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# Massive and permanent decline of symbiont bearing morozovellids and $\delta^{13}$C perturbations across the Early Eocene Climatic Optimum at the Possagno section (Southern Alps of northeastern Italy)

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## Abstract

The Early Eocene Climatic Optimum (EECO) records the highest prolonged global temperatures over the past 70 Ma. Understanding the causes and timing of Eocene climate change remains a major challenge in Cenozoic paleoceanography, which includes the biotic response to climate variability and the changes among planktic foraminiferal assemblages across the EECO. The symbiont bearing and shallow dwelling genera *Morozovella* and *Acarinina* were important calcifiers in the tropical-subtropical early Paleogene oceans but almost completely disappeared at about 38 Ma, near the Bartonian/Priabonian boundary. We show here that morozovellids record a first critical step across the EECO through a major permanent decline in relative abundance from the Tethyan Possagno section and ODP Site 1051 in the western subtropical North Atlantic. Possible causes may include increased eutrophication, weak water column stratification, changes in ocean chemistry, loss of symbiosis and possible complex interaction with other microfossil groups. Relative abundances of planktic foraminiferal taxa at Possagno parallel negative shifts in both $\delta^{13}$C and $\delta^{18}$O of bulk sediment from Chron C24r to basal Chron C20r. The post-EECO stable isotopic excursions towards lighter values are of modest intensity. Significant though ephemeral modifications in the planktic foraminiferal communities occur during these minor isotopic excursions. These modifications are marked by pronounced increases in relative abundance of acarininids, in a manner similar to their behaviour during pre-EECO hyperthermals in the Tethyan settings, which suggest a pronounced biotic sensitivity to climate change of planktic foraminifera even during the post-EECO interval.

## 1 Introduction

The Early Eocene Climatic Optimum (EECO) is the interval in which the Earth's climate attained its warmest state of the past 90 Ma and it represents a major turning point in the Cenozoic climate, as it was followed by a long term cooling throughout the remainder of the Eocene, which culminated with the formation of permanent large ice sheets on Antarctica at the end of the Eocene (Zachos et al., 2001; Coxall et al., 2005). Superimposed on the long term early Eocene climate trend, short lived ($< 200$ kyr) warm events occurred, named hyperthermals, the most extreme of which is the well known Paleocene Eocene Thermal Maximum (PETM) (Agnini et al., 2009; Coccioni et al., 2012; Cramer et al., 2003; Kennett and Stott, 1991; Lourens et al., 2006; Nicolò et al., 2007; Quillévéré et al., 2008; Zachos et al., 2008). Massive, rapid releases of isotopically light carbon are linked to hyperthermals and concomitant deep-sea carbonate dissolution events (Dickens, 2011; Dickens et al., 1995, 1997; Zachos et al., 2005, 2008). The series of early Eocene hyperthermals (Littler et al., 2014; Slotnick et al., 2012; Zachos et al., 2010) has been suggested to continue into the earliest middle Eocene, with an additional thirteen brief ($\sim 40$ kyr) and less pronounced events (Kirtland Turner et al., 2014; Sexton et al., 2011).

Although the EECO still lacks a formal definition in terms of absolute age and duration (Slotnick et al., 2012), this interval is thought to represent a ca 2–3 Ma long early Eocene interval of extreme warmth between about 52 and 50 Ma (Zachos et al., 2001) or between about 53 and 51 Ma (Zachos et al., 2008). Current thought about the placement of the EECO thus encompasses the interval from approximately 50 to 53 Ma. Regardless of the exact duration and position on the chronometric scale of the EECO, it is clearly much longer than any of the brief early Eocene hyperthermals (Zachos et al., 2001, 2008, 2010). Exceptionally high and long lasting atmospheric $p\text{CO}_2$ conditions are considered to have played a primary control on the EECO warmth (Fletcher et al., 2008; Hyland and Sheldon, 2013; Komar et al., 2013; Lowenstein and Demicco, 2006; Lunt et al., 2011; Pearson and Palmer, 2000; Royer et al., 2007; Smith et al., 2010). Slow addition of depleted carbon dioxide from volcanism, the second emplacement phase of the North Atlantic Igneous Province, and increased weathering of silicate rocks are often invoked as the main trigger of the EECO warming and the subsequent long term cooling trend (Demicco, 2004; Raymo and Ruddiman, 1992; Sinton and Duncan, 1998; Vogt, 1979; Zachos et al., 2008). The influence of a major switch from continental to island arc volcanism around 50 Ma may also have played a role in perturbing the carbon cycle change that helped end the warm EECO interval (Dickens et al., 2014; Lee et al., 2013).

It is well established that major plant and mammal faunal evolutionary turnovers occurred during the EECO (Falkowski et al., 2005; Figueirido et al., 2012; Wilf et al., 2003; Wing et al., 1991; Woodbourne et al., 2009; Zonneveld et al., 2000). In the marine realm, changes in evolutionary trends have also been observed, for example the inception to the modern structure among calcareous nannofossil communities (Agnini et al., 2006; Shamrock and Watkins, 2012; Schneider et al., 2011) and possibly in diatom lineages (Oreshkina, 2012; Sims et al., 2006). These observations both from continents and the oceans support the hypothesis of a primary interaction between climate change and biotic evolution.

The relationship between the EECO and the paleoecology and evolution of planktic foraminifera is insufficiently known. Within this plankton group, the symbiont bearing and shallow dwelling morozovellids and acarininids are of particular interest because they dominated the tropical and subtropical assemblages of the early Paleogene oceans. These genera are also known as muricates, from the muricae that form conical pustules on the test wall. Among calcareous microplankton, the muricates were one of the major calcifiers in the low latitude early Paleogene oceans and almost completely disappeared at about 38 Ma, near the Bartonian/Priabonian boundary (Agnini et al., 2011; Luciani et al., 2010; Wade, 2004; Wade et al., 2012).

The hemipelagic Possagno sedimentary succession is located in the Venetian Prealps of northeastern Italy (Fig. 1). This section represents continuous deposition of the early through early middle Eocene interval (55–46 Ma) from a bathyal setting in the central-western Tethys. A robust Eocene biomagnetostratigraphy was established by Agnini et al. (2006). The Possagno section thus spans the EECO interval, here agreed as the interval from about 53 to 50 Ma (Slotnick et al., 2012).

According to Agnini et al. (2006), the Possagno section is 66 m thick extending from the Paleocene/Eocene boundary at 55 Ma to the early middle Eocene (lower Chron

C20r) at 46 Ma on the time scale of Cande and Kent (1995). The aim here is to investigate the response of the muricates in terms of relative abundance throughout the early and early middle Eocene, including the EECO interval, in the 55 through 46 Ma interval at Possagno, encompassing biozones planktic foraminiferal Zones E1 to lower E8 (Luciani and Giusberti, 2014). In addition, the planktic foraminiferal changes recorded at Possagno are compared with those observed from ODP Site 1051 in the western subtropical North Atlantic. Additional aims include (1) to document planktic foraminiferal changes in the Possagno section in relation to stable carbon and oxygen isotopes for the purpose to unravel paleoenviromental conditions of the upper water column and (2), to distinguish ephemeral biotic modifications during brief peaks of warming from permanent evolutionary changes in the Tethyan and North Atlantic realms.

## 2 The Possagno section and Site 1051: setting and stratigraphy

An upper Cretaceous-Miocene succession crops out at the bottom of the Monte Grappa Massif in the Possagno area, about 60 km NW of Venice. The lower to middle Eocene interval, which is the focus of this study, is represented by pelagic to hemipelagic Scaglia facies sediments. The Scaglia beds at Possagno are considered to have been deposited at middle to lower bathyal depths (Cita, 1975; Thomas, 1998) in the western part of the Belluno Basin, a Mesozoic–Cenozoic paleogeographic unit of the Southern Alps characterized by Jurassic to Eocene pelagic sequences (Bosellini, 1989). The basal part of the Possagno section straddles a 30 cm thick interval of dark-red clayey marls (Arenillas et al., 1999; Agnini et al., 2006), referred to as the Clay Marl Unit (CMU) by Giusberti et al. (2007). The CMU is the lithological expression of the main carbon isotope excursion (CIE) of the Paleocene Eocene Thermal Maximum (PETM), the base of which defines the Paleocene-Eocene boundary (Aubry et al., 2007). The bio-lithostratigraphic assignment of the Possagno sediments follows Luciani and Giusberti (2014), and the magnetostratigraphy is from Agnini et al. (2006) (Figs. 2 and 3).

The Blake Nose is a gentle ramp extending from 1000 to 2700 m water depth at the Blake Escarpment in the western North Atlantic (Norris et al., 1998). ODP Site 1051 is located well above the local lysocline and the carbonate compensation depth. The sediments studied here are from 452.24 to 353.10 m below sea floor (mbsf) and consists of lower to middle Eocene carbonate ooze and chalk (Norris et al., 1998). This part of the Eocene section shows good recovery except between 382 mbsf and 390 mbsf (Fig. 4) and contains abundant calcareous plankton. Magnetostratigraphy is from Ogg and Bardot (2001). Paleodepth estimates from benthic foraminiferal assemblages indicate lower bathyal depth (1000–2000 m) during late Paleocene-middle Eocene (Norris et al., 1998). The paleodepth was about 2200 m during the lower Eocene according to Bohaty et al. (2009).

## 3 Methods

Analyses of foraminifera and stable isotopes were performed from the identical sample set of the Possagno section previously used for calcareous nannofossils (Agnini et al., 2006). Relative abundances have been determined from about 300 specimens extracted from each of the 110 samples investigated in the > 63 µm size fraction. A sampling interval of 2–5 cm was used in the basal 0.7 m of the Possagno section, followed by 50 cm spacing for the 0.7–14 m interval, and 20 cm for the 14–66 m interval. Washed residues were prepared following standard procedures, which varied with the different lithologies. Foraminifera were successfully extracted from the indurated marly limestones and limestones using the cold-acetolyse technique (Lirer, 2000; Luciani and Giusberti, 2014), a highly successful method for disaggregating strongly lithified samples (Fornaciari et al., 2007; Luciani et al., 2007), otherwise analyzable only in thin section. The marly samples were disaggregated using 30 % hydrogen peroxide and subsequently washed and sieved using a 63 µm sieve. In most cases, gentle ultrasonic treatment improved the cleaning of the tests. In the Possagno section, foraminifera are continuously present and diverse throughout the studied interval with a preservation varying from moderate to fairly good.

The weight percent of the > 63 µm size fraction relative to the weight of the bulk sample, typically 100 g/sample, for the 110 Possagno samples is referred to as the coarse fraction (CF), following Hancock and Dickens (2005). Investigation of fifty Eocene samples at Site 1051 (Hole 1051A) from 452.24 to 353.1 mbsf, corresponding to ∼ 52–47 Ma, had a spacing varying from 2.0 to 0.5 m. These were prepared using disaggregation using distilled water and washing over 38 and 63 µm sieves. Washed residues were dried at < 50 °C. Planktic foraminifera from Site 1051 are abundant and well preserved.

The degree of dissolution, expressed as fragmentation index (*F* index), has been evaluated by counting the number of planktic foraminiferal fragments or partially dissolved tests vs. entire tests on 300 elements, following Hancock and Dickens (2005). These data are expressed in percentages. Fragmented foraminifera include specimens showing missing chambers and substantial breakage.

Carbon and oxygen stable isotope data of bulk sediment samples 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 ±0.07 ‰ for oxygen isotopes. Stable isotopes values are calibrated to the Vienna Pee Dee Belemnite standard (VPDB) and converted to conventional delta notation ($\delta^{13}$C and $\delta^{18}$O).

# 4 Results

## 4.1 Foraminiferal fragmentation

The *F* index recorded at Possagno (Fig. 3) displays a large variability throughout the interval investigated. The highest values, up to 70 %, were observed in the 14–22 m interval. The maximum *F* index values correspond to the minimum values in the $\delta^{13}$C record. A number of *F* index peaks mimic the $\delta^{13}$C negative peaks below 16 m, showing values between 60 and 70 %.

*F* index values at Site 1051 (Fig. 4) show less variability with respect to Possagno. A maximum value of 60 % is reached in Zone E5, just below an interval of uncertain magnetostratigraphic attribution (Norris et al., 1998), here referred to as Chron C23r. Relatively high *F* index values around 50 % occur the upper portions of Chrons C24n and C22r. The interval across the EECO, on the basis of biomagnetostratigraphic correlation and here placed between ca. 405 and 432 mbsf, displays low *F* index values ($<$ 20 %). The relatively lower *F* index values at Site 1051 are presumably caused by less carbonate dissolution at that site and, to some extent, the lower resolution of the investigated samples at Site 1051.

### 4.2 Weight percent coarse fraction

Carbonate dissolution generally causes the bulk sediment coarse fraction to decrease because of fragmentation of foraminiferal tests (Hancock and Dickens, 2005). The coarse fraction and *F* index data from Possagno (Fig. 3) do not show such an anti-phasing, especially in the post-EECO interval. The coarse fraction at Possagno shows minor fluctuations with a mean value of 5.3 ± 1.5 % from the base of the EECO and upsection, with pre-EECO values varying around 10 %.

### 4.3 Carbon and oxygen isotopes

The $\delta^{13}$C data from Possagno show a negative shift of about 1.5 ‰ at the 0 m level, which corresponds to the Paleocene-Eocene boundary (Agnini et al., 2009). There are nine additional negative carbon isotope excursions above the Paleocene-Eocene boundary in the lower 21.4 m of the Possagno section (Fig. 2, Table S1 in the Supplement):

1. 0.9 ‰ at 21.4 m (C22r) within EECO

2. 1.1 ‰ at 20.8 m (C22r) within EECO
3. 0.6 ‰ at 19.8 m (C23n) within EECO
4. 0.8 ‰ at 18.0 m (C23n) within EECO
5. 0.9 ‰ at 16.8 m (C23n) within EECO
6. 0.4 ‰ at 14.8 m (C24n.1n) within EECO (X event)
7. 0.3 ‰ at 12.5 m (near C24n.2n/C24n.2r boundary; J event)
8. 0.3 ‰ at 10.5 m (mid C24n.3n; I event)
9. 0.3 ‰ at 8.0 m (upper C24r; ETM2/ELMO event)

The two oldest of these carbon isotope excursions are determined using 45–50 cm sample spacing, implying that their true magnitudes are probably not fully captured. Their precise positions may also change as higher resolution data become available from this relatively condensed part of the section showing sedimentation rates $< 0.5\,\mathrm{cm\,kyr^{-1}}$. The remaining five are determined using 20 cm sample spacing. The number, magnitudes and stratigraphy of the above carbon isotope excursions are similar to the results of other studies (Agnini et al., 2009; Slotnick et al., 2012; Zachos et al., 2010).

Above Chron C22r, a series of additional minor negative carbon isotope excursions (CIEs) are recorded in Chron C22n, Chron C21r and Chron C21n from the Possagno section. By combining the chron identification with the number of CIEs starting at the old end of the chron, these CIEs are coined C22n-CIE1, C22n-CIE2, etc., up to C21n-CIE5 (Fig. 2). As the Possagno section is measured from the base of the PETM (0 m) and upsection, increasing distance from the PETM level yields increasing positive meter values:

1. C21n-CIE5 – 0.3 ‰ from 56.6 to 57.0 m

2. C21n-CIE4 – 0.3 ‰ from 55.6 to 56.2 m
3. C21n-CIE3 – 0.3 ‰ from 54.8 to 55.0 m
4. C21n-CIE2 – 0.4 ‰ from 52.8 to 53.2 m
5. C21n-CIE1 – 0.8 ‰ from 48.8 to 49.4 m
6. C21r-CIE4 – 0.3 ‰ from 39.6 to 39.8 m
7. C21r-CIE3 – 0.5 ‰ from 38.8 to 39.2 m
8. C21r-CIE2 – 0.7 ‰ from 37.6 to 38.2 m
9. C21r-CIE1 – 0.9 ‰ from 32.8 to 33.2 m
10. C22n-CIE3 – 0.5 ‰ from 31.2 to 31.4 m
11. C22n-CIE2 – 0.5 ‰ from 30.0 to 30.2 m
12. C22n-CIE1 – 0.6 ‰ from 27.2 to 27.4 m

Oxygen isotopes of bulk rock measurements from indurate marly limestones and limestones may be affected by diagenetic overprints (Marshall, 1992), which presumably apply also to the rocks in the Possagno section. Despite of this preservation caveat, it is assumed that oscillations in oxygen isotopes chiefly represent temperature fluctuations during the ice-free early Eocene world. Lighter oxygen isotope values in the Possagno section indeed show a clear correspondence with lighter carbon isotope values (CIEs) and vice versa in the post-EECO interval (Fig. 2). Thus, despite the possibility of some diagenetic overprinting in several individual samples, especially in the lower part of our record, a three-point moving average of oxygen isotope data should reveal early to early middle Eocene climate variability in the Possagno section.

### 4.4 Planktic foraminiferal quantitative analysis

The planktic foraminiferal assemblages show significant modifications in the early to early middle Eocene interval at Possagno (Fig. 3). The mean relative abundance of *Acarinina* is about 46 % of the total assemblage throughout the section. Members of this genus show peak abundances of 60–70 % of the total assemblage during the early to early middle Eocene CIEs. Particularly prominent is the increase to ~ 80 % during the EECO interval (Fig. 3). Acarininids clearly thrived and expanded in abundance during the CIEs, including the EECO.

This increase of acarininids is counter balanced by a transient decrease in members of subbotinids. This latter group recovers above the EECO interval and increases moderately from ~ 24 to ~ 36 % in terms of mean relative abundance of the total assemblage, up to the top of the section. The North Atlantic Site 1051 also shows a slight increase of ca 7 % in the mean value among the subbotinids during the corresponding time interval.

A permanent reduction in the abundance of members of the genus *Morozovella* represents a major change within the planktic foraminiferal assemblages within Zone E5. This group collapses from a mean value of ~ 24 % in the 0–15 m interval to less than 6 % above 15 m. Morozovellids never recover to their pre-EECO abundances, even if including the appearance of the ecologically comparable genus *Morozovelloides* (Pearson et al., 2006) in samples above 36 m. Genera and species with low abundances show minor changes throughout the interval studied at Possagno (Fig. S1 in the Supplement).

The major change in planktic foraminiferal assemblages at Site 1051 includes a distinct decrease of *Morozovella*, from mean values around 40 to 10 % in the middle part of Zone E5 (Fig. 4). The differences in the relative abundance of morozovellids at Possagno and Site 1051 indicate a morozovellid preference for open ocean settings. Like at Possagno, morozovellids never recover at Site 1051 in the Zone E5 through E8 interval. The abundance of subbotinids shows little variations around mean values of 20 %

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at Site 1051. *Acarinina* displays an increase in mean relative abundance from 35 % (base to ca 450 mbsf) to around 50 % (ca 430 mbsf), with maximum values of about 60 %. The relatively low resolution used here does not permit comparison between the early Eocene CIEs at Site 1051 (Cramer et al., 2003) and how the relative abundance of planktic foraminiferal genera varies with respect to CIEs.

### 4.5 Radiolarian abundance

Radiolarians are rare to absent in the Possagno section. Brief temporary occurrences of this group have been observed in coincidence with some of the most negative $\delta^{13}$C excursions. Specifically, they reach a maximum relative abundance of 28 % in the lower part of the major $\delta^{13}$C perturbation recorded in the lower to middle part of C23n, of ~ 10 % at 27.5 m and of 15 % at 31.4 m (Fig. 3). At Site 1051, radiolarians fluctuate in abundance from 0 to 78 % throughout the studied interval.

## 5 Discussion

### 5.1 The $\delta^{18}$O and $\delta^{13}$C stratigraphies at Possagno

The $\delta^{18}$O and $\delta^{13}$C records from the Possagno section display both details and trends (Fig. 2) that are similar to those observed in several other late Paleocene through early middle Eocene stable isotope stratigraphies (Cramer et al., 2009; Schmitz et al., 1997; Shackleton et al., 1985; Slotnick et al., 2012; Zachos et al., 2001, 2008). For example, the major CIE (−1.5 ‰) close to the base of the Possagno section represents the PETM, followed upsection by hyperthermals ETM2, I, J, and ETM3 (Agnini et al., 2009). The older and younger sides of the EECO are not well constrained in any single sedimentary record (Slotnick et al., 2012), nor so at Possagno, yet the interval between 16 and 22.5 m in Possagno shows the lightest $\delta^{18}$O values during the entire post-PETM interval of the early Eocene and early middle Eocene (Fig. 2) and is considered to represent at least part of the EECO. In terms of oxygen isotope stratigraphy, both the EECO and post-EECO intervals are characterized by a series of rapid oscillations. The oxygen isotope amplitude range shows up to 1.5 ‰ differences between adjacent samples, which possibly may reflect potential diagenetic overprint. By running a 3-point running mean of the oxygen isotope data, single overprint outliers are dampened. Even so, these data show rapid amplitude changes of up to 0.5 ‰, suggesting correspondingly rapid temperature changes in the western Tethys on the order of 2 °C during the ice-free early and early middle Eocene world. The underlying cause of these distinct and rapid temperature changes may be sought in the stable carbon isotope data.

Several lines of evidence suggest that high $CO_2$ concentrations were driving the EECO global warmth as well as the hyperthermal events of the early Eocene (Fletcher et al., 2008; Hyland and Sheldon, 2013; Komar et al., 2013; Lowenstein and Demicco, 2006; Lunt et al., 2011; Pearson and Palmer, 2000; Royer et al., 2007; Smith et al., 2010). A series of CIEs occur within and above the EECO interval at Possagno. A number of CIEs have been observed from ODP Site 1258 in the western tropical Atlantic (Kirtland Turner et al., 2014; Sexton et al., 2006, 2011), which they interpreted as minor hyperthermals and referred to as 21 numbered H-events (H for Hyperthermal) in Chrons C23r through C21r. Sedimentation rates at Possagno are 2–6 times lower than those at Site 1258 in the indentical time interval. The number of CIEs within individual magntochron zones at Possagno and Site 1258 differ slightly, presumably because of differences in sedimentation rates and sample resolution. Kirtland Turner et al. (2014) listed three CIEs/H-events in Chron C23r, none of which are evident in the Possagno record at the present sample resolution, probably due to strongly condensed sedimentation or presence of a hiatus. At Possagno, three events are recorded in C23n, compared with the two CIEs/H-events from Demerara Rise, whereas only two of the six CIEs/H-events in Chron C22r are distinguishable in Possagno. Five CIEs/H-events are listed in Chron C22n from Demerara Rise, three of which are evident in the Possagno record. Finally, five CIEs/H-events are listed in Chron C21r, four of which are evident in the Possagno record. It follows that the lower sample resolution at Possagno likely has blurred both the number and true magnitudes of the isotopic amplitude changes. It remains uncertain if the CIEs and H-events at Site 1258 and the CIEs in the Possagno section are in synchrony.

Regardless of the potential synchrony between Possagno and Site 1258 at the Demerara Rise, both regions clearly demonstrate that after the EECO, from ca 50 to ca. 46–47 Ma during a trend of cooling (2–2.4 °C) climate, about 18 brief negative CIEs coincide with hyperthermal-like brief episodes of warming. These brief CIEs induced environmental perturbations that are expressed in the planktic foraminiferal data from the Possagno section. This points to a primary relationship between increased $CO_2$ concentration and warmth during early through early middle Eocene times (Dickens et al., 2005; Quillévéré et al., 2008; Zachos et al., 2005, 2008).

### 5.2 The EECO interval and hyperthermals at Possagno: acarininids dominated or dissolution controlled assemblages?

One of the most prominent changes in the planktic foraminiferal assemblages is the dominance of acarininids across the EECO interval, resulting in a corresponding decrease in relative abundance of morozovellids and subbotinids (Fig. 3). These changes parallel relatively high values of the $F$ index and coincide with the most negative parts in the $\delta^{13}C$ record. The increase in shell fragmentation suggests some carbonate dissolution. The high $pCO_2$ atmospheric concentration during the EECO may have induced carbonate dissolution at the deep-water Possagno setting, resulting from deep-water acidification and a rise of the lysocline, similar to patterns observed during the main hyperthermal events. This interpretation for the Possagno section should however imply a considerable shallowing of the CCD/lysocline, assuming that the section was deposited in a middle to lower bathyal setting. Further studies on the Tethyan CCD in the Eocene interval will help investigate the hypothesis that the CCD was shallower there, with respect to the open ocean CCD. Intensified water column remineralization of organic matter, forced by augmented metabolic rates at elevated temperatures, may have caused pH to decrease in the uppermost water column, inducing dissolution of calcitic tests (Brown et al., 2004; John et al., 2013, 2014; O'Connor et al., 2009; Olivarez Lyle and Lyle, 2006).

Questions arise on how to estimate the possible dissolution artefacts from the primary ecological signal. Nguyen et al. (2011) and Petrizzo et al. (2008) studied Pacific Ocean assemblages of latest Paleocene to initial Eocene age, and suggested that subbotinids are more dissolution susceptible than morozovellids and acarininds, which previously were thought to be the most dissolution prone forms (Berggren and Norris, 1997; Boersma and Premoli Silva, 1983). Paleogene assemblages affected by extensive dissolution could be expected to be impoverished with respect to the more dissolution susceptible subbotinids. These results have been challenged by other analyses that document a dominance of subbotinids within intervals affected by a high *F* index and enhanced carbonate dissolution (Luciani et al., 2010), who suggested that dissolution has affected the planktic assemblages rather equally. The degreee of dissolution of planktic foraminifera appears to have varied during different time intervals, being species related rather than exclusively associated with different genera. However, since data on dissolution susceptibility on different genera are so far lacking for early and early middle Eocene times, we cannot exclude that dissolution may have changed the pristine planktic foraminifera assemblages.

When assuming that dissolution has affected assemblages, it follows that the dominance of acarininids during the EECO and hyperthermal events may represent a taphonomic artifact. This assumption appears yet to conflict with the results from the upper part of Possagno in the Chron C21n interval, where significant decreases of subbotinids, associated with distinct acarininid increases, correspond to negative shifts in $\delta^{13}$C values in the absence of carbonate dissolution, as expressed in low *F* index values (Fig. 3).

The similarity in the major planktic foraminiferal modifications throughout the EECO at Site 1051 (Fig. 4), which appears only marginally affected by dissolution, suggests that the Possagno assemblages represent a reasonably genuine paleoecological response rather than assemblages primarily modified by carbonate dissolution.

The decrease of CF values (Fig. 3) in the EECO interval might indicate loss of carbonate shells due to carbonate dissolution. Similarly, relatively low CF-values with only minor fluctuations are recorded to the top of the section, independently from changes in the *F* index values. The CF curve parallels the EECO/post-EECO trend of the morozovellid abundance thus suggesting a relationship with the morozovellid decline rather than carbonate dissolution.

### 5.3 The Possagno and Site 1051 records: planktic foraminiferal response to the EECO

The planktic foraminiferal assemblages show significant variations in the Possagno material that correlate with the pronounced $\delta^{13}$C perturbations in the EECO interval (Fig. 3). When the warm preferring acarininids become dominant during the EECO, this results in a reduction in relative abundance of the warm preferring morozovellids. This feature is recurring in planktic foraminiferal assemblages across some hyperthermals (PETM and *X* events), as recorded from a number of Tethyan successions of northeastern Italy and it has been interpreted as a result of relatively enhanced eutrophication of surface waters in a near continental setting (Agnini et al., 2009; Arenillas et al., 1999; Luciani et al., 2007; Molina et al., 1999).

Planktic foraminiferal analyses of the pre-EECO hyperthermals ETM2, I, J and ETM3 at Possagno show PETM-like responses, consisting of strongly increasing relative abundances of acarininids, as in the PETM interval of the nearby Forada section (Luciani et al., 2007). The multi-proxy analyses of the *X* event at the nearby Farra section (Agnini et al., 2009) corroborate at higher resolution the record from Possagno. Increased surface water eutrophication has been proposed to favour acarininids, in being able to temporarily colonize deeper waters that previously were occupied by subbotinids and in being able to tolerate relatively high eutrophic conditions that suppressed the abundances of morozovellids (Agnini et al., 2009; Luciani et al., 2007). The increased surface water eutrophication during hyperthermals was forced by strengthening of the hydrological cycle and increased weathering as a consequence to strengthened greenhouse conditions. The effects improved the nutrient availability in this near continental, pelagic setting of the western Tethys (Agnini et al., 2009; Giusberti et al., 2007; Luciani et al., 2007). The hypothesis of increased nutrient availability in the lower part of the EECO interval at Possagno is supported by the entry of relatively high concentration of radiolarians, considered as eutrophic indices (Hallock, 1987).

The decline of morozovellids across the EECO at Possagno and Site 1051 is irreversible and cannot be explained by brief perturbations, as during the pre-EECO hyperthermals. The morozovellid crisis is coupled with the gradual disappearances of several species, including *M. aequa, M. gracilis, M. lensiformis, M. marginodentata*, and *M. subbotinae*, and it is not counterbalanced by the appearance of species of *Morozovelloides*, a minor component of middle Eocene assemblages. The latter genus appeared at Possagno around the Ypresian/Lutetian boundary (Luciani and Giusberti, 2014) and it is morphologically highly convergent with *Morozovella* although probably did evolve from *Acarinina* (Pearson et al., 2006).

The similar behaviour across the EECO of morozovellids in the Tethyan Possagno section and Site 1051 in the western subtropical North Atlantic supports the hypothesis of a geographically wide spread morozovellid crisis that is caused by climate change. This change must be a consequence of the major modifications across the EECO, both in terms of temperature and $p\mathrm{CO}_2$, which in turn must have induced water column reorganizations leading to a reduction of the morozovellid habitat. Because morozovellids exhibit transient reduction in abundance during pre-EECO hyperthermals, and due to the imprecise definition of this event, it is not possible to precisely pinpoint the exact turning point of the morozovellid decline, i.e. whether it began just at the onset, within, or at the termination of the EECO event. Current data from Possagno and Site 1051 however record that their massive drop in abundance began across the C24n1n–C23r transition. The decrease apparently started at the top of C24n1n at Possagno, but it has not been possible to determine whether or not this decrease is transitory because a potential recovery may be hidden by condensation/hiatus across the C24n1n–C23r interval. Present data from Site 1051 record the decline in lower C23r, even though some uncertainties are caused by the low resolution in the foraminiferal analysis and magnetostratigraphic attribution.

In contrast to the deterioration of the morozovellid habitat, relatively favourable conditions for thermocline dwellers such as subbotinids and parasubbotinids are suggested by the new species appearing progressively during the post-EECO interval at Possagno (Luciani and Giusberti, 2014), in good agreement with the low latitude data presented by Pearson et al. (2006). Most of the new species will characterize the thermocline of the middle and late Eocene oceans: *Subbotina corpulenta, S. eocena, S. hagni, S. senni, S. yeguanesis, Parasubbotina griffinae,* and *P. pseudowilsoni*. The appearance of the radially chambered *Parasubbotina eoclava*, which is considered to be the precursor of the truly clavate chambered *Clavigerinella* (Coxall et al., 2003; Pearson and Coxall, 2014) occurs at 19.8 m (Luciani and Giusberti, 2014)*. Clavigerinella* is the ancestor of the genus *Hantkenina* that successfully inhabited the sub-surface middle through late Eocene oceans. Prior to the evolution of genuine *Clavigerinella, P. eoclava* made several aborted attempts to evolve towards the genus *Clavigerinella.* This is reflected in presence of rare and scattered specimens that are morphologically close to *Clavigerinella* within the EECO interval even though true representative of genus *Clavigerinella* were not observed in the Possagno section.

The EECO and post-EECO intervals indeed proved to be crucial in Eocene planktic foraminferal evolution.

### 5.4 Possible causes of morozovellids decline across the EECO

The data from Possagno and Site 1051 demonstrate that the early Paleogene planktic foraminiferal symbiont bearing groups were strongly affected by a habitat deterioration across the EECO. This early Eocene crisis was followed by a second step, involving the large sized acarininids and *Morozovelloides,* documented through their reduction in abundance as well as test size during the Middle Eocene Climate Optimum (MECO) at ca 40 Ma in Tethyan (Fig. 5), Southern Ocean, and northwest Atlantic settings (Edgar et al., 2012; Luciani et al., 2010). Furthermore, the muricate crisis culminates near the

Bartonian/Priabonian boundary with a major demise in the *Acarinina* lineage and the extinction of *Morozovelloides*. Only small (< 125 µm) and relatively rare acarininids survived into the late Eocene and Oligocene (Agnini et al., 2011; Berggren et al., 2006; Wade, 2004; Wade et al., 2012). An episode with loss of symbiosis resulting in bleaching caused by global warming has been proposed to explain the second muricate crisis (Edgar et al., 2012). If the MECO warmth has been the main cause of bleaching of acarininids, we would expect that this phenomenon also involved morozovellids during the EECO, as this warm interval records the highest temperatures of the Paleogene. Considering the importance of photosymbiosis in extant species for foraminiferal test calcification and ecology (Bé, 1982; Bé et al., 1982; Hemleben et al., 1989), we may assume similar requirements for fossil taxa. The algal-symbiotic relationship is considered one of the most successful strategies adopted by muricates during the earliest Paleogene (Norris, 1996; Quillévéré et al., 2001). A crisis in that relationship may represent one possible hypothesis to explain the decline of early Eocene morozovellids. Further studies that include stable isotope analyses, including $\delta^{13}$C gradients, on morozovellid tests are needed to further elucidate this scenario. There is however scarce documentation on mechanisms responsible for bleaching and besides elevated sea surface temperature, a number of other factors, for example high ultraviolet radiation, in pH decrease, increase in $CO_2$, changes in salinity and nutrient availability, may have been involved (Douglas et al., 2003; Wade et al., 2008).

The protracted exceptional warming of the EECO is expected to have increased metabolic rates particularly in heterotrophs that are more sensitive to temperature than rates of primary production (Brown et al., 2004; O'Connor et al., 2009; Olivarez Lyle and Lyle, 2006). This effect may have increased water column remineralization of organic matter and caused pH to decrease in the uppermost water column (John et al., 2013, 2014; O'Connor et al., 2009; Olivarez Lyle and Lyle, 2006). The potential lowering of pH in surface waters, which could have been further enhanced by the huge EECO $CO_2$ pressure, may have affected calcification (De Moel et al., 2009; Moy et al., 2009; Zeebe

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et al., 2008) of most surface dwellers such as the morozovellids, also by reducing or completely halting their symbiont relationships.

Complex interactions with other microfossil groups, such as radiolarians, diatoms or dinoflagellates, may have contributed to the morozovellid crisis across the EECO, for example by competing for the use of the same algal-symbionts in the case of radiolarians, or symbiont-providers. Detailed comparisons of trends in other fossil groups are necessary to investigate this hypothesis.

Seawater chemistry influences the biomineralization of organisms producing $CaCO_3$ skeletons, especially for many algae and invertebrates that have less control over the chemical composition of their mineralized parts (Stanley, 2006, 2008). High magnesium/calcium ratios are known to have favoured aragonitic and high-Mg calcite skeletons throughout the Phanerozoic. This insight is corroborated by experiments with living organisms, confirming, for example, population growth among the calcitic coccolithophores in conditions of low concentration of Mg and high concentration of calcium in seawater (Stanley et al., 2005). A strong reduction in Ca concentration occurred during the Cenozoic, following the "calcitic" Cretaceous ocean, possibly driven by changes in rates of deep-sea igneous activity (Hardie, 1996). We cannot exclude that a decrease of Ca concentration in seawater chemistry may have affected morozovellid calcification. Planktonic foraminifera have not been widely employed to study the effects of the Mg/Ca ratio of the seawater on calcification, however, they have been found to produce heavier skeleton when the saturation state of the ambient seawater with respect to calcite is elevated. It would be interesting to compare flux data of calcareous nannofossils before and after the major evolutionary change recorded across the EECO (Agnini et al., 2006; Schneider et al., 2011) to test a potential reduction in their overall productivity.

Extended time intervals of weak water column stratification and increased eutrophication are known to provide hostile ecological conditions for the highly specialized oligotrophic morozovellids (Boersma et al., 1987; Bralower et al., 1995; Pearson et al., 2006; Premoli Silva and Boersma, 1989). Such conditions are documented in several ocean sites by the recorded decline in surface-to-benthic $\delta^{13}$C gradients across the EECO (Hilting et al., 2008) and have been considered linked to evolutionary turnovers among calcareous nannofossil assemblages (Schneider et al., 2011). Weakened thermal stratification with increased vertical mixing is predicted for many, although not all, oceanic areas during hyperthermals. The fact that the permanent morozovellid collapse occurs during the EECO implies that a threshold was surpassed, not previously experienced by the morozovellid communities.

Available data indicate that the protracted conditions of extreme warmth and high $CO_2$ pressure during the EECO may have been the key element inducing a permanent impact in the marine surface water ecosystem that became detrimental for the morozovellids. Even the peculiar PETM, that records the most dramatic changes among the hyperthermals both in terms of temperature increase and carbon cycle perturbation, did not adversely affected the morozovellid habitat in a permanent way. On the contrary, morozovellids increased in abundance in open oceanic settings (Kelly et al., 1996, 1998, 2002; Lu and Keller, 1993; Petrizzo, 2007), and only a transient decrease in abundance is recorded in pelagic Tethyan near continental settings (Luciani et al., 2007). It is intriguing to note that the second main crisis of the muricate symbiont bearing forms occurred during the MECO (Fig. 5), that is also a warming event of much longer duration (about 400–500 kyr) than the early Paleogene hyperthermals (Bohaty et al., 2009; Westerhold and Röhl, 2013).

### 5.5 Planktic foraminiferal changes during post-EECO stable-isotope perturbations at Possagno

The small $\delta^{13}$C excursions recorded in the post-EECO interval at Possagno, from C22n to C21n, induced perturbations on the planktic foraminiferal assemblages that mirror those recorded in the pre-EECO interval (Fig. 3). These perturbations are expressed as marked increases of acarininids, representing warmer thriving taxa that were tolerant to relatively enhanced surface water eutrophic conditions. Peaks in surface water eutrophication could have been reached during the C22n-CIE1 and C22n-CIE3 events, as indicated by the relatively high production of radiolarians.

The post-EECO CIEs are concomitant with $\delta^{18}$O excursions and coupled to distinct modifications in the planktic foraminiferal assemblages comparable to those recorded at other early Eocene brief warming events in Tethyan settings. These data make it tenable to refer to these events as hyperthermals, although of less intensity and magnitude compared to some of the pre-EECO hyperthermals. A number of these $\delta^{13}$C and $\delta^{18}$O excursions, of much smaller magnitude and intensity with respect to the PETM, probably correlate with the recently discovered late early Eocene through early middle Eocene post-EECO hyperthermals in the Atlantic and Pacific (Kirtland Turner et al., 2014; Sexton et al., 2006, 2011). According to Sexton et al. (2011) and Kirtland Turner et al. (2014) their shorter duration and more rapid recovery phases, with respect to the PETM, imply a different forcing and feedback mechanism involving redistribution of carbon among the ocean reservoirs rather than release of greenhouse gases from buried sediments. This mechanism was active also during the EECO interval and was similar to the orbital forcing of the carbon cycle operating during the Oligocene and Miocene.

## 6 Summary and conclusions

The investigation of planktic foraminifera from the Possagno section in northern Italy represents a first case history recording changes in relative abundance among planktic foraminiferal assemblages across the EECO warm interval and post-EECO climatic variability in the Tethys realm from about 55 to 46 Ma.

The most crucial change emerging from the Possagno and ODP Site 1051 data is the irreversible decline across the EECO of the symbiont bearing genus *Morozovella,* one of the most important calcifiers of the early Paleogene tropical and subtropical oceans. The Possagno data indicate that the EECO event had a permanent impact on the planktic foraminiferal communities, representing a critical phase in the reorganization of Eocene pelagic ecosystems. Possible causes for this reorganization, that deserve further investigations, include increased eutrophication, changes in ocean chemistry, weak water column stratification, loss of symbionts, complex interaction with other microplankton groups such us radiolarians, diatoms or dinoflagellates that represented possible competitors in the use of symbionts or as symbiont providers. A critical threshold was reached across the EECO, evidently never reached before, which induced unfavourable habitats for continued morozovellid diversification and proliferation but not harsh enough to cause their extinction. This threshold appears to be related to the duration of extreme conditions characterizing the extended warmth during the EECO.

Even though several questions still remain to be answered, the data presented from Possagno add significant information about the complex evolution of the muricate planktic foraminifera and stimulate additional investigations across the EECO from different paleoceanographic settings.

The post-EECO interval at Possagno is punctuated by relatively small, negative $\delta^{13}$C shifts, interpreted as potential minor hyperhthermals in the light of available oxygen isotope data, a number of which probably are in synchrony with those recorded in the tropical Atlantic by Sexton et al. (2011) and Kirtland Turner et al. (2014). These modest post-EECO $\delta^{13}$C and $\delta^{18}$O perturbations are associated with significant, though ephemeral, modifications in the planktic foraminiferal communities showing distinct increases of the warm acarininids in a manner similar to their behaviour during pre-EECO hyperthermals in Tethyan settings. Changes in planktic foraminiferal assemblages occur during environmental perturbations associated with minor negative carbon and oxygen isotope excursions, which suggest a pronounced biotic sensitivity to climate change of planktic foraminifera even during the post-EECO interval.

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**Table A1.** Taxonomic list of species cited in text and figures.

*Globanomalina australiformis* (Jenkins, 1965)
*Morozovella aequa* (Cushman and Renz, 1942)
*Morozovella gracilis* (Bolli, 1957)
*Morozovella lensiformis* (Subbotina, 1953)
*Morozovella marginodentata* (Subbotina, 1953)
*Morozovella subbotinae* (Morozova, 1939)
*Parasubbotina eoclava Coxall* (Huber and Pearson, 2003)
*Parasubbotina griffinae* (Blow, 1979)
*Parasubbotina pseudowilsoni* (Olsson and Pearson, 2006)
*Subbotina corpulenta* (Subbotina, 1953)
*Subbotina eocena* (Guembel, 1868)
*Subbotina hagni* (Gohrbandt, 1967)
*Subbotina senni* (Beckmann, 1953)
*Subbotina yeguanesis* (Weinzierl and Applin, 1929)
*Planoglobanolamina pseudoalgeriana* (Olsson and Hemleben, 2006)

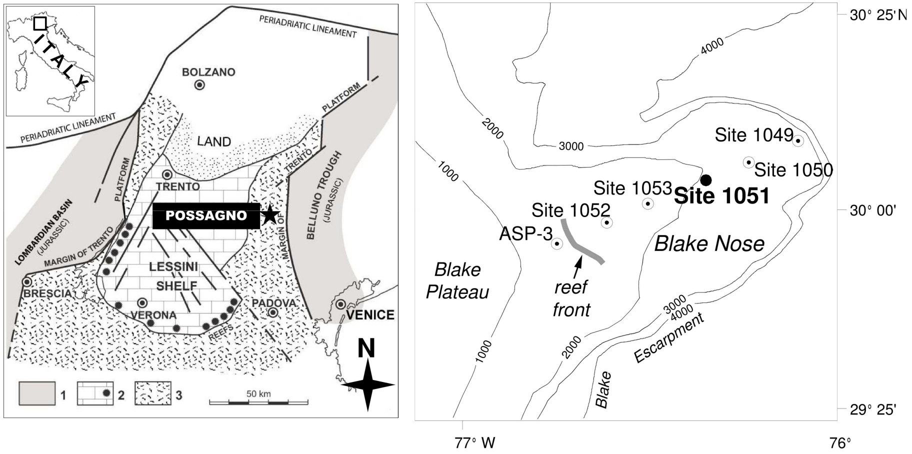


**Figure 1.** Left: paleogeographic location of the Possagno section (star) in the Belluno Basin, a Mesozoic–Cenozoic pelagic sequence, delimited during the Eocene by the shallow water carbonates of the Lessini Shelf to the west (Modified from Bosellini, 1989). 1 – deep water mudstones of the Jurassic basins; 2 – Paleogene shallow water limestones, lagoons, and shelf-edge reefs of the Lessini Shelf; 3 – Paleogene deep water pelagic claystones and marlstones of the Belluno and Lombardian Basin. Right: blake Nose map and location of Site 1051 in the western North Atlantic, modified from Norris et al. (1998).

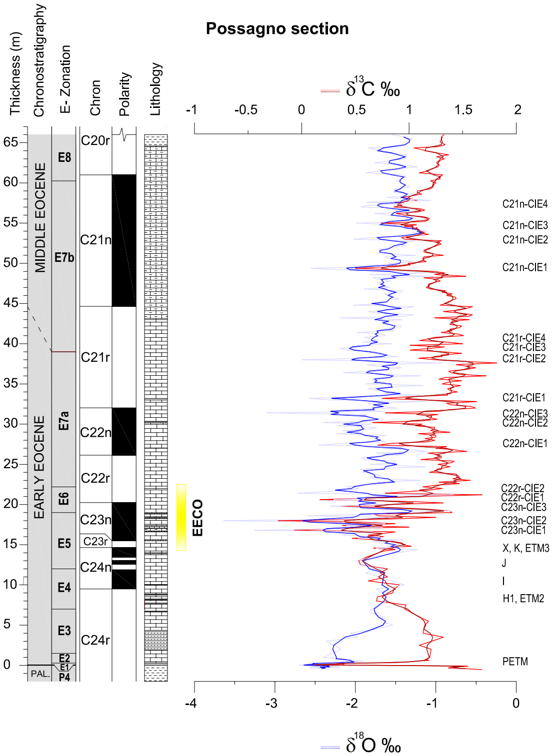


**Figure 2.** Carbon and oxygen isotopes of bulk sediment from the Possagno section plotted against lithology and planktic foraminiferal E-Zonations from Wade et al. (2011), modified by Luciani and Giusberti (2014). Magnetostratigraphy is from Agnini et al. (2006). Thinner lines: original data; thicker lines average 3-points. The average 3-point curve is utilized to dampen some of the potential diagenetic overprint on the $^{18}$O data. Pre-EECO CIEs are labelled according to current literature; the post-EECO CIEs are labelled according to Kirtland Turner et al. (2014) and Sexton et al. (2011) by substituting H (hyperthermals) with CIE (carbon isotope excursion). The yellow band band highlights the interval tentatively referred to the EECO.

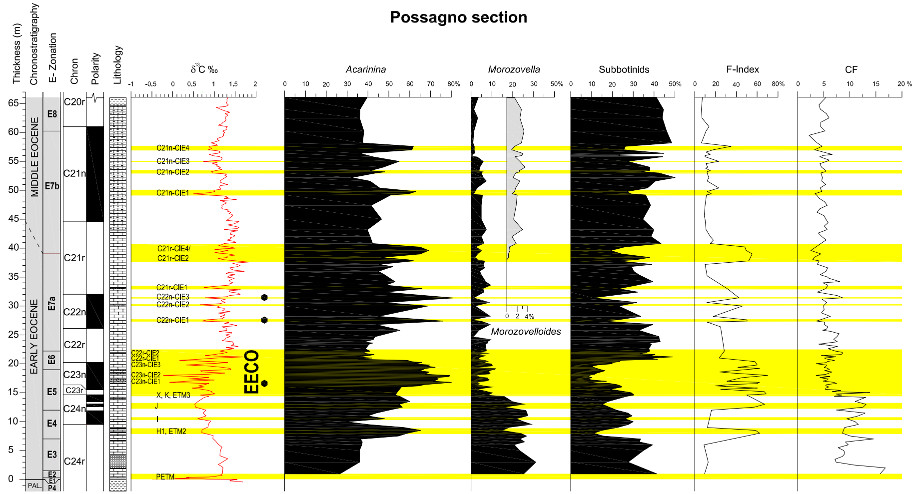


**Figure 3.** The Possagno $\delta^{13}$C record and relative abundance of main planktic foraminifera across the early and basal middle Eocene interval, plotted against lithology, fragmentation index (*F* index) and coarse fraction (CF) data. The subbotinids includes the genera *Subbotina* and *Parasubbotina*. Magnetostratigraphy is from Agnini et al. (2006). The biozonal scheme is from Wade et al. (2011), modified by Luciani and Giusberti (2014). The yellow bands highlight the interval tentatively referred to the EECO, the pre-EECO hyperthermals and post-EECO stable isotope excursions that are considered to represent hyperthermals. Pre-EECO CIEs are labelled according to current literature; the post-EECO CIEs are labelled according to Kirtland Turner et al. (2014) and Sexton et al. (2011) by substituting H (hyperthermals) with CIE (carbon isotope excursion). Filled circles show occurrences of abundant radiolarians.

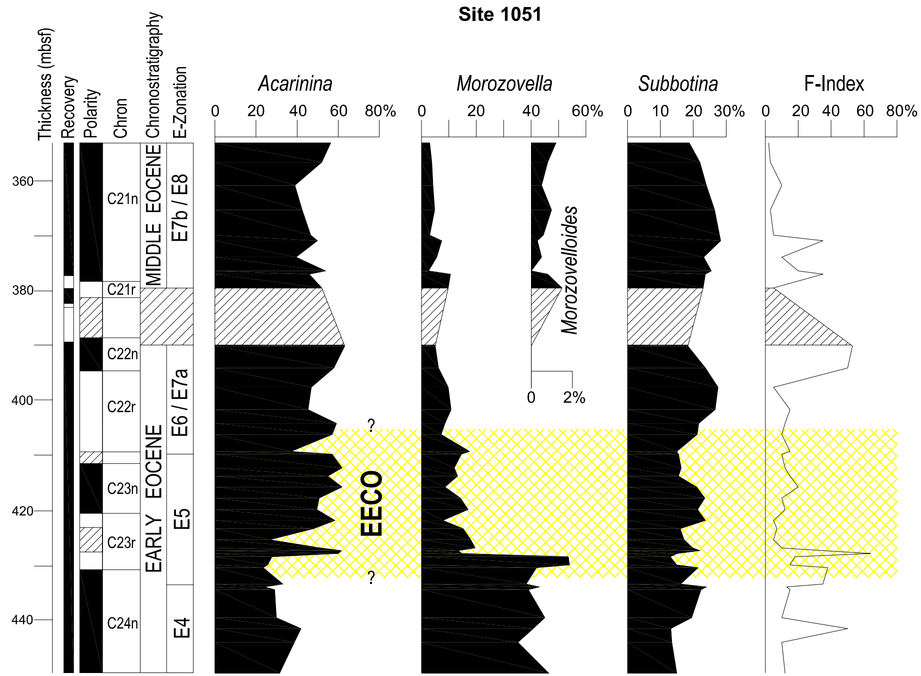
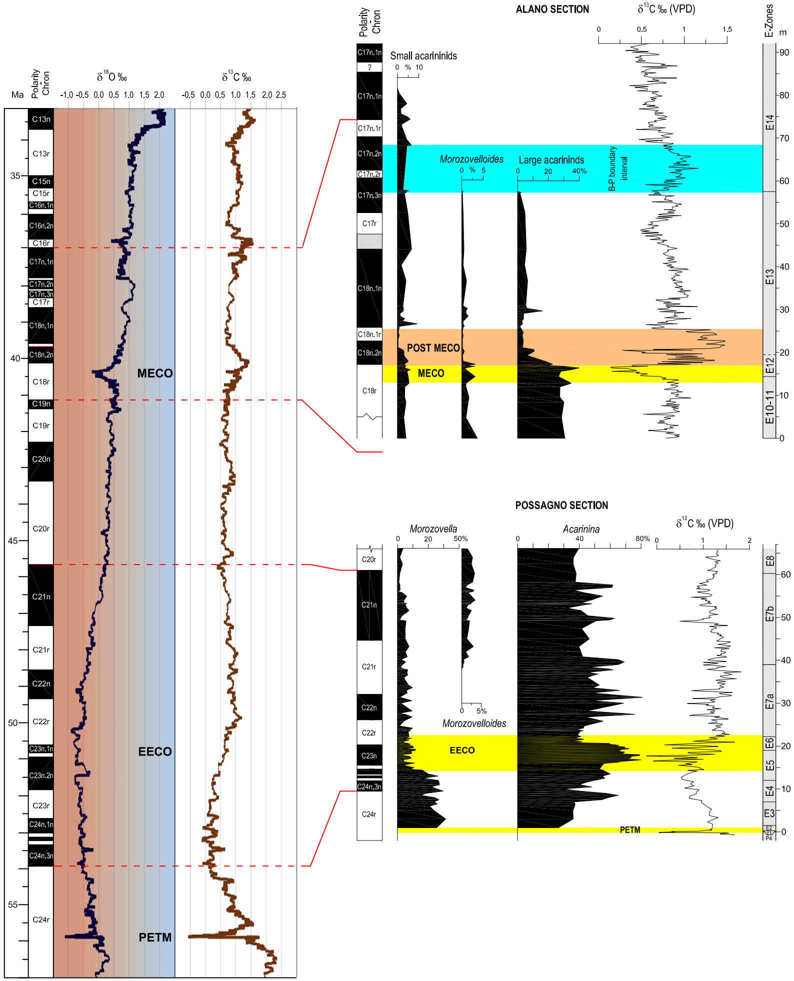


**Figure 4.** Relative abundance of the main planktic foraminiferal genera from ODP Site 1051, plotted against the biozones of Wade et al. (2011), partly modified by Luciani and Giusberti (2014), and *F* index data. The subbotinid group includes the genera *Subbotina* and *Parasubbotina*. Magnetostratigraphy is from Ogg and Bardot (2001); striped bands are intervals of uncertainty in magnetostratigraphic boundaries. The yellow band highlights the interval tentatively referred to the EECO.



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## Early Eocene massive and permanent decline of morozovellids

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**Figure 5.** The record of warm-indices muricates morozovellids and large acarininids (> 200 micron) and carbon isotope curves in the western Tethyan setting from the Possagno (below, this paper) and Alano sections (above, from Luciani et al., 2010) plotted against the generalized oxygen and carbon isotopic curves, slightly modified, shown in Gradstein et al. (2012, Fig. 28.11). The original oxygen and carbon isotopic values from Cramer et al. (2009) are re-calibrated to GTS2012 (Gradstein et al., 2012). The Tethyan record shows that the long-lasting EECO and MECO intervals mark two main steps in the decline of relative abundance within this group of important early Paleogene calcifiers. E-Zones follow Wade et al. (2011), partly modified by Luciani and Giusberti (2014). B-P = Bartonian-Priabonian; PETM = Paleocene Eocene Thermal maximum.