

1 **Major perturbations in the global carbon cycle and photosymbiont-bearing**
2 **planktic foraminifera during the early Eocene**

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19 **Abstract.** A marked switch in the abundance of the planktic foraminiferal genera
20 *Morozovella* and *Acarinina* occurred at low-latitude sites near the start of the Early Eocene
21 Climatic Optimum (EECO), a multi-million-year interval when Earth surface temperatures
22 reached their Cenozoic maximum. Stable carbon and oxygen isotope data of bulk sediment
23 are presented from across the EECO at two locations: Possagno in northeast Italy, and DSDP
24 Site 577 in the northwest Pacific. Relative abundances of planktic foraminifera are presented
25 from these two locations, as well as from ODP Site 1051 in the northwest Atlantic. All three
26 sections have good stratigraphic markers, and the $\delta^{13}\text{C}$ records at each section can be
27 correlated amongst each other and to $\delta^{13}\text{C}$ records at other locations across the globe. These
28 records show that a series of negative carbon isotope excursions (CIEs) occurred before,
29 during and across the EECO, which is defined here as the interval between the "J" event and
30 the base of *Discoaster subloboensis*. Significant though ephemeral modifications in planktic
31 foraminiferal assemblages coincide with some of the short-term CIEs, which were marked by
32 increases in the relative abundance of acarininids, similar to what happened across
33 established hyperthermal events in Tethyan settings prior to the EECO. Most crucially, a
34 temporal link exists between the onset of the EECO, carbon cycle changes during this time,
35 and the decline of morozovellids. Possible causes are multiple, and may include temperature
36 effects on photosymbiont-bearing planktic foraminifera and changes in ocean chemistry.

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45 **1 Introduction**

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47 Cenozoic Earth surface temperatures attained their warmest long-term state during the Early
48 Eocene Climatic Optimum (EECO). This was a 2-4 Myr time interval (discussed below)
49 centered at ca. 51 Ma (**Figure 1**), when average high latitude temperatures exceeded those at
50 present-day by at least 10°C (Zachos et al., 2008; Huber and Caballero, 2011; Hollis et al.,
51 2012; Pross et al., 2012; Inglis et al., 2015). Several short-term (<200 kyr) global warming
52 events (**Figure 1**) occurred before the EECO. The Paleocene Eocene Thermal Maximum
53 (PETM) provides the archetypical example: about 55.9 Ma (Vandenbergh et al., 2012;
54 Hilgen et al., 2015) temperatures soared an additional 5-6°C relative to background
55 conditions (Sluijs et al., 2006, 2007; Dunkley Jones et al., 2013). Evidence exists for at least
56 two other significant Eocene warming events (Cramer et al., 2003; Lourens et al., 2005; Röhl
57 et al., 2005; Thomas et al., 2006; Nicolo et al., 2007; Agnini et al., 2009; Cocconi et al.,
58 2012; Lauretano et al., 2015; Westerhold et al., 2015): one ca. 54.1 Ma and named H-1 or
59 Eocene Thermal Maximum 2 (ETM-2, also referred as the ELMO event), and one at 52.8 Ma
60 and variously named K, X, or ETM-3 (hereafter called K/X). However, additional brief
61 warming events may have spanned the early Eocene (above references; Kirtland-Turner et al.,
62 2014), and the EECO may comprise a series of successive events (Slotnick et al., 2012). Both
63 long-term and short-term intervals of warming corresponded to major changes in global
64 carbon cycling, although the precise timing between these parameters remains insufficiently
65 resolved.

66 In benthic foraminiferal stable isotope records for the early Paleogene (**Figure 1**), $\delta^{18}\text{O}$
67 serves as a proxy for deep-water temperature, while $\delta^{13}\text{C}$ relates to the composition of deep-
68 water dissolved inorganic carbon (DIC). The highest $\delta^{13}\text{C}$ values of the Cenozoic occurred at
69 ca. 58 Ma. From this Paleocene Carbon Isotope Maximum (PCIM), benthic foraminiferal

70 $\delta^{13}\text{C}$ values plunge by approximately 2.5 ‰ to reach a near Cenozoic minimum at or near the
71 start of the EECO, and subsequently rise by approximately 1.5 ‰ across this interval (Zachos
72 et al., 2001, 2008; Cramer et al., 2009). Benthic foraminiferal $\delta^{13}\text{C}$ records also exhibit
73 prominent negative carbon isotope excursions (CIEs) across the three hyperthermals
74 mentioned above (Kennett and Stott, 1991; Littler et al., 2014; Lauretano et al., 2015).
75 Crucially, at least from the late Paleocene to the start of the EECO, similar $\delta^{13}\text{C}$ records occur
76 in other carbon-bearing phases, such as bulk marine carbonate, planktic foraminifera, and
77 various marine and terrestrial organic carbon compounds (Shackleton, 1986; Schmitz et al.,
78 1996; Lourens et al., 2005; Nicolo et al., 2007; Agnini et al., 2009, submitted; Leon-
79 Rodriguez and Dickens, 2010; Abels et al., 2012; Coccioni et al., 2012; Sluijs and Dickens,
80 2012; Slotnick et al. 2012, 2015a; Clyde et al., 2013). This strongly suggests that observed
81 changes in $\delta^{13}\text{C}$, both long-term trends as well as short-term perturbations, represent
82 variations in the input and output of ^{13}C -depleted carbon to the exogenic carbon cycle
83 (Shackleton, 1986; Dickens et al., 1995; Dickens, 2000; Kurtz et al., 2003; Komar et al.,
84 2013).

85 Significant biotic changes occur in terrestrial and marine environments during times
86 when the early Paleogene $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ records show major variations. This has been
87 recognized for the PETM, where land sections exhibit a prominent mammal turnover
88 (Gingerich 2001, 2003; McInerney and Wing, 2011; Clyde et al., 2013), and where marine
89 sections reveal a profound benthic foraminiferal extinction (Thomas, 1998), turnovers in
90 calcareous nannoplankton, ostracods, corals and larger benthic foraminifera (Raffi and De
91 Bernardi, 2008; Scheibner and Speijer, 2008; Yamaguchi and Norris, 2012; Agnini et al.,
92 2014), and appearances of excursion taxa in calcareous nannoplankton, dinoflagellates and
93 planktic foraminifera (Kelly et al., 1996, 1998; Crouch et al., 2001; Sluijs et al., 2006; Self-
94 Trail et al., 2012). Major plant and mammal turnovers also occurred on land during the longer

95 EECO (Wing et al., 1991; Zonneveld et al., 2000; Wilf et al., 2003; Falkowski et al., 2005;
96 Woodbourne et al., 2009; Figueirido et al., 2012). In the marine realm, evolutionary trends
97 across the EECO have been noted, in particular the inception of modern calcareous
98 nannofossil community structure (Agnini et al., 2006, 2014; Schneider et al., 2011; Shamrock
99 et al., 2012) and possibly the same for diatoms (Sims et al., 2006; Oreshkina, 2012). These
100 observations, both from continents and the oceans, support an overarching hypothesis that
101 climate change drives biotic evolution, at least in part (Ezard et al., 2011).

102 Planktic foraminiferal assemblages are abundant in carbonate bearing marine sediments
103 and display distinct evolutionary trends that often can be correlated to climate variability
104 (Schmidt et al., 2004; Ezard et al., 2011; Fraass et al., 2015). This is especially true in the
105 early Paleogene, even though the relationship between climate variability and planktic
106 foraminiferal evolution remains insufficiently known. At the beginning of the Eocene,
107 planktic foraminifera had evolved over ca. 10 Myr following the Cretaceous-Paleogene mass
108 extinction event. Several early Paleogene phylogenetic lines evolved, occupying different
109 ecological niches in the upper water column. Subsequently, a major diversification occurred
110 during the early Eocene, which resulted in a peak of planktic foraminiferal diversity during
111 the middle Eocene (Norris, 1991; Schmidt et al., 2004; Pearson et al., 2006; Aze et al., 2011;
112 Ezard et al., 2011; Fraass et al., 2015).

113 In this study, we focus on the evolution of two planktic foraminiferal genera:
114 morozovellids and acarininids (**Figure 1**). These two genera belong to the “muricate group”,
115 a term derived from the muricae that form layered pustules on the test wall. These two genera
116 are of particular interest because of their dominance among tropical and subtropical
117 assemblages of the early Paleogene oceans, and because these genera show a major turnover
118 in taxonomic diversity close to the beginning of the EECO, one that comprises species
119 reduction among morozovellids and species diversification among acarininids (Lu and

120 Keller, 1995; Lu et al., 1998; Pearson et al., 2006; Aze et al., 2011).

121 Numerous lower Eocene sedimentary sections from lower latitudes contain well-
122 preserved (albeit often recrystallized) planktic foraminiferal tests. Changes in foraminiferal
123 assemblages presumably reflect relationships between climate and carbon cycling across the
124 EECO. The present problem is that no section examined to date provides counts of
125 foraminiferal assemblages, detailed stable isotope records and robust planktic foraminiferal
126 biostratigraphies across the entire EECO. Indeed, at present, only a few sites have detailed
127 and interpretable stable isotope records across much of the EECO (Slotnick et al., 2012,
128 2015a; Kirtland-Turner et al., 2014). Furthermore, the EECO lacks formal definition. As a
129 consequence, any relationship between climatic perturbations during the EECO and the
130 evolution of planktic foraminifera remains speculative. Here, we add new data from three
131 locations: the Possagno section from the western Tethys, DSDP Site 577 from the tropical
132 Pacific Ocean, and ODP Site 1051 from the subtropical Atlantic Ocean (**Figure 2**). These
133 sections hence represent a wide longitudinal span of low latitude locations during the early
134 Paleogene. By comparing stable isotope and planktic foraminiferal records at these three
135 locations, we provide a new foundation for understanding why the abundances of acarininids
136 and morozovellids changed during the EECO.

137

138 **2 The Early Eocene Climatic Optimum**

139

140 Evidence for extreme Earth surface warmth during a multi-million year time interval of the
141 early Eocene is overwhelming, and comes from many studies, utilizing both marine and
142 terrestrial sequences, and both fossil and geochemical proxies (Huber and Caballero, 2011;
143 Hollis et al., 2012; Pross et al., 2012). However, a definition for the EECO, including the
144 usage of “optimum”, endures as a perplexing problem. This is for several reasons, including

145 the basic facts that: (i) proxies for temperature should not be used to define a time increment,
146 (ii) clearly correlative records across the middle of the early Eocene with temporal resolution
147 less than 50 kyr remain scarce, and (iii) absolute ages across the early Eocene have changed
148 significantly (Berggren et al., 1995; Vandenberghe et al., 2102). As a consequence, various
149 papers discussing the EECO give different ages and durations spanning from 2 to 4 Myr long
150 sometime between circa 49 and 54 Ma (e.g., Yapp, 2004; Lowenstein and Demicco, 2006;
151 Zachos et al., 2008; Woodburne et al., 2009; Bijl et al., 2009; Smith et al., 2010; Hollis et al.,
152 2012; Slotnick et al., 2012; Puljalte et al., 2015).

153 The EECO, at least as presented in many papers, refers to the time of minimum $\delta^{18}\text{O}$
154 values in “stacked” benthic foraminifera stable isotope curves (**Figure 1**). These curves were
155 constructed by splicing together multiple $\delta^{18}\text{O}$ records generated at individual locations onto
156 a common age model (originally Berggren et al., 1995). However, the stacked curves (Zachos
157 et al., 2001, 2008; Cramer et al., 2009), while they can be adjusted to different time scales,
158 show significant variance in $\delta^{18}\text{O}$ across the middle to late early Eocene. Some of this
159 variance belies imprecisely calibrated records at individual sites, where cores do not align
160 properly in the depth domain (Dickens and Backman, 2013). Some of this variance probably
161 reflects a dynamic early Eocene climate regime, where average temperatures and atmospheric
162 $p\text{CO}_2$ across Earth changed significantly, perhaps on orbital time scales (Smith et al., 2010;
163 Slotnick et al., 2012, 2015a; Kirtland-Turner et al., 2014).

164 There is also the root problem as to where EECO starts and ends. At a basic level, the
165 interval characterized by the lowest Cenozoic benthic foraminiferal $\delta^{18}\text{O}$ values begins at a
166 time that closely corresponds with a long-term minimum in $\delta^{13}\text{C}$ values (**Figure 1**). This is
167 important for stratigraphic reasons because the two stable isotope curves were generated
168 using the same benthic foraminiferal samples, but $\delta^{13}\text{C}$ records at different locations should
169 necessarily correlate in the time domain (unlike $\delta^{18}\text{O}$ and temperature). The rationale for such

170 carbon isotope stratigraphy lies in the rapid cycling of carbon across Earth's surface
171 (Shackleton, 1986; Dickens, 2000).

172 The Eocene minimum in $\delta^{13}\text{C}$ corresponds to the K/X event (**Figure 1**), which happened
173 in polarity chron C24n.1n and approximately 3 Myr after the PETM (Agnini et al., 2009;
174 Leon-Rodriguez and Dickens, 2010; Slotnick et al., 2012; Dallanave et al., 2015; Lauretano
175 et al., 2015; Westerhold et al., 2015). However, in several detailed studies spanning the early
176 Eocene, changes in long-term trends appear to have occurred about 400 kyr before the K/X
177 event, and at an event called "J" (after Cramer et al., 2003), which happened near the
178 boundary of polarity chrons C24n.2r and C24n.3n (Slotnick et al., 2015a; Lauretano et al.,
179 2015). Notably, the long-term late Paleocene-early Eocene decrease in detailed benthic
180 foraminiferal $\delta^{18}\text{O}$ records at Site 1262 on Walvis Ridge ceases at the J event (Lauretano et
181 al., 2015).

182 The end of the EECO has received limited attention from a stratigraphic perspective. In
183 Paleogene continental slope sections now uplifted and exposed in the Clarence River Valley,
184 New Zealand, a major lithologic change from limestone to marl coincides with the J event
185 (Slotnick et al., 2012, 2015a; Dallanave et al., 2015). The marl-rich unit, referred to as
186 "Lower Marl", has been interpreted to reflect enhanced terrigenous supply to a continental
187 margin because of greater temperature and enhanced seasonal precipitation. It has been
188 suggested further that Lower Marl expresses the EECO (Slotnick et al., 2012; Dallanave et
189 al., 2015). The top of Lower Marl, and a return to limestone deposition, lies within the upper
190 part of polarity chron C22n (Dallanave et al., 2015). This is interesting because it
191 approximates the time when general long-term Cenozoic cooling initiates at several locations
192 that have records of polarity chrons and proxies for temperature (Hollis et al., 2012; Pross et
193 al., 2012). It is also useful from a stratigraphic perspective because the end of the EECO thus
194 lies close to a well documented and widespread calcareous nannofossil biohorizon, the base

195 of *Discoaster sublodoensis*. This marks the base of CP10, NP12 or CNE4, depending on the
196 chosen calcareous nannofossil zonal scheme (Okada and Bukry, 1080; Martini, 1971; Agnini
197 et al., 2014).

198 Without an accepted definition in the literature, we tentatively present the EECO as the
199 duration of time between the J event and the base of *D. sublodoensis*. This interval thus
200 begins at about 53 Ma and ends at about 49 Ma on the 2012 Time Scale (GTS; Vandenberghe
201 et al., 2012). However, while the EECO was characterized by generally warm conditions,
202 numerous fluctuations in average temperature likely occurred during the 4 Myr interval.

203

204 **3 Sites and stratigraphy**

205

206 **3.1 Possagno, Venetian Prealps, Tethys**

207

208 An Upper Cretaceous through Miocene succession crops out at the bottom of the Monte
209 Grappa Massif in the Possagno area, about 60 km northwest of Venice. The lower to middle
210 Eocene, of primary focus to this study, is represented by the Scaglia beds. These
211 sedimentary rocks represent pelagic and hemipelagic sediment that accumulated at middle to
212 lower bathyal depths (Cita, 1975; Thomas, 1998) in the western part of the Belluno Basin, a
213 Mesozoic–Cenozoic paleogeographic unit of the Southern Alps (Bosellini, 1989). The basin
214 very likely was an embayment connected to the western Tethys, with a paleolatitude of ca.
215 42° during the early Eocene (**Figure 2**).

216 A quarry at 45°51.0' N and 11°51.6' E exposed in 2002-2003 a 66 m thick section of
217 the Scaglia beds (Figure 3), although it is at present largely covered and inaccessible. This
218 section was examined for its stratigraphy (Agnini et al., 2006; Luciani and Giusberti, 2014),
219 and shown to extend from just below the PETM to within lower Chron C20r in the lower

220 middle Eocene. Like other lower Paleogene sections of the Venetian Pre-alps (Giusberti et
221 al., 2007; Agnini et al., submitted), a Clay Marl Unit (CMU) with a prominent negative CIE
222 marks the PETM.

223 The Possagno section appears to be continuous, but with an important decrease in
224 sedimentation rate (to below 1.4 m/Myr) between 14.66 m and 15.51 m (Agnini et al., 2006).
225 This interval lies within Chron C23r and near the start of the EECO, and predates the onset
226 of a major increase in discoaster abundance (Agnini et al., 2006).

227

228 **3.2 Site 577, Shatsky Rise, Western Pacific**

229

230 Deep Sea Drilling Project (DSDP) Leg 86 drilled Site 577 at 32°26.5' N, 157°43.4' E, and
231 2680 m water depth, on Shatsky Rise, a large igneous plateau in the NW Pacific with a
232 relatively thin veneer of sediment (Shipboard Scientific Party 1985). During the early
233 Eocene, this site was located closer to 15° N (**Figure 2**), and probably at a slightly shallower
234 water depth (Ito and Clift, 1998).

235 Two primary holes were drilled at Site 577. Both Hole 577* and Hole 577A recovered
236 portions of a nominally 65 m thick section of Upper Cretaceous through lower Eocene
237 nannofossil ooze. Similar to the Possagno section, the lower Paleogene interval has
238 biomagnetostratigraphic information (Bleil, 1985; Monechi et al., 1985; Backman, 1986; Lu
239 and Keller, 1995; Dickens and Backman, 2013). Stable isotope records of bulk carbonate
240 have been generated for sediment from several cores at low sample resolution (Shackleton,
241 1986), and for much of Cores 577*-9H and 577*-10H at fairly high sample resolution
242 (Cramer et al. 2003).

243 The composition and relative abundances of planktic foraminifera were nicely
244 documented at Site 577 (Lu, 1995; Lu and Keller, 1995), and show a marked turnover

245 between morozovellids and acarainids during the early Eocene. These data, however, have
246 remained on an out-dated view for the stratigraphy at this location, where cores were not
247 originally aligned to account for gaps and overlaps (Dickens and Backman, 2013). As will
248 become obvious later, the main phase of the EECO spans Cores 577*-8H and 577A-8H,
249 where detailed stable isotope records have not been generated previously.

250

251 **3.3 Site 1051, Blake Nose, Western Atlantic**

252

253 The Blake Nose is a gentle ramp extending from 1000 m to 2700 m water depth east of
254 Florida (Norris et al, 1998). The feature is known for a relatively thick sequence of middle
255 Cretaceous through middle Eocene sediment with minimal overburden. Ocean Drilling
256 Program (ODP) Leg 171B drilled and cored this sequence at several locations, including Site
257 1051 at 30°03.2' N, 76°21.5' W, and 1994 m water depth (Shipboard Scientific Party 1998).
258 The site was located slightly to the south during the early Eocene (**Figure 2**). Benthic
259 foraminiferal assemblages indicate a lower bathyal depth (1000-2000 m) during the late
260 Paleocene and middle Eocene (Norris et al., 1998), although Bohaty et al. (2009) estimated a
261 paleodepth of about 2200 m for sedimentation ca. 50 Ma.

262 Sediments from 452.24 to 353.10 meters below sea floor (mbsf) at Site 1051 consist of
263 lower to middle Eocene carbonate ooze and chalk (Shipboard Scientific Party, 1998). The
264 site comprises two holes (1051A and 1051B), with core gaps and core overlaps existing at
265 both (Shipboard Scientific Party, 1998). However, the impact of these depth offsets upon
266 age is less than at Site 577, because of higher overall sedimentation rates.

267 The Eocene section at Site 1051 has good sediment recovery, except an interval between
268 382 mbsf and 390 mbsf, which contains significant chert. Stratigraphic markers across the
269 Eocene interval include polarity chrons (Ogg and Bardot, 2001), calcareous nannofossil

270 biohorizons (Mita, 2001), and planktic foraminiferal biohorizons (Norris et al., 1998; Luciani
271 and Giusberti, 2014). As first noted by Cramer et al. (2003), though, there is a basic
272 stratigraphic problem with the labelling of the polarity chrons. The intervals of normal
273 polarity between approximately 388 and 395 mbsf, and between approximately 412 and 420
274 mbsf were tentatively assigned to C22n and C23n, respectively (Ogg and Bardot, 2001). This
275 age assignment was assumed to be correct by Luciani and Giusberti (2014), who therefore
276 considered the last occurrence of *Morozovella subbotinae* as happening near the top of C23n,
277 an assumption that was also made for the revision of Eocene foraminiferal biozones (Wade et
278 al., 2011).

279 These age assignments, however, cannot be correct, because calcareous nannofossil
280 biohorizons that lie below or within C22n (top of *T. orthostylus*, top of *Toweius*, base of *D.*
281 *sublodoensis*) occur above 388 mbsf (Mita, 2001). Instead, there must be a significant hiatus
282 or condensed interval at the chert horizon, and the above noted intervals of normal polarity
283 are C23n and C24n.1n.

284

285 **4 Methods**

286

287 **4.1 Samples for isotopes and foraminifera**

288

289 The three sites provide a good stratigraphic background and key existing data for
290 understanding the temporal link between the EECO, carbon isotope perturbations and
291 planktic foraminiferal evolution. Our analytical aim was to obtain comparable data sets
292 across the sites. More specifically, a need existed to generate stable isotope and planktic
293 foraminiferal assemblage records at the Possagno section, to generate stable isotope records
294 at DSDP Site 577, and to generate planktic foraminiferal assemblage records at ODP Site

295 1051.

296 In total, 298 samples were collected from the originally exposed Possagno section in
297 2002-2003 for isotope analyses. The sampling interval was 2 to 5 cm for the basal 0.7 m, and
298 at variable spacing from 20 to 50 cm for the interval between 0.7 m and 66 m. Bulk sediment
299 samples previously were examined for their calcareous nannofossil assemblages (Agnini et
300 al., 2006). One hundred and ten of these samples were selected for the foraminiferal study.

301 Aliquots of the 110 samples were weighed, and then washed to obtain foraminifera using
302 two standard procedures, depending on lithology. For the indurated marly limestones and
303 limestones, the cold-acetolyse technique was used (Lirer, 2000; Luciani and Giusberti, 2014).
304 This method disaggregates strongly lithified samples, in which foraminifera otherwise can be
305 analyzed only with thin sections (Fornaciari et al., 2007; Luciani et al., 2007). For the marls,
306 samples were disaggregated using 30 % hydrogen peroxide and subsequently washed and
307 sieved at 63 μm . In most cases, gentle ultrasonic treatment (e.g., low-frequency at 40 kHz for
308 30–60 seconds) improved the cleaning of the tests.

309 Relative abundance data of planktic foraminiferal samples were generated for 65 samples
310 at Site 577 (Lu, 1995; Lu and Keller, 1995). We collected new samples for stable isotope
311 measurements that span their previous effort.

312 Fifty samples of Eocene sediment were obtained from Hole 1051A between 452 to 353
313 mbsf. Sample spacing varied from 2.0 m to 0.5 m. As the samples are ooze and chalk, they
314 were prepared using disaggregation using distilled water and washing over 38 μm and 63 μm
315 sieves. Washed residues were dried at $<50^{\circ}\text{C}$.

316

317 **4.2 Stable Isotopes**

318

319 Carbon and oxygen stable isotope data of bulk sediment samples from the Possagno section

320 and Site 577 were analysed using a Finnigan MAT 252 mass spectrometer equipped with a
321 Kiel device at Stockholm University. Precision is within ± 0.06 ‰ for carbon isotopes and
322 within ± 0.07 ‰ for oxygen isotopes. Stable isotope values were calibrated to the Vienna Pee
323 Dee Belemnite standard (VPDB) and converted to conventional delta notation ($\delta^{13}\text{C}$ and
324 $\delta^{18}\text{O}$).

325

326 **4.3 Foraminifera analyses**

327

328 The mass percent of the >63 μm size fraction relative to the mass of the bulk sample,
329 typically 100 g/sample was calculated for the 110 Possagno samples. This is referred to as the
330 weight percent coarse fraction, following many previous works. Due to the consistent
331 occurrence of radiolarians at Site 1051, the coarse fraction cannot give information on
332 foraminiferal productivity.

333 Relative abundances for both Possagno and Site 1051 have been determined from about
334 300 complete specimens extracted from each of the 110 samples investigated in the >63 μm
335 size fraction from random splits.

336 The degree of dissolution, expressed as the fragmentation index (F index) was evaluated
337 according to Petrizzo et al. (2008) on ca. 300 elements, by counting planktic foraminiferal
338 fragments or partially dissolved tests versus complete tests. These data are expressed in
339 percentages. Fragmented foraminifera include specimens showing missing chambers and
340 substantial breakage. The taxonomic criteria for identifying planktic foraminifera follows the
341 work by Pearson et al. (2006).

342

343 **5 Results**

344

345 **5.1 Carbon isotopes**

346

347 Possagno

348 Carbon isotopes of bulk carbonate at Possagno vary between +1.8 and -0.3 ‰ (**Figure 4,**
349 **Table S1**). Overall, $\delta^{13}\text{C}$ decreases from 1.8 ‰ at the base of the section to about 0.6 ‰ at 14
350 m. Generally, values then increase to 1.5 ‰ at 24 m, and remain between 1.5 ‰ and 0.8 ‰
351 for the remainder of the studied interval.

352 Superimposed on these trends are a series of negative CIEs. The most prominent of these
353 (~1.5 ‰) occurs at the 0 m level, and marks the PETM (Agnini et al., 2009). However, other
354 negative CIEs lie above this marker and within the lowermost 21.4 m, albeit some are only
355 defined by one data point (**Figure 4, Table S1**). The lower two at ~8 m and ~12.5 m probably
356 represent the H-1/ETM-2 and J event, respectively, as they lie at the appropriate stratigraphic
357 horizons in relation to polarity chrons. The K/X event may lie at 14.8 m, although this height
358 marks the start of the condensed interval.

359 The complex interval between 15.5 m and 24 m broadly corresponds to all of Chron
360 C23n and the bottom half of Chron C22r. A series of CIEs occur in that interval on the order
361 of 1.4 ‰, superimposed on a background trend of increasing $\delta^{13}\text{C}$ values (about 0.7 ‰). We
362 tentatively label these CIEs with even numbers for internal stratigraphic purposes (**Figure 4**),
363 as will become obvious below; their magnitudes range between 0.9 and 0.3 ‰ (**Table S1**).
364 However, the sample spacing through this interval varies from 20 to 50 cm. The precise
365 magnitudes and positions certainly could change with higher sample resolution, given the
366 estimated compacted sedimentation rate of ~0.5 cm/kyr for this part of the section (Agnini et
367 al., 2006).

368 Above Chron C22r, the Possagno $\delta^{13}\text{C}$ record contains additional minor CIEs (**Figure 4**).
369 The most prominent of these CIEs, at least relative to baseline values (~1.2 ‰), occurs within

370 Chron C21n. More important to understanding the EECO, a ~ 0.6 ‰ CIE nearly coincides
371 with the base of *D. sublodoensis* within the lower part of Chron C22n.

372

373 DSDP Site 577

374 The $\delta^{13}\text{C}$ record of bulk carbonate at DSDP Site 577 from just below the PETM through
375 Chron C22n ranges between 2.3 and 0.6 ‰ (**Figure 5; Table S2**). Overall, $\delta^{13}\text{C}$ decreases
376 from 1.4 ‰ at 84.5 mcd to about 0.6 ‰ at ~ 76 mcd. Values then generally increase to 2.1 ‰
377 at ~ 68 mcd, and remain between 2.3 ‰ and 1.6 ‰ for the rest of the studied interval. Thus,
378 the ranges and general trends in $\delta^{13}\text{C}$ for the two sections are similar, but skewed at DSDP
379 Site 577 relative to Possagno by about +0.6 ‰.

380 Like at Possagno, the early Eocene $\delta^{13}\text{C}$ record at DSDP Site 577 exhibits a series of
381 CIEs (**Figure 5**). The portion of this record from the PETM through the K/X event has been
382 documented and discussed elsewhere (Cramer et al., 2003; Dickens and Backman, 2013). The
383 new portion of this record, from above the K/X event through Chron C22n, spans the
384 remainder of the EECO. Within this interval, where background $\delta^{13}\text{C}$ values rise by ~ 1.5 ‰,
385 there again occur a series of minor CIEs with magnitudes between 0.3 and 0.5 ‰ (**Table S2**).
386 Here, however, multiple data points define most of the CIEs. We again give these an internal
387 numerical labelling scheme. A ~ 0.4 ‰ CIE also nearly coincides with the base of *D.*
388 *sublodoensis* within the lower part of C22n.

389

390 **5.2 Oxygen isotopes**

391

392 Possagno

393 Oxygen isotopes of bulk carbonate at Possagno range between -3.3 and 0.8 ‰ with a mean
394 value of -1.7 ‰ (**Figure 4, Table S1**). In general, considerable scatter exists across the data

395 set with respect to depth, as adjacent samples often display a difference in $\delta^{18}\text{O}$ that exceeds
396 0.5 ‰. Nonetheless, some of the more prominent lows in $\delta^{18}\text{O}$ show a clear correspondence
397 with negative $\delta^{13}\text{C}$ values (CIEs) and vice versa. This correspondence occurs across the
398 PETM and other known hyperthermals, as well as within and after the EECO. Indeed, the
399 main phase of the EECO corresponds with a broad has the lowest $\delta^{18}\text{O}$ values.

400

401 DSDP Site 577

402 The $\delta^{18}\text{O}$ record at Site 577 noticeably deviates from that at Possagno (**Figure 5, Table S2**).
403 This is because values range between -1.1 ‰ and 0.2 with an average value of -0.4 ‰. Thus,
404 relative to Possagno, the record at Site 577 has less scatter, and an overall shift of about -1.3
405 ‰. There ~~is~~ exists again a modest correlation between decreases in $\delta^{18}\text{O}$ and negative $\delta^{13}\text{C}$
406 values, as well as a general low in $\delta^{18}\text{O}$ across the main phase of the EECO.

407

408 **5.3 Coarse fraction**

409

410 The coarse fraction of samples from Possagno shows two distinct trends (**Figure 6, Table**
411 **S3**). Before the EECO, values are $10.4\% \pm 2.67\%$. However, from the base of the EECO
412 and up through the section, values decrease to $5.3 \pm 1.3\%$.

413

414 **5.4 Foraminiferal preservation and fragmentation**

415

416 Planktic foraminifera are consistently present and diverse throughout the studied intervals at
417 Possagno and at ODP Site 1051. Preservation of the tests at Possagno varies from moderate
418 to fairly good (Luciani and Giusberti, 2014). However, planktic foraminiferal tests at
419 Possagno are recrystallized and essentially totally filled with calcite. Planktic foraminifera

420 from samples at Site 1051 are readily recognizable throughout the studied interval. Planktic
421 foraminifera from Site 577, at least as illustrated by published plates (Lu and Keller, 1995),
422 show a very good state of preservation (albeit possibly recrystallized).

423 The *F* index record at Possagno (**Figure 6, Table S3**) displays large amplitude variations
424 throughout the investigated interval. The highest values, up to 70 %, were observed between
425 16 and 22 m. In general, highs in *F* index values correspond to lows in the $\delta^{13}\text{C}$ record.

426 The *F* index record at Site 1051 (**Figure 8, Table S4**) shows less variability compared to
427 that at Possagno, although some of this may reflect the difference in the number of samples
428 examined at the two locations. A maximum value of 60 % is found in Zone E5, just below an
429 interval of uncertain magnetostratigraphy (Norris et al., 1998), but corresponding to the J
430 event (Cramer et al., 2003). Relatively high *F* index values, around 50 %, also occur in
431 several samples below this horizon. The interval across the EECO generally displays low *F*
432 index values (<20 %).

433

434 **5.5 Planktic foraminiferal quantitative analysis**

435

436 Possagno

437 Planktic foraminiferal assemblages at Possagno show significant changes across the early to
438 early middle Eocene (**Figure 6, Table S3**). Throughout the entire section, the mean relative
439 abundance of *Acarinina* is about 46 % of the total assemblage. However, members of this
440 genus ~~show~~ exhibit peak abundances of 60-80 % of the total assemblage ~~occur~~ across several
441 intervals, often corresponding to CIEs. Particularly prominent is the broad abundance peak of
442 *Acarinina* coincident with the main phase of the EECO.

443 The increases in acarininid relative abundance typically are counterbalanced by transient
444 decreases of subbotinids (**Figure 6**). This group also shows a general increase throughout the

445 section. Below the EECO the relative abundances of subbotinids average ~24 %. Above the
446 EECO, this average rises to ~36 %.

447 The trends of acarininids and subbotinids contrast with that of morozovellids (**Figure 6**),
448 which exhibit a major and permanent decline within Zone E5. This group collapses from
449 mean abundances ~24 % in the 0-15 m interval to <6 % above 15 m. Qualitative examination
450 of species shows that, in the lower part of Zone E5, where relatively high morozovellids
451 abundances are recorded, there is no dominance of any species. *M. marginodentata*, *M.*
452 *subbotinae* and *M. lensiformis* are each relatively common, and *M. aequa*, *M. aragonensis*,
453 *M. formosa* and *M. crater* are each less common. By contrast, in the upper part of Zone E5,
454 where low abundances of morozovellids occur, *M. aragonensis*, *M. formosa*, *M. crater* and
455 *M. caucasica* are the most common species. The general decrease of morozovellids
456 abundances appears unrelated to the disappearance of a single, dominant species.

457 At Possagno, morozovellids never recover to their pre-EECO abundances. This is true
458 even if one includes the morphologically and ecologically comparable genus *Morozovelloides*
459 (Pearson et al., 2006), which first appears in samples above 36 m.

460 Other planktic foraminiferal genera are always less than 15 % of the total assemblages
461 throughout the studied interval at Possagno (**Figure S1, Table S3**).

462

463 ODP Site 577

464 Samples from Site 577 were disaggregated in water and washed through a >63 sieve (Lu,
465 1995; Lu and Keller, 1995). They determined relative abundances of planktic foraminifera
466 from random splits of about 300 specimens (Lu, 1995; Lu and Keller, 1995). The resulting
467 data are shown in **Figure 7**, placed onto the composite depth scale by Dickens and Backman
468 (2013). Major changes in planktic foraminiferal assemblages are comparable to those
469 recorded at Possagno. Such changes include indeed a distinct decrease of morozovellids

470 within Zone E5. The decrease at Site 577 is from mean values of 26.6 % to 6.7 % (**Table S4**).
471 This marked drop occurs at ca. 78 mcd close to the J event and at the start of the EECO. Like
472 at Possagno, morozovellids never recover to their pre-EECO abundances.

473 The morozovellids decrease is counter balanced by the trend of acarininid abundances
474 that increase from mean values of 30.4 % to 64.8 % in correspondence to the level of the
475 morozovellid collapse. Subbotinids fluctuate in abundance throughout the interval
476 investigated from 1 % to 18 %, with a mean value of ca. 8 %.

477

478 ODP Site 1051

479 Planktic foraminifera show distinct changes in abundance at Site 1051 (**Figure 8, Table S5**).

480 The changes of the main taxa are similar to the variations observed at Possagno. The genus
481 *Acarinina* displays an increase in mean relative abundance from 35 % (base to ca. 450 mbsf)
482 to around 50 % (ca. 430 mbsf), with maximum values of about 60 %. The relatively low
483 resolution used here does not permit comparison to the early Eocene CIEs at Site 1051
484 (Cramer et al., 2003), or how the relative abundance of planktic foraminiferal genera varies
485 with respect to CIEs.

486 The abundance of subbotinids shows ~~little~~ small variations around mean values of 20 %
487 at Site 1051. Like at Possagno, samples from Site 1051 also record a slight increase in
488 abundance toward the end of the EECO and above.

489 The major change in planktic foraminiferal assemblages at Site 1051 includes a distinct
490 decrease of *Morozovella*, from mean values around 40 % to 10 % in the middle part of Zone
491 E5 (**Figure 7**). Similar to Possagno, the lower part of Zone E5 with the higher percentages of
492 morozovellids does not record the dominance of selected species, but at Site 1051 *M.*
493 *aragonensis* and *M. formosa* besides *M. subbotinae* are relatively common whereas *M.*
494 *marginodentata* is less frequent. Within the interval of low morozovellids abundances, *M.*

495 *aragonensis* and *M. formosa* are the most common taxa. The general decline of
496 morozovellids does not appear therefore related, both at Possagno and at Site 1051, to the
497 extinction or local disappearance of a dominant species.

498

499 **6 Discussion**

500

501 **6.1 Dissolution, recrystallization, and bulk carbonate stable isotopes**

502

503 The bulk carbonate stable isotope records within the lower Paleogene sections at Possagno
504 and at Site 577 need thought, considering how such records are produced and modified in
505 much younger strata dominated by pelagic carbonate. In open ocean environments, carbonate
506 preserved on the seafloor principally consists of calcareous tests of nannoplankton
507 (coccolithophores) and planktic foraminifera (Bramlette and Riedel, 1954; Berger, 1967;
508 Vincent and Berger, 1981). However, the total amount of carbonate and its microfossil
509 composition can vary considerably across locations because of differences in deep-water
510 chemistry and in test properties (e.g., ratio of surface area to volume; mineralogical
511 composition). For regions at low to mid latitudes, a reasonable representation of carbonate
512 components produced in the surface water accumulates on the seafloor at modest (<2000 m)
513 water depth. By contrast, microfossil assemblages become heavily modified in deeper water,
514 because of increasingly significant carbonate dissolution (Berger, 1967). Such dissolution
515 preferentially affects certain tests, such as thin-walled, highly porous planktic foraminifera
516 (Berger, 1970; Bé et al., 1975; Thunell and Honjo, 1981).

517 The stable isotope composition of modern bulk carbonate ooze reflects the mixture of its
518 carbonate components, which mostly record water temperature and the composition of
519 dissolved inorganic carbon (DIC) within the mixed layer (<100 m water depth). The stable

520 isotope records are imperfect, though, because of varying proportions of carbonate
521 constituents, and “vital effects”, which impact stable isotope fractionation for each
522 component (Anderson and Cole, 1975; Reghellin et al., 2015). Nonetheless, the stable isotope
523 composition of bulk carbonate ooze on the seafloor can be related to overlying temperature
524 and chemistry of surface water (Anderson and Cole, 1975; Reghellin et al., 2015).

525 Major modification of carbonate ooze occurs during sediment burial. This is because,
526 with compaction and increasing pressure, carbonate tests begin to dissolve and recrystallize
527 (Schlanger and Douglas, 1974; Borre and Fabricus, 1998). Typically within several hundred
528 meters of the seafloor, carbonate ooze becomes chalk and, with further burial, limestone
529 (Schlanger and Douglas, 1974; Kroencke et al., 1991; Borre and Fabricus, 1998). Carbonate
530 recrystallization appears to be a local and nearly closed system process, such that mass
531 transfer occurs over short distances (i.e., less than a few meters) (above references and Matter
532 et al., 1975; Arthur et al., 1984; Frank et al., 1999).

533 In pelagic sequences with appreciable carbonate content and low organic carbon content,
534 bulk carbonate $\delta^{13}\text{C}$ records typically give information of paleoceanographic significance
535 (Scholle and Arthur, 1980; Frank et al., 1999). Even when transformed to indurated
536 limestone, the $\delta^{13}\text{C}$ value for a given sample should be similar to that originally deposited on
537 the seafloor. This is because, for such sediments, almost all carbon within small ~~sedimentary~~
538 volumes exists as carbonate. Bulk carbonate $\delta^{18}\text{O}$ records are a different matter, especially in
539 indurated marly limestones and limestones (Marshall, 1992; Schrag et al., 1995; Frank et al.,
540 1999). This is because pore water dominates the total amount of oxygen within an initial
541 parcel of sediment, and oxygen isotope fractionation depends strongly on temperature. Thus,
542 during dissolution and recrystallization of carbonate, significant exchange of oxygen isotopes
543 occurs. At first, carbonate begins to preferentially acquire ^{18}O , because shallowly buried
544 sediment generally has lower temperatures than surface water. However, with increasing

545 burial depth along a geothermal gradient, carbonate begins to preferentially acquire ^{16}O
546 (Schrag et al., 1995; Frank et al., 1999).

547

548 **6.2 Carbon isotope stratigraphy through the EECO**

549

550 Stratigraphic issues complicate direct comparison of various records from Possagno and Site
551 577. The two sections have somewhat similar multi-million year sedimentation rates across
552 the early Eocene. However, the section at Possagno contains the condensed interval, where
553 much of C23r spans a very short distance (Agnini et al., 2006), and the section at Site 577 has
554 a series of core gaps and core overlaps (Dickens and Backman, 2013).

555 An immediate issue to amend is the alignment of Cores 8H and 9H in Hole 577* and
556 Core 8H in Hole 577A (**Figure 5**). On the basis of GRAPE density records for these cores,
557 Dickens and Backman (2013) initially suggested a 2.6 m core gap between Cores 8H* and
558 9H*. However, a 3.5 m core gap also conforms to all available stratigraphic information. The
559 newly generated $\delta^{13}\text{C}$ (and $\delta^{18}\text{O}$) records across these three cores show the latter to be correct.

560 Once sedimentation rate differences at Possagno are recognized and coring problems at
561 Site 577 are rectified, early Eocene $\delta^{13}\text{C}$ records at both locations display similar trends and
562 deviations in relation to polarity chrons and key microfossil events (**Figures 4, 5**). Moreover,
563 the $\delta^{13}\text{C}$ variations seemingly can be correlated in time to those found in bulk carbonate $\delta^{13}\text{C}$
564 records at other locations, including Site 1051 (**Figure 8**) and Site 1258 (**Figure 9**). As noted
565 previously, such correlation occurs because the bulk carbonate $\delta^{13}\text{C}$ signals reflect past global
566 changes in the composition of surface water DIC, even after carbonate recrystallization.

567 For the latest Paleocene and earliest Eocene, nominally the time spanning from the base
568 of C24r through the middle of C24n, detailed stable carbon isotope records have been
569 generated at more than a dozen locations across the globe (Cramer et al., 2003; Agnini et al.,

570 2009; Galeotti et al., 2010; Zachos et al., 2010; Slotnick et al., 2012; Littler et al., 2014;
571 Agnini et al., in review). These records can be described consistently as a long-term drop in
572 $\delta^{13}\text{C}$ superimposed with a specific sequence of prominent CIEs that include those
573 corresponding to the PETM, H-1, and J events. In continuous sections with good
574 magnetostratigraphy and biostratigraphy, there is no ambiguity in the assignment of CIEs
575 (Zachos et al., 2010; Littler et al., 2014; Slotnick et al., 2012, 2105a; Lauretano et al., 2015).
576 This “ $\delta^{13}\text{C}$ template” can be found at the Possagno section and at Site 577 (**Figure 9**); it is
577 found at Site 1051 for the depth interval where carbon isotopes have been determined
578 (**Figure 8**).

579 After the J event and across the EECO, very few detailed $\delta^{13}\text{C}$ records have been
580 published (Slotnick et al., 2012, 2015a; Kirtland-Turner et al., 2014). Moreover, the available
581 records are not entirely consistent. For example, the K/X event in Clarence River valley
582 sections manifests as a prominent CIE within a series of smaller $\delta^{13}\text{C}$ excursions (Slotnick et
583 al., 2012, 2015a), whereas the event has limited expression in the $\delta^{13}\text{C}$ record at Site 1258
584 (Kirtland-Turner et al., 2014; **Figure 9**).

585 The new records from Possagno and Site 577 emphasize an important finding regarding
586 bulk carbonate $\delta^{13}\text{C}$ records across the EECO. Between the middle of C24n and the upper
587 part of C23r, there appears to be a sequence of low amplitude, low frequency CIEs. (Note
588 that this portion of the record is missing at Possagno because of the condensed interval;
589 **Figure 9**). However, near the C23r/C23n boundary, a long-term rise in $\delta^{13}\text{C}$ begins, but with
590 a series of relatively high amplitude, high frequency CIEs (Kirtland-Turner et al., 2014;
591 Slotnick et al., 2014). The number, relative magnitude and precise timing of CIEs within this
592 interval remain uncertain. For example, the CIE labelled “4” appears to occur near the top of
593 C23r at Site 577 but near the bottom of C23n.2n at Site 1258 and at Possagno. Additional
594 $\delta^{13}\text{C}$ records across this interval are needed to resolve the correct sequence of CIEs and to

595 derive an internally consistent labelling scheme for these perturbations. It is also not clear
596 which of these CIEs during the main phase of the EECO specifically relate to significant
597 increases in temperature, as clear for the “hyperthermals” in the earliest Eocene. Nonetheless,
598 numerous CIEs, as well as an apparent change in the mode of these events, characterize the
599 EECO (Kirtland-Turner et al., 2014; Slotnick et al., 2014).

600 The causes of $\delta^{13}\text{C}$ changes during the early Paleogene lie at the crux of considerable
601 research and debate (Dickens et al., 1995, 1997; Zeebe et al., 2009; Dickens, 2011; Lunt et
602 al., 2011; Sexton et al., 2011; De Conto et al., 2012; Lee et al., 2013; Kirtland Turner et al.,
603 2014). Much of the discussion has revolved around three questions: (1) what are the sources
604 of ^{13}C -depleted carbon that led to prominent CIEs, especially during the PETM? (2) does the
605 relative importance of different carbon sources vary throughout this time interval? and, (3)
606 are the geologically brief CIEs related to the longer secular changes in $\delta^{13}\text{C}$? One might
607 suggest, through several papers, a convergence of thought as to how carbon cycled across
608 Earth’s surface during the early Paleogene, at least between the late Paleocene and the K/X
609 event (Cramer et al., 2003; Lourens et al., 2005; Galeotti et al., 2010; Hyland et al., 2013;
610 Zachos et al., 2010; Lunt et al. 2011; Littler et al., 2014; Lauretano et al., 2015; Westerhold et
611 al., 2015). Changes in tectonics, volcanism, and weathering drove long-term changes
612 atmospheric $p\text{CO}_2$ (Vogt, 1979; Raymo and Ruddiman, 1992; Sinton and Duncan, 1998;
613 Demicco, 2004; Zachos et al., 2008), which was generally high throughout the early
614 Paleogene, but increased toward the EECO (Pearson and Palmer, 2000; Fletcher et al., 2008;
615 Lowenstein and Demicco, 2006; Smith et al., 2010; Hyland and Sheldon, 2013). However, as
616 evident from the large range in $\delta^{13}\text{C}$ across early Paleogene stable isotope records, major
617 changes in the storage and release of organic carbon must have additionally contributed to
618 variability in atmospheric $p\text{CO}_2$ and ocean DIC concentrations (Shackleton, 1986; Kurtz et
619 al., 2003; Komar et al., 2013). When long-term increases in $p\text{CO}_2$, perhaps in conjunction

620 with orbital forcing, pushed temperatures across some threshold, such as the limit of sea-ice
621 formation (Lunt et al., 2011), rapid inputs of ^{13}C -depleted organic carbon from the shallow
622 geosphere served as a positive feedback to abrupt warming (Dickens et al., 1995; Bowen et
623 al., 2006; DeConto et al., 2012).

624 Our new $\delta^{13}\text{C}$ records do not directly address the above questions and narrative
625 concerning early Paleogene carbon cycling. However, they do highlight two general and
626 related problems when such discussion includes the EECO. First, surface temperatures appear
627 to stay high across an extended time interval when the $\delta^{13}\text{C}$ of benthic foraminifer (**Figure 1**)
628 and bulk carbonate (**Figure 9**) increase. Second, numerous brief CIEs mark this global long-
629 term rise in $\delta^{13}\text{C}$. Whether the aforementioned views need modification or reconsideration
630 (Kirtland Turner et al., 2014) is an outstanding issue, one that depends on how long-term and
631 short-term $\delta^{13}\text{C}$ changes relate across the entire early Paleogene.

632 The overall offset between bulk carbonate $\delta^{13}\text{C}$ values at Possagno and Site 577 may hint
633 at an important constraint to any model of early Paleogene carbon cycling. Throughout the
634 early Eocene, $\delta^{13}\text{C}$ values at Site 577 exceed those at Possagno by nominally 0.8 ‰ (**Figure**
635 **9**). This probably does reflect recrystallization or lithification, because similar offsets appear
636 across numerous records independent of post-depositional history but dependent on location
637 (Schmitz et al., 1996; Cramer et al., 2003; Slotnick et al., 2012, 2015a; Agnini et al.,
638 submitted). In general, absolute values of bulk carbonate $\delta^{13}\text{C}$ records increase from the
639 North Atlantic and western Tethys (low), through the South Atlantic and eastern
640 Tethys/Indian, to the Pacific (high), although suggestively with a latitudinal component to
641 this signature.

642

643 **6.3 Stable oxygen isotope stratigraphy across the EECO**

644

645 Bulk carbonate $\delta^{18}\text{O}$ values for Holocene sediment across the Eastern Equatorial Pacific
646 relate to average temperatures in the mixed layer (Shackleton and Hall, 1995; Reghellin et al.,
647 2015). Indeed, values are close to those predicted from water chemistry ($\delta^{18}\text{O}_w$) and
648 equilibrium calculations for calcite precipitation (e.g., Bemis et al., 1998) if vital effects in
649 the dominant nanoplankton increase $\delta^{18}\text{O}$ by nominally 1‰ (Reghellin et al., 2015).

650 Site 577 was located at about 15°N latitude in the eastern Pacific during the early
651 Paleogene. Given that sediment of this age remains “nanofossil ooze” (Shipboard Scientific
652 Party, 1985), one might predict past mixed layer temperatures from the $\delta^{18}\text{O}$ values with
653 three assumptions: early Paleogene $\delta^{18}\text{O}_w$ was 1.2 ‰ less than that at present-day to account
654 for an ice-free world; local $\delta^{18}\text{O}_w$ was equal to average seawater, similar to modern chemistry
655 at this off-Equator location (LeGrande and Schmidt, 2006); and, Paleogene nanoplankton
656 also fractionated $\delta^{18}\text{O}$ by 1.0 ‰. With commonly used equations that relate the $\delta^{18}\text{O}$ of
657 calcite to temperature (Bemis et al., 1998), these numbers render temperatures of between
658 16°C and 21°C for the data at Site 577. Such temperatures seem too cold by at least 10°C,
659 given other proxy data and modelling studies (e.g., Pearson et al., 2007; Huber and Caballero,
660 2011; Hollis et al., 2012; Pross et al., 2012; Inglis et al., 2015). At low latitudes, bottom
661 waters are always much colder than surface waters. Even during the EECO, deep waters
662 probably did not exceed 12°C (Zachos et al., 2008). The calculated tepid temperatures likely
663 indicate partial recrystallization of bulk carbonate near the seafloor. Examinations of
664 calcareous nanofossils in Paleogene sediment at Site 577 show extensive calcite
665 overgrowths (Shipboard Scientific Party, 1985; Backman, 1986). Relatively low $\delta^{18}\text{O}$ values
666 mark the H-1 and K/X events, as well as the main phase of the EECO (**Figure 5**). Both
667 observations support the idea that the bulk carbonate $\delta^{18}\text{O}$ at Site 577 represents the
668 combination of a primary surface water $\delta^{18}\text{O}$ signal and a secondary shallow pore water $\delta^{18}\text{O}$
669 signal.

670 Lithification should further impact bulk carbonate $\delta^{18}\text{O}$ records (Marshall, 1992; Schrag
671 et al., 1995; Frank et al., 1999). Because this process occurs well below the seafloor, where
672 temperatures approach or exceed those of surface water, the $\delta^{18}\text{O}$ values of pelagic marls and
673 limestones should be significantly depleted in ^{18}O relative to partially recrystallized
674 nannofossil ooze. This explains the nominal 2‰ offset in average $\delta^{18}\text{O}$ between correlative
675 strata at Possagno and at Site 577. While temperature calculations using the $\delta^{18}\text{O}$ record at
676 Possagno render reasonable surface water values for a mid-latitude location in the early
677 Paleogene (26-31°C, using the aforementioned approach), any interpretation in these terms
678 more than likely reflects happenstance. The fact that planktic foraminifera are completely
679 recrystallized and totally filled with calcite at Possagno supports this inference.

680 One might suggest, at least for the Possagno section, that meteoric water might have also
681 impacted the $\delta^{18}\text{O}$ record. This is because rainwater generally has a $\delta^{18}\text{O}$ composition less
682 than that of seawater. However, samples were collected at Possagno in 2002-2003 from fresh
683 quarry cuts.

684 As observed at Site 577, however, horizons of lower $\delta^{18}\text{O}$ at Possagno may represent
685 times of relative warmth in surface water. This includes the broad interval between 16 and
686 22.5 m, which marks the main phase of the EECO, as well as many of the brief CIEs, at least
687 one that clearly represents the PETM (**Figure 4**). That is, despite obvious overprinting of the
688 original $\delta^{18}\text{O}$ signal, early to early middle Eocene climate variations appear manifest in the
689 data.

690

691 **6.4 The EECO and planktic foraminiferal abundances**

692

693 Bulk carbonate $\delta^{13}\text{C}$ records, especially in conjunction with other stratigraphic markers,
694 provide a powerful means to correlate early Paleogene sequences from widely separated

695 locations (**Figure 9**). They also allow for placement of planktic foraminiferal assemblage
696 changes into broader context.

697 The most striking change in planktic foraminiferal assemblages occurred near the start of
698 the EECO. Over a fairly short time interval and at multiple widespread locations, the relative
699 abundance of acarininids increased significantly whereas the relative abundance of
700 morozovellids decreased significantly. This switch, best defined by the decline in
701 morozovellids, happened just before the condensed interval at Possagno (**Figure 6**), just
702 above the J event at Site 577 (**Figure 7, Table S4**), and during the J event at Site 1051
703 (**Figure 8**). At the Farra section, cropping out in the same geological setting of Possagno at
704 50 km NE of the Carcoselle quarry, it also appears to have occurred close to the J event
705 (**Figure 10**). Indeed, the maximum turnover in relative abundances may have been coincident
706 with the J event at all locations. Importantly, the relative abundance of subbotinids only
707 changed marginally during this time.

708 The morozovellid decline across the start of the EECO did not rebound afterward. At
709 Possagno, at Site 1051, and at Site 577, it was coupled with the gradual disappearances of
710 several species, including *M. aequa*, *M. gracilis*, *M. lensiformis*, *M. marginodentata*, and *M.*
711 *subbotinae*. Furthermore, the loss of morozovellids was not counterbalanced by the
712 appearance of the *Morozovelloides* genus, which shared with *Morozovella* the same
713 ecological preferences. This latter genus appeared in C21r, near the Ypresian/Lutetian
714 boundary, and well after the EECO (Pearson et al., 2006; Aze et al., 2011), including at
715 Possagno (Luciani and Giusberti, 2014; **Figure 6**). Though *Morozovelloides* were
716 morphologically similar to *Morozovella*, they probably evolved from *Acarinina* (Pearson et
717 al., 2006; Aze et al., 2011; **Figure 1**).

718 At Possagno, higher abundances of acarininids also correlate with pronounced negative
719 $\delta^{13}\text{C}$ perturbations before and after the EECO (**Figure 6**). This includes the H-1 event, as well

720 as several unlabelled CIEs during C22n, C21r and C21n. Such increases in the relative
721 abundances of acarininids have been described for the PETM interval at the nearby Forada
722 section (Luciani et al., 2007), and for the K/X event at the proximal Farra section (Agnini et
723 al., 2009). Unlike for the main switch near the J event, however, these changes are transient,
724 so that relative abundances in planktic foraminiferal genera are similar before and after the
725 short-term CIEs.

726

727 **6.5 The impact of dissolution**

728

729 Carbonate dissolution at or near the seafloor presents a potential explanation for observed
730 changes in foraminifera assemblages. Some studies of latest Paleocene to initial Eocene age
731 sediments, including laboratory experiments, suggest a general ordering of dissolution
732 according to genus, with acarininids more resistant than morozovellids, and the latter more
733 resistant than subbotinids (Petrizzo et al., 2008; Nguyen et al., 2009, 2011).

734 Carbonate solubility horizons that impact calcite preservation and dissolution on the
735 seafloor (i.e., the CCD and lysocline) also shoaled considerably during various intervals of
736 the early Eocene. The three most prominent hyperthermals that occurred before the main
737 phase of the EECO (PETM, H-1, K/X) were clearly marked by pronounced carbonate
738 dissolution at multiple locations (Zachos et al., 2005; Agnini et al., 2009; Stap et al., 2009;
739 Leon-Rodriguez and Dickens, 2010). A multi-million year interval characterized by a
740 relatively shallow CCD also follows the K/X event (Leon-Rodriguez and Dickens, 2010;
741 Pálike et al., 2012; Slotnick et al., 2015b).

742 Should changes in carbonate preservation primarily drive the observed planktic
743 foraminiferal assemblages, it follows that the dominance of acarininids during the EECO and
744 multiple CIEs could represent a taphonomic artefact. Limited support for this idea comes

745 from our records of fragmentation (*F* index). In general, intervals with relatively high
746 abundances of acarininids (and low $\delta^{13}\text{C}$) correspond to intervals of fairly high fragmentation
747 at Possagno and at Site 1051 (**Figures 6, 8**). This can suggest carbonate dissolution, because
748 this process breaks planktic foraminifera into fragments (Berger, 1967; Hancock and
749 Dickens, 2005).

750 Carbonate dissolution can cause the coarse fraction of bulk sediment to decrease (Berger
751 et al., 1982; Broecker et al., 1999; Hancock and Dickens, 2005). This happens because whole
752 planktic foraminiferal tests typically exceed 63 μm , whereas the resulting fragments often do
753 not exceed 63 μm . The decrease in CF values at the start of the EECO at Possagno (**Figure 6**)
754 may therefore further indicate loss of foraminiferal tests. However, relatively low CF values
755 continue to the top of the section, independent of changes in the *F* index. The CF record
756 parallels the trend of morozovellids abundance, and thus might also suggest a loss of larger
757 morozovellids rather than carbonate dissolution.

758 The cause of the long-term rise in carbonate dissolution horizons remains perplexing, but
759 may relate to reduced inputs of ^{13}C -depleted carbon into the ocean and atmosphere (Leon-
760 Rodriguez and Dickens, 2010; Komar et al., 2013). Should the morozovellids decline and
761 amplified *F* index at the Possagno section mostly represent dissolution, it would imply
762 considerable shoaling of these horizons in the western Tethys, given the inferred deposition
763 in middle to lower bathyal setting. As with open ocean sites (Slotnick et al., 2015b), further
764 studies on the Eocene lysocline and CCD are needed from Tethyan locations. One idea is that
765 remineralization of organic matter intensified within the water column, driven by augmented
766 microbial metabolic rates at elevated temperatures during the EECO; this may have decreased
767 pH at intermediate water column depths (Brown et al., 2004; Olivarez Lyle and Lyle, 2006;
768 O'Connor et al., 2009; John et al., 2013, 2014).

769 Despite evidence for carbonate dissolution, this process probably only amplified primary

770 changes in planktic foraminiferal assemblages. The most critical observation is the similarity
771 of the abundance records for major planktic foraminiferal genera throughout the early Eocene
772 at multiple locations (**Figures 6-8**). This includes the section at Site 1051, where carbonate
773 appears only marginally modified by dissolution according to the F index values (**Figure 7**).
774 Subbotinid abundance also remains fairly high throughout the early Eocene. One explanation
775 is that, in contrast to laboratory experiments (Nguyen et al., 2009, 2011), subbotinids are
776 more resistant to dissolution than morozovellids (Boersma and Premoli Silva, 1983; Berggren
777 and Norris, 1997), at least once the EECO has transpired. In the proximal middle-upper
778 Eocene section at Alano, Luciani et al. (2010) documented a dominance of subbotinids within
779 intervals of high fragmentation (F index) and enhanced carbonate dissolution. The degree of
780 dissolution across planktic foraminiferal assemblages may have varied through the early
781 Paleogene, as distinct species within each genus may respond differently (Nguyen et al.,
782 2011). So far, data on dissolution susceptibility for different species and genera are limited
783 for early and early middle Eocene times (Petrizzo et al., 2008).

784 There is also recent work from the Terche section (ca. 28 km NE of Possagno) to
785 consider. This section is located in the same geological setting as Possagno, but across the H-
786 1, H-2 and I1 events, there are very low F index values and marked increases of acarininids
787 coupled with significant decreases of subbotinids (D'Onofrio et al., 2014). Therefore,
788 although the Possagno record may be partially altered by dissolution, an increase of warm
789 water acarininids concomitant with decrease of subbotinids seems to be a robust finding
790 during early Paleogene warming events in Tethyan settings.

791

792 **6.6 A record of mixed water change**

793

794 The switch in abundance between morozovellids and acarininids at the start of the EECO

795 supports a hypothesis whereby environmental change resulted in a geographically widespread
796 overturn of planktic foraminiferal genera. During the PETM and K/X events, acarininids
797 became dominant over morozovellids in a number of Tethyan successions. This has been
798 interpreted as signifying enhanced eutrophication of surface waters near continental margins
799 (Arenillas et al., 1999; Molina et al., 1999; Ernst et al., 2006; Guasti and Speijer, 2007;
800 Luciani et al., 2007; Agnini et al., 2009), an idea consistent with evidence for elevated (albeit
801 more seasonal) riverine discharge during these hyperthermals (Schmitz and Pujalte, 2007;
802 Giusberti et al., 2007; Schulte et al., 2011; Slotnick et al., 2012; Pujalte et al., 2015).
803 Increased nutrient availability may also have occurred at Possagno during the early part of the
804 EECO, given the relatively high concentration of radiolarians, which may reflect
805 eutrophication (Hallock, 1987).

806 However, the fact that the major switch at the start of the EECO can be found at Sites
807 1051 (western Atlantic) and Site 577 (central Pacific) suggests that local variations in
808 oceanographic conditions, such as riverine discharge, was not the primary causal mechanism.
809 Rather, the switch must be a consequence of globally significant modifications related to the
810 EECO, most likely sustained high temperatures, elevated $p\text{CO}_2$, or both. Given model
811 predictions for our Earth in the coming millennia (IPCC, 2014), indirect effects also could
812 have contributed, especially including increased ocean stratification and decreased pH.

813 An explanation for the shift may lie in habitat differences across planktic foraminifera
814 genera. Although both morozovellids and acarininids likely had photosymbionts,
815 morozovellids may have occupied a shallower surface habitat than the latter genus as
816 indicated by minor variations in their stable isotope compositions (Boersma et al., 1987;
817 Pearson et al., 1993; 2001).

818 One important consideration to any interpretation is the evolution of new species that
819 progressively appear during the post-EECO interval. In good agreement with studies of lower

820 Paleogene sediment from other low latitude locations (Pearson et al., 2006), thermocline
821 dwellers such as subbotinids and parasubbotinids seem to proliferate at Possagno (Luciani
822 and Giusberti, 2014). These include *Subbotina corpulenta*, *S. eocena*, *S. hagni*, *S. senni*, *S.*
823 *yeguanesis*, *Parasubbotina griffinae*, and *P. pseudowilsoni*. The appearance of the radially-
824 chambered *Parasubbotina eoclava*, considered to be the precursor of the truly clavate
825 chambered *Clavigerinella* (Coxall et al., 2003; Pearson and Coxall, 2014), also occurs at 19.8
826 m, and in the core of the EECO (Luciani and Giusberti, 2014). *Clavigerinella* is the ancestor
827 of the genus *Hantkenina* that successfully inhabited the sub-surface and surface waters during
828 the middle through late Eocene (Coxall et al., 2000).

829 A second consideration is the change in planktic foraminiferal assemblages during the
830 Middle Eocene Climate Optimum (MECO), another interval of anomalous and prolonged
831 warmth ca. 40 Ma (Bohaty and Zachos, 2003). At Alano (**Figure 11**) and other locations
832 (Luciani et al., 2010; Edgar et al., 2012), the MECO involved the reduction in the abundance
833 and test size of large acarininids and *Morozovelloides*. This has been attributed to “bleaching”
834 and the loss of photosymbionts resulting from global warming (Edgar et al., 2012), although
835 related factors, such as a decrease in pH, a decrease in nutrient availability, or changes in
836 salinity, may have been involved (Douglas, 2003; Wade et al., 2008). The symbiotic
837 relationship with algae is considered an important strategy adopted by muricate planktic
838 foraminifera during the early Paleogene (Norris, 1996; Quillévéré et al., 2001). Considering
839 the importance of this relationship in extant species (Bé, 1982; Bé et al., 1982; Hemleben et
840 al., 1989), the loss of photosymbionts may represent a crucial mechanism to explain the
841 relatively rapid decline foraminifera utilizing this strategy, including morozovellids at the
842 start of the EECO.

843 Available data suggest that the protracted conditions of extreme warmth and high $p\text{CO}_2$
844 during the EECO were the key elements inducing a permanent impact on planktic

845 foraminiferal evolution, and the decline of the morozovellids. Even during the PETM, the
846 most pronounced hyperthermal, did not adversely affect the morozovellids permanently.
847 While “excursion taxa” appeared, morozovellids seem to have increased in abundance in
848 open ocean settings (Kelly et al., 1996; 1998, 2002; Lu and Keller, 1995; Petrizzo, 2007);
849 only in some continental margin settings did a transient decrease in abundance occur (Luciani
850 et al., 2007).

851

852 **6.7 Post-EECO changes at Possagno**

853

854 Several small CIEs appear in the $\delta^{13}\text{C}$ record at Possagno during polarity chrons C22n, C21r,
855 and C21n. Some of these post-EECO excursions coincide with planktic foraminiferal
856 assemblage changes similar to those recorded in lower strata. Specifically, there are marked
857 increases of acarininids (**Figure 6**). These “post-EECO” CIEs are concomitant with $\delta^{18}\text{O}$
858 excursions and coupled to distinct modifications in the planktic foraminiferal assemblages
859 comparable to those recorded across known hyperthermals in Tethyan settings (Luciani et al.,
860 2007; Agnini et al., 2009; D’Onofrio et al., 2014). Additional hyperthermals, although of less
861 intensity and magnitude, may extend through the entirety of the early and middle Eocene, as
862 suggested previously (Sexton et al., 2006; 2011; Kirtland-Turner et al., 2014). Whether these
863 imply different forcing and feedback mechanisms compared to the PETM remains an open
864 discussion.

865

866 **7 Summary and conclusions**

867 The symbiont-bearing planktic foraminiferal genera *Morozovella* and *Acarinina* were
868 among the most important calcifiers of the early Paleogene tropical and subtropical oceans.
869 However, a remarkable and permanent switch in the relative abundance of these genera

870 happened in the early Eocene, an evolutionary change accompanied by species reduction of
871 *Morozovella* and species diversification of *Acarinina*. We show here that this switch probably
872 coincided with a carbon isotope excursion (CIE) presently coined J. Although the Early
873 Eocene Climatic Optimum (EECO), a multi-million year interval of extreme Earth surface
874 warmth, lacks an accepted definition, we propose that the EECO is best defined as the
875 duration of time between the J event and the base of *D. subloboensis* (about 53 Ma to 49 Ma
876 on the 2012 GTS).

877 Our conclusion that the planktic foraminiferal switch coincides with the start of the
878 EECO derives from the generation of new records and collation of old records concerning
879 bulk sediment stable isotopes and planktic foraminiferal abundances at three sections. These
880 sections span a wide longitude range of the low latitude Paleogene world: the Possagno
881 section from the western Tethys, DSDP Site 577 from the central Pacific Ocean, and ODP
882 Site 1051 from the western Atlantic Ocean. Importantly, these locations have robust
883 calcareous nannofossils and polarity chron age markers, although the stratigraphy required
884 amendment at Sites 577 and 1051.

885 An overarching problem is that global carbon cycling was probably very dynamic during
886 the EECO. The interval appears to have been characterized not only by numerous CIEs, but
887 also a major switch in the timing and magnitude of these perturbations. Furthermore, there
888 was a rapid shoaling of carbonate dissolution horizons in the middle of the EECO. A key
889 finding of our study is that the major switch in planktic foraminiferal assemblages happened
890 at the start of the EECO. Significant, though ephemeral, modifications in planktic
891 foraminiferal assemblages coincide with numerous short-term CIEs, before, during and after
892 the EECO. Often, there are marked increases in the relative abundance of acarininids, similar
893 to what happened permanently across the start of the EECO.

894 Although we show for the first time that the critical turnover in planktic foraminifera

895 clearly coincided with the start of the EECO, the exact cause for the switch (aka the decline
896 of morozovellids) remains elusive. Possible causes are multiple, and may include temperature
897 effects on photosymbiont-bearing planktic foraminifera, changes in ocean chemistry, or even
898 interaction with other microplankton groups such as radiolarians, diatoms or dinoflagellates
899 that represented possible competitors in the use of symbionts or as symbiont providers. For
900 some reason, a critical threshold was surpassed at the start the EECO, and this induced an
901 unfavourable habitat for continued morozovellid diversification and proliferation but a
902 favourable habitat for the acarinids.

903

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921

922 **References**

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1492

1493 **Figure Captions**

1494

1495 **Figure 1.** Evolution of climate, carbon cycling, and planktic foraminifera across the middle
1496 Paleogene on the GPTS 2012 time scale. Left side shows polarity chrons, and smoothed
1497 oxygen and carbon isotope records of benthic foraminifera, slightly modified from
1498 Vandenberghe et al. (2012). Original oxygen and carbon isotope values come from
1499 compilations by Zachos et al. (2008) and Cramer et al. (2009). Middle of the figure indicates
1500 planktic foraminiferal biozones by Wade et al. (2011) with three modifications. The lower
1501 boundary for Zone E7a is now based on the first occurrence of *Astrorotalia palmerae* due to
1502 diachroneity in the first appearance of the previously selected marker *Acarinina*
1503 *cuneicamerata* (Luciani and Giusberti, 2014). The base of Zone E5, identified by the first
1504 appearance of *Morozovella aragonensis*, occurs within the middle of C24n instead of lower
1505 C23r (see text). A question marks the top of *Morozovella subbotinae* because there is
1506 diachroneity for this occurrence (see text). Right side shows a partial view of morozovellid
1507 and acarininid evolution as envisioned by Pearson et al. (2006) and Aze et al. (2011). It does
1508 not include several “root taxa” that disappear in the earliest Eocene (e.g., *M. velascoensis*) or
1509 “excursion taxa” that appear during the Paleocene-Eocene Thermal Maximum (PETM) (e.g.,
1510 *M. allisonensis*). Superimposed on these records are key intervals of climate change,
1511 including the Early Eocene Climatic Optimum (EECO), the Middle Eocene Climatic
1512 Optimum (MECO) and the three well documented early Eocene hyperthermal events. The
1513 extent of the EECO is not precise, because of stratigraphic issues (see text). Red and blue
1514 triangles= top and base of the morozovellid and acarininid zonal markers.

1515

1516 **Figure 2.** Approximate locations of the three sites discussed in this work during the early
1517 Eocene. Also shown is Site 1258, which has a bulk carbonate $\delta^{13}\text{C}$ record spanning the
1518 EECO. Base map is from <http://www.odsn.de/services/paleomap.html>.

1519

1520 **Figure 3.** The Possagno section. Upper panel: geological map (modified from Braga, 1970).

1521 1 = Quaternary deposits; 2, 3 = Calcarenite di Castelcuoco (Miocene); 4 = glauconitic

1522 arenites (Miocene); 5 = siltstones and conglomerates (upper Oligocene-lower Miocene); 6 =

1523 Upper Marna di Possagno (upper Eocene); 7 = Formazione di Pradelgiglio (upper Eocene); 8

1524 = Marna di Possagno (upper Eocene); 9 = Scaglia Cinerea (middle-upper Eocene); 10 =

1525 Scaglia Rossa (upper Cretaceous-lower Eocene); 11 = faults; 12 = traces of stratigraphic

1526 sections originally studied by Bolli (1975); red circle = the Carcoselle quarry. Lower panel:

1527 the exposed quarry face during Summer 2002 (Photo by Luca Giusberti).

1528

1529 **Figure 4.** Lithology, stratigraphy, and bulk sediment stable-isotope composition of the

1530 Possagno section aligned according to depth. Lithologic key: 1 = limestone; 2 = marly

1531 limestone and calcareous marl; 3 = cyclical marl-limestone alternations, 4 = marl; 5= Clay

1532 Marl unit (CMU). Planktic foraminiferal biozones follow those of Wade et al. (2011), as

1533 modified by Luciani and Giusberti (2014). Magnetostratigraphy and key calcareous

1534 nannofossil events come from Agnini et al. (2006); NP-zonation is from Martini (1971).

1535 Nannofossil events are shown as red triangles (tops), blue triangles (bases), and purple

1536 diamonds (evolutionary crossovers); *S. rad.* = *Sphenolithus radians*; T.c./T.o. = *Tribrachiatus*

1537 *contortus*/ *Tribrachiatus orthostylus*; *D. lod.* = *Discoaster lodoensis*; Tow. = *Toweius*; *T. orth.*

1538 = *Tribrachiatus orthostylus*; *D. sublod.* = *Discoaster sublodoensis*. Stable isotope records

1539 determined in this study. Established early Eocene “events” are superimposed in light red;

1540 suggested carbon isotope excursions (CIEs) within the EECO are shown with numbers.

1541

1542 **Figure 5.** Cores, stratigraphy, and bulk sediment stable isotope composition for the early

1543 Eocene interval at Deep-Sea Drilling Project (DSDP) Site 577 aligned according to

1544 composite depth (Dickens and Backman, 2013). Note the increased length for the gap
1545 between Core 577*-8H and Core 577*-9H (see text). The Wade et al. (2011) E-zonation,
1546 partly modified by Luciani and Giusberti (2014), has been applied to Site 577 given
1547 assemblages presented by Lu (1995) and Lu and Keller (1995). Note that: (a) the base of
1548 Zone E3 (top of *Morozovella velascoensis*) lies within a core gap; (b) the E4/E5 zonal
1549 boundary (base of *M. aragonensis*) occurs within C24n, in agreement with Luciani and
1550 Giusberti (2014); (c) the E5/E6 zonal boundary is problematic because the top of *M.*
1551 *subbotinae* occurs in middle C24n, much earlier than the presumed disappearance in the
1552 upper part of C23n (Wade et al., 2011). We have therefore positioned the E5/E6 boundary at
1553 the lowest occurrence of *Acarinina aspensis*, according to the original definition of Zone E5
1554 (Berggren and Pearson, 2005); (d) we cannot differentiate between Zone E6 and Zone E7a
1555 due to the absence of *Astrorotalia palmerae* and to the diachronous appearance of *A.*
1556 *cuneicamerata* (Luciani and Giusberti, 2014). Magnetostratigraphy and key calcareous
1557 nannofossil events are those summarized by Dickens and Backman (2013). For the latter and
1558 beyond that noted for **Figure 4**: *F. spp.* = *Fasciculithus spp.*; *D. dia.* = *Discoaster diastypus*.
1559 Stable isotope records: black - Cramer et al. (2003), red and blue - this study. Early Eocene
1560 “events” are the same as those in **Figure 4**.

1561

1562

1563 **Figure 6.** The Possagno section and its $\delta^{13}\text{C}$ record (**Figure 4**) with measured relative
1564 abundances of primary planktic foraminiferal genera, fragmentation index (*F* index) and
1565 coarse fraction. The subbotinid abundance includes both *Subbotina* and *Parasubbotina*
1566 genera. Note that a significant increase in *Acarinina* abundance marks the EECO and several
1567 carbon isotope excursions (CIEs). Note also the major decline in abundance of *Morozovella*
1568 at the start of the EECO. Filled yellow hexagons show occurrences of abundant radiolarians.

1569 Lithological symbols and early Eocene “events” are the same as those in **Figure 4**.

1570

1571 **Figure 7.** The early Eocene succession at DSDP Site 577 and its $\delta^{13}\text{C}$ record (**Figure 5**) with
1572 relative abundances of primary planktic foraminiferal genera (Lu, 1995; Lu and Keller,
1573 1995). Note the major switch in *Morozovella* and *Acarinina* abundances approximately
1574 coincides with the J-event, the top of polarity chron C24n, and the start of the EECO. Early
1575 Eocene “events” are the same as those in **Figure 4**.

1576

1577 **Figure 8.** Stratigraphy, bulk sediment $\delta^{13}\text{C}$ composition, relative abundances of primary
1578 planktic foraminiferal genera, and fragmentation index (*F* index) for the early Eocene interval
1579 at ODP Site 1051. Planktic foraminiferal biozones follow those of Wade et al. (2011), as
1580 modified by Luciani and Giusberti (2014; see **Figure 1** caption). Magnetostratigraphy and
1581 positions of key calcareous nannofossil events come from Ogg and Bardot (2001) and Mita
1582 (2001), but with an important modification to polarity chron labelling (see text and Cramer et
1583 al., 2003). Calcareous nannofossil horizons are the same as in previous figures. Foraminiferal
1584 information comes from this study; subbotinids include both *Subbotina* and *Parasubbotina*.
1585 Early Eocene “events” are the same as those in **Figure 4**.

1586

1587 **Figure 9.** Carbon isotope and paleomagnetic records across the early Eocene for the
1588 Possagno section, DSDP Site 577, and ODP Site 1258 (Kirtland-Turner et al., 2014). This
1589 highlights the overall framework of carbon cycling in the early Eocene, but also stratigraphic
1590 problems across the EECO at each of the three sites. At Possagno, the coarse resolution of
1591 $\delta^{13}\text{C}$ records and the condensed interval makes correlations difficult. At ODP Site 1258 the
1592 prominent K/X event seems missing. At DSDP Site 577, the entire record is compressed in
1593 the depth domain. Nonetheless, a major shift in frequency and amplitude of carbon isotope

1594 excursions (CIEs) appears to have happened during the EECO. CIEs that suggestively
1595 correlate within the EECO are shown with numbers.

1596

1597 **Figure 10.** Records of magnetostratigraphy, bulk sediment $\delta^{13}\text{C}$, CaCO_3 content, F index and
1598 abundance patterns for primary planktic foraminiferal taxa at the Farra section, which crops
1599 out 50 km NE of Possagno. All data are from Agnini et al. (2009). Note that the switch in
1600 abundance between *Morozovella* and *Acarinina* occurs close the J event.

1601

1602 **Figure 11.** Records of morozovellids and large acarininids (>200 micron) in the western
1603 Tethyan setting from the Possagno section (this paper) and the Alano section (Luciani et al.,
1604 2010), plotted with generalized $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ curves for benthic foraminiferal on the
1605 GTS2012 time scale (as summarized by Vandenberghe et al., 2012; slightly modified). These
1606 records suggest that the long-lasting EECO and MECO intervals of anomalous warmth mark
1607 two main steps in the decline of morozovellids and acarininids. The plankic foraminiferal
1608 biozones follow those presented by Wade et al. (2011), as partly modified by Luciani and
1609 Giusberti (2014).

1610

1611 **Supplementary material**

1612

1613 **Table S1.** Carbon and oxygen isotopes from the Possagno section.

1614

1615 **Table S2.** Carbon and oxygen isotopes from DSDP Site 577.

1616

1617 **Table S3.** Foraminiferal abundances, fragmentation index (%) and coarse fraction (%) from
1618 the Possagno section.

1619

1620 **Table S4.** Foraminiferal abundances from DSDP Site 577.

1621

1622 **Table S5.** Foraminiferal abundances from ODP Site 1051.

1623

1624 **Figure S1.** The Possagno $\delta^{13}\text{C}$ data and relative abundance of minor planktic foraminiferal
1625 genera and selected species plotted against lithology and fragmentation index (*F* index) data.
1626 Magnetostratigraphy is from Agnini et al. (2006). The planktic foraminiferal biozonal scheme
1627 is from Wade et al. (2011), as modified by Luciani and Giusberti (2014). Various symbols are
1628 the same as in **Figure 4**.

1629

1630 **Appendix A: Taxonomic list of planktic foraminiferal species cited in text and figures**

1631

1632 *Globanomalina australiformis* (Jenkins, 1965)

1633 *Morozovella aequa* (Cushman and Renz, 1942)

1634 *Morozovella gracilis* (Bolli, 1957)

1635 *Morozovella lensiformis* (Subbotina, 1953),

1636 *Morozovella marginodentata* (Subbotina, 1953)

1637 *Morozovella subbotinae* (Morozova, 1939)

1638 *Parasubbotina eoelava* Coxall, Huber and Pearson, 2003

1639 *Parasubbotina griffinae* (Blow, 1979)

1640 *Parasubbotina pseudowilsoni* Olsson and Pearson, 2006

1641 *Subbotina corpulenta* (Subbotina, 1953)

1642 *Subbotina eocena* (Gümbel, 1868)

1643 *Subbotina hagni* (Gohrbandt, 1967)

- 1644 *Subbotina senni* (Beckmann, 1953)
1645 *Subbotina yeguanesis* (Weinzierl and Applin, 1929)
1646 *Planoglobanomalina pseudoalgeriana* Olsson & Hemleben, 2006

1647

1648 **Appendix B: Taxonomic list of calcareous nannofossil taxa cited in text and figures**

1649

- 1650 *Globanomalina australiformis* (Jenkins, 1965)
1651 *Morozovella aequa* (Cushman and Renz, 1942)
1652 *Morozovella gracilis* (Bolli, 1957)
1653 *Morozovella lensiformis* (Subbotina, 1953),
1654 *Morozovella marginodentata* (Subbotina, 1953)
1655 *Morozovella subbotinae* (Morozova, 1939)
1656 *Parasubbotina eoelava* Coxall, Huber and Pearson, 2003
1657 *Parasubbotina griffinae* (Blow, 1979)
1658 *Parasubbotina pseudowilsoni* Olsson and Pearson, 2006
1659 *Subbotina corpulenta* (Subbotina, 1953)
1660 *Subbotina eocena* (Gümbel, 1868)
1661 *Subbotina hagni* (Gohrbandt, 1967)
1662 *Subbotina senni* (Beckmann, 1953)
1663 *Subbotina yeguanesis* (Weinzierl and Applin, 1929)
1664 *Planoglobanomalina pseudoalgeriana* Olsson & Hemleben, 2006

1665

1666 **Appendix B: Taxonomic list of calcareous nannofossil taxa cited in text and figures**

1667

- 1668 *Discoaster diastypus* Bramlette and Sullivan, 1961

- 1669 *Discoaster lodoensis* Bramlette and Sullivan, 1961
- 1670 *Discoaster sublodoensis* Bramlette and Sullivan, 1961
- 1671 *Fasciculithus* Bramlette and Sullivan, 1961
- 1672 *Fasciculithus tympaniformis* Hay and Mohler in Hay et al., 1967
- 1673 *Sphenolithus radians* Deflandre in Grassé, 1952
- 1674 *Toweius* Hay and Mohler, 1967
- 1675 *Tribrachiatus contortus* (Stradner, 1958) Bukry, 1972
- 1676 *Tribrachiatus orthostylus* (Bramlette and Riedel, 1954) Shamrai, 1963
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1694 **Major perturbations in the global carbon cycle and photosymbiont-bearing**
1695 **planktic foraminifera during the early Eocene**

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1697

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1712 **Abstract.** A marked switch in the abundance of the planktic foraminiferal genera
1713 *Morozovella* and *Acarinina* occurred [at low-latitude sites](#) near the start of the Early Eocene
1714 Climatic Optimum (EECO), a multi-million-year interval when Earth surface temperatures
1715 reached their Cenozoic maximum. Stable carbon and oxygen isotope data of bulk sediment
1716 are presented from across the EECO at two locations: Possagno in northeast Italy, and DSDP
1717 Site 577 in the northwest Pacific. Relative abundances of planktic foraminifera are presented
1718 from these two locations, as well as from ODP Site 1051 in the northwest Atlantic. All three
1719 sections have good stratigraphic markers, and the $\delta^{13}\text{C}$ records at each section can be
1720 correlated amongst each other and to $\delta^{13}\text{C}$ records at other locations across the globe. These
1721 records show that a series of negative carbon isotope excursions (CIEs) occurred before,
1722 during and across the EECO, which is defined here as the interval between the "J" event and
1723 the base of *Discoaster subloboensis*. Significant though ephemeral modifications in planktic
1724 foraminiferal assemblages coincide with some of the short-term CIEs, which were marked by
1725 increases in the relative abundance of acarininids, similar to what happened across
1726 established hyperthermal events in Tethyan settings prior to the EECO. Most crucially, a
1727 temporal link exists between the onset of the EECO, carbon cycle changes during this time,
1728 and the ~~demise~~ [decline](#) of morozovellids. Possible causes are multiple, and may include
1729 temperature effects on photosymbiont-bearing planktic foraminifera and changes in ocean
1730 chemistry.

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1739 **1 Introduction**

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1741 Cenozoic Earth surface temperatures attained their warmest **long-term** state during the Early
1742 Eocene Climatic Optimum (EECO). This was a 2-4 Myr **time** interval (discussed below)
1743 centered at ca. 51 Ma (**Figure 1**), when average high latitude temperatures exceeded those at
1744 present-day by at least 10°C (Zachos et al., 2008; Huber and Caballero, 2011; Hollis et al.,
1745 2012; Pross et al., 2012; Inglis et al., 2015). Several short-term (<200 kyr) global warming
1746 events (**Figure 1**) occurred before the EECO. The Paleocene Eocene Thermal Maximum
1747 (PETM) provides **the** archetypical example: about 55.9 Ma (Vandenbergh et al., 2012;
1748 Hilgen et al., 2015) temperatures soared an additional 5-6°C relative to background
1749 conditions (Sluijs et al., 2006, 2007; Dunkley Jones et al., 2013). Evidence exists for at least
1750 two other significant **Eocene** warming events (Cramer et al., 2003; Lourens et al., 2005; Röhl
1751 et al., 2005; Thomas et al., 2006; Nicolo et al., 2007; Agnini et al., 2009; Coccioni et al.,
1752 2012; Lauretano et al., 2015; Westerhold et al., 2015): one ca. 54.1 Ma and named H-1 or
1753 Eocene Thermal Maximum 2 (ETM-2, also referred as the ELMO **event**), and one at 52.8 Ma
1754 and variously named K, X, or ETM-3 (hereafter called K/X). However, additional brief
1755 warming events may have spanned the early Eocene (above references; Kirtland-Turner et al.,
1756 2014), and the EECO may comprise a series of successive events (Slotnick et al., 2012). Both
1757 long-term and short-term intervals of warming corresponded to major changes in global
1758 carbon cycling, although the precise timing between these parameters remains insufficiently
1759 resolved.

1760 In benthic foraminiferal stable isotope records for the early Paleogene (**Figure 1**), $\delta^{18}\text{O}$
1761 serves as a proxy for deep-water temperature, while $\delta^{13}\text{C}$ relates to the composition of deep-
1762 water dissolved inorganic carbon (DIC). The highest $\delta^{13}\text{C}$ values of the Cenozoic occurred at
1763 ca. 58 Ma. From this Paleocene Carbon Isotope Maximum (PCIM), benthic foraminiferal

1764 $\delta^{13}\text{C}$ values plunge by approximately 2.5 ‰ to reach a near Cenozoic minimum at or near the
1765 start of the EECO, and subsequently rise by approximately 1.5 ‰ across this interval (Zachos
1766 et al., 2001, 2008; Cramer et al., 2009). Benthic foraminiferal $\delta^{13}\text{C}$ records also exhibit
1767 prominent negative carbon isotope excursions (CIEs) across the three hyperthermals
1768 mentioned above (Kennett and Stott, 1991; Littler et al., 2014; Lauretano et al., 2015).
1769 Crucially, at least from the late Paleocene to the start of the EECO, similar $\delta^{13}\text{C}$ records occur
1770 in other carbon-bearing phases, such as bulk marine carbonate, planktic foraminifera, and
1771 various marine and terrestrial organic carbon compounds (Shackleton, 1986; Schmitz et al.,
1772 1996; Lourens et al., 2005; Nicolo et al., 2007; Agnini et al., 2009, submitted; Leon-
1773 Rodriguez and Dickens, 2010; Abels et al., 2012; Coccioni et al., 2012; Sluijs and Dickens,
1774 2012; Slotnick et al. 2012, 2015a; Clyde et al., 2013). This strongly suggests that observed
1775 changes in $\delta^{13}\text{C}$, both long-term trends as well as short-term perturbations, represent
1776 variations in the input and output of ^{13}C -depleted carbon to the exogenic carbon cycle
1777 (Shackleton, 1986; Dickens et al., 1995; Dickens, 2000; Kurtz et al., 2003; Komar et al.,
1778 2013).

1779 Significant biotic changes occur in terrestrial and marine environments during times
1780 when the early Paleogene $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ records show major variations. This has been
1781 recognized for the PETM, where land sections exhibit a prominent mammal turnover
1782 (Gingerich 2001, 2003; McInerney and Wing, 2011; Clyde et al., 2013), and where marine
1783 sections reveal a profound benthic foraminiferal extinction (Thomas, 1998), **turnovers in**
1784 **calcareous nannoplankton, ostracods, corals and larger benthic foraminifera (Raffi and De**
1785 **Bernardi, 2008; Scheibner and Speijer, 2008; Yamaguchi and Norris, 2012; Agnini et al.,**
1786 **2014), and appearances of excursion taxa in calcareous nannoplankton, dinoflagellates and**
1787 **planktic foraminifera (Kelly et al., 1996, 1998; Crouch et al., 2001; Sluijs et al., 2006; Self-**
1788 **Trail et al., 2012).** Major plant and mammal turnovers also occurred on land during the longer

1789 EECO (Wing et al., 1991; Zonneveld et al., 2000; Wilf et al., 2003; Falkowski et al., 2005;
1790 Woodbourne et al., 2009; Figueirido et al., 2012). In the marine realm, evolutionary trends
1791 across the EECO have been noted, in particular the inception of modern calcareous
1792 nannofossil community structure (Agnini et al., 2006, 2014; Schneider et al., 2011; Shamrock
1793 et al., 2012) and possibly the same for diatoms (Sims et al., 2006; Oreshkina, 2012). These
1794 observations, both from continents and the oceans, support an overarching hypothesis that
1795 climate change drives biotic evolution, [at least in part \(Ezard et al., 2011\)](#).

1796 Planktic foraminiferal assemblages are abundant in carbonate bearing marine sediments
1797 and display distinct evolutionary trends that often can be correlated to climate variability
1798 (Schmidt et al., 2004; [Ezard et al., 2011](#); Fraass et al., 2015). This is especially true in the
1799 early Paleogene, even though the relationship between climate variability and planktic
1800 foraminiferal evolution remains insufficiently known. At the beginning of the Eocene,
1801 planktic foraminifera had evolved over ca. 10 Myr following the Cretaceous-Paleogene mass
1802 extinction event. Several early Paleogene phylogenetic lines evolved, occupying different
1803 ecological niches in the upper water column. Subsequently, a major diversification occurred
1804 during the early Eocene, which resulted in a peak of planktic foraminiferal diversity during
1805 the middle Eocene (Norris, 1991; Schmidt et al., 2004; Pearson et al., 2006; Aze et al., 2011;
1806 [Ezard et al., 2011](#); Fraass et al., 2015).

1807 In this study, we focus on the evolution of two planktic foraminiferal genera:
1808 morozovellids and acarininids (**Figure 1**). These two genera belong to the “muricate group”,
1809 a term derived from the muricae that form ~~conical~~ [conical layered](#) pustules on the test wall. These
1810 two genera are of particular interest because of their dominance among tropical and
1811 subtropical assemblages of the early Paleogene oceans, and because these genera show a
1812 major turnover in taxonomic diversity close to the beginning of the EECO, one that
1813 comprises ~~and~~ species reduction among morozovellids and species diversification among

1814 acarininids (**Figure 1**)(Lu and Keller, 1995; Lu et al., 1998; Pearson et al., 2006; Aze et al.,
1815 2011).

1816 Numerous lower Eocene sedimentary sections from lower latitudes contain well-
1817 preserved (*albeit often recrystallized*) planktic foraminiferal tests. *Changes in These*
1818 foraminiferal assemblages presumably reflect relationships between climate and carbon
1819 cycling across the EECO. The present problem is that no section examined to date provides
1820 counts of foraminiferal assemblages, detailed stable isotope records and robust planktic
1821 foraminiferal biostratigraphies across the entire EECO. Indeed, at present, only a few sites
1822 have detailed and interpretable stable isotope records across much of the EECO (Slotnick et
1823 al., 2012, 2015a; Kirtland-Turner et al., 2014). Furthermore, the EECO lacks formal
1824 definition. As a consequence, any relationship between climatic perturbations during the
1825 EECO and the evolution of planktic foraminifera remains speculative. Here, we add new data
1826 from three locations: the Possagno section from the western Tethys, DSDP Site 577 from the
1827 tropical Pacific Ocean, and ODP Site 1051 from the subtropical Atlantic Ocean (**Figure 2**).
1828 These sections hence represent a wide longitudinal span of low latitude locations during the
1829 early Paleogene. By comparing stable isotope and planktic foraminiferal records at these
1830 three locations, we provide a new foundation for understanding why the abundances of
1831 acarininids and morozovellids changed during the EECO.

1832

1833 **2 The Early Eocene Climatic Optimum**

1834

1835 Evidence for extreme Earth surface warmth during a multi-million year time interval of the
1836 early Eocene is overwhelming, and comes from many studies, utilizing both marine and
1837 terrestrial sequences, and both fossil and geochemical proxies (Huber and Caballero, 2011;
1838 Hollis et al., 2012; Pross et al., 2012). However, a definition for the EECO, including the

1839 usage of “optimum”, endures as a perplexing problem [eirea-2015](#). This is for several reasons,
1840 including the basic facts that: (i) [proxies for temperature should not be used to](#) define a time
1841 increment, (ii) clearly correlative records across the middle of the early Eocene with temporal
1842 resolution less than 50 kyr remain scarce, and (iii) absolute ages across the early Eocene have
1843 changed significantly (Berggren et al., 1995; Vandenberghe et al., 2102). As a consequence,
1844 various papers discussing the EECO give different ages and durations [spanning from 2 to 4](#)
1845 [Myr long sometime between circa 49 and 54 Ma](#) (e.g., Yapp, 2004; Lowenstein and
1846 Demicco, 2006; Zachos et al., 2008; Woodburne et al., 2009; [Bijl et al., 2009](#); Smith et al.,
1847 2010; Hollis et al., 2012; Slotnick et al., 2012; Puljalte et al., 2015).

1848 The EECO, at least as presented in many papers, refers to the time of minimum $\delta^{18}\text{O}$
1849 values in “stacked” benthic foraminifera stable isotope curves (**Figure 1**). These curves were
1850 constructed by splicing together multiple $\delta^{18}\text{O}$ records generated at individual locations onto
1851 a common age model (originally Berggren et al., 1995). However, the stacked curves (Zachos
1852 et al., 2001, 2008; Cramer et al., 2009), while they can be adjusted to different time scales,
1853 show significant variance in $\delta^{18}\text{O}$ across the middle to late early Eocene. Some of this
1854 variance belies imprecisely calibrated records at individual sites, where cores do not align
1855 properly in the depth domain (Dickens and Backman, 2013). Some of this variance probably
1856 reflects a dynamic early Eocene climate regime, where average temperatures and atmospheric
1857 $p\text{CO}_2$ across Earth changed significantly, perhaps on orbital time scales (Smith et al., 2010;
1858 Slotnick et al., 2012, 2015a; Kirtland-Turner et al., 2014).

1859 [There is also the root problem as to where EECO starts and ends. At a basic level, the](#)
1860 [interval characterized by the lowest Cenozoic benthic foraminiferal \$\delta^{18}\text{O}\$ values begins at a](#)
1861 [time that](#) closely corresponds with a long-term minimum in $\delta^{13}\text{C}$ values (**Figure 1**). This is
1862 important for stratigraphic reasons because the two stable isotope curves were generated
1863 using the same benthic foraminiferal samples, but $\delta^{13}\text{C}$ records at different locations should

1864 necessarily correlate in the time domain (unlike $\delta^{18}\text{O}$ and temperature). The rationale for such
1865 carbon isotope stratigraphy lies in the rapid cycling of carbon across Earth's surface
1866 (Shackleton, 1986; Dickens, 2000).

1867 The Eocene minimum in $\delta^{13}\text{C}$ corresponds to the K/X event (**Figure 1**), which happened
1868 in polarity chron C24n.1n and approximately 3 Myr after the PETM (Agnini et al., 2009;
1869 Leon-Rodriguez and Dickens, 2010; Slotnick et al., 2012; Dallanave et al., 2015; Lauretano
1870 et al., 2015; Westerhold et al., 2015). However, in several detailed studies spanning the early
1871 Eocene, changes in long-term trends appear to have occurred about 400 kyr before the K/X
1872 event, and at an event called "J" (after Cramer et al., 2003), which happened near the
1873 boundary of polarity chrons C24n.2r and C24n.3n (Slotnick et al., 2015a; Lauretano et al.,
1874 2015). Notably, the long-term late Paleocene-early Eocene decrease in detailed benthic
1875 foraminiferal $\delta^{18}\text{O}$ records at Site 1262 on Walvis Ridge ceases at the J event (Lauretano et
1876 al., 2015).

1877 The end of the EECO has received limited attention from a stratigraphic perspective. In
1878 Paleogene continental slope sections now uplifted and exposed in the Clarence River Valley,
1879 New Zealand, a major lithologic change from limestone to marl coincides with the J event
1880 (Slotnick et al., 2012, 2015a; Dallanave et al., 2015). The marl-rich unit, referred to as
1881 "Lower Marl", has been interpreted to reflect enhanced terrigenous supply to a continental
1882 margin because of greater temperature and enhanced seasonal precipitation. It has been
1883 suggested further that Lower Marl expresses the EECO (Slotnick et al., 2012; Dallanave et
1884 al., 2015). The top of Lower Marl, and a return to limestone deposition, lies within the upper
1885 part of polarity chron C22n (Dallanave et al., 2015). This is interesting because it
1886 approximates the time when general long-term Cenozoic cooling initiates at several locations
1887 that have records of polarity chrons and proxies for temperature (Hollis et al., 2012; Pross et
1888 al., 2012). It is also useful from a stratigraphic perspective because the end of the EECO thus

1889 lies close to a well documented and widespread calcareous nannofossil biohorizon, the base
1890 of *Discoaster subloedoensis*. This marks the base of CP10, NP12 or CNE4, depending on the
1891 chosen calcareous nannofossil zonal scheme (Okada and Bukry, 1980; Martini, 1971; Agnini
1892 et al., 2014).

1893 Without an accepted definition in the literature, we tentatively present the EECO as the
1894 duration of time between the J event and the base of *D. subloedoensis*. This interval thus
1895 begins at about 53 Ma and ends at about 49 Ma on the 2012 Time Scale (GTS; Vandenberghe
1896 et al., 2012). However, while the EECO was characterized by generally warm conditions,
1897 numerous fluctuations in average temperature likely occurred during the 4 Myr interval.

1898

1899 **3 Sites and stratigraphy**

1900

1901 **3.1 Possagno, Venetian Prealps, Tethys**

1902

1903 An Upper Cretaceous through Miocene succession crops out at the bottom of the Monte
1904 Grappa Massif in the Possagno area, about 60 km northwest of Venice. The lower to middle
1905 Eocene, of primary focus to this study, is represented by the Scaglia beds. These
1906 sedimentary rocks represent pelagic and hemipelagic sediment that accumulated at middle to
1907 lower bathyal depths (Cita, 1975; Thomas, 1998) in the western part of the Belluno Basin, a
1908 Mesozoic–Cenozoic paleogeographic unit of the Southern Alps (Bosellini, 1989). The basin
1909 very likely was an embayment connected to the western Tethys, with a paleolatitude of 42°
1910 during the early Eocene (**Figure 2**).

1911 A quarry at 45°51.0' N and 11°51.6' E exposed in 2002-2003 a 66 m thick section of
1912 the Scaglia beds (Figure 3), although it is at present largely covered and inaccessible. This
1913 section was examined for its stratigraphy (Agnini et al., 2006; Luciani and Giusberti, 2014),

1914 and shown to extend from just below the PETM to within lower Chron C20r in the lower
1915 middle Eocene. Like other lower Paleogene sections of the Venetian Pre-alps (Giusberti et
1916 al., 2007; Agnini et al., submitted), a Clay Marl Unit (CMU) with a prominent negative CIE
1917 marks the PETM.

1918 The Possagno section appears to be continuous, but with an important decrease in
1919 sedimentation rate (to below 1.4 m/Myr)-between 14.66 m and 15.51 m (Agnini et al., 2006).
1920 This interval lies within Chron C23r and near the start of the EECO, and predates the onset
1921 of a major increase in discoaster abundance (Agnini et al., 2006).

1922

1923 **3.2 Site 577, Shatsky Rise, Western Pacific**

1924

1925 Deep Sea Drilling Project (DSDP) Leg 86 drilled Site 577 at 32°26.5' N, 157°43.4' E, and
1926 2680 m water depth, on Shatsky Rise, a large igneous plateau in the NW Pacific with a
1927 relatively thin veneer of sediment (Shipboard Scientific Party 1985). During the early
1928 Eocene, this site was located closer to 15° N (**Figure 2**), and probably at a slightly shallower
1929 water depth (Ito and Clift, 1998).

1930 Two primary holes were drilled at Site 577. Both Hole 577* and Hole 577A recovered
1931 portions of a nominally 65 m thick section of Upper Cretaceous through lower Eocene
1932 nannofossil ooze. Similar to the Possagno section, the lower Paleogene interval has
1933 biomagnetostratigraphic information (Bleil, 1985; Monechi et al., 1985; Backman, 1986; Lu
1934 and Keller, 1995; Dickens and Backman, 2013). Stable isotope records of bulk carbonate
1935 have been generated for sediment from several cores at low sample resolution (Shackleton,
1936 1986), and for much of Cores 577*-9H and 577*-10H at fairly high sample resolution
1937 (Cramer et al. 2003).

1938 The composition and relative abundances of planktic foraminifera were nicely

1939 documented at Site 577 (Lu, 1995; Lu and Keller, 1995), and show a marked turnover
1940 between morozovellids and acarainids during the early Eocene. These data, however, have
1941 remained on an out-dated view for the stratigraphy at this location, where cores were not
1942 originally aligned to account for gaps and overlaps (Dickens and Backman, 2013). As will
1943 become obvious later, the main phase of the EECO spans Cores 577*-8H and 577A-8H,
1944 where detailed stable isotope records have not been generated previously.

1945

1946 **3.3 Site 1051, Blake Nose, Western Atlantic**

1947

1948 The Blake Nose is a gentle ramp extending from 1000 m to 2700 m water depth east of
1949 Florida (Norris et al, 1998). The feature is known for a relatively thick sequence of middle
1950 Cretaceous through middle Eocene sediment with minimal overburden. Ocean Drilling
1951 Program (ODP) Leg 171B drilled and cored this sequence at several locations, including Site
1952 1051 at 30°03.2' N, 76°21.5' W, and 1994 m water depth (Shipboard Scientific Party 1998).
1953 The site was located slightly to the south during the early Eocene (**Figure 2**). Benthic
1954 foraminiferal assemblages indicate a lower bathyal depth (1000-2000 m) during the late
1955 Paleocene and middle Eocene (Norris et al., 1998), although Bohaty et al. (2009) estimated a
1956 paleodepth of about 2200 m for sedimentation ca. 50 Ma.

1957 Sediments from 452.24 to 353.10 meters below sea floor (mbsf) at Site 1051 consist of
1958 lower to middle Eocene carbonate ooze and chalk (Shipboard Scientific Party, 1998).

1959 ~~Although~~ The site comprises two holes (1051A and 1051B), with core gaps and core
1960 overlaps existing at both (Shipboard Scientific Party, 1998). However, the impact of these
1961 depth offsets upon age is less than at Site 577, because of higher overall sedimentation rates.

1962 The Eocene section at Site 1051 has good sediment recovery, except an interval between
1963 382 mbsf and 390 mbsf, which contains significant chert. Stratigraphic markers across the

1964 Eocene interval include polarity chrons (Ogg and Bardot, 2001), calcareous nannofossil
1965 biohorizons (Mita, 2001), and planktic foraminiferal biohorizons (Norris et al., 1998; Luciani
1966 and Giusberti, 2014). ~~However,~~ As first noted by Cramer et al. (2003), though, there is a
1967 basic stratigraphic problem with the labelling of the polarity chrons. The intervals of normal
1968 polarity between approximately 388 and 395 mbsf, and between approximately 412 and 420
1969 mbsf were tentatively assigned to C22n and C23n, respectively (Ogg and Bardot, 2001). ~~The~~
1970 ~~original~~ This age assignment was ~~adopted~~ assumed to be correct by Luciani and Giusberti
1971 (2014), who therefore considered the last occurrence of *Morozovella subbotinae* as ~~happened~~
1972 ~~happening~~ near the top of C23n, an assumption that was also made for the revision of Eocene
1973 foraminiferal biozones (Wade et al., 2011).

1974 These age assignments, however, cannot be correct, because calcareous nannofossil
1975 biohorizons that lie below or within C22n (top of *T. orthostylus*, top of *Toweius*, base of *D.*
1976 *sublodoensis*) occur above 388 mbsf (Mita, 2001). Instead, there must be a significant hiatus
1977 or condensed interval at the chert horizon, and the above noted intervals of normal polarity
1978 are C23n and C24n.1n.

1979

1980 **4 Methods**

1981

1982 **4.1 Samples for isotopes and foraminifera**

1983

1984 The three sites provide a good stratigraphic background and key existing data for
1985 understanding the temporal link between the EECO, carbon isotope perturbations and
1986 planktic foraminiferal evolution. Our analytical aim was to obtain comparable data sets
1987 across the sites. More specifically, a need existed to generate stable isotope and planktic
1988 foraminiferal assemblage records at the Possagno section, to generate stable isotope records

1989 at DSDP Site 577, and to generate planktic foraminiferal assemblage records at ODP Site
1990 1051.

1991 A In total, of 298 samples were collected from the originally exposed Possagno section
1992 in 2002-2003 for isotope analyses. The sampling interval was 2 to 5 cm for the basal 0.7 m,
1993 50 cm, and 20 cm and at variable spacing from 20 to 50 cm for the interval between 0.7 m
1994 and 66 m. Bulk sediment samples previously were examined for their calcareous nannofossil
1995 assemblages (Agnini et al., 2006). One hundred and ten of these samples were selected for
1996 the foraminiferal study.

1997 Aliquots of the 110 samples were weighed, and then washed to obtain foraminifera using
1998 two standard procedures, depending on lithology. For the indurated marly limestones and
1999 limestones, the cold-acetolyse technique was used (Lirer, 2000; Luciani and Giusberti, 2014).
2000 This method disaggregates strongly lithified samples, in which foraminifera otherwise can be
2001 analyzed only with thin sections (Fornaciari et al., 2007; Luciani et al., 2007). For the marls,
2002 samples were disaggregated using 30 % hydrogen peroxide and subsequently washed and
2003 sieved at 63 μm . In most cases, gentle ultrasonic treatment (e.g., low-frequency at 40 kHz for
2004 30–60 seconds) improved the cleaning of the tests.

2005 Relative abundance data of planktic foraminiferal samples were generated for 65 samples
2006 at Site 577 (Lu, 1995; Lu and Keller, 1995). We collected new samples for stable isotope
2007 (~~below~~) measurements that span their previous effort.

2008 Fifty samples of Eocene sediment were obtained from Hole 1051A between 452 to 353
2009 mbsf. Sample spacing varied from 2.0 m to 0.5 m. As the samples are ooze and chalk, they
2010 were prepared using disaggregation using distilled water and washing over 38 μm and 63 μm
2011 sieves. Washed residues were dried at $<50^{\circ}\text{C}$.

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2013 **4.2 Stable Isotopes**

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Carbon and oxygen stable isotope data of bulk sediment samples from the Possagno section and Site 577 were analysed using a Finnigan MAT 252 mass spectrometer equipped with a Kiel device at Stockholm University. Precision is within ± 0.06 ‰ for carbon isotopes and within ± 0.07 ‰ for oxygen isotopes. Stable isotope values were calibrated to the Vienna Pee Dee Belemnite standard (VPDB) and converted to conventional delta notation ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$).

4.3 Foraminifera analyses

The mass percent of the >63 μm size fraction relative to the mass of the bulk sample, typically 100 g/sample was calculated for the 110 Possagno samples. This is referred to as the weight percent coarse fraction, following many previous works. (~~Hancock and Dickens, 2005~~). Due to the consistent occurrence of radiolarians at Site 1051, the coarse fraction cannot give information on foraminiferal productivity.

Relative abundances for both Possagno and Site 1051 have been determined from about 300 complete specimens extracted from each of the 110 samples investigated in the >63 μm size fraction from random splits.

The degree of dissolution, expressed as the fragmentation index (F index) was evaluated according to Petrizzo et al. (2008) on ca. 300 elements, by counting planktic foraminiferal fragments or partially dissolved tests versus complete tests. These data are expressed in percentages. Fragmented foraminifera include specimens showing missing chambers and substantial breakage. The taxonomic criteria for identifying planktic foraminifera follows the work by Pearson et al. (2006).

2039 **5 Results**

2040

2041 **5.1 Carbon isotopes**

2042

2043 *Possagno*

2044 Carbon isotopes of bulk carbonate at Possagno vary between +1.8 and -0.3 ‰ (**Figure 4,**
2045 **Table S1**). Overall, $\delta^{13}\text{C}$ decreases from 1.8 ‰ at the base of the section to about 0.6 ‰ at 14
2046 m. Generally, values then increase to 1.5 ‰ at 24 m, and remain between 1.5 ‰ and 0.8 ‰
2047 for the remainder of the studied interval.

2048 Superimposed on these trends are a series of negative CIEs. The most prominent of these
2049 (~1.5 ‰) occurs at the 0 m level, and marks the PETM (Agnini et al., 2009). However, *other*
2050 negative CIEs lie above this marker and within the lowermost 21.4 m, *albeit some are only*
2051 *defined by one data point* (**Figure 4, Table S1**). The lower two at ~8 m and ~12.5 m probably
2052 represent the H-1/ETM-2 and J event, respectively, as they lie at the appropriate stratigraphic
2053 horizons in relation to polarity chrons. The K/X event may lie at 14.8 m, although this height
2054 marks the start of the condensed interval.

2055 The complex interval between 15.5 m and 24 m broadly corresponds to all of Chron
2056 C23n and the bottom half of Chron C22r. A series of CIEs occur in that interval on the order
2057 of 1.4 ‰, superimposed on a background trend of increasing $\delta^{13}\text{C}$ values (about 0.7 ‰). We
2058 tentatively label these CIEs with even numbers for internal stratigraphic purposes (**Figure 4**),
2059 as will become obvious below; their magnitudes range between 0.9 and 0.3 ‰ (**Table S1**).
2060 However, the sample spacing through this interval varies from 20 to 50 cm. The precise
2061 magnitudes and positions certainly could change with higher sample resolution, given the
2062 estimated compacted sedimentation rate of ~0.5 cm/kyr for this part of the section (Agnini et
2063 al., 2006).

2064 Above Chron C22r, the Possagno $\delta^{13}\text{C}$ record contains additional minor CIEs (**Figure 4**).
2065 The most prominent of these CIEs, at least relative to baseline values ($\sim 1.2\text{‰}$), occurs within
2066 Chron C21n. More important to understanding the EECO, a $\sim 0.6\text{‰}$ CIE nearly coincides
2067 with the base of *D. sublodoensis* within the lower part of Chron C22n.

2068

2069 DSDP Site 577

2070 The $\delta^{13}\text{C}$ record of bulk carbonate at DSDP Site 577 from just ~~prior to~~ below the PETM
2071 through Chron C22n ranges between 2.3 and 0.6 ‰ (**Figure 5; Table S2**). Overall, $\delta^{13}\text{C}$
2072 decreases from 1.4 ‰ at 84.5 mcd to about 0.6 ‰ at ~ 76 mcd. Values then generally increase
2073 to 2.1 ‰ at ~ 68 mcd, and remain between 2.3 ‰ and 1.6 ‰ for the rest of the studied
2074 interval. Thus, the ranges and general trends in $\delta^{13}\text{C}$ for the two sections are similar, but
2075 skewed at DSDP Site 577 relative to Possagno by about $+0.6\text{‰}$.

2076 Like at Possagno, the early Eocene $\delta^{13}\text{C}$ record at DSDP Site 577 exhibits a series of
2077 CIEs (**Figure 5**). The portion of this record from the PETM through the K/X event has been
2078 documented and discussed elsewhere (Cramer et al., 2003; Dickens and Backman, 2013). The
2079 new portion of this record, from above the K/X event through Chron C22n, spans the
2080 remainder of the EECO. Within this interval, where background $\delta^{13}\text{C}$ values rise by $\sim 1.5\text{‰}$,
2081 there again occur a series of minor CIEs with magnitudes between 0.3 and 0.5 ‰ (**Table S2**).
2082 Here, however, multiple data points define most of the CIEs. We again give these an internal
2083 numerical labelling scheme. A $\sim 0.4\text{‰}$ CIE also nearly coincides with the base of *D.*
2084 *sublodoensis* within the lower part of C22n.

2085

2086 **5.2 Oxygen isotopes**

2087

2088 Possagno

2089 Oxygen isotopes of bulk carbonate at Possagno range between -3.3 and 0.8 ‰ with a mean
2090 value of -1.7 ‰ (**Figure 4, Table S1**). In general, ~~there exists~~ considerable scatter exists
2091 across the data set with respect to depth, as adjacent samples often ~~having~~ display a
2092 difference in $\delta^{18}\text{O}$ that exceeds 0.5 ‰. Nonetheless, some of the more prominent lows in $\delta^{18}\text{O}$
2093 show a clear correspondence with negative $\delta^{13}\text{C}$ values (CIEs) and vice versa. This
2094 correspondence occurs across the PETM and other known hyperthermals, as well as within
2095 and after the EECO. Indeed, the main phase of the EECO ~~appears to~~ corresponds with a
2096 broad has the lowest $\delta^{18}\text{O}$ values.

2097

2098 DSDP Site 577

2099 The $\delta^{18}\text{O}$ record at Site 577 noticeably deviates from that at Possagno (**Figure 5, Table S2**).
2100 This is because values range between ~~0.2 and -1.1 ‰~~ -1.1 ‰ and 0.2 with an average value of
2101 -0.4 ‰. Thus, ~~both records have somewhat similar scatter~~ relative to Possagno, the record at
2102 Site 577 has less scatter, and an overall shift of about -1.3 ‰. There ~~is~~ exists again a modest
2103 correlation between decreases in $\delta^{18}\text{O}$ and negative $\delta^{13}\text{C}$ values, as well as a general low in
2104 $\delta^{18}\text{O}$ across the main phase of the EECO.

2105

2106 **5.3 Coarse fraction**

2107

2108 The coarse fraction of samples from Possagno shows two distinct trends (**Figure 6, Table**
2109 **S3**). Before the EECO, values are $10.4 \pm 2.67 \%$. However, from the base of the EECO
2110 and up through the section, values decrease to $5.3 \pm 1.3 \%$.

2111

2112 **5.4 Foraminiferal preservation and fragmentation**

2113

2114 Planktic foraminifera are consistently present and diverse throughout the studied intervals at
2115 Possagno and at ODP Site 1051. Preservation of the tests at Possagno varies from moderate
2116 to fairly good (Luciani and Giusberti, 2014). However, planktic foraminiferal tests at
2117 Possagno are recrystallized and essentially totally filled with calcite. Planktic foraminifera
2118 from samples at Site 1051 are readily preserved recognizable throughout the studied interval.
2119 Planktic foraminifera from Site 577, at least as illustrated by published plates (Lu and Keller,
2120 1995), show a very good state of preservation (albeit possibly recrystallized).

2121 The *F* index record at Possagno (Figure 6, Table S3) displays large amplitude variations
2122 throughout the investigated interval. The highest values, up to 70 %, were observed between
2123 16 and 22 m. In general, highs in *F* index values correspond to lows in the $\delta^{13}\text{C}$ record.

2124 The *F* index record at Site 1051 (Figure 8 7, Table S4) shows less variability compared
2125 to that at Possagno, although some of this may reflect the difference in the number of samples
2126 examined at the two locations. A maximum value of 60 % is found in Zone E5, just below an
2127 interval of uncertain magnetostratigraphy (Norris et al., 1998), but corresponding to the J
2128 event (Cramer et al., 2003). Relatively high *F* index values, around 50 %, also occur in
2129 several samples below this horizon. The interval across the EECO generally displays low *F*
2130 index values (<20 %).

2131

2132 **5.5 Planktic foraminiferal quantitative analysis**

2133

2134 Possagno

2135 Planktic foraminiferal assemblages at Possagno show significant changes across the early to
2136 early middle Eocene (Figure 6, Table S3). Throughout the entire section, the mean relative
2137 abundance of *Acarinina* is about 46 % of the total assemblage. However, members of this
2138 genus show exhibit peak abundances of 60-80 % of the total assemblage ~~occur~~ across several

2139 intervals, often corresponding to CIEs. Particularly prominent is the broad abundance peak of
2140 *Acarinina* coincident with the main phase of the EECO.

2141 The increases in acarininid relative abundance typically are counterbalanced by transient
2142 decreases of subbotinids (**Figure 6**). This group also shows a general increase throughout the
2143 section. Below the EECO the relative abundances of subbotinids average ~24 %. Above the
2144 EECO, this average rises to ~36 %.

2145 The trends of acarininids and subbotinids contrast with that of morozovellids (**Figure 6**),
2146 which exhibit a major and permanent decline within Zone E5. This group collapses from
2147 mean abundances ~24 % in the 0-15 m interval to <6 % above 15 m. Qualitative examination
2148 of species shows that, in the lower part of Zone E5, where relatively high morozovellids
2149 abundances are recorded, there is no dominance of any species. *M. marginodentata*, *M.*
2150 *subbotinae* and *M. lensiformis* are each relatively common, and *M. aequa*, *M. aragonensis*,
2151 *M. formosa* and *M. crater* are each less common. By contrast, in the upper part of Zone E5,
2152 where low morozovellids abundances of morozovellids occur, *M. aragonensis*, *M. formosa*,
2153 *M. crater* and *M. caucasica* are the most common species. The general decrease of
2154 morozovellids abundances appears unrelated to the disappearance of a single, dominant
2155 species.

2156 At Possagno, morozovellids never recover to their pre-EECO abundances. This is true
2157 even if one includes the morphologically and ecologically comparable genus *Morozovelloides*
2158 (Pearson et al., 2006), which first appears in samples above 36 m.

2159 Other planktic foraminiferal genera are always less than 15 % of the total assemblages
2160 throughout the studied interval at Possagno (**Figure S1, Table S3**).

2161

2162 ODP Site 577

2163 Samples from Site 577 were disaggregated in water and washed through a >63 sieve (Lu,
2164 1995; Lu and Keller, 1995). They determined relative abundances of planktic foraminifera
2165 from random splits of about 300 specimens (Lu, 1995; Lu and Keller, 1995). The resulting
2166 data are shown in **Figure 7**, placed onto the composite depth scale by Dickens and Backman
2167 (2013). Major changes in planktic foraminiferal assemblages are comparable to those
2168 recorded at Possagno. Such changes include indeed a distinct decrease of morozovellids
2169 within Zone E5. The decrease at Site 577 is from mean values of 26.6 % to 6.7 % (**Table S4**).
2170 This marked drop occurs at ca. 78 mcd close to the J event and at the start of the EECO. Like
2171 at Possagno, morozovellids never recover to their pre-EECO abundances.

2172 The morozovellids decrease is counter balanced by the trend of acarininids abundances
2173 that increase from mean values of 30.4 % to 64.8 % in correspondence to the level of the
2174 morozovellids collapse. Subbotinids fluctuate in abundance throughout the interval
2175 investigated from 1 % to 18 %, with a mean value of ca. 8 %.

2176

2177 ODP Site 1051

2178 Planktic foraminifera show distinct changes in abundance at Site 1051 (**Figure 8, Table S5**).
2179 The changes of the main taxa are similar to the variations observed at Possagno. The genus
2180 *Acarinina* displays an increase in mean relative abundance from 35 % (base to ca. 450 mbsf)
2181 to around 50 % (ca. 430 mbsf), with maximum values of about 60 %. The relatively low
2182 resolution used here does not permit comparison to the early Eocene CIEs at Site 1051
2183 (Cramer et al., 2003), or how the relative abundance of planktic foraminiferal genera varies
2184 with respect to CIEs.

2185 The abundance of subbotinids shows ~~little~~ small variations around mean values of 20 %
2186 at Site 1051. Like at Possagno, samples from Site 1051 also record a slight increase in
2187 abundance toward the end of the EECO and above (~~ca. 7%, mean value~~).

2188 The major change in planktic foraminiferal assemblages at Site 1051 includes a distinct
2189 decrease of *Morozovella*, from mean values around 40 % to 10 % in the middle part of Zone
2190 E5 (**Figure 7**). Similar to Possagno, the lower part of Zone E5 with the higher percentages of
2191 morozovellids does not record the dominance of selected species, but at Site 1051 *M.*
2192 *aragonensis* and *M. formosa* besides *M. subbotinae* are relatively common whereas *M.*
2193 *marginodentata* is less frequent. Within the interval of low morozovellids abundances, *M.*
2194 *aragonensis* and *M. formosa* are the most common taxa. The general decline of
2195 morozovellids does not appear therefore related, both at Possagno and at Site 1051, to the
2196 extinction or local disappearance of a dominant species.

2197

2198 **6 Discussion**

2199

2200 **6.1 Dissolution, recrystallization, and bulk carbonate stable isotopes**

2201

2202 The bulk carbonate stable isotope records within the lower Paleogene sections at Possagno
2203 and at Site 577 need ~~thought, consideration~~ considering how such records are produced and
2204 modified in much younger strata dominated by pelagic carbonate. In open ocean
2205 environments, carbonate preserved on the seafloor principally consists of calcareous tests of
2206 nannoplankton (coccolithophores) and planktic foraminifera (Bramlette and Riedel, 1954;
2207 Berger, 1967; Vincent and Berger, 1981). However, the total amount of carbonate and its
2208 microfossil composition can vary considerably across locations because of differences in
2209 deep-water chemistry and in test properties (e.g., ratio of surface area to volume;
2210 mineralogical composition). For regions at low to mid latitudes, a reasonable representation
2211 of carbonate components produced in the surface water accumulates on the seafloor at
2212 modest (<2000 m) water depth. By contrast, microfossil assemblages become heavily

2213 modified in deeper water, because of increasingly significant carbonate dissolution (Berger,
2214 1967). Such dissolution preferentially affects certain tests, such as thin-walled, highly porous
2215 planktic foraminifera (Berger, 1970; Bé et al., 1975; Thunell and Honjo, 1981).

2216 The stable isotope composition of modern bulk carbonate ooze reflects the mixture of its
2217 carbonate components, which mostly record water temperature and the composition of
2218 dissolved inorganic carbon (DIC) within the mixed layer (<100 m water depth). The stable
2219 isotope records are imperfect, though, because of varying proportions of carbonate
2220 constituents, and “vital effects”, which impact stable isotope fractionation for each
2221 component (Anderson and Cole, 1975; Reghellin et al., 2015). Nonetheless, the stable isotope
2222 composition of bulk carbonate ooze on the seafloor can be related to overlying temperature
2223 and chemistry of surface water (Anderson and Cole, 1975; Reghellin et al., 2015).

2224 Major modification of carbonate ooze occurs during sediment burial. This is because,
2225 with compaction and increasing pressure, carbonate tests begin to dissolve and recrystallize
2226 (Schlanger and Douglas, 1974; Borre and Fabricus, 1998). Typically within several hundred
2227 meters of the seafloor, carbonate ooze becomes chalk and, with further burial, limestone
2228 (Schlanger and Douglas, 1974; Kroencke et al., 1991; Borre and Fabricus, 1998). Carbonate
2229 recrystallization appears to be a local and nearly closed system process, such that mass
2230 transfer occurs over short distances (i.e., less than a few meters) (above references and Matter
2231 et al., 1975; Arthur et al., 1984; Frank et al., 1999).

2232 In pelagic sequences with appreciable carbonate content **and low organic carbon content**,
2233 bulk carbonate $\delta^{13}\text{C}$ records typically give information of paleoceanographic significance
2234 (Scholle and Arthur, 1980; Frank et al., 1999). Even when transformed to indurated
2235 limestone, the $\delta^{13}\text{C}$ value for a given sample should be similar to that originally deposited on
2236 the seafloor. This is because, **for such sediments**, almost all carbon within small ~~sedimentary~~
2237 volumes exists as carbonate. Bulk carbonate $\delta^{18}\text{O}$ records are a different matter, especially in

2238 indurated marly limestones and limestones (Marshall, 1992; Schrag et al., 1995; Frank et al.,
2239 1999). This is because pore water dominates the total amount of oxygen within an initial
2240 parcel of sediment, and oxygen isotope fractionation depends strongly on temperature. Thus,
2241 during dissolution and recrystallization of carbonate, significant exchange of oxygen isotopes
2242 occurs. At first, carbonate begins to preferentially acquire ^{18}O , because shallowly buried
2243 sediment generally has ~~older~~ lower temperatures than surface water. However, with
2244 increasing burial depth along a geothermal gradient, carbonate begins to preferentially
2245 acquire ^{16}O (Schrag et al., 1995; Frank et al., 1999).

2246

2247 **6.2 Carbon isotope stratigraphy through the EECO**

2248

2249 Stratigraphic issues complicate direct comparison of various records from Possagno and Site
2250 577. The two sections have somewhat similar multi-million year sedimentation rates across
2251 the early Eocene. However, the section at Possagno contains the condensed interval, where
2252 much of C23r spans a very short distance (Agnini et al., 2006), and the section at Site 577 has
2253 a series of core gaps and core overlaps (Dickens and Backman, 2013).

2254 An immediate issue to amend is the alignment of Cores 8H and 9H in Hole 577* and
2255 Core 8H in Hole 577A (**Figure 5**). On the basis of GRAPE density records for these cores,
2256 Dickens and Backman (2013) initially suggested a 2.6 m core gap between Cores 8H* and
2257 9H*. However, a 3.5 m core gap also conforms to all available stratigraphic information. The
2258 newly generated $\delta^{13}\text{C}$ (and $\delta^{18}\text{O}$) records across these three cores show the latter to be correct.

2259 Once sedimentation rate differences at Possagno are recognized and coring problems at
2260 Site 577 are rectified, early Eocene $\delta^{13}\text{C}$ records at both locations display similar trends and
2261 deviations in relation to polarity chrons and key microfossil events (**Figures 4, 5**). Moreover,
2262 the $\delta^{13}\text{C}$ variations seemingly can be correlated in time to those found in bulk carbonate $\delta^{13}\text{C}$

2263 records at other locations, including Site 1051 (**Figure 8**) and Site 1258 (**Figure 9**). As noted
2264 previously, such correlation occurs because the bulk carbonate $\delta^{13}\text{C}$ signals reflect past global
2265 changes in the composition of surface water DIC, even after carbonate recrystallization.

2266 For the latest Paleocene and earliest Eocene, nominally the time spanning from the base
2267 of C24r through the middle of C24n, detailed stable carbon isotope records have been
2268 generated at more than a dozen locations across the globe (Cramer et al., 2003; Agnini et al.,
2269 2009; Galeotti et al., 2010; Zachos et al., 2010; Slotnick et al., 2012; Littler et al., 2014;
2270 Agnini et al., in review). These records can be described consistently as a long-term drop in
2271 $\delta^{13}\text{C}$ superimposed with a specific sequence of prominent CIEs that include those
2272 corresponding to the PETM, H-1, and J events. In continuous sections with good
2273 magnetostratigraphy and biostratigraphy, there is no ambiguity in the assignment of CIEs
2274 (Zachos et al., 2010; Littler et al., 2014; Slotnick et al., 2012, 2105a; Lauretano et al., 2015).
2275 This “ $\delta^{13}\text{C}$ template” can be found at the Possagno section and at Site 577 (**Figure 9**); it is
2276 found at Site 1051 for the depth interval where carbon isotopes have been determined
2277 (**Figure 8**).

2278 After the J event and across the EECO, very few detailed $\delta^{13}\text{C}$ records have been
2279 published (Slotnick et al., 2012, 2015a; Kirtland-Turner et al., 2014). Moreover, the available
2280 records are not entirely consistent. For example, the K/X event in Clarence River valley
2281 sections manifests as a prominent CIE within a series of smaller $\delta^{13}\text{C}$ excursions (Slotnick et
2282 al., 2012, 2015a), whereas the event has limited expression in the $\delta^{13}\text{C}$ record at Site 1258
2283 (Kirtland-Turner et al., 2014; **Figure 9**).

2284 The new records from Possagno and Site 577 emphasize an important finding regarding
2285 bulk carbonate $\delta^{13}\text{C}$ records across the EECO. Between the middle of C24n and the upper
2286 part of C23r, there appears to be a sequence of low amplitude, low frequency CIEs. (Note
2287 that this portion of the record is missing at Possagno because of the condensed interval;

2288 **Figure 9**). However, near the C23r/C23n boundary, a long-term rise in $\delta^{13}\text{C}$ begins, but with
2289 a series of relatively high amplitude, high frequency CIEs (Kirtland-Turner et al., 2014;
2290 Slotnick et al., 2014). The number, relative magnitude and precise timing of CIEs within this
2291 interval remain uncertain. For example, the CIE labelled “4” appears to occur near the top of
2292 C23r at Site 577 but near the bottom of C23n.2n at Site 1258 and at Possagno. Additional
2293 $\delta^{13}\text{C}$ records across this interval are needed to resolve the correct sequence of CIEs and to
2294 derive an internally consistent labelling scheme for these perturbations. It is also not clear
2295 which of these CIEs during the main phase of the EECO specifically relate to significant
2296 increases in temperature, as clear for the “hyperthermals” in the earliest Eocene. Nonetheless,
2297 numerous CIEs, as well as an apparent change in the mode of these events, characterize the
2298 EECO (Kirtland-Turner et al., 2014; Slotnick et al., 2014).

2299 The causes of $\delta^{13}\text{C}$ changes during the early Paleogene lie at the crux of considerable
2300 research and debate (Dickens et al., 1995, 1997; Zeebe et al., 2009; Dickens, 2011; Lunt et
2301 al., 2011; Sexton et al., 2011; De Conto et al., 2012; Lee et al., 2013; Kirtland Turner et al.,
2302 2014). Much of the discussion has revolved around three questions: (1) what are the sources
2303 of ^{13}C -depleted carbon that led to prominent CIEs, especially during the PETM? (2) does the
2304 relative importance of different carbon sources vary throughout this time interval? and, (3)
2305 are the geologically brief CIEs related to the longer secular changes in $\delta^{13}\text{C}$? One might
2306 suggest, through several papers, a convergence of thought as to how carbon cycled across
2307 Earth’s surface during the early Paleogene, at least between the late Paleocene and the K/X
2308 event (Cramer et al., 2003; Lourens et al., 2005; Galeotti et al., 2010; Hyland et al., 2013;
2309 Zachos et al., 2010; Lunt et al. 2011; Littler et al., 2014; Lauretano et al., 2015; Westerhold et
2310 al., 2015). Changes in tectonics, volcanism, and weathering drove long-term changes
2311 atmospheric $p\text{CO}_2$ (Vogt, 1979; Raymo and Ruddiman, 1992; Sinton and Duncan, 1998;
2312 Demicco, 2004; Zachos et al., 2008), which was generally high throughout the early

2313 Paleogene, but increased toward the EECO (Pearson and Palmer, 2000; Fletcher et al., 2008;
2314 Lowenstein and Demicco, 2006; Smith et al., 2010; Hyland and Sheldon, 2013). However, as
2315 evident from the large range in $\delta^{13}\text{C}$ across early Paleogene stable isotope records, major
2316 changes in the storage and release of organic carbon must have additionally contributed to
2317 variability in atmospheric $p\text{CO}_2$ and ocean DIC concentrations (Shackleton, 1986; Kurtz et
2318 al., 2003; Komar et al., 2013). When long-term increases in $p\text{CO}_2$, perhaps in conjunction
2319 with orbital forcing, pushed temperatures across some threshold, such as the limit of sea-ice
2320 formation (Lunt et al., 2011), rapid inputs of ^{13}C -depleted organic carbon from the shallow
2321 geosphere served as a positive feedback to abrupt warming (Dickens et al., 1995; Bowen et
2322 al., 2006; DeConto et al., 2012).

2323 Our new $\delta^{13}\text{C}$ records do not directly address the above questions and narrative
2324 concerning early Paleogene carbon cycling. However, they do highlight two general and
2325 related problems when such discussion includes the EECO. First, surface temperatures appear
2326 to stay high across an extended time interval when the $\delta^{13}\text{C}$ of benthic foraminifer (**Figure 1**)
2327 and bulk carbonate (**Figure 9**) increase. Second, numerous brief CIEs mark this global long-
2328 term rise in $\delta^{13}\text{C}$. Whether the aforementioned views need modification or reconsideration
2329 (Kirtland Turner et al., 2014) is an outstanding issue, one that depends on how long-term and
2330 short-term $\delta^{13}\text{C}$ changes relate across the entire early Paleogene.

2331 The overall offset between bulk carbonate $\delta^{13}\text{C}$ values at Possagno and Site 577 may hint
2332 at an important constraint to any model of early Paleogene carbon cycling. Throughout the
2333 early Eocene, $\delta^{13}\text{C}$ values at Site 577 exceed those at Possagno by nominally 0.8 ‰ (**Figure**
2334 **9**). This probably does reflect recrystallization or lithification, because similar offsets appear
2335 across numerous records independent of post-depositional history but dependent on location
2336 (Schmitz et al., 1996; Cramer et al., 2003; Slotnick et al., 2012, 2015a; Agnini et al.,
2337 submitted). In general, absolute values of bulk carbonate $\delta^{13}\text{C}$ records increase from the

2338 North Atlantic and western Tethys (low), through the South Atlantic and eastern
2339 Tethys/Indian, to the Pacific oceans (high), although suggestively with a latitudinal
2340 component to this signature.

2341

2342 **6.3 Stable oxygen isotope stratigraphy across the EECO**

2343

2344 Bulk carbonate $\delta^{18}\text{O}$ values for Holocene sediment across the Eastern Equatorial Pacific
2345 relate to average temperatures in the mixed layer (Shackleton and Hall, 1995; Reghellin et al.,
2346 2015). Indeed, values are close to those predicted from water chemistry ($\delta^{18}\text{O}_w$) and
2347 equilibrium calculations for calcite precipitation (e.g., Bemis et al., 1998) if vital effects in
2348 the dominant nanoplankton increase $\delta^{18}\text{O}$ by nominally 1‰ (Reghellin et al., 2015).

2349 Site 577 was located at about 15°N latitude in the eastern Pacific during the early
2350 Paleogene. Given that sediment of this age remains “nanofossil ooze” (Shipboard Scientific
2351 Party, 1985), one might predict past mixed layer temperatures from the $\delta^{18}\text{O}$ values with
2352 three assumptions: early Paleogene $\delta^{18}\text{O}_w$ was 1.2 ‰ less than that at present-day to account
2353 for an ice-free world; local $\delta^{18}\text{O}_w$ was equal to average seawater, similar to modern chemistry
2354 at this off-Equator location (LeGrande and Schmidt, 2006); and, Paleogene nanoplankton
2355 also fractionated $\delta^{18}\text{O}$ by 1.0 ‰. With commonly used equations that relate the $\delta^{18}\text{O}$ of
2356 calcite to temperature (Bemis et al., 1998), these numbers render temperatures of between
2357 16°C and 21°C for the data at Site 577. Such temperatures seem too cold by at least 10°C,
2358 given other proxy data and modelling studies (e.g., Pearson et al., 2007; Huber and Caballero,
2359 2011; Hollis et al., 2012; Pross et al., 2012; Inglis et al., 2015). At low latitudes, bottom
2360 waters are always much colder than surface waters. Even during the EECO, deep waters
2361 probably did not exceed 12°C (Zachos et al., 2008). The calculated tepid temperatures likely
2362 indicate partial recrystallization of bulk carbonate near the seafloor. Examinations of

2363 calcareous nanofossils in Paleogene sediment at Site 577 show extensive calcite
2364 overgrowths (Shipboard Scientific Party, 1985; Backman, 1986). Relatively low $\delta^{18}\text{O}$ values
2365 mark the H-1 and K/X events, as well as the main phase of the EECO (**Figure 5**). Both
2366 observations support the idea that the bulk carbonate $\delta^{18}\text{O}$ at Site 577 represents the
2367 combination of a primary surface water $\delta^{18}\text{O}$ signal and a secondary shallow pore water $\delta^{18}\text{O}$
2368 signal.

2369 Lithification should further impact bulk carbonate $\delta^{18}\text{O}$ records (Marshall, 1992; Schrag
2370 et al., 1995; Frank et al., 1999). Because this process occurs well below the seafloor, where
2371 temperatures approach or exceed those of surface water, the $\delta^{18}\text{O}$ values of pelagic marls and
2372 limestones should be significantly depleted in ^{18}O relative to partially recrystallized
2373 nanofossil ooze. This explains the nominal 2‰ offset in average $\delta^{18}\text{O}$ between correlative
2374 strata at Possagno and at Site 577. While temperature calculations using the $\delta^{18}\text{O}$ record at
2375 Possagno render reasonable surface water values for a mid-latitude location in the early
2376 Paleogene (26-31°C, using the aforementioned approach), any interpretation in these terms
2377 more than likely reflects happenstance. The fact that planktic foraminifera are completely
2378 recrystallized and totally filled with calcite at ~~this site~~ Possagno supports this inference.

2379 One might suggest, at least for the Possagno section, that meteoric water might have also
2380 impacted the $\delta^{18}\text{O}$ record. This is because rainwater generally has a $\delta^{18}\text{O}$ composition less
2381 than that of seawater. However, samples were collected at Possagno in 2002-2003 from fresh
2382 quarry cuts.

2383 As observed at Site 577, however, horizons of lower $\delta^{18}\text{O}$ at Possagno may represent
2384 times of relative warmth in surface water. This includes the broad interval between 16 and
2385 22.5 m, which marks the main phase of the EECO, as well as many of the brief CIEs, at least
2386 one that clearly represents the PETM (**Figure 4**). That is, despite obvious overprinting of the
2387 original $\delta^{18}\text{O}$ signal, early to early middle Eocene climate variations appear manifest in the

2388 data.

2389

2390 **6.4 The EECO and planktic foraminiferal abundances**

2391

2392 Bulk carbonate $\delta^{13}\text{C}$ records, especially in conjunction with other stratigraphic markers,
2393 provide a powerful means to correlate early Paleogene sequences from widely separated
2394 locations (**Figure 9**). They also allow for placement of planktic foraminiferal assemblage
2395 changes into broader context.

2396 The most striking change in planktic foraminiferal assemblages occurred near the start of
2397 the EECO. Over a fairly short time interval and at multiple widespread locations, the relative
2398 abundance of acarininids increased significantly whereas the relative abundance of
2399 morozovellids decreased significantly. This switch, best defined by the decline in
2400 morozovellids, happened just before the condensed interval at Possagno (**Figure 6**), just
2401 above the J event at Site 577 (**Figure 7, Table S4**), and during the J event at Site 1051
2402 (**Figure 8**). At the Farra section, cropping out in the same geological setting of Possagno at
2403 50 km NE of the Carcoselle quarry, it also appears to have occurred close to the J event
2404 (**Figure 10**). Indeed, the maximum turnover in relative abundances may have been coincident
2405 with the J event at all locations. Importantly, the relative abundance of subbotinids only
2406 changed marginally during this time.

2407 The “morozovellid ~~crisis~~ decline across the start of the EECO ~~was irreversible~~ did not
2408 rebound afterward. At Possagno, at Site 1051, and at Site 577, it was coupled with the
2409 gradual disappearances of several species, including *M. aequa*, *M. gracilis*, *M. lensiformis*,
2410 *M. marginodentata*, and *M. subbotinae*. Furthermore, the loss of morozovellids was not
2411 counterbalanced by the appearance of the *Morozovelloides* genus, which shared with
2412 *Morozovella* the same ecological preferences. This latter genus appeared in C21r, near the

2413 Ypresian/Lutetian boundary, and well after the EECO (Pearson et al., 2006; Aze et al., 2011),
2414 including at Possagno (Luciani and Giusberti, 2014; **Figure 6**). Though *Morozovelloides*
2415 were morphologically similar to *Morozovella*, they probably evolved from *Acarinina*
2416 (Pearson et al., 2006; Aze et al., 2011; **Figure 1**).

2417 At Possagno, higher abundances of acarininids also correlate with pronounced negative
2418 $\delta^{13}\text{C}$ perturbations before and after the EECO (**Figure 6**). This includes the H-1 event, as well
2419 as several unlabelled CIEs during C22n, C21r and C21n. Such increases in the relative
2420 abundances of acarininids have been described for the PETM interval at the proximal nearby
2421 Forada section (Luciani et al., 2007), and for the K/X event at the proximal Farra section
2422 (Agnini et al., 2009). Unlike for the main switch near the J event, however, these changes are
2423 transient, so that relative abundances in planktic foraminiferal genera are similar before and
2424 after the short-term CIEs.

2425

2426 **6.5 The impact of dissolution**

2427

2428 Carbonate dissolution at or near the seafloor presents a potential explanation for observed
2429 changes in foraminifera assemblages. Some studies of latest Paleocene to initial Eocene age
2430 sediments, including laboratory experiments, suggest a general ordering of dissolution
2431 according to genus, with acarininids more resistant than morozovellids, and the latter more
2432 resistant than subbotinids (Petrizzo et al., 2008; Nguyen et al., 2009, 2011).

2433 Carbonate solubility horizons that impact calcite preservation and dissolution on the
2434 seafloor (i.e., the CCD and lysocline) also shoaled considerably during various intervals of
2435 the early Eocene. The three most prominent hyperthermals that occurred before the main
2436 phase of the EECO (PETM, H-1, K/X) were clearly marked by pronounced carbonate
2437 dissolution at multiple locations (Zachos et al., 2005; Agnini et al., 2009; Stap et al., 2009;

2438 Leon-Rodriguez and Dickens, 2010). A multi-million year interval characterized by a
2439 relatively shallow CCD also follows the K/X event (Leon-Rodriguez and Dickens, 2010;
2440 Pälke et al., 2012; Slotnick et al., 2015b).

2441 Should changes in carbonate preservation primarily drive the observed planktic
2442 foraminiferal assemblages, it follows that the dominance of acarininids during the EECO and
2443 multiple CIEs could represent a taphonomic artefact. Limited support for this idea comes
2444 from our records of fragmentation (*F* index). In general, intervals with relatively high
2445 abundances of acarininids (and low $\delta^{13}\text{C}$) correspond to intervals of fairly high fragmentation
2446 at Possagno and at Site 1051 (**Figures 6, 8**). This can suggest carbonate dissolution, because
2447 this process breaks planktic foraminifera into fragments (Berger, 1967; Hancock and
2448 Dickens, 2005).

2449 Carbonate dissolution can cause the coarse fraction of bulk sediment to decrease (Berger
2450 et al., 1982; Broecker et al., 1999; Hancock and Dickens, 2005). This happens because whole
2451 planktic foraminiferal tests typically exceed 63 μm , whereas the resulting fragments often do
2452 not exceed 63 μm . The decrease in CF values at the start of the EECO at Possagno (**Figure 6**)
2453 may therefore further indicate loss of foraminiferal tests. However, relatively low CF values
2454 continue to the top of the section, independent of changes in the *F* index. The CF record
2455 parallels the trend of morozovellids abundance, and thus might also suggest a loss of larger
2456 morozovellids rather than carbonate dissolution.

2457 The cause of the long-term rise in carbonate dissolution horizons remains perplexing, but
2458 may relate to reduced inputs of ^{13}C -depleted carbon into the ocean and atmosphere (Leon-
2459 Rodriguez and Dickens, 2010; Komar et al., 2013). Should the morozovellids decline and
2460 amplified *F* index at the Possagno section mostly represent dissolution, it would imply
2461 considerable shoaling of these horizons in the western Tethys, given the inferred deposition
2462 in middle to lower bathyal setting. As with open ocean sites (Slotnick et al., 2015b), further

2463 studies on the Eocene **lysocline and** CCD are needed from Tethyan locations. One idea is that
2464 remineralization of organic matter intensified within the water column, driven by augmented
2465 microbial metabolic rates at elevated temperatures during the EECO; this may have decreased
2466 pH at intermediate water column depths (Brown et al., 2004; Olivarez Lyle and Lyle, 2006;
2467 O'Connor et al., 2009; John et al., 2013, 2014).

2468 Despite evidence for carbonate dissolution, this process probably only amplified primary
2469 changes in planktic foraminiferal assemblages. The most critical observation is the similarity
2470 of the abundance records for major planktic foraminiferal genera throughout the early Eocene
2471 at multiple locations (**Figures 6-8**). This includes the section at Site 1051, where carbonate
2472 appears only marginally modified by dissolution according to the *F* index values (**Figure 7**).
2473 Subbotinid abundance also remains fairly high throughout the early Eocene. One explanation
2474 is that, in contrast to laboratory experiments (Nguyen et al., 2009, 2011), subbotinids are
2475 more resistant to dissolution than morozovellids (Boersma and Premoli Silva, 1983; Berggren
2476 and Norris, 1997), at least once the EECO has transpired. In the proximal middle-upper
2477 Eocene section at Alano, Luciani et al. (2010) documented a dominance of subbotinids within
2478 intervals of high fragmentation (*F* index) and enhanced carbonate dissolution. The degree of
2479 dissolution across planktic foraminiferal assemblages may have varied through the early
2480 Paleogene, as distinct species within each genus may respond differently (Nguyen et al.,
2481 2011). So far, data on dissolution susceptibility for different species and genera are ~~lacking~~
2482 **limited** for early and early middle Eocene times (**Petrizzo et al., 2008**).

2483 There is also recent work from the Terche section (ca. 28 km NE of Possagno) to
2484 consider. This section is located in the same geological setting as Possagno, but across the H-
2485 1, H-2 and I1 events, there are very low *F* index values and marked increases of acarininids
2486 coupled with significant decreases of subbotinids (D'Onofrio et al., 2014). Therefore,
2487 although the Possagno record may be partially altered by dissolution, an increase of warm

2488 water acarininids concomitant with decrease of subbotinids seems to be a robust finding
2489 during early Paleogene warming events in Tethyan settings.

2490

2491 **6.6 A record of mixed water change**

2492

2493 The switch in abundance between morozovellids and acarininids at the start of the EECO
2494 supports a hypothesis whereby environmental change resulted in a geographically widespread
2495 overturn of planktic foraminiferal genera. During the PETM and K/X events, acarininids
2496 became dominant over morozovellids in a number of Tethyan successions ~~of northeast Italy~~.
2497 This has been interpreted as signifying enhanced eutrophication of surface waters near
2498 continental margins (Arenillas et al., 1999; Molina et al., 1999; Ernst et al., 2006; Guasti and
2499 Speijer, 2007; Luciani et al., 2007; Agnini et al., 2009; ~~Arenillas et al., 1999; Luciani et al.,~~
2500 ~~2007; Molina et al., 1999~~), an idea consistent with evidence for elevated (albeit more
2501 seasonal) riverine discharge during these hyperthermals (Schmitz and Pujalte, 2007;
2502 Giusberti et al., 2007; Schulte et al., 2011; Slotnick et al., 2012; Pujalte et al., 2015).
2503 Increased nutrient availability may also have occurred at Possagno during the early part of the
2504 EECO, given the relatively high concentration of radiolarians, which may reflect
2505 eutrophication (Hallock, 1987).

2506 However, the fact that the major switch at the start of the EECO can be found at Sites
2507 1051 (western Atlantic) and Site 577 (central Pacific) suggests that local variations in
2508 oceanographic conditions, such as riverine discharge, was not the primary causal mechanism.
2509 Rather, the switch must be a consequence of globally significant modifications related to the
2510 EECO, most likely sustained high temperatures, elevated $p\text{CO}_2$, or both. Given model
2511 predictions for our Earth in the coming millennia (IPCC, 2014), indirect effects also could
2512 have contributed, especially including increased ocean stratification and decreased pH.

2513 An explanation for the shift may lie in habitat differences across planktic foraminifera
2514 genera. Although both morozovellids and acarainids likely had photosymbionts,
2515 morozovellids may have occupied a shallower surface habitat than the latter genus as
2516 indicated by minor variations in their stable isotope compositions (Boersma et al., 1987;
2517 Pearson et al., 1993; 2001).

2518 One important consideration to any interpretation is the evolution of new species that
2519 progressively appear during the post-EECO interval. In good agreement with studies of lower
2520 Paleogene sediment from other low latitude locations (Pearson et al., 2006), thermocline
2521 dwellers such as subbotinids and parasubbotinids seem to proliferate at Possagno (Luciani
2522 and Giusberti, 2014). These include *Subbotina corpulenta*, *S. eocena*, *S. hagni*, *S. senni*, *S.*
2523 *yeguanesis*, *Parasubbotina griffinae*, and *P. pseudowilsoni*. The appearance of the radially-
2524 chambered *Parasubbotina eoclava*, considered to be the precursor of the truly clavate
2525 chambered *Clavigerinella* (Coxall et al., 2003; Pearson and Coxall, 2014), also occurs at 19.8
2526 m, and in the core of the EECO (Luciani and Giusberti, 2014). *Clavigerinella* is the ancestor
2527 of the genus *Hantkenina* that successfully inhabited the sub-surface [and surface waters](#) during
2528 the middle through late Eocene (Coxall et al., 2000).

2529 A second consideration is the change in planktic foraminiferal assemblages during the
2530 Middle Eocene Climate Optimum (MECO), another interval of anomalous and prolonged
2531 warmth ca. 40 Ma (Bohaty and Zachos, 2003). At Alano (**Figure 11**) and other locations
2532 (Luciani et al., 2010; Edgar et al., 2012), the MECO involved the reduction in the abundance
2533 and test size of large acarainids and *Morozovelloides*. This has been attributed to “bleaching”
2534 and the loss of photosymbionts resulting from global warming (Edgar et al., 2012), although
2535 related factors, such as a decrease in pH, a decrease in nutrient availability, or changes in
2536 salinity, may have been involved (Douglas, 2003; Wade et al., 2008). The symbiotic
2537 relationship with algae is considered an important strategy adopted by muricate planktic

2538 foraminifera during the early Paleogene (Norris, 1996; Quillévéré et al., 2001). Considering
2539 the importance of this relationship in extant species (Bé, 1982; Bé et al., 1982; Hemleben et
2540 al., 1989), the loss of photosymbionts may represent a crucial mechanism to explain the
2541 relatively rapid decline foraminifera utilizing this strategy, including morozovellids at the
2542 start of the EECO.

2543 Available data suggest that the protracted conditions of extreme warmth and high $p\text{CO}_2$
2544 during the EECO were the key elements inducing a permanent impact on planktic
2545 foraminiferal evolution, and the demise decline of the morozovellids. Even during the PETM,
2546 the most pronounced hyperthermal, did not adversely affect the morozovellids permanently.
2547 While “excursion taxa” appeared, morozovellids seem to have increased in abundance in
2548 open ocean settings (Kelly et al., 1996; 1998, 2002; Lu and Keller, 1995; Petrizzo, 2007);
2549 only in some continental margin settings did a transient decrease in abundance occur (Luciani
2550 et al., 2007).

2551

2552 **6.7 Post-EECO changes at Possagno**

2553

2554 Several small CIEs appear in the $\delta^{13}\text{C}$ record at Possagno during polarity chrons C22n, C21r,
2555 and C21n. Some of these post-EECO excursions coincide with planktic foraminiferal
2556 assemblage changes similar to those recorded in lower strata. Specifically, there are marked
2557 increases of acarininids (**Figure 6**). These “post-EECO” CIEs are concomitant with $\delta^{18}\text{O}$
2558 excursions and coupled to distinct modifications in the planktic foraminiferal assemblages
2559 comparable to those recorded across known hyperthermals in Tethyan settings (Luciani et al.,
2560 2007; Agnini et al., 2009; D’Onofrio et al., 2014). Additional hyperthermals, although of less
2561 intensity and magnitude, may extend through the entirety of the early and middle Eocene, as
2562 suggested previously (Sexton et al., 2006; 2011; Kirtland-Turner et al., 2014). Whether these

2563 imply different forcing and feedback mechanisms compared to the PETM remains an open
2564 discussion.

2565

2566 **7 Summary and conclusions**

2567 The symbiont-bearing planktic foraminiferal genera *Morozovella* and *Acarinina* were
2568 among the most important calcifiers of the early Paleogene tropical and subtropical oceans.
2569 However, a remarkable and permanent switch in the relative abundance of these genera
2570 happened in the early Eocene, an evolutionary change accompanied by species reduction of
2571 *Morozovella* and species diversification of *Acarinina*. We show here that this switch probably
2572 coincided with a carbon isotope excursion (CIE) presently coined J. Although the Early
2573 Eocene Climatic Optimum (EECO), a multi-million year interval of extreme Earth surface
2574 warmth, lacks an accepted definition, we ~~agree~~ **propose** ~~with others~~ that the EECO is best
2575 defined as the duration of time between the J event and the base of *D. subladoensis* (about 53
2576 Ma to 49 Ma on the 2012 GTS).

2577 Our conclusion that the planktic foraminiferal switch coincides with the start of the
2578 EECO derives from the generation of new records and collation of old records concerning
2579 bulk sediment stable isotopes and planktic foraminiferal abundances at three sections. These
2580 sections span a wide longitude range of the low latitude Paleogene world: the Possagno
2581 section from the western Tethys, DSDP Site 577 from the central Pacific Ocean, and ODP
2582 Site 1051 from the western Atlantic Ocean. Importantly, these locations have robust
2583 calcareous nannofossils and polarity chron age markers, although the stratigraphy required
2584 amendment at Sites 577 and 1051.

2585 An overarching problem is that global carbon cycling was probably very dynamic during
2586 the EECO. The interval appears to have been characterized not only by numerous CIEs, but
2587 also a major switch in the timing and magnitude of these perturbations. Furthermore, there

2588 was a rapid shoaling of carbonate dissolution horizons in the middle of the EECO. A key
2589 finding of our study is that the major switch in planktic foraminiferal assemblages happened
2590 at the start of the EECO. Significant, though ephemeral, modifications in planktic
2591 foraminiferal assemblages coincide with numerous short-term CIEs, before, during and after
2592 the EECO. Often, there are marked increases in the relative abundance of acarininids, similar
2593 to what happened permanently across the start of the EECO.

2594 Although we show for the first time that the critical turnover in planktic foraminifera
2595 clearly coincided with the start of the EECO, the exact cause for the switch (aka the demise
2596 [decline](#) of morozovellids) remains elusive. Possible causes are multiple, and may include
2597 temperature effects on photosymbiont-bearing planktic foraminifera, changes in ocean
2598 chemistry, or even interaction with other microplankton groups such as radiolarians, diatoms
2599 or dinoflagellates that represented possible competitors in the use of symbionts or as
2600 symbiont providers. For some reason, a critical threshold was surpassed at the start the
2601 EECO, and this induced an unfavourable habitat for continued morozovellid diversification
2602 and proliferation but a favourable habitat for the acarininids.

2603

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2621

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3195

3196 **Figure Captions**

3197

3198 **Figure 1.** ~~The~~ Evolution of climate, carbon cycling, and planktic foraminifera across the
3199 middle Paleogene on the GPTS 2012 time scale. ~~The~~ Left side shows polarity chrons, and
3200 smoothed oxygen and carbon isotope records of benthic foraminifera, slightly modified from
3201 Vandenberghe et al. (2012). ~~The~~ Original oxygen and carbon isotope values come from
3202 ~~numerous source~~ compilations by Zachos et al. (2008) and Cramer et al. (2009). ~~The~~ Middle
3203 of the figure indicates planktic foraminiferal biozones by ~~(~~Wade et al. ~~(~~2011), ~~and partly~~
3204 ~~modified by Luciani and Giusberti (2014)~~ with three modifications. The lower boundary for
3205 Zone E7a is now based on the first occurrence of *Astrorotalia palmerae* due to ~~diachronous~~
3206 diachroneity in the first appearance of the previously selected marker ~~A.~~ *Acarinina*
3207 *cuneicamerata* (Luciani and Giusberti, 2014). ~~In addition,~~ The base of Zone E5, identified by
3208 the first appearance of *Morozovella aragonensis*, occurs within the middle of C24n instead of
3209 lower C23r (see text). ~~We add a~~ A question marks the top of *Morozovella subbotinae* because
3210 ~~the present study highlights a remarkable diachronism of this event~~ there is diachroneity for
3211 this occurrence (see text). ~~The~~ Right side ~~of the figure~~ shows a partial view of morozovellid
3212 and acarininid evolution as ~~suggested~~ envisioned by Pearson et al. (2006) and Aze et al.
3213 (2011). It does not include several “root taxa” that disappear in the earliest Eocene (e.g., *M.*

3214 *velascoensis*) or “excursion taxa” that appear during the Paleocene-Eocene Thermal
3215 Maximum (PETM) (e.g., *M. allisonensis*). Superimposed on these records are key intervals of
3216 climate change, including the Early Eocene Climatic Optimum (EECO), the Middle Eocene
3217 Climatic Optimum (MECO) and the three well documented early Eocene hyperthermal
3218 events. ~~The shown alignment of these records and~~The extent of the EECO ~~are~~ is not precise,
3219 because of stratigraphic issues (see text). ~~Nevertheless, there appears a major switch from~~
3220 ~~morozovellids to acarininids at the species level, independent of abundance, sometime within~~
3221 ~~the EECO~~. Red and blue triangles= top and base of the morozovellid and acarininid zonal
3222 markers.

3223

3224

3225 **Figure 2.** Approximate locations ~~for~~ of the three sites discussed in this work during the early
3226 Eocene. Also shown is Site 1258, which has a bulk carbonate $\delta^{13}\text{C}$ record spanning the
3227 EECO. Base map is from <http://www.odsn.de/services/paleomap.html>.

3228

3229 **Figure 3.** The Possagno section. ~~in northeast Italy when sampled in the Carcoselle quarry~~
3230 ~~between Summer 2002 and Spring 2003 (Photo by Luca Giusberti, Summer 2002). Lower~~
3231 ~~panel shows the then-exposed quarry face.~~ Upper panel ~~shows the~~: geological map (modified
3232 from Braga, 1970). 1 = Quaternary deposits; 2, 3 = Calcarenite di Castelcucco (Miocene); 4 =
3233 glauconitic arenites (Miocene); 5 = siltstones and conglomerates (upper Oligocene-lower
3234 Miocene); 6 = Upper Marna di Possagno (upper Eocene); 7 = Formazione di Pradelgiglio
3235 (upper Eocene); 8 = Marna di Possagno (upper Eocene); 9 = Scaglia Cinerea (middle-upper
3236 Eocene); 10 = Scaglia Rossa (upper Cretaceous-lower Eocene); 11 = faults; 12 = traces of
3237 stratigraphic sections originally studied by Bolli (1975); red circle = the Carcoselle quarry.
3238 Lower panel: the exposed quarry face during Summer 2002 (Photo by Luca Giusberti). ~~The~~

3239 ~~outerop sampled in 2003 was located very close to the outerops sampled in the sixties (dotted~~
3240 ~~red circle).~~

3241

3242 **Figure 4.** Lithology, stratigraphy, and bulk sediment stable-isotope composition of the
3243 Possagno section aligned according to depth. Lithologic key: 1 = limestone; 2 = marly
3244 limestone and calcareous marl; 3 = cyclical marl-limestone alternations, 4 = marl; 5= Clay
3245 Marl unit (CMU). Planktic foraminiferal biozones follow those of Wade et al. (2011), as
3246 modified by Luciani and Giusberti (2014). Magnetostratigraphy and key calcareous
3247 nannofossil events come from Agnini et al. (2006); NP-zonation is from Martini (1971).
3248 Nannofossil events are shown as red triangles (tops), blue triangles (bases), and purple
3249 diamonds (evolutionary crossovers); *S. rad.* = *Sphenolithus radians*; T.c./T.o. = *Tribrachiatus*
3250 *contortus*/ *Tribrachiatus orthostylus*; *D. lod.* = *Discoaster lodoensis*; Tow. = *Toweius*; *T. orth.*
3251 = *Tribrachiatus orthostylus*; *D. sublod.* = *Discoaster sublodoensis*. ~~The~~ Stable isotope
3252 records ~~come from~~ determined in this study. Established early Eocene “events” are
3253 superimposed in light red; suggested carbon isotope excursions (CIEs) within the EECO are
3254 shown with numbers. ~~1=Limestone, 2= Marly limestones and calcareous marls, 3= cyclical~~
3255 ~~marl-limestone alternations, 4= Marls, 5=Clay marly units (CMU).~~

3256

3257 **Figure 5.** Cores, stratigraphy, and bulk sediment stable isotope composition for the early
3258 Eocene interval at Deep-Sea Drilling Project (DSDP) Site 577 aligned according to
3259 composite depth (Dickens and Backman, 2013). Note the increased length for the gap
3260 between Core 577*-8H and Core 577*-9H (see text). The Wade et al. (2011) E-zonation,
3261 partly modified by Luciani and Giusberti (2014), has been applied to Site 577 ~~on the basis of~~
3262 ~~the events recorded~~ given assemblages presented by Lu (1995) and Lu and Keller (1995).
3263 Note that: (a) the base of Zone E3 ~~has been positioned at the~~ (top of *Morozovella*

3264 *velascoensis*) lies within a core gap; even though this event is uncertain due to the lowest
3265 core gap. The lowest occurrence of *Morozovella formosa* occurs within C24r in agreement
3266 with Wade et al. (2011) and defines the E3/E4 zonal boundary. (b) the E4/E5 zonal boundary
3267 (base of *M. aragonensis*) occurs within C24n, in agreement with Luciani and Giusberti
3268 (2014); and The base of *M. aragonensis*, defining the E4/E5 zonal boundary, is recorded
3269 within C24n. (c) the E5/E6 zonal boundary is problematic because the top of *M. subbotinae*
3270 occurs in middle C24n, much earlier than the presumed disappearance in the upper part of
3271 C23n The boundary between Zones E5 and E6 cannot be placed by means of the *M.*
3272 *subbotinae* top because this species disappears (at Site 577) much earlier with respect to the
3273 expected C23n top (Wade et al., 2011). i.e., in middle C24n, even below the base of *M.*
3274 *aragonensis*. Our new interpretation of the magnetostratigraphy at Site 1051, based on
3275 calcareous nannofossil events (see text), substantiates the significant diachrony of this
3276 biohorizon. We have therefore positioned, at Site 577, the E5/E6 boundary upper boundary of
3277 Zone E5 at the lowest occurrence of *Acarinina aspensis*, according to the original definition
3278 of Zone E5 by (Berggren and Pearson, 2005); (d) we cannot differentiate between Zone E6
3279 and Zone E7a due to the absence of *Astrorotalia palmerae* at Site 577 and to the
3280 diachronous appearance of *A. cuneicametrata* base (Luciani and Giusberti, 2014).
3281 Cores are aligned following Dickens and Backman (2013), with an increased gap between
3282 Core 577*-8H and Core 577*-9H (see text). Magnetostratigraphy and key calcareous
3283 nannofossil events are those summarized by Dickens and Backman (2013). For the latter and
3284 beyond that noted for Figure 4: *F. spp.*= *Fasciculithus spp.*; *D. dia.*= *Discoaster diastypus*;
3285 *T.c./T.o.*= *Tribrachiatus contortus/ Tribrachiatus orthostylus*; *D. lod.*= *Discoaster lodoensis*;
3286 *T. orth.*= *Tribrachiatus orthostylus*; *D. sublod.*= *Discoaster sublodoensis*. The stable isotope
3287 records: come from black – Cramer et al. (2003), and red and blue – this study. Established
3288 Early Eocene “events” are the same as those in Figure 4. are superimposed in light red;

3289 suggested carbon isotope excursions (CIEs) following the “L event” (yellow band) are shown
3290 with numbers.

3291

3292 **Figure 6.** The Possagno section and its $\delta^{13}\text{C}$ record (**Figure 4**) with measured relative
3293 abundances of primary planktic foraminiferal genera, fragmentation index (*F* index) and
3294 coarse fraction. The subbotinid abundance includes both *Subbotina* and *Parasubbotina*
3295 genera. Note that a significant increase in *Acarinina* abundance marks the EECO and several
3296 carbon isotope excursions (CIEs). before and after it are marked by a significant increase in
3297 *Acarinina* abundance. Note also the major decline in abundance of *Morozovella* at the start
3298 of the EECO. Filled yellow circles hexagons show occurrences of abundant radiolarians.
3299 Lithological symbols and early Eocene “events” are the same as those in **Figure 4**.

3300

3301 **Figure 7.** The early Eocene succession at DSDP Site 577 and its $\delta^{13}\text{C}$ record (**Figure 5**) with
3302 measured relative abundances of primary planktic foraminiferal genera (Lu, 1995; Lu and
3303 Keller, 1995). The Wade et al. (2011) E-zonation, partly modified by Luciani and Giusberti
3304 (2014), has been applied to Site 577 on the basis of the events recorded by Lu (1995) and Lu
3305 and Keller (1995). *F. spp.* = *Fasciculithus spp.*; *D. dia.* = *Discoaster diastypus*; *T.c./T.o.* =
3306 *Tribrachiatus contortus*/*Tribrachiatus orthostylus*; *D. lod.* = *Discoaster lodoensis*; *T. orth.* =
3307 *Tribrachiatus orthostylus*; *D. sublod.* = *Discoaster sublodoensis*. Suggested carbon isotope
3308 excursions (CIEs) following the “L event” are shown with numbers. The subbotinid
3309 abundance includes both *Subbotina* and *Parasubbotina* genera. Note also that the major
3310 switch in *Morozovella* and *Acarinina* abundances approximately coincides with the J-event,
3311 the top of polarity chron C24n, and the start of the EECO. Early Eocene “events” are the
3312 same as those in **Figure 4**.

3313

3314 **Figure 8.** ~~Lithology~~, Stratigraphy, bulk sediment $\delta^{13}\text{C}$ composition, relative abundances of
3315 primary planktic foraminiferal genera, and fragmentation index (*F* index) for the early
3316 Eocene interval at ODP Site 1051. ~~The~~ Planktic foraminiferal biozones follow those of Wade
3317 et al. (2011), as modified by Luciani and Giusberti (2014; see **Figure 1** caption).
3318 Magnetostratigraphy and positions of key calcareous nannofossil events come from Ogg and
3319 Bardot (2001) and Mita (2001), but with an important modification to polarity chron labelling
3320 (see text and Cramer et al., 2003). *S. rad.* = *Sphenolithus radians*; *D. lod.* = *Discoaster*
3321 *lodoensis*; *Tow.* = *Toweius*; *T. orth.* = *Tribrachiatus orthostylus*; *D. sub.* = *Discoaster*
3322 *sublodoensis*. Calcareous nannofossil horizons are the same as in previous figures.
3323 Foraminiferal information comes from this study; ; subbotinids include both *Subbotina* and
3324 *Parasubbotina*.
3325 Early Eocene “events” are the same as those in **Figure 4**.

3326
3327 **Figure 9.** Carbon isotope and paleomagnetic records across the early Eocene for the
3328 Possagno section, DSDP Site 577, and ODP Site 1258 (Kirtland-Turner et al., 2014). This
3329 highlights the overall framework of carbon cycling in the early Eocene, but also stratigraphic
3330 problems across the EECO at each of the three sites. At Possagno, the coarse resolution of
3331 $\delta^{13}\text{C}$ records and the condensed interval makes correlations difficult. At ODP Site 1258, the
3332 ~~entire record is compressed in the depth domain~~ the prominent K/X event seems missing. At
3333 DSDP Site 577, the entire record is compressed in the depth domain. Nonetheless, a major
3334 shift in frequency and amplitude of carbon isotope excursions (CIEs) appears to have
3335 happened during the EECO. ~~Suggested Carbon isotope excursions~~ CIEs that suggestively
3336 ~~probably~~ correlate within the EECO are shown with numbers.

3337
3338 **Figure 10.** ~~Abundance patterns of primary planktic foraminiferal taxa from the Farra section,~~

3339 cropping out 50 km NE of Possagno, plotted against bulk sediment $\delta^{13}\text{C}$, CaCO_3 content, F
3340 index and magnetostratigraphy. Records of magnetostratigraphy, bulk sediment $\delta^{13}\text{C}$, CaCO_3
3341 content, F index and abundance patterns for primary planktic foraminiferal taxa at the Farra
3342 section, which crops out 50 km NE of Possagno. ~~The *Subbotina* group includes besides~~
3343 ~~*Subbotina* the genera *Parasubbotina* and *Globorotaloides*, that constitute the minor~~
3344 ~~components of this group.~~ All data are from Agnini et al. (2009). Note that the switch in
3345 abundance between *Morozovella* and *Acarinina* occurs close the “J event”.

3346

3347 **Figure 11.** ~~The~~ Records of ~~warm indices symbiont-bearing~~ morozovellids and large
3348 acarininids (>200 micron) in the western Tethyan setting from the Possagno section (~~below,~~
3349 this paper) and the Alano section (Luciani et al., 2010), plotted with generalized $\delta^{13}\text{C}$ and
3350 $\delta^{18}\text{O}$ curves for benthic foraminiferal on the GTS2012 time scale (as summarized by
3351 Vandenberghe et al., 2012; slightly modified). ~~The original oxygen and carbon isotopic~~
3352 ~~values from Cramer et al. (2009) are recalibrated to GTS2012 (Vandenberghe et al., 2012).~~
3353 ~~The Tethyan~~ These records suggest that the long-lasting EECO and MECO intervals of
3354 anomalous ~~intense~~ warmth mark two main steps in the decline of ~~morozovellids and~~
3355 ~~acarininids. within this group of important early Paleogene calcifiers, which almost~~
3356 ~~completely disappeared at about 38 Ma, near the Bartonian/Priabonian boundary (Agnini et~~
3357 ~~al., 2011; Luciani et al., 2010; Wade, 2004; Wade et al., 2012).~~ E-Zones-The planktic
3358 foraminiferal biozones follow those presented by Wade et al. (2011), as partly modified by
3359 Luciani and Giusberti (2014).

3360

3361 **Supplementary material**

3362

3363 **Table S1.** Carbon and oxygen isotopes from the Possagno section.

3364

3365 **Table S2.** Carbon and oxygen isotopes from DSDP Site 577.

3366

3367 **Table S3.** Foraminiferal abundances, fragmentation index (%) and coarse fraction (%) from
3368 the Possagno section.

3369

3370 **Table S4.** Foraminiferal abundances from DSDP Site 577.

3371

3372 **Table S5.** Foraminiferal abundances from ODP Site 1051.

3373

3374 **Figure S1.** The Possagno $\delta^{13}\text{C}$ data and relative abundance of minor planktic foraminiferal
3375 genera and selected species plotted against lithology and fragmentation index (*F* index) data.
3376 Magnetostratigraphy is from Agnini et al. (2006). ~~The biozonal scheme is from Wade et al.~~
3377 ~~(2011), modified by Luciani and Giusberti (2014).~~ The planktic foraminiferal biozonal
3378 scheme is from Wade et al. (2011), as modified by Luciani and Giusberti (2014). **Established**
3379 **early Eocene “events” are superimposed in light red; suggested carbon isotope excursions**
3380 **(CIEs) within the EECO are shown with numbers. Lithological** Various symbols are the same
3381 as in **Figure 4.**

3382

3383 **Appendix A: Taxonomic list of planktic ~~foraminiferal~~ foraminiferal species cited in text**
3384 **and figures**

3385

3386 *Globanomalina australiformis* (Jenkins, 1965)

3387 *Morozovella aequa* (Cushman and Renz, 1942)

3388 *Morozovella gracilis* (Bolli, 1957)

- 3389 *Morozovella lensiformis* (Subbotina, 1953),
- 3390 *Morozovella marginodentata* (Subbotina, 1953)
- 3391 *Morozovella subbotinae* (Morozova, 1939)
- 3392 *Parasubbotina eoelava* Coxall, Huber and Pearson, 2003
- 3393 *Parasubbotina griffinae* (Blow, 1979)
- 3394 *Parasubbotina pseudowilsoni* Olsson and Pearson, 2006
- 3395 *Subbotina corpulenta* (Subbotina, 1953)
- 3396 *Subbotina eocena* (Gümbel, 1868)
- 3397 *Subbotina hagni* (Gohrbandt, 1967)
- 3398 *Subbotina senni* (Beckmann, 1953)
- 3399 *Subbotina yeguanesis* (Weinzierl and Applin, 1929)
- 3400 *Planoglobanomalina pseudoalgeriana* Olsson & Hemleben, 2006
- 3401
- 3402 **Appendix B: Taxonomic list of calcareous nannofossil taxa cited in text and figures**
- 3403
- 3404 *Discoaster diastypus* Bramlette and Sullivan, 1961
- 3405 *Discoaster lodoensis* Bramlette and Sullivan, 1961
- 3406 *Discoaster sublodoensis* Bramlette and Sullivan, 1961
- 3407 *Fasciculithus* Bramlette and Sullivan, 1961
- 3408 *Fasciculithus tympaniformis* Hay and Mohler in Hay et al., 1967
- 3409 *Sphenolithus radians* Deflandre in Grasse, 1952
- 3410 *Toweius* Hay and Mohler, 1967
- 3411 *Tribrachiatus contortus* (Stradner, 1958) Bukry, 1972
- 3412 *Tribrachiatus orthostylus* (Bramlette and Riedel, 1954) Shamrai, 1963
- 3413

Figure 1

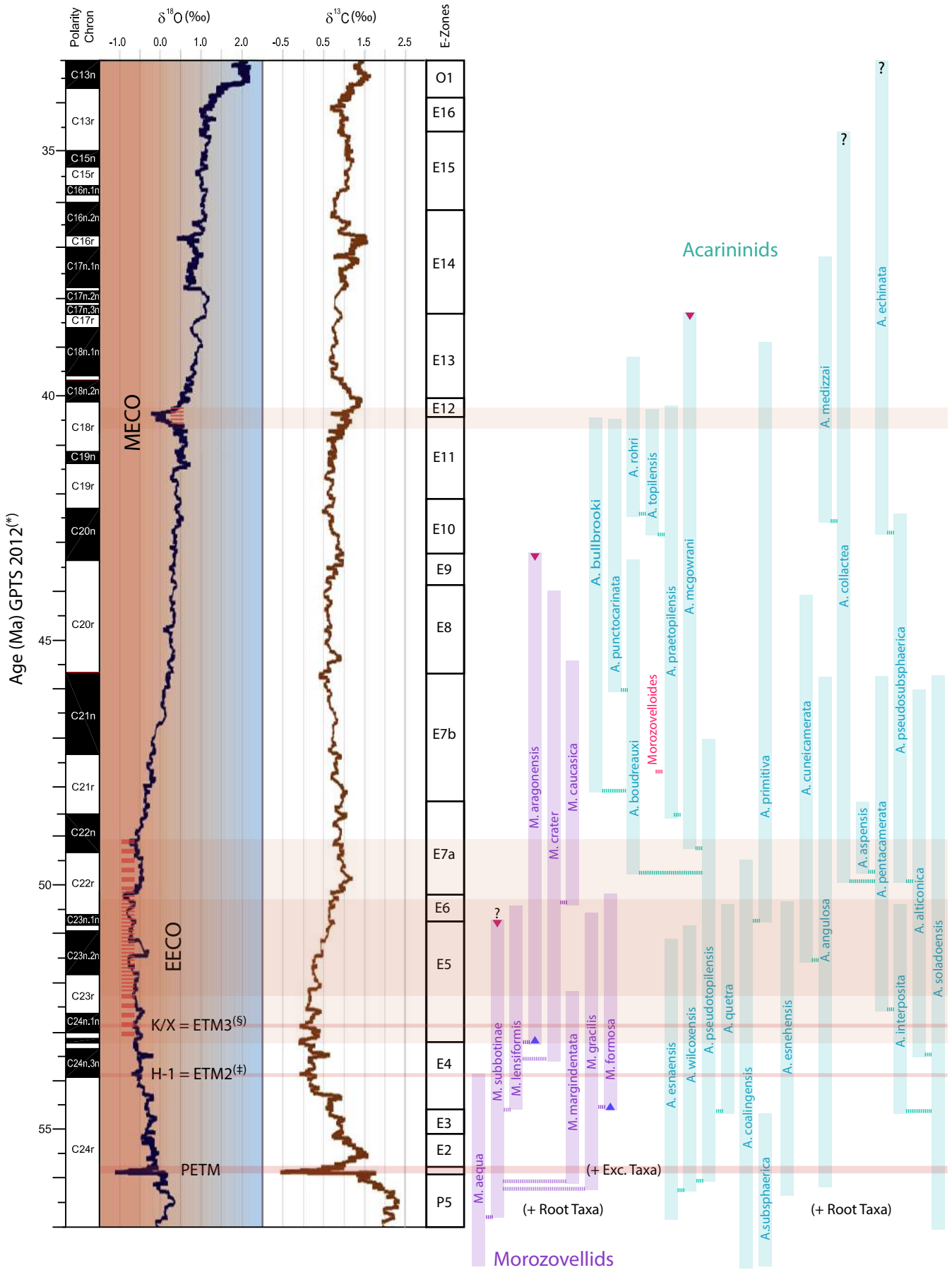
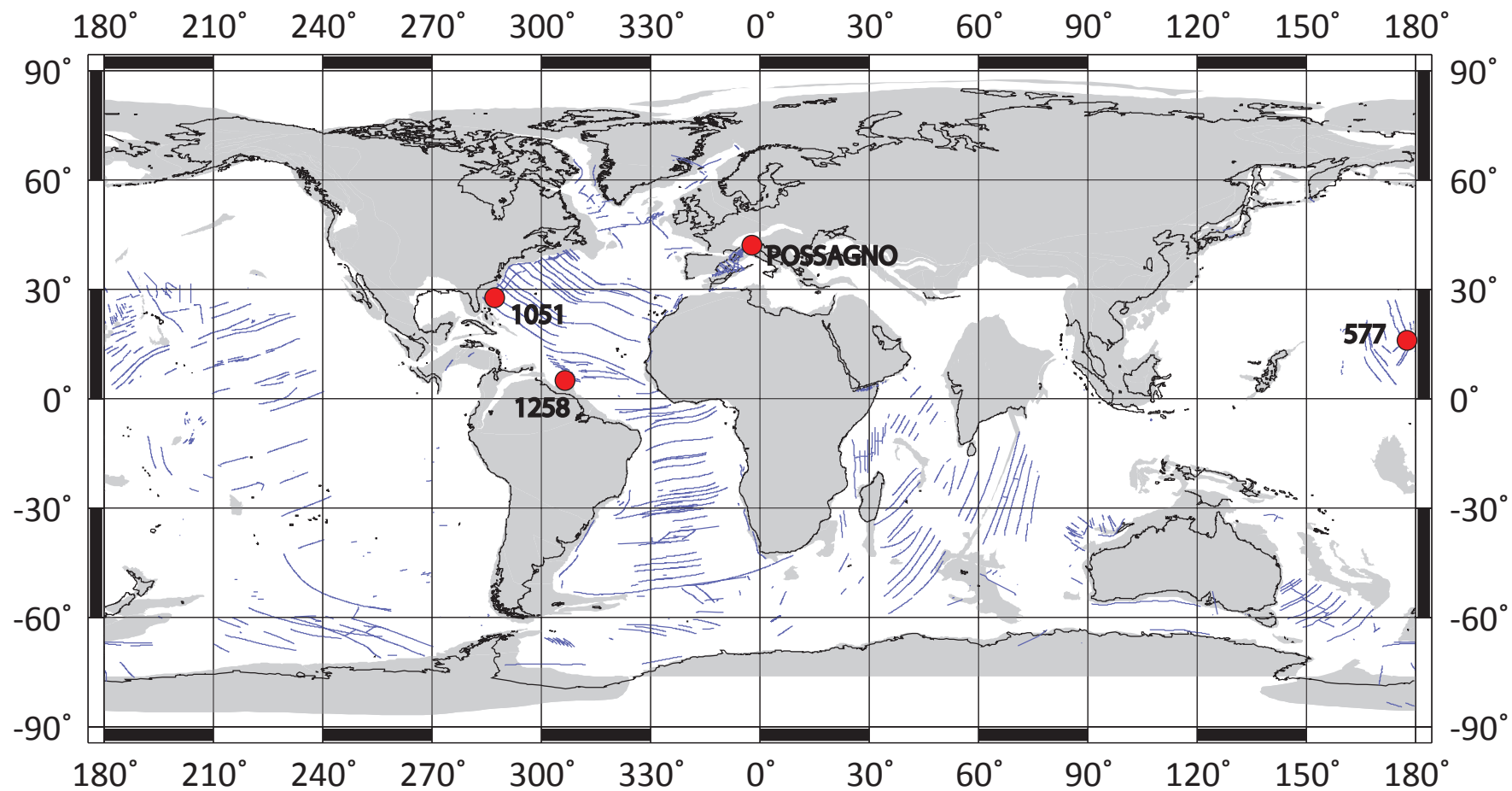


Figure 2



50 Ma Reconstruction

Figure 3

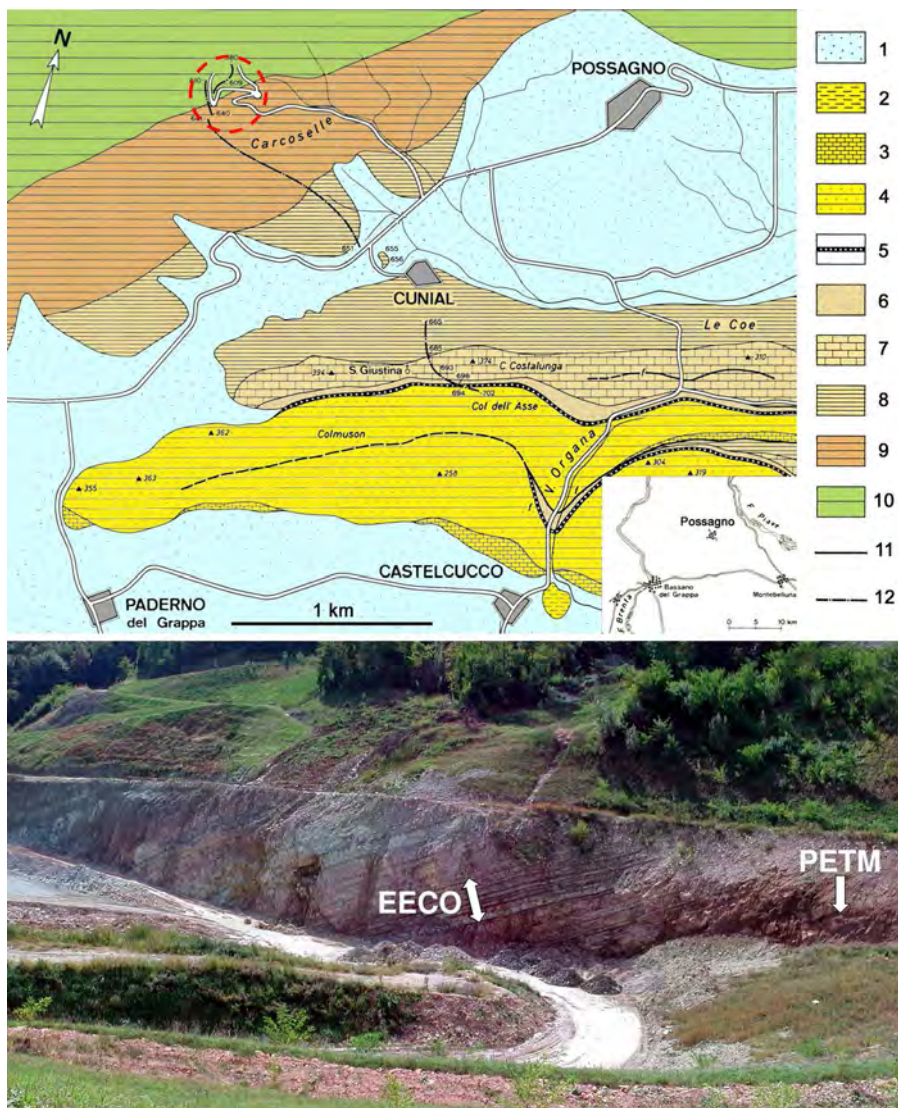


Figure 4

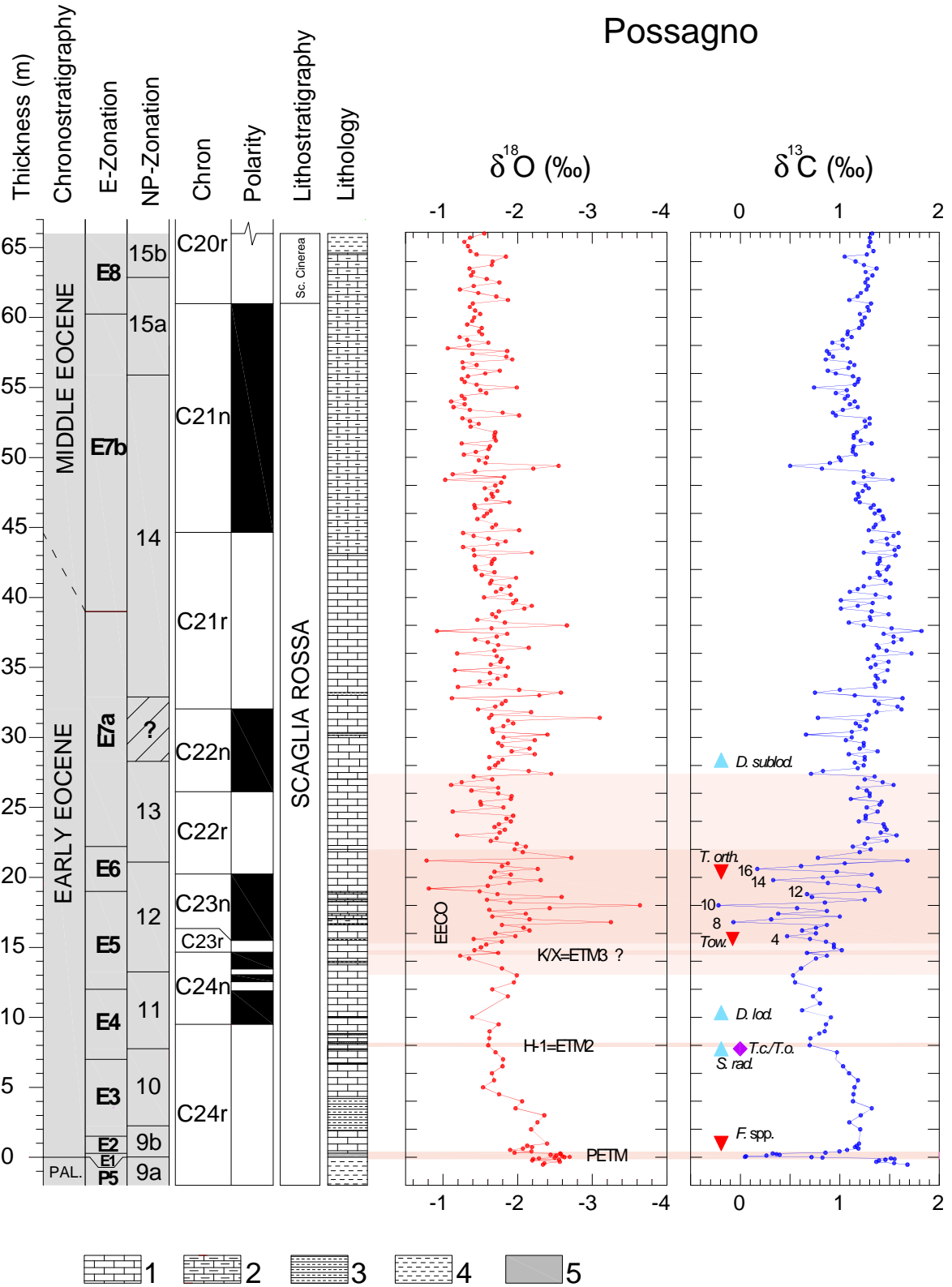


Figure 5

DSDP Site 577

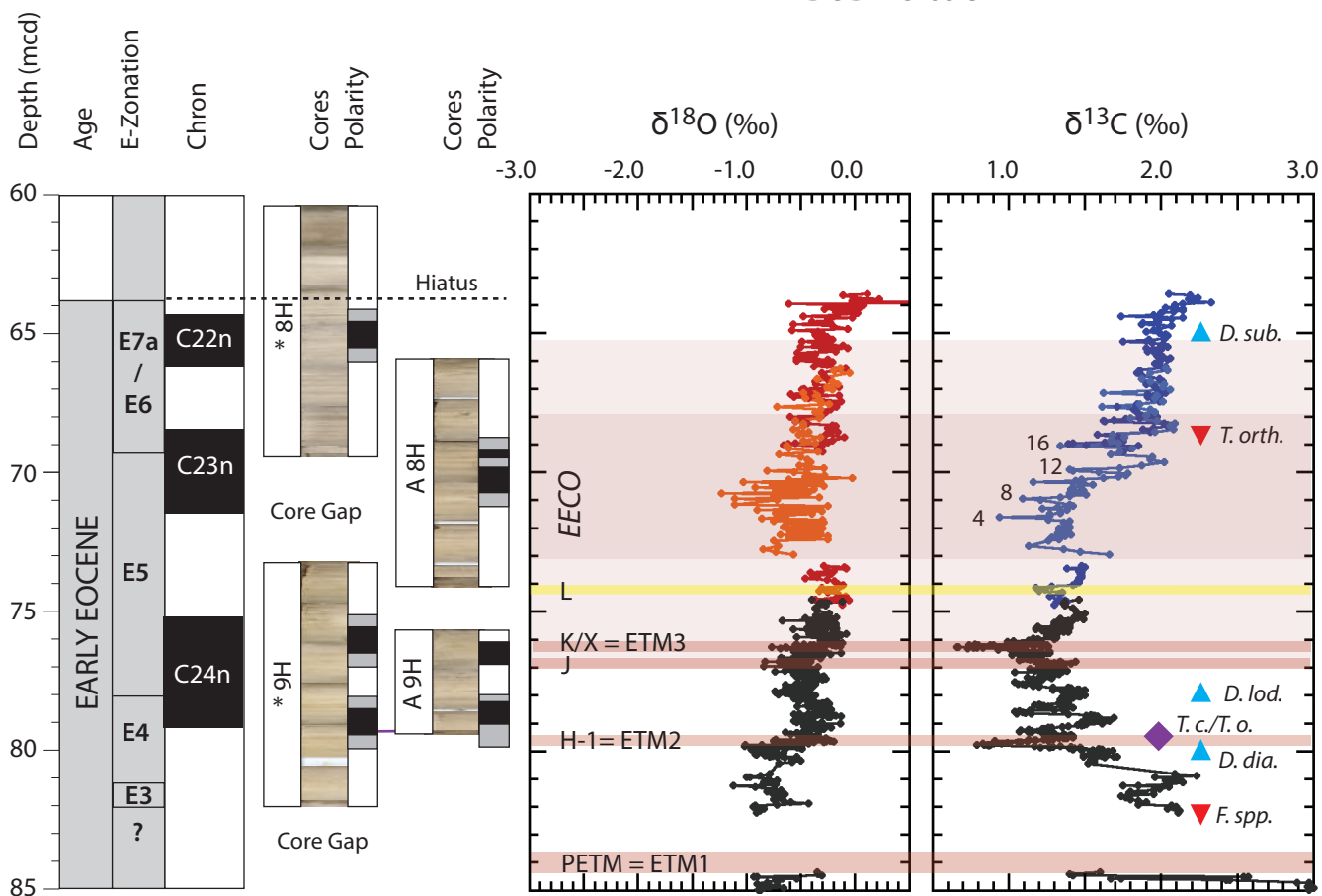
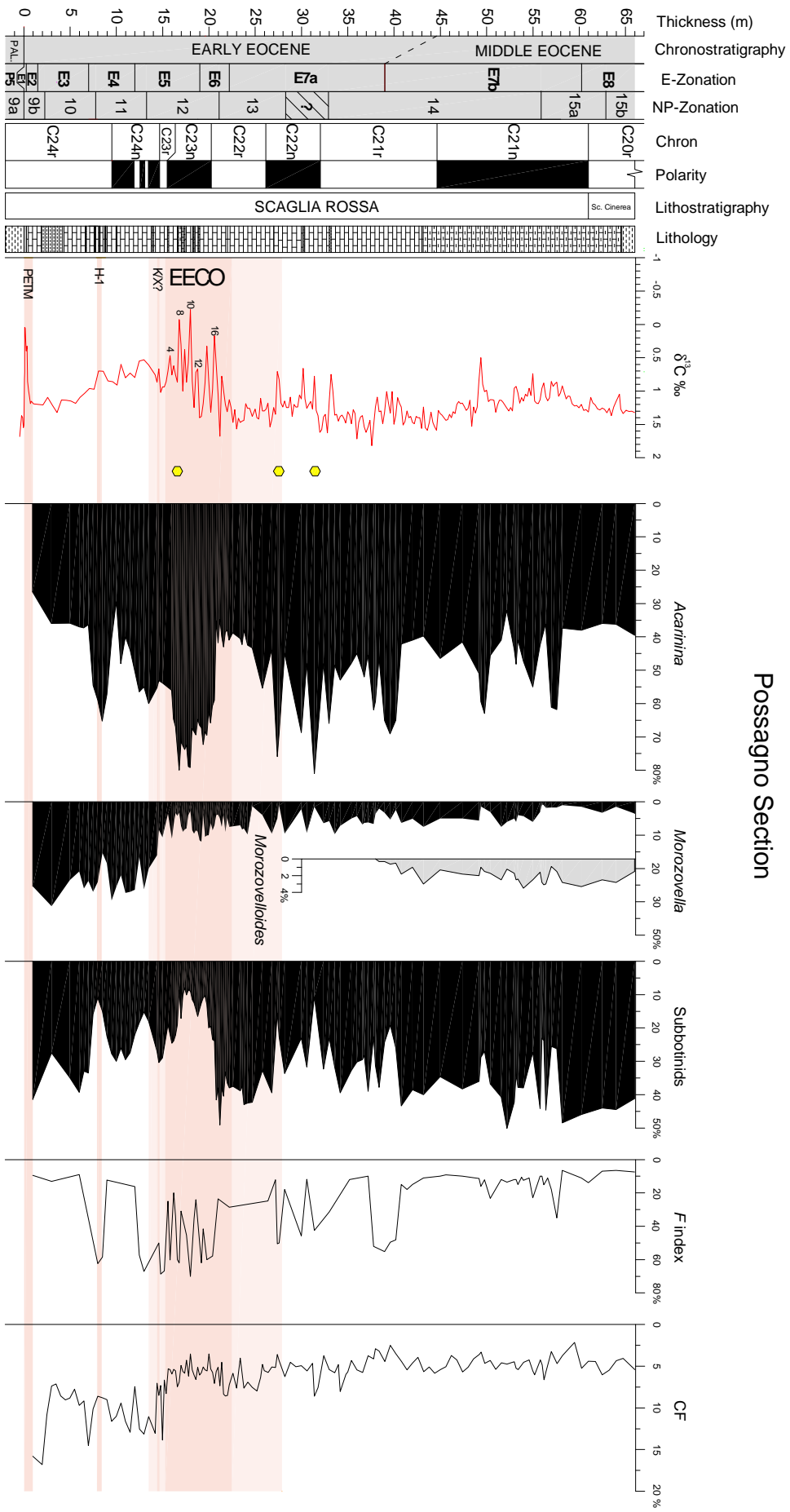


Figure 6



Possagno Section

Figure 7

DSDP Site 577

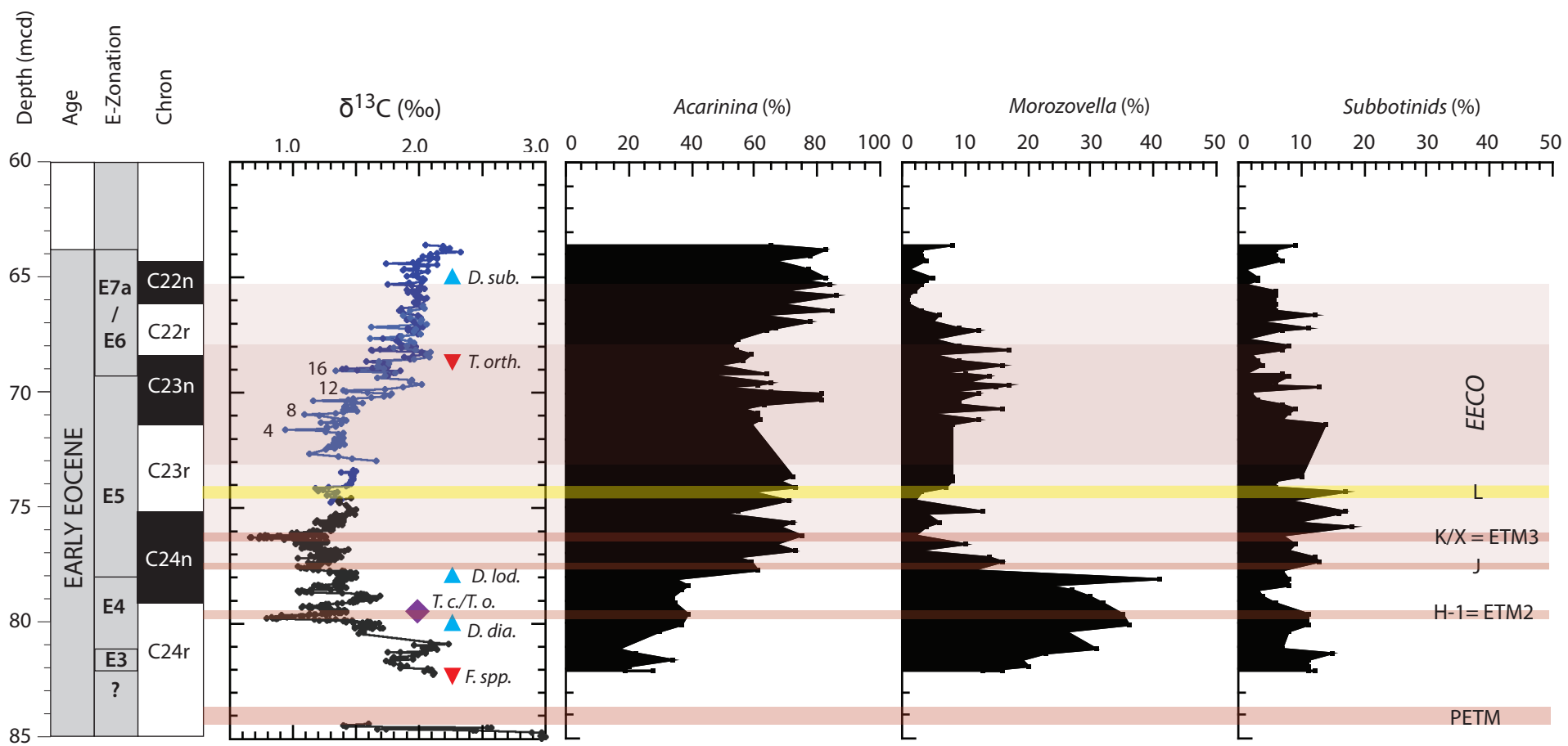
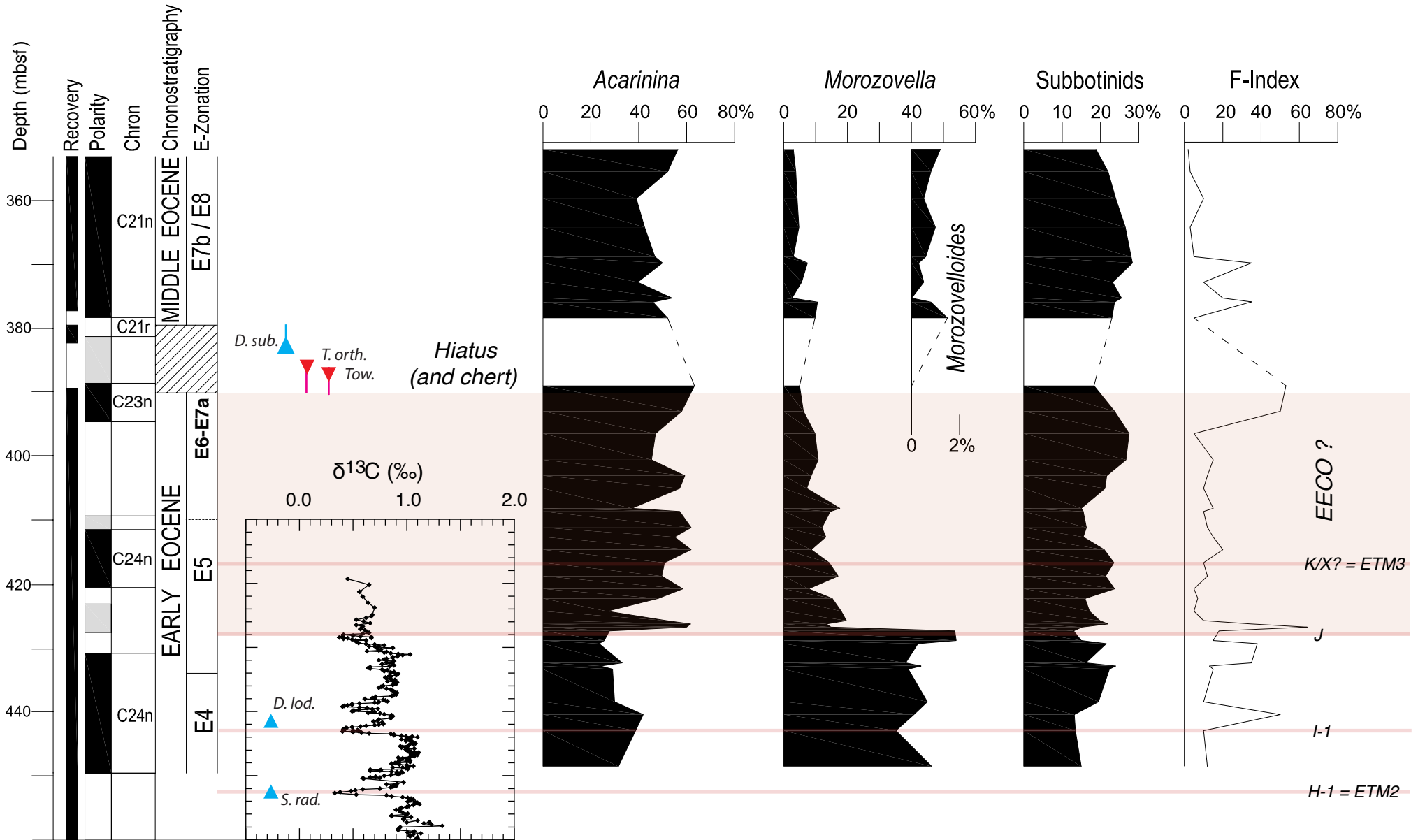
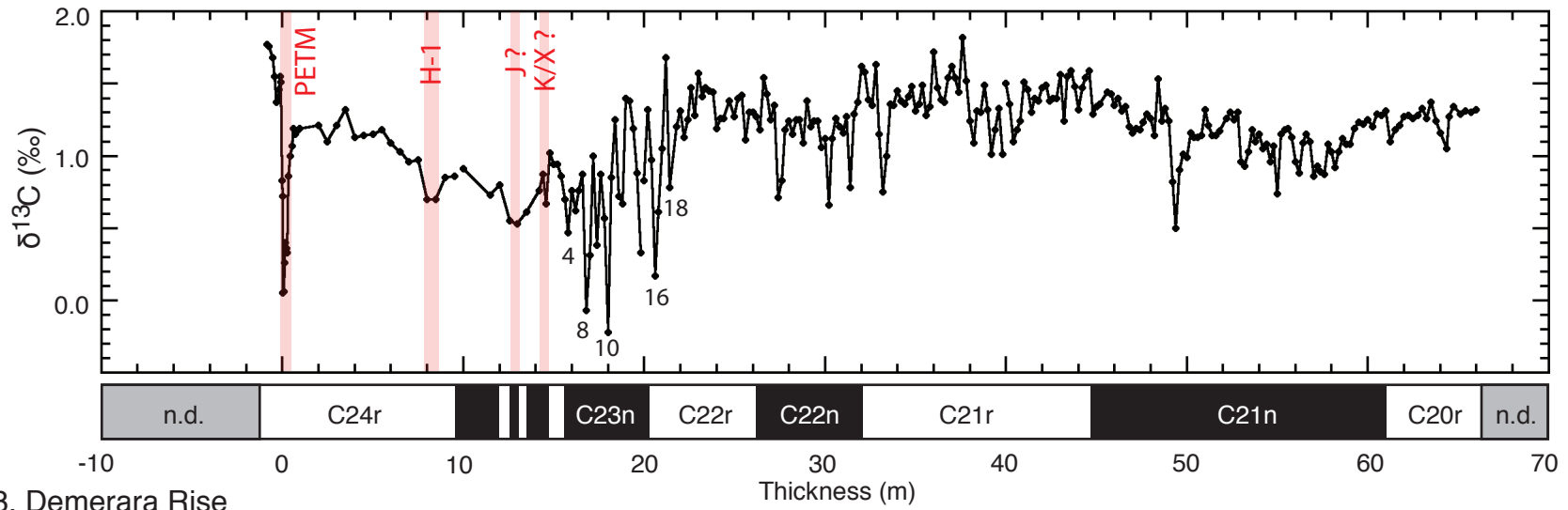


Figure 8

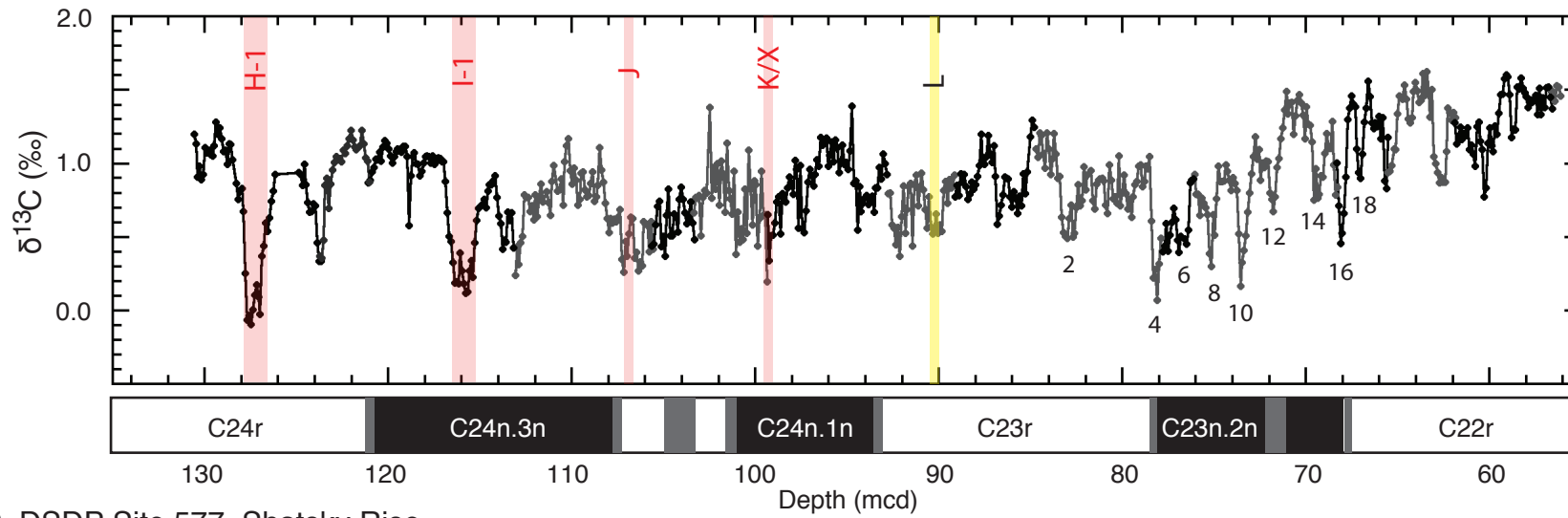
ODP Site 1051



A. Possagno, northeast Italy



B. ODP Site 1258, Demerara Rise



C. DSDP Site 577, Shatsky Rise

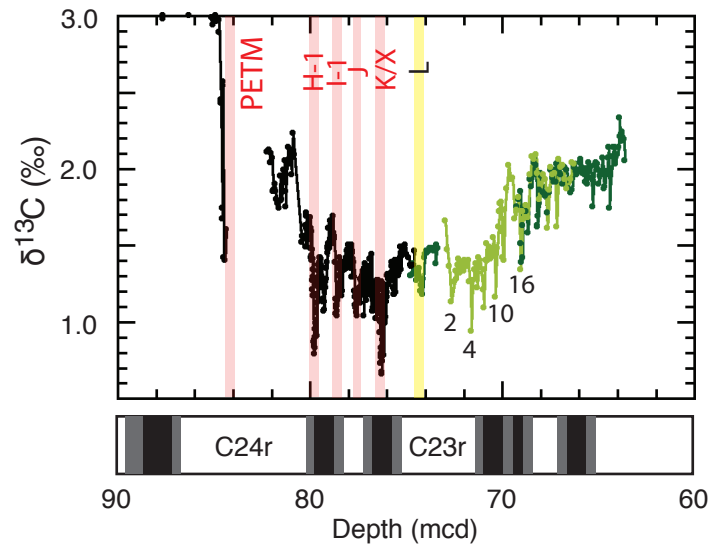


Figure 9

Figure 10

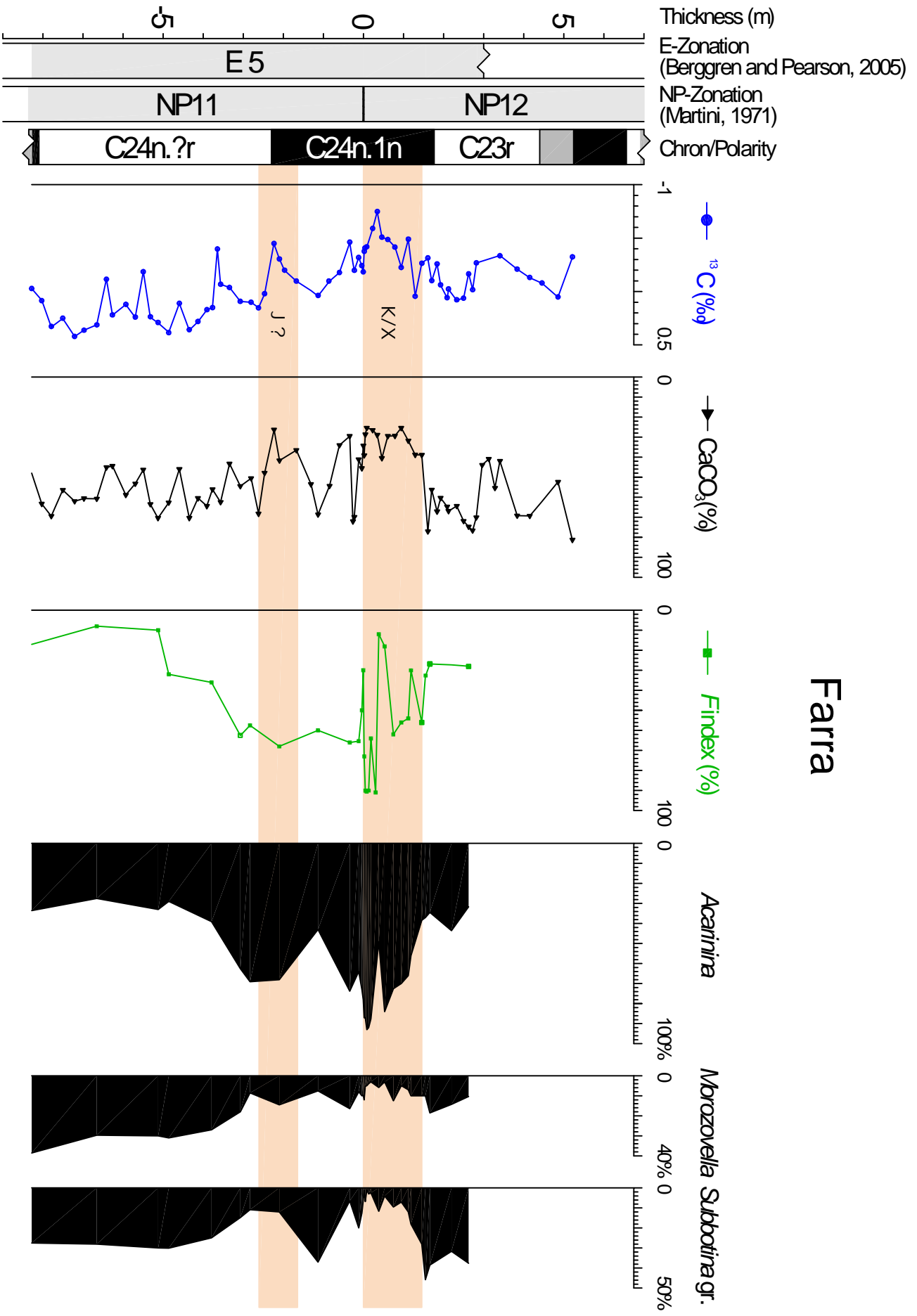


Figure 11

