Distribution and significance of foraminiferal biofacies on an aphotic Danian bryozoan mound, Karlstrup, Denmark

EMILIE GRØNBÆK SPRINGER, JAN AUDUN RASMUSSEN & LARS STEMMERIK

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In this study, the distribution of benthic foraminifers across a Danian bryozoan mound in Karlstrup quarry, Denmark, is analysed in 22 samples using multivariate analysis. Three foraminiferal biofacies are established, each representing a distinct part of the mound. The *Anomalinoides-Cibicides-Osangularia* Biofacies is characteristic of the relatively pure carbonate sediments on the crest and flanks of the bryozoan mound. The *Patellina* Biofacies occurs at the mound flanks and is particularly common in marly sediments. The *Spirillina* Biofacies characterises the crest of the bryozoan mound, in both marly and pure carbonate sediments.

Variations in the plankton/benthos ratio indicate that the benthic foraminifers prefer the marly sediments to pure limestone and mound flanks relative to the mound top. It is likely that the benthic foraminifers avoided the more powerful currents at the mound crest. The common occurrence of spirillinids on the mound top may represent the remnant of a rich, siliceous sponge community.

Keywords: Palaeoecology, benthic foraminifers, biofacies, Danian, Karlstrup quarry, bryozoan mounds.

Emilie Grønbæk Springer [emiliegspringer@gmail.com], Gentofte Kommune, Natur og Miljø, Bernstorffsvej 161, DK-2920 Charlottenlund, Denmark. Jan Audun Rasmussen [janr@snm.ku.dk] and Lars Stemmerik [lars. stemmerik@snm.ku.dk], Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5–7, DK-1350 Copenhagen K, Denmark. JAR from April 1st 2016: [jan.rasmussen@museummors.dk], Museum Mors/Fossil and Mo-clay Museum, Skarrehagevej 8, DK-7900 Nykøbing Mors, Denmark.

Corresponding author: Jan Audun Rasmussen

Lower Danian cool-water bryozoan mounds are common in a NW–SE trending facies belt along the north-eastern margin of the Danish Basin from eastern Sjælland to northern Jylland, Denmark (Fig. 1; Thomsen 1995; Bjerager & Surlyk 2007). The mounds are believed to reflect deposition in relatively deep water, below the photic zone, and pass south- and westwards into deep water chalk deposits (Thomsen 1995). The Danian mounds are 50–110 m long with a relief of 5 to more than 10 m above the sea floor (Cheetham 1971; Thomsen 1976, 1983; Bjerager & Surlyk 2007). The benthic fauna is dominated by bryozoans in a carbonate mud matrix. Octocorals are locally common while echinoids, crinoids, serpulid worms, brachiopods, bivalves, calcareous sponges and benthic foraminifers are minor elements (Bjerager & Surlyk 2007). The mounds are poorly cemented and samples therefore easy to disintegrate, making them ideal for faunal studies.

Studies of fossil and recent epifaunal and infaunal benthic foraminifers have demonstrated that shell morphology usually reflects adaptions to life strategies in the different microhabitats (e.g. Bernhard 1986; Corliss & Chen 1988; Koutsoukos & Hart 1990; Kaiho 1991; Murray 1991, 2006). The usually high abundance of benthic foraminifers in seabed samples and their ability to react quickly to environmental changes make them well suited for ecological and palaeoecological studies. In the present study, we analyse the distribution of benthic foraminifers across a single Danian bryozoan mound exposed in an old quarry at Karlstrup some 25 km southwest of Copenhagen (Fig. 1, Fig. 2), with the aim to improve the understanding of its evolution over time and its dependency on the sea-floor conditions. We have established three palaeoecological biofacies based on multivariate analysis of the benthic foraminifer assemblage in 22 samples, each of them characterising certain parts of the bryozoan mound. Five genera, *Anomalinoides*, *Cibicides*, *Osangularia*, *Patellina* and *Spirillina*, constitute 73% of the benthic foraminiferal assemblage. The relative variations in abundance between these genera have shown to be useful in the palaeoecological analysis.

The analysis of the benthic foraminifers in the Karlstrup mound supplements earlier analyses of the benthic macrofauna in Danian bryozoan mounds from Jylland and Stevns Klint (Fig. 1; Thomsen 1976; Bjerager & Surlyk 2007).

Geological setting

The Danish Basin forms part of an extensive basin that covered north-western Europe during the late Cretaceous and earliest Danian (Surlyk 1997). The basin was bounded to the north by the inverted Sorgenfrei–Tornquist fault zone and to the south by the Ringkøbing–Fyn basement high (Fig. 1).

The study area of Karlstrup quarry is located in the south-eastern part of the basin. Quarrying in the area started in 1843 and ended in 1975; the quarry is now a recreational area and the walls are either flooded or partly overgrown (Gravesen 1983, 1993). The studied bryozoan mound is located along the western wall of the quarry. It forms part of the Stevns Klint Formation, and the occurrence of the planktic foraminifers *Parasubbotina pseudobulloides* and *Subbotina trivialis* in all the studied samples, together with the lack of younger species such as *Subbotina triloculinoides* and *Globanomalina compressa*, show that the mound was deposited during the early Danian *P. pseudobulloides* Subzone (P1a) of Berggren & Miller (1988). Thus, it correlates biostratigraphically with the top of the Cerithium Limestone Member and the lower part of the overlying bryozoan mounds of the Korsnæb Member at Stevns Klint (Rasmussen *et al.* 2005). Additionally, the occurrence of the echinoid *Tylocidaris oedumi* in the mound shows that it correlates with the *T. oedumi* Zone of Rosenkrantz (1937). The bryozoan-rich limestones were included in the Korsnæb Member of the Stevns Klint Formation by Surlyk *et al.* (2006). They dominate the lower Danian in a facies belt across northern Sjælland and northern Jylland where they form important groundwater reservoirs. The thickness varies from 30–45 m in northern Jylland to 5–20 m on Sjælland (Thomsen 1995; Surlyk *et al.* 2006).

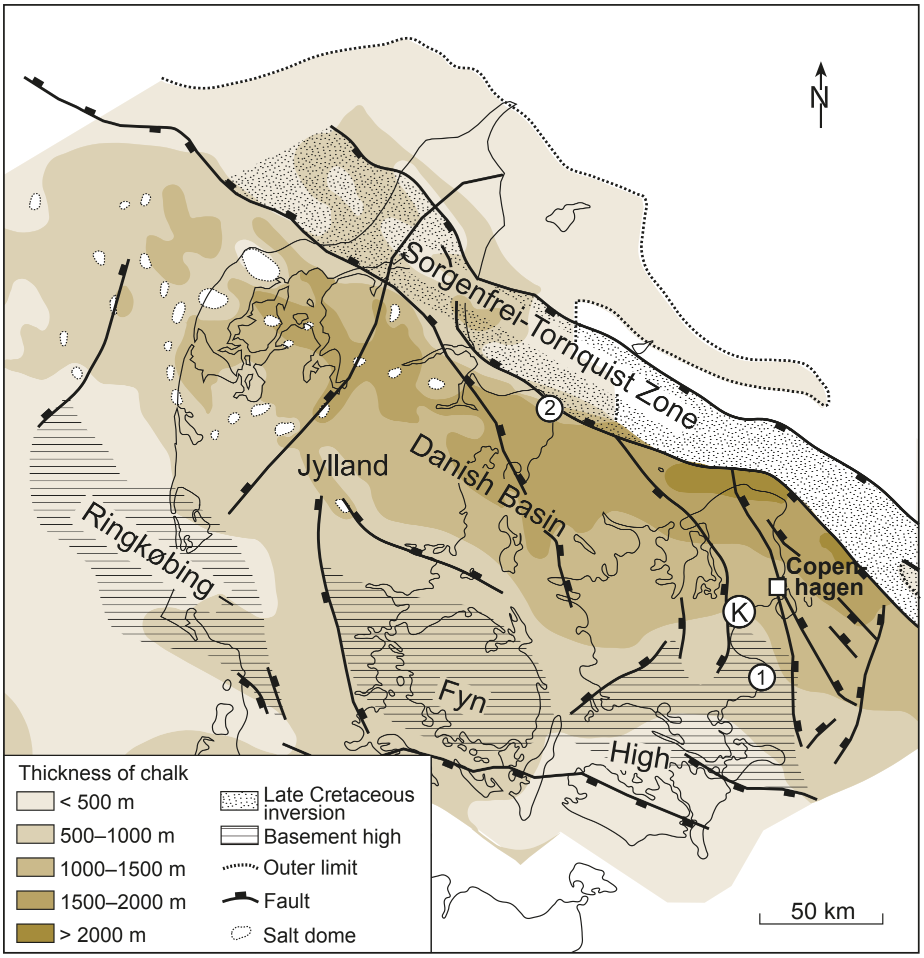

Fig. 1. Karlstrup quarry (K) is situated approximately 25 km south-west of Copenhagen, Denmark (map modified after Stemmerik *et al.* 2006). Additional localities mentioned in the text are Stevns Klint (1) and Karlby Klint (2).

The shape and growth of the bryozoan mounds are controlled by availability of food and bottom currents. The mounds are asymmetric and the highest density of bryozoans is found on the steep flanks facing the currents, where higher availability of food gave favourable conditions for colony growth (Thomsen 1976, 1983). The palaeocurrents were flowing towards WNW under the influence of the palaeotopography and the Coriolis force, and accordingly the bryozoan mounds migrated in a direction varying from SW to SE (Surlyk *et al.* 2006; Bjerager & Surlyk 2007). The bryozoan mounds in the Karlstrup quarry have the steepest flanks towards the SSW and S, which agrees with the orientation at Karlby Klint (Thomsen 1983) and Stevns Klint (Bjerager & Surlyk 2007).

Material and methods

Twenty-two samples of approximately 200 g were collected for analysis from two bryozoan packstone beds with thin marly layers. The limestone beds, which are separated by flint horizons, can be traced across the selected mound. Samples were taken at eight vertical sections across the mound (Fig. 2). Where possible, three samples were taken at each section: one in the basal part of each of the two selected limestone beds and one in a marly layer in the upper bed. The lower limestone bed is referred to as bed A, the upper limestone is bed B, and the marly horizon is referred to as the M layer (Fig. 3).

Sixty grams of each sample were placed in a drying

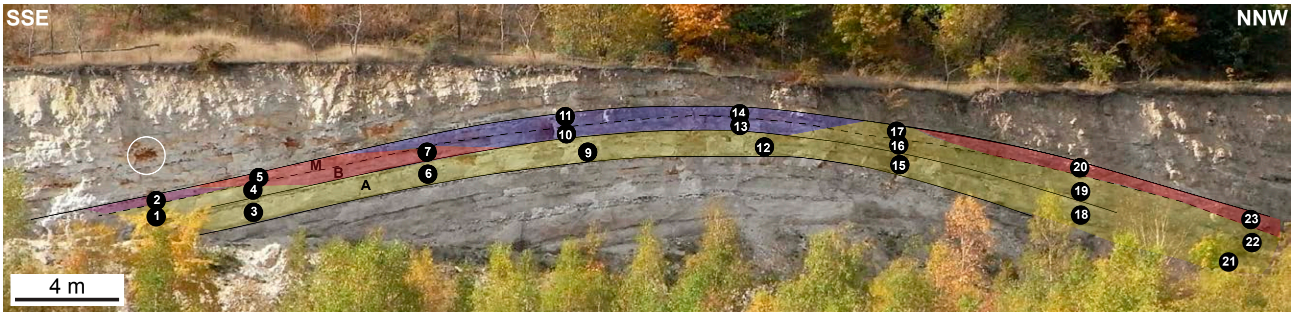

Fig. 2. The studied lower Danian bryozoan mound in the western wall of Karlstrup quarry. Twenty-two samples (numbers 1–7, 9–23, all with prefix P not shown here) were collected across the mound in two limestone beds (A and B) and one marly layer (M). Yellow shading marks the distribution of the *Anomalinoides*-*Cibicides*-*Osangularia* Biofacies, red shading corresponds to the *Patellina* Biofacies, and blue shading marks the *Spirillina* Biofacies. Layer M at sample 2 is shaded purple, as sample 2 shares characteristics of both the *Spirillina* and the *Patellina* biofacies. The white circle is a characteristic area also visible in Fig. 3.

Fig. 3. Close-up of the southern flank of the bryozoan mound. Limestone beds A and B are separated by continuous flint bands. Samples were collected from the basal part of beds A and B and in the distinct marly layer (M) towards the top of bed B. The white circle is a characteristic area also visible in Fig. 2. Persons for scale.

cabinet for 24 hours, then reduced to 50 g and put in a dish soap solution for at least a week. The solution was stirred approximately every other day. Thereafter the material was wet-sieved through 1 mm and 63 μm sieves. The 1 mm to 63 μm fractions were dried, weighed, and split into suitable volumes. Splits from each sample were examined through a binocular microscope.

The ratio between planktic and benthic foraminifers is named the P/B ratio. It is expressed as 100×P/(P+B), which is the percentage of planktic foraminifera in the total foraminiferal assemblage. Approximately 200 foraminifers were picked from each sample to establish the P/B ratio, resulting in 2741 benthic and 5555 planktic foraminifers. Subsequently, additional splits were picked for palaeoecological analysis, resulting in 100–200 benthic specimens per sample and 4194 benthic specimens in total. The benthic foraminifers and selected planktic foraminifers were assigned to order, family, genus, or species level. Selected benthic species from the present data set have been taxonomically described and photographed using a Scanning Electron Microscope (Springer 2013).

The distribution of benthic foraminifers, especially the so-called reduced benthic assemblage (see below), was analysed statistically with two different multivariate statistical methods – correspondence analysis and cluster analysis – using the PAST software package (Hammer *et al*. 2001, Hammer 2012).

Ordination and clustering are the two main categories of multivariate methods employed in palaeoecological analyses. The principal method used in this study is Correspondence Analysis, which is a nonparametric ordination method that maximizes the correspondence between genus scores and sample scores. It is based on relative rather than absolute numbers from the data set. In this case it means that the relative number of the selected genera in each sample is more important than the absolute abundance. The advantage of the Correspondence Analysis is that genera and samples are ordinated simultaneously and scaled similarly. Thus, it is possible to plot the genus scores (R-mode) and the sample scores (Q-mode) in the same scatter diagram to show the relationship between them. Genera which plot close to each other in the CA plot show a related distribution and are typically relatively common in the same samples. Similarly, closely spaced localities are characterised by the occurrence of similar foraminiferal assemblages.

Data set reduction

A total of 4194 benthic foraminifers were counted and identified using the methods described above. The total number of benthic foraminifers collected from each sample varies between 82 and 506, and all samples except P12 and P19 contained more than 100 benthic foraminifers (Table 1). All observed benthic foraminifers are calcareous with a hyaline test. Approximately 85% of the benthic foraminifers were identified to the order level and 80% to genus level.

Based on a study of benthic foraminifers, Fatela & Taborda (2002) analysed the importance of both the total and relative abundance of taxa in palaeoecological studies. They showed that approximately 300 specimens of a population give a reliable statistical result, but concluded also that in studies primarily focusing on dominant taxa that each comprise >5% of the total fauna a collection of 100 specimens gives a sufficient degree of statistical reliability. These recommendations are followed here, and our statistical analyses were carried out on a reduced genus group, where genera comprising less than 5% were discarded. Consequently, the five dominating genera – *Cibicides*, *Anomalinoides*, *Osangularia*, *Patellina* and *Spirillina* – which each constitute more than 5% of the total benthic foraminiferal assemblage were treated statistically. In total, this reduced benthic assemblage includes 3070 specimens constituting 73% of the total benthic assemblage. The four most abundant species are *Cibicides succedens, Osangularia lens, Anomalinoides ?midwayensis* and *Anomalinoides* sp. A.

Results

P/B – the ratio between planktic and benthic foraminifers

Gibson (1989) investigated the P/B ratio in a variety of settings and showed that the relative portion of planktic foraminifers generally correlates with distance from shore and/or water depth, and thus they are relatively more abundant with increasing depths in shelf and slope settings. In this work, the P/B ratio varies from 40.9% to 91.8% and is generally lower in the marly M layer (average 50.6%) than in the more pure limestone beds A and B (average 71.3%). Furthermore, in all three layers the P/B ratios are slightly higher near the mound crest (average 70%) than at the mound flanks (average 61%).

Multivariate statistical analyses

The Morisita similarity index was selected for the unweighted pair-group average (UPGMA) cluster analysis. This index is widely used in ecological studies and is favoured by its independence of sample size and diversity (Wolda 1981).

Table 1. Number of identified benthic foraminiferal specimens in each sample

Sample	P1	P2	P3	P4	P5	P6	P7	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20	P21	P22	P23	Total
Anomalinoides midwayensis ?	12	2	10	6	0	13	5	6	7	4	0	12	14	5	8	4	6	6	7	3	6	7	143
Anomalinoides sp. A	11	6	26	4	9	24	8	18	9	3	10	40	37	18	32	21	20	7	16	64	13	15	411
Anomalinoides spp.	7	1	1	2	0	0	0	2	2	4	1	5	4	4	3	1	0	3	1	5	0	0	46
Buliminida morfotype A	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3
Charltonina spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Charltonina ? sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cibicides spp.	21	4	18	7	8	6	10	13	3	4	6	3	30	3	15	25	17	9	13	33	9	12	269
Cibicides succedens	19	9	16	20	9	14	4	17	7	5	4	9	18	5	11	17	27	8	10	41	8	15	293
Cibicidoides spp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	7	1	0	0	0	0	0	0	9
Discorbidae morfotype A	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	5
Eponides spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Gavelinopsis spp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Globulina ?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Guttulina sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Gyroidinoides spp.	0	0	0	0	0	2	0	0	0	0	0	1	1	0	1	0	0	0	0	2	1	0	8
Lagena sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
Lagenida morfotype A	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Lagenidae morfotype A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Lenticulina spp.	0	0	1	1	0	1	0	2	0	0	0	0	0	1	1	0	1	1	0	1	1	1	12
Nodosaria cf. *spinescens*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Nodosariidae morfotype A	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Nonionella ?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
cf. *Nonionella* sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Osangularia lens	36	11	21	21	5	25	30	9	19	18	14	18	47	17	67	35	25	12	17	30	25	21	523
Patellina spp.	4	40	28	2	73	38	50	7	44	20	9	7	61	20	0	32	13	2	58	24	3	60	595
Planulina ? spp.	1	0	0	0	0	1	0	1	0	2	1	0	1	0	0	0	0	0	0	2	0	0	9
Polymorphinidae morfotype A	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	3
aff. *Pyrulina* sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
cf. *Pyrulinoides* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Pullenia spp.	0	0	0	2	2	1	0	0	0	0	0	0	0	1	0	0	1	2	0	1	0	2	12
Pullenia ?	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Pyrulina sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Rosalina aff. *globularis*	0	1	4	0	1	11	2	0	0	2	0	3	11	0	1	5	5	4	0	5	3	2	60
Rosalina sp. A	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	3
Rosalina sp. C	0	0	0	0	0	0	0	2	6	0	0	1	0	1	1	3	0	0	1	0	0	0	15
Rosalina sp. D	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2
Rosalina sp. E	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	2
Rosalina sp. F	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	3	7
Rosalina sp. AA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Rosalina spp.	0	0	0	0	0	0	0	0	6	0	0	13	8	0	0	0	0	0	0	0	0	0	27
cf. Rosalina	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2
Rosalina sp. B	0	0	0	0	0	0	0	0	0	0	0	14	0	0	1	0	0	0	0	0	0	0	15
Rotaliida A.	1	1	0	2	1	2	2	0	16	10	0	28	41	3	5	0	3	0	1	3	3	0	122
Rotaliida B.	0	0	0	1	0	0	0	0	0	7	0	0	20	0	0	0	1	0	0	0	0	0	29
Rotaliida C.	0	0	0	0	0	0	0	0	3	7	0	11	11	2	0	0	1	0	0	0	0	1	36
Spirillina spp.	5	44	55	2	42	34	22	10	76	57	8	71	159	11	23	27	11	8	34	67	7	17	790
Stilostomella spp.	1	0	5	1	1	2	0	1	0	0	0	3	7	3	3	2	2	0	3	4	0	0	38
Tappanina selmensis	1	0	0	0	0	2	7	0	8	5	0	8	23	1	3	1	0	0	0	2	0	4	65
Genus et species indet. A	2	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5
Genus et species indet. B	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	1	0	0	0	0	0	8
Genus et species indet. C	18	5	14	21	12	28	9	11	0	0	17	0	0	28	37	17	12	10	22	18	33	30	342
Genus et species indet. D	9	0	3	5	0	3	8	0	0	0	5	0	0	7	17	8	11	10	2	4	13	3	108
Genus et species indet. E	0	0	0	3	0	0	1	0	0	0	0	0	0	2	6	0	2	0	1	0	0	2	17
Genus et species indet. F	1	1	1	5	0	3	15	0	0	4	10	19	12	1	22	4	2	0	9	11	6	10	136
Total	160	125	204	105	164	211	175	110	207	154	86	266	506	135	270	208	164	82	196	324	134	208	4194

In the correspondence analysis, *Cibicides* and *Osangularia* plot closely together near *Anomalinoides* in the left-hand side of the diagram (Fig. 4), whereas *Patellina* and *Spirillina* plot near the two corners in the right-hand side.

The R-mode dendrogram for the cluster analysis based on the Morisita similarity index differs from the correspondence analysis plot in showing a closer relation between *Cibicides* and *Anomalinoides* than between *Cibicides* and *Osangularia.* Otherwise, the resulting R-mode dendrogram (Fig. 5A) is in agreement with the correspondence analysis plot. Both methods show that the genera divide into two main groups consisting of *Cibicides, Anomalinoides* and *Osangularia* in one group, and *Patellina* and *Spirillina* in the other. Furthermore, the distribution of *Anomalinoides*, *Cibicides* and *Osangularia* show a higher degree of similarity than that of *Patellina* and *Spirillina.* The Q-mode dendrogram (Fig. 5B) corresponds well with the correspondence analysis results, and the three main sample clusters form a basis for the distribution of foraminiferal biofacies described below.

Foraminiferal biofacies

Based on the correspondence analysis, the cluster analysis, and the quantitative distribution of the five analysed genera, three biofacies are recognised: *Anomalinoides-Cibicides-Osangularia* Biofacies, *Patellina* Biofacies and *Spirillina* Biofacies (Fig. 4, Fig. 5A, B).

Anomalinoides-Cibicides-Osangularia Biofacies

Definition. Together, *Anomalinoides, Cibicides* and *Osangularia* constitute more than 50% of the reduced genus group (see above).

Characteristics. Dominated by the nominate genera, this biofacies also includes relatively common specimens of *Spirillina* (14%) and *Patellina* (8%). Specimens of *Rosalina* (2.2%), *Stilostomella* (1.1%), *Lenticulina* and *Cibicidoides* occur sporadically.

Distribution. The biofacies characterises the relatively pure carbonate sediments on both the crest and flanks of the bryozoan mound.

Occurrence. P1, P3, P4, P6, P9, P12, P15, P16, P17, P18, P19, P21 and P22.

Patellina Biofacies

Definition. *Patellina* constitutes more than 33% of the reduced genus group (see above).

Characteristics. *Patellina* dominates the biofacies, but *Spirillina* (18%), *Cibicides* (10.8%), *Osangularia* (10%) and *Anomalinoides* (9%) are also common. Additional, scattered genera include *Tappanina* (1.3%), *Rosalina* (1.3%), *Stilostomella*, *Pullenia* and *Eponides.*

Distribution. The biofacies characterises the bryozoan mound flanks and is particularly common in the marly sediments.

Occurrence. P5, P7, P20 and P23. P2 shares characteristics of both the *Spirillina* Biofacies and the *Patellina* Biofacies.

Spirillina Biofacies

Definition. *Spirillina* constitutes more than 33% of the reduced genus group.

Characteristics. Dominated by *Spirillina*, this biofacies also includes *Patellina* (13.7%), *Anomalinoides* (12.0%), *Osangularia* (9%) and *Cibicides* (7%). Less common benthic genera include *Rosalina* (4.5%), *Tappanina* (3.5%) and *Stilostomella*.

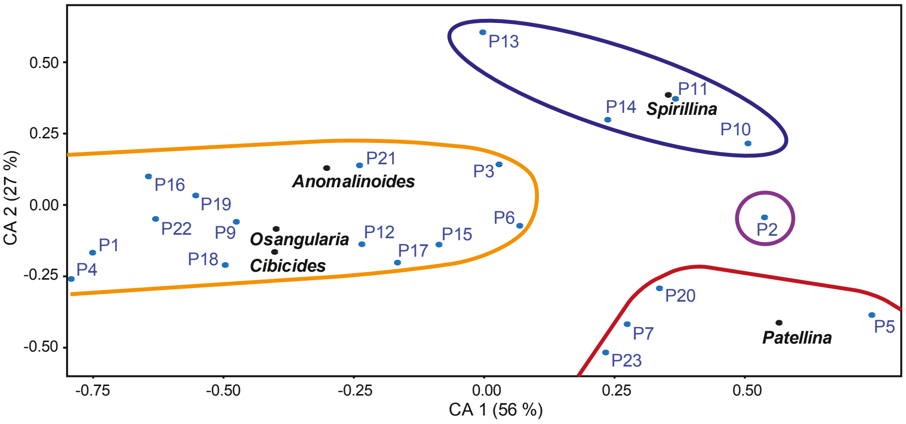

Fig. 4. Correspondence analysis plot based on a reduced benthic foraminiferal assemblage including all genera that comprise more than 5% of the total assemblage. Samples P1, P3, P4, P6, P9, P12, P15–19, P21 and P22 belong to the *Anomalinoides-Cibicides-Osangularia* Biofacies (enclosed by an orange curve). Sample P2 shares characteristics of both the *Spirillina* and *Patellina* Biofacies (enclosed in a purple ring). Samples P5, P7, P20 and P23 represent the *Patellina* Biofacies (enclosed by a red curve). Samples P10, P11, P13 and P14 belong to the *Spirillina* Biofacies (enclosed by a blue curve). Note that 56% of the overall variation is seen along the CA 1 axis and only 27% along the CA 2 axis.

Distribution. The biofacies characterises the crest of the bryozoan mound where it occurs in both marls and pure carbonate facies.

Occurrence. P10, P11, P13 and P14. P2 shares characteristics with both the *Spirillina* Biofacies and the *Patellina* Biofacies.

Following the definitions of Corliss & Chen (1988), epifaunal foraminifers are recognised as those that live on or within the uppermost centimetre of the substrate, while infaunal foraminifers live below the uppermost centimetre of the substrate. Typically, epifaunal species are characterised by trochospirally coiled, plano-convex or biconvex tests, while infaunal species commonly have unornamented, elongate, biserially or triserially coiled torpedo-shaped or flattened tests or are planispiral with a rounded periphery (Corliss & Chen 1988, Kaiho 1991). In addition, anaerobic specimens are generally smaller than aerobic (Bernhard 1986). Epifaunal specimens represent 98% of the total benthic assemblage from the bryozoan mounds of Karlstrup. The content of infaunal benthic specimens is insignificant and averages 2% (Table 2). The scattered infaunal specimens are represented by *Tappanina selmensis*, *Stilostomella* spp. and a species of Buliminida morphotype A which are confined to the area near the crest of the mound. Infaunal specimens are typically most common in assemblages of the *Spirillina* Biofacies.

Palaeoenvironmental significance

Overall, the foraminiferal assemblage contains 65% planktic specimens. According to the empirical equation of Van der Zwaan *et al*. (1990), this indicates a depositional depth of about 350 m. However, as discussed recently by Rasmussen & Sheldon (2015), this value is probably biased towards a deeper setting because the equation was based on depositional settings other than those of the very fine-grained chalk sea sediments. The common occurrence of azooxanthellate octocorals within the Danian deposits (Bernecker & Weidlich 2006) strongly indicates a palaeo-depth below the photic zone, but probably not deeper than 200–300 m as indicated by the common occurrence of the typical inner shelf foraminifer genera *Spirillina* and *Patellina* documented in the present paper. Hennig (1899) suggested a comparable depth for the middle Danian bryozoan mounds of the Faxe quarry. A recent study on cold-water, stylasterine corals from the middle Danian Faxe Formation (Lauridsen & Bjerager 2014) indicate a similar depositional depth of 200–400 m by comparison with modern stylasterine corals.

It is assumed that the relatively small variations in the P/B ratios on the bryozoan mound are not related to changes in water depth but instead to other environmental changes. If it is further assumed that the deposition of planktic foraminifers was uniform across the

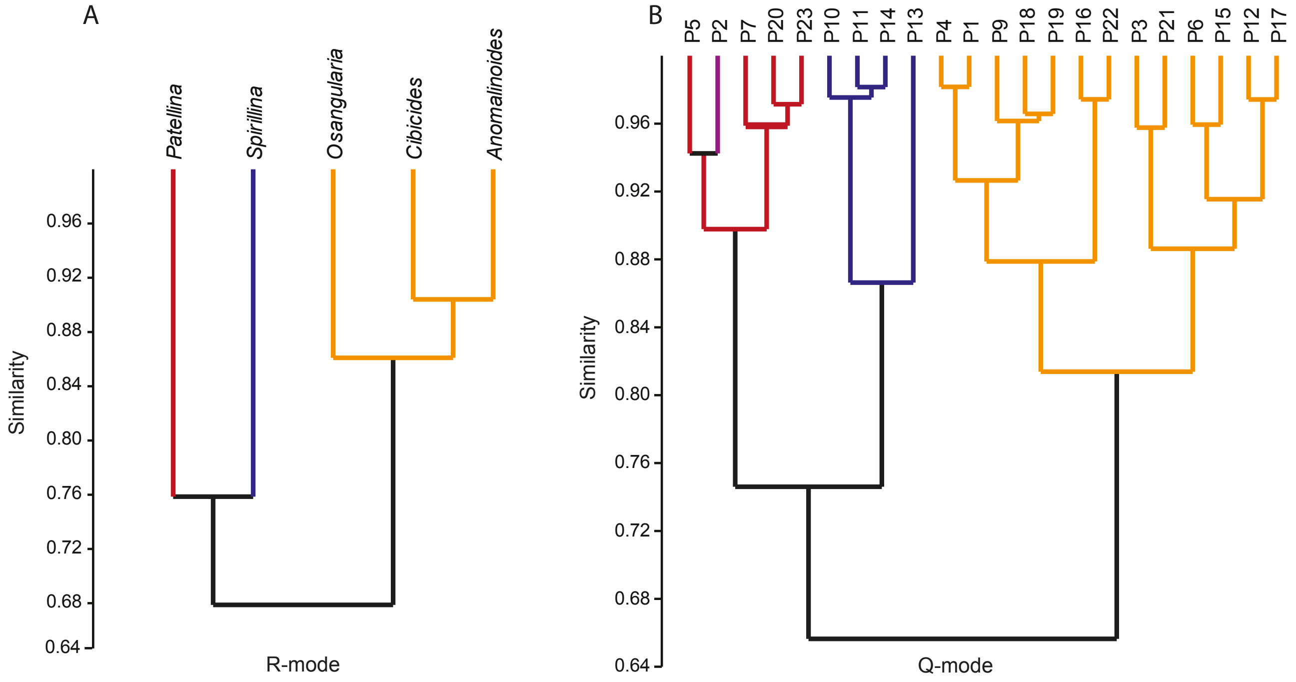

Fig. 5. Cluster analysis using the Morisita similarity index on a reduced benthic foraminiferal assemblage including all genera that comprise more than 5% of the total assemblage. **A**: R-mode dendrogram showing the level of similarity between the five dominating genera: *Anomalinoides, Cibicides, Osangularia, Patellina* and *Spirillina*. **B**: Q-mode dendrogram showing the level of similarity between the content of the five dominating genera in each sample. See Fig. 4 for explanation of colours.

mound with minimal secondary transportation, the variation in the P/B ratio is best explained by relative changes in the abundance of benthic foraminifers. Following that assumption, the P/B ratio reflects a tendency towards a higher concentration of benthic foraminifers in the marl layer (M layer) compared to the two pure limestone layers (A and B beds), and on the flanks relative to the mound top. Thus, the benthic foraminifers seem to follow the same pattern as the bryozoans described by Thomsen (1983), avoiding the most powerful currents near the crest of the mound.

Several studies have indicated that the epifaunal/infaunal foraminiferal ratio reflects the organic carbon flux to the sea floor and/or the oxygen content near the sea floor and the uppermost centimetres of the underlying sediment (e.g. Bernard 1986; Corliss & Chen 1988; Corliss 1991; Kaiho 1991, 1994), but also other factors such as competition for food and space is important (Van der Zwaan *et al*. 1999). As a rule, an increase in the organic matter content triggers a decrease in the oxygen content of the pore water caused by microbial metabolism (Reolid & Martinez-Ruiz 2012). The Danian mounds contain a rich and diverse fauna of benthic organisms indicating excellent ecological conditions including well-oxygenated bottom water and a high food supply. It seems likely that the sparse infaunal fauna is related to the relatively coarse-grained structure of the bottom sediments (average 57 wt% > 63 μm), especially at the crest (70 wt% > 63 μm), and the relatively strong bottom currents that swept the mounds. Several modern studies have shown that these factors are inhibiting for infaunal foraminifers, but enhancing for epifaunal foraminifers (e.g. Schönfeld 2002; Schönfeld *et al*. 2011).

Lithological influence on the distribution of biofacies

The lower of the two relatively pure limestone layers, bed A (Fig. 2, Fig. 3), is strongly dominated by the *Anomalinoides-Cibicides-Osangularia* Biofacies which contains 65.8% of the analysed benthic foraminifers. Of these, the two first-mentioned genera are most common and make up 25.6% and 23.2% of the analysed genera, respectively, while *Osangularia* accounts for 17% of the specimens. Similarly, the *Anomalinoides-Cibicides-Osangularia* Biofacies dominates the overlying limestone layer, bed B, but here the abundance of *Osangularia* increases from 17% to 26.1%, while *Anomalinoides* and *Cibicides* decrease to 22.9% and 21.5%, respectively. *Spirillina* and *Patellina* constitute less than 20% on average in both limestone beds.

The marl layer (M) deposited in the upper part of bed B is characterised by a foraminiferal fauna that is strikingly different from the fauna in the two studied limestone beds. The relative abundance of the *Anomalinoides-Cibicides-Osangularia* Biofacies drops significantly to 39.3%, while the *Spirillina* and *Patellina* Biofacies increase to 29.8% and 30.8%, respectively; these genera seem to be able to take advantage of the higher content of siliciclastic mud and silt in this layer. The reason for this change is not clear. The three nominate genera of the *Anomalinoides-Cibicides-Osangularia* Biofacies are recognised as epifaunal taxa. *Anomalinoides* had its convex, umbilical side buried in the substrate, and it has been interpreted as having various feeding strategies. More precisely, it has been considered an active herbivorous, detrivorous, or omnivorous deposit feeder with a broad test that probably was well-suited for muddy substrates (Koutsoukos & Hart 1990). This is comparable to *Osangularia*, which Koutsoukos & Hart (1990) interpreted as an active herbivorous, detrivorous, or omnivorous deposit feeder. A different mode of life is seen in *Cibicides*, which may have been passive, attached and herbivorous (Koutsoukos & Hart 1990) or possibly an attached passive suspension feeder (Murray 1991). Many Palaeogene species of *Cibicides* preferred the inner and middle

Table 2. Samples on bryozoan mound. Karlstrup quarry

Samples	Position on mound	Layer/Bed (Fig. 2)	Biofacies	P/B ratio 100*(P/P+B) (%)	Infaunal specimens (%)
P1	SSE flank	B	ACO	77.1	1.3
P2	SSE flank	M	P/S	45.6	0.0
P3	SSE flank	A	ACO	44.7	2.5
P4	SSE flank	B	ACO	75.4	1.0
P5	SSE flank	M	P	42.9	0.6
P6	SSE flank	A	ACO	75.7	1.9
P7	SSE flank	B	P	69.0	4.0
P9	Crest	A	ACO	79.7	2.7
P10	Crest	B	S	55.0	3.9
P11	Crest	M	S	53.2	3.2
P12	Crest	A	ACO	91.8	0.0
P13	Crest	B	S	67.1	4.1
P14	Crest	M	S	54.9	5.9
P15	Crest	A	ACO	79.1	3.0
P16	Crest	B	ACO	85.5	2.6
P17	Crest	M	ACO	66.7	1.4
P18	NNW flank	A	ACO	64.7	1.2
P19	NNW flank	B	ACO	76.2	0.0
P20	NNW flank	M	P	40.9	1.5
P21	NNW flank	A	ACO	67.5	1.9
P22	NNW flank	B	ACO	61.0	0.0
P23	NNW flank	M	P	50.3	1.9

ACO: *Anomalinoides-Cibicides-Osangularia* Biofacies; P: *Patellina* Biofacies; S: *Spirillina* Biofacies

P/B: The percentage of planktic foraminifers (P) of the total foraminiferal assemblage (planktic+benthic (P+B)) shelf environments (Murray *et al*. 1989), but they also occur in deeper, marine settings (Murray 1991).

The distinctive increase in the abundance of *Spirillina* within the marl layer may be related to its mode of life as attached or semi-attached to hard substrates favouring epifaunal suspension feeding (Langer 1993) or grazing (Reolid *et al*. 2008), commonly occurring on the inner shelf at depths less than 100 m (Murray 1991). An alternative view was presented by Koutsoukos & Hart (1990) who suggested that *Spirillina* was an epifaunal, active herbivorous, detrivorous, or omnivorous deposit feeder on muddy substrates where the broad test may have functioned as a snow-shoe. Murray (1991) interpreted *Patellina* as an attached, epifaunal suspension feeder, but it was also suggested that the genus may have been capable of an active life mode, with the umbilical side buried in the sediment, as an herbivorous or detrivorous deposit feeder (Koutsoukos & Hart 1990).

Distribution of foraminiferal biofacies across the bryozoan mound

Seven samples from the SSE flank (samples P1–P7), nine from the mound crest (samples P9–P17), and six from the NNW flank (samples P18–P23) were analysed. Although genera of the *Anomalinoides-Cibicides-Osangularia* Biofacies are most common at both the flanks and at the mound top, a more complex pattern appears when the mean abundances of the five main genera are analysed. Overall, *Patellina* (24.3%) characterises the SSE flank, while *Spirillina* (28.1%) typifies the crest of the mound. Similarly, when both the A, B and M (marl) beds are considered, *Cibicides* (25.4%) dominates the NNW flank, but also *Anomalinoides* (22.5%) and *Osangularia* (19.1%) are common here. If only the marl layer is considered, *Patellina* characterises the two flanks and *Spirillina* the mound top. The most common infaunal species observed, *Tappanina selmensis*, constitutes 2% of the total benthic assemblage in the B and M beds at the mound crest. It is absent from the A bed. It inhabited primarily the outer neritic environments (Van Morkhoven *et al*. 1986). Although *T. selmensis* is rare, its presence indicates that at least sporadic areas with soft seabottom sediments existed at the mound top allowing an infaunal mode of life.

A survey of seven sample splits from three samples from the SSE flank, one sample from the mound crest and three samples from the NNW flank revealed that bryozoans are, by far, the most dominating supplementary fossil group, followed by serpulid worms and echinoids. Moreover, the concentration of bryozoan fragments are 2.1 times more common in the flank samples than in the top sample in the 1–2 mm fraction, measured as bryozoan fragments per gram of sediment. Very small bryozoan fragments (63–250 μm) are distinctly more common at the NNW flank (lee side) than at the SSE flank, while large bryozoan and serpulid fragments (> 2 mm) are more common at the SSE flank. Thomsen (1976, 1983) observed this difference in the size of the bryozoan fragments between the two flanks from bryozoan mounds of the lower Danian Karlby Klint. The difference is caused by a reinforcement of the bryozoans due to the stronger influence of currents on the steep flank.

A number of physical, chemical and biological factors that affected the bryozoan mound controlled the distribution of foraminiferal biofacies. Significant limiting factors include food availability (organic matter) and oxygenation (Van der Zwaan *et al*. 1999), but also light, temperature, salinity, depth, substrate, water flow velocity and competition from other organisms are important.

Reolid *et al*. (2008) found that in the Jurassic the abundance of *Spirillina* was linked to the food supply, and the genus was usually common during high mesotrophic conditions characterised by a moderate amount of dissolved nutrients. *Spirillina* was considered an epifaunal grazer that indicate the presence of significant bacterial populations related to organic carbon particles (Reolid *et al*. 2008; Reolid & Martinez-Ruiz 2012). Moreover, Reolid & Martinez-Ruiz (2012) concluded that the abundance of *Spirillina* decreased during intervals with oxygen depletion.

Interestingly, Reuter *et al*. (2013) observed that spirillinid foraminifers (*Spirillina* and/or *Patellina*) appeared in high abundances in both Miocene and Late Jurassic sponge reefs but the group was less common in the surrounding sediments; they concluded that the spirillinids populated the water channels within the internal parts of sponges, which provided both food and protection. Accordingly, it may be speculated that the mound crest at Karlstrup was originally populated by siliceous sponges which served as habitats for the spirillinids. This is supported by a comprehensive study on the Danian bryozoan mounds of Stevns Klint by Bjerager & Surlyk (2007), who showed that siliceous sponge spicules were dissolved during burial but are preserved as voids in hardgrounds. They estimated that siliceous sponges might have constituted possibly 10–30% of the mound fauna, given that they were the main source of the silica forming the very common thick flint bands and nodules in the mounds. Accordingly, the common occurrence of spirillinids in the mound crest sediments of the Karlstrup quarry may be the remains of a former, rich, siliceous sponge community which was inhabited by grazing and/or filter feeding *Spirillina* and *Patellina*.

Conclusions

Three foraminiferal biofacies have been established by multivariate analysis of the benthic foraminifer assemblage. The distribution of biofacies across the bryozoan mound shows an obvious preference in both mound area and environmental setting between the pure limestone and marly layers. The *Anomalinoides-Cibicides-Osangularia* Biofacies is characteristic of the relatively pure carbonate sediments on the crest and flanks of the mound. The *Patellina* biofacies occurs on the bryozoan mound flanks and is particularly common in the marly sediments, whereas the *Spirillina* Biofacies characterizes the crest of the bryozoan mound in both marly and pure carbonate sediments.

Spirillina and *Patellina* may be associated with siliceous sponges (Reuter *et al*. 2013) and the common occurrence of spirillinids on the mound crest may reflect that a rich community of siliceous sponges originally inhabited this part of the mound. The sponges later became the main source of silica for the flint bands and nodules of the bryozoan mound (Bjerager & Surlyk 2007).

The ratio between planktic and benthic foraminifers (P/B) and the common occurrence of the typical inner shelf genera *Spirillina* and *Patellina* indicate a depositional depth below the photic zone but probably not deeper than 200–300 m. This is comparable with previously suggested depositional depth estimates for the middle Danian bryozoan mounds of the Faxe quarry, eastern Denmark (Hennig 1899; Lauridsen & Bjerager 2014).

It is proposed that the P/B ratio further reflects a tendency of the benthic foraminifers to prefer the marly sediments (M layer) compared to the pure limestone (beds A and B), and the mound flanks relative to the mound top. This pattern is similar to that of the bryozoans avoiding the powerful currents near the mound crest (Thomsen 1983).

The very low number of infaunal species within the assemblage strongly indicates well-oxygenated conditions during the time of mound formation, which is further supported by the presence of very common *Spirillina*.

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