

Symbiont bleaching in fossil planktonic foraminifera

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Abstract Size restricted carbon isotopes ($\delta^{13}\text{C}$) are used to track changes in the ontogenetic life strategies of two species of extinct planktonic foraminifera and demonstrate that the species *Morozovelloides crassatus* lost their photosymbiotic association prior to their extinction in the latest middle Eocene. *M. crassatus* exhibit a strong positive correlation between test size and $\delta^{13}\text{C}$ between 39.5 Ma and 38.7 Ma and a $\Delta\delta^{13}\text{C}$ shift of 1.0‰/100 μm , this is analogous with modern species that possess an association with algal photosymbionts. *Turborotalia cerroazulensis* is interpreted as an asymbiotic, thermocline dweller and consistently shows no size related $\delta^{13}\text{C}$ trends and greater $\delta^{18}\text{O}$ values in comparison to *Morozovelloides*. We show a long-term (1.5 million year) deterioration of *Morozovelloides* ecology that culminated in their extinction at 38.021 Ma. The $\Delta\delta^{13}\text{C}$ / 100 μm in *M. crassatus* is dramatically reduced from 1.0‰ at 39.53 to only 0.2‰ at 38.026 Ma, 5 kyr before their extinction. The decline in ontogenetic $\delta^{13}\text{C}$ suggests diminished photosymbiotic activity (bleaching) and disruption of foraminiferal ecology in the interval preceding their extinction. We conclude that the demise of *Morozovelloides* was directly related to the deterioration of photosymbiotic partnerships with algae.

Keywords Photosymbionts · Planktonic foraminifera · Eocene · Site 1052 · Carbon isotopes · Extinction

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Introduction

Planktonic foraminifera are a group of marine, single-celled protists that shield their cytoplasm within a secreted calcareous (CaCO_3) skeleton (Hemleben et al. 1989). The preservation and accumulation of foraminifera tests within marine sediments yields a long and valuable fossil record, which can be exploited to document and understand mechanisms controlling extinction and diversification and their relationship to climatic and palaeoceanographic controls.

Many extant species of planktonic foraminifera (e.g., *Globigerinoides ruber*, *G. sacculifer*, *Orbulina universa*) have a symbiotic relationship with photosynthetic algae (Bé 1982; Bé et al. 1982; Hemleben et al. 1989; Gast and Caron 2001). There are several potential advantages to planktonic foraminifera harbouring algal symbionts. These endosymbionts (dinoflagellates) play an important role in foraminiferal reproduction, calcification and growth (Caron et al. 1981; Bé 1982; Bé et al. 1982) and allows them to succeed in low nutrient environments and niche space unavailable to the rest of the assemblage. Algal symbiosis allows the exploitation of both organic and inorganic carbon in reproduction and metabolism and is particularly valuable in oligotrophic ecosystems where nutrients are limited but radiant energy is abundant (Hallock 1981). Even though the importance of photosymbiosis in foraminiferal calcification and ecology has been documented in modern species (Bé 1982; Bé et al. 1982; Hemleben et al. 1989), the role of photosymbionts in extinct taxa and through geological time is not well understood as symbionts are not preserved in the fossil record. Here we use stable isotope analyses to investigate the palaeoecology and symbiotic associations in two extinct species of planktonic foraminifera.

A well-established tool utilised in the study of palaeoclimatology and palaeoceanography is the ratio between the stable oxygen isotopes (^{16}O , ^{18}O) and carbon isotopes (^{12}C , ^{13}C) recorded in the tests of foraminifera during the biomineralization of calcite. At higher temperatures, there is less fractionation of ^{18}O relative to ^{16}O , so foraminifera inhabiting warmer waters and calcifying in the mixed layer will be depleted in ^{18}O (Fig. 1a), whilst those species living in colder waters and calcifying in the thermocline will be enriched in ^{18}O (Urey 1947; Shackleton and Opdyke 1973).

The carbon isotope composition ($\delta^{13}\text{C}$) of planktonic foraminifera is influenced by a variety of factors including the presence and activity of algal photosymbionts. Foraminifera do not inherit their photosymbionts, but acquire them throughout their life cycle from the ambient sea water (Hemleben et al. 1989; Bijma et al. 1990). Carbon isotope signatures within fossil planktonic foraminifera can be used as a proxy for symbiotic presence and activity in extinct taxa (Pearson et al. 1993; D'Hondt et al. 1994; Norris 1996). This offers a quantitative method for identifying symbiotic associations and life strategy in fossil foraminifera, and serves as a proxy for photosymbiosis. Modern symbiotic planktonic foraminiferal species show an increasing size to $\delta^{13}\text{C}$ relationship (Fig. 1b), as algal symbionts preferentially remove the lighter, more weakly bonded ^{12}C isotope during photosynthesis, leaving the ambient water enriched in ^{13}C (Fig. 1a; Spero and DeNiro 1987; Spero and Williams 1988; Spero et al. 1991). Larger (adult) hosts support greater symbiont density and enhanced photosynthetic activity (Fig. 1b) in comparison to juveniles (Spero and DeNiro 1987; Spero and Williams 1988; Spero et al. 1991; Spero 1992; Spero and Lea 1993; D'Hondt et al. 1994). This symbiotic activity results in the ^{13}C enrichment of the foraminiferal test in relation to the ambient seawater (Erez 1978). Higher $\delta^{13}\text{C}$ values with increasing test size in photosymbiotic foraminifera of

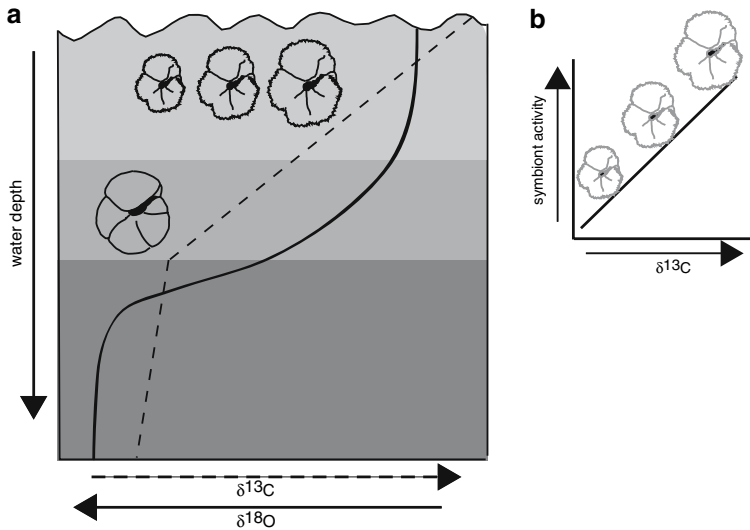


Fig. 1 (a) Schematic representation of changes in stable isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) through depth of the water column. Dashed line = $\delta^{13}\text{C}$; solid line = $\delta^{18}\text{O}$. The isotopic signature of fossil planktonic foraminifera reflects the ambient water in which their calcareous tests were precipitated. The surface waters of the ocean are depleted in ^{12}C and ^{18}O relative to deeper waters. (b) Schematic representation of changes in $\delta^{13}\text{C}$ with increased symbiotic activity in foraminifera

approximately 1‰ or greater have been recorded (Bouvier-Soumagnac and Duplessy 1985; Berger and Vincent 1986; Spero and DeNiro 1987; Spero and Williams 1988; Spero et al. 1991). Isotopic analysis has demonstrated this relationship in both modern and extinct planktonic foraminiferal species, including Paleocene and early Eocene *Praemurica*, *Morozovella* and *Acarinina* (Pearson et al. 1993; D’Hondt et al. 1994; Kelly et al. 1996; Norris 1996; Quillévéré et al. 2001).

The muricate planktonic foraminiferal *Morozovelloides* (Fig. 2), *Morozovella* and *Acarinina* were highly successful shallow dwelling groups that dominated subtropical and tropical oceans of the early Paleogene. During the late middle Eocene ~ 38 Ma (magnetostratigraphic chron C17n.3n), a faunal turnover in planktonic foraminifera occurred which saw a major decline in the *Acarinina* lineage and the extinction of the *Morozovelloides* genus (Wade 2004; Berggren et al. 2006). *Morozovelloides crassatus* (previously *Morozovella crassata*) and its synonym *M. spinulosa* (Pearson and Berggren 2006) have been widely recognised in middle Eocene sediments and employed extensively in palaeoclimatic studies. The extinction of *Morozovelloides* and the decline in the acarininid lineage in the latest middle Eocene at 38.02 and 38.03 Ma respectively (Wade 2004) are important biostratigraphic indicators and mark a significant change in the ecology of the surface ocean (see Wade 2004 for discussion).

Morozovelloides, like extant photosymbiotic foraminiferal species, were abundant in low to mid latitudes. Stable isotope analyses of *M. crassatus* indicate that these forms occupied the near-surface photic zone and consistently record the most depleted $\delta^{18}\text{O}$ and enriched $\delta^{13}\text{C}$ values compared to other species in the assemblage (Boersma et al. 1987; Pearson et al. 1993, 2001; Wade and Kroon 2002; all recorded as *Morozovella spinulosa*).

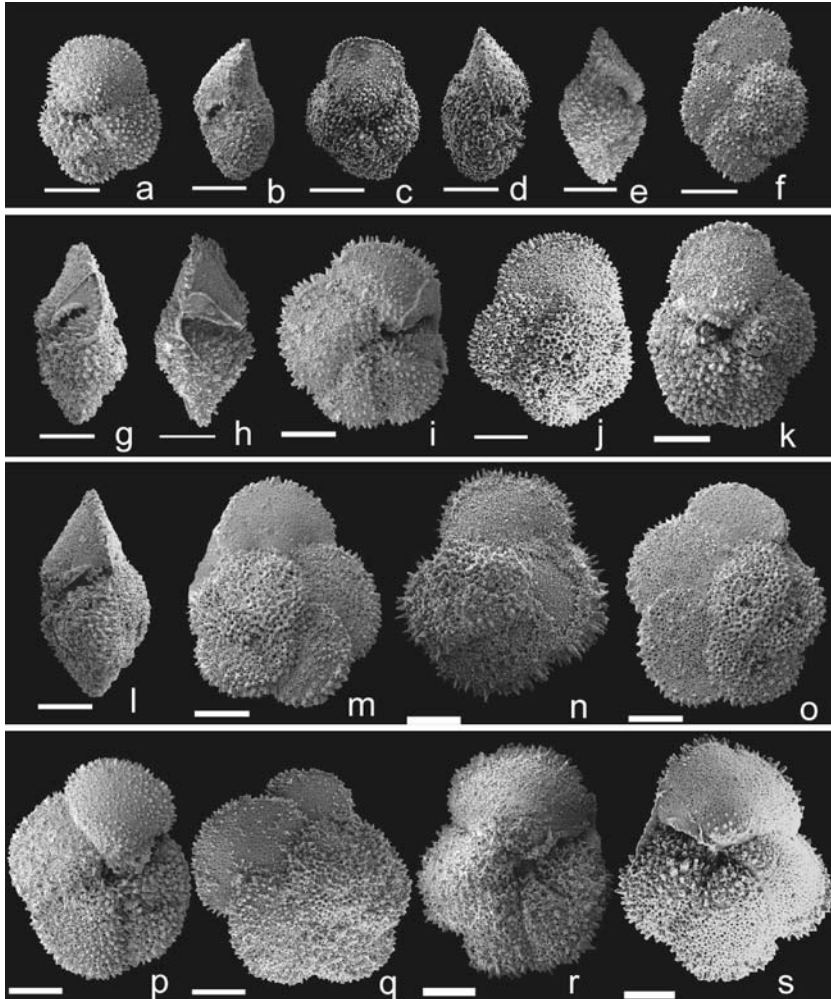


Fig. 2 Planktonic foraminifera *Morozovelloides crassatus* from the western North Atlantic (Ocean Drilling Program, Site 1052). All scale bars represent 100 μm , all specimens are from Planktonic Foraminifera Biozone E13 (P14). (a) Sample 171B-1052B-11H4, 103–106 cm, umbilical view (b) Sample 171B-1052B-11H4, 103–106 cm, edge view (c) Sample 171B-1052B-13H4, 43–46 cm, umbilical view (d) Sample 171B-1052B-11H4, 143–146 cm, edge view (e) Sample 171B-1052B-11H4, 103–106 cm, edge view (f) Sample 171B-1052B-11H4, 103–106 cm, spiral view (g) Sample 171B-1052B-11H4, 103–106 cm, edge view (h) Sample 171B-1052B-11H4, 103–106 cm, edge view (i) Sample 171B-1052B-11H4, 103–106 cm, umbilical view (j) Sample 171B-1052F-14H4, 23–26 cm, spiral view (k) Sample 171B-1052B-11H4, 103–106 cm, umbilical view (l) Sample 171B-1052B-11H4, 103–106 cm, edge view (m) Sample 171B-1052B-11H4, 103–106 cm, spiral view (n) Sample 171B-1052B-11H4, 93–96 cm, spiral view (o) Sample 171B-1052B-11H4, 103–106 cm, spiral view (p) Sample 171B-1052B-11H4, 103–106 cm, umbilical view (q) Sample 171B-1052B-13H4, 43–46 cm, spiral view (r) Sample 171B-1052B-11H4, 93–96 cm, umbilical view (s) Sample 171B-1052F-14H4, 23–26 cm, umbilical view

High $\delta^{13}\text{C}$ values and $\delta^{13}\text{C}$ to size related trends suggest that muricate taxa (*Morozovella*, *Acarinina*) harboured photosymbionts (Shackleton et al. 1985; Pearson et al. 1993; D’Hondt et al. 1994; Kelly et al. 1996; Norris 1996; Quillévéré et al. 2001).

However, while studies have examined symbiotic associations during the muricate diversification in the late Paleocene (D'Hondt et al. 1994; Norris 1996; Quillévéré et al. 2001), prior to this investigation the changes in foraminiferal ecology in later representatives of muricate taxa and during the demise of the muricate group have not been studied. Wade (2004) concluded that the extinction of the planktonic foraminiferal genus *Morozovelloides* (recorded as *Morozovella*) at 38.02 Ma was not related to climatic change, but possibly to a demise in relationships with photosymbiotic algae. Here we test this hypothesis and ascertain any change in photosymbiotic relationships prior to their extinction. Monospecific size segregated $\delta^{13}\text{C}$ data were used to track changes in the ecology and symbiotic associations of morozovelloidids (*Morozovelloides crassatus*) and turborotaliids (*Turborotalia cerroazulensis*) through the late middle Eocene (39.5–38.0 Ma) and in the 1.5 myr prior to the extinction of *M. crassatus*. Although we are studying specific taxa in the middle Eocene, our data have wider implications for understanding of the role of photosymbiosis in ecological strategies through geological time and mechanisms controlling extinction. We examine the significance of photosymbiosis in the late middle Eocene extinction of muricate taxa.

To track changes in the $\delta^{13}\text{C}$ gradient through the water column and as a comparison to changes in *Morozovelloides* through time, we use size fraction analysis of *Turborotalia cerroazulensis*. *T. cerroazulensis* (Fig. 3) is a distinctive, cosmopolitan species ranging from the middle Eocene, to just below Eocene/Oligocene boundary (Coccioni et al. 1988; Pearson et al. 2006). No previous size fraction isotope data has been published on turborotaliids, but the depleted $\delta^{13}\text{C}$ in comparison with *Morozovelloides* (Boersma et al. 1987; Pearson et al. 2001; Wade 2004) would suggest that they were asymbiotic,

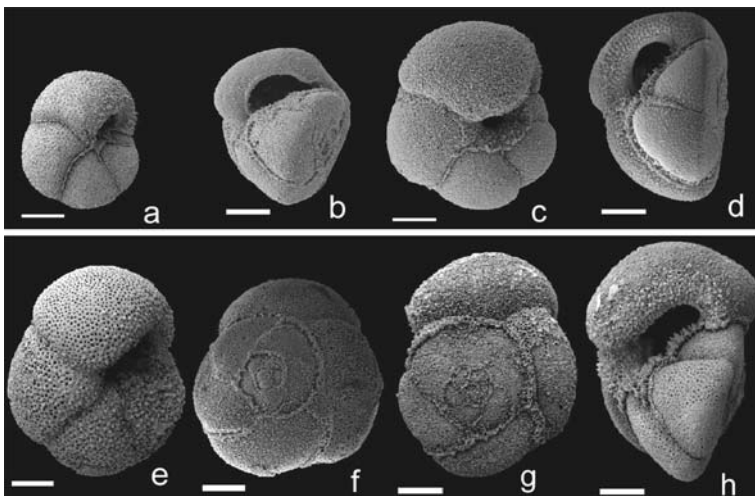


Fig. 3 Planktonic foraminifera *Turborotalia cerroazulensis* from the western North Atlantic (Ocean Drilling Program, Site 1052). All scale bars represent 100 μm , all specimens are from Planktonic Foraminifera Biozone E13 (P14), except specimen 3f from Biozone E14 (P15) (a) Sample 171B-1052B-11H4, 103–106 cm, umbilical view (b) Sample 171B-1052B-11H4, 133–136 cm, edge view (c) Sample 171B-1052B-11H4, 103–106 cm, umbilical view (d) Sample 171B-1052B-11H4, 133–136 cm, edge view (e) Sample 171B-1052B-11H4, 103–106 cm, umbilical view (f) Sample 171B-1052B-10H1, 93–96 cm, spiral view (g) Sample 171B-1052B-11H4, 103–106 cm, spiral view (h) Sample 171B-1052B-11H4, 103–106 cm, edge view

thermocline dwellers, like modern *Globorotalia*. We use stable isotope results of *T. cerroazulensis* as a model for asymbiotic, thermocline patterns and as a comparison to *M. crassatus*.

Materials and methods

Ocean Drilling Program (ODP) Site 1052 (29°57' N, 76°37' W) is located ~1345 m below sea level, on the Blake Nose (western North Atlantic). The middle Eocene sequence contains abundant and diverse planktonic foraminifera typical of open ocean assemblages (Norris et al. 1998; Wade 2004). The high sedimentation rates and good age control (Norris et al. 1998; Wade 2004) make Blake Nose an excellent site to study foraminiferal palaeoecology. Planktonic foraminifera show evidence of recrystallisation, but are free of carbonate infilling and overgrowth.

Stable isotope analyses were conducted on late middle Eocene *Morozovelloides crassatus* and *Turborotalia cerroazulensis*. Specimens were analysed from five samples from ODP Site 1052 from cores 11H to 14H, 92.57–127.21 m composite depth (mcd). This interval corresponds to 38.02–39.53 Ma and spans the *M. crassatus* biozone P14 (E13 as per Berggren and Pearson 2005) and corresponds to the last 1.5 myr of *Morozovelloides* existence. We choose samples to incorporate the interval at the base of P14, 1.5 myr before the extinction and also concentrated samples prior to the extinction event.

To document changes in $\delta^{13}\text{C}$ values through ontogeny as a proxy for photosymbiotic relationships and examine the extinction in response to foraminiferal ecology, we picked multiple specimens of *M. crassatus* and *T. cerroazulensis* from several narrowly constrained size fractions. Samples were washed over a 63 μm mesh and dry sieved into various size fractions. *Morozovelloides crassatus* and *T. cerroazulensis* were analysed from size fractions ranging from 63 to >425 μm . The number of specimens analysed varied from a maximum of 80 to a minimum of 5 specimens depending on the size fraction. Analyses were undertaken on a ThermoFinnigan MAT 252 coupled with a Kiel III Carbonate Preparation Device at Cardiff University, UK. Stable isotope results are expressed using the δ notation which defines the deviation in parts per thousand (‰) or per mil of the sample analysed from the fossil belemnite Pee Dee Belemnite (PDB) standard, as follows:

$$\delta^{13}\text{C}\text{‰} = \left[\left(\frac{^{13}\text{C}/^{12}\text{C}_{\text{sample}}}{^{13}\text{C}/^{12}\text{C}_{\text{standard}}} - 1 \right) \right] * 1000$$

External reproducibility for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ is better than 0.03 and 0.08‰ respectively. Duplicate analyses were conducted on *M. crassatus* from the 125–150 μm and 150–180 μm size fraction of sample 1052B 11H-4, 103–106 cm. This indicates reproducibility is good and results are consistent within a given size fraction $\pm 0.03\%$.

Results

The changes in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ through ontogeny of *Morozovelloides crassatus* and *Turborotalia cerroazulensis* are shown in Figs. 4 and 5 respectively. Values of $\delta^{18}\text{O}$ in *M. crassatus* are variable, between a maximum of -0.31% at 92.67 mcd to minimum values of -1.20% at 112.50 mcd. *T. cerroazulensis* $\delta^{18}\text{O}$ is consistently greater than values for *M. crassatus* $+0.46 \pm 0.23\%$. There is no relationship between size and $\delta^{18}\text{O}$ in either species (Fig. 4). All $\delta^{13}\text{C}$ values of *M. crassatus* fall between 2.0 and 3.6‰ and

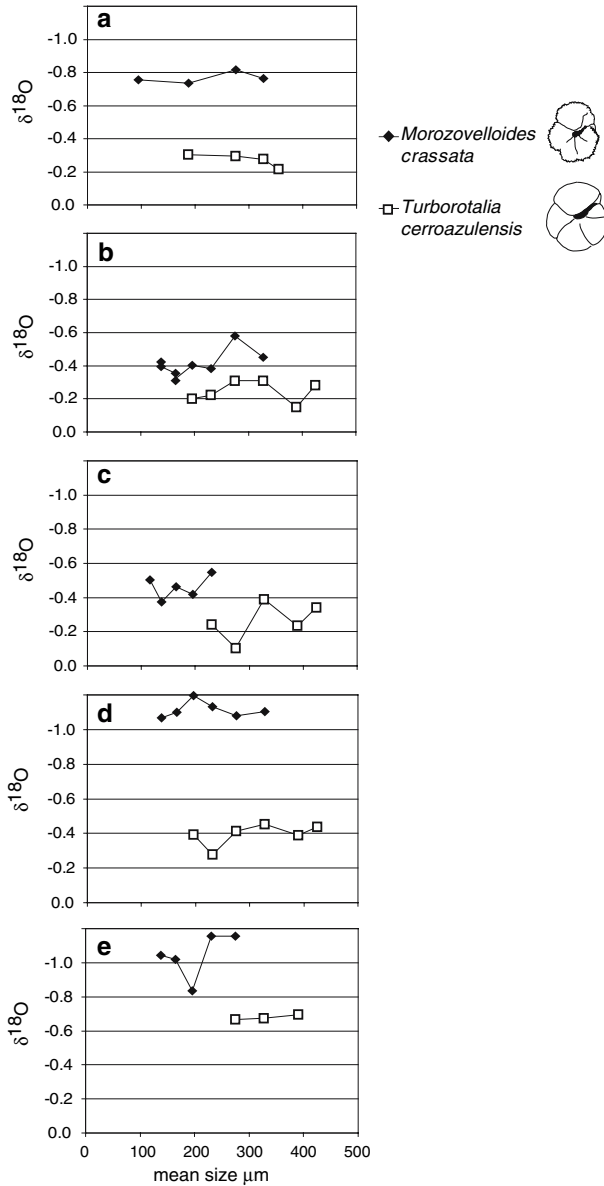
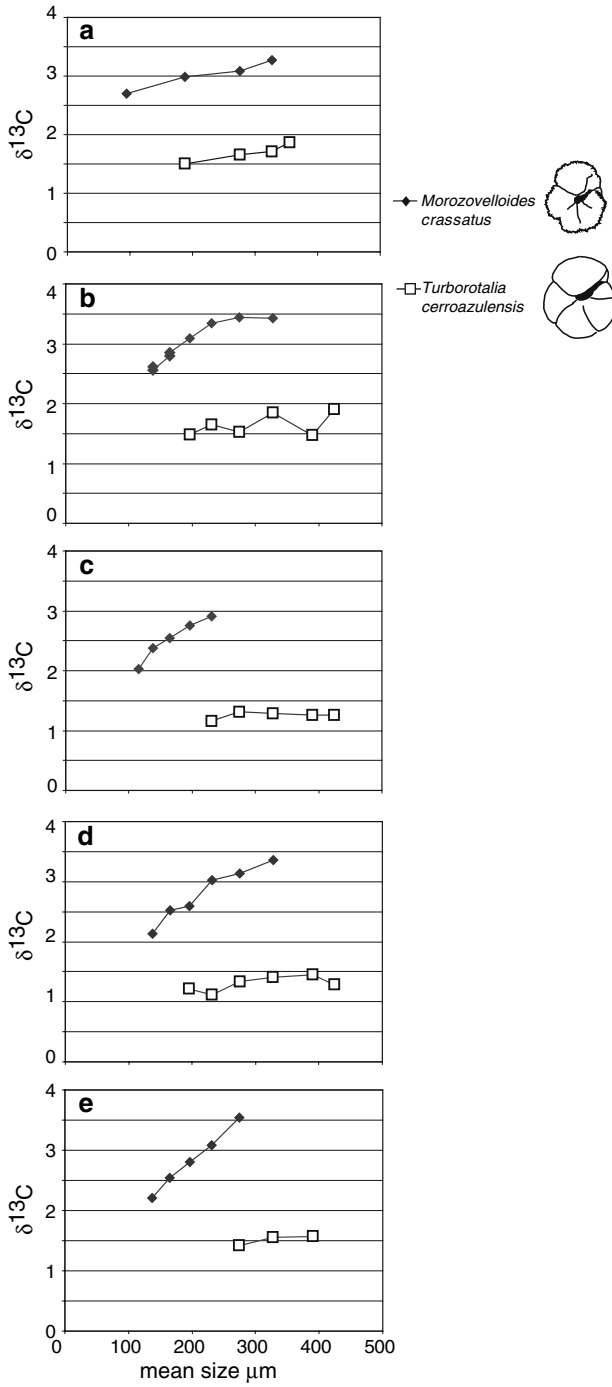


Fig. 4 Variation in $\delta^{18}\text{O}$ with test size in *Morozovelloides crassatus* and *Turborotalia cerroazulensis* from Ocean Drilling Program Site 1052. The core, section and interval (cm) are given for each sample. Ages are calculated to the Berggren et al. (1995) time-scale. Analytical precision for $\delta^{18}\text{O} < 0.08\text{‰}$. Note y-axis reversed. (a) Sample 1052B 11H4, 93–96 cm, 92.57 m composite depth (mcd), 38.026 Ma. (b) Sample 1052B 11H4, 103–106 cm, 92.67 mcd, 38.029 Ma. (c) Sample 1052B 11H4, 143–146 cm, 93.07 mcd, 38.039 Ma. (d) Sample 1052B 13H4, 43–46 cm, 112.50 mcd, 38.745 Ma. (e) Sample 1052F 14H4, 23–26 cm, 127.21 mcd, 39.530 Ma



◀ **Fig. 5** Variation in $\delta^{13}\text{C}$ with test size in *Morozovelloides crassatus* and *Turborotalia cerroazulensis* from Ocean Drilling Program Site 1052. The core, section and interval (cm) are given for each sample. Ages are calculated to the Berggren et al. (1995) time-scale. Analytical precision for $\delta^{13}\text{C} < 0.03\text{‰}$. (a) Sample 1052B 11H4, 93–96 cm, 92.57 m composite depth (mcd), 38.026 Ma. (b) Sample 1052B 11H4, 103–106 cm, 92.67 mcd, 38.029 Ma. (c) Sample 1052B 11H4, 143–146 cm, 93.07 mcd, 38.039 Ma. (d) Sample 1052B 13H4, 43–46 cm, 112.50 mcd, 38.745 Ma. (e) Sample 1052F 14H4, 23–26 cm, 127.21 mcd, 39.530 Ma

consistently record higher $\delta^{13}\text{C}$ values in the larger size fractions ($>250\ \mu\text{m}$) (Fig. 5). *Turborotalia* $\delta^{13}\text{C}$ values fall between 1.2 and 1.9‰ (mean values of $1.41 \pm 0.22\text{‰}$) and change by a maximum of 0.42‰. To quantify the changes in carbon isotope gradient through time we have calculated the change in $\delta^{13}\text{C}$ per 100 μm ($\Delta\delta^{13}\text{C}/100\ \mu\text{m}$) for *M. crassatus* in each sample (Fig. 6).

Discussion

The palaeoecology of *Morozovelloides* and *Turborotalia*

Previous studies have reported that inferred symbiotic species generally have shifts in $\delta^{13}\text{C}$ through ontogeny of $>0.72\text{‰}$, whilst asymbiotic taxa have a smaller $\delta^{13}\text{C}$ change of

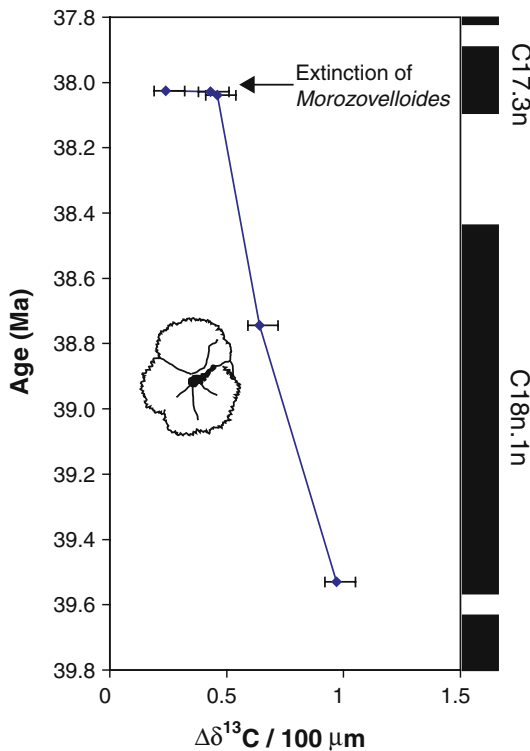


Fig. 6 Change in carbon isotopes per 100 μm ($\Delta\delta^{13}\text{C}/100\ \mu\text{m}$) in *Morozovelloides crassatus*. Magnetostratigraphy at Site 1052 (Norris et al. 1998) is shown on the right. A significant reduction (0.8‰) in $\Delta\delta^{13}\text{C}/100\ \mu\text{m}$ occurs from 39.5 Ma to 38.0 Ma

<0.47‰ (D'Hondt et al. 1994; Norris 1996). Sieve isolated size intervals of *Morozovelloides* from 127.21 mcd (39.5 Ma) exhibit a large change in $\delta^{13}\text{C}$ with size and a $\Delta\delta^{13}\text{C}$ shift of 1.0‰/100 μm (Figs. 5 and 6). The magnitude of $\delta^{13}\text{C}$ variation through ontogeny in *M. crassatus* in samples at 127.21 and 112.50 mcd (Figs. 5d, e) is characteristic of an ecology associated with active photosymbionts. Following previous studies (Pearson et al. 1993; D'Hondt et al. 1994; Norris 1996; Kelly et al. 1996; Quillévéré et al. 2001) and analogies with living species, the increasing $\delta^{13}\text{C}$ signature through ontogeny within *Morozovelloides* may be interpreted as an indication of photosymbiotic associations.

In all samples *Morozovelloides crassatus* records heavier $\delta^{13}\text{C}$ in comparison with *Turborotalia cerroazulensis* by $1.36\pm 0.31\%$ (Fig. 5). *Turborotalia cerroazulensis* are ontogenetically consistent and there is no trend of increasing $\delta^{13}\text{C}$ with test size. The lack of ontogenetic $\delta^{13}\text{C}$ to size trends suggests that *T. cerroazulensis* were asymbiotic in nature. *Turborotalia* $\delta^{18}\text{O}$ values are consistently heavier than co-occurring morozovelloidids (Boersma et al. 1987; Pearson et al. 2001; Wade and Kroon 2002; this study), suggesting that the turborotaliid group occupied a deeper niche in the water column (thermocline) compared to *Morozovelloides*. Although there is a minor ($\sim 0.1\%$) change in turborotaliid $\delta^{13}\text{C}$ through ontogeny, this is interpreted as kinetic fractionation, similar to variations in extant *Globigerina bulloides* (Spero 1991).

Symbiont expulsion and extinction

Our results show a change in the ecology of *Morozovelloides* through the latest middle Eocene (Figs. 5 and 6). In the youngest samples stratigraphically there is an abrupt decrease in the $\delta^{13}\text{C}$ to size relationship through ontogeny (Fig. 5a). The $\Delta\delta^{13}\text{C}/100\ \mu\text{m}$ in *M. crassatus* is dramatically reduced from 1.0‰ at 39.530 (127.21 mcd) to only 0.2‰ at 38.026 Ma (92.57 mcd), 5 kyr before their extinction (Fig. 6). This suggests that the last representatives of the muricate clade *Morozovelloides* at 38 Ma had a very different ecology than early and middle Eocene taxa of *Morozovella* and *Acarinina*. The marked decrease in $\Delta\delta^{13}\text{C}$ indicates a progressive change in the ecological strategy of *Morozovelloides* and diminished levels of symbiont photosynthetic activity in the interval preceding their extinction. The decline in ontogenetic $\delta^{13}\text{C}$ would suggest either the expulsion of photosymbionts or inhibition of endosymbiont photosynthesis in *Morozovelloides* at 38.03 Ma. The small change in *M. crassatus* $\delta^{13}\text{C}$ at 38.03 Ma is comparable to the variation recorded in *T. cerroazulensis* (Fig. 5) indicating that the final *Morozovelloides* were essentially asymbiotic in nature.

Bleaching, is the short-term or permanent loss of photosymbionts or of their pigments (Glynn 1996; Talge and Hallock 2003). This has been widely recognised in corals where the loss of symbiotic algae during bleaching events can result in extensive coral mortality and degradation. Bleaching in corals is associated with significantly lower $\delta^{13}\text{C}$ in comparison to non-bleached corals, resulting from depressed coral metabolism, reduced calcification and lower rates of photosynthesis during bleaching events (Suzuki et al. 2003; Grottoli et al. 2004). Other hosts of endosymbionts are also susceptible to bleaching, including larger benthic foraminifera (Talge and Hallock 1995; Hallock 2000; Hallock et al. 1995; Talge and Hallock 2003) anemones (Peters 1993), and giant clams (Addessi 2001). However, causes of zooxanthellae expulsion remain unknown, and have been attributed to a number of stress causing factors including, elevated sea surface temperature, increased ultraviolet radiation, hypersalinity, starvation and/or increased CO_2 (Douglas 2003 and references therein). Symbiont loss in benthic foraminifera is associated with a decrease in viable

offspring, shell deformities, increased foraminiferal susceptibility to predation and infestation, compromised immunity and population decline (Hallock et al. 2003).

The $\delta^{18}\text{O}$ record at Site 1052 (Wade and Kroon 2002) would suggest that this decline in photosymbiotic activity in *Morozovelloides crassatus* was not related to increased sea surface temperatures (Wade 2004). Like bleaching in the modern benthic foraminifer *Amphistegina gibbosa* (Talge and Hallock 1995), it is impossible to know whether the *Morozovelloides* expelled their photosymbionts or whether the photosymbionts left their host. Was this an extreme and detrimental reaction to an unfavourable environment? The expulsion of endosymbiotic algae may have been an adaptive change to adverse environmental conditions during the late middle Eocene.

Throughout the interval studied *Morozovelloides* are common, with the largest specimens $>250\ \mu\text{m}$. The exception is the 4 kyr prior to their extinction where specimens are smaller in size ($<250\ \mu\text{m}$) and we were unable to obtain sufficient specimens for isotopic analysis during this interval. A decrease in size is common to many extinction events in planktonic foraminifera (Wade 2006) and suggests an interval of elevated stress prior to their extinction.

Factors other than photosymbiosis can also influence the $\delta^{13}\text{C}$ signature incorporated into foraminiferal calcite (Berger and Vincent 1986; Spero 1992; Spero and Williams 1988; Spero et al. 1991). It should be noted that the juveniles are recording heavier $\delta^{13}\text{C}$ ratios in sample 92.57 mcd. This may relate to global changes in the carbon reservoir or simply the broader size ranges used for this sample (125–250 μm). Even if $\delta^{13}\text{C}$ changes are not reflecting symbiotic associations but some kind of vital activity then there is nevertheless a progressive change in the $\delta^{13}\text{C}$ size trend of *Morozovelloides* and a shift in vital effects in the final stage of their stratigraphic range. While size fraction analysis of acarininids was beyond the scope of this study, the almost synchronous extinctions (10 kyr) of *M. crassatus* and *Acarinina mcgowrani* (Wade 2004, previously recorded as *A. praetopilensis*) would suggest a related causal mechanism.

Photosymbionts are extremely valuable to foraminifer ecology. Modern planktonic foraminifera depend heavily on photosymbionts for nutrition, and retaining algal symbionts may have been vital for the successful life cycle of *Morozovelloides*, as in modern *G. sacculifer* (Bé 1982; Bé et al. 1982). Carbon isotope results indicate an ontogenetic change in the ecology and life strategy of *Morozovelloides* in the interval preceding their extinction. Our data support the hypothesis that the extinction was related to a deterioration of their symbiotic relationship with algae and suggests a direct relationship between foraminifer ecology and the major turnover at this time. The reduction in $\Delta\delta^{13}\text{C}$ suggests that *Morozovelloides* may have failed to establish and sustain photosymbiotic populations. The breakdown of this ecological strategy would have impacted *Morozovelloides* ecological success, nutrition, and calcification rates and may have led to chronic stress that acted as the catalyst for the extinction event. We conclude that the demise of the *Morozovelloides* lineage was related to a strong reliance of photosymbionts and the destruction of this ecological partnership was a mechanism involved in their extinction.

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