

Benthic foraminifera: indicators for a long-term improvement of living conditions in the Late Valanginian of the NW German Basin

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ABSTRACT – Foraminiferal occurrences in marine sediments of Late Valanginian age (Early Cretaceous) are described from NW Germany. The distribution patterns of benthic foraminifera are discussed with respect to their abundance and diversity. Benthic foraminifera are characterized in terms of moderate diversity and abundance. Vertical fluctuations in foraminifera contents are discussed with respect to their palaeoecology and palaeobiogeography. Benthic foraminifera, which are represented by a total of 101 species, show a gradual increase of diversity throughout the Late Valanginian. This improvement of living conditions in an epicontinental sea over a period of approximately 2 million years indicates a gradual recolonization of the formerly non-marine semi-restricted basin. The associations are dominated by agglutinated taxa with common *Ammobaculites*, *Ammoverrella*, *Bulbobaculites*, *Haplophragmoides*, *Protonina*, *Psammospaera* and *Reophax*. The calcareous species *Epistomina caracolla*, which is extremely common in certain intervals, may reach significant abundances. Further agglutinated and calcareous taxa occur rarely. The early Late Valanginian is marked by the occurrence of the Tethyan species *Cerobertinella subhercynica*, reflecting a major sea-level highstand. *J. Micropalaeontol.* 20(1): 81–95, July 2001.

INTRODUCTION

Early studies dealing with earliest Cretaceous benthic foraminifera from NW Germany concentrated mainly on stratigraphic and taxonomic aspects (e.g. Bartenstein & Brand, 1951; Bartenstein & Bettenstaedt, 1962). It is only in the late 1980s and early 1990s that interest in benthic foraminifera of the Valanginian of this area was revitalized by studies of Niedziolka (1988) on stratigraphic aspects and by Meyn & Vespermann (1994) on taxonomic problems. The only study which covers palaeoecological and sequence stratigraphical aspects was published by Stadtler (1998) and concentrates on the Early Valanginian Bentheim Sandstone and its sequence stratigraphic interpretation. The most recent account of Valanginian foraminifera has been presented by Mutterlose *et al.* (2000). No attempt has hitherto been made to understand benthic foraminifera from the palaeoecological–palaeogeographical point of view. During the last fifteen years extensive sampling of Lower Cretaceous sediments from outcrops in northern Germany has been performed.

For the current study fifty-four samples derived from four outcrops were analysed qualitatively and quantitatively. Abundance fluctuation of various taxa is discussed with respect to its palaeoecological context in order to decipher the role of autoecological factors on the composition of foraminiferal assemblages. Variations of diversity and abundance of benthic foraminifera are clearly controlled by palaeoceanographic changes on a regional scale. Thus these shifts in marine communities are here used to reconstruct the Valanginian Boreal sea.

GEOLOGICAL BACKGROUND

Palaeogeography of the NW German Basin

In Early Cretaceous times the NW German Basin (NWGB) formed the southernmost extension of the North Sea Basin, which itself was the southernmost extension of the Boreal–

Arctic sea. Due to its palaeogeographical position between the Tethys and the Boreal Realm the NWGB and the adjoining proto-North Sea Basin formed an important marine passage for marine biota. Apart from this northward-directed seaway which existed throughout Valanginian–Albian times, the NWGB also had connections via seaways to the Tethys in the south. These were less stable than those to the north and were interrupted during regressive periods in Berriasian and Barremian/Early Aptian times.

The NWGB was about 280 km long and 80 km wide. More than 2000 m of Lower Cretaceous sediments accumulated in this epeirogenic basin. Lithological changes and different sediment accumulation rates within the basin allow for a differentiation of a western part (area Rheine–Bentheim–Meppen–Groningen), a central part (area Osnabrück–Bielefeld–Minden–Vechta) and an eastern part (area Hannover–Braunschweig–Salzgitter) (Schott *et al.*, 1967/1969).

Marine sediments of Valanginian age are widespread in a 50 km wide belt from Bentheim in the west up to the Hannover/Braunschweig area in the east. These sediments show a clear lithological variation. Dark shales and mudstones with a low CaCO₃ content and abundant sideritic nodules represent the basin-facies. High subsidence and accumulation rates went along with a low oxygen-content.

MATERIAL AND METHODS

Fieldwork was performed from 1984 to 1999. All existing clay pits with known Valanginian strata were logged lithologically and sampled subsequently for micropalaeontological studies. In addition, macrofossils were collected bed-by-bed to allow for detailed biostratigraphic zonation based on ammonites. Macrofossils were also used to indicate changes in the provenance of marine biota, in particular to date the timing and influx of tethyan-derived ammonite faunas. Material from four clay pits (Twiehausen, Hollwede, Varlheide, Diepenau), situated in the

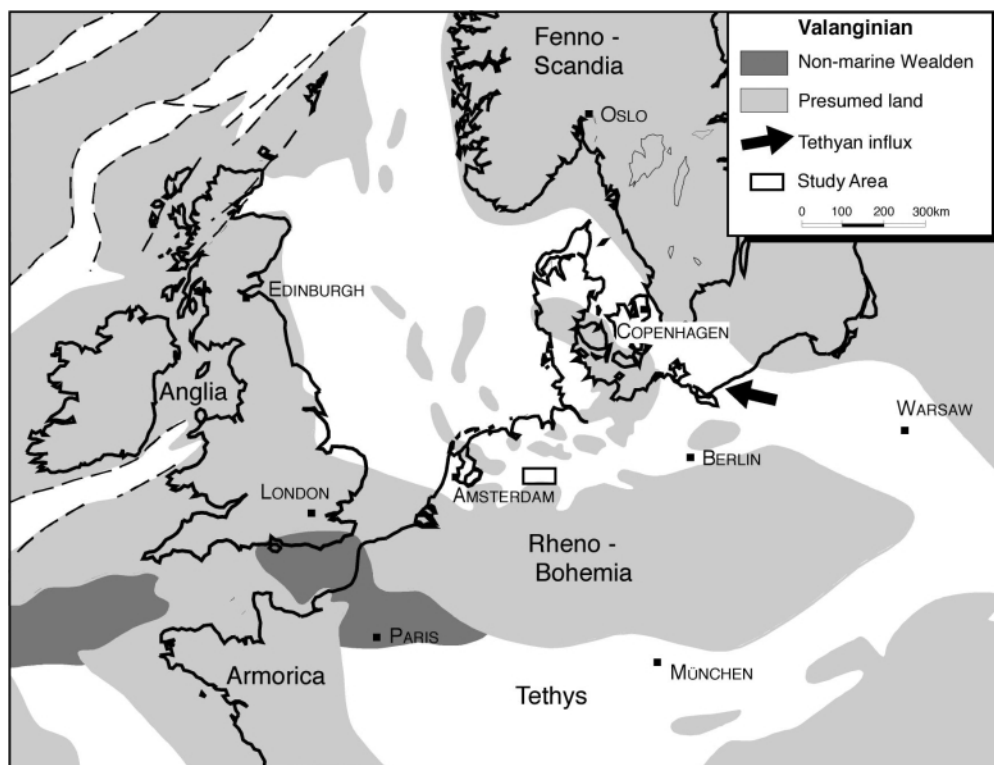


Fig. 1. Palaeogeographical map for the Valanginian of northwestern Europe, showing the studied area.

northern part of North Rhine Westphalia was considered for this study (Fig. 1). A detailed description of the lithology, biostratigraphy and faunal contents of these sites is given by Mutterlose (1992) and Mutterlose *et al.* (2000). Apart from Twiehausen, mining has been stopped in these pits and the outcrop conditions of these abandoned pits is extremely poor. A total of 74 samples were collected bed-by-bed and, subsequently, 54 of these samples were investigated for foraminifers.

For the foraminiferal investigation different amounts of dried sediment samples were processed with tenside (REWOQUAT[®] W 3690 PG), since the standard hydrogen peroxide method proved to be ineffective. The weight of the processed samples varied from 120–400 g for sample. After crushing, the raw material was covered with a tenside/ethanol mixture. Several times a week the sample was stirred up and after one or two weeks it was washed through a 200 µm and a 63 µm sieve. The dry insoluble residue was weighed and subtracted from the original weight of the sample. After drying and weighing the sieved material was divided into three fractions (>315 µm, 200–315 µm and <200 µm). The two large fractions (>315 and 200–315 µm) were picked completely. Occasionally, foraminiferal abundances in these fractions were extremely high, requiring splits to be made (Broelsma, 1978). These were obtained by using the classical method. A minimum of 300 individuals was picked for each sample. The finest fraction (<200 µm) was only picked quantitatively and is not considered in the absolute counts.

All specimens, which were picked from the two large fractions, were counted. Only few taxa attain abundances higher than 1%. These were chosen for a more detailed discussion of the

palaeoenvironment. A complete list of all foraminifera encountered is given in the taxonomic index (Appendix A). Relative abundances are given by using the following abbreviations: very common (VC: >20%); common (C: 19.9–5%); rare (R: 4.9–1%); very rare (VR <0.9%), see Appendix B. The numbers of specimens, as discussed in the text, is always based on 200 g raw material. The abbreviation AF is used for agglutinated foraminifera and CF for calcareous foraminifera.

The generic classification used here is based on Loeblich & Tappan (1987), the classification at species level follows Bartenstein & Brand (1951) and Meyn & Vespermann (1994). SEM photographs were taken on a LEO 1530, all specimens and samples are located at the Institut für Geologie, Mineralogie und Geophysik of the Ruhr-Universität Bochum. The CaCO₃ content of the samples was measured on an AAS (Atomic-Absorption-Spectrometer), the organic carbon (TOC) content on a coulometer.

LOCATIONS AND STRATIGRAPHY

The four investigated sections (Twiehausen, Hollwede, Varlheide, Diepenau) are located in the western part of NW Germany, north of the Wiehengebirge approximately 20 km west of Minden (Fig. 1). Detailed descriptions of their lithology, biostratigraphy and faunal content is given by Mutterlose (1992) and Mutterlose *et al.* (2000).

The 32 m thick succession of the Twiehausen section [grid reference R: 34 67080, H: 58 07400] is of early Late Valanginian age (*Prodichotomites hollwedensis* ammonite zone and lower part of the *Prodichotomites polytomus* ammonite zone; Fig. 2). The succession is well known for its rich and diverse ammonite

STAGE	Ammonite zones NW-Germany	Belemnite zones NW-Europe	Biostrat. Units	Foraminifera and Ostracods NW-Germany	Zone	Nannoplankton NW-Germany	Zone	Sequence	Lithology bm bc	Range of sections	
VALANGINIAN	UPPER	<i>Acroteuthis acmonoides</i> pars	Astieria - Beds		UV 4	FO <i>C. rothii</i>	<i>C. rothii</i>	MFS	G	Diepenau	
			Arnoldia - Beds		UV 3		<i>T. striatum</i>	MFS	D		
			Dichotomites - Beds	FO <i>Lenticulina eichenbergi</i>	UV 2						
				FO <i>P. franki</i>	UV 1						
				FO <i>Pr. kummi</i>							
				FO <i>Protocythere praetriplacata</i>							
				FO <i>T. striatum</i>							
	LOWER	<i>Acroteuthis kemperi</i>	Polyptychites - Beds		LV 2						MFS
					FO <i>A. cellensis</i>	LV 1			MFS	SB	
			Platylenticeras - Beds			LV 1			MFS		
					FO <i>P. pseudopropria pseudopropria</i>						

Fig. 2. Stratigraphic range of the studied sections. FO, first occurrence; LV, Lower Valanginian; UV, Upper Valanginian; MFS, maximum flooding surface; SB, sequence boundary; bm, basin margin; bc, basin centre; B, Bentheim Sandstone; D, *Dichotomites* Sandstone; G, Grenz Sandstone. Foraminifera and Ostracods: P, *Protocythere*; Pr, *Protomarssonella*; A, *Ammovertella*. Nannoplankton: C, *Conusphaera*; T, *Tegementum*.

faunas (Kemper *et al.*, 1981; Mutterlose, 1992; Mutterlose *et al.*, 2000). Apart from boreal taxa several tethyan-derived ammonites have been described from this section, which consists of CaCO₃- and TOC-poor dark claystones.

The Hollwede pit [grid reference R: 34 65950, H: 58 07500] exposed 7 m of Upper Valanginian claystones (*Prodichotomites polytomus* ammonite zone; Fig. 2). The boreal ammonite faunas of this clay pit were described by Kemper (1978), Kemper *et al.* (1981) and Jeletzky & Kemper (1988). Tethyan ammonites recorded from Hollwede were derived from the underlying *P. hollwedensis* zone, which was no longer accessible when the fieldwork was carried out for the current study. The CaCO₃ content varies from 1.2% (sample 99/3) to 8.3% (sample 101/1), the TOC contents from 0.2% (sample 101/1) to 0.7% (sample 97/2).

A 12 m thick succession of claystones of mid-Late Valanginian age (upper part of the *Dichotomites crassus* ammonite zone; Fig. 2) was exposed in the Varlheide pit [grid reference R: 34 70875, H: 58 06875]. Diverse boreal ammonites assemblages, yielding minor tethyan influences are known from Varlheide (Seitz, 1950; Kemper, 1978; Rawson & Kemper, 1978; Kemper *et al.*, 1981). The CaCO₃ content varies from 3% (sample 93/2) to 13% (sample 109/1).

The Diepenau pit [grid reference R: 34 80700, H: 58 08670] covers a 5 m thick claystone sequence of latest Valanginian age (*Dichotomites tuberculata* ammonite zone; Fig. 2). Diverse tethyan and boreal ammonite assemblages have been figured from Diepenau (Seitz, 1950; Kemper, 1978; Kemper *et al.*, 1981; Mutterlose, 1992). The CaCO₃ content varies from 2% (sample 93/1) to 6% (sample 99/1).

BENTHIC FORAMINIFERA

The distribution patterns of benthic foraminifera (Figs 3–6) are discussed in the order of the stratigraphic succession. Following the ammonite zonation schemes, typical assemblages of foraminifera (see Plates 1 and 2) are described for each outcrop.

These assemblages are discussed with respect to palaeoenvironmental aspects.

The earliest Late Valanginian assemblage (A1)

These foraminiferal assemblages are dominated by agglutinated taxa including *Ammobaculites agglutinans*, *Ammovertella cellensis*, *Bulbobaculites inconstans erectum*, *Haplophragmoides* spp., *Protonina difflugiformis*, *Psammospaera fusca* and *Reophax scorpiurus* (Figs 7, 8). *Epistomina caracolla* is the only calcareous taxon which occurs in large numbers, up to 22% (sample 93/2). Additional, less common taxa of agglutinated and calcareous foraminifera have been observed. A total of 23 agglutinated and 34 calcareous taxa have been found. Sample 95/1 is marked by a diverse fauna consisting of 29 taxa. It is only in this sample that *Cerobertinella subhercynica* was observed (4 individuals). This decrease of diversity is caused by changes in the composition of calcareous taxa which vary from 0–16 species per sample. In the lower part of the succession (samples 71–101) diversity is significantly higher than in the upper part (samples 103–119). This is clearly reflected by the AF/CF ratio. Calcareous foraminifera, which have a ratio from 0–35% attain a significant maximum in the middle part of the section (samples 91/1–101/1).

The abundance patterns show three maxima (samples 71–75, 85–89, 111–119). Abundance increases from 1900 specimens (sample 75/1) to 3200 specimens (sample 85/4) and to a maximum of 8500 specimens (sample 119/1). All three parameters (diversity, AF/CF ratio, abundance) show a similar trend that may reflect environmental changes. This shift marks the base of the *P. polytomus* zone and may be used as a biostratigraphic marker in the future.

A. cellensis, a common index species of the lower Upper Valanginian, is present in all samples, except for samples 115–119. Samples 85/1 to 89/4 show a distinctive maximum of *A. cellensis* (sample 89/2, 1174 specimens). In this sample *A. cellensis* represents 47.2% of all specimens encountered. A second peak is visible in the upper part of the section (samples

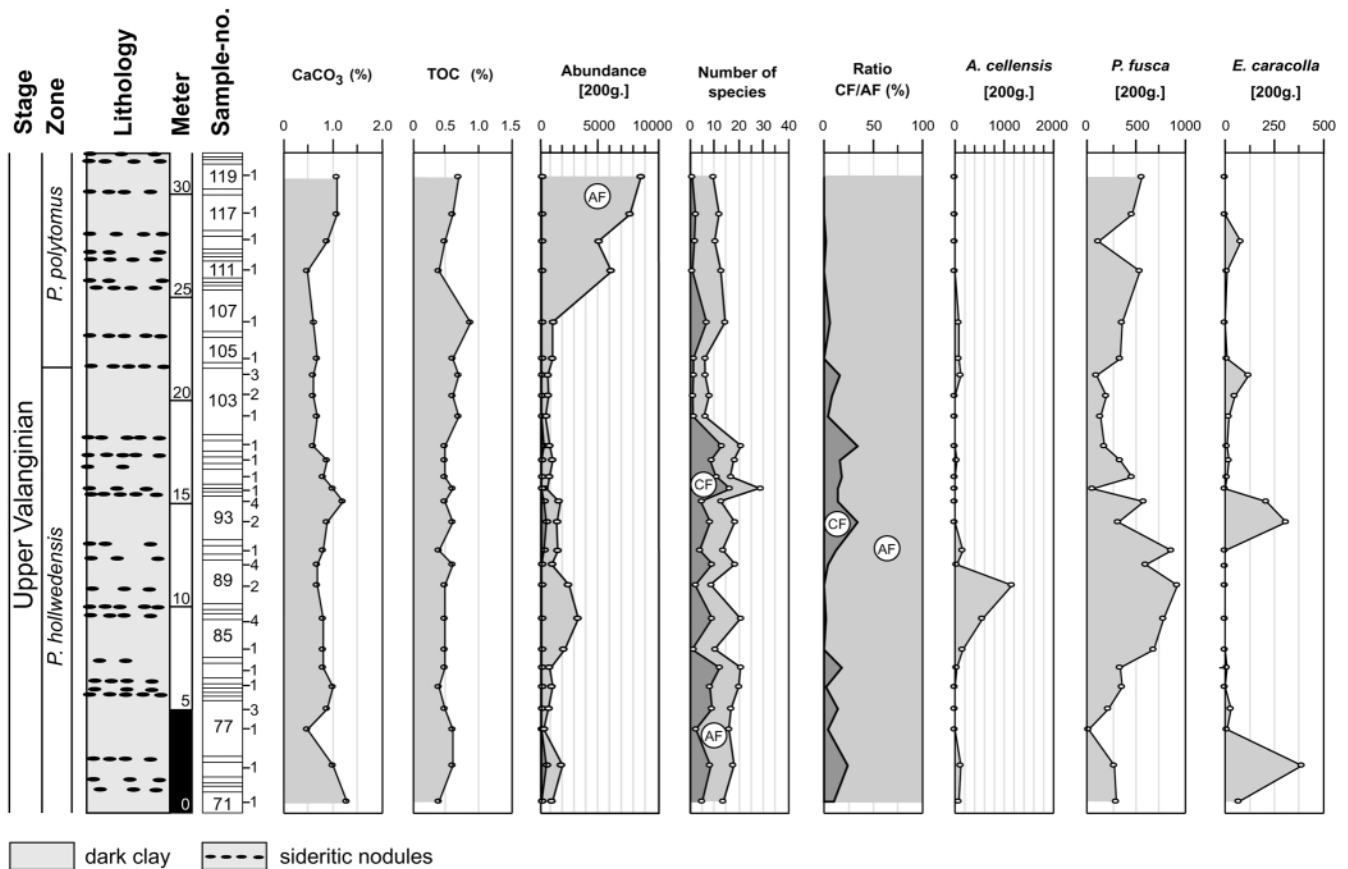


Fig. 3. Fluctuations in the benthic foraminiferal content of the Twiehausen section (A1) on a high resolution scale. Ammonites: P., *Prodichotomites*. Foraminifera: A., *Ammovertella*; P., *Psammosphaera*; E., *Epistomina*. CF, calcareous foraminifera; AF, agglutinated foraminifera.

103, 107). In sample 103/3 *A. cellensis* represents 19.8 % of all specimens.

Psammosphaera fusca, another common species, dominates the assemblages throughout the succession. This species attains more than 50% of the whole foraminiferal assemblage in samples 89/4, 91/1 and 97/1.

The only common calcareous species is *E. caracolla* with a maximum of 390 specimens (sample 75/1, 22% of all individuals). Samples 75, 93 103 and 115 are characterized by *E. caracolla* peaks, with a general increase of this species towards the top of the succession.

The early Late Valanginian assemblage (A2)

Most common foraminifera of this assemblage include *A. agglutinans*, *Ammobaculites irregulariformis*, *Bulbobaculites inconstans inconstans*, *E. caracolla*, *E. ornata*, *Lenticulina muensteri*, *P. difflugiformis* and *R. scorpiurus* (Figs 7, 8). These species are associated with additional taxa of agglutinated and calcareous foraminifera which are, however, less common. Twenty-four taxa of agglutinated and 24 calcareous taxa were observed in the 9 samples investigated from this interval.

Diversity varies insignificantly from 18 (sample 95/1) to 27 (samples 97/1, 101/1). Diversity of agglutinated taxa is rather stable (10–16 taxa), while it varies considerably for calcareous

taxa (3–14 taxa). The AC/CF ratio ranges from 0.8% (sample 99/3) to 84% (sample 99/3), showing three maxima for calcareous forams (samples 95/2, 99/1 and 101/1). The ratio of calcareous foraminifera always exceeds 65%.

Abundance varies considerably, with two maxima recognizable (sample 95/1, 10 000 specimens; samples 99/2 and 99/3, 6000 specimens). The lowest abundances were observed in the middle of the section (sample 99/1, 1300 specimens). The maxima have a positive correlation with agglutinated foraminifera. The high abundance in sample 95/2 is caused by an acme of *E. caracolla*; 4652 of a total of 7466 foraminifera were attributed to this species. Diversity of foraminifera shows a uniform pattern.

Both *E. caracolla* and *E. ornata* are common throughout the interval. *E. caracolla* is present in all samples with the number of specimens varying from 19 (sample 99/3) to 4652 (sample 95/2). The species has its maximum in the lower part of the section (sample 95/2), though it is also common near the top of the section (sample 101/1, 402 individuals=26.7% of all foraminifers). Remarkable is the occurrence of *E. ornata*, since it is the earliest recorded occurrence in the NWGB. *E. ornata* has a maximum in the middle part of the section (sample 99/1, 429 specimens). Samples 95/1, 99/3 and 103/1 did not yield *E. ornata*, which is always less frequent than *E. caracolla*.

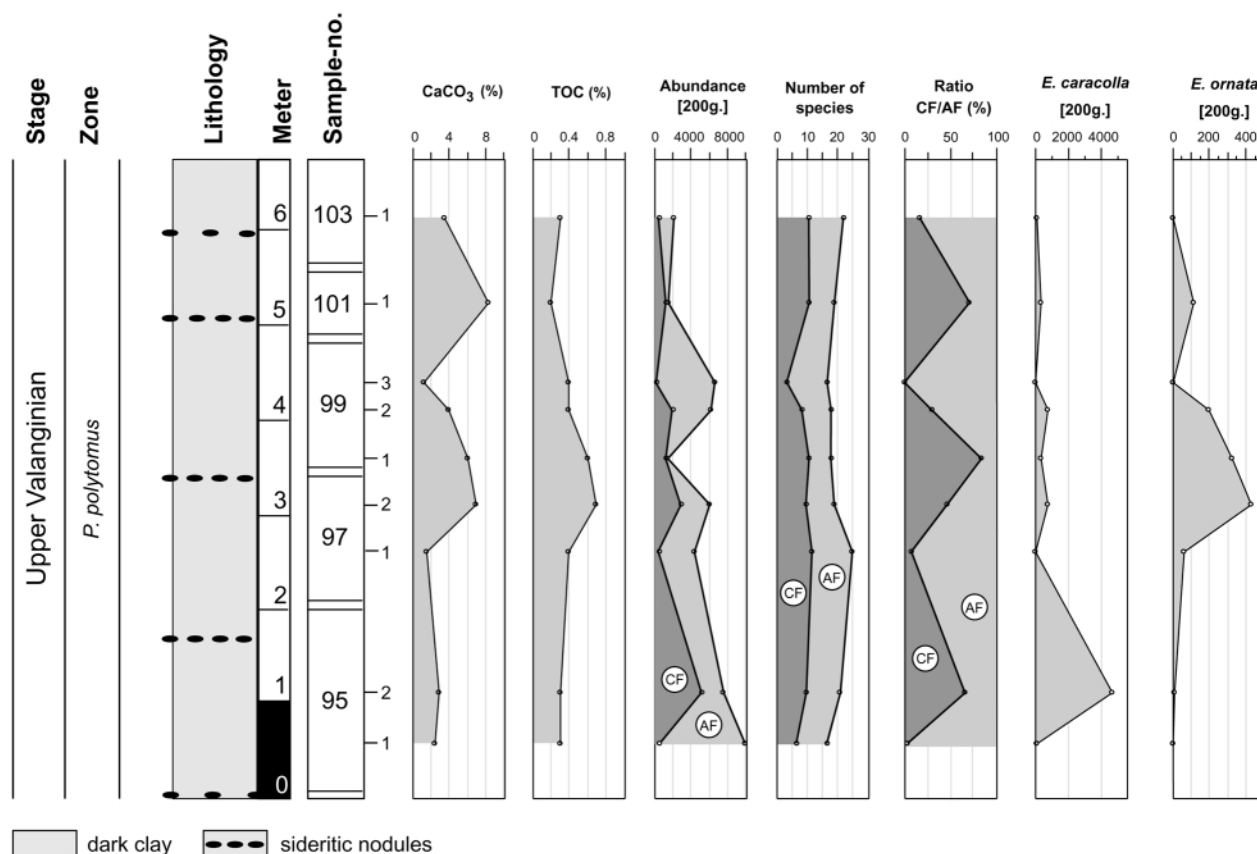


Fig. 4. Fluctuations in the benthic foraminiferal content of the Hollwede section (A2) on a high resolution scale. Ammonites: P., *Prodichotomites*. Foraminifera: E., *Epistominia*. CF, calcareous foraminifera; AF, agglutinated foraminifera.

The mid-Late Valanginian assemblage (A3)

The most common species of this assemblage are *A. agglutinans*, *A. irregulariformis*, *E. caracolla*, *L. muensteri* and *R. scorpiurus* (Figs 7, 8). In particular *A. irregulariformis* is extremely common in this interval and thus characterizes the assemblage. Additional taxa of agglutinated and calcareous foraminifera add up to a diverse fauna of 21 taxa of agglutinated and 39 calcareous taxa.

Diversity ranges from 16 species (sample 87/3) to 31 (sample 109/1) with fluctuations mainly caused by changes in the composition of calcareous foraminifera (varying from 2–19 taxa). Agglutinated foraminifera show a more stable distribution, with 9–15 taxa. Both diversity and the AC/CF ratio reach a maximum for calcareous foraminifera at the top of the section (sample 107/1, 91.9%).

Abundance varies considerably from 305 (sample 87/1) to 3097 specimens (sample 89/1). Two maxima occur (samples 89/1–93/2, up to 3097 specimens; samples 99/3–101/1, up to 2572 specimens). A high percentage is represented by *E. caracolla*; e.g. in sample 99/3 *E. caracolla* represents 1811 out of 2307 specimens. Due to the common occurrence of *E. caracolla* the abundance of calcareous foraminifera is always higher than 50% except for sample 87/3 (35.5%).

The distribution of *E. caracolla* is clearly reflected by the AC/CF ratio. There are two maxima (samples 89/1–93/2, 1510 and 1009 specimens; samples 99/3–103/1, 1029 and 1811 speci-

mens). *E. caracolla* varies throughout the section from 140 (sample 87/1) to 1811 specimens (sample 99/3). The highest percentage of *E. caracolla* marks sample 107/1 (86.5%), the lowest sample 87/3 (35.4%). All other calcareous foraminifera only occur in smaller numbers, varying from sample 87/3 (2 specimens=0.13%) to 121 (sample 93/2=6%).

The latest Valanginian assemblage (A4)

Common foraminifera of this assemblage consist of the agglutinated species *A. agglutinans*, *A. irregulariformis*, *B. subaequale* and *R. scorpiurus*. Among calcareous foraminifera only *E. caracolla* and *L. muensteri* occur in higher numbers (Figs 7, 8). These foraminifera are associated with additional taxa, resulting in a total of 23 agglutinated and 37 calcareous taxa which have been identified in the 8 samples of this interval.

Diversity varies from 22 species (sample 97/1) to 37 (sample 99/1), with higher values characterizing the upper part of the section. Diversity of calcareous foraminifera varies from 8 (sample 95/1) to 23 species (sample 101/1), while the diversity of agglutinated foraminifera is more constant. It fluctuates from 11 (sample 97/1) to 18 species (sample 99/1). The AC/CF ratio shows a dominance of agglutinated foraminifera, with two minor maxima for calcareous foraminifera; one at the base (sample 91/1, 32.2%) and in the upper part (samples 97/1–103/1, 20–27.83%).

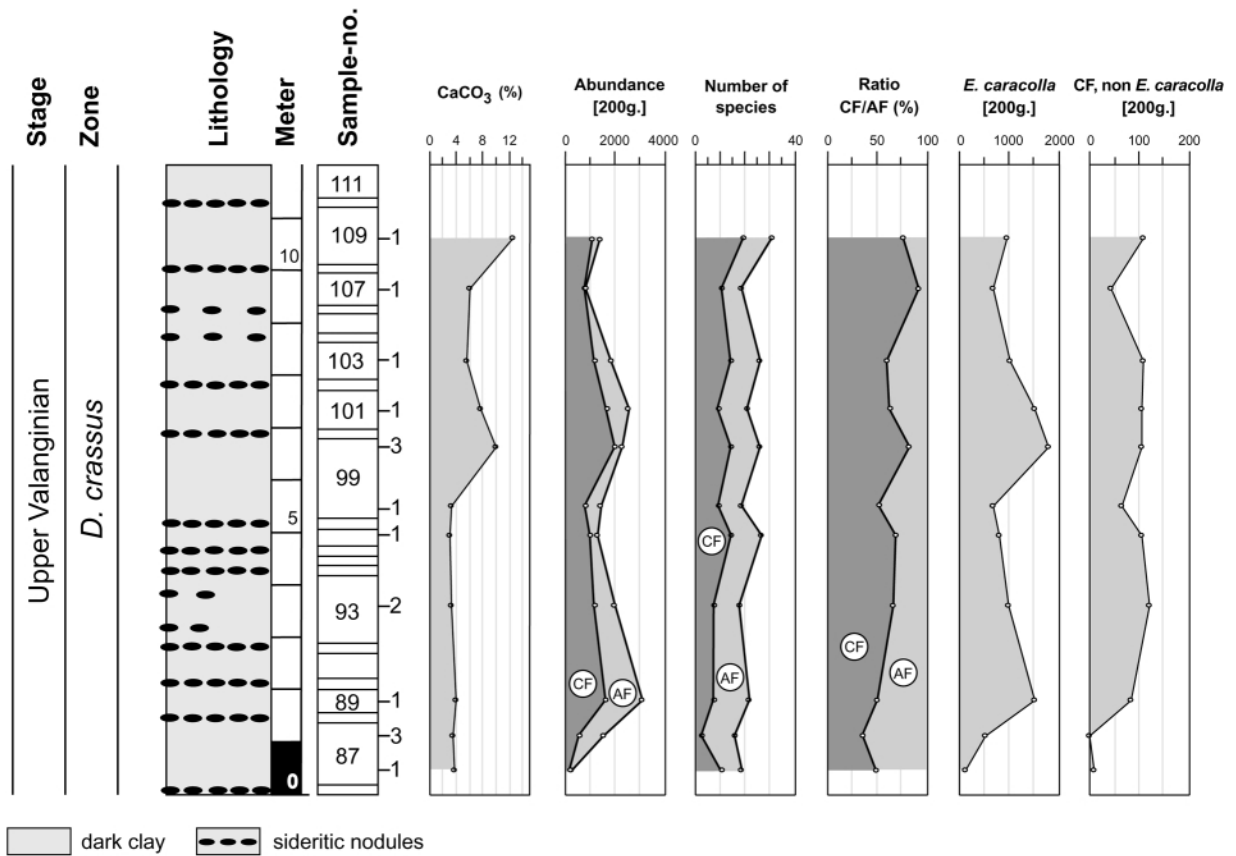


Fig. 5. Fluctuations in the benthic foraminiferal content of the Varlheide section (A3) on a high resolution scale. Ammonites: *D.*, *Dichotomites*. Foraminifera: *E.*, *Epistomina*. CF, calcareous foraminifera; AF, agglutinated foraminifera.

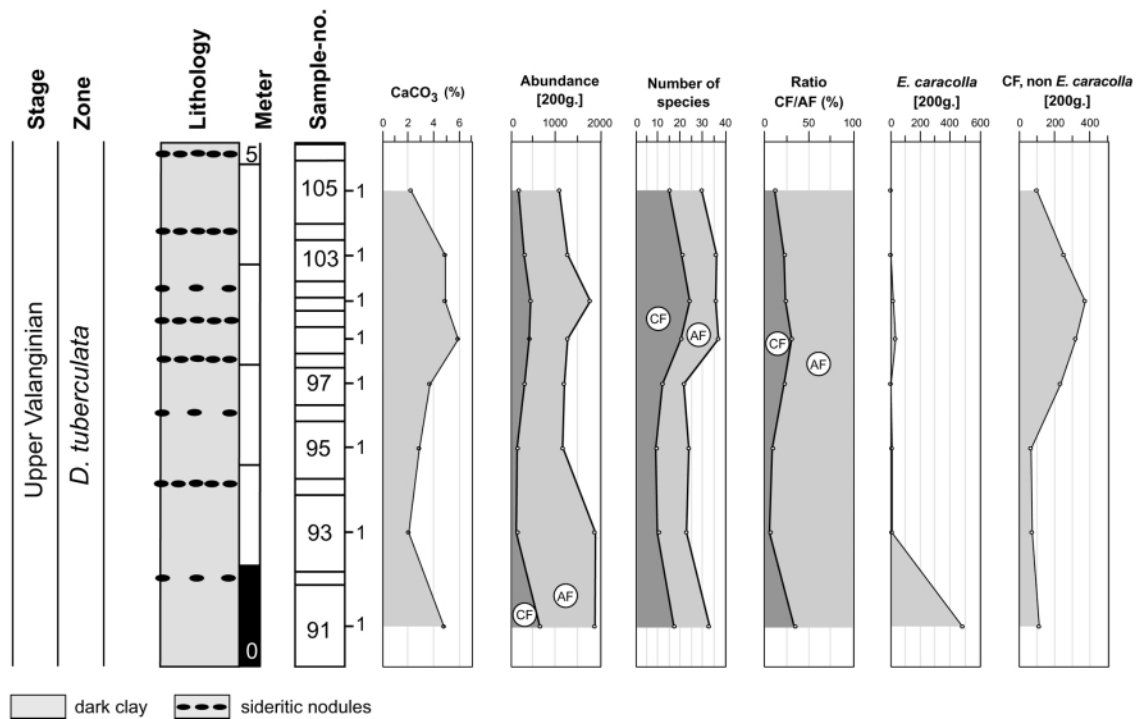
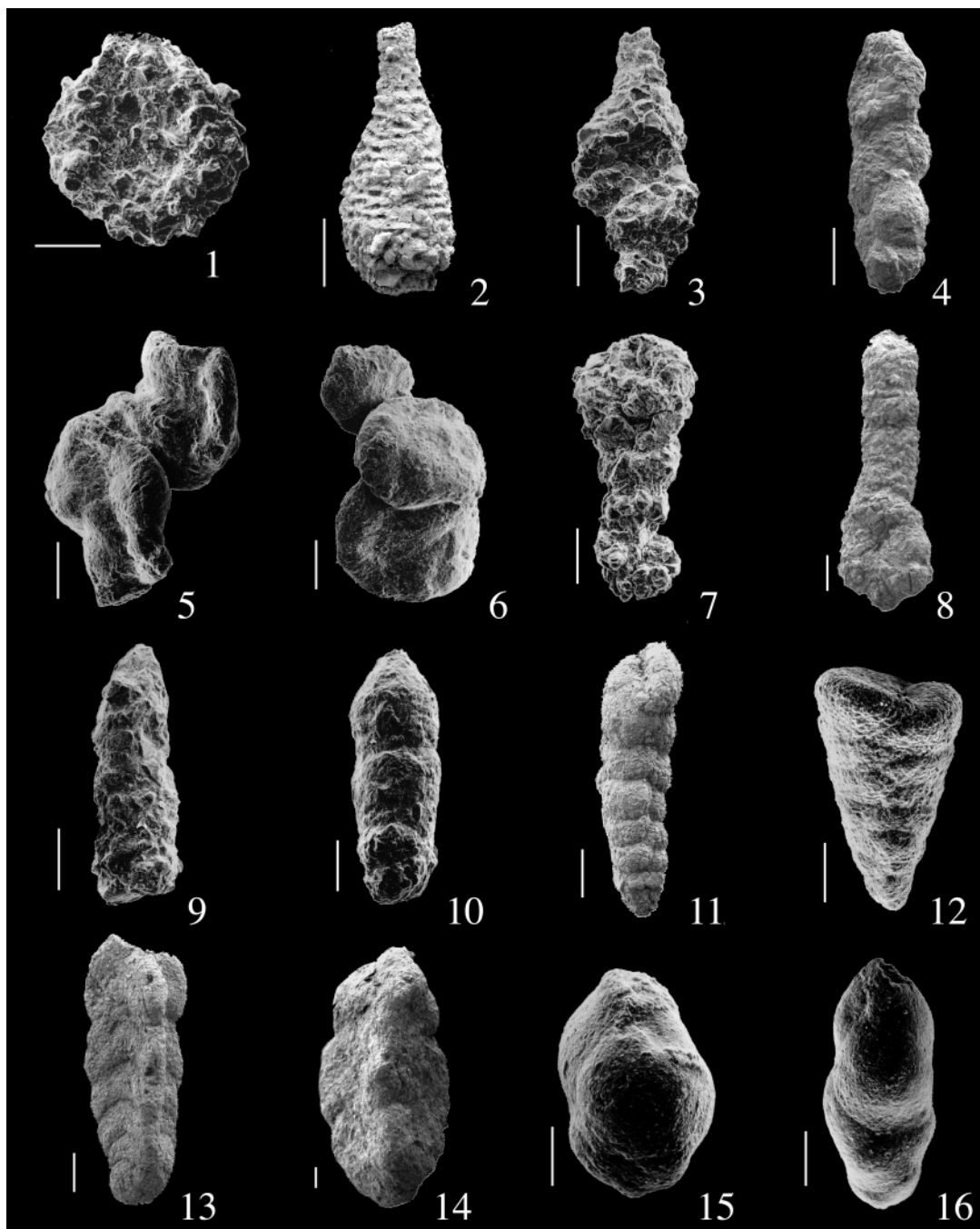


Fig. 6. Fluctuations in the benthic foraminiferal content of the Diepenau section (A4) on a high resolution scale. Ammonites: *D.*, *Dicostella*. Foraminifera: *E.*, *Epistomina*. CF, calcareous foraminifera; AF, agglutinated foraminifera.

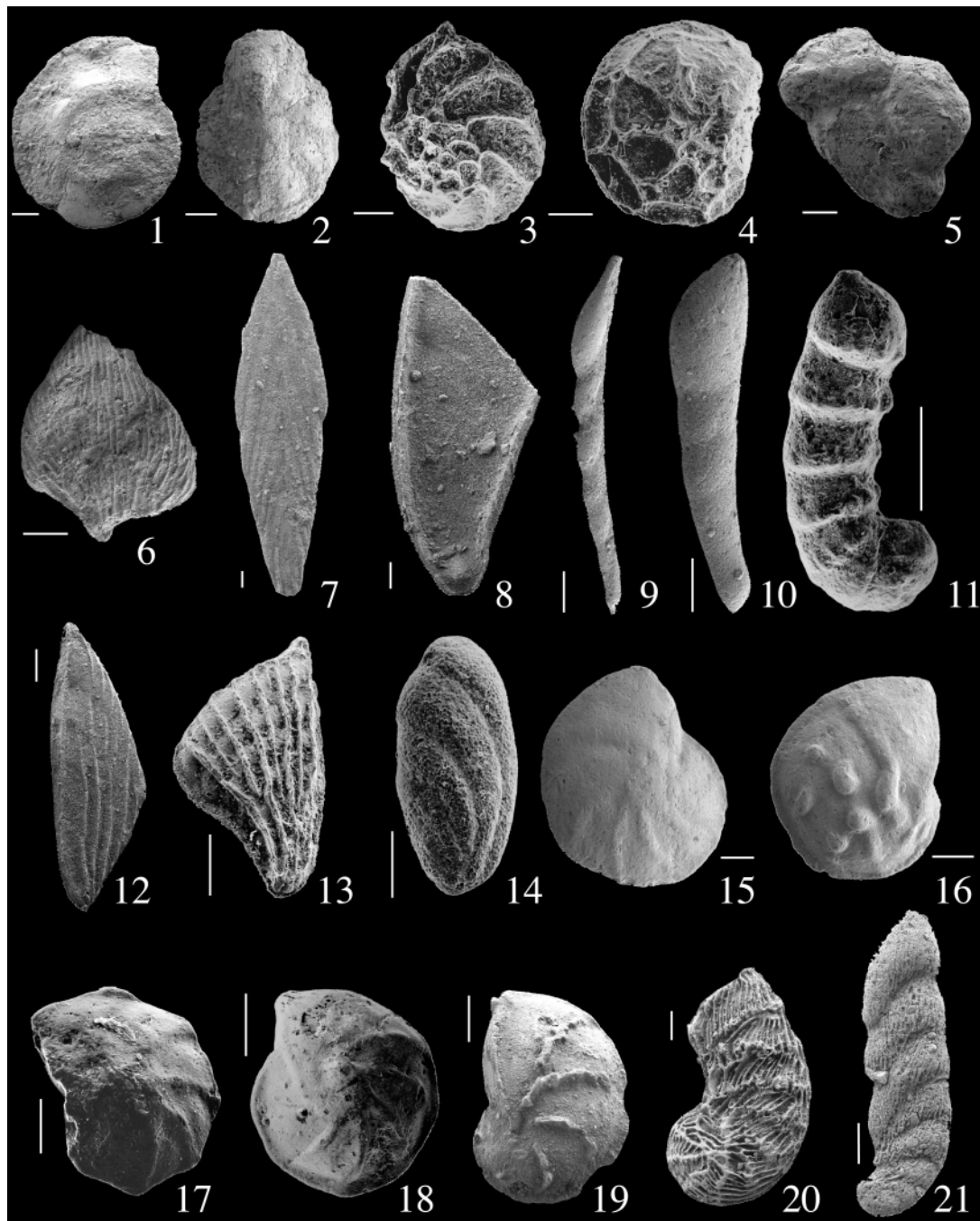


Explanation of Plate 1

Fig. 1. *Psammospharea fusca*, sample Tw 93/4/90. Scale bar=200 µm. **Fig. 2.** *Proteonina difflugiformis*, sample Va 99/3/90. Scale bar=100 µm. **Fig. 3.** *Reophax scorpiurus*, sample Tw 93/2/90. Scale bar=200 µm. **Fig. 4.** *Gaudryinella hannoverana*, sample Di 105/1/88. Scale bar=100 µm. **Figs 5–6.** *Ammovertella cellensis*, sample TW 89/2/90. Scale bar=200 µm. **Fig. 7.** *Ammobaculites agglutinans*, sample Hw 99/2/90. Scale bar=100 µm. **Fig. 8.** *Ammobaculites irregulariformis*, sample Va 89/1/90. Scale bar=200 µm. **Fig. 9.** *Bulbobaculites inconstans inconstans*, sample Hw 99/3/90. Scale bar=200 µm. **Fig. 10.** *Bulbobaculites inconstans erectum*, sample Tw 99/1/90. Scale bar=200 µm. **Fig. 11.** *Verneulinoides neocomiensis*, sample Va 103/1/90. Scale bar=100 µm. **Fig. 12.** *Protomarssonella kummi*, sample Hw 95/2/90. Scale bar=100 µm. **Fig. 13.** *Triplasia emslandensis emslandensis*, sample Va 97/1/90. Scale bar=200 µm. **Fig. 14.** *Triplasia emslandensis emslandensis*, sample Va 97/1/90. Scale bar=100 µm. **Fig. 15.** *Falsogaudryinella* sp, sample Hw 97/2/90. Scale bar=50 µm. **Fig. 16.** *Falsogaudryinella* sp, sample Hw 97/2/90. Scale bar=100 µm.

Abundance varies only little from 1100 individuals (sample 105/1) to 1892 (sample 91/1). Abundance of calcareous foraminifera is high with 605 individuals (sample 91/1), domi-

nated by 488 specimens of *E. caracolla*. Higher values exist again in the upper part of the section (samples 97/1–103/1) with 239–393 individuals caused by increasing numbers of *Lenticulina* spp.



Explanation of Plate 2

Figs 1–2. *Epistomina caracolla* sample Di 95/1/88, scale bar=100 μ m; 1, spiral side; 2, umbilical side. **Figs 3–4.** *Epistomina ornata*, sample HW 99/1/88, scale bar=100 μ m; 3, spiral side; 4, umbilical side. **Fig. 5.** *Hechtina praeantiqua*, sample Di 99/1/88. Scale bar=100 μ m. **Fig. 6.** *Frondicularia concinna*, sample Di 103/1/88. Scale bar=200 μ m. **Fig. 7.** *Frondicularia hastata*, sample Va 109/1/90. Scale bar=100 μ m. **Fig. 8.** *Psilocitharella kochi prolaevis*, sample Va 93/2/90. Scale bar=100 μ m. **Fig. 9.** *Laevidentalina debilis*, sample Va 109/1/90. Scale bar=100 μ m. **Fig. 10.** *Laevidentalina legumen*, sample Di 103/1/88. Scale bar=100 μ m. **Fig. 11.** *Marginulinopsis oldenburgensis*, sample Tw 85/4/90. Scale bar=200 μ m. **Fig. 12.** *Citharina discors discors*, sample Va 103/1/90. Scale bar=100 μ m. **Fig. 13.** *Citharina harpa*, sample Tw 93/2/90. Scale bar=200 μ m. **Fig. 14.** *Cerobertinella subhercynika*, sample Tw 95/1/90. Scale bar=100 μ m. **Fig. 15.** *Lenticulina muensteri*, sample Di 97/1/88. Scale bar=100 μ m. **Fig. 16.** *Lenticulina eichenbergi*, sample Di 99/1/88. Scale bar=100 μ m. **Fig. 17.** *Lenticulina nodosa*, sample Hw 99/1/90. Scale bar=100 μ m. **Fig. 18.** *Lenticulina roemeri*, sample Hw 97/2/90. Scale bar=200 μ m. **Fig. 19.** *Lenticulina saxonica*, sample Va 97/1/90. Scale bar=100 μ m. **Fig. 20.** *Vaginulinopsis reticulosa*, sample Va 109/1/90. Scale bar=100 μ m. **Fig. 21.** *Astacohus mutterlosei*, sample Va 99/3/90. Scale bar=100 μ m.

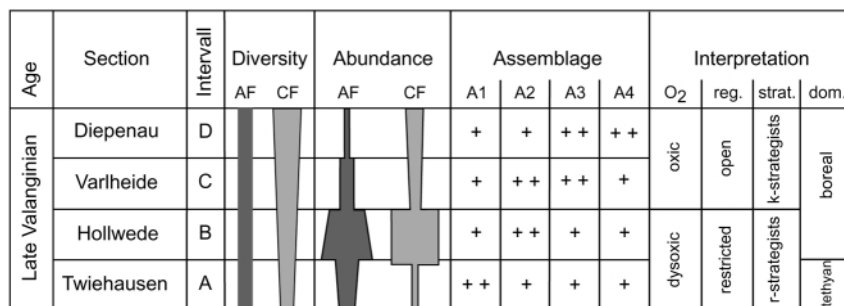


Fig. 7. Synthesis of micropalaeontological data from the late Valanginian of NW Germany. The intervals (A–D) are described in detail in the text. AF, agglutinated foraminifera; CF, calcareous foraminifera. reg., regime; strat., strategy; dom., domain.

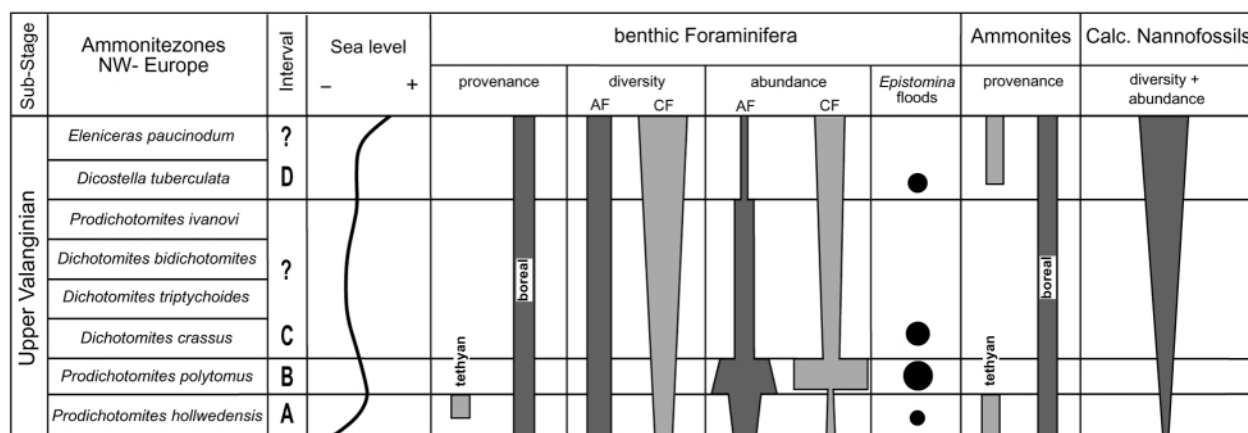


Fig. 8. Synthesis of distribution patterns of various groups of benthic foraminifera, ammonites and calcareous nannofossils for intervals A–D. AF, agglutinated foraminifera; CF, calcareous foraminifera.

Discussion

The four Upper Valanginian intervals under discussion are characterized by assemblages of medium high diversity. A total of 101 taxa of benthic foraminifera have been identified out of which only 32 species are agglutinated and 69 are calcareous foraminifera. These abundances are significantly higher than those observed by Niedziolka (1988) who identified 73 species over the same interval from sections further east in the NWGB. This implies a higher diversity for the western part of the NWGB. On the other hand our data agree with the findings of Bartenstein & Brand (1951), who identified 167 different taxa for the Upper Valanginian in several boreholes.

Ecological factors that control the abundance and diversity of benthic foraminifera include food availability (organic matter flux), temperature, substrate characteristics and oxygen content of bottom waters. In general, the benthic foraminifera have been used in the following ways as interpretative proxies.

- The highest total diversity and a high diversity of calcareous foraminifera is indicative of well oxygenated, shallow tropical to sub-tropical seas (Michael, 1974; Kemper, 1987; Murray, 1991).
- Associations of low diversity but high abundance are considered to be typical of an unstable environment, in particular low oxygen or low temperature conditions (Michael, 1979; Kemper, 1987; Kaminski *et al.*, 1995).

- A dominance of simple agglutinated foraminifera (e.g. *Psammospaera* spp., *Trochammina* spp., *Haplophragmoides* spp.) has been suggested to indicate cool water (Michael, 1979; Kemper, 1987). During the Cretaceous these forms are more common in the Boreal and deep-sea basins such as the Norwegian Sea and the Carpathian flysch.
- *Cerobertinella subhercynica* is considered to be a stenothermal warm water species, indicative of higher water temperatures (Vespermann, 1998). This assumption is based on the common occurrence of *Cerobertinella* in Tethyan warm water settings of Aptian and Albian age.
- *Hechtina praeantiqua* has been interpreted as a thermophile species (Michael, 1974, 1979). Furthermore, *H. praeantiqua* indicates areas with high oxygenation (Bartenstein & Brand, 1951).

Results of this work can summarized as follows (Fig. 7). Diversity fluctuations throughout the four intervals are thought to reflect palaeoenvironmental changes of the bottom waters. After an earliest Late Valanginian diversity peak of 57 species (interval A) diversity decreases to 48 species (interval B) and increases subsequently to 60 species (intervals C & D). It has to be kept in mind that the results for the intervals B and D may not be representative due to the low number of samples investigated from those sections (interval B, 9 samples). A general increase of diversity throughout the Late Valanginian is, however, observable. Diversity of agglutinated foraminifera is fairly

constant throughout the Late Valanginian. Since the latter are more sensitive to environmental change, decreases of diversity indicate trends towards more restricted conditions. Variation of diversity is mainly caused by the diversity fluctuations of the calcareous foraminifera. The diversity of calcareous foraminifera is, in each section, higher than the diversity of agglutinated foraminifera. Most of the calcareous taxa can be included in the Nodosariidae, with common *Lenticulina* spp. and rarer *Astacolus* spp. and *Laevidentalina* spp. According to these data, interval A reflects rather suitable bottom water conditions, interval B impoverishment and intervals C & D rather stable bottom water conditions. Most abundant are agglutinated foraminifera, with the only common calcareous species being *Epistomina* spp. Highest abundances of benthic foraminifera are observed in interval B, showing a clearly negative correlation with diversity. From the observation that low diversity accompanies high abundances it may be deduced that the assemblages of interval B reflect a primary ecological signal. This indicates R-mode selection, which reflects unstable, rather stressful, palaeoecological conditions. Short-term floods of *Epistomina* spp. occur in all four intervals. Interval A is characterized by four distinctive floods of *E. caracolla*, interval B by an *E. caracolla*/*E. ornata* flood while interval C yields common *E. caracolla* throughout the sequence and interval D yet another *E. caracolla* flood. These floods are always restricted to intervals of 20–50 m thickness, reflecting a period of 4000–10 000 years (1 m/22 000 years; 200 m/4.5 Ma).

The most common taxa, which include *Ammobaculites* spp., *A. cellensis*, *Bulbobaculites* spp., *P. difflugiformis*, *P. fusca*, *R. indivisa* and *R. scorpiurus*, represent 70–90% of the abundance. These agglutinated taxa may be viewed as ecologically robust forms.

High abundances of *Reophax*, *Rhizammina* and *Haplophragmoides*, which have been interpreted as a proxy of a restricted basin biofacies (King *et al.*, 1989), were observed in intervals A & B of the early Late Valanginian. This correlates positively with low diversity and high abundances of certain agglutinated taxa in these lowermost intervals. The overall pattern may be best explained by a slow, stepwise recolonization of the NWGB in Valanginian times after non-marine conditions prevailed in Berriasian times. Marine biota began to spread into the basin in earliest Valanginian times from the northwest via the Netherlands. It is also, at this time, that the Carpathian seaway via Poland opened towards the Tethys. The increase in diversity and the changes in the abundance patterns in Late Valanginian times may be evidence of increasing oxygenation and improved living conditions for foraminifera, as well as rising sea-level. This trend of a general improvement of ecological conditions throughout the Late Valanginian is based on the high diversity patterns in interval A.

The early Late Valanginian *P. hollwedensis* zone, is characterized by high diversity and the occurrence of the tethyan-derived foraminifera species *C. subhercynica*. The genus *Cerobertinella*, established by Mjatluk (1980), was previously only known from the Aptian and Albian of the Tethys (Kazakhstan). *C. subhercynica* has been described by Vespermann (1998) from the Upper Barremian of the Braunschweig area. These records of *C. subhercynica* coincide with a short-term influx of tethyan-derived ammonites into the

Boreal Realm. Kemper *et al.* (1981) described the tethyan ammonite taxa *Saynoceras verrucosum*, *Karakaschiceras* spp., *Neohoplaceras* aff. *Karakaschiceras* spp., *Valanginites* spp., *Bochianites* sp. which migrated into the Boreal Realm during a sea-level highstand. It is from the same interval that a Boreal nannofossil excursion has been observed from sections of Tethyan affinities in Romania (Melinte & Mutterlose, in press). It is only in this particular interval that Boreal taxa (ammonites, nannofossils) migrated into the Tethys, which clearly correlates with the emigration of tethyan taxa out of the Tethyan area. It seems unlikely that the simultaneous emigration of tethyan taxa into the Boreal Realm and the immigration of Boreal taxa into the Tethys is controlled by climate. These migration patterns and shifts in the composition of marine faunas and floras in the early Late Valanginian may be best explained by a global sea-level rise and related changes in the palaeogeographical framework. It is the sea-level highstand of the early Late Valanginian *Saynoceras verrucosum* ammonite Zone, which allowed an exchange of ammonites in both directions. The gradual sea-level rise in Late Valanginian times may be viewed as the driving factor in the short-term exchange of faunas. The early Late Valanginian sea-level highstand is known from many different areas (e.g., France, Germany) and has been identified as a 3rd order sea-level highstand.

CONCLUSIONS

The distribution pattern of benthic foraminifera of the NWGB is controlled by distinctive palaeoenvironmental signals on different scales. Abundance and diversity patterns, negatively correlated to each other, clearly reflect a regional long term trend throughout the Late Valanginian (Fig. 8). The ecological conditions improved only slowly in this epicontinental sea, over a period of approximately 2 million years, indicated by a gradual recolonization of the formerly non-marine semi-restricted basin. This is supported by diversity patterns throughout Valanginian and Hauterivian times. Similar patterns of a gradual improvement throughout the Valanginian of the NWGB has been demonstrated for calcareous nannofossils.

Short-term sea-level-controlled signals are superimposed on the long-term trends. The early Late Valanginian sea-level highstand, which is well known from ammonites (e.g., Rawson, 1999) and calcareous nannofossils (Melinte & Mutterlose, in press) is also indicated by benthic foraminifera. Foraminiferal diversity is high during this period and tethyan taxa (*C. subhercynica*) do occur in this interval, which probably corresponds to a maximum flooding surface in a sequence stratigraphic context. This immigration of tethyan benthic species is a clearly short-term sea-level-related event on the order of half an ammonite zone (c. 200 000 years). Various acmes of *Epistomina* spp., occurring throughout the Valanginian, may be viewed as short term fluctuations of benthic foraminifera. Each interval investigated yielded at least one of these *Epistomina* floods. For interval A, which covers slightly less than one complete ammonite zone (=400 000 years), four short *Epistomina* spp. floods were observed. Each of these is restricted to a few consecutive samples (3 m of sediment), individual floods are separated by 5–8 m thick intervals, with only rare *Epistomina*.

Valanginian benthic foraminifera

Thus the acmes occur on a scale of approximately 100 000 years, which is on the Milankovitch scale.

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APPENDIX A

List of species cited in the text and figures, in alphabetical order by generic name.

Agglutinated Foraminifera

Ammobaculites agglutinans (d'Orbigny, 1846)
Ammobaculites eocretaceus Bartenstein & Brand, 1951
Ammobaculites goodlandensis Cushman & Alexander, 1930
Ammobaculites irregulariformis Bartenstein & Brand, 1951
Ammodiscus gaultinus Berthelin, 1880
Ammodiscus tenuissimus (Gümbel, 1862)
Ammovertella cellensis Bartenstein & Brand, 1951
Bulbobaculites inconstans erectum (Bartenstein & Brand, 1951)
Bulbobaculites inconstans gracile (Bartenstein & Brand, 1951)
Bulbobaculites inconstans inconstans (Bartenstein & Brand, 1951)
Bulbobaculites subaequale (Mjatliuk, 1939)
Falsogaudryinella Bartenstein, 1977
Gaudryina vetustissima Bartenstein & Brand, 1951
Gaudryinella hannoverana Bartenstein & Brand, 1951
Glomospira gordialis (Jones & Parker, 1860)
Haplophragmoides concavus (Chapman, 1892)
Haplophragmoides cushmani Loeblich & Tappan, 1946
Proteonina difflugiformis Brady, 1879
Protomarssonella kummi (Zedler, 1961)
Psammospaera fusca Schulze, 1875
Reophax nodulosa Brady, 1879
Reophax scorpiurus Montfort, 1808
Rhizammina indivisa Brady, 1884
Tetraplasia quadrata Bartenstein & Brand, 1951
Triplasia emslandensis emslandensis Bartenstein & Brand, 1951
Triplasia Reuss, 1854
Trochammina depressa Lozo, 1944
Trochammina inflata (Montagu, 1808)
Trochammina squamata Jones & Parker, 1860
Verneuilinoides inaequalis Bartenstein & Brand, 1951
Verneuilinoides neocomiensis (Mjatliuk, 1939)
Webbinella subhemisphaerica Franke, 1936

Calcareous Foraminifera

Astacolus bronni (Roemer, 1841)
Astacolus calliopsis (Reuss, 1863)
Astacolus exilis (Reuss, 1863)
Astacolus humilis (Reuss, 1863)
Astacolus linaris (Reuss, 1863)
Astacolus mutterlosei Bartenstein & Malz, in press
Astacolus schloenbachi (Reuss, 1863)
Buliminella loeblichii Bartenstein & Brand, 1951
Bullopara laevis (Sollas, 1877)
Cerobertinella subhercynica Vespermann, 1998
Citharina cristellarioides (Reuss, 1863)
Citharina discors discors (Koch, 1851)
Citharina harpa (Roemer, 1841)
Citharina krobothi Meyn & Vespermann, 1994
Citharina sparsicostata (Reuss, 1863)

Conorbis valendisensis Bartenstein & Brand, 1951
Epistomina caracolla (Roemer, 1841)
Epistomina ornata (Roemer, 1842)
Frondicularia concinna Koch, 1851
Frondicularia hastata Roemer, 1842
Frondicularia microdisca dichotomiana Bartenstein & Brand, 1951
Frondicularia rehburgensis Bartenstein & Brand, 1951
Globulina prisca Reuss, 1863
Hechtina praeantiqua Bartenstein & Brand, 1949
Histopomphus cervicornis (Chapman, 1892)
Laevidentalina debilis (Berthelin, 1880)
Laevidentalina distincta (Reuss, 1860)
Laevidentalina legumen (Reuss, 1845)
Laevidentalina linearis (Roemer, 1841)
Laevidentalina nana (Reuss, 1863)
Laevidentalina serrata (Eichenberg, 1934)
Laevidentalina soluta (Reuss, 1851)
Laevidentalina terquemi (d'Orbigny, 1849)
Laevidentalina varians (Terquem, 1866)
Lagena apiculata neocomiana Bartenstein & Brand, 1951
Lagena laevis (Montagu, 1803)
Lenticulina dunkeri (Reuss, 1863)
Lenticulina eichenbergi Bartenstein & Brand, 1951
Lenticulina muensteri (Roemer, 1839)
Lenticulina nodosa (Reuss, 1863)
Lenticulina ouachensis Sigal, 1952
Lenticulina pulchella (Reuss, 1863)
Lenticulina roemeri (Reuss, 1863)
Lenticulina saxonica Bartenstein & Brand, 1951
Lenticulina subalata (Reuss, 1854)
Lenticulina subangulata (Reuss, 1863)
Lenticulina subaperta (Reuss, 1863)
Marginulina pyramidalis (Koch, 1851)
Marginulinopsis ? gracilissima (Reuss, 1863)
Marginulinopsis jonesi (Reuss, 1863)
Marginulinopsis oldenburgensis (Bartenstein & Brand, 1951)
Marginulinopsis striatocostata (Reuss, 1863)
Nodosaria loeblichae Ten Dam, 1948
Nodosaria regularis Terquem, 1862
Pseudonodosaria humilis (Roemer, 1841)
Psilocitharella costulata (Roemer, 1842)
Psilocitharella kochi kochi (Roemer, 1841)
Psilocitharella kochi prolaevis Meyn & Vespermann, 1994
Pyramidulina paucicosta (Roemer, 1841)
Pyramidulina sceptrum (Reuss, 1863)
Pyrulina gutta d'Orbigny, 1826
Pyrulina longa Tappan, 1940
Ramulina laevis (Jones, 1875)
Saracenaria pyramidata (Reuss, 1863)
Saracenaria valanginiana (Bartenstein & Brand, 1951)
Sprillina minima Schacko, 1892
Tristix acutangula (Reuss, 1863)
Tristix insignis (Reuss, 1863)
Vaginulinopsis reticulosa Ten Dam, 1946

APPENDIX B

Foraminiferal distribution in the sections at Twiehausen and Hollwede

TWIEHAUSEN																						
Stage	Zone	Sample-no.	CF in %	AF in %	number of species (AF)	number of species (CF)																
Upper Valanginian	P. polytomus	127/1	99.73	0.27	7	1	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		125/1	98.98	1.02	6	1	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		123/3	82.79	17.21	6	1	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		123/1	95.82	4.18	6	1	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		121/1	98.55	1.45	9	1	VC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		119/1	90.95	9.05	8	8	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		115/1	75.26	24.74	10	10	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		111/2	97.97	2.03	8	3	VC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		107/1	93.12	6.88	8	7	VC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		103/2	91.80	8.20	7	1	VC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		101/1	65.43	34.57	8	13	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		99/1	83.70	16.30	10	8	VC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		97/1	80.93	19.07	6	11	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		95/1	85.96	14.04	13	16	VC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		93/4	84.38	15.62	9	4	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		93/2	65.49	34.51	11	8	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	91/1	86.60	13.40	10	4	C	VR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	89/4	94.94	5.06	10	9	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	89/2	99.76	0.24	7	2	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	85/4	97.46	2.54	12	9	R	-	VR	VR	-	-	-	-	-	-	-	-	-	-	-	-	
	85/1	100	0.00	11	0	R	-	-	VR	-	-	-	-	-	-	-	-	-	-	-	-	
	83/1	80.63	19.37	9	12	R	-	VR	VR	VR	C	-	-	-	-	-	-	-	-	-	-	
	81/1	97.88	2.12	12	8	C	-	VR	VR	VR	R	-	-	-	-	-	-	-	-	-	-	
	77/3	85.10	14.90	8	9	VR	-	-	VR	-	-	-	-	-	-	-	-	-	-	-	-	
	77/1	95.72	4.28	13	3	R	-	VR	VR	VR	VR	-	-	-	-	-	-	-	-	-	-	

TWIEHAUSEN																						
Stage	Zone	Sample-no.	AF in %	CF in %	number of species (AF)	number of species (CF)																
Upper Valanginian	P. polytomus	127/1	99.73	0.27	7	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		125/1	98.98	1.02	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		123/3	82.79	17.21	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		123/1	95.82	4.18	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		121/1	98.55	1.45	9	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		119/1	90.95	9.05	8	8	VR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		115/1	75.26	24.74	10	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		111/2	97.97	2.03	8	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		107/1	93.12	6.88	8	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		103/2	91.80	8.20	7	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		101/1	65.43	34.57	8	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		99/1	83.70	16.30	10	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		97/1	80.93	19.07	6	11	-	VR	VR	-	-	-	-	-	-	-	-	-	-	-	-	-
		95/1	85.96	14.04	13	16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		93/4	84.38	15.62	9	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		93/2	65.49	34.51	11	8	-	-	VR	-	-	-	-	-	-	-	-	-	-	-	-	-
	91/1	86.60	13.40	10	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	89/4	94.94	5.06	10	9	-	-	VR	-	-	-	-	-	-	-	-	-	-	-	-	-	
	89/2	99.76	0.24	7	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	85/4	97.46	2.54	12	9	-	-	VR	VR	-	-	-	-	-	-	-	-	-	-	-	-	
	85/1	100	0.00	11	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	83/1	80.63	19.37	9	12	-	-	-	-	R	VR	-	-	-	-	-	-	-	-	-	-	
	81/1	97.88	2.12	12	8	VR	-	-	VR	VR	VR	-	-	-	-	-	-	-	-	-	-	
	77/3	85.10	14.90	8	9	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	
	77/1	95.72	4.28	13	3	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	

