FINN SURLYK

MORPHOLOGICAL ADAPTATIONS AND POPULATION STRUCTURES OF THE DANISH CHALK BRACHIOPODS
(MAASTRICHTIAN, UPPER CRETACEOUS)

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Synopsis

The study is based on a large number of 5 or 10 kg samples from all major Danish chalk localities. After washing, the samples yielded a material of about 50.000 brachiopods representing 37 articulate and 6 inarticulate species.

In order to give a comprehensive description of the brachiopod ecology an analysis has been made of spatial and stratigraphical variations, morphological adaptations, population structures, enemies, and inter- and intraspecific competition of the fauna. Special emphasis has been laid upon comparison between the different types of morphological adaptations and the corresponding population structures as well as comparison with closely related living species.

CONTENTS

Introduction

In recent years the trend in palaeoecological work has been focused especially on morphological adaptations of the animals to different environments and on fossil communities and evolution at the community level.

Somewhat unexpected, palaeoecological research has concentrated on the evaluation of fossil community successions and parallel communities (sensu THORSON, 1957) mainly in Palaeozoic rocks. Particularly worthy of mention are the studies of early Palaeozoic faunas in North America and Europe by ZIEGLER, 1965, ZIEGLER et. al. 1968, BRETSKY, 1970 a, 1970 b, FOX, 1968, and WALKER & LAPORTE, 1970.

The Upper Cretaceous (topmost Campanian–Maastrichtian) white chalk of Denmark contains a very rich macrofauna dominated by several hundred species of bryozoans associated with bivalves, brachiopods, echinoids, crinoids, ophiuroids, asteroids, belemnites etc.

In the present study the work is concentrated on the brachiopods which comprise 43 species representing 23 genera. In order to give a comprehensive description of the brachiopod ecology, an analysis has been made of spatial and stratigraphical variations, morphological adaptations, population structures, enemies, and inter- and intraspecific competition of the fauna. A special emphasis has been laid upon comparison between the different types of morphological adaptations and the corresponding population structures as well as comparison with closely related living species.

Acknowledgements

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The drawings which play an important role in the paper were prepared by H. Egelund.

Esther Ebjerg, Erna Nordmann, J. Aagaard, C. Heinberg, G. Jessen, and N. Svendsen all contributed with highly appreciated help in collecting, washing and sorting the numerous large bulk samples.

Special thanks are directed to Annelise Nørgaard Jensen who undertook the main part of the sorting and together with J. Fuglsang Nielsen assisted in taking the electron micrographs.

R. Bromley undertook the great task of improving the English language.

Method

The study is based on a large number of samples or series of samples from all major Danish white chalk localities (fig. 1). The weight of each sample in the more important sections is 5 or 10 kg, but in many cases additional 2.5 kg samples have been collected.

The samples are dried at about 30°, overheating being avoided since this hardens the chalk. The dry samples are weighed out to 5 or 10 kg and poured over with a supersaturated solution of glaubersalt ($Na_2SO_4 \cdot 10H_2O$) with a temperature of 40°. After cooling for some hours the superfluous glaubersalt solution is poured off and the sample deep-frozen. The sample is then reheated until the glaubersalt solution liquifies again (glaubersalt has a maximum solubility at about 40°). This proces is repeated 16–18 times, after which the sample is washed through a 0.25 mm sieve. The residue is then dried and hand-sieved into three fractions: 0.25–0.5 mm, 0.5–1.0 mm and > 1.0 mm. The brachiopods are picked only from the two upper fractions, the 0.25–0.5 mm fraction containing practically none. When the brachiopods have been picked out (under binocular microscope at ×6 or ×12 magnification) and determined to species, the number of individuals is estimated by adding whichever the greater number of dorsal or ventral valves to the number of whole shells, thus obtaining the minimal number of individuals. In addition, the number of fragments is counted in order to check if the estimated minimal number of individuals is representative. The term individual is used throughout in this sense to avoid confusion with the term specimen, which is used for any ventral or dorsal valve or whole shell.

A sample weight of 5 kg was found to be ideal. Samples of greater weight only rarely show additional species while the number of individuals seems to vary proportionally with the size of the sample.

Fig. 1. Localities. The signature shows the distribution of the Upper Cretaceous sediments on the Prequarter-
nary map of Denmark. The investigated chalk localities are marked with an asterisk. The positions of the most
important localities mentioned in the text are shown.

Material

About 150 samples from 47 localities (13 of which are situated at Møns Klint)
have been examined. These have yielded a total of about 50.000 brachiopod individuals
representing 37 articulate and 6 inarticulate species. The brachiopod collections of the
Mineralogical Museum of the University of Copenhagen have also been examined.

Stratigraphy

Brachiopods have shown themselves to be valuable for the detailed stratigraphical subdivision of the chalk of Rügen, East Germany (STEINICH, 1965) and Denmark (SURLYK, 1970 a, 1970 b). Thus it is possible to divide the Danish Maastrichtian into 10 zones on the basis of the brachiopods (fig. 2). Furthermore, it is possible to correlate precisely the most important Lower Maastrichtian sections in Denmark, north-west Germany and Rügen (SURLYK, 1970 b) by means of the brachiopods.

Besides the zonal stratigraphy, STEINICH (1965, fig. 296) showed that variations in the quantitative distributions of the brachiopods from bed to bed through the chalk sections on Rügen made it possible to correlate neighbouring localities. This is also possible in the Danish chalk, where the glacially folded and faulted chalk of the cliff of Møn can be correlated by means of quantitative brachiopod diagrams.

Sedimentology

The Danish white chalk is a soft, friable, almost pure carbonate sediment of biogenic origin. Although the chalk never has been the subject of a detailed sedimentological investigation, its petrographical composition is rather well known. BLACK (1953) showed, that the English Senonian chalk was composed of whole or broken coccoliths in the 5–$10 \, \mu$ fraction and of fragments of molluscs and foraminifera in the sand fraction. The coccoliths of the Danish chalk are well known (PERCH-NIELSEN, 1968, 1969) and constitute the major part of the sediment.

Münzberger (cit. NESTLER, 1965 p. 9) analyzed the quantitative composition of the chalk of Rügen (table 1). His results fit well with those on preliminary work on the Danish chalk.

TABLE 1.

Coccoliths	72.0	weigth %
Foraminifera	1.0	–
Bryozoans	1.8	–
Ostracods	0.1	–
Non-carbonate	1.2	–
Carbonate > 0.1 mm	5.3	–
Carbonate < 0.1 mm	18.0	–

(After Münzberger in Nestler, 1965)

HONJO (1969) classified the Danish chalk as a friable, semiconsolidated nanno-agorite.

The problem of the non-hardening of the chalk has attracted the attention of many authors (e.g. HANCOCK, 1963, TERMIER & TERMIER, 1963, HANCOCK & KENNEDY, 1967, HONJO, 1969), but only in recent years have acceptable explanations been put forward. The lack of hardening of the chalk seems to be due chiefly to the high diagenetic stability of the coccoliths, presumably on account of the persistence of the organic

Fig. 2. Stratigraphy. The stratigraphical distribution of the most important brachiopods and the corresponding 10 brachiopod zones shown. The correlation with the belemnite zones used in the European standard Maastrichtian zonation is according to SURLYK (1970b). It must be mentioned that in the *Belemnitella junior* Zone no specimen of the index fossil has been found as this species is extremely rare in Danmark. The stratigraphical positions of some of the sections illustrated in the quantitative diagrams on figs. 3, 14 and 15 are shown.

membranes surrounding the single coccolith plates (HONJO, 1969). Furthermore the shells of almost all the organism groups found in the chalk are composed of the most stable form of $CaCO_3$, low-Mg-calcite. The only major exceptions are the shells of the

gastropods, the cephalopods (except belemnite rostra) and some of the bivalves, which were originally composed of aragonite. The shells of the echinoderms are composed of high-Mg-calcite and are well preserved.

Impressions of ammonites are quite common whereas remains of aragonite-shelled bivalves and gastropods are rare except in a few hardgrounds. Therefore the rarity of the bivalves and the gastropods seems in part to be primary and not merely caused by solution of the aragonitic shells. However, borings in shells of brachiopods and bivalves which are attributable to muricid and naticid gastropods are not uncommon. (For details of the mineralogical composition of the shells of the fossils see CLARKE & WHEELER, 1922, CHAVE, 1954 a, 1954 b, SCHOPF & MANHEIM, 1967, RUCKER & CARVER, 1969, LOWENSTAM, 1954).

The non-carbonate content of the Danish chalk normally varies between 0.5 and 5% and consists of clay minerals, dessiminated FeS_2, rare well-rounded æolian quartz grains, and siliceous sponge spicules. The chalk of Zone 8 and 9 (fig. 2) has a higher non-carbonate content (6–12%).

Flint nodules are common in the most horizon of the chalk, especially in Zone 3–5 and 10 (fig. 3). Tabular flint layers occur more rarely. The flint nodules were formed diagenetically under a varying cover of sediment. There is certain evidence that some flint, at least, formed by processes of very early diagenesis (e. g. STEINICH, 1965 p. 205). On the other hand the silicification of fossils after they have been crushed by overburden of sediment, and the existence of oblique to nearly vertical tabular layers following joints shows that flint also formed through processes of late diagenesis (FAIRBRIDGE, 1967).

According to STÖRR, 1966 and ERNST, 1966 flint seems only to be formed in very pure carbonate sediment and that might explain why flint is missing in Zones 8 and 9 where the non-carbonate content is high.

More or less distinct marl layers are common at many horizons. Several 4–5 cm thick, distinct, grey marl layers occur in Zone 2. At the boundary between Zones 7 and 8 two prominent marl layers seem to be good marker horizons for the boundary between Lower and Upper Maastrichtian in Denmark and northern Germany (SURLYK, 1970 b). In Zones 8, 9 and 10 light grey, marly horizons c. 50 cm thick are common (one of the

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Fig. 3. Standardsuccession. As the stratigraphy for some parts of the succession is based on numerous small scattered localities and not on borings the correct thicknesses of all the zones are not known. The relative thicknesses of Zones 1–7 and Zone 10 are approximately correct, whereas the relative thicknesses of Zone 8–9 are rough estimates. The samples used in the construction of the three curves were not chosen at random, but it has been attempted to select samples typical for each zone. There is a pronounced parallelism between the washing residue curve ($\approx$ the bryozoa curve) and the curve illustrating the number of brachiopod individuals. The number of species curve follows roughly the two other curves except for the very rich horizons (Zones 4 and 10) where the number of species decreases. The overall trends of the three curves reveal two pronounced maxima of the benthonic fauna (Zones 4 and 10) and a minimum between them (Zones 7–9). HG = hardground. Incip. HG = incipient hardground. M = marl layer. P = platy flintlayer. Black spots indicate flintnodules.
The following samples have been used in the construction of the curves (from bottom to top): Hvide Klint 1, 3, 4. Hvidskud 28, 18, 7, 5, 2. Lille Taler. Rørdal 1, 4, 6. Lindholm 2. Nørre Flødal 1. Linds Kalkværk. Stevns Klint 7, 2, 1. The total thickness increases from c. 350 m to 700 m in the central part of the Danish basin.
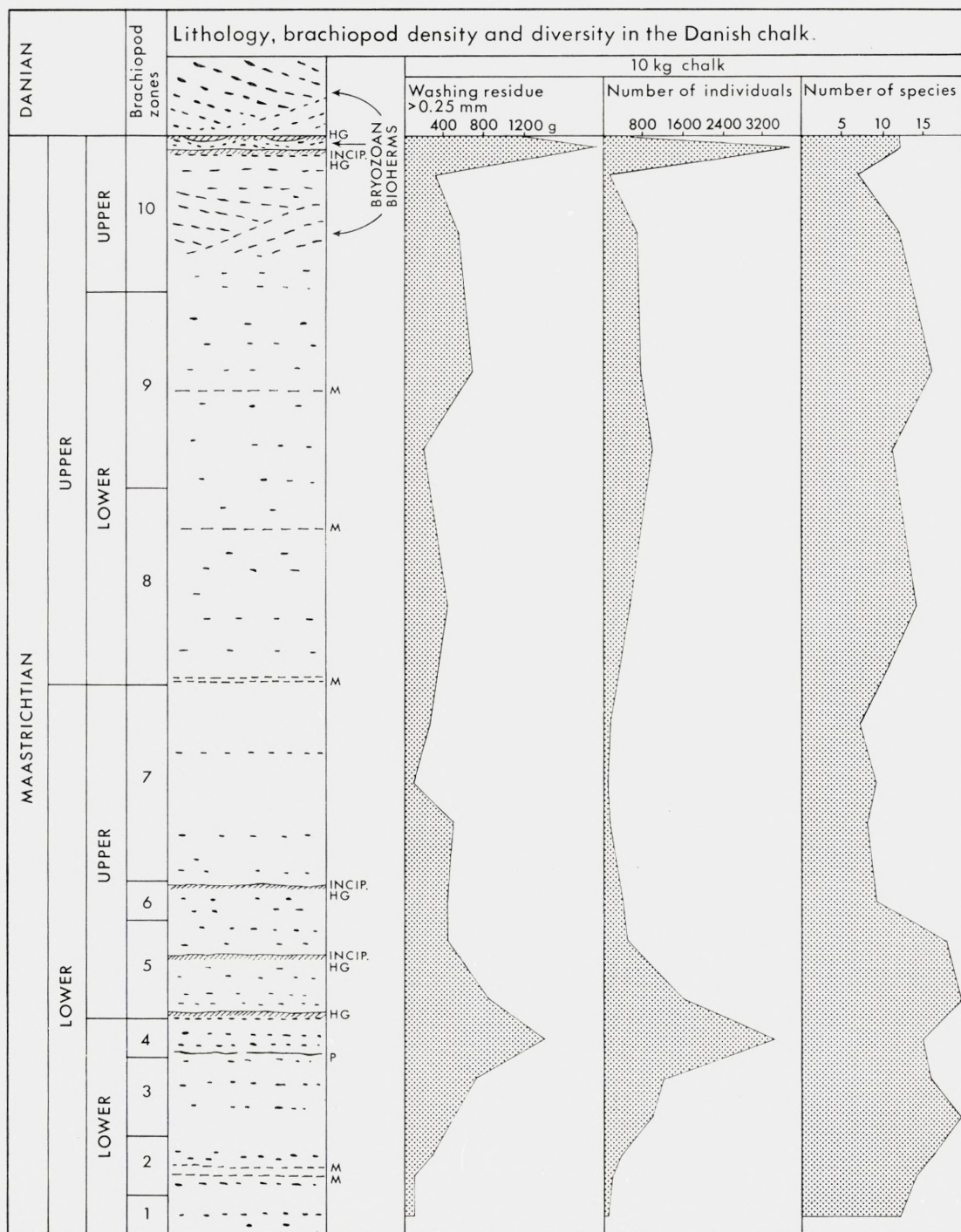
Fig. 3.

most important was named the Kjølbygård Marl by TROELSEN, 1955). At some localities
(Dania, Limhamn) the marl layers occur very regularly at a distance of a few metres in
a somewhat rhytmic manner.

Stratigraphical variations in the sediment

The Danish Maastrichtian is developed as a rather uniform sequence of white
chalk with scattered flint nodules arranged in horizontal layers. The regular horisontal
layering is however interrupted in Zone 10, where the bryozoans have developed small
bioherms (ROSENKRANTZ & RASMUSSEN, 1960) (fig. 3).

The bryozoan bioherms found at several localities in the uppermost part of the
chalk have recently been interpreted as the result of wave action, i. e. that they represent
a sort of mega ripples (RASMUSSEN, 1971). No arguments are however forwarded to
substantiate this hypothesis. The fossils (e.g. the bryozoans and the brachiopods) in the
bioherms are extremely well preserved and show absolutely no signs of transport.
Furthermore, the bioherms are asymmetrical, the southern flank of each bioherm
overlapping the northern flank of the neighbouring bioherm. At Karlstrup (fig. 15) the
Maastrichtian chalk bioherms are conformably overlain by Danian bioherms and the
same asymmetry and overlapping is found as at Stevns Klint. It is not possible to explain
these features as structures produced by wave action.

In addition to the bioherms, many smaller variations in the Maastrichtian sequence
occur (fig. 3). 2 m above the boundary between Zones 4 and 5 a thin hardground is
developed (fig. 14) (TROELSEN, 1937). It consists of a distinct discontinuity surface
beneath which nodules of rather hard, yellow chalk in a softer matrix of only weakly
hardened chalk extend downwards for some 10 cm. This nodular hardening is rather
common in the Danish chalk and might be considered an initial stage in hardground
development (BROMLEY, 1967, 1968). 3.5 m below the Maastrichtian Danian boundary
at Stevns Klint (fig. 3) there is a sharp junction between normal white chalk and grey
chalk with bryozoan bioherms. This discontinuity surface is developed as the initial
stage of formation of a hardground with nodular hardening (SURLYK, 1969).

The Maastrichtian-Danian boundary is at some localities very complex, especially
at Stevns Klint (ROSENKRANTZ, 1924, 1940, 1966), but normally the stop in sedimen-
tation is marked by small-scale erosion and nodular hardening of the top 20–30 cm of
the Maastrichtian.

Ecology

Stratigraphical variations in the benthonic fauna

The Danish Maastrichtian white chalk can be divided into three ecological units
based on the major variations in the richness of the benthonic fauna (fig. 3).

From Zones 1–4 there is a steady increase in the benthonic fauna illustrated by
the washing residue curve in fig. 3. The washing residue consists in the main of cyclo-
stome and cheilostome bryozoans with smaller amounts of bivalves, calcareous sponges,

brachiopods etc. The benthos reaches a clear maximum in Zone 4. A second very pronounced maximum is reached in Zone 10 in the bioherms, where bryozoans comprise almost 20% of the sediment. The chalk between the two maxima (Zones 7–9) is very poor in benthonic organisms.

The variations in the richness of the benthonic fauna are not only illustrated by the weight of the washing residue (approximately equal to the weight of the bryozoans), but are also seen in the number of brachiopod individuals per 10 kg of chalk (fig. 3). The two curves are almost parallel. This feature was previously observed in the Rügen chalk by STEINICH (1965).

The number-of-species curve is in part parallel to the two other curves but in the samples richest in benthos the number of species seems to decrease (this is most characteristic in Zone 4).

This phenomenon is found not only in the samples represented in fig. 3, but it seems to be a general principle that the number-of-species curve is roughly parallel to the number-of-individuals curve except in the samples very rich in benthonic organisms (fig. 14). These samples are dominated by a few species. The exclusion of some of the rare species is presumably due to interspecific competition.

Preservation

All fossils are extremely well preserved. The small fossils, as for instance the bryozoans, are especially well preserved with the most delicate structures and spines intact. Also the brachiopods are preserved with unbroken brachidia, and traces of wear are never found.

It is well known that in recent terebratuloid brachiopods the lophophore is supported by the brachidium and by mesodermal calcite spicules, which sometimes form a nearly coherent endoskeleton (SCHUMANN, 1970). Isolated spicules are described for a few fossil brachiopods (STEINICH, 1965, 1967 b, POPIEL-BARCZYK, 1968) but from the Rügen chalk STEINICH (1963 a, 1965) for the first time succeeded in finding complete spicular skeleton in fossil brachiopods. SURLYK (1970 a) described complete spicular skeletons in *Rugia tegulata* SURLYK, from the Danish chalk. Outside the north European chalk only one fossil brachiopod with complete spicular skeleton is known, viz. *Terebratulina wardenensis* from the Eocene London Clay (ROWELL & RUNDLE, 1967).

Steinich's discovery not only proved that fossil terebratuloids also were provided with spicules, but it permitted detailed description of the structure and form of the lophophore of these chalk brachiopods. Spicular skeletons from three Danish chalk brachiopods are shown on Pl. 1, 2.

In recent *Terebratulina* the spicules are often isolated, but in some species they form a continuous mesh in parts of the lophophore and mantle (SCHUMANN, 1970). When the animal dies the spicules of the mantle, body wall and median sides of the lateral arms of the lophophore disintegrate as the flesh decomposes. It is rare to find spicules at all in dead, dredged specimens of recent brachiopods (Dr. D. SCHUMANN, 1970, personal communication).

Transport

With very few exceptions, signs of current transport of the chalk fossils have not been found. Nevertheless, at two localities in the vicinity of Rørdal (fig. 1) a few specimens of parallel orientated *Baculites* and echinoid spines have been found, which might be referred to current action.

STEINICH (1967 a) showed that at a few horizons in the Rügen chalk very early diagenetic, submarine slides of soft chalk had occurred on the sea-bottom. In the Danish chalk traces of submarine slides can be found on the flanks of the bryozoan bioherms, where breccia-like structures occur.

As the chalk is highly bioturbated, practically all fossils have been shifted or rotated, but the movements seem to be only a matter of a few mm.

The very delicate, coherent spicular skeletons found in the chalk brachiopods described above (pl. 1, 2) indicate that no preburial transport of the brachiopods can have occurred and that the smaller brachiopods must have been buried in the sediment rapidly after or even before death.

The chalk sea bottom as substratum for brachiopods

The existence of brachiopods in a rock which must have accumulated as soft fine grained sediment on the sea bottom has often aroused interest among palaeontologists. Inspired by flume experiments of MENARD & BOUCOT (1951), ELLIOTT (1956) forwarded the hypothesis that these brachiopods might have been transported over rather long distances without being notably worn on the outside of the shell, and used as an example the occurrence of brachiopods in the English chalk.

AGER (1962, 1965) forwarded another hypothesis, namely that many of the small brachiopods found in the chalk could be epiplanktonic forms which lived attached to floating seaweeds of sargasso type.

Both hypotheses may explain isolated occurrences of brachiopods in fine grained sediments, but seem to be of rather limited value in explaining more regular occurrences. RUDWICK (1961), however, pointed out that many recent brachiopods are able to attach themselves to organic materials that will normally escape fossilization. As examples he mentioned ascidians, seaweeds, sponges and horny worm tubes.

The Danish chalk contains a very well preserved brachiopod fauna rich in species as well as individuals. The species composition is almost constant within each zone

Fig. 4. The chalk as substratum for brachiopods. The chalk yielded a number of substrates suitable for the brachiopods. The cocolithic mud in itself was a good substrate for burrowing brachiopods and for free living brachiopods of different shapes corresponding to different adaptive lines.

The numerous small hard objects (bryozoans, serpulids etc.) were excellent substrates for very small brachiopods or for brachiopods with a pedicle split into fine rootlets. Larger hard substrates (echinoids, belemnites etc.) were very rare on the chalk sea bottom and larger brachiopods with a normal functional pedicle are correspondingly extremely rare. Cementing brachiopods with small attachment surface are rather common, whereas forms with a large attachment surface are rare. RUDWICK (1961) mentioned a large variety of substrates which normally would not have been fossilized (e. g. algae, horny worm tubes, ascidians) and some of these have of course also played a role in the chalk sea. The fine grained nature of the chalk as well as the depth of the sea seems, however, to exclude sea-weeds as possible substrates.

THE CHALK AS SUBSTRATUM FOR BRACHIOPODS.

Ī. THE COCCOLITHIC MUD:

    1. Burrowing:

    2. Free living:

        ideal forms
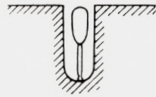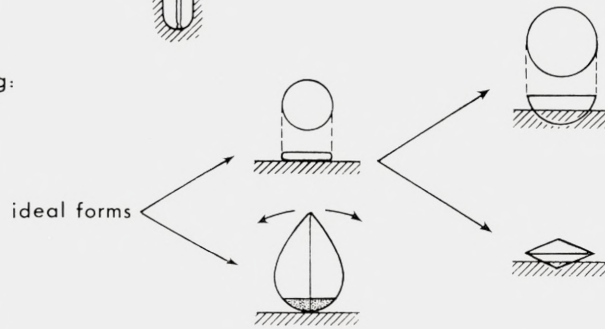
ĪI. HARD SUBSTRATES:

    1. Attached with a pedicle:

        a. to single small, hard substrates:

        b. to several small, hard substrates:

        c. to rare, large, hard substrates:
          ("secondary hardbottoms")

    2. Cemented to the substratum:
        a. with a minute attachment surface:

        ideal forms

        b. with extensive attachment surface:

        ← large "secondary hardbottom"

Fig. 4.

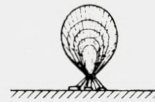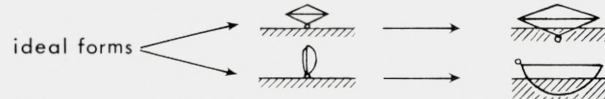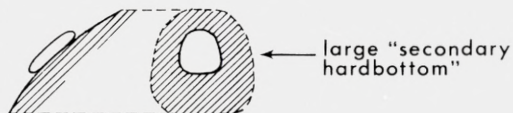(fig. 2) and each species has a characteristic size-frequency distribution whereever it is found in greater numbers. Further the whole fauna is very well adapted to the chalk substratum where practically all the major niches seem to be occupied. Thus the fauna includes burrowing, free-living, cementing and pedunculate brachiopods. Therefore it is not necessary to invoke the hypotheses of ELLIOTT (1956) and of AGER (1962, 1965) to explain the occurrence of brachiopods in the Danish chalk.

In the chalk several major groups of substrates can be distinguished (fig. 4):

1. *The fine grained chalk mud.*

This substrate would normally be expected to be unsuitable for brachiopods. Nevertheless the chalk contains 1 burrowing species and 9 free living species well adapted to a life directly in or on the coccolithic mud.

2. *Hard subjects.*

As shown on p. 8 the chalk besides the coccoliths normally contains about 5–10% small bryozoans, bivalves, serpulids and other hard subjects in the size of a few mm. Large hard subjects such as oysters, echinoids and belemnites are much rarer. Correspondingly the chalk contains a great variety of very small brachiopod species which were able to use the small substrates and only a few large pedunculate species which were restricted to the rare large hard subjects.

3. *Substrates which will escape fossilization.*

This group has of course been of some importance as substrates for the pedunculate brachiopods. In all horizons of the chalk there is a remarkable parallelism between the number of brachiopods and the rest of the benthonic fauna especially the bryozoans. The "soft" substrates have probably followed the numerical variations of the rest of the benthonic fauna, but have presumably always been of minor importance. In this connection it must be mentioned that sea-weeds are unknown from the Danish chalk. The sea-bottom was not ideal for their attachment and the sea was probably too deep in the main part of the Maastrichtian Stage. Finally all accounts from the brachiopod literature as well as inspection of collections of recent brachiopods seem to show that brachiopods absolutely prefer attachment to hard subjects - predominantly stones or the mineral shells of other marine invertebrates.

Ecological groups

Based on their mode of life the chalk brachiopods can be divided into 4 groups (fig. 5):

I.   Brachiopods attached to the substrate by means of a pedicle.
This group can be divided into 3 subgroups according to the nature and especially the size of the preferred substrate.
II.   Brachiopods living free on the substrate.

I) ATTACHED TO THE SUBSTRATE BY MEANS OF A PEDICLE: 24 species.

a) Minute forms able to use very small substrates: 20 species

Terebratulina faujasii (Roemer) - 4.6 mm

Terebratulina longicollis Steinich - 5.2 mm

Terebratulina subtilis Steinich - 2.5 mm

Rugia tenuicostata Steinich - approx. 3 mm

Rugia acutirostris Steinich - 2.5 mm

Rugia tegulata Surlyk - 2.5 mm

Rugia spinosa Surlyk - 1.3 mm

Gisilina gisii (Roemer) - 5.5 mm

Gisilina jasmundi Steinich - 4.5 mm

Dracius carnifex Steinich - approx. 4 mm

Aemula inusitata Steinich - 3.6 mm

Scumulus inopinatus Steinich - 2.5 mm

Argyrotheca bronnii (Roemer) - 5 mm

Argyrotheca coniuncta Steinich - 3.7 mm

Argyrotheca n. sp. aff. coniuncta - approx. 4 mm

Argyrotheca hirundo (Hagenow) - 4 mm

Argyrotheca obstinata Steinich - 4 mm

Argyrotheca stevensis (Nielsen) - 2.5 mm

Argyrotheca bronnii s.l. (late form) - 5 mm

Dalligas nobilis Steinich - approx. 5 mm

b) Medium to very large sized forms confined to large, hard substrates: 3 species.

Neoliothyrina obesa Sahni - 70 mm

Neoliothyrina fittoni (Hagenow) - 15 mm

Kingena pentangulata (Woodward) - 17 mm

c) Attached directly to the sediment: 1 species.

Terebratulina chrysalis (Schlottheim) - 22 mm

II) SECONDARILY FREE-LIVING FORMS, MEDIUM TO LARGE SIZED: 10 species.

Cretirhynchia limbata (Schlottheim) - 12 mm

Cretirhynchia retracta (Roemer) - 25 mm

Cretirhynchia sp. - approx. 30 mm

Carneithyris subcardinalis (Sahni) - 45 mm

Terebratulina gracilis (Schlottheim) - 13 mm

Trigonosemus pulchellus (Nilsson) - 20 mm

Gemmarcula humboldtii (Hagenow) - 20 mm

Magas chitoniformis (Schlottheim) - 11 mm

Meonia semiglobularis (Posselt) - 4 mm

Thecidea pappilata (Schlottheim) - 10 mm

III) BURROWING FORMS: 1 species.

Lingula cretacea Nilsson - 8 mm

IV) ATTACHED TO THE SUBSTRATE BY CEMENTATION: 8 species.

a) Attached to the very small substrates: 2 species.

Isocrania costata (Sowerby) - approx. 7 mm

Isocrania barbata (Hagenow) - approx. 7 mm

b) Confined to large, hard substrates: 6 species.

Ancistrocrania tubulosa (Nielsen) - 8 mm

Crania antiqua Defrance - 14 mm

Crania aff. craniolaris (Linnaeus) - 7 mm

Vermiculothecidea vermicularis (Schlottheim) - 12 mm

Thecidea recurvirostra Defrance - 7 mm

Bifolium wetherelli (Morris) - 4 mm

Fig. 5. All brachiopod species found in the Danish chalk distributed on ecological groups. The approx. maximum length of each species, and a sketch is given together with the species name.

III. Brachiopods burrowing in the substrate.

IV. Brachiopods attached to the substrate by cementation of the ventral valve.

This group can be divided into 2 subgroups according to the size of the substrate.

I. Brachiopods attached to the substrate by means of a pedicle.

I a. *Minute forms able to use very small, hard substrates.*

Small Cancellothyridid brachiopods.

The following species are only separated by minor differences in shell sculpture and shape of the brachidium. They never reach a length above 5.5 mm and are therefore treated under the same heading. The greatest length of each species in the Danish chalk is added after the name of the species.

> *Terebratulina faujasii* (ROEMER, 1841) – 4.6 mm.
> *Terebratulina longicollis* STEINICH, 1965 – 5.2 mm.
> *Terebratulina subtilis* STEINICH, 1965 – 3.5 mm.
> *Rugia tenuicostata* STEINICH, 1963 – appr. 3 mm.
> *Rugia acutirostris* STEINICH, 1965 – 2.5 mm.
> *Rugia tegulata* SURLYK, 1970 – 2.5 mm.
> *Rugia spinosa* SURLYK, 1970 – 1.3 mm.
> *Gisilina gisii* (ROEMER, 1841) – 5.5 mm.
> *Gisilina jasmundi* STEINICH, 1965 – 4.5 mm.

Terebratulina subtilis (fig. 6) and the species belonging to the genera *Rugia* and *Gisilina* only rarely dominate the brachiopod assemblages, but are nevertheless almost always found in some quantities.

Fig. 6. Growth stages of *Terebratulina subtilis* STEINICH (sample Hvidskud 9, Zone 4). a: 1.1 mm long, b: 1.7 mm long, c: 2.3 mm long, d: 3.1 mm long. All specimens drawn to scale.

Terebratulina faujasii (fig. 7) appears with a very varying frequency in the chalk. In the most samples it constitutes only a minor part of the brachiopod assemblage, but in the bryozoan rich horizons (Zones 4 and 10) it often occurs in enormous quantities (fig. 15 b, sample no. 3). In this species STEINICH (1965, p. 194) noted common a-symmetrical growth combined with displaced spicular skeletons. Asymmetrical lophophores are sometimes met with among recent living brachiopods (e.g. ELLIOTT, 1958), and SCHUMANN (personal communication, 1970) has photographed an asymmetrical

living brachiopod (*Platidia anomioides*) with displaced lophophore, which was caused by the attachement position close to the commisure of a *Spondylus*.

The distortion in the shell of *Terebratulina faujasii* is also common in the Danish specimens and similar distortions are found in several of the other species, e.g. *Terebratulina subtilis* and *Rugia tenuicostata*. The irregularities are due almost certainly to crowding on the very small available substrates—a theory substantiated by the fact that the distorted shells are in every case most common at the horizons very rich in benthonic life, where small brachiopods occur in thousands in each sample.
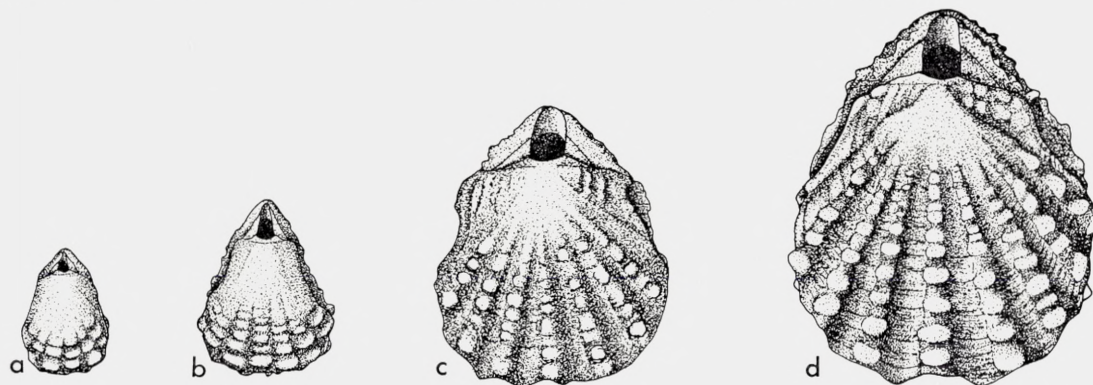
Fig. 7. Growth stages of *Terebratulina faujasii* (ROEMER) (sample Hvidskud 7, Zone 4). a: 1.0 mm long, b: 1.4 mm long, c: 2.2 mm long, d: 3.0 mm long. All the specimens are drawn to scale. Note the great similarity between the juveniles of this minute species and the juveniles of the larger *Terebratulina gracilis* (figs. 9 a, b).

Dracius carnifex STEINICH, 1967 – approx. 4 mm.

In external appearance this species is very close to the terebratelloid brachiopods *Platidia* and *Megerlia* although as demonstrated by STEINICH (1967 b) it in fact represents a very unusual terebratuloid form. Nevertheless, *Dracius carnifex* seems to be specialized to the same mode of life as these two terebratelloid genera. The very irregular shell and the large amphithyrid foramen show that like e.g. the recent *Platidia anomioides* (see ATKINS, 1959) it lived with the dorsal valve pressed firmly against the substrate.

Aemula inusitata STEINICH, 1968 – 4.6 mm.

The mode of life demonstrated by *Dracius carnifex* is even more obvious in *Aemula inusitata* (Pl. III e, f, h). This species is close to the recent species of *Platidia* and *Amphithyris* and it is very difficult to distinguish between *Aemula inusitata* and the recent *Platidia anomioides*. The major differences are found in the development of the brachidium and the lophophore. In complete spicular skeletons of *Aemula inusitata* it can be seen that the lophophore is of exactly the same type as in *Amphithyris*, viz. a schizolophe (THOMSON, 1927). The lophophore of the recent species belonging to *Platidia* has reached a more complex stage of development. Thus *Platidia anomioides* has an early plectolophe (ATKINS, 1959).

2*

According to ATKINS, living *Platidia* press their dorsal valve firmly against the substrate. Individuals of *P. anomioides* which settle on larger, more even substrates e.g. oysters, have a regular, symmetrical shell in contrary to the individuals that settle on small irregular substrates like e.g. bryozoans and corals. A similar difference in shape is found in specimens of *Aemula inusitata* from the chalk. This species is extremely variable in shape and there is a tendency for the most irregular forms to occur at horizons richest in benthos (Zones 4 and 10), whereas the regular forms dominate in the chalk of Zones 7 and 8, which is poor in small substrates (fig. 3).

Scumulus inopinatus STEINICH, 1968 – 3.5 mm.

Dalligas nobilis STEINICH, 1968 – 5 mm.

These two species are very small and show a remarkable frequency distribution. They are either represented by a few individuals or they dominate the assemblage completely (e.g. Hvidskud samples 7 and 18, fig. 14). Moreover, the two species, which are very much alike morphologically seem to substitute each other. Thus in sample 7 (fig. 14) 442 individuals of *S. inopinatus* were found, comprising 12.7% of the total number of brachiopod individuals, whereas *D. nobilis* was missing. On the other hand, in sample 18 (13 m below sample 7), *D. nobilis* was found in enormous quantities, 886 individuals comprising 73.2% of the total number of brachiopod individuals, whereas only 14 individuals (1.2%) of *S. inopinatus* were found.

D. nobilis is rather constant in shape in contrast to *S. inopinatus* which displays a considerable morphological variability. This great variability of *S. inopinatus* together with is amphithyrid foramen suggest a similar mode of life to that of the *Platidia* species i.e. with the dorsal valve pressed against the substrate.

Argyrotheca bronnii (ROEMER, 1841) – 5 mm.
Argyrotheca hirundo (HAGENOW, 1842) – 4 mm.
Argyrotheca obstinata STEINICH, 1965 – 4 mm.
Argyrotheca stevensis (NIELSEN, 1928) – 2.5 mm.
Argyrotheca coniuncta STEINICH, 1965 – 3.7 mm.
Argyrotheca n. sp. aff. *coniuncta* – approx. 4 mm.
Argyrotheca bronnii s.l. – late form – 5 mm.

The 7 species of *Argyrotheca* found in the chalk are only separated by minor differences in number and shape of the ribs, profile of the median septum, general outline etc. However, they have the same size and general morphology and are considered to have had approximately the same mode of life.

The recent species of *Argyrotheca* are closely related to the chalk species. As they have a short pedicle and sit almost perpendicular to the substrate (Pl. III, a, g) their beaks suffer attrition (ATKINS, 1960). Attrite beaks are common also in the chalk species. The lophophore and the feeding mechanisms of the recent megathirids (to which *Argyrotheca* belongs) are described in detail by ATKINS (1960) and because of the

great morphological similarity between the fossil and recent *Argyrotheca* there can be little doubt that the two groups lived in the same way.

Substrates used by recent *Argyrotheca* include the ahermatypic corals *Lophelia* and *Dendrophyllia*, solitary coral thecae and crustaceans (ATKINS, 1960), algae (RUD-WICK, 1962), other brachiopods (DAVIDSON, 1880), bryozoans, worm tubes and shell gravel. Recent species of *Argyrotheca* are shallow water forms normally not found below 200 m depth (U. ASGAARD, 1971, personal communication).

I b. *Medium to large sized brachiopods confined to large, hard substrates.*
Neoliothyrina obesa SAHNI, 1925 – approx. 7 cm.

This species is by far the largest brachiopod in the chalk. The shell is thin and the pedicle opening is labiate and about 3 mm wide, suitable for a normal, functional pedicle. The surroundings of the pedicle opening are often strongly worn showing that the pedicle was short and the shell thus pressed closely against the substrate.

Neoliothyrina fittoni (HAGENOW, 1842) – 1.5 cm.
Kingena pentangulata (WOODWARD, 1833) – 1.7 cm.

These two species are medium sized and are provided with a pedicle opening of "normal" size allowing the passage of a functional pedicle.

All three species belonging to this group are very rare, those of *Neoliothyrina* being the rarest in the Danish chalk. This rarity can no doubt be correlated with the rarity of suitable large hard substrates e.g. echinoids, oysters, belemnites etc.

I c. *Medium sized brachiopods attached directly to the sediment.*

The only species which almost certainly has lived attached directly to the sediment by a root-like, divided pedicle is *Terebratulina chrysalis* (SCHLOTTHEIM, 1813) – 2.2 cm. This mode of life is well known from its close recent relatives *Terebratulina retusa* (*L.*) and *Terebratulina septentrionalis* COUTHOUY (Pl. IV, a, d, e, and EKMAN, 1896, SCHUMANN, 1969). In these brachiopods the pedicle is able to etch slender holes or furrows in foraminifera, small fragments of shells, bryozoans etc. This feature of the pedicle of articulate brachiopods has possibly developed independently in different groups (SCHUMANN, 1969), and AGER (1965) proposed this attachment type for Cretaceous terebratulinids. Nevertheless, AGER (1965 p. 160) mentioned a specimen of *Terebratulina* cf. *chrysalis* from Czekoslovakia which had a "snowshoe-like" frill comparable to the frill by some Atrypids (COPPER, 1967) indicating a completely different mode of life. As the shell of adult specimens of *T. chrysalis* is very thin, the species is often found with the anterior part of the shell compressed as a result of compaction under the burden of overlying sediment and in that way a "frill" could be developed diagenetic-ally. Pl. IV b shows a slightly compressed specimen with a thickness of hardly 1 mm where its normal thickness before compression is approximately 3 mm. Thus there
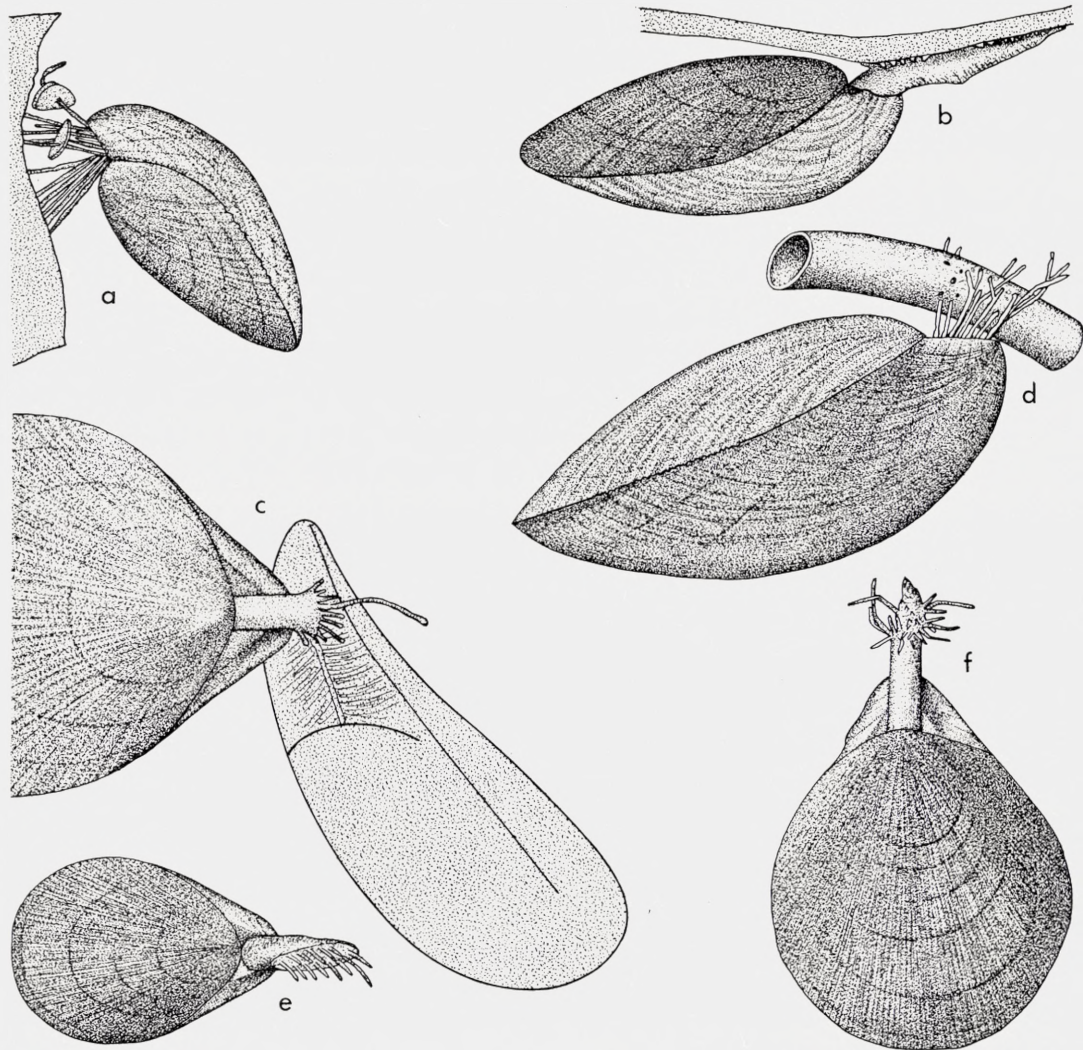
Fig. 8. Variation in the pedicle of recent *Terebratulina retusa* (L.). The specimens are drawn to scale. The length of the largest specimen (d) is 13 mm.

seems to be no evidence of a snowshoe-like frill to suggest a free living mode of life for this species in the Danish chalk.

Two different lines of evidence suggest the mode of life of *T. chrysalis:* Studies of its occurrence in the sediments and comparison with living relatives.

Terebratulina chrysalis is the only Danish chalk brachiopod which was found in all samples from all localities and it is almost the only species which occurs also in marginal facies e. g. the near-shore carbonate sediments in Scania (Sweden). Moreover, the species is a member of a morphologically very stable group which started in Ceno-

manian and continued through the Tertiary to recent times (*T. retusa* and *T. septentrio-nalis* are the recent representatives). This indicates that the group is very tolerant and only little specialized compared to the other chalk brachiopods. In detrital carbonate siltstones of Danian (Lower Paleocene) age *T. chrysalis* is found in beds where there are practically no larger fossils as potential substrates. It is also rather common in parts of the Danish chalk which consists almost solely of coccoliths and small foramini-fera (Zone 7) and with extremely few larger fossils. These observations indicates that *Terebratulina chrysalis* was able to attach itself to almost all kinds of available substrates.

Comparison with the recent *Terebratulina retusa* (fig. 8 and pl. IV a-e) shows that the two species are very close relatives differing only in minor details of the rib pattern, *T. chrysalis* having coarser and more sculptured ribs. (On pl. IV the ribs of *T. retusa* appear deceptively smooth, because the specimens are overgrown with a thin sponge layer. Thus the difference in morphology is even smaller than indicated by the figure). Apart from the rare *Neoliothyrina obesa*, *N. fittoni* and *Kingena pentangulata*, *Terebratu-lina chrysalis* is the only larger chalk brachiopod with a normal pedicle opening, which surrounded a functional pedicle. As shown above, the three first mentioned species are extremely rare in the chalk in sharp contrast to *T. chrysalis*. Their pedicles were probably not split up into fine rootlets and they were thus restricted to large substrates, while *T. chrysalis*, on the contrary was able to settle down almost everywhere on the soft Cretaceous sea bottom independant of such restrictions.

Terebratulina chrysalis is not only found in all samples, but is by far the most com-mon brachiopod in the Danish chalk. The sea bottom, sometimes a pure coccolithic mud, at other times rich in a great variety of small shells (bryozoans, foraminifera, serpulids, brachiopods etc.), seems to have been an excellent biotope for *T. chrysalis* due to its low degree of specialization and correspondingly high adaptibility.

The great variability of the pedicle of the recent *T. retusa* is shown in fig. 8. There seems to be a tendency for the pedicle to split up more finely in response to finer sub-strates. The manner in which it may be split varies more than normally accepted.

The pedicles of the small Cancellothyridid brachiopods (group I a) were probably also split into fine rootlets, as in recent *Terebratulina*, but this is more difficult to prove than for *T. chrysalis*.

II. Free living brachiopods.

The second group comprises species which, as adults, lie unattached on the sea bottom. All the species belonging to this group, except *Thecidea pappilata*, were attached to the substrate in the young stages by means of a pedicle. At the early ontogenetic stages the brachiopods had the same general shape as the terebratulinid brachiopods of group I a, i.e. longer than wide and biconvex, with normal pedicle openings. But during ontogenetic growth (figs. 9, 10) the pedicle openings were closed by secondary shell or at least narrowed to a "pin hole foramen". Furthermore, in 6 (7) of the species there was a very characteristic tendency towards a hemispherical shape in late ontogenetic stages (fig. 11). This shape is not very common among Mesozoic brachiopods and is

here developed in a group of species which are not closely related. The hemispherical shape would seem to be ideal for a free-living brachiopod (fig. 4) and it is remarkable that this shape is not found among the brachiopods provided with a functional pedicle (group I and III).

Cretirhynchia limbata (SCHLOTTHEIM, 1813) – 12 mm.

Cretirhynchia retracta (ROEMER, 1841) – 25 mm.

Cretirhynchia sp. – 30 mm (figured as *Rhynchonella limbata* by NIELSEN, 1909 pl. 1, figs. 24, 25).

STEINICH (1963 c) showed that the pedicle opening of *Cretirhynchia retracta* was closed from the inside by a hollow, conical plug. In addition, the pedicle openings of all three species are closed by secondary shell.

Cretirhynchia sp. seems to be especially well adapted to the free living mode of life as the lateral parts of the shell are considerably expanded.

Carneithyris subcardinalis (SAHNI, 1925) – approx. 45 mm.

The pedicle opening of this species is closed during ontogeny by secondary shell. It is the only common large brachiopod in the chalk and morphologically it seems to fit well with one of the ideal shapes of a free living brachiopod i. e. a self-righting "tumbler" (Fig. 4). It is strongly biconvex to almost spherical and thin-shelled except for the posterior part of the shell where the cardinalia are thickened by secondary shell, especially in adult specimens. The thickening is not sufficient to keep the shell in a permanent position on the sea bottom. However, the posterior position of the centre of gravity ensures that the commisure is always kept free of the sediment surface. This inferred mode of life explains the abundance of the species at all horizons of the chalk in spite of its large size, and irrespective of the presence of larger substrates.

Terebratulina gracilis SCHLOTTHEIM, 1813 – 13 mm.

The juveniles of *T. gracilis* are very difficult to distinguish from juveniles of the small *Terebratulina* species of group I (figs. 6, 7, 9) but at a length of a few mm the shells begin to approach the final hemispherical shape. The pedicle opening is not closed, but very narrow, and this combined with the incurved umbo (figs. 9, 11) would seem to reduce the likelihood of attachment by a pedicle. Stratigraphically slightly older forms of the *Terebratulina gracilis* group (e.g. forms found in the lowermost Maastrichtian and Upper Campanian of England) have a more biconvex shape and the evolution towards a perfectly hemispherical shape does not appear to have been completed until early Maastrichtian time.

Trigonosemus pulchellus (NILSSON, 1827) – 20 mm.

Gemmarcula humboldtii (HAGENOW, 1842) – 20 mm.

The pedicle opening in adults of *T. pulchellus* (figs. 10, 11) and *G. humboldtii* were closed with secondary shell. The shape is not completely hemispherical in *G. hum-*
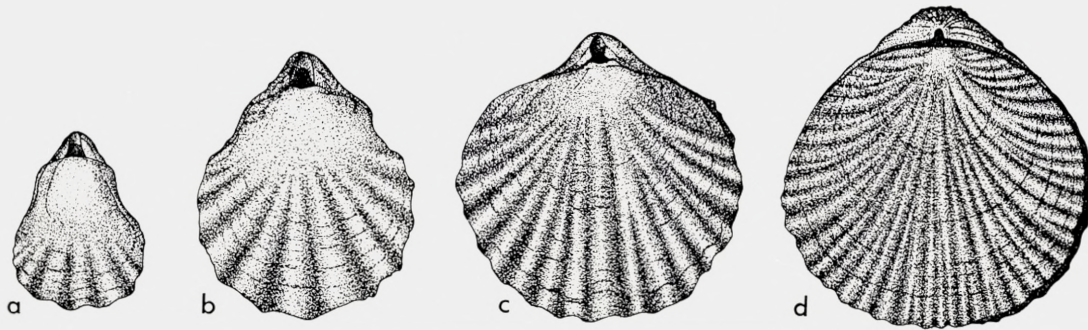
Fig. 9. Growth stages of *Terebratulina gracilis* (SCHLOTTHEIM) (sample Rordal 4, Zone 7). a: 1.4 mm long, b: 2.1 mm long, c: 4.8 mm long, d: 10.7 mm long. The specimens are not drawn to scale.
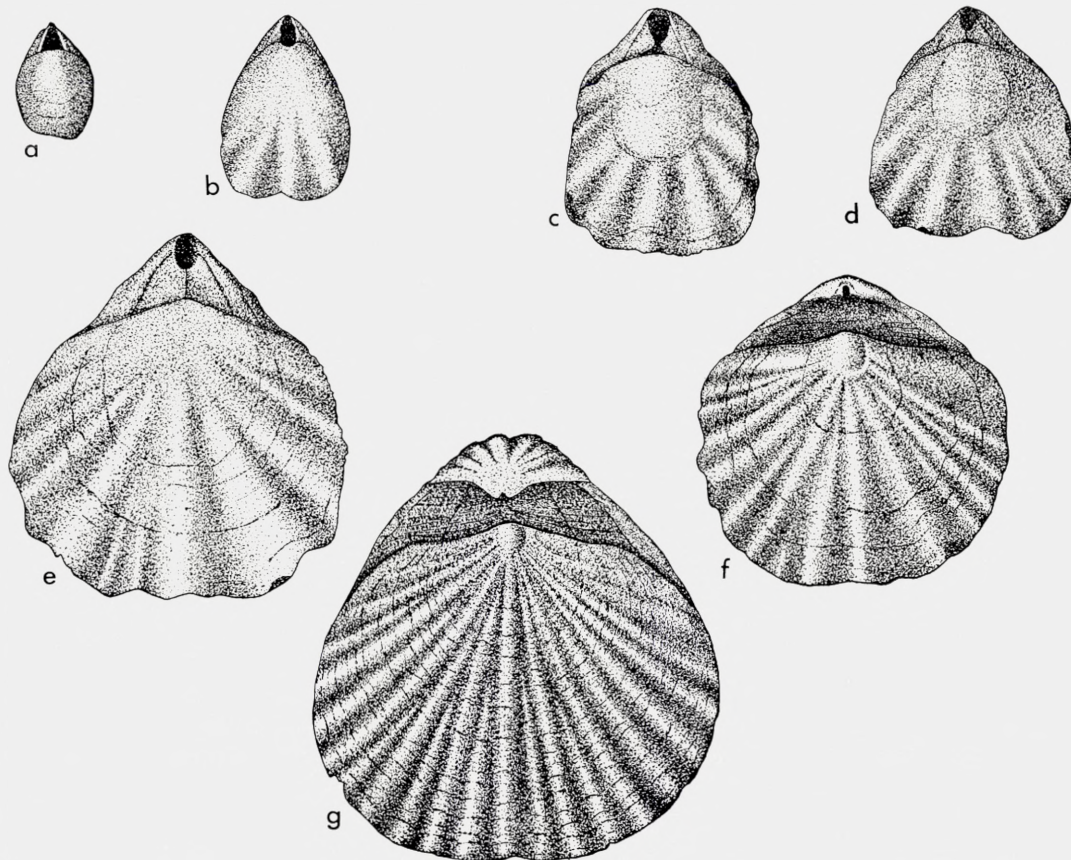
Fig. 10. Growth stages of *Trigonosemus pulchellus* (NILSSON) (sample Hvidskud 5, Zone 5). a: 0.9 mm long, b: 1.5 mm long, c: 2.0 mm long, d: 1.9 mm long, e: 2.9 mm long, f: 5.1 mm long, g: 14.2 mm long. Except f and g, all the specimens are drawn to scale.
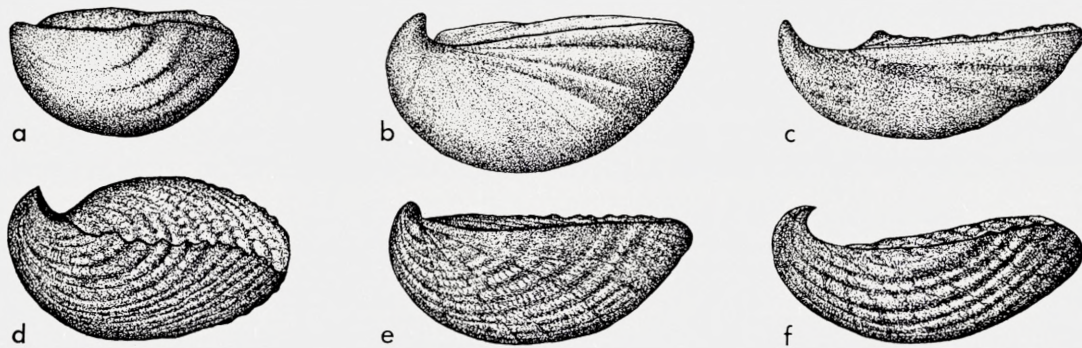
Fig. 11. Hemispherical free living brachiopods belonging to group II. a: *Meonia semiglobularis* (POSSELT), b: *Magas chitoniformis* (SLOTTHEIM), c: *Thecidea pappilata* (SCHLOTTHEIM), d: *Gemmarcula humboldtii* (HAGENOW), e: *Terebratulina gracilis* (SCHLOTTHEIM), f: *Trigonosemus pulchellus* (NILSSON). The specimens are not drawn to scale.

boldtii, the dorsal valve being flat-convex, but the shape of this species varies considerably. *T. pulchellus* is almost perfectly hemispherical and like *Terebratulina gracilis* its Campanian predecessors have a more biconvex shape (e.g. *Trigonosemus elegans* KOENIG).

Magas chitoniformis (SCHLOTTHEIM, 1813) – 11 mm.

M. chitoniformis is reminiscent of *Terebratulina gracilis* in several ways. Juveniles are extremely difficult to distinguish from small individuals of some of the brachiopods belonging to group I a, viz. *Dalligas nobilis* and *Scumulus inopinatus* and the adults are almost perfectly hemispherical (fig. 11). Furthermore, the pedicle opening is not closed but is narrow and more or less hidden by the umbo which is often strongly incurved (fig. 11).

At horizons where conditions for the small brachiopods (group I) deteriorated, *Magas chitoniformis* and *Terebratulina gracilis* become increasingly dominant (fig. 15 a) and together with *Terebratulina chrysalis* they are in many cases the only species found. This is especially characteristic in the upper part of the section at Hemmoor (north Germany) where the diverse brachiopod fauna gradually disappears upwards corresponding to coarsening of the sediment (F. SCHMID, 1969, written communication) to leave a limited, but individualrich, fauna dominated by *M. chitoniformis* and *T. gracilis*.

Meonia semiglobularis (POSSELT, 1894) – 4 mm.

M. semiglobularis is smaller than the rest of the brachiopods in the group, but nevertheless attains a perfectly hemispherical shape (fig. 11). The pedicle opening is not closed, but extremely narrow and often covered by the incurved umbo. The species is thick-shelled, perhaps for reasons of stability.

Thecidea pappilata (SCHLOTTHEIM, 1813) – 10 mm.

T. pappilata occupies an intermediate position between groups II and IV, since in the young stages it is cemented to the substrate. However, the attachment area is very

small and impression of small bryozoans are found in only a few cases. Nevertheless, the very small substrates and its hemispherical shape (fig. 11) indicate that the species lived free on the bottom.

III. Burrowing brachiopods.

The third group includes only one species, *Lingula cretacea* LUNDGREN, 1885. The species is small (8 mm in max. length) and very thin-shelled but not uncommon. However, owing to the fragility of its shell, it is found only rarely in the washed samples. There is no direct evidence for the burrowing mode of life in this case, but this seems to have been a characteristic activity of the family since early Palaeozoic time (CRAIG, 1952).

In the palaeoecological literature, lingulids are normally described as near-shore animals capable of surviving occasional brackish conditions, but according to JONES & BARNARD (1963) the recent lingulid brachiopod *Glottidia albida* reaches its peak of abundance at about 34 m depth in a sediment of compact fine sand mixed with coarse silt.

IV. Brachiopods attached by cementation.

This group comprises brachiopods that live attached to the substrate by cementation of the ventral valve. The group can be divided into 2 subgroups based on the size of the substrate.

IV a. Two species, *Isocrania costata* (SOWERBY, 1823) – 7 mm and *Isocrania barbata* (HAGENOW, 1842) – 8 mm have very small attachment surfaces. In *Isocrania costata* this surface is almost invisible and the species in fact occupies a position intermediate between the cemented and the free living forms. Its shape is very close to one of the ideal forms of a free living brachiopod, i. e., discoid (fig. 4). The species is rather common at all horizons, especially where the sediment contains only a few larger substrates e. g. in the Rørdal section (fig. 15 a). Thus the larva seems to have settled on bryozoans and other small objects and as the brachiopod grew, its discoid shape allowed it to become totally independant of this substrate, and to live free on the sea bottom.

Isocrania barbata has a larger attachment surface and is very rare.

IVb. *Crania antiqua* DEFRANCE, 1818 – 14 mm.
     Crania aff. *craniolaris* (L., 1758) – 7 mm.
     Crania tubulosa NIELSEN, 1909 – 8 mm.
     Thecidea recurvirostra DEFRANCE, 1828 – 7 mm.
     Vermiculothecidea vermicularis (SCHLOTTHEIM, 1913) – 12 mm.
     Bifolium wetherelli (MORRIS, 1851) – 4 mm.

The 6 species belonging to this subgroup are rare and are normally not found in the washing residues, as they are cemented to large, hard substrates, especially irregular echinoids. The size of the attachment surface of *Thecidea recurvirostra*, however, seems
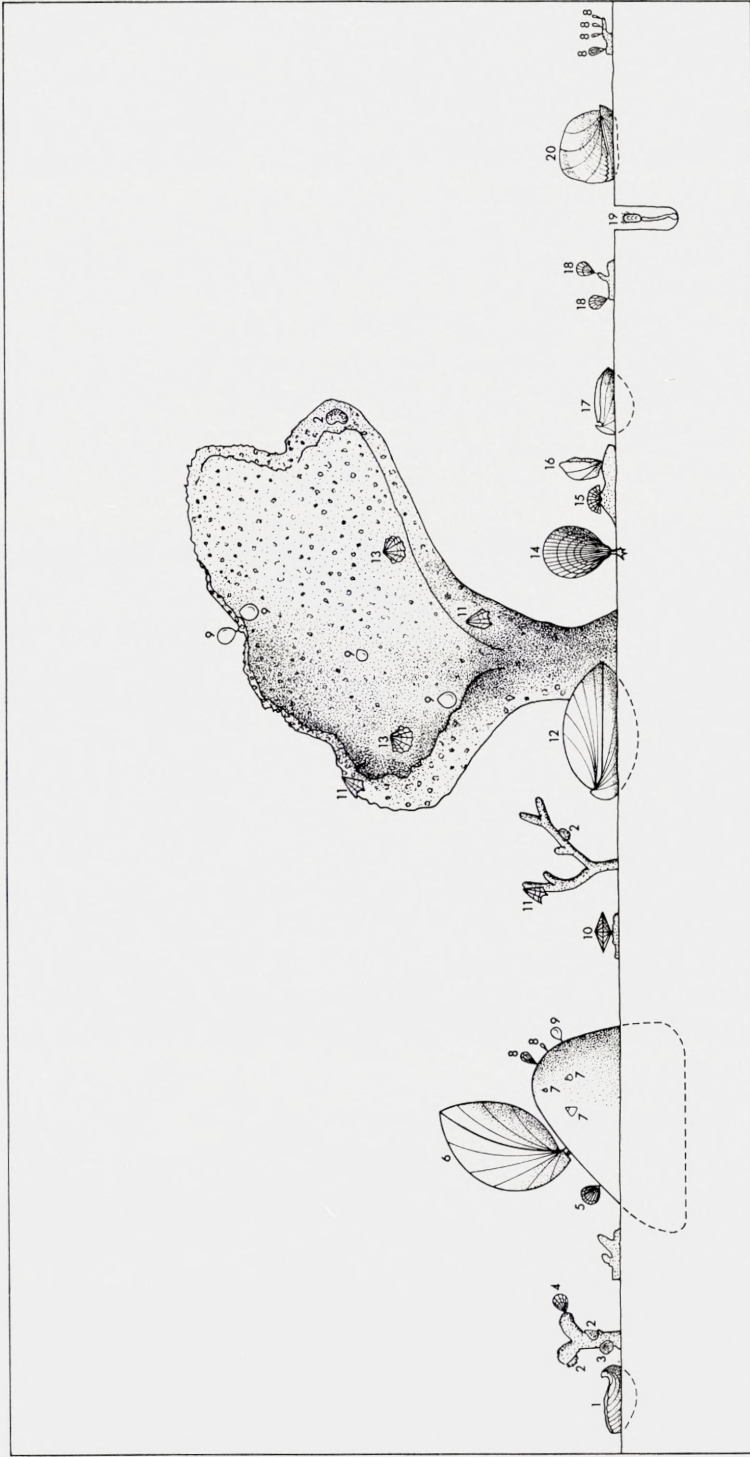
Fig. 12. Lower Maastrichtian brachiopod assemblage.—It has not been attempted to reconstruct the ancient sea bottom, but only to show the morphological adaptations to the different substrates of the brachiopods found in this part of the succession.—The sketches of the substrates here and in fig. 13 are based on actual specimens found in the chalk. 1: *Trigonosemus pulchellus* (NILSSON), 2: *Aemula inusitata* STEINICH, 3: *Dracius carnifex* STEINICH, 4: *Terebratulina faujasii* (ROEMER), 5: *Gisilina gisii* (ROEMER), 6: *Neoliothyrina obesa* SAHNI, 7: *Bifolium wetherelli* (MORRIS), 8: *Terebratulina longicollis* STEINICH, 9: *Scamulus inopinatus* STEINICH, 10: *Isocrania costata* (SOWERBY), 11: *Argyrotheca hirundo* (HAGENOW), 12: *Carneithyris subcardinalis* (SAHNI), (shown in one of many possible positions), 13: *Argyrotheca bronnii* (ROEMER), 14: *Tererbratulina chrysalis* (SCHLOTTHEIM), 15: *Argyrotheca coniuncta* STEINICH, 16: *Vermiculothecidea vermicularis* (SCHLOTTHEIM), 17: *Magas chitoniformis* (SCHLOTTHEIM), 18: *Rugia tenuicostata* STEINICH, 19: *Lingula cretacea* NILSSON, 20: *Cretirhynchia retracta* (ROEMER).—The substrates comprise bryozoans, an irregular echinoid (*Echinocorys*) and a siliceous sponge.
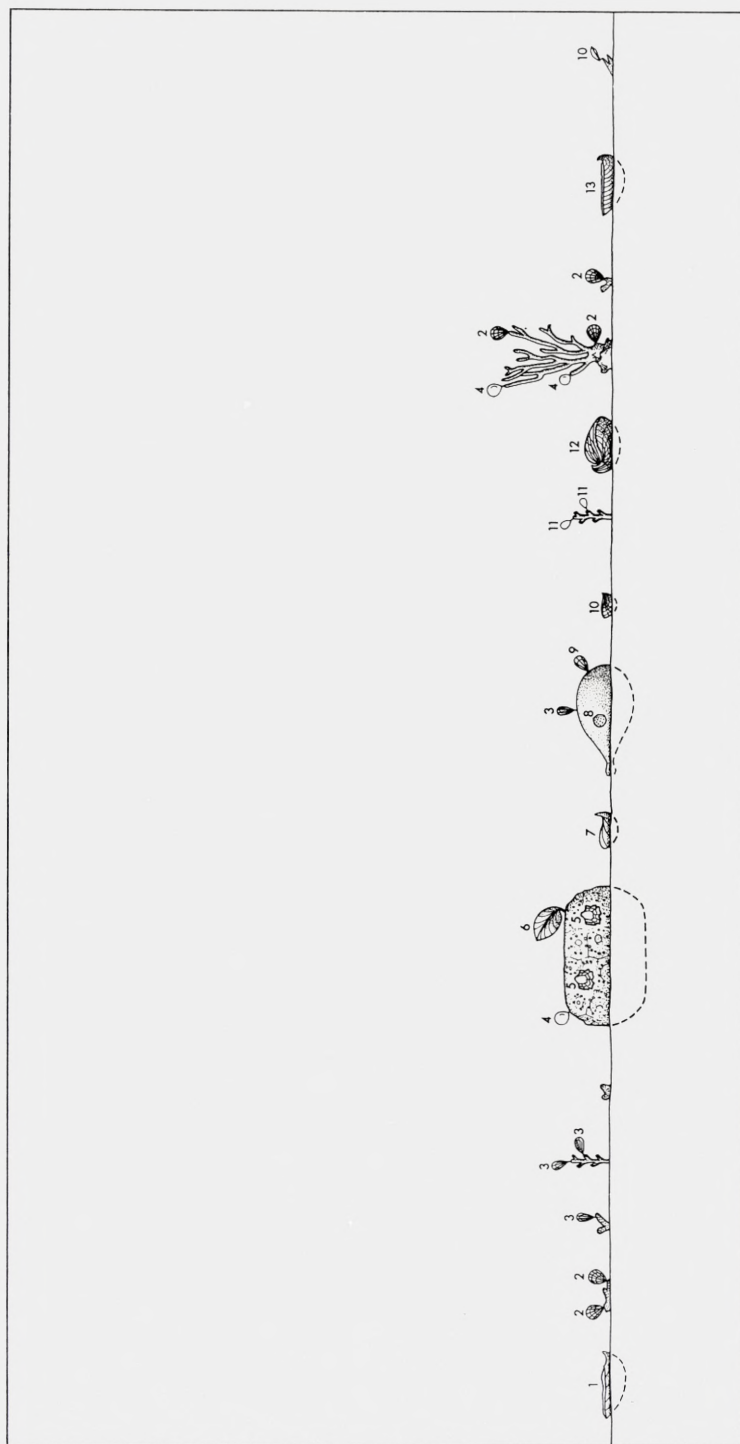
Fig. 13. Upper Maastrichtian brachiopod assemblage. — 1: *Thecidea pappilata* (SCHLOTTHEIM), 2: *Gisilina jasmundi* STEINICH, 3: *Terebratulina longicollis* STEINICH, 4: *Scumulus inopinatus* STEINICH, 5: *Argyrotheca stevensis* (NIELSEN), 6: *Neoliothyrina fittoni* (HAGENOW), 7: *Thecidea recurvirostra* DEFRANCE, 8: *Aemula inusitata* STEINICH, 9: *Terebratulina chrysalis* (SCHLOTTHEIM), 10: *Meonia semiglobularis* (POSSELT), 11: *Dalligas nobilis* STEINICH, 12: *Gemmarcula humboldtii* (HAGENOW), 13: *Terebratulina gracilis* (SCHLOTTHEIM). — The substrates comprise bryozoans, a test and a spine of a regular echinoid (*Tylocidaris baltica*).

to be variable and in some specimens it is not visible at all. This last variety must have been free living and its dorsal valve is correspondingly flat, giving a hemispherical shape although with a very large incurved umbo (fig. 13).

The 3 *Crania* species are all attached with nearly the whole surface of the ventral valve. All species show a very characteristic geotropic orientation on the substrate (SCHMID, 1949).

Distribution in the sediment

The small brachiopod species dominating the chalk brachiopod fauna seem to have a rather random distribution in the sediment. If a 10 kg chalk sample is divided into smaller samples of very varying size (down to 20–50 g) each partsample normally contains representatives of almost all the species found in the large samples. The number of species decreases markedly in samples of less than 100–200 g. The number of individuals is not so closely correlated with sample size as is the number of species.

Patchy distribution of brachiopods has been described very often in the literature (e.g. HALLAM, 1962, RUDWICK, 1965, 1970); each individual nest of brachiopods is normally comprised of one species. It is remarkable, however, that the small chalk brachiopods are apparently randomly distributed and that local concentrations, correlated with local concentrations of bryozoans and other small potential substrates, are never monospecific but display the same quantitative composition as the whole population contained in the sample.

These features are well documented from washing numerous small samples, e.g. core samples from borings. Another technique is further used in combination with the washing of samples of different size to give a more detailed picture of the spatial distribution of the brachiopods. Small orientated blocks of chalk (e.g. $10 \times 10 \times 10$ cm) are cut out with a saw. As described above the chalk consists of numerous small fossils (bryozoans etc.) embedded in a soft groundmass composed mainly of coccoliths. This groundmass is selectively removed by use of an "Airbrasive unit" (the method is described by SPRENG, 1962) with which the block is methodically dissected. When a few mm of groundmass have been removed the remaining harder fossils stand free of sediment. The position of any brachiopods exposed are measured relative to one of the corners of the block and the brachiopod is determined to species. When the positions have been measured the sediment-free fossils are removed and the abrasion is continued. The method is very time consuming, because the speed of the sand-beam must be rather low in order not to damage the larger fossils. Nevertheless, this technique yields so much complementary information on the structure of the chalk that it is much recommended. In thin sections, on ground surfaces, on replicas or on X-radiographs the rock is only seen in two dimensions. From the washing residues the form and size of the larger constituents of the rock are known. But the orientation of these constituents can only be studied by methodical dissection with an "Airbrasive unit".

Throughout most of the Danish Maastrichtian chalk the orientation of the bryozoan stems and other small fossils are almost completely random and they seem to be

preserved very close to the place where they lived. At the most they have been moved only a few mm by bioturbation except those which occur in the fill of larger burrows. Only in Zone 10 in the bryozoan bioherms are the stems of the small bryozoans found to be orientated more or less parallel to the surface of the bioherms. Nevertheless, no signs of wear are found on the fossils in the bioherms and the orientation might be explained by the assumption of a reduced coccolith sedimentation. This is supported by the evidence of total interruption of sedimentation at an initial hardground (fig. 3) immediately below the bioherms and at the complex Maastrichtian-Danian hardground topping the bioherms at Stevns Klint.

The distribution of the brachiopods in the sand-blown blocks confirms the distribution inferred on basis of the washed samples. A statistical treatment is not possible due to the rather limited number of brachiopods contained in each block. (It is not possible to prepare larger samples because of the size of the airbrasive unit).

Contrary to the small brachiopods, the larger brachiopods are sometimes found in small aggregations composed of one to three species. Owing to their rarity, the larger brachiopods are normally collected as isolated specimens, but at some horizons they are found in greater quantities. There is a very pronounced correlation between aggregations of larger brachiopods and absence of potential substrates. The aggregations are thus found almost exclusively in the chalk of Zones 7–9 where the benthonic fauna is reduced (fig. 3). The small brachiopods were well adapted to the bryozoan rich chalk sea bottom and, where the bryozoans were less important or totally absent, the small brachiopods with their great juvenile mortality were not able to survive (figs. 16, 17, 18). The larger brachiopods, dominated by the hemispherical species, all had insignificant juvenile mortality rates (see p. 40) probably due to a rapid initial growth rate. In their early stages they had a functional pedicle, and were thus capable of settling on hard substrates. If only a few larvae succeeded in settling they passed the dangerous juvenile stages rapidly due to high initial growth rate and assumed their free living mode of life and may thus have functioned as substrates for other brachiopods. This may explain the dominance of aggregation of hemispherical brachiopods in environments where the remaining brachiopod fauna has disappeared.

Quantitative variations in the brachiopod fauna

Figs. 14 and 15 a, b show quantitative diagrams for three important Danish chalk sections. Hvidskud (Møns Klint) includes the boundary between the lower and the upper part of Lower Maastrichtian i.e. Zone 4/Zone 5 (BIRKELUND, 1957, SURLYK, 1970 b). Rørdal includes the Lower-Upper Maastrichtian boundary (SURLYK, 1970 b) and Karlstrup includes the Maastrichtian-Danian boundary. Moreover, the three sections are good representatives for each of the three main ecological units described on p. 12. In Hvidskud the horizons below the hardground are very rich in benthonic animals (fig. 14). Upwards the fauna decreases to reach a pronounced minimum in the Rørdal section (fig. 15 a). At Karlstrup the Maastrichtian is topped by small, slightly asymmetrical bioherms yielding profuse benthonic faunas.

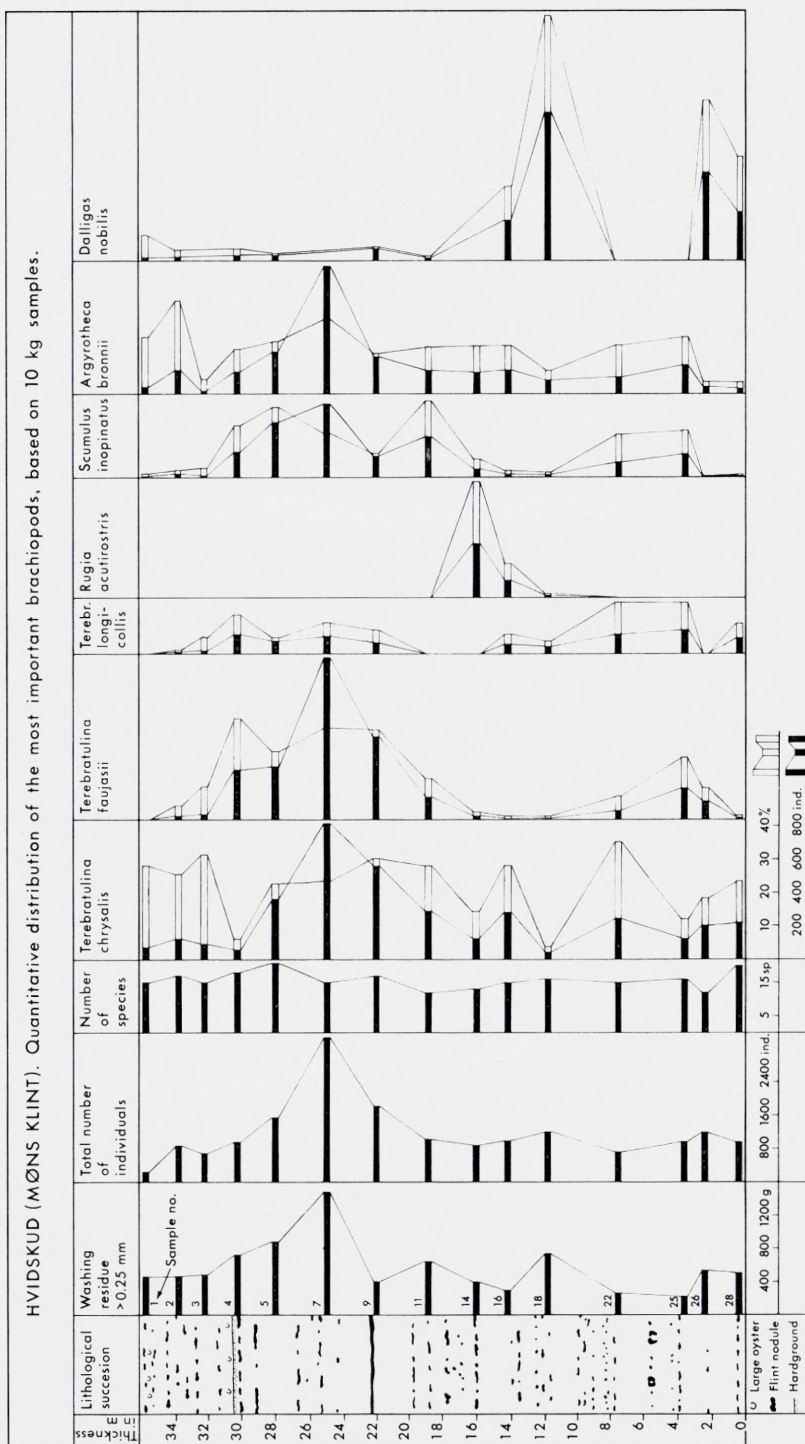Fig. 14. The quantitative distribution of the most important brachiopods in the Hvidskud section.
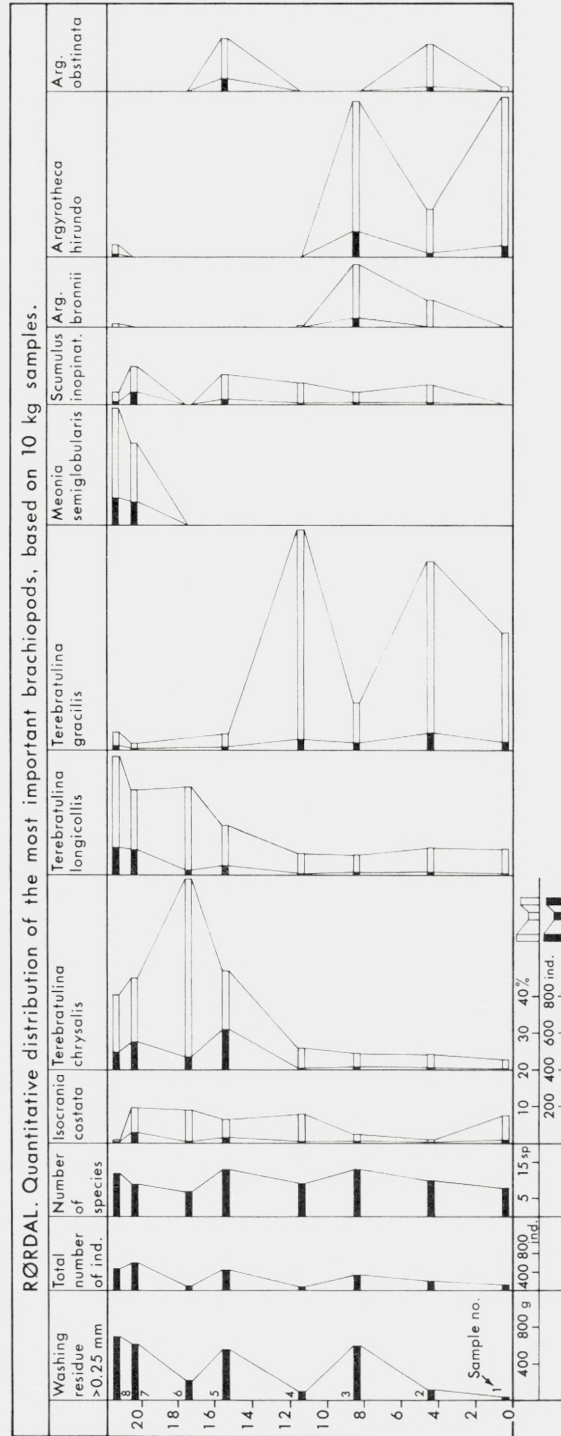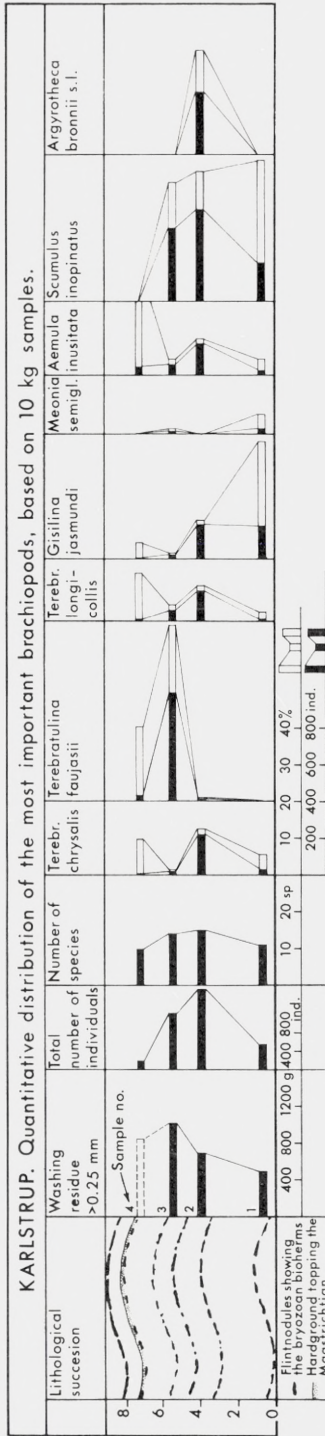
Fig. 15, a: The quantitative distribution of the most important brachiopods in the Rørdal section. The lithology is not shown as it comprises uniform white chalk without flint. Only at the top of the section two thin marl layers occur. b: The quantitative distribution of the most important brachiopods in the Karlstrup section.

The specific composition of the brachiopod fauna is rather constant for each zone, but the abundance of each species is very variable. The quantitative distributions of the most important brachiopods in the Hvidskud section is shown in fig. 14. There is a close agreement between the curve showing the weight of the washing residues (more or less equivalent to the quantity of bryozoans) and the curve illustrating the total number of brachiopod individuals. The number of species is rather constant but follows more or less the two other curves except for the samples richest in individuals, where the number of species decreases (most notably in sample 7). A closer examination the frequency curves of each species reveals that only a few species follow the "bryozoa-curve". This is the case with *Terebratulina chrysalis*, *Terebratulina faujasii*, *Argyrotheca bronnii* and to a smaller degree *Scumulus inopinatus*. On the contrary, *Dalligas nobilis* is rather unimportant in the main part of the section except for sample 26 and especially sample 18 where it outnumbers all the other species.

The correlation between the washing residue curve (i.e. the benthos curve) and the number of individuals curve is remarkable. Steinich (1965) found a similar accordance in the Rügen chalk.

The parallelism of the curves is mainly primary, the bryozoans and the other small benthonic animals playing the role of substrates for the brachiopods, and is only to a small degree secondary, due to variations in the pelagic sedimentation.

Diversity of the brachiopod fauna

a. Diversity indices.

The concept of diversity and of diversity indices have been much used in ecological studies. Diversity understood as simple species diversity, has been used very often to characterize a fauna or a succesion of faunas. The species diversity is sometimes modified so that rare species (e.g. comprising less than 5% of the total number of individuals) are omitted.

As mentioned by Ager (1963 p. 235): "mere numbers of species in themselves are not an adequate ecological guide, however, for obviously a flora of three species may be quite as dense as one of fifty". To compensate for this, different diversity indices have been constructed e.g. $sp/\sqrt{ind}$. (Menhinick, 1964), $sp/\log ind$. (Ziegler et. al. 1968). In these simple indices the total number of individuals are compared to the number of species, but nothing is inferred about the relative importance of each species. Thus 10 spp totalling 100 individuals, where each species comprises 10 individuals give the same index as where 1 species comprises 91 individuals and the rest of the species are each represented by 1 individual. Simpson (1949) suggested the formula $\dfrac{N(N-1)}{\Sigma n(n-1)}$ where N is the total number of individuals and n is the number of individuals in each species. In this formula the relative frequency of each species is included. Thus the last mentioned example gives $\dfrac{100 \times 99}{(10 \times 9) \times 10} = 11$ in the first case and $\dfrac{100 \times 99}{91 \times 90} = 1.2$ in the

second. A thorough review of different diversity indices including the so-called FISCHER's α-index was given by MURRAY (1968). The rather teoretical α-index gives good results in recent lagoonal sediments, but seems to be somewhat too elaborate to be used in older rocks.

b. Application to the chalk brachiopod populations.

An important disadvantage of the formula of SIMPSON (1959) and most other comparable formulas is that they are almost impossible to use when the populations are not of approximately the same size. Thus, a sample from Zone 7 with few species each represented by a few individuals will have a greater diversity index than a sample from e.g. Zone 5 with more species many of which are represented by great numbers of individuals, because no species plays a really dominating role in the Zone 7 sample. Formulae of this kind are therefore considered to be of little value in palaeoecological studies based on bulk samples or on square counts.

As it is equally important to know the density as it is the diversity of the fossil fauna, formulae based on counts of equal numbers of specimens must be avoided. We must therefore return to the more simple formulae where the relative importance of the different species is not taken into consideration.

As the total number of species is not usually related linearly to the total number of individuals, but rather, the chance of collecting a new species decreases as sampling increases, MENHINICK (1964) sought a ratio (index) of species to individuals which would be constant for samples of different sizes. He considered $sp/\sqrt{ind.}$ usable while $sp/\log$ ind., $sp-1/\log e$ of ind., and $\log sp/\log$ ind. were considered inappropriate. Nevertheless, for use on the chalk brachiopods the $sp/\sqrt{ind.}$ diversity index was found to be no more useful than MENHINICK's other indices. Thus the very poor faunas from the middle part of the Maastrichtian (Zone 7) e.g. Rørdal (fig. 15 a) give higher diversity indices than the very rich samples from Zone 4 e.g. Hvidskud (fig. 14). The number of species compared to the percent frequency of the most important species gives a more precise picture of the diversity of the investigated fauna and is used here in figs. 14 and 15.

Dominant, accessory and rare species

It is clear from figs. 14, 15 a, b that the different species have different frequency patterns. Some species represented by *Terebratulina chrysalis* and *Argyrotheca bronnii* are present in almost all samples and dominate the fauna. Other species represented by *Terebratulina faujasii* dominate in a few samples but are otherwise rare or totally absent.

A third group of species represented by e.g. *Isocrania costata*, *Carneithyris sub-cardinalis* and *Aemula inusitata* are present in the majority of samples in small but rather constant numbers and never dominate. Finally, there is a group of species, represented by e.g. *Kingena pentangulata*, which are found in a minority of the samples

and always in small numbers. A statistical treatment of this subject would be interest-
ing, but has been avoided since not all samples are comparable from a statistical point
of view, and since many of the species only have a limited vertical distribution in
the succesion.

Size-frequency distribution

a. Premises.

The construction of size-frequency distributions is a mush used technique in
palaeoecological studies. Nevertheless the evaluation of the histograms is dubious in
many earlier publications. The most common mistake is to compare the size-frequency
distribution of a fossil assemblage directly with a survivorship curve. Further, the
shape of the histograms is used to determine the nature of the assemblage, that is, if the
assemblage is residual or if it is a so-called life assemblage (BOUCOT, 1953) or fossil
community (FAGERSTROM, 1964) etc.

A firm basis for work on size-frequency distributions of fossil assemblages was
first established in the very important paper by CRAIG & OERTEL (1966). Here, a clear
distinction was drawn between the living and the resulting dead population. These au-
thors emphasized (op. cit. p. 349) that the size-frequency distributions of living and
dead populations of organisms in these steady-state experiments depend on five fac-
tors. These were: 1) the length of the period(s) of annual recruitment, 2) the growth-
rate and its coefficient of variation, 3) the period of cessation of growth, 4) the mortality
rate and 5), on which the shape of the histograms primarily depends, the interplay
between the growth-rate and the mortality rate.

It is therefore evident that the shape of the size-frequency distributions can be used
in only a few cases as a criterion of the nature of the investigated population. A strongly
right (= positively) skewed curve will normally be indicative of the presence of a fossil
community (sensu FAGERSTROM, 1964), but on the other hand a bellshaped curve might
equally represent a fossil community.

The use of the shape of the size-frequency distributions as criteria for different
kinds of fossil assemblages is a reversal of cause and effect. As a consequence of the
results obtained by CRAIG & OERTEL (1966) it is necessary to establish the nature of the
fossil assemblage before the size-frequency distribution can be interpreted. The life
history of an organism from birth to the time of death and its subsequent burial is
ably summarized by HALLAM (1967). Among the most important post mortal factors
modifying the structure of the fossil community may be mentioned: sorting by currents,
size-selective crushing and diagenetic dissolution of certain size classes. Dissolution
of small, thin shells is often mentioned in the literature as an important modifying
factor, e.g. FAGERSTROM, 1964, HALLAM, 1967. However, it should be emphasized that
in the chalk the shells are better preserved the smaller they are and that dissolution
only occurs in very large fossils e.g. the anterior part of the 5–7 cm long *Neoliothyrina
obesa*.

b. Size-frequency distributions of the chalk brachiopods.

Size-frequency histograms are constructed for all species found in three chalk samples (figs. 16, 17, 18). Sample Hvidskud 9 is representative for the lower benthos-rich part of the chalk (figs. 3, 14). No samples from Zone 6 and 7 have been investigated because of the small number of individuals found at these horizons. Sample Lindholm 8 belongs to Zone 8 and sample Karlstrup 2 is representative of the upper benthos-rich part of the chalk (figs. 3, 15).

Before the ecological evaluation of the size-frequency distributions can begin, several controls must be made:

1) It is of great importance to determine if any size-selective transport, crushing or solution has taken place. As shown on p. 13, these agents are of no importance in the Danish chalk.

2) It must be ascertained that each sample has been deposited under stable conditions, as the brachiopod population contained in the sample is a sum of many generations. If conditions are stable the shape of the size-frequency distributions will remain constant, irrespective of the number of generations added to the population. From the inspection of the size-frequency distribution of the same species from numerous samples of all sizes from all horizons of the Danish chalk, it is evident that each species has its own distinct size-frequency distribution. Thus the shape of the histograms are results of factors characteristic for the biology of each species and not of changes in sedimentation rate etc.

3) Finally it is of great importance that the taxonomy of the fauna is well known and that it is possible to determine juvenile specimens with absolute certainty. In many ecological papers published in recent years the fossils are only identified to a rather high taxonomical level. This may be useful in the first broad grouping of localities but has only little ecological significance. A detailed and profound knowledge of the taxonomy at species or subspecies level is necessary before a study of size-frequency distributions, species-frequency diagrams and morphological adaptations can be attempted.

c. Types of size-frequency distributions.

In figs. 16, 17 and 18 all species contained in each sample are size-frequency measured to present a view of the whole fauna. Nevertheless, it is evident that only the histograms of the more common species have any value in the population studies.

From only a superficial view of the histograms it is seen that in all the more common species the populations are dominated by large quantities of juvenile individuals. In *Terebratulina faujasii* (fig. 16) only about $3^0/_0$ of the population exceeds $^1/_2$ the size of an adult individual. This is even more clearly the case in *Terebratulina chrysalis* (fig. 16). This species reaches an adult length of about 2 cm, but except for one specimen all 235 individuals found in the sample are under 4 mm in length.

This right (= positively) skewed type of distribution is found in all the common species in the three measured samples. Most of the histograms have quite gentle slopes
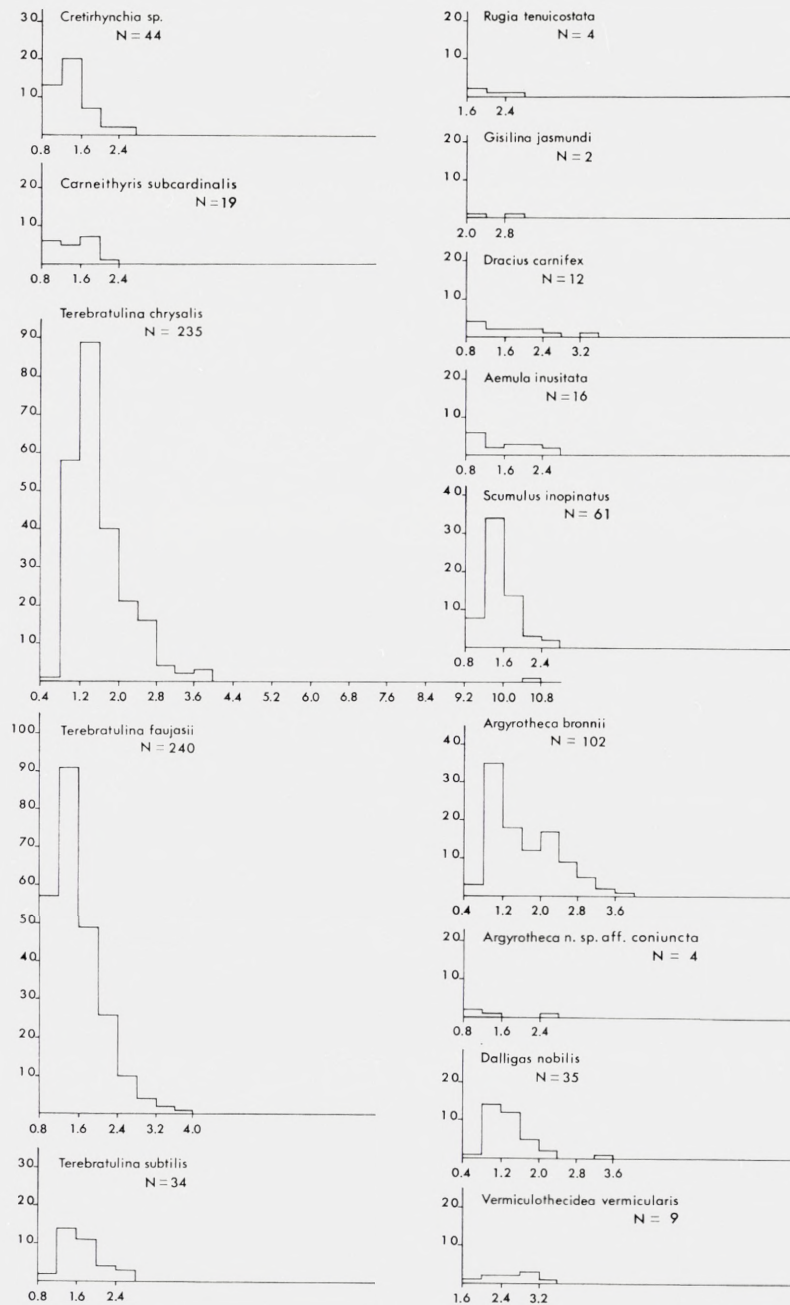
Fig. 16. Size-frequency diagrams of the species found in sample Hvidskud 9 (Fig. 14, Zone 4). The number of individuals (N) of each species is in some cases somewhat smaller than the corresponding number on fig. 14 as some of the specimens were too damaged to be measured.—*Cretirhynchia* sp. includes all rhynchonelloid specimens found in the sample as it is impossible to distinguish between juveniles belonging to the three *Cretirhynchia* species found in the chalk. They are nevertheless measured to give a clear picture of the size distribution of all brachiopods found in the sample. The following species have been omitted due to small number and bad preservation: *Isocrania costata* (SOWERBY), *Isocrania barbata* (HAGENOW), *Gisilina gisii* (ROEMER) and a dubious *Terebratulina gracilis* (SCHLOTTHEIM). Abscissa is length of pedicle valve in mm, ordinate is number of individuals.
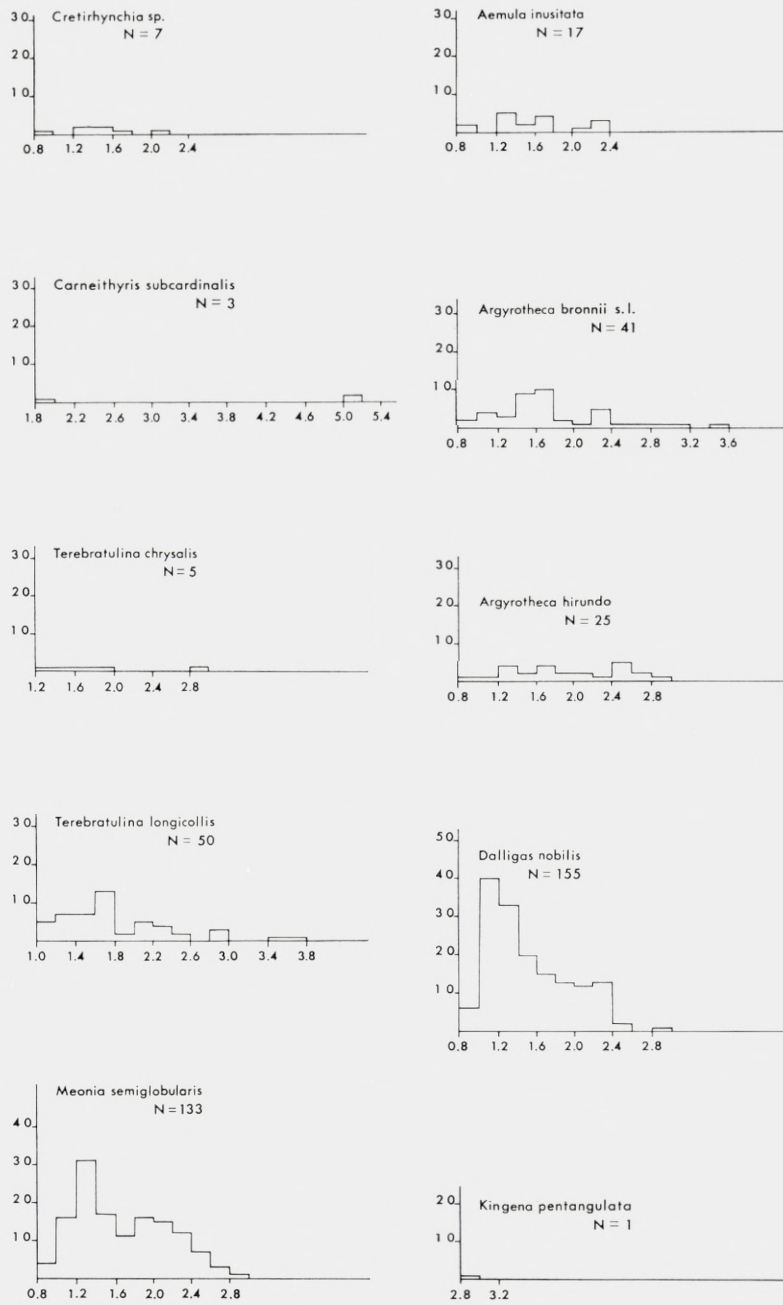
Fig. 17. Size-frequency diagrams of the species found in sample Lindholm 8 (Zone 8). The remarks in the legend to fig. 16 are also valid here. The following species have been omitted due to small numbers and bad preservation: *Terebratulina gracilis* (SCHLOTTHEIM), *Rugia tegulata* SURLYK, *Scumulus inopinatus* STEINICH, *Vermiculothecidea vermicularis* (SCHLOTTHEIM).

and secondary peaks are only rarely seen. This is of course partly a function of the chosen class-boundaries, but the formation of the fossil populations by summing of many generations will also have a smoothing effect on the distribution. From inspection of the three figured samples and many other samples it is seen that, where they are common, all the small pedunculate brachiopods (group I a, fig. 5) have strongly positively skewed distributions.

The size-frequency distributions of the burrowing and the cemented brachiopods (group III and IV, fig. 5) as well as of the large brachiopods of group I b are unknown because these brachiopods were only rarely found in the samples.

The hemispherical free living brachiopods (group II) are normally quite rare, but where they are common they show a size-frequency distribution quite different from the remarkably uniform, positively skewed histograms of the small pedunculate brachiopods.

The size-frequency curves of the hemispherical brachiopods (notably *Magas chitoniformis*, *Terebratulina gracilis* and *Trigonosemus pulchellus*) are in some cases almost bell shaped or in a small number of cases negatively (= left) skewed, but never right skewed with an overweight of juvenile individuals. The most common histograms are those with a concentration of forms which have reached the final adult shape but not the maximum size of the species.

The great difference in size-frequency distributions among two ecologically very different groups of brachiopods makes it possible to draw some important conclusions on the biology of two groups. The species belonging to group II are not taxonomically closely related. On the other hand, juveniles of these hemispherical brachiopods closely resemble juveniles of some of the small brachiopods (group I a). Thus the early ontogenetic stages of *Terebratulina gracilis* are morphologically very similar to *Terebratulina faujasii* of comparable size (figs. 9 a and 7 a) and juveniles of *Magas chitoniformis* are similarly very close to small individuals of *Dalligas nobilis* and *Scumulus inopinatus*.

As no selective removal of certain size classes has occurred and as the juveniles of members of each of the two groups find their counterparts in the other group, the difference in the histograms cannot find its explanation in simple ecological reasons as e.g. different enemies or different feeding habits.

d. Size-frequency distributions compared to the morphological adaptations.

The two types of distribution are due to differences in mortality, growth rate and adult size and must be seen in connection with the different adaptations of the two groups.

The small pedunculate brachiopods are adapted to a life attached to the very small hard substrates on the sea-bottom, i.e. mainly small, delicate bryozoans. This implies that they spend their life very close to the surface of the sediment. This position is dangerous to small, sessile suspension feeders, which are very susceptible of becoming overturned by vagile benthonic animals and more less buried in the uppermost soft
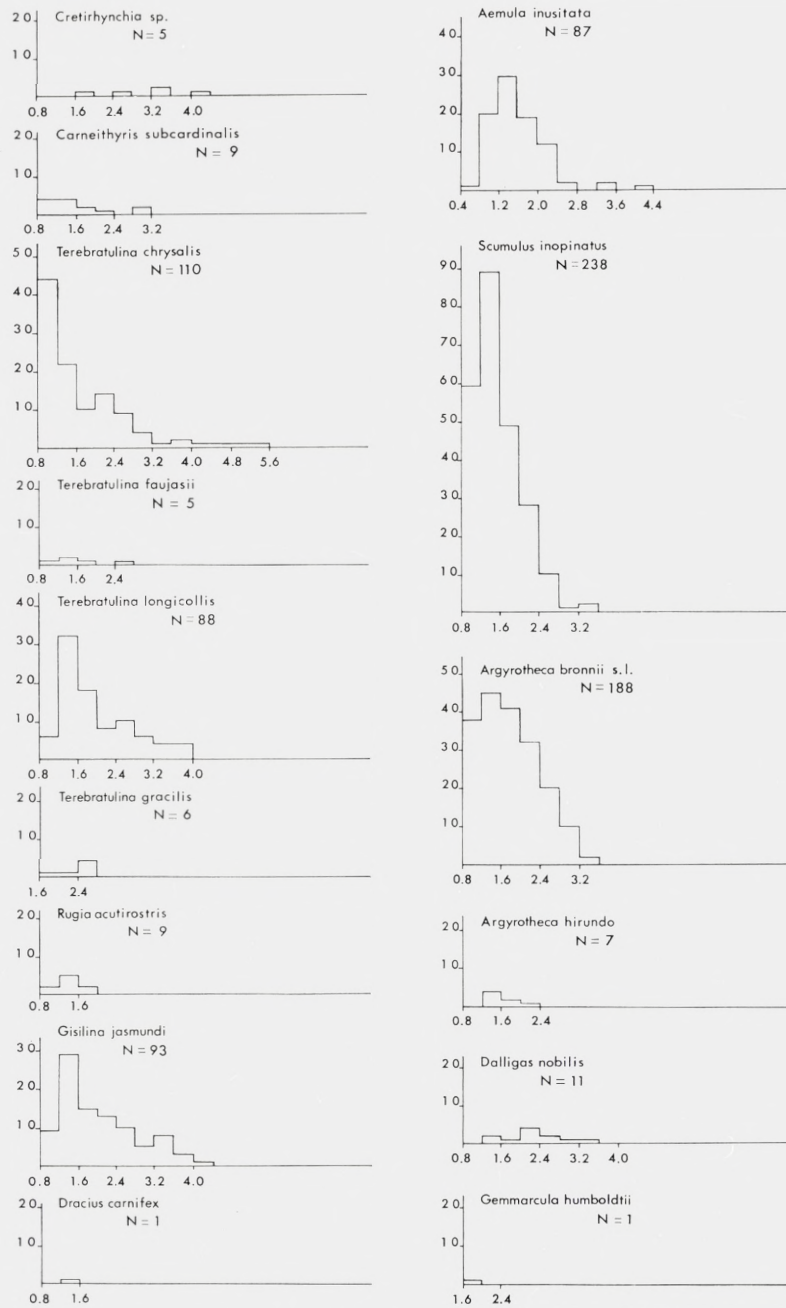
Fig. 18. Size-frequency diagrams of the species found in sample Karlstrup 2 (fig. 15 b, Zone 10). The remarks in the legend to fig. 16 are also valid here.
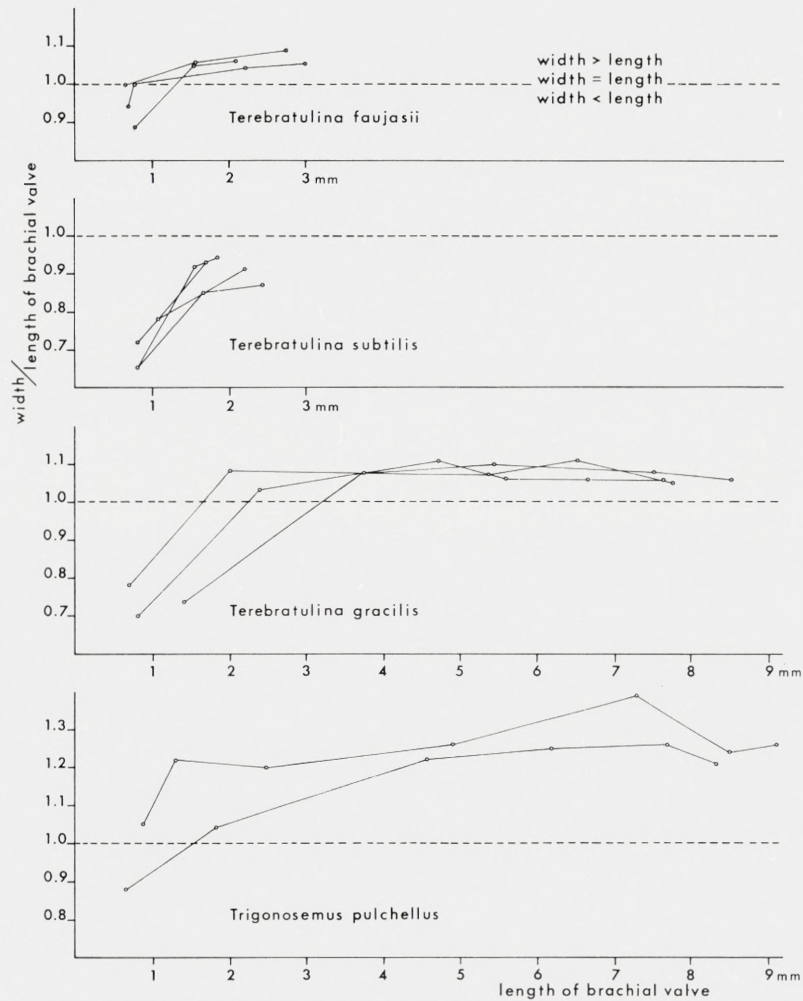
Fig. 19. Growth curves of the four species shown on figs. 6, 7, 9 and 10 (not the same individuals). In all 4 cases the relation between width and length of the brachial valve starts well below 1.0, corresponding to the very long juvenile shell characteristic of most brachiopods. This relation changes rapidly during growth and at a length of 1–2 mm the width becomes larger than the length. In the two hemispherical species *Terebratulina gracilis* (SCHLOTTHEIM) and *Trigonosemus pulchellus* (NILSSON) the final shape is reached already at about 3–4 mm length and the relation remains constant during the rest of the ontogenetic growth. Only the minute *Terebratulina subtilis* STEINICH never reaches a size where the width becomes greater than the length of the brachial valve. The measurements have been carried out on the basis of growth lines on individual specimens.

layer of the sediment. Furthermore, there must have been considerable competition for space on the small substrates. These factors favour the evolution of small, short-lived forms which become sexually mature at an early age.

RUDWICK (1965, 1970) mentioned that many recent brachiopods are sexually mature when they have reached $^2/_3$ their final size. An early maturity for the small

chalk brachiopods would seem to have been necessary in order to maintain a constant population in an environment which caused high juvenile mortality.

The juveniles of the medium sized, hemispherical free living forms ran the same risk as the juveniles of the minute pedunculate brachiopods as they are in all respects very closely alike (figs. 6, 7, 9). The fact that the free living species had a very low juvenile mortality therefore deserves an explanation.

A rather large size would appear to be necessary for the free living mode of life, and it takes some years to attain this size. It is therefore of great importance that the animals belonging to this group rapidly pass through the vulnerable small growth-stages and reach their final size and shape as soon as possible. The initial growth rate of these species must therefore be much greater than that of the small species, a fact that again influences the size-mortality pattern.

It is remarkable that this growth-rate/mortality pattern inferred on theoretical grounds for the two groups is clearly illustrated by the empirical size-frequency diagrams.

e. Growth rates.

In order to substantiate the explanation for the two types of size-frequency distributions an attempt is made to estimate the ontogenetic age of some of the brachiopods. Some authors have used growth rings in age studies (HALLAM, 1967, CRAIG & HALLAM, 1963, VOGEL, 1959) but the growth rings of the chalk brachiopods normally do not occur in regular positions as year-rings or spawning rings. In the majority of species it is not possible to distinguish between year-rings and disturbance rings, and thus the age determination methods of VOGEL (1959) and SHELDON (1965) cannot be used directly. A tendency towards a constant grouping of about 5 growth rings is found only in a few species.

To compensate for the occurrence of disturbance rings the technique used by CRAIG & HALLAM (1963) was followed.

All growth rings were measured and the measurements considered as frequency groups. Compensation of disturbance rings in this way revealed potential year rings as peaks on the histograms.

The position of class boundaries and size of classes has a considerable influence on the position of the peaks. However, the application of several class limits showed that the minima in the histograms corresponding to the position between the year rings are rather regular in distribution. The position of the year rings is interpreted as the mean of the measurements between the minima.

This technique gives a minimum age of adult *Terebratulina gracilis* of 4 years (fig. 20). At greater ages the growth rings become crowded and it is not possible to distinguish isolated peaks on the curve. As the average position of the first three year rings is known the total adult age can then be estimated by aid of the method described by SHELDON (1965). L_t (size at one year) is plotted against L_{t+1} (size the following year) which gives a linear curve, converging on the point $L_t = L_{t+1}$ (= the average maximum
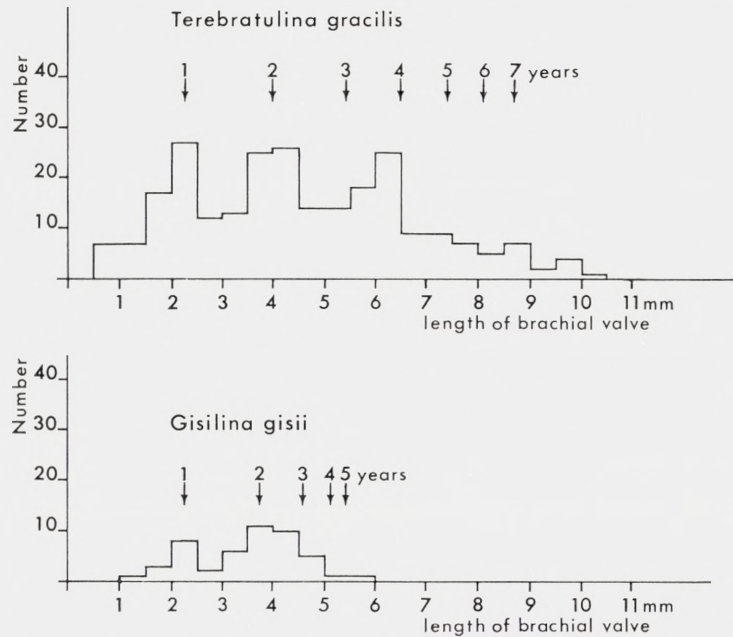
Fig. 20. Frequency distribution of the growth lines of *Terebratulina gracilis* (Schlottheim) and *Gisilina gisii* (Roemer). Due to crowding the last growth rings have only been measured in a few specimens of each species. The growth rings of *Terebratulina gracilis* (Schlottheim) show pronounced peaks at about 2.3 mm, 4.0 mm and 6.5 mm length of the brachial valve. At *Gisilina gisii* (Roemer) there is a pronounced peak at 2.3 mm and a more obscure one at 3.8 mm. The size at each year of ontogenetic growth has been estimated by the method described by Sheldon (1965)—see fig. 21.

size). This method gives for an individual of *Terebratulina gracilis* 1 cm long an age of 10 years. Only a very few age studies on living brachiopods are published (e.g. Rudwick, 1962, 1965, Paine, 1963, 1969) and it is therefore difficult to check the estimated age, but compared with the available data the estimate seems to be rather high.

Several of the small brachiopod species have numerous growth rings (*Argyrotheca*) and seem to be unsuited for age studies, but some of the species have only 1–3 distinct growth rings. This is in good agreement with the theory that the small brachiopods are short-lived and mature early in contrast with the free living brachiopods.

Growth rings were also measured in the small species *Gisilina gisii* (fig. 20) and the first rings were found to be fairly regularly distributed. As the crowding of growth rings in this small species occurs rather early in the ontogenetic growth compared to *Terebratulina gracilis* the positions of the 2. and 3. maximum do not emerge clearly from the histograms. A closer inspection of the measurements reveals, however, that the 2. maximum is situated at about 3.8 mm length of the brachial valve. By using the technique of Sheldon (1965) the maximum age of *Gisilina gisii* is estimated at 5 years. By plotting the estimated age-sizes of *T. gracilis* and *G. gisii* on an age-length curve (fig. 22) it is clearly revealed that the initial growth rate of *T. gracilis* is much larger than of *G. gisii*, thus substantiating the theory that the low juvenile mortality of the medium
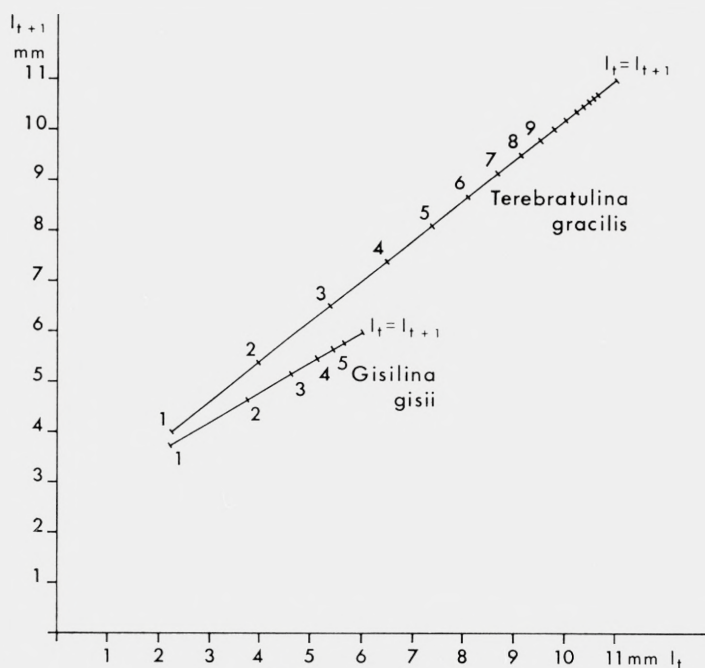
Fig. 21. The size at different years of *Terebratulina gracilis* (Schlottheim) and *Gisilina gisii* (Roemer) has been estimated on the basis of the growth ring diagrams (fig. 20) and of the final size of each species. The method is adopted from Sheldon (1965) and is described on p. 43.
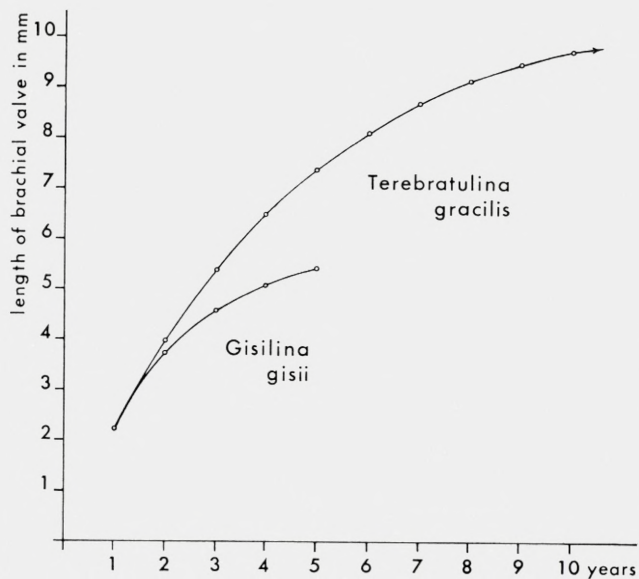

Fig. 22. Age-length curves of *Terebratulina gracilis* (Schlottheim) and *Gisilina gisii* (Roemer) based on fig. 21. It is clearly seen that the initial growth rate of *Terebratulina gracilis* is much greater than of *Gisilina gisii*.
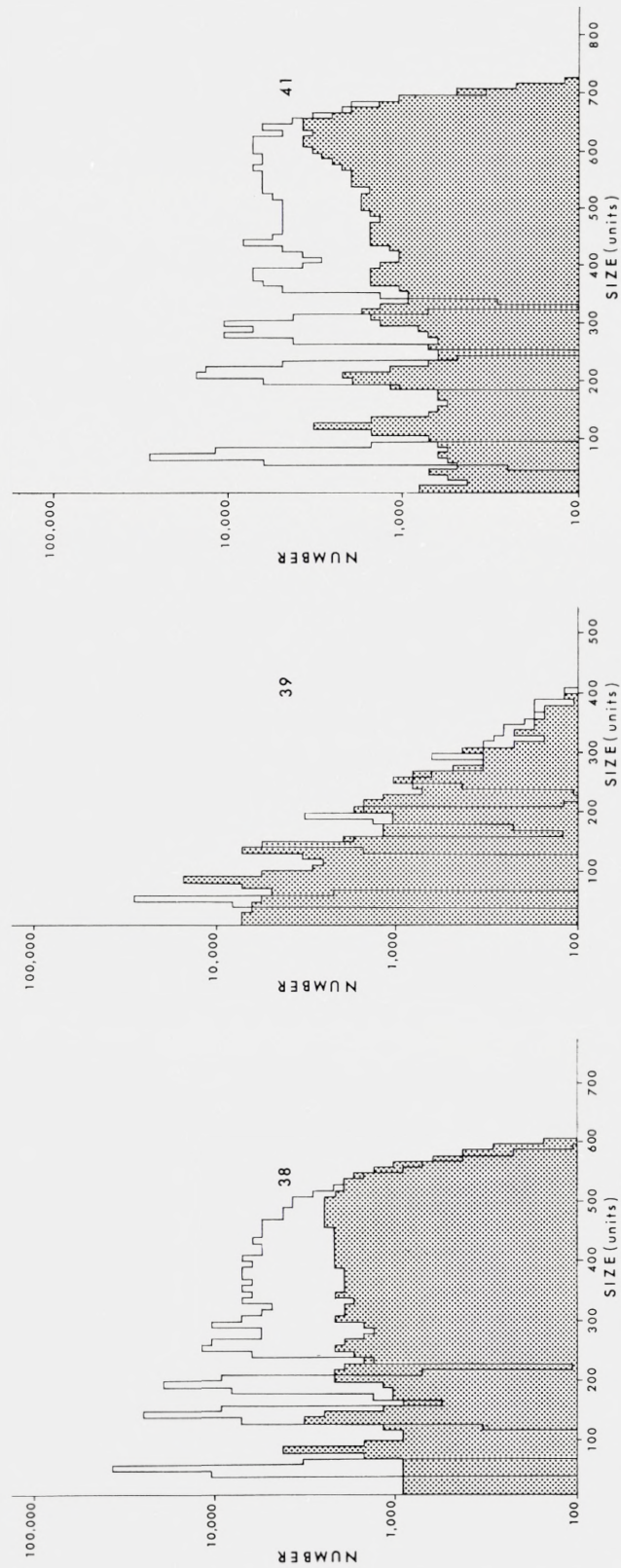
Fig. 23. Theoretical size-frequency distributions. From CRAIG & OERTEL (1966).—Size-frequency histograms of living and dead (shaded) populations derived from "boreal" recruitment, 3 months cessation of growth (December, January, and February) with mortality ×2, high-to-low growth rate, and coefficient of variation 2. Expt. 38: increasing mortality, 39: decreasing mortality, 41: increasing mortality and very high-to-low growth-rate.

sized hemispherical, free living species is a result of a high early growth rate of these species allowing a rapid passage of the vulnerable early stages.

f. Comparison with theoretical size-frequency distributions.

To ease comparison with the theoretical size frequency distributions calculated by CRAIG & OERTEL (1966) the population characteristics of the two ecologically different groups are summarized below.

1. The free living hemispherical forms (group II):
    High (or very high) → low growth rate
    Increasing mortality
    "Boreal" recruitment.
2. The minute pedunculate brachiopods (group I a):
    High → low growth rate
    Decreasing mortality
    "Boreal" recruitment.

The type of recruitment can of course only be roughly estimated, but as the chalk sea is considered to have had a depth varying between about 50 and several hundred meters the "boreal" recruitment type of CRAIG & OERTEL (1966) seems to be the most likely.

In comparison with the experiments of CRAIG & OERTEL the supposed mortality rates, growth rates and recruitment type of the two groups correspond with experiment 38 (possibly 41) and 39 respectively refigured here. Experiment 38 (fig. 23) shows a pronounced left skewed curve with relatively low juvenile mortality and with a maximum in the adult stages corresponding well with all observations on the population structures of the free living hemispherical brachiopods. Experiment 39 (fig. 23) on the contrary is markedly right skewed with high juvenile mortality and only a very few individuals reaching the maximum size. This curve corresponds even better with the size-frequency distributions of the minute pedunculate brachiopods.

Stunting or small brachiopods ?

The problems concerning stunting in fossil faunas have attracted many authors (e.g. CLOUD, 1948, HALLAM, 1965, TASCH, 1953).

The numerous 2–5 mm long brachiopod species found in the Danish chalk are naturally suggestive of a stunted fauna. However, this quite conclusively seems not to be the case, for the following reasons:

1. The small species are found in all horizons throughout the Upper Campanian and Maastrichtian Stages of northern Germany and Denmark i.e. through a period of several million years. They are known almost without exception, only from the north European chalk.

2. The maximum adult size of all the species is well known on account of the crowding of growth rings in the largest individuals. This maximum size is about constant throughout the chalk and no localities with individuals of the same species attaining greater sizes are known.

3. The small size, as shown in the foregoing pages, may be considered a positive life adaptation in response to the numerous very small, hard substrates available on the chalk sea bottom.

It is therefore considered that no stunting has occurred and the fauna must be characterized as comprising naturally small-sized species.

Epifauna

In the literature there are numerous accounts of brachiopods more or less covered by a rich epifauna (e.g. Rudwick, 1970). However, an almost total absence of epifauna is characteristic for the majority of the brachiopod species in the Danish chalk. This absence is easily explained in the case of the small species (group I a) owing to their short life and to rapid burial of the small shells after death. At horizons with a supposed reduced rate of sedimentation, however, (e.g. in the upper part of the succesion at Hemmoor in North Germany) epifauna is often found even on the smallest brachiopods.

An epifauna is likewise almost totally absent on the hemispherical free living species (group II). The three *Cretirhynchia* species, *Carneithyris subcardinalis* and the large species belonging to groups I b & c would appear to represent ideal substrates for a rich epifauna. Nevertheless, while an epifauna is only rarely found in *C. subcardinalis*, *Kingena pentangulata* and *Neoliothyrina fittoni* it is sometimes well-developed on the very large *Neoliothyrina obesa* and especially on the three *Cretirhynchia* species.

The reason for this pronounced difference is not clear, but it might be explained by the past existence of a periostracum of different thickness in the different species (Dr. R. Bromley, 1971, in conversation). In species with a thick periostracum the epifauna will be separated from the brachiopod when the periostracum disintegrates. However, the recent species of *Terebratulina* and many terebratelloids have a very thin periostracum.

An examination of the recent brachiopods in the collection of professor N. Spjeld-næs showed that even from the same locality some species are almost covered by epifauna while others are completely free of overgrowth. This difference might be due to unknown features of the periostracum.

Recent *Terebratulina retusa* and *Terebratulina septentrionalis* are often covered by a thick layer of encrusting sponge. Dall (1920 p. 300) wrote that *T. septentrionalis* is subject to the (commensal ?) growth of a sponge which when young "appears like a normal pubescence, as in *T. retusa*, but when full grown becomes a spongy ball in which the brachiopod is entirely concealed".

The spongy layer prevents attachment of other epifaunal organisms. After death it disintegrates rapidly and there is no reason to believe that it would normally be preserved in the fossil state. By analogy this seems to be a reasonable explanation of the almost total absence of epifauna on *Terebratulina chrysalis* in the chalk.

Only in a few cases is it possible to judge if the epifauna was attached to living brachiopods or dead shells. In some examples bryozoans have closely followed the commisure or growth lines. No orientation of epifauna relative to inhalant or exhalant current has been observed. The most common epifaunal organisms are bryozoans, encrusting foraminifera, calcareous sponges, bivalves (*Atreta*), brachiopods (*Crania*) and serpulids.

Borings

Two types of borings have been found in the brachiopods viz. thallophyte and gastropod borings. At some horizons the majority of the specimens are penetrated by thallophyte borings. It is not known if the borings are caused by fungi or algae, but an algal origin seems most likely according to the branching pattern and dimensions of the borings (BROMLEY, 1971, personal communication). There is a pronounced correlation between slow sedimentation and number of thallophyte borings. Thallophyte borings are normally restricted to large disarticulated and broken shells indicating that the borings were not made in the shells of living brachiopods.
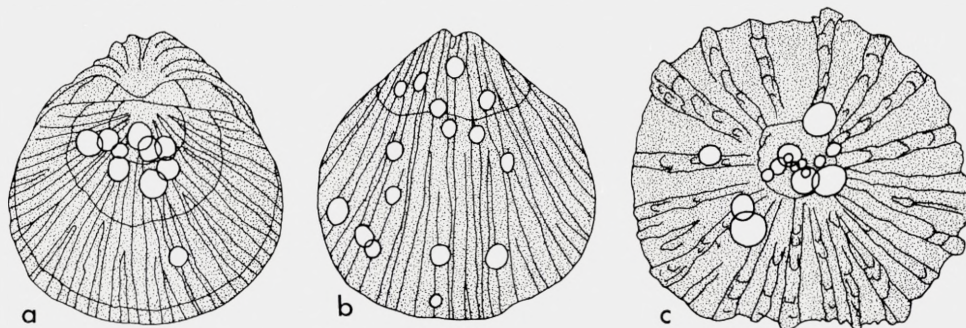

Fig. 24. The relative positions of muricid? borings on the outline of: a: a brachial valve of *Trigonosemus pulchellus* (NILSSON) b: a pedicle valve of *Trigonosemus pulchellus* (NILSSON) c: a dorsal valve of *Isocrania costata* (SOWERBY). a and b are based on a population of *Trigonosemus pulchellus* from Dronningestolen, Møns Klint. c is based on a population of *Isocrania costata* from Lindholm.

The gastropod borings are more significant from an ecological point of view, as they must have been made on living brachiopods. STEINICH (1965 p. 196) mentioned that in the Rügen chalk 12% of all specimens of *Terebratulina gracilis* had been bored by gastropods. In the Danish chalk, borings are only found in a few species and not at all horizons. The borings are cylindrical and, by comparison with modern examples, were apparently made by muricid gastropods (BROMLEY, 1971, personal communication) indicating that the brachiopods were attacked at the surface of the sediment and not by burrowing naticid gastropods. Only in *Isocrania costata* and *Trigonosemus*

pulchellus are borings common. Thus 20% of a *T. pulchellus* population from Møns Klint were bored by gastropods. In *Isocrania costata* the borings are concentrated in the thick umbonal region (fig. 24 c) where the soft parts of the body were situated. Un-finished borings are very common. In *T. pulchellus* a very characteristic distribution is found of the borings in the dorsal and ventral valves respectively (figs. 24 a, b). In the dorsal valve the borings are concentrated in the umbonal part where the soft parts were situated, but on the ventral valve the borings are found in a ring around the central part of the valve, where borings are absent. This is in good agreement with the supposed mode of life of *T. pulchellus*—lying free on the sea bottom with the ventral valve down.

Fossil communities

PETERSEN (1913, 1918) developed the concept of communities as statistical units based on recurring combination of certain animals (a discussion of PETERSEN's community concept is given by THORSON, 1957 p. 467).

In the present study several of the brachiopod species are found in recurrent combinations. THORSON (1957) noticed that epifaunal organisms were not ideal as "characterizing animals" for a community due to their less constant occurence. Never-theless some of the chalk brachiopods are suitable as characterizing animals as they are found in all samples in the part of the column where they occur. Brachiopods have also been used as such in the Ordovician communities defined by BRETSKY (1970 b). As mentioned by WALKER & LAPORTE (1970 p. 934) it is misleading to name a fossil community after one or more of the type animals as different taxa may be involved at different times when dealing with temporarily separated communities. They therefore chose to name the communities after the presumed biotopes. This is almost impossible in the very monotonous chalk sequence and it seems to be most convenient to delay any designation of fossil communities in the Danish chalk until the taxonomy and strati-graphy of all major fossil groups are known in detail.

Summary

The present study is based on a large number of samples or series of samples from all major Danish chalk localities (fig. 1).

The samples, normally weighing 5 or 10 kg were washed and yielded a total of about 50.000 brachiopods representing 37 articulate and 6 inarticulate species.

The white chalk is a soft, friable, almost pure carbonate sediment of biogenic origin classified as a nannoagorite by HONJO (1969). It consists of coccolith detritus with an admixture of up to 20% smaller macrofossils, chiefly bryozoans.

The brachiopods have shown themselves to be valuable for a detailed strati-graphical subdivision of the Maastrichtian chalk of northern Germany and Denmark

(Surlyk, 1970 b). Thus it is possible to divide the Danish Maastrichtian into 10 zones on the basis of the brachiopods.

The Danish chalk can be divided into three ecological units based on the major variations in the richness of the benthonic fauna (fig. 3). From Zones 1–4 (fig. 2) there is a steady increase in the benthonic fauna with a very pronounced maximum in Zone 4. In Zones 6–7 the benthonic fauna has almost disappeared but upwards the fauna becomes richer again and a second maximum is reached in Zone 10.

All fossils are extremely well preserved. In the brachiopods, mesodermal spicules and even coherent spicular skeletons revealing the whole structure of the mantle, the body wall and the lophophore are commonly found (pl. 1, 2). Furthermore there is a complete mixture of fossils of all size classes. Preburial transport can thus be excluded. Traces of early diagenetic slides have been found only on the flanks of the bryozoan bioherms of Zone 10 (figs. 3, 15).

On the basis of their mode of life, the chalk brachiopods can be divided into 4 groups (fig. 5):

I.   Attached to the substrate by means of a pedicle: 24 spp. This group can be divided into 3 subgroups according to the nature and especially the size of the preferred substrate.

II. Living free on the surface of the sediment: 10 spp.

III. Burrowing in the sediment: 1 sp.

IV. Attached to the substrate by cementation: 8 spp. This group can be divided into 2 subgroups according to the size of the substrate.

Group I is completely dominated by minute brachiopods with a very high juvenile mortality. These brachiopods seem to be well adapted to a life attached to the very small hard substrates, especially bryozoans, available in the chalk.

The brachiopods of group II show several kinds of adaptations to the free living mode of life. Six of the species are hemispherical (fig. 11), one species seems to have functioned like a self-righting "tumbler" (fig. 4), and the three last species are rhynchonelloids with the lateral parts of the shell considerably expanded. The pedicle openings of all the species belonging to this group are closed or at least hidden by the incurved umbo.

The small brachiopods (group I) dominating the chalk brachiopod fauna seem to have a rather random distribution in the sediment. On the contrary, the larger, free living brachiopods (group II) are sometimes found in small aggregations composed of one to three species (pl. 5 c). There is a pronounced correlation between aggregations of the larger brachiopods and absence of potential substrates. The aggregations are thus found almost exclusively in the chalk of Zones 7–9 where the benthonic fauna is very reduced.

The quantitative distribution of the most important brachiopods in three sections is shown on figs. 14 and 15. There is a close agreement between the curve showing the weight of the washing residue (more or less equivalent to the quantity of bryozoans)

and the curve illustrating the total number of brachiopod individuals. The parallelism of the curves is mainly primary, the bryozoans playing the role of substrates for the brachiopods, and is only to a small degree secondary, due to variations in the pelagic sedimentation.

Size-frequency diagrams have been constructed for all brachiopods found in three samples (figs. 16, 17 and 18). It is seen that in all the more common species (all belonging to group I) the populations are dominated by large quantities of juvenile individuals. The hemispherical free living brachiopods (group II) are normally quite rare, but where they are common they show a bell-shaped or left (= negatively) skewed size-frequency distribution. The two types of distribution are due to differences in mortality, growth rate and adult size and must be seen in connection with the different adaptations of the two groups.

The small pedunculate brachiopods are adapted to a life attached to the very small hard substrates on the sea bottom, i.e. mainly small, delicate bryozoans. This implies that they spent their life very close to the surface of the sediment. This position is dangerous to small, sessile suspension feeders, which are very susceptible of becoming overturned by vagile benthonic animals and more or less buried in the topmost soft layer of the sediment. The juveniles of the free living larger brachiopods run the same risk as the juveniles of the minute pedunculate brachiopods as they are in all respects very closely alike (figs. 6, 7 and 9). A rather large size would appear to be necessary for the free living mode of life, and it takes some years to attain this size. It was therefore of great importance that the animals belonging to this group rapidly passed through the vulnerable small growth-stages and reached their final size and shape as soon as possible. The initial growth rate of these species must therefore have been much greater than that of the small species, a fact that again influenced the size-mortality pattern. This difference in growth rate is shown for *Gisilina gisii* (group I) and for *Terebratulina gracilis* (group II) in figs. 20, 21 and 22.

There is a good agreement between the actual size-frequency distributions and the theoretical distributions computed by CRAIG & OERTEL (1966).

It is shown that no stunting has occurred and the fauna of minute brachiopods must be characterized as comprising naturally small-sized species.

Thus the Danish chalk contains a rich fauna of brachiopods which were remarkably well adapted to the life on the level, relatively soft and fine grained chalk sea bottom.

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PLATES

PLATE I

Plate II

a–b: *Terebratulina longicollis* Steinich.

a: Ventral valve. Internal view. Spicular skeleton of the plectolophous lophophore showing the lateral arms with long, slender filaments and the recrystalized median spire. ×55.

b: Ventral valve. Like a, but median spire of plectolophe more strongly recrystalized. ×58.

c–g: *Terebratulina faujasii* (Roemer).

c: Dorsal valve. Internal view showing brachidium. ×30.

d: Spicular skeleton of plectolophous lophophore. Oblique anterio-lateral view. Note the filament bases along the lateral arm and the partially spiculated median spire. ×74.

e: Ventral view of d. Complete spicular skeleton of plectolophous lophophore. Anterior downwards. Mouth opening visible as a white spot at the upper part of the figure. The ventral side of the arms are not spiculated thus making it possible to see the great brachial canal in each arm. ×53.

f: Lateral view of d. ×74.

g: Isolated spicular skeleton of the anterior body wall. Dorsal view. Anterior downwards. Compare with pl. 1 a. ×60.

d–g are all isolated from the specimen on fig. c.
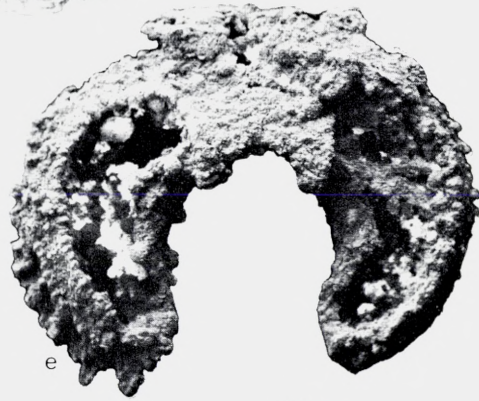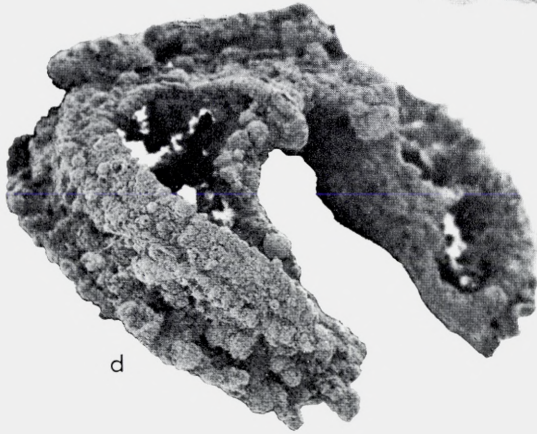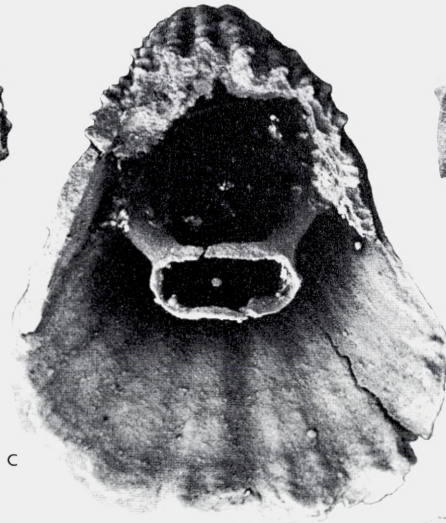
PLATE II

a: Recent *Argyrotheca* from Barbados attached to lunulitiform bryozoa. Note the very close attachment. ×29.

b: Large recent *Argyrotheca* from Barbados closely attached to lunulitiform bryozoa. ×29.

c: Recent *Argyrotheca* from Barbados attached to bryozoa. ×36.

d: As c. ×14.

e: *Aemula inusitata* STEINICH from the Danish chalk. ×57.

f: As e. ×73.

g: Lateral view of the specimen on fig. a. ×30.

h: As e and f. ×55. e, f and h show the great variability of this species. Note the large amphithyrid foramen.
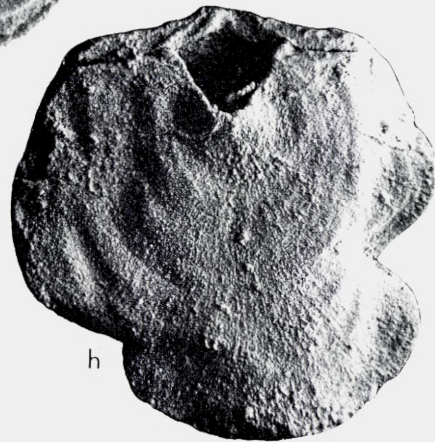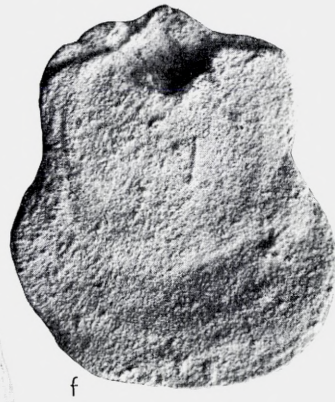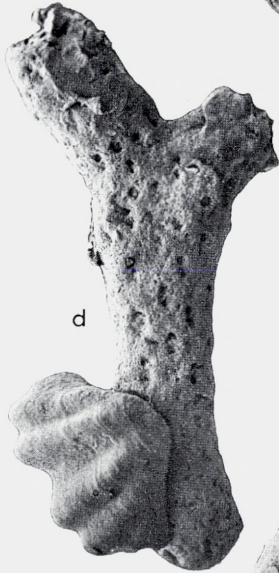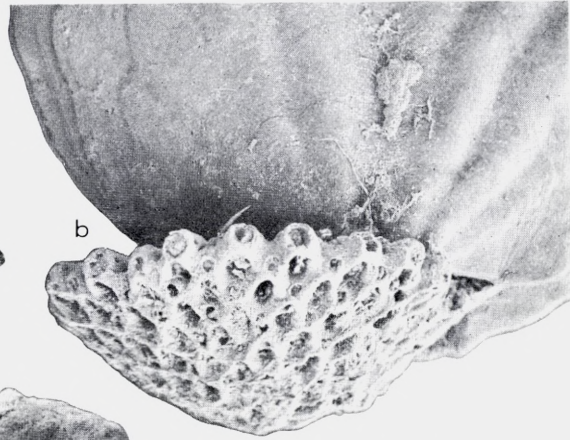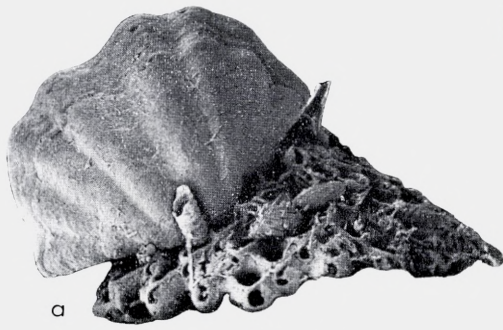
PLATE III

a: Recent *Terebratulina retusa* (L.) attached to bryozoans and shell gravel with a rootlike divided pedicle. ×10.

b: *Terebratulina chrysalis* (SCHLOTTHEIM) from the Danish chalk. Note the large foramen and the great similarity to a, e, d. ×9.

c: As b. ×5.7.

d–e: Two specimens of recent *Terebratulina retusa* (L.) with rootlike divided pedicle. a and e are covered with a thin sponge layer. d: ×10. e: ×5.5.

f: *Lunulites* sp. from the Danish chalk. ×42. Compare with pl. 3, a, b.

g: *Argyrotheca bronnii* (ROEMER) from the Danish chalk. ×25. Compare pl. 3, a, b, c, d, g.

h: *Terebratulina chrysalis* (SLOTTHEIM) from the Danish chalk with anterior commisure damaged by a bite. ×5.5.

PLATE IV

a

b

c

d

e

f

g

h

PLATE V