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Contribution to the History of Growth of the *Chordoperculinoides* Shell

By Paul Arni (Zürich)¹⁾

with two text figures and two plates (1 and 2)

INTRODUCTION

In the systematics of the nummulitids the evolute and involute forms are roughly separated on the level of generic diagnostics. *Nummulites* s. str. comprises roughly the involute forms; most evolute or nearly evolute forms are placed under the genera *Operculina* and *Assilina*. It was hitherto also admitted that many species of *Assilina* are having a hidden involute coiling. Other peculiar forms were discovered, as such which have a nummulitic or an operculina morphology on a compressed involute or a mixed coiling. These observations urged the introduction of new genera or sub-generic names. Forms which appeared to be unfit for the criterion of the three main genera were named *Operculinoides* and *Operculinella* or *Nummulites (Operculinoides)* and more recently *Palaeonummulites* (part.). In recent publications the writer proposed to incorporate all real «nummulites cordelées» in a sub-genus, namely *Nummulites (Chordoperculinoides)* and to leave the thicker forms of the early Paleocene, showing also an operculinoid morphology, under *Nummulites (Ranikothalia)*. The spiral cord of the latter is of a nummulitic size but has the coarse texture; N.(R.) is the direct descendant of the Upper Senonian *Sulcoperculina*. The relation of certain old forms, such as *Nummulites (Nummulites) scotlandica* M. DE CIZANCOURT with *Sulcoperculina* is striking.

In view of the inconstancy of certain morphological diagnostics, such as papillae, and of other diagnostics, such as the thickness of the shell and of the walls and sometimes even of the spiral step, the resulting species determinations are often condemned to remain uncertain. The puzzle becomes still more intricate if we consider also the fact that there are forms or groups of forms which intimate the existence of transitions between valid genera. The effect of this situation is well known and unreasonably one always has to rely upon the personal judgement of the paleontologist who deals with the matter in question and, consequently, we are then left with the problem of finding a compromise between various personal judgements.

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The coordination, however, of these judgements is only possible by profound studies of the diagnostics in use. This means the gathering of as many details as possible on the history of growth of the shell elements, and on genetic relations; it also implies a sufficient comprehension of the effect of the environmental conditions on the development of the various shell elements and the shape and size of the whole nummulites shell. Upon the completion of these detailed studies conclusive results such as improvements on the systematics, will in time evolve.

It is very important to know how and in which succession the different shell elements received their development. What is the actual purpose of the so-called secondary skeleton? In which way is the new chamber added on a living nummulites shell? Is it brought about by the exposure to the open of the rather delicate septal wall?

The writer had occasion to collect new data on the nature and the history of growth of nummulites shell elements when studying Libyan nummulites. The following notes deal with observations on nummulites cordelées from Fogaha (around 16° E and 27° or 28° N); the samples were collected by Dr. M. Sommer of Mobil Oil Company, in 1959²). The fossils here discussed simply originate in the surface sand of the Fogaha depression, which, according to SILVESTRI and others who published papers on the area, is extremely rich in larger foraminifera. In a lecture at the stratigraphic colloquium in Dakar (May 1963) the writer was dealing with the systematic position of these forms which (in 1934) were put under *Operculina* by SILVESTRI and DESIO. The following details on the texture of the spiral cord illustrate a unique type of texture which eventually could be used as a sub-generic or even generic criterion.

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The Spiral Cord

The thin walled primary, primitive stage of a microspheric nummulites shell, which bears resemblance with a *Globigerinella* shell, reached its approximate end form with the fifth or seventh chamber; this is about one whorl. The primitive stage rarely goes on beyond the first whorl. Upon its completion a coarse-textured corpus rises on the spiral crest as from the fifth or seventh chamber. The crestal thickening may occasionally begin earlier, as from the fourth chamber.

²) The specimens used for the photomicrographs, on plate I & II, are deposited in the Museum of Natural History, Basel.

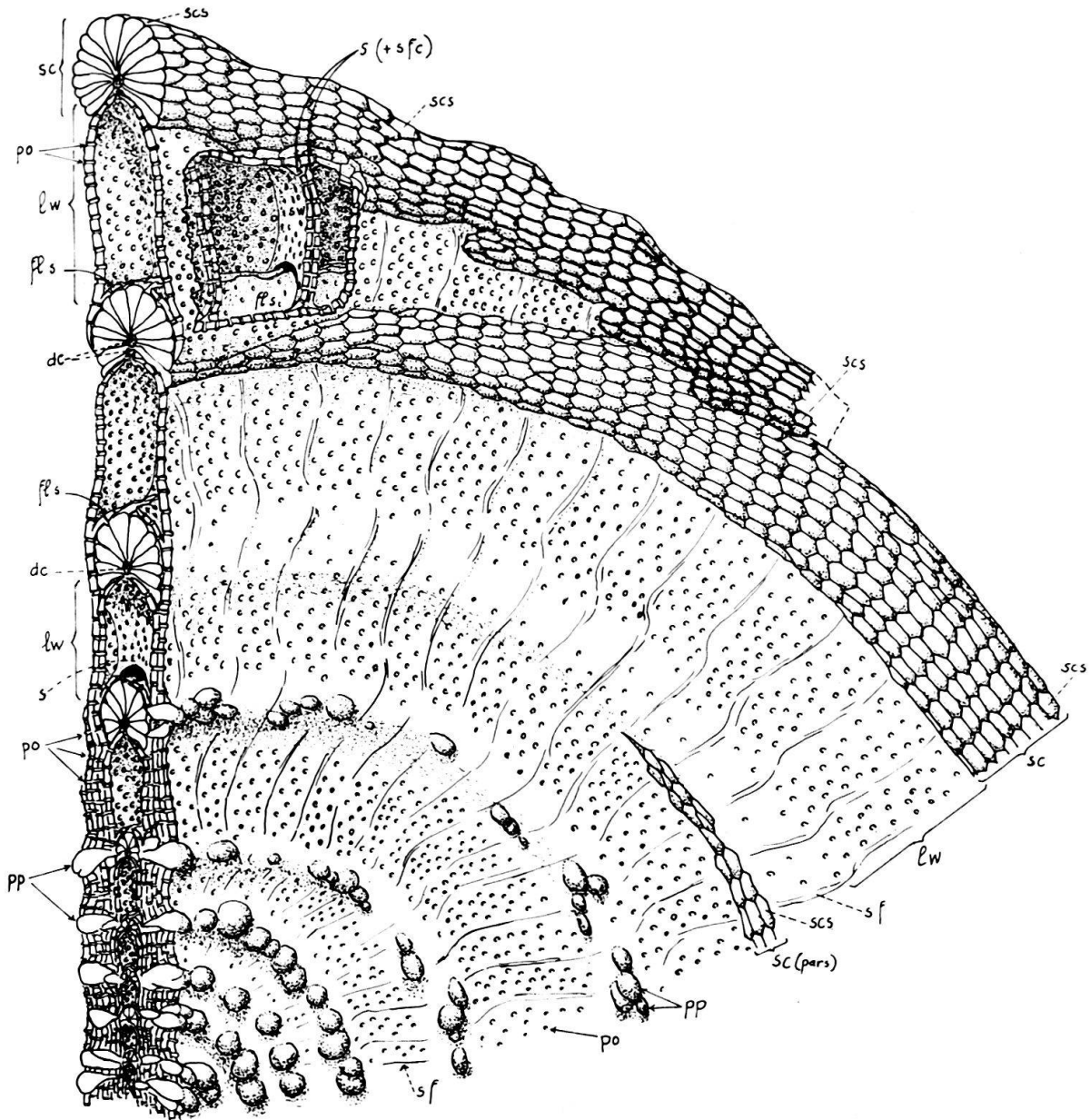


Fig. 1. A diagrammatic sketch of a sector of the *Nummulites* (*Chordoperculinoides*) shell (B-form) illustrating the morphology, the cross section and also the last phase of the shell formation. sc - Spiral cord.

scs - Segment of which the spiral cord is composed.

dc - Dorsal canal system. It is usually one pipe-shaped way which is often accompanied by bifurcating or parallel small canals of shorter extension. This dorsal canal system, or plexus marginalis, is located in the basal central part of the spiral cord; it runs over the whole extension of the spiral cord. Irregularly shaped communications with the chambers seem to exist just where the lateral walls are sparsely fused together, leaving a gap in the chamber roof.

lw - Lateral chamber wall.

sw - Septal wall (half of the septum).

fls - Chamber floor segment.

po - Pores in the chamber and septal walls.

s - Septum, consisting of two septal walls and the interseptal space or film including the interseptal canals.

sfc - Interseptal film and canal space.

sf - Septal filaments, the morphological feature created by the prolongations of the septal walls across the lateral chamber walls to the surface of the shell.

pp - Spindle shaped pillars and their morphological feature the papillae or warts.

The manifestation of the additional spiral corpus, the crestal secondary skeleton or supplementary mass, as it is called in the literature, is in fact the inauguration of the actual nummulitic growth.

The spiral cord or spiral lamina together with the lateral secondary skeleton (pillars etc.) constitute the essential diagnostics of the nummulitids.

The spiral cord of most nummulites shells covers the crestal (outer) end of the chambers. In *Chordoperculinoïdes* it embraces, to a limited extent, the distal portion of the chambers. As is well known, the spiral lamina or cord bears near its basal margin a «canal system», the plexus marginalis. The central position of the latter and its presence over practically the whole spiral extension of the cord are diagnostics of functions which, though not specifically known, appear to be important with respect to the development of the spiral cord and the shell as a whole. The cross section of *Chordoperculinoïdes* offers a striking example of the disposition in question. Here the elements (building blocks) of the spiral cord have a fan-shaped arrangement over three quarters of the plexus marginalis' circumference.

Much has already been written about the plexus marginalis of the nummulitids and in view of this fact the writer originally did not intend to search for additional suggestive explanations. But, by taking a few new observations on *Chordoperculinoïdes* into account, he feels urged to venture some tentative conclusions and suggestions of his own. Among these observations two finds are deemed as particularly valuable and conclusive, namely the extension of the spiral cord over the youngest not yet fully grown last chambers of the *Chordoperculinoïdes* shell and the often scarce, rudimental or even missing bottom wall of the plexus marginalis.

The photomicrographs 1, 4 and 5, pl. I, distinctly reveal the spiral cord protectively overlapping the youngest chambers including those in statu nascendi. The photomicrograph 5, pl. I, shows groups of two or three chambers, of various stages of development at the growing end of the spire, which are covered with a surprisingly strong spiral cord, and it appears logical to assume that on most living nummulites the spiral cord stepped down, embracing lower and lower groups of the youngest chambers in formation and extended even further to reach its youngest end over the naked crest of the previous whorl (see Fig. 1).

Obviously, the building elements of this end portion of the spiral cord must have been mobile within the controlling protoplasm (see Fig. 2). Besides the protective purpose, this secondary skeleton served as carbonate supplier for the growing chamber walls, but at the same time it received further completion and adjustments. The extensive cementation of the elements of the cord structure took place step by step with the completion of the corresponding chambers.

The death of the protoplasm logically involved the disintegration of the not yet cemented youngest portion of the spiral cord. Therefore specimens with a complete end of the spiral cord are not found among the fossil nummulites. Shells showing a still partly preserved end of the spiral cord which, as seen in the photomicrographs 5 and 4, pl. I, climbs down over a few unfinished chambers, are rare fossils and always represent a gerontic state of development. Specimens which died at a juvenile or early adult stage of development are deprived of any end portion of the spiral cord, the last whorl ending with a high or the highest chamber and an abrupt cut of the spiral cord.

The Plexus Marginalis

On a previous page it was emphasised that special importance should be attributed to the central position of the plexus marginalis. The fan-shaped arrangement of the carbonate elements of the spiral cord suggests that the plexus marginalis had an important function right from the beginning of the spiral cord's growth. Assuming, as above, that the growth of the spiral cord of *Chordoperculinoidea* preceded the first stage of the chambers, the germination of the new septum and the lateral walls occurred underneath a complete cover of secondary skeleton. The apertural outlet of the growing chamber must have been effected through this juvenile spiral cord, probably through the corresponding portion of the plexus marginalis. Assuming, that this configuration conforms with the correct history of the shell development, the plexus marginalis in front of the chamber in formation functioned as the outlet from the aperture in the new septum to the open. (see Fig. 2).

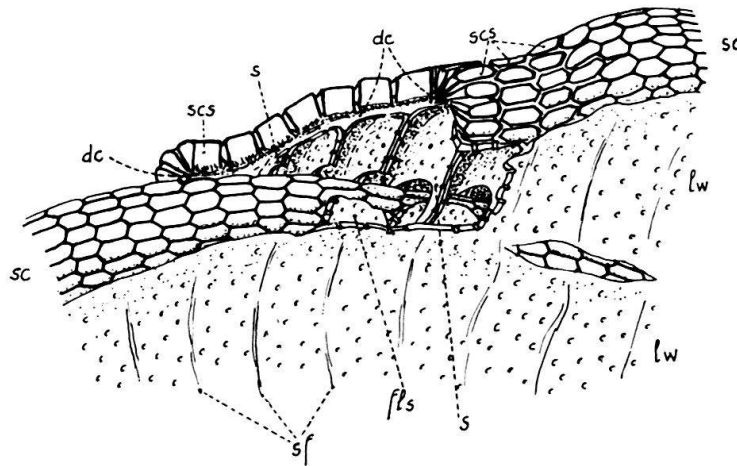


Fig. 2. A hypothetical picture of the growing end of a *Chordoperculinoidea* spire. The here diagrammatically shaped building elements of the youngest portion of the spiral cord are considered as not yet cemented; they represent a more or less loosely arranged skeleton in the protoplasm. Half of this youngest portion of the living spire is cut away in order to expose the septa and chambers in formation and the plexus marginalis; this shows the obvious purpose of the p.m. opposite the aperture of the youngest septum. Sc – spiral cord; lw – lateral wall of chambers; sf – septal filament; s – septum (at various stages of development); scs – building blocks, not yet cemented, of the spiral cord; dc – dorsal canal system or plexus marginalis.

The floor wall of this canal, being irregular, has gaps, which may be seen in cross sections and equatorial sections of *Chordoperculinoidea*. The basal wall of the p.m. is mostly a thin layer of the same type of carbonate as the elements of the spiral cord; in places it is fragmentary, but occasionally mended by distal extensions of septal walls or through the fusion of the lateral chamber walls in the roof of the chambers. In *Chordoperculinoidea* these chamber walls are often not completely fused together.

Function of the Secondary Skeleton

These various aspects of the genesis of the spiral canal and the spiral cord may lead to the assumption of two initial conditions of the growth principle of *Chordo-*

perculinoides; namely, (1) a sort of current running through the apertural opening at the juvenile end of the spire, and (2) the accumulation of carbonate, forming building elements, in the protoplasma in the outer circumference of that current.

The secondary skeleton of the spiral cord probably served the following main purposes: It formed a certain stabilising, protective shield, or skeleton, in respect to the germination and the growth of the various finely perforated chamber walls. It served also as a carbonate reserve within the protoplasma for the edification of the chamber walls.

Also, the spiral lamina of the nummulites often function as a kind of hinge between the two chamber walls when, in connection with the development (e.g. widening) of the chambers, the position and width of the spiral cord receive adjustments. The hinge function is brought about by changes in the size and location of the mobile elements in *Chordoperculinoides* or the dissolution and deformation or addition of irregular columns in the spiral cord of most nummulites.

This capacity, to accept changes in the form of the spiral lamina of the nummulites, reminds one of the imperforate carbonate agglomerations in the keel of *Globorotalia* and *Globotruncana*. Here coarse shell mass links perforated wall segments of growing chambers (see figs. 6–11, page 641, of H. LUTERBACHER, *Studies in some Globorotalia from the Paleocene and Lower Eocene of the Central Apennines*, *Eclogae*, 57, 1965).

The Pillars and Papillae

The pillars and papillae form the secondary skeleton in the side walls of the nummulites and probably served also the purpose of a handy carbonate reserve and a protection and strengthening of the side walls. It is most probable that these pillars grew from distal points in the protoplasma, outside the so far existing shell, towards the equatorial plain. In certain cases small nummulites pillars may have developed also in a distal direction.

In some *Nummulites* species the pillars do not reach the surface of the adult form and are then mostly neglected as diagnostic items. Other forms, occasionally, bear only papillae on the shell surface. These are but small carbonate agglomerations in the last whorl.

The difference in the development of pillars is presumably chiefly a result of variform conditions such as the temperature and the availability of calcium carbonate rather than the expression of species characteristics.

The adult or gerontic B-form of *Chordoperculinoides bermudezi* from Libya bears the pillars and warts in the wider polar area, rarely further on to beyond the second last whorl. Often the papillae are not conspicuous, and often they are rare or sporadic. Occasionally they are, though irregular in size, well arranged in a single row over the inner edge of the spiral cord, thus distinctly earmarking parts of the whorls. This secondary skeleton, located within the earlier whorls, developed during the growth of the shell from outside towards the median plain.

The juvenile and many adult forms of *Chordoperculinoides bermudezi* from the Libyan Paleocene lack all morphological manifestations of pillars. Even in cross sections many of these forms are free of indications of pillars. The adult pillar-free

form is very thin and certainly originates in argillaceous sediments which belong to deposits of the transitional zones between the true littoral character and the realm of the *Globigerina* marls and limestones. One may perhaps discern between pillared and non-pillared variations of *Chordoperculinoides bermudezi*; however, this should not be meant in the sense of systematic classification.

Synoptic Remarks and Some Conclusions

Reviewing the observations sketched above on *Chordoperculinoides* and nummulitids in general, one can discern, as already proposed by ROZLOZSNIK, two major shell elements: the finely perforated chamber walls including the septum, and the secondary skeleton, consisting primarily of the spiral cord or lamina and of a supplementary, not regularly appearing, corpus – the pillars.

One day the details and the genesis of the different shell elements of nummulites will be sufficiently ascertained and satisfactorily defined, so that the various shell elements can be classified systematically. The two major building elements in the *Chordoperculinoides* shell are so far found unequivocal with respect to their nature, but only approximately known regarding their history and function.

Chordoperculinoides fundamentally preserves its type of perforated chamber wall over the whole shell, and the thickening of the wall remains considerably under the proportion known of *Nummulites* s. str. The area of the first few whorls mostly contains a pile of several layers of primitive lateral walls. This succession of wall layers is sometimes more or less moulded into one finely perforated body.

A tentative idea of the functions of the spiral cord has been sketched above. The mobile nature of the spiral cord during growth furnished qualities of a hinge between the two chamber walls. The mosaic texture on the rounded edge of the shell and sometimes in narrow portions of the previous whorl is caused by the polygonal elongated blocks of which the spiral cord is composed. The distinct pattern on the surface of the spiral cord is typical for *Chordoperculinoides*; it is illustrated by text figures 1 and 2 and may also be seen in the photomicrographs of plate I.

The spiral lamina of *Nummulites* s. str., such as *Nummulites gizehensis*, *Nummulites beaumonti*, etc., and of *Assilina*, is finer in texture than the spiral cord of *Chordoperculinoides*. The irregular columns of which this secondary skeleton of *Nummulites* is composed, are so fine that it would be more adequate to speak of a fibrous texture of the spiral lamina, the packing being much tighter than in *Chordoperculinoides*. After the first whorl of the B-form of *Nummulites*, the lateral walls of the chambers gain considerably in strength and grow much thicker than the *Globigerina* type wall or the septal wall. The remarkable strength of the finely perforated wall is a characteristic of *Nummulites* s. str. and will be a point of special interest in a future systematics of the building elements of the nummulites shell.

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Plate I

Chordoperculinoides bermudezi (PALMER), B-forms, 10×. Originating in the surface sand of the Fogaha depression, west of the Pliocene-Recent Basalt flows of Gebel Harug el Eswed.

Fig. 1 (sample No. 98 I Fogaha); No. in Museum Nat. Hist.: C 25548/1

Fig. 2 (sample No. 98 II Fogaha); C 25548/2

Fig. 3 (sample No. 97 Fogaha); C 25548/3

Fig. 4 (sample No. 101 Fogaha); C 25548/4

Fig. 5 (sample No. 102 Fogaha); C 25548/5

Fig. 6 (sample No. 103 Fogaha); C 25548/6

These are all adult specimens; some with, some without (figs. 1-3) pillars. Two specimens, figs. 5 and 6, distinctly show pillars (warts) which are distributed over the inner whorls. The texture of the spiral cord can be noted in figs. 4, 5 and 6. The stepping down of the spiral cord over the crest of the youngest not yet fully grown chambers is visible in fig. 5 and fairly well marked on the specimens of figs. 4, 1 and 3. In places the spiral cord of the second last whorl is partly visible. The wavy circumference, which can be seen on all photomicrographs, is the result of an irregular completion of the chamber height. The irregularity is possibly the consequence of an early cementation of the spiral cord's building elements.

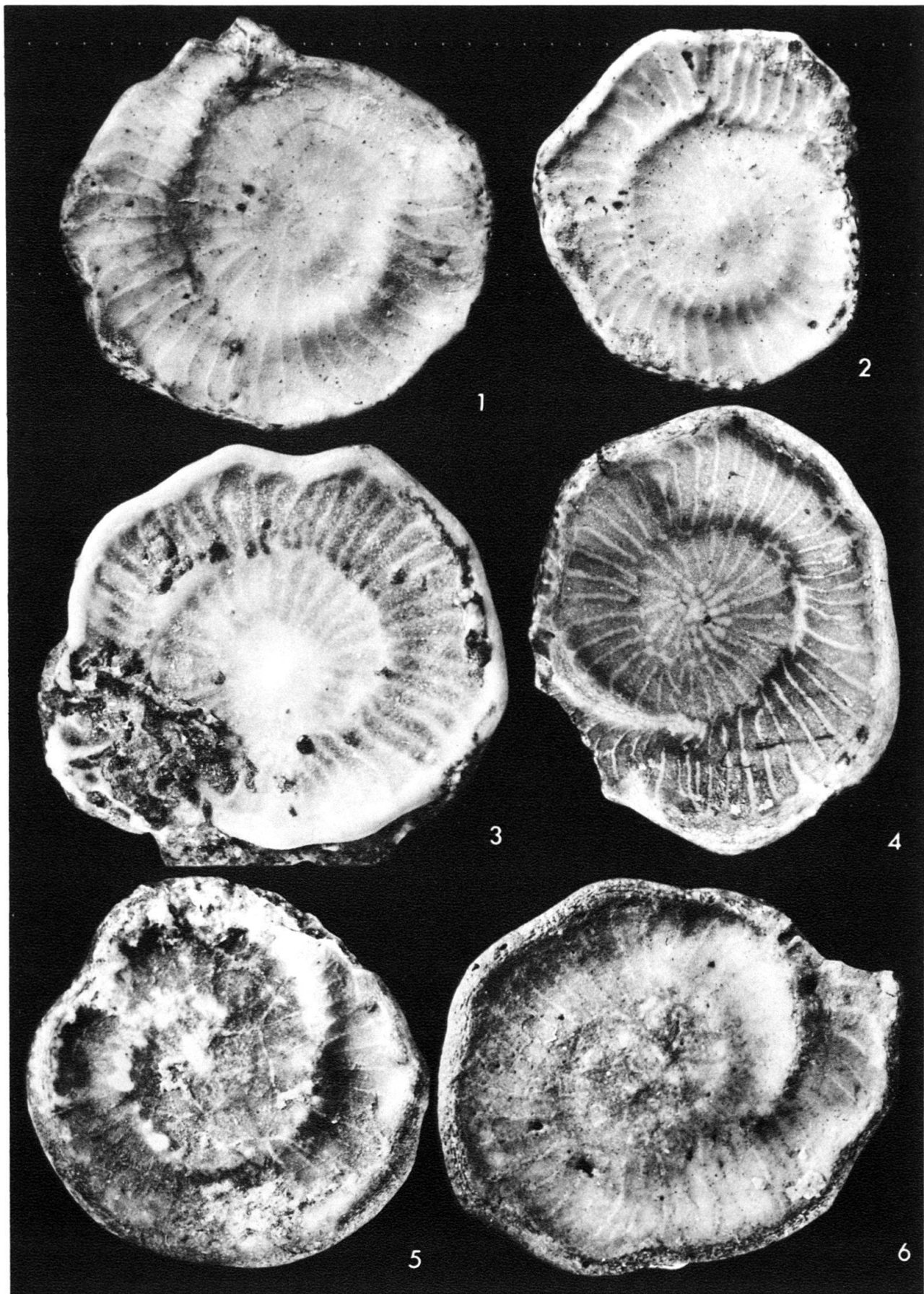


Plate II

- Fig. 7 (sample No. 105 Fogaha); C25548/7³), *Chordoperculinooides bermudezi* (PALMER) B-form. 10 ×. It originates in the surface sand of the Fogaha depression (west of the Basalt hills of Gebel Harug el Eswed). This specimen is comparatively well fortified with pillars. The texture of the spiral cord is partly visible.
- Fig. 8 (sample No. 109 Fogaha); C 25548/8. Polished equatorial cut of a *Chordoperculinooides bermudezi* (PALMER) B-form. 5.7 ×. See the rather rounded distal corners of the chambers.
- Fig. 9a, b (sample No. 106 Fogaha); C 25548/9. *Chordoperculinooides bermudezi* (PALMER) A-form. 10 ×. The chambers of at least one quarter of the last whorl are partly broken off. Fig. 9a illustrates the morphological features; conspicuous pillars are frequent in the polar area; other pillars are arranged in a single row over the spiral cord from the poles, to about one quarter of the last whorl. Fig. 9b shows the natural cut in the equatorial plain. The initial chamber is comparatively small; it is obviously smaller than the beginning of the *Ranikothalia* A-form. The megalospheric *Chordoperculinooides* is distinctly involute but less compressed than the B-form. As a consequence of this the spiral cord of the A-form is thinner than the spiral cord of the microspheric generation.
- Fig. 10 (sample No. 108 Fogaha); C25548/10, *Chordoperculinooides bermudezi* (PALMER) A-form. 10 ×. The surface of the slightly inflated megalospheric generation shows smaller warts (pillars) than the specimen of Fig. 9a; the warts are densely distributed over the inner 2¹/₂ whorls, the distribution tending to become radial rather than spiral in arrangement.
- Fig. 11 (sample No. 107 Fogaha); C25548/11, *Chordoperculinooides bermudezi* (PALMER) A-form. 10 ×. This equatorial (natural) cut represents a specimen which is similar in shape and size to the specimen of Fig. 10. The somewhat globular form of the two chambers after the nucleocoenoch are noteworthy.
- Fig. 12 (sample No. 111 Fogaha); C 25548/12, *Chordoperculinooides bermudezi* (PALMER) B-form. 9 ×. Cross section showing the spiral cord and the incomplete basal wall of the chambers. The compressed involuteness of the spire is clearly visible, especially in the inner whorls.
- Fig. 13 a-f (sample No. 110 Fogaha); C 25548/13-18, *Chordoperculinooides bermudezi* (PALMER) B-form. 6.5 ×. Cross sections of specimens of varying thickness and of diverse grade of compression. Noteworthy also are the irregularities in the ratio of involuteness and the unique fact that the chamber over a very strong spiral cord is always the least involute one.

³) No. in Museum Nat. Hist. Basel.

