

1 **Complex response of dinoflagellate cyst distribution patterns to cooler early**

2 **Oligocene oceans**

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22

23 **Abstract**

24 Previous studies have made extensive use of dinoflagellate cysts to reconstruct past

25 sea surface temperature (SST). Analysis of associations of dinoflagellate cysts using

26 two new ocean datasets for the mid Eocene (Bartonian) and early Oligocene
27 (Rupelian) reveals clear latitudinally constrained distributions for the Bartonian, but
28 unexpected changes in their Rupelian distribution; a significant number of species
29 with low and mid-latitude northern hemisphere occurrences in the Bartonian extend
30 their northward ranges in the Rupelian, including some forms characterised as ‘warm
31 water’ by previous studies. This suggests either that dinoflagellates are faithfully
32 tracking a complex oceanographic response to Rupelian cooling, or that dinoflagellate
33 sensitivity/adaptability to a range of ecological variables means that at a global scale
34 their distributions are not primarily controlled by sea surface temperature-variability.

35

36 Previous use of dinoflagellate cysts for palaeoclimate work has relied on rather
37 subjective and inconsistent identification of ‘warm’ and ‘cold’ water forms, rather
38 than comprehensive analysis of community associations at the global-scale. It is clear
39 from this study that a better understanding of the (palaeo-)ecology of dinoflagellates
40 and their cysts is required.

41

42 Rupelian dinoflagellate cyst distribution may reflect changes in a range of
43 environmental variables linked to early Oligocene climate-cooling, for example
44 changes in nutrient fluxes triggered by glacially-induced base-level fall; complex
45 reorganisation of ocean current systems between the Bartonian and Rupelian, or
46 muted changes to Rupelian summer SSTs in the northern hemisphere that have
47 previously been reported. Many extant dinoflagellate species also exhibit relatively
48 broad temperature tolerance. Moreover, they have potentially extensive cryptic
49 diversity, and are able to produce dormant cysts during short-lived environmental

50 deterioration, all of which may act to limit the value of undifferentiated dinoflagellate
51 cyst assemblages for identifying climate signals.

52

53 Keywords: dinoflagellate cysts; Eocene; Oligocene; palaeoclimatology

54

55 **1. Introduction**

56

57 Previous work by Salzmann et al. (2008) and Pound et al. (2011, 2012) has
58 established a robust database methodology (Tertiary Environments Vegetation System
59 – TEVIS) for interpreting patterns of Cenozoic vegetation using data ‘mined’ from
60 historical literature. Similarly, Vandenbroucke et al. (2010) used multivariate analysis
61 of published occurrences of the enigmatic Chitinozoa to examine sea surface
62 temperature (SST) relationships in the Late Ordovician. Here, we adapt the TEVIS
63 methodology to obtain data from published literature on dinoflagellate cysts, and use
64 them as a proxy for investigating the response of the marine realm to cooling at the
65 Eocene – Oligocene transition. Dinoflagellates have formed a component of the
66 microplankton in aquatic ecosystems since the Mid Triassic. They are ubiquitous in
67 modern oceans, as well as brackish and freshwater environments, and include
68 phototrophic, heterotrophic and mixotrophic species (Fensome et al., 1993; Jeong et
69 al., 2010). Their fossilised organic remains (cysts) are the basis for biostratigraphical
70 schemes (Brinkhuis and Biffi, 1993; Van Simaey et al., 2005; Williams et al., 2004)
71 and palaeoenvironmental analysis (Sluijs et al., 2005; Versteegh and Zonneveld,
72 1994). Their use to discriminate between offshore to near-shore environments (Dale,
73 1996; Wall et al., 1977) has made them invaluable for the identification of different
74 systems tracts in sequence stratigraphy (Brinkhuis, 1994; Sluijs et al., 2005), and the

75 apparent strong relationship between the global distribution of extant marine
76 dinoflagellates and SST (e.g. Marret and Zonneveld, 2003; Zonneveld et al., 2013)
77 has formed the basis of their widespread use in palaeoclimate reconstruction and
78 tracking palaeoclimate oscillations (Brinkhuis and Biffi, 1993; Brinkhuis et al., 1998;
79 Esper and Zonneveld, 2007; Masare and Vrielynck, 2009; Mudie et al., 2001; Sluijs et
80 al., 2005; Wall et al., 1977).

81

82 This work reconstructs global distributions of dinoflagellate cysts between a warmer
83 mid Eocene (Bartonian) Earth and a cooler early Oligocene (Rupelian) Earth, and
84 uses multivariate analysis and range data to investigate the extent to which these
85 patterns are significant for understanding the pattern of ocean temperature change
86 across the Eocene – Oligocene boundary. We also explore how our results might
87 reveal potential weaknesses in the ability of dinoflagellate cysts to track global
88 climate change. We examine the hypothesis that at a global scale, dinoflagellate cyst
89 latitudinal distributions shifted equatorward from the late mid Eocene to the early
90 Oligocene in response to climate cooling. Published data on planktonic foraminifera
91 in Tanzania, showing a major faunal turnover and size reduction of individual species
92 at the Eocene/Oligocene boundary, suggests that even the modest SST reductions at
93 low latitudes had a significant impact on marine habitats (Wade and Pearson, 2008),
94 and a strong biotic signal in dinoflagellate cyst data from this time interval might
95 therefore be anticipated. Previous studies using dinoflagellate cysts to track Eocene
96 and/or Oligocene climate change (e.g. Bijl et al., 2011; Brinkhuis, 1994; Brinkhuis
97 and Biffi, 1993; Guerin et al., 2008) have tended to focus on relatively limited
98 geographical areas, rather than adopting a methodology to track ocean-wide species
99 responses across this time interval.

100 **2. Background**

101

102 A transition in global climate state began in the latest Eocene (Wade et al., 2012),
103 probably triggered by a reduction in atmospheric CO₂ below a critical threshold
104 (Anderson et al., 2011; DeConto and Pollard, 2003; Pagani et al., 2011; Pearson et al.,
105 2009). It culminated in the establishment of the East Antarctic Ice Sheet associated
106 with further cooling in the early Oligocene, termed Oi-1. The widely recognised early
107 Oligocene cooling event (Eldrett et al., 2009; Liu et al., 2009; Wei, 1991) lasted about
108 400,000 years, and is dated to about 34 Ma (Fig. 1).

109

110 In the mid Eocene, annual mean SSTs ranged from c. 35°C at the equator to 15 to >20
111 °C at high latitudes (Bijl et al., 2009). Corresponding values for the early Oligocene
112 were reduced by about 5°C at mid to high latitudes, with smaller temperature
113 reductions in tropical and equatorial regions (Liu et al., 2009). Oxygen isotope data
114 from benthic foraminifera show that the Bartonian was a relatively warm and stable
115 climatic interval compared to the relatively cooler Rupelian (Fig. 1). Apart from a
116 transient warming event at 40 Ma (Bohaty et al., 2009), termed the Middle Eocene
117 Climate Optimum (Bohaty and Zachos, 2003), temperatures in the Bartonian mostly
118 show a gradual fall from their peak in the late Paleocene and early Eocene (Bijl et al.,
119 2009). Imprinted on this overall trend are higher frequency cycles of orbitally-driven
120 climate change that variably affected SST values (Sloan and Huber, 2001; Burgess et
121 al., 2008; Pälike et al., 2006; Wade and Pälike, 2004), as well as larger regional
122 temperature oscillations in SST, of perhaps 10°C, that have been reported in the
123 uppermost middle Eocene (presumably Bartonian) of the subtropical western North
124 Atlantic (Wade and Kroon, 2002). However, none of these fluctuations are inferred to

125 have had a sustained impact on marine ecology. In the lower and middle Eocene,
126 coccolithophores exhibit maximum species richness for the Paleogene (Bown et al.,
127 2004), and data from Eocene benthonic foraminifera suggests relatively stable
128 phyletic composition (Less and Özcan, 2012). As remarked by MacLeod et al. (2000),
129 middle Eocene planktonic foraminifera from low and mid-latitudes show a broad and
130 fairly uniform distribution of morphotypes, with almost constant relative abundance
131 between zones P9 (Ypresian) and P14 (Bartonian) (Fig. 2); significant changes in both
132 Paleogene planktonic foraminifera (MacLeod et al., 2000) and coccolithophores
133 (Bown et al., 2004) coincided with major climate-change events, including the Eocene
134 – Oligocene transition.

135

136 **3. Material**

137

138 Two stratigraphically well-defined time slabs were selected for dinoflagellate cyst
139 analysis; the Bartonian (late mid Eocene; 41.2 – 37.8 Ma) and Rupelian (early
140 Oligocene; 33.9 – 28.1 Ma) (Figs 2, 3). Time slabs were chosen for optimum potential
141 for climate contrast between them, whilst minimising both temporal separation and
142 the influence of transient climate effects within them. The Priabonian (latest Eocene)
143 is less attractive for investigation. It straddles the onset of the climate cooling event
144 that extends into the Rupelian (Houben et al., 2012), but variable quality of
145 stratigraphical data in published accounts means that accurate and consistent
146 interpretation of the dinoflagellate cyst record with respect to the cooling event
147 would be problematic, or would require a subjective interpretation to be imposed.
148 Literature records of dinoflagellate cysts in Bartonian and Rupelian successions were
149 used to construct two new global datasets of taxa present within these time slabs at

150 different localities. These datasets contain species (presence/absence) and location
151 data, chronostratigraphical, biostratigraphical, lithostratigraphical and
152 palaeoenvironmental information. Raw data were obtained by searches of digital
153 reference indexes, institutional library catalogues, and thematic literature collections,
154 the latter particularly including the global palynological reference collection
155 assembled by John Williams at the Natural History Museum (London). Potential
156 limitation of Rupelian data as a consequence of sea level fall associated with early
157 Oligocene glaciation of Antarctica is not reflected by the relative sizes of our two
158 datasets, although it may potentially affect its relative completeness in particular
159 palaeoenvironments.

160

161 *Dating: chronostratigraphy, biostratigraphy, magnetostratigraphy*

162 Geochronometric, biostratigraphical (dinoflagellate cyst, planktonic foraminifera,
163 calcareous nannofossil) and magnetostratigraphical criteria are used to recognise the
164 Bartonian and Rupelian. These stratigraphical criteria are summarised in Figures 2
165 and 3. Confidence of assignment to a particular time slab is based on assessment of
166 published stratigraphical data (1 = high confidence; 3 = low confidence), and this is
167 indicated in a separate field in the data compilation (see Supplementary Data).

168 Brinkhuis and Biffi (1993) noted that long-range biostratigraphical correlation using
169 dinoflagellate cysts is problematic because of the effects of provincialism and
170 palaeoenvironment, and this may affect the confidence of age assignment of sites
171 where dinoflagellate cysts alone are the basis of age diagnosis. Generally, sites dated
172 with low confidence are those that are likely to contain at least parts of
173 chronostratigraphical intervals adjacent to either the Bartonian or Rupelian.

174 Nevertheless, in all these cases their dinoflagellate cyst floras are highly likely to span

175 the time slabs critical to this investigation; other sites that potentially include the
176 Bartonian or Rupelian, but for which confirmatory stratigraphical data were scant,
177 were excluded from this study. In some cases age confidence was enhanced by
178 omitting sample data from parts of successions where dating evidence was much less
179 certain.

180

181 *Location*

182 Location data are recorded as longitude and latitude, either directly transcribed from
183 the relevant publication, or derived from Google Earth™ using published
184 geographical details. Where the quality of published data precludes a precise location
185 fix, then a site is defined by a radius from a designated point. All modern longitude
186 and latitude data for sites were converted to values relevant to the Bartonian or
187 Rupelian (Fig. 4C, D) using PALEOMAP PointTracker software for global
188 palaeogeography reconstructions at 40 Ma (early Bartonian) and 30 Ma (mid
189 Rupelian).

190

191 *Lithostratigraphy and palaeoenvironment*

192 Where available, lithostratigraphical and palaeoenvironmental information has been
193 included in the datasets. Together, these data provide an indication of how nearshore
194 or basinal a succession is likely to be, and are a guide to the likely influence of local
195 palaeogeographical factors on dinoflagellate cyst composition.

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199

200 *Dinoflagellate cyst data, taxonomy and nomenclature*

201 Following the rationale used to build the Cenozoic vegetation databases using TEVIS
202 (Salzmann et al., 2008; Pound et al., 2011, 2012), there is minimal reinterpretation of
203 the primary published data, which in this study represents the dedicated work of
204 dinoflagellate specialists. This is an essential feature of our methodology, which
205 permits rapid construction of global-scale databases, focusing on large-scale trends
206 that are beyond the scope of individual studies. The sheer quantity of data assembled,
207 and the broad-scale of the analysis, militate against problems caused by variable
208 taxonomic interpretation in source literature used to build the databases. There are
209 obvious practical problems in attempting to directly re-interpret such large volumes of
210 data. Extensive indirect re-interpretation of published records is also undesirable,
211 because strict application of current understanding of taxonomic and range concepts is
212 likely to falsely eliminate data that represent genuine records of taxa that were
213 previously differently interpreted.

214

215 Notwithstanding the above, some limited screening of taxonomic nomenclature has
216 been applied where this is clearly beneficial for data analysis, including removal of
217 obvious species synonyms. In a few cases, where clear doubt existed about species
218 records, these were checked against any associated published figures/plates, or the
219 records deleted. Only taxa identified to species-level are included in the datasets;
220 identifications qualified by “?” and “cf.” are regarded as definite for the purposes of
221 the statistical analyses, but records qualified by “aff.” are excluded. No informal
222 nomenclature, prevalent in some older publications, has been included, but data fields
223 describing the higher taxonomic classification of species have been added. An
224 important consequence of the methodology adopted in this study is that the species

225 names appearing in our dataset largely reflect understanding of dinoflagellate cyst
226 taxonomy at the time of publication. Current species concepts, and the stratigraphical
227 ranges of taxa, may be broader or narrower than those appearing in historical
228 literature.

229

230 Potential distortion of ecological conclusions based on this methodology can arise
231 where there is reworking of dinoflagellate cysts, either through erosion of pre-existing
232 rock successions, or by pre-burial lateral transport of dinoflagellate cysts within
233 sedimentary basins. Reworked taxa, identified in published source data for this study
234 (e.g. De Coninck, 1986; Frith, 1996; Heilmann-Clausen and Van Simaey, 2005;
235 Jaramillo and Oboh-Ikuenobe, 1999; McMahon, 1997; Schiøler, 2005) or inferred
236 from known range data, were excluded from the analysis. The possibility that some
237 reworked taxa form part of our analysis cannot be excluded. However, the large
238 quantity of data analysed in this study coupled with evidence of limited reworking of
239 dinoflagellate cysts in younger sediments (Mertens et al., 2009; Verleye and Louwye,
240 2010), suggest that this factor is unlikely to bias our results. Mertens et al. (2009)
241 reported that reworking affected a maximum of 7% of the cysts recorded in
242 Quaternary sediments at four widely distributed sites, and statistical analysis of shelf
243 to basin transects in the south-east Pacific found negligible evidence of lateral
244 transport of cysts, including by near-shore and bottom water currents (Verleye and
245 Louwye, 2010).

246

247 The datasets contain presence/absence data for dinoflagellate cysts from 71 Bartonian
248 sites and 123 Rupelian sites (Fig. 4; Appendix 1A). Figure 4 shows that there is a
249 general paucity of low latitude and southern hemisphere data for each time interval,

250 but in the northern hemisphere data coverage is good. A total of 460 taxa are
251 represented in the Bartonian dataset, and 492 taxa in the Rupelian dataset, with 268
252 taxa occurring in both time slabs, representing more than 50% of the taxa in each
253 individual time slab. Information about relative species abundance in samples was
254 collected or derived where possible, but inconsistency in the quality of these data
255 precluded their use in statistical analyses. Similar problems with abundance data were
256 encountered by Masure and Vrielynck (2009) in their global analysis of Upper Albian
257 dinoflagellate cysts. The large percentage of taxa shared by the Bartonian and
258 Rupelian is reflected in the global plot of dinoflagellate generic diversity across the
259 Eocene – Oligocene boundary, which is almost flat (MacRae et al., 1996).
260 Assessments of individual localities show that, despite the range of
261 palaeoenvironments represented in this study, many Bartonian and Rupelian sites
262 have more than 70% of taxa common to both time slabs; localities with a lower
263 proportion of shared taxa tend to occur at higher palaeolatitudes. The high percentage
264 of shared taxa between the time slabs mitigates the impact of biological factors (e.g.
265 evolutionary change) on the interpretation of our results.
266 Copies of all the datasets, and the references from which they were compiled, are
267 provided as Supplementary Data. The author citations, with the relevant
268 bibliographical references, of all the dinoflagellate cyst taxa at and below generic
269 level which are quoted in this contribution and associated Supplementary Data can be
270 found in Fensome and Williams (2004), or online at:
271 <http://dinoflaj.smu.ca/~macrae/pdf/dinoflaj.pdf>.

272

273 **4. Method**

274

275 We used ordination techniques to study relationships between sample sites on the
276 basis of their full dinoflagellate cyst composition (presence/absence data). Ordination
277 techniques allow visualisation of large datasets in low-dimensional (usually two-
278 dimensional) ordination diagrams, in which the ordination axes represent the most
279 important gradients in species composition (Jongman et al. 1995). These can then be
280 related to known environmental variation, i.e. palaeolatitude, depositional basin
281 (North Sea, Arctic, Atlantic, Tethys, Indian and Pacific Ocean) and
282 palaeoenvironment (position of sites with respect to the shore, i.e. inshore vs.
283 offshore). Multivariate analysis has previously been used by Versteegh and
284 Zonneveld (1994), Marret and Zonneveld (2003), Esper and Zonneveld (2007), and
285 Zonneveld et al. (2013) to investigate the relationship between dinoflagellate cyst
286 distribution and environmental parameters.

287

288 Three primary datasets have been investigated: (1) a Bartonian dataset comprising
289 460 species and 71 sites, (2) a Rupelian dataset with 492 species and 123 sites, and (3)
290 a combined dataset comprising only those species that occurred in both time slabs
291 (268 species and 175 sites). Analysis of the latter dataset allowed comparison of
292 potential latitudinal shifts in species distributions between the Bartonian and Rupelian
293 sites. All ordination analyses were performed using the program CANOCO for
294 Windows 4.5 (ter Braak and Smilauer 1998). To aid the analysis of particular
295 variables other than latitudinal position, key features of the primary data (for example,
296 ocean basin, inshore/offshore palaeoenvironment) were introduced as qualitative
297 (dummy) variables (cf. ter Braak and Smilauer, 1998).

298

299 Preliminary Detrended Correspondence Analyses (DCA) revealed strong turnover in
300 species composition between the samples in all datasets investigated ('length of
301 gradient' > 4), indicating that unimodal ordination techniques were the most
302 appropriate for all analyses (Jongman et al., 1995). DCA was used instead of
303 Correspondence Analysis (CA) to eliminate the arch effects in the analyses (ter Braak
304 and Smilauer 1998). Analyses were initially performed on datasets (1) and (2) (Figs 5
305 and 6); subsequently the data were 'filtered' by removing groups of samples from
306 further analyses, in order to eliminate confounding basin-specific effects
307 (provincialism) (see Supplementary Data: Suppl. Figs 1 and 2). In a final analysis of
308 the combined Bartonian and Rupelian data (dataset (3), Fig. 7), a further data
309 reduction (sample elimination) was performed in order to minimise basin-specific and
310 potential palaeoenvironmental effects. In this last analysis, the Bartonian samples
311 were active (i.e. the DCA was only based on these samples) and the Rupelian samples
312 were supplementary (i.e. they were passively plotted in the Bartonian DCA, only on
313 the basis of their resemblance in dinoflagellate cyst composition to the Bartonian
314 samples).

315

316 To further understand the changes in the global distribution of dinoflagellate cyst taxa
317 that are common to both time slabs, simplified latitudinal range plots (using 5° bins;
318 see Supplementary Data: Latitudinal Ranges) were generated for all species in dataset
319 (3), and global occurrence maps plotted for selected species. These distributions,
320 plotted using corrected palaeolatitudes on modern geographical base maps, are shown
321 in Figure 8. Taxa were selected on the basis of having been consistently designated as
322 'temperature sensitive' in previous studies (Table 1). Opinion is divided about the

323 temperature sensitivity of some dinoflagellate cysts (Table 1), and the present study is
324 open-minded about the significance of the plots we illustrate for understanding SST.

325

326 **5. Results**

327

328 DCA of the global Bartonian and Rupelian datasets shows that southern hemisphere
329 communities are clearly different from northern hemisphere communities in both time
330 slabs (Fig. 5; see 7). Because latitudinal coverage of sample sites is poor in the
331 southern hemisphere, we decided to restrict further ordination analyses to the northern
332 hemisphere sites.

333

334 After omitting the 14 southern hemisphere samples and two outlier samples (B57 and
335 B58), we performed DCA on the remaining northern hemisphere Bartonian data (365
336 species, 55 samples). Along the first axis, sites are separated on the basis of their
337 palaeolatitudinal position, with low latitude samples (from three separate basins:
338 Atlantic, Indian and Pacific oceans) on the right side of the first axis, high latitude
339 samples on the left side, and samples from intermediate latitudes (50 – 30° N)
340 occupying a somewhat intermediate position (Fig. 6B). The latitudinal gradient in cyst
341 composition appears to be mainly driven by the low latitude samples, with high
342 latitude samples (80 – 60° N) having a species composition that is more-or-less
343 similar to samples from the many mid-latitude sites. As well as a latitudinal signal, we
344 can also distinguish a clear ‘basin-effect’, with sites in the North Sea and the palaeo-
345 Tethys Ocean being more or less separated along the second axis (Fig. 6A).

346 In contrast with the Bartonian dataset, DCA of the northern hemisphere Rupelian data
347 (449 species and 106 sites, after omitting 15 southern hemisphere samples and the

348 outliers R41 and R77) revealed no distinct latitudinal trend in species composition.
349 The Pacific sites are separated from most other samples which form a tight cluster on
350 the right side of the first ordination axis (Figs. 6C, D). The single (Indian Ocean)
351 sample from the 10 – 0° N latitude class does not appear to be very different from the
352 other samples, nor do the samples from the 30 – 20° N class (Fig. 6D). Basin
353 specificity is also less pronounced (except for the Pacific samples), although Atlantic
354 and North Sea samples do seem to be separated along the second axis (Fig. 6C). It is
355 likely that a general lack of tropical samples (only one sample after omission of
356 outliers R77 (Nigeria) and R41 (Indian Ocean)) is at least partly responsible for the
357 absence of a latitudinal trend in the Rupelian dataset, with most samples being located
358 between 45 – 65 °N.

359

360 To get a clearer insight into any underlying latitudinal control on the Bartonian and
361 Rupelian data, basin-specific effects were initially reduced by confining analyses to
362 samples from the palaeo-North Sea, Atlantic and Arctic oceans; basins for which
363 palaeogeographical data suggest few barriers to North – South migration during the
364 Eocene – Oligocene transition. However, these results appear to show the persistent
365 influence of basin-setting and inshore to offshore environmental gradients (Suppl. Fig.
366 1), predominantly caused by the inclusion of samples from the palaeo-North Sea
367 region which are predominantly ‘inshore’. Therefore, in a final analysis of the
368 combined Bartonian and Rupelian dataset (dataset (3)), residual basin-effects and
369 palaeoenvironmental influences were minimised by removing the North Sea samples
370 (Fig. 7). As the latitudinal signal was strongest in the Bartonian dataset (cf. Fig. 6A),
371 we used the 15 remaining (Atlantic and Arctic) Bartonian samples as active samples,
372 thus providing a (latitudinal) scaffold onto which the Rupelian samples are plotted as

373 supplementary ('passive') samples. The underlying idea is that if, as hypothesized,
374 dinoflagellate communities shift southward in a cooler climate, Rupelian communities
375 from a specific latitudinal belt would become more similar to Bartonian communities
376 from a higher latitudinal belt, since in a warmer period the same communities would
377 be found at higher latitudes. Surprisingly, there is no evidence supporting this
378 hypothesis at the community level. On the contrary, Fig. 7 clearly shows that
379 Rupelian high latitude communities (60 – 80 °N) appear to become more similar to
380 mid-latitude (30 – 60 °N) Bartonian samples. While as a result of the stringent data
381 reduction, the number of samples included in the analysis is rather low, and some
382 latitudinal belts (20 – 30, 40 – 50, 50 – 60 °N) are poorly or not represented in the
383 Bartonian latitudinal scaffold, the signal from the Rupelian high northern latitudinal
384 samples is clear: we find little evidence for a southward shift of dinoflagellate
385 communities from the Bartonian to the Rupelian.

386

387 Examination of latitudinal range plots of taxa that are common to both time slabs (see
388 Supplementary Data: Latitudinal Ranges), as well as the distributions of some
389 'temperature sensitive' taxa, also suggest lack of a clear cooling signal in Rupelian
390 dinoflagellate cyst data. Latitudinal range plots for all taxa occurring in both the
391 Bartonian and Rupelian reveals three predominant patterns (Appendix 1B): 1) taxa
392 showing negligible change in their most northerly limit in the northern hemisphere; 2)
393 taxa with a lower northern latitudinal limit in the northern hemisphere in the Rupelian
394 compared to the Bartonian; 3) taxa extending their northern latitudinal limit in the
395 northern hemisphere in the Rupelian compared to the Bartonian. Numbers of species
396 in categories (1) and (3) significantly exceed those in category (2), and category (3) is
397 the largest (Appendix 1B). Amongst the taxa previously interpreted as temperature-

398 sensitive, some warm/cold-water forms exhibit trends consistent with Rupelian
399 cooling, such as the southward movements of ‘warm-water’ *Deflandrea arcuata* (Fig.
400 8C) and ‘cold-water’ *Rottnestia borussica* (Fig 8F) and *Svalbardella cooksoniae* (Fig.
401 8B). Other taxa suggest the opposite trend, with persistence or northward extension of
402 the Rupelian ranges of ‘warm-water’ forms (e.g. *Tectatodinium pellitum*,
403 *Lingulodinium machaerophorum*; Fig. 8A, D). *Polysphaeridium zoharyi*, regarded as
404 a tropical to subtropical indicator species in modern oceans (Marret and Zonneveld,
405 2003; Zonneveld et al., 2013), extends from equatorial and subtropical latitudes in the
406 Bartonian to high mid-latitudes in the Rupelian (Fig. 8E). The plot for the Rupelian
407 occurrence of all selected warm-water indicator species shows a local concentration
408 immediately south of Australia (Fig. 9B), and published data for this region suggests a
409 persistent warm-water influence from the Late Eocene to Quaternary (Brinkhuis et al.,
410 2004). Overall, between the Bartonian and Rupelian there appears to be negligible
411 change in the global distributions of all cold-water/high-latitude and warm-water/low-
412 latitude taxa (Fig. 9). An important caveat concerning these trends is that they are also
413 affected by lack of data rather than purely reflecting a palaeoecological response.
414 However, the consistency of these trends across significant numbers of taxa suggests
415 that data-paucity alone is insufficient to explain them.

416

417 **6. Interpretation**

418

419 The starting hypothesis for this paper was that, based on previous use of dinoflagellate
420 cysts in palaeoclimate work (Brinkhuis and Biffi, 1993; Brinkhuis et al., 1998; Esper
421 and Zonneveld, 2007; Masure and Vrielynck, 2009; Mudie et al., 2001; Sluijs et al.,
422 2005; Wall et al., 1977), and on current understanding of extant dinoflagellate

423 distributions (Marret and Zonneveld, 2003; Zonneveld et al., 2013): 1) dinoflagellate
424 cyst assemblages as a whole would robustly track global climate change at the Eocene
425 – Oligocene transition; 2) there would be a well established palaeolatitudinal gradient
426 of dinoflagellate cyst taxa in both the Bartonian and Rupelian; 3) that the effect of
427 global cooling in the latest Eocene and early Oligocene would be manifest as a
428 steepening of this palaeolatitudinal gradient, and that this would be accompanied by
429 significant equator-ward movement of taxa that are present in both time slabs. Our
430 analysis of dinoflagellate cyst data actually reveals more complex patterns that may
431 reflect a more complex oceanography, or suggests that across the Eocene – Oligocene
432 transition the predominant control on dinoflagellate cyst distributions may not be
433 SST. There is a relatively well-defined palaeolatitudinal gradient in northern
434 hemisphere data for the Bartonian. Low latitude sites have a distinct dinoflagellate
435 cyst composition whilst high and mid-latitude cyst taxa are more similar, suggesting a
436 weak thermal gradient. In contrast, there is no clear latitudinal gradient in northern
437 hemisphere Rupelian data. Partly this reflects lack of low-latitude data points (a single
438 site, R77), but it is also consistent with latitudinal range data that suggest both
439 northward and southward movement of a significant number of taxa in the northern
440 hemisphere in the Rupelian (Appendix 1B).

441

442 **7. Discussion**

443

444 Zonneveld et al. (2013) determined that latitudinal gradient was the most important
445 influence on their dataset of modern dinoflagellates, and that SST, phosphate and
446 nitrate concentrations are the most significant environmental variables that can be
447 related to modern distribution patterns. In this context, it is striking that both

448 community-level analysis of the northern hemisphere dinoflagellate cyst assemblages
449 (i.e. DCA results) and latitudinal range plots identify apparently paradoxical
450 palaeolatitudinal range shifts of taxa between the Bartonian and Rupelian. These
451 unexpected results may, in part, be explained by the uneven global coverage of our
452 dataset as well as methodological limitations; they may also reflect complex changes
453 in oceanography (for example patterns of warm and cool currents) that confuses the
454 global relationship of dinoflagellate cysts to palaeolatitude, or show that ecological
455 tolerance/adaptability of dinoflagellate cysts caused SST to be subordinate to other
456 factors in controlling their net latitudinal distribution in the Rupelian.

457

458 *7.1. Data coverage, methodological assumptions and limitations*

459 Our methodology assumes that the time intervals (slabs) we have analysed are broadly
460 representative of two different global climatic states, one warm (Bartonian) and one
461 cool (Rupelian). For each time interval we assume that the contained taxa have
462 consistent ecology, have not been significantly affected by re-working (*4 above*), and
463 that orbitally driven patterns of climate change within each have had less impact on
464 the global distributions of taxa than the climate change events that occur between the
465 time intervals (MacLeod et al., 2000; Less and Özcan, 2012). Finally, because of
466 historical and on-going revisions to the definition of the selected time intervals, it is
467 possible that there is some error in how stratigraphical successions have been assigned
468 to time intervals, although this is partly addressed by assigning confidence levels to
469 stratigraphical assignments in our datasets. The degree to which the above assumptions
470 are not fully met will affect the fidelity of our results and interpretations, and may
471 explain in part why we have difficulty in discerning a clear latitudinal signal from the
472 Rupelian data.

473

474 In mitigation, our methodology outlines procedures and describes published evidence
475 that seeks to reduce or acceptably quantify the adverse potential impact of our
476 inherent assumptions. Also, the large size of both datasets helps to reduce the
477 statistical effect of individual sites that strongly depart from our ideal criteria; data
478 classes for age precision, depositional basin and environment allow statistical filtering
479 of potentially problematic data. Any residual bias in our data might be expected to
480 equally affect both Bartonian and Rupelian datasets, but whilst data for the Bartonian
481 yield a good latitudinal signal, a reliable signal for the Rupelian (the larger of the two
482 datasets) is not detectable.

483

484 *7.2. Oceanography*

485 Pole-ward range shifts of Rupelian dinoflagellate cysts in the northern hemisphere
486 may suggest that aspects of environmental change related to Eocene – Oligocene
487 cooling modulated the response of dinoflagellate cysts to this event, compared to the
488 much more direct impact reported for planktonic foraminifera and calcareous
489 nannofossils (Wade and Pearson, 2008; Wei, 1991). Alternatively, the complex
490 response patterns of Rupelian dinoflagellates might reflect their sensitivity to local
491 patterns of marine circulation with different temperature profiles. In both central Italy
492 and the Southern Ocean, the sensitivity of dinoflagellate cysts to warm ocean currents
493 has been detected (Brinkhuis and Biffi, 1993; Brinkhuis et al., 2004). This has
494 produced low-latitude dinoflagellate cyst associations in Eocene – Quaternary
495 successions off the coast of Tasmania (palaeolatitude 59°S) (Brinkhuis et al., 2004),
496 and in Italy, warm and cool phase dinoflagellate cyst associations in Eocene –
497 Oligocene strata (Brinkhuis and Biffi, 1993) may reflect the intermittent influence of

498 the Subtropical Neotethys Current (STENT) (Jovane et al., 2009). Warm ocean
499 currents may also be the cause of inexplicably high SSTs at mid to high latitudes in
500 the late Eocene and early Oligocene of the northern hemisphere (Liu et al., 2009), and
501 explain some of the unexpected results of our study.

502

503 *7.3. Nutrient regime*

504 Although the distribution of modern organic walled dinoflagellate cysts is
505 predominantly related to SST and latitude, the next biggest controls are salinity and
506 nutrients (Zonneveld et al., 2013), which to a greater or lesser degree reflect the
507 offshore to onshore gradient (Marret and Zonneveld, 2003). It is therefore likely that
508 related environmental changes to global cooling at the Eocene – Oligocene boundary
509 could have an impact on the results of our study.

510

511 A modelled c. 70 m fall in sea level is associated with early Oligocene cooling and the
512 onset of Antarctic glaciation (Coxall et al., 2005), and both palaeontological and
513 sedimentological data (Alegret et al., 2008; Brinkhuis and Biffi, 1993; Śliwińska et
514 al., 2010) show that this time coincides with enhanced riverine input of eroded
515 sediments into marine basins. The effects of enhanced nutrient delivery to the marine
516 realm would be amplified across flooded continental shelves and enclosed basins;
517 palaeogeographical settings that are strongly represented in our northern hemisphere
518 data for the Rupelian. In the North Sea, this fall in sea level produced prograding
519 muddy and sandy sediments derived from Fennoscandia, overlying Eocene
520 hemipelagic clays (Śliwińska et al., 2010). Elsewhere, contemporary tectonism
521 combined with eustatic sea level fall radically altered the nature and volumes of
522 sediment entering marine basins, for example in the Mediterranean (Brinkhuis and

523 Biffi, 1993) and off the coast of southern Spain, where foraminifera provide evidence
524 for increases in nutrient fluxes to deep marine early Rupelian settings (Alegret et al.,
525 2008). This, and the lack of DCA evidence for equator-ward movement of Rupelian
526 dinoflagellate cysts from predominantly open-ocean sites, suggests that any changes
527 in the nutrient regime of the marine realm in the Rupelian may not have been limited
528 to shelfal regions.

529

530 The importance of nutrients in driving the evolution of the dinoflagellates is
531 exemplified by the distinct character of southern hemisphere Eocene – Oligocene
532 dinoflagellate cysts. These high southern latitude dinoflagellates developed their
533 endemic character (‘Transantarctic Flora’) in the early mid Eocene (Bijl et al., 2011),
534 initially in response to increases in ocean fertility, but probably later became
535 modulated by reductions in SST (Bijl et al., 2011). Mathematical ‘decision-making’
536 models also reveal the influence of light and nutrients on the diurnal movements of
537 modern dinoflagellates, suggesting that changes in the relative balances of these two
538 variables can trigger different responses (Yamazaki and Kamykowski, 2000). This
539 raises the possibility that at least part of the distribution of dinoflagellate taxa in the
540 Rupelian is the result of an ecological trade-off between several simultaneously
541 varying factors that are important for dinoflagellate well-being.

542

543 *7.4. Ecological tolerance and adaptability*

544 Data from our study, particularly the large percentage of shared taxa between the
545 Bartonian and Rupelian and the apparent pole-ward Rupelian migration of many
546 dinoflagellate cyst species in the northern hemisphere, suggests that dinoflagellate
547 cyst taxa are relatively robust to environmental change. This may partly reflect the

548 astonishing cryptic diversity recently discovered in extant dinoflagellates (Stern et al.,
549 2010; Murray et al., 2012). Broad temperature tolerance is also suggested by
550 comparison of Pliocene dinoflagellate cysts with analytically determined temperature
551 measurements (De Schepper et al., 2011); the SST range of many dinoflagellate cyst
552 taxa is large compared to the average cooling of 5.4°C (polar regions; Liu et al., 2009)
553 to 2.5°C (tropical regions; Lear et al., 2008) at the Eocene – Oligocene transition.
554 Unlocking the SST signal from dinoflagellate cyst data may ultimately depend on
555 analysis of their abundance (De Schepper et al., 2011), although challenges exist to
556 applying this methodology at a global scale across numerous sites. In a quantitative
557 analysis of dinoflagellate cysts to track Eocene – Oligocene climate change in central
558 Italy, Houben et al. (2012) were careful to select particular ‘warm’ or ‘cool’ oceanic
559 taxa, aware that inclusion of all taxa could create unwanted ‘noise’.

560

561 Investigation of high-latitude northern hemisphere climate at the Eocene – Oligocene
562 transition suggests a complex response to cooling, with limited ice growth (Peck et
563 al., 2010) and extreme seasonality; modelled climate simulations suggest very cold
564 winters contrasting with warm summers with high precipitation (Eldrett et al., 2009).
565 This climate response in the northern hemisphere could help explain why our
566 Rupelian data (overwhelmingly concentrated in the northern hemisphere) do not show
567 a dominant latitudinal effect. Cyst formation could also have mitigated the effects of
568 seasonally adverse conditions (Dale, 1983; Matsuoka and Fukyo, 2000; Sarjeant et al.,
569 1987), and may partly explain why diversity plots of dinoflagellate cysts show only a
570 small drop between the Ypresian/Bartonian and Rupelian (MacRae et al., 1996).

571

572

573

574 **8. Conclusions**

575 This study has sought to investigate Eocene – Oligocene climate change using
576 published data on the occurrence of dinoflagellate cysts; to understand the pattern of
577 change in distribution between the Bartonian and Rupelian; the extent to which this
578 distribution is likely to faithfully track changes in SST, and the implications this has
579 for understanding the consequences of early Oligocene global cooling; the extent to
580 which these distributions are likely to be unrelated to changes in SST, and the
581 consequences for use of dinoflagellate cyst data in palaeoclimate work.

582 Our results suggest the following:

583

584 1) Global distributions of dinoflagellate cysts in the Bartonian show a good latitudinal
585 relationship and suggest a weak thermal gradient, in agreement with global SST
586 estimates for this time interval (Bijl et al., 2009). This suggests that our methodology
587 is reliable, and our assumptions and data coverage acceptable.

588

589 2) Rupelian dinoflagellate cyst distributions do not show a clear relationship to
590 latitude. Statistical analyses and range data suggest that mid- to high-latitude
591 dinoflagellate cyst associations in the cooler Rupelian are more like lower latitude
592 associations in the globally warmer Bartonian.

593

594 3) It is possible that at least part of the Rupelian dinoflagellate cyst distribution
595 reflects latitudinally discordant influences on SST, such as warm ocean currents
596 (Brinkhuis et al., 2004), or perhaps unusual northern hemisphere seasonality that
597 maintained relatively high summer temperatures at high latitudes (Eldrett et al., 2009).

598

599 4) To some extent, the distributions of dinoflagellate cysts in the Rupelian may be
600 significantly influenced by factors other than SST, potentially complicating how their
601 distributions are interpreted with respect to climate change events. The factors
602 affecting dinoflagellate cyst distribution in the Rupelian may be connected to related
603 environmental changes associated with Rupelian cooling, such as sea level fall
604 associated with the onset of Antarctic glaciation. Studies of Pliocene and extant
605 dinoflagellates also suggest that many have broad temperature ranges (De Schepper et
606 al., 2011) and high genetic diversity (Stern et al., 2010; Murray et al., 2012); whilst
607 dinoflagellate cysts appear to have optimised distributions to SST in the Bartonian,
608 their biology may have allowed greater flexibility of response to Rupelian climate
609 change. Our work highlights the need for better understanding of the biology and
610 (palaeo-) ecology of dinoflagellates, and how this affects their response to changes in
611 key environmental parameters and governs their distribution in present and past
612 oceans.

613

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623

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965

966 **Appendix 1A. Summary of locality data.**

967

968 Longitude and latitude co-ordinates are decimalised. Where precise positions are

969 uncertain, the co-ordinates are the origin of a specified geographical radius that the

970 locality falls within. For full details see Supplementary Data.

971

Mid Eocene (Bartonian)

Locality	General	Modern	Rotated		Locality	General	Modern	Rotated			
Code	Location	Lat.	Long.	Lat.	Long.	Code	Location	Lat	Long.	Lat.	Long.
B1	UK	50.72N	1.75W	48.55N	5.64W	B37	Southern Ocean	46.78S	144.96E	67.23S	149.59E
B2	Siberia, Russia	64.16N	73.15E	64.56N	65.54E	B38	North Sea	59N	1E	56.87N	3.49W
B3	UK	50.7N	1.32W	48.53N	5.23W	B39	North Sea	57.76N	1.95E	55.65N	2.51W
B4	Germany	53.05N	11.45E	51.17N	6.85E	B40	Slovakia	49.22N	19.35E	43.89N	16.97E
B5	Germany	52.38N	9.96E	50.46N	5.47E	B41	South Carolina, USA	33.15N	80.46W	33.2N	71.45W
B6	North Atlantic	29.98N	76.52W	29.74N	67.86W	B42	Antarctica	61.85S	42.93W	61.74S	51.57W
B7	Siberia, Russia	62.66N	64.36E	62.7N	57.04E	B43	Venezuela	9.78N	71.06W	7.32N	63.63W
B8	Siberia, Russia	61.76N	63.6E	61.77N	56.46E	B44	Venezuela	9.32N	70.68W	6.87N	63.24W
B9	New Zealand	41.53S	173.58E	-53.73S	176.39W	B45	Venezuela	9.38N	70.55W	6.94N	63.11W
B10	India	23.25N	72.5E	8.79N	66.03E	B46	Venezuela	9.2N	70.78W	6.75N	63.33W
B11	Antarctica	64.28S	56.75W	64.09S	59.81W	B47	Georgia, USA	32.93N	81.65W	33.08N	72.66W
B12	Antarctica	64.22S	56.63W	64.03S	59.69W	B48	Georgia, USA	33.03N	81.7W	33.18N	72.69W
B13	North Atlantic	45N	53W	42.97N	43.08W	B49	Georgia, USA	33.18N	81.78W	33.34N	72.76W
B14	Siberia, Russia	66.76N	77.46E	67.33N	69.26E	B50	Georgia, USA	33.23N	81.9W	33.39N	72.87W
B15	Siberia, Russia	66.4N	74.85E	66.86N	66.71E	B51	Georgia, USA	33.2	81.96	33.37	72.94
B16	Siberia, Russia	67.46N	75.96E	67.96N	67.54E	B52	New Zealand	45.66S	170.65E	53.13S	167.83E
B17	Japan	34.45N	134.85E	42.11N	129.39E	B53	New Zealand	45.28S	170.85E	52.77S	167.52E
B18	New Zealand	45.28S	170.83E	52.77S	167.54W	B54	New Zealand	45.9S	170.43E	53.35S	168.14E
B19	India	22.83N	88.43E	4.34N	80.1E	B55	China	39.5N	75.98E	39.12N	70.15E

B20	Argentina	53.95S	68.25W	56.29S	58.2W	B56	Australia	34.9S	138.6E	56.78S	133.52E
B21	North Atlantic	67.65N	56.68W	65.38N	41.45W	B57	North Sea	58.5N	0.5W	56.34N	4.87W
B22	North Atlantic, Greenland Sea	75.48N	6.95E	70.53N	13.07E	B58	Kamchatka, Russia	57.92	160.63	61.63	162.59
B23	France	48.85N	2.32E	46.76N	1.66W	B59	Turkey	41.65N	33.68E	38.63N	41.42E
B24	Netherlands	51.45N	4.3E	49.4N	0.11E	B60	Novosibirsk, Russia	54.58N	77.02E	55.18N	71.05E
B25	North Atlantic, Norwegian Sea	67.7N	1.03W	63.95N	4.78W	B61	Kazakhstan	51.98N	76.15E	52.55N	70.48E
B26	Denmark	56.02N	10.26E	54.11N	5.5E	B62	Ukraine	50.16N	30E	48.86N	24.98E
B27	India	16.68N	81.9E	0.06S	72.6E	B63	India	27.06N	95.02E	7.17N	86.88E
B28	Labrador Sea	53.32N	45.25W	50.75N	34.5W	B64	Aral Sea	47.16N	61.13E	47.11N	55.9E
B29	New Zealand	42S	173.75E	54.08S	175.82W	B65	Italy	39.93N	16.46E	34.79N	13.37E
B30	India	25.33N	90.68E	6.31N	82.68E	B66	Hungary	47.06N	19.55E	41.72N	16.91E
B31	France	48.88N	2.58E	46.79N	1.41W	B67	Volgograd, Russia	48N	44.46E	47.25N	39.31E
B32	France	48.86N	2.35E	46.77N	1.63W	B68	Borneo	3.25N	110.72E	7.31N	113.7E
B33	France	48.83N	2.48E	46.74N	1.5W	B69	Spain	41.48N	1.38E	39.7N	1.85W
B34	France	48.93N	2.45E	46.84N	1.54W	B70	Slovakia	48.66N	19.65E	43.31N	17.17E
B35	Argentina	51.58S	72.22W	54.04S	62.6W	B71	Texas, USA	30.63N	96.55W	31.92N	87.86W
B36	Southern Ocean	45.03S	144.32E	65.71S	147.17E						

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Early Oligocene (Rupelian)

Locality Code	General Location	Modern Lat.	Modern Long.	Rotated Lat.	Rotated Long.	Locality Code	General Location	Modern Lat.	Modern Long.	Rotated Lat.	Rotated Long.
R1	Belgium	51.4N	4.9E	50.87N	1.35E	R63	Germany	51.42N	6.5E	50.93N	2.93E
R2	Belgium	51.2N	5.1E	50.67N	1.56E	R64	North Atlantic	33.15N	77.43W	32.92N	71.14W
R3	Belgium	51.1N	5.36E	50.58N	1.82E	R65	Egypt	30.65N	29.15E	27.56N	26.15E
R4	Germany	53.05N	11.45E	52.67N	7.72E	R66	North Atlantic	53.32N	45.25W	51.82N	38.03W
R5	Germany	52.53N	7.3E	52.05N	3.65E	R67	Turkey	38.82N	42.12E	36.01N	47.62E
R6	Germany	52.38 N	9.96E	51.97N	6.29E	R68	Turkey	38.82N	42.12E	36.01N	47.62E
R7	Italy	40.16N	16.5E	37.44N	14.35E	R69	Germany	51.25N	12.35E	50.9N	8.73E
R8	Italy	43.38N	12.56E	40.8N	10.77E	R70	Poland	52.83N	16.55E	52.58N	12.8E

R9	Italy	43.53N	13.58E	40.91N	11.75E	R71	Germany	54N	10.06E	53.59N	6.28E
R10	Italy	43.56N	12.56E	40.98N	10.78E	R72	Germany	49.45N	8.52E	49N	5.04E
R11	Italy	45.63N	11.36E	43.09N	9.78E	R73	Germany	52.2N	8.58E	51.75N	4.94E
R12	Italy	45.65N	11.4E	43.11N	9.82E	R74	Germany	52.38N	7.28E	51.9N	3.64E
R13	Belgium	51.25N	4.38E	50.71N	0.84E	R75	Germany	52.52N	13.42E	52.19N	9.71E
R14	Poland	49.33N	20.93E	46.45N	19.14E	R76	Turkey	41.45N	26.75E	38.42N	24.24E
R15	North Sea	55N	6E	54.49N	2.2E	R77	Nigeria	5.35N	6.5E	3.05N	2.9E
R16	North Pacific	52.56N	161.2W	45.17N	143.71W	R78	Belgium	50.82N	5.43E	50.3N	1.9E
R17	Japan	42.92N	142.03E	44.57N	139.41E	R79	Germany	49.9N	8.03E	49.44N	4.53E
R18	Japan	43.06N	143.83E	44.72N	141.26E	R80	France	48.96N	2.18E	48.37N	-1.2W
R19	Japan	37N	140.85E	44.22N	137.42E	R81	France	48.93N	2.56E	48.34N	0.83W
R20	North Atlantic	45N	53W	43.78N	46.22W	R82	France	48.95N	2.92E	48.37N	0.47W
R21	India	22.83N	88.43E	9.42N	83.94E	R83	France	48.8N	2.12E	48.2N	1.25W
R22	Australia	34.33S	142.4E	51.08S	138.85E	R84	Barents Sea	73.52N	16.43E	73.23N	9.79E
R23	Australia	34.22S	140.85E	51.1S	136.8E	R85	Southern Ocean	42.25S	143.48E	58.84S	142E
R24	North Atlantic	63.35N	7.78W	62.53N	12W	R86	Southern Ocean	43.92S	154.28E	58.97S	157.63E
R25	North Atlantic	67.78N	5.38E	67.24N	0.25E	R87	Deleted due to poor age constraint				
R26	North Atlantic	75.48N	6.95E	73.04N	11.82E	R88	Argentina	53.83S	67.7W	55.5S	58.19W
R27	North Atlantic	78.38N	1.35E	75.96N	7.2E	R89	Poland	49.62N	21.38E	49.49N	17.81E
R28	South Atlantic	51S	46.96W	51.67S	37.32W	R90	Mississippi, USA	31.66N	88.63W	31.91N	82.42W
R29	South Atlantic	47.56S	24.63W	47.08S	15.43W	R91	Alabama, USA	31.58N	88.1W	31.81N	81.89W
R30	North Atlantic	66.95N	6.45W	66.15N	11.12W	R92	Mississippi, USA	31.72N	88.66W	31.97N	82.44W
R31	Tunisia	36.26N	8.9E	33.83N	6.78E	R93	Mississippi, USA	31.83N	88.7W	32.08N	82.48W
R32	Tunisia	36.95N	8.75E	34.53N	6.68E	R94	North Sea	57.76N	1.95E	57.15N	2W
R33	Southern Ocean	43.95S	149.92E	59.7S	151.64E	R95	Antarctica	77.18S	163.7E	77.66S	155.45E
R34	Southern Ocean	42.6S	144.4E	59.09S	143.4E	R96	North Atlantic	55.25N	22.08W	54.17N	25.32W
R35	France	48.85N	2.32E	48.26N	1.06W	R97	North Atlantic	67.78N	5.38E	67.24N	0.25E
R36	Italy	43.53N	13.58E	40.91N	11.75E	R98	Florida, USA	27.03N	81.75W	27N	75.8W
R37	Netherlands	51.45N	4.3E	50.9N	0.75E	R99	Florida, USA	27.36N	81.43W	27.31N	75.46W
R38	North	67.7N	1.03W	67.02N	5.98W	R100	Florida, USA	27.15N	81.35W	27.1N	75.39W

R39	Atlantic Denmark	56.02N	10.26E	55.61N	6.33E	R101	Florida, USA	27.7N	80.43W	27.61N	74.44W
R40	UK	50.68N	1.3W	50.01N	4.73W	R102	Dunedin, New Zealand	45.18S	170.9E	51.89S	173.0W
R41	India	16.68N	81.9E	4.7N	76.58E	R103	Fiordland, New Zealand	46.05S	166.53E	52.42S	178.16W
R42	Poland	49.4N	19.93E	46.56N	18.2E	R104	Westland, New Zealand	41.75S	171.46E	53.22S	178.19E
R43	Poland	49.4N	19.95E	46.56N	18.22E	R105	China	39.5N	75.98E	39.68N	72.02E
R44	Poland	49.4N	20.05E	46.55N	18.31E	R106	Kazakhstan	43.26N	55.55E	43.97N	52.47E
R45	Poland	49.4N	20.13E	46.55N	18.39E	R107	Poland	53.23N	15.2E	52.95N	11.43E
R46	Poland	49.35N	20.18E	46.5N	18.43E	R108	Poland	53.52N	20.96E	53.38N	17.13E
R47	Poland	49.36N	20.3E	46.5N	18.55E	R109	Poland	54.62N	18.08E	54.41N	14.19E
R48	Poland	49.36N	19.85E	46.52N	18.12E	R110	Poland	52.93N	18.8E	52.74N	15.02E
R49	Poland	49.33N	19.86E	46.49N	18.13E	R111	Kamchatka, Russia	57.92N	160.63E	60.07N	163.41E
R50	Poland	49.33	19.96E	46.48N	18.22E	R112	Albania	41.33N	19.82E	38.5N	17.6E
R51	Poland	49.33N	19.93E	46.49N	18.2E	R113	Rostov, Russia	57.2N	39.42E	57.52N	35.33E
R52	Poland	49.35N	19.93E	46.51N	18.2E	R114	Hungary	47.06N	19.55E	44.23N	17.68E
R53	Poland	49.38N	20.13E	46.53N	18.39E	R115	Volgograd, Russia	48N	44.46E	48.45N	41.04E
R54	Poland	49.3N	19.86E	46.46N	18.13E	R116	Slovakia	48.66N	19.65E	45.83N	17.88E
R55	Poland	49.28N	19.83E	46.44N	18.1E	R117	Romania	47.22N	23.18E	44.28N	21.14E
R56	Poland	49.28N	19.95E	46.44N	18.21E	R118	Ukraine	48.63N	23.88E	45.67N	21.88E
R57	Poland	49.28N	19.86E	46.44N	18.13E	R119	Romania	46.28N	26.58E	46.29N	23.18E
R58	Poland	49.28N	19.95E	46.44N	18.21E	R120	France	46.08N	6.48E	45.59N	3.2E
R59	Poland	49.3N	19.92E	46.46N	18.18E	R121	France	46.05N	6.38E	45.56N	3.1E
R60	Poland	49.36N	19.82E	46.52N	18.09E	R122	Egypt	31.03N	30.08E	27.92N	27.06E
R61	Poland	49.38N	20.02E	46.53N	18.28E	R123	Antarctica	77S	163.72E	77.48S	155.55E
R62	South China Sea	18.83N	116.56E	20.98N	116.86E	R124	Antarctica	61.85S	42.93W	61.74S	51.57W

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978 **Appendix 1B. Major categories of northern hemisphere latitudinal response, and**
 979 **constituent taxa, for dinoflagellate cysts occurring in both the Bartonian and**
 980 **Rupelian (see also: Supplementary Data: latitudinal ranges)**

981

982 W = low latitude / warm water form

983 C = high latitude / cold water form

984 M = mid-latitude/temperate form

985 H = heterotrophic

986

987 NB: taxa with broader ecological ranges, or for which different ecological

988 assignments have previously been published, have not been classified below. For full

989 details see Supplementary Data.

990

991 (i) Dinoflagellate species showing negligible change in their maximum northern hemisphere range between the
 992 Bartonian and Rupelian.

993

<i>Achilleodinium biformoides</i>	<i>Deflandrea leptodermata</i>	H W	<i>Phelodinium pumilum</i>	H
<i>Achilleodinium latispinosum</i>	<i>Deflandrea musculopsis</i>	H	<i>Phthanoperidinium geminatum</i>	H
<i>Achomospaera multifurcata</i>	<i>Deflandrea phosphoritica phosphoritica attenuata</i>	H	<i>Phthanoperidinium levimurum</i>	H
<i>Achomospaera triangulata</i>	<i>Deflandrea phosphoritica spinulosa</i>	H	<i>Samlandia reticulifera</i>	
<i>Amphorosphaeridium multispinosum</i>	<i>Diphyes colligerum</i>		<i>Sentusidinium stipulatum</i>	
<i>Apteodinium maculatum</i>	<i>Distatodinium scariosum</i>		<i>Spiniferites microceras</i>	
<i>Areoligera undulata</i>	<i>Enneadocysta arcuata</i>		<i>Spiniferites ramosus granomembranceus</i>	
<i>Areosphaeridium diktyoplokum</i>	<i>Florentinia laciniata</i>		<i>Spiniferites twistringiensis</i>	

			<i>propria</i>			
<i>Batiacasphaera baculata</i>			<i>Gerdicysta aciculata</i>		<i>Svalbardella cooksoniae</i>	H C
<i>Batiacasphaera micropapillata</i>			<i>Heteraulacacysta porosa</i>	M	<i>Thalassiphora patula</i>	
<i>Bellatodinium hokkaidoanum</i>			<i>Homotryblium caliculum</i>		<i>Wetzeliiella articulata</i>	H
<i>Cerebrocysta bartonensis</i>			<i>Homotryblium tenuispinosum</i>		<i>Wetzeliiella cf. clathrata</i>	H
<i>Cerodinium leptodermum</i>	H		<i>Impagidinium disperitum</i>	W	<i>Wetzeliiella gochtii</i>	H
<i>Cerodinium wardense</i>	H	M	<i>Lejeunecysta hyalina</i>	H	<i>Wetzeliiella lunaris</i>	H
<i>Cyclonephelium compactum</i>			<i>Membranilarnacia angustivela</i>		<i>Wilsonidinium echinosuturatum</i>	H C
<i>Deflandrea granulata</i>	H	W	<i>Pentadinium taeniagerum</i>			

No. heterotrophic species = 18

994

995 (ii) Dinoflagellate species extending their maximum northern limit in the northern hemisphere in the Rupelian compared
996 to the Bartonian

997

<i>Achomosphaera crassipellis</i>			<i>Heteraulacacysta fehmannensis</i>		<i>Phthanoperidinium comatum</i>	H
<i>Adnatospaeridium robustum</i>			<i>Homotryblium floripes</i>		<i>Phthanoperidinium coreoides</i>	H
<i>Adnatospaeridium vittatum</i>			<i>Homotryblium oceanicum</i>		<i>Polysphaeridium asperum</i>	
<i>Apectodinium homomorphum</i>	H		<i>Homotryblium plectilum</i>		<i>Polysphaeridium subtile</i>	
<i>Apectodinium hyperacanthum</i>	H		<i>Homotryblium vallum</i>		<i>Polysphaeridium zoharyi</i>	W
<i>Apteodinium australiense</i>			<i>Hystrichokolpoma granulatum</i>		<i>Polysphaeridium zoharyi subsp. ktana</i>	
<i>Apteodinium emslandense</i>			<i>Hystrichokolpoma poculum</i>		<i>Rhombodinium perforatum</i>	H M
<i>Caligodinium amiculum</i>			<i>Hystrichokolpoma rigaudiae</i>		<i>Riculacysta perforata</i>	
<i>Cleistospaeridium ancyreum</i>			<i>Hystrichospaeropsis rectangularis</i>		<i>Selenopemphix armata</i>	H
<i>Cleistospaeridium diversispinosum</i>			<i>Hystrichostrogylon coninckii</i>		<i>Selenopemphix nephroides</i>	H

<i>Cleistosphaeridium placacanthum</i>			<i>Hystrichostrogylon membraniphorum</i>		<i>Selenpempix selenoides</i>	H
<i>Cordosphaeridium cantharellus</i>			<i>Impagidinium maculatum</i>	W	<i>Spiniferella cornuta</i>	
<i>Cordosphaeridium minimum</i>			<i>Impagidinium paradoxum</i>		<i>Spiniferites bulloideus</i>	
<i>Cordosphaeridium robustum</i>			<i>Impletosphaeridium kroemmelbeinii</i>		<i>Spiniferites hyperacanthus</i>	
<i>Dapsilidinium pastielsi</i>			<i>Impletosphaeridium ligospinosum</i>		<i>Spiniferites membranaceus</i>	
<i>Deflandrea heterophlycta</i>	H		<i>Impletosphaeridium multispinosum</i>		<i>Spiniferites mirabilis</i>	W
<i>Deflandrea oebisfeldensis</i>	H	M	<i>Impletosphaeridium rugosum</i>		<i>Spiniferites perforatus</i>	
<i>Deflandrea phosphoritica</i>	H		<i>Lejeunecysta cinctoria</i>	H	<i>Spiniferites pseudofurcatus</i>	
<i>Deflandrea phosphoritica australis</i>	H		<i>Lejeunecysta fallax</i>	H	<i>Spiniferites ramosus</i>	
<i>Dinopterygium cladoides</i>		M	<i>Lejeunecysta tenella</i>	H	<i>Spiniferites ramosus gracilis</i>	
<i>Diphyes ficusoides</i>		M	<i>Lingulodinium machaerophorum</i>	W	<i>Surculosphaeridium? oceaniae</i>	
<i>Distatodinium paradoxum</i>			<i>Lingulodinium pycnospinosum</i>		<i>Tectatodinium pellitum</i>	W
<i>Distatodinium tenerum</i>			<i>Litosphaeridium mamellatum</i>		<i>Thalassiphora pelagica</i>	
<i>Dracodinium laszczynskii</i>	H		<i>Melitasphaeridium asterium</i>		<i>Thalassiphora reticulata</i>	
<i>Elytrocysta brevis</i>			<i>Membranophoridium aspinatum</i>		<i>Thalassiphora velata</i>	W
<i>Fibrocyta vectensis</i>			<i>Nematosphaeropsis reticulensis</i>		<i>Trinovantedinium boreale</i>	
<i>Glaphyrocysta intricata</i>			<i>Operculodinium centrocarpum</i>	W	<i>Tubiosphaera magnifica</i>	
<i>Glaphyrocysta microfenestrata</i>			<i>Operculodinium eisenackii</i>		<i>Turbiosphaera symmetrica</i>	
<i>Glaphyrocysta pastielsi</i>			<i>Operculodinium tiara</i>		<i>Wetziella ovalis</i>	H
<i>Glaphyrocysta paupercula</i>			<i>Operculodinium</i>		<i>Wetziella simplex</i>	H

	<i>uncinispinosum</i>		
<i>Glaphyrocysta reticulosa</i>	<i>Operculodinium</i>		cf. <i>Wetzeliella symmetrica</i>
	<i>xanthium</i>		
<i>Glaphyrocysta vicina</i>	<i>Palaeocystodinium</i>	H	<i>Xenicodinium conispinum</i>
	<i>golzowense</i>		
<i>Glyphanodinium facetum</i>	<i>Pentadinium laticinctum</i>		<i>Ynezidium brevisulcatum</i>
	<i>granulatum</i>		
<i>Gonyaulacysta giuseppi</i>	<i>Pentadinium</i>		
	<i>lophophorum</i>		
<i>Heteraulacacysta campanula</i>	<i>Phthanoperidinium</i>	H	
	<i>eocenicum</i>		

No. heterotrophic species = 20

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1001

(iii) Dinoflagellate species with a reduced maximum northern limit in the northern hemisphere in the Rupelian compared to the Bartonian

<i>Achomospaera alcicornu</i>	<i>Eocladopyxis peniculata</i>		<i>Pentadinium goniferum</i>
<i>Achomospaera ramulifera</i>	<i>Fibrocyta axialis</i>		<i>Pentadinium laticinctum</i>
<i>Adnatosphaeridium</i>	<i>Glaphyrocysta</i>		<i>Phthanoperidinium</i>
<i>multispinosum</i>	<i>divaricata</i>		<i>alectrolophum</i>
<i>Areoligera coronata</i>	<i>Glaphyrocysta</i>		<i>Phthanoperidinium</i>
	<i>exuberans</i>		<i>filigranum</i>
<i>Areoligera senonensis</i>	<i>Glaphyrocysta</i>		<i>Phthanoperidinium</i>
	<i>laciniiformis</i>		<i>multispinum</i>
<i>Areoligera sentosa</i>	<i>Glaphyrocysta ordinata</i>		<i>Phthanoperidinium</i>
			<i>resistente</i>
<i>Areoligera tauloma</i>	<i>Glaphyrocysta semitecta</i>		<i>Phthanoperidinium</i>
			<i>stockmansii</i>
<i>Areosphaeridium michoudii</i>	<i>Glaphyrocysta texta</i>		<i>Polysphaeridium</i>
			<i>congregatum</i>
<i>Batiacasphaera compta</i>	<i>Heteraulacacysta</i>		<i>Pterodinium cingulatum</i>
	<i>leptalae</i>		
<i>Batiacasphaera hirsuta</i>	<i>Homotryblium</i>		<i>Pyxidiella scrobiculata</i>
	<i>abbreviatum</i>		

<i>Charlesdownia reticulata</i>	H		<i>Homotryblium pallidum</i>		<i>Rhombodinium draco</i>	H	M
<i>Charlesdownia variabilis</i>	H		<i>Homotryblium floripes</i>		<i>Rhombodinium</i>	H	
			<i>breviradiatum</i>		<i>longimanum</i>		
<i>Cordosphaeridium exilimurum</i>			<i>Hystrichokolpoma</i>	M	<i>Rhombodinium porosum</i>	H	
			<i>cinctum</i>				
<i>Cordosphaeridium fibrospinosum</i>			<i>Hystrichokolpoma globulus</i>	W	<i>Rotnestia borussica</i>		C
<i>Cordosphaeridium funiculatum</i>			<i>Hystrichokolpoma salacia</i>		<i>Samlandia chlamydophora</i>		
<i>Cordosphaeridium gracile</i>			<i>Hystrichosphaeridium tubiferum</i>	M	<i>Selenopemphix coronata</i>	H	
<i>Cordosphaeridium inodes</i>			<i>Impagidinium aculeatum</i>	W	<i>Spiniferites cornuta</i>		
<i>Corrudinium incompositum</i>			<i>Impagidinium velorum</i>		<i>Spiniferites monilis</i>		
<i>Cribroperidinium giuseppeii</i>			<i>Impletosphaeridium insolitum</i>		<i>Spiniferites ramosus</i>		
<i>Dapsilidinium pseudocolligerum</i>			<i>Lentinia serrata</i>	H	<i>Sumatradinium hispidum</i>	H	
<i>Dapsilidinium simplex</i>			<i>Lentinia? wetzelii</i>	H	<i>Tanyosphaeridium regulare</i>		
<i>Deflandrea arcuata</i>	H	W	<i>Melitasphaeridium pseudorecurvatum</i>		<i>Thalassiphora delicata</i>		
<i>Deflandrea denticulata</i>	H		<i>Microdinium reticulatum</i>		<i>Thalassiphora fenestrata</i>		
<i>Distatodinium craterum</i>			<i>Nematosphaeropsis lemniscata</i>		<i>Turbiosphaera galatea</i>		
<i>Distatodinium ellipticum</i>			<i>Operculodinium divergens</i>		<i>Wilsonidium intermedium</i>	H	
<i>Enneadocysta multicornuta</i>			<i>Operculodinium microtriainum</i>		<i>Wilsonidium tabulatum</i>	H	
<i>Enneadocysta pectiniformis</i>		M	<i>Paucisphaeridium inversibuccinum</i>				

No. heterotrophic species = 19

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1007 **Figure and Table captions**

1008

1009 Fig. 1. Eocene – Oligocene geochronology and temporal $\delta^{18}\text{O}$ curve showing key
1010 climate events. Based on Gradstein et al. (2012, fig. 28.11). NB: Wade et al (2012)
1011 show the Eocene – Oligocene boundary at about 33.7 Ma

1012

1013 Fig. 2. Bartonian stratigraphy and age ranges of successions investigated as part of
1014 this study. Range bars do not necessarily imply the presence of all the corresponding
1015 stratigraphical units. Ages and correlations of stratigraphical units based on Gradstein
1016 et al. (2012). Locality details are summarised in Appendix 1A. For source literature
1017 and comprehensive data relating to these localities, see Supplementary Data.

1018

1019 Fig. 3. Rupelian stratigraphy and age ranges of successions investigated as part of this
1020 study. Range bars do not necessarily imply the presence of all the corresponding
1021 stratigraphical units. Ages and correlations of stratigraphical units based on Gradstein
1022 et al. (2012). Locality details are summarised in Appendix 1A. For source literature
1023 and comprehensive data relating to these localities, see Supplementary Data.

1024

1025 Fig. 4. Global data and palaeogeography maps. (A, B): maps showing the modern and
1026 Bartonian/Rupelian palaeo co-ordinates of data points used in this study. See
1027 Supplementary Data for individual locality details; (C, D): Eocene and Oligocene
1028 palaeogeography based on maps produced by Ron Blakey, Colorado Plateau
1029 Geosystems.

1030

1031 Fig. 5. DCA sample scatter plots of the (A) Bartonian (460 species, 71 samples) and
1032 (B) Rupelian (486 species, 122 samples) datasets (note that outlier sample R41 was
1033 omitted). Northern Hemisphere samples = filled symbols, Southern Hemisphere
1034 samples = open symbols

1035

1036 Fig. 6. DCA sample scatter plots of the Bartonian (A, B - 365 species, 55 samples)
1037 and Rupelian (C, D - 449 species, 106 samples) Northern Hemisphere datasets. (A,
1038 C): symbols represent ocean basins. Arctic Ocean: black squares; Atlantic Ocean: dark
1039 grey circles; Tethys Ocean: brown diamonds; North Sea: pink diamonds; Indian
1040 Ocean: beige stars; Pacific Ocean: light grey squares. (B, D): colours represent
1041 northern latitude classes. 80 – 70°: darkest blue-purple; 70 – 60°: dark blue; 60 – 50°:
1042 light blue; 50 – 40°: green; 40 – 30°: yellow; 30 – 20°: orange; 10 – 0°: red.

1043

1044 Fig. 7. DCA sample scatter plot of combined Bartonian-Rupelian dataset (only
1045 offshore Atlantic and Arctic locations, see text for more details) with 15 active
1046 Bartonian samples (filled symbols) and 21 supplementary Rupelian samples (open
1047 symbols). For colour coding of latitude classes, see legend Fig. 6 B, D.

1048

1049 Fig. 8. Geographical plots for selected species showing change in global occurrence
1050 between the Bartonian and Rupelian. Species are plotted using palaeo co-ordinates on
1051 a modern base map.

1052

1053 Fig. 9. Global plots of temperature sensitive / latitudinally diagnostic dinoflagellate
1054 cyst taxa that occur in both the Bartonian and Rupelian. (A): Bartonian global

1055 distribution of warm-water/ low-latitude indicator dinoflagellate cyst taxa; (B):
1056 Rupelian global distribution of warm-water / low-latitude indicator dinoflagellate cyst
1057 taxa; (C): Bartonian global distribution of cool-water / high-latitude indicator
1058 dinoflagellate cyst taxa; (D) Rupelian global distribution of cold-water / high-latitude
1059 indicator dinoflagellate cyst taxa.

1060

1061 Table 1. The temperature/latitude affinities of dinoflagellate cyst taxa occurring in
1062 both the Bartonian and Rupelian, based on published literature. Excludes species
1063 interpreted as broad-ranging / mid-latitude / temperate or cosmopolitan, except for
1064 instances where this is contradicted by multiple literature records. Latitude
1065 assignments are qualified NH (Northern Hemisphere) or SH (southern hemisphere),
1066 where it is not known from the source literature if this can be extrapolated to both
1067 hemispheres.

1068

1069 Supplementary Fig. 1. DCA sample scatter plots, Northern Hemisphere datasets,
1070 showing North Sea, Atlantic Ocean and Arctic Ocean samples only. Bartonian: 39
1071 samples (318 species), outliers (20, 35) removed; Rupelian: 49 samples (356 species),
1072 outliers (77, 28, 29, 88) removed. Symbols represent ocean basins: Arctic Ocean =
1073 black squares; Atlantic Ocean = dark grey circles; North Sea = pink diamonds. Fill of
1074 symbols distinguishes inshore (open) and offshore (filled). Also see TextFig. 6 (A, C).

1075

1076 Supplementary Fig. 2. DCA sample scatter plots, Northern Hemisphere datasets,
1077 showing North Sea and Atlantic Ocean samples only. Bartonian : 31 samples (282
1078 species), outliers (20, 35) removed; Rupelian: 48 samples (350 species), outliers (77,
1079 28, 29, 88) removed. Symbols represent ocean basins: Atlantic Ocean = dark grey

1080 circles; North Sea = pink diamonds. Fill of symbols distinguishes inshore (open) and
1081 offshore (filled). Also see TextFig. 6 (A, C).
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1083
1084