

Author: Below, we have copied the review by the referee, and have added our responses in blue and between square brackets.

R1 - Severine Fauquette (Referee)

5 Cramwinckel et al. present a study of the surface-circulation change in the Southern Ocean during the Middle Eocene Climatic Optimum based on dinoflagellate cysts and biomarker paleothermometry. The manuscript submitted by Cramwinckel et al. is of good quality. This manuscript is within the scope of 'Climate of the Past' and is well written and structured. This will be a very useful paper on the MECO period in the Southern Ocean that is not well known. This study
10 will certainly help climate modelers who can introduce consistent boundary conditions into the models for this part of the globe. I recommend publication of their paper in Climate of the Past with however some revisions.

[AR: We thank the Referee, Severine Fauquette, for her positive evaluation of our manuscript and the constructive suggestions. We hope to adequately address these below.]

15 Main comments:

- Authors should give, in supplementary data, a detailed description of the pollen morphology (apertures, ornamentation of the exine surface...) and some photos of the main palynomorphs (dinocysts and pollen grains). This
20 period in this region is not well known and it could help for further studies.

[AR: Referee 3 also suggested adding plates of the most important palynomorphs. We propose to add a plate containing light microscope photos of the main marine and terrestrial palynomorphs from the studied sites to the revised
25 manuscript. We feel however, that a detailed description of pollen morphology is beyond the scope of this paper, which focuses on paleoceanography and paleoclimate rather than taxonomy, systematics and morphology of palynomorphs. Regarding the latter topic, future pollen-based studies for this region are being worked on, which will contain the requested morphological and taxonomic data.]

- The fossil pollen and spores should be identified, by comparing them to modern pollen grains, following current
30 taxonomy of recent taxa, instead of using morphotaxa names. By applying such approach, pollen and spores may be assigned to family, genus, and sometimes, but rarely, even to species levels. Once they are botanically identified, their paleoecological requirements may be defined based on the modern taxa. This botanical approach allows reliable paleoenvironmental reconstructions, as described and done by Suan et al. (Geology, 2017) for the Early Eocene of the Arctic Siberia.

[AR: We agree regarding the utility of correlating fossil pollen to modern botanical taxa with known environmental preferences, to facilitate paleoenvironmental reconstruction. In the current version of the manuscript, we therefore
35 provide the names of the pollen taxa followed by the known botanical affinity in brackets. As these are Eocene taxa, indeed, this is often at the level of family or genus instead of a modern species-level designation.]

40 - Biostratigraphy: A table with the regional occurrences of the dinocysts could be interesting.

[AR: Bijl et al. 2013 ESR and Bijl et al. 2011 Paleoceanography already document the regional biogeographic occurrence of dinocysts. We cite these papers in our manuscript. We think that publication of this same dataset again is not
45 necessary, and do not include the data in this work. We will more clearly state in the revised manuscript where these tables can be found.]

- A simplified diagram with the stratigraphic log and the percentages of the main terrestrial palynological data of Latrobe-1 borehole is lacking.

5 [AR: In the revised manuscript, we will add a supplementary figure including a stratigraphic log and palynological data from the Latrobe-1 borehole.]

Minor (technical) comments:

- p5, L1: add a S to metre; L10: call figure 2a; L11: remove one "was not".
- p6, L8: How many samples have been studied for this site?; L25: add "concentration" for the dinocyst content.
- 10 - p10, L32: add a reference for the ages given by *Lophocysta* spp .
- p14, L19: remove the "cf" in front of the reference Bijl et al..
- Figure 5, L17: add a "c" in the word dinocyst.
- Figure 2, L21: in (a), it is not the bathymetry that is illustrated as there is no mention of the depth of the ocean.

15 [AR: We will adapt all of these technical comments. Instead of adding "concentration" to p6, L25 we propose to adapt wording to "content in specimens per gram".]

Author: Below, we have copied the review by the referee, and have added our responses in blue and between square brackets.

R2 - Chris Hollis (Referee)

5

General comments

10 This is an interesting and important study, comparing and contrasting dinocyst assemblage changes between ODP sites 1170 and 1172, one within the Australo-Antarctic Gulf and one in the SW Tasman Sea, during a time of major climate change in the middle Eocene. The study uses evidence from the assemblages to unravel the interplay of changes in ocean circulation due to tectonics and climate changes. Additional sites and data are used to build the case for a significant regional response to the middle Eocene climatic optimum (MECO) – in terms of changes in plankton communities, terrestrial vegetation and sea level. The interpretations are reasonable in most cases but there are a few areas where the argument is weakened by over-interpretation of what the authors admit are ambiguous data.

15

[AR: We thank the referee, Chris Hollis, for his positive evaluation of our manuscript, and constructive criticism and comments. We hope we adequately respond to these below.]

20

The key areas are: the definition of the MECO at Site 1170 based on the TEX86 record, which is clearly open to interpretation;

[AR: While the definition of the MECO at Site 1170 is indeed open to interpretation, we prefer the correlation presented in the current manuscript. We are however open to additionally presenting an alternative interpretation in the revised manuscript. We elaborate on this in response to the comment below regarding p11, line 8.]

25

the lumping together of cosmopolitan and low/mid latitude taxa, when the latter group is the one that is best able to signal the influence of the EAC and PLC;

30

[AR: We agree this will be a good addition and will separate these groups in a revised version of Figure 3. This further distinction will however not change our main results or conclusions.]

the lack of convincing evidence for the presence of the MECO in the Latrobe-1 borehole;

[AR: As noted below in the AR to the comment on p12, line 17, presence of the dinocyst species *Dracodinium rhomboideum* in two samples from the Latrobe-1 borehole tightly constrains this interval to the MECO. However, also in light of comments by Referee #3 on this topic, in the revised manuscript, we will refrain from separating the four studied Latrobe-1 samples into pre-/post-MECO and MECO samples, and will present these data together without describing trends through time.]

40

and the very tenuous correlation of middle Eocene transgression to a purported MECO-related glacioeustatic event.

[AR: In the current version of the manuscript, we tried to convey that this correlation is tentative. We propose to elaborate on this in the revised version of the manuscript, as outlined in the AR to the comment on p16, line 28.]

45

I have made numerous comments on these and other issues at the places they occur in the text.

However, there is a hidden gem in this dataset that I'm disappointed the authors appear to have overlooked. In our warming world, we are increasingly concerned about the ways ecosystems will be adversely affected by warmer oceans

and changes in ocean circulation. For dinoflagellates there is the further concern of how toxic blooms may impact coastal fisheries. The authors provide a dataset that clearly shows the MECO in this region is linked to dramatic increases in the abundance of single species, analogous to present day blooms. And intriguingly, a species of one genus dominates at Site 1170 whereas another species of the same genus dominates at 1172. Even more intriguing, both species have short-lived blooms leading up to the MECO at 1172. Much of the paper simply combines the data for these two species with their respective biogeographic groups (cosmopolitan and endemic) but these two taxa clearly dominate these groups (as shown by DCA and NMDS) and it is certainly worth considering that the rise and fall of these two species is more directly related to local watermass conditions than to current transport. I'd like to know if there is any indication of EAC or PLC influence with *E. multicornuta* removed. And I'd like to see more discussion on the watermass conditions that might lead to monospecific blooms of these two species.

[AR: We thank the referee for his interest in, and suggestions on, this specific part of our results. Although it would be very useful to be able to reconstruct harmful dinoflagellate blooms in the past, we unfortunately do not possess enough information to be able to make such assertions here. While we record acmes of fossils in the sediment, we cannot know what kind of paleo-concentrations of plankton in seawater on what timescales (short seasonal blooms? dominance of species throughout the year?) are actually represented by the data. Furthermore, it is not known if dinocyst species within the genus *Enneadocysta* have a blooming-type ecology, as they are not represented by extant dinoflagellate species with a known ecology. From the fossil record, they typically seem to be mid-shelfal species rather than near-coastal. We are therefore hesitant to claim more than a possibility of paleo-blooms, which we suggest in the present manuscript paragraph 5.3, e.g. p15 line 18–20: "The relatively low diversity of the dinocyst assemblages in combination with the high dominance of a single taxon (*Enneadocysta dictyostila* in the MECO interval) suggests a generally eutrophic setting that could have been characterised by seasonal plankton blooms." Especially at Site 1172, the dinocyst assemblage as a whole is characterized by alternating dominance of different taxa (*Enneadocysta*, *Deflandrea*, *Spinidinium/Vozzhennikovia* and *Phthanoperidinium*). We interpret this succession of dominance of different species as changing conditions rather than as a succession of blooms. Therefore, while we certainly agree with the referee on the relevance and appeal of this topic, we are hesitant to include more speculation on the possibility of (harmful) plankton blooms.]

Specific comments/Corrections by page, line:

1, 20: I see the term "Tasman Gateway" or "Tasman Seaway" has been used in the literature but it's incorrect. The proper term is "Tasmanian Gateway", being the gateway between Tasmania and Antarctica (see any Leg 189 publication).
[AR: we will correct to "Tasmanian Gateway" throughout the paper]

1, 22: ", including the organic walled cysts of dinoflagellates (dinocysts). I'd like to see a distinction made between dinoflagellates (plankton) and dinoflagellate cysts or dinocysts (fossil remains of the plankton)
[AR: we will clarify this distinction where appropriate in the manuscript]

1, 23: prefer "geographic" to "spatiotemporal" (here and elsewhere)
[AR: we respectfully feel this is a matter of preference and prefer to retain "spatiotemporal", also because the "temporal" aspect is less clearly represented in the word "geographic"]

1, 24: "geographic" here is superfluous. And is it primarily controlled by tectonism? What about the rotation of the Earth? I wonder if this simplistic separation of tectonic and climatic controls is warranted or needed in an abstract? Sentence is awkward, so how about rephrasing: "The extent to which the climatic and tectonic controls on the distribution and composition of surface currents have influence the composition of fossil assemblages ...".
1, 26: This sentence is also a little awkward. "Indeed, the extent to which climate change affects oceanographic processes is still poorly understood"?

- 1, 29: Also, an awkward sentence. "trend, the Middle Eocene Climatic Optimum (MECO, 40 Ma). This 500 kyr-long episode of global warming is unrelated to ..."
- 1, 31: "ocean's"; replace "only" with "alone"
[AR: we will change wording in the abstract according to above suggestions]
- 5
- 2, 1: "our new results...", no hyphen between surface and ocean
[AR: we will change the text accordingly]
- 10
- 2, 2: replace "southward" with "south"
[AR: we will change the text accordingly]
- 2, 3: Explain how "warm temperate with paratropical elements" MECO assemblage differs from the general middle Eocene pollen assemblage?
[AR: We elaborate on this in the relevant discussion section on the terrestrial palynology of the Latrobe-1 core (5.4). Here we note that this warm flora overlaps with the MECO interval, based on the dinocyst species that are present in the samples, but, p 16 line 15–17: "Future regional pollen studies focussing on the Nirranda group might therefore elucidate whether the relatively warm-loving flora described here was restricted to the MECO interval, or to a broader interval of middle-late Eocene "background" conditions."]
- 15
- 20
- 2, 8: change "into" to "to"
[AR: we will change the text accordingly]
- 2, 13: does "intermediate-deep" mean somewhere between upper and lower deep water or is it shorthand for "intermediate and deep", in which case this formulation is less ambiguous.
[AR: we will change the text accordingly]
- 25
- 2, 15: None of these sites are close enough to the Antarctic margin to be sources of deep water and are all north of the 60S demarcation for the SO, using pmag reference frame (although noting the uncertainty).
[AR: In these lines, we did not have the intention of suggesting that these sites precisely represent the locations of Eocene deep water formation, but instead, that model simulations suggest that these sites lie close to the region of intermediate-deep water formation. In this we mean to distinguish and refer to intermediate-deep water formation. According to model simulations, while bottom waters formed on the Antarctic continental shelf, intermediate-deep waters formed at southern high latitudes, not necessarily only on the Antarctic margin. We will better clarify the above in a revised version of the text.]
- 30
- 35
- 2, 18: change "marine-based" to "sea" and, no, they are not supported by estimates for land temperatures from NLR approaches, which are in general closer to the modelled temperatures (add Pancost et al. 2013), so SST estimates are 5-10C warmer than models and LAT estimates.
[AR: we will add the land temperatures from NLR approaches to this section of the introduction, citing Pancost et al. 2013]
- 40
- 2, 21: add comma after processes
[AR: we will change the text accordingly]
- 45
- 2, 22: remove parentheses around global
[AR: we will change the text to "regional and global"]
- 2, 31: plural "changes". Lord Howe Rise is part of Zealandia so rephrase: "submerged parts of NW Zealandia..."

[AR: we will change the text accordingly]

3, 1: that's a lot of potential effects but rather speculative. Suggest you keep it simple. "... should have affected ocean circulation in the region with likely impacts for global heat transport and climate."

5 [AR: we will change the text accordingly]

3, 4: change "of" to "from"

[AR: we will change the text accordingly]

10 3, 5: Change "Southern Ocean" to "SO".

[AR: we will change the text accordingly, and verify use of abbreviations after first definition is consistent throughout]

3, 6: Rephrase: "... endemism are characteristic of a diverse range of fossil groups ..." (circum-Antarctic is tautological when you've already said Southern Ocean)

15 [AR: we will change the text accordingly]

3, 9: here is where I'd prefer you to use "dinoflagellates". If you use cysts here, you really also need to use frustules for diatoms and tests for forams and rads. Personally, I don't think you need to use "dinocyst" at all, but certainly should not be used when you are talking about plankton as opposed to assemblages in sediment.

20 [AR: we respectfully disagree on this point, and prefer to restrict the discussion to dinocysts, not dinoflagellates. In contrast to diatom frustules and foraminifera and radiolaria tests, dinoflagellate cysts, being vegetative resting cysts, do not have a 1:1 relationship to the living organism. (The body of the motile dinoflagellate is composed of labile organic material and in general does not preserve in the sediment.) While the abovementioned frustules and tests of other microfossils are truly body fossils of the living organism, the dinocyst is a resting cyst produced during the life cycle of the dinoflagellate. Since we know that not all dinoflagellates produce resting cysts (Head 1996), a single species of cyst-producing dinoflagellate can produce multiple species of dinocyst (Rochon et al. 2009) and dinoflagellate taxonomy is distinct from dinocyst taxonomy, there is a big discrepancy between the dinocyst assemblage and the dinoflagellate assemblage. For the Paleogene, relationships between this plankton group and its biogeography and environmental preferences are all based on dinocyst species and groups, typically without knowledge of which dinoflagellate produced them, certainly as most Paleogene cyst types are extinct. Therefore, we should refrain from extrapolating to dinoflagellates and restrict the discussion to dinocysts. Since, in p3 line 9, we are enumerating types of fossil assemblages, we are referring to dinocysts, not dinoflagellates.]

35 [Author comment: below, we have grouped a few of the referees comments on the topic of biogeographic terminology, to answer these collectively.]

3, 12: Query use of "cosmopolitan". This is unconventional usage. Cosmopolitan means found everywhere, so hard to see why this group signals the influence of the PLC or EAC.

40 4, 2: low-latitude and cosmopolitan are not the same thing.

7, 14, 16: Key problem issue for this paper. Definition of "cosmopolitan" is ambiguous and not in line with convention: cosmopolitan = found everywhere. I recommend you use only low and mid-latitude taxa as your guide to PLC and EAC influence.

45 10, 12: Differentiate cosmopolitan from low/mid latitude.

12, 24: Differentiate cosmopolitan from low/mid latitude taxa.

14, 7: This statement further serves to highlight why it would be helpful to differentiate cosmopolitan from low/mid latitude taxa

5 [AR: In our dinocyst grouping, we consider species that occur everywhere with respect to latitude, and do not have a specific latitudinal affinity, as “cosmopolitan” species. However, it is definitely likely that within this group of cosmopolitan species there are different habitat preferences, even though these species are principally able to occur at all latitudes (as seems indicated by the ordination analysis and statement on p 14, line 7). Regarding surface currents, the EAC and PLC are expected to bring an assemblage consisting of both cosmopolitan and low/mid latitude taxa, and no Southern Ocean endemic taxa, whereas the TC primarily transports an SO endemic assemblage. During MECO dominance of *Enneadocysta multicornuta* (cosmopolitan ecogroup) is recorded at Site 1172, at the expense of Antarctic endemic species. Although presence of a cosmopolitan assemblage by itself might not be very informative, this change from dominantly Antarctic endemic species to cosmopolitan species during MECO provides information, signalling a change in surface currents. We propose to better explain the above reasoning in paragraph 3.1.2 on “Dinocyst biostratigraphy and palaeogeographic affinity”. Furthermore, we propose to better differentiate the cosmopolitan from low/mid latitude group where the referee is asking for a distinction.]

3, 13: NZ is not in the Tasman Sea. It is east of it.

[AR: we will change the text accordingly]

20 3, 26: change “biogeographical patterns” to “biogeography”

[AR: we will change the text accordingly]

3, 27: why the “cf.”?

[AR: upon reflection, we think the “cf.” in front of the reference is redundant and will remove it]

25

3, 28: Why is “orbital scale” mentioned? Is it relevant? Why the “cf.”?

[AR: upon reflection, we think the “cf.” in front of the reference is redundant and will remove it. We would like to mention “orbital scale” variability here as an indication for the timescale on which these assemblage changes can occur.]

30 3, 32: Why is deep ocean warming described as “transient” and surface-water warming described as “widespread”

[AR: “transient” is meant to describe both deep- and surface-water warming, whereas “widespread” is meant to describe surface-water warming. We will change wording to clarify.]

3, 34: be a little more specific than “global perturbations”

35 [AR: we will change the text to more specifically describe oceanographic and environmental changes during the MECO at the sites studied in the cited papers]

4, 3: change “outstanding” to “unresolved”

[AR: we will change the text accordingly]

40

4,5: Sentences in this paragraph from “In addition ...” to end of paragraph should come before the description of the dinocyst assemblages. These sentences are part of the general description of the MECO.

[AR: agree and we will change the text accordingly]

45 4, 8: The two factors mentioned do not “imply” a volcanic explanation. Revise this sentence and provide a reference for the volcanic carbon hypothesis.

[AR: we omitted to mention carbon isotope trends over the MECO here. As $d^{13}C$ of DIC does not show a negative trend over the MECO, this rules out a depleted source of carbon. Together with the cited reconstructions of carbon cycling

during MECO, a more heavy source of carbon, such as volcanic carbon, thus was the more likely cause. We will add these additional constraints in the revised text to clarify this sentence.]

4, 11: Last sentence of paragraph is poorly worded. Revise.

5 [AR: we propose to simplify this sentence to “, constraints on global sea level change during the MECO are lacking”]

4, 25: Revise: “in the 2–3 km-deep and 50 km-wide Ninene Basin”.

[AR: here we meant to describe that Site 1170 is located in one of the grabens within the Ninene Basin, and that this certain graben is 2-3 km deep and 50 km wide. We will revise the text to clarify.]

10

5, 18: Delete “interval”; no hyphen between shallow and marine, as for 5, 21.

[AR: we will change the text accordingly]

5, 31: Sentence doesn't make sense. What covers the unconformity and overlies basal Nirranda Group?

15 5, 32: “Latrobe-1 borehole”

[AR: we will combine this sentence with the next to “The Latrobe-1 borehole (38.693009° S, 143.149995° E) was drilled in 1963–1964 near the Port Campbell Embayment depocenter, reaching a total depth of 620 metres.” The information on stratigraphy then follows in the following lines.]

20 6, 2: change “overlying” to “underlying”; What's the age of the Dilwyn Fm?

[AR: we will change wording here to clarify that the middle Eocene Narraturk Fm overlies the early Eocene Dilwyn Fm.]

6, 11: Elsewhere in text it is referred to as Hampden section. Be consistent. Why no mention of the work on the rest of the Eocene / Paleogene section (e.g. Morgans, 2009; Hollis, et al., 2012; Inglis et al., 2015)

25 [AR: to conform to the other location descriptions, we will add more background information on this section, including these appropriate references for which we thank the reviewer.]

6, 12: missing comma after “...E)”

[AR: we will change the text accordingly]

30

6, 13: “end-member” is not the right word. How about “analysed to identify influences from the TC or EAC in the middle Eocene prior to the MECO”.

[AR: we will change the text accordingly]

35 6, 28: lower case “s” for section.

[AR: we will change the text accordingly]

7, 2: 50 and 90 are normally seen as too few for robust statistical analysis.

[AR: we agree and will add discussion on this to paragraph 3.3 on statistical analyses]

40

7, 5: and identified to what taxonomic level?

[AR: typically to the level of genus - we will add this to the text]

7, 27: Again, ambiguous terminology. Your example is not of a taxon with unknown biogeographic affinities, but with conflicting biogeographic affinities.

45

[AR: We do mean to use the term “unknown” here. Regarding the specific *Deflandrea* example - different species within the genus *Deflandrea* have different geographic ranges. For example, *Deflandrea antarctica* is endemic to the Southern Ocean, whereas *Deflandrea phosphoritica* occurs globally. In our samples, we encountered specimens of *Deflandrea* that

we could only bring to the genus level, because of poor preservation. For those specimens of *Deflandrea* spp., no biogeographic grouping could therefore be made, and they are categorized as “unknown”.]

- 5 9, 7: What is meant by “spatial”? Lateral? Geographic might be a better term.
[AR: we will change the text accordingly]
- 9, 24: U is not a direct proxy for TOC.
[AR: we agree and will remove the part in between brackets here]
- 10 9, 26: Change “like” to “As with”.
[AR: we will change the text accordingly]
- 10, 2: Change “for” to “of”.
[AR: we will change the text accordingly]
- 15 10, 5: Change “dinocysts” to “assemblage”
[AR: we will change the text accordingly]
- 20 10, 7: Can low salinity be consistent with low BIT?
[AR: since the BIT index is the relative proportion between a (chiefly) terrestrially- and a (chiefly) marine-produced set of components, changing either terrestrial input or marine production can change the BIT index. In terms of BIT index, an increase in influx of terrestrially produced components can thus be offset by an increase in the accumulation of marine components. Therefore, in some settings, low salinity can indeed be consistent with low BIT indices, if marine GDGT production is relatively high.]
- 25 10, 9: Change “most dominant” to “most abundant”.
[AR: we will change the text accordingly]
- 30 10, 13: What does “a.o.” mean?
[AR: we will change this to “i.a.”, inter alia]
- 10, 20: delete “at this site”; redundant.
[AR: we will change the text accordingly]
- 35 10, 23: Provide error values for SST estimates and show on Fig. 3.
[AR: we will add error bars to Fig. 3, incorporating calibration and analytical uncertainty]
- 11, 8: “Precarious” is the wrong word, but a good choice nevertheless, because the whole interpretation of this section is precarious due to the subjective way the SST record has been interpreted. This is only one possible interpretation.
40 Another is that the warming at 670 m precedes the MECO and perhaps can be correlated with the broad peak around 440 m at 1172. Thus, the MECO is the interval between 5570 and 600 m at 1170. This shorter duration is consistent with the biostrat and would mean that the cyst accumulation rate is not so untenably high. Both options should be considered.
45 [AR: As we agree the age constraints for Site 1170 are not conclusive, we present the data for Site 1170 in the depth domain. Our dinocyst age constraints indicate the oldest layers studied (around 770 mbsf) contain *Impagidinium parvireticulatum* (FO 44 Ma), implying they are younger than 44 Ma. Therefore, it is highly unlikely that the temperature optimum around 675 mbsf represents the EECO. While we interpret this temperature optimum to represent peak MECO conditions, we cannot exclude the possibility that a “pre-MECO warming phase” occurred at Site 1170. Although we note

- that such a warming, to temperatures above peak MECO, would likely be regional in nature, as it does not seem to occur in MECO SST records from other sites (e.g. Bijl et al. 2010; Boscolo-Galazzo et al. 2014; Cramwinckel et al. 2018) or the global deep ocean (e.g. Zachos et al. 2008). Furthermore, we do note that high sedimentation rates are plausible given the seismic interpretation, as shown in Figure 2B. However, we agree that both temperature correlations cannot be excluded and propose to present the alternative explanation in the revised manuscript. We will then revise our (very rough) estimate of cyst accumulation rates to consider both options. We note however, that tenfold lower dinocyst accumulation rates would still be very high, and dinocyst concentrations are very high regardless. All of our other analyses and conclusions are neutral to which interpretation is chosen, as the dinocyst assemblages are highly similar over the interval ~575-680 mbsf at Site 1170.]
- 11, 16: Poorly worded. "sufficient numbers of dinocysts were encountered for counts of 50-100 specimens to be undertaken. Other marine palynomorphs such as prasinophytes and acritarchs, were rare/common?"
[AR: we will change the text accordingly (using "rare")]
- 11, 31: Revise sentence beginning "Furthermore..." to "Cycadopites ... are also present but rare."
[AR: we will change the text accordingly]
- 12, 1. Simultaneously is the wrong word. Delete. The abundance of Dilwynites, Protea... also decrease towards the top of the borehole.
[AR: in light of comments by Referee 3, we will remove the description of trends in these four samples.]
- 12, 17. Very poorly worded but crucial sentence. The FO of this species is said to be at 40 Ma. When is the LO? It can only be used to define the MECO if it's restricted to the MECO. I conclude from the biostrat presented that the interval may include the MECO but equally may be younger (anywhere between 40 to 35.95 Ma).
[AR: In fact, the stratigraphic range of *Dracodinium rhomboideum* in the South Pacific Dinocyst Zonation of Bijl et al. 2013 is very restricted, as *D. rhomboideum* was only recorded in one sample at Site 1172 with an age of 40 ± 0.1 Ma, within Chron 18n.2n. This corresponds to peak MECO in a compilation of deep sea stable isotope records (Bohaty et al. 2009) as well as coinciding with peak SST based on TEX₈₆ at Site 1172 itself. Notably, the range of *D. rhomboideum* in the North Atlantic Ocean (Eldrett et al. 2004 Marine Geology) is also restricted to the MECO interval (from C18n.2n 0% to C18n.1r 50%, or from 40.14 Ma to 39.66 Ma in GTS2012). Therefore, even a few specimens (1 in sample L85, 3 in sample L86 in this case - we will add the counts in addition to the relative proportions in the supplementary datafile) of this dinocyst species firmly correlate this interval to the MECO.]
- 12, 29: Which species help to constrain the age? And revise to "this 4 m-thick interval within the section".
[AR: we will change to: "This dinocyst assemblage is in agreement with the age of c. 41.7 Ma as previously assigned to this 4 m-thick interval within the section"]
- 13, 6: Use of "records" implies plural, meaning more than just the Hampden section. Are there data from other NZ sections?
[AR: In addition to the here presented data from the Hampden section there are also a few records from other NZ sections as presented in Bijl et al. 2011 Paleooceanography Figure 2f. We will add a citation here.]
- 13, 10: What is meant by "60degS front"? Do you mean the polar front? What evidence is presented for it lying north of the gateway?
[AR: Here we are indeed referring to the polar front. As further elaborated in the response to Referee 3, the fossil plankton evidence is suggestive of a Tasmanian Gateway that is influenced by a westward surface circulation, i.e. the polar front separating the polar easterlies from the westerlies to the north.]

- 13, 12: This SST range excludes the high SSTs in the MECO and possible MECO intervals. Why?
[AR: we could indeed expand this range to also include MECO SSTs, and not just “background” SSTs and will do so.]
- 5 13,14: Surely we are not interested in mantle-based paleolatitudes, which are not linked to the Earth’s spin axis. Restrict discussion to the uncertainty on the pmag reconstruction.
[AR: Since, as far as we can judge, there is still discussion within the community over which reference frame to use, we prefer to be inclusive and shortly mention both. This is also relevant in model-proxy comparison, as several GCMs use mantle-based absolute reference frames.]
- 10 13, 19. This is a key part of the argument, so needs a stronger word than “may”. How about “is more likely to”
[AR: In response to comments by Referee 3 we will adapt the section including this line in two ways. First, we will support the possibility of further southward extent of the EAC during MECO by citing literature on model simulations and modern observations illustrating wind-driven intensification of the EAC under conditions of enhanced global warmth.
- 15 Next to this, we will also discuss the suggestion of weak eastward surface transport through the northern part of the Tasmanian Gateway (see response to Referee 3 for more details.)
- 13, 20. This is an observation, so replace “suggest” with “find”, but I suggest you drop the word “transported”, which is interpretation.
20 [AR: we will change the text accordingly]
- 13, 21: “transported” is similarly redundant here - “southward reach of the warm EAC...”
[AR: we will change the text accordingly]
- 25 13, 24: “Additionally” is not needed.
[AR: we will change the text accordingly]
- 14, 1: This is an interesting finding, and should be investigated further (see general comments)
[AR: see AR above under the general comments]
- 30 14, 15: You don’t explain how this species responded and consequently miss the opportunity of expanding on a major discovery: mono-specific blooms of different species of *Enneadocysta* during the MECO at Sites 1170 and 1172 warrants more discussion.
[AR: as outlined above, correlating fossil acmes to ecological blooms warrants caution and we are therefore hesitant to call these acmes “blooms”.]
- 35 14, 26: This section is based on the so-called “precarious” use of the SST record to define the EECO at 1170. The alternative correlation noted above also needs to be considered.
[AR: In this section we primarily discuss dinocyst concentrations, not accumulation rates. These concentrations are very high, regardless of age model. With our preferred MECO correlation, cyst accumulation rates, although with large error, would also have been extremely high. We will add the alternative correlation to generate a low-end estimate on accumulation rates.]
- 40 Note too that the MECO has not been identified for sure on the Otway Basin and is not described at Hampden.
- 45 15, 18: Again, a stronger word than “might” is needed here: “most likely”?
[AR: we prefer the word “might” here, since more positive evidence would be necessary to improve certainty]

- 15, 25: "production OF dinoflagellate prey ..."
[AR: we will change the text accordingly]
- 5 16, 3: Again "seem" is too weak a word. If there is evidence, specify it.
[AR: we will change to "but also include a small proportion of meso- and megathermal components"]
- 10 16, 4: Repetition. Replace "sporomorph record at" with "assemblages in"
[AR: we will change the text accordingly]
- 16, 10: Numerous terms introduced here, either for the first time or with limited context: Wilson Bluff, Latrobe unconformity, Lutetian gap, Khirthar transgression. Consider which ones are actually needed for the argument and explain them more fully.
- 15 [AR: we agree and will make this more concise, focussing on the sequence of early Eocene sedimentation followed by erosion (Latrobe unconformity, Lutetian gap) followed by middle Eocene sedimentation (Wilson Bluff transgression, Khirthar transgression).]
- 20 16, 28. Highly tenuous to suggest a short-lived event like the MECO could be linked to such a large- scale change in base level, accommodation space. A more fruitful approach may be to consider the longer-term climate shift from EECO to MECO, where significant cooling is inferred for early middle Eocene and the MECO is seen in the context of generally warmer conditions in the later middle Eocene (e.g. Pekar et al. 2005)
- 25 [AR: In a largely ice-free world such as the middle Eocene, accommodation space on the continental shelf (on time scales of 10⁶-10⁷ years) would have been determined indeed not only by thermal expansion, but also by sediment supply and basin subsidence. The renewed drowning of the continental shelf, as reflected in the Wilson Bluff transgression, seems unlikely to be related to slow and continuous basin subsidence. Instead, ocean warming during the MECO would have caused thermal expansion of seawater, and climate and environmental change could have altered sediment supply. As we note in the Conclusion section, the current age control on these sections is not nearly sufficient to be able to correlate these transgressive surfaces to the MECO with certainty. We are merely noting the curious coincidence in
- 30 timing, which we feel is worthy of further investigation. We shall express this point more clearly in the revised text.]
- 17, 15 and 18: STR and ETP are areas of ocean floor not localities, so the plankton communities are found "on" them not "at" them.
[AR: we will change the text accordingly]
- 35 17, 20: Difficult to reconcile, but you suggest it may be related to the nature of preexisting assemblages. Something on this idea needs to be added to the conclusions.
[AR: With this statement, we meant to indicate that similar sea surface temperatures above the STR and ETP are not expected, if indeed an extension of the (warmer) EAC reaches the ETP, while the (colder) proto-ACC influences the STR. We will rephrase to clarify.]
- 40 17, 21: This conclusion is contingent upon age model assumptions.
[AR: We will add the accumulation rate estimates based on alternative age constraints, but note that absolute concentrations of dinocyst are very high given the setting, independent of accumulation rates.]
- 45 17, 25: Correlation with the MECO is uncertain.
[AR: As noted above, we will better illustrate the stratigraphic usability of *Dracodinium rhomboideum* to strengthen this correlation.]

17, 26: SLR link to MECO is too speculative. Is there evidence for SLF after the MECO?

[AR: We agree the SLR link to the MECO is speculative. Higher resolution age control combined with a more detailed paleoenvironmental and/or sedimentological study could better resolve the timing of SLR and SLF. However, as noted above, the stratigraphic range of *Dracodinium rhomboideum* is very short and strongly tied to the MECO. We would like to include this curious timing of the regional transgression in a final discussion paragraph, to be able to present this as a promising direction for further investigation to the paleoceanography community.]

References:

Morgans, H. E. G., 2009, Late Paleocene to middle Eocene foraminiferal biostratigraphy of the Hampden Beach section, eastern South Island, New Zealand: *New Zealand Journal of Geology and Geophysics*, v. 52, no. 4, p. 273-320.

Pancost, R. D., Taylor, K. W. R., Inglis, G. N., Kennedy, E. M., Handley, L., Hollis, C. J., Crouch, E. M., Pross, J., Huber, M., Schouten, S., Pearson, P. N., Morgans, H. E. G., and Raine, J. I., 2013, Early Paleogene evolution of terrestrial climate in the SW Pacific, Southern New Zealand: *Geochemistry, Geophysics, Geosystems*, p. doi: 10.1002/2013gc004935.

Pekar, S. F., Hucks, A., Fuller, M., and Li, S., 2005, Glacioeustatic changes in the early and middle Eocene (51-42 Ma); shallow-water stratigraphy from ODP Leg 189 Site 1171 (South Tasman Rise) and deep-sea $\delta^{18}O$ records: *Geological Society of America Bulletin*, v. 117, no. 7-8, p. 1081-1093.

[AR references not cited in the main paper:

Head, M. J.: Modern dinoflagellate cysts and their biological affinities, in *Palynology: principles and applications*, vol. 3, edited by J. Jansonius and D. C. McGregor, pp. 1197-1248, American Association of Stratigraphic Palynologists Foundation., 1996.

Rochon, A., Lewis, J., Ellegaard, M. and Harding, I. C.: The *Gonyaulax spinifera* (Dinophyceae) "complex": Perpetuating the paradox?, *Review of Palaeobotany and Palynology*, 155(1-2), 52-60, doi:10.1016/j.revpalbo.2008.12.017, 2009.

Author: Below, we have copied the review by the referee, and have added our responses in blue and between square brackets.

R3 - G. Raquel Guerstein (Referee)

5 The Middle Eocene Climatic Optimum (MECO) is a global warming event at about 40 Ma that interrupted the long-term
Cenozoic cooling trend. Up to now only a few studies have focused with enough resolution to evaluate the
paleoenvironmental and paleobiotic consequences of this hyperthermal event. In this work Cramwinckel and coauthors
10 have investigated the paleoecological and paleoceanographic repercussions of the MECO in the Southwest Pacific
Ocean (SWPO) primarily based on organic walled dinoflagellate cysts (dinocysts) and TEX86 palaeothermometry. The
most important site analysed in this study is the ODP Site 1170 located on the western side of the South Tasman Rise
(STR). The area where this site was drilled is characterised by a notably high sedimentation rate, especially the
15 stratigraphical interval here interpreted as part of the middle Eocene including the MECO. Despite the absence of key
biostratigraphic markers to validate a robust age-depth frame, the results from this study, together with the
information from the Site 1172 (Bijl et., 2010, 2011 and 2013a), conform a dataset of very good quality and high potential
to respond the questions posed by the authors. However, I have identified several unsubstantiated interpretations and
important methodological shortcomings that reduce the relevance of the paper. In the following I list some points that
20 may be of assistance to make the contribution stronger. I am positive that the authors can carry out the proposed
modifications, and I recommend publication of the manuscript after major revisions.

[AR: We thank the referee, G. Raquel Guerstein, for her positive evaluation of our dataset and manuscript, and critical but
constructive concerns and comments. We hope to adequately respond to these below and in a revised version of the
manuscript.]

25 My primary concern is related to the lack of physical arguments to explain the proposed change in the Southern Ocean's
surface circulation through the MECO. According to the authors (page 13, lines 8 to 11): Throughout the studied middle
Eocene interval, dinocyst assemblages at Site 1170 are dominated by Antarctic-endemic taxa. This implies that the
Tasman Gateway was influenced by westward atmospheric and surfaceoceanic circulation (i.e., the polar easterlies)
30 around 40 Ma, with the 60 S front thus located to the north of the gateway and the proto-ACC flowing through the
Tasman Gateway (Figure 1b). Then (page 13, line 19), the authors suggest that during the MECO the East-Australian
Current (EAC) waters would reach paleolatitudes somewhat less than 60 S, represented by the dinocyst assemblages at
Site 1172 on the East Tasman Plateau (ETP) (Fig 1C). Such changes in the path of a Western Boundary Current (WBC) have
to be driven by a substantial modification of the global wind pattern.

35 [AR: In this study, we use our fossil dinocyst data as a tool to reconstruct surface ocean currents. In the MECO interval we
find cosmopolitan dinocysts at Site 1172 but not Site 1170, and consequently explore ocean circulation changes that can
account for this biogeographic distribution. We explore several mechanisms and identify the one we consider most likely
(southward extent of the EAC). Indeed, such changes in surface ocean circulation would follow changes in the wind
40 pattern - given bathymetric and geographic constraints. We would like to emphasize that the
bathymetric/paleogeographic constraints are just as important as the wind patterns, and both are much less well-
constrained than the existing model simulations seem to suggest. As discussed below, we thank the referee for bringing
another potential mechanism to our attention and will add this to the discussion.

We respond to the specific comments a-d below.]

45 a. Add a schematic wind distribution in Fig. 1 A, B and C indicating the latitude of zero wind stress curl.

[AR: While we agree that it would be insightful to draw in the prevailing wind directions in the Eocene, unfortunately these reconstructions do not reliably exist, so we respectfully refrain from drawing them. The middle Eocene ocean circulation patterns that we draw are based on fossil plankton biogeography, but we prefer to not infer wind circulation patterns from this, as this additional step would introduce a lot of uncertainty. Alternatively, drawing wind circulation patterns as derived from model simulations does not provide a solution either. Atmospheric simulations as derived from fully-coupled coarse resolution GCMs (that are tuned to reproduce modern conditions), are still limited by the poorly-constrained Eocene boundary conditions. Detailed model output is too dependent on these poorly resolved boundary conditions in order to be leading in drawing atmospheric reconstructions.]

10 b. Explain the physical mechanisms conducting to the intensification and southward displacement of the the EAC shown in Fig. 1C.

c. If the changes in the EAC are wind driven, then explain the physical mechanisms by which the MECO was able to change the present distribution of wind stress.

15 [AR to b and c: We thank the referee for noticing we did not elaborate on this mechanism. Given the present constraints on MECO temperature (Bohaty et al. 2009 Paleoclimatology; Bijl et al. 2010 Science; Boscolo-Galazzo et al. 2014 Paleoclimatology; Cramwinckel et al. 2018 Nature; Giorgioni et al. 2019 Scientific Reports), the MECO was likely a global warming event, possibly driven by atmospheric CO₂ increase (Bijl et al. 2010 Science; Steinthorsdottir et al. 2019 Geology). For the modern ocean, climate model simulations using modern boundary conditions indicate that increased CO₂ forcing (with associated global warming) causes changes in zonal wind stress (maximum change around 60 °S) and large increases in positive wind stress curl south of the Tasman Sea and New Zealand (Cai et al. 2005 GRL). In these simulations, the changes in wind stress curl drive changes in ocean surface circulation characterized by intensification of the southern midlatitude circulation, including strengthening and further southward extent of the EAC. Indeed, 20 observational data indicate a strengthening of the South Pacific Gyre over the past six decades, including a southward extent of the EAC at the expense of the Tasman Front (Hill et al. 2008 GRL; Hill et al. 2011 GRL). SST anomaly reconstructions over the peak interglacial Marine Isotope Stage 5e (~125 ka) similarly indicate strengthening and further southward extent of the EAC to offshore Tasmania (Cortese et al. 2013 Paleoclimatology). We propose a similar atmospheric and oceanographic response to global warming occurred during MECO and will add the above discussion to our discussion paragraph on ocean circulation change during MECO.]

25 d. According of Fig. 1C (representing the MECO situation) the latitude of zero wind stress curl should be about 10-15 to the south of its present location. In that case the southern portion of the Australo-Antarctic Gulf (AAG) would have been under the influence of the westerlies instead of the polar easterlies. Explain how a proto-Antarctic Counter Current (proto-ACC) would flow through a shallow, partially open Tasman Gateway (TG) as proposed by Bijl et al (2013a and b) under such conditions.

30 [AR: Notably, the 60 °S line we draw in Figure 1C has quite some uncertainty. First, there is the choice of (and discussion on) which reference frame to use in order to reconstruct paleolatitude, with the first-order choice being between mantle- and paleomagnetic-based absolute reference frames. Second, there is an intrinsic error or uncertainty associated with the paleolatitude reconstructions of every chosen reference frame. For example, in Figure 1C, Site 1170 is drawn at 61.6 °S at 40 Ma, according to the Torsvik et al. (2012) paleomagnetic reference frame, but the uncertainty margins on this are between 58.76 °S and 64.55 °S (www.paleolatitude.org; Hinsbergen et al. 2015). Using the Besse and Courtillot (2002) reference frame gives a range of 57.52 °S – 64.12 °S. Given these uncertainties on the precise location of the 60 °S paleolatitude that approximately separates the westerlies from polar easterlies, we prefer to instead follow the paleobiogeographical data in order to infer circulation. These data suggest westward flow through the southern portion of the Tasmanian Gateway, which is within the uncertainty limits of the paleolatitude reconstructions (pointing more

towards the more southerly latitudes within the uncertainty). To clarify the above, we propose to add uncertainty to the lines of paleolatitude in Figure 1.]

5 I suggest to consider another hypothesis to explain the observed dyncocysts distribution. Bearing in mind a TG area located at 60 S during the middle Eocene, the cosmopolitan taxa could actually have been transported eastward through the northern portion of an incipient TG from a PLC source, very much like similar interpretations for an early incipient opening of the Drake Passage (see Scher and Martin, 2006; Livermore et al., 2007, Lagabrielle et al., 2009, González Estebenet et al., 2014). This weak flow would reach the ETP (Site 1172) but not the STR (Site 1170), dominated by the TC and a proto-ACC (Fig 1B with slight modifications). Then it would be easy to explain why the surface temperature rise during the MECO would have resulted in increased production of the cosmopolitan *Enneadocysta multicornuta* on the ETP but not on the STR, where the dominant species is *Enneadocysta dictyostila*. This species is the member of the Antarctic endemic assemblage most tolerant to warm surface waters (Fig 4C). The data matrix included in the SI reinforces this hypothesis: *E. multicornuta* is present in Latrobe-1 borehole but has not been recorded in Hampden Section.

15 This interpretation doesn't need Figure 1C but implies changes in the title and a reorganization of some of the sections accordingly.

20 [AR: We thank the referee for this suggestion. We agree that weak continuous eastward flow through the northern portion of the Tasmanian Gateway, or discontinuous eddy transport, could have been a mechanism that brought cosmopolitan dinocysts to Site 1172, but not Site 1170. We will add this potential mechanism to our discussion section in the revised version of the manuscript. We note that this explanation, similar to the EAC extending further south, raises the question why this process would only occur during MECO warmth. We propose that eastward eddy or weak continuous transport could principally occur throughout the middle Eocene, but transported species were only able to dominate the assemblage under sufficiently warm temperatures during MECO. We will add the above considerations to our revised text.]

25 There are also some methodological weaknesses that are important to take into consideration:

30 **Data and Statistical analyses**

a. According to the supplementary information it seems that the statistical analyses are based on proportions (not on counts) and this should be indicated. If they are actually based on proportions the total number of dinocysts counted in each sample should be included in the data tables.

35 [AR: Indeed, the ordination analyses are based on proportions, or relative abundances. In the revised version, we will clearly state this in the methods section. Furthermore, we will add the total number of dinocysts counted per sample to the data tables, as we agree this is important information.]

40 b. Figure 3 illustrates the relative abundances of selected dinocyst biogeographic groups using 4 categories. In the Figure 3B (site 1172) the sum of the 4 categories is not 100% but is not far from it. However, in Fig. 3A (site 1170) it appears that some important information is not taken into account. Indicate which species or groups have not been considered in these cumulative plots and why.

45 [AR: Unfortunately, especially the younger part of the Site 1170 record contained a high proportion of poorly preserved *Deflandrea* specimens that we could only determine to the level of genus. Therefore, these could not be given a biogeographic grouping, as described on page 7, lines 26–30 of the present manuscript. We will note the relevance of this to the Site 1170 dinocyst record in the caption of Figure 3 in the revised version of the manuscript.]

c. In view of the high number of species included in the data tables and that many of them are underrepresented is reasonable that only some of the species were plotted in Figures 4A and 4B. Indicate which criteria were followed for the selection of species.

[AR: This is indeed the case. In the figure caption, the sentence "For visual clarity, only the most abundant taxa (taxa that occur in >10% of the samples, have a mean relative abundance >1%, and have a maximum relative abundance of >5%) are shown in these plots" contains our criteria. We will change "in these plots" to "in all three panels" to clarify this applies to panel A and B as well as C.]

d. Only 4 samples from the Latrobe-1 borehole were studied and the number of of cyts counted in each sample is very small (based on a minimum of 50 cyst in each sample). The data available from this site is not of good quality for statistical analyses nor are some of the Hampden Beach samples (based on a minimum of 90 cyst in each sample). I hardly recommend not to include these samples in the unconstrained NMDS analysis, unless additional counts can make these dinocyst assemblages part of a reliable dataset.

[AR: We agree with the referee that caution should be taken in doing statistical analyses on assemblage counts of <150–200 palynomorphs. We prefer, however, to present the results for the reader to assess, adding the cautionary note that these analyses are based on low count data.]

e. Figure 5. Explain the meaning of *Enneadocysta* – *Oligosphaeridium*. What is *Enneadocysta* spp besides *Enne-Oli*, *E.dic* and *E.mul*?

[AR: We encountered these *Enneadocysta-Oligosphaeridium* intermediates (as we have designated them) only at the Latrobe-1 borehole. These specimens have a morphology in between *Enneadocysta (multicornuta)* and *Oligosphaeridium* spp., being dorsoventrally compressed and following the tabulation pattern of *Enneadocysta* spp. and having several processes conform *Enneadocysta* (thin, solid, distally radiating), but also having multiple processes conform *Oligosphaeridium* (much thicker, tubiform, distally less complex). The preservation and quantity of the material is not sufficient for description of this as a new species, which is why we describe them as "*Enneadocysta-Oligosphaeridium* intermediate". To clarify, we will add a short description to our datafile, in the sheet "Dinolist" column "notes". *Enneadocysta* spp. are species of *Enneadocysta* with insufficient characteristics preserved to bring their determination to the species level, but that do not fall into the category of *Enneadocysta-Oligosphaeridium* intermediates.]

Indicate the criteria followed for the selections of species or groups to be plotted in this figure.

[AR: The criteria are the same as for Figure 4, which we will add to the caption of Figure 5.]

Illustration of key markers, taxonomy and dinocyst paleogeographic affinity

a. The middle Eocene dinocysts assemblages are mainly composed of cysts of extant dinoflagellates. Thus, the illustration of key biostratigraphic and palaeoenvironmental markers is a matter of major relevance and should be part of the main paper or included as Supplementary Information.

[AR: Referee 1 also commented that a plate with key markers would make a useful addition to the manuscript. We propose to add a plate with key palynomorph species to the revised manuscript as a supplementary figure, including the below mentioned *Dracodinium rhomboideum*.]

- 5 b. The taxonomy of the Subfamily Wetzelielloideae is an issue of discussion, which is still open (Williams et al., 2015; Iakovleva, 2016; Bijl et al., 2016; Williams et al., 2017). In this context the illustration of the key biomarkers is essential. As things are stand now different research groups can use the same name for different morphotypes and the same morphotype can be named in different ways. One of the key biostratigraphic markers for the MECO, here called *Dracodinium rhomboideum*, has previously found only at Site 1172 and has not been illustrated by Bijl et al. (2013a).
10 Every research group can call this taxa with different names, but a good illustration allows the dinocyst specialist to know if they are talking about the same thing or not. Unquestionably, the authors have the right to follow the taxonomy they consider better and more useful. However, if they reference a "Comment on a paper", they cannot ignore that there is a "Response to that comment" and it should be mentioned (Williams et al., 2017). The authors are free to follow Fensome et al., 2004 for the wetzelielloid taxonomy, of course, but they have to do it for all the members of the subfamily. For
15 example, *Rhombodinium rhomboideum* had already been transferred to *Dracodinium rhomboideum* 15 years ago. A taxonomic appendix should be included to avoid these mistakes.

[AR: We will add an illustration of *Dracodinium rhomboideum* to a supplementary plate. In the supplementary datafile, we will add author references to the dinocyst species, to change this into a taxonomic appendix. Furthermore, we will add a citation to the response to the comment at the appropriate place in the text.]
20

c. Which is the difference between "endemic SO" and the "so called TF"? I suggest to consider all these taxa as "Antarctic endemics" in order to leave the old name "Transantartic Flora" behind.

25 [AR: We agree and will group the "endemic SO" and "so called TF" as "Antarctic endemics.]

d. Dinolist (Excell file of SI): Indicate the meaning of "biogeo alt" and "g" and "p" Add a column indicating the source of the biogeo (Bijl et al., 2011, Bijl et al., 2013b, Frieling, Apy Sluijs, 2018... or others).

30 [AR: We will make these additions to the datafile.]

Terrestrial palynomorphs from the Latrobe-1 borehole

- This section is the weakest part of the manuscript. The authors overinterpreted a poor set of data coming from the Latrobe-1 borehole based on only 4 samples within the interval representing the MECO. The section 4.2.2 Terrestrial Palynology (pages 11-12) is merely descriptive using an open taxonomy with broad links to the modern types and no references to their present-day distribution. The section is closed with the following report: "Within the sporomorph assemblages, there is a slight dominance shift between the major pollen groups towards the top of the interval: the percentages of saccate pollen increase from 15–20 % to 40 % upsection, while angiosperms decrease from 40–60 % to 25 %".... Actually, it is not consistent to describe a palaeoenvironmental trend based on four samples. Moreover, an
40 avaluation of the vegetational modifications as a consequence of the climatic change during the MECO with no records of the pre and post MECO intervals does not have any sense. Furthermore, the authors concluded (page 17, lines 23-25): "Terrestrial palynomorph assemblages suggest a warm temperate rainforest with some paratropical elements that grew along the southeast Australian margin during the MECO", which can be possible, but the statement clearly does not arise
45 from this unsupported analysis. I suggest to remove this section unless it can be substantially improved.

[AR: While we agree with the referee that 4 palynological samples comprise a limited set of data, we respectfully disagree that this would make the data less suitable for publication in our manuscript. While limited in number, these

palynological assemblages provide crucial additional information on middle Eocene warmth on the nearby continent, supporting the marine-based reconstructions. This is important, as land and ocean temperatures did not necessarily change synchronously in this region throughout the Eocene (e.g., Pancost et al. 2013 G³; Bijl et al. 2013 PNAS). The presence of dinocyst marker species *Dracodinium rhomboideum* strongly indicates a MECO age (see the author response to Referee 2). Nevertheless, we agree that our description of trends based on 4 samples might not be sensible, so we propose to omit this in the revised version.]

Other comments

- 10 When different sources are used to reference a concept the references have to follow a chronological order, from the oldest to the youngest. (not in alphabetical order). Example: Page 2, line 22: (Kennett et al., 1974; Cande and Stock, 2004) instead of (Cande and Stock, 2004; Kennett et al., 1974). Check this aspect throughout the manuscript since there are many of these mistakes.
Page 2, line 28: (Scher and Martin, 2004; Lagabrielle et al., 2009; González Estebenet et al., 2014) instead of (Lagabrielle et al., 2009; Scher and Martin, 2004)
- 15 Page 3 line 9: (Wrenn and Beckman, 1982; Wrenn and Hart, 1988; Mao and Mor, 1995; Guerstein et al., 2008; Bijl et al., 2011, 2013a) instead of (Wrenn and Beckman, 1982; Wrenn and Hart, 1988; Bijl et al., 2011, 2013a)
[AR: Although the CP formatting guidelines leave these decisions to the authors, we will adjust to a chronological reference order.]
- 20 Page 3. Lines 8 and 9: organic walled dinoflagellate cyst assemblage instad of organic dinoflagellate cyst assemblage
[AR: we will change the text accordingly]
- Page 3, line 18: dinocyst assemblages instead of dinocysts assemblages
- 25 [AR: we will change the text accordingly]
- Page 5, line 11: delete a repeted "was not"
[AR: we will change the text accordingly]
- 30 Page 5, line: The overlying Wilson Bluff transgressive deposits have an age.... instead of "The overlying Wilson Bluff transgression has an age"
[AR: we will change the text accordingly]
- Page 5, line 28: Narrawaturk Formation instead of Narrawaturk formation
- 35 [AR: we will change the text accordingly]
- Page 6, line 7: Narrawaturk Formation (or Fm) instead of Narrawaturk formation
[AR: we will change the text accordingly]
- 40 Page 6, line 13: The Hampden section at Hampden Beach, New Zealand (Figure 2a).... which could have recorded influences of both TC and/or EAC. Explain.
[AR: we will change this sentence following the suggestion by Referee 2, who also commented on it]
- Page 7. Line 6: wetzelielloids or Subfamily Wetzelielloideae insted of "Wetzelioid family"
- 45 [AR: we will change to "wetzelielloids"]

Page 7. Lines 16-18: "We label taxa without a clear temperature affinity as cosmopolitan, such as those taxa with a distribution that is primarily controlled by other parameters like salinity (e.g., *Senegalinium* cpx.) or nutrient availability (e.g., protoperidinioids) Add references

[AR: we will add appropriate references to Sluijs et al. 2005; Sluijs and Brinkhuis 2009; Frieling and Sluijs 2018.]

5

Page 7, line 31: where the only species of *Deflandrea* recorded was *D. antarctica* insted of: where only the *Deflandrea* species *D. antarctica* is present

[AR: we will change the text accordingly]

10 Page 9 lines 31 -32: Middle Eocene palynomorphs at Site 1170 are generally well preserved and assemblages are dominated (>95%) by marine forms, mainly dinocysts. Terrestrial palynomorphs occur consistently, but in low relative abundances (<2% of palynomorphs). 95 or 97%? vs. 2 or 5%?

[AR: we will change "<2%", to "<5%". This was a small inconsistency, because there is only one sample with 95% marine and 5% terrestrial palynomorphs.]

15

Page 10, lines 2: "possibly from the north". Why?

[AR: because this was a relatively nearby land mass for offshore transport of material]

20 Page 10, lines 6-8: "High abundances of *Enneadocysta* spp. and peridinioid dinocysts in combination with low diversity indicate a somewhat restricted, eutrophic assemblage with possible low-salinity influences." Add references

[AR: we will cite Sluijs et al. 2005 for these environmental inferences]

25 Page 11, line 3: MECO cooling ?

[AR: we will change this to "MECO recovery"]

25

Page 17, lines 2 and 3: Annenberg Formation.... Helmstedt Formation Annenberg Formation instead Annenberg formation.... Helmstedt formation Annenberg formation

[AR: we will capitalize "Formation" here]

30 Illustrations Be consistent using upper or lower case for the figures. Figure 1 shows A, B and C and the figure caption explains the Figure 1 a, b and c. See also Figs 2, 3, 4, 6 and supplementary figures.

[AR: we will be consistent and change these to lower case between brackets, in accordance with the CP house style]

References mentioned in this comments and not included in the reference list of the manuscript

35

González Estebenet, M. S., Guerin, G. R., and Alperin, M. I., 2014. Dinoflagellate cyst distribution during the Middle Eocene in the Drake Passage area: paleoceanographic implications. *Ameghiniana*, 51(6):500-510. DOI: 10.5710/AMGH.06.08.2014.2727.

40 Guerin, G.R., Guler, M.V., Williams, G.L., Fensome, R.A., Chiesa, J.O., 2008. Mid Palaeogene dinoflagellate cysts from Tierra del Fuego, Argentina: biostratigraphy and palaeoenvironments. *Journal of Micropalaeontology* 27: 75-94.

Iakovleva, A. I., 2016. Did the PETM trigger the first important radiation of wetzelielloideans? Evidence from France and northern Kazakhstan, *Palynology*, DOI: 10.1080/01916122.2016.1173121

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Surface-circulation change in the Southern Ocean across the Middle Eocene Climatic Optimum: inferences from dinoflagellate cysts and biomarker paleothermometry

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Abstract

Global climate cooled from the early Eocene hothouse (~52–50 Ma) to the latest Eocene (~34 Ma). At the same time, the tectonic evolution of the Southern Ocean was characterized by the opening and deepening of circum-Antarctic gateways, which affected both surface- and deep-ocean circulation. The Tasmanian Gateway played a key role in regulating ocean throughflow between Australia and Antarctica. Southern Ocean surface currents through and around the Tasmanian Gateway have left recognizable tracers in the spatiotemporal distribution of plankton fossils, including organic-walled dinoflagellate cysts. This spatiotemporal distribution depends on both physico-chemical properties of the water masses as well as the path of surface ocean currents. The extent to which climate and tectonics have influenced the distribution and composition of surface currents and thus fossil assemblages has, however, remained unclear. In particular, the contribution of climate change to oceanographic changes, superimposed on long-term and gradual changes induced by tectonics, is still poorly understood.

To disentangle the effects of tectonism and climate in the southwest Pacific Ocean, we target a climatic deviation from the long-term Eocene cooling trend, the Middle Eocene Climatic Optimum (MECO; ~40 Ma). This 500 thousand year long phase of global warming was unrelated to regional tectonism, and thus provides a test case to investigate the ocean's physiochemical response to climate change alone. We reconstruct changes in surface-water circulation and temperature in and around the Tasmanian Gateway during the MECO through new palynological and organic geochemical records from the central Tasmanian Gateway (Ocean Drilling Program Site 1170), the Otway Basin (southeastern Australia) and the Hampden Beach section (New Zealand). Our results confirm that dinocyst communities track specific surface ocean currents, yet the variability within the communities can be driven by superimposed temperature change. Together with published results from the east of the Tasmanian Gateway, our new results suggest that as surface ocean temperatures rose, the East Australian

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Current likely extended further south during the peak of MECO warmth. Simultaneous with high sea-surface temperatures in the Tasmanian Gateway area, pollen assemblages indicate warm temperate rainforests with paratropical elements along the southeastern margin of Australia. Finally, based on new age constraints we suggest that a regional southeast Australian transgression might have been caused by sea-level rise during MECO.

5 1 Introduction

The Eocene epoch (~56–34 millions of years ago; Ma) was characterised by gradual ocean cooling from the early Eocene hothouse (~52–50 Ma) to the early Oligocene icehouse (33 Ma), accompanied by decreasing atmospheric CO₂ concentrations (Zachos et al., 2008; Inglis et al., 2015; Anagnostou et al., 2016; Cramwinckel et al., 2018). In the framework of Eocene climate evolution, the Southern Ocean (SO) and its circulation are of particular interest. Geochemical tracers (Thomas et al., 2003; Huck et al., 2017) and model simulations using specific Eocene boundary conditions (Huber and Caballero, 2011) indicate that the SO, and the Southwest Pacific (SWP) in particular (Sijp et al., 2014; Baatsen et al., 2018), was the main source of intermediate, and deep water formation during the early Paleogene. This effectively relays SO surface conditions to the global deep ocean. Several sites from the SWP sector of the SO have yielded proxy-based sea-surface temperatures (SSTs) (Bijl et al., 2009; Hollis et al., 2009, 2012) that are 5–10°C higher than the temperatures derived from the current generation of fully coupled climate models (Huber and Caballero, 2011; Lunt et al., 2012; Cramwinckel et al., 2018). These high sea water temperatures are supported by biomarker-based continental air temperature estimates, and vegetation reconstructions on the surrounding continents that indicate paratropical conditions (Pross et al., 2012; Carpenter et al., 2012; Contreras et al., 2013, 2014), although land and ocean temperatures did not necessarily change synchronously in this region (Pancost et al., 2013). This mismatch between proxy- and model-based temperatures has remained a conundrum.

As a result of tectonic processes, the bathymetry and geography of the Southern Ocean experienced major reorganizations in the Eocene (Kennett et al., 1974; Cande and Stock, 2004) that strongly affected regional and global ocean circulation (Huber et al., 2004; Sijp et al., 2014) (Figure 1). In the earliest Eocene, the Australian and South American continents were much closer to Antarctica (e.g., Cande and Stock, 2004) and obstructed circum-Antarctic ocean circulation. Instead, sub-polar gyres dominated circulation patterns in the southern sectors of the Indian and Pacific Ocean, transporting relatively warm surface waters to the Antarctic coast (Huber et al., 2004; Sijp et al., 2011; Baatsen et al., 2018) (Figure 1a). Tectonic activity in the Eocene led to the opening and subsequent deepening of the Tasmanian Gateway (Bijl et al., 2013b; Stickley et al., 2004b) and Drake Passage (Lagabrielle et al., 2009; Scher and Martin, 2004). Furthermore, a transition from northwesterly to accelerated northerly displacement of the Australian continent (Cande and Stock, 2004; Hill and Exon, 2004; Williams et al., 2019) and post-rift collapse of the outer continental shelf on both the Australian and Antarctic margins (Totterdell et al., 2000; Close et al., 2009) occurred. Subduction initiation affected vertical motion of submerged parts of northwestern

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Zealandia including the Lord Howe Rise in the Tasman Sea (Sutherland et al., 2017, 2018). This complex tectonic evolution should have affected ocean circulation, and, in turn, heat transport and regional climate.

Along with the indirect inferences from modelling and heat distribution based on SST reconstructions, biogeographic patterns of surface-water plankton may be used as a tool to reconstruct surface-ocean circulation. In the Paleogene, SO, high levels of endemism characterise a diverse range of fossil groups, including molluscs (Zinsmeister, 1979), radiolarians and diatoms (Harwood, 1991; Lazarus et al., 2008; Pascher et al., 2015; Stickley et al., 2004b), calcareous nannoplankton and planktonic foraminifera (Nelson and Cooke, 2001; Villa et al., 2008), and organic-walled dinoflagellate cysts (dinocysts) (Wrenn and Beckman, 1982; Wrenn and Hart, 1988; Bijl et al., 2011, 2013a). The endemic dinocyst assemblage from the Southern Ocean is traditionally referred to as “Transantarctic Flora” (Wrenn and Beckman, 1982). Here, following more recent extensive biogeographic mapping (Huber et al., 2004; Warnaar et al., 2009; Bijl et al., 2011, 2013b), we use these “Antarctic endemic dinocysts” to track Antarctica-derived surface currents, while cosmopolitan assemblages track currents sourced from the low latitudes. Throughout the Eocene, the Australian margin of the Australo-Antarctic Gulf (AAG) as well as New Zealand east of the Tasman Sea were characterised by high percentages of cosmopolitan dinocysts, implying an influence of the low-latitude-sourced Proto-Leeuwin Current (PLC) and the East Australian Current (EAC), respectively (Figure 1). In contrast, coeval assemblages on the eastern side of the Tasmanian Gateway were Antarctic-endemic, showing influence of the Antarctica-derived northward-flowing Tasman Current (TC) (Bijl et al., 2011, 2013b; Huber et al., 2004). From about ~50 Ma onwards, endemic dinocyst assemblages were established on both the Antarctic margin in the Australo-Antarctic Gulf and the eastern boundaries of the Tasmanian Gateway and Drake Passage (Bijl et al., 2011, 2013b). This indicates surficial westward flow through the Tasmanian Gateway of a proto-Antarctic Counter Current (proto-ACC), which is supported by simulations using an intermediate-complexity coupled model (Sijp et al., 2016). Pronounced widening and deepening of the gateway did not start until the late Eocene (Stickley et al., 2004b), although some subsidence already took place during the middle Eocene (Röhl et al., 2004).

These biogeographical patterns broadly confirm the Paleogene ocean circulation patterns as simulated by numerical climate models (Huber et al., 2004). Thus, on tectonic timescales (i.e., tens of Myrs), plankton biogeographical patterns predominantly follow changes in surface-ocean circulation (Bijl et al., 2011). During periods with a relatively stable ocean-current configuration, such as the middle Eocene, SO dinocyst assemblage variability was instead driven by (orbital-scale; Warnaar et al., 2009) climatic factors such as SST (Bijl et al., 2011). Superimposed changes in SWP dinocyst assemblages also occur during transient climate change such as the Paleocene-Eocene Thermal Maximum (PETM, ~56 Ma, (Sluijs et al., 2011)) and the Middle Eocene Climatic Optimum (MECO, ~40 Ma, (Bijl et al., 2010)). During the PETM, global warming of ~5 °C occurred within millennia, associated with the injection of a large mass of reduced carbon into the ocean-atmosphere system, which resulted in the appearance of tropical dinocyst taxa at the East Tasman Plateau (Sluijs et al., 2011; Frieling and Sluijs, 2018a). In contrast, although with similar magnitude of warming, the MECO was a 500 thousand year

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(kyr) period of transient warming of the global deep ocean (Bohaty et al., 2009; Bohaty and Zachos, 2003) and surface ocean (Boscolo-Galazzo et al., 2014; Cramwinckel et al., 2018). Regionally, the MECO was associated with changes in oceanic productivity and oxygenation, reflected by changes in planktic and benthic assemblages (e.g., Spofforth et al., 2010; Boscolo-Galazzo et al., 2015; Cramwinckel et al., 2019). However, the mechanism that caused MECO warming remains enigmatic. Deep-ocean carbonate dissolution (Bohaty et al., 2009), indications for $p\text{CO}_2$ rise (Bijl et al., 2010; Steinhilber et al., 2019) and a diminished weathering feedback (van der Ploeg et al., 2018) during the MECO imply that climate change was forced by an accumulation of carbon in the exogenic carbon pool. The lack of a negative trend in stable carbon isotope ratios ($\delta^{13}\text{C}$) over the MECO suggests this carbon to be volcanic, rather than organic, in origin (Bohaty et al., 2009). One of the proposed MECO carbon-cycle scenarios suggests a global sea-level rise in order to shift the locus of carbonate deposition from the deep ocean to the continental shelves (Sluijs et al., 2013). Although speculative isotopic evidence for a MECO-associated change in glacioeustasy exists (Dawber et al., 2011), constraints on global sea level change during the MECO are lacking. At the East Tasman Plateau, the MECO is characterised by an incursion of low-latitude dinocyst taxa that temporarily replaced the largely endemic Antarctic community (Bijl et al., 2010). The origin of these cosmopolitan dinocysts remains an unresolved question. Potentially, cosmopolitan dinoflagellates outcompeted the Antarctic-endemic taxa in the warming TC, similar to during the PETM. Alternatively, a southward extension of the EAC from the north or leakage of the PLC from the west through the Tasmanian Gateway supplied cosmopolitan assemblages to the region east of Tasmania, possibly even associated with sea level rise.

To disentangle the effects of tectonism and climate change in the southwest Pacific Ocean, we here assess the biotic and oceanographic response in that region to MECO warming. The MECO allows us to assess oceanographic response to climate change, independent of tectonic change. We reconstruct surface-ocean circulation and temperature by generating new dinocyst and organic geochemical records from Ocean Drilling Program (ODP) Site 1170 on the South Tasman Rise in the central Tasmanian Gateway. We place these records into their broader regional context by comparing them to newly generated middle Eocene palynological records, including pollen from terrestrial plants, from the Otway Basin (SE Australia) and the Hampden Beach section (New Zealand) (Figure 2a).

2 Material

2.1 South Tasman Rise (ODP Site 1170) and East Tasman Plateau (ODP Site 1172)

Ocean Drilling Program Site 1170 is located at a water depth of ~2704 m, 400 km south of Tasmania at 47.1507° S and 146.0498° E (Exon et al., 2001) (Figure 2a). It was drilled on the western side of the South Tasman Rise (STR), a continental block to the south of present-day Tasmania. The site is located in a 2–3 km deep and 50 km wide graben within the Ninene Basin (Figure 2b). A ~300 m thick package of shallow marine silty claystones of middle Eocene age overlies an erosional unconformity. Northwest-southeast rifting between Australia and Antarctica accelerated after 51 Ma, resulting in

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prominent NW-SE structural trends in seabed seismic topography associated with seafloor spreading between Tasmania-STR on the one side and Antarctica on the other (Exon et al., 2004; Bijl et al., 2013b; Williams et al., 2019) (**Figure 2a**). This coincided with renewed subsidence of both conjugate continental margins (Totterdell et al., 2000) and the STR (Hill and Exon, 2004). Marked lateral thinning of middle Eocene deposits at Site 1170 is apparent in the seismic profile, suggesting synsedimentary growth faulting caused local subsidence (**Figure 2c**). Middle Eocene sediments are present in Hole 1170D as a thick sequence from ~500 metres below sea floor (mbsf) to the total depth at 780 mbsf (Exon et al., 2001). The precise age of the middle Eocene strata at Site 1170 has thus far not been well constrained (Stickley et al., 2004a). Nevertheless, the thickness of the middle Eocene sequence implies high sedimentation rates (Exon et al., 2001), together with the seismic evidence suggesting that the surrounding graben was a depocenter that formed as rifting developed. Middle Eocene sediments are overlain by latest Eocene-earliest Oligocene glauconite-rich clayey siltstones (Exon et al., 2001; Sluijs et al., 2003; Stickley et al., 2004a). Here, we target the middle Eocene claystones from the interval ~500–780 mbsf for dinocyst biogeography and organic geochemistry, to gain a central **Tasmanian Gateway** perspective on regional effects of the MECO.

Ocean Drilling Program Site 1172 is located at a water depth of ~2620 m on thinned continental crust on the western side of the East Tasman Plateau (ETP), ~170 km southeast of Tasmania at 43.9598° S and 149.9283° E (Exon et al., 2001) (**Figure 2a**). While the ETP has a similar tectonic history to the STR, Site 1172 was not affected by growth faulting and subsidence like Site 1170 during the middle Eocene (Hill and Moore, 2001). Palynological and organic geochemical results for the middle Eocene of the East Tasman Plateau are presented in Bijl et al. (2009, 2010, 2011, 2013a), and are compared to our results from the South Tasman Rise in this study.

2.2 Latrobe-1 borehole, Otway Basin (Australo-Antarctic Gulf, Southeast Australia)

Sediment cores from the Otway Basin, on the Australian margin of the AAG (**Figure 2a**), were analysed as a location under influence of the PLC during the MECO. The Otway Basin contains a regionally thick sequence of shallow marine Paleogene deposits (Gallagher et al., 1999; Gallagher and Holdgate, 2000). These deposits developed due to Paleocene-Eocene post-rift extension on the edge of the continental margin, causing subsidence of extensive troughs that served as depocentres of terrigenous sediment in deltaic and shallow marine environments (Krassay et al., 2004; Stacey et al., 2013; Frieling et al., 2018a). In southeast Australia, the middle Eocene to early Oligocene Nirranda Group unconformably overlies the early Eocene Dilwyn Formation (Wangerrip Group) (Abele, 1994; Krassay et al., 2004; Tickell et al., 1993). This unconformity can be traced throughout southeast Australia (Holdgate et al., 2003). The overlying Wilson Bluff **transgressive deposits have** an age between 44 and 40 Ma (Holdgate et al., 2003; McGowran et al., 2004). In the Portland Trough and Port Campbell Embayment of the Otway Basin, the basal part of the Nirranda Group consists mainly of the Burrungule and Sturgess Point members. Outside of these main depocentres and on the ridges in between, the basal part of the Nirranda Group is

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represented by the Narrawaturk Formation. Planktonic foraminiferal biostratigraphy indicates a Bartonian age for the Sturgess Point Member (Abele, 1994; Gallagher and Holdgate, 2000).

The Latrobe-1 borehole (38.693009° S, 143.149995° E) was drilled in 1963–1964 near the Port Campbell Embayment, reaching a total depth of 620 metres. It spans Cretaceous to Eocene sediments, with initial biostratigraphic age constraints (Archer, 1977; Taylor, 1964; Tickell et al., 1993) and well log data (White, 1963) placing the middle Eocene Narrawaturk Fm at a depth of 60–76 metres below surface (mbs), overlying the early Eocene Dilwyn Fm (76–289 mbs). The Dilwyn Fm in the Latrobe-1 core consists largely of light- to dark brown sandstones with some contributions of mud- and siltstone, while the Narrawaturk Fm is a dark brown muddy sandstone (Frieling et al., 2018a). Based on the occurrence of the stratigraphic marker dinocysts *Achilleodinium biformoides* and *Dracodinium rhomboideum*, and in accordance with the regional dinocyst zonation (Bijl et al., 2013a) sediments around a depth of 67.35 metres below surface (mbs) in the Narrawaturk Fm (Nirranda Group) of the Latrobe-1 borehole have an age near the MECO (Frieling et al., 2018a). Here, we target 4 samples from the Latrobe-1 core Narrawaturk Fm (interval ~60-90 mbs) for palynology and organic geochemistry.

2.3 Hampden Beach section (South Island, New Zealand)

The Hampden Beach section at Hampden Beach, New Zealand (**Figure 2a**) (45.30° S, 170.83° E), was analysed to identify influences of TC and/or EAC at southern New Zealand in the middle Eocene prior to the MECO (Hines et al., 2017). This 256.5 m thick section spans the Paleocene to late Eocene and has a well-resolved foraminiferal biostratigraphy (Morgans, 2009). Middle Eocene sediments of the Hampden Beach section consist of calcareous clay-rich siltstone to very fine sandstone. Benthic foraminiferal assemblages suggest a depositional environment near the shelf-slope transition. An interval of 4 m was previously selected for high-resolution investigation (Burgess et al., 2008). This interval spans 70 kyr around 41.7 Ma, based on biostratigraphy and orbital interpretation of lithological cycles. Sea-surface temperature (SST) reconstructions based on Mg/Ca and $\delta^{18}\text{O}$ of excellently preserved foraminifera and TEX_{86} indicate values of 23–25 °C (Burgess et al., 2008), which is consistent with regional Eocene SST reconstructions (Hollis et al., 2012; Inglis et al., 2015). We have analysed the same 4 m interval for dinocyst biogeography.

3 Methods

3.1 Palynology

3.1.1 Processing and analysis

A total of 43 samples from ODP Site 1170 (Hole 1170D), 8 samples from the Latrobe-1 core, and 39 samples from the Hampden Beach section were processed for palynology following standard procedures. A known amount of *Lycopodium*

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clavatum spores was added for quantification of the dinocyst content in specimens per gram. Sediment samples were crushed and oven dried (60 °C), followed by treatment with 30% HCl and ~40% HF to dissolve carbonate and silicate minerals, respectively. After each acid step, samples were washed with water, centrifuged or settled for 24 h, and decanted. The residue was sieved over nylon mesh sieves of 250 µm and 10 µm (Site 1170) or 15 µm (Otway Basin, Hampden Beach section) and subjected to an ultrasonic bath to break up agglutinated particles of the residue. A drop of the homogenised residue was mounted on a glass microscope slide with glycerine jelly and sealed. All slides are stored in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht University. Palynomorphs were counted up to a minimum of 200 identified dinocysts for ODP Site 1170, typically to the taxonomic level of genus or species. Because the dinocyst yield was relatively low for the other localities, palynomorphs were counted up to a minimum of 90 (Hampden Beach section) or 50 (Otway Basin) identified dinocysts. Terrestrial palynomorphs were counted in broad categories of gymnosperm pollen, angiosperm pollen and spores for Site 1170 and the Hampden Beach section. As the Otway Basin samples yielded diverse and abundant sporomorph assemblages, a minimum of 300 sporomorphs was counted per sample. Dinocyst taxonomy as cited in Williams et al. (2017) was generally followed, with the exception of the wetzelielloids. For this group, we follow the suggestion made in Bijl et al. (2016) to use the taxonomy of Fensome and Williams (2004) instead of (Williams et al., 2015, 2017a). Sporomorph taxonomy follows Stover and Partridge (1973), Macphail et al. (1994), and Raine et al. (2011).

3.1.2 Dinocyst biostratigraphy and palaeogeographic affinity

Regional dinocyst biostratigraphy for the middle Eocene is based on Bijl et al. (2013a) (ages presented in table 2 of that work). Dinocyst-based environmental interpretation follows Sluijs et al. (2005), Sluijs and Brinkhuis (2009), and Frieling and Sluijs (2018). For biogeographic analysis, dinocyst taxa were binned into Antarctic endemics, cosmopolitan taxa, and mid-/low-latitude taxa (Supplementary Data). Shifts in relative abundance between these groups signal changes in surface ocean currents. Surface ocean currents deriving from the water surrounding Antarctica are dominated by Antarctic endemics, whereas low-latitude derived current such as the EAC and PLC transport more cosmopolitan and mid-/low-latitude taxa. We primarily follow the biogeographical groupings of Bijl et al. (2011) and (2013b), based on occurrence and stratigraphic range of species at different latitudes. Cosmopolitan dinocysts are those taxa that have been recorded globally, at low (tropics), middle (subtropical and temperate) and high (polar) latitudes. The Antarctic endemic group consists of species endemic to either the Southern Ocean (including the Transantarctic Flora (TF) cf. Wrenn and Beckman (1982)) or both the Southern Ocean and northern high latitudes (bipolar taxa). To the mid-/low-latitude group we add those taxa that are considered thermophilic (all wetzelielloids and goniodomids) based on recent empirical information on ecological affinities of Paleogene dinocysts (Frieling and Sluijs, 2018b). We note that this addition only constitutes a minor change in biogeographic grouping for this study (Supplementary Data).

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Taxa with unknown biogeographic affinities were excluded from biogeographical analysis. For instance, a large fraction of *Deflandrea* specimens that lost their outer bodies could not be identified to the species level. As some *Deflandrea* species are endemic to the **SO**, while others are cosmopolitan, we have excluded these specimens (and other taxa with unknown affinity) from biogeographic analysis. We note that a different choice was made for the published middle Eocene dinocyst assemblages from Site 1172, where **the only *Deflandrea* species recorded was *D. antarctica***; consequently, *Deflandrea* inner bodies were counted as *D. antarctica* (Bijl et al., 2011). **Endemic and cosmopolitan dinocysts during the MECO at Sites 1170 and 1172 largely consist of two species belonging to the genus *Enneadocysta*, i.e., the cosmopolitan species *Enneadocysta multicornuta* and the Southern Ocean endemic *Enneadocysta dictyostila*. **These** species are morphologically similar, **but differ** by their tabulation patterns and the morphology of the distal ends of the processes (Fensome et al., 2006) (**Supplementary Figure 1**). The species morphology has been crosschecked with the original Site 1172 material and dinocyst counts to validate consistency in species determination. The above biogeographical affinity of dinocysts, in particular the relative abundance of endemic vs. non-endemic dinocyst taxa, is used here to distinguish the relative influence of the Antarctic-derived TC vs. the lower-latitude-derived EAC and PLC.**

3.2 Organic geochemistry

To quantify SST changes, 52 samples from ODP Hole 1170D and one sample from the Latrobe-1 core were processed for TEX₈₆ palaeothermometry based on isoprenoid glycerol **dibiphytanyl** glycerol tetraether (GDGT) membrane lipids of marine archaea (Schouten et al., 2002). The GDGTs were extracted from freeze-dried, powdered samples (~8–10 g dry weight) with dichloromethane (DCM):methanol (MeOH) (9:1, v:v) using a Dionex accelerated solvent extractor (ASE) 350, at a temperature of 100°C and a pressure of 7.6×10^6 Pa. Lipid extracts were subsequently separated by Al₂O₃ column chromatography into 4 fractions, using hexane:dichloromethane (DCM) (9:1, v/v), ethyl acetate (100%), DCM:MeOH (95:5, v/v) and DCM:MeOH (1:1, v/v). For quantification purposes, 9.9 ng of a C₄₆ GDGT internal standard (*m/z* 744) was added to the DCM:MeOH (95:5, v/v) fraction after this. This fraction, containing the GDGTs, was subsequently dissolved in hexane:isopropanol (99:1, v/v) to a concentration of ~3 mg/mL, passed through a 0.45 µm polytetrafluoroethylene (PTFE) filter and analysed using ultra-high performance liquid chromatography-mass spectrometry (UHPLC-MS) following (Hopmans et al., 2016). We note that the published TEX₈₆ records from Site 1172 and the **Hampden Beach section** were generated using high performance liquid chromatography-mass spectrometry (HPLC-MS) after (Schouten et al., 2007), but differences in TEX₈₆ values between the two methods have been shown to be negligible (Hopmans et al., 2016). Samples with very low concentrations (i.e., peak area < 3000 mV and/or peak height < 3x background signal) of any GDGT included in TEX₈₆ were excluded from analysis. Based on relative abundances of GDGTs, the TEX₈₆ and Branched versus Isoprenoid Tetraether (BIT) index values were calculated following Schouten et al. (2002) and Hopmans et al. (2004), respectively. The BIT index is used as an indicator for the **contribution of terrestrially-derived organic material to the marine realm, relative to influence of marine production. High BIT index values indicate a primarily terrestrial origin of GDGTs and/or low marine production of GDGTs**, whereas **low BIT values indicate dominance of marine-produced GDGTs over a smaller contribution**

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of terrestrial GDGTs. BIT index values >0.3 imply TEX₈₆ might not correctly reflect SST due to an overprint by a terrestrial-derived signal (Weijers et al., 2006). In addition, several other ratios were calculated to evaluate GDGT sourcing and thus the reliability of TEX₈₆-based SST estimates. In short, the Methane Index (MI) (Zhang et al., 2011) and GDGT-2/crenarchaeol (Weijers et al., 2011), GDGT-0/crenarchaeol (Blaga et al., 2009), and GDGT-2/GDGT-3 (Taylor et al., 2013) indices are calculated to investigate potential contributions by methanotrophic, methanogenic, and deep-dwelling GDGT producers to the GDGT pool in the sediments. The analytical precision for TEX₈₆ is ±0.3°C based on long-term analysis of in-house standards. TEX₈₆-to-SST calibrations include those based on mesocosm experiments and core-top datasets. We prefer the latter for paleoreconstructions, as these integrate ecological, water-column and diagenetic effects that are not incorporated in mesocosm experiments. Since our measured TEX₈₆ values are within the range of the modern core-top dataset (±0.73), no extrapolation of the modern TEX₈₆-to-SST relationship is necessary, and differences between linearly and exponentially fitted calibrations are small (see for example extended data figure 2 in Cramwinckel et al. (2018)). Here we calculate SST from TEX₈₆ values using both the exponential calibration of Kim et al. (2010) and the linear calibration of O'Brien et al. (2017) (Supplementary Data). Since the resulting values are highly similar, we present only the values from a single calibration, the TEX₈₆^H calibration, in our figures. We note that however, the interest of this study primarily lies in comparing geographic differences in SST and not absolute temperature values.

3.3 Statistical analyses

To assess the main patterns within the changing dinocyst assemblages at the studied sites, unconstrained ordination was applied on the proportional abundances. Both Nonmetric MultiDimensional Scaling (NMDS) and Detrended Correspondence Analysis (DCA) were performed, using the R Package Vegan (Oksanen et al., 2015). Whereas DCA assumes a unimodal species response to the environment, NMDS is a distance-based method that does not assume any relationship, which can be considered more neutral because it introduces less assumptions (Prentice, 1977). For NMDS, the Bray-Curtis measure was used as an appropriate dissimilarity index for (paleo-) ecological community data (e.g., Faith et al., 1987), and recommendations by Clarke (1993) were followed to set the number (two or three) of dimensions used in the ordination. Unconstrained ordination was performed on the full dinocyst assemblages from Site 1170 and Hampden Beach (this study) and Site 1172 (Bijl et al., 2010, 2011, 2013a). Furthermore, unconstrained ordination was applied to the combined dinocyst assemblages of Site 1170, Site 1172, Otway Basin and Hampden Beach. We note that caution should be taken when performing statistical analyses on microfossil assemblage counts of less than 150–200 palynomorphs (minimum 50 for Latrobe-1, minimum 90 for Hampden Beach), as diversity will likely be underrepresented. While this introduces biases into measures of diversity and variability of the assemblage, ordination-type analyses that establish the dominant patterns within the data should be more robust for low count data.

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To investigate whether dinocyst assemblage change at Site 1170 correlates with environmental change, constrained ordination using Canonical Correspondence Analysis (CCA) was performed with the R Package Vegan. We assess different sets of environmental proxy data, including SST (based on TEX₈₆; this study), input of terrestrial material (BIT; this study), shipboard-generated clay contents from smear slide analysis, uranium contents, magnetic susceptibility, and colour reflectance data (Masclé et al., 1996). Higher-resolution environmental data were interpolated to the sampling resolution used here for palynology. As with DCA, CCA assumes a unimodal species response to the input environmental variables.

4 Results

4.1 Site 1170

4.1.1 Palynology

Middle Eocene palynomorphs at Site 1170 are generally well preserved and assemblages are dominated (>95%) by marine forms, mainly dinocysts. Terrestrial palynomorphs occur consistently, but in low relative abundances (<5% of palynomorphs). The presence of *Impagidinium* spp. in all samples indicates an open marine setting (Dale, 1996), suggesting that palynomorphs characteristic of inshore environments have been transported off-shelf, possibly from the north. Absolute concentrations of dinocysts are extremely high, averaging ~175,000 dinocysts per gram of dry sediment over the studied section, with maxima of over 400,000 cysts per gram. The dinocyst assemblages are generally of low diversity and consist of three dominant groups that typically comprise over 90% of the total assemblage. These groups are: *Enneadocysta dictyostila*, *Deflandrea* spp. and spiny peridinioids *sensu* Sluijs et al. (2009). High abundances of *Enneadocysta* spp. and peridinioid dinocysts in combination with low diversity indicate a somewhat restricted, eutrophic assemblage with possible low-salinity influences (Sluijs et al., 2005). Endemic taxa dominate the record, typically accounting for more than half of the assemblage (Figure 3). The most abundant endemic species is *E. dictyostila*, particularly from 570–690 mbsf. Endemic *Vozzhennikovia apertura* also has a high average relative abundance (~20%). Other, rarer endemics include *Arachnodinium antarcticum*, *Deflandrea antarctica*, *Enneadocysta brevistila*, *Octodinium askinae*, *Spinidinium macmurdoense*, *S. schellenbergii*, and *Vozzhennikovia netrona*. Cosmopolitan and mid-/low-latitude dinocyst species on average make up about 10% of the assemblage, consisting among others of *Cerebrocysta* spp., *Cordosphaeridium* spp., *Enneadocysta multicornuta*, *Eocladopyxis peniculata*, *Operculodinium centrocarpum*, and *Thalassiphora pelagica*. Selected taxa are illustrated in Supplementary Figure 1.

4.1.2 Organic geochemistry and sea-surface temperatures

Out of 52 samples from Hole 1170D, five were disregarded for TEX₈₆ analysis due to low GDGT concentrations, particularly in the lower part of the section. The remaining 47 samples have isoprenoid GDGT concentrations of on average 18 ± 10 ng per g sediment. BIT index values (Hopmans et al., 2004) are consistently below 0.25, indicating a dominant marine source of the isoprenoid GDGTs (Weijers et al., 2006). Furthermore, MI values (Zhang et al., 2011) and GDGT-

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2/Cren ratios (Weijers et al., 2011) are below 0.3 and 0.2, respectively, indicating no substantial GDGT contributions by methanotrophic archaea. Finally, GDGT-0/Cren ratios (Blaga et al., 2009) are never above 1.2, indicating normal marine conditions, without substantial contributions by methanogenic archaea. Based on the TEX₈₆^H calibration, TEX₈₆-derived SSTs are mostly between 20–28°C, similar to time-equivalent temperatures at the East Tasman Plateau (Bijl et al., 2010) (Figure 3). Maximum temperatures of ~28°C are reached around 670 mbsf, and temperatures decline gradually towards the top of the studied section. Large temperature variability of several degrees between consecutive samples is recorded particularly in the interval from 600 to 550 mbsf (Figure 3).

4.1.3 Biostratigraphic framework

Some biostratigraphically informative dinocyst species are present. *Selenopemphix* spp. and *Impagidinium parvireticulatum* occur sparsely throughout the investigated samples from Site 1170, with their oldest occurrence at ~766 mbsf (second-to-lowermost sample). Their regional first occurrences are at 48.6 Ma and 44.0 Ma (GTS2012), respectively (Bijl et al., 2013a). Presence of *Impagidinium parvireticulatum* thus constrains the studied sediments to an age younger than 44 Ma. The single occurrence of *Lophocysta* spp. at 569 mbsf provides a narrow age range around the MECO for this part of the investigated core, from 41.39 to 39.66 Ma (Bijl et al., 2013a). Additional age constraints from magnetostratigraphy are not possible, as inclination data suffered from a persistent large overprint (Stickley et al., 2004a). The few available shipboard nannofossil datums do not add further constraints, but confirm sediments of MECO age should lie within the studied interval (Stickley et al., 2004a). Based on the above constraints, we consider the recorded TEX₈₆-based temperature maximum at ~670 mbsf to reflect the peak of the MECO and the subsequent surface ocean cooling trend to represent the MECO recovery phase (“Option 1” in Figure 3a). An alternative interpretation would be to consider the warming interval from ~610 to ~580 mbsf as MECO warming (“Option 2” in Figure 3a), which would suggest peak MECO temperatures at ~580 mbsf. However, this would imply a pre-MECO peak in temperature at ~670 mbsf. This would strongly conflict with temperature evolution across the middle Eocene and MECO as recorded at numerous sites across the global ocean, including the nearby Site 1172 (e.g., Bijl et al., 2010; Boscolo-Galazzo et al., 2014; Cramwinckel et al., 2018). We therefore prefer the first interpretation, even though it implies (very) high sedimentation rates of 10s of centimetres per thousand years. Such rates are consistent with the middle Eocene locality of Site 1170 in a depocenter on the northeast-southwest rifting South Tasman Rise (Figure 2b-c). While these constraints are valuable in delimiting our study interval to the MECO, stratigraphic correlation based on temperature records is precarious and the lack of precise and consistent age-depth tie-points impedes the construction of a solid age–depth model. We therefore present the data for Site 1170 in the depth domain.

4.2 Otway Basin

4.2.1 Marine palynology

The palynomorph assemblages from the Latrobe-1 borehole consist predominantly of sporomorphs. Absolute concentrations of dinocysts are in the order of 100–1,000 cysts per gram of dry sediment, while sporomorphs total 2,000–5,000 grains per

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gram of dry sediment. ~~Sufficient dinocysts were encountered for counts of ~50–100 identified dinocysts to be undertaken.~~ Other marine palynomorphs such as prasinophytes and acritarchs were rare. The *Spiniferites* complex is dominant (averaging ~40 %), and *Enneadocysta* spp. (mostly consisting of *E. multicornuta*) are common (averaging ~20 %). Other minor constituents include *Cleistosphaeridium* spp., *Cordosphaeridium* spp., *Deflandrea* spp., *Elytrocysta* spp., *Hystrichosphaeridium* spp., and *Phthanoperidinium* spp. Notably, the dinocyst assemblages do not yield Antarctic endemic taxa; instead, they are composed solely of cosmopolitan and low-/mid-latitude taxa. Combined, the marine palynology indicates a proximal marine setting.

4.2.2 Terrestrial palynology

The middle Eocene sporomorph assemblage from the Latrobe-1 borehole consists of abundant gymnosperm (30–50 %) and angiosperm (30–50 %) pollen, with pteridophyte spores as a minor component of the assemblage (10–15 %). Saccate pollen are mainly represented by *Podocarpidites* spp. (*Podocarpus*), *Lygistepollenites* (*Dacrydium*) and *Phyllocladites* spp. (*Lagarostrobus*); other gymnosperms are Araucariaceae (10–20 %), which consist mainly of *Dilwynites* spp. (*Agathis/Wollemlia*) and, to a lesser extent, of *Araucariacites* spp. (*Araucaria*). Angiosperm pollen are dominated by *Myricipites* spp. (Casuarinaceae; *Gymnostoma*), *Nothofagidites* (including *Nothofagus* sg. *Brassospora*) and *Malvacipollis* spp. (*Austrobuxus/Dissilaria*), with *Proteacidites* spp. and *Rhoipites* spp. as minor elements. Pteridophyte spores are mainly represented by *Cyathidites* spp. and *Laevigatosporites* spp. Furthermore, *Cycadopites* spp. (Cycadophyta), *Arecipites* spp. (Arecaceae), and *Santalumidites* spp. (*Santalum*) are also present but rare. Selected taxa are illustrated in Supplementary Figure 1. A stratigraphic log of the Latrobe-1 borehole and a pollen diagram are presented in Supplementary Figure 2.

4.2.3 Organic geochemistry

The analysed sample from the Latrobe-1 borehole contains predominantly terrestrial-derived branched GDGTs, resulting in a BIT index of 0.79, making the sample unsuitable for TEX₈₆ analysis.

4.2.4 Stratigraphy

Our new palynological data further constrain the position of the early-middle Eocene hiatus that was recognised in the Latrobe-1 borehole between 67.35 and 97.84 mbs (Frieling et al., 2018a) to a depth between 78.98 and 70.32 mbs. The hiatus therefore likely corresponds to the transition between the Dilwyn Formation (Wangerrip Group) and the Narrawaturk Marl (Nirrandra Group) at ~70.5 mbs. Dinocyst species with biostratigraphic utility in strata above the unconformity include *Phthanoperidinium comatum* (FO 45.70 ± 0.20 Ma) and *Phthanoperidinium stockmansii* (FO 57.20 ± 0.20 Ma), *Achilleodinium biformoides* (recorded in ODP Site 1171 South Pacific Dinocyst Zone (SPDZ) 13), and *Dracodinium rhomboideum* (Supplementary Figure 1c) (Bijl et al., 2013a). Occurrence of this last species is especially informative, as the stratigraphic range of *Dracodinium rhomboideum* in the South Pacific Dinocyst Zonation of Bijl et al. (2013a) is very restricted. In fact, it was only present in one sample at Site 1172, with an age of 40.00 ± 0.10 Ma, within Chron 18n.2n. This

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corresponds to peak MECO in the compilation of deep sea stable isotope records (Bohaty et al. 2009) as well as coinciding with peak MECO SSTs based on TEX₈₆ at Site 1172. Notably, the range of *D. rhomboideum* in the North Atlantic Ocean (Eldrett et al., 2004) is similarly restricted to the MECO interval (from C18n.2n 0% to C18n.1r 50%, corresponding to 40.14 Ma – 39.66 Ma, indicating this species to be a useful biostratigraphic marker for the MECO). The interval from 61.46 to 70.32 mbs in the Latrobe-1 borehole is therefore assigned to SPDZ13 (40.0–35.95 Ma), based on the regional dinocyst zonation of Bijl et al. (2013a). Moreover, the presence of *Dracodinium rhomboideum* in samples at 63.82 and 67.35 mbs indicate coverage of the MECO.

4.3 Hampden Beach

4.3.1 Palynology

Middle Eocene palynological assemblages at Hampden Beach are dominated by dinocysts (~65 %), with abundant sporomorphs (~30 %) and some acritarchs and prasinophytes. Sediments yield several thousand dinocysts per gram of dry sediment. The consistent presence of *Impagidinium* spp. (mean: ~7 %) indicates an open-ocean setting. The dinocyst assemblages comprise predominantly cosmopolitan and low-/mid-latitude taxa. Similar to the assemblages from the Latrobe-1 borehole, the outer neritic *Spiniferites* sp. is dominant (averaging ~40 %). Other common cosmopolitan and low-/mid-latitude taxa include *Cordosphaeridium fibrospinosum*, *Dapsilidinium* spp., *Elyrocysta brevis*, *Hystriocholpoma rigaudiae*, *Hystriochosphaeridium tubiferum*, and *Senegalinium* spp. (together averaging ~35 %). Antarctic endemic species occur sparsely (averaging ~6 %) and consist of *Deflandrea antarctica*, *Enneadocysta dictyostila* and *Pyxidropsis delicata*. This dinocyst assemblage is in agreement with the age of c. 41.7 Ma as previously assigned to this 4 m-thick interval within the section (Burgess et al., 2008).

5 Discussion

5.1 Surface-ocean circulation in the Southwest Pacific during the MECO

Our new dinocyst biogeographic data are generally consistent with previous interpretations of Tasmanian Gateway surface-ocean circulation based on plankton biogeography and model simulations (Bijl et al., 2011; Huber et al., 2004; Sijp et al., 2016) (Figure 1b). By the middle Eocene, the Antarctic endemic dinocyst assemblage associated with the proto-ACC and TC had become firmly established, while the northern bound of the AAG was primarily influenced by the low-latitude-derived PLC. Records from southern New Zealand yield a predominantly warm EAC signal, with a minor, yet constant influx of Antarctic endemics indicating limited TC influence (this study and Bijl et al., 2011). Throughout the studied middle Eocene interval, dinocyst assemblages at Site 1170 are dominated by Antarctic-endemic taxa. This implies that the Tasmanian Gateway was influenced by westward atmospheric and surface-oceanic circulation (i.e., the polar easterlies) around 40 Ma, with the polar front thus located to the north of the gateway and the proto-ACC flowing

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westward through the **Tasmanian Gateway** (Figure 1b). This is supported by the similar range of TEX₈₆ SSTs of 20–28°C within (Site 1170) and east of (Site 1172) the **Tasmanian Gateway** (Figure 3). In terms of paleolatitude reconstructions, placing Site 1170 within the **Tasmanian Gateway** south of 60°S at this time is within the uncertainty limits of **current generation** mantle (e.g., Matthews et al., 2016) **as well as** paleomagnetic reference frames (e.g., Torsvik et al., 2012). Notably, however, the **shift in dominance from endemic to cosmopolitan** dinocysts that occurs at the zenith of MECO warmth on the East Tasman Plateau (Site 1172) has no equivalent on the South Tasman Rise (Site 1170) (Figure 3). **The dominance of cosmopolitan dinocysts at Site 1172 therefore cannot be explained by the warming TC and Ross Sea gyre alone, as this effect would have resulted in a dinocyst assemblage similar to Site 1170.** **Two possible oceanographic features could have resulted in a dominantly cosmopolitan dinocyst assemblage at Site 1172 and not at Site 1170. First, weak eastward flow could have occurred through Bass Strait and/or the northern portion of the Tasmanian Gateway from the AAG (Figure 1c).** The uncertainty on paleolatitude in principle allows for weak continuous eastward flow (or discontinuous eddy transport) under influence of the westerlies through the northern part of the TG. While this remains a possible scenario, we consider it unlikely that such a nearby current would not be reflected in the plankton assemblages at the depocenter of Site 1170, particularly since the widest opening in the TG would be located south of the **South Tasman Rise (Bijl et al., 2013)**, close to Site 1170. In addition, the Bass Strait, or Bass Basin, to the north of Tasmania was likely too restricted at its eastern end for throughflow (Cande and Stock, 2004). **As the second option, southward extension and/or intensification of the EAC could have sustained cosmopolitan assemblages at Site 1172 (Figure 1c).** Increased southward reach of the relatively warm EAC has been suggested before as a mechanism to warm the SWP throughout the hot early Eocene (Hines et al., 2017; Hollis et al., 2012). Model simulations (using modern boundary conditions) indicate that a wind-driven strengthening and further southward extent of the EAC is expected under conditions of enhanced global warmth, as part of intensification of the southern midlatitude circulation (Cai et al., 2005). Indeed, observational data indicate a strengthening of the South Pacific Gyre over the past six decades, including a southward extent of the EAC at the expense of the Tasman Front (Hill et al., 2008, 2011). Similarly, SST anomaly reconstructions over the peak interglacial Marine Isotope Stage 5e (~125 ka) indicate intensification of the EAC to offshore Tasmania (Cortese et al., 2013). Possibly a similar atmospheric and oceanographic response to global warming occurred during MECO.

5.2 Drivers of dinocyst assemblage change in the **Tasmanian Gateway**

Unconstrained ordination using a unimodal (DCA) or non-metric (NMDS) model shows that the primary variability in the dinocyst assemblage at Site 1170 is governed by *E. dictyostila* and follows SST quite closely (Figure 4a, **Supplementary Figure 3**), suggesting that the abundance of *E. dictyostila* responds to temperature. The first NMDS and DCA axes are virtually identical, with DCA1 accounting for 33 % of the variance in the dataset. Both DCA2 (accounting for 17 %) and MDS2 contrast *D. antarctica* and *T. pelagica* at one end of the axis with *Vozzhennikovia* spp. at the other end. Ordination results of the MECO and the surrounding interval at Site 1172 are closely comparable with those of Site 1170 (Figure 4b, **Supplementary Figure 3**). At Site 1172, the abundance of *E. dictyostila* also controls the first axis (DCA1 accounting for 42

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Deleted: , as was recently shown to be plausible based on simulations with the Community Earth System Model 1 using 38 Ma geographic boundary conditions (Baatsen et al., 2018). Additionally, ic boundary conditionsuplift of shallow rises in the Tasman Sea during the Eocene may have reoriented the EAC (Sutherland et al., 2018), which could be a promising scenario for modelling studies to investigate.

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% of the variance), and the second axis (accounting for 17 %) places *D. antarctica* and *T. pelagica* vs. *Vozzhennikovia* spp. No clear patterns in biogeographic or coastal proximity grouping emerge from the ordination results of Site 1170 and Site 1172. However, unconstrained ordination of the combined dinocyst assemblages from Site 1170, Site 1172, the Otway Basin, and Hampden Beach results in a biogeographic separation on the first axis (DCA1 accounting for 77 % of the variance, DCA2 accounting for 38 %) (**Figure 5**). DCA1 and MDS1 separate the Site 1170 and Site 1172 assemblages from the Otway Basin and Hampden Beach assemblages, as these axes separate endemic (and some cosmopolitan) taxa on the left vs. mid-/low-latitude (and some cosmopolitan) taxa on the right. The second axis further separates Site 1170 from Site 1172.

The role of temperature in determining assemblage variability at Site 1170 is further supported by constrained ordination (CCA), in which the first axis has high explanatory power (~67 % of the total accounted variance by the environmental variables), and has TEX₈₆ as the dominant component (**Figure 4c**; environmental variables as time series in **Supplementary Figure 4**). Therefore, although no peak of low-latitude species characterizes the MECO at Site 1170, the ordination analyses suggest that the dinocyst assemblage as a whole, and in particular *E. dictyostila*, responded to temperature change during MECO.

Taken together, these results confirm previous evidence that once a surface-oceanography-tracking plankton community has become established, relative abundance changes within the community correspond closely with changes in SST (Bijl et al., 2011). In the modern ocean, phytoplankton distribution patterns are driven by the interplay of passive transport by surface currents and temperature selection (Hellweger et al., 2016; Thomas et al., 2012). A similar dual selection mechanism seems to have affected the middle Eocene dinocyst assemblages in the region. Regional surface-ocean circulation determined which assemblage was established and where. This spatial pattern (**Figure 5**) could change over tectonic timescales as paleogeography changed (Bijl et al. 2011). Dominance shifts and variability within these assemblages were then driven by superimposed surface-ocean changes (such as in temperature), which typically occur on shorter timescales.

5.3 Massive middle Eocene dinocyst productivity on the South Tasman Rise

At the South Tasman Rise, MECO sediments are not only characterised by rapid sedimentation rates (in the order of 10s of cms per kyr according to our age models; compare Section 4.1.3), but also by high concentrations of dinocysts (**Figure 6**). High sedimentation rates are readily explained by the location of Site 1170 as a middle Eocene depocenter affected by rifting between Australia and Antarctica and associated subsidence (Exon et al., 2004). However, the extraordinarily high dinocyst concentrations are more difficult to explain. They are 100–1,000 times higher than in the studied strata from the Otway Basin and Hampden Beach. They also stand out when compared to other time intervals and settings where high dinocyst concentrations are expected and found. Specifically, they are about an order of magnitude higher than those typically found in Mediterranean sapropels (e.g., Sangiorgi et al., 2006; van Helmond et al., 2015; Zwiep et al., 2018), Cretaceous Oceanic

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Anoxic Event 2 shelf sediments (van Helmond et al., 2014) and the Holocene Adélie drift underlying a highly productive polynya system (Hartman et al., 2018).

The high sedimentation rates and silty claystone facies make it unlikely that high dinocyst content was the result of sediment starvation and/or winnowing, respectively. Furthermore, such conditions would also have facilitated oxidation and degradation of organic-walled palynomorphs, while they are instead well-preserved and abundant. Therefore, these high concentrations seem to represent extreme dinocyst productivity and/or preservation. Enhanced sediment accumulation rate by itself facilitates burial of organic matter, in particular through adsorption of organics to clay minerals (Berner, 2006; Hedges and Keil, 1995), so preservation **could have** played a role. However, total organic carbon (TOC) contents are not extremely high (mean: ~1 % over the studied interval), the sediment is well bioturbated, and there is no significant correlation between dinocysts/gram and shipboard TOC contents, uranium contents or magnetic susceptibility (**Supplementary Figure 5**), which suggests preservation was not the driving factor leading to high dinocyst concentrations. Rather, surface ocean productivity **may have** been elevated. The relatively low diversity of the dinocyst assemblages in combination with the high dominance of a single taxon (*Enneadocysta dictyostila* in the MECO interval) suggests a generally eutrophic setting that could have been characterised by seasonal plankton blooms. Notably, in several records from the Paleocene-Eocene Thermal Maximum (Harding et al., 2011; Sluijs et al., 2011; Frieling et al., 2018b), and a record from Oceanic Anoxic Event 2 at Bass River (van Helmond et al., 2014), highest concentrations of dinocysts reach 10,000–100,000 cysts per gram sediment, and also correspond to low diversity - high dominance assemblages, suggestive of dinoflagellate blooms. Dinocysts deriving from heterotrophic dinoflagellates are present at Site 1170, but not in high abundance (**Supplementary data**). This **indicates** that primary production **of** dinoflagellate prey species such as diatoms (Jeong, 1999) was not necessarily high during the studied interval. Combined, the above suggests that high surface-ocean dinoflagellate-based productivity **combined** with increased production of resting cysts, was the most likely cause of rapid accumulation of dinocysts at Site 1170, with possible secondary roles for sediment transport and organic matter preservation. Indications why conditions in the middle Eocene **Tasmanian Gateway** would have been extremely favourable for dinoflagellate or dinocyst production are, however, yet lacking.

5.4 Southeast Australian vegetation during the MECO

The middle Eocene sporomorph assemblages from the Latrobe-1 borehole are generally similar to those identified in previous studies (Macphail et al., 1994; Greenwood et al., 2003; Hill, 2017), but **also** include a **small** proportion of meso-megathermal components. **Although the small amount of analysed samples prohibits a description of pre-, syn-, and post-MECO vegetation, the assemblages from Latrobe-1 reveal that this middle Eocene vegetation of coastal southeast Australia consisted of a mosaic of mesothermal rainforest flora. These forests were dominated by warm temperate angiosperms Casuarinaceae (*Gymnostoma*), *Austrobuxus/Dissilaria* and Proteaceae as shrubs and trees, with rare (paratropical) tree palms**

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(Arecaceae) and cycads (Cycadophyta). Overstorey elements included *Nothofagus* sp. *Brassospora* and gymnosperms of the Araucariaceae and Podocarpaceae (*Podocarpus*, *Dacrydium* and *Lagarostrobos*). The low abundance of saccate Podocarpaceae pollen, *i.e.*, pollen with high transport capability that are often overrepresented in pollen assemblages, suggests that these taxa were not a major part of the coastal vegetation in the lower interval. Together with small trees and shrubs, ground ferns (Gleicheniaceae and Osmundaceae) and tree ferns (Cyatheaceae) occupied the understorey in these rainforests. While the MECO marker dinocyst species *Dracodinium rhomboideum* was recorded in two of four studied samples, further stratigraphic constraints are lacking. Future regional pollen studies focussing on the Nirranda Group might therefore elucidate whether the relatively warm-loving flora described here was restricted to the MECO interval, or to a broader interval of middle-late Eocene “background” conditions.

10 5.5 Sea-level rise during the MECO?

Glacial eustacy might have played a minor role in middle Eocene sea level changes (Dawber et al., 2011), but Earth’s polar regions are generally thought to have been largely ice-free during that time. Thus, accommodation space on the continental shelves (on time scales of 10^6 – 10^7 years) was primarily determined by the interplay of thermal expansion of seawater, sediment supply and basin subsidence. In general, warm and wet early Eocene conditions are expected to have saturated passive continental shelves, resulting in relatively flat and shallow shelf platforms (Somme et al., 2009). In the Otway Basin, sediments of middle Eocene age (basal Nirranda Group) overlie a large unconformity at the top of early Eocene sediments of the Wangerrip Group (e.g., Krassay et al., 2004). These middle Eocene sediments were deposited during the Wilson Bluff transgression, which is recognised throughout southeast Australia (Holdgate et al., 2003; McGowran et al., 2004) and has been linked to a major transgressive phase in the Indo-Pacific (the Khirthar transgression) (Jauhri and Agarwal, 2001; McGowran et al., 2004). While there is seismostratigraphic evidence for regional tectonic rifting, normal faulting and subsidence during the Paleocene and early Eocene in southeast Australia (Krassay et al., 2004; Close et al., 2009), it is unknown when subsidence terminated, and renewed. Additionally, a progressive decrease in terrigenous sediment supply throughout the Eocene might have affected accommodation space, as the Australian hinterland aridified (Sauermilch et al., 2019). Whatever the relative contributions of these mechanisms, the hiatus between the Wangerrip Group and the Nirranda Group suggests no or negative accommodation space by the end of the early Eocene (51 Ma) or later. The renewed drowning of the continental shelf, as reflected in the Wilson Bluff transgression, seems unlikely to be related to slow and continuous basin subsidence. Instead, ocean warming during the MECO may have raised global average sea level by several meters by thermal expansion, while warmer and wetter regional climate could have increased sediment supply. The resumption of sedimentation accumulation above the top Latrobe unconformity has been previously dated to between 44 and 40 Ma (Holdgate et al., 2003; McGowran et al., 2004). Based on our new dinocyst-based age constraints, it is likely that the sediments overlying the Wangerrip group are close to the MECO in age, suggestive of a causal link between the Wilson Bluff transgression and MECO warming. A similar timing of renewed sedimentation occurred in the Schöningen section in

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the North German Basin, where the transgressive, fully marine Annenberg Formation unconformably overlies the Lutetian coal-bearing Helmstedt Formation (Riegel et al., 2012). The Annenberg Formation has been assigned an age around the MECO (Gürs, 2005), possibly ~41 Ma (Brandes et al., 2012). Based on a compilation of New Jersey coastal plain sections, a highstand (sequence E8) is also interpreted at ~41–40 Ma (Browning et al., 2008).

Sea-level rise and warming during the MECO may have accommodated increased burial of biogenic carbonate on continental shelves, explaining a reduction in carbonate burial in the deep sea (Sluijs et al., 2013), along with a diminished silicate weathering feedback (Van der Ploeg et al., 2018). However, it should be noted that the above inferences regarding global sea-level rise during the MECO are tentative. Although these transgressive surfaces all have an age around the MECO, current age control is not nearly sufficient to correlate them to MECO with certainty. A dating accuracy of $\leq 100,000$ years would be required for these transgressive surfaces to indicate their relationship to MECO warming, which is presently not available. It is therefore crucial to improve these constraints in order to assess the potential influence of sea-level change on the carbon cycle during the MECO.

6 Conclusions

Comparison of plankton and sea-surface temperature patterns during the MECO above the South Tasman Rise indicate that while dinocyst assemblages responded to surface-water warming, the acme in cosmopolitan taxa above the East Tasman Plateau at peak MECO is not mirrored at the STR. This implies either eastward throughflow through the northern portion of the Tasmanian Gateway, or a southward extension of the EAC during the zenith of MECO warmth. This illustrates, how profoundly surface-ocean currents can respond to external climate forcing in these regions of the Southern Ocean. Terrestrial palynomorph assemblages indicate a warm temperate rainforest with some paratropical elements grew along the southeast Australian margin during the MECO. Finally, we suggest that the southeast Australian Wilson Bluff Transgression may be related to sea-level rise during the MECO, but improvement of the available age constraints is necessary to establish a possible causal link.

Acknowledgements

This research used samples and data provided by the International Ocean Discovery Program (IODP) and its predecessors. This work was carried out under the program of the Netherlands Earth System Science Centre (NESSC), financially supported by the Dutch Ministry of Education, Culture and Science. This study was made possible by the Netherlands Organisation for Scientific Research (NWO) grant number 834.11.006, which enabled the purchase of the UHPLC-MS system used for GDGT analyses. Funding was provided by the Australian IODP office and the ARC Basins Genesis Hub (IH130200012) to SJG. We thank Natasja Welters, Jan van Tongeren and Arnold van Dijk (Utrecht University Geolab) for

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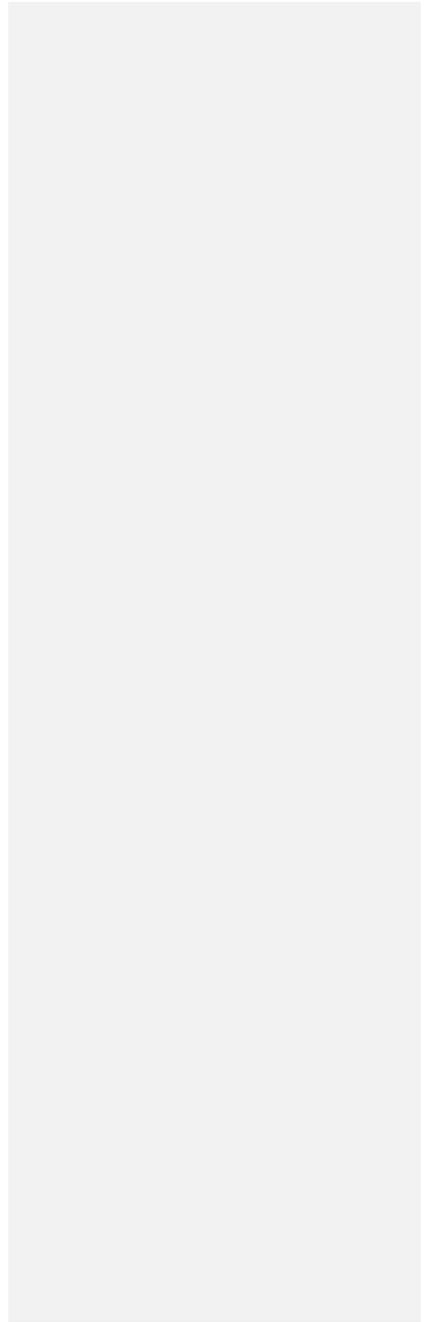
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analytical support. [We thank the reviewers Severine Fauquette, Chris Hollis and G. Raquel Guerstein for their constructive reviews of the initial version of the manuscript.](#)



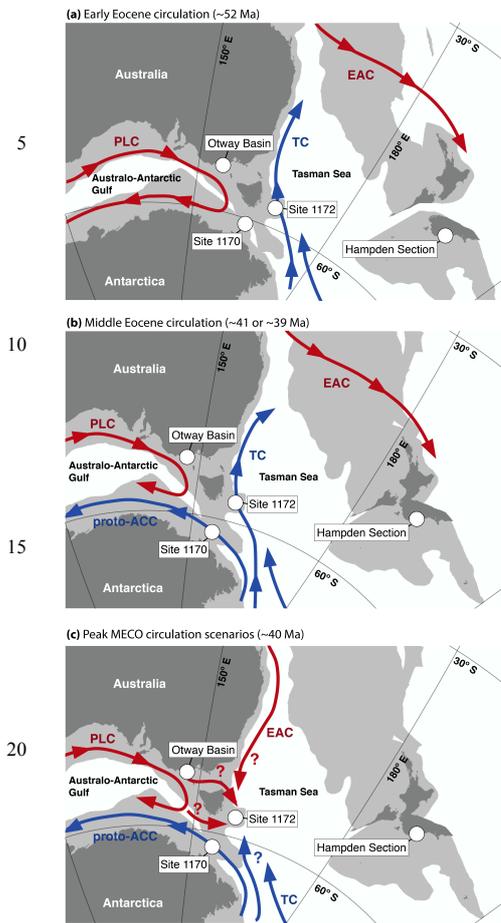
Automatic citation updates are disabled. To see the bibliography, click Refresh in the Zotero toolbar.

Author: References are available in the manuscript pdf

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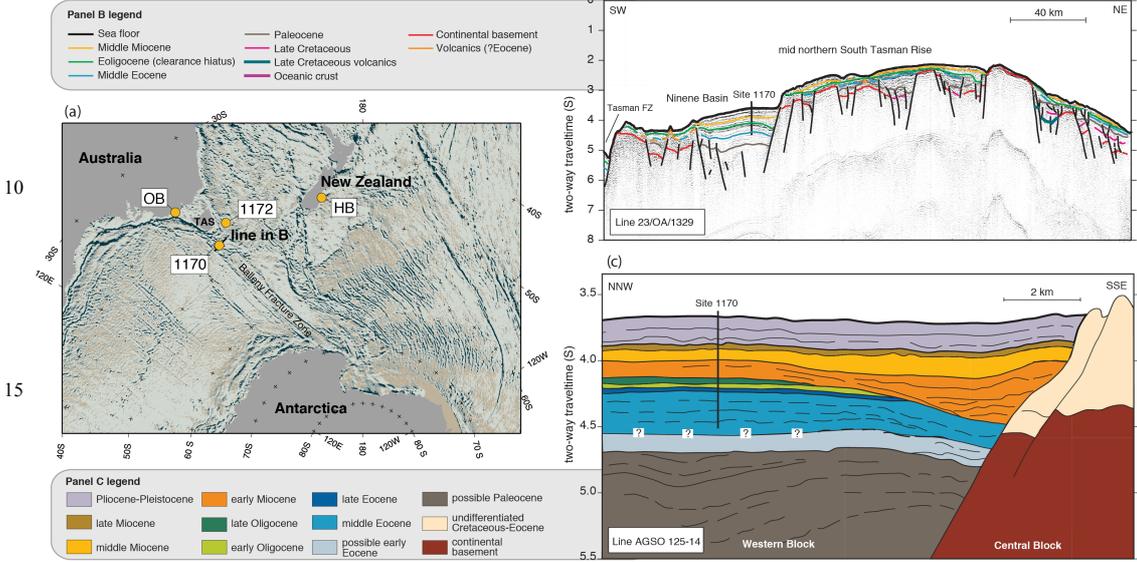
Main figures



25 **Figure 1. Generalised Eocene surface ocean circulation patterns in the southwest Pacific Ocean.** (a) Generalised early Eocene (~52 Ma) circulation. (b) Generalised middle Eocene circulation pre-MECO (~41 Ma) and post-MECO (~39 Ma). (c) Generalised peak MECO (~40 Ma) circulation. Maps constructed with GPlates, using Torsvik et al. (2012) paleomagnetic rotation frame and Matthews et al. (2016) continental polygons and coastlines for 52 Ma (a) and 40 Ma (b and c). Note that, within this rotation frame, there is uncertainty on the drawn paleolatitudes. For example, Site 1170 is drawn at 61.6 °S at 40 Ma, but the uncertainty margins on this are between 58.76 °S and 64.55 °S (van Hinsbergen et al., 2015). Currents drawn after reconstructions by Bijl et al. (2011, 2013b, 2013a) and this study. EAC = East-Australian Current; PLC = Proto-Leeuwin Current; TC = Tasman Current; proto-ACC = proto-Antarctic Counter Current.

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20 | **Figure 2. Tectonic setting of ODP Site 1170 and other studied sites** (a) Present-day map of the Australo-Antarctic sector of the Southern Ocean, with present-day locations of sites and sections used in this study as yellow circles (ODP Site 1170; ODP Site 1172; OB, Otway Basin; HB, Hampden Beach). NW-SE structural trends mark the direction of rifting between Australia and Antarctica, clearly visible in the (labelled) Balleny Fracture Zone. Seismic profile line 23/OA/1329, as shown in panel b, drawn as thick black line. Seismic profile line AGSO125-14 not drawn due to its small scale. Adapted from Bijl et al. (2013b) and Cande and Stock (2004). (b) Interpreted SW-NE seismic profile (line SO36-58) across the South Tasman Rise, illustrating the Site 1170 location in a graben structure. Profile and interpretation adapted from Hill and Moore (2001). (c) Interpreted NNW-SSE seismic profile (line AGSO125-14) across the South Tasman Rise, including Site 1170, illustrating laterally thinning seismic layers of interpreted middle Eocene age. Profile and interpretation adapted from Exxon et al. (2001).

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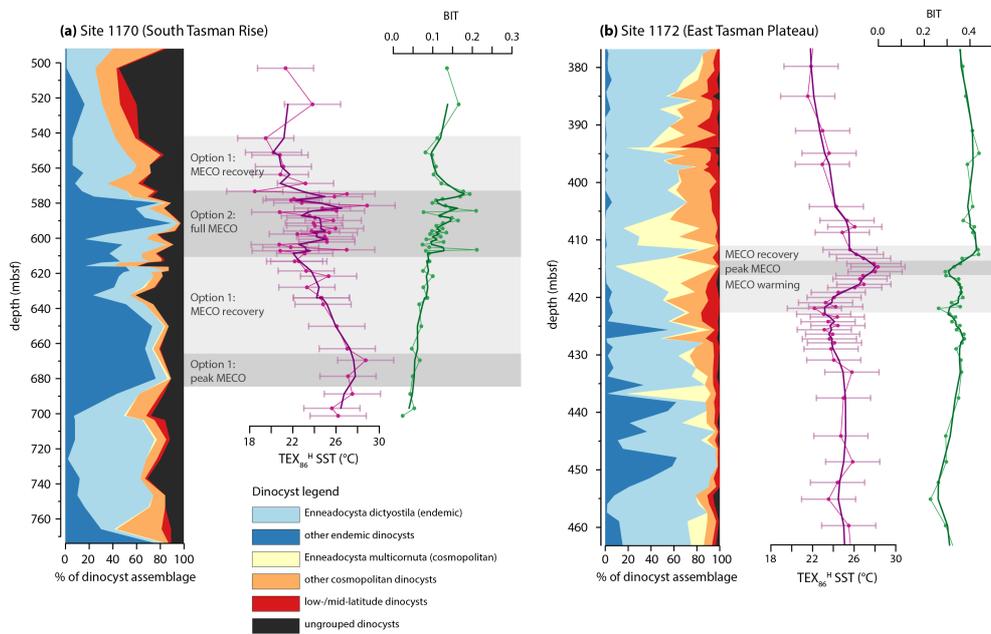


Figure 3. Dinocyst and temperature data from ODP Site 1170 and Site 1172. (a) Left: cumulative silhouette plot of relative abundances of dinocyst biogeographic groups at Site 1170. Especially for the younger part of the 1170 record, a high proportion of specimens of the genus *Deflandrea* could not be identified to the species level, causing the high abundance of the “others” group. Middle: TEX₈₆^H-based SST (in degrees celsius) in pink, with 5 point moving average in purple. Error bars are combined calibration and analytical error (1 s.d.) (± 2.6 °C). Right: BIT in green, with 5 point moving average in dark green. Plotted against depth in metres below seafloor on the vertical axis. Gray horizontal bars visualize the two different options for extent of the MECO, as presented in paragraph 4.1.3. (b) Same as a, but for Site 1172. Data from (Bijl et al., 2010, 2011).

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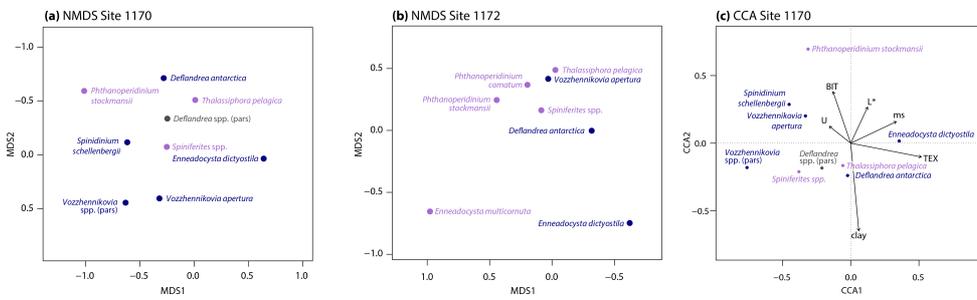


Figure 4. Ordination results. (a) Nonmetric multidimensional scaling ordination diagram for the dinocyst assemblage data of Site 1170. Species scores as circles, colour-coded by biogeographic affinity (purple, cosmopolitan; blue, endemic; grey, not assigned). (b) Nonmetric multidimensional scaling ordination diagram for the dinocyst assemblage data of Site 1172. Species colour-coding as in panel a. (c) Canonical correspondence analysis ordination diagram for the dinocyst assemblage data of Site 1170. Species colour-coding as in panel a. Abbreviations are as follows: BIT, BIT index; clay, clay fraction (%); L*, CIELAB lightness variable; ms, magnetic susceptibility; TEX, TEX₈₆; U, uranium content. Total amount of inertia in species data explained by environmental variables is 34%. For visual clarity, only the most abundant taxa (taxa that occur in >10% of the samples, have a mean relative abundance >1%, and have a maximum relative abundance of >5%) are shown in [all three panels](#). Ordination plots showing all taxa are provided as Supplementary Figure 3.

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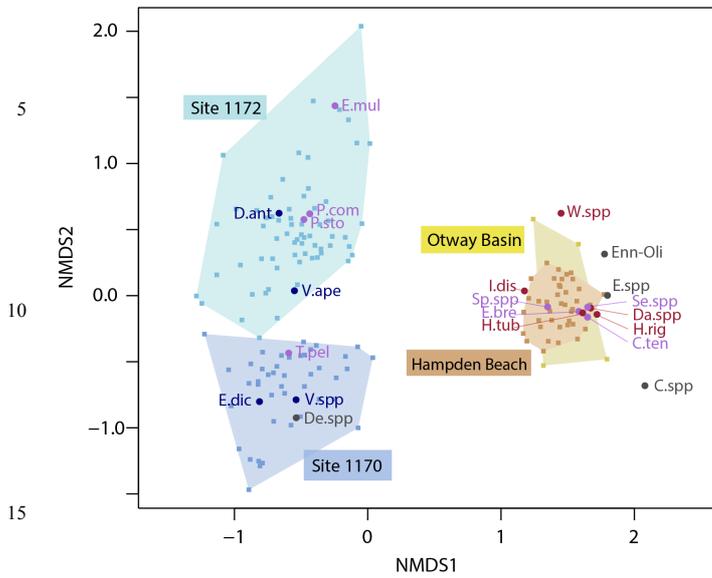


Figure 5. Nonmetric multidimensional scaling ordination diagram for the combined dinocyst assemblage data of Site 1170, Site 1172, Hampden Beach and Otway Basin. Species scores as circles, colour-coded by biogeographic affinity (red, mid-/low-latitude; purple, cosmopolitan; blue, endemic; grey, not assigned). Samples scores as squares, colour-coded by location (light blue, Site 1170; dark blue, Site 1172; orange, Hampden Beach; yellow, Otway Basin), with shading connecting same-location samples. Abbreviations are as follows: C.spp, *Corrudinium* spp. (pars); C.ten, *Cribroperidinium tenuitabulatum*; Da.spp, *Dapsilidinium* spp.; D.ant, *Deflandrea antarctica*; De.spp, *Deflandrea* spp.; E.bre, *Elytrocysta brevis*; E.dic, *Enneadocysta dictyostila*; E.mul, *Enneadocysta multicornuta*; Enn-Oli, *Enneadocysta-Oligosphaeridium* intermediate; E. spp, *Enneadocysta* spp. (pars); H.rig, *Hystrichokolpoma rigaudiae*; H.tub, *Hystrichosphaeridium tubiferum*; I.dis, *Impagidinium dispertitum*; P.com, *Phthanoperidinium comatum*; P.sto, *Phthanoperidinium stockmansii*; Se.spp, *Senegalinium* spp. (pars); Sp.spp, *Spiniferites* spp. (pars); T.pel, *Thalassiphora pelagica*; V.ape, *Vozzhennikovia apertura*; V.spp, *Vozzhennikovia* spp. (pars); W.spp, Wetzellioids. For visual clarity, only the most abundant taxa are shown.

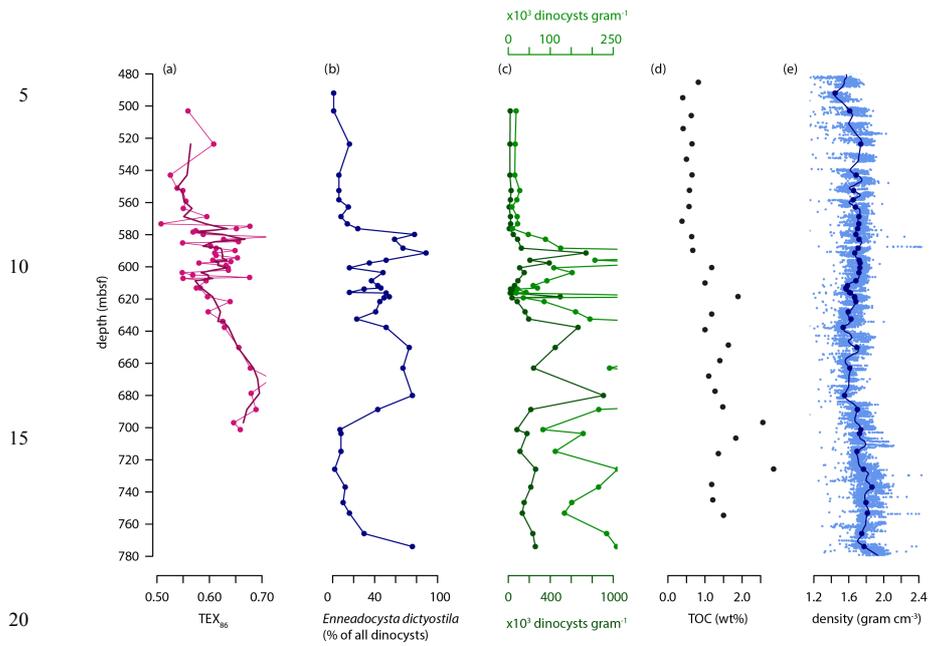
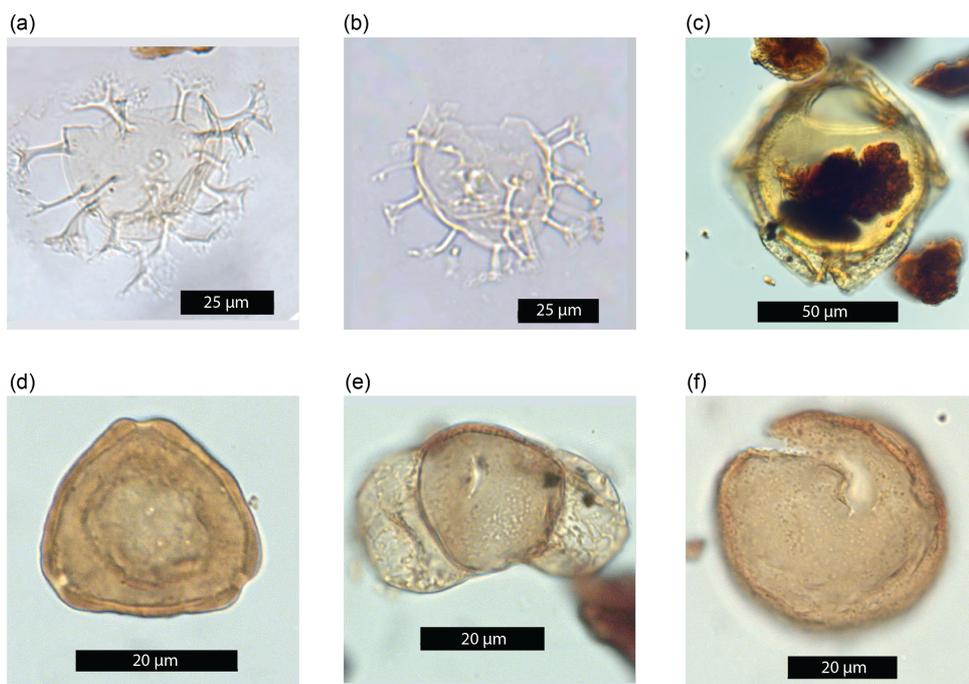
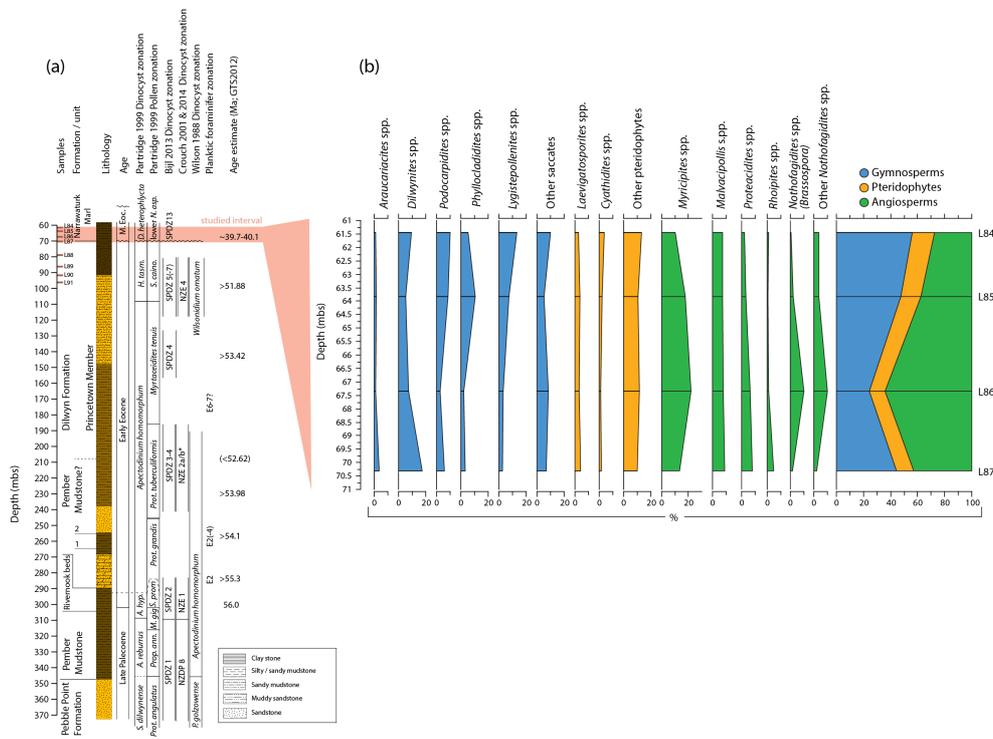


Figure 6. Selected proxy records over the MECO interval of Site 1170, plotted against depth in metres below sea level. **(a)** TEX_{86} (pink dots and line), with three-point moving average (purple lines). **(b)** Relative abundance of *Enneadocysta dictyostila* (percentage of total dinocyst assemblage; dark blue dots and line). **(c)** Dinoflagellate cyst content (cysts per gram of dry sediment; two different scales shown for visual clarity in dark green and light green). **(d)** Total organic carbon (weight percentage; black dots) (from Exon et al., 2001). **(e)** GRA sediment density in (gram per cubic centimetre; light blue dots original data; dark blue line LOESS fit; dark blue dots interpolated LOESS fit to depth of dinocyst samples) (from Exon et al., 2001).

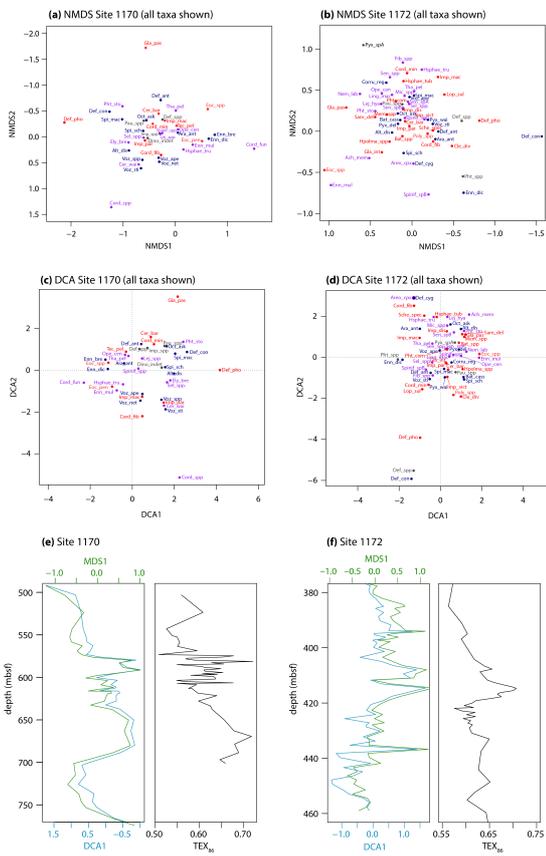
Supplementary figures



Supplementary Figure 1. Plate with light microscope images of relevant palynomorphs encountered in this study. (a) Dinocyst *Enneadocysta dictyostila* from sample 1170D 21R 4W 85-87 cm (EFC unavailable), scale bar 25 µm. (b) Dinocyst *Enneadocysta multicornuta* from sample 1170D 23R 2W 85-87 cm (EFC unavailable), scale bar 25 µm. (c) Dinocyst *Dracodinium rhomboideum* from sample L86 slide 2 (EFC E48.1), scale bar 50 µm. (d) Pollen *Myricipites harrisii* from sample L85 slide 1 (EFC J15.4), scale bar 20 µm. (e) Pollen *Podocarpidites ellipticus* from sample L84 slide 1 (EFC G19.2), scale bar 20 µm. (f) Pollen *Dilwynites granulatus* from sample L87 slide 1 (EFC J16.1), scale bar 20 µm.

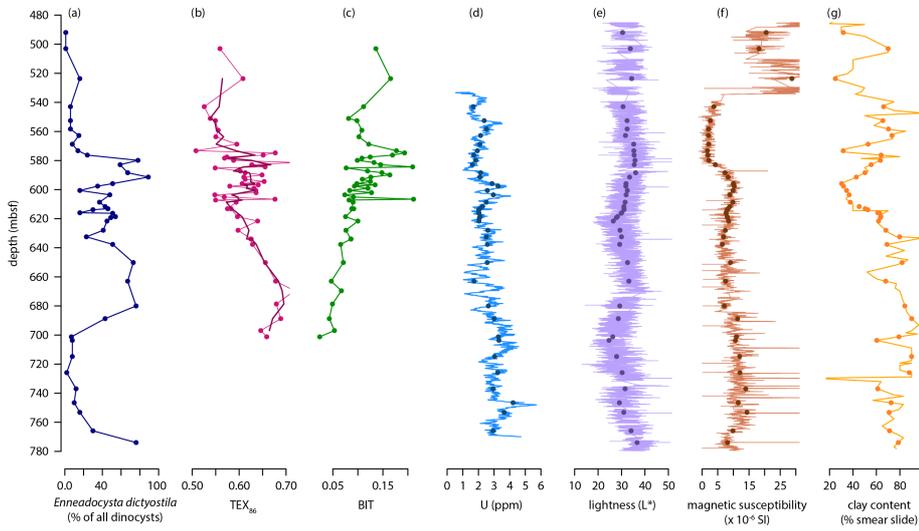


Supplementary Figure 2. (a) Stratigraphy of the Latrobe-1 borehole, including studied samples, lithologic units, lithology and age constraints based on microfossil biostratigraphy. The interval analysed in this study is highlighted in pink. Figure adapted from (Frieling et al., 2018a). (b) Relative abundances of representative sporomorph taxa in samples L84-L87 from the Latrobe-1 borehole, in percentage of total sporomorph assemblage.



5 | **Supplementary Figure 3.** Additional ordination results. Nonmetric multidimensional scaling (NMDS) ordination diagram for the dinocyst assemblage data of Site 1170 (a) and Site 1172 (b). Detrended correspondence analysis (DCA) ordination diagram for the dinocyst assemblage data of Site 1170 (c) and Site 1172 (d). Species scores in a-d as circles, colour-coded by biogeographic affinity (red, mid-low latitude; purple, cosmopolitan; blue, endemic; grey, not assigned). Full names for dinocyst abbreviations can be found in the Supplementary Datafile. First axis of DCA (blue) and NMDS (green) analysis of Site 1170 (e) and Site 1172 (f), together with the respective TEX₈₆ records (black).

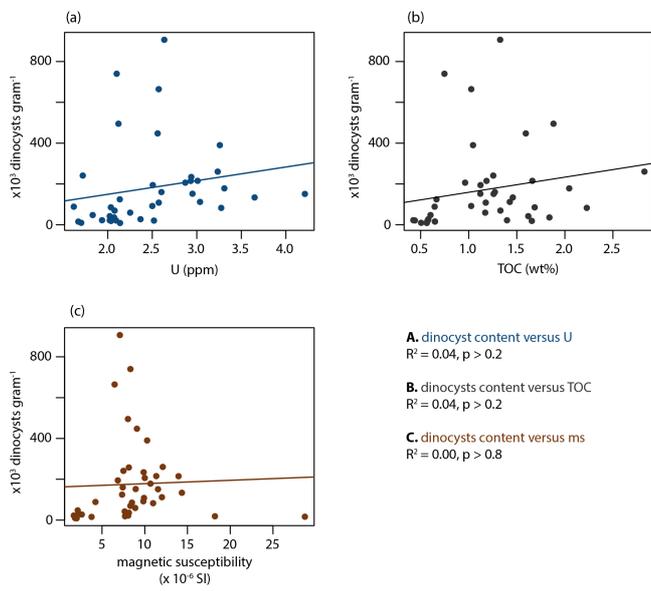
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Supplementary Figure 4. Environmental proxy records over the MECO interval of Site 1170, as used in CCA analysis (b-g). Original data plotted as line, data interpolated to depth of dinocyst samples plotted as dots. Plotted against depth in metres below sea level. (a) Relative abundance of *Enneadocysta dicyostila* (percentage of total dinocyst assemblage; dark blue dots and line). (b) TEX_{86} (pink dots and line), with three-point moving average (purple lines). (c) BIT (green dots and line). (d) Sedimentary uranium content (ppm; blue dots and line). (e) Spectrophotometric lightness (CIELAB L^* ; purple dots and line). (f) Core-measured magnetic susceptibility ($\times 10^{-6}$ SI). (g) Clay content (% of smear slide). Data in panels d-g from Exon et al. (2001).

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5 | **Supplementary Figure 5.** Scatter plots and regression analysis of sedimentary dinocyst content as a function of selected proxy records of Site 1170, indicating no significant correlation. (a) Dinoflagellate cyst content (cysts per gram of dry sediment) against uranium content (ppm). (b) Dinoflagellate cyst content (cysts per gram of dry sediment) against total organic carbon content (weight percentage). (c) Dinoflagellate cyst content (cysts per gram of dry sediment) against magnetic susceptibility ($\times 10^{-6}$ SI). U, TOC and ms data from Exon et al. (2001).

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