Referee #1: Dr. Dodsworth

Referee: Page 4, line 6. For clarity, it would be worth spelling out *Cyclonephelium compactum* at first mention, to avoid potential confusion with *Cauveridinium*.

Response: We have spelled out *Cyclonephelium* completely as suggested by the referee.


Response: Spelling corrected.

Referee: Page 4, line 30. "...reporting of Ccm [at the other 15 localities]."

Response: We have followed the referee’s suggestion and added “at the other 15 locations.”


Response: Corrected.


Response: Corrected.

Referee: Page 12. I can’t find Voigt et al. (2004) cited in the manuscript. It should be removed from the reference list if it is not cited.

Response: Voigt et al. (2004) was indeed not cited in the current version of the manuscript we have therefore removed it from the reference list.

Referee: Figure 4 caption. Write out ‘mbs’ in full at first mention.

Response: We have written out “meters below surface (mbs)” in full at first mention.

Referee: Figure 6 caption, line 3. “, open symbols[are]...”

Response: We have corrected the spelling here, i.e. "is” replaced by “are”.

Referee: If a quantitative / semi-quantitative distribution chart of all palynomorphs at genera/ species level is available for the Pratts Landing section, it could be added to the supplementary file, although this is not a requirement given the scope of the article.

Response: A quantitative distribution chart for all palynomorphs is available. We are currently looking to extend the dataset, which as such could form the basis for a second manuscript. Since it is not a requirement given the scope of the present article, we choose to not add the quantitative distribution chart to the supplementary file.
Referee #2: Dr Schiøler

Referee: The ms presents new data and compiles existing data on the Plenus Cold Event at the Cenomanian-Turonian boundary and shows that the Ccm Complex of dinoflagellates migrated towards the Equator during the cold event. It thereby shows that yet another group of dinoflagellates responded to temperature changes by migrating. This is an important observation because it elucidates how environmental factors need to be taken into consideration when biostratigraphic interpretations and correlations are made and also indicates how certain plankton groups can be used as proxies for temperature changes in the far past. The ms is very well written in clear language. It is brief and concise and makes it point without any irrelevant ado. The illustrations are informative, of good quality and well captioned. I have seen this manuscript before and notice that all my previous comments and suggestions to changes have been taken on-board, and I therefore believe that the ms should be published in Biogeosciences as is.

Response: As the referee notes, we have incorporated the comments and suggestions he raised in his review on an earlier version of the manuscript for a different journal.
Referee #3: Anonymous

**Referee:** This study establishes a link between the first consistent occurrence of dinoflagellate cysts grouped in the Cyclonephelium compactum-membraniphorum (Ccm) morphological plexus with the Plenus cold event during OAE 2. Whereas most data were literature derived one additional section was added which represents a locality in northern Alberta. This locality is presented as a High Latitude northern hemisphere site. Data for this locality are shown in Figure 3, which is not very informative. The segment of the featured carbon Isotope curve can be anywhere within the Cretaceous history. No correlations to biostratigraphic zones that are mentioned in the text are indicated. No lithostratigraphy is mentioned either. Since this is the only new data point, more information would be desirable.

**Response:** Despite the distinctive, >2‰, positive excursion in δ13Corg which is indicative for the OAE2 interval, we agree with the referee that more information for the Pratts Landing outcrop locality is desirable. We have changed the title of section 2.1 (Page 3; line 4) from “The Pratts Landing section” into “Stratigraphic setting of the Pratts Landing section”. Most of this section is new text, the section now reads:

“In northwest Alberta and northeast British Columbia, upper Cenomanian and Turonian strata of the Kaskapau Formation form a thick, mudstone-dominated and north-eastward-thinning wedge that spans the foredeep of the Western Canada Foreland Basin (Varban and Plint, 2005). Well-exposed sections in the Rocky Mountain Foothills on the western margin of the foredeep can be correlated with sections in the Peace River Valley, located close to the forebulge. Correlation has been established by using abundant, publically-accessible wireline log data (Fig. 2). Detailed correlation through a grid of 756 wireline logs showed that 28 allomembers, bounded by marine flooding surfaces, could be mapped across the foredeep (Varban and Plint, 2005). In the western part of the foredeep, exemplified by the section at Mount Robert (Figs. 2, 3), nearshore and shoreface sandstones form stacked successions that prograded only 20-40 km seaward from the preserved basin margin; shoreface progradation was limited by a consistently high rate of flexural subsidence (Varban and Plint, 2005, 2008). Traced eastward from Mount Robert, successive allomembers become thinner and finer-grained, and some allomembers (e.g., allomembers 7, 9, 10), pinch out completely before reaching outcrop in the Peace River Valley, exemplified by the section at Pratts Landing (Figs. 2, 3). The section at Pratts Landing, the focus of this study, is located on the north bank of the Peace River (56°01′14″N, 118°48′47″W; Fig. 4), and comprises stacked siltier- and sandier-upward successions, capped, at a prominent flooding surface, by weakly bioturbated, organic-rich claystones and silty claystones characterized by a very high radioactivity (i.e., boundary of allomembers 6 and 8; Figs. 3, 5). Outcrop spectral gamma ray profiles allow the Pratts Landing section to be correlated with confidence to nearby wireline logs (Fig. 3). In the west, the Cenomanian-Turonian boundary was recognized at the top of Kaskapau allomember 6 at Mount Robert, based on the distribution of inoceramid bivalves (Fig. 3). At that section, Late Cenomanian Inoceramus ex gr. pictus (Sowerby) is widely distributed through allomembers 2 to 6, whereas Mytiloides puebloensis (Walsaszczyk and Cobban) is present 2 m above the allomember 6-7 contact, indicating that the lowest Zone of the Turonian is present in the lower part of allomember 7 (cf. Kennedy et al., 2000). The upper bounding surface of allomember 6 can be traced, through well logs, for 220 km eastward to Pratts Landing where it corresponds to the sharp basal surface of a gypsum-cemented silty claystone. That sharp surface, separating allomembers 6 and 8, corresponds to an abrupt increase in radioactivity, and lies 25 cm below the first appearance...
of the Early Turonian inoceramids Mytiloides goppelnensis (Badillet and Sornay) and Mytiloides kossmati (Heinz; Figs. 3, 5). The wireline log correlation shows that, at Pratts Landing, all of allomember 7 is missing, and the earliest Turonian Zone of M. puebloensis also appears to be un-represented, emphasizing the hiatal character of the allomember 6-8 boundary (Fig. 3).

During the Late Cretaceous, the study site was located at ~61°N, ±5 (van Hinsbergen et al., 2015; paleolatitude.org), on the eastern flank of the foredeep, about 160 km from the contemporaneous western shoreline of the Western Interior Seaway (Varban and Plint, 2005, 2008). We generated carbon isotope and dinoflagellate cyst data across about 23 m of upper Cenomanian to lower Turonian strata, based on stable carbon isotope stratigraphy and inoceramid biostratigraphy (Figs. 3, 6).”

To support the above text, we have added three new figures:

"Figure 2. Map of northwest Alberta and adjacent British Columbia showing distribution of well logs, cores and outcrops used to establish the regional stratigraphic framework that forms the basis for the present study. Outcrop sections at Mount Robert in the west, and Pratts Landing in the east are correlated via wireline well logs (gamma ray and resistivity pairs)."
Figure 3. Regional cross-section (located in Fig. 2) showing how allomembers of the Kaskapau Formation can be correlated across the foredeep from Mount Robert to Pratts Landing. Cross-section is condensed from more detailed lines in Varban and Plint (2005). The Cenomanian-Turonian boundary is shown as a broken line at the top of allomember 6. Note how allomember 7 laps out eastward onto allomember 6, and that both allomembers 6 and 8 become increasingly radioactive towards the east. Spectral gamma ray profiles taken at Pratts Landing confirm the correlation of the various stratal units at outcrop with their equivalents in subsurface. The inset stratigraphic logs show more detailed representations of the lithological successions, gamma ray profiles, and the distribution of inoceramid bivalves at Mount Robert and Pratts Landing. Detailed legend in figure 6."
Figure 5. Field photographs of the Pratt's Landing site. With a, showing an overview of upper part of the section showing resistant, gypsum-cemented ledge that marks a sharp erosional boundary between two claystone units. Immediately above the boundary there is a large increase in the uranium content of the sediment. The Early Turonian inoceramid bivalves Mytiloides goppelnensis and Mytiloides kossmati appear 25 cm above the erosion surface. Photograph b. shows an overview of the lower part of the section showing highly bioturbated silty sandstone of Kaskapau allomember 6, sharply overlain, at a major flooding surface (13.6 m level in Fig. 6) by thinly-bedded claystones. Rocks embracing the Plenus Cold Event are represented by a 1.4 m thick, shallowing (sandier)-upward succession bounded above by a major flooding surface. The Cenomanian-
Turonian boundary, marked by a resistant ledge, lies at the 15.3 m level. Note that all of Kaskapau allomember 7 is absent at the erosion surface marking the Cenomanian-Turonian boundary, as illustrated in Figure 3.

We also added the lithostratigraphy to Figure 3, which after addition of the extra information on the Pratts Landing section became Figure 6. Unfortunately no planktonic foraminifer or ammonite zonation is available for Pratts Landing. The only biostratigraphic data that is available for Pratts Landing is based on inoceramids. We added this information to Figure 6 (old figure 3):

"Figure 6. Lithostratigraphy, detailed lithological log, δ¹³Corg, abundances of Cyclonephelium compactum–membraniphorum morphological plexus (Ccm) and inoceramid bivalve stratigraphy for Pratts Landing. Sample intervals for palynology are indicated by horizontal black lines."

Referee: The Ccm occurs throughout and shows an increase within the OAE 2, but not only during the interval that was designated as the Plenus Event. Two other peaks occur above which would indicate that the increased productivity signal prevalent throughout this interval and the possibly increased preservation potential of organic matter during this interval could also be regarded as causes for these occurrences.

Response: We treated the post-Plenus occurrences of the Ccm at lower latitudes in section 3.2 of the manuscript with the following text: "The sustained presence of Ccm after the PCE at all sites, except Bass River (after addition of new figures Fig. 9 – former figure 6), suggests that, in addition to sea surface temperature, other environmental and paleoceanographic factors became dominant in determining the distribution of Ccm once it had occupied niches at lower latitudes.
For example, salinity and proximity to the shoreline may have been important (Harris and Tocher, 2003)."

The reviewer suggests that productivity may have been more important than the factors we mention to explain sustained presence of Ccm after the Plenus Cold Event. Based on modern analogue paleoecology and empirical information, we do not expect this taxon to be particularly sensitive to sea surface water nutrient budgets. We would expect other taxa, notably peridinioid dinocysts, to more strongly respond to such changes (e.g., Sluijs et al., 2005; Earth-science Reviews). We do not note these, nor other productivity indicators along with the additional Ccm occurrences (Van Helmond et al., 2014; Geology and 2015; Climate of the Past) and therefore surmise that productivity was unlikely a dominant factor. However, to accommodate the comment by the reviewer, we will include productivity (i.e. enhanced nutrient availability) as a potential factor.

Preservation of the palynomorphs is variable within sections and between sections but is unrelated to the occurrences of Ccm.

We have included the information mentioned above in the revised manuscript as follows:

(Page 6, Line 20-23) "For example, salinity, (enhanced) nutrient availability and proximity to the shoreline may have been important (Harris and Tocher, 2003). Preservation of palynomorphs, e.g. dinocysts, is variable within sections and between sections but is unrelated to the occurrences of certain species."

Referee: This illustration is then repeated in Figure 6, which is unreadable in the small format as presented.

Response: We will upload the figure again in landscape format and have increased font sizes.

Referee: In Figure 6 five localities are compared, all in the northern hemisphere of which Pratts Landing from Alberta is the only locality that shows the Ccm throughout the Cenomanian. Other localities show the first occurrence within the Plenus Event, but several sections show increased abundances during the warmer interval of the OAE 2 further up section. These occurrences do not confirm the interpretation presented here namely that this species group is a marker for a cold spell. This species group appears to range throughout the Cenomanian to Turonian. The Plenus Cold Event is near the base of the OAE 2 interval, where a number of global paleoenvironmental changes take place. The distribution of this fossil as shown here does not convince me that it is indeed the cold spell that is the main control.

Response: As stated on Page 2, lines 33-38, for two of the five locations, Bass River (van Helmond et al., 2014; Geology) and Wunstorf (van Helmond et al., 2015; Climate of the Past) the FCO of Ccm co-occurs with a pronounced cooling in sea surface temperatures, reconstructed using the biomarker-based proxy TEX86 (e.g., Schouten et al., 2002; EPSL). For the Eastbourne succession the FCO of Ccm occurs in the interval where a Boreal fauna was found (Pearce et al., 2009; Palaeo3), i.e. colder conditions. While for the Iona-1 core the FCO of Ccm occurs in a period of reoxygenation, e.g. minima in sedimentary organic carbon and redox sensitive elements (Eldrett et al., 2014; Geology), which previously have been shown to correlate with a phase of cooling (e.g., Sinninghe Damsté et al., 2010; EPSL). This implies that the FCO coincides with Plenus cooling at all five locations and therefore a causal link is by far the most likely explanation for the observations.
Only at Bass River the occurrence of Ccm is strictly confined to the interval of lowered sea surface temperatures (Figure 6, van Helmond et al., 2014; Geology). We therefore suggest that once Ccm arrived in the mid-latitudes other paleoenvironmental factors became important in controlling its distribution, as discussed above and more elaborately in the revised manuscript.

Referee: Page 1, Line 41: Jenkyns et al. is the wrong reference, their work addressed Arctic sections of Campanian age, not late Cenomanian.

Response: We have removed this sentence and reference. The sentence now reads: (Page 1, lines 39-41) “The Cenomanian–Turonian boundary interval (ca. 94 Ma) was an episode of extreme warmth, with tropical and mid-latitude sea surface temperatures exceeding 35 °C (e.g., Huber et al., 2002; Forster et al., 2007; Van Helmond et al. 2014a).”

Referee: Figure 1: Occurrences of Boreal fauna: Hamulus sp., sp should not be italicized. Why does the carbon curve leave some dots out?

Response: We have corrected Figure 1. The carbon isotope curve in Figure 1 is based on two different records. The high resolution line is based on the data derived from Paul et al. 1999 (Palaeo3), while the low resolution dots are derived from Pearce et al., 2009 (Palaeo3). We have now clarified this in the caption:

“Figure 1. Biozonation, lithology, Plenus Marl beds (Jefferies, 1963) and δ¹³C_carb (low-resolution data (dots and dotted line) derived from Pearce et al., 2009; high-resolution data (solid line) derived from Paul et al., 1999) for the Cenomanian-Turonian boundary reference section at Eastbourne, combined with occurrences of Boreal fauna (Gale and Christensen, 1996). On the right side the ranges of the different definitions for the Plenus Cold Event are indicated.”
Referee: Biostratigraphic and lithostratigraphic information should be added. Figure 3: See comments above. In addition, what is the wavy line, normally indicating a disconformity. Is that the case here? Its meaning should be added to the legend.

Response: We have added the lithostratigraphy to Figure 3, which after addition of the extra information on the Pratts Landing section became Figure 6. The only biostratigraphic data that is available for Pratts Landing is based on inoceramids.
We added this information to Figure 6 (old figure 3). Furthermore the legend was updated.

Referee: Page 4, Line 23: The genus of a species named for the first time, should be spelled out. Page 6, Line 22: zone should be plural.

Response: Both issues have been corrected.
**Additional changes**

We inserted "relatively" before "widespread marine anoxia" in the first sentence of the abstract. Simply using "widespread" could be interpreted in the wrong way, i.e. large areas of the seafloor were not anoxic.

As a result of the addition of three new figures (Figs. 2,3,5), most figure numbers have changes. Fig. 1 remains Fig. 1; Fig. 2 became Fig. 4; Fig. 3 became Fig. 6; Fig. 4 became Fig. 7; Fig. 5 became Fig. 8; Fig. 6 became Fig. 9.

We slightly changed the sentence discussing the placement of the Cenomanian-Turonian boundary, this sentence was:

(Page 4, lines 20-21) "The Cenomanian-Turonian boundary is placed at 15.3 m, at the sharp base of a 20 cm thick, siltstone-rich and heavily gypsum-cemented mudstone lacking macrofauna."

Which now reads:

(Page 5, lines 12-13) "The Cenomanian-Turonian boundary is placed at 15.3 m, at the sharp base of a 20 cm thick, heavily gypsum-cemented silty claystone lacking macrofauna (Fig. 5)."

We also changed the next sentence to make clear we are talking about biostratigraphy based on inoceramid bivalves, this sentence was:

(Page 4, lines 21-25) "The base Turonian marker species Mytiloides puebloensis was not found, but the succeeding Zone, characterized by M. goppelnensis and M. kossmati starts approximately 25 cm above the basal surface (Fig. 3). Ccm is a general constituent (1-4%) of the dinocyst assemblage at Pratts Landing throughout the section, i.e., also below the onset of OAE2 (Fig. 3)."

Which now is:

(Page 5, lines 13-17) "The base Turonian marker inoceramid species Mytiloides pueblensis was not found, but the succeeding inoceramid Zone, characterized by M. goppelnensis and M. kossmati starts approximately 25 cm above the basal surface (Fig. 3). Ccm is a general constituent (1-4%) of the dinocyst assemblage at Pratts Landing throughout the section, i.e., also below the onset of OAE2 (Fig. 6)."

We slightly changed the section describing the author contributions, this now reads:

"N. van Helmond, A. Sluijs and H. Brinkhuis designed the research. Samples and fossils at the Pratts Landing section were collected in the field by G. Plint and I. Walaszczyk. Palynological analyses were carried out by N. van Helmond, N. Papadomanolaki and B. van de Schootbrugge. Carbon isotope stratigraphy was carried out by D. Gröcke and J. Trabuco-Alexandre. Inoceramid biostratigraphy was carried out by I. Walaszczyk. Regional stratigraphy was compiled by G. Plint. Compilation of the global biogeographical distribution of Ccm was carried out by N. van Helmond, H. Brinkhuis, M. Pearce and J. Eldrett. N. van Helmond and A. Sluijs prepared the manuscript with input from all authors."

We changed the acknowledgements to thank the reviewers. The second sentence of the acknowledgements now reads:
"We thank Paul Dodsworth, Poul Schiøler and an anonymous reviewer for helpful comments and suggestions and J. van Tongeren and N. Welters for laboratory assistance."
Equatorward phytoplankton migration during a cold spell within the Late Cretaceous supergreenhouse

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Abstract. Oceanic Anoxic Event 2 (OAE2), a ~600 kyr episode close to the Cenomanian-Turonian boundary (ca. 94 Ma), is characterized by relatively widespread marine anoxia and ranks amongst the warmest intervals of the Phanerozoic. The early stages of OAE2 are, however, marked by an episode of widespread transient cooling and bottom water oxygenation: the Plenus Cold Event. This cold spell has been linked to a decline in atmospheric CO₂, resulting from enhanced global organic carbon burial. To investigate the response of phytoplankton to this marked and rapid climate shift we examined the biogeographical response of dinoflagellates to the Plenus Cold Event. Our study is based on a newly generated geochemical and palynological dataset from a high-latitude Northern Hemisphere site, Pratts Landing (western Alberta, Canada). We combine this data with a semi-quantitative global compilation of the stratigraphic distribution of dinoflagellate cyst taxa. The data show that dinoflagellate cysts grouped in the Cyclonephelium compactum-membraniphorum morphological plexus migrated from high- to mid-latitudes during the Plenus Cold Event, making it the sole widely found (micro)fossil to mark this cold spell. In addition to earlier reports from regional metazoan migrations during the Plenus Cold Event, our findings illustrate the effect of rapid climate change on the global biogeographical dispersion of phytoplankton.

1. Introduction

The Cenomanian–Turonian boundary interval (ca. 94 Ma) was an episode of extreme warmth, with tropical and mid-latitude sea surface temperatures exceeding 35 °C (e.g., Huber et al., 2002; Forster et al., 2007; Van Helmond et al. 2014a) and subtropical conditions at high latitudes (e.g., Jenkyns et al. 2004). This interval corresponds to an Oceanic Anoxic Event (OAE2), during which an increase in the
production of organic carbon and a reduction in the oxygen content of seawater resulted in unusually high organic matter content of marine sediments (e.g., Schlanger and Jenkyns, 1976; Jenkyns, 2010). The OAE2 interval is stratigraphically marked by a positive carbon isotope excursion in all active carbon reservoirs, resulting from elevated organic carbon burial rates (e.g., Tsikos et al., 2004).

The early stages of OAE2 are characterized by a short-lived (ca. 40 kyr; Jarvis et al., 2011) colder interval as recorded in several marine paleotemperature records (e.g., Gale and Christensen, 1996; Forster et al., 2007; Sinninghe Damsté et al., 2010). It was first recognized as the co-occurrence of Boreal fauna with a positive oxygen isotope excursion of about 1.5‰, recorded in biogenic calcite from Beds 4–8 of the Plenus Marl in mid-latitude shelf sites of northwest Europe (Gale and Christensen, 1996). This interval was termed the ‘Plenus Cold Event’ (PCE; Fig. 1), after the Boreal belemnite Praeactinocamax plenus (Blainville). Subsequently, the PCE was restricted only to Bed 4 of the Plenus Marl, being the sole bed containing abundant Boreal fauna (Voigt et al., 2006; Fig. 1). Bed 4 corresponds precisely to the upper trough and second build-up of the carbon isotope excursion, the upper part of the Metoicoceras geslinianum ammonite Zone and basal Whiteinella archaeocretacea planktonic foraminifer Zone (Gale et al., 2005). More recently, Jarvis et al. (2011) extended the PCE down to Beds 2 and 3 of the Plenus Marl (Fig. 1), based on a positive excursion in carbonate oxygen isotopes.

The PCE interval is characterized by a 3–7°C cooling of sea surface temperatures in the proto-North Atlantic and the European shelf (e.g., Forster et al., 2007; Sinninghe Damsté et al., 2010; van Helmond et al., 2014a; 2015). In several regions, such as the Western Interior Seaway (Eldrett et al., 2014) and proto-North Atlantic (e.g., Forster et al., 2007), the stratigraphic position of the PCE is characterized by minima in sediment organic carbon content and redox-sensitive element concentrations, which indicates improved oxygenation of bottom waters (e.g., van Helmond et al., 2014b). Furthermore the stratigraphic position of the PCE coincides with a decline in atmospheric $p$CO$_2$ (e.g., Kuypers et al., 1999; Sinninghe Damsté et al., 2008; Barclay et al., 2010), which is thought to be a consequence of enhanced sequestration of organic carbon in sediments during the early stages of OAE2 (e.g., Barclay et al., 2010; Sinninghe Damsté et al., 2010). The incursion of Boreal fauna into lower latitudes has only been documented for the European shelf. A causal relation between $p$CO$_2$ drawdown, sea surface cooling, bottom water oxygenation and the PCE has been proposed (e.g., Forster et al., 2007; Sinninghe Damsté et al., 2010; Jarvis et al., 2011; van Helmond, 2014b).

Previously, it remained unclear whether the migration of Boreal fauna was related to a migration of multiple components of marine food webs. Recently, van Helmond et al. (2014a, 2015) showed that the first consistent presence (FCP; presence of multiple specimens in consecutive samples) of dinoflagellate cysts (dinocysts) belonging to the Cyclonephelium compactum-membraniphorum morphological plexus (Ccm; see below for a detailed discussion on taxonomic status) in two sections on the proto-North Atlantic and European shelf coincided with a cooling of sea surface temperatures at the stratigraphic level of the PCE. To test whether Ccm was truly a high latitude taxon and if widespread migration of these dinoflagellates occurred during the PCE, we studied a high-latitude site in northwest Alberta, Canada (Pratts Landing) and compiled a global distribution of Ccm across OAE2, calibrated using biostratigraphy and carbon isotope stratigraphy.
Materials and methods

2.1 Stratigraphic setting of the Pratts Landing section

In northwest Alberta and northeast British Columbia, upper Cenomanian and Turonian strata of the Kaskapau Formation form a thick, mudstone-dominated and north-eastward-thinning wedge that spans the foredeep of the Western Canada Foreland Basin (Varban and Plint, 2005). Well-exposed sections in the Rocky Mountain Foothills on the western margin of the foredeep can be correlated with sections in the Peace River Valley, located close to the forebulge. Correlation has been established by using abundant, publically-accessible wireline log data (Fig. 2). Detailed correlation through a grid of 756 wireline logs showed that 28 allomembers, bounded by marine flooding surfaces, could be mapped across the foredeep (Varban and Plint, 2005). In the western part of the foredeep, exemplified by the section at Mount Robert (Figs. 2, 3), nearshore and shoreface sandstones form stacked successions that prograded only 20-40 km seaward from the preserved basin margin; shoreface progradation was limited by a consistently high rate of flexural subsidence (Varban and Plint, 2005, 2008). Traced eastward from Mount Robert, successive allomembers become thinner and finer-grained, and some allomembers (e.g., allomembers 7, 9, 10), pinch out completely before reaching outcrop in the Peace River Valley, exemplified by the section at Pratts Landing (Figs. 2, 3). The section at Pratts Landing, the focus of this study, is located on the north bank of the Peace River (56°01′14″N, 118°48′47″W; Fig. 4), and comprises stacked siltier- and sandier-upward successions, capped, at a prominent flooding surface, by weakly bioturbated, organic-rich claystones and silty claystones characterized by a very high radioactivity (i.e., boundary of allomembers 6 and 8; Figs. 3, 5). Outcrop spectral gamma ray profiles allow the Pratts Landing section to be correlated with confidence to nearby wireline logs (Fig. 3).

In the west, the Cenomanian-Turonian boundary was recognized at the top of Kaskapau allomember 6 at Mount Robert, based on the distribution of inoceramid bivalves (Fig. 3). At that section, Late Cenomanian Inoceramus ex gr. pictus (Sowerby) is widely distributed through allomembers 2 to 6, whereas Mytiloides pueblosensis (Walszczysz and Cobban) is present 2 m above the allomember 6-7 contact, indicating that the lowest Zone of the Turonian is present in the lower part of allomember 7 (cf. Kennedy et al., 2000). The upper bounding surface of allomember 6 can be traced, through well logs, for 220 km eastward to Pratts Landing where it corresponds to the sharp basal surface of a gypsum-cemented silt claystone. That sharp surface, separating allomembers 6 and 8, corresponds to an abrupt increase in radioactivity, and lies 25 cm below the first appearance of the Early Turonian inoceramids Mytiloides goppelnensis (Badillet and Sornay) and Mytiloides kossmatei (Heinz; Figs. 3, 5). The wireline log correlation shows that, at Pratts Landing, all of allomember 7 is missing, and the earliest Turonian Zone of M. pueblosensis also appears to be un-represented, emphasizing the hiatal character of the allomember 6-8 boundary (Fig. 3).

Pratts Landing is an outcrop locality in the Peace River valley in northwest Alberta, Canada (56°01′14″N, 118°48′47″W). During the Late Cretaceous, the study site was located at ~61°N, ±5 (van Hinsbergen et al., 2015; paleolatitude.org), on the eastern flank of the foredeep basin, about 160 km from the contemporaneous western shoreline of the Western Interior Seaway (Fig. 2). Varban and Plint,
We generated carbon isotope and dinoflagellate cyst data across about 23 m of upper Cenomanian to lower Turonian strata, based on stable carbon isotope stratigraphy and inoceramid biostratigraphy (Figs. 3, 6).

2.2 Stable isotope geochemistry

The carbon isotope composition of bulk organic carbon (δ\(^{13}\)C\(_{\text{org}}\)) was measured at 20 cm intervals across OAE2 in order to constrain its exact position, and at 50 cm intervals for the remainder of the section. Analyses were performed in the Stable-Isotope Biogeochemistry Laboratory of the School of Geography and Earth Sciences, McMaster University, Hamilton, Ontario, Canada. In total, 77 samples were treated with 3N HCl to remove carbonates, rinsed with demineralised water, freeze-dried and powdered. Between 1 and 3 mg of powdered sediment sample was weighed in tin capsules, and put in a rotating carousel for subsequent combustion in an elemental analyser. After purification of the gas sample it was passed through a SIRA II Series 2 dual-inlet isotope-ratio mass-spectrometer to determine the stable carbon isotopic composition of organic matter. Carbon isotope ratios were measured against an international standard, NBS-21. The analytical reproducibility, based on replicate samples, was better than 0.1‰.

2.3 Palynological processing

Dinocyst abundances were determined for 21 samples, covering the entire section, using standard palynological methods. About 5 grams of freeze-dried sediment was processed following a standardized quantitative method (e.g., Sluijs et al., 2003), which involves the addition of a known amount of *Lycopodium* marker spores (Stockmar, 1971). To dissolve carbonates and silicates, HCl (~30%) and HF (~38%) were added, respectively. After centrifugation, acids were discarded. The remaining residues were sieved over a 15 µm nylon mesh and the >15 µm fraction was mounted on slides for analysis by light microscopy. Samples were counted to a minimum of 250 dinocysts, which were identified to genus, or species level at 500x magnification, following the taxonomy of Fensome and Williams (2004). All samples and slides are stored in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht University, the Netherlands. All data (δ\(^{13}\)C\(_{\text{org}}\) and palynology) are listed in a supplementary file (Table S1).

2.4 Taxonomy and literature survey

Originally the cysts *Cyclonephelium membraniphorum* (Cookson and Eisenack, 1962), which was renamed *Cauveridinium membraniphorum* (Masure in Fauconnier and Masure, 2004), were differentiated from *Cyclonephelium compactum* (Deflandre and Cookson, 1955), based on the generally higher and structurally ordered crests and membranes of *C. membraniphorum*. Additionally, cysts of *C. membraniphorum* form a series of funnel-shaped structures bordering unornamented mid-dorsal and mid-ventral areas. However, the apparent morphological variation regarding ornamentation
within the two species exceeds the defined difference between the two species. Therefore it was proposed to refer to the dinocyst morphological complex *Cyclonephelium compactum-membraniphorum*, rather than separating both species (Marshall and Batten, 1988). We agree that the two species are members of a morphological continuum and therefore group all these morphotypes of this continuum from our study site and the literature under the *Cyclonephelium compactum-membraniphorum* morphological plexus (*Ccm*) (Fig. 24; Table 1). For the compilation of the global biogeographical distribution of *Ccm* prior to, during and after OAE2, a literature survey was conducted.

3. Results and Discussion

3.1 Dinocyst biogeography

At Pratts Landing the OAE2 interval is recorded between 10.2 m and 16.8 m, based on a 2‰ positive shift in δ¹³Corg (Fig. 63). The Cenomanian-Turonian boundary is placed at 15.3 m, at the sharp base of a 20 cm thick, siltstone-rich and heavily gypsum-cemented *silty claystone mudstone* lacking macrofauna (Fig. 5). The base Turonian marker *inoceramid* species *Mytiloides puebloensis* was not found, but the succeeding *inoceramid* Zone, characterized by *M. goppelnensis* and *M. kossmati* starts approximately 25 cm above the basal surface (Fig. 3). *Ccm* is a general constituent (1–4%) of the dinocyst assemblage at Pratts Landing throughout the section, i.e., also below the onset of OAE2 (Fig. 64).

All localities (*n*=35) with reported cysts of *Ccm* (i.e. *Cauveriplinimum membraniphorum, Cyclonephelium membraniphorum, Cyclonephelium compactum and/or Cyclonephelium compactum-membraniphorum*) are listed in Table 1 and shown in Figure 85. The first common presence (FCP) of *Ccm* could only be determined for 20 of the localities as a result of poor stratigraphic constraints and only qualitative reporting of *Ccm* at the other 15 localities.

Recent dinocyst biostratigraphic studies from the East Coast Basin, New Zealand, show that the FCP of *Cc* was ca. 500 kyr before the onset of OAE2 (Schlisler and Crampton, 2014). At northern high latitudes, notably Pratts Landing and the Norwegian Sea (Radmacher et al. 2015), *Ccm* is a consistent constituent of the dinocyst assemblage throughout the late Cenomanian. In contrast, at most Northern Hemisphere mid-latitude sites, *Ccm* has not been reported before OAE2, with the exception of a few spot occurrences at Eastbourne and Iona-1 (Pearce et al., 2009; Eldrett et al., 2014). Crucially, *Ccm* was never a consistent constituent of mid-latitude dinocyst assemblages before OAE2. This indicates that *Ccm* had a high-latitude biogeographical distribution in both hemispheres before OAE2.

Five Northern Hemisphere shelf sites in Europe and North America, namely Pratts Landing, Iona-1 (southwest Texas, USA), Bass River (New Jersey, USA), Eastbourne (East Sussex, UK) and Wunstorf (Lower Saxony, Germany), were selected to compare established biozonation, high-resolution records of δ¹³C, and the relative abundances of *Ccm* (Fig. 96; Pearce et al., 2009; Eldrett et al., 2014; van Helmond et al., 2014a; 2015). Maximum relative abundances of *Ccm* (i.e., >10%) are recorded during the first maximum in the OAE2 characterizing carbon isotope excursion (point “A” — cf. Voigt et al., 2008), at Pratts Landing (Figs. 64, 96). At the same stratigraphic position, *Ccm* becomes abundant at several other Northern Hemisphere mid-latitude sites, for example, the southern part of the Western
Interior Seaway, the proto-North Atlantic shelf, the European shelf, and the Tethys (Figs. 85, 96; Table 1). Despite a spot occurrence at point “A”, the FCP of Ccm seems somewhat delayed at Eastbourne (i.e., Plenus Marl Bed 7 – Fig. 96; Pearce et al., 2009), this is a local phenomenon, because in other English Chalk sections (e.g., Dodsworth, 2000) the FCP of Ccm coincides with that of other Northern Hemisphere mid-latitude sites.

### 3.2 Ecology

At Bass River and Wunstorf the FCP of Ccm precisely correlates with a drop in sea surface temperature (van Helmond et al., 2014a; 2015), leading to the suggestion that the dinoflagellate taxon that produced Ccm migrated to these sites in response to climatic cooling. We therefore suggest that sea surface temperature was the primary control on the biogeographical distribution of Ccm outside high latitude regions. For the Shell Iona-1 core the FCP of Ccm coincides with a minimum in organic carbon, redox-sensitive elements and relatively high abundances of benthic foraminifera and trace fossils indicative of a period of improved oxygenation of bottom waters (Eldrett et al., 2014). This is in agreement with previous observations for the interval showing PCE-related cooling of sea surface temperature in the proto-North Atlantic (Forster et al., 2007; Sinninghe Damsté et al., 2010; van Helmond et al., 2014b). The sustained presence of Ccm after the PCE at all sites, except Bass River (Fig. 96), suggests that, in addition to sea surface temperature, other environmental and paleoceanographic factors became dominant in determining the distribution of Ccm once it had occupied niches at lower latitudes. For example, salinity, enhanced nutrient availability and proximity to the shoreline may have been important (Harris and Tocher, 2003). Preservation of palynomorphs, e.g. dinocysts, is variable within sections and between sections but is unrelated to the occurrences of certain species.

The migration of Ccm towards lower latitudes in response to cooling resembles dinoflagellate migration events during other periods of marked climatic change. Dinocysts referable to the Arctic Paleogene taxon Svalbardella were encountered in mid- and low-latitudes during the most pronounced Oligocene glaciations (ca. 30–25 Ma; van Simaeys et al., 2005). In contrast, during the Paleocene–Eocene Thermal Maximum, tropical species of the dinocyst genus Apectodinium moved from low toward high latitudes in response to peak warmth (Crouch et al., 2003; Sluijs et al., 2007). Studies across the Cretaceous–Paleogene boundary indicate initial high latitude to equatorial dinoflagellate migration at the boundary, followed by a reverse migration. This presumably took place in response to impact-related initial climatic cooling followed by a return to warmer conditions (Brinkhuis et al., 1998; Galeotti et al., 2004; Vellekoop et al., 2014).

The biogeographical expansion of Ccm towards the equator seems to be a relatively strong response to a moderate change in sea surface temperature (ca. 3–5°C). The southward migration of Ccm over relatively large distances, i.e. 20°–30° of latitude southwards, may have been amplified by the flatter meridional temperature gradients across OAE2 (e.g., Sinninghe Damsté et al., 2010). Compared to the present day, which is characterized by a much steeper meridional temperature gradient, relatively small changes in temperature in the mid-Cretaceous and early Paleogene may have had a much larger impact on the distribution of marine organisms.
3.3 A new stratigraphic marker

Most of the Cretaceous is covered by the Normal Superchron C34n (ca. 126–84 Ma; Gradstein et al., 2012), hampering application of magnetostratigraphy. Stratigraphic correlation for the Cenomanian–Turonian boundary interval therefore relies on biostratigraphy and carbon isotope stratigraphy (Gale et al., 2005) as well as on recent advances in astrochronology (e.g., Meyers et al., 2012; Eldrett et al., 2015). Pelagic sediments are often carbonate-poor, because the calcite compensation depth was relatively shallow during OAE2, complicating planktonic foraminifer and calcareous nanofossil biostratigraphy (e.g., Erba, 2004). Consequently, carbon isotope stratigraphy is the main stratigraphic tool for OAE2 because the positive carbon isotope excursion is recognized in all active carbon reservoirs (Tsikos et al., 2004). Calibration of carbon isotope stratigraphy with bioevents is, however, essential to establish detailed stratigraphic frameworks.

The coincidence of the FCP of Ccm with the base of the W. archaeocretacea and the upper part of the M. geslinianum zones close to the first maximum in the positive carbon isotope excursion (point “A”, Fig. 9e), suggests that dinoflagellate migration probably occurred within thousands to ten thousand years. The FCP of Ccm thus represents a useful biostratigraphic marker, being, to date, the only widely found microfossil to mark the PCE, except at high latitudes.

4. Conclusions

A global compilation of dinocyst assemblage records combined with new data from a high-latitude site spanning OAE2 illustrates the migration of dinoflagellates, that produced the dinocyst morphological complex Ccm, from high-latitudes to mid-latitudes during the early stages of OAE2 (latest Cenomanian). The first consistent presence of this taxon at mid-latitudes correlates with the stratigraphic position of the Plenus Cold Event, following its original definition by Gale and Christensen (1996), making it the sole widely distributed microfossil to mark this cold spell. The coincidence of the first consistent presence of Ccm in the mid-latitudes with this transient cooling, implies lasting reorganization of phytoplankton biogeography in response to rapid climate change during the Late Cretaceous supergreenhouse. The migration of Ccm in response to climatic cooling resembles previously recognized dinoflagellate migration events during comparable periods of transient climate change, e.g., the Oligocene glaciations and the Paleocene–Eocene Thermal Maximum.

Author contributions

N. van Helmond, A. Sluijs and H. Brinkhuis designed the research. Samples and fossils at the Pratts Landing section were collected in the field by G. Plint and I. Walaszczyk and D. Gröcke. Palynological analyses were carried out by N. van Helmond, N. Papadomanolaki and B. van de Schootbrugge. Carbon isotope stratigraphy was carried out by D. Gröcke, G. Plint and J. Trabucho-Alexandre. Inoceramid biostratigraphy was carried out by I. Walaszczyk. Regional stratigraphy was compiled by G. Plint. Compilation of the global biogeographical distribution of Ccm was carried out by
N. van Helmond, H. Brinkhuis, M. Pearce and J. Eldrett. N. van Helmond and A. Sluijs prepared the manuscript with input from all authors.

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References


Table 1. Overview of the localities where cysts of *Cyclonephelium compactum-membraniphorum* morphological plexus (Ccm) have been reported across the Cenomanian-Turonian boundary interval. In the fourth and fifth column an “X” marks whether the first consistent presence (FCP) of Ccm was before OAE2 or if it was associated with the first maximum in the positive carbon isotopic excursion (CIE), point “A” cf. Voigt et al., 2008. Question marks indicate that the FCP could not be determined accurately, resulting from insufficient supporting information, e.g. high-resolution carbon isotope stratigraphy or unquantified abundances of Ccm. Localities further discussed in the article are in bold.
<table>
<thead>
<tr>
<th>Site ID</th>
<th>Region</th>
<th>Locality</th>
<th>FCP of Ccm prior to OAE2</th>
<th>FCP of Ccm associated with CIE-“A”</th>
<th>References</th>
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<td>Eldrett et al., 2014</td>
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Figure 1. Biozonation, lithology, Plenus Marl beds (Jefferies, 1963) and δ¹³C_carb (low-resolution data (dots and dotted line) derived from Pearce et al., 2009; high-resolution data (solid line) derived from Paul et al., 1999) for the Cenomanian-Turonian boundary reference section at Eastbourne, combined with occurrences of Boreal fauna (Gale and Christensen, 1996). On the right side the ranges of the different definitions for the Plenus Cold Event are indicated.
Figure 2. Map of northwest Alberta and adjacent British Columbia showing distribution of well logs, cores and outcrops used to establish the regional stratigraphic framework that forms the basis for the present study. Outcrop sections at Mount Robert in the west, and Pratts Landing in the east are correlated via wireline well logs (gamma ray and resistivity pairs).
Figure 3. Regional cross-section (located in Fig. 2) showing how allomembers of the Kaskapau Formation can be correlated across the foredeep from Mount Robert to Pratts Landing. Cross-section is condensed from more detailed lines in Varban and Plint (2005). The Cenomanian-Turonian boundary is shown as a broken line at the top of allomember 6. Note how allomember 7 laps out eastward onto allomember 6, and that both allomembers 6 and 8 become increasingly radioactive towards the east. Spectral gamma ray profiles taken at Pratts Landing confirm the correlation of the various stratal units at outcrop with their equivalents in subsurface. The inset stratigraphic logs show more detailed representations of the lithological successions, gamma ray profiles, and the distribution of inoceramid bivalves at Mount Robert and Pratts Landing. Detailed legend in figure 6.
Figure 42. Map showing the southern part of Alberta. The study site at Pratts Landing is located on the Peace River about 70 km east of the Alberta-British Columbia border. Inset map shows details of the Peace River area in the vicinity of the town of Fairview, with the outcrop locality and access roads indicated.
Figure 5. Field photographs of the Pratts Landing site. With **a**, showing an overview of upper part of the section showing resistant, gypsum-cemented ledge that marks a sharp erosional boundary between two claystone units. Immediately above the boundary there is a large increase in the uranium content of the sediment. The Early Turonian inoceramid bivalves *Mytiloides goppelnensis* and *Mytiloides fossimati* appear 25 cm above the erosion surface. Photograph **b**, shows an overview of the lower part of the section showing highly bioturbated silty sandstone of Kaskapau allomember 6, sharply overlain.
at a major flooding surface (13.6 m level in Fig. 6) by thinly-bedded claystones. Rocks embracing the Plenus Cold Event are represented by a 1.4 m thick, shallowing (sandier)-upward succession bounded above by a major flooding surface. The Cenomanian-Turonian boundary, marked by a resistant ledge, lies at the 15.3 m level. Note that all of Kaskapau allomember 7 is absent at the erosion surface marking the Cenomanian-Turonian boundary, as illustrated in Figure 3.
Figure 6. Lithostratigraphy, detailed lithological log, δ¹³C Org and abundances of Cyclonephelium compactum–membraniphorum morphological plexus (Ccm) and inoceramid bivalve stratigraphy for Pratts Landing. Sample intervals for palynology are indicated by horizontal black lines.
Figure 74. Various specimens of the *Cyclonephelium compactum-membraniphorum* morphological plexus (*Ccm*), gradually changing from the *C. membraniphorum* end-member (a-e) to the *C. compactum* end-member (g-i). Specimens a. (England Finder coordinates (EFc): U59/2-slide 1) and i. (EFc: L70/1-slide 2) are from Wunstorf sample 42.21 meters below surface (mbs), specimen b. (EFc: H13-slide 1) is from Bass River sample 590.69 mbs, specimen c. (EFc: R65/1-slide 1) is from Wunstorf sample 45.81 mbs, specimens d. (EFc: M59/2-slide 1) and h. (EFc: V53/2-slide 1) are from Pratts Landing sample 6.5 m, specimens e. (EFc: E59/2-slide 1) and g. (EFc: T64/3-slide 2) are from Bass River sample 590.08 mbs and specimen f. (EFc: J8/1-slide 1) is from Pratts Landing sample 12 m. Scale bars represent 50 µm.
Figure 85. Compilation of the first consistent presence (FCP) of *Cyclonephelium compactum–membraniphorum* morphological plexus (*Ccm*) across Oceanic Anoxic Event 2. Numbers in white boxes refer to localities compiled in Table 1. Letters in orange boxes refer to the sites selected for comparison of established biozonation, high-resolution records of δ¹³C and the relative abundances of *Ccm* (Fig. 96) also compiled in Table 1. The Mollweide projected paleogeographic map for the Cenomanian–Turonian boundary interval was generated at http://www.odsn.de/odsn/services/paleomap/paleomap.html. Continental plates are in light gray. Dry land in dark gray after Scotese (2001).
Figure 9c. Overview of δ¹³Corg and/or δ¹³Ccarb abundances of Cyclonephelium compactum–membraniphorum morphological plexus (Ccm) and foraminiferal and/or ammonite zonation for the studied sections; (a) Shell Iona-1 core (Eldrett et al., 2014); (b) Pratts Landing (this study); (c) Bass River (van Helmond et al., 2014a) open symbols are δ¹³Corg derived from Bowman and Bralower (2005); (d) Eastbourne (Pearce et al., 2009), high-resolution δ¹³Ccarb data derived from Paul et al. (1999); (e) Wunstorf — relative abundances of Ccm from van Helmond et al. (2015), δ¹³Corg from Du Vivier et al. (2014) and δ¹³Ccarb from Voigt et al. (2008), a red cross marks a barren sample. Age is from the astronomically tuned age model for the Shell Iona-1 core (Eldrett et al., 2015). Dashed line represents the first maximum in the carbon isotope excursion, point “A” (cf. Voigt et al., 2008). Solid lines represent the Cenomanian–Turonian boundary. The blue shaded area represents the Plenus Cold Event according to its original definition (Gale and Christensen, 1996), the cooling in reconstructed sea surface temperatures at Bass River and Wunstorf (van Helmond et al., 2014a, 2015), and the (re)oxygenation of bottom waters in the Shell Iona-1 core (Eldrett et al., 2014). Note: the sections are plotted using different depth scales.