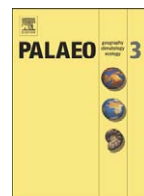




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Oceanographic conditions as a trigger for the formation of an Early Miocene (Aquitanian) *Konservat-Lagerstätte* in the Central Paratethys Sea

Patrick Grunert^{a,*}, Mathias Harzhauser^b, Fred Rögl^b, Reinhard Sachsenhofer^c, Reinhard Gratzer^c, Ali Soliman^a, Werner E. Piller^a

^a Institute for Earth Sciences (Geology and Paleontology), University of Graz, Heinrichstraße 26, A-8010 Graz, Austria

^b Natural History Museum Vienna, Geological-Paleontological Department, Burggring 7, A-1014 Vienna, Austria

^c Department of Applied Geosciences and Geophysics, Montanuniversität Leoben, Peter-Tunner Straße 5, A-8700 Leoben, Austria

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ABSTRACT

An exceptional Early Aquitanian *Konservat-Lagerstätte* with well-preserved vertebrate and invertebrate fossil assemblages has been studied in the North Alpine Foreland Basin of Upper Austria. The finely laminated sediments were deposited along the northern shelf of the Central Paratethys Sea. Micropaleontological (foraminifers, dinoflagellates) and geochemical (organic carbon, sulphur, carbonate content, biomarker, stable isotopes) proxies indicate intense upwelling. In addition, episodically increased coastal runoff provided large amounts of nutrients stimulating primary productivity. All evidence suggests deposition within dysoxic–anoxic bottom waters of an oxygen minimum zone along the outer shelf and upper slope. Fossil assemblages show specific planktic and nektic associations in distinct intervals of the section. Various mechanisms are discussed to explain their origin: (1) blooms of pteropods and calcareous nannoplankton reflect short-term peaks in primary productivity. Increased coastal runoff and/or intensified upwelling activity are considered as trigger mechanisms for providing the nutrients. (2) Allochthonous associations of the cephalopod *Aturia* with brown algae suggest a two-fold transport mechanism: shells of the offshoring cephalopods were transported post mortem to the coast by surface currents and/or wind currents. Episodic flooding events and storms mixed the accumulated shells with the algae and moved them offshore. The latter process also seems to apply to several pipefish accumulations observed in the section. (3) Multi-species vertebrate accumulations of fish and dolphins are considered parautochthonous as their habitat is in good agreement with the reconstructed paleoenvironment. (4) Benthic macrofauna is scarce and of low diversity. It mainly consists of bivalves adapted to dysoxic environments and is thus interpreted to be autochthonous.

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1. Introduction

The fossil record is strongly biased by the preferred preservation of hard parts (Donovan and Paul, 1998). Conservation of organic material and soft tissue is generally scarce and bound to specific conditions. Such, often spectacular occurrences are summarized as *Konservat-Lagerstätten* (Seilacher, 1970). Studies on their genesis are manifold. They have led to different scenarios explaining their origin and identified two primary triggers (Allison, 1988): (1) burial by rapid and/or catastrophic sedimentation (obtrusion) and (2) bottom-water anoxia. Due to facies prevalence and evolutionary patterns, *Konservat-Lagerstätten* are not evenly distributed through time (Allison and Briggs, 1993; Briggs, 2003). In the Cenozoic – contrasting the extensive black-shale deposits of the Mesozoic – most *Konservat-Lagerstätten* originate from marginal

marine carbonate environments (e.g. Schwark et al., 2009) or limnic deposits (e.g. Wuttke, 1983) while marine shales are scarce (Allison and Briggs, 1993).

In this study we present well-preserved fossil assemblages of different composition from a shaley Early Miocene *Konservat-Lagerstätte* in the Central Paratethys. Based on an analysis of the depositional environment these accumulations will be evaluated for characteristic patterns and different scenarios for their origin will be discussed.

2. Geological setting and stratigraphy

The presented material comes from a temporary outcrop exposed during the construction of a hydroelectric power plant near the small town of Pucking in Upper Austria (N 48° 12' 22"; E 14° 13' 27") and belong to the North Alpine Foreland Basin (NAFB) fill (Figs. 1 and 2A). The c. 3-m-thick section was described by Kovar (1982), who had already documented an uneven distribution of the floral and faunal elements. In addition, one sample from a nearby section at Linz-

* Corresponding author. Tel.: +43 316 380 8735; fax: +43 316 380 9871.

E-mail address: patrick.grunert@uni-graz.at (P. Grunert).

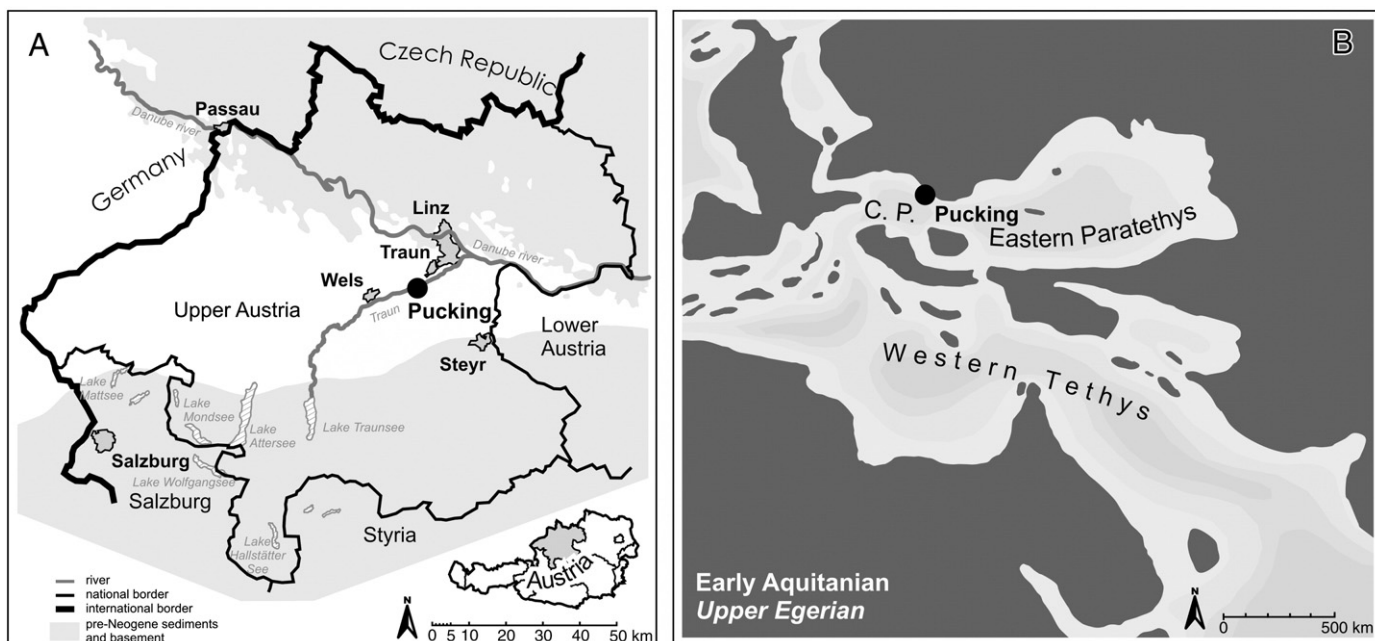


Fig. 1. (A) Location of the study area. (B) Paleogeographic location of the study area based on Harzhauser and Piller (2007).

Ebelsberg (12.5 km NE Pucking) has been included in the foraminiferal analysis. The deposits are part of the Ebelsberg Formation consisting of laminated sandy and silty clay to silty clay with mm-thick intercalations of silt (Wagner, 1998; Krenmayr and Schnabel, 2006). Single beds range from a few mm to 2–3 cm. Based on the regional stratigraphy and palynological assemblages, the Ebelsberg Formation has been considered as Upper Oligocene (Hochuli, 1978; Roetzel, 1983; Harzhauser and Mandic, 2002). Recent investigations of the herein described section near Pucking, however, proved an Aquitanian age (zone lower NN2) based on a nannoplankton assemblage with *Reticulofenestra minuta*, *R. pseudumbilica* and *R. haqii* (Gregorova et al., 2009). According to the regional stage system for the Central Paratethys, the deposits are part of the upper Egerian stage (Piller et al., 2007; Fig. 3).

The section was situated on the northern shelf of the Central Paratethys Sea (Fig. 1B). During the Early Aquitanian, the NAFB was covered by a deep sea (Rögl, 1998). The Paratethys was a huge sea at that time, reaching far into Asia. Within that system, the NAFB acted as a relatively narrow passage between the Mediterranean and the wide basins of the Carpathian Foredeep.

3. Materials and methods

The investigated material was collected at the Pucking section in the 1980s by private and scientific collectors. One of the samples bears a specimen of the sunfish *Austromola angerhoferi* described in Gregorova et al. (2009, fig. 5). High resolution sampling for micropaleontology and geochemical analyses was performed across an 8-cm-thick section on this rock slab (Fig. 2D).

Macrofauna. Well-preserved macrofossils have been recovered from various levels in the section. Rock slabs containing these fossils are stored in the collection of the Natural History Museum Vienna (NHMW; Plate 1). For the present study, this material is described and paleoecologically and paleoceanographically evaluated for the first time.

Foraminifers. Thirteen samples (F1–13) have been investigated from different levels in the Pucking section (including eight samples from the sunfish horizon; Fig. 2A). One sample (F14) is from the Ebelsberg locality. From each sample, 100 g of dried sediment were soaked in dilute H_2O_2 and wet sieved under running water with a

minimum mesh size of 63 μm . Planktic and benthic foraminifers have been identified based on Cicha et al. (1998). The sample material is stored at the NHMW.

Dinoflagellates. Two samples (D1–2) from the sunfish horizon have been analysed for dinoflagellate cysts. From each sample, 20 g were treated by standard palynological techniques following Green (2001). Two microscope slides per sample were investigated with a light microscope and the first 300 specimens were counted. Additionally, two SEM stubs were prepared from sample D2 and scanned using a DSM 982 Gemini SEM operating at a working voltage of 10kv. Dinoflagellate cyst nomenclature generally follows Fensome and Williams (2004) and Fensome et al. (2008). The material is stored in the collection of the Institute for Earth Sciences at the University of Graz.

Geochemical analyses. Eleven bulk sediment samples (I1–11) from the sunfish horizon were measured for $\delta^{18}O$ and $\delta^{13}C$ at the Institute for Earth Sciences at the University of Graz, using an automatic Kiel II preparation line and a Finnigan MAT Delta Plus mass spectrometer. Samples were dried and reacted with 100% phosphoric acid at 70 °C. Analytical precision, based on replicate analysis of international standards NBS-19 and NBS-18 and an internal laboratory standard, is better than 0.08‰ for $\delta^{18}O$ and 0.04‰ for $\delta^{13}C$. Results are reported in conventional δ -notation relative to the Vienna Pee Dee Belemnite standard (VPDB) in ‰ units.

Five samples (Bio1-5) from the sunfish horizon were selected for biomarker analysis. Representative portions of these samples were extracted for 1 h using dichloromethane in a Dionex ASE 200 accelerated solvent extractor at 75 °C and 50 bar. Asphaltenes were precipitated from a hexane–dichloromethane solution (80:1 according to volume) and separated by centrifugation. The fractions of the hexane-soluble organic matter were separated into saturated and aromatic hydrocarbons and resins using medium-pressure liquid chromatography with a Köhnen–Willsch MPLC instrument (Radke et al., 1980). The hydrocarbon fractions were analysed by a gas chromatograph equipped with a 30 m DB-5MS fused silica capillary column (i.d. 0.25 mm; 0.25 μm film thickness) coupled to a Finnigan MAT GCQ ion trap mass spectrometer. The oven temperature was programmed from 70 to 300 °C at a rate of 4 °C min^{-1} followed by an isothermal period of 15 min. Helium was used as the carrier gas. The mass spectrometer was operated in the EI (electron ionisation) mode over a mass range from m/z 50 to m/z 650 (0.7 s total scan time).

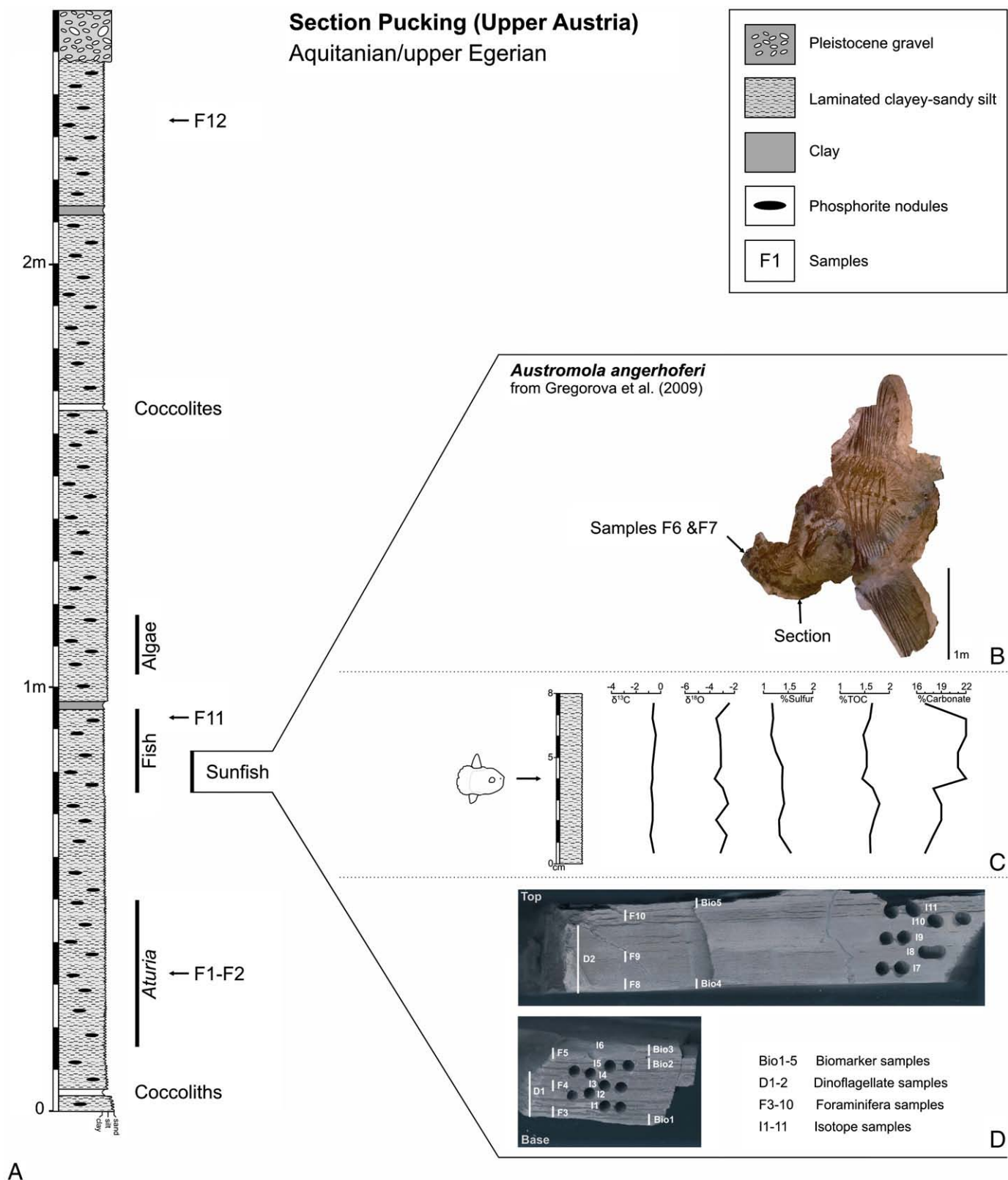


Fig. 2. The Pucking section. (A) Lithology and position of the fossil accumulation horizons and the micropaleontological samples. The exact position of sample F13 from a *Limacina* accumulation above the sunfish layer is not known. (B) Position of the section and samples F6–7 across the giant sunfish *Austromola angerhoferi*. (C) Results for the geochemical evaluation ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$, TOC, S, carbonate) of samples I1–11. Stable isotope ratios relative to VPDB. (D) Position of the samples within the sunfish layer.

Identification of individual compounds was accomplished on the basis of retention times in the total ion current chromatogram and comparison of mass spectra with published data.

Additionally, samples I1–11 and Bio1–5 were powdered and analysed for sulphur (S), total carbon (TC), and total organic carbon contents (TOC, after acidification of samples to remove carbonate)

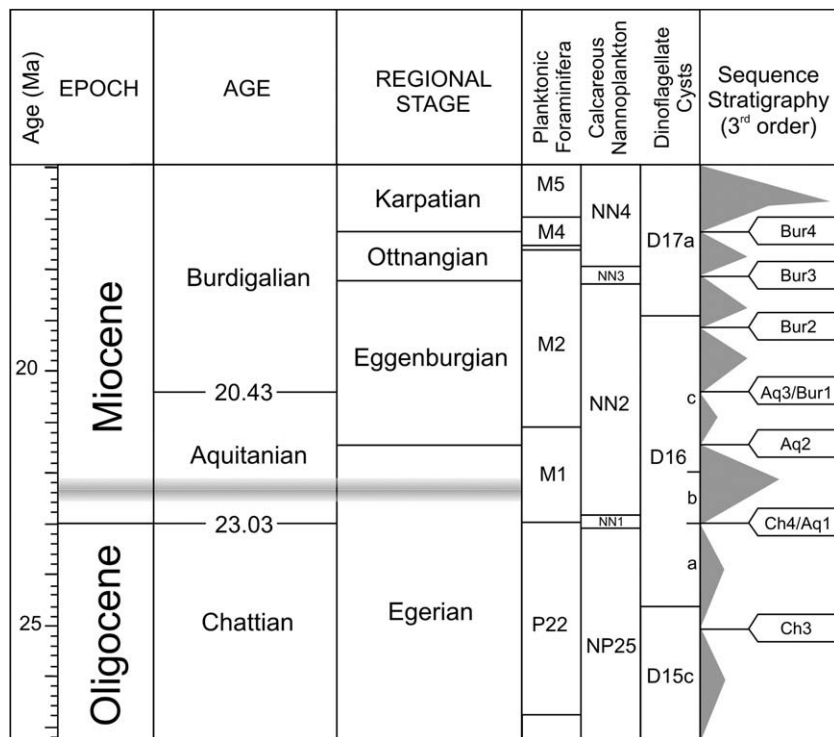


Fig. 3. Lower Miocene stratigraphy for the Central Paratethys based on Piller et al. (2007). The stratigraphic position of the studied sections is indicated by grey bar. Geochronology, biozonations of planktic foraminifers, calcareous nannoplankton and dinoflagellate cysts after Lourens et al. (2004), sequence stratigraphy and sea level curve after Hardenbol et al. (1998).

using a Leco CS-300 analyser. The difference between TC and TOC is the total inorganic carbon content (TIC). TIC contents were used to calculate calcite equivalent percentages ($= 8.34 * TIC$).

Rock-Eval pyrolysis (Espitalié et al., 1977) for samples Bio1–5 was carried out using a Rock-Eval 2+ instrument. By this method, the amount of hydrocarbons (mgHC/grock) present in the rock sample (S1) and released from kerogen during gradual heating (S2) were determined. The S2 content was normalised against TOC to give the Hydrogen Index ($HI = S2 * 100 / TOC$). T_{max} was measured as a thermal maturation indicator.

4. Results

4.1. Fossil mass occurrences

Only the palynoflora and leaf flora of Pucking and associated outcrops have been studied previously (Hochuli, 1978; Kovar, 1982). A detailed description of the fauna is largely missing aside from single descriptions of a rare echinoid (Kroh, 2005), a razorbill (Mlíkovský, 1987) and the giant sunfish *Austromola* (Gregorova et al., 2009).

The survey of the collections of the NHMW clearly showed that the Pucking section is outstanding in the composition of the fauna and sheer number of species. Although total diversity is impressive, taxa are not distributed evenly. They appear in distinct associations in peculiar layers, sometimes forming nearly monospecific occurrences with the exception of driftwood associations.

In the basal part of the section, several horizons occur with accumulations of the nautilid cephalopod *Aturia* (Fig. 2A; Plate I, fig. 9). The shells are distinctly larger than those of the widespread Miocene *Aturia aturi* (Basterot, 1825) and might represent an undescribed species. The compressed mode of preservation, however, hampers serious taxonomic analysis. All *Aturia* accumulations are associated with thalli of the brown seaweed *Cystoseirites altoaustriacus* Kovar, 1982 and other unidentified thalli of phycophytes.

A second type of accumulation consists mainly of fish skeletons (Plate I, figs. 2–4). These are largely articulated, although most specimens display initial stages of decay (e.g. scales are detached). An analysis of the fish fauna has yet to be undertaken, but some comments are given by Pfeil (1983). Based on the collections of the NHMW, the diversity is moderate, with about 10 common taxa out of which four predominate: pipefish (Syngnathidae), hake (Merlucciidae), herring

Plate I. Compilation of various macrofossils contributing to the mass-accumulations.

1. Undescribed dolphin (length: 230 cm).
2. Partly disarticulated skeleton of a hake (Merlucciidae; length: 140 mm; 2003z0026/0477).
3. Largely complete skeleton of a herring (Clupaeidae; length of head: 60 mm; 2003z0026/0397).
4. Slab with several specimens of pipefish (Syngnathidae; length of largest specimen: 125 mm; 2003z0026/0159).
5. Undescribed lepadid cirripedes attached to driftwood (height: 160 mm; NHM2003z0026/0487).
6. Pteropod bloom consisting of *Limacina* sp. in association with algae (length: c. 150 mm; NHM 1980/25).
7. Pteropod bloom consisting of *Clio* sp. from the near Ebelsberg locality (length: 185 mm; NHM 2003z0026/0926).
8. Brown seaweed *Cystoseirites altoaustriacus* Kovar, 1982 with aerocysts (length: 120 mm).
9. *Aturia* sp. (diameter: 80 mm) in association with phycophyta thalli.
10. Articulated shells of the lucinids bivalve *Megaxinus bellardianus* (Mayer, 1864) (diameter: 52 mm; NHM 2003z0026/01919). These bivalves are frequently found in situ within the sediment.

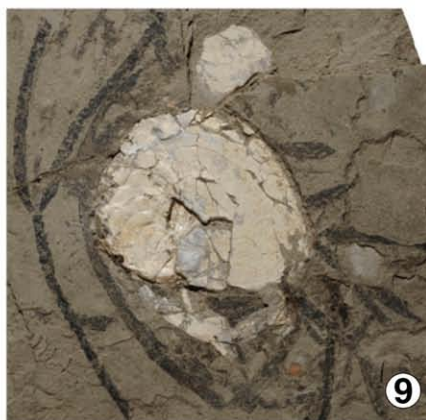
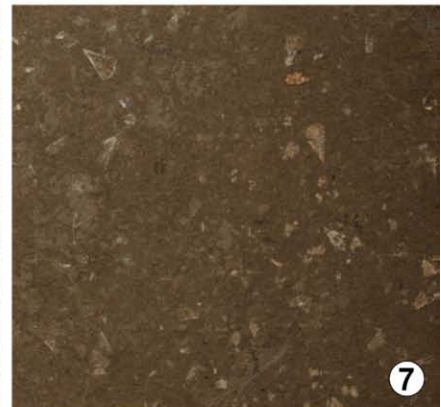
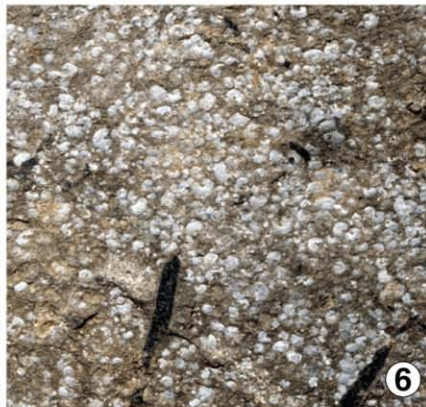


Table 1
Distribution and abundance of benthic foraminifers from samples F1–14. Single (s) = 1; rare (r) = 2–9; abundant (a) = ≤10.

Species	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13	F14
<i>Ammodiscus tenuissimus</i>		s	r	s	r			a	r		s			
<i>Bathysiphon filiformis</i>		r												
<i>Budashevaella?</i>		r												
<i>Gaudryinopsis austriacus</i>		a						r				r		
<i>Haplophragmoides laminatus</i>	a	a	s	r	s	r	s	a		a		a	a	
<i>Haplophragmoides peripheroexcavatus</i>								r						
<i>Haplophragmoides vasiceki</i>								r				r		
<i>Milliammina</i> sp.										s				
<i>Recurvoides</i> sp.		r						s						
<i>Semivulvulina</i> sp.									s					
<i>Alabamina wolterstorffi</i>														r
<i>Ammonia discigera</i>						s	r	s	r	r		r	s	
<i>Ammonia pseudobeccarii</i>			s						r					
<i>Ammonia tepida</i>									s					
<i>Ammonia viennensis</i>												s		
<i>Amphicoryna badenensis</i>								s		r	r			
? <i>Amphicoryna</i> sp.														s
<i>Amphimorphina haueriana</i>						s	s		r					a
<i>Angulogerina angulosa</i>											r		s	
<i>Angulogerina esuviensis</i>													r	
<i>Angulogerina cf. muralis</i>											r			
<i>Asterigerinata planorbis</i>				s										
<i>Aubignyna kiliani</i>				s		s		r	r	r				
<i>Baggina dentata</i>												r		
<i>Biapertorbis alteconicus</i>								r	r		s		s	
<i>Biapertorbis biaperturatus</i>				s		r		r	r	r				
<i>Bolivina beyrichi</i>													r	
<i>Bolivina crenulata</i>	s	r	s	a	a	a	a	a	a	a	r	a	r	a
<i>Bolivina fastigia</i>		s			s	s		s	r	r		r		r
<i>Bolivina grabenensis</i>														r
<i>Bolivina korynoides</i>			s	r	s	a	a	s		a				
<i>Bolivina subalpina</i>														a
<i>Bolivina trunensis</i>	r	r	a	a	a	a	a	a	a	a		a	a	a
<i>Bolivina versatilis</i>													r	
<i>Buccella propinqua</i>			s	s		r								
<i>Bulimina striata</i>														r
<i>Buliminella acicula</i>		r										a		
<i>Cancris primitivus</i>									s					
<i>Cancris turgidus</i>								s				r		
<i>Cassidulina laevigata</i>												s		
<i>Caucasina coprolithoides</i>		r								a			a	a
<i>Caucasina schischkinskayae</i>		a	s	r	s		r	r	r	r		r	a	a
<i>Cibicidoides lopjanicus</i>		s			r		s	r	a			s	r	
<i>Cibicidoides lucidus</i>						r								
<i>Cibicidoides punctatus</i>									s					
<i>Cibicidoides slovenicus</i>													s	
<i>Cibicidoides tenellus</i>		s											r	
<i>Cibicidoides ungerianus</i>								r						
<i>Cibicidoides</i> spp.	s						r		r				r	
<i>Cycloforina ludwigi</i>										s				
<i>Cycloforina</i> sp.				s										
<i>Elphidiella cryptostoma</i>							s							
<i>Elphidiella dollfusi</i>				s		s		r	a	a				
<i>Elphidiella heteropora</i>										s				s
<i>Elphidiella minuta</i>				s		r							s	
<i>Elphidiella roemeri</i>				s										
<i>Elphidiella subcarinata</i>				r			r	s	r					
<i>Elphidiella subnodosa</i>			s	s	s	r	r	r	r	r				
<i>Elphidium crispum</i>									r					
<i>Elphidium felsense</i>									s	s				
<i>Elphidium karpaticum</i>			r		s			r	r		s			
<i>Elphidium cf. matzenense</i>					s									
<i>Elphidium cf. ortenburgense</i>					s				r					
<i>Elphidium praeforme</i>									r	s				
<i>Eoeponidella ampliportata</i>	s		s	a		a	a	r	r	a		r	r	
? <i>Epistominella</i> sp.														s
<i>Escomebovina cuvillieri</i>	r		r		r	r	r	r	a		r	r		
<i>Escomebovina orthorapha</i>			s		s		r	r		r		r		
<i>Escomebovina trochiformis</i>	s			r	s	a	a	r	a	a		r	r	
<i>Escomebovina</i> sp.														s
? <i>Escomebovina</i> sp.														s
<i>Fissurina buchneri</i>										s			s	
<i>Fissurina corrosa</i>														s
<i>Fissurina marginata</i>										s				

Table 1 (continued)

Species	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13	F14
<i>Fursenkoina acuta</i>				s	s									r
<i>Fursenkoina cf. mustoni</i>												r		
<i>Globobulimina pupoides</i>											r			
<i>Globocassidulina subglobosa</i>				s	s		s		r	r		r	r	a
<i>Globulina gibba</i>								r						s
<i>Grigelis pyrula</i>											s			
? <i>Gyroidina brockerti</i>				s										
<i>Gyroidinoides parvus</i>										r				r
<i>Gyroidinoides soldanii</i>					s								s	
<i>Hanzawaia boueana</i>			s	r	s			r	r	a			r	
<i>Hanzawaia hovcici</i>														a
<i>Hemirobulina sp.</i>											s			
<i>Heterolepa dutemplei</i>											s			
<i>Laevidentalina inornata</i>	r						r	s			r	s	r	
<i>Laevidentalina intermedia</i>												r		
<i>Laevidentalina reussi</i>											r			
<i>Lagena catenulata</i>										s				
<i>Lagena filicosta</i>										r				
<i>Lagena haidingeri</i>									s					s
<i>Lagena striata</i>										s				
<i>Lenticulina inornata</i>	s		s	r	s	s	r	r	a	a	r			
<i>Lenticulina spp.</i>		r							r			a	r	a
<i>Marginulina subregularis</i>		r										r		r
<i>Marginulina sp.</i>	s													
<i>Melonis pompilioides</i>										s				
<i>Myllostomella advena</i>	s		r	a	h	a	a	a	a	a		s	r	a
? <i>Neoconorbina sp.</i>									r	r			s	
<i>Neugeborina longiscata</i>								r	s			r		
<i>Nonion commune</i>		r	s	s	s			s	s	a	s	s	r	a
<i>Nonionellina sp.</i>														a
<i>Nuttallides convexus</i>				r			r			r		r		
<i>Parrelloides sp.</i>				r		r								
<i>Planularia moravica</i>														s
<i>Plectofrondicularia sp.</i>												s		a
<i>Porosonion roemeri</i>							r	s	r	a				
? <i>Porosonion sp.</i>														s
<i>Pseudoparrella exigua</i>	r			r	s	a	r	r	s	r		r	a	r
<i>Pseudoparrella sp.</i>	r			a	s	r	r	r	r	a		r	a	a
<i>Sigmoilinita sp.</i>									s					r
<i>Siphonodosaria adolphina</i>											s			r
<i>Siphonodosaria cf. consobrina</i>														s
<i>Siphonodosaria scripta</i>													s	
<i>Sphaeroidina variabilis</i>														r
? <i>Stomatorbina sp.</i>				s										
<i>Trochulina uhligi austriaca</i>							r			s				
<i>Turrilina alsatica</i>							s	r	r	r				
<i>Uvigerina cf. gracilis</i>												s		
<i>Uvigerina cf. rudlingensis</i>												r		
<i>Valvulineria complanata</i>												s		
<i>Valvulineria palmarealensis</i>										s				r
<i>Valvulineria sp.</i>														s
<i>Virgulopsis tuberculatus</i>			s						s					

(Clupeidae) and mackerel (Scombridae). The syngnathids tend to form monospecific accumulations, whereas the other fishes are less exclusive. Comber (Serranidae), jack fish (Carangidae) and boarfish (Caproidae) are distinctly less frequent. Most eye catching is the occurrence of at least three almost complete specimens of the giant sunfish *Austromola angerhoferi* Gregorova et al. (2009), which attained a diameter up to c. 3 m. This is the largest fossil Cenozoic teleost known so far. Sharks are represented only by few isolated teeth. Within the same horizon, a near complete dolphin skeleton (undescribed; Plate I, fig. 1) and a skeleton of the razorbill *Petalca austriaca* Mlíkovský, 1987 have been found.

Pteropod mass occurrences consisting either of *Limacina sp.* or of *Clio sp.* are intercalated several times within the section (Plate I, figs. 6–7). These horizons lack fish skeletons or *Aturia* shells but may contain algal thalli.

Aside from these accumulations, several mollusc taxa are found throughout the section. The mollusc fauna is of low diversity and

dominated by few species. Among the gastropods, a single unidentified turrid species and the naticid *Euspira helicina* (Brocchi, 1814) predominate. Bivalves are represented by the lucinid *Megaxinus bellardianus* (Mayer, 1864), the nuculid *Nucula*, and the small pectinid *Deletopecten*. Most bivalves are articulated with only slightly gaping valves (Plate I, fig. 10). Lucinids occur in life position perpendicular to the bedding.

Echinoderms are rare at Pucking. Only few specimens of spatangoids and *Linthia summesbergeri* Kroh (2005) have been reported (Kroh, 2005).

Frequently found are centimetre to decimetre long pieces of lignite which are often completely penetrated by teredinid bivalves (Plate I, fig. 5). These are interpreted as driftwood falls. The bivalves *Perna aquitana* (Mayer-Eymar, 1858) and an isognomid bivalve are also typical driftwood associates along with unidentified bryozoans and polychaetes. At least two species of probably undescribed barnacles of the family Lepadidae occur attached to the driftwood.

Table 2
Distribution and abundance of planktic foraminifers from samples F1–14. Single (s) = 1; rare (r) = 2–9; abundant (a) = ≤ 10 .

Species	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13	F14
<i>Globigerina anguliofficialis</i>				r	s						r			a
<i>Globigerina dubia</i>												r		
<i>Globigerina cf. falconensis</i>				s							a			
<i>Globigerina gnaucki</i>					s					r	a	a		a
<i>Globigerina lentiana</i>								s		r	a	a	s	
<i>Globigerina officinalis</i>			s		s				s	a	a	r	a	a
<i>Globigerina ottmangiensis</i>			s								r	a	a	a
<i>Globigerina ouachitaensis</i>											r		r	s
<i>Globigerina praebulloides</i>				s	s		r	s		a	a	a	a	
<i>Globigerina steiningeri</i>											s	a	r	r
<i>Globigerina sp.</i>														r
<i>Globigerinella cf. obesa</i>										r	r			
<i>Globoturborotalita connecta</i>												r		
<i>Globoturborotalita woodi</i>														a
<i>Tenuitella brevispira</i>		r	s	r	s	a	r	r	a	a		a	a	r
<i>Tenuitella clemenciae</i>			s	r	s		r							r
<i>Tenuitella minutissima</i>			s		s	r			r	r		r	r	
<i>Tenuitellinata angustiumbilitata</i>		r	s	r	s	a	r	r	a	a		a	a	
<i>Tenuitellinata pseudoedita</i>				r	s		r		a	a			r	s
<i>Tenuitellinata sp.</i>				a	s	a	a	r	a	a		a	a	s

4.2. Foraminifers

The distribution of foraminifers is summarized in Tables 1 and 2. Benthic assemblages at Pucking are dominated by *Haplophragmoides laminatus*, *Bolivina* spp., *Caucasina* spp., *Eoepionidella* spp., *Myllostomella advena* and *Pseudoparella* spp. throughout the section (Plate II). The sample from Ebelsberg revealed a similar benthic fauna dominated by *Bolivina* spp., *Caucasina* spp., *Globocassidulina subglobosa*, *Lenticulina* spp., nonionids, *Plectofrondicularia* sp. and *Pseudoparella exigua*. The observed foraminifers display very small test sizes.

Planktic assemblages consist of globigerinid and microperforate tenuitellid species. While the latter are dominant in the samples from the *Aturia* and sunfish horizons in the lower part of the section, globigerinids predominate in samples F11–13. The sample from Ebelsberg (F14) revealed a planktic fauna dominated by globigerinids.

The composition of the assemblages differs according to the macrofaunal accumulations with which they are associated. From the *Aturia* accumulations only few foraminifers were revealed. *Caucasina schischkinskayae* and the agglutinated species *Haplophragmoides laminatus* and *Gaudryinopsis austriacus* dominate the benthic assemblages. Planktic foraminifers are scarce, with only two tenuitellid species documented from sample F2. In contrast, the samples from the sunfish horizon revealed a rich fauna. Benthic communities are dominated by small species of *Bolivina*, *Caucasina*, *Eoepionidella*, *Escornebovina* and

Myllostomella. Mass occurrences of tenuitellid species are recorded while globigerinids occur only in small numbers. Finally, benthic foraminifers from a *Limacina* accumulation (F13) are dominated by *H. laminatus*, *Bolivina trunensis*, *Caucasina* spp. and *Pseudoparella* spp. Tenuitellid and globigerinid species are equally abundant.

4.3. Dinoflagellates

The two investigated samples revealed fairly well-preserved specimens. The recorded assemblages are mainly composed of *Cordosphaeridium cantharellus*, *Glaphyrocysta* spp., *Homotryblium tenuispinosum*, *Lejeunecysta* spp., *Lingulodinium machaerophorum*, *Polysphaeridium zoharyi*, *Selenopemphix* spp., *Spiniferites/Achomosphaera* spp. and round brown cysts (*Brigantedinium?* spp.) (Table 3; Plate III). Other dinoflagellate cyst taxa occur only in small numbers. Additionally, acritarchs (*Paralecaniella indentata* and *Cyclopsella* spp.) and foraminiferal test linings are common.

Many of the revealed taxa have a long biostratigraphic range and extend from Paleogene to mid-Miocene (e.g., *Apteodinium spiridoides*, *Cleistosphaeridium placacanthum*, *Cordosphaeridium cantharellus*, *Cribroperidinium* spp., *Distatodinium paradoxum*, *Glaphyrocysta* spp., *Homotryblium tenuispinosum*, *Hystrichokolpoma* spp., *Reticulosphaera actinocoronata*, *Thalassiphora pelagica* and *Tuberculodinium vancampoae*). However, in agreement with the calcareous nannoplankton data of

Plate II. Compilation of the most common planktic and benthic foraminifers.

- Tenuitella brevispira* Subbotina, 1960; sample F10.
- Tenuitellinata angustiumbilitata* Bolli, 1957; sample F10.
- Tenuitella minutissima* Bolli, 1957; sample F9.
- Globigerina praebulloides* Blow, 1959; sample F11.
- Globigerina gnaucki* Blow and Banner, 1962; sample F11.
- Globigerina ottmangiensis* Rögl, 1969; sample F12.
- Myllostomella advena* Cushman and Laiming, 1931; sample F9.
- Haplophragmoides laminatus*; Voloshinova, 1961; sample F13.
- Escornebovina cuvillieri* Poignant, 1965; spiral view; sample F9.
- Caucasina schischkinskayae* Samoylova, 1947; sample F10.
- Caucasina coprolithoides* Andreae, 1884; sample F10.
- Bolivina trunensis* Hofmann, 1967; sample F7.
- Bolivina korynoides* Hofmann, 1967; sample F7.
- Bolivina crenulata* Cushman, 1936; sample F7.
- Bolivina fastigia* Cushman, 1936; sample F9.
- Pseudoparella exigua* Brady, 1884; spiral view; sample F7.
- Pseudoparella exigua* Brady, 1884; umbilical view; sample F7.
- Escornebovina trochiformis* Andreae, 1884; spiral view; sample F7.
- Escornebovina trochiformis* Andreae, 1884; umbilical view; sample F7.
- Eoepionidella ampliportata* Reiser, 1987; sample F7.

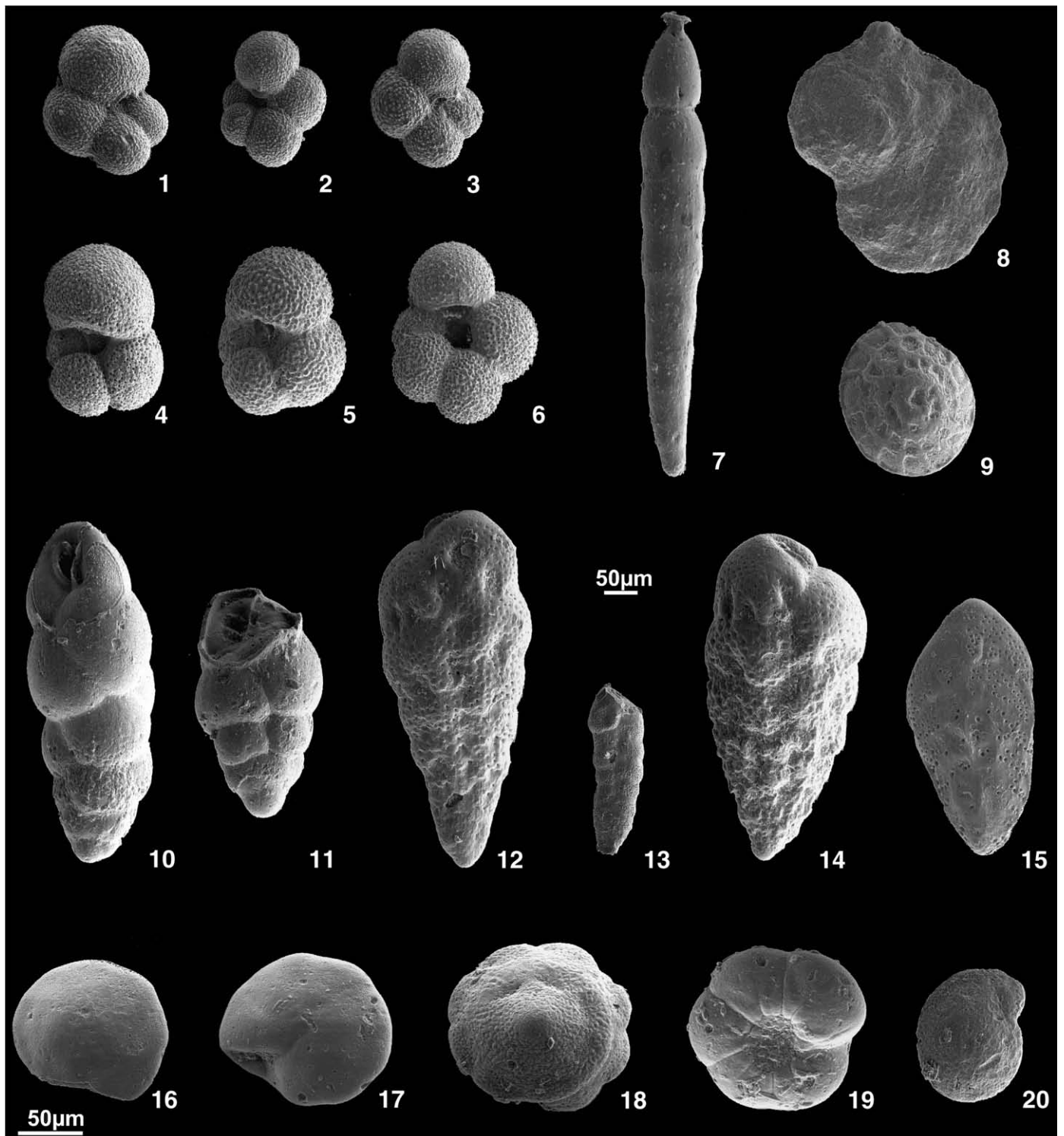


Table 3
Frequency of dinoflagellate cysts, acritarchs and other marine microfossils from samples D1 and D2. “x” marks single specimens of taxa documented outside the routine counting.

Species	D1	D2
Dinoflagellate cysts		
<i>Apteodinium spiridoides</i>	0	1
<i>Batiacasphaera sphaerica</i>	1	x
<i>Cleistosphaeridium placacanthum</i>	2	x
<i>Cordosphaeridium cantharellus</i>	24	31
<i>Cordosphaeridium minimum</i>	0	x
<i>Cribroperidinium giuseppi</i>	0	1
<i>Dapsilidinium pseudocolligerum</i>	2	3
<i>Deflandrea phosphoritica</i>	5	5
<i>Distatodinium apenninicum?</i>	0	x
<i>Distatodinium paradoxum</i>	2	x
<i>Glaphyrocysta</i> spp.	25	25
<i>Heteraulacacysta</i> sp.	0	x
<i>Homotryblium tenuispinosum</i>	29	42
<i>Hystrichokolpoma denticulatum</i>	1	x
<i>Hystrichokolpoma cinctum</i>	1	1
<i>Hystrichosphaeropsis obscura</i>	0	x
<i>Hystrichokolpoma rigaudiae</i>	2	1
<i>Lejeunecysta</i> spp.	12	18
<i>Lingulodinium machaerophorum</i>	14	5
<i>Melitasphaeridium choanophorum</i>	0	x
<i>Melitasphaeridium pseudorecurvatum</i>	0	x
<i>Nematosphaeropsis labyrinthus</i>	1	3
<i>Operculodinium israelianum</i>	0	x
<i>Operculodinium</i> spp.	6	6
<i>Polysphaeridium zoharyi</i>	16	23
<i>Reticulatosphaera actinocoronata</i>	5	1
<i>Selenopemphix nephroides</i>	4	2
<i>Selenopemphix quanta</i>	4	16
<i>Spiniferites/Achomospaera</i> spp.	57	39
<i>Stoveracysta conerae</i>	x	0
<i>Thalassiphora pelagica</i>	8	1
<i>Tuberculodinium vancampoeae</i>	5	7
<i>Xandarodinium xanthum</i>	1	1
Round brown cysts (? <i>Brigantedinium</i>)	71	60
Cysts indet.	2	8
Total dinoflagellate cysts	300	300
Acritarchs and other marine microfossils		
<i>Paralecaniella indentata</i>	7	19
<i>Cyclopsiella</i> spp.	2	5
Foraminiferal test lining	15	14

Gregorova et al. (2009), the co-occurrence of *Deflandrea phosphoritica*, *Distatodinium apenninicum?*, *Hystrichosphaeropsis obscura* and *Stoveracysta conerae* suggests an Early Miocene, most likely Aquitanian age (Biffi and Manum, 1988; Brinkhuis et al., 1992; Zevenboom, 1995; de Verteuil and Norris, 1996; Lourens et al., 2004; Munsterman and Brinkhuis, 2004).

The highest occurrence of *Deflandrea phosphoritica* has been used to define the top of dinocyst zone DN1 (latest Oligocene–earliest

Miocene) of the eastern U.S.A. (de Verteuil and Norris, 1996). Accordingly, Munsterman and Brinkhuis (2004) recorded the highest occurrence of *D. phosphoritica* within their SNSM1a subzone of latest Chattian–earliest Aquitanian age from the Southern North Sea Basin. In the Lemme section of northern Italy, *D. phosphoritica* extends into the Early Miocene *Membranilamacia? picena* (Mpi) Interval Zone (Zevenboom, 1995). The highest occurrence of *Distatodinium apenninicum* has been used to identify the base of the Early Miocene Dap Interval Subzone of northern Italy (Brinkhuis et al., 1992). Thus, the co-occurrence of *D. phosphoritica* and *D. apenninicum* indicates an Early Miocene age (Zevenboom, 1995; Williams et al., 2004).

Biffi and Manum (1988) used the lowest occurrence of *Stoveracysta conerae* to define the base of their Early Miocene DM2 Zone of northern Italy. In the NW Atlantic, the lowest occurrence of *S. conerae* is recorded within DN1 and its highest occurrence defines the top of the DN2 Interval Zone (early–middle Early Miocene; de Verteuil and Norris, 1996). *Hystrichosphaeropsis obscura* has been recorded in DN2 (de Verteuil and Norris, 1996) and SNSM2 Zone (Munsterman and Brinkhuis, 2004).

4.4. Geochemistry

4.4.1. Stable isotopes

Stable isotope ratios are rather constant, ranging from -0.8% to -0.41% (mean: -0.62%) for $\delta^{13}\text{C}$ and -2.55% to -3.69% (mean: -3.12%) for $\delta^{18}\text{O}$ (Table 4). No distinct change or trend is observed.

4.4.2. Organic carbon, sulphur and carbonate content

The evaluation of organic carbon, sulphur and carbonate content revealed relatively uniform results (Table 4; Fig. 2C; TOC: 1.5–1.9%; S: 1.0–1.6%; carbonate: 17–22; TOC/S: 1–1.7). While TOC and S do not show distinctive trends, a slight rise in carbonate content is documented for the upper part of the section. TOC/S ratios in the order of 1.1 to 1.7 suggest oxygen depleted conditions during deposition of the sediments (Bernier, 1984).

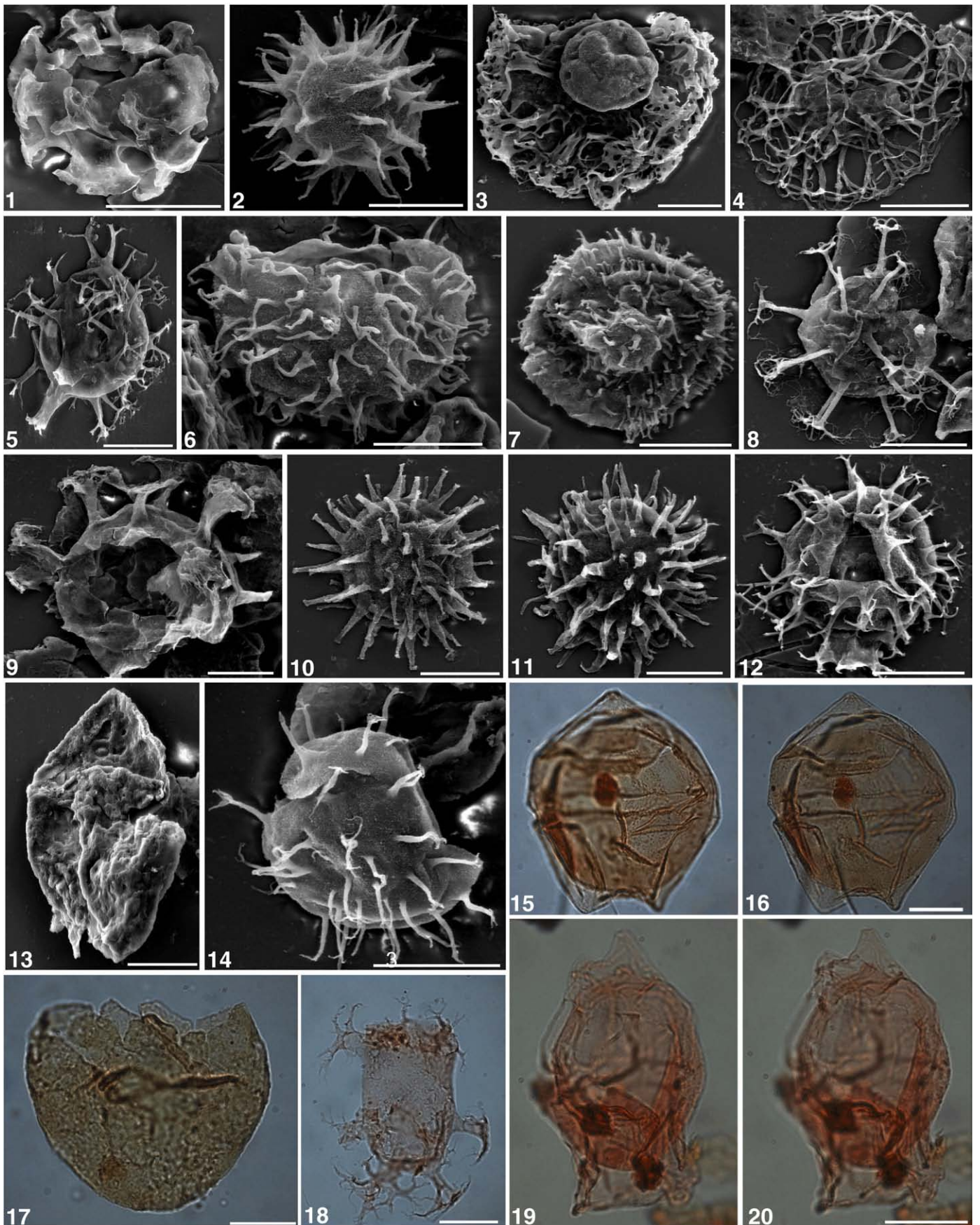
4.4.3. Biomarker composition

GC traces of the five samples studied are very similar (Tables 5,6). Representative examples of the distribution of revealed compounds are given in Figs. 4 and 5.

n-Alkanes and isoprenoids. All samples are characterized by bimodal *n*-alkane distributions with similar contributions of short-chain (C_{15} – C_{19}) and long-chain (C_{27} – C_{31}) *n*-alkanes relative to the sum of total *n*-alkanes (C_{15} – C_{33}). This suggests a contribution of both, algal material and higher terrestrial plants (Peters et al., 2005). Pristane/phytane (Pr/Ph) ratios vary in a narrow range between 0.9 and 1.4. According to Didyk et al. (1978), Pr/Ph ratios below 1.0 indicate anaerobic conditions during early diagenesis, and values between 1.0 and 3.0 reflect dysaerobic environments. However, Pr/Ph

Plate III. Compilation of selected dinoflagellate cysts from samples D1 and D2. Scale bar 20 μm .

1. *Distatodinium apenninicum?* Brinkhuis et al., 1992; dorsal view.
2. *Dapsilidinium pseudocolligerum* Stover, 1977 Bujak et al., 1980; uncertain orientation.
3. *Glaphyrocysta* sp.; ? ventral view.
4. *Nematosphaeropsis labyrinthus* Ostfeld Reid, 1974; uncertain orientation.
5. *Achomospaera ramulifera* Deflandre Evitt, 1963; later view.
6. *Cleistosphaeridium placacanthum* Deflandre and Cookson Eaton et al., 2001; ?ventral view.
7. *Operculodinium israelianum* Rossignol Wall, 1967; uncertain orientation.
8. *Reticulatosphaera actinocoronata* Benedek Bujak and Matsuoka, 1986; uncertain orientation.
9. *Cordosphaeridium cantharellus* Brosius Gocht, 1969; ?dorsal view.
10. *Polysphaeridium zoharyi* Rossignol Bujak, Downie, Eaton and Williams, 1980; uncertain orientation.
11. *Lingulodinium machaerophorum* Deflandre and Cookson Wall, 1967; uncertain orientation.
12. *Spiniferites mirabilis* Rossignol Sarjeant, 1970; dorsal view.
13. *Apteodinium spiridoides* Benedek, 1972; dorsal view.
14. *Melitasphaeridium pseudorecurvatum* Morgenroth, 1966 Bujak et al., 1980; left-lateral view.
- 15, 16. *Deflandrea phosphoritica* Eisenack, 1938; dorsal view, successive foci.
17. *Stoveracysta conerae* Biffi and Manum, 1988; ventral view.
18. *Distatodinium paradoxum* Brosius Eaton 1976; uncertain orientation.
- 19, 20. *Hystrichosphaeropsis obscura* Habib, 1972; right lateral view.



ratios are known to be affected also by maturation (Tissot and Welte, 1984) and by differences in the precursors of acyclic isoprenoids (i.e. bacterial origin; Volkman and Maxwell, 1986; ten Haven et al., 1987). Moreover, a bacterial origin for phytane from phytanyl ether lipids found in archaeobacteria, as well as the formation of pristane from tocopherols (vitamin-E) or chromans (Goossens et al., 1984), cannot be excluded. Maturity variations within the studied sample set can be excluded. Therefore and because oxygen depleted conditions are supported by very low TOC/S ratios, we consider Pr/Ph ratios as an appropriate redox indicator in the present case.

Sesquiterpenoids. In all samples, aromatic sesquiterpenoids of the cadinane-type, dominated by cadalene (Fig. 5), are observed (Simoneit and Mazurek, 1982). This compound, together with retene, is specific for resinous input from higher plants.

Steroids and hopanoids. There is little variation in the relative amounts of C₂₇, C₂₈ and C₂₉ steranes. All samples are dominated by C₂₉ steranes (55–60%), which are typically related to land plants (Volkman, 1986). In contrast, relative abundances of C₂₈ steranes are low (12–21%). Whereas high amounts of C₂₇ steranes are indicative of algal material, C₂₈ steranes have been related to phytoplankton including diatoms, coccolithophorides and dinoflagellates (Grantham and Wakefield, 1988).

The steranes/hopanes ratio is a measure of organic matter production by autotrophic eukaryotes (e.g. algae, land plants) versus bacterial activity. The determined ratios (0.9–1.0) are nearly identical in all samples. Nevertheless a positive correlation between the steranes/hopanes ratio and the relative contribution of long-chain *n*-alkanes can be observed (correlation coefficient r^2 : 0.78), suggesting that the ratio is mainly controlled by the relative input of land plants.

Chromans. In all samples 2,5,7,8-tetramethyl-2-(4',8',12'-trimethyltridecyl) chroman (tri-MTTC) predominates over the 2,5,8-trimethyl-2-(4',8',12'-trimethyltridecyl) chroman (di-MTTC). Although the origin of methylated MTTCs is not yet understood, methylated MTTCs have been widely used for palaeosalinity reconstruction (Sinninghe Damsté et al., 1993; Barakat and Rullkötter, 1997). The ratio between tri-MTTC and the sum of MTTCs is proportional to salinity. The detected ratios (0.6–1.0) suggest normal saline conditions.

4.4.4. Rock-Eval pyrolysis

Hydrogen Index values ranging from 170 mgHC/gTOC to 200 mgHC/gTOC indicate a type III kerogen. Calculated T_{\max} -values around 425 °C suggest that the organic matter is thermally immature.

5. Discussion

5.1. The paleoceanographic setting

5.1.1. Paleogeography

The investigated section was situated on the northern shelf of the NAFB (Fig. 1B). The Aquitanian coastline of the Paratethys Sea in the area of the Bohemian Massif cannot be reconstructed due to erosion. Nevertheless a minimum distance of the Pucking section to the coast can be calculated on the ancient coastline represented by the escarpment of the Bohemian Massif in the Linz area. This formed the coast, with characteristic lithologies and fauna, during the late Oligocene (Harzhauser and Mandic, 2002), whereas during the Aquitanian the coast was located further to the NNE due to the transgressive character of the Ebelsberg Formation. This assumption suggests an offshore position of the Pucking section at the time of deposition, at a minimum distance of c. 10 km to the north and c. 20 km to the northeastern coast. In any case, the Pucking section is located offshore of the many tectonically induced embayments, such as the Linz Bay, the Gallneukirchen Bay and others that structured the rocky shore. To the west and the south the shelf passed into the deep North Alpine Foreland Basin with estimated depths of 1000–1500 m (Rögl et al., 1979).

Table 4

Stable isotope values, TOC-, S-, CaCO₃-content and TOC/S ratios of samples I1–I11. Isotopic values are given relative to VPDB.

Sample	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	S	TOC	Carbonate	TOC/S
I1	−0.54	−3.19	1.57	1.61	17	1.0
I2	−0.8	−2.68	1.33	1.6	18	1.2
I3	−0.65	−3.53	1.31	1.69	19	1.3
I4	−0.66	−2.55	1.41	1.81	19	1.3
I5	−0.76	−2.95	1.37	1.67	18	1.2
I6	−0.64	−3.69	1.37	1.47	22	1.1
I7	−0.65	−3.08	1.39	1.55	21	1.1
I8	−0.52	−3.1	1.25	1.55	21	1.2
I9	−0.41	−3.18	1.15	1.48	22	1.3
I10	−0.63	−3.55	1.2	1.59	22	1.3
I11	−0.55	−2.87	1.18	1.65	17	1.4

Depth estimates for the investigated deposits are not precise due to the wide range of bathymetric distributions of the revealed benthic foraminifers. The common occurrence of *Haplophragmoides* indicates a water depth greater than 100 m (Murray, 2006). The scarce occurrence of the shallow-water taxa *Ammonia* and *Elphidium* is interpreted as transport from the coast. Furthermore, recent tenuitellids are exclusively described from offshore sites in basins deeper than 100 m (Li and McGowran, 1998) and from oceanic environments (Li et al., 1992). This interpretation is in good agreement with an outer shelf to slope position for the Ebelsberg Formation suggested by Wagner (1998).

5.1.2. Upwelling-induced primary productivity as trigger of an oxygen minimum zone

Low oxygen conditions prevailed on the shelf, favouring the preservation of organic matter. The benthic foraminiferal assemblages, dominated by bolivinids and buliminids, bear strong evidence of oxygen depleted environments with concentrations below 1 ml/l (Bernhard and Sen Gupta, 1999). The agglutinated taxa *Gaudryinopsis* and *Haplophragmoides* have been reported previously from dysoxic environments in the Central Paratethys (Spezzaferri et al., 2002). The scarce occurrence of epifaunal taxa seems to be linked to low oxygen conditions too (Murray, 2001): for recent benthic communities it has been shown that the critical oxygen concentration for epifaunal taxa is around 1 ml/l. Below this threshold only infaunal foraminifers better adapted to low oxygen environments occur. Finally, the overall small test size points to stressful conditions hampering carbonate precipitation.

Accordingly, the extremely depleted mollusc fauna with the sulphur-oxidizing bacterial symbiosis of the lucinids documents a low oxygen environment (Schweimanns and Felbeck, 1985). The presence of sulphur bacteria, indirectly recorded by pyrite framboids, further supports this interpretation. Finally, the absence of bioturbation documents that the sediment was probably dysoxic from a few mm downwards. Oxygen depletion culminated in repeated episodes of anaerobic conditions in the bottom water, allowing the

Table 5

Bulk organic geochemical parameters and concentration ratios of selected compound groups and biomarkers.

Sample	TOC (%)	Calcite S (%)	TOC/S (%)	T_{\max} (°C)	S1 (mg _{HC} /g _{Rock})	S2	HI (mg _{HC} /g _{TOC})	
BIO1	1.76	17.4	1.06	1.67	425	0.24	3.40	200
BIO2	1.72	18.9	1.49	1.15	425	0.22	2.88	180
BIO3	1.77	19.5	1.21	1.46	427	0.23	2.89	193
BIO4	1.90	18.4	1.25	1.52				
BIO5	1.66	17.2	1.42	1.16	425	0.20	2.69	168

Table 6

Concentration ratios of selected compound groups and biomarkers.

Sample	$n\text{-C}_{15-19}/n\text{-C}_{15-33}$	$n\text{-C}_{21-25}/n\text{-C}_{15-33}$	$n\text{-C}_{27-31}/n\text{-C}_{15-33}$	CPI	Pristane/ phytane	Steranes (%)			Steranes/ hopanes	di-MTTC/ tri-MTTC
						C ₂₇	C ₂₈	C ₂₉		
BIO1	0.37	0.11	0.39	2.50	0.89	29	16	55	0.94	0.77
BIO2	0.44	0.10	0.35	2.91	1.07	31	12	57	0.89	0.97
BIO3	0.40	0.09	0.42	3.04	1.08	29	13	58	1.00	0.59
BIO4	0.39	0.11	0.36	3.08	1.02	19	21	60	0.95	0.59
BIO5	0.34	0.12	0.39	3.48	1.35	29	13	58	0.97	0.71

preservation of fish corpses. This is clearly indicated by the revealed low TOC/S and PR/Ph ratios from the sunfish horizon (Berner, 1984).

Two models have been established to explain the development of anoxic bottom waters and the deposition of organic-rich shales (see e.g., Rohling, 1994; Rullkötter, 2000; Negri et al., 2009 for reviews): (1) the stagnation model emphasizes a strong stratification of the water-column limiting mixing of surface and bottom waters.

Restricted connections to open-ocean waters and increased freshwater input by rivers or intensified rainfall force a permanent halocline that hampers ventilation (Meyers, 2006). The development of anoxic bottom waters thus triggers the preservation of organic matter. Restricted basins such as the Black Sea are modern analogues for such conditions. Schulz et al. (2005) suggested similar conditions for the Early Oligocene Central Paratethys. For the Ebelsberg Fm., however,

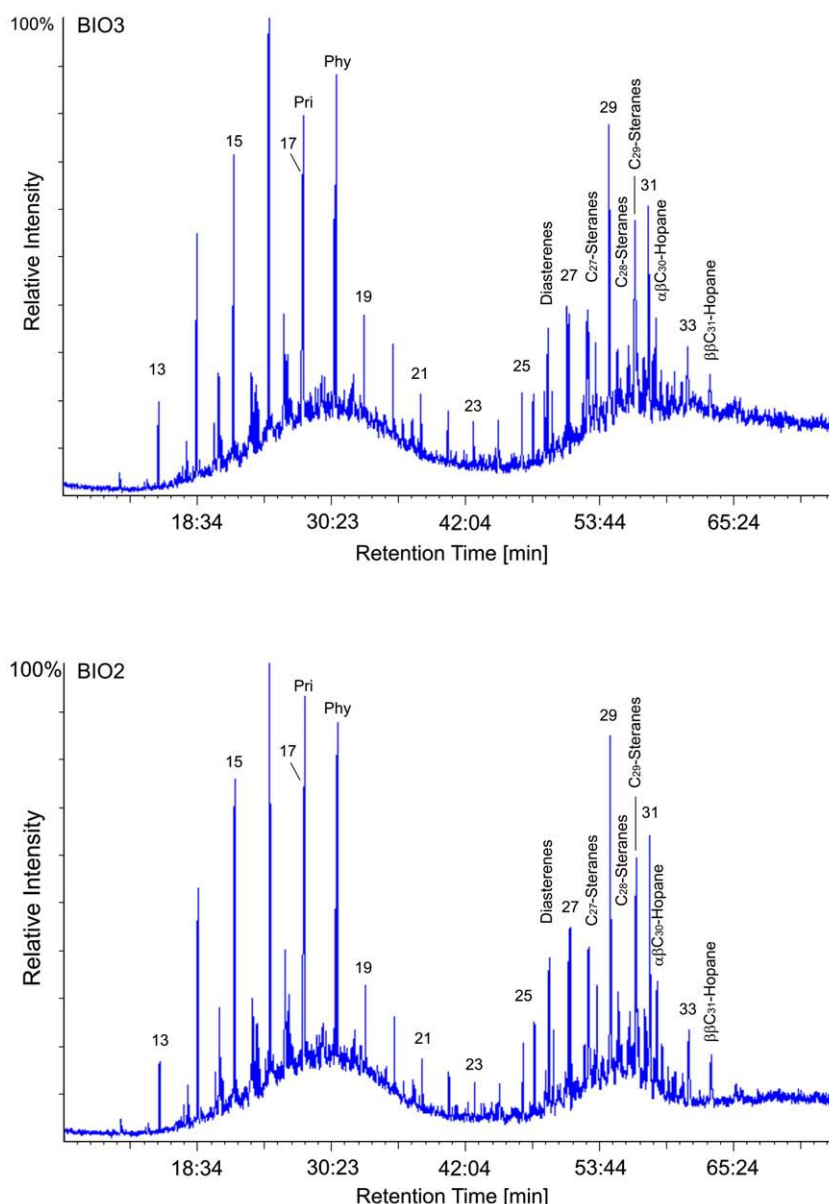


Fig. 4. Gas chromatograms (total ion current) of the saturated hydrocarbon fractions of samples Bio2 and Bio3. *n*-Alkanes are labelled according to their carbon number.

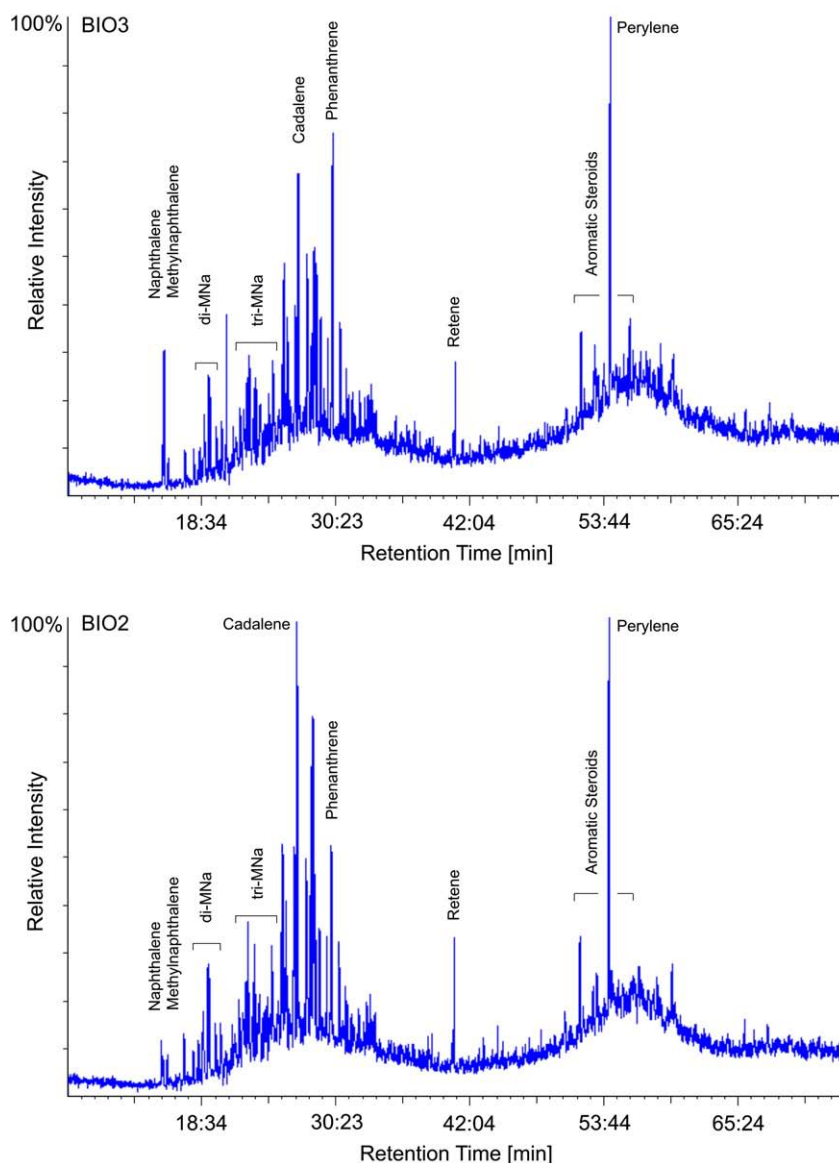


Fig. 5. Gas chromatograms (total ion current) of the aromatic hydrocarbon fractions of samples Bio2 and Bio3.

such a scenario is unlikely since broad connections to the Mediterranean and Atlantic seas did exist (Rögl, 1998). A major input of freshwater should result in an upper water-layer with reduced salinity. The planktic foraminifers, however, do not show any indications of diluted surface waters, and the distribution of chromans also indicates normal salinity.

(2) The productivity model focuses on the importance of high primary productivity in surface waters creating elevated levels of organic matter accumulation. Large amounts of sinking biomass consume much oxygen during decay and thus cause anoxic conditions in the water-column. Such conditions are often associated with upwelling, where an oxygen minimum zone (OMZ) is established covering the outer shelf and upper slope (e.g. Maas, 2000; Gooday, 2003; Schumacher et al., 2007).

In the present case, a scenario favouring the productivity model has been suggested by Wagner (1996, 1998). He links the deposition of fish shales and intercalated diatomites in the Upper Austrian NAFB during the Oligocene and Early Miocene to upwelling activity along the northern slope. This model is clearly supported by our data. Indications of cool and highly productive surface waters are observed

in planktic foraminifers which revealed blooms of cold-water tenuitellids (Li et al., 1992), opportunistic high-productivity taxa such as *Globigerina praebulloides* and cold-water indicators including *Globigerina ottangiensis*. These are all commonly associated with upwelling sites (e.g. Peeters et al., 2002; Roetzel et al., 2006; Grunert et al., 2010). The temperate surface-water conditions indicated by both groups contrast the subtropical climate suggested by Kovar (1982) and thus further document the influence of cold currents. High export rates of organic matter are indicated by the dominance of bolivininid species. Observations from recent upwelling sites in the Indian Ocean have shown that their peak abundance is restricted to the upper OMZ (Schumacher et al., 2007). A relationship between foraminiferal assemblages dominated by calcitic taxa and the hypoxic environment of an OMZ has been reported from the same study area (Larkin and Gooday, 2009). Studies by Gooday (1993) and Kawagata (2001) further showed that increased abundances of buliminds, *Mylostomella* spp. and *Pseudoparella exigua* are linked to elevated surface-water productivity and intermittent food supply. Highly productive surface waters are also documented in the heterotrophic dinoflagellate taxa *Lejeunecysta* spp., *Paralecaniella indentata*, *Selenopemphix*

spp., *Xandarodinium thanxum* and round brown cysts (*Brigantedinium* spp.) reaching an abundance of 30–32% (Dale, 1996; Louwye and Laga, 2008). Furthermore, the absence of oceanic dinoflagellate cyst taxa, usually adapted to oligotrophic conditions, can be linked to surface waters enriched in nutrients (Deville and de Vernal, 2000). The common occurrence of phosphorite nodules throughout the section also points to increased nutrient flux as they are often described from upwelling sites (e.g. Schenau et al., 2000). Finally, the revealed bulk stable isotope data are close to those of a mid-Burdigalian upwelling site in the NAFB (Grunert et al., 2010).

5.1.3. Coastal runoff

The faunas indicate that most of the nutrient input was caused by upwelling of deeper water masses. However, the sediments also bear evidence for at least episodically strong coastal runoff providing an additional source of nutrients. Deposits of the ancient coastline are lost due to erosion, and information on the hinterland is sparse. Leaf communities (Kovar, 1982) and the palynoflora (Hochuli, 1978) from Pucking and adjacent outcrops point to a warm, humid climate with a precipitation maximum in the warmest months and a lack of dry seasons. The annual precipitation may have ranged between 1100 and 2000 mm (Kovar, 1982).

Episodic flooding events are indicated by the dinoflagellate cysts: in contrast to the foraminiferal fauna, the occurrence of thermophilic dinoflagellate taxa such as *Lingulodinium machaerophorum*, *Melitasphaeridium choanophorum*, *Polysphaeridium zoharyi*, *Selenopemphix nephroides* and *Tuberculodinium vancampoe* suggest warm surface-water conditions (Marret and Zonneveld, 2003). As most of these taxa are associated with a neritic or inner neritic environment (Dale, 1996), transport from marginal areas close to the coast towards the outer shelf is a plausible explanation. This is further supported by the observation that most revealed species related to high productivity do not belong to the thermophilic taxa. A considerable input of land plants is also indicated by the distributions of steranes and sesquiterpenoids in the samples from the sunfish layer.

5.2. Types of fossil mass occurrences

The fossil mass occurrences can be divided into planktic and nektic ones. The planktic ones are formed by pteropod and nannoplankton blooms. The nektic category is threefold: *Aturia*-algae accumulations, pipefish mass occurrences and multi-species vertebrate accumulations. The different compositions of the mass occurrences point to quite different trigger mechanisms.

5.2.1. Blooms of pteropods and nannoplankton

The pteropods *Limacina* and *Clio* are adapted to pelagic life in the upper ocean layers. They are diel migrants with nocturnal upward migration and produce large mucous webs to catch suspended organic material (Mackas and Galbraith, 2002; Gilmer and Harbison, 1986). Fossil pteropod blooms have been linked to flooding events (Gürs and Janssen, 2004) allowing immigrations from adjacent ecosystems. Similarly, recent blooms are suggested to result from climate driven eddy intensification and the northward shift of warm-water fauna into subarctic waters (Tsurumi et al., 2005). Both mechanisms focus on import from a distant source area and are inadequate to explain the blooms in the subtropical Paratethys Sea with its wide oceanic connections.

An alternative scenario is described from Quaternary settings in the Red Sea, the Gulf of Aqaba, the Arabian Sea and the Sargasso Sea (Almogi-Labin, 1982; Almogi-Labin et al., 1986, 1988; Mohan et al., 2006). According to these studies, high primary productivity is the main trigger for large standing stocks of pteropods. Highly productive areas such as upwelling regions and boundary currents are favourable for many *Limacina* species. A correlation of *Limacina* blooms with abundance peaks of the upwelling index foraminifer *Globigerina bulloides*, coccolithophorid blooms, and a rise of buliminid foraminifera,

indicating low oxygen bottom conditions, has been observed frequently (Almogi-Labin, 1982; Mohan et al., 2006). This pattern can also be observed in the fossil record of the Central Paratethys, as *Limacina* accumulations have been reported from Oligocene and Middle Miocene shales in the Carpathian Foredeep and related to anoxic environments (Báldi, 1986; Báldi, 2006).

Thus, the episodic occurrence of pteropod and nannoplankton blooms suggests temporarily changing conditions. These short-term events might either be related to intensification of upwelling or increased coastal runoff.

5.2.2. Allochthonous accumulations of *Aturia* and brown algae

Aturia is interpreted the most active and deeply living Cenozoic nautiloid, judging from the shell's large size, streamlining, and siphuncle configuration (Ward, 1987). Although many findings derive from coastal settings (Lukeneder and Harzhauser, 2002), the original habitat of *Aturia* was most likely deep water. However, the specimens from Pucking are frequently associated with brown algae, which grew in littoral environments. Therefore, the mass occurrences might have resulted from a complex succession of processes. First, the *Aturia* shells floated post mortem to the surface and were transported by surface currents and/or wind to the coast. Examples from recent nautiloid shells show that transport over large distances is a common phenomenon (e.g. Toriyama et al., 1964). There, they became mixed with the algae and became transported offshore at the surface. The same coastal area was probably also the origin for the monospecific pipefish accumulations. Syngnathids prefer lagoons and sheltered bays with sea-grass (Polard, 1984; Howard and Koehn, 1985) and thrive also between brown algae (Browne and Smith, 2007) but not in the open ocean.

Storms and catastrophic flooding events might be the trigger for the offshore transport. This idea is supported by an increased input of sand in the lower part of the section (Kovar, 1982). Furthermore, fluvial influx might be the reason for the scarce occurrence of planktic foraminifera.

5.2.3. Autochthonous multi-species vertebrate accumulations

The multi-species fish accumulations point to an epipelagic origin. A relationship between these fish accumulations and intensified upwelling and surface-water productivity is indicated by the planktic and benthic foraminiferal assemblages from the sunfish horizon. Offshore hake prefer the shelf and upper slope from few tens of metres down to several hundred metres. These fish are benthic and undertake diel vertical migrations to prey on small crustaceans, squid and other fish (Cohen et al., 1990). Mackerel are mainly plankton feeders filtering crustaceans out of the water. They are epipelagic, schooling fish and prefer surface waters in shelf environments (Collette and Nauen, 1983). Herring, as one of the most frequent constituents of the Pucking fish fauna, are mainly offshore, pelagic, schooling fishes down to 200 m water depth (Whitehead, 1985). The sunfish *Austromola angerhoferi* might have lived in very similar habitats to its modern relative *Mola mola*, which is a pelagic fish living from surface waters down to several hundred metres depth (Parenti, 2003). Thus it fits very well in the epipelagic pattern represented by the schooling fish – a habitat which is also suitable for the undescribed dolphin. Therefore, these mass occurrences were formed by “autochthonous” offshore species.

The autochthonous deep water fish fauna is still largely undescribed. Some comments are given by Pfeil (1983). Among sharks, the deep water category is represented by the bramble shark *Echinorhinus pollerspoeki* Pfeil, 1983. Its modern relatives are deep water sharks, living close to the bottom of the shelf (Compagno, 1984). A second representative is the benthic one-finned shark *Heptanchias* sp. which today lives in deep water down to 400–1000 m close to the shelf edge (Serena, 2005). Teleost index taxa of the deep water fauna are lanternfishes (Myctophidae) which are bathypelagic, adapted to lightless depths but display a diel migration to the epipelagic zone (Paxton and Hulley, 1999). Similarly, the hatchetfish *Argyropelecus* is a bathypelagic fish (Quero et al., 1990).

5.2.4. Benthic communities

Benthic mass occurrences are missing entirely. The only autochthonous benthic macrofauna, always low in number, consists of few specialists. The lucinids are adapted to low oxygen habitats and survive by utilizing sulphide-oxidizing, chemosymbiotic bacteria as symbionts (Taylor and Glover, 2000; Zuschin et al., 2001). *Megaxinus bellardianus* occurs close to the sunfish skeletons, indicating hypoxic bottom conditions close to the sunfish fall. This hostile environment may also explain the near absence of gastropods, represented only by two small-sized carnivorous species. The absence of infaunal molluscs and echinoderms, the lack of bioturbation, and the good preservation of the fishes all support the interpretation of a sea bottom close to and sometimes under anoxic conditions.

6. Conclusions

The Aquitanian Ebelsberg Formation bears a *Konservat-Lagerstätte* with a variety of macrofossil assemblages. An evaluation of macrofossils recovered from a section near Pucking (Upper Austria) shows that besides the enormous number of specimens these assemblages are bound to specific levels in the rather uniform sediments of the section.

Micropaleontological (foraminifers, dinoflagellates) and geochemical (biomarker, organic carbon, sulphur, carbonate contents, stable isotopes) proxies have been used to reconstruct the paleoceanographic setting. The finely laminated sediments were deposited in the NAFB along the northern shelf of the Central Paratethys. Upwelling and episodically increased coastal runoff provided large amounts of nutrients stimulating primary productivity. All revealed data suggest dysoxic–anoxic bottom waters of an oxygen minimum zone along the outer shelf and upper slope.

The revealed fossil assemblages show specific associations occurring during distinct intervals within the section. Different mechanisms are discussed to explain their origin:

- (1) Mass occurrences of pteropods and calcareous nannoplankton occur in several horizons across the section. These accumulations are interpreted as a response to an episodic rise in nutrient availability resulting in blooms of primary productivity. Increased coastal runoff or intensified upwelling activity is considered as the trigger mechanism.
- (2) Allochthonous associations of the nautiloid *Aturia* with brown algae indicate a complex transport mechanism. Shells of the offshore-living cephalopods were transported to the coast by surface currents and/or wind currents. Episodic flooding events and storms then mixed the accumulated shells with the algae and drew them offshore again. The latter process also seems to apply to pipefish accumulations observed in the section.
- (3) The multi-species vertebrate accumulations of fish and dolphins are considered as parautochthonous as their habitat is in good agreement with the reconstructed paleoenvironment.
- (4) Benthic mollusc communities are scarce and of low diversity. They mainly consist of bivalves adapted to anoxic environments and thus are regarded as parautochthonous.

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