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 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 pCO$_2$, 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

5   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

10   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

15   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

20   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

25   stratigraphic position of the PCE coincides with a decline in atmospheric pCO$_2$ (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 pCO$_2$ drawdown, sea surface

30   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

35   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.

2. Materials and methods

2.1 The Pratts Landing section

5   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 shoreline of the Western Interior Seaway (Fig. 2; Varban and Plint, 2008). The studied section of predominantly thinly bedded silt- and claystones spans about 23 m of upper
10   Cenomanian to lower Turonian strata, based on stable carbon isotope stratigraphy and inoceramid biostratigraphy (Fig. 3).

2.2 Stable isotope geochemistry

The carbon isotope composition of bulk organic carbon ($\delta^{13}C_{org}$) 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
15   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
20   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

25   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
30   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 ($\delta^{13}C_{org}$ 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

5   renamed *Cauveridinium membraniphorum* (Masure in Fauconnier and Masure, 2004), were differentiated from *C. 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

10   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

15   (*Ccm*) (Fig. 4; 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

20   shift in $\delta^{13}C_{org}$ (Fig. 3). 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. 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,

25   i.e., also below the onset of OAE2 (Fig. 3).

    All localities (n=35) with reported cysts of *Ccm* (i.e. *Cauverodinium membraniphorum*, *Cyclonephelium membraniphorum*, *Cyclonephelium compactum* and/or *Cyclonephelium compactum-membraniphorum*) are listed in Table 1 and shown in Figure 5. The first common presence (FCP) of *Ccm* could only be determined for 20 of the localities as a result of poor stratigraphic constraints and

30   only qualitative reporting of *Ccm*.

    Recent dinocyst biostratigraphic studies from the East Coast Basin, New Zealand, show that the FCP of *Ccm* was ca. 500 kyr before the onset of OAE2 (Schiøler 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

35   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
5 (Lower Saxony, Germany), were selected to compare established biozonation, high-resolution records of δ^{13}C, and the relative abundances of *Ccm* (Fig. 6; 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. 3, 6). At the same stratigraphic position, *Ccm* becomes abundant at
10 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. 5, 6; 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. 6; 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
15 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
20 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
25 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. 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
30 important (Harris and Tocher, 2003).

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–
35 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 nannofossil 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* zone close to the first maximum in the positive carbon isotope excursion (point "A"; Fig. 6), 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 found 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 of the Pratts Landing section were collected in the field by G. Plint, I. Walaszczyk and D. Gröcke. Palynological analyses were carried out by N. van Helmond, N. Papadomanolaki and B. van de Schootbrugge. Carbon isotope
5   stratigraphy was carried out by D. Gröcke, G. Plint and J. Trabucho-Alexandre. Inoceramid biostratigraphy was carried out by I. Walaszczyk. 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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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. Western Interior Seaway (WIS).

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Site ID	Region	Locality	FCP of *Ccm* prior to OAE2	FCP of *Ccm* associated with CIE-"A"	References
North America					
1	WIS	Blue Point, Arizona, USA		X	Li and Habib, 1996; Harris and Tocher, 2003
a	**WIS**	**Shell Iona-1, Texas, USA**		**X**	**Eldrett et al., 2014**
2	WIS	Pueblo, Colorado, USA		X	Dodsworth, 2000; Harris and Tocher, 2003
3	WIS	Wahweap Wash, Utah, USA	?	?	Harris and Tocher, 2003
4	WIS	Bunker Hill, Kansas, USA	?	?	Harris and Tocher, 2003
5	WIS	Rebecca K. Bounds Core, Kansas, USA	?	?	Harris and Tocher, 2003
b	**WIS**	**Pratts Landing, Alberta, Canada**	**X**		**this study**
c	**proto-N. Atlantic shelf**	**Bass River, New Jersey, USA**		**X**	**van Helmond et al., 2014a**
Europe					
6	European shelf	Lulworth, Dorset, UK		X	Dodsworth, 2000
7	European shelf	Culver Cliff, Isle of Wight, UK		X	Lignum, 2009
8	European shelf	Folkstone, Kent, UK		X	Jarvis et al., 1988; Lignum, 2009
d	**European shelf**	**Eastbourne, East-Sussex, UK**		**X**	**Pearce et al., 2009**
9	European shelf	Eastern UK	?	?	Dodsworth, 1996
e	**European shelf**	**Wunstorf, Lower Saxony, Germany**		**X**	**Marshall and Batten, 1988; Prauss, 2006; Lignum, 2009; van Helmond et al., 2015**
10	European shelf	Misburg, Lower Saxony, Germany		X	Marshall and Batten, 1988
11	European shelf	Norwegian Sea, Norway	X		Radmacher et al, 2015
12	European shelf	Gröbern, Saxony Anhalt, Germany		X	Lignum, 2009
13	European shelf	Ratssteinbruch, Saxony, Germany		X	Lignum, 2009
14	European shelf	Pulawy, central Poland		X	Dodsworth, 2004a
15	European shelf	Nymburk, Central Bohemia, Czech Republic	?	?	Čech et al., 2005
16	European shelf	Aksudere, Crimea, Ukraine	?	?	Dodsworth, 2004b
17	European shelf	Bois du Gallet, St.-Sylvestre-de-Cormeilles, Normandy, France	?	?	Tocher and Jarvis, 1995
18	European shelf	Les Fosses Blanches, Duneau, Maine, France	?	?	Tocher and Jarvis, 1995
19	European shelf	Ganuza, Castillian Platform, Spain	?	?	Lamolda and Mao, 1999
20	European shelf	Puentedey, Castillian Platform, Spain	?	?	Peyrot et al., 2011
21	European shelf	Fuentetoba, Castillian Plateau, Spain	?	?	Peyrot et al., 2011
22	European shelf	Tamajon, Castillian Plateau, Spain	?	?	Peyrot et al., 2011
23	European shelf	Condemios, Castillian Plateau, Spain	?	?	Peyrot et al., 2012
24	Tethys	Ultrahelvetic Rehkogelgraben, Austria	?	?	Pavlishina and Wagreich, 2012
25	Tethys	Pont d'Issole, Provence-Alpes-Côte d'Azur, France		X	Lignum, 2009
26	Tethys	Vergons, Provence-Alpes-Côte d'Azur, France		X	Courtinat et al., 1991; Lignum, 2009
Southern Hemisphere					
27	Southern Ocean	Central Kerguelen Plateau	?	?	Mohr et al., 2002
28	Indian Ocean	Northwestern Australia	X		McMinn, 1988
29	Pacific Ocean	East Coast Basin, New Zealand	X		Hasegawa et al., 2013; Schiøler and Crampton, 2014
30	Pacific Ocean	Mangaotane Stream, Raukumara Peninsula, New Zealand	X		Crampton et al., 2001
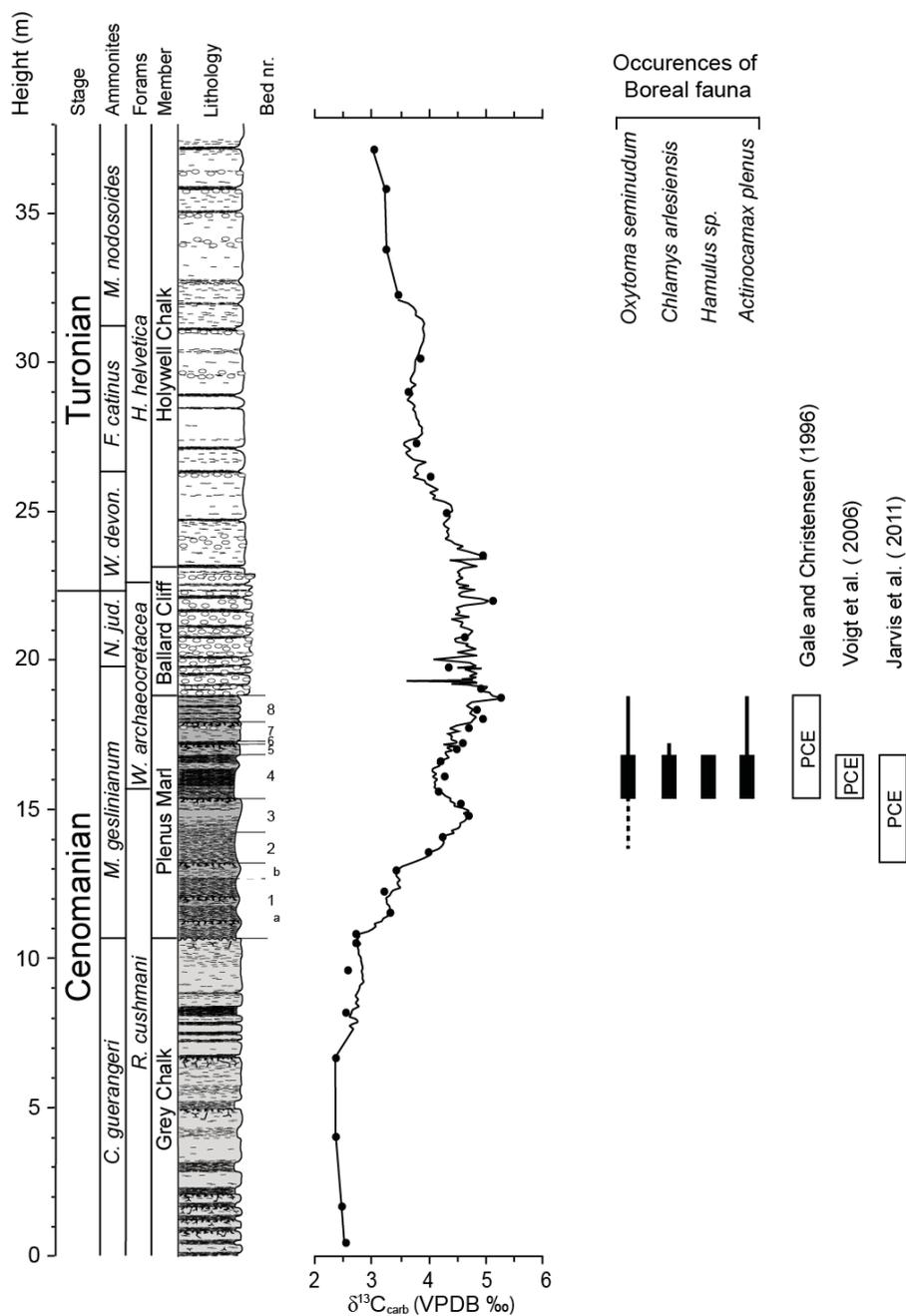
Figure 1. Biozonation, lithology, Plenus Marl beds (Jefferies, 1963) and δ^{13}C$_{carb}$ (Pearce et al., 2009; high-resolution data derived from Paul et al.,1999) for the Cenomanian-Turonian boundary reference section at Eastbourne, combined with occurrences of Boreal fauna (Gale and Christensen, 1996). On the right side the ranges of the different definitions for the Plenus Cold Event are indicated.
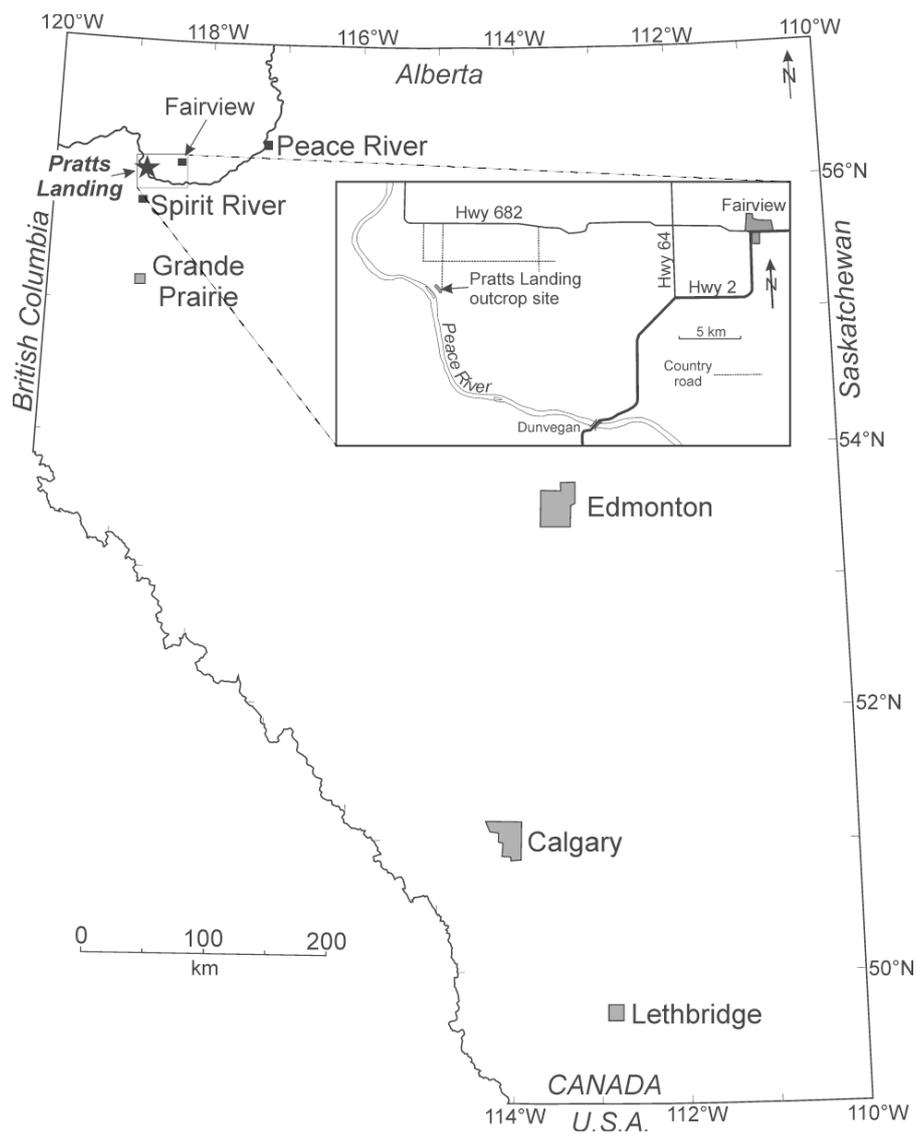
Figure 2. Map showing the southern part of Alberta. Study site at Pratts Landing is located on the Peace River about 70 km east of the Alberta-British Columbia border. Inset map shows details of the Peace River area in the vicinity of the town of Fairview, with the outcrop locality and access roads indicated.
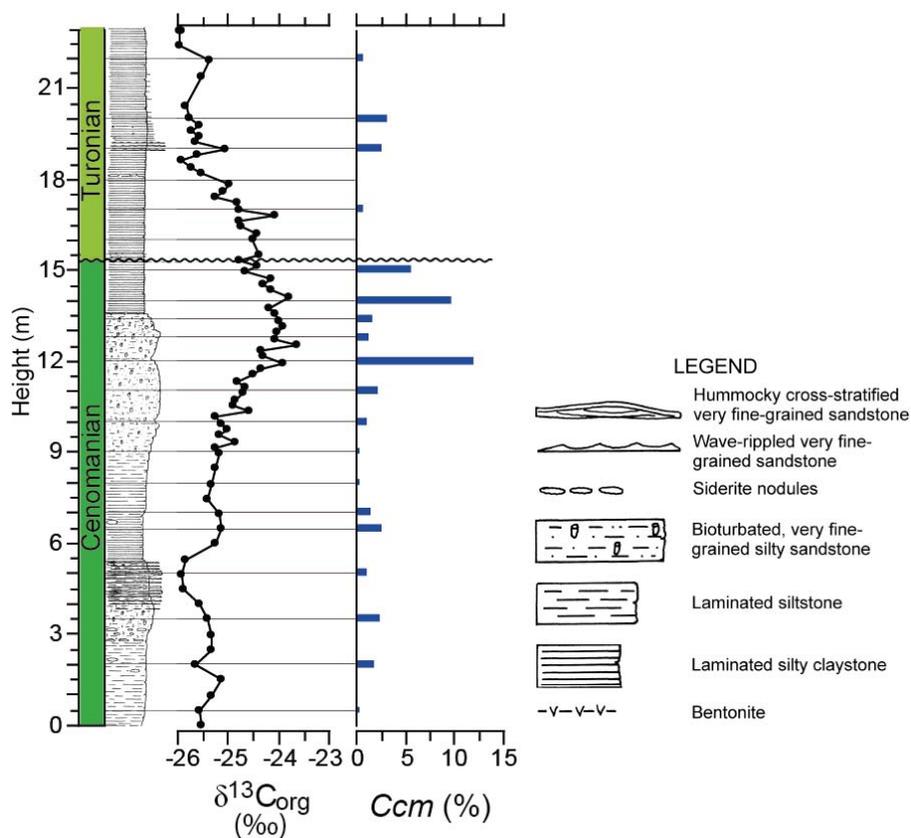
Figure 3. Lithology, $\delta^{13}C_{org}$ and abundances of *Cyclonephelium compactum–membraniphorum* morphological plexus (*Ccm*) for Pratts Landing. Sample intervals for palynology are indicated by horizontal black lines.
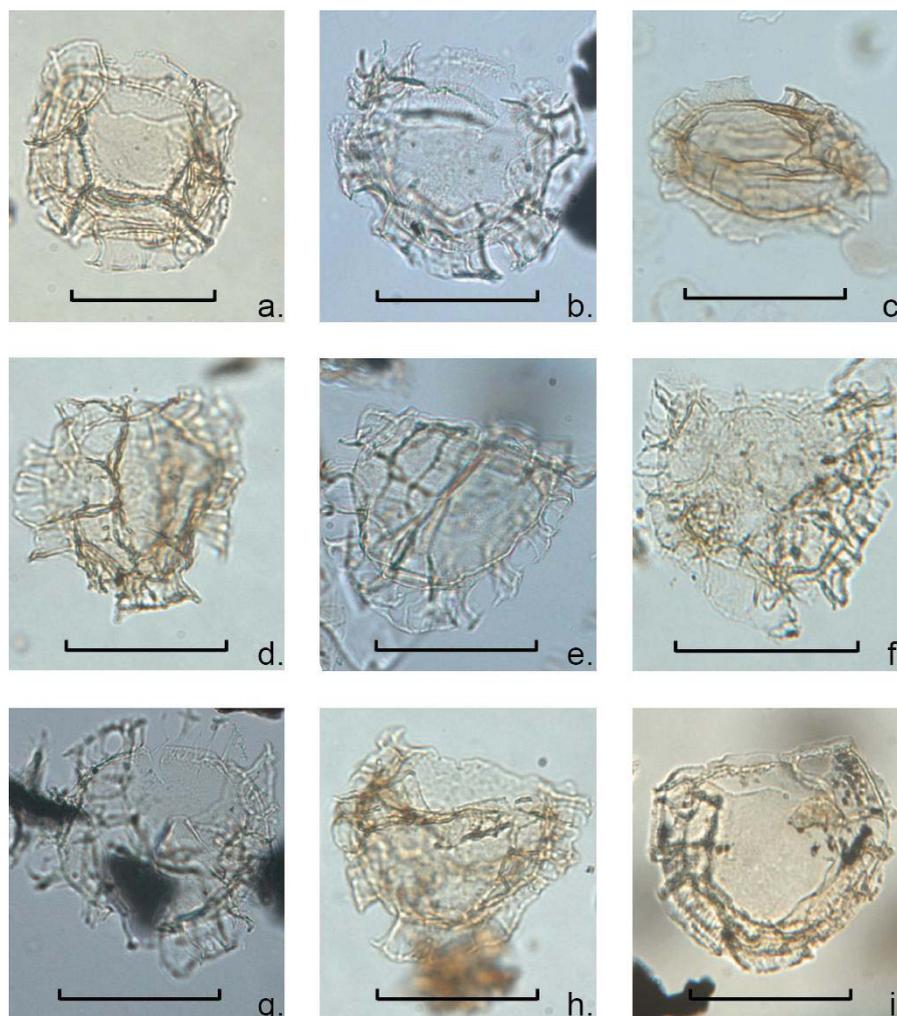
Figure 4. Various specimens of the *Cyclonephelium compactum-membraniphorum* morphological plexus (*Ccm*), gradually changing from the *C. membraniphorum* end-member (**a-c**) to the *C. compactum* end-member (**g-i**). Specimens **a.** (England Finder coordinates (EFc): U59/2-slide 1) and **i.** (EFc: L70/1-slide 2) are from Wunstorf sample 42.21 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.
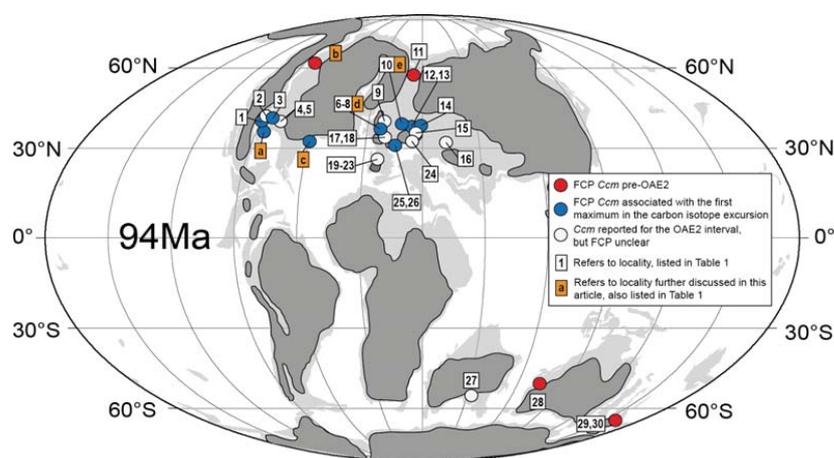
Figure 5. Compilation of the first consistent presence (FCP) of *Cyclonephelium compactum–membraniphorum* morphological plexus (*Ccm*) across Oceanic Anoxic Event 2. Numbers in white boxes refer to localities compiled in Table 1. Letters in orange boxes refer to the sites selected for comparison of established biozonation, high-resolution records of δ^{13}C and the relative abundances of *Ccm* (Fig. 6) 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).
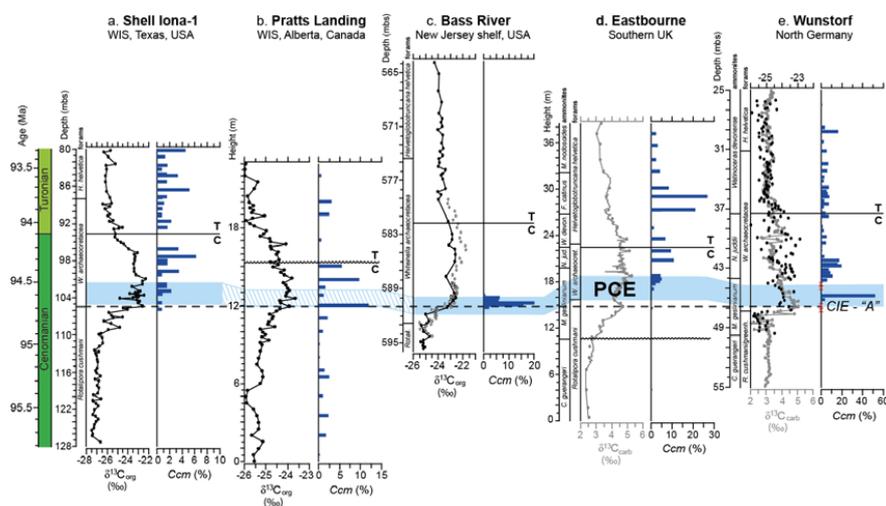
Figure 6. Overview of δ[13]C_org and/or δ[13]C_carb, abundances of *Cyclonephelium compactum–membraniphorum* morphological plexus (*Ccm*) and foraminiferal and/or ammonite zonation for the studied sections; (a) Shell Iona-1 core (Eldrett et al., 2014); (b) Pratts Landing (this study); (c) Bass River (van Helmond et al., 2014a) open symbols is δ[13]C_org derived from Bowman and Bralower (2005); (d) Eastbourne (Pearce et al., 2009), high-resolution δ[13]C_carb data derived from Paul et al. (1999); (e) Wunstorf — relative abundances of *Ccm* from van Helmond et al. (2015), δ[13]C_org from Du Vivier et al. (2014) and δ[13]C_carb 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.