

BIVALVES FROM THE LATEST  
MAASTRICHTIAN OF STEVNS KLINT  
AND THEIR STRATIGRAPHIC AFFINITIES

Claus Heinberg

Institute of Historical Geology  
and Palaeontology  
Øster Voldgade 10, DK-1350 Copenhagen K

The topmost Upper Maastrichtian bryozoan chalk of Stevns Klint, Sjælland, is among the youngest Mesozoic strata yielding abundant macrofossils. Locally, this chalk has been cemented by early Danian hardground processes (Heinberg, 1976, Bromley, this volume; Surlyk, this volume).

In addition to calcitic skeletons, which are normally preserved in the chalk, the hardground limestone contains void moulds after originally aragonitic skeletons (Bromley, this volume) that are normally not preserved in the chalk. The presence of this aragonitic faunal element imparts a considerable importance to this bed for comparison of Cretaceous and Tertiary faunas (discussion by Russel, 1976). This importance has been accentuated by recent studies, which have revealed 14 aragonitic bivalve genera hitherto only known from the Cenozoic (Heinberg, 1976, 1979 and in prep.).

The stratigraphic range of genera present in the hardground is shown diagrammatically in Fig. 1. Three major types of time-range can be distinguished: (1) genera ranging from Upper Cretaceous (some appearing as late as the Upper Maastrichtian) to Recent, (2) genera ranging from Mesozoic (or earlier) to Cenozoic, (3) genera exclusively known from pre-Cenozoic deposits.

Genera originating in the Upper Cretaceous and continuing into the Cenozoic (group 1) are of special interest. The majority of these genera originated at the very top of the Maastrichtian (in the sediment beneath the hardground) within a community of extreme diversity and habitat diversification. It is noteworthy that it is among these highly specialized animals that we find the bulk of bivalve genera crossing the boundary.

Long-ranging Mesozoic-Cenozoic genera (group 2) are of limited

stratigraphic interest, but important in the discussion of extinctions simply because they did survive the Cretaceous/Tertiary boundary.

Group 3, consisting of genera that became extinct at the Cretaceous/Tertiary boundary, gives little information about the nature of the boundary events. They simply died out. The new genera occurring together with them and finally replacing them may very well tell more about the nature of these events.

In order to shed light on the reasons for the changes at the boundary, different aspects of the three groups will be compared.

When discussing faunal extinctions on a larger scale, so-called mass extinctions, at least three aspects must be taken into consideration with regard to biological properties:

- 1) Community structures and ecology of the faunas on both sides of the boundary.
- 2) The age of taxa that becomes extinct compared to those that survive.
- 3) The taxonomic change across the boundary with special reference to the new taxa following the event.

#### COMMUNITY STRUCTURE AND ECOLOGY

The community structure of the present Upper Maastrichtian bivalve fauna has been dealt with elsewhere (Heinberg, in press). The bivalves comprise a high number of species, many of which belong to the same genera, and which were members of an extremely diversified ecosystem. Low internal stability is characteristic of such a system (May, 1973), necessitating high environmental stability.

The ecology of the present genera is listed in Fig. 2, where the individual time-range classes are subdivided into four ecological groups. The bivalves are assigned to these groups on the basis of taxonomic and shell morphological criteria. The ecological groups are:

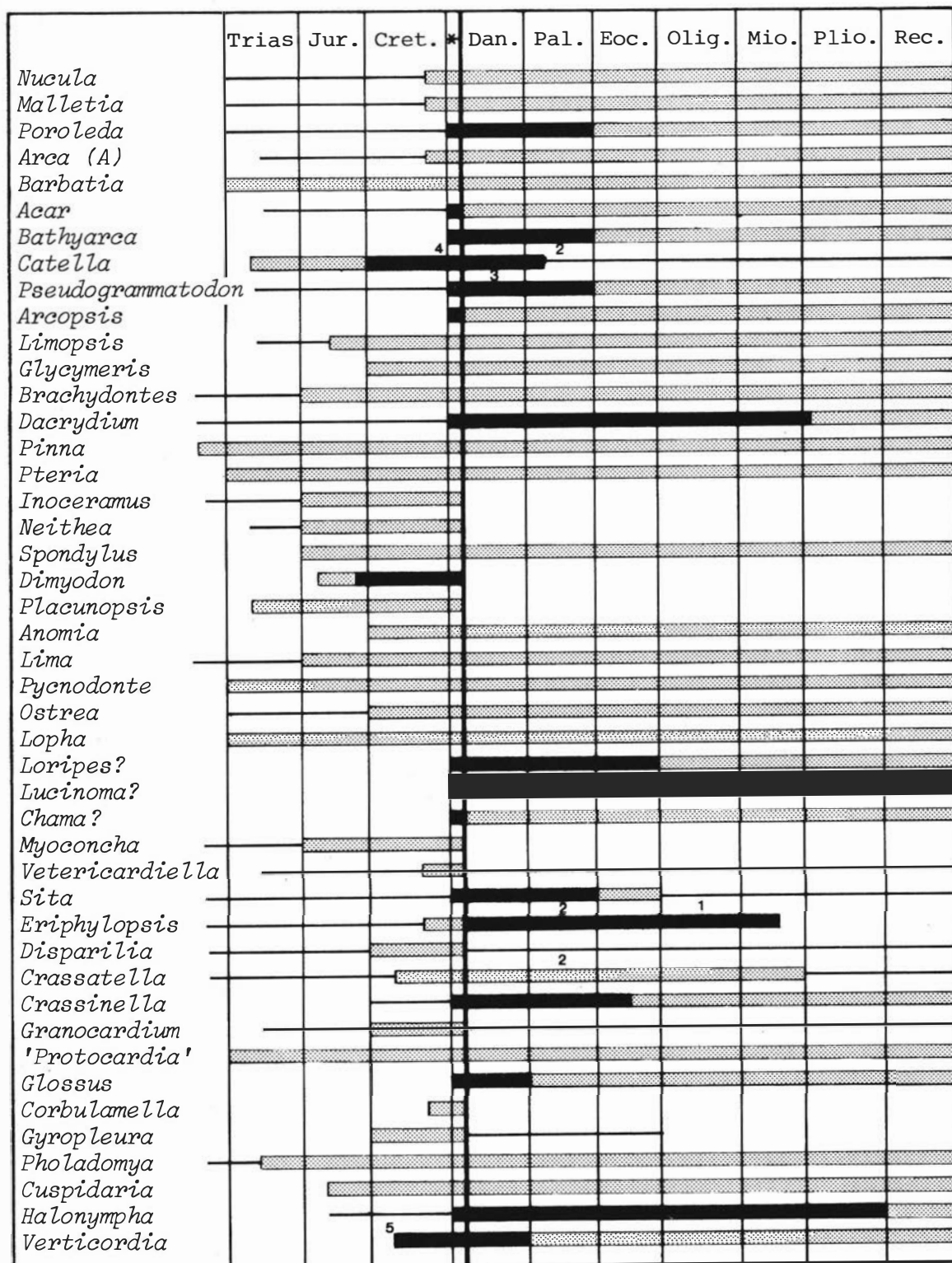
- 1) Endofaunal, deposit feeding prosobranchs.
- 2) Low level suspension feeders (Turpaeva's group 'filter A' 1957) comprising freely burrowing forms (e.g. *Protocardium*), endobyssate species (e.g. *Limopsis*) and byssate semi-infaunal species (*Pinna*, *Inoceramus*).

Fig. 1. Range of genera occurring in the Upper Maastrichtian hard-ground at Stevns Klint. The hardground is marked by an asterisk. White bars show the range according to Moore (1969), while black bars represent extensions based on the fauna in the hardground, plus data from a few other sources: von Koenen, 1893(1); Ravn, 1933, 1939(2,3); Speden, 1970(4) and Kauffman, 1976(5). Thin lines indicate family range.

Ten genera are entirely Mesozoic: *Inoceramus*, *Neithea*, *Dimyodon*, *Placunopsis*, *Myoconcha*, *Vetericardiella*, *Disparilia*, *Granocardium*, *Corbulamella* and *Gyropleura*. Five of these are also restricted to the Mesozoic at family level.

The Mesozoic genera may be weighted differently as to their stratigraphic significance. *Corbulamella* is extremely restricted in its range, being hitherto known only from the Maastrichtian of North America (Speden, 1970). The recorded stratigraphic ranges of *Eriphylopsis* and *Disparilia* (Moore, 1969) are obviously too limited, owing to inadequate taxonomic knowledge, especially for Tertiary material. *Eriphylopsis*, e.g., is probably represented by *Astarte trigonula* from the Paleocene of Copenhagen (Ravn, 1939). There remain as significant Mesozoic elements: *Inoceramus*, *Myoconcha*, *Neithea*, *Granocardium* and *Placunopsis*, all being Mesozoic also at family level.

New records for the Mesozoic are: *Poroleda*, *Acar*, *Bathyarca*, *Pseudogrammatodon*, *Arcopsis*, *Dacrydium*, *Sita*, *Crassinella*, *Glossus*, *Halenympha* and *Verticordia*; except for *Crassinella*, all are well defined genera. Especially important are the occurrence of *Acar* and *Arcopsis*, two genera widely distributed and relatively abundant in Cenozoic deposits. It is worth mentioning that *Acar* already appears in a Lower Maastrichtian hardground in Møns Klint. Two lucinids are tentatively referred to *Loripes* and *Lucinoma*, genera ranging from Oligocene to recent time. The species referred to '*Protocardia*' is an intermediate between the Mesozoic genus *Protocardia* and the Cenozoic genus *Nemocardium*, thus illustrating the danger of circular argument by referring a species to a certain genus not only because of morphology, but also under the impact of the stratigraphic distribution of the species.



- 3) High level suspension feeders (Turpaeva's group 'filter B' either byssate (e.g. *Limopsis*) or cemented (e.g. *Dimyodon*) epifauna.
- 4) Carnivores, exclusively septibranchs.

The individual behaviour of these ecological groups is of great significance to the elucidation of the extinction process. Disappearance of whole groups will indicate the operation of an extrabiological process, whereas extinction of only restricted numbers of several groups would indicate that the reason lies in community evolution, involving successional (evolutionary) shifts, where new species replace old. It is clear from Fig. 2 that the boundary was crossed by representatives of the whole ecological spectrum. The fact that all the genera that became extinct were filter feeders cannot lead to the conclusion that filter feeders were affected more severely than other ecological groups, since the majority of genera that crossed the boundary were filter feeders themselves.

The deposit feeding genera are the modern representatives of a very old mode of life among bivalves. In contrast, the carnivores represent a pioneering stage in bivalve history, dating back to the Jurassic, but with their major radiation in the Cenozoic.

In general, the Maastrichtian material contains representatives of all the important niches occupied by bivalves through the Cenozoic. It is noteworthy that within an advanced group like the carnivores a profound radiation took place prior to the Cretaceous/Tertiary event as exemplified by the presence of 7 coexisting species belonging to the genus *Cuspidaria*.

#### AGE OF THE GENERA

Not surprisingly it is seen that the genera that die out are relatively older than many of the genera that cross the boundary. Among the 34 genera that cross the boundary, 17 are new and 17 old. Of the 17 new, 5 originated in the Upper Cretaceous and 12 even within the Upper Maastrichtian. 8 old genera as opposed to 2 new die out at the boundary. It can thus be concluded that new genera present in the Upper Maastrichtian have a longer future than older ones. This conclusion supports the normal course of evolution, in contrast to the 'catastrophic' theories that underlie many interpretations of the events of the boundary.

Fig. 2. Distribution of genera according to ecological groups and time-range classes. A: aragonitic forms, X: genera restricted to the hardground in the Mesozoic part of their range.

	DEPOSIT FEEDERS	FILTER A	FILTER B	CARNIVORES
U. Cret. (U. Maastr. = X) to Recent New genera passing the boundary	<i>Nucula</i> A <i>Malletia</i> A <i>Poroleda</i> XA	<i>Bathyarca</i> XA <i>Dacrydium</i> XA <i>Sita</i> XA <i>Eriphylopsis</i> A <i>Crassatella</i> A <i>Crassinella</i> XA <i>Glossus</i> XA <i>Loripes?</i> A <i>Lucinoma?</i> A	<i>Arca</i> A <i>Acar</i> XA <i>Pseudo-</i> <i>grammatodon</i> XA <i>Arcopsis</i> XA ( <i>Chama?</i> X)	<i>Halonympha</i> XA <i>Verticordia</i> XA
Mesozoic (Palaeozoic) to Recent Old genera passing the boundary		<i>Glycymeris</i> A <i>Limopsis</i> A <i>Brachydontes</i> <i>Pinna</i> <i>Spondylus</i> <i>Anomia</i> ' <i>Protocardia</i> ' A <i>Pholadomya</i> <i>Pycnodonte</i> <i>Ostrea</i>	<i>Barbatia</i> A <i>Limopsis</i> A <i>Pteria</i> <i>Lima</i> <i>Lopha</i>	<i>Cuspidaria</i> A
Mesozoic (Palaeozoic) Old genera becoming extinct		<i>Inoceramus</i> <i>Neithea</i> <i>Granocardium</i> A <i>Disparilia</i> A	<i>Myoconcha</i> A <i>Dimyodon</i> <i>Placunopsis</i> <i>Gyropleura</i>	
U. Maastrichtian New genera becoming extinct		<i>Corbulamella</i> A <i>Veteri-</i> <i>cardiella</i> A		

## MINERALOGY

All 17 of the new genera that cross the boundary are aragonitic (Fig. 2). Among the 17 old genera that cross, only 7 are aragonitic, and among 8 genera that become extinct at the boundary only 3 are aragonitic (the range of one is doubtful). The apparently drastic faunal change in bivalves at the boundary (e.g. Rosenkrantz, 1966) may be explained, therefore, largely by this mineralogical distribution and the different preservation potential of the minerals.

Within the North European region aragonitic fossils are far better preserved in Tertiary rocks than in Cretaceous. This is mainly due to the lithology and diagenesis of the rocks. The Maastrichtian is dominated by chalk from which aragonite was lost soon after burial (Håkansson *et al.*, 1974; Bromley, this volume).

Evidence taken exclusively from the chalk facies has led to the 'catastrophic' view of the faunal change, the old fauna disappearing before the appearance of the new. Thanks to the early diagenetic hardening of the last 20 cm of the Mesozoic chalk this picture is now totally changed, showing a rich 'Tertiary' fauna living together with the last representatives of ammonites, inoceramids, myoconchids and mosasaurs.

In evolutionary perspective it is important to note that all the new taxa were already present as important members of a complex fauna before the faunal break at the Cretaceous/Tertiary boundary, occurring together with the taxa that were to die out at the boundary. In the case of the bivalves, therefore, there is no need to incorporate drastic external selective mechanisms in order to explain the extinctions. Adjustments within the ecosystem, caused by the development and introduction of novelties, were sufficient for the elimination of a few older and apparently adaptively inflexible taxa.