

1 **NEOGENE DINOFLAGELLATE CYSTS AND ACRITARCHS FROM THE HIGH**
2 **NORTHERN LATITUDES AND THEIR RELATION TO SEA SURFACE TEMPERATURE**

3

4 **Michael Schreck^{1,2,*}, Nam Seung-II², Caroline Clotten³, Kirsten Fahl⁴, Stijn De Schepper³,**
5 **Matthias Forwick¹, Jens Matthiessen⁴**

6

7 ¹ *Department of Geosciences, UiT The Arctic University of Norway in Tromsø, P.O. Box 6050*
8 *Langnes, 9037 Tromsø, Norway.*

9 ² *Arctic Research Centre, Korea Polar Research Institute, 26 Songdomirae-ro, Yeonsu-gu,*
10 *406-840 Incheon, Korea.*

11 ³ *Uni Research Climate, Bjerknes Centre for Climate Research, Nygårdsgaten 112–114, 5008*
12 *Bergen, Norway.*

13 ⁴ *Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Am Alten Hafen*
14 *26, 27568 Bremerhaven, Germany.*

15

16

17

18

19

20

21

22

23

24 ^{*} *Corresponding author: Michael Schreck, Michael.Schreck@uit.no*

25

26 **Abstract**

27 Organic-walled dinoflagellate cysts and acritarchs are a vital tool for reconstructing past
28 environmental change, in particular in the Neogene of the high northern latitudes where
29 marine deposits are virtually barren of traditionally used calcareous microfossils. Yet only
30 little is known about the paleoenvironmental value of fossil assemblages that do not have
31 modern analogues, so that reconstructions remain qualitative. Thus, extracting their
32 paleoecological signals still poses a major challenge, in particular on pre-Quaternary
33 timescales. Here we unravel the relationship between species relative abundance and sea
34 surface temperature for extinct dinoflagellate cyst and acritarch taxa from the Neogene of the
35 Iceland Sea using palynological assemblages and organic geochemical (alkenone) data
36 generated from the same set of samples. The reconstructed temperatures for the Miocene to
37 Pliocene sequence of Ocean Drilling Program Site 907 range from 3 to 26°C and our database
38 consists of 68 dinoflagellate cyst and acritarch samples calibrated to alkenone data. The
39 temperature range of five extant species co-occurring in the fossil assemblage agrees well
40 with their present-day distribution providing confidence to inferred temperature ranges for
41 extinct taxa. The 14 extinct dinoflagellate cyst and acritarch species clearly exhibit a
42 temperature dependency in their occurrence throughout the analysed section. The
43 dinoflagellate cyst species *Batiacasphaera hirsuta*, *Labyrinthinium truncatum*,
44 *Cerebrocysta irregulare*, *Cordosphaeridium minimum*, *Impagidinium elongatum* and
45 *Operculodinium centrocarpum* s.s., and the acritarch *Lavradosphaera elongatum*, which are
46 confined to the Miocene, have highest relative abundances and restricted temperature ranges
47 at the warm end of the reconstructed temperature spectrum. The latter five species disappear
48 when Iceland Sea surface temperatures permanently drop below 20°C, thus indicating a
49 distinct threshold on their occurrence. In contrast, species occurring in both the Miocene and
50 Pliocene interval (*Batiacasphaera micropapillata*, *Habibacysta tectata*, *Reticulatosphaera*
51 *actinocoronata*, *Cymatiosphaera? invaginata*) show a broader temperature range and a

52 tolerance towards cooler conditions. *Operculodinium? eirikianum* may have a lower limit on
53 its occurrence at around 10°C.

54 The calibration of species relative abundance versus reconstructed sea surface
55 temperature provides a quantitative assessment of temperature ranges for extinct Miocene to
56 Pliocene species indicating that temperature is a decisive ecological factor for regional
57 extinctions that may explain the frequently observed asynchronous highest occurrences across
58 different ocean basins. It demonstrates that qualitative assessments of ecological preferences
59 solely based on (paleo) biogeographic distribution should be treated with caution. In addition
60 to enhancing knowledge on marine palynomorph paleoecology, this study ultimately
61 improves the application of palynomorphs for paleoenvironmental reconstructions in the
62 Neogene of the Arctic and subarctic seas, a region essential for understanding past global
63 climate.

64

65

66

67

68

69

70

71

72

73

74

75

76 **Keywords**

77 Iceland Sea | Neogene | dinoflagellate cyst | acritarch | alkenones | paleotemperatures

78

79 **Introduction**

80 Due to the nearly complete absence of biosiliceous and calcareous microfossils in Neogene
81 deposits at high northern latitudes, organic-walled marine palynomorphs (dinoflagellate cysts
82 and acritarchs) are important proxies for the establishment of a regional biostratigraphy and
83 paleoenvironmental reconstructions in the Arctic and sub-arctic realm (e.g. Schreck et al.,
84 2012, 2013; De Schepper et al., 2015, 2017). They have been proven particularly useful in
85 upper Quaternary deposits where assemblages are comparable to modern assemblages (de
86 Vernal et al., 2005). The distribution of modern dinoflagellate cysts (dinocysts) at high
87 northern latitudes was first studied on locally restricted data sets, which were subsequently
88 expanded and combined within a Northern Hemisphere reference database that currently
89 comprises 1492 sites (Fig. 1; e.g. de Vernal et al., 2013 and references therein). The present-
90 day n=1492 database documents the relationship between species relative abundance and
91 observed surface water parameters, which control assemblage composition. This extensive
92 reference dataset has been widely used to quantitatively reconstruct sea surface temperature,
93 salinity, productivity and sea ice cover in upper Quaternary sediments (e.g. Radi and de
94 Vernal, 2008; de Vernal et al., 2001, 2013; Van Nieuwenhove et al., 2016) using transfer
95 functions (e.g. Modern Analogue Technique, Guiot and de Vernal 2007).

96 Reconstructions of Neogene high latitude paleoceanographic and paleoclimatic
97 variability relies heavily on marine palynomorphs, which are often the only microfossil group
98 with a continuous record in pre-Quaternary sediments in this region. However, when going
99 further back in the Neogene, palynomorph assemblages are increasingly dominated by extinct
100 species of which the ecological affinities are poorly constrained. Therefore, it is of crucial
101 importance to unravel the (paleo)ecology of these Neogene marine palynomorphs in order to
102 improve their application for paleoceanographic studies in a region essential for
103 understanding the Cenozoic transition from greenhouse to icehouse climates.

104 In the past decades, significant progress has been made in deciphering the
105 paleoecology of extinct species using statistical analyses (e.g. Versteegh and Zonneveld,
106 1994), the definition of paleoenvironmental indices (Edwards et al., 1991; Versteegh, 1994),
107 and analysis of the biogeographic distribution (Head, 1997; Masure and Vrielynck, 2009;
108 Schreck and Matthiessen, 2013). The derived information, however, solely remains
109 qualitative (e.g. warm/cold, oceanic/neritic). Recently, geochemical proxies for sea surface
110 conditions have been employed to directly assess the paleoecology of extinct species (De
111 Schepper et al., 2011; Hennissen et al., 2017). De Schepper et al. (2011) correlated the
112 relative abundance of extant species to a sea surface temperature (SST) proxy derived from
113 the same sample and then compared to the species' modern temperature distribution using the
114 n=1171 dataset (the n=1492 precursor) of Radi and de Vernal (2008) and a subset thereof.
115 The subset was restricted to 518 samples located mainly in the North Atlantic Ocean between
116 75°W and 15°E, and north of 25°N, with samples from the Mediterranean and northern part
117 of Baffin Bay being omitted (De Schepper et al., 2011). Based on a dataset containing 204
118 samples from four drilling sites across the Plio-Pleistocene North Atlantic (Fig. 1), the authors
119 demonstrated a strong correlation between reconstructed and present-day SST ranges of
120 extant species. Because modern species occurring in fossil assemblages have a comparable
121 temperature distribution as today, De Schepper et al. (2011) argued that SST ranges of extinct
122 species could be determined with confidence. Using this approach, they documented past
123 temperature ranges of 16 extinct dinocyst species from the Plio-Pleistocene North Atlantic in
124 their n=204 paleo-database.

125 Based on this approach, we establish a quantitative relationship between high latitude
126 marine palynomorph species and alkenone-based SST for the Miocene to Pliocene interval of
127 Ocean Drilling Program (ODP) Hole 907A in the Iceland Sea. Both palynological assemblage
128 and organic geochemical data are extracted from the same sample to ensure one-to-one
129 comparability. Therefore, this study provides independently derived temperature affinities of

130 extinct species, and refines previous ecological interpretations that were solely based on
131 biogeographic distribution and stratigraphic ranges. Ultimately, our study enhances the
132 application of fossil palynomorph assemblages for paleoenvironmental reconstructions in the
133 Neogene of the Arctic and subarctic seas, and improves our understanding of
134 paleoceanographic implications of assemblages that do not have a modern analogue.

135

136 **Material and Methods**

137 ***Material***

138 Located on the eastern Iceland Plateau (69°14.989' N, 12°41.894' W; 2035.7 m water depth;
139 Fig. 1), ODP Hole 907A was drilled in an undisturbed hemipelagic sequence, terminating at a
140 total depth of 224.1 meters below sea floor (Shipboard Scientific Party, 1995). The lithology
141 mainly consists of unlithified silty clay and clayey silt. Five lithostratigraphic units were
142 distinguished based on their siliciclastic, biogenic calcareous, and biogenic siliceous contents
143 (Fig. 2). Unit III is subdivided into Subunit IIIA which is nannofossil ooze bearing, and
144 Subunit IIIB lacking calcareous nannofossils, but having higher biogenic silica content
145 (Shipboard Scientific Party, 1995).

146 Previous studies (e.g. Schreck et al., 2012, 2013) used the revised composite
147 magnetostratigraphy of ODP Site 907 (Channell et al., 1999) adjusted to the Astronomically
148 Tuned Neogene Time Scale 2004 (ATNTS 2004, Lourens et al., 2005). Here, we update the
149 paleomagnetic reversals to the Geological Time Scale 2012 (Hilgen et al., 2012), which is
150 identical to the ATNTS 2004 back to 8.3 Ma. The investigated interval spans the entire
151 Pliocene and extends back to the early Middle Miocene. In addition to the 126 samples from
152 Hole 907A, we included five samples from the Pliocene of Hole 907B, resulting in a total of
153 131 samples analysed for palynology and biomarkers.

154

155 ***Palynology***

156 Subsamples (~ 15 cm³) were processed using standard palynological techniques including acid
157 treatment (cold HCl [10%], cold HF [38–40%]), but without oxidation or alkali treatments
158 (see Schreck et al., 2012 for details). Two *Lycopodium clavatum* tablets were added to each
159 sample during the HCl treatment to calculate palynomorph concentrations (Stockmarr, 1977).
160 The residue was sieved over a 6 µm polyester mesh and mounted with glycerine jelly on
161 microscope slides.

162 Six samples from Hole 907A (indicated by asterisk on Fig. 2) and the five sample
163 from Hole 907B (not shown on Fig. 2) were processed by Palynological Laboratory Services
164 Ltd (Holyhead, UK) using a similar processing technique, also without oxidation (details in
165 De Schepper et al., 2017). For those samples, only one *Lycopodium clavatum* tablet was
166 added. The residue was sieved on 10 µm and mounted with glycerine jelly on microscope
167 slides.

168 Wherever possible, marine palynomorphs have been counted until a minimum of 350
169 dinocysts had been enumerated. All counts were conducted at 40x and 63x magnification
170 respectively, using a Zeiss Axioplan 2 and Zeiss Axio Imager.A2 microscope. Dinocyst and
171 acritarch nomenclature follows Williams et al. (2017), De Schepper and Head (2008a),
172 Schreck et al. (2012), and Schreck and Matthiessen (2013, 2014). However, in contrast to De
173 Schepper and Head (2008a), we have not distinguished *Operculodinium? eirikianum* on
174 variety level. Percentage calculations for dinocysts (Figs. 3, 5–7) are based on the sum of all
175 cysts counted to ensure comparability with previously published data. The relative abundance
176 of acritarchs (Figs. 3 and 8) is based on the total marine palynomorph assemblage (=
177 dinocysts + acritarchs). To evaluate the reliability of relative abundances as a function of total
178 cyst counts and dissemination of individual species, we have calculated the simultaneous
179 confidence intervals (95%) for each sample following Sison and Glaz (1995; Fig. 4). Except
180 for six samples from Hole 907A (indicated with asterisk on Fig. 2) and five samples from
181 Hole 907B (not shown on Fig. 2), all palynological data have previously been published by

182 Schreck et al. (2012, 2013). These data can be accessed at www.pangaea.de via
183 doi:10.1594/PANGAEA.805377 and doi:10.1594/PANGAEA.807134.

184

185 *Alkenone paleothermometry*

186 This study uses alkenone SST estimates previously published by Schreck et al. (2013), De
187 Schepper et al. (2015), and Stein et al. (2016), but adds another 11 samples (see above) to the
188 Site 907 SST record (Figs. 2 and 3). All data have been generated in the organic geochemistry
189 laboratory of the Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research
190 (Bremerhaven, Germany) using the following procedure: bulk sediments (2 to 7g) from the
191 same samples as used for palynology were extracted using accelerated solvent extraction
192 (DIONEX, ASE 200; 100°C, 1000 psi, 15min, solvent dichloromethane). Compounds have
193 been separated by open column chromatography. The composition of alkenones was analysed
194 with a Hewlett Packard HP 6890 gas chromatograph (n=120 samples) and an Agilent 7890A
195 gas chromatograph (n=11 samples). Individual alkenone ($C_{37:3}$, $C_{37:2}$) identification is based on
196 retention time and the comparison with an external standard. The instrument stability has
197 been continuously controlled by reruns of the external alkenone standard (extracted from
198 coccolithophore *Emiliana huxleyi* (Lohman) cultures with known growth temperature) during
199 the analytical sequences. The range of the total analytical error calculated by replicate
200 analyses is less than 0.4°C. The alkenone unsaturation index U_{37}^k and the global core top
201 calibration (Müller et al., 1998) were used to calculate sea surface temperature (SST in °C).
202 We used the Müller et al. (1998) calibration versus summer SSTs. U_{37}^k shows the best
203 statistical relationship to mean annual SST on a global scale (Müller et al., 1998), but
204 coccolithophore production in the modern Nordic Seas is significantly higher (factor of 10)
205 during summer than during autumn to spring due to the availability of light for
206 photosynthesis. This may cause a shift towards a summer bias in temperature (Schröder-
207 Ritzrau et al., 2001; see also discussion below). The summer calibration is similar to the

208 annual mean calibration of Müller et al. (1998) frequently used in the literature, but results in
209 SSTs higher by a constant value of 1.2°C independent of the U_{37}^k value. The standard error of
210 this calibration is reported as $\pm 0.055 U_{37}^k$ units or 1.7°C. Due to this uncertainty, we only
211 present integral numbers for the alkenone SSTs. Full details of the method and the reliability
212 of the U_{37}^k index in Neogene deposits of the high northern latitudes are discussed in Schreck et
213 al. (2013) and Stein et al. (2016). The alkenone datasets can be accessed at www.pangaea.de
214 via doi:10.1594/PANGAEA.807107, doi:10.1594/PANGAEA.848671 and,
215 doi:10.1594/PANGAEA.855508.

216

217 ***Comparison database***

218 To test whether extant taxa have a comparable SST distribution in the Neogene as in the
219 modern ocean, we follow the approach of De Schepper et al. (2011) and first compare
220 selected species to the Northern Hemisphere reference database n=1492 (Fig. 1). In a second
221 step, the n=1492 database was restricted to 101 samples (n=101 database) located in the
222 Iceland Sea and adjacent areas (between 67–78°N, and between 10°E–20°W) to provide a
223 spatially confined representation of our study site and to exclude sites less suitable for
224 comparison. In both datasets species relative abundance is given as a function of summer and
225 winter SSTs derived from the World Ocean Atlas 2001 (WOA01, Stephens et al., 2002). For
226 the purpose of this study, we use the summer (July–September) SSTs given in the WOA01
227 for comparison as dinoflagellate and coccolithophore production in the Nordic Seas today is
228 mainly restricted to the summer season (e.g. Matthiessen et al., 2005; see discussion below).
229 We refrain from a detailed comparison with the global dataset of modern cyst distribution
230 (Zonneveld et al., 2013), which presently consists of 2405 data points (including the Northern
231 Hemisphere reference database), as it contains sites less suitable for meaningful comparison
232 with our high latitude data.

233 In addition, the distribution of extant and extinct dinocyst species is compared to the
234 North Atlantic paleo-database of De Schepper et al. (2011) where possible. This dataset
235 compares Plio-Pleistocene dinocyst relative abundances with (spring–summer) SST estimates
236 derived from the same sample by measuring Mg/Ca ratios on the planktonic foraminifera
237 *Globogerina bulloides* (d’Orbigny). It currently comprises 204 samples (n=204 paleo-
238 database) from four DSDP/ODP/IODP sites in the North Atlantic (Fig. 1) spanning the Late
239 Pliocene through Early Pleistocene, and can be accessed at www.pangaea.de via
240 doi:10.1594/PANGAEA.758713.

241 For most dinocyst species discussed here, however, no previous calibration of relative
242 abundance vs. SST is available. This also applies to the acritarch taxa presented.

243

244 ***Comparability of proxies and general limitations of the approach***

245 The approach used here, i.e. combining marine palynomorph assemblages with geochemical
246 SST reconstructions, has previously been proposed by De Schepper et al. (2011). The authors
247 show that extant species (both dominant and less abundant) occurring in fossil assemblages
248 have a similar temperature distribution compared to today, and that these SST reconstructions
249 can therefore be used to assess temperature ranges of extinct species. In contrast to the study
250 of De Schepper et al. (2011), who used the Mg/Ca ratio of planktonic foraminifera
251 *Globogerina bulloides* as a SST proxy, the virtual absence of planktonic foraminifera in the
252 Miocene-Pliocene section of ODP Site 907 (Shipboard Scientific Party, 1995) prevents the
253 application of the same SST proxy for calibration of species relative abundance. However,
254 previous studies have shown that the alkenone unsaturation index U_{37}^k can be applied to
255 reliably reconstruct SSTs on pre-Quaternary timescales at high northern latitudes (see
256 discussion in Schreck et al., 2013; Stein et al., 2016; Herbert et al., 2016).

257 While sea surface temperature is the primary ecological factor determining the
258 distribution of dinoflagellates (e.g. Taylor 1987), we note that the relationship between

259 temperature and phytoplankton species abundance might be more complex. In order to
260 compare dinoflagellate cyst abundance, alkenone-based SSTs (this study) and Mg/Ca SSTs
261 (De Schepper et al., 2011), the producing organisms (dinoflagellates, coccolithophores,
262 foraminifera) should have comparable habitat depth and seasonality, as these parameters
263 determine the recorded signal.

264

265 *1) Habitat depth*

266 All dinocysts discussed here are cysts of phototrophic dinoflagellate species because of
267 fluorescent properties of the cyst wall (cf. Brenner and Biebow, 2001). Apart from
268 temperature, phototrophic dinoflagellates respond to light availability, and consequently they
269 are restricted to the photic zone of the surface waters. Although capable of vertically adjusting
270 their position in the water column, they generally inhabit a shallow and thin surface layer (e.g.
271 Dale, 1996).

272 Alkenones are biosynthesized by haptophytes (e.g. coccolithophores, Herbert, 2003)
273 and, given their phytoplanktonic source, the alkenone production must originate from the
274 photic zone. Direct measurements of alkenones in the upper water column indicate that the
275 zone of maximum alkenone production is in the isothermal surface mixed layer (0–20m)
276 rather than within the deeper chlorophyll maximum layer (e.g. Rosell-Melé and McClymont,
277 2007, and references therein). Indeed, calibration of the U_{37}^k is best when using temperatures
278 from 0–10m water depth (Müller et al., 1998), suggesting that temperatures derived from
279 alkenone producing coccolithophores reflect surface conditions.

280 The planktonic foraminifera *Globogerina bulloides* generally occupies a habitat
281 restricted to the upper 60m in the North Atlantic (Ganssen and Kroon, 2000; Chapman, 2010)
282 and the average calcification depth lies around ± 50 m (Vázquez-Riveiros et al., 2016).
283 Therefore, this species records slightly deeper surface water conditions compared to
284 alkenones.

285

286 2) *Seasonality of production*

287 In the Nordic Seas, a generally restricted production period has been observed and the export
288 of fossilizable plankton groups (including dinoflagellates, coccolithophores, foraminifera)
289 occurs during 4–6 months of the year. Hence, the signal recorded in the sediments mainly
290 represents the summer to autumn seasons (Schröder-Ritzrau et al., 2001, and references
291 therein).

292 While studies of dinocysts in surface sediments are numerous, sediment trap studies
293 focussing on the seasonal production of dinoflagellates and their cysts are rare. Most studies
294 are limited to coastal marine environments, upwelling regions and very restricted marine
295 settings such as fjords and inlets. While on global scale dinoflagellate cyst relative abundance
296 in surface sediments shows a good correlation to summer, autumn and annual mean SSTs
297 (Zonneveld et al., 2013), in the Arctic and Subarctic realm dinoflagellates undergo a
298 pronounced seasonal cycle in production. They are most abundant during summer due to the
299 prevailing light regime and nutrient availability, but never during the spring bloom (see
300 Matthiessen et al., 2005, and references therein). Indeed, the few sediment trap studies from
301 the high latitudes revealed a trend towards summer production of dinoflagellate cysts (e.g.
302 Dale and Dale, 1992; Howe et al., 2010; Heikkilä et al., 2016). Therefore, we consider
303 dinoflagellate cysts as recorders of summer surface conditions in the study area.

304 The same limitations as discussed for dinocysts also apply to production of
305 coccolithophores in high latitude settings. In the modern Nordic Seas, the production of
306 coccolithophores is significantly higher (factor of 10) during summer than in the non-
307 production period from late autumn to early summer due to the availability of light for
308 photosynthesis (Andruleit, 1997; Schröder-Ritzrau et al., 2001), and high cell densities are
309 usually not observed before August (Samtleben et al., 1995). This is also documented by the

310 vertical flux of coccolithophores recorded in sediment traps (Samtleben and Bickert, 1990).

311 Therefore, we interpret the alkenone-derived SSTs to reflect summer SSTs in the study area.

312 The foraminifer *Globogerina bulloides* reflects the northward migrating North Atlantic
313 spring bloom, February-March between 30° and 40°N, and May-June at higher latitudes
314 (Ganssen and Kroon, 2000). In fact, recently published isotopic temperatures suggest *G.*
315 *bulloides* to calcify their tests during the summer season between 40–60°N (Vázquez-Riveiros
316 et al., 2016). In the eastern North Atlantic it reaches highest abundances in late spring and
317 summer (Chapman, 2010). Therefore, De Schepper et al. (2011) discussed this species as a
318 recorder of spring to summer SSTs in the North Atlantic n=204 paleo-database. The SST
319 estimates presented by De Schepper et al. (2011) are derived using the North Atlantic
320 calibration of Elderfield and Ganssen (2000).

321

322 3) Limitations of the approach

323 Despite the fact that dinoflagellate cysts and alkenone producing coccolithophores have a
324 comparable habitat and seasonality in the study area, certain limitations apply to this
325 approach. In particular, dispersal with ocean currents has to be considered when comparing
326 fossil and modern species distribution (Dale and Dale, 1992), but also alkenone distribution
327 (e.g. Mollenhauer et al., 2005) The East Greenland current flowing along the Greenland
328 continental shelf and slope is the main oceanographic feature influencing the Iceland Sea (e.g.
329 Blindheim and Østerhus, 2005). Its north to south configuration limits lateral transport from
330 the Greenland fjords and shelf into the open waters of the study site. Indeed, palynological
331 assemblages of ODP Site 907 indicate an open ocean environment throughout most of the
332 analysed interval with only occasional input from the outer shelf (De Schepper et al., 2015).
333 Thus, ODP Site 907 reflects local conditions with only minimal influence by oceanic
334 transport. Another bias to the fossil assemblage may be introduced by species-selective
335 degradation (e.g. Zonneveld et al., 2008). However, this factor does not exert a major

336 influence on the ODP Site 907 palynomorph assemblages in the productive intervals of both
337 the Miocene and the Pliocene (see Schreck et al., 2013 for discussion). Finally, the overall
338 SST range reconstructed for ODP Site 907 (3–26°C) is largely comparable to that in the
339 present-day n=1492 database (-1.8–30.5°C, de Vernal et al., 2013) and the Plio-Pleistocene
340 North Atlantic paleo-dataset (7.7–25.2°C, De Schepper et al., 2011). However, our dataset
341 contains more samples from the presumably warmer Middle to Late Miocene than from the
342 cooler Pliocene, thus partially introducing an offset towards higher SSTs when compared to
343 the modern n=1492 and n=101 reference datasets (de Vernal et al., 2013). Therefore, we may
344 record the warm end of species distribution rather than its minimum SST requirements. Due
345 to these limitations, we refrain from defining exact upper and lower temperature limits for the
346 occurrence of extinct species, but rather provide temperature ranges in which extinct species
347 occurred based on independently derived SST estimates. We note that additional data from
348 different sites needs to be incorporated into the developing paleo-database to allow for more
349 precise assessment of species temperature affinities.

350

351 **Results and Discussion**

352 *Alkenone sea surface temperatures*

353 The alkenone SST data used here represent a stack record of data previously published by
354 Schreck et al. (2013), De Schepper et al. (2015) and Stein et al. (2016). They are discussed in
355 detail in the respective publications. In addition, this study adds 11 samples with alkenone-
356 based SST estimates to the ODP Site 907 record. In summary, 86 of the 131 analysed samples
357 yielded sufficient alkenones to allow the application of the U_{37}^k index to calculate summer
358 SST. The U_{37}^k index varies from 0.116 to 0.863, which translates into SSTs ranging from 3 to
359 26°C (Figs. 2–3). Modern mean annual SSTs are 2°C at the study site while summer SSTs are
360 5°C (Fig. 3). Thus, the ODP Site 907 record suggests warmer than present-day conditions
361 throughout most of the analysed interval. Highest temperatures are observed in the Middle

362 Miocene. SSTs subsequently decrease towards the end of the latest Pliocene (Figs. 2–3),
363 where SSTs close to modern values have been recorded. The long-term temperature evolution
364 in the Iceland Sea therefore follows the general global Neogene cooling trend (Zachos et al.,
365 2008). However, samples with low amounts of alkenones preventing a reliable calculation of
366 the U_{37}^k index cluster in the early Middle Miocene (Langhian stage) and latest Pliocene. The
367 Late Pliocene interval coincides with samples almost barren of palynomorphs (Figs. 2–3;
368 Schreck et al., 2013) and diatoms (Stabell and Koç, 1996), which has been assigned to a
369 combination of factors such as sea ice cover, nutrient availability, bottom water ventilation
370 and selective degradation in relation to waxing and waning of the Greenland Ice Sheet. That
371 may also account for the low amounts of alkenones. In contrast, the Langhian (Middle
372 Miocene) samples are characterized by high palynomorph and diatom abundance and
373 diversity, so that the controlling factors for the low alkenone abundance remains speculative.

374

375 *Dinoflagellate cysts and acritarchs*

376 The details and raw data of the palynological investigation are presented in Schreck et al.
377 (2013) and summarized together with our new data in Figs. 2–3. Several species exhibit
378 restricted stratigraphic ranges with well-defined range tops. This is exemplified in clusters of
379 highest occurrences (HO) in the early Late Miocene and Early Pliocene (Fig. 3). From the 86
380 samples with SST estimates (see above) 18 were virtually barren (< 50 palynomorphs
381 counted, Fig. 2). These 18 samples have been removed from the dataset due to the large
382 statistical uncertainty introduced by the low number of counts. Of the remaining 68 samples,
383 48 samples yielded more than 350 cysts while 7 samples contained less than 150 cysts (Figs.
384 2 and 4). In order to account for the variability in the number of counts per sample and to
385 evaluate the statistical error it introduces, we have calculated the simultaneous confidence
386 interval (95%) for each sample using the method of Sison and Glaz (1995), which takes the
387 total number of counts per sample into account, but also the distribution of counts for each

388 individual species. This corresponds to confidence intervals on the relative abundance of \pm
389 0.6 to \pm 12.9% in any given sample, and an average of 5.3% on the entire dataset (Fig. 4). In
390 general, higher count numbers result in smaller confidence intervals (represented by larger
391 dots in Figs. 5–8) and are thus more reliable. This allows to objectively assess the reliability
392 of the relative abundance and avoid over-interpretation.

393 In summary, this study provides 68 samples with marine palynomorph relative
394 abundance calibrated to SST estimates from the Miocene through Pliocene. The temperature
395 affinities of extinct species discussed in the text are summarized in Fig. 9.

396

397 ***Extant dinoflagellate cysts***

398 Even though extant species are recorded almost continuously in the Middle Miocene to Late
399 Pliocene of ODP Site 907, their relative abundances are usually low ($< 1\%$) thus rendering
400 conclusions on their paleoecology difficult. Extant species recorded include *Bitectatodinium*
401 *tepikiense*, *Impagidinium aculeatum*, *Impagidinium patulum*, *Impagidinium striatum*,
402 *Operculodinium israelianum*, *Selenopemphix nephroides*, *Tectatodinium pellitum* and several
403 *Brigantedinium* species. Only *Nematosphaeropsis labyrinthus*, *Impagidinium pallidum*,
404 *Ataxiodinium choane*, *Spiniferites elongatus* s.l. and *Lingulodinium machaerophorum* occur
405 continuously and in higher relative abundances (up to $\sim 80\%$) in parts of the analysed interval,
406 and are hence discussed here (Fig. 5). Species abundance is plotted against alkenone-based
407 SSTs (yellow dots) and compared with their modern distribution in the Northern Hemisphere
408 reference dataset (black and grey dots) and the n=101 subset (grey dots only). The present-
409 day data are plotted as a function of summer SST derived from the WOA01 (Stephens et al.,
410 2001) because they provide the best comparison with our alkenone-based SSTs, which reflect
411 summer temperatures at the study site (see discussion above). In addition, we compare their
412 Miocene-Pliocene distribution with that observed in the n=204 paleo-dataset from the Plio-

413 Pleistocene North Atlantic (blue dots), where species relative abundance is plotted against
414 Mg/Ca spring-summer SST (De Schepper et al., 2011).

415 At ODP Site 907, *Lingulodinium machaerophorum* is restricted to the comparatively
416 warm Miocene, where it occurs at SSTs ranging from 15 to 24°C (Fig. 5). This compares
417 favourably with its distribution in the present-day n=1492 database where it is restricted to
418 SSTs between 14 to 30°C (de Vernal et al., 2013), and also with its distribution in the Plio-
419 Pleistocene North Atlantic where it mainly occurs between 16 to 24°C (De Schepper et al.,
420 2011). *Lingulodinium machaerophorum* is a temperate to tropical species today (Zonneveld et
421 al., 2013) and accordingly has not been observed in the n=101 subset from the Nordic Seas,
422 where present-day summer SSTs are around 5°C. It is only a minor component of the ODP
423 Site 907 dinocyst record and thus the data has to be treated with caution due to the
424 uncertainties related to the low numbers of counts. However, our paleo-dataset suggests a
425 preference for warm waters during the Neogene in accordance with its present-day and its
426 Plio-Pleistocene distribution, indicating a similar lower limit on its occurrence as observed
427 today (> 15°C).

428 *Nematosphaeropsis labyrinthus* exhibits a broad temperature range in both the Mio-
429 Pliocene Iceland Sea (Fig. 5, 7–26°C) and the modern ocean (-1.8–30°C). Its Neogene
430 distribution compares particularly well at the warm end of its temperature distribution with
431 both present-day datasets (n=1492 and n=101), but clearly misses elevated relative
432 abundances below 5°C. A similar distribution is observed in the n=204 paleo-database (De
433 Schepper et al., 2011), which compares favourably with our data. However, both paleo-
434 datasets (n=204 and this study), do not facilitate comparison at the lowermost end of this
435 species present day SST range as they only contain two samples with temperatures < 5°C
436 compared to the strong representation of this temperature interval in the modern dataset.
437 Nonetheless, it is interesting to note that *N. labyrinthus* becomes successively more abundant
438 over the course of the gradual Neogene cooling observed in ODP Hole 907A (Fig. 3). Besides

439 few exceptions, however, relative abundances > 40% are confined to the interval from 8 to
440 15°C in both paleo-datasets, while such relative abundances are observed between 7–12°C in
441 the present-day distribution of this cosmopolitan species.

442 *Ataxiodinium choane* occurs in subpolar to temperate regions of the Northern
443 Hemisphere today and has been rarely observed in the Southern Hemisphere (Zonneveld et al.,
444 2013). In the Mio-Pliocene of the Iceland Sea, it occurs at temperatures ranging from 8 to
445 21°C, exceptionally as high as 26°C, which is similar to its present-day distribution in the
446 n=1492 database (0–25°C, Fig. 5, de Vernal et al, 2013), in particular at the warm end of its
447 temperature distribution. It can apparently occur at lower temperatures today (< 5°C) but then
448 it is only rare (< 1%). *Ataxiodinium choane* accounts for up to 3% of the modern dinocyst
449 assemblage but constitutes as much as 8–14% of the dinocyst assemblage in the Neogene of
450 the Iceland Sea. It is important to note that its maximum relative abundance at the study site is
451 related to similar SSTs (10–15°C) as its maximum abundance in the modern ocean, thus
452 lending confidence to our reconstruction. In the Plio-Pleistocene North Atlantic this species is
453 only a rare component of the dinocyst assemblage (< 0.5%, data supplement in De Schepper
454 et al., 2011), but it occurs at temperatures ranging from 11 to 21°C in the n=204 paleo-
455 database, thereby more or less supporting our Mio-Pliocene temperature assessment.

456 In the modern ocean, *Spiniferites elongatus* s.l. is a polar to subtropical species
457 restricted to the Northern Hemisphere (Zonneveld et al., 2013). It occurs at SSTs ranging
458 from -1.8 to 25°C (Fig. 5), occasionally as high as 30°C, but has highest relative abundances
459 (> 10%) between 2 and 15°C (de Vernal et al., 2013). At ODP Site 907, *S. elongatus* s.l. is
460 mainly confined to the cooler Pliocene interval and is present in only two samples from the
461 Miocene. It occurs at restricted SSTs between 7 to 13°C, and is particularly abundant between
462 5–4 Ma when ODP Site 907 received increased IRD input (Fronval and Jansen, 1996), which
463 may suggest a tolerance for colder surface waters similar to its present-day distribution.

464 In contrast, the Middle Miocene to Pliocene record of *Impagidinium pallidum* suggests
465 a preference for warmer conditions than its distribution in the modern ocean. Today this
466 species occurs at SSTs ranging from -2.1 to 25.7°C (Zonneveld et al., 2013), but is most
467 abundant (> 10% of the assemblage) in the Northern Hemisphere at SSTs ranging between -
468 1.8 and 6.5°C, clearly suggesting a cold-water affinity (Fig. 5, de Vernal et al., 2013). This
469 species apparently has a similar overall SST range (7–26°C) and reaches highest relative
470 abundance (6–8% of the assemblage) at the colder end of its temperature spectrum (7–10°C)
471 in the Mio-Pliocene Iceland Sea, but does not exhibit increased abundances at similarly lower
472 temperatures as observed in the present-day database. In fact, *I. pallidum* never constitutes
473 more than 10% to the dinocyst assemblage at ODP Site 907, which is in contrast to its high
474 relative abundance in the present-day Iceland Sea (Matthiessen, 1995; Marret et al., 2004).
475 The overall temperature range in the Iceland Sea agrees well with the distribution observed in
476 the Plio-Pleistocene North Atlantic and, in particular, its occurrence at temperatures
477 exceeding 15°C supports the tolerance of *I. pallidum* for higher SSTs in the past as suggested
478 by De Schepper et al. (2011). However, De Schepper et al. (2011) reported highest relative
479 abundances (> 10%) of *I. pallidum* at SST values between 10–15°C only at DSDP Site 610
480 from the eastern North Atlantic, while in the Iceland Sea it reaches maximum relative
481 abundance at SSTs between 7–10°C, thus being closer to present-day values. Nonetheless, the
482 occurrence of *I. pallidum* at warmer conditions in the geological past, in particular in the
483 eastern North Atlantic, is in clear contrast with its present-day distribution (Fig. 5), which
484 suggests other factors, such as nutrient availability, may play a decisive role in controlling its
485 occurrence. While its present-day distribution reflects affinities with cold and rather
486 oligotrophic environments this might have been different in the past. However, we note that
487 the modern database does not include warm oligotrophic sites. It is worth mentioning, that *I.*
488 *pallidum* is stratigraphically long-ranging and extends back into at least the Middle Eocene
489 (Bujak, 1984; Head and Norris, 1989). Its existence during those periods, which were much

490 warmer than today, already suggests some tolerance for warmer conditions. Moreover, its
491 longevity, in particular from the late Paleogene to the present-day, also suggests a potential
492 for adaption to changing environments. However, given the fact that *I. pallidum* reaches
493 highest relative abundances in the present-day Nordic Seas and the eastern Arctic Ocean
494 (Matthiessen, 1995), reduced habitat competition in these hostile environments may also
495 explain the observed differences. On the other hand, it may also reflect the existence of two
496 cryptic species and therefore explain the observed differences in distribution. We therefore
497 corroborate the questionable value of *I. pallidum* as a reliable cold-water indicator in older
498 (pre-Quaternary) deposits (this study, De Schepper et al., 2011).

499

500 ***Extinct dinoflagellate cysts***

501 The majority of the Miocene to Pliocene samples of ODP Site 907 is dominated by extinct
502 species. Despite the high diversity of the palynomorph record, however, only 10 dinocyst
503 species continuously occur in significant numbers to reliably perform a correlation exercise.
504 Most species are rare (< 2% of the assemblage) or occur in a few samples only (see Schreck
505 et al., 2013 for details), thus circumventing conclusions on their ecological affinities.
506 Therefore, only the most relevant species are shown in Figs. 6–7 and 9, and discussed here.
507 All Miocene to Pliocene data (yellow dots) are plotted versus alkenone-derived summer
508 SSTs. *Habibacysta tectata* and *Operculodinium? eirikianum* have also been recorded by De
509 Schepper et al. (2011) from the Plio-Pleistocene North Atlantic, hence allow to compare their
510 distribution with the n=204 paleo-database (Fig. 6).

511 Based on its geographical distribution in the Pliocene of the Labrador Sea, North
512 Atlantic and North Sea basin, *Habibacysta tectata* has been considered a cool-water tolerant
513 (Head 1994) to cold-water species (Versteegh 1994), while recent quantitative data indicate a
514 broader temperature tolerance with a cool-water affinity (De Schepper et al., 2011; Hennissen
515 et al., 2017). This species has also been recorded from the Middle Miocene of the

516 Mediterranean (Jiménez-Moreno et al., 2006), and the upper Miocene of the Gulf of Mexico
517 (as *Tectatodinium* sp. B in Wrenn and Kokinos, 1986) and the Caribbean Sea (Wrenn pers.
518 com. in Head 1994) respectively, suggesting a much wider thermal preference. In Iceland Sea
519 ODP Hole 907A, which covers both the Miocene and the Pliocene, *H. tectata* indeed exhibits
520 a much broader temperature range (8–26°C, Figs. 6 and 9) than in the study of De Schepper et
521 al. (11–17°C, 2011), suggesting that temperature may not be the only factor controlling this
522 species distribution. Even though it can occur at temperatures below 10°C, it clearly shows a
523 centre of distribution at temperatures > 15°C. Given its wide temperature distribution across
524 the Middle Miocene to Pliocene in the Iceland Sea (this study), its more restricted range in the
525 Plio-Pleistocene North Atlantic and its overall biogeographic distribution ranging from
526 subtropical/tropical (in the Miocene) to subpolar (in the Plio-Pleistocene), this may suggest an
527 adaptation of this species towards cooler conditions occurring in concert with the general
528 global cooling observed during the Neogene, with optimum temperatures > 15°C. Based on
529 the clear decrease in relative abundance around 10°C, and comparable to the conclusion of
530 Hennissen et al. (2017) we consider *H. tectata* as a cold-tolerant species rather than a strictly
531 cold-water indicator.

532 *Operculodinium?* *eirikianum* is only a minor component of the Mio-Pliocene
533 palynomorph assemblage in the Iceland Sea, and thus conclusions should be treated with
534 caution. However, similarly low counts of *O.?* *eirikianum* have been reported from the
535 Miocene and Pliocene of the North Atlantic and North Sea basin suggesting this species is
536 typically a minor but consistent component of Neogene assemblages (e.g. Louwye, 2002;
537 Louwye et al., 2007; Louwye and De Schepper et al., 2010; De Schepper et al., 2011;
538 Quaijtaal et al., 2014). It is present from 8 to 26°C in the Mio-Pliocene of the Iceland Sea
539 (Figs. 6 and 9), but in significant numbers (> 5%) only in one sample at 12°C, thus clearly
540 restricting interpretations of its paleoecological preferences. Nonetheless, the lower limit of
541 distribution compares well with the n=204 North Atlantic paleo-database where both

542 subspecies (*O.?* *eirikianum* var. *eirikianum* and *O.?* *eirikianum* var. *crebrum*) have not been
543 recorded at SSTs below 9°C (De Schepper et al., 2011). This may suggest a certain
544 temperature threshold on its occurrence and supports the interpretation of this species being
545 cold-intolerant (Head, 1997).

546 The species stratigraphically restricted to the Miocene (*Cerebrocysta irregulare*,
547 *Cordosphaeridium minimum*, *Operculodinium centrocarpum* s.s., *Impagidinium elongatum*,
548 *Batiacasphaera hirsuta*, and *Labyrinthodinium truncatum*) all show a preference towards
549 higher temperatures (Figs. 7 and 9). *Cerebrocysta irregulare*, *Cordosphaeridium minimum*,
550 *Operculodinium centrocarpum* s.s. and *Impagidinium elongatum* are all confined to the early
551 Late Miocene and occur at SSTs between 19 and 26°C, with only one sample recorded at a
552 lower temperature (16°C) outside this restricted SST range. All four species disappear around
553 10.5 Ma when temperatures permanently drop below 20°C (Figs. 2–3). In addition,
554 siliciclastic sedimentation becomes predominant and the first drop stone is recorded at the
555 study site (Shipboard Scientific Party, 1995). This suggests incisive environmental changes in
556 the study area causing these species to disappear. It seems likely that a critical temperature
557 threshold on the occurrence of these species might have been crossed, but a lower temperature
558 limit cannot be assessed with certainty based on the limited data available. Similarly,
559 *Batiacasphaera hirsuta* persistently occurs with relative abundances greater than 1% of the
560 dinocyst assemblage at SSTs in excess of 20°C (Fig. 7). In contrast to *C. irregulare*, *C.*
561 *minimum*, *O. centrocarpum* s.s., and *I. elongatum*, which all disappear around 10.5 Ma, *B.*
562 *hirsuta* still occurs, although sporadically and in very low numbers only, at temperatures as
563 low as 16°C until its highest occurrence (HO) in ODP Hole 907A at around 8.5 Ma (Figs. 2–
564 3). *Labyrinthodinium truncatum* clearly shows a centre of distribution at SSTs between 16
565 and 22°C, occasionally occurring at even higher temperatures (Figs. 7 and 9). It has a similar
566 stratigraphic range as *B. hirsuta*, but in contrast to the latter it occurs continuously and in
567 greater numbers until its HO around 8.5 Ma (Fig. 3). While the contemporaneous

568 disappearance suggests a similar temperature threshold for the occurrence of both species, *L.*
569 *truncatum* appears to be more tolerant towards cooler conditions than *B. hirsuta* judged by its
570 higher relative abundances.

571 All six Miocene species exhibit very restricted temperature ranges in ODP Hole 907A,
572 but with distinctively varying thermal affinities indicating a strong individual adaptation to
573 the warm conditions prevailing during most of the Miocene. *Cerebrocysta irregulare*, *C.*
574 *minimum*, *O. centrocarpum* s.s. and *I. elongatum* disappear in an interval when the first drop
575 stone is observed and temperatures constantly drop below 20°C, suggesting an intolerance
576 towards cooler conditions. *Batiacasphaera hirsuta* and *L. truncatum* occur at SSTs as low as
577 16°C, the latter probably being more tolerant to these temperatures judged by its higher
578 relative abundances. However, none of the six taxa has been recorded at temperatures lower
579 than 15°C clearly suggesting them all to be warm-water species. They all disappear from the
580 Nordic Seas and the North Atlantic in the early Late Miocene in concert with general
581 Neogene climate deterioration (Figs. 2–3).

582 In contrast, the *Batiacasphaera micropapillata* complex and *Reticulosphaera*
583 *actinocoronata*, which both range up into the Early Pliocene across the North Atlantic, occur
584 at a much broader temperature range (Figs. 7 and 9). The *B. micropapillata* complex ranges
585 from 8 to 26°C, but highest relative abundances are recorded at the warm end of the SST
586 spectrum reconstructed for Iceland Sea ODP Site 907. It contributes to the dinocyst
587 assemblage at temperatures below 10°C, but relative abundance only starts to increase at
588 SSTs > 10°C. Previous interpretations of this species complex as being warm- to cool-
589 temperate based on its (paleo) biogeographic distribution (Schreck and Matthiessen, 2013)
590 may have to be reconsidered since high relative abundances at SSTs in excess of 15°C clearly
591 suggests a warm water affinity. *Reticulosphaera actinocoronata* has a similar temperature
592 range and occurs at SSTs between 9 and 25°C. Relative abundances of 2.5% and above are
593 usually associated with SST values greater than 18°C and it only occurs sporadically at

594 temperatures lower than 15°C. This indicates a lesser tolerance of this species versus colder
595 waters compared to the *B. micropapillata* complex, which is still common (e.g. > 10%) at
596 SSTs between 10 and 15°C (Fig 3). In addition, *R. actinocoronata* disappears earlier than the
597 *B. micropapillata* complex across the North Atlantic during Pliocene cooling supporting the
598 interpretation of *R. actinocoronata* being less tolerant towards colder conditions. However,
599 both taxa tolerate a wide range of temperatures, thus favouring their cosmopolitan distribution
600 in the Neogene (see Schreck et al., 2012, and references therein). Both species disappear in
601 the Iceland Sea during the Early Pliocene in concert with a fundamental reorganisation of the
602 Nordic Seas surface circulation (Schreck et al., 2013; De Schepper et al., 2015).

603 *Operculodinium tegillatum* is only a minor constituent of the dinocyst assemblage at
604 ODP Site 907, and interpretations should thus be considered tentative. It is largely confined to
605 the Early Pliocene interval and only occurs sporadically in the warmer Miocene (Figs. 2–3). It
606 exhibits a restricted temperature range and its occurrence is related to SSTs between 7 and
607 15°C (Figs. 7 and 9), indicating a tolerance versus cool-temperate conditions. We note,
608 however, that occurrences at both ends of the temperature spectrum are confined to very low
609 relative abundances. Contemporaneously with *B. micropapillata* and *R. actinocoronata*, this
610 species disappears at 4.5 Ma from the record of ODP Hole 907A (Fig. 3). This disappearance
611 event has been related to a general reorganisation of surface water circulation in the entire
612 Nordic Seas (De Schepper et al., 2015). As these changes in oceanographic conditions
613 certainly affected different surface water mass properties, it leaves the question whether
614 species disappearance is exclusively a function of temperature (e.g. cooling). As all three
615 species have slightly different thermal preferences it seems likely that other factors such as
616 salinity and nutrient availability also played a crucial role in their coeval disappearance.

617

618 ***Acritarchs***

619 Due to their small size, unknown biological affinity and challenging taxonomy, acritarchs
620 have often received considerably less attention than dinocysts during palynological analyses,
621 in particular during stratigraphic studies, resulting in a loss of information (De Schepper and
622 Head, 2014). However, significant progress in their taxonomy has been made over the last
623 two decades, and their stratigraphic and paleoenvironmental value is progressively explored.
624 The fossil acritarch genera *Cymatiosphaera* and *Lavradosphaera* have been frequently
625 recorded in the Neogene of the high northern latitudes and exhibit high relative abundances in
626 certain intervals where they may even outnumber the dinocysts (de Vernal and Mudie, 1989;
627 Piasecki, 2003; De Schepper and Head, 2014; Schreck et al., 2013). Despite providing
628 valuable biostratigraphic marker events (Matthiessen et al., 2009; De Schepper and Head,
629 2014; Mattingsdal et al., 2014; Grøsfjeld et al., 2014), the application of these high abundance
630 intervals (acmes) for paleoenvironmental reconstructions is still restricted due to limited
631 knowledge on their paleoecological implications. At ODP Site 907, acritarchs occur
632 throughout most of the analysed interval and contribute substantially to the palynomorph
633 assemblage (Figs. 2–3). Unfortunately, the Middle Miocene assemblage is dominated by
634 various spinous forms that could not be assigned to a particular genus but have only
635 collectively been referred to as acanthomorphic acritarchs (Schreck et al., 2013), and are
636 hence not discussed here.

637 *Lavradosphaera elongata* is restricted to the Middle Miocene in ODP Site 907 and its
638 highest occurrence in the upper Serravallian (Figs. 2–3) has been related to the global Mi-5
639 cooling event leading to the interpretation of *L. elongata* being a warm-temperate species
640 (Schreck and Matthiessen, 2014). Indeed, its occurrence is confined to SSTs higher than 20°C
641 (Figs. 8–9) indicating a warm water preference. It exhibits a restricted temperature range
642 between 20 and 24°C suggesting an adaptation to warmer surface waters, which likely
643 explains its disappearance during times of high latitude cooling. However, this species has
644 only been recorded in the Iceland Sea to date and relative abundances are usually low, thus

645 conclusions should be regarded tentative until more data on its distribution are available to
646 validate the temperature range given in this study.

647 The acritarch *Decahedrella martinheadii* is endemic to the high northern latitudes and
648 an excellent stratigraphic marker for the Late Miocene in the Arctic and sub-arctic seas
649 (Schreck et al., 2012). Based on its biogeographic distribution it has been considered a cold-
650 water species (Manum, 1997; Matthiessen et al., 2009). Indeed, its first occurrence in Iceland
651 Sea ODP Hole 907A around 10.5 Ma is contemporaneous with the occurrence of the first
652 drop stone, the onset of predominantly siliciclastic deposition at the site (Figs. 2–3, Shipboard
653 Scientific Party, 1995) and a permanent drop of SSTs below 20°C. In combination with
654 simultaneously declining dinocyst diversity and the disappearance of several dinocyst and
655 acritarch taxa, this suggests initiation of cooler surface water conditions in the study area at
656 that time (Schreck et al., 2013). However, alkenone data from ODP Hole 907A indicate a
657 broad temperature tolerance for this species as it occurs at SSTs ranging from 3 to 21°C (Figs.
658 8–9). Although its presence in significant numbers until 21°C contrasts previous
659 interpretations of this species being a cold-water indicator based on biogeographic
660 distribution, highest relative abundances (> 40% of the total marine palynomorph assemblage
661 [dinocysts and acritarchs]) are found $\leq 12^\circ\text{C}$. In the central Arctic Ocean, *D. martinheadii*
662 continuously occurs in samples with alkenone SST estimates ranging from 4 to 6°C (Stein et
663 al., 2016), which indicates that, even though this species can tolerate a wide range of
664 temperatures, it is well adapted to colder conditions in the Arctic and subarctic realm.

665 The genus *Cymatiosphaera* has been assigned to the prasinophytes, which today forms
666 an important element of high latitude phytoplankton communities (Tyson, 1995, and
667 references therein). In modern and Quaternary sediments, prasinophytes (in particular
668 *Cymatiosphaera* species) are often associated with cooler surface waters and/or less saline
669 conditions (Wall and Dale, 1974; Tappan, 1980; Sorrel et al., 2006). In the Pliocene of

670 Iceland Sea ODP Hole 907A, *Cymatiosphaera? invaginata* reaches relative abundances > 5%
671 of the total marine palynomorph assemblage at temperatures lower than 15°C (Fig. 8), indeed
672 indicating a cold-water tolerance of this species. The Early Pliocene interval with elevated *C.?*
673 *invaginata* abundance is characterized by severe cooling (Figs. 2–3, De Schepper et al., 2015)
674 and increased occurrence of ice-rafted debris (Fronval and Jansen, 1996), both supporting this
675 interpretation. In the generally warmer Middle Miocene, however, it can occur at
676 temperatures of up to 26°C, but then never exceeds more than 2% of the total marine
677 palynomorph assemblage suggesting an occurrence close to its upper temperature limit. This
678 species apparently tolerates a broad range of temperatures, but relative abundances in ODP
679 Hole 907A clearly suggest an affinity for cooler surface waters.

680

681 **Conclusion**

682 Information on the paleoecology of extinct marine palynomorphs has been mainly derived
683 from their biogeographic distribution and thus, remained qualitative. However, the
684 combination of dinocyst and acritarch assemblages with independently derived alkenone-
685 based SST estimates from the same sample presented here provide an initial quantitative
686 assessment of temperature preferences for Miocene through Pliocene species in a high latitude
687 setting. We refrain from defining exact upper and lower temperature limits for the occurrence
688 of extinct species, but provide temperature ranges in which extinct species may have occurred
689 based on independently derived SST estimates, thus improving previous qualitative
690 assignments that were solely based on biogeographic distribution. Our results indicate that:

- 691 • The Miocene dinocyst species *Cerebrocysta irregulare*, *Cordosphaeridium minimum*,
692 *Operculodinium centrocarpum* s.s., *Impagidinium elongatum*, *Batiacasphaera hirsuta*
693 *and Labyrinthodinium truncatum*, and the acritarch *Lavradosphaera elongata* are
694 restricted to a narrow temperature interval and none of these are recorded at SSTs
695 below 15°C. Therefore, these species are considered as warm-water species. Their

696 disappearance during late Neogene cooling, indicated by a SST decrease and the first
697 drop stone, suggests a strong adaptation to the warmer conditions prevailing during
698 most of the Miocene.

699 • The stratigraphically higher ranging species *Operculodinium?* *eirikianum*,
700 *Reticulatosphaera actinocoronata*, *Batiacasphaera micropapillata* complex and
701 *Habibacysta tectata* tolerate a broader temperature range. The latter two taxa still
702 contribute to the palynomorph assemblage at temperatures below 10°C, but our data
703 indicate that *H. tectata* is not a cold-water species as previously suggested based on
704 (paleo)biogeographic distribution. In contrast, *B. micropapillata* complex may have a
705 preference for warmer surface conditions than previously suggested by biogeography.
706 *Operculodinium?* *eirikianum* is considered a cold-intolerant species that may have a
707 lower SST limit for its occurrence at around 10°C.

708 • The acritarchs *D. martinheadii* and *C.?* *invaginata* have a broad temperature
709 distribution across the Miocene to Pliocene, but high relative abundances at
710 temperatures < 10°C in the Iceland Sea clearly suggest a preference for cooler surface
711 water conditions. Based on our data quantitative data, however, *D. martinheadii*
712 should not be regarded as an indicator for cold waters exclusively.

713 • The Miocene-Pliocene distribution of the extant *L. machaerophorum*, *N. labyrinthus*,
714 *A. choane* and *S. elongatus* compares well with its occurrence in the Plio-Pleistocene
715 North Atlantic and in the modern ocean. However, it rather corresponds to the warm
716 end of its distribution in the modern ocean for *S. elongatus* s.l. and *N. labyrinthus*.

717 • Compared to present-day, the extant *I. pallidum* does not exhibit increased relative
718 abundances at the lower end of its temperature range in both paleo-datasets, but rather
719 show a preference for somewhat warmer waters (> 10°C) in the geological past. We
720 thus question its use as a reliable cold-water indicator in pre-Quaternary sediments.

721

722 Although our Miocene to Pliocene record may be slightly biased towards warmer SSTs when
723 compared to the present-day reference database, fossil and modern distribution of extant
724 species is largely comparable. It is in good agreement with the species distribution recorded in
725 the North Atlantic Plio-Pleistocene paleo-dataset (De Schepper et al., 2011) and therefore
726 provides first indications on how to interpret Miocene assemblages with no modern analogue.
727 In particular, when combining the SST range of several individual species it allows to narrow
728 the interval of co-occurrence and thus to infer the prevailing SSTs at the study site (Fig. 9).
729 Our new data complement the previously published paleo-dataset from the North Atlantic and
730 expands its spatial (high northern latitudes) and temporal (into the Miocene) coverage.
731 However, we note that our data represent an initial assignment of paleoecological affinities of
732 extinct Mio-Pliocene species and there is a strong need to further augment data from different
733 sites to this dataset in order to confirm the proposed relationships and to further increase the
734 reliability of ecological assessments of extinct species.

735 Despite its limitations, this approach helps to decipher the paleoecology of extinct
736 species and improves their application for paleoenvironmental reconstructions, in particular in
737 the high northern latitudes where other microfossil groups are rare to absent. A refined
738 understanding of temperature preferences of Neogene high latitude species and its
739 quantitative assessment will be particularly important to better understand
740 paleoenvironmental changes in the Arctic Ocean and marginal seas during Earth's transition
741 from Greenhouse to Icehouse conditions.

742

743 **Acknowledgments**

744 This research uses samples and data provided by the Ocean Drilling Program. We gratefully
745 thank W. Luttmer (AWI-Bremerhaven) for technical support with the alkenone analyses and
746 M. Jones (Palynological Laboratory Services Ltd, Holyhead, UK) for palynological
747 preparation. MS and JM acknowledge financial support from the German Research

748 Foundation (DFG MA 3913/2), and MS is additionally thankful to the Basic Research
749 Program (No. PE16062) of the Korea Polar Research Institute, and a National Research
750 Foundation of Korea grant from the government of Korea (MSIP) (No.
751 2014R1A2A2A09049496). SDS and CC acknowledge funding from the Norwegian Research
752 Council (project 229819).

753

754 **Appendix: List of taxa discussed in the text and their full authorial citations.**

755 *Ataxiodinium choane* Reid, 1974

756 *Batiacasphaera hirsuta* Stover, 1977

757 *Batiacasphaera micropapillata* Stover, 1977

758 *Cerebrocysta irregulare* Schreck et al., 2012

759 *Cordosphaeridium minimum* (Morgenroth, 1966) Benedek, 1972

760 *Habibacysta tectata* Head et al., 1989

761 *Impagidinium elongatum* Schreck et al., 2012

762 *Impagidinium pallidum* Bujak, 1984

763 *Labyrinthodinium truncatum* Piasecki, 1980

764 *Lingulodinium machaerophorum* (Deflandre and Cookson, 1955) Wall, 1967

765 *Nematosphaeropsis labyrinthus* (Ostenfeld, 1903) Reid, 1974

766 *Operculodinium centrocarpum* (Deflandre and Cookson, 1955) Wall, 1967

767 *Operculodinium tegillatum* Head, 1997

768 *Operculodinium? eirikianum* Head et al, 1989 emend. Head, 1997

769 *Reticulosphaera actinocoronata* (Benedek, 1972) Bujak and Matsuoka, 1986 emend. Bujak
770 and Matsuoka, 1986

771 *Spiniferites elongatus* Reid, 1974

772

773 *Cymatiosphaera? invaginata* Head et al., 1989

774 *Decahedrella martinheadii* Manum, 1997

775 *Lavradosphaera elongata* Schreck and Matthiessen, 2014

776

777 **References**

778 Andruleit, H., 1997. Coccolithophore fluxes in the Norwegian-Greenland Sea: seasonality and
779 assemblage alterations. *Marine Micropaleontology* 31, 45–64.

780 Blindheim, J., Østerhus, S., 2005. The Nordic Seas, main oceanographic features. In: Drange,
781 H., Dokken, T., Furevik, T., Gerdes, R. (Eds.), *The Nordic Seas - An integrated*
782 *perspective*. American Geophysical Union, Washington D.C., pp. 11–38.

783 Brenner, W., Biebow, N., 2001. Missing autofluorescence of recent and fossil dinoflagellate
784 cysts - an indicator of heterotrophy? *Neues Jahrbuch für Geologie und Paläontologie -*
785 *Abhandlungen* 219, 229–240.

786 Bujak, J.P., 1984. Cenozoic dinoflagellate cysts and acritarchs from the Bering Sea and
787 northern North Pacific, DSDP Leg 19. *Micropaleontology* 30, 180–212.

788 Channell, J.E.T., Amigo, A.E., Fronval, T., Rack, F., Lehman, B., 1999. Magnetic
789 stratigraphy at Sites 907 and 985 in the Norwegian-Greenland Sea and a revision of
790 the Site 907 composite section. In: Raymo, M.E., Jansen, E., Blum, P., Herbert, T.D.
791 (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results 162*. College
792 Station, TX, pp. 131–148.

793 Chapman, M., 2010. Seasonal production patterns of planktonic foraminifera in the NE
794 Atlantic Ocean: implications for paleotemperature and hydrographic reconstructions.
795 *Paleoceanography* 25, PA1101. doi:10.1029/2008PA001708.

796 Dale, B., 1996. *Dinoflagellate Cyst Ecology: Modelling and Geological Applications*. In:
797 Jansonius, J., McGregor, D.C. (Eds.), *Palynology: principles and applications*, Vol. 3.
798 AASP Foundation, Dallas, TX, pp. 1249–1275.

799 Dale, A.L., Dale, B., 1992. Dinoflagellate contributions to the sediment flux of the Nordic
800 Sea. In: Honjo, S. (Eds.), *Dinoflagellate contribution to the deep sea*. Ocean
801 Biocoenosis Series No. 5, Woods Hole Oceanographic Institution, Massachusetts, pp.
802 45–75.

803 Dale, B., Dale, A., 2002. Environmental applications of dinoflagellate cysts and acritarchs. In:
804 Haslett, K. (Eds.), *Quaternary environmental micropaleontology*. Oxford University
805 Press, London, pp. 207–240.

806 De Schepper, S., Head, M.J., 2008a. New dinoflagellate cyst and acritarch taxa from the

807 Pliocene and Pleistocene of the eastern North Atlantic (DSDP Site 610A). *Journal of*
808 *Systematic Palaeontology* 6, 101–107.

809 De Schepper, S., Head, M.J., 2008b. Age calibration of dinoflagellate cyst and acritarch
810 events in the Pliocene-Pleistocene of the eastern North Atlantic (DSDP Hole 610A).
811 *Stratigraphy* 5, 137–161.

812 De Schepper, S., Head, M.J., 2014. New Pliocene and Pleistocene acritarchs: correlation
813 potential in high latitude oceans. *Journal of Systematic Palaeontology* 12, 493–519.

814 De Schepper, S., Fischer, E.I., Groeneveld, J., Head, M.J., Matthiessen, J., 2011. Deciphering
815 the palaeoecology of Late Pliocene and Early Pleistocene dinoflagellate cysts.
816 *Palaeogeography, Palaeoclimatology, Palaeoecology* 309, 17–32.

817 De Schepper, S., Schreck, M., Beck, K.M., Matthiessen, J., Fahl, K., Mangerud, G., 2015.
818 Early Pliocene onset of modern Nordic Seas circulation related to ocean gateway
819 changes. *Nature Communication* 6, doi:10.1038/ncomms9659.

820 De Schepper, S., Beck, K.M., Mangerud, G., 2017. Late Neogene dinoflagellate cyst and
821 acritarch biostratigraphy for Ocean Drilling Program Hole 642B, Norwegian Sea.
822 *Review of Palynology and Palaeobotany* 236, 12–32.

823 de Vernal, A., Mudie, P., 1989. Pliocene and Pleistocene palynostratigraphy at ODP Sites 646
824 and 647, eastern and southern Labrador Sea. In: Srivastava, S.P., Arthur, M., Clement,
825 B. (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results 105*. College
826 Station, TX, pp. 401–422.

827 de Vernal, A., Henry, J., Matthiessen, J., Mudie, P., Rochon, A., Boessenkool, K.P., Eynaud,
828 F., Grosfjeld, K., Guiot, J., Hamel, D., Harland, R., Head, M.J., Kunz-Pirrung, M.,
829 Levac, E., Loucheur, V., Peyron, O., Pospelova, V., Radi, T., Turon, J.L., Voronina,
830 E., 2001. Dinoflagellate cyst assemblages as tracers of sea-surface conditions in the
831 northern North Atlantic, Arctic, and sub-Arctic seas: the new "n=677" data base and
832 its application for quantitative paleoceanographic reconstruction. *Journal of*
833 *Quaternary Science* 16, 681–698.

834 de Vernal, A., Eynaud, F., Henry, M., Hillaire-Marcel, C., Londeix, L., Mangin, S.,
835 Matthiessen, J., Marret, F., Radi, T., Rochon, A., Solignac, S., Turon, J.L., 2005.
836 Reconstruction of sea-surface conditions at middle to high latitudes of the Northern
837 Hemisphere during the Last Glacial Maximum (LGM) based on dinoflagellate cyst
838 assemblages. *Quaternary Science Reviews* 24, 897–924.

839 de Vernal, A., Rochon, A., Fréchet, B., Henry, M., Radi, T., Solignac, S., 2013.
840 Reconstructing past sea ice cover of the Northern Hemisphere from dinocyst

841 assemblages: status of the approach. *Quaternary Science Reviews* 79, 122–134.

842 Edwards, L.E., Mudie, P.J., de Vernal, A., 1991. Pliocene paleoclimatic reconstruction using
843 dinoflagellate cysts: Comparison of methods. *Quaternary Science Reviews* 10, 259–
844 274.

845 Elderfield, H., Ganssen, G., 2000. Past temperature and $\delta^{18}\text{O}$ of surface ocean waters inferred
846 from foraminiferal Mg/Ca ratios. *Nature* 405, 442–445.

847 Fronval, T., Jansen, E., 1996. Late Neogene paleoclimates and paleoceanography in the
848 Iceland-Norwegian Sea: Evidence from the Iceland and Vøring Plateaus. In: Thiede,
849 J., Myhre, A.M., Firth, J.V., Johnson, G.L., Ruddiman, W.F. (Eds.), *Proceedings of*
850 *the Ocean Drilling Program, Scientific Results 151*. College Station, TX, pp. 455–468.

851 Ganssen, G.M., Kroon, D., 2000. The isotopic signature of planktonic foraminifera from NE
852 Atlantic surface sediments: implications for the reconstruction of past oceanic
853 conditions. *Journal of the Geological Society* 157, 693–699.

854 Grøsfjeld, K., De Schepper, S., Fabian, K., Husum, K., Baranwal, S., Andreassen, K., Knies,
855 J., 2014. Dating and palaeoenvironmental reconstruction of the sediments around the
856 Miocene/Pliocene boundary in Yermak Plateau ODP Hole 911A using marine
857 palynology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 414, 382–402.

858 Guiot, J., de Vernal, A., 2007. Transfer functions: methods for quantitative paleoceanography
859 based on microfossils. In: Hillaire-Marcel, C., de Vernal, A. (Eds.), *Proxies in Late*
860 *Cenozoic Paleoceanography*. Elsevier, Amsterdam, pp. 523–563.

861 Head, M.J., 1994. Morphology and paleoenvironmental significance of the Cenozoic
862 dinoflagellate genera *Tectatodinium* and *Habibacysta*. *Micropaleontology* 40, 289–
863 321.

864 Head, M.J., 1997. Thermophilic dinoflagellate assemblages from the mid Pliocene of eastern
865 England. *Journal of Paleontology* 71, 165–193.

866 Head, M.J., Norris, G., 1989. Palynology and dinocyst stratigraphy of the Eocene and
867 Oligocene in ODP Leg 105, Hole 647A, Labrador Sea. In: Srivastava, S.P., Arthur,
868 M., Clement, B. (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results*
869 *105*. College Station, TX, pp. 515–550.

870 Heikkilä, M., Pospelova, V., Forest, A., Stern, G.A., Fortier, L., Macdonald, R.W., 2016.
871 Dinoflagellate cyst production over an annual cycle in seasonally ice-covered Hudson
872 Bay. *Marine Micropaleontology* 125, 1–24.

873 Hennissen, J.A., Head, M.J., De Schepper, S., Groeneveld, J., 2017. Dinoflagellate cysts
874 paleoecology during the Pliocene-Pleistocene transition in the North Atlantic.

875 Palaeogeography, Palaeoclimatology, Palaeoecology 470, 81–108.

876 Herbert, T., 2003. Alkenone Paleotemperature Determinations. In: Holland, H.D., Turekian,
877 K.K. (Eds.), Treatise of Geochemistry - Volume 6: The Oceans and Marine
878 Geochemistry. Elsevier, Amsterdam, pp. 391–432.

879 Herbert, T., Lawrence, K.T., Tzanova, A., Peterson, L.C., Caballero-Gill, R., Kelly, C.S.,
880 2016. Late Miocene global cooling and the rise of modern ecosystems. Nature
881 Geoscience 9, 843–847.

882 Hilgen, F.J., Lourens, L.J., Van Dam, J.A., 2012. The Neogene Period. In: Gradstein, F., Ogg,
883 J., Schmitz, M., Ogg, G. (Eds.), The Geological Time Scale 2012. Elsevier,
884 Amsterdam, pp. 923–978.

885 Howe, J.A., Harland, R., Cottier, F.R., Brand, T., Willis, K.J., Berge, J.R., Grøsfjeld, K.,
886 Eriksson, A., 2010. Dinoflagellate cysts as proxies for palaeoceanographic conditions
887 in Arctic fjords, in: Howe, J.A., Austin, W.E.N., Forwick, M., Paetzel, M. (Eds.),
888 Fjord Systems and Archives. Geological Society of London, London, pp. 61–74.

889 Jiménez-Moreno, G., Head, M.J., Harzhauser, M., 2006. Early and Middle Miocene
890 dinoflagellate cyst stratigraphy of the Central Paratethys, Central Europe. Journal of
891 Micropalaeontology 25, 113–119.

892 Lourens, L., Hilgen, F., Shackleton, N.J., Laskar, J., Wilson, J., 2005. The Neogene. In:
893 Gradstein, F.M., Ogg, J.G., Smith, A.G. (Eds.), A Geological Timescale 2004
894 Cambridge University Press, Cambridge, U.K., 409–430. (Imprinted).

895 Louwye, S., 2002. Dinoflagellate cyst biostratigraphy of the Upper Miocene Deurne Sands
896 (Diest Formation) of northern Belgium, southern North Sea Basin. Geological Journal
897 37, 55–67.

898 Louwye, S., De Schepper, S., 2010. The Miocene–Pliocene hiatus in the southern North Sea
899 Basin (northern Belgium) revealed by dinoflagellate cysts. Geological Magazine 147,
900 1–17.

901 Louwye, S., Foubert, A., Mertens, K., Van Rooij, D., and IODP Expedition 307 Scientific
902 Party, 2007. Integrated stratigraphy and palaeoecology of the Lower and Middle
903 Miocene of the Porcupine Basin. Geological Magazine 145, 321–344.

904 Manum, S.B., 1997. *Decahedrella martinheadii* gen. et sp. nov. - a problematic palynomorph
905 from the Northern Atlantic Miocene. Palynology 21, 67–77.

906 Marret, F., Eiríksson, J., Knudsen, K.L., Turon, J.-L., Scourse, J.D., 2004. Distribution of
907 dinoflagellate cyst assemblages in surface sediments from the northern and western
908 shelf of Iceland. Review of Palaeobotany and Palynology 128, 35–53.

- 909 Masure, E., Vrielynck, B., 2009. Late Albian dinoflagellate cyst paleobiogeography as
910 indicator of asymmetric sea surface temperature gradient on both hemispheres with
911 southern high latitudes warmer than northern ones. *Marine Micropaleontology* 70,
912 120–133.
- 913 Mattingsdal, R., Knies, J., Andreassen, K., Fabian, K., Husum, K., Grøsfjeld, K., De
914 Schepper, S., 2014. A new 6 Myr stratigraphic framework for the Atlantic–Arctic
915 Gateway. *Quaternary Science Reviews* 92, 170–178.
- 916 Matthiessen, J., 1995. Distribution patterns of dinoflagellate cysts and other organic-walled
917 microfossils in recent Norwegian-Greenland Sea sediments. *Marine*
918 *Micropaleontology* 24, 307–334.
- 919 Matthiessen, J., De Vernal, A., Head, M.J., Okolodkov, Y., Puerto, A., Zonneveld, K.A.F.,
920 Harland, R., 2005. Modern organic-walled dinoflagellate cysts in Arctic marine
921 environments and their (paleo-) environmental significance. *Paläontologische*
922 *Zeitschrift* 79, 3–51.
- 923 Matthiessen, J., Brinkhuis, H., Poulsen, N.E., Smelror, M., 2009. *Decahedrella martinheadii*
924 Manum 1997 - a stratigraphically and paleoenvironmentally useful Miocene acritarch
925 of the northern high latitudes. *Micropaleontology* 55, 171–186.
- 926 Mollenhauer, G., Kienast, M., Lamy, F., Meggers, H., Schneider, R.R., Hayes, J.M., Eglinton,
927 T.I., 2005. An evaluation of ^{14}C age relationships between co-occurring foraminifera,
928 alkenones, and total organic carbon in continental margin sediments.
929 *Paleoceanography* 20, PA1016
- 930 Müller, P.J., Kirst, G., Ruhland, G., von Storch, I., Rosell-Melé, A., 1998. Calibration of the
931 alkenone paleotemperature index U_{37}^k based on core-tops from the eastern South
932 Atlantic and the global ocean (60°N – 60°S). *Geochimica et Cosmochimica Acta* 62,
933 1757–1772.
- 934 Radi, T., de Vernal, A., 2008. Dinocysts as proxy of primary productivity in mid-high
935 latitudes of the Northern Hemisphere. *Marine Micropaleontology* 68, 84–114.
- 936 Piasecki, S., 2003. Neogene dinoflagellate cysts from Davis Strait, offshore West Greenland.
937 *Marine and Petroleum Geology* 20, 1075–1088.
- 938 Rosell-Melè, A., McClymont, E., 2007. Biomarkers as paleoceanographic proxies. In:
939 Hillaire-Marcel, C., de Vernal, A. (Eds.), *Proxies in Late Cenozoic Paleocyanography*.
940 Elsevier, Amsterdam, pp. 441–490.
- 941 Samtleben, C., Bickert, T., 1990. Coccoliths in sediment traps from the Norwegian Sea.
942 *Marine Micropaleontology* 16, 39–64.

943 Samtleben, C., Schäfer, P., Andruleit, H., Baumann, A., Baumann, K.H., Kohly, A.,
944 Matthiessen, J., Schröder-Ritzrau, A., 1995. Plankton in the Norwegian-Greenland
945 Sea: from living communities to sediment assemblages - an actualistic approach.
946 *Geologische Rundschau* 84, 108–136.

947 Schreck, M., Matthiessen, J., Head, M.J., 2012. A magnetostratigraphic calibration of Middle
948 Miocene through Pliocene dinoflagellate cyst and acritarch events in the Iceland Sea
949 (Ocean Drilling Program Hole 907A). *Review of Palaeobotany and Palynology* 187,
950 66–94.

951 Schreck, M., Meheust, M., Stein, R., Matthiessen, J., 2013. Response of marine
952 palynomorphs to Neogene climate cooling in the Iceland Sea (ODP Hole 907A).
953 *Marine Micropaleontology* 101, 49–67.

954 Schreck, M., Matthiessen, J., 2013. *Batiacasphaera micropapillata*: Palaeobiogeographic
955 distribution and palaeological implications of a critical Neogene species complex. In:
956 Lewis, J., Marret, F., Bradley, L. (Eds.), *Biological and Geological Perspectives of*
957 *Dinoflagellates*. The Micropalaeontological Society, Special Publications: Geological
958 Society, London, pp. 301–314.

959 Schreck, M., Matthiessen, J., 2014. *Batiacasphaera bergenensis* and *Lavradosphaera*
960 *elongata* - New dinoflagellate cyst and acritarch species from the Miocene of the
961 Iceland Sea (ODP Hole 907A). *Review of Palaeobotany and Palynology* 211, 97–106.

962 Schröder-Ritzrau, A., Andruleit, H., Jensen, S., Samtleben, C., Schäfer, P., Matthiessen, J.,
963 Hass, C., Kohly, A., Thiede, J., 2001. Distribution, Export and Alteration of
964 Fossilizable Plankton in the Nordic Seas. In: Schäfer, P., Ritzrau, W., Schlüter, M.,
965 Thiede, J. (Eds.), *The Northern North Atlantic - A changing environment*. Springer-
966 Verlag, Berlin, pp. 81–104.

967 Shipboard Scientific Party, 1995. Site 907. In: Myhre, A.M., Thiede, J., Firth, J.V. (Eds.),
968 *Proceedings of the Ocean Drilling, Initial Reports 151*. College Station, TX, pp. 57–
969 111.

970 Sison, C.P., Glaz, J., 1995. Simultaneous confidence intervals and sample size determination
971 for multinomial proportions. *Journal of the American Statistical Association* 90, 366–
972 369.

973 Sorrel, P., Popescu, S.M., Head, M.J., Suc, J.P., Klotz, S., Oberhänsli, H., 2006.
974 Hydrographic development of the Aral Sea during the last 2000 years based on a
975 quantitative analysis of dinoflagellate cysts. *Palaeogeography, Palaeoclimatology,*
976 *Palaeoecology* 234, 304–327.

977 Stabell, B., Koç, N., 1996. Recent to Middle Miocene diatom productivity at Site 907, Iceland
978 Plateau. In: Thiede, J., Myhre, A.M., Firth, J.V., Johnson, G.L., Ruddiman, W.F.
979 (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results 151. College
980 Station, TX, pp. 483–492.

981 Stein, R., Fahl, K., Schreck, M., Knorr, G., Niessen, F., Jensen, L., Forwick, M., Gebhardt,
982 C., Kaminski, M., Kopf, A., Matthiessen, J., Jokat, W., Lohmann, G. (2016). Evidence
983 for ice-free summers in the late Miocene central Arctic Ocean. Nature
984 Communications 7, doi:10.1038/ncomms11148.

985 Stephens, C., Conkright, M.E., Boyer, T.P., Antonov, J.I., Baranova, O.K., Garcia, H.E.,
986 Gelfeld, R., Johnson, D., Locarnini, R.A., Murphy, P.P., O'Brien, T.D., Smolyar, I.,
987 2002. In: Levitus, S. (Ed.), World Ocean Database 2001, Volume 3: temporal
988 distribution of conductivity–temperature–depth (pressure) profiles. NOAA Atlas
989 NESDIS 44. U.S. Government Printing Office, Washington, D.C., 47 p.

990 Stockmarr, J., 1977. Tablets with spores used in absolute pollen analysis. Pollen et Spores 13,
991 615–621.

992 Tappan, H., 1980. The paleobiology of plant protists. W.H. Freeman and Company, San
993 Francisco, 1028 pp.

994 Taylor, F. J. R., 1987. The Biology of Dinoflagellates. Oxford: Blackwell Scientific
995 Publications, 785 pp.

996 Tyson, R.V., 1995. Sedimentary Organic Matter - Organic Facies and Palynofacies. Chapman
997 & Hall, London, 615 pp.

998 Van Nieuwenhove, N., Baumann, A., Matthiessen, J., Bonnet, S., de Vernal, A., 2016. Sea
999 surface conditions in the southern Nordic Seas during the Holocene based on
1000 dinoflagellate cyst assemblages. The Holocene 26, 722–735.

1001 Vázquez-Riveiros, N., Govin, A., Waelbroeck, C., Mackensen, A., Michel, E., Moreira, S.,
1002 Bouinot, T., Caillon, N., Orgun, A., Brandon, M., 2016. Mg/Ca thermometry in
1003 planktic foraminifera: Improving paleotemperature estimations for *G. bulloides* and *N.*
1004 *pachyderma* left. Geochemistry, Geophysics, Geosystems 17, 1–16.

1005 Versteegh, G.J.M., 1994. Recognition of cyclic and non-cyclic environmental changes in the
1006 Mediterranean Pliocene: A palynological approach. Marine Micropaleontology 23,
1007 147–183.

1008 Versteegh, G.J.M., Zonneveld, K.A.F., 1994. Determination of (palaeo-)ecological
1009 preferences of dinoflagellates by applying Detrended and Canonical Correspondence
1010 analysis to Late Pliocene dinoflagellate cyst assemblages of the south Italian Singa

1011 section. *Review of Palaeobotany and Palynology* 84, 181–199.

1012 Wall, D., Dale, B., 1974. Dinoflagellates in the Late Quaternary deep-water sediments of the
1013 Black Sea. In: Degens, E.T., Ross, D.A. (Eds.), *The Black Sea - Geology, Chemistry
1014 and Biology*. American Association of Petroleum Geologists, Tulsa, TX, pp. 364–380.

1015 Williams, G.L., Fensome, R.A., MacRae, R.A., 2017. *The Lentin and Williams Index of
1016 Fossil Dinoflagellates, 2017 Edition*. American Association of Stratigraphic
1017 Palynologists, Contribution Series 48, TX, 1097 pp.

1018 Wrenn, J.H., Kokinos, J.P., 1986. Preliminary comments on Miocene through Pleistocene
1019 dinoflagellate cysts from De Soto Canyon, Gulf of Mexico. *American Association of
1020 Stratigraphic Palynologists, Contributions Series 17, TX, pp. 169-225*.

1021 Zachos, J.C., Dickens, G.R., Zeebe, R.E., 2008. An early Cenozoic perspective on greenhouse
1022 warming and carbon-cycle dynamics. *Nature* 451, 279–283.

1023 Zonneveld, K.A.F., Versteegh, G., Kodrans-Nsiah, M., 2008. Preservation and organic
1024 chemistry of Late Cenozoic organic-walled dinoflagellate cysts: A review. *Marine
1025 Micropaleontology* 68, 179–197.

1026 Zonneveld, K.A.F., Marret, F., Versteegh, G.J.M., Bogus, K., Bonnet, S., Bouimetarhan, I.,
1027 Crouch, E., de Vernal, A., Elshanawany, R., Edwards, L., Esper, O., Forke, S.,
1028 Grøsfjeld, K., Henry, M., Holzwarth, U., Kieft, J.-F., Kim, S.-Y., Ladouceur, S., Ledu,
1029 D., Chen, L., Limoges, A., Londeix, L., Lu, S.H., Mahmoud, M.S., Marino, G.,
1030 Matsouka, K., Matthiessen, J., Mildenhall, D.C., Mudie, P., Neil, H.L., Pospelova, V.,
1031 Qi, Y., Radi, T., Richerol, T., Rochon, A., Sangiorgi, F., Solignac, S., Turon, J.-L.,
1032 Verleye, T., Wang, Y., Wang, Z., Young, M., 2013. Atlas of modern dinoflagellate
1033 cyst distribution based on 2405 data points. *Review of Palaeobotany and Palynology*
1034 191, 1–197.

1035

1036 **Figures**

1037 **Figure 1:** Location of the study site ODP Site 907 (yellow dot) together with the n=1492
1038 present-day Northern Hemisphere reference database of de Vernal et al., 2013 (black and grey
1039 dots) and the n=101 Nordic Seas subset (grey dots only). Blue dots represent the Pliocene to
1040 Pleistocene North Atlantic sites of the n=204 paleo-database (De Schepper et al., 2011).

1041

1042 **Figure 2:** Raw counts of selected dinocyst and acritarch species (data from Schreck et al.,
1043 2013) and their relation to alkenone-based sea surface temperature (data from Schreck et al.,
1044 2013; De Schepper et al., 2015; Stein et al., 2016) in ODP Hole 907A. Light shading
1045 illustrates the total stratigraphic range and dark shading the first and last occurrence
1046 respectively. * = species only encountered outside regular counts, (n) or (*) = suspected
1047 reworking. Also shown is the magnetostratigraphy (Channell et al., 1999) and the
1048 lithostratigraphic units (Shipboard Scientific Party, 1995) of ODP Hole 907A.

1049

1050 **Figure 3:** Relative abundance of extant and extinct dinoflagellate cysts and acritarchs in ODP
1051 Site 907. Also shown is the reconstructed alkenone sea surface temperature (SST in °C).
1052 Black line depicts the gradual cooling trend observed in ODP Site 907. Red line presents the
1053 present-day sea surface temperature in the study area, while the blue line presents the present-
1054 day annual mean sea surface temperature.

1055

1056 **Figure 4:** The calculated simultaneous confidence interval (95%) using the method of Sison
1057 and Glaz (1995) for all samples in our Miocene-Pliocene database (n=68). Samples with less
1058 than 50 palynomorph counts have been omitted from that figure. Larger confidence intervals
1059 (i.e. less reliable samples) are represented by smaller dots in Figs. 4–7.

1060

1061 **Figure 5:** Relative abundance (in %) of extant dinoflagellate cysts in relation to sea surface
1062 temperatures (SST in °C). Species relative abundance (yellow dots) is plotted against
1063 alkenone-based SST. Species relative abundance in the modern ocean (n=1492 = black and
1064 grey dots, n=101 = grey dots only) is plotted against present-day summer SST derived from
1065 the World Ocean Atlas 2001 (Stephens et al., 2002). For the Pliocene-Pleistocene n=204
1066 paleo-database (blue dots) species relative abundances is plotted vs. foraminiferal Mg/Ca-
1067 derived (spring-summer) SST (De Schepper et al., 2011).

1068

1069 **Figure 6:** Relative abundance (in %) of extinct dinoflagellate cysts in relation to sea surface
1070 temperatures (SST in °C). Species relative abundance (yellow dots) is plotted against
1071 alkenone-based SST, and for the Pliocene-Pleistocene n=204 paleo-database (light blue dots)
1072 species relative abundance is plotted vs. foraminiferal Mg/Ca-derived (spring-summer) SST
1073 (De Schepper et al., 2011).

1074

1075 **Figure 7:** Relative abundance (in %) of extinct dinoflagellate cysts in relation to sea surface
1076 temperatures (SST in °C). Species relative abundance (yellow dots) is plotted against
1077 alkenone-based SST.

1078

1079 **Figure 8:** Relative abundance (in %) of extinct acritarchs in relation to sea-surface
1080 temperatures (SST in °C). Species relative abundance (yellow dots) is plotted against
1081 alkenone-based SST.

1082

1083 **Figure 9:** Summary of the temperature ranges of the extinct dinoflagellate and acritarch
1084 species discussed in the text. Highlighted area (back) represents the centre of distribution.
1085 Blue line indicates the total reconstructed temperature range in ODP Site 907.















