SVERIGES GEOLOGISKA UNDERSÖKNING

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WITH 9 PLATES

STOCKHOLM 1968

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Edited by the author and R. Becker

C. DAVIDSONS BOKTRYCKERI AB, VÄXJÖ

TO

Fritz Brotzen

SCIENTIST,

INSPIRING TEACHER AND FRIEND

THIS WORK IS DEDICATED

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ABSTRACT

In delimiting taxonomic units within fossil Foraminifera, the diagnostics have mainly been based on external characters. However, during the Early Mesozoic many representatives of the family *Nodosariidae* EHRENBERG 1838 exhibit a great instability in the external characters, which has caused great classificatory problems. According to the present investigation, the wall-structure in certain Liassic nodosariids seems to be more stable and thus of great importance for the classification. In this paper, the texture, perforation, layering and lamination, and ornamentation of the test have been treated. Notes are also given on the aperture. Certain features in the wall-structure have justified a subdivision of the genus *Dentalina* D'ORBIGNY 1826, into *Prodentalina* n. gen., *Mesodentalina* n.gen., and *Dentalina* s.str. No representatives of the latter genus (type species: *Nodosaria obliqua* D'ORBIGNY 1826, Recent) have been found in the Lower Lias of Sweden. New descriptions, in which the wall-structure plays an important role, are given some species of the new genera proposed, and species of other genera as well. The Liassic stratigraphy of the sampling localities is briefly treated.

ACKNOWLEDGEMENTS

The present paper has been prepared at the Geological Survey of Sweden (SGU), Stockholm. To Dr. F. Brotzen, former Director of the Department for Research and Applied Geology, SGU, I wish to acknowledge my great indebtedness for providing the working facilities, for generous advice and valuable discussions, and for his kindness in putting his own material to my disposal. To Professor P. Thorslund, former Director of the Paleontological Institute, Uppsala University, I tender my sincere gratitude for critical reading of the manuscript, and for extensive personal help. The author wishes to thank Professor V. Pokorný, Prague, during his visit in Stockholm in April, 1966, for helpful advice and criticism.

Further thanks are due to Professor I. Hessland, Director of the Paleontological Institute, Stockholm University, for his kindness in allowing me to use the electron microscope at his institute, and to his assistant, Dr. R. Hallberg for obtaining the electron micrographs. The writer is also greatly indebted to Dr. J. Cornwell, SGU, for revising the language. The final preparation of the drawings in this paper has been carried out by Mrs. I. Berglund, I. Palmaer, G. Hellström, and Mr. E. Ståhl to whom I wish to express my thanks. Thanks are also due to Mrs. I. Signorelli and Mr. G. Andersson for careful photographic copying.

INTRODUCTION

The foraminifers grouped within the family *Nodosariidae* EHRENBERG 1838 very likely began with ancestral forms in the upper Paleozoic. True nodosariids constitute a notable element of the foraminiferal fauna in the Triassic and, in certain facies, they dominate in the beginning of the Jurassic. After the Jurassic they show a negative trend in the geological succession.

As seen in publications by Gerke (1957), Nørvang (1957), Furssenko & Rauzer-Chernousova (1959), Reiss (1958, 1963), Brotzen (1963), Glaessner (1963), Loeblich & Tappan (1964) et. al., the problems concerning the evolution of this group, and consequently also the taxonomy, have been in the centre of the discussion. In this connection it has also been a main problem whether or not the wall-structure is different in different taxonomic units.

In addition to investigations by Gerke (1957) and Sellier de Civrieux & Dessauvagie (1965) on certain older nodosariid Foraminifera, most records on the wall-structure of Upper Paleozoic and Lower Mesozoic *Nodosariidae* were hitherto based on isolated observations. On the other hand, observations on the wall-structure in Cretaceous, Tertiary and Recent forms of *Nodosariidae*, treated in many papers, are usually based on fairly extensive material. The great knowledge of the wall-structure in Upper Mesozoic and younger nodosariids, and the imperfect knowledge of that in older ones, have resulted in a tendency to apply certain generalisations on younger nodosariids to the whole family *Nodosariidae*.

The present writer is aware of that the problems concerning the taxonomy and the evolution of the large family *Nodosariidae* need extensive studies of material from the Upper Paleozoic, the Triassic, and younger systems as well. However, he hopes that his observations will contribute to a better knowledge of the wall-structure in older representatives of the family.

ACTUAL PROBLEMS IN THE DISCUSSION OF THE WALL-STRUCTURE IN *NODOSARIIDAE*

More comprehensive references of works dealing with general problems concerning the wall-structure in the Foraminifera will be found in Wood (1949), Reiss (1963), and Loeblich & Tappan (1964).

Discussions on the wall-structure of the family *Nodosariidae* deal with evolutionary and taxonomic problems including the origin of the family, the changes and varying development of the wall-structure within it, and the content of the family from a generic point of view. According to Glaessner (1963) and Brotzen (1963), the origin of the *Nodosariidae,* as seen from the aspect of the wall-structure, would be an evolutionary trend from the Upper Paleozoic agglutinate test-walls, via calcareous granular, to compound walls, the different layers of the latter having different crystalline structures, and finally to the simple fibrous-radiate test-wall.

According to Glaessner, one line would be:

Astrorhizidae — Aschemonellidae — Nodosinellidae — Nodosariidae.

He thinks also that another line is possible, since the compound wall with an inner fibrous and an outer microgranular layer characterising the *Nodosinellidae,* also occurs in the *Paleotextulariidae.* According to Cummings (1956), the latter family is assumed to be derived from coiled endothyrid ancestors, one line leading to *Nodosinella* (syn. *Monogenerina ?)* in the Permian. The other line of origination would then be:

Endothyrid ancestor — *Paleotextularia — Paleobigenerina — Nodosinella — Nodosariidae.*

Brotzen (1963) accounts for the opinion that the inner fibrous layer of the Upper Paleozoic *Nodosinellidae* can be regarded as one of the characters which the Mesozoic *Nodosariidae* retained after a reduction of the outer layer of the compound wall of ancestral groups. Nørvang (1957) united the families *Nodosinellidae* and *Nodosariidae* in the superfamily *Nodosariidea.* He reclassified certain Liassic species previously referred to the nodosariid genera *Lingulina* and *Frondicularia.* Mainly owing to a stated absence of perforation of the test-wall and a lack of a true radiate aperture, Nørvang referred these forms to the genera *Geinitzina* SPANDEL 1901 and *Spandelina* CUSHMAN & WATERS 1928. Without giving his opinion of the wall-structure in the Upper Paleozoic genera *Geinitzina* and *Spandelina,* the present writer will just point out that at least Liassic forms of *"Spandelina"* sensu Nørvang actually are perforated, and often have a radiate aperture (Norling 1966).

Sellier de Civrieux & Dessauvagie (1965) have stated that the differences in the wall-structure between the Lower Mesozoic foraminifers referred to *Nodosariidae* and the Upper Paleozoic foraminifers referred to *Nodosinellidae* probably are caused by recrystallisation of the latter. Concequently, they consider the family *Nodosinellidae* not valid and place the genus *Geinitzina* with the *Nodosariidae*. The genus *Spandelina* is considered insufficiently documented and its validity doubtful.

The taxonomic importance of the presence or absence of perforation through the test-wall has been discussed in many papers since the nineteenth centuary. A brief review of these discussions will be given later in this paper (p. 20).

Not until the last decades has the lamination of the test-wall in nodosariid Foraminifera received due attention, although Beissel had already clearly demonstrated this character in 1891. Most studies on lamellar test-walls have in common that they are based on materials from systems younger than the Jurassic, inter alia in papers by Beissel (1891), Johannesen (1952), Smout (1954, 1955) and Reiss (1958, 1963).

Concerning the Jurassic and older nodosariids, Gerke (1957) discussed in a short paper the evolution of the lamination of the test-wall in certain Permian, Triassic and Liassic forms, illustrated by several stages of lamination between the nonlamellar and completely lamellar wall. He divided the lamination into primary and secondary lamination. The primary lamination affects both the septa and the test-wall. Its formation is not yet fully understood. Probably it is not of secretory origin, but a special type of crystalline aggregate of the calcite (see p. 18). The secondary lamination, on the other hand, is due to superposition of calcareous material secreted by the animal. In a secondarily lamellar foraminifer the primary wall of every chamber covers completely and adheres to the previously formed test. The septa are never secondarily lamellar (Reiss 1963).

Brotzen (1963) was also aware of the fact that the wall-structure of the Upper Paleozoic and Lower Mesozoic *Nodosariidae* diverges from that of younger forms of the family. He suggests that the test-wall in *Nodosariidae* has undergone an evolution from a compound test-wall in its Paleozoic ancestors, via a nonlamellar test-wall in Triassic and Early Jurassic forms, to the true lamellar test-wall, which should appear for the first time in the Middle Jurassic.

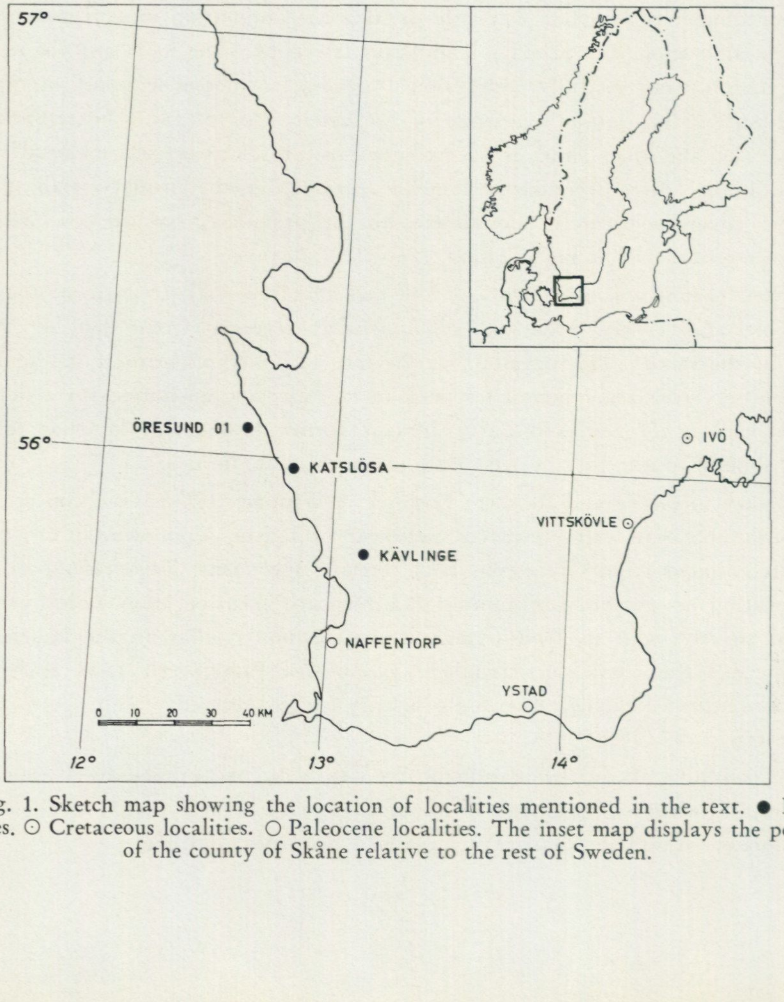
Contrary to Gerke and Brotzen, Loeblich & Tappan (1964) state, concerning the wall-structure, that well preserved specimens of Liassic *Nodosariidae* can scarcely be differentiated from Cretaceous and Tertiary specimens. Reiss (1963) in his reclassification of perforate Foraminifera, does not mention any successive evolution of the test-wall in *Nodosariidae* from the nonlamellar to the lamellar one. He describes the whole superfamily *Nodosariidea* EHRENBERG 1838 as having a distinctly septate, calcitic radiate, primarily single layered, finely perforate, lamellar test-wall.

The evolution of the lamination of the test-wall, as outlined by Gerke (1957) is essentially accepted by Sellier de Civrieux & Dessauvagie (1965) in their reclassification of certain Permian, Triassic and Liassic *Nodosariidae*.

As seen above, there are many controversal opinions concerning the wall-structure in *Nodosariidae.* Most of them seem to be due to an imperfect knowledge of the wall-structure in older nodosariids, and a tendency to generalize characters found in younger nodosariids to apply to the whole family.

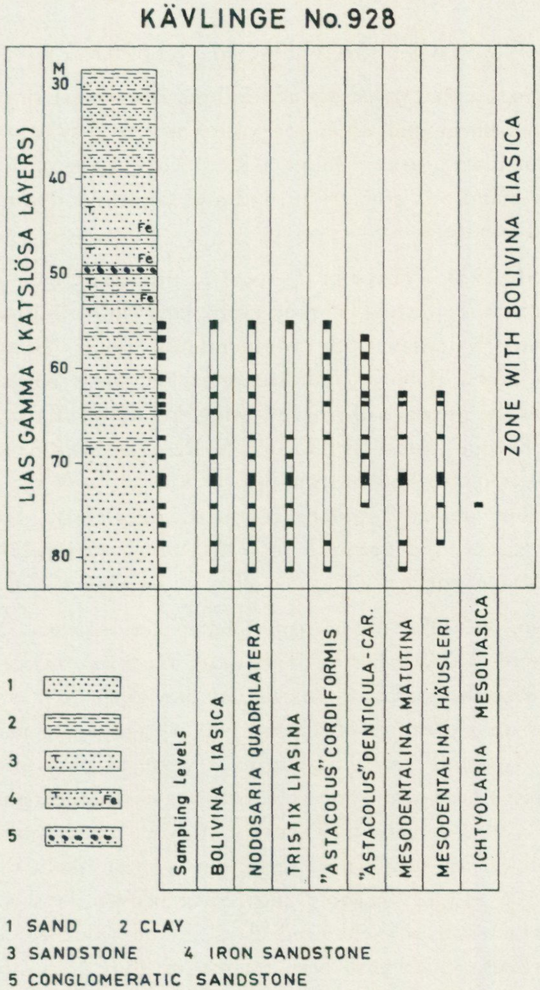
METHODS AND MATERIAL

METHODS. — To obtain thin-sections, the foraminifers have been embedded in a transparent medium, ground with the aid of carborundum powder, and finally polished with aluminium oxide. Notes on methods applied for the present work have been given in a previous paper (Norling 1966). The photomicroscope used was a Zeiss Ultraphot II, equipped with phase contrast condensor, polarisor and analysor, allowing magnifications up to 2,500 x. The film has invariably been Agfa Isopan 13 DIN, 9×12 cm. The preparations for electron micrographs were carried out by Dr. R. Hallberg, the Paleontological Institute of Stockholm University. A comparable procedure has been described by Krinsley & Bé (1965).



Text-fig. 1. Sketch map showing the location of localities mentioned in the text. ● Liassic localities. ⊙ Cretaceous localities. ○ Paleocene localities. The inset map displays the position of the county of Skåne relative to the rest of Sweden.

LIASSIC MATERIAL. — The foraminifers examined, including numerous species by most previous students referred to the genera *Lingulina, Nodosaria, Dentalina, Marginulina, Astacolus, Planularia,* and *Lenticulina,* are from the Lower Lias of Skåne, S Sweden. They were taken in cores of two borings at Kävlinge, 12 km NW of Lund, one boring in Öresund, offshore from Hälsingborg, and from the classical outcrop at Katslösa, 10 km SE of Hälsingborg. The Kävlinge and Katslösa material was collected by Dr F. Brotzen, the Öresund material by the author. In addition, material from the Upper Lower Lias of England has been examined, collected at Waddington Brick Pit, Lincolnshire, and kindly placed to my disposal by Dr V. Jaanusson, Uppsala.



Text-fig 2. Kävlinge core no. 928. Range of foraminiferal species within Upper Lias γ (Lower Pliensbachian).

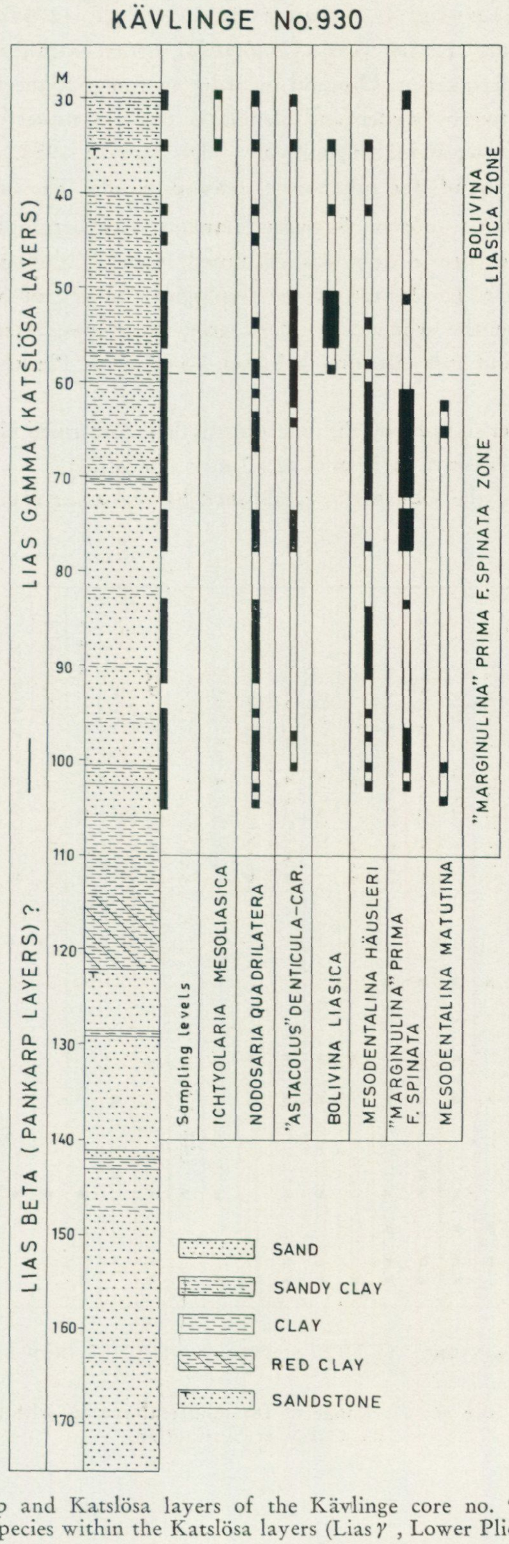
MATERIAL FOR COMPARISON. — For comparative studies on wall-structures of nodosariids from different geological systems great use was made of Dr. Brotzen's collections of Cretaceous and Paleocene foraminifers. The Cretaceous material was collected in cores of borings at Ivö, Vittskövle, and St. Köpinge in E Skåne, the Paleocene foraminifers in cores of borings at Ystad in S Skåne and Klagshamn and Naffentorp in SW Skåne (Fig. 1, p. 00). The recent nodosariids studied were collected in the Mediterranean, offshore from Bastia (Corsica) and Cagliori (Sardinia) by Dr. Tregouboff, Ville Franche, France. These collections were kindly forwarded to me by Mrs. K. Wängberg-Eriksson, the Paleontological Institute of Uppsala University. The repository of the collections is the Geological Survey of Sweden, Stockholm.

STRATIGRAPHICAL REMARKS

In 1951, three borings were carried out at Kävlinge (fig. 1) for the Geological Survey of Sweden. Two of them, placed in the valley of the Kävlinge River, W of the village, passed into Liassic strata. Below a Pleistocene cover of about 30 m in both borings, sequences mainly of grey-green sand and sandstone occur, intercalated with layers of clay and claystone.

KÄVLINGE NO. 928. (Text-fig. 2) — The pre-Quaternary sequence between 28.75 m and 83.25 m, consisting of grey-green sand and sandstone, rich in oolitic chamosite, contains a fairly rich foraminiferal fauna between 54 m and 83.25 m. Certain fauna elements indicate that these beds belong to Lias γ. This seems evident from the presence of the following species: *Bolivina liasica* (TERQUEM) occurring in NW Europe from Lias γ to Lias δ, *Mesodentalina häusleri* (SCHICK) and *Tristix liasina* (BERTHELIN) known from beds of Lias β — γ age. Furthermore, the lack of "*Marginulina*" *prima f. spinata* TERQUEM, index fossil of uppermost Lias β and Lower Lias γ, and the presence of "*Astacolus*" *denticula-carinata* FRANKE, suggest that the above portion could be referred to Upper Lias γ .

KÄVLINGE No. 930 (Text-fig. 3) (pre-Quaternary sequence: 29.20—176 m +). — The occurrence of *Bolivina liasica* (TERQUEM), *Ichthyolaria mesoliasica* (BRAND), and "*Astacolus*" *denticula-carinata* FRANKE in the upper part of the core section has been taken as an indication of Upper Lias γ age, since neither *Ichthyolaria mesoliasica* nor "*Astacolus*" *denticula-carinata* seem to pass into Lias δ in NW Europe. Lower Lias γ beds also seem to be present, as is indicated by the occurrence of "*Marginulina*" *prima f. spinata* TERQUEM. Below 103 m no foraminifers have been found. However, for lithological reasons it is most likely that Lias β also is present. Between 106 and 122 m, grey and red or brown clays occur. The location of these very characteristically coloured clays in the sequence, indicates the presence of Pankarp Beds, which have been referred to Lias β by Bölau (1954, 1959). However, without further studies, the limit between Lias γ and Lias β cannot be drawn in the core section.

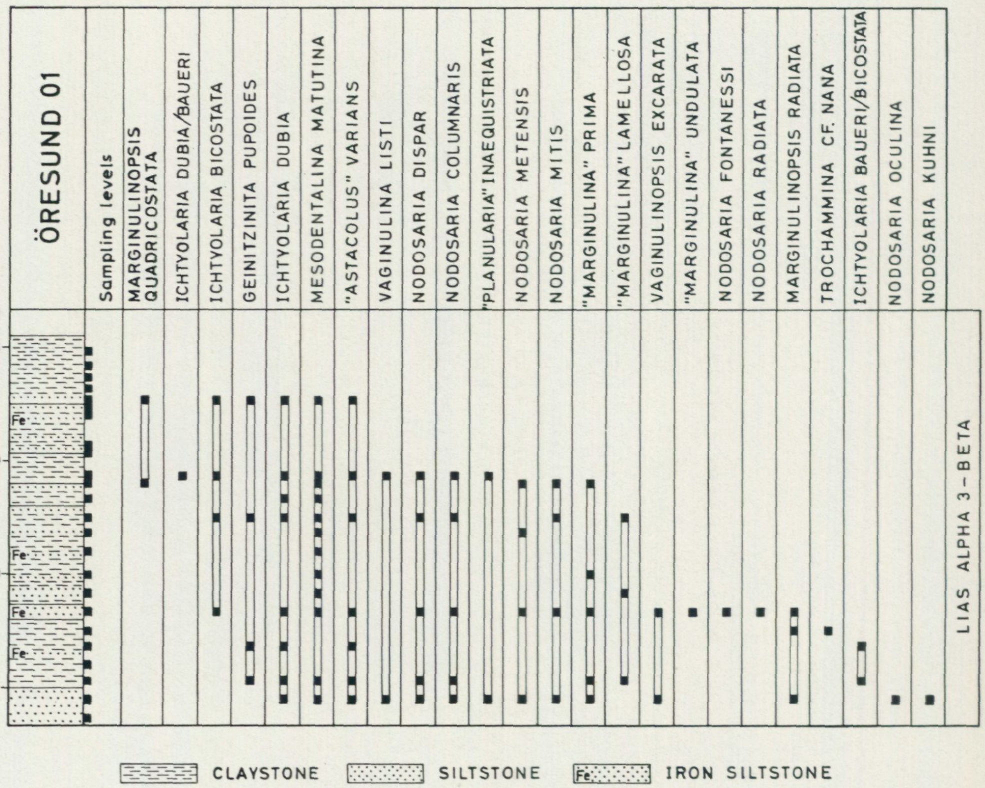


Text-fig. 3. Pankarp and Katslösa layers of the Kävlinge core no. 930. Range of foraminiferal species within the Katslösa layers (Lias γ , Lower Pliensbachian).

ÖRESUND 01 (Text-fig. 4) (Location: N 56°4′3″, E 12°39′30″. Water depth: 17 m). — During the last ten years, geophysical, geotechnical, and geological surveys have been undertaken in Öresund in order to find out the best location for a bridge or tunnel between Sweden and Denmark. For this project, two borings were made in Öresund between Hälsingborg and Helsingør in 1958, one boring on the Danish side of the sound, the other on the Swedish side. The latter boring, ÖRESUND 01, was carried out by Svenska Diamant Bergborrnings AB (Craelius) as a core drilling. The core section was examined from a lithological-stratigraphical point of view by Dr. E. Mohrén at the Geological Survey of Sweden. According to his interpretation the sequence of dark grey claystones, intercalated with thin layers of siltstone and iron siltstone, below a 3.5 m thick Pleistocene cover, should be of Liassic age.

The present writer's study of the microfossils has confirmed this result as far as the core portion between 9.16 m and 42.80 m is concerned.

The Liassic age of the sequence is established by the occurrence of *Mesodentalina*



Text-fig. 4. Öresund core no. 01. Range of foraminiferal species within Lias α_3 — Lower Lias β (Lower Sinemurian).

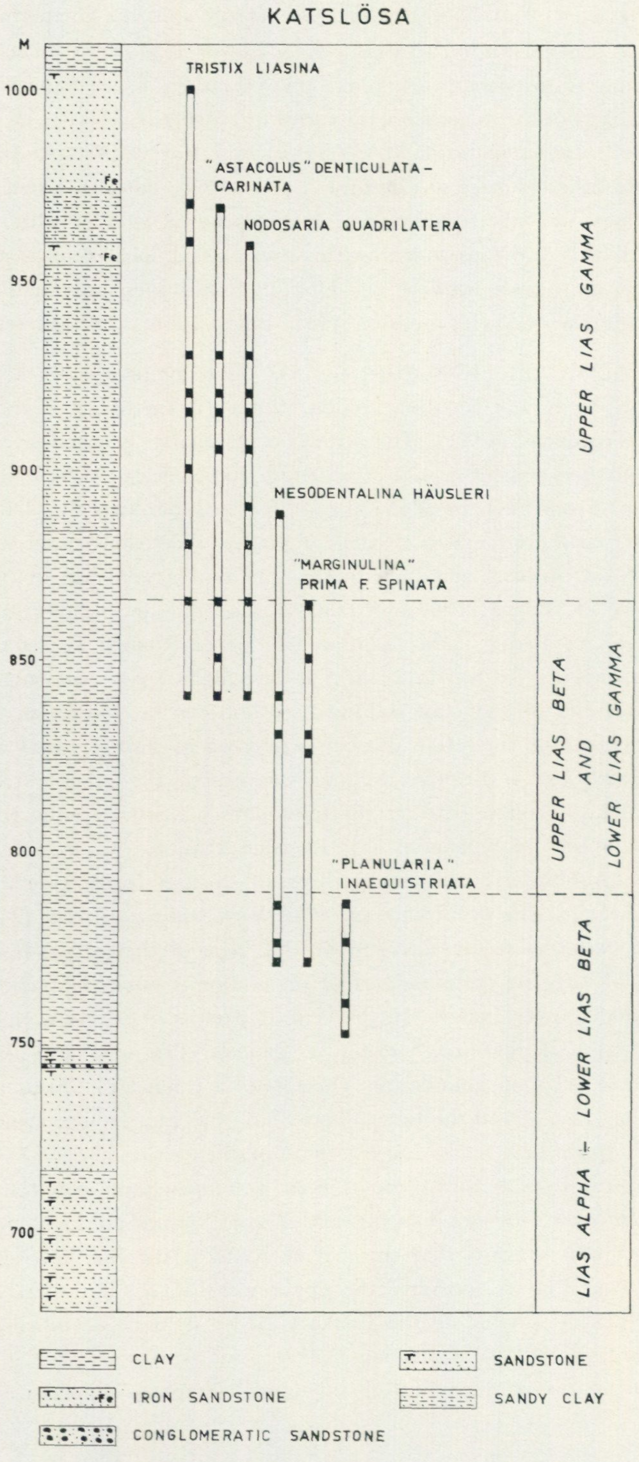
matutina (D'ORBIGNY) and "*Marginulina*" *prima* D'ORBIGNY. Furthermore, the age of the sequence can be limited to Lias α_3 — Lower Lias β, as an assembledge is found containing forms disappearing in Lower Lias β, for instance "Planularia" inaequistriata (TERQUEM), together with forms appearing in Lias α_3 in NW Europe, inter alia *Mesodentalina matutina* (D'ORBIGNY) and *Vaginulina listi* (BORNEMANN). As known from other borings in Öresund (Larsen 1965, Bang in Larsen 1965), neither the lithology nor the foraminiferal fauna provide evidence for locating the limit between Lias α and Lias β within this area. Using local geological terms, this claystone formation occurs between the Döshult Sandstones and the Pankarp Beds of grey and redbrown clays (Troedsson 1951; Bölau 1954, 1959; Larsen 1965).

THE KATSLÖSA SECTION (Text-fig. 5). — A comprehensive account of the Liassic stratigraphy of the Katslösa section, about 10 km SE of Hälsingborg, was published by Troedsson (1951). The strata, occasionally exposed in 1945 at the bottom of a ditch-system of c. 400 m in length, were measured by Drs. F. Brotzen and E. Mohrén. From ENE to WSW the section includes Lias α_3 (Döshult Stage), the uppermost Lias β and Lias γ (Katslösa Stage). Troedsson stated that the main part of Lias β was missing, not only in the Katslösa section, but in NW Skåne as a whole. However, Bölau (1959) has shown that red and grey-green clays and sandstones (Pankarp Beds), earlier supposed to be of Rhaetic age, actually should be referred to Lias β. At Katslösa, the Pankarp Beds are represented only by a 0.24 m thin horizon of red clay followed by non-marine, yellowish sandstone of small vertical extension, the latter also being referred by him to Lias β.

Reyment (1959) has a different opinion concerning the Liassic stratigraphy of NW Skåne, for he considers that certain ammonites indicate that the Katslösa Stage (sensu Troedsson) should belong to Lias β rather than to Lias γ.

Among the foraminifers collected by Brotzen, certain forms give a hint of the stratigraphical range. The occurrence of "*Planularia*" *inaequistriata* (TERQUEM) and *Mesodentalina matutina* (D'ORBIGNY) in the NE part of the section (Loc. 700—775 sensu Troedsson), suggests that this part of the section is not older than Lias α_3 and not younger than Lower Lias β. In the central part of the section (Loc. 825—875 sensu Troedsson), "*Marginulina*" *prima f. spinata* TERQUEM and *Mesodentalina häusleri* (SCHICK) occur in abundance. These two characteristic forms are restricted to the uppermost Lias β and the Lower Lias γ in NW Europe, the latter form being found also in Upper Lias γ. In the SW part of the section (Loc. 875—1000 sensu Troedsson) typical Lias γ forms occur, such as *Ichthyolaria mesoliasica* (BRAND), "*Astacolus*" *denticula-carinata* FRANKE and *Tristix liasina* (BERTHELIN). The foraminiferal fauna thus suggests that the marine parts of the Katslösa section include Lias α_3 — Lower Lias β, possibly the uppermost Lias β, and Lias γ, while the main part of Lias β (including the Pankarp Beds) seem to be missing, as already stated by Troedsson (1951) and Bölau (1959).

Certain Lower Liassic foraminifers of biostratigraphic importance are figured in pl. IX.



Text-fig. 5. Katslösa exposure. Range of foraminiferal species within Lias α_3 — Lias γ (Sinemurian and Lower Pliensbachian). After F. Brotzen.

THE TEST

NOTES ON THE TEST AND CHAMBER FORMATION. — Before entering into the description of certain characters of the calcareous test of Liassic *Nodosariidae,* the test and chamber formation in the *Foraminifera* will be briefly treated. According to Reiss (1963), the foraminiferal test must be regarded as an intraectoplasmatic skeleton, and not as an enveloping shell, since the cytoplasm coats both the inner and the outer side of the test.

The test may be simple or extremely complex. The test-wall may be a deformable membrane, or constructed by extraneous material cemented in an organic, ferriginous, calcareous, or silicious matrix, or formed by calcite or aragonite of varying structure, secreted by the animal. As far as is known to the present writer, most authorities hold the opinion that the inorganic component of the test in *Nodosariidae* always is calcite. The chamber formation in the *Foraminifera* is on the whole very little known, except for a few genera. Concerning recent *Nodosariidae,* nothing has been published on the chamber formation, as far as is known to the present writer. However, this process has been described by Myers (1935, 1952) in the genera *Patellina* and *Glabratella,* and by Le Calvez (1950) in the genus *Discorbinella.*

Even if these genera differ widely from the nodosariid genera, a review of the chamber formation in the genera mentioned, given by Loeblich & Tappan (1964), will give an idea of the process.

"In each of the genera *Glabratella, Patellina* and *Discorbinella,* a temporary cyst consisting of a thin membrane and debris collected by the pseudopodia is built for protection during secretion of a new chamber. When the cyst is completed, the pseudopodia withdraw; the test and cyst then are separated opposite the last chamber by an expanding mass of clear cytoplasm, which extends the width of a chamber below and beyond the margin. Indication of calcification of the surface membrane of the forming chamber first appears as bright points in reflected light. Pseudopodia extend through minute pores along the margin and the calcification gradually increase, shown as an increase in the amount of light reflected from its surface. In *Patellina* about 5 hours is required for completion of a chamber (Myers 1935). In *Glabratella* it can be seen that a new layer of calcite is added to the entire test at the time of formation of a new chamber. In *Tretomphalus* it has been observed that the pores are due to deposition of shell material around the base of short pseudopodia extending through the pseudochitinous membrane to the wall of the cyst and that they are not formed secondarily after the wall is completed. About 12 hours is required for making an adult chamber in *Glabratella* (Myers 1940).

In *Discorbinella* chamber formation is similar; the test and growth cyst around the margin are shown with pseudopodia extending out to the cyst margin. Rapid circulation of granules occurs at this time. The main pseudopodia then retract, leaving only fine extensions to the cyst, and the border changes in refringence, with perforations of the pseudochitinous pellicle that appears, showing as small, conical spaces. This pellicle, which is the first element of the test, first becomes enriched with lime salts at tiny points (e. g. *Patellina),* which by gradual coalescence produce the calcareous test. The pseudopodia then protrude from the new aperture and the completed chamber fills with ectoplasm.

About 8 hours is required for making a chamber in *Discorbinella.* The test is secreted by the ectoplasm and the pseudopodia, the endoplasm being found only in previously constructed chambers (Le Calvez 1950)."

Smout (1954) has stated five different ways of test and chamber formation in the Foraminifera:

1) by formation of a tube growing at its lip.
2) by addition of adherent chambers, each with its own wall.
3) by addition of "shell" material to the exterior of the test as a whole, spaces being thus formed by local interruption, or arching of the layers of the wall material.
4) by secretion at a single episode.
5) by intergration of spicules into a skeleton.

Concerning the *Nodosariidae,* the statements under 2) and 3) are of a special interest. If, as in 2), a new chamber wall is added to the previously constructed test without covering the latter, the foraminiferal test is said to be secondarily nonlamellar. If, as in 3), the new-formed chamber wall covers completely the previously formed test, the test-wall is referred to as secondarily lamellar. These statements will be more thoroughly discussed later on.

CRYSTALLINE AGGREGATES. — Since numerous terms, more or less adequate and sometimes incompletely explained, are used in papers on foraminiferal wall-structures for various types of texture, the most common types of crystalline aggregates of calcium carbonates will be described here.

Calcite, as well as aragonite, may occur in aggregates of crystals elongated in a particular direction, which is generally one of the crystallographic axes. The elongation is then described as being parallel to a, b, or c, as the case may be. The form is said to be bladed, if each crystal in the aggregate is flattened. If the crystals are small and needle-like, the form is acicular. Crystals being so tiny that they look like fibers, form a fibrous aggregate. When the individuals in a crystalline aggregate show no marked elongation, the form is said to be granular. When the crystals are diverging from a common center, they are said to be radiating. Calcite, as well as aragonite (together with many other minerals), may occur in aggregates of flattened plates, a form referred to as lamellar by the mineralogist. The individual plates or laminae are generally parallel, but can also be curved around a common center, giving a concentric form (Berry & Mason, 1959).

The crystallographic type of lamination must not be confused with the lamination of secretory origin in the so called lamellar Foraminifera. Both types of lamination occur. To avoid confusion, the crystallographic type of lamination will be called primary lamination, while the secretory lamination will be called secondary lamination.

When studying the chamber formation in living foraminifers it has been observed that the first indication of calcification may appear as small granules, seen as bright points in reflected light (p. 17). The nature of these granules is uncertain, but some laboratory experiments have given an idea of it. When mixing concentrated solutions of $CaCl_2$, $Ca(NO_3)_2$-acetate with $NaCO_3$ or K_2CO_3, Harting (1872) found, as the first indication of precipitation, a transparent gel consisting of numerous small globules, the globules first being isolated from each others, but as precipitation continued, becoming closely packed, producing complex and interfering textures. Similar experiments have been carried out inter alia by Bütschli (1880), Lehmann (1880), and Biedermann (1914). As examples of different textures found in such experiments Biedermann (1914) mentions: straight or bent rows of globules arranged into concentric patterns, "honey-comb" patterns etc. As known, such types of textures can be found also in microgranular foraminiferal tests. The relationship between the small granules, being the first indication of calcification in some cases at least, and the acicular or fibrous texture in the nodosariid foraminiferal test is not known. The granule, known as the spherulite, which is composed of radiating fibers of calcite is supposed to play an important role in the test formation. Under certain conditions the spherulite becomes an oriented growth; which means that only some sectors of the sphere increase, thus forming elongated crystal elements. A number of closely packed spherulites restricted to a thin layer are thus able to grow normal to the layer they are forming, with an acicular or fibrous texture as the final result.

Textures of the test

In the nodosariid foraminifers examined, four basic types of texture have been found: 1) vesicular, 2) granular, 3) acicular, and 4) fibrous.

Vesicular texture (Pl. I, fig. 4). — Under normal magnification, c. 250—500 x, this texture often gives the impression of being granular, but when examined under high magnification the calcite is found to have a lot of hollow spaces (vesiculi). The vesiculi, having a polygonal form, may vary greatly in size (1—10 microns). In thin-sections the open spaces form a reticulate pattern. The vesicular texture is found in many ornamentations, e. g. in ribs and costae, especially at the surface of the ornamental elements. Towards the inner part of the ornamental elements, this texture pass into a granular one.

A *granular texture* occurs as unequidimensional or equidimensional, closely packed polygonal grains (1—10 microns) in ribs, costae, and keels in most of the ornamented Liassic nodosariid Foraminifera, inter alia in the genera *Mesodentalina* nov., *Ichthyolaria, Nodosaria, "Marginulina"*, and *"Planularia"*. It also occurs in the granular interior layer found in some forms (p. 22, Pl. II, fig. 5).

Globulites arranged in rows normal to the surface of the test, reported to occur in some *Textularia* (Cummings 1955) are not found in the nodosariids examined.

An *acicular texture* (p. 18, Pl. V, fig. 4) is found in specimens of the genera *Prodentalina* nov. and *"Astacolus"*.

The *fibrous texture* (p. 18, Pl. III, fig. 3) is the most common texture in the material examined. The fibrous and the acicular textures only occur in the inter-ornamental parts of the test, while the granular and the vesicular texture are restricted to the ornamental elements and a thin interior layer.

Perforation

Pl. II, fig. 4; Pl. III, figs. 1, 2, 4; Pl. IV, figs. 2, 3; Pl. VI, figs. 1—4; Pl. VII, figs. 1, 3.

Although more than one hundred years have passed since the perforation of the test-wall in the Foraminifera was used for classification for the first time, it is still discussed to which degree this feature is of taxonomic importance. Nowadays, no one dealing with foraminifers, recent or fossil, will accept either the two-fold division into Perforate and Imperforate Foraminifera (Reuss 1861, Carpenter 1862), or the three-fold division into Arenaceous, Perforate and Imperforate Foraminifera used in the classification by many early workers, including Jones (1876), Zittel (1876), Schwager (1877), and Bütschli (1880). In fact, the death-blow to these classifications was given by the discovery of perforated arenaceous forms (Moebius 1880), and the perforate initial chamber of *Peneroplis*, a typical "imperforate" genus (Rhumbler 1894). In consequence of these discoveries, the three-fold division mentioned above, was later abandoned by Kenma (1903), Douvillé (1906), Rhumbler (1911), and Schubert (1920), though Rhumbler considered the perforate nodosariids and rotaliids to be natural groups. However, the fact that a classification mainly based on the absence or presence of pores was abandoned early, does not mean that the perforation has lost its position as an important taxonomic character. Chapman & Parr (1936) used it in their classification, as did Cushman (1940, 1947). Originally, the perforation was one of few main characters used in the classification, but was found to give rise to unnatural groups. It has subsequently approached the position of being one of many characters used in the classification. Wood (1949) held the opinion that composition and texture are characters of greater taxonomic importance than the perforation, which has been found to occur in completely unrelated groups. Hofker (1951, 1956) stated that the perforation has proved to be of high importance in respect to taxonomy. According to this author, the size, form, and distribution of the pores are features very characteristic for different species. He also stated that in geologically older species, the pores in most groups are very fine (protopores c. 0.5—5 microns). In geologically younger species, he found that a second kind of pores had been developed from the protopores in such a way that a certain proportion of protopores end in a common large pore (deuteropore c. 5—15 microns). Hofker also stated the pore index to be of great importance in the classification (pore index = the relation between pore diameter and the number of pores per unit area).

Reiss (1963) also stated that there is little doubt that size and distribution per unit area of pores are features of great taxonomic significance. However, giving examples of earlier forms having coarse pores and their (probable) descendants having fine pores, and also giving examples of groups where pore size changes during ontogeny, Reiss warns of wide conclusions concerning the evolution from fine to coarse pores. He thus thinks that too little is known on pores as a biocharacter to use them as a basic criterion in classification.

Höglund (1947) studied the size, form and distribution of pore openings in the outer, as well as the inner surfaces of tests in certain species of recent *Bulimina* and *Globobulimina* (Pl. 22, figs. 1—6), and found great differences in the patterns of the two surfaces. Such differences have not been observed in the Liassic *Nodosariidae* described here.

As has been pointed out by many workers on foraminiferal wall-structures, the test is not evenly perforated. There are always certain imperforate regions; the apertural area, the main parts of septa (former apertural areas), the chamber sutures, and the ornamental elements (ribs, costae, marginal keels).

According to Reiss (1963), apertural areas, canals, chamber margins and edges (at the same time regions of ornamentation), are regions of strong cytoplasmic activity and streaming. It seems therefore, he states, that parts of the test formed in regions of strong cytoplasmic activity and streaming, or formed within the cytoblast, are essentially imperforate.

Many authors have supposed the pores to be passageways for pseudopodia with locomotory functions; to gather food and to transport excretory products. Glaessner (1945), Smout (1954) et. al., believed the pores to be communication channels for cytoplasm inside and outside the test. It seems however, that very little is known about the functions of the pores and their relationship to pseudopodia, although careful examinations have been undertaken on living perforate Foraminifera (Le Calvez 1930, 1938, 1947; Myers 1935, 1942; Jepps 1942) et. al.

It has been observed that a newly built chamber in perforate foraminifers is perforate from the beginning, and that the pseudopodia definitely take part in the chamber formation, but none of the above mentioned authors could observe the actual relationship between the pseudopodia and the pores.

Some perforated foraminifers are reported to have finely perforated plugs (sieve plates) deposited in the pore canals. This has been beautifully illustrated with electron micrographs by Jahn (1953). Arnold (1954) believed that these micro-perforated sieve plates allowed actual pseudopodial transfer, while Le Calvez (1947) was of the opinion that the pores are blind and that effective exchange of cytoplasm inside and outside the test is possible by osmotic processes only.

Until the neontologists have clarified the function of the pores and their connection with the pseudopodia, the taxonomic value of the perforation can scarcely be definitely established.

Concerning the perforation of Lower Liassic nodosariids, the present investigation seems to show that:

1. Contrary to the opinion of some authors, there rarely exist forms actually being imperforate. Thus, all examined specimens of *Geinitzinita pupoides* (Nørvang)

and "*Astacolus*" *varians* (BORNEMANN) from Lias α_3 — Lower Lias β lack pores. However, representatives of these genera from Lias γ are finely perforated.

2. All Liassic specimens of *Ichthyolaria* WEDEKIND (by most previous students referred to *Frondicularia)* are shown to be perforate (Norling, 1966).
3. There is a relation between the presence, size and frequency of pores and the degree of secondary lamination of the test-wall. Thus, forms having a secondarily nonlamellar test-wall are either imperforate, or perforated with extremely fine pores (< 1 microns in diam.), or perforated with somewhat larger pores (1—2 microns) with a low frequency. On the other hand, the secondarily lamellar foraminifers examined are always perforated with a high frequency of pores (1—5 microns in diam.).

The correlation between the type of perforation and the degree of lamination of the test-wall suggests that the pores have some function in the formation of lamellae, as was already suspected by Le Calvez (1950). Compared with Cretaceous, Tertiary, and Recent representatives of the family, Liassic lamellar *Nodosariidae* have about the same pore size (< 5 microns). It means that no evolution from protopores to deuteropores (sensu Hofker) has been found in the *Nodosariidae*.

Layering and Lamination

THE BASAL ORGANIC LAYER. — In foraminifers with fibrous-radiate and granular, calcareous, secreted tests, as well as in agglutinate forms, a basal organic layer is reported, which is usually supposed to constitute the originally formed wall layer. It then becomes calcified or adds foreign matter to its surface. This basal organic layer has been isolated in decalcified preparations of many Recent forms, and in some fossil ones as well (Wetzel 1957). It has been variously regarded as chitinous, chitinoid, pseudochitinous, keratinous, proteinous or techtinous. Averintzev (1903) studied the organic component of the test in *Peneroplis* and found a protein *(albuminoid)* chemical reaction, wherefore it must be unrelated to true chitin. This discovery has been verified by many later workers. According to Hedely (1958), the organic lining underlying the agglutinated testwall of *Haliphysema,* gives the reaction of carbohydrate and a protein, and is therefore regarded as a mucopolysaccaride or a mucoprotein. According to Reiss (1963), the existence of such a basal organic layer is also proved in nodosariid Foraminifera, at least in some genera.

THE INTERIOR GRANULAR LAYER. — As mentioned before (p. 19), a thin interior layer of granular calcareous material is present in some Liassic nodosariids examined. This layer is composed of inequidimensional polygonal grains in some cases (Text-figs. 7 A, C—E, p. 32; Pl. II, fig. 5), and, in other cases, of small globulites, often arranged to form a reticulate pattern. In species with a granular layer, this layer completely covers the internal surfaces of the test-wall and septa.

It is obviously not a secondary formation deposited during fossilisation, since it actually has pores inside perforated parts of the main test-wall. Possibly it is formed as the first calcified layer outside the basal organic layer during the test-formation (see p. 17). A similar interior granular layer has been observed in Paleozoic nodosaroid Foraminifera (Cummings 1955, Sellier de Civrieux & Dessauvagie 1965). On the other hand, it has not been reported to exist in *Nodosariidae* younger than from the Lias, as far as is known to the present writer. It is therefore believed to be a primitive feature.

THE EXTERIOR FIBROUS LAYER (The main test-wall). — In non-ornamented Liassic nodosariids, the main test-wall is homogeneously composed of radiate calcite, the crystals being elongated (fibrous or acicular) with their c-axis oriented normal to the surface of the test. In perforated forms, the pores are essentially situated in between the radially disposed crystals, the pores thus being also radiating. In ornamented Liassic nodosariids, the main test-wall is composed of calcite in two basic types of textures: 1) granular in longitudinal ribs, costae, and marginal keels, which usually penetrate the test-wall; 2) fibrous or acicular in interornamental parts of the test. In perforated, ornamented *Nodosariidae,* the pores are restricted to the fibrous (or acicular) parts of the test, while the granular ornamental elements are essentially imperforate. In many ornamented forms, the granular component of the test (consisting of penetrative ornamental elements and the interior granular layer) clearly dominates over the fibrous (or acicular) component; hence it is not correct to describe nodsariids on the whole as having a fibrous-radiate test-wall, as has been done in many cases.

LAMINATION. — As mentioned before, Gerke (1957) divides the lamination of the test-wall into; 1) primary lamination, and 2) secondary lamination.

The primary lamination affects both the septa and the main test-wall. Its formation is not fully understood as yet. The present writer is inclined to support Sellier de Civrieux & Dessauvagie (1965) in their opinion that this type of lamination is an aggregation type of the calcite, and not of secretory origin (p. 18). In the present material it has been observed in forms of the genera *Ichthyolaria* WEDEKIND and *Mesodentalina* nov. only. The primary lamination is often indistinct, observable only under crossed nichols. According to Gerke (1957) and Sellier de Civrieux & Dessauvagie (1965) it is common in Permian and Triassic nodosariids, but rare in Liassic ones.

The secondary lamination is due to superposition of calcareous material secreted by the animal. In his examinations of Permian, Triassic, and Middle Liassic nodosariids, Gerke (1957) has found that there are different stages of secondary lamination of the test-wall, and that in different groups of *Nodosariidae,* the present type of secondary lamination is a stable and characteristic feature within the respective groups. The present investigation on Lower Liassic nodosariids seems to support Gerke's opinion. Based on examinations of thin-sections of many forms, by previous students referred to the genera *Frondicularia, Lingulina, Nodosaria, Dentalina, Marginulina, Astacolus, Planularia,* and *Lenticulina,* a three-fold division of the observed types of secondary lamination is proposed here:

1. Nonlamellar
2. Mesolamellar
3. Lamellar

1. The test-wall is said to be secondarily nonlamellar (Text-figs. 8 A, p. 35; 12 A, D, E, p. 50; Pl. III, figs. 1—4; Pl. V, figs. 1—4), when, in the polythalamous Foraminifera, the new chamber wall is added to the preceeding chamber in such a manner, that it is attached to and covers only a part of the latter (Smout 1954, 1955; Reiss 1963).

2. The secondarily mesolamellar test-wall (Text-figs. 8 B, p. 35; 12 B, p. 50; Pl. III, fig. 5; Pl. VI, figs. 2, 4), a term introduced here, is regarded an intermediate between the nonlamellar and the lamellar test-wall and can be defined as follows: When in the polythalamous Foraminifera, the newly built chamber wall is attached to and covers at least one preceeding chamber, but not the entire previously formed test, the test is said to have a secondarily mesolamellar wall.

3. The test-wall is referred to as secondarily lamellar (Text-figs. 8 C—D, p. 35; 12 C, F, p. 50; Pl. II, figs. 1, 2; Pl. III, fig. 6; Pl. VI, figs. 1, 3; Pl. VII, fig. 3), when in the polythalamous Foraminifera, the new chamber wall covers completely and adheres to the previously formed test (Reiss, 1963).

The nonlamellar test-wall clearly dominates in the Lower Liassic nodosariids examined, in orthoserial and curviserial, as well as in spiroserial forms. The mesolamellar test-wall has been found in forms referred to *Mesodentalina matutina* (D'ORBIGNY) and *Mesodentalina häusleri* (SCHICK), and in some formes of the *"Lenticulina plexus"*. A true secondarily lamellar test-wall has only been found in forms referred to genus *Nodosaria,* and in some forms of the genus *Lenticulina* as well. The basic types of secondary lamination will be further discussed at some length in the descriptions of species.

Ornamentation

Ornamental features are very common in Liassic nodosariids and play an important role in the taxonomy. In many cases the ornaments show a certain evolutionary trend during the Lias, which is of great importance for the biostratigraphy. In several papers, Barnard (1950, 1957, 1963) has dealt with the ornamentation in the species groups represented by *Ichthyolaria ("Frondicularia") sulcata* and *Geinitzinita ("Lingulina") tenera.*

As far as *Ichthyolaria ex gr. sulcata* is concerned, Barnard states that it exhibits a "progressive evolution" in the ornament of the test throughout the Lower Lias, in that early forms having eight to twelwe longitudinal ribs are followed by forms having six to eight ribs. Degeneration of the peripheral ribs usually takes place first and slowly spreads to the central ribs. A reduction then occurs to four ribs and after that to two. During the evolution forms often show remains of early ribs, discontinuous or badly developed. Finally, completely smooth forms are developed, assigned to *Ichthyolaria terquemi.*

Geinitzinita ex gr. tenera (Lingulina tenera by Barnard and most other previous authors) also exhibits an evolution from costate to more or less smooth forms during the Jurassic. Barnard's observations have been verified by other workers, inter alia by Nørvang (1957).

Although the appearance and evolution of the ornamentation in Liassic nodosariid Foraminifera are well-known, the very texture of the ornamental elements has not received due attention.

The present study on transverse and longitudinal thin-sections has given many interesting results concerning the ornamentation. It has been found that most ornamental elements, such as longitudinal costae, ribs, striae, and keels usually affect not only the external parts of the test but also the internal; it means that these elements penetrate the test-wall. In ribbed forms of *Ichthyolaria,* remains of "degenerated" ribs sometimes can be seen as tiny granular parts in the fibrous test-wall, even in cases where these remains are not visible on the surface of the test (cfr Norling 1966).

It has been postulated many times that the test-wall of Liassic *Ichthyolaria (Frondicularia, Spandelina* sensu Nørvang) is finely granular and imperforate. However, in the Lower Liassic forms of *Ichthyolaria* examined (including *I. bicostata, I. dubia, I. baueri,* and *I. sulcata),* the interornamental parts of the test are always fibrous-radiate and perforate. As mentioned above, the granular (or vesicular) and imperforate ornamental elements penetrate the test-wall, giving rise to a textural alternation of granular and fibrous sectors in the wall. Because of this penetrative ability of the ornamental elements, a longitudinal thin-section may completely fall within a granular zone of the test. It is believed therefore that the texture of the test-wall in Liassic *Ichthyolaria* often has been erroneously interpreted (Norling 1966).

In the lamellar forms examined the penetrative ornamental elements are also laminated (Text-figs. 7 B, D, p. 32).

Using Smout's terminology (1954), the ornamentation mentioned above should be referred to the inflational-textural type, possibly with single exception of the peripheral keel in certain smooth forms. Such a keel occurs in many Liassic forms usually referred to the genera *Astacolus* and *Lenticulina.* In addition to the longitudinal ribs traversing the test of many forms, this peripheral keel has a granular (and/or vesicular) texture and is also essentially imperforate. However, it is uncertain whether or not this keel is penetrative. In some cases, inter alia in "*Astacolus*" *varians* (BORNEMANN) it rather seems to be restricted to the surface of the test.

In addition to the longitudinally arranged ornamental elements, inflational, or inflational-textural ornamentation may occur as local thickenings of imperforate "shell" material along the suture lines.

In many forms of the *"Marginulina" prima* group, especially in forms from Lias γ, the often strong longitudinal costae are connected at every chamber suture by transverse ridges, giving rise to a peculiar surface morphology of the test. The chamber wall of perforate, fibrous-radiate calcite often outcrops in small oval windows only (Text-fig. 11 A—C, p. 47).

Another two basic types of ornamentation are mentioned by Smout (1954); the incised ornamentation, and the residual one. The incised ornamentation concerns isolated portions of "shell" material on the surface of the test, giving rise to pillars and plate-like structures. The residual ornamentation concerns a special type of pillar arising as masses of lamellar material, more or less cylindrical in shape and formed by interruptions in the lamellae (Reiss 1963).

Concerning the Liassic *Nodosariidae,* these last mentioned types of ornamentation seem to be of subordinate importance and will not be discussed here.

Notes on the aperture

The term aperture is used only for the single or multiple opening in the distal wall of the last chamber. The openings between consecutive chambers are referred to as foramina.

Being a character of great importance in evolutionary and taxonomic studies, as well as in physiological, great attention has long been paid to the aperture. Many papers have been written in which its function, various positions and shapes have been dealt with. Here some comments will be given on the "radiate" aperture only. Data on the apertures studied are given in the description of species.

As is well-known, the apertures of many nodosariid foraminifers are usually described as radiate. This term does not say very much. It will be very difficult for the reader to get an idea of what the radiate aperture looks like, unless the descriptions are accompanied by good illustrations. In this connection, a differentiation into four basic types of radiate apertures is proposed, even if the present writer is aware that the shape of the aperture may change considerably in the course of ontogeny and phylogeny:

1. *Apertures with radiating grooves.* — The grooves are often narrow, suture-like depressions in the wall, radiating towards a common centre, the aperture. All grooves may be of the same length, which is usually the case in foraminifers with a circular transverse section of the aperture chamber. In flattened forms, the grooves may be extended in the direction of the longest axis. This type of aperture is common in forms referred to the genera *Nodosaria* (smooth forms), *Prodentalina* nov. gen., *"Marginulina", Marginulinopsis, "Astacolus"* and *"Planularia"*. It is also frequent in the genus *Pseudonodosaria* and the family *Polymorphinidae.*

2. *Apertures with radiating slits.* — The radiating slits are united into a common centre giving a stellar shape to the aperture. It is common in forms referred to the genus *Ichthyolaria (Frondicularia* by most previous students), and also in many forms of the *Lenticulina* plexus.

3. *Apertural chamberlets with radiating slits.* — The radiating slits are usually not united, but leave a little cap of "shell" material in the centre. The slits may be of about the same length, or extended in the direction of the longest axis. Often, one median slit broader and longer than the others occurs. In this case, the radiating slits form a secondary aperture in the chamberlet covering the primary aperture. The function of the slitted chamberlet is supposed to be a kind of a filter. It has been well figured by Johannesen (1952). The apertural chamberlet is resorbed in earlier ontogenetic stages of geologically older forms, but persists in all stages of most of the Late Mesozoic, Tertiary and Recent ones (Reiss, 1963).

The slitted apertural chamberlet seems to be very rare in Liassic *Nodosariidae*. It has only been found in specimens of *Prodentalina vasta* (FRANKE) and *Prodentalina vetusta* (D'ORBIGNY) (p. 38, 37; Text-figs. 9 A_2, B_2, p. 39; Pl. IV, fig. 1).

4. *Apertures with a textural radiation.* — In many Liassic nodosariids, the border of the aperture is radiated by alternating granular and fibrous sectors. This type of aperture is especially common among ornamented forms (costate). The granular sectors may be raised to form radiating ridges, or planed to the same level as the fibrous sectors. In all cases, the granular sectors seem to be connected with the granular costae or ribs, traversing the foraminiferal test. The fibrous sectors of the aperture correspond to the interornamental, fibrous parts of the test-wall. This type of aperture has been found in many *Nodosariae*, inter alia in forms referred to *Nodosaria radiata, N. metensis, N. mitis, N. columnaris, N. oculina, N. costata, N. dispar*, and *N. issleri*. It also occurs in ribbed forms of *Mesodentalina* nov. gen. The shape of the aperture with a textural radiation may vary greatly.

Brotzen (1963, p. 68) has presented an interesting theory concerning the radiate aperture in *Nodosariidae*. He holds that the radiate aperture may be the only persistent character originating from an interior septation of the chambers. Such an interior septation is present in the Devonian genus *Multiseptida* BYKOVA, and in the Permian genus *Collaniella* LICHAREV. The last mentioned genus has been redescribed and placed with the *Nodosariidae* by Sellier de Civrieux & Dessauvagie (1965).

By virtue of the knowledge received concerning the nature of the ornamentation in Liassic *Nodosariidae,* and the found connection between the ornamental elements and the radiate aperture, the present author is disposed to support Brotzen's theory. The radiate aperture may not be the only character originating from an interior septation, but the longitudinal ribs and costae may be also closely connected with it. In ornamented Liassic *Nodosariidae,* the ornamental elements (ribs, costae) are radiating and penetrate the test-wall. In ornamented forms of *Colaniella,* e. g. in the Upper Permian species *Colaniella cylindrica* MIKLUCHO-MAKLAJ, the ribs also penetrate the test-wall but are extended to form an interior septation.

DESCRIPTION OF FOSSILS

Family *NODOSARIIDAE* Ehrenberg 1838

Genus *Geinitzinita* Sellier de Civrieux & Dessauvagie 1965

TYPE SPECIES. — *Geinitzinita oberhauseri* Sellier de Civrieux & Dessauvagie 1965.

Geinitzinita pupoides (Nørvang)

Textfig. 6 a—g; Pl. I, figs. 1—3

1957 *Geinitzina tenera* (Borneman) ssp. *pupoides* Nørvang. — p. 60, figs. 25—29.

1965 *Geinitzinita pupoides* (Nørvang). — Sellier de Civrieux & Dessauvagie. — p. 81, Pl. X, fig. 7; Pl. XX, figs. 7—8.

HOLOTYPE and TYPE STRATUM. — A well preserved specimen figured by Nørvang, 1957; Fig. 27. Lower Lias γ (L. Pliensbachian); boring Gassum 1; depth 4349′ — 4350′, Denmark.

SWEDISH MATERIAL. — Numerous specimens, boring Öresund 01.

DESCRIPTION. — Test oval to subtriangular in frontal view; transverse section oval to bilobate, sometimes tricarinate.

Chamber arrangement uniserial, orthoserial. Number of chambers 5—7 in megalospheric forms; 7—10 in microspheric forms. Proloculum more or less spherical, the following chambers oblate. Chamber sutures indistinct, hidden by the ornamental elements.

Aperture slitlike, elliptical or oval, with a smooth border, in frontal contour usually plane or slightly protruding. Seldom depressed.

Foramina similar to the aperture.

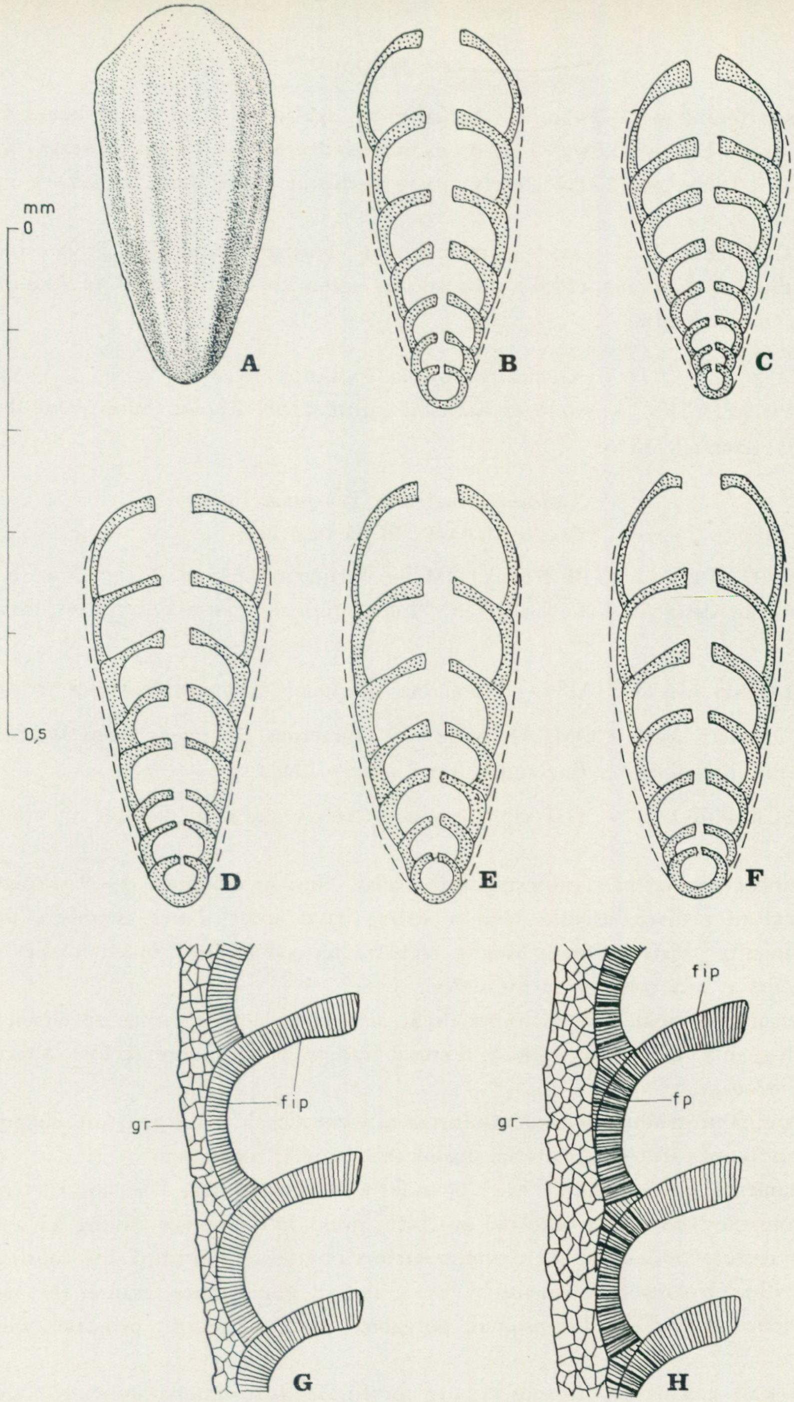
Ornamentation consists of two longitudinal, median ribs interspaced with several smaller, continuous or discontinuous ribs.

Between the ribs, additional fine striae may occur. Texture of ornamental elements microgranular.

Test-wall calcareous, fibrous, apparently imperforate, without primary and secondary lamination. The wall of one chamber not overlapping that of the preceeding chamber.

Septa fibrous-radiate, arched in frontal view; without primary lamination and interstratifications. Thickness of septa about the same as for the test-wall. Measurements in table 1, p. 31.

REMARKS. — According to Nørvang (1957), *G. pupoides* is derived from *G. tenuistriata* (Nørvang) from which it sometimes can hardly be distinguished. *G. pupoides* is said to be generally much more compressed and to have finer, lower, and much more regular ribs than *G. tenuistriata*. In their description of *G. pupoides*, Sellier de Civrieux and Dessauvagie (1965) report the thickness of the test-wall (excluding peripheral costae) to be 0.22—0.25 microns. These figures must be at least fifty times too small. As seen from the description, no perforation of the test



Text-fig 6 A—G. *Geinitzinita pupoides* (NØRVANG 1957). Specimens from boring Öresund 01, Lias α_3/Lower Lias β. Schematic drawings based on photograps.
A. Megalospheric form in frontal view.
B. Megalospheric form, longitudinal section.
C. Microspheric form, longitudinal section.
D—F. Megalospheric forms, longitudinal sections. Note the triangular form (D), and the depressed aperture (F).
G. Longitudinal section showing the granular marginal keel, the fibrous-radiate, imperforate, nonlamellar test-wall and septa.
Fig. 6 H. *Geinitzinita sp*. Longitudinal section showing the granular marginal keel, the fibrous-radiate, perforate, nonlamellar test-wall, and the fibrous-radiate, imperforate septa. Note the slight overlap of primary wall layers. Kävlinge No 930; 63 m. Lias γ.

has been found in *G. pupoides*. Actually, all specimens (c. 150) of genus *Geinitzinita* from Lias α_3/Lower Lias β examined are obviously imperforate, whereas specimens from Lias γ are clearly finely perforate (pore diam. c. 0.5—1 micron) (Text-fig. 6 h).

OCCURRENCE. — Lias α_3/Lower Lias β: boring Öresund 01; 21.08—40.30 m. According to Nørvang (1957), this species seems to be restricted to Lias β and Lies γ in Denmark.

Genus *Nodosaria* Lamarck 1812

TYPE SPECIES. — *Nautilus radicula* Linné 1758. Recent. Subsequent designation by Lamarck 1816.

Nodosaria metensis Terquem 1864

Textfig. 7 A—E; Pl. II figs. 1—5

HOLOTYPE and TYPE STRATUM. — Terquem 1864; pl. 7, figs. 5 a—b. Type stratum not designated. Levels given: "Lias inférieur. Assise à gryphées; Am. planorbis."

SWEDISH MATERIAL. — Numerous specimens from all localities treated.

MATERIAL FOR COMPARISON. — Numerous specimens from Waddington Brick Pit, Lincolnshire, England (Upper Lower Lias.)

DESCRIPTION. — Test elongate, sides nearly parallel, circular in transverse section.

Chamber arrangement uniserial, orthoserial. Nos. of chambers 5—9. Proloculum spherical to prolate, usually with a strong basal spine. Later chambers prolate, exceptionally oblate. Growth usually regular, but sometimes a much smaller chamber occurs at any position in the series.

Aperture terminal, central, on a neck, always radiate; in some specimens with radiating slits, in others with a textural radiation (granular sectors alternating with fibrous).

Foramina protruding, but not elongated to form a neck as the aperture, suggesting a resorption of calcareous material during the chamber formation.

Ornamentation consists of 12—20, usually 16 strong ribs. The ribs traverse the test from the basal spine onto the apertural neck. In specimens having an aperture with a textural radiation, the granular sectors obviously constitute the continuation of the ribs. Ornamental elements have a granular, imperforate texture, the granules being more or less equidimensional, polygonal grains. The ribs penetrate the test-wall.

Test-wall calcareous, fibrous-radiate, perforate with interruptions for the penetrative, granular, imperforate ornamental elements. The thickness of the test-wall increases towards the initial part of the test caused by lamellar superposition. Test-wall secondarily lamellar. Border lines between consecutive lamellae often accentuated by dark-brown non-calcareous material, supposed to contain matter

TABLE 1. *Geinitzinita pupoides* (Nørvang). Length and max. breadth of the test in mm. Proloculum diameter and wall thickness (exclusive peripheral keels) in microns.

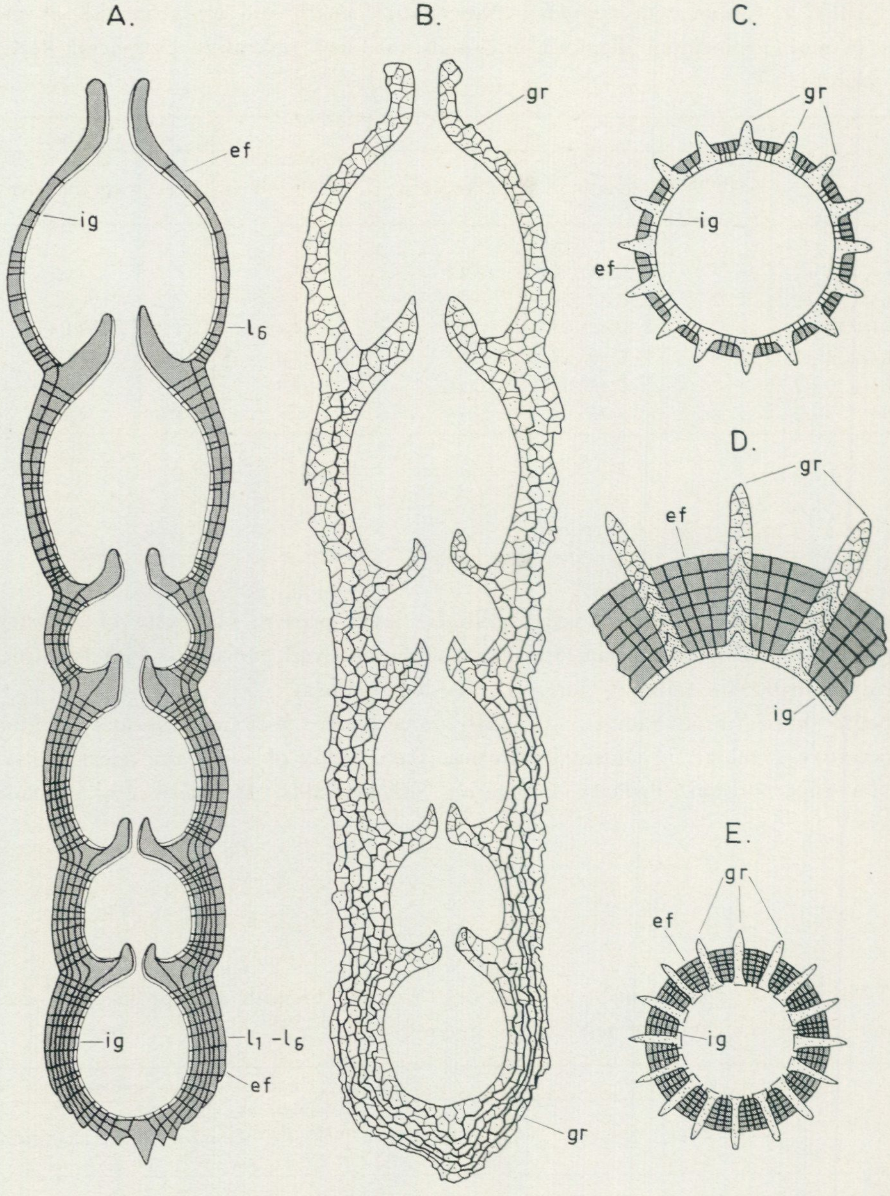
no	nos. of chambers	test		proloculum diameter	wall thickness	
		length	max. breadth		prol.	ap. chamber
64—32—1	7	0.41	0.17	57.2	7.2	5.7
63—32—2	7	0.37	0.16	42.9	7.2	7.2
64—32—3	7	0.40	0.17	64.4	11.4	11.4
64—33—1	8	0.39	0.17	57.2	14.3	11.4
64—33—2	7	0.44	0.16	64.4	11.4	7.2
64—33—3	8	0.46	0.16	50.1	8.6	11.4

of organic nature. A thin interior, granular layer present, obviously of primary origin (pp. 19, 22). Interornamental parts of the test-wall perforated with frequent, evenly distributed, radiating pores (D.: 1—1.5 microns).

Septa short, fibrous-radiate, essentially imperforate, with interruptions for the penetrative granular, ornamental elements. Basal parts of septa thickened by lamellar superposition. Primary lamination inappreciable. Measurements in table below.

TABLE 2. *Nodosaria metensis* Terquem. Length, breadth and proloculum diameter in mm. Thickness of test-wall in microns.

no	nos. of chambers	test		proloculum max. diam.	test-wall	
		length	max. breadth		prol.	ap. chamber
65—50	6	1.22	0.23	0.18	18.0	7.6
65—51	6	1.01	0.23	0.20	30.0	15.0
65—52	6	1.03	0.26	0.20	26.0	18.0
N 1	9	1.65	0.20	0.15	20.0	12.0
N 2	5	0.75	0.14	0.12	—	—
N 3	7	0.80	0.25	0.20	—	—
N 4	8	1.20	0.28	0.21	—	—
N 5	7	0.91	0.18	0.16	—	—



Text-fig. 7. *Nodosaria metensis* TERQUEM 1864. Figs. A—C, and E magnified c. 120 X, fig. D c. 400 X. Schematic drawings based on thin-sections of several specimens.

A) Longitudinal section between two pairs of opposite costae. Interornamental parts of the test composed of an interior granular layer (ig), and an exterior fibrous layer (ef). Lamellae (1_1—1_6) of ef increase in number towards the proloculum. Note the radiating pores penetrating ig, as well as ef. Number of pores very much reduced in the figure.

B) Longitudinal section through two opposite costae showing a granular, imperforate texture (gr). Note the lamination.

C) Transverse section through the apertural chamber showing granular, penetrative costae (gr), interior granular layer (ig), and exterior fibrous, perforate layer (ef).

D) Detail of fig. E.

E) Transverse section through proloculum showing interior granular layer (ig), penetrative granular costae (gr), and exterior fibrous, perforate layer (ef) composed of several lamellae.

REMARKS. — Concerning exceptionally small chambers occurring at any position in a series of regular chambers, Barnard (1950) comments: "It has been suggested by some American authors experimenting with living *Discorbis,* that if a chamber is broken off, the living animal will secrete an almost identical chamber, except that this will be much smaller." This is well illustrated by Pl. II, fig. 2 in the present paper, where a broken test-wall (upper right corner) indicates a former chamber, much larger than the one replacing it.

Of the Liassic genera examined, *Nodosaria* (together with some few forms of the *"Lenticulina plexus")* is outstanding in having a secondarily lamellar test-wall of principally the same type as the one described in *Nodosariidae* from the Upper Mesozoic, Caenozoic and Recent. However, there also exist characters in *Nodosaria* suggesting relationship to Paleozoic forms, suspected to be ancestors of the *Nodosariidae.* One of these characters may be the interior granular layer reported here (text-fig 7, p. 32, Pl. II, fig. 5). Such a layer is observed inter alia by Cummings (1956) and Sellier de Civrieux & Dessauvagie (1965) in other Early Mesozoic and Paleozoic nodosariids and related forms.

OCCURRENCE. — Lias α_3/Lower Lias β: Öresund 01; 21.31—22.97 m, 25.97—26.88 m, 33.40—33.79 m, 40.30—40.70 m.

Lias γ: Kävlinge No. 928 and No. 930, and Katslösa (occurring, but the levels are not registered).

Notes on the *Dentalina* plexus

To be placed with the genus *Dentalina* D'ORBIGNY 1826, a foraminifer has usually had to display the following features: To have a calcareous, elongate, more or less arquate test, uniserially arranged chambers and a radiate, terminal, eccentric aperture. Unfortunately, a great number of foraminifers from the Carboniferous up to Recent fulfil these requests, including forms having widely diverging internal characters, usually being insufficiently examined. Besides, even the smallest differences in the exterior have many times promoted forms of *"Dentalina"* to the rank of species. On the other hand, it has happened that certain Early Mesozoic dentalinoid foraminifers have been assigned to the same species of *Dentalina* as Recent forms. Persistent species indeed!

Even if attempts have been made to bring order and system into the confusing *Dentalina plexus* (inter alia by Barnard 1963), by putting together morphologically closely related "species" into larger groups, the main part of the *"Dentalinae"* described (especially smooth forms), seems to be a hopeless muddle of true species, homeomorphs and synonyms. However, as pointed out above (p. 24), studies of internal characters have shown that there exist different types of wall-structure of classificatory importance within the *Dentalina plexus.* As mentioned in the introduction, the wall-structure in Cretaceous, Tertiary and Recent *Nodosariidae* (including the genus *Dentalina)* is on the whole rather well known, thanks to works by Beissel (1891), Wood (1949), and Reiss (1958, 1963) et. al. Concerning the Liassic forms, smooth as well as ornamented, referred to the genus *Dentalina* by most previous students, the present investigation has shown that many species placed with the genus should be divided into two new genera, *Prodentalina* and *Mesodentalina,* a division mainly based on differences in the lamination of the test-wall. The genera can briefely be characterized as follows (text-fig. 8; Pl. III, figs. 1, 3, 5, 6; Pl. IV, figs. 1—3; Pl. VII, figs. 1—3; Pl. VIII, figs. 1—2).

1. *Dentalina s.str.* D'ORBIGNY 1826. — (type species: *Nodosaria obliqua* D'ORB. 1826). Test calcareous, elongate, arquate, polythalamous, uniserial; sutures commonly oblique; aperture radiate, terminal, eccentric. Test-wall fibrous-radiate, perforate, secondarily lamellar.
2. *Mesodentalina n. gen.* — Shape as in *Dentalina,* distinguished by its wall-structure, which is fibrous-radiate, perforate, secondarily mesolamellar.
3. *Prodentalina n. gen.* — Shape as in *Dentalina,* distinguished by its wall-structure, which is fibrous-radiate, perforate, secondarily nonlamellar.

Hitherto, no representatives of the genus *Dentalina s. str.,* have been found in the Lower Lias. Diagnoses of the new genera proposed, and descriptions of species within them are given below.

Prodentalina nov. gen.

TYPE SPECIES. — *Dentalina terquemi* D'ORBIGNY 1849.

SPECIES. — *Dentalina terquemi* D'ORBIGNY 1849, *Dentalina vetusta* D'ORBIGNY 1849, *Dentalina vasta* FRANKE 1936.

Further investigations will probably show that many other Lower Liassic and Triassic smooth forms, previously referred to genus *Dentalina* should be placed with the new genus.

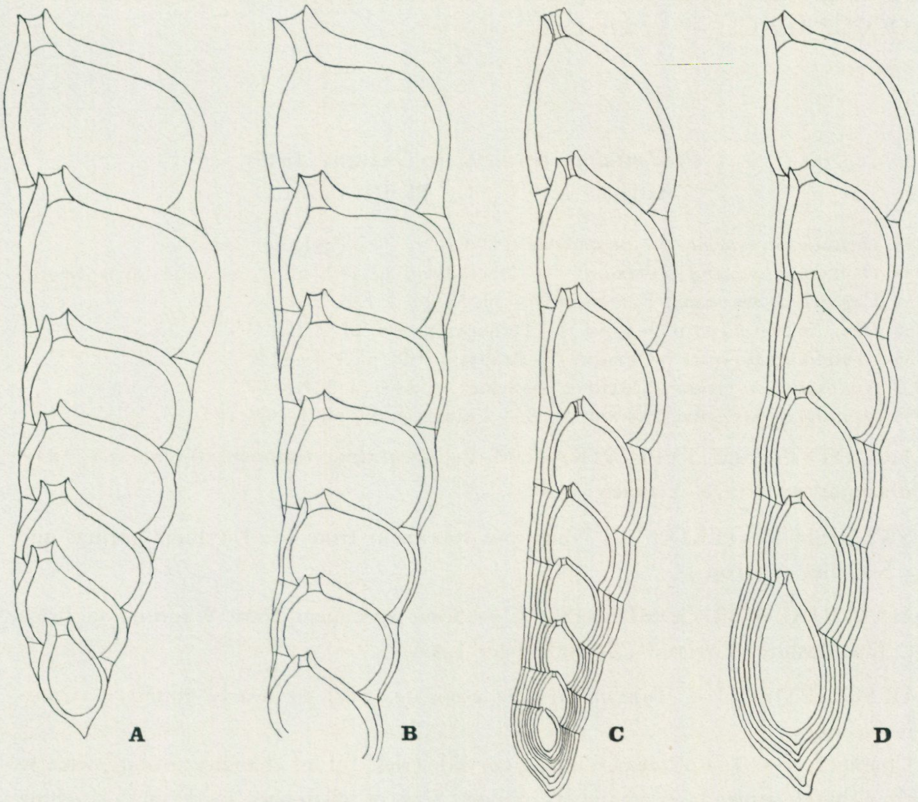
DIAGNOSIS. — Test elongate, ventral side convex, dorsal side concave, or nearly straight. In transverse section oval, or nearly round. Size variable; length usually 0.5—1.5 mm, Breadth 0.15—0.40 mm. Polythalamous.

Chambers 3—10, oblate or prolate, in an uniserial, curviserial arrangement. Chamber sutures distinct, oblique.

Aperture distinct, terminal, eccentric (at the dorsal side of the test), protruding. Form oval to round, radiate (with radiating grooves or slits). An apertural chamberlet present in some species.

Foramina protruding, resembling the aperture, but as a rule they have lost the radiation. In forms with an apertural chamberlet, the foramina lack chamberlets due to resorption. Apertural and foraminal areas imperforate. Species hitherto examined lack ornamentation.

Test-wall calcareous, fibrous- (or acicular-) radiate, finely perforate, secondarily nonlamellar. No primary lamination has been observed.



Text-fig. 8 A—D. Schematic drawings showing different stages of secondary lamination in dentalinoid *Foraminifera* from Lower Lias (A, B), Middle Lias (C), and Upper Cretaceous (D).

A) N o n l a m e l l a r test-wall in *Prodentalina nov. gen.* Drawing based on a sectioned specimen of *Prodentalina terquemi* (D'ORBIGNY 1849). Lias α_3 Katslösa. c. 150 X.

B) M e s o l a m e l l a r test-wall in *Mesodentalina nov. gen.* Drawing based on sectioned specimen of *Mesodentalina matutina* (D,ORBIGNY 1849). Lias γ. Waddington Brick Pit, Lincolnshire, England. c. 100 X.

C) L a m e l l a r test-wall in *Dentalina ex gr. communis* D'ORBIGNY. Note that the lamination is not complete in the distal part of the test. Middle Lias. After Gerke (1957).

D) L a m e l l a r test-wall in *Dentalina s. str.* D'ORBIGNY 1826. Drawing based on sectioned specimen of *Dentalina sp.* (smooth form). Upper Campanian. Vittsköfle No. 15, Skåne. ca 160 X.

Perforation consists of straight to slightly curved pores, more or less evenly distributed, or restricted to "pore bundles". Often, the basal parts of each chamber have a greater number of pores than other parts of the test.

Septa fibrous- (or acicular-) radiate, essentially imperforate. Ventral septa usually much longer than the dorsal ones due to the eccentric positions of the foramina.

OCCURRENCE. — Lower Lias.

Prodentalina terquemi (D'ORBIGNY 1849)

Textfigs. 8 A, 9 C_1, C_2; Pl. III, figs. 1, 3

1849 *Dentalina terquemi (pro terquiemi)* D'ORBIGNY. — p. 241, no. 257.
1936 *Dentalina terquemi* D'ORBIGNY. — Macfadyen, p. 149, pl. 1, fig. 257 (type figure).
1854 *Vaginulina hausmanni* BORNEMANN. — p. 38, pl. 3, figs. 25 a, b.
1858 *Dentalina terquemi* D'ORBIGNY. — Terquem, p. 596, pl. 2, figs. 1 a—c, 23.
1865 *Dentalina pauperata* D'ORBIGNY. — Brady, p. 108, pl. 1, fig. 14.
1903 *Nodosaria pauperata* D'ORBIGNY. — Schick, p. 143, pl. 5, fig. 11.
1936 *Dentalina hausmanni* (BORNEMANN). — Franke, p. 29, pl. 2, figs. 15 a, b.

HOLOTYPE and TYPE STRATUM. — *Dentalina terquemi* D'ORBIGNY 1849. "Jurasique, 8 e Étage, Liassien."

SWEDISH MATERIAL. — Numerous specimens from the Kävlinge borings and the Katslösa outcrop.

MATERIAL FOR COMPARISON. — Some specimens from Waddington Brick Pit, Lincolnshire, England (Upper Lower Lias).

DESCRIPTION. — Test calcareous, elongate, oval to nearly round in transverse section.

Chambers 6—10 in a linear, slightly curved series. Initial chamber prolate, usually with a basal spine, later chambers oblate. Size of chambers increasing, reaching maximum in the latest or penultimate chamber. Chamber sutures distinct, slightly depressed.

Aperture terminal, eccentric, at the dorsal side of the test, protruding, oval or round, radiate (with radiating grooves). Without an apertural chamberlet.

Foramina protruding, resembling the aperture, but lack radiation.

Ornamentation of the test absent.

Test-wall acicular-radiate, perforate, without primary and secondary lamination. With the exception of the always imperforate areas (apertural and foraminal areas, chamber sutures), the test-wall is perforated with straight to slightly curved pores occurring in pore bundles. Usually, heavily perforated borders occur above the imperforate chamber sutures. Pore diameter: 1—1.5 microns.

Septa acicular-radiate, essentially imperforate. Without primary lamination. Thickness: 15—20 microns in the initial chamber, 20—30 microns in the final chambers. Other measurements in table below.

TABLE 3. *Prodentalina terquemi* (d'Orbigny). Wall thickness in microns, other measurements in mm.

no	nos. of chambers	test		proloculum max. diam.	wall thickness	
		length	max. diam.		prol.	aperture ch.
64—1	7	1.03	0.24	0.10	—	36
64—6	7	1.03	0.25	0.14	22	36
64—8	7	1.07	0.27	0.16	29	29
64—9	8+	—	—	0.14	29	—
64—10	6	1.00	0.26	0.11	29	36
64—11	9	0.97	0.22	0.11	22	25
64—12	7+	—	0.24	0.16	22	—
66—1	7	0.80	0.21	0.10	—	—

OCCURRENCE. — Lias β (?) — Lias γ : Katslösa, 762—818 m. Lias γ : Kävlinge No. 928, 54—83 m; Kävlinge No. 930, 30—103 m.

Prodentalina vetusta (d'Orbigny)

Textfigs. 9 A_1—A_2

1849 *Dentalina vetusta* d'Orbigny. — p. 242, No. 258.
1936 *Dentalina vetusta* d'Orbigny. — Macfadyen, p. 150, pl. 1, fig. 258 (type figure).
1936 *Dentalina subsiliqua* Franke. — p. 30, pl. 2, fig. 21 a.
1937 *Dentalina subsiliqua* Franke. — Bartenstein & Brand, p. 136, pl. 1A, fig. 5; pl. 1B, fig. 16; pl. 2, fig. 6; pl. 3, fig. 7; pl. 4, fig. 22; pl. 5, fig. 11.

HOLOTYPE and TYPE STRATUM. — A badly preserved specimen figured by Macfadyen, 1936. "Jurassique, 8e Étage, Liassien."

SWEDISH MATERIAL. — Some few specimens from Katslösa, Kävlinge No. 928 and No. 930.

DESCRIPTION. — Test calcareous, elongate, oval in transverse section. Dorsal side concave, ventral side convex. Length: 0.50—0.65 mm. Breadth: 0.11—0.16 mm.

Chambers 4—6 in a linear, slightly curved series. All chambers prolate, proloculum with a basal spine. Chamber sutures more or less distinct, slightly depressed, oblique.

Aperture terminal, protruding, at the peripheral angle.

Apertural chamberlet present, penetrated by 6 radiating slits.

Foramina not protruding, lacking chamberlets.

Ornamentation of the test absent.

Test-wall fibrous-radiate, perforate; the pores being concentrated into bundles, leaving nearly imperforate the small areas in between them. Test-wall secondarily nonlamellar; at the dorsal side of the test with overlapping of primary chamber walls, at the ventral side without such an overlapping. No primary lamination observed. Thickness of the test-wall: 5—7 microns in the proximal part, 8—10 microns in the distal part of the test.

Septa. — Ventral septa forming a smooth bend, extending for almost the full breadth of the test, dorsal septa very short, due to the eccentric position of foramina. Texture of septa fibrous-radiate, essentially imperforate. Thickness from 2—3 microns in the proximal part to 7—8 microns in the distal part of the test. Without a primary lamination.

REMARKS. — *Prodentalina vetusta* shows a close resemblance to *P. vasta* in many characters (inter alia in the shape of the test and chambers, and the presence of an apertural chamberlet). The species can be distinguished by the presence of a basal spine of the proloculum in *P. vetusta*, and probably also by the pore pattern.

OCCURRENCE. — Lias β (?) — Lias γ: Katslösa, 760—877 m. Lias γ : Kävlinge No. 928, 62.5—63 m; Kävlinge No. 930, 30.2—31.2 m.

Prodentalina vasta (Franke)

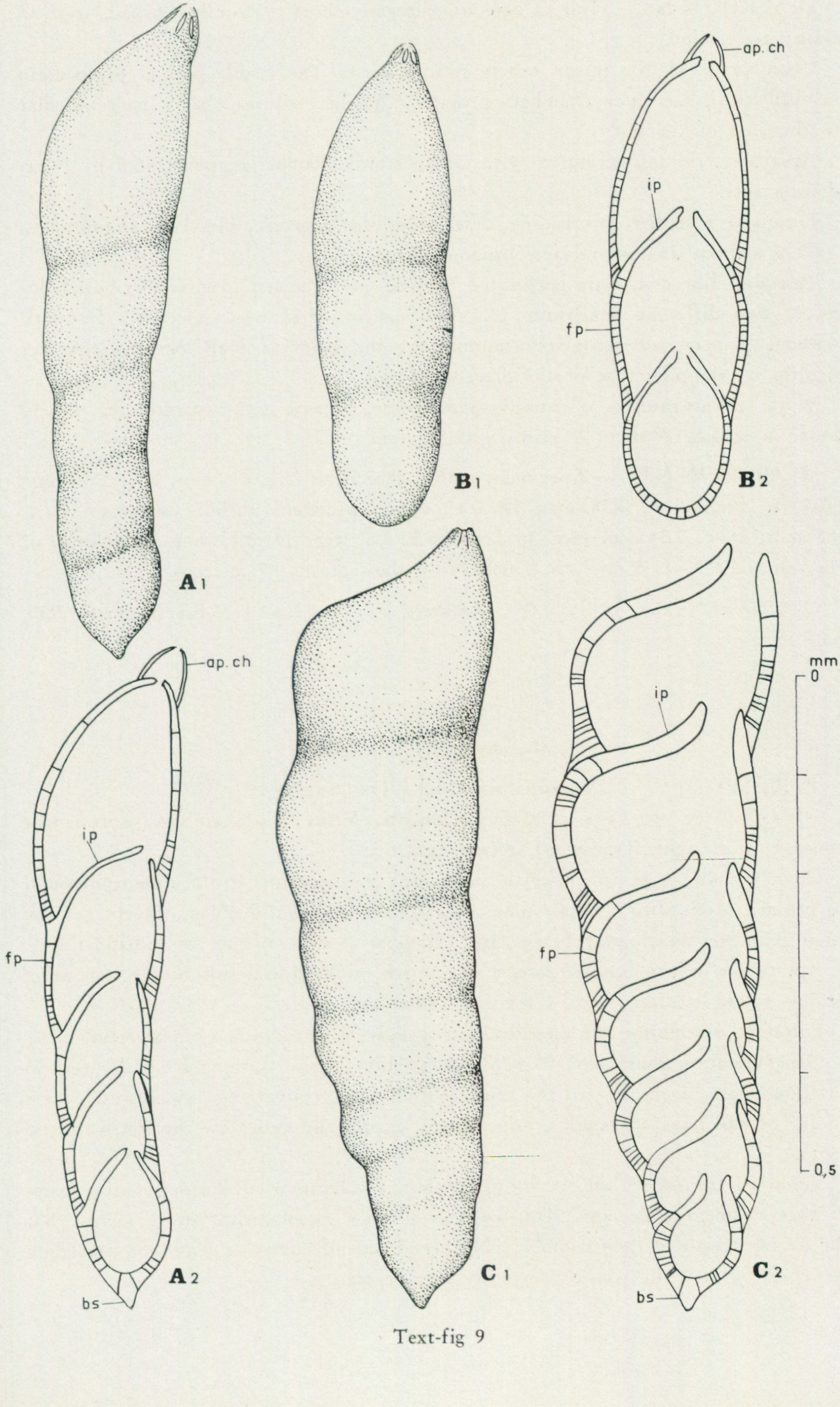
Text-figs. 9 B_1—B_2; pl. IV, figs. 1—3

1936 *Dentalina vasta* Franke. — p. 32, pl. 2; figs. 27 a, b.
1937 *Dentalina vasta* Franke. — Bartenstein & Brand, p. 140, pl. 2 B; fig. 7.

HOLOTYPE and TYPE STRATUM. — A specimen with 5 chambers, figured by Franke 1936, pl.2; fig. 28a. Lias γ.

SWEDISH MATERIAL. — Some few specimens from Katslösa and Kävlinge no. 930.

Text-fig. 9 A_1—A_2. *Prodentalina vetusta* (d'Orbigny 1849). Lias γ, Kävlinge No. 928.
A_1. Megalospheric specimen, side view.
A_2. Megalospheric specimen; longitudinal section showing nonlamellar, perforate test-wall, imperforate septa, apertural chamberlet, and basal spine of proloculum.
B_1—B_2. *Prodentalina vasta* (Franke 1936). Lias γ, Katslösa.
B_1. Megalospheric specimen, side view.
B_2. Megalospheric specimen; longitudinal section showing nonlamellar, perforate test-wall, imperforate septa, and apertural chamberlet. Note the absence of a basal spine of prolocolum.
C_1—C_2. *Prodentalina terquemi* (d'Orbigny 1849). Upper Lias β/Lower Lias γ, Katslösa.
C_1. Megalospheric specimen, side view.
C_2. Megalospheric specimen; longitudinal section showing nonlamellar test-wall with pore-bundles, imperforate septa, and basal spine of proloculum.



Text-fig 9

DESCRIPTION. — Test calcareous, elongate, short and rather broad, oval in transverse section.

Chambers 3—5 in a linear, nearly straight series. The visible part of proloculum hemispherical, the later chambers prolate. Chamber sutures nearly perpendicular to the axes of the test.

Aperture terminal, eccentric, with an apertural chamberlet, penetrated by 6 radiating slits.

Foramina eccentric, protruding, resembling the aperture, but lack chamberlets.

Test without any appreciable ornamentation.

Test-wall fibrous-radiate perforated by fine, more or less evenly distributed pores of two different dimensions (0.4—0.6 microns and 1—2 microns). Test-wall without primary or secondary lamination; the primary wall of one chamber slightly overlapping that of the preceeding one.

Septa fibrous-radiate, essentially imperforate. Dorsal and ventral septa nearly equal in length. Without a primary lamination.

MEASUREMENTS. — Specimens with 3 chambers: L. c. 0.5 mm; D. c. 0.14 mm (Acc. to Franke: L. 0.38 mm; D. 0.12 mm). Specimens with 5 chambers: L. c. 0.8 mm; D. c. 0.25 mm (acc. to Franke: L. 0.7 mm; D. 0.13 mm). Thickness of the test-wall, 9—11.5 microns. Thickness of the septa: 5—7 microns.

OCCURRENCE. — Lias β/γ : Katslösa, 771 m. Lias γ : Kävlinge no. 930, 34—35 m.

Mesodentalina nov. gen.

TYPE SPECIES. — *Dentalina matutina* D'ORBIGNY 1849.

DIAGNOSIS. — Test calcareous, elongate. Ventral side convex, dorsal side concave to straight. Transverse section oval.

Chambers 8—14 in an uniserial, curviserial arrangement. Proloculum spheroidal to prolate, often with a basal spine. Later chambers usually oblate, except for the final chamber, which may be prolate. Chamber sutures distinct or indistinct.

Aperture terminal, eccentric, on a short neck at the dorsal side of the test; more or less round, radiate (with a textural radiation).

Foramina resembling the aperture, but usually the radiation is inappreciable.

Ornamentation consists of 10—25 strong, oblique ribs, running from the ventral proximal part of the test to the dorsal, distal part, converging towards the aperture. The ribs have a granular, imperforate texture and penetrate the test-wall and septa.

Test-wall fibrous-radiate, perforate, with the exceptions of the penetrative parts of the ornamental elements. Test-wall secondarily mesolamellar in the sense that the primary wall of each chamber is attached to and covers at least one preceding chamber, but not the whole previously formed test.

Septa fibrous-radiate, with interruptions for the penetrative, granular ornamental elements. A primary lamination of the septa is present.

REMARKS. — The line of evolution from the secondarily non-lamellar *Prodentalina* to the secondarily lamellar *Dentalina* is easily traced by means of the mesolamellar test-wall in *Mesodentalina*. Thus, *Mesodentalina* is looked upon as an intermediate genus between *Prodentalina* and *Dentalina*.

OCCURRENCE. — Lower Jurassic to ?.

Mesodentalina matutina (D'ORBIGNY)

Text-figs. 8 B; 10 A—F; pl. III, fig. 5.

1849 *Dentalina matutina* D'ORBIGNY. — p. 242, no. 259.
1849 *Dentalina primaeva* D'ORBIGNY. — p. 242, no. 260.
1936 *Dentalina matutina* D'ORBIGNY. — Macfadyen, p. 150, pl. 1; no. 259 (type figure).
1936 *Dentalina primaeva* D'ORBIGNY. — Macfadyen, p. 150, pl. 1; no. 260.
1866 *Dentalina fasciata* TERQUEM. — p. 485, pl. 19; fig. 25.
1876 *Dentalina funiculosa* TERQUEM. — Tate & Blake, p. 461, pl. 18; fig. 28.
1903 *Dentalina obliquistriata* (REUSS). — Schick, p. 148, pl. 5; figs. 18, 19.
1957 *Dentalina matutina* D'ORBIGNY *subsp. matutina* D'ORBIGNY. — Nørvang, p. 83, figs. 88, 90—93.

HOLOTYPE and TYPE STRATUM. — A complete, well preserved specimen figured by Macfayden, 1936. Jurassic, 8th Etage, Lias.

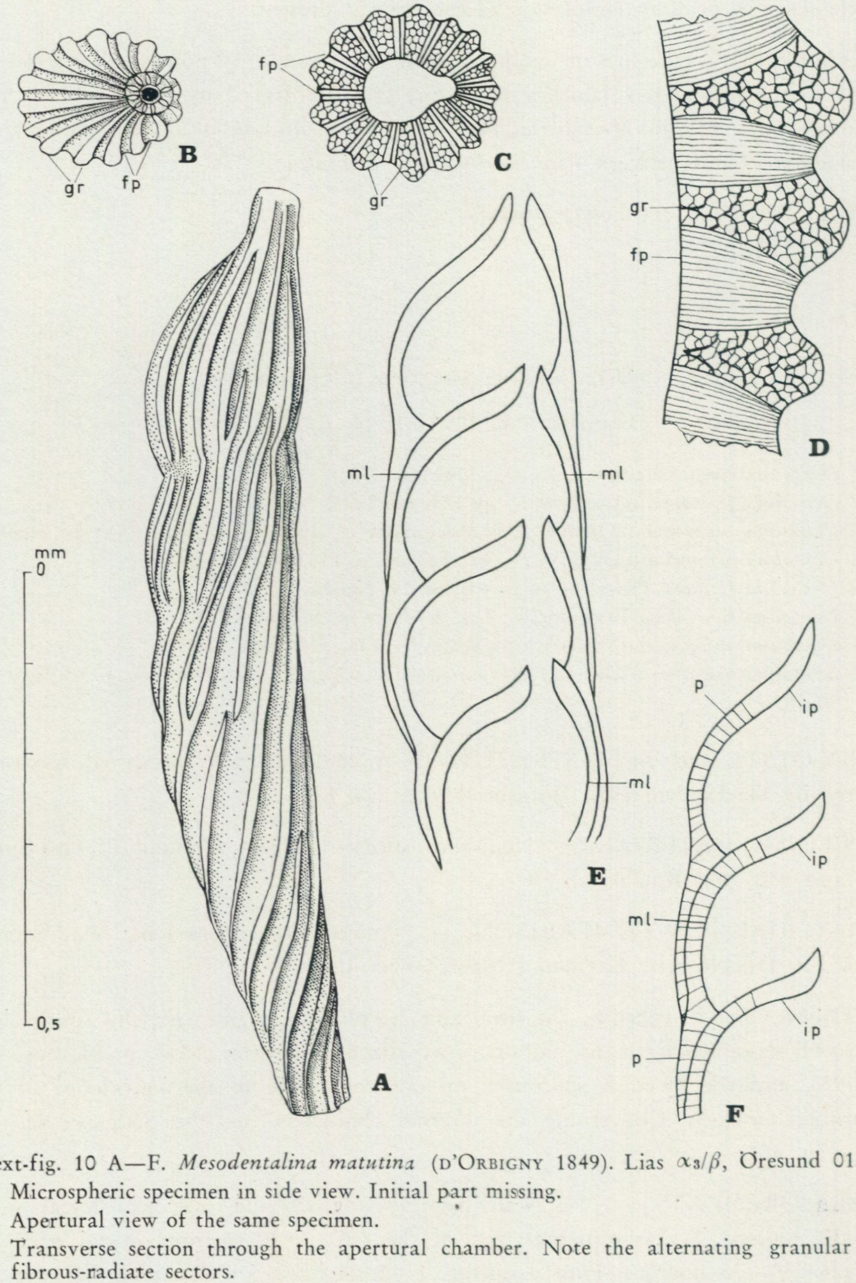
SWEDISH MATERIAL. — Numerous specimens from Öresund 01, Kävlinge 928 and 930, and Katslösa.

MATERIAL FOR COMPARISON. — Numerous specimens from Waddington Brick Pit, Lincolnshire, England (Upper Lower Lias).

REMARKS. — Regarding the form and morphology of the test, this species has been well described by many authors, inter alia by Nørvang (1957, p. 83, figs. 88, 90—93), and the Swedish specimens do not contribute to the knowledge of its external characters. Concerning the internal characters, see the diagnosis of the genus (p. 40).

MEASUREMENTS. — Test-wall, ventral side: 20—25 microns; dorsal side: 25—30 microns. Septa, proximal part of the test: c. 20 microns; distal parts of the test: 30—35 microns. Pore diameter: 1—2 microns. See also table below.

OCCURRENCE. — Lias α_3/Lower Lias β: Öresund 01; 14.90—49.70 m. Lias β (?) — Lias γ: Katslösa; 762—960 m. Lias γ: Kävlinge no. 928; 62—83 m, Kävlinge no. 930; 62—103 m.



Text-fig. 10 A—F. *Mesodentalina matutina* (D'ORBIGNY 1849). Lias α_3/β, Öresund 01.

A. Microspheric specimen in side view. Initial part missing.

B. Apertural view of the same specimen.

C. Transverse section through the apertural chamber. Note the alternating granular and fibrous-radiate sectors.

D. Detail of C.

E. Longitudinal section showing the strong overlap of primary wall layers, typical for the secondarily mesolamellar test-wall.

F. Longitudinal section showing radiate perforation of the test-wall and the basal parts of septa. Number of pores very much reduced.

TABLE 4. *Mesodentalina matutina* (D'ORBIGNY).
Dimensions in mm.

no.	nos. of chambers	test		proloculum max. diam.	form
		length	max. diam.		
R 55—7	6	1.14	0.30	0.15	megalospheric
66—5	9	1.57	0.35	0.13	,,
66—1	10	1.27	0.27	0.09	,,
66—4	10	1.65	0.26	0.11	,,
R 55—8	11	1.49	0.29	0.14	,,
R 55—2	8	0.64	0.17	0.07	microspheric

Genus *Marginulina* D'ORBIGNY, 1826

TYPE SPECIES. — *Marginulina raphanus* D'ORBIGNY, 1826, designated by Deshayes, 1832. Lectotype for *Marginulina raphanus;* the specimen figured by D'Orbigny, 1826; pl. 10; fig. 7, designated by Loeblich and Tappan, 1961.

"*Marginulina*" *prima* D'ORBIGNY, 1849

Text-fig. 11 A—C; pl. III, figs. 2, 4

1849 *Marginulina prima* D'ORBIGNY. — p. 242, no. 262.
1936 *Marginulina prima* D'ORBIGNY. — Macfadyen, p. 151, pl. 1; fig. 262 (type figure).
1854 *Marginulina rugosa* BORNEMANN. —p. 39, pl. 3; figs. 26 a, b.
1858 *Marginulina prima* D'ORBIGNY. — Terquem, p. 53, pl. 3; figs. 5—10 (including varieties *gibbosa, recta, acuta, spinata, alata, ornata).*
1863 *Marginulina burgundae* TERQUEM. — p. 196, pl. 9; fig. 3.
1866 *Marginulina interrupta* TERQUEM. — p. 426, pl. 17; figs. 4 a—c.
1875 *Marginulina prima var. praelonga* TERQUEM & BERTHELIN. — p. 54, pl. 4; fig. 18.
1875 *Marginulina gibberula* TERQUEM & BERTHELIN. — p. 53, pl. 4; figs. 21 a, b.
1876 *Dentalina burgundae* TATE & BLAKE. — p. 461, pl. 18; fig. 29.
1881 *Marginulina dentalina* HAEUSLER. — p. 17, fig. 24.
1903 *Marginulina costata* SCHICK. — p. 137, pl. 4; figs. 20, 21.
1936 *Dentalina insignis* FRANKE. — p. 36, pl. 3; figs. 11 a, b.
1936 *Marginulina prima* D'ORBIGNY. — Franke, pl. 8; figs. 1—7 (including the forms *rugosa, gibbosa, recta, acuta,* and *ornata* TERQUEM, and *praelonga, gibberula* TERQUEM & BERTHELIN).
1936 *Marginulina incisa* FRANKE. — p. 78, pl. 8; figs. 11, 12.
1947 *Nodosaria unguis* PAYARD, p. 172, pl. 2; fig. 23.
1957 *Marginulina prima* D'ORBIGNY. — Nørvang, p. 87, figs. 96—104 (including form *burgundae* TERQUEM and *subsp. prima* D'ORBIGNY, *rugosa* BORNEMANN, *praerugosa* NØRVANG, and *spinata* TERQUEM.

HOLOTYPE and TYPE STRATUM. — *Marginulina prima* D'ORBIGNY 1849, "Jurassique 8e Etage, Liassien".

SWEDISH MATERIAL. — Numerous specimens from Katslösa, Öresund 01, Kävlinge no. 928 and no. 930.

DESCRIPTION. — Test calcareous, elongate, subcircular in transverse section. Length variable, 0.4—1.6 mm, usually around 1 mm; breadth 0.15—0.35 mm (excl. ornamental elements).

Chambers 6—14, in the early portion of the test often arranged in an open coil, later on in a rectilinear or slightly curved series. All chambers oblate to spherical, proloculum often with a basal spine. Size of the chambers increases regularly.

Aperture terminal, eccentric, on a short neck. Form round to oval, radiate (with radiating slits or grooves).

Foramina lack the short neck typical for the aperture. Their radiation is inappreciable.

Ornamentation. — Test ornamented with 5—10 (usually 7) strong, longitudinal ribs or costae, often connected by straight or arching ridges at every chamber suture. Ornamental elements have a granular, imperforate texture, the granules being more or less equidimensional, closely packed calcareous grains. The longitudinal ornamental elements penetrate the test-wall. The granular transverse ridges are not penetrative, but are attached to and cover a certain amount of the fibrous-radiate test-wall. Apertural area often covered by a thin cap of granular, calcareous material.

Test-wall composed of fibrous-radiate, perforate, longitudinal sectors alternating with granular, imperforate sectors, the latter being the penetrative ornamental elements. Pores (D. 0.75—1.50 microns) more or less evenly distributed in the interornamental parts of the wall. Test-wall clearly nonlamellar. Thickness variable usually 4—6 microns in the proximal part of the test, 12—18 microns in the distal part.

Septa usually nearly transverse due to the oblate form of the chambers. Their texture essentially fibrous-radiate, imperforate, with interruptions for the penetrative, granular ornamental elements. No primary lamination has been observed. Thickness c. 4—10 microns, increasing towards the apertural chamber.

REMARKS. — As seen in Gerke (1957), several forms from the Middle Lias, referred by him to the genus *Marginulina* D'ORB., have a secondarily lamellar test-wall, and thus widely diverge in the wall-structure from specimens of "*Marginulina*" *prima* from the Lower Lias of Sweden. Concerning the Pliocene genotype *Marginulina raphanus* D'ORBIGNY, neither the type figures nor the diagnoses inform about its wall-structure. However, Reiss (1963), in his reclassification of perforate Foraminifera, mainly based on examinations of Cretaceous, Tertiary and Recent foraminifers, includes the genus *Marginulina* in the group of lamellar Foraminifera. Thus, there are good reasons to believe, that most Upper Mesozoic, Caenozoic and Recent representatives of the genus (including the genotype) are lamellar. On the other hand, the present investigation and that of Gerke (1957) suggest that Lower

Mesozoic forms, usually referred to genus *Marginulina* actually have undergone an evolution from a nonlamellar to a lamellar test-wall, more or less analogous to that of many other nodosariids. Until a more comprehensive investigation of marginulinoid foraminifers of different geological ages has been undertaken, the present writer suggests that forms having a wall-structure widely diverging from the one used in the classification of the genus, preliminarily should have the generic name within quotation marks.

OCCURRENCE. — "*Marginulina*" *prima* D'ORBIGNY: Lias α_3/Lower Lias β : Öresund 01; 21.31—40.70 m. Lias β —Lias γ : Katslösa; 750—1 000 m. Lias γ : Kävlinge 928; 54—83 m, Kävlinge 930; 30—103 m.

"*Marginulina*" *prima* D'ORB. form *spinata* TERQUEM: Upper Lias β (?) — Lower Lias γ : Katslösa; 826—860 m. Lias γ : Kävlinge 930; 60—80 m.

Notes on the wall-structure in certain forms of *Lenticulina* and associated genera

In spite of comprehensive studies of the *Lenticulina plexus* by several authors, including Bartenstein (1948), Barnard (1950, 1960), Nørvang (1957), and Gordon (1965, 1966), no generally accepted classification of the group resulted. This appears natural in view of the great instability in the different characters usually studied in Jurassic forms. In delimiting genera, subgenera and species within the *Lenticulina plexus* most workers have based their diagnostics on the following characters: the size of the test, the degree of coiling, the angle between the sutures and the peripheral wall, the shape and size of the chambers, the degree of lateral compression of the test, and the ornamentation.

Adams (1957) has statistically studied the variation in the mentioned characters in thousands of specimens of certain lenticulinoid forms. His studies have led him to the conlusion that not one of the characters mentioned is sufficiently stable to be of decisive importance in delimiting species. Adams suggests that, "in delimiting a species care must be taken to indicate the complete range of variation exhibited by its component individuals, otherwise an unnecessary multiplication of specific names will result." However, first of all, a greater accuracy and unity in delimiting genera must be reached. Concerning the Jurassic lenticulinoid foraminifers, the wall-structure has seldom been taken into account as a character of classificatory importance, with the exception for some general comments like; test calcareous, fibrous-radiate, perforate. However, there actually exist different types of wall-structure in lenticulinoid foraminifers, believed by the present writer to be useful in the classification. The present investigation suggests that they have undergone an evolution in the wall-structure, more or less analogous to that of uncoiled nodosariids. Concerning the secondary lamination of the test-wall (which seems to be correlated with the perforation), three basic types have been found, as mentioned before (p. 24):

1. NONLAMELLAR FORMS (text-fig. 12 A, D, E; pl. V, figs. 1—4)
   a) Test imperforate
   b) Test perforate; pores fine (diam. < 1 micron), evenly distributed or restricted to pore bundles.
2. MESOLAMELLAR FORMS (text-fig. 12 B; pl. VI, fig. 2)
   Test always perforate; relatively low frequency of more or less evenly distributed pores (diam. > 1 micron).
3. LAMELLAR FORMS (Text-figs. 12 C, F; pl. VI, figs. 1, 3)
   Test always perforate; high frequency of pores (diam. > 1 micron).

The "*Astacolus*" *varians* group

Text-figs. 12 D—E; pl. V, figs. 1—4

The group includes forms comparable to the following "species":

1854 *Cristellaria varians* BORNEMANN. — p. 41, pl. 4, figs. 32—34.
1854 *Cristellaria deformis* BORNEMANN. — p. 41, pl. 4, figs. 35 a, b.
1854 *Cristellaria minuta* BORNEMANN. — p. 42, pl. 4, figs. 37 a, b.
1854 *Cristellaria convoluta* BORNEMANN. — p. 42, pl. 4, fig. 38 a.
1854 *Cristellaria major* BORNEMANN. — p. 40, pl. 4, figs. 31 a, b.
1936 *Cristellaria (Astacolus) major* BORNEMANN. — Franke, p. 101, pl. 9, fig. 36.
1936 *Cristellaria (Lenticulina) subquadrata* TERQUEM. — Franke, p. 111, pl. 11, fig. 7.
1936 *Cristellaria (Lenticulina) minuta* BORNEMANN. — Franke, p. 112, pl. 11, figs. 8 a, b.

Text-fig. 11 A—C. "*Marginulina*" *prima* D'ORBIGNY 1849.

A. Megalospheric specimen showing position of transverse sections A1—A3. Lias γ, Katslösa.

A1—A3. Schematic drawings of transverse sections based on observations in several specimens.

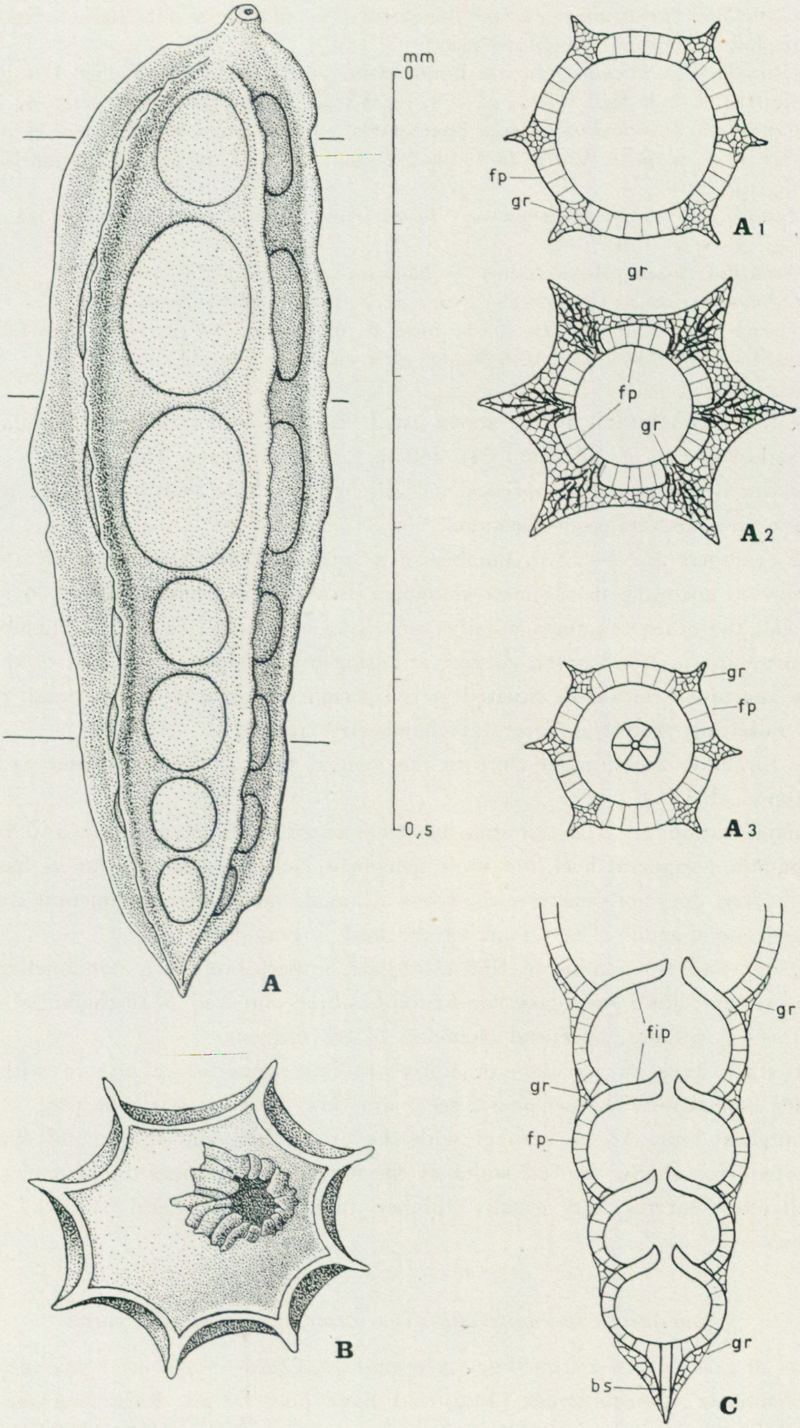
A1. Transverse section through the apertural chamber showing a fibrous-radiate, perforate test-wall, penetrated by granular, imperforate ornamental elements.

A2. Transverse section through the test-wall close to the junction of two consecutive chambers showing a fibrous-radiate test-wall and penetrative granular costae connected by ridges of granular material.

A3. Transverse section through the wall of one chamber and the septum of the preceeding chamber showing a fibrous-radiate, perforate test-wall, penetrative, granular costae and fibrous-radiate septum with foramen.

B. Apertural view. Specimen from Lias γ, Kävlinge no. 928. C. 270 X.

C. Part of a longitudinal section through an intercostal part of the test, showing the secondarily nonlamellar, fibrous-radiate, perforate test-wall, imperforate septa, and a strong basal spine of proloculum. Note the granular regions at the junctions of consecutive chambers. Specimen from Lias γ, Katslösa.



Text-fig 11

1936 *Cristellaria (Lenticulina) varians* Bornemann. — Franke, p. 112, fig. 11, figs. 9—13 (including the forms typica and recta).
1937 *Cristellaria (Lenticulina) varians* Bornemann. — Barnstein & Brand, p. 176, pl. 1 A, fig. 18; pl. 2 A, figs. 16, 20; pl. 2 B, fig. 32, pl. 3, figs. 31, 32; pl. 5, rig. 60.
1937 *Cristellaria (Lenticulina) minuta* Bornemann. — Bartenstein & Brand p. 176, pl. 1 A, figs. 17 a, b; pl. 2 A, fig. 18 a; pl. 2 B, fig. 31; pl. 3, fig. 33; pl. 4, fig. 70; pl. 5, fig. 61.
1947 *Lenticulina varians* (Bornemann) *forma recta* Franke. — Payard, p. 86, pl. 7, figs. 3—5.
1957 *Astacolus varians* (Bornemann). — Nørvang, p. 99, figs. 123—134.
1957 ? *Planularia stilla* (Terquem). — Nørvang, figs. 136—140, 142, 145.
1960 Forms Aa—Af, pl. 1, figs. 1—6; form B, pl. 1, figs. 8—10; forms Ea—Ef pl. 2, figs. 1—4, 6, 7; pl. 4, figs, 1—6, 8—12; pl. 6, fig. 1. — Barnard.

The forms comparable to the above listed "species", occur in great abundance in Lias α_3/Lower Lias β (Öresund 01), and in Lias γ, Kävlinge No. 930.

The test is elongated, compressed, usually oval in side view, lenticular to oval in front view and transverse section.

The chambers are 9—12 in number in a spiroserial arrangement, with a strong tendency to uncoiling in the later chambers. Proloculum (diam. 0.03—0.06 mm) is spherical, the other chambers usually very low, broad and thin. The chamber sutures are more or less distinct, curved, radiating towards the initial part of the test.

The aperture is terminal, situated at the peripheral angle, oval to round, radiate (with radiating grooves). Apertural chamberlet lacking.

The foramina are situated close to the ventral side of the test. Their radiation is inappreciable.

Ornamentation. — The test may be ornamented with a very thin and fragile, transparent, peripheral keel, but most specimens lack this keel. As far as has been seen, the keel does not penetrate the test-wall, as do most other ornamental elements in Liassic nodosariids. The texture of the keel is granular.

The test-wall is acicular- or fibrous-radiate, imperforate. It is nonlamellar; neither a primary, nor a secondary lamination has been observed. Wall thickness: proloculum; 4—8 microns, apertural chamber; 6—12 microns.

The septa have an acicular- or fibrous-radiate, imperforate texture without a primary lamination. The peripheral septa are very short or nearly lacking. Most of the umbilical septa are in contact with the proloculum and the second chamber, and extend for almost the full width of the test. They are more or less curved like the chamber sutures and usually thinner than the peripheral test-wall (3—5 microns).

"*Planularia*" *inaequistriata* (Terquem) and associated forms.

In beds of Lias α_3/Lower Lias β age (Öresund 01; 21.08—40.70 m), some specimens of "*Planularia*" *inaequistriata* (Terquem) have been found. Regarding the form and morphology of the test, this easily identified species has been well described

TABLE 5. Dimensions of some specimens referred to the "*Astacolus*" *varians* group. In mm.

no	nos. of chambers	length	max. width	max. thickness
1	9	0.41	0.25	0.13
2	10	0.47	0.22	0.12
3	10	0.51	0.21	0.10
4	10	0.49	0.21	0.11
64—27	10	0.43	0.27	0.12
64—28	11	0.47	0.33	0.11
64—25	11	0.49	0.29	0.09

in many papers, and the Swedish specimens do not contribute to the knowledge of its external characters. In Lias γ beds (Kävlinge No. 928, No. 930, and Katslösa), forms referrable to "*Planularia*" *eugenii* (TERQUEM) are rather common. Apparently, this species is closely related to "*Planularia*" *inaequistriata*, and can be distinguished from the latter in the reduced number of ribs. A higher degree of lateral compression is also said to be characteristical for "*Planularia*" *eugenii*. Concerning the wall-structure, the two species seem to be almost identical.

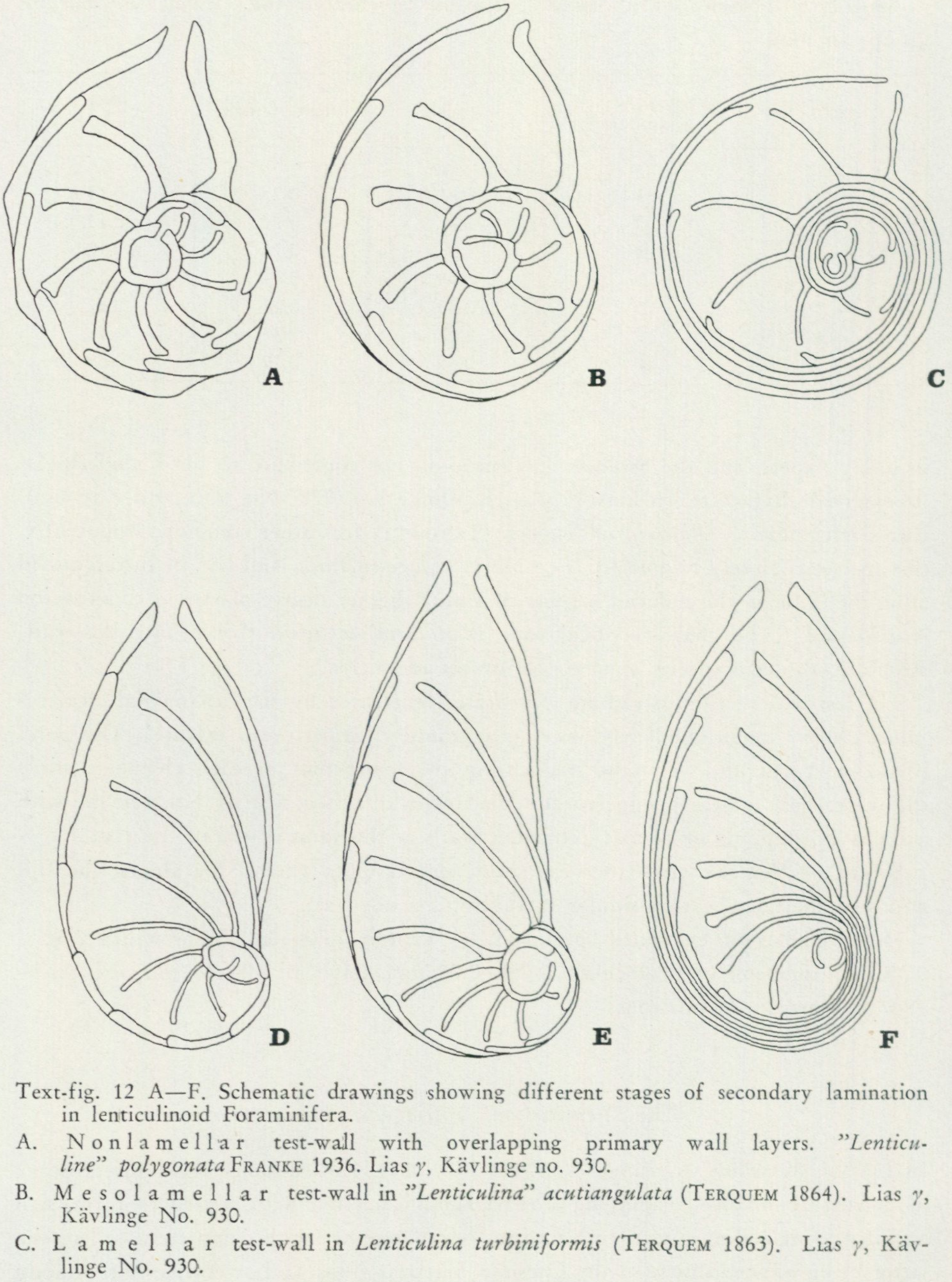
The test-wall is fibrous-radiate, perforate, penetrated by the ornamental elements (more or less longitudinal ribs, having a granular, imperforate texture). The pores (diam. c. 1 micron), are most frequent in the lower half of each chamber, while the upper half is nearly imperforate. The test-wall is secondarily nonlamellar with a slight overlapping of primary chamber walls at the ventral side of the test.

Septa. — Ventral septa are very short, dorsal septa extend for almost the full width of the test. Texture similar to that of the test-wall.

Measurements of examined specimens. — Length 0.70—0.85 mm, width 0.30—0.35 mm, diameter of proloculum 0.05—0.07 mm, test-wall 10—15 microns, thickness of septa 8—12 microns.

The "*Lenticulina*" *gottingensis* group

In Lias γ (Katslösa, Kävlinge No. 928, No. 930), lenticulinoid foraminifers occur in a great abundance, displaying a remarkable variation with regard to form, size and degree of coiling. Open coiled forms occur together with completely coiled, the latter being almost absent in the Öresund material (Lias α_3/Lower Lias β). Among the completely coiled foraminifers, there are certain forms, by many authors grouped around *Lenticulina gottingensis* (BORNEMANN). The present writer has examined thin sections of a few specimens referrable to *Lenticulina gottingensis* (BORNEMANN), *Lenticulina polygonata* FRANKE, *Lenticulina acutiangulata* (TERQUEM), and *Lenti-*



Text-fig. 12 A—F. Schematic drawings showing different stages of secondary lamination in lenticulinoid Foraminifera.

A. N o n l a m e l l a r test-wall with overlapping primary wall layers. *"Lenticuline" polygonata* FRANKE 1936. Lias γ, Kävlinge no. 930.

B. M e s o l a m e l l a r test-wall in *"Lenticulina" acutiangulata* (TERQUEM 1864). Lias γ, Kävlinge No. 930.

C. L a m e l l a r test-wall in *Lenticulina turbiniformis* (TERQUEM 1863). Lias γ, Kävlinge No. 930.

D. N o n l a m e l l a r test-wall in *"Astacolus" ex gr. varians* (BORNEMANN 1854). Lias α 3/ Lower Lias β, Öresund 01.

E. N o n l a m e l l a r test-wall in *"Astacolus" ex. gr. varians.* Lias γ, Kävlinge No. 930.

F. L a m e l l a r test-wall in *Astacolus paleocenicus* BROTZEN 1948. Paleocene, Ystad.

culina turbiniformis (TERQUEM). Even if the material examined is too small to allow any other conclusions to be drawn, it demonstrates the existence of different stages of lamination within the group. Thus, specimens referrable to *Lenticulina gottingensis* and *Lenticulina polygonata* have been found to have a secondarily nonlamellar test-wall with a rather high degree of overlapping of primary wall layers (text-fig. 12 A). A secondarily mesolamellar test-wall is found in specimens referred to *Lenticulina acutiangulata* (text-fig. 12 B), and a secondarily lamellar test-wall in *Lenticulina turbiniformis* (text-fig. 12 C).

DISCUSSION. — The examined material seems to demonstrate that nonlamellar and mesolamellar test-walls dominate in spiroserial forms during the Lower Lias, while lamellar forms are very rare. Unfortunately, no information about the wall-structures is given in the diagnoses of the genera *Astacolus* DE MONTFORT, *Planularia* DEFRANCE, and *Lenticulina* LAMARCK. Their genotypes are Recent, Pliocene, and Late Cretaceous respectively. As all Recent specimens of these genera (from the Mediterranean), as well as Tertiary and Cretaceous (form S Sweden), examined by the present writer, have a fibrous-radiate, perforate, and secondarily lamellar test-wall, there are strong arguments for a lamellar test-wall in their genotypes too. It means that many Lower Liassic forms of the "*Lenticulina*" plexus, including forms usually referred to the genera *Astacolus, Planularia,* and *Lenticulina,* have a wall-structure widely diverging from the one which can be expected in their genotypes. The present writer therefore suggests that the wall-structure must be taken into account in a necessary revision of the "*Lenticulina*" plexus.

SUMMARY

The great expansion of the family *Nodosariidae* EHRENBERG 1838 took place in the Early Mesozoic. As late as in the Lower Lias it appears to be a very primitive family with a great instability in many groups in the external characters of the test causing problems in the classification. Most Liassic forms were originally referred to distinct Cretaceous, Tertiary and Recent genera, mainly on the basis of external similarities. However, the present investigation has shown that the wall-structure in Liassic representatives of the family widely diverge from that of younger forms, as previously has been postulated by Gerke (1957), Brotzen (1963) et. al. The term wall-structure includes several characters of importance in the classification, of which the texture, the perforation, the lamination and layering, and the ornamentation have been studied by the present writer.

The family *Nodosariidae* has usually been described as having a fibrous-radiate, perforate, lamellar test-wall. As to the texture, this description is not adequate, since, in a great number of Liassic ornamented representatives of the family, the granular component of the test (penetrative ornamental elements and, rarely, an interior granular layer) clearly dominates over the fibrous-radiate component.

Concerning the perforation it has been found that there exist rare Liassic forms with an imperforate test-wall (e. g. *Geinitzinita pupoides* (NØRVANG) and *"Astacolus" varians* (BORNEMANN) from beds dated to Lias α_3/Lower Lias β). Contrary to the opinion of some authors, Liassic species of genus *Ichthyolaria* WEDEKIND have been found to be perforate (Norling, 1966).

A relation between the type of perforation (pore size and frequency) and the degree of secondary lamination of the test-wall has been found, suggesting that the pores have some function in the formation of lamellae, as was previously suspected by Le Calvez (1950).

In agreement with the opinion of Gerke (1957), the present study demonstrates that there exist different types of secondary lamination of the test-wall in Liassic nodosariids, representing different stages in an evolution from a nonlamellar to a lamellar test-wall, and that the different stages are sufficiently stable and characteristic to be useful in the classification. In the present study, a three-fold division of the secondary lamination is proposed: — nonlamellar, mesolamellar, and lamellar test-walls.

The nonlamellar test-wall clearly dominates in the Lower Liassic nodosariids examined, in orthoserial and curviserial, as well as in spiroserial forms. This type of lamination has been found in forms previously referred to the genera *Ichthyolaria* WEDEKIND *(Frondicularia* by some authors, *Spandelina* sensu Nørvang), *Geinitzinita* SELLIER DE CIVRIEUX & DESSAUVAGIE *(Lingulina* by some authors), *Dentalina* D'ORBIGNY (in part), *Marginulina* D'ORBIGNY, *Astacolus* DE MONTFORT, *Planularia* DEFRANCE, and *Lenticulina* LAMARCK (in part).

The mesolamellar test-wall has been found in forms previously referred to the genera *Dentalina* D'ORBIGNY (in part) and *Lenticulina* (in part).

A true lamellar test-wall has only been found in representatives of the genera *Nodosaria* LAMARCK and *Lenticulina* LAMARCK (in part).

Concerning the ornamentation of the test, its appearance and evolution in Liassic nodosariid Foraminifera is, on the whole, well known thanks to works by Barnard (1950, 1957, 1960, 1963), Nørvang (1957) et. al. In the present investigation the texture itself of the ornamental elements has been studied. Most ornamental elements have a granular texture, being composed of more or less equidimensional, rounded, calcareous grains (0.5—1.5 microns) in some cases, and of inequidimensional, polygonal grains (1—10 microns) in other cases. At the surface, ornamental elements often show another texture, referred to as vesicular, in which the calcite is found to have a lot of hollow spaces (vesiculi) forming a reticulate pattern. The vesiculi have a polygonal form and may vary greatly in size (1—10 microns). It has been found that most of the ornamental elements, such as longitudinal costae, ribs and striae, usually affect not only the external parts of the test, but also the internal; they penetrate the test-wall so to say. It means that ornamented foraminiferal tests have a textural alternation of granular, imperforate, and fibrous-radiate, perforate sectors. This fact has obviously never or seldom been paid attention to, and the texture of the test in ornamented nodosariids thus has often been erroneously interpreted as being completely granular, or completely fibrous-radiate, depending on how the thin section has been oriented.

Based on main differences in the wall-structure, a subdivision of the genus *Dentalina* D'ORBIGNY has been proposed, into *Dentalina* s. str., *Mesodentalina* n. gen., and *Prodentalina* n. gen. No representatives of the genus *Dentalina* s. str., with its completely lamellar test-wall, have hitherto been found in the Lower Lias, but, as seen in Gerke (1957) they occur in the Middle Lias. Actually, though there exist close external resemblances, most Lower Liassic nodosariids have wall-structures widely diverging from those in younger forms, which justifies a thorough revision of the family, affecting most of the genera with Upper Mesozoic, Caenozoic, and Recent genotypes. The present investigation clearly shows that, in addition to genus *Dentalina,* the genera *Marginulina, Astacolus, Planularia* and *Lenticulina* should also be subdivided into new genera. However, a comprehensive reclassification of these and other nodosariid genera need more extensive studies of materials from different geological systems.

The Liassic stratigraphy of the sampling localities has been briefly treated in this, and a previous paper (Norling 1966). The core sections Kävlinge no. 928 (Upper Lias γ), Kävlinge no. 930 (Lias β—Lias γ), and Öresund 01 (Lias α_3/Lower Lias β) have been dated by the present writer, mainly with the aid of nodosariid Foraminifera, whereas the strathigraphic range of the Katslösa section (Lias α_3/Lower Lias β, Upper Lias β (?)—Lias γ) was known previously (Troedsson (1951), Bölau (1959) et. al.).

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Abbreviations

GFF = Geologiska Föreningens i Stockholm Förhandlingar.
SGU = Sveriges Geologiska Undersökning.
DGU = Danmarks Geologiske Undersøgelse.

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Abbreviations used in explanatories to figures and plates

ap.ch. = apertural chamberlet
bs = basal spine
ef = exterior fibrous layer
f = foramen
fip = fibrous imperforate
fp = fibrous perforate
gr = granular
ig = interior granular layer
ip = imperforate
l = lamella, lamellar
ml = mesolamellar
p = perforate, pore, pores
pb = pore bundle
r.ap. = radiate aperture
s = septum

PLATE I

Figs. 1—3 *Geinitzinita pupoides* (Nørvang 1957). Lias α_3/Lower Lias β. Öresund 01. Longitudinal sections. 200 x.
1. Microspheric form.
2. Megalospheric form.
3. Megalospheric form.

Figs. 4—5 *Ichthyolaria dubia* (Bornemann 1854). Upper Lias β/Lower Lias γ. Katslösa. Longitudinal sections.
4. Megalospheric form. Detail of fig. 5 showing a fibrous testwall and vesicular-granular marginal keels (gr). Phase contrast. c. 200 x.
5. Megalospheric form.

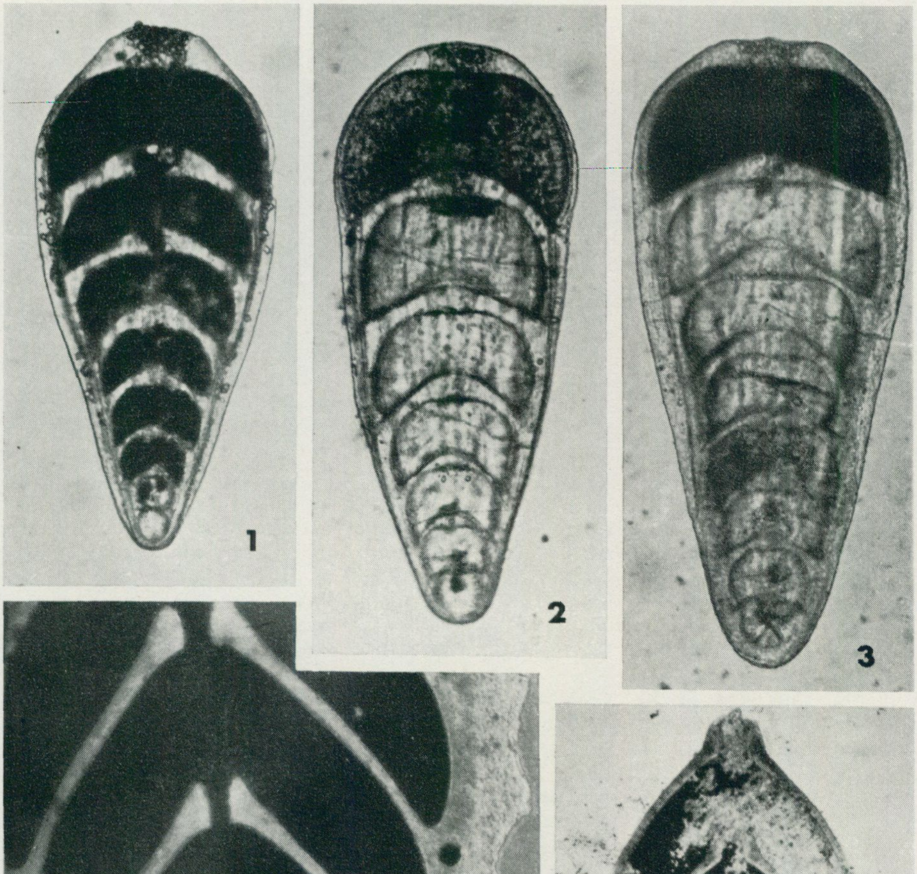


PLATE I

PLATE II

Figs. 1—5 *Nodosaria metensis* Terquem 1864.

1. Longitudinal section through the two last chambers showing an radiate aperture (r.ap.) on a short neck, foramen (f), imperforate septa (s), imperforate granular costae (gr), and a perforate, lamellar test-wall (1). Specimen from Upper Lower Lias, Waddington Brick Pit, Lincolnshire. 200 x.
2. The same specimen as in fig. 1. Longitudinal section through three consecutive chambers showing protruding foramina (f), imperforate septa (s), imperforate granular costae (gr), and a perforate, secondarily lamellar test-wall (1). Note that broken chamber has been replaced by a much smaller chamber. 200 x.
3. Detail of fig. 1 showing the apertural neck and the radiate aperture. C. 400 x.
4. A part of the internal surface of the test showing a granular imperforate costa (gr), surrounded by heavy perforated regions (p). Dark angular spots are grains of carborundum. Specimen from Lias α_3/Lower Lias β, Öresund 01. c. 1000 x.
5. Detail of a longitudinal section through the test showing an interior granular layer (ig), and an exterior fibrous layer (ef). Specimen from Lias α_3/Lower Lias β, Öresund 01. 2500 x.

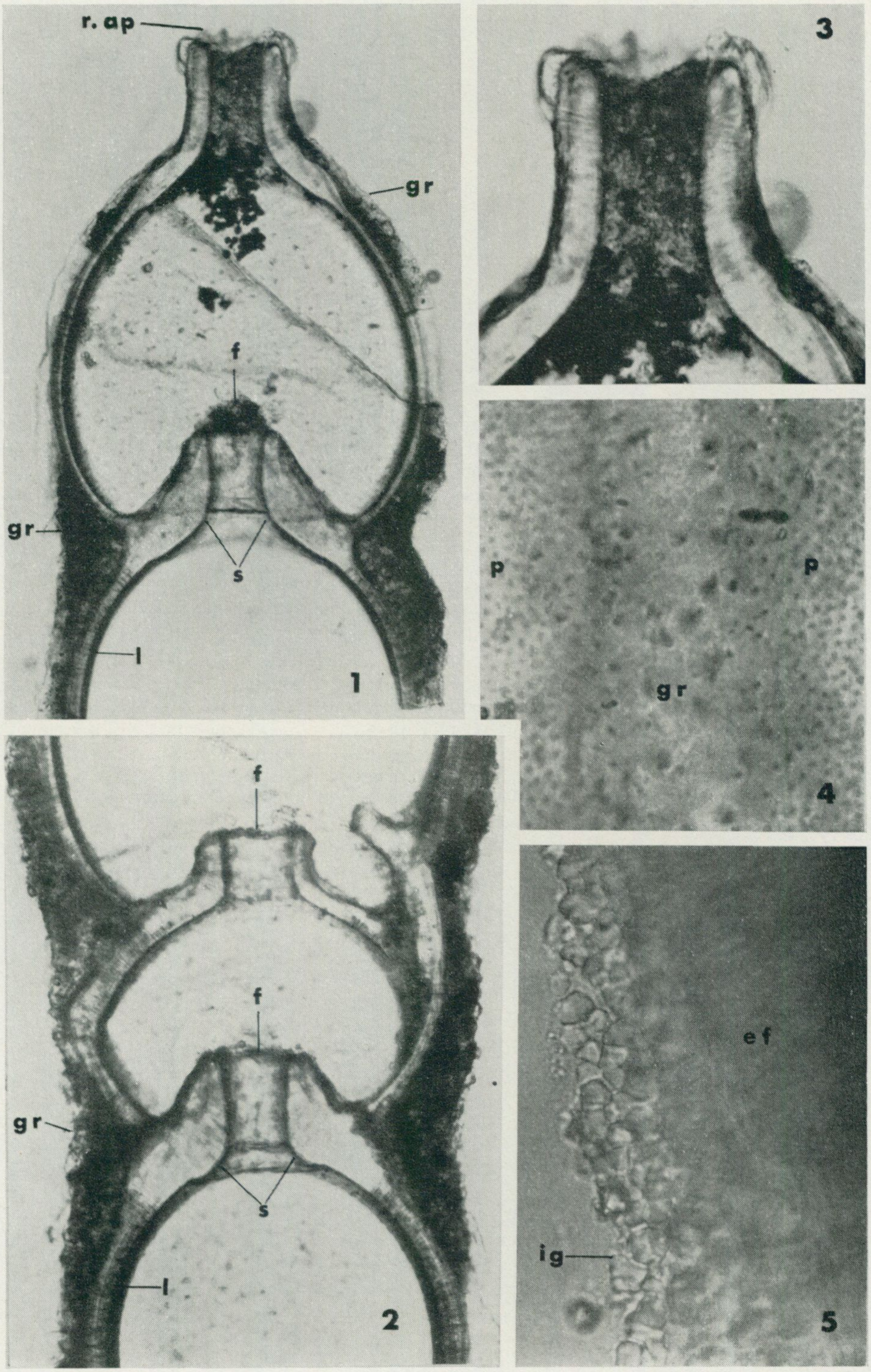


PLATE II

PLATE III

Fig. 1 *Prodentalina terquemi* (D'ORBIGNY 1849). Lias γ, Katslösa. Longitudinal section through the apertural and preceeding chamber showing imperforate apertural area and septa and pore-bundles (pb) in the test-wall. 200 x.

Fig. 2 *"Marginulina" prima* D'ORBIGNY 1849. Lias γ, Kävlinge No. 930. Longitudinal section through the three first chambers showing the circular form of proloculum, the perforate nonlamellar test-wall, and imperforate areas around the chamber sutures. 250 x.

Fig. 3 *Prodentalina terquemi* (D'ORBIGNY 1849). Lias γ, Katslösa. Part of a longitudinal section showing the nonlamellar, fibrous-radiate test-wall. 300 x.

Figs. 4—6 Three different stages of secondary lamination.

Fig. 4 *"Marginulina" prima* D'ORBIGNY 1849. Lias γ, Kävlinge no. 930. Longitudinal section through an interornamental part of the test, showing the secondarily nonlamellar test-wall with perforate (p), and imperforate (ip) regions. 500 x.

Fig. 5 *Mesodentalina matutina* (D'ORBIGNY 1849). Lias α 3/Lower Lias β, Öresund 01. Part of a longitudinal section through an interornamental part of the test, showing the secondarily mesolamellar test-wall with its high degree of overlapping of primary wall-layers, perforate and imperforate regions. 500 x.

Fig. 6 *Dentaitna sulcata* (NILSSON 1827). Upper Campanian/Lower Maastrichtian, St. Köpinge, Skåne. Part of a longitudinal section showing secondary and primary lamination of the test-wall and septa. 100 x.

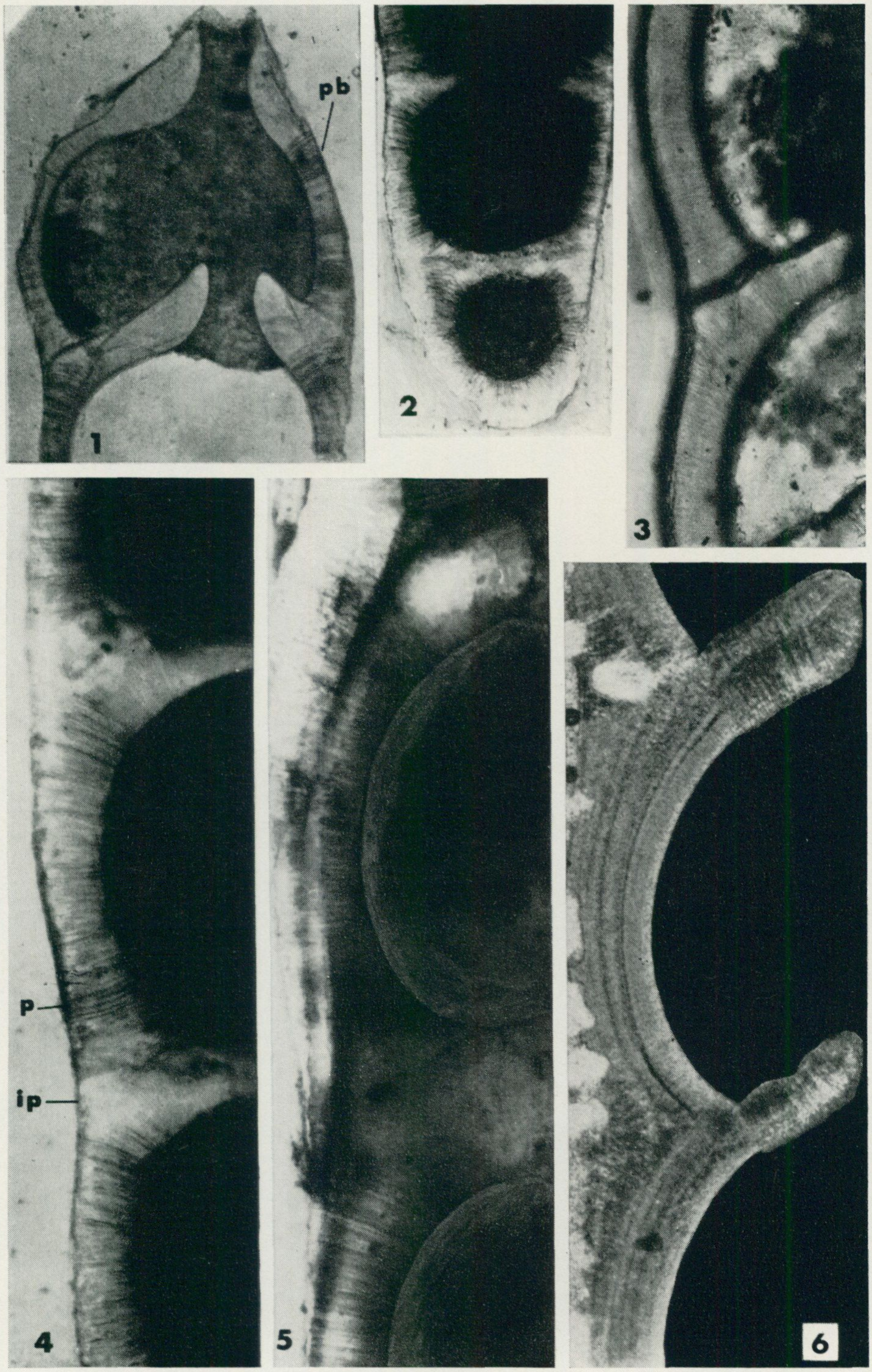
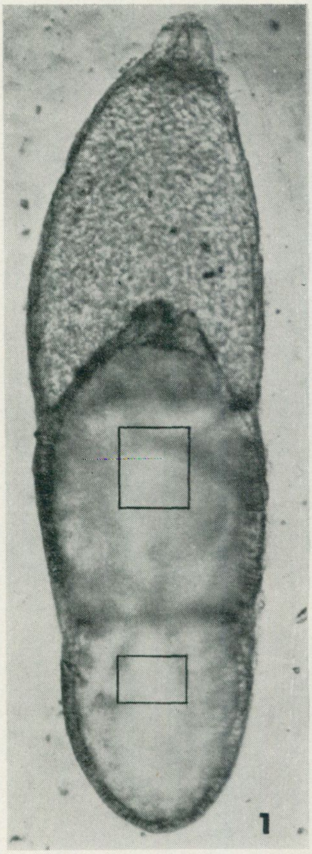


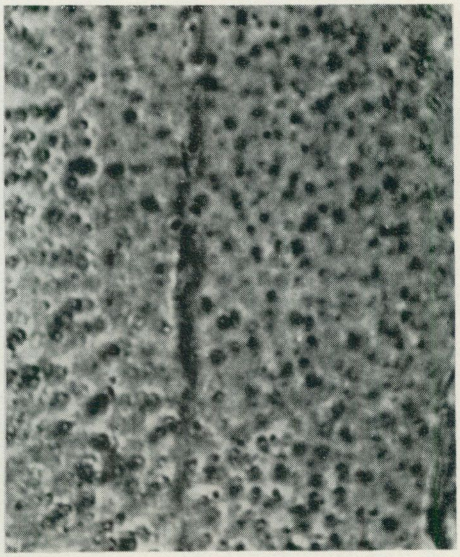
PLATE III

PLATE IV

Figs. 1—3 *Prodentalina vasta* (FRANKE 1936). Lias γ, Katslösa

1. Sectioned specimen to lay open the nonlamellar, fibrous-radiate, perforate test-wall. Note the apertural chamberlet. Black rectangles show the position of photographed areas (figs. 2, 3). 220 x.
2. Internal pore pattern of the central chamber. Note the two different sizes of pores. 1500 x.
3. Internal pore pattern of proloculum. 1500 x.





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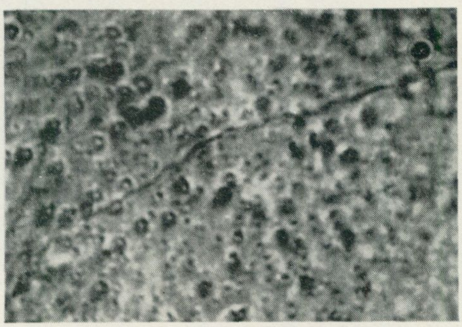


3

PLATE IV

PLATE V

Figs. 1—4 "*Astacolus*" *ex gr. varians* (BORNEMANN 1854). Lias α_3/Lower Lias β, Öresund 01.

1. Section in plane of coiling showing the chamber arrangement, and the secondarily nonlamellar, imperforate test-wall and septa. 200 x.
2. Detail of fig. 1. Phase contrast. 400 x.
3. Longitudinal section perpendicular to plane of coiling. 200 x.
4. Detail of specimen in fig. 1 showing the acicular texture of test-wall and septa. Nichols X. 400 x.

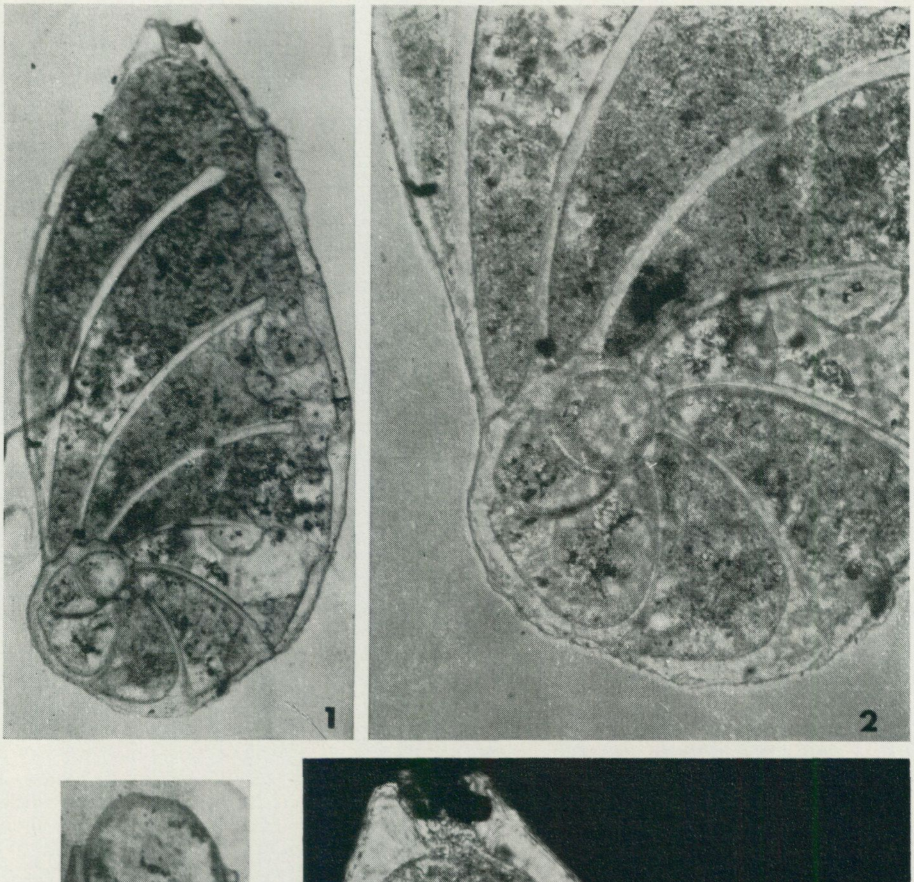


PLATE V

PLATE VI

Fig. 1 *Lenticulina turbiniformis* (TERQUEM 1863). Lias γ, Kävlinge No. 930. Specimen sectioned in plane of coiling. Note the thick wall of proloculum typical for a lamellar foraminifer. 82 x.

Fig. 2 "*Lenticulina*" *acutiangulata* (TERQUEM 1864). Lias γ, Kävlinge No. 930. Specimen sectioned in plane of coiling showing chamber arrangement, imperforate septa, perforate test-wall, and indistinctly, the mesolamellar nature of the wall. 100 x.

Fig. 3 *Lenticulina turbiniformis* (TERQUEM 1863). The same specimen as in fig. 1. Section in plane of coiling showing the fibrous texture and the radiating pores. Indistinct limits between consecutive lamellae can also be seen. Note the thick wall of proloculum. 165 x. Phase contrast.

Fig. 4 *Lenticulina cf. turbiniformis* (TERQUEM 1863). Part of a section in plane of coiling showing the fibrous texture and radiating pores. Note the decreasing thickness of the wall in the ontogenetically later chamber, and the indistinct limits between consecutive lamellae. 300 x.

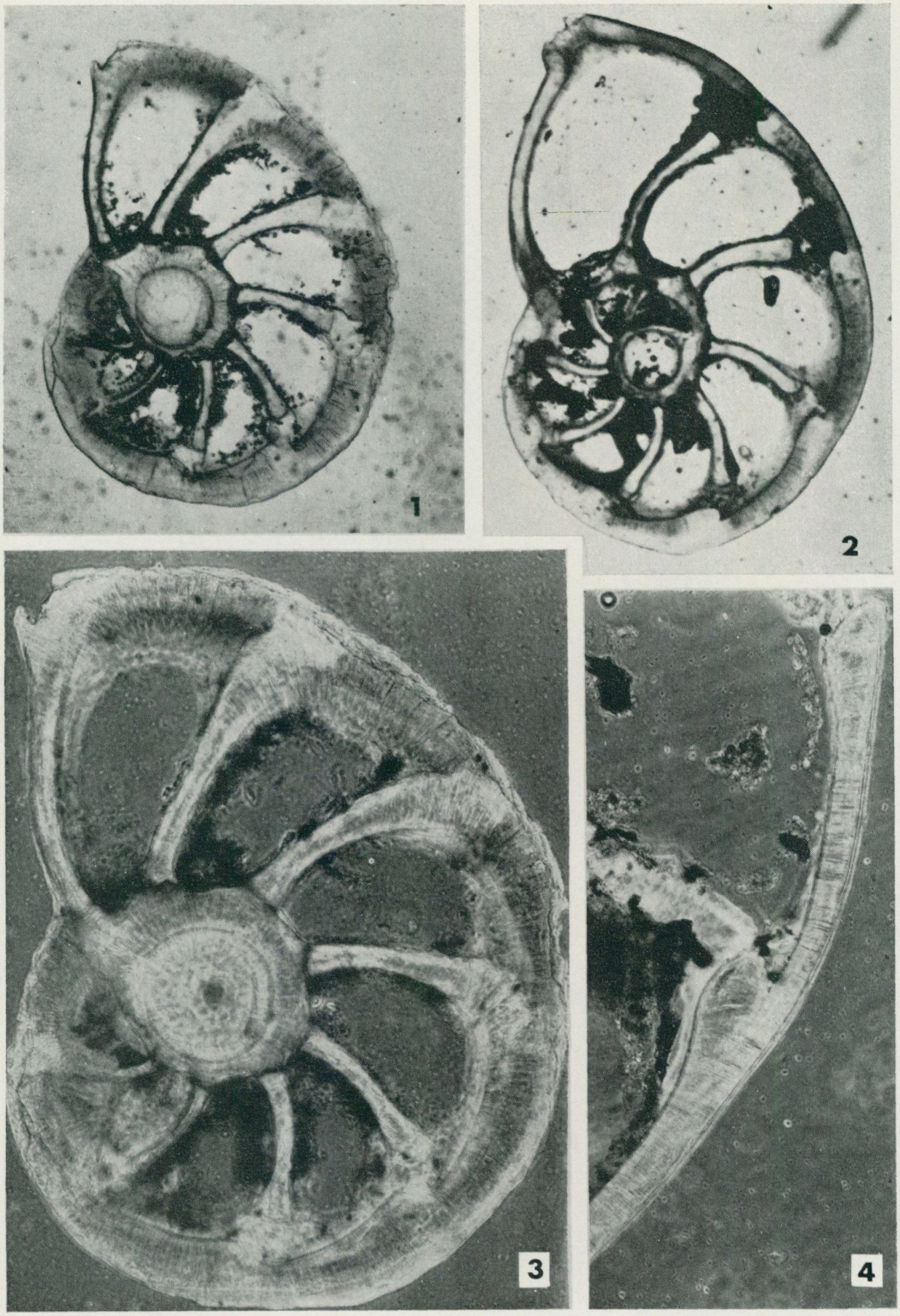


PLATE VI

PLATE VII

Electron micrographs

Figs. 1—3 *Dentalina sulcata* (NILSSON 1827). Upper Campanian/Lower Maastrichtian. St. Köpinge Skåne, S Sweden.

1. Internal mouth of a pore. c. 6,500 x.
2. Globulitic texture of the internal part of a septum. c. 3,300 x.
3. Part of the test-wall in longitudinal section showing parallel crystal elements and pore canals. Perpendicular to them, limits between consecutive lamellae are seen. The canals, which penetrate the crystal elements, and partly follow the limits between lamellae, are probably caused by a parasite. c. 3,300 x.

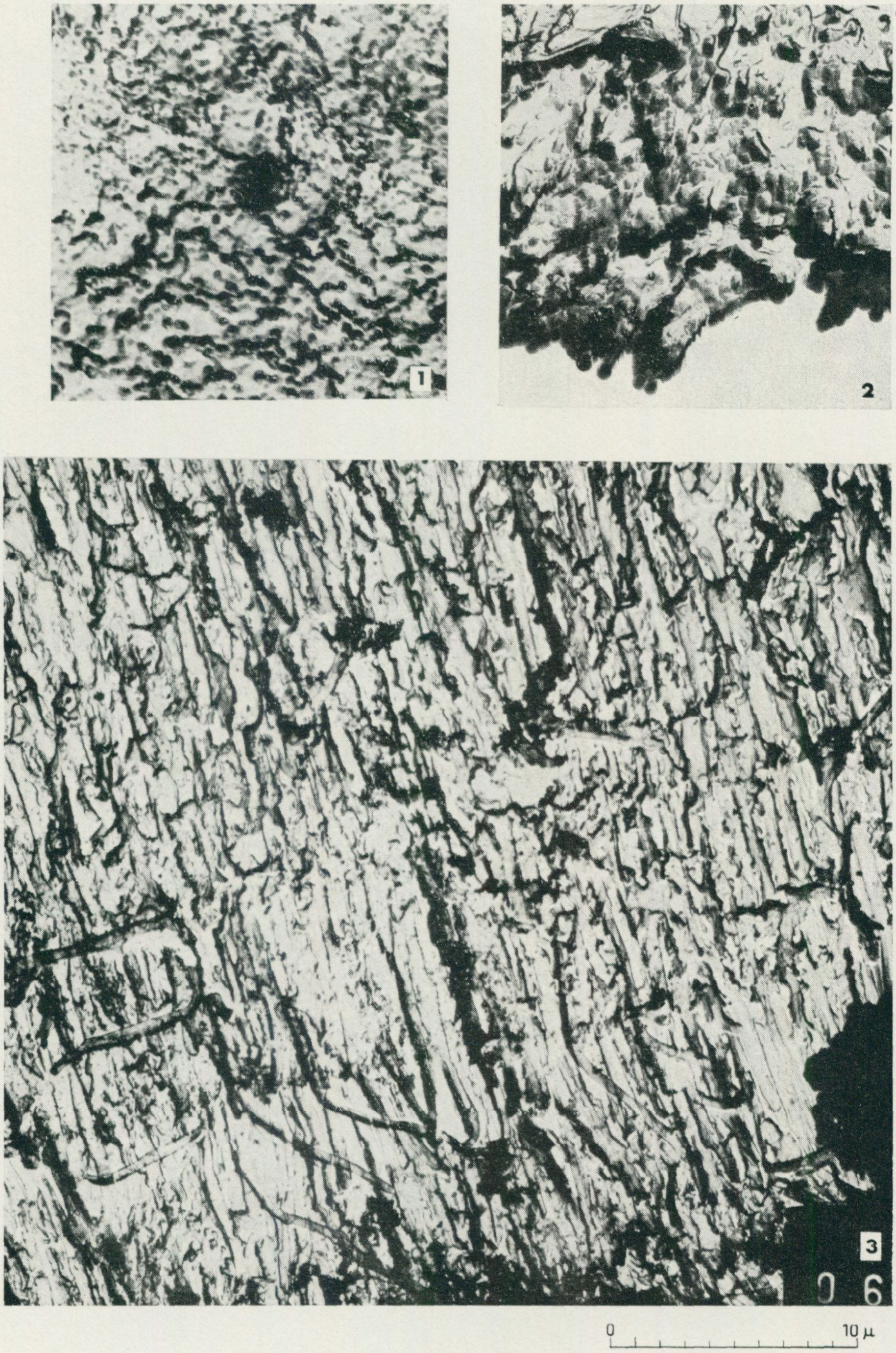


PLATE VII

PLATE VIII

Electron micrographs

Figs. 1—2 *Dentalina sulcata* (NILSSON 1827). Upper Campanian/Lower Maastrichtian, St. Köpinge, Skåne, S Sweden.

Part of the test-wall in longitudinal section showing parallel crystal elements in two different directions on each side of a chamber suture. c. 3,300 x.

2. Part of the test-wall in longitudinal section showing parallel pore canals. c. 3,300 x.

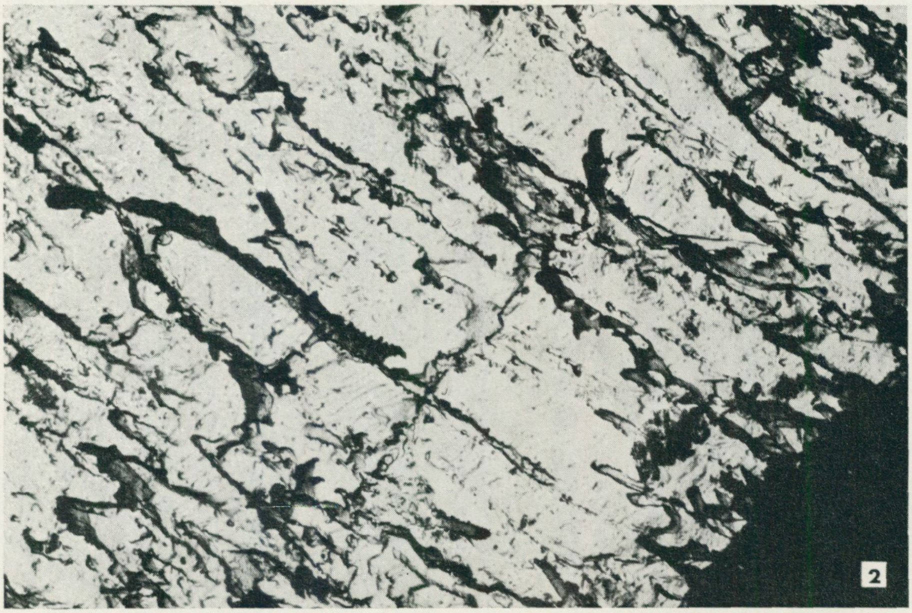
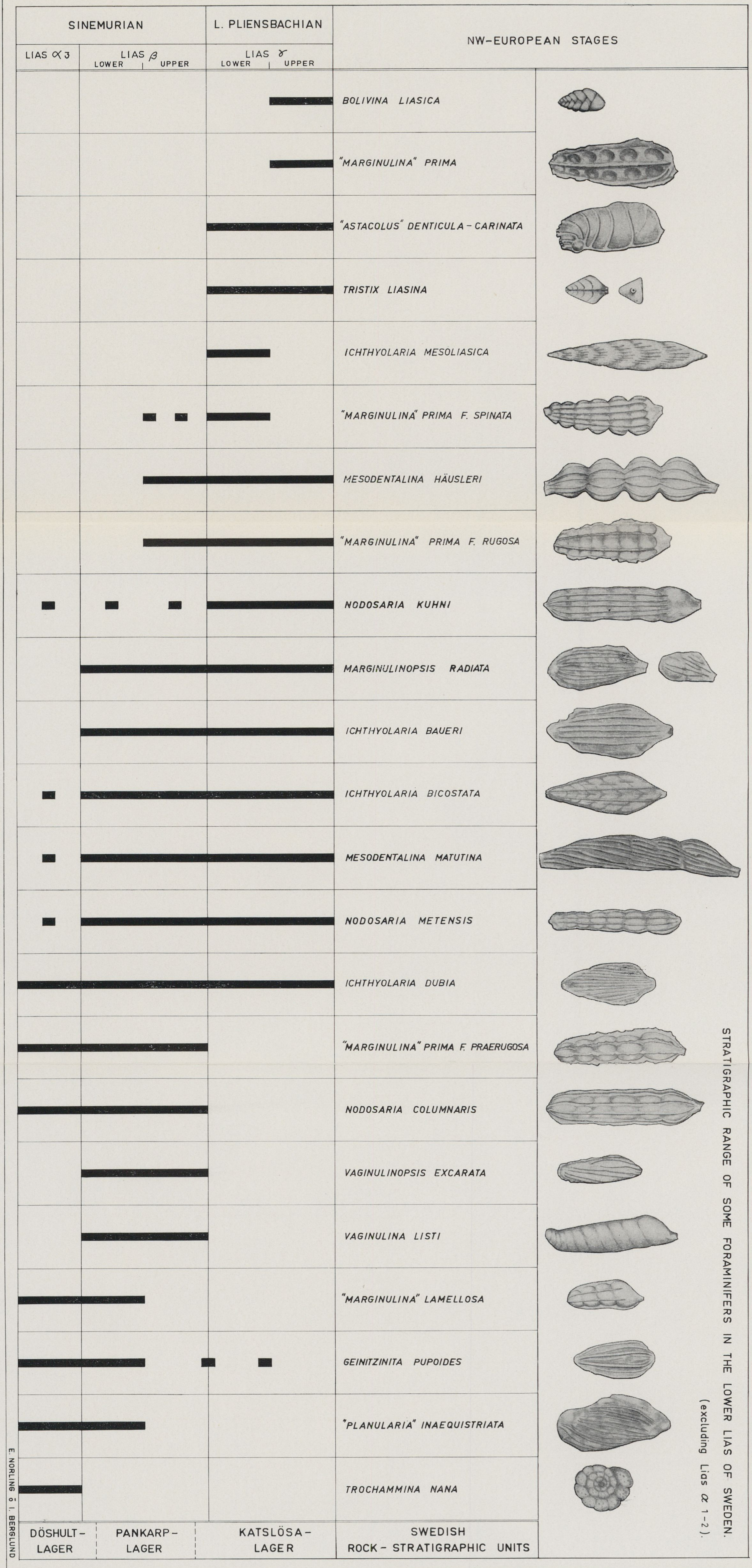


PLATE VIII

PLATE IX



STRATIGRAPHIC RANGE OF SOME FORAMINIFERS IN THE LOWER LIAS OF SWEDEN.
(excluding Lias α 1-2).

PRISKLASS D

Distribution

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