

Voilà de quoi à s'occuper.

Bien à toi

Perch 79

- es tu vraiment pour le premier dans le Tethyan  
le Cretacé? Tu es la seule à côté des Prot. Vingt ...

# Calcareous Nannofossils from the Cretaceous between the North Sea and the Mediterranean

## Kalkige Nannofossilien (Coccolithen) aus der Kreide zwischen Nordsee und Mittelmeer

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with 24 text-figures and 2 plates

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**Abstract:** Calcareous nannofossils make important contributions to the Cretaceous biostratigraphy of the Boreal as well as the Tethyan Realm. Several zonal subdivisions of the Cretaceous by calcareous nannofossils have been proposed and the stratigraphical positions of the European Cretaceous stratotypes in these zonations have been documented. Moreover, continuous sections from the Boreal and Tethyan Realms have been investigated and zoned. Correlations with other fossil groups and with the magnetic reversals have been established. Provincialism of certain forms seems evident, but statements about paleoprovinces are still also (mainly?) statements about the availability of investigations of well preserved material of a given age in a given area. Some evolutionary lineages are reviewed and others are proposed; however, much more detailed work still needs to be done in this field.

7 new coccolith species are described: *Calicalathina alta*, *Ceratolithoides verbeekii*, *Eprolithus antiquus*, *Micrantholithus speetonensis*, *Micula prinsii*, *Nannoconus borealis*, *Prediscosphaera grandis*.

**Kurzfassung:** Coccolithen leisten einen wichtigen Beitrag zur Biostratigraphie der Borealen sowie der Tethydischen Kreide. Verschiedene Zonierungen der Kreide durch kalkige Nannofossilien sind bereits vorgeschlagen worden, und die stratigraphische Ausdehnung der Europäischen Stratotypen der Kreide ist mehrfach mit diesen Zonierungen korreliert worden. Zusätzlich sind mehrere längere Profile des Borealen sowie des Mittelmeerraumes untersucht und zoniert worden. Korrelationen mit anderen Fossilgruppen und mit der magnetischen Stratigraphie sind erarbeitet worden. Ein gewisser Provinzialismus verschiedener Formen ist augenscheinlich; Aussagen über Palaeoprovinzen sind jedoch immer noch stark abhängig vom Vorhandensein von detaillierten Untersuchungen an gut erhaltenem Material. Einige Entwicklungsreihen werden besprochen, andere vorgeschlagen – auf diesem Gebiet wartet jedoch noch viel Arbeit.

7 neue Arten werden beschrieben: *Calicalathina alta*, *Ceratolithoides verbeekii*, *Eprolithus antiquus*, *Micrantholithus speetonensis*, *Micula prinsii*, *Nannoconus borealis*, *Prediscosphaera grandis*.

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## Introduction

*Purpose of this paper.* The purpose of this paper is to summarize and present the current knowledge of Cretaceous calcareous nannofossils. It also discusses their importance and use in biostratigraphical and paleoecological studies of the Cretaceous from the North Sea to the Mediterranean.

During the past few years, great progress has been made in coccolith biostratigraphy with the investigation and publication of the coccolith content of all marine European stratotypes of the Cretaceous. Moreover, some nearly continuous sections have been studied from both the boreal and the tethyan realm, so that comparisons between these two paleoecologic provinces are more reliable, but still far from "final". Some of this information has been published recently; the rest, however, is in preparation and may not get published, as it is contained in English Ph. D. theses or in oil-company files. Thanks to the generosity of some of these investigators, I was allowed to use their work and add this information to the already published data.

I hope that the many illustrations will help coccolith specialists gain an overview over at least some of the more important families and genera of the Cretaceous. They also will show up the amount of detailed work still needed to understand the relations between the genera and families and their origin. There are still many forms that seem to appear from "nowhere". Some families and genera are only treated superficially or not at all, since most of their species are not (yet?) considered to be of stratigraphical interest.

It is to be hoped that this paper encourages specialists of other fossil groups and stratigraphers to co-operate more frequently with coccolith specialists, to have their samples studied by them and to include coccolith age-determinations in their stratigraphies. It will help them to correlate more precisely their material with that from other areas and it could help everyone to find more continuous sections and/or especially well preserved assemblages.

*Methods of investigation.* Several methods of investigation are used at present for the study of calcareous nannofossils. For a rapid age determination it is usually enough to prepare a smear slide for investigation under the light microscope. In samples where coccoliths are rare, a settling technique or the use of a centrifuge to concentrate the desired fraction (2–20 microns) are advisable. In clay-rich samples, the use of a sonic cleaner is also recommended. The latter techniques are also used when the sample is to be investigated by TEM or SEM, which is essential for the study of the fine structure of the coccoliths, the description of new species and the detection of small differences between two similar forms.

*Preservation.* Many problems now occurring when working with calcareous nannofossils are based on the variable state of preservation of the material:

- taxonomic concepts of species are unclear due to different appearances in etched, overgrown or well preserved specimens. This results not only in more species names than necessary, but also in the "lumping" of some useful species. It also leads to the creation of "preservation" zones rather than biostratigraphic zones.
- many species originally living in the Cretaceous waters were either not fossilized or can only be found in ideally preserved assemblages. A list of relatively solution resistant and less resistant species has been presented by Thierstein (1976: 327, 329).
- the reliability of an age assignment in moderately well to poorly preserved material is not necessarily less than in well preserved material, as it is dependent on the availability of solution resistant forms in the interval studied. It depends on the presence of the same species in well preserved material, since the ranges of delicate species are not very reliable and can increase beyond their "normally" accepted ranges in exceptionally well preserved assemblages. The biostratigraphic events used for the zonation of the Cretaceous were mainly based on moderately well preserved material; thus they are also most reliable in such material. Deviations in both directions, to better or poorer preservation, will decrease this reliability for practical purposes. There are benefits from the additional knowledge gained from very well preserved



material; but for practical purposes it tends to complicate matters rather than clarify them. In any case, every range chart should show the abundance and preservational status of the coccoliths in the samples studied, in order to allow the reader to judge the reliability of the resulting biozonation.

– most new species described recently are likely to be relatively easily dissolved, and/or provincial, and/or very rare, or part of a "splitting" of a long known and used, but too broadly or poorly defined species (i.e. *Prediscosphaera cretacea*, *Eiffellithus turrisseiffeli*). In the latter case, the dividing of these species may be possible in well preserved material, but not in poorly preserved material.

## Biostratigraphy

### Previous and current work

*General.* When Stradner (1963) published his "New contributions to Mesozoic stratigraphy by means of nannofossils" at the VI World Petroleum Congress in Frankfurt, he was the first to propose clearly defined coccolith associations for the Cretaceous stages. Stradner (1965) also presented the first biostratigraphic account of a borehole in the German (Westphalia) Upper Cretaceous: Donar 5 in southern Münsterland. Stover (1966) suggested many new species and biostratigraphy from the Cretaceous of France and the Netherlands; Reinhardt (1966) gave the same for material from East Germany. Since then there has been a steady flow of papers dealing with mainly Upper and "Mid" Cretaceous coccoliths. Thierstein (1971, 1973) and Deres & Acheriteguy (1972) dealt with the Lower Cretaceous after early attempts by Brönnimann (1955), who examined the nannoconids of Cuba. With the thesis of Manivit (1971) and the contributions of Verbeek (1976, 1977), Sissingh (1977, 1978) and Barrier (1977a, b), the investigations of the European stratotypes are completed. Verbeek (1977) also gives an extensive overview of previous studies of the "Mid" and Upper Cretaceous coccoliths.

The biostratigraphy of the entire Mesozoic was summarized by Thierstein (1976), and is based on land as well as on DSDP sections from the whole world. Sissingh (1977) on the other hand, presented a more detailed zonation based mainly on outcrops from Europe and North Africa and subsurface data from the North Sea area. In the following work, these two zonations are given and their application discussed in some detail.

*Germany.* The first coccoliths described were those found by Ehrenberg (1836) in the chalk of Rügen and were assigned to inorganic calcite structures.

Besides the summary report on Donar 5 by Stradner (1965), few other papers have dealt with the German Cretaceous. Martini (1967) discussed the nannofossil assemblage of the Middle Albian from Salzgitter Watenstedt (N. Germany). The Maastrichtian of the Aachen area was dealt with by Vangerow & Schloemer (1967), and Cepek (1970) reported on the investigations of eleven localities of stratigraphically well documented Cenomanian through Maastrichtian ages, but giving generalized range charts only. Cepek (1973) listed the coccoliths from the Santonian of the Gehrdener Mountains and Stradner & Grün (1973) described *Nannoconus abundans*, from the Barremian of Schacht Konrad I near Salzgitter. Sissingh (1977) mentions a few German localities. At present R. Taylor (University College, London) is working on Lower Cretaceous samples from NW Germany; also A. Afejuku (University College, London) worked on Albian samples from some German localities. In E Germany, Reinhardt (1964, 1965, 1966a, 1966b, 1967, 1969) presented an early biostratigraphic scheme (1966a), while Reinhardt & Gorka (1967)





Jurassic/Cretaceous boundary

The Jurassic/Cretaceous boundary seems unlikely to be characterized satisfactorily by calcareous nannofossils, since the Upper Jurassic stratotypes lack suitable calcareous

MY	STAGES	NANNOFOSSIL EVENTS			KPN & BP	
		Thierstein 1976	Sissingh 1977	zones		
65-70	MAASTRICHTIAN	M. murus	N. frequens	26 c	M. prinsi* N. frequens*, C. kampneri	
		N. frequens	L. quadratus	25 b	M. murus* L. quadratus*	
		L. quadratus	A. cymbiform.	a	A. cymbiformis*	
		T. trifidus	R. levis	24	R. levis* T. phacelosus*, Q. trifidum	
		T. trifidus	T. phacelosus	b	T. phacelosus*, Q. trifidum	
	70-85	CAMPANIAN	T. trifidus	A. parvus	23 a	A. parvus*
			T. trifidus	R. anthophorus	b	R. anthophorus*, E. eximius*
			T. trifidus	R. levis	22 a	R. levis* L. grillii*
			T. trifidus	T. trifidus	b	Q. trifidum
			T. trifidus	C. arcuatus	a	C. arcuatus
SANTONIAN		T. aculeus	T. nitidus	21 b	Q. nitidum	
		T. aculeus	C. aculeus	20	C. aculeus	
		T. aculeus	B. hayi	b	B. hayi	
		T. aculeus	M. furcatus	a	M. furcatus* C. verbeekii, A. parvus*	
		T. aculeus	B. hayi	18 b	B. hayi*, A. sp. 5	
85-90	CONIACIAN	M. furcatus	A. parvus	a	A. sp. 1	
		M. furcatus	C. obscurus	17 a	P. obscurus*, E. floralis*	
	TURONIAN	M. furcatus	L. cayeuxii	16	L. cayeuxii*, L. septenarius*	
		M. furcatus	R. anthophorus	15	R. anthophorus*, L. grillii*, M. conca- va	
		M. furcatus	M. decussata	14	M. decussata*, L. septenarius*	
90-95	CENOMANIAN	M. staurophora	M. furcatus	13	M. furcatus*	
		G. obliquum	L. maleformis	12	E. eximius*	
	ALBIAN	L. alatus	T. pyramidus	11	Q. gartneri* G. nanum*	
		E. turrisseiffeli	M. decoratus	10	A. octoradiata*, C. chiastia* M. decoratus*, L. acutum, C. exiguum	
		P. albianus	E. turrisseiffeli	9	C. cympletum*, E. br. tannica* → B. Halpensis, C. anglicum*, Africana* E. prolithus sp. 1* E. turrisseiffeli*	
100-105	APTIAN	P. cretacea	P. cretacea	8	T. phacelosus*, C. signum, Cribrospha.	
		P. angustus, E. floralis	M. obtusus	7 b	R. angustus*, N. wassallii*, E. ant- iquus*	
	C. litterarius	C. litterarius	a	E. floralis*, B. africana* N. kampneri		
	R. irregularis, N. colanii	C. litterarius	6	N. steinmannii*, C. mexicana* Chiasiozygus ssp. → N. bermudezi		
	105-115	BARREMIAN	C. oblongata	C. oblongata	5	C. oblongata*
C. oblongata			S. colligata	4	S. colligata*, C. striatus*	
HAUTERIVIAN		C. cuvillieri	C. cuvillieri	b	C. cuvillieri*	
		L. bollii	P. salebrosa	a	E. antiquus*	
		L. bollii	C. lariei	3	C. striatus*	
115-135	VALANGINIAN	D. rectus	D. rectus	2	M. speetonensis*	
		D. rectus	D. rectus	3	M. speetonensis*	
	C. oblongata	C. oblongata	2	C. oblongata*		
	BERRIASIAN	C. angustiforatus	C. crenulatus	1	C. angustiforatus* C. cuvillieri*, N. steinmannii*	
		C. angustiforatus	N. steinmannii	1	C. angustiforatus* C. cuvillieri*, N. steinmannii*	

Fig. 2. Calcareous nannofossil events according to Thierstein (1976), Sissingh (1977) and this paper. Correlation to stages and numeric time-scale after Thierstein (1976), used as scale. \* = species also useful in the boreal area.

nannofossils. According to Thierstein (1975, 1976), several species first appear at the base of the Berriasian, just above the Jurassic/Cretaceous boundary: *Cruciellipsis chiastia*, *Lithraphidites carniolensis*, *Micrantholithus obtusus*, *Rucinolithus wisei* and *Staphanolithion laffittei*. Only *Polycostella beckmannii*, which extends from the Tithonian into the lowermost Berriasian, is thought to have its highest occurrence near the boundary. Medd (Institute of Geological Sciences, Leeds, UK) investigates at present the Jurassic/Cretaceous boundary, using DSDP cores.

*Nannoconus* specimens are considered by Thierstein (1975, 1976) to first occur in the Berriasian, while Trejo (1960), Stradner (1963), Baldi-Beke (1964), Geel (1966), Moshkovitz (1972) and Grün & Allemann (1975) suggested that *N. colomii* (*N. steinmannii*) first appears in the uppermost Jurassic sediments.

### Zonations

Zonation of part or the whole Cretaceous has been proposed by Čepék & Hay (1969, 1970), Čepék (1970), Manivit (1971), Worsley (1971), and recently by Verbeek (1977), based on material from Tunisia, Southern Spain and France; Sissingh (1977), from Tunisia, France, Holland, Germany and England; and Perch-Nielsen (1977) from the South Atlantic. Hojjatzadeh (1977) zones the "Mid" Cretaceous of Western Morocco and Manivit *et al.* (1977) dealt with the "Mid" Cretaceous in a general way. Only Sissingh (1977), Gartner (1977), Hay (1977) and Thierstein (1976) cover the entire Cretaceous. Their zonations are based on the first as well as the last occurrences of species and the zonal markers used by Sissingh (1977) and Thierstein (1976) are shown in Fig. 2, together with an even more complete sequence of events suggested by B. Prins (written communication, 1978) and the author.

While Thierstein uses 16 cosmopolitan, 8 tethyan and 2 boreal "biohorizons" to subdivide the Cretaceous, Sissingh gives a more detailed zonation including 26 zones and 18 subzones, thus a 36-fold subdivision of the whole Cretaceous. 14 marker species are common to these two biostratigraphies. Gartner (1977) gives no formal zones but uses Thierstein's (1976) range-chart. Hay (1977) bases his scheme on Manivit (1971) and Thierstein (1973).

*Berriasian to Aptian.* According to Thierstein (1976), only 4 reliable biohorizons are cosmopolitan in the Berriasian through Aptian interval, while 6 more are found in tropical regions. Taylor (in press) and the author have independently studied the Lower Cretaceous section at Speeton (UK), which was studied also by Black (1971) and Sissingh (1977), but not by Thierstein (1976). Although this excellent boreal section was the object of extensive TEM work by Black (1971), we found additional species, including scattered occurrences of *Nannoconus* and, in the middle Barremian, even a bed where *Nannoconus* is common. For the interval covered by the Speeton section – Berriasian through Barremian – Thierstein (1976) suggests only two cosmopolitan markers: the base of *C. angustiforatus* (*C. crenulatus* of Sissingh, 1977) in the middle of the Berriasian and the last occurrence of *C. cuvillieri* in the Upper Hauterivian. In the same interval, he also suggests 6 tropical markers. With the exception of *L. bollii*, all of them also were found at Speeton, but their occurrences are rare and, in the case of *D. rectus*, outside the range given by Thierstein. Thus they are not likely to be useful as zonal markers in this part of the boreal realm.

In the northern North Sea, however, the occurrence of *C. oblongata* is sufficiently consistent to make it a reliable zonal marker as suggested by Thierstein. Here, also *Nannoconus* occur consistently and can be used stratigraphically much in the same way as in the tethyan



realm (Brönnimann 1955, Deres & Acheriteguy 1972, Moshkovith 1972). Sissingh (1977) paid less attention to the lower Lower Cretaceous: nevertheless, he studied the Speeton section and suggested the use of the last occurrence of *Speetonia colligata* as a zonal marker and that of the last occurrence of *Paleopontosphaera salebrosa* as a subzonal marker within the Hauterivian. While the former species seems to be useful at Speeton, as well as in the North Sea, in Germany and in the tethyan realm, *P. salebrosa* was found both by Taylor (1978) and the author up into the Lower Barremian at Speeton and reaches also the Aptian/Albian (Prins, written communication 1978). The first occurrence of *C. loriei*, suggested by Sissingh (1977) as a zonal boundary in the Hauterivian, was found difficult to establish due to difficulties in recognizing or differentiating the species from other species of *Cretarhabdus* (Taylor 1978).

In Fig. 3 a revised zonation for the Speeton section is given. It includes two new subzonal markers, *Micrantholithus speetonensis* and *Eprolithus antiquus*. No general "boreal zonation" of the lower Lower Cretaceous interval can be given, since the presence of some of the markers seems to be facies dependent rather than latitude dependent as had hitherto been assumed.

For the subdivision of the Aptian, Thierstein (1976) and others suggest the first occurrences of *Chiastozygus litterarius*, *Parhabdolithus angustus* and *Eprolithus floralis*. According to Taylor (1978), *C. litterarius* is also found in the Barremian and uppermost Hauterivian at Speeton. This discrepancy may be due to differing opinions on the species *C. litterarius* by various authors. Forms attributed from the Lower Cretaceous to *C. litterarius*, a species originally described from the Upper Maastrichtian of Poland, are likely to differ from the original forms as well as from each other. Small forms hardly distinguishable from *R. angustus* were found as low down as the Upper Hauterivian in Speeton. They show parallel to slightly convex sides and the granules in the central area are not visible. Typical *R. angustus*, with parallel to slightly concave sides and clearly visible granules, however, do not occur before the Upper Aptian.

SPEETON, Yorkshire, England	Bed (Neale, Koye Fletcher)	KPN Sample 261	W. barnesae	S. crenulata	P. embergeri	S. laffittei	S. horticus	M. haechulzii	G. meddii	P. salebrosa	M. speetonensis	L. carniolensis	S. colligata	C. cuvillieri	C. striatus	E. antiquus	S. fossilis	R. cf. Rangustus	C. tenuis	N. abundans	N. borealis	C. litterarius	Abundance Preservation	coccolith events ↗ last occurrence ↘ first	
																									Stage
Barremian	UB	58																						F M	C. litterarius
	MB	56																						C M	
	MB	55																						C M	
	LB 2D	53																						C M	N. borealis
	LB 4	10																						F M	
	LB 5A	52																						C M	
Hauterivian	LB 5E	51																						A M	
	LB 6	49																						C M	
	C 1	13																						C M	
	C 2C	14																						C M	
	C 3	15																						A M	S. colligata
	C 4	16																						C M	C. striatus
	C 4	18																						C M	C. cuvillieri
	C 10	22																						F M	
	C 11	23																						C M	
	D 1	24																						C M	E. antiquus
Valanginian	D 2D	25																						C M	C. striatus
	D 2E	47																						F P	
	D 3B	45																						F P	
	D 3C	44																						R P	M. speetonensis
	D 4A	42																						C M	
	D 6A	29																						C M	
Berriasian	D 6	30																						C M	S. crenulata
	D 7	31																						R P	
	D 7	31																						R P	
	E	32																						- -	

Fig. 3. Distribution of coccoliths in the Speeton Clay. Symbols see Fig. 1.

*Albian to Turonian*. Special attention has been given to the "Mid" Cretaceous calcareous nannofossils in the context of the "Mid Cretaceous Events" IUGS Project. A paper concerning mid Cretaceous calcareous nonnofossil biostratigraphy (Manivit *et al.* 1977) was the outcome of a meeting held in Nice 1976 and was followed by another meeting in The Hague, 1977.

Thierstein (1976), Sissingh (1977) and Manivit *et al.* (1977) in the Albian recognize the first occurrence of *Prediscosphaera columnata* (*P. cretacea* of Thierstein and Sissingh) followed by the first occurrence of *Eiffelithus turriseiffeli*. These events have been observed worldwide at this stratigraphical level. The recognition of the Albian/Cenomanian boundary presents problems due to the correlation of coccolith stratigraphy with the stratotypes, but the following events occur near the boundary: the last occurrences of *Hayesites albiensis*, *Braarudosphaera quinqucostata*, *B. regularis*, and *B. stenorhetha*. The first occurrence of *Lithraphidites alatus* was considered by Thierstein (1976) to coincide with the base of the Cenomanian, but was since found to be older than the first occurrence of *E. turriseiffeli* in the Albian (Verbeek 1977). In the southern part of the North Sea region, T. Afejuku (personal communication 1978) could not find *H. albiensis* in Albian samples studied from the UK, the Channel tunnel or from northern Germany.

In the Middle Cenomanian, the first occurrences of *Lithraphidites acutum* and *Microrhabdulus decoratus* respectively were used for the zonation by Sissingh (1977) and Manivit *et al.* (1977). The latter suggested a further subdivision using the last occurrence of *Crucellipsis chiesta*, while Verbeek (1977) used the first occurrence of *Gartnerago obliquum*. The latter is shown by Thierstein (1976) to first occur in the Lower Turonian, while similar forms seem to occur all the way down to the Upper Albian. A very detailed study of the early species of *Gartnerago* and related genera is needed before this discrepancy can be resolved. Thierstein (1976) does not subdivide the Cenomanian.

Due to different views on the exact position of the Cenomanian/Turonian boundary in the European stratotypes, the next widely used event, the base of *Quadrum gartneri* (*Micula staurophora/decussata* and *Tetralithus gothicus* of other authors) is found below, at, or above that boundary.

For the subdivision of the Turonian, the first occurrence of *Eiffelithus eximius* and *Lucianorhabdus maleformis* is used by Manivit *et al.* (1977) and by Sissingh (1977) respectively. Hill (1976) refers to forms very similar to *E. eximius* from the Albian of Texas and Oklahoma (see p. ).

*Coniacian to Maastrichtian*. The base of the Coniacian is often correlated with the base of *Marthasterites furcatus*. The first occurrence of *M. decussata* (*M. staurophora* of many authors) is observed in the upper part of the Coniacian. Since *M. decussata* and *Q. gartneri* have only recently been separated (Manivit *et al.* 1977), *M. decussata* often shows up in range-charts below the level at which it is now believed to have evolved.

While Thierstein (1976) does not suggest a cosmopolitan subdivision of the Coniacian-Santonian interval, Sissingh (1977) introduces the first occurrence of *Reinhardtites anthophorus* and later of *Lucianorhabdus cayeuxii* as zonal markers for the Santonian. The base of *Tetralithus obscurus* is considered by Thierstein (1976) to be a marker for the boreal and austral base of the Santonian, while Sissingh notes it as a zonal marker for the base of the Campanian. Again, species concepts and/or correlation of biohorizons to stratotypes are not seen the same way by the two (and other) authors. Verbeek (1977) subdivides the Santonian, but he uses different species to those of Sissingh (1977): with *Broinsonia lacunosa* marking the base of the Santonian, he also notes the base of *Micula concava* still in the Lower Santonian, the base of *Rucinolithus*



(should be *Bukryaster hayi* in the Middle Santonian and the base of *Zygodiscus spiralis* just below the Upper Santonian. Verbeek follows Thierstein in correlating the base of *Broinsonia parca* with the lower boundary of the Campanian, Sissingh (1977) sets the first occurrence of *Calculites obscurus* (*Tetralithus* and *Phanulithus* of other authors) at this boundary, and the base of *Aspidolithus parvus* (*Broinsonia* of other authors) as the next younger event. With this, he suggests the opposite to Thierstein regarding the sequence of these two events. He also disagrees with Verbeek on the lower boundary of *Bukryaster hayi*, which he sets as a subzonal marker above the base of *A. parvus*. The last occurrence of *M. furcatus* and then *B. hayi* further subdivide the Campanian according to Sissingh (1977). All three authors then use the base of *Ceratolithoides aculeus* (*Tetralithus* of other authors) as a zonal marker. Sissingh and Verbeek continue with the base of *Tetralithus nitidus* (*Quadrum gothicum* of Verbeek) and then all three authors again agree with the base of *Tetralithus trifidus* (*Quadrum trifidum* of Verbeek), in the uppermost part of the Campanian. All of these forms (*C. aculeus*, *Q. gothicum*, *Q. trifidum*), and *C. arcuatus*, whose range constitutes a subzone in the *T. trifidus* Zone of Sissingh (1977), have not been found in the North Sea area. However, the base and the top of *Reinhardtites levis* and the last occurrence of *R. anthophorus* can be used as zonal markers and subzonal markers, as suggested by Sissingh (1977). With the subdivision of the *Reinhardtites anthophorus* group into three forms, Sissingh made it possible to subdivide also the high latitude Upper Campanian – Lower Maastrichtian interval, for which he additionally suggests the last occurrence of *A. parvus* and then *Tranolithus phacelosus* as subzonal markers and zonal markers respectively. The position of the Campanian/Maastrichtian boundary is not marked by a calcareous nannofossil event in Thierstein (1976) and Verbeek (1977), while Sissingh (1977) correlates the last occurrence of *A. parvus* with it. The latter is found to continue into the Lower Maastrichtian by most other authors.

For the subdivision of the Maastrichtian, Thierstein and Verbeek use the subsequent bases of *Lithraphidites quadratus* and *Micula murus*, while Sissingh uses the last occurrence of *R. levis*, the base of *A. cymbiformis* (by others usually placed in the Upper Campanian), the base of *L. quadratus* and the base of *N. frequens*. Thierstein considered *N. frequens* to be useful in the boreal/austral realm, while *M. murus* was restricted to the tropical areas. Although *N. frequens* is more common in high latitudes, it does occur also in low latitudes, and *M. murus* also has been found in the boreal realm. Where they occur together, *N. frequens* precedes "*M. murus*"; if this species is taken as a form with distinct, long and sometimes bifurcated arms, and is here introduced as the new species, *M. prinsii*. Forms with short or almost no arms occur below *N. frequens*. The writer has found *A. cymbiformis* to overlap with *R. levis* near to the Campanian/Maastrichtian boundary in Denmark, and thus does not agree with Sissingh's zonation. This is probably due to a different species concept of the genus *Arkhangelskiella*, in that the writer includes Sissingh's "*Arkhangelskiella* (large forms)" in *A. cymbiformis*.

Thus there seem to be differences in the sequence of events at the Kef section as reported by Verbeek (1977), the Kef section as reported by Sissingh (1977) and the writer's own observations of the Kef section and of the Campanian/Maastrichtian interval of the North Sea area. Differences also are found between the various observations of the type Maastrichtian, in that Sissingh (1977), Bramlette & Martini (1964) and the writer found *N. frequens*, while Verbeek (1977) did not find this species. Instead he reports *M. murus*, which was not found by the others. Whether this is due to the fact that different samples were studied or that these authors have different species concepts or have published incomplete inventories of species is not resolved; however, this contested information is presented, when the zonal schemes are established and compared, or when the data are used to establish paleoprovinces of certain species.

## Cretaceous/Tertiary boundary

Most Cretaceous coccoliths disappear shortly below or at the Cretaceous/Tertiary boundary, but are found in varying amounts reworked into the overlying Danian. Such Danian "Cretaceous assemblages" are usually richer in *Biscutum*, *Crepidolithus* and *Markalius* species than the Maastrichtian assemblages. It is therefore likely that these forms survived the "Cretaceous-Tertiary boundary events" – whatever they were – together with *Braarudosphaera*, *Cyclagelosphaera*, *Goniolithus*, *Lapideacassis*, *Micrantholithus*, *Phanulithus*, *Scampanella*, *Scapholithus*, *Zygodiscus*, and the calcareous dinoflagellate *Thoracosphaera* (Perch-Nielsen 1969, 1972; Percival & Fischer 1977; Romein 1977; Worsley 1974; Monechi 1977).

## Conclusions

The biozonation of the Cretaceous by calcareous nannofossils has made substantial progress since Thierstein presented his 1976 paper in Kiel 1974. Some experience has been gained as to the usefulness of his "cosmopolitan" markers in the North Sea area and it has been found that some of them cannot be used, namely *C. aculeus*, *Q. trifidum*, *L. alatus* and *L. bollii*. However, some of his "tropical" biohorizons can be used in parts of the North Sea, namely *N. colomii*, *L. carniolensis*, *C. oblongata* and *M. murus*. The absence of the latter in most northern Maastrichtian sequences might be taken as an indication that the youngest "Maastrichtian" was not deposited or not preserved, rather than that the species was primarily absent. The presence of *Nannoconus* and *C. oblongata* in the Northern North Sea and their absence in the Central and Southern part of the North Sea seem to be due to facies differences rather than to latitudinal differences.

Other, and more numerous, biohorizons than those of Thierstein (1976) were chosen to be reliable markers by Sissingh (1977) and Verbeek (1977), by Manivit *et al.* (1977) and are suggested by the author to come from tethyan as well as from boreal areas. Contradictions do exist as to the sequence of events and more work is needed to determine whether they are due to different species concepts of various authors, facies dependence of some species or to migration of species. This type of work was attempted successfully at the "Mid Cretaceous Events" second calcareous nannofossil specialist meeting, where microscope work, the study of holotypes etc. clarified the concept of many species among the 17 participants. The lumping of similar forms or the splitting of species with only small differences obviously leads to quite different possibilities of biostratigraphical resolution. Whilst there is often poor resolution, when working with poorly preserved material, it seems clear now, that a still finer subdivision can be attained by a more careful investigation of evolutionary lineages.

## Stratotypes and other important sections

Fig. 4 shows the correlation of coccolith biohorizons and the European stratotypes of the Cretaceous. This topic has been dealt with mainly by Manivit (1976, 1971), Thierstein (1973), Smith (1975), Verbeek (1976a, 1977a, b) Verbeek & Wonders (1977), Sissingh (1977) and Barrier (1977a, b). Thierstein and Barrier discuss the Lower Cretaceous stages and their coccolith content, Manivit, Sissingh and Verbeek deal mainly with the Upper Cretaceous stratotypes. As is evident from Fig. 4, the stratotypes do not contain all of the coccolith zones recognizable from the more complete sections. Furthermore, the facies of most stratotypes is less favourable to the deposition and/or preservation of calcareous nannofossils, than the sediments of some other sections, which were usually deposited in deeper waters. Therefore, any further effort to study



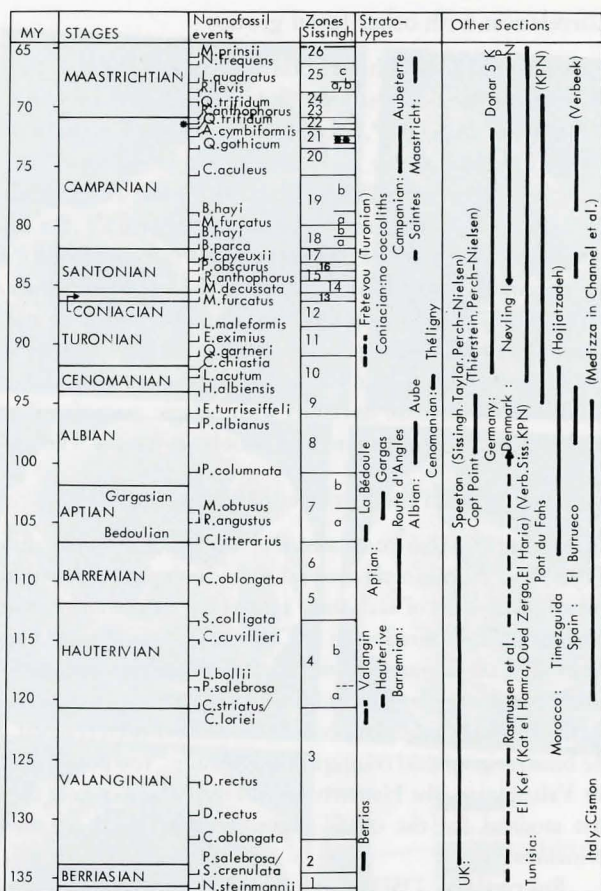


Fig. 4. Correlation of calcareous nannofossil events, stratotypes and other sections. \* = *R. levis*; \*\* = subzone 21b defined by range of *C. arcuatus*.

their coccoliths is unlikely to yield better results. From this must be accepted the fact that boundaries between stages cannot be defined by coccolith zones, but only by common consent, since first order correlation in most cases is impossible, and second or third order correlations are unsatisfactory. The careful inventory of the calcareous nannofossils of more complete Cretaceous sections is therefore essential. It has been undertaken by several authors during the past few years, using both surface outcrop and an offshore material. While the former also allows correlation with the macrofossils, the latter furnishes better correlation between planktonic foraminifera and coccoliths. In Fig. 4 some more complete and expanded sequences studied recently from the North Sea area down to North Africa are also shown. It seems still meaningful to establish and control the sequence of events in various latitudinal and environmental provinces – certainly more meaningful than to question the various published correlations with the stages. For practical purposes and for communication of these findings to other workers, it will, however, be necessary to agree on the correlation of at least a rough framework of the zonation, such as that given by Thierstein (1976), who also correlated the coccolith events with the magnetic anomalies and with foraminifera and calpionellid biohorizons.

### Correlation with other fossil groups

Correlation of coccolith zonations and other zonations are given for the Lower Cretaceous by Thierstein (cephalopods, foraminifera, 1973, and foraminifera and calpionellid biohorizons, 1976), by Sissingh (1977, coccoliths-planktonic foraminifera-stratotypes, p. 57: the two groups being compared at the Kef section, where the foraminifera zonation is derived from an unpublished report by Postuma and 1978) and Perch-Nielsen (1977b, foraminifera). Manivit (1971, table 8) compares the macrofaune, mainly the ammonite zones according to the "Colloque sur le Crétacé supérieur (1959)/inférieur (1963)" to the planktonic foraminifera and the coccolith zones based on material from the Aptian to the Maastrichtian of France. Verbeek (1977) summarizes his previous investigations and the new findings from Spain and Tunisia in presenting the correlation of coccolith and foraminiferal zones with the European stratotypes of the Albian to the Maastrichtian. Van Hinte (1976) presented a correlation of calcareous nannofossil horizons with pelagic macrofossil zones, planktonic foraminifera and calpionellids, benthic forams and radiolaria, for the whole Cretaceous.

### Correlation with the Cretaceous numerical scale

Thierstein (1976) has correlated also the "absolute" time-scale with the nannofossil biohorizons (Fig. 4) and the magnetic reversal scale. Sissingh (1977) pointed out that a plot of the number of formal zonal units of each stage against the approximate duration of each Late Cretaceous stage as proposed by Obradovich & Cobban (1974) indicated a fairly regular zonal subdivision over the entire Late Cretaceous interval. If the same calculations are applied to the Lower Cretaceous, where every stage only includes between half and two zones, it is evident that the stratigraphical resolution that should be possible has not yet been reached. Either the stages are "too long" or the biostratigraphical resolution is generally "too poor" in the Lower Cretaceous, especially in the Valanginian, the Hauterivian and the Albian, where the resolution is well below the one of that attained for the other stages. Further work on these stages should result in further refinement.

Bukry (1974, DSDP Legs 26 and 27; 1975, DSDP Leg 32) already correlated Cretaceous coccolith zones with a numerical time-scale. Van Hinte (1976) in his "Cretaceous time scale" also correlated calcareous nannofossil horizons with a numerical scale based on Thierstein's (1973) and Roth's (1973) zonations; Martini (1976) correlated Campanian and Maastrichtian events with the numerical scale. Their findings were compared in Perch-Nielsen (1977: 702), where minor and major differences are evident: 3 my in the case of the first occurrence of *Q. trifidum*, 4 my with the first occurrence of *A. parvus*; and 6 my with the first occurrence of *L. alatus*. The interval from the first occurrence of *L. alatus* to the first occurrence of *A. parvus* lasted 12 my according to Thierstein (1976) and 22 my according to van Hinte (1976) – the result of different correlations of stage boundaries with the numerical time-scale.

### Correlation of Calcareous Nannofossil Events with the magnetic stratigraphy

Thierstein (1976) correlated coccolith biohorizons with the magnetic reversal scale on the basis of three reference points only: the oldest nannofossils at DSDP Site 20 (latest Maastrichtian overlying anomaly 30), Site 166 (Hauterivian overlying Anomaly M-7/M-8) and Sites 100 and 105 (Oxfordian overlying anomaly M-25). Channel *et al.* (1978) studied the Valanginian to Campanian Cismon section in Northern Italy and there directly correlated coccolith biohorizons with the magnetic stratigraphy. Their results for the Lower Cretaceous are shown



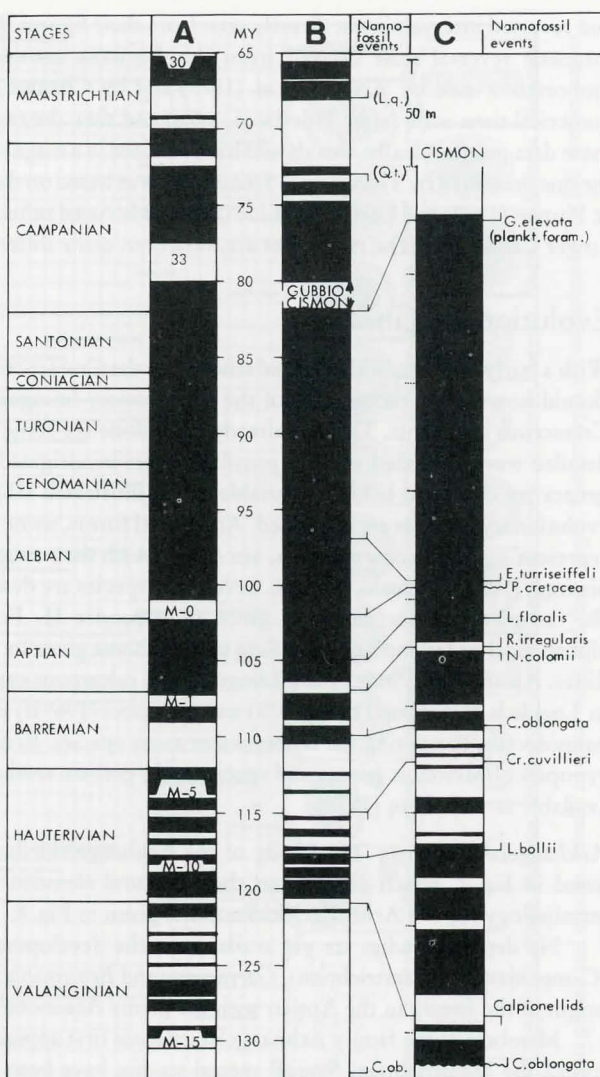


Fig. 5. Stages, magnetic stratigraphy, numeric time-scale and calcareous nannofossil events. A = magnetic anomaly pattern derived from ocean floor. B = magnetic anomaly pattern derived from correlating the pattern measured at Gubbio and Cismone to the numeric time-scale given by Thierstein (1976). C = Polarity pattern measured and coccolith events found at Cismone.

in Fig. 5. For the Upper Cretaceous, both Channel *et al.* (1978) and Alvarez *et al.* (1977), who studied the section at Gubbio, Italy, only show correlation of the magnetic stratigraphy with the planktonic foraminifera biohorizons due to the poor preservation or absence of coccoliths in the limestones at Gubbio (Premoli-Silva 1977; Monechi 1977). Thus the correlation of coccolith biohorizons with the magnetic reversal sequence is inferred from their correlation with the planktonic foraminifera zones (correlation used by Thierstein 1976) for the sequence younger than the Albian.

Alvarez *et al.* (1977) and Channel *et al.* (1978) use the actual thickness of the sections studied as a scale for the presentation of their results. Arthur & Fischer (1977) show, that the sedimentation rates for the various stages studied at Gubbio varied from 2–3 m/my in the Albian shales to 8–13 m/my in more calcareous Upper Cretaceous stages. Thus the duration of normal

and reversed intervals is not directly seen from their figures. Nor is it directly comparable to the magnetic reversal scale derived from the magnetic anomalies of the oceans. In Fig. 5 the biohorizons used by Alvarez *et al.* (1977) and by Channel *et al.* (1978) are correlated to the numerical time-scale (after Thierstein, 1976) and then the reversals are interpolated in between these data points. Ideally, this should have resulted in a magnetic anomaly pattern comparable to the one presented by Thierstein (1976), which was based on the magnetic reversal scale of Larson & Pitman (1972) and Larson & Hilde (1975), who used other absolute ages for the stages of the Lower Cretaceous. The two scales are, however, quite different.

## Evolutionary Lineages

With a fairly well established zonal scheme for the Cretaceous at hand, the emphasis of the work should now be the recognition of the evolutionary lineages, to allow a further subdivision of Cretaceous sediments. This has already been done for some genera and families, but still more detailed work is needed, until all possibilities are investigated. Some families, genera or group of genera are discussed below in variable detail, illustrated range-charts are presented, and a few evolutionary lineages are suggested. Additional forms, some stratigraphically important, others representing little known genera, are shown with their ranges set against the zonal scheme of Sissingh (1977) as a scale, in Fig. 6. Seven new species are described in appendix I and a list with the complete species names is given in appendix II. Families and genera are treated in alphabetical order and not according to the scheme given by Hay (1977), since family concepts differ. An annotated index and bibliography of calcareous nannoplankton up to 1972 is available in Loeblich & Tappan (1966–1973) and Farinacci (1969ff) publishes a catalogue of calcareous nanofossils, presenting the holotypes of many species. Reinhardt (1970a, b, 1971) presented a synopsis of Mesozoic genera and species and a German textbook (1972). An English textbook is available as well: Haq (1978).

*Arkhangelskiellaceae.* The family of the Arkhangelskiellaceae at present includes the genera listed in Fig. 7, which also shows the structural elements that characterize these genera. A terminology for the Arkhangelskiellaceae is given in Fig. 8.

No detailed studies are yet available on the development of the genera *Arkhangelskiella* (Campanian and Maastrichtian), *Gartnerago* and *Broinsonia* (Albian to Maastrichtian) or on the origin of the family in the Aptian with the genus *Acaenolithus* (Aptian to Cenomanian?).

Members of the family Arkhangelskiellaceae first appear in the Aptian and disappear at the top of the Maastrichtian. Several special studies have been made on members of this family. Gartner (1968), Perch-Nielsen (1968), Bukry (1969) and Noël (1969) as well as Roth & Thierstein (1972), Forchheimer (1972) and others published electron microscope and light microscope pictures of forms belonging to this family. Recently Lauer (1975) reported on evolutionary trends in the Arkhangelskiellaceae. Verbeek (1977) showed measurements of *Broinsonia lacunosa* and *Broinsonia parca*, where the width of the margin increases relative to the width of the coccolith, and the total width of the coccolith increases from 5–7 microns in the uppermost Santonian to 9–11 microns in the Lower Campanian; the width then remains about the same through the rest of the range of *B. parca*, reaching an absolute maximum as well as maximum size-differences in the *Quadrum gothicum* Zone of Verbeek (Upper Campanian). Lauer (1975) used the same ratios and the reduction of the number of perforations in the central field to subdivide the Santonian/Campanian sediments of Oman. Verbeek (1977) could not confirm this, due to obliteration of the pores in his material. Also, he did not observe any



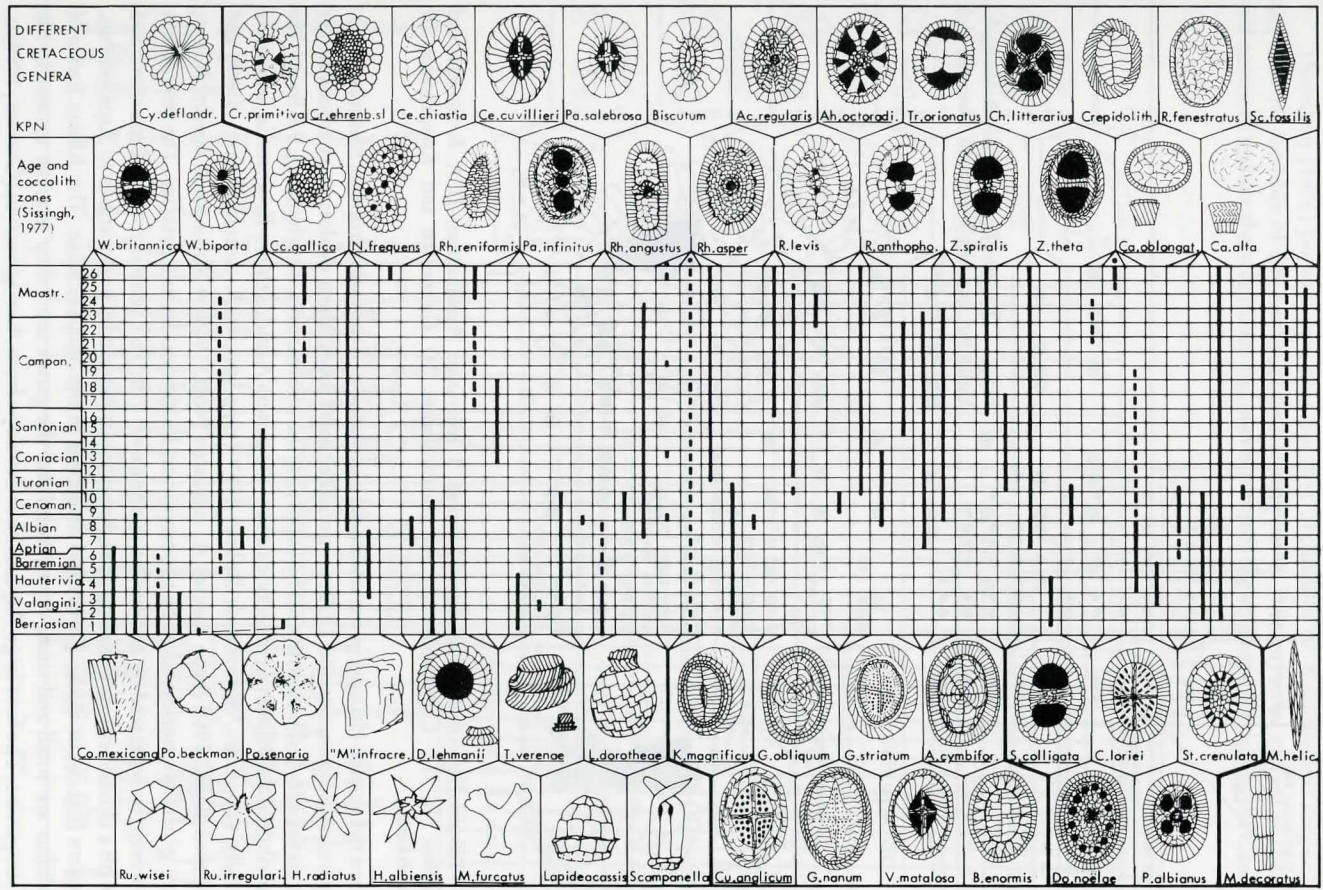


Fig. 6. Important Cretaceous genera and species, usually in distal view, and their ranges. Generotypes are underlined. For full species names see Appendix II

ARKHANGELSKIELLAEE structural elements	view:												
	general	distal	proxim.	side	tiers								
Genera	central cross	central plate	perforations	central net	flange	knob or spine	outer rim	inner rim	zeugoid rim	outer rim	inner rim	?	3 or more
<i>Acaenolithus</i> BLACK	●											?	
<i>Arkhangelskiella</i> VEKSHINA	●	●											?
<i>Aspidolithus</i> NOEL		●	●										●
<i>Broinsonia</i> BUKRY	●												●
<i>Cribricatillus</i> BLACK	●	●											
<i>Crucicribrum</i> BLACK	●	●	●										●
<i>Gartnerago</i> BUKRY		●											●
<i>Kamptnerius</i> DEFLANDRE		●	●										●
<i>Misceomarginatus</i> WIND & WISE	●	●											●

Fig. 7. The genera of the family Arkhangelskiellaceae and the structural elements that characterise them.

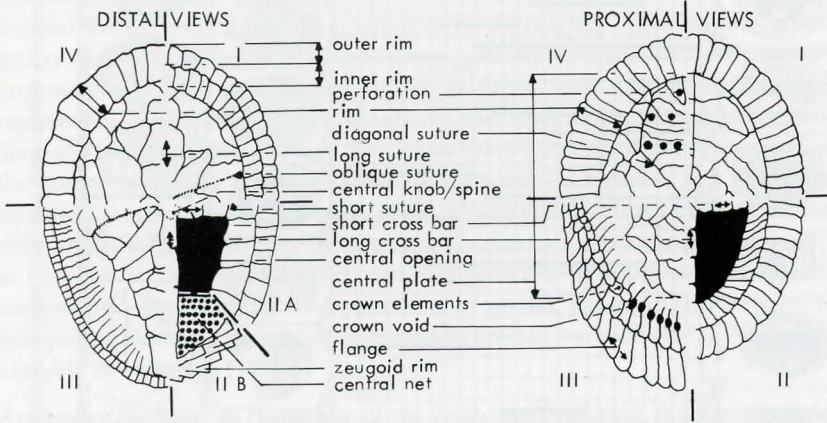


Fig. 8. Terminology of the Arkhangelskiellaceae. I represents *Aspidolithus*, II A *Broinsonia* and *Acaenolithus* (?), II B *Cribricatillus* (?) and *Crucicribrum*, III *Gartnerago* and *Kamptnerius*, IV *Arkhangelskiella*.

significant systematic changes in the unimodal distribution of the ratios from his measurements. Prins (personal communication 1978) on the other hand found these evolutionary trends also in Tunisia and reinforced his comments by supplying the information, on which Fig. 9 is based. He also contributed the following reflections about the genera *Aspidolithus* - *Broinsonia*, which the writer fully supports: "*Broinsonia* Bukry, 1969 (type species *B. dentata* Bukry, 1969) and *Aspidolithus* Noël, 1969 (type species *A. angustus* Noël, 1969 = *Broinsonia bevieri* Bukry, 1969) are generally considered to be synonymous, *Broinsonia* having priority. The two genera can, however, be separated by attributing species with a distinct central cross to *Broinsonia* and forms with a closed centre consisting of eight segments pierced by perforations to *Aspidolithus*. Both genera first occur in the Albian and disappear in the Maastrichtian. The Albian forms of *Aspidolithus* are small and small forms dominate the genus until they become extinct in the Early Campanian. The first large *Aspidolithus* develops from *A. magnacavus* (Gartner, 1968) n. comb. (basonym *Arkhangelskiella magnacava* Gartner, 1968; 38, pl. 18, figs 24, 25; pl. 22, fig. 9) in the Early Campanian. Most forms indicated here as "large" in Fig. 9 were attributed to "*Aspidolithus* ex gr. *parcus*" by Sissingh (1977) and are generally assigned to *A. parcus* (or *B. parca*) by many authors.



Thierstein (1976) pointed out, that the first occurrence of *Kamptnerius magnificus*, an asymmetric member of this family, is time transgressive. It seems to be earliest in the high to mid northern and southern latitudes and moves towards the equator only during the Campanian

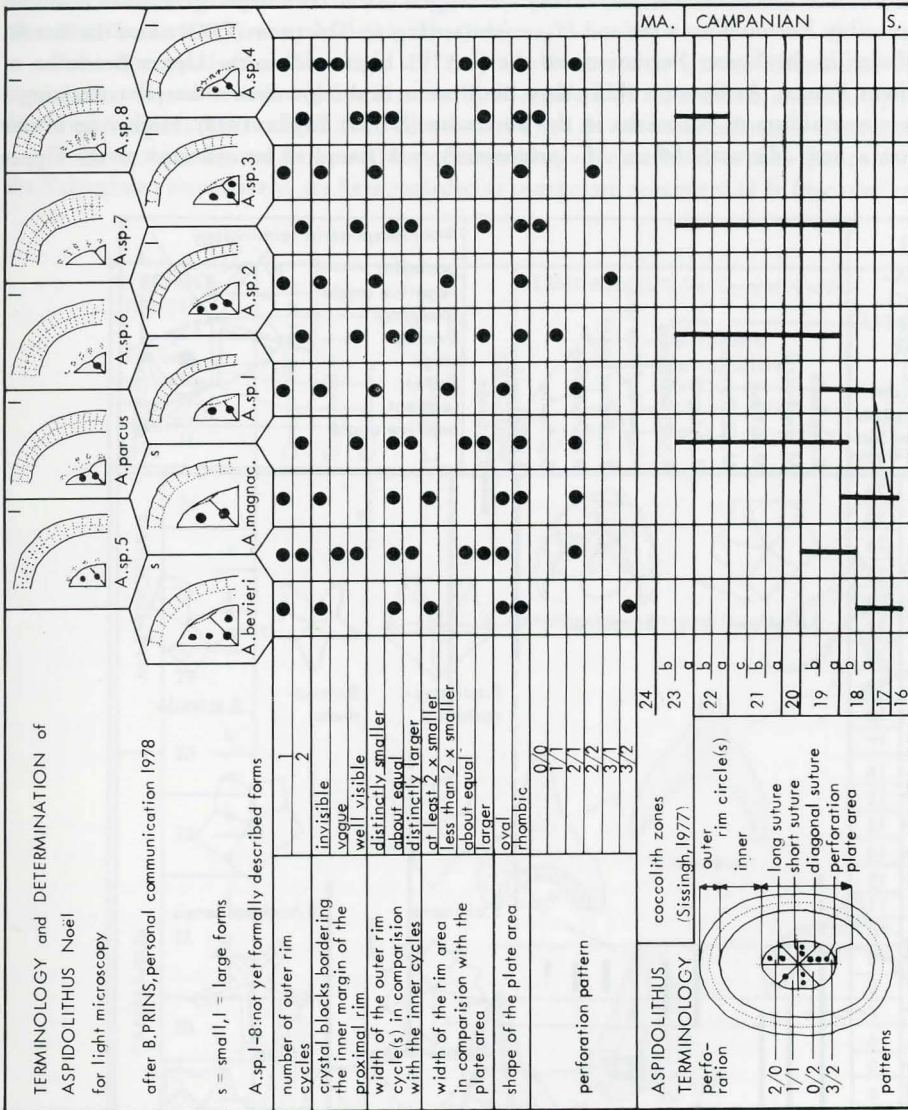


Fig. 9 The genus *Aspidolithus*.

and Maastrichtian. He also suggested, that forms with perforations are well preserved morphotypes, while those without them represent overgrown specimens of the perforated species. For other members of this family see Fig. 6.

*Braarudosphaera* and *Micrantholithus*. The oldest typical forms of *Braarudosphaera* and *Micrantholithus* are reported from the lowermost Cretaceous, with the exception of older occurrences of "*B. bigelowii*" mentioned by Noël (1956) from the Portlandian of Algeria. In samples with well preserved *Polycostella senaria* and *Hexalithus*-like forms, B. Prins and S. van Heck (written communication 1978) observed intermediate specimens between the above mentioned taxa and *Micrantholithus*. They also suggest that *P. beckmannii* gave rise to *P. senaria* and possibly *Rucinolithus wisei* and *Hayesites* (see Fig. 6). Thierstein (1973) noted the first *M. hoschulzii* in the Lower Berriasian and the first "*B. bigelowii*" in the Upper Berriasian of Southern France. At Speeton (UK) they both occur in the lowermost sample containing a diverse assemblage of coccoliths in the Berriasian (D 7D; Taylor 1978). Higher up in this section a new *Micrantholithus*, *M. speetonensis*, was found to be confined to the Upper

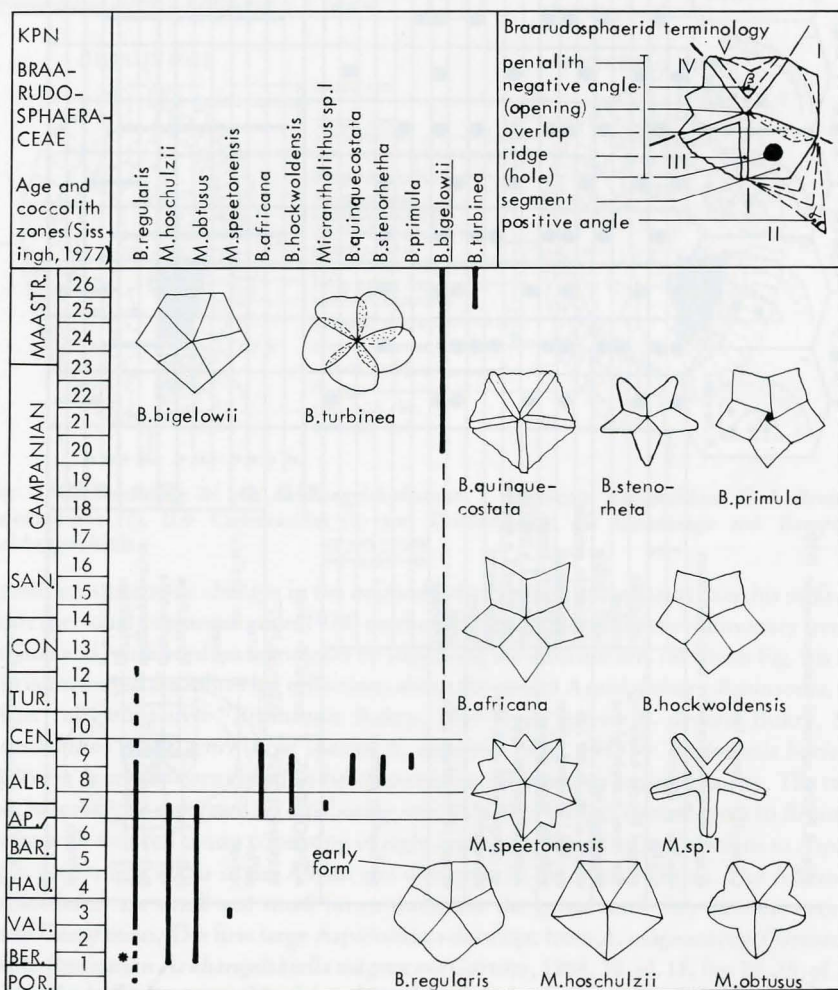


Fig. 10 Terminology and stratigraphical distribution of the species of Braarudosphaeraceae. I-V represent the different species. \* = earliest *B. regularis* uncertain.



Valanginian (D 4A through D 2E). The next members of this group are assigned to *Braarudosphaera* and occur in the Upper Aptian and Albian. *M. hoschulzii* and *M. obtusus* disappear at the end of the Aptian, where their niche seems to have been taken over successfully by the new species of *Braarudosphaera* and by *Micrantholithus* sp. 1, a form similar to the Tertiary *M. vesper* (see Fig. 10). From the Cenomanian on, occasional occurrences of *B. regularis* and later *B. bigelowii* constitute the link to the Maastrichtian/Danian *B. turbinea* and the numerous Lower Tertiary braarudosphaerids.

Prins (personal communication 1977) pointed out, that Lower Cretaceous forms commonly referred to as *B. bigelowii*, are really *B. regularis* or allied forms, and that typical *B. bigelowii* with asymmetrical pentaliths as in the holotype, do not occur before the Cenomanian.

*B. bigelowii imbricata* Bukry and *B. imbricata* Manivit from the Santonian-Campanian and the Valanginian respectively, are here regarded as overgrown specimens of *B. bigelowii* and *B.*

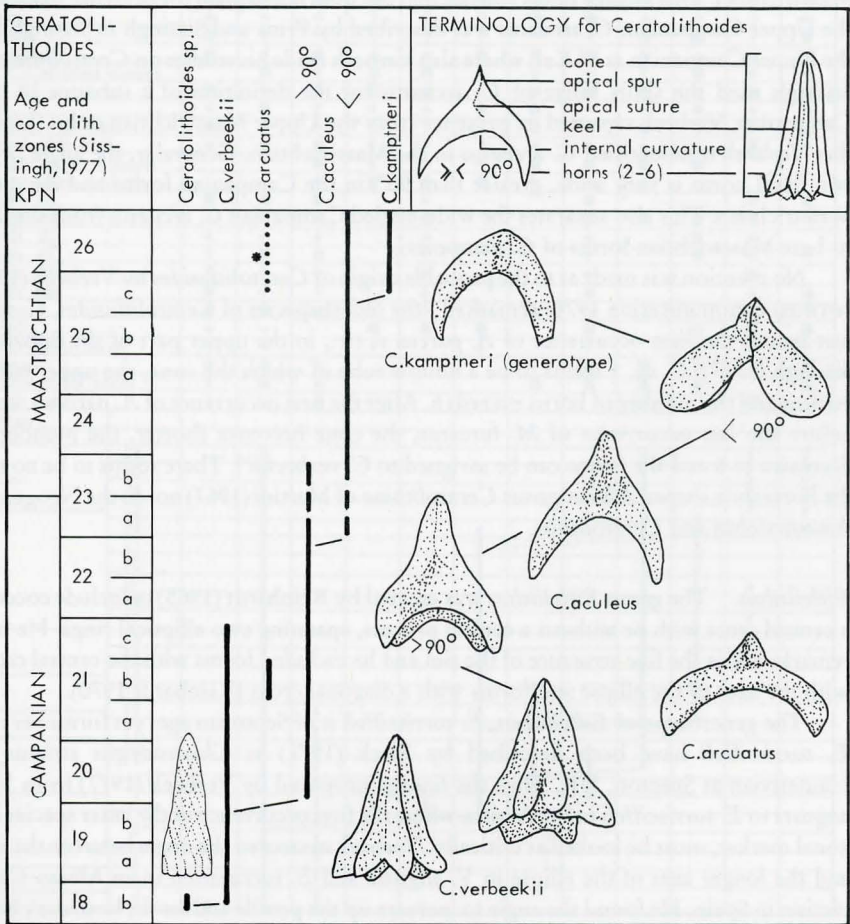


Fig. 11 Terminology and stratigraphical distribution of the species of *Ceratolithoides*. \* = Maastrichtian range (Verbeek 1977) questionable.

*regularis* respectively. *B. hexalitha* Vekshina and *B. tetralitha* Vekshina are considered to belong to other genera of the Maastrichtian, since they have six and four sectors respectively. *M. lidiae* Gorka is considered to be an eroded specimen of *B. bigelowii* from the Maastrichtian. *B. gartneri* Filewicz, Wind & Wise and *B. minuta* Filewicz, Wind & Wise are junior synonyms of *B. quinquecostata* and *B. stenorhetha*, respectively. An opening is only found in *B. primula*, where the sutures between the segments run tangentially instead of radially as in most other species of the family. Overlapping segments are characteristic for *B. turbinea* only and holes are only found in *Pemma*, a Tertiary genus of the family.

*Ceratolithoides*. Four species are currently assigned to *Ceratolithoides*: *C. aculeus*, *C. arcuatus*, *C. kamptneri* and *C. verbeekii* (Fig. 11). Verbeek (1977) discussed their evolution from the early forms of *Ceratolithoides*, with six short, basal horns and long, apical elements in the Early Campanian to forms with two long, arched horns and an apical point only, in the Late Maastrichtian. This lineage looks convincing, but does not explain the presence of *C. arcuatus* in the Upper Campanian. *C. arcuatus* was described by Prins and Sissingh in Sissingh 1977 from the Upper Campanian at El Kef, where also Verbeek made his studies on *Ceratolithoides*. While Sissingh used the short range of *C. arcuatus* for the definition of a subzone in the Upper Campanian, Verbeek reported its presence from the Upper Maastrichtian only. It seems likely that Verbeek misidentified *C. arcuatus* in the Maastrichtian. Generally, the angle between the two basal horns is very wide, greater than 90°, in the Campanian forms and decreases in the Maastrichtian. This also separates the wide-angled Campanian *C. arcuatus* from similar Middle to Late Maastrichtian forms of *C. kamptneri*.

No mention was made as to the probable origin of *Ceratolithoides* by Verbeek (1977). Prins (written communication 1978) remarked "the oldest species of *Ceratolithoides*, *C. sp. 1*, occur just before the first occurrence of *A. parvus* s. str., in the upper part of the Subzone 18b of Sissingh (1977). *C. sp. 1* seems to be a hollow tube of which the cone, the upper part, is often broken and the number of horns exceeds 6. After the first occurrence of *A. parvus* s. str., but still before the last occurrence of *M. furcatus*, the cone becomes shorter, the number of horns decreases to 6 and the forms can be assigned to *C. verbeekii*". There seems to be no relation to the horseshoe shaped Albian genus *Ceratolithina* of Martini (1967) nor to the Neogene forms of *Amaurolithus* and *Ceratolithus*.

*Eiffellithus*. The genus *Eiffellithus* was erected by Reinhardt (1965) to include coccoliths with a central cross with or without a central process, spanning two elliptical rings. He later added remarks about the fine structure of the rim and he included forms with the central cross aligned with the axes of the ellipse and forms with a diagonal cross (Reinhardt 1970).

The generotype of *Eiffellithus*, *E. turriseiffeli* is of Senonian age, yet forms very similar to *E. turriseiffeli* have been described by Black (1971) as *Chiasozygus striatus* from the Hauterivian at Speeton, UK. Thus the lineage proposed by Verbeek (1977) from *Vekshinella angusta* to *E. turriseiffeli* in the Albian, where the first occurrence of the latter species is used as a zonal marker, must be looked at critically. Verbeek measured the angle between the longer bars and the longer axes of the ellipse in *V. angusta* and *E. turriseiffeli* in an Albian-Cenomanian section in Spain. He found the angle to increase up the profile and set the boundary between the two species at a jump from a mean value of 14° to a mean value of 25°, due to a hiatus in the section. Below, no angle was larger than 20°, above none smaller than 20°, thus the boundary could conveniently be set at 20°. Verbeek also noted a gradual closing of the central area, but



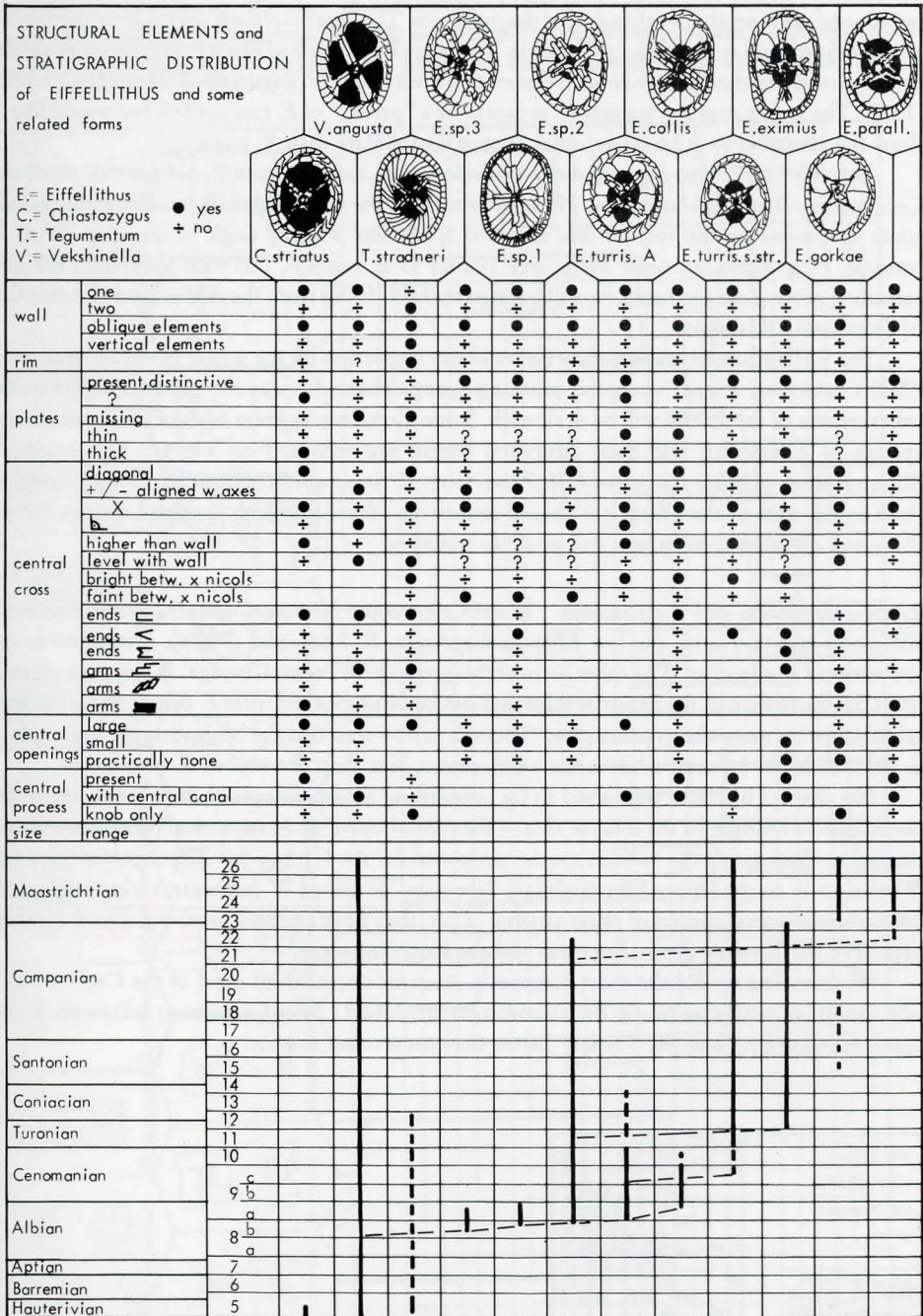


Fig. 12 Eiffellithus and related forms: stratigraphical distribution and structural elements.

mentioned nothing about a thinning of the outer rim. The latter is always very thin in any species of *Eiffellithus* and is also thin in *C. striata*. The latter has a circle of blocky elements very similar to those of *E. turriseiffeli*, while such elements are missing in *V. angusta* as illustrated by Verbeek (1977). The writer does not suggest *C. striata* to be a "parent" of *E. turriseiffeli*, but would like to draw the attention to at least one other ancestral candidate than *V. angusta*.

Verbeek (1977) also suggested the evolution of *E. eximius* from *E. turriseiffeli* above the Cenomanian-Turonian boundary. He again measured the same angle and found it to decrease in some specimens up the section. He assigned specimens with an angle of less than 20° to *E. eximius*. Here again, an older form very similar to *E. eximius*, but with a different rim and including more plate segments, was illustrated by Hill (1976) from the Albian and Cenomanian of Texas and Oklahoma.

The Eiffellithaceae are currently under closer inspection by the writer in the context of the "Mid Cretaceous Event" coccolith working group. There, besides the genus *Eiffellithus*, the other genera of the family will be dealt with. Some Cretaceous genera of the Eiffellithaceae and species of *Eiffellithus* and their structural details are recorded on Fig. 12. This enables a differentiation of other species of *Eiffellithus* from *E. turriseiffeli* (oblique bars) and *E. eximius* (bars in the axes of the ellipse); it should encourage others to search for these species, record them and establish their ranges and possible relations.

*Ellipsagelosphaera* and *Watznaueria*. In the Cretaceous, *Ellipsagelosphaera* and *Watznaueria* still occur together until the last *Ellipsagelosphaera*, *E. britannica* (Fig. 6), disappears in the lowermost Cenomanian. The other form of this group with a central bridge, *W. biporta*, extends from the Barremian to the Maastrichtian and can be distinguished from *E. britannica* in the light microscope by using the gypsum plate. There, it can be seen that the bridge has the same colour as the wall in *W. biporta*, while it has a different colour than the wall in *E. britannica*.

No attempt has been published so far concerning measurements of the overall size of the coccoliths or changes in the relative size of the central opening. Systematical measurements are needed to distinguish the various species proposed for the Cretaceous *Ellipsagelosphaera* and *Watznaueria*. In the Upper Maastrichtian, "aberrant" forms of *W. barnesae*, a longranging and often very common species of *Watznaueria*, occur; they have a double proximal shield, a feature typical of the Tertiary genus *Ericsonia* and the Coccolithaceae.

*W. barnesae*, by far the most diagenesis-resistant coccolith of most of the Cretaceous, is often found in nearly monospecific assemblages in lithified Lower Cretaceous sediments. It also survives reworking into the Tertiary better than most other species.

EPROLITHUS, LITHASTRINUS and ? related genera	wall elements			central diaphragm					
	5	9	8 - 20	none	small	large	"proximal" "equatorial"	radial segments	overlapping segm.
Bukryaster PRINS	●			●					
Eprolithus STOVER				●	●	●	●	●	?
Hexalithus GARDET		●							
Hexangulolithus BUKRY			?		?		●		●
Lithastrinus STRADNER	●	●		?			●	?	?
Polycyclolithus FORCHH.				●	●	●	●	●	●
Radialithus STOVER				●		●	●	●	
Rhombogyrus BLACK							●		●
Rucinolithus STOVER	●	●		●					

Fig. 13 *Eprolithus*, *Lithastrinus* and ? related genera and their characteristics.



*Eprolithus*, *Lithastrinus*, *Micula*. In the context of the "Mid Cretaceous Events" project, the group of *Eprolithus-Lithastrinus* (Fig. 13) and *Eprolithus-Quadrum-Micula* is at present under special investigation by B. Prins, who, however, kindly furnished the information already

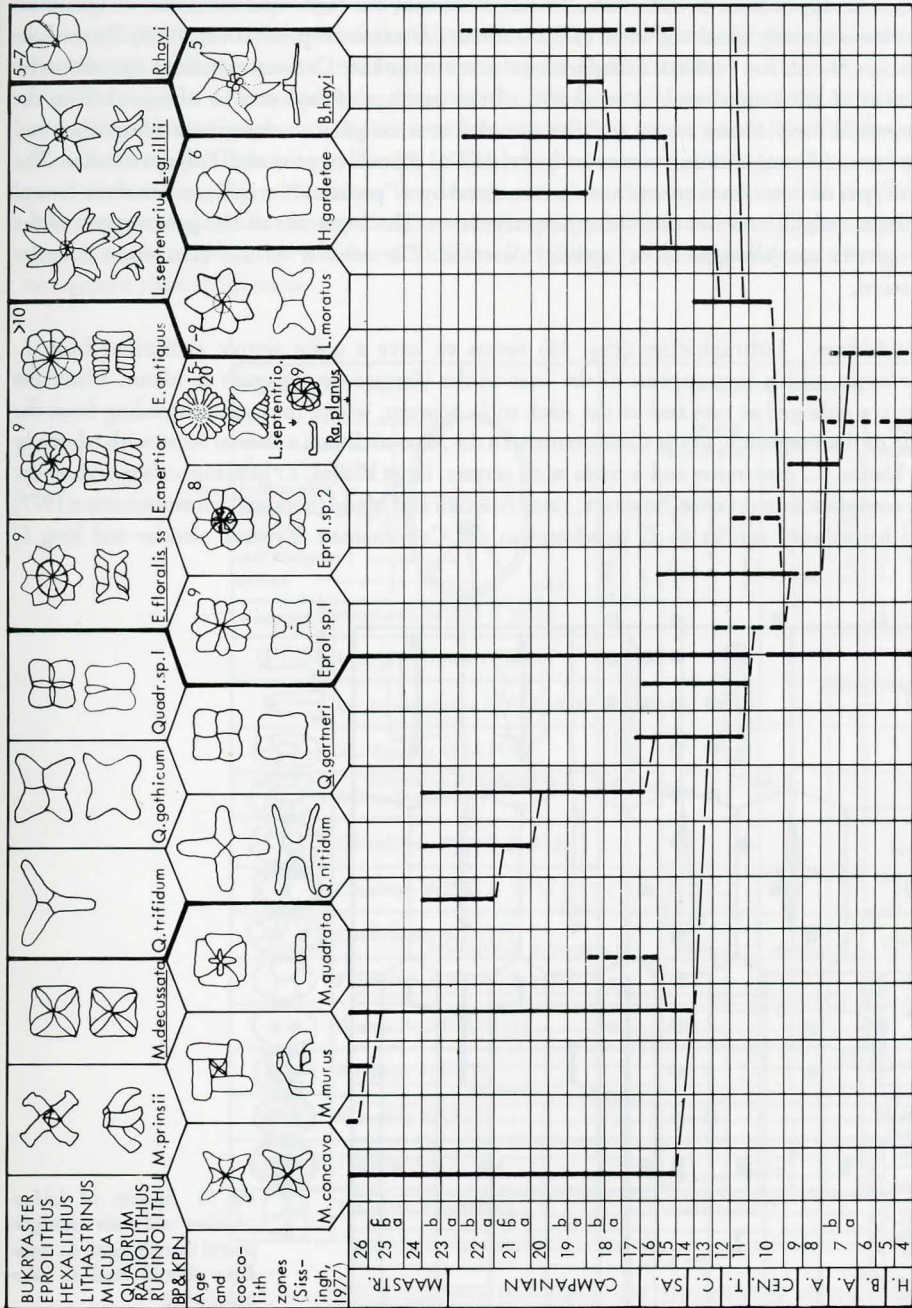


Fig. 14 Species of *Eprolithus*, *Lithastrinus*, *Micula* and ? related genera and their stratigraphical distribution.

available for the compilation of Fig. 14 (personal communication 1978). Prins suggests the evolution of *Eprolithus* from forms with more than 10 rays in the Hauterivian (*E. antiquus* n. sp., see appendix I) to forms with fewer rays in the Aptian through the Cenomanian. *E. floralis* and related species also show a narrowing of the equatorial plane, giving the specimens a spindle-like appearance in side view. In the Turonian, the first representatives of *Quadrum* evolve from a nearly quadratic form of *Eprolithus* (*Lithastrinus* sp. of Stover, 1966). By the Late Coniacian *Micula* has evolved. *Lithastrinus* evolves in the Late Cenomanian from *Eprolithus* by reduction of the central area; a reduction of the number of rays can be observed from the seven-armed early forms to six and five-rayed forms assigned to the genera *Hexalithus* and *Bukryaster*. *Hexangulolithus* seems to be related to *Rhombogyrus* and *Polycyclolithus*. The generotypes of these three genera are characterized by a "proximal" emplacement of the central diaphragm, which consists of overlapping segments. The segments of the generotypes of the other genera are (thought to be) radially oriented. The validity of this distinction is under discussion.

**Lithraphidites.** Lithraphidites (Fig. 15) seems to have a quite simple evolution: from *L. carniolensis*, which first appears at the base of the Cretaceous, through *L. alatus*, where the blades are enlarged at one end of the stick to *L. acutum*, where they are protruding from the middle of the long stick, in the Cenomanian. In the Maastrichtian, a shorter form with relatively wide blades, *L. quadratus* and a form with serrate, large blades, *L. grossopectinatus* develop. Some complications do arise, however, since Afejuku and Medd (personal communication 1977) found forms very similar to *L. quadratus* in the Cenomanian. Typical, slender and long *L.*

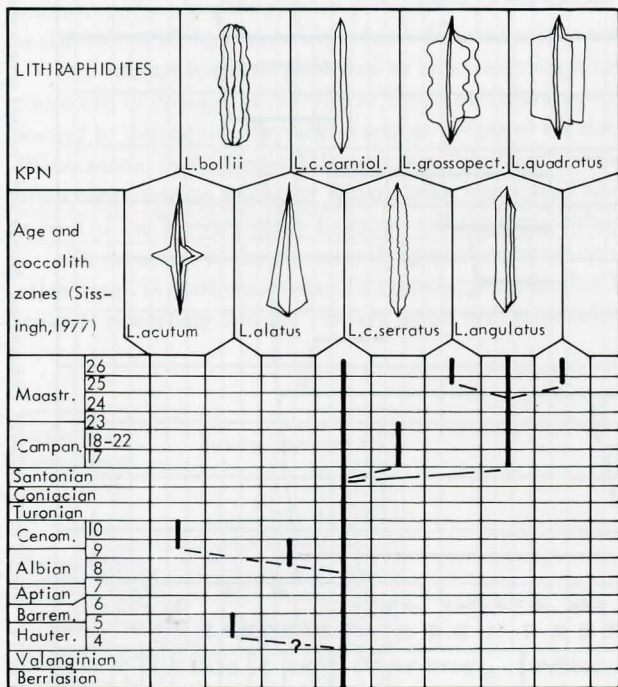


Fig. 15 Species of *Lithraphidites* and their stratigraphical distribution. *L. angulatus* should read *L. praequadratus*.



*carniolensis* can be assigned to *L. carniolensis carniolensis*, while forms between *L. carniolensis* and *L. quadratus* can be assigned to *L. praequadratus*. Manivit (1971) described a form similar to *L. carniolensis*, with a small, round base as *Rhabdolithes moeslensis*. The latter and *Rhabdolithes aquitanicus*, also described by Manivit (1971) and *L. serratus* described by Shumenko (1970) are here regarded as the subspecies *L. carniolensis serratus*. There appears to be a trend to serrated blades from the Albian onwards, reaching its most extreme forms, when also the size of the blades is a maximum in the Upper Maastrichtian.

The origin of *Lithraphidites* is unknown, the first *L. carniolensis* appearing quite suddenly at the base of the Cretaceous. It seems to have no relation to the genus *Pseudolithraphidites* described from the Tithonian by Keupp (1976), which consists of at least four long, cylindrical, parallel elements. No connections are known either to the similar forms of the Tertiary: *Pseudotriquetrorhabdulus* in the Eocene and *Triquetrorhabdulus* in the Oligocene/Miocene. Also, it seems questionable whether *L. bollii* really belongs to *Lithraphidites*, or whether it is an overgrown rhabdolith stem.

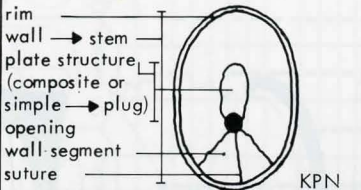














HOLOCOCCOLITHS		structural elements										
		plate structure		openings			wall segments					
		rim (thin)	wall (wide)	one element	composite	1	2	3 or more	1-3	4-5	6 or more	
	Acuturris WIND & WISE	●	●			●				●		
	Isocrystallithus VERBEEK	●	●		●						?	
	Lucianorhabdus DEFLANDRE	●	●	●	●						●	
	Multipartis RISATTI			●	●							●
	Munarinus RISATTI			●	●							●
	Okkolithus WIND & WISE			●		●						●
	Orastrum WIND & WISE	●					●				●	
	Ottavianus RISATTI			●				●				●
	Phanulithus WIND & WISE	●		●							●	
	Pharus WIND & WISE	●		●				●		●		
	Ramsaya RISATTI			●	?	?		●				●
	Russellia RISATTI			●	●							●
	Tegumentum? sp.1	?	●	●		●			●			?
	Tetralithus GARDET	"wastebasket"										

Fig. 16 Holococcolithic genera, their terminology and characteristic structural elements.

*Lucianorhabdus* and related forms. Gardet (1955) described *Tetralithus pyramidus* n. gen. n. sp., a simple rectangular plate divided into four segments, from the Miocene of Algeria. Subsequently, many Cretaceous forms, holococcoliths and heterococcoliths alike, were assigned to *Tetralithus*. Since the genotype of the genus is Miocene, it seemed preferable to have another genus for the Cretaceous forms. Thus Wind & Wise (1977) erected the genus *Phanulithus*, taking *Tetralithus obscurus* Deflandre as genotype. Later in 1977, Prins & Sissingh (*in* Sissingh, 1977) erected *Calculites* on the same species for "heterococcoliths composed of a narrow rim and a broad wall consisting of a limited number of calcite blocks, but lacking a plate structure", thus creating a junior synonym. *Phanulithus* is distinguished from the

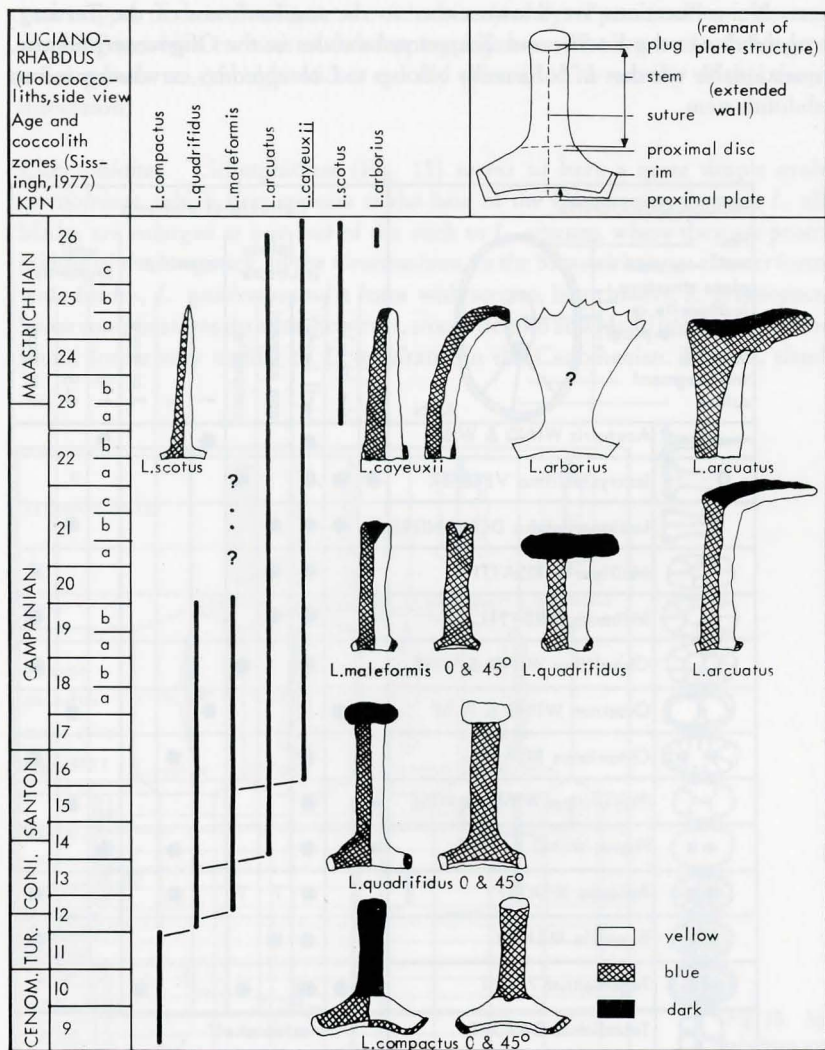


Fig. 17 Stratigraphical distribution, evolution and terminology of *Lucianorhabdus*. Sideviews in the lightmicroscope, crossed nicols and gypsum red I plate inserted.



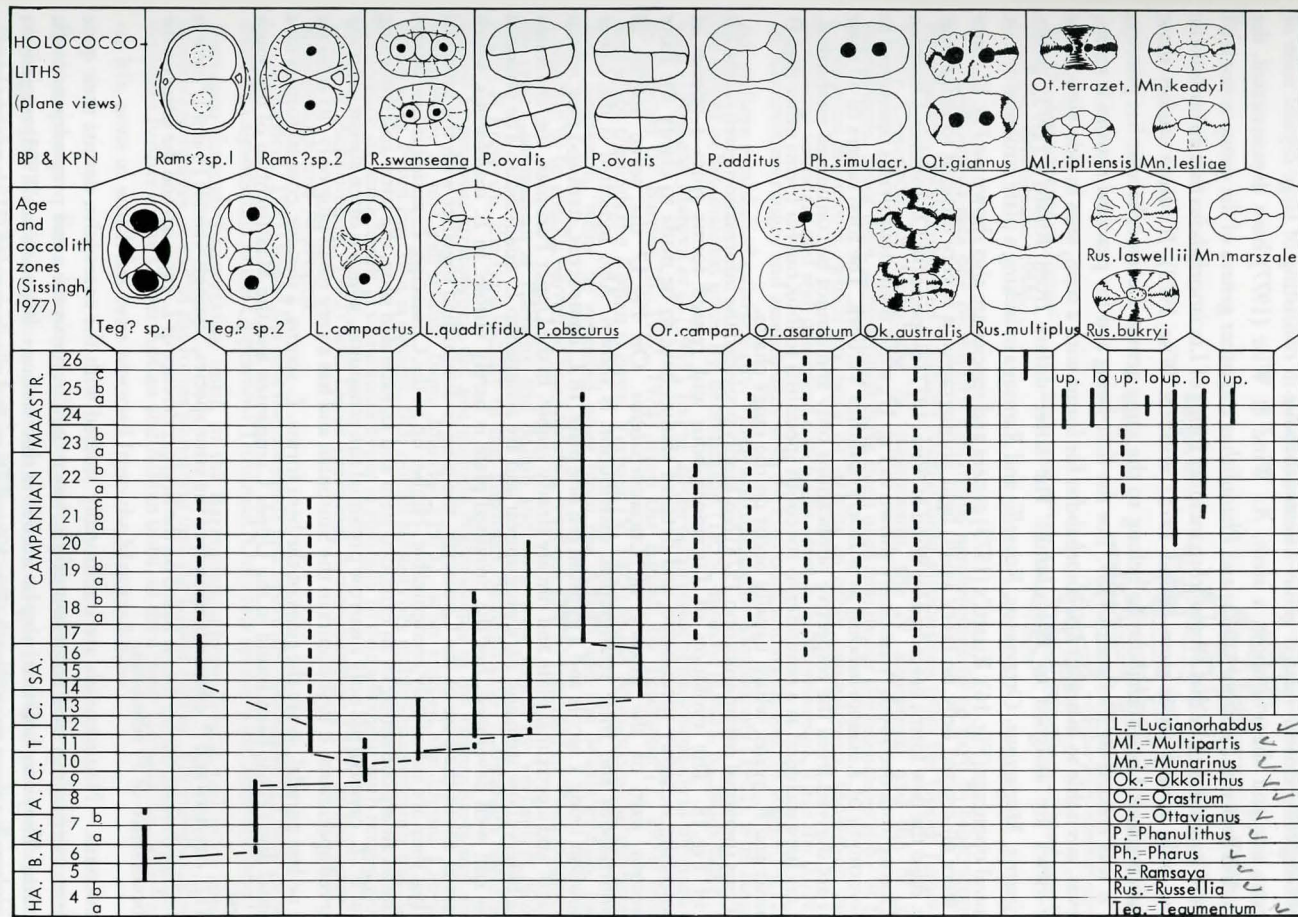


Fig. 18 Holococcoliths in plane view. Ranges in right half of figure are very tentative.

morphologically closely related genus *Lucianorhabdus* in consisting of large crystal units of different size and shape without a stem. As Wind & Wise (1977) have demonstrated, the distinction between *Lucianorhabdus* and *Phanulithus* and other genera of the group is not at all clear and it could well be that *Phanulithus* includes forms of *Lucianorhabdus* that do not have or possess only a very short stem (Wind 1975; Wind & Wise 1978). If future studies show *Phanulithus* and *Lucianorhabdus* to belong to the same genus, *Lucianorhabdus* has priority, since it was erected by Deflandre 1959. For the time being and for practical reasons it seems, however, advisable to maintain *Lucianorhabdus* for forms with a stem, seen in side-view, while plane-views are assigned to *Phanulithus*. The latter differs from Risatti's (1973) genera *Multipartis*, *Munarinus*, *Ottavianus*, *Russellia* and *Ramsaya* in lacking a plate structure or a set of central openings (Fig. 16). Risatti's (1973) genera and species are also shown on Fig. 17. Since they were all erected only on (very small) light photographs, it is very difficult to judge their value. Also the new forms described by Wind & Wise (1977) as species of *Okkolithus*, *Orastrum* and *Pharus* from the South Atlantic are shown in Fig. 17, while their *Acuturris* is considered to be a synonym of *Lucianorhabdus*, as is *Isocrystallithus* Verbeek. The total ranges of all these forms are derived from the respective publications only and cannot be considered established. They are here included as a reminder to coccolith specialists to look out for forms other than *P. obscurus* and *P. ovalis*, which usually occur on the range charts.

Prins (personal communication 1978) has kindly provided the information given on the left side of Fig. 18. The evolution of *Lucianorhabdus* and related forms from a species of *Tegumentum* is highly speculative, and detailed studies have to be made to clarify the Early Cretaceous part of the history of *Lucianorhabdus*. On Fig. 17 the seven species of *Lucianorhabdus* and their stratigraphic distribution is shown. Also indicated is the colour distribution using x nicols and a gypsum red one plate. In *L. compactus*, stem and plug remain dark at 0° and a proximal plate and rim are clearly visible. In the Upper Turonian, the first forms with a blue/yellow stem and dark plug appear and are assigned to *L. quadrifidus*. The proximal disc is still well developed, but the proximal plate is barely visible. In *L. maleformis*, which appears at about the base of the Coniacian, the plug is diminished together with the proximal disc, but they are still clearly recognizable. Higher up in the Coniacian, *L. arcuatus* first occurs and shows an arc consisting of an extended stem and an extended plug, the latter still remaining dark at 0°. *L. cayeuxii* has only a narrow proximal rim remaining, which is often absent in poorly preserved specimens; it first occurs in the Santonian and has a very small plug only. Its sides are more or less parallel, as are the sides of the bent forms. *L. scotus*, a slender, conical form with a proximal disc (?) has been found in the Upper Campanian and the Maastrichtian of the South Atlantic.

If *L. cayeuxii* and *P. obscurus* are indeed the same species, Sissingh's zones 16 and 17 have to be combined, since the former is based on the first occurrence of *L. cayeuxii* and the latter on the first occurrence of *P. obscurus*.

*Nannoconus*. Nannoconids are traditionally studied with the coccoliths, despite their quite different morphology and unknown origin, since they occur in the same preparations as the coccoliths. They can, however, also be studied in thin sections. Brönnimann (1955) suggested a terminology for these nannofossils (Fig. 19) and Deres & Acheriteguy (1972) proposed a key for the determination of the morphotypes of the nannoconids and illustrated over 50 Lower Cretaceous forms, most of which have not yet been formally described as species. Aubry (1974) discussed – and rejected – the species concept of the few forms occurring in the French chalk (Turonian – Campanian).



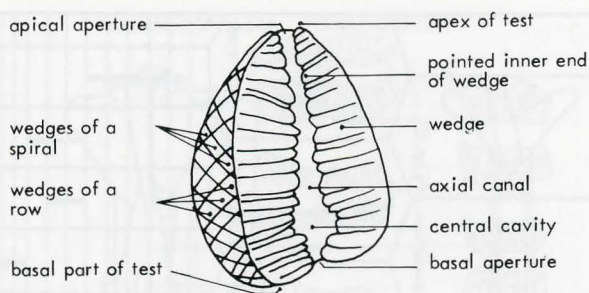


Fig. 19 Terminology of *Nannoconus* after Brönnimann (1955).

*Nannoconus* was one of the first calcareous nannofossils to be used in biostratigraphy. Brönnimann (1955) suggested 3 distinct *Nannoconus* associations from the Upper Jurassic and Lower Cretaceous of Cuba: the *N. steinmannii*, the *N. kamptneri* and the *N. truittii* assemblages. Since then, nannoconids have been used mainly for the biostratigraphy of Lower Cretaceous sediments, which are poor or lacking in other nannofossils. However, samples containing abundant and well preserved coccoliths often lack *Nannoconus*. Thus the correlation of *Nannoconus* ranges and assemblages with the coccolith zonations and the stages (Fig. 20) has not yet been established satisfactorily. This was discussed by Moshkovitz (1972), who compared the ranges of associations given by Brönnimann (1955), Bouché (1963a, b), Baldi-Beke (1964), Geel (1966) and Manivit *et al.* (1969). In Fig. 20 the occurrence of nannoconids in the stratotypes as reported by Barrier (B, 1977, 1978) from the Aptian, by Thierstein (T, 1973) from the Berriasian through the Aptian is given. Verbeek (V, 1977) found *Nannoconus* in the Santonian and Campanian, while he reported none from the Albian and the Maastrichtian, and the Coniacian to be totally barren of nannofossils. Verbeek (1976) reported no *Nannoconus* from the type Cenomanian at Théligny and Ballon and none were found by Verbeek & Wonders (1976) at Frêtevou, the type locality of the *Turonian*. Sissingh (1977), although reporting on several Cretaceous stratotypes, did not include *Nannoconus* in his range charts and detailed information is not extractable from Manivit (1971), who studied the Upper Cretaceous stratotypes. From Fig. 20 it is evident, that not all stratotypes include nannoconids and that the occurrence of some forms at some stratotypes is strongly in disagreement with ranges given by Deres & Acheriteguy (1972) and Deres (personal communication 1977) in the cases of *N. brönnimannii* and *N. truittii*.

Thierstein (1975) found the first nannoconids just below the *Berriasian* at Pomet, a section dated by calpionellids as the Uppermost Tithonian. Only few species and forms are found in the *Berriasian* through *Hauterivian*, until, in the Barremian, a more diverse and more abundant assemblage evolves, many of the forms persisting into the Lower Aptian. The number of species decreases further in the Upper Aptian and Albian until, in the Upper Cretaceous, only 4 species are left, none of which has been reported from the Maastrichtian.

*Prediscosphaera*. For a long time, all more or less elliptical coccoliths with a low number of wall elements – 16 to be precise – and central cross were assigned to "*Coccolithophora cretacea*" Arkhangelsky, 1912. Since then, the species has been assigned to different genera, the established one being *Prediscosphaera*, which was erected 1959 by Vekshina. The first separation came by the introduction of another name – *P. spinosa* – for forms with a cross aligned with the axes of the ellipse by Bramlette & Martini, 1964. Since then, more than a dozen species have been described, but in most range-charts, only *P. cretacea* and *P. spinosa* are present. And so, even

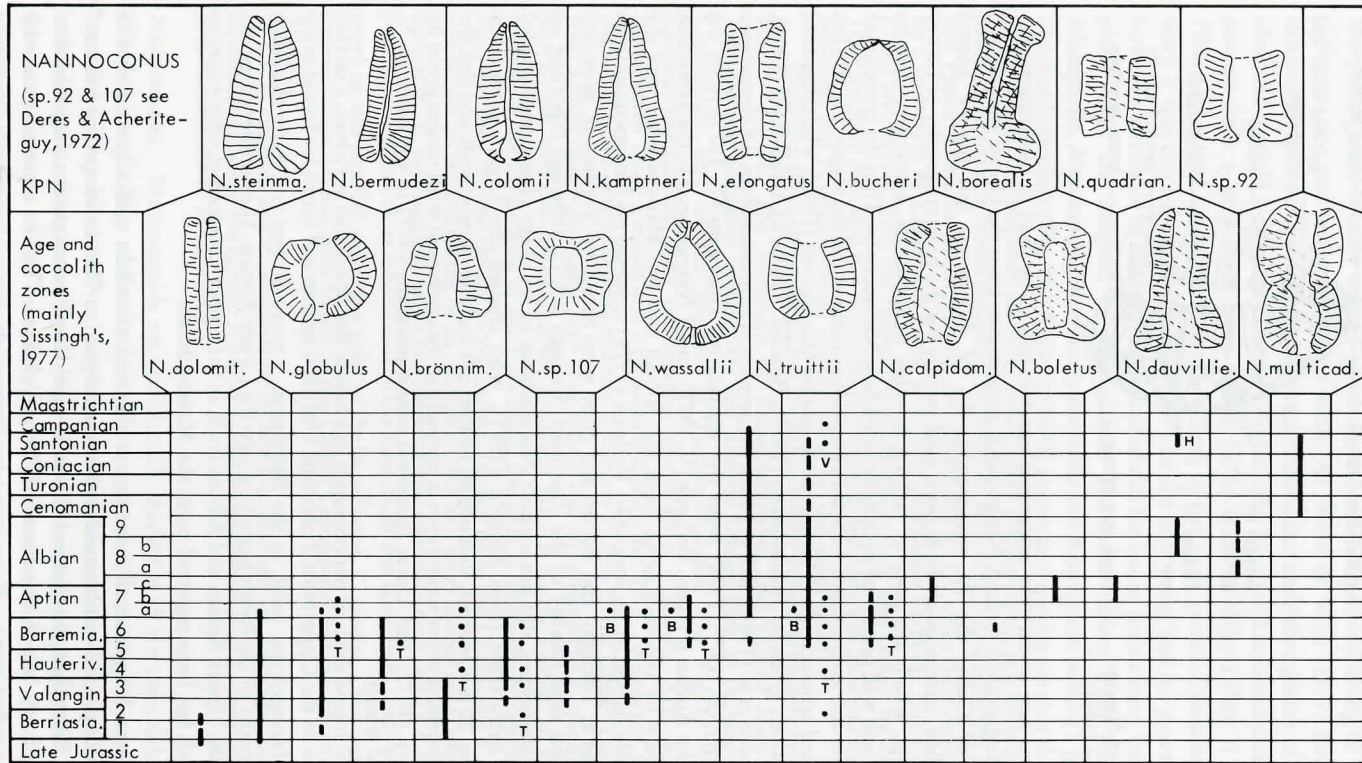


Fig. 20 Selected species of *Nannoconus* and their stratigraphic distribution. B, T, V see text. H = holotype.



PREDISCOSPHAERA TERMINOLOGY

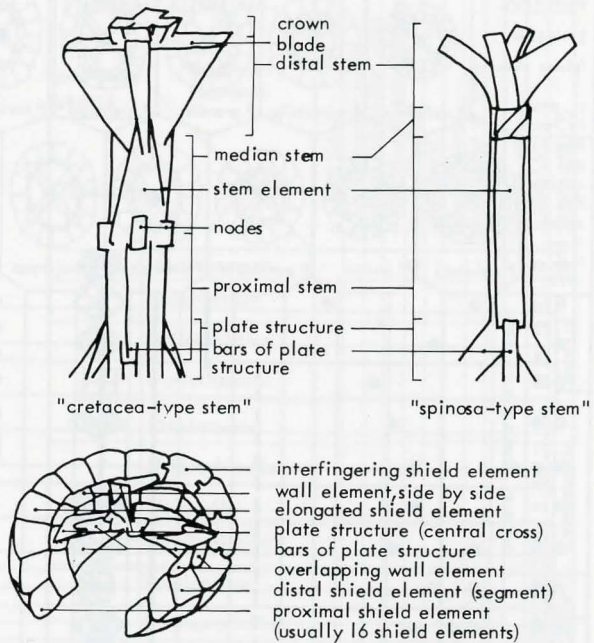


Fig. 21 Terminology of *Prediscosphaera*.

though many different forms are described, little has been published as to the ranges of them. The species of *Prediscosphaera* are distinguished by the orientation of the central cross, by the relative width of the two circles of elements, (Fig. 21), their shape (round/elliptic) and to a certain extent by their size. Unlike in other genera, where the number of elements in the wall increases with the size of the specimen, *Prediscosphaera* has always 16 elements. Fig. 22 shows the stratigraphic distribution of most species of *Prediscosphaera*. It is strongly suggested here, that more attention be given to this genus, especially in the study of well preserved material derived from long sections and in the Albian/Cenomanian, where its species first occur and evolve rapidly.

It is generally accepted, that the first elliptical forms of *Prediscosphaera* appear in the Upper Aptian. The first round forms are small and occur above the Aptian/Albian boundary. Their two cycles of the wall are of about equal width. With time, they become larger and the width of the outer circle increases, while the inner circle narrows or stays the same. By the Turonian, the forms become more elliptical, but still show a relatively narrow inner circle (*P. intercisa*). *P. cretacea*, with a broad inner circle, only evolves in the Lower Campanian and the extremely large forms of *P. grandis* have only been observed in the Maastrichtian (and Upper Campanian?) so far. *P. honjoi* and *P. bukryi* are small forms with relatively small central areas and a diagonal and axes-aligned central cross respectively. While *P. spinosa* has a relatively narrow inner circle of elements, this circle is broader in *P. arkhangelskyi* and consists of overlapping elements in *P. stoveri*, which also is smaller. The elements of the distal shield are wedge-shaped in *P. bukryi* while they are trapezoid in most other forms of *Prediscosphaera*. *P. rhombica*, with its more complicated central structure, might even belong to another genus (*Sollasites*) according to

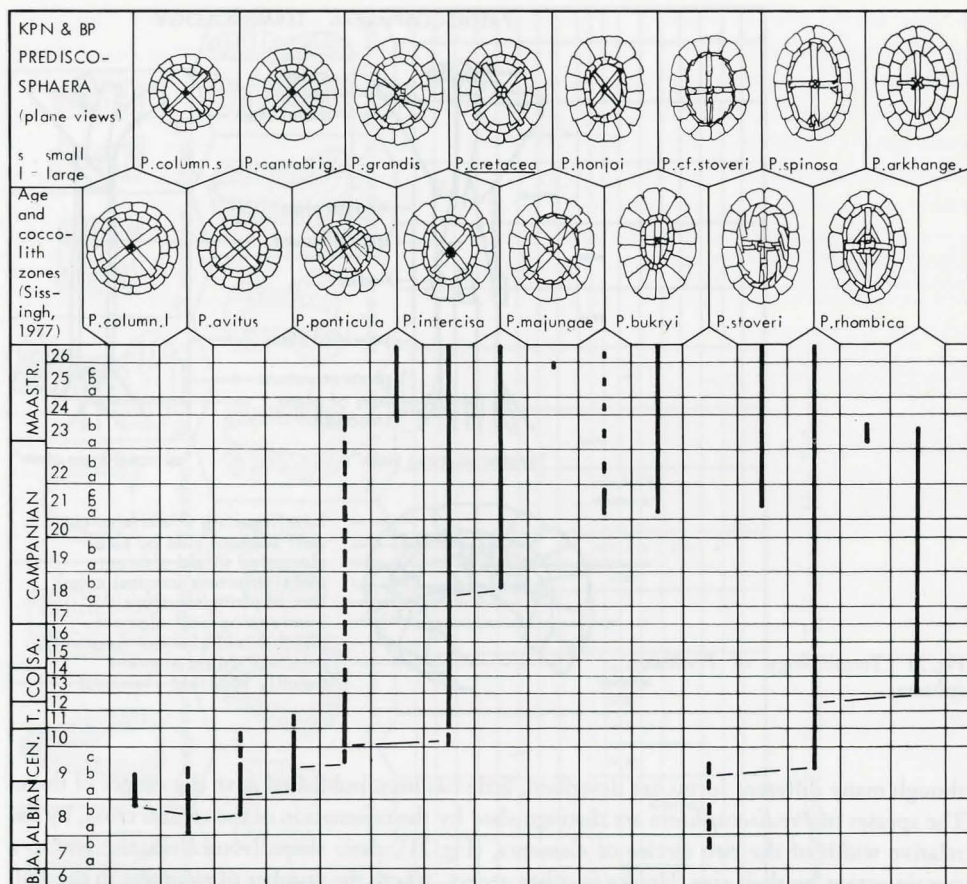


Fig. 22 Species of *Prediscosphaera* and their stratigraphical distribution.

observations by B. Prins (written communication 1978). The Aptian "*Prediscosphaera spinosa*" described and illustrated by Barrier (1977b) includes forms with the usual 16 as well as a form with more shield elements (pl. III, fig. 3). They are included as *P. cf. P. stoveri* on Fig. 22, since they seem to have a wall differing from the one of "typical" *P. spinosa*.

*Stephanolithionaceae* and similar forms. The Stephanolithionaceae comprise round, elliptical and polygonal forms with a wall consisting of vertical or nearly vertical elements, some of which can be extended into lateral spines. The central or plate area is spanned with four or more bars which often support a plate spine or knob. The genera usually assigned to this family plus some similar genera are listed in Fig. 23.

Noël (1972), Rood *et al.* (1971) and Rood & Barnard (1972) have published on the Jurassic members of this family. Their findings are also included on Fig. 24, since most genera of this family have originated in the Jurassic and reworking of Jurassic forms into the Cretaceous seems likely when looking at the ranges of some forms. The ranges given for most species in Fig. 24
















STEPHANOLITHIONACEAE and other genera		structural elements										Generotype		Genera	
		6 equal sides	6 (4 elongate) sides	4 near rectangular sides	4 near rhomboedrical sides	near elliptical	near round	lateral spines	plate spine or knob	inner wall	invalid genus	JURASSIC	CRETACEOUS		
	(Actinozygus)											•	•		
	Corollithion	•											•		
	Cylindralithus							•					•		
	Diadorhombus			•									•		
	(Diadozygus)				•								•		
	? Ellipsochiastus					•						•	•		
	Nodosella						•						•		
	Rhombolithion				•				•				•		
	Rotelapillus							•		•			•		
	Stephanolithion					•		•	•				•		
	Stradnerlithus					•			•				•		
	Tegumentum					•				•			•		
	Truncatoscapus	•											•		

Fig. 23 The genera of the family Stephanolithionaceae, *Actinozygus*, *Cylindralithus* and *Tegumentum*, and the structural elements that characterise them.

must be taken with caution, since very few authors have dealt with these forms, many of which are very small, usually less than 5 microns. The generotypes of the various genera are underlined in Fig. 24. Far too few data are yet available to make even an educated guess as to the course of evolution in this family. Therefore, no species have been transferred into the genus to which generotype they were grouped in Fig. 24. The species are arranged partly according to quite well defined genera (*Truncatoscapus* and *Stephanolithion*) and partly in groups around an appropriate generotype. The forms assigned to the genus *Actinozygus*, which is based on a very poorly described species (*Tremalithus regularis* Gorka, 1957) could conveniently be assigned to *Stradnerlithus*, the latter including most elliptical forms of the family without lateral spines. *A. regularis* has eight segments of elements filling the central area completely and a wall consisting of inclined elements, and thus does not belong to the Stephanolithionaceae (see Reinhardt & Gorka 1967). Another of Gorka's forms commonly assigned to a genus of this family, *Discolithus geometricus* Gorka, 1957, should be "forgotten", since it was not redefined by Reinhardt & Gorka (1967). Forms commonly assigned to *A. regularis* belong to *S. tortuosus* and those assigned to *D. geometricus* can be put into *C. ellipticum*.

If *Corollithion* is restricted to hexagonal forms, it becomes an entirely Cretaceous genus. *Diadorhombus* should include nearly rectangular forms with or without the near round forms with a central cross like *C. achylosum*. *Diadozygus* is, like the few months older *Rhombolithion*, a nearly rhomboedrical form. *Rotelapillus* could include the near round forms

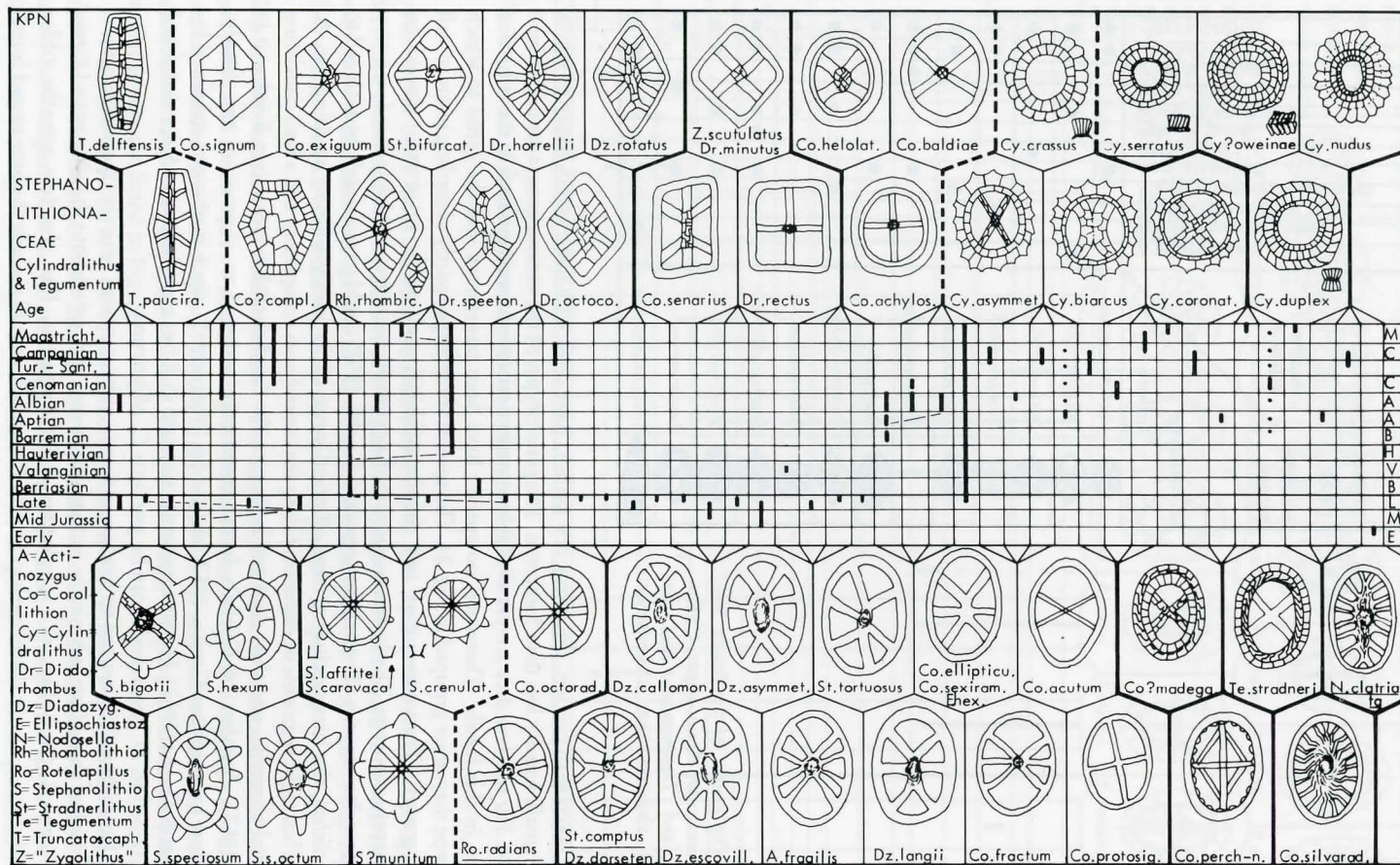


Fig. 24 The stratigraphical distribution of species of the family Stephanolithionaceae and ? related genera. Heavy lines separate groups of possibly related species. Generotypes are underlined.



with eight central bars and the round forms with eight central bars so far assigned to *Stephanolithion*. These mainly Cretaceous forms of *Stephanolithion* have no lateral spins, but protruding ring elements. *Tegumentum* is included here, since it also has a wall consisting of vertical elements. It differs from the genera of Stephanolithionaceae by its inner circle of oblique elements. *Truncatoscapus* has two short and four elongated sides and its patchy occurrence in the Cretaceous might be due to reworking from the Upper Jurassic, from where the two forms are also reported. Some forms commonly assigned to *Corolithion*, as *C. achylosum*, may be related to forms commonly attributed to *Cylindralithus* as *C. biarcus* and *C. coronatus* (but not with the genotype of *Cylindralithus*, *C. serratus*).

## Paleoecology

Thierstein (1976) summarized the paleoecologic observations made by previous authors and by himself. While some of his observations could be confirmed by later investigations, others need to be revised as a result of the newer sections that have been studied from high northern and southern latitude Cretaceous.

### Tropical – boreal

Localities from Great Britain, Holland, Northern Germany, Scandinavia and the North Sea are considered to belong to the boreal realm, those from the countries surrounding the Mediterranean, as representatives of the tethyan, tropical province.

*Early Cretaceous.* Considerably more information is available now concerning the Early Cretaceous floral distribution than when Thierstein (1976) wrote his paper (1974). Half the taxa he considered to be restricted to tropical and subtropical paleolatitudes occur in what is here considered the boreal realm: *Conusphaera mexicana*, *Nannoconus* spp. *Calcicalathina oblongata* and *Rucinolithus irregularis* also occur in northern Germany, at Speeton and/or in the North Sea. *Nannoconus* has been found as far north as Spitzbergen (Verdenius, written communication 1978). Together with the occurrences reported from Brazil by Troelsen & Quadros (1971) and Wind & Wise (1977) from the Falkland Plateau in the South Atlantic, this genus has become a truly cosmopolitan form. This is in contrast with Berger & Roth (1975), who regarded it as a typical tethyan genus. One reason for this is that only four years ago no Lower Cretaceous sections in a suitable facies had been studied which allowed the recognition of paleoprovinces.

"*Cribrosphaera*" *primitiva* was proposed by Thierstein (1976) to be the only form restricted to the boreal and austral realms.

However, as many of the species described by Black from the Lower Cretaceous at Speeton (1971) and from the Gault of Great Britain (1972, 1973 and 1975) have still not been found in the tethyan realm or at any other locality, Thierstein's comment may be premature. A possible reason for this is that only very few monographs on Lower Cretaceous coccoliths have been published since Black's descriptions of the British material. Similarly, Wind & Wise (1977) found a few new Lower Cretaceous species and many new species in the Maastrichtian of the Falkland Plateau, thus clearly there is provinciality, whose limits have not yet been determined. Much more work has to be done on well preserved coccolith assemblages to give a better understanding about the paleodistribution of coccolith species.

*Late Cretaceous.* Thierstein (1976) suggests that *Kamptnerius magnificus* preferred cooler waters and that *Lucianorhabdus cayeuxii* was fairly abundant in samples from above 30° paleolatitude only. He recorded it only from one tropical site, DSDP Site 152 in the Caribbean. Since then, *L. cayeuxii* was also found in Southern Spain and Tunisia (Verbeek 1977), but not in another Tunisian nor in a Moroccan section (Hojjatzadeh, personal communication 1978). It also occurs in the Maastrichtian at DSDP Site 354 on Ceara Rise in the equatorial Atlantic (Perch-Nielsen 1977). *K. magnificus* was also found at this site. This might suggest that the controlling factor is facies rather than paleolatitude (or temperature).

*Nephrolithus frequens* was considered by Worsley and Martini (1970) as a boreal/austral form, but has since been found also in Egypt and at DSDP Sites 354 in the equatorial Atlantic (Perch-Nielsen, 1973, 1977 and Perch-Nielsen *et al.* 1971). *Micula murus*, on the other hand, was thought to be a tropical form by Worsley & Martini (1970), but has been found also in Dania, the youngest Maastrichtian of Denmark (Perch-Nielsen 1977, and Plate I: 12). Its absence in most high latitude Maastrichtian deposits thus might be indicative of the missing of the youngest Cretaceous in the section or of the ease with which *M. murus* dissolves in chalk facies.

*Lithraphidites quadratus* and *Marthasterites furcatus*, while quite reliable markers in the tethyan realm, occur less consistently in higher latitude sequences. *Quadrum trifidum*, *C. aculeus* and *Q. gothicum* also are forms which may be restricted to tropical areas and which have not yet been found in Denmark or the North Sea area. Sissingh (1977:55) does, however, mention the *T. trifidus* Zone from the Netherlands.

In conclusion it may be said that, while *Nannoconus* and other forms mentioned above are found more abundantly in the tethyan rather than boreal/austral realms, many of these forms do, nevertheless, occur in the other realm and so are cosmopolitan. However, their stratigraphic usefulness is less in sections of the other realm than in the one from where they are thought to be typical. Most of the long-ranging species are cosmopolitan.

### Epicontinental – marginal

Thierstein (1976) reasoned that forms common in the Tethys area but absent at the Pacific DSDP sites were related to the general paleogeographic setting of the two oceans: marginal for the Tethys and oceanic for the Pacific. He found the following forms to be favored by epicontinental seas and large shelf areas:

*Nannoconus* spp.  
*Conusphaera mexicana*  
*Calcicalathina oblongata*  
*Lithraphidites bollii*  
*Micrantholithus obtusus*  
*Lithastrinus floralis*

and observed a similar preference for marginal conditions for:

*Lucianorhabdus cayeuxii*  
*Tetralithus obscurus*  
*Braarudosphaera bigelowii*

*Arkhangelskiella cymbiformis* and *K. magnificus* should be added to this list as both species are usually more common in marginal than in oceanic environments.



## Conclusions and Outlook

The following conclusions can be drawn from the observations presented here:

– Preservation of coccoliths varies in different lithologies; it is usually better in slightly marly chalks and marls than in pure chalks or limestones. Dissolution and overgrowth are limiting factors for species identification.

– For practical purposes like age-dating for mapping, and in boreholes, long-range and local correlations on- and offshore, useful zonations have been established and correlated to the European stages, the magnetic and the radiometric time-scales.

– a still finer subdivision of sequences with well preserved calcareous nannofossils can be expected.

– Evolutionary lineages have been worked out for a few "families" and genera or groups of genera.

– Calcareous nannofossils show some provincialism, however, some species previously considered as tethyan have been found to be cosmopolitan (i.e. *Nannoconus*). At the moment, there are more species restricted to the boreal and austral realm respectively than to the tethyan realm!

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The following work still needs to be done:

### Preservation

– detailed studies on the distribution of coccolith species in selected, sedimentologically well defined samples are needed to interpret results from quantitatively investigated Cretaceous samples, which are not as yet available.

### Biostratigraphy

– the sequence of events has to be tested further on continuous sections from different latitudes and from different facies, to check and map its applicability (local – regional – cosmopolitan) and/or limitations (facies).

– further splitting of usually lumped species is necessary. Sections with well preserved forms should be found and investigated in detail. There seems little need for too detailed work on too poorly preserved assemblages.

### Evolution

– many of these lineages are still incomplete and have an abrupt beginning and/or end. For many forms no attempts have yet been published as to the origin or course of evolution.

### Paleoecology

– monographs on Cretaceous calcareous nannofossils are unevenly spread, more well preserved high latitude assemblages having been studied. Investigations of well preserved material from the tethyan/tropical realm are needed to rectify this imbalance, which will make qualitative and quantitative comparisons meaningful.

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## Appendix I

*Calcicalathina alta* n. sp.

Plate 2, Fig. 1–7

Holotype: Plate 2, Fig. 5

Type level: Cenomanian,

Type locality: Pont du Fahs, Tunisia



Diagnosis: Form of *Calcicalathina* with a very high central area.

Description: Basket like elliptical forms with a low wall and a central area filled with calcite crystals of different orientation that rise highly above the distal margin of the wall, which consists of vertical to slightly oblique elements.

Remarks: *C. alta* differs from the generotype of *Calcicalathina*, *C. oblongata*, by the high elevation of the central area. In the light microscope, the first impression of *C. alta* is that of a rectangular piece of *Schizosphaerella* or *Thoracosphaera*. But on closer inspection, especially with the use of a gypsum red I plate, the thin wall is clearly visible.

Occurrence: Early Cenomanian through Late Cenomanian and E. Turonian (?) of Pont du Fahs, Tunisia. Not observed in other areas so far.

*Ceratolithoides verbeekii* n. sp.

Plate 2, Fig. 10–13

1977 *Ceratolithoides aculeus* (Stradner) Prins & Sissingh, in Verbeek: Plate 1, Fig. 1–4 only.

Holotype: Plate 1, Fig. 4 of Verbeek (1977).

Type level: Campanian.

Type locality: El Kef, Tunisia.

Diagnosis: A form of *Ceratolithoides* with a high cone and six horns.

Description: The base of the nannolith consists of six horns. A ridge continues from each horn to form the high cone.

Remarks: *C. verbeekii* includes *C. aculeus* forms I and II of Verbeek (1977). These forms can be well distinguished from *C. aculeus* by the six horns, the longer cone and the ridges in the former.

Occurrence: *C. verbeekii* was found to overlap with *M. furcatus* in Tunisia in the Lower Campanian and is found up to the first occurrence of *Q. trifidum* (zones 18b through 21c of Sissingh 1977), in the Upper Campanian.

*Eprolithus antiquus* n. sp.

Plate 1, Fig. 5–9

Holotype: Plate 1, Fig. 5, 9.

Type level: Hauterivian.

Type locality: Speeton, U.K.

Diagnosis: A form of *Eprolithus* with about 12 wall elements.

Description: *E. antiquus* is round or has a slightly elliptical outline. The wall elements stand vertical and are about the same height as the width of the central area and show no incisure in the equatorial plane. They seem to be less pointed than those of younger *Eprolithus*, which might, however, be due to calcite overgrowth.

Remarks: *E. antiquus* is a relatively large species of the genus and has, accordingly, more wall elements than those. *E. planus* and *E. floralis* have usually 9 wall elements only. The number of wall elements decreases from older to younger forms of *Eprolithus*. The construction of the central area is not clear from the pictures, due to the not ideal preservation of the forms found.

Occurrence: *E. antiquus* is quite common in one sample from the Hauterivian C 11 bed at Speeton, but only few specimens were found in younger Hauterivian samples. *E. antiquus* is the oldest representative of *Eprolithus* found so far.

*Micrantholithus speetonensis* n. sp.

Plate 1, Fig. 10, 13

Holotype: Plate 1, Fig. 10.

Type level: Valanginian.

Type locality: Speeton, U.K.

Diagnosis: A form of *Micrantholithus*, where the free side of the segment has two negative and one positive angles.

Description and Remarks: *M. speetonensis* is a small form of the genus. It resembles the Eocene *M. bramlettei*, from which it can be distinguished by the wider positive angle in the former. No similar forms have been reported from the sediments of Hauterivian through Paleocene age and it is therefore believed, that *M. speetonensis* is, indeed, a proper species of *Micrantholithus*. A similar form then evolved again in the Eocene. Only few pentaliths and no complete coccospheres were found.

Occurrence: Upper Valanginian (D4A through D2E) at Speeton, U.K.

*Micula prinsii* n. sp.

Plate 1, Fig. 11, 14–16

Holotype: Plate 1, Fig. 16.

Type level: Maastrichtian (reworked into Danian).

Type locality: DSDP Site 356, Sao Paulo Plateau, South Atlantic.

Diagnosis: Form of *Micula* with a very reduced cross and a cross with long arms meeting tangentially in the middle. The arms are bent and their ends bifurcated or slightly turning.

Description: The reduced cross is very small and shows sutures aligned more or less with the direction of the longer arms of the larger cross. The arms of the latter are long and protrude well away from the "body". They are bent and meet tangentially in the middle. Their ends turn slightly or, in later forms, are bifurcated.

Remarks: It became necessary to define this new species to differentiate between the *M. murus* with the short arms hardly protruding from the "body" and this later form with the long arms, to use the two forms better stratigraphically.

Occurrence: *M. prinsii* occurs in the Latest Cretaceous of Denmark, SW France, Spain and Tunisia above the first occurrence of *Abathomphalus mayaroensis*. While *M. murus* s. str. (without forms now to be assigned *M. prinsii*) can be found before *N. frequens* (see the *M. murus* Zone of Sissingh 1977), *M. prinsii* appears higher than *N. frequens*.

*Nannoconus borealis* n. sp.

Plate 1, Fig. 1–4

Holotype: Plate 1, Fig. 3.

Type level: Barremian.

Type locality: Speeton, U.K.

Diagnosis: A large form of *Nannoconus* with an enlarged basal part, a relatively long, slender and slightly curved middle part and a slightly enlarged distal part. The central canal is barely visible in the basal part and narrow in the middle and distal part.

Description: The basal part is often twice as wide as the middle part and about half as high. It consists of coarser elements than the middle part or stem. Like in the stem, they are arranged in a spiral. The stem and the distal part are also decorated with ridges running at about 90° to the



spirals of the elements building them. They are probably a preservational feature. The elements building the stem and the distal part are flatter than those of the base.

Remarks: *N. borealis* resembles *N. boletus*, but its stem is longer and its base larger. *N. dauvillieri* also has a smaller base and no distally enlarged part.

Occurrence: *N. borealis* is quite common in one sample from the Barremian of Speeton (layer MB), where also *Nannoconus abundans* and other forms of this genus occur. With the repeated findings of *Nannoconus* in the North Sea area, *Nannoconus* must now be regarded as a cosmopolitan genus rather than a strictly tethyan one as claimed by Berger & Roth 1975.

*Prediscosphaera grandis* n.sp.

Plate 2, Fig. 8

1968 *Deflandrius cretaceus* (Archangelsky) Bramlette & Martini, in Perch-Nielsen Plate XIII, Fig. 1, 5 & 6 and Plate XIV, Fig. 2.

Holotype: Plate XIII, Fig. 1 in Perch-Nielsen 1968.

Type level: Maastrichtian.

Type locality: Mon's Klint, Denmark.

Diagnosis: Very large, broad elliptical form of *Prediscosphaera*.

Description: The rim consists of 16 elements, as is usual for the forms of this genus. The central cross lies diagonal and supports a prominent stem. The inner circle of elements is relatively narrow.

Remarks: While *P. cretacea* in the Maastrichtian is usually 6–8  $\mu$  long, *P. grandis* is over 10  $\mu$  long and reaches over 15  $\mu$ .

Occurrence: *P. grandis* is found in the Maastrichtian of Denmark and other high latitude areas.

## Appendix II

List of species in Figures, with Figure number and \* = illustration.

- |  |  |
|--|--|
| abundans, <i>Nannoconus</i> 3                                    | angusta, <i>Vekshinella</i> 12*                              |
| <i>Aceanolithus</i> 7, 8*  | angustifloratus, <i>Cretarhabdus</i> 2                       |
| achylosum, <i>Corrollithion</i> 24*                              | angustus, <i>Rhagodiscus</i> ( <i>Parhabdolithus</i> ) 2, 3, |
| <i>Actionozygus</i> 6, 23*, 24*                                  | 4, 6*  |
| aculeus, <i>Ceratolithoides</i> ( <i>Tetralithus</i> ) 2, 4, 11* | anthophorus, <i>Reinhardtites</i> 1, 2, 4, 6*                |
| acutum, <i>Corollithion</i> 21*                                  | antiquus, <i>Eprolithus</i> 2, 3, 14*, Pl. 1*                |
| acutum, <i>Lucianorhabdus</i> 2, 4, 15*                          | apertior, <i>Eprolithus</i> 14*                              |
| <i>Acuturris</i> 16*   | arborius, <i>Lucianorhabdus</i> 17*                          |
| additus, <i>Phanulithus</i> 18*                                  | arcuatus, <i>Ceratolithoides</i> 2, 11*                      |
| africana, <i>Braarudosphaera</i> 2, 10*                          | arcuatus, <i>Lucianorhabdus</i> 17*                          |
| <i>Ahmuelerella</i> 6*   | <i>Arkhangelskiella</i> 6*, 7, 8*                            |
| alatus, <i>Lithraphidites</i> 2, 15*                             | arkhangelskiyi, <i>Prediscosphaera</i> 22*                   |
| albianus, <i>Podorhabdus</i> 2, 4, 6*                            | asarotium, <i>Orastrum</i> 18*                               |
| albiensis, <i>Hayesites</i> 2, 4, 6*                             | <i>Aspidolithus</i> 7, 8*, 9*                                |
| alta, <i>Calcicalatina</i> 6*, Pl. 2*                            | <i>Aspidolithus</i> sp. 1–8 2, 9*                            |
| anglicum, <i>Crucicribrum</i> 2, 6*                              | asper, <i>Rhagodiscus</i> 6*                                 |
|  | asymmetricus, <i>cylindralithus</i> 24*                      |

- asymmetricus, Diadozygus 24°  
 australis, Okkolithus 18°  
 avitus, Prediscosphaera 22°  
  
 baldiae, Corollithion 24°  
 barnesae, Watznaueria 1, 3  
 beckmannii, Polycostella 6°  
 bermudezii, Nannoconus 2, 20°  
 bevieri, Aspidolithus 9°  
 biarcus, Cylindralithus 24°  
 bifurcatus, Stradnerlithus 24°  
 bigelowii, Braarudosphaera 1, 10°  
 bigotii, Stephanolithion 24°  
 biporta, Watznaueria 6°  
 Biscutum 1, 6°  
   bohotnicae, Staurolithites 1  
   boletus, Nannoconus 20°  
   bollii, Lithraphidites 2, 4, 5, 15°  
   borealis, Nannoconus 3, 20, Pl. 1°  
 Braarudosphaera 10°  
 Braarudosphaeraceae 10°  
 Broinsonia 6°, 7, 8°  
   britannica, Watznaueria 2, 6°  
   brönnimannii, Nannoconus 20°  
   bucheri, Nannoconus 20°  
 Bukryaster 13, 14°  
   bukryi, Prediscosphaera 22°  
   bukryi, Russellia 18°  
  
   campanensis, Orastrum 18°  
 Calccalatina 6°  
   callomonii, Diadozygus 24°  
   calpidomorphus, Nannoconus 20°  
   cantabrigensis, Prediscosphaera 22°  
   caravacaensis, Stephanolithion 24°  
   carniolensis, Lithraphidites 1, 3, 15°  
   cayeuxii, Lucianorhabdus 1, 4, 17°  
 Ceratolithoides 11°  
   Ceratolithoides sp. 1 11°  
   chiastia, Cruciellipsis 2, 4, 6°  
 Chiastozygus 6°, 12°  
   clatriata, Nodosella 24°  
   colligata, Speetonia 2, 3, 4, 6°  
   collis, Eiffellithus 12°  
   colonii, Nannoconus 2, 5, 20°  
   columnata, Prediscosphaera 2, 4, 22°  
   compactus, Glaukolithus 1  
   compactus, Lucianorhabdus 15°, 18°  
   completum, Corollithion? 2, 24  
   comptus, Stradnerlithus 24°  
   concava, Micula 2, 14°  
 Conusphaera 6°  
 Corollithion 23°, 24°  
   coronatus, Cylindralithus 24°  
   crassus, Cylindralithus 24°  
   crenulata, Stradneria (Cretarhabdus) 1, 2, 3, 4,  
   6°  
   crenulatum, Stephanolithion 24°  
 Crepidolithus 6°  
   cretacea, Prediscosphaera 1, 2, 5, 22°, Pl. 2°  
 Cretarhabdus 6°  
 Cribricatillus 7, 8°  
 Cribrocorona 6°  
 Cribrosphaerella 6°  
 Crucicribrum 6°, 7, 8°  
 Cruciellipsis 6°  
   cuvillieri, Cruciellipsis 2, 3, 4, 5, 6°  
 Cyclagelosphaera 6°  
 Cylindralithus 23°, 24°  
   cymbiformis, Arkhangelskiella 1, 2, 4, 6°  
  
   dauvillieri, Nannoconus 20°  
   decoratus, Microrhabdulus 2, 6°  
   decorus, Podorhabdus 1, 3  
   decussata, Micula 1, 4, 14°  
   deflandrei, Cylindralithus 6°  
   deltensis, Truncatoscapus 24°  
 Diadorhombus 23°, 24°  
 Diadozygus 23°, 24°  
 Diazomatolithus 6°  
   diplogrammus, Glaukolithus 1  
   disgregatus, Glaukolithus 1  
 Dodekapodorhabdus 6°  
   dolomiticus, Nannoconus 20°  
   dorotheae, Laguncula 6°  
   dorsetense, Diadozygus 24°  
   duplex, Cylindralithus 24°  
  
   ehrenbergii, Cribrosphaerella 1, 6°  
 Eiffellithus 12°  
 Ellipsochiastus 23°, 24°  
   ellipticum, Corollithion 24°  
   elongatus, Nannoconus 20°  
   embergeri, Parhabdolithus 1, 3  
   enormis, Broinsonia 6°  
 Eprolithus 13, 14°  
   Eprolithus sp. 1 2, 14°  
   Eprolithus sp. 2 14°  
   escovillensis, Diadozygus 24°  
   exiguum, Corollithion 1, 2, 24°  
   eximus, Eiffellithus 1, 2, 4, 12°  
  
   fenestratus, Reinhardtites 6°  
   fessus, Glaukolithus 1  
   floralis, Eprolithus (Lithastrinus) 1, 2, 5, 14°  
   fossilis, Scapholithus 3, 6°  
   fractum, Corollithion 24°  
   fragilis, Actinozygus 24°  
   frequens, Nephrolithus 2, 4, 6°  
   furcatus, Marthasterites 1, 2, 4, 6°  
  
   gallica, Cribrocorona 1, 6°  
   gardetae, Hexalithus 13°  
 Gartnerago 6°, 7, 8°



- gartneri, *Quadrum* 1, 2, 4, 14<sup>\*</sup>  
 giannus, *Ottavianus* 18<sup>\*</sup>  
 globulus, *Nannoconus* 20<sup>\*</sup>  
 gorkae, *Eiffellithus* 12<sup>\*</sup>  
 gothicum, *Quadrum* (*Tetralithus*) 4, 14<sup>\*</sup>  
 grandis, *Prediscosphaera* 22<sup>\*</sup>, Pl. 2<sup>\*</sup>  
 grillii, *Lithastrinus* 1, 2, 14<sup>\*</sup>  
 grossopectinatus, *Lithraphidites* 15<sup>\*</sup>
- Hayesites* 6<sup>\*</sup>  
 hayi, *Bukryaster* 1, 2, 4, 14<sup>\*</sup>  
 hayi, *Rucinolithus* 14<sup>\*</sup>  
 helicoides, *Microrhabdulus* 1, 6<sup>\*</sup>  
 helolatus, *Corollithion* 24<sup>\*</sup>
- Hexalithus* 13, 14<sup>\*</sup>  
*Hexangulolithus* 13  
 hexserratus, *Ellipsochastus* 24<sup>\*</sup>  
 hexum, *Stephanolithion* 24<sup>\*</sup>  
 hockwoldensis, *Braarudosphaera* 10<sup>\*</sup>  
 honjoi, *Prediscosphaera* 22<sup>\*</sup>  
 horrellii, *Diadorhombus* 24<sup>\*</sup>  
 horticus, *Sollasites* 3  
 hoschulzii, *Micrantholithus* 3, 10<sup>\*</sup>
- infinitus, *Parhabdololithus* 6<sup>\*</sup>  
 infracretacea, „*Micula*“ 6<sup>\*</sup>  
 intercisa, *Prediscosphaera* 22<sup>\*</sup>  
 irregularis, *Rucinolithus* 2, 5, 6<sup>\*</sup>
- Isocrystallithus* 16<sup>\*</sup>  
 kamptneri, *Ceratolithoides* 2, 11<sup>\*</sup>  
 kamptneri, *Nannoconus* 2, 20<sup>\*</sup>
- Kamptnerius* 6<sup>\*</sup>, 7, 8<sup>\*</sup>  
 keadyi, *Munarinus* 18<sup>\*</sup>
- laffittei, *Stephanolithion* 1, 3, 24<sup>\*</sup>
- Laguncula* 6<sup>\*</sup>  
 langii, *Diadozygus* 24<sup>\*</sup>
- Lapideacassis* 6<sup>\*</sup>  
 laswellii, *Russellia* 18<sup>\*</sup>  
 lehmanii, *Diazomatolithus* 6<sup>\*</sup>  
 lesliae, *Munarinus* 18<sup>\*</sup>  
 levis, *Reinhardtites* 2, 4, 6<sup>\*</sup>
- Lithastrinus* 13, 14<sup>\*</sup>  
*Lithraphidites* 15<sup>\*</sup>  
 litterarius, *Chiastozygus* 1, 2, 3, 4, 6<sup>\*</sup>  
 loriei, *Cretrarhabdus* 2, 4, 6<sup>\*</sup>
- Lucianorhabdus* 16<sup>\*</sup>, 17<sup>\*</sup>, 18<sup>\*</sup>  
 madagaskarensis, *Corollithion*? 24<sup>\*</sup>  
 magnacavus, *Aspidolithus* 9<sup>\*</sup>  
 magnificus, *Kamptnerius* 1, 6<sup>\*</sup>  
 majungae, *Prediscosphaera* 22<sup>\*</sup>  
 maleformis, *Lucianorhabdus* 1, 2, 4, 17<sup>\*</sup>  
 marszalekii, *Munarinus* 18<sup>\*</sup>
- Marthasterites* 6<sup>\*</sup>  
 matalosa, *Vekshinella* 6<sup>\*</sup>  
 meddii, *Grantarhabdus* 2  
 mexicana, *Conusphaera* 2, 6<sup>\*</sup>  
*Micrantholithus* 10<sup>\*</sup>  
*Micrantholithus* sp. 1 10<sup>\*</sup>  
*Microrhabdulus* 6<sup>\*</sup>  
*Micula* 14<sup>\*</sup>  
 moratus, *Lithastrinus* 14<sup>\*</sup>  
 multicaudus, *Nannoconus* 20<sup>\*</sup>  
*Multipartis* 16<sup>\*</sup>, 18<sup>\*</sup>  
 multiplus, *Russellia* 18<sup>\*</sup>  
*Munarinus* 16<sup>\*</sup>, 18<sup>\*</sup>  
 minutus, *Diadorhombus* 24<sup>\*</sup>  
 munitum, *Stephanolithion*? 24<sup>\*</sup>  
 murus, *Micula* 2, 14<sup>\*</sup>, Pl. 1<sup>\*</sup>
- Nannoconus* 1, 19<sup>\*</sup>, 20<sup>\*</sup>  
*Nannoconus* sp. 92 20<sup>\*</sup>  
*Nannoconus* sp. 107 8<sup>\*</sup>  
 nanum, *Gartnerago* 2, 6<sup>\*</sup>
- Nephrolithus* 6<sup>\*</sup>  
 nitidum, *Quadrum* (*Tetralithus*) 2, 14<sup>\*</sup>
- Nodosella* 23<sup>\*</sup>, 24<sup>\*</sup>  
 noelae, *Dodekapodorhabdus* 6<sup>\*</sup>  
 nudus, *Cylindralithus* 24<sup>\*</sup>
- obliquum, *Gartnerago* 1, 2, 6<sup>\*</sup>  
 oblongata, *Calcalatina* 2, 4, 5, 6<sup>\*</sup>  
 obscurus, *Phanulithus* 1, 2, 4, 18<sup>\*</sup>  
 obtusus, *Micrantholithus* 2, 4, 10<sup>\*</sup>  
 octocostatus, *Diadorhombus* 24<sup>\*</sup>  
 octoradiata, *Ahmuelerella* 1, 2, 6<sup>\*</sup>  
 octoradiatum, *Corollithion* 24<sup>\*</sup>  
 octum, *Stephanolithion*, *speciosum* 24<sup>\*</sup>
- Okkolithus* 16<sup>\*</sup>, 18<sup>\*</sup>  
*Orastrum* 16<sup>\*</sup>, 18<sup>\*</sup>  
 orionatus, *Tranolithus* 1, 6<sup>\*</sup>
- Ottavianus* 16<sup>\*</sup>, 18<sup>\*</sup>  
 ovalis, *Phanulithus* (*Tetralithus*) 1, 18<sup>\*</sup>  
 oweinae, *Cylindralithus* 24<sup>\*</sup>
- Palaeopontosphaera* 6<sup>\*</sup>  
 parallelus, *Eiffellithus* 12<sup>\*</sup>  
 parvus, *Aspidolithus* (*Broinsonia*) 1, 2, 4, 9<sup>\*</sup>
- Parhabdololithus* 6<sup>\*</sup>  
 pauciramossus, *Truncatoscapus* 24<sup>\*</sup>  
 perch-nielsenae, *Corollithion* 24<sup>\*</sup>  
 phacelosus, *Tranolithus* 2
- Phanulithus* (*Calculites*) 16<sup>\*</sup>, 18<sup>\*</sup>  
 planus, *Radiolithus* 1, 14<sup>\*</sup>
- Podorhabdus* 6<sup>\*</sup>  
*Polycostella* 6<sup>\*</sup>  
*Polycyclolithus* 13<sup>\*</sup>  
 ponticula, *Prediscosphaera* 15<sup>\*</sup>  
 praequadratus, *Lithraphidites* 22<sup>\*</sup>
- Prediscosphaera* 21<sup>\*</sup>, 22<sup>\*</sup>  
 primitiva, *Cribrosphaerella* 6<sup>\*</sup>  
 primula, *Braarudosphaera* 10<sup>\*</sup>

- prinsii, Micula 2, 4, 14\*, Pl. 1\*  
 protosignum, Corollithion 24\*  
 pyramidus, Tetralithus 2
- quadrata, Micula 14\*  
 quadratus, Lithraphidites 2, 4, 5, 15\*  
 quadriangulus, Nannoconus 2, 20\*  
 quadrifidus, Lucianorhabdus 17\*, 18\*  
 Quadrum 14\*  
 Quadrum sp. 1 14\*  
 quinquecostata, Braarudosphaera 10\*
- Radiolithus 13, 14\*  
 Ramsaya 16\*, 18\*  
 Ramsaya? sp. 1 18\*  
 Ramsaya? sp. 2 18\*  
 radians, Rotelapillus 24\*  
 radiatus, Hayesites 6\*  
 rectus, Diadorhombus 2, 4, 24\*  
 reinhardtii, Markalius 1  
 regularis, Actinozygus (Tremalithus) 6\*  
 regularis, Braarudosphaera 10\*
- Reinhardtites 6\*  
 reniformis, Rhagodiscus 6\*  
 Rhagodiscus 6\*  
 rhombica, Prediscosphaera 22\*  
 rhombicum, Rhombolithion 24\*  
 Rhombogyrus 13\*  
 Rhombolithion 23\*, 24\*  
 ripliensis, Multipartis 18\*  
 rotatus, Diadozygus 24\*  
 Rotelapillus 23\*, 24\*  
 Rucinolithus 6\*, 13, 14\*  
 Russellia 16\*, 18\*
- salebrosa, Palaeopontosphaera 2, 3, 4, 6\*  
 Scampanella 1, 6\*  
 Scapholithus 6\*  
 scotus, Lucianorhabdus (Acuturris) 17\*\*  
 scutulatus, „Zygodiscus“ 24\*  
 senaria, Polycostella 6\*  
 senarius, Corollithion 24\*  
 septenarius, Lithastrinus 2, 14\*  
 septentrionalis, Lithastrinus 14\*  
 serratus, Cylindralithus 24\*
- serratus, Lithraphidites carniolensis 15\*  
 sexiradiatus, Corollithion (Zygodiscus) 24\*  
 signum, Corollithion 1, 2, 24\*  
 silvaradion, Corollithion 24\*  
 simulacrum, Pharus 18\*  
 speciosum, Stephanolithion 24\*  
 speetonensis, Diadorhombus 24\*  
 speetonensis, Micrantholithus 2, 3, 10\*, Pl. 1\*  
 Speetonia 6\*  
 spinosa, Prediscosphaera 1, 22\*  
 spiralis, Zygodiscus 1, 6\*  
 staurophora, Micula 2  
 steinmannii, Nannoconus 2, 4, 20\*  
 stenorheta, Braarudosphaera 10\*  
 Stephanolithion 23\*, 24\*  
 Stephanolithionaceae 23\*, 24\*  
 stoveri, Prediscosphaera 22\*  
 cf. stoveri, Prediscosphaera 22\*  
 stradneri, Tegumentum 12\*, 24\*  
 Stradneria 6\*  
 Stradnerlithus 23\*, 24\*  
 striatum, Gartnerago 6\*  
 striatus, Chiastozygus 2, 3, 4, 12\*  
 swanseana, Ramsaya 18\*
- Tegumentum 12\*, 18\*, 23\*, 24\*  
 Tegumentum? sp. 1 16\*, 18\*  
 Tegumentum? sp. 2 18\*  
 tenuis, Chiastozygus 3  
 terrazetus, Ottavianus 18\*  
 Tetralithus 16\*  
 theta, Zygodiscus 6\*  
 tortuosus, Stradnerlithus 24\*  
 trifidum, Quadrum (Tetralithus) 2, 4, 5, 14\*  
 truittii, Nannoconus 20\*  
 Truncatoscapus 23\*, 24\*  
 turbinea, Braarudosphaera 10\*  
 turriseiffeli 1, 2, 4, 5, 12\*
- Vekshinella 12\*  
 verenae, Tubodiscus 6\*  
 verbeekii, Ceratolithoides 2, 11\*, Pl. 2\*
- wassallii, Nannoconus 2, 20\*  
 wisei, Rucinolithus 6\*

### Explanation of plates

#### Plate 1

- Fig. 1–4: *Nannoconus borealis* n.sp. LM (1,4) and SEM pictures from sample KPN 261/55 from the Barremian of Speeton, UK. Fig. 3 = holotype.
- Fig. 5–9: *Eprolithus antiquus* n.sp. LM (7,8) and SEM pictures from sample KPN 261/23 from the Hauterivian of Speeton, UK. Figures 5, 9 = holotype.
- Fig. 10, 13: *Micrantholithus speetonensis* n.sp. LM from sample KPN 261/42 from the Valanginian of Speeton, UK. Fig. 10 = holotype.



Fig. 11, 14–16: *Micula prinsii* n. sp. LM (11) and SEM pictures from sample KPN 553/23 from the Upper Maastrichtian of El Kef, Tunisia (11) and from the Danian of DSDP Site 356, sample 29–3, 24 cm (reworked). Fig. 16 = holotype.

Fig. 12: *Micula murus* (Martini) Bukry. LM from sample KPN 81/13 from Dania, Upper Maastrichtian of Denmark.

Magnification: Fig. 13: 2000 x, all other LM 3200 x. Fig. 2, 3: 2500 x. Fig. 5, 9: 7500 x, Fig. 6: 5000 x.

#### Plate 2

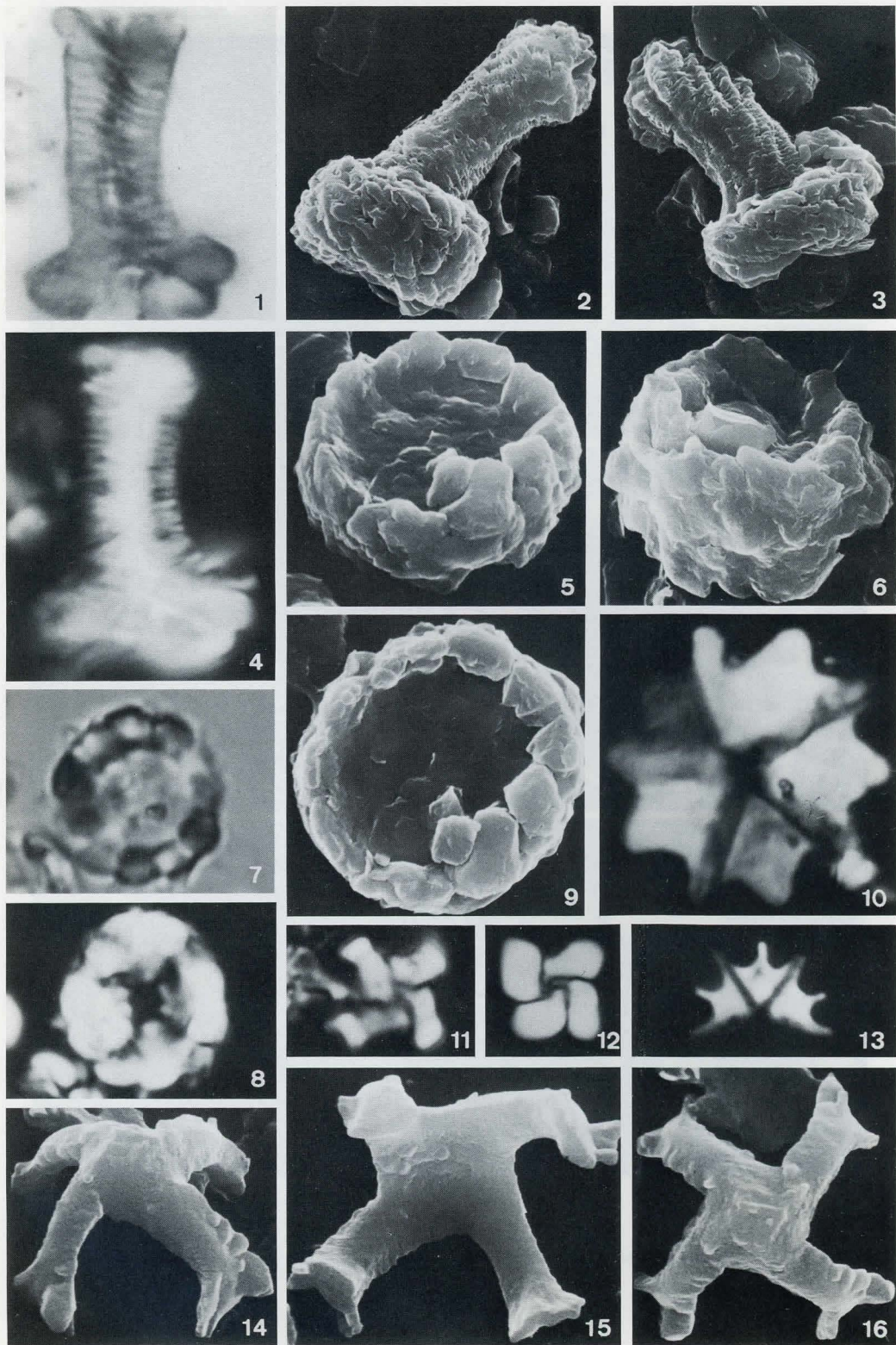
Fig. 1–7: *Calicalathina alta* n.sp. LM (1–3) and SEM pictures from sample KPN 551/4 from the Lower Cenomanian of Pont du Fahs, Tunisia. Fig. 5 = holotype.

Fig. 8: *Prediscosphaera grandis* n.sp. LM from sample KPN 81/13 from Dania, Upper Maastrichtian of Denmark.

Fig. 9: *Prediscosphaera cretacea* (Arkhangelsky) Gartner. LM from sample 81/13 from Dania, Upper Maastrichtian of Denmark.

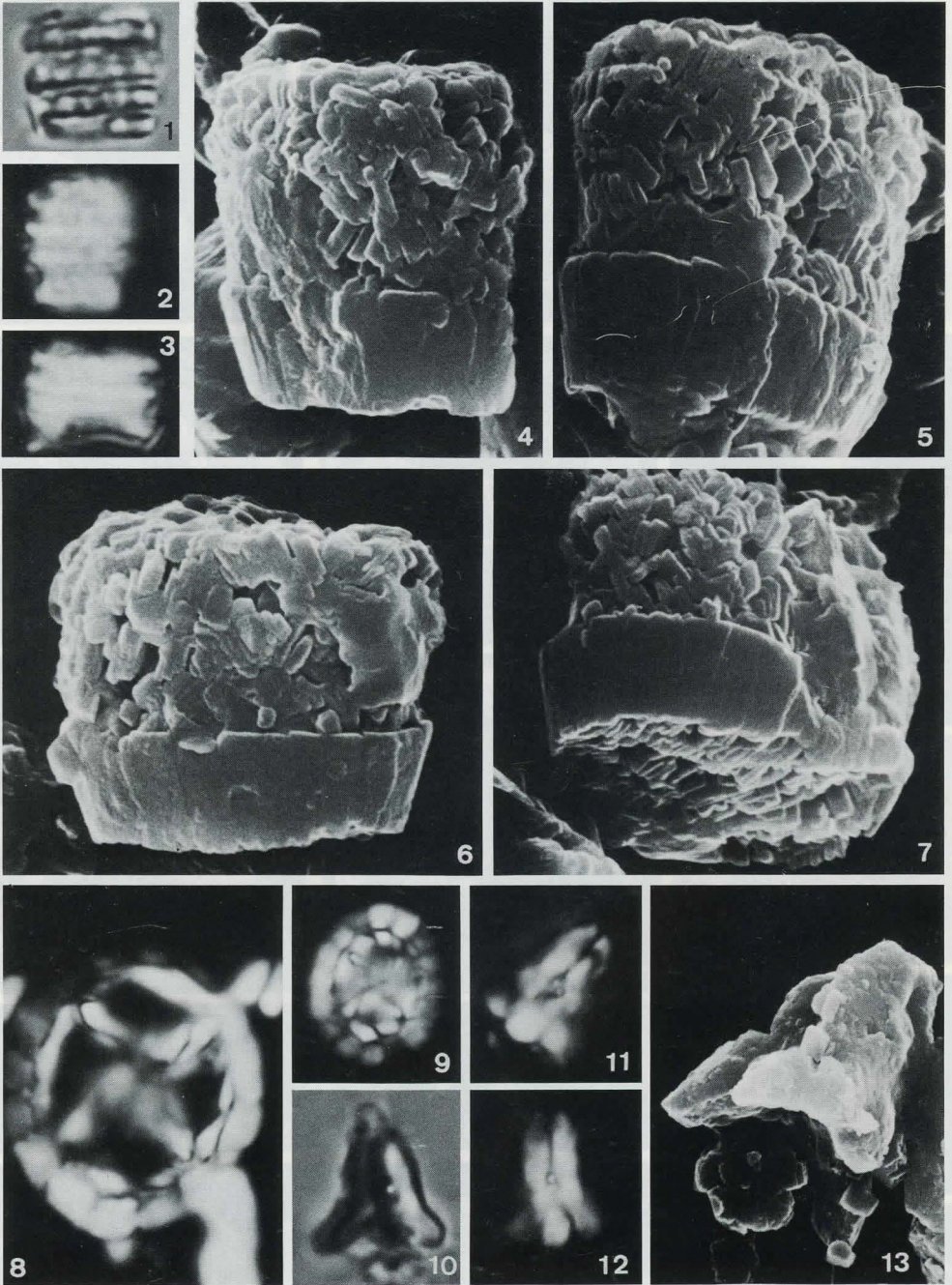
Fig. 10–13: *Ceratolithoides verbeekii* n.sp. LM (10–12) and SEM picture from sample KPN 553/3, Lower Campanian of El Kef, Tunisia and from sample KPN 551/33, Lower Campanian of Pont du Fahs, Tunisia.

Magnification: All LM: 3200 x. Fig. 4–7: 10000 x. Fig. 13: 7000 x.



Calcareous Nannofossils between the North Sea and the Mediterranean





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