

Interactive comment on “A dynamic climate and ecosystem state during the Paleocene-Eocene Thermal Maximum – inferences from dinoflagellate cyst assemblages at the New Jersey Shelf” by A. Sluijs and H. Brinkhuis

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AUTHOR COMMENT

We thank referee 2 for his/her positive review and constructive comments. They have enabled us to improve the quality of the manuscript tremendously. Below we discuss all points raised.

Appy Sluijs and Henk Brinkhuis

REFEREE #2

C1352

Referee's comments on manuscript by Sluijs & Brinkhuis, entitled "A dynamic climate state during the Paleocene-Eocene Thermal Maximum; inferences from dinoflagellate cyst assemblages at the New Jersey Shelf" Overall The authors present some interesting findings which present one of the first studies to examine environmental variability within the pronounced greenhouse warming event of the Paleocene-Eocene Thermal Maximum. Whilst similar palynological data have been presented previously from other sites (e.g ACEX), these data have not yet been discussed in the context of intra-PETM variability, nor have they been interpreted using results from multivariate data analysis. The paper is in the main very well written and contains some interesting arguments, the figures are well drafted, the illustrations provided in the plates are of good quality, and the manuscript is largely internally consistent. The paper is appropriate for publication in Biogeosciences, and represents an elucidation of intra-event environmental fluctuations associated with a pulse of rapid global warming that is being taken as an ancient analogue for anthropogenically induced warming. Palynological data is notoriously complex and difficult to interpret, it being extremely difficult to determine which single or combination of different ecological variable(s) is/was responsible for the fluctuations in abundances observed. The DCA/CCA data analysis methods employed provide a very good indication of some of the likely controls on some of the taxonomic groups discussed in this manuscript. However, although the authors indicate that there are no major increases in the terrestrially derived palynological fraction associated with periods they invoke as being characterised by increased runoff, by only presenting data on marine organic-walled phytoplankton, an opportunity to provide more robust palaeoenvironmental interpretations by integrating the remaining palynofacies components (e.g. sporomorphs and phytoclasts) has been missed. The findings that are presented will be of general interest to a wide audience of palaeoceanographers, palaeoclimatologists, micropalaeontologists and climate modellers. Many of the technical arguments presented stand up to close scrutiny, but some cases the authors regrettably perpetuate misconceptions that have permeated the literature for several years, the most notable of which concerns the most significant genus of dinocysts associated with the

C1353

PETM, *Apectodinium*. Whilst many palynologists reading the new text will be aware of such problems, non-specialist readers may not, and thus could easily be misled into believing that there is no debate as to the biological affinities of this genus – this is absolutely not the case, and a more accurate articulation of affinities should be presented. However, once this has been rectified the manuscript will provide a very useful contribution to the literature concerning the PETM. This referee believes the majority of the content and argument presented in this paper are scientifically sound and supported by the integrated nature of the different data sets provided (e.g. dinocyst data, sedimentology, TEX86, MS, etc.), but has a couple of major points to raise which must be attended to prior to final publication of the manuscript (see below).

Specific comments:

Whilst the use of species complexes has been proven to have (palaeo-)ecological utility when interpreting dinocyst distribution data in previous publications, in one case in the present submission the authors construct the *Senegalinium* complex from all hexa-2a peridiniod dinocyst taxa present in the samples. This complex thus comprises numerous different peridiniod taxa, many with quite different morphologies, sizes and even differences in tabulation. There is no hard proof that all these taxa, even the majority of these taxa were all governed by the same ecological controls on their distribution. However, as the authors once again do not provide any raw species count data for the reader to consult, it is impossible for the reader to conduct an independent assessment of the effects that grouping such often disparate taxa into a single complex might have had on the abundance data. Thus given the importance of such genera as *Senegalinium* itself in many PETM sections, the reader is totally unable to determine the percentages or absolute abundances of these important taxa, whether this single genus might contribute 1% or 99% of the abundance peaks in this species complex. In any circumstances it ought to be a matter of scientific protocol to provide the reader with the raw count data in order firstly for the authors to demonstrate to the reader that they have confidence in their datasets, secondly for the reader to have access to the

C1354

raw data to independently verify the interpretations put forward, and thirdly for future readers to have access to raw data so that they may be used in hitherto unforeseen ways or utilised using new analytical methodologies.

Reply: We completely agree with the referee and we include the raw data as a Supplementary Table. Within the *Senegalinium* complex, only two taxa are dominant in our samples: *Senegalinium* and *Phthanoperidinium*, as now indicated in the table.

In all cases in the text where a complex of dinocyst taxa is referred to, the authors would be advised to use the word 'complex' in full; whilst 'cpx' is a necessary abbreviation in the context of diagrams/figures, it is quite unnecessary and even potentially confusing for the non-specialist when employed in the main text.

Reply: done

Section 4.1.2 Heterotrophy. This referee does not take any pleasure in doing so, but feels that it must be pointed out that many of the arguments presented in this section are simply incorrect or founded on extremely tenuous/dubious information, and are regrettably becoming entrenched in the literature with little, if any, hard data to back them up. In many cases the arguments presented are simply incorrect and are being perpetuated fallaciously in successive publications. The authors are extremely capable taxonomists with a familiarity with the literature and thus they will be aware that there is actually NO morphological evidence from the paratabulation schemes of *Apectodinium* (or even the wider Subfamily Wetzelioideae to which it belongs) to suggest that the group has affinities with the protoperidinoids (or more properly the Subfamily Congruentidioideae). All palynologists would probably agree that there is no disputing the fact that morphologically *Apectodinium* is a typical wetzelioidean dinocyst. The most authoritative publication on higher systematic levels of dinoflagellate classification, Fensome et al. (1993), quite clearly allocates *Apectodinium*, and all other related peridiniods with quadra-style mid-dorsal anterior intercalary (2a) plates, to the Subfamily Wetzelioideae, based on observations of sub-divided paracingular plates

C1355

in typical wetzelielloideans (also confirmed by such taxa as Charlesdowniea, etc.), which contrast with Evitt's (1985) statement of an undivided paracingular area. The quadrastyle 2a plate arrangement is remarkably stable within the wetzelielloideans, and indeed episomal tabulation is remarkably conservative within this long lived fossil group, in striking contrast to extant and fossil congruentidioid/protoperidinioid cysts, which have extremely variable, cinctioid or even bipesioid episomal tabulation (even when the diplopsalioideans are excluded). Nor does a pentagonal outline (ambitus) to many (but not all, cf. *A. homomorphum*, *A. parvum*) species of *Apectodinium* serve to identify the genus as protoperidinioid, as many other peridinioids also have outlines of this shape (cf. the majority of non-primarily pigmented non-protoperidinoioid peridinioid fossil cysts), whereas many protoperidinioids have outlines that are anything but pentagonal. Whilst the possession of primary pigmentation in extant and most fossil congruentidioids can serve to identify their biological affinity, this is should also be verified by recognition of other morphological characteristics confirming such an assignation. The few congruentidioids for which we have nutritional information to infer a heterotrophic life-style produce pigmented cysts today. It is thus by inference that a heterotrophic nutritional life-style has been suggested for primarily pigmented fossil congruentidioid cysts. As only some of the *Apectodinium* specimens described here apparently show pigmentation – are the authors thus implying only some of these specimens were heterotrophic? One would presume not? However, no explanation for this unusual phenomenon is provided, or even speculated upon. If the genus *Apectodinium* cannot unequivocally be demonstrated to be a congruentidioid/protoperidinioid, then this line of argument for heterotrophy falls apart. In some cases, such as the North Sea, *Apectodinium* is accompanied by assemblages of pyritized diatoms, sometimes believed to be the 'prey' for the dinoflagellates, however, the dinoflagellates could simply be responding to the one of the same ecological parameter that was causing the diatoms to bloom, not specifically feeding on the diatoms (without sub-lamina scale studies there is no way of determining whether the two taxa were even blooming at the same time). The authors should further bear in mind that other nutritional modes

C1356

have been described for extant peridinioids other than heterotrophy. The arguments presented above also impinge on lines 384-5.

Reply: As the referee indicates there is an active discussion going on within the dinoflagellate community on the paleoecology of *Apectodinium* as well as the morphological resemblances with modern heterotrophic dinoflagellates. In fact, there is active discussion whether wetzelielloideans have just one dorsal cingular plate or multiple (cf. Evitt, 1985 versus Fensome et al. 1993, as well as some unpublished information by one of the authors). Fensome et al., 1993 base their analyses on a line drawing by Lentin and Vozzhennikova (1989), which is not based on an actual photograph and cannot be evaluated. Hence, as there is discussion, the last thing we intended to do in this paper is to solve the indeed outstanding issue and we were careful to only suggest the distinct possibility that *Apectodinium* was heterotrophic. The only new thing we add to the present discussion is the brown color of many specimens in New Jersey that resembles that of Modern heterotrophic protoperidinioids. We have rewritten this section to make this clearer, and still indicate this is a matter of debate.

Section 4.3 Fresh water forcing l.346-349. The construction of this sentence is not terribly clear. Dickens' (2008) paper indicates that the magnetotactic, bacterially produced magnetite grains were not dissolved post-depositionally from the PETM sediments in which they were deposited as these sediments were not subject to corrosive sulphidic conditions due to the presence of oxygenated sediments immediately underlying them. The way in which the present sentence is phrased (the use of 'while') makes it appear that the authors believe the oxygenated conditions to be present during the deposition of the PETM clays – this referee is sure that this is not what the authors intended to convey, and recommends the sentence be rephrased to avoid ambiguity.

Reply: done

Much is made in this section of enhanced runoff driving the increased availability of nutrients, which in turn raised productivity levels of low-salinity dinoflagellates. This

C1357

is an argument that has been put forward on many occasions, and indeed there is palynological evidence from some locations to substantiate this theory. However, the authors state that on the NJ Shelf there is no supporting palynological evidence for enhanced runoff in the form of increased terrestrial sporomorphs, contrasting markedly with the situation at such sites as ACEX. It is therefore surprising that the authors do not even mention the work of Knies et al. (2008, Paleoceanography) on nitrogen isotopes from ACEX, who argued that they saw no evidence for increased surface water productivity driven by increased input of terrestrially sourced nitrogen during the PETM (at a locality where the Senegalium complex has also been used to infer low surface water salinities and enhanced productivity resulting from enhanced runoff). Instead they saw changes in the nitrogen inventory driven by a coupling of denitrification and N₂ fixation, and suggested that nitrogen supply to the photic zone from enhanced river runoff was an insignificant source of nitrogen compared to bacterial diazotrophy. I would be useful if the authors could provide some discussion of this phenomenon in the context of the present work, given its stress on increased runoff being responsible for driving the increases in productivity in certain dinocyst groups.

Reply: Point 1: terrestrial palynomorphs. As (still) indicated in the papers, we record on average 1 terrestrial palynomorph grain per slide and it is just impossible to gain any statistically significant number for the change in the flux of terrestrial palynomorphs, unfortunately. This section thus indeed differs markedly from all other PETM section from the shelf ever studied. Either way, whatever proxy for organic matter input by rivers will also be affected by sea level rise (Cramer et al. 1999; Sluijs et al., 2008), rates of organic matter remineralization and marine production. Point 2: We have actually not argued for an increase in river run off to explain dinocyst assemblage changes during the PETM of the ACEX core. Percentages of the low-salinity-tolerant group remain rather constant at ~80-90%, as also shown by Sluijs et al. (2006, *Nature*; 2008, *Paleoceanography*). It goes beyond the scope of this paper to discuss some of the somewhat debatable conclusions of Knies et al. 2008 (there are many potential problems with using bulk nitrogen isotopes which is why hardly anyone has done it) from

C1358

another site. Regardless, yes, of course is it possible that eutrophication can happen due to several mechanisms, although Lippert and Zachos (2007, *Paleoceanography*) assign this to increased supply from rivers because of the vast concomitant increase in sediment (clay) supply, which must come from rivers. We indicate that this suggests a causal link. We have included that latter point on the sediment supply to the discussion to make this point more clear.

Section 5 (lines 364-375) The authors discuss the possibility of winnowing as a process which may have modified the pre-PETM assemblages, but not the possibility that oxygenation levels may have also played a role. Lowered oxygen conditions (even if restricted to below the sediment-water interface) during the PETM would increase the likelihood of the preservation of more labile/less refractory cyst types, whereas the more energetic, coarser grain-sized sediments before the PETM would have been deposited in higher oxygen conditions and thus less oxidation-resistant cysts could be preferentially removed from the assemblages – the peridinioid taxa mentioned as being largely absent from these earlier sediments are just those which would be affected by such conditions. Some discussion or refutation of such a mechanism to account for these discrepancies should be provided. Reply: Good point. We have included the following sentence: It is unlikely that the record is affected by preferential oxidation of some peridinioid taxa, as these are present throughout the record and well preserved. I.388-389. The authors should be quite transparent about where these abundance peaks occur, namely prior to and immediately after the main CIE, so far as the rather small diagrams can be interrogated, but confirmed by Table 1.

Reply: done

Stratification: mechanisms and implications? The authors introduce seasonal hyperstratification and hypersaline surface waters as a reason for the acme abundances of the goniodomids (I.386-398), thus this would imply a phase of hyperstratification/hypersalinity prior to the CIE, the origin of which the authors do not explain. This should be accounted for if such an interpretation is going to be presented – e.g. is

C1359

there any supporting evidence from the rest of the dinoflagellate assemblages in these samples? The mechanism of stratification is discussed time and again, each time with a different outcome: the goniiodomids were responding to hyperstratification and hypersalinity, the Apectodinium peaks (e.g. lines 241-245) are related to temperature-induced stratification, and the Senegaliniun complex is interpreted as responding to salinity induced stratification due to surface water hyposalinity. It would be useful for the reader if the authors could forward a more in-depth explanation of the development of these three methods of stratification – after all, the tenet of the paper is environmental variability during the PETM, and the ways in which different forms of stratification have been invoked is an interesting but under-discussed aspect of that variability.

Reply: Proposed mechanisms for stratification are quite elaborately included in the MS: We suggest that Senegaliniun blooms were forced by fresh water runoff, which is consistent with increased riverine clay flux and the development of seafloor suboxia (and magnetic grains causing higher MS). For Apectodinium we are, we feel, quite clear in that we have not unraveled the ultimate cause of its acme. The section that the reviewer points to is obviously a speculative one where we actually particularly touch on the aspect of seasonality (rather than warming or stratification) as a potential but unrestricted forcing mechanism. Also for the goniiodomid case, we are quite clear by suggesting a mechanism proposed in another paper to explain goniiodomid blooms. We have rewritten some of the sections to make these mechanisms of stratification even more clear.

Minor comments/corrections: This seems like a long list, but concerns only minor grammatical or spelling errors.

Reply: We have followed all below suggestions. We thank the reviewer for his detailed reading and comments.

Title: substitute 'on' for 'at' I.20, 76, the term 'thermophilic' might be preferred to 'thermophilious' I.30, insert comma after CIE I.32, insert 'with' after 'contrast' I.38, replace

C1360

'to' with 'regarding' I.47, replace 'lasting' with 'long' I.50-52, awkwardly worded, suggest: "The onset of the PETM is marked by a pronounced negative stable carbon isotope (del13C) excursion (CIE), measured in marine and terrestrial sedimentary components (refs), and an additional warming of ~5- 9C (refs)." I.70, move 'particularly' to after 'companies' I.75, "This is most notably shown by the quasi-globally..." I.87, replace 'by' with 'a' I.88, "by using dinocyst distribution patterns set against..." I.89, delete 'e.g.' I.93-95, "processes which underlie this event, and the effects of rapid global warming and exogenic carbon release during greenhouse conditions" I.113, replace 'upper' with 'late' I.116, upper case 'F' for Formation I.117, insert 'any' before siliciclastic I.125, delete 'e.g.' I.134-5, "represent the hypnozygotic stage of certain species of dinoflagellates – however, less than 20% of living dinoflagellate species produce fossilizable cysts (Fensome et al., 1996)." 'in the Modern' is an awkward phrase. I.135, "Living organic cysts", the authors actually refer to the cyst, not the cell contents – the cyst itself is not alive! They mean "Cysts produced by living dinoflagellates". In addition, there are numerous other published references that can be referred to here, in addition to the now-published Rochon et al. (2009). I.142, replace 'tiniest' with 'smallest'. I.150, replace 'based' with 'founded'. I.157, rather clumsy phraseology, suggest replacement of "marine, or even freshwater" with "stressed aquatic". I.159, "taxonomic" I.167, add refs. for magnetic susceptibility papers mentioned elsewhere. I.173, replace 'early' with 'lower' and 'Upper' with 'Late' – the authors confuse chronostratigraphic and lithostratigraphic terminology here. I.179, "in both the Recent (refs) and the Palaeogene (ref)." There is no geological period known as the "Modern". I.182, lower case for 'peridinoid' I.191, delete 'at' I.195, insert "of dinocyst-defined events" after 'correlation' I.198, insert 'dinocyst' after 'correlation,' I.209, move 'mutually' to after 'plot in' I.210, 'in' instead of 'into' I.212, if I read this correctly, the reference to Fig 2B should actually be to Figure 3A? I.215, replace 'as well as' with 'and' I.216, insert 'µm' after '>63' I.222, insert hyphen after global for internal consistency (see I.75). I.225, delete comma and 'which' and replace 'span' with 'spanning' Headings in I.227227, 246, 259, 300 all require capital initial letters. I.228, delete apostrophe, this is not a possessive noun.

C1361

I.229, replace 'than' with 'to' I.241-244, a complex and somewhat opaque sentence, suggest rewording as follows: "However, many dinoflagellates bloom in a particular season (ref), which indicates that warming/stratification and blooming of *Apectodinium* may have been seasonal in nature and the warming would thus not necessarily have influenced MAT" I.254, delete first hyphen. I.263, replace 'Modern' with 'extant' I.266, a poorly worded sentence and one which frankly is not terribly helpful – many of the living and fossils members of the Family *Congruentidiaceae* produce cysts that do not have pentagonal outlines, this is a very tenuous support for the affinities of *Apectodinium*. I.272, replace 'Modern' with 'living' I.273-4, place square brackets round '[even zooplankton]' I.280 'foraminiferal' – adjective, insert hyphen between 'organic-rich' I.286, replace 'at' with 'in', and 'in' by 'around' I.292, suggest "have caused mixing of deeper nutrient-rich waters into the photic zone on a regional scale thereby..." I.294-5, insert 'probably' before 'only', and replace 'part' with 'percentage', delete 'organisms' and replace with 'assemblages'. I.307, some mention should be made of reports of the published report of pre-PETM acmes of *Apectodinium* in the North Sea – even if the authors argue against this being correct. I.308, replace 'the above' with 'these' I.323, replace 'an Upper' with 'a Late' – a transgressions were events in time. I.333, insert 'in a manner' after 'Hence,' I.334, upper case initial for 'Axis' I.340, insert 'the' after 'CCA,' I.341, insert '(MS)' after 'susceptibility' I.344, replace 'But' with 'However' I.356, replace 'to' with 'of' I.357, replace 'food' with 'nutrients' I.366, insert full stop after 'spp' I.386, delete third 'of' I.390, replace 'have been' with 'were' I.399, "...often informally referred to by several authors..." I.401, "occur abundantly" I.403, replace 'gone' with 'became' – yuk: they had no choice in the matter! I.407, replace 'Only few' with 'Little' I.409, delete comma after 'sections' and insert one after the closed bracket. I.421, delete 'e.g.' and replace with 'for example'; lower case 'g' for 'goniodomid' I.423, capital initial for 'Milankovitch' I.426, too colloquial, replace 'even stunning' with '(even extremely) abundant' I.431-3, awkward sentence, suggest: "high accumulation, marine and terrestrial PETM sites from around the world.or larger scale phenomena." I.463-465, suggest insertion of 'Plate' before each bracketed plate reference, to avoid confusion

C1362

with paraplate terminology. I.472, 474-5, do the authors mean the 'endocyst' (I suspect not), or 'main body' of the cyst? Care needed to avoid ambiguity. I.476-7, numbering not necessary, remove '(1)' and '(2)' and replace 'besides' with 'or' I.479, "with a usually detached.." I.487, start sentence with "However, *F. ferox* has more..." List of species: suggest 'cpx' is rendered in full, as 'complex' I.517-8: is this a quote? If so a ref. needed, if not, loose the inverted commas and the capital for 'gonyaulacoid' is not needed. I.533, 'horrific' is hardly a scientific term! I.534., replace 'Upper' with 'Late' I.538, delete superfluous full stop I.541, if not accessory sutures (such faint tabulation), is this the right genus to allocate this taxon too? I.543, italicise *Cribroperidinium* I.522, no need for capital 'G' for goniodomid. I.555, 557, insert full stop before 'Part' I.586, remark is poorly phrased: "...in distribution of ornamentation"? I.625, 'Drill' not needed. I.628, 631, replace 'distribution' with 'abundances' Table 1: 'goniodomid' (events B and I) does not need an initial capital letter The heading for plates 9-11 are wrongly labelled as plates 1, 2 & 3...

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C1363