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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

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 monsoon activity in both Africa and
58 Asia.

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 (CH₄) 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).

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).

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 hystrix*, *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 (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 1σ uncertainties, and speleothem $\delta^{18}\text{O}$ with 1σ 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}O enrichment/depletion (Schrag et al., 2002)
241 associated with ice-volume changes (Grant et al., 2012). Next, we calculated the 1st
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 (16th–84th percentile) and 95% (2.5th–97.5th 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;

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

299

300 5 –Chronology

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

The LC21 chronology follows Grant et al. (2012) (see section 6.1). The mean sedimentation rate is about 4.4 cm kyr⁻¹, with a mean sampling resolution of about 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 CH₄ 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

radiometrically constrained chronology of Grant et al. (2012), as natural logarithm of the original data. Within uncertainties of the various records, we note a strong similarity between the LC21 *F. profunda* record and variations of both Sanbao Cave speleothem $\delta^{18}\text{O}$ (Fig. 2a) and EDC CH_4 (Fig. 2b). Notably, a distinct *F. profunda* peak at ~129 ka appears contemporaneous with upper mixed layer thinning, with a maximum in the rates of Sanbao Cave $\delta^{18}\text{O}$ change and with the CH_4 overshoot in EDC. This suggests: (i) synchronous intensification of the African and Asian monsoons at the onset of the last interglacial period, in line with what has been documented for the early Holocene (Fleitmann et al., 2003; Marino et al., 2009; Nicholson et al., 2020; Tierney et al., 2008); and (ii) a rapid increase in freshwater discharge into the eastern Mediterranean at the onset of the last interglacial monsoon maximum, quantified as up to ~8.8 times the modern pre- Aswan Nile discharge and responsible for the most intense thinning of the upper summer mixed layer (Amies et al., 2019). Observation (ii) is particularly relevant because it alludes to the influence of the rates of monsoon intensification on stratification in the eastern Mediterranean. When large amounts of monsoon-fuelled freshwater are rapidly added to the basin, the strong evaporative climate of the Levant cannot keep up with sea-surface dilution (Rohling et al., 1991b) and the water column becomes strongly stratified (Rohling and Gieskes, 1989; Rohling et al., 2006; Marino et al., 2007; Athanasiou et al., 2015, 2017; Amies et al., 2019), causing shoaling of the pycnocline, the nutricline to be positioned at the base of the photic layer and the attendant development of a pronounced DCM.

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

(Hodell et al., 2015; Martrat et al., 2007) unequivocally indicate that AMOC had collapsed during Heinrich event HS11 (Böhm et al., 2015); we find that, at the same time, holococcolith preservation was enhanced. A similar relationship is evident above sapropel S5, especially with C₂₆OH ratio data (Fig. 2f), and may be correlated with North Atlantic cold event C26 (Oppo et al., 2006, 2001; Tzedakis et al., 2018). Coupled ocean-atmosphere hindcasts suggest that the AMOC slowdown/shutdown may have propagated through the Mediterranean Sea in the form of major cooling and intense atmospheric perturbations (Manabe and Stouffer, 1997; Vellinga and Wood, 2002). Both cooling and atmospheric perturbations are major prerequisites for surface water buoyancy loss and deep-water formation, explaining enhanced Mediterranean bottom water ventilation during Heinrich and Stadial events in the last glacial, based on benthic foraminifera $\delta^{13}\text{C}$ and alcohol index records (Cacho et al., 2000; Sprovieri et al., 2012; Toucanne et al., 2012). Our new results from the Aegean Sea explicitly link holococcolith preservation to Heinrich and Stadial events in response to deep-water formation and seafloor ventilation increases in the 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 21st 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; Girone 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

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

However, the coccolith record at Site 967 suggests that *F. profunda* increases are a recurring feature of the record that is not necessarily associated with the deposition of organic-rich layers deposition on the eastern Mediterranean seafloor, especially in glacial episodes (Fig. 5A). The Ba/Al signal indicates that many sapropel layers have been partially oxidized (Fig. 5G), so that their currently visible extents do not represent the original thickness of anoxic sediments. Yet, we argue that *F. profunda* peaks are not exclusively linked to the environmental changes associated with sapropel formation. Positive *Florisphaera profunda* peaks without a corresponding sapropel layer (be it visible, or oxidized) are evident in all eastern Mediterranean records that span sufficiently long time intervals (Castradori, 1993; Giunta et al., 2003; Maiorano et al., 2013; Negri et al., 1999; Triantaphyllou et al., 2010). The occurrence of *F. profunda* during glacial periods identifies a second mode of DCM development in the eastern Mediterranean, as proposed on the basis of planktonic foraminiferal assemblages (Rohling and Gieskes, 1989) and modeling (Myers et al., 1998; Rohling, 1991a). Again, the DCM development would be driven by the pycnocline and nutricline shoaling within the lower part of the photic zone. But, for glacials, the eustatic sea-level drop (Fig. 5C) would have been the main trigger mechanism, after reducing water mass transport at both Gibraltar and Sicily Straits 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 CH₄ 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 CH₄ 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 CH₄ 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 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

Fig. 2: plot of coccolith data in the Aegean Sea core LC21 and comparison with selected records. a) *Florisphaera profunda* percentage values (blue circles), expressed as natural logarithm (Grelaud et al., 2012). The 1st derivative of Sanbao Cave speleothem $\delta^{18}\text{O}$ (orange line) for each of the 10,000 ice-volume corrected ‘stacks’, following the chronology by Cheng et al. (2009) and after ice-volume correction. b) *Florisphaera profunda* percentage values (blue line), expressed as natural logarithm (Grelaud et al., 2012). Epica Dome C CH_4 (grey circles and grey line), following the Antarctic Ice Core chronology AICC2012 (Bazin et al., 2013) c) *Florisphaera profunda* percentage values (blue line), expressed as natural logarithm (Grelaud et al., 2012). Upper Summer Mixed Layer depth in the three different experiments by Amies et al. (2019) (respectively pink, orange and red lines for experiments A, B and C). d) Alkenone-derived SST (red circles) from the Alboran Sea (Martrat et al., 2014). e) Holococcoliths percentage values (blue circles, this study) and superimposed $\delta^{13}\text{C}$ values of the benthic foraminifera species *Cibicidoides wuellerstorfi* from the Iberian Margin (green circles) (Martrat et al., 2007). f) Ca/Ti ratio, expressed as logarithm (green line), in sediments from the Iberian Margin (Hodell et al., 2015), superimposed to the C_{26}OH ratio from the same area (red circles) (Martrat et al., 2007). Thick lines represent the 3-pt running average and coloured shadows indicate the 95% confidence level. The sapropel S5 and HS11 extent is also shown.

Fig. 3: plot of coccolith data at ODP Site 967 and comparison with selected records. A) June 21st insolation curve at 65°N (Laskar et al., 2004). B) Benthic $\delta^{18}\text{O}$ composite record from ODP Sites 967 and 968 (Konijnendijk et al., 2015). C) LR04 benthic $\delta^{18}\text{O}$ stack (Lisiecki and Raymo, 2005). D) Downcore percentage variations of Placoliths. E) Downcore percentage variations of *F. profunda*. F) Downcore percentage variations of UPZ taxa. G) Downcore percentage variations of Miscellaneous taxa. H) Downcore percentage variations of holococcoliths. Black 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 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

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

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

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

1 – Introduction

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

Coccolithophores are marine unicellular phytoplankton organisms living in the upper part of the water column. ~~The ecology of c~~Coccolithophore species' ~~ecology is shows~~ a strong sensitivity ~~very sensitive~~ to modern gradients within the Mediterranean Sea and different species thrive in different areas, mainly in response to West-East temperature and nutrient gradients, water column dynamics, and meso-scale oceanographic features (Bonomo et al., 2012; D'Amario et al., 2017; 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 (CH₄) 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 ~~ex-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 (Millet, 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 cCoccolith 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 histricea*, *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 (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 1σ uncertainties, and speleothem $\delta^{18}\text{O}$ with 1σ 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}O enrichment/depletion (Schrag et al., 2002)
 244 associated with ice-volume changes (Grant et al., 2012). Next, we calculated the 1st
 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 (16th–84th percentile) and 95% (2.5th–97.5th percentile) probability intervals and the
 254 probability maximum (PMAX, 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 \(Athanasίου et al., 2015\)](#). 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⁻¹ to 3.9 cm kyr⁻¹, 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⁻¹, 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 CH₄ concentrations and the Sanbao Cave $\delta^{18}\text{O}$ stack, ~~both~~ which are expected ~~thought~~

to reflect fluctuations in ~~the boreal monsoon~~ intensity ~~of the boreal monsoon~~ and attendant changes in the ~~wetland~~ spatial coverage of tropical wetlands (Cheng et al., 2016, 2009, 2006; Möller et al., 2013; Petrenko et al., 2009). We present tThe *F. profunda* time series (Grelaud et al., 2012) ~~is here presented~~ on the radiometrically constrained chronology of Grant et al. (2012), as natural logarithm of the original data. Within uncertainties of the various records, we note a strong similarity between the LC21 *F. profunda* record and variations of both Sanbao Cave speleothem $\delta^{18}\text{O}$ (Fig. 2a) and EDC CH_4 (Fig. 2b). Notably, a distinct *F. profunda* peak at ~129 ka appears contemporaneous with upper mixed layer thinning, with a maximum in the rates of Sanbao Cave $\delta^{18}\text{O}$ change and with the CH_4 overshoot in EDC. This suggests: (i) synchronous intensification of the African and Asian monsoons at the onset of the last interglacial period, in line with what has been documented for the early Holocene (Fleitmann et al., 2003; Marino et al., 2009; Nicholson et al., 2020; Tierney et al., 2008); and (ii) a rapid increase in freshwater discharge into the eastern Mediterranean at the onset of the last interglacial monsoon maximum, quantified as up to ~8.8 times the modern pre- Aswan Nile discharge and responsible for the most intense thinning of the upper summer mixed layer (Amies et al., 2019). Observation (ii) is particularly relevant because it alludes to the influence of the rates of monsoon intensification on stratification in the eastern Mediterranean. When large amounts of monsoon-fuelled freshwater are rapidly added to the basin, the strong evaporative climate of the Levant cannot keep up with sea-surface dilution (Rohling et al., 1991b) and the water column becomes strongly stratified (Rohling and Gieskes, 1989; Rohling et al., 2006; Marino et al., 2007; Athanasiou et al., 2015, 2017; Amies et al., 2019), causing shoaling of the pycnocline, the nutricline to be positioned at the base of the photic layer and the attendant development of a pronounced DCM.

In Figure 2d-f, LC21 holococcolith data are compared with North Atlantic and western Mediterranean Sea records. It is evident that there is no or poor preservation 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 C_{26}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 C_{26}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

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 21st 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~~ indicatessuggests 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

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

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

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

6.4 – AMOC slowdown, holococcolith preservation and monsoon weakening

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

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

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

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

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

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

The atmospheric CH₄ record from Antarctica ice cores (Fig. 6E) reflects emissions from boreal and monsoonal wetlands (Guo et al., 2012; Landais et al., 2010). The signal has been separated into three principal components, a glacial-interglacial forced component, a bi-hemispheric insolation driven component, and a millennial-scale oscillatory component, ~~that~~ which respectively explain 80%, 15% and 5% of the variance (Guo et al., 2012). Glacial-interglacial cycles force ~~a~~ globally synchronous monsoonal variations in methane emission. The other two forcings are hemispheric in nature, because of the two hemispheres' anti-phasing for low-latitude summer 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 CH₄ 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 CH₄ 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 CH₄ 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

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

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

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Captions

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

Fig. 2: plot of coccolith data in the Aegean Sea core LC21 and comparison with selected records. a) *Florisphaera profunda* percentage values (blue circles), expressed as natural logarithm (Grelaud et al., 2012). The 1st derivative of Sanbao Cave speleothem $\delta^{18}\text{O}$ (orange line) for each of the 10,000 ice-volume corrected ‘stacks’, following the chronology by Cheng et al. (2009) and after ice-volume correction. b) *Florisphaera profunda* percentage values (blue line), expressed as natural logarithm (Grelaud et al., 2012). Epica Dome C CH_4 (grey circles and grey line), following the Antarctic Ice Core chronology AICC2012 (Bazin et al., 2013) c) *Florisphaera profunda* percentage values (blue line), expressed as natural logarithm (Grelaud et al., 2012). Upper Summer Mixed Layer depth in the three different experiments by Amies et al. (2019) (respectively pink, orange and red lines for experiments A, B and C). d) Alkenone-derived SST (red circles) from the Alboran Sea (Martrat et al., 2014). e) Holococcoliths percentage values (blue circles, this 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 C₂₆OH 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.

1281 Fig. 3: plot of coccolith data at ODP Site 967 and comparison with selected records.
1282 A) June 21st 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).

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, R² correlation index
1296 and number of samples are also reported.

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

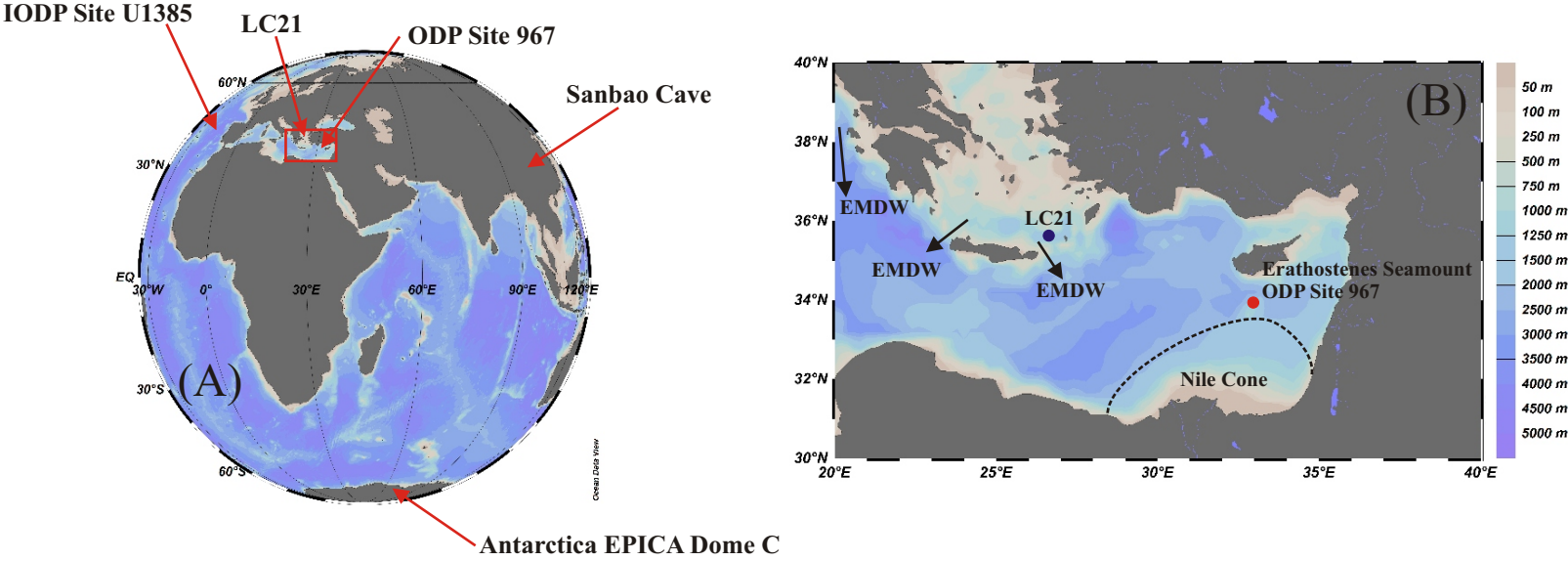
1303 layers (Grant et al., 2017). E) The Aeolian residual by Larrasoña et al. (2003)
1304 plotted by the Grant et al. (2017) chronology. F) The North Africa humidity/aridity
1305 index (Grant et al., 2017). G) The Ba/Al ratio (Grant et al., 2017). Horizontal thick
1306 black lines indicate MIS boundaries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

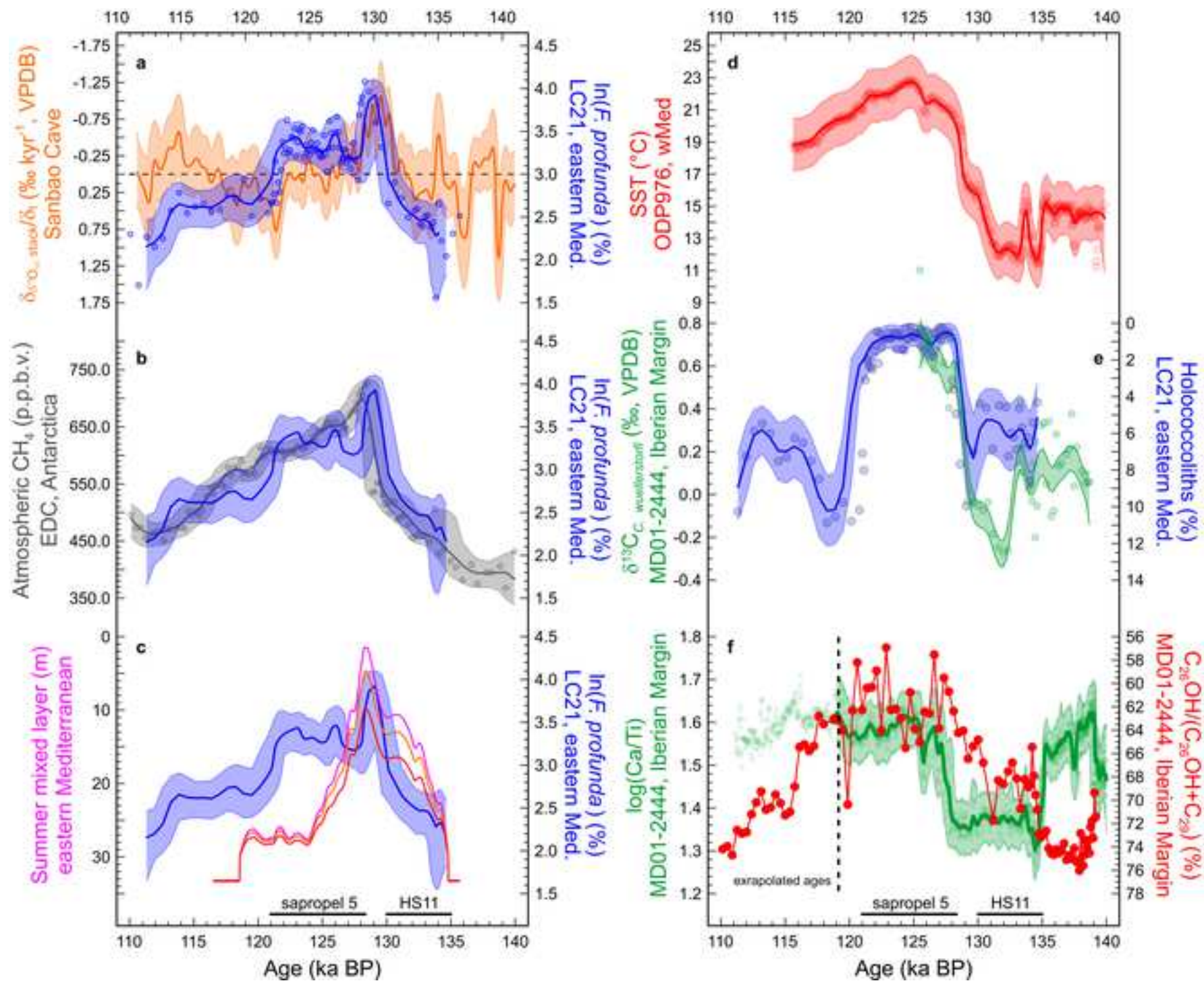
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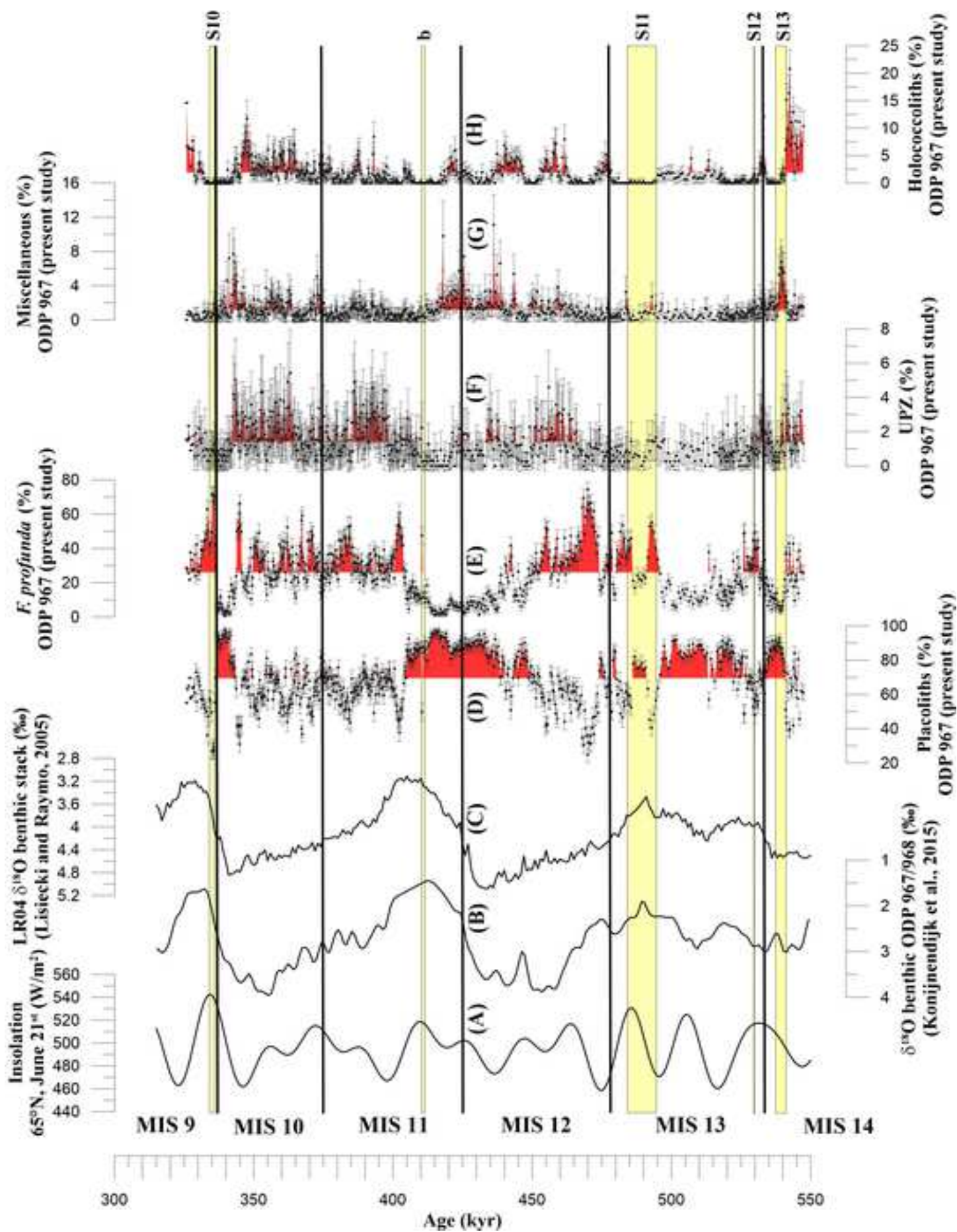
1310 Fig. 6: correlation among Mediterranean, North Atlantic, Asian and Antarctica
1311 records. A) Alkenone-based SSTs (°C) at Site MD01-2444, Iberian Margin (Martrat
1312 et al., 2007). B) Log (Ca/Ti) at IODP Site U1385, Iberian Margin (Hodell et al.,
1313 2015). Note the reversed axis. C) 3-pt running 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 CH_4 , Antarctica (Bazin et al., 2013).

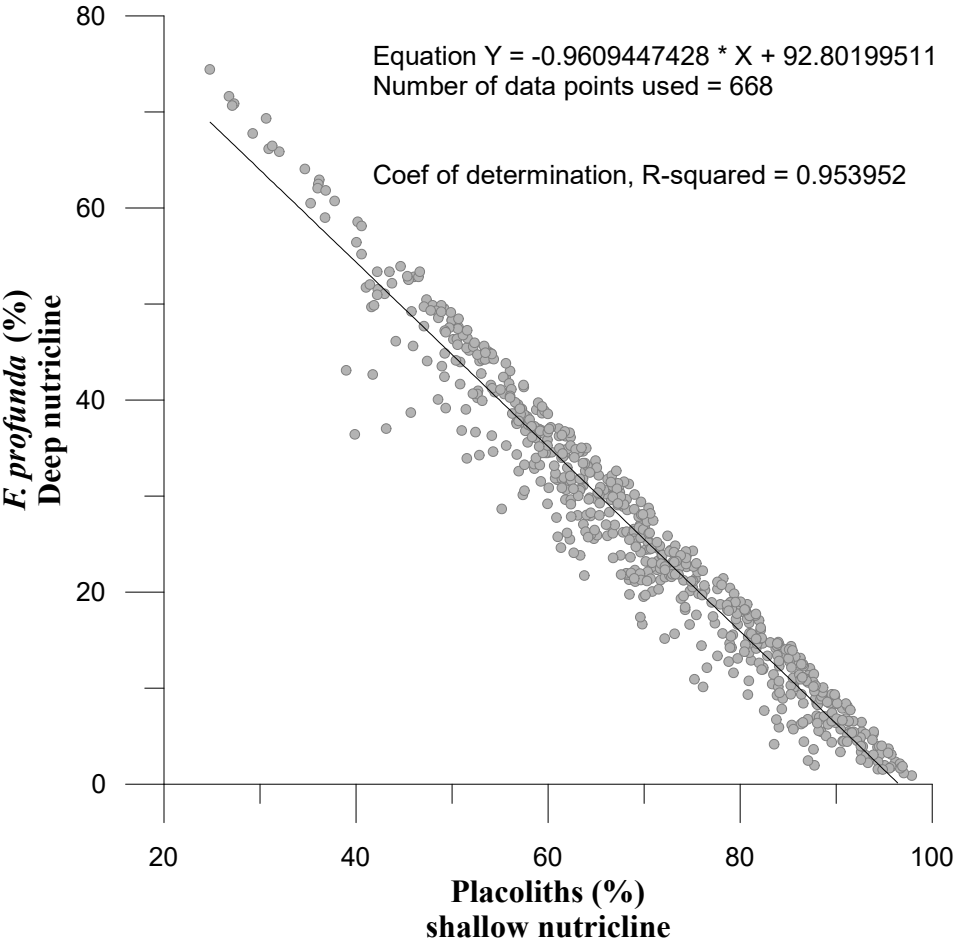
1317 Grey boxes indicate correlations among different records: cooling and AMOC
1318 weakening/shutdown in the Iberian Margin (A, B), holococcolith preservation in the
1319 eastern Mediterranean seafloor (C), monsoon activity weakening in China (D) and
1320 EDC methane concentration decrease in Antarctica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

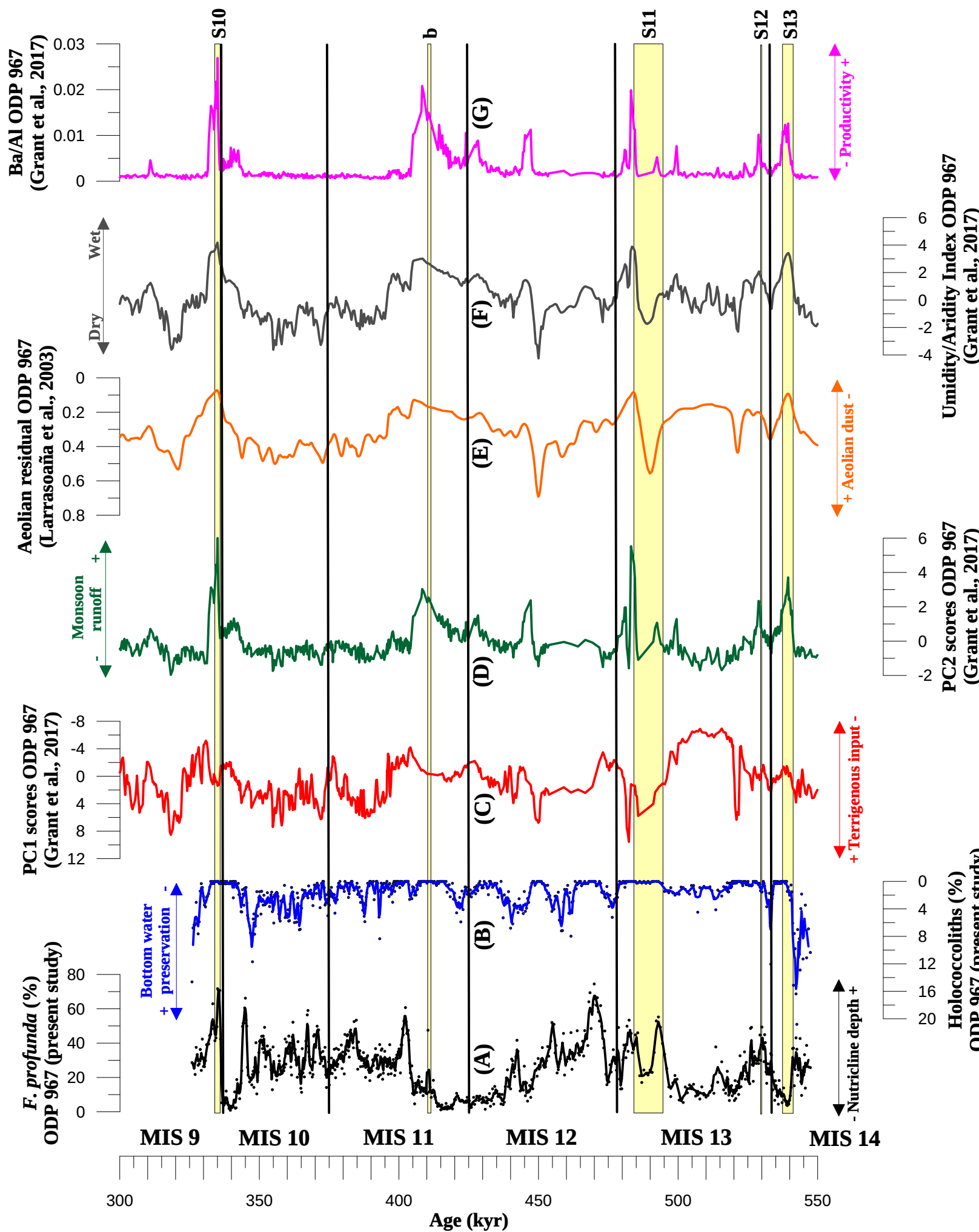
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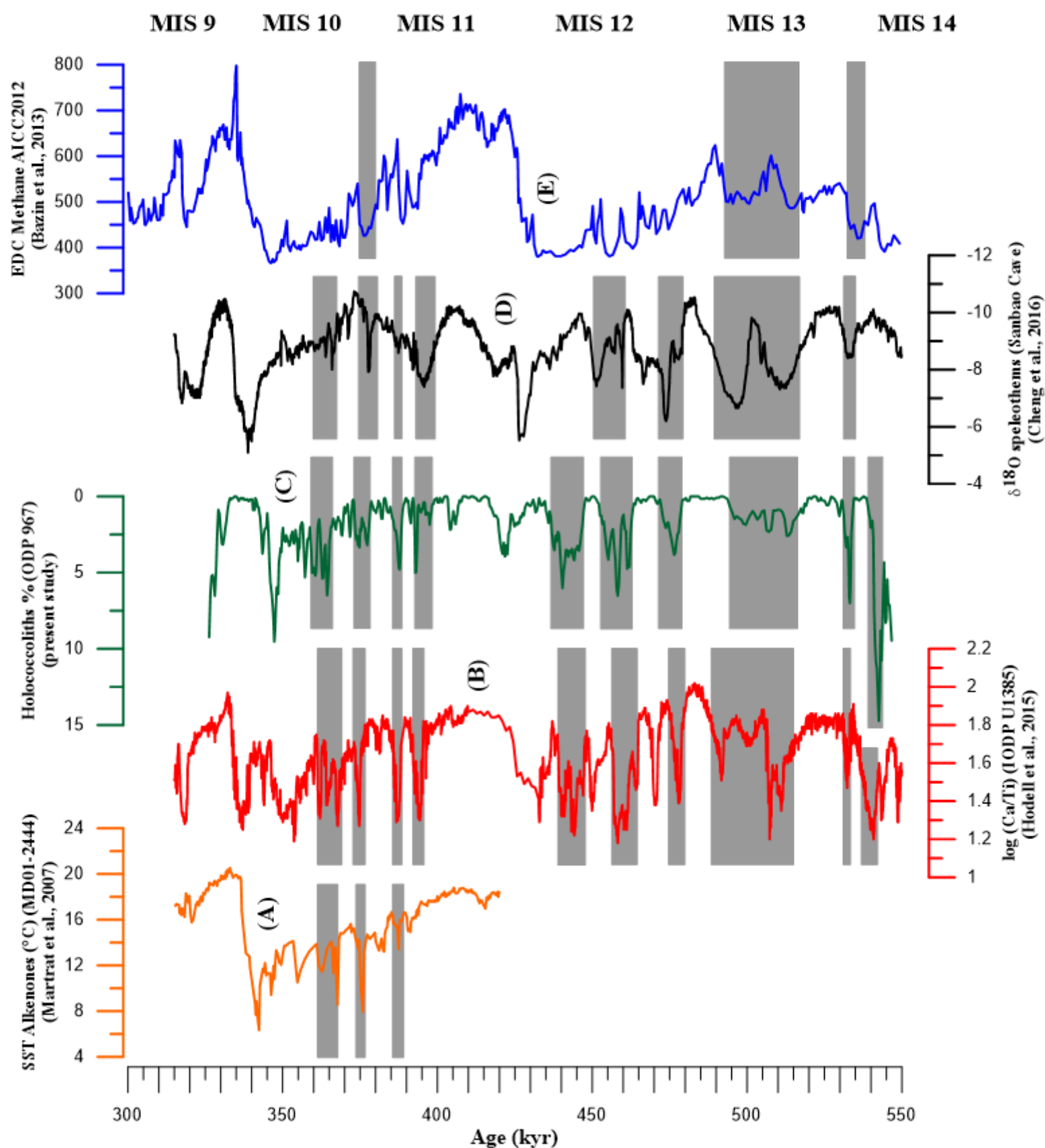












Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: