

# Scanning electron microscopy of some recent and fossil nodosariid foraminifera

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23 recent and fossil species representing 15 genera within the Nodosariacea have been studied with respect to lamellarity. All forms were found to be monolamellar. However, four different categories of the monolamellar construction pattern were found. Of these the ortho-monolamellar type has a one-layered chamber with an enveloping secondary lamella covering the earlier exposed shell. If the secondary lamella covers only part of the earlier exposed shell it is termed plesio-monolamellar while a lack of secondary lamination is called atelo-monolamellar. Multiple lamination in the septa covering also the earlier exposed shell parts is called poly-monolamellar. The microgranular layer in Jurassic forms is of diagenetic origin.

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The superfamily Nodosariacea *sensu* Loeblich & Tappan (1964) is an important stratigraphical foraminiferal group particularly in the Mesozoic Era and has accordingly attracted the interest of stratigraphers. The wall structure of this group has mainly been studied in specimens from older geological horizons, while the recent representatives have received considerably less attention.

The obvious disadvantage in studying geologically older tests relates to the fact that diagenetic processes play a varying rôle veiling the primary structures. Earlier works (Gerke 1957; Sellier de Civrieux & Dessauvage 1965; Norling 1968; Reiss 1963) all used light microscopy in their studies. The present work utilizes the higher spatial resolution power of the scanning electron microscope, and the main emphasis has been placed on the study of recent representatives in order to avoid the inherent diagenetic problems of fossil specimens.

A part of the present work constitutes a partial fulfilment of the requirements for the cand. scient. degree of the senior author.

## Methods and materials

Specimens to be sectioned were embedded in Lakeside 70 cement on glass slides and oriented by aid of a heated needle. In some cases not all chambers were filled in after the initial embedding. Such specimens were ground to a level where the chambers in question were opened. The cement was reheated and the shell turned over so that the sectioned plane was brought in contact with the surface of the glass slide. After this procedure the test was sectioned to the desired level on wet grinding paper no. 600.

Subsequently the section was polished on a velvet rotating disc using 1  $\mu\text{m}$   $\text{Al}_2\text{O}_3$  paste as polishing medium.

After this treatment the section was rinsed thoroughly by washing with grease-free sulfonated soap followed by etching in an aqueous unbuffered saturated solution of EDTA for varying periods of time. The etching process was made in gradual steps interrupted by inspection of the dried section under the binocular microscope. The etching was considered sufficient when, under the light microscope in reflected light, the relief at boundaries between lamellae was seen.

The glass slides were fractured by a diamond pencil and a vice, and the sections were

mounted onto SEM stubs by the aid of double adhesive tape. Whole specimens were mounted on the stubs directly on tape.

The preparations were coated with 200–500 Å gold from two tungsten filaments under an angle of 5° and 45° respectively. They were studied in a Cambridge MK IIa scanning electron microscope housed in the Laboratory of Electron Microscopy of the University of Copenhagen.

The material used in this investigation originates from the 'Nørvang Collection' housed in the Micropalaeontological Laboratory of the University of Copenhagen. It involves specimens determined by Jan Hofker sen., by the late A. Nørvang and by the authors. All preparations are deposited in the above-mentioned laboratory.

Material of Cretaceous and Tertiary age for comparison was generously furnished by Prof. Krystina Pozaryska, Warsaw.

### Terminology

Through the works of Smout (1954), Reiss (1963) and later authors a terminology regarding lamellarity of foraminiferal tests has gradually evolved. Thus a *monolamellar* form secretes a primary chamberwall consisting of one carbonate layer; the same layer continues as one layer covering also the exposed parts of the ontogenetically younger parts of the shell. A *bilamellar* form secretes a primary chamberwall consisting of two carbonate layers separated by an organic layer of varying thickness; the outer layer of the primary chamberwall continues as one layer covering also the exposed parts of the ontogenetically younger parts of the shell. A variant of the bilamellar form exists in the so-called '*rotaliid*' model, in which the inner carbonate layer of the primary chamberwall continues to cover partly or completely the face of the preceding chamber.

The term *nonlamellar* is applied to forms other than those belonging to the suborder Rotaliina (compare Loeblich & Tappan 1964).

The term *primary lamination* is applied to lamination occurring in one of the above-mentioned carbonate layers. These lines (as

seen on the etched sections) cannot be followed throughout the shell but only for shorter distances, i. e. unlike the boundary between secondary lamellae.

### Observations

Species with monolamellar septa and complete enveloping secondary lamellae (ortho-monolamellar).

*Nodosaria vertebralis* (Batsch, 1791); Recent, Kei Islands, depth 200–300 m.; coll. Th. Mortensen, 1922; det. J. Hofker sen.. This very large and costate species (fig. 1) showed in longitudinal section a different reaction towards etching depending on whether the sectioned area consisted of imperforate material or whether pore tubules were present. The latter areas responded more willingly to etching (figs. 2 & 3). Secondary lamellae are added to the earlier exposed shell with one lamella per chamber-forming event. Multiple primary lamination was observed in various regions.

*Dentalina frobisherensis* Loeblich & Tappan, 1953; Recent, Brønlunds Fjord, North Greenland, depth 40 m.; coll. J. Just, 1966; det. H. J. Hansen. This species is large but carries no ornamentation (fig. 4). Sections demonstrated a construction identical to that of *N. vertebralis* (figs 5 & 6).

*Lenticulina iota* (Cushman, 1923); Recent, off Frederikssted, Virgin Islands, depth 950

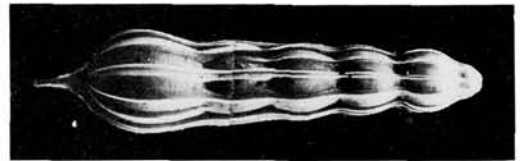


Fig. 1. *Nodosaria vertebralis* (Batsch, 1791). Megaspherical specimen;  $\times 10$ .

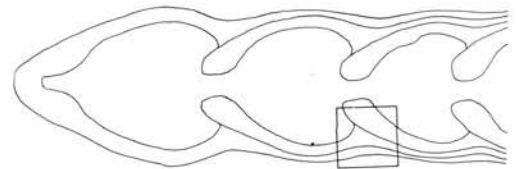


Fig. 2. Section plane of *N. vertebralis* (Batsch, 1791). Framed area shown in fig. 3.

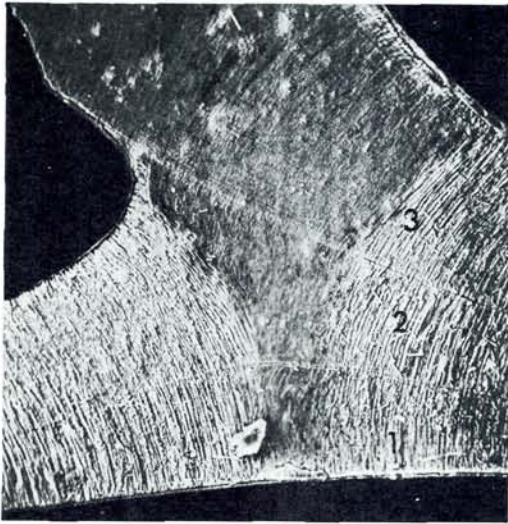


Fig. 3. Detail indicated in fig. 2. Polished and etched section through the junction between the penultimate and antepenultimate chambers showing configuration of lamellae.

NOTE the numbering system of the lamellae is arranged so that number 1 corresponds to the lamel deposited continuously with the lamel constituting the wall of the ultimate chamber et cetera. Note the slight traces of primary lamination;  $\times 190$ .

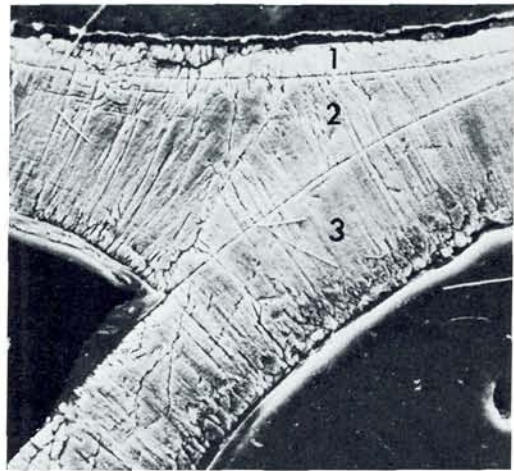


Fig. 6. Detail indicated in fig. 5. Polished and etched section through the junction between penultimate and antepenultimate chamber. Numbers as in fig. 3;  $\times 460$ .

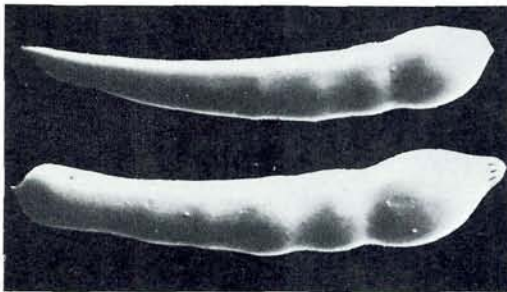


Fig. 4. *Dentalina frobisherensis* Loeblich & Tappan, 1953. Micro- and megalospheric specimens;  $\times 25$ .

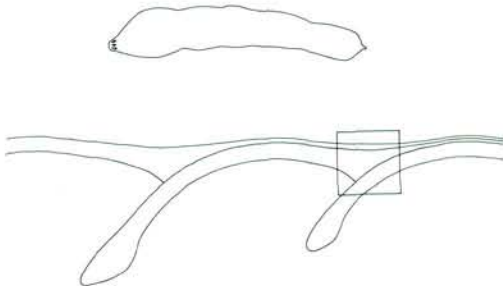


Fig. 5. Section plane of *D. frobisherensis* Loeblich & Tappan, 1953. Framed area shown in fig. 6.

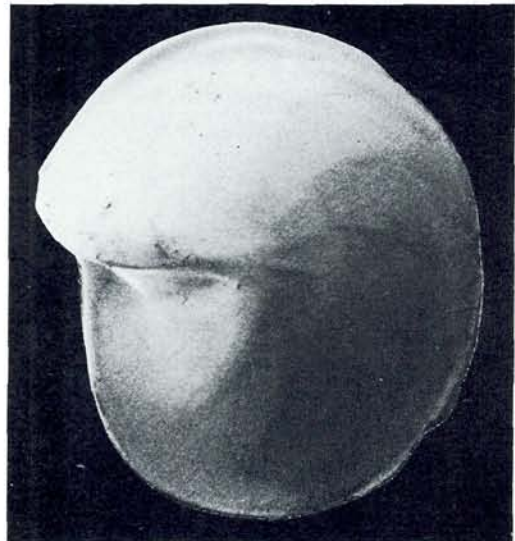


Fig. 7. *Lenticulina iota* (Cushman, 1923);  $\times 20$ .

m.; coll. Th. Mortensen, 1906; det. A. Nørvang. *L. iota* is smooth and large with a well-developed peripheral keel (fig. 7). Polished and etched sections in the SEM demonstrated the septa to be constructed of one layer (monolamellar septa) which layer continues over the earlier exposed shell parts to form secondary lamination each lamel of which corresponds to one chamber-forming event (figs 8 & 9).

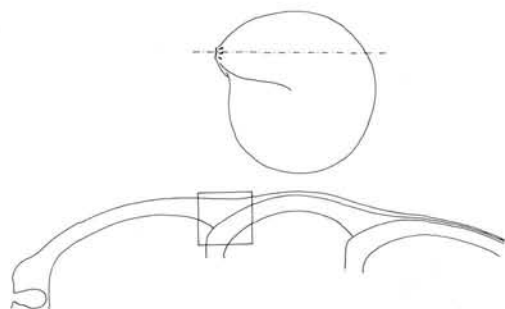


Fig. 8. Section plane (dotted line) of *L. iota* (Cushman, 1923). Framed area shown in fig. 9.

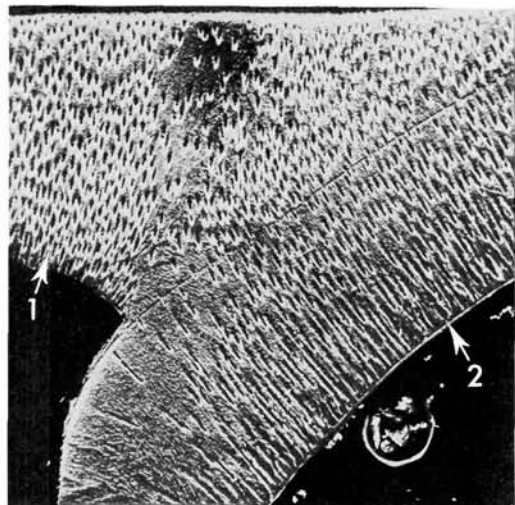


Fig. 9. Detail indicated in fig. 8. Polished and etched section through the junction between ultimate and penultimate chambers. Numbers as in fig. 3;  $\times 400$ .

One specimen of *Lenticulina* sp.; Upper Jurassic, Pomerania, Poland; being smooth without any ornamentation was identical to *L. iota* with respect to wall structure (fig. 10).

Identical structures were observed in *Lenticulina costata* (Fichtel & Moll, 1798); Recent, Kei Island, depth 200 m.; coll. Th. Mortensen, 1922; det. A. Nørvang. By contrast to the above-mentioned species of the genus *Lenticulina*, this species carries costae as well as limbate sutures (fig. 11). In etched sections in SEM the lamellar boundaries were found to conform to the ornamentation (fig. 12) but did not differ in construction principle from the other representatives of the genus *Lenticulina* here studied.

The closely allied genus *Marginulina* is here



Fig. 10. *Lenticulina* sp.. Detail of polished and etched vertical tangential section through monolamellar septum and the corresponding secondary lamella. Note secondary lamellae in the earlier coil;  $\times 440$ .



Fig. 11. *Lenticulina costata* (Fichtel & Moll, 1798);  $\times 28$ .

represented by *Marginulina albatrossi* (Cushman, 1923); Recent, Salhus, Norway, depth 350 m.; coll. K. Stephensen, 1905; det. H. Grønlund. The shell is smooth and unornamented (fig. 13) and showed in etched sections in the SEM a characteristic monomellar pattern like in the previously mentioned species (figs 14 & 15).

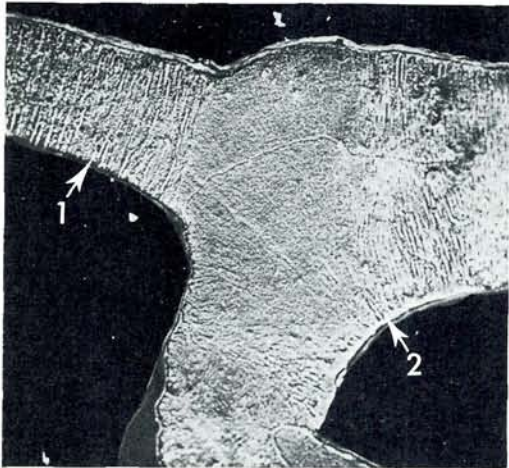


Fig. 12. *L. costata* (Fichtel & Moll, 1798). Detail of polished and etched section showing junction between ultimate and penultimate chambers (section plane as in fig. 8);  $\times 310$ .

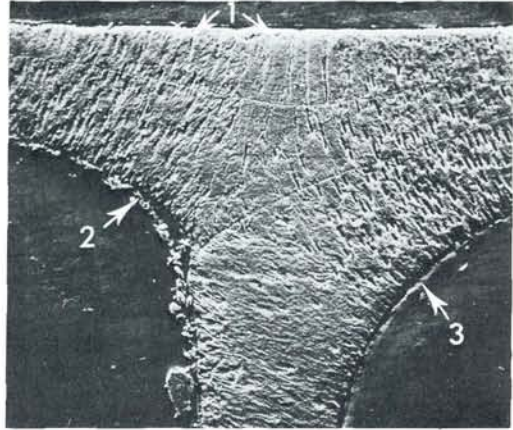


Fig. 15. Detail indicated in fig. 14 of polished and etched section through the junction between the penultimate and antepenultimate chamber;  $\times 355$ .

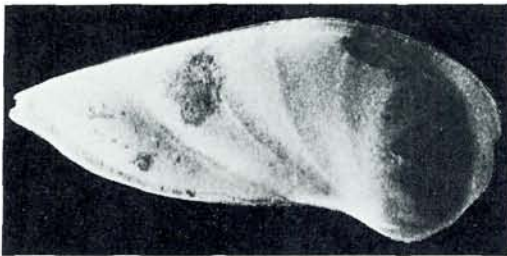


Fig. 13. *Marginulina albatrossi* (Cushman, 1923);  $\times 21$ .

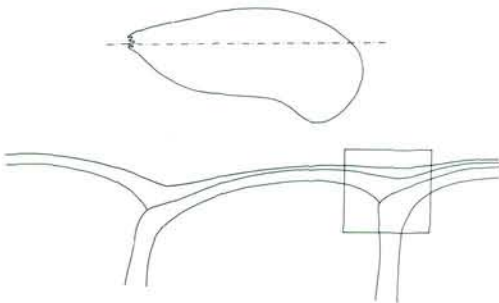


Fig. 14. Section plane of *M. albatrossi* (Cushman, 1923). Framed area shown in fig. 15.

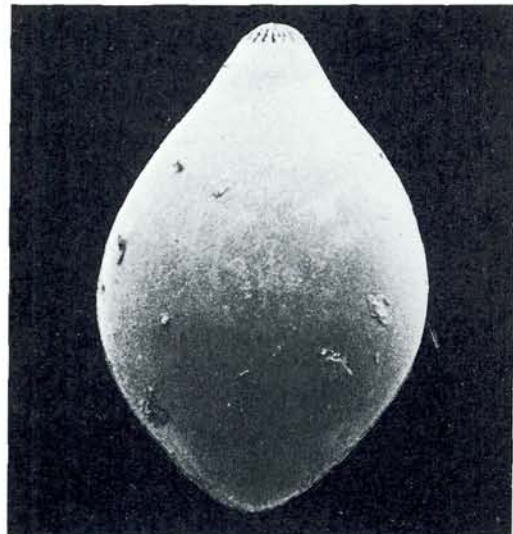


Fig. 16. *Glandulina laevigata* d'Orbigny, 1826;  $\times 60$ .

As representative of the family Glandulinidae the type species of the genus *Glandulina* i. e. *Glandulina laevigata* d'Orbigny, 1826; Recent, Salhus, Norway, depth 350 m.; coll. K. Stephensen, 1905; det. A. Nørvang, has been studied (fig. 16). Etched sections in the SEM demonstrated that the septa are mo-

nolamellar and that the secondary lamellae envelope the earlier exposed shell completely (figs 17 & 18).

Species with monolamellar septa and incomplete enveloping secondary lamellae (plesiomonolamellar).

In the material studied only one species was met that fits into this group, namely *Dentalina pauperata* d'Orbigny, 1846; Recent, off Godhavn, Disko, Greenland, depth 425 m.; coll. "Tjalfe", 1908; det. A. Nørvang (fig. 19). Longitudinal sections in the SEM demonstra-

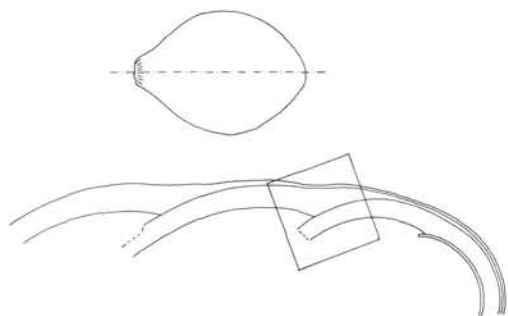


Fig. 17. Section plane of *G. laevigata* d'Orbigny, 1826. Framed area shown in fig. 18.



Fig. 18. Detail of polished and etched section through junction between penultimate and antepenultimate chamber indicated on fig. 17;  $\times 450$ .



Fig. 19. *Dentalina pauperata* d'Orbigny, 1846;  $\times 21$ .

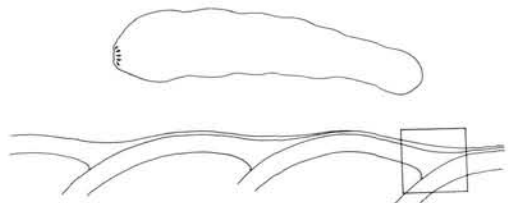


Fig. 20. Section plane of *D. pauperata* d'Orbigny, 1846. The framed area is shown in fig. 21.

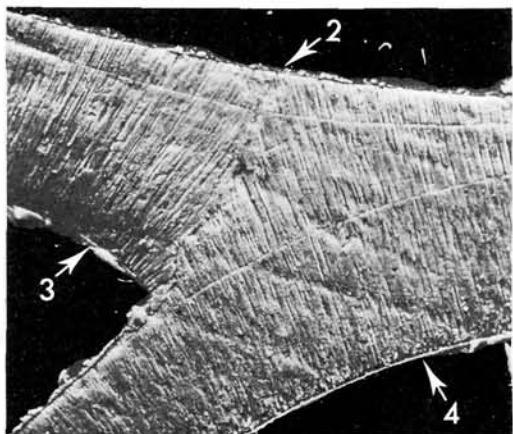


Fig. 21. Polished and etched section at chamber junction as indicated on fig. 20;  $\times 325$ .

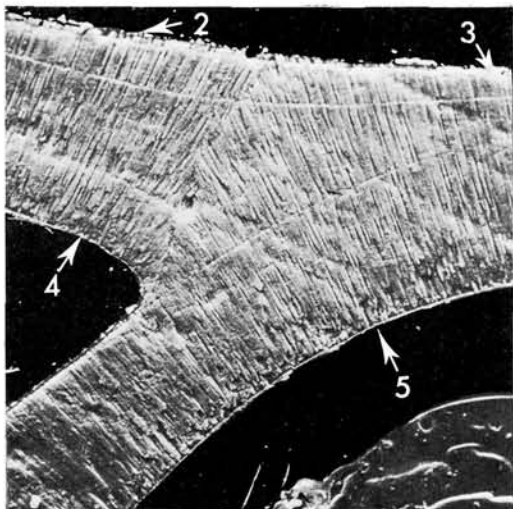


Fig. 22. Detail of the section shown in fig. 21 at the preceding chamber junction. Note the wedging out of lamella number 2 at top of micrograph;  $\times 325$ .

ted that the septa are monolamellar and that the wall continues to cover also the exposed parts of the preceding two chambers beyond which it does not continue (figs 20, 21 & 22).

Species with monolamellar septa and no enveloping secondary lamellae (atelo-monolamellar).

In the recent material here studied only one species belonging to the above-defined group was found. *Nodosaria subsoluta* Cushman, 1923, Recent, Virgin Islands, depth 950 m.; coll. Th. Mortensen, 1906; det. A. Nørvang.

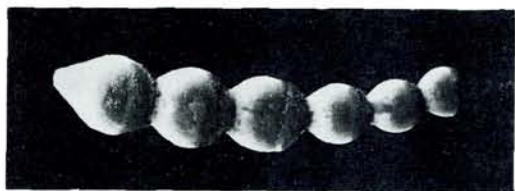


Fig. 23. *Nodosaria subsoluta* Cushman, 1923;  $\times 9$ .

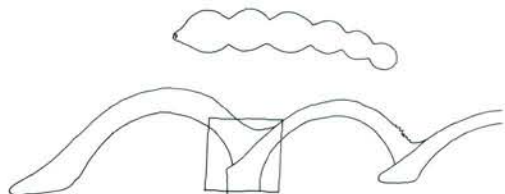


Fig. 24. Section plane of *N. subsoluta* Cushman, 1923. Framed area shown in fig. 25.

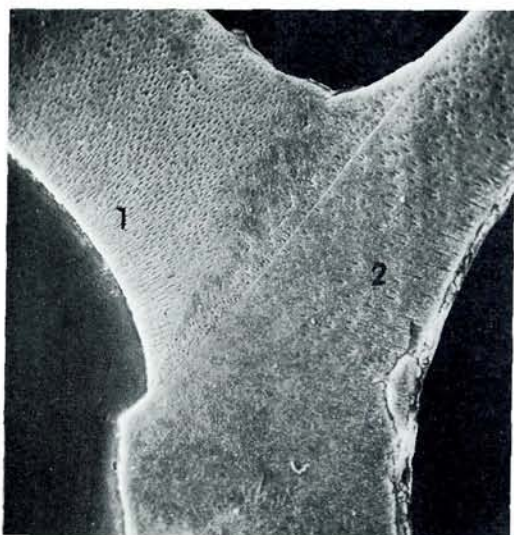


Fig. 25. Polished and etched section showing the junction between ultimate and penultimate chamber as indicated on fig. 24;  $\times 240$ .

Longitudinal sections in the SEM showed that the septa and primary chamber-walls are monolamellar and that the chamber material does not extend beyond the attachment zone (figs 23, 24 & 25).

Species with monolamellar septa and complete enveloping secondary lamellae with additional enveloping carbonate layers covering the entire shell including the last-formed chamber (poly-monolamellar).

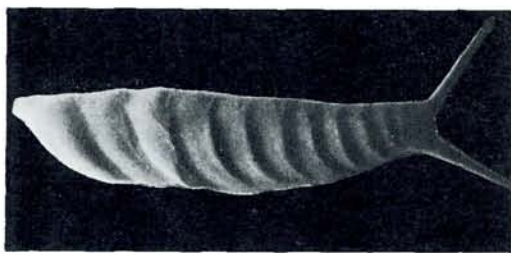


Fig. 26. *Vaginulina spinigera* Brady, 1881;  $\times 12$ .

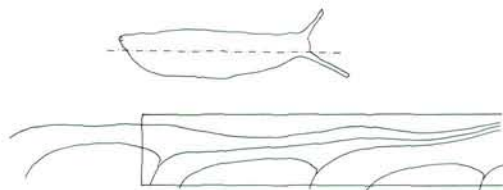


Fig. 27. Section plane of *V. spinigera* Brady, 1881.

*Vaginulina spinigera* Brady, 1881; Recent, Virgin Islands, depth 950 m.; coll. Th. Mortensen, 1906; det. A. Nørvang. This large species is unornamented except for two prominent apical spines (fig. 26). Longitudinal sections in the SEM demonstrated that the septa are constructed of one, two or more layers. When constructed of a single layer the structural pattern of the wall is identical to that of the ortho-monolamellar group described above. When a septum consists of more than one layer, each of these layers envelops the entire exposed previously formed shell (figs 27 & 28).

*Saracenaria italica* DeFrance, 1824; Recent, Kei Islands, depth 200 m.; coll. Th. Mortensen, 1922; det. J. Hofker senior. This is a large and smooth species (fig. 29). Sections studied in the SEM showed a construction pattern identical to that observed in *V. spinigera*; however, the number of layers in the septa was generally higher in *S. italica* (figs 30 & 31).

*Lingulina seminuda* Hantken, 1873; Recent, Virgin Islands, depth 950 m.; coll. Th. Mortensen, 1906; det. A. Nørvang. This species is very large and robust (fig. 32) and is without ornamentation except for the peripheral keels. Longitudinal sections in the SEM showed the septa to be constructed of a varying number of lamellae ranging from two to five. Each lamella covers the earlier exposed shell

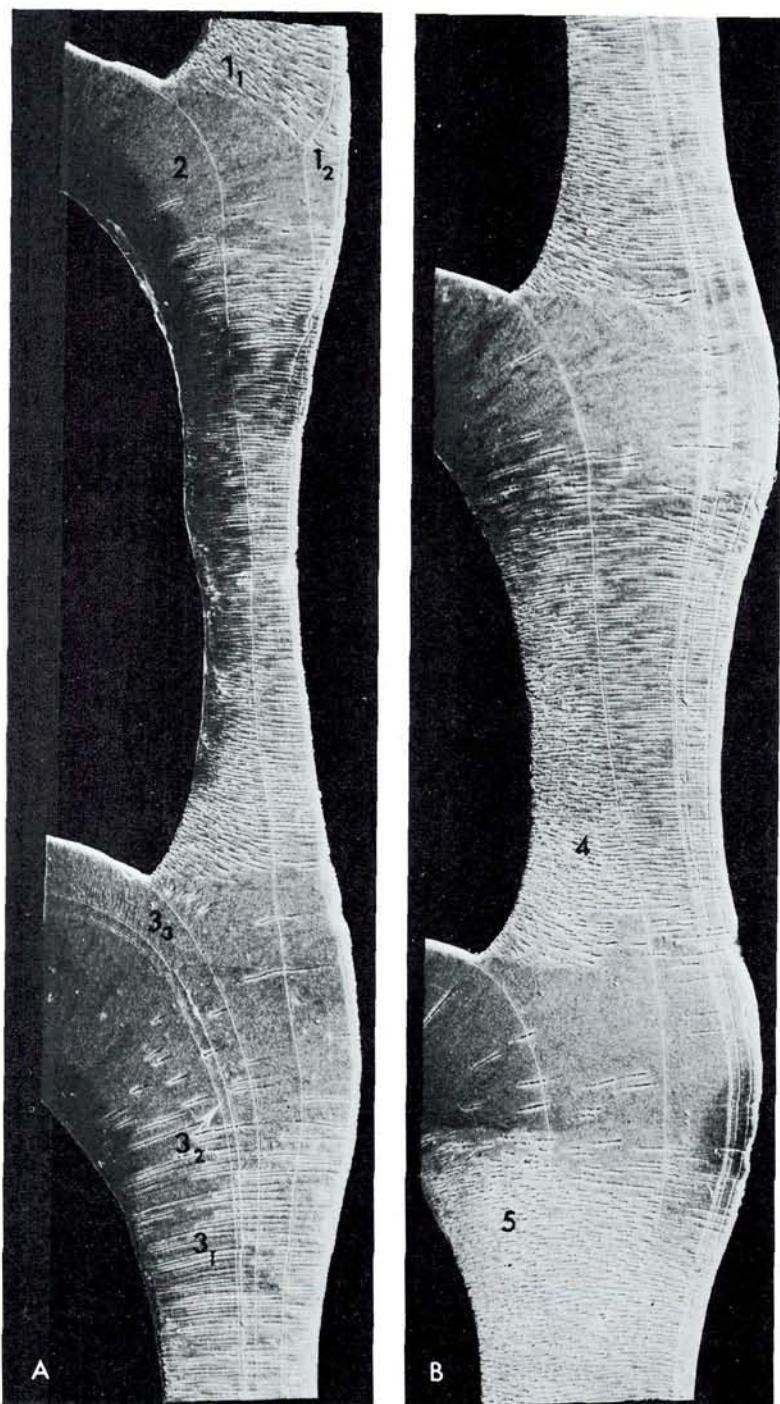


Fig. 28. Polished and etched section through four consecutive chambers starting with the junction between ultimate and penultimate one. Fig. 28 B is the continuation of fig. 28 A. The first lamel formed is marked as  $1_1$ , the next as  $1_2$ , et cetera. Note traces of primary lamination;  $\times 200$ .





Fig. 29. *Saracenaria italica* DeFrance, 1824;  $\times 24$ .

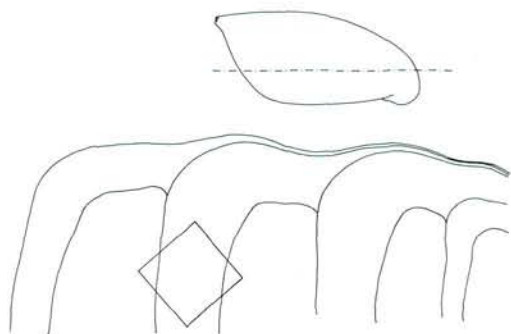


Fig. 30. Section plane in *S. italica* DeFrance, 1824. Framed area shown in fig. 31.

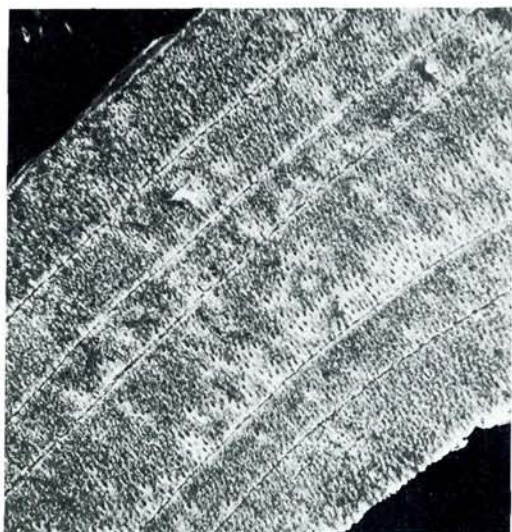


Fig. 31. Detail of polished and etched section as indicated on fig. 30 showing a septum with six lamellae;  $\times 460$ .



Fig. 32. *Lingulina seminuda* Hantken, 1873;  $\times 19$ .

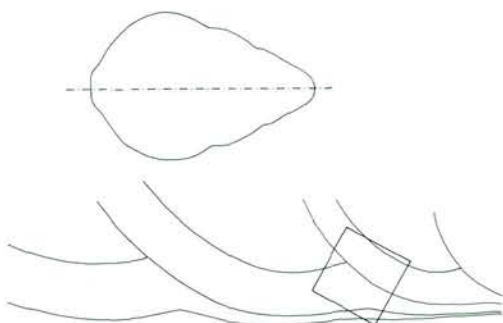


Fig. 33. Section plane in *L. seminuda* Hantken, 1873. Framed area shown in fig 34.

parts as described above for *V. spinigera* (figs 33 & 34).

The following species were studied as well. However, since these forms do not differ from the above described ultrastructural patterns and accordingly convey no further information they have not been illustrated.

*Amphicoryna scalaris* (Batsch, 1791). Recent, ortho-monolamellar.

*Citharina plummoides* (Plummer, 1926). Palaeocene, shell recrystallized, ortho-monolamellar (?).

*Fronicularia tenuissima* Hantken, 1875. Palaeocene, shell recrystallized, ortho-monolamellar (?).

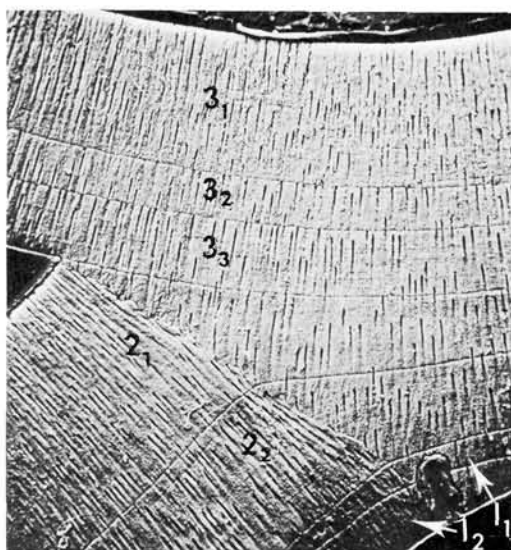


Fig. 34. Detail of polished and etched section showing junction between penultimate chamber and antepenultimate chamber. Numbering like in fig. 28;  $\times 320$ .

*Lagena sulcata* (Walker & Jacob, 1798). Recent, monolamellar.

*Lagena laevis* (Montagu, 1803). Recent, monolamellar.

*Lenticulina orbicularis* (d'Orbigny, 1826). Recent, ortho-monolamellar.

*Lenticulina inornata* (d'Orbigny, 1846). Palaeocene, ortho-monolamellar.

*Guttulina lactea* (Walker & Jacob, 1798). Recent, poly-monolamellar.

*Guttulina roemeri* (Reuss, 1856). Palaeocene, poly-monolamellar.

*Oolina melo* d'Orbigny, 1839. Recent, monolamellar.

*Fissurina* sp. Recent, monolamellar.

*Citharina plummoides* and *Fronicularia tenuissima* were recrystallized, but the still observable structures in the SEM would suggest that both forms originally were monolamellar with complete enveloping secondary lamellae.

From the results presented herein it is immediately evident that the genus *Lagena* cannot possibly fit into any of the subcategories here reported (ortho-, plesio-, atelo- or poly-monolamellar). Whether the genus *Lagena* should be placed within the Nodosariacea is an open question, but the optically radiate wall

and apertural character strongly point in this direction.

The Glandulinidae (containing forms like *Fissurina* and *Oolina*) represents a particular problem since they have a so-called entosolenian tube and one form is known to be an endoparasite of another foraminifer (Loeblich & Tappan 1964). Whether this is a reduction of a multichambered member within the Nodosariacea is not known. Anyway, by analogy with the one-chambered *Lagena*, they (i. e. *Oolina melo* and *Fissurina* sp.) are not to be classified in the subcategories mentioned above. Two specimens of *Oolina melo* were studied. One showed a monolamellar chamber-wall, the other was two-layered. This lamination might represent either a well-developed primary lamination or a poly-monolamellar chamber-wall.

The species belonging to the family Polymorphinidae (i. e. *Guttulina lactea* and *G. roemeri*) showed multilayered septa and a complete enveloping secondary lamination.

## Discussion and conclusions

Hansen and Reiss (1972) pointed out that discrepancies in findings by various authors with regard to foraminiferal wall structures apparently are due to different methods of study applied (involving also different preparational techniques and limitations in resolution power).

Hansen and Reiss further pointed out that all lamellar species so far examined by them showed a bilamellar pattern of test construction. They did, however, also stress that the Nodosariacea require further study.

Our find of undoubtedly monolamellar forms within the Nodosariacea offers the possibility of dealing with two groups of foraminifera within the Rotaliina (not including the superfamilies Spirillinacea and Carterinacea):

1. Bilamellar forms (with or without septal flap, with or without deeply depressed sutures, with optically radiate or granulate walls).
2. Monolamellar forms (with optically radiate walls), fig. 35.
  - a. Ortho-monolamellar forms (the entire exposed part of the earlier test is cove-

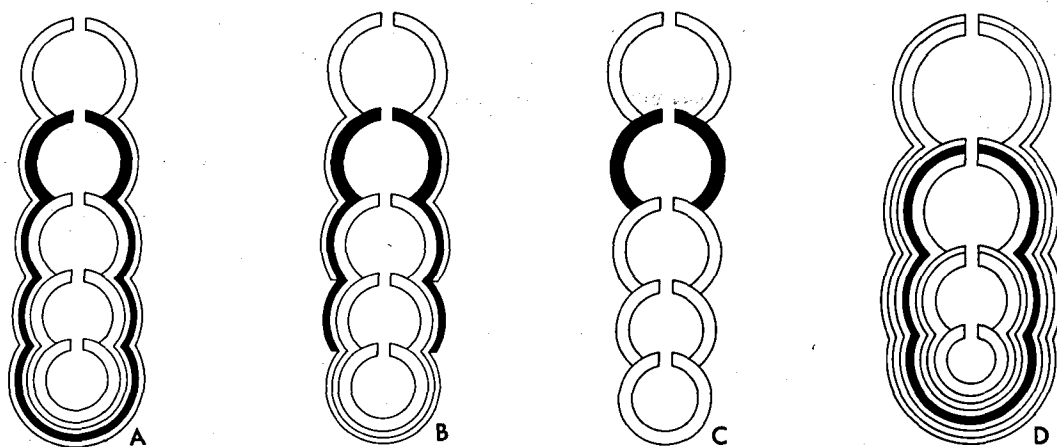


Fig. 35. Lamellar construction pattern in A: ortho-monolamellar forms, B: plesio-monolamellar forms,

C: atelo-monolamellar forms and D: poly-monolamellar forms.

red by a secondary lamella corresponding to one chamber-forming event).

- b. Plesio-monolamellar forms (the secondary lamella corresponding to the chamber-forming event does cover only part of the exposed earlier formed test).
- c. Atelo-monolamellar forms (no covering of the earlier formed shell).
- d. Poly-monolamellar forms (the entire exposed part of the earlier test is covered by a secondary lamella corresponding to one chamber-forming event with additional lamellae covering not only the exposed earlier test but also the last-formed chamber).

The terminology here suggested is purely descriptive and does not *per se* involve any evolutionary or taxonomic implications. In this connection it must be emphasized that Gerke (1957) reported species in which the microspheric individuals showed 'multilamellar structure' (probably corresponding to the ortho-monolamellar model) while the megalospheric individuals were 'monolamellar' (corresponding to the atelo-monolamellar model).

The above-mentioned categories of monolamellar forms have previously been recorded by Gerke (1957) from deposits of Permian, Triassic and Liassic age in the U.S.S.R. Forms having what is here termed ortho-monolamellar structure were recorded to have their first occurrence at the transition from Lower to Upper

Rotliegendes. This also applies to the poly-, plesio- and atelo-monolamellar forms. Thus there is no geological indication as to one lamellar group being ancestral to another.

Later studies of nodosariid wall-structures by Sellier de Civrieux & Dessauvagie (1965) and Norling (1968) dealing with Palaeozoic and Mesozoic material have confirmed observations by Gerke (1957) while the terminology applied differs somewhat.

Norling (1968) distinguished three categories of lamellar forms, namely: (1) Nonlamellar, (2) Mesolamellar and (3) Lamellar, corresponding to atelo-, plesio- and ortho-monolamellar respectively. The term nonlamellar would seem less attractive in this context since traditionally this term has been used to describe foraminiferal wall structures in forms not belonging to the suborder Rotaliina.

The existence of the poly-monolamellar construction principle has considerable bearing upon the present discussion of wall structure as related to classification. It is generally accepted that the formation of secondary lamination is intimately connected with the chamber forming process, see e.g. Smout (1954), Reiss (1963) and Hansen & Reiss (1971, 1972). However, the poly-monolamellar forms bear witness to the independence of formation of additional layers structurally indistinguishable from true secondary lamellae. Thus there exists within the suborder Rotaliina a wide variety of possibilities for shell growth. The

chamber-forming process may be connected with the deposition of a complete enveloping secondary lamella, the lamella may only partly cover or it may be totally absent. The poly-monolamellar model releases the deposition of a lamella from the chamber-forming event so that within the monolamellar group (apparently confined to the superfamily Nodosariacea) a broad spectrum of combinations exists. We have not been able to find within the large group of bilamellar forms any species showing incomplete or no secondary lamellar covering.

It is a general assumption that the Nodosariacea represents a highly conservative group within the Foraminiferida. The results of the present study of the recent representatives considered together with the results of works dealing with Palaeozoic and Mesozoic forms show that not only does the morphology remain constant but that the constancy also applies to wall structures. Accordingly the present authors consider it justified to use the same generic names for the older and younger forms even though the period of time in question may be as long as 260 million years.

The existence of an outer and (in some cases) an inner 'microgranular' layer (Norling 1968; Hohenegger & Piller 1975) has especially attracted the interest of the present authors. Norling (1968) showed drawings of e. g. *Nodosaria metensis* with 'microgranular' imperforate costae as well as light-micrographs of *N. metensis* described as having imperforate 'granular costae' and an 'interior granular layer'. Hohenegger & Piller (1975) showed a light-micrograph of a Triassic '*Astacolus*' *varians* that was stated to have a microgranular keel. Gerke (1957) considered such structures to be of diagenetic origin and not related to the primary shell secreted by the animal. Sellier de Civrieux & Dessauvage (1965) in some detail demonstrated diagenetic alterations of the primary wall (e. g. by dissolution and precipitation of iron compounds in lamellar boundaries inside the shell wall).

In our recent material we have never encountered any structures like microgranular layers on the inside or on the outside of the shells. This, however, does not preclude the existence of microgranular layer(s) in early Nodosariacea since a loss of the ability to

secrete such layer(s) might have happened during some evolutionary process, although it does not seem very likely in view of the conservatism seen in the Nodosariacea.

To test the hypothesis of the existence of primary microgranular layers the present authors picked specimens from a sample from Gantofta, Lias alpha<sub>3</sub>, Sweden, from our collection and in addition examples from Jurassic deposits in Poland and France.

In our Swedish material of *Nodosaria* (fig. 36) the structure is fully compatible with that of Palaeocene *Nodosaria latejugata* Gümbel, illustrated by Hansen (1970), in showing imperforate keels and fine pores terminating solely in the intercostal regions. We were unable to find structures identical to those drawn by Norling (1968). However, under the light microscope using dark field illumination of thin sections, a granular appearance of some costae was seen, but that is believed to be due to cracking of the material during the grinding process. It did not affect the optical orientation of the wall material as seen between crossed nicols.

*Dentalina matutina matutina* d'Orbigny, 1849; Lias beta, Nancy, France; det. A. Nørvang; was sectioned (figs. 37 & 38). In SEM these sections show layers comparable to the



Fig. 36. Detail of polished and etched cross section of *Nodosaria* sp. from Gantofta, Sweden showing imperforate costae, and perforate chamberwall between the costae;  $\times 700$ .



Fig. 37. *Dentalina matutina matutina* d'Orbigny, 1849, Nancy, France; det. A. Nørvang. Megaospheric specimen with typical "hairy" overgrowth in the intercostal regions;  $\times 42$ .

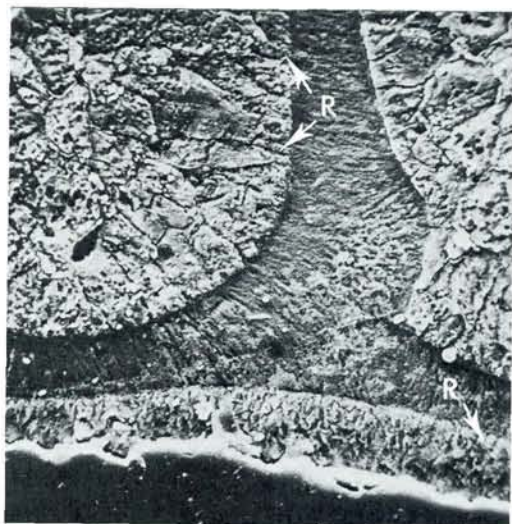


Fig. 38. Detail of polished and etched horizontal section through specimen shown in fig. 37 showing junction between chamber no. 3 and 4 (according to the numbering system used in fig. 3). The chamber interior is filled with sparry calcite in the central part while the areas close to the chamberwall is developed in a finely radiating manner (R). Identical finely radiating crystals are seen in the outer layer closest to the chamber outer surface, while the crystal size appear larger in the outer part of the surface layer. NOTE the identical etching of the infilling material and the layer on the surface, being different from the true perforate wall;  $\times 390$ .

outer 'microgranular' layer recorded by Norling (1968). However, these outer granular layers were invariably connected with surface areas of the shells, being covered with a layer giving the shell sculpture and outline a 'hairy' appearance. This is seen also on the SEM micrographs published by Norling (1972, see e. g. his fig. 42 A & C) and Hohenegger & Piller (1975, pl. 7, fig. 1). The present authors therefore are confident that this layer is of diagenetic origin. The boundary between the 'mi-

crogranular' layers and the shell wall proper is generally well marked on etched sections.

The partly microgranular costae in *Nodosaria metensis* drawn by Norling (1968) may well represent a progressive recrystallization which is more easily traced in the imperforate costae than in the perforate chamber-wall in which the pore tubules give the impression of a more orderly structure.

In the electron microscope the fine structure of the 'microgranular' layer is seen as an aggregation of grains; these are apparently carbonate particles since they react to etching (fig. 38). Often the wall proper reacts differently towards etching than does the outer 'microgranular' layer. The reaction of the outer 'microgranular' layer is identical to that of the sparry calcite filling in the chamber lumina. Moreover, it is remarkable that the 'microgranular' outer layer as well as the part of the infilling sparry calcite lying closest to the shell wall exhibits a slight columnar structure indicative of an initial diagenetic epitaxial growth corresponding to the crystal units of the optically radiate wall. Such growth is well known from e. g. the Maastrichtian white chalk of Denmark, see e. g. Jørgensen (1975). With the growth of these initial crystals, larger crystals are formed that lead in the later stages to the formation of sparry calcite. This stage is reached in the chamber infilling area but not on the surface of the shell.

The light-micrograph of a sectioned specimen of *Nodosaria metensis* shown by Norling (1968, pl. 2, fig. 1) would appear to demonstrate that the so-called imperforate granular costae are not granular. On fig. 1 on the left hand side of the section of the final chamber is seen an imperforate keel (recognizable owing to its glassy appearance) that does not exhibit any granular structure. The same is seen on the right hand side of the final chamber where a piece of the secondary overgrowth seems to have fallen off.

Norling's section is not perfectly axial (i. e. the one section level is in the axial plane while the other is deeper, resulting in the preservation in the section of the upper or lower half of the aperture/foramina). Since the costae lie in the axial plane they disappear out of the section when the suture is approached and

reappear on the following chamber as is seen on the micrograph shown by Norling (1968). The area in the lower left side of the micrograph indicated as being granular accordingly represents neither a keel nor a part of the perforate chamber wall. The present authors therefore interpret the granular material shown on Norling's micrograph as being caused by diagenetic overgrowth as discussed above.

The present authors agree with Gerke (1957) in regarding microgranular layers and parallel phenomena in the Nodosariacea as of secondary origin not related to the primary shell of the organism.

### Dansk sammendrag

23 recente og fossile arter, der repræsenterer 15 slægter fra overfamilien Nodosariacea, er undersøgt med hensyn til lamellaritet. Alle 23 arter var monolamellære, men det var muligt at skelne mellem 4 forskellige typer af monolamellær konstruktion, se fig. 35. Den ortho-monolamellære type har en een-laget kammervæg, der fortsætter i en såkaldt sekundær lamel, som dækker hele den ydre overflade af den ældre del af skallen. Den plesio-monolamellære type adskiller sig fra den ortho-monolamellære type ved, at den sekundære lamel kun dækker en del af den ældre del af skallen; og den atelo-monolamellære type er karakteriseret ved, at den sekundære lamel mangler. Hos nogle arter er septa opbygget af flere lag, der alle fortsætter ned over den ældre del af skallen. Denne type af lamellaritet kaldes poly-monolamellær.

Forskellige forfattere har beskrevet ydre, mikrogranulære lag, der skulle dække den hyaline, perforate kammervæg hos jurassiske arter tilhørende Nodosariacea. Det ydre, mikrogranulære lag er ikke en del af den skal, det levende dyr afsondrede, men må tolkes som værende af diagenetisk oprindelse (fig. 38).

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