Morphotype biostratigraphy, diachronism, and bivalve recovery in the earliest Danian of Denmark

CLAUS HEINBERG

Morphotype ratios among planktonic foraminifers are used as a stratigraphic tool within the Cerithium Limestone, part of the lowermost Danian type sequence at Stevns Klint, Denmark. Enhanced stratigraphic resolution provided by the method indicates that the base of the limestone is diachronous, becoming progressively younger northwards. The bivalve fauna of the Cerithium Limestone represents an early recovery fauna exhibiting a gradual recovery pattern from zero species at the stratigraphic base of the limestone to a rather constant level about 20 species through the upper half of the unit. A continuous cline, covering the entire stratigraphic interval, results when using evenness or dominance, rather than species number, as a community measure. This reflects a continued growth in equitability and decline in dominance, also after the levelling of the species number.

Keywords: Cerithium Limestone, diachroniety, planktonic foraminifer morphotype stratigraphy, Danian, Stevns Klint, K–T boundary, bivalve recovery.

Claus Heinberg [heinberg@ruc.dk] Department of Environment, Technology and Social Studies, Roskilde University Center, P.O. Box 260, DK 4000, Roskilde, Denmark.

The Cerithium Limestone, exposed along the Stevns Klint section, constitutes, together with the underlying Fish Clay, the lowermost Danian. Together with the nearby limestone quarry at Faxe, the section is part of the classical type Danian, and thus a classical site for the study of the biotic turnover across the Cretaceous–Paleogene (K–T) boundary. Studies of recovery from mass extinctions, are highly dependent on comparability between 'above' and 'below' the event horizon, otherwise pseudo-recovery patterns may originate from comparing faunas of different environments, faunas with different taphonomic histories, or, in the presence of considerable hiati, from exaggeration of faunal change. The high content of microfauna and mesofauna, the setting within a carbonate succession and the stratigraphic position within the lowermost Danian overlying the iridium bearing boundary marl, the Fish Clay, gives the Cerithium Limestone an important role in the discussion of recovery from mass extinction, also in a global context. In addition, the faunas from both below and above the boundary represent a marine soft bottom carbonate palaeoenvironment, and both originate from the same hardground sharing almost the same aragonite-calcite preservational potential and taphonomic history. The preservational quality is outstanding, and the succession is complete involving all known biozones.

Localities

The Cretaceous–Paleogene boundary is exposed at a number of localities in Denmark along the axial part of the relatively narrow strait that connected the North Sea and the Polish basin (Fig. 1). The westernmost localities in the north, e.g. Nye Kløv are located 300 km from the easternmost localities in the south, Stevns Klint, and the maximum width of the strait is estimated to have been around 100 km (Thomsen 1995). Most prominent among the exposures is Stevns Klint (klint: Danish for cliff), south of Copenhagen, a 15 km long coastal cliff with easy access to the boundary. The remaining boundary exposures in Denmark are all of very restricted size.

Boundary setting

The geology of the K–T boundary succession at Stevns Klint is rather complicated (Rosenkrantz 1924,
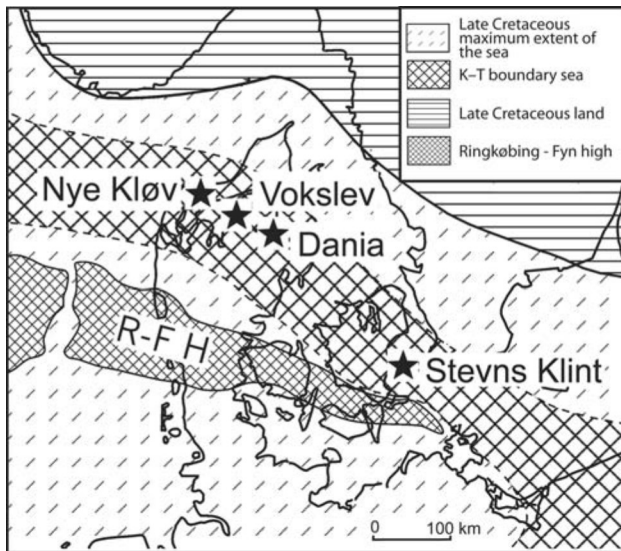
Fig. 1. Palaeogeography of the Danish region at the time of the K–T boundary. Important K–T localities indicated (from Thomsen 1995).

Schmitz *et al.* 1992; Surlyk 1997; Surlyk & Håkansson 1999; Heinberg 1999), especially with respect to the immediate post-boundary strata where a complex mix of deposition, bioturbation, lithification, glauconite formation, phosphoritization and erosion still has to be sorted out in detail. The uppermost Maastrichtian chalk was deposited as low bryozoan mounds, resulting in an undulating bottom topography where mounds and inter-mound troughs alternate in a regular pattern (Surlyk 1997). This topography formed the basis for the deposition of the iridium-bearing Fish Clay (Christensen *et al.* 1973) that terminated carbonate sedimentation and produced what must be regarded an isochronous global marker. Following deposition of the boundary marl, carbonate sedimentation gradually resumed with deposition of the Cerithium Limestone, which may

have originated as a chemically precipitated lime mud (Hansen 1990), though a possible biogenic origin of the sediment must also be considered (see Machalski & Heinberg 2005, this volume). Heavy bioturbation of *Thalassinoides* and *Spongeliomorpha* type (Ekdale & Bromley 1984) penetrated the unit to the top of the Fish Clay. After deposition and consolidation of the Cerithium Limestone, erosion removed an unknown thickness, including the crests of the Maastrichtian mounds. Accordingly, the Cerithium Limestone is preserved in a disjunct series of basin fills, separated by truncated Maastrichtian mounds (Fig. 2). Subsequent lithification produced a prominent hardground, cutting through both the Maastrichtian white chalk (mound crests) and Danian Cerithium Limestone (mound basins).

The Hardground Fauna

The hardground is rich in an aragonitic fauna of bivalves, gastropods, benthonic foraminifers, solitary corals (Rosenkrantz 1924, 1966; Heinberg 1999). This is of crucial importance for recovery studies, because aragonitic fossils are otherwise exceedingly rare in the non-lithified basal Danian carbonates and in the soft Maastrichtian white chalk, where the preservation potential of aragonite is extremely low, limiting aragonitic remains to imprints from ammonites and very rare silicified gastropods. The lowermost Danian hardground thus represents a taphonomic window into the rich aragonite-shelled faunas of the K–T boundary carbonates, otherwise barren in aragonitic fossils (Heinberg & Håkansson 2000).

The presence of the aragonite faunas completely changes the faunal patterns across the boundary (Heinberg 1999) compared to the picture derived from non-lithified chalk containing almost exclusively calcitic faunas. In the latter situation, a rich Maas-
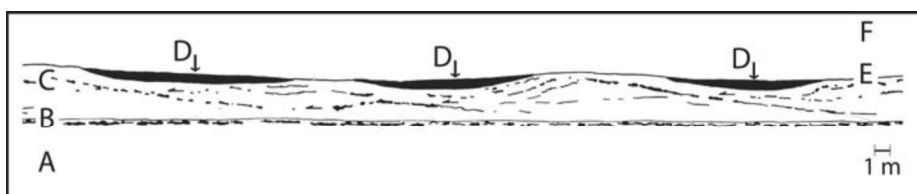
A: White chalk
B: Incipient hardground over nodular flint layer
C: Bryozoan chalk with mounds outlined by flint nodules
D: Cerithium Limestone and Fish clay
E: Hardground and erosion surface
F: Bryozoan limestone

Fig. 2. K–T boundary profile just north of Højerup old church. Three Cerithium Limestone basins marked with black, situated between the low bryozoan mounds of the uppermost Maastrichtian chalk. Line drawing based on photo mosaic. Modified from Surlyk (1997).

trichtian fauna of calcitic bivalves goes extinct at the boundary, with virtually no bivalve replacement in the early Danian. The actual situation with hardground preservation of fossils of both aragonitic (moulds) and calcitic origin, shows a continuation of nearly all higher bivalve taxa, the majority of which have aragonitic shells, into the Danian (Heinberg 1979). It is, however, a challenging fact that the lowermost Danian Cerithium Limestone contains no remains of low magnesium calcite-shelled animals, including bivalves, despite the high preservation potential of the limestone. Accordingly, this absence must be considered as primary.

In Jylland, lack of chalk lithification at Nye Kløv has facilitated quantitative collecting and comparison of calcite-shelled organisms across the boundary, including planktonic foraminifers (Berggren 1960; Bang 1980), bryozoans (Håkansson & Thomsen 1999), micromorphic brachiopods (Johansen 1987), and a prominent example of a K–T boundary transition among micromorphic brachiopods (Surlyk & Johansen 1984). A detailed planktonic foraminifer stratigraphy was established by Keller et al. (1993). This stratigraphy is based on 50 samples and more that 10,000 specimens of planktonic foraminifers. The Nye Kløv material of Keller et al. (1993) covers the PF zones P0–P1c, which includes the lowermost 4 m of Danian deposits, the socalled 'Dead Layer' (Jessen & Ødum 1923).

Fortunately, the nearby quarry at Voxlev exposes a lower Danian nodular hardground with voids after aragonitic shells (bivalves, gastropods). This fauna is similar to the Cerithium Limestone fauna, also with respect to the nearly complete absence of cal-

citic faunal elements. The Voxlev hardground thus links the Danian hardground fauna from Stevns Klint to the remaining part of the soft basal Danian chalk of northern Jylland, barren in aragonitic fossils, rendering the Cerithium Limestone fauna representative for the earliest Danian fauna throughout the basin.

Planktonic foraminifers

Due to the lithification of the Cerithium Limestone, it is difficult to process planktonic foraminifers from the rock. As a consequence, previous datings are based on rather restricted collections, covering only one or a very small number of localities.

In this study, samples for planktonic foraminifers were collected from five Cerithium Limestone basins, from south to north: 1) Rødvig, 2) Højerup, 3) Sigerslev quarry, 4) Mandehoved, 5) Holtug quarry (Fig. 3); the Rødvig and Højerup localities comprise respectively the Korsnæb and Knøsen localities in Heinberg (1999). All the Cerithium Limestone basins do not produce planktonic foraminifers with the same ease (Table 1). All basins are increasingly lithified upwards, and thus less productive in foraminifers, and the harder upper part increases in thickness northwards. In the extreme north, lithification is complete, and the northernmost of the larger basins (at Kulsti Rende), the thickest known, has not yielded any foraminifers. Each sample covers a 5–10 cm interval, dependent on the nature of the rock, which in most places is riddled with burrows. Care was taken to ensure that samples represent Cerithium

Table 1. Planktonic foraminifers. Relative abundance of serial specimens (%), and total number of specimens at five localities. * = 65–125 µm fraction, ** = >125 µm.
A–F are the sampling levels (bottom to top) within the Cerithium Limestone basins.

	RØDVIG		HØJERUP		SIGERSLEV		MANDEHOVED		HOLTUG	
F	30%	112								
E	73%	164								
	76%	162	69%	110					33%	158
D	88%	237								
C	87%	203								
B					48%	101				
					47%	89			48%	312
	89%	148	97%	106	59%	108			39%	52
A									**35%	159
	84%	63			95%	56			*43%	120
	76%	127	96%	142	95%	112	55%	240	33%	232
									30%	437
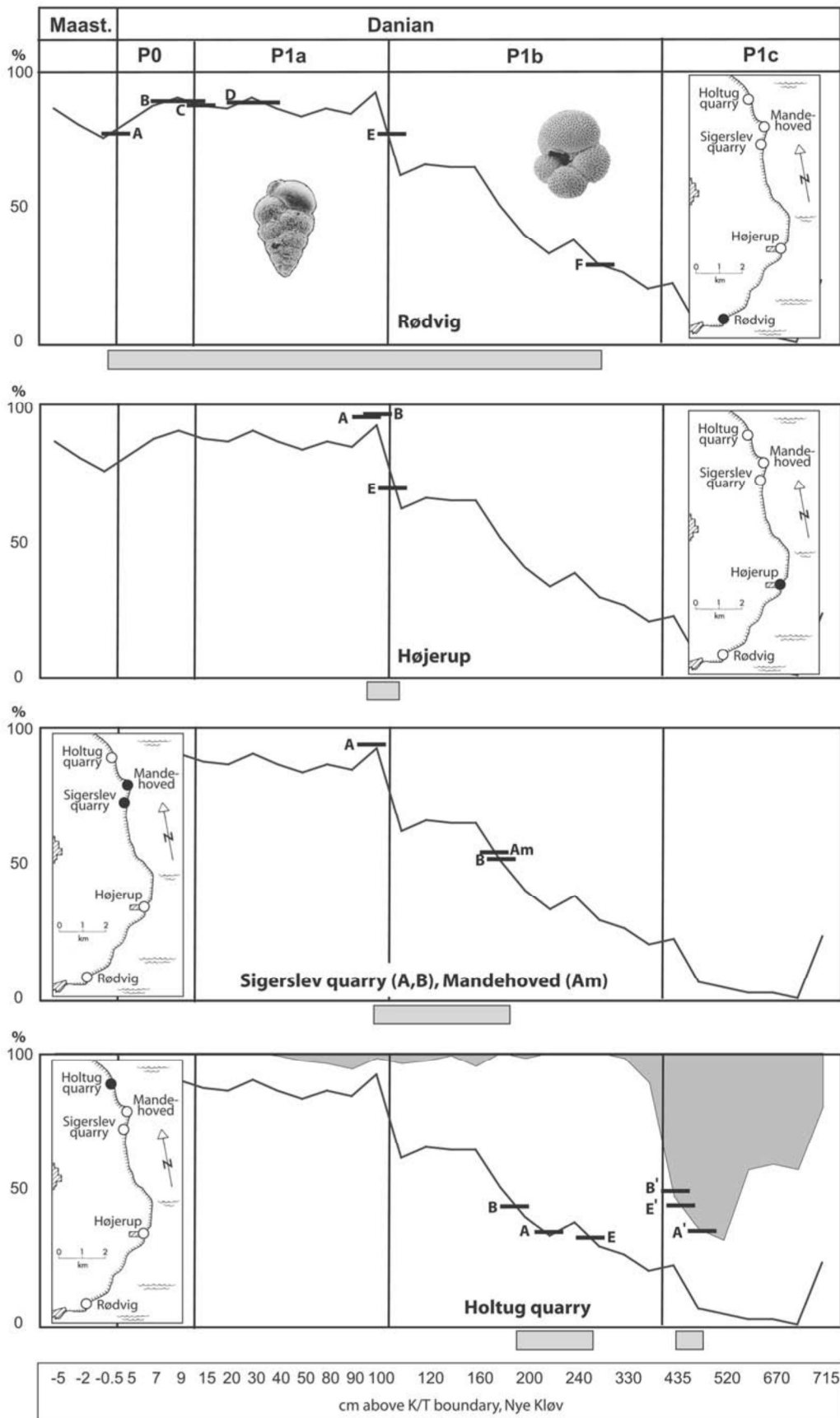
Limestone proper and not burrow fills from above. A good indication of Cerithium Limestone proper, is the presence of small (1 mm) sphaerical voids with a green glauconitic lining, supposed to represent prasinophytic algae.

Processing the samples started with the disintegration of the rock (hammer and anvil). The resulting powder was washed through a series of sieves (>500 mm, >250 mm, >125 mm, >40 mm). The finest fraction was suspended in water in a 40 cm glass tube. After settling, a thin, extremely fine-grained white layer is seen on top of the coarser material. This top layer is carefully sucked with a pipette, and pored through the 43 mm mesh. Finally the remaining water in the tube is poured through the 40 mm mesh. The material thus obtained (40–125 mm) is sorted in the conventional manner, and mounted with water on black photographic paper.

Biostratigraphy

There is contrasting evidence as well as opinions concerning age and duration of the Cerithium Limestone (see Rasmussen *et al.* 2005, this volume). Hultberg & Malmgren (1986), Schmitz (1988), Håkansson & Thomsen (1999) and Heinberg (1999) have argued that the boundary section is complete, covering the entire P0–P1a interval in the zonation of Keller (1988; Keller *et al.* 1993), while Schmitz *et al.* (1992) have suggested the presence of a hiatus on top of the Fish Clay. This conclusion is based on a restricted assemblage of planktonic foraminifers from the lower third of the Cerithium Limestone. This assemblage has a possible range from P0–P1c, and in the absence

of a few normally extremely rare species restricted to the P0–P1a zones, it was concluded that the hiatus covered the entire P1a zone, and possibly the P1b zone as well. This placed the entire Cerithium Limestone at the top of the P1b or even base of the P1c zone. This interpretation is questioned for several reasons, mainly because it is based on the absence of a few extraordinarily rare species in a sample of only 24 specimens (Keller *et al.* 1993). Occurrence in the Cerithium Limestone of coccoliths indicating the lower part of nannoplankton zone NP1, also favours a P1a age.

The present study is based on collections totalling more than 4000 specimens (24 samples, five localities) of planktonic foraminifers from the Cerithium Limestone. The samples have been collected stratigraphically from five Cerithium Limestone basins, covering the entire length of Stevns Klint. The massive increase in numbers of specimens from 28 (Schmitz *et al.* 1992) to more than 4000 provided only two additional species, increasing the number from 11 to 13. The zonation of Keller *et al.* (1993) is used throughout this work because of the permanent reference to the Nye Kløv section.

Morphotype stratigraphy

The planktonic foraminifers from the lowermost 7 m of the Danian at Nye Kløv exhibit a gradual stratigraphic transition in terms of the morphotype ratio of spiral versus biserial and triserial forms ('serial' in the following; Fig. 3). The transition constitutes a gradient from dominance (80–90%) of serial genera just above the K–T boundary (P0 zone), to a near complete dominance of spiral forms 7 m higher up, in the P1c zone. This morphotype gradient is tentatively termed the 'Nye Kløv gradient' (Fig. 3). Provided that the gradient is common to the Nye Kløv and Stevns Klint sections, such a regular stratigraphic change may serve as a stratigraphic tool or standard, simply by comparing the spiral/serial ratio of Stevns Klint samples with the Nye Kløv gradient. A high degree of similarity in ratios between the Rødvig section at Stevns Klint, and the lower part of the Nye Kløv section, even in the finer details, indicates that the entire basin did share the same planktonic history. In the following, the stratigraphic position of samples from within the Cerithium Limestone at Stevns Klint is expressed in terms of 'centimetres above the K–T boundary at Nye Kløv'. The large new material of planktonic foraminifers from the Cerithium Limestone (4000 specimens from five localities) provides the specimens necessary for such quan-

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Fig. 3. Morphotype frequencies. The four diagrams represent five sections along the coastal cliff of Stevns Klint. The position of the sections are indicated by the black dots on the inserted maps. The curve running from the upper left to the lower right of the diagrams, shows the stratigtraphic change in the ratio of spiral *versus* serial planktonic foraminifers at the locality Nye Kløv. Cerithium Limestone samples A–F are fitted to the Nye Kløv curve by the horizontal black bars, based on their morphotype frequencies. For stratigraphic position in centimetres of the samples (A–F), see box in Fig. 4. The horizontal grey bars below each diagram show the stratigraphic range of the Stevns Klint sections, in centimetres above the K–T boundary at Nye Kløv (lowermost box).
A′, B′, E′ in the Holtug diagram is based on the abundance of *Globoconusa daubjergensis* (shaded area).
Note: The Rødvig and Højerup localities correspond respectively to the Korsnæb and Knøsen localities in Heinberg (1999).
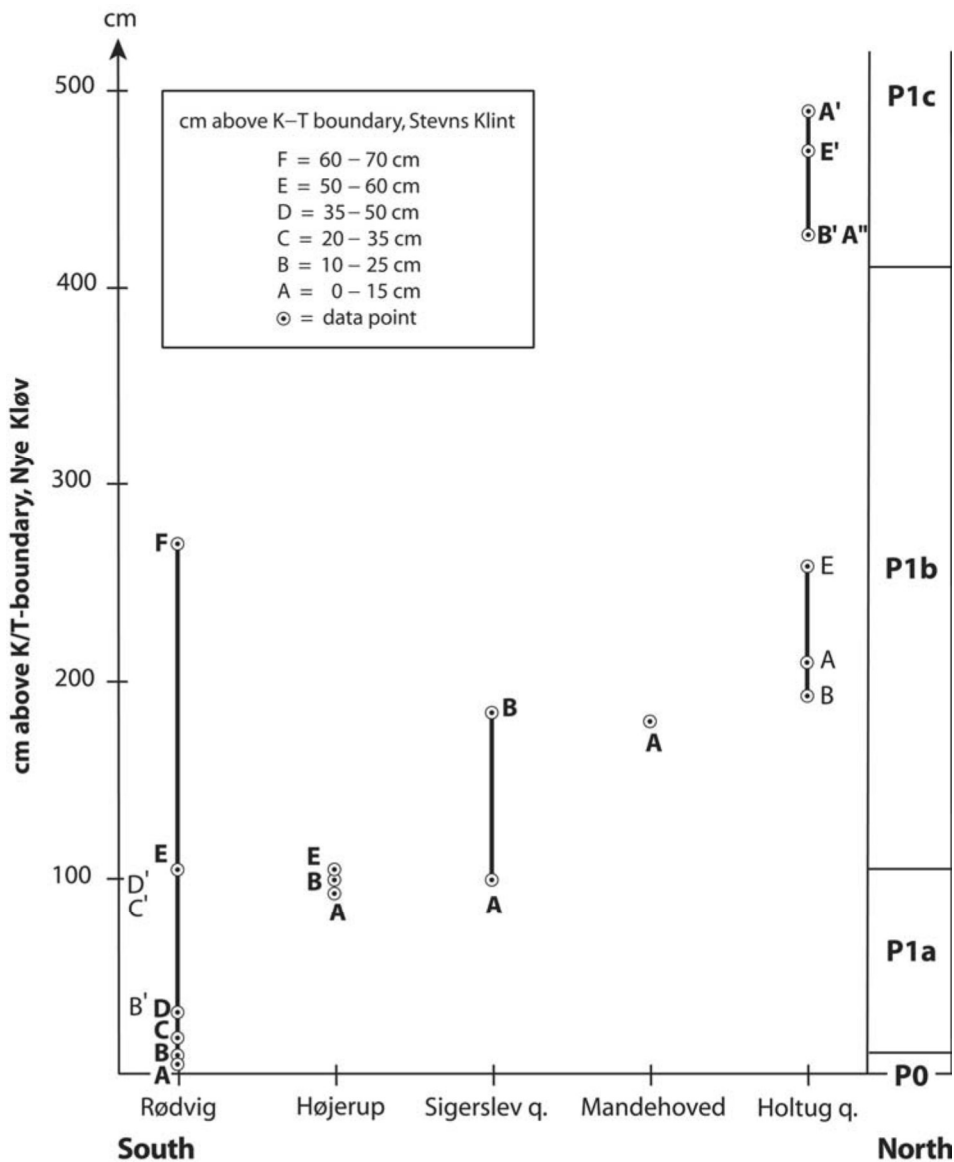
Fig. 4. Stratigraphic compilation of the Stevns Klint samples, relative to the Nye Kløv standard (centimetres above the K–T boundary at Nye Kløv) and to the position along the cliff. Letters (A–F) indicate the position of the samples in centimetres above the K–T boundary at Stevns Klint. Rødvig B′, C′, D′ refers to alternative fitting (se text) of Stevns samples, Holtug A′, B′, E′ and A″ are positions based on the frequency of *Globoconusa daubjergensis* only.

'Best Fit'

The Rødvig section may serve as an example of the procedure, when the Nye Kløv curve is used as stratigraphic standard (Fig. 3), as exemplified in the following. Fitting the spiral/serial-ratio data from the Cerithium Limestone to the Nye Kløv curve, is quite simple as long as the curve exhibits a gradient, as is the situation in the P1b – P1c interval, whereas the P0 – P1a interval, where the Nye Kløv figures vary close to a common value (90%), leaves more room

titative comparison. The outcome is an increased resolution of the stratigraphy within the Cerithium Limestone.

for interpretation. The Rødvig section is represented by six samples (samples A–F). As one of two alternatives, fitting of the samples starts with the lowermost sample (A). This sample has a spiral/serial-ratio of 78%, which places it right on the K–T boundary on the Nye Kløv gradient (Fig. 3 top) in good accordance with its position in the lowermost 5 cm of the Cerithium Limestone. Viewed in isolation, sample A could equally well be fitted to the curve at the P1a – P1b zone boundary (100–110 centimetres above the K–T boundary at Nye Kløv). However, that choice leaves no space for the B, C, and D samples. Next, the position of sample B is chosen as the first interception of the B value (89% serials) with the gradient. B could equally well be fitted a bit higher, but that would leave no space for C, D, and E.

Table 2. Relative number of *Globoconusa daubjergensis* (A), and total spiral specimen (B), with different minimum mesh dimensions. Note the positive correlation between minimum mesh size and abundance of *G. daubjergensis*.

A	B
43 µm: 60%	43 µm: 69%
65 µm: 42%	65 µm: 57%

To test the robustness of the positions obtained by this method, an alternative fitting procedure has been followed, still using Rødvig as an example, starting with the fitting of sample F and followed by the remaining samples in downward stratigraphic order. The discrepancy between the two procedures is limited, and only concerns samples B, C, D, which find their alternative position somewhat higher in the P1a zone (30–100 cm at Nye Kløv, indicated as B', C' and E' in Fig. 4) instead of in the lower part (10–30 cm above the K–T boundary at Nye Kløv). The stratigraphic positions (Fig. 3) of the analysed samples are compiled in Figure 4 with reference to both the locality at Stevns Klint and the stratigraphic position in terms of centimetres above the K–T boundary at Nye Kløv.

The A-level (bottom samples) is illustrative. All A-samples are from the lowermost 0–13 cm interval of the studied Cerithium Limestone basins (Rødvig, Højerup, etc.), and it is evident that the stratigraphic position of the base of the Cerithium Limestone becomes progressively younger to the north (Holtug). The base of the Cerithium Limestone is time-transgressive, leaving space northwards for either an increasing hiatus, or increased condensation. This overall pattern is confirmed by conventional foraminifer stratigraphy (Rasmussen *et al.* 2005, this volume) and on the high abundance of the planktonic foraminifer *Globoconusa daubjergensis* at Holtug (shaded area in the Holtug diagram of Fig. 3). At high latitude nearshore settings, the *G. daubjergensis* is a strong indicator of the P1c zone (Keller 1989; Olsson *et al.* 1999). In the present example, it accounts for up to more than 50% of the planktonic foraminifers.

There is some discrepancy between the stratigraphic positions of the Holtug samples (A, B and E) dependent on whether the morphotype ratio or the density of *G. daubjergensis* is used. Stratigraphic positions determined on the basis of the *G. daubjergensis* data alone are indicated as A', B', E' (Fig. 3) and occur well within the P1c zone, a few metres higher (Nye Kløv standard) than the stratigraphic position based on the spiral/serial ratio, in the upper half of P1b.

However, the high position of the *G. daubjergensis* acme may be an exaggeration, due to differences in the processing procedure of this work and that of Keller *et al.* 1993. The Cerithium Limestone material is processed with 40 mm as the smallest mesh size, while the Nye Kløv material has a minimum mesh size of 63 mm. Since *G. daubjergensis* is a very small species, it is likely to be overrepresented in the Stevns Klint material, resulting in too high a position. The influence of mesh size on the relative abundance of *G. daubjergensis* is shown in Table 2, where sample 9A from Holtug chalk pit has been sieved through different minimum mesh dimentions (40 mm, 63 mm and 125 mm, respectively). Using a 63 mm mesh size instead of 40 mm, reduces the fraction (whole sample) of *G. daubjergensis* from approximately 60 to 40% equivalent to a stratigraphic downshift of sample A from 470 cm to 420 cm (Holtug A" in Fig. 4). No correlation is seen between minimum mesh size and ratio of spiral/serial specimens. Therefore, the general strength of the *G. daubjergensis* acme is acknowledged and the Holtug samples accordingly placed in the lowermost part of the P1c zone in the analysis.

Bivalve recovery

The diachronous nature of the base of the Cerithium Limestone has consequences both for the interpretation of the post K–T boundary depositional history, and for the recovery of the Cerithium Limestone fauna. Revision is therefore needed with respect to the continuity of the bivalve fauna across the boundary in the Danish region (Heinberg 1996, 1999). Arrangement of the bivalve assemblages along the cliff and in accordance with the interpreted diachroneity setting forms the basis for such a revision.

The locality Rødvig is of crucial importance in this context as it shows the most complete stratigraphic section, as well as the longest range within a single basin, ranking it among the most complete K–T boundary sections worldwide with rich benthonic micro, meso and macrofaunas as well as with planktonic microfauna and flora. Brazos River and Seymour Island (Zinsmeister & Macellari 1988; Macellari 1988; Hansen *et al.* 1993) are among the few localities, which may offer a match (see also Stilwell 2003; Hart *et al.* 2004).

The analysis of the bivalve recovery is based on 64 samples, yielding 2004 bivalve specimens from different stratigraphic levels within seven Cerithium Limestone basins. Five of these basins coincide with those used in the planktonic foraminifer study. The collection has resulted in a rich additional fauna of
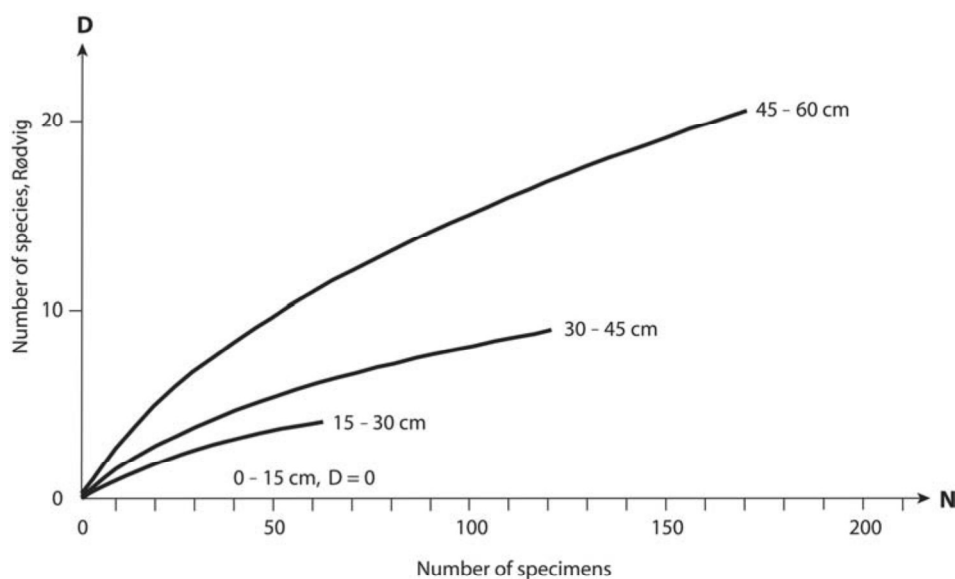
Fig. 5. Rarefaction curves, showing bivalve abundances in the Cerithium Limestone up through the Rødvig profile (0–15, 15–30, 30–45 and 45–60 cm above the K–T boundary). The basal 15 cm contains no bivalves. D: number of species, N: number of specimens.

gastropods, sponges, aragonitic benthonic foraminifers, solitary corals, scaphopods, otoliths etc., contributing to a general picture of a numerous and diversified fauna. The overwhelming part of the bivalve fauna is aragonitic, reducing the relative proportion of calcitic specimens from the Cerithium Limestone to less than one percent (Heinberg & Håkansson 2000). The generally minute size of the shells, and the void preservation, makes quantitative sampling inaccurate and troublesome, but the procedure is simple. Pieces of Cerithium Limestone are collected in place. Care is taken to avoid burrow fills. Where possible, the samples are collected stratigraphically from three, in one case (Rødvig) four levels, i.e. base (B), middle (M), and top (T) of the bed. Each interval is approximately 15–20 cm thick. The samples are dried, weighed, and hammered to small pieces in the laboratory. Larger samples are subdivided into smaller (2–3 kg) in order to check robustness of species composition and relative abundances. The re-

sult is promising. The split samples add up nicely with respect to species richness and especially to relative abundances of the more common species.

The recovery pattern of the bivalve fauna has been analysed quantitatively in terms of stratigraphic changes of three different parameters: 1) Richness (species number), 2) Broken-stick distribution (difference between observed rank–frequency and calculated broken-stick distribution) and 3) Dominance (abundance of the most common species).
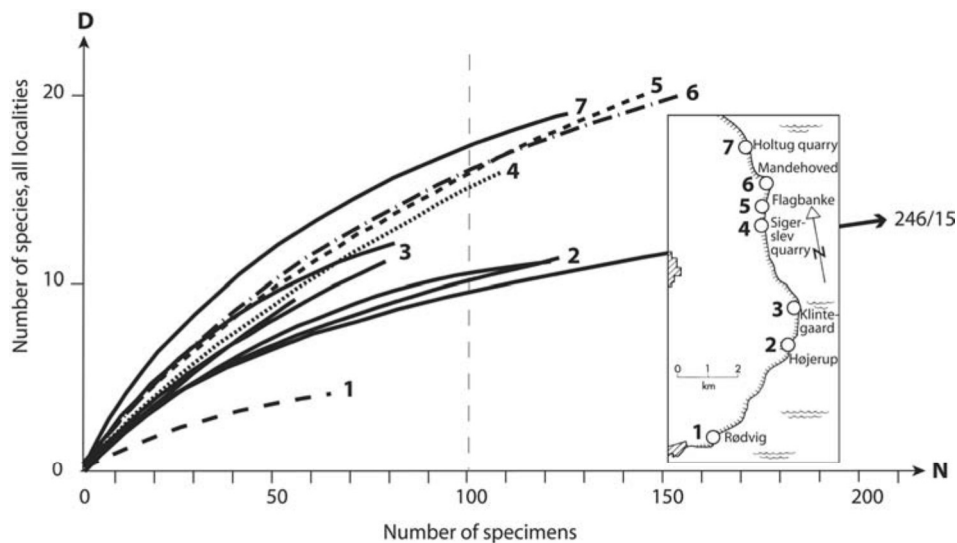
Species number

The diversity values of table 3 (raw data), show a wide range in number of species and sample sizes. To permit a more direct comparison between the differently sized samples, rarefaction curves (Sanders 1968, Hammer et al. 2001) have been constructed

Table 3. Bivalve diversity (number of species) and sample size (in brackets). Each sample interval comprises approximately 15–20 cm of rock, the two larger intervals the double thickness. The figures of the lower line are total values, including samples of unknown stratigraphic position within the individual localities.
Total number of specimens = 2004.

1	2	3	4	5	6	7
RØDVIG	HØJERUP	KLINTEGÅRD	SIGERSLEV	FLAGBANKE	MANDEHOVED	HOLTUG
17 (129)						
10 (119)	12 (119)	13 (78)		3 (16)		20 (124)
5 (63)	15 (246)	10 (54)	14 (60)	8 (22)		
0	12 (121)	12 (77)	15 (82)	17 (105)	23 (167)	
26 (411)	27 (602)	25 (280)	24 (204)	20 (143)	23 (167)	21 (197)

Fig. 6. Rarefaction curves for all localities (Rødvig, se also Fig. 5). Numbers are localities indicated on the map. Localities 2 and 3 are represented by three solid curves each (base, middle, top of the Cerithium Limestone). D: number of species, N: number of speci-

(Figs 5–6) for each locality, covering all samples larger than 54 specimens (average sample size: 120, range 54–246, total number of specimens: 1544). Species number, sample size and position of each sample are shown in Table 3.

The rarefaction method has been questioned (Tipper 1979), and even recommended not to be used (Wignall 1990), due to an alleged lack of significance. However, palaeontological data of this kind, filtered through preservational biases, taphonomic processes and problems with obtaining comparable data sets, have to be dealt with as approximations, permitting semi-quantitative and qualitative conclusions only, which is exactly what the method offers, and authors still benefit from this simple procedure for comparison among different sample sizes within the most diverse range of subjects (Fürsich & Werner 1986; Fürsich 1993; Sheehan *et al*. 1991; Hansen *et al*. 2001). It is accordingly adopted here using the PAST program (Hammer *et al*. 2001).

The results are presented in Figures 5 and 6. The close stratigraphic spacing (centimetres to tents of centimetres) of the different samples do not permit significant statistical separation (95% confidence) between neighbouring samples, but certainly among the more widely spaces ones, e.g. the Rødvig figures (Fig. 6). For comparison, number of species representing a sample size of N=100 are plotted against the Nye Kløv standard in Figure 7. Thus arranged, the bivalve data exhibit three important trends:

1) A stratigraphic upwards increase in species number at localities with sufficient data: Rødvig, Højerup, Klintegård.
2) a gradient in species number from south to north

along Stevns Klint (and up through the Rødvig section) with highest number of species to the north,
3) samples which are stratigraphically close (Fig. 4), produce similar rarefaction curves (Højerup, curve 2 in Fig. 6), while samples with large stratigraphic separation (Rødvig, Fig. 5) have widely spaced rarefaction curves.

The wide spacing of the four rarefaction curves (including base level, 0–15 cm = 0 species) from Rødvig (Fig. 5), and the almost overlapping curves from Højerup are interpreted as indicating differences in sedimentation rates at the two localities, rather than assuming differences in bivalve entry rates at the two closely adjacent localities. This implies that the Cerithium Limestone at Rødvig represents a long time span compared to the Højerup section. Klintegård (loc. 3 in Fig. 6) exhibits a similar pattern with overlapping or closely spaced curves, though not reaching the N=100 specimen level. The remaining localities (locs 4–7) are represented by only one sample each.

Broken-stick

Diversity, in the sense of species number, is commonly used as a community or assemblage character, open for interpretation. However, species richness (number of species) is a very sample-size sensitive measure, where 'the next species to be found', adding to the accumulated species number, becomes increasingly rarer (Murray 2003) as species number increases. Possible measures, dependent on the more
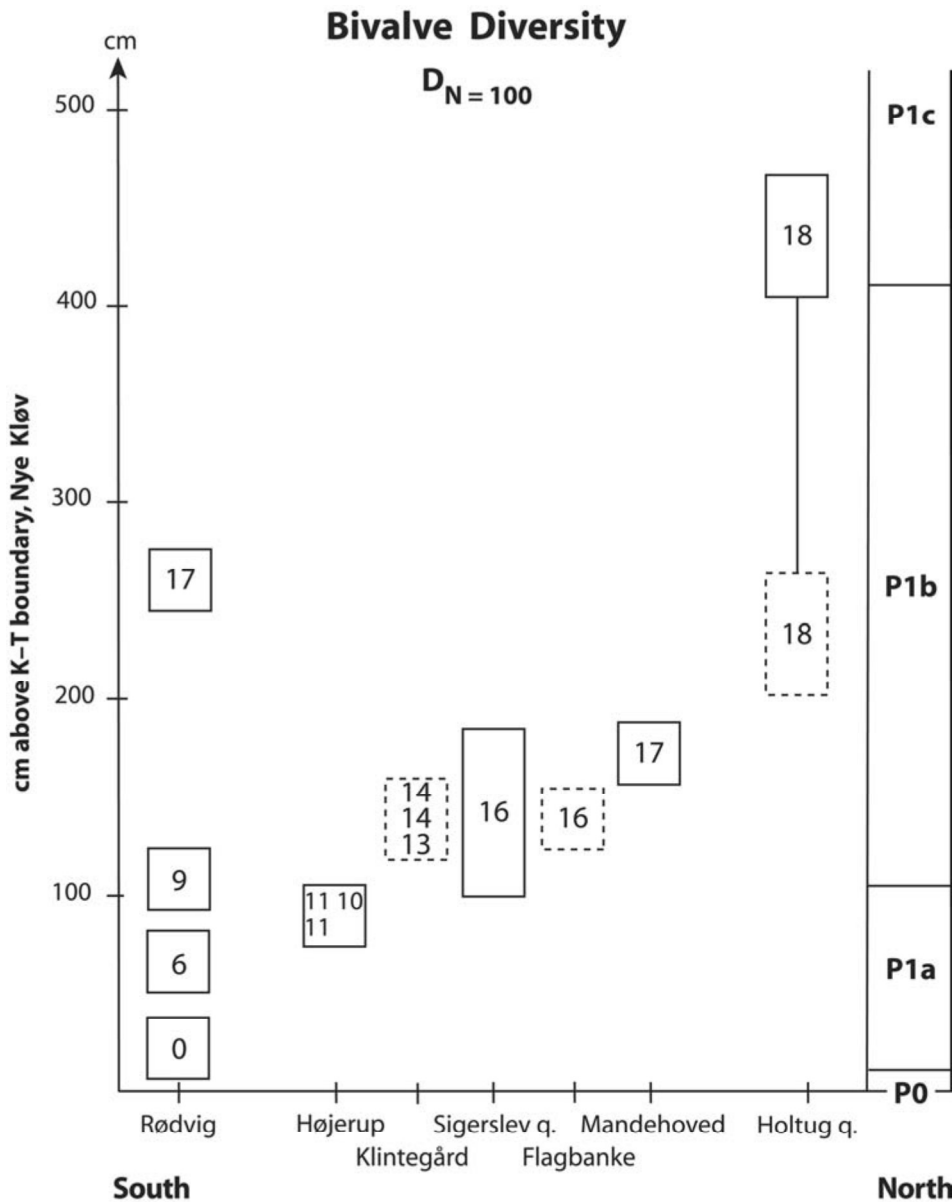
Bivalve Diversity

$D_{N = 100}$

Fig. 7. Number of bivalve species rarefied to a sample size of N = 100 and arranged according to the stratigraphic position in terms of centimetres above the K–T boundary at Nye Kløv (Fig. 4). Stratigraphic position of boxes with dashed lining is not known, or open to interpretation (Holtug). The selected stratigraphic position of Holtug is based on the frequency of *Globoconusa daubjergensis*.

common species instead of the rarer ones, may thus be preferred as indicator of community structure. Diversity indices are widely used (Shannon, Simpson, Weaver), but have drawbacks, thanks to the inverse relationship between richness (S) and equitability (E) inherent in these indices, where identical diversity values (D) may originate from very different rank–frequency distributions.

A better solution is to compare either the entire rank-frequency distribution, or its trophic nucleus (Fürsich 1977), with the calculated broken-stick rank–frequency distribution ($N_i = N_T / S_T \, \Sigma 1/n$) of the individual assemblages (MacArthur 1957, 1960). The dissimilarity between the two distributions is a quantitative measure of differences in community struc-

ture. Irrespective and independent of any theoretical aspects which may be associated with the broken-stick distribution (May 1975; Grey 1987; Seligmann 1999), it serves a purpose simply by offering a standard for comparison of frequency distributions (Stefanova 2003). The procedure used in this study is to calculate the difference (RMS, root mean square) between the calculated (broken-stick) and the observed frequency distributions, and use the dissimilarity (%) as a community index (Fig. 8). There are several advantages in this. One is that the broken-stick distribution takes both species number (S) and species abundance (N) into account, an other that by using frequencies, and weighting the most common species relatively high (a consequence of the RMS

Fig. 8. Rank–Frequency distribution of bivalve species, Holtug sample. Curve: Calculated broken-stick frequences. Columns: Actual frequences. Difference between calculated and actual species frequencies: RMS = 9.6%. X-axes: Species in rank order. Y-axes: Frequency in percentage.

Holtug

□ % Actual frequences

— % Calculated frequences (Broken stick)

N = 124
D = 20
RMS = 9.6 %
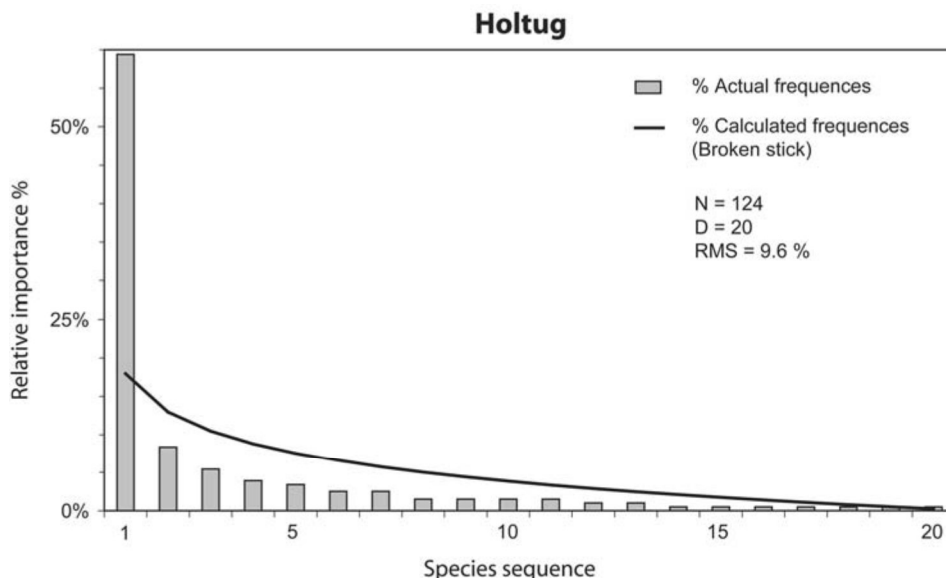
calculation), focus is on the 'common' instead on the 'rare', reducing the importance of sample size. In the present case, the RMS values, presented in stratigraphic order (Fig. 9, curve A), exhibit a more gradual trend than the one expressed through the species number alone (Fig. 9, curve C).

The empirical 'fact', that the broken-stick distribution is the most equal (highest 'evenness' or 'equitability') rank-frequency distribution to be expected within guilds of ecologically homogeneous samples provides an additional advantage, due to its potential in ecological interpretation (Tsukada 1972; Bussenschutt 1999; Peters 1999; Scott *et al*. 2001). High evenness (low dominance), especially in combination with high species richness, is often taken as indication for a balanced or climax community, while high dominance is indicative of either stress or an early or pioneer successional state of a community.

Dominance

The dominating role of the common species, inherent in the 'RMS' measure, offers a methodological short-cut to the broken-stick index. The easy alternative is to use 'dominance' in the simplest possible sense, meaning the 'frequency of the most common species' as community index. In case of less extreme dominance than in the present case, the sum of the two most common species has proved useful (Goodman 1979).

The plot of 'dominance' values (Fig. 9, curve B) shows a strong correlation with the broken-stick val-

ues (curve A), and a reverse relation to the number of species (curve C). Species number levels out relatively early, whereas the RMS and the dominance values continue to decrease to the top of the section. The simple %-value of the most common species, may thus serve as a sufficient alternative to the broken-stick measure, at least as long as the style of the involved rank–frequency distributions are sufficiently homogeneous to permit comparison. It should be kept in mind that this simple measure of dominance totally ignores anything but the one or two most common species. Fürsich (1993) using MacArthur's (1972) evenness index, reached the same conclusion, that while species richness shows a fairly irregular pattern along an environmental cline, evenness values constitute an almost uninterrupted cline. If frequency of most common species had been used instead, the same, or an even 'better' result would have resulted.

Discussion

The recovery pattern of the Cerithium Limestone bivalves exhibits a double trend, easily compatible with conventional successional theory. The initial period following the K–T crisis is characterized by a very low number of species, starting with zero at the base. The subsequent assemblages are characterized by extreme dominance (62–90%) of a single species (disaster species of Kauffman & Erwin 1995). From thereon, the number of species increases rapidly, reaching a constant level of 17–18 species (sample size N=100) early in zone P1b time. Equitability, on
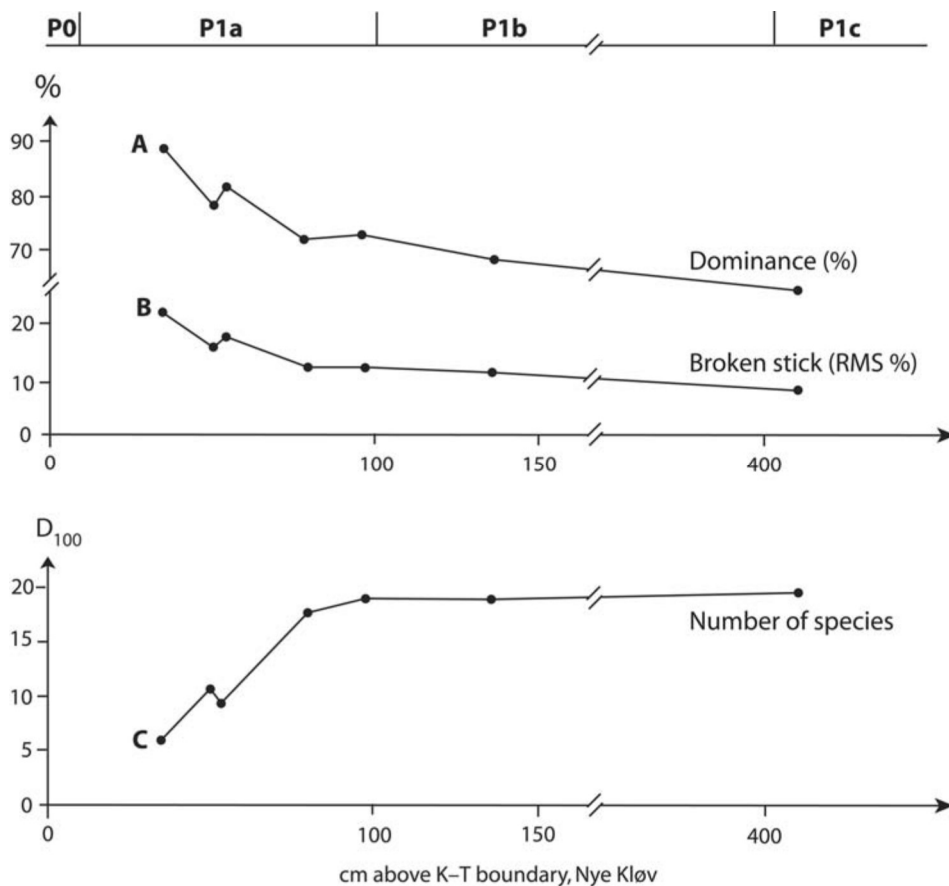
Fig. 9. Trends in bivalve diversity. Stratigraphic change in (A) dominance, (B) broken stick and (C) species number at a sample size of 100 specimens (N = 100). Planktonic foraminifer zones at top of the figure. X-axis: centimetres above the K–T boundary at Nye Kløv. D_{100}: Number of species at sample size N=100.

the contrary, continues to increase also after the levelling of the species number curve, expressed by an increasingly better fit between the actual species frequencies and the calculated broken-stick distribution. The most likely interpretation is a continued accommodation of the community, also after a constant level in species number is reached. The species stock in the sense of potential immigrants is emptied so to say, while the community structure continues the development towards a more equilibrium stage. Dominance exhibits a similar gradual trend, decreasing from the 90% level at the base to a frequency of 62% at the top of the succession.

The dominant species in all Cerithium Limestone samples, a *Corbulamella*, is a regular, though rare species in the upper Maastrichtian chalk, where it never exceeds values of more than a few percentages, quite different from its minimum value of 62% in the Cerithium limestone. On the other hand, the most common species in the Maastrichtian chalk, a *Limopsis*, never exceeds 25% in the chalk, compared to the 90% reached by *Corbulamella* in the Cerithium Limestone.

The number of species also differs considerably. The Maastrichtian bivalve fauna, including bivalves from both the mounds and the mound basins, totals 104 species (69 aragonitic), while the Cerithium Limestone bivalve fauna counts 45 species (41 aragonitic) (Heinberg 1999).

Two major patterns thus characterize the K–T transition, in terms of community structure:
1) A change from a high number of species and low dominance in the Maastrichtian to a much more uneven distribution in the Danian with one extremely dominant species, and a restricted number of additional species.
2) The poor fauna of the basal Cerithium Limestone undergoes a rapid increase in species numbers, finally reaching species numbers equalling those of the Maastrichtian chalk, as far as the infauna is concerned (Heinberg 1999).

Depositional Pattern

The diachroneity and northwards younging of the base of the Cerithium Limestone may find its explanation in the recently documented large-scale topography of the chalk seafloor during time of deposi-

Fig. 10. Graphic correlation of the Stevns Klint (Rødvig) and Nye Kløv sections. Each Cerithium Limestone sample is arranged according to centimetres above the K–T boundary at Stevns Klint, and centimetres above the K–T boundary at Nye Kløv, as determined by the morphotypic frequencies of the planktonic foraminifers.
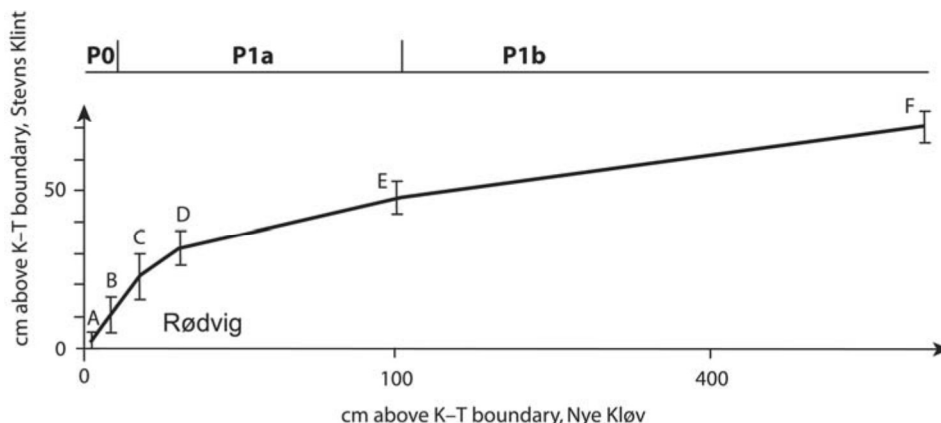
tion. Using offshore seismic data, Lykke-Andersen & Surlyk (2004) demonstrated that the culmination of the early Danian erosional surface at Stevns Klint, reaching 35 m at Sigerslev quarry equivalent to a sea-floor relief at about 40 m, is deeply rooted and of depositional origin, and not, as previously thought, caused by late or post-Danian Laramide folding (Rosenkrantz 1938). This observation provides the southwards sloping ramp which can explain the apparently onlapping pattern of the sequence, at least as far as the Rødvig-Sigerslev interval is concerned.

Initially coccolith ooze and planktonic foraminifers settling from the water column may have resulted in an isochronous cover of fine sediment along the entire topographic range. Subsequently, due to winnowing, clouds of resuspended ooze with planktonic foraminifers resettled downslope, filling the southernmost and deepest positioned basins first and in stratigraphic order. The resulting overall setting on the ramp thus mimics the onlap patterns typical for clastic sediments.

A graphic correlation between Rødvig and Nye Kløv (Fig. 10) shows that the depositional rate in the lower half of the Rødvig succession is equal to or slightly higher than the depositional rate at Nye Kløv. This tendency changes gradually upwards, where the sedimentation rate at Rødvig becomes very low compared to Nye Kløv. The high initial accumulation rate in the Rødvig basin may be interpreted as a result of the sea-floor relief.

Conclusions

1) The present study has demonstrated that the stratigraphy of the lowermost Danian Cerithium Limestone at Stevns Klint is more complicated than previously thought. On the basis of plank-tonic foraminifer morphotypes, it is demonstrated that the base of the limestone is time transgressive, younging from south to north with a corresponding northwards increasing hiatus between the K–T boundary and the Cerithium Limestone.

2) The post K–T recovery pattern exhibited by the bivalves from the Cerithium Limestone is characterized by a gradual buildup of species richness accompanied by a simultaneous reduction in dominance and increase in equitability. The two latter tendencies continue also after the species richness curve has levelled out. Such a pattern is in accordance with ordinary successional theory on recolonization following a biological crisis.

3) The gradual recovery patterns of the bivalve community parameters emerge only when the bivalve data are arranged in accordance with the foraminifer morphocline stratigraphy. The regularity of the bivalve patterns when organized in accordance with this cline, is regarded as a mutual corroboration of both gradients.

4) Accepting the diachronous nature of the Cerithium Limestone, previously opposing points of view can be reconciled. The claim of some authors that the Stevns Klint K–T section is complete, and the statement of others that there is a hiatus below the Cerithium Limestone, may thus both be correct, but at different localities along the cliff, reflecting the diachronous base of the Cerithium Limestone.

5) The Rødvig section is demonstrated to be complete in terms of the tree lowermost Danian planktonic foraminifer zones. The Rødvig section also covers the longest time range of the investigated sections. These properties underline the impor-

tance of the Rødvig section at the southernmost
extremity of Stevns Klint as a key K–T boundary
locality, also on a global scale.

Acknowledgements

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