REVISTA ESPAÑOLA DE PALEONTOLOGÍA, **n.º Extraordinario,** 41-56. 1988.
Palaeontology and Evolution: Extinction Events

BRACHIOPOD EXTINCTIONS IN THE UPPER CRETACEOUS TO LOWERMOST TERTIARY CHALK OF NORTHWEST EUROPE

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ABSTRACT

The white monotonous chalk from the Upper Cretaceous-lowermost Tertiary of Northwest Europe spans at least 24 million years and contains a rich, well preserved fauna of minute brachiopods. Based on taxonomical range charts and time-specific diversities this fauna is studied in terms of mean species longevity, rate of species origin and rate of extinction. The brachiopod fauna initially appears to have colonized the chalk sea in mid-Coniacian times. From there on there is a slow build-up of species diversity reflecting a gradual niche diversification of the chalk. A climax in adjustment and evolutionary stability is reached in Late Maastrichtian time. During the Coniacian-Maastrichtian interval mean rate of extinction is low (0.07 My^{-1}) and mean rate of origination equally low (0.10 My^{-1}). A sudden mass extinction at the Maastrichtian-Danian boundary, however, eliminated more than 70 per cent of the species. The most specialized species, in particular the secondarily free-lying species, apparently became extinct at the boundary. Only six species are known to cross the Maastrichtian-Danian boundary. These are all relatively featureless, non-specialized forms and gave, together with possible survivors in basin margin areas, rise to a rapidly formed highly diverse Early Danian fauna through adaptive radiation. The Early Danian fauna differs in taxonomic composition from the Maastrichtian fauna both on species as well as on higher levels. A dichotomous classification of extinction seems real for the brachiopods from the chalk as their mass extinction at the Maastrichtian-Danian boundary both quantitatively and qualitatively differ from their Late Cretaceous background extinction.

Keywords: Mass extinction, background extinction, brachiopods, chalk, Northwest Europe, Upper Creataceous, Cretaceous-Tertiary boundary.

RESUMEN

La creta blanca y monótona del Cretácico superior-Terciario basal del NO europeo abarca, al menos, 24 millones de años y contiene una fauna rica y bien preservada de microbraquiópodos. En base a sus distribuciones estratigráficas y diversidades específicas se estudian sus índices de especiación y de extinción. Inicialmente, la fauna de braquiópodos colonizó el mar de la creta en el Coniaciense medio. Desde entonces hubo un aumento lento de la diversidad específica, que reflejaba una diversificación gradual de los nichos en las facies de la creta. El clímax se alcanzó durante el Maastrichtiense superior. Durante ese intervalo el índice medio de extinción es bajo (0.07 My^{-1}), así como la especiación (0.10 My^{-1}). Sin embargo, una extinción en masa en el límite Maastrichtiense-Daniense eliminó más del 70 % de las especies. Las más especializadas, en particular las formas libres secundarias, aparentemente se extinguieron. Sólo seis especies sobrevivieron, todas ellas relativamente poco características y no especializadas, que dieron lugar mediante una radiación adaptativa a una fauna muy diversificada en el Daniense inferior, que difiere de la fauna Maastrichtiense tanto a nivel específico como supraespecífico. Por tanto, en base a las extinciones de los braquiópodos de la creta, parece real una distinción entre la extinción de fondo durante el Cretácico superior y la extinción en masa del final del Cretácico, no sólo cuantitativamente sino también cualitativamente.

Palabras clave: Extinción en masa; extinción de fondo; braquiópodos; creta; Europa noroccidental; Cretácico superior; límite Cretácico-Terciario.

https://doi.org/10.7203/sjp.25158

INTRODUCTION

"In order to contract a thing, one should surely expand it first.

In order to weaken, one will surely strengthen first.

In order to overthrow, one will surely exalt first.

"In order to take, one will surely give first".

This is called subtle wisdom..."

(From Chapter 36 of Tao Te Ching)

During the last years an intense debate has taken place internationally on the primary causes of the Cretaceous-Tertiary boundary mass extinctions. This discussion includes scenarios involving a sudden extra-terrestrial triggering mechanism (e.g. Alvarez *et al.*, 1980, 1984; Hsü, 1980; Smit & ten Kate, 1982), increased volcanism as well as involving climatic deterioration and lowering of the sea level (e.g. papers in Birkelund & Bromley, 1979 and in Christensen & Birkelund, 1979; Kauffman, 1984).

The debate also led to a vast number of papers concerning extinction patterns and dynamics through time. As pointed out (Raup, 1987) an important question is whether extinction through time is a continuous rather than an episodical process. Raup and Sepkoski (1982, 1986) thus defined background level of extinction per million year to decline through the Phanerozoic and mass extinctions to be identified as significant peaks above this trend. Jablonski (1986a, b) suggested that major extinction events were separated by periods of lower extinction rates, typically referred to as background extinction, and that there were qualitative as well as quantitative differences between these two macroevolutionary regimes. Opposed to this, McKinney (1987) argued that there is no clear distinction between background and mass extinction rates, that the mass extinction events appear to be qualitatively similar to background extinctions and that a dichotomous classification of extinctions thus may be artificial.

The debate concerning patterns of extinction is, unfortunately, until now characterized by arguments and statistical skirmishes based on data lumped from the "Treatise on Invertebrate Paleontology". Most of the studies do furthermore concentrate on analyses of families or even higher taxonomic levels.

Based on the assumption that the species is a true basic and stable evolutionary unit, optimal conditions for evolutionary studies must be present among fossils represented by entire communities on species-level and over the full span of the geographical and temporal ranges (Gould & Eldredge, 1977; Boucot, 1987). These conditions are seldom, if ever, fulfilled, but still, as quoted from Gould & Eldredge (1977, p. 148): "It is ironic that so much palaeontological activity has been devoted to the description of species, but virtually all interpretative studies concentrate on generic or higher ranks".

To comply with this is here presented data on species longevities, species originations and extinctions of a rich fauna of brachiopods present in the Upper Cretaceous-lowermost Tertiary chalk of Northwest Europe.

The chalk has long been known to contain numerous and well preserved brachiopods (eg. Davidson, 1852; 1854; Bosquet, 1860; Schloenbach, 1866; Nielsen, 1909; Steinich, 1965; Asgaard, 1968; Surlyk, 1972; Bitner & Pisera, 1979; Ernst, 1984a; Johansen, 1987a, b, c). These brachiopods are especially suitable for evolutionary studies, as they in the chalk are characterized by high diversity, large numer of individuals, by being documented to species level, and by their wide biogeographic distribution within the chalk (Surlyk & Birkelund, 1977; Steinich, 1965; Surlyk, 1972; Surlyk & Johansen, 1984; Johansen, 1986, 1987a, b).

The chalk, which formed the substrate for the brachiopods, is characterized by its relatively great uniformity, by being deposited through a long span of time, its relatively high rate of deposition, by its high biostratigraphical resolution, by its relatively resemblance to both recent deep-sea and recent shallow-water environments and by its capacity of being totally broken down so that precise quantitative measurements can be obtained (Nestler, 1965; Håkansson *et al.*, 1974; Surlyk & Birkelund, 1977).

The sedimentological and faunistic qualities of the chalk do thus in many ways provide a unique possibility of following a group of fossils from their initial stages of colonization of the chalk environment early in the Late Cretaceous, through the gradual development of the fauna to its absolute climax in evolution, to its sudden devastation at the end of the Cretaceous and finally to its renewed adaptive radiation and recolonization in the Early Tertiary.

MATERIAL

The total material investigated includes more than 100.000 specimens of brachiopods present in several hundred bulk samples of chalk obtained from a more than thousand metres thick combined sequence of chalk. Distance between individual chalk samples vary from a few metres to a few centimetres, the samples being most closely spaced across the Cretaceous-Tertiary boundary (Steinich, 1965; Bitner & Pisera, 1979; Surlyk, 1972, 1982, 1984; Ernst, 1984b; Johansen & Surlyk, in press pending revision; Johansen, 1986, 1987a). The majority of these brachiopod species are only a few millimetres in adult length. A 5 kilogram chalk sample is considered ideal, as larger samples only seldom provide any additional new species to the fauna (Surlyk, 1972). Most of the populations investigated are obtained from chalk samples each weighing between 5 and 150 Kg.

The brachiopod data are derived from Middle Coniacian-Lower Maastrichtian chalk strata at Lägerdorf and Kronsmoor, West Germany (Surlyk, 1982; Ernst, 1984a; Johansen, 1986, 1987b), Lower Maastrichtian chalk of Rügen, East Germany (e.g. Steinich, 1965), Upper Maastrichtian chalk of Hemmoor, West Germany (Ernst, 1984a; Surlyk, 1984), Upper Campanian-Maastrichtian of Norfolk, England (Johansen & Surlyk, in press pending revision) and Mielniek, Poland (Bitner & Pisera, 1979) and from Maastrichtian-Lower Danian chalk strata in Denmark (e.g. Nielsen, 1909; Ødum, 1926; Surlyk, 1972, 1984; Johansen, 1987a). A few rare or poorly known species are omitted from the range chart and diversity diagram (Figs. 1, 2).

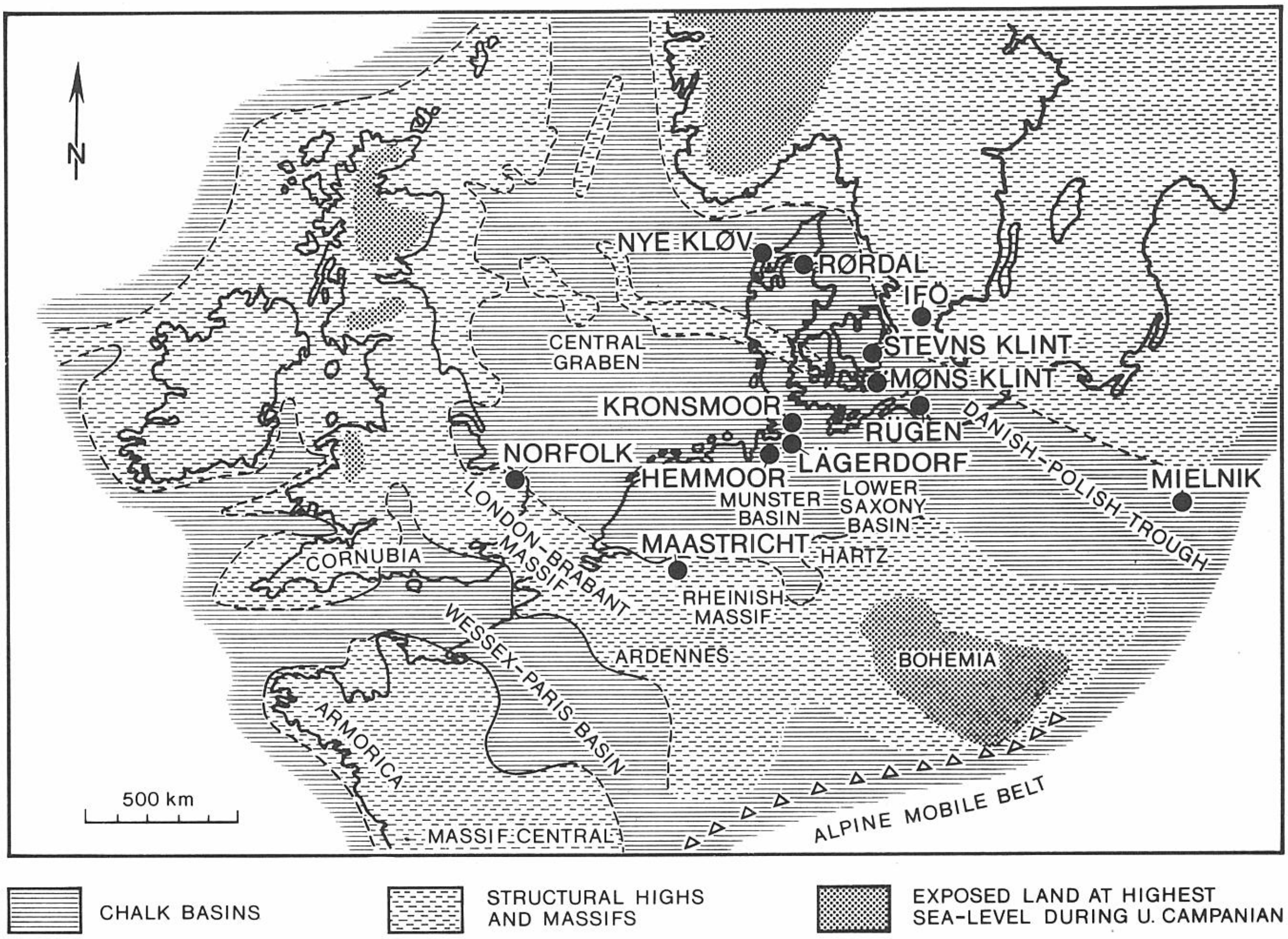

Figure 1. Map showing the position of Upper Cretaceous-lowermost Tertiary chalk localities in Northwest Europe (based on Hancock, 1975).

Several additional species are known from benthos-rich chalk of a more shallow water nature and deposited during the Late Maastrichtian to the Early to Middle Danian in the Limburg area, the Netherlands, Stevns Klint, Denmark and Fakse, Denmark (e.g. Bosquet, 1860; Posselt, 1894; Asgaard, 1968). These species are not included here either, as this study for reasons of homogeneity has its emphasis on brachiopods from the fine-grained chalk facies.

A low diversity fauna of minute brachiopods was established already in the Cenomanian-Turonian chalks of Northern France, Southern England and Northwest Germany (Schmid, 1971; Johansen, unpublished data). The pre-chalk ancestry of this fauna is, however, only poorly known. Species of *Terebratulina* are reported as far back as from the Speton Clay of Late Hauterivian –Aptian age (e.g. *T. martiana* d'Orbigny) and from the Red Chalk of Mid Aptian– Late Albian age from France and from northwest Germany (*T.* cf. *martiana* e.g.) (Schmid, 1971; Middlemiss, 1976). Species of *Argytotheca* are likewise recorded from the Red Chalk of Valanginian age from the northern Norfolk, England (Davidson, 1854) and from Cenomanian? - Lower Turonian sandy limestone and calcareous claystone from the Bohemian Cretaceous Basin. Other minute brachiopods occurring here are species of the genera *Terebratulina, Praelacazella, Thecidiopsis* and *Ancistocrania* (Nekvasilova, 1983). But, as the phylogeny and geographic control of these brachiopods is scarcely known, and as only little is known about the ancestors of the brachiopods concerned here, this paper deals only with a fauna younger than mid-Coniacian (Fig. 2).

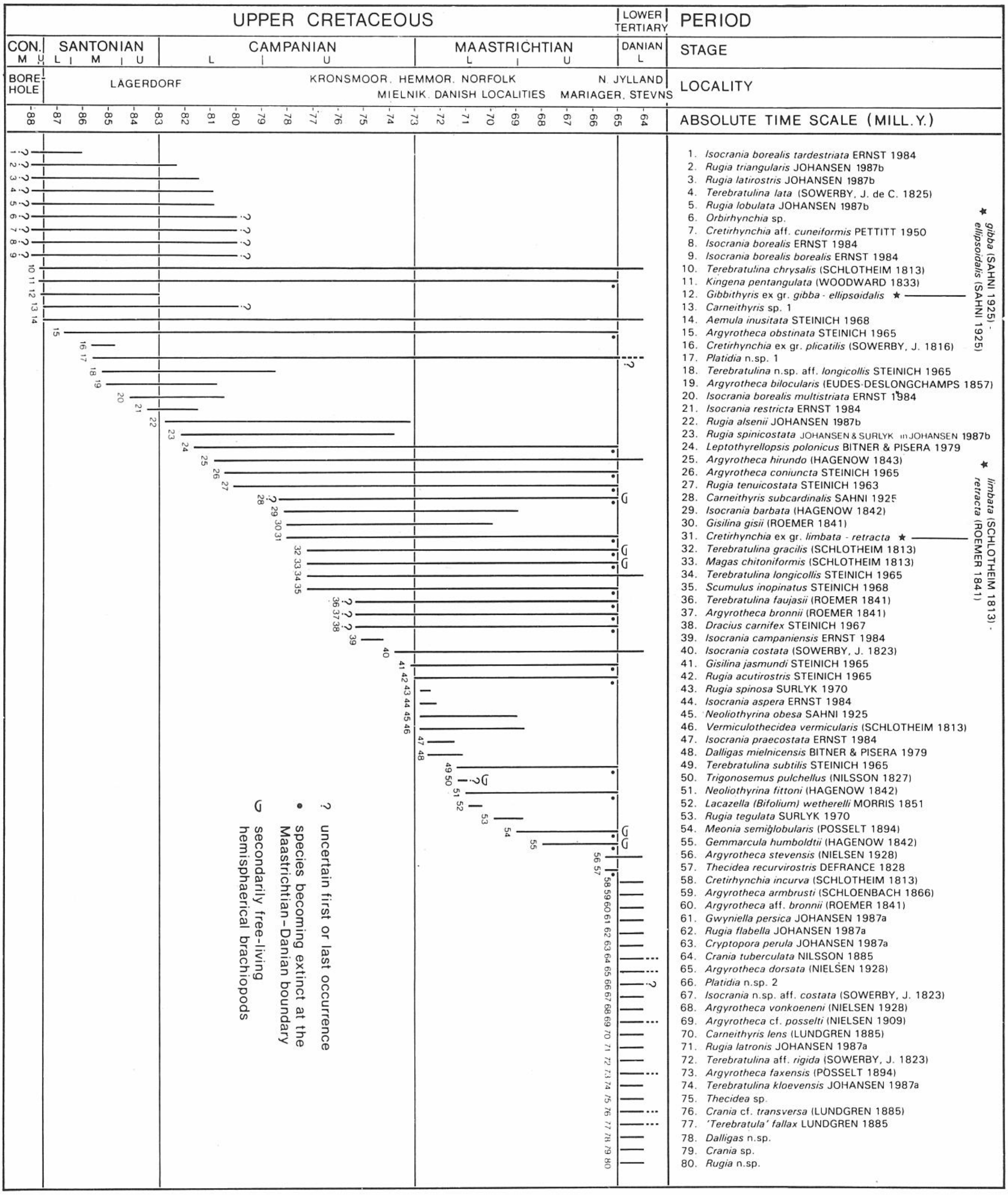

Figure 2. Taxonomic range chart for the 80 most common brachiopod species present in the Middle Coniacian to Lower Danian chalk of Northwest Europe. A few rare or poorly known species are omitted from this diagram (updated from Johansen, 1986). The absolute time scale is based on Harland *et al.* (1982).

On the basis of lithology and faunal content the Northwest European chalk has been subdivided into two faunal provinces, a Northern Province including North Norfolk, Denmark, Northwest and East Germany and Poland, and a Southern Province including North France and South England. (e.g. Mortimore, 1983). The Northern Province was situated adjacent to the North Sea basin and was thus separated from the Anglo-Paris basin by a swell, the London-Brabant Massif. This study only deals with faunas from the Northern Province (Fig. 1).

TAXONOMIC FREQUENCY

The term *taxonomic frequency* rate was introduced by Simpson (1944, 1953), who demonstrated that rigorous rates of origination and extinction can be obtained from measurements of simple diversity measured as number of taxa present per time unit. This concept has since been widely applied to studies of evolutionary histories (e.g. Van Valen, 1973; Stanley, 1979; Jones & Nicol, 1986; Valentine & Walker, 1987), but still needs to be supplemented by community analyses.

Taxonomic range chart

The first step in analysing the evolutionary trends of the Chalk brachiopods is to convert their biostratigraphical ranges into absolute time ranges. Fig. 2 shows a combined taxonomic range chart for the 80 most common species of brachiopods occurring in the Middle Coniacian-Lower Danian interval. Rate of sedimentation is a much debated matter. As to the chalk it is well known that the chalk sequences in North Germany are among the most continuous, in as much as no hardgrounds are present neither are any major biostratigraphic gaps thought to be present (e.g. Schulz *et al.*, 1984). Based on the sections in Lägerdorf, Kronsmoor and Hemmoor several workers have estimated mean rate of sedimentation accumulation for the Santonian and Campanian to 2.5 cm/1000 years and for the Maastrichtian 3.5 cm/1000 years (e.g. Schulz *et al.*, 1984; Ehrmann, 1986). These figures are adapted for the present study. Although indicators of reduced sedimentation are present throughout the sequence (e.g. pyrite-impregnated burrow-horizons, marly beds), the uncertainties introduced by these are assumed to be equally distributed throughout the sequence.

Ernst & Schmid (1979) established a more regional absolute time scale for the Upper Cretaceous of Northwest Germany. The ages are, however, based on K/Ar-dates derived from glauconite, which in many cases is allochtonous, reworked and/or altered by diagenesis. These dates are thus very uncertain and for the present study is thus chosen the well-documented and up-dated, although global, time scale of Harland *et al.* (1982) as the best basis for conversion of the thickness into absolute time-units. The absolute time scale applied to this range chart has thus been constructed from age determinations compiled for the Coniacian to the Danian Stages by Harland *et al.* (1982) and adopted to the most detailed and widely used biostratigraphical subdivisions already set out by e.g. Martini (1971), Ernst & Schulz (1974), Perch-Nielsen (1979), Schulz *et al.* (1984), Surlyk (1984) and Schulz (1985). Together these schemes constitute the probably most reliable tabulations of relative and absolute time

The distribution of the Upper Campanian and Maastrichtian species are already known from comparable sections in Denmark, Sweden, Northwest and East Germany, England and Poland. The Coniacian to Upper Campanian part of the sequence is represented primarily in Northwest Germany.

The distribution of the Upper Maastrichtian-Lower Danian species is primarily known from sections in Denmark, sections which in many ways approach the demands necessary to illustrate the detailed nature of the Maastrichtian-Danian boundary extinction (Håkansoon & Hansen, 1979; Surlyk & Johansen, 1984). Supplementary material has been obtained from virtually all other Danian localities exposing the Cretaceous-Tertiary boundary.

The absolute time scale on Fig. 2 covers more than a total of 24 million years, that is from 88 to 64 million years B.P. It must, however, be borne in mind that the Createaceous-Tertiary boundary event, approximately 65 million years ago, in itself represent a time interval of unknown duration. The stratigraphical record over the most critical interval in boundary sections is often obscured by low sedimentation rates and absence of fossils and it is thus very difficult using stratigraphic evidence alone, to estimate the time interval representing the boundary hiatus (Alvarez et al., 1982). Compared to the total span of time investigated, this interval is, however, probably short (e.g. Smit & Hertogen, 1980; Harland *et al.*, 1982; Hsü *et al.* (1982).

Diversity

Diversity is here defined as time specific diversity expressed as number of species present within a given interval of one million years. Phyletic evolution probably only contributes in a minor way to the total large-scale evolution of the brachiopods. By far the majority of the species appear in the chalk without any apparent ancestor, persist through their ranges without undergoing any substantial morphological change and become extinct without gradually transforming into a descendant. Biometrical measurements support this pattern (Johansen, 1987a, b). No distinction has thus been made here between true first appearances and first occurrences or between phyletic extinction and termination of a lineage.

Standing diversity is measured at estimated million year boundaries. Species which seem to become extinct at these boundaries are considered as occurring in the oldest of the two intervals only. Species which seem to originate at estimated million years boundaries are considered as belonging to the youngest of the two intervals only.

Rate of origination is calculated as number of species originations during a given million years interval divided by the numer of species surviving from the preceding interval plus all those that originated during the interval in question (Tab. 1).

Rate of extinction is measured as number of species extinctions in a given interval divided by the number of species surviving from the preceding interval plus all those that originated during the concerned interval (Tab. 2).

MILLION YEARS	TOTAL NUMBER OF SPECIES	NUMBER OF NEW SPECIES	RATE OF ORIGINATION	ACCUMULATED RATE OF ORIGINATION
64	30	23	0.767	3.177
65	27	2	0.074	2.410
66	25	0	0.000	2.336
67	25	1	0.000	2.336
68	25	1	0.040	2.336
69	28	1	0.036	2.296
70	28	1	0.036	2.260
71	29	4	0.138	2.224
72	27	6	0.222	2.086
73	23	3	0.130	1.864
74	22	0	0.000	1.734
75	23	4	0.174	1.734
76	19	0	0.000	1.560
77	19	4	0.210	1.560
78	15	4	0.267	1.350
79	12	0	0.000	1.083
80	17	2	0.118	1.083
81	19	2	0.105	0.965
82	19	2	0.105	0.860
83	19	1	0.053	0.755
84	18	1	0.056	0.702
85	18	4	0.222	0.646
86	15	1	0.067	0.424
87	14	5	0.357	0.357
88	9(–14?)	0(–5?)	0.000?	0.000?

Table 1. Number of new species per million years and rate of origination (million year^{-1}) of the brachiopod fauna occurring through the Middle Coniacian-Early Danian of Northwest Europe. Mean rate of origination for the Upper Cretaceous: $\frac{2.410}{24} = 0.100$. Rate of origination in the Early Danian: 0.767. Data are based on Fig. 2. 65 million year refers to rate of origination in the uppermost Upper Maastrichtian immediately before the Maastrichtian-Danian boundary.

MILLION YEARS	TOTAL NUMBER OF SPECIES	NUMBER OF SPECIES BECOMING EXTINCT	RATE OF EXTINCTION	ACCUMULATED RATE OF EXTINCTION
64/65	27	20	0.741	2.324
65	27	0	0.000	1.583
66	25	0	0.000	1.583
67	25	0	0.000	1.583
68	25	4	0.160	1.583
69	28	1	0.036	1.432
70	28	2	0.071	1.387
71	29	2	0.069	1.316
72	27	2	0.074	1.247
73	23	1	0.087	1.173
74	22	1	0.045	1.086
75	23	0	0.000	1.041
76	19	0	0.000	1.041
77	19	0	0.000	1.041
78	15	1	0.067	1.041
79	12	5	0.417	0.974
80	17	4	0.235	0.557
81	19	2	0.105	0.322
82	19	2	0.105	0.217
83	19	0	0.000	0.112
84	18	1	0.056	0.112
85	18	1	0.056	0.056
86	15	0	0.000	0.000
87	14	0	0.000	0.000
88	9(–14?)	0	0.000	0.000

Table 2. Number of species becoming extinct per million years and rate of extinction (million year^{-1}) of the brachiopod fauna occurring throught the Middle Coniacian-Early Danian of Northwest Europe. Mean rate of extinction for the Upper Cretaceous: $\frac{1.583}{24} = 0.066$. Rate of extinction at the Cretaceous-Tertiary boundary: 0.741. Data are based on fig. 2. 64/65 million year refers here to the rate of extinction at the Maastrichtian-Danian boundary, whereas 65 million year refers to rate of extinction in the uppermost Upper Maastrichtian inmediately before the Maastrichtian-Danian boundary.

Time-specific diversity changes are illustrated in Fig. 3. This diagram shows the relative magnitudes or originations and extinctions plotted against the total number of species occurring from the Middle Coniacian to the Lower Danian. Fig. 4 shows accumulated rates of origination and extinction through this interval.

From the time-diversity scheme the following pattern emerges: during the mid-Coniacian-Early Santonian diversity is low (10-12 species) reflecting initial stages of brachiopod colonization of the chalk. Nine species seem to appear in the Middle Coniacian, but as their first occurrences coincide with the lowermost chalk sample available, their true first appearances may well have occurred much earlier.

Through mid-Santonian-Late Maastrichtian times there is a slow build-up of species diversity reflecting a gradual niche diversification of the chalk.

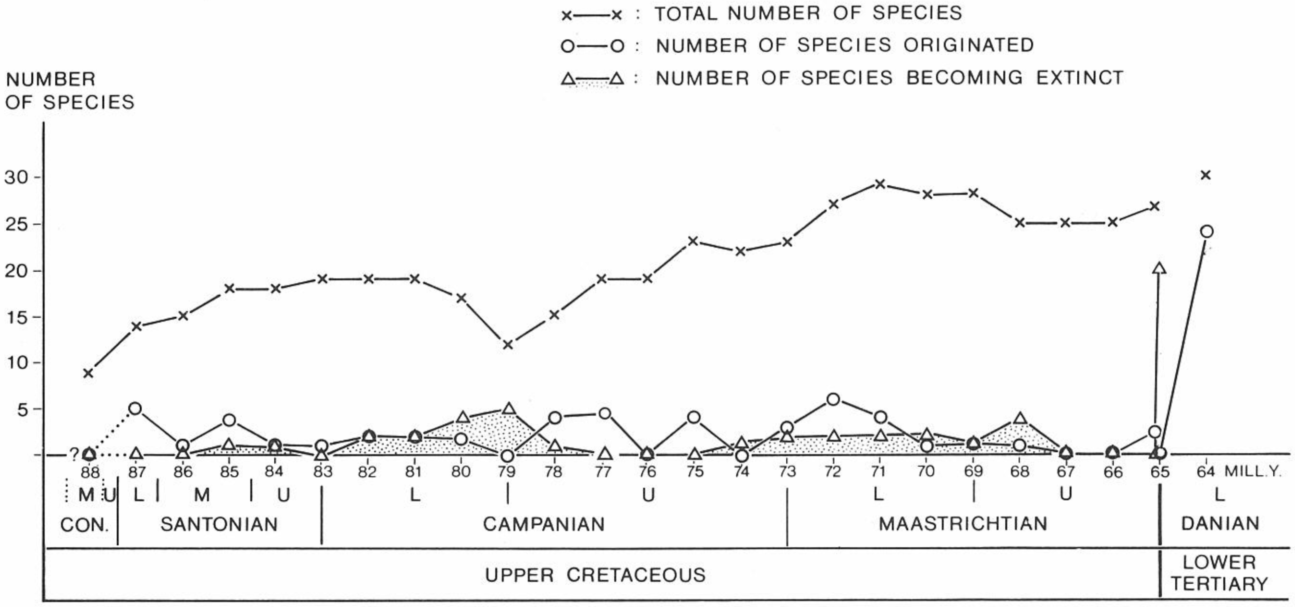

Figure 3. Diagram showing the time-specific diversity changes. The relative magnitudes of species origination and extinction are plotted against the total number of species occurring from the Middle Coniacian to the Early Danian (updated from Johansen, 1986). For details on diversity on the Maastrichtian-Danian boundary, see Surlyk & Johansen (1984) and Johansen (1987a).

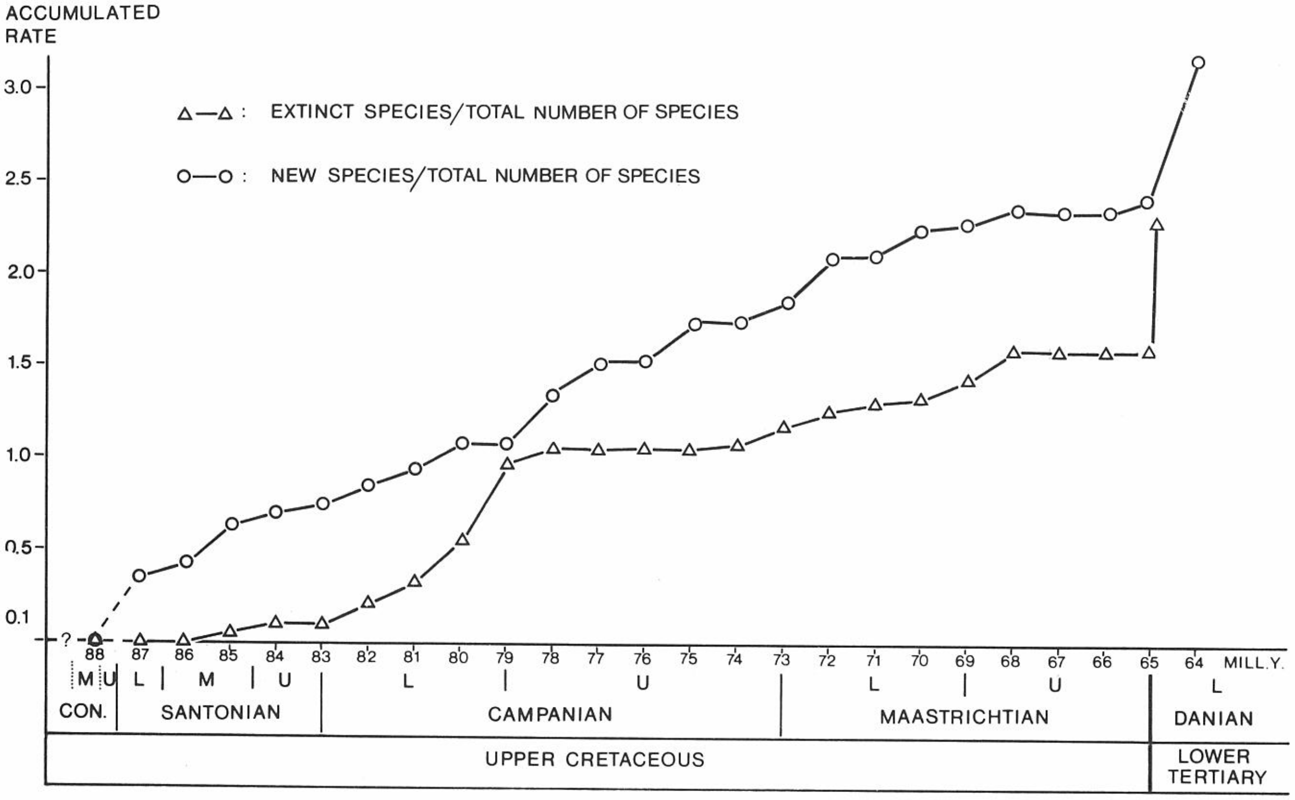

Figure 4. Diagram showing accumulated rates of origination and extinction through the Middle Coniacian to the Early Danian (updated from Johansen, 1986).

Diversity increases during this interval from 10 (—12) to (25—) 30 species. Through the Maastrichtian, the fauna reached optimal adjustment and evolutionary stability. Community analyses are, however, still needed to illuminate the details of this diversification pattern. In end-Maastrichtian time, when the fauna was at its climax, a sudden and conspicuous drop in diversity was experienced, coinciding with the Maastrichtian-Danian boundary (Surlyk & Johansen, 1984; Johansen, 1987a). This drop in diversity was in Early Danian times followed by a phase of renewed adaptive radiation and recolonization. It is characteristic here that the diversity in the Early Danian is fully comparable to Maastrichtian climax-diversity.

Species longevity

Assuming that rate of species evolution is a function of time, one would expect to find some relationship between species longetivy and the size of the species group. Fig. 5 thus shows the frequency distribution of brachiopod species according to their longevities estimated in intervals of 1.0 million years each.

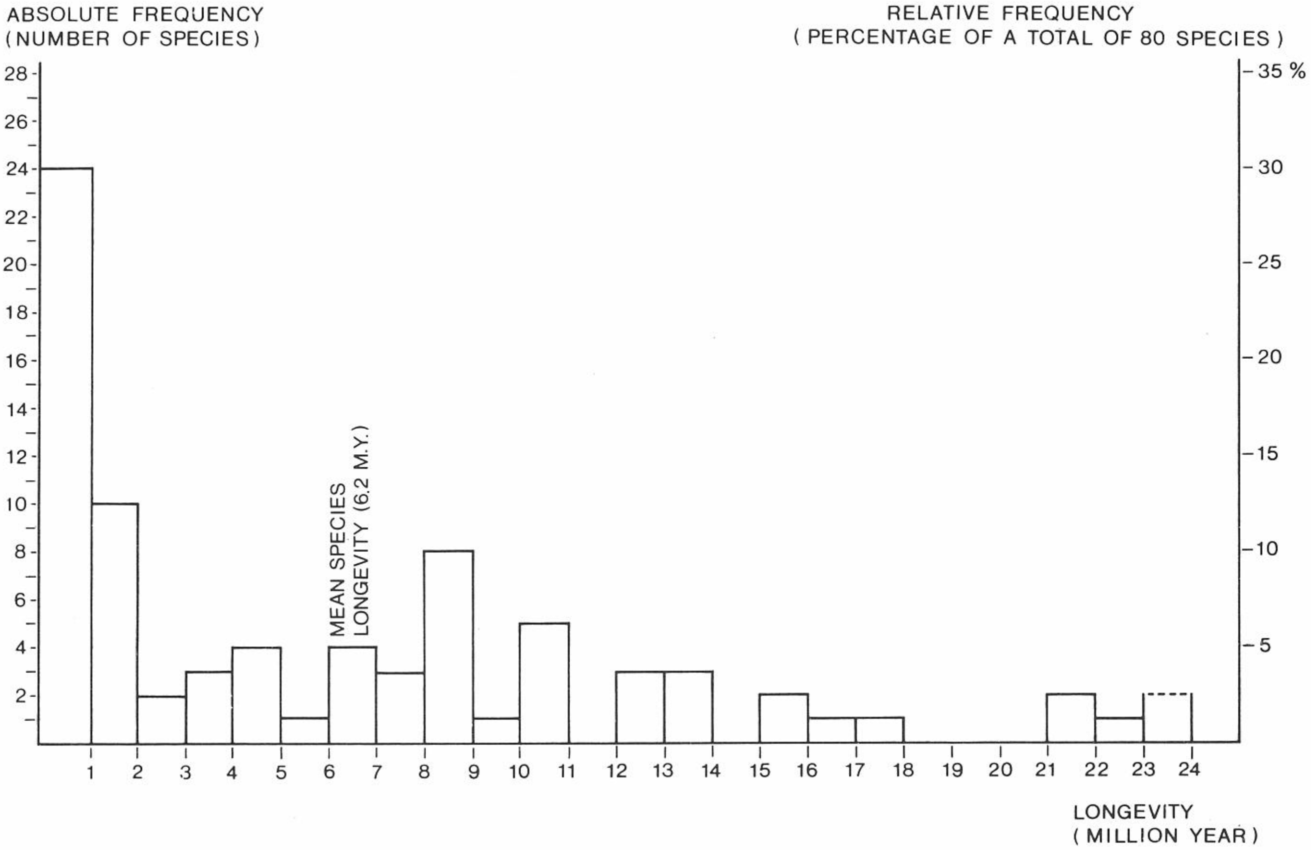

Figure 5. Histogram showing the frequency distribution of the longevities of the 80 most common brachiopod species present in the Middle Coniacian to the Early Danian chalk of Northwest Europe (updated from Johansen, 1986).

The histogram shows an overall strongly right skewed distribution relative to absolute time. The shortest species longevities were less than 1.0 million years and the most long-ranging more than 23 million years. The majority of the short-ranging species are those restricted to the Early Danian. Of a total of 80 species 34 had a longevity of less than 2.0 million year and 23 of these are restricted to the Early Danian. According to both literature and own observations the majority of the species from the Early Danian are furthermore restricted to the Lower Danian chalk facies itself and thus have a range around one million years or less. Exceptions are *Crania tuberculata, Crania transversa, Argyrotheca dorsata, Argyrotheca posselti, "Terebratula" fallax* and probably also *Platidia* n.sp 2 all of which are present in more benthos-rich chalk of the Middle Danian as well (Ødum, 1926; Asgaard, 1968; Johansen, unpublished data).

Subsidiary peaks occur around 8 and 23 million years. The most long-ranging species are *Terebratulina chrysalis, Argyrotheca obstinata, Aemula inusitata* and *Kingena pentangulata* which all ranges through 21 million years or more.

Mean species longevity, L, is derived from the equation

$$L = \frac{\Sigma F \times M}{N}$$

where F is the frequency of species in each class, M is the mean of each age class and N is the total number of species, Williams (1984).

Mean duration for a Late Cretaceous-Early Danian brachiopod species is hence 6.2 million years, an estimate which is fully comparable to mean species durations both for other groups of brachiopods (Waterhouse, 1977) and for other groups of fossil marine, benthic invertebrates (Stanley, 1979, 1985).

The strongly right skewed longevity distribution, dominated as it is by short-lived species, constitute a so-called horotelic pattern (sensu Simpson, 1944, 1953; Williams & Hurst, 1977). Horotely expresses the usual pace of evolution, including faster and slower episodes of evolutionary opportunities for a group of organisms. A horotelic pattern is opposed to a bradytelic pattern, representing lineages, whose adaptive zone happen to endure indefinitely (associated with exceedingly low evolutionary rates) and to tachytely, which is associated with very rapid evolution recording the first invasion of new adaptive zones. The horotelic pattern of the brachiopod longevity histogram thus a *priori* suggest a normal, progressive pattern of evolution for these brachiopods.

The shape of the longevity histogram (Fig. 5) depends, however, primarily on the interplay between times of origin and extinction as well. Although the time-specific diversity patterns (Figs. 3, 4) show that the brachiopods display a remarkable degree of evolutionary stability partly reflected by their *in general* low rates of origination and low rates of linage terminations and partly reflected by their wide biogeographical distribution in the chalk, the observed horotely is primarily a product of the conspicuous taxonomic turn-over occurring at the Maastrichtian-Danian boundary.

EXTINCTION AND ORIGINATION

Rates of extinction clearly fluctuated through Middle Coniacian-Maastrichtian times, but it is highly significant that the extinction peak coinciding with the Cretaceous-Tertiary boundary is by far the most prominent (Figs. 3, 4). It is furthermore characteristic that general Late Cretaceous extinction differs both quantitatively and qualitatively from the Cretaceous-Tertiary boundary mass extinction.

Rates of extinction through the Middle Coniacian-latest Maastrichtian interval are thus typically low, reaching a mean rate of 0.07 My^{-1} varying between 0.00 and 0.41 (Tab. 2). Rate of extinction at the Maastrichtian-Danian boundary is, compared to this, as high as 0.74 My^{-1}, roughly an order of ten times that of the mean rate of extinction.

Accumulated rates of origination have throughout the Late Cretaceous been higher than the accumulated rates of extinction although the progress of these two curves was almost parallel (Fig. 4). Mean rate of origination is thus 0.10 My^{-1} varying between 0.00 and 0.36, and rate of origination subsequent to the Maastrichtian-Danian boundary event as high as 0.77 My^{-1} (Tab. 1).

Background extinction

During the Late Cretaceous, extinction seems to have been random with respect to taxonomic groups and morphologic adaptations. Through this interval there seems to have been a gradual replacement of species along with a gradual process of adjustment to the chalk sea botton. From Fig. 2 can be seen that a minimum of 80 species are present in the Middle Coniacian-Lower Danian interval. Of these, 57 species representing 24 genera occur in the Upper Cretaceous. In the Lower Danian are recorded about 30 species representing 13 genera, and about 25 species and two genera of these are new compared to the Upper Cretaceous.

Mainly micromorphic cancellothyridid, megathyridid, platidiid and craniid brachiopods dominate the fauna in both number of species and number of individuals. Of these the genera *Terebratulina, Rugia, Argyrotheca and Isocrania* are the most species-rich of the genera present. *Isocrania* is thus represented by at least eleven species, *Terebratulina* by at least nine species and *Rugia* and *Argyrotheca* by at least twelve species each. *Aemula*, Platidia and *Scumulus*, all platidiids, are low in number of species (Fig. 2, Pls. I, II, III).

In the Upper Cretaceous, diversification took place primarily within this group of minute, relatively featureless brachiopods, all of which were pedically attached or cemented to tiny, hard substrates on the chalk sea bottom. This group seemingly formed a non-specialized basic stock already in the Coniacian. Diversification also took place within a group of larger brachiopods which were specialized to a secondarily free-lying life habit on the muddy sea bottom itself. The free-lying forms developed either through a hemisphaerical, reclining adaptation within a group of brachiopods which were not closely related (Surlyk, 1972) (e.g. *Terebratulina gracilis, Meonia semiglobularis, Magas chitoniformis, Trigonosemus pulchellus* and *Gemmarcula humboldtii*), or through adaptation of a so-called "snow-shoe" morphology (e.g. Thayer, 1975) within a group of closely related rhychonellids (Surlyk, 1972) (Fig. 2, Pl. I). Whereas the "snow-shoe" adaptation was present as early as in the Coniacian, the hemisphaerical recliners did not appear until Late Companian times (Surlyk, 1972; Johansen, 1987a). The secondarily free-lying brachiopods are all represented by monotypic genera or by genera represented by a few species only.

Mass extinction

At least four factors could have contributed to extinction of the brachiopods namely random fluctuations, competition, predation and habitat changes. It has, however, been argued that competition apparently is not of primary importance for rate of extinction for brachiopods (Alexander, 1979), and that brachiopod population fluctuations most likely are promoting extinction of narrowly distributed species with low population density rather that of widely distributed and abundant species (Jackson, 1974). Increased predation of brachiopods during Late Cretaceous may have influenced population dynamics (Jablonski & Bottjer, 1983), but so far no evidence has been published that substantiates predation as a cause of extinction for any particular species.

Increasing specialization and niche diversification/splitting resulted in extinction following even minor environmental fluctuations. For the extinction at the Maastrichtian-Danian boundary, habitat change is considered to be of primary importance. The dramatic decrease in nannoplankton productivity and the succeeding deposition of the basal Danian clay layer, the Fish Clay and its equivalents, represented a geologically instantaneous destruction of the chalk as a macrohabitat in the end-Maastrichtian (Surlyk & Johansen, 1982, 1984; Johansen, 1987a). Marly layers are, however, present and common throughout the monotonous Middle Coniacian-Upper Maastrichtian chalk, some of which are of diagenetic origin and some of which are of uncertain origin (e.g. Schulz *et al.,* 1984), but the stratigraphical distribution of these marly layers does not seem to be correlated with any of the species lineage terminations occurring in this interval.

Other details characterizing the brachiopod extinctions at the Maastrichtian-Danian boundary are in themselves peculiar. This extinction event shows a drastic increase in rate of extinction eliminating more than 70 per cent of the species. It took place at a time when the fauna was at its evolutionary summit and no significant changes in diversity or population structure has been observed towards the boundary. The recolonization and subsequent adaptive radiation that followed relatively soon after the boundary event is reflected as a conspicuous increase in rate of origination in the Early Danian times. This course mimics in essence the evolutionary radiation of survivors into the ecospace cleared by mass extinction (Sepkoski, 1984). Adaptive radiation led to a fauna which was highly diverse but which at the specific level as well as at higher levels differs in taxonomic composition, and which also in community-type differs from the Maastrichtian (Johansen, 1987a). Among extinct species are thus the highly specialized hemisphaerical reclining brachiopods. Wheter the preferential extinction of these forms is a biological event or rather a statistical phenomenon is difficult to say at the present stage. To illuminate this, further study is needed to show whether other specialized species also were selected against or whether there are other characteristics that could beadded to strengthen the general conclusions regarding selective extinction (Johansen, in prep.). At present one can say that they apparently disappeared at the boundary and that their niches were not exploited in the Lower Danian chalk. The few surviving species are all morphologically conservative, comparatively featureless brachiopods.

These characteristics are difficult to explain solely in terms of the long-term changes in the biotic and physical environments of the Upper Cretaceous-Lower Tertiary shelf sea and the mutually reinforcing interaction of these and the brachiopod fauna, the process which most likely accounts for the main part of the evolution through the Upper Cretaceous.

In conclusion the complete graph for brachiopod species extinction rates shows, that the Maastrichtian-Danian boundary mass extinction represents a short-

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Plate I. Specimens from Norfolk and Nye Kløv have MGUH as prefix to their registration numbers. MGUH refers to the formal numbering system of Geological Museum, the University of Copenhagen, Denmark. Specimens from Lägerdorf and Kronsmoor are prefixed SPGIH, referring to the formal numbering system of the Institute of Geology and Palaeontology, the University and Museum of Hamburg, Germany. For illustration purposes are used both normal photography of specimens coated with aluminium chloride and scanning electron microscope photography of specimens coated with gold.

1.—*Cretirhynchia* aff. *cuneiformis* Pettitt, 1950. Large adult specimen in dorsal view, × 4. Sample G54, Lägerdorf, Germany. Upper Santonian. SPGIH 3551.
2a, b.—*Meonia semiglobularis* (Posselt, 1984). a, large, adult specimen in dorsal view, × 14. Sample NK8, Nye Kløv, Denmark. Maastrichtian-Danian boundary clay. MGUH 16903. b, 2a in oblique lateral view showing hemisphaerical shell.
3a, b.—*Trigonosemus pulchellus* (Nilsson, 1827). a, large, adult specimen in dorsal view, × 4. Sample G159, Kronsmoor, Germany. Upper Lower Maastrichtian. SPGIH 3552. Note the very incurved umbo and that the pedicle opening is closed by secondary shell. b, 3a in lateral view showing plano-convex shell and incurved umbo.
4.—*Isocrania costata* (Sowerby, J. de C., 1823). Interior of adult ventral valve, × 12. Trimingham, Norfolk, England. Upper Lower Maastrichtian. MGUH 16843.
5.—*Terebratulina gracilis* (Schlotheim, 1813). a. large specimen in dorsal view, × 13, G148, Kronsmoor, Germany. Lower Lower Maastrichtian. SPGIH 3553. Note the pin-hole type foramen. b, 5a in lateral view showing plano-convex shell.

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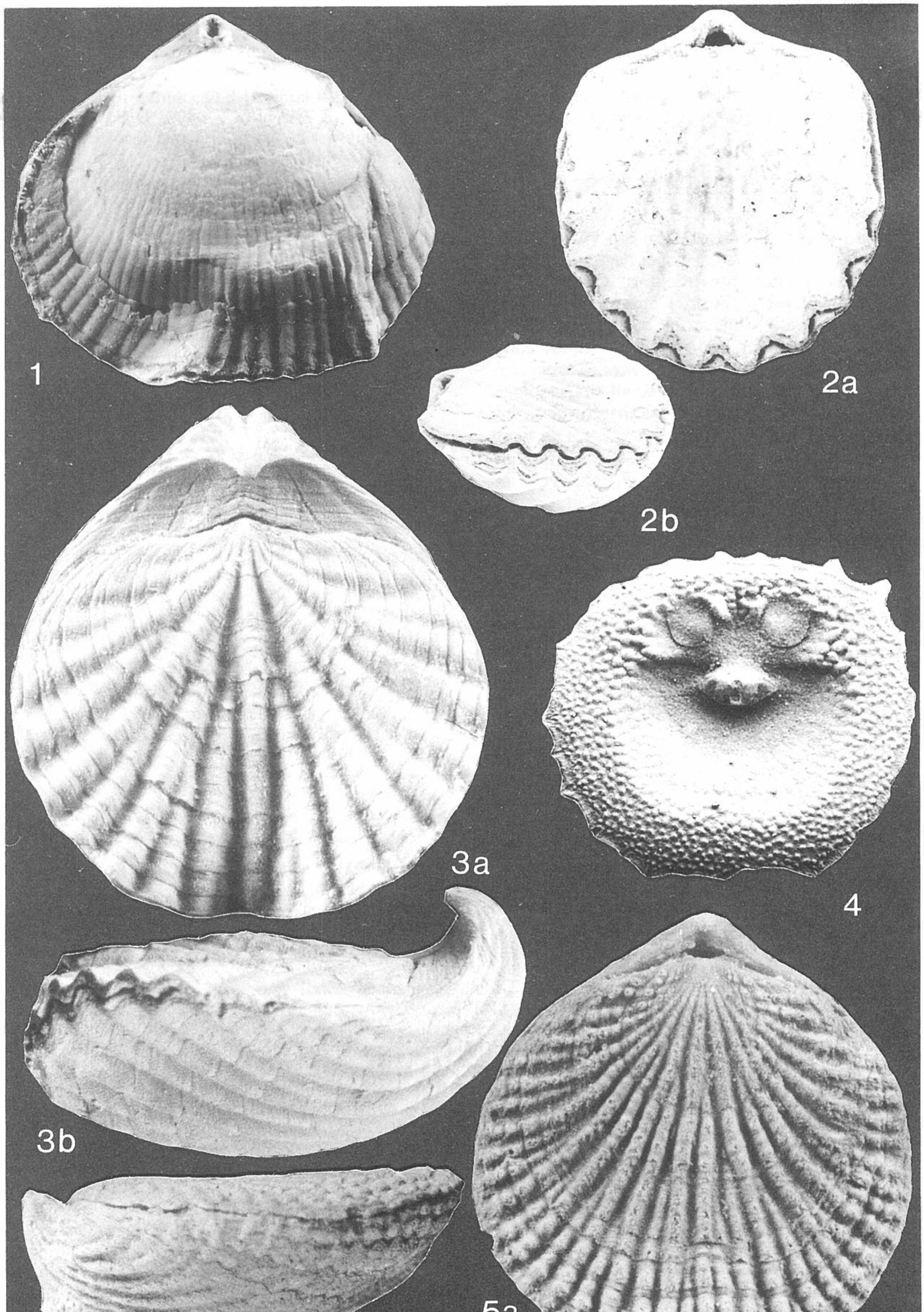
Plate I



term acceleration of extinction rates with neither the timing nor the magnitude predictable from its position on the background curve. This mass extinction thus seems to be a pertubation of the faunal system produced by forces external to and basically independent of long-term growth and decay of the fauna.

ACKNOWLEDGEMENTS

I want to thank Professor Finn Surlyk, the Geological Survey of Greenland, Copenhagen, Professor Marcos A. Lamolda, Department of Geology, Bilbao, Professor Derek V. Ager, Department of Earth Sciences, University College of Swansea and one anonymous referee, for criticism and helpful comments, Mrs. Annemarie Brantsen, Mrs. Ragna Larsen and Mr. Christian Rasmussen, all the Geological Museum, the University of Copenhagen for typing and drawing and Mr. Jan Aagaard and Mr. Ole Bang Berthelsen, both the Institute of Historical Geology and Palaeontology, University of Copenhagen for doing the dark-room work.

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Plate II. 1.—*Rugia tenuicostata* Steinich, 1963. Adult specimen in dorsal view, × 27. Sample G155, Kronsmoor, Germany. Lower Lower Maastrichtian. SPGIH 3529.

2.—*Rugia spinicostata* Johansen & Surlyk in Johansen, 1987b. Adult specimen in dorsal view, × 30. Sample G60, Lägerdorf, Germany. Lower Lower Campanian. SPGIH 3522 (Holotype).

3.—*Rugia acutirostris* Steinich, 1965. Adult specimen in dorsal view, × 30. Sample G147. Kronsmoor, Germany. Lower Lower Maastrichtian SPGIH 3525.

4.—*Rugia triangularis* Johansen, 1987b. Adult specimen in dorsal view, × 22. Sample G5, uppert Middle Coniacian Lägerdorf, Germany. SPGIH 3501 (Holotype).

5.—*Rugia latronis* Johansen, 1987a. Adult specimen in dorsal view, × 25. Sample NK26, Nye Kløv, Denmark. Lower Danian. MGUH 16948 (Holotype).

6.—*Rugia flabella* Johansen, 1987a. Adult specimen in dorsal view, × 20. Sample NK19, Nye Kløv, Denmark. Lower Danian. MGUH 16941 (Holotype).

7.—*Terebratulina chrysalis* (Schlotheim, 1813). Large juvenile specimen in dorsal view, × 28. Sample NK30, Nye Kløv, Denmark. Lower Danian. MGUH 16917.

8.—*Terebratulina chrysalis* (Schlotheim, 1813). Interior of juvenile dorsal valve showing brachidium and part of recrystallized plectolophe, × 20. Sample NK30, Nye Kløv, Denmark. Lower Danian. MGUH 16915.

9.—*Terebratulina chrysalis* (Schlotheim, 1813). Broken large adult specimen in dorsal view showing complete ring-shaped brachidium, × 10. Sample G20, Lägerdorf, Germany. Upper Lower Santonian. SPGIH 3554.

10.—*Terebratulina chrysalis* (Schlotheim, 1813). Large adult specimen in dorsal view, × 8. Sample G26, Lägerdorf, Germany. Upper Middle Santonian. SPGIH 3555.

11.—*Terebratulina longicollis* Steinich, 1965. Adult specimen in dorsal view, × 18. Sample NK5, Nye Kløv, Denmark. Upper Maastrichtian. MGUH 16932.

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Plate II

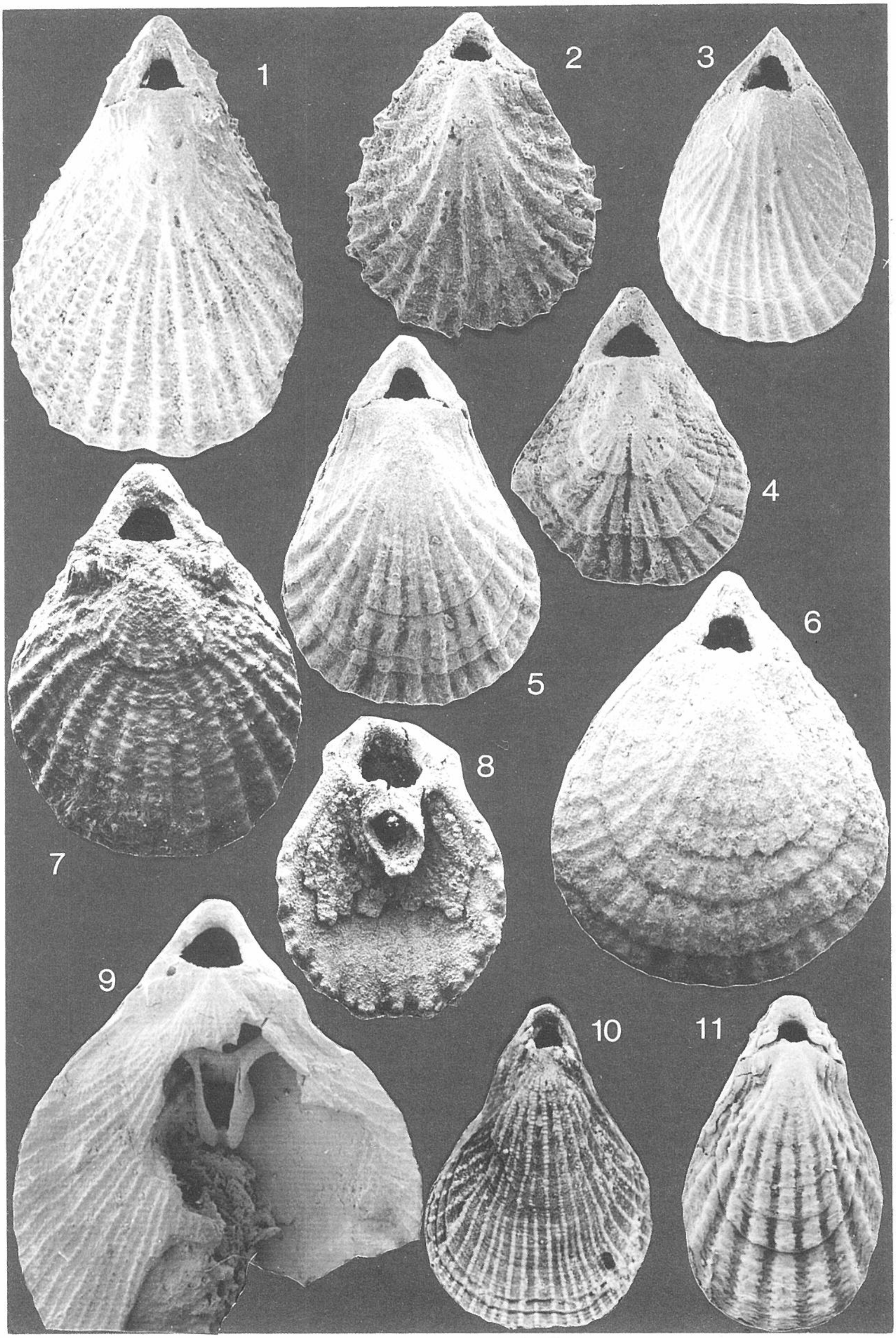

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Plate III. 1.—*Argyrotheca obstinata* Steinich, 1965. Adult specimen in dorsal view, × 26. Sample G79, Lägerdorf, Germany. Upper Lower Campanian. SPGIH 3556.

2.—*Argyrotheca hirundo* (Hagenow, 1843). Adult specimen in dorsal view, × 28. Sample NK23, Nye Kløv, Denmark. Lower Danian. MGUH 16980.

3.—*Argyrotheca stevensis* (Nielsen, 1928). Adult specimen in dorsal view, × 25. Sample NK26, Nye Kløv, Denmark. Lower Danian. MGUH 16966.

4a, b.—*Aemula inusitata* Steinich, 1968. Two-valved adult specimen in ventral view, × 36. Sample NK25, Nye Kløv, Denmark. Lower Danian. a, dextral half showing surface sculpture, amphithyridid foramen and median septum. MGUH 16999A. b, sinistral half. MGUH 16999B.

5.—*Aemula inusitata* Steinich, 1968. Adult ventral valve in exterior view, × 25. Trimingham, Norfolk, England. Upper Lower Maastrichtian. MGUH 18237. Note the characteristically tuberculate shell surface.

6.—*Aemula inusitata* Steinich, 1968. Adult specimen in dorsal view, × 24. Sample G147. Kronsmoor, Germany. Lower Lower Maastrichtian SPGIH 3557.

Note the characteristically smooth surface of the dorsal valve.

7.—*Platidia* n.sp. Adult specimen in dorsal view, × 45. Sample NK21, Nye Kløv, Denmark. Lower Danian. MGUH 17004.

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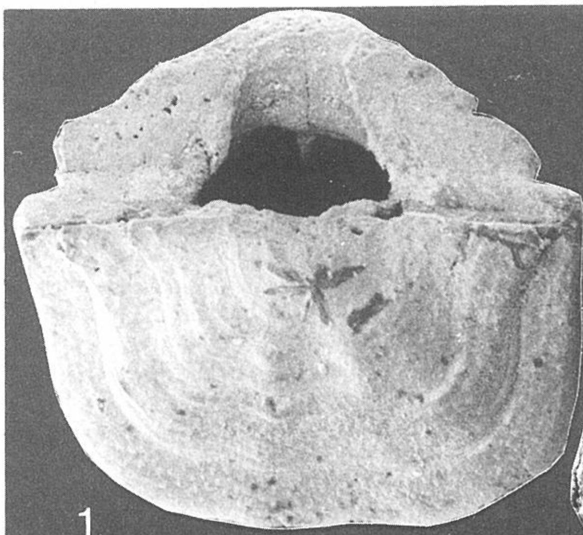
Plate III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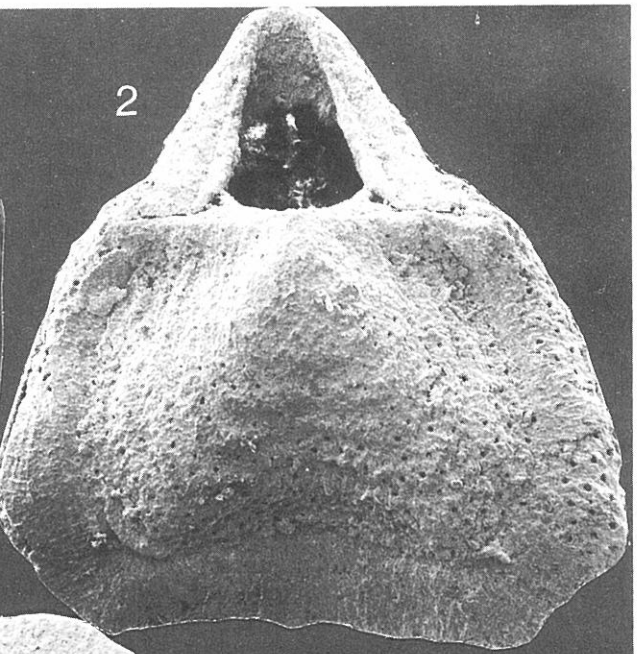
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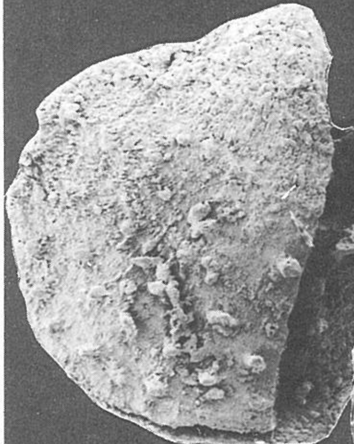
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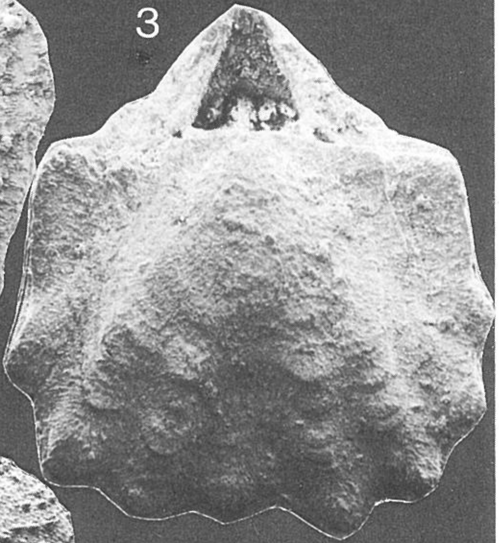
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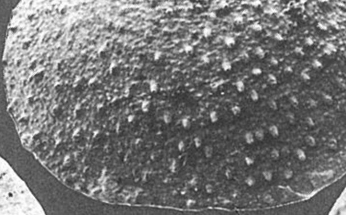
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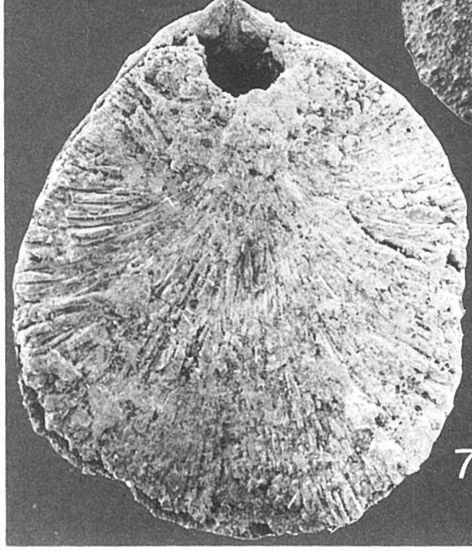
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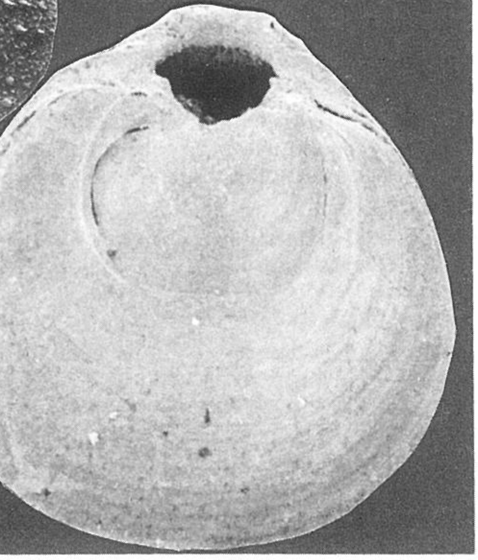
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