibration in the warmest
739	intervals, and progressively less with lower SSTs (Fig. 9a). The BAYSPAR method,
740	which uses a linear relation between SST and TEX86 generates the lowest SSTs for
741	the low TEX_{86} values in the Maastrichtian, Paleocene and middle–late Eocene, and
742	SSTs in between those based on the linear and exponential calibrations for the
743	highest TEX $_{86}$ index values (Fig. 9a). U $^{K\prime}_{37}$ -based SSTs (Bijl et al., 2010, with
744	BAYSPLINE calibration) around the MECO are most consistent with the high SSTs
745	based on the linear TEX_{OBL} calibration, although in this TEX_{86} range all calibrations
746	yield SSTs within error (Fig. 9a).
747	In general, Maastrichtian (70.5–66.7 Ma) SSTs show a gradual cooling trend
748	towards the late Maastrichtian–early Danian hiatus of $\sim\!800$ kyrs. The early Danian
749	(\sim 65 Ma) is roughly 3 °C warmer than the late Maastrichtian (\sim 67 Ma). The mid-
750	Paleocene (62–59 Ma) shows two cooling steps: a \sim 2 °C cooling at 62 Ma, followed by
751	a return to higher SSTs roughly at 60 Ma, and a ${\sim}5$ °C cooling to minimum values of
752	around 18°C around 59.5 Ma, where the record is truncated by a hiatus.
753	A hiatus straddling the early Thanetian (59.0–57.7 Ma) likely obscures the
754	onset of late Paleocene warming out of the mid-Paleocene temperature minimum.
755	Background latest Paleocene SSTs fluctuate considerably, but the PETM warming
756	clearly stands out (Sluijs et al., 2011), with a magnitude (5-7 $^{\circ}\text{C}$ depending on the
757	calibration) comparable to that in other mid- to high latitude sections and similar to
758	the global average (Frieling et al., 2017). Post-PETM SSTs drop back to pre-PETM
759	values completely, followed by renewed warming towards the EECO. The magnitude
760	of warming is 6 to 11 $^{\circ}\text{C}$ depending on the choice of calibration. Smaller early Eocene
761	hyperthermal events, if represented in our record, do not clearly stand out at Site
762	1172.
763	Highest SSTs of the EECO are slightly lower than peak PETM values in all
764	calibrations, consistent with other records (Inglis et al., 2020). However, a hiatus





between 52.7 and 51.4 Ma may conceal peak EECO temperatures (Hollis et al., 2019; Lauretano et al., 2018). A gradual SST decline commences around 49.2 Ma and terminates the EECO, which is broadly coeval with cooling inferred from benthic foraminiferal isotope records (Lauretano et al., 2018) and proxy records from New Zealand (Dallanave et al., 2016; Crouch et al., 2020).



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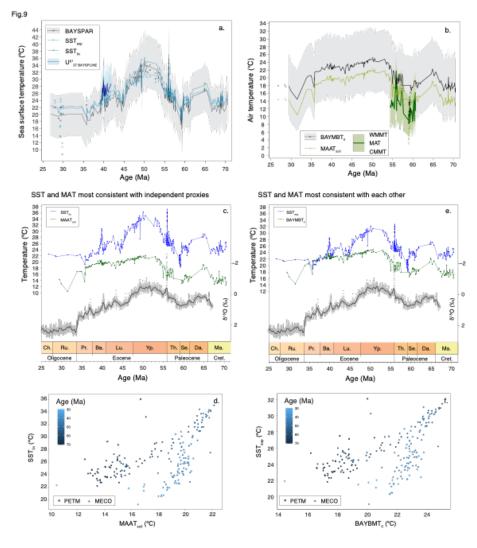


Figure 9. Paleothermometers. a. TEX_{86} based SST reconstructions, using a Bayesian (BAYSPAR; black, with 90% confidence interval in grey envelope; Tierney and

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774 Tingley, 2015) an exponential (SST_{exp}; light blue; Kim et al., 2010) and a linear (SST_{lin}; 775 dark blue; O'Brien et al., 2017) calibration. Also plotted are U^{K'}37 -based SSTs (thick 776 blue line; from Bijl et al., 2010, recalculated using BAYSPLINE of Tierney and Tingley, 777 2018). Discarded samples are indicated by the crosses. b. brGDGT-based MAAT 778 reconstructions using the Bayesian (BayMBT₀; black, with 90% confidence interval in 779 grey envelope; Dearing Crampton-Flood et al., 2020) and soil (MAAT_{soil}; light green; 780 Naafs et al., 2017b) calibrations. Discarded samples are indicated in crosses. Also 781 plotted are pollen-based NLR-approach MAT reconstructions (thick dark green, with 782 light green envelope representing coldest and warmest month mean temperatures; 783 from Contreras et al., 2014). c. SST and MAAT reconstructions using the calibrations 784 that are most consistent with independent proxies from this site (Bijl et al., 2010; 785 Contreras et al., 2014), with the CENOGRID benthic foraminifer oxygen isotope splice 786 of Westerhold et al., 2020 (10pnt loess smooth in grey, 500 pnt loess smooth in 787 black). d. cross-correlation between SST_{lin} and MAAT_{soil}. e. SST and MAAT 788 reconstructions using the calibrations that are, in absolute temperature, most 789 consistent with each other, with the CENOGRID benthic foraminifer oxygen isotope 790 splice of Westerhold et al., 2020 (10pnt loess smooth in grey, 500 pnt loess smooth in 791 black). f. cross-correlation between SST_{exp} and BAYMBT₀. 792 793

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Post-EECO cooling is gradual and of small magnitude (2 °C from peak EECO values) until about 46.4 Ma, after which it accelerates (5 °C) between 46.2 Ma and 44.4 Ma. The age model in this particular part of the sequence is complicated, due to a problematic assignment of chron C21n (Bijl et al., 2010; 2013b). Following the minimum SSTS at 44.4 Ma, SSTs rise again towards a plateau at 42.7 Ma. An SST minimum of ~22 °C is observed just prior to the MECO, at 40.2 Ma, followed by MECO warming of about 5-7 °C reached at 39.9 Ma. Post-MECO cooling seems more gradual than MECO warming, although this might be the result of sedimentation rate changes (Bijl et al., 2010), which are not accounted for in our age model. SSTs are almost identical to those for the MECO at nearby Site 1170 on the South Tasman Rise (Cramwinckel et al., 2020). Post-MECO cooling transitions into gradual late Eocene

cooling, down to a minimum of \sim 19 °C at 35.7 Ma. The following latest Eocene to





806	Oligocene TEX ₈₆ -based SSTs (35–27 Ma) are 3 °C warmer, with surprisingly no
807	cooling associated to the Eocene-Oligocene transition (Houben et al., 2019).
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809	4.2.2 MAAT
810	After excluding samples with IR values above those of local soils, we present
811	MBT' $_{5\text{me}}\text{-}\text{based}$ MAAT reconstructions. These differ substantially (up to 5°C) per
812	calibration chosen (Fig. 9b). The $MAAT_{soil}$ calibration yield consistently cooler MAATs
813	(2–3°C) compared to the BAYMBT $_0$ calibration (Fig. 9b), which may be because the
814	$MAAT_{soil}$ is calibrated against average temperature of the days above freezing, while
815	$BAYMBT_0$ is calibrated against mean annual temperature. Both MAAT calibrations fall
816	between the MAT and the warmest month mean temperature reconstruction of the
817	sporomorph nearest living relative (NLR)-based temperature reconstruction
818	(Contreras et al., 2014), and calibration errors largely overlap.
819	Independent of the calibration chosen, MAAT evolution reveals late
820	Maastrichtian-early Danian warming of 3°C, gradual 4°C cooling towards the mid-
821	Paleocene, gradual 8°C warming towards the EECO, with a conspicuous absence of
822	warming at the PETM. Gradual cooling of 4°C starts at 49.5 Ma and continues into the
823	Late Eocene. MAAT reaches a minimum at 43 Ma, followed by a plateau-phase. There
824	is little warming that can be associated to the MECO. MAAT shows a conspicuous
825	transient 3 $^{\circ}\text{C}$ cooling in the Late Eocene, at the onset of glauconite deposition. The
826	Eocene-Oligocene Transition is characterized by another 5°C MAAT cooling.





Fig. 10

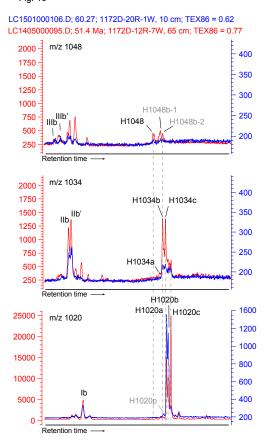


Figure 10. Stack of 2 UHPLC-MS chromatograms (1172D-12R-7W, 65cm in red and 1172D-20R-1W, 10cm in blue) of m/z 1048, 1034 and 1020 traces, between \sim 40 and \sim 60 minutes retention time, showing the pattern of peaks corresponding to brGDGTs and brGMGTs. Peak labels refer to the molecular structures in Fig. 3.

4.3 brGMGTs

We detected brGMGTs throughout the record (see Fig. 10 for typical chromatograms). The exact molecular structure and position of the C-C bridge is still unknown but based on visual comparison with chromatograms of brGMGTs in African lake sediments (Baxter et al., 2019), all 7 known brGMGTs can be identified.





Next to H1020a, b, and c as most abundant brGMGTs, also H1034a, b and c are detected, although in some samples in the Maastrichtian, individual peaks could not be separated. Traces of H1048 can be seen at times, suggesting presence of this compound as well, albeit in low relative abundance. Next to these previously described peaks, we here recognized several other peaks that consistently occur at Site 1172: one compound that elutes just prior to H1020a, which we term H1020p (Fig. 10). \sim 1 minute after H1048 elutes, two more peaks appear which we here term H1048b-1 and H1048b-2 (Fig. 10). Because these have so far unknown affinities or molecular structure, we do not include them here further in our calculations.

Fig. 11

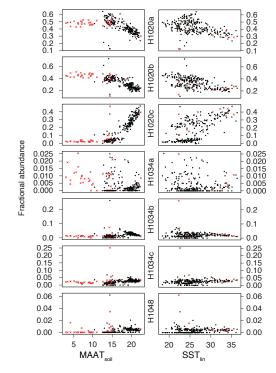


Figure 11. Fractional abundances of brGMGTs plotted against BAYMBT₀ and SST_{exp}.

The fractional abundances of the H1020 isomers show qualitatively similar relations to temperature as in the East African lake dataset of Baxter et al. (2019): H1020b abundance has a negative relationship with MAAT, while H1020c has a





856 positive relationship (Fig. 11). In addition, H1020a seems negatively correlated with 857 MAAT in our data, although this compound does not show any relation to 858 temperature in lakes (Baxter et al., 2019). The relative abundances of the H1034 859 isomers do not show a clear relationship with MAAT (Fig. 11), similar as in the 860 tropical lake dataset, where the scatter increases at lower (H1034b) or higher 861 (H1034a, c) temperatures (Baxter et al., 2019). 862 Downcore trends in brGMGTI are primarily controlled by the relative 863 abundance of H1020c and closely follow those in both SST and MAAT. Upon cross-864 correlation, we note that brGMGTI has a higher correlation with MAAT (R = 0.89) 865 than with SST (R=0.57; Fig. 12). Interestingly, the correlations between brGMGTI and 866 temperature indices only hold for part of the dataset. Samples with high IR values, for 867 which brGDGT-based MAAT could not be reliably interpreted, fall outside the 868 correlation (grey crosses in Fig. 12). This is probably due to the supposed 869 contribution of river-derived brGDGTs that may bias MAAT towards lower 870 temperatures. In addition, we also note that brGMGTI approaches 'saturation' 871 (brGMGTI = 0) at reconstructed MAAT of 15°C. The correlation with temperature 872 (MAAT and SST) is divided into 2 clusters. BrGMGTI values for samples from the 873 younger part of the record, with BIT index $<\sim$ 0.3, seem to correlate better to 874 temperature than those from the older part of tha record, with BIT index values 875 >~0.3 (Fig. 12). In the Oligocene, where many isoGDGT signals were evidently 876 overprinted, the %brGMGTs increases (Fig. 3, 12d), and the brGMGT composition is 877 characterized by a relatively higher abundance of H1020c, H1034b and H1048 878 compared to the rest of the record (Fig. 3; 12). 879 There is no clear relationship between %brGMGTs and MBT'_{5me}-based MAAT 880 (Fig. 12h, i). This slightly differs from the Paleocene-Eocene Arctic Ocean record 881 (Sluijs et al., 2020), where the brGMGTI has no correlation to temperature, while 882 %brGMGTs do. This may indicate differences in sources of brGMGTs between the 883 sites, differences in oceanographic settings, or a non-temperature control on their 884 distribution. $HMBT_{acyclic}$ does seem to show similar trends to the MBT'_{5me} -based 885 MAAT (Fig. 12g), like in the Arctic Ocean (Sluijs et al., 2020). 886



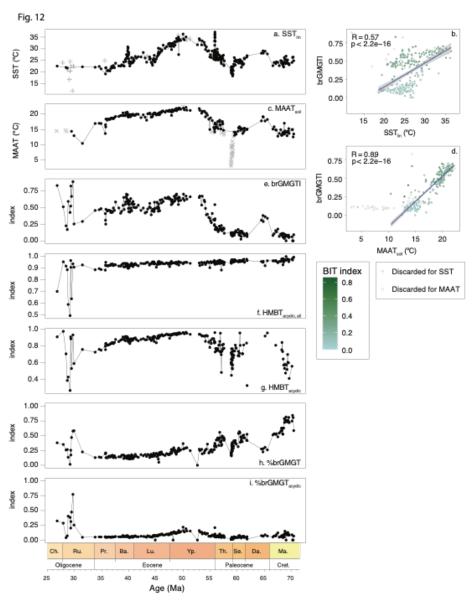


Figure 12. Time series and crossplots of brGMGT-based indices with MAAT and SST reconstructions. (a) SST $_{\rm lin}$ (b) crossplot of SST $_{\rm lin}$ and brGMGTI, (c) MAAT $_{\rm soil}$, (d) crossplot of MAAT $_{\rm soil}$ and brGMGTI, (e) brGMGTI, (f) HMBT $_{\rm acyclic}$, all, (g) HMBT $_{\rm acyclic}$, (h) %brGMGT (Baxter et al., 2019), (i) %brGMGT $_{\rm acyclic}$ (Naafs et al., 2018). For equations see Table 1). Colour variable in the crossplots indicate the BIT index value.

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4.4 Palynology 895 4.4.1 Assemblages 896 Dinocyst assemblages are dominated by *Manumiella* spp. throughout the 897 Maastrichtian, together with Goniodomideae (notably Dinopterygium spp.), and 898 Cerebrocysta cpx. (Fig. 13). From the late Maastrichtian onwards, Senegalinium cpx. 899 increases gradually in relative abundance, interrupted by acmes of Palaeoperidinium 900 pyrophorum in the Danian and Glaphyrocysta cpx. in the lower Selandian. Relative 901 abundances of Senegalinium cpx. reach maximum values during the mid-Paleocene 902 and during the Paleocene-Eocene transition, while the PETM itself is characterised by 903 abundant Apectodinium (~30%) and common Senegalinium cpx. and Goniodomideae 904 (Sluijs et al., 2011). After the PETM, Senegalinium cpx. abundances temporarily 905 increase, and are then replaced by Deflandrea cpx, Spinidinium cpx and Elytrocysta 906 spp. and low abundances of various other genera, e.g., Wetzeliella, Hystrichokolpoma, 907 Goniodomideae (Fig. 13). From 45 Ma to ~37 Ma, *Enneadocysta* spp. alternates 908 dominance with Deflandrea cpx. and Spinidinium/Vozzhennikovia cpx, with 909 contributions of Phthanoperidinium spp. (Röhl et al., 2004a). Protoperidinioid 910 dinocysts appear commonly in the late Eocene, around 35.5 Ma (Houben et al., 2019; 911 Sluijs et al., 2003; Fig. 13). 912 913 4.4.2 Diversity and variability 914 Together with the changing assemblage composition are some strong and 915 coherent changes in all diversity and variability indices (Fig. 14). First, results are 916 highly similar for the full species-level dataset and the grouped assemblages, 917 indicating robustness of both the grouping and diversity analysis. The Maastrichtian-918 Paleocene assemblages are characterized by relatively low diversity, which increases 919 towards the EECO, as variability indicated by the Gibbs index decreases. After this, 920 diversity drops and variability increases during middle-late Eocene cooling ~49-38 921 Ma, with an interruption around 41–39 Ma. Towards the top of the record, both 922 diversity and variability increase. 923





Fig. 13

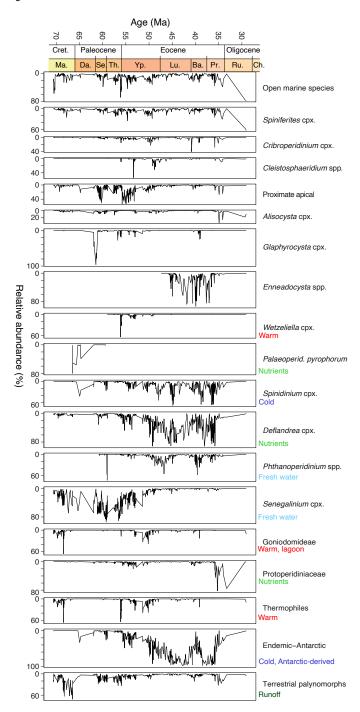






Figure 13. Dinocyst ecogroups and %terrestrial palynomorphs from Site 1172. From left to right, ecogroups are ordered in an in-shore-to-offshore transect. Relative abundance ticks represent 20%.

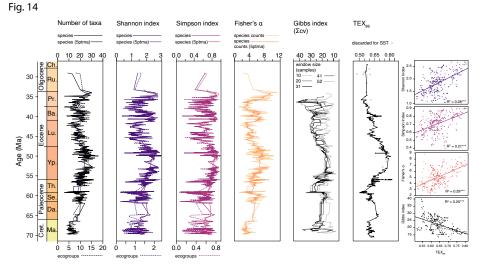


Figure 14. Dinocyst taxonomic diversity and variability through time. From left to right are plotted number of taxa (black), Shannon index (purple), Simpson index (pink), Fisher's alpha (orange) (species-based dataset in solid lines; ecogrouped dataset in dashed lines) and Gibbs index (different window sizes in gray-black). TEX₈₆ plotted for comparison. Crossplots show correlation of these indices with TEX₈₆.

5. Discussion

5.1 Air and sea surface temperature evolution compared

The near-shore depositional setting of our record should have captured a coastal terrestrial environment with similar MAATs similar to the local SSTs. Indeed, the brGDGT-based MAAT record shows strong similarities to SST particularly in multi-million year trends (Fig. 9). Specifically, the early Danian is warmer than the Maastrichtian, and bothe records show a 2-step Paleocene cooling, late Paleocene warming towards peak values in the EECO, and middle–late Eocene cooling. On shorter time scales both records, occasionally even on sample-to-sample level, show synchronous variability (Fig. 9c, d). The independent SST (based on alkenones; Bijl et





946 al., 2010) and air temperature reconstructions (based on pollen assemblages; 947 Contreras et al., 2014) show the best fit with the absolute SST values derived from the 948 linear calibration for TEX₈₆ (BAYSPAR or SST_{lin}; generating the highest SST 949 estimates), and MAATs based on the calibration using Deeming regression (MAATsoil), 950 respectively. These are the two calibrations with the largest absolute temperature 951 offset, particularly in the warm EECO (Fig. 9c). If the local terrestrial climate in the 952 nearby river catchment is largely controlled by ocean temperature, the absolute mean 953 annual SST and MAAT should be broadly similar in the integrated signal of our 954 samples. This could be an argument to choose transfer functions for SST and MAAT 955 whereby absolute temperature estimates overlap most: SST_{exp} and the Bayesian 956 BAYMBT₀. These generate overlapping absolute temperatures for the colder middle-957 late Eocene and Paleocene, but in the warmer Eocene time intervals SSTs remain 958 consistently warmer (by ~8 °C). The lower MAATs cannot be explained by a 959 saturation of the MBT'_{5me} index that is underlying the paleothermometer, as 960 maximum recorded MBT'_{5me} values are around 0.85 in the EECO. Accounting for the 961 calibration errors of SST (± 2.5 °C) and the large calibration error bar of BAYMBT $_0$ in 962 principle could resolve the offset but applying the extremes in calibration error to 963 TEX₈₆ and MBT'_{5me} to make them consistent would make both profoundly 964 inconsistent to the other independent SST and MAAT proxies from the same samples. 965 More importantly, the colder MAAT compared to SST seems to be a consistent feature 966 in many regions where TEX₈₆ and MBT'_{5me} were applied together (see e.g., Hollis et 967 al., 2019 and compare Willard et al., 2019 and Sluijs et al., 2020). The offset between 968 MAAT and SST would have been more variable between sites if it were only the result 969 of calibration errors. TEX₈₆ -based SSTs in the southwest Pacific realm have been on 970 the high end of many multi-proxy-based temperature reconstructions for the Eocene 971 (Hollis et al., 2012), and therefore may be assumed to have an as yet poorly 972 understood warm bias. However, the consistency of TEX₈₆-based SSTs with other SST 973 proxies for specific time intervals and locations (Bijl et al., 2010; Hines et al., 2017) 974 suggests the SST-MAAT offset cannot be easily reconciled by only invoking a warm 975 bias in TEX₈₆. MAAT reconstructions on the other hand have been broadly consistent 976 with nearest living relative based temperature reconstructions on pollen assemblages 977 in many applications in the Eocene (Contreras et al., 2013; Contreras et al., 2014;





978 Pancost et al., 2013; Pross et al., 2012; Willard et al., 2019), but both brGDGT and 979 plant-based temperature estimates are arguably prone to cold biases at the high-980 temperature end (e.g. Naafs et al. 2018, Van Dijk et al., 2020). In addition, it may be 981 that the same evolutionary or bacterial community factors that make Paleogene 982 brGDGT assemblages deviate from that in modern soils, may also cause a deviation in 983 the calibration to MAAT. This may resolve some of the offset between MAAT and SST 984 reconstructions. Although this implies that quantitative MAAT estimates based on 985 MBT'_{5me} in non-analogue settings such as the present one should be taken with care, 986 the strong temperature dependence in Paleogene brGDGTs cannot be ignored. 987 Another surprising result is that the brGDGT-based MAAT record does not 988 capture PETM and MECO warming (Fig. 9c), independent of the calibration chosen. 989 This is remarkable for several reasons: (1) brGDGTs were measured on the same 990 samples as isoGDGTs, which precludes a sampling bias; (2) SST changes of longer 991 duration (Maastrichtian-Danian warming, mid-Paleocene cooling and early Eocene 992 warming towards the EECO) are represented in the MAAT record; (3) The duration of 993 PETM (~150-250 kyrs; Röhl et al., 2007, Zeebe & Lourens, 2019) and MECO (~400 994 kyrs; Bohaty et al, 2009) is too long to explain the absence in MAAT warming with a 995 lag in soil-derived OM delivery to the ocean (up to several kyr, see, e.g., Feng et al., 996 2013; Schefuß et al., 2016; Huurdeman et al., 2020); (4) seems incompatible with the 997 fact that other low-amplitude, shorter-term SST changes are reflected in the MAAT 998 record (Fig. 9c, d), which suggests that soil-derived OM did capture short-term 999 climate variability on the time resolution of the samples; (5) Other PETM records in 1000 the region do show a temperature response in the PETM in various proxies including 1001 brGDGTs (Hollis et al., 2012; Pancost et al., 2013, Huurdeman et al. 2020). A lack of 1002 MAAT rise during the PETM and the MECO could be explained by a switch from 1003 brGDGT sourcing from soils to (peaty) lakes, which are notoriously cold-biased 1004 (Tierney et al., 2010). Paleocene–Eocene peats are abundant in southeast Australia 1005 (Holdgate et al., 2009), and it is possible that a contribution from peat lakes at times 1006 of global warming, contributed to a dampening of the proxy-response. This may also 1007 explain the lack of response at the EECO and explain why MBT'_{5me} does not reach 1008 saturation in that interval. The final option, which, although unlikely, cannot be





excluded, is that a dominant fraction of the brGDGT was produced in situ and subdues the temperature response during these warming phases.

The subdued middle-late Eocene cooling in the air temperature record compared to the strong decrease in SST is particularly clear when cross-plotting SST *versus* MAAT (Fig. 9c, d): the relationship between the two proxies is different in the Maastrichtian–early Eocene compared to the middle–late Eocene. This may be related to the start of a progressive northward tectonic drift of the Tasmanian hinterland, which occurred around the same time (Fig. 1). This puts the hinterland of the soilderived brGDGTs into warmer climate zones throughout the middle–late Eocene, while the ETP remained under influence of the Antarctic-derived Tasman Current (TC) through that time (Huber et al., 2004). The TC cools and likely strengthens in the middle and late Eocene. The terrestrial climate cooled as well, but this signal will be subdued if the soil material is sourced from a progressively lower-latitude environment as Australia drifted northward. Yet, one would expect that the close coupling between land- and seawater temperature in near-shore environments would not capture such tectonic effects.

The correlation between both temperature proxies changes once more during the late Eocene–Oligocene, when they show a sharp cooling of 2–3 °C at the onset of greensand deposition, at ~35.5 Ma. Whereas this is merely a continuation of progressive late Eocene cooling in the SST record, the decrease in MAAT is strongly accelerated compared to middle–late Eocene trends. Another 3–4 °C MAAT drop occurs sometime between the late Eocene and the early Oligocene (likely associated with the Eocene–Oligocene transition), while SSTs returns to warmer, middle Eocene values in this interval. The continued sea surface warmth across the EOT has been related to persistent influence of the proto-Leeuwin Current (Houben et al., 2019), which apparently retained a constant temperature across the EOT. Since MAAT decreased while SSTs remained high, the influence of regional oceanographic changes did not impact climate changes in the source region of brGDGTs during this time interval. This is surprising given the proximity of the sediment record to the coastline.

Minimum mid-Paleocene SSTs are lower than those for the early Oligocene. However, the site migrated northward by \sim 7 ° of latitude between the mid-Paleocene and the early Oligocene (Fig. 1) and the oceanographic regime changed with





throughflow of the proto-Leeuwin Current through the TG in the Late Eocene (Houben et al., 2019). More remarkably, the mid-Paleocene SSTs approach those of the warmest interglacial intervals of Oligocene Wilkes Land Margin, east Antarctica (Hartman et al., 2018), at a similar paleolatitude as the Paleocene ETP. This suggests that mid-Paleocene Antarctic-proximal temperatures were similar to those at times of major Antarctic glaciation during EOT. Previous work has indeed presented widespread evidence for low sea level during this time interval (Frieling et al., 2014; 2018; Guasti et al., 2006; Hollis et al., 2014), which combined with low SSTs suggests the presence of some continental ice on the Antarctic continent during this mid-Paleocene interval.

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5.2 BrGMGTs

The continuous presence of brGMGTs in our record appears unrelated to depositional conditions or varying relative contributions of terrestrial material, suggesting that at least part of the brGMGTs have a marine origin. This confirms previous observations from the modern sediments and water column (Liu et al. 2012, Xie et al. 2014) and Paleogene Arctic Ocean sediments (Sluijs et al., 2020). Their sparse presence in modern soils (Peterse et al., pers comm based on metadata from De Jonge et al., 2019; Kirkels et al., 2020) is also in line with this, although abundant occurrence in peats and lakes (Naafs et al., 2018, Baxter et al. 2019, Tang et al., 2021) shows clear potential for terrestrial input. Despite the uncertainties in sourcing of brGMGTs, we find a strong resemblance with the signals from tropical lakes. The brGMGTI, which was derived to quantify the temperature relation of brGMGTs in surface sediments of East African lakes (Baxter et al., 2019), seems to correlate to temperature in our record as well (Fig. 12a-d), although the better correlation of brGMGTI with MAAT than with SST (Fig. 12a-d) seems to be at odds with the presumed marine source of brGMGTs in our record. Despite all potential complications, our study provides additional evidence that a temperature signal may be governing the distribution of the different brGMGT isomers, as proposed by (Baxter et al., 2019), but there are differences as well. For instance, H1020c is altogether absent in the cold mid-Paleocene part of our record. There are numerous



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above a certain temperature, or the microbes that biosynthesize H1020c do not live at low temperatures, or the site receives brGMGTs from a different catchment in colder climates. Indeed, H1020c was almost absent in the cold (<12°C), high-altitude tropical lake samples (Baxter et al. 2019). However, those cold lakes did have high relative abundance of H1048 (Baxter et al., 2019), which our record lacks in the cold mid-Paleocene, illustrating the differences between modern lakes and our marine depositional setting. The HMBT record does not reflect a temperature signal when using all brGMGT isomers in the calculation (Fig. 12f), as H1020 isomers are by far the most abundant brGMGTs at Site 1172, and any change in the abundance of H1020c is compensated by both H1020b and H1020a in our record. In contrast, only using the H1020c and H1034b isomers, which following the chromatographic peak identification of Sluijs et al. (2020) match the compounds used to derive the HMBT index based on brGMGTs in peats (Naafs et al., 2018), does show a correlation to temperature in our record (Fig. 12g). %brGMGT as calculated in Naafs et al., (2018) or as in Baxter et al., (2019) does not show a clear relation with temperature (Fig. 12h, i), in contrast to observations in modern peats (Naafs et al., 2018a) and lake sediments (Baxter et al., 2019). We do note the extremely high %brGMGT (~80%) in the Maastrichtian and Oligocene, much higher than seen anywhere so far. We also do not see a clear inverse relationship between %brGMGT and BIT index, as in Sluijs et al. (2020). This may be because of the complexity in the relative abundance of brGDGTs in the record, which does not necessarily reflect the variation in terrestrial versus marine sourcing. The higher relative abundance and change in composition of brGMGT

composition in the Oligocene that coincides with abundant signs of overprints in all

isoGDGTs. The differences in brGMGT signals between our record, the Eocene Arctic

Ocean record and modern sediments demonstrate that more research is needed on

their sources and environmental dependencies to further assess their use and value

br- and isoGDGT indices may indicate a source change of brGMGTs in this interval,

e.g., related to the same changes in contribution that cause the overprints in

ways in which this can be explained, e.g., the biosynthesis of H1020c occurs only

in paleoreconstructions.

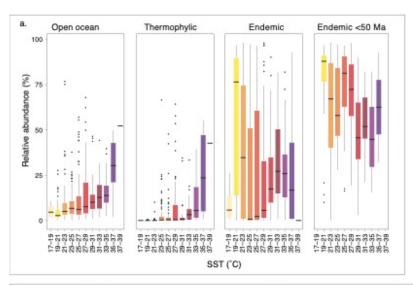


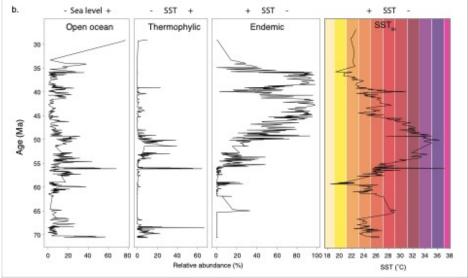


1105 1106 1107 5.3 Integrated paleoenvironmental and -climatological reconstruction 1108 5.3.1 Sea level and ecosystem response to SST changes 1109 The abundance of temperature-responsive dinocyst eco-groups qualitatively 1110 confirm our SST trends. The thermophile dinocyst eco-group shows higher relative 1111 abundance at higher SSTs (Fig. 15). This eco-group has been empirically associated to 1112 SST based on its strong affinity to high SST in the global compilation of late 1113 Paleocene-early Eocene records (Frieling and Sluijs, 2018), and we here confirm this 1114 relationship for the longer early Paleogene. The relationship between isoGDGT-based 1115 SSTs and relative abundance of the supposedly cold-affiliated endemic dinocysts (Bijl 1116 et al., 2011) is not as clear. This might be because the majority of dinocyst species 1117 within the Endemic-Antarctic dinocyst ecogroup are restricted to the Eocene (Bijl et 1118 al., 2011). 1119 Indeed, from 50 Ma onwards, SST does have a correlation with the %endemic 1120 Antarctic dinocyst abundance in the record (Fig. 15; Bijl et al., 2011), which may 1121 indicate a more distinct biogeographical separation through the development of 1122 stronger meridional gradients or evolutive adaptation of the endemic dinocyst 1123 community to more polar environments following the extreme warmth of the EECO. 1124 We particularly note the strong correlation between TEX₈₆-based SST and relative 1125 abundance of more open ocean-affiliated dinocysts (Fig. 13), which suggests that SST 1126 correlates with regional sea level. SST-induced sea level changes hint at steric effects 1127 as driver. Indeed, because of the flatness of continental shelf areas during long-term 1128 greenhouse climates (Somme et al., 2009) small changes in regional sea level will 1129 cause large changes in distance to shore and associated characteristics, including e.g. 1130 salinity, nutrients and suspended sediment loads, which subsequently shapes the 1131 dinocyst assemblages. 1132



Fig.15 GDGT- and palynology-based proxies for SST





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Figure 15. isoGDGT- and palynology-based proxies for SST. a. relative abundance of open ocean, thermophylic and endemic-Antarctic dinocysts (total dataset and samples <50Ma only) plotted against linearly interpolated (resampled) TEX $_{86}$ -based SST, in 2 degree bins. b. Time series of the same dinocyst ecogroups and SST.





1140 and assemblage variability indices. Throughout the long time interval covered in our 1141 record, dinocyst richness and diversity show a remarkably similar pattern to TEX86-1142 based SST. Species richness, as well as diversity expressed in the Shannon and 1143 Simpson indices and Fisher's alpha reach a maximum during the prolonged warmth 1144 of the EECO and drop during middle-late Eocene cooling. These relationships are 1145 demonstrated by modest correlation coefficient between diversity and TEX₈₆ (Fig. 1146 13). This pattern holds for the long-term trends, as well as for the short-term PETM, 1147 but not for the MECO. Dinocyst diversity is known to vary in an inshore-to-offshore 1148 transect in the modern and Eocene (Brinkhuis, 1994; Pross and Brinkhuis, 2005). As 1149 our assemblages indeed consist of many mid-shelf species, the strong correlation 1150 between diversity and SST might thus be indirectly related through habitat size, with 1151 expansion of the flat shelf area and thereby increase in shelf niches during the EECO 1152 (Somme et al., 2009). Variability as indicated by the Gibbs index records the opposite 1153 pattern to diversity for the long-term trends into and out of the EECO (Fig 14). That 1154 is, the lower-diversity assemblages in general have a higher variability, or sample-to-1155 sample fluctuations within the relative abundances. This indicates the higher 1156 diversity dinocyst assemblages might be more ecologically resilient. 1157 5.3.2 Marine environmental response to runoff changes 1158 Senegalinium cpx. abundance broadly correlates with the IR (Fig. 16), which 1159 signals input of river-produced brGDGTs. Senegalinium cpx. is generally thought to 1160 have tolerated low salinity environments (Barke et al., 2011; Sluijs et al., 2005; Sluijs 1161 and Brinkhuis, 2009). These two proxies together confirm a large input of fresh water 1162 at this site during the mid-to-late Paleocene in line with high relative abundance of 1163 terrestrial palynomorphs, low abundances of open ocean dinocysts and high IR values 1164 (Fig. 16). Interestingly, Phthanoperidinium spp., which is also generally associated 1165 with low-salinity to near fresh-water conditions (Barke et al., 2011; Frieling and 1166 Sluijs, 2018; Sluijs and Brinkhuis, 2009) does not correlate to IR (Fig. 16). Because we 1167 find different species of *Phthanoperidinium* spp. than those previously associated to fresh-water conditions (e.g., Barke et al., 2011), it could be that the fresh-water 1168 1169 tolerance of *Phthanoperidinium* spp. was not shared among all species. It could also 1170 be that *Phthanoperidinium* spp. is slightly less euryhaline than *Senegalinium*.

The SST control on dinocyst assemblages is further demonstrated in diversity



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Tasmania was located at latitudes between 55° and 60° S, in the middle of the region of strong westerly winds, within the range of low atmospheric pressure and received a large amount of precipitation during the Paleocene (Huber and Caballero, 2011). River input from Tasmania and perhaps also Australia could have reached the site. Interestingly, while Tasmania migrated northwards only a few degrees latitude between 60 and 40 Ma (Fig. 1), the freshwater input decreased, based on both Senegalinium cpx., terrestrial palynomorph abundance (decimated abundance from 50 Ma onwards) and the IR (decrease to normal values around 54 Ma; Fig. 16). This suggests either a rerouting of river input or a drying of the hinterland. Support for the latter comes from clay mineralogical data, showing an increase in kaolinite starting at 50 Ma (Fig. 2; Robert, 2004). Kaolinite forms abundantly at the base of acidic peats (Staub and Cohen, 1978; Korasidis et al., 2019) and in old, leached soils, which were ubiquitous in the Eocene Australian hinterland (Holdgate et al., 2009). While the hinterland could well retain the kaolinite-rich clays during the Maastrichtian and Paleocene, because the site was under a year-round high precipitation regime, it was less efficient in doing so when the hinterland experienced drier, more variable climatic conditions as Australia migrated northward. The increase in kaolinite delivery to Site 1172 is hence interpreted as a signal of enhanced soil (or peat) erosion from the catchment areas in Tasmania and SW, as a result of a more variable climate regime.

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5.4 Environmental and climatological changes in the catchment

The long-term trends in the BIT index are at odds with all the river runoff indicators in our data. BIT remains low during the presumed interval with increased river water discharge, as indicated by the high IR and abundance of *Senegalinium* and increases when this river-input signal ceases. This is unexpected, because the BIT index should reflect high input of soil-derived brGDGTs into the marine sediments, associated with increased discharge (Hopmans et al., 2004). There are two ways to explain this signal. The BIT index could be responding to marine crenarchaeol production, rather than to the terrestrial brGDGT flux. Indeed, marine productivity could have been spurred by runoff and associated nutrient delivery to the coastal zone during the Paleocene, and decreased in the Eocene, affecting BIT index values.

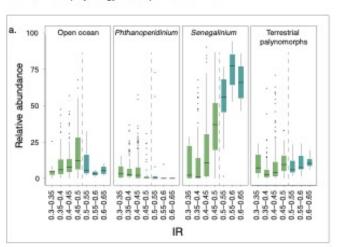


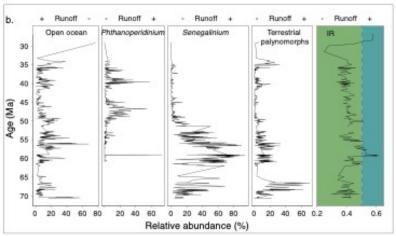


1203 Another explanation is that the BIT index has been influenced by crenarchaeol 1204 production in the river (Zell et al., 2013), although the river-produced crenarchaeol 1205 concentrations are normally negligible compared to that produced in the marine 1206 realm. Decreasing BIT index values with increasing river-and soil input has been 1207 related to catchment dynamics in the late Quaternary Zambezi river (Lattaud et al., 1208 2017), involving vegetation dynamics controlling soil-OM input. Studies on modern 1209 soil-river-ocean pathways in the Amazon River system show that whereas river-1210 suspended brGDGTs in its upper tributaries reflect catchment soils (Kirkels et al., 1211 2020), brGDGTs in the lower Amazon receive increasing contributions of in situ 1212 produced brGDGTs (Zell et al., 2013), and marine surface sediments of the Amazon 1213 fan contain a mix of soil, riverine, and marine brGDGTs (Zell et al., 2014). In a high-1214 precipitation, soil-rich environment like the Amazon basin, this can only occur if the 1215 river-produced brGDGT production progressively exceeds the soil-derived brGDGTs 1216 input in river water along the trajectory of the river, or when the soil-derived 1217 brGDGTs are preferentially remineralized during river transport. We here propose 1218 the following scenario to explain the BIT index trends: In the Paleocene-early Eocene, 1219 excessive, year-round precipitation-fed river runoff caused strong fresh-water 1220 delivery into the sw Pacific. Soil-derived brGDGTs were partly remineralized in the 1221 river catchment, and the strongly diluted soil-derived OM was dominated by river-1222 produced brGDGTs and crenarchaeol, both in river production and on the continental 1223 shelf, which suppressed the BIT index. This explains the unexpectedly cold MAATs 1224 derived from the mid-Paleocene samples with high IR. The high riverine input did 1225 promote pelagic isoGDGT production: crenarchaeol which decreases the BIT index 1226 and isoGDGTs in general. In the early Eocene, precipitation in the hinterland 1227 decreased as the hinterland gradually drifted out of the zone of intense precipitation. 1228 This reduced river discharge, but at the same time the more dynamic climate regime 1229 caused more seasonal precipitation which increased destabilization of Australian and 1230 Tasmanian soils, leading to a higher abundance of soil-derived brGDGTs and kaolinite 1231 from destabilized soils in the river discharge, and relatively little river-produced 1232 brGDGTs (because enhanced soil-OM content increased turbidity) and river-produced 1233 crenarchaeol, which increased BIT index at the ETP.



Fig. 16 GDGT- and palynology-based proxies for runoff





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Figure 16. BrGDGT- and palynology-based proxies for river runoff. a. relative abundance of Open Ocean, *Phthanoperidinium* spp., *Senegalinium* cpx. and terrestrial palynomorphs in 0.05 index unit bins of the resampled IR. Dashed line separates elevated IR bins from non-elevated IR bins. b. Time series of the same palynology ecogroups and the IR.

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1244 6. Conclusions 1245 We have critically reviewed the GDGT- and dinoflagellate cyst data in samples from 1246 the Maastrichtian-lower Oligocene sediments at ODP Site 1172. IsoGDGTs represent 1247 a pelagic signal throughout the Maastrichtian-Eocene and are influenced by 1248 sedimentary-produced isoGDGTs in the Oligocene. BrGDGTs at our site are likely 1249 primarily soil- or peat-derived, albeit evolutionary changes in brGDGT prodcution 1250 may have altered the Paleogene soil brGDGT composition. Exceptions are the mid-1251 Paleocene, where river-produced brGDGTs influence the record, and the Oligocene, 1252 where marine in situ produced brGDGTs dominate. TEX₈₆ and MBT'_{5me} records reveal 1253 the SST and MAAT evolution of the region, respectively, consistent with independent 1254 existing paleotemperature reconstructions from the same samples. A temperature 1255 offset between the SST and MAAT proxies remains poorly reconciled with the coastal 1256 proximity of the site but is likely a combined effect of evolutionary differences in 1257 MBT'_{5me}-MAAT relationships and a disparate integration of climate signals by both 1258 proxies. The subdued air temperature cooling in the middle Eocene compared to the 1259 SST cooling could in part reflect progressive northward tectonic drift of the 1260 hinterland, while SSTs remained continuously influenced by the Antarctic-derived 1261 Tasman Current. Strong MAAT cooling occurred step-wise around the Eocene-1262 Oligocene transition. The absence of SST cooling around the Eocene-Oligocene 1263 transition suggests some disconnection between oceanographic reorganisations and 1264 regional MAAT changes. The absence of a MAAT response at the PETM and MECO 1265 remains unresolved but might be related to shifting sources of brGDGTs during these 1266 warm phases. 1267 The relatively high IR, and low #rings_{tetra} confirm dinocyst assemblages characteristic 1268 of an inner mid-shelf depositional setting. We reconstruct strong river-runoff in the 1269 Paleocene–early Eocene at this site, and normal open-marine conditions thereafter. 1270 The latter reflects a drying and increased seasonality in precipitation in the 1271 catchment as the continent tectonically migrates northwards, out of the region of 1272 strong precipitation during the middle and late Eocene. The correlation between SST 1273 and changes dinoflagellate cyst assemblages and biodiversity metrics suggest 1274 temperature-controlled sea level changes influenced the site, probably through steric 1275 effects. We find corroborating evidence for a temperature signal in brGMGT





1276 assemblages, further demonstrating the potential to develop novel proxies with more 1277 extensive studies on modern affinities. 1278 1279 7.Supplements 1280 Table S1: Age tie points 1281 Table S2: grouping of dinocysts in ecogroups 1282 1283 8. Data availability 1284 Raw GDGT/GMGT and palynological data presented in this paper, as well as R 1285 markdown code for data analysis and visualization can be found on Github 1286 (https://github.com/bijlpeter83/RGDGT.git). Data was deposited at zenodo under 1287 DOI:10.5281/zenodo.4471204. 1288 1289 9. Author contributions 1290 AS (PETM) and PKB (part) prepared samples for GDGT analyses. PKB (part), AS 1291 (PETM) and CB (part) integrated UHPLC-MS results. AS (PETM) and PKB (part) 1292 analysed palynological samples. All authors contributed to the interpretation of the 1293 OG results, and PKB, AS, JF and MC interpreted dinocyst results. PKB wrote the R 1294 script for data analyses and visualization, drafted the figures and wrote the paper 1295 with input from all authors. 1296 1297 10. Acknowledgements 1298 This research used samples from the Ocean Drilling Program, which was funded 1299 through U.S. National Science foundation under the management of joined 1300 oceanographic institutions, inc. We thank Klaas Nierop, Desmond Eefting and Natasja 1301 Welters for technical/analytical support. PKB acknowledges funding through NWO 1302 Vernieuwingsimpuls Veni grant no. 863.13.002. This work was carried out under the 1303 program of the Netherlands Earth System Science Centre (NESSC), financially 1304 supported by the Dutch Ministry of Education, Culture and Science. MC and AS thank 1305 the Ammodo Foundation for funding unfettered research of laureate AS. PB and AS 1306 thank the European Research Council for Starting Grant 802835 OceaNice and 1307 Consolidator Grant 771497 SPANC, respectively. 1308



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