

DISTRIBUTION AND TYPES OF BRYOZOAN COMMUNITIES AT THE BOUNDARY IN DENMARK

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In most Maastrichtian and Danian sediments in the North Sea region, bryozoans constitute the dominant macrofossil group both in terms of density and diversity (Berthelsen, 1962; Cheetham, 1971; Håkansson *et* al, 1974) totalling well over 500 species in Denmark. The region was part of the western European sea which undoubtedly constituted the most significant centre of bryozoan evolution during late Cretaceous and Danian times. The development of the bryozoan fauna in the region during the Cretaceous/Tertiary boundary event may therefore be attributed global significance, particularly in view of the very short hiatus recorded at the boundary in most of the Danish Basin (Hansen, 1977, 1979; Håkansson & Hansen, this volume).

The immense bryozoan fauna of the Maastrichtian and Danian of this region has attracted the attention of several authors through the last 140 years, resulting in a number of impressive monographs (e.g. Pergens & Meunier, 1886; Marsson, 1887; Levinsen, 1925; Voigt, 1930; Berthelsen, 1962; Brood, 1973). Nevertheless, in spite of these efforts, a noticeable proportion of the fauna remains undescribed and, particularly important in the present context, only a few papers have been devoted to the development across the boundary (Voigt, 1959b, 1960, 1967, 1972). and then only in fairly broad terms. It is evident, however, that the turn-over in the bryozoan fauna at the Maastrichtian/Danian boundary is in no way comparable to the dramatic changes noted in other groups, although it may appear somewhat more noticeable than at the preceeding Upper Cretaceous stage boundaries (Voigt, 1967).

Comparing the Maastrichtian Stage in its entirety with the Danian it becomes evident that virtually no change is recorded at family (or higher) level (Larwood *et al.*, 1967); all developments are confined to low taxonomic levels. Also it appears that the cheilostomes uniformly constitute the more diverse group whereas in the Danian the cyclostomes



Fig. 1. Rate of evolution in cheilostome bryozoans expressed in number of families per stage. Two major episodes are discernible, and it appears that the Cretaceous/Tertiary boundary event falls within the interjacent plateau. (Modified from Cheetham (1971, fig. 1 with the timescale adjusted according to Obradowich & Cobban (1975) and Berggren (1972)).

commonly show the highest density. However, more detailed considerations are necessary in order to distinguish differences in development patterns in the Cyclostomata and the Cheilostomata (classified in separate bryozoan classes).

Cyclostome bryozoans have an extended geological record reaching back to the Ordovician and in general may be characterized as conservative, having a slow evolutionary rate and a correspondingly low diversity. In accordance with this, the diversity of the cyclostome fauna during the Danian is of the same order as the Maastrichtian diversity, and approximately 75% of the species occur in both faunas (in part based on data from Brood, 1973).

In contrast to this, the cheilostome bryozoans develop from a slow start late in the Jurassic, through their first, rapid radiation in the

Upper Cretaceous to reach an evolutionary plateau by the end of the Cretaceous (Fig. 1). The Maastrichtian/Danian boundary event is perhaps merely accidentally - concordant with this evolutionary standstill (Cheetham, 1971), and is totally overshadowed by the spectacular effects of the second major episode in cheilostome evolution (mainly during the Eocene). Boundary-related changes at the specific and generic level are, nevertheless, much more widespread than in the cyclostome fauna. Most readily, this is observed in the significant decrease in the total diversity as well as in community diversities; and, in strong contrast to the cyclostomes, less than 20% of the Maastrichtian cheilostome species survive into the Danian (in part based on data from Voigt (1930) and Berthelsen (1962)).

In spite of their abundance, bryozoans apparently have never been particularly attractive to biostratigraphers working in the Cretaceous and Paleogene, and the few studies that have been made have been on a broad scale (Berthelsen, 1962; Voigt, 1967; Brood, 1973). The obvious potential value, especially of the rapidly evolving cheilostome bryozoans in detailed stratigraphic investigations of the Maastrichtian and Danian, has so far remained largely unexplored. However, comparisons of the stratigraphic occurrence of the free-living cheilostome species in Denmark and northwest Germany indicate this potential to be very promising (Håkansson, 1978), approaching the level of the local brachiopod zonation (Surlyk, 1970).

Though overall comparisons of the Maastrichtian and Danian faunas as those presented above have a general significance, the faunal development through the Cretaceous/Tertiary boundary event in actual sequences is, of course, also of the utmost importance. Investigations of this kind based on bryozoans have not previously been published and we now present the preliminary results of a first attempt. The very detailed picture arising from investigations of actual boundary sequences is evidently influenced significantly by the local environment and, accordingly, is expected to be highly variable. Therefore, in order to maximize the general applicability of such results, understanding of the ecological tolerance of individual species plays a paramount role and, ideally, sequences having a uniform lithology and no depositional breaks should be preferred.

As one of the best approximations to this ideal we have chosen the sequence at the small abandoned chalk pit Nye Kløv as an example.

Fig. 2. Bryozoan faunal properties across the Maastrichtian/Danian boundary at Nye Kløv, based on samples of 1-1.2 kg. (Lithology after Håkansson & Hansen, this volume).



FAUNAL DEVELOPMENT AT NYE KLØV

The lithology at Nye Kløv may be briefly characterized as follows (cf. Håkansson & Hansen, this volume): A Maastrichtian white chalk comparatively poor in macrofossils is overlain by a thin Danian marl rapidly changing upwards into a slightly granular chalk which in turn develops gradually into a bryozoan limestone (Fig. 2).

The Maastrichtian part of the section contains about 1% skeletal material > 0.5 mm (Fig. 2A). The material is dominated by bryozoans making up between 50% and 80% of the preserved fauna. Apart from the lowermost sample (NK 21) the Danian pelagic chalk is less fossiliferous than the Maastrichtian, particularly in regard to the amount of bryozoans. Within the first 2 m of the Danian, bryozoans are virtually absent and the fauna here is totally dominated by crinoids belonging to the genus *Bourgueticrinus*. Reworked fossils - distinguishable through a somewhat whitish appearance - are quite common in these levels, but have been excluded from faunal considerations. From approximately 2 m above the boundary the bryozoan content gradually increases, and in the higher parts of the section skeletal fragments constitute up to 10% of the sediment, with bryozoans making up almost 90% of the fauna. Towards the top of the sequence the amount of bryozoans drops again.

Cheilostome bryozoans dominate over cyclostomes throughout the sequence af Nye Kløv (Fig. 2B). This deviation from the general pattern, where cyclostomes typically dominate the Danian fauna, is noteworthy, especially since no cyclostomes at all were found in the four lowermost Danian samples. However, in the bryozoan rich level higher in the sequence, the picture approaches the normal situation with almost 50% cyclostomes.

The Cretaceous/Tertiary boundary is clearly reflected in the diversity index of the cheilostome bryozoans (Figs 2C, 3). The Maastrichtian populations are highly diverse, having a total of some 70 species. In strong contrast to this, the first Danian samples contain an extremely poor fauna comprising only four species; indeed, of these only a single species appears in the lowermost sample (NK 21). Following this extreme reduction, the diversity gradually rises to a maximum of more than 40 species in the bryozoan limestone (NK 30). The populations in the uppermost more pelagic sediments again show lower diversities. Thus, within the Danian part of the sequence, low diversity and low density are correlated as are high diversity and high density. In the Maastrichtian populations, on the other hand, high diversity associated with low density is characteristic. Moreover, in terms of species composition, the two faunas are quite different.



Fig. 3. Species rarefaction curves calculated for populations of cheilostome bryozoans across the Maastrichtian/Danian boundary at Nye Kløv (sample numbers refer to Fig. 2). Dashed lines: Maastrichtian populations; solid lines: Danian populations.

A total of 115 cheilostome species were recognized during the investigation of Nye Kløv. According to their stratigraphic distribution they may be classified into four distinct groups (Fig. 2D): (1) 60 species were recorded only from the Maastrichtian part of the sequence; (2) 11 species were found in both the Maastrichtian and the Danian part of the sequence; (3) 4 species have their main distribution in the lowermost part of the Danian, but also occur sporadically in other parts of the sequence; (4) 40 species were found only in the higher part of the Danian (a few of these occur in the Maastrichtian elsewhere in the basin).

Species showing a group 3 distribution constitute a very characteristic, low diversity bryozoan community which has been recognized immediately on top of the basal Danian marl layer at a number of localities in Jylland. This community appears to be dominated everywhere by freeliving and radicelled ('rooted') species, with one free-living species (*Pavolunulites* n.sp.) constituting between 50% and 100% of the bryozoan fauna. It should be stressed that none of the species found in both the Maastrichtian and the Danian part of the sequence at Nye Kløv do in fact occur in this group 3 community; gradually they reappear in the higher, more bryozoan rich parts.

BRYOZOAN COMMUNITIES AND DEPOSITIONAL ENVIRONMENT

The Maastrichtian and Danian rocks of the entire region are uniformly developed in carbonate facies, typically having a significant carbonate mud component (see Bromley, this volume). Near-shore deposits are rare and associated with substantial sedimentary breaks, and are hence of little relevance in context with the detailed development in the boundary event. Basinal conditions, on the other hand, are more likely to preserve a sedimentary record containing negligible hiati in association with this event (Håkansson & Hansen, this volume).

Broadly speaking, bryozoans are, of course, as dependant on the sedimentary environment in which they live as are other benthic invertebrates. However, in the case of the Maastrichtian and Danian sediments in the Danish region the bryozoans themselves have a noticeable impact on this environment as is conspicuously expressed in the widespread bryozoan mounds.

The total range of carbonate environments in the Danish area during Maastrichtian and Danian time is most conveniently classified into two main types, i.e. pelagic chalk and bryozoan limestone, each supporting a number of bryozoan communities. Nevertheless it must be stressed that the two sediment types are merely portions of a continuum ranging from pure pelagic muds containing virtually no benthic skeletal material to limestones containing more than 50% of bryozoans by weight.

Pelagic chalk communities

These are particularly widespread in the Maastrichtian, but occur commonly in the Danian as well. They are associated with mud-supported chalks, dominated by coccoliths and planktic foraminifera and with varying, subordinate amounts of benthic forms (Håkansson *et al.*, 1974; Bromley, this volume). Most often the benthic fauna of pelagic chalk is dominated by bryozoans, but local concentrations of other phyla occur. Great variation is recorded in the composition of the bryozoan communities, with the water/sediment interface consistency and substrate availability as the main determining factors.

A considerable faunal element of the pelagic chalk communities is confined as encrusters to the rare, larger secondary hardbottoms (such as echinoid tests), and is accordingly not necessarily restricted to the chalk environment. Apart from the encrusting forms the chalk communities contain three main growth forms in varying proportions. Rigidly erect, more or less bushy colonies attached by a solid encrusting base constitute the most diverse and commonly the dominant group. On the other hand, flexible erect colonies with chitinous joints and, in particular, free-living colonies may occasionally dominate the fauna - probably as pioneer communities capable of direct colonisation of soft mud (Håkansson, 1974, 1976).

The chalk environment apparently was strongly influenced by changes in connection with the Cretaceous/Tertiary boundary event. While Maastrichtian chalks usually contain highly diverse, albeit thin, bryozoan communities (sample diversity commonly exceeding 100 species), the Danian chalks virtually lack bryozoans and exhibit very low diversities (sample diversity below 10 species).

Bryozoan limestone and bryozoan chalk communities

These communities occur commonly in both the Maastrichtian and the Danian. As noted above, the limit between pelagic chalk and bryozoan limestone is arbitrary in terms of depositional environment, and we do not feel it justified to suggest a definite limit expressed by, for example, bryozoan content. As, moreover, most coarse grains in these rock types are branching bryozoans, it is commonly impossible to establish whether a bryozoan limestone was originally grain-supported or not (cf. also Nielsen, 1976). Nevertheless, within the range of facies accepted as bryozoan limestones, both mud-supported and grainsupported types occur, and typically they are composed of coccoliths and planktic foraminifera in addition to substantial amounts of benthic remains (Håkansson et al., 1974; Thomsen, 1976; Bromley, this volume). The benthic faunas in bryozoan limestones contain very little but bryozoans. Rigidly erect, branching colonies attached by a solid base dominate (by weight) in all bryozoan limestone communities, and commonly a certain amount of flexible, erect forms are present as well. A high proportion of the branching colonies support a highly diverse encrusting fauna (Thomsen, 1977b), which may have some resemblance to the encrusting communities of the secondary hardbottoms in pelagic chalk. Free-living bryozoans, on the other hand, play a very limited role in bryozoan limestone communities.

With regard to diversity, the bryozoan limestone communities of the Maastrichtian and Danian are very similar (diversity typically well over 75 species). However, the cyclostomes generally dominate by weight in the Danian communites, whereas they play a more subordinate role in the Maastrichtian communities.



Fig. 4. Bryozoan community fluctuation patterns in a highly accommodated, stable community framework as in the Maastrichtian/Danian Upper curve indicates the level of the period in the Danish region. total energy (food) input to the benthic community, and the lower curve indicates the amount of this energy exploited by bryozoans. To each horizontal portion of the lower curve corresponds a unique bryozoan community, whereas oblique portions of this curve indicate transitional periods with mixed communities or - more precisely - rapid changes through a number of communities. Event A signifies a change in the total environment favouring bryozoan competition (as one likely example a diminishing accumulation of carbonate mud may be mentioned). Event B, on the other hand, signifies a similar change with the adverse effect (as for instance increase in the accumulation of carbonate mud). Events C and D illustrate changes in the amount of food available and possible effects on bryozoan compatibility (see the text for further discussion).

Bryozoan community adjustments

The sediments in the Maastrichtian and Danian of Denmark represent a broad, yet continuous range of environments, and it may be predicted that the gradational series of communities preserved in these sediments will closely follow changes in the environment (Nestler, 1967). As bryozoans are very important constituents of most communities, changes recorded in this part of the fauna, i.e. in the bryozoan communities as outlined above, in many instances may qualify as a sufficient approximation to the total community. Thus, changes recorded in the bryozoan communities may serve as a major tool in unravelling most of the significant changes in the overall environment, in particular as detailed bryozoan biofacies are more easily defined than ordinary sedimentary facies (Håkansson, 1974).

Fundamentally, these benthic communities were in perfect balance with the environment in which they lived and to which they were adapted. Environmental changes thus immediately led to adjustments in the community structure as expressed in both the relative importance of individual species and the species composition. Innumerable factors may be envisaged to have influenced the communities under study. However, in the environment of the Maastrichtian and Danian bottom dwelling communities, gradational changes in the amount of food (energy) and substrate quality or availability may be regarded as basic.

Speculating now that the food supply (energy input) was in general fairly stable through substantial lengths of time in the very stable depositional environment, competition among groups would lead to a very fine balance, i.e. mature, stable communities. Even minor changes in the substrate situation, as in any other basic factor, necessarily will alter the compatibility of the individual groups of organisms in this type of community and, thus, produce changes in their relative importance. This is expressed graphically in Fig. 4, where events A and B signify changes in some basic parameter in a constant food supply situation. In one case (A), bryozoan compatability on the whole is improved, with the result that a larger proportion of the available energy is exploited by bryozoans. Event B, on the other hand, reduces bryozoan compatibility once more and leads to a balance with a somewhat lower bryozoan component.

In bryozoan communities in a depositional regime dominated by pelagic mud, events A and B may illustrate changes in substrate availability, either numerically or perhaps qualitatively. In this depositional regime an important means for increasing the amount of substrate is a decrease in accumulation of pelagic mud. This decrease may result from a reduction in the actual supply owing either to reduced productivity in the pelagic community or to minor increase in calcite dissolution in the water column or on the sea floor.

An important aspect of this process is that even a small increase in the amount of substrate may trigger a self-increasing process based on the fact that most bryozoans utilize other bryozoans as substrate (cf. Surlyk & Birkelund, 1977).

Moving water is another plausible means of reducing mud deposition. More important still, this is likely to increase the amount of food available to the benthic community simply by giving access to larger water masses. If, therefore, event C (Fig. 4) signifies the onset of moving water conditions, it combines the effect of more food (energy) to the community and increased substrate availability, with the probable result that bryozoan growth will be strongly promoted. This chain of events may lead to the overwhelming dominance of bryozoans recorded in some flat-bedded limestones where bryozoans constitute more than 50% (by weight) of the sediment.

Unidirectional water movement in particular is likely to have significantly changed the general environment of the benthic realm. Thus Thomsen (1976) concluded that fairly uniform northwesterly directed currents were the main controlling factor in the development of the lower Danian mounds in Karleby Klint. The proposed model accounts for the strong faunal differences on the upstream and downstream sides of the elongate mounds and suggests that baffling processes in the dense bryozoan cover on the upstream side caused the asymmetrical mound accretion (Thomsen, 1977a).

BRYOZOAN BIOFACIES DISTRIBUTION

The results of Håkansson *et al.* (1974) and Hansen (1977) reveal that changes in the sedimentary environment comparable to those detected through actual sequences occur also along time planes traceable through major parts of the basin. By inference, this is valid also for the range of bryozoan communities associated with these variations, i.e. the bryozoan biofacies distribution. Moreover, it is likely that the entire range of bryozoan communities was present at any one time in the Maastrichtian and Danian within the Danish area - with the possible exception of the period of time represented by the hiatus and the marl layer at the Maastrichtian/Danian boundary. Within a given area, provided that the distribution of community types and the time frame are reasonably well documented, the biofacies distribution may be mapped in some detail.

Fig. 5. Generalized Danian facies distribution. In the late Danian transgression (map C) the bryozoan limestone south of the Ringkøbing-Fyn High is somewhat marly towards the south, and it is not known whether the Danian was originally deposited also on top of the numerous north German salt structures (not shown here). Localities mentioned in the text are marked with numbers (in map A): 1) Nye Kløv, 2) Karleby Klint, 3) Stevns Klint, 4) Limhamn. In addition to extensive field observations data from the following sources have been included: Ødum (1926, 1928), Brotzen (1959), Berthelsen (1962), Sorgenfrei & Buch (1964), Larsen (1965), Rasmussen *et al.* (1971, 1973), Rasmussen (1974, 1978), Thomsen (1974), Dunn (1975), Stenestad (1976), Hansen (1977), and Baldschuhn (in press).



Very few levels within the Maastrichtian are represented at more than a few localities, so it is rather unrewarding at present to attempt detailed Maastrichtian facies maps for this region. It is noteworthy, however, that the ultimate Maastrichtian zones have hitherto been found only in the central part of the Danish Basin, i.e. in northern Jylland (cf. Håkansson & Hansen, this volume).

From the Danian, the areal coverage is significantly better and fairly reliable facies charts may be constructed (Fig. 5). This sequence of maps shows that early in the Danian, extended areas became covered with dense bryozoan growth (Fig. 5A), perhaps facilitated by extensive hardground development during lowermost Danian time in many areas. The apparent coast-parallel distribution of the mounds suggests that much of the facies distribution was related to depth and, thus, that the northwesterly directed current assumed to be responsible for the mound formation was restricted to a fairly narrow interval of depth. In close agreement with this notion, it is found that halokinetically induced local highs in areas otherwise characterized by pelagic mud deposition commonly are capped by bryozoan limestones (N. Svendsen, pers. comm. 1979).

Deposition of pelagic mud gradually increased in area up through the Danian, and by mid-Danian time bryozoans continued to flourish only along the south eastern margins of the Danish Basin (Fig. 5B). Early in the late Danian, parts of the Ringkøbing-Fyn High as well as large areas to its south were transgressed, probably for the first time since the Cretaceous/Tertiary boundary event (Fig. 5C). Here, bryozoan limestones were deposited, apparently without mound development, and in the Danish Basin pelagic mud totally dominated. Later in the Danian the preparation of subsequent facies maps is prevented by inadequacy of the stratigraphic and distributional data.

The facies distribution through the Danian traditionally has been interpreted to be the result of a general, slow regression lasting throughout the Danian (Ødum, 1926; Rosenkrantz, 1937; Hansen, 1977). However, in view of the probable depth relation of the main facies in the early Danian example (Fig. 5A) and the great extension of the late Danian sea (Fig. 5C) it may be suggested, on the contrary, that a prolonged transgressional phase was only replaced by a regression shortly before the close of the Danian.

In relation to the Danian facies pattern just described, a few notes on the Maastrichtian may be attempted as well. It is conceivable that Maastrichtian bryozoan chalk likewise developed mainly in areas where there were comparatively strong currents within a definite depth interval as, for instance, on the Ringkøbing-Fyn High (Thomsen, 1974) or in the moderately near-shore area around Stevns Klint in eastern Sjælland. In the latter area, the Maastrichtian bryozoan chalk forms low bryozoan mounds very similar to the Danian mounds (Håkansson, 1971; Surlyk, this volume), and it is interesting to note that this region comprising eastern Sjælland and southwestern Scania is apparantly the location for the most prolonged mound formation (cf. Holland & Gabrielson, this volume, and Floris, this volume).