

The planktic foraminifer *Planorotalites* in the Tethyan middle Eocene

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Abstract: Morphologically uniform, low-trochospiral foraminifera are a common, though not very well-preserved component of foraminiferal assemblages across the interval including the Middle Eocene Climatic Optimum (MECO) at the Alano (northeastern Italy) and Monte Cagnero (central Italy) Tethyan sections. The morphology of these specimens, combined with their state of preservation, made it difficult to assign them to a benthic or planktic group. We measured their stable isotope (oxygen and carbon) composition and compared them with those of trochospiral, epifaunal benthic (*Nuttallides truempyi* (Nuttall, 1930)) and planktic foraminifera (*Acarinina* and *Subbotina*) in the same samples. Despite the preservation, the isotopic analysis showed that the low-trochospiral forms were undoubtedly planktic foraminifera calcifying in the mixed layer. We assign them to the species *Planorotalites capdevilensis* (Cushman & Bermudez, 1949). Their abundance, distribution and stable isotope values suggest that *P. capdevilensis* may have been mixed-layer dwellers without photosymbionts, adapted to slightly more mesotrophic conditions than symbiont-bearing, larger acarininids and morozovelloidids. The oxygen isotope data for benthic and planktic species in the two sections are similar, but the carbon isotopic values of all foraminifera are 1.0–1.5 lower at the Alano section than at Monte Cagnero, probably because the Alano sediments were deposited in the more restricted Belluno Basin, the Monte Cagnero sediments in the more open oceanic setting of the Umbria-Marche Basin.

Keywords: *Planorotalites*; Eocene; stable isotopes; Tethys; MECO

Supplementary material: The full dataset is available at <http://www.geolsoc.org.uk/SUP18868>

Received 24 November 2014; accepted 22 March 2015

Middle Eocene foraminiferal assemblages from the Alano section (Southern Alps, northeastern Italy; Fig. 1) contain common, small, low-trochospiral foraminifera of problematic taxonomic assignment. This morphologically variable, but overall uniform group of low-trochospiral specimens is common in the 63–150 µm size fraction throughout the stratigraphic interval analysed, spanning planktic foraminiferal Zones E11–12 to E13.

The test morphology shares similarities with some benthic foraminiferal genera, specifically species assigned to the genera *Nuttallides*, *Nuttallinella*, *Parrella* and *Cibicidoides*. They are, however, also similar to planktic foraminifera in the genus *Planorotalites*. Detailed morphological investigation through scanning electron microscopy (SEM) was not sufficient to taxonomically assign these specimens to genus and species with confidence, in part because the exact size and shape of the aperture in many specimens cannot be observed. Luciani *et al.* (2010) included the ≥63 µm size fraction in their study of planktic foraminifera at Alano, but *Planorotalites* was not recognized as a planktic taxon due to its state of preservation and resemblance to benthics.

Similar low-trochospiral forms are abundant in coeval samples from the Tethyan Monte Cagnero (M. Cagnero; Fig. 1) section (northeastern Apennines, Central Italy). The specimens from the M. Cagnero section present the same problems in test morphology, i.e. small size and not optimal preservation. In the Trieste–Pazin Basin, to the east of Alano (Fig. 1), similar middle Eocene small low-trochospiral forms were assigned to *Cibicidoides praemundulus* Berggren & Miller, 1986, but do not have a typical *Cibicidoides* aperture, and strongly resemble our forms (Zivkovic & Glumac 2007, pl. 2, figs 3a, b).

It is of primary importance to resolve whether these small forms are benthic or planktic foraminifera. Their occurrence across different geological and palaeogeographical settings suggests that they represent a widespread, but not well-documented component of middle Eocene Tethyan foraminiferal assemblages. In the absence of significant carbonate dissolution, planktic foraminifera outnumber benthics by one to several orders of magnitude in most deep-water settings (e.g. van der Zwaan *et al.* 1990), so that even moderately abundant planktic foraminifera will be highly abundant compared to benthics (see, for example, Smart & Thomas 2006, 2007). Incorrect assignment to either the benthic or the planktic category thus will cause severe bias in palaeoceanographic reconstructions, lead to misinterpretation of biotic data and miss potentially important palaeoecological information. This is especially relevant in sections of major stratigraphic importance.

The Belluno Basin (Alano section) and Umbria–Marche Basin (M. Cagnero section) are classical areas for the study of the Palaeogene in the Tethys (Giusberti *et al.* 2007; Coccioni *et al.* 2012a). The Alano section is a candidate for the Global Stratotype Section and Point (GSSP) for the Bartonian–Priabonian boundary (Agnini *et al.* 2011, 2014). The M. Cagnero section is a candidate for the GSSP for the Rupelian– Chattian boundary (Coccioni *et al.* 2008) and is close to the Massignano section, the GSSP for the Eocene/Oligocene boundary (e.g. Premoli Silva & Jenkins 1993; Coccioni *et al.* 2009). Sections a few kilometres away from the Alano and M. Cagnero outcrops, and thus likely to have a similar microfossil content, have been and continue to be extensively used in studies of Paleocene–Eocene hyperthermals, and in the

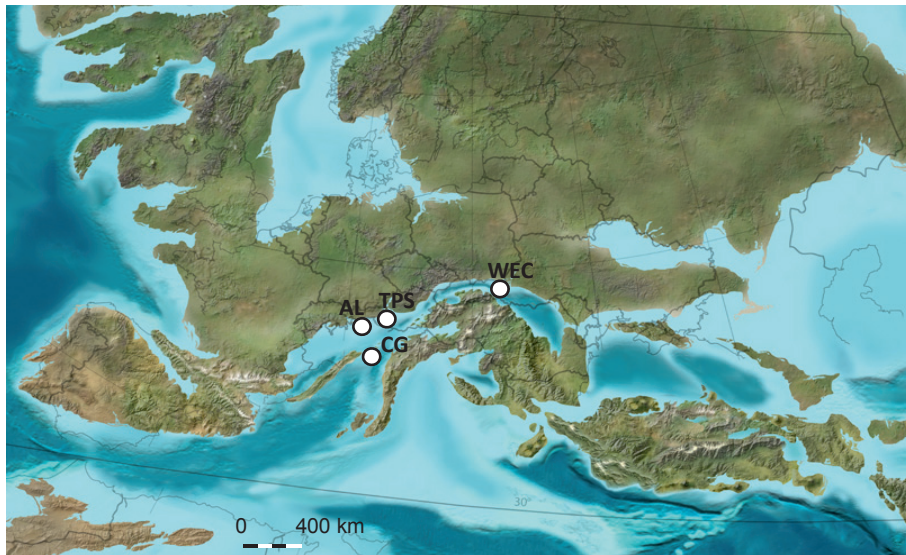


Fig. 1 Eocene palaeogeographical map (modified after Ron Bakley, NAU Geology), showing the approximate location of the Tethyan sections discussed in the text where *Planorotalites capdevilensis* has been reported. (AL) Alano, present paper; (CG) Monte Cagnero, present paper; (TPS) Trieste–Pazin Basin sections (Zivkovic & Glumac 2007); (WEC) sections in the Western Carpathians (Samuel 1972).

refinement of Eocene biostratigraphy (e.g. Contessa Road Section; Forada Section; Galeotti *et al.* 2000, 2005, 2010; Giusberti *et al.* 2007, 2009; Luciani *et al.* 2007; Agnini *et al.* 2009; Coccioni *et al.* 2010, 2012*b*; Coccioni & Bancalà 2012; Luciani & Giusberti 2014; D’Onofrio *et al.* 2014).

In both the M. Cagnero and Alano sections the studied interval includes the Middle Eocene Climatic Optimum (MECO), an important global warming event at about 40 Ma, which interrupted the Eocene cooling trend (Bohaty & Zachos 2003; Bohaty *et al.* 2009; Luciani *et al.* 2010; Boscolo Galazzo *et al.* 2013, 2014, 2015). This time interval was of major importance in the evolution of planktic foraminifera, and the diachronous range of the short-lived, warm-water species *Orbulinoides beckmanni* (Saito, 1962), the zonal marker for Zone E12 (or P13), largely overlaps with the MECO (Edgar *et al.* 2010; Luciani *et al.* 2010). The morozovellidoids and large acarininids, dominant warm-water forms of the middle Eocene, became extinct a few million years later (Wade 2004), after suffering a crisis attributed to loss of photosymbionts during the MECO at least in some locations (Edgar *et al.* 2012).

The distribution pattern of the abundant, small, trochospiral foraminifera across the MECO thus may provide important information on environmental and biotic effects in central-western Tethys of this still poorly understood climatic perturbation.

With this paper, we provide the first documentation and isotopic characterization of these enigmatic low-trochospiral specimens from the Tethys. We used stable isotopic data and the abundance of this group in samples from the Alano and M. Cagnero sections to document that they had a planktic habitat, and to speculate on possible explanations for their fluctuating abundance patterns across the MECO.

Setting, lithology and biostratigraphy

The Alano section (45° 54′ 50″ N–11° 54′ 55″ E; Fig. 1) contains a continuous and expanded middle to upper Eocene succession of grey marls in an outcrop along the Calcino riverbed, close to the village of Alano di Piave (Venetian Prealps, northeastern Italy). The section consists of 120–130 m of monotonous grey marls, with intercalated silty–sandy tuff and biocalcarenic–calciruditic beds (Agnini *et al.* 2011). It spans the upper part of Chron C18r (c. 41.5 Ma) to the base of Chron C16r (c. 36.5 Ma). The marls were deposited at middle bathyal palaeodepth (Agnini *et al.* 2011; Boscolo Galazzo *et al.* 2013) in the Belluno Basin (Fig. 1). An integrated magnetobiostratigraphic study was completed by Agnini *et al.* (2011). Spofforth *et al.* (2010) recognized that the section contains an expanded and continuous record of the MECO,

which was the focus of studies on the response of planktic foraminifera (Luciani *et al.* 2010), calcareous nannoplankton (Toffanin *et al.* 2011) and benthic foraminifera (Boscolo Galazzo *et al.* 2013).

The MECO spans the interval between 13 and 17 m (Spofforth *et al.* 2010). At 17 m, directly above the upper boundary of the MECO interval, an 8 m-thick sapropelic interval interrupts the predominantly marly lithology. This interval has a high total organic carbon (TOC) content (up to 3%; Fig. 3) and has been subdivided into two subunits, ORG1 and ORG2, separated by a 2 m interval with a normal marly lithology (Spofforth *et al.* 2010). This study focuses on the interval from 10 to 32 m above the base of the section, within planktic foraminiferal Zones E10–11, E12 and lower E13 (Berggren & Pearson 2005), corresponding to P12 to lower P14 (Berggren *et al.* 1995).

The M. Cagnero section (43° 38′ 50″ N–12° 28′ 05″ E; Fig. 1) exposes a continuous sedimentary sequence of pelagic sediments on the southeastern flank of the Monte Cagnero, near the town of Urbania, northeastern Apennines (Italy). The section spans the middle Eocene through lower Oligocene, with sediments deposited at a lower bathyal palaeodepth in the Umbria–Marche Basin (Jovane *et al.* 2013; Savian *et al.* 2013, 2014; Fig. 1). The lithology consists of the alternating reddish/greenish-grey calcareous marl and marly limestones from the Scaglia Variiegata and Scaglia Cinerea formations (Jovane *et al.* 2013). We focus on the interval between 61 and 65 m, within foraminiferal Zones E10–11, E12 and lower E13 (Berggren & Pearson 2005) or P12 to lower P14 (Berggren *et al.* 1995; Jovane *et al.* 2013), including the MECO (Savian *et al.* 2013, 2014).

Material and methods

For the Alano section, we used the same samples as Boscolo Galazzo *et al.* (2013). Foraminifera were extracted through 1–2 h disaggregation with 10–30% H₂O₂, followed by washing over ≥63 and ≥450 μm sieves (Boscolo Galazzo *et al.* 2013). When necessary, samples were additionally soaked in a surface-tension-active solution (Desogen). Foraminifera were extracted from the marly-limestone and limestone of the M. Cagnero section using the cold acetolysate technique (Lirer 2000). Residues were sieved through a 63 μm mesh and dried at 50°C. The size fraction ≥63 μm was weighed and split into two equal parts with a precision micro-splitter. The absolute abundance (number of specimens per gram bulk sediment; *n/g*) of the low-trochospiral form was calculated, as well as that of benthic foraminifera, counting all the specimens in the analysed sediment fraction.

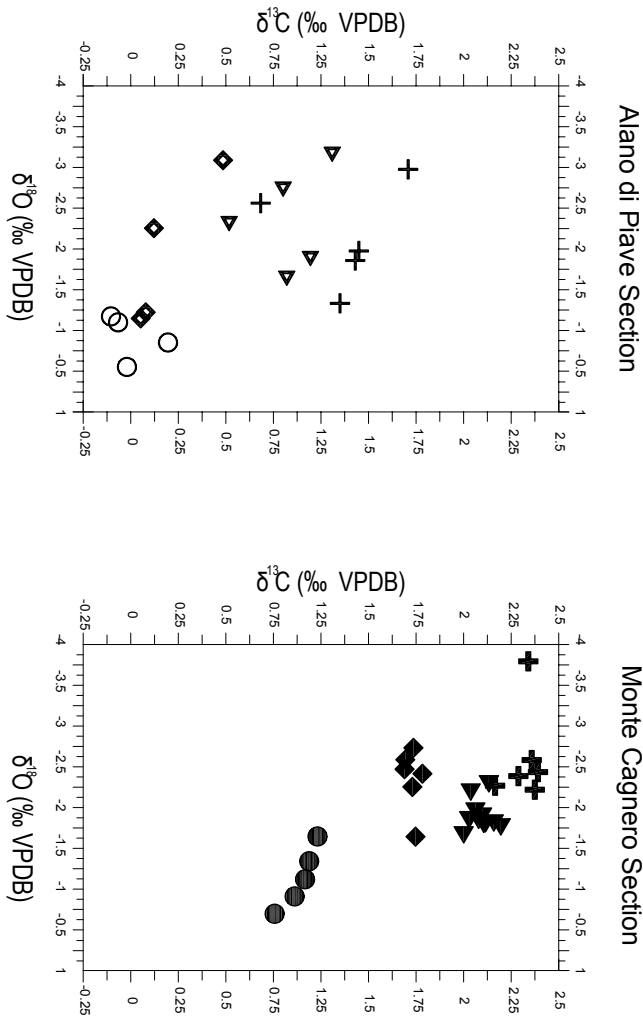


Fig. 2. $\delta^{18}\text{O}$ v. $\delta^{13}\text{C}$ crossplots. Cross denotes *Acarinina topilensis*–*praetopilensis* group; square denotes *Subbotina* spp.; triangle denotes *Planorotalites capdevilensis*; circle denotes *Nuttallides truempyi*. All the values are from specimens analysed for this work.

The number of specimens analysed for stable isotopes varied depending on the size fraction. To account for interspecies isotopic variability, we used more than three specimens per analysis. About 150 low-trochospiral specimens were picked from the 63–150 μm size fraction, in which this small taxon was especially abundant. About 10–20 specimens of *Acarinina* belonging to the *topilensis*–*praetopilensis* group, 4–5 *Subbotina* spp., and 20–25 *Nuttallides truempyi* (Nuttall, 1930) were picked from the 150–450 μm size fraction for both sections. *Nuttallides truempyi* is an epifaunal benthic foraminiferal species (Bralower *et al.* 1995; Thomas 1998; Katz *et al.* 2003) and *Acarinina* species are symbiont-carrying, mixed-layer calcifying planktic foraminifera (e.g. Bralower *et al.* 1995; Pearson *et al.* 2001; Sexton *et al.* 2006a). *Subbotina* is a deeper-dwelling, usually asymbiotic genus, calcifying in the lower part of, or below, the thermocline (Pearson *et al.* 2001; Sexton *et al.* 2006a).

Stable isotope samples were analysed on a Thermo Scientific Delta plus XP coupled with a Gas Bench II at Yale University Earth Systems Center for Stable Isotopic Studies (ESCSIS). External precision of analysis for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was $\pm 0.1\text{‰}$ and $\pm 0.15\text{‰}$, respectively, based on replicate analysis of NBS-19 and NBS-18. Corrected delta values are expressed relative to international standards VPDB (Vienna Pee Dee Belemnite) for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$.

Figured material is housed in the Department of Geosciences, University of Padova.

Results

Stable isotopes

Planktic foraminiferal tests are generally recrystallized on the seafloor, so that their stable oxygen isotopic values become closer to those of benthic foraminifera (Pearson *et al.* 2001; Kozdon *et al.* 2011, 2013). Seafloor diagenetic alteration of bulk carbonate may lower the $\delta^{18}\text{O}$ -derived paleotemperature by *c.* 5°C (Schrag *et al.* 1995). Our low-trochospiral species has overgrowths and infillings, and most specimens have ‘frosty’ tests, suggesting recrystallization (Pls 1 and 2) of and around muricae (Kozdon *et al.* 2011, 2013). Despite recrystallization, we note significant differences between the isotope values of the small trochospiral foraminifera, the planktic genera and the epifaunal benthic species *N. truempyi*. The isotopic ratios of the analysed planktic taxa match the profile obtained by the same genera from pristine carbonates from Tanzania (Pearson *et al.* 2001; Sexton *et al.* 2006b). Our $\delta^{18}\text{O}$ values for *Acarinina* are close to those reported by Sexton *et al.* (2006a) for the NW Atlantic.

The low-trochospiral forms in the $\delta^{18}\text{O}$ – $\delta^{13}\text{C}$ crossplots for the Alano and M. Cagnero sections display a position very close to that occupied by ‘glassy’ specimens of *Planorotalites capdevilensis* from Tanzania (Pearson *et al.* 2001).

The oxygen isotope values of the low-trochospiral forms from both sections cluster with those for the mixed-layer-dwelling planktic foraminiferal genus *Acarinina*, whereas they are considerably lower ($\Delta\delta^{18}\text{O}\approx 0.5$ – 3‰) than values for the benthic species *N. truempyi* (Fig. 2; Tables 1 and 2).

The carbon isotope values, less affected by recrystallization (e.g. Pearson *et al.* 2001; Sexton *et al.* 2006b; Boscolo Galazzo *et al.* 2014), also place the low-trochospiral forms decisively close to the mixed-layer calcifying *Acarinina*, further from deeper calcifying benthic or planktic forms (Fig. 2). The low-trochospiral specimens from both the Alano and M. Cagnero sections have slightly lower values ($\Delta\delta^{13}\text{C}\approx 0.2\text{‰}$) than the mixed-layer symbiont-bearing genus *Acarinina* (Fig. 2; Tables 1 and 2). Carbon isotope values of the low-trochospiral forms are higher ($\Delta\delta^{13}\text{C}\approx 0.8\text{‰}$ Alano specimens; $\Delta\delta^{13}\text{C}\approx 0.4\text{‰}$ M. Cagnero specimens) than those for the deep-dwelling *Subbotina*, and in the M. Cagnero section they are much higher than the values for *N. truempyi* ($\Delta\delta^{13}\text{C}\approx 1\text{‰}$; Fig. 2; Tables 1 and 2).

Stable isotope analyses from both the Alano and M. Cagnero sections unquestionably, and despite recrystallization, indicate a planktic habitat for the small trochospiral forms (Fig. 2; Tables 1 and 2). The plot of $\delta^{18}\text{O}$ versus $\delta^{13}\text{C}$ values for the M. Cagnero section shows better defined and much more separated clusters than that for the Alano section (Fig. 2). There are no significant differences in the $\delta^{18}\text{O}$ values for the genera at the two sections, but the $\delta^{13}\text{C}$ values for all the analysed groups are *c.* 1‰ more negative at Alano than at M. Cagnero (Fig. 2; Tables 1 and 2).

Taxonomic assignment of the problematic low-trochospiral foraminifera

The preservation of the small trochospiral forms is rather poor, and the apertures are not clearly visible (Pl. 2). However, their general test morphology allows us to refer them confidently to the genus *Planorotalites* (Berggren *et al.* 2006). Their tests are small, low-trochospiral, biconvex, circular to subcircular, with lobate outline of the last chambers, and they are variably, but generally weakly keeled. They have six to eight chambers in the last whorl, triangular in shape on the umbilical side, and the chambers increase in size slowly. The umbilicus is shallow and narrow, the walls are normally perforate, muricate and pustulate on the umbilical side. Early chambers on the ventral side are covered with dense pustules, probably at least in part recrystallized and overgrown muricae

Table 1. *Alano di Piave section*

Sample ID	Thickness (m)	<i>Acarinina</i>		<i>Subbotina</i>		<i>Planorotalites</i>		<i>N. truempyi</i>	
		$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
COL1385B	30.7					0.96	-2.76		
COL1265B	29.5	1.32	-1.85	0.08	-1.14	0.92	-1.66	0.00	-0.55
COL865B	25.5	1.63	-2.97	0.55	-3.08	1.19	-3.19	0.24	-0.85
COL865B	25.5								-1.17
COL365B	20.5	0.77	-2.56	0.15	-2.55	0.59	-2.34	-0.08	-1.17
COL40A	10.8	1.34	-1.97	0.11	-1.22	1.06	-1.91	-0.04	-1.10
COL40A	10.8	1.23	-1.33						
Mean	n/a	1.26	-2.14	0.22	-1.92	0.93	-2.37	0.02	-0.97
Std dev.	n/a	0.30	0.64	0.22	0.92	0.22	0.61	0.14	0.26

Table 2. *Monte Cagnero section*

Sample ID	Thickness (m)	<i>Acarinina</i>		<i>Subbotina</i>		<i>Planorotalites</i>		<i>N. truempyi</i>	
		$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
CAG65.40	65.4					2.12	-1.81		
CAG65.40	65.4					2.02	-1.96		
CAG65.40	65.4	2.34	-2.58	1.71	-2.41	2.10	-2.29	1.10	-1.65
CAG63.00	63	2.38	-2.44			2.08	-1.80		
CAG63.00	63	2.36	-2.22	1.65	-2.25			0.86	-0.70
CAG62.55	62.55	2.27	-2.39	1.66	-2.73	1.98	-1.85		
CAG62.55	62.55					2.04	-1.84	0.97	-0.91
CAG62.00	62			1.67	-1.64	1.95	-1.66		
CAG62.00	62	2.32	-3.79	1.61	-2.47	1.99	-2.19	1.03	-1.12
CAG61.00	61	2.13	-2.27	1.61	-2.59	2.06	-1.89	1.06	-1.34
CAG61.00	61					2.16	-1.76		
Mean	n/a	2.30	-2.61	1.65	-2.35	2.04	-1.86	1.00	-1.14
Std dev.	n/a	0.09	0.59	0.04	0.38	0.06	0.15	0.10	0.37

(as in Kozdon *et al.* 2011), and sutures in this part of the test cannot be clearly seen. Sutures between later chambers on the umbilical side are broadly depressed. Sutures on the spiral side are flat to slightly raised and limbate. The aperture is not visible in most specimens due to the poor preservation, but in some specimens it is an umbilical–extraumbilical low-arc, bordered by a thin lip (Pl. 2, fig. 5). These features enable us to identify the genus confidently despite the recrystallization, the lack of a clear view of the aperture and the generally poor preservation (Pl. 1). *Planorotalites* is the only Eocene planktic genus with such general morphology.

It is more difficult to assign our specimens confidently to a species. Berggren *et al.* (2006) provide the most recent taxonomical revision of species in the genus *Planorotalites* Morozova, 1957, and include two Palaeogene species: *P. pseudoscitula* and *P. capdevilensis*. After detailed comparison to figured specimens, and study at the Smithsonian Institution of the type material of *P. capdevilensis* and *Planorotalites renzi*, a junior synonym of *P. capdevilensis* according to Berggren *et al.* (2006), as well as numerous specimens assigned to *P. pseudoscitula* by various authors (e.g. the A. Loeblich collection), we conclude that our specimens most probably can be assigned to the species *Planorotalites capdevilensis* (Cushman & Bermudez, 1949), rather than to *P. pseudoscitula* (Glaessner, 1937). Specimens of these two species (as well as *Planorotalites renzi*), both show considerable morphological variability and differences between them are subtle, as evident from the specimens figured in Berggren *et al.* (2006). These authors state (p. 393) that *Planorotalites capdevilensis* can be distinguished from its ancestor *P. pseudoscitula* by its

flush to slightly raised) suture on spiral side, and flatter, more equally biconvex test.

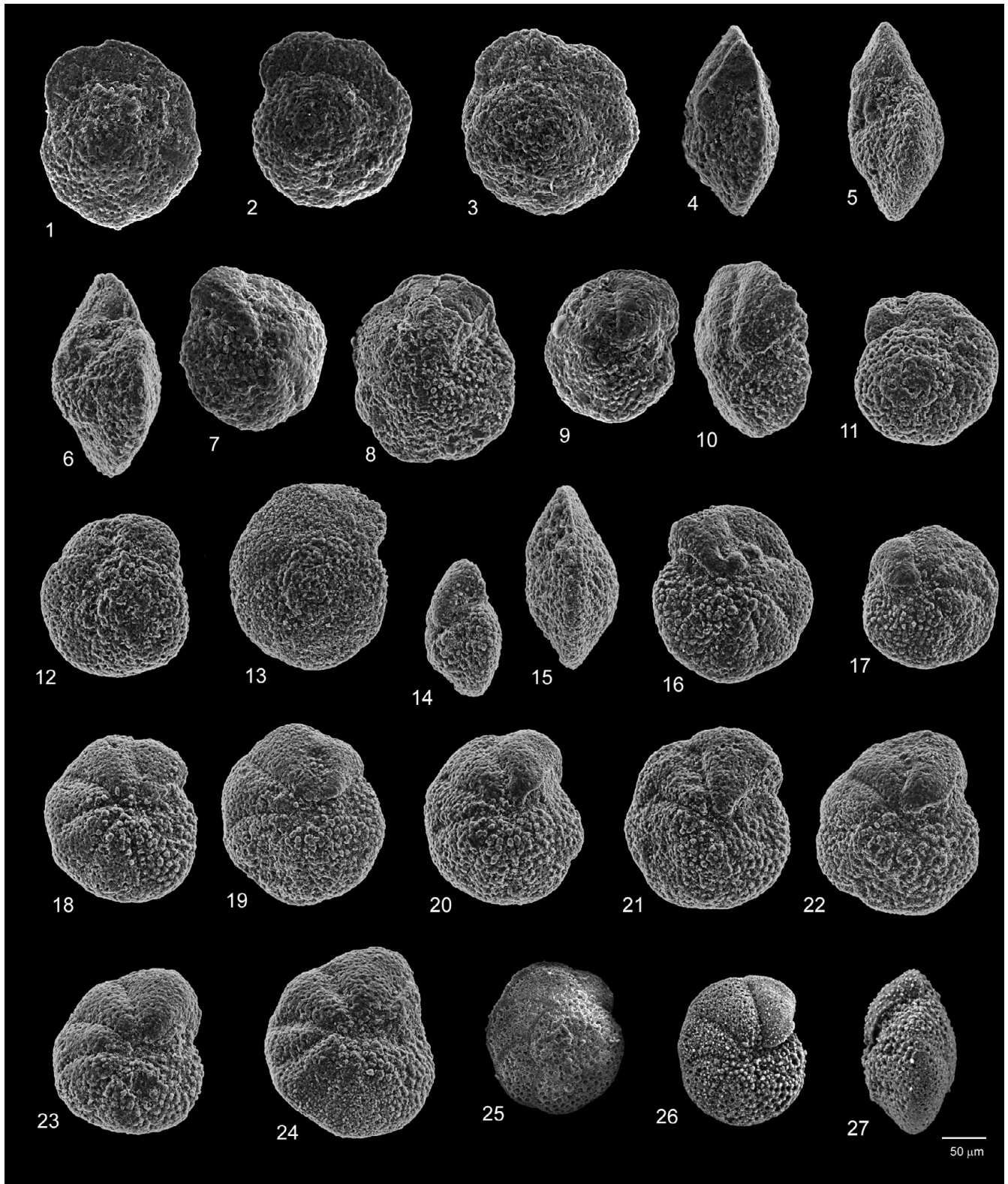
In addition, they state that

P. capdevilensis evolved from *P. pseudoscitula* in the late early Eocene through the development of a flatter, more lenticular and more coarsely muricate test, and the development of flush to slightly raised limbate sutures on the spiral side.

These are subtle differences, and both species show variability exactly in these features used to distinguish between the species, as our specimens do (Pl. 1). Both species can have a subcircular, biconvex, weakly keeled test. Many of our specimens have a subacute to rounded, rather strongly convex profile in cross-section and chambers increase in size slowly, features described as more typical for *P. pseudoscitula* (e.g. specimens in Samuel (1972), Benjamini (1980), Berggren *et al.* (2006, pl. 12.5, figs 1–3, 4–8)) than for *P. capdevilensis*. Many of our specimens are less distinctively lenticular and have a less acute periphery than described as typical for *P. capdevilensis* (e.g. specimens in Cushman & Bermudez (1949), Samuel (1972), Cifelli & Belford (1977), Snyder & Waters (1985)). On the other hand, our specimens are more coarsely pustulate than typical for *P. pseudoscitula* and generally show flush to slightly limbate sutures on the spiral side (Pl. 1, figs 11–13, 25).

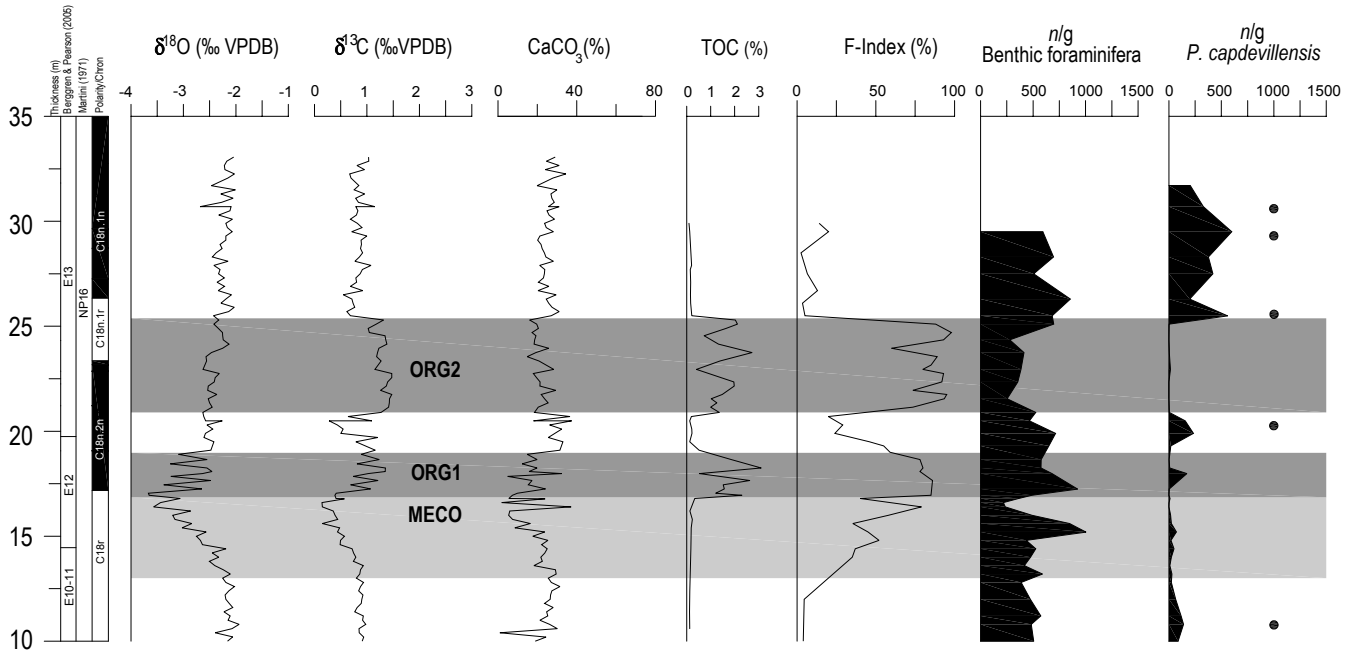
We conclude that there is considerable morphological variability in populations assigned to *P. pseudoscitula* and *P. capdevilensis* (e.g. as seen in specimens in the Smithsonian Institution) and that there is considerable overlap in the morphological range of these two species, although the type specimens show the differences as

stronger pustulation and muricate wall, higher rate of increase in chambers, more distinct and less depressed (essentially



Explanation of Plate 1. *Planorotalites capdevilensis* (Cushman & Bermudez, 1949). **fig. 1.** spiral view, Alano section COL1065B – 27.5 m. **fig. 2.** spiral view, Alano section COL1265B – 29.5 m. **fig. 3.** spiral view, Alano section COL945B – 26.3 m. **figs 4–6.** lateral view, Alano section COL945B – 26.3 m. **fig. 7.** umbilical view, Alano section COL1385 – 30.7 m. **fig. 8.** umbilical view, Alano section COL1265B – 29.5 m. **fig. 9.** umbilical view, Alano section COL945B – 26.3 m. **fig. 10.** lateral view, M. Cagnero section CAG 61.60 – 61.6 m. **fig. 11.** spiral view, M. Cagnero section CAG 61.60 – 61.6 m. **figs 12–13.** spiral view, M. Cagnero section CAG 62 – 62 m. **fig. 14.** lateral view, M. Cagnero section CAG 62.55 – 62.55 m. **fig. 15.** lateral view, M. Cagnero CAG 62 – 62 m. **figs 16–20.** umbilical view, M. Cagnero CAG 61.60 – 61.6 m. **figs 21–24.** umbilical view, M. Cagnero section CAG 62.55 – 62.55 m. **fig. 25.** spiral view, M. Cagnero section CAG 62.55 – 62.55 m. **fig. 26.** umbilical view, M. Cagnero section CAG. 62.55 – 62.55 m. **fig. 27.** lateral view, M. Cagnero 62.55 – 62.55 m.

Alano di Piave section



Monte Cagnero section

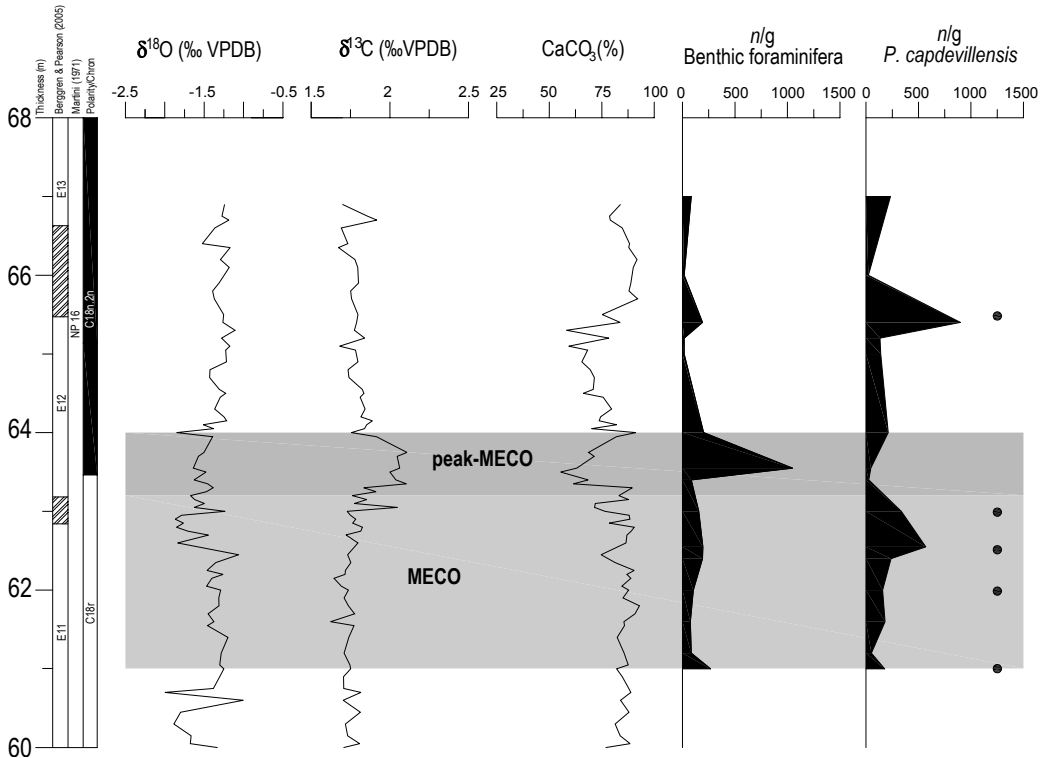


Fig. 3. Total abundance (n/g = number of specimens per gram) of *Planorotalites capdevillensis* and benthic foraminifera across the MECO at Alano and Cagnero sections plotted against bio-magnetostratigraphy. Black dots on the right indicate the stratigraphic position of samples used for stable isotope analysis. Alano section stable isotopes ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$), total organic carbon (TOC%) and $\text{CaCO}_3\%$ records after Spofforth *et al.* (2010), magnetobiostratigraphy after Agnini *et al.* (2011), fragmentation index after Luciani *et al.* (2010), benthic foraminifera n/g after Boscolo Galazzo *et al.* (2013). Cagnero section stable isotope ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$), $\text{CaCO}_3\%$ records, and magnetostratigraphy after Savian *et al.* (2013). MECO interval in the Cagnero section according to Savian *et al.* (2014).

described by Berggren *et al.* (2006) and cited above. Our assemblages contain specimens that appear to share features described as more typical for both species, so that species assignment is not clear. However, our specimens include features that arose only in the descendant species *P. capdevilensis* (i.e. the coarse pustules and flat to raised sutures on the spiral side) and we, therefore, assign them to this species.

Berggren *et al.* (2006) described the stratigraphic range of the species *P. pseudoscutula* as not extending above the uppermost lower Eocene Zone E7 (upper Ypresian), and we assign our specimens to the younger, descendant species. However, at least some of the specimens in our middle Eocene assemblage have features (e.g. weak keel, biconvex test) that have been described as more typical for *P. pseudoscutula* than for *P. capdevilensis*.

Abundance of *Planorotalites capdevilensis* at Alano and M. Cagnero sections

At Alano, *P. capdevilensis* is moderately abundant in the lowermost part of section (mean $n/g=86$; Fig. 3), then progressively decreases in abundance across the MECO interval and is virtually absent within the sapropel-like beds that characterize the post-MECO interval (Spofforth *et al.* 2010; Fig. 3). The highest abundances are reached at the top of the studied interval, above the organic-rich layers (mean $n/g=382$; Fig. 3). This pattern contrasts with that of benthic foraminiferal abundances, which increase across the MECO, and are relatively high in the sapropelic intervals (Boscolo Galazzo *et al.* 2013; Fig. 3).

In the M. Cagnero section, the abundance of *P. capdevilensis* (n/g) fluctuates throughout the studied interval (mean $n/g=208$), slightly increasing across the MECO with a maximum in its later part (Fig. 3). At *c.* 63.5 m *Planorotalites* are very rare, whereas the absolute abundance of benthic foraminifera attains the highest value for the studied interval (Fig. 3). This thin interval coincides with a dissolution level, causing a decrease in percentage of CaCO_3 and more severe loss of planktic foraminifera (including *P. capdevilensis*) than of benthic tests (Fig. 3).

Discussion

The upper water column, where planktic foraminifera live, is characterized by the largest vertical gradients in the oceans in such parameters as temperature, nutrient concentration and density (Talley *et al.* 2011). Temperature and the functioning of the biological carbon pump are reflected in the $^{18}\text{O}/^{16}\text{O}$ and $^{13}\text{C}/^{12}\text{C}$ values of planktic foraminifera calcifying at different levels in the water column, whereas benthic foraminifera record bottom or pore-water properties (e.g. Ravizza & Zachos 2004; Pearson 2012). Stable isotope ratios in planktic and benthic foraminifera are routinely used to reconstruct depth-gradients and the ecology of extinct foraminifera species (e.g. Shackleton 1977; Killingley *et al.* 1981; Berger & Vincent 1986; Wefer & Berger 1991; Pearson *et al.* 1993; Katz *et al.* 2003; Sexton *et al.* 2006a, b, c; John *et al.* 2013, 2014), with highly ^{13}C -enriched tests associated with the presence of photosynthetic symbionts preferentially uptaking ^{12}C (Spero & Williams 1988, 1989). Our carbon isotopic data show clear offsets between the analysed genera, coherent with their known palaeoecology, and reflecting different depth habitats in the water column, in agreement with the oxygen isotope data (Fig. 2).

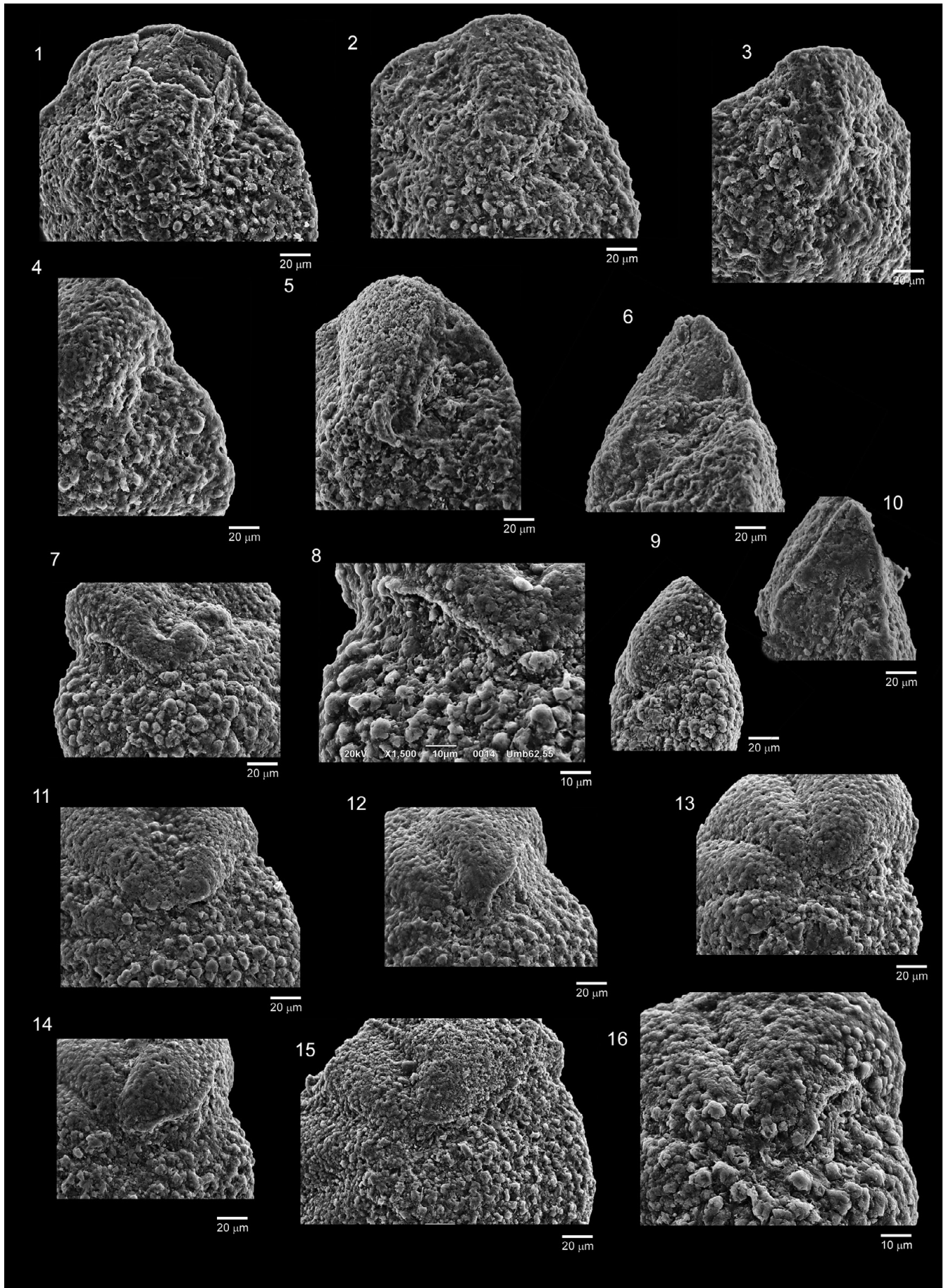
Subbotina carbon isotope values are the lowest among those of the analysed planktic genera, compatible with the thermocline or sub-thermocline habitat generally attributed to this genus (Pearson *et al.* 2006; Sexton *et al.* 2006a, b). *Acarinina* specimens display more positive carbon isotope values, consistent with a shallower habitat, and hosting of symbionts (Pearson *et al.* 2006). The carbon stable isotope values of *P. capdevilensis* are higher than those

of *Subbotina*, and, combined with the low oxygen isotope values, suggest that these forms were mixed-layer dwellers (Fig. 2). Our stable isotope data thus indicate that it was a surface-water species, in agreement with Pearson *et al.* (2001). The lower carbon isotope signature relative to that of *Acarinina* may result from the combined effect of a lack of photosymbionts, the very small size or rapid growth rates (e.g. Killingley *et al.* 1981; Wefer & Berger 1991; Birch *et al.* 2013; John *et al.* 2013). Smaller planktic foraminifera show more kinetic fractionation, because their relatively high metabolic activity causes incorporation of more respired, isotopically light carbon into the test (e.g. Wefer & Berger 1991). Larger planktic foraminifera generally grow more slowly, thus having less kinetic fractionation (Birch *et al.* 2013).

Our oxygen stable isotope data show offsets between the genera, indicating that these differences have not been fully obliterated by diagenesis, with *Acarinina* and *P. capdevilensis* having 0.5 to 3‰ lighter values than the benthic *N. truempyi* (Fig. 2). Benthic foraminiferal oxygen isotope values at the two sites are similar, reflecting an average temperature of *c.* 17.5°C, using the equation of Shackleton (1974) and assuming a global mean $\delta^{18}\text{O}$ for seawater of -1‰ in an ice-free world (Zachos *et al.* 1994; Huber *et al.* 2003). Adjusted for vital effects, the mean of the $\delta^{18}\text{O}$ values of *N. truempyi* gives 18.5°C, using an offset of 0.4‰ (Zachos *et al.* 2001), or 19.5°C following Katz *et al.* (2003). Even this highest estimate is much lower than the surface water temperature of about 24°C, estimated from the average $\delta^{18}\text{O}$ value of surface-dwelling planktic foraminifera (assuming no vital effects; Sexton *et al.* 2006a). This value is probably an underestimate due to at least partial recrystallization on the seafloor.

All analysed groups (benthic foraminifera, deep-dwelling planktic foraminifera and mixed-layer dwelling planktic foraminifera) have a lower carbon-isotope signature at Alano than at M. Cagnero (Fig. 2; Tables 1 and 2). In addition, the M. Cagnero $\delta^{13}\text{C}$ - $\delta^{18}\text{O}$ crossplot shows a better separation of the four groups along the $\delta^{13}\text{C}$ axis than the Alano plot (Fig. 2). The overall lower values and the broad scatter of benthic and planktic $\delta^{13}\text{C}$ values in the Alano section may reflect its location in the rather shallow and marginal Belluno Basin. Generally, carbon isotope values in coastal waters are lower than in the open ocean, due to advection of isotopically lighter organic matter and total dissolved inorganic carbon from river waters (e.g. Thomas *et al.* 2000). Even the $\delta^{13}\text{C}$ values of *Acarinina* from the Tethyan M. Cagnero section, though higher than at Alano, are about 0.5–1‰ lower than those of middle Eocene *Acarinina* from pelagic oceanic areas (e.g. *A. praetopilensis*, *A. topilensis*, *A. rohri*, *A. mcgowrani*, *A. matthewsae*; see Wade 2004; Sexton *et al.* 2006b; John *et al.* 2013; Boscolo Galazzo *et al.* 2014). Lower carbon isotope values in Tethyan specimens are expected, as they record the isotopic signature of Tethys water masses that were probably ^{12}C enriched as an effect of more restricted circulation within the Tethys basins, which were not fully open to the global ocean (Fig. 1).

The reported time range of *P. capdevilensis* spans from the late early Eocene (*c.* 50 Ma) up to *c.* 36 Ma, when it became extinct, i.e. about two million years after the extinction of large acarininids and the genus *Morozovella* (Wade 2004; Pearson *et al.* 2006; Agnini *et al.* 2011). *Planorotalites capdevilensis* has been described as widely distributed in essentially (sub)tropical regions (Caribbean, Tethys) and austral (New Zealand) regions. The species originally named *P. pseudoscutula* by Pearson *et al.* (2001) from hemipelagic sediments in Tanzania was later assigned to *P. capdevilensis* (Pearson *et al.* 2006). *Planorotalites capdevilensis* is rather abundant (up to 40% of planktic foraminifera) in sediments from the mid-latitude SE Atlantic, across the same stratigraphic interval as investigated here (Luciani, unpublished data). Wade (2004) reported *P. capdevilensis* at ODP Site 1052 (mid-latitude NW Atlantic) across the middle to late Eocene.



Within the Tethys, *P. capdevilensis* has been reported from the Western Carpathians (Fig. 1), like its ancestor, *P. pseudoscitula* (in Samuel 1972), which was reported also in the NW Caucasus (Glaessner 1937; Subbotina 1947, 1953) and the southern margin of the Tethys (Hillebrandt 1976; Benjamini 1980).

Planorotalites capdevilensis may have been abundant in the middle Eocene of the Tethyan Trieste–Pazin Basin (Fig. 1), where it probably has been misidentified as the benthic form *C. praemundulus* (in Zivkovic & Glumac 2007). This may explain the unusually high percentages of *Cibicidoides* in some samples recorded by Zivkovic & Glumac (2007), which are in sharp contrast to those in assemblages from similar palaeodepths in the coeval Alano section (Boscolo Galazzo *et al.* 2013) as well as in other Eocene Tethyan sections (Beniamovski *et al.* 2003; Ortiz & Thomas 2006; Alegret *et al.* 2008, 2009; Ortiz *et al.* 2008; Giusberti *et al.* 2009; Stassen *et al.* 2012), where *Cibicidoides* spp. are never >5–10%.

Planorotalites capdevilensis is not reliably reported from high latitudes (Pearson *et al.* 2006).

These distributional data suggest that *P. capdevilensis* (and potentially its ancestral species) occupied a broad latitudinal area, spanning the warm tropical to temperate latitudes of early to middle Eocene oceans, and overlapping with the biogeographical range of other warm-water muriculates. With the progressive increase of the meridional temperature gradient over the middle Eocene, species of the genus *Planorotalites* might have become increasingly constrained to lower latitudes or to semi-enclosed and warmer Tethyan basins.

Planorotalites capdevilensis is quite abundant in both the Tethyan sections investigated. At Alano (0.6–0.8 km palaeodepth), in most samples it is less abundant than at the M. Cagnero section (palaeodepth *c.* 1–2 km), but it is more abundant in the samples above the sapropelic intervals. However, different sedimentation rates at the Alano and M. Cagnero sections do not allow comparisons of absolute abundances of *P. capdevilensis* between the sections (Agnini *et al.* 2011; Jovane *et al.* 2013; Savian *et al.* 2014).

At Alano, *P. capdevilensis* has a very low abundance across the MECO and is absent in the upper organic-rich layers directly post-dating the event (Fig. 3), i.e. during eutrophication of surface waters (Luciani *et al.* 2010; Toffanin *et al.* 2011). Dissolution of *Planorotalites* could have influenced our data, because its lowest abundance occurs in intervals with high values of the fragmentation index (Luciani *et al.* 2010). In the organic-rich layers above the MECO interval, foraminiferal tests show marked signs of dissolution and assemblage preservation deteriorates (Luciani *et al.* 2010; Boscolo Galazzo *et al.* 2013). However, foraminiferal preservation remains uniform throughout the pre-MECO and MECO intervals and is better than in the organic-rich levels, with tests without signs of dissolution (Boscolo Galazzo *et al.* 2013).

At Alano, benthic foraminiferal absolute abundance increases across the MECO (Fig. 3; Boscolo Galazzo *et al.* 2013), so that dilution of tests of *P. capdevilensis* due to increased sedimentation rates appears unlikely. The decrease in abundance of *P. capdevilensis* across the MECO is paralleled by an increase in tiny, opportunistic biserial and triserial planktics, indicative of an eutrophic and low-oxygenated upper water column (Luciani *et al.* 2010). The decrease in abundance of *P. capdevilensis* thus could reflect a

low tolerance for an unstable water column or for changes in oxygenation and salinity, due to enhanced precipitation and run-off during the MECO (Spofforth *et al.* 2010). However, the lower carbon isotope signature at Alano throughout the water column (Fig. 2) might reflect stronger remineralization of organic matter, indicating that *P. capdevilensis* was, to some degree, able to thrive in surface waters which were not strictly oligotrophic.

Planorotalites capdevilensis increased strongly in abundance after the deposition of the uppermost organic-rich layer, when the larger muriculates began to recover after the MECO (Fig. 3). According to the age model, the Alano section records a higher sedimentation rate following the post-MECO interval (Agnini *et al.* 2011). The substantial increase in *P. capdevilensis* after the post-MECO interval thus might be related to a return to normally productive surface waters and a more stable water column. It is also possible that planorotaliids occupied to some extent the ecological niches permanently vacated by the large acariniids, which decreased in abundance during the MECO and never fully recovered (e.g. Luciani *et al.* 2010; Edgar *et al.* 2012).

At the M. Cagnero section, the abundance of *P. capdevilensis* overall increased gradually during the MECO (Fig. 3). Data on planktic foraminiferal assemblages (Luciani, unpublished data) suggest that there was no marked eutrophication during the MECO, in contrast with Alano. Further, planktic foraminiferal $\delta^{13}\text{C}$ values at M. Cagnero indicate stable water-column stratification, thus probably also water-column properties such as oxygen and nutrient concentration, during the MECO. Assuming no changes in sedimentation rates, the increase in abundance of *P. capdevilensis* during the MECO suggests a preference for warmer waters, in agreement with its latitudinal distribution in the Eocene, similar to that of other muriculates. The more distal setting of the M. Cagnero section may have been less affected by hydrological changes during the MECO, favouring stenotopic, non-opportunistic, warm-water taxa, such as *P. capdevilensis*.

In conclusion, *P. capdevilensis* was probably a mixed-layer dweller, preferring warm waters and lacking photosymbionts. It might have been adapted to slightly more mesotrophic conditions than the symbiont-bearing large acariniids and morozovelloidids, but less eutrophic than biserial and triserial planktic species.

Conclusions

Stable isotope data show that the low-trochospiral specimens that are common to abundant in middle Eocene samples from the Alano and M. Cagnero sections (and possibly other Tethyan sections) are planktic foraminifera belonging to the genus *Planorotalites*. The dense pustulation on the umbilical side and flat to raised sutures on the spiral side make an assignment to the species *Planorotalites capdevilensis* most probable, although its biconvex, subacute to rounded profile and slow rate of increase in chamber size are similar to these features in *P. pseudoscitula*. Our oxygen and carbon stable isotope data indicate that the taxon calcified in the mixed layer. Its relatively low carbon isotope signature may indicate the combination of a lack of photosymbionts, its small size and possibly rapid growth rate. The widespread distribution of *Planorotalites capdevilensis* in subtropical to tropical regions during the middle Eocene, together with the differences in its abundance pattern

Explanation of Plate 2. *Planorotalites capdevilensis* (Cushman & Bermudez, 1949). **fig. 1.** umbilical view, detail of the aperture, Alano section COL1265B – 29.5 m. **fig. 2.** umbilical view, detail of the aperture, Alano section COL945B – 26.3 m. **fig. 3.** umbilical view, detail of the aperture, Alano section COL1385 – 30.7 m. **fig. 4.** umbilical view, detail of the aperture, Alano section COL1385 – 30.7 m. **fig. 5.** umbilical view, detail of the aperture, Alano section COL945B – 26.3 m. **fig. 6.** lateral view, detail of the aperture, Alano section, COL945B – 26.3 m. **figs 7–8.** umbilical view, detail of the aperture, M. Cagnero CAG 61.60 – 61.6 m. **fig. 9.** lateral view, detail of the aperture, M. Cagnero section CAG 62.55 – 62.55 m. **fig. 10.** lateral view, detail of the aperture, Alano section COL945B – 26.3 m. **figs 11–12.** umbilical view, detail of the aperture, M. Cagnero section CAG 61.60 – 61.6 m. **figs 13–14.** umbilical view, detail of the aperture, M. Cagnero section CAG 62.55 – 62.55 m. **fig. 15.** umbilical view, detail of the aperture, M. Cagnero section CAG 65.40 – 65.4 m. **fig. 16.** umbilical view, detail of the aperture, M. Cagnero section CAG 62.55 – 62.55 m.

across the MECO at the Alano and M. Cagnero sections, suggest that the species was rather flexible, adapted to slightly more mesotrophic conditions than the symbiont-bearing large acarionids and morozovelloidids, although with a similar preference for warm waters and stable water-column properties.

Acknowledgements and Funding

FBG's stay at Yale was funded by Padova University (Progetto di Ateneo GIUSPRAT10 CPDA108242/10 assigned to LG and ex-60% funding by Eliana Fornaciari) and a grant by the Geological Society of America to ET, who also thanks the Leverhulme Foundation and recognizes funding through NSF Grant OCE-0903014. VL was financially supported by FAR from Ferrara University. We are grateful to Paul Pearson and Mark Leckie for the insightful reviews. Thanks are due to Lorenzo Franceschin for processing samples. SEM images were acquired at the CUGAS (Centro Universitario Grandi Apparecchiature Scientifiche) of Padova University.

Scientific editing by Sigal Abramovich

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