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## Middle-Late Pleistocene Eastern Mediterranean nutricline depth and coccolith preservation linked to Monsoon activity and Atlantic Meridional Overturning Circulation

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### Abstract :

The eastern Mediterranean Sea lies under the influence of high- and low-latitude climatic systems. The northern part of the basin is affected by Atlantic depressions and continental and polar air masses that promote intermediate and deep-water formation. The southern part is influenced by subtropical conditions and monsoon activity. Monsoon intensification results in enhanced freshwater discharge from the Nile River and other (now dry) systems along the North African margin. This freshwater influx into the Mediterranean Sea reduces surface water buoyancy loss. Disentangling the influences of these diverse climatic forcings is hindered by inherent proxy data limitations and by interactions between the climatic forcings. Here we use a wealth of published and new paleoclimate records across Termination II to understand the impacts of the higher latitude and subtropical/monsoon climate influences on coccolithophore ecology and holococcolith preservation in Aegean Sea sediment core LC21. We then use these findings to interpret coccolith assemblage variations at Ocean Drilling Program Site 967 (located nearby LC21, at the Eratosthenes Seamount) during multiple glacial-interglacial cycles across the Middle Pleistocene (marine isotopic stages 14–9). The LC21 analysis suggests that holococcolith preservation was enhanced during Heinrich Stadial 11 (~133 ka) and cold spell C26 (~119 ka). These two events have been previously linked to cold conditions in the North Atlantic and Atlantic Meridional Overturning Circulation weakening. We propose that associated atmospheric perturbations over the Mediterranean Sea promoted deep-water formation, and thus holococcolith preservation. Similarly, in the

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Middle Pleistocene (MIS 14-9) of Site 967, we observe temporal coincidence between ten episodes of enhanced holococcolith preservation and episodes of Atlantic Meridional Overturning Circulation slowdown. In Site 967, we also identified repeated fluctuations in placoliths and in *Florisphaera profunda*, which indicate nutricline depth variations. The development of a deep chlorophyll maximum is associated with the North Africa and wet phases, as recently observed using elemental proxy records at Site 967, during the deposition of sapropel layers. A further deep chlorophyll maximum development is identified during MISs 12 and 10, as a result of pycnocline and nutricline shoaling within the lower part of the photic zone due to glacial sea-level lowering and water mass transport reduction at both the Gibraltar and Sicily Straits. Finally, enhanced holococcolith preservation during cold/dry events is clearly correlated to weakened monsoon activity in both Africa and Asia.

### Highlights

► *F. profunda* in sapropel S5 is in line with maximum rates of  $\delta^{18}\text{O}$  Asian speleothems and with the  $\text{CH}_4$  overshoot in EDC; ► *F. profunda* DCM development in glacials, due to sea-level lowering that reduced water-mass transport through straits; ► Holococcolith enhanced preservation during cold spells, in response to AMOC slowdown and weakened monsoon activity;

**Keywords** : Coccolith, F, profunda, Holococcolith, Eastern Mediterranean, Middle Pleistocene, Monsoon

59

60 1 – Introduction

61 Paleoclimate reconstructions document the competing influence of southern *versus*  
62 northern climate systems on the hydrography and hydrology of the eastern  
63 Mediterranean Sea and its borderlands over a range of timescales (Emeis et al.,  
64 2000b; Grant et al., 2017, 2016; Lourens, 2004; Rohling et al., 2002b). During  
65 precession minima (Northern Hemisphere insolation maxima), the African monsoon  
66 intensified and shifted northward, with attendant enhancement of the freshwater  
67 release into the Mediterranean basin via large North African river systems and/or  
68 currently inactive wadis (Amies et al., 2019; Marino et al., 2009; Osborne et al.,  
69 2008; Rohling et al., 2002a; Rohling et al., 2015; van der Meer et al., 2007). This  
70 impacted the basin's hydrography and weakened or even shut down dense water  
71 formation, leading to oxygen starvation at depth and deposition of layers (sapropels)  
72 with elevated organic carbon concentrations (De Lange et al., 2008; Rohling et al.,  
73 2015; Rossignol-Strick et al., 1982). Millennial-scale climatic variations have been  
74 less well documented and appear to be associated with variations in the strength of  
75 the Atlantic Meridional Overturning Circulation (AMOC) (Grant et al., 2017, 2016;  
76 Stockhecke et al., 2016).

77

78 Coccolithophores are marine unicellular phytoplankton organisms living in the upper  
79 part of the water column. The ecology of coccolithophore species shows a strong  
80 sensitivity to modern gradients within the Mediterranean Sea and different species  
81 thrive in different areas, mainly in response to West-East temperature and nutrient  
82 gradients, water column dynamics, and meso-scale oceanographic features (Bonomo  
83 et al., 2012; D'Amario et al., 2017; Knappertsbusch, 1993; Oviedo et al., 2015). In  
84 the sedimentary archive, calcite coccolithophore remains (coccoliths) have been used  
85 successfully to infer orbital and suborbital variations in climate, productivity, and  
86 nutricline depth in oceans and marginal seas (Beaufort et al., 1997; Flores et al.,  
87 1997; Incarbona et al., 2013, 2010a; Marino et al., 2008; Molfino and McIntyre,

88 1990a; Rogalla and Andrulleit, 2005). In the eastern Mediterranean Sea, coccolith-  
89 based paleoenvironmental reconstructions have been mostly aimed at assessing the  
90 shallow *versus* deep position of the nutricline within the photic layer and its  
91 relationship with the basin's freshwater budget, water mass circulation, and deep-sea  
92 ventilation during sapropel deposition (e.g., Grelaud et al., 2012). These studies attest  
93 to the development of a deep chlorophyll maximum (DCM) while organic carbon-  
94 rich layers were accumulating on the oxygen-starved eastern Mediterranean seafloor  
95 (Castradori, 1993; Giunta et al., 2003; Grelaud et al., 2012; Incarbona et al., 2019,  
96 2011; Incarbona and Di Stefano, 2019; Maiorano et al., 2013; Negri et al., 1999;  
97 Principato et al., 2006; Triantaphyllou et al., 2009b, 2009a), corroborating findings  
98 based on other marine planktonic groups (Kemp et al., 1999; Meier et al., 2004;  
99 Rohling and Gieskes, 1989).

100

101 Here we present new data that complement a previous dataset of coccolith  
102 assemblages from south-eastern Aegean Sea core LC21 (Grelaud et al., 2012), across  
103 the penultimate glacial termination (termination II, T-II) and the last interglacial  
104 period, with a precise, radiometrically constrained chronology (Grant et al., 2012).  
105 This allows comparison of LC21 “coccolith proxies” with time series of  
106 palaeoclimate variability in the monsoon and the North Atlantic region (Cheng et al.,  
107 2009; Hodell et al., 2013), as well as atmospheric methane (CH<sub>4</sub>) concentrations. Our  
108 combined dataset is probabilistically evaluated to decipher the amplitude and timing  
109 of change by quantitatively assessing the impact of chronological, analytical, and  
110 proxy uncertainties. We use this analysis as a proof of concept for new, highly  
111 resolved coccolith data from Ocean Drilling Program (ODP) Site 967 from the  
112 Eratosthenes Seamount, South of Cyprus, within the Nile Delta Basin province  
113 (Emeis et al., 1996). The new ODP 967 time series spans, at centennial-scale  
114 resolution, three glacial/interglacial cycles of the Middle Pleistocene, from glacial  
115 Marine Isotope Stage (MIS) 14 to interglacial MIS 9. Collectively, our new data and  
116 analyses provide insights into climate variability at orbital and sub-orbital timescales

117 during both glacial and interglacial periods, complementing a wealth of existing  
118 knowledge of the intervals of sapropel deposition. Specifically, we explore  
119 modifications in nutrient dynamics and holococcolith preservation during the Middle  
120 Pleistocene. These changes are compared with recently acquired variations in  
121 elemental abundances, elemental ratios, and climate indices for ODP Site 967  
122 (Section 6.3) that portray the alternation of wet and dry North Africa periods at both  
123 orbital and sub-orbital timescales (Grant et al., 2017). Finally, we centre on the  
124 correlation between holococcolith preservation, AMOC, and boreal monsoon activity  
125 (both in Africa and in a wider Asian context) to assess: (i) the atmospheric impact of  
126 continental/polar air outbreaks on the eastern Mediterranean deep-sea ventilation and  
127 seafloor calcite preservation during cold stadials; and (ii) impact of millennial-scale  
128 atmospheric perturbations on the eastern Mediterranean Sea.

129

## 130 2 – Environmental Setting

131 A negative hydrological balance maintains a robust antiestuarine thermohaline  
132 circulation pattern in the Mediterranean Sea (Robinson and Golnaraghi, 1994).  
133 Surface Atlantic water (Modified Atlantic Water – MAW) enters the Mediterranean  
134 Sea and occupies the uppermost 100-200 m depth (Millot, 1999; POEM group,  
135 1992). MAW spread out into the eastern Mediterranean Sea *via* the Mid-  
136 Mediterranean Jet and reaches the Eratosthenes Seamount where a quasi-permanent  
137 anticyclonic summer circulation exists, that is known as the Shikmona Gyre  
138 (Malanotte-Rizzoli et al., 2014; Pinardi and Masetti, 2000; POEM group, 1992).  
139 Levantine Intermediate Water (LIW) formation takes place close to the Eratosthenes  
140 Seamount (Ovchinnikov I.M., 1984; POEM group, 1992). Eastern Mediterranean  
141 Deep Water (EMDW) forms in the Adriatic and Aegean Sea (Fig. 1) due to winter  
142 heat loss under the influence of intense Bora and Vardar winds (Malanotte-Rizzoli et  
143 al., 2014; POEM group, 1992).

144

145 Today, the eastern Mediterranean Sea is one of the most oligotrophic areas globally.  
146 Primary productivity is more than three times lower than in the western basin, in  
147 accordance with a similar nutrient depletion trend (Krom et al., 2010, 1991). Primary  
148 production is also seasonally controlled: higher productivity occurs in winter, after  
149 winter convection, while severe oligotrophy occurs in summer due to deepening of  
150 the thermocline and nutricline (Allen et al., 2002; Klein and Coste, 1984). The  
151 Eratosthenes region is classified as a no-bloom area by satellite-based chlorophyll  
152 analyses. The severe late spring-summer oligotrophy is followed by relatively higher  
153 chlorophyll values in winter (D'Ortenzio and Ribera d'Alcalà, 2009).

154  
155 High- and low-latitude climate systems impact on the eastern Mediterranean Sea. In  
156 summer, subtropical high-pressure conditions cause stable dry and warm conditions  
157 throughout the Mediterranean area (Lionello, 2012). In winter, the North African  
158 subtropical high pressure is shifted southward, and cold and dry polar/continental air  
159 outbreaks occur into the eastern Mediterranean from the north (Lionello, 2012;  
160 Rohling et al., 2019, 2015). Expansion of the Siberian High is an important driver for  
161 advection of cold air toward the eastern Mediterranean. Intensification of the Siberian  
162 High during Holocene rapid climatic changes is thought to be an important driver of  
163 surface water cooling and atmospheric perturbations in the central-eastern  
164 Mediterranean Sea (Incarbona et al., 2008; Rohling et al., 2002b; Rohling et al.,  
165 2019). Prolonged and strengthened polar/continental air outbreaks promote sea  
166 surface heat loss and deep-water formation (Josey et al., 2011; Rohling et al., 2019;  
167 Velaoras et al., 2017).

168

### 169 3 – Material and Methods

#### 170 3.1 - Sediment cores

171 ODP Site 967 (34°04.098'N, 32°43.523'E, 2,553 m water depth) is located at the  
172 base of the northern slope of the Eratosthenes Seamount, a structure that emerges  
173 from the Nile Delta Cone (Fig. 1). Sediments are dominated by horizontal and sub-

174 horizontal brown and light gray, bioturbated nannofossil ooze and nannofossil clay,  
175 intercalated with sapropels and turbidites (Emeis et al., 1996). Specifically, there are  
176 five sapropel layers that show signs of moderate bioturbation (S13, S12, S11, b and  
177 S10) in the studied interval (Emeis et al., 1996), while no turbidites and/or other  
178 sedimentary disturbances were identified (Konijnendijk et al., 2014).

179  
180 Sediment core LC21 (35°40'N, 26°35'E; 1,522 m water depth) was recovered in  
181 1995 by *RV Marion Dufresne* in the southeastern Aegean Sea (Fig. 1). Lithology  
182 consists of hemipelagic sediments, with visible sapropels (S1, S3, S4, and S5) and  
183 tephra layers (Grant et al., 2016; Satow et al., 2015).

184

### 185 3.2 - Coccolith data

186 We carried out coccolith analyses at ODP Site 967 at 1 cm resolution between 14.80  
187 and 21.49 m composite depth (mcd) (Emeis et al., 1996), for a total of 668 samples,  
188 which were analysed with a polarized microscope at ~ 1000× magnification. Rippled  
189 smear slides were prepared following standard procedures (Bown and Young, 1998).  
190 On average 350 specimens were identified following the taxonomic concepts for  
191 living coccolithophores of Young et al. (2003) and Jordan et al. (2004). Taxa were  
192 grouped as ‘placoliths’, ‘miscellaneous group’, ‘upper photic zone (UPZ) group’,  
193 ‘lower photic zone (LPZ) group’ and ‘holococcoliths’ (Di Stefano and Incarbona,  
194 2004; Incarbona et al., 2010). Placoliths include small placoliths, small  
195 *Gephyrocapsa*, *Gephyrocapsa muellerae*, and *Gephyrocapsa oceanica*. The  
196 miscellaneous group includes *Helicosphaera* spp., *Coccolithus pelagicus*,  
197 *Syracosphaera histrica*, *Pontosphaera* spp., *Calcidiscus leptoporus*, *Coronosphaera*  
198 spp., *Braarudosphaera* spp., *Oolithotus fragilis*, *Calciosolenia* spp., and specimens of  
199 all the other species. UPZ group includes *Syracosphaera pulchra*, *Umbellosphaera*  
200 spp., *Discosphaera tubifera*, *Rhabdosphaera* spp., *Umbilicosphaera* spp., and  
201 *Ceratolithus* spp.. LPZ group comprises *F. profunda*, which dominates the group,  
202 with negligible amounts of *Gladiolithus flabellatus* in a few samples. Holococcoliths

203 include all the coccoliths produced during the haploid life-cycle stage (Incarbona et  
204 al., 2019).

205

206 The holococcolith analysis at Aegean Sea core LC21 was carried out by observation  
207 with a polarized microscope at about 1000× magnification, following the standard  
208 procedure for rippled smear slides (Bown and Young, 1998). Holococcolith  
209 percentage values were evaluated on 102 samples *versus* heterococcoliths specimens,  
210 examining about 500 coccoliths. *Florisphaera profunda* percentage values at LC21  
211 Aegean Sea core were presented before (Grelaud et al., 2012), following the same  
212 procedure adopted in this study, and that earlier dataset is available at  
213 <https://doi.pangaea.de/10.1594/PANGAEA.805357>.

214

### 215 3.3 - Statistical analysis of the time series

216 We use a Monte Carlo approach based on MATLAB coding (Marino et al., 2015;  
217 Thirumalai et al., 2016) to: (i) stack the  $\delta^{18}\text{O}$  time series for different stalagmites  
218 (SB11, SB23, and SB25) from Sanbao Cave, China, that cover T-II and the last  
219 interglacial period (Cheng et al., 2009); (ii) calculate rates of  $\delta^{18}\text{O}$  change in the  
220 Sanbao Cave stalagmites; (iii) probabilistically evaluate the chronological (Bazin et  
221 al., 2013; Veres et al., 2013) and measurement uncertainties associated with the time  
222 series of atmospheric methane ( $\text{CH}_4$ ) concentrations from EPICA Dome C (EDC)  
223 (Loulergue et al., 2008); and (iv) probabilistically evaluate chronological and  
224 counting uncertainties associated with the *F. profunda* (Grelaud et al., 2012) and new  
225 holococcolith records for core LC21.

226

227 Speleothem  $\delta^{18}\text{O}$  time series from Sanbao Cave have been probabilistically evaluated  
228 and stacked across the 140-110 ka interval. Input data for the Monte Carlo routine are  
229 sample ages with  $1\sigma$  uncertainties, and speleothem  $\delta^{18}\text{O}$  with  $1\sigma$  uncertainties (Cheng  
230 et al., 2009). For each stalagmite (SB11, SB23, and SB25), individual data points are  
231 then separately and randomly sampled 10,000 times within their chronological and



232  $\delta^{18}\text{O}$  uncertainties. The chronological uncertainties are evaluated using a random  
233 walk Monte Carlo routine that employs a Metropolis–Hastings approach to reject  
234 steps in the random walk that will result in age reversals (Rodríguez-Sanz et al.,  
235 2017). That is, we imposed a stratigraphic constraint (monotonic increase of age with  
236 depth, analogous to Rohling et al., 2014) to the data that are measured in a  
237 stratigraphically coherent manner along individual stalagmites. All realizations are  
238 then linearly interpolated on an equally spaced time scale and stacked to produce  
239 10,000 speleothem  $\delta^{18}\text{O}$  stacks with and without a correction that probabilistically  
240 quantifies the impacts of the global  $^{18}\text{O}$  enrichment/depletion (Schrag et al., 2002)  
241 associated with ice-volume changes (Grant et al., 2012). Next, we calculated the 1<sup>st</sup>  
242 time derivative, to obtain rates of speleothem  $\delta^{18}\text{O}$  change for each of the 10,000 ice-  
243 volume corrected ‘stacks’. This is done by smoothing each realization using 0.75 kyr  
244 Gaussian window to remove sample-to-sample noise, which would result in spurious  
245 jumps in the estimated rates of change, and by then differentiating the smoothed  
246 realizations. Monte Carlo analysis of the EDC methane record and of the eastern  
247 Mediterranean coccolith time series are performed using the same approach. Finally,  
248 the 10,000 iterations of each of these time series are linearly interpolated and the  
249 probability distribution assessed at each time step, thereby determining the 68%  
250 (16<sup>th</sup>–84<sup>th</sup> percentile) and 95% (2.5<sup>th</sup>–97.5<sup>th</sup> percentile) probability intervals and the  
251 probability maximum (PMAX, modal value) of the data.

252

#### 253 4 – Coccolith taxon ecology

254 Placoliths are so-called ‘r-strategist taxa’ that rapidly exploit nutrients in the photic  
255 zone (Baumann et al., 2005; Young, 1994). In the eastern Mediterranean Sea,  
256 placoliths bloom in winter, after nutrient fertilization (Di Stefano et al., 2011;  
257 Knappertsbusch, 1993; Triantaphyllou et al., 2004; Ziveri et al., 2000).

258 *Florisphaera profunda* is a deep photic zone species that indicates the occurrence of a  
259 deep nutricline (McIntyre and Molino, 1996; Molino and McIntyre, 1990a). In low-  
260 and middle-latitude open ocean regions, the relative abundance of this species is

261 anticorrelated with primary productivity (Beaufort et al., 2001, 1997; Hernández-  
262 Almeida et al., 2019).

263

264 In the Mediterranean Sea, except for a limited area in the central part of the basin,  
265 there is no apparent relationship between *F. profunda* abundance and satellite-  
266 observed (surface) primary productivity levels (Hernández-Almeida et al., 2019;  
267 Incarbona et al., 2008). However, *F. profunda* has been generally used to decipher  
268 water column stratification and development of a deep nutricline due to monsoon-  
269 fuelled freshwater discharge in the eastern Mediterranean and entrainment of  
270 nutrients into the lower photic zone from below (Castradori, 1993; Grelaud et al.,  
271 2012; Incarbona et al., 2019; Negri et al., 1999; Triantaphyllou et al., 2009b). This  
272 occurs through the development of a distinct DCM in the eastern Mediterranean during  
273 sapropel deposition. DCM development resulted from nutrient entrainment into the  
274 photic zone from relatively buoyant intermediate waters that likely originated from  
275 the Adriatic Sea, while the volume of MAW inflow through the Sicily Strait was  
276 reduced (Myers et al., 1998; Rohling, 1991b; Rohling and Gieskes, 1989).

277 Accordingly, relative abundances of placoliths and *F. profunda*, or their ratio, provide  
278 a robust indication of the depth of the nutricline in the eastern Mediterranean Sea.  
279 Specifically, presence (absence) of placoliths (*F. profunda*) in the coccolith  
280 assemblage reflects a shallow (deep) nutricline (Di Stefano et al., 2015; Flores et al.,  
281 2000; Molino and McIntyre, 1990b).

282

283 The UPZ group consists of so-called ‘K-strategist taxa’, specialized to exploit a  
284 minimum uptake of nutrients in surface water (Bazzicalupo et al., 2020; Di Stefano  
285 and Incarbona, 2004; Young, 1994). Miscellaneous taxa reflect the lack of either an  
286 apparent distinctive ecological preference or of an understanding of their ecological  
287 preferences, with a potential weak K-strategy (Incarbona et al., 2010; Young, 1994).  
288 Holococcoliths prefer dwelling in warm, oligotrophic surface water and are abundant  
289 in the eastern Mediterranean Sea (D’Amario et al., 2017; Kleijne, 1991;

290 Knappertsbusch, 1993; Dimiza et al., 2015; Oviedo et al., 2015; Skampa et al., 2019).  
291 Poor preservation of holococcoliths in sapropel S1 sediments was firstly recognised  
292 by Crudeli et al. (2006) and was later confirmed across the whole eastern  
293 Mediterranean, included the Eratosthenes Seamount (Incarbona et al., 2019;  
294 Incarbona and Di Stefano, 2019) and Pliocene sapropel layers in sedimentary  
295 sequences on Cyprus (Athanasidou et al., 2015). Importantly, potential preservation of  
296 tiny holococcolith crystals improves when dense water renewal ensures vigorous  
297 ventilation/oxygenation of the seafloor, even during short reventilation episodes that  
298 “interrupt” sapropel deposition (Incarbona et al., 2019).

299

## 300 5 –Chronology

301 The original shipboard age model by Sakamoto et al. (1998) at ODP Site 967 has  
302 since been revised, because of some inconsistent tuning to orbital insolation  
303 (Konijnendijk et al., 2014; Lourens et al., 2001). More recently, Grant et al. (2017)  
304 developed a monsoon runoff (sapropel) proxy from the principal component analysis  
305 of sedimentary elemental data in ODP Site 967 that they tuned to precession minima.  
306 They use a zero phase lag, which relies upon the assumption that little or no lag exists  
307 when monsoon maxima did not immediately follow a high-amplitude glacial  
308 termination (Grant et al., 2016; Lourens et al., 2001). In this study, we adopt the  
309 chronology by Grant et al. (2017) for the coccolith data. Sedimentation rates between  
310 MIS 14 and MIS 9 range from 1.4 cm kyr<sup>-1</sup> to 3.9 cm kyr<sup>-1</sup>, implying that the mean  
311 sampling resolution of our coccolith time series is about 340 years.

312 The LC21 chronology follows Grant et al. (2012) (see section 6.1). The mean  
313 sedimentation rate is about 4.4 cm kyr<sup>-1</sup>, with a mean sampling resolution of about  
314 225 years.

315

## 316 6 – Results and Discussion

### 317 6.1 – Coccolith assemblages in Aegean Sea core LC21

318 *Florisphaera profunda* (Grelaud et al., 2012) and holococcoliths across T-II and the  
319 last interglacial in south-eastern Aegean core LC21 are used to evaluate their  
320 relationship with water column stratification and deep-sea ventilation, respectively.  
321 Several features make this core and the timespan that we target ideal to provide a  
322 ‘proof of concept’ for the interpretation of the new records from ODP Site 967 that  
323 spans multiple glacial-interglacial cycles. First, core LC21 has a radiometrically  
324 constrained chronology across T-II and the last interglacial period (Grant et al.,  
325 2012). This has been corroborated through comparison with western Mediterranean  
326 sediment cores and speleothem records, and it is consistent with the latest ice core  
327 chronology across the study interval (Marino et al., 2015). Second, prominent  
328 episodes of climate change punctuated T-II, including a multi-millennial Heinrich  
329 stadial associated with major freshwater discharge into the North Atlantic and AMOC  
330 slowdown (Deaney et al., 2017; Marino et al., 2015). Third, during the last  
331 interglacial period, an organic rich layer (sapropel S5) was deposited in the eastern  
332 Mediterranean under persistently anoxic or even euxinic conditions (Marino et al.,  
333 2007; Rohling et al., 2015, 2006). Sapropel S5 conditions developed in response to  
334 extensive monsoon-fuelled freshwater discharge along the North African Margin  
335 (Amies et al., 2019; Osborne et al., 2008; Rohling et al., 2002a; Rohling et al., 2004)  
336 that reduced surface salinity (van der Meer et al., 2007) and produced strong water  
337 column stratification (Amies et al., 2019; Grelaud et al., 2012; Marino et al., 2007;  
338 Rohling et al., 2006).

339

340 In Figure 2a-c we show *F. profunda* relative abundances from core LC21 (Grelaud et  
341 al., 2012) with upper mixed layer depth fluctuations reconstructed for the same core  
342 (Amies et al., 2019), and with the contemporaneous EDC time series of atmospheric  
343 CH<sub>4</sub> concentrations and the Sanbao Cave  $\delta^{18}\text{O}$  stack, which are thought to reflect  
344 fluctuations in boreal monsoon intensity and attendant changes in the spatial coverage  
345 of tropical wetlands (Cheng et al., 2016, 2009, 2006; Möller et al., 2013; Petrenko et  
346 al., 2009). We present the *F. profunda* time series (Grelaud et al., 2012) on the

347 radiometrically constrained chronology of Grant et al. (2012), as natural logarithm of  
348 the original data. Within uncertainties of the various records, we note a strong  
349 similarity between the LC21 *F. profunda* record and variations of both Sanbao Cave  
350 speleothem  $\delta^{18}\text{O}$  (Fig. 2a) and EDC  $\text{CH}_4$  (Fig. 2b). Notably, a distinct *F. profunda*  
351 peak at  $\sim 129$  ka appears contemporaneous with upper mixed layer thinning, with a  
352 maximum in the rates of Sanbao Cave  $\delta^{18}\text{O}$  change and with the  $\text{CH}_4$  overshoot in  
353 EDC. This suggests: (i) synchronous intensification of the African and Asian  
354 monsoons at the onset of the last interglacial period, in line with what has been  
355 documented for the early Holocene (Fleitmann et al., 2003; Marino et al., 2009;  
356 Nicholson et al., 2020; Tierney et al., 2008); and (ii) a rapid increase in freshwater  
357 discharge into the eastern Mediterranean at the onset of the last interglacial monsoon  
358 maximum, quantified as up to  $\sim 8.8$  times the modern pre- Aswan Nile discharge and  
359 responsible for the most intense thinning of the upper summer mixed layer (Amies et  
360 al., 2019). Observation (ii) is particularly relevant because it alludes to the influence  
361 of the rates of monsoon intensification on stratification in the eastern Mediterranean.  
362 When large amounts of monsoon-fuelled freshwater are rapidly added to the basin,  
363 the strong evaporative climate of the Levant cannot keep up with sea-surface dilution  
364 (Rohling et al., 1991b) and the water column becomes strongly stratified (Rohling  
365 and Gieskes, 1989; Rohling et al., 2006; Marino et al., 2007; Athanasiou et al., 2015,  
366 2017; Amies et al., 2019), causing shoaling of the pycnocline, the nutricline to be  
367 positioned at the base of the photic layer and the attendant development of a  
368 pronounced DCM.

369

370 In Figure 2d-f, LC21 holococcolith data are compared with North Atlantic and  
371 western Mediterranean Sea records. It is evident that there is no or poor preservation  
372 of holococcoliths during sapropel S5 (Fig. 2e). Peaks of holococcoliths below S5  
373 correlate with low alkenone-derived SSTs in the Alboran Sea (Martrat et al., 2014)  
374 (Fig. 2d) and with variations in AMOC strength proxies (Figs. 2e,f) from the Iberian  
375 Margin. Specifically,  $\log(\text{Ca}/\text{Ti})$ , benthic foraminiferal  $\delta^{13}\text{C}$ , and  $\text{C}_{26}\text{OH}$  ratios

376 (Hodell et al., 2015; Martrat et al., 2007) unequivocally indicate that AMOC had  
377 collapsed during Heinrich event HS11 (Böhm et al., 2015); we find that, at the same  
378 time, holococcolith preservation was enhanced. A similar relationship is evident  
379 above sapropel S5, especially with C<sub>26</sub>OH ratio data (Fig. 2f), and may be correlated  
380 with North Atlantic cold event C26 (Oppo et al., 2006, 2001; Tzedakis et al., 2018).  
381 Coupled ocean-atmosphere hindcasts suggest that the AMOC slowdown/shutdown  
382 may have propagated through the Mediterranean Sea in the form of major cooling  
383 and intense atmospheric perturbations (Manabe and Stouffer, 1997; Vellinga and  
384 Wood, 2002). Both cooling and atmospheric perturbations are major prerequisites for  
385 surface water buoyancy loss and deep-water formation, explaining enhanced  
386 Mediterranean bottom water ventilation during Heinrich and Stadial events in the last  
387 glacial, based on benthic foraminifera  $\delta^{13}\text{C}$  and alcohol index records (Cacho et al.,  
388 2000; Sprovieri et al., 2012; Toucanne et al., 2012). Our new results from the Aegean  
389 Sea explicitly link holococcolith preservation to Heinrich and Stadial events in  
390 response to deep-water formation and seafloor ventilation increases in the  
391 Mediterranean Sea during those events.

392

## 393 6.2 – Coccolith assemblages at ODP Site 967

394 At ODP Site 967, coccolith distribution patterns are compared (Figure 3) with: (i)  
395 June 21<sup>st</sup> insolation at 65°N (Laskar et al., 2004); (ii) the benthic  $\delta^{18}\text{O}$  composite  
396 record from ODP Sites 967 and 968 (Konijnendijk et al., 2015); and (iii) the LR04  
397 benthic  $\delta^{18}\text{O}$  stack (Lisiecki and Raymo, 2005). Overall, coccolith assemblages are  
398 dominated by placoliths, with percentages between 25 and 98% (average = 70%, Fig.  
399 3D). The deep photic zone species *F. profunda* features high-amplitude fluctuations  
400 between intervals in which it is barely occurring (1%) and intervals in which it  
401 becomes the dominant (up to 74%), ~~and an average of 26%~~ (Fig. 3E). Placoliths'  
402 peak (low) abundances occur when *F. profunda* percentages are at a minimum  
403 (maximum), as highlighted by the pronounced anticorrelation ( $R^2= 0.95$ ,  $n = 668$ )  
404 displayed in Figure 4.

405

406 The observed alternating dominance of the placoliths and *F. profunda* (see above) at  
407 ODP Site 967 suggests that between MIS 14 and MIS 9 the upper water column in  
408 the easternmost Mediterranean Sea repeatedly switched between dominant winter-  
409 induced fertilization (placoliths' peaks, shallow nutricline), similar to today's winter  
410 conditions (Knappertsbusch, 1993), and a predominantly DCM-focused productivity  
411 (*F. profunda*'s peaks, deep nutricline) during both glacial and interglacial periods.  
412 Shoaling of the pycnocline, which promoted a deep nutricline (DCM), in association  
413 with intensifications of the North African monsoon and sea-level lowering (Rohling  
414 and Gieskes, 1989; Rohling, 1991a, 1991b) is the most plausible explanation for the  
415 peak abundance of *F. profunda* at ODP Site 967 during sapropels and glacial periods,  
416 respectively. Accordingly, *F. profunda* would be particularly sensitive to nutrient  
417 (re)distribution within the photic zone, with intervals of positive shifts in the basins  
418 freshwater budget (monsoon maxima, Rohling, 1991b) and reduced water exchange  
419 at straits (glacial lowstands, Rohling, 1991a) both leading to enhanced stratification  
420 in the upper water column, shoaling of the pycnocline, and development of a  
421 nutricline at the based of the photic layer. This conceptual framework indicated by  
422 box-model calculations (Rohling, 1991a,b) provides an explanation for the *F.*  
423 *profunda* peaks both in sapropel layers (e.g., S12, S11, b, S10) and during MIS 12  
424 and MIS 10 glacial periods (see also Section 6.3).

425 The remaining three coccolith groups at Site 967 are largely subordinate. Low  
426 abundance of UPZ taxa (0.0-5.4%, 1.4% on average, Fig. 3F) and Miscellaneous taxa  
427 (0.0-11.1%, 1.2% on average, Fig. 3G) is unexpected in the severe oligotrophy of the  
428 eastern Mediterranean Sea, especially for UPZ taxa that include dominant  
429 coccolithophore species in summer/autumn (Knappertsbusch, 1993; Malinverno et  
430 al., 2009; Oviedo et al., 2015). However, living coccolithophore surveys show that  
431 winter production (placolith blooming) is about an order of magnitude higher than  
432 summer production, thereby explaining the apparent ecological contradiction in taxa  
433 proportions (Knappertsbusch, 1993).

434 Holococcolith percentage values range between 0.0 and 20.8%, 1.9% on average  
435 (Fig. 3H). As was the case in late Quaternary sapropels, tiny holococcoliths are again  
436 not preserved in sapropel layers, but we also note that that poor preservation extends  
437 far beyond sapropel layers.

438

439 6.3 – Comparison between coccoliths, element ratios and climatic indices at ODP  
440 Site 967

441 *Florisphaera profunda* and holococcolith distribution patterns at ODP Site 967 (Figs.  
442 5A-B) are compared with sedimentary elemental ratios and climatic indices from the  
443 same sedimentary sequence (Grant et al., 2017). A principal component analysis  
444 carried out on elemental proxies by these authors highlighted that principal  
445 components PC1 (not shown) and PC2 (Fig. 5D) account for 79% of variance and  
446 reflect terrigenous input and sapropel deposition (enhanced monsoon runoff),  
447 respectively. Moreover, aeolian dust fluxes (Fig. 5E) and a North Africa  
448 humidity/aridity index (Fig. 5F) were calculated and are also compared with  
449 coccolith abundance fluctuations.

450

451 Intensification of East African monsoon precipitation coincided with northward  
452 displacement of the Intertropical Convergence Zone (ITCZ) and subsequent  
453 intensification of precipitation over the catchment basins of the Nile and other rivers,  
454 which fuelled enhanced freshwater discharge along the wider North African margin  
455 into the eastern Mediterranean (Ehrmann et al., 2016; Rohling et al., 2002a; Rohling  
456 et al., 2015). *Florisphaera profunda* proliferates because it benefits from the  
457 nutricline positioned in deep photic zone and the establishment of a DCM  
458 (Castradori, 1993; Gironé et al., 2013; Grelaud et al., 2012; Incarbona et al., 2011;  
459 Negri et al., 1999), following the rationale outlined above (Myers et al., 1998;  
460 Rohling, 1991a; Rohling and Gieskes, 1989). This scenario has been described for  
461 eastern Mediterranean sapropels and is further supported by the coupling of the *F.*  
462 *profunda* signal and enhanced humidity in North Africa that leads to enhanced



463 monsoon runoff into the eastern Mediterranean, especially during S12, S11, b and  
464 S10 (Fig. 5). Also evident is decoupling between *F. profunda* and the  
465 humidity/aridity index, for instance during glacial sapropel S13 and during sapropel  
466 layer b. This suggests that the climatic indices at ODP Site 967 reflect increased  
467 rainfall over North Africa and Sahara, without sufficient northward monsoon  
468 penetration that determines the intensity of monsoon-related runoff into the eastern  
469 Mediterranean Sea (Grant et al., 2017). Also, different nutrient dynamics may have  
470 developed during the glacial sapropel S13, with surface fertilization that supports  
471 placolith-bearing species competition.

472  
473 However, the coccolith record at Site 967 suggests that *F. profunda* increases are a  
474 recurring feature of the record that is not necessarily associated with the deposition of  
475 organic-rich layers deposition on the eastern Mediterranean seafloor, especially in  
476 glacial episodes (Fig. 5A). The Ba/Al signal indicates that many sapropel layers have  
477 been partially oxidized (Fig. 5G), so that their currently visible extents do not  
478 represent the original thickness of anoxic sediments. Yet, we argue that *F. profunda*  
479 peaks are not exclusively linked to the environmental changes associated with  
480 sapropel formation. Positive *Florisphaera profunda* peaks without a corresponding  
481 sapropel layer (be it visible, or oxidized) are evident in all eastern Mediterranean  
482 records that span sufficiently long time intervals (Castradori, 1993; Giunta et al.,  
483 2003; Maiorano et al., 2013; Negri et al., 1999; Triantaphyllou et al., 2010). The  
484 occurrence of *F. profunda* during glacial periods identifies a second mode of DCM  
485 development in the eastern Mediterranean, as proposed on the basis of planktonic  
486 foraminiferal assemblages (Rohling and Gieskes, 1989) and modeling (Myers et al.,  
487 1998; Rohling, 1991a). Again, the DCM development would be driven by the  
488 pycnocline and nutricline shoaling within the lower part of the photic zone. But, for  
489 glacials, the eustatic sea-level drop (Fig. 5C) would have been the main trigger  
490 mechanism, after reducing water mass transport at both Gibraltar and Sicily Straits  
491 and ultimately shoaling the pycnocline and nutricline depth up to ~ 80 m (Myers et

492 al., 1998; Rohling, 1991a). However, the scattered *F. profunda* abundance signal in  
493 MISs 12 and 10 suggests that other factors may operate in conjunction with sea-level  
494 fall, for reducing water transport across the Gibraltar and Sicily Straits. Among these,  
495 less frequent and intense northern outbreaks in deep water production sites and the  
496 inflow of low-density meltwater from the Atlantic Ocean may have weakened the  
497 Mediterranean thermohaline circulation and may have caused transient reductions in  
498 the water transport at straits, like during last glacial cold spells (Sierro et al., 2005;  
499 Sprovieri et al., 2012; Toucanne et al., 2012; Azibeiro et al., 2021).

500

501 Holococcoliths are made of small calcite rhombohedra, arranged in different patterns.  
502 They are the most vulnerable coccoliths to selective dissolution (Roth and Coulbourn,  
503 1982). Comparison between the new ODP 967 holococcolith record and the  
504 humidity/aridity index (Figs. 5B, F) shows strong similarities throughout the time  
505 span studied, which clearly point to the dissolution of haploid-life calcite remains at  
506 the Erathostenes seamount during humid phases. This agrees with the notion that  
507 surface buoyancy gain by freshwater river discharge negatively impacted deep-water  
508 formation in the eastern Mediterranean Sea, which enhanced organic carbon  
509 preservation (De Lange et al., 2008; Myers et al., 1998; Rohling et al., 2015) and,  
510 thus, worsened holococcolith preservation, like during sapropel S1 (Crudeli et al.,  
511 2006; Incarbona et al., 2019; Incarbona and Di Stefano, 2019) and sapropel S5 (Fig.  
512 2, this study).

513

514 It is worth noting that the three major aeolian dust peaks during MIS 13-12 (Fig. 5E)  
515 did not match with increasing holococcolith preservation but fall within ‘no  
516 preservation’ intervals. Aeolian dust peaks are associated with weakened monsoon  
517 activity and North Africa dry periods, as seen from the Ti/Al ratio (Konijnendijk et  
518 al., 2015; Lourens et al., 2001; Wehausen and Brumsack, 2000; Ziegler et al., 2010),  
519 and would imply a lower freshwater input into the eastern Mediterranean Sea.

520 Ideally, these conditions would enhance deep water formation, reduce organic matter

521 preservation on the seafloor and increase preservation of holococcolith calcite.  
522 However, dust accumulation in marine cores depends on wind strength and direction  
523 (Moulin et al., 1997; Zabel et al., 1999). Thus, aeolian dust peaks are not necessarily  
524 tied to cooling and atmospheric perturbations that, for instance during the latest  
525 Quaternary, led to enhanced Mediterranean bottom water ventilation in coincidence  
526 of glacials and stadials (Cacho et al., 1999; 2000; Sprovieri et al., 2012; Toucanne et  
527 al., 2012).

528

529 6.4 – AMOC slowdown, holococcolith preservation and monsoon weakening  
530 In Figure 6, North Atlantic geochemical records (Fig. 6A-B), Mediterranean  
531 holococcolith data (Fig. 6C), and oxygen isotopes of China speleothems (Fig. 6D) are  
532 plotted using their own original age models (Cheng et al., 2016; Grant et al., 2017;  
533 Hodell et al., 2015; Martrat et al., 2007). The grey boxes used for correlation are  
534 drawn and link correlative events in these various Northern Hemisphere records.  
535 Records shown in Figure 6 help with outlining a concept of atmosphere/ocean  
536 interactions that resulted in the correlation between Northern Hemisphere climate  
537 variability and surface water ecosystem modifications and seafloor diagenesis in the  
538 eastern Mediterranean.

539

540 The correlation boxes in Figure 6 are drawn assuming that AMOC  
541 slowdown/shutdown caused an atmospheric perturbation that impacted a vast area of  
542 the northern Hemisphere, including the eastern Mediterranean Sea, East African and  
543 Asian monsoon sites (Vellinga and Wood, 2002). The log (Ca/Ti) record from the  
544 Iberian Margin (Fig. 6B) is a proxy for millennial-scale variability (Hodell et al.,  
545 2015): minima indicate stadial/Heinrich phases during which the AMOC was  
546 severely weakened or collapsed (McManus et al., 2004, 1999). Previous studies based  
547 on  $\delta^{13}\text{C}$ , alcohol index and sortable silt records support the hypothesis that  
548 Mediterranean bottom water ventilation at least in the western sub-basin was more  
549 intense during glacial periods and stadial events (Cacho et al., 2000, 1999; Frigola et

550 al., 2008; Sprovieri et al., 2012; Toucanne et al., 2012) and strengthened  
551 Mediterranean outflow into the Gulf of Cadiz and in the Iberian Margin (Sierro et al.,  
552 2020). Simultaneous enhancement of EMDW ventilation would have enhanced  
553 holococcolith preservation, as observed below and above sapropel S1 (Incarbona et  
554 al., 2019; Incarbona and Di Stefano, 2019) and during HS11 and C26 in the Aegean  
555 Sea (this study, Fig. 2). The physico-chemical processes in the seafloor microsystem  
556 by which tiny holococcolith calcite rhombohedra are preferentially preserved under  
557 oxic conditions is not clear yet. Incarbona et al. (2019b) hypothesized a possible  
558 detrimental action of organic acid produced by bacteria under a dysoxic/anoxic state  
559 on the water/sediment interface, in analogy with results from modern surveys in the  
560 Gulf of California (Ziveri and Thunell, 2000). However, specific studies are needed  
561 to better understand the processes involved.

562

563 The link between AMOC slowdown/shutdown and East African, Indian, and Asian  
564 monsoon weakening is well-established (Deplazes et al., 2014; Porter and Zhisheng,  
565 1995; Rohling et al., 2002; Rohling et al., 2006; Schulz et al., 1998; Sirocko et al.,  
566 1993; Tjallingii et al., 2008), and may involve severe drought development due to  
567 southward ITCZ displacement (Krebs and Timmermann, 2007; Vellinga and Wood,  
568 2002; Zhang and Delworth, 2006). Yet, an ITCZ shift and associated Hadley cell  
569 changes likely explain only part of the impacts on monsoon circulation, which also  
570 depends on regional and local processes (Donohoe et al., 2013; Geen et al., 2020).  
571 For example, recent modeling shows that Northern Hemisphere glacial cooling,  
572 increased ice-sheet albedo, and sea-level lowering produce an anomalous thermal  
573 gradient between the Arabian Peninsula and the Arabian Sea that results in a  
574 weakened Walker circulation in the Indian Ocean and drought in the monsoon  
575 systems of the Indo-Pacific region (DiNezio et al., 2018). As mentioned before for  
576 the HS 11 and C26 cold spells (section 6.1), AMOC slowdown/shutdown also  
577 produces cooling and intense atmospheric perturbations in the Mediterranean region  
578 (Manabe and Stouffer, 1997; Vellinga and Wood, 2002), facilitating deep-water

579 formation and bottom water ventilation (Cacho et al., 2000; Sprovieri et al., 2012;  
580 Toucanne et al., 2012). Thus, AMOC slowdown/shutdown may have both  
581 strengthened cold and dry polar/continental air outbreaks and reduced Indian-African  
582 monsoon activity, with both processes conducive to enhanced EMDW production  
583 (the prerequisite for holococcolith preservation).

584 In Fig. 6, grey correlation boxes indicate a link between AMOC slowdown/shutdown  
585 phases (Fig. 6B) and both the heaviest oxygen isotopic values in Chinese Sanbao  
586 Cave speleothems (Fig. 6D) and enhanced holococcolith preservation in the  
587 Mediterranean (Fig. 6C).

588 The atmospheric CH<sub>4</sub> record from Antarctica ice cores (Fig. 6E) reflects emissions  
589 from boreal and monsoonal wetlands (Guo et al., 2012; Landais et al., 2010). The  
590 signal has been separated into three principal components, a glacial-interglacial  
591 forced component, a bi-hemispheric insolation driven component, and a millennial-  
592 scale oscillatory component, which respectively explain 80%, 15% and 5% of the  
593 variance (Guo et al., 2012). Glacial-interglacial cycles force globally synchronous  
594 monsoonal variations in methane emission. The other two forcings are hemispheric in  
595 nature, because of the two hemispheres' anti-phasing for low-latitude summer  
596 insolation changes in ITCZ oscillations and for millennial-scale bipolar see-saw  
597 (strengthening/weakening) AMOC circulation (Guo et al., 2012). The limited number  
598 of grey correlation boxes between the Antarctic CH<sub>4</sub> signal and of Asian monsoon  
599 activity (Fig. 6D-E) suggests that the activity of Southern Hemisphere monsoon  
600 systems (South America, South Africa, Australia) have been a major driver of  
601 methane emission between 550 and 300 ka. However, we note the occurrence of three  
602 different peaks of Antarctic CH<sub>4</sub> during MIS 13, a signal which is also visible in  
603 Mediterranean holococcoliths and the China speleothem record (Fig. 6). This feature  
604 supports reduced emission from southern hemisphere methane sources during MIS 13  
605 and an increased and synchronous emission from northern monsoons and boreal  
606 wetlands (Guo et al., 2012).

607

608 7 – Conclusions

609 The chronology and age uncertainties of SE Aegean Sea core LC21 coccolith data,  
610 Iberian Margin geochemical records,  $\delta^{18}\text{O}$  in the Sanbao Cave stalagmites, and  
611 atmospheric methane concentrations from EDC have been probabilistically assessed  
612 for the last interglacial and TII. The *F. profunda* peak at the base of sapropel S5 layer  
613 is contemporaneous with a maximum in the rates of  $\delta^{18}\text{O}$  change in Sanbao Cave and  
614 with the  $\text{CH}_4$  overshoot in EDC, which suggests an African and Asian monsoon  
615 intensification at the onset of the last interglacial and the raising of the summer upper  
616 mixed layer depth. Holococcolith preservation was enhanced during Heinrich event  
617 HS11 and the C26 cold spell, when AMOC was severely weakened or collapsed.  
618 Cooling and atmospheric perturbations promoted surface-water buoyancy loss and  
619 deep-water formation, and thus increased Mediterranean bottom water ventilation  
620 rates. These results for LC21 explicitly link holococcolith preservation to episodes of  
621 enhanced deep-water formation and seafloor ventilation in the eastern Mediterranean  
622 Sea during Heinrich and Stadial events.

623

624 We also analysed 668 samples from ODP Site 967 to reconstruct variations in  
625 coccolithophore ecology in the region of the Eratosthenes Seamount (eastern  
626 Mediterranean Sea) between about 550 and 300 ka (Middle Pleistocene, MIS 14-9).  
627 Placoliths and *F. profunda* abundance fluctuations are strongly anticorrelated ( $R^2 =$   
628  $0.95$ ,  $n = 668$ ) and together dominate the coccolith assemblages at Site 967, which  
629 suggests that the surface water environment repeatedly switched between  
630 predominant winter-induced fertilization (shallow nutricline) and predominant  
631 monsoon-induced deep nutricline conditions (and Deep Chlorophyll Maximum  
632 development) associated with a shoaling of the pycnocline to a position within the  
633 lower photic zone. In analogy with results for core LC21, Middle Pleistocene phases  
634 of enhanced monsoon runoff into the eastern Mediterranean appear to have caused  
635 shoaling of the pycnocline into the lower photic layer, which provides a deep  
636 nutricline that fosters *F. profunda* proliferation. A second mode of *F. profunda*

637 proliferation and DCM development is seen in glacials, when the nutricline shoaled  
638 into the lower photic zone due to sea-level lowering that reduced water-mass  
639 transport through the main Mediterranean straits. Thus, our coccolithophore  
640 assemblage analyses corroborate earlier suggestions of such a phenomenon based on  
641 planktonic foraminiferal analyses (Rohling and Gieskes, 1989) and modeling (Myers  
642 et al., 1998; Rohling, 1991a).

643

644 Scattered but statistically significant peaks of holococcoliths (up to ~ 20%) mark  
645 increased carbonate preservation on the seafloor due to enhanced production of  
646 EMDW, which match changes in recently proposed North Africa aridity indices  
647 (Grant et al., 2017). Finally, holococcolith enhanced preservation during cold spells is  
648 linked to increased deep-water formation in the Mediterranean Sea, in response to  
649 Atlantic Meridional Overturning Circulation slowdown and weakened monsoon  
650 activity during Northern Hemisphere cold events.

651

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659

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### 1235 Captions

1236 Fig. 1: location of ODP Site 967 and of records used for correlation. A) Red arrows  
1237 indicate the location of International Ocean Discovery program (IODP) Site U1385 in  
1238 the Iberian Margin, ODP Site 967 in the eastern Mediterranean, Core LC21 in the  
1239 Aegean Sea, Sanbao Cave in China and EPICA Dome C in Antarctica. B) Inset map  
1240 of the red box in A). The blue and red circles respectively indicate the location of  
1241 core LC21 and ODP Site 967. The dashed line shows the Nile cone province. Black  
1242 arrows point out the path of Eastern Mediterranean Deep-water from Adriatic and  
1243 Aegean Sea.

1244

1245 Fig. 2: plot of coccolith data in the Aegean Sea core LC21 and comparison with  
1246 selected records. a) *Florisphaera profunda* percentage values (blue circles),  
1247 expressed as natural logarithm (Grelaud et al., 2012). The 1<sup>st</sup> derivative of Sanbao  
1248 Cave speleothem  $\delta^{18}\text{O}$  (orange line) for each of the 10,000 ice-volume corrected  
1249 ‘stacks’, following the chronology by Cheng et al. (2009) and after ice-volume  
1250 correction. b) *Florisphaera profunda* percentage values (blue line), expressed as  
1251 natural logarithm (Grelaud et al., 2012). Epica Dome C  $\text{CH}_4$  (grey circles and grey  
1252 line), following the Antarctic Ice Core chronology AICC2012 (Bazin et al., 2013) c)  
1253 *Florisphaera profunda* percentage values (blue line), expressed as natural logarithm  
1254 (Grelaud et al., 2012). Upper Summer Mixed Layer depth in the three different  
1255 experiments by Amies et al. (2019) (respectively pink, orange and red lines for  
1256 experiments A, B and C). d) Alkenone-derived SST (red circles) from the Alboran  
1257 Sea (Martrat et al., 2014). e) Holococcoliths percentage values (blue circles, this  
1258 study) and superimposed  $\delta^{13}\text{C}$  values of the benthic foraminifera species *Cibicidoides*  
1259 *wuellerstorfi* from the Iberian Margin (green circles) (Martrat et al., 2007). f) Ca/Ti  
1260 ratio, expressed as logarithm (green line), in sediments from the Iberian Margin  
1261 (Hodell et al., 2015), superimposed to the  $\text{C}_{26}\text{OH}$  ratio from the same area (red  
1262 circles) (Martrat et al., 2007). Thick lines represent the 3-pt running average and  
1263 coloured shadows indicate the 95% confidence level. The sapropel S5 and HS11  
1264 extent is also shown.

1265

1266 Fig. 3: plot of coccolith data at ODP Site 967 and comparison with selected records.  
1267 A) June 21<sup>st</sup> insolation curve at 65°N (Laskar et al., 2004). B) Benthic  $\delta^{18}\text{O}$   
1268 composite record from ODP Sites 967 and 968 (Konijnendijk et al., 2015).  
1269 C) LR04 benthic  $\delta^{18}\text{O}$  stack (Lisiecki and Raymo, 2005). D) Downcore percentage  
1270 variations of Placoliths. E) Downcore percentage variations of *F. profunda*. F)  
1271 Downcore percentage variations of UPZ taxa. G) Downcore percentage variations of  
1272 Miscellaneous taxa. H) Downcore percentage variations of holococcoliths. Black  
1273 horizontal bars show the error associated to countings for a 95% confidence level.

1274 Red filling indicates values higher than the total average percentage. Horizontal thick  
1275 black lines indicate MIS boundaries from Lisiecki and Raymo (2005). Horizontal  
1276 yellow boxes show visible sapropel layers in the ODP 967 composite section (Emeis  
1277 et al., 2000a).

1278

1279 Fig. 4: scatter plot of placoliths and *F. profunda* percentage values at ODP Site 967.  
1280 The black line shows the linear fit. The equation of the linear fit,  $R^2$  correlation index  
1281 and number of samples are also reported.

1282

1283 Fig. 5: coccolith, element ratios, indices and principal component scores at ODP Site  
1284 967. A) *Florisphaera profunda* percentage values (black circles, the black line is the  
1285 3-pt running average, this study). B) Holococcolith percentage values (blue circles,  
1286 the blue line is the 3-pt running average, this study). C) Relative sea-level (Spratt and  
1287 Lisiecki, 2016). D) PC2 of elemental proxies that reflects sapropel/monsoon runoff  
1288 layers (Grant et al., 2017). E) The Aeolian residual by Larrasoana et al. (2003)  
1289 plotted by the Grant et al. (2017) chronology. F) The North Africa humidity/aridity  
1290 index (Grant et al., 2017). G) The Ba/Al ratio (Grant et al., 2017). Horizontal thick  
1291 black lines indicate MIS boundaries from Lisiecki and Raymo (2005). Horizontal  
1292 yellow boxes show visible sapropel layers in the ODP 967 composite section (Emeis  
1293 et al., 2000a).

1294

1295 Fig. 6: correlation among Mediterranean, North Atlantic, Asian and Antarctica  
1296 records. A) Alkenone-based SSTs ( $^{\circ}\text{C}$ ) at Site MD01-2444, Iberian Margin (Martrat  
1297 et al., 2007). B) Log (Ca/Ti) at IODP Site U1385, Iberian Margin (Hodell et al.,  
1298 2015). Note the reversed axis. C) 3-pt running average of holococcolith percentage  
1299 values at ODP Site 967, eastern Mediterranean Sea (present study). Note the reversed  
1300 axis. D)  $\delta^{18}\text{O}$  speleothem data at Sanbao Cave, China (Cheng et al., 2016). Note the  
1301 reversed axis. E) Epica Dome C  $\text{CH}_4$ , Antarctica (Bazin et al., 2013).

1302 Grey boxes indicate correlations among different records: cooling and AMOC  
1303 weakening/shutdown in the Iberian Margin (A, B), holococcolith preservation in the  
1304 eastern Mediterranean seafloor (C), monsoon activity weakening in China (D) and  
1305 EDC methane concentration decrease in Antarctica (see Section 6 for further  
1306 explanation).  
1307

1 Middle-Late Pleistocene Eastern Mediterranean nutricline depth and coccolith  
2 preservation linked to Monsoon activity and Atlantic Meridional Overturning  
3 Circulation  
4

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22  
23  
24 Abstract

25 The eastern Mediterranean Sea lies under the influence of high- and low-latitude  
26 climatic systems. The northern part of the basin is affected by Atlantic depressions  
27 and continental and polar air masses that promote intermediate and deep-water  
28 formation. The southern part is influenced by subtropical conditions and monsoon  
29 activity. Monsoon intensification results in enhanced freshwater discharge from the

30 Nile River and other (now dry) systems along the North African margin. This  
31 freshwater influx into the Mediterranean Sea reduces surface water buoyancy loss.  
32 Disentangling the influences of these diverse climatic forcings is hindered by inherent  
33 proxy data limitations and by interactions between the climatic forcings. Here we use  
34 a wealth of published and new paleoclimate records across Termination II to  
35 understand the impacts of the higher latitude and subtropical/monsoon climate  
36 influences on coccolithophore ecology and holococcolith preservation in Aegean Sea  
37 sediment core LC21. We then use these findings to interpret coccolith assemblage  
38 variations at Ocean Drilling Program Site 967 (located nearby LC21, at the  
39 Eratosthenes Seamount) during multiple glacial-interglacial cycles across the Middle  
40 Pleistocene (marine isotopic stages 14-9). The LC21 analysis suggests that  
41 holococcolith preservation was enhanced during Heinrich Stadial 11 (~ 133 ka) and  
42 cold spell C26 (~ 119 ka). These two events have been previously linked to cold  
43 conditions in the North Atlantic and Atlantic Meridional Overturning Circulation  
44 weakening. We propose that associated atmospheric perturbations over the  
45 Mediterranean Sea promoted deep-water formation, and thus holococcolith  
46 preservation. Similarly, in the Middle Pleistocene (MIS 14-9) of Site 967, we observe  
47 temporal coincidence between ten episodes of enhanced holococcolith preservation  
48 and episodes of Atlantic Meridional Overturning Circulation slowdown. In Site 967,  
49 we also identified repeated fluctuations in placoliths and in *Florisphaera profunda*,  
50 which indicate nutricline depth variations. The development of a deep chlorophyll  
51 maximum is associated with the North Africa and wet phases, as recently observed  
52 using elemental proxy records at Site 967, during the deposition of sapropel layers. A  
53 further deep chlorophyll maximum development is identified during MISs 12 and 10,  
54 as a result of pycnocline and nutricline shoaling within the lower part of the photic  
55 zone due to glacial sea-level lowering and water mass transport reduction at both the  
56 Gibraltar and Sicily Straits. Finally, enhanced holococcolith preservation during  
57 cold/dry events is clearly correlated to weakened ~~Asian~~-monsoon activity in both



58 ~~Africa and Asia, establishing a vast Northern Hemisphere link for stadial~~  
59 ~~perturbations.~~

60

61 1 – Introduction

62 Paleoclimate reconstructions document the competing influence of southern *versus*  
63 northern climate systems on the hydrography and hydrology of the eastern  
64 Mediterranean Sea and its borderlands over a range of timescales (Emeis et al.,  
65 2000b; Grant et al., 2017, 2016; Lourens, 2004; Rohling et al., 2002b). During  
66 precession minima (Northern Hemisphere insolation maxima), the African monsoon  
67 intensified and shifted northward, with attendant enhancement of the freshwater  
68 release into the Mediterranean basin via large North African river systems and/or  
69 currently inactive wadis (Amies et al., 2019; Marino et al., 2009; Osborne et al.,  
70 2008; Rohling et al., 2002a; Rohling et al., 2015; van der Meer et al., 2007). This  
71 impacted the basin's hydrography and weakened or even shut down dense water  
72 formation, leading to oxygen starvation at depth and deposition of layers (sapropels)  
73 with elevated organic carbon concentrations (De Lange et al., 2008; Rohling et al.,  
74 2015; Rossignol-Strick et al., 1982). ~~Superimposed upon these orbital scale changes~~  
75 ~~in basin hydrography, circulation, and biogeochemistry are regional m~~Millennial-  
76 scale climatic variations ~~that~~ have been less well documented and appear to be  
77 associated with variations in the strength of the Atlantic Meridional Overturning  
78 Circulation (AMOC) (Grant et al., 2017, 2016; Stockhecke et al., 2016).

79

80 Coccolithophores are marine unicellular phytoplankton organisms living in the upper  
81 part of the water column. ~~The ecology of c~~Coccolithophore species' ~~ecology is shows~~  
82 ~~a strong sensitivity~~very sensitive to modern gradients within the Mediterranean Sea  
83 and different species thrive in different areas, mainly in response to West-East  
84 temperature and nutrient gradients, water column dynamics, and meso-scale  
85 oceanographic features (Bonomo et al., 2012; D'Amario et al., 2017;  
86 Knappertsbusch, 1993; Oviedo et al., 2015). In the sedimentary archive, calcite

87 coccolithophore remains (coccoliths) have been used successfully to infer orbital and  
88 suborbital variations in climate, productivity, and nutricline depth in oceans and  
89 marginal seas (Beaufort et al., 1997; Flores et al., 1997; Incarbona et al., 2013, 2010a;  
90 Marino et al., 2008; Molfino and McIntyre, 1990a; Rogalla and Andruleit, 2005). In  
91 the eastern Mediterranean Sea, coccolith-based paleoenvironmental reconstructions  
92 ~~were~~have been mostly aimed at assessing the shallow *versus* deep position of the  
93 nutricline within the photic layer and its relationship with the basin's freshwater  
94 budget, water mass circulation, and deep-sea ventilation during sapropel deposition  
95 (e.g., Grelaud et al., 2012). These studies attest to the development of a deep  
96 chlorophyll maximum (DCM) while organic carbon-rich layers were accumulating on  
97 the oxygen-starved eastern Mediterranean seafloor (Castradori, 1993; Giunta et al.,  
98 2003; Grelaud et al., 2012; Incarbona et al., 2019, 2011; Incarbona and Di Stefano,  
99 2019; Maiorano et al., 2013; Negri et al., 1999; Principato et al., 2006; Triantaphyllou  
100 et al., 2009b, 2009a), corroborating findings based on other marine planktonic groups  
101 (Kemp et al., 1999; Meier et al., 2004; Rohling and Gieskes, 1989).

102  
103 Here we present new data that complement a previous dataset of coccolith  
104 assemblages from south-eastern Aegean Sea core LC21 (Grelaud et al., 2012), across  
105 the penultimate glacial termination (termination II, T-II) and the last interglacial  
106 period, with a precise, radiometrically constrained chronology (Grant et al., 2012).  
107 This allows comparison of LC21 “coccolith proxies” with time series of  
108 palaeoclimate variability in the monsoon and the North Atlantic region (Cheng et al.,  
109 2009; Hodell et al., 2013), as well as atmospheric methane (CH<sub>4</sub>) concentrations. Our  
110 combined dataset is probabilistically evaluated to decipher the amplitude and timing  
111 of change by quantitatively assessing the impact of chronological, analytical, and  
112 proxy uncertainties. We use this analysis as a proof of concept for new, highly  
113 resolved coccolith data from Ocean Drilling Program (ODP) Site 967 from the  
114 Eratosthenes Seamount, South of Cyprus, within the Nile Delta Basin province  
115 (Emeis et al., 1996). The new ODP 967 time series spans, at centennial-scale

116 resolution, three glacial/interglacial cycles of the Middle Pleistocene, from glacial  
117 Marine Isotope Stage (MIS) 14 to interglacial MIS 9. Collectively, our new data and  
118 analyses provide insights into climate variability at orbital and sub-orbital timescales  
119 ~~both~~ during both glacial and interglacial periods, complementing ~~the a~~ wealth of  
120 existing knowledge of the intervals of sapropel deposition. Specifically, we explore  
121 modifications in nutrient dynamics and holococcolith preservation during the Middle  
122 Pleistocene. These changes are compared with recently acquired variations in  
123 elemental abundances, elemental ratios, and climate index ~~variation~~ ices recently  
124 ~~acquired at for~~ ODP Site 967 (Section 6.3) that portray the alternation of wet and dry  
125 North Africa periods at both orbital and sub-orbital timescales (Grant et al., 2017).  
126 Finally, we centre on the correlation between holococcolith preservation, AMOC,  
127 ~~Asian~~ and boreal monsoon activity (both in Africa and in a wider Asian context)  
128 ~~activity~~ to assess: (i) the atmospheric impact of continental/polar air outbreaks on the  
129 eastern Mediterranean deep-sea ventilation and seafloor calcite preservation during  
130 cold stadials; and (ii) impact of millennial-scale atmospheric perturbations on the  
131 eastern Mediterranean Sea.

132

## 133 2 – Environmental Setting

134 A negative hydrological balance maintains a robust antiestuarine thermohaline  
135 circulation pattern in the Mediterranean Sea (Robinson and Golnaraghi, 1994).  
136 Surface Atlantic water (Modified Atlantic Water – MAW) enters the Mediterranean  
137 Sea and occupies the uppermost 100-200 m depth (Millot, 1999; POEM group,  
138 1992). MAW spread out into the eastern Mediterranean Sea *via* the Mid-  
139 Mediterranean Jet and reaches the Eratosthenes Seamount where a quasi-permanent  
140 anticyclonic summer circulation exists, that is known as the Shikmona Gyre  
141 (Malanotte-Rizzoli et al., 2014; Pinardi and Masetti, 2000; POEM group, 1992).  
142 Levantine Intermediate Water (LIW) formation takes place close to the Eratosthenes  
143 Seamount (Ovchinnikov I.M., 1984; POEM group, 1992). Eastern Mediterranean  
144 Deep Water (EMDW) forms in the Adriatic and Aegean Sea (Fig. 1) due to winter

145 heat loss, ~~when~~ under the influence of intense Bora and Vardar winds ~~blow~~  
146 (Malanotte-Rizzoli et al., 2014; POEM group, 1992).

147

148 Today, the eastern Mediterranean Sea is one of the most oligotrophic areas globally.  
149 Primary productivity is more than three times lower than in the western basin, in  
150 accordance with a similar nutrient depletion trend (Krom et al., 2010, 1991). Primary  
151 production is also seasonally controlled: higher productivity occurs in winter, after  
152 winter convection, while severe oligotrophy occurs in summer due to deepening of  
153 the thermocline and nutricline (Allen et al., 2002; Klein and Coste, 1984). The  
154 Eratosthenes region is classified as a no-bloom area by satellite-based chlorophyll  
155 analyses. The severe late spring-summer oligotrophy is followed by relatively higher  
156 chlorophyll values in winter (D’Ortenzio and Ribera d’Alcalà, 2009).

157

158 High- and low-latitude climate systems impact on the eastern Mediterranean Sea. In  
159 summer, subtropical high-pressure conditions cause stable dry and warm conditions  
160 throughout the Mediterranean area (Lionello, 2012). In winter, the North African  
161 subtropical high pressure is shifted southward, and cold and dry polar/continental air  
162 outbreaks occur into the eastern Mediterranean from the north (Lionello, 2012;  
163 Rohling et al., 2019, 2015). Expansion of the Siberian High is an important driver for  
164 advection of cold air toward the eastern Mediterranean. Intensification of the Siberian  
165 High during Holocene rapid climatic changes is thought to be an important driver of  
166 surface water cooling and atmospheric perturbations in the central-eastern  
167 Mediterranean Sea (Incarbona et al., 2008; Rohling et al., 2002b; Rohling et al.,  
168 2019). Prolonged and strengthened polar/continental air outbreaks promote sea  
169 surface heat loss and deep-water formation (Josey et al., 2011; Rohling et al., 2019;  
170 Velaoras et al., 2017).

171

## 172 3 – Material and Methods

### 173 3.1 - Sediment cores

174 ODP Site 967 (34°04.098'N, 32°43.523'E, 2,553 m water depth) is located at the  
175 base of the northern slope of the Eratosthenes Seamount, a structure that emerges  
176 from the Nile Delta Cone (Fig. 1). Sediments are dominated by horizontal and sub-  
177 horizontal brown and light gray, bioturbated nannofossil ooze and nannofossil clay,  
178 intercalated with sapropels and turbidites (Emeis et al., 1996). Specifically, there are  
179 five sapropel layers that show signs of moderate bioturbation (S13, S12, S11, b and  
180 S10) in the studied interval (Emeis et al., 1996), while no turbidites and/or other  
181 sedimentary disturbances were identified (Konijnendijk et al., 2014).

182  
183 Sediment core LC21 (35°40'N, 26°35'E; 1,522 m water depth) was recovered in  
184 1995 by *RV Marion Dufresne* in the southeastern Aegean Sea (Fig. 1). Lithology  
185 consists of hemipelagic sediments, with visible sapropels (S1, S3, S4, and S5) and  
186 tephra layers (Grant et al., 2016; Satow et al., 2015).

187  
188 3.2 - Coccolith data

189 We carried out coccolith analysis analyses at ODP Site 967 ~~was carried out~~ at 1 cm  
190 resolution between 14.80 and 21.49 m composite depth (mcd) (Emeis et al., 1996),  
191 for a total of 668 samples, which were analysed with a polarized microscope at ~  
192 1000× magnification. Rippled smear slides were prepared following standard  
193 procedures (Bown and Young, 1998). On average 350 specimens were identified  
194 following the taxonomic concepts ~~on~~ for living coccolithophores of Young et al.  
195 (2003) and Jordan et al. (2004). Taxa were grouped ~~in~~ as 'placoliths', 'miscellaneous  
196 group', 'upper photic zone (UPZ) group', 'lower photic zone (LPZ) group' and  
197 'holococcoliths' (Di Stefano and Incarbona, 2004; Incarbona et al., 2010). Placoliths  
198 include small placoliths, small *Gephyrocapsa*, *Gephyrocapsa muelleriae*, and  
199 *Gephyrocapsa oceanica*. The miscellaneous group includes *Helicosphaera* spp.,  
200 *Coccolithus pelagicus*, *Syracosphaera histrica*, *Pontosphaera* spp., *Calcidiscus*  
201 *leptoporus*, *Coronosphaera* spp., *Braarudosphaera* spp., *Oolithotus fragilis*,  
202 *Calciosolenia* spp., and specimens of all the other species. UPZ group includes

203 *Syracosphaera pulchra*, *Umbellosphaera* spp., *Discosphaera tubifera*,  
204 *Rhabdosphaera* spp., *Umbilicosphaera* spp., and *Ceratolithus* spp.. LPZ group  
205 comprises *F. profunda*, which dominates the group, with negligible amounts of  
206 *Gladiolithus flabellatus* in a few samples. Holococcoliths include all the coccoliths  
207 produced during the haploid life-cycle stage (Incarbona et al., 2019).

208

209 The holococcolith analysis at Aegean Sea core LC21 was carried out by observation  
210 with a polarized microscope at about 1000× magnification, following the standard  
211 procedure for rippled smear slides (Bown and Young, 1998). Holococcolith  
212 percentage values were evaluated on 102 samples *versus* heterococcoliths specimens,  
213 examining about 500 coccoliths. *Florisphaera profunda* percentage values at LC21  
214 Aegean Sea core were presented before (Grelaud et al., 2012), following the same  
215 procedure adopted in this study, and that earlier dataset is available at  
216 <https://doi.pangaea.de/10.1594/PANGAEA.805357>.

217

### 218 3.3 - Statistical analysis of the time series

219 ~~A-We use a~~ Monte Carlo approach based on MATLAB coding (Marino et al., 2015;  
220 Thirumalai et al., 2016) ~~has been used~~ to: (i) stack the  $\delta^{18}\text{O}$  time series for ~~the~~  
221 different stalagmites (SB11, SB23, and SB25) from Sanbao Cave, China, ~~(Cheng et~~  
222 ~~al., 2009)~~ that cover T-II and the last interglacial period (Cheng et al., 2009); (ii)  
223 calculate rates of  $\delta^{18}\text{O}$  change in the Sanbao Cave stalagmites; (iii) probabilistically  
224 evaluate the chronological (Bazin et al., 2013; Veres et al., 2013) and measurement  
225 uncertainties associated with the time series of atmospheric methane ( $\text{CH}_4$ )  
226 concentrations from EPICA Dome C (EDC) (Loulergue et al., 2008); and (iv)  
227 probabilistically evaluate chronological and counting uncertainties associated with  
228 the *F. profunda* (Grelaud et al., 2012) and new holococcolith records for core LC21.

229

230 Speleothem  $\delta^{18}\text{O}$  time series from Sanbao Cave have been probabilistically evaluated  
231 and stacked across the 140-110 ka interval. Input data for the Monte Carlo routine are



232 sample ages with  $1\sigma$  uncertainties, and speleothem  $\delta^{18}\text{O}$  with  $1\sigma$  uncertainties (Cheng  
233 et al., 2009). For each stalagmite (SB11, SB23, and SB25), individual data points are  
234 then separately and randomly sampled 10,000 times within their chronological and  
235  $\delta^{18}\text{O}$  uncertainties. The chronological uncertainties are evaluated using a random  
236 walk Monte Carlo routine that employs a Metropolis–Hastings approach to reject  
237 steps in the random walk that will result in age reversals (Rodríguez-Sanz et al.,  
238 2017). That is, we imposed a stratigraphic constraint (monotonic increase of age with  
239 depth, analogous to Rohling et al., 2014) to the data that are measured in a  
240 stratigraphically coherent manner along individual stalagmites. All realizations are  
241 then linearly interpolated on an equally spaced time scale and stacked to produce  
242 10,000 speleothem  $\delta^{18}\text{O}$  stacks with and without a correction that probabilistically  
243 quantifies the impacts of the global  $^{18}\text{O}$  enrichment/depletion (Schrag et al., 2002)  
244 associated with ice-volume changes (Grant et al., 2012). Next, we calculated the 1<sup>st</sup>  
245 time derivative, to obtain rates of speleothem  $\delta^{18}\text{O}$  change, for each of the 10,000 ice-  
246 volume corrected ‘stacks’. This is done by smoothing each realization using 0.75 kyr  
247 Gaussian window to remove sample-to-sample noise, which would result in spurious  
248 jumps in the estimated rates of change, and by then differentiating the smoothed  
249 realizations. Monte Carlo analysis of the EDC methane record and of the eastern  
250 Mediterranean coccolith time series are performed using the same approach. Finally,  
251 the 10,000 iterations of each of these time series are linearly interpolated and the  
252 probability distribution assessed at each time step, thereby determining the 68%  
253 (16<sup>th</sup>–84<sup>th</sup> percentile) and 95% (2.5<sup>th</sup>–97.5<sup>th</sup> percentile) probability intervals and the  
254 probability maximum (P<sub>MAX</sub>, modal value) of the data.

255

#### 256 4 – Coccolith ~~taxa~~ taxon ecology

257 Placoliths are so-called ‘r-strategist taxa’ that rapidly exploit nutrients in the photic  
258 zone (Baumann et al., 2005; Young, 1994). In the eastern Mediterranean Sea,  
259 placoliths bloom in winter, after nutrient fertilization (Di Stefano et al., 2011;  
260 Knappertsbusch, 1993; Triantaphyllou et al., 2004; Ziveri et al., 2000).

261 *Florisphaera profunda* is a deep photic zone species that indicates the occurrence of a  
262 deep nutricline (McIntyre and Molino, 1996; Molino and McIntyre, 1990a). In low-  
263 and middle-latitude open ocean regions, the relative abundance of this species is  
264 anticorrelated with primary productivity (Beaufort et al., 2001, 1997; Hernández-  
265 Almeida et al., 2019).

266  
267 In the Mediterranean Sea, except for a limited area in the central part of the basin,  
268 there is no apparent relationship between *F. profunda* abundance and satellite-  
269 observed (surface) primary productivity levels (Hernández-Almeida et al., 2019;  
270 Incarbona et al., 2008). However, *F. profunda* has been generally used to decipher  
271 water column stratification and development of a deep nutricline due to monsoon-  
272 fuelled freshwater discharge in the eastern Mediterranean and entrainment of  
273 nutrients into the lower photic zone from below (Castradori, 1993; Grelaud et al.,  
274 2012; Incarbona et al., 2019; Negri et al., 1999; Triantaphyllou et al., 2009b). This  
275 occurs through the development of a distinct DCM in the eastern Mediterranean during  
276 sapropel deposition, ~~with. DCM development resulted from~~ nutrients ~~entraining~~  
277 ~~entrainment into~~ the photic zone from ~~below, injected by more buoyant relatively~~  
278 ~~buoyant~~ intermediate waters. ~~These were possibly that likely forming in~~ ~~originated~~  
279 ~~from~~ the Adriatic Sea, while ~~the~~ volume of MAW ~~inflow across through~~ the Sicily  
280 Strait was ~~plausibly~~ reduced (Myers et al., 1998; Rohling, 1991b; Rohling and  
281 Gieskes, 1989). Accordingly, relative abundances of placoliths and *F. profunda*, or  
282 their ratio, provide a robust indication of the depth of the nutricline in the eastern  
283 Mediterranean Sea. Specifically, presence (absence) of placoliths (*F. profunda*) in the  
284 coccolith assemblage reflects a shallow (deep) nutricline (Di Stefano et al., 2015;  
285 Flores et al., 2000; Molino and McIntyre, 1990b).

286  
287 ~~The~~ UPZ ~~are group consists of~~ so-called ‘K-strategist taxa’, specialized to exploit a  
288 minimum uptake of nutrients in surface water (Bazzicalupo et al., 2020; Di Stefano  
289 and Incarbona, 2004; Young, 1994). Miscellaneous taxa reflect the lack of either an



290 apparent distinctive ecological preference or of an understanding of their ecological  
291 preferences, with a potential weak K-strategy (Incarbona et al., 2010; Young, 1994).  
292 Holococcoliths prefer dwelling in warm, oligotrophic surface water and are abundant  
293 in the eastern Mediterranean Sea (D’Amario et al., 2017; Kleijne, 1991;  
294 Knappertsbusch, 1993; [Dimiza et al., 2015](#); Oviedo et al., 2015; [Skampa et al., 2019](#)).  
295 Poor preservation of holococcoliths in sapropel S1 sediments was firstly recognised  
296 by Crudeli et al. (2006) and was later confirmed across the whole eastern  
297 Mediterranean, included the Eratosthenes Seamount (Incarbona et al., 2019;  
298 Incarbona and Di Stefano, 2019) [and Pliocene sapropel layers in sedimentary](#)  
299 [sequencess on Cyprus Island sediments \(Athanasidou et al., 2015\)](#). Importantly,  
300 potential preservation of tiny holococcolith crystals improves when dense water  
301 renewal ensures vigorous ventilation/oxygenation of the seafloor, even during short  
302 reventilation episodes that “interrupt” sapropel deposition (Incarbona et al., 2019).

303

## 304 5 –Chronology

305 The original shipboard age model by Sakamoto et al. (1998) at ODP Site 967 has  
306 [since](#) been ~~later~~ revised, because of some inconsistent tuning to orbital insolation  
307 (Konijnendijk et al., 2014; Lourens et al., 2001). More recently, Grant et al. (2017)  
308 developed a monsoon runoff (sapropel) proxy from the principal component analysis  
309 of sedimentary elemental data in ODP Site 967 that they tuned to precession minima.  
310 They use a zero phase lag, which relies upon the assumption that little or no lag exists  
311 when monsoon maxima did not immediately follow a high-amplitude glacial  
312 termination (Grant et al., 2016; Lourens et al., 2001). In this study, we adopt the  
313 chronology by Grant et al. (2017) for the coccolith data. Sedimentation rates, between  
314 MIS 14 and MIS 9, range from 1.4 cm kyr<sup>-1</sup> to 3.9 cm kyr<sup>-1</sup>, implying that the mean  
315 sampling resolution of our coccolith time series is about 340 years.

316 The LC21 chronology follows Grant et al. (2012) [\(see also-section 6.1\)](#). The mean  
317 sedimentation rate is about 4.4 cm kyr<sup>-1</sup>, with a mean sampling resolution of about  
318 225 years.

319

## 320 6 – Results and Discussion

### 321 6.1 ~~—~~ Coccolith assemblages in Aegean Sea core LC21

322 *Florisphaera profunda* (Grelaud et al., 2012) and holococcoliths across T-II and the  
323 last interglacial in south-eastern Aegean core LC21 are used to evaluate their  
324 relationship with water column stratification and deep-sea ventilation, respectively.  
325 Several features make this core and the timespan that we target ideal to provide a  
326 ‘proof of concept’ for the interpretation of the new records from ODP Site 967 that  
327 spans multiple glacial-interglacial cycles. First, core LC21 has a radiometrically  
328 constrained chronology across T-II and the last interglacial period (Grant et al.,  
329 2012). This has been corroborated through comparison with western Mediterranean  
330 sediment cores and speleothem records, and it is consistent with the latest ice core  
331 chronology across the study interval (Marino et al., 2015). Second, prominent  
332 episodes of climate change punctuated T-II, including a multi-millennial Heinrich  
333 stadial associated with major freshwater discharge into the North Atlantic and AMOC  
334 slowdown (Deaney et al., 2017; Marino et al., 2015). Third, during the last  
335 interglacial period, an organic rich layer (sapropel S5) was deposited in the eastern  
336 Mediterranean under persistently anoxic or even euxinic conditions (Marino et al.,  
337 2007; Rohling et al., 2015, 2006). Sapropel S5 conditions developed in response to  
338 extensive monsoon-fuelled freshwater discharge along the North African Margin  
339 (Amies et al., 2019; Osborne et al., 2008; Rohling et al., 2002a; Rohling et al., 2004)  
340 that reduced surface salinity (van der Meer et al., 2007) and produced strong water  
341 column stratification (Amies et al., 2019; Grelaud et al., 2012; Marino et al., 2007;  
342 Rohling et al., 2006).

343

344 In Figure 2a-c we show *F. profunda* relative abundances from core LC21 (Grelaud et  
345 al., 2012) with upper mixed layer depth fluctuations reconstructed for the same core  
346 (Amies et al., 2019), and with the contemporaneous EDC time series of atmospheric  
347 CH<sub>4</sub> concentrations and the Sanbao Cave  $\delta^{18}\text{O}$  stack, ~~both~~ which are expected ~~thought~~

348 to reflect fluctuations in ~~the boreal monsoon~~ intensity ~~of the boreal monsoon~~ and  
349 attendant changes in the ~~wetland~~ spatial coverage of tropical wetlands (Cheng et al.,  
350 2016, 2009, 2006; Möller et al., 2013; Petrenko et al., 2009). We present tThe *F.*  
351 *profunda* time series (Grelaud et al., 2012) ~~is here presented~~ on the radiometrically  
352 constrained chronology of Grant et al. (2012), as natural logarithm of the original  
353 data. Within uncertainties of the various records, we note a strong similarity between  
354 the LC21 *F. profunda* record and variations of both Sanbao Cave speleothem  $\delta^{18}\text{O}$   
355 (Fig. 2a) and EDC  $\text{CH}_4$  (Fig. 2b). Notably, a distinct *F. profunda* peak at  $\sim 129$  ka  
356 appears contemporaneous with upper mixed layer thinning, with a maximum in the  
357 rates of Sanbao Cave  $\delta^{18}\text{O}$  change and with the  $\text{CH}_4$  overshoot in EDC. This  
358 suggests: (i) synchronous intensification of the African and Asian monsoons at the  
359 onset of the last interglacial period, in line with what has been documented for the  
360 early Holocene (Fleitmann et al., 2003; Marino et al., 2009; Nicholson et al., 2020;  
361 Tierney et al., 2008); and (ii) a rapid increase in freshwater discharge into the eastern  
362 Mediterranean at the onset of the last interglacial monsoon maximum, quantified as  
363 up to  $\sim 8.8$  times the modern pre- Aswan Nile discharge and responsible for the most  
364 intense thinning of the upper summer mixed layer (Amies et al., 2019). Observation  
365 (ii) is particularly relevant because it alludes to the influence of the rates of monsoon  
366 intensification on stratification in the eastern Mediterranean. When large amounts of  
367 monsoon-fuelled freshwater are rapidly added to the basin, the strong evaporative  
368 climate of the Levant cannot keep up with sea-surface dilution (Rohling et al.,  
369 1991b) and the water column becomes strongly stratified (Rohling and Gieskes,  
370 1989; Rohling et al., 2006; Marino et al., 2007; Athanasiou et al., 2015, 2017; Amies  
371 et al., 2019), causing shoaling of the pycnocline, the nutricline to be positioned at the  
372 base of the photic layer and the attendant development of a pronounced DCM.  
373  
374 In Figure 2d-f, LC21 holococcolith data are compared with North Atlantic and  
375 western Mediterranean Sea records. It is evident that there is no or poor preservation  
376 of holococcoliths during sapropel S5 (Fig. 2e). Peaks of holococcoliths below S5

377 correlate with low alkenone-derived SSTs in the Alboran Sea (Martrat et al., 2014)  
378 (Fig. 2d) and with variations in AMOC strength proxies (Figs. 2e,f) from the Iberian  
379 Margin. Specifically, log (Ca/Ti), benthic foraminiferal  $\delta^{13}\text{C}$ , and  $\text{C}_{26}\text{OH}$  ratios  
380 (Hodell et al., 2015; Martrat et al., 2007) unequivocally indicate that AMOC ~~was~~  
381 ~~severely~~had collapsed during Heinrich event HS11 (Böhm et al., 2015); we find that,  
382 at the same time, holococcolith preservation was enhanced. A similar relationship is  
383 evident above sapropel S5, especially with  $\text{C}_{26}\text{OH}$  ratio data (Fig. 2f), and may be  
384 correlated with ~~the~~ North Atlantic cold event C26 (Oppo et al., 2006, 2001; Tzedakis  
385 et al., 2018). Coupled ocean-atmosphere hindcasts suggest that the AMOC  
386 slowdown/shutdown may have propagated through the Mediterranean Sea as-in the  
387 form of major cooling and intense atmospheric perturbations (Manabe and Stouffer,  
388 1997; Vellinga and Wood, 2002). Both cooling and atmospheric perturbations are  
389 major prerequisites for surface water buoyancy loss and deep-water formation,  
390 explaining enhanced Mediterranean bottom water ventilation during Heinrich and  
391 ~~stadial~~ Stadial events in the last glacial, based on benthic foraminifera  $\delta^{13}\text{C}$  and  
392 alcohol index records (Cacho et al., 2000; Sprovieri et al., 2012; Toucanne et al.,  
393 2012). Our new results from the Aegean Sea explicitly link holococcolith  
394 preservation to Heinrich and Stadial events in response to deep-water formation and  
395 seafloor ventilation increases in the Mediterranean Sea during those events.

396

## 397 6.2 – Coccolith assemblages at ODP Site 967

398 At ODP Site 967, coccolith distribution patterns are compared (Figure 3) with: (i)  
399 June 21<sup>st</sup> insolation at 65°N (Laskar et al., 2004); (ii) the benthic  $\delta^{18}\text{O}$  composite  
400 record from ODP Sites 967 and 968 (~~Konijnendijk et al., 2015~~), (~~Konijnendijk et al.,~~  
401 ~~2015~~); and (iii) the LR04 benthic  $\delta^{18}\text{O}$  stack (Lisiecki and Raymo, 2005). Overall,  
402 coccolith assemblages are dominated by placoliths, with percentages between 25 and  
403 98% (average = 70%, Fig. 3D). The deep photic zone species *F. profunda* features  
404 high-amplitude fluctuations between intervals in which it is barely occurring (1%)  
405 and intervals in which it becomes the dominant (up to 74%), ~~and an average of 26%~~

406 (Fig. 3E). Placoliths' peak (low) abundances occur when *F. profunda* percentages are  
407 at a minimum (maximum), as highlighted by the pronounced anticorrelation ( $R^2=$   
408  $0.95$ ,  $n = 668$ ) displayed in Figure 4.

409  
410 The observed alternating dominance of the placoliths and *F. profunda* (see above) at  
411 ODP Site 967 suggests that between MIS 14 and MIS 9 the upper water column in  
412 the easternmost Mediterranean Sea repeatedly switched between ~~a~~-dominant winter-  
413 induced fertilization (placoliths' peaks, shallow nutricline), similar to today's winter  
414 conditions (Knappertsbusch, 1993), and a predominantly DCM-focused productivity  
415 ~~mostly occurring within the DCM~~ (*F. profunda*'s peaks, deep nutricline) during both  
416 glacial and interglacial periods. Shoaling of the pycnocline, which promoted a deep  
417 nutricline (DCM), in association with intensifications of the North African monsoon  
418 and sea-level lowering (Rohling and Gieskes, 1989; Rohling, 1991a, 1991b) is the  
419 most plausible explanation for the peak abundance of *F. profunda* at ODP Site 967  
420 during sapropels and glacial periods, respectively. Accordingly, *F. profunda* would  
421 be particularly sensitive to ~~the~~-nutrient (re)distribution within the photic zone, with  
422 intervals of positive shifts in the basins freshwater budget (monsoon maxima,  
423 Rohling, 1991b) and reduced water exchange at straits (glacial lowstands, Rohling,  
424 1991a), both leading to enhanced stratification in the upper water column, shoaling  
425 of the pycnocline, and development of a ~~deep~~-nutricline at the based of the photic  
426 layer. This conceptual framework indicated by box-model calculations (Rohling,  
427 1991a,b) provides an explanation for the *F. profunda* peaks both in sapropel layers  
428 (e.g., S12, S11, b, S10) and during MIS 12 and MIS 10 glacial periods (see also  
429 Section 6.3).

430 The remaining three coccolith groups at Site 967 are largely subordinate. Low  
431 abundance of UPZ taxa (0.0-5.4%, 1.4% on average, Fig. 3F) and Miscellaneous taxa  
432 (0.0-11.1%, 1.2% on average, Fig. 3G) is unexpected in the severe oligotrophy of the  
433 eastern Mediterranean Sea, especially for UPZ taxa that include dominant  
434 coccolithophore species in summer/autumn (Knappertsbusch, 1993; Malinverno et

435 al., 2009; Oviedo et al., 2015). However, living coccolithophore surveys show that  
436 winter production (placolith blooming) is ~~even about one an~~ order of magnitude  
437 higher than summer production, thereby explaining the apparent ecological  
438 contradiction in taxa proportions (Knappertsbusch, 1993).

439 Holococcolith percentage values range between 0.0 and 20.8%, 1.9% on average  
440 (Fig. 3H). As ~~was the case infor~~ late Quaternary sapropels, tiny holococcoliths are  
441 ~~again~~ not preserved ~~during in~~ sapropel layers, but ~~it is evident~~ we also note that that  
442 poor preservation extends far beyond sapropel layers.

443

444 6.3 – Comparison between coccoliths, ~~and~~ element ratios and climatic indices at ODP  
445 Site 967

446 *Florisphaera profunda* and holococcolith distribution patterns at ODP Site 967 (Figs.  
447 5A-B) are compared with sedimentary elemental ratios and climatic indices from the  
448 same sedimentary sequence (Grant et al., 2017). A principal component analysis  
449 carried out on elemental proxies by these authors highlighted that principal  
450 components PC1 (not shown) and PC2 (Fig. 5D) account for 79% of variance and  
451 reflect terrigenous input and sapropel deposition (enhanced monsoon runoff),  
452 respectively. Moreover, aeolian dust fluxes (Fig. 5E) and a North Africa  
453 humidity/aridity index (Fig. 5F) were calculated and are also compared with  
454 coccolith abundance fluctuations.

455

456 Intensification of East African monsoon precipitation coincided with northward  
457 displacement of the Intertropical Convergence Zone (ITCZ) and subsequent  
458 intensification of precipitation over the catchment basins of the Nile and other rivers,  
459 which fuelled enhanced freshwater discharge along the wider North African margin  
460 into the eastern Mediterranean (Ehrmann et al., 2016; Rohling et al., 2002a; Rohling  
461 et al., 2015). *Florisphaera profunda* proliferates because it benefits from the  
462 nutricline positioned in deep photic zone and the establishment of a DCM  
463 (Castradori, 1993; Girone et al., 2013; Grelaud et al., 2012; Incarbona et al., 2011;



464 Negri et al., 1999), following the rationale outlined above (Myers et al., 1998;  
465 Rohling, 1991a; Rohling and Gieskes, 1989). This scenario has been described for  
466 eastern Mediterranean sapropels and is further supported by the coupling of the *F.*  
467 *profunda* signal and enhanced humidity in North Africa that leads to enhanced  
468 monsoon runoff into the eastern Mediterranean, especially during S12, S11, b and  
469 S10 (Fig. 5). Also evident is decoupling between *F. profunda* and the  
470 humidity/aridity index, for instance during glacial sapropel S13 and during sapropel  
471 layer b. This ~~can be explained by the meaning of~~ indicates suggests that the climatic  
472 indices at ODP Site 967 ~~that~~ reflect increased rainfall over North Africa and Sahara,  
473 without ~~a clear indication of the~~ sufficient northward monsoon penetration that  
474 determines the intensity of monsoon-related runoff into the eastern Mediterranean  
475 Sea (Grant et al., 2017). Also, different nutrient dynamics may have developed  
476 during the glacial sapropel S13, with surface fertilization that supports placolith-  
477 bearing species competition.

478  
479 However, the coccolith record at Site 967 suggests that *F. profunda* increases are a  
480 recurring feature of the record that is not necessarily associated with the deposition of  
481 organic-rich layers deposition on the eastern Mediterranean seafloor, especially in  
482 glacial episodess (Fig. 5A). The Ba/Al signal indicates that many sapropel layers  
483 likely were have been partially oxidized (Fig. 5G) ~~and, so that their currently visible~~  
484 extents do not represent the ~~real original~~ thickness of anoxic sediments. Yet, we argue  
485 that *F. profunda* peaks are not exclusively linked to the environmental changes ~~driven~~  
486 ~~by these hydrographic perturbations associated with sapropel formation.~~ Positive  
487 *Florisphaera profunda* ~~positive~~ peaks, without a corresponding sapropel layer, (be it  
488 visible, or oxidized) are evident in all eastern Mediterranean records that span  
489 sufficiently long time intervals (Castradori, 1993; Giunta et al., 2003; Maiorano et al.,  
490 2013; Negri et al., 1999; Triantaphyllou et al., 2010). The occurrence of *F. profunda*  
491 during glacial periods identifies a second mode of DCM development in the eastern  
492 Mediterranean, as proposed on the basis of planktonic foraminiferal assemblages

493 (Rohling and Gieskes, 1989) and modeling (Myers et al., 1998; Rohling, 1991a).  
494 Again, the DCM development would be driven by the pycnocline and nutricline  
495 shoaling within the lower part of the photic zone. But, for glacials, the eustatic sea-  
496 level drop (Fig. 5C) would have been the main trigger mechanism, after reducing  
497 water mass transport at both Gibraltar and Sicily Straits and ultimately shoaling the  
498 pycnocline and nutricline depth up to ~ 80 m (Myers et al., 1998; Rohling, 1991a).  
499 However, the scattered *F. profunda* abundance signal in MISs 12 and 10 suggests that  
500 other factors may operate in conjunction with sea-level fall, for reducing water  
501 transport across the Gibraltar and Sicily Straits. Among these, less frequent and  
502 intense northern outbreaks in deep water production sites and the inflow of low-  
503 density meltwater from the Atlantic Ocean may have weakened the Mediterranean  
504 thermohaline circulation and may have caused transient reductions in reduced the  
505 water transport at straits, like during last glacial cold spells (Sierro et al., 2005;  
506 Sprovieri et al., 2012; Toucanne et al., 2012; Azibeiro et al., 2021).

507  
508 Holococcoliths are made of small calcite rhombohedra, arranged in different patterns.  
509 They are the most vulnerable coccoliths to selective dissolution (Roth and Coulbourn,  
510 1982). Comparison between the new ODP 967 holococcolith record and the  
511 humidity/aridity index (Figs. 5B, F) shows strong similarities throughout the time  
512 span studied, which clearly point to the dissolution of haploid-haploid-life calcite  
513 remains in-at the Erathostenes seamount during humid phases. This agrees with the  
514 notion that surface buoyancy gain by freshwater river discharge negatively impacted  
515 deep-water formation in the eastern Mediterranean Sea, which enhanced organic  
516 carbon preservation (De Lange et al., 2008; Myers et al., 1998; Rohling et al., 2015)  
517 and, thus, worsened holococcolith preservation, like during sapropel S1 (Crudeli et  
518 al., 2006; Incarbona et al., 2019; Incarbona and Di Stefano, 2019) and sapropel S5  
519 (Fig. 2, this study).

520



521 It is worth noting that the three major aeolian dust peaks ~~of dust~~ during MIS 13-12  
522 (Fig. 5E) did not match with increasing holococcolith preservation but fall within ‘no  
523 preservation’ intervals. Aeolian dust peaks are associated ~~to~~ with a-weakened  
524 monsoon activity and North Africa dry periods, as seen from the Ti/Al ratio  
525 (Konijnendijk et al., 2015; Lourens et al., 2001; Wehausen and Brumsack, 2000;  
526 Ziegler et al., 2010), and would imply a lower freshwater input into the eastern  
527 Mediterranean Sea. Ideally, these conditions would enhance deep water formation,  
528 less-reduce organic matter preservation on the seafloor, and increased preservation of  
529 holococcolith calcite. However, dust accumulation in marine cores depends on wind  
530 strength and direction (Moulin et al., 1997; Zabel et al., 1999). Thus, aeolian dust  
531 peaks are not necessarily tied to cooling and atmospheric perturbations that, for  
532 instance during the latest Quaternary, led to enhanced Mediterranean bottom water  
533 ventilation in coincidence of glacials and stadials (Cacho et al., 1999; 2000; Sprovieri  
534 et al., 2012; Toucanne et al., 2012).

535

536 6.4 – AMOC slowdown, holococcolith preservation and monsoon weakening  
537 In Figure 6, North Atlantic geochemical records (Fig. 6A-B), Mediterranean  
538 holococcolith data (Fig. 6C), and oxygen isotopes of China speleothems (Fig. 6D) are  
539 plotted using their own original age models (Cheng et al., 2016; Grant et al., 2017;  
540 Hodell et al., 2015; Martrat et al., 2007). The grey boxes used for correlation are  
541 drawn and link correlative events in these various Northern Hemisphere records.  
542 Records shown in Figure 6 help with outlining a concept of atmosphere/ocean  
543 interactions that resulted in the correlation between Northern Hemisphere climate  
544 variability and surface water ecosystem modifications and seafloor diagenesis in the  
545 eastern Mediterranean.

546

547 The correlation boxes in Figure 6 are drawn assuming that AMOC  
548 slowdown/shutdown caused an atmospheric perturbation that impacted a vast area of  
549 the northern Hemisphere, including the eastern Mediterranean Sea, East African and

550 Asian monsoon sites (~~REFS for this assumption— from modelling would be best~~  
551 ~~here?~~ Vellinga and Wood, 2002). The log (Ca/Ti) record from the Iberian Margin  
552 (Fig. 6B) is a proxy for millennial-scale variability (Hodell et al., 2015): minima  
553 indicate stadial/Heinrich phases during which the AMOC was severely weakened or  
554 collapsed (McManus et al., 2004, 1999). Previous studies based on  $\delta^{13}\text{C}$ , alcohol  
555 index and sortable silt records support the hypothesis that Mediterranean bottom  
556 water ventilation at least in the western sub-basin was more intense during glacial  
557 periods and stadial events (Cacho et al., 2000, 1999; Frigola et al., 2008; Sprovieri et  
558 al., 2012; Toucanne et al., 2012) and strengthened Mediterranean outflow ~~water into~~  
559 the Gulf of Cadiz and in the Iberian Margin (Sierro et al., 2020). ~~The Simultaneous~~  
560 ~~enhancement of EMDW renewal ventilation on the seafloor~~ would have enhanced  
561 holococcolith preservation, as ~~already~~ observed below and above sapropel S1  
562 (Incarbona et al., 2019; Incarbona and Di Stefano, 2019) and during HS11 and C26 in  
563 the Aegean Sea (this study, Fig. 2). The physico-chemical processes in the seafloor  
564 microsystem by which tiny holococcolith calcite rhombohedra are preferentially  
565 preserved under oxic conditions is not clear yet. Incarbona et al. (2019b)  
566 hypothesized a possible detrimental action of organic acid produced by bacteria under  
567 a dysoxic/anoxic state on the water/sediment interface, in analogy with ~~today's~~  
568 ~~results from modern~~ surveys in the Gulf of California (Ziveri and Thunell, 2000).  
569 However, specific studies are needed to better understand the processes involved.

570  
571 The link between AMOC slowdown/shutdown and East African, Indian, and Asian  
572 monsoon weakening is well-established (Deplazes et al., 2014; Porter and Zhisheng,  
573 1995; Rohling et al., 2002; Rohling et al., 2006; Schulz et al., 1998; Sirocko et al.,  
574 1993; Tjallingii et al., 2008), ~~possibly operating by the and may involve severe~~  
575 ~~drought development due to southward ITCZ southward shift and severe~~  
576 ~~drought displacement~~ (Krebs and Timmermann, 2007; Vellinga and Wood, 2002;  
577 Zhang and Delworth, 2006). Yet, ~~we acknowledge that the an~~ ITCZ shift, and ~~the~~  
578 ~~associated~~ Hadley cell ~~activity, changes may likely~~ explain only part of the ~~impacts on~~

579 monsoon circulation, which also depends on regional and local processes (Donohoe  
580 et al., 2013; Geen et al., 2020). For example, A-recent modeling shows that Northern  
581 Hemisphere glacial cooling, increased ice-sheet albedo, and sea-level fall, lowering  
582 produce an anomalous thermal gradient between the Arabian Peninsula and the  
583 Arabian Sea, that producing resultings in a weakened Walker circulation in the  
584 Indian Ocean and drought in the monsoon systems of the Indo-Pacific region  
585 (DiNezio et al., 2018). As already-mentioned before for the HS 11 and C26 cold  
586 spells (section 6.1), AMOC slowdown/shutdown also produces cooling and intense  
587 atmospheric perturbations in the Mediterranean region (Manabe and Stouffer, 1997;  
588 Vellinga and Wood, 2002), facilitating deep-water formation and bottom water  
589 ventilation (Cacho et al., 2000; Sprovieri et al., 2012; Toucanne et al., 2012). Thus,  
590 AMOC slowdown/shutdown may have both strengthened cold and dry  
591 polar/continental air outbreaks and reduced Indian-African monsoon activity, with  
592 both processes conducive to enhanced EMDW production (the prerequisite for  
593 holococcolith preservation).

594 In Fig. 6, grey correlation boxes indicate a link between AMOC slowdown/shutdown  
595 phases (Fig. 6B) and both the heaviest oxygen isotopic values in Chinese Sanbao  
596 Cave speleothems (Fig. 6D) and enhanced holococcolith preservation in the  
597 Mediterranean (Fig. 6C).

598  
599 The atmospheric CH<sub>4</sub> record from Antarctica ice cores (Fig. 6E) reflects emissions  
600 from boreal and monsoonal wetlands (Guo et al., 2012; Landais et al., 2010). The  
601 signal has been be separated into three principal components, a glacial-interglacial  
602 forced component, a bi-hemispheric insolation driven component, and a millennial-  
603 scale oscillatory component, that-which respectively explain 80%, 15% and 5% of the  
604 variance (Guo et al., 2012). Glacial-interglacial cycles force a-globally synchronous  
605 monsoonal variations in methane emission. The other two forcings are hemispheric in  
606 nature, because of the two hemispheres' anti-phasing for low-latitude summer  
607 insolation changes in ITCZ oscillations and for millennial-scale bipolar see-saw

608 ~~(strengthening/weakening)~~ AMOC circulation (Guo et al., 2012). The limited number  
609 of grey correlation boxes between the Antarctic CH<sub>4</sub> signal and of Asian monsoon  
610 activity (Fig. 6D-E) suggests that the activity of ~~southern~~ Southern Hemisphere  
611 monsoon systems (South America, South Africa, Australia) ~~has~~ have been a major  
612 driver of methane emission between 550 and 300 ka. However, we note the  
613 occurrence of three different peaks of Antarctic CH<sub>4</sub> during MIS 13, a signal which is  
614 also visible in Mediterranean holococcoliths and the China speleothem record (Fig.  
615 6). This feature supports reduced emission from southern hemisphere methane  
616 sources during MIS 13 and an increased and synchronous emission from northern  
617 monsoons and boreal wetlands (Guo et al., 2012).

618

## 619 7 – Conclusions

620 The chronology and age uncertainties of SE Aegean Sea core LC21 coccolith data,  
621 Iberian Margin geochemical records,  $\delta^{18}\text{O}$  in the Sanbao Cave stalagmites, and  
622 atmospheric methane concentrations from EDC have been probabilistically assessed  
623 for the last interglacial and TII. The *F. profunda* peak at the base of sapropel S5 layer  
624 is contemporaneous with a maximum in the rates of  $\delta^{18}\text{O}$  change in Sanbao Cave and  
625 with the CH<sub>4</sub> overshoot in EDC, ~~which suggesting suggests the an intensification of~~  
626 ~~the~~ African and Asian monsoon intensification at the onset of the last interglacial and  
627 the raising of the summer upper mixed layer depth. Holococcolith preservation was  
628 enhanced during Heinrich event HS11 and the C26 cold spell ~~C26~~, ~~while when~~  
629 AMOC was severely weakened or collapsed. Cooling and atmospheric perturbations  
630 promoted ~~surface-surface-~~water buoyancy loss and deep-water formation-, and thus  
631 increased higher Mediterranean bottom water ventilation rates. These results ~~from the~~  
632 ~~Aegean Sea for LC21~~ explicitly link holococcolith preservation to episodes of  
633 enhanced deep-water formation and seafloor ventilation in the eastern Mediterranean  
634 Sea during Heinrich and Stadial events.

635

636 ~~We also analysed A total of~~ 668 samples ~~were analysed~~ from ODP Site 967 Site to  
637 reconstruct variations in coccolithophore ~~ecological variations of coccolithophoresy~~  
638 in the region of the Eratosthenes Seamount (eastern Mediterranean Sea) between  
639 about 550 and 300 ka (Middle Pleistocene, MIS 14-9). Placoliths and *F. profunda*  
640 abundance fluctuations are strongly anticorrelated ( $R^2 = 0.95$ ,  $n = 668$ ) and together  
641 dominate the coccolith assemblages at Site 967, ~~which suggesting suggests~~ that the  
642 surface water environment repeatedly switched between predominant winter-induced  
643 fertilization (shallow nutricline) and predominant monsoon-induced deep nutricline  
644 ~~deepening conditions (and Deep Chlorophyll Maximum development) associated with~~  
645 ~~, through~~ a shoaling of the pycnocline to a position within the lower photic zone. In  
646 analogy with results for core LC21, Middle Pleistocene phases of enhanced monsoon  
647 runoff into the eastern Mediterranean ~~may have appear to have~~ caused shoaling of the  
648 pycnocline into the ~~base of the lower~~ photic layer, which provides a deep nutricline  
649 that fosters *F. profunda* proliferation. A second mode of *F. profunda* proliferation  
650 and DCM development is seen in glacials, when the nutricline shoaled into the lower  
651 photic zone due to sea-level lowering that reduced water-mass transport through the  
652 main Mediterranean straits. Thus, our coccolithophore assemblage analyses  
653 corroborate earlier suggestions of such a phenomenon based on planktonic  
654 foraminiferal analyses (Rohling and Gieskes, 1989) and modeling (Myers et al.,  
655 1998; Rohling, 1991a).

656  
657 Scattered but statistically significant peaks of holococcoliths (up to ~ 20%) mark  
658 increased carbonate preservation on the seafloor ~~by due to enhanced~~ production of  
659 EMDW, ~~that which~~ match changes in recently proposed North Africa aridity indices  
660 ~~as recently proposed on the basis of elemental analysis~~ (Grant et al., 2017). Finally,  
661 holococcolith enhanced preservation during cold spells is linked to increased deep-  
662 water formation in the Mediterranean Sea, in response to Atlantic Meridional  
663 Overturning Circulation slowdown and weakened monsoon activity during Northern  
664 Hemisphere cold events.

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## 1250 Captions

1251 Fig. 1: location of ODP Site 967 and of records used for correlation. A) Red arrows  
1252 indicate the location of International Ocean Discovery program (IODP) Site U1385 in  
1253 the Iberian Margin, ODP Site 967 in the eastern Mediterranean, Core LC21 in the  
1254 Aegean Sea, Sanbao Cave in China and EPICA Dome C in Antarctica. B) Inset map  
1255 of the red box in A). The blue and red circles respectively indicate the location of  
1256 core LC21 and ODP Site 967. The dashed line shows the Nile cone province. Black  
1257 arrows point out the path of Eastern Mediterranean Deep-water from Adriatic and  
1258 Aegean Sea.

1259

1260 Fig. 2: plot of coccolith data in the Aegean Sea core LC21 and comparison with  
1261 selected records. a) *Florisphaera profunda* percentage values (blue circles),  
1262 expressed as natural logarithm (Grelaud et al., 2012). The 1<sup>st</sup> derivative of Sanbao  
1263 Cave speleothem  $\delta^{18}\text{O}$  (orange line) for each of the 10,000 ice-volume corrected  
1264 ‘stacks’, following the chronology by Cheng et al. (2009) and after ice-volume  
1265 correction. b) *Florisphaera profunda* percentage values (blue line), expressed as  
1266 natural logarithm (Grelaud et al., 2012). Epica Dome C  $\text{CH}_4$  (grey circles and grey  
1267 line), following the Antarctic Ice Core chronology AICC2012 (Bazin et al., 2013) c)  
1268 *Florisphaera profunda* percentage values (blue line), expressed as natural logarithm  
1269 (Grelaud et al., 2012). Upper Summer Mixed Layer depth in the three different  
1270 experiments by Amies et al. (2019) (respectively pink, orange and red lines for  
1271 experiments A, B and C). d) Alkenone-derived SST (red circles) from the Alboran  
1272 Sea (Martrat et al., 2014). e) Holococcoliths percentage values (blue circles, this  
1273 study) and superimposed  $\delta^{13}\text{C}$  values of the benthic foraminifera species *Cibicidoides*

1274 *wuellestorfi* from the Iberian Margin (green circles) (Martrat et al., 2007). f) Ca/Ti  
1275 ratio, expressed as logarithm (green line), in sediments from the Iberian Margin  
1276 (Hodell et al., 2015), superimposed to the C<sub>26</sub>OH ratio from the same area (red  
1277 circles) (Martrat et al., 2007). Thick lines represent the 3-pt running average and  
1278 coloured shadows indicate the 95% confidence level. The sapropel S5 and HS11  
1279 extent is also shown.

1280

1281 Fig. 3: plot of coccolith data at ODP Site 967 and comparison with selected records.  
1282 A) June 21<sup>st</sup> insolation curve at 65°N (Laskar et al., 2004). B) Benthic  $\delta^{18}\text{O}$   
1283 composite record from ODP Sites 967 and 968 (Konijnendijk et al., 2015).  
1284 C) LR04 benthic  $\delta^{18}\text{O}$  stack (Lisiecki and Raymo, 2005). D) Downcore percentage  
1285 variations of Placoliths. E) Downcore percentage variations of *F. profunda*. F)  
1286 Downcore percentage variations of UPZ taxa. G) Downcore percentage variations of  
1287 Miscellaneous taxa. H) Downcore percentage variations of holococcoliths. Black  
1288 horizontal bars show the error associated to countings for a 95% confidence level.  
1289 Red filling indicates values higher than the total average percentage. Horizontal thick  
1290 black lines indicate MIS boundaries from Lisiecki and Raymo (2005). Horizontal  
1291 yellow boxes show visible sapropel layers in the ODP 967 composite section (Emeis  
1292 et al., 2000a).

1293

1294 Fig. 4: scatter plot of placoliths and *F. profunda* percentage values at ODP Site 967.  
1295 The black line shows the linear fit. The equation of the linear fit, R<sup>2</sup> correlation index  
1296 and number of samples are also reported.

1297

1298 Fig. 5: coccolith, element ratios, indices and principal component scores at ODP Site  
1299 967. A) *Florisphaera profunda* percentage values (black circles, the black line is the  
1300 3-pt running average, this study). B) Holococcolith percentage values (blue circles,  
1301 the blue line is the 3-pt running average, this study). C) Relative sea-level (Spratt and  
1302 Lisiecki, 2016). D) PC2 of elemental proxies that reflects sapropel/monsoon runoff

1303 layers (Grant et al., 2017). E) The Aeolian residual by Larrasoaña et al. (2003)  
1304 plotted by the Grant et al. (2017) chronology. F) The North Africa humidity/aridity  
1305 index (Grant et al., 2017). G) The Ba/Al ratio (Grant et al., 2017). Horizontal thick  
1306 black lines indicate MIS boundaries from Lisiecki and Raymo (2005). Horizontal  
1307 yellow boxes show visible sapropel layers in the ODP 967 composite section (Emeis  
1308 et al., 2000a).

1309

1310 Fig. 6: correlation among Mediterranean, North Atlantic, Asian and Antarctica  
1311 records. A) Alkenone-based SSTs (°C) at Site MD01-2444, Iberian Margin (Martrat  
1312 et al., 2007). B) Log (Ca/Ti) at IODP Site U1385, Iberian Margin (Hodell et al.,  
1313 2015). Note the reversed axis. C) 3-pt running average of holococcolith percentage  
1314 values at ODP Site 967, eastern Mediterranean Sea (present study). Note the reversed  
1315 axis. D)  $\delta^{18}\text{O}$  speleothem data at Sanbao Cave, China (Cheng et al., 2016). Note the  
1316 reversed axis. E) Epica Dome C  $\text{CH}_4$ , Antarctica (Bazin et al., 2013).

1317 Grey boxes indicate correlations among different records: cooling and AMOC  
1318 weakening/shutdown in the Iberian Margin (A, B), holococcolith preservation in the  
1319 eastern Mediterranean seafloor (C), monsoon activity weakening in China (D) and  
1320 EDC methane concentration decrease in Antarctica (see Section 6 for further  
1321 explanation).

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