

Benthic macroinvertebrate associations
from the Boreal Upper Jurassic of Milne Land,
central East Greenland

by

Franz T. Fürsich



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Abstract

From the Upper Oxfordian to the Middle Volgian of Milne Land twenty-two marine benthic macroinvertebrate associations and ten assemblages are described. They occur in silici-clastic, shallow near-shore to offshore shelf sediments. Most of the associations are dominated by bivalves, some by brachiopods, and one by a serpulid polychaete. They are based on 135 samples containing close to 24 000 specimens. For each association, statistical data on faunal composition, trophic composition and life habits are given. The depositional environment of the Milne Land sequence is briefly discussed as are the faunal relationships with other parts of the Boreal Sea (North-East Greenland, Spitsbergen, and northern Siberia).

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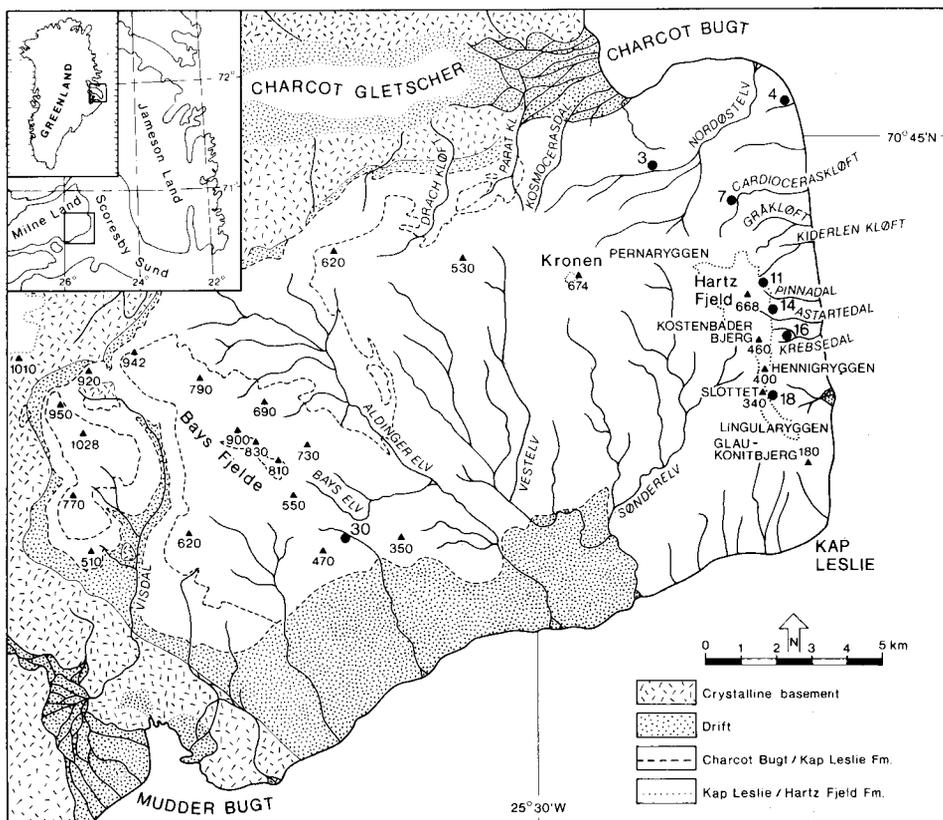


Fig. 1. Locality map, southeast Milne Land, East Greenland. Dots refer to localities mentioned in the text.

INTRODUCTION

Marine benthic macroinvertebrate associations from the Boreal Jurassic are little known. Solely Žakharov (1966) gives an outline of the synecology of Upper Jurassic faunas from northern Siberia without, however, providing any quantitative data. The present study is a description of the benthic macroinvertebrate associations and assemblages occurring in the Upper Jurassic (Upper Oxfordian – Middle Volgian) sequence of Milne Land. Like taxonomic studies of populations, these descriptions serve as the basis for more interpretative studies dealing with interspecific relations, fauna/facies relationships, faunal evolution, and faunal provincialism which will be published elsewhere.

Locally, the Upper Jurassic of Milne Land is very fossiliferous so that quantitative bed by bed fossil collecting was possible. Furthermore, most faunas are preserved *in situ*, transported assemblages being relatively rare. Finally, diagenetic distortion caused by preferential dissolution of specific faunal elements appears to have been insignificant. These three facts make the Upper Jurassic of Milne Land ideal for palaeoecological investigations.

The Jurassic sea transgressed onto Milne Land, an island in the Scoresby Sund (fig. 1), in Bathonian times. These lowermost Jurassic sediments rest on a Caldonian crystalline basement and are very coarse grained arkoses and quartzose sandstones (Charcot Bugt Formation, Upper Bathonian – Middle Callovian). They are followed by offshore fine-sandy silty shale and siltstone of the Kosmocerasdal Member of the Kap Leslie Formation (Upper Callovian – Upper Oxfordian). The next lithological unit is the Upper Oxfordian Aldinger Elv Member which represents well sorted, frequently cross-bedded fine to medium-grained sand and sandstone reflecting very shallow water conditions. A return to somewhat deeper, quieter environments is suggested by the partly glauconitic sandstone and siltstone of the Bays Elv Member (Upper Oxfordian – Lower Kimmeridgian) and the siltstone and sandstone of the Cardioceraskløft Member (Lower Kimmeridgian). Largely anoxic conditions and a very low energy environment is represented by black laminated silty shale of the Gråkløft Member (Lower Kimmeridgian – Lower Volgian). The Lower – Middle Volgian Krebsedal Member, a unit of bioturbated silt, siltstone, and fine-grained sandstone, shows a return to shallower, well oxygenated conditions. Authigenic glauconite and shell beds are very abundant in the Middle Volgian Krebsedal Member, whilst the silty shales of the Astartedal Member (Middle Volgian) are characterized by their extremely high mica content. All these units belong to the Kap Leslie Formation. It is overlain, with a slight unconformity, by the Hartz Fjeld Formation: cross-bedded medium to coarse-grained sand and sand-

stone which are of nearshore origin and represent the youngest Mesozoic rocks exposed in the area. Only the lowermost part (lower part of the Hennigryggen Member) is still Jurassic in age. The preserved sedimentary record extends to the Hauterivian.

A detailed description of the biostratigraphy and lithology of the Upper Jurassic sequence is found in Birkelund *et al.* (1984). Sections of the three main outcrop areas are shown in fig. 2.

Although benthic macroinvertebrate faunas occur through much of this sequence, they are particularly common at the following levels:

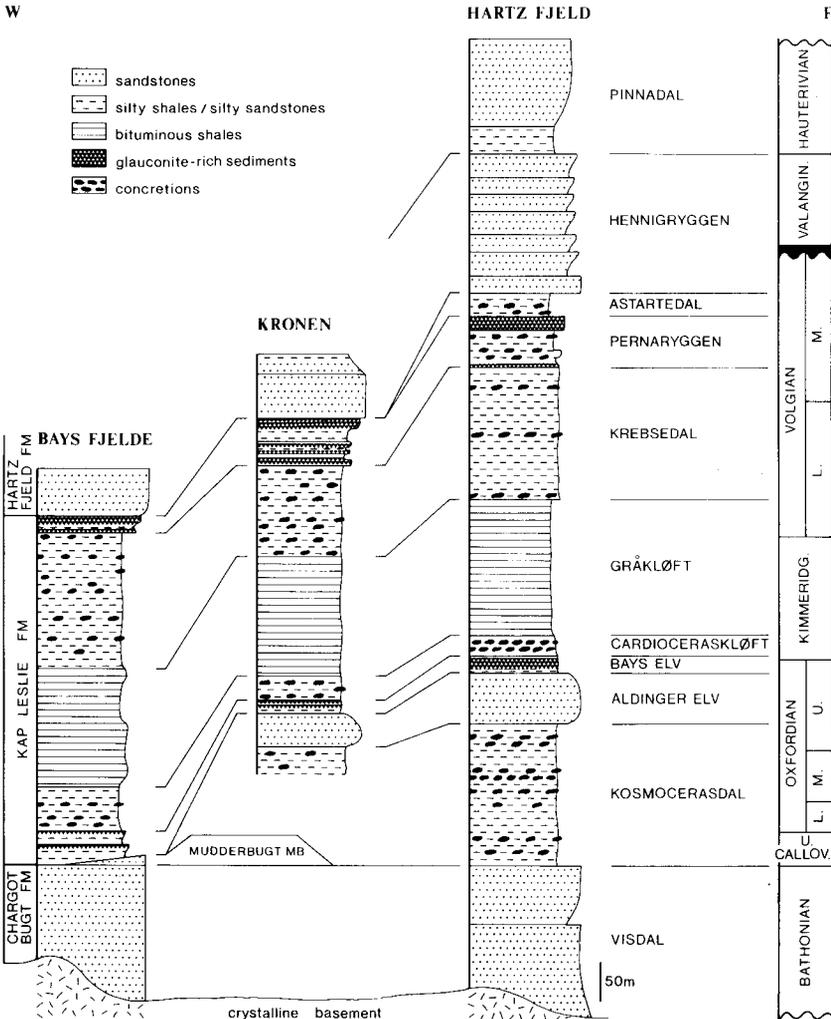


Fig. 2. Schematic sections and lithostratigraphy of the three main outcrop areas of the Upper Jurassic in southeast Milne Land.

- a) sandstone of the Kosmocerasdal Member;
- b) the Aldinger Elv Member;
- c) some concretion levels in the Cardioceraskløft Member;
- d) in concretions in the upper part of the Krebsedal Member;
- e) the numerous shell beds of the Pernaryggen Member;
- f) some concretion levels of the Astartedal Member; and
- g) the *Lingula* bed, a concretion horizon in the lower part of the Hennigryggen Member.

The geology of the Mesozoic sequence of Milne Land is comparatively well known. Jurassic sediments occur in the southeast corner of the island (fig. 1). First mentioned by Bay (1895), they were subsequently studied by Rosenkrantz (1929), Parat & Drach (1933, 1934), Aldinger (1935), Donovan (1957), Callomon (1961), Sykes & Brand (1976), and mapped by Håkansson *et al.* (1971). During an expedition of the Geological Survey of Greenland to East Greenland in 1977, additional data on the biostratigraphy, sedimentology and palaeoecology were collected by T. Birkelund, J. H. Callomon, F. T. Fürsich, C. Heinberg and S. Piasecki. First results were published by Birkelund *et al.* (1978), Callomon & Birkelund (1980, 1982), Piasecki (1980), Fürsich (1982a), and Fürsich & Heinberg (1983).

The invertebrate fauna was described by Spath (1935, 1936) and the bivalves were monographed by Fürsich (1982b). As bivalves are the dominant benthic group, there exists a sound taxonomic basis for palaeosynecological studies.

METHODS OF STUDY AND TERMINOLOGY

Bed by bed sampling of fossiliferous horizons resulted in 135 samples with approximately 23 850 specimens of invertebrate fossils. Samples were partly counted in the field, partly broken up in the laboratory. Taxa with two valves were only counted as one individual when articulated. Among disarticulated specimens the commoner valve was counted. Where distinction between right and left valve or pedicle and brachial valve was not possible, the number of disarticulated specimens was divided by two to reach the final count. Of each sample the relative abundance was calculated, and the trophic nucleus, that is the most abundant faunal elements accounting for approximately 80% of the fauna, was established (see Walker, 1972).

The term assemblage is used for faunas which are autochthonous, but not recurrent, or else are allochthonous. The term association, in contrast, is used for faunas which are recurrent and autochthonous and therefore represent preserved relics of former communities. Samples with identical or very similar trophic nuclei were thus grouped in associations. For each association, the relative abundance percentage and the presence percentage (as an expression of the homogeneity of an

association; giving the percentage of samples of the association in which a particular species occurs) were calculated. In addition, the percentage of the various trophic groups (suspension-feeders, deposit-feeders, herbivores) was established. Biostratinomic data refer to the percentage of uncemented faunal elements preserved in life position, percentage of still articulated taxa, and the degree of fragmentation. The latter was estimated and therefore is only approximate. Where possible, plan-view and side-view orientation of shells was measured.

Two aspects of faunal diversity were calculated: species richness and evenness. Species richness was simply expressed by the number of species present. As most samples have well over 100 specimens and are only of moderate diversity, distortion of the species richness by differing sample sizes is thought to be minimal. Evenness was calculated as $D = 1/\sum_i p_i^2$ where p_i is the relative frequency of the i th species (e.g. MacArthur, 1972, p. 197).

For each association, members of the trophic nucleus were reconstructed in their growth positions. The growth position was inferred from either field observations, oriented epizoans, or else by functional analysis of the species. Notes on the life habits of the bivalves are found in Fürsich (1982b).

BENTHIC MACROINVERTEBRATE FAUNA

In the following, the various benthic faunal groups are briefly characterized and their distribution discussed.

Scaphopods

Scaphopods are only represented by one species of *Dentalium*. It occurs as a characteristic element of the *Grammatodon schourovskii* association in the Kребседal and Astartedal Members and is absent or rare anywhere else.

Gastropods

There are 20 species of gastropods in the Upper Jurassic of Milne Land, a surprisingly low number when compared with similar sequences from the subboreal or submediterranean faunal provinces. Most species probably were herbivores, grazing on algal films and seaweed or feeding on dead plant material. More rarely they were specialized suspension-feeders such as *Turritella* aff. *T. molarium*. The most abundant forms are *Sulcoactaeon peroskianus*, *Pseudomelania* sp., *Turritella* aff. *T. molarium*, *Delphinula* sp. and *Amberleya* cf. *A. jasikofiana*. There are only three levels where gastropods play a significant role: At the *Rasenia* concretion level II (Cardioceraskløft Member) where *Amberleya* cf. *A. jasikofiana* is abundant; within the lower part of the Pernaryggen Member, where *Turritella* aff. *T. molarium* is the diagnostic species of an association; and in the so-called *Pinna* bed

(upper part of the Pernaryggen Member) where several gastropod species (*Sulcoataeon* sp., *Delphinula* sp., *Pseudomelania* sp.) are conspicuous. An abundance of herbivorous gastropods probably characterizes well vegetated parts of the sea floor. The scarcity or absence of gastropods from many associations may indicate that the environments were generally too deep to support rich gastropod faunas whose maximum distribution is in shallow shelf areas.

Bivalves

Bivalves are the dominant element of most associations from the Upper Jurassic of East Greenland. With 90 to 95 species they are also the most diverse group. Particularly common are species of the genera *Grammatodon*, *Lopatinia*, *Buchia*, *Pinna*, *Astarte*, *Arctica*, *Isocyprina*, *Isognomon*, *Entolium*, *Camptonectes* and *Pleuromya*. Deposit-feeding nuculids are common only in one association; the overwhelming majority of the bivalves are suspension-feeders. Byssate and free living pectinids dominate many associations. Noteworthy are several very large species of *Camptonectes*, particularly in the Pernaryggen Member, where giant *Camptonectes praecinctus* appears. Also of interest is the scarcity of oysters. The most abundant form, *Liosrea plastica*, most likely lived attached to floating ammonites (Fürsich, 1982b) and therefore does not belong to the benthos. The same is true of a wood boring bivalve which is frequently found in pieces of drift wood in the Pernaryggen Member.

Most bivalves appear to have been adapted to life on or in relatively firm substrates. Several species are known so far from East Greenland only (e.g. the eleven new species described in Fürsich (1982b)), and several genera apparently are restricted to the boreal faunal province (e.g. *Hartwellia*, *Buchia*, *Lopatinia*, *Strimodiolus*). Many other species, however, are also common faunal elements of Upper Jurassic sequences belonging to the subboreal and submediterranean faunal provinces (e.g. southern England, Germany, France and Portugal).

Annelids

Annelids are represented by encrusting or free living serpulids. Encrusting forms are surprisingly rare considering that many of the epifaunal bivalves or brachiopods must have remained unburied for considerable spans of time, due to generally low rates of sedimentation, and thus provided ideal settling grounds for serpulid larvae. Free living *Cycloserpula* is common in the *Pinna* bed of the Pernaryggen Member, and the free living *Ditrupa* is a characteristic element of the Aldinger Elv Member and of certain horizons in the Kosmocerasdal Member, sometimes occurring in huge numbers (e.g. fig. 11). *Ditrupa* appears to be characteristic of the boreal faunal province in the Upper Jurassic as it occurs also in other parts of East Greenland (Frebald, 1933; Ravn, 1911).

Crustaceans

Not uncommonly, crustaceans are preserved in concretions within silty shale of the Krebsedal, Pernaryggen and Astartedal Members. Two species (*Glyphea ros-trata* and *Eryma* cf. *E. ventrosa*) are present although in low numbers only. *Glyphea* has been repeatedly encountered within *Thalassinoides* systems (e.g. Bromley & Asgaard, 1972; Fürsich, 1974) and members of this genus apparently were able to construct such burrow systems.

Bryozoans

Bryozoans are extremely rare. A crustose and a fan-shaped type occur in the *Pinna* bed of the Hartz Fjeld region. Bryozoans are generally rare in boreal sequences.

Brachiopods

Brachiopods are represented by two inarticulate (*Orbiculoidea* sp., *Lingula* sp.) and two articulate species. The two articulates are new species of *Taimyrothyris* and '*Rhynchonella*' (E. F. Owen, London, written communication, 1982).

Although of low diversity, the brachiopods occur locally in great abundance, frequently in life position. *Orbiculoidea latissima* is common in the vicinity of the *Epi-pallasiceras* bed (Pernaryggen Member); *Lingula* is typical of the *Lingula* bed of the Hennigryggen Member. The two articulates are common at numerous levels

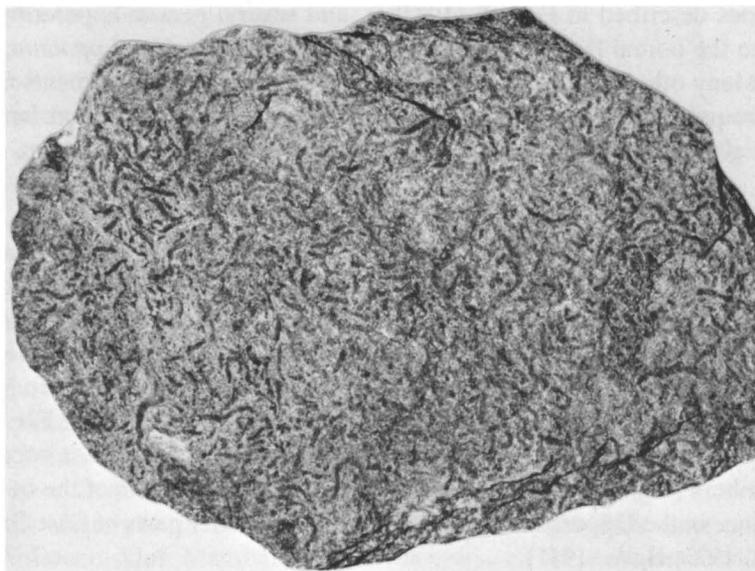


Fig. 3. *Macaronichnus segregatis*, back-filled tubes of a deposit-feeder. Pernaryggen Member at Pernaryggen. Scale: $\times 0.8$.

within the Pernaryggen Member where they dominate one and are characteristic members of several other associations. *Taimyrothyris* and the rhynchonellid apparently preferred habitats below fair weather wave base.

Echinoderms

Echinoderms are another rare group in the Upper Jurassic of Milne Land. Cidaroid spines and plates have been found at one locality in the Krebsedal Member. Scattered *Pentacrinites* columnals occasionally occur in the Pernaryggen Member, particularly in the *Pinna* bed. More often, large portions of the stem, crown, or arms of *Pentacrinites* are found at certain horizons of the Aldinger Elv Member and possibly are relics of a former community dominated by this crinoid. The rarity of echinoderms is difficult to explain. Diagenetic dissolution can be ruled out, as the high-Mg calcite of their skeleton is less easily dissolved than aragonitic shells of gastropods and some bivalves which are often preserved with their (recrystallized) shell.

Trace fossils

Trace fossils are common at numerous levels. Seventeen ichnogenera have been recognized. Table 1 gives their distribution in the various members. Traces of sus-

Table 1. Distribution of trace fossils in the Upper Jurassic of Milne Land

r: rare; o: occurs; c: common; a: abundant; x: abundance not recorded.

Trace fossil	Member	Kosmocerasedal	Bays Elv	Aldinger Elv	Cardioceraskløft	Gråkløft	Krebsedal	Pernaryggen	Astartedal	Hennigryggen	(Lingula Bed)
<i>Ancorichnus ancorichnus</i>				x							
<i>Arenicolites</i> sp.				x							
<i>Chondrites</i> sp.		x						r		r	
<i>Curvolithus</i> sp.				x	x		x	o		x	
<i>Diplocraterion habichi</i>								r		a	
<i>Gyrochorte comosa</i>				x				r		x	
<i>Gyrophyllites</i> sp.				r							
<i>Helminthopsis</i> sp.				c							c
<i>Macaronichnus segregatis</i>				x	a		a	a	o		o
mantled vertical tubes							x	c	o		
<i>Muensteria</i> sp.		x		x							
<i>Ophiomorpha</i> sp.										a	
<i>Planolites</i> sp.				x			x	c	o	x	
<i>Skolithos</i> sp.		x		x	x		x	c	c	x	c
<i>Teichichnus rectus</i>								r			
<i>Thalassinoides suevicus</i>		x		x	x		x	a	o	r	c
<i>Urohelminthoida</i> sp.				x							
escape structures				x							x

pension-feeders (e.g. *Ophiomorpha*, *Diplocraterion*, *Arenicolites*, *Skolithos*) indicative of raised energy levels preferentially occur at some levels within the Aldinger Elv Member and in the Hennigryggen Member; they are less diverse than traces of deposit-feeders (e.g. *Macaronichnus*, *Muensteria*, *Gyrochorte*, *Gyrophylites*). *Macaronichnus*, possibly of polychaete origin, is by far the most abundant trace fossil (fig. 3) and accounts for most of the mottling in the silty shale facies. The occurrence of a meandering trace (*Helminthopsis*) and a graphoglyptid (*Urohelminthoida*) in high energy environments of the Aldinger Elv Member and the Lingula Bed is surprising, as both forms are typical of flysch deposits rather than shallow water environments. The occurrence of a graphoglyptid in horizontal laminated sands is interpreted as a special adaptation to life in frequently reworked sediments (Fürsich & Heinberg, 1983).

As most trace fossils record the activity of soft-bodied organisms which were not preserved, they have been included in the description of the associations thus reducing, to some extent, the degree of diagenetic distortion of the former communities, caused by loss of soft-bodied organisms. The trace fossil assemblages do not differ much from those known from the Jurassic elsewhere. Solely *Ancorichnus* appears to be restricted to Greenland not having been reported from anywhere else.

BENTHIC MACROINVERTEBRATE ASSOCIATIONS AND ASSEMBLAGES

Twenty-one benthic associations and ten assemblages have been recognized in the Upper Jurassic of Milne Land. Each association is described, and statistical data are given. The depositional environment of each lithostratigraphical member is briefly discussed as reconstructed from facies and benthic fauna.

Kosmocerasdal Member

The Kosmocerasdal Member (Upper Oxfordian) consists predominantly of micaceous very fine-sandy to silty shale with only rare remains of benthic invertebrates. Within the *tenuiserratum* Zone, however, well-sorted fine-grained micaceous sand and sandstone is developed, which is exposed in a valley north of Cardioceraskløft (locality 4). The locality has been visited by A. Rosenkrantz (1929) and, in 1933, by M. Parat, P. Drach and H. Aldinger. Only limited time for sampling was available when the locality was visited in 1977, but the following descriptions are thought to provide a reasonably accurate picture of the benthic fauna and biofacies.

Biofacies distribution

The well-sorted fine-grained micaceous sands and sandstones only rarely exhibit sedimentary structures (such as horizontal lamination), but for the most part are bioturbated and contain a variety of trace fossils. The shelly fauna is usually randomly distributed, and burrowing forms are frequently found in life positions. At irregular intervals, however, thin shell beds up to 10 cm in thickness occur, which contain a transported and often highly fragmented fauna. They obviously represent high energy episodes during which sediment and fauna were reworked and the latter sometimes selectively enriched. Of the benthic associations only the *Grammatodon keyserlingii*/*Ditrupa nodulosa* association which prevails in the lower part of the section is found reworked in shell beds, whilst the *Entolium corneolum*/*Pleuromya uniformis* association, which is rare in the lower part but widespread in the upper part, invariably occurs with burrowing forms in life position and clearly represents a quieter environment than the former.

Towards the top of the valley, the sediments become slightly glauconitic, and fine-grained sand alternates with concretion levels. The benthic fauna is represented by the *E. corneolum*/*P. uniformis* association throughout. The only change in faunal composition is the slight increase in the numbers of *Camptonectes broenlundii* towards the top, a species which is so profuse in the overlying sandstone of the Aldinger Elv Member.

No section was measured, but the biofacies sequence is tentatively given in fig. 4.

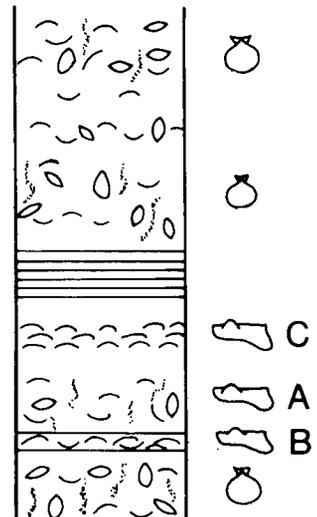


Fig. 4. Schematic section through the upper part of the Kosmo-cersdal Member. Not to scale. A, B and C refer to fig. 8.

Entolium corneolum/*Pleuromya uniformis* association

Table 2, figs 5, 6

Although sampled only at two horizons, the *E. corneolum*/*P. uniformis* association was found also at several other levels and indeed dominates the upper part of the section. The four species in the trophic nucleus are the free living pectinid *Entolium corneolum*, the deep burrowing *Pleuromya uniformis*, the epibyssate *Camptonectes milnelandensis* and the deep burrowing *Pholadomya hemicardia*. All species were suspension-feeders apart from the rare detritus-feeding gastropod *Dicroloma*. Epifauna (*Entolium*, *Camptonectes*, *Meleagrinea*, *Praebuchia*) constitutes 59.1% of the fauna, semi-infauna (*Pinna*, *Modiolus*) 2.9%, and infauna (e.g. the pholadomyids, *Protocardia*, *Thracia*) 38%. Trace fossils are common and represent deposit-feeders (*Muensteria*, *Chondrites*), detritus-feeders (*Thalassinoides suevicus*), and suspension-feeders (*Skolithos*). Ammonites and belemnites comprise 16.7% of the total fauna. Faunal diversity is moderate with species richness ranging from 11 to 17, and evenness values from 1.86 to 3.69. Only 2% of the fauna occur in life position (*Pleuromya*) and 30% of the bivalved fauna are still articulated. Fragmentation varies from 20 to 75%. Even thin-shelled *Pleuromya* are preserved with shell so that diagenetic distortion of the fauna can be ruled out.

In one of the samples, young individuals of *E. corneolum* are arranged in a nar-

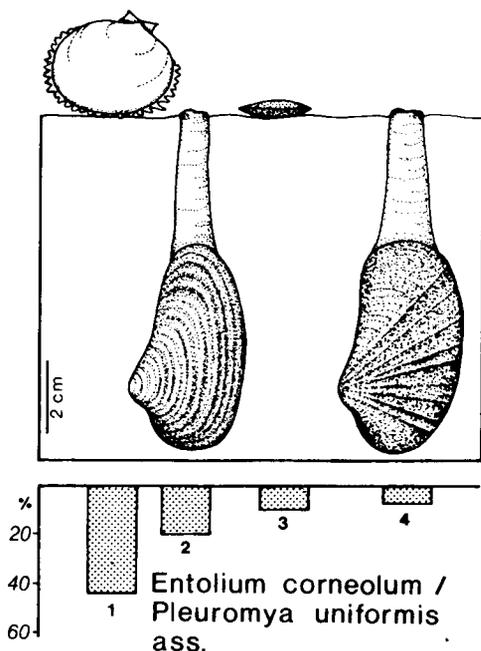


Fig. 5. Trophic nucleus of the *Entolium corneolum*/*Pleuromya uniformis* association. 1: *Entolium corneolum*; 2: *Pleuromya uniformis*; 3: *Camptonectes milnelandensis*; 4: *Pholadomya hemicardia*.

Table 2. *Entolium corneolum*/*Pleuromya uniformis* association

	Relative abundance (%)	Presence (%)
Bivalves (99.1%)		
* <i>Entolium corneolum</i>	43.2	100
* <i>Pleuromya uniformis</i>	20.6	100
* <i>Camptonectes milnelandensis</i>	10.7	100
* <i>Pholadomya hemicardia</i>	7.8	50
<i>Protocardia striatula</i>	6.1	100
<i>Pleuromya uralensis</i>	1.7	100
<i>Camptonectes auritus</i>	1.4	50
<i>Thracia depressa</i>	1.4	50
<i>Meleagrinea ovalis</i>	1.1	100
<i>Modiolus strajeskianus</i>	1.1	100
<i>Goniomya literata</i>	0.6	100
<i>Oxytoma</i> sp.	0.6	50
<i>Praebuchia kirghisensis</i>	0.6	50
<i>Camptonectes broenlundii</i>	0.6	50
<i>Pinna lanceolata</i>	0.6	50
<i>Limatula</i> sp.	0.3	50
<i>Nicaniella</i> sp.	0.3	50
Gastropods (0.3%)		
<i>Dicroloma bononiensis</i>	0.3	50
Serpulids (0.6%)		
<i>Serpula intestinalis</i>	0.6	100
Trace fossils		
<i>Thalassinoides suevicus</i>		100
<i>Muensteria</i> sp.		50
<i>Chondrites</i> sp.		50
<i>Skolithos</i> sp.		50

2 collections, 414 specimens.

Members of the trophic nucleus are marked with an asterisk.

row strip on the bedding plane. This arrangement can be explained in that the bivalves were trapped inside a *Thalassinoides* burrow of which the sediment fill does not differ from the surrounding sediment. Alternatively, the shells could represent a stringer indicative of current influence. The *E. corneolum*/*P. uniformis* association appears to be the autochthonous relic of a former community. It occurs in micaceous, fine-grained, slightly glauconitic and carbonaceous sand and sandstone in which pieces of driftwood are common.

Grammatodon keyserlingii/*Ditrupa nodulosa* association

Table 3, figs 6, 7

Represented by only one quantitative sample with 167 specimens the *G. keyserlingii*/*D. nodulosa* association is nevertheless thought to represent a true association as it was found also at several other horizons, although there somewhat distorted by either selective transport or differential fragmentation. The following brief description is therefore based on one sample only.

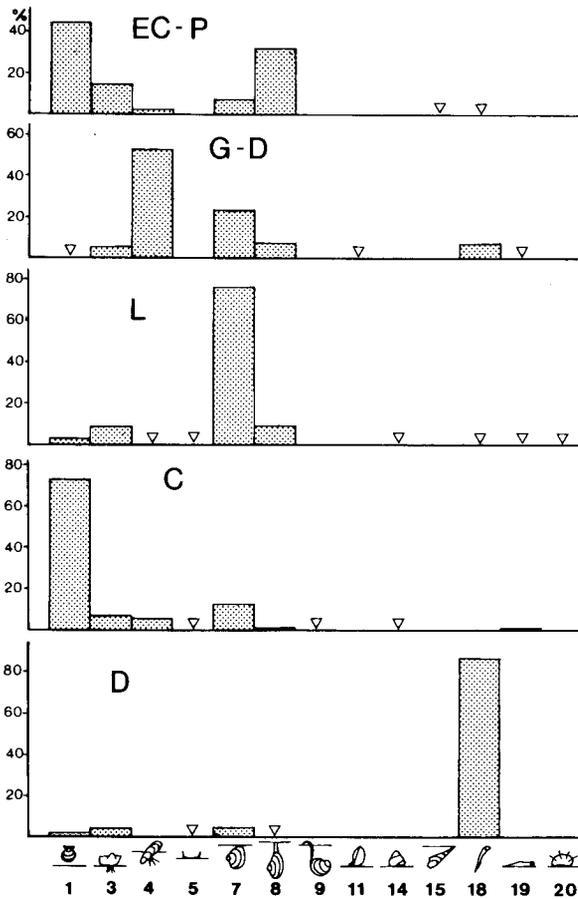


Fig. 6. Distribution of life habit groups in five associations from the Kosmocerasdal and Aldinger Elv Members. For symbols 1–20 see fig. 24. EC-P: *Entolium corneolum*/*Pleuromya unifornis* ass.; G-D: *Grammatodon keyserlingii*/*Ditrupa nodulosa* ass.; L: *Lopatinia callomoni* ass.; C: *Camptonectes broenlundii* ass.; D: *Ditrupa nodulosa* ass.

The association is dominated by *G. keyserlingii* which represents over 50% of the fauna. Other important elements are the small shallow burrowing bivalves *Nicaniella* and *Protocardia* as well as the epifaunal polychaete *Ditrupa*. All species are suspension-feeders with the exception of *Ditrupa*. Due to the abundance of *G. keyserlingii* the semi-infauna constitutes 54.3% of the fauna, epifauna 14.6%, infauna the rest. Eight out of nine deep burrowing *Pholadomya hemicardia* were found in life position, but only 11.3% of bivalved forms were still articulated. Faunal density is low and fragmentation around 50–75%.

Species richness of the sample is 12, the evenness value 3.01. The sample comes from fine-grained, micaceous bioturbated sandstone with abundant plant debris.

Whilst there is little doubt that the sample represents the autochthonous relic of a former community, several other samples show clear indications of distortion by biostratinomic processes. Fig. 8 illustrates the change taking place from an auto-

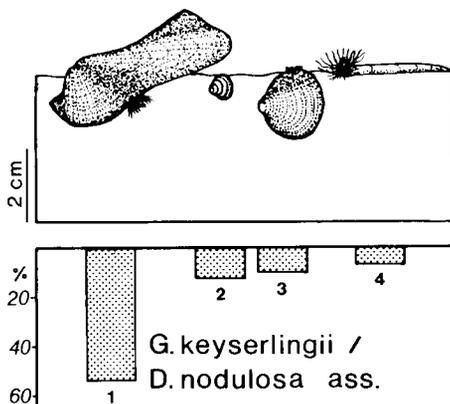


Fig. 7. Trophic nucleus of the *Grammatodon keyserlingii*/*Ditrupa nodulosa* association from the Kosmocerasdal Member. 1: *Grammatodon keyserlingii*; 2: *Nicaniella* sp.; 3: *Protocardia striatula*; 4: *Ditrupa nodulosa*.

chthonous fauna to an increasingly reworked and transported assemblage. Sample A represents the *in situ* preserved fauna as described above. In sample B, a 10 cm thick shell bed, the species richness is higher than in A, probably due to admixture from adjacent communities. No specimens are articulated or preserved in life position and 6% are bored by acrothoracican barnacles. Fragmentation is very high (95%). Whilst sorting by currents appears to have been negligible (*Grammatodon* shells are present in a wide variety of sizes), selective fragmentation of thin-shelled faunal elements by wave action is thought to have led to preferential preservation of the comparatively thick-shelled *G. keyserlingii* and *D. nodulosa*.

In sample C, a shell bed only one centimetre in thickness, the species richness is extremely low (3) and the fragmentation even higher than in B. Selective transport caused the dominance of *Ditrupa* over *Grammatodon*, the former representing

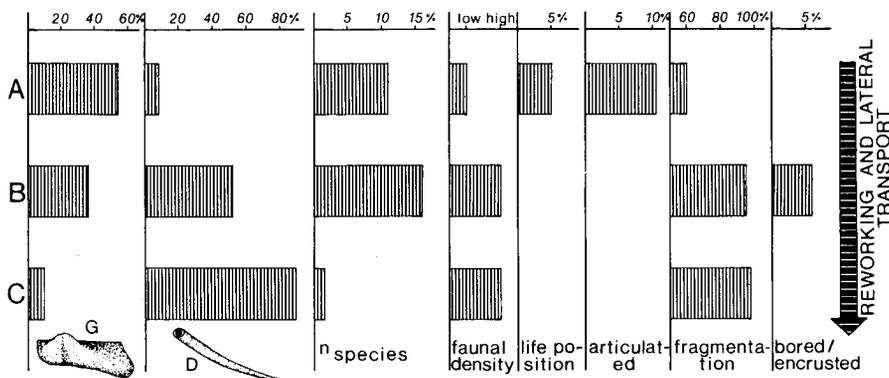


Fig. 8. Biostratinomy of three shell beds of the *Grammatodon keyserlingii*/*Ditrupa nodulosa* association from the upper part of the Kosmocerasdal Member indicating various stages of reworking and transport. G: *G. keyserlingii*; D: *D. nodulosa*.

Table 3. *Grammatodon keyserlingii*/*Ditrupa nodulosa* association

	Relative abundance (%)
Bivalves (91.5%)	
* <i>Grammatodon keyserlingii</i>	54.3
* <i>Nicaniella</i> sp.	12.2
* <i>Protocardia striatula</i>	10.4
<i>Pholadomya hemicardia</i>	5.5
<i>Camptonectes milnelandensis</i>	4.9
tancrediid bivalve	1.8
heterodont bivalve	1.2
<i>Limatula</i> sp.	0.6
<i>Entolium corneolum</i>	0.6
Brachiopods (0.6%)	
' <i>Terebratula</i> ' sp.	0.6
Annelids (7.9%)	
* <i>Ditrupa nodulosa</i>	7.3
<i>Serpula (Cycloserpula)</i> sp.	0.6

1 collection, 167 specimens.

Members of the trophic nucleus are marked with an asterisk.

84% of all individuals. This last sample clearly illustrates the decrease in diversity and increase in dominance of one or very few faunal elements, so characteristic of extensive lateral transport.

Discussion

The two associations of the Kosmocerasdal Member represent two different environments: The *E. corneolum*/*P. uniformis* association apparently lived below fair weather wave base on relatively firm sediments (dominance of epifauna!) which are highly bioturbated. The sedimentation rate was low, enabling glauconite to form on the sea floor. Large-scale reworking, erosion, or sedimentation did not take place.

The *G. keyserlingii*/*D. nodulosa* association, in contrast, represents a higher energy environment. Although the substrate was firm, reworking was frequent and led to formation of shell beds and, more rarely, to sudden burial of autochthonous benthic faunas. Sedimentation rates seem to have varied considerably, and there was not sufficient time for the burrowing fauna to obliterate all sedimentary structures.

Most likely, the sandy intercalation in the shale of the Kosmocerasdal Member was some kind of offshore subtidal sand bar complex the crest of which was above wave base (colonized by the *G. keyserlingii*/*D. nodulosa* association), whilst the remainder characterizes a low energy environment colonized by the *E. corneolum*/*P. uniformis* association. This sand unit is probably comparable to the sand bar com-

plex of the Aldinger Elv Member (see below) except for the much larger dimensions of the latter.

Aldinger Elv Member

The well-sorted sand and sandstone of the Aldinger Elv Member (Upper Oxfordian) contains a rich fauna of benthic invertebrates, chiefly bivalves. Most of them occur as allochthonous assemblages (e.g. figs 11, 12) and only few have been preserved *in situ*. They have been briefly described by Fürsich & Heinberg (1983) and interpreted as characterizing an offshore shallow subtidal sand bar complex. Apart from the three associations described below there occur possibly several other associations for which no statistical data are available. For example, *in situ* preserved clusters of *Modiolus strajeskianus* and *Aguilerella aldingeri* suggest the existence of a *Modiolus* and *Aguilerella* community respectively. They occur in low energy parts of the sand bar complex. Assemblages dominated by the crinoid *Pentacrinites* may represent yet another association, as the *Pentacrinites* are still largely articulated.

Lopatinia callomoni association

Table 4, figs 6, 9

The *L. callomoni* association is represented by 567 specimens in three samples. Members of the trophic nucleus are three bivalves, the shallow burrowing *L. callomoni* and *Arctica syssoillae* and the deep burrowing *Pleuromya zakharovi*. Over 97% of the fauna are bivalves, the rest gastropods, annelids and echinoderms. All

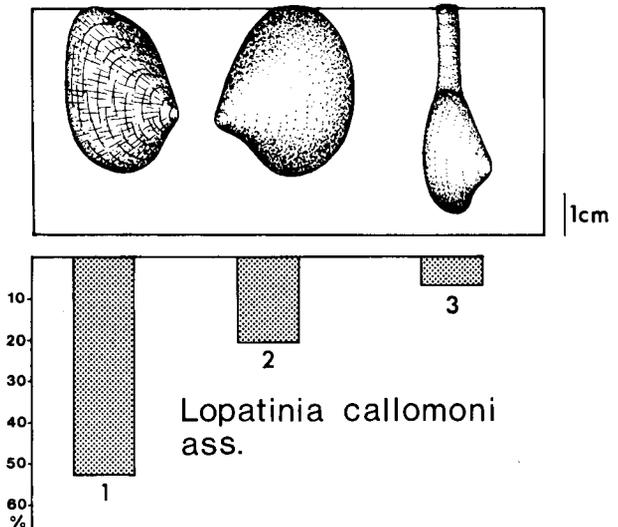


Fig. 9. Trophic nucleus of the *Lopatinia callomoni* association from the Aldinger Elv Member. 1: *Lopatinia callomoni*; 2: *Arctica syssoillae*; 3: *Pleuromya zakharovi*.

Table 4. *Lopatinia callomoni* association

	Relative abundance (%)	Presence (%)
Bivalves (97.9%)		
* <i>Lopatinia callomoni</i>	53.1	100
* <i>Arctica syssollae</i>	20.6	100
* <i>Pleuromya zakharovi</i>	7.0	67
<i>Praebuchia kirghisensis</i>	6.3	100
<i>Camptonectes broenlundii</i>	2.3	100
<i>Tancredia magna</i>	2.3	67
<i>Aguilerella aldingeri</i>	1.2	67
<i>Corbicellopsis lorioli</i>	1.2	33
<i>Protocardia striatula</i>	0.9	33
<i>Corbicellopsis laevis</i>	0.7	67
<i>Meleagrinnella ovalis</i>	0.5	67
<i>Modiolus strajeskianus</i>	0.5	67
<i>Nanogyra nana</i>	0.5	33
<i>Camptonectes auritus</i>	0.3	33
? <i>Liostrea</i> sp. 2	0.2	33
<i>Goniomya literata</i>	0.2	33
<i>Grammatodon keyserlingii</i>	0.2	33
Gastropods (0.9%)		
<i>Ampullina</i> sp.	0.5	33
neritimid sp. A	0.3	67
Annelids (1.1%)		
<i>Ditrupa nodulosa</i>	0.7	33
<i>Serpula (Cycloserpula)</i> sp.	0.4	67
Echinoderms (0.2%)		
<i>Pentacrinites</i> sp.	0.2	33
Trace fossils		
<i>Talpina ramosa</i>		33

3 collections, 567 specimens.

Members of the trophic nucleus are marked with an asterisk.

bivalves are suspension-feeders. Infauna accounts for 85% of the benthos, epifauna (*Nanogyra*, *Praebuchia*, *Camptonectes*) for 11%, semi-infauna (*Modiolus*, *Grammatodon keyserlingii*) for the rest. Borers (*Talpina ramosa*) and encrusters (*Cycloserpula*) are rare. Nektic ammonites constitute 4.2% of the total fauna. Species richness varies between 11 and 13 (mean: 12), evenness from 2.29 to 5.97 (mean: 3.7). 23.9% of the bivalves are still articulated, but none occur in life position. Fragmentation varies between 50 and 90%. In two of the three samples wood fragments are common.

The *L. callomoni* association occurs in loosely to densely packed shell beds in which shells are randomly oriented. Whilst gentle reworking (winnowing) must be postulated to explain the concentration of shells, lateral transport can be excluded.

Camptonectes broenlundii association

Table 5, figs 6, 10

Three samples with 1056 specimens were grouped into the *Camptonectes broenlundii* association. It is dominated by the large free living *C. broenlundii* which accounts for nearly three-quarters of the fauna. The shallow burrowing *Arctica syssoillae* is the second species in the trophic nucleus. Again, bivalves account for nearly 99% of the fauna with epifaunal forms clearly dominating (*Camptonectes*, *Praebuchia*). Apart from rare grazing or detritus-feeding gastropods (neritimid sp. A, *Amberleya*), all species are suspension-feeders. Species richness varies from 14 to 19 (mean: 16.3), evenness from 1.58 to 2.87 (mean: 2.11). The *C. broenlundii* association occurs as *in situ* reworked shell beds. 21% of the shells are still articulated, shell orientation is random, and there are no signs of abrasion.

Camptonectes occurs in a wide size range. Many articulated specimens are filled with sparite. One-fourth of the shells, chiefly *Camptonectes*, are bored by acrothor-

Table 5. *Camptonectes broenlundii* association

	Relative abundance (%)	Presence (%)
Bivalves (98.7%)		
* <i>Camptonectes broenlundii</i>	72.3	100
* <i>Arctica syssoillae</i>	8.0	100
<i>Praebuchia kirghisensis</i>	5.9	100
<i>Modiolus strajeskianus</i>	4.4	100
<i>Corbicellopsis laevis</i>	1.7	100
<i>Protocardia striatula</i>	1.2	100
<i>Grammatodon keyserlingii</i>	1.0	67
<i>Unicardium aceste</i>	0.7	67
<i>Pleuromya zakharovi</i>	0.6	33
<i>Discomiltha lirata</i>	0.5	33
<i>Lopatinia callomoni</i>	0.4	100
? <i>Liostrea</i> sp. 2	0.4	33
<i>Corbicellopsis lorioli</i>	0.4	33
<i>Tancredia donaciformis</i>	0.3	33
<i>Tancredia</i> sp.	0.2	33
<i>Tancredia magna</i>	0.2	33
<i>Camptonectes</i> cf. <i>C. auritus</i>	0.2	33
<i>Plagiostoma</i> sp.	0.1	33
<i>Oxytoma</i> sp.	0.1	33
Gastropods (0.3%)		
<i>Amberleya</i> sp.	0.2	33
neritimid sp. A.	0.1	33
Annelids (1.0%)		
<i>Serpula (Cycloserpula)</i> sp.	1.0	100
Trace fossils		
<i>Talpina ramosa</i>		100
acrothoracian borings		100

3 collections, 1056 specimens.

Members of the trophic nucleus are marked with an asterisk.

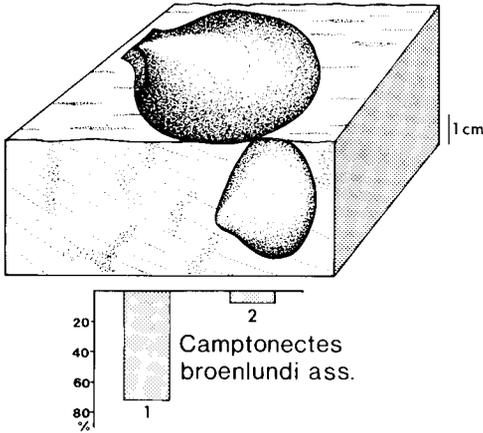


Fig. 10. Trophic nucleus of the *Camptonectes broenlundii* association from the Aldinger Elv Member. 1: *Camptonectes broenlundii*; 2: *Arctica syssollae*.

acican cirripeds and *Talpina ramosa*; 4.5% are encrusted by serpulids. An analysis of the boring pattern revealed that boring on most *Camptonectes broenlundii* shells took place *prae-mortem*, as the bivalves reacted in depositing additional shell layers at the boring sites (Fürsich, 1982b, fig. 20).

Ditrupa nodulosa association

Table 6, figs 6, 11

Very widespread as transported assemblage (e.g. fig. 11), the *D. nodulosa* association is only rarely preserved *in situ*. Consequently, only one autochthonous sample was available for analysis. The ?detritus-feeding polychaete *D. nodulosa* strongly dominates the fauna which, in addition, contains 8 bivalve species. Apart

Table 6. *Ditrupa nodulosa* association

	Relative abundance (%)
Bivalves (12.2%)	
<i>Aguilerella aldingeri</i>	4.1
<i>Lopatinia callomoni</i>	3.7
<i>Camptonectes broenlundii</i>	1.2
bivalves indet.	1.2
<i>Camptonectes</i> sp.	0.8
<i>Pleuromya zakharovi</i>	0.4
? <i>Liostrea</i> sp. 2	0.4
<i>Arctica syssollae</i>	0.4
Annelids (87.8%)	
* <i>Ditrupa nodulosa</i>	87.8

1 collection, 246 specimens.

Members of the trophic nucleus are marked with an asterisk.

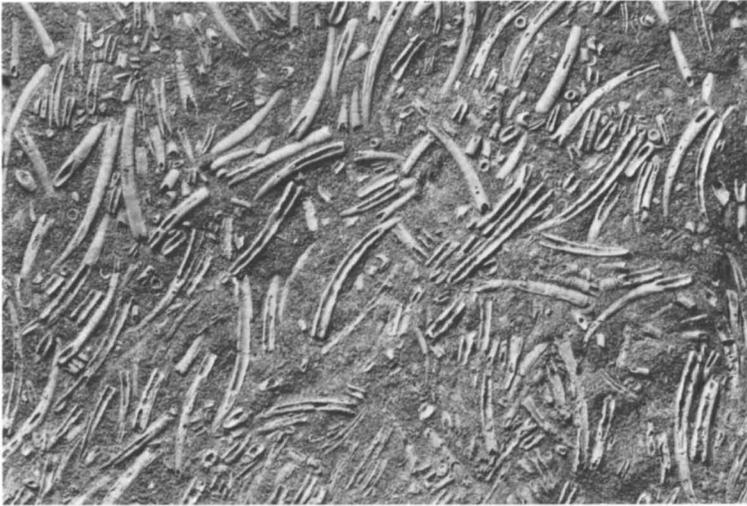


Fig. 11. Monospecific *Ditrupa nodulosa* shell layer indicative of sorting. Note preferred orientation of the tubes. Aldinger Elv Member, locality 3. Scale: $\times 0.8$.

from *Ditrupa*, all species are suspension-feeders and most (94%) belong to the epifauna. The faunal elements other than *Ditrupa* (e.g. *Aguilerella*, *Lopatinia*) occur also in other benthic associations and are non-diagnostic. Diversity is low: species richness is 9, evenness 1.29.

The *D. nodulosa* association occurs scattered on bedding planes; only 2% of the bivalves are articulated. *Ditrupa* tubes do not exhibit any preferred orientation.

Assemblages

Most shells occur in shell pavements or shell beds which exhibit clear signs of reworking, sorting and selective destruction of delicate faunal elements. As a rule, the associations can be observed in various stages of reworking and transport (see also Fürsich & Heinberg, 1983). Diversity decreases in the direction of transport as does the degree of shell articulation. In contrast, side-view and plan-view orientation increases. The final stages are near-monospecific shell pavements (figs 11,12). Shell beds of the *Camptonectes broenlundii* association frequently underwent a different genesis. They record only short-term reworking events and do not indicate extensive lateral transport. Most likely, they were formed by storms (for details see Fürsich & Heinberg, 1983).

Discussion

The three benthic associations are characterized by mobile epifaunal forms (*Ditrupa*, *C. broenlundii*) and rapid shallow burrowers (*Arctica*, *Lopatinia*). This is in

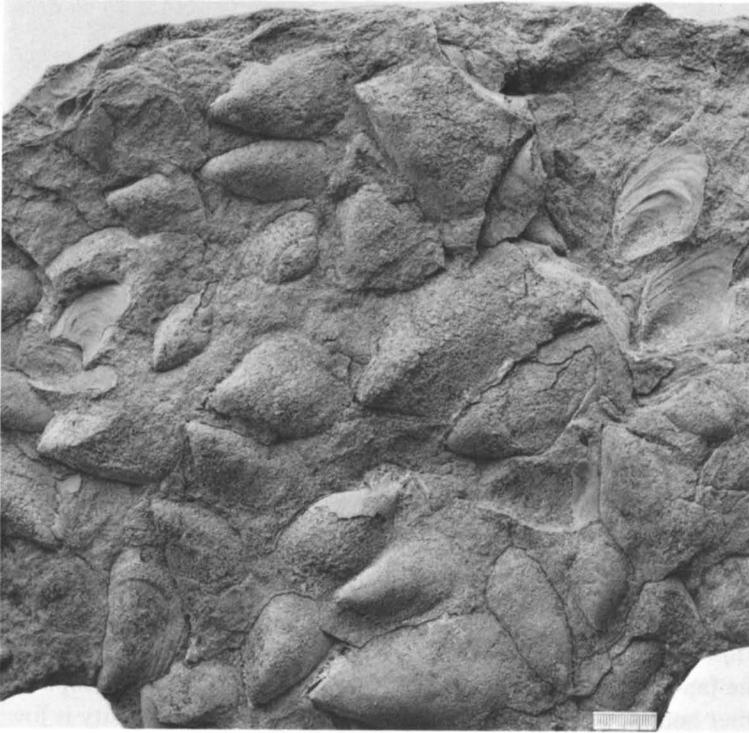


Fig. 12. Monospecific shell pavement of *Aguilerella aldingeri*, a transported and sorted relic of a former community. Aldinger Elv Member, valley east of Bays Fjelde. Scale in cm.

agreement with their proposed environment, a sandbar complex where adaptations to cope with rapid sedimentation or erosion are essential for successful colonization. The mobile substrate representing a high stress environment is thought to be responsible for the low diversity.

Cardioceraskløft Member

Benthic faunas are rare in the Cardioceraskløft Member (Lower Kimmeridgian) and confined largely to concretion horizons containing different ammonite faunas (*Rasenia* concretion levels I to IV of Callomon & Birkelund, 1980). The most fossiliferous exposures are in the upper course of the Cardioceraskløft (locality 7) and southeast of Bays Fjelde (locality 30). Three autochthonous associations and one transported and mixed assemblage have been encountered which form a link to the fossiliferous parts of the still higher Krebsedal and Pernaryggen Members.

Amberleya cf. *A. jasikofiana* association

Table 7, fig. 13

Known from 2 samples with 120 specimens, the *A. cf. A. jasikofiana* association is found in large rubbly, yellow weathering concretions which laterally pass into shale. They correspond to the *Rasenia* concretion level II of Callomon & Birkelund (1980). There are six species in the trophic nucleus: the gastropod *Amberleya* cf. *A. jasikofiana*, the epibyssate *Limatula consobrina*, the deep burrowing *Pleuromya uralensis* and *Pholadomya* sp., the endobyssate *Modiolus strajeskianus*, and the epibyssate *Camptonectes morini*. Epifauna represents 60%, semi-infauna (*Modiolus*) 10%, and infauna 30% of the fauna. Assuming that *A. cf. A. jasikofiana* (22.5%) is a herbivore, suspension-feeders constitute 76.7% of the benthic fauna, and deposit-feeders represented by the nuculanid *Mesosaccella* 0.8%.

Trace fossils are represented by *Thalassinoides suevicus*, *Macaronichnus segregatis*, *?Curvolithus* and *?Skolithos*. Ammonites and belemnites are very common (42% of the total fauna); in addition, some cephalopod hooks occur.

Nearly half the fauna is still articulated and 10% are found in life position (the deep burrowing *Pleuromya* and *Pholadomya*). Only 20% of the shells are fragmented and shell density is low. Faunal diversity is high with an evenness value of 6.7 and a species richness of 18. Preservational bias of the fauna can be excluded as aragonitic organisms are partly preserved with shell. The *A. cf. A. jasikofiana* asso-

AMBERLEYA CF. A. JASIKOFIANA ASS.

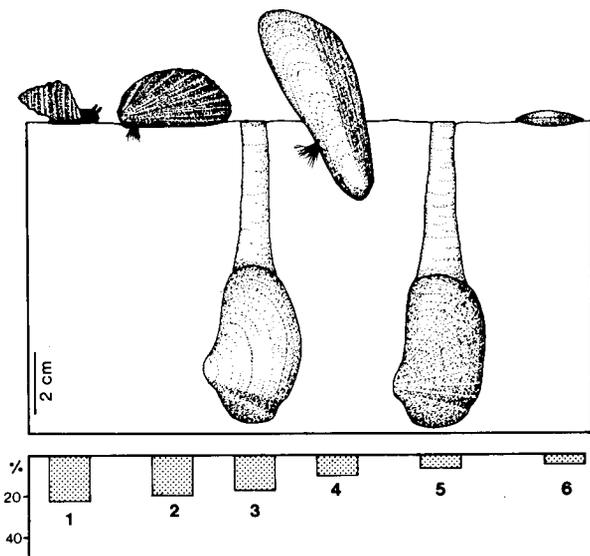


Fig. 13. Members of the trophic nucleus of the *Amberleya* cf. *A. jasikofiana* association from the Cardioceraskløft Member. 1: *Amberleya* cf. *A. jasikofiana*; 2: *Limatula consobrina*; 3: *Pleuromya uralensis*; 4: *Modiolus strajeskianus*; 5: *Pholadomya* sp.; 6: *Camptonectes morini*.

Table 7. *Amberleya* cf. *A. jasikofiana* association

	Relative abundance (%)	Presence (%)
Bivalves (75.8%)		
* <i>Limatula consobrina</i>	18.5	100
* <i>Pleuromya uralensis</i>	16.2	100
* <i>Modiolus strajeskianus</i>	9.3	100
* <i>Pholadomya</i> sp.	6.9	100
* <i>Camptonectes morini</i>	5.4	100
<i>Liostraea</i> sp.	5.4	100
<i>Entolium orbiculare</i>	5.4	100
<i>Buchia</i> sp.	3.1	100
<i>Thracia depressa</i>	1.6	100
<i>Goniomya literata</i>	1.6	50
<i>Protocardia</i> sp.	0.7	50
<i>Inoceramus</i> sp.	0.7	50
<i>Grammatodon schourovskii</i>	0.7	50
<i>Camptonectes</i> cf. <i>C. validus</i>	0.7	50
<i>Oxytoma inequivalve</i>	0.7	50
<i>Mesosacella</i> sp.	0.7	50
Gastropods (22.5%)		
* <i>Amberleya</i> cf. <i>A. jasikofiana</i>	20.8	100
Brachiopods (1.7%)		
' <i>Terebratula</i> ' sp.	1.6	50
Trace fossils		
<i>Thalassinoides suevicus</i>		100
<i>Macaronichnus segregatis</i>		100
? <i>Curvolithus</i> sp.		100
? <i>Skolithos</i> sp.		50

2 samples, 207 specimens.

Members of the trophic nucleus are marked with an asterisk.

ciation can thus be regarded as the autochthonous relic of a former community. It occurs in highly micaceous, very fine-grained concretionary sandstone with occasional wood fragments.

Pleuromya uniformis/*Camptonectes* cf. *C. validus* association

Table 8, fig. 14

Although represented only by one quantitative sample, the fauna occurs at several levels within large, up to 100 cm thick concretions of the *Rasenia* concretion level I and thus can be regarded as representing a true association. The sample has been taken from the top level of the concretions which exhibited a moderately high faunal density. In the remaining parts of the concretions, faunal density was considerably lower.

P. uniformis (68.4%) and the free living large thin-shelled *Camptonectes* cf. *C. validus* (15.8%) dominate the fauna which is of moderately low diversity (richness: 8; evenness: 2.0). Nearly three-quarters of the fauna lived in the sediment (*P. uniformis*, *P. uralensis*), the rest on the substrate (*Entolium*, *Buchia*, *Limatula*, *Camp-*

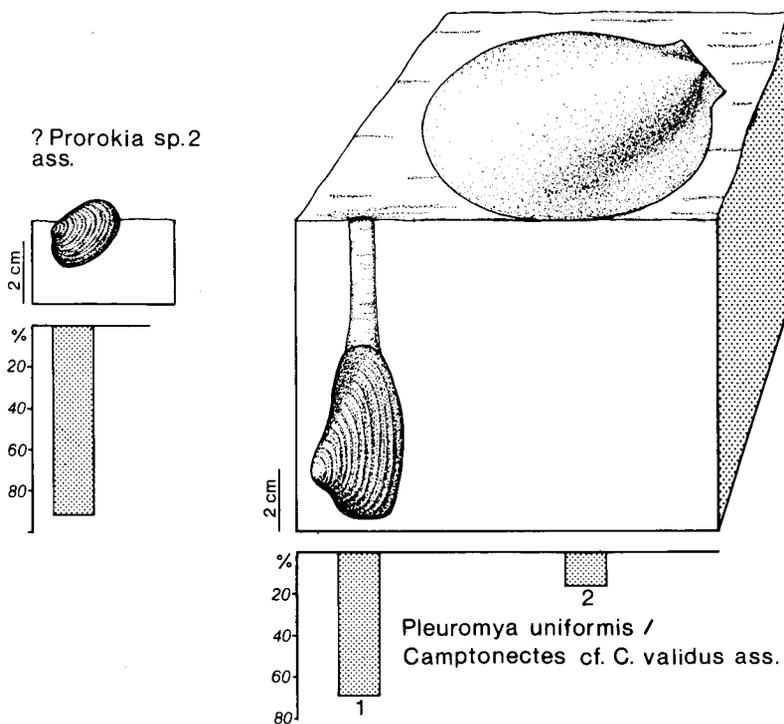


Fig. 14. Trophic nucleus of two associations from the Cardioceraskløft Member. 1: *Pleuromya uniformis*; 2: *Camptonectes* cf. *C. validus*.

tonectes). Only few life habit groups are represented and apart from the ?herbivorous gastropod *Pseudomelania*, all species were suspension-feeders. The trace fossil *Curvolithus*, made by a scavenging or predating gastropod, is abundant, and *Chondrites* is common. Ammonites and belemnites constitute over one-fourth of the total fauna. 86.7% of the bivalved fauna are still articulated, and 56.3% are preserved in life position (most burrowers). Fragmentation is very low (10%) except in some shell nests which most likely were made by organisms. As reworking of the fauna can be excluded, the *P. uniformis*/*C. cf. validus* association is consequently the autochthonous relic of a former community. It occurs in highly micaceous, moderately glauconitic fine-grained sandstones which contain occasional pieces of drift wood.

Amberleya/Camptonectes assemblage

A faunal assemblage containing elements of both associations occurs in the upper part of the concretions representing the *Rasenia* level II. Only three species are

Table 8. *Pleuromya uniformis*/*Camptonectes* cf. *C. validus* association

	Relative abundance (%)
Bivalves (95.3%)	
* <i>Pleuromya uniformis</i>	68.4
* <i>Camptonectes</i> cf. <i>C. validus</i>	15.8
<i>Pleuromya uralensis</i>	5.3
<i>Entolium orbiculare</i>	2.6
<i>Buchia</i> cf. <i>B. lindstroemi</i>	2.1
<i>Limatula consobrina</i>	1.0
Gastropods (0.5%)	
<i>Pseudomelania</i> sp.	0.5
Annelids (4.2%)	
<i>Serpula</i> (<i>Cycloserpula</i>) sp.	4.2
Trace fossils	
<i>Curvolithus</i> sp.	
<i>Chondrites</i> sp.	

1 sample, 253 specimens.

Members of the trophic nucleus are marked with an asterisk.

present: a rare serpulid (*Dorsoserpula* sp.), *C. cf. validus* and *A. cf. A. jasikofiana*. *Camptonectes* shells form a pavement of disarticulated valves with most valves in a current stable convex-up position. *Amberleya*, in contrast, is found together with shell hash in a large *Thalassinoides* burrow which obviously acted as trap.

Biostratigraphic data and comparison with the two autochthonous associations show that the fauna has undergone transport and sorting, a rare feature in the otherwise fairly low energy environment of the Cardioceraskløft Member.

?*Prorokia* sp. 2 association

Table 9, figs 14,15

In the Cardioceraskløft Member southeast of Bays Fjelde (locality 30), corresponding to the *Rasenia* concretion level IV of Callomon & Birkelund (1980), a very low diversity association occurs scattered in micaceous silt, concretionary very fine-grained sandstone, and densely packed in lenticular shell beds up to 15 cm thick. The only quantitative sample (521 specimens) comes from such a lenticular redbrown weathering shelly sandstone bed. The heterodont bivalve ?*Prorokia* sp. 2 constitutes over 90% of the fauna, a rhynchonellid and terebratulid species form the rest. Ammonites are common (8.9% of the total fauna). Species richness is 3 and the evenness value is 1.15, both indicating very low diversities.

The fauna consists solely of suspension-feeders. ?*Prorokia* most likely was a shallow burrowing species, being relatively elongate for an astartid, but it cannot be excluded that it just lay on the sediment surface. 84% of the fauna are articulated, and only 10 to 20% of the shells are fragmented. Most specimens have been

Table 9. ?*Prorokia* sp. 2 association

	Relative abundance (%)
Bivalves (92.9%)	
*? <i>Prorokia</i> sp. 2	92.9
Brachiopods (6.9%)	
' <i>Rhynchonella</i> ' sp.	6.5
' <i>Terebratula</i> ' sp.	0.4
Ecological composition	
epifauna: 6.9%	
infauna: 92.9%	
suspension-feeders: 100%	
nekton percentage of total fauna: 8.9%	
Biostratigraphic data	
uncemented fauna in life position: ?10%	
bivalved fauna still articulated: 84.6%	
fragmentation: 10–20%	
Diversity	
evenness: 1.15	
richness: 3	

1 sample, 572 specimens.

Members of the trophic nucleus are marked with an asterisk.

compressed and distorted during compaction, which made a precise identification impossible. Some specimens have been embedded obliquely, which might indicate a vertical orientation of the commissure line during life, altered subsequently during compaction. ?*Prorokia* occurs in all size classes; '*Rhynchonella*' in small clusters of 4 to 6 individuals. These data strongly suggest that the shell bed does not represent a transported and sorted assemblage, but accumulated *in situ* with only minor reworking. The lenticular nature of the shell bed possibly indicates an original patchy distribution of the fauna. The autochthonous nature of the fauna is corroborated by the fact that the same fauna, albeit in lower densities, occurs both above and below the shell bed. In nearby giant sandstone doggers, *Pleuromya* in growth position is an additional rare faunal element.

Discussion

The *A. cf. A. jasikofiana* association characterizes a subtidal shelf environment below fair weather wave base. This is indicated by the nature of the sediment, extensive bioturbation, the low percentage of fragmented shells, the high proportion of articulated shells and by specimens preserved in life position. These features also suggest a fairly stable substrate. The abundance of the herbivorous gastropod *Amblerleya* probably points to a vegetated sea floor which would place the depositional environment within the photic zone. The very common nektonic ammonites and bellerophonts indicate fully marine conditions.

A very similar environment can be envisaged for the *P. uniformis*/C. cf. *C. validus* association. It differs mainly in that the substrate is slightly coarser and the

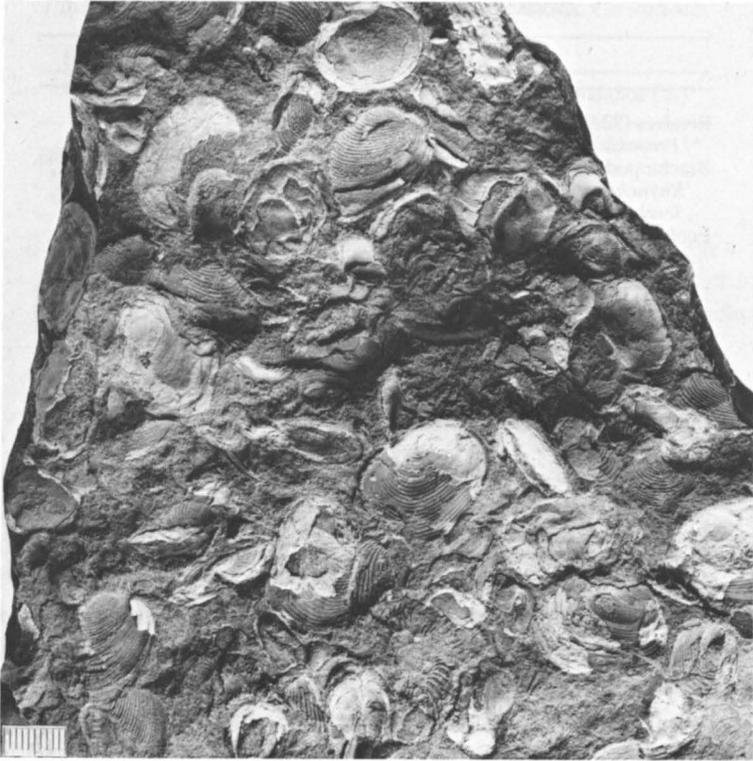


Fig. 15. Bedding plane view of slab with abundant *?Prorokia* sp. 2. *Rasenia* concretion level IV, Cardio-ceraskløft Member southeast of Bays Fjelde. Scale in cm.

sedimentation rate fairly low (presence of glauconite grains). Vegetation cover was probably of lesser significance. In contrast to the former association most faunal elements lived deeply buried in the sediment.

The *Amberleya/Camptonectes* assemblage clearly represents a mixture of the two associations. The shell pavement and other biostratigraphic features (high degree of disarticulation, evidence of sorting) indicate that currents (possibly in connection with storms) were responsible for the faunal mixing.

The *?Prorokia* sp. 2 association, in contrast, is again the autochthonous relic of a community which lived below fair weather wave base. The very low faunal diversity appears to be a genuine feature and to have been caused by adverse environmental factors. As salinity variations can be excluded (presence of brachiopods and abundant ammonites), it was more likely a low oxygen level or the substrate consistency which excluded most of the 'normal' benthic fauna from successful colonization. *?Prorokia* would then have to be regarded as an opportunistic species being able to flourish under conditions of high environmental stress.

In conclusion, sediments, high degree of bioturbation, and benthic faunas of the Cardioceraskløft Member record open marine subtidal environments below fair weather wave base, which were only occasionally disturbed by events causing faunal mixing and extensive sediment reworking.

Gråkløft Member

The Gråkløft Member (Kimmeridgian) consists of up to 160 m black bituminous shale which, for the most part, does not contain any benthic faunas. The most likely explanation is that anoxic conditions at the sea bottom were widespread. There are, however, several horizons in which benthic faunas, although of extremely low diversity, are abundant. Several samples were obtained from the upper course of the Cardioceraskløft (close to locality 7) where, in the *eudoxus* Zone, finely laminated concretions exhibit near-monospecific benthic faunas. All shells were completely flattened during compaction making a precise identification impossible. The following associations and assemblages could be distinguished (see also table 10 and figs 16–18).

?Prorokia sp.. 1 association

On several bedding planes high numbers of articulated *?Prorokia* sp. 1 occur, an astartid bivalve which most likely lived partly buried in the sediment. The only other species is an epibyssate *Buchia* sp. *?Prorokia* represents over 99% of the benthic fauna. Nectic belemnites (rare) and the occasional ammonite *Hoplocardioceras* constitute 1.8% of the total fauna. *?Prorokia* and *Buchia* are both suspension-feeders. Diversity is extremely low, species richness being 2, the evenness 1.01.

Table 10. Composition of benthic associations from the Gråkløft Member

	Relative abundance (%)
Example of the <i>?Prorokia</i> sp. 1 association (388 specimens)	
Bivalves (100%)	
<i>?Prorokia</i> sp. 1	99.2
<i>Buchia</i> sp.	0.8
Example of the <i>Buchia</i> sp. association (120 specimens)	
Bivalves (100%)	
<i>Buchia</i> sp.	93.3
<i>?Prorokia</i> sp. 1	6.7

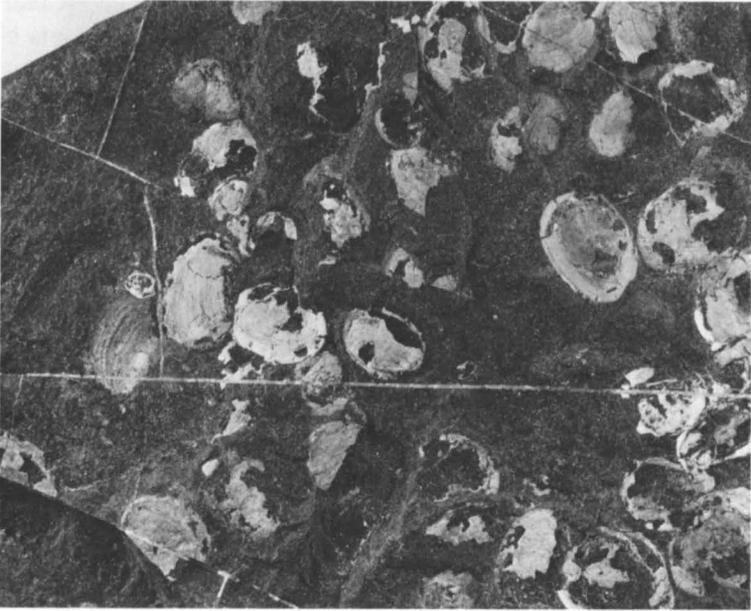


Fig. 16. Bedding plane view of slab with abundant ?*Prorokia* sp. 1. Gråkløft Member northeast of Hartz Fjeld (locality 7). Scale: $\times 1.1$.

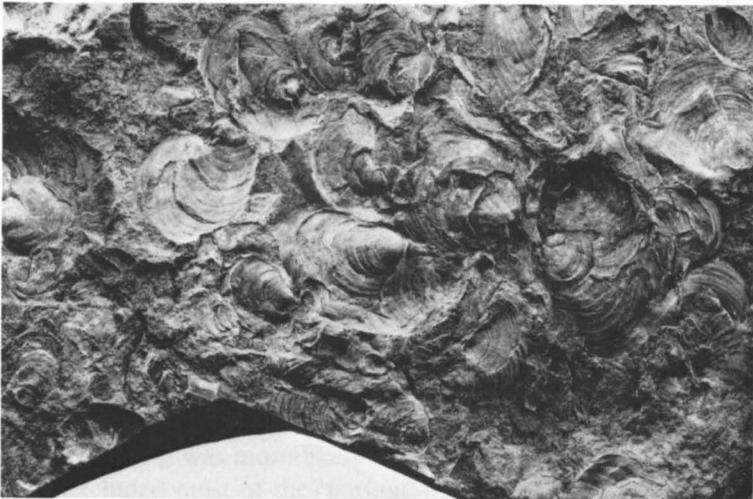


Fig. 17. Bedding plane view of *Buchia* sp. shell bed. Slab from the Gråkløft Member northeast of Hartz Fjeld (locality 7). Scale: $\times 1.1$.

Biostratigraphic data (e.g. complete lack of fragmentation) indicate that the fauna is preserved *in situ*.

Buchia sp. association

Thin shell layers up to several centimetres thick consist overwhelmingly of *Buchia* sp. (93.3%), the only other species being *?Prorokia* sp. 1. Again, all shells are still articulated, and the *Buchia* sp. occur in a wide size range. Species richness is 2, evenness 1.14. Biostratigraphic data exclude any disturbance of the fauna.

?Inoceramus sp. 1 assemblage

Only available as a slab collected by T. Birkelund and J. H. Callomon close to the so-called *Hoplocardioceras* bed, this assemblage consists solely of one-valved individuals of a small (1–1.5 cm high) species of *?Inoceramus* which form a 5 to 10 mm thick shell bed. The individuals are preferentially in a convex-up position indicative of lateral transport by currents. Nevertheless, it is well possible that the assemblage represents a hardly altered relic of a former benthic settlement.

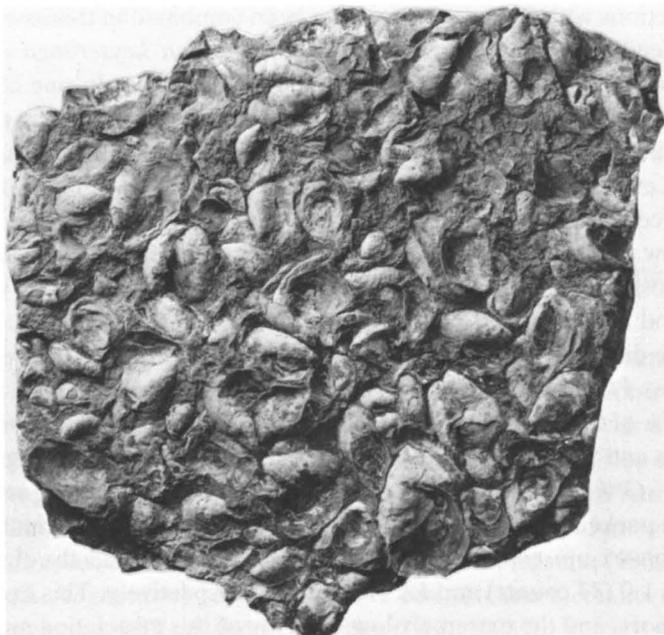


Fig. 18. *?Inoceramus* shell bed from the Gråkløft Member, northeast of Hartz Fjeld (locality 7). Scale: $\times 0.8$.

Discussion

All benthic faunas of the Gråkløft Member have in common an extremely low diversity. They occur in close association with laminated bituminous shale signifying anoxic conditions. The levels with benthic faunas most likely represent periods when the oxic/anoxic boundary was lowered below the sediment/water interface allowing colonization of the sea floor by a well adapted species (compare also Kauffman's (1981) interpretation of the southern German Posidonienschiefer). That the oxygen level varied considerably during time of deposition of the Gråkløft Member is shown by the presence of small-scale ripple lamination indicative of currents, and levels which have been heavily bioturbated so that no original bedding features are preserved. Both ripples and bioturbated layers occur in close contact with the benthic shelly faunas thus illustrating the variable environmental conditions. Depth of deposition was well below wave base.

Krebsedal, Pernaryggen and Astartedal Members

Grammatodon keyserlingii association

Table 11, figs 19–21

Five collections with 850 specimens have been combined in this association. The suspension-feeding endobysate bivalve *Grammatodon keyserlingii* is by far the dominant species, accounting for nearly 95% of the fauna. In one collection, *G. keyserlingii* is the only faunal element present, thus documenting a monospecific association. The diversity is generally very low: species richness varies from 1 to 11 (mean: 4.8), evenness from 1.0 to 1.31 (mean: 1.12). Nearly all faunal elements are suspension-feeders (99.9%), but a variety of life habit groups is present, though in extremely low numbers (fig. 21). Nectic elements (ammonites, belemnites) are absent. Trace fossils occur in 40% of the samples and are represented by vertical mantled tubes and *Macaronichnus*.

Diagenetic distortion of the fauna can be excluded as thin-shelled aragonitic bivalves such as *Pleuromya* are preserved as internal moulds.

Nearly 30% of the fauna are still articulated, but only 0.3% occurs in growth position (*Pinna* and *Pleuromya*). No shells are encrusted or bored; fragmentation is around 20%. *G. keyserlingii* occurs either scattered throughout the sediment or in thin, loosely packed shell beds (fig. 20). In both cases the shell orientation is random (e.g. convex up: convex down: vertical = 29:29:14) and the right valve/left valve ratio is 1.0 (77 counts) and 1.2 (130 counts) respectively. This excludes major lateral transport, and the extremely low diversity of this association must therefore be regarded as a genuine feature of the former community. As the percentage of articulated specimens differs in closely adjacent layers, they most likely represent

Table 11. *Grammatodon keyserlingii* association

	Relative abundance (%)	Presence (%)
Bivalves (98.9%)		
* <i>Grammatodon keyserlingii</i>	94.5	100
<i>Camptonectes morini</i>	0.6	20
<i>Grammatodon schourovskii</i>	0.5	40
<i>Pinna lanceolata</i>	0.5	20
<i>Pleuromya uniformis</i>	0.5	20
<i>Buchia mosquensis</i>	0.3	40
<i>Hartwellia</i> sp.	0.2	20
<i>Mesosaccella choroschowensis</i>	0.1	20
<i>Modiolus elongatus</i>	0.1	20
<i>Camptonectes praecinctus</i>	0.1	20
<i>Entolium orbiculare</i>	0.1	20
<i>Isognomon volaticum</i>	0.1	20
<i>Astarte</i> sp.	0.1	20
<i>Pholadomya hemicardia</i>	0.1	20
Gastropods (0.2%)		
neritidid sp. B	0.2	20
Brachiopods (1.8%)		
<i>Taimyrothyris</i> sp. nov.	1.8	40
Annelids (0.1)		
<i>Serpula intestinalis</i>	0.1	20
Trace fossils		
mantled vertical tubes		40
<i>Macaronichnus segregatis</i>		40

5 collections, 850 specimens.

Members of the trophic nucleus are marked with an asterisk.

different stages of gentle *in situ* reworking of the benthic fauna. The *G. keyserlingii* association occurs in fine to very fine-grained micaceous shales and sandstones, which contain only few glauconite grains.

Grammatodon keyserlingii/*Taimyrothyris* sp. nov. association

Table 12, figs 19, 21

The *G. keyserlingii*/*Taimyrothyris* sp. nov. association is represented by eight collections with 1083 specimens. There are three species in the trophic nucleus: the semi-infaunal bivalve *G. keyserlingii*, the brachiopod *Taimyrothyris* and the semi-infaunal bivalve *Isognomon volaticum*. Suspension-feeders (98.7%; e.g. all members of the trophic nucleus) again dominate. The infauna (e.g. *Pleuromya*, *Hartwellia*, *Mesosaccella*) constitutes only 6.3% of the association with epifauna (43.6%; e.g. *Entolium*, *Camptonectes*, *Buchia*) and semi-infauna (50%; e.g. *Pinna*, *G. keyserlingii*, *Isognomon*) representing the rest. Nekitic elements (ammonites, belemnites) make up 4.6% of the whole faunal assemblage. Trace fossils are relatively rare and are represented by *Skolithos*, *Macaronichnus* and *Thalassinoides suevicus*. The species richness varies from 7 to 18 (mean: 11.4) and the evenness

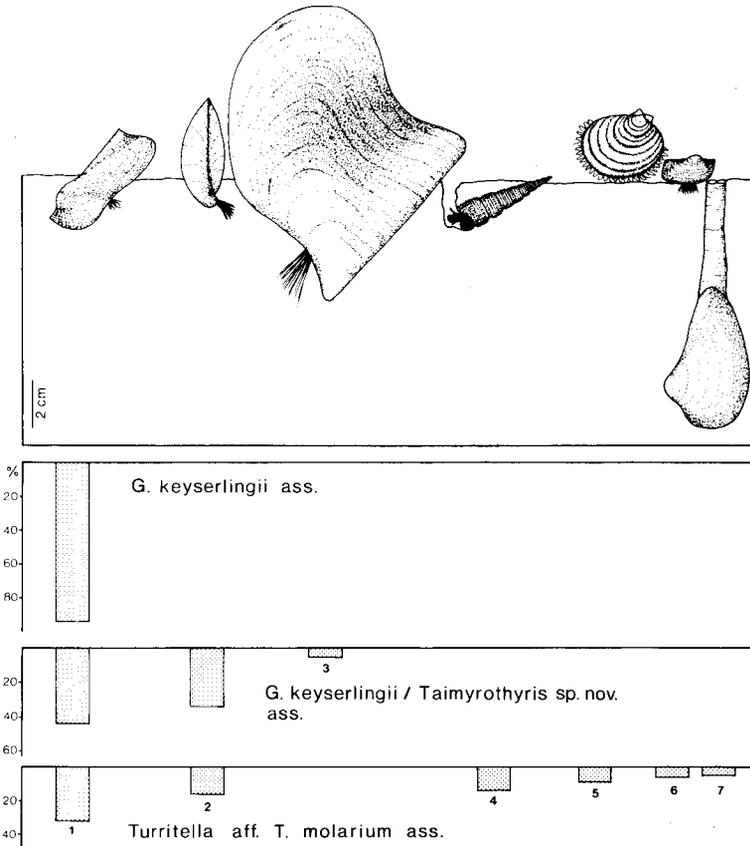


Fig. 19. Trophic nuclei of three *Grammatodon keyserlingii* dominated associations from the Pernaryggen Member. 1: *Grammatodon keyserlingii*; 2: *Taimyrothyris* sp. nov.; 3: *Isognomon volaticum*; 4: *Turritella* aff. *T. molarium*; 5: *Entolium orbiculare*; 6: *Grammatodon schourovskii*; 7: *Pleuromya triangularis*.

from 2.03 to 3.22 (mean: 2.65). Diversity is thus distinctly higher than in the preceding association.

No specimens show signs of boring and only 0.1% are encrusted by *Liostrea*. 56% of bivalved individuals were still articulated and 23% found in life position. Whilst *G. keyserlingii* has been encountered in growth position only rarely, but thus confirming its assumed semi-infaunal mode of life, the epifaunal brachiopod *Taimyrothyris* frequently occurs in clusters of up to 50 individuals which often are in life position. Other species found in growth position are *Pleuromya uralensis*, *P. uniformis* and *Pinna lanceolata*. Whilst *Taimyrothyris* clearly shows a clumped distribution, the remaining faunal elements are randomly dispersed throughout the sediment.

Table 12. *Grammatodon keyserlingii/Taimyrothyris* sp. nov. association

	Relative abundance (%)	Presence (%)
Bivalves (64.0%)		
* <i>Grammatodon keyserlingii</i>	44.2	100
* <i>Isognomon volaticum</i>	5.6	100
<i>Entolium orbiculare</i>	4.2	100
<i>Pleuromya uralensis</i>	1.6	37
<i>Grammatodon schourovskii</i>	1.2	62
<i>Pleuromya uniformis</i>	1.2	62
<i>Buchia mosquensis</i>	0.9	50
<i>Camptonectes praecinctus</i>	0.8	37
<i>Camptonectes morini</i>	0.7	50
<i>Pleuromya triangularis</i>	0.7	25
<i>Liostraea plastica</i>	0.5	37
<i>Hartwellia borealis</i>	0.5	37
<i>Mesosacella choroschowensis</i>	0.5	12
<i>Isocyprina birkelundi</i>	0.4	25
<i>Pinna lanceolata</i>	0.2	12
<i>Pseudolimea</i> cf. <i>P. arctica</i>	0.2	12
<i>Astarte praevenensis praevenensis</i>	0.2	12
<i>Plagiostoma incrassatum</i>	0.1	12
? <i>Liostraea</i> sp. 1	0.1	12
<i>Protocardia striatula</i>	0.1	12
<i>Unicardium aceste</i>	0.1	12
<i>Pholadomya hemicardia</i>	0.1	12
burrowing heterodont	0.1	12
Gastropods (0.8%)		
neritid sp. B	0.6	12
<i>Turritella</i> aff. <i>T. molarium</i>	0.1	12
<i>Neritopsis</i> sp.	0.1	12
<i>Brachytrema incerta</i>	0.1	12
Brachiopods (34.7%)		
* <i>Taimyrothyris</i> sp. nov.	34.4	100
' <i>Rhynchonella</i> ' sp. nov.	0.3	12
<i>Orbiculoidea latissima</i>	0.1	12
Annelids (0.4%)		
<i>Serpula intestinalis</i>	0.4	50
Trace fossils		
<i>Skolithos</i> sp.		
<i>Thalassinoides suevicus</i>		25
<i>Macaronichnus segregatis</i>		25
Nekton: ammonites and belemnites		

8 collections, 1083 specimens.

Members of the trophic nucleus are marked with an asterisk.

The *G. keyserlingii/Taimyrothyris* sp. nov. association thus clearly represents undisturbed relics of a former community. The association occurs in fine-grained micaceous silty shale and sandstone as well as in heavily glauconitic fine-grained and rarely medium-grained sandstone.



Fig. 20. Monospecific *Grammatodon keyserlingii* shell bed. Concretion from the Pernaryggen Member at Pernaryggen. Scale: $\times 0.4$.

Turritella aff. *T. molarium* association

Table 13, figs 19,21

The *T. molarium* association was encountered in three collections with 632 specimens. There are six species in the trophic nucleus (*G. keyserlingii*, *Taimyrothyris* sp., *T. aff. T. molarium*, *Entolium orbiculare*, *G. schourovskii* and *Pleuromya triangularis*). Although *Turritella* occupies only third rank, this rank of the gastropod, which is absent or very rare in other collections, is regarded as very significant. Epifauna (40.6%; e.g. *Taimyrothyris*, '*Rhynchonella*' sp. nov., *G. schourovskii*, *Entolium*, *Buchia mosquensis*), semi-infauna (33.8%; e.g. *G. keyserlingii*, *Isognomon*) and infauna (25.6%; e.g. *Turritella*, *Pl. triangularis*, *Astarte* aff. *A. veneris*, *Hartwellia borealis*) are nearly equally important. As in most associations from Milne Land, suspension-feeders represent over 99% of the fauna. Rare scavengers are represented by a decapod crustacean, and deposit-feeders by *Mesosaccella* and the trace fossil *Macaronichnus*. The other trace fossil (*Skolithos*) most likely represents a suspension-feeder.

The nekton constitutes 3.5% of the total fauna.

Diversity is relatively high. The species richness ranges from 16 to 18 and the evenness from 3.82 to 4.85 (mean: 4.32). Over 50% of the bivalved fauna are still articulated and 12.3% are preserved in life position (*Taimyrothyris*, '*Rhynchonella*'

Table 13. *Turritella* aff. *T. molarium* association

	Relative abundance (%)	Presence (%)
Bivalves (62.8%)		
* <i>Grammatodon keyserlingii</i>	32.1	100
* <i>Entolium orbiculare</i>	7.9	100
* <i>Grammatodon schourovskii</i>	6.7	100
* <i>Pleuromya triangularis</i>	5.6	100
<i>Hartwellia borealis</i>	1.9	100
<i>Buchia mosquensis</i>	1.6	100
<i>Isognomon volaticum</i>	1.6	100
<i>Astarte</i> aff. <i>A. veneris</i>	1.5	100
<i>Camptonectes praecinctus</i>	0.8	100
<i>Camptonectes morini</i>	0.8	100
<i>Astarte praeveneris praeveneris</i>	0.5	33
<i>Isocyprina birkelundi</i>	0.3	33
<i>Thracia depressa</i>	0.3	67
<i>Pleuromya uralensis</i>	0.3	33
<i>Oxytoma inequivalve</i>	0.2	33
<i>Protocardia striatula</i>	0.2	33
<i>Mesosacella choroschowensis</i>	0.2	33
<i>Modiolus</i> sp.	0.2	33
Gastropods (14.6%)		
* <i>Turritella</i> aff. <i>T. molarium</i>	14.6	100
Brachiopods (21.9%)		
* <i>Taimyrothyris</i> sp. nov.	16.5	100
* <i>Rhynchonella</i> sp. nov.	5.4	100
Annelids (0.3%)		
<i>Serpula intestinalis</i>	0.3	33
Arthropods (0.2%)		
crustacean	0.2	33
Echinoderms (0.2%)		
cidaroid (spines)	0.2	33
Trace fossils		
<i>Macaronichnus segregatis</i>		33
<i>Skolithos</i> sp.		33

3 collections, 632 specimens.

Members of the trophic nucleus are marked with an asterisk.

sp. nov. and the deep burrowing *Pleuromya triangularis*. The brachiopods commonly occur in nests and sometimes exhibit a large variation in size. No faunal elements are encrusted or bored.

Fragmentation varies from 0 to 50%. This and the remaining biostratigraphic evidence indicate only minimal disturbance of a former community.

The *T.* aff. *T. molarium* association occurs in micaceous, fine-grained glauconitic sand and sandstone. In contrast to most other associations (with the exception of the *Isocyprina birkelundi*/*Pinna lanceolata* and the *Astarte praeveneris maimchaensis* associations), the *T.* aff. *T. molarium* association occurs only at one level within any section.

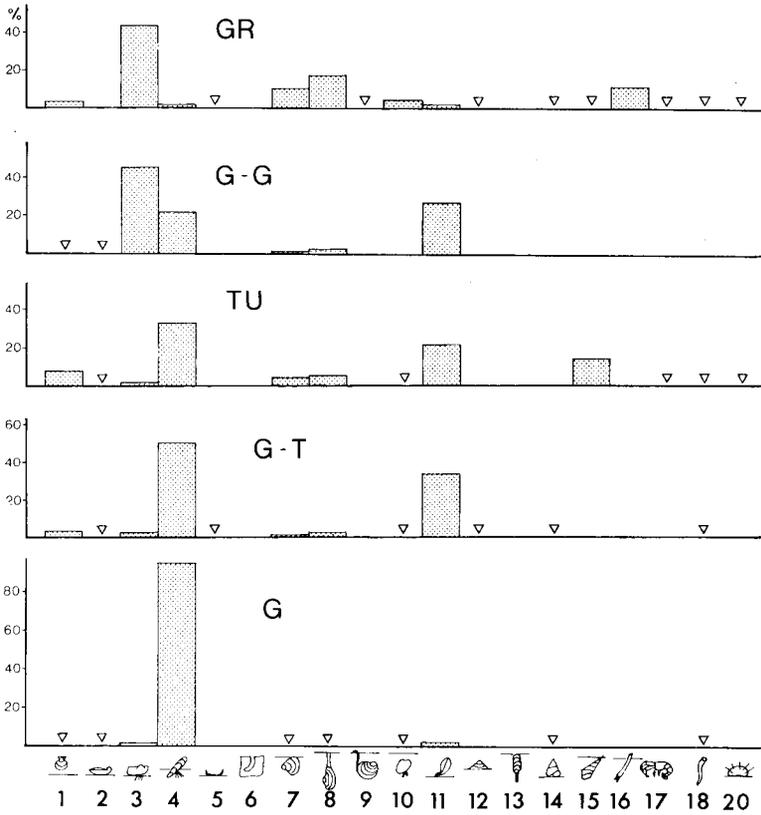


Fig. 21. Distribution of life habit groups in five associations from the Pernaryggen Member. For symbols 1–20 see fig. 24. GR: *Grammatodon schourovskii* ass.; G-G: *Grammatodon schourovskii*/*Grammatodon keyserlingii* ass.; TU: *Turritella* aff. *T. molarium* ass.; G-T: *Grammatodon keyserlingii*/*Taimyrothyris* sp. nov. ass.; G: *Grammatodon keyserlingii* ass.

Grammatodon schourovskii/*Grammatodon keyserlingii* association

Table 14, figs 21, 22

The *G. schourovskii*/*G. keyserlingii* association, represented by 451 specimens in two collections, differs from the preceding associations in *G. schourovskii* being the most abundant species (45.6%), followed by *Taimyrothyris* sp. nov. (27.5%) and *G. keyserlingii* (18.1%). In contrast to the endobysate *G. keyserlingii*, the much shorter *G. schourovskii* was most likely an epibysate species, resembling in shape other epifaunal *Grammatodon* species. The association is dominated by epifauna (74.5%) with infauna (3.8%; *Thracia depressa*, *Hartwellia kharoschovensis*) being insignificant. Only few life habit groups are represented (fig. 21) and apart from some ammonites and belemnites the fauna consists of bivalves, brachiopods

Table 14. *Grammatodon schourovskii*/*Grammatodon keyserlingii* association

	Relative abundance (%)	Presence (%)
Bivalves (72.5%)		
* <i>Grammatodon schourovskii</i>	45.6	100
* <i>Grammatodon keyserlingii</i>	18.1	100
<i>Isognomon volaticum</i>	2.9	100
<i>Thracia depressa</i>	1.3	100
<i>Pleuromya uralensis</i>	0.9	100
<i>Hartwellia kharoschovensis</i>	0.9	50
<i>Camptonectes morini</i>	0.7	100
<i>Pinna lanceolata</i>	0.7	50
<i>Isocyprina birkelundi</i>	0.4	50
<i>Pachymya sinuata</i>	0.2	50
<i>Camptonectes praecinctus</i>	0.2	50
<i>Entolium orbiculare</i>	0.2	50
<i>Plagiostoma incrassatum</i>	0.2	50
Brachiopods (27.5%)		
* <i>Taimyrothyris</i> sp. nov.	27.5	100
Trace fossils		
<i>Macaronichnus segregatis</i>		100

2 collections, 451 specimens.

Members of the trophic nucleus are marked with an asterisk.

and ?polychaetes only (the latter represented by the trace fossil *Macaronichnus segregatis*).

The diversity is moderate: species richness ranges from 9 to 12 (mean 10.5) and evenness from 2.57 to 3.29 (mean: 2.93). Most individuals are still articulated, and at least 12.5% occur in life position, in particular *G. keyserlingii*, *Isognomon volaticum*, *Pinna lanceolata* and *Taimyrothyris*. *Isognomon*, *Taimyrothyris* and both *Grammatodon* species occur in clusters in some horizons and scattered in others. In the latter, fragmentation may reach up to 75%, demonstrating disturbance such as *in situ* reworking of the fauna. Clusters of *Taimyrothyris* are usually not monospecific, but also contain *G. schourovskii* or *G. keyserlingii*. Such horizons indicate minimum disturbance, and the high density of individuals appears to be due to slow sedimentation rather than to reworking.

The association occurs in concretionary micaceous fine-grained sandstone.

Grammatodon schourovskii association

Table 15, figs 21, 22

The *G. schourovskii* association is very widespread in the Krebsedal, Pernarygen and Astartedal Members and was established in fifteen samples with 1867 specimens. It is characterized by the dominance of the presumably weakly byssate, epifaunal *G. schourovskii* and by the deep burrowing suspension-feeding bivalve *Thracia depressa*, the infaunal deposit-feeding bivalve *Mesosaccella choroschowen-*

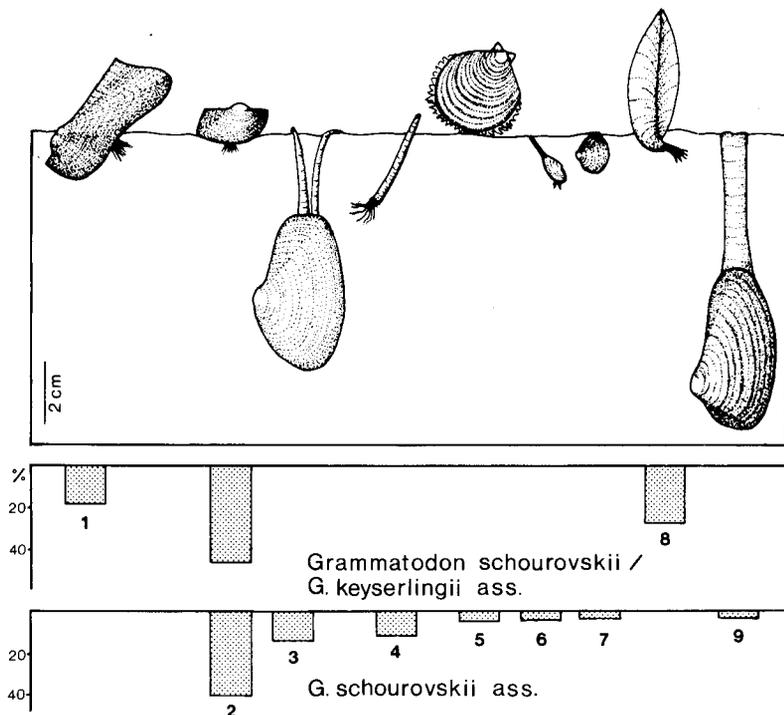


Fig. 22. Trophic nuclei of two *Grammatodon schourovskii*-dominated associations. 1: *Grammatodon keyserlingii*; 2: *Grammatodon schourovskii*; 3: *Thracia depressa*; 4: *Dentalium* sp.; 5: *Entolium orbiculare*; 6: *Mesosaccella choroschowensis*; 7: *Protocardia striatula*; 8: *Taimyrothyris* sp. nov.; 9: *Pleuromya uniformis*.

sis and the scaphopod *Dentalium*. The number of life habit groups is larger than in the preceding associations (fig. 21) with epi- and infauna of roughly the same importance, whilst semi-infauna which dominated previously described associations represents only 1.6%. This is the only association in which deposit-feeders (*M. choroschowensis*, *Nuculoma variabilis*) constitute a significant part of the fauna (17.3%), suspension-feeders (*Grammatodon*, shallow and deep burrowing bivalves such as *Protocardia*, *Thracia*, *Pleuromya*) representing the remainder; scavenging/detritus-feeding arthropods (*Glyphea*) and herbivorous gastropods are very rare (0.4%).

The diversity is high: species richness ranges from 9 to 18 (mean: 12.3) and evenness from 1.44 to 7.33 (mean: 3.71).

A variety of trace fossils occurs with the body fauna, but apart from *Macronichnus segregatis* and *Thalassinoides suevicus* most are found in some collections only (e.g. *Chondrites*, *Skolithos*, *Planolites*, vertical mantled tubes and *Diplocraterion*). In terms of trophic groups, they represent deposit- and suspension-feeders.

Table 15. *Grammatodon schourovskii* association

	Relative abundance (%)	Presence (%)
Bivalves (83,7%)		
* <i>Grammatodon schourovskii</i>	39.4	100
* <i>Thracia depressa</i>	14.7	93
* <i>Entolium orbiculare</i>	3.7	73
* <i>Mesosaccella choroschowensis</i>	3.5	87
* <i>Protocardia striatula</i>	2.8	67
* <i>Pleuromya uniformis</i>	2.7	40
<i>Buchia mosquensis</i>	2.6	73
<i>Isocyprina birkelundi</i>	2.1	60
<i>Hartwellia kharoschovensis</i>	1.9	53
<i>Hartwellia groenlandica</i>	1.8	20
<i>Nuculoma variabilis</i>	1.3	40
<i>Pleuromya triangularis</i>	0.9	13
<i>Hartwellia borealis</i>	0.9	7
<i>Isognomon volaticum</i>	0.9	20
<i>Camptonectes morini</i>	0.7	47
<i>Pinna lanceolata</i>	0.7	40
<i>Astarte</i> aff. <i>A. veneris</i>	0.7	13
<i>Eriphyla saemanni</i>	0.5	20
<i>Oxytoma inequivalve</i>	0.3	33
<i>Astarte</i> (A.) sp.	0.2	27
<i>Pleuromya uralensis</i>	0.1	7
<i>Corbulomima</i> sp.	0.1	13
<i>Plagiostoma incrassatum</i>	0.1	13
<i>Limatula consobrina consobrina</i>	0.1	13
<i>Placunopsis radiata</i>	0.1	7
<i>Solemya</i> sp.	0.1	7
shallow burrowing heterodont	0.1	7
' <i>Lucina</i> ' sp.	0.1	7
<i>Inoceramus</i> sp.	0.1	7
Small astartid	0.1	7
<i>Myophorella ingens</i>	0.1	7
<i>Corbicellopsis lorioli</i>	0.1	7
deep burrowing pholadomyacean	0.1	7
<i>Modiolus</i> (<i>Strimodiolus</i>) sp.	0.1	7
Gastropods (0.6%)		
<i>Turritella</i> aff. <i>T. molarium</i>	0.2	7
<i>Brachytrema keyserlingiana</i>	0.1	7
<i>Neritopsis</i> sp.	0.1	7
<i>Purpurina</i> sp.	0.1	7
<i>Pseudorhytidopilus</i> sp.	0.1	7
<i>Pseudomelania</i> sp.	0.1	7
gastropod indet.	0.1	7
Scaphopods (12.5%)		
* <i>Dentalium</i> sp.	12.5	73
Brachiopods (2.9%)		
* <i>Taimyrothyris</i> sp. nov.	2.8	20
<i>Orbiculoidea latissima</i>	0.1	7
Annelids (0.2%)		
<i>Serpula intestinalis</i>	0.2	13
Arthropods (0.1%)		
<i>Glyphea</i> sp.	0.1	7
Echinoderms (0.1%)		
<i>Pentacrinites</i> sp.	0.1	7
Trace fossils:		
<i>Thalassinoides suevicus</i>		60

15 collections, 1867 specimens.

Members of the trophic nucleus are marked with an asterisk.

Ammonites and belemnites are commonly associated with the benthic fauna and constitute 7.3% of the total fauna. Small pieces of drift wood and plant debris are widespread in collections from the Astartedal Member and Krebsedal Member.

36.4% of bivalved forms are still articulated, but only 4.4% occur in life position, in particular the deep burrowing bivalves *Pleuromya* and *Thracia*. Rarely *Taimyrothyris* and *Buchia mosquensis* form small clusters, the latter preferentially on ammonites. No shells are bored and only 0.05% encrusted by a serpulid. Calcitic shells are preserved, whilst aragonitic forms occur as internal moulds.

Fragmentation is very variable ranging from 0 to over 90%. Commonly shell debris is concentrated in small pockets, whilst in the surrounding sediment shells are largely complete. Some of these pockets consist predominantly of fragmented *Dentalium*. This strongly suggests that breakage was largely due to the activity of pre-dating or scavenging organisms and less to currents or wave movements.

The *G. schourovskii* association occurs in micaceous silty to fine-grained sand and concretionary sandstone. Glauconite grains are very rare or absent. Within the Astartedal Member, the layers containing the association are bioturbated, but adjacent beds exhibit a variety of sedimentary structures such as wavy lamination, small-scale cross-lamination or large-scale trough cross-bedding.

Taimyrothyris sp. nov. association

Table 16, figs 23, 24

The *Taimyrothyris* sp. nov. association (4 collections, 713 specimens) is strongly dominated by the brachiopod *Taimyrothyris* which forms 85.3% of the total fauna. In the shelled fauna, only suspension-feeders are present, whilst the trace fossils represent both, deposit (*Macaronichnus*, *Planolites*) and suspension-feeders (*Skolithos*). The free living *Serpula intestinalis* and bivalves constitute the remainder of the fauna: semi-infaunal *G. keyserlingii* and *Isognomon volaticum*, epibyssate *G. schourovskii* and the deep burrowing *Pleuromya uniformis* are the commonest forms. Nektic ammonites and belemnites constitute less than 1% of the total fauna. Epifauna predominates (91.2%), with semi-infauna and infauna sharing the rest. 85% of the bivalved fauna are still articulated and nearly two-thirds of the fauna occurs in life position indicating minimal disturbance of the sea floor life. Apart from *Pinna*, it is particularly *Taimyrothyris* which occurs in position of growth. The brachiopods frequently occur in clusters of usually less than 100 individuals which exhibit a large variation in size. Some individuals show signs of crowding such as deviations from the normal bilateral-symmetrical growth. Often the brachiopod shells exhibit geopetal fills or have, on their inside, at thin line of drusy calcite only, the rest of the shell cavity being empty. Fragmentation ranges from 0 to 50%. All these features point to a sea floor which was patchily colonized by brachiopods. Considering that the overwhelming majority of the fauna lived epifaunally, the total lack of encrusting or boring faunal elements is surprising.

Table 16. *Taimyrothyris* sp. nov. association

	Relative abundance (%)	Presence (%)
Bivalves (14.4%)		
<i>Grammatodon keyserlingii</i>	3.8	75
<i>Grammatodon schourovskii</i>	3.2	25
<i>Isognomon volaticum</i>	1.7	100
<i>Pleuromya uniformis</i>	1.4	75
<i>Hartwellia borealis</i>	1.3	50
<i>Buchia mosquensis</i>	0.7	25
<i>Entolium orbiculare</i>	0.6	50
<i>Camptonectes praecinctus</i>	0.4	50
<i>Camptonectes morini</i>	0.3	25
<i>Oxytoma inequivalve</i>	0.1	25
<i>Pinna lanceolata</i>	0.1	25
<i>Liostrrea plastica</i>	0.1	25
<i>Isocyprina birkelundi</i>	0.1	25
<i>Protocardia striatula</i>	0.1	25
<i>Pachymya sinuata</i>	0.1	25
<i>Thracia depressa</i>	0.1	25
Brachiopods (85.4%)		
* <i>Taimyrothyris</i> sp. nov.	85.3	100
<i>Orbiculoidea latissima</i>	0.1	25
Annelids (0.1%)		
<i>Serpula intestinalis</i>	0.1	25
Trace fossils		
<i>Planolites</i> sp.		25
<i>Macaronichnus segregatis</i>		25
mantled vertical tubes		25

4 collections, 713 specimens.

Members of the trophic nucleus are marked with an asterisk.

Due to the strong dominance of *Taimyrothyris* the evenness values are very low (range: 1.1–1.5; mean: 1.37). Species richness ranges from 3 to 15 (mean: 8.7).

The *Taimyrothyris* sp. nov. association occurs in very fine to fine-grained sandstones which may be strongly glauconitic.

Taimyrothyris sp. nov./*Isognomon volaticum* association

Table 17, figs 23, 24

Five collections with 1171 specimens have been grouped in this association. There are three species in the trophic nucleus: *Taimyrothyris* sp. nov. (57.9%), the semi-infaunal *I. volaticum* (14.9%) and the free-swimming pectinid *Entolium orbiculare* (8.3%). Deposit-feeders and herbivores are very rare, the fauna consisting nearly exclusively of suspension-feeders (99.5%). Three-quarters of the benthos lived epifaunally (*Taimyrothyris*, *G. schourovskii*, *Entolium*, *Camptonectes praecinctus*), 18.3% semi-infaunally (*Isognomon*, *G. keyserlingii*) and only 6.5% infaunally (*Pleuromya uralensis*, *Hartwellia borealis*). The nekton represents 9.5% of the total fauna. 83.7% of the bivalved fauna are still articulated and 20.8% pre-

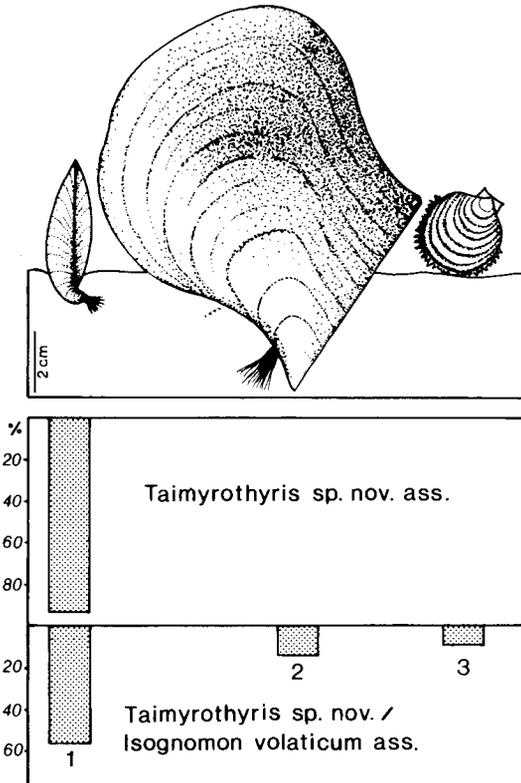


Fig. 23. Trophic nucleus of two *Taimyrothyris*-dominated associations from the Pernaryggen Member. 1: *Taimyrothyris* sp. nov.; 2: *Isognomon volaticum*; 3: *Entolium orbiculare*.

served in life position (*Pleuromya uniformis*, *Thracia*, *Pinna* and *Taimyrothyris*). Encrustation (0.7%) and boring are still insignificant, but considerably more common than in most other associations. Encrusted and bored organisms include *Liostraea*, *Camptonectes praecinctus*, *Isognomon* and belemnites. Encrusters are foraminifera, *Liostraea* and *Cycloserpula*, borers phoronid worms (producing *Talpina*), acrothoracican cirripeds, and an organism producing cylindrical tunnels.

Apart from borings trace fossils are represented by *Chondrites* and *Thalassinoides suevicus*. In two of the five samples drift wood is common.

The species richness is moderate, 8 to 20 species being present in each sample (mean: 13.25), as are the evenness values ranging from 1.88 to 6.15 (mean: 3.10).

A generally low percentage of fragmentation (10 to 20, rarely up to 75), the very high number of articulated shells and the preservation of epifaunal species in life position testify that very little disturbance has taken place. As usual *Taimyrothyris* forms small to medium-sized clusters, but also occurs scattered throughout the sediment. Diagenetic distortion can be ruled out, as aragonitic forms are preserved as moulds.

The *Taimyrothyris* sp. nov./*I. volaticum* association occurs in slightly to heavily glauconitic very fine to fine-grained sand and sandstone.

Table 17. *Taimyrothyris* sp. nov./*Isognomon volaticum* association

	Relative abundance (%)	Presence (%)
Bivalves (41.2%)		
* <i>Isognomon volaticum</i>	14.9	100
* <i>Entolium orbiculare</i>	8.3	100
<i>Grammatodon schourovskii</i>	3.6	40
<i>Grammatodon keyserlingii</i>	2.3	80
<i>Camptonectes praecinctus</i>	2.3	60
<i>Pleuromya uralensis</i>	2.1	60
<i>Buchia mosquensis</i>	1.6	60
<i>Pleuromya triangularis</i>	1.2	40
<i>Pinna lanceolata</i>	1.1	60
<i>Hartwellia borealis</i>	0.9	60
<i>Pleuromya uniformis</i>	0.7	60
<i>Astarte</i> aff. <i>A. veneris</i>	0.4	40
<i>Isocyprina birkelundi</i>	0.3	40
<i>Liostraea plastica</i>	0.3	40
<i>Nuculoma variabilis</i>	0.2	20
shallow burrowing bivalves	0.2	20
tiny burrowing bivalve	0.2	20
<i>Mesosaccella choroschowensis</i>	0.1	20
<i>Plagiostoma incrassatum</i>	0.1	20
<i>Thracia depressa</i>	0.1	20
<i>Discomiltha</i> sp. A	0.1	20
<i>Camptonectes morini</i>	0.1	20
<i>Oxytoma inequivalve</i>	0.1	20
Gastropods (0.1%)		
<i>Pleurotomaria</i> sp.	0.1	20
Brachiopods (57.9%)		
* <i>Taimyrothyris</i> sp. nov.	57.9	100
Annelids (0.6%)		
<i>Serpula (Cycloserpula)</i> sp.	0.2	40
<i>Serpula intestinalis</i>	0.4	20
Arthropods (0.1%)		
<i>Glyphea rostrata</i>	0.1	20
Echinoderms (0.3%)		
<i>Pentacrinites</i> sp.	0.3	40
Trace fossils		
<i>Thalassinoides suevicus</i>		60
<i>Chondrites</i> sp.		40
<i>Talpina</i> sp.		40

5 collections, 1171 specimens.

Members of the trophic nucleus are marked with an asterisk.

Entolium orbiculare association

Table 18, figs 24, 25

In three samples with 460 specimens, *Entolium orbiculare* represents over 80% of the benthic fauna. Its thin, symmetrical shell suggests that, whilst living byssally attached at the juvenile stage, it was capable of swimming at the adult stage.

Apart from one specimen of a grazing gastropod (*Delphinula*), all other benthic organisms were suspension-feeders. Semi-infaunal and infaunal forms are rare compared to epifaunal ones.

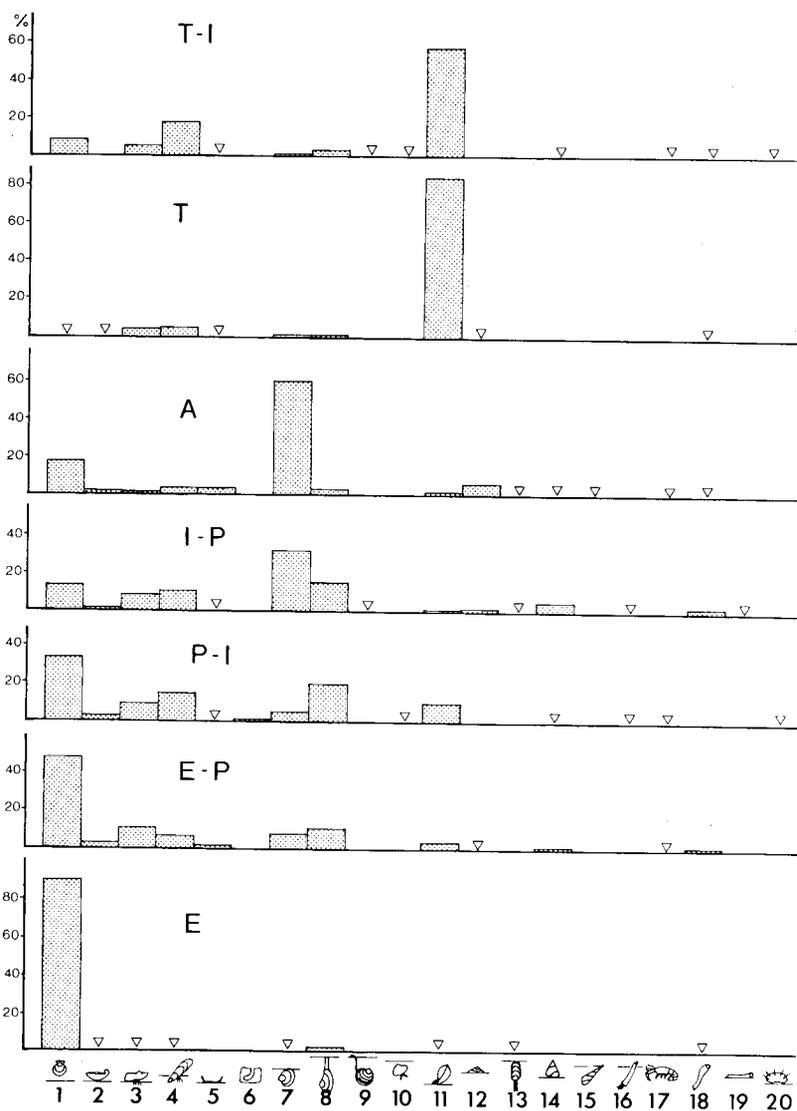


Fig. 24. Distribution of life habit groups in seven associations from the Pernaryggen Member. Triangles indicate occurrences of less than one percent. T-I: *Taimyrothyris* sp. nov./*Isognomon volaticum* ass.; T: *Taimyrothyris* sp. nov. ass.; A: *Astarte praeveneris maimchaensis* ass.; I-P: *Isocyprina birkelundi*/*Pinna lanceolata* ass.; P-I: *Pleuromya uniformis*/*Isognomon volaticum* ass.; E-P: *Entolium orbiculare*/*Pleuromya triangularis* ass.; E: *Entolium orbiculare* ass.; 1-20: life habit groups; 1: mobile epibenthic suspension-feeders; 2: reclining epibenthic susp.-feeders; 3: epibyssate susp.-feeders; 4: endobyssate semi-infaunal susp.-feeders; 5: epibenthic cemented susp.-feeders; 6: wood borers; 7: shallow burrowing susp.-feeders; 8: deep burrowing susp.-feeders; 9: deposit-feeders at the depositional interface; 10: infaunal mobile deposit-feeders; 11: pedicle-attached epibenthic articulate brachiopods; 12: epibenthic inarticulate brachiopods; 13: burrowing brachiopods; 14: epifaunal herbivorous gastropods; 15: infaunal suspension-feeding gastropods; 16: infaunal detritus-collecting scaphopods; 17: scavenging detritus-feeding crustaceans; 18: free living serpulids; 19: encrusting serpulids; 20: echinoderms.

Table 18. *Entolium orbiculare* association

	Relative abundance (%)	Presence (%)
Bivalves (98.1%)		
* <i>Entolium orbiculare</i>	92.7	100
<i>Pleuromya uniformis</i>	1.9	100
<i>Thracia depressa</i>	0.9	33
<i>Astarte</i> sp.	0.5	33
<i>Buchia mosquensis</i>	0.5	67
<i>Grammatodon schourovskii</i>	0.2	33
<i>Isognomon volaticum</i>	0.2	33
<i>Camptonectes morini</i>	0.2	33
<i>Camptonectes praecinctus</i>	0.2	33
<i>Protocardia striatula</i>	0.2	33
Gastropods (0.2%)		
<i>Delphinula</i> sp.	0.2	33
Brachiopods (0.9%)		
<i>Taimyrothyris</i> sp.	0.5	33
' <i>Rhynchonella</i> ' sp. nov.	0.2	33
<i>Lingula zeta</i>	0.2	33
Annelids (0.7%)		
<i>Serpula intestinalis</i>	0.7	33
Trace fossils		
<i>Thalassinoides suevicus</i>		33
<i>Macaronichnus segregatis</i>		33

3 collections, 460 specimens.

Members of the trophic nucleus are marked with an asterisk.

Ammonites and belemnites represent 7.8% of the total fauna. The trace fossils *Macaronichnus segregatis* and *Thalassinoides suevicus* occur in one of the samples; wood fragments were encountered in two.

No specimens are encrusted or bored and only 0.2% are found in life position (*Pleuromya uniformis*). On the other hand, 64.7% of the fauna are still articulated; in one sample, 254 of 267 *Entolium* were still articulated demonstrating that in this case minimal disturbance and rapid burial of the fauna must have taken place. The low percentage of specimens recorded in life position is thus misleading: Infaunal and semi-infaunal forms are usually very easily recognised when preserved in life position which, in most cases, differs from a current stable position; in free living epifaunal species such as some pectinids or gastropods, however, the life position often does not differ drastically from the orientation of transported shells. In these cases the preservation of a shell in life position cannot be inferred with certainty.

As the fragmentation is relatively low (20–50%), it appears most probable that the *Entolium orbiculare* association is not the winnowed or transported product of a former community, but represents its *in situ* relic. Thus, the low diversity values (mean evenness: 1.25; mean species richness: 7) are a primary feature and not distorted by biostratigraphic processes. The *E. orbiculare* association occurs in fine to medium-grained moderately to heavily glauconitic sandstone.

Astarte praevenensis maimechaensis association

Table 19, figs 24,25

This widespread association is represented by 1369 specimens in nine collections. Characteristic species are the shallow burrowing bivalve *Astarte praevenensis maimechaensis* (59.8%) and the encrusting inarticulate brachiopod *Orbiculoidea latissima* (6%) although the latter occurs in just over half the samples. Member of the trophic nucleus is also *E. orbiculare* (17.2%). Suspension-feeders (99.7%) again dominate the association, the rest consisting of some ?herbivorous gastropods (*Delphinula*, *Leptomaria*) and the crustacean *Glyphea*. Shallow burrowing bivalves prevail (*Astarte*, *Eriphyla*, *Hartwellia*) followed by free living epifaunal bivalves (*Entolium*, *Camptonectes praecinctus*) and encrusting brachiopods (*Orbi-*

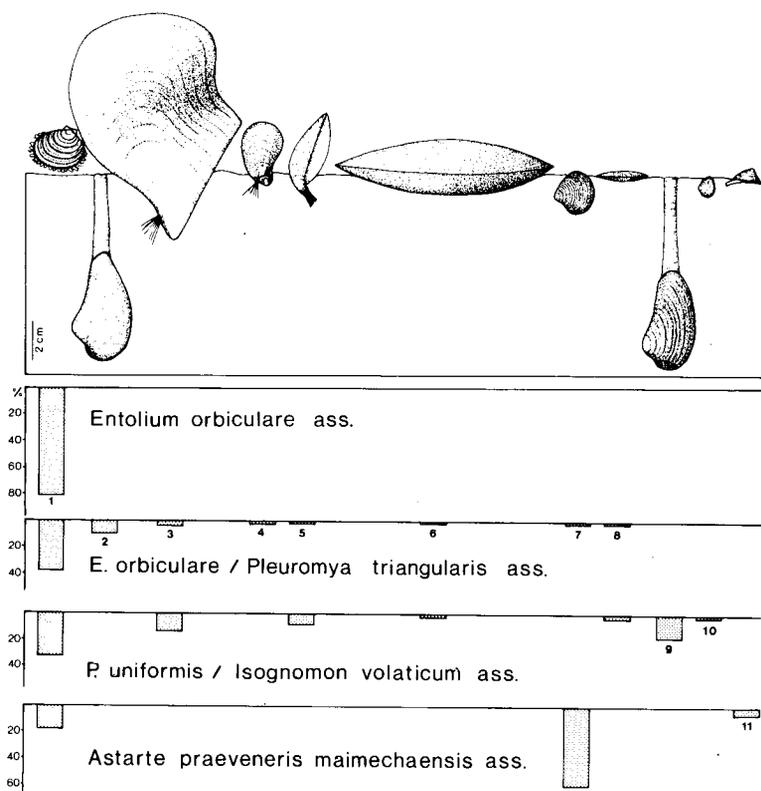


Fig. 25. Trophic nuclei of four associations from the Pernaryggen Member. 1: *Entolium orbiculare*; 2: *Pleuromya triangularis*; 3: *Isognomon volaticum*; 4: *Buchia mosquensis*; 5: *Taimyrothyris* sp. nov.; 6: *Camptonectes praecinctus*; 7: *Astarte praevenensis maimechaensis*; 8: *Camptonectes morini*; 9: *Pleuromya uniformis*; 10: *Isocyprina birkelundi*; 11: *Orbiculoidea latissima*.

Table 19. *Astarte praevenensis maimechaensis* association

	Relative abundance (%)	Presence (%)
Bivalves (91.0%)		
* <i>Astarte praevenensis maimechaensis</i>	59.8	100
* <i>Entolium orbiculare</i>	17.2	88
<i>Isognomon volaticum</i>	3.4	55
<i>Liostraea plastica</i>	2.8	55
<i>Camptonectes praecinctus</i>	2.1	77
<i>Pleuromya triangularis</i>	1.8	44
<i>Pleuromya uralensis</i>	0.8	66
<i>Buchia mosquensis</i>	0.8	66
<i>Camptonectes morini</i>	0.5	33
<i>Hartwellia kharoschovensis</i>	0.4	11
<i>Eriphyla saemanni</i>	0.2	22
? <i>Liostraea</i> sp. 1	0.1	11
<i>Plagiostoma incrassatum</i>	0.1	22
<i>Pleuromya uniformis</i>	0.1	11
<i>Corbicellopsis</i> cf. <i>C. lorioli</i>	0.1	11
<i>Nanogyra nana</i>	0.1	11
<i>Plagiostoma</i> sp. A	0.1	11
<i>Oxytoma inequivalve</i>	0.1	11
<i>Grammatodon</i> sp.	0.1	11
<i>Limatula consobrina</i>	0.1	11
Gastropods (0.4%)		
<i>Delphinula</i> sp.	0.1	22
<i>Turrítella</i> sp.	0.1	11
<i>Leptomaria</i> sp.	0.1	11
<i>Pseudomelania</i> sp.	0.1	11
Brachiopods (8.3%)		
* <i>Orbiculoidea latissima</i>	6.1	55
<i>Taimyrothyris</i> sp. nov.	1.5	55
' <i>Rhynchonella</i> ' sp. nov.	0.5	33
<i>Lingula zeta</i>	0.3	33
Annelids (0.2%)		
<i>Serpula intestinalis</i>	0.2	33
Arthropods (0.9%)		
<i>Glyphea rostrata</i>	0.1	11
Trace fossils		
mantled vertical tubes		33
<i>Skolithos</i> sp.		11
<i>Chondrites</i> sp.		11
<i>Thalassinoides suevicus</i>		11

9 collections, 1369 specimens.

Members of the trophic nucleus are marked with an asterisk.

culoidea). The variety of remaining life habit groups is high, but most are represented by few individuals only (fig. 24).

Trace fossils are rare and consist of mantled vertical tubes, *Skolithos*, *Chondrites*, and *Thalassinoides suevicus*, the latter most likely produced by *Glyphea*. Ammonites and belemnites form 4.9% of the total fauna. Wood fragments, some of them up to 30 cm in length, occur in most samples. Compared to other associations, only very little (0.4%) of the uncemented fauna occurs in life position (small clusters of *Taimyrothyris*, semi-infaunal *Isognomon*, deep burrowing *Pleuromya uralensis* and

P. triangularis). In some samples, disarticulated *Entolium* shells preferentially occur in nests. The percentage of articulated organisms is generally not very high (26.4%). *Astarte praevenensis* sometimes occurs in loosely packed shell layers indicative of some degree of reworking. The degree of fragmentation is moderate, varying from 30 to 75%. These features suggest that post-mortem disturbance of the fauna was greater than in most other associations, but significant lateral faunal mixing appears unlikely.

The percentage of bored (0.7%) and encrusted (0.8%) organisms again is very low. Borers are acrothoracican cirripeds, encrusters *Liostrea plastica* (found commonly on ammonites).

The diversity is moderate: evenness values range from 1.45 to 3.98 (mean: 2.42), species richness from 8 to 15 (mean: 11.1). The *A. praevenensis maimechaensis* association occurs in moderately to heavily glauconitic fine-grained sandstone (size of glauconite grains usually medium). In many cases it was found associated with the so-called *Pseudaperta* bed, a layer rich in shells of the ammonite *Epipallasiceras pseudaperta* which can be followed for several kilometres around Hartz Fjeld and from there to Kronen and Bays Fjelde. The close, but not absolute correlation between the ammonite shell bed and the association suggests that the distribution of the latter was isochronous. Consequently, a relatively uniform depositional environment across the region is envisaged for that time interval.

Entolium orbiculare/*Pleuromya triangularis* association

Table 20, figs 24, 25

The *E. orbiculare*/*P. triangularis* association is represented by ten collections with 1824 specimens. There are eight species in the trophic nucleus with *E. orbiculare* constituting nearly 50% in terms of relative abundance. Other members are the deep burrowing *Pleuromya triangularis*, the endobysate *Isognomon volaticum*, the epibysate *Buchia mosquensis*, *Camptonectes morini*, the pedicle-attached *Tai-myrothyris*, the reclining *Camptonectes praecinctus* and the shallow burrower *Astarte* aff. *A. veneris*. Thus, a variety of life habit groups are represented in the trophic nucleus, and it is only due to the abundance of *Entolium* that free living epi-

Table 20. *Entolium orbiculare*/*Pleuromya triangularis* association

	Relative abundance (%)	Presence (%)
Bivalves (92.2%)		
* <i>Entolium orbiculare</i>	48.6	100
* <i>Pleuromya triangularis</i>	9.2	100
* <i>Isognomon volaticum</i>	4.9	90
* <i>Buchia mosquensis</i>	4.1	80
* <i>Camptonectes praecinctus</i>	3.6	90
* <i>Astarte</i> aff. <i>A. veneris</i>	2.9	80

	Relative abundance (%)	Presence (%)
* <i>Camptonectes morini</i>	2.9	60
<i>Isocyprina birkelundi</i>	2.1	60
<i>Grammatodon schourovskii</i>	1.6	50
<i>Liostrea plastica</i>	1.5	50
<i>Pleuromya uralensis</i>	1.2	60
<i>Oxytoma inequivalve</i>	1.1	60
<i>Grammatodon keyserlingii</i>	0.9	40
<i>Eriphyla saemanni</i>	0.8	30
<i>Plagiostoma incrassatum</i>	0.8	70
<i>Pinna lanceolata</i>	0.7	50
<i>Limatula consobrina multicostata</i>	0.6	30
<i>Astarte praevenensis maimechaensis</i>	0.6	30
<i>Hartwellia borealis</i>	0.4	40
<i>Protocardia striatula</i>	0.4	20
<i>Pleuromya uniformis</i>	0.4	10
<i>Modiolus czekanowskii</i>	0.3	20
? <i>Liostrea</i> sp. 1	0.2	10
shallow burrowing heterodont A	0.2	20
<i>Hartwellia kharoschovensis</i>	0.2	10
<i>Modiolus bipartitus</i>	0.2	20
<i>Modiolus elongatus</i>	0.1	10
<i>Thracia depressa</i>	0.1	20
<i>Hartwellia groenlandica</i>	0.1	20
<i>Corbicellopsis</i> sp.	0.1	20
<i>Pachymya sinuata</i>	0.1	10
<i>Pholadomya hemicardia</i>	0.1	10
' <i>Tancredia</i> ' sp.	0.1	10
deep burrowing heterodont	0.1	10
<i>Goniomya literata</i>	0.1	10
<i>Corbicellopsis lorioli</i>	0.1	10
<i>Placunopsis radiata</i>	0.1	10
<i>Nicanella</i> sp.	0.1	10
<i>Nanogyra nana</i>	0.1	10
<i>Plagiostoma</i> sp. A	0.1	10
? <i>Liostrea</i> sp. 2	0.1	10
? <i>Solemya</i> sp.	0.1	10
<i>Camptonectes (Camptochlamys)</i> sp.	0.1	10
Gastropods (1.2%)		
<i>Sulcoactaeon peroskianus</i>	0.6	10
<i>Brachytrema</i> sp.	0.2	10
<i>Pseudomelania</i> sp.	0.2	10
<i>Amberleya</i> cf. <i>A. pulchra</i>	0.2	10
Brachiopods (4.4%)		
* <i>Taimyrothyris</i> sp. nov.	3.9	70
' <i>Rhynchonella</i> ' sp. nov.	0.3	30
<i>Orbiculoidea latissima</i>	0.2	30
Annelids (2.0%)		
<i>Serpula intestinalis</i>	2.0	60
Arthropods (0.1%)		
<i>Glyphea rostrata</i>	0.1	10
Trace fossils		
<i>Chondrites</i> sp.		30
<i>Planolites</i> sp.		20
<i>Skolithos</i> sp.		20
<i>Diplocraterion habichi</i>		10
<i>Macaronichnus segregatis</i>		10

10 collections, 1824 specimens.

Members of the trophic nucleus are marked with an asterisk.

faunal species dominate (fig. 24). Apart from some rare herbivorous gastropods (*Brachytrema*, *Amberleya*, *Sulcoactaeon*) and detritus feeding crustaceans (*Glyphea*) the association is dominated by suspension-feeders (98.8%). Three-fourth of the fauna lived on the substrate, one-fifth in the sediment, and 7% had a semi-infaunal mode of life (*Pinna*, *Modiolus*, *Isognomon*). Trace fossils occur in only few samples and represent deposit-feeders (*Chondrites*, *Planolites*, *Macaronichnus*) as well as suspension-feeders (*Diplocraterion habichi*, *Skolithos*). Nektic ammonites and belemnites are very common and make up 14.5% of the total fauna. Wood fragments occur in all but one of the samples.

Due to the abundance of free living epifaunal *Entolium*, only 2.7% of the fauna are found in life position (some small clusters of *Taimyrothyris*, the endobysate *Modiolus czezanowski*, *M. elongatus*, *Pinna*, *Isognomon* and the deep burrowing *Goniomya literata*, *Pleuromya triangularis* and *P. uralensis*). The percentage of still articulated bivalved individuals is relatively low (16.5%). Encrusters (*Liostrea*) and borers (acrothoracican cirripeds, ?polychaetes) are very rare, *Liostrea plastica* being largely confined to ammonites, the borers to large shells of *Isognomon* and *Camptonectes praecinctus*. Fragmentation varies from 10 to 50%, most commonly being around 20%.

The diversity is high: species richness ranges from 9 to 25 (mean: 18.8) and evenness from 1.94 to 8.66 (mean: 3.92). Although some samples represent shell beds up to 20 cm in thickness, it is unlikely that they indicate extensive reworking as the fragmentation rate is relatively low and there are no signs of sorting. More likely, the shell accumulations can be accounted for by a reduced rate in sedimentation and short term *in situ* reworking. Parts of successional sequences seem to be preserved in some beds. For example, a 20 cm thick shell bed on the north slope of Krebsedal (locality 16) is topped in places by a pavement of articulated *Isognomon volaticum*. Conversely, at the base of another sandstone unit from Pernaryggen a level with *Pleuromya triangularis* in life position is followed by a layer of large articulated *Camptonectes praecinctus* (see also Fürsich, 1978).

The *E. orbiculare*/*P. triangularis* association preferentially occurs in strongly glauconitic fine-grained sandstone, but also in micaceous fine sand.

Isocyprina birkelundi/*Pinna lanceolata* association

Table 21, figs 24, 26-28

The *I. birkelundi*/*P. lanceolata* association is the commonest association encountered in the Pernaryggen Member, represented by 17 collections and 4960 specimens. It occurs in the so-called *Pinna* bed, a shell-rich layer (fig. 27) up to 190 cm in thickness, which can be traced from Kap Leslie to the northern slopes of Hartz Fjeld and to Kronen. The association is also by far the most diverse, with 13 species in the trophic nucleus. Diagnostic species are *Isocyprina birkelundi*, a small, shallow burrowing bivalve, and the semi-infaunal bivalve *Pinna lanceolata*.

Characteristic is also the relative abundance of gastropods (especially *Pseudomelania* and *Delphinula*) as well as of the free living serpulid *Serpula intestinalis*. Rarer species which also characterize the association are the shallow burrowing bivalve *Myophorella* and the inarticulate brachiopods *Lingula* and *Orbiculoidea*. Remaining species of the trophic nucleus (the bivalves *E. orbiculare*, *P. uniformis*, *P. triangularis*, *Buchia mosquensis*, *Astarte praevenensis praevenensis*, *Camptonectes morini*, *I. volaticum* and the brachiopod *Taimyrothyris*) occur in a wide variety of associations and reach the peaks of their distribution somewhere else.

Epifauna comprises 36.2%, semi-infauna 10.9% and infauna 52.8% of the benthic fauna. The dominance of infauna is due largely to several species of *Pleuromya*, *Astarte*, and in particular to the small *Isocyprina*. Although the latter occupies the first rank in terms of numerical abundance, it is probably the large *Pinna lanceolata* which, though occupying rank four in terms of numerical abundance, dominates the association in terms of biomass. As in most other associations, nearly all organisms were suspension-feeders (97%).

A wide range of different life habit groups is represented, the commonest being shallow infaunal suspension-feeding bivalves. Amongst the rarer groups are brows-

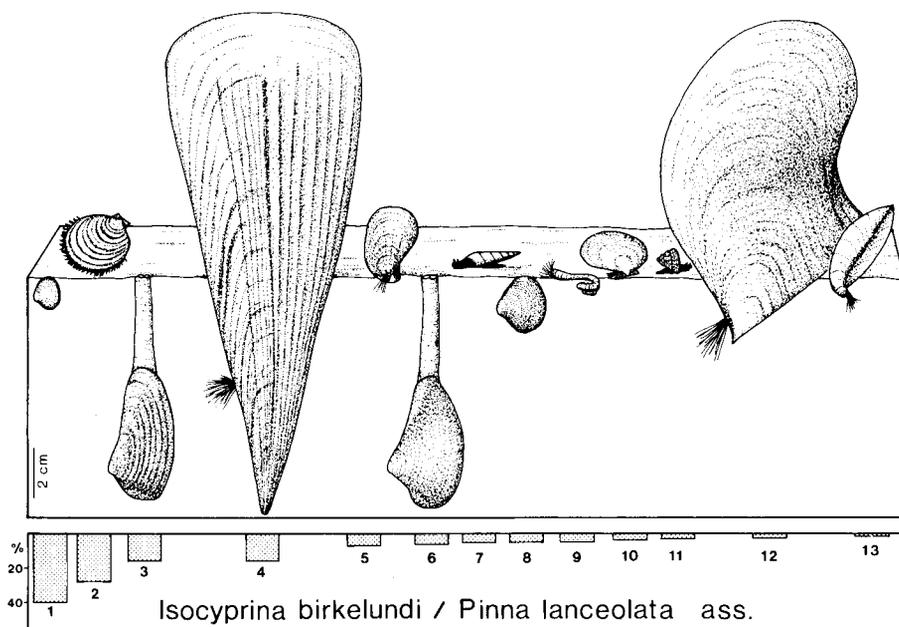


Fig. 26. Trophic nucleus of the *Isocyprina birkelundi*/*Pinna lanceolata* association from the Pernaryggen Member. 1: *Isocyprina birkelundi*; 2: *Entolium orbiculare*; 3: *Pleuromya uniformis*; 4: *Pinna lanceolata*; 5: *Buchia mosquensis*; 6: *Pleuromya triangularis*; 7: *Pseudomelania* sp.; 8: *Astarte praevenensis praevenensis*; 9: *Cycloserpula intestinalis*; 10: *Camptonectes morini*; 11: *Delphinula* sp.; 12: *Isognomon volaticum*; 13: *Taimyrothyris* sp. nov.

ing echinoids, infaunal bivalves feeding at the depositional interface (*Discomiltha*), detritus collecting scaphopods, fan-shaped and crustose bryozoans and high level suspension-feeding crinoids (*Pentacrinites*).

A wide variety of trophic groups is also represented by the trace fossils: infaunal scavengers/predators (*Curvolithus*), deposit-feeders (*Teichichnus*, *Chondrites*, *Macaronichnus*, *Planolites*), suspension-feeders (mantled vertical tubes, *Skolithos*) and detritus-feeding crustaceans (*Thalassinoides*). Nektic ammonites and belemnites are common and constitute 4.2% of the total fauna. Wood fragments occur in

Table 21. *Isocyprina birkelundi*/*Pinna lanceolata* association

	Relative abundance (%)	Presence (%)
Bivalves (85.6%)		
* <i>Isocyprina birkelundi</i>	20.8	94
* <i>Entolium orbiculare</i>	14.7	100
* <i>Pleuromya uniformis</i>	8.6	88
* <i>Pinna lanceolata</i>	8.2	100
* <i>Buchia mosquensis</i>	4.4	94
* <i>Pleuromya triangularis</i>	4.2	59
* <i>Astarte praevenensis praevenensis</i>	3.6	59
* <i>Camptonectes morini</i>	2.6	88
* <i>Isognomon volaticum</i>	1.8	82
<i>Protocardia striatula</i>	1.6	82
<i>Pleuromya uralensis</i>	1.6	76
<i>Grammatodon schourovskii</i>	1.3	53
<i>Eriphyla saemanni</i>	1.3	59
<i>Astarte</i> aff. <i>A. veneris</i>	1.2	29
<i>Camptonectes praecinctus</i>	1.1	82
<i>Astarte praevenensis maimechaensis</i>	0.9	6
<i>Oxytoma inequivalve</i>	0.9	71
<i>Hartwellia kharoschovensis</i>	0.9	47
<i>Nanogyra nana</i>	0.6	29
<i>Myophorella ingens</i>	0.4	53
<i>Modiolus elongatus</i>	0.3	23
<i>Corbicellopsis</i> cf. <i>C. lorioli</i>	0.3	41
<i>Thracia depressa</i>	0.3	47
<i>Modiolus czekanowskii</i>	0.3	35
<i>Pholadomya hemicardia</i>	0.2	23
<i>Corbicellopsis lorioli</i>	0.2	23
<i>Hartwellia groenlandica</i>	0.2	18
<i>Liostrea plastica</i>	0.2	41
<i>Limatula consobrina multicostata</i>	0.2	23
? <i>Discomiltha</i> sp. A	0.2	12
<i>Neocrassina pelops</i>	0.1	12
shallow burrowing heterodont	0.1	23
<i>Plagiostoma incrassatum</i>	0.1	29
<i>Hartwellia</i> sp. A	0.1	12
<i>Hartwellia borealis</i>	0.1	12
deep burrowing pholadomyacean	0.1	18
<i>Goniomya literata</i>	0.08	23
<i>Pachymya sinuata</i>	0.08	18
<i>Grammatodon keyserlingii</i>	0.08	18
<i>Placunopsis radiata</i>	0.08	23
<i>Modiolus bipartitus</i>	0.06	18

	Relative abundance (%)	Presence (%)
<i>Discomiltha lirata</i>	0.06	12
<i>Corbulomima</i> sp.	0.06	18
' <i>Pleuromya elongata</i> '	0.06	12
cyprinid	0.06	12
<i>Quenstedtia parallela</i>	0.06	12
<i>Goniomya bicarinata</i>	0.06	12
<i>Tancredia</i> sp.	0.04	12
<i>Corbicellopsis unioides</i>	0.04	6
large <i>Isocyprina</i> sp.	0.04	12
<i>Falcimytilus suprajurensis</i>	0.04	12
<i>Musculus fischerianus</i>	0.04	6
<i>Unicardium aceste</i>	0.04	6
<i>Trichites</i> sp.	0.02	6
<i>Plagiostoma</i> sp. A	0.02	6
<i>Bakevella</i> sp.	0.02	6
epibyssate pteriacean	0.02	6
<i>Buchia</i> ? <i>rugosa</i>	0.02	6
<i>Buchia</i> ex gr. <i>B. russiensis</i>	0.02	6
<i>Pseudolimea</i> cf. <i>P. arctica</i>	0.02	6
<i>Corbicellopsis</i> cf. <i>C. laevis</i>	0.02	6
<i>Pleuromya uniformis peregrina</i>	0.02	6
<i>Isocyprina</i> sp. indet.	0.02	6
' <i>Cyprina birostrata</i> '	0.02	6
<i>Isocyprina</i> cf. <i>I. cyreniformis</i>	0.02	6
burrowing heterodont A	0.02	6
Gastropods (6.5%)		
* <i>Pseudomelania</i> sp.	3.6	94
* <i>Delphinula</i> sp.	2.4	76
<i>Sulcoactaeon peroskianus</i>	0.5	59
neritid sp. B	0.02	6
<i>Brachytrema incerta</i>	0.02	6
Scaphopods (0.06%)		
<i>Dentalium</i> sp.	0.06	18
Brachiopods (4.0%)		
* <i>Taimyrothyris</i> sp. nov.	1.7	76
<i>Orbiculoidea latissima</i>	1.4	76
<i>Lingula zeta</i>	0.9	53
Annelids (3.7%)		
* <i>Serpula intestinalis</i>	3.4	94
<i>Serpula</i> (<i>Tetraserpula</i>) sp.	0.2	35
<i>Serpula</i> (<i>Cycloserpula</i>) sp.	0.02	6
<i>Serpula</i> (<i>Dorsoserpula</i>) sp.	0.02	6
Bryozoans (0.1%)		
fan-shaped bryozoan	0.1	6
crustose bryozoan	0.04	6
Echinoderms (0.02%)		
<i>Pentacrinites</i> sp.	0.02	6
Trace fossils		
mantled vertical tubes		41
<i>Skolithos</i> sp.		18
<i>Thalassinoides suevicus</i>		18
<i>Planolites</i> sp.		12
<i>Macaronichnus segregatis</i>		6
<i>Teichichnus rectus</i>		6
<i>Chondrites</i> sp.		6
<i>Curvolithus</i> sp.		6

17 collections, 4960 specimens.

Members of the trophic nucleus are marked with an asterisk.

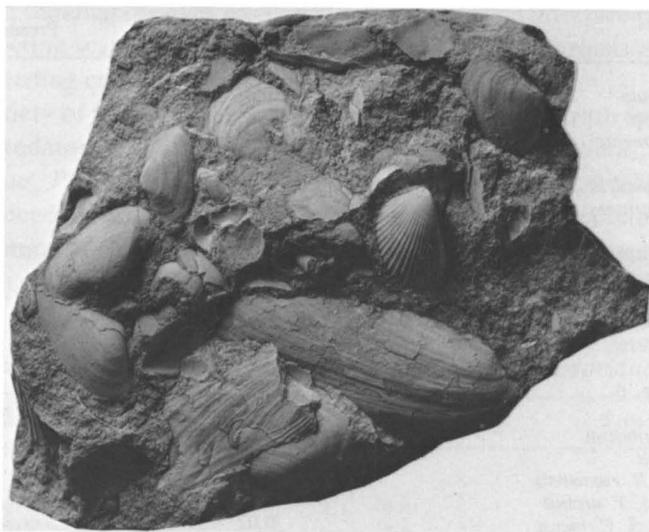


Fig. 27. Shell accumulation in the *Pinna* bed, Pernaryggen Member, eastern slopes of Hartz Fjeld. Scale: $\times 0.8$.

most samples. Bored and/or encrusted shells are very rare. Encrusters include *Liostrea*, *Nanogyra*, serpulids, *Orbiculoidea* and bryozoans, whilst borers are represented by bivalves, ?polychaetes, acrothoracican barnacles and the trace fossil *Dendrina*. On some large *Camptonectes praecinctus* etch marks of brachiopod pedicles (*Podichnus*) were encountered.

40% of the bivalved fauna are still articulated, among them epifaunal forms such as *Entolium*, *Buchia* and *Camptonectes*. Only 7% of the semi-infaunal (*Pinna*) and infaunal organisms are preserved in life positions. Such preservation is particularly common in deep burrowing forms (various species of *Pleuromya*, *Goniomya*, *Pholadomya*, *Pachymya* and *Discomiltha*) and rare in endobysate *Isognomon volaticum* which occurred in small clusters. Individuals of *Buchia mosquensis* were observed close to life position as small clusters on an ammonite shell. Particularly noticeable are, however, populations of *Pinna lanceolata* preserved in life position (fig. 28). They have been mentioned already by Aldinger (1935) who recognised them as relics of an *in situ* preserved community. Frequently, *Pinna* shells are closely stacked and must, at some stage, have formed dense settlements on the sea floor, although only of limited lateral extent. In some samples ossicles and calice fragments of *Pentacrinites* occur. Although the crinoids are disarticulated, the elements occur in nests and any significant lateral transport is therefore unlikely.

Patchy distribution is also found in *Isocyprina* where sometimes 20 to 100 mainly bivalved individuals occur in nests and pockets. In this case, however, the con-

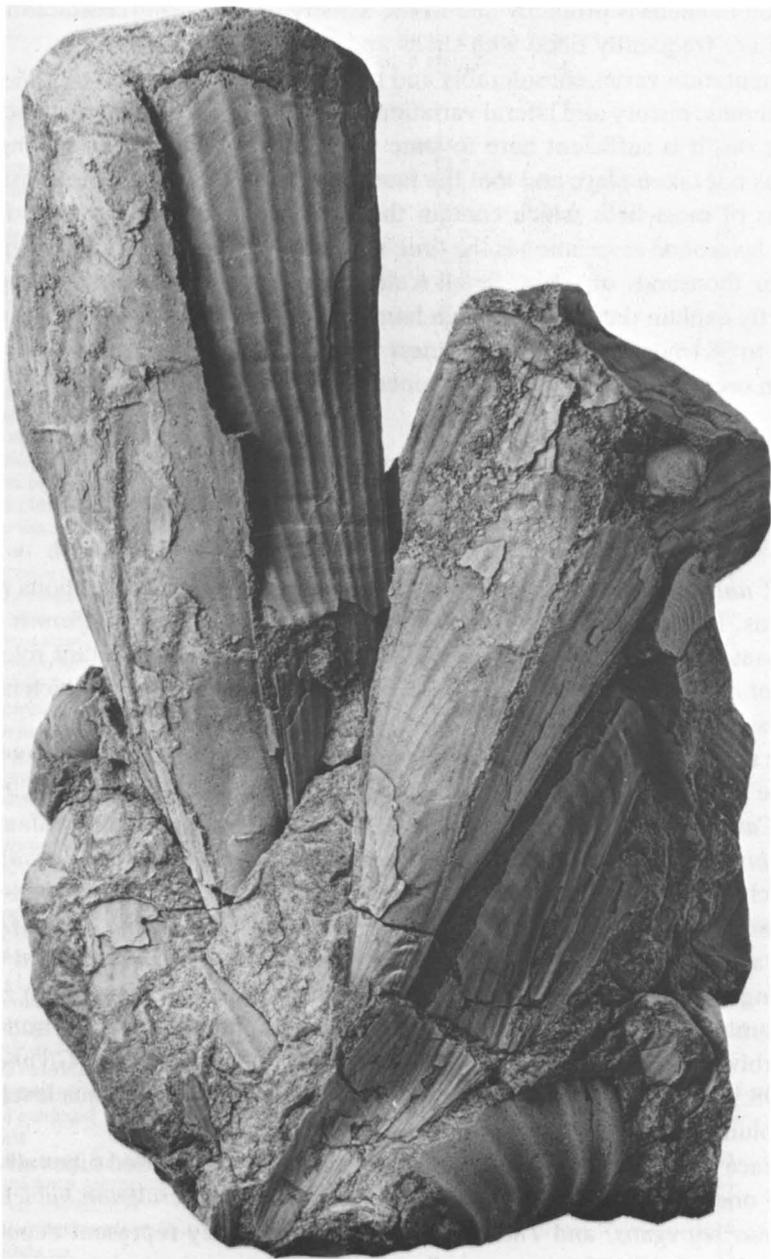


Fig. 28. *Pinna lanceolata* in life position. *Pinna* bed (Pernaryggen Mb), eastern slopes of Hartz Fjeld.
Scale: $\times 0.8$.

centration of shells is probably due to the activity of burrowing crustaceans whose burrows are frequently filled with shells and shell debris.

Fragmentation varies considerably and may be less than 10 or up to 95%. As the biostratigraphic history and lateral variation of the *Pinna* bed will be discussed in detail later on, it is sufficient here to state that lateral transport and sorting of the fauna has not taken place and that the fauna accumulated *in situ*. The considerable thickness of most beds which contain the association suggests that the *I. birkelundi*/*P. lanceolata* association is the time-averaged relic of a community which persisted for thousands of years. Small-scale fluctuations in taxonomic composition may partly explain the relatively high faunal diversity: The species richness ranges from 17 to 38 (mean: 28.5), the evenness from 3.71 to 11.36 (mean: 7.62). The association occurs in fine to medium-grained slightly to moderately glauconitic sandstone.

Pleuromya uniformis/*Isognomon volaticum* association

Table 22, figs 24, 25

The *P. uniformis*/*I. volaticum* association is represented by 7 collections with 976 specimens. It is characterized by the deep burrowing bivalve *P. uniformis* and the endobyssate bivalve *I. volaticum*. Both species play also an important role in several other associations, but it is their co-occurrence and abundance which is unique to this association.

There are seven species in the trophic nucleus: Apart from the two index species, there are the free living pectinid *Entolium*, the brachiopod *Taimyrothyris*, two species of *Camptonectes* (*C. praecinctus* and *C. morini*) and the shallow infaunal *Iso-cyprina birkelundi*. Due to the abundance of pectinids, *Grammatodon schourovskii* and brachiopods, the epifauna constitutes 58.1% of the fauna, the semi-infauna (*Isognomon*, some *Grammatodon keyserlingii* and rare *Pinna* and *Modiolus*) 15.3%, and the infauna (deep burrowing *Pleuromya*, *Pholadomya* and shallow burrowing *Hartwellia*, *Iso-cyprina* and *Corbicellopsis*) 26.6%. Apart from rare mobile infaunal deposit-feeding nuculids (*Mesosaccella chorschowensis*) and equally rare herbivorous gastropods (e.g. *Sulcoactaeon*) and arthropods (*Glyphea*), the fauna (98.9%) consists of suspension-feeders which exploited various levels of the water column for food.

The trace fossil fauna is diverse, but apart from vertical mantled tubes all of them occur in one collection only (*Curvolithus*, *Skolithos*, *Diplocraterion habichi*, *Macaronichnus segregatis*, and *Thalassinoides suevicus*). They represent deposit-, detritus- and suspension-feeders as well as predators/scavengers.

Ammonites and belemnites are very common and constitute nearly one-fifth of the total fauna. Pieces of drift wood are found in most samples.

Nearly half the bivalved fauna is still articulated and 13.5% are preserved in life position (nests of *Taimyrothyris*, *P. uniformis*, *P. uralensis*, clusters of *Buchia*).

Table 22. *Pleuromya uniformis*/*Isognomon volaticum* association

	Relative abundance (%)	Presence (%)
Bivalves (87.9%)		
* <i>Entolium orbiculare</i>	33.5	100
* <i>Pleuromya uniformis</i>	17.5	100
* <i>Isognomon volaticum</i>	14.1	100
* <i>Camptonectes praecinctus</i>	3.2	100
* <i>Camptonectes morini</i>	3.0	86
* <i>Isocyprina birkelundi</i>	2.3	29
<i>Grammatodon schourovskii</i>	1.9	29
<i>Buchia mosquensis</i>	1.6	43
<i>Pleuromya uralensis</i>	1.5	71
xylophagan bivalve	1.5	14
<i>Eriphyla saemanni</i>	1.1	57
<i>Plagiostoma incrassatum</i>	1.0	43
<i>Grammatodon keyserlingii</i>	0.9	43
<i>Buchia</i> cf. <i>B. rugosa</i>	0.8	14
<i>Hartwellia borealis</i>	0.5	29
<i>Oxytoma inequivalve</i>	0.4	29
<i>Liostraea plastica</i>	0.4	43
<i>Protocardia striatula</i>	0.4	43
<i>Astarte</i> aff. <i>A. veneris</i>	0.2	29
<i>Mesosacella choroschowensis</i>	0.2	14
<i>Limatula consobrina multicostata</i>	0.2	14
<i>Placunopsis radiata</i>	0.2	29
<i>Pleuromya triangularis</i>	0.2	14
<i>Pholadomya hemicardia</i>	0.2	14
<i>Inoceramus</i> sp.	0.1	14
cf. <i>Corbicellopsis</i>	0.1	14
<i>Goniomya</i> sp.	0.1	14
<i>Modiolus elongatus</i>	0.1	14
<i>Pinna lanceolata</i>	0.1	14
Gastropods (0.5%)		
<i>Sulcoactaeon peroskianus</i>	0.2	14
<i>Pseudomelania</i> sp.	0.2	29
Scaphopods (0.1%)		
<i>Dentalium</i> sp.	0.1	14
Brachiopods (10.3%)		
* <i>Taimyrothyris</i> sp. nov.	8.5	57
' <i>Rhynchonella</i> ' sp. nov.	1.8	29
Annelids (1.0%)		
<i>Serpula intestinalis</i>	0.9	29
<i>Serpula</i> (<i>Cycloserpula</i>) sp.	0.1	14
Arthropods (0.1%)		
<i>Glyphea rostrata</i>	0.1	14
Echinoderms (0.1%)		
cidaroid echinoid	0.1	14
Trace fossils		
mantled vertical tubes		43
<i>Macaronichnus segregatis</i>		14
<i>Diplocraterion habichti</i>		14
<i>Thalassinoides suevicus</i>		14
<i>Curvolithus</i> sp.		14
<i>Skolithos</i> sp.		14

7 collections, 976 specimens.

Members of the trophic nucleus are marked with an asterisk.

Fragmentation ranges from 0 to 90%. In one horizon, complete and fragmented ammonites are densely packed in nests and lenses. They suggest the activity of scavenging organisms rather than high turbulence levels. In contrast, rare thin layers of densely packed undamaged *Entolium* and occasional *Taimyrothyris* reflect small-scale physical disturbance.

No shells are bored and only very few (0.5%) encrusted by *Cycloserpula* or *Lios-trea plastica*. Faunal diversity is moderately high: species richness varies from 12 to 21 (mean: 16.4) and evenness values from 2.72 to 5.24 (mean: 3.59). The *P. uniformis*/*I. volaticum* association occurs in fine-sandy micaceous shale and concretions as well as in fine-grained heavily glauconitic sandstone.

Faunal assemblages

In the following and table 23 usually unique occurrences of distinct faunal assemblages are briefly described which, in some cases, may represent associations, in others have clearly suffered lateral transport and/or faunal mixing.

Orbiculoidea latissima assemblage

(Pernaryggen Member, locality 16)

The *Orbiculoidea latissima* assemblage occurs immediately below the *A. praevenaris maimechaensis* association, which also contains a considerable number of *Orbiculoidea* (6%). In this assemblage, however, the inarticulate brachiopod represents 82.1% of the fauna. Apart from *Orbiculoidea* only the bivalves *Entolium* (4.4%), *Astarte* aff. *A. veneris* (3.4%) and *Isognomon* (3.6%) are of any significance, the remaining species being very rare.

The assemblage consists solely of suspension-feeders among which epifaunal forms strongly dominate. Due to the dominance of *Orbiculoidea*, evenness is low (1.47), whilst species richness is moderate (15). Only 6.5% of the bivalved organisms are still articulated and no individuals occur in life position apart from one *Orbiculoidea* which was found attached to *Serpula intestinalis*. Fragmentation reaches only 20%. *Orbiculoidea* occurs in nests and lenses and may form a shell layer 2–3 cm thick. However, the species also occurs dispersed throughout the sediment, a fine-sandy micaceous shale.

The sample consists of two subsamples, one taken 20 cm, the other 220 cm above the base of this rock unit. In between the fossil density is very low. The fact that both samples are nearly identical in terms of species composition and relative abundance, suggests that more or less identical environmental conditions prevailed during growth of the fauna. Possibly *Orbiculoidea* was an opportunistic species whose high productivity under favourable conditions resulted in the clear dominance of the benthic fauna by this species. On the other hand, the mode of occurrence of the brachiopod points to some lateral transport, and it cannot be excluded that the

Table 23. Taxonomic, ecological and biostratigraphic data on the various faunal assemblages occurring in the Krebsedal, Pernarygen and Astartedal Members

Assemblage	dominant faunal elements	%	evenness	species richness	articulated (%)	in life position (%)	bored (%)	en-crusted (%)	fragmentation (%)
<i>Discomiltha lirata</i> (131 specimens; 1 coll.)	<i>Grammatodon schourovskii</i>	52.7	2.36	9	56.6	24.0	0	0	<20
	<i>Discomiltha lirata</i>	39.5							
<i>Pleuromya uralensis</i> (78 specimens; 1 coll.)	<i>Pleuromya uralensis</i>	60.0	2.50	10	55.0	10.0	0	0	20
	<i>Buchia mosquensis</i>	14.3							
	<i>Entolium orbiculare</i>	12.9							
<i>Grammatodon keyserlingii</i> <i>Liostraea plastica</i> (300 specimens; 2 coll.)	<i>Grammatodon keyserlingii</i>	50.5	3.35	16	21.7	1.0	0	1.0	50–90
	<i>Entolium orbiculare</i>	14.0							
	<i>Isognomon volaticum</i>	9.2							
	<i>Liostraea plastica</i>	7.2							
<i>Orbiculoidea latissima</i> (615 specimens; 2 coll.)	<i>Orbiculoidea latissima</i>	82.1	1.46	15	6.6	0.2	0	0.2	20
<i>Buchia mosquensis</i> (281 specimens; 2 coll.)	<i>Buchia mosquensis</i>	96.2	1.12	5	1.9	0	0	0	95
<i>Plagiostoma incrassatum</i> (120 specimens; 1 coll.)	<i>Plagiostoma incrassatum</i>	32.5	1.12	19	3.3	0	5.8	0	75
	<i>Liostraea plastica</i>	17.5							
	<i>Oxytoma inequivalve</i>	9.2							
	<i>Buchia mosquensis</i>	9.2							
	<i>Entolium orbiculare</i>	6.7							
	<i>Isocyprina birkelundi</i>	6.7							
<i>Camptonectes praecinctus</i> (103 specimens; 4 coll.)	<i>Camptonectes praecinctus</i>	25.0	1.12	12	58.5	2.1	0	0	0
	<i>Entolium orbiculare</i>	16.7							
	<i>Serpula intestinalis</i>	16.7							
	<i>Isognomon volaticum</i>	16.7							
	<i>Pinna lanceolata</i>	6.2							
	<i>Pleuromya uralensis</i>	6.2							

shells are, due to their light weight and particular shape, well sorted relics of another community.

Buchia mosquensis assemblage
(Astartedal Member, localities 11 and 14)

Twice within the Astartedal Member on the eastern slope of Hartz Fjeld thin shell beds were found which consist nearly exclusively of *Buchia mosquensis* (96 and 92% respectively). Other benthic faunal elements are *Entolium*, *Discomiltha*, *Dentalium* and *Delphinula*. Ammonites are also common. Articulated specimens are extremely rare and fragmentation is around 95%. Transport by currents appears to be the main agent for shell accumulation. This is corroborated by the fact that at one locality, the shell bed occurs in highly micaceous fine-grained and concretionary sandstone which exhibits large-scale cross-bedding. At the other locality (11) the sediment consists of micaceous coarse sand with *Skolithos* and *Planolites*. The *B. mosquensis* assemblage thus clearly is the transported and sorted relic of a former community.

Plagiostoma incrassatum assemblage
(Pernaryggen Member, Pernaryggen)

The *Plagiostoma incrassatum* assemblage is moderately diverse and characterized by the limid bivalve *P. incrassatum* and the oyster *Liostrea plastica*. Nearly all faunal elements are disarticulated and none preserved in life position. *Plagiostoma* occurs largely within one layer and the shells appear to have undergone lateral transport (preferred orientation is convex up). A comparatively high percentage (16%) is bored by cirripeds and a phoronid represented by *Talpina ramosa*.

The sediment is a medium to coarse-grained glauconitic sandstone containing the trace fossils *Macaronichnus*, *Skolithos* and *Curvolithus*. Laterally these bioturbated sediments give way to large-scale trough cross-beds which indicate periodic high energy conditions.

The assemblage appears to be a transported and distorted relic of a former community.

Pleuromya uralensis assemblage
(Pernaryggen Member, ridge north of Krebsedal)

This unique assemblage is dominated by the deep burrowing *Pleuromya uralensis* (60%) which is of little significance in other associations. While 10% of the bivalves are preserved in life position, 55% are still articulated, no shells are bored or encrusted. The fragmentation rate is low (20%) and the sediment is a fine-grained glauconitic sandstone which has been heavily churned by the producers of *Chon-*

drites, *Thalassinoides* and *Planolites*. There can be no doubt that the assemblage is the autochthonous relic of a former benthic settlement. The fact that *P. uralensis* formed clusters may explain its high abundance: thus, the sample representing a particular dense cluster of *P. uralensis* may not adequately reflect the composition of hard-shelled taxa of the former community.

Grammatodon keyserlingii/Liostrea plastica assemblage

(Pernaryggen Member, localities 11 and 18)

This assemblage is represented by 293 specimens in two collections. Dominated by *G. keyserlingii* (50.5%) the fauna is further characterized by the relative abundance of *L. plastica* (7.2%). Semi-infaunal species prevail (60%), followed in abundance by epifauna (33.8%) and infauna (6.2%). All benthic organisms were suspension-feeders. About one-fifth of the fauna is still articulated, but only 1% occurs in life position (*Isognomon*, *Pleuromya*). The biostratigraphic data do not indicate a significant disturbance of the fauna which accumulated most likely *in situ*.

For two reasons, however, the fauna is not regarded as an association:

- 1) *Liostrea plastica* only colonized ammonites, usually on both sides, although plenty of other large substrates (such as *Isognomon*) were available. This, together with the thin shell of the oyster suggests that *Liostrea* may have lived commensally on the shells of live ammonites and thus did not belong to the benthos (see also Fürsich, 1982b, p. 62).
- 2) None of the other species of the trophic nucleus (*G. keyserlingii*, *Entolium*, *Isognomon*) are diagnostic as they occur in similar abundance in other associations as well.

It therefore appears safer to regard this fauna as an assemblage rather than an association. Close links exist undoubtedly with the *G. keyserlingii* association which, however, exhibits a much lower evenness and species richness.

The assemblage occurs in fine-grained micaceous sandstone which, in one case, is glauconitic.

Discomiltha lirata assemblage

(Krebsedal Member, locality 14)

The *D. lirata* assemblage, represented by 129 specimens occurs only at one level in micaceous, very fine-grained concretionary sandstone of the Krebsedal Member. The assemblage is dominated by the epibyssate *Grammatodon schourovskii* (52.7%) and the deep burrowing detritus-feeding *D. lirata* (39.5%). 56% of the fauna are still articulated and 24% in life position (*Pinna*, *Discomiltha*). No shells are bored or encrusted, and fragmentation is less than 20%. Evenness and species richness are moderately low. The sediment is highly bioturbated (*Macaronichnus*).

There is little doubt that the assemblage is undisturbed and thus the relic of a onetime benthic settlement. If we discount *Discomiltha*, the remaining fauna is typical of the *Grammatodon schourovskii* association which characterizes large parts of the Krebsedal Member. The occurrence of abundant *D. lirata* in life position may then be explained by an unusually successful settling of larvae of this species within this community which drastically altered the numerical abundance pattern. Within a time-averaged community such variation in faunal composition will be considerably tuned down. In the present case, however, relatively rapid burial of the community left us with only few generations of organisms representing but a very short glimpse of time.

Camptonectes praecinctus assemblage
(Pernaryggen Member, numerous localities)

In eight samples from the Pernaryggen Member, the faunal density was so low that no representative collections could be made (as a rule, only between 5 and 20 specimens were obtained).

Characteristic of these samples is the dominance of large, usually articulated shells (*C. praecinctus*, *Isognomon volaticum*) which in most other associations are relatively rare. As in some of these samples only calcitic shells are present (e.g. *Entolium*, *Camptonectes*, *Isognomon*, *Liostrea*), they might represent diagenetically distorted relics of former communities where small and particularly aragonitic shells have been selectively removed. In four of these samples, however, aragonitic shells (*Pleuromya*, *Goniomya*, *Thracia* and ammonites) are present, in two cases as moulds and in the two others even with shell. This contradicts widespread diagenetic shell dissolution. Data on these four samples are presented in table 23.

Thus, whilst in some samples diagenetic bias cannot be ruled out, others appear to represent a very patchy, low density colonization phase of the sea floor, either due to relatively high sedimentation rates or to unfavourable conditions.

Discussion

As details of the palaeosynecology of these associations will be discussed elsewhere, only a short summary of the environmental conclusions drawn from the faunas will be presented here.

The faunas of the Krebsedal, Pernaryggen and Astartedal Members represent communities that lived on the open shelf in fully marine, well oxygenated waters. The sea floor was below fair weather wave base and was only occasionally disturbed by deep-reaching storms. Although usually occurring in shell beds, most faunas are autochthonous. Sedimentation took place partly out of suspension (clay particles and smaller mica flakes), partly by bedload transport (silt and sand-sized particles and larger mica flakes). Sedimentation rates were generally very low as is

demonstrated by the thorough reworking of the sediments by organisms and by the presence of abundant authigenic glauconite grains. Even byssate and pedicle attached epifaunal species are commonly preserved in growth position stressing the low energy nature of the environment.

Only in the *Grammatodon schourovskii* association do deposit-feeding bivalves and scaphopods represent a significant part of the faunal spectrum. This does not imply that the sediments were generally poor in organic matter as in other associations deposit-feeders are represented by the ubiquitous trace fossil *Macaronichnus*. It is interesting, however, that epifaunal suspension-feeders were so widespread in these offshore lower shelf deposits, quite in contrast to the situation on present-day shelves. Apparently plenty of suspended organic matter must have been present to support the rich suspension-feeding communities.

Gastropods are only abundant in the *Isocyprina birkelundi*/*Pinna lanceolata* association. As most of them appear to have been herbivorous, it is reasonable to assume that the sea floor was, at that time, well vegetated and thus within the photic zone.

Biostratigraphic data show that only two associations, the *Isocyprina birkelundi*/*Pinna lanceolata* and the *Astarte praevenensis maimechaensis* associations have a synchronous distribution across most of the outcrop belt (Fürsich, 1984). Most other associations can be traced only for short distances laterally. This implies a mosaic distribution of the former communities across the sea floor.

Faunas from the Hennigryggen Member

The medium to coarse-grained sand and sandstone of the Hennigryggen Member (Middle Volgian) only rarely contain benthic faunas, apart from one particular horizon, the so-called *Lingula* bed. The scarcity of fossils may partly be due to diagenetic dissolution of shells, but surely also reflects the environment: large-scale cross-beds evidence rapid sedimentation and the scattered trace fossils (e.g. *Ophiomorpha*, *Diplocraterion*) also testify a relatively high energy environment. Similar environments at present are usually devoid of shelly macrobenthos. The fauna of the Hennigryggen Member, which occurs at several levels, consists predominantly of poorly preserved *Pleuromya* and *Entolium orbiculare*. More rarely, *Thracia*, *Pinna*, *Pholadomya*, *Eriphyla* and *Lingula* occur. They represent most likely relics of the *E. orbiculare*/*P. triangularis* association (see under Pernaryggen Member).

Lingula zeta assemblage

Within concretionary medium-grained and slightly glauconitic sandstone of the lower part of the Hennigryggen Member at Lingularyggen, a rich well preserved fauna occurs. This so-called *Lingula* bed is not a uniform shell bed, but consists of several levels at some of which shells are reworked, at others some faunal elements

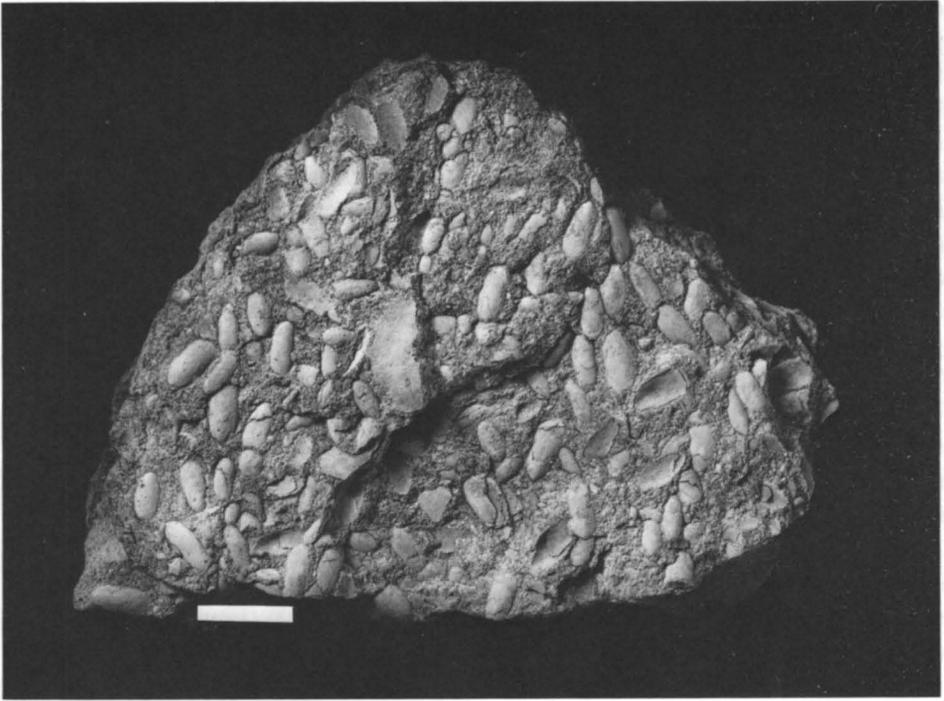


Fig. 29. Slab from the *Lingula* bed with numerous *Lingula zeta*. Lingulargygen. Scale: 2 cm.

(e.g. *Pinna*, *Modiolus*) are preserved in life position. As the hard sandstone did not allow quantitative sampling, no precise data are available on the composition of the fauna. Dominant faunal element is the inarticulate brachiopod *Lingula zeta* (fig. 29). Other common forms include *Eriphyla saemanni*, *Unicardium aceste*, *Modiolus elongatus*, *Pleuromya uniformis*, *Entolium orbiculare* and *Isocyprina birkelundi*. Lateral transport frequently caused sorting of shells so that relative abundance figures of samples would not reflect the original biological distribution pattern. Towards the north (Hartz Fjeld), the *Lingula* Bed thins rapidly from about 300 cm and disappears on the slopes of Hennigryggen.

The dominance of *Lingula* in the fauna agrees with sedimentological evidence (frequent scours, small-scale ripple bedding, parallel lamination) which places the *Lingula* bed above wave base, in a nearshore, but still fully marine environment.

COMPARISON WITH OTHER BOREAL UPPER JURASSIC ASSOCIATIONS

Comparisons with other parts of the Boreal Upper Jurassic are hampered by the lack of detailed palaeoecological studies. In most cases, faunal lists are the only basis for evaluating the occurrence of the Milne Land associations in other parts of Greenland, on Spitsbergen, or in northern Siberia.

North-East Greenland

The Upper Jurassic of North-East Greenland (e.g. Hochstetter Forland, Wollaston Forland, Kuhn Ø., Store Koldewey) consists of clastic sequences ranging in grain size from silty clays to conglomerates. Kimmeridgian and Volgian benthic faunas are sparse and dominated by *Buchia* (e.g. Surlyk, 1977). In contrast, Oxfordian sandstones frequently contain shell beds in which *Grammatodon keyserlingii*, *Camptonectes broenlundi*, *Tancredia* spp., *Arctica syssollae*, 'Perna' *groenlandica*, terebratulids, and *Ditrupa nodulosa* abound (e.g. Ravn, 1911; Frebold, 1933; Maync, 1947; Sykes & Surlyk, 1976). The faunas are very similar in composition to those of the Kosmocerasdal and Aldinger Elv Members. Scattered remarks about the dominant faunal elements of some of these shell beds in Frebold (1933) and Maync (1947) reveal the presence of assemblages dominated by either *Grammatodon keyserlingii* (1), *Arctica syssollae* and *Tancredia* (2), *Ditrupa nodulosa* (3), 'Perna' (= *Aguilerella?*) *groenlandica* (4) and terebratulids (5).

Assemblages 1–3 clearly correspond to associations found in beds of equivalent age on Milne Land, whilst assemblage 4 probably corresponds to the *Aguilerella aldingeri* assemblage on Milne Land. The occurrence of assemblages dominated by terebratulids is not known from the Milne Land Oxfordian. As on Milne Land, some of the faunas have apparently been transported and monotypic assemblages dominated, for example, by *Ditrupa* or 'Perna' *groenlandica* occur. The faunal composition between the two regions differs to some degree: *Tancredia jarneri* is not known from Milne Land; its niche is occupied by *Tancredia magna*. Similarly, the niche of the epibyssate 'Perna' *groenlandica* is filled, on Milne Land, by *Aguilerella aldingeri*. At some levels in the Upper Oxfordian of North-East Greenland, oysters are much more common than they are on Milne Land.

It is interesting that in North-East Greenland *Ditrupa* and *Grammatodon keyserlingii* are also common in beds of Late Bathonian and Callovian age, but are there accompanied by abundant *Meleagrinnella braamburiensis*. *G. keyserlingii* dominated associations existed therefore in the Boreal Jurassic from Late Bathonian to Mid-Volgian times, that is for at least 20 million years.

Spitsbergen

The Upper Jurassic faunas of Spitsbergen are impoverished when compared to those from Milne Land. The dominant facies, black micaceous shales, are characterized by species of *Buchia*. Horizons with abundant *Pholadomya* and *Camptonectes validus* in the Lower Kimmeridgian (Sokolov & Bodylevski, 1931) may be equivalents of the *Camptonectes* cf. *C. validus*/*Pleuromya uniformis* association of the Cardioceraskløft Member.

Northern Siberia

In northern Siberia, the boreal sea supported a rich benthic fauna during the Upper Jurassic. Zakharov (1966, 1970) and Zakharov & Shurygin (1979) discuss the life habits, ecological preferences and taphonomy of the bivalves and sum up the environmental distribution of the benthic fauna. Zakharov (1966) briefly outlines the dominant faunal assemblages which are characterized by oysters and large camptonectids of the subgenus *Boreionectes*. As on Milne Land, many faunal elements occur in life position allowing a fairly precise characterization of the life habits of particular species.

In Oxfordian strata which are represented by shallow water nearshore sandstones, *Camptonectes* (*Boreionectes*) *broenlundi* is the dominant faunal element. Other common forms include 'Cyprina' (= *Arctica?*), *Pleuromya*, *Isognomon*, *Modiolus*, *Tancredia*, and *Meleagrinnella*. *C. broenlundi*, 'Cyprina' and *Isognomon* occasionally form near-monospecific layers.

Shallow water nearshore sandstones and glauconitic sandstones of the Kimmeridgian are characterized by *C. broenlundi* and *Deltoideum delta*. Locally abundant are 'Cyprina', *Entolium*, *Pleuromya*, *Meleagrinnella*, *Inoceramus*, *Grammatodon*, *Tancredia*, *Buchia*, limids, and *Dentalium*. 'Cyprina' appears to have occupied shallower, more agitated waters than *C. broenlundi*.

In sandy to silty sediments of the Lower Volgian oysters and *Boreionectes* again prevail. In nearshore agitated waters *C. broenlundi* dominates, whilst quieter environments are characterized by *Liostrea praeanaabarensis* and *Camptonectes* (*B.*) *breviauris*. Together with them *Isognomon*, *Pleuromya*, *Homomya* and brachiopods occur. *Liostrea praeanaabarensis* and *Astarte* are typical of nearshore lagoonal/open sea transitional systems.

These faunas are closest to the *C. broenlundi* association of the Aldinger Elv Member. It is interesting to note the persistence in northern Siberia of a *Camptonectes broenlundi* dominated biofacies into the Lower Volgian, while it terminates at the end of the Upper Oxfordian on Milne Land. Quite clearly the replacement of the various large species of *Camptonectes* on Milne Land is largely an ecological and not an evolutionary feature.

It is possible that several other associations from Milne Land have close analogues or even occur in the Upper Jurassic of northern Siberia. However, the lack of quantitative data precludes further detailed statements.

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REFERENCES

- Aldinger, H. 1935: Geologische Beobachtungen im Oberen Jura des Scoresbysundes (Ostgrönland). *Meddr Grønland* **99**(1), 128 pp.
- Bay, E. 1895: Geologie. *Meddr Grønland* **19**(6), 145–177.
- Birkelund, T., Callomon, J. H. & Fürsich, F. T. 1978: The Jurassic of Milne Land, central East Greenland. *Rapp. Grønlands geol. Unders.* **90**, 99–106.
- Birkelund, T., Callomon, J. H. & Fürsich, F. T. 1984: The stratigraphy of the Upper Jurassic and Lower Cretaceous sediments of Milne Land, central East Greenland. *Bull. Grønlands geol. Unders.* **147**, 56 pp.
- Bromley, R. G. & Asgaard, U. 1972: Notes on Greenland trace fossils. II. The burrows and microcoprolites of *Glyphea rosenkrantzi*, a Lower Jurassic palinuran crustacean from Jameson Land, East Greenland. *Rapp. Grønlands geol. Unders.* **49**, 15–21.
- Callomon, J. H. 1961: The Jurassic system in East Greenland. In Raasch, G. O. (edit.) *Geology of the Arctic*. **1**, 258–268.
- Callomon, J. H. & Birkelund, T. 1980: The Jurassic transgression and the mid-late Jurassic succession in Milne Land, central East Greenland. *Geol. Mag.* **117**, 211–226.
- Callomon, J. H. & Birkelund, T. 1982: The ammonite zones of the Boreal Volgian (Upper Jurassic) in East Greenland. In Embry, A. F. & Balkwill, H. R. (edit.) *Arctic geology and geophysics. Canad. Soc. Petrol. Geol. Mem.* **8**, 349–369.
- Donovan, D. T. 1957: The Jurassic and Cretaceous systems in East Greenland. *Meddr Grønland* **155**(4), 214 pp.
- Frebald, H. 1933: Untersuchungen über die Verbreitung, Lagerungsverhältnisse und Fauna des Oberen Jura von Ostgrönland. *Meddr Grønland* **94**(1), 81 pp.
- Fürsich, F. T. 1974: Corallian (Upper Jurassic) trace fossils from England and Normandy. *Stuttgarter Beitr. Naturk., Ser. B* **13**, 52 pp.
- Fürsich, F. T. 1978: The influence of faunal condensation and mixing on the preservation of fossil benthic communities. *Lethaia* **11**, 243–250.
- Fürsich, F. T. 1982a: Rhythmic bedding and shell bed formation in the Upper Jurassic of East Greenland. In Einsele, G. & Seilacher, A. (edit.) *Cyclic and event stratification*, 208–222. Berlin: Springer.
- Fürsich, F. T. 1982b: Upper Jurassic bivalves from Milne Land, East Greenland. *Bull. Grønlands geol. Unders.* **144**, 126 pp.
- Fürsich, F. T. 1984: Distribution patterns of benthic associations in offshore shelf deposits (Upper Jurassic, central East Greenland). *Géobios. Mém. spec.* **8**, 75–84.
- Fürsich, F. T. & Heinberg, C. H. 1983: Sedimentology, biostratigraphy, and palaeoecology of an Upper Jurassic off-shore sand bar complex. *Bull. geol. Soc. Denmark* **32**, 67–95.
- Håkansson, E., Birkelund, T., Heinberg, C. & Willumsen, P. 1971: Preliminary results of mapping the Upper Jurassic and Lower Cretaceous sediments of Milne Land. *Rapp. Grønlands geol. Unders.* **37**, 32–41.

- Kauffman, E. G. 1981: Ecological reappraisal of the German Posidonienschiefer (Toarcian) and the stagnant basin model. In Gray, J., Boucot, A. J. & Berry, W. B. N. (edit.) *Communities of the Past*, 311–381. Stroudsburg, Pa.: Hutchinson, Ross Publ. Co.
- MacArthur, R. H. 1972: *Geographical Ecology*. 269 pp. New York: Harper & Row.
- Maync, W. 1947: Stratigraphie der Jurabildungen Ostgrönlands. *Meddr Grønland* 132(2), 223 pp.
- Parat, M. & Drach, P. 1933: Le Portlandien du Cap Leslie dans le Scoresby Sund (Groenland). *C. r. hebdomadaire des Séances Acad. Sci. Paris* 196, 1909–1911.
- Parat, M. & Drach, P. 1934: Rapport sur les observations d'histoire naturelle et de géographie physique. *Annls hydrograph.* 1934, 1–17.
- Piasecki, S. 1980: Hauterivian dinoflagellate cysts from Milne Land, East Greenland. *Bull. geol. Soc. Denmark* 28, 31–37.
- Ravn, J. P. J. 1911: On Jurassic and Cretaceous fossils from Northeast Greenland. *Meddr Grønland* 45, 433–500.
- Rosenkrantz, A. 1929: Preliminary account of the geology of the Scoresby Sound district. In Koch, L. The geology of East Greenland. *Meddr Grønland* 73(2), 135–154.
- Sokolov, D. & Bodylevsky, W. 1931: Jura- und Kreidefaunen von Spitzbergen. *Skr. Svalbard Ishavet* 35, 151 pp.
- Spath, L. F. 1935: The Upper Jurassic invertebrate faunas of Cape Leslie, Milne Land. I. Oxfordian and Lower Kimmeridgian. *Meddr Grønland* 99(2), 82 pp.
- Spath, L. F. 1936: The Upper Jurassic invertebrate faunas of Cape Leslie, Milne Land, II. Upper Kimmeridgian and Portlandian. *Meddr Grønland* 99(3), 180 pp.
- Surlyk, F. 1977: Stratigraphy, tectonics and palaeogeography of the Jurassic sediments of the areas north of Kong Oscars Fjord, East Greenland. *Bull. Grønlands geol. Unders.* 123, 56 pp.
- Sykes, R. M. & Brand, R. P. 1976: Fan-delta sedimentation: an example from the Late Jurassic – Early Cretaceous of Milne Land, central East Greenland. *Geol. Mijnb.* 55, 195–203.
- Sykes, R. M. & Surlyk, F. 1976: A revised ammonite zonation of the Boreal Oxfordian and its application in northeast Greenland. *Lethaia* 9, 421–436.
- Walker, K. R. 1972: Trophic analysis: a method for studying the function of ancient communities. *J. Paleont.* 46, 82–93.
- Zakharov, V. A. 1966: [Late Jurassic and early Cretaceous Bivalvia (Anisomyaria) in northern Siberia and the conditions of their existence.] *Akad. Nauk SSSR, Siber. Otd. Inst. Geol. Geofiz.*, 184 pp. Moscow. (In Russian)
- Zakharov, V. A. 1970: [Late Jurassic and early Cretaceous bivalves of northern Siberia and their ecology, Part 2, Fam. Astartidae.] *Trudy Inst. Geol. Geofiz. sib. Otd.* 113, 136 pp. (In Russian)
- Zakharov, V. A. & Shurygin, B. N. 1979: [The Jurassic Sea in the north of Middle Siberia.] In Saks, V. N. & Zakharov, V. A. (edit.) [Conditions of existence of Mesozoic marine boreal fauna.] *Trudy Inst. Geol. Geofiz. sib. Otd.* 411, 56–81. (In Russian)

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