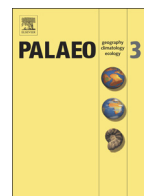




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## Assessing pelagic palaeoenvironments using foraminiferal assemblages – A case study from the late Campanian *Radotruncana calcarata* Zone (Upper Cretaceous, Austrian Alps)

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## ABSTRACT

Two upper Campanian sections in the Austrian Alps representing the north western Tethyan biogeographic realm from either sides of the Penninic Ocean (Alpine Tethys) have been examined aiming at a high-resolution assessment of foraminiferal assemblages: the Postalm section from the Northern Calcareous Alps (southern active margin) and the Oberhehenfeld section from the Ultrahelvetics (northern passive margin). This study focuses on plankton biostratigraphy and foraminiferal palaeoecology of the *Radotruncana calcarata* Total Range Zone.

The Postalm section displays cyclic red deposits with marls and marly limestones, while we find uniform grey marls at Oberhehenfeld. The Oberhehenfeld section from the Ultrahelvetics can be correlated stratigraphically to the Postalm section using foraminifera, calcareous nannoplankton and stable isotope stratigraphy, and provides a point of comparison from the northern margin of the Penninic Ocean.

The two sections show minimal difference in faunal composition and few distinct local stratigraphic signals. Palaeoenvironmental trends from the late Campanian can be recognised relating the two sections from the Austrian Alps. The depositional water depth can be reconstructed as some 500–800 m. Plankton assemblages show a remarkable stability despite the sudden appearance and disappearance of *R. calcarata*, hinting at the late Campanian as a time interval of general foraminiferal stasis without significant evolutionary events. We speculate that the origin and extinction of *R. calcarata* are related to the prolonged evolution of ocean stratification during the Campanian from the mid-Cretaceous sluggish hothouse during a time of general slow greenhouse climate decline.

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## 1. Introduction

The Campanian stage, introduced by Coquand (1857), is the longest stage of the Late Cretaceous with a duration of more than 10 Ma (Ogg and Hinnov, 2012). Climate change is evident during this period displaying a shift from a hot greenhouse climate to more moderate temperatures (e.g., Huber et al., 2002; Hay and Floegel, 2012; Price et al., 2013). This general trend in Late Cretaceous climate history is marked by small-scale short-term palaeoenvironmental and climatic changes (e.g., Jarvis et al., 2002; Hu et al., 2012).

Durations in Earth history and related rates of change have always been a major issue for reconstructing palaeoenvironmental changes and for the understanding of fundamental processes and their application to recent global change issues. The implementation of an

astronomically calibrated time scale (ATS) by Laskar et al. (1993) has, in many cases, shed light on the actual amount of time, especially in the younger part of Earth history. Thus, the ATS offers good solutions for the Cenozoic in general and a precise calibration for the Neogene (Lourens et al., 2004). However, an accurate calibration for the Mesozoic is still largely limited to the 405 kyr orbital eccentricity cycle on a floating ATS (Laskar et al., 2004, 2011; Hinnov and Ogg, 2007). Contributing to the effort of establishing a record for this period, several studies on cyclic intervals from the Late Cretaceous and their astronomical calibration were conducted throughout the last years (Locklair and Sageman, 2008; Hennebert et al., 2009; Husson et al., 2011, 2014; Batenburg et al., 2012, 2014; Thibault et al., 2012; Wagneich et al., 2012; Dinarès-Turell et al., 2013; Sprovieri et al., 2013).

To improve biostratigraphic control, studies on Late Cretaceous foraminiferal stratigraphy provide an invaluable tool. Foraminiferal biozonation within the Campanian stage has been subject to discussion on many occasions. The reliability of certain taxa as zonal markers has been reviewed and reassessed in the last years, for instance

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*Globotruncana ventricosa*. This species is reported to be diachronous in the stratigraphic record and was in the following replaced by *Contusotruncana plummerae* (Petrisso et al., 2011) as an index fossil for the mid-Campanian.

However, the planktonic foraminifer *Radotruncana calcarata* is still considered as a reliable marker at lower latitudes in the Late Cretaceous, and the established *R. calcarata* Total Range Zone (TRZ) can be identified globally (e.g. Robaszynski et al., 1984; Chungkham and Jafar, 1998; Premoli Silva et al., 1998; Puckett and Mancini, 1998; Huber et al., 2008; Wendler et al., 2011). The short time duration of only ca. 800 kyr, as identified by Wagreich et al. (2012: 806 kyr) and Robaszynski and Mzoughi (2010: 790 kyr) based on cyclostratigraphy (other works e.g., Odin, 2002; Hennebert et al., 2009 and Odin, 2010, suggest similar durations for this interval based on various evidence), and its distinct morphology makes this species a most favourable tool in Late Cretaceous biostratigraphy. Huber et al. (2008) indicate a stratigraphic age of 76.18 to 75.71 Ma for the *R. calcarata* TRZ (determined by chronostratigraphic correlations based on magnetostratigraphy) (Anthonissen and Ogg, 2012). In contrast, Gardin et al. (2012) indicated a duration from 75.785 (base) to 74.190 Ma (top) based on bio-magnetostratigraphy from the Gubbio area, Italy. Provisionally, we combined the Anthonissen and Ogg (2012) top age datum with the published cyclostratigraphic duration (Wagreich et al., 2012), ending in a most probable minimum age range from 75.71 to 76.51 Ma.

The development in knowledge on Late Cretaceous benthic foraminiferal communities supports detailed palaeoecological reconstructions. Considering their recent analogues, this group can be used to establish proxies for palaeodepth, palaeoproductivity and environmental factors like oxygenation or salinity (e.g., Sliter and Baker, 1972; Corliss and Chen, 1988; Corliss, 1991; Nagy et al., 1992, 2009; Kaiho, 1994; Speijer, 1994; Hohenegger, 2005).

The study of Wagreich et al. (2012) in the Austrian Alps focused on the astronomically calibrated duration and the fit to a floating timescale, thus, it gave a framework to examine late Campanian foraminiferal communities in stratigraphically well defined sections. During this interval, the ongoing convergence of Eurasia and Africa, tectonically controlled active margin subsidence (Wagreich, 1993) and marine transgression caused fully marine conditions in the study area at the margins of the Penninic Ocean (Alpine-Tethys) within the north western Tethyan biogeographic realm. Cyclic pelagic sequences on the southern active and flysch - type and hemipelagic to pelagic deposits on the northern passive continental margin of the Penninic Ocean are preserved (e.g., Butt, 1981; Wagreich, 1993).

This work focuses on foraminiferal communities present throughout the *R. calcarata* TRZ. By investigation of two outcrops in Austria – each representing opposite margins of the Penninic Ocean – a palaeoenvironmental reconstruction of foraminiferal communities during a cooling greenhouse climate (Hay and Floegel, 2012) on the brink of the late Campanian/early Maastrichtian cooling event (Friedrich et al., 2009; Jung et al., 2013) is possible.

## 2. Geological setting

The Postalm section (POST) (coordinates 13° 23' 11"E; 47° 36' 44" N) is part of the Nierental Formation of the Upper Gosau Subgroup in the Northern Calcareous Alps (Krenmayr, 1996; Wagreich and Krenmayr, 2005; Wagreich et al., 2012).

The geological setting of POST is discussed in Wagreich et al. (2012). The bathyal pelagic to hemipelagic succession comprising Santonian to Maastrichtian deposits displays distinct marly limestone - marl cycles. The marly-limestones can be addressed as reddish foraminiferal packstone. No signs of transport or dissolution of microfossils were noticed.

The Oberhehenfeld section (OBH) (coordinates 13° 38' 09" E; 47° 55' 19" N) is part of the Ultrahelvetetic units of the Austrian Alps. The outcrop is located alongside the Schönbach creek (Hradecka and Lobitzer, 2003).

The Ultrahelvetics are associated with the "Buntmergelserie", an informal lithostratigraphic unit of the Austrian Alps. The Buntmergelserie is characterised by variegated marls and depicts Upper Cretaceous to Eocene deposits (Neuhuber et al., 2007; Egger and Mohamed, 2010, Fig. 1).

Originally, the two localities examined in this work were positioned on the northern and southern margin of the Penninic Ocean at palaeolatitudes of approximately 30°–40° N. Fig. 2 shows the approximate location of Postalm and Oberhehenfeld section on a palaeotectonic reconstruction of the Penninic realm in a broader sense in the Late Cretaceous (Stampfli et al., 2002, see also Schettino and Turco (2011)). Before the polyphase Alpine shortening, these sections were some 400 to 1500 km apart, depending on varying plate tectonic models involving different amounts of shortening and strike-slip movements (see Handy et al. (2010), for a thorough recent review). Both sections show a pelagic to hemipelagic depositional environment well above the CCD.

Units forming the Northern Calcareous Alps (NCA) were deposited along the northern margin of the Austroalpine domain on the Adriatic microplate (Wagreich, 1993), at the southern margin of the Penninic Ocean ("Alpine Tethys" of Stampfli et al., 2002; Handy et al., 2010). The Gosau Group of the NCA can be separated in the Lower and the Upper Gosau Subgroup. The Lower Gosau Subgroup predominantly displays shallow water deposits of Turonian to Santonian age deposited in pull-apart basins alongside an oblique subduction zone (Wagreich, 1993). After a short phase of tectonically induced uplift of the NCA, rapid subsidence processes set in. Hemipelagic to pelagic, and in some areas turbiditic sedimentation of late Santonian/Campanian to Eocene age (Krenmayr, 1999), defines the Upper Gosau Subgroup.

POST is part of the Nierental Formation and reflects a northward deepening slope of at least 500 m water-depth (Wagreich and Krenmayr, 2005). The deposits at this section can be defined as a Cretaceous Oceanic Red Bed (CORB), indicating well oxygenated bottom waters (Hu et al., 2005; Wagreich and Krenmayr, 2005).

OBH is located on the European continental slope, along the northern margin of the Penninic Ocean (Faupl and Wagreich, 2000). The Ultrahelvetetic units have their origin within the Helvetic palaeogeographic realm. In the north, continental shelf deposits can be found. Abyssal palaeo water-depths prevail to the south. The two sections display different sediment accumulation rates; at POST 20 mm/kyr are estimated, while OBH displays only 3 mm/kyr (Neuhuber et al., 2007; Wagreich et al., 2012). Figs. 3 and 4 show sketches of the stratigraphical and lithological framework at POST and OBH.

## 3. Methods and material

### 3.1. Sampling

The exposed *R. calcarata* TRZ was sampled following a biostratigraphic investigation of the two sections yielding Upper Cretaceous deposits (Wagreich et al., 2012; Neuhuber, Wagreich, Gier, Strauss, Hohenegger, Wolfgring and Spötl, submitted for publication). As POST shows distinct cycles, samples were taken bed-by-bed, no standard distance between samples was applied. OBH displays no visible cycles; therefore a standard sample distance of 10 cm was applied.

At POST the *R. calcarata* interval displays a thickness of approximately 16 m – 25 samples from marls were examined. OBH exhibits a 2.4 m thick *R. calcarata* Zone. 34 samples from this interval were processed for qualitative foraminiferal data. Marl and marlstone samples were dissolved with hydrogen peroxide and the tenside Rewoquad®. Samples and microslides are stored in the Earth science collections at the University of Vienna, Department of Geodynamics and Sedimentology.

### 3.2. Qualitative data

Qualitative data (i.e. presence–absence data) were assessed at POST and OBH to unveil local biostratigraphic events and to estimate species richness in these two localities. The use of qualitative data enforces

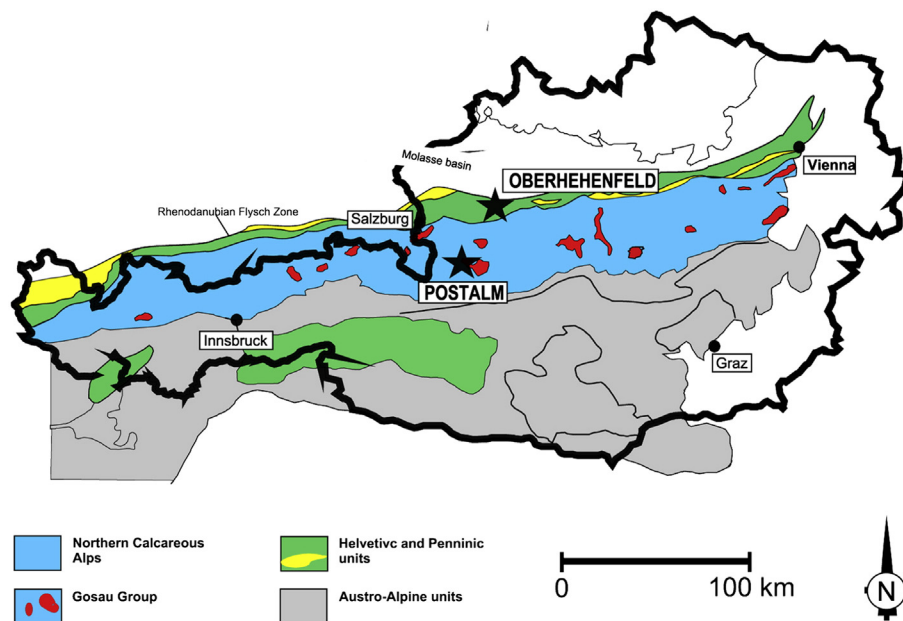


Fig. 1. Geological sketch map of the Austrian Alps including Postalm and Oberhehenfeld sections.

index species in ecological investigations, because index species are rare and often underrepresented in quantitative analyses because overwhelmed by abundant, not indicative species.

Samples were sieved for 63, 150, 300 and 600  $\mu\text{m}$  fractions. 150  $\mu\text{m}$  and 300  $\mu\text{m}$  fractions were investigated for presence or absence of foraminiferal taxa.

### 3.3. Preservation of microfossils

With few exceptions, the state of preservation of foraminifera from POST can be considered as moderate to poor. Most spiral and trochospiral forms (both planktic and benthic) appear with fully intact tests. Elongated forms, especially benthic taxa, frequently appear fragmented. Samples from OBH show an overall slightly better preservation.

### 3.4. Statistical methods

Samples from POST and OBH were clustered hierarchically using Ward's (1963) method requiring Euclidian distances. Furthermore, a Principal Components Analysis (PCA) was applied to help for defining the palaeoenvironmental characteristics of POST and OBH (Davis,

1986; Harper, 1999). Principal components (PC) determined in this analysis are variables accounting for most of the variance in the dataset. A biplot shows the original axes, thus making the interpretation of palaeoenvironmental trends possible (Hammer et al., 2001).

Trends and changes in  $\beta$ -diversity (the diversity between samples, as well as the global  $\beta$ -diversity) of benthic foraminifera along POST and OBH were examined as described in Harrison et al. (1992), with

$$\beta = \frac{\frac{S}{\bar{\alpha}} - 1}{N - 1} \quad (1)$$

$\bar{\alpha}$ : average number of species;  $N$ : the number of samples;  $S$  the total number of species.  $\beta$ -diversity was calculated over all section samples and between succeeding samples for indicating changes in faunal composition. Statistical analyses were conducted using the program packages R (R Development Core Team, 2015) and PAST (Hammer et al., 2001).

### 3.5. Taxonomic remarks

The state of preservation did not allow the definite taxonomic assignment of some individuals at species level. Thus, morphogroups for certain taxa were established. Some double keeled globotruncanid taxa (*Globotruncana arca*, *G. lapparenti*, *G. orientalis*) have subsequently been merged into one group (*G. arca-lapparenti-orientalis*) as morphological transitions were observed and the state of preservation did not always permit an assignment to a species. In general, planktic foraminifera taxonomy follows Robaszynski and Caron (1995), Nederbragt (1991) and Premoli Silva and Verga (2004). Benthic foraminifera were assigned to groups, predominantly following the parameters applied in Alegret et al. (2003) (following the works of Corliss and Chen (1988); Corliss (1991); Nagy (1992)), based on habitat preferences and the mode of benthic life. Information on morphotypes of agglutinated foraminifera also follows Kuhnt and Kaminski (1990), Kaminski and Gradstein (2005), Kaminski et al. (2005) and Nagy et al. (2009). As far as applicable, a classification of benthic foraminifera referring to their oxygenation preference, applying the "Benthic Foraminifera Oxygenation Index" (BFOI) (Kaiho, 1994) and general information on oxygenation preference of taxa provided in Murray (1991, 2006), is conducted. The suprageneric classification follows Loeblich and Tappan (1988).

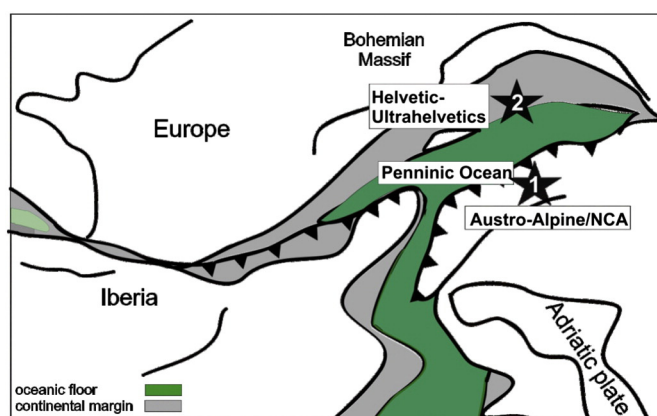
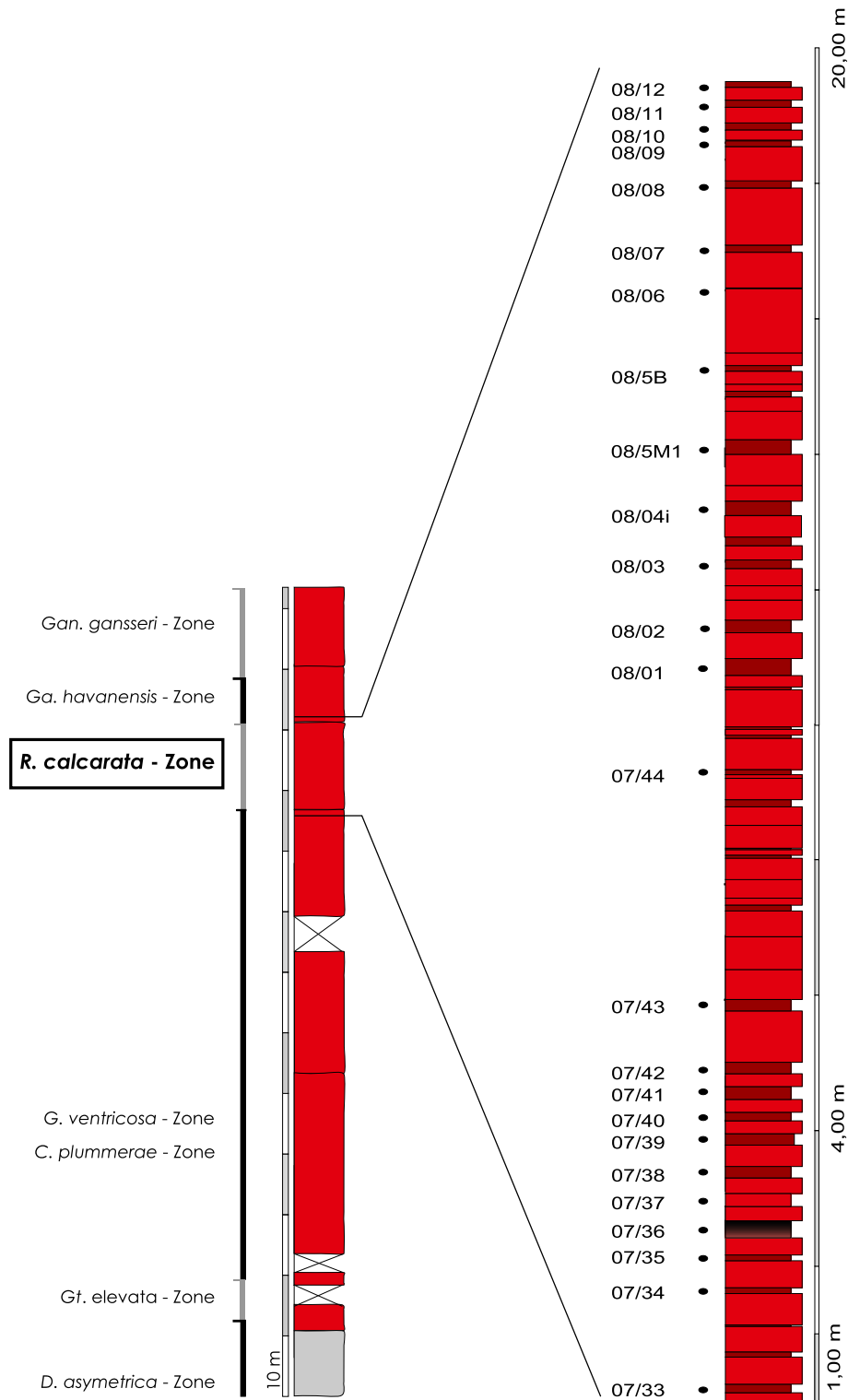


Fig. 2. Palaeogeographic reconstruction of the Penninic realm (after the Santonian Alpine Tethys, Stampfli et al., 2002). The Postalm section (1) is situated on the southern active margin of the Penninic Ocean, Oberhehenfeld (2) on the European continental margin.



**Fig. 3.** This figure displays an overview of Postalm section as well as the *R. calcarata* interval in detail. POST predominantly yields cyclic reddish marly limestone - marl alternations. The section seems to provide a continuous record of the upper Campanian. In this work the *R. calcarata* interval is examined. Black dots indicate samples used for a qualitative assessment of foraminiferal assemblages.

## 4. Results

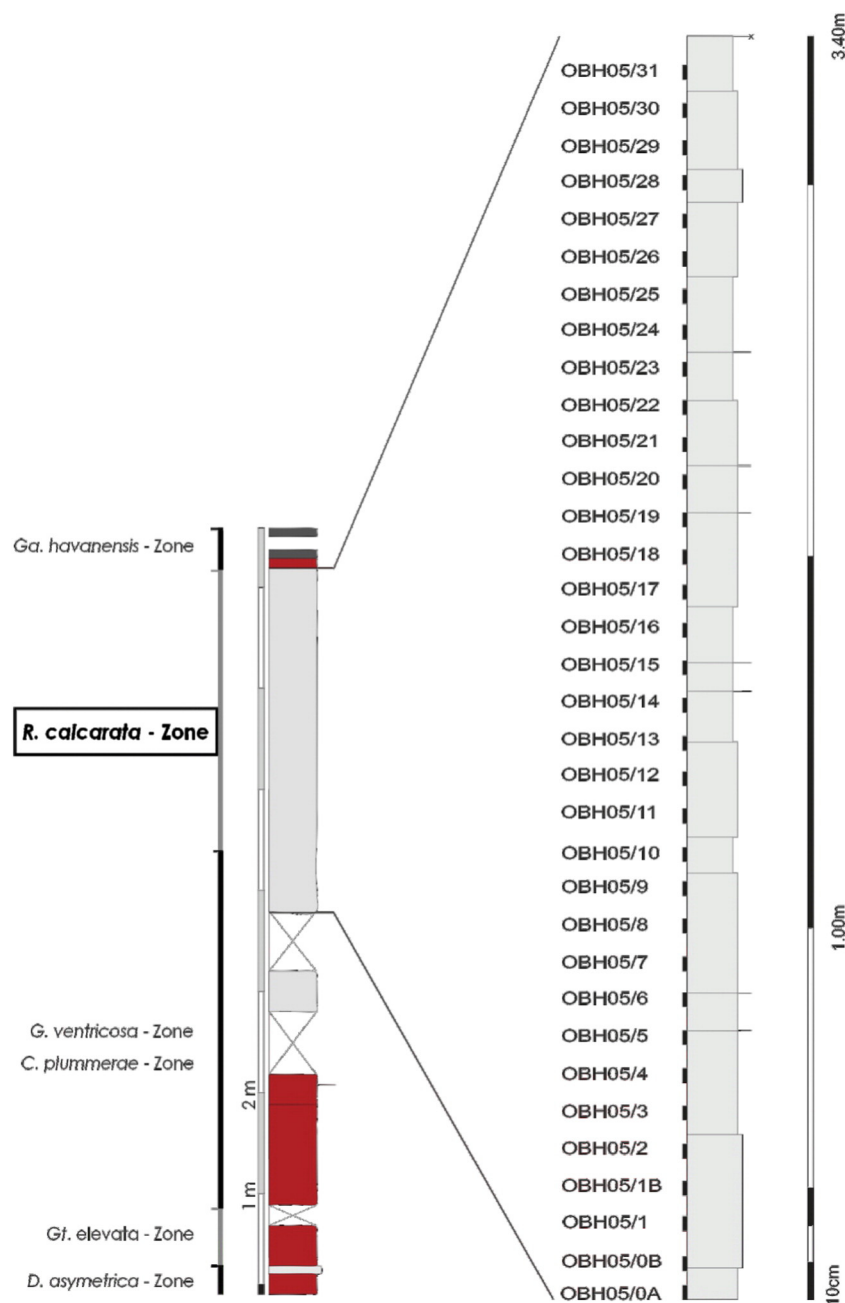
### 4.1. Qualitative data

POST: The investigation of the 150 and 300  $\mu\text{m}$  fraction of 25 samples from marls provided an overall taxonomic richness of 103 foraminiferal taxa at POST. 21 planktic and 82 benthic species could be distinguished.

OBH: 34 samples from OBH displayed 119 species, divided into 29 planktic and 90 benthic species (see Tables 1 and 2). The 150 and 300  $\mu\text{m}$  were examined.

#### 4.1.1. Planktic foraminifera biostratigraphy

Very similar planktic foraminifera communities could be detected at both localities. In both sections, the *R. calcarata* Zone displays an



**Fig. 4.** This figure shows an overview of Oberhehenfeld section and the *R. calcarata* interval in detail. At the base, OBH displays reddish marls. Greyish marls are present towards the top. The *R. calcarata* Zone at OBH is recorded in the greyish marls (note the different scales of Fig. 3 and 4).

occurrence of the nominative taxon in every sample. Globotruncanids are represented by the genera *Radotruncana* El Naggar, 1971, *Globotruncana* Cushman, 1927, *Globotruncanella* Reiss, 1957, *Globotruncanita* Reiss, 1957 and *Contusotruncana*, Korchagin, 1982. OBH yields all of the above, while the genus *Globotruncanella* could not be identified at POST. OBH shows the frequent appearance of *Macroglobigerinelloides bolli* in the stratigraphically older part of the section. *Macroglobigerinelloides* aff. *multispinus* also appears in this section. Species assigning to *M. bolli* and *M. multispinus* could not be identified at POST. Individuals assigning to *Archaeoglobigerina* occur occasionally – *A. cretacea* and *A. blowi* were identified. However, OBH displays a more continuous appearance of archaeoglobigerinids than POST. No members of the genus *Rugoglobigerina* were identified. The most abundant planktic taxa in both sections are the *G. arca-lapparenti-orientalis* group, *G. ventricosa*, *G. linneiana*, *Contusotruncana fornicata* and *C. patelliformis*. All of the above constantly appear throughout both sections. *Globotruncanita*

*subspinosa* was frequently identified in both localities. *Globotruncanella havanensis* can be reported only from a single sample in OBH. Specimens displaying transitional forms between *Contusotruncana fornicata* and *C. plummerae* were frequently found throughout both sections. Furthermore, OBH displays a higher abundance of biserial taxa than POST. Neither of the sections exhibits a high diversity in this group. The most abundant biserial form is *Heterohelix globulosa* in POST and *Pseudotextularia nuttalli* in OBH. *Heterohelix striata* frequently occurs in both sections, *Heterohelix labellosa* is sparsely found (Fig. 5, Fig. 6). SEM images of biostratigraphically relevant taxa are provided in Fig. 7.

#### 4.1.2. Benthic foraminifera

The two sections yield diverse benthic foraminiferal communities. POST and OBH display an almost equal ratio of calcareous and agglutinated benthic foraminiferal species.

**Table 1**  
Presence–absence data of benthic foraminifera taxa recorded at Postalm section.

	POST_07/33	POST_07/34	POST_07/35	POST_07/36	POST_07/37	POST_07/38	POST_07/39	POST_07/40	POST_07/41	POST_07/42	POST_07/43	POST_07/44
<i>Allomorpha cretacea</i>												
<i>Ammodiscus cretaceus</i>												1
<i>Ammosphaeroidina pseudopauciloculata</i>		1				1	1					
<i>Anomalinoidea larseni</i>						1						
<i>Bathysiphon</i> sp.	1					1						
<i>Bolivinoidea clavatus</i>	1			1					1			
<i>Bulimina obtusa</i>		1									1	
<i>Caudamina excelsa</i>								1			1	
tubular agglutinates (cf. <i>Ammobaculites</i> )				1	1	1					1	
<i>Clavulina amorpha</i>		1							1			
<i>Clavulina trilatera</i>			1	1	1	1	1				1	
<i>Conglophragmium irregularis</i>					1							
<i>Conorboidea</i> sp.						1						
<i>Cribrostomoides</i> spp.	1	1		1	1	1	1	1	1	1	1	1
<i>Dentalina annulata</i>	1			1								
<i>Dentalina catemula</i>			1									
<i>Dentalina</i> sp. ( <i>solvata</i> ?)	1											
<i>Dentalina</i> sp.		1		1	1	1			1		1	
<i>Dentalina</i> sp.1 (thick wall)						1						
<i>Dentalina</i> sp.2 (pustules)						1		1				
<i>Dentalina</i> sp.3 (aculeate term. chmb.)												
<i>Dentalina</i> sp.4 (aculeate term. chamber)			1									
<i>Dorothia conula</i>				1				1	1	1	1	
<i>Dorothia pupoides</i>												
<i>Dorothia</i> sp.						1	1					
<i>Eponides beisseli</i>	1	1	1	1		1	1	1	1	1		1
<i>Eponides</i> sp.1												
<i>Gaudryina laevigata</i>												
<i>Gaudryina pyramidata</i>	1	1	1		1			1			1	1
<i>Gaudryina rugosa</i>							1		1			
<i>Gaudryina</i> sp.	1	1		1	1		1					
<i>Gaudryina</i> sp.2	1	1							1			
<i>Globorotalites multiseptus</i>			1	1	1	1		1	1	1	1	
<i>Guttulina communis</i>												
<i>Guttulina</i> sp.		1					1	1			1	
<i>Gyroidinews nitidus</i>					1							1
<i>Gyroidinoides lenticulus</i>												
<i>Hyperammia</i> sp.												1
<i>Lagena apiculata</i>		1	1				1		1		1	1
<i>Lagena emaciata</i>												
<i>Lagena</i> sp.		1				1	1		1		1	

<i>Lenticulina</i> sp.			1	1	1		1			1											
<i>Lenticulina</i> sp.1																					1
<i>Lenticulina subangulata</i>																					
<i>Lenticulina velascoensis</i>	1		1					1													
<i>Lenticulinites rotulata</i>			1		1																
<i>Marginulina</i> sp.	1		1																		
<i>Marssonella oxycona</i>								1													1
<i>Marssonella</i> sp.								1		1											
<i>Marssonella trochus</i>																					
<i>Nodogeneria pseudoscripta</i>																					1
<i>Nodosaria paupercula</i>																					1
<i>Nodosaria</i> sp.			1																		1
<i>Nothia excelsa</i>																					1
<i>Osangularia cordieriana</i>																					
<i>Osangularia</i> sp.																					
<i>Paratrochamminoides deflexiformis</i>																					
<i>Placentammina placenta</i>			1																		1
<i>Pleurostomella</i> sp.	1		1							1											
<i>Pleurostomella wadow</i>										1											
<i>Praebulimina</i> sp.	1																				1
<i>Pullenia</i> sp.																					1
<i>Ramulina</i> sp.																					1
<i>Ramulina wrightyi</i>																					1
<i>Reussella</i> sp. 1			1		1					1				1							1
<i>Reussella szajnochae</i>			1		1					1				1							1
<i>Spiroplectammina praelonga</i>	1																				
<i>Spiroplectinella dentata</i>			1		1					1				1							1
<i>Spiroplectinella</i> sp.1														1							1
<i>Stensioina pommerana</i>			1		1									1							
<i>Stilostomella alexanderi</i>																					1
<i>Stilostomella</i> sp.																					1
<i>Textularia</i> sp.	1																				1
<i>Thalmannammina</i> sp.																					
<i>Tritaxia</i> sp.1 (tripleura ?)			1																		1
<i>Tritaxia</i> sp.																					
<i>Tritaxia eggeri</i>																					1
<i>Trochammina boehmi</i>																					
<i>Trochammina</i> sp.																					1
<i>Trochamminoides proteus</i>																					1
<i>Verneulina muensteri</i>																					
<i>Verneulina</i> sp.			1																		1

Table 1 (continued)

	POST_08/01	POST_08/02	POST_08/03	POST_08/04	POST_08/05b	POST_08/05a	POST_08/06	POST_08/07	POST_08/08	POST_08/09	POST_08/10	POST_08/11	POST_08/12
<i>Allomorpha cretacea</i>								1					
<i>Ammodiscus cretaceus</i>								1					
<i>Ammosphaeroidina pseudopauciloculata</i>	1			1									
<i>Anomalinoidea larseni</i>								1					
<i>Bathysiphon</i> sp.								1		1			
<i>Bolivinoidea clavatus</i>													
<i>Bulimina obtusa</i>							1		1		1		
<i>Caudamina excelsa</i>			1				1					1	
tubular agglutinates (cf. <i>Ammobaculites</i> )												1	
<i>Clavulina amorpha</i>	1			1		1			1				
<i>Clavulina trilatera</i>													
<i>Conglophragmium irregularis</i>													
<i>Conorboidea</i> sp.					1				1				
<i>Cribrostomoides</i> spp.	1	1		1	1	1				1	1		
<i>Dentalina annulata</i>									1				
<i>Dentalina catemula</i>			1			1		1				1	
<i>Dentalina</i> sp. ( <i>solvata</i> ?)													
<i>Dentalina</i> sp.		1					1		1				
<i>Dentalina</i> sp.1 (thick wall)				1									
<i>Dentalina</i> sp.2 (pustules)			1										
<i>Dentalina</i> sp.3 (aculeate term. chmb.)				1									
<i>Dentalina</i> sp.4 (aculeate term. chamber)													
<i>Dorothia conula</i>		1							1		1	1	
<i>Dorothia pupoides</i>	1								1				
<i>Dorothia</i> sp.	1												
<i>Eponides beisseli</i>	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Eponides</i> sp.1												1	
<i>Gaudryina laevigata</i>	1									1			1
<i>Gaudryina pyramidata</i>	1	1	1	1	1		1	1	1				
<i>Gaudryina rugosa</i>							1	1					
<i>Gaudryina</i> sp.		1		1		1	1				1		
<i>Gaudryina</i> sp.2							1	1	1				
<i>Globorotalites multiseptus</i>												1	1
<i>Guttulina communis</i>									1				
<i>Guttulina</i> sp.			1						1				
<i>Gyrodinews nitidus</i>					1		1	1			1		
<i>Gyroidinoides lenticulus</i>					1		1						
<i>Hyperammia</i> sp.				1				1					1
<i>Lagena apiculata</i>											1		
<i>Lagena emaciata</i>										1			
<i>Lagena</i> sp.									1	1		1	



<i>Lenticulina</i> sp.											1							
<i>Lenticulina</i> sp.1											1							
<i>Lenticulina subangulata</i>										1		1						1
<i>Lenticulina velascoensis</i>																		
<i>Lenticulinites rotulata</i>	1				1													
<i>Marginullina</i> sp.	1											1	1					
<i>Marssonella oxycona</i>																		
<i>Marssonella</i> sp.													1					
<i>Marssonella trochus</i>												1						
<i>Nodogeneria pseudoscripta</i>																		1
<i>Nodosaria paupereule</i>																		
<i>Nodosaria</i> sp.	1																	
<i>Nothia excelsa</i>													1					
<i>Osangularia cordieriana</i>													1	1				1
<i>Osangularia</i> sp.																		1
<i>Paratrochamminoides deflexiformis</i>	1												1					
<i>Placentamina placenta</i>																		
<i>Pleurostomella</i> sp.	1																	1
<i>Pleurostomella wadow</i>	1												1	1				
<i>Praebulimina</i> sp.																		
<i>Pullenia</i> sp.																		
<i>Ramulina</i> sp.																		
<i>Ramulina wrightyi</i>																		
<i>Reussella</i> sp. 1	1																	1
<i>Reussella szajnochae</i>	1																	
<i>Spiroplectamina praelonga</i>																		
<i>Spiroplectinella dentata</i>	1																	1
<i>Spiroplectinella</i> sp.1																		
<i>Stensioina pommerana</i>	1																	
<i>Stilostomella alexanderi</i>																		
<i>Stilostomella</i> sp.																		1
<i>Textularia</i> sp.																		
<i>Thalmannammina</i> sp.																		
<i>Tritaxia</i> sp.1 ( <i>tripleura</i> ?)	1																	1
<i>Tritaxia</i> sp.																		
<i>Tritaxia eggeri</i>																		
<i>Trochammina boehmi</i>																		
<i>Trochammina</i> sp.																		
<i>Trochamminoides proteus</i>																		
<i>Verneulina muensteri</i>																		
<i>Verneulina</i> sp.																		1

**Table 2**  
Presence–absence data of benthic foraminifera taxa recorded at Oberhehenfeld section.

	OBH_0b	OBH_1	OBH_1b	OBH_2	OBH_3	OBH_4	OBH_5	OBH_05/0A	OBH_6	OBH_7	OBH_8	OBH_9	OBH_10	OBH_11	OBH_12	OBH_13
<i>Allomorpha cretacea</i>									1					1		
<i>Ammobaculites agglutinans</i>									1							
<i>Ammodiscus cretaceus</i>				1						1			1			
<i>Ammodiscus</i> sp.																
<i>Ammosphaeroidina pseudopauciloculata</i>														1		
<i>Anomalinoidea larseni</i>						1				1		1				
<i>Astacolus</i> sp.																
<i>Bathysiphon</i> sp.									1		1					
<i>Caudamina excelsa</i>																
tubular agglutinates (cf <i>Ammobaculites</i> )					1		1		1							
<i>Cibicidoides pseudoacutus</i>									1							
<i>Cibicidoides voltzianus</i>									1							
<i>Clavulina trilatera</i>			1	1	1					1						
<i>Conorboides</i> sp.													1			
<i>Cribrostomoides</i> spp.													1	1		
<i>Dentalina annulata</i>		1				1	1							1		
<i>Dentalina catenula</i>																
<i>Dentalina filiformis</i>						1										
<i>Dentalina oligostegia</i>													1			
<i>Dentalina</i> sp. (solvata?)																
<i>Dentalina</i> sp.											1			1		1
<i>Dentalina</i> sp.1 (thick wall)																
<i>Dentalina</i> sp.3 (aculeate term. chmb.)																
<i>Dorothia conula</i>								1		1		1		1		
<i>Dorothia pupoides</i>																
<i>Dorothia</i> sp.																
<i>Ellipsodimorphia hrubieszowiensis</i>		1									1					
<i>Entosolenia</i> / <i>Fissurina orbignyana</i>		1	1													
<i>Eponides beisseli</i>		1		1		1		1				1	1	1	1	1
<i>Eponides</i> sp.1																
<i>Fronicularia canaliculata</i>							1									
<i>Gaudryina laevigata</i>		1		1					1					1		1
<i>Gaudryina pyramidata</i>	1	1	1	1		1	1	1	1	1	1	1	1	1	1	
<i>Gaudryina rugosa</i>		1						1		1		1				
<i>Gaudryina</i> sp.																1
<i>Gavellinopsis involuta</i>					1											
<i>Glandulina pygmaea</i>											1					
<i>Globorotalites multiseptus</i>						1		1						1		1
<i>Guttulina communis</i>															1	
<i>Guttulina</i> sp.	1									1						
<i>Guttulina trigonula</i>		1														
<i>Gyroidinews nitidus</i>				1							1		1			
<i>Gyroidinoides bandyi</i>																
<i>Gyroidinoides girarianus</i>												1				

<i>Gyroidinoides lenticulus</i>		1					1		1				
<i>Gyroidinoides sp.</i>													
<i>Gyroidinoides umbilicatus</i>													
<i>Hyperammina sp.</i>			1										1
<i>Laevidentalina sp.</i>			1										
<i>Lagena apiculata</i>						1							
<i>Lagena laevis</i>													
<i>Lenticulina (Robulus) subalatus</i>							1						
<i>Lenticulina sp.</i>					1								
<i>Lenticulina subangulata</i>								1					1
<i>Lenticulina trachyomphalus</i>													
<i>Lenticulinites rotulatus</i>									1				
<i>Marginulina sp.2</i>													
<i>Marginullina sp.</i>											1		
<i>Marssonella oxycona</i>		1	1							1		1	1
<i>Marssonella sp.</i>								1					
<i>Marssonella trochus</i>					1					1		1	
<i>Neoflabellina sp.</i>	1												
<i>Nodosaria aspera</i>										1			
<i>Nodosaria limbata</i>								1					
<i>Nodosaria monile</i>												1	
<i>Nodosaria paupercula</i>						1	1						
<i>Nodosaria sp.</i>													
<i>Nothia excelsa</i>	1												
<i>Nothia? sp. 1</i>	1	1						1	1	1	1	1	1
<i>Osangularia cordieriana</i>				1	1						1	1	
<i>Paratrochamminoides deflexiformis</i>													
<i>Placentammina placenta</i>							1			1	1		
<i>Pleurostomella sp.</i>				1									
<i>Pleurostomella spinosa</i>												1	
<i>Pleurostomella wadow</i>												1	
<i>Ramulina sp.</i>	1	1	1		1		1	1				1	
<i>Ramulina wrightyi</i>													
<i>Reophax globosus</i>									1				
<i>Reussella sp. 1</i>	1	1	1		1	1							
<i>Reussella szajnochae</i>		1	1	1	1	1		1	1		1	1	1
<i>Rzehakina lata</i>													
<i>Saracenaria triangularis</i>													
<i>Spiroplectammina praelonga</i>							1						
<i>Spiroplectinella dentata</i>		1										1	
<i>Spiroplectinella sp.1</i>													
<i>Subreophax sp.</i>					1								
<i>Tritaxia sp.1 (tripleura ?)</i>		1	1	1		1			1				1
<i>Tritaxia sp.</i>										1			
<i>Tritaxia eggeri</i>			1								1		1
<i>Trochammina sp.1</i>													
<i>Verneulina sp.</i>													

	OBH_14	OBH_15	OBH_16	OBH_17	OBH_18	OBH_19	OBH_20	OBH_21	OBH_22	OBH_23	OBH_24	OBH_25	OBH_26	OBH_27	OBH_28	OBH_29	OBH_30	OBH_31
<i>Allomorpha cretacea</i>							1		1	1								
<i>Ammobaculites agglutinans</i>								1										
<i>Ammodiscus cretaceus</i>			1	1				1			1	1	1				1	
<i>Ammodiscus</i> sp.																	1	
<i>Ammosphaeroidina pseudopauciloculata</i>											1							
<i>Anomalinoidea larseni</i>																	1	
<i>Astacolus</i> sp.							1					1						
<i>Bathysiphon</i> sp.																		
<i>Caudammina excelsa</i>				1		1									1		1	
tubular agglutinates (cf <i>Ammobaculites</i> )									1									
<i>Cibicidoides pseudoacutus</i>				1							1		1					
<i>Cibicidoides voltzianus</i>													1					
<i>Clavulina trilatera</i>																		
<i>Conorboides</i> sp.	1																	
<i>Cribrostomoides</i> spp.											1	1	1	1			1	
<i>Dentalina annulata</i>																	1	
<i>Dentalina catenula</i>											1			1			1	
<i>Dentalina filiformis</i>							1											
<i>Dentalina oligostegia</i>																		1
<i>Dentalina</i> sp. (solvata?)																		
<i>Dentalina</i> sp.													1					
<i>Dentalina</i> sp.1 (thick wall)												1						
<i>Dentalina</i> sp.3 (aculeate term. chmb.)							1											
<i>Dorothyia conula</i>						1	1		1	1	1	1	1	1	1			1
<i>Dorothyia pupoides</i>																	1	
<i>Dorothyia</i> sp.						1												
<i>Ellipsodimorphia hrubieszowiensis</i>																		
<i>Entosolenia/ Fissurina orbignyana</i>																		
<i>Eponides beisseli</i>	1			1		1	1	1		1	1			1	1	1	1	
<i>Eponides</i> sp.1																		1
<i>Fronicularia canaliculata</i>																		
<i>Gaudryina laevigata</i>						1										1		
<i>Gaudryina pyramidata</i>		1		1		1	1		1				1			1	1	
<i>Gaudryina rugosa</i>																	1	1
<i>Gaudryina</i> sp.					1	1									1			1
<i>Gavellinopsis involuta</i>																		
<i>Glandulina pygmaea</i>																		
<i>Globorotalites multiseptus</i>				1			1	1					1					
<i>Guttulina communis</i>																		
<i>Guttulina</i> sp.																		
<i>Guttulina trigonula</i>																		
<i>Gyroidinews nitidus</i>	1			1						1			1	1	1	1	1	
<i>Gyroidinoides bandyi</i>				1														
<i>Gyroidinoides girarianus</i>													1					

<i>Gyroidinoides lenticulus</i>		1							1		1							
<i>Gyroidinoides</i> sp.													1					1
<i>Gyroidinoides umbilicatus</i>																		1
<i>Hyperammina</i> sp.	1										1		1					1
<i>Laevidentalina</i> sp.																		1
<i>Lagena apiculata</i>																		
<i>Lagena laevis</i>																		1
<i>Lenticulina (Robulus) subalatus</i>	1										1							
<i>Lenticulina</i> sp.			1															1
<i>Lenticulina subangulata</i>		1																1
<i>Lenticulina trachyomphalus</i>																		1
<i>Lenticulinites rotulatus</i>																		1
<i>Marginulina</i> sp.2																		1
<i>Marginulina</i> sp.																		1
<i>Marssonella oxycona</i>			1															1
<i>Marssonella</i> sp.																		1
<i>Marssonella trochus</i>																		1
<i>Neoflabellina</i> sp.																		1
<i>Nodosaria aspera</i>																		1
<i>Nodosaria limbata</i>																		1
<i>Nodosaria monile</i>																		1
<i>Nodosaria paupereule</i>																		1
<i>Nodosaria</i> sp.																		1
<i>Nothia excelsa</i>																		1
<i>Nothia?</i> sp. 1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Osangularia cordieriana</i>				1	1													1
<i>Paratrochamminoides deflexiformis</i>																		1
<i>Placentammina placenta</i>																		1
<i>Pleurostomella</i> sp.																		1
<i>Pleurostomella spinosa</i>																		1
<i>Pleurostomella wadow</i>																		1
<i>Ramulina</i> sp.																		1
<i>Ramulina wrightyi</i>																		1
<i>Reophax globosus</i>																		1
<i>Reussella</i> sp. 1																		1
<i>Reussella szajnochae</i>		1																1
<i>Rzehakina lata</i>																		1
<i>Saracenaria triangularis</i>																		1
<i>Spiroplectammina praelonga</i>																		1
<i>Spiroplectinella dentata</i>																		1
<i>Spiroplectinella</i> sp.1																		1
<i>Subreophax</i> sp.																		1
<i>Tritaxia</i> sp.1 (tripleura ?)	1																	1
<i>Tritaxia</i> sp.																		1
<i>Tritaxia eggeri</i>	1																	1
<i>Trochammina</i> sp.1																		1
<i>Vermeulina</i> sp.																		1

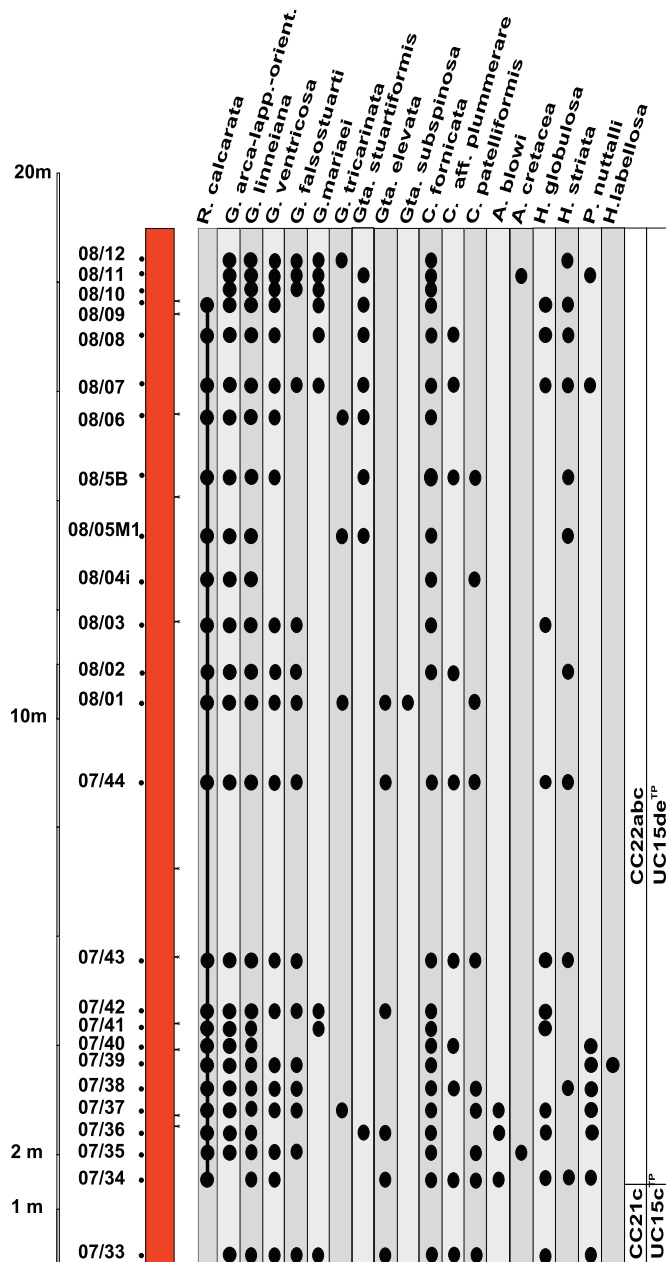


Fig. 5. Distribution of planktic foraminiferal taxa at POST, including nannofossil zonation from Wagreich et al. (2012).

4.1.2.1. Section POST. 45 calcareous benthic species assigning to 21 genera were identified. 37 species within 17 genera of agglutinated foraminifera are present. The mean taxonomic richness in benthic foraminifera is 15 taxa per sample. Some taxa are present throughout the *R. calcarata* Zone: *Eponides* spp. are frequent and show high taxonomic richness in POST. *Eponides beisseli* is present in 21 of 26 samples, other species assigning to the genus *Eponides* appear in 11 samples. *Spiroplectinella dentata*, *Reussella* sp.1 and *Gaudryina pyramidata* appear in 15, *Cribrostomoides cretaceus* and *Reussella szajnochae* in 14 samples.

The highest species richness can be reported within the genus *Dentalina* with 7 species and the genus *Lenticulina* with 5 species (Table 1).

4.1.2.2. OBH. OBH displays 53 calcareous benthic species within 23 genera and 34 agglutinated benthic species belonging to 19 genera,

documenting a mean benthic foraminiferal taxonomic richness of 11 species per sample. The most frequent taxon in this section is *Reussella szajnochae* appearing in 22 of the 35 samples. *Ramulina* sp., *Tritaxia eggeri*, *Marssonella oxycona*, *Gyroidinoides nitidus* and *Ammodiscus cretaceus* are present in 10 to 13 samples. Furthermore, high occurrence of *Trochammina* spp., *Dentalina* spp. and *Eponides* spp. was identified throughout the section. *Dentalina* spp. also shows the highest taxonomic diversity with 9 species (Table 2).

4.1.3. Benthic foraminifera morphogroups and habitat preference

Benthic foraminiferal taxa were assigned to their preferred mode of life and clustered in groups in respect of their habitat preference (Table 3). Epifaunal calcareous or agglutinated taxa, infaunal calcareous or agglutinated taxa and calcareous or agglutinated taxa that do not depict a clear preference between in- or epifaunal habitats can be distinguished.

Counting species richness in reference to the preferred mode of life (habitat preference) can give information on the palaeoecological regime. Table 4 shows the absolute numbers of species per category. Fig. 8 shows the relative distribution of foraminiferal species by habitat preference.

Species counts by habitat preference reveal only minor changes at POST, while at OBH the alterations between succeeding samples are strong. In 19 out of 25 samples agglutinated species represent the majority in benthic foraminiferal taxa.

Epifaunal agglutinated taxa are sparse at POST, species showing a preference for infaunal habitats prevail. OBH seems to show a less stable palaeoenvironment. The distribution of taxa in respect to their preferred mode of life hints to a cyclic pattern.

4.1.4. Overlaps between POST and OBH

Hierarchical clustering clearly separates both localities (Fig. 9). Seven clusters can be distinguished. Samples from OBH can predominantly be found in clusters a, b and d. Cluster c is defined by the single sample OBH 26. Because 24 taxa were identified therein, OBH 26 depicts a unique association of taxa quite different from other samples. Clusters e, f and g predominantly include samples from POST.

Based on the combined Q- and R-mode cluster analyses, indicator species responsible for the formation of the eight clusters could be determined (Table 5). Cluster a is characterised by the dominance of *Nothia* ? sp.1, together with *Dorothyia conula* and *Reussella szajnochae*, while in Cluster b *Nothia* ? sp.1 is less dominant similar to *Tritaxia eggeri*. *Gaudryina pyramidata* characterises Cluster d in combination with the less frequent *Eponides beisseli*, while both species in combination with *Reussella* sp. determine Cluster c. The remaining clusters f and g are quite different in their composition to the former clusters, inducing the strong separation in cluster analysis (Fig. 9). *Spiroplectinella dentata* dominates in Cluster f in combination with *Globorotalites multiseptus*, *Lenticulina* spp. and *Cribrostomoides* spp. The latter species together with *Marginulina* sp. are prominent elements of Cluster g, that is dominated by *Eponides beisseli* and *Gaudryina pyramidata*.

5. Discussion

5.1. Biostratigraphy and palaeoenvironment – implications from qualitative data

5.1.1. Planktic foraminifera biostratigraphy

In both sections, the studied interval starts in the uppermost part of the *G. ventricosa* partial range zone (Robaszynski and Caron, 1995). This zone was first introduced by Dalbiez (1955) and is defined by the interval between the FO of *G. ventricosa* and the FO of *R. calcarata*. Petrizzo et al. (2011) proposed the *C. plummerae* zone to replace the *G. ventricosa* zone, defining the biostratigraphic interval between the FO of the nominate taxon and the FO of *R. calcarata*.

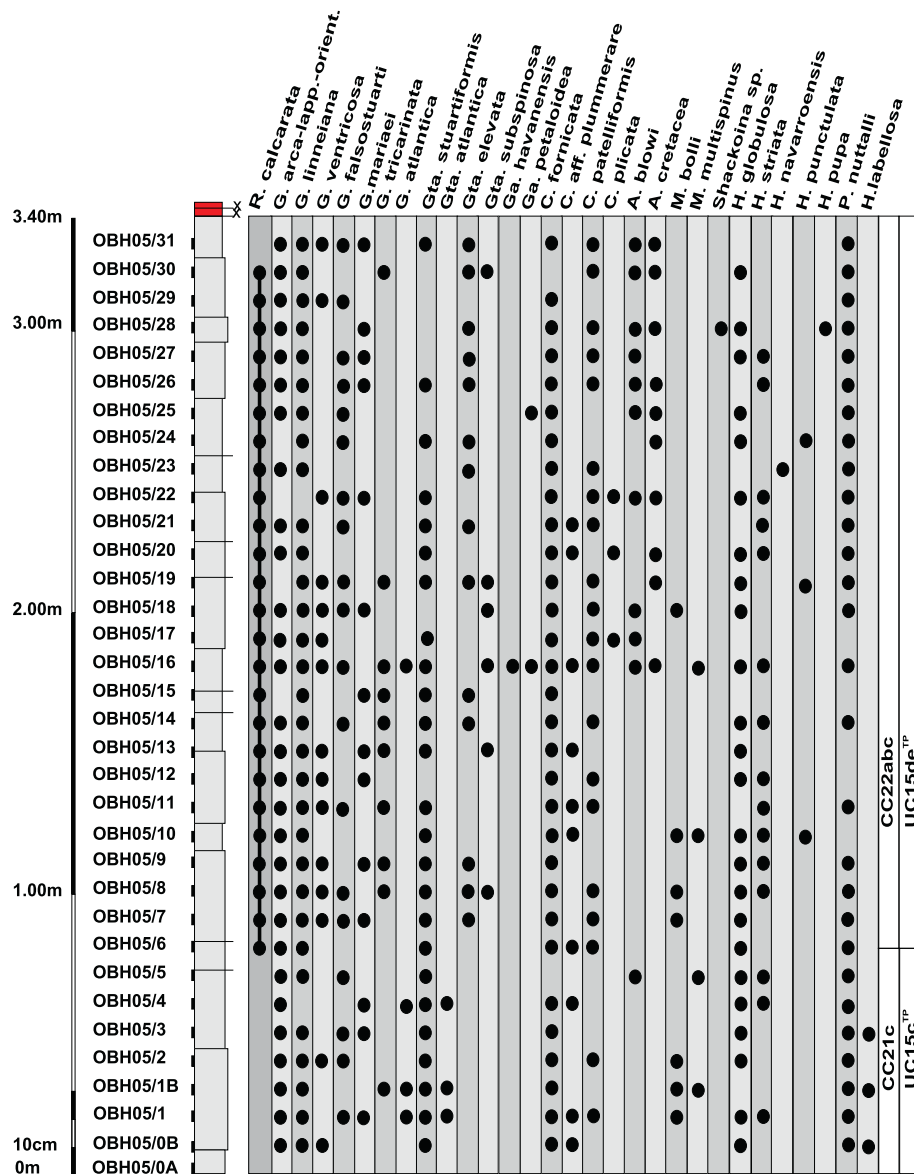


Fig. 6. Distribution of planktic foraminiferal taxa at OBH, including nannofossil zones.

The *R. calcarata* total range zone (TRZ) was first defined by Herm (1962). This interval was placed originally in the uppermost Campanian (e.g. Caron, 1985; Sliter, 1989). Following works (e.g. Robaszynski and Caron, 1995 - as *Globotruncana calcarata* TRZ, Premoli and Sliter, 1999; Huber, et al., 2008; Robaszynski and Mzoughi, 2010) locate the *R. calcarata* TRZ in the middle to late Campanian.

By absence of the taxon *R. calcarata* in the topmost parts of the sections the lowermost part of the *Ga. havanensis* Zone, introduced by Caron (1978), can be identified. This zone defines the interval between the LO (last occurrence) of *R. calcarata* and the FO of *G. aegyptiaca* (Robaszynski and Caron, 1995; Premoli and Sliter, 1999).

Most works covering this interval in the Tethyan realm report the LO of the taxon *Globotruncana elevata* before or within the *R. calcarata* TRZ. Robaszynski et al. (1984) see the stratigraphic range from the late Santonian to the Campanian *G. ventricosa* Zone. Cetean et al. (2011) record the extinction of this taxon in the *G. ventricosa* Zone, Petrizzo et al. (2011) locate the LO of *Gta. elevata* at Bottaccione section right below the FO of *R. calcarata*. Robaszynski and Mzoughi (2010) also report the LO in the uppermost *G. ventricosa* Zone for the Aboid Formation at Elles. The LO of *Gta. elevata* within the *R. calcarata* Zone is reported by Chacón et al. (2004).

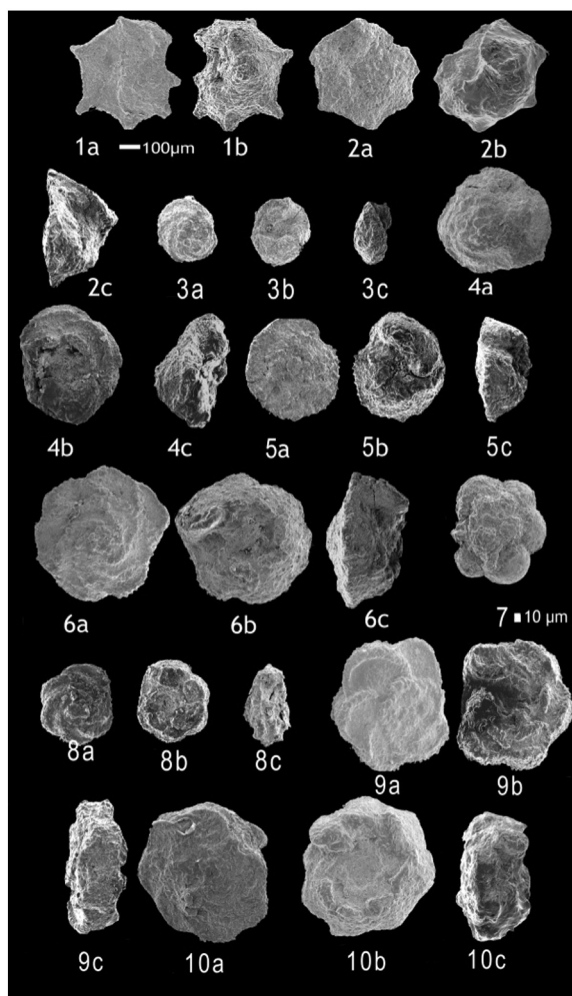
*Globotruncana elevata* is present in both sections investigated in this study. POST seems to display the LO of *Gta. elevata*. At OBH, this taxon appears to be present throughout the *R. calcarata* interval. *Globotruncana stuartiformis* and *Gta. subspinosa*, both present in either section, exhibit a constant appearance in OBH.

No specimen of *Macroglobigerinelloides* could be identified at POST. OBH displays 2 taxa assigned to this genus. In this time interval, members of *Macroglobigerinelloides* usually appear in the size fractions smaller than 150  $\mu\text{m}$ . The same applies principally to rugoglobigerinids, however, the latter could not be identified in either of the sections.

Other studies on the *R. calcarata* interval also identified *G. rosetta* (Salaj, 1974; Robaszynski and Mzoughi, 2010 from Tunisia), *G. aegyptiaca* (Chacón et al., 2004, from Spain) and *G. bulloides* (e.g. Janoschek, 1968, from the Austrian Alps). These taxa could not be identified in either of the two sections examined in this study.

#### 5.1.2. Benthic foraminifera and palaeoenvironment

POST and OBH yield very similar benthic foraminifera communities. Both display elements of "Deep Water Agglutinated Foraminifera" (DWAF) assemblages (Kuhnt and Kaminski, 1990) as well as elements



**Fig. 7.** 1a,b: *Radotruncana calcarata* (sample POST 7/38), 2a, b, c: *Globotruncana subspinosus* (8/1), 3a, b, c: *Contusotruncana fornicata* (7/38), 4a, b, c: *C. patelliformis* (7/38), 5a, b, c: *Gta. stuartiformis* (8/7), 6a, b, c: *Gta. elevata* (7/36), 7: *Archaeoglobigerina cretacea* (7/39), 8a, b, c: *Globotruncana arca* (7/38), 9a, b, c: *G. linneiana* (7/38), 10a, b, c: *G. ventricosa* (7/38). Note the different scale used in the SEM micrograph of *Archaeoglobigerina cretacea* (7.).

assigning to higher productivity environments represented by lenticulinids, dentalinids and nodosariids.

We can report similarities of the benthic foraminiferal assemblages assessed at POST and OBH, to “Slope-Marl” and “Flysch-type” assemblages (as described in Kuhnt et al., 1989; Kaminski and Gradstein, 2005). The assemblage assessed at POST particularly displays some diagnostic elements of the “Slope-Marl” fauna: *Dorothia* spp., *Clavulina* spp., *Cribrostomoides* spp. and *Spiroplectammina* spp. appear frequently. *Nothia* spp., *Hyperammina* sp. and *Placentammina* spp. are not exclusively, but frequently found in OBH, and are indicative taxa of a “Flysch-type” assemblage.

POST yields only slightly more infaunal morphotypes than morphotypes depicting an epifaunal habitat preference. At OBH the infaunal/epifaunal ratio in species counts is balanced. Thus, following Widmark and Speijer (1997), the assemblages at POST and OBH can be described as “Deep Bathyal Assemblages”. POST and OBH can therefore be addressed as upper to middle slope settings of some 500 to 800 m water depth.

In the mean, we could identify 18 different benthic foraminiferal species per sample at POST and 15 at OBH.

The benthic foraminifera *Reussella szajnochae*, a biostratigraphic marker for the Upper Cretaceous, has been identified in both sections.

Stratigraphically indicative agglutinated species, such as *Caudammina gigantea*, could not be unanimously identified.

**5.1.2.1. Analysing (dis)similarities of POST and OBH.** Q- and R-mode analyses reveal the determining elements for the separation of the two sections. Distinct factors separating POST and OBH are the presence of *Nothia* (?) sp.1, *Reussella szajnochae*, *Dorothia conula* and *Tritaxia eggeri* at OBH, as well as the presence of *Spiroplectinella dentata*, *Cribrostomoides* spp. and *Gaudryina pyramidata* at POST.

For the better understanding of the palaeoecology of the two sections, it is also necessary to examine the taxa in respect to their environmental preference and ecological characteristics. Table 5 provides a listing of taxa indicative for each cluster (except for c) determined by hierarchical clustering (see Fig. 9).

**5.1.2.2. Differences in palaeoecological conditions inferred from benthic foraminifera habitats.** By the distribution of agglutinated and calcareous foraminiferal species and their habitat preference we can assume certain environmental characteristics for both sections.

Calculating a PCA, the amount of benthic foraminiferal species grouped by habitat preference confirms that POST and OBH depict very similar palaeocommunities (Fig. 10a, b).

Comparing the two sections, we find a predominantly homogenous dataset at POST, while data from OBH appear more scattered.

POST: Species richness ( $\alpha$ -diversity) and the global  $\beta$ -diversity (diversity between all samples:  $\beta_{global} = 0.174$ ) is lower than at OBH. Though POST is considered to be a typical CORB deposited in (highly) oxic bottom waters (Wagreich and Krenmayr, 2005; Wagreich et al., 2009), a diverse DWAF assemblage was identified. Only at the base and the top of the *R. calcarata* section calcareous species prevail in numbers, other parts of this section show a mixed agglutinated and calcareous benthic foraminifera community. According to the low amount of epifaunal calcareous foraminifera species and the continuously high proportion of infaunal calcareous species in this section, dysoxic conditions as a driving factor behind the migration to infaunal habitats should be taken into consideration (Koutsoukos and Hart, 1990; Jorissen et al., 1995; Van der Zwaan et al., 1999; Gooday, 2003; Murray, 2006). Furthermore, the presence of *Gaudryina* can be associated with dysoxic conditions (Holburn et al., 1999). Consequently, considering species indicative for the calculation of the “BFOI” (Kaiho, 1994), we sparsely find benthic species requiring oxic environments at POST. At the lowermost parts of the *R. calcarata* Zone and at the top, species like *Cibicides* or *Osangularia* occur together with indicators for high productivity.

The hierarchical clustering after Ward sees the lowermost as well as the uppermost parts of the section assign to Cluster g (Fig. 10c). This cluster seems to be defined by taxa adapted to dysoxic environments. Throughout the stratigraphically older part of POST, *Spiroplectammina* and *Spiroplectinella* were frequently detected. These taxa occur together with morphogroups indicative of high productivity, such as *Lenticulina* or *Dentalina*.

The fauna of this part of the section belongs to Cluster f, according to the indicative species (Table 5). *Spiroplectammina* and *Spiroplectinella* are known as indicators for “shallow” water depths from the deeper sublittoral to the upper bathyal. Changes in the abundance of indicative taxonomic groups give information on changes in the bathymetry. The presence of these taxa in a bathyal Campanian sequence has also been recorded by Cetean et al. (2011) from the Carpathians. Cetean et al. (2011) interpret the occurrence of *Spiroplectammina* and *Spiroplectinella* as a shallow water fauna invasion event. Assumingly, more favourable conditions at greater depths could be found for these taxa during times of high sea level. The presence at frequent intervals could in the following be interpreted as an indicator for a high sea level (or a small scale sea-level rise?) during the stratigraphically older *R. calcarata* interval.

The fauna of the younger section part belongs to clusters e and g. Taxa like *Gaudryina*, *Eponides*, *Reussella* and *Cribrostomoides* define



**Table 3**

Habitat preferences of benthic foraminiferal species.

## Group “A” – epifaunal calcareous taxa:

*Anomalinoidea larseni*  
*Cibicidoides pseudoacutus*  
*Cibicidoides voltzianus*  
*Eponides beisseli*  
*Eponides* sp.1  
*Gavellinopsis involuta*  
*Globorotalites multiseptus*  
*Gyroidinoides nitidus*  
*Gyroidinoides bandyi*  
*Gyroidinoides girardanus*  
*Gyroidinoides lenticulus*  
*Gyroidinoides* sp.  
*Gyroidinoides umbilicatus*  
*Osangularia cordieriana*  
*Osangularia* sp.  
*Ramulina* sp.  
*Ramulina wrighyti*  
*Stensioina pommerana*

## Group “B” – calcareous taxa without clear vertical (infaunal or epifaunal) habitat preference:

*Astacolus* sp.  
*Conglophragmium irregularis*  
*Dentalina annulata*  
*Dentalina catenula*  
*Dentalina filiformis*  
*Dentalina oligostegia*  
*Dentalina* aff. *solvata*  
*Dentalina* sp.  
*Dentalina* sp.1 (thick wall)  
*Dentalina* sp.1 *pustulae* (?)  
*Dentalina* sp.2 (aculeate terminal chamber)  
*Dentalina* sp.3 (aculeate terminal chamber)  
*Ellipsodimorphia hrubieszowiensis*  
*Entosolenia/Fissurina orbignyana*  
*Fronidularia canaliculata*  
*Laevidentalina* sp.  
*Lenticulina (Robulus) subalatus*  
*Lenticulina* sp.  
*Lenticulina* sp.1  
*Lenticulina subangulata*  
*Lenticulina trachyomphalus*  
*Lenticulina velascoensis*  
*Lenticulites rotulata*  
*Neoflabellina* sp.  
*Nodogeneria pseudoscripta*  
*Nodosaria aspera*  
*Nodosaria limbata*  
*Nodosaria monile*  
*Nodosaria pauperula*  
*Nodosaria* sp.  
*Saracenaria triangularis*

## Group “C” – calcareous taxa with preference for infaunal habitats:

*Allomorphina cretacea*  
*Bolivinoidea clavatus*  
*Bulimina obtusa*  
*Conorboidea* sp.  
*Glandulina pygmaea*  
*Guttulina communis*  
*Guttulina* sp.  
*Guttulina trigonula*  
*Lagena apiculata*  
*Lagena emaciata*  
*Lagena laevis*  
*Lagena* sp.  
*Marginulina* sp.  
*Marginullina* sp.1  
*Pleurostomella* sp.  
*Pleurostomella spinosa*  
*Pleurostomella wadow*  
*Praebulimina* sp.  
*Pullenia* sp.  
*Reussella* sp.1  
*Reussella szajnochae*  
*Stilostomella alexanderi*  
*Stilostomella* sp.

**Table 3 (continued)**

## Group “D” – epifaunal agglutinating taxa:

*Ammosphaeroidina pseudopauciloculata*  
*Ammodiscus cretaceus*  
*Ammodiscus* sp.  
*Bathysiphon* sp.  
*Nothia excelsa*  
*Nothia?* sp.1  
*Paratrochamminoides deflexiformis*  
*Rzehakia lata*  
*Spiroplectinella dentata*  
*Spiroplectammina praelonga*  
*Spiroplectinella* sp.1  
*Trochammina boehmi*  
*Trochammina* sp.  
*Trochammina* sp.1  
*Trochamminoides proteus*

## Group “E” – agglutinating taxa with a preference for infaunal habitats:

*Ammobaculites agglutinans*  
*Ammobaculites* sp.  
*Caudammina excelsa*  
*Clavulina amorpha*  
*Clavulina trilatera*  
*Cribrostomoides* spp.  
*Dorothia conula*  
*Dorothia pupoides*  
*Dorothia* sp.  
*Gaudryina laevigata*  
*Gaudryina pyramidata*  
*Gaudryina rugosa*  
*Gaudryina* sp.  
*Gaudryina* sp.2  
*Hyperammina* sp.  
*Marssonella* sp.  
*Marssonella* sp.1  
*Marssonella trochus*  
*Placentammina placenta*  
*Reophax globosus*  
*Subreophax* sp.  
*Textularia* sp.  
*Thalmanammina* sp.  
*Tritaxia (tripleura ?)*  
*Tritaxia* sp.  
*Tritaxia eggeri*  
*Verneulina muensteri*  
*Verneulina* sp.

these clusters and seem to be indicative for a stable upper to middle slope environment. This assumption is also supported by low values for  $\beta$ -diversity between samples from POST (see Fig. 10c).

Resuming, we can interpret POST as a bathyal, distal slope environment displaying dysoxic conditions.

OBH: Higher species richness ( $\alpha$ -diversity) and  $\beta$ -diversity over all section samples ( $\beta_{global} = 0.217$ ) is recorded from OBH. Fluctuations in  $\beta$ -diversity between succeeding samples are also more intense than at POST. Compared to POST, this section shows a higher frequency of “epifaunal to infaunal calcareous” taxa. These morphogroups are represented by species like *Lenticulina* or *Dentalina*, representing many opportunistic high-productivity taxa. Although this section depicts a higher number of benthic foraminifera species, only a mean of 15 different benthic taxa per sample could be found that is also documented in the high  $\beta$ -diversities between samples. Benthic foraminiferal species richness records mostly calcareous species, most of them showing a shallow infaunal to epifaunal mode of life.

Agglutinated foraminiferal taxa found at OBH assign mostly to the infaunal and epifaunal morphogroups and are in a large part represented by *Nothia* spp. or *Ammobaculites* spp. The frequent appearance of *Nothia* spp. together with *Ammodiscus* sp. could be indicative for an oxygen-depleted environment (Kuhnt et al., 1989).

However, in addition to indicators for oxygen-depleted environments, OBH also yields some taxa requiring oxic conditions such as

**Table 4**  
Benthic foraminiferal taxa categorised in respect to their habitat preference.

	Epifaunal Calcareous	Epifaunal/ infaunal Calcareous	Infaunal Calcareous	Epifaunal Agglutinated	Infaunal Agglutinated
OBH_0b	0	0	2	0	1
OBH_1	2	4	3	3	4
OBH_1b	2	1	0	1	5
OBH_2	3	1	2	2	6
OBH_3	2	1	2	0	3
OBH_4	5	3	2	0	3
OBH_5	0	3	4	1	4
OBH_05/0A	3	0	0	0	3
OBH_6	2	1	2	1	4
OBH_7	1	1	2	2	7
OBH_8	2	3	1	2	4
OBH_9	3	2	1	1	6
OBH_10	3	1	4	3	2
OBH_11	4	3	2	2	4
OBH_12	2	0	2	0	4
OBH_13	2	2	1	1	5
OBH_14	2	1	1	1	3
OBH_15	0	0	0	0	1
OBH_16	1	1	1	2	1
OBH_17	6	1	0	2	4
OBH_18	2	2	1	1	3
OBH_19	1	0	0	1	8
OBH_20	3	5	3	1	3
OBH_21	2	0	0	2	1
OBH_22	0	1	3	1	3
OBH_23	2	4	3	1	2
OBH_24	4	3	2	3	2
OBH_25	1	3	2	2	3
OBH_26	8	4	4	3	6
OBH_27	2	1	2	1	5
OBH_28	2	1	0	2	5
OBH_29	3	0	1	0	5
OBH_30	4	3	1	5	8
OBH_31	2	1	3	1	4
POST_07/33	1	3	4	2	5
POST_07/34	2	2	6	1	6
POST_07/35	3	5	4	1	4
POST_07/36	3	4	6	1	7
POST_07/37	3	4	2	1	7
POST_07/38	3	2	7	4	5
POST_07/39	2	5	6	2	7
POST_07/40	2	1	2	3	5
POST_07/41	2	1	4	2	8
POST_07/42	2	2	5	2	4
POST_07/43	1	3	5	3	8
POST_07/44	2	1	3	1	4
POST_08/01	2	2	5	3	7
POST_08/02	1	2	1	3	7
POST_08/03	1	4	3	3	3
POST_08/04	1	3	4	2	7
POST_08/05a	3	0	3	1	3
POST_08/05b	1	1	1	0	5
POST_08/06	2	1	3	0	4
POST_08/07	4	1	5	4	5
POST_08/08	3	1	7	0	7
POST_08/09	4	2	2	1	9
POST_08/10	3	1	3	2	4
POST_08/11	3	2	3	3	7
POST_08/12	3	1	2	1	5

*Cibicides* sp. or *Ramulina* sp.. Groups obtained by cluster analysis show a fluctuation between clusters *a*, *b* and *d*. Only samples OBH 5/30 and OBH 5/5 were assigned cluster *g* and *e*. *Nothia* sp.1 can, according to cluster analysis, be seen as a determining element for the clusters *a* and *b*. Cluster *d* shows strong influence of *Gaudryina pyramidata*, *Eponides beisseli* and *Reussella szajnochae* and could therefore hint to an occasionally dysoxic environment.

Considering the combined Q- and R-mode cluster analyses, it can be reasonably assumed, that samples from OBH record an instable slope

environment. We find evidence for high productivity and in some samples evidence for a suboxic to dysoxic regime with high nutrient availability (also visible in the distribution and peculiarity of factor loadings inferred from the PCA, see Fig. 10c). The presence of species requiring oxygen-saturated environments could refer to frequent faunal ingression or transport downslope from environments with better oxygen saturation.

## 5.2. The Penninic Ocean as a part of the Tethys ocean system

The foraminiferal fauna of the two sections from the northern and southern margin of the Penninic Ocean, originally a few hundred kilometres apart in north-south direction, also sheds light onto the palaeoceanography and the palaeobiogeographic evolution at the north-western Tethys. Biogeographically, both sections clearly belong to the Tethyan pelagic realm, characterised by abundant and diverse globotruncanids. The Tethyan realm involves the whole European margin, i.e. the classical Upper Cretaceous Helvetic shelf (e.g. Föllmi, 1989; Wiese, 2010) and their northern foreland (e.g. the Danubian Group, Wilmsen and Niebuhr, 2010), where abundant globotruncanids are still present (see Küpper (1963); Fuchs and Wessely (1977), as well as Oberhauser (1965) for the western foreland). According to Küpper (1963) and Fuchs and Wessely (1977), the late Campanian *R. calcarata* Zone was identified also in this area.

Connections to the Neotethys Ocean(s) to the south are, at least in the late Campanian, wide and deep enough (e.g. Handy et al., 2010) to facilitate faunal exchange from Italy and Tunisia to the Penninic Ocean. Although the Penninic Ocean in the Eastern Alps transect already started to close (subduct?) since the Aptian–Albian (Wagreich, 2001; Mandic and Lukeneder, 2008), in the late Campanian sea ways were unrestricted for faunal exchange.

The benthic foraminiferal marker for the Campanian, *Bolivinooides draco draco*, is missing in our sections, but generally known from other Campanian sections of the NCA and the Ultrahelvetic (e.g. Oberhauser, 1965; Hradecká and Lobitzer, 2003). The absence of this taxon at POST and OBH is not necessarily related to lacking faunal exchange, but presumably to environmental conditions (such as water depth). Overall, we can reconstruct a typical late Campanian foraminiferal fauna. This is also different from results concerning the Cenomanian–Turonian boundary interval in the Ultrahelvetic, where Gebhardt et al. (2010) speculated in terms of a restricted, “relic” biogeographic realm in the Penninic, with a semi-closed basin where global high productivity events cannot be evidenced based on foraminiferal assemblages.

### 5.2.1. Implications for sea-level

No detailed, clear-cut sea level record exists for the *R. calcarata* Zone. Given the two most recent and detailed sea-level curves for the Late Cretaceous, i.e. the data published by Miller et al. (2005a, b) and Haq (2014), the long-term trend is rather stable, but indicates high sea level (more than 200 m above present day sea-level according to Haq (2014)). In the short-term record, i.e. at 3rd order cycles and sequences, Haq (2014) records a minor sequence boundary KCa6 (= lowstand) at 75.4 Ma, within the *calcarata* Zone (although his correlations may have some uncertainties). Ogg et al. (2012) also indicate a sequence boundary (Cam6) within the *calcarata* Zone, dated around 75.6 Ma. Miller et al. (2005a,b), in contrast, indicate a sequence boundary below the *calcarata* Zone (below the base of nannofossil standard zone CC22a), and another one significantly above the *calcarata* Zone near the Campanian/Maastrichtian boundary within nannofossil zone CC 23. According to the stable foraminiferal communities in our sections, we see no evidence for major sea-level fluctuations within the *calcarata* Zone, thus no major sequence boundary seems to correlate with the zone corroborating the sequence stratigraphy correlation of Miller et al. (2005a,b).

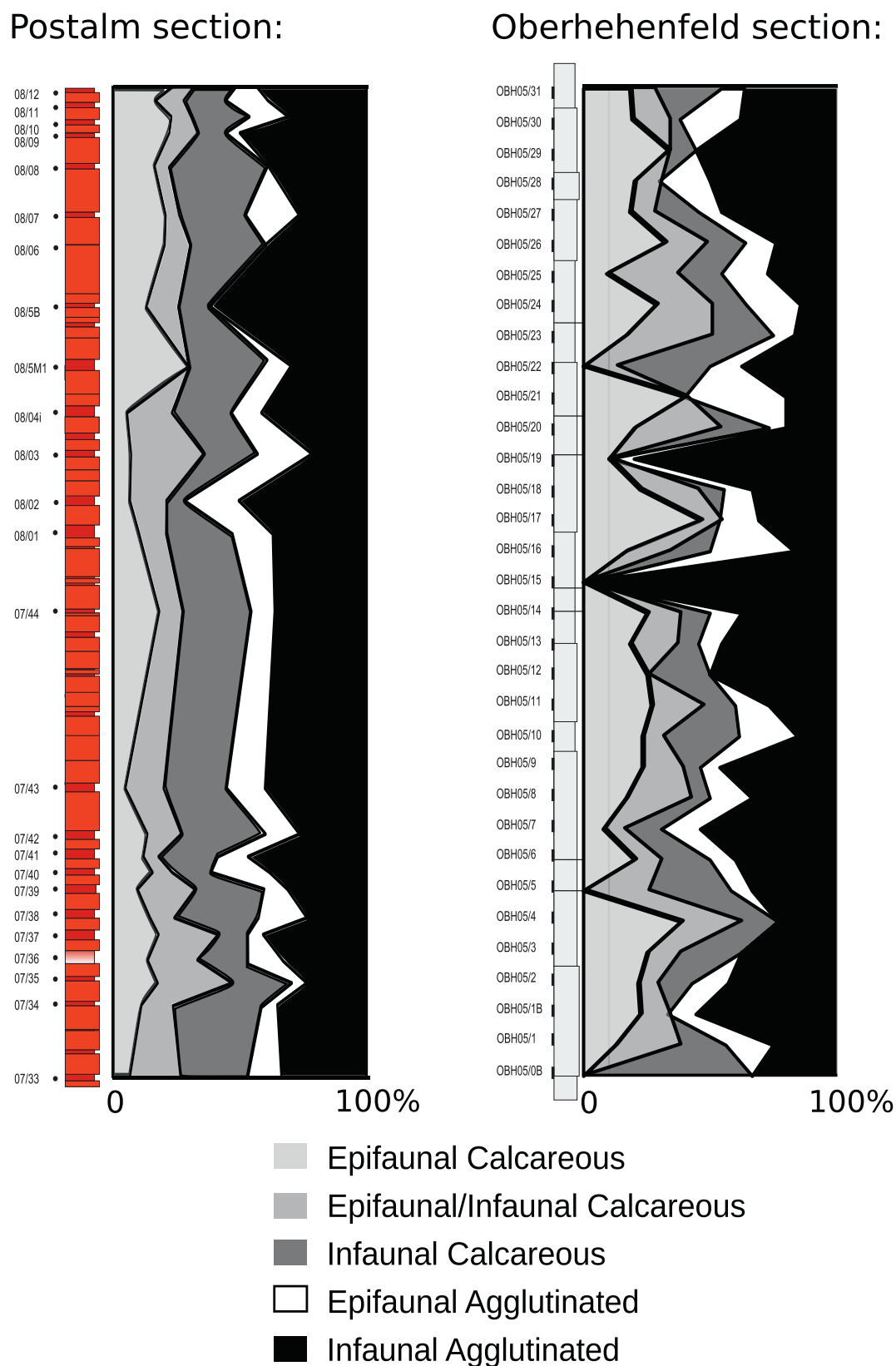
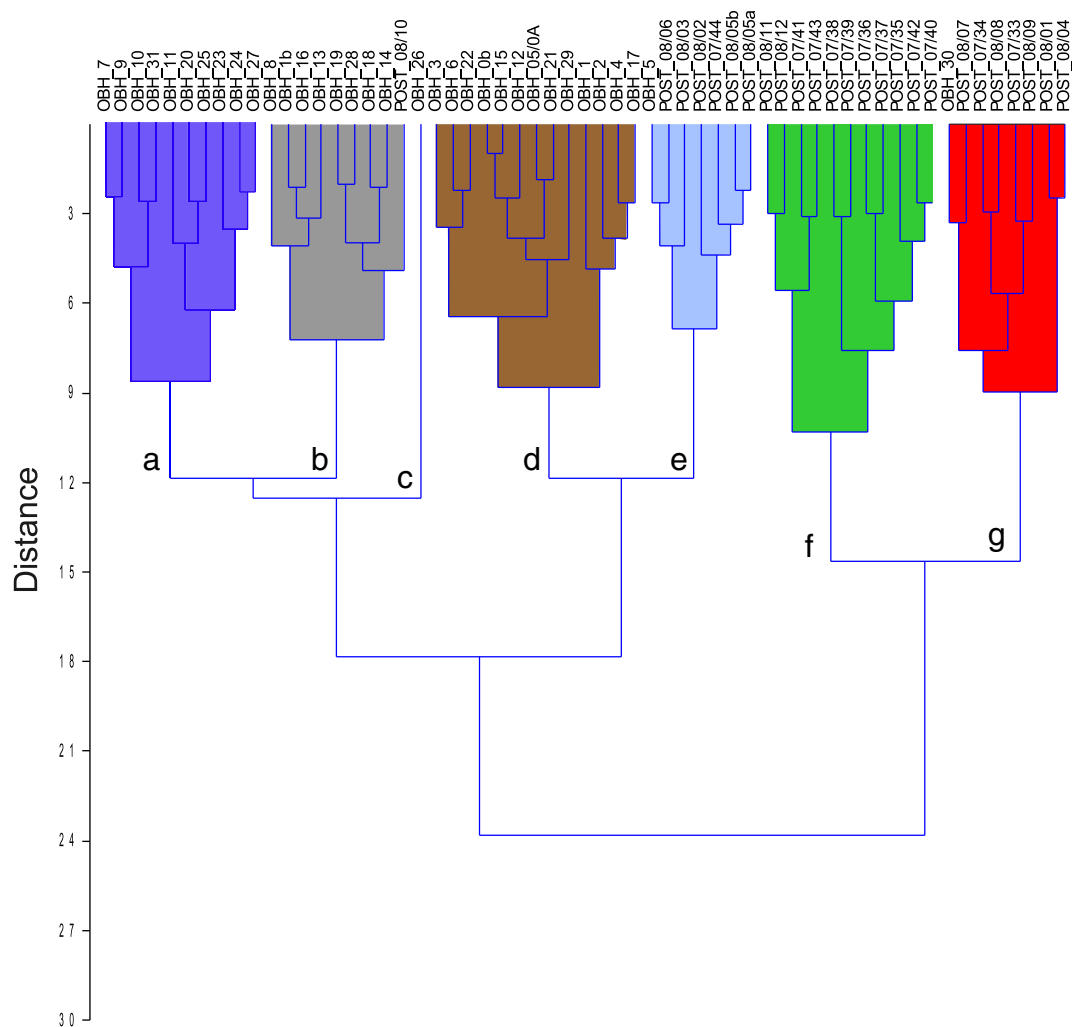


Fig. 8. Relative distribution of benthic foraminiferal taxa in respect to their habitat preference within the *R. calcarata* Zone (scale = time equivalents).

Minor relative sea-level changes may be indicated by the presence of shallow water taxa in POST, i.e. *Spiroplectammina* spp. However, especially in the Postalm section at the active Austroalpine

margin, regional sea-level changes are possibly controlled by tectonics, but nevertheless not well expressed in our foraminiferal data. *Radotruncana calcarata* seems to show no relation to sea-level stands



**Fig. 9.** Classification of samples using qualitative benthic foraminifera data on species level. Hierarchical clustering after Ward allocates most samples from Postalm and Oberhehenfeld in clearly separated groups.

as well as no relation to palaeoclimate, as also expressed by its independent evolution in regard to Milankovitch-type climate cycles (Wagreich et al., 2012).

Despite the influence of minor sea-level changes and other palaeoecological events, i.e. as expressed by minor carbon isotope peaks (Wagreich et al., 2012; Wendler, 2013) or geochemical proxy data (Neuhuber et al., 2015), or the clear-cut Milankovitch cyclicity of the sections, the foraminiferal assemblages of the *calcarata* Zone in the Austrian Alps show remarkable stability. It can be concluded that, although major changes and cycles (sequences) in the range of several Ma may influence foraminiferal communities, those short-term changes within the 800 kyr *calcarata* Zone did not significantly influence or alter the foraminiferal communities in the bathyal realm of water depth between 500–800 m. There are only some subtle changes, easily overlooked, and/or challenging to interpret, i.e. the occurrence of *Spiroplectammmina* at POST or the changes in the dominant morphogroups in benthic foraminifera.

### 5.3. The *R. calcarata* Zone as interval of palaeoenvironmental stability in the northwestern Tethyan realm?

The late Campanian was in general identified as a time of low planktonic foraminifera turnover (Premoli and Sliter, 1999). During the 806 kyr long *R. calcarata* interval we experience no major change in neither benthic nor planktonic foraminiferal communities. This interval does

not display any FO in planktic taxa except *R. calcarata* itself. *G. elevata* becomes a rare faunal element in POST, probably depicting its local LO, while it seems to be present throughout OBH. Furthermore, no evolutionary trend or any noticeable environmentally influenced change in the composition of foraminiferal assemblages, neither planktic nor benthic, was observed. Isotopic data, assessed by Wagreich et al. (2012), give clear signals for Milankovitch cycles. Three carbon isotope excursions visible during the *calcarata* interval correlate well to carbon isotope data recorded by Jarvis et al. (2002).

Therefore, we interpret the *R. calcarata* Zone in general to show very stable conditions in terms of palaeoecology and planktonic foraminiferal evolution. We can consider a palaeoecological stasis, or at least presume a certain stability in foraminiferal communities despite the general cooling trend of the Cretaceous greenhouse.

The development of the zonal marker itself can be seen as the only major event in planktonic foraminiferal evolution, not paralleled by any other evolutionary event in planktonic foraminifera, giving a precise point of correlation, between the FO of *G. ventricosa* or *C. plummerae* and the uppermost Campanian foraminiferal evolution and radiation pulses leading to development of new forms in planktonic foraminifera (Premoli and Sliter, 1999). Rugoglobigerinids and the genus *Globotruncanella* are already present in the *R. calcarata* Zone and seem to get more common towards the late Campanian. The development in biserial taxa happened even later. Apart from the FO of *H. rajagopalani* in the middle to late Campanian (Petruzzo, 2003), changes in this

**Table 5**

Indicator species for each Cluster (see Fig. 10) inferred from combined Q- and R-mode cluster analyses.

Cluster a): <i>Nothia</i> ? sp.1 <i>Dorothia conula</i> <i>Reussella szajnochae</i>	Cluster b): <i>Nothia</i> ? sp.1 <i>Tritaxia eggeri</i>	Cluster d): <i>Gaudryina pyramidata</i> <i>Eponides beisseli</i>
Cluster e): <i>Reussella</i> sp. <i>Gaudryina pyramidata</i> <i>Eponides beisseli</i>	Cluster f): <i>Spiroplectinella dentata</i> <i>Globorotalites multiseptus</i> <i>Lenticulina</i> spp. <i>Cribristomoides</i> spp.	Cluster g): <i>Eponides beisseli</i> <i>Gaudryina pyramidata</i> <i>Marginulina</i> sp. <i>Cribristomoides</i> spp.

group (strongly dominated by *H. globulosa* during the Campanian) get noticeable only at the beginning of the Maastrichtian (Premoli and Sliter, 1999).

In terms of evolution, *R. calcarata* cannot be considered the result of the *stuartiformis-elevata-subspinosa* progression, but has its origin directly in an archaeoglobigerinid ancestor (Longoria and VonFeldt, 1991), the sudden appearance and disappearance after only 806kyr seems puzzling as no environmental proxies regarding palaeoclimate or sea-level coincide directly neither with the appearance nor the extinction of this taxon, and no species in a line of succession of *R. calcarata* are known.

Here we present an alternative hypothesis for the evolution of *R. calcarata*, based on the principal characteristics of the Cretaceous ocean system. During the Cretaceous several factors provoked an intense stratification of the ocean's water masses, for instance Ocean Anoxic Events and (mutual) sea level highstands (Huber and Watkins, 1992; Price et al., 1998; Friedrich et al., 2012). Using the difference in oxygen isotope values of benthic and planktic foraminifera, highly stratified water masses can be reconstructed for the mid-Cretaceous, while during the late Campanian and towards Maastrichtian the deep-water circulation seems to have increased and accordingly, we find a decrease in the difference in oxygen isotope values (e.g., Norris et al., 2001; Otto-Bliesner et al., 2002; Hasegawa et al., 2012). Evidence for stable surface and bottom water temperatures in the late Campanian is presented in Jung et al. (2013), following the investigation of Nd isotope signatures. This period (79–74.5 Ma) is characterised by stable environmental conditions and was followed by a cooling trend in the latest Campanian (Friedrich et al., 2012). Considering the chronostratigraphic framework given by Huber et al. (2008) for the *R. calcarata* Zone (76.18 to 75.57 Ma), the possible impact of changes in oceanwater properties on highly specialised taxa like *R. calcarata* should be taken into account.

Changes in the vertical gradients and properties of the water column and the presence of regional intermediate and deep-waters (e.g. Voigt et al., 2013) could open up ecological niches for deeper dwelling planktic foraminifera. Considering the possibility of a reticulate evolutionary pattern (see Hohenegger, 2014) for this group of single keeled globotruncanids, the short stratigraphic range of *R. calcarata* could be caused by the opening and closing of an adaptive zone during palaeoceanographic, i.e. water mass reorganisation (that also can be understood as the emergence of an ecological opportunity, permitting the further specialisation or development of a taxon) for this species, the latter causing the sudden extinction.

Developments in planktonic foraminiferal morphology, particularly the elongation of chambers or the development of tubulospines, is generally understood as a reaction to environmental change (Leckie, 1989; Hart, 1980; Hart, 1999; Coccioni et al., 2006). Adaptations in schackoinids and leupoldinids might be related to severe changes in the Cretaceous hothouse ocean dynamics, resulting in black shale events and widespread anoxia, and can therefore be seen as an adaptation to changes in oxygen availability (e.g.: Magniez-Jannin et al., 1997; Coccioni et al., 2006). A striking similarity in morphological traits is

known from the genus *Hantkenina*. The gradual evolution and changes in the *Hantkenina* lineage follow and adapt to climatic changes throughout the Eocene; Evidence from isotopic data suggests a shift from a planktonic deep marine habitat to an adaptation to shallow water depths close to the surface (Coxall et al., 2000). It is discussed that the development of tubulospines in hantkeninids correlates to the Eocene cooling event and that these adaptations were favourable in order to remain in the preferred position in the water column (Coxall et al., 2003; Pearson and Coxall, 2014).

The late Campanian records significant changes in ocean temperatures i.e. the late Campanian/early Maastrichtian cooling event (Friedrich et al., 2009; Jung et al., 2013). The similar morphology, as well as the development in comparable palaeoecological settings could hint towards similar factors influencing the evolution of *Radotruncana* and *Hantkenina*.

Anyhow, the distinctive morphology of *R. calcarata* most certainly suggests an adaptation to environmental parameters. As the functional morphology of Cretaceous planktic foraminifera is probably related to the hydrodynamic regime (Leckie, 1989), we can assume that the prominent spines in *R. calcarata* aid in keeping the preferred position in the water column at an intermittent adaptive zone.

In contrast to the gradual disappearance of *Gta. elevata* in POST, *R. calcarata* displays an abrupt disappearance in the Alpine sections as well as in other sections (e.g. from the Tunisian Aboid at Ellès section, Robasynski and Mzoughi, 2010), seemingly contemporaneous according to cyclostratigraphic data. The occurrence pattern of *R. calcarata* still could be a consequence of immigration and disappearance into and from the Penninic Ocean – however, as the studies of Robasynski and Mzoughi (2010) from the Tethyan Tunisia and Wagerich et al. (2012) from the Penninic Ocean, give a similar duration for the *R. calcarata* TRZ, we are confident that the total (global) range of this taxon is recorded reliably.

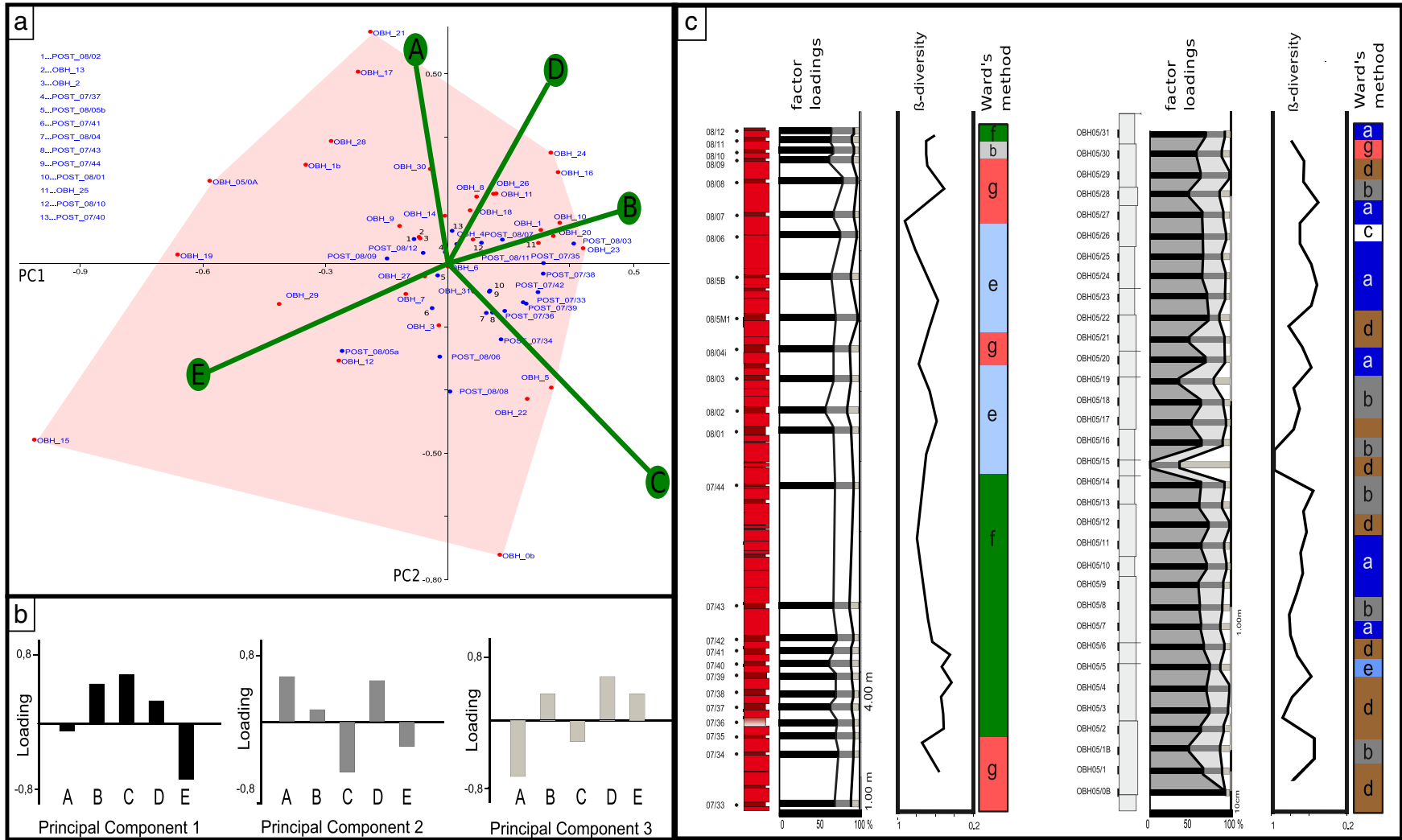
## 6. Conclusion

A well resolved assessment of foraminiferal communities in the Austrian Alps during the *R. calcarata* TRZ was established. Using astronomically calibrated intervals in Earth history and scaling them with biostratigraphic events (and considering the general outline of microfossil communities) is vital for tuning and correlating an astronomically calibrated timescale of the Mesozoic. Studies on planktic foraminifera biostratigraphy of the Austrian Alps point out that, although lacking well preserved individuals in the middle to late Campanian, a precise biostratigraphic framework spanning the Penninic Ocean can still be established. *R. calcarata* serves as an excellent marker. Biostratigraphic events, such as the extinction of *Gta. elevata* and the development of intermediate forms of *Gta. stuartiformis* and other single keeled planktic foraminifera in the Penninic realm, still require further investigation.

The examination of benthic foraminifera species represented at the Postalm and the Oberhehenfeld sections provides valuable insights into the bathymetry and palaeoenvironments.

Although classified as CORB, the Postalm foraminiferal assemblages do not indicate oxic bottom waters, but a dysoxic palaeoenvironment, and thus question the strict association of CORBs with highly oxic bottom waters as published by, e.g., Hu et al. (2005).

Though qualitative data gives only insight into the presence or absence of certain taxa, we can expect the continuous presence of a taxon – within several samples of a succession – to be indicative for a common faunal element of the section examined. During the ca. 800 kyr duration of the *calcarata* Zone, a remarkable stability in the taxonomic composition of foraminiferal assemblages has been recognised, with only minor and local perturbations. This exemplifies a longer interval of palaeoecologic stability in foraminiferal communities in the northwestern Tethyan realm during the late Campanian. Based on these data we speculate on the evolution of *R. calcarata* within an



**Fig. 10.** a.: Principal component analysis considering the preferred mode of life of foraminiferal species per sample; a. arrows indicate the five different habitat groups: "A": epifaunal calcareous, "B": infaunal/epifaunal calcareous, "C": infaunal calcareous, "D": epifaunal agglutinating, "E": infaunal agglutinating. The two sections overlap with a comparatively wider scatter at OBH; b.: factor loadings for the first three principal components explaining 86.8% of variance. PC 1 mainly explains the influence of habitat group "E". The influence of infaunal agglutinated and infaunal calcareous taxa is best explained along PC 1. Higher values in PC 1 can be found at POST, while OBH is rather influenced by PC 2 (predominantly defining the relation between epi- and infaunal calcareous taxa). PC 3 plays a minor role in the explanation of palaeoenvironments and predominantly explains the influence of the epifaunal calcareous, "A", and epifaunal agglutinated group, "D". c.: explains the factor loadings per sample spot, the units based on Q- and R-mode cluster analysis, as well as changes in  $\beta$ -diversity over the sections. Comparing the two sections, POST constantly shows a stronger influence of infaunal calcareous taxa, "C" (expressed in high loadings of PC 1).

opening and closing adaptive zone within changing water masses of the Late Cretaceous.

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### Appendix A. List of benthic foraminiferal taxa in alphabetic order

- Allomorphina cretacea* Reuss 1851  
*Ammobaculites agglutinans* (d'Orbigny, 1846)  
*Ammobaculites* sp.  
*Ammodiscus cretaceus* (Reuss, 1845)  
*Ammodiscus* sp.  
*Ammosphaeroidina pseudopauciloculata* (Mjatluk, 1966)  
*Anomalinoidea larseni* Huber 1988  
*Astacolus* sp.  
*Bathysiphon* sp.  
*Bolivinoidea clavatus* Plotnikova 1967  
*Bulimina obtusa* d'Orbigny, 1840  
*Caudamina excelsa* (Dylążanka, 1923)  
*Cibicidoides pseudoacutus* (Nakkady)  
*Cibicidoides voltzianus* (d'Orbigny, 1840)  
*Clavulina amorpha* Cushman, 1926  
*Clavulina trilatera* Cushman, 1926  
*Conglophragmium irregularis* (White, 1926)  
*Conorboides* sp.  
*Cribrostomoides* spp.  
*Dentalina annulata* Reuss, 1845  
*Dentalina catenula* Reuss, 1860  
*Dentalina filiformis* (d'Orbigny, 1845)  
*Dentalina oligostegia* Reuss  
*Dentalina aff. solvata* Cushman, 1938  
*Dentalina* sp.  
*Dentalina* sp.1 (thick wall)  
*Dentalina* sp.2 (aculeate terminal chamber)  
*Dentalina* sp.3 (aculeate terminal chamber)  
*Dentalina* sp.4 (pustulae)  
*Dorothia conula* (Reuss, 1845)  
*Dorothia pupoides* (d'Orbigny)  
*Dorothia* sp.  
*Ellipsodimorphia hrubieszowiensis* Gabor–Biedowa, 1992  
*Entosolenia/Fissurina orbignyana* Sequenza, 1862  
*Eponides beisseli* (White, 1928)  
*Eponides* sp.1  
*Globorotalites multiseptus* Brotzen, 1936  
*Frondicularia canaliculata* Reuss, 1844  
*Gaudryina pyramidata* Cushman, 1926  
*Gaudryina rugosa* (d'Orbigny, 1840)  
*Gaudryina laevigata* Franke, 1914  
*Gaudryina* sp.  
*Gaudryina* sp.2  
*Gavelinopsis involuta* Reuss, 1862  
*Glandulina pygmaea* Reuss  
*Globorotalites multiseptus* Brotzen, 1936  
*Guttulina communis* d'Orbigny, 1826  
*Guttulina* sp.  
*Guttulina trigonula* (Reuss, 1845)  
*Gyroidinoides bandyi* (Trujillo)  
*Gyroidinoides girardanus* (Reuss, 1851)  
*Gyroidinoides lenticulus* (Reuss, 1845)  
*Gyroidinoides* sp.  
*Gyroidinoides umbilicatus* (d'Orbigny, 1840)  
*Laevidentalina* sp.  
*Lagena apiculata* (Reuss 1851)  
*Lagena emaciata* Reuss  
*Lagena laevis* (Montagu, 1803)  
*Lagena* sp.  
*Lenticulina (Robulus) subalatus* (Reuss 1860)  
*Lenticulina* sp.  
*Lenticulina* sp.1  
*Lenticulina subangulata* (Reuss 1863)  
*Lenticulina trachyomphalus* (Reuss, 1851)  
*Lenticulina velascoensis* White  
*Lenticulinites rotulata* Lamarck, 1804  
*Marginulina* sp.  
*Marginullina* sp.1  
*Marssonella* sp.  
*Marssonella* sp.1  
*Marssonella trochus* (d'Orbigny)  
*Neoflabellina* sp.  
*Nodogenerina pseudoscripta* (Cushman, 1937)  
*Nodosaria aspera* Reuss, 1845  
*Nodosaria limbata* D'Orbigny, 1840  
*Nodosaria monilis* Silvestri, 1872  
*Nodosaria paupercula* Reuss 1845  
*Nodosaria* sp.  
*Nothia excelsa* (Grzybowski, 1898)  
*Nothia?* sp.1  
*Osangularia cordieriana* (d'Orbigny, 1840)  
*Osangularia* sp.  
*Paratrochamminoides deflexiformis* (Noth, 1912)  
*Placentamina placenta* (Grzybowski, 1898)  
*Pleurostomella* sp.  
*Pleurostomella spinosa* Cushman, 1911  
*Pleurostomella wadowicensis* Grzybowski, 1896  
*Praebulimina* sp.  
*Pullenia* sp.  
*Ramulina* sp.  
*Ramulina wrightii* Barnard, 1972  
*Reophax globosus* Sliter 1968  
*Reussella* sp. *szajnochae* Grzybowski, 1896  
*Reussella* sp.1  
*Rzehakina lata*  
*Saraceneria triangularis* (d'Orbigny, 1840)  
*Spiroplectinella dentata* (Alth, 1850)  
*Spiroplectammina praelonga* Vasilenko, 1961  
*Spiroplectinella* sp.1  
*Stensioeina pommerana* Brotzen  
*Stilostomella alexanderi* (Cushman)  
*Stilostomella* sp.  
*Subreophax* sp.  
*Textularia* sp.  
*Thalmanammina* sp.  
*Tritaxia (tripleura?)*  
*Tritaxia* sp.  
*Tritaxia eggeri* (Cushman, 1936)  
*Trochammina boehmi* Franke, 1928  
*Trochammina* sp.  
*Trochammina* sp.1  
*Trochamminoides proteus* (Karrer, 1866)  
*Verneulina muensteri* Reuss  
*Verneulina* sp.

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