FACIES	22	103-138	Taf. 26-33	12 Abb.	4 Tab.	ERLANGEN 1990

The Danian (Paleocene) Coral Limestone of Fakse, Denmark: A Model for Ancient Aphotic, Azooxanthellate Coral Mounds

Der Korallenkalk aus dem Dan (Paläozän) von Fakse, Dänemark: Ein Modell für fossile aphotische, azooxanthellate Korallenriffe

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KEYWORDS: FACIES ANALYSIS - CARBONATE DIAGENESIS - REEFS - DEEP-WATER CORAL MOUNDS - APHOTIC ENVIRONMENT - SCLERACTINIAN CORALS - HYDROZOANS - OCTOCORALS - DENMARK - TERTIARY (DANIAN)

Research Project:
EVOLUTION
of
REEFS

General Location: Southern Denmark
Age: Danian C (Lowermost Paleocene)
Reef Type: Deep water coral mound
Dimensions: Up to 200 x 80 x 30 m
Lithology: Unbedded coral limestone
Depositional Setting: Deep-water shelf
Tectonic Region: Danish-Polish Trough
Foundation below Reef: Bryozoan limestone, Maastrichtian limestone
Overlying Sediments: Bryozoan limestone?
Termination of the Reef: Shallowing upwards?
Bathymetric Range: Subtidal, below the photic zone, probably 200-300 m
Reef-forming Process: Baffling by corals, bioaccumulation
Dominant Organisms: Colonial corals, hydrozoans, octocorals, bryozoans
Destruction Process: Predominantly biological (borings by sponges, bryozoans)
Diagenesis: Early marine-phreatic, cementation; late meteoric-phreatic cements and replacement by quartz
Porosity: Intraskeletal moldic porosity

CONTENT

SUMMARY

The Danish-Polish Trough - a northwest to southeast striking basin - is bordered by the Fennoscandian Shield in the north and the Ringköbing-Fyn High in the south. During the Late Cretaceous and Early Tertiary carbonate sedimentation prevailed. Locally small bryozoan mounds were formed during the Upper Maastrichtian. The bulk of bryozoan bioherms originated during the Danian B to C. Coral communities and coral mounds are confined to the Danian C. About five coral limestone localities occur within the Danish-Polish Trough; Fakse is the most important one.

Paleontological and sedimentological data of the coral

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limestones point to the interpretation of the coral reefs as "cold- and deep-water coral bioherms".

Important criteria are the (1) absence of algae, (2) low-diverse azooxanthellate coral community, (3) dominance of dendroid growth forms in the corals, (4) surrounding pelagic facies adjacent to the coral mounds, (5) occurrence of pelagic organisms (globigerinid foraminifera, coccoliths) within the micrite of the mound facies and intermound facies, (6) breakdown of framebuilders predominantly by bioerosion instead of mechanical destruction, (7) mound- or bank-like structure of the buildups, (8) occurrence at a high paleolatitude.

Three major facies types can be distinguished: (1) bryozoan limestones, (2) transitional facies, and (3) coral limestones which include five subfacies types defined by the predominating coral taxa. Most coral mounds are composed of facies types 2 and 3.

Diagenesis is characterized by the formation of early marine-phreatic fibrous and bladed cements and by late diagenetic meteoric-phreatic dog-tooth cements and the replacement of calcite cements by quartz.

The mounds have an asymmetrical shape caused by unidirectional currents from the south. The maximum length is 200 m, the height 30 m and the width 80 m. The distribution of colonial corals within the mounds indicates a zonation pattern.

Framebuilders are represented only by azooxanthellate organisms: Colonial scleractinian corals, stylasterine hydrozoans and octocorals. Scleractinian corals have dendroid and arborescent growth forms, whereas hydrozoans and octocorals form fan-like colonies. Strong bioerosion of the framebuilding organisms was responsible for the breakdown of the skeletons; the bioclasts formed the substrate for other framebuilders. The soft bottom between the framebuilders was burrowed by bivalves and crustaceans.

The comparison with coral mounds occurring in the eastern Atlantic at similar latitudes and in a position comparable with that of the Paleocene Danish-Polish Trough suggests a paleodepth between 100 and 300 m.

ZUSAMMENFASSUNG

In der Oberkreide und im Alttertiär wurden im Dänisch-Polnischen Trog überwiegend Karbonate abgelagert. Erste Bryozoenbioherme sind bereits aus der Oberkreide bekannt. Die meisten der Bryozoen-Mounds entstanden jedoch im Dan B und C. Korallen bauten erst im Dan C biogene Strukturen auf. Von den etwa fünf Korallenkalk-Lokalitäten im Dänisch-Polnischen Trog ist Fakse aufgrund der Aufschlußverhältnisse und der Mächtigkeit der Korallenkalke (ca. 50m) die wichtigste.

Paläontologische und sedimentologische Daten machen eine Deutung der Korallen-Mounds als "Kalt- und Tiefwasser-Riffe" wahrscheinlich.

Kriterien hierfür sind: (1) Fehlen von Algen, (2) geringdiverse azooxanthellate Korallenassoziation, (3) Überwiegen von dendroiden Wuchsformen unter den Korallen, (4) die die Mounds umgebende pelagische Fazies, (5) Beteiligung von pelagischen Organismen an der Mikritbildung, (6) Zerstörung der Gerüstbildnerskelette überwiegend durch Bioerosion (7) moundförmige Struktur der Riffe, (8) Vorkommen in einer hohen Paläobreite.

Innerhalb der Mounds treten drei Faziestypen auf:
(1) Bryozoenkalk,
(2) Übergangsfazies Korallenkalk/Bryozoenkalk,
(3) Korallenkalk mit fünf Subfaziestypen, die anhand der jeweils dominierenden Korallengattungen unterschieden werden. Die Korallenmounds bestehen überwiegend aus den Faziestypen 2 und 3.

Die Diagenese ist durch frühdiagenetische marin-phreatische fibröse Zemente und spätdiagenetisch entstandene meteorisch-phreatische Hundezahnzemente sowie durch Verdrängung der karbonatischen Zemente durch Quarz charakterisiert.

Die Mounds wachsen asymmetrisch einer aus südlicher Richtung kommenden Strömung entgegen. Die maximale Länge der Mounds beträgt 200 m, die Höhe mindestens 30 m und die Breite 80 m. Die moundförmige Gestalt wird durch die interne Fazieszonierung verdeutlicht.

Die Gerüstbildner - koloniale Korallen, Hydrozoen und Oktokorallen - lebten, wie sich anhand der Morphologie nachweisen läßt, ohne Symbiose mit Zooxanthellen. Koloniebildende Scleractinier waren durch arborescente und dendroide Wuchsformen, die meisten Oktokorallen und Hydrozoen durch eine fächerförmige Wuchsform an eine heterotrophe Ernährung angepaßt. Durch starke Inkrustationen und intensive Anbohrung wurden die Gerüstbildner instabil und brachen leicht zusammen. Das Sediment zwischen ihnen war nicht lithifiziert.

Korallenmounds im SE-Atlantik in einer mit dem Dänisch-Polnischen Trog vergleichbaren Breite und Position legen eine Entstehung der Korallenmounds von Fakse in einer Tiefe von 100 - 300 m nahe.

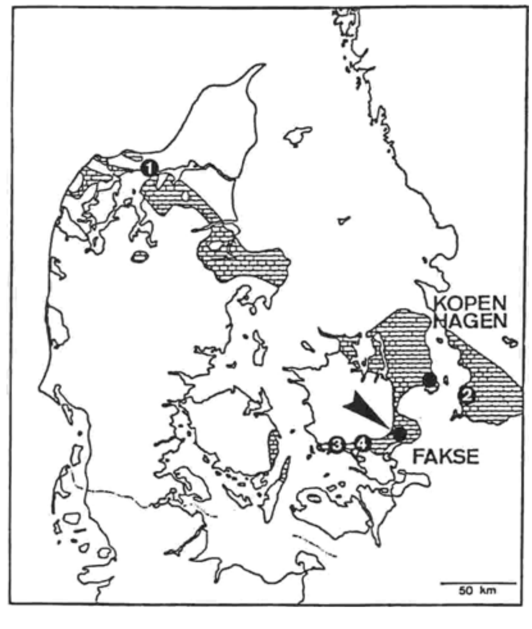


Fig. 1. Distribution of the Danian coral limestone localities. 1 = Aggersborggaard, 2 = Limhamn, 3 = Spjelderup, 4 = Herlufsholm.

Author	Locality	Time	Depth (m)	Temp. (C)	Coral Association
COATES & KAUFFMAN (1973)	Lamy, New Mexico	Turonian, Cretaceous	450 – 2850m	cold	*Septastrea crassa*
FLORIS (1980)	Fakse, Denmark	Danian Tertiary	50m	18	*Dendrophyllia candelabrum* *Faksephyllia faxoensis* *Oculina becki*
FLORIS (1972)	Nugssuaq, Greenland	Danian, Tertiary	80m	?	*Dendrophyllia candelabrum* *Faksephyllia faxoensis* *Oculina becki* *Lophelia sp.?*
HOLLAND & GABRIELSON (1979)	Limhamn, Sweden	Danian, Tertiary	photic	?	*Dendrophyllia candelabrum* *Faksephyllia faxoensis* *Oculina becki*
SQUIRES (1964)	Hinakura, New Zealand	Miocene, Tertiary	1500 – 2500m	2–3	*Lophelia parvisepta*
SQUIRES (1964)	Lake Ferry, New Zealand	Pliocene, Tertiary	150 – 600m	?	*Lophelia parvisepta*
BAILEY & TEDESCO (1986)	North Carolina	Pliocene, Tertiary	< 30m	cold	*Septastrea crassa*

Tab. 1. Summarized physical and biological data of fossil deep-water coral mounds.

1 INTRODUCTION

Reefs do form not only in warm, shallow waters of the circum-equatorial realm but also in cooler temperate waters and at greater depths. Examples of such organic buildups are found both in Recent environments and in Mesozoic and Tertiary rocks (Eliuk 1988, Stanley & Cairns 1988). The symbiosis between the vegetative stage of endosymbiotic dinoflagellate algae (zooxanthellae) and coral polyps is of major importance to the overall success of reefs growing in the photic zone and preferring warm clear water. However, the absence of symbiosis does not prevent the growth of reefs in the aphotic zone (Fagerstrom 1987). Azooxanthellate corals occur both within the aphotic and the photic zone. Zooxanthellate as well as azooxanthellate corals may act as framebuilding (hermatypic) organisms or as non-framebuilding (ahermatypic) organisms within the photic zone as well as within the aphotic zone. Schuhmacher & Zibrowius (1985) distinguished between constructional and non-constructional corals, describing the moundbuilding or non-moundbuilding potential of the corals.

Many of these cold and deep-water coral mounds have undergone a multi-stage development from colony to thicket to coppice to bank (Squires 1964). This evolution is accomplished by a breakdown of the framebuilders and by baffling of fine-grained carbonate sediment.

Recent and subrecent deep-water scleractinian banks have been described, among others, by Gruvel (1923), Dons (1944), Le Danois (1948), Moore & Bullis (1960), Allen & Wells (1962), Stetson et al. (1962), Squires (1965), Neumann & Ball (1970), Neumann et al. (1977), Reed (1980), Mullins et al. (1981), Fricke & Hottinger (1983), Dullo (1984), Newton et al. (1987) and Eliuk (1988).

The fossil record of constructional azooxanthellate and ahermatypic corals is scanty, partly because of difficulties in the differentiating them from shallow-water corals. Examples are sporadic in stratigraphic distribution and might extend back to the Triassic (Stanley 1981), perhaps to the Paleozoic (Talent 1988). The most notable reports are from the Tertiary (Tab. 1).

The criteria used for the recognition of Ancient deep-water coral banks include (Teichert 1958, Mullins et al. 1981, Cairns & Stanley 1982, Stanley & Cairns 1988, Talent 1988):

— absence of calcareous algae and algal borings
— low-diversity azooxantellate coral communities
— dominance of colonial corals with large individual coralla
— arborescent to dendroid coralla with relatively thin fragile branches
— breakdown of coral framework predominantly by bioerosion rather than by mechanical destruction
— admixture of open-marine planktonic organisms and corals
— mound-like or bank-like shapes of the biogenic structures

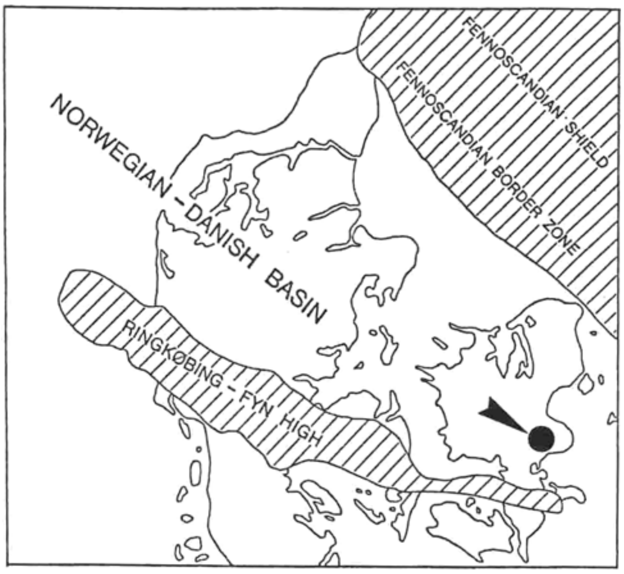


Fig. 2. Paleogeographic reconstruction of the Danish-Polish Trough.

- interfingering with pelagic sediments
- occurrence at high paleolatitudes
- C- and O isotope patterns

These criteria are tested by a case study resulting from the paleontological and microfacies analysis of lowermost Tertiary coral mounds in southern Denmark (Fig. 1).

2 CASE STUDY: DANIAN CORAL LIMESTONES OF FAKSE

The coral limestones were studied with regard to facies types (based on field observations and microfacies), diagenesis (based on thin-section and SEM analysis) and paleontological criteria. The paleontological investigation focussed on the major framebuilders as well as on the biogenic encrustation patterns. The coral mounds are defined by geometry and by the composition of the predominantly bioclastic sediment. These data are used in the reconstruction of the development of the coral mounds and in the discussion of the paleobathymetry.

2.1 Location, stratigraphy, paleogeography

The quarry of Fakse (Fig. 1) and the cliffs of Stevns Klint are type localities of the Danien stage (Desor 1847). Fakse is located in the Danish-Polish Trough (Fig. 2), which is bordered by the Fennoscandian Shield in the north and the Ringköbing-Fyn High in the south. During the Maastrichtian and Danian carbonate sedimentation prevailed. Using the spines of the echinid *Tylocidaris*, the Danian has been subdivided into four members (A - D). Recent zonations are based on planktonic foraminifera (Blow 1979), dinoflagellates (Hansen 1977) and coccoliths (Perch-Nielsen 1979). Member A starts with the Fish Clay, a thin marl layer containing fish-scales and -bones. The overlying Cerithium Chalk is heavily bioturbated. Descriptions of the Danian member A and B are given by Rosenkrantz (1937). Danian B is characterized by bryozoan mounds investigated by Thomsen (1976, 1977 a,b, 1983). Bryozoan limestones prevailed during the Danian B to D, whereas coral limestones are confined to the Danian C. In addition to the Fakse area, coral limestone outcrops are known from Aggersborggaard, Denmark (Ødum, 1926), Limnham, Sweden (Holland & Gabrielson, 1979; also called Annetorp: Steenstrup, 1867) and Nûgssuaq, Greenland (Floris, 1972).

In Fakse, the coral limestone reaches its greatest thickness (about 50 m). It is also known from boreholes at Spjelderup (Milthers, 1907) and Herlufsholm, Denmark (Rosenkrantz, 1937) (Fig. 1). For other localities see Floris (1980).

Bryozoan limestones of Danian D age occur together with resediments ("Trümmerkalk"), partly covered by Selandian clays and sands.

2.2 Facies patterns

Three facies types can be differentiated according to the number of bryozoans and corals. Quantitative criteria are based on point-counter analysis of thin-sections as well as on field observations.

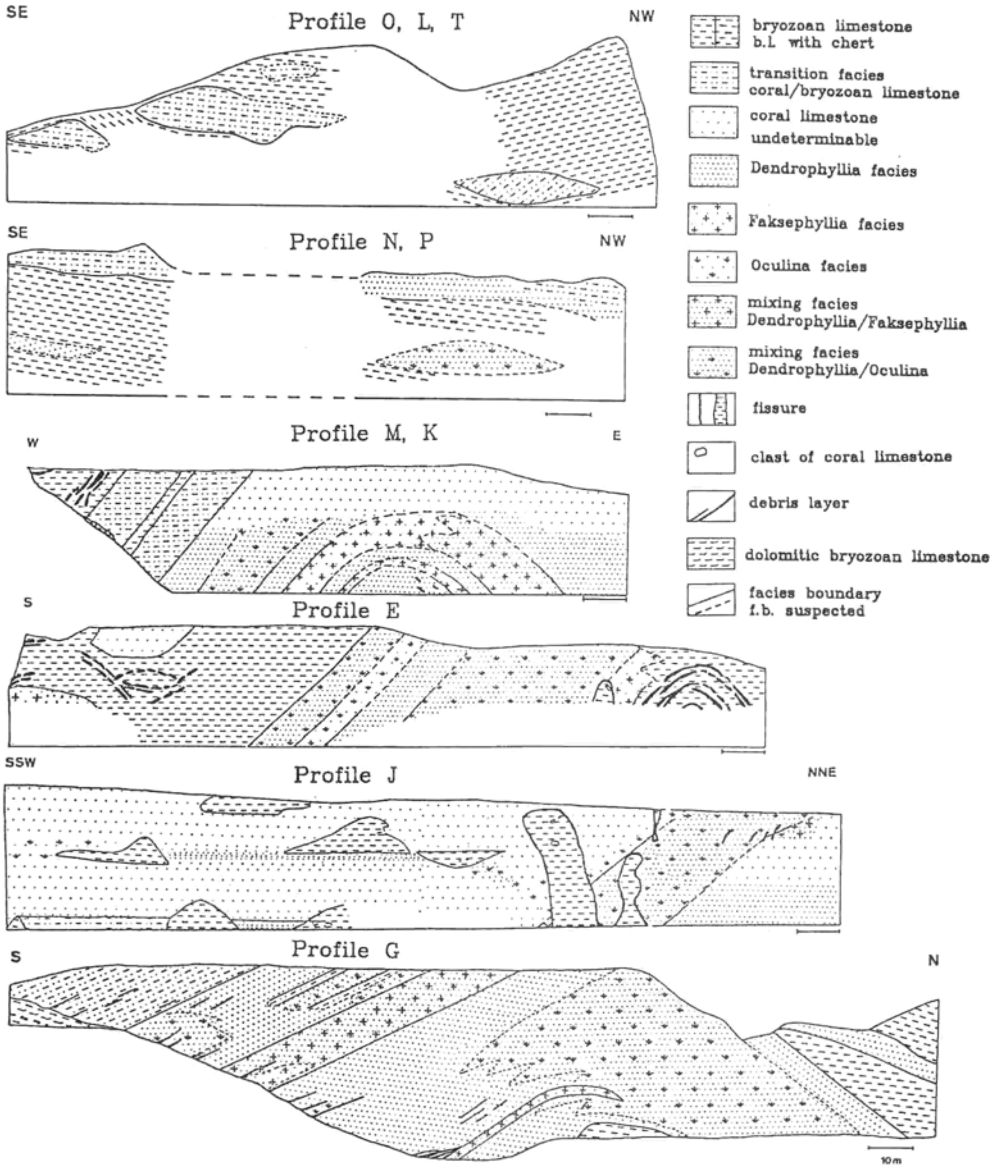
The main facies types, represented by bryozoan limestones and coral limestones, can easily be differentiated in the quarry and they have already been described by Fischer-Benzon (1866). Profiles described by Rosenkrantz (1937) and Floris (1979 b, 1980) show the distribution of these facies types. Parautochthonous layers within coral limestones were recognized by Rosenkrantz (1937, "raslaeg") and Floris (1980, "zonated coral limestone"), but a description of the internal structure and the mound-like shape is missing.

2.2.1 Definition of facies types

Bryozoan limestones

The typical bryozoan limestone is a chalky, poorly lithified sediment. Bedding and a mound structure are emphasized by cherts and dolomitic concretions. Dolomitization is confined to small areas only. The faunal assemblage clearly differs from that of the coral limestones and of the transitional facies:

- the bulk of the skeletal grains consists of cheilostome and cyclostome bryozoans
- the bryozoan/micrite ratio varies greatly and may be less than 1
- colonial scleractinians and hydrozoans are missing
- octocorals, especially *Moltkia isis*, are represented by large colonies
- the associated fauna is low-diverse



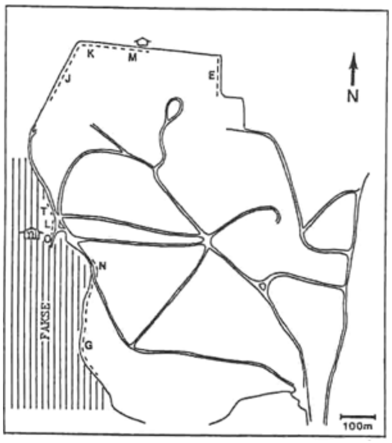


Fig. 3. Profiles of the coral limestone with internal zonation.

The "*Moltkia* limestone" differentiated by Rosenkrantz (1937) is included within the bryozoan limestone because of its similar microfacies.

Transitional facies coral/bryozoan limestones (Pl. 33/1, 2)

This type, occurring at the top of the coral mounds, is characterized by massive limestones containing more than 50% bryozoans and a varying number of coral colonies. Some smaller, lenticular-shaped bioherms consist only of this facies. The facies type is defined by the following criteria:

-- the number of corals varies strongly
-- *Dendrophyllia* and *Oculina* are more common than *Faksephyllia*
-- the ratio bryozoans/corals is >1
-- bryozoan encrustations of corals are thicker than within the coral limestones
-- octocorals and hydrozoans are rare
-- occurrence of sponges and sponge spicules
-- burrows of thallassinoid crustaceans

Coral limestones (Pl. 26)

Field observations resulted in a subdivision of the coral limestones into five subfacies types according to the dom-

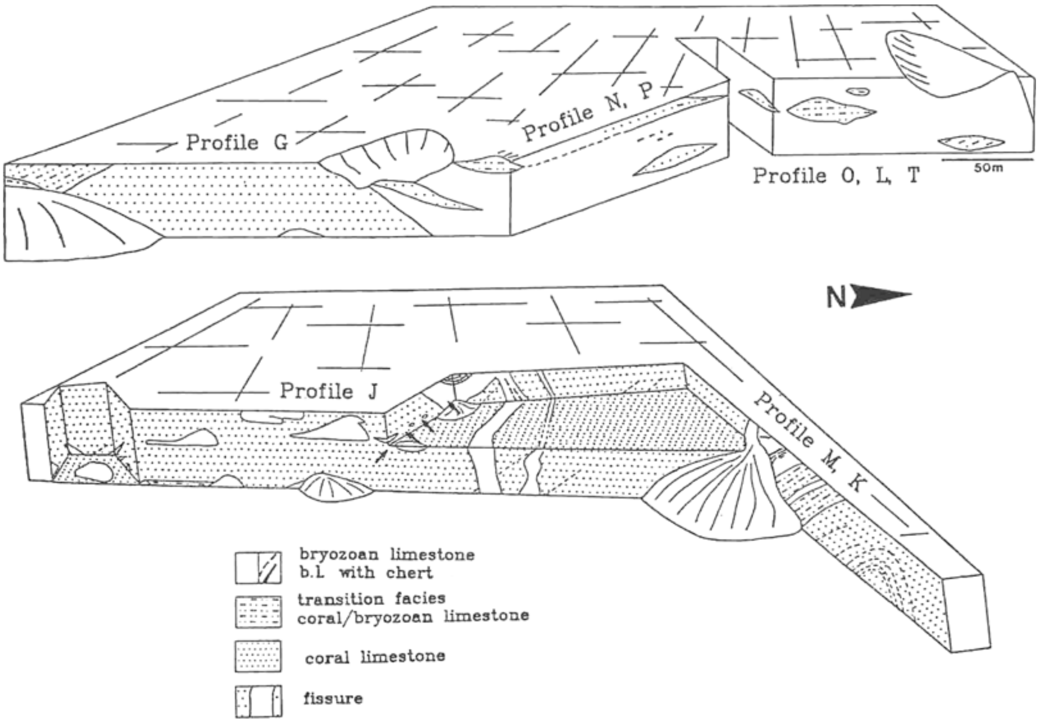


Fig. 4. Distribution of the facies types in the northern (profiles J, K, M) and southern part (profiles G, L, N, O, P) of the Fakse quarry.

inance of *Dendrophyllia candelabrum, Faksephyllia faxoensis* and *Oculina becki* (Fig. 3). Microfacies analysis offered no additional possibilities for defining subfacies types. Bryozoans, hydrozoans and octocorals are present everywhere within the coral facies, but occur with varying frequencies. Characteristic facies fossils are missing. The associated fauna of the coral limestones is more highly diverse than that of the bryozoan limestones.

Dendrophyllia subfacies (Pl. 26/1, 2)

- the dominating coral species is *Dendrophyllia candelabrum*.
- octocorals and stylasterine hydrozoans are abundant
- bryozoans are more common than within the *Faksephyllia* subfacies.

Faksephyllia subfacies (Pl. 26/3, 4)

- the dominating coral species is *Faksephyllia faxoensis*
- octocorals and stylasterine hydrozoans are rare
- bryozoans are rare

Oculina subfacies (Pl. 26/5, 6)

- the dominating coral species is *Oculina becki*
- octocorals and stylasterine hydrozoans are rare
- bryozoans are more common than in the *Faksephyllia* subfacies

Dendrophyllia/Oculina subfacies and *Dendrophyllia/Faksephyllia* subfacies

- *Dendrophyllia candelabrum* and *Oculina becki* respectively *D. candelabrum* and *Faksephyllia faxoensis* occur with approximately the same proportions
- octocorals and stylasterine hydrozoans are less common than within the *Dendrophyllia* subfacies
- bryozoans are rare

Transitions between *Dendrophyllia* facies and *Oculina* facies (mixing facies *Dendrophyllia/Oculina*) or *Dendrophyllia* facies and *Faksephyllia* facies (mixing facies *Dendrophylia/Faksephyllia*) occur.

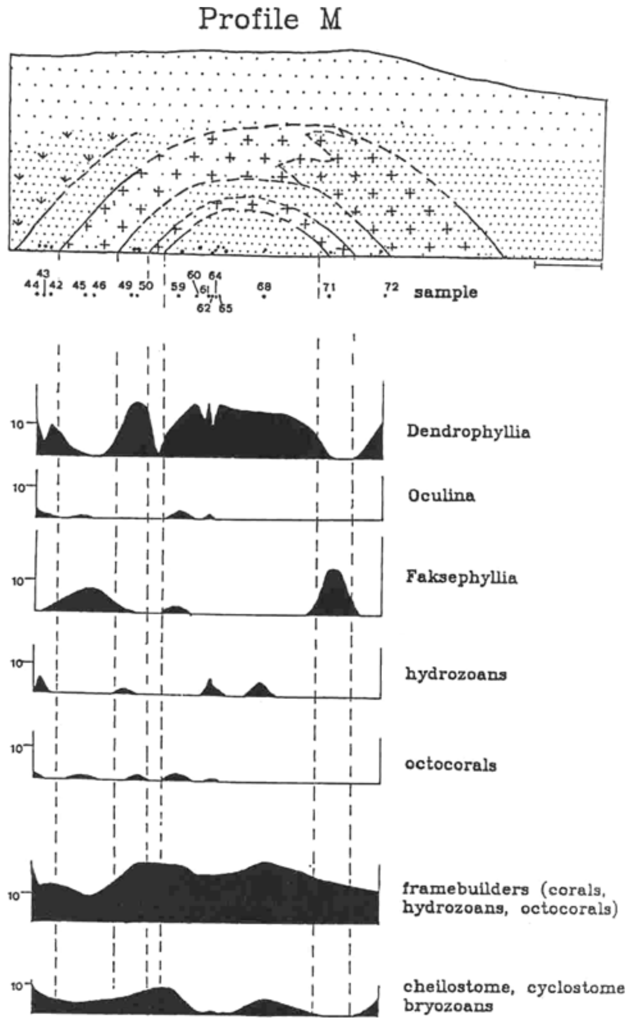
2.2.2 Facies boundaries

The coral mounds are underlain by the bryozoan facies and overlain by bryozoan limestones or by the transitional facies. There is a distinct boundary between the underlying bryozoan limestones and the coral limestone. The transitional facies develops from the coral facies by a decrease in the number of corals. Generally, the transional facies is overlain by the bryozoan facies (Profile G; cf Chapter 2.2.3).

The boundaries between the subfacies types within the coral limestone (except those of the *Faksephyllia* subfacies) are characterized by a gradual change in the dominating coral taxa.

2.2.3 Profiles

Profiles exhibiting different sections of a few mounds are drawn at a scale of 1: 500 (Fig. 3, 4). Profiles G and E are interpreted as longitudinal sections through large, extremely differentiated mounds. The base is formed by bryozoan mounds. Flint layers underscore the bedding. The zonation



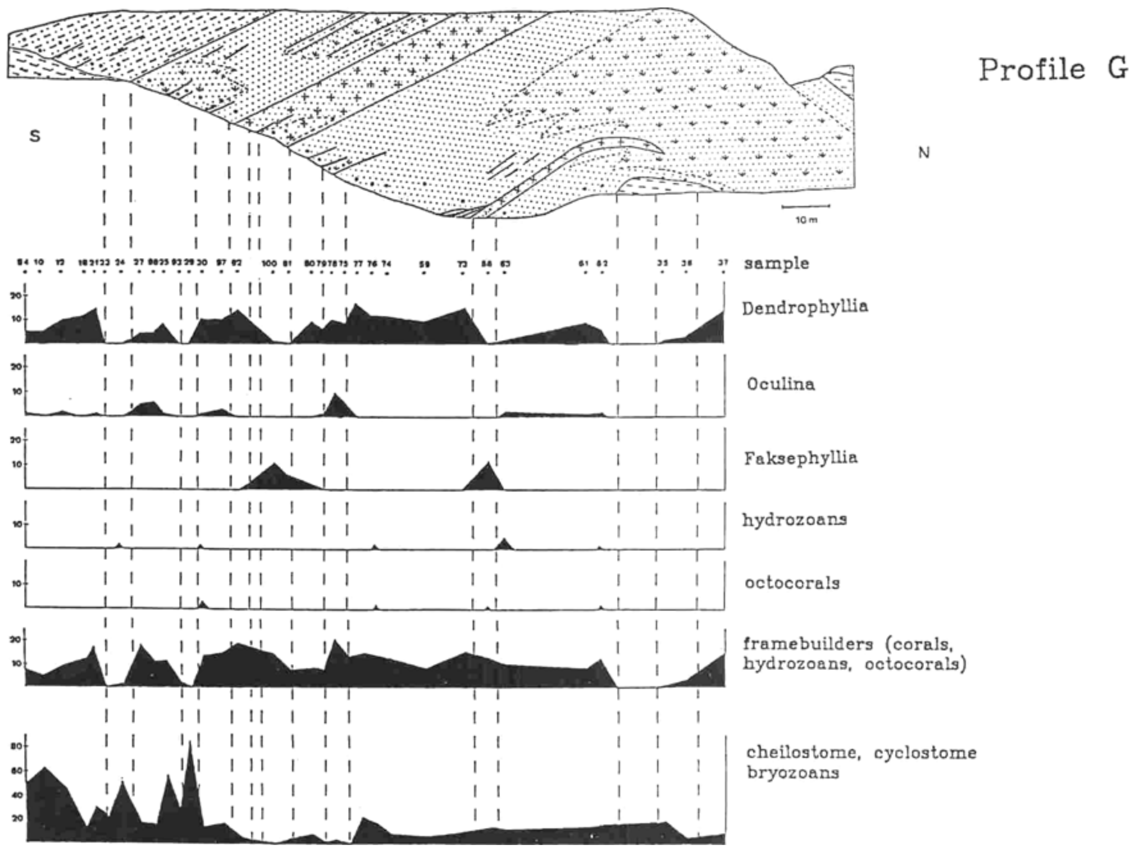


Fig. 5. Longitudinal section (profile G) and cross section (profile M) showing the statistical distribution of the corals and bryozoans (grain number analysis).

of the coral limestone in profile G emphasizes the asymmetrical shape. The southern flank containing several thin debris layers (see Chapter 2.5.3) is thicker and more differentiated than the northern flank. The dipping of the facies boundaries and the debris layers is 20°- 25°. The top of the coral mounds is formed by bryozoan limestones. The coral facies of the northern flank interfingers with the bryozoan facies. The transition facies occurs at the southern flank. It grades into the bryozoan limestone by alternating with the coral facies.

Two mounds seem to adjoin, forming an intermound facies in the southern part of profile E. This is indicated by the different dipping of the flanks and by a bowl structure of the chert layers. Profile J, a parallel section to profile E, shows southward dipping flanks in the northern part and interfingering of coral and bryozoan limestones in the southern part. The facies boundaries and the bedding within the bryozoan mounds are horizontal. The bowl structure in the center of profile J is comparable with that of profile E. Coral limestone clasts within the chalky bryozoan limestone point to an interpretation as an intermound facies.

Several fissures (10 cm to 10 m in diameter, cf Fig. 12) intersect the coral mounds vertically. They are filled by partly graded bryozoan packstone and angular coral limestone clasts, up to 50 cm in size.

Profile M is regarded as a cross section of a mound. The facies types underscore the symmetrical shape. The west-

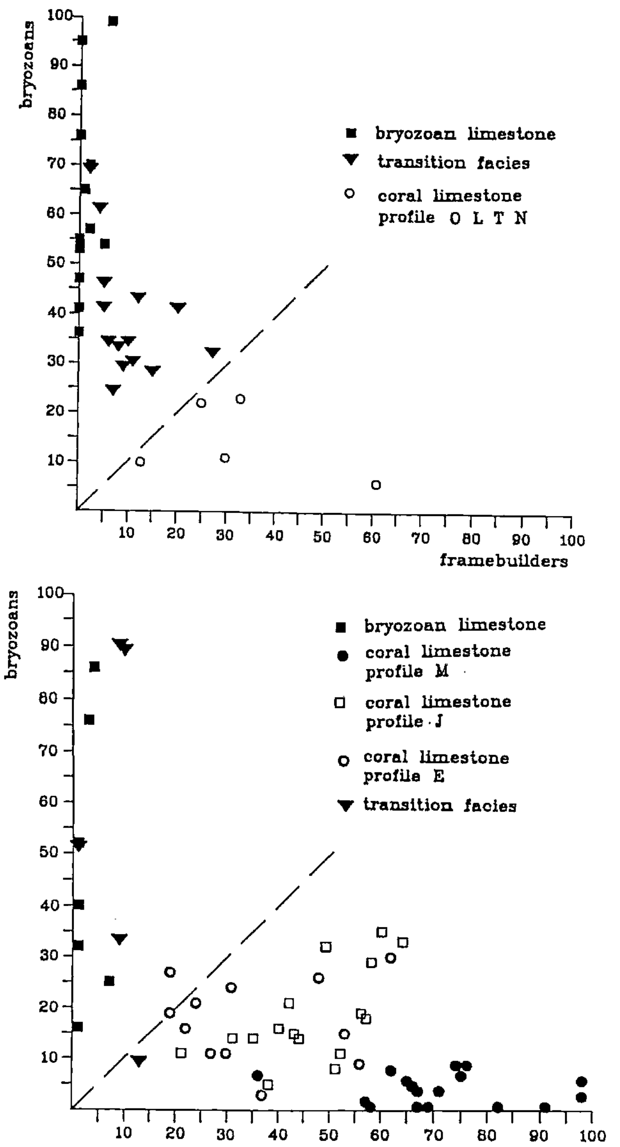


Fig. 6. Proportion of framebuilders and bryozoans (point counting analysis) in different facies types and different profiles. Note the characteristic proportion in each profile.

ward dipping flank shows the transition to the overlying bryozoan limestone.

The small lenticular mounds represented by the profiles N, P, O, L, and T cannot be differentiated. An internal structure is missing. The facies type corresponds to the transitional facies. Profiles N, P, O describe a single mound; profile O is a cross section, N and P are longitudinal sections. Profile T exhibits only transitional facies with southward dipping beds containing a significant number of corals. In the center of profile L, large autochthonous or toppled corals belonging to *Dendrophyllia*, *Oculina* and *Faksephyllia*, are relatively frequent. Large colonies occurring in situ or having just toppled were observed in the profiles M, G and L.

Quantitative facies analysis

The frequency of framebuilding organisms and bryozoans was measured by using the point-counter method (300 point grid, spacing 2 mm) and by grain number analysis (unit area 3x4 cm) in 130 thin-sections (Fig. 5). The number of corals and bryozoans in the coral limestones is more strongly controlled by the local situation represented by the profiles than by the facies types (Fig. 6). Nevertheless, the ratio of corals and bryozoans may be used to separate the coral facies and the transitional facies.

The subfacies types of the coral facies can be not distinguished by the number of micrite, framebuilders or open pores (Fig. 7).

Quantitative investigations of the total biota emphasize the low diversity of the bryozoan limestones and the lack of characteristic facies fossils within the coral limestones (Tab. 2). The diversity of framebuilding organisms was calculated using the Shannon-Weaver Information Theory Index. Data were collected from the statistical analysis of thin-sections. Bryozoans were not considered because they could not be determined in thin-sections. Only corals, octocorals and hydrozoans were used. The index varies within the *Faksephyllia* subfacies and *Oculina* subfacies between 0 and 0.6. In *Dendrophyllia* facies and the *Dendrophyllia/Oculina* facies the intervall extends from 0 to 1. Compared with tropical reefs (Crame 1980; Dullo 1987) the diversity is low.

2.3 Diagenesis

Diagenetic criteria of the corals, already observable in the quarry, led to the recognition of four diagenesis types (Tab. 3), which correspond in part to those described by Rosenkrantz & Rasmussen (1960). These types are defined by the preservation of the corals, by the preservation of coccoliths and by the lithification type of the calcareous ooze. Aragonitic skeletons (e.g. corals or gastropods) are either converted into calcite or dissolved. Well-preserved fossils within unlithified micrite characterize diagenesis type 1 (Pls. 29/1-3; 30/5-12; 32/1-4, 6-9).

Distribution of diagenesis types does not seem be not controlled by primary facies types.

The diagenetic criteria were studied by thin-section and cathodoluminescence analysis (Technosyn 8200 MK 2; 15 kV, 400 nA), the preservation of the coccoliths by SEM. The carbonate content of 16 samples from different facies varies between 98 - 99 % $CaCO_3$. Calcite cement and quartz cement were distinguished by staining with Alizarine-S.

The diagenetic stages are summarized in Tab. 4 and illustrated in Fig. 8.

2.3.1 Early diagenesis

Bioturbation (Pl. 26/1) and the lack of encrustations and borings indicate slow lithification of the lime mud. The first lithification probably took place within the sediment. This is indicated by the sealing of early marine-phreatic cements within intraskeletal voids of calcitic bioclasts (e.g. brachiopod shells, Pl. 28/4). These fibrous or bladed cements some-

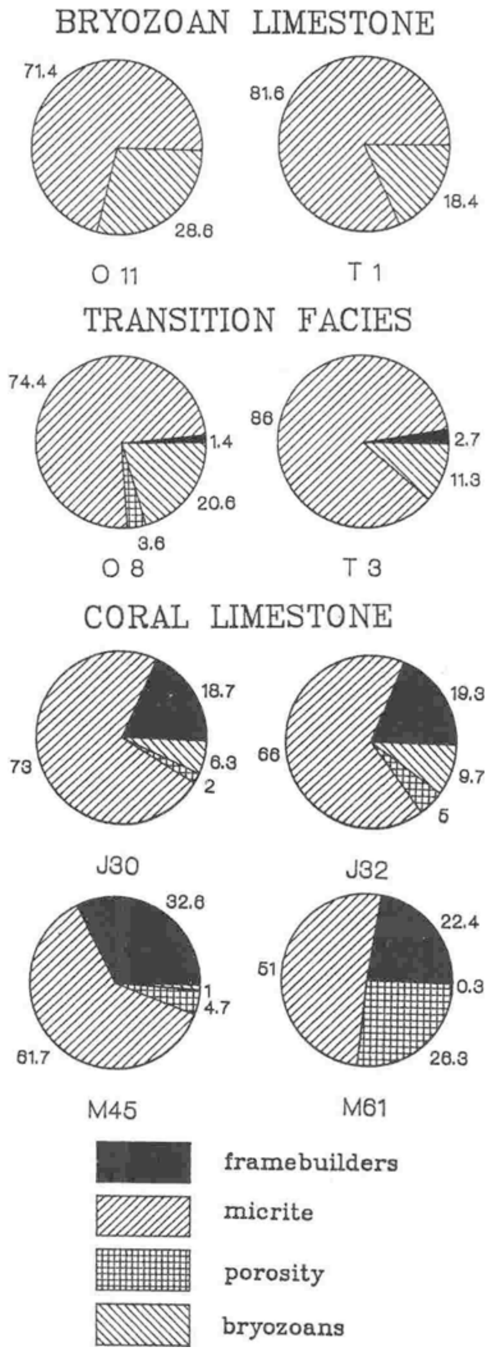


Fig. 7. Percentage of skeletal grains (framebuilders), micrite and open porosity in the facies types of the Danian reef limestones of Fakse (point counting analysis).

times consist of two generations. The first generation is formed by smaller crystals (0.88 mm in size), the second by larger crystals (3 mm). Layers with variously sized and packed peloids occur below these cements and alternating with them. Similar peloids were described by MACINTYRE (1985) and CHAFETZ (1986). Some cavities were geopetally filled with a homogenous sediment withoutfossils subsequent to cementation (Pl. 28/1). Rim cements are developed within debris layers and in fissures (Pl. 28/2). They are believed to be of marine phreatic origin.

2.3.2 Late diagenesis

During late diagenesis aragonitic skeleton were either dissolved or converted into calcite. Recrystallization of the marine phreatic cements resulted in the formation of cloudy rims showing no crystal boundaries under plane polarized light. Blocky cements are visible under crossed Nicols, relictic fibrous structures by cathodoluminescence.

Cathodoluminescence investigation of distinct dog-tooth cements of late diagenetic origin resulted in the recognition of a characteristic sequence (Fig. 8):

- -- dark non-luminescent phase
- -- small bright luminescent phase
- -- broad red luminescent phase.

Quartz cements are represented by two varieties: (1) Microquartz displaces calcite cements. The displacement

	sample	facies type	octocorals	hydrozoans	echinoderms	echinoid spines	globigerinids	lenticulinids	ostracods	*Porina salebrosa*	*Floridina gothica*	*Columnotheca cribrosa*	encrusting bryozoans	brachiopods	serpulid worms	sponge spicules
PROFILE G	82	D	■		■		■		■							
	100	F					■							■		
	81	F			■	■	■	■		■						
	80	D			■	■	■	■	■	■		■	■	■		
	79	D			■	■	■					■		■	■	
	78	D/O				■	■		■			■	■			
	75	D/O	■			■	■		■			■	■			
	77	D	■		■	■	■		■			■	■	■		
	76	D	■	■	■	■	■		■	■		■	■			
	74	D	■	■	■	■	■		■			■	■			
	59	D		■	■		■		■				■			
	73	D		■		■	■	■	■	■			■			
	60	F	■		■		■	■		■			■			
	56	F					■	■					■			
	63	D		■			■		■				■			
	61	D			■	■	■	■					■			
	62	D	■	■	■	■							■			
	57	D	■		■					■			■			
	58	D					■						■			
	54	D/O							■	■			■			
	55	D/O	■	■		■			■				■			
	35	D	■			■				■		■	■			
	36	D					■		■						■	
	37	D		■			■			■			■			
	38	D/O	■		■	■							■		■	
	39	D					■		■							
	53	D	■		■	■									■	
	44	D	■		■	■	■	■		■		■	■	■	■	
	95	D	■	■		■	■					■	■	■	■	
PROFILE T	4	U	■			■	■			■			■			
	5	U					■			■	■		■		■	■
	6	D			■		■			■	■				■	
	7	D	■		■	■	■		■			■		■		■
	10	U	■		■	■					■		■		■	
	11	U			■	■	■	■	■	■			■	■	■	■
	12	BK			■	■	■							■	■	
	13	U			■	■	■			■				■		
	14	U	■			■	■			■		■	■			
	15	U	■		■	■	■			■			■	■	■	■
PROFILE M	73	D/O	■	■	■	■					■	■		■		
	44	D	■	■		■		■	■				■	■	■	
	43	D	■	■								■		■		
	42	D	■	■		■	■		■			■	■			■
	45	F	■	■		■		■				■	■			■
	46	F		■		■		■	■			■	■			
	49	D	■	■		■			■			■	■			■
	50	D	■	■	■	■						■				
	59	D	■		■	■	■	■				■	■			■
	60	D				■		■	■			■	■			
	64	D		■	■	■		■	■		■	■	■	■		■
	62	D	■	■		■		■	■							
	61	D	■			■		■								■
	65	D		■		■	■	■				■	■			■
	66	D	■					■				■	■			■
	68	D	■	■	■	■	■	■	■			■	■	■		■
	71	F			■	■	■	■	■			■				■
	72	D	■	■	■		■	■	■			■	■	■		■

Tab. 2. Quantitative distribution of fossils in thin-sections . D = *Dendorphyllia* subfacies, O = *Oculina* subfacies, F = *Faksephyllia* subfacies, D/O = *Dendrophyllia/Oculina* subfacies, BK = bryozoan limestone; U = Transitional facies

	micrite	preservation of corals
1	unlithified coccoliths well preserved	converted into calcite
2	strongly cemented coccoliths well preserved framework porosity	converted into calcite
3	cemented coccoliths dissolved moldic and vug porosity	partly dissolved or sediment casts
4	weakly cemented coccoliths strongly dissolved	sediment casts or soluted

Tab. 3. Diagenesis types of the coral limestone of Fakse. The types are defined by the preservation of corals and coccoliths and by the different cementation of the limestones.

marine phreatic	$CaCO_3$	fibrous cement
		rim cement
meteoric phreatic	$CaCO_3$	rim cement
		blocky cement
		dog tooth
	SiO_2	microquartz
		blocky cement

Tab. 4. Diagenetic stages occurring in the coral limestones of Fakse, Denmark.

starts at the boundary sediment/cement affecting predominantly fibrous cements. In the beginning microquartz occurs only as a small rim. Later it increases to form a brecciated texture (Fig 9). (2) Blocky cement seals the remaining pores (Pl. 28/3).

The solution of aragonite, neomorphism of calcite and dog tooth cements indicate diagenesis both under meteoric-phreatic conditions or within a deeper and colder marine phreatic environment. Meteoric-phreatic diagenesis is more reasonable because of the regression during the Danian D (Ödum 1926) and the increase in water temperatures subsequent to the Danian (Buchhardt 1978).

2.4 Paleontological criteria

The interpretation of the coral mounds and of the paleoenvironment is based primarily on the composition, diversity and ecological patterns of the biota.

2.4.1 Framebuilding organisms

The framebuilders of the coral limestone are azooxanthellate, ahermatypic and constructional. A rigid framework is missing. Colonial corals, stylasterine hydrozoans and octocorals are the most important groups. Solitary corals are of no importance.

Colonial scleractinian corals

The aragonitic skeleton is converted into calcite or dissolved (sediment casts, diagenesis type 2 and 3, cf Chap-

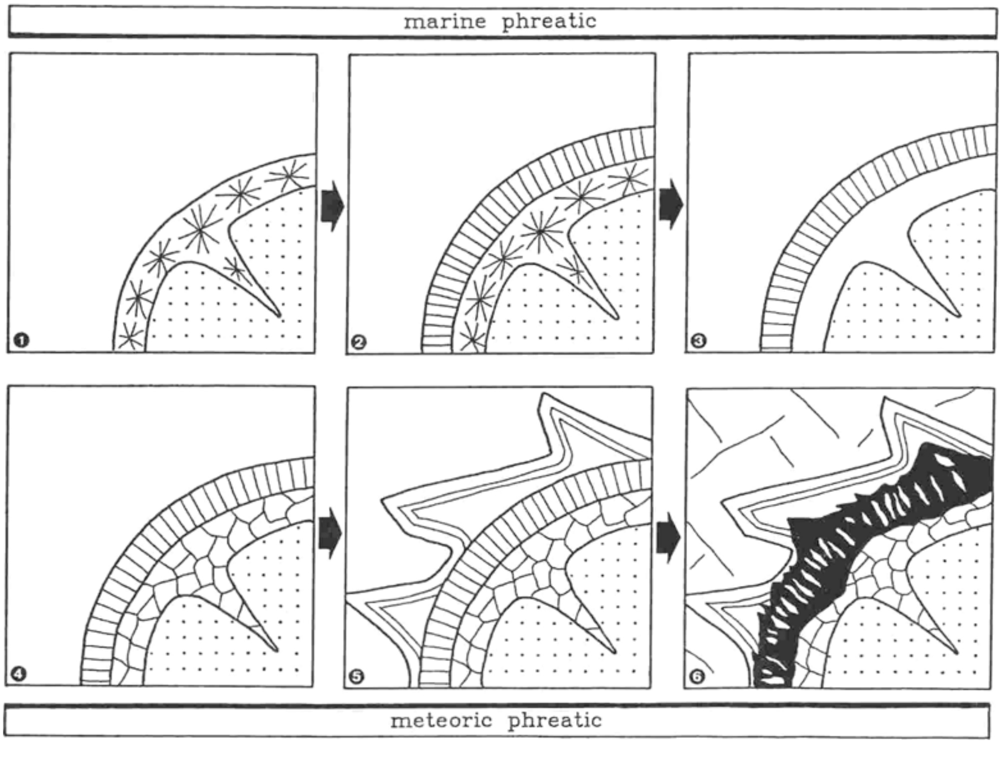


Fig. 8. Coral diagenesis:
(1) primary aragonitic structure
(2) marine fibrous cement
(3) solution of the aragonitic skeletal grains
(4) blocky calcite
(5) dog-tooth cement with three generations
(6) microquartz replaces calcite leaving relictic structures of fibrous cement; blocky quartz seales the remaining pores.

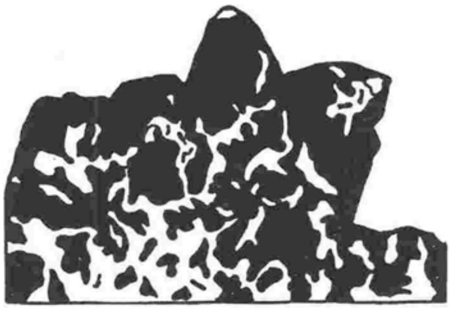


Fig. 9. Late diagenetic microquartz (white) replaces calcite (black). Width of figure is 1.5 mm.

ter2.3). Dissolved corals can only be distinguished by the diameter of the molds (Fig. 10) and by the mode of budding. The corals were described by LYELL (1835), HENNIG (1899a), NIELSEN (1922) and FLORIS (1972, 1979a). *Dendrophyllia candelabrum* HENNIG was compared with a Recent species of *Dendrophyllia* (WELLS 1954; CAIRNS 1979; ZIBROWIUS 1980).

Dendrophyllia candelabrum HENNIG 1899
(Pls. 26/1, 2; 29/1-4; 30/1, 2)

Dendrophyllia candelabrum is the most frequent coral in Fakse. It is represented by dendroid colonies with extratentacular, normally rectangular budding. The spacing of the budding varies between a few millimeters and 3 cm. Subsequent to the budding the coral branches grow parallel to the parent branch. If neighbouring corallites approach each other, they fuse by building a coenosteum or change their directions without touching each other. The colonies reach at last 50 cm in height. A synapticulothecal, distinctly porous wall is formed by septal sclerodermites. Septa are inserted in four cycles, following Pourtalès Plan. The fourth cycle is incomplete. The number of septa varies between 28 and 34. A spongy columella is developed. Small calyces are circular to elliptical in outline. Their diameters vary between 0.20 and 0.35 cm, the diameter of the branches between 0.2 and 0.4 cm (Fig. 10). The wall is sculptured by costae and granules or is smooth.

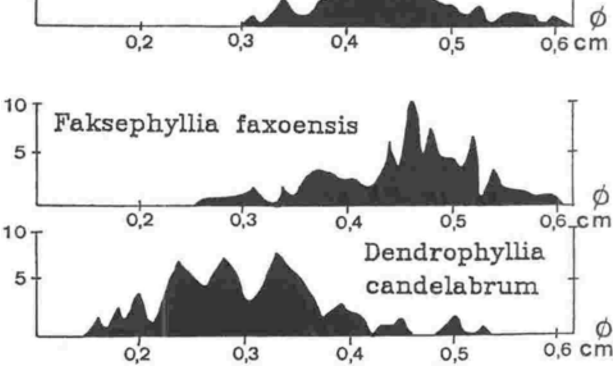


Fig. 10. Branch diameter of colonial corals from Fakse.

Molds of *Dendrophyllia candelabrum* can be easily distinguished from *Faksephyllia faxoensis* by extratentacular budding and a smaller branch diameter, and from *Oculina becki* by the asymmetrical budding spacing.

Faksephyllia faxoensis (BECK, 1835)
(Pls. 26/3,4 ; 29/5-8; 30/3, 4)

The monospecific genus *Faksephyllia* is known only from the Danian of Fakse, Limhamn and from West Greenland (Nûgssuaq). The species is characterized by large (up to 1 m in height) phaceloid colonies with extratentacular budding (mostly distomodaeal). The spacing of the budding varies between 1 and 2 cm. The angle of budding varies between 20° and 30°. The wall is septothecal. Septae are arranged in 4 cycles, seldom following the Pourtalès Plan. The last cycle is incompletely developed. The number of septa varies between 32 and 36. The wall is smooth, costae are rare. Dissepiments may be present. A columella is weakly developed. The branch diameter varies between 0.4 and 0.5 cm (Fig. 10).

Molds are characterized by an irregular budding spacing and large diameters.

Oculina becki (NIELSEN, 1922)
(Pls. 26/5, 6; 29/9-12)

Dendroid colonies formed by extratentacular budding. The buds alternate regularly in two opposite rows and have a constant spacing of 1 and 1.2 cm. The angle of the buds varies between 50° and 55°. The growth form of the colony is unknown, because only broken branches have been found. Septa are arranged in three cycles (usually 24 septa). Septa belonging to older cycles may exhibit granules. Older specimens thickened their walls by stereome, they are often bored by clionid sponges. The wall is smooth or slightly granulated. Younger calyces have a deep fossa, whereas older calyces develop a papillose columella and pali. The diameter of the calyces varies between 0.20 and 0.30 cm; the diameter of the branches between 0.20 and 0.55 cm.

Compared with the original branch, the diameter of the sedimentary casts is very small. Isolated sedimentary casts can be easily confused with solitary corals. Imprints can be recognized by regular budding. Many sedimentary casts of clionid sponges represent heavily bored branches of this coral.

Hydrozoans

Recent species of *Millepora* are common constituents of tropical reefs occurring at depths not exceeding 30 m, whereas species of *Stylasterina* do not seem to be controlled by depth and latitudes.

Nielsen (1919) described 9 species of *Stylasterina* and one *Millepora* from the coral limestone of Fakse. Hickson (1906: 261-262) and Boschma (1951: 4-5) expressed doubt about the existence of Tertiary *Milleporids*. Boschma (1951: 15-16) questioned the assignment of *M. parva* to *Millepora*: "This arrangement of the dactylopores gives the coral an aspect entirely different from that of the recent species of the genus, so that it must remain doubtful whether or not the species really belongs to *Millepora*."

Criteria for the recognition of stylasterine hydrozoans are:

-- Growth form: Fan-shaped colonies with branches arranged in one plane having pores concentrated in the anterior direction (Pls. 30/ 9,10; 31/1). The pores of bushy colonies are irregularly scattered over the whole colony
-- The individual branches may anastomose or not, the cross section of the branches can be circular or elliptical.
-- Tabulae may occur in the gastropores
-- Gastropores and dactylopores
-- Gastrostyle and dactylostyle (vertical spine in the gastropores or dactylopores)
-- Cyclosystem, geometrically arranged dactylopores around one gastropore
-- Ampullae, round cavities in the coenosteum or at the surface
-- Type of the surface of the coenosteum.

Hydrozoans were described by Nielsen (1919), Boschma (1956) and Cairns (1983). Hydrozoans in thin-sections could not be determined (Pl. 27/5, 7). Most common hydrozoans are:

Sporadopora faxensis Nielsen,1919 (Pl. 30/9,10)

Only broken branches are known, but the concentration of the pores on the anterior side suggests a fan-like growth. The individual branches do not anastomose. The branch diameter ranges between 0.38 and 0.41 cm. In cross sections, individual branches are distally rounded. With increasing age, the cross-sections become more elliptical and long gastropore tubes with tabulae are developed. The dactylopores and gastropores of younger specimens are situated at the distal part of the branches. In older specimens the pores are concentrated at the anterior side. A fragile gastrostyle is only rarely preserved, a dactylostyle and a cyclosystem are missing. The surface of the coenosteum is smooth and slightly granulated. Ampullae are not visible; they are hidden within the coenosteum.

Errina lobata (Nielsen, 1919)
(Pls. 30/11; 32/6)

This common hydrozoan forms fan-like colonies up to 20 cm in height. One specimen is encrusted on *Dendrophyllia candelabrum*. The branch diameter varies between 0.28 and 0.88 cm, often 0.5 cm. *E. lobata* differs in size from other hydrozoans. Basal branches tend to anastomose strongly. Young specimens have gastro- and dactylopores on the distal part of their branches, whereas in older branches the pores are concentrated on the anterior side. A gastrostyle may be preserved, a dactylostyle and a cyclosystem are missing. Dactylopores are situated on grooved spines adjacent to the gastropores or on the branches.This arrangement of gastropores causes a nodular surface. Ampullae are hidden in the coenosteum. There are only a few pores on the surface of the coenosteum; the pores may be connected by narrow channels.

The genus *Errina* is restricted to the Danian.

Conopora arborescens Nielsen, 1919

Colonies are irregularly branched. The diameter of the thin juvenile branches measures 0.15 cm; it increases to 0.4 cm, attaining an elliptical shape. The branches may anastomose at the base of the colony. There is a cyclosystem composed of 8-10 dactylopores surrounding one gastropore. The dactylopores occur on an elevation, the gastropores at the base of the coenosteum. In young distal branches, the cyclosystems are situated at the two lateral edges. On older branches, cyclosystems are scattered over the whole branch. In this case, the cyclosystem may be covered by stereome. In well-preserved material the gastropore tube is constricted, forming two chambers. There is no gastrostyle and dactylostyle. Ampullae are superfically developed all over the colony. The surface of the coenosteum is smooth or slightly sculptured by dots.

Astya crassus (Nielsen, 1919)
(Pls. 30/12; 31/1-3, 5-6)

Hydrozoans with typical fan-like growth form. The largest colony is 17 cm in height. The branches tend to be extremely anastomosized. The cyclosystem is arranged in an anterior direction. The development of the cyclosystem is similar to *C. arborescens*.

Other not so common hydrozoans are represented by broken branches of *Congregopora nasiformis* Nielsen, 1919, *Errina (Inferiolabiata) irregularis* (Nielsen, 1919) and *Pliobothrus laevis* Nielsen, 1919.

Octocorals

The octocoral fauna of Fakse is well-known for its good preservation. Many species have been described by Nielsen (1913 b, 1917, 1918, 1925). Voigt (1958) summarized and illustrated four ontogenetic stages of the calcareous internodes of *Moltkia* :

-- juvenile specimens have distinct calyces, the articulation planes are visible at the proximal and distal side (Pl. 30/ 5, 7)
-- adult specimen have few or overgrown calyces; the surface of the internodes is granulated (Pl. 30/8).

Two species of *Moltkia* are framebuilding organisms in the coral limestone and important constituents of the bryozoan limestone as well. Only a few specimens of *Graphularia groenwalli* NIELSEN, 1915, *Primnoa costata* NIELSEN, 1913 and *Isis steenstrupi* NIELSEN, 1913 were collected in the bryozoan limestone. Specimens of *Gorgonella torta* NIELSEN, 1913, *Epiphaxum auloporides* LONSDALE, 1850 and *Primnoa costata* were found in the coral limestone and in the transition facies. They have no importance as framebuilders.

Moltkia isis STEENSTRUP, 1846
(Pls. 30/5, 6; 31/4; 32/5)

Juvenile internodes are compressed, with sympodially arranged elliptical calyces lying in a vertical row. They may fuse in places forming a groove. With increasing age the internodes become more cylindrical and the calyces spread all over the surface. Old internodes can be recognized by an absence of calyces and by large diameters up to 1.8 cm. In this stage they tend to overgrow the horny nodes by layers of calcite creating a massive corallum. An axial channel is missing. Adult specimens are heavily bored by clionid sponges. Investigations of recent Isididae show that calcification of the primary horny nodes reduces the flexibility of the colony. This has been interpreted as an adaptation to deeper water environments and slow current velocity (GRASSHOFF & ZIBROWIUS, 1983).

The bryozoan limestone of the northern part of profile G (Chapter 2.2.3) is interpreted as leeward sedimentation; it is colonized by many large fan-like colonies of *Moltkia isis*. The colonies have toppled. The observation of colonies exhibiting different ontogenetic stages permits a reconstruction of the growth form. The largest colony studied is 12 cm in height and 7 cm in width. The growth form is fan-like, emphasizing a unidirectional current pattern (Chapter 2.5.2).

In contrast only single internodes of mostly juvenile stages were found in the coral limestone. The colonial corals were probably better adapted for life in the coral mounds.

Moltkia lyelli NIELSEN, 1913
(Pls. 30/7, 8; 31/3)

Juvenile specimens are club-like with a round handle. An axial channel with tabulae is developed. The calyces are scattered over the surface. *M. lyelli* occurs in both the bryozoan limestones and coral limestones. The growth form of this species can be reconstructed by new paleontological data, showing an irregularly branching colony creeping around *Dendrophyllia candelabrum* and stylasterine hydrozoans. Interestingly, only very young specimens form this colony. Different ontogenetic stages occur in the bryozoan limestones. Life conditions of this species were probably less favourable in the coral facies, similar to *M. isis*.

Heliopora incrustans NIELSEN, 1917
(Pls. 31/5; 32/4)

This octocoral is confined to the coral limestone facies. It is of no importance as a framebuilder. The small encrusting colonies comprise 3 - 70 calyces. The coenosteum is composed of many vertical tubes. Large autopores (0.9 - 1.1 cm) and small siphonopores (0.1 - 0.2 cm) are visible at the surface of the colony. The autopores are rimmed and surrounded by 18 - 22 pseudosepta. They are 0.2 - 0.3 cm long and 0.1 - 0.2 cm broad.

2.4.2 Azooxanthellate character of the framebuilders

The recent species *H. coerulea* is an important zooxanthellate framebuilding organism in the Indopacific, forming rigid wave-resistent skeletons (see WELLS, 1954: Pl. 182). It occurs from the intertidal to the subtidal, down to a water depth of 30 m (COLGAN 1984). The life habit of this species has been considered to be similar to that of *H. incrustans*. This comparison was used in order to interprete the depositional environment of the coral limestones as being in the photic zone (FLORIS, 1980; see Chapter 3.2.1).

This interpretation is contradicted by the different grwoth form of *H. coerula* which forms large rigid colonies not comparable with the small incrusting colonies of *H. incrustans*. The genus *Heliopora* probably includes zooxanthellate species (*H. coerula* and *H. japonica*, described by EGUCHI 1948, from the Early Cretaceous) and azooxanthellate species (*H. lindströmi* and *H. tenera*, described by TRAUTH (1911) from the Late Cretaceous of Czechoslovakia). H. *incrustans* most probably should be included within the azooxantellate species. The existence of zooxantellate and azooxanthellate species within one genus is a widespread phenomenon in Recent corals (FAGERSTROM 1988).

Based on the criteria established by ROSEN (1977), MULLINS et al. (1981), GEISTER (1984) and COATES & JACKSON (1987) for azooxanthellate corals, most of the corals and hydrozoans occurring in Fakse should be regarded as azooxanthellate:

Colonial corals

- All corals have a bushy growth form (Pl. 30/1-4)
- Edge zone and coenosteum are only weakly developed
- The coral branches are separated and do not fuse. Each branch develops one calyx only (Pls. 29; 30/1-4).
- Compared with dendroid zooxanthellate counterparts, like *Acropora* or *Porites* the corallum consists only of relatively few calyces: *Dendrophyllia candelabrum* develops 50 - 60 and *Faksephyllia faxoensis* 40 - 50 calyces within an area of 6 x 6 cm
- The calyces have larger diameters (*Dendrophyllia candelabrum*: 0.20 - 0.35 cm; *Faksephyllia faxoensis*: 0.4 - 0.5 cm; *Oculina becki*: 0.2 - 0.3 cm) than those of zooxanthellate dendroid corals
- Recent and subrecent species of *Dendrophyllia* are cosmopolitic, azooxanthellate, constructional and ahermatypic corals. They form coral mounds in the Eastern Atlantic between Ireland and North Africa (LE DANOIS 1948: depth 200 - 450 m; GRUVEL 1923: 100 m), Niger Delta (ALLEN & WELLS 1962: 50 - 120 m) and in the Red

Sea (Fricke & Hottinger 983: 120 m; Dullo 1984: 500 m)

- Oculina occurs with and without zooxanthellae. Large colonies of *O. varicosa* up to 2 m in height live in deep waters off Florida, whereas in the photic zone smaller colonies with a diameter of less than 50 cm occur (Reed 1980, 1981)
- The endemic *Faksephyllia* belongs to the Parasmiliinae; this family is exclusively "ahermatypic" (Wells 1956)

Stylasterine hydrozoans and octocorals

- All hydrozoans of Fakse have similar growth forms., characterized by slender arborescent or fan-like colonies (Pl. 31/1, 3). Recent counterparts of these hydrozoans live preferentially in deeper and colder water (Cairns 1983)
- The growth form of *Moltkia isis* (Pl. 31/4) and *M. lyelli* is similar to that of hydrozoans, it resembles that of Recent octocorals living in the aphotic zone

2.4.3 Associated organisms

The biota of the coral facies associated with the framebuilders are highly diverse (Nielsen 1919, Ödum 1926).

Bryozoans

Berthelsen (1962) described 117 species occuring in Fakse. Five frequent species of erect cheilostome bryozoans can be used in paleoecological interpretations (Thomsen, 1977a):

Porina salebrosa Marsson, 1887 (Pl. 27/1, 2)
Floridina gothica d'Orbigny, 1850 (Pl. 27/4)
Columnotheca cribrosa Marsson, 1887 (Pl. 27/3)
Pachythecella lundgreni Pergens & Meunier, 1886
Onychocella columella Berthelsen, 1962

Incrusting bryozoans prefer framebuilders (Pls. 27/6, 8; 32/5) and oysters (Pl. 32/7) as substrates because of the smooth and extended surface. The minimal grain size for encrustation is 0.3 - 0.5 mm (Thomsen 1977b).

Morphology and distribution of bryozoans within the coral facies of the mounds permit the following generalizations:

- Paleoenvironment: Water movement was the most important factor controlling the morphology and distribution of bryozoans in the mounds (Cheetham 1971; Thomsen 1977a, b). Based on combined sedimentological and paleontological studies of the lower Danian bryozoan mounds of Karlby Klint and on flume channel experiments Thomsen (1976, 1977a, b, 1983) postulated a SE-NW current with low to medium velocity. This velocity was modified by the mound shape. It increased upslope on the southeastern flank, reached a maximum across the summit and decreased rapidly downslope on the leeward flank.
- Distribution: Rigid cylindrical branches with circular stem diameter (*Floridina gothica, Pachythecella lundgreni, Columnotheca cribrosa*) prefer low current velocities and occur preferentially on the downstream flank Bilamellar forms with elliptical cross sections (*Porina salebrosa, Onychocella columella*) and encrusting colonies are adapted to stronger water movement and dominate on the upstream flank
- Density: The proportion of the bryozoans is significantly higher on the upstream flank, depending on an increased nutrient supply carried by the water currents
- Morphological variation: *Porina salebrosa, Floridina gothica* and *Onychocella columella* are highly variable with respect to the size and thickness of walls. Stem diameter and wall thickness are larger on the upstream flank than on the downstream flank (Pl. 27/1, 2).

Solitary corals

Nielsen (1919) described 9 species, but only specimens of the genera *Smilotrochus, Parasmilia* and *Caryophyllia* (Pl. 32/1) were found during the study.

- Relation coral/substrate: Juvenile corals are attached to framebuilding organisms. In contrast, adult specimens are often found lying in the sediment, exhibiting a slightly eroded base. With increasing age and increasing thickness the corals become unstable and break off easily. Lying in the sediment they were able to survive and to change their growth direction by up to 90°.

Mollusks

- Bivalves were studied by Hennig (1899 c) and Ravn (1902b, 1933). *Isoarca obliquendata* Lundgren, 1867, *Chlamys monotiformis* (Hennig, 1899) and *Meiocardia faxensis* (Lundgren, 1867) are common. Apart from numerous epibenthonic species, other bivalves lived as endobenthos (e.g., *Cardium vogeli* Hennig, 1899). Two species of oysters, attached upon coral branches, are conspicuous (*Exogyra lateralis* Nilsson, 1827; Pls. 27/9; 1/2; 32/2; and *Ostrea semiplana* Sowerby; Pl. 32/7,9)
- Gastropods are represented by many species (Ravn 1902a, 1933; Schilder 1928). *Eocypraea bullaria* (Schlotheim, 1820), *Palaeocypraea spirata* (Schlotheim, 1820), *Pleurotomaria niloticiformis* Schlotheim (1820), *Tritonium subglabrum* Ravn (1902) and specimens of *Cerithium* are widespread within the coral limestone
- Cephalopods are represented only by rare nautilids (Ravn 1902) belonging to three species.

Arthropods

The coral limestone of Fakse is well known for its highly diverse decapod fauna (Fischer-Benzon 1866). *Dromiopsis rugosa* (Schlotheim, 1820), *Dromiopsis elegans* (Steenstrup & Forchhammer) and *Galathea strigifera* (Fischer-Benzon, 1866) are common. Y-shaped crustacean burrows with a diameter up to one centimeter seem to be restricted to the transitional facies.

Brachiopods

Common brachiopods of coral limestones are *Rhynchonella flustracea* (Schlotheim, 1820), *Rhynchonella danica* (Schlotheim, 1820) and Thecideidae (Pl. 32/7). The brachiopods were described by Nielsen (1911, 1914, 1921, 1928) and Backhaus (1959), the paleoecology was studied by Asgaard (1968).

Echinoderms

In comparison with crinoids (Nielsen 1913a) echinoids are abundant (Ravn 1927, 1928; Wind 1954, Brotzen 1959, Hennig1989). Undeterminable echinoderm plates are common in thin-sections.

Serpulids (Pl. 27/6, 8)

Framebuilding organisms and oysters are often encrusted by serpulids (*Serpula* and *Spirorbula*). They were described by Nielsen (1931).

Sponges

Siliceous sponges are rare within the coral limestone facies (Nielsen 1929, Rasmussen 1973, Clausen 1982). They are more frequent within the transitional facies. *Aphrocallistes* and *Scyphia* as well as spicula were found in thin-sections of samples this facies type.

2.4.4 Bioerosion

Boring organisms are common within framebuilders and shells. SEM investigations of plastic casts resulted in the recognition of clionid borings (Pl. 28/7, 8) and bryozoan borings (*Iramena*, cf. Boeckschoten 1970). Microborings of algae were not observed.

2.4.5 Biogenic encrustations

The sediment between the framebuilding organisms was not lithified. The soft bottom was bioturbated (Pl. 26/1) by various organisms (e.g., *Cardium vogeli*, irregular echinoids) but not encrusted or bored. In the transitional facies burrow structures, probably of *Thalassinoides* without bryozoan encrustations (Voigt 1959, 1988) were observed. Hardgrounds described for the Danian of Limhamn (Holland & Gabrielsson 1979) and Stevns Klint (Surlyk 1979) are missing in the coral limestones of Fakse.

Biogenic encrustations took place preferentially on framebuilding organisms or skeletal grains:

- colonial and solitary corals (Pl. 32/1)
- stylasterine hydrozoans (Pls. 27/5; 30/11; 32/3, 6;)
- octocorals (Pls. 26/5; 31/3, 5; 32/8)
- bryozoans (Pls. 27/6, 8; 32/3, 5, 7)
- serpulids (Pls. 27/6, 8; 31/2; 32/3)
- brachiopods (Pl. 32/7)
- oysters (Pl. 32/9)

Framebuilding organisms were often incrusted in life position. This is supported by:

-- Unidirectional encrustations predominantly by *Heliopora incrustans* (see Nielsen, 1919; Pl. 31/5,6)
-- Different framebuilding organisms growing around each other with calyces pointing in the same direction (Pl. 32/1)
-- Encrustations by octocorals and hydrozoans covering the substrate completely (Pls. 26/5; 32/3, 6, 8).

Although encrustations occur frequently, no significant succession has been observed.

Encrustation was an important factor in increasing the weight of the framebuilders, colonization of the framebuilding organisms by various invertebrates was another. In addition, the stability of the colony was gradually weakened by the network of boring . This resulted in the breakdown of the framebuilders, perhaps intensified by the activities of feeding fishes which produced inhomogeneous bioclastic debris. Mechanical destruction might have played a minor part only because there are no indications of transport and stronger wave energy. Broken colonies or branches produced new hard substrates for a further colonization.

This interpretation is supported by the investigation of Recent *Lophelia* colonies at Rockall Bank (Wilson 1979 a, b) producing bioclastic debris in a similar way.

2.4.6 Diversity

The framebuilding community is low diverse, the associated fauna is significantly high-diverse. This contradicts strongly the pattern seen in many shallow-marine reefs which are characterized by typically high species diversity compared with adjacent level-bottom communities.

2.5 Sedimentological criteria of the coral mounds

2.5.1 Mound geometry

Basic information on the geometry of the coral mounds originate from longitudinal sections (profile G and E) and a cross section (profile M). A combination of these profiles exhibits an asymmetrical mound with an elliptical plan. The largest coral mounds are 200 m long, 80 m broad and at least 30 m high (Fig. 11). The exact height could not be measured, because the top of all the buildups has been removed by glaciers. Smaller mounds, consisting exclusively of sediments of the transitional facies (profile T, L) reach 50 m in length, a width of 20 m and a height of 15 m.

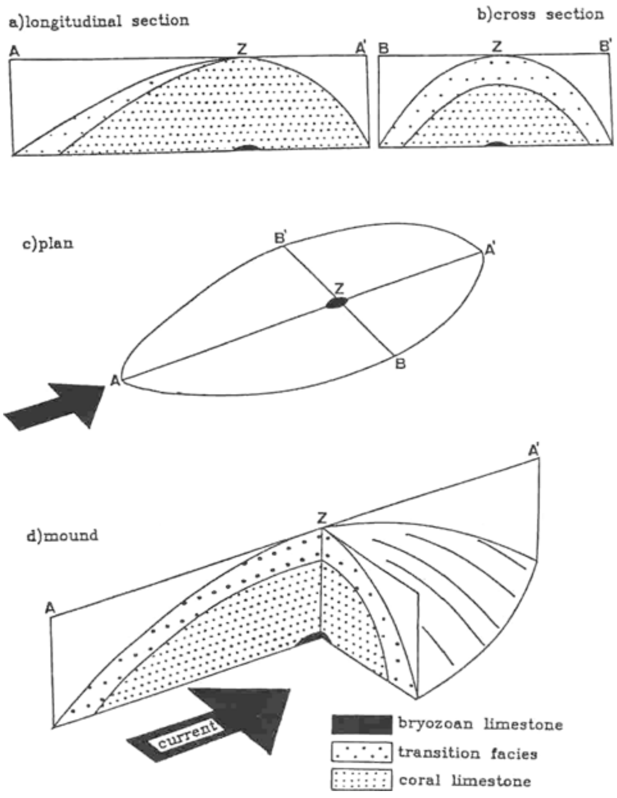


Fig. 11. Schematic reconstruction of a coral mound. Coral limestones (Danian), Fakse.

2.5.2 Paleocurrents

Directions of the paleocurrents

The current direction can be derived from

-- longitudinal sections oriented north/south and having a length of up to 200 m, cf profile G and E (Fig. 11 a, d)

-- cross sections running east/west, cf profile M (Fig. 11 b, d)

-- longitudinal sections exhibiting a asymmetrical shape of the mound with an extended southern flank (Fig. 11 a, d). In profile G the ratio of the southern to the northern flank is 2 : 1. The southern flanks of profile G and E exhibit the largest thickness of all the profiles (150 m at profile G, 80 m at profile E)

-- conspicuous southward dipping flanks which were already been recognized by Fischer-Benzon (1866)

-- distribution and functional morphology of cheilostome bryozoans, influenced by current velocity (Thomsen 1976, 1977 a,b, 1983). Bryozoans are generally more common on the southern flank. *Porina salebrosa* Marsson, 1887, *Floridina gothica* d'Orbigny,1850 and *Onychocella columella* Berthelsen, 1962, occurring on the southern flank, are characterized by large diameters and thick walls. Colonies with cylindrical zooecia dominate on the northern flank, bilamellar and encrusting bryozoans on the southern flank of profile G

-- unidirectional currents are indicated by the one-sided encrustation by *Heliopora incrustans*, by calyces of different framebuilding organisms oriented in the same direction, and by fan-like growth forms of octocorals (*Moltkia isis*) and stylasterine hydrozoans (*Errina lobata, Sporadopora faxensis, Astya crassus*).

These criteria point to the assumption of a south to north current direction. On nutrient-rich southern flanks framebuilding organisms grew under favourable conditions, trapping a large amount of sediment. Bryozoans were adapted to this environment by bilamellar or incrusting growth. Owing to a minor food supply on the northern flank, fewer framebuilding organisms and bryozoans, mainly with cylindrical morphologies, grew on the northern flank. As a consequence, the southern flank is longer and is more distinct than the northern flank.

This reconstruction corresponds with that given by Thomsen (1976) for the bryozoan mounds of the Danian B. He postulated a current direction from the southeast.

Current velocity

Older specimen of *Moltkia isis* show horny nodes covered by layers of calcite. This stabilization of the colony is interpreted as an adaptation to a low current velocity. Grasshoff & Zibrowius (1983) described Recent Isididae exhibiting the same features. Skeletal grains (composed of bryozoans or thin brachiopod shells) are only rarely broken, probably caused by bioerosion or mechanical compaction subsequent to sedimentation, but not by the action of waves or a strong current velocity. Weak current velocities might have existed; most sediments can be attributed to Energy Type II and IV (Plumley et al 1962).

2.5.3 Sedimentation patterns

Most of the sediments occurring within the mounds and surrounding the mounds seem to be of parautochthonous origin.

Parautochthonous sedimentation

The varying content of broken coral branches is obvious in rock slabs . Modal analysis indicates that the percentage of framebuilding organisms varies between 10 % and 30 %. The size of the broken corals ranges between 0.1 mm and 50 cm. Coral colonies in life position are common. There are no indications for transport or resedimentation. A parautochthonous deposition can be assumed, therefore. In addition, pelagic skeletal grains, such as coccoliths (Pl. 28/6), globigerinid foraminifera (Pl. 28/5) and ostracods are important constituents of the calcarous ooze. Globigerinid foraminifera are frequent and occur in all subfacies types of the coral limestone (Tab. 2).

Allochthonous sedimentation

Allochthonous sedimentation (Pl. 33/5, 6) is of little importance. Small southward dipping debris fans occur in profile G (thickness 2 - 10 cm, length up to 3 m). They have an erosional base and consist of grain-supported coral debris with a few limestone intraclasts. Micrite is winnowed.

Other allochthonous sediments occur within vertical fissures (Fig. 12; Pl. 33/3, 4). The width varies between 10

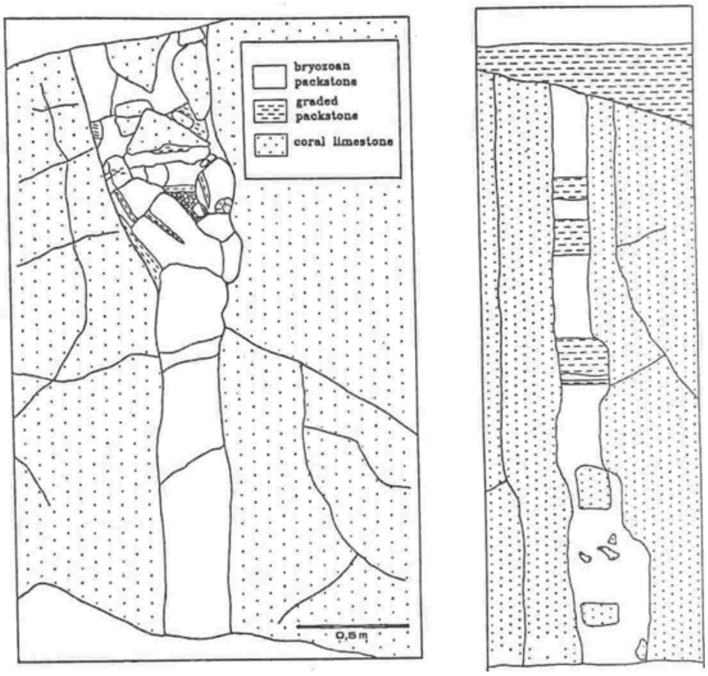


Fig. 12. Fissures within the Fakse coral limestone.

cm and 10 m. The sediment corresponds to bioclastic packstone with heavily broken bryozoans and angular lithoclasts derived from the surrounding coral limestones. They are 10 cm to 10 m broad.

3 ENVIRONMENTAL INTERPRETATION

The interpretation deals with the development of the mounds over time and with the critical question of the water depth.

3.1 Development of the mounds

The growth of the corals starts preferentially on bryozoan mounds as indicated by the profiles E and G (Chapter 2.2.3). The base of the coral mounds is very distinct. Bioclasts (mostly bryozoans), derived from the underlying bryozoan limestones, decrease towards the base of the coral mounds. This suggests that the first corals, colonizing the soft sediment, required only few skeletal grains for settlement. No transitional facies was observed at the base.

Soft substrates (lime mud, formed by pelagic bioclasts and bryozoan debris), indicated by strong bioturbation, dominated at the beginning of mound building. Hard substrates were available only from the skeletons of framebuilding organisms, especially corals, stylasterine hydrozoans and octocorals. Strong biogenic encrustations multiplied the number of hard bottoms, acting as substrates for further framebuilders. Intensive bioerosion caused fine-grained bioclastic sediment. This sediment and the pelagic grains were deposited parautochthonously within a low-energy environment which was controlled by weak bottom currents.

3.2 Water depth

The paleobathymetrical position of the coral "reefs" of Fakse is controversial (Asgaard 1968). Various parts of deeper-marine environments as well as a shallow-marine environment have been considered.

3.2.1 Discussion of previous interpretations

Lyell (1835:149) assumed a shallow-water environment for the coral reefs of Fakse, inspired by Darwin's investigations of Recent coral reefs. A similar interpretation was given by Fischer-Benzon (1866) who interpreted the west and the south flanks as being exposed to waves. Nielsen (1913a) postulated a water depth between 200 - 250 m studying the crinoids. Hadding (1941) and Teichert (1958:1078) compared the coral banks of Fakse with Recent deep-water reefs growing in depths between 100 and 300 m and assumed paleodepth reefbuilding in depths > 100 m and in colder water.

Floris (1980), however, postulated a high energy environment at a depth of 50 m and a temperature of 18°C. He used the following paleontological arguments:

-- occurrence of *Millepora parva* Nielsen. *Millepora* is a zooxanthellate hydrozoan occurring in many Recent coral reefs at a depth of down to 30 m (Boschma 1956). *Millepora parva* probably does not belong to *Millepora.*

-- *Heliopora incrustans* Nielsen. Recent helioporid octocorals are zooxanthellate. They are widespread framebuilding reef organisms (Wells, 1954). *Heliopora incrustans,* however, should be regarded as azooxanthellate, taking into account the morphology and dimension of the corallites

-- *Cyathidium holopus* Steenstrup. These crinoids were found in caves, burrows of crustaceans and in oyster shells. Nielsen (1913 a) assumed that the crinoids lived on the top of the coral mounds during a shallowing phase, at a depth of 90 m. Recent *Cyathidium* live at a depth of more than 380 m within an aphotic environment (Rasmussen & Sieverts-Doreck 1978). Rasmussen (1973) interpreted the occurrence of *Cyathidium holopus* as an adaptation to the darkness of burrows and cavities. The occurrence might, however, also be interpreted as a result of increased competition with framebuilding organisms

-- Doubtful algal mats (Floris, 1962:151: "slamflader paa hovedet, som kan vaere dannet med unterstötning med autokton algeslim") have been used together with some borings in aragonitic shells as indications for a shallow-marine environment. No calcareous algae have been observed in the thin-sections, algal microborings are missing in thin-sections as well as in SEM samples

-- The depth distribution of the Recent brachiopod *Argyrotheca* indicates a possible water depth of about 50-80 m (Asgaard 1968).

3.2.2 Paleobathymetrical interpretation

Our investigations indicate that the coral mounds most probably grew within the aphotic zone. The criteria fit those for "deep and cold-water bioherms" as proposed by Teichert (1958), Mullins et al. (1981) and Stanley & Cairns (1988).

(1) Calcareous and boring algae are missing
(2) All framebuilding organisms are optimally adapted to heterotrophic nourishment and can be regarded as azooxanthellate
(3) Compared with Recent tropical shallow-marine reefs, the diversity of the framebuilding organisms is low
(4) The cheilostome and cyclostome bryozoans occurring in the bryozoan limestones surrounding the coral limestones predominantly of cheilostome and cyclostome bryozoans correspond to deeper water species (Voigt 1929; 80-150 m). Similar depths can be derived from morphological criteria of the bryozoans studied by Thomsen (1976)
(5) Pelagic organisms (coccoliths, globigerinid foraminifera and ostracods) are constituents of the micrite in both the coral limestones and the bryozoan limestones
(6) Breakdown of framebuilding organisms took place predominantly by bioerosion instead of mechanical destruction
(7) The asymmetrical shape of the mound points to the existence of unidirectional bottom currents which are more likely in deeper than in shallower environments
(8) The coral limestones occur at a high paleolatitude
(9) Diversity of the facies types of the coral limestones is significantly low as compared with the facies diversity of shallow-marine tropical reef carbonates.

The discussion of the paleobathymetry should take into account the configuration of the Danish-Polish trough which corresponds to an elongated, not too deep basin. A paleodepth exceeding 100 m, perhaps between 200 and 300 m, might be reliable for the coral mounds of Fakse. This is also supported by the occurrence of Recent azooxanthellate coral communities at similar latitudes and in a comparable topographic position in depths between 230 and 300 m (*Lophelia pertusa*, Rockall Bank, Scoffin et al. 1980); bryozoans occur in more shallow waters (80-120 m; Australian shelf: 100-200 m, Wass et al. 1970). Other Recent counterparts (coral thickets with *Madrepora oculata* and *Dendrophyllia cornigera*) have been found in the eastern Atlantic shelf edge area off Europe in a depth of 200-1200 m.

It is even possible that the corals of the coral mounds in Fakse grew in deeper waters than the bryozoans. The coral buildups of Limhamn are smaller then those in Fakse. This may be a consequence of less favourable conditions (and different paleobathymetry ?) at the border of the Fennoscandian Shield.

Similar paleobathymetrical interpretations of the Fakse limestone were given by Hennig (1899b), who concluded that the bryozoans grew at a depth of 200-300 m. Nielsen (1913a: 74) assumed that the corals lived in a depth between 180 and 220 m. Voigt (1929) suggested a depth of 80-150 m for the bryozoan limestones. Hadding (1941) thought that the corals lived in a depth of 100 - 150 m.

Based on a comparision with Recent *Lophelia* thickets Teichert (1958) proposed the model of "cold- and deep-water coral banks" which is strongly supported by our investigations. The Danian coral "reefs" of Fakse illustrate well the Ancient buildups formed by azooxanthellate, constructional and ahermatypic corals.

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Plate 26 Coral limestone facies, Fakse: Thin-sections of subfacies types
Korallenkalk-Fazies von Fakse: Dünnschliffe der Subfaziestypen

Dendrophyllia Facies

Fig. 1. Cross section of a *Dendrophyllia* colony with open framework porosity; the soft bottom between the frame-building organisms was bioturbated. The debris consists to a high percentage of broken coral skeletons. Diagenesis type 2. Sample M 71. x 5

Fig. 2. Cross section of a coral branch; note the synapticulothecal wall and the septa following Pourtalès plan. The septa are arranged in 4 cycles, the last cycle is incomplete. Sample G 55. x 14

Faksephyllia Facies

Fig. 3. *Faksephyllia* facies; some corals are partly dissolved. Diagenesis type 2-3. Sample M 68. x 8

Fig. 4. Cross section through the intratentacular (distomodaeal) budding of a coral branch. Sample D 19.5. x 10

Oculina Facies

Fig. 5. Longitudinal section of *Oculina becki* exhibiting the characteristic extratentacular budding. The speciman is totally encrusted by the octocoral *Moltkia isis;*. Diagenesis type 3. Sample J 33. x 8

Fig. 6. Cross section of a juvenile branch with three septal cycles. Sample M 37. x 5

Fig. 7. Adult specimen. The wall is thickened by stereome; note the penetration by *Cliona*, sample M 33. x 10

Dendrophyllia Fazies

Fig. 1. Querschnitt durch eine *Dendrophyllia*-Kolonie mit offener Gerüstporosität. Das Sediment zwischen den Gerüstbildnern war nicht lithifiziert und wurde bioturbat verwühlt. Der Detritus besteht zu einem hohen Prozentsatz aus feinem Korallenschutt. Diagenesetyp 2. Probe M 71. x 5

Fig. 2. Korallenquerschnitt mit synapticulothekaler Wand und Septen, die nach Pourtalès Plan auffächern. Die Septen sind in 4 Zyklen eingeschaltet. Der letzte Zyklus ist unvollständig. Probe G 55. x 14

Faksephyllia Fazies

Fig. 3. Querschnitt durch eine *Faksephyllia*-Kolonie. Einige Korallen sind teilweise gelöst. Diagenesetyp 2-3. Probe M 68. x 8

Fig. 4. Querschnitt durch eine intratentakulare (distomodaeale) Knospung. Probe D 19,5. x 10

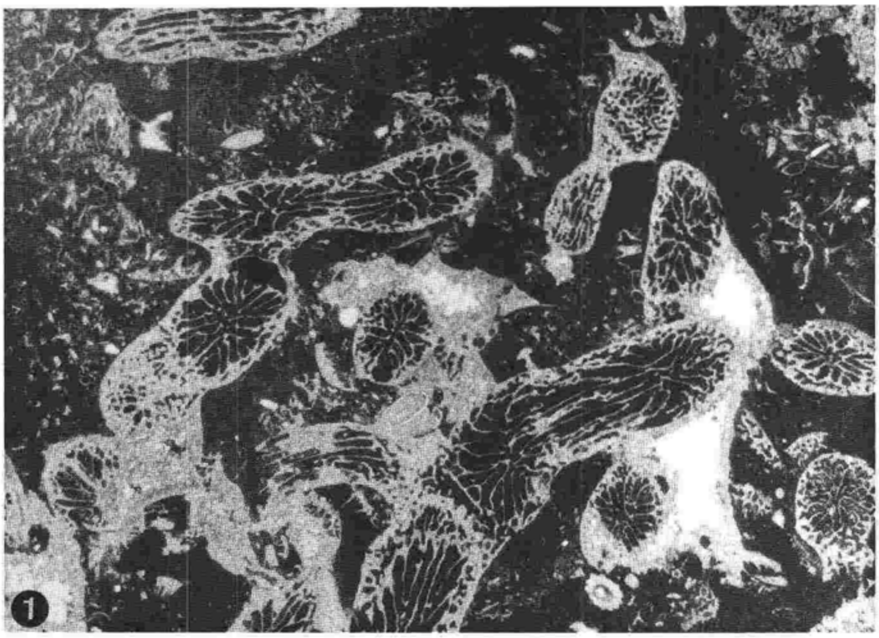
Oculina Fazies

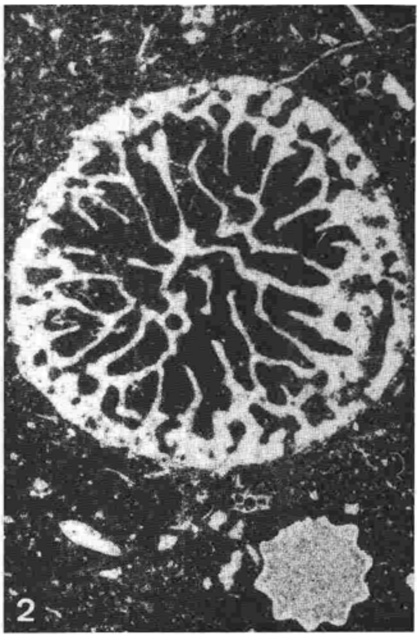
Fig. 5. Längsschnitt durch *Oculina becki* mit extratentakularer, alternierender Knospung. Das Exemplar ist vollständig von der Octokoralle *Moltkia isis* inkrustiert. Diagenesetyp 3. Probe J 33. x 8

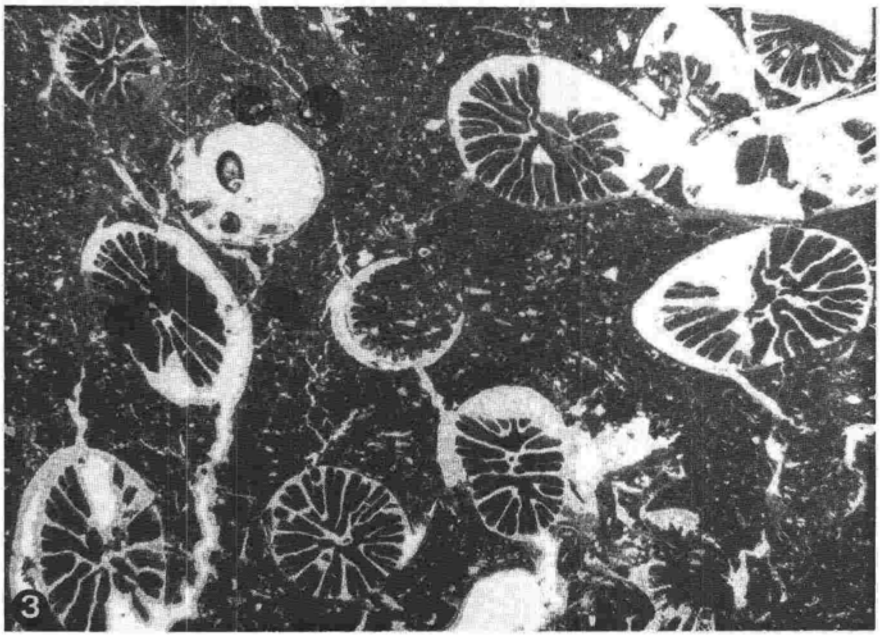
Fig. 6. Querschnitt durch ein juveniles Exemplar mit 3 Septenzyklen. Probe M 37. x 5

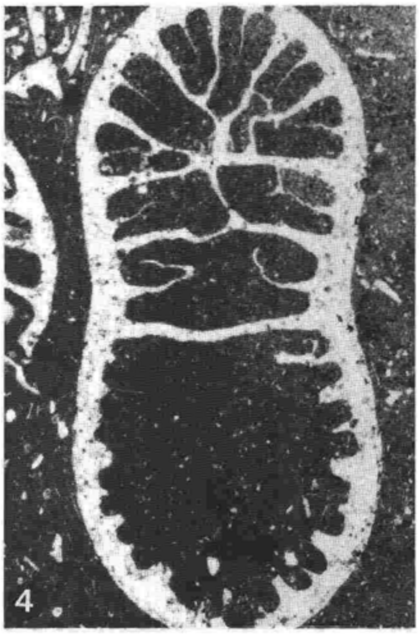
Fig. 7. Adultes Exemplar mit stereomverdickter Wand und Anbohrung durch den Bohrschwamm *Cliona*. Probe M 33. x 10

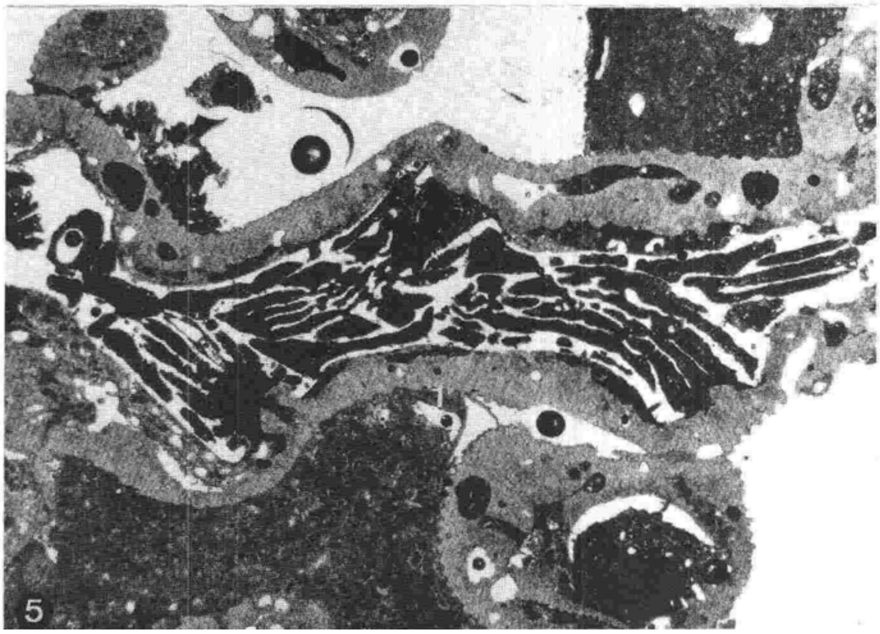
Plate 26

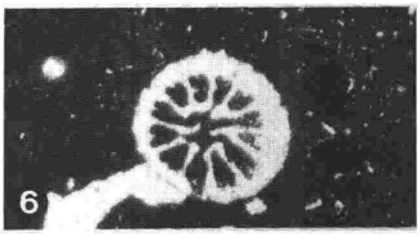












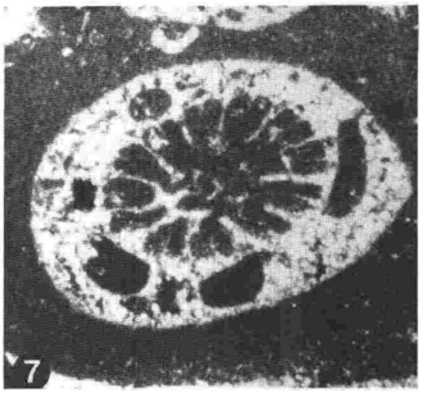


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Plate 27 The Danian coral limestone of Fakse, Denmark: Fossils in thin-sections
Der Korallenkalk von Fakse, Dänemark (Dan): Fossilien im Dünnschliff

Bryozoans

Fig. 1. *Porina salebrosa* Marsson, 1887. The thin wall indicates the existence of slow currents on the downstream flank of a coral mound Sample K 5. x 30

Fig. 2. Thick-walled *Porina salebrosa* from the south flank of profile G indicating higher current velocity on the upstream flank. Sample G 9. x 30

Fig. 3. Cross section of *Columnotheca cribrosa* Marsson, 1887. Sample G 77. x 30

Fig. 4. Cross section of *Floridina gothica* d'Orbigny, 1850. Sample G 16. x 30

Octocorals and scleractinian corals

Fig. 5. *Moltkia sp.* (1) encrusting a fragment of a stylasterine hydrozoan (2) and bored by *Cliona* (arrow). Sample E 42. x 7

Fig. 6. Encrustation of partly dissolved *Dendrophyllia candelabrum* by bryozoans and a serpulid worm. Note the cone-in-cone structure (arrow). Sample E 37. x 7.5

Fig. 7. Longitudinal and cross section of a stylasterine hydrozoan. Note the gastropores. Sample M 37. x 15

Fig. 8. *Moltkia lyelli* exhibiting the characteristic axial channel. Two calyces are visible in the internode. Sample M 44. x 13.5

Oysters and serpulid worms

Fig. 9. Longitudinal section of *Exogyra lateralis*. The calcitic microstructure is preserved. Sample M 66. x12

Fig. 10. A serpulid worm encrusting a recrystallized bioclast. Sample M 17. x 18

Bryozoen

Fig. 1. *Porina salebrosa* Marsson, 1887. Die dünne Wand läßt auf die Existenz einer geringen Strömung auf der strömungsabgewandten Seite des Mounds schließen. Probe K 5. x 30

Fig. 2. Die dickwandige *Porina salebrosa* der südlichen Moundflanke (Profil G) weist auf eine höhere Strömungsgeschwindigkeit an der strömungsexponierten Flanke hin. Probe G 9. x 30

Fig. 3. Querschnitt durch *Columnotheca cribrosa* Marsson, 1887. Probe G 77. x 30

Fig. 4. Querschnitt durch *Floridina gothica* d'Orbigny, 1850. Probe G 16. x 30

Octokorallen und Hexakorallen

Fig. 5. *Moltkia sp.* (1) inkrustiert ein Bruchstück einer stylasterinen Hydrozoe.(2) und wurde von *Cliona* (Pfeil) angebohrt. Probe E 42. x 7

Fig. 6. Inkrustation einer teilweise gelösten *Dendrophyllia candelabrum* durch Bryozoen und eine Serpel (mit cone-in-cone structure, Pfeil). Probe E 37. x 7,5

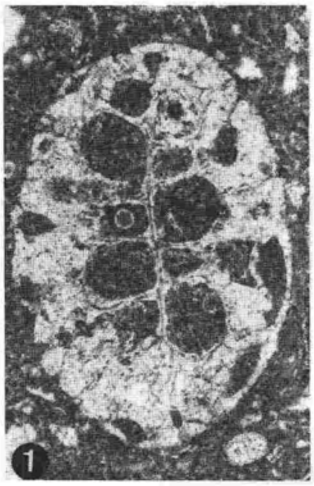
Fig. 7. Längs- und Querschnitt einer stylasterinen Hydrozoe. Probe M 37. x 15

Fig. 8. *Moltkia lyelli* mit typischen Achsenkanal. Es sind zwei Kelchgruben zu erkennen. Probe M 44. x 13,5

Austern und serpulide Würmer

Fig. 9. Längsschnitt von *Exogyra lateralis* mit erhaltener kalzitischer Mikrostruktur. Probe M 66. x 12

Fig. 10. Eine Serpel inkrustiert auf Bioklasten. Probe M 17. x 18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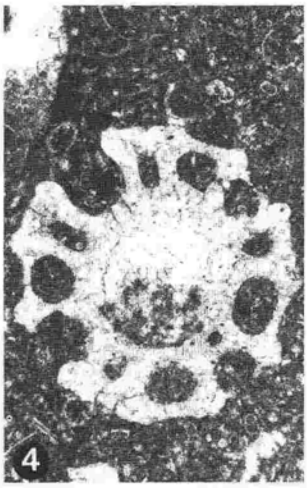
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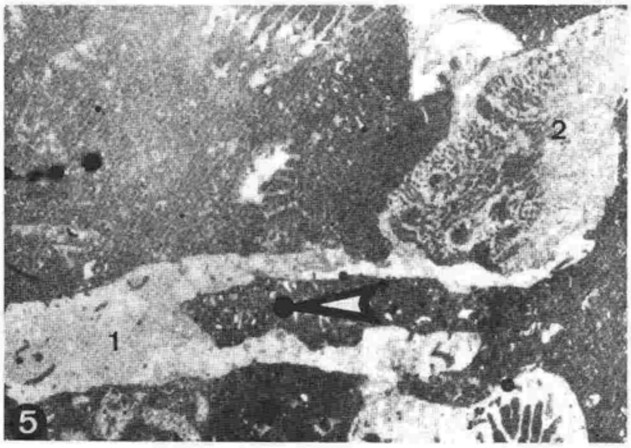
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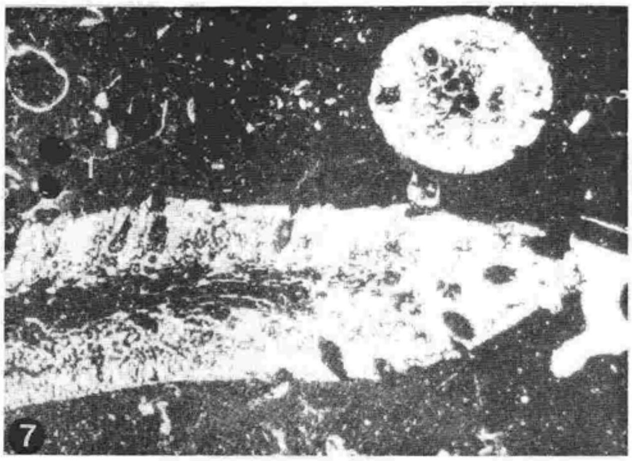
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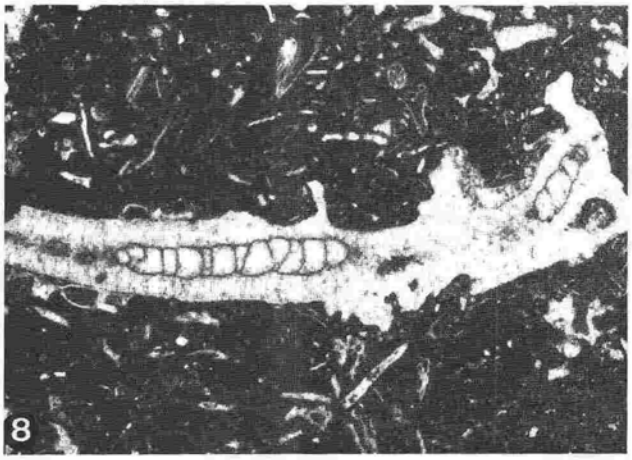
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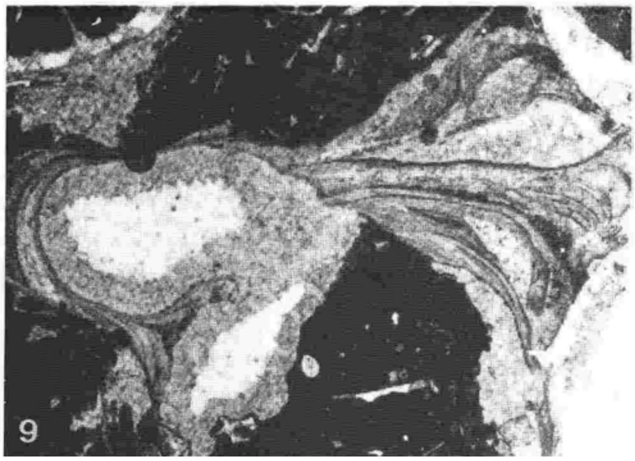
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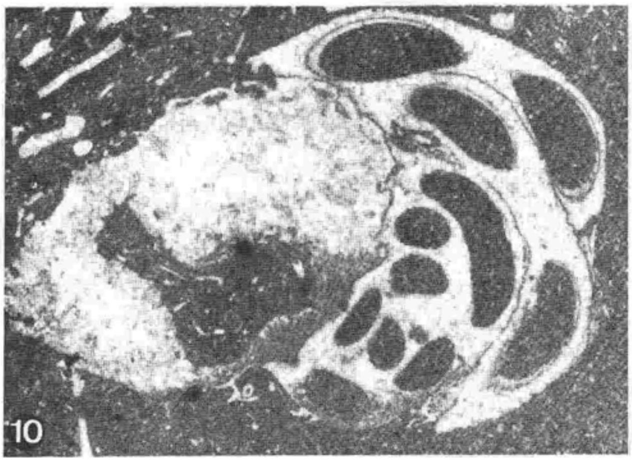
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Plate 28 The coral limestone of Fakse, Denmark (Danian): Diagenesis and microborings
Der Korallenkalk von Fakse, Dänemark (Dan): Diagenese und Bohrspuren

Fig. 1. Subsequent to early marine cementation the cavities were filled with geopetal sediment. The sediment is fine-grained and contains no fossils. Sample M 14.2. x 12

Fig. 2. Rim cement around an echinoid spine. Sample G 74. x 55

Fig. 3. Typical diagenetic alteration of a coral branch: The coral skeleton is converted into calcite. Marine fibrous cements have been recristallized under meteoric-phreatic conditions to blocky calcite. Relictic fibrous structures are revealed only by cathodoluminescence.Clear dog-tooth crystals are typical for this meteoric-phreatic diagenesis. The remaining pores were sealed by coarse blocky quartz cement. Crossed nicols. Sample D 14.2. x 14

Fig. 4. Fibrous cements are only preserved within intraskeletal pores of calcitic shells (e.g., brachiopods). The crystals directly growing upon the calcitic shell are distinctly longer than crystals growing on the geopetal sediment. Crossed nicols. Sample M 32. x 15

Fig. 5. Planktonic organisms are common within the micritic sediment: Globigerinid foraminifera. SEM photo

Fig. 6. Well-preserved coccolith (diagenesis type 1) within the matrix of the coral limestone. SEM photo

Fig. 7. Microborings originate mainly from clionid sponges. SEM photo

Fig. 8. Detail of a clionid boring exhibiting the typical chips. SEM photo

Fig. 1. Primäre Hohlräume wurden nach frühdiagenetischer Zementation geopetal mit Sediment verfüllt. Das Sediment ist feinkörnig und enthält keine Fossilien. Probe M 14.2. x 12

Fig. 2. Rim Zement um einen Seeigelstachel. Probe G 74. x 55

Fig. 3. Typische diagenetische Veränderung einer Koralle: Das primär aragonitische Skelett ist in Kalzit umgewandelt. Marin-fibröse Zemente rekristallisierten unter meteorisch-phreatischen Bedingungen zu Blockzementen. Reliktische fibröse Strukturen sind unter Kathodolumineszenz erkennbar. Klare Hundezahnkristalle sind für diese meteorisch-phreatische Diagenese typisch. Der noch offene Porenraum wurde durch blockigen Quarz-Zement plombiert. Gekreuzte Polarisatoren. Probe D 14,2. x 14

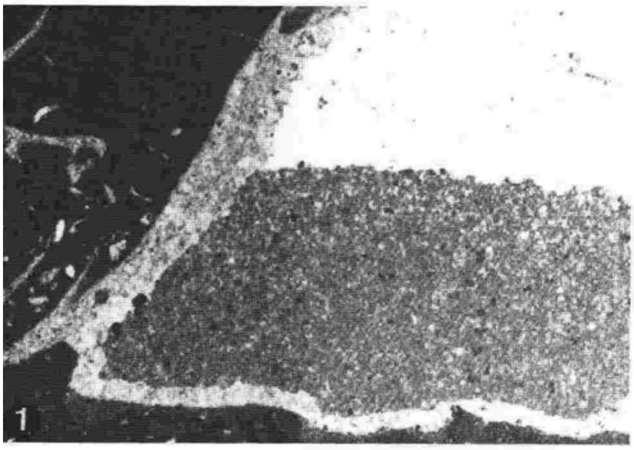
Fig. 4. Marin-fibröse Zemente sind nur iHohlräumen von kalzitischen Organismen, z. B. Brachiopoden, erhalten. Kristalle, die direkt auf den Kalzitprismen der Schale aufgewachsen sind, haben eine größere Länge als Kristalle, die auf der geopetalen Sedimentfüllung wachsen. Gekreuzte Polarisatoren. Probe M 32. x 15

Fig. 5. Planktonische Organismen (z.B. Globigerinen) sind wichtige Bestandteile der feinkörnigen Matrix des Korallenkalkes. REM Photo

Fig. 6. Gut erhaltener Coccolith (Diagenesetyp 1) in der mikritischen Matrix des Korallenkalkes. REM Photo

Fig. 7. Mikrobohrungen von clioniden Bohrschwämmen. REM Photo

Fig. 8. Detail einer *Cliona*-Bohrung. REM Photo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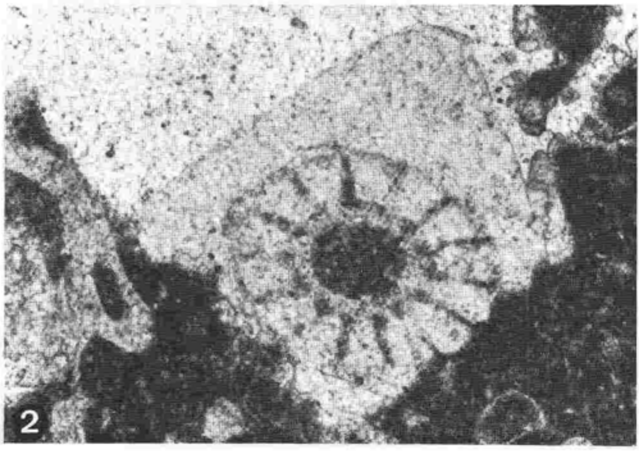
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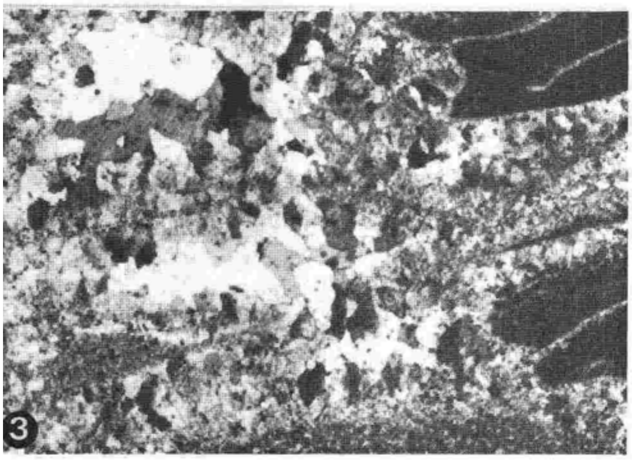
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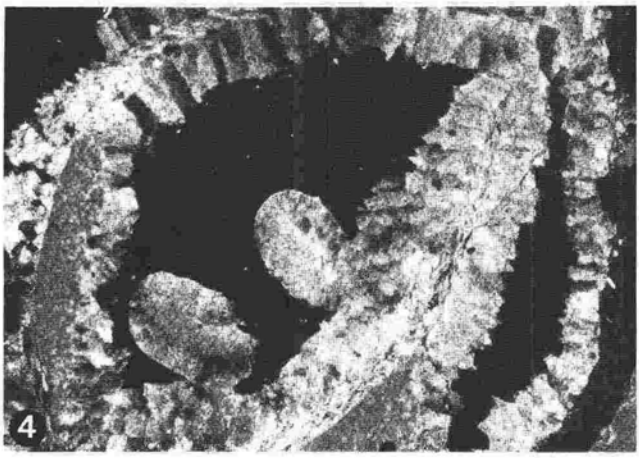
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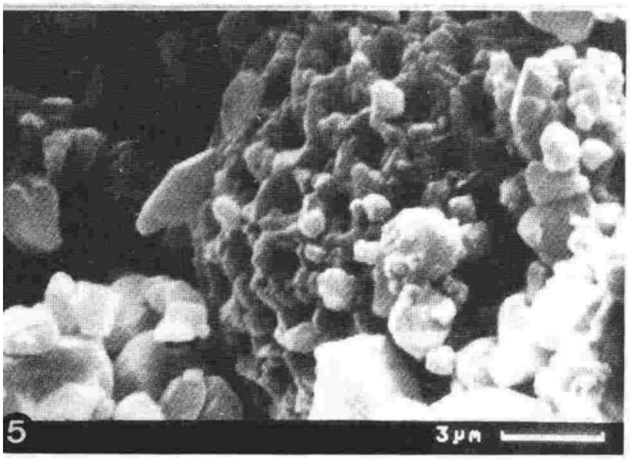
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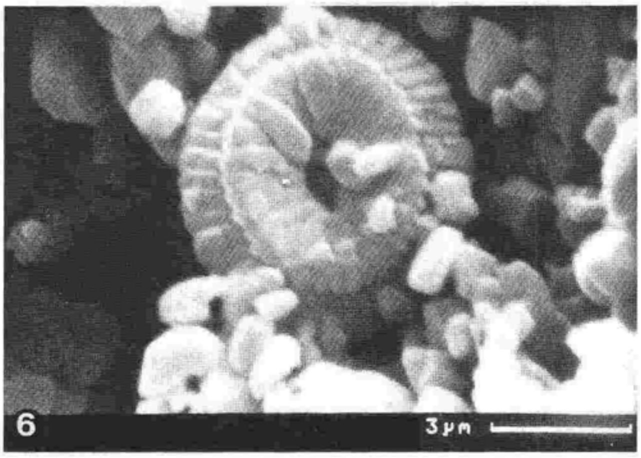
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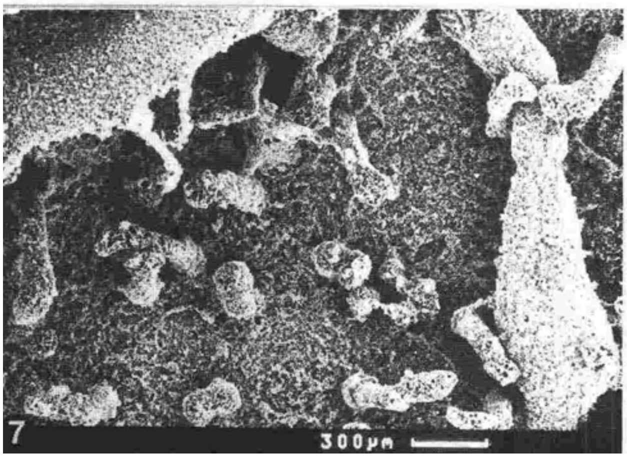
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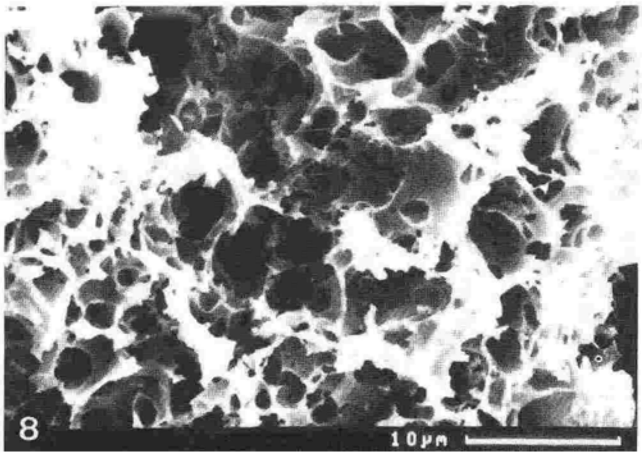
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Plate 29 Colonial corals from the Danian coral limestone of Fakse: Preservational and diagenetic stages
Korallen aus dem Korallenkalk (Dan) von Fakse, Dänemark: Erhaltung und diagenetische Stadien

Dendrophyllia candelabrum Hennig, 1899
Fig. 1. Broken coral branch with extratentacular budding and slight costae. The skeleton is converted into calcite; this preservation is characteristic for diagenesis type 1. Sample M 2. x 2
Fig. 2. Sediment cast with characteristic synapticulothecal wall; typical sample of diagenesis type 3. x 10
Fig. 3. Longitudinal section of a coral branch exhibiting septa and spongy columella. Sample M 2. x 10
Fig. 4. Calyx with extratentacular, rectangular budding. Sample M 2. x 10

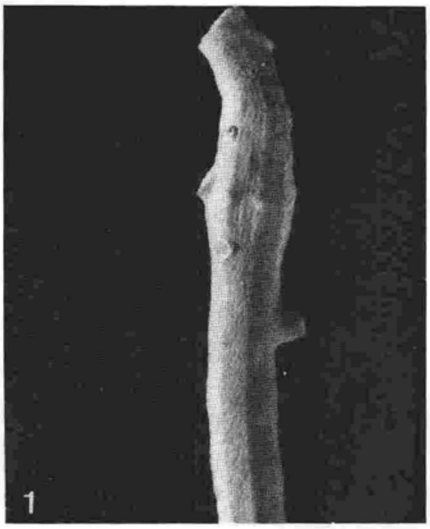
Faksephyllia faxoensis (Beck, 1835)
Fig. 5. Coral branch with intratentacular budding in an angle from 20° to 30° and smooth wall. The skeleton is converted into calcite; typical preservation of diagenesis type 1. Sample M 2. x 2
Fig. 6. Sediment cast showing the septa; the septothecal wall is not preserved,. Sample of diagenesis type 3. x 10
Fig. 7. Longitudinal section of a coral branch; septa and dissepiments are visible. Sample M 2. x 10
Fig. 8. Calyx with intratentacular budding. Sample M 2. x 10

Oculina becki (Nielsen, 1922)
Fig. 9. Coral branch with characteristic extratentacular budding, the buds alternate in two opposite rows. The skeleton is converted into calcite; typical preservation of diagenesis type 1. Sample M 2. x 2
Fig. 10. Similar small sediment casts are abundant and have been found isolated; they can easily be confused with solitary corals. Typical sample of diagenesis type 3. x 10
Fig. 11. Cross-section of an adult speciman; the wall is thickened by stereome and bored by clionid sponges. Sample M 2. x 10
Fig. 12. Calyx with papillose columella. Sample M 2. x 10

Dendrophyllia candelabrum Hennig, 1899
Fig. 1. Bruchstück mit extratentakularer Knospung und angedeuteten Costae. Das Skelett ist kalzitisch erhalten. Diagenesetyp 1. Probe M 2. x 2
Fig. 2. Steinkern mit charakteristischer synapticulothekaler Wand. Diagenesetyp 2. x 10
Fig. 3. Längsschnitt mit Septen und spongiöser Columella. x 10
Fig. 4. Kelch von *Dendrophyllia candelabrum* mit extratentakularer Knospung. x 10

Faksephyllia faxoensis (Beck, 1835)
Fig. 5. Bruchstück mit intratentakularer Knospung und glatter Wand. Der Knospungswinkel schwankt zwischen 20 und 30°. Das Skelett ist kalzitisch erhalten. Typische Erhaltung für Diagenesetyp 1. Probe M 2. x 2
Fig. 6. Steinkern mit schlammverfüllten Interseptalräumen. Die septothekale Wand ist gelöst. Diagenesebereich 3. x 10
Fig. 7. Längsschnitt mit sichtbaren Septen und Dissepimenten. Probe M 2. x 10
Fig. 8. Kelche mit intratentakularer Knospung. Probe M 2. x 10

Oculina becki (Nielsen, 1922)
Fig. 9. Bruchstück mit charakteristischer iextratentakularer Knospung. Die Knospungsstellen alternieren mit regelmäßigem Abstand in einer Ebene. Das Skelett ist kalzitisch erhalten. Diagenesetyp 1. Probe M 2. x 2
Fig. 10. Die kleinen Steinkerne findet man oft isoliert. Sie können deshalb mit Solitärkorallen verwechselt werden. Diagenesetyp 3. x 10
Fig. 11. Querschnitt durch ein adultes Exemplar. Die Wand ist stereomverdickt und von *Cliona* angebohrt. Probe M 2. x 10
Fig. 12. Kelch von *Oculina becki* mit papilloser Columella. x 10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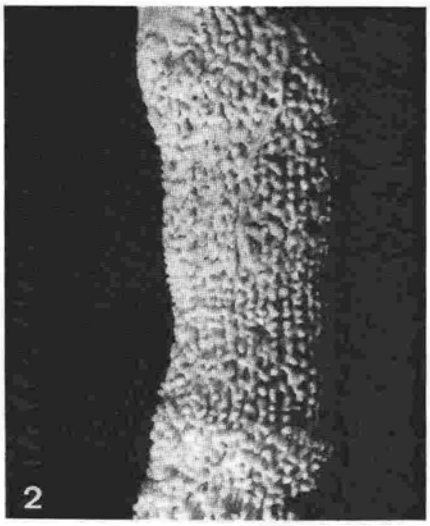
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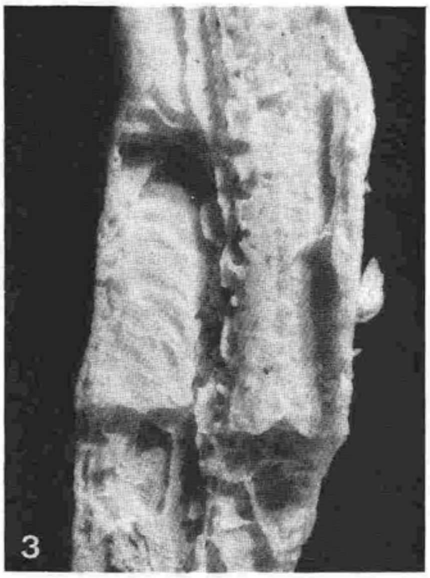
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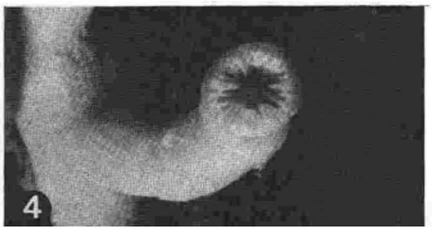
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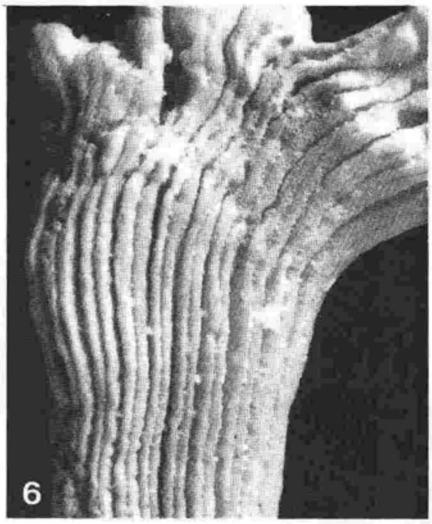
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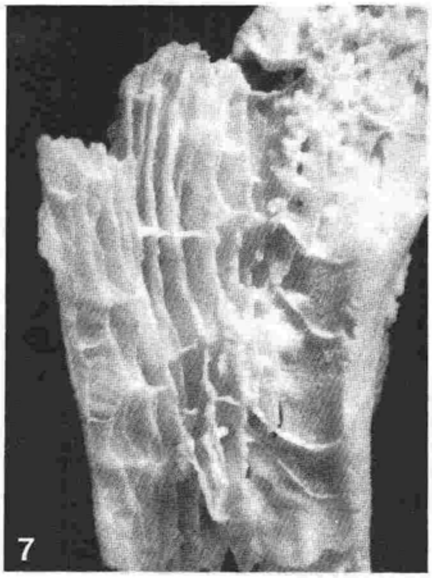
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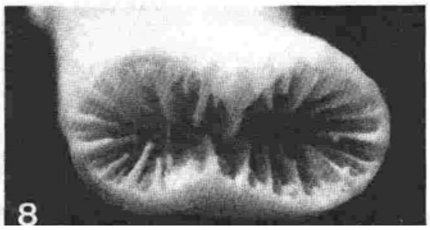
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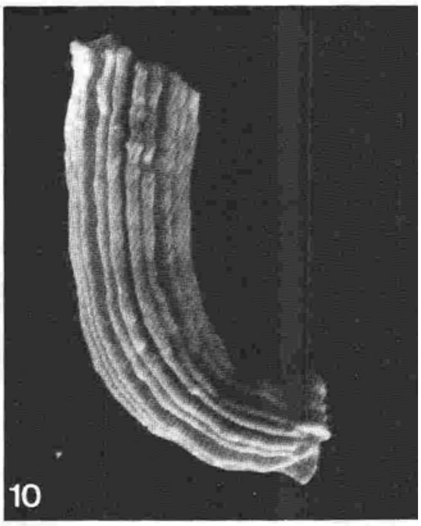
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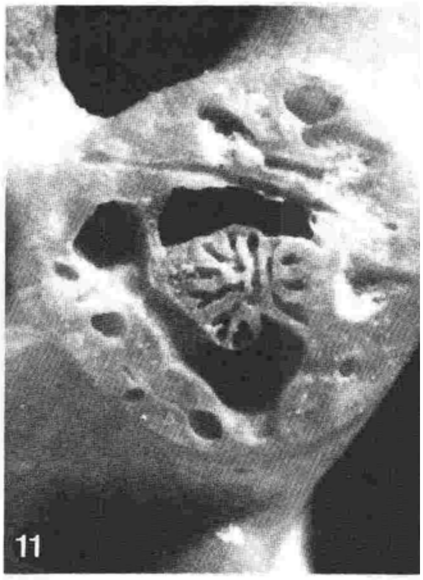
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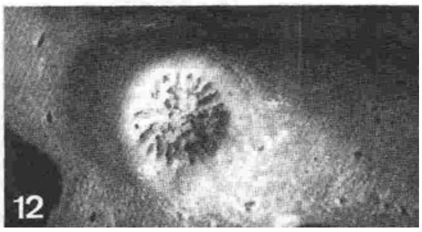
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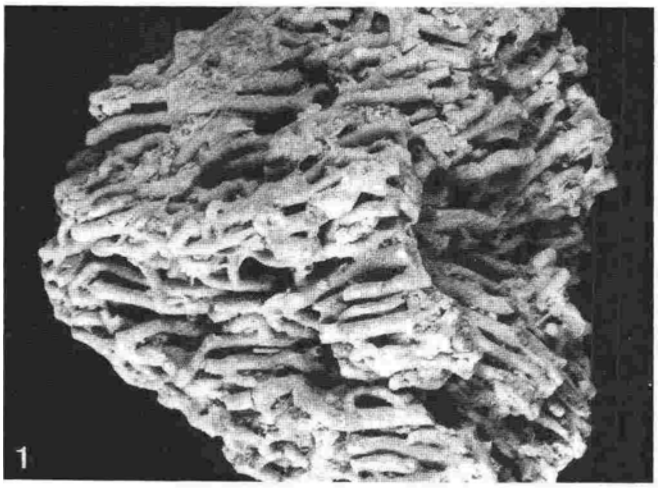
Plate 30 Danian coral limestone, Fakse: Framebuilding organisms (scleractinian corals, stylasterine hysdrozoans, octocorals)
Gerüstbildner aus dem Korallenkalk von Fakse, Dänemark: Hexakorallen, stylasterine Hydrozoen, Octokorallen

Scleractinian corals
Dendrophyllia candelabrum Hennig, 1899
Fig. 1. Lateral view of a dendroid colony. Subsequent to budding the coral branches grew parallel to the parent branch, but did not fuse. The growth form is regarded as adaptation to a heterotrophic life habit and indicates the azooxanthellate character of the coral. x 0.5
Fig. 2. View of the top; each branch with only one calyx . x 0.5
Faksephyllia faxoensis (Beck, 1835)
Fig. 3. Lateral view of the phaceloid colony with intratentacular budding. *Faksephyllia faxoensis* shows similar adaptation to a heterotrophic life habit as *Dendrophyllia candelabrum.* x 0.5
Fig. 4. View of the top. The calyces are separated butnot fused by stereome. x 0.5
Octocorals
Moltkia isis Steenstrup, 1846
Fig. 5. Juvenile specimen with sympodially arranged caliyces. Sample M 2. x 4
Fig. 6. Adult specimen with different layers of calcite (arrow); note the borings by *Cliona*,. Sample G 52. x 5
Moltkia lyelli Nielsen, 1917
Fig. 7. Juvenile specimen which is club-shaped. Sample M 2. x 5
Fig. 8. Adult specimen with several calyces. Sample M 2. x 5
Stylasterine hydrozoans
Fig. 9-10. Anterior and posterior side of *Sporadopora faxensis* Nielsen. Note the one-sided arrangement of the pores, indicating the existence of an unidirectional current pattern. Sample M 2. x 3.5
Fig. 11. Cyclosystem of *Astya crassus* (Nielsen, 1919). 8-10 dactylopores surround one gastropore. Sample M 2. x 25
Fig. 12. Gastropores and dactylopores cause the nodular surface of *Errina lobata* (Nielsen, 1919). A cyclosystem is missing . Sample M 2. x 6
Fig. 13. A juvenile hydrozoan, encrusting the substrate (probably a colonial coral) with a wide basal area. Sample M 2. x 5

Dendrophyllia candelabrum Hennig, 1899
Fig. 1. Seitenansicht einer dendroiden Kolonie. Nach der Knospung wachsen die Korallenäste parallel zum Hauptstamm ohne miteinander zu verschmelzen. Diese Wuchsform ist eine Anpassung an eine heterotrophe Lebensweise und läßt auf einen azooxanthellaten Charakter der Koralle schließen. x 0,5
Fig. 2. Blick auf die Kolonie von oben; jeder Zweig endet mit nur einem Kelch. x 0,5
Faksephyllia faxoensis (Beck, 1835)
Fig. 3. Seitenansicht einer phaceloiden Kolonie mit intratentakularer Knospung. *Faksephyllia faxoensis* ist in ihrer Wuchsform in ähnlicher Weise an heterotrophe Ernährung angepaßt wie *Dendrophyllia candelabrum.* x 0,5
Fig. 4. Blick auf die Kolonie von oben. Die Kelche sind nicht miteinander verschmolzen. x 0,5
Octokorallen
Moltkia isis Steenstrup, 1846
Fig. 5. Juveniles Internodium mit bilateral angeordneten Kelchgruben,.Probe M 2. x 4
Fig. 6. Adultes Internodium mit konzentrischen Kalzitlagen (Pfeil) und Bohrspuren von *Cliona.* Probe G 52. x 5
Moltkia lyelli Nielsen, 1917
Fig. 7. Junges Internodium mit charakteristischer Keulenform. Probe M 2. x 5
Fig. 8. Adultes Internodium mit zahlreichen Kelchgruben. Probe M 2. x 5
Stylasterine Hydrozoen
Fig. 9-10. Vorder- und Rückseite von *Sporadopora faxensis* Nielsen, 1919. Die Konzentration der Poren auf einer Seite weist auf die Existenz einer gerichteten Strömung hin. Probe M 2. x 3,5
Fig. 11. Cyclosystem von *Astya crassus* (Nielsen, 1919). 8-10 Dactyloporen umgeben eine Gastropore. Probe M 2. x 25
Fig.12. Die Anordnung der Gastroporen und Dactyloporen verursacht die narbige Oberfläche von *Errina lobata* (Nielsen, 1919). Ein Cyclosystem ist nicht ausgebildet. Probe M 2. x 6
Fig. 13. Eine juvenile Hydrozoe inkrustierte einen Korallenast mit einer breiten Basis. Probe M 2. x 5

Plate 30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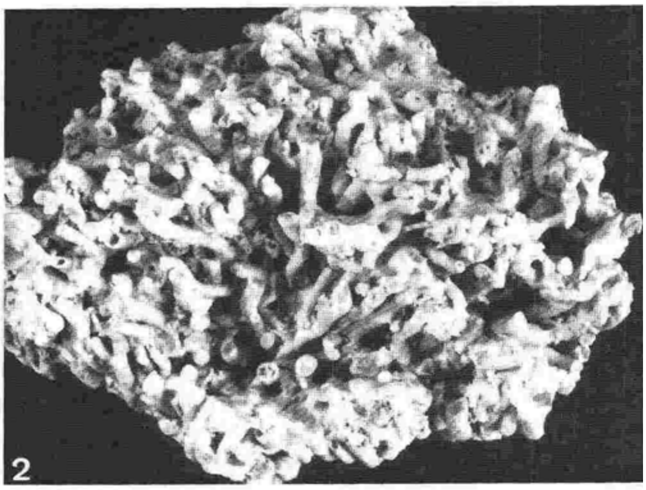
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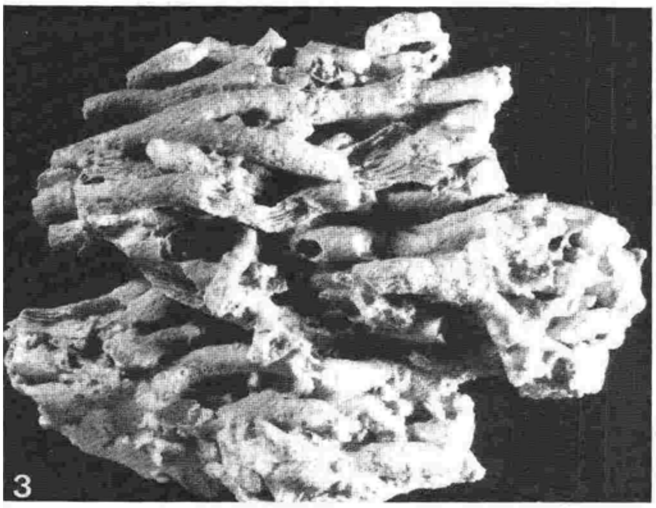
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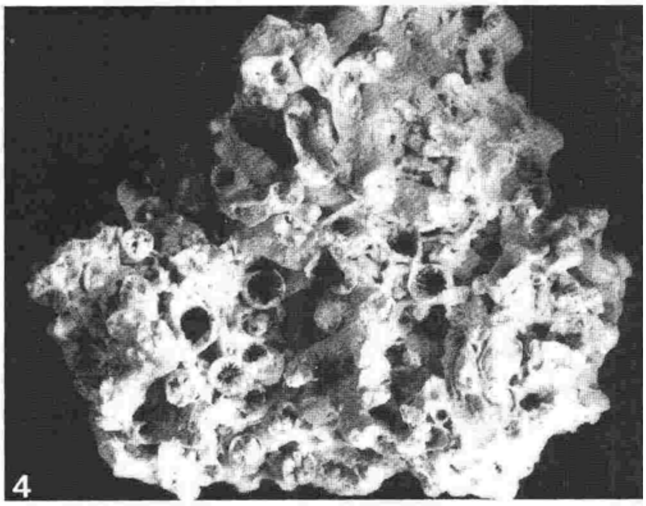
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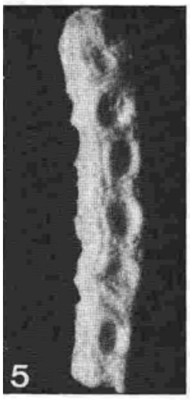
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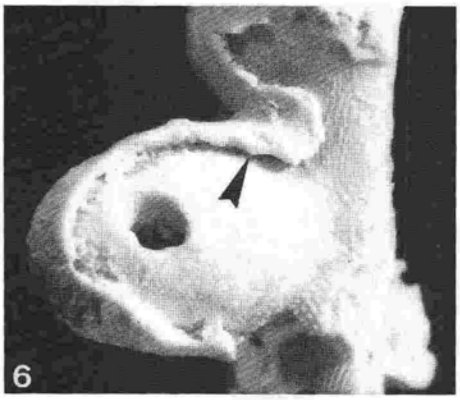
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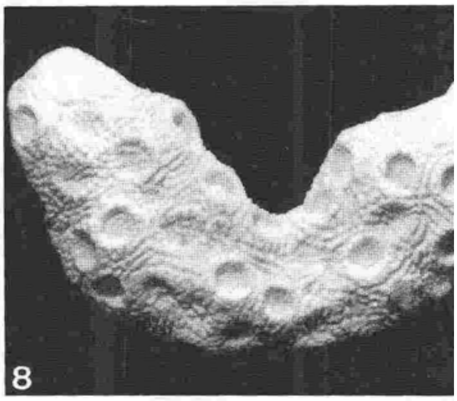
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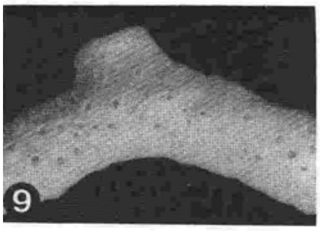
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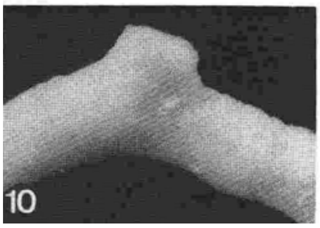
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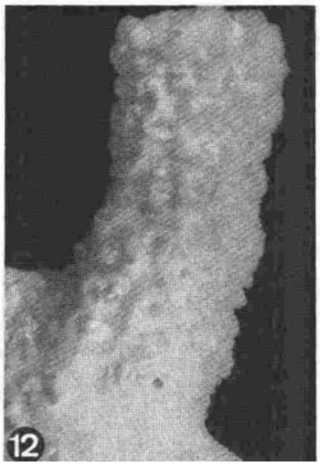
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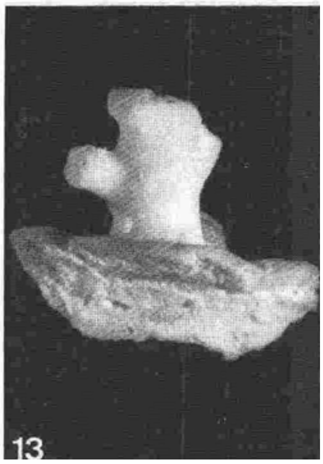
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Plate 31 Danian coral limestone of Fakse, Denmark: Growth forms of framebuilders and biogenic encrustations

Der Korallenkalk von Fakse, Dänemark: Wuchsform der Gerüstbildner und biogene Inkrustationen

Fig. 1. Typical fan-like colony of *Astya crassus*. The cyclosystems are arranged in the anterior direction and the branches tend to be highly anastomosized. This colony was colonized in life position by *Dendrophyllia candelabrum, Moltkia lyelli, Exogyra lateralis*, bryozoans and serpulid worms. The stability of the colony was gradually weakened by the network of boring organisms. Diagenesis type 2-3. x 0.9

Fig. 2. Detail of Fig. 1 (insert 2): *Exogyra lateralis* Nilsson, 1827 attached on framebuilders and encrusted by serpulids. x 3

Fig. 3. Detail of Fig. 1 (insert 3): *Astya crassus* is encrusted by *Dendrophyllia candelabrum* (A) and *Moltkia lyelli* (B). All the organisms are growing in the same direction, indicating that *Astya crassus* was colonized in life position. The skeleton is bored by clionid sponges. Note the overgrowth of calcite cements. x 3.5

Fig. 4. *Moltkia isis* is adapted to a unidirectional current by its fan-like growth form. This colony exhibits different ontogenetic stages. Some of the primary horny nodes are covered by layers of calcite. This suggests a low current velocity and a deposition in deeper water. x 0.6

Fig. 5. *Heliopora incrustans* Nielsen, 1917 encrusted *Astya crassus* on the anterior side. The cyclosystems of the hydrozoan (preserved as slight elevations) and the autopores of the octocoral point in the same direction, indicating the existence of a unidirectional current. x 1.2

Fig. 6. Posterior side of *Astya crassus* without cyclosystems. x 1.2

Fig. 1. Fächerförmige Kolonie von *Astya crassus*. Die Cyclosysteme sind auf einer Seite angeordnet, die Äste sind häufig verzweigt. Diese Kolonie wurde in Lebensstellung von *Dendrophyllia candelabrum, Moltkia lyelli, Exogyra lateralis*, Bryozoen und Serpeln besiedelt. Die Stabilität der Kolonie wurde durch diese Inkrustationen und durch bohrende Organismen geschwächt. Diagenesetyp 2-3. x 0,9

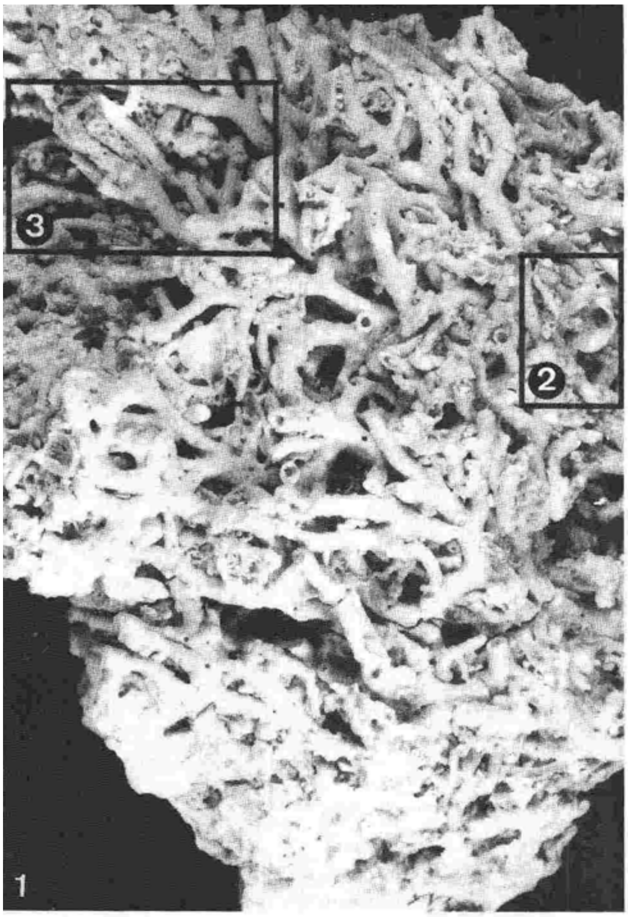
Fig. 2. Ausschnitt von Fig. 1 (Feld 2): *Exogyra lateralis* Nilsson, 1827 zementierte auf Gerüstbildnern und inkrustiert von Serpeln. x 3

Fig. 3. Ausschnitt von Fig. 1 (Feld 3): *Astya crassus* wurde von *Dendrophyllia candelabrum* (A) und *Molkia lyelli* (B) bewachsen. Für eine Besiedlung in Lebensstellung spricht, daß alle Kelche in die gleiche Richtung orientiert sind. Die Kalkskelette sind von *Cliona* angebort. Kalzitzemente erschweren die systematische Bestimmung der Organismen. x 3,5

Fig. 4. *Moltkia isis* ist durch eine fächerförmige Wuchsform an eine gerichtete Strömung angepasst. Diese Kolonie besteht aus verschiedenen Altersstadien. Einige der ehemals hornigen Nodien sind von Kalkkrusten umgeben. Dies ist ein Hinweis auf geringe Strömungsgeschwindigkeit und und größere Wassertiefe. x 0,6

Fig. 5. *Heliopora incrustans* besiedelte *Astya crassus* nur auf einer Seite. Die Cyclosysteme der Hydrozoe (in Form von Erhebungen erhalten) und die Autoporen der Octokoralle zeigen in die gleiche Richtung und weisen somit auf die Existenz einer gerichteten Strömung hin. x 1,2

Fig. 6. Rückseite von *Astya crassus* ohne Cyclosysteme und ohne Inkrustation von *Heliopora incrustans*. x 1,2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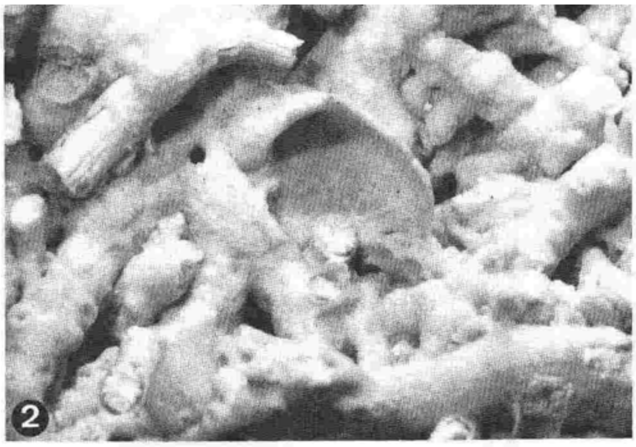
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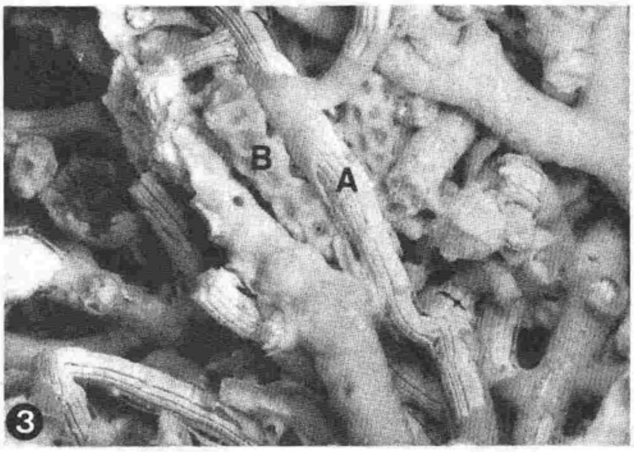
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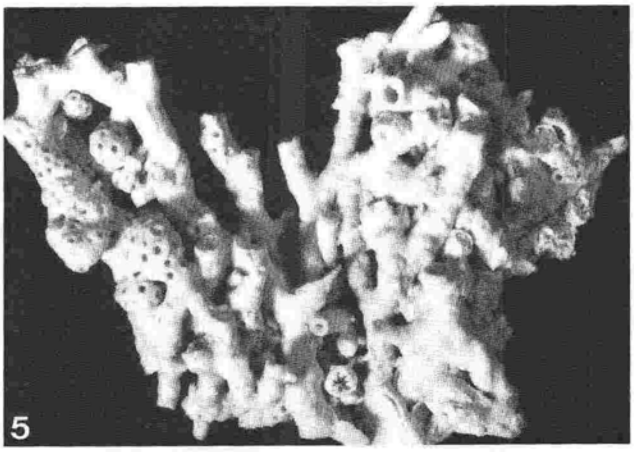
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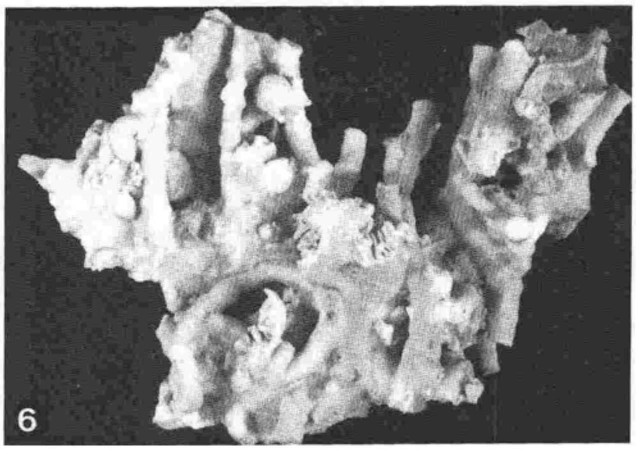
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Plate 32 Danian coral limestone of Fakse, Denmark: Biogenic encrustations
Korallenkalk von Fakse, Dänemark: Biogene Inkrustationen

Fig. 1. *Caryophyllia sp.* attached on *Faksephyllia faxoensis* with a broad base. The calyces point in the same direction, indicating the existence of unidirectional currents. Sample M 2. x 4.5

Fig. 2. *Exogyra lateralis* Nilsson, 1827 is fixed on a stylasterine hydrozoan. These oysters seem to be confined to the coral limestone facies. Sample M 2. x 5

Fig. 3. Encrustation of a coral branch by serpulid worms, bryozoans and a stylasterine hydrozoan. Sample M 2. x 5

Fig. 4. Detail of *Heliopora incrustans* Nielsen, 1919, exhibiting large autopores, pseudosepta and small siphonopores. Colonies of *Heliopora incrustans* are very small and consist only of a few calyces (up to 30). They cannot be compared with the recent light-dependent zooxanthellate species *Heliopora coerulea* exhibiting hundreds of corallites and a massive growth form. Sample M 2. x 10

Fig. 5. Bryozoans encrusting on an adult internode of *Moltkia isis*. Note the multiple overgrowth of several generations of bryozoans. x 2.5

Fig. 6. Encrustation of *Errina lobata* on *Faksephyllia faxoensis* in life position. The arrows point to the calyces of the coral. Sample M 2. x 4.5

Fig. 7. Colonization of oysters (*Ostrea semiplana* Sowerby) by bryozoans and a thecideidean brachiopods. Sample J 24. x 2.5

Fig. 8. Encrustation of a coral calyx (*Dendrophyllia candelabrum*) by the octocoral *Moltkia isis*. Sample M 2. x 6

Fig. 9. *Ostrea semiplana* lived attached on *Dendrophyllia candelabrum*. Note the characteristic imprint (arrow) showing extratentacular budding and costae. Sample J 24. x 2.5

Fig. 1. *Caryophyllia sp.* inkrustiert *Faksephyllia faxoensis* mit einer breiten Basis. Die Kelche zeigen in eine Richtung; dies spricht für die Existenz von gerichteten Strömungen. Probe M 2. x 4,5

Fig. 2. *Exogyra lateralis* Nilsson, 1827, zementiert auf einer stylasterinen Hydrozoe. Diese Auster scheint nur im Korallenkalk vorzukommen. Probe M 2. x 5

Fig. 3. Inkrustation einer Koralle durch Serpeln, Bryozoen und eine stylasterine Hydrozoe. Probe M 2. x 5

Fig. 4. Ausschnitt von *Heliopora incrustans* Nielsen, 1917 mit großen Autoporen, Pseudosepten und kleinen Siphonoporen. Kolonien von *Heliopora incrustans* sind klein und bestehen aus nur wenigen Kelchen (bis zu 30). Die Art kann deshalb nicht mit der rezenten zooxanthellaten (und damit lichtabhängigen) Art *Heliopora coerulea* verglichen werden, die aus hunderten von Individuen besteht und massige Skelette bildet. Probe M 2. x 10

Fig. 5. Bryozoen, inkrustiert auf einem adulten Internodium von *Moltkia isis*. Mehrere Bryozoengenerationen wachsen übereinander. x 2,5

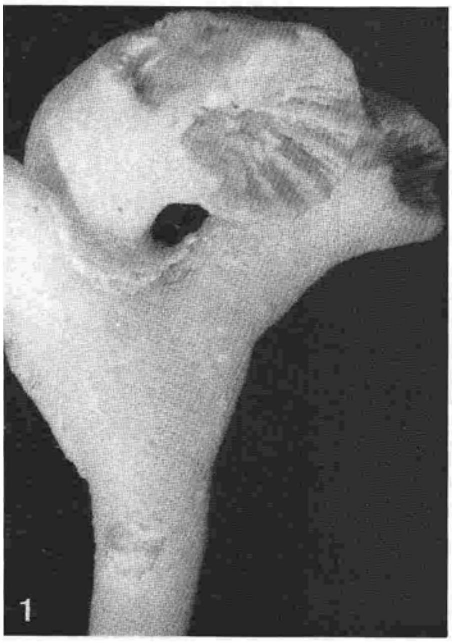
Fig. 6. Allseitige Inkrustation von *Errina lobata* auf *Faksephyllia faxoensis* in Lebensstellung. Die Pfeile weisen auf die Kelche der Koralle hin. Probe M 2. x 4,5

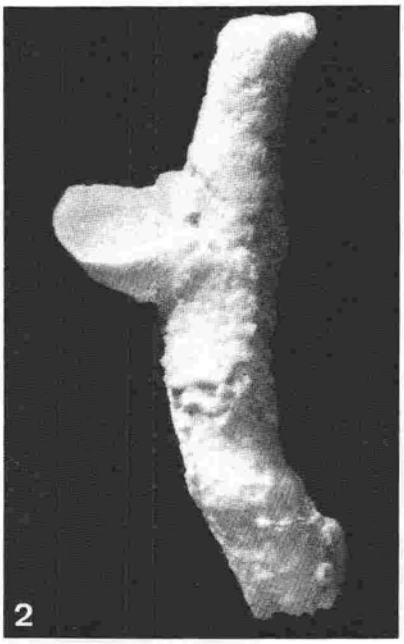
Fig. 7. *Ostrea semiplana* Sowerby wurde postmortal von Bryozoen und Brachiopoden (Thecideidae) bewachsen. Probe J 24. x 2,5

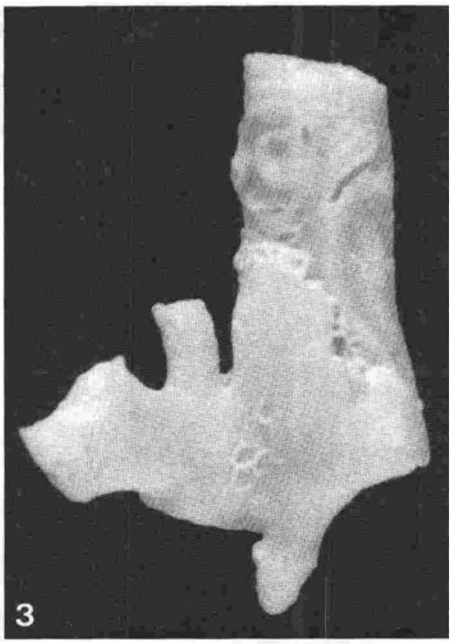
Fig. 8. Inkrustation eines *Dendrophyllia*-Kelches durch die Oktokoralle *Moltkia isis*. Probe M 2. x 6

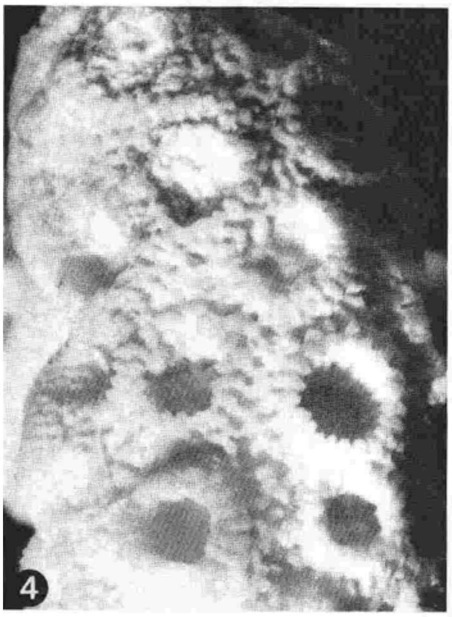
Fig. 9. *Ostrea semiplana* zementiert auf *Dendrophyllia candelabrum*. Charakteristisch ist der Abdruck (Pfeil) des Korallenastes mit extratentakularer Knospung und Costae. Probe J 24. x 2,5

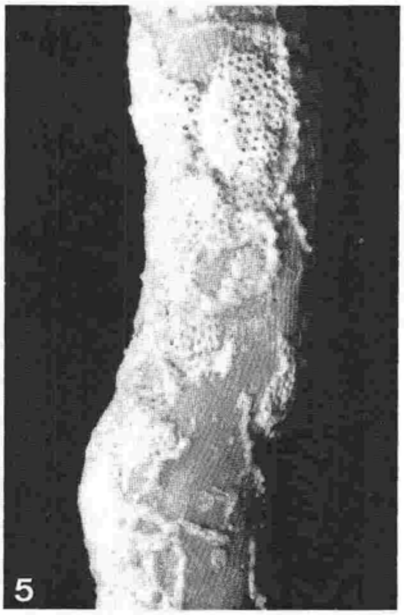
Plate 32

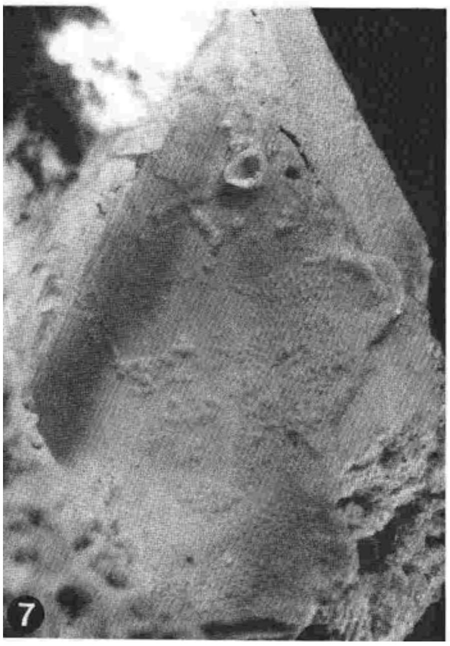


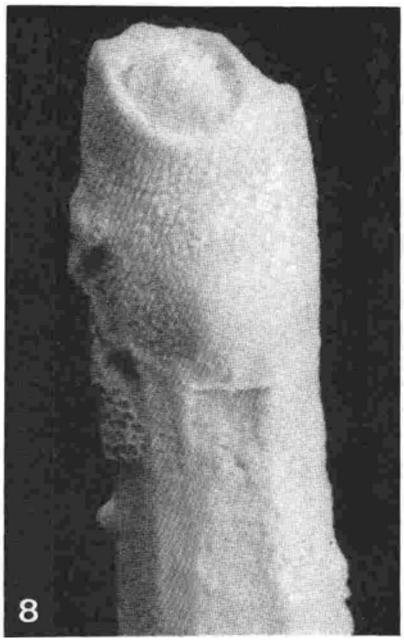












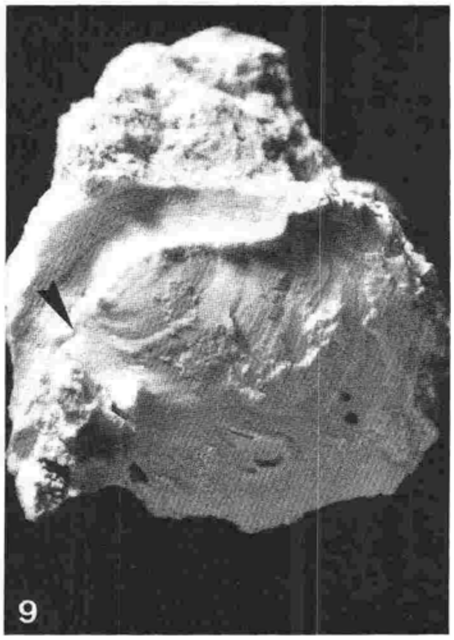


Plate 33 Danian coral limestone of Fakse, Denmark: Parautochthonous and allochthonous sedimentation Der Korallenkalk von Fakse, Dänemark (Dan): Parautochthone und allochthone Sedimentation

Transitional facies

Fig. 1 Typical sample of the transitional facies showing a few imprints of coral branches (arrows) and some large fragments of bryozoans (up to 3 cm in size). x 0.9

Fig. 2. Thin-section. Abundant bryozoans and a cross-section of *Oculina becki*. Sample O 8. x 3

Fissures

Fig. 3. Fissure filling with bryozoan packstone. The surrounding coral limestone is dominated by *Oculina becki*. Sample G 55. x 1

Fig. 4. Thin-section showing the difference between allochthonous and parautochthonous sedimentation: The bioclasts of the fissure (at the right) are more densely packed and heavily broken. Micrite is missing. Sample G 55. x 3

Debris layer

Fig. 5. The debris layer consists of broken coral branches and angular lithoclasts (arrow). In the lower part of the sample parautochthonous coral limestone is visible. Sample G 78. x 1

Fig. 6. Thin section of a debris layer. Note the erosive base. Sample G78. x 3

Übergangsfazies

Fig. 1. Typisches Handstück mit häufigen Bryozoen (gut sichtbar in den Hohlräumen) und nur wenigen Korallen (Pfeile). Die Bryozoenbruchstücke können eine Länge von 3 cm erreichen. x 0,9

Fig. 2. Dünnschliff mit häufigen Bryozoen und nur einem *Oculina*-Querschnitt. Probe O 8. x 3

Spalten

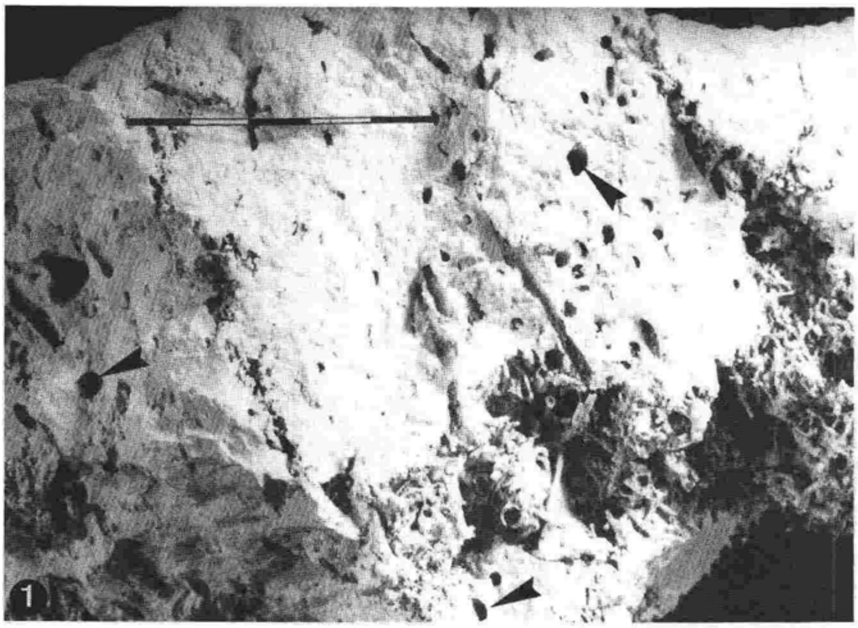
Fig. 3. Spaltenfüllung mit Bryozoen-Packstone. Im umgebenden Korallenkalk dominiert *Oculina becki*. Probe G 55. x 1

Fig. 4. Der Dünnschliff verdeutlicht die Unterschiede zwischen allochthoner und autochthoner Sedimentation: Die Bioklasten der Spalte (im Bild rechts) sind dichter gepackt und stärker zerbrochen. Mikrit fehlt zwischen den Komponenten. Probe G 55. x 3

Schuttlagen

Fig. 5. Die Schuttlage besteht aus stark zerbrochenen Korallen und angularen Lithoklasten (Pfeil). Im unteren Bereich des Handstückes ist parautochthoner Korallenkalk zu erkennen. Probe G 78. x 1

Fig. 6. Dünnschliff einer Schuttlage mit erosiver Basis. Probe G 78. x 3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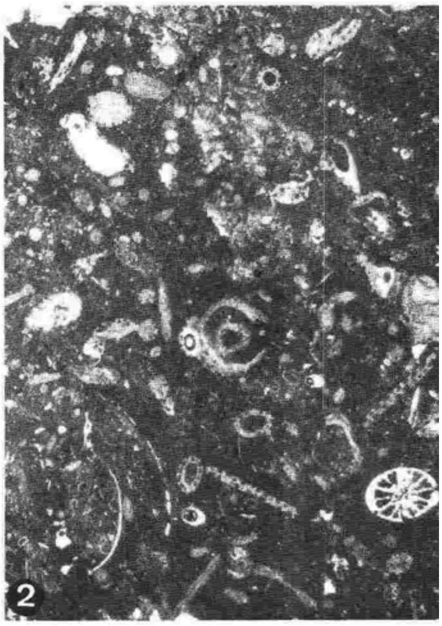
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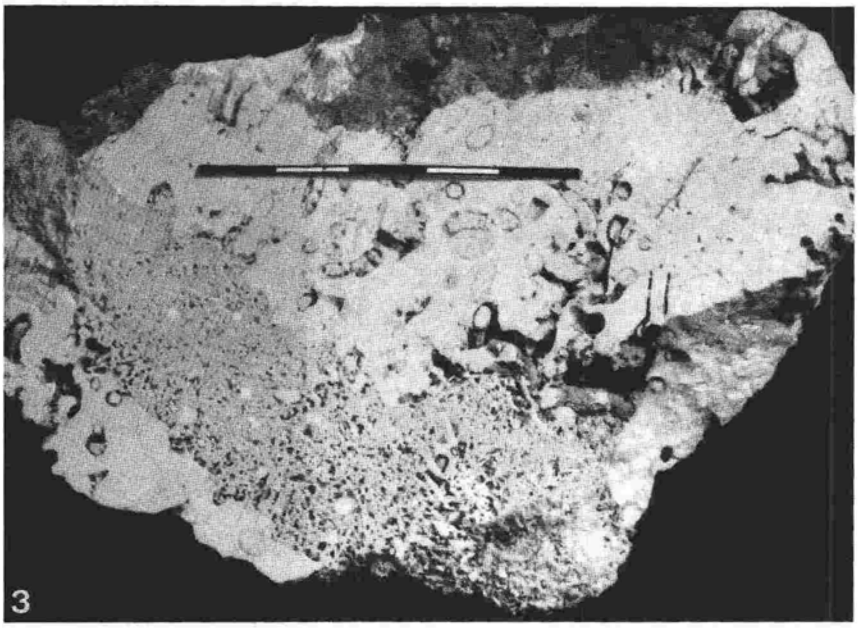
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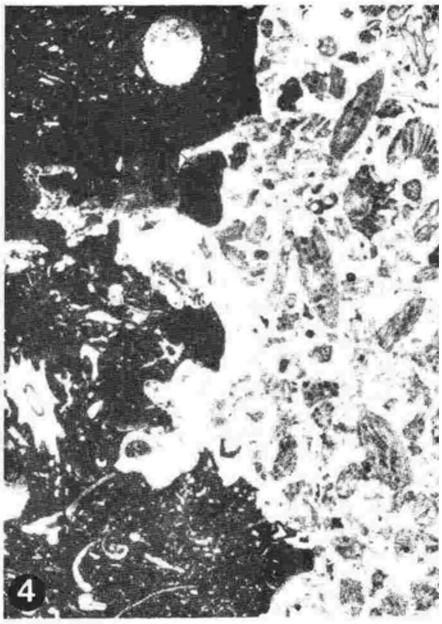
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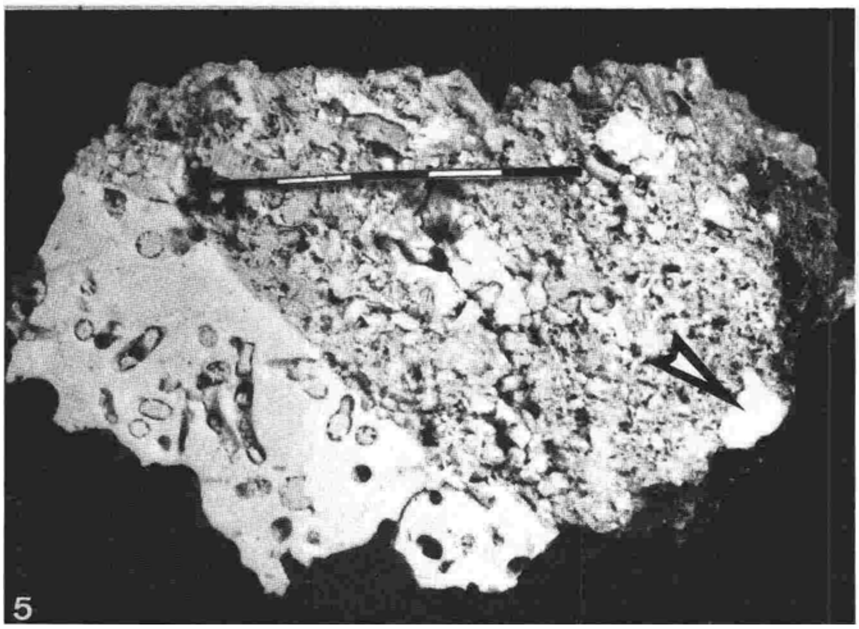
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