SUBMICROSCOPIC SHELL STRUCTURES IN EARLY GROWTH-STAGES OF MAASTRICHTIAN AMMONITES (*SAGHALINITES* AND *SCAPHITES*)

A preliminary note

by

TOVE BIRKELUND
Geological Institute of the University of Copenhagen

Abstract

Remarkable successive changes of the shell structure in early ontogenetic stages of the Upper Cretaceous ammonites *Saghalinites* WRIGHT & MATSUMOTO and *Scaphites (Discoscaphites)* MEEK have been found. The protoconch is composed of a thin porcellaneous layer. At the beginning of the first whorl this is gradually replaced by another porcellaneous layer. At the constriction about one volution from the apex a prominent nacreous layer gradually appears and the porcellaneous layer of the first whorl gradually wedges out. Finally at the edge of this nacreous layer the porcellaneous and nacreous layers of the later part of the shell wall appear. The changes in shell structure between the protoconch and the first whorl and at the constriction about one volution from apex confirm that these mark important stages in the development of ammonites.

ACKNOWLEDGEMENTS

In 1963 Professor H. K. ERBEN, Bonn, and the author discussed the possibility that the shell structures of the early whorls of some Maastrichtian ammonites from West Greenland might be so well preserved that they could throw further light on the early growth-stages of ammonites.

The present work shows that certain changes in shell structure of the early whorls of these ammonites do occur, and the author is greatly indebted to Professor ERBEN for stimulating discussion of the problem.

The practical part of the electron-microscopy was carried out by mag. scient. H. J. HANSEN. The author is most indebted to him for his careful work and helpfulness.

The drawings were prepared by Mr. O. KJÆRGAARD, and T. C. R. PULVERCRAFT, B.A., corrected the English manuscript.

MATERIAL

Saghalinites wrighti BIRKELUND and *Scaphites (Discoscaphites)* sp., the shell structures of which are described in the present paper, are from the Maastrichtian of West Greenland. The material was collected by Professor A. ROSENKRANTZ and described by the author (1965, p. 30–37, pp. 116–129). The species occur in great numbers in a Danian basal conglomerate (Oyster-ammonite Conglomerate) exposed in Agatdalen, Nûgssuaq. The ammonites are derived from Maastrichtian deposits. They are enclosed in calcareous concretions and the aragonitic shell material (compare BØGGILD, 1930, pp. 323–324) is excellently preserved and suitable for submicroscopic investigations.

PREPARATION

Carbon replicas of polished and etched median dorso-ventral sections and cross sections of the two species have been investigated by electron-microscope. The technique, described by HANSEN (1967, p. 130), made it possible to prepare composite photographs of the protoconch and the first and second whorls. By means of these it is possible to demonstrate all the successive changes of the shell structure of the outer shell wall during the early growth stages.

THE SHELL STRUCTURES OF *SAGHALINITES*

The protoconch (text-fig. 1; pl. 1, figs. 1,2).

The protoconch is thin, about 5 micron. It is composed of a porcellaneous layer, the inner part of which is made up of elongated crystals set at right angles to the inner face. The outer part is composed of crystals without any apparent orientation. In the latest part of the protoconch the outer irregular part gradually becomes thicker, and the outermost part acquires an irregular prismatic structure.

The first whorl (text-fig. 1; pl. 2, figs. 3,4).

At the beginning of the first whorl a new porcellaneous layer appears on the inner side of the porcellaneous layer of the protoconch (pl. 1, fig. 2). This layer gradually grows thicker and replaces the porcellaneous layer of the protoconch, which wedges out.

The porcellaneous layer of the first whorl is thicker than that of the protoconch, about 15 micron, but very similar in structure, being composed of an inner prismatic part and an outer part with crystals showing no particular orientation. In the later part of the first whorl the boundary between the two different parts of the porcellaneous layer becomes sharper.

Changes in shell structure between first and second whorl (text-figs. 1–2; pl. 3, figs. 5,6).

At the constriction, which seems to occur in all ammonites about one volution from apex, the most remarkable changes in shell structure occur. At this stage a nacreous layer gradually appears. It shows the brick-wall configuration of mother-of-pearl and looks very similar to the nacreous layer of living *Nautilus* described by GREGOIRE (1962). This nacreous layer rapidly grows thicker and simultaneously the porcellaneous layer of the first whorl wedges out. The inner prismatic part of the porcellaneous layer wedges out more rapidly than the outer part. At the stage where

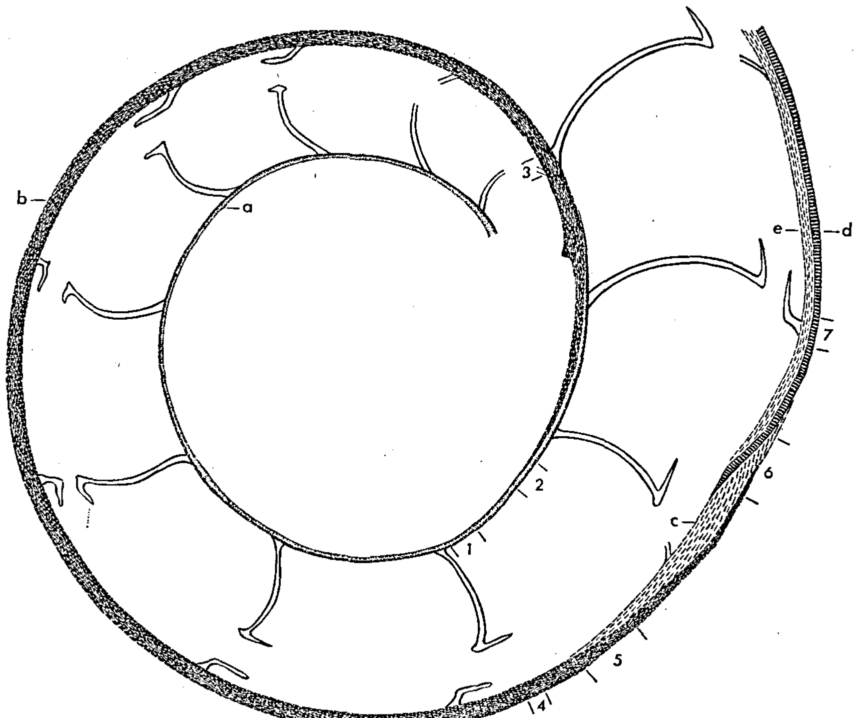


Fig. 1. *Saghalinites wrighti* BIRKELUND. Median dorso-ventral section of the adapical portion of the shell, showing diagrammatically the various structures of the shell wall. × 85.

a: Porcellaneous layer of the protoconch.
b: Porcellaneous layer of the first wall.
c: Nacreous layer of the constricted area.
d: Porcellaneous layer of the later whorls.
e: Nacreous layer of the later whorls.

the nacreous layer attains its greatest thickness, corresponding to the deepest part of the constriction mentioned above, the final porcellaneous layer of the outer ostracum appears at the inner surface of the nacreous layer and crosses to the outer side. The final nacreous layer of the outer ostracum develops along the inner surface of the final porcellaneous layer*).

The second whorl (text-figs. 1,2; pl. 4, fig. 7).

The porcellaneous layer of the outer ostracum is composed of elongated crystals generally disposed in palisades at right angle to the outer face.

*) In the present paper the provisional terminology of the shell layers recommended by STENZEL (1964, p. K78) in 'Treatise on Invertebrate Paleontology' has been used.

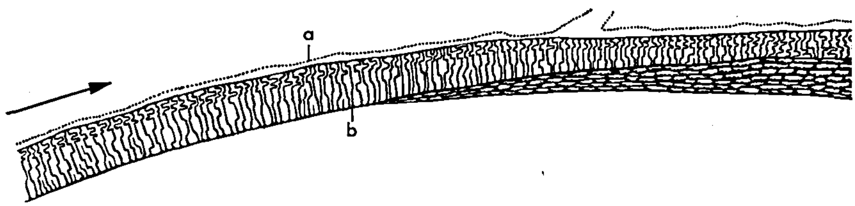


Fig. 2. *Saghalinites wrighti* BIRKELUND. Median dorso-ventral section of the constricted area about one volution from the apex, showing diagrammatically the various structures of the shell wall. ×450.

a: Outline of the dorsal shell wall of the succeeding volution.
b: Porcellaneous layer of the first wall.
c: Nacreous layer of the constricted area.
d: Porcellaneous layer of the later whorls.
e: Nacreous layer of the later whorls.

It is less complicated than the porcellaneous layer of living *Nautilus* as described by MUTVEI (1964, pp. 257–258) and GREGOIRE (1962, pp. 7–8). The structure is more similar to the inner prismatic part of the porcellaneous layer of *Nautilus,* whereas the outer "spherulitic" part (MUTVEI, 1964, p. 257) is absent in this ammonite at least in the early whorls. The nacreous layer of the outer ostracum is slightly thicker than the porcellaneous layer and shows the usual brick-wall configuration. Within the adoral part of the whorl the hypostracum can be recognized.

Later whorls.

The shell wall of later whorls of *Saghalinites* gradually grows thicker and the hypostracum grows more prominent.

Closer examination of the sub-microscopic structures of the walls of the later whorls, the septa and the siphuncle has not yet been carried out.

THE SHELL STRUCTURES OF *SCAPHITES (DISCOSCAPHITES)* SP.

The inner whorls of *Scaphites (Discoscaphites)* (text-fig. 3) show similar shell patterns as the inner whorls of *Saghalinites.* It thus looks as if the changes in shell structures described here occur generally in lytoceratid ammonites. Non-lytoceratid ammonites have not yet been closely investigated.

DISCUSSION

ERBEN (1964a, pp. 161–162) gave a short historical review of the most important interpretations of the early ontogenetic stages in ammonites and described in detail (pp. 162–164) the ontogenetic phases of primitive Ammonoidea. The first phase comprises the protoconch, the second phase reaches from the protoconch to the shell constriction about one volution from the apex. The third phase includes all the later part of the shell.

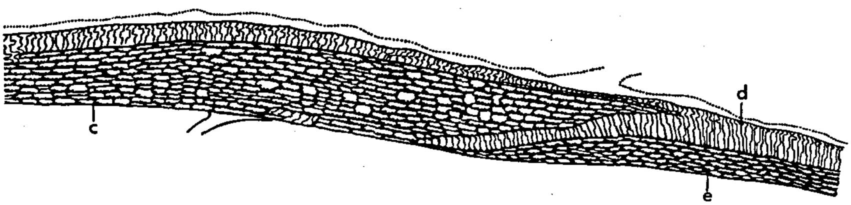


Fig. 2. (continued)

The phases are expressed by shell constrictions and changes of the configuration of growth-lines. ERBEN points out that several characters in the two first phases pass through an evolution completely unlike that of their evolution in the third phase, for example the growth lines and presumably the sutures. The different stages of development of the suture, of course, cannot be exactly correlated with the three phases, for each septum is formed at a later stage than the corresponding part of the conch in which it appears. According to ERBEN (1964b, p. K494) it seems as if the first septum appeared in the late stages or at the end of the second ontogenetic phase.

Early ontogenetic stages of Mesozoic ammonites have been investigated in Jurassic forms by CURRIE (i. a. 1942, 1944). In these ammonites the transition from the second to the third ontogenetic phase can be recognized by a remarkable change in growth rate between 2nd and 3rd half-whorl. In the ammonites investigated here the change in growth rate between these ontogenetic phases is also very distinct (text-figs. 1, 3). Unfortunately the growth lines of the early phases of Mesozoic ammonites are unknown.

In living *Nautilus* a constriction can be distinguished about 1.25 volution from the apex. This constriction may be analogous to the constriction near the adoral end of the first volution in ammonites (MILLER & UNKLESBAY, 1943, p. 3), but it is much weaker. At this stage of growth the shell of *Nautilus* is 25 to 27 mm in diameter. As described by STENZEL (1964, p. K82, figs. 64,65) certain changes take place at this stage and originally WILEY (1896, p. 225) interpreted this constriction or line of discontinuous growth ("nepionic line") as the end of the embryonic stage. However, the changes are by no means so radical as in ammonites and the main structures of the shell wall seem to be established at a much earlier stage in *Nautilus* (compare APPELLÖF (1893) and MUTVEI (1964)).

On the basis of morphologic and isotopic evidence EICHLER & RISTEDT (1966) suggested that living *Nautilus,* when it hatches from the egg, has a shell diameter of about 12 mm and that the constriction about 1.25 volution from the apex marks migration from warm to cooler water.

ERBEN (1964a, p. 177) suggested, as did WILEY (1896) and many later authors, that *Nautilus* has no larval stages outside the egg, whereas ammonites, according to ERBEN, might pass through a metamorphosis similar to that of gastropods with free-swimming larvae. This opinion is

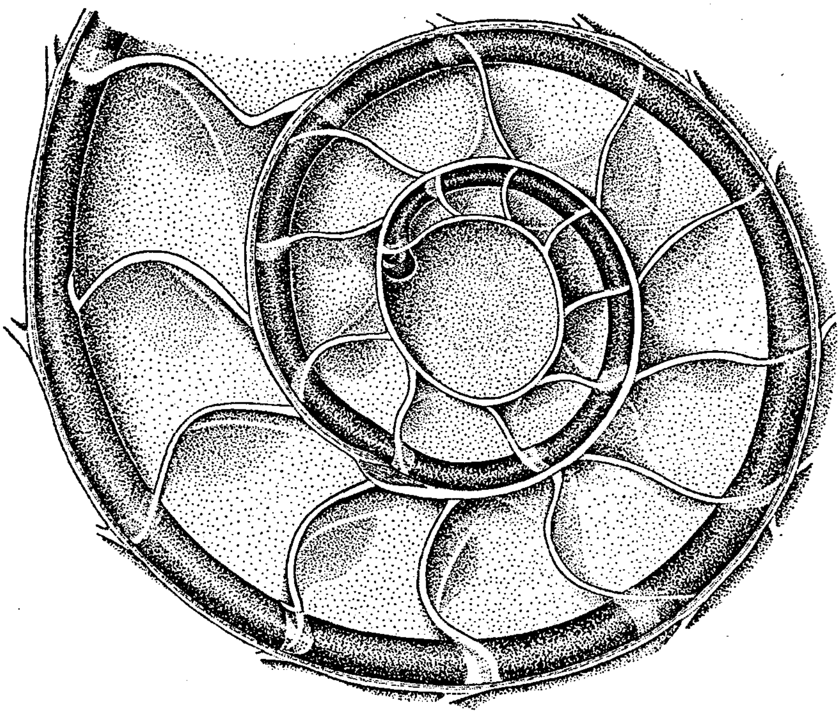


Fig. 3. *Scaphites (Discoscaphites)* sp. Polished dorso-ventral section of the adapical portion of the shell, showing the constriction about one volution from the apex. The nacreous shell layer is dotted. The caecum and the siphuncle are visible through the transparent calcite filling. ×60.

based on the distinct changes in growth lines and sutures between the second and the third phase in ammonite ontogeny. The small size of the early ontogenetic stages of ammonites in comparison with those in *Nautilus* also supports this suggestion. ERBEN (1964a, p. 167) interprets the first ontogenetic phase in ammonites as an embryonic stage, while the second may be correlated with larval and the third one with post larval development.

The remarkable changes of shell structure at the constriction between the second and third ontogenetic phase in the ammonites here investigated, accentuate the difference in ammonoid and nautiloid development and support ERBEN's conclusion.

In order to be able to make a closer comparison of the shell structures of early ontogenetic stages of gastropods and ammonites, the author has begun an examination of the structures of the termination of gastropod protoconchs.

REFERENCES

APPELLÖF, A., 1893. Die Schalen von Sepia, Spirula und Nautilus. Studien über den Bau und das Wachsthum.—K. svenska Vetensk. Akad. Handl., Bd. 25, No. 7, pp. 1–106, 3 text-figs., 7 pls. Stockholm.

BIRKELUND, T., 1965. Ammonites from the Upper Cretaceous of West Greenland.—Medd. Grønland, Bd. 179, Nr. 7, pp. 1–194, 125 text-figs., 49 pls. København.

BØGGILD, O. B., 1930. The shell structure of the mollusks.—K. danske Vidensk. Selsk., Skr., Nat.-Mat. Afd., 9 Rk. Bd. 2, pp. 231–325, 10 text-figs., 15 pls. København.

CURRIE, E. D., 1942. Growth stages in the ammonite *Promicroceras marstonense* SPATH.—Proc. roy. Soc. Edinb., Sect. B, Vol. 61, Part 3, No. 25, pp. 344–367, 13 textfigs., Edinburgh.

EICHLER, R. & RISTEDT, H., 1966. Untersuchungen zur Frühontogenie von *Nautilus pompilius* (LINNÉ). – Paläont. Zeitschr., Bd. 40, pp. 173–191, 4 text-figs., 2 pls. Stuttgart.

ERBEN, H. K., 1964 a. Die Evolution der ältesten Ammonoidea.—Neues Jb. Geol. Paläont., Abh., Bd. 120, Nr. 2, pp. 107–212, 15 text-figs., pl. 7–10. Stuttgart.

— 1964 b. Bactritoidea.—In: MOORE, R. C. (ed.): Treatise on Invertebrate Paleontology, Part K, Mollusca 3, pp. K491–K505. Kansas.

GREGOIRE, Ch., 1962. On submicroscopic structure of the Nautilus shell.—Inst. roy. Sci. nat. Belgique, Tome 38, no. 49, pp. 1–71, 8 text-figs. 24 pls. Bruxelles.

HANSEN, H. J., 1967. A technique for depiction of grind sections of Foraminifera by aid of compiled electromicrographs.—Medd. Dansk Geol. Foren. Bd. 17, p. 128, 2 pls. København.

MILLER A. K. & UNKLESBAY, A. G., 1943. The siphuncle of Late Paleozoic ammonoids.—J. Paleont., Vol. 17, No. 1, pp. 1–25, 9 text-figs., 5 pls. Tulsa.

MUTVEI, H., 1964. On the shells of Nautilus and Spirula with notes on the shell secretion in non-cephalopod molluscs.—K. svenska Vetensk. Akad. Handl., Ark. Zool., Bd. 16, nr. 14, pp. 221–278, 30 text-figs., 22 pls. Stockholm.

STENZEL, H. B., 1964. Living Nautilus.—In: MOORE, R. C. (ed.): Treatise on Invertebrate Paleontology, Part K, Mollusca 3, pp. K59–K93. Kansas.

WILLEY, A., 1896. Zoological observations in the South Pacific.—Quart. J. micro. Sci., new ser., Vol. 39, no. 154, pp. 219–231, pl. 13. London.

Plates 1–4. *Saghalinites wrighti* BIRKELUND. Electron micrographs of dorso-ventral median sections of the adapical portion of the shell wall. The arrow at the outer face of the shell wall indicates the adoral direction. The position of the sections is shown in text-fig. 1.

Pl. 1. Fig. 1: Protoconch, ×3750. Fig. 2: Adoral part of protoconch, showing the beginning of the porcellaneous layer of the first whorl, ×3750.

Pl. 2. Fig. 3: Adapical part of first whorl, ×3750. Fig. 4: Adoral part of first whorl; this part shows a sharper boundary between the inner and the outer part of the porcellaneous layer than does the adapical part, ×3750.

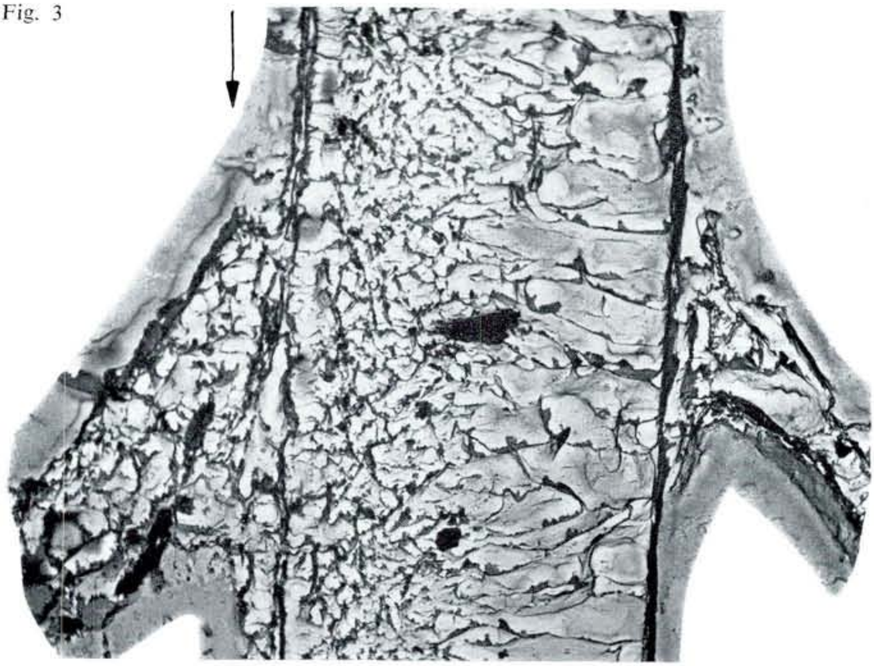
Pl. 3. Fig. 5: Adapical part of the constricted area, showing the beginning of the nacreous layer of the constriction and the beginning of the reduction of the porcellaneous layer of the first whorl, ×1875. Fig. 6: Adoral part of the constricted area, showing the nacreous layer of the constriction, the wedging out of the porcellaneous layer of the first whorl and the appearance of the porcellaneous and nacreous layers of the later whorls, ×1875.

Pl. 4. Fig. 7: Adapical part of the second whorl, showing the final nacreous and porcellaneous layers.

Fig. 1

Fig. 2

Fig. 3



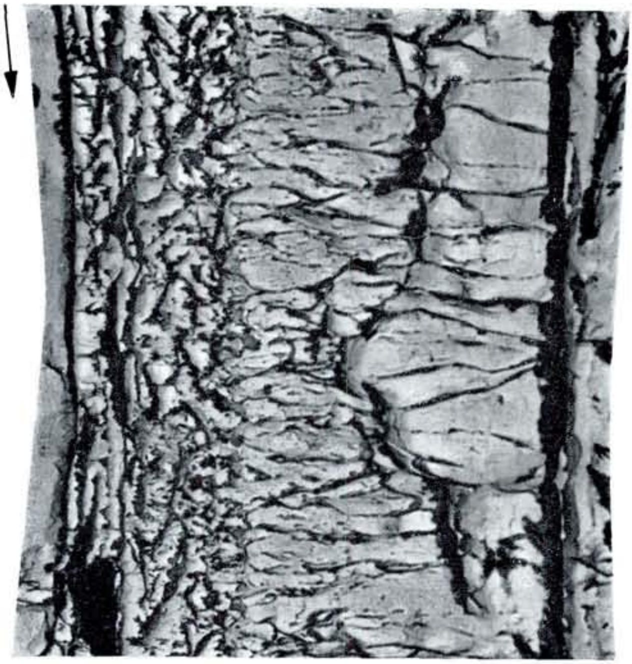
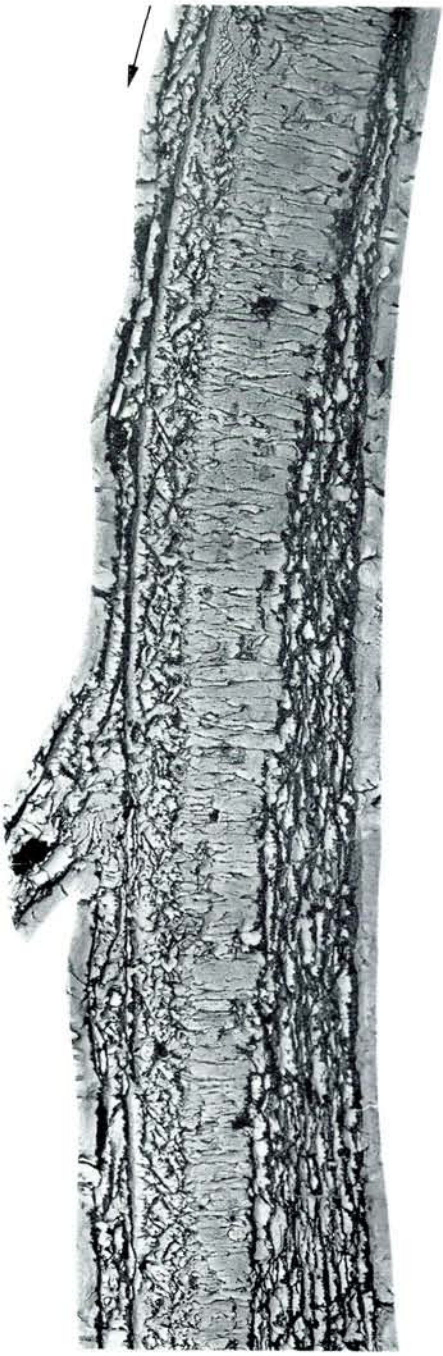


Fig. 4



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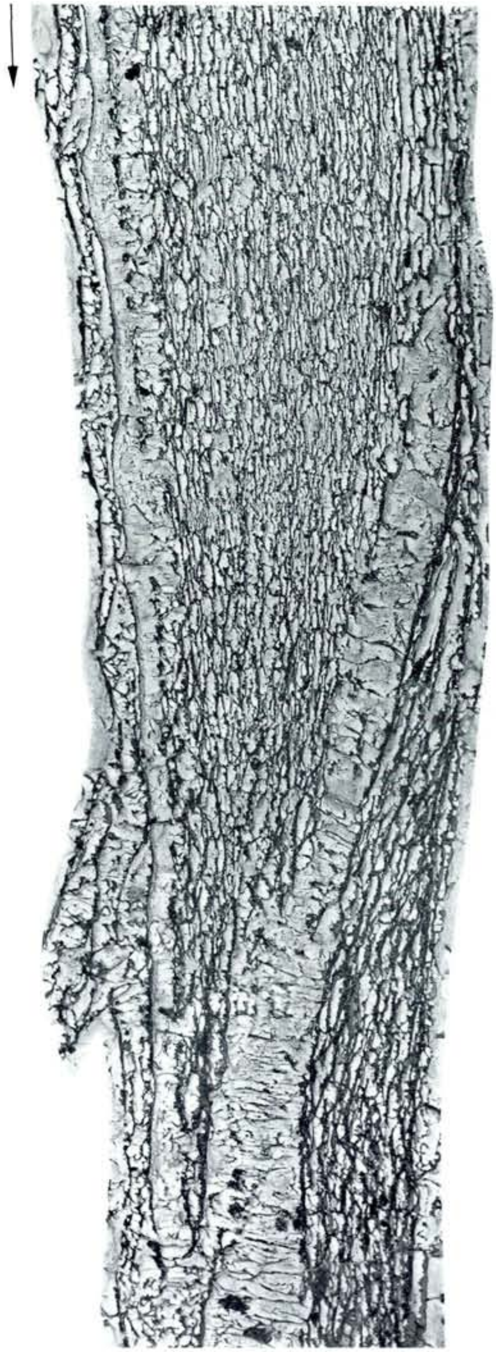

Fig. 6

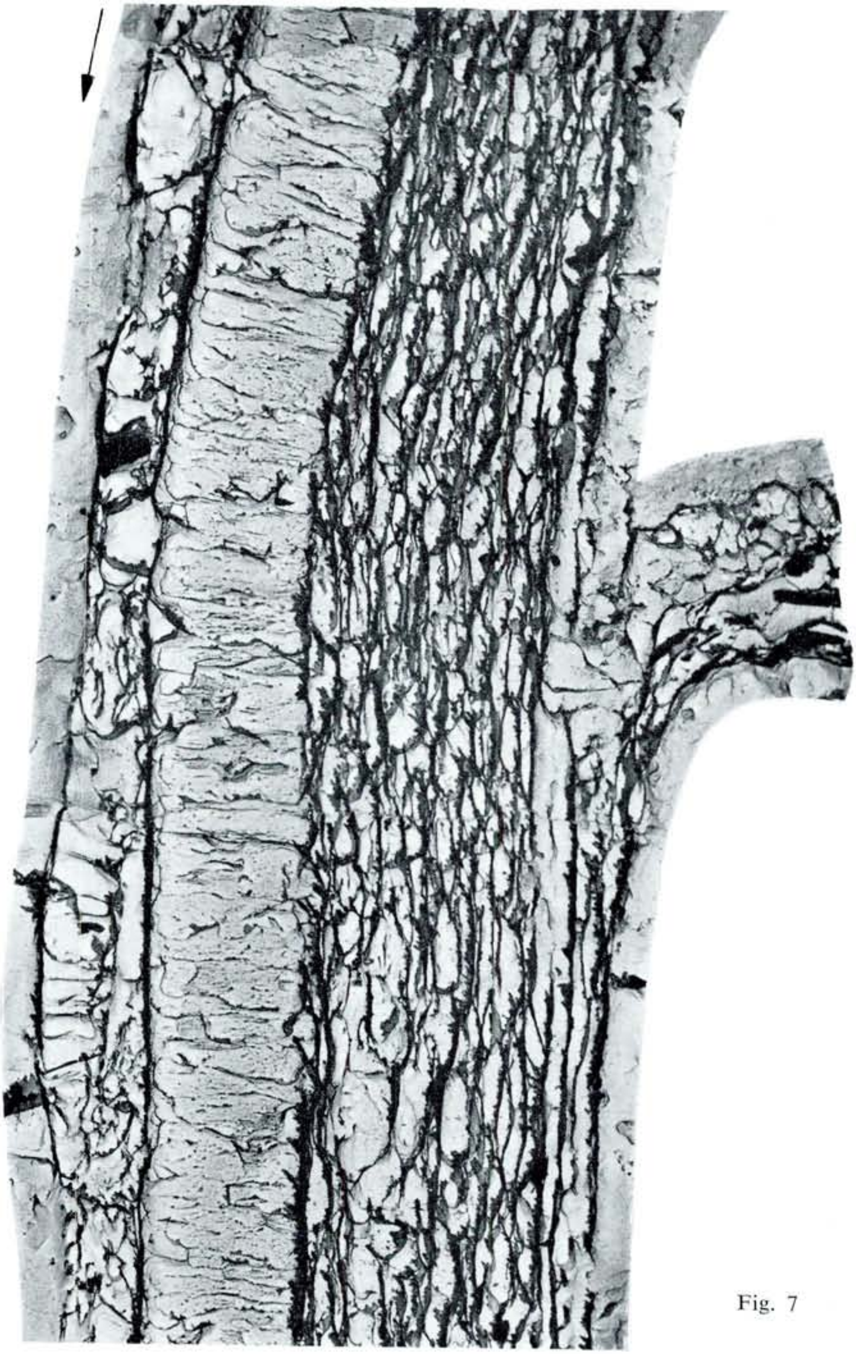

Fig. 7