Meyer, Bernhard Ludwig (1956) *A monograph on the morphology of stigmarioid branches.* PhD thesis.

A MONOGRAPH ON THE MORPHOLOGY OF STIGMARIOID BRANCHES.

Thesis presented by
BERNHARD LUDWIG MEYER, Dr.rer.nat.
for the degree of Doctor of Philosophy of the
University of Glasgow.

September, 1954

Contents:

PART I

INTRODUCTION

1. Historical review:

a) Geological occurrence:

Few of the palaeozoic plant remains are as common as the casts, impressions and structurally preserved parts of Stigmaria. Common all through the Carboniferous period, the branches of Stigmaria are especially numerous in the underclays of certain coal-seams and the appendages are ubiquitous in the coal ball flora. Stigmaria is reported to occur throughout the Carboniferous in all parts of the world. It is known from the Lower Permian but is not as common in this period as in the Carboniferous. DAWSON (1871) reported Stigmaria from the Middle Devonian and Upper Devonian of Canada but the identification is not certain; hence the lower age limit for Stigmaria has to remain an open question.

b) Early records:

The cylindrical casts with the circular appendage scars were known from an early period and were figured for the first time by PETIVER (1704) in England. He called the Stigmaria he had in his collection from Beverley/Yorks. "Cylindrus lapideus Beverleus". VOLKMANN (1720) in Silesia called the Stigmariae he had investigated and figured "Anthracodendron oculatum" and "Lithophyllum opuntiae maioris facie", the latter because he thought the remains to be related to the Opuntiae. WOODWARD (1729) in England noted the quincuncial arrangement of the appendage scars and saw the vascular axis in the compression though he mistook this for the medulla.

MARTIN (1809) figured a Stigmaria in his work "Petrificata Derbiensia" and gave it the name "Phytolithes verrucosus" while STERNBERG (1820) called the fossil "Variolaria ficoides". As STERNBERG's name Variolaria was already used for a modern species of lichens, BRONGIART (1822) described and figured the cylindrical casts with the circular scars for the first time as Stigmaria, the name which was retained by later authors. Only Artis (1838) in his "Antediluvian Phytology" chose once again another name and called it Ficoidites furcatus.

After BRONGIART's (1822) publications many authors in England and other European countries described Stigmaria and distinguished a large number of species after the external features. Many of these species, however, are only different stages of preservation and have little systematic value.

c) Stigmaria, a root-organ:

For a long time the nature of Stigmaria remained a subject for speculation. Commonly it was thought either to belong to Ficus or the Cactaceae. In 1839 HAWKSHAW reported the discovery of a group of erect fossil trees with their basal parts preserved. In 1844 other fossil trees, Sigillariae, were recorded by BINNEY, which had their root-organs preserved. These "roots" showed the external features of Stigmaria and since then many other specimens have been found suggesting that stigmarioid branches are the basal organs of not only Sigillariae but also of Lepidodendron.

d)First reports about anatomy:

LINDLEY and HUTTON (1837) were the first to publish about the internal structure of Stigmaria when they had obtained a specimen which showed both the external features and internal structure preserved. Many authors after LINDLEY and HUTTON described the anatomical features, especially BRONGIART (1839), GOEPPERT (1841), CORDA (1845) and BINNEY (1859) until finally WILLIAMSON (1887) in his "Monograph on Stigmaria ficoides" summarized all the previous work and added numerous new observations. He for the first time gave a comprehensive account of both casts and petrifactions of Stigmaria but named all the structurally preserved parts Stigmaria ficoides, apparently still under the impression that all stigmarioid branches had a uniform structure.

e)Stigmaria species based on anatomical features:

RENAULT (1893) reported the first fossil showing the external features of Stigmaria but having a different anatomical structure distinguished from Stigmaria ficoides chiefly by the development of centripetal wood. HICK (1891) described a fossil from English coal measures bearing the Stigmaria characteristics on its outer surface as Xenophyton radiculosum. WEISS (1902) ascertained WILLIAMSON's opinion to be that Xenophyton was probably a Stigmaria. The importance of HICK's description of Xenophyton lies in the fact that this specimen is the only Stigmaria hitherto found in which all tissues except the most peripheral cortex are preserved. Thus Xenophyton, now known as Stigmaria radiculosa, furnishes much evidence relating to the structure of tissues otherwise not known and only assumed to have been present.

f)Modern workers on the anatomy of Stigmaria:

No description of the structure of Stigmaria would be complete without mentioning the many studies F.E.WEISS has published about the subject. Prof.WEISS described the vascular connection between the stele and cortex of the appendages (19o2,1904), re-examined Xenophyton and demonstrated its affinities with Stigmaria (1902) and especially drew attention to Stigmariae with centripetal wood in the English coal ball flora (1908,1929,1930). LANG (1925) made observations on small and probably young specimens of Stigmaria bacupensis which indicated that appendages may be inserted slightly endogenously and so contributed some evidence towards the real morphological nature of Stigmaria. LECLERCQ (1925,1928) described specimens of Stigmaria with centripetal wood from the Belgian coal measures and 193o with her "Monograph on Stigmaria bacupensis" she described an entirely new type of Stigmaria.

Finally there may be mentioned the work of DUERDEN and WRIGHT (1952) who discovered on a specimen bearing Stigmarian appendages that these latter may bear leaves and ligules in some instances.

2.The problems in Stigmaria:

a)The systematic position:

The basal parts of the Lepidodendraceae and Sigillariae are known under the name *Stigmaria* Brongiart and *Stigmariopsis* Grand Eury. A specific identification was (because of the uniformity of the structure) hitherto not possible. It was, however, assumed that the form genus Stigmaria comprises the basal parts of the Lepidodendraceae as well as some of the Eu-Sigillariae whilst those fossils described as Stigmariopsis are probably the basal organs of Sub-Sigillariae. There is indication that some of the other arborescent paleozoic Lycopods had Stigmarioid basal organs.

Only in one case has a Stigmarioid species been successfully related to the arborescent part of Carboniferous Lycopods (*Stigmaria rimosa* Goldenberg - *Stigmariopsis rimosa* - Sub-Sigillariae, SOLMS,1894) whilst in all other instances the external features of casts and impressions did not show significant enough features to make such relations evident.

Basing on similar anatomical features of Stigmariae and Lepidodendraceae more attempts have been made to unite both. WEISS (1902) thought of *Xenophyton* (*Stigmaria radiculosa*) as ~~of~~ the basal part of *Lepidophloios fuliginosus* and a Stigmarian appendage which he described in the same publication was considered to be of the same species. The same author (1930) also suggested that *Stigmaria weissiana* might be the Stigmarian axis of *Bothrodendron mundum*.

The first correlation, however, does not seem to be completely justified since it is known today that the features on which the correlation is based are shared by a great number of other species of stigmarioid as well as aerial parts of the arborescent Lycopods.

WALTON (1935) suggests that Stigmaria arranensis might be the basal part of Lepidophloios wünschianus. The evidence supporting this correlation will be considered on a later page (p.88).

b)Anatomical Problems:

The Stigmarian stele is usually medullated but the pith tissue is rarely preserved. Many authors (SCOTT,1920) have therefore assumed that the pith may have been fistular, disintegrating relatively early and forming a medullary cavity similar to that of Calamites. The pith is surrounded by wedge-shaped bundles, consisting of mainly radially arranged tracheids although some of the innermost tracheids may be irregularly arranged. The bundles anastomose, thus forming a network through the meshes of which the appendage traces pass out. Annular tracheids, which are described as protoxylem elements are sometimes observed on the inner edge of the vascular bundles.

These protoxylem elements on the inside of the xylem wedges have been a puzzle to palaeobotanists for they implied that all tracheids outside were differentiated in a centrifugal direction. As it was the custom to regard the few irregularly arranged tracheids on the inside of the xylem wedges as "metaxylem" it was stated that in Stigmaria the metaxylem is developed centrifugally in contrast to all the aerial parts of the palaeozoic Lycopods in which the metaxylem is developed in a centripetal direction (HIRMER,1927).

Although it has never been really described how and why the "metaxylem" is differentiated centrifugally in the stele of the basal organ and centripetally in the stele of the shoot, comparison has been made with the rhizophore of *Selaginella spinulosa* and *S.kraussiana* (SCOTT,1920) in which plants the upper parts have a centripetally developed metaxylem whilst in the creeping stem all xylem is centrifugally developed.

Not in all Stigmariae, however, is centripetal xylem absent. WEISS (1908) and LECLERCQ (1925) described a stigmarioid species in which primary xylem was differentiated centripetally. WEISS (1930) found that the Stigmaria he had described (1908) has great affinities with Bothrodendron. RENAULT (1893) had described a Stigmarian axis with centripetal primary wood before, *Stigmaria brardii*.

The regular radial seriation of the secondary xylem elements is sometimes interrupted by tangential bands of much smaller tracheids, a feature which has found different explanations (p. 57).

Remains of the delicate tissue at the exterior of the xylem has always been interpreted as cambium and phloem ? but a concise description of these tissues has never been published.

The xylem strands of the appendage traces terminate level with the inner edge of the xylem wedges. The appendage trace consists of few protoxylem elements and of mainly radially arranged scalariform tracheids. In most appendages this radial arrangement is lost in the distal parts of the appendage stele.

In fact every stage of transition from completely radial arrangement to completely irregular arrangement of tracheids was observed and especially in the case of the appendages all authors have found it extremely difficult to distinguish between "meta-" and "secondary xylem".

The opinion held by most authors about the structure and development of the cortex is summed up by HIRMER(1927) who writes:

"The primary inner cortex of Stigmaria seems to have been more lacunar than in the aerial shoots of Lepidodendron, which is suggested by the imperfect preservation.The outer primary cortex consists of rather uniform and large celled parenchyma.Only in younger stages of Stigmaria, larger parts of it are preserved because, in contrast to the aerial shoots of the Lepidophytes,the formation of the periderm takes place farther inside in the outer primary cortex and the cells outside of the periderm are rather early exfoliated.As far as the formation of the periderm is concerned several types are known: Types in which -at least for a longer period- only endo-phelloderm was formed and on the other hand, types in which only exo-phelloderm was developed; in addition there are types in which both exo- and endo-phelloderm are produced. In the older parts of Stigmaria the prosenchymatous endo-phelloderm seems to have been the major part of the periderm.In this tissue layers of secretory tissue are distributed in zonal order".

Considerable disagreement exists in literature about Stigmaria as to the position of the cambium producing the secondary cortical cells.Whilst HIRMER(1927) is of the opinion that the secondary cortex is formed by successive meristems other authors,cited in SCOTT(1920),were of the opinion that the secondary cortex was formed either in centrifugal,centripetal or both directions.

Cells in the outer primary cortex,which are filled with a dark substance,have been described by most authors as sclerotic elements (SCOTT,1920). These sclerotic cells lie beneath a number of layers of thin-walled cells ~~to~~ which SCOTT referred to as "hypodermal zone".

The quincuncial arrangement of the appendages on the axis resembles the phyllotaxy of the aerial shoots of Lepidodendron and Sigillaria.This feature has many authors (HICK,1892) led to the belief that the appendages of Stigmaria are modified leaves.The slightly endogenous insertion (LANG,1923) as well as the recent findings of DUERDEN and WRIGHT (1952),however, seem to have contradicted this theory.

The appendages show a variable structure especially of their cortex.SCOTT(192o) suggested that this variation might be of systematic value but an attempt to catalogue all the features of the Stigmarian appendages has hitherto not been made.

The descrepancy between the amount of secondary xylem in the axis and the absence or little amount of secondary growth in the appendage steles has already been mentioned.

The stele of an appendage may be connected with the outer cortex by a narrow band of parenchymatous tissue in which tracheids,branching from the protoxylem, pass out obliquely to the cortex.They terminate there in "transfusion tracheids" (WEISS,1904).RENAULT(1882) made an attempt to interpret these tracheids as traces of abortive branches of the appendages.In the opinion of WEISS(19o4),however, these tracheids act as transfusion tissue and bridge the gap left by early disintegration of the middle cortex.

c)Morphological problems:

Ever since it was discovered that Stigmaria was the basal organ of the arborescent Lycopods speculations as to its real morphological nature have been made by botanists and paleobotanists.WILLIAMSON (1887) referred to Stigmaria as to the root of Sigillaria and implies that it must have had the mechanical and physiological function of roots of higher plants although in its structure it is unlike a true root. RENAULT (1882) regards Stigmaria as a rhizome from which under certain circumstances the aerial shoot of a Sigillaria may have risen.HICK(1892) also supports the rhizome theory,basing his arguments mainly on the "phyllotaxy" of the appendages,against the strong opposition of WILLIAMSON(1892).SCOTT(1920) seems to be the initiator of the"rhizophore theory" which has then been so fervently defended by TROLL(1934) who saw the problem completely solved in comparing Stigmaria with the rhizophore of Selaginella.

HIRMER(1927) is of the opinion:"Entgegen der oft fälschlicherweise ausgesprochenen Annahme der Wurzelnatur der Stigmarien sei ausdrücklich betont,dass es keinem Zweifel unterliegen kann,dass die Stigmaria als ganzes die Auflösung der unteren Stammpartie der Lepidophytenbäume in rhizomatische Verzweigungen darstellen,die der durch wiederholte Gabelteilung zustande kommenden Auflösung der oberen Partie des Hauptstammes der meisten Lepidophyten vollkommen homolog ist und sich prinzipiell in nichts davon unterscheidet.Erst die von den Stigmaria Gabelästen getragenen Appendices sind Wurzeln."

DUERDEN and WRIGHT(1952) described ligulate leaves on appendages probably of Stigmaria bacupensis. This discovery throws some doubts on the root-nature of the Stigmarian appendages and WALTON(1953,p.49) suggests that there might not be such a clear cut distinction between shoot and root in the Lepidodendrales as in the higher plants.

3. Material investigated:

For this thesis slides of the Kidston Collection (Botany Dept. University of Glasgow), of the D.H.Scott Collection (British Museum of Natural History,London) and of the Botanical Collections,Manchester Museum were investigated.

I am indebted to Dr.J.Walton,Professor of Botany in Glasgow,Mr.W.N.Edwards, Keeper of the Geological Collections of the British Museum and to Dr.I.M.Rosser,Keeper of the Botanical Collections,Manchester Museum for kindly permitting me to study sections of these collections.

In addition to the slides of these collections, which supplied most of the specimens described in this thesis, cellulose acetate peels (WALTON,1951) were taken from the Arran petrifactions (WALTON,1935) stored in the Botany Dept. Glasgow and in the Hunterian Museum,Glasgow University. A coal ball sent to Glasgow University by Prof.H.Andrews (St.Louis,Mo/USA,see p.77) was also sectioned.

All figured slides from these peels are to be stored at the Botany Dept. Glasgow.

Drawings of tissues in this thesis are camera lucida drawings. The Scale of the drawings is given on page A.

The magnification of the photographs is given in the explanation of the plates. An attempt has been made to apply statistical methods to an investigation of the effects of size as a factor influencing the anatomy of Stigmaria and some results are included in chapter 8 o of this thesis. Studies in the relationship between size and form were initiated by Prof. F.O.BOWER (1930) but this relationship has not been previously investigated in Stigmaria.

4.The general appearance of Stigmaria:

Ever since it was discovered that Stigmaria is the "root- organ" of the arborescent palaeozoic Lycopods (HAWKSHAW,1835;BINNEY,1844;BROWN,1849) descriptions of tree stumps have been published and figured showing Stigmaria as part of a ramification system. The best specimens, trunks with lateral ramifications bearing the circular appendage scars of Stigmaria, are those described by WILLIAMSON (1887) and POTONIE (1892) (pl.I,figs.1,1a,2,2a). The tree stumps of the "Fossil Grove" Whiteinch/Glasgow are often figured and described and well known to readers of palaeobotanical textbooks.

a)The system of ramification:

The stumps divide in a downward direction into four main branches (pl.I,fig.1 and 2) which then continue to divide dichotomously. POTONIE (1892) suggested that the partition of the main stem into four branches may be due to a rapid succession of dichotomies and this seems to be supported by the specimens he described:

"Der Grundriss (pl.I,fig.2a) demonstriert,dass sich die Wurzel ohne jede Deutelei als von vorne herein dichotom betrachten lässt.Denn die gegenüber befindlichen Buchten b und c liegen dem in derselben Ebene genommenen Stammmittelpunkt am nächsten.Sie sind besonders stumpf und machen aus diesen Gründen den Wurzelkörper von vorneherein zweiteilig.Durch die Linie b-a-c wird also die Achsel der ersten Dichotomie markiert.Es erinnert an das gewöhnlich zweilappige Isoetes Stämmchen".

But further on POTONIE mentiones that in another specimen he has not observed such an obvious dichotomy and comes to the conclusion that the dichotomies must have followed each other more quickly.

Careful study of the diagram (pl.I,fig.2a) of the Stigmaria described by POTONIE shows,however,that the evidence brought forward by POTONIE of two successive dichotomies,is not entirely convincing.It is evident on first sight that the system of ramification is asymmetrical, as the dichotomies of the more or less horizontal branches shown in the upper part of the figure occur at a far greater distance from the base of the trunk than those on the lower part of the figure.These branches,which according to POTONIE are of the second order of dichotomy,are also narrower and therefore the branches of the same order i - n are necessarily farther apart from h - m (same f - k from g - l) than the dichotomies m - l and k - n from each other. Thus we can also assume for this specimen,that the trunk was divided into four main branches almost instantaneously.The first division of the trunk takes place in the vertical plane. Later branchings may occur in both the vertical and the horizontal plane in different specimens.

The second forking (II) of the Stigmarian branches, if we assume the division of the trunk into four branches one incident (I)(eventually Ia and Ib) occurs in the specimen described by WILLIAMSON from Clayton, in the vertical plane. The same order of dichotomy in the Piesberg Stigmaria, described by POTONIE, occurs in the horizontal plane and in some instances at a considerable distance from the centre of the trunk,(1.50 m).This gives the two Stigmariae a distinctively different appearance (pl.I,fig.1 to 2a).

The "Fossil Grove" Stigmariae show their second dichotomy in the horizontal plane but apparently still in the immediate vicinity of the trunk.We can therefore distinguish between three types:

fig.1 and 1a	Clayton Stigmaria,branching	II	in vertical plane
	Fossil Grove Stigm., "	II	in horizont. pl. at base of trunk
fig.2 and 2a	Piesberg Stigmaria, "	II	in horizontal pl. at some distance from base of trunk.

The other Stigmariae,from Dixon Fold (fig.4 and 5) show the same arrangement as the Fossil Grove Stigmariae: Dichotomy II occurs at the base of the trunk.

At varying distances from the Dichotomy II,the branches of the second order dichotomize again into branches of the third order.These branches then can be sometimes pursued (WILLIAMSON,1887) for a long distance and remain undivided. Branches of the third order of the Clayton Stigmaria could be pursued to a distance of 37 feet from the base of the trunk where they tapered away completely.

In the Piesberg Stigmaria (fig.2) the branches of the last order (indicated only on the right hand side of the diagram) taper away much more quickly and it seems unlikely that they ever reached a greater length.

It may be mentioned here that the Clayton Stigmariae were found embedded in shale but the Piesberg Stigmaria was found on top of a coal seam.

b) Stigmaria casts and species:

The branches of the last order are the parts of Stigmaria most commonly found in the coal measures and in the underclays of coal seams. As casts they are cylindrical and of rather uniform diameter showing the quincuncially arranged circular appendage scars. In many specimens (WALTON,1953,fig.19) appendages can still be found attached to these Stigmarioid branches and can be observed radiating into the surrounding rock in all directions.

The surface of the casts often bears in addition to the appendage scars, striations, flutings, ridges and furrows. These marks have been used as criteria for the identification of species of Stigmaria. Although JONGMANS (1937) cites 57 of these Stigmaria species, excluding the 16 varieties of Stigmaria ficoides, he himself points out that few of these species withstand critical examination and that many of them may be preservational stages of Stigmaria ficoides only. Some species, however, can be undoubtedly distinguished. Stigmaria stellata, the most conspicuous of them, is distinguished by ridges radiating from the appendage scars. Stigmaria minuta and St. minor show very small appendage scars. Stigmaria rugulosa is distinguished by striations between the appendage bases.

Stigmaria rimosa, another conspicuous species with a fluted surface and small appendage scars, has been referred to (SOLMS, 1894, GRAND EURY 189o) as a cast of Stigmariopsis.

c) Branch apices:

Different opinions exist about the terminations of the branches of the last order. WILLIAMSON observed on the Clayton Stigmaria that the branches of the last order tapered away to a point whilst SOLMS(1887) describes a specimen with a blunt end on which appendages are attached on all, including the front side. SOLMS(1887) mentiones further that the appendages increase in size from the tip towards the base of his described specimen. Other authors have also observed the blunt ends of Stigmarioid branches of the last order and it seems that this type of apex is more common.

d) The ramification of Stigmariopsis:

The basal organ of Sigillariae described by BROWN(1849) has an altogether different appearance. The division of the trunk into four main branches is only faintly recognizable. All dichotomies appear to occur in the horizontal plane and a higher number of dichotomies are reached in the ultimate branches. Similar tree bases have been figured by GRAND EURY (1890). Thus 32 branches have been counted in the Sigillarian bases in contrast to the 16 ultimate branches of Stigmaria. It appears from the description of SOLMS(1894), GRAND EURY (1890) and BROWN(1849) that some of these branches were superimposed, which is also suggested by fig.6, pl.I. Therefore forkings of the higher order must have occurred in the vertical plane.

The ultimate branches are described as very short and only branches of this order show appendage scars. In addition, short vertical branches may be given off which have been described as conical tap-roots and it seems that each branch of a certain order produced one tap-root only. According to GRAND EURY(1890) the tap-roots also show the quincuncial arrangement of appendage scars and dichotomize at their ends.

Another Sigillarian base showing tap-roots is also described by GRAND EURY (1890) and SOLMS (1894). In this type the trunk divides in the vertical plane into four main arms on which tap-roots are borne (pl.I,fig.7). These two types were then named Stigmariopsis since their characters deviated from those diagnostic of Stigmaria and were considered to be the basal organs of Sigillariae.

e) Ecological factors influence ramification:

It has been indicated already that the tree bases and the system of ramification may very considerably. Three types of ramification systems of Stigmaria, excluding those of Stigmariopsis, were mentioned. It was also noted that the length of the branches of different orders of dichotomy may vary within the system of ramification of one trunk and from specimen to specimen.

Many of these features may be due to ecological factors. Different soil conditions especially seem to have influenced the development of the rooting system. WILLIAMSON (1887) directs attention to the difference between the basal ramifications of the fossil tree trunks found at Dixon Fold and St.Helens. In the latter locality the four main branches of the stump bent downwards in an oblique outward direction and at a change in the facies of the embedding rock (WILLIAMSON: Silty clay - fire clay), the branches bent horizontally on the harder fire clay. The Dixon Fold Stigmariae are preserved standing on top of a coal seam but their lateral ramifications, probably extending into and forming part of the coal, were not preserved as distinct fossils.

The chemical properties of the soil in which Stigmaria is preserved do not seem to have influenced the growth of the rooting system. Stigmaria is recorded as being preserved "in situ" in clay, shale, limestone, cannel coal and coal. It has also been found in sandstones, but there it is uncertain whether it was preserved in situ.

f) Preservation of Stigmariae:

Stigmariae are usually preserved in clay or in shale, the casts being usually formed of sandstone. It is a generally accepted opinion that the Stigmariae were growing in fine mud which after diagenesis turned into clay or shale. The aerial part of the plant disintegrated but the Stigmaria covered by the mud decayed more slowly, the resulting cavity was then filled up with mineral substance, usually sand, of the overlying facies (fig.1).

WILLIAMSON (1887) has pointed out that the parts of Stigmaria filled with mineral substance are preserved as cylindrical casts whilst the tips of the ultimate branches into which the filling could not penetrate are preserved as compressions.Excellent specimens of Stigmariae preserved in shale are those described by WILLIAMSON (1887) and those of the Fossil Grove,Glasgow (MACGREGOR and WALTON,1948)!

The question has to remain open whether Stigmariae were growing in water covered soil or on dry land but it may be mentioned here that in the strata of the Fossil Grove on a slightly higher level than the stumps , ripple marks are reported (YOUNG and GLEN,1888) which are on the same surface as a prostrate trunk (MACGREGOR and WALTON,1948).

The Stigmariae at the base of coal seams grew apparently in more or less the same substratum as those in the barren clay or shale sediments.All authors who have commented on the origin of coal have described the features of these clay deposits underneath the coal seams in which Stigmaria is such a common fossil. They regarded this stratum as the fossil soil on which the initial flora,later constituting the coal, grew.Furthermore they have argued that the abundance of Stigmaria suggests that the major part of this initial flora in many localities consisted of arborescent Lycopods. This may be true as long as only compressions or impressions of appendages and Stigmarian axes are preserved in the underclays. The presence of tree stumps and casts (WILLIAMSON, 1887) in the"seat-earth",however,appears to prove rather the contrary,namely,that these Stigmariae can have nothing to do with the overlying coal seam.

As explained above, the general assumption is that the hollow Stigmariae, after the decay of the aerial parts of the plants, were filled with mineral substance of the same facies as the overlying strata. Thus the casts are separate from the surrounding medium. If the "seat earth" had been overlain by coal, the hollow spaces of Stigmaria could only have been filled with coal, unless a trunk attached to Stigmaria had reached through the coal to the roof of the coal seam. This, however, has not been recorded. WILLIAMSON (1887) goes even farther and claims to have seen a sandstone cast of a Stigmarian base in the seat earth and the sandstone cast of the tree trunk belonging to it in the roof of the coal seam. This is entirely impossible, for if the Stigmaria and the trunk had been filled with sand then the sandstone casts could be recognizable in the coal seam. Stigmarioid branches preserved as casts can therefore not have been in organic connection with the plants constituting the coal flora. If a seat earth containing casts of Stigmaria is overlain by coal then the facies filling the cavities left by the decay of the plant tissue has either been eroded before the coal was deposited or observation has not been accurate and the Stigmariae are in fact separated from the coal by a sterile layer. Beds of casts and coal seams may represent each other in a horizontal direction but the first cannot be the true base of the second.

g) Stigmariae and Coal:

Records of Stigmariae in coal can be obtained mainly from coal balls and it is from these that most of our knowledge of the tissues of Stigmaria is obtained. The great abundance of Stigmariae in these concretions makes it probable that the coal forming substance was penetrated by Stigmarian appendages and that the Stigmariae were actually growing in this substance. It is notable that the majority of Stigmariae structurally preserved are probably those of Lepidodendron and Lepidophloios whilst casts of Stigmaria were observed mainly in connection with Sigillariae.

STOPES and WATSON (1908) report the abundance of Stigmarian appendages and axes in coal balls obtained from the bottom of coal seams and infer that the lower part of the coal forming substance was penetrated completely by them. As, however, coal balls obtained from other horizons of a seam may show the same feature, penetration of the coal forming substance by Stigmarian appendages does not seem to be significant for the lower part of the seam only and may be rather due to local palaeo-ecological factors.

Impressions of Stigmariae, especially Stigmaria stellata are commonly observed in cannel coal (LESQUEREUX, 1875).

5.Introduction into the terminology used:

a)New terminology necessary:

In structurally preserved specimens of Stigmaria as well as of Lepidodendron and Sigillaria a varying number of different tissues can be recognized.The absence of serial sections renders an understanding of the development and nature of the tissues difficult and direct evidence bearing on these questions can only be obtained from the apical regions of both the aerial shoots and the Stigmarian branches.Such evidence is also required for an understanding of the morphological nature of the Stigmariae and their appendages.Unfortunately petrifactions of such growing points have not yet been found, or possibly not been recognized as such,and even about the apical morphology of the probably most closely related,living plant,Isoetes,different opinions exist although the interpretation of LANG(1915) seems to be now generally accepted.

In previous descriptions of the anatomy of the fossil Lycopodiales several morphological and histological terms have been used which, while applicable to perhaps most vascular plants,do not describe the morphological peculiarities of Stigmaria satisfactorily;misunderstandings have therefore occurred.

For this thesis, which is based on the examination of a great number of sections of different Stigmaria specimens,new terms are used which,I hope,will simplify the explanations given of the nature and development of Stigmaria and which may prove to be applicable to the explanation of the anatomical features of the erect shoots of Lepidodendrales and Sigillariae.It may be noted that similar difficulties in terminology are encountered in description of the anatomy of Isoetes.In this plant too there are anomalies both in histological detail and in the development and distribution of the vascular tissues.

b)The Stigmarian axis:

For convenience the tissues will be dealt with under the headings :Stele,Cortex and Epidermis.Close observation however proves that these three tissue groups may not be so distinctly separable as in modern plants.

The Stele:

Three different types of elements occur in the xylem of Stigmaria steles.These are:

1. Annular tracheids - long,narrow,tubular elements with annular thickenings.
2. Scalariform tracheids - long but relatively wide elements with scalariform thickenings on both radial and tangential walls;the pits are traversed by fine threads (WILLIAMSON, 1869), pl.IX,fig.36.
3. Short scalariform tracheids - short wide cells with irregular pitting (ray tissue tracheids).

Four different types of steles are known of Stigmarioid branches, which differ in the arrangement of the vascular tissue particularly as regards the xylem. These four different stelar types named after the species first described with this stele are illustrated in the diagrams 2 - 5 (p.25 and 27) and are named:

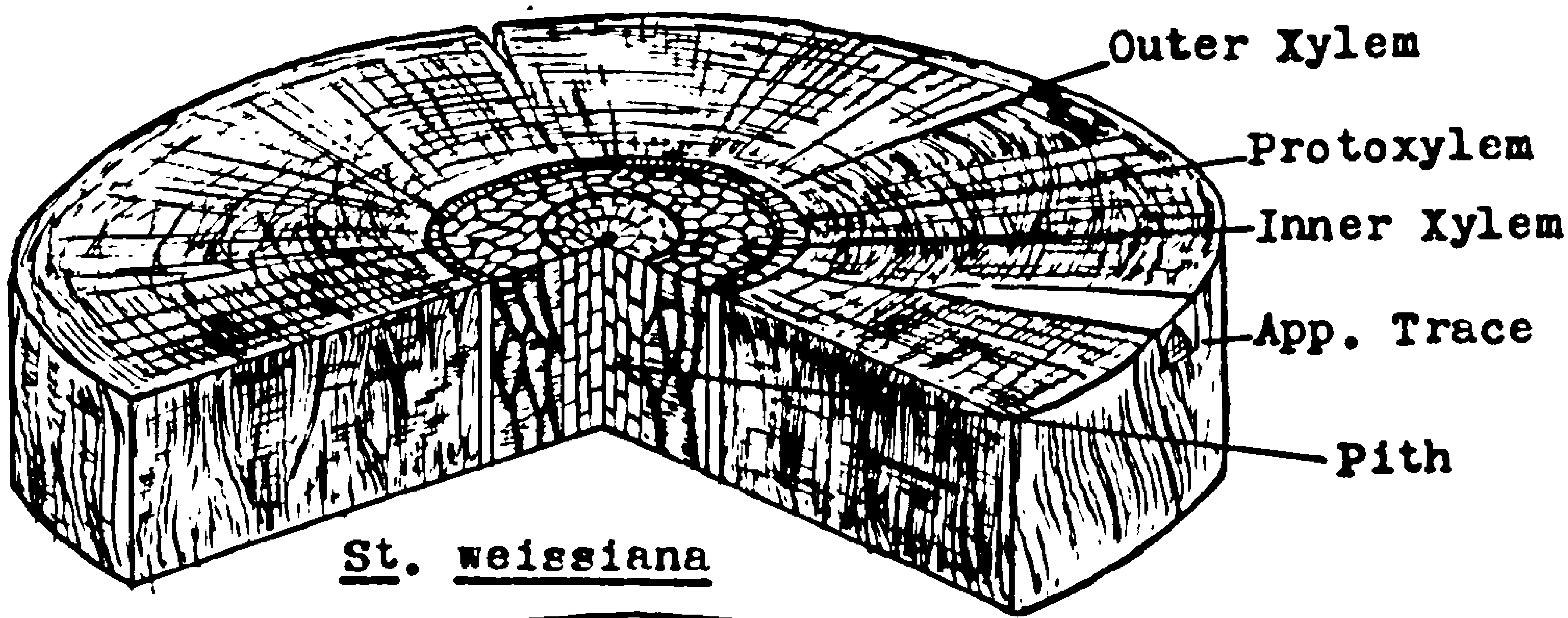
1) *Stigmaria weissiana* type
2) *Stigmaria lohesti* type
3) *Stigmaria bacupensis* type
4) *Stigmaria ficoides* type

1) In steles of the *Stigmaria weissiana* type (p.25, fig.2) parenchymatous tissue occupies the centre of the stele. Surrounding this in centrifugal order are: A narrow zone of irregularly arranged scalariform tracheids, a ring of annular tracheids and a broad zone of radially arranged scalariform tracheids. In the description of the species the tissues are named as follows:
The parenchymatous centre of the stele is the pith. The tissue consisting of irregularly arranged scalariform tracheids will be referred to as inner xylem. The groups of annular tracheids may be called protoxylem but it should be emphasized here that it is an open question whether these annular tracheids are the protoxylem elements of appendage traces or those of the vascular strand of the axis. The radially arranged scalariform tracheids will be referred to as outer xylem.

2) Of the *Stigmaria lohesti* type of stele (p.25, fig.3) only the xylem part is known. It consists of a solid core of irregularly arranged tracheids, these are surrounded by groups of annular tracheids. The bulk of the tissue consists of radially arranged scalariform tracheids which surround the solid core.

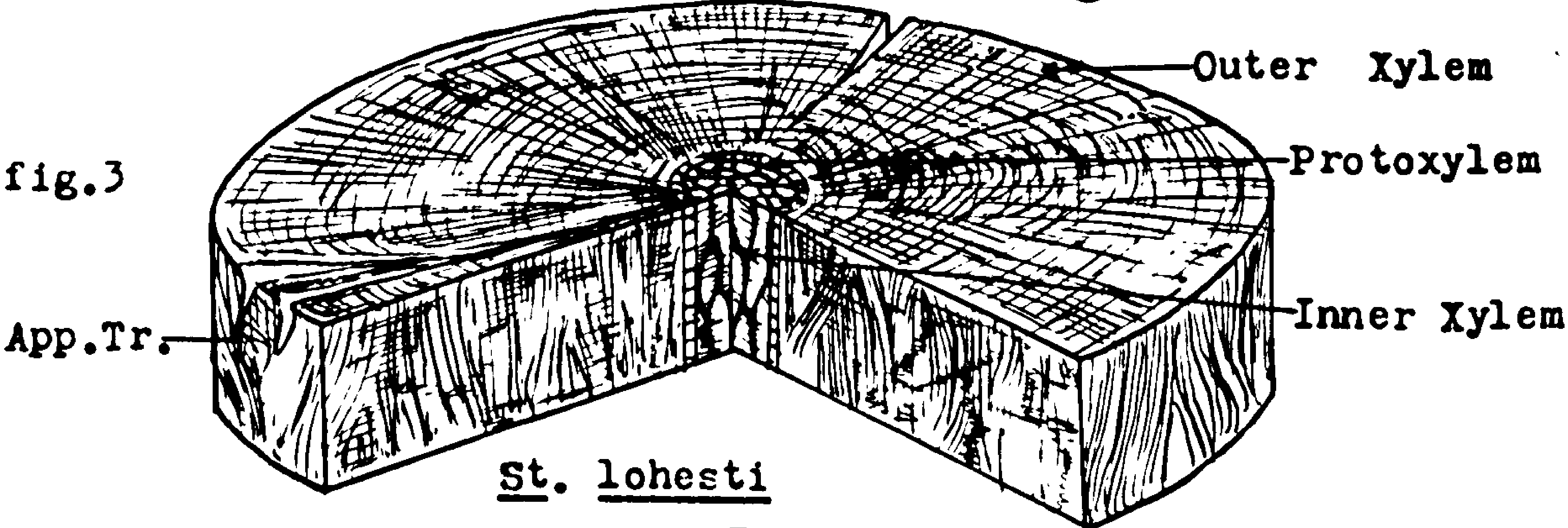
Stelar Types of Stigmaria

fig.2



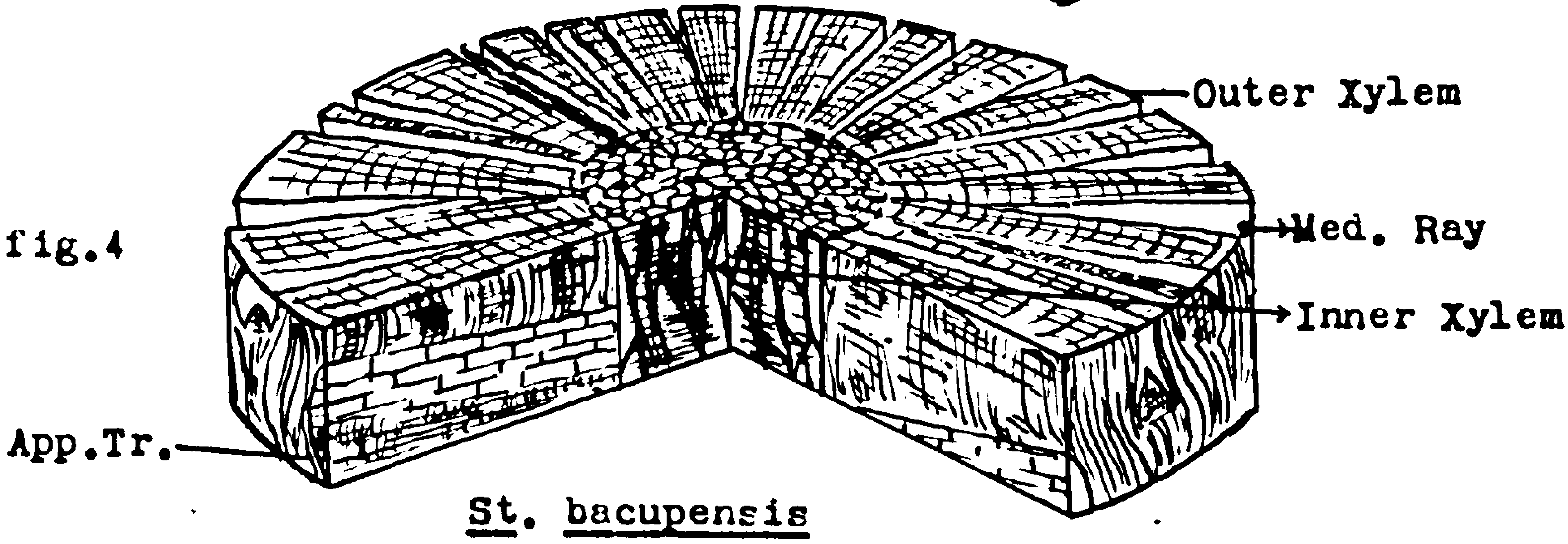
St. weissiana

fig.3



St. lohesti

fig.4



St. bacupensis

3) The Stigmaria bacupensis type of stele (p.25,fig.4) has a solid core of irregularly arranged short scalariform, scalariform and annular tracheids. Parenchymatous cells may occur in this part but a pith is not observed. This vascular tissue, the inner xylem, is surrounded by a cylinder of radially arranged scalariform tracheids, the outer xylem. Groups of annular tracheids between the inner and outer xylem are not observed. Tissues outside the xylem were not found preserved.

4) The centre of the stele of the Stigmaria ficoides type (p.35),(p.27,fig.5) is occupied by the pith which, however, is seldom completely preserved. When the medullary tissue is not or only partly preserved, the empty space is referred to as the medullary cavity. The pith is surrounded by a parenchyma of different structure in which annular tracheids can be sometimes observed. This is the endo-xylem. Outside this are radially arranged scalariform tracheids constituting the outer xylem. The parenchymatous tissue outside the outer xylem is the exo-xylem. Secretory strands represent the phloem and are surrounded by the pericycle. The outer xylem of both the Stigmaria ficoides and the Stigmaria bacupensis type appears to be split into a number of wedges by the appendage traces, which originate between the inner and the outer xylem.
A varying number of wedges in transverse sections of the stele does however not indicate variation in the number of appendage traces but is often due to a difference in height of the principal medullary rays in which the appendage traces pass out.

Stelar Types of Stigmaria.

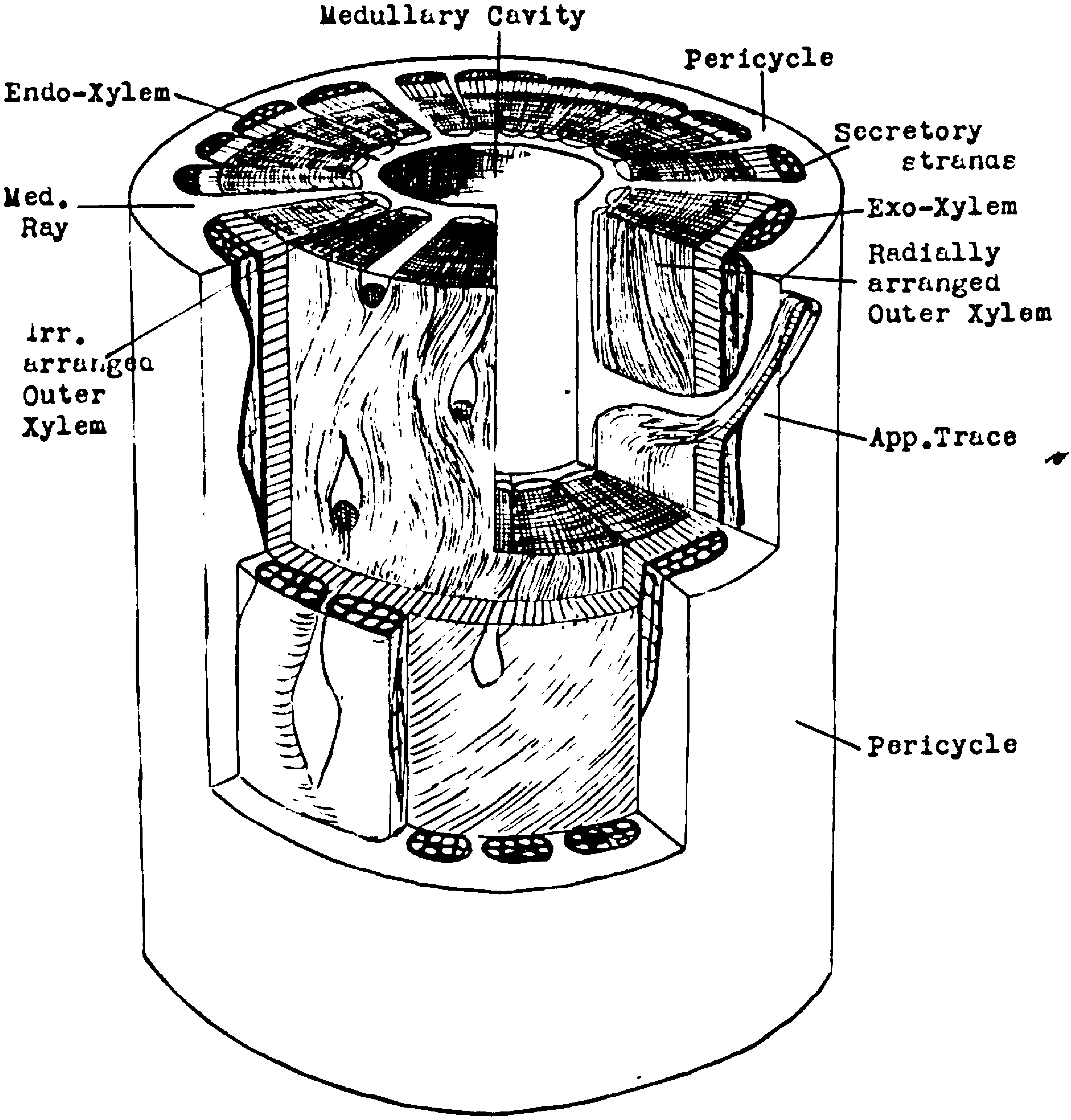


fig.5 Stigmaria ficoides type

The Cortex of the Stigmarian axis:

The Stigmarian cortices appear to consist of a large number of different tissues. Early start of secondary growth in the cortex renders the recognition of the true succession and distribution often difficult and a number of different terms has been used to describe the same tissue in Lepidodendron, Lepidophloios or Stigmaria.

In the order of their development three groups of tissues can be recognized in the cortex of Stigmaria:

Fundamental cortical tissue = primary cortex
Accessory cortical tissue = expansion tissue
Secondary cortical tissue = radially arranged.

The fundamental cortex:

The anatomy of the apical region of Stigmaria is not known but it may be assumed that a uniform primary cortex was present in this region. Patches and zones of this tissue left unchanged by differentiation and secondary growth provide evidence that the entire cortex consisted once of this fundamental cortical tissue. Towards the outside the cells of the fundamental cortex become smaller in size and this area is described in this thesis as the superficial cortex, especially when it is separated from the inner part of the fundamental tissues by the sclerotic elements.

The accessory tissue:

These tissues are derived from the fundamental tissue by irregular or cambiform division of cells of the fundamental cortex. The secretory ducts within the outer cortex are also assumed to be accessory developments.

The development of the accessory middle cortex separates the fundamental tissue into an outer and inner part, the outer primary and the inner primary cortex.

In this stage, probably, the cortical secretory ducts and the sclerotic elements are differentiated.
The whole cortex now consists of four zones(p.31, fig.6):
1)The superficial cortex, separated from the outer primary cortex by the differentiation of sclerotic elements between both tissues.
2)The outer primary cortex (p1 + p2)
3)The middle cortex (M)
4)The inner primary cortex (p3)
The cells of the inner primary cortex, which is a fundamental tissue, may eventually become completely differentiated into accessory cortical tissue also, so that in a later stage of development the "middle cortex" may appear to be adjacent to the stele.

<u>The secondary cortical tissue:</u>

Meristematic activity may commence in both primary and accessory tissues and may lead to the formation of radially arranged, secondary tissues. Secondary growth commences after, or more probably, during differentiation of accessory tissues.

Meristematic activity in the outer primary cortex (p1+p2) divides the outer cortex into an outer (p1) and inner zone (p2). In branches of the last order of dichotomy the secondary cortex is a small band of radially arranged cells of uniform size. In sections of Stigmarioid branches of a lower order the secondary cortex is much thicker and can be divided into an external (Se) and internal(Si) zone.

The external zone shows cells tangentially stretched and radially arranged (zone of dilatation);the cells of the internal secondary cortex are isodiametric in transverse section.

Epidermis:

An epidermis has not been recognized in a Stigmarian axis.The superficial cortex of the axis and the corresponding zone of the appendages - the limiting layer and the cells immediately underneath- may prove to be multiple epidermal layers (p.132).Until such evidence has been submitted these zones are described in this thesis as peripheral zones of the cortex.

c)The Stigmarian appendages:

The anatomy of the appendages corresponds in many respects to that of the axes.

The stele:

The stele of the appendage consists of a strand of annular tracheids which can considered to be the protoxylem. To the inside of this (p.33,fig.7)is a triangular strand of scalariform tracheids,the xylem. This vascular tissue is assumed to correspond to the outer xylem of the axis and may therefore consist of either radially or irregularly arranged tracheids.Endo-xylem can be observed sometimes, surrounding the vascular strand,exo-xylem is frequently preserved between the xylem and the secretory strand,which represents the phloem.In the phloem area there are a few thick-walled large cells surrounded by parenchyma.It corresponds to the phloem zone of the axis.

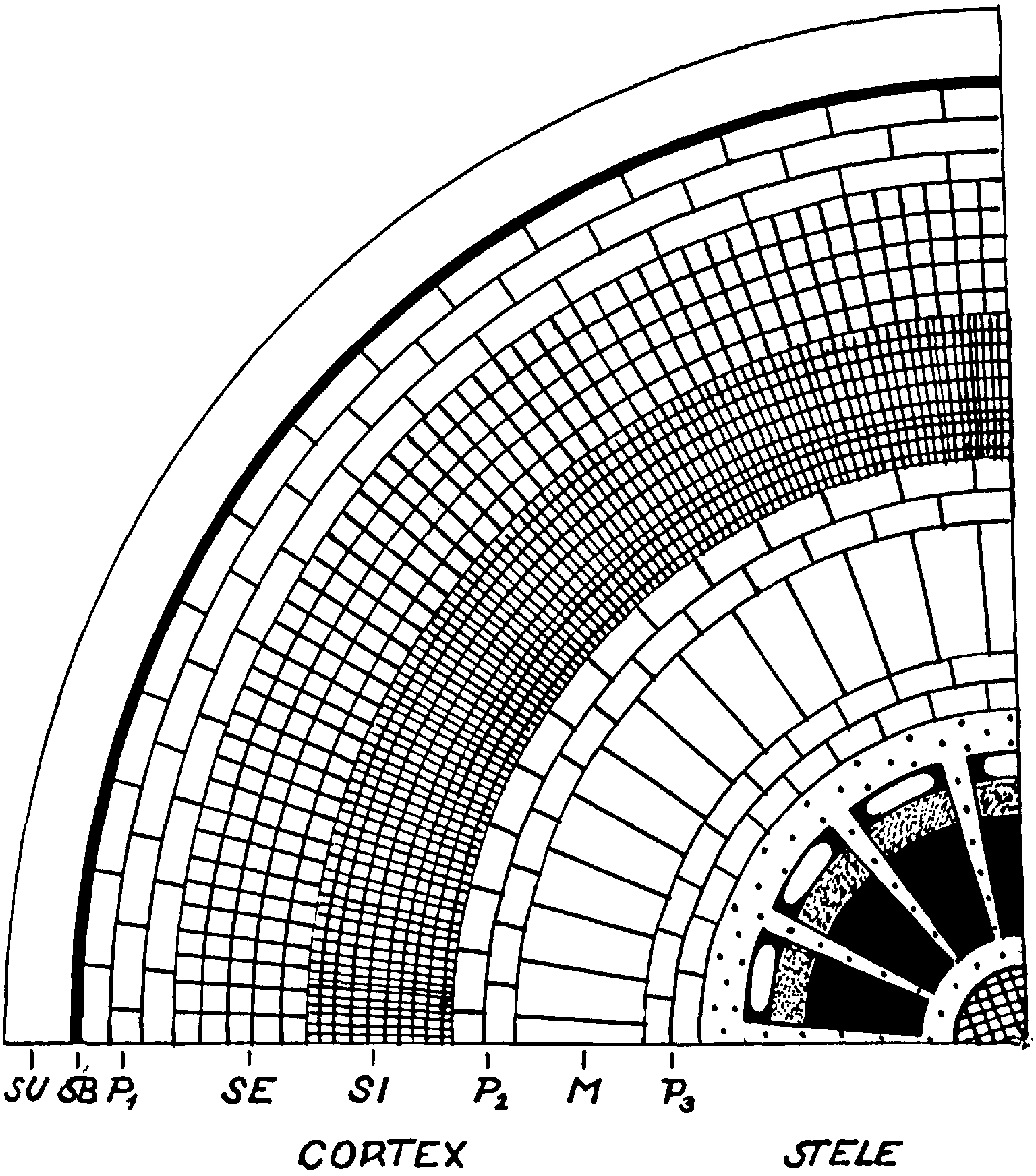


fig. 6: Diagrammatic drawing of a transverse section through part of a Stigmarian axis, showing the distribution of cortical tissues

The vascular tissue is surrounded by a sheath of parenchymatous tissue.The nature of this tissue is not always the same in all appendage types and species.In some instances this parenchymatous sheath may be considered to be pericycle whilst in others the outer part of it must be considered to be cortex.In most appendages as well as in the axes,cortex and stele are histologically not distinctly separated. delimited ?

The cortex:

The cortex of the appendage,like that of the axis, consists of three tissue groups:Outer,middle and inner cortex. As in the axis it can be assumed that the middle cortex is differentiated from the primary cortex and separates the primary tissue secondarily into outer and inner cortex.In many instances the inner cortex is completely differentiated into middle cortex.The middle cortex itself is,however,rarely preserved.Only in small appendages, in the region of dichotomies of appendages and in appendage bases can it be frequently found.Patches of the tissue may, however, be preserved in other parts of the appendages.

In most appendages the outer cortex can be seen to consist of two to four different zones which correspond to the tissues of the axis.

The surface layer of cells in the appendage is called limiting layer when it is made up of cells of uniform size and shape,but different in size from the underlying layers.This layer can possibly be an epidermis and not part of the cortex.

A zone of thin-walled tissue underneath the limiting layer or the outermost zone of cells in appendages without such a limiting layer is called outer zone.

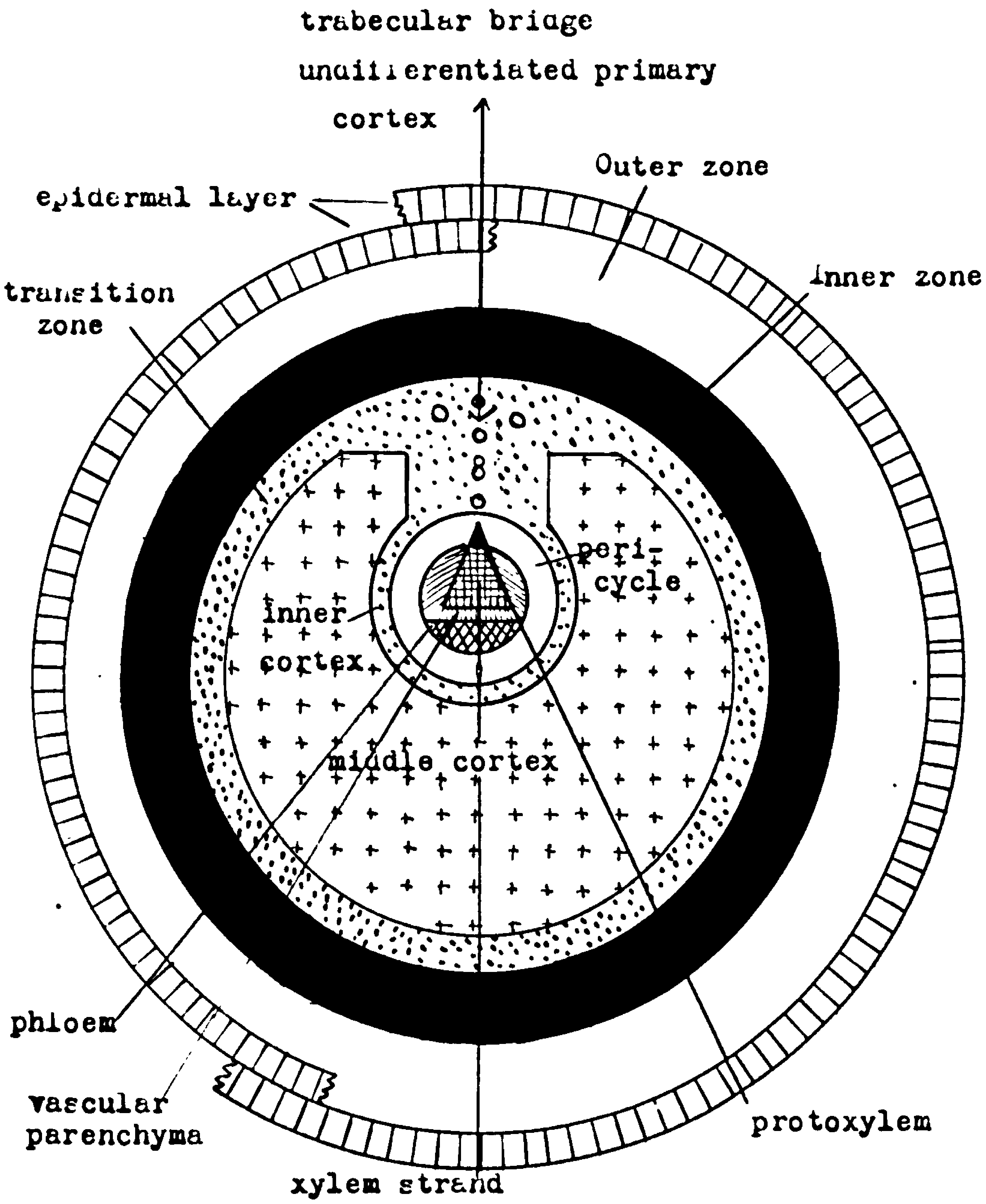


fig.7: Diagrammatic drawing of Stigmarian appendage
in transverse section

It generally corresponds to the superficial cortex of the axis.Within this is the inner zone of the appendage cortex which may be of different structure in different species. It may correspond to the outer primary cortex and may also in some instances correspond to the sclerotic zone of the axis.In some appendages it probably represents both zones.

A few layers of thin-walled cells are sometimes preserved inside the inner zone.This tissue is called transition zone and may in some instances be completely differentiated into middle cortex.The transition zone is considered to represent the outer primary cortex of the axis.

Secondary growth in the cortex of Stigmarian appendages was observed in few specimens only.One of these showed a pathological condition,following the intrusion of a fungus into the cortex.Secondary growth in the cortex of appendages will be described seperately.

In many appendages a strand of undifferentiated cortical tissue connects the stele with the outer cortex. This bridge normally consists of undifferentiated primary cortex. The cortical bridge surrounds a strand of tracheids, annular or scalariform,or both,which appears to originate in the endo-xylem.These strands of tracheids,terminating in short annular tracheids in the cortex,are the trabecular strands.

PART II

ANATOMY OF STIGMARIA FICOIDES TYPES

6. Anatomy of the *Stigmaria ficoides* type species:

In 1837 LINDLEY and HUTTON figured a fossil showing the external features of *Stigmaria ficoides*. Within this cast~~s~~ a cylinder consisting of radially seriated tracheids was preserved and this proved to be the xylem of the Stigmarian axis. This xylem consisted of a number of wedge shaped bundles anastomosing with each other and thus forming a network, the spaces left free being occupied by parenchyma, the medullary rays. In transverse section the wedges surrounded a circular space which was subsequently recognized as the cavity left by the disintegration of the medullary tissue. The wedges appeared to consists almost solely of radially seriated xylem. No other type of xylem was found associated with it.

After LINDLEY and HUTTON (1837) it was usual to describe specimens showing these steles, as *Stigmaria ficoides* and it seems to have been a general opinion among early palaeobotanical authors that a Stigmaria, showing the quincuncial arrangement of circular scars on the outside, always had this type of stele. Specific identification was based on minor differences (CORDA,1845) which might easily have been different stages of preservation.

RENAULT (1893) described and figured for the first time a Stigmaria showing the quincuncial arrangement of scars on the surface but having an entirely different type of stele and later authors (WEISS,1908,LECLERCQ,1925) have described other species of Stigmaria with steles different in the general structure from *Stigmaria ficoides* described by LINDLEY and HUTTON (1837).

In this thesis it is demonstrated that several species of Stigmaria showing the Stigmaria ficoides type of stele can be distinguished by cortical features.Therefore the name Stigmaria ficoides is used for anatomical description, only to describe a stelar type and its use as a specific name is discontinued.

a)A re-examination of Stigmaria radiculosa Hick:

In 1891 T.HICK published a paper in which he described an apparently new fossil plant found at Cinder Hills,Siddal near Halifax.He called this plant Tylophora radiculosa but changed the name later into Xenophyton radiculosum.WILLIAMSON was,according to WEISS(1902),of the opinion that "this plants affinities were with Stigmaria" but HICK left the relationship of Xenophyton an open question.WEISS(1902) showed that Xenophyton was indeed a Stigmaria and suggested that it might be the basal organ of Lepidophloios fuliginosus.

The external view,figured by HICK(1891,pl.16,f.1), shows a quincuncial arrangement of circular scars,typical of Stigmaria.The internal structure seems to be different at first sight from the common preservations of Stigmaria, but typical appendages branching off on the periphery of Xenophyton place this plant in the form genus Stigmaria.

For this re-examination of Stigmaria radiculosa slides were studied which are sections of the same specimen described by HICK(1891) and WEISS(1902).They are apparently taken at different levels and therefore a fair impression about longitudinal changes could be obtained.The slides were from Kidston Coll. and Class Coll.Glasgow,Manch.Mus. Coll. and D.H.Scott Coll. London.

Anatomical Structure:

1) Stele:

In contrast to the common preservation of Stigmaria, the pith is completely preserved in Stigmaria radiculosa. Some slides show the medullary tissue intact; in others, however, it may be partly destroyed or crushed by the intrusion of Stigmarian appendages into the vascular cylinder.

The pith cells are cylindrical in shape, of varying size and the medullary tissue has intercellular spaces (pl.II, fig.8). The cells are arranged in longitudinal rows and are separated from each other by horizontal or slightly oblique walls (pl.II, fig.10).

Towards the periphery of the pith, cells are small and of uniform size; this region may be called endo-xylem. The walls of the endo-xylem cells are markedly thinner than those of the pith cells and the latter are frequently filled with dark brown matter. Such fillings do not occur in cells of the endo-xylem. The endoxylem is three to five cells wide, has no intercellular spaces and lines the inside of the xylem cylinder. In contrast to the rectangular pith cells the endo-xylem cells are pointed at their ends (pl.II, fig.10) and resemble the cells of the pericycle. A zone of blackened cells along the border between pith and endo-xylem is similar to the band of black cells between pericycle and cortex in both the axis and appendages of Stigmaria radiculosa, (pl.II, fig.9 and pl.VII, fig.25).

Within the undifferentiated endo-xylem annular tracheids may occur, single or in groups. These have been considered to be the protoxylem elements of the vascular strand (HICK, 1891;WEISS,1902) but this is not altogether clear. Until really good tangential sections prove the course of the protoxylem elements, both possibilities, that the annular tracheids are the protoxylem of the vascular strand or that they are the terminations of the protoxylem strands of the appendage traces have to be taken into consideration.

The differentiated xylem is very little developed in Stigmaria radiculosa. This fact among others suggested that the type specimen of St. radiculosa might be the region of a Stigmaria near the growing point. The xylem cylinder is split into a number of wedge shaped bundles (between 30 and 40) which ~~consists~~ consist of scalariform tracheids. The innermost of these (pl.II,fig.9) commonly show no trace of radial arrangement and are similar in size and arrangement to the cells of the endo-xylem. This zone with irregularly arranged tracheids has frequently been described as centrifugally differentiated metaxylem, corresponding to the solid core of xylem (inner xylem) in the Stigmaria lohesti and Stigmaria weissiana type. This however cannot be considered correct as will be pointed out on p.53,54.

The whole of the differentiated xylem in *Stigmaria radiculosa* corresponds to the outer xylem of the *St.weissiana* or *St.lohesti* type stele. In some wedges of the outer xylem of *Stigmaria radiculosa* tracheids are radially arranged throughout and some endo-xylem cells show this radial arrangement also (pl.II,fig.8).

A tissue consisting of small tracheids and small parenchymatous cells surrounds the outer xylem of *St.radiculosa* (pl.II,fig.9) and is named exo-xylem. The exo-xylem cells are of the same size and arrangement as those of the endo-xylem and those irregularly arranged tracheids of the outer xylem. Also the cells of the secretory strands (pl.II,fig.9) are of the same arrangement and size as in the exo-xylem. Beginning meristematic activity can be observed in this tissue (pl.III,fig.14).

Secondary xylem, exo-xylem and secretory strands are divided into wedge-shaped bundles by the principal medullary rays. In these, the xylem strands of the appendage traces pass out. To the inside of the vascular cylinder the parenchyma of the medullary rays is connected with the endo-xylem and to the outside with the pericycle. The medullary rays are high and narrow and overlap one another deeply so that a large number of vascular bundles appear in transverse section. Pl.II,fig.11 shows a tangential section through the stele near the pith. The protoxylem strand in the medullary ray can be seen coming off one side and bending into the centre of the medullary ray. The tissue in this ray is made up of narrow elongated cells and has the same appearance as the tissue of the endo-xylem.

Outer xylem tissue is attached to the protoxylem as it passes out in a steep course through the xylem cylinder. Exo-xylem and secretory tissue are added to the appendage trace opposite its protoxylem as it traverses the meristematic zone and secretory strands. When the appendage trace leaves the vascular strand of the axis, the protoxylem of the trace is pointing towards the centre of the axis. The protoxylem and the two adjacent sides of the outer xylem are surrounded by the medullary ray tissue, probably the tissue of the endo-xylem, which then is continuous with the exo-xylem and the secretory strands of the appendage trace. In the pericycle all this tissue is surrounded with pericyclic tissue and then passes out into the cortex (pl.III,fig.12) where the trace bends and continues on its course more or less vertically in the axis (pl.III,fig.15).

The secondary xylem wedges are split up further by the secondary medullary rays which are only one or few cells high and usually only one cell broad. They consist mainly of parenchyma but scalariform cells may also occur.

The secretory strands (phloem zone) are not very well preserved in <u>Stigmaria radiculosa</u>. In their place are wide lacunae opposite each xylem wedge. In some instances the tissue is partly preserved but obscured by dark masses (pyrite). Around this opaque substance patches of cells of the secretory strands can sometimes be observed (pl.II,fig.9). The cells do not differ in structure from the cells of the pericycle but their walls are thinner and they are slightly smaller in diameter.

In longitudinal section the cells of the secretory strands appear to be narrow cylinders (pl.II,fig.10) separated from each other by oblique walls.Sieve elements were never observed. In some places it can be observed that the secretory tissue has broken down to form large sacs defined by blackened walls, a feature seen in Lepidophloios steles and not so far observed in other Stigmariae,but I will submit evidence later that it occurs in Stigmaria also.

Outside the "phloem" region and surrounding the whole stele is a parenchymatous tissue which may be called pericycle.The cell walls are thin compared with those of the cortex outside it and the cells are far smaller in diameter than those of the latter. The cells of the pericycle are elongated whilst the cortical cells are isodiametrical. The cells surrounding the secretory strands are small in diameter but the size increases towards the periphery of the pericycle (pl.II,fig.9).Sometimes, especially near appendage traces,pitted cells may occur in the pericycle.

An endodermis separating the pericycle from the cortex has not been observed. Although the pericyclic and cortical cells differ from each other in appearance, there is no distinct layer of cells separating them. Pl.II,fig.9 shows that the innermost cells of the cortex are often filled with an opaque substance and a clear line of separation is thereby apparent between cortex and stele.

2)Cortex:

Unlike the commonly incomplete preservation of the cortex of most Stigmariae, the cortex of Stigmaria radiculosa is preserved completely i.e. solid tissue extends from the stele to the periphery where appendages are attached.

The cortex consists of three different types of tissues, the fundamental-, accessory-, and secondary cortical tissues.

A superficial cortex is preserved (pl.V, fig.20) and is composed of thin-walled mostly tangentially stretched cells which are elongated in longitudinal direction. As far as the superficial cortex is preserved it is in continuation with the outer zone of the cortex of the appendages. A narrow zone of cells which can be followed all round the cortex separates the superficial cortex from the outer primary cortex (pl.V, fig.20). This layer in which cells have dark brown contents is figured as sclerotic band.

Situated inside the sclerotic band is a tissue with isodiametric cells of rather uniform size arranged in a peculiar manner similar to that of the cells found in the cortex of some Stigmarian appendages. Four to five larger cells are grouped around a smaller cell (pl.III, fig.9a). The cell walls in this tissue are dark brown and they appear tp be rather thick in pl.V, fig.20. This, however, is due to the fact that the section figured was rather thick and parts of the longitudinal cell walls are visible in the figure.

The whole of the cortex of St.radiculosa originally consisted entirely of the primary cortical tissue.It extended from the stele to the superficial cortex.Out of this fundamental cortex,the middle cortex,the radicular tissue of HICK (1892),was secondarily derived by repeated divisions of the original cells of the primary cortex.

The inner cortex is not very distinct in St.radiculosa. all the cells are in a differentiating stage, as it is figured from the outer cortex (pl.V,fig.21a,transition zone) and some divisions have already taken place. In pl.III,fig.12 the dark cell walls of the inner cortex, within which the cells of the middle cortex were formed, are still recognizable.It can be assumed that these cell walls may disappear completely in the course of development in which case the middle cortex will be adjacent to the stele.

The accessory tissues, developed from the primary cortical cells, are the middle cortex and the secretory ducts in the outer cortex. The cells of the primary cortex underwent irregular and cambiform division to form new cells of which the middle cortex is constituted.This division probably started in layers near the stele and proceeded both centrifugally and centripetally. An indication of the differentiation of a new tissue out of an already existing one is shown in pl.V,fig.21a. There the cells after irregular division have proceeded to cambiform meristematic activity.

The remains of the darker cell walls of the primary cortex can be found all over the middle cortex and especially, as mentioned above, around the stele and near appendage traces (pl.III,fig.13).

Patches of primary cortical tissue left undifferentiated for some reason or the other can be seen extending from the outer cortex to the stele (pl.VI,fig.24).They strongly suggest that the cortex was made up of uniform tissue of the type of the outer cortex,the primary cortical tissue.

A second type of differentiation in the primary cortical tissue is shown by the groups of cells figured in pl.IV,fig.16,fig.18 and pl.V,fig.20a and provisionally described as secretory ducts. These ducts arranged concentrically around the cortex are situated immediately underneath the secondary cortex (pl.V,fig.20 a). In transverse section these ducts appear as concentric cluster of cells. In longitudinal section (pl.IV,fig.18) their innermost cells appear to be isodiametric whilst the outer layers of cells are elongated.The groups of cells are arranged in longitudinal rows parallel to the axis. The centre cells of these groups seem to have broken down easily and thus formed long canals which are well known in the primary and secondary cortices of Lepidodendron and Lepidophloios. They will be described later in the cortex of Stigmaria arranensis and other species.

After and possibly during the differentiation of the primary cortex into its various regions,meristematic activity resulting in the formation of radially seriated cells started in various zones of the tissues.

Three radially successive meristems are figured in the outer primary cortex. The outermost meristematic layer (pl.V,fig.20a and fig.21) produced radially seriated cells of the same type as the primary tissue.

In contrast to the polygonal and isodiametric primary cells, the secondary cells are rectangular in T.S. and elongated longitudinally.

The next meristematic layer may be seen a little deeper in the cortex. It is still in an initial stage and is associated with the secretory ducts (pl.V,fig.20a). Further in, and separated from the second by a band of primary cortex, a third meristematic layer is present between the outer and the middle cortex.The meristem evidently originated in the differentiating cells of the primary cortex (pl.V,fig.21a) and is together with the meristem on the outside of the inner cortex mainly responsible for the production of middle cortical tissue. In the specimen studied there is usually a gap between the outer and the middle cortex (pl.VI,fig.22) or where the two tissues are joined together a layer of crushed cell walls marks the border between them. The meristematic layer (pl.V,fig.20a) traverses this gap (pl.VI,fig.22).

The position of meristems in the middle cortex is shown by pl.VI,fig.24;they mainly tend to surround appendage traces.A concentric meristem is present around the stele and,originating from the primary inner cortex,produces middle cortex cells in centripetal direction. A meristem passing through the middle cortex in radial direction is shown in pl.VI,fig.23.These radial meristems probably serve to equalize tangential stresses originating during radial expansion.

The rise of meristematic activity in the outer cortex is illustrated by pl.IV,fig.17.

3)Appendage traces:

When the appendage traces leave the stele they bend to a horizontal course in the axis. Pl.VI,fig.24, shows many appendage traces cut longitudinally. The appendage trace is accompanied by a meristem usually on one side only. In the middle cortex the appendage traces bend upwards and then pass obliquely outwards through the outer cortex. In this area the meristem has added to the inner cortex of the trace and this tissue is arranged radially arround the stele of the trace. In some of the traces, in the region of the outer margin of the middle cortex (pl.VI,fig.24) the meristem is arranged all round the trace; in most other cases the meristem reaches half way round the outward side. In the sector of the trace without meristematic activity the middle cortex of the appendage merges into the middle cortex of the axis. On the meristematic side there is a gap,or a streak of crushed cells,or both between the meristem and the middle cortex of the axis. Thus the impression of a "secondary endogenous insertion" of the appendage in the middle cortex can be obtained,(pl.III,fig.13).

In the outer cortex the presence of an appendage trace seems to have stimulated meristematic activity in the surrounding cells. Meristematic activity in the middle cortex then seems to have ceased as appendage bases in the outer cortex of the axis were not observed to have meristems in their middle cortex.

Part of an appendage base, as seen in a tangential section through the superficial cortex, is shown in pl.VII,fig.25. The stele consisting of xylem, endo- and exo-xylem,secretory strand and pericycle, is surrounded by black cells very much of the same nature as the cells surrounding the stele of the axis(pl.II,fig.9).A few cells of the inner cortex of this appendage base can be observed between the black substance.The middle cortex of this appendage base appears to consist of a loose parenchyma and is separated from the outer cortex by a layer of cells of uniform size (pl.VII,fig.25).The outer cortex appears to be of the same nature as that of the axis but the cells are slightly smaller in size.The outer zone of the appendage is necessarily the same as the superficial cortex of the axis.

4)Appendages:

Only one specimen of Stigmaria radiculosa is known, the type specimen and it has no free appendages preserved. But pl.VII,fig.26 shows an appendage of another specimen of Stigmaria of exactly the same structure as the appendage base figured in pl.VII,fig.25.

Appendages of this type are quite commonly found. This appendage (pl.VII,fig.26) comes from an axis of the common incomplete Stigmaria preservation (p.49).From the stele of this Stigmaria only a little of the apparently well developed xylem is preserved but the outer cortical tissues,the sclerotic band and the superficial cortex are of the same type as St. radiculosa. Middle cortex, inner cortex and other stelar tissues than xylem are not preserved in this specimen.

The secondary cortex of this specimen is further developed than in the St. radiculosa type specimen.It can be assumed that this specimen is Stigmaria radiculosa in an advanced stage of growth.

Other appendages coming from the same axis,in which, however,the middle cortex is not preserved show a similar structure as figured in pl.VII,fig.26.

Within the middle cortex of the appendage (pl.VII,fig.26) tracheids surrounded by cortical tissue can be observed (tr) which indicate the presence of a trabecular bridge.

The stele of the appendage is surrounded by cells filled with an opaque substance in which at one point the inner cortical cells can be observed.The middle cortex consists of loose parenchyma and is separated from the outer cortex by a layer of cells very uniform in size.The outer zone has the same structure as in St. radiculosa. A limiting layer is developed.

b) Stigmaria radiculosa, other than the type specimen:

It has been mentioned above (p.47,48) that some incomplete Stigmariae show great similarity to the type specimen of Stigmaria radiculosa. When they correspond in the structure of the outer cortex, the stele and the appendage bases to the type specimen they are assumed to be of the same species.

The stele in all specimens is split into 3o to 35 wedges, each wedge being from 4 to 8 radial rows of tracheids wide. The radial width of the xylem is 3 mm as an average and varies only slightly in the studied specimens, except in the probably younger type specimen. The xylem strands of the Stigmaria radiculosa specimens thus have a rather uniform shape which, however, is shared also by the xylem strands of Stigmaria asteroidea.

In some specimens patches of the middle cortex are preserved and prove to consist of the same tissue as in the type specimen.

Of the greatest importance for the specific identification is the outer cortex.

The external secondary cortex is very narrow, dilatation was observed only in a specimen with a very large circumference of the outer cortex (4oo mm), Glasgow Class Coll. 185,

The outer cortex always consists of isodiametric cells, the sclerotic band which is one or two layers of cells wide, but never wider, and small isodiametric, thin-walled cells in the superficial cortex (pl.IV, fig.19).

All the specimens showing this structure are considered to be of the same species as the specimen described by HICK (1891) and WEISS (1902),Stigmaria radiculosa.

One specimen (Kidst.Coll.646,Dulesgate) shows a slight variation.The medullary cavity in the stele appears to be wider, but this cannot be dicided with certainty because the stele is crushed.In the superficial cortex outside the typical Stigmaria radiculosa sclerotic band a few layers of small isodiametric cells are followed by a zone of radially elongated cells. An outermost zone consisting of a few layers of very small cells is preserved in a few small patches.Appendages seem to break through this outermost layer and may be inserted slightly endogenously.

In the appendage bases,another typical feature in Stigmaria radiculosa three zones can be distinguished in the outer cortex in all specimens.The middle cortex is always a wide celled parenchyma (pl.VII,f.26).

One specimen of Stigmaria radiculosa has,as mentioned, a very large circumference of the outer cortex(4oo mm). The average circumference of all other specimens observed, reached from about 14o mm(type specimen) to 18o mm.

The large specimen shows extensive development of the secondary cortex.The external secondary cortex is wider than in the other specimens and shows some signs although not very marked,of dilatation. Secretory ductsn seem to have been present in the internal secondary cortex. On the inner side of this tissue the radial rows of cells widen and thus indicate the presence of the inner zone of the outer primary cortex.The outer cortex is fissured deeply,apparently by the tangential expansion and the superficial cortex is,except in some places exfoliated. This specimen could be described as the truncate stage of Stigmaria radiculosa.

c)Stigmaria sewardi,a new species with a preserved stele:

In most specimens of Stigmaria the stelar tissues, except the xylem, are not preserved.Small specimens, as the type specimen of Stigmaria radiculosa and a specimen of Stigmaria arranensis in a similar stage of development,may show stelar tissues more perfectly preserved but Stigmaria sewardi frequently shows stelar tissues inside and outside the xylem,even in steles of large diameter.

A series of slides,now in different collections (Kidston Coll.656 A-D,Glasgow Class Coll.34-35,Manch.Mus. coll.R 355,R 875 and D.H.Scott Coll.111,116,905) present the species in long,tang. and transverse sections. All these sections mentioned above seem to be cut from the same block and are probably sections of the same plant. All show the same state of preservation,They were prepared by LOMAX and are from Oldham/Lancs.All slides show "Liesegang's rings" in the mineral substance a phenomenon rarely observed in coal balls. Certain rings occupy the same position in all slides. The six transverse sections are in three pairs, the section in each pair being almost identical in size and structure;the pairs are:
905 Scott Coll. - R 355 Manch.Coll; 656 Kidst.Coll - R 875 Manch.Coll; 111 Scott Coll. - 34 Glasgow Cl.Coll.
The circumferences are in mm:

	Outer xylem	medullary cavity
111 Scott C.	103	43
656 Kidst. C.	91	4o
R 355 Manch.C.	62	28

Another specimen of the same species,var,minor (Kidst.Coll.1350 from Shore/Littleborough) has less developed outer xylem. The circumference of the outer xylem is 31 mm and that of the medullary cavity is 28 mm. Of the third, large variety of this species, var.boonvillensis, the stele is unfortunately not preserved.

The stelar tissues outside the xylem, usually well preserved in this species, show great similarity with the so called meristematic zone in Lepidodendron and Lepidophloios,first described by SEWARD (1902). I therefore propose to name this species Stigmaria sewardi.

Anatomical structure:

1)The Stele:

Remains of the medullary tissue have been observed in one specimen only (pl.VIII,fig.27).The pith seems to have consisted of more or less isodiametric cells,varying in size, with relatively thick walls. In long. direction they are elongated and are of the same appearance as the pith cells of St. radiculosa. The pith is surrounded by thin-walled tissue, the endo-xylem,which is more frequently preserved than the pith.The endo-xylem cells are smaller, have thinner walls than the pith cells (pl.VIII,fig.27) and are frequently radially arranged. Annular or , in some instances, scalariform tracheids may occur in the endo-xylem. Unfortunately too few scalariform tracheids are differentiated in the endo-xylem for their relation to the annular tracheids to be established. A clear centrifugal or centripetal differentiation of the scalariform tracheids,regarding the annular tracheids as protoxylem groups could not be established.

Whilst additional specimens may yield further information about the direction of differentiation of scalariform tracheids in the endo-xylem, I am, at present, of the opinion, that differentiation was proceeding in all directions just as it is assumed to have done in the inner xylem of Stigmaria bacupensis. Supporting this opinion is the fact that distinct groups of annular tracheids, protoxylem groups, observed in the Stigmaria weissiana and Stigmaria lohesti types are neither observed in Stigmaria sewardi nor in any other Stigmaria of the ficoides type.
The radially arranged outer xylem merges with the endo-xylem in very much the same way as the outer xylem merges with the inner xylem in Stigmaria bacupensis.

The outer xylem, distinctly differentiated, is very well developed in Stigmaria sewardi. Sect.111 (Scott Coll.) shows one of the largest vascular strands so far observed in any Stigmaria (circ.103 mm). The innermost cells of the outer xylem (pl.VIII, fig.27) are, as in Stigmaria radiculosa irregularly arranged. This zone was by many previous authors regarded as the primary xylem. Though this can be considered correct in some respects, this zone cannot be compared with the centripetally differentiated xylem of the Stigmaria weissiana and the Stigmaria lohesti types and consequently not with the metaxylem of Lepidodendron, Lepidophloios or Sigillaria.

Five facts make it improbable that this zone in the outer xylem of Stigmaria sewardi as well as all the Stigmariae of the ficoides type is homologous to the metaxylem in diploxyloid steles:

1)The innermost cells of the outer xylem in the diploxyloid steles may show exactly the same arrangement as in St. sewardi i.e. the irregularly arranged small scalariform tracheids are succeeded on the outside by radially seriated tracheids. The innermost tracheids together with the radially arranged tracheids have been regarded as secondary xylem by most authors.
2)Groups of irregularly arranged tracheids frequently occur within the secondary xylem in Stigmariae of the weissiana and ficoides type.
3)Some xylem wedges in other specimens show radial arrangement throughout without irregularly arranged tracheids on the inside of the wedges.
4)"Metaxylem" is not recognizable in appendage traces within or immediately outside the xylem cylinder.
5)Centrifugally developed metaxylem is not yet reported in the paleozoic Lycopodiales.

In conformity with the definition for outer and inner xylem used for the St.lohesti,St.weissiana and St.bacupensis type,viz. that the zone in which the appendage traces terminate,separates inner from the outer xylem (LANG,1915) it is assumed that these irregularly arranged tracheids at the inner side of the xylem wedges belong to the outer xylem.

They are,however,in fact primary xylem elements. Confusion arises at this point when the terms "metaxylem" and "secondary xylem" are used.The term secondary xylem implies that the tissue is produced by a meristem of cambial nature following the differentiation of primary xylem.

Such secondary xylem does not,however, occur in Stigmaria although the preservation of a tissue,the "meristematic zone", has led many authors to assume the presence of a cambium. Again many facts contradict the assumption that the outer xylem was produced by a single layered cambium:

1)Only radially arranged tracheids are observed,radially arranged phloem tissue, "secondary phloem" is not known.

2)In spite of the complete preservation of the stele in _Stigmaria sewardi_ and _Stigmaria radiculosa_ a cambium was not observed in the tissue between the xylem and the secretory strands,a tissue for which the non-comittal name exo-xylem was applied. This exo-xylem, the cells of which are much smaller than the normal tracheids of the xylem, may be completely parenchymatous as in _St.radiculosa_ (pl.II,fig.9) or may be in an early stage of meristematic activity (pl.III,fig.14). As such it can hardly be responsible for the amount of radially arranged xylem already produced. It may also be meristematic but then tracheids differentiated from cells produced by this tissue are much smaller than the average sized tracheids of the radially arranged xylem.

3)Irregularities in growth occur among the radially arranged tracheids which can hardly have been produced by a cambium as within these zones the cells are not only smaller but also irregularly arranged.

4)Appendage traces immediately outside the stele consist entirely of radially arranged xylem.When appendages leave the cortex of the axis their vascular strand consists in most cases entirely of irregularly arranged tracheids. Only in few cases radial arrangement is recognizable in the xylem.

All these points suggest that it cannot be assumed that the outer xylem is produced by a normally functioning cambium therefore the misleading term secondary xylem is avoided. It will be suggested later that lignification of the irregularly arranged cells and all the radially arranged tracheids probably occurred practically simultaneously hence it seems inappropriate also to use the term metaxylem for the groups of irregularly arranged tracheids on the inside of the xylem wedges.

Irregularities in growth of the radially arranged outer xylem have already been mentioned. This feature although observed in most Stigmariae and in the wood of many Lepidodendroid steles, is very conspicuous in Stigmaria sewardi and may therefore be discussed in relation to this species.

Pl.VIII,fig.28 shows these irregularities in growth in the outer part of the outer xylem. Small irregularly arranged tracheids abut on larger tracheids outwardly. Some radial rows of tracheids,however,can be observed to go through these zones without any change in diameter of tracheids; in another row (pl.VIII,fig.28) an increase in the diameter of the tracheids can be observed in these zones.The size,shape and arrangement of the tracheids in these zones of irregularity is exactly the same as in the endo-xylem, the irregular zone on the inside of the xylem wedges and in the exo-xylem. Furthermore the irregular tissues do not differ in arrangement and size of their cells from the secretory strands,so far preserved,or from the pericycle.

NOÉ (1931) suggests that these zones might be comparable to growth rings in modern plants and caused by external influences which resulted in the shedding of leaves etc. This can hardly be considered correct because, though a cambium or meristematic layer might produce small cells under such circumstances it could not produce irregularly arranged cells. Most other authors who have referred to the feature of irregular growth in the outer wood of the Lepidodendrales (esp. SEWARD, 1910) join WILLIAMSON (1896) in the opinion expressed in his account of the Arran trees: "that these perished in consequence of the mephitic vapours which filled the atmosphere" and he also added: " it may be that in the striking difference in the diameter of the conducting elements on the margin of the wood we have evidence of approaching death"

As these irregularities in growth, however less common they may be in the Lepidodendroid steles, are a regular feature in Stigmaria and are present even in the very little developed wood of <u>Stigmaria radiculosa</u>, it cannot be assumed that they are related to extraordinary atmospheric or climatic circumstances; otherwise it must be assumed that extraordinary circumstances were a constant feature of the habitat. Furthermore the occurence of tracheids, running through the zones of irregularities with unchanged or even larger diameters than normal, would speak against this theory.

The irregularly arranged cells, which cannot be produced by a cambium, their similarity to the endo-xylem, the inner part of the xylem wedges, the exo-xylem, secretory strands and pericycle all tissues which are assumed to be primary tissues, strongly suggests, that these zones of irregularities in the outer xylem are primary tissues embedded in secondary, radially arranged tissues.

The full theory of the growth of the xylem in the Stigmaria ficoides type of stele will be discussed on the basis of this view after the other stelar tissues have been described but it may be mentioned here that primary tissues unaffected by secondary growth were observed also in the secondary cortex of Stigmaria specimens (p.115) and will be described there (pl.XVI,fig.62).

The exo-xylem consists of thin-walled, radially or irregularly arranged cells; few tracheids are developed in it (pl.VIII,fig.30).This tissue,referred to in many accounts of Lepidodendron as the meristematic zone (SEWARD,1910) was considered to be the cambial zone of the secondary wood. But while giving this explanation it was realized that cells produced by this tissue were always smaller than the average tracheids in the secondary xylem in all specimens in which this tissue outside the xylem was preserved. HICK (1891) came to the conclusion that this tissue might be the remainder of the procambium left undifferentiated between xylem and phloem in Stigmaria radiculosa. Pl.III,fig.14 suggests,however, that meristematic activity was going on in this tissue and also, that tracheids were differentiated in this region.The term "remnant procambium" and its explanation does therefore not appear to be sufficient.

SEWARD(1910) pointed out that the way in which the exo-xylem is connected with the radially arranged cells of the outer xylem shows great similarity to the irregularities in growth of the outer xylem and he therefore came to the conclusion that another zone of irregular growth was just developing when the specimen was fossilized.

Whilst this can be considered correct in some respects it is not, as is explained later,an extraordinary development.

The tissue in the phloem zone corresponds to that observed in the corresponding zone of Lepidophloios steles. Characterized by the thick black walls (pl.VIII, fig.30) it is made up of small cells of the same nature as the tissue of the exo-xylem. The resemblance is very striking when the irregularly arranged groups of differentiated tracheids are compared with the small celled tissue of the secretory strands (pl.VIII,fig.30). Disagreement exists as to the use of the terms "phloem" or "secretory elements" for the tissue in the position outside the exo-xylem.

WEISS (1901) together with most other authors spoke of phloem and he well described and figured this zone from a section of _Lepidophloios fuliginosus_. Although he did not observe any sieve elements in this tissue, he came to the conclusion that the tissue must have functioned as phloem and could therefore be named as such. SEWARD (1902) described the phloem area in _Lepidophloios_ and figured the tissue as wide and elongated sacs, which originated from broken down cells. The same author interpreted the conspicuous black walls as indications of secretory activity of this tissue and therefore used the term "secretory strands". SEWARD (1902) agrees that these secretory strands might have functioned as phloem. The preservation of _Stigmaria sewardi_ provides further evidence and supports SEWARD's assumption that the blackwalled,partly decomposed tissue described by him, might be a developmental stage of the tissue described as phloem in _Lepidophloios fuliginosus_ by WEISS (1901).

Pl.VIII,fig.30 shows part of such a secretory strand in which both,small celled tissue as described by WEISS and large sacs (SEWARD) probably originating from small celled tissue, occur together.In other strands of the same specimen, the tissue was completely turned into these secretory sacs.

The uniformity of the tissues outside the xylem has already been referred to. This uniformity, also clearly seen in longitudinal sections of <u>St. radiculosa</u> provides a further feature supporting the theory of development of the vascular tissues put forward in this thesis.

Surrounding the phloem and forming the outermost layer of the stelar tissue is a thin-walled parenchymatous tissue, the pericycle (pl.VIII,fig.30). In its appearance it is similar to the endo and exo-xylem and where the preservation is sufficiently complete,as in <u>Stigmaria radiculosa</u>, it can be observed that it is also of the same structure as the secretory strands.

2)The development of the stele:

Before any secondary growth occurred, the tissues now described as endo-xylem,exo-xylem,secretory strands and pericycle must have been placed closely together forming one radial succession from the margin of the medulla to the periphery of the stele. It has already been emphasized that the appearance of all these tissues in transverse section as well as in longitudinal section is uniform.Doubtless all these tissues are primary tissues and it seems unlikely that they underwent any further differentiation, as their structure in the specimens showing considerable secondary growth is still the same, where,after the tissues have been serving different functions, differentiation might be expected.

It may therefore be assumed that, as HICK (1891) suggested, the endo-xylem,the exo-xylem,the secretory strands (in part) and the pericycle represent the primary tissues differentiated from the procambial strand behind the apex.

The first stage in the development of the stele appears to have been the differentiation of annular tracheids in the procambium. It seems likely that this ocurred as in _Isoetes_, i.e. the protoxylem elements of the appendage traces differentiated first in the growing stele of Stigmaria. As pointed out, there is no evidence whether there are any other protoxylem elements in the stele of the _Stigmaria ficoides_ type than the terminations of appendage traces.

The explanation LANG (1915) gave for the growth of the stem of Isoetes lacustris can be applied almost entirely for Stigmaria. LANG showed that secondary growth was already going on in the tissue he called outer xylem when the inner xylem was not differentiated at all and the first vascular elements recognizable near to the apex of Isoetes were the protoxylem elements of the leaf traces. If the same is assumed for Stigmaria it can explain why metaxylem is not differentiated in the Stigmaria ficoides type.

In the description of the cortex of Stigmaria radiculosa it was mentioned that the secondary growth of the cortex is somewhat anomalous as compared with secondary growth in modern plants although the periderm formation in monocotyledons has some similarity. Itbwas observed there that certain cells or groups of cells become meristematic and give rise to a secondary tissue in which every cell continues to divide in the same direction. This obviously results in the rapid production of a great bulk of secondary tissue. If we assume that the secondary growth in the stele of Stigmaria was prodeeding in the same manner, as suggested by the growth of the outer xylem in Isoetes, most of the conspicuous features of the stele can be explained.

The sequence in the development is also explained in p.64, fig.8.

Stage 1: The entire stele is assumed to have consisted of undifferentiated primary tissue. (The pith may have been recognizable in this stage)

Stage 2. The vascular elements of the appendage traces are differentiated in the primary tissue.

Stage 3. The tissue between the appendage traces becomes meristematic. Divisions take place in a whole group of cells and each daughter cell continues to divide.

Stage 4. All tissues outside the protoxylem terminations (primary and secondary) are differentiated into xylem and phloem and meristematic activity ceases.

In this last stage the following tissues can be observed in the stele of Stigmaria:The pith, differing from the outer tissues of the stele by its rectangular cells,undifferentiated pointed cells inside the xylem,tracheids,undifferentiated pointed cells outside the differentiated xylem,secretory tissue representing the phloem and undifferentiated pointed cells surrounding the vascular cylinder.

In Isoetes, and this may probably be true for Stigmaria also,LANG (1915) observed that phloem is differentiated early, probably during meristematic activity in the stelar tissues.

The zone in which the protoxylem elements terminate separates the inner from the outer xylem in diploxyloid steles or, in the Stigmaria ficoides type stele it separates the endo-xylem from the outer xylem. Meristematic activity does normally not start immediately adjacent to this zone but a few layers of cells outside it. Differentiation of vascular tissues,however,occurred in all cells (primary and secondary) outside this zone. Therefore,when the xylem of Stigmaria ficoides type steles is fully differentiated it can be observed that the inner part of each wedge consists of irregularly arranged small tracheids, differentiated from primary tissue and the outer part of the wedge consists of radially seriated tracheids differentiated from secondary tissue.

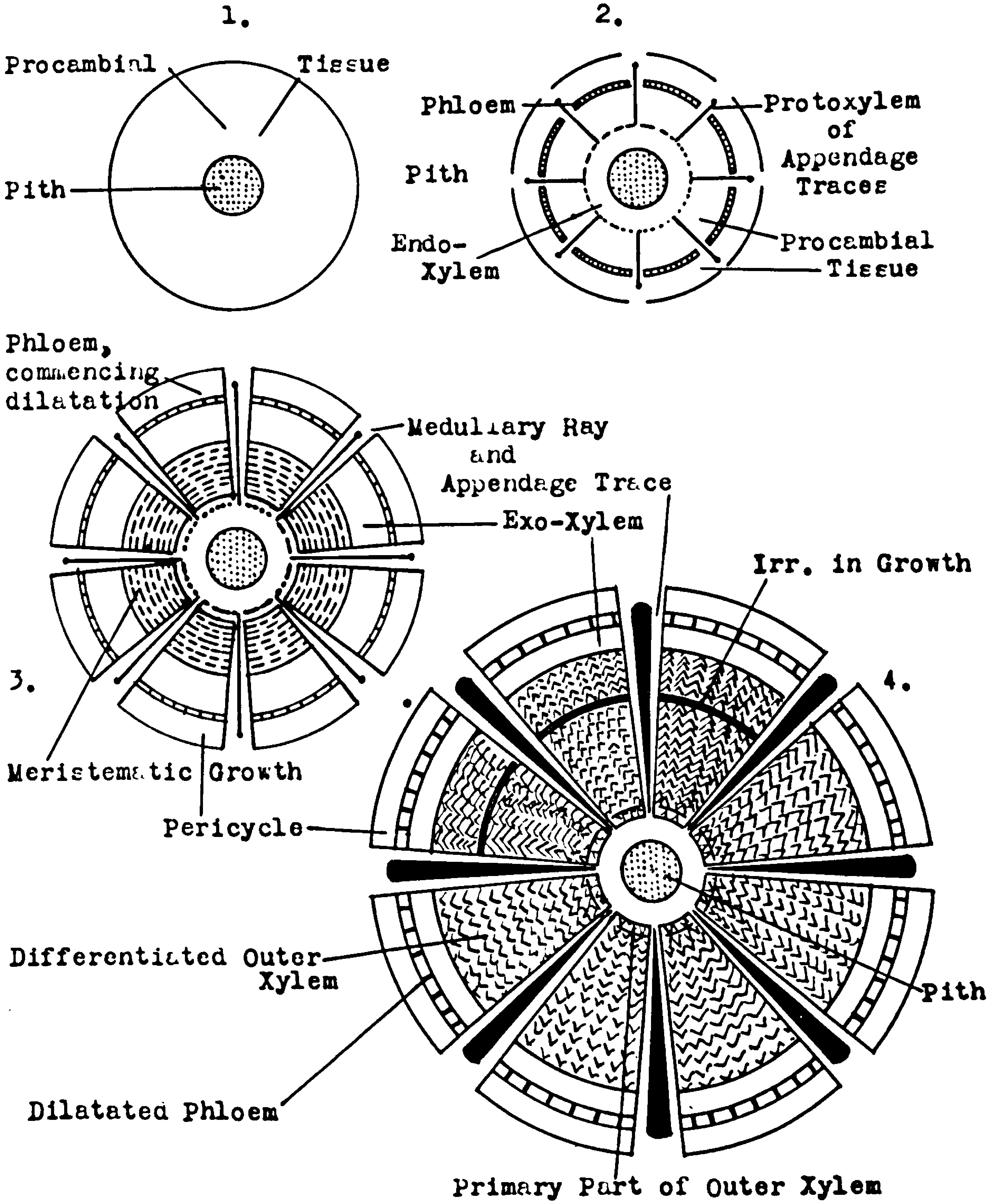


fig.8: The Development of the Stele in Stigmaria

The tissue inside the protoxylem is not,or only for a negligible part,differentiated.

A little further out, these irregularly arranged cells outside the protoxylem terminations,merge more or less gradually into a zone of radially arranged cells.It can be said that the further out in the xylem the more regularly are the cells arranged. The reason for this feature seems to be, that, though at first cells of all sizes took part in the rec$\overset{\text{ru}}{\text{on}}$descence of meristematic activity, those below a certain size were soon suppressed, (pl.II,fig.8 and 9). This feature can be explained on purely mechanical grounds. We assumed that tissues like endo and exo-xylem are primary in nature. It is observed that these tissues consist of cells of different diameter. During meristematic activity in these primary cells, it seems likely that the daughter cells produced would be of the same size as the respective parent cells,an assumption borne out by the observed arrangement of the tissues. It is this feature which underlies the increasingly regular radial arrangement in zones successively further from the endo-xylem.An example may be considered where a primary cell is half the size of a neighbouring cell and both proceed to divide at the same speed. Since this relative size difference is maintained in the derivative cells it follows that after two,or,at the most,three divisions the smaller cells will be completely surrounded by large and still dividing cells and no space is left for further division of the smaller cells.

This theory can be easily applied to the development of the xylem of Stigmaria although the growth seems to be more complicated. It can,however, be observed on the radial rows of tracheids of many Stigmaria specimens that those originating from a large cell in the primary part can be followed through the wedge for a great distance whilst those originating in the smaller cells of the primary part are not persistent and are quickly suppressed.

Further out in the xylem only tracheids of a more or less uniform diameter have continued growth.

These facts are in keeping with the proposed theory relating to the mode of secondary growth in Stigmaria and,in particular,they strongly suggest that a true single layered cambium was not present. The irregularities on the periphery of the Stigmaria xylem can find an easy explanation. Meristematic activity of the type suggested,can,of course, only proceed when the cells are undifferentiated.
As soon as they are differentiated, growth must stop and radially arranged xylem of the usual appearance can be observed in transverse section but in the undifferentiated parenchyma separating the xylem from the secretory strands growth may still continue. If so,the procedure described for the initial secondary growth in the xylem apparently starts again. Immediately outside the differentiated radially arranged tracheids lie primary cells of the exo-xylem region. Some of the outer layers of these primary cells become meristematic and radially arranged cells are produced again and the smaller cells become suppressed until the cells reach the same diameter and a uniform xylem is produced.

This process may be repeated several times, apparently depending on the amount of undifferentiated parenchyma left between the xylem and the phloem zone.

Differentiation is not at all regular as SEWARD (1910) has already observed for the exo-xylem of Lepidophloios wünschianus. The process of irregular differentiation of tracheids will be described later in relation to the appendages of Stigmaria sewardi var. boonvillensis.

This irregular differentiation offers an explanation as to why these patches of irregularly arranged primary xylem in the radially arranged tissue are not disposed in distinct zones and why, in certain instances, radial rows of tracheids may also show tracheids of larger diameter whilst in neighbouring rows irregularities in growth may occur. Pl.VIII, fig.3o shows that differentiation of tracheids does not take place as a continuous process although the general trend is in centripetal direction. It is, rather, a discontinuous process showing areas of lignified tracheids separated by patches of meristematic parenchyma. The vicinity of appendage traces and secondary medullary rays, however, seems to influence the cells towards an earlier differentiation.

Thus it can be assumed that the tissue called meristematic tissue by SEWARD and WEISS (1902, 1901) was not responsible for the production of radially arranged xylem. It is the remains of the procambial tissue separated from the other primary tissues of the stele by differentiation and secondary growth of cells in certain intervening zones.

The foregoing account has assumed that the irregularities in the size and arrangement of the tracheids of the outer xylem are due to the fact that the differentiation of a zone of secondary tracheids is followed by a renewal of meristematic activity in the parenchyma of the exo-xylem region.

A similar arrangement might arise if meristematic activity occurred in more than one zone of the procambium. In this case also the radially arranged tissue would appear tp be separated by irregularly arranged tissue. But it is easier to imagine that the tissues outside the radial meristem were undifferentiated because they had to equalize the tangential stresses by radial division an extension of which,however, no indication could be found.

At this point also the phloem question comes up again. If any phloem was differentiated before or during secondary growth in the outer xylem then it must have been displaced and torn as secondary growth continued in the outer xylem, since such peripheral tissues would no longer be able to keep pace with the tangential expansion. This result can indeed be observed. In Lepidophloios wünschianus, a species with an extraordinary development of radially arranged outer xylem, SEWARD(1910) has described the areas formerly occupied by the functional "phloem" as beeing filled with partly desintegrated cells and as having the appearance of a tissue which has been torn and turned into large lysiganous sacs.

On the other hand, the tissue described as phloem by WEISS (1901) in Lepidophloios fuliginosus is in a stele showing practically no secondary growth at all, except for a thin band of tissue which the same author described as cambium.

This supports the assumption that the tissue in the phloem area is differentiated early and it may be mentioned here that LANG (1915) showed that it is differentiated before the xylem in Isoetes.Subsequently the cells are turned into lysigenous sacs, described by SEWARD (1910) as secretory strands, by the tangential stresses caused by the radial growth of xylem.

3)Appendage Traces:

The principal medullary rays in Stigmaria sewardi are of a characteristic shape especially in tangential sections taken through the outer part of the outer xylem. The medullary rays are broad and drawn out to a slender tip. The tissue accompanying the appendage trace is normally parenchymatous but a few short scalariform tracheids may occur in it.

The appendage trace in the medullary ray appears to consist entirely of the radially arranged outer xylem tracheids, except for a few annular tracheids on the tip of the tongue shaped trace (pl.VIII,fig.29). All other tracheids are scalariform and appear to be radially arranged. The tongue shape of the appendage trace is typical in this species and differs from the triangular shape of the appendage traces of Stigmaria arranensis (pl.XI,fig.46).

The trace in Stigmaria sewardi appears to sit on a stalk which is formed by tracheids diverging outwards from the main mass of outer xylem. These tracheids join the appendage trace in outward direction and are, in contrast to other Stigmaria species, separated from the vertically orientated tracheids by parenchymatous tissue (pl.VIII,fig.29) for some distance before they join the appendage trace

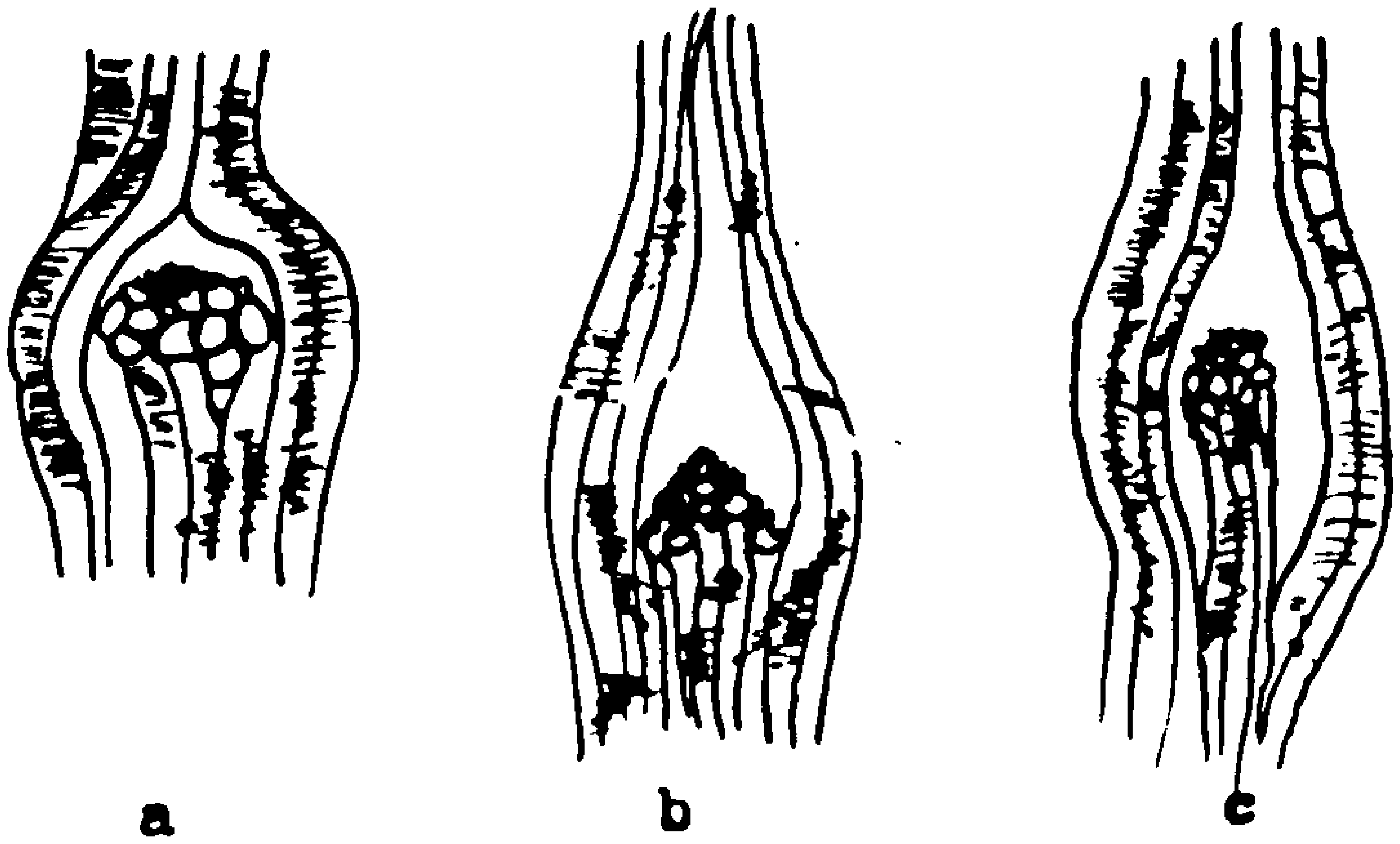


fig.9: Medullary Rays of Stigmaria in Tang.Section through outer Xylem

a) St.lohesti b) St.arranensis c) St.sewardi

The appendage traces pursue a slightly oblique course within the xylem but bend sharply upwards when they leave the outer xylem cylinder. There the exo-xylem and the secretory tissue (phloem) become attached to the appendage trace, which then passes out from the stele in a steep course. In transverse sections through the stele of the axis appendage traces are also cut almost transversely (pl.VIII,fig.30 and pl.IX,fig.31).

The first figure shows an appendage trace still within the secretory (phloem) zone.It can be observed that phloem tissue and exo-xylem is attached to the trace whilst on the protoxylem side of the appendage trace the vascular tissue is still surrounded by parenchyma of the medullary ray. The parenchyma of the medullary ray is continuous with the endo-xylem inside and the pericycle outside the xylem cylinder. In appendage traces in or outside the pericycle zone it can be observed in the tissue of the trace (pl.IX, fig.32) that the protoxylem is surrounded by tissue of the same arrangement and nature as the endo-xylem (p.52). The radial arrangement of cells around the protoxylem, produced by tensions set up in the tissues, is indicated by pl.IX, fig.32. The tissue on the side of the vascular strand of the trace shows some differences from the surrounding tissue, the pericycle. These cells, surrounding the vascular strand of the appendage trace may be compared with those of the medullary ray and are thought to be remnants of the medullary ray parenchyma,i.e. probably endo-xylem which is continuous with the exo-xylem.

In the description of Stigmaria arranensis it is mentioned that these cells surrounding the vascular strand of the appendage trace on all sides may in some instances be differentiated (p.100).

This leads to the conclusion that the xylem strand consisting of annular and scalariform tracheids is surrounded by undifferentiated vascular parenchyma. The difference between this undifferentiated parenchyma and the pericycle immediately outside it is well shown by pl.IX,fig.35 and page 181 ,fig.26. The latter figure depicts a transverse section through the vascular strand of a Stigmaria bacupensis appendage. The small cells of the endo- and exo-xylem and the large regular cells of the pericycle can be observed.

Most authors call the parenchyma surrounding the vascular strand, inner cortex. Whilst this may be true in some cases it is evident in Stigmaria sewardi that the parenchymatous tissue surrounding the xylem is comparable to the pericycle in pl.VIII,fig.30. The vascular strand is surrounded with this tissue before it passes out into the cortex as it is suggested by pl.IX,fig.31.

4)The Cortex:

The cortex of *Stigmaria sewardi* was not found completely preserved. In the slides mentioned only the external and internal secondary cortex (SE and SI) and the outer primary cortex are preserved. A superficial cortex is not differentiated in this species; the outer cortex consists of uniform tissue. The appendages are inserted in deep pits in this tissue but there is no evidence of an endogenous insertion. Towards the periphery of the preserved outer cortex the cells become gradually smaller in size. This zone may correspond to the superficial cortex observed in other species but no difference in the arrangement or structure of the tissues can be observed.

This uniform outer cortex of *Stigmaria sewardi* is similar to the corresponding region in *Stigmaria arranensis* from which *Stigmaria sewardi* differs, however, in the structure of the stele. Another Stigmaria found to have a uniform outer cortex is a specimen from Boonville/Indiana/USA. This specimen corresponds in many respects to the species under consideration, as will be described later, but has larger appendage bases.Therefore this Stigmaria is considered to be a variety, var. *boonvillensis* of *Stigmaria sewardi*. Another specimen, with a very small stele,had small appendage bases and is referred to as *Stigmaria sewardi* var. *minor* because in all other anatomical features it is identical with the described species.

The secondary cortex of *Stigmaria sewardi* is very little developed compared with that of *Stigmaria arranensis* although the former has the larger stele. The external secondary cortex is only ten to fifteen cells broad, the internal secondary cortex may reach a thickness of about 1 cm.

Remnants of the inner zone of the outer cortex (p2) are present on the inner side of the secondary cortex. Patches of middle cortex tissue can be observed in the empty space between cortex and stele but they are crushed and provide no evidence as to the structure of this tissue.

The cells of the inner secondary cortex are isodiametric in transverse and slightly elongated in longitudinal section. Pl.IX,fig.33, showing a longitudinal section through this zone, shows that some of these cells in the secondary cortex have annular thickening and thus resemble tracheids.

One zone of secretory ducts similar to those described in detail later in *Stigmaria arranensis* was observed in the internal secondary cortex of *Stigmaria sewardi*. So far this feature is concerned, *Stigmaria sewardi* is intermediate between its.var.*boonvillensis*, where there are no such secretory ducts in its relatively broad inner secondary cortex and *Stigmaria arranensis*, which has many zones of ducts.

5)Appendages:

The appendages of *Stigmaria sewardi*, found attached to the type specimen prove to be of a very simple structure especially as far as their cortex is concerned.

It has been mentioned that the appendages are inserted in deep pits in the outer cortex. An endogenous insertion as in *Stigmaria bacupensis* has not been observed but was probably, if present, not very deep in the cortex. The outermost layers of the cortex of *Stigmaria sewardi* do not seem to be preserved and so this question cannot be satisfactorily answered.

The specimens of *Stigmaria sewardi* fall into three size groups and on this basis three varieties have been named.

Stigmaria sewardi var. *minor* is an axis of small circumference.The xylem is little developed (p.52) and the appendage bases are small (diam. 6 mm).

Many specimens are known of *Stigmaria sewardi* var. *sewardi*. The xylem cylinder in this variety is well developed and in contrast to var.*minor* a relatively thick secondary cortex can be observed. The diameter of appendage bases is 8 mm.

One specimen is known of *Stigmaria sewardi* var. *boonvillensis* and unfortunately this specimen is without stele.A thick primary and secondary cortex is developed and the average diameter of appendages at their base is 12 mm.

A common feature of *St. sewardi* is that the vascular strand of the appendage trace dichotomizes whilst still in the cortex of the axis.Thus it may happen that appendage bases are sometimes in pairs with a short stretch of axial cortex left between them.

All three varieties show the middle cortex preserved in the appendage bases (pl.X,fig.41 and pl.XIII,fig.53). The tissue is similar to that in *Stigmaria arranensis.*

The vascular strand of the appendages frequently shows signs of a radial arrangement of scalariform tracheids.

Phloem tissue, as described by WEISS(1901), consisting of a few rounded thick-walled cells surrounded by parenchyma is present in appendage bases of several specimens.

The protoxylem, consisting of few annular tracheids, is usrrounded by small-celled parenchymatous tissue, the endo-xylem,which can be observed also on both sides of t the differentiated vascular strand adjacent to the protoxylem(pl.IX,fig.35).Annular tracheids can be observed branching off from the protoxylem but a trabecular bridge was never observed in an appendage attached to the *Stigmaria sewardi* axis.

The vascular strand is surrounded by parenchymatous tissue which appears to consist of an inner pericyclic region surrounded by a zone of inner cortex(pl.XXIV,fig.92). Frequently the border between pericycle and inner cortex is made conspicuous by black matter deposited between these two tissues but it does not seem possible to separate these tissues on histological differences except that the pericycle seems to consist of more uniform and smaller cells.

Middle cortex was not observed in the appendages but it is usually preserved in appendage bases and disappears at the point at which the appendage leaves the pit in the cortex of the axis. The structure of the middle cortex which is typical for this species, all its varieties and for *Stigmaria arranensis* will be discussed in the description of var. *boonvillensis*.

The outer cortex of the appendages consists of the four tissues common in Stigmarian appendages: Limiting layer,outer,inner and transition zones. The appearance of the outer cortex is uniform as described for the axis. The limiting layer is distinct,(pl.IX,fig.34) and consists of small cells slightly elongated in longitudinal direction.

This layer seems to be shed (p.87,fig.12) and replaced by the layer of cells underneath soon after the appendage leaves the cortex of the axis.The uniformity of the most peripheral tissue of the appendage cortex leaves the alternative that these tissues,i.e. the limiting layer and the layers of cells immediately underneath, may be a multiple epidermis and not, as described, part of the cortex (p. 132).

The three zones of the outer cortex show the same arrangement and type of cells although the diameter of the cells is small in the outer zone increasing in size towards the inner zone and decreasing again in the transition zone (p.154).The outer zone and the transition zone consist of thin-walled cells whilst the inner zone consists of thick-walled cells (pl.IX,fig.34).

As in the outer cortex of the axis the arrangement of cells is peculiar.Four to five larger cells are grouped around a cell of very small diameter. This small centre cell which is also shorter than the surrounding cells, is commonly filled with some brown substance.

Whilst the outer cortex near the appendage bases is relatively thick it becomes progressively thinner in the distal parts of the appendage . This seems to be due to a disintegration of the transition zone.

d)Stigmaria sewardi var.boonvillensis n.sp.n.var.:

Among a number of coal balls sent by Prof.H.N.Andrews of George Washington University,St.Louis/Mo.USA to the University of Glasgow early in 1953 was a section of a coal ball from Boonville/Indiana showing a Stigmarian cortex and very conspicouous large appendages attached to it.Peel sections of this Stigmaria showed a number of excellently preserved tissues in the cortex and appendages. Remains of the stele were unfortunately not found in our section of the coal ball. The Stigmaria proved to have the same cortical features as Stigmaria sewardi and was therefore considered to belong to this species but because of the larger dimensions of the appendage bases and the generally larger development I propose to call this form Stigmaria sewardi var.boonvillensis.

Anatomical Structure:

1)Cortex:

As in Stigmaria sewardi the outer cortex of this variety consists of uniform tissue. A superficial cortex and sclerotic elements are not differentiated.

The cells of the outer primary cortex (pl) are very large so that the structure of the tissue can be studied with a hand lens. The size of the cells is uniform in large parts of the tissue but the cells become gradually smaller towards the outside of the cortex in the zone which might correspond to the superficial cortex of other species. The appendages are inserted in deep pits in this cortex but no evidence of endogenous insertion was found.

A broad zone of external secondary cortex was found, similar to the corresponding zone in *Stigmaria arranensis*. The cells in this tissue are radially arranged and tangentially elongated. Growth has proceeded in such a way that the tangential diameter of the cells increases towards the inside and then decreases again until the original diameter is reached. This gives the secondary cortex the appearance as if being made up of lens-shaped units which consist of radially arranged cells of varying tangential diameter. These "lenses" may form a network or may also be separated by radial rows of isodiametric cells which are continuous with the isodiametric cells of the internal secondary cortex.

It seems important to mention that not all of the external secondary cortex is of this appearance. Between concentric zones of secondary tissue, zones of irregularly arranged primary tissues may occur which, however, show signs of dilatation. This indicates that secondary growth in the cortex of this Stigmaria was not initiated in and confined to one zone but started in two zones leaving a zone of primary tissue between.

In *Stigmaria arranensis*, however, the transition from external to internal secondary cortex is generally gradual. The number of radial rows consisting of isodiametric cells increases towards the inside of the cortex until finally only tissue consisting of isodiametric cells can be observed. It may be mentioned here that, whilst the bulk of the tissue in *Stigmaria arranensis* is made up of the internal secondary cortex, this tissue seems to be only little developed in *Stigmaria sewardi* var. *boonvillensis* but the external secondary cortex is very broad.

The internal secondary cortex in var.boonvillensis consists of isodiametric cells smaller than the average cortical cells, and the walls of these secondary cells appear to be thicker than those of the cells of the primary and external secondary cortex.

Cortical tissues other than those described, as middle or inner cortex, were not found preserved.

2)Appendage traces:

Pl.XIII,fig.52 shows an excellently preserved part of the cortex which clearly demonstrates the correlation which exists between the meristematic activity of the cortex and that of the appendage tissues. As was described in Stigmaria radiculosa,all the tissue surrounding the appendage trace, apparently including the pericycle, become meristematic when passing through the meristematic zones of the cortex, thus keeping pace with the radial expansion. For mechanical reasons we can therefore not assume that any vascular elements, apart from the protoxylem were differentiated during the period of meristematic activity in the external secondary cortex. It should be noted here that this mode of secondary growth of appendage traces occurs in the external secondary cortex. Appendage traces in the internal secondary cortex were hardly ever observed.

Appendage bases in St. sewardi var.boonvillensis show a feature which, though it was observed also in St.arranensis and the other varieties of St.sewardi, may be described here since it is best preserved in the specimen under consideration.

The middle cortex of the appendage trace,which can be seen in a state of meristematic activity and elongation of cells in pl.XIII,fig.52, terminates in rather elongated cells in the outer cortex of the axis as shown by pl.XIII, fig.53,bottom.Close investigation shows that these cells are very loosely connected and many intercellular spaces occur. These intercellular spaces gradually become more numerous as the appendage trace passes out through the outer cortex of the axis.

The base of the appendage is separated from the outer cortex of the axis by a mass of dark brown substance which apparently fills the intercellular spaces. The inner cortex in the appendages is filled the same way but the stele of the appendage passes without change through this "basal plate". Outside the basal plate of brown substance the middle cortex of the appendage forms a typical aerenchyma in which the cells are connected by arm like protuberances (pl.XIII,fig.53). This tissue,which resembles the parichnos of Lepidodendron, disintegrates in the more distal parts of the appendage where it leaves the pit in the outer cortex of the axis. This tearing of middle cortical tissue appears to be due to the considerable expansion of the outer cortex of the appendage in this region.

There can be little doubt that this middle cortical tissue served to keep up an exchange of air between appendage and axis, but in a certain stage, probably rather early,the connection was sealed by brown substance.

The middle cortex in form of this aerenchyma was only observed in Stigmaria arranensis and Stigmaria sewardi (all three varieties) and may serve as a guide for the identification of the species.A similar aerenchyma has been described from the roots of Isoetes australis (WILLIAMS,1943) which is, according to the same author also present in the root branchings of Isoetes lacustris, has been named by him "arm parenchyma".

It has been mentioned that dichotomies in the vascular strand of the appendages may occur in this species whilst the appendage is still within the cortex of the axis. Pl.X,fig.41 shows such a dichotomy of an appendage trace in the outer cortex of the axis, in transverse section. Inner cortex, the aerenchyma and remains of the basal plate can also be observed in this figure.

3)Appendages:

The appendages of St.sewardi var. boonvillensis are conspicuous by their large diameter. They are certainly the largest appendages reported and vary in size from 34 to 44 mm in circumference. Their outer cortex is made up of uniform tissue (p.85,fig.10 - 12). A limiting layer of cells can be recognized. Underneath this outermost layer is a zone of thin-walled tissue,in some cells of which tangential divisions could be observed. This occurs especially in layers of cells immediately underneath the epidermal layer when the latter shows signs of disintegration and seems to indicate that a new limiting layer is developed.

The size of the cells gradually increases towards the inside of the outer cortex (p.154), but the arrangement of the cells is the same in all parts of the cortex. A zone in which the cells are larger and have thicker walls can be described as inner zone and probably corresponds to a similar zone (thick walls and large cells) in the outer primary cortex of the axis.

The innermost part of the outer cortex, rarely observed, consists again of smaller, thinwalled cells.

Middle cortical tissue was not observed in appendages except in appendage bases, as already described.

The inner cortex, still recognizable in appendage bases seems to disappear along with the middle cortex and was not observed in free appendages. A dark brown layer around the stele, apparently consisting of disintegrated cell walls indicates the presence of the former inner cortex.

The vascular strand is surrounded by uniform parenchyma, the pericycle (pl.X, fig.39). Its cells are elongated with transverse end walls (pl.IX, fig.35) in contrast to the cells of the inner cortex the end walls of which are oblique. Previous authors have generally described the parenchyma surrounding the vascular strand as inner cortex but the course of the appendage traces in the stele of <u>Stigmaria sewardi</u> (p.71) showed that at least part of it must be considered to belong to the stele. Pl.X, fig.4o, a magnified part of the appendage trace in pl.X, fig.41 shows both tissues, inner cortex and pericycle, a slight difference in the arrangement of their cells being recognizable.

The vascular strand consists of parenchyma, annular and scalariform tracheids and the phloem elements. The phloem is shown in pl.X,fig.4o and seems to consist of a few thick-walled round cells surrounded by parenchymatous cells as described by WEISS(1901) for Lepidophloios fuliginosus. Unfortunately a longitudinal section of this tissue could not be obtained. In free appendages the phloem tissue has disappeared and only the remains of black cell walls can be found in this area (pl.X,fig.37).

Groups of annular tracheids at one corner of the triangular shaped vascular strand (pl.X,fig.37 - 4o) can be regarded as the protoxylem elements of the vascular strand. Some tracheids diverge from the protoxylem strand (pl.X,fig.38) and this feature may indicate the presence of a trabecular bridge although no such structure was observed in the appendages of St. sewardi var. boonvillensis.

The protoxylem is situated in parenchyma which extends on both sides of the vascular strand and is connected with the parenchyma separating the xylem from the phloem (pl.X, fig.38,39).This xylem parenchyma probably corresponds to the endo- and exo-xylem described in Stigmaria sewardi.
The differentiated xylem may consist of scalariform tracheids of different size and their arrangement leaves hardly any doubt that these tracheids are primary xylem (pl.X,fig.37 - 40). Pl.X,fig.38,39 shows radially arranged small tracheids in the area between xylem and phloem. These have been referred to as secondary xylem by most authors (SCOTT,1920).But this terminology leads to some misunderstanding as this xylem apparently does not plainly correspond to the so-called"secondary xylem" (the outer xylem) of the axis stele.

Pl.X,fig.37, shows primary parenchyma, irregularly arranged,between the primary xylem and the phloem and shows that this tissue is distinctly different in size from the primary xylem. In view of the structure of the appendage traces in <u>Stigmaria</u> <u>sewardi</u> it is assumed to represent the exo-xylem of the axis. Pl.X,fig.38 and 39 show that tracheids may be differentiated in this parenchyma from both radially arranged and primary tissue. The differentiation of the vascular tissues thus seems to follow a course comparable to that described in the axis and, as in the latter, some of the primary tissue is left undifferntiated. In this relict primary tissue secondary growth may occur as a result of cambiform divisions in some of the cells. Pl.X,fig.40 shows such dividing cells between phloem and xylem. Divisions and the subsequent secondary differentiation occur entirely irregularly as described for the exo-xylem of the axis (p.67) and SEWARD(1910), This irregularity is shown in pl.X,fig.37 - 39. The appendages figured were lying closely together in one coal ball and all have about the same circumference (42,40,41 mm). The vascular strands of these appendages which all belong to the same Stigmarian axis are also approximately equal in size. Nevertheless,they show very variable differentiation of the exo-xylem. It will be necessary to discuss this secondary growth of the vascular strands of appendages later in a comparative survey of the appendages (p.139).There may be mentioned here a specimen of <u>Stigmaria</u> <u>arranensis</u> (p.90) which shows both secondary growth of the exo-xylem of the axis and of the attached appendages and which suggests a connection between these two features.

fig.10: Outer Cortex of Appendage of Stigmaria sewardi
var. boonvillensis. Magn. 2
Ac-o.

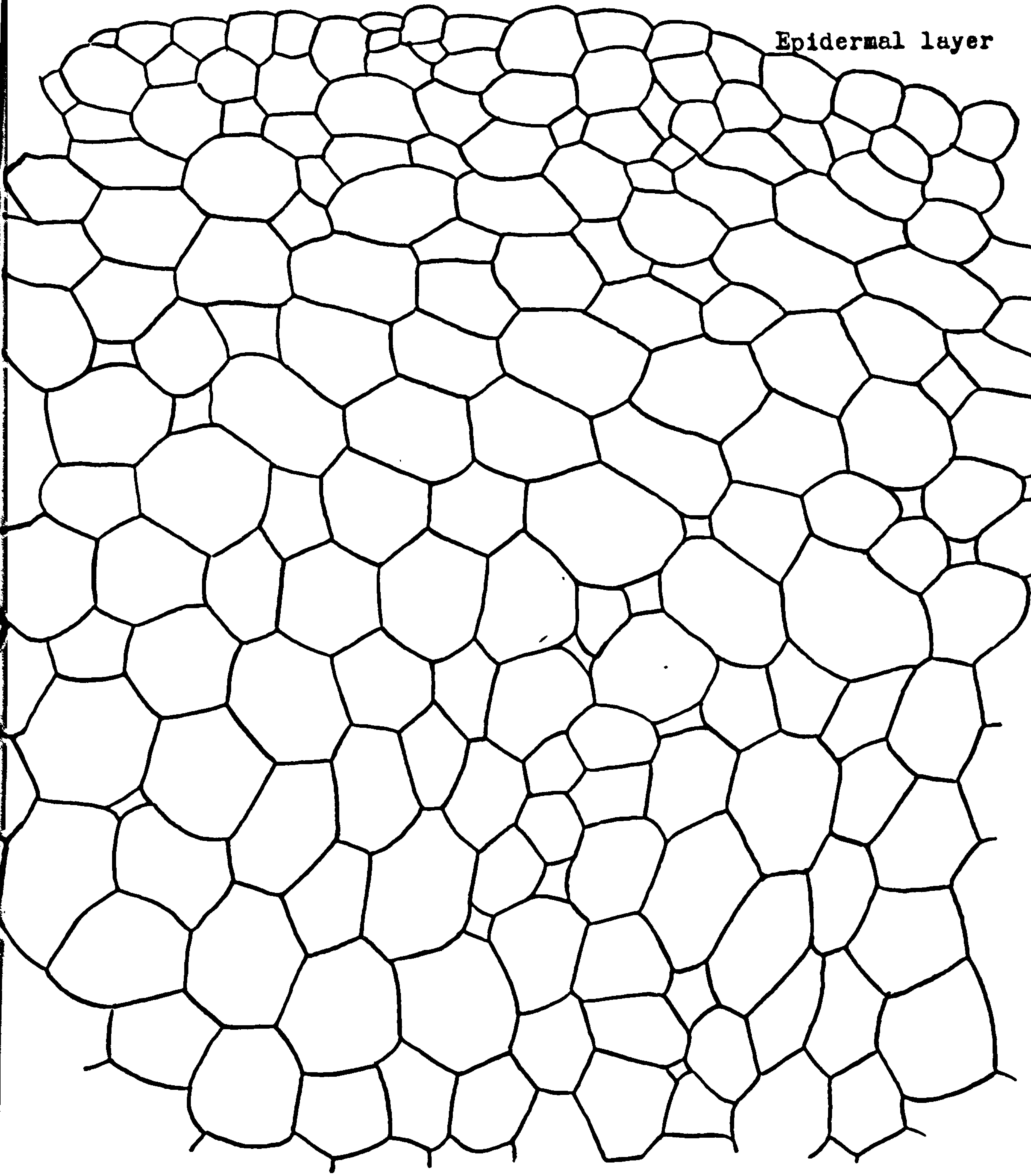


fig.10: Outer Cortex of Appendage of <u>Stigmaria sewardi</u> var. <u>boonvillensis</u>. Magn. 2

Ac-o.

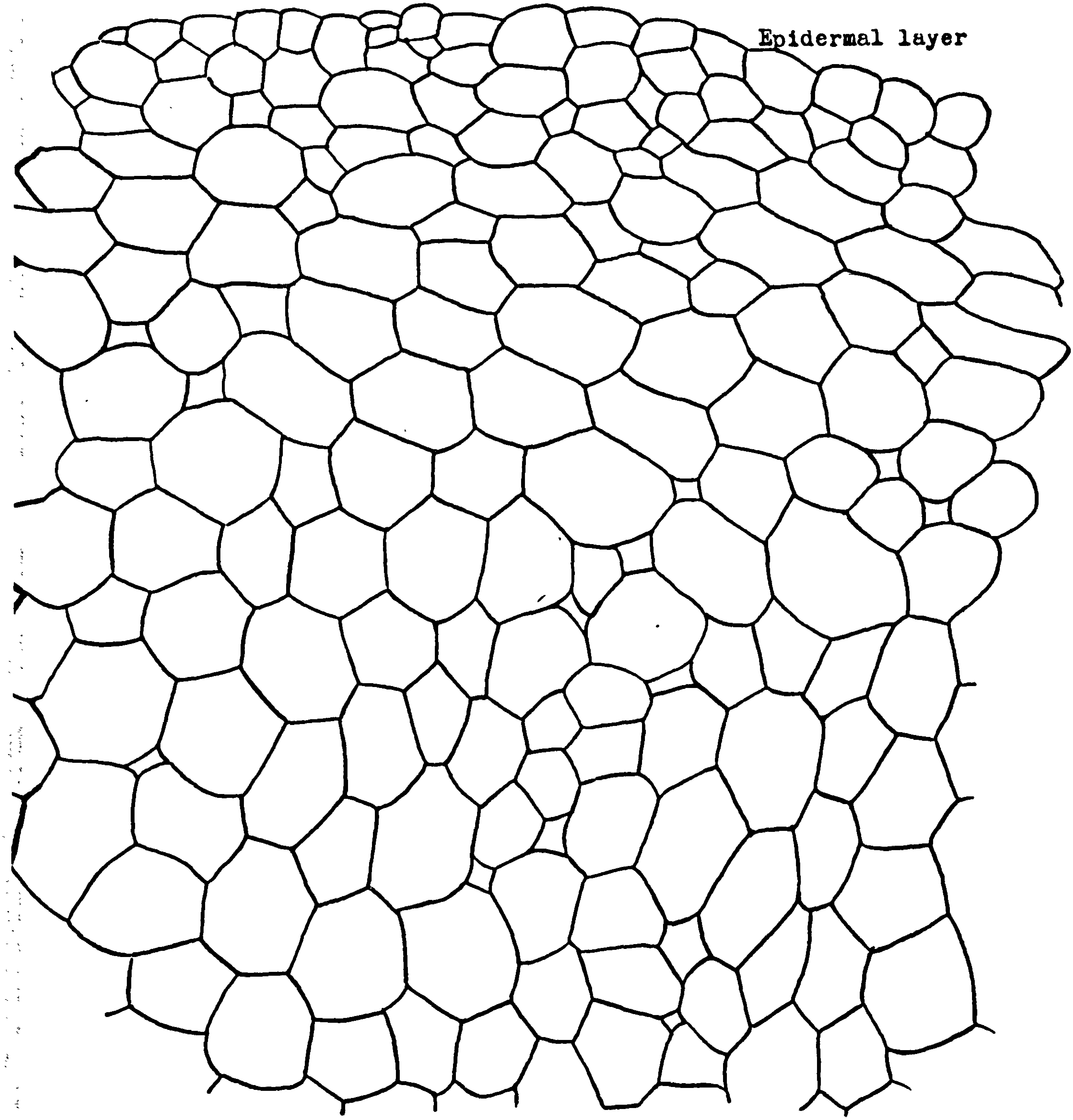
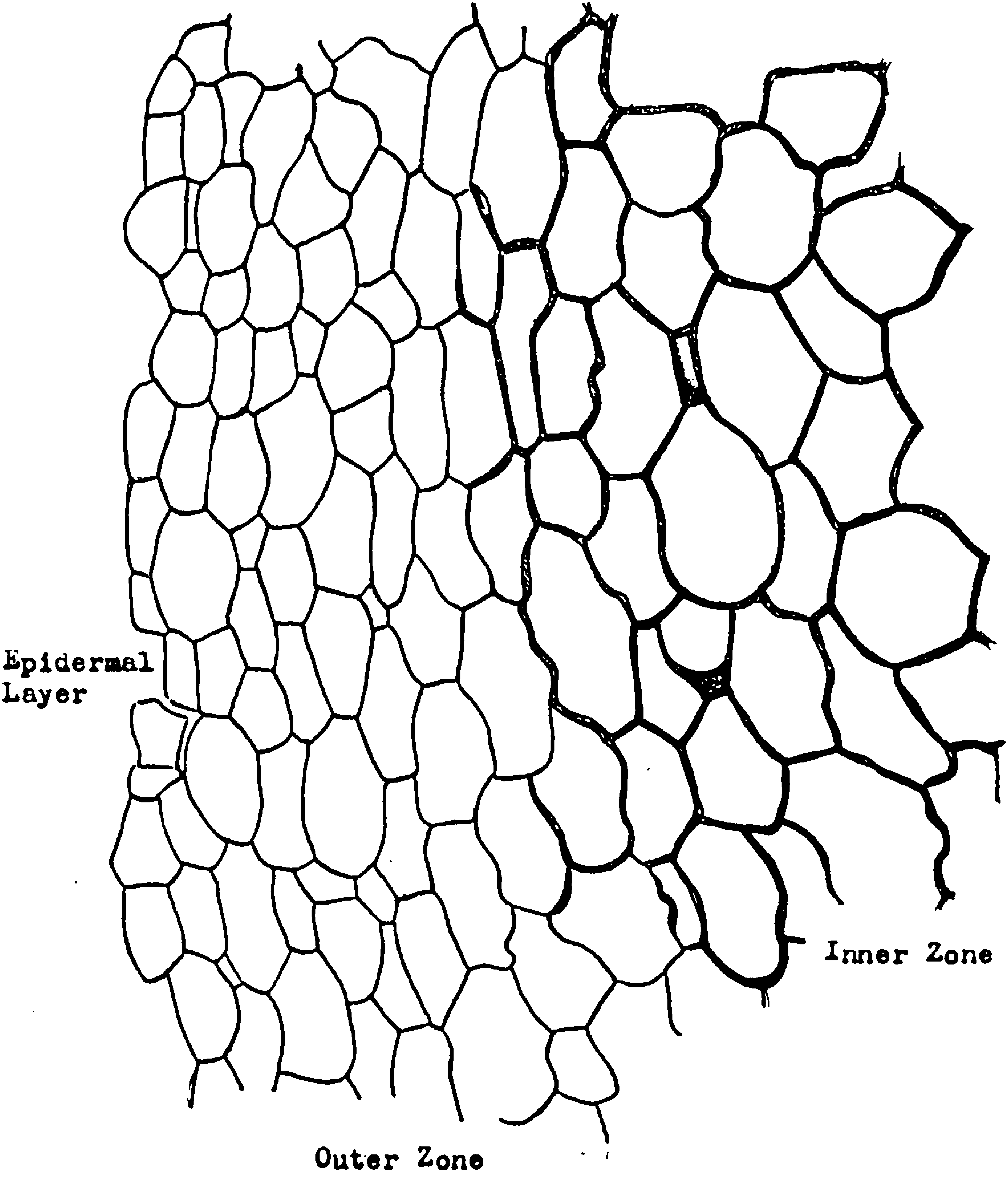


fig.11: Outer Cortex of Appendage of *Stigmaria sewardi* var. *boonvillensis*. Scale 2. Ac-6.



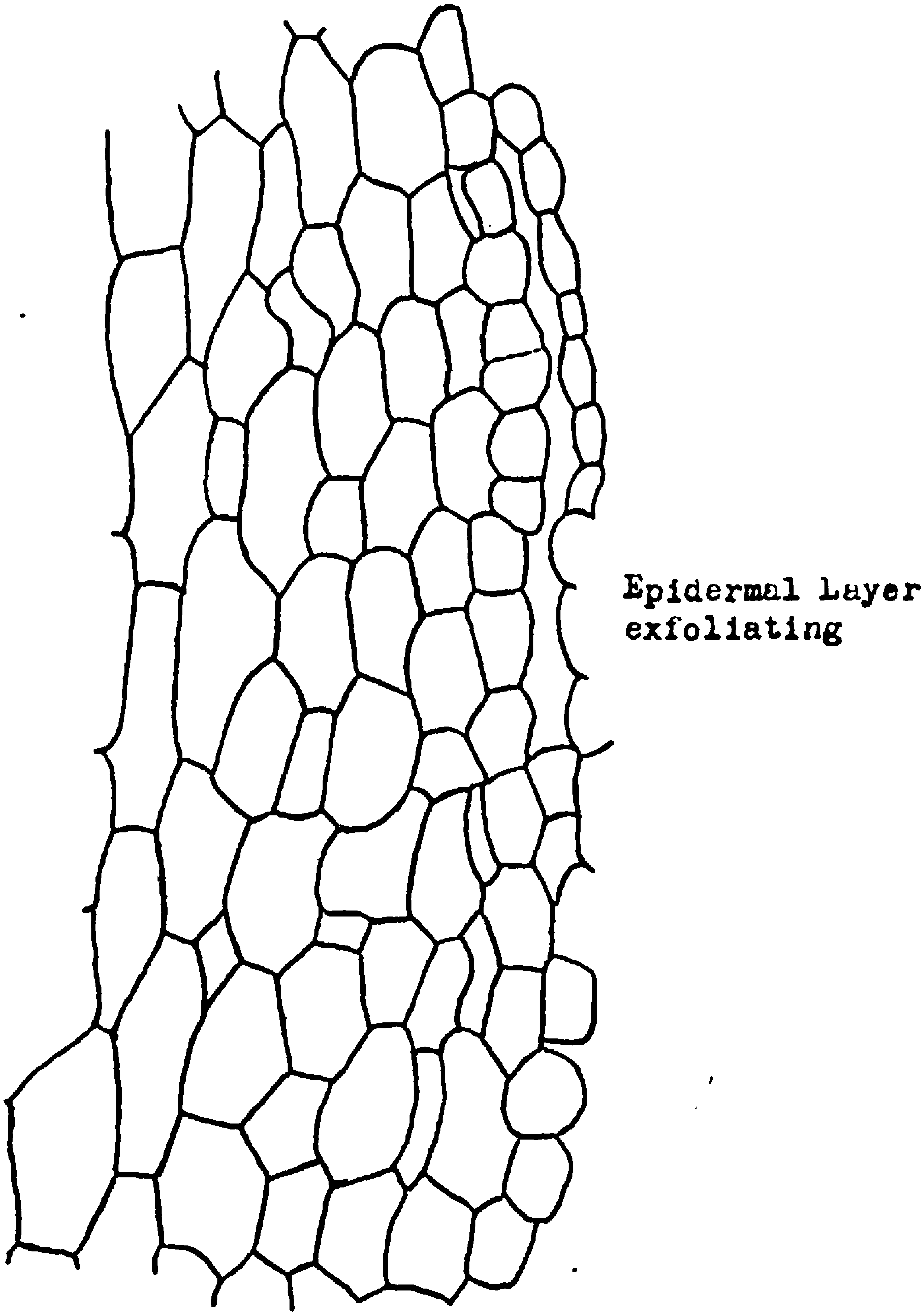


fig.12: Longitudinal section through Outer Cortex of Appendage of Stigmaria sewardi var. boonvillensis.

Scale 2. Ac-48.

e) Stigmaria arranensis, a new species from the lower Carboniferous of Scotland.

In the tree stumps which were discovered in the lower Carboniferous ash beds of the Isle of Arran (WÜNSCH,1865) structurally preserved Stigmariae,consisting of axes and attached appendages, were found by WALTON (1935). Prof.Walton figures and mentions these Stigmariae in his memoir on the "Arran trees" but the specimens have never been described in detail. A description of them seemed desirable because the Stigmariae show, apart from some well preserved tissues, certain features which place these specimens in a new species. Sections of the species are in the Glasgow Class Coll. and in Prof.Walton's own collection of slides. In addition, peel sections of slabs of the Arran trees, now in the Hunterian Museum and Botany Dept. University of Glasgow were studied.

The Stigmariae were of varying size and show different stages of development. The smallest Stigmarian axis observed had a xylem cylinder of 8 x 3 mm diameter (maximal thickness of xylem 1 mm). The xylem cylinder of the largest axis observed was 29 x 19 mm (thickness of xylem 9 mm). Appendages of the species are relatively large and are numerous within the "Arran trees".

The basal parts of the tree stumps have never been observed and the Stigmariae preserved were, as WALTON (1935) suggested, probably the basal organs of plants from a higher plant bed. Stigmaria arranensis, however, shows considerable affinities with the Arran trees, Lepidophloios wünschianus, and it seems possible that Stigmaria arranensis and Lepidophloios wünschianus are parts of one plant species.

Anatomical Structure:

1) Stele:

The pith is preserved in one specimen (pl.XI, fig.42,44); the medullary tissue, consisting of rather large cells of uniform size. Longitudinal sections show the arrangement of the pith cells in rows (pl.XI, fig.44). The pith is surrounded by a zone in which the cells are smaller and have thinner walls, the endo-xylem. Whilst the pith has intercellular spaces, these are absent in the endo-xylem. The endo-xylem shows great uniformity with the innermost zone of the wedges of outer xylem. Annular tracheids may occur between the endo-xylem and the differentiated outer xylem, but are rarely observed.

The cylinder of outer xylem is usually split into about 16 wedges by the appendage traces. This number is conspicuously lower than that in other Stigmariae in which the number is usually around 30 wedges.

The innermost zone of these wedges consists of rather irregularly arranged tracheids and in this type of preservation, it is, as mentioned, difficult to distinguish it from the endo-xylem. This zone of irregularly arranged tracheids then passes gradually in an outward direction into the zone of radially arranged tracheids (pl.XI, fig.42). The xylem wedges are deeply split by a large number of secondary medullary rays which, from one to a few cells high, can be observed in pl.XII, fig.47.

The exo-xylem, small celled tissue, consists of parenchymatous cells and tracheids. Little or no meristematic activity could be observed in the exo-xylem of the examined specimens. The cells of the exo-xylem are of the same size as those of the endo-xylem (pl.XI, fig.43).

The phloem zone shows patches of large celled tissue in transverse section. The diameter of the cells is the same as that of the tracheids of the outer xylem. No sign of disintegration of cell walls could be observed in transverse sections. The phloem tissue in this specimen (pl.XI,fig.43) has therefore much the same appearance as that of Lepidophloios fuliginosus, described by WEISS (1901). The end walls of the "phloem cells" seem to have broken down easily thus forming long canals as they are described by WALTON (1953). Parenchymatous tissue outside the phloem, consisting of cells of the same size as those of the endo-xylem, indicates the presence of a pericycle.

Appendage traces immediately outside the xylem cylinder consist of a few annular tracheids at the protoxylem corner whilst the main part of the vascular tissue consists of radially arranged, scalariform tracheids(pl.XI,fig.45). Some of the larger specimens of Stigmaria arranensis show the development of small radially arranged tracheids on the periphery of the xylem cylinder (pl.XI,fig.45). These, corresponding to the irregularities in growth described in Stigmaria sewardi, were considered to be signs of approaching death (WILLIAMSON,1896). Their probable nature is explained in the description of Stigmaria sewardi. A feature of interest is, that in a specimen showing these "irregularities" on the periphery of the outer xylem all the appendage traces outside the xylem show the same feature, viz. rows of small radially arranged tracheids abutting on large radially arranged tracheids. Furthermore, most of the appendages found attached to this specimen show radial rows of small tracheids adjoining the xylem strand on the side opposite to the protoxylem (p.102,fig.17).

The medullary rays in Stigmaria arranensis are slender and show a triangular vascular strand in them. The appendage trace appears to consist of radially arranged xylem only (pl.XI,fig.46,pl.XII,fig.47).

2)Cortex:

The development of the cortex is very similar to that of the Stigmaria radiculosa type specimen. The cortical tissue, which is preserved from the stele to the appendage bases, shows, however, more marked secondary developments than are shown in Stigmaria radiculosa, a fact which may be correlated with the smaller development of the outer xylem in the latter. The inner cortex is preserved in patches around the stele. As in Stigmaria radiculosa, the tissue is partly differentiated into middle cortex but the remains of the cell walls of the primary cells can still be recognized(p.43).

The middle cortex consists of hyphal tissue such as has often been described in the cortex of Lepidodendron and Stigmaria (pl.XII,fig.50).This tissue can be observed in a state of meristematic activity in some areas. Appendage traces in this zone seem to pursue a course almost parallel to the axis as they are all cut in transverse section in a transverse section through the axis.

The connection between middle and outer cortex could not be observed. It seems, however, that the middle cortex was not very wide and was narrower than in Stigmaria radiculosa. The inside of the outer cortex is defined by irregularly arranged parenchymatous tissue, the inner zone of the outer primary cortex (p2). Secretory ducts, as those described from Stigmaria radiculosa (p.44) are present (pl.XII,fig.48, fig.49). Towards the outside of the cortex, the cells become more radially arranged, smaller, and of uniform size. This tissue may then be called the internal secondary cortex.

Intercellular spaces are very common in the secondary cortex, as in the cortex of Lepidophloios wünschianus (WALTON,1935), but the thickening of the radial walls of these cells, as described by the same author, was not observed, only in a few radial rows an indication of it is recognizable. A section in the D.H.Scott Coll (No.112, no locality given, but probably a section of a coal ball) shows the same stele as Stigmaria arranensis and might belong to this species. Only the inner zone of the primary cortex and the internal secondary cortex are preserved. The inner zone of the primary cortex is, however, very well preserved and shows, that this tissue persists with the secretory ducts in it even after extensive secondary growth(pl.XII,fig.48).

Some of the cells of the internal secondary cortex of this specimen also show the thickening of radial walls (WALTON,1935) and it may be mentioned here that the secretory ducts in it are frequently accompanied by tracheids (pl.XII,fig.49).

The secretory ducts in the internal secondary cortex of Stigmaria arranensis form almost continuous concentric rings, equally spaced. In the small specimen described, only few rings were observed but in the larger specimens the internal secondary cortex makes up the bulk of the cortical tissue and up to ten concentric rings of secretory ducts were counted. The average distance between two rings is 2 mm.

The secretory ducts (pl.XIII,fig.51a) have the same appearance as those figured in the inner primary cortex of Stigmaria radiculosa and probably arose in the same way i.e. by differentiation of certain groups of cells. In longitudinal section they resemble the ducts of Stigmaria vulgaris the only other species so far known to posess a broad zone of internal secondary cortex, and were probably of the same nature.

The cells of the internal secondary cortex are elongated longitudinally, correspond to the cells described in Stigmaria vulgaris and have the same shape as the cells figured there (pl.XVI,fig.64).

In large specimens with a thick internal secondary cortex, the inner zone of the primary cortex is often missing but the cells of the secondary cortex become larger in diameter towards the inside, thus indicating that the inner zone of the primary cortex was present there, although it has not been preserved.

The external secondary cortex of Stigmaria arranensis is not very thick. It consists, as mentioned in the description of Stigmaria sewardi var. boonvillensis, of tangentially stretched cells of varying diameter (pl.XIII,fig.51). The tangential diameter increases in one radial row of cells gradually towards the inside of the cortex until a maximum width is reached and then decreases again. Thus lens-shaped tissue groups are formed which interlace with each other. They probably result from tangential stresses on the cells during meristematic activity. Radial rows of uniform cells, whose dimensions are similar to those of the internal secondary cortex, may occur between groups of lenses . We thus get some more evidence from Stigmaria arranensis as to the mode of secondary growth in the cortex.

We can hardly speak of a phellogen, as many authors do, because meristematic activity occurred everywhere in the region in which the secondary growth is now found. Secondary growth in the cortical tissue must have led to considerable stresses in the outer parts of the cortex.

These stresses were equalized in the outer parts of the secondary cortex by the tangential stretching of certain cell groups while radial division of cells in the outer primary cortex seems to indicate that this tissue equalized the stresses by production of additional cells.Secondary thickening of cell walls seems to have occurred in a late stage of growth and to have only affected the cells of the internal secondary cortex and the radial rows of cells of equal size in the external secondary cortex. Thus the external secondary cortex has an outline like a cog-wheel, the spaces between the cogs being occupied by tangentially stretched cells. Thus the internal secondary cortex appears to have the same outline as the secondary phloem in modern plants with cambial growth.

It seems necessary to mention here some further observations. As described and figured, remains of the inner zone of the outer cortex were observed in *Stigmaria arranensis* and in another specimen. We can assume from the uniform structure of the outer and the inner zone of the primary cortex that as in *Stigmaria radiculosa* these regions are parts of the originally homogenous primary cortex which were later separated by the development of secondary tissue.

The inner zone shows a clear transition from irregularly arranged cells (pl.XII,fig.48,lower side) into radially arranged cells(pl.XII,fig.48,upper side) of the inner secondary cortex. The small elongated cells of the inner secondary cortex are probably the product of normal secondary growth and show no sign of tangential stretching, characteristic of the external secondary cortex. The tangential stretching may, in fact, be regarded as a sign of dilatation and the external secondary cortex as a zone of dilatation.

The outer zone of the outer primary cortex consists of isodiametric cells of uniform size. In this zone cells can be observed in an initial stage of meristematic activity and it seems apparent in fig.51,pl.XIII, that, as in Stigmaria radiculosa, cells divide in radial rows by means of tangential cell walls and that consequently one lens-shaped tissue unit in the external secondary cortex ,consisting of radially arranged cells of varying diameter, correspond to one original cell of the primary cortex, The extremely wide tangential diameters of the cells in the external secondary cortex are caused by the tangential stresses originating during continuation of growth on the inside of the secondary cortex, thus forcing the outer zone, in which meristematic growth has occurred earlier, to expand.

Summarizing the secondary growth in the cortex of Stigmaria arranensis it can be said:

1. Meristematic growth must have occurred at a very early stage. The stele may be little developed but the secondary cortex is very thick.
2. Growth seems to have occurred in two successive stages; in the initial stage the external secondary cortex was produced which was then dilatated in the second stage in which the internal secondary cortex grew. Both stages, however, are probably part of a single continuous process of secondary growth.
3. The tissues of the external secondary cortex are dilatated and not produced in the shape they can now be observed in.

A superficial cortex is not differentiated in Stigmaria arranensis and sclerotic elements were not observed. Towards the outside, the cells of the primary outer cortex are smaller and have thinner walls. These may, as in Stigmaria sewardi, correspond to the superficial cortex. Appendage bases are inserted in deep pits in the outer cortex but an endogenous insertion is not observed. The structure of the appendage traces in the secondary cortex is the same as described in Stigmaria sewardi var. boonvillensis, the stele and middle cortex of the trace showing elongation of the cells and meristematic activity to keep pace with the radial expansion of the cortex.

3)Appendages:

The appendages of St.arranensis are rather large. The largest reach the size of those of the Boonville specimens (p. 81) although on the average they are of the same size as the appendages of Stigmaria sewardi var. sewardi. The structure of appendages coming from one axis is far from uniform. How much the structure of the outer cortex can vary is illustrated on p.97 - 99, figs.13 - 16.

Whilst the division of the outer cortex into outer, inner and transition zones can be recognized in most appendages it is not clear whether all appendages originally possessed a limiting layer. This layer could be observed in some appendages (fig.13,15,16) but was absent, possibly exfoliated, in others.

The outer zone consists of cells, slightly smaller and thin-walled but of the same arrangement as in the inner zone. Different thickenings may occur in the inner zone.

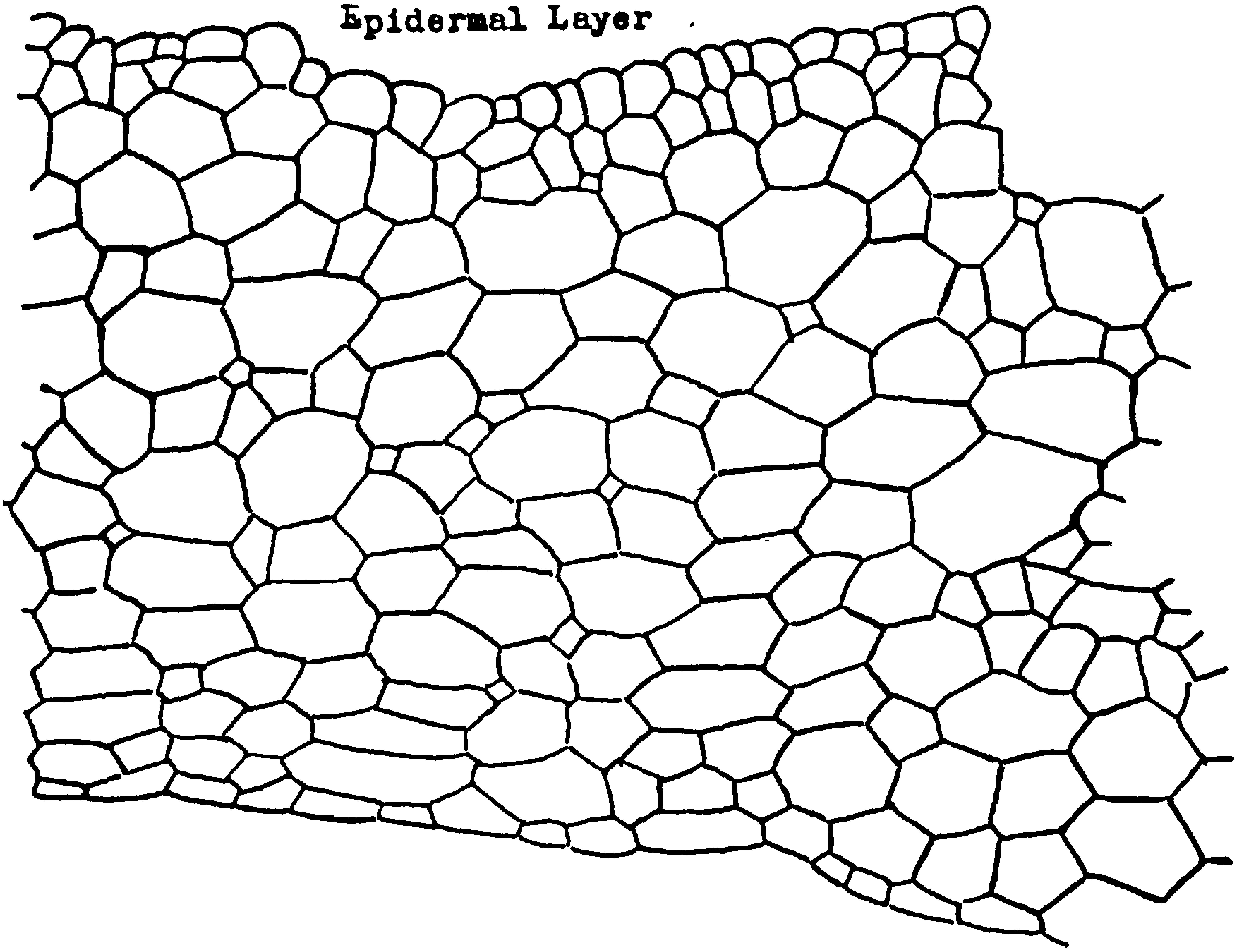


fig.13: Tv.S. through Outer Cortex of Appendage of *Stigmaria arranensis*. Magn. 2. Ac-4o.

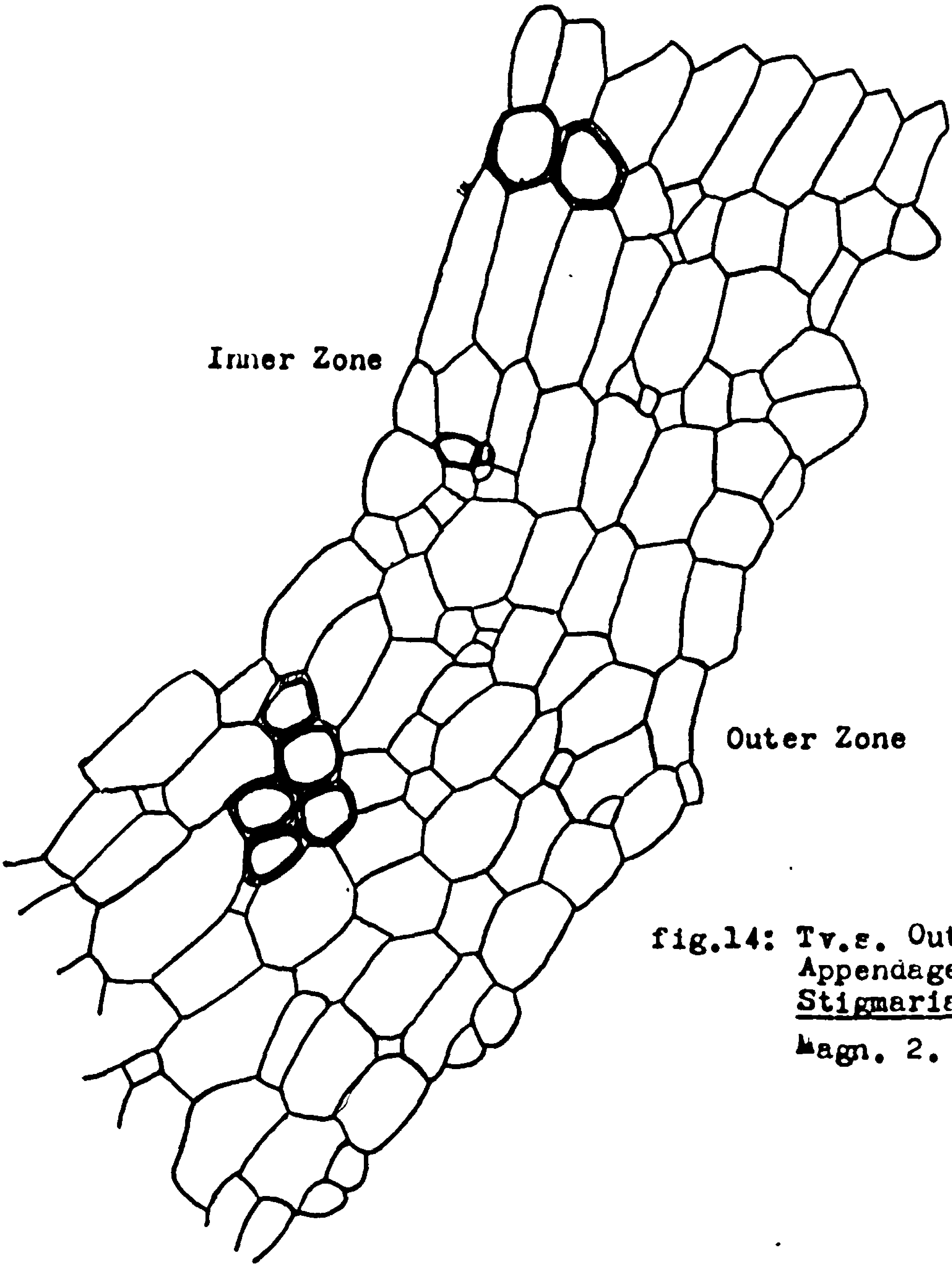


fig.14: Tv.s. Outer Cortex of Appendage of *Stigmaria arranensis*.
Magn. 2. Ac-42

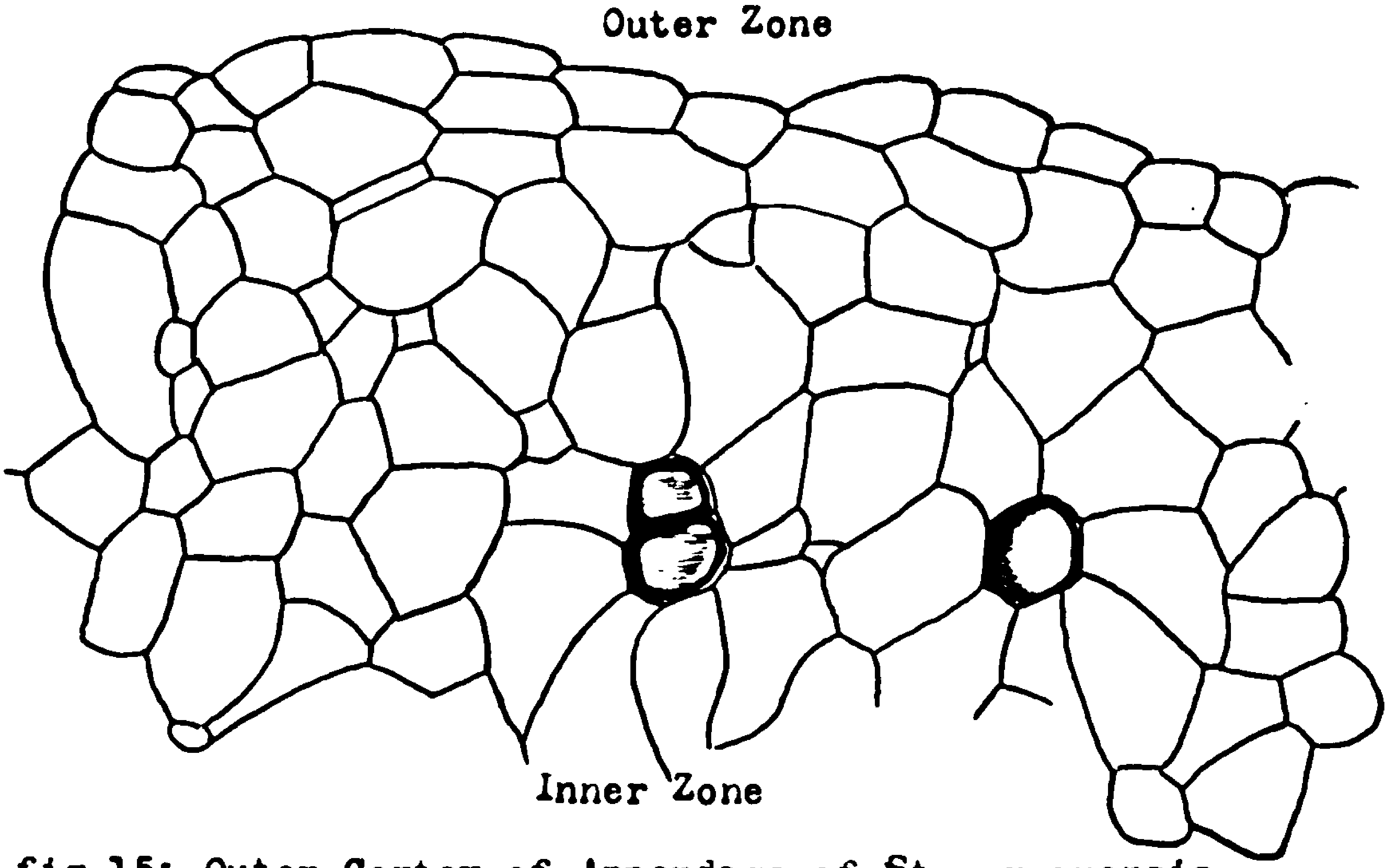


fig.15: Outer Cortex of Appendage of *St. arranensis*.
Scale 2. Ac-31

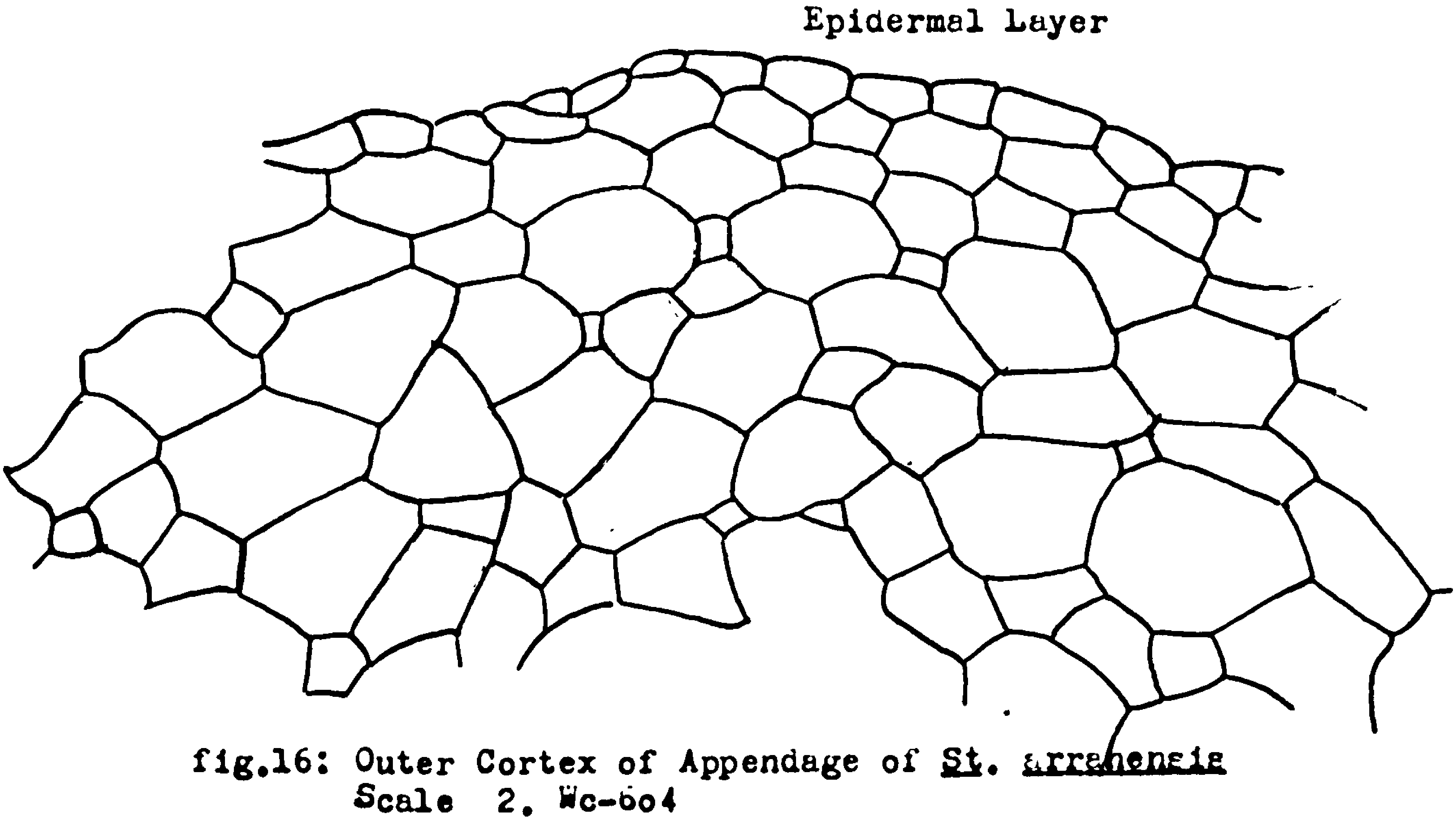


fig.16: Outer Cortex of Appendage of *St. arranensis*
Scale 2. Wc-604

Whilst in some appendages isodiametric cells are thickened and the cells in between stretched (p.98,fig.14) in other appendages of the same axis all of the cells of this zone are thickened, or as in some instances, no thickening may occur at all. The innermost or transition zone, where it is preserved, often shows signs of slight meristematic activity. The middle cortex is preserved in the appendage bases only, where it consists of a very loose parenchyma in which the cells are connected by arm-like protuberances just like it is described and figured for Stigmaria sewardi var. boonvillensis (p.81,pl.XIII,fig.53).

The pericycle may vary strikingly in thickness, being from 3 to 10 cells deep in the radial direction. Some of the tissue might belong to the inner cortex but the deposition of some dark matter around it rather suggests that the parenchymatous ring ensheathing the vascular strand is part of the stele. Of the vascular strand only the xylem part is preserved. The central part of the xylem does not differ in any way from that seen in other Stigmariae, especially Stigmaria sewardi, but it can be observed that around these large scalariform tracheids small tracheids are frequently differentiated(pl.XIV,fig.54,55). These tracheids probably are differentiated from the parenchyma described as endo- and exo-xylem in Stigmaria sewardi but these parenchymatous tissues are unfortunately not preserved in appendages of Stigmaria arranensis.

Secondary growth in the exo-xylem is very common in the appendages and can reach considerable extent(p.102,fig.17).

It has already been mentioned (p.90) in relation to that specimen of Stigmaria arranensis, which shows irregular growth at the periphery of the outer xylem of the axis, that the majority of the appendages borne by it also show secondary development of their exo-xylem. It may be concluded therefore that a revival of meristematic activity took place in the exo-xylem of both appendages and axis after the outer xylem of the axis and the xylem strand of the appendage were differentiated.

The protoxylem of the appendages may be of variable arrangement. Annular tracheids may be arranged in groups at one corner of the vascular strand from which a radial band of tracheids extends through the pericycle (pl.XIV, fig.54,55). In some instances (pl.XIV,fig.55) the tracheids appear to be disconnected and surrounded by cells of the pericycle, but their arrangement in line can still be demonstrated and it seems likely that these tracheids are connected with each other in longitudinal direction. These tracheids seem to constitute the connection with the so called trabecular bridges of other appendage species (p.151) but such trabecular bridges connecting stele and cortex have not been seen in the appendages of Stigmaria arranensis. Between the cortex and stele, however, tracheids can be observed (pl.XIV,fig.56) which are surrounded by four or five parenchymatous cells and thus form miniature steles branching off the stele of the appendage.

Tracheids in the cortex of the appendages are observed in one specimen only (pl.XIV,fig.56) and are situated in the transition zone.

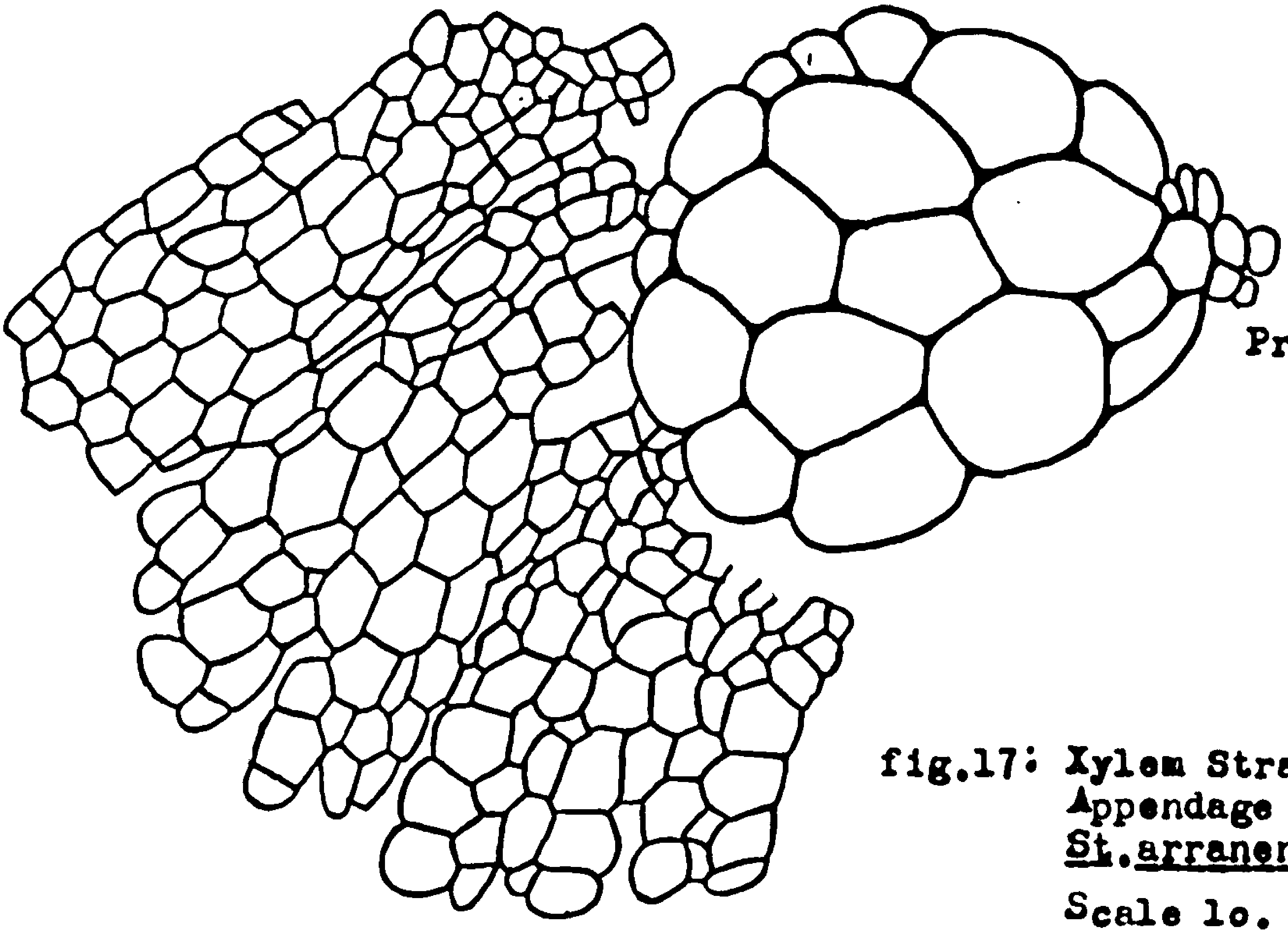
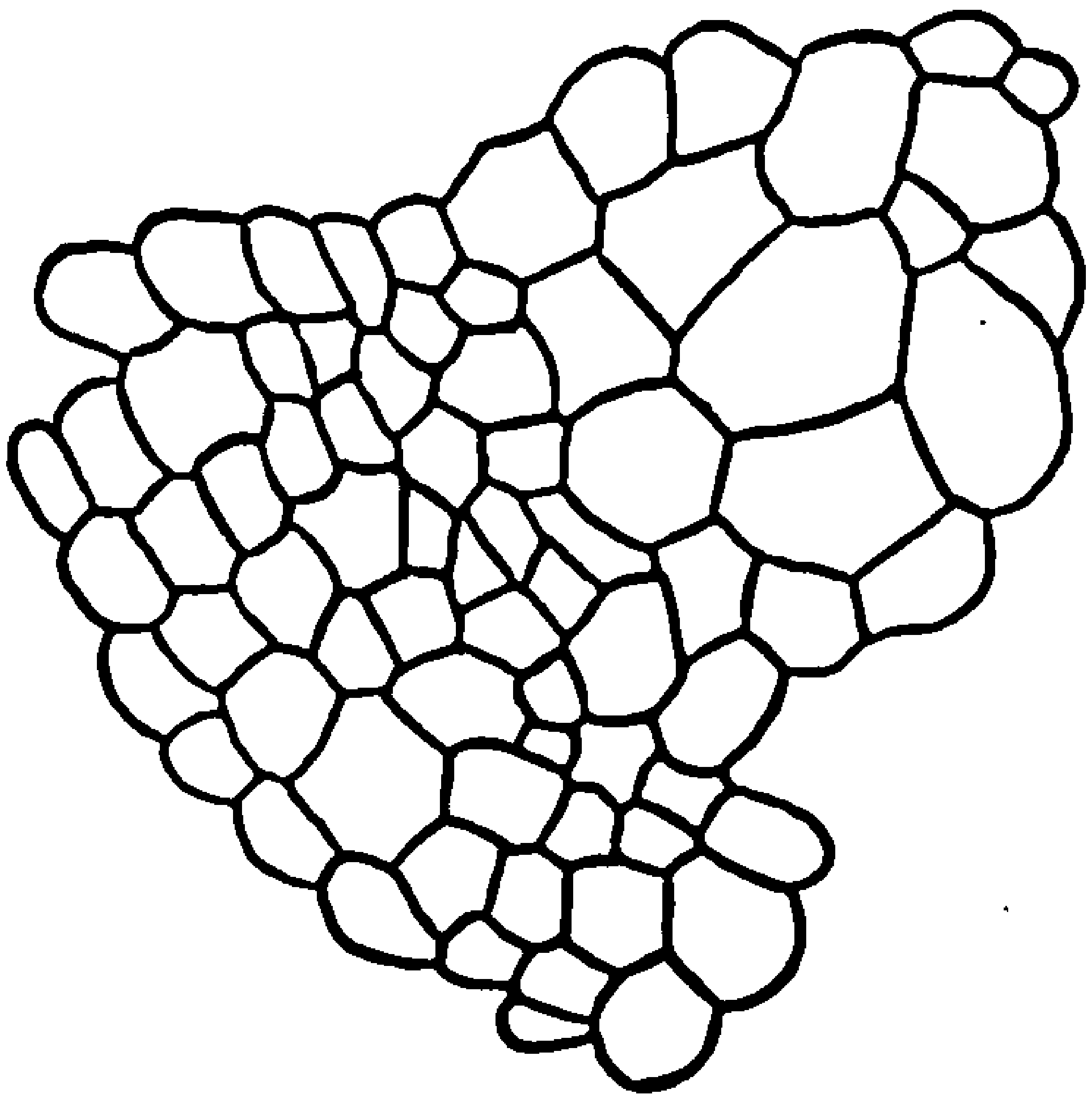


fig.17: Xylem Strand of Appendage of <u>St.arranensis</u>.
Scale 10. Wc-604

fig.18: Xylem Strand of Appendage of <u>Stigmaria pettycurensis</u>.
Scale 10. Kc-545 N.



f) Stigmaria pettycurensis Scott:

The species was named by SCOTT but never described. SCOTT who had several specimens of this species in his collection from Pettyour,Fife (Lower Carboniferous / Calciferous Sandstone Series) mentioned in his notebook (No.XVIII,p-111):
"The Stigmaria is a large axis, trans. about 45 x 16 mm with a thin layer of cortex. Pith obliterated. Wood appears wholly centrifugal and secondary. Medullary rays narrow. Cortex much crushed, apparently outer cortex best preserved. Embedded in the cortex are a number of rootlet bundles, sometimes with secondary xylem".

The Kidston collection contains other slides of the species in the same state of preservation. These are described here. The species presents in some respects an intermediate stage between the undifferentiated outer cortex of Stigmaria sewardi - Stigmaria arranensis and the simple differentiation of Stigmaria radiculosa but shows more affinities with Stigmaria radiculosa.

Anatomical Structure:

1) Stele:

Of the stelar tissues only the outer xylem is preserved. The tracheids in this tissue are radially arranged throughout,no irregular arrangement being observed within the xylem wedges. The outer xylem is split by the appendage traces into 38 - 40 narrow wedges.

The xylem cylinder of the specimens in the Kidston Coll. have average diameters of 50 x 25 mm and are therefore larger than the Scott specimens. The maximal radial length of the xylem wedges measured was 14 mm. The medullary cavity, the differentiation of only the outer xylem and the fact that this is split into numerous wedges places this Stigmaria with the ficoides type.

Appendage traces immediately outside the xylem cylinder show irregularly arranged tracheids of very small diameter at the protoxylem corner. Outside this are a few irregularly arranged tracheids of larger diameter but the major part of the tissue consists of radially arranged tracheids. The medullary rays were found to be broad and high, compared with those of Stigmaria sewardi but the appendage traces in them are shorter and narrower. Very few secondary medullary rays were observed in Stigmaria pettycurensis and these are not more than one cell high.

2) Cortex:

Of the cortical tissue only the outer primary cortex and the superficial cortex were found preserved. The outer primary cortex consists, as usual, of isodiametric cells of uniform size and arrangement. Between outer cortex and stele patches of tissue with radially arranged and small cells can be observed, which were possibly part of the internal secondary cortex.

Towards the outside of the outer cortex the diameter of the cells decreases. In this tissue some of the cells are filled with dark substance, but the distribution of this substance is very irregular.

These dark cells may represent the sclerotic elements of other Stigmariae and for some stretches in the outer cortex of Stigmaria pettycurensis where more of these dark elements are present they resemble the sclerotic band of Stigmaria radiculosa.

3)Appendages:

Appendage bases and appendages were found attached to this Stigmaria and prove, except for minor differences, to be of the same structure as those of Stigmaria radiculosa. The outer cortex can be divided into four zones, the limiting layer,outer,inner and transition zone. The outer zone and epidermal layer is preserved in all appendages. The inner zone, broad at the base of the appendages and consisting of thick-walled dark brown cells thins out and disappears at some distance from the appendage base. This however is not, as in Stigmaria asteroidea (p.119) due to the disintegration of the inner zone for it seems that only the thickening of the walls disappears in the inner zone of the appendage which then consists of uniform tissue. In some appendages, however, a few blackened cells can be observed, separating the outer from the inner zone, just as the superficial cortex is separated from the outer cortex of the axis. The middle cortex is preserved only in the appendage bases and consists of loose parenchyma of the same type as described for Stigmaria radiculosa (pl.VII,fig.25,26).The middle cortex is separated from the outer cortex by a band of parenchyma which may consist of one or of a few layers of cells, the transition zone.

Towards the inside, the middle cortex merges with the inner cortex which has the same structure as the transition region and is likewise preserved only in appendage bases. The inner cortex is separated from the pericycle by a layer of cells filled with dark substance. The pericycle is three to five layers of cells wide and, as seen in longitudinal section, these layers have elongated cells with horizontal end-walls.

Of the vascular tissues only the xylem strand is preserved. This consists of a group of annular tracheids (protoxylem) a few irregularly arranged tracheids and a large bulk of radially arranged tissue (p.102,fig.18). In some appendages there are indications of endo-xylem.

An appendage base similar to those described from Stigmaria pettycurensis was found in a section of a coal ball from Langendreer, Westfalia, Germany (pl.XXI,fig.81).

g) Stigmaria vulgaris, a new species common in the English Coal Ball Flora:

The species described in this chapter is, judging from the number of specimens in the various collections examined, the most common type in the English coal ball flora. It shows affinities with both Stigmaria radiculosa and Stigmaria asteroidea and combines features of both species in its superficial cortex, i.e. it shows the sclerotic band of Stigmaria radiculosa plus the sclerotic strands of Stigmaria asteroidea. The outer cortex of the smallest specimen studied shows about the same circumference as that of Stigmaria radiculosa type specimen (12o to 14o mm) but the stele is much larger than in the latter species. The medullary cavity, however, is generally smaller or of the same size as that of the St. radiculosa type specimen. On the other hand the stele of this species is smaller than in specimens of St. asteroidea with approximately the same cortical circumference and the xylem wedges of the latter species are much broader. 30 xylem wedges are observed in average transverse sections of Stigmaria vulgaris. Because of its common occurrence in the English coal ball flora I propose the name Stigmaria vulgaris.

Anatomical Structure:

1) Stele:

Only the xylem is preserved of the stelar tissues. The medullary cavity is small and in none of the studied specimens does it exceed 1 x 5 mm diameter. The average diameters observed were 1 x 3 mm. In the medullary cavity patches of thin-walled tissue can be observed which in some parts are in organic connection with the xylem and appear to be remains of the medullary tissue. This tissue apparently consisted of cells of uniform size, having the same diameter as the innermost elements of the xylem. Some cells of this tissue appear to have had annular thickening.

The xylem consists of radially arranged, scalariform tracheids throughout. It is most striking in this species that practically no irregularly arranged tracheids at all are present on the inside of the wedges. The tracheids on the inside of the wedges are, however, of very small diameter and are similar in size to the few annular tracheids between medulla and outer xylem. These annular tracheids occur near medullary rays.

The outer xylem wedges are normally five to eight cells wide. The growth is regular to the periphery of the xylem cylinder and the diameter of the tracheids steadily increases in this direction.

The principal medullary rays are short (pl.XV,fig.57) and almost no parenchyma separates the appendage trace from the vertical tracheids but the tip on the protoxylem side is very long and thin and is filled with parenchymatous tissue, together with short scalariform or annular tracheids. Tissues outside the xylem were not observed in steles of this species.

2)Cortex:

Sections of this species show three different types of cortex. These are assumed to correspond to the order of dichotomy (p.14) and it may be mentioned here that the specimens with little development of the secondary cortex have the smallest stele, those with a medium development a larger stele and in those with the thickest secondary cortex the xylem cylinder has the largest diameter.

Small specimens (order of dichotomy III):

In these specimens which show about the same circumference as the type specimen of Stigmaria radiculosa the cortex consists of the following zones:

a) A wide superficial cortex,

b) outer primary cortex with isodiametric and relatively thick-walled cells. This is divided into an outer and inner zone by a relatively thin band of radially arranged cells, the secondary cortex, which was formed in the same way as in Stigmaria radiculosa. The inner zone of the outer primary cortex has secretory ducts lying just beneath the band of secondary cortex.

c) Patches of tissue in the cavity between the stele and the outer cortex show appendage traces in longitudinal section. A middle cortex is not recognizable in small specimens of St. vulgaris and its normal position seems to be occupied by a tissue of the same type as the primary cortex.

The superficial cortex is typical for the species (pl.XV, fig.59).It consists of a concentric "sclerotic band" separating the outer from the superficial cortex and of clusters of cells with black contents resembling those described for Stigmaria asteroidea.

In one instance three zones of such clusters are present. These, in transverse section isodiametric cells are surrounded by elongated cells, the long axis of which points to the centre of the black clusters, suggesting that these clusters of dark cells stopped enlarging before the surrounding tissues did so. In some instances the cells of these clusters are not filled with black matter but show distinct black walls (pl.XV,fig.59). In some regions the superficial cortex appears to be very thick and the cells decrease in diameter towards the outside. Unfortunately the superficial cortex is not well preserved near appendage bases but the thick cortex in other places suggests that insertion of appendages was slightly endogenous.

In tangential section through the outer cortex (pl.XV, fig.58) the black clusters seen in transverse sections appear to be short strands of elongated cells, with or without black contents, surrounded by tangentially elongated cells. In some instances these cells, especially in the vicinity of appendage bases, show annular thickenings (pl.XV,fig.60).

It is probable that in casts of this Stigmaria species fine striations may appear on the surface of the cast as the result of different speed of disintegration of these black strands and the surrounding cells. No evidence as to whether these strands were sclerotic or glandular in nature could be obtained. The tracheids in the vicinity of these strands may point, as LECLERCQ (1930) suggested for <u>Stigmaria bacupensis</u>, to a glandular nature. Even so, the black band (sclerotic band) of <u>Stigmaria radiculosa</u> and the similar band of <u>Stigmaria vulgaris</u> might still have been sclerotic in nature.

3)Appendages:

Appendage bases of Stigmaria vulgaris show exactly the same structure as those of Stigmaria radiculosa (p.47). The appendages of St. vulgaris have a thin outer cortex (usually only five cells wide) at some distance from the base. A limiting layer is indistinct but appears to be present. The inner zone is distinguished by the fact that one layer of cells shows thickening of the outer tangential walls only (p.112,fig.20). Appendages of this type are very common in English coal balls.

A layer of thinwalled small cells, the transition zone, can be observed in many appendages. A middle cortex was not preserved except in the appendage bases and was found to be of the same type as in St. radiculosa. Remains of the inner cortex are found surrounding the pericycle and appear to consist of the same type of cells as the transition zone. The stele of the appendage is of the same type as described in Stigmaria radiculosa. Trabecular bridges have not been observed in appendages of this species.

Medium sized specimens (Order of dichotomy II):

In specimens of this order considerable secondary growth took place in the cortex; whilst in the specimens of St. vulgaris previously described the secondary cortex consisted of a narrow band (usually about 2o cells wide) of radially arranged cells. The larger specimens show differentiation of the secondary cortex into an external and internal zone.

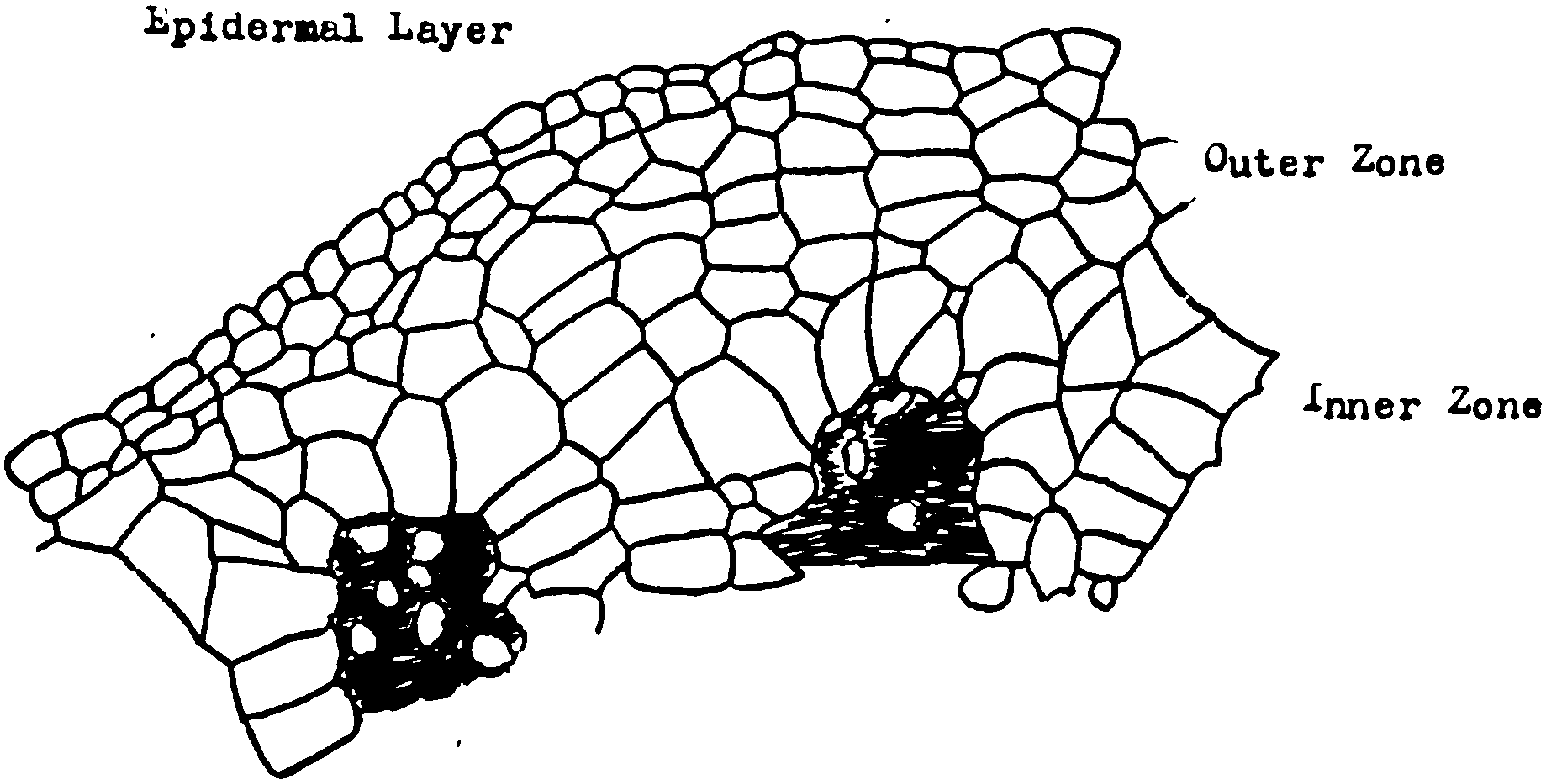


fig.19: Outer Cortex of Appendage :<u>Stigmaria</u> <u>arachnoidea</u>.
Scale 2 . Kc-431 .

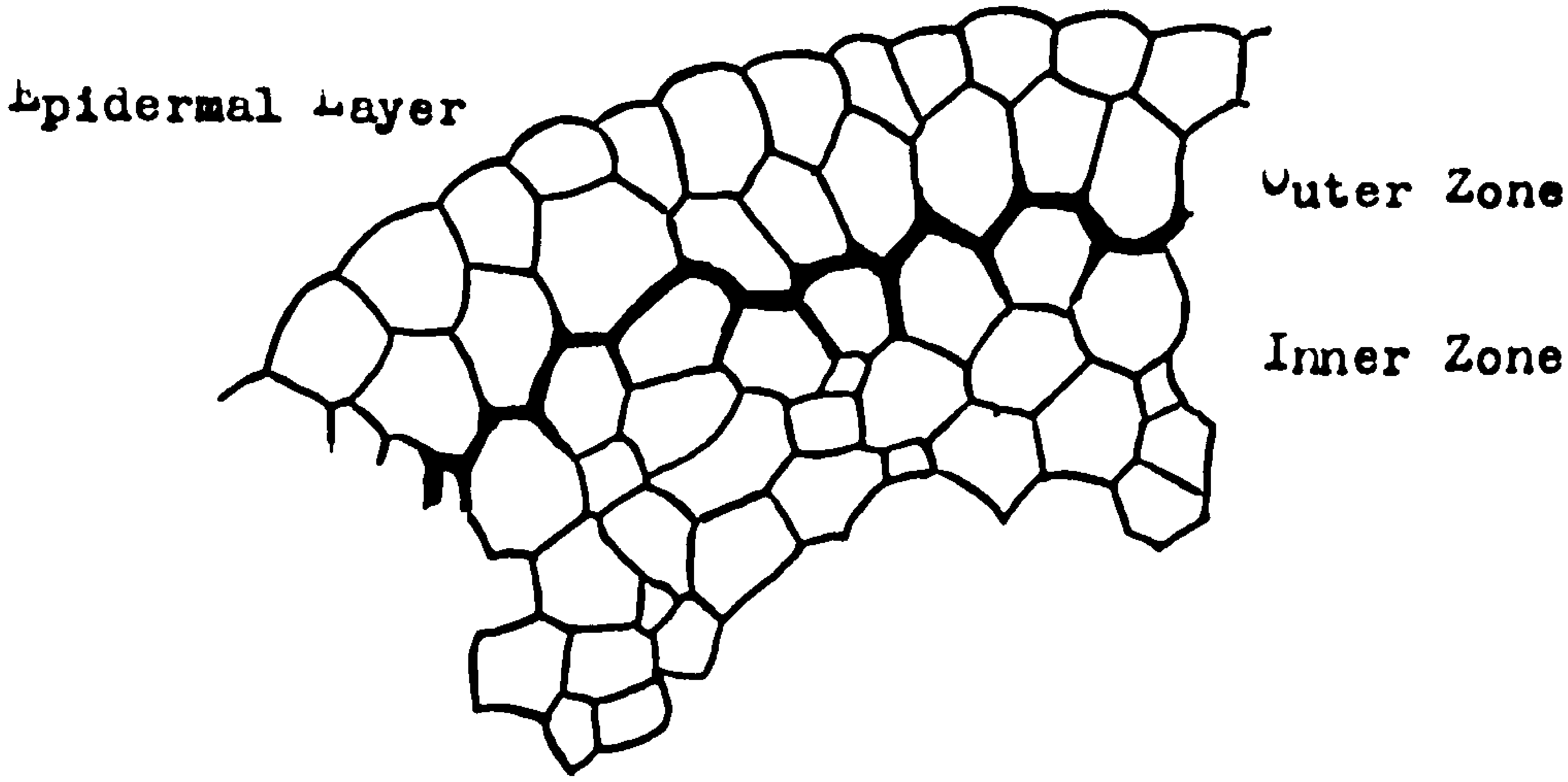


fig.20: Outer Cortex of Appendage of <u>Stigmaria</u> <u>vulgaris</u>.
Scale 10. Gc- 196.

The inner zone of the outer primary cortex is of the same type as in the small specimens. The inner secondary cortex consists of cells of uniform diameter (pl.XVI,fig.63) and elongated in longitudinal direction (pl.XVI,fig.64). Within this tissue, which corresponds to the internal secondary cortices described in other species of the *Stigmaria ficoides* type, concentric zones of strands can be observed which are described by SEWARD and HILL (1900). Pl.XVI,fig.63 shows that in these zones the cells are slightly elongated in a radial direction and have thinner walls. Some walls show signs of disintegration. In longitudinal section (pl.XVI,fig.64) it can be observed that also the horizontal walls tend to break down easily and thus long vertical canals are formed in the inner secondary cortex.

The outer secondary cortex consists of tangentially stretched (dilatated) cells only. The lens-shaped tissue elements observed in *Stigmaria arranensis* are not very conspicuous in this species. Pl.XVI,fig.61 shows the transition from the outer to the inner secondary cortex and this zone appears to be narrower than that of *Stigmaria arranensis*.

Stigmaria vulgaris also shows that we must discard the assumption of cambia in the cortex producing two different types of tissues, the external and internal secondary cortex, as so often made by authors describing the cortex of Stigmaria and Lepidodendron.

The cells of the outer primary cortex in the medium sized specimens are also tangentially stretched (dilatated) and in many instances renewed division is indicated by the presence of thin anticlinal walls.

The outer primary cortex is fissured, apparently by the stresses produced by the growth of the inner secondary cortex and the superficial cortex together with the appendage bases appears to be largely exfoliated. Only in some areas are the superficial cortex and the strands in it preserved and these provide the evidence that these specimens belong to *Stigmaria vulgaris*.

Large specimens (order of dichotomy I):

The stele of this specimen is the largest observed in the species. The cortex, corresponding in structure to that described in the specimens of medium size, is still further developed. The inner and outer secondary cortex are much thicker. Few remnants of the outer primary cortex and the superficial cortex are preserved. They show the same structure as figured in pl.XV,fig.59. The outer secondary cortex does not show the same degree of dilatation as that of the medium sized specimens. Instead the outer secondary cortex is deeply fissured. It also seems that the outer secondary cortex was detached from the inner secondary cortex thus forming a space which is penetrated by Stigmarian appendages of different species.

The cortex of the large specimens shows therefore the same preservation as the bark of the bases of Lepidodendron trunks (SEWARD and HILL,1900) and it seems probable that the specimens already described as branches of the first order of dichotomy (Ib) are sections of a Stigmaria taken in a vicinity of a tree base.

Pl.XVI,fig.62 shows part of the outer secondary cortex of a large truncate specimen (Manch.Mus.Coll. 873 R). This figure demonstrates that within secondary radially arranged cells, irregularly arranged cells which are apparently patches of primary tissue, may occur. This figure strongly suggests that the radially arranged cells are not produced by a single layered cambium but by meristematic activity of many cells in the primary cortex. Some of the cells of the primary cortex seem to have failed to attain meristematic activity or to differentiate and thus to have remained unchanged as the patches of primary tissue within the secondary tissues.

h) Stigmaria asteroidea n.sp.:

The structure of the superficial cortex and the sclerotic elements therein was found to vary in species previously described but there are other Stigmariae in which the tissue in this zone is different from any of these.

The Kidston Coll. contains three slides (No.586,587, 654), the first two are sections of the same specimen of Stigmaria asteroidea, which show this Stigmaria species. Although the typical appendages of this Stigmaria are quite common I could not find any other specimen of this Stigmaria in the collections examined. In the specimens described, only the xylem of the stele, a few layers of the outer primary cortex and the superficial cortex with attached appendages are preserved. The latter however is so characteristic that the specimens can instantly be placed in a new species, which I propose to name Stigmaria asteroidea.

Anatomical structure:

1) Stele:

Anatomically this Stigmaria belongs to the Stigmaria ficoides type. The medullated xylem cylinder is split into about 30 wedges by the appendage traces. The growth of the outer xylem, which alone is preserved, is very irregular and the presence of many patches of irregularly arranged tissue (regarded as primary tissue) (pl.XVII, fig.65) supports the theory of growth of the Stigmarian stele of which an account was given in the description of Stigmaria sewardi.

The innermost part of the xylem wedges consists of groups of small, irregularly arranged tracheids. It is, however, not possible to decide from transverse sections where annular tracheids are situated and longitudinal sections of this species have not been available. This zone of irregularly arranged tracheids merges into radial rows of tracheids, each tracheid~~s~~ usually being slightly elongated in the radial direction. The radial rows of tracheids are separated by numerous secondary medullary rays within which annular tracheids may occur. Further out in the xylem patches of primary tissue, which in many instances seem to have remained in a parenchymatous state, are enclosed in the radial rows(pl.XVII,fig.65). This figure strongly supports the opinion (p. 67) that a broad zone of the procambium became meristematic thus making it possible for primary tissue to become enclosed in secondary tissue. The exo-xylem found in a few patches only consists, as in Stigmaria sewardi, of cells of much smaller diameter than those of the differentiated xylem but of the same diameter as the primary cells enclosed in the secondary tissue. Phloem tissue and a pericycle were not found preserved.

Appendage traces immediately outside the xylem cylinder show a group of very small tracheids at the protoxylem corner (pl.XVII,fig.66) irregularly arranged tracheids at the protoxylem end and radially seriated tracheids at the opposite side of the vascular strand.

2)Cortex:

Only parts of the cortical tissue are preserved. These include patches of small celled tissue (which probably belongs to the inner cortex), the outer primary cortex and the superficial cortex.

The inner zone of the preserved cortical tissue shows signs of secondary growth and may represent the transition zone between the secondary cortex and the outer primary cortex. The latter consists of isodiametric cells of uniform size and shape. Outside this zone the cells decrease in size and are stretched tangentially, forming the superficial cortex in which occur clusters of isodiametric cells filled with a black substance. There are several concentric zones of these clusters which may be called sclerotic strands. (The parenchymatous cells of the superficial cortex are radially elongated around these black clusters (pl.XVII,fig.67). Towards the periphery both cells of the superficial cortex and the sclerotic strands become gradually smaller. Patches of tissue preserved on the outside of *Stigmaria asteroidea* suggest that the superficial cortex was rather thick (pl.XVII,fig.68). Some of the cells on the periphery of the superficial cortex show annular thickening which suggests that they are short tracheids. In the innermost zone the blabk clusters may in certain regions be connected tangentially. Where this is so, this zone locks similar to the sclerotic band described in *Stigmaria radiculosa* and the superficial cortex in *Stigmaria vulgaris*, but can be distinguished from these by the peculiar arrangement of the cells of the superficial cortex and by the typical appendages of *Stigmaria asteroidea.* The clusters of black cells have more similarity with those in *Stigmaria bacupensis* (LECLERCQ,1930) which however are in a different position.

3)Appendages:

The appendages of this species are quite conspicuous because they donot show any sign of a limiting layer. The cells of the outer zone of the cortex are very irregularly distributed (p.121,fig.21 and pl.XXII,fig.84) and the outermost cells have papilla like protrusions. The cells of the outer zone are of equal size with those of the inner zone, another unusual feature compared with other appendages. The cells of the inner zone of the outer cortex have thick walls and are sometimes filled with dark substance just as are the cells of the superficial cortex of the axis. There is, however, no regularity in the distribution of those black cells in the appendage cortex. No tissue is preserved internal to the inner zone of the outer cortex. In fact in longitudinal sections through appendages it can be observed that the inner zone soon disintegrates when the appendage has left the cortex of the axis and the remaining tissue is the outer, thin-walled zone with occasionally one layer of inner zone cells (pl.XVII,fig.68). This then is the usual type of appendage found in many transverse sections. It appears as if the inner zone of the outer cortex forms a funnel and as soon as the appendage is through the cortex of the axis, it disintegrates.

Though the superficial cortex of the axis is never completely preserved near the appendage bases, the thickness of the superficial cortex in other places suggests that the insertion of appendages was endogenous in this tissue (pl.XVII,fig.68).

The vascular strand in the appendages also differs from the usual type. Pl.XXII,fig.84 shows that the xylem is entirely radially arranged except for a few elements near the protoxylem end of the vascular strand. Of the phloem only a few cells, thin-walled and in some instances filled with dark brown substance are present. The parenchyma surrounding the vascular strand can be observed radiating from the protoxylem in much the same way as was described and figured for an appendage trace of Stigmaria sewardi.

This suggests that the inner part of parenchyma represents endo-xylem. The outer part is probably the pericycle. No indications of trabecular bridges were observed in appendages of this species.

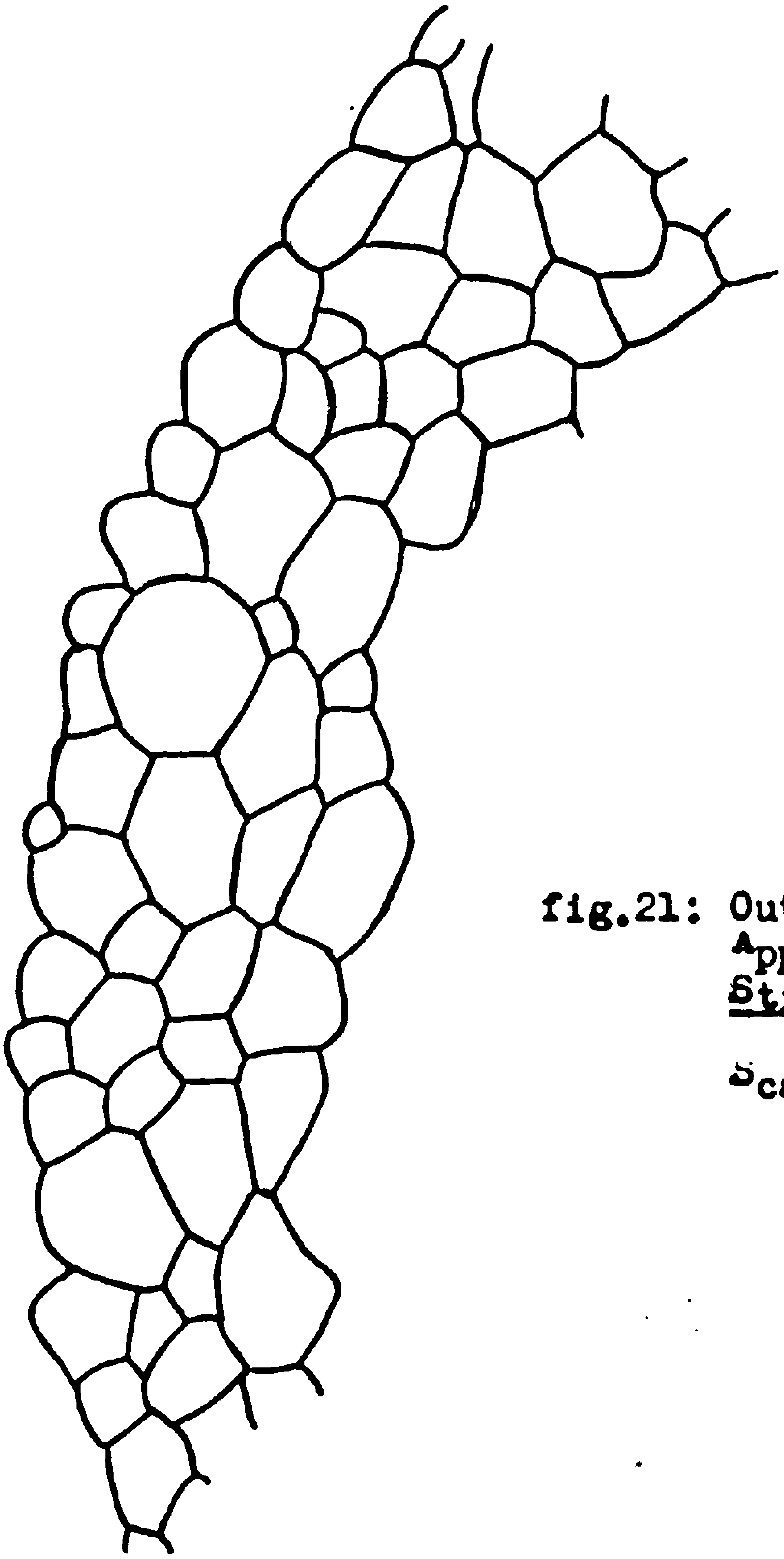


fig.21: Outer Cortex of
Appendage of
Stigmaria asteroidea

Scale 1o. Gc.157.

7. Summary of Features of Systematic Value:

The systematics of Stigmariae of the ficoides type is based upon the structure of the superficial cortex of the axis and the sclerotic elements therein. Other features, as the structure of the stele, the middle cortex and the appendage bases are secondary features in recognition.

Stigmaria sewardi and Stigmaria arranensis (p.123, fig.22a and b) show no differentiation in the outer cortex, i.e. a differentiation into superficial cortex and sclerotic elements is not recognizable. Towards the periphery the cells of the outer cortex of these species become smaller and this zone may possibly correspond to the superficial cortex of other species but it seems more appropriate to refer to this type of cortex as of uniform structure (p.72).

In Stigmaria pettycurensis (p.123, fig.22c) a superficial cortex is not really differentiated i.e. as in Stigmaria sewardi the cells are becoming gradually smaller in centrifugal direction but in a certain zone, a few layers from the preserved margin of the cortex, single cells may be filled with black substance or may have thickened walls. This structure is intermediate between St. sewardi and Stigmaria radiculosa.

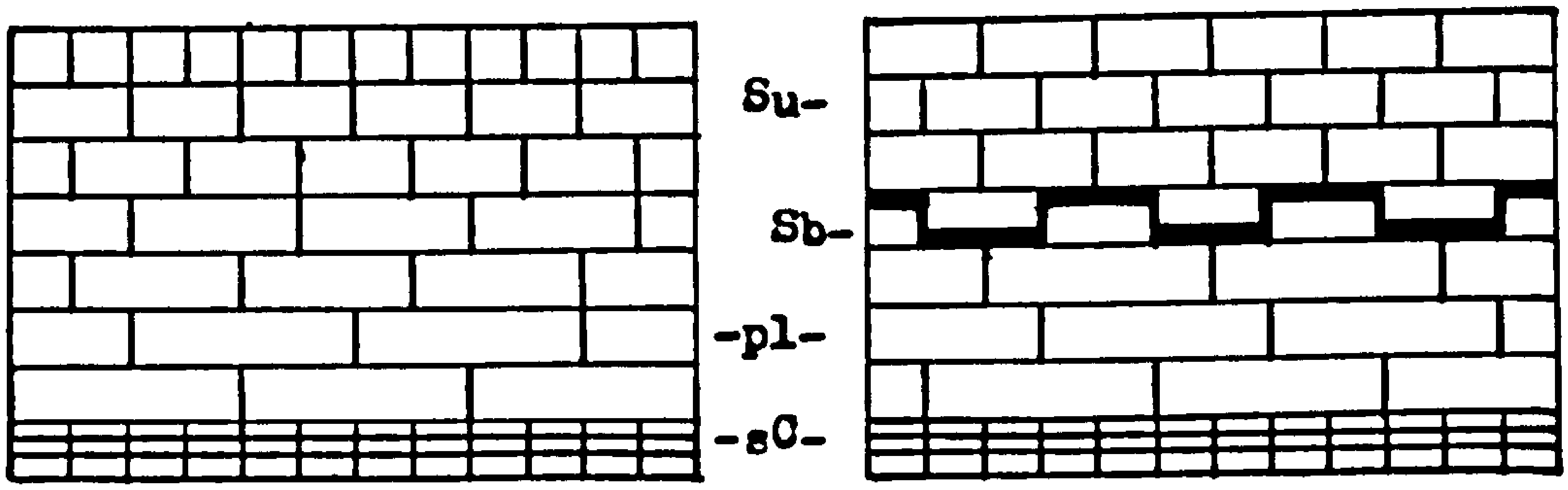
In the latter species (p.123, fig.22d) a superficial cortex is already distinctly recognizable, the cells being smaller and having thinner walls. Furthermore is the superficial cortex clearly separated from the outer cortex by a band of blackened cells, usually one cell wide, the sclerotic band.

A further differentiation of the superficial cortex can be recognized in *Stigmaria vulgaris* (p.123,fig.22e). In this species the sclerotic band can be also observed and in addition to it there are clusters of black cells in the superficial cortex outside the sclerotic band. The clusters of black cells have been shown to be black strands and were called sclerotic strands. The cells of the superficial cortex between these strands are tangentially stretched.

In *Stigmaria asteroidea* (p.123,fig.22f) the last species of the *Stigmaria ficoides* type, described in this thesis, the sclerotic band is absent. The sclerotic strands however are more distinct, larger and the cells of the superficial cortex are arranged radially around these black strands. The superficial cortex can be rather thick in this species; the outermost parts consist of very small isodiametric cells. *St. asteroidea* can also be distinguished by the appendages which show, significantly enough, no limiting layer of cells.

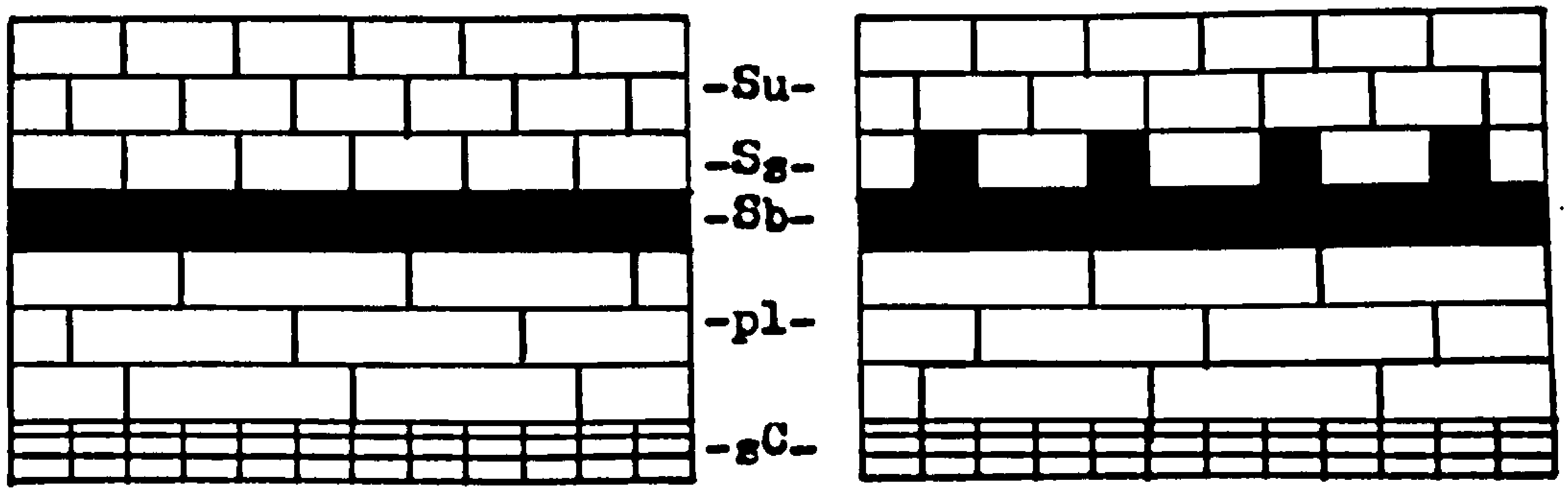
The species without differentiation in the outer cortex i.e.*Stigmaria sewardi* and *Stigmaria arranensis* have been kept apart by the structure of their vascular strand. They differ in the number of medullary rays visible in transverse section and it seems, since the height of the medullary rays of both species is about the same that the number of appendage traces in *St. arranensis* per unit xylem surface is less than in *Stigmaria sewardi* for the same area. Different are also the appendages which always have a uniform cortex in *Stigmaria sewardi* but often show a sclerotic inner zone in *Stigmaria arranensis*.

fig.22 :Variation in the Structure of the Superficial Cortex and the Sclerotic Elements in Stigmaria of the ficoidea type.



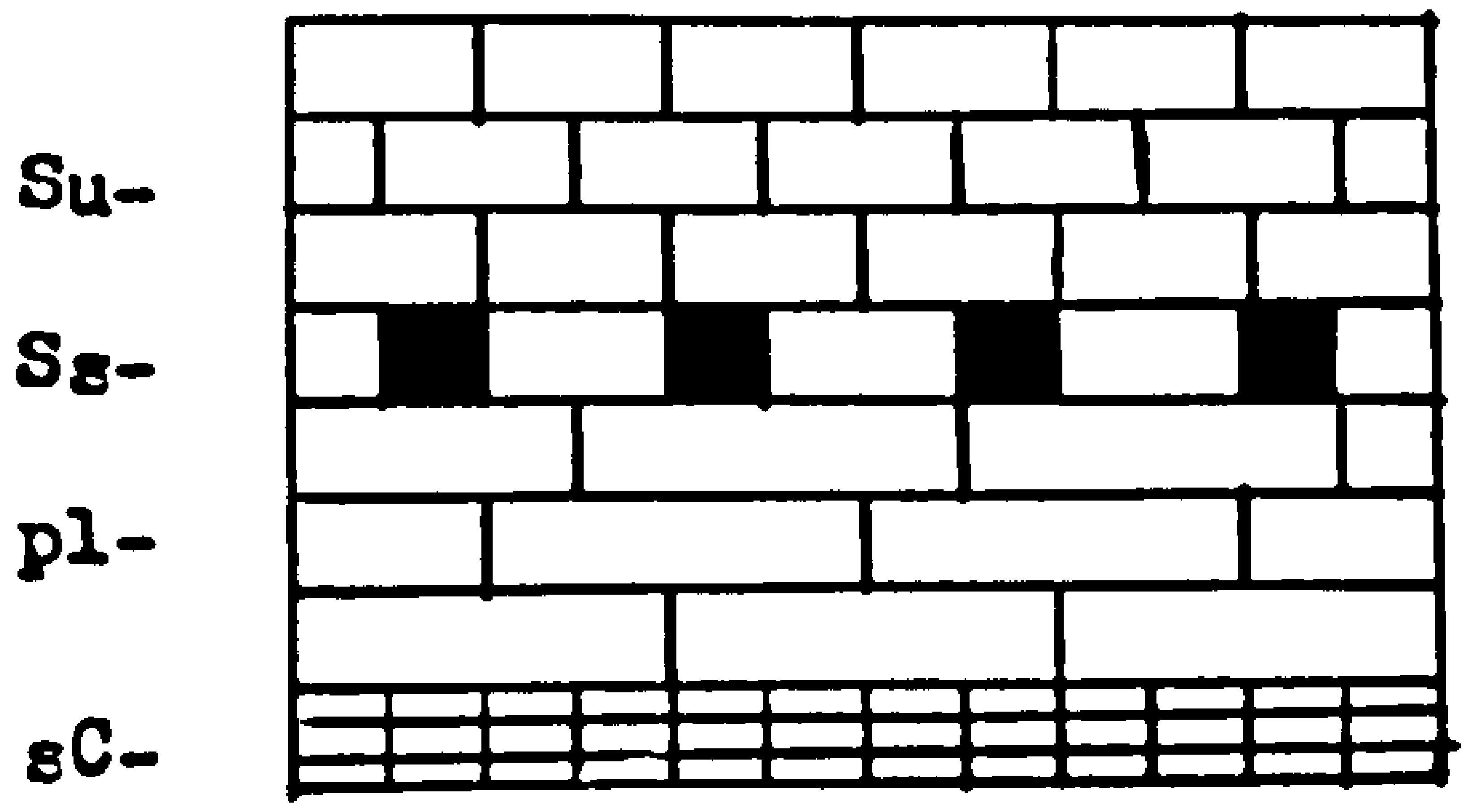
a) *Stigmaria sewardi*
b) *Stigmaria arranensis*

c) *Stigmaria pettycurensis*



d) *Stigmaria radiculosa*

e) *Stigmaria vulgaris*



f) *Stigmaria asteroidea*

Su - Superficial Cortex
pl - Outer Primary Cortex
sC - Secondary Cortex

Sb - Sclerotic Band
Ss - Sclerotic Strands

Furthermore is the cortex more developed in Stigmaria arranensis in specimens with a smaller stele than in Stigmaria sewardi. Both species seem to be, however, related.

Of Stigmaria sewardi three varieties were described, These, grouped according to their size, were named var. minor (a small specimen with small appendage bases and little developed xylem), var. sewardi, the type specimen, and var. boonvillensis (a fragment of a very large Stigmaria with large appendage bases from U.S.A.).

8. Comparative Anatomy:

The stele of the Stigmaria ficoides type is always medullated and has a single xylem cylinder in contrast to the aerial parts of the fossil Lycopods in which a cylinder consisting of two different types of xylem (diploxyloid) is developed.

The medullary tissue is preserved in few specimens only. which probably are the ultimate branches of Stigmaria. It consists of rather thick-walled cylindrical cells which are arranged in longitudinal rows(pl. II, fig. 10). These cylindrical cells differ considerably from the medullary cells of Lepidodendron and Lepidophloios. In the latter plants the medullary parenchyma is formed by septations of potential tracheids (WALTON, 1935, pl. IV, fig. 27). This seems to indicate that the pith in the Lepidodendroid shoots consists of undifferentated but potential tracheids whilst Stigmaria has a true medullated stele.

The pith in Lepidodendron consists of uniform tissue but in the Stigmaria ficoides type the cells are considerably smaller towards the outside of the pith, have thinner walls and are tapered on both ends (pl.II, fig.11). This area is called the endo-xylem. The cells of the pith are frequently filled with some dark substance, the cells of the endo-xylem are clear. This feature marks the border between endo-xylem and pith conspicuously. Tracheids may be occasionally differentiated in the endo-xylem of Stigmaria and are assumed to be the protoxylem elements of either the axis or the appendage traces.

The single cylinder of xylem is split into anastosmosing bundles by the medullary rays. These bundles, wedge-shaped in transverse section consist of mainly radially arranged scalariform tracheids. On the inside of those wedges, normally a few irregularly arranged scalariform tracheids of small diameter can be found. These are assumed to be differentiated from primary tissues (p.54), but are not as has been described, metaxylem. Within the radially arranged tracheids patches of small irregularly arranged cells (pl.XVII,fig.65) or tracheids(pl.VII,fig.28) may occur in concentric zones or isolated areas. The presence of these tissues suggests that the xylem in Stigmaria as well as probably in the aerial parts of the Lepidodendrales is not produced by a normally functioning cambium.

The xylem cylinder of radially arranged tracheids, which is in conformity with LANG (1915) called outer xylem (p.54) is surrounded by a sheath of parenchymatous tissue in which occasionally small tracheids may be differentiated.

This zone has previously been considered to be the cambial zone of the outer xylem (SEWARD,1910) but all authors were at loss to explain how the large tracheids of the outer xylem could be produced by a small celled tissue like in this zone. In this thesis therefore a non-committal name, "exo-xylem", was applied for the tissue. Adjacent to the exo-xylem is the phloem which is, so far observed, of the same type as described by WALTON (1953) for Lepidophloios wünschianus and may therefore in conformity with WALTON and SEWARD (1910) be called "secretory strands".

The outermost layers of the stele consists of small parenchymatous cells which, of the same structure as the exo-xylem, has been called pericycle. The separation of stele and cortex of Stigmaria seems in certain cases rather arbitrary and many authors (SCOTT,1923) have described the tissue outside the phloem zone as inner cortex. As,however, the parenchyma is of the same type as the other undifferentiated stelar tissues and quite different from the cortical cells (pl.III,fig.15) it may be more justified to call this area pericycle. Furthermore are the cortical tissues separated from the stele by a layer of blackened cells (pl.II,fig.9) which can be regarded as an endodermal layer (HOVELACQUE,1892).

The stele of the Stigmaria ficoides type is unique in fossil botany and cannot be directly compared with the stele of any other plant. Naturally, however, it has some relation to the stele of Lepidodendroid shoots and can in some respects considered to be the medullated form of the Stigmaria bacupensis type of stele and the stele of the Isoetes lacustris shoot.

The whole of the differentiated xylem in the *Stigmaria ficoides* type, the outer xylem, corresponds to the outer (secondary) xylem of the diploxyloid steles. In these, the irregularly arranged inner parts and the patches of irregular growth are also present and although these tissues are undoubtedly primary they have been classified with the secondary xylem. In conformity with this definition it would have to be maintained that in the *Stigmaria ficoides* type no primary xylem is differentiated and the vascular strand consists only of secondary xylem.

The tissue described as exo-xylem in this thesis is known from Lepidodendroid steles also and was described by SEWARD and HILL (1900) and SEWARD (1910) as meristematic zone.

WALTON (1953) states that these cells are, however, not cambial cells. The tissue in the phloem zone corresponds to the secretory tissue in the same position known of *Lepidophloios fuliginosus* and *Lepidophloios wünschianus* (WALTON, 1953). A pericycle is not known of Lepidodendroid steles but may however have been present.

The growth of the steles appears to correspond in many respects to that of *Isoetes lacustris* (LANG, 1915) with the difference that the stele of the shoot of the latter is not medullated. Meristematic growth probably occurred very early, before vascular elements, except the protoxylem elements of the appendage traces, were differentiated. In many instances the meristematic activity was cambiform but each daughter cell seems to have retained the power of further division. Inside and outside this zone of meristematic activity procambial cells retained their primary nature.

The differentiation of the phloem i.e. the secretory strands, divided the otherwise completely uniform tissue into two zones, the pericycle outside and the exo-xylem inside the secretory strands. Differentiation of the xylem elements took place in all cells outside the terminations of the appendage traces but ceased in a certain, in no case uniform, position inside the phloem. Since meristematic growth in the procambial tissue did probably not, similar as in Isoetes (LANG,1915), start at the terminations of the appendage traces but few layers outside, differentiation, however, started at the terminations of the appendage traces and involved all cells outside, it is clear why the innermost cells are irregularly arranged whilst further out the cells become more radially arranged (p.63).

In this view,however, it seems to be inaccurate to talk of primary or even metaxylem because both the irregularly and the radially arranged tracheids appear to be differentiated simultaneously. Taking the terminations of the appendage traces and the terminations of the leaf traces as the same relative level in both Stigmaria and Lepidodendroid shoot, as done by many authors, it seems to be wrong entirely to compare these innermost cells of the outer xylem with the centripetally developed primary xylem ring. This point will be more clear after the structure of Stigmaria bacupensis has been described.

The medullary rays and the appendage bases of Stigmaria are of different shape and size, according to the species and to the distance of the section from the inner margin of the xylem. The medullary rays are generally narrow and high on the inside and tend to shorten and widen towards the outside of the xylem cylinder.

This however seems to be done in different ways in different species. The appendage traces in the medullary rays are generally triangular in shape, the protoxylem on the free corner of the triangle points towards the apex of the axis. Opposite the protoxylem the tracheids of the outer xylem are attached to the appendage trace. The trace may be separated from the surrounding tracheids of the xylem by parenchyma the amount and the arrangement of which seems to vary with the species.

The leaftraces of Lepidodendron usually have no outer xylem attached and the medullary rays appear to be lens-shaped in tangential section through the outer xylem. In Lepidophloios wünschianus (SEWARD and HILL,1900,WALTON, 1935) it was observed that outer xylem tissue may be attached to the leaf traces when they pass through this tissue and in tangential section through the outer xylem the medullary rays of these species resemble those of Stigmaria.

The course of the appendage traces in the outer xylem is almost horizontal but when leaving the xylem cylinder the appendage traces bend sharply upwards and exo-xylem and secretory tissue is attached to their outer side when they pass through the respective zones. In the pericycle the appendage traces are surrounded with pericyclic tissue and then pass out into the cortex.

Cortex:

All the cortical tissues have been found in a state of preservation of Stigmaria radiculosa and although their structure may differ from that of other species the arrangement of the tissues seems to be the same.

In Stigmaria radiculosa three types of tissues can be recognized: Fundamental cortex, accessory cortex and the secondary cortex.

The fundamental cortex consists of primary tissue and since patches of this tissue can be observed all over the cortex of Stigmaria radiculosa, even amidst the accessory tissue, it has led to the conclusion that the latter is derived from the primary tissue and not directly differentiated from the promeristem and furthermore, that the cortex near the growing point consisted of uniform tissue, except for the outermost layers. By irregular and cambiform division of primary cells, continuing in layers around the stele and on the inside of the outer cortex, coinciding with a general expansion, a zone of loose tissue originated, the middle cortex, which separated the primary tissue into an outer and inner cortex.

In some instances the inner cortex is completely transformed into middle cortex and has disappeared. In the middle cortex cambiform meristematic activity continued. As these meristems (pl.VI,fig.24) mostly produce cells in tangential they apparently served to equalize stresses originating during tangential expansion by radial growth.

In the outer cortex, cambiform meristematic activity started at an apparently very early stage. The secondary tissue is again not produced by a cambium but, similar to certain monocotyledon stems, by a number of cells in which each daughter cell continues to divide. The meristematic zone divides the outer primary cortex into an outer and inner zone. Immediately inside the meristematic band, in the inner zone concentric rings of cells are situated which have been named secretory ducts (WEISS,1904,CALDER,1933). The ducts are also known of Bothrodendron mundum, Lepidophloios wünschianus and Lepidophloios fuliginosus and may possibly occur in several other species of Lepidodendroid cortices. In these strands tracheids have been observed (pl.XII,fig.49) also by CALDER (1933).

Deeper in the inner zone of the outer primary cortex, the transition to the middle cortex can be observed. The above mentioned secretory ducts and the course of the appendage traces may serve as a guide in identifying the homologous tissues in the aerial parts of the Lepidodendroid plants. While the inner cortex is recognizable also in the shoots and shows sometimes cells with black fillings as in Stigmaria, the middle cortex of Lepidodendron is known to be of varying structure. It may be hyphal, or, in other cases small strands of tissue bridge a gap similar to the cortex of Astromyelon (HIRMER,1927). The middle cortex of Stigmaria is less well known but the more common preservation of the middle cortex in appendages suggests that it was also in Stigmaria of varying type.

In the inner part of the middle cortex, the leaf traces pursue a course at right angles to the stele of Lepidodendroid shoots but in the outer part they bend steeply upwards. The same is the case in the middle cortex of Stigmaria. Thessecretory ducts, observed in *Stigmaria radiculosa*, can be found again inside the meristematic layer underneath the leaf cushions in Lepidodendron and there can be little doubt that the periderm of Lepidodendron is in the identical position as the band of secondary cortex in *Stigmaria radiculosa*.

Therefore the outer zone of the outer primary cortex in Stigmaria, the primary tissue outside the meristematic zone, corresponds to the leaf cushion region in Lepidodendron and Lepidophloios.

The outer zone is bordered by a sclerotic band in *Stigmaria radiculosa* which in position corresponds to the, often suberized, epidermal zone of Lepidodendron. The superficial cortex has then no counterpart in the aerial shoots. It seems that both the superficial cortex and the sclerotic band correspond to the epidermal zone of Lepidodendroid shoots. This assumption is supported by the sclerotic elements developed in the superficial cortex of other Stigmaria species, as *Stigmaria vulgaris*. In the latter species tracheids are developed along the sclerotic strands in the superficial cortex and it may be, as LECLERCQ (1930) suggests for similar strands in *Stigmaria bacupensis* that these are in reality of glandular nature.

It is, however, more probable that the superficial cortex is a multiple epidermis similar as the velamen of orchid roots,the sclerotic band corresponding to the exodermis and the superficial cortex with its storage tracheids to the hypodermis.

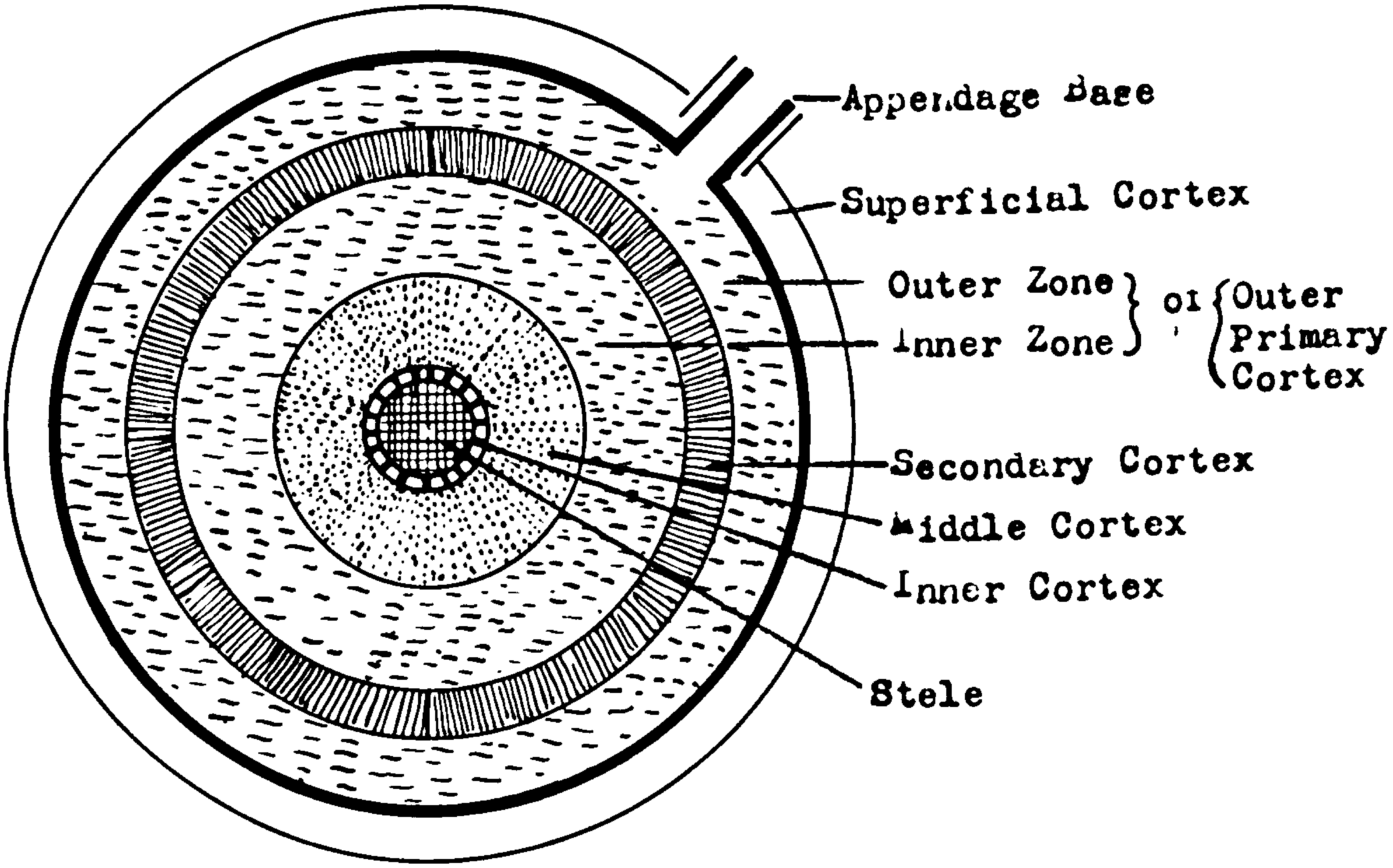


fig.23a:Diagrammatic Transverse Section of a Stigmarian Branch.

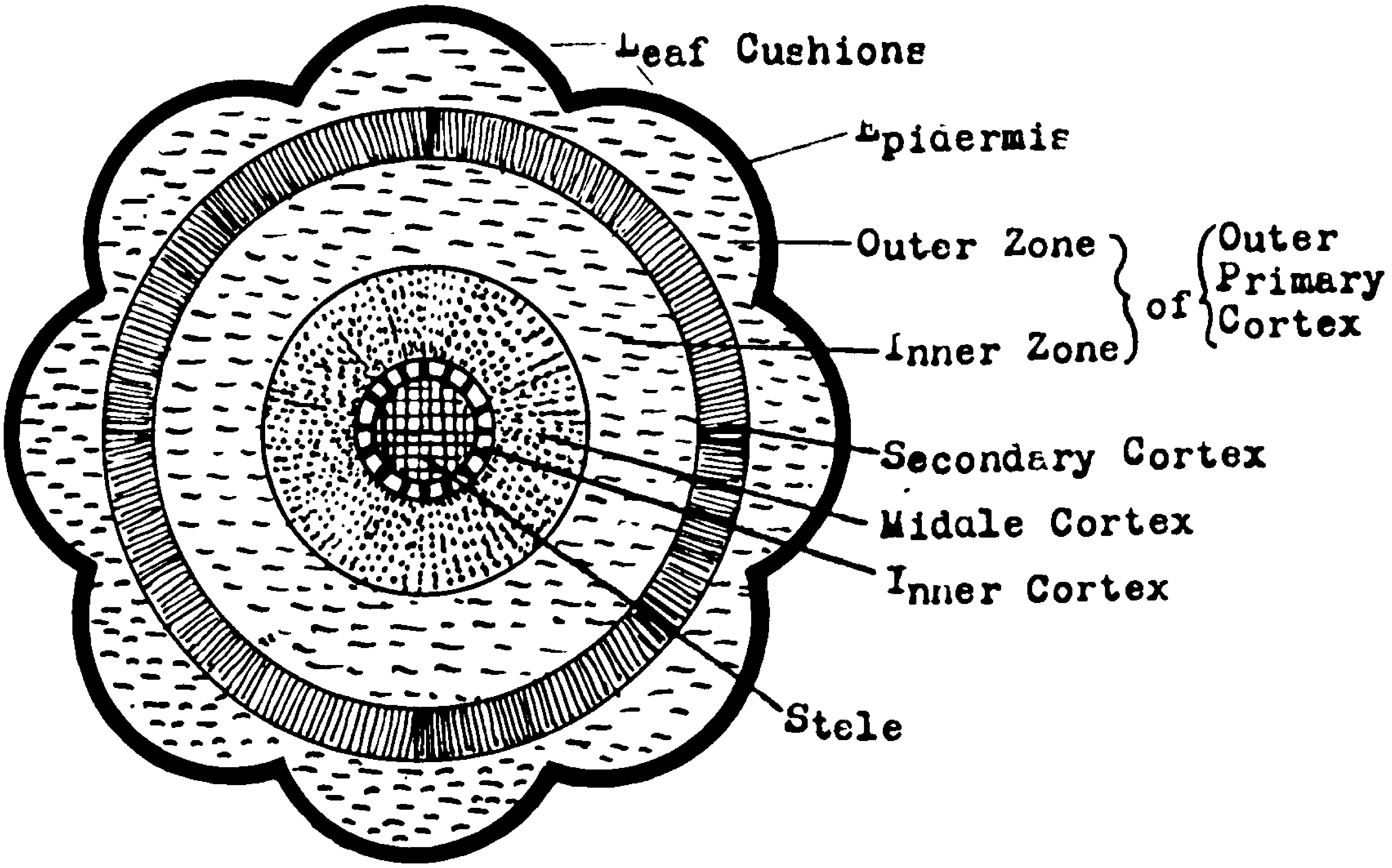


fig.23b :Diagrammatic Transverse Section of a small Lepidodendron Branch .

Sections through ramifications of a lower order show, as some of the trunks of Lepidodendron, a considerably larger development of the cortex. By cambiform meristematic growth secondary tissue is added to the inside of the band of secondary cortex (periderm in Lepidodendron). This additional tissue, recognizable in branches of a lower order only is called the inner secondary cortex.

The cells of the inner secondary cortex are prismatic to fibrous in shape and show in some instances thickening of the walls. A similar tissue is observed in *Lepidophloios wünschianus* and WALTON (1935) describes the thickening of the cell walls in this tissue. This indicates that the inner secondary cortex of the erect shoots of Lepidodendron is in the main the supporting tissue. In addition to that concentric zones of ducts occur in some species of Lepidodendron and Stigmaria in the inner secondary cortex. These ducts are probably derived from the prismatic cortical fibers by disintegration of certain longitudinal and horizontal cell walls. They have been called secretory ducts (SEWARD and HILL,1900) and may represent additional phloem tissue since secondary phloem is not produced in the stele. If this assumption is correct the inner secondary cortex would correspond to the"secondary prismatic tissue" (LANG,1915) of Isoetes. The assumption is supported by the fact that tracheids have been observed to be differentiated from both the inner secondary cortex of Stigmaria (p.73 and pl.IX,fig.33) and the prismatic tissue of Isoetes (SEWARD, 1910).

It is clear that the internal secondary cortex must arise from meristematic activity between the band of secondary cortex (*Stigmaria radiculosa*,p.44) since the primary tissue with these secretory ducts (p.91) is observed on the inside of a fairly thick internal secondary cortex. The position in which the inner secondary cortex arises may vary in different species and even in single specimens. Whilst in some cases undoubtedly (pl.XIII,fig.51) (pl.XVI,fig.61) the periderm continued to grow , in other cases, as described from *Stigmaria sewardi* var. *boonvillensis* a narrow zone of primary tissue may remain between the outer secondary cortex and the inner secondary cortex.

The outer secondary cortex was described as a zone of tangential expansion (dilatation) and probably represents at least in its outer part the first formed secondary cortex (the periderm of Lepidodendron) which, after continuation of secondary growth on its inner side becomes dilatated by tangential expansion. Thus it seems clear why appendage traces (leaf traces in Lepidodendron) can be observed in the outer secondary cortex but not in the inner secondary cortical tissue.

In the course of this secondary growth, the cells of the outer primary cortex are tangentially stretched and respond to the stresses by division in tangential direction, (pl.XII,fig.51). During secondary growth which, corresponding to the trunk of Lepidodendron, might be called the truncate stage of Stigmaria, the superficial cortex, the sclerotic zone and the appendage bases become more or less exfoliated and it seems quite evident that the Stigmarian branches of a lower order of ramification did not bear functioning appendages.

In branches probably of the lowest order of ramification, the outer primary and the outer secondary cortex could not keep pace with the tangential expansion and both tissues became deeply fissured by cracks extending normally as far inside as the outermost layers of the inner secondary cortex. In many cases the outer secondary cortex seems to be separated from the inner secondary cortex by a concentric fissure which indicates that in some instances and in very late stages of growth the outer secondary cortex and the outer primary cortex was exfoliated completely. As a cast these Stigmariae must have the same appearance as the decorticated Lepidodendron branches.

Insertion of appendages:

LANG (1923) discovered that the insertion of appendages in a young axis of Stigmaria bacupensis is slightly endogenous. As this feature had hitherto not been observed on larger specimens of the same or other species of Stigmariae he concluded that the outermost layers of the cortex through which the appendages break may normally be exfoliated and that therefore the insertion of appendages appears to be exogenous. Whilst slightly endogenous insertion of appendages appears to be a regular feature of the Stigmariae with a diploxyloid stele especially Stigmaria bacupensis (p.179) it seems that this feature is not of constant occurrence in Stigmaria ficoides types and it is only in Stigmaria asteroidea which shows cortical similarities to Stigmaria bacupensis that an endogenous insertion perhaps exists, (pl.XVII,fig.68).

It is difficult to estimate how much of the superficial cortex in which the appendages are inserted (p.138,fig.24) is exfoliated in the other species of the *Stigmaria ficoides* type. In some specimens (especially in *Stigmaria vulgaris*) the appendages seem to have broken through the outermost layers of the superficial cortex. In *Stigmaria sewardi* on the other hand this may not have occurred for here the appendages are inserted in deep pits in the outer cortex and it seems unlikely that these pits could have been subject of much expansion. The outermost layers of the superficial cortex are probably preserved there. They are, however, continuous with the outer cortex of the appendage.

Summarizing it can be said that the appendages of *Stigmaria ficoides* type axes were inserted endogenously only slightly if at all and break only through the outer layers of the superficial cortex. This is illustrated by p.138,fig.24 which shows in a diagrammatic drawing an appendage base in which a slight endogenous insertion in the superficial cortex is assumed.

The insertion of appendages in *Stigmaria bacupensis* (LANG,1923) is much deeper in the cortex as in probably all other Stigmariae with a diploxyloid stele; but this will be described later.

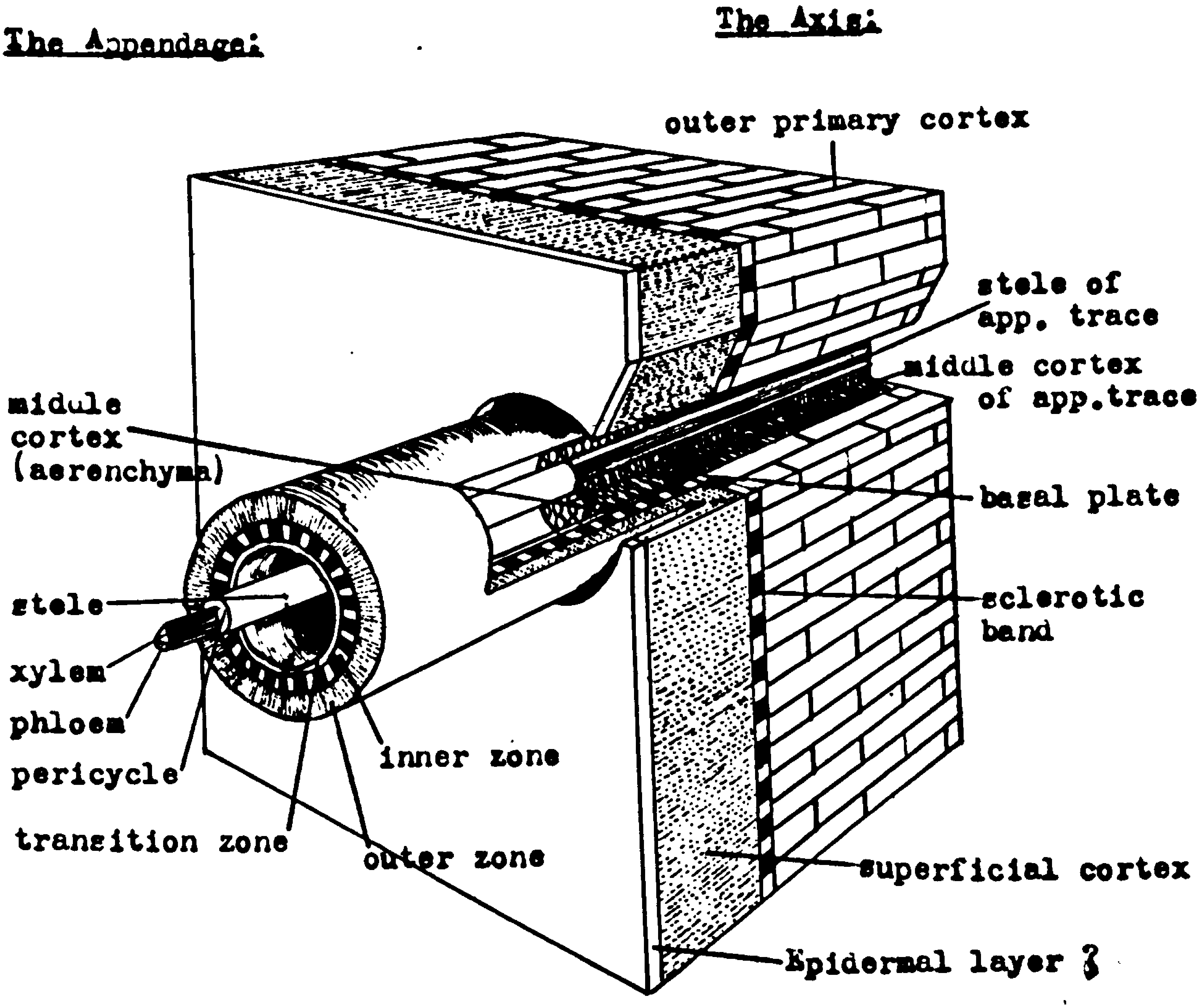


fig.24: The slightly endogenous insertion of appendages in the outer cortex of Stigmaria. Diagrammatic Drawing.

B.M.53

Appendages:

The cortex of Stigmarian appendages is normally preserved in the form of a hollow tube in which the stele is, frequently eccentrically, situated. The stele of the appendage may be attached to the cortex by a narrow band of cortical tissue and consists of xylem, phloem (secretory strand) and parenchyma, part of which is probably the pericycle.

The vascular strand is normally triangular in transverse section and at one corner, in relation to the Stigmarian axis the adaxial corner, the protoxylem is situated. It consists of two to five elements with annular or spiral thickening. The xylem strand consists of scalariform tracheids which are narrow in diameter near the protoxylem but become wider the further they are away from it.

In certain appendages radially seriated tracheids appear on the outside of the xylem strand. This feature may be observed in three different developments. In the first instance the xylem may appear to consist almost entirely of radially seriated tracheids (pl.XXII,fig.84). In other cases the inner tracheids may be irregularly and the outer tracheids radially arranged (pl.XVII,fig.66) but in that case the diameter of the tracheids in both parts is the same. Among the appendages showing radially seriated tracheids the third development is the most common one in which very small radially seriated tracheids abut on the larger tracheids of the primary vascular strand. These tracheids may be in actual connection with the primary strand (p.102,fig.17) or may be separated from it by a sheath of undifferentiated parenchyma (pl.XXIV, fig.93).

As in the stele of the axis it would be inaccurate to call the irregularly arranged tracheids metaxylem and the radially arranged tissue secondary xylem.

The xylem strand is surrounded by parenchyma which is normally undifferentiated procambial tissue. In some instances, as in the appendages of Stigmaria arranensis tracheids may be differentiated in it (p.100). This parenchyma corresponds to the endo-xylem, the exo-xylem and to the medullary ray tissue of the axis and is, as there, a potential meristem.

Tracheids may be differentiated from this primary tissue or from tissue in which some meristematic activity had occurred. But in the latter case differentiation of primary and secondary tissue most probably occurred simultaneously, as was described for the similar development in the stele of the axis and therefore a distinction between metaxylem and secondary xylem cannot be drawn. Only in the last mentioned case where small radially seriated tracheids abut on large primary elements, these small scalariform tracheids are differentiated secondarily and it seems also that the cambiform growth occurred after the differentiation of primary xylem. This is the only case in Stigmaria ficoides types in which truly secondary xylem can be observed.

Most appendages branching from a certain axis of Stigmaria arranensis (p.90) show this feature. The xylem and the appendage traces of the same axis show the described irregularities on their outer margin and there seems to be some connection between the secondary growth in appendage steles and the irregularities in growth of the xylem of the axis.

During the investigation of appendages it was observed that the size of the vascular strand and the number of xylem elements therein varied with the size of the whole appendage. Statistical results demonstrate this in a simple mathematical function:

A slide in the Kidston collection (No.120) showed a number of Stigmarian appendages lying closely together. Most of them are of a uniform cortical type and are probably, judging from their position, from one axis. They are probably appendages of Stigmaria vulgaris but this identification is not certain. The cortex of these appendages is figured on p.182,fig.28. Of all these appendages with the same cortical structure in the same slide measurements of the circumference of the outer cortex and of the number of tracheids in the vascular strand were taken and compared with each other. These measurements are compiled in page 142. Entered into a diagram (p.143) the data suggest that with an increasing circumference of the appendage the number of xylem elements increases proportionally in the same way as, of course, the circumference of the stele is increasing with the number of tracheids.
On p.144 Camera lucida drawings of the xylemstrands of the measured appendages are arranged according to the circumference of the appendages (p.142) and it is obvious again that the number and diameter of the xylem elements increases with the circumference of the outer cortex of the appendage. In the larger appendages however this increase does not seem to be so conspicuously regular but in measuring these appendages allowance has to be made for a larger margin of error because these specimens had been slightly distorted before fossilisation and an exact determination of the circumference was not possible,

Sizes of Stigmarian Appendages in Slide 120 Kidst. Coll.

	Outer Cortex			Stele		Vasc. Bundle	
Number	Outer Diameter	Inner Diameter	Circumference	Diameter	Circumference	Diameter (maximal)	Number of Cells
1	1.14	0.81	3.57	0.238	0.74	0.028	6
2	1.26	0.81	3.95	0.250	0.78	0.070	5
3	1.26	0.81	3.95	0.280	0.87	0.070	8
4	1.30	0.92	4.08	0.154	0.48	0.070	9
5	1.40	1.14	4.39	0.230	0.42	0.070	6
6	2.30	1.72	7.22	0.160	0.50	0.070	6
7	2.60	2.10	8.16	0.370	1.16	0.070	8
8	2.65	1.85	8.32	0.420	1.31	0.120	13
9	3.05	2.35	9.57	0.490	1.53	0.140	14
10	3.35	2.40	10.51	0.420	1.31	0.140	9
11	3.35	2.75	10.51	0.530	1.66	0.190	12
12	3.90	3.20	11.11	0.700	2.19	0.322	22
13	4.15	3.45	13.03	0.700	2.19	0.300	19
14	4.45	4.05	13.97	0.700	2.19	0.260	19
15	5.45	4.55	17.11	0.700	2.19	0.250	20
16	6.15	5.30	19.31	0.770	2.41	0.210	21

KIDSTON COLL. 120
STIGMARIAN APPENDAGES

10.4.1953

Xylem strands of Stigmarian
appendages arranged after the
circumference of the outer cortex.
(Kidst.Coll. 120)Magn.about 185 X.

TEXT BOUND
INTO
THE SPINE

STIGMARIAN ROOTLETS ALL CORTICAL TYPES
ALL LOCALITIES

⊙ = SEC. GROWTH IN VASCULAR STRAND

9.4.1983

A similar result is obtained when the circumference of the xylem strand, or the number of tracheids therein, or the circumference of the stele is compared with the circumference of the outer cortex of the appendage, regardless of the species (p.145,146). The graphs also suggest that the number of tracheids or the size of the xylem strand is directly dependent upon the circumference of the appendage. Furthermore it can be observed that the appendages of *Stigmaria arranensis* and those of *Stigmaria sewardi* var. *boonvillensis* are the largest measured and, as previously mentioned in this thesis, secondary growth in the vascular strand can be most commonly observed in appendages of this species. In view of these results the assumption seems to be justified that the number and size of primary vascular elements is related to the size of the appendage. Furthermore, if, compared with the size of the appendage, too few or too small tracheids are differentiated, secondary tracheids are developed to subsidize the primary strand. The very small appendages of *Stigmaria bacupensis* normally show no sign of secondary growth in their vascular strand; however, in a slide (Kidston coll. 1932) an appendage of this species can be observed which shows secondary growth of its vascular strand and at the same time secondary growth in its outer cortex. This supports the assumption that secondary growth of the vascular strand is initiated when the circumference of the appendage is relatively too large either in a primary state or after secondary growth in the cortex. An excellent example of such an appendage in which secondary growth has taken place in both cortex and stele is figured in pl.XXIV,fig.91,93.

The stele of the appendage is shown in pl.XXIV,fig.93 and in this figure it is apparent that the secondary xylem resulted from growth of the parenchyma surrounding the primary strand. Pl.XXIV,fig.91, shows the cortex of the same specimen and it is evident that meristematic growth took place in this tissue in the usual irregular way. Another appendage showing cambiform secondary growth in the outer cortex and stele, similar to the above mentioned specimen is shown in pl.XXII,fig.86. It was already described (p.67) that growth and differentiation of secondary xylem may be very irregular and this fact is well illustrated by the xylem strands of the appendages of _Stigmaria_ _sewardi_ var. _boonvillensis_ (pl.X,fig.37 - 39). The latter species again suggests that the secondary xylem of appendages is not produced by a single layered cambium.

The whole of the differentiated xylem of the Stigmarian appendage corresponds to the outer xylem of the axis. It is differentiated simultaneously from primary and eventually also from secondary parenchyma, as described from the outer xylem of the axis (p.127) and only in exceptional cases secondary xylem is added to the primary strand. The xylem strand is surrounded by small celled parenchymatous tissue from the outer part of which the secondary xylem may be produced. This parenchyma, which is probably a remainder of the procambial tissue and in which some tracheids may occasionally be differentiated is most clearly shown by pl.XXIV,fig.93, but can be observed in other well preserved appendages also. It corresponds to the remnant procambial tissues of the axis i.e. the endo-xylem and theexo-xylem. The part capable of secondary growth seems to reach half way round the outer side of the appendage vascular strand (pl.XXII,fig.86 and pl.XXIV fig.93).

The inner part of this parenchyma surrounding the protoxylem corner of the vascular strand is connected with the pericycle of the appendage and may be considered part of this tissue. This is most clearly shown by pl.XXIV,fig.93 in which the pericycle, after the considerable secondary growth of the xylem, shows signs of dilatation. The cells of the pericycle as well as those of the vascular parenchyma in the protoxylem region show signs of tangential elongation and are considerably stretched. A stretched pericycle cell in the phloem region of the same specimen shows inserted radial cell walls. The same features can be seen in appendages in a similar state of preservation.

In appendages with a normal primary stele the pericyclic cells are very regular and cylindrical in shape. Owing to the absence of a well defined endodermis the border between cortex and stele cannot be clearly distinguished but in some appendages (p.82) and pl.VII,fig.25) the cortex is separated from the stele, as in the axis, by a dark brown deposit. The phloem of the appendages, so far it is preserved, is of the same type as in the axis (secretory strands).

Cortex:

The inner cortex of the appendages is, as mentioned, rarely recognizable and may have disintegrated completely in most specimens. It is recognizable when, as mentioned above, the cells are filled with brown substance; this occurs mainly in appendage bases. In pl.X,fig.40, a gradual transition from pericycle to inner cortex can be observed whereby the cells of the latter can be recognized only by their more irregular shape and slightly thicker walls.

As in the Stigmarian axis (p.43) the inner cortex is part of the primary cortex and has been separated from the outer primary cortex by the development of the middle cortex. Pl.X,fig.41 and pl.XXIV,fig.91, show the transformation of the inner cortex into middle cortex. Other evidence supporting this assumption was found in Kidston coll. slide no.1524 in which two solid appendages of Stigmaria bacupensis are preserved. These two specimens show uniform tissue, although very thin-walled, extending from the stele to the outer margin of the cortex and suggest that within this uniform cortex differentiation of the middle cortex took place.

The middle cortex may be of different structure. It is observed as"hyphal tissue", loose parenchyma,"arm-parenchyma" or may connect the stele with the outer cortex in the form of narrow bands of tissue. The hyphal tissue is, as in the axis, probably produced by a meristem arising in the innermost cells of the outer cortex. In one instance (pl.XXII,fig.85) this meristem can be observed. The appendage was previously described by WEISS (1902) as probably belonging to Stigmaria radiculosa. This assumption is however unfounded as the appendage has no similarity with the appendage bases and appendages observed with Stigmaria radiculosa. The "hyphal" middle cortex is shared by many other species of Stigmarian appendages. SEWARD (1910) also figured the same specimen and described the meristem although he omitted that the meristem originally arises in cells of the outer primary cortex. This is however I think, shown in pl.XXII,fig.85.

The bands of cells in the middle cortex region are recognizable in pl.XXIV,fig.91. A similar appendage has been described by LECLERCQ (1927). The "arm-parenchyma" in the middle cortex region of Stigmaria arranensis and St. sewardi and the loose parenchyma in Stigmaria radiculosa appendages have already been described (p.80,47). In the latter species the middle cortex is separated from the outer cortex by a single layer of very uniform cells, which is also present in a few other species but nowhere so perfectly preserved.

In the middle cortex groups of tracheids may be observed which, surrounded by uniform parenchymatous cells, branch from the protoxylem of the vascular strand and connect the stele with the cortex. The strands, called trabecular bridges, are in most cases surrounded by remnants of the undifferentiated primary cortex and not by middle cortex as STEWART (1947) suggests. They may however, as described by WEISS (1902), be surrounded by tissue of the same type as the middle cortex, in which case it seems probable that the primary cells surrounding the tracheids have been transformed into middle cortex also similar to the meristems around the appendage traces in Stigmaria radiculosa.

The outer cortex in most Stigmarian appendages can be divided into four zones which although greatly reduced correspond to the outer cortex of the Stigmarian axis. The transition zone is the innermost of these four and from this tissue usually the middle cortex is differentiated. It corresponds to the transition zone described of the Stigmarian axis and figured in pl.V,fig.21a. The cells of this transition zone are thin walled and must have disintegrated together with the middle cortex very quickly.

In the appendage often referred to already (pl.XXIV,fig.91) this zone and its transitional character can be observed although it is of course greatly enlarged.

Meristematic activity in the transition zone (apart from the mentioned specimen in which the middle cortex is produced,WEISS,1902) has been observed by WEISS (1904) who describes a Stigmarian appendage in which at the intrusion of a fungus the transition zone (WEISS:"middle cortex") is stimulated to considerable meristematic activity.

The remaining outer primary cortex may be divided into three zones, the limiting layer, the outer zone and the inner zone. In the appendages of Stigmaria asteroidea a limiting layer is missing; in other appendages, especially in very small specimens, it is difficult to distinguish between outer and inner zone. With few exceptions as in Stigmaria arachnoidea (pl.XXI,fig.80) the arrangement of cells is the same in the outer as in the inner zone.

The outer zone consists of thin-walled parenchyma and in larger appendages the cells in this zone are frequently tangentially stretched; in layers underneath the limiting layer, cells in a stage of radial division may be observed. The cells of the outer zone are larger than those of the limiting layer but generally smaller than those of the inner zone.

Thickened cell walls and cells filled with black substance make the inner zone of the appendage conspicuous. There are many variations in the way the cell walls are thickened and it may be that in some instances these are of specific value.

It was shown however that appendages coming from one axis may vary in the structure of their inner zone (p.100) and it seems also probable that the type of thickening varies in different levels of the appendage. It may therefore not be entirely justified to describe these different appendage types as species, as this was done by KOOPMANS (1928) who named a conspicuous appendage Stigmaria arachnoidea. Some of these different types of inner zones of appendages are figured and described in different parts of this thesis (pl.XXI and pl.XXII). The thickened cells of the inner zone of the outer cortex were not dead cells and in some instances evidence of meristematic activity can be seen in this zone (pl.XXII,fig.86). The inner zone corresponds in position (p,138,fig.24) to the outer primary cortex of the axis and in some instances to the sclerotic elements separating the superficial cortex from the outer cortex, or both. The outer zone of the appendage cortex is therefore probably the equivalent of the superficial cortex of the axis and may correspond to the innermost layers of it.

The relative size of cells varies according to their position in the cortex. Generally it can be said that the cells increase in size towards the middle of the outer cortex and decrease again towards the inside. In the case of the var. boonvillensis appendages this was measured. One radial row of cells furnished the following results:

Diameter of cells in mm:

Lim.layer	1	2	3	4	5	6	7	8 Inside
Long.ø:	0.10	0.14	0.15	0.17	0.28	0.28	0.21	0.21 mm
Rad. ø:	0.07	0.07	o.10	0.12	0.19	0.19	0.10	0.07 mm

Another row of cells of the same appendage showed the data:

Lim.Layer	1	2	3	4	5	6	7	8	Inside
Long.ø:	0.10	0.13	0.14	0.21	0.26	0.31	0.28	0.17	mm
Rad. ø:	0.04	0.07	0.09	0.14	0.12	0.10	0.10	0.07	mm

A third measurement was taken from a longitudinal section of a var. boonvillensis appendage. The outer cortex in this specimen was thicker and therefore data from 14 cells could be obtained:

From outside to inside, radial diameter in mm:

1	2	3	4	5	6	7	8	9	10
0.03	0.09	0.10	0.10	0.13	0.14	0.17	0.17	0.17	0.21

11	12	13	14
0.19	0.13	0.10	0.07

The fact that the diameter of the cells in the outer cortex increases towards the middle and decreases again towards the inner side of the outer cortex can also be shown by data obtained from Stigmaria bacupensis appendages. It may be recalled here that the cortical cells of the Stigmaria bacupensis appendage are practically isodiametric in transverse section.

Diameter of cells from outside to inside of outer cortex in mm:

Measurement I	Measurement II	
0.015	0.015	= Lim.layer
0.030	0.022	
0.037	0.030	
0.030	0.035	
0.030	0.045	
0.022	0.022	
	0.016	

The largest diameter of a cortical cell in this appendage (Ko 2592) was 0.052 mm. This large cell was far from the attachement of the trabecular bridge to the cortex.

For _Stigmaria_ _bacupensis_ the increase in size of outer cortical cells near the tracheids of the trabecular bridge (p.178) was measured as an example:

Diameters in mm:

Row with enlarged cells	nearest normal row
0.015	0.015 = lim.layer
0.095	0.017
0.030	0.030
0.035	0.033
0.030	0.030
0.030	0.022
0.035	
0.022	

It indicates that not only the cells near the trabecular bridge are larger but also that in this place the outer cortex is thicker i.e. there are more cells in radial direction.

Most of the Stigmarian appendages studied have a distinct superficial layer of cells, the limiting layer. It does not seem to be an epidermis in _sensu_ _stricto_ and all the walls of the cells in the limiting layer are of the same thickness. Only by the difference in size, arrangement and shape of cells a limiting layer can be recognized (pl.XXi,fig.80,82).

An appendage of _St._ _sewardi_ var. _boonvillensis_ (Ac 6) showed the limiting layer quite clearly. Measurements of a subsequent series of cells in tangential direction furnished the following data:

Diameters of cells of limiting layer in mm:

tangential	radial	ratio
0.105	0.090	1.16
0.111	0.105	1.05
0.127	0.097	1.30
0.067	0.067	1.00
0.067	0.060	1.11
0.082	0.075	1.09
0.105	0.075	1.40
0.105	0.052	2.01
0.150	0.060	2.50

When these diameters are compared with those of cortical cells (p.153,154) it is quite evident that the cells of the limiting layer are smaller than the average cortical cells. The var. boonvillensis appendage from which the above measurements are taken has a circumference of 40 mm. It will be explained later (p.158) that the size of cortical cells is also related to the circumference of the appendage. Because of this rule the diameters of cortical cells of smaller circumference are much smaller. An appendage of Stigmaria arranensis (Ac 31) has the circumference of 18 mm.

The diameters of cells in the limiting layer are in mm:

tangential	radial	ratio
0.030	0.060	0.50
0.045	0.030	1.50
0.030	0.030	1.00
0.030	0.030	1.00
0.037	0.037	1.00
0.037	0.045	0.82
0.030	0.060	0.50
0.030	0.045	0.66
0.045	0.045	1.00

It is evident that the cells have in the average a much smaller diameter. A comparison shows furthermore that the cells in the limiting layer of the St. arranensis appendage are stretched in radial direction whilst the limiting layer cells of the boonvillensis appendage are elongated in tangential direction. This fact is also expressed by the ratios : $\frac{\text{Tang.diameter}}{\text{Rad. diameter}}$.

The cells underneath the limiting layer are usually considerably larger than the limiting layer cells. In the St. arranensis appendage already cited, the cells underneath the limiting layer have the following diameters: Radial from 0.07 to 0.14 mm and tang. from 0.05 to 0.07 mm. The largest diameter of a cell in the outer cortex was 0.24 mm.

The cells of the limiting layer are elongated in longitudinal direction but are shorter than the cortical cells underneath. A longitudinal section through a St. sewardi var. boonvillensis appendage showed that the cells of the limiting layer had a longitudinal diameter ranging from 0.07 to 0.1 mm. The radial diameters of the same group of cells ranged from 0.03 to 0.05 mm. A similar result is obtained from longitudinal sections through the appendages of St. bacupensis (pl.XX,fig.79). The longitudinal diameter of the epidermal cells in these appendages is uniformly about 0.05 mm (average radial diameter = 0.02 mm).

In some cases, especially in the larger appendages the limiting layer can be observed in a state of exfoliation. P.87,fig.12, shows the limiting layer bursting off in groups of cells. The limiting layer may be chafed off as the appendage is growing through the substratum or it may burst at the increase in diameter of the appendage and is replaced by layers of cells of the outer zone of the outer cortex.

Where the cortical bridge is attached to the outer cortex tracheids may be observed in the cortical tissue of the appendage. These may occur in the transition zone but in the appendages of Stigmaria bacupensis the tracheids of the trabecular bridge terminate underneath the limiting layer where they merge with a strand of annular elements,parallel to the appendage stele. This strand (WEISS,1902) can be observed in pl.XXII,fig.87 which shows a tangential section through the outer zone of an appendage.

The maximal size of the cortical cells seems to be, as the size of the tracheids in the vascular strand, related to the circumference of the appendage. This is demonstrated by the graph on p.159 which also suggests that the total width of the outer cortex is, of course, dependent on the circumference of the appendage.


40
30
20
10
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44 mm
CIRCUMFERENCE OUTER CORTEX


0.4
0.3
0.2
0.1
0.0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44 mm
CIRCUMFERENCE OUTER CORTEX

11/4/1933

It is natural at first sight to compare the Stigmarian appendages with leaves since their phyllotaxy and their insertion in the stele of the axis resembles that of Lepidodendron and other arborescent Lycopod leaves.

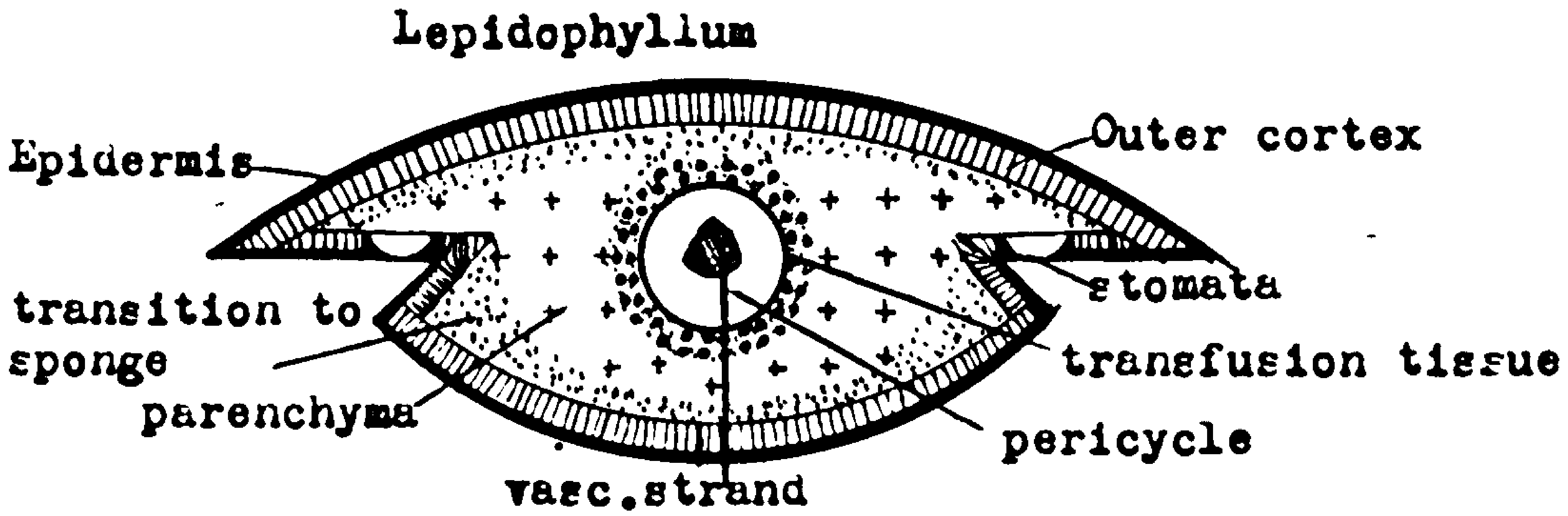
The tissues in the appendages are of the same arrangement as in the leaves although in both some specialization according to their function can be recognized. The vascular strand, essentailly the same in leaves and appendages, is surrounded by the pericycle in both species. Under the epidermis the cortex of the leaf can be divided into inner cortex or transfusion tissue, middle cortex or aerenchyma and outer cortex. These tissues have their equivalent in the Stigmarian appendages. The inner cortex of the appendage is rarely observed. Examples have been stated in which the inner cortex is transformed into middle cortex. The same is the case in the leaves although in these a thick sheath of inner cortex surrounding the stele usually remains. In this sheath tracheids may be differentiated which are called "transfusion tissue" in recognition of their resemblance to a similar tissue in the needles of modern conifers. An equivalent area in the appendages would be the so-called cortical bridge which is, as described, primary cortex with tracheids.

The inner cortex (transfusion tissue) is in the larger leaves surrounded by an aerenchyma, the equivalent of the middle cortex of the appendages. In smaller leaves (the narrower part of leaves respectively), as in small appendages, the cortex is solid and uniform from the epidermal layer to the stele.

The outer cortex of the appendages is far more differentiated than the outer cortex of the leaves. In the latter only a few layers of very thick walled cells are underneath the epidermal layer which seems to have suberized walls. In the Stigmarian appendages several zones can be recognized, the inner zone probably corresponds to the thick walled outermost cortex of the leaf whilst the outer zone may be a multiple epidermis as this was described for the Stigmarian axis in comparison with the Lepidodendroid shoots.

There is therefore some justification for supposing a certain degree of homology between the leaves of the arborescent Lycopods and the appendages of Stigmaria.

Anatomically and morphologically similar to the appendages of Stigmaria are the roots of Isoetes.



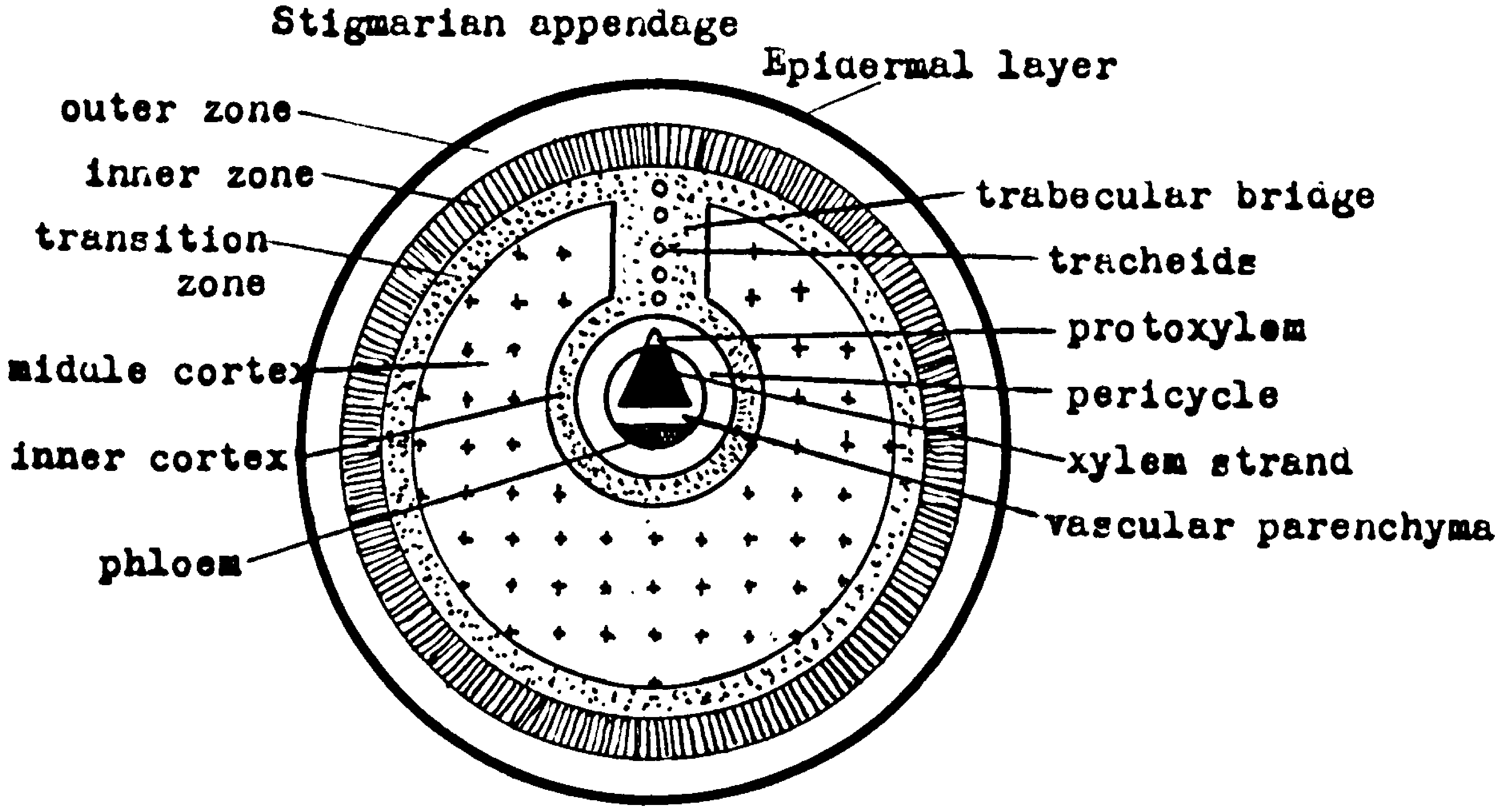


fig.25: Diagrammatic drawing of Lepidophyllum sp. and an appendage of the *Stigmaria ficoides* type in transverse section.

Summary:

Six species of the Stigmaria ficoides type have been described. This type is characterized by its medullated stele and the uniform type of outer xylem. The phloem is of the same type as that observed in several Lepidophloios species. The cortex is of the same structure and shows the same variations as in Lepidodendron and Lepidophloios. It is probable that Stigmariae of the ficoides type with the exception of, perhaps, Stigmaria asteroidea the relation of which is not so obvious, are the basal organs of Lepidodendron and Lepidophloios.

The outermost parts of the cortex of Stigmaria vary from the corresponding region in the Lepidodendroid shoot in as much as in Stigmaria a superficial cortex is present, probably a multiple epidermis, whilst in Lepidodendron a single suberized epidermal layer is present.

The appendages of Stigmaria have a certain degree of homology with the leaves of the aerial shoot and break through the superficial cortex of the axis.

PART III

STIGMARIAE WITH A DIPLOXYLOID STELE

9. Stigmariae with a diploxyloid stele:

The contrast between the apparently purely centrifugal development of the wood of Stigmaria and the centripetally developed primary wood of the arborescent parts of the Carboniferous Lycopods had for long puzzled paleobotanists. WEISS (1908) drew attention to a Stigmaria with a diploxyloid stele in the English coal ball flora but RENAULT (1893) had still earlier reported a similar Stigmaria in French coal deposits which he named Stigmaria brardii. This is probably the basal organ of Sub-Sigillariae, Stigmariopsis (SOLMS'LAUBACH, 1894).

In all, four species of Stigmariae with a diploxyloid stele have already been described. These are Stigmaria bacupensis Scott et Lang, Stigmaria lohesti Leclercq, both species with a solid core of primary xylem, Stigmaria weissiana Leclercq with a medullated stele and Stigmaria brardii Renault with both a medullated and a solid stele in branchings of different order.

Three new species are described in this thesis which judging from the number of sections in the various collections are quite common in the English coal ball flora. It seems however from fragments of Stigmariae in different slides that the number of species is greater than commonly realized and it may well be that future studies will reveal the existance of yet more species. On the other hand it seems possible for reasons explained later that Stigmariae cited in this thesis among different species are part of one plant. Stigmariae in this group are mainly identified on differences in the stelar structure. The cortex proved to be uniform in all species with the exception of St. weissiana

a) Stigmaria weissiana Leclercq:

This species was first described by WEISS (1908). LECLERCQ (1928) reported the species in the Belgian coal ball flora and named it after its first author, WEISS. He (1930) pointed out in a second memoir on the species its affinities with Bothrodendron mundum and called it Stigmaria bothrodendroni.

Of the stele of this species only the pith and the xylem are preserved. The outer xylem consisting, except for a few irregularities (p.57), of radially arranged scalariform tracheids, appears to be solid. Tang. sections show that the medullary rays are in fact very short in the longitudinal direction. Longer principal medullary rays have merged with secondary medullary rays as is suggested by WEISS (pl.XV, fig.3 and 4) and are similar in structure as the principal medullary rays of Stigmaria shurneyensis (p.167), but in principal medullary rays of Stigmaria weissiana tracheids of the outer xylem are attached to the appendage trace. The secondary medullary rays differ in height and width from those of the Stigmaria ficoides type and Stigmaria bacupensis but are similar to those of Stigmaria shurneyensis.

The inner xylem consists of only a few layers of cells with the smaller tracheids to the outside. Some of these small elements may be, as WEISS (1908) suggests, protoxylem elements. The innermost, scalariform tracheids of the inner xylem have a very large diameter, in fact larger than any other tracheid in the outer xylem. This very conspicuous feature distinguishes the stele of Stigmaria weissiana from any other diploxyloid stele. Only the axis of Stigmaria shurneyensis shows a similar development in a solid core of inner xylem and, of course, Bothrodendron mundum has the same type of stele.

This uniformity of the stelar structure in both *Bothrodendron mundum* and *Stigmaria weissiana* has led WEISS (1908,1930) to the assumption that *Stigmaria weissiana* is the basal organ of Bothrodendron, in fact the first *Stigmaria weissiana* specimens discovered were described as vascular axis of Bothrodendron by WILLIAMSON (1889). The stele of the latter is known to be either solid or medullated. In conformity with this, the diameter of the medulla of *Stigmaria weissiana* may vary considerably. WEISS (1930) figures a specimen with a very large medulla, the pith cells are cylindrical and arranged in longitudinal rows as, described in p.37, in the pith of *Stigmaria radiculosa*. A specimen with a much smaller pith is described earlier by the same author (1908) and the specimen of *Stigmaria weissiana* described by LECLERCQ (1928) shows a still smaller medulla, consisting of few cells only.

Stigmaria shurneyensis showing great affinities with *Stigmaria weissiana* and differing from any other Stigmaria in structure may be the protostelic type of the same species. But the stele of *Stigmaria weissiana* is generally very small, the largest observed is 2.35 cm in circumference, whilst *Stigmaria shurneyensis* may have an extremely large stele (circ. 12.5 cm).

Cortex:

Of the cortex of *Stigmaria weissiana* very little is preserved. Only parts of the secondary cortex and small fragments of the outer primary cortex can be observed, the latter consist of uniform,small cells. Appendage traces have been observed in the secondary cortex which consists of conspicuously large rectangular cells , relatively larger than in any other species of Stigmaria.

Appendage bases and appendages of Stigmaria weissiana are not known. So far the cortex of Stigmaria weissiana is preserved it is of the same structure as that of Stigmaria shurneyensis but differs from all other species of Stigmariae with a diploxyloid stele especially in the appearance of the secondary cortex.

b) Stigmaria shurneyensis, a new species with a solid stele:

The Kidston coll. contains a series of sections (No.652 A-F,653 A,B,) of coal balls from Shurney Ford near Bacup,Lancs. containing a Stigmaria which consists of a solid core of inner xylem surrounded by a very large amount of outer xylem.

The vascular cylinder of the specimen in slide 653 has a circumference of 12.5 cm whilst the specimen in slide 652 is smaller and the circumference of its xylem cylinder is about 6 cm. The inner xylem core of the latter specimen has a diameter of 0.5 mm and consists of few scalariform tracheids of large diameter (pl.XVIII,fig.69). Thus the specimen shows affinities with Stigmaria weissiana. Annular tracheids are not observed, the smaller cells on the outer margin of the inner xylem may, however, possibly be protoxylem elements.

The outer xylem is regularly developed, on the outer margin, however, irregularities in growth (p.57) may occur. The principal medullary rays are small and short and only the appendage trace in them distinguishes them from secondary medullary rays. In tangential section the medullary rays are lens-shaped, the appendage trace is normally situated in the centre of the principal medullary ray and the walls of the neighbouring tracheids bulge out around it (pl.XVIII,fig.70).

Elements of the outer xylem do not seem to be attached to the appendage trace, the only point in which these medullary rays differ from those of Stigmaria weissiana. The xylem cylinder is surrounded by a Stigmarian cortex with attached appendages. This cortex probably belongs to the described stele. The outer zone of the primary outer cortex and the secondary cortex are preserved but the inner and middle cortex is missing. The outer primary cortex consists of cells of fairly uniform size and shape, the cells seem to become gradually smaller towards the outside of the cortex but a superficial cortex as in some of the Stigmariae of the ficoides type is not observed. Towards the inside of the outer cortex the cells are radially arranged and show in their regularity of the diameters great similarity to the secondary cortex of Stigmaria weissiana.

Pl.XXI,fig.83, shows an appendage base attached to the outer cortex. It is, like the few other appendage bases preserved, of very small diameter. The xylem strand of the appendage base is arranged in the same manner as in the appendage traces in the medullary rays and resembles more the vascular strand of leaves than that of a Stigmarian appendage. There is no indication for phloem or secretory tissue for in the zone in which it was probably situated the tissues are badly preserved. The xylem is surrounded by a narrow parenchymatous zone into which the protoxylem projects, the pericycle. The stele of the appendage is surrounded by an inner cortex. The outer cortex of the appendage base shows no differentiation into zones. A limiting layer was not observed.

c)Stigmaria lohesti Leclercq:

This species, observed in small specimens only, consists of a solid strand of centripetally developed inner xylem and a solid cylinder of outer xylem. The inner xylem consists, in contrast to that of Stigmaria shurneyensis and Stigmaria weissiana of tracheids of a uniform diameter only on the outer margin are very small xylem elements which, according to WEISS (1929) are the protoxylem elements. The tracheids of the outer xylem are regularly arranged and are approximately of the same diameter in the inner and the outer xylem. In contrast to this WEISS (1929,fig.2) shows another specimen (Scottcoll.93) under the same name in which the tracheids of the outer xylem show a considerably larger diameter than in the inner xylem. Furthermore is the outer xylem of this specimen far more dissected by appendage traces and medullary rays. It seems that the latter specimen should better be placed in a new species.

The principal medullary rays are very short and relatively wide (WEISS,1929,fig.4) and are accompanied by a very small amount of parenchyma. The narrow long parenchymatous tip of the medullary rays as in Stigmariae of the ficoides type is missing but the appendage trace has the triangular shape of the latter type. WEISS (1929) compares Stigmaria lohesti with the specimens described as Stigmaria shurneyensis in this thesis but since the inner xylem and the medullary rays vary in both species this correlation is unfounded. The affinities of Stigmaria lohesti are rather with Stigmaria vascularis and

Stigmaria sigillarioides and it may be that the species represents the ultimate ramifications of the main branches of the latter two. Other tissues than the xylem are not known of *Stigmaria lohesti*

d)*Stigmaria brardii* Renault:

RENAULT (1893) described a Stigmarian axis as *Stigmaria brardii*, apparently under the impression that it is the basal organ of *Sigillaria brardii*. It has most unfortunately received little attention in the literature about Stigmaria. The main reason for this neglect seems to be that RENAULT described it as a rhizome, an opinion WILLIAMSON (1892) talking about an entirely different structure had so sternly opposed.

The inner xylem of *Stigmaria brardii* has a crenulate inner and outer margin, as it is typical of a Sigillarian stele. RENAULT's figure (1893,pl.XXXIX,fig.5) suggests that the inner xylem is on the verge of being dissected into bundles of primary xylem as they are known of *Sigillaria menardi*. This is a transitional stage which has been described of the stele of the trunk of *Sigillaria brardii*. The outer xylem appears to be rather solid and the appendage traces outside the xylem show a great amount of radially arranged outer xylem, both features which have also been observed on Stigmariae which are described in this thesis as *Stigmaria sigillarioides*.

The cortex of *Stigmaria brardii* is of the dictyoxylon structure same as that of the Sub-Sigillaria stems.

It is most probable that *Stigmaria brardii* is the anatomical structure of a Stigmariopsis species. The crenulate margin of the inner xylem would most likely produce the peculiar "calamitoid" pith casts observed of Stigmariopsis and the "dictyoxylon" cortex would, as has been suggested by SOLMS (1894), produce the Stigmaria rimosa or Stigmaria flexuosa relief in impressions. Furthermore, Stigmariopsis has been found in connection with Sub-Sigillariae to which group of the arborescent Lycopods the dictyoxylon structure is restricted.

Together with the medullated stele of Stigmaria brardii another Stigmarioid stele is described by RENAULT which is significant by its solid core of inner xylem (1893, pl.XXXIX,fig.11). The inner xylem is most unfortunately not clearly drawn in this figure but it seems to have consisted of irregularly arranged, very small cells. The outer xylem is largely dissected and it is in this and the size of the stele that the specimen has such a great similarity with Stigmaria bacupensis (p.172). RENAULT describes the figure:"Coupe transversale d'un rameau de Stigmaria pri dans le voisinage de la tige principale", indicating for the first time that a Stigmaria (i.e.Stigmariopsis) may have branches of varying anatomical structure, one type, having a medullated stele and a solid ring of outer xylem, the main branch, and another type with a solid inner and a dissected ring of outer xylem, a side branch.

Further evidence, confirming RENAULT's findings, was obtained from specimens in the Kidston coll. and these will be described later in this thesis,(p.189).

e) *Stigmaria bacupensis* Scott et Lang:

Specimens of this species are always of a small diameter. The smaller variety which has been described by LANG (1923) shows no or little secondary growth in the cortex. Larger specimens showing considerable secondary growth are described by LECLERCQ (1930) in her "Monograph on *Stigmaria bacupensis*".

Axes in the state represented by LANG's specimen are very small and in their total diameter they are of the same average diameter as appendages attached to *Stigmariae* of the *ficoides* type. The specimens described by LECLERCQ may be larger but even these are far smaller than any other Stigmarian axis described. This leads to the conclusion that *Stigmaria bacupensis* may either be the basal organ of a very small plant or an ultimate branch of a larger Stigmaria species.

The conspicuously small appendages of *Stigmaria bacupensis* are figured in many paleobotanical textbooks as more or less typical"Stigmarian rootlets" mostly under the name *Stigmaria ficoides* or *Stigmaria* sp. They differ however from most types of Stigmarian appendages and cannot considered to be typical.

DUERDEN and WRIGHT (1952) described a specimen of a plant which bears a resemblance to *Stigmaria bacupensis* in the structure of the vascular system and the cortex. The appendages attached to this specimen are slightly endogenous and bear small leaves each of which has a ligule attached to its adaxial surface near the base (WALTON,1953).

After the examination of slides of different collections containing Stigmaria bacupensis it seems that there are slight variations in the structure of the cortex and the stele. Two varieties have been mentioned already, the specimens described by Lang and Leclercq, which are, however, connected by transitional forms. It seems quite possible that these differences in structure are not only different stages of growth, as LECLERCQ (1930) suggests, but also indicative of different species and it may be advisable to consider Stigmaria bacupensis as a form species.

Stele:

The stele of Stigmaria bacupensis consists of a core of very small irregularly arranged tracheids, the inner xylem, which is surrounded by a cylinder of radially arranged scalariform elements forming the outer xylem. The inner xylem may be completely differentiated into tracheids, as in the specimen figured by LECLERCQ (1930, pl.1,fig.1) or may be a mixture of parenchyma and tracheids. Steles of Stigmaria bacupensis observed in connection with Stigmaria sigillarioides (p.189) always show a completely differentiated inner xylem whilst in the small specimens, in the state represented by LANG's specimen, only few tracheids can be observed in the centre of the stele. On the inside of the outer xylem tracheids are however differentiated (pl.XIX,fig.73,pl.XX,fig.78). In one instance (Kc-382) no tracheids at all were differentiated in the centre of the stele, the specimen appeared to be medullated and thus resembled a Stigmaria of the ficoides type, such as Stigmaria asteroidea. Practically all transitional stages of differentiation of tracheids in the inner xylem can be observed.

In contrast to Stigmaria weissiana and other Stigmariae with a diploxyloid stele, the inner xylem is not separated from the outer xylem by annular tracheids, i.e. protoxylem elements. In fact, as in some specimens of the Stigmaria ficoides type, a gradual transition from the inner to the outer xylem exists and it is difficult to draw the line between both elements of the xylem cylinder. Pl.XIX,fig.73 shows the transition zone of inner to outer xylem and is a larger magnification of pl.XX,fig.78. It is evident in this figure that elements, undoubtedly belonging to the inner xylem, protrude into an area in which in other places the outer xylem is recognizable by the radial arrangement of cells.

This coincides with the mode of secondary growth of the vascular tissue explained in the description of Stigmaria sewardi (p.61).

In Stigmaria bacupensis it would seem that undifferentiated cells at the surface of the inner xylem gained meristematic activity and by repeated division formed radially arranged tissue between the appendage traces which were probably the first vascular elements differentiated. The growth of the outer xylem may have occurred before the outer xylem was differentiated. In this respect Stigmaria bacupensis shows considerable affinities with the apex of the shoot of Isoetes lacustris. In Isoetes, as LANG (1915) points out, protoxylem strands other than those of the leaf traces are not recognizable. The procambium can be divided into an inner and outer zone (inner and outer xylem in Stigmaria), meristematic activity starts very early, before any lignification of vascular elements other than those of the leaftraces is recognizable.

The outer xylem of Stigmaria bacupensis is split into a great number of bundles by the appendage traces. These, although smaller, show the tongue shape, observed in species of the St.ficoides type. It seems, however, that the number of appendage traces per length unit of xylem is greater then in any other Stigmaria.

The xylem strand of a specimen of Stigmaria brardii with a solid stele resembles, as has already been mentioned, the xylem of Stigmaria bacupensis.

Appendage traces outside the xylem cylinder consist of both irregularly and radially arranged tissue and are surrounded by parenchyma in which the phloem (secretory strands) seems to have been situated.

Other stelar tissues than the xylem are not known of Stigmaria bacupensis.

Cortex of small specimens:

Only the outer parts of the cortex, the outer primary cortex and in some instances the secondary cortex are known of this species. Other tissues are normally not preserved. In one specimen remains of the tissue of the same appearance as shown in pl.XIX,fig.74 were observed in the cavity between outer cortex and stele and it may be that these were the remains of the middle cortex. This would suggest that Stigmaria bacupensis had the same type of middle cortex as the axes of Stigmaria sigillarioides.

The structure of the appendage traces in the middle cortex area of Stigmaria bacupensis (LECLERCQ,1930,pl.VI, fig.45) agrees with the appendage trace in pl.XIX,fig.74, and therefore it seems likely that the middle cortex in both Stigmaria bacupensis and Stigmaria sigillarioides was of the same type.

The outer cortex may show different structural features which probably represent different stages of growth but may in some cases also indicate specific difference. The youngest state of cortical tissues so far observed has been described by LANG (1923). This specimen is figured in pl.XX,fig.77,77a. The outer cortex of this specimen and few other, little larger, axes consists of uniform tissue made up of small thin-walled cells which gradually decrease in size in centrifugal direction. On the inside of this tissue few radially arranged cells may occasionally be observed, which suggest commencing secondary growth. Immediately outside this zone or in a corresponding level in regions where secondary growth has not taken place groups of cells filled with black substance may occur (pl.XX,fig.77a). In the same region, i.e. in the zone of these black strands, the appendages are inserted and break through the outer layers of the primary cortex,as described by LANG (1923). This endogenous insertion is also demonstrated by pl.XX,fig.77.

Appendages:

It is most striking in transverse sections of axes of Stigmaria bacupensis, especially the smaller specimens, that the appendages and appendage bases outside the axis are all cut in transverse section. This indicates that the appendages must have had a course more or less parallel to the axis, the appendages probably being directed forward towards the growing point of the axes in contrast to the species of the Stigmaria ficoides type in which the appendages are more or less vertically upon the axis.

In the appendage base it is possible to correlate the tissues of the base (pl.XX,fig.77) with the cortical tissues of the axis. The stele of the appendage base is of the usual triangular shape, the protoxylem being situated at one corner of the triangle. Secondary growth in the appendage stele has been observed only in one instance (Kc-1932). This appendage is larger than in the usual specimens and the middle cortex in it is preserved, which is of the same structure as in pl.XX,fig.79. The secondary xylem of the specimen is separated from the primary strand by undifferentiated parenchyma, similarly as is shown in pl.XXIV,fig.93. The primary xylem strand is surrounded by parenchyma (p.181,fig.26) which in its inner part corresponds to the vascular parenchyma of the appendages attached to axes of the Stigmaria ficoides type whilst the outer part may be the pericycle. In some instances remains of this parenchyma may be observed surrounding the xylem of the axis (Kc-2592).

Phloem tissue or the equivalent secretory strands could not be observed in appendages of Stigmaria bacupensis.

Whilst the similarity in the growth of the axis of Stigmaria bacupensis and the shoot of Isoetes lacustris has already been mentioned (p.174) the appendages show affinities with the roots of Isoetes australis (WILLIAMS, 1943). In these, the innermost layers of cortical cells have been named endodermis.

Regularly the stele is connected with the cortex of the appendages by a strand of cortical tissue in which tracheids are developed.These tracheids branch from the protoxylem elements, pursue an oblique outward course in the middle cortex region and terminate in short transfusion tracheids underneath the limiting layer of the appendage.

The cortical cells in the vicinity of these "transfusion tracheids" are greatly enlarged. This is in striking contrast to the appendages of Stigmariae of the ficoides type in which the tracheids of the trabecular bridge always terminate in a strand of tracheids parallel to the appendage stele and situated in the transition zone,viz. far deeper in the cortex.

The outer cortex of the appendage of Stigmaria bacupensis may be, as the appendages of Stigmariae of the ficoides type, divided into three zones an outer,inner and transition zone and a limiting layer, although the zones in appendages of the both types are not clearly homologous.

In Stigmaria ficoides types the inner zone of the appendages was described (p.153) as corresponding to the sclerotic elements of the outer cortex and the outer zone as corresponding to the superficial cortex of the axis, i.e. is probably a multiple epidermis. In Stigmaria bacupensis appendages the correlation must be different, according to the completely different structure of the cortex of the axis. The nature of the latter will be more clear after the sigillarioid Stigmariae and their correlation with the aerial parts have been described.

The main differences between Stigmaria bacupensis and the cortex of Stigmaria ficoides types may be mentioned here. In species of the latter type the appendages are inserted in the superficial cortex with the inner zone of the appendages continuous with the sclerotic elements between superficial and outer cortex.

These sclerotic elements are separated from the secondary cortex by a primary tissue, varying in width, the outer zone of the outer primary cortex. In Stigmaria bacupensis, however, sclerotic elements are immediately outside the secondary tissues and the outer primary cortex is outside the sclerotic elements. Since the appendages are inserted in the zone of the sclerotic strands they therefore break through the outer primary cortex in Stigmaria bacupensis in contrast to the appendages of the ficoides type which are, as mentioned above, breaking through the layers of the superficial cortex only.

Thus appendages of both types originate in the zone of the cortex in which sclerotic elements are developed and the inner zone of the appendages corresponds to the sclerotic zone of the axis. But in the Stigmaria bacupensis appendages the outer zone corresponds to the outer primary cortex whilst in the appendages of Stigmariae of the ficoides type the outer zone corresponds to the superficial cortex of the axis and the transition zone is the equivalent of the outer primary cortex.

Because of this difference between the appendages of both species it is clear why the tracheids of the trabecular bridge terminate in apparently different levels of the appendage cortex i.e. outside and inside the inner zone. Morphologically they terminate in the homologous zones, the outer primary cortex.In other words, if the superficial cortex of Stigmaria ficoides types is a multiple epidermis appendages have the same multiple epidermis whilst the limiting layer of appendages of Stigmaria bacupensis is only a single epidermal layer.

Appendages of the Stigmaria bacupensis type really correspond more to shoots, since their epidermal layer is underlain by the outer primary cortex whilst, if our assumption is correct that the outer zone of the Stigmaria ficoides type appendages is a multiple epidermis, appendages of the latter type are, from the point of view of cortical structure, more root-like. It was on appendages similar to those of Stigmaria bacupensis on which the ligulate leaves were observed (DUERDEN and WRIGHT,1952).

In slide 1392 (Kidston coll.) two very small appendages of Stigmaria bacupensis can be observed in which solid tissue extends from the stele to the limiting layer,i.e. a middle cortical cavity is not present. These specimens may be sections near the growing point of appendages in which the tangential expansion had not yet taken place, however, tracheids in the stele of these specimens were already differentiated.

The cortical tissue in these specimens is fairly uniform. The cells become gradually larger towards the inner zone of the cortex which is marked by slightly thicker cell walls. From there they decrease in size again, without altering shape or arrangement, towards the stele. The cells are very thin-walled in the middle cortex area. This slide seems to prove that the middle cortex is not produced by the apical meristem but is a secondary development in a primary tissue. The cells of the outer cortex in the area where the tracheids of the trabecular bridge terminate are greatly enlarged,(p.178) similarly as the cells in the corresponding transition zone of Stigmaria ficoides type appendages.

Fig.26: Vascular Strand of Appendage of <u>Stigmaria bacupensis</u>. Kc-2529

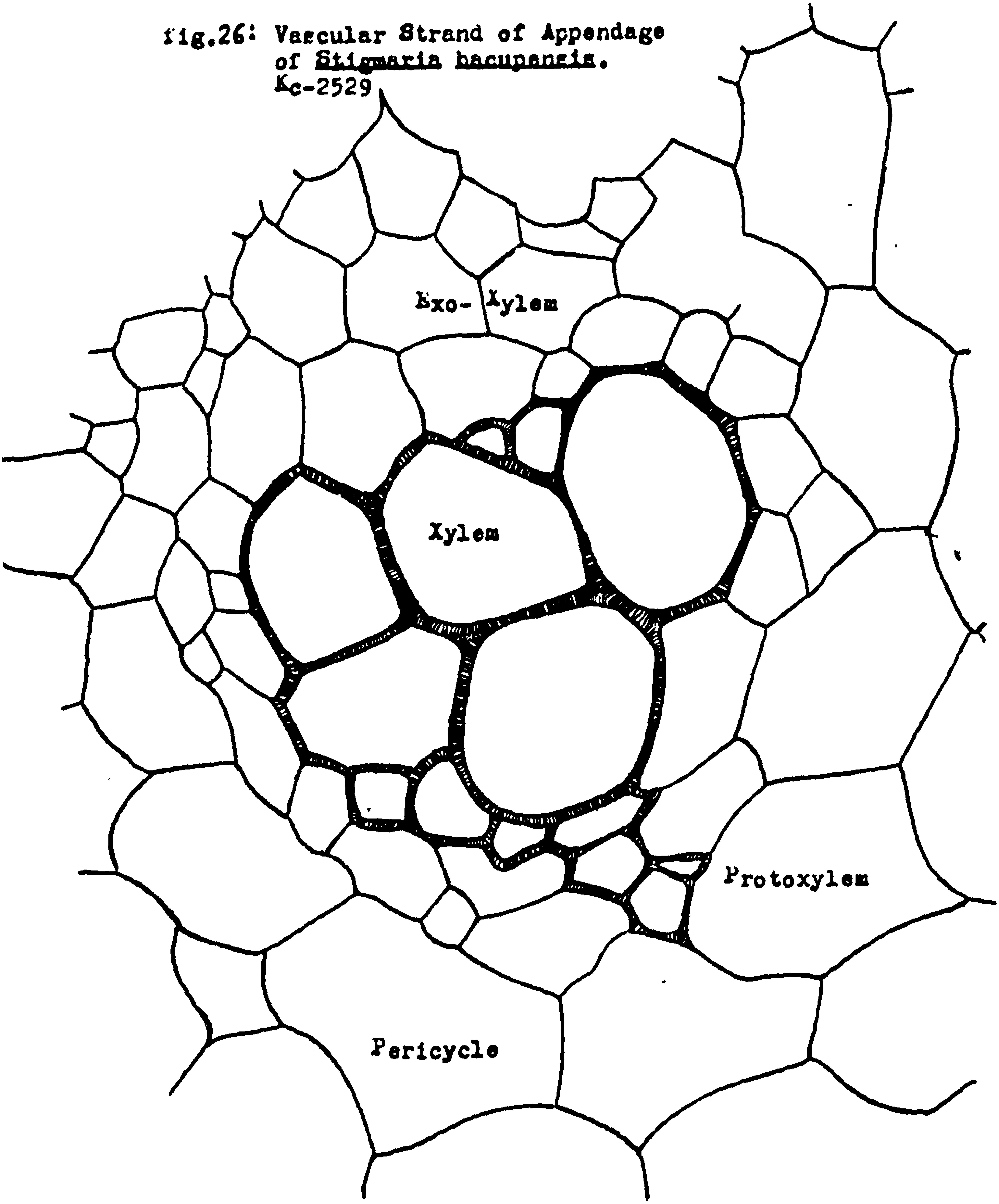


Fig.27: Outer Cortex of Appendage of Stigmaria bacupensis.
Scale lo. Gc-365.

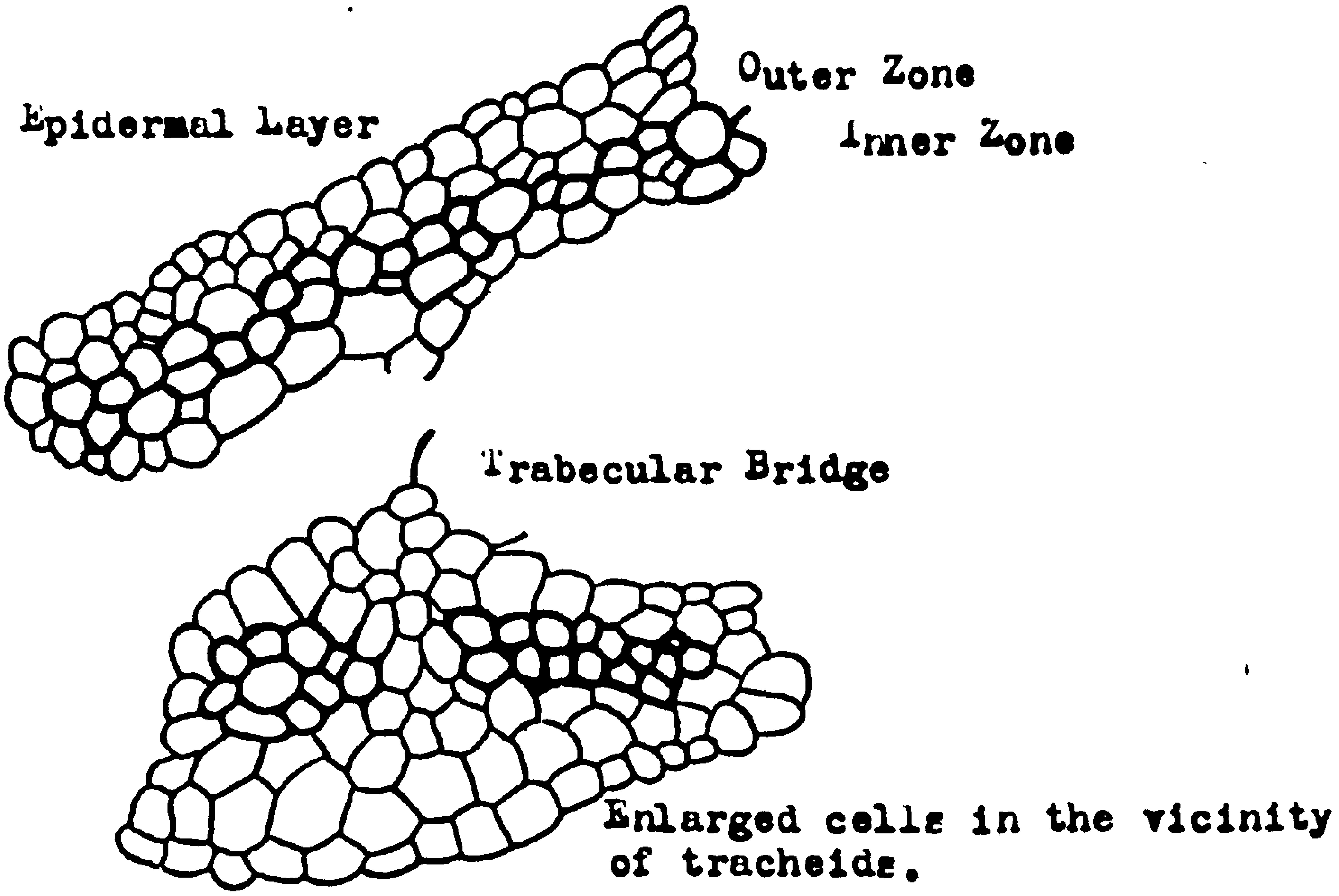
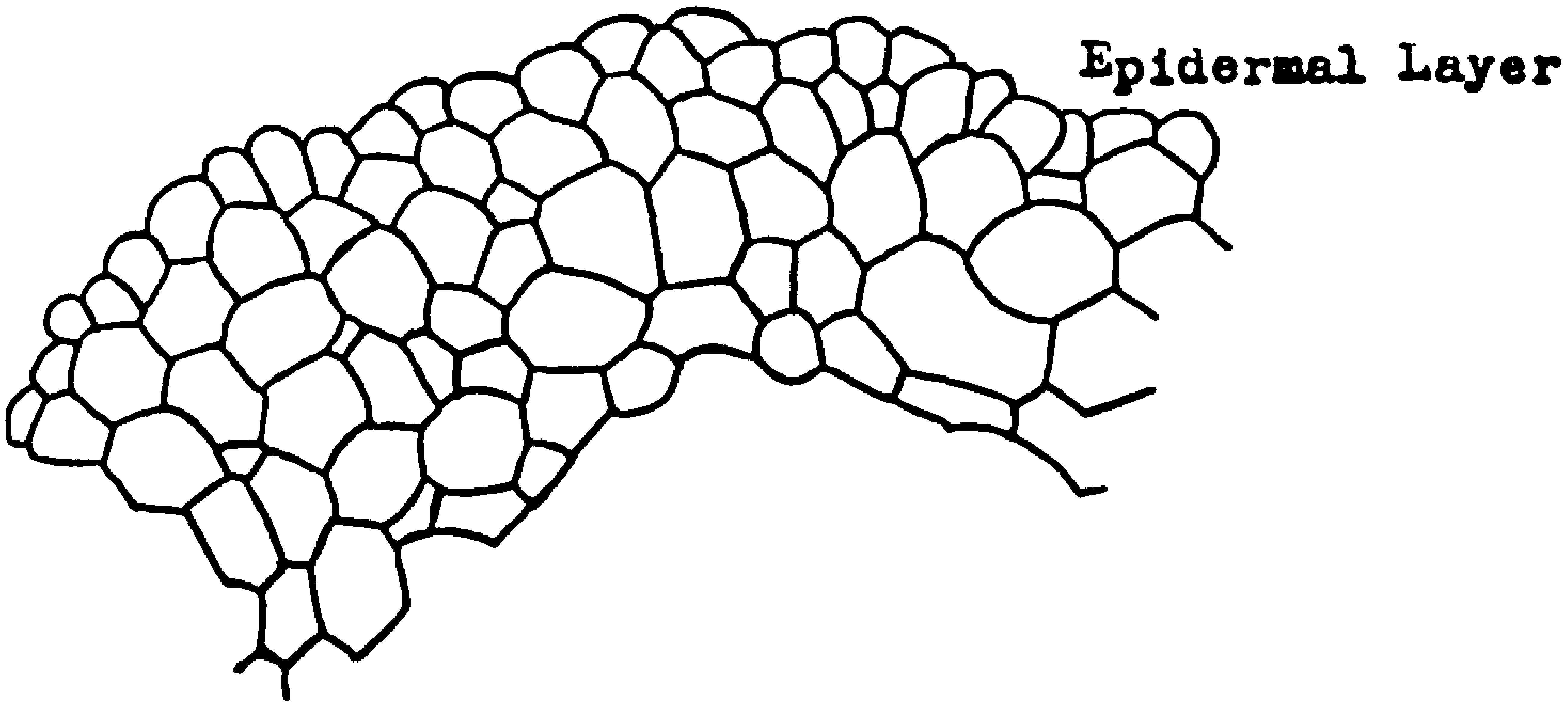


Fig.28: Outer Cortex of Stigmarian Appendage.(See page)
Scale lo. Kc-12o



The cortex of large specimens:

The larger forms of Stigmaria bacupensis, represented by the specimens figured by LECLERCQ (1930) show considerable secondary growth in the inner part of the outer cortex going hand in hand with a dilatation of the primary tissues in the outer part. Although the shape and size of cells forming the outer cortex may vary, possibly due to specific differences within the form species Stigmaria bacupensis the arrangement of tissues remains the same in both Stigmaria bacupensis and Stigmaria sigillarioides.

At the inside of the secondary cortex the radially arranged cells are of uniform diameter. In many specimens it can be observed that the innermost cells have a very narrow radial diameter but they gradually widen in centrifugal direction (pl.XIX,fig.75). This zone is probably near the meristem, or is the meristematic zone itself, which produces the secondary cortex. Slight irregularities occurring inmthis zone of growth suggest (pl.XIX,fig.75), that again, as was found for other Stigmaria species, the secondary cortex of Stigmaria bacupensis and Stigmaria sigillarioides is not produced by a normal single layered cambium, but by meristematic activity of a broad zone of tissue, in which each produced daughter cell retains the power of division. Only by this it can be explained why patches of primary tissue are enclosed in the rows of, undoubtedly, secondary cells.

Further outward, the cells of the secondary cortex are isodiametric and elongated in longitudinal direction resembling the cells of the inner secondary cortex of the Stigmaria ficoides types. Towards its periphery the secondary cortex consists of both isodiametric and tangentially stretched cells.

This tissue is arranged, as exhibited diagrammatically in p.193,fig.29, in such a way, that bands of the radially arranged isodiametric cells connect the primary outer cortex with the growing zone whilst the area in between is occupied by the tangentially extended cells. This structure obviously enables the plant to equalize the stresses originating during enlargement of girth.

The dictyoxylon cortex of the Sub-Sigillariae shows the same arrangement. There, the isodiametric cells have thickened walls and may be called truly fibrous. Such thickened cells, or, their equivalent, cells filled with a black substance, may occur in the <u>Stigmaria</u> <u>bacupensis</u> cortex also and have been called "sclerotic strands" (p.110) although LECLERCQ (1930) is of the opinion that they may have been of glandular nature.

These strands are situated on the outside of the bands of isodiametric cells (p.193,fig.29) and consist mostly of primary tissue. This can be observed in those specimens in which these cells are not filled with black matter(pl.XIX,fig.76). They seem to be strengthening elements for the radial bands of the isodiametric secondary cells but it is not clear when, in the development of the cortex, they are differentiated.

In many instances they are situated immediately outside the secondary cells and on the outside they are surrounded by, although greatly deformed and stretched, primary cells, In this case, they may have been present before any secondary growth occurred, as is suggested by pl.XX,fig.77a. In other cases, however, cells outside these sclerotic strands may still be radially arranged, as can be commonly observed in the cortices of <u>Stigmaria</u> <u>sigillarioides</u> and as is indicated by p193,fig.29.

This radially disposed tissue outside can mean two things, either that the sclerotic strands are differentiated after secondary growth, from secondary tissue or, that after differentiation, growth occurred outside the sclerotic strands. Evidence, obtained from similar structures in Sigillarian cortices points to the aletrnative, that both possibilities may occur together (p.192). Secondary growth may commence in the outer primary tissues after the formation and independently from the secondary cortex, whereby cells of the outer primary cortex divide by means of tangential cell walls into a usually small number of daughter cells. In some instances this may involve all the cells of the primary cortex in the leafcushions of Sigillaria, in other cases as indicated by fig.89,pl.XXIII, few cells may proceed to do so.

In Stigmaria bacupensis although in a lesser degree the same may happen and is figured by LECLERCQ (1930, pl.IV,fig.26). In one specimen (Kc-1011)two zones of sclerotic strands may be observed. The outer is situated outside the secondary cortex and the sclerotic elements are primary cells. The second zone is in the secondary cortex and secondary, radially arranged cells, are filled with black substance. Another specimen (pl.XXIV,fig.94) showed considerable secondary growth outside the sclerotic strands and in the outer primary cortex radially arranged tissue can be observed. The appendages appear to be, because of this broad zone of cortical tissue, inserted very deeply. It is highly probable however, that the secondary growth in the outer cortex of this specimen ocurred after the development of the appendages and affected only stretches of tissue between the appendage bases since in other parts of the cortex of the same specimen the development is normal (pl.XXIV,fig.94,right side).

In the larger specimens, undilatated cells of the outer part of the primary cortex are rarely observed and seem to have been cast off during the initial stages of secondary cortical growth. The endogenous insertion is not easily recognized in these forms, except in specimens like that in pl.XXIV,fig.94.

f) Stigmaria sigillarioides, a new type of Stigmaria:

The Kidston Collection of slides contains a great number of sections of different specimens, showing a Eu-Sigillarian stele (*Sig.elegans* or *Sig.mammillaris* type) surrounded by a cortex, identical in structure with that of *Stigmaria bacupensis*. In some instances this cortex bears appendage bases on its outer parts and proves therefore to be of the stigmarioid type.

Although the cortices were never really in organic connection with the Sigillarian steles it is highly probable that cortex and Sigillarian stele are part of one plant since a coincidental deposition of a stele in the cortex would hardly have occurred in so many different specimens in the same way. Many of these slides were already named, apparently by Dr.Kidston himself, "Sigillarian root?" and another set "*Stigmaria vasculare*" (also *Stigmariopsis vasculare*). The specimens named *Stigmaria vasculare* vary slightly in cortical and stelar structure from the specimens named "Sigillarian roots?" and may therefore be described separately. The specimens named "Sigillarian root?" shall be described as *Stigmaria sigillarioides* nov.spec.

Stele:

The centripetally developed inner xylem of Stigmaria sigillarioides shows the same feature as the steles of Sigillariae, the crenulate outer margin of the inner xylem. The inner margin of the inner xylem as well as the outer margin of the outer xylem follow this contour slightly. The arrangement of small elements, for the greater part probably protoxylem elements, on the periphery of the inner xylem mainly causes these undulations.

The centre of the stele of all the investigated specimens was hollow and this may be described as the medullary cavity. The diameter of the inner xylem cylinder may vary considerably whilst the total diameter of the xylem cylinder (including the outer xylem) is fairly uniform. In another mode of saying: The larger the cylinder of primary xylem, the less is the outer xylem developed. This same relationship was observed in the stele of Lepidophloios wünschianus for which WALTON (1935) suggested that, although the diameter of the vascular cylinder remains the same, the primary xylem is of very small diameter at the base of the plant whilst in the more distal parts it increases considerably pari passu with a decrease in the amount of secondary xylem.

It seems most probable that the same happened in Stigmaria sigillarioides in which species the diameter of the primary xylem may vary from 1.5 mm (Kc-2679) total diameter of the stele 9 mm, to a diameter of primary xylem of lo mm (Kc-1574, total diameter of the stele 21 mm). A third specimen showed a primary stele of an average diameter of 8 mm (slight compression) and the secondary stele had the diameter of 22 mm (Kc-1461).

These and other measurements suggest that the stele in the main branches of Stigmaria sigillarioides has a fairly uniform total diameter whilst the primary xylem cylinder in it is tapered, similar as in Lepidophloios wünschianus (WALTON,1935).

Assuming that the primary stele of Stigmaria sigillarioides is conical it has to be considered in which direction the part with the smaller diameter points. There is no direct evidence bearing on this, but it was observed that,as a rule, the specimens with the smallest primary stele are surrounded by the thickest secondary cortex whilst the specimens with the largest stele have the least developed secondary cortex. It also seems that the diameter of the specimen increases with a decrease of the diameter of the primary stele, but one cannot be quite sure of this because the specimens are all compressed or the cortex is broken into fragments. It can however be deducted that the narrow end of the stele pointed towards the base of the plant, in this case probably towards the base of Sigillaria. If all these assumptions are correct, a Stigmaria sigillarioides branch would show the same development as the shoot of Lepidophloios wünschianus and could therefore considered to be a shoot and the whole system of ramification a shoot system.

But the cortex of Stigmaria sigillarioides bears no leaf cushions, shows a development of the cortex varying from the leafy shoots of Sigillaria and the smaller specimens bear appendage bases which suggest that it was the water absorbing part of the plant, i.e. functioned as a root system.

2)Relation of *St.sigillarioides* and *St.bacupensis*:

a)The stele of *Stigmaria sigillarioides* is frequently accompanied by steles like those of *Stigmaria bacupensis* which in certain specimens (Ko-2679) surround the stele of *Stigmaria sigillarioides* like leaf or appendage traces. Other specimens (Ko-1460) show only one stele of *Stigmaria bacupensis* together with the *Stigmaria sigillarioides* stele. All these *Stigmaria bacupensis* steles have a fully differentiated inner xylem (p. 173). Remains of the cortex of these *Stigmaria bacupensis* specimens have never been observed inside the *Stigmaria sigillarioides* cortex.

b)In some specimens (Ko-1931) a fully developed *Stigmaria bacupensis* is situated immediately outside a *Stigmaria sigillarioides* cortex.

c)The cortex of *Stigmaria bacupensis* and *Stigmaria sigillarioides* are identical in structure.

d)The appendage bases of both species are identical in structure

e)RENAULT (1893) figured a specimen (p.171) on which he could show that the stele of the main branch was of the sigillarioid type whilst a ramification of it had the appearance of *Stigmaria bacupensis*.

All these above mentioned points lead to the conclusion that *Stigmaria bacupensis* is a branch of *Stigmaria sigillarioides* which is in conformity with the opinion (p.172) that *Stigmaria bacupensis* because of its extremely small size must be either a basal organ of a very small plant or a ramification of ultimate order

It seems that the latter alternative is the more likely to be the correct one and that *Stigmaria bacupensis* is a branch of *Stigmaria sigillarioides* but is probably not resulting from a dichotomy of the latter. Branches of a similar order are the "tap-roots" of Stigmariopsis and in this connection it seems likely that these "tap-roots" (SOLMS,1894) have the anatomical structure of *Stigmaria bacupensis*. This assumption is also supported by the forward directed appendages (p.176) of *Stigmaria bacupensis*. The dichotomizing horizontal arms of Stigmariopsis from which the "calamitoid" pith casts are known (SOLMS,1894) probably had the *Sigmaria sigillarioides* structure or , in other species, the *Stigmaria brardii* structure.

3)The cortex of *Stigmaria sigillarioides*:

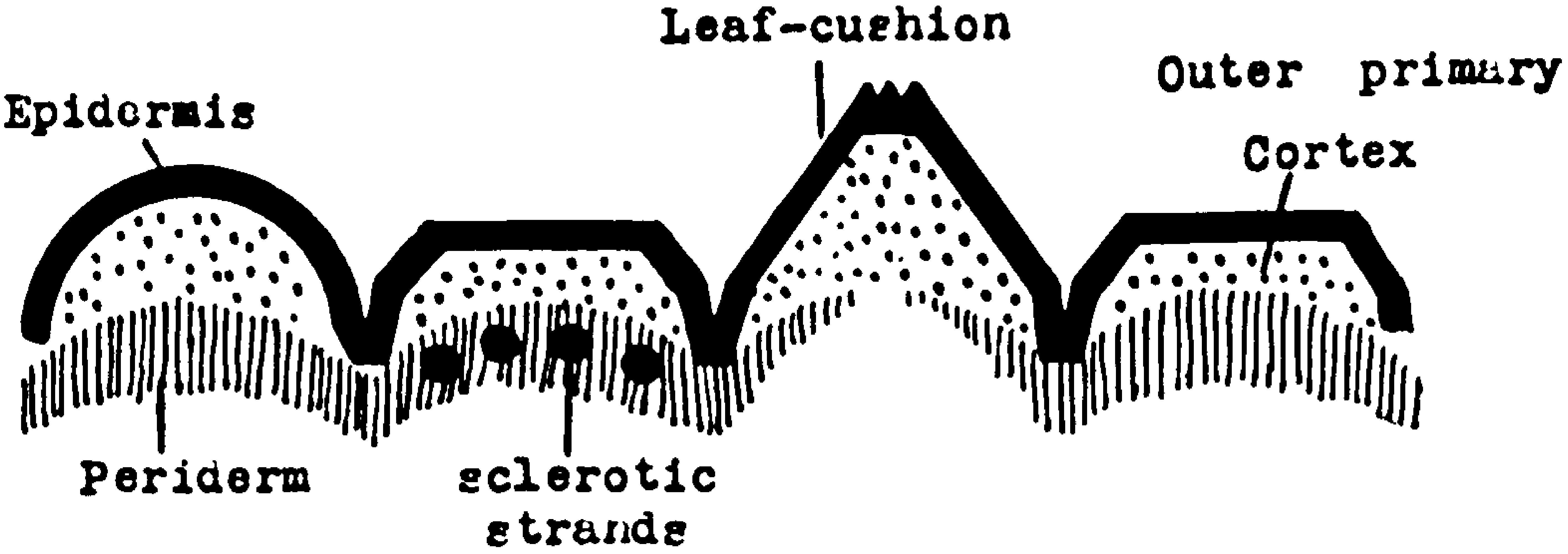
In one specimen of *Stigmaria sigillarioides* the middle cortex was preserved, still connected with the outer cortex. The middle cortex consists of a hyphal tissue (pl.XIX,fig.74) and is produced by a meristem between the middle and outer cortex. Probably, as in *Stigmaria radiculosa*, a meristem around the stele and several in the middle cortex itself partizipated in the production of middle cortex tissue, but these were not preserved. Appendage traces in the middle cortex pursue, as in *Stigmaria radiculosa* a steep outward courseand seem to consist mainly of radially arranged tracheids. The primary xylem is represented by few, very small elements (pl.XIX,fig.74) presumably the protoxylem elements. The phloem area is occupied by the same type of tissue as in *Stigmaria ficoides* types, "secretory strands".

Separated from the middle cortex by a meristematic band is the inner zone of the outer primary cortex. This tissue consists of very thin-walled, irregularly arranged, isodiametric cells. Towards the outside follows the growing zone of the secondary cortex (pl.XIX,fig.75) and this is succeeded in centrifugal direction by a zone in which the cells are tangentially stretched (pl.XIX,fig.76). The structure of these outer secondary cortical parts is identical with those of Stigmaria bacupensis and has been described there. Traces, as leaf or appendage traces, are extremely rare in the secondary cortex. One specimen with an extremely thick secondary cortex (pl.XXIII,fig.90) showed a trace, the course of which is also indicated in p.191,fig.29. Few cells on the outside of the secondary tissue were preserved but judging from these, the vascular elements in pl.XXIII,fig.90 are part of an appendage trace.

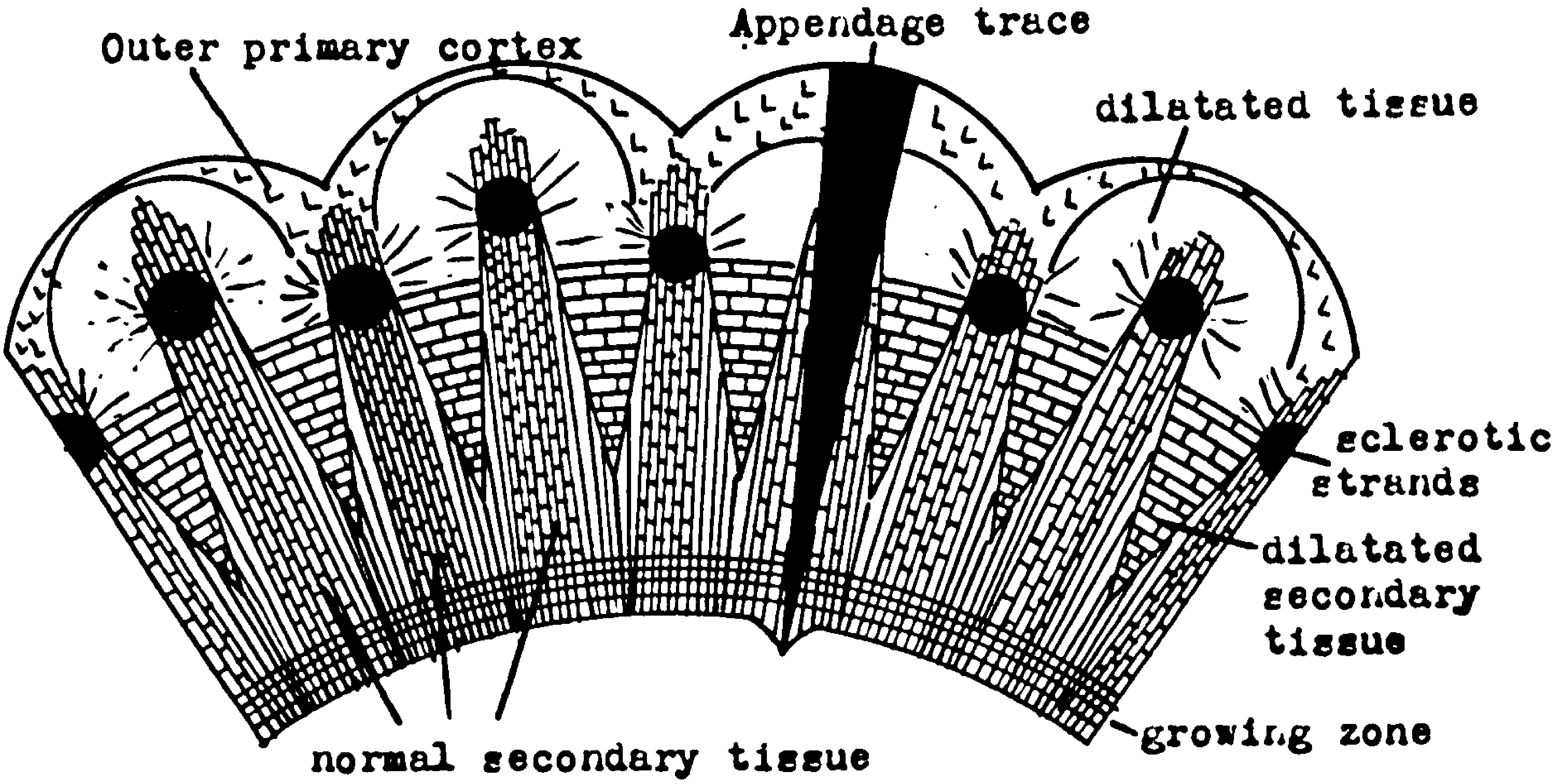
Specimens of Stigmaria sigillarioides with a large circumference show complete exfoliation of the tissue outside the sclerotic strands and often have a deeply fissured secondary cortex. The tangentially stretched cells may be torn in specimens of this size. Appendage bases, so far preserved, are of the same structure as those of Stigmaria bacupensis and it seems that appendages were also endogenously inserted in the outer primary cortex.

4)The cortex of St.sigillarioides and Sig.mamillaris:

The secondary cortex of Stigmaria sigillarioides is fundamentally of the same structure as the dictyoxylon cortex of the Sub-Sigillariae. It consists of radial sheets of fibrous tissue whilst the tissue between these sheets served to equalize stresses and tensions originating during the expansion of girth. In the cortex of the dictyoxylon structure these fibers have, however, thickened walls, whilst in Stigmaria sigillarioides their walls are only slightly thickened and on their outside the sclerotic strands are situated. An arrangement similar as in the cortex of Stigmaria sigillarioides can be observed in the outer cortex of Sigillaria mamillaris, in which species the sclerotic strands are situated in the periderm (pl.XXIII,fig.88). These strands are differentiated from secondary tissue. The same specimen shows that the cells in the shadow of the sclerotic strands are more thickened than those in between and also that in some instances the cells in between are slightly radially stretched. It is easy to imagine that after tangential expansion a cortex of this type would be similar to the cortex of Stigmaria bacupensis or Stigmaria sigillarioides. There can be little doubt therefore, that the secondary cortex of Stigmaria bacupensis and Stigmaria sigillarioides is homologous to the periderm and that the tissue outside corresponds to the outer primary cortex,i.e. the leaf-cushion region of the shoot. In the Sigillarian shoot as well as in Stigmaria bacupensis the cells of the outer cortex decrease in size in centrifugal direction, but the suberized hypodermis of Sigillaria is missing entirely in Stigmaria bacupensis in which the outer cells, so far preserved, are not thickened at all.



cf. *Sigillaria mammillaris*



cf. *Stigmaria sigillarioides*

fig29: Diagrammatic drawing of a Sigillarioid outer cortex of aerial and Stigmarioid branch.

g)Stigmaria vascularis, a new sigillarioid species:

Apart from the specimens described as Stigmaria sigillarioides, the Kidston Collection contains slides showing other Stigmariae with a similar stele which however vary from St. sigillarioides in the structure of their outer cortex.

The slides containing these specimens were apparently named by Kidston himself Stigmaria vascularis Weiss. A species with that name has, however, not been described but it seems probable that Kidston was referring to WEISS (1908). The Stigmarian axis described in this publication, Stigmaria weissiana Leclercq, shows however a different development of the inner xylem as well as the cortex and therefore I propose to call the in the following chapter described specimens Stigmaria vascularis nov.spec.

Anatomical structure:

1)Stele:

The vascular cylinder consists of centripetally differentiated inner xylem and radially arranged tracheids, the outer xylem. The distribution of tissues is the same as in specimens of Stigmaria sigillarioides with a small primary stele. In Stigmaria vascularis however the crenulate outer margin of the inner xylem is not so conspicuous (pl.XVIII,fig.71). The outer xylem is dissected by principal and even more by secondary medullary rays and this forms one of the most striking contrasts between this species and St. sigillarioides. The diameter of the inner xylem seems to be fairly constant in all the examined specimens but the diameter of the outer xylem varies from 18 to 40 mm; (diameter of the primary stele varies from 4 mm in the specimens with the smallest diameter of secondary xylem and 1 mm of those with a large amount).

A specimen of Stigmaria vascularis with a solid primary stele was not found but the specimen of Stigmaria lohesti (p.169) figured by WEISS (1930,fig.2) is of the same type, especially because of the many medullary rays. Irregularities in growth occur frequently on the outer margin of the outer xylem.

2)Cortex:

Of the cortex of Stigmaria vascularis only the parts outside the secondary cortex are preserved. The cells of the inner part of the secondary cortex are of uniform size but of extremely wide radial diameter, as compared with cells in the same region of Stigmaria sigillarioides and Stigmaria bacupensis. Further out in the cortex all the cells are tangentially stretched and unlike Stigmaria sigillarioides bands of isodiametric cells are absent. This zone of dilatation is succeeded centrifugally by a narrow band of primary tissue the cells of which are also tangentially extended. In this primary tissue black strands, as those of Stigmaria bacupensis, may occur. In this zone which might correspond to the outer primary cortex all the cells have rather thick walls (pl.XVIII,fig.72). On the outer side of the cortex a tissue consisting of very small cells with thin walls is situated. This tissue might be called the superficial cortex. In it nests of cells with thickened walls (pl.XVIII,fig.72) and tracheids may occur.

Appendages are inserted in the outer primary cortex and break through the superficial cortex. The appendage bases are very small and similar to those of Stigmaria bacupensis. Appendages of the species are not known.

h)Summary:

The group "Stigmariae with a diploxyloid stele" comprises all Stigmariae in which the outer and the inner xylem is clearly differentiated. There are three different stelar types among this group of species:

1)The Stigmaria weissiana type;stele medullated, primary xylem differentiated centripetally.

2)The Stigmaria lohesti type; solid stele, centripetally differentiated primary xylem.

3)The Stigmaria bacupensis type;protoxylem groups and direction of differentiation in primary xylem not recognizable.

In contrast to the species of the Stigmaria ficoides type, the species with a diploxyloid stele are distinguished by the variation in the structure of their steles.Except in Stigmaria weissiana - Stigmaria shurneyensis the cortex is uniform in all Stigmariae with a diploxyloid stele. For this reason it seems likely that some of these different Stigmaria species are part of one plant species and represent only branches of different order.

Stigmaria weissiana has a pith of varying diameter and the tracheids in the inner xylem are extremely wide. The stele thus shows great affinities with Bothrodendron mundum and it seems probable that this species is the basal organ of Bothrodendron. The cortex of Stigmaria weissiana has no sclerotic elements in its outer parts in contrast to the other Stigmariae with a diploxyloid stele. Only Stigmaria shurneyensis has a similar cortex.

This species, however, has a stele consisting of a solid primary xylem, pith being absent. The tracheids of the inner xylem are of the same wide diameter as in Stigmaria weissiana and it seems probable that St.shurneyensis is a protostelic branch or the protostelic base of Stigmaria weissiana and therefore also part of a Bothrodendron tree.

In the stele of Stigmaria brardii the ring of primary xylem is partly dissected, as it is known from the steles of Sub-Sigillariae. Furthermore, Stigmaria brardii shows the dictyoxylon cortex, so there is hardly any doubt that Stigmaria brardii is the basal organ of Sub-Sigillariae.

Stigmaria sigillarioides has a medullated stele which resembles that of Eu-Sigillariae. The margin between inner and outer xylem undulates owing to the protruding protoxylem groups on the surface of the primary xylem cylinder. Similar is the stele of Stigmaria lohesti, but this species has a protostele. It seems probable that Stigmaria lohesti is a protostelic branch of Stigmaria sigillarioides. The cortex of Stigmaria sigillarioides is identical in structure with the cortex of Stigmaria bacupensis and similar to the cortices of Eu-Sigillarian shoots. It seems probable that Stigmaria sigillarioides is the basal organ of Sub-Sigillariae and that Stigmaria bacupensis is a side branch of St. sigillarioides.

Stigmaria bacupensis has a solid primary stele which consists of annular and scalariform tracheids and parenchyma. The outer xylem is deeply dissected by medullary rays and in this Stigmaria bacupensis shows affinities with species of the Stigmaria ficoides type

Stigmaria vascularis has a similar stele as Stigmaria sigillarioides but the cortex shows no sclerotic fibers as in the latter species.

PART IV

CONCLUSIONS

10. Conclusions:

a) Occurence of Stigmaria:

Stigmarioid branches are the basal organs of the palaeozoic arborescent Lycopods. They occur in strata extending from the Lower Carboniferous to the Lower Permian but are especially abundant in the coal measures. For reasons explained in this thesis it seems however unlikely that beds of casts of Stigmaria are, as previously assumed, usually the true bases of coal seams.

b) Nomenclature of Stigmaria:

The generic name Stigmaria was originally applied to casts, impressions, or compressions of cylindrical branches, bearing quincuncially arranged appendages or circular appendage scars. These branches are part of a symmetric dichotomous ramification system and the name Stigmaria is now also applied to the whole system.

Stigmarioid branches attached to certain Sigillaria trunks deviate in their arrangement from the pattern typical of Stigmaria. This system of ramification has been called Stigmariopsis.

Structurally preserved specimens are called Stigmaria when either appendages are attached to them, appendage bases are preserved in the cortex, or when it can be inferred from the structure of the stele that it is that of Stigmaria.

A systematic description of Stigmaria specimens , preserved as casts, impressions or compressions has not been attempted in this thesis. The following systematic classification is based on the investigation of petrified, structurally preserved specimens.

The steles of Stigmarioid branches were found to be of two types, the *Stigmaria ficoides* type, in which a uniform xylem is developed and the diploxyloid type in which, similarly as in the aerial shoots, the xylem consists of a centripetally differentiated inner and a centrifugally differentiated outer part.

I.Species of the *Stigmaria ficoides* type:

Diagnosis: Stele medullated; xylem uniform, consisting of wedge-shaped bundles, separated from each other by the principal medullary rays in which appendage traces pass out.

Specimens with this type of xylem were first described as *Stigmaria ficoides*. This species is ill defined and a type specimen does not exist. Since several species can be identified having this type of stele the name *Stigmaria ficoides* is used to describe a certain type of stele but its use as a specific name is discontinued.

1)*Stigmaria sewardi* nov.spec. (p.51):

Type specimen: Glasgow Class Coll.34
Locality : Oldham/Lancs.
Horizon : Halifax Hard Bed/U.Carb.
Affinities : Sim. with *Lepidophloios* sp.

Stele : Medullated;Endo-xylem;30-35 xylem wedges; irregularities in growth frequent; exo-xylem frequently preserved;phloem = secretory strands;pericycle.
Med.rays : High and slender;app.trace - tongue shaped.
Cortex : Outer cortex uniform;no sclerotic elements, no superficial cortex.
Appendages : Secondary xylem frequent;middle cortex = arm parenchyma;uniform outer cortex.
Conspicuous : Med.rays;arm-parenchyma of appendages.

2)*Stigmaria arranensis* nov.spec. (p.88):

Reference : WALTON (1935)
Type specimen: J.Walton Coll.605 / Glasgow
Locality : Laggan Bay, Arran, Scotland.
Horizon : Calc.Sandst.Ser./L.Carb.
Affinities : Sim. with *Lepidophloios wünschianus*

Stele : Medullated;endo-xylem;16-20 xylem wedges; irregularities in growth on periphery frequent;exo-xylem;phloem + secretory strands.
Med.rays : High and slender;app.trace triangular.
Cortex : Hyphal middle cortex;thick secondary cortex with zones of secretory ducts;zone of dilatation;secretory ducts in primary cortex;uniform outer cortex.
Appendages : Secondary xylem;pericycle;middle cortex = arm parenchyma;trabecular bridge.
Conspicuous : Thick secondary cortex;low number of xylem wedges.

3)*Stigmaria pettycurensis* Scott,(p.103):

Reference :SCOTT,notebook no.XVIII in British Museum of Natural History,p.111.
Type specimen:Kidston Coll.545,a,b,/ Glasgow
Locality :Pettycur/Fife, Scotland
Horizon :Calc.Sandst.Ser./L.Carb.
Affinities :Similarities with *Lep.veltheimianum*.
16

Stele :Medullated;40-45 xylem wedges;extremely large xylem cylinder.
Med.ray :Broad and high;triangular trace.
Cortex :Narrow uniform outer cortex;few irregular sclerotic cells differentiated;no superficial cortex.
Appendages :Secondary xylem;distinct zonation of outer cortex.
Conspicuous :Extremely large xylem cylinder.

4)*Stigmaria radiculosa* Hick (p.36):

Reference: HICK (1891);WEISS (1902).
Type specimen: Manch.Mus.Coll. R 354
Locality : Cinder Hills near Siddal,Halifax.
Horizon : Upper Carboniferous
Affinities : Sim. with ?*Lepidophloios fuliginosus*.

Stele : Medullated;30-35 narrow xylem wedges; exo-xylem;phloem = secretory strands; pericycle;
Med.rays : High and slender;triangular appendage trace.
Cortex : Hyphal middle cortex;narrow secondary cortex; secretory ducts in outer primary cortex; sclerotic band;superficial cortex.
Appendages : Pericycle and inner cortex;middle cortex-loose parenchyma;distinct zonation of outer cortex.
Conspicuous : Sclerotic band;black layer between stele and cortex.

5)*Stigmaria vulgaris* nov.spec. (p.107):

Type specimen: Kidston Coll.649 / Glasgow
Locality : ?
Horizon : Halifax Hard Bed / U.Carb.
Affinities : Sim. with *Lepidodendron vasculare*.

Stele : Medullated;30 xylem wedges;
Med. rays : High and narrow;very short triangular app.trace.
Cortex : Thick secondary cortex with secretory ducts; Sclerotic band and sclerotic strands; superficial cortex;

6)*Stigmaria asteroidea* nov.spec. (p.116):

Type specimen: Kidston Coll.654 / Glasgow
Locality : ?
Horizon : Halifax Hard Bed / U.Carb.
Affinities : ?

Stele : Medullated;30 xylem wedges.
Cortex : Narrow primary cortex;sclerotic strands; broad superficial cortex.
Appendages : Narrow outer cortex;no limiting layer.
Conspicuous : Sclerotic strands and superficial cortex.

II.Stigmariae with a Diploxyloid Stele:

This group comprises all specimens in the stele of which a primary inner and a secondary outer xylem is distinctly differentiated. The steles of these Stigmariae thus have a similar appearance ~~as~~ to the steles of the aerial parts of the Lepidodendrales.

7)*Stigmaria weissiana* Leclercq (p.165):

Reference : LECLERCQ (1928); WEISS (1908).
Affinities : Sim. with *Bothrodendron mundum*

Stele : Medullated;varying Ø of pith;inner xylem tracheids extremely large;few primary elements;solid secondary xylem.
Med.rays : Lens-shaped;only primary tracheids in app.trace.
Conspicuous : Large tracheids of inner xylem;medullary rays.

8)*Stigmaria shurneyensis* nov.spec.(p.167):

Type specimen: Kidston Coll.652 A / Glasgow
Locality : Shurney Ford near Bacup/Lancs.
Horizon : Upper Foot Coal / U.Carb.
Affinities : Similarities with *Bothrodendron mundum*.

Stele : Solid;little primary xylem;large tracheids.
Med.rays : Lens-shaped;only primary elements in app. trace.
Conspicuous : Med.rays.

9)*Stigmaria lohesti* Leclercq (p.169):

Reference : LECLERCQ (1925)
Affinities : Probably ultimate branch of *St.sigillarioides* or *St.vascularis*.

Stele : Solid;centripetal primary xylem;outer xylem dissected by primary and secondary med.rays.
Med.rays : Very short;broad triang.app.trace.
Conspicuous : Solid stele.

10)*Stigmaria bacupensis* Scott et Lang (p.172):

Reference : LECLERCQ (1930).
Affinities : Probably branch of *St.sigillarioides*.

Stele :Inner xylem consisting of annular and scalariform tracheids and parenchymatous cells;outer xylem dissected by many principal medullary rays.
Med.rays : High,narrow;app.trace triangular.
Cortex : Sclerotic strands;fibrous and expansion tissue;outer primary cortex wide.
Appendages : Endogenously inserted;trabecular bridge; tracheids of tr.bridge terminate underneath limiting layer.
Conspicuous : Stele;appendages.

11)*Stigmaria brardii* Renault (p.170):

Reference : RENAULT (1893).
Affinities : Sim. with Sub-Sigillaria sp.

Stele : Partly dissected primary xylem;solid secondary xylem.
Cortex : Dictyoxylon cortex.
Conspicuous : Cortex.

12) *Stigmaria sigillarioides* nov.spec. (p.186):

Type specimen: Kidston Coll. 2679
Locality : Dulesgate
Horizon : Halifax Hard Bed
Affinities : Sim.with *Eu-Sigillaria* sp.

Stele : Medullated;varying diameter of primary stele;crenulate inner and outer margin of xylem cylinder;outer xylem solid.
Cortex : Middle cortex hyphal;sclerotic strands; fibrous and expansion tissue.
Conspicuous : Sigillarioid stele surrounded by cortex bearing appendages.

13) *Stigmaria vascularis* nov.spec. (p.194):

Type specimen: Kidston Coll. 2314
Locality : ?
Horizon : Upper Carboniferous
Affinities : Sim. with Sigillariae.

Stele : Medullated;centripetal primary xylem; outer xylem deeply dissected by primary and secondary medullary rays.
Cortex : All cells tang.stretched;thick outer primary cortex;no fibrous tissue.
Appendages : Endogenous.
Conspicuous : Outer cortex.

c) Anatomy of Stigmaria:

The xylem of Stigmariae of the ficoides type was found to correspond solely to the outer xylem of the diploxyloid steles. Its tracheids are differentiated simultaneously from primary and secondary parenchyma, therefore a strict distinction between metaxylem and secondary xylem cannot be made.

Between xylem and pith the endo-xylem is situated, a parenchyma of procambial origin in which occasionally tracheids may be differentiated. Even these are probably not centripetally differentiated; the direction of their development is, as in Stigmaria bacupensis, not clear. The stele of the latter corresponds most closely to the stele of the shoot of Isoetes and in this plant, owing to the absence of protoxylem elements, the direction of differentiation in the inner xylem cannot be made out. In the Stigmaria ficoides and Stigmaria bacupensis type of stele, the outer xylem is split into a varying number of wedges by medullary rays, in which the appendage traces pass out. In this feature both stelar types correspond but differ from stigmarioid branches with a centripetally developed inner xylem, in which the medullary rays and the appendage traces therein may be of varying structure. It seems therefore that branches with a Stigmaria ficoides type and those with a Stigmaria bacupensis type of stele, are homologous organs. The first of the medullated type, the latter of the protostelic type.

Branches with a diploxyloid stele probably have a primary stele consisting of a protostelic and a siphonostelic part, analogous to aerial shoots. Stigmaria bacupensis is probably a side branch of the sigillarioid Stigmariae and seems to be the anatomical structure of the "tap-roots" as known of Stigmariopsis.

Because of their similar cortical structure it was concluded that branches with steles of the _Stigmaria ficoides_ type are the basal organs of the Lepidodendrales. At least two of the stigmarioid species with a diploxyloid stele, described in this thesis, constitute the basal organs of Sigillariae (_St.brardii_ and _St.sigillarioides_). Other Stigmariae with a diploxyloid stele are possibly also the basal ramifications of Sigillariae. _St.weissiana_ and _St.shurneyensis_ are probably the basal organ of Bothrodendron.

d)Histology of Stigmaria:

1)Secondary growth:

All specimens described in this thesis suggested that secondary tissues were not produced by normally functioning linear cambia. The position of primary tissues within radially arranged cells rather seemed to indicate that secondary tissues in both stele and cortex of stigmarioid branches originated from meristematic activity of a deep zone of tissue within which inactive primary patches may remain. These results of the investigation of stigmarioid branches also seem to have bearing upon the anatomy of the aerial parts of the palaeozoic arboreseent Lycopods, therefore the use of terms referring to such cambia as for instance "Phellogen" in the description of their anatomy is no longer advisable.

2)Accessory tissues:

Two types of "secondary growth" were recognized in the stigmarioid branches. The first produces radially arranged tissue and the second parenchyma often of a hyphal appearance.

The meristems arise in primary cortical cells. This accessory tissue has been called middle cortex in this thesis and is in the aerial parts of Lepidodendron and Lepidophloios of the same origin and not, as has been claimed, laid down by the apical meristem.

3)Dilatation of tissues in Stigmaria:
Tissues on the periphery of larger branches frequently show considerable tangential stretching. These tissues have not been produced in that shape but were stretched by the tangential stresses during expansion of the branch. In several specimens the elasticity of the cells and tissues in the arborescent Lycopods could be demonstrated.

4)Epidermis of Stigmaria:
Certain species of the Stigmaria ficoides type show thin-walled parenchyma described as superficial cortex, separated from the outer primary cortex by a sclerotic band. A single epidermal layer was not observed but it may be that this outermost zone, similar in structure as the velamen of orchid roots, is a multiple epidermis. Appendages are inserted endogenously in the superficial cortex, which has no equivalent in the tissues of the aerial shoot. In the diploxyloid species in which no such superficial cortex was observed, the appendages are inserted endogenously in the outer primary cortex.

e) Morphology of Stigmaria:

LANG(1915) and HIRMER(1927) brought forward the theory that the Lepidodendrales were bi-polar plants and both suggested that Stigmaria is homologous to the aerial shoot. This opinion has frequently been attacked and the arguments against were mainly based on the anatomical difference between the stele of Stigmaria, especially that of the ficoides type, and the aerial shoots of the Lepidodendrales. In this thesis the similarity between the stigmarioid and lepidodendroid cortex has been pointed out.

The results of the investigation of relatively few specimens of Stigmaria with a diploxyloid stele supports the theory brought forward by LANG and HIRMER and supplements it by suggesting the following relations between Stigmariae and aerial shoots:

If the assumption is correct that St.shurneyensis as well as St.weissiana are the basal parts of Bothrodendron, then Bothrodendron has had the simplest type of Stigmaria and it was absolutely homologous to the aerial ramification. The solid stigmarioid as well as shoot stele open up to a siphonostele in parts of the ramification system. The increase in the diameter of the primary stele of St.weissiana has been referred to in this thesis. An argument in favour of the strict homology between Stigmaria and shoot of Bothrodendron is the structure of the principal medullary rays and the appendage traces therein. In both St.weissiana and St.shurneyensis these traces show no secondary xylem attached and are similar to leaf traces in contrast to the structure of appendage traces of species of the Stigmaria ficoides type. A specimen of St.shurneyensis has attached appendages and there is no doubt that it is a true Stigmaria.

There is much evidence supporting the view that aerial and stigmarioid branches of Bothrodendron are strictly homologous, the only difference being that the stigmarioid branches bore appendages in place of leaves.

In the Sigillariae the layout of the stigmarioid ramification system and the anatomical relation are more complicated. It is remarkable that Sigillaria, the aerial shoot of which is only little branched, shows the most elaborate system of ramification in the Stigmaria organ. It has previously in this thesis been suggested that the main branches of *St.sigillarioides* had, similar as *Stigmaria weissiana*, an opening primary stele e.g. that near the base the stele of *St.sigillarioides* is solid whilst in the distal parts of the ramification system the stele is medullated. These branches of *St.sigillarioides* bear appendages and the conclusion is that they are strictly homologous to the aerial shoots. But *St.sigillarioides* bears additional branches whose structure is known under the name of *Stigmaria bacupensis*. *St.bacupensis* is probably identical with the "tap-roots" of *Stigmariopsis*. How these *St.bacupensis* branches come off the *St.sigillarioides* branches is not known and their order in the ramification system has to remain anoopen question.

The anatomical structure of species of the *Stigmaria ficoides* type is very similar to that of *Stigmaria bacupensis* e.g. the side branches of sigillarioid Stigmariae. Especially from the point of view of xylem development the stele of the *Stigmaria ficoides* type can be regarded as the medullated form of the *Stigmaria bacupensis* stele. The tissue described as endo-xylem in the *Stigmaria ficoides* stele corresponds to the inner xylem of *Stigmaria bacupensis* especially in the peculiar way primary xylem elements are differentiated.

The outer xylem of St.bacupensis and especially the medullary rays in it are of the same structure as those of the Stigmaria ficoides steles but vary considerably from those of the diploxyloid Stigmariae. It has furthermore been pointed out in this thesis that the cortex of Stigmaria asteroidea although the stele of this species is of the ficoides type, shows considerable affinities with that of St.bacupensis.

All this suggests that St.bacupensis and the species of the Stigmaria ficoides type are homologous organs. Whilst Stigmaria bacupensis is borne on branches equivalent to the aerial shoots (St.sigillarioides), such equivalents of aerial ramifications are not known in the Stigmariae of the ficoides type, are not developed or possibly reduced in the course of evolution. Whilst it seems likely that the aerial shoot of Bothrodendrales and Sigillariae grew simultaneously with the Stigmaria or even that the Stigmaria was developed first for the greater part, the shoot of Lepidodendrales may have risen first and the Stigmariae developed later.

f)Evolution of Stigmaria:

Although all Stigmariae are very similar in their external appearance, three distinctly different types can be distinguished from the anatomical point of view. These three types can be related to the three genera of arborescent Lycopods: Bothrodendrales, Sigillariae and Lepidodendrales. The evolution of these different systems, between which a phylogenetic link is recognizable, seems to have taken place in the Devonian since in the Lower Carboniferous the different systems are already present.

A further development in the course of evolution can be deduc~~t~~ed from the variation of anatomy within the species groups. The Lower Carboniferous *Stigmaria arranensis* a species with the *Stigmaria ficoides* type of stele, shows a shoot-like undifferentiated outer cortex. In the other Lower Carboniferous species, *Stigmaria pettycurensis*, differentiation of the outer cortex is in an initial stage. The Upper Carboniferous species *Stigmaria radiculosa* and *St.vulgaris*, however, show a fully differentiated superficial cortex e.g. probably a multiple epidermis, and have therefore more root-like features.

The basal organs of Sigillariae are represented by *St.vascularis* and *St.sigillarioides* in the Upper Carboniferous as more primitive types whilst in the Stephanian and in the lower Permian *St.brardii* with the more elaborate dictyoxylon cortex prevails.

g) Summary:

Stigmarioid branches are of two different types. They can have a diploxyloid stele or one consisting of uniform xylem. 13 species of Stigmaria have hitherto been identified. Seven of these are newly described in this thesis. Certain Stigmariae are homologous to the aerial ramification of the plants. The sigillarioid Stigmariae bear side branches which have no equivalent in the aerial ramification and are special developments of the absorbing system. *Stigmaria ficoides*, the basal organ of Lepidodendrales, is morphologically equivalent to these side branches of the sigillarioid Stigmariae.

11. Acknowledgements:

I am grateful for this opportunity to express my sincerest thanks to Professor J.Walton for the continous advice and counsel I received during the preparation of this thesis. I am also greatly indebted to Dr.S.Williams for his kind and invaluable assistance in the formulation of the text.

My thanks are due to the British Council and to the University of Glasgow who kindly assisted me with a grant thus enabling me to study the subject of the thesis.
I gratefully acknowledge the permission to use laboratory, libraries and material of the University of Glasgow during the preparation of this thesis.

12. Literature cited:

ARTIS, E.T. Antediluvian Phytology London 1838

BINNEY, E.W. On the Remarkable Fossil Trees Lately
Discovered near St. Helens.
Edinb. and Dublin Phil. Mag. Vol. XXIV, No. 3, 1844.

Observations on *Stigmaria ficoides*.
Quart. Journ. Geol. Soc. London XV, 1859 p.76-80.

BOWER, F.O. Size and Form in Plants London 1930

BRONGIART, A. Sur la Classification et la Distribution
des Vegetaux Fossiles.
Mem. du Mus. d'Hist. Nat. Vol. III, Paris 1838

Observ. sur la struct. int. du *Sigillaria*
elegans comparee a celle des Lepidodendron
et Stigmaria.
Arch. du Mus. d'Hist. Nat. Vol. I Paris 1839

BROWN, R. Description of Errect Sigillariae with
Conical Tap-Roots, Found in the Roof of
the Sidney Main Coal, in the Island of
Cape Breton.
Proc. Geol. Soc. London, March 21st, 1849

CALDER, M.G. Notes on the Kidston Collection of Fossil
Plant Slides:
Note II: The Anatomy of the Axis of
Bothrodendron mundum Williamson sp.
Trans. Roy. Soc. Edinb. Vol. LVII, Part III, (No. 26)
Edinburgh 1933

CORDA, A.J. Flora Protogaea; Beiträge zur Flora der
Vorwelt. 1845
(2nd Ed. Berlin 1867)

DAWSON, J.W. The Fossil Plants of the Devonian and
Upper Silurian Formations of Canada.
Geol. Survey of Canada p.23 1871

DUERDEN, H. and WRIGHT, A.S. A Ligulate Pteridophyte from the Lower
Coal Measures of Bacup/Lancs.
Nature, Vol. 170, p.41, July 1952

GÖPPERT,H.R.	Die Gattungen der Fossilen Pflanzen Bonn 1841
GOLDENBERG,F.	Flora Saraepontana Fossilis Die Pflanzenversteinerungen des Steinkohlengebirges von Saarbrücken. Saarbrücken 1855
GOTHAN,W.	Lehrbuch der Paläobotanik von H.Potonié. 2.Aufl. Berlin 1921
GRAND EURY,M.C.	Geologie et Palaeontologie du Bassin Houiller du Gard. St.Etienne 1890
HAWKSHAW,J.	Description of the Fossil Trees Found in the Excavations for the Manchester and Bolton Railway. Trans.Geol.Soc.London (2) VI, 1893
HICK,Th.	On a New Fossil Plant from the Lower Coal Measures. Linn.Soc.Journ. Bot.Vol.XXIX 1891
	Is Stigmaria a Root or Rhizome? Natural Science, July 1892
HIRMER,M.	Handbuch der Paläobotanik Bd.1 München und Berlin 1927
Hovelacque,M.	Rech. sur le *Lepidodendron selaginoides* Mem.Soc.Linn.Normandie Vol.XVII I Fasc. Caen 1892
JONGMANS,W.	Fossilium Catalogus II Plantae Pars 21 et 22 's Gravenhage 1937
KOOPMANS,R.G.	Researches on the Flora of the Coal Balls from the Finefrau Nebenbank Horizon in the Province of Limburg (The Netherlands). Heerlen 1928

LANG, W.H.
Studies in the Morphology of Isoetes:
I. The general Morphology of the Stock of *Isoetes lacustris*.
Mem.&Proc.Manch.Lit.&Phil.Soc.
Vol.59, Part 1, No.3, Feb.16th, 1915

II. The Analysis of the Stele of the Shoot of *Isoetes lacustris* in the Light of Mature Structure and Apical Development.
Mem.&Proc.Manch.Lit.&Phil.Soc.
Vol.59, Part 2, No.8, May 31st, 1915

On the Apparently Endogenous Insertion of the Roots of Stigmaria.
Mem.&Proc.Manch.Lit.&Phil.Soc.
Vol.67, Part 2, No.8, June 30th, 1923

LECLERCQ, S.
Les Coal Balls de la Couche Bouxharmont des Charbonnages de Werister.
Mem.Soc.Geol.Belgique Vol.4 Liege 1925

Certains Appendices de Stigmaria presentent une ecorce lacuneuse.
Ann.Soc.Geol.Belgique Bull. Liege 1927

Les Vegetaux a Structure Conservee du Houiller Belge.
Note II: Sur un Stigmaria a bois primaire centripete des Coal Balls de la Couche Bouxharmont.
Ann.Scc.Geol.Belg. T.21 Bull. Liege 1928

A Monograph of *Stigmaria bacupensis* Scott et Lang.
Ann. of Botany Vol. XLIV, No.CLXXIII Jan.1930

LESQUEREUX, L.
Third Report Geol.Survey, Kentucky, 1857
p.529, 532, 548.

LINDLEY, J. and HUTTON, W.
The Fossil Flora of Great Britain.
London 1837.

MacGregor, M. and WALTON, J.
The Story of the Fossil Grove.
Glasgow Publ.Parks and Bot.Gardems Dept.1948

MARTIN, W.	Petrificata Derbiensia Wigan 18o9
NOE, A.C.	Evidence of Climate in the Morphology of Pennsylvanian Plants. Illinois State Geol. Survey Bull. 60 1931
PETIVER, J.	Gazophylacii Naturae Dec. II, pl. 18, fig. 2
POTONIE, H.	Der im Lichthof der Königl. Geologischen Landesanstalt und Bergakademie aufgestellte Baumstumpf mit Wurzeln aus dem Karbon des Piesberges. Jahrbuch Preuss. Geol. L.A. 1889 Berlin 1890.
RENAULT, B.	Etude sur les Stigmaria Rhizomes et Racines de Sigillaria. Ann. de Scienc. Geol. Vol. XII 1882
	Etudes des Gites Mineraux de la France: Bassin Houiller et Permien d'Autun et d'Epinac. Part II Paris 1893
SCOTT, D.H.	Studies in Fossil Botany Vol. I, Pteridophyta 3rd Ed. London 1920
SEWARD, A.C.	On the so-called Phloem of Lepidodendron. New Phytologist Feb. 19th, 1902
	Fossil Plants, Vol. II, Cambridge 1910
SEWARD, A.C. and HILL, A.W.	On the Structure and Affinities of a Lepidodendroid Stem from the Calciferous Sandstone Series of Dalmeny, Scotland. Trans. Roy. Soc. Edinb. Vol. XXXIX Part IV Edinb. 1900

SOLMS-LAUBACH, H.v.
Einleitung in die Paläophytologie.
Leipzig 1887

Über *Stigmariopsis* Grand Eury
Paläont.Abh. N.F. Bd.II, Heft 5, Jena 1894

Über die seinerzeit von Unger beschriebenen strukturbietenden Pflanzenreste des Unterkulm von Saalfeld.
Abh.Preuss.Geol.L.A. N.F. ,Heft 23,
Berlin 1896

STERNBERG, K.v.
Versuch einer Geognostisch-Botanischen Darstellung der Flora der Vorwelt.
Fasc. 1 Regensburg 1820

Stevenson, J.J.
Formation of Coal Beds.
Proc.American Phil.Soc.
Vol.L 1911
Vol.LI 1912
Vol.LII 1913

STEWART, W.N.
A Comparative Study of Stigmarian Appendages and Isoetes Roots.
American Journ. of Botany Vol.34 No.6
June 1947

STOPES, M.C. and
WATSON, D.M.S.
On the present Distribution and Origin of the Calcareous Concretions in Coal Seams known as Coal Balls.
Phil.Trans.Roy.Soc.London Ser. B.
Vol.200 1908

TROLL, W.
Grundsätzliches zum Stigmarienproblem.
Flora, Neue Folge, Bd.29 Jena 1934-35

VOLKMANN, G.A.
Silesia Subterranea
Leipzig 1720

WALTON, J.
Scottish Lower Carboniferous Plants: The Fossil Hollow Trees of Arran and their Branches (*Lepidophloios wünschianus*, Carr).
Trans.Roy.Soc.Edinb.Vol.LVIII, Part II No.13
Edinburgh 1935

Notes on the Preparation and Permanence of Peel Sections.
Comte Rendu /3ieme Congres de Strat.et de Geol. du Carbonifere Heerlen 1951

An Introduction to the Study of Fossil Plants.
2nd Ed. London 1953

WEISS, F.E.
On the Phloem of Lepidophloios and Lepidodendron.
Mem.Proc.Manch.Lit.&Phil.Soc.
Vol.45 Part III No.7 July 1901

On *Xenophyton radiculosum* (HICK) and on a Stigmarian Rootlet, probably related to *Lepidophloios fuliginosus*.
Mem.&Proc.Manch.Lit.&Phil.Soc.
Vol.46 Part III No.9 March 10th, 1902

The Vascular Branches of Stigmarian Rootlets.
Ann.of Botany Vol.XVI No.LXIII Sept.1902

The Vascular Supply of Stigmarian Rootlets.
Ann.of Botany Vol.XVIII No.LXIX Jan.1904

A Probable Parasite of Stigmarian Rootlets.
New Phytologist Vol.III No.3 March 1904

A Stigmaria with Centripetal Wood.
Ann.of Botany Vol.XXII No.LXXXVI April 1908

On the Occurrence of *Stigmaria lohesti* in the British Coal Measures.
Mem.&Proc.Manch.Lit.&Phil.Soc.
Vol.73 No.8 June 1929

The Probable Stigmarian Axis of *Bothrodendron mundum*.
Mem.&Proc.Manch.Lit.&Phil.Soc.
Vol.74 No.8 June 1930

A Re-examination of the Stigmarian Problem.
Proc.Linn.Soc.London 144 (1931-32) 1932

WILLIAMS,S.
On *Isoetes australis*, a new species from Western Australia. Part I.
Proc.Roy.Soc.Edinb.Sect.B. Vol.LXII Part 1 (No.1) Edinburgh 1943

WILLIAMSON,W.C.
On the Structure and Affinities of some Exogenous Stems from the Coal Measures.
Monthly Microscop.Journal Aug.1869

A Monograph on the Morphology and Histology of *Stigmaria ficoides*.
Palaeontol. Soc.London Volume for 1886
London 1887

Organization of the Fossil Plants of the Coal Measures. Part.XVI
Phil.Trans.Roy.Soc.London 1889

Is Stigmaria a Root or Rhizome?
A Reply to Mr.Hick.
Natural Science July 1892

On the Light thrown upon the Question of the Growth and Development of the Carboniferous Arborescent Lepidodendra by a Study of the Details of their Organization.
Mem.&Proc.Manch.Lit.&Phil.Soc.
Vol.IX Ser.4 1895

WOODWARD,J.
An Attempt towards a Natural History of the Fossils of England. London 1729

WÜNSCH,E.A.
Discovery of Er~~r~~ect Stems of Fossil Trees in the Trappean Ash in Arran.
Geol.Magazin Vol.II Glasgow 1865

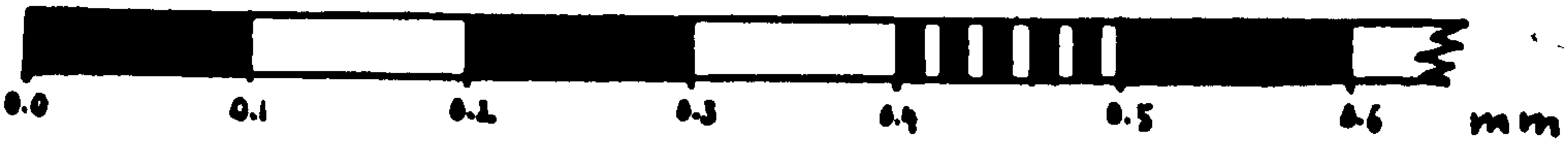
YOUNG,J. and GLEN,D.C.
Notes on a Section of Carboniferous Strata Containing Er~~r~~ect Stems of Fossil Trees and Beds of Intrusive Dolerite in the Victoria Park, Whiteinch.
Trans.Geol.Soc.Glasgow 1888

PART V

PLATES

Scale for all Camera lucida drawings.

Oc. 2x



Oc. 10 x

Explanation of Plates:

Collections of slides:
Kc = Kidston Collection
Mc = Manchester Museum Collection
Sc = D.H.Scott Collection London
Gc = Glasgow Class Collection
Wc = Prof.Waltons Collection
Ac = Authors Collection.

P L A T E I

fig.1 : Stigmaria from Clayton/Yorks.; now in Manchester Museum (from HIRMER,1927, after WILLIAMSON,1887).

fig.1a: Map of Stigmaria in fig.1 (from WILLIAMSON,1887).

fig.2 : Stigmaria from Piesberg/Osnabrück, now in Geologische Landesanstalt Berlin (from GOTHAN,1921).

fig.2a: Map of the Stigmaria in fig.2 (from POTONIE,1890).

fig.3 : Small Stigmaria specimen (diameter of upper extremety 6 inches). From WILLIAMSON (1887).

fig.3a: View of the under surface of specimen in fig.3.

fig.4 and 5: Casts of tree bases from Dixon Fold/Lancs. now in Manch.Museum (from Williamson,1887).

fig.6 : View of the under surface of a Sigillarian tree base from Cape Breton/Nova Scotia (from WILLIAMSON,1887, after BROWN,1849).

fig.7 : Diagrammatic sketch of a Sigillarian tree base from St.Etienne (from SOLMS-LAUBACH,1894,after GRAND EURY,1890).

PLATE II

Stigmaria radiculosa Hick

fig.8 : Transverse section through stele; Magn. 90x; Mc - R 354.

Me = pith
Ms = endo-xylem
Mr = medullary ray
pX = protoxylem
oX = outer xylem
exX = exo-xylem
Sz = secretory zone (phloem)
Pc = pericycle
p3 = inner cortex

fig.9 : Transv.sect. through stele and inner cortex; magn. 90x; Mc - R 354

lettering as in fig.8

fig.10: Long.sect. through stele; magn.90x; Mc - Q 153

lettering as in fig.8

fig.11: Tang.sect. through stele; magn.90x; Kc - 766 k.

lettering as in fig.8

PLATE III

fig.12: Transv.sect.through appendage trace leaving stele; magn 90x; Mc - R 354

lettering as in fig.8

fig.13: Transv.sect.through app.trace in middle cortex; magn. 90x; Mc - R 354

M = middle cortex
pc = pericycle of appendage trace
Vs = vascular strand

fig.14: Transv.sect. through outer and exo-xylem; magn. 350x Sc - 475. Lettering as in fig.8

fig.15: Long.sect. through stele and app.trace; magn.90x; Mc - Q 153; lettering as in fig.8.

PLATE IV

Stigmaria radiculosa Hick

fig.16 : Transv.sect.of outer cortex. Magn.90x; Ko - 657

sC = secondary cortex
Ss = secretory ducts
p2 = inner zone of outer primary cortex.

fig.17 : Transv.sect.of meristematic outer cortex; magn.30x; Mc - R 354

Mm = meristem
p1 = outer zone of outer primary cortex

fig.18 : Long.sect. of outer cortex and secretory ducts in fig 16; magn.90x; Mc - Q 161

lettering as in fig.16

fig.19 : Transv.sect.of superficial cortex; magn.30x; Ko - 731.

Su = superficial cortex
Sb = sclerotic band
p1 = outer primary cortex

PLATE V

Stigmaria radiculosa Hick

fig.20 : Transv.sect.of outer cortex; magn.30x; Ko - 657;

Su = superficial cortex
Sb = sclerotic band
p1 = outer zone of outer primary cortex
sC = secondary cortex
p2 = inner zone of outer primary cortex
Ss = secretory ducts
Mm = meristem
trans = transition zone

fig.20a: Transv.sect. of inner zone of outer cortex; magn. 30x; Go - 158.

fig.21 : Transv.sect. of inner zone of outer cortex; magn. 30x; Mc - R 354.

fig.21a: Transv.sect. of inner zone of outer cortex; magn. 30; Go - 158.

PLATE VI

Stigmaria radiculosa Hick

fig.22: Transv.sect. of outer and middle cortex; magn. 30x; Kc - 657;lettering as in fig.24.

fig.23: Transv.sect. of meristem in middle cortex; magn. 30x; Kc - 657; lettering as in fig.24.

fig.24: Transv.sect. of *Stigmaria radiculosa*; magn. 3x; Kc - 657;

x = appendage trace
M = middle cortex
Mm = meristem
p1 = outer primary cortex, outer zone
p2 = outer primary cortex, inner zone
p3 = inner primary cortex
Sc = secondary cortex
shaded areas = meristematic zones

PLATE VII

Stigmaria radiculosa Hick:

fig.25: Transverse section of appendage base; magn.60x; Mc - Q 162.

iZ = inner zone of outer cortex
trans= transition zone
Mc = middle cortex
iC = inner cortex
Pc = pericycle
pX = protoxylem
xyl = xylem strand
exX = exo-xylem
Sz = secretory strand (phloem)
Tr = tracheid of trabecular bridge

fig.26: Transv, sect. of appendage; magn. 60x; Kc - 1529; lettering as in fig.25.

PLATE VIII

Stigmaria sewardi nov.spec.

fig.27: Transv.sect.of stele;magn. 90x; Gc - 244;

Me = pith
Ms = endo-xylem
Mr = medullary ray
oX = outer xylem

fig.28: Transv.sect. of outer xylem; magn.30x; Gc - 34;

irr = irregularities in growth

fig.29: Tang.sect. of outer xylem with principal medullary ray; magn. 90x; Kc - 656 D.

prX = protoxylem
Mr = parenchyma of the medullary ray
oX = outer xylem
sMr = secondary medullary ray

fig.30: Transv.sect. stele; magn. 30x; Gc - 34;

oX = outer xylem
exX = exo-xylem
Sz = secretory zone (phloem)
Pc = pericycle
Mr = medullary ray

PLATE IX

Stigmaria sewardi nov.spec.

fig.31: Transv.sect. of stele with app.trace; magn. 90x; Gc - 34; lettering as in fig.30.

fig.32: Transv.sect. of appendage trace outside the stele; magn. 90x; Gc - 34; lettering as in fig.29 and 3o.

fig.33: Long.sect. of secondary cortex; magn.90x; Sc - 116;

Tr = tracheid

fig.34: Transv.sect. of outer appendage cortex; magn.30x;Kc-651.

trans= transition zone
iZ = inner zone
oZ = outer zone
eL = limiting layer

fig.35: Long.sect. of appendage stele; magn. 90x;Kc - 651;

endX = endoxylem
xyl = xylem strand
Sz = secretory zone
pc = pericycle

fig.36: Tracheid in fig.35; magn. 1100x.

PLATE X

Stigmaria sewardi var.*boonvillensis* nov.sp.nov.var.

fig.37: Transv.sect.of app.stele; magn. 90x; Ac - 6;
fig.38: " " " " " ; " 90x; Ac - 6;
fig.39: " " " " " ; " 90x; Ac - 6;

prX = protoxylem
xyl = xylem strand
exX = exo-xylem
Sz = secretory zone (phloem)
Pc = pericycle

fig.40: Tang.sect. of outer cortex showing appendage base; magn.90x; Ac - 11.

fig.41: Same section as fig.40; magn. 30x;

pc = pericycle
iC = inner cortex
mC = middle cortex
iZ = inner zone of outer cortex

PLATE XI

Stigmaria arranensis nov.spec.

fig.42: Transv.sect.of stele; magn. 90x; Wo - 605 lettering as in fig.27.

fig.43: Transv.sect.of stele; magn. 90x; Wo - 605 lettering as in fig.30.

fig.44: Long.sect. of pith; magn. 90x; Ac - 22.

fig.45: Transv.sect. of stele and appendage trace;magn. 30x; Ac - 54;

irr = irregularities in growth

fig.46: Tang.sect. of outer xylem and primary med.ray; magn. 90x; Ac - 50;

prX = protoxylem

PLATE XII

Stigmaria arranensis nov.spec.

fig.47: Tang.sect. of outer xylem with medullary rays; same as fig.46; magn. 30x;

Mr = medullary ray
sMr = secondary medullary ray

fig.48: *Stigmaria* cf. *arranensis*, transv.sect. of inner zone of outer primary cortex; magn. 30x; Sc - 112;

p2 = inner zone of outer cortex
Ss = secretory ducts
Tr = tracheids

fig.49: Same as fig.48; magn. 90x; lettering as in fig.48.

fig.50: Transv. sect. middle cortex; magn. 30x; Wc - 606;

PLATE XIII

Stigmaria arranensis nov.spec.

fig.51: Transv.sect. of outer primary and secondary cortex;
51a: magn. 30x; Ac - 53.

pl = outer primary cortex
Se = external secondary cortex
Si = internal secondary cortex
Ss = secretory ducts

fig.52: *Stigmaria sewardi* var.*boonvillensis*, transv.sect. of secondary cortex; appendage trace; magn. 30x; Ac - 51.

fig.53: *Stigmaria sewardi* var *boonvillensis*, long.sect. of appendage base in outer cortex; magn. 30x; Ac - 48;

Aer = middle cortex as aerenchyma
bpl = basal plate

PLATE XIV

Stigmaria arranensis n.sp.

fig.54: Transv.sect.of appendage stele; magn. 90x; Ac - 5;

prX = protoxylem
xyl = xylem strand
Pc = pericycle
Tr = tracheids

fig.55: Transv.sect. of appendage stele; magn. 90x; Ac - 5; lettering as in fig.54.

fig.56: Transv.sect. of appendage stele; magn. 90x; Ac - 40; lettering as in fig.54.

PLATE XV

Stigmaria vulgaris nov.spec.

fig.57: Tang.sect. of outer xylem with principal medullary rays; magn. 30x; Gc - 183.

fig.58: Tang.sect. through superficial cortex; magn. 30x; Kc - 833.

fig.59: Transv.sect. of outer cortex; magn. 30x; Kc - 649.

Su = superficial cortex
Ss = sclerotic strand
Sb = sclerotic band
pl = outer primary cortex

fig.60: Same as fig.58; magn. 90x; tr = tracheids

PAGE
NUMBERING
AS ORIGINAL

PLATE XVI

Stigmaria vulgaris nov.spec.

fig.61: Transv.sect.of secondary cortex; magn. 30; Gc - 179;

Se = external secondary cortex
Si = internal secondary cortex
Ss = secretory ducts

fig.62: Transv.sect.of secondary cortex, primary tissue surrounded by secondary tissue; magn. 30x; Mc - R 873;

fig.63: Transv.sect. of internal secondary cortex; magn.90x; lettering as in fig.61. Gc - 179.

fig.64: Long.sect. of internal secondary cortex; magn.30x; Gc - 185; lettering as in fig.61.

PLATE XVII

Stigmaria asteroidea nov.spec.

fig.65: Transverse sect. of outer xylem; magn. 90x; Kc - 654;

irr = irregularities in growth

fig.66: Transverse sect. of outer xylem and app. traces; magn. 90x; Kc - 654.

fig.67: Transv. sect. of superficial cortex and sclerotic strands; magn. 90x; Kc - 587;

Su = superficial cortex
Ss = sclerotic strands
pl = outer primary cortex
bpl = basal plate
iz = inner zone
oz = outer zone

fig.68: Transverse section of outer cortex and appendage base; magn. 30x; Kc - 654; lettering as in fig.67

P L A T E XVIII

fig.69: *Stigmaria shurneyensis* n.sp., transv. sect. of stele; magn. 90x; Kc - 652 A;

iX = inner xylem
oX = outer xylem
Mr = medullary ray

fig.70: *Stigmaria shurneyensis* n.sp., tang.sect.of outer xylem showing principal and secondary medullary rays; magn. 30x; Kc - 652 F.

sMr = secondary medullary rays

fig.71: *Stigmaria vascularis* n.sp.transv.sect. of stele; magn. 90x; Kc - 2314;

Me = pith
iX = inner xylem
oX = outer xylem
prX = protoxylem groups

fig.72: *Stigmaria vascularis* n.sp., transv.sect. of outer cortex; magn. about 90x; Kc - 2314;

Ss = sclerotic strands
Su = superficial cortex
pl = outer primary cortex

P L A T E XIX

fig.73: *Stigmaria bacupensis*,transv.sect.of stele; magn. 350x; Kc - 2592; lettering as in fig.71.

fig.74: *Stigmaria sigillarioides* n.sp. transv.sect.of middle cortex; magn. 90x; Kc - 2679;

mC = middle cortex
sZ = secretory strand (phloem) of appendage trace

fig.75: *Stigmaria sigillarioides* n.sp.,transv.sect.of secondary cortex; magn. 90x; Gc - 196;

Mm = meristematic zone

fig.76: *Stigmaria sigillarioides* n.sp.,transv.sect. of outer part of cortex; magn. 90x; Gc - 196;

oC = outer primary cortex
Ss = sclerotic strands

PLATE XX

Stigmaria bacupensis Scott et Lang

fig.77: Transv.sect.of outer cortex; magn.90x;Kc - 2592;
a.77a : (figd in LANG,1923);

Pl = outer primary cortex
Ss = sclerotic strands

fig.78: Transv.sect.of stele; magn.90x; Kc - 2592;

iX = inner xylem
oX = outer xylem

fig.79: Long.section of appendage base; magn.90x; Kc - 2592;

xyl = xylemstrand of appendage
pc = pericycle
mC = middle cortex
iz = inner zone
oz = outer zone

PLATE XXI

fig.80: *Stigmaria arachnoidea* Koopmans; transv.sect. of outer cortex of appendage; magn. 90x; Kc - 431.
El = limiting layer
oZ = outer zone
iZ = inner zone

fig.81: *Stigmaria* cf. *pettycurensis*; transverse sect. of appendage magn. 30x; Kc - 257; lettering as in fig.80.

fig.82: *Stigmaria* sp., transverse section of outer cortex of appendage; magn. 90x; Gc - 183; lettering as in fig.80.

fig.83: *Stigmaria shurneyensis* n.sp., transverse sect. of appendage base. Magn. 30x; Kc - 652 F.

PLATE XXII

fig.84: *Stigmaria asteroidea* n.sp., transverse section of appendage; magn.30x;Kc - 586; lettering as in fig.80.

fig.85: *Stigmaria* sp., transv. sect. of appendage;secondary growth in middle cortex;magn.30x;Sc - 563;

oZ = outer zone
iZ = inner zone
Mm = meristem
mC = middle cortex

fig.86: *Stigmaria* sp., oblique transv.sect. of appendage; secondary growth in xylem and outer cortex; magn. 30x; Go - 179;lettering as in fig.85

fig.87: *Stigmaria* sp. tang.sect.of outer cortex, outer zone of appendage with tracheids therein; magn.90x; Kc - 121; tr = tracheids.

PLATE XXIII

fig.88: *Sigillaria* cf. *mamillaris*, transv.sect.of outer cortex; magn.30x; Kc - 1960.

Ep = epidermis and suberized subepidermal layers
oC = outer primary cortex
Pd = periderm
Ss = sclerotic ? strands

fig.89: *Sigillaria* cf. *mamillaris*, transv.sect. of leaf cushion; magn.30x; Kc - 1960;

par = parichnos strands

fig.90: *Stigmaria sigillarioides* n.sp., transv.sect.of secondary cortex; magn. 30x; Kc - 2829.
trace = probably appendage trace.

PLATE XXIV

fig.91: Stigmaria sp. appendage, transv. sect. of cortex; magn.30x; Kc - 1846;

El = limiting layer
oZ = outer zone
iZ = inner zone
trZ = transition zone
mC = middle cortex
iC = inner cortex

fig.92: Stigmaria sewardi n.sp, transv.sect. of app.base; magn.30x; Kc - 651; lettering as in fig.93

fig.93: Stigmaria sp.appendage, same specimen as fig.91; transv.sect. of stele; magn. 90x

pX = protoxylem
xyl = primary xylem strand
endX= endo-xylem
exX = exo-xylem
pc = pericycle
sZ = secretory zone

fig.94: Stigmaria bacupensis, long.sect.of appendage base; magn.30x;Kc - 659;
Endogenous insertion of appendage.

sC = secondary cortex
Ss = sclerotic strands
Mm = meristematic zone
oC = outer primary cortex

Plate I

fig.1

fig.1a

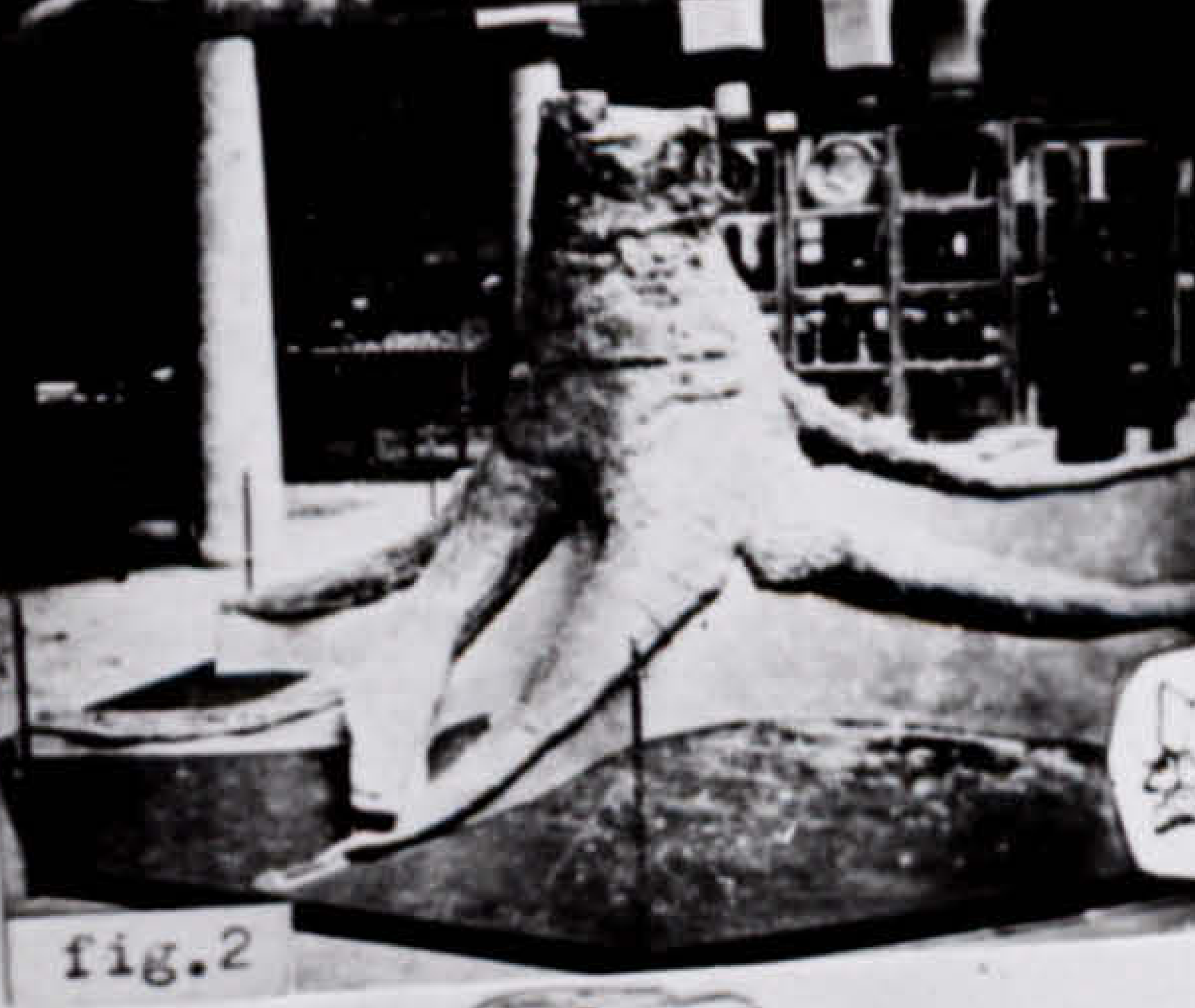


fig.2

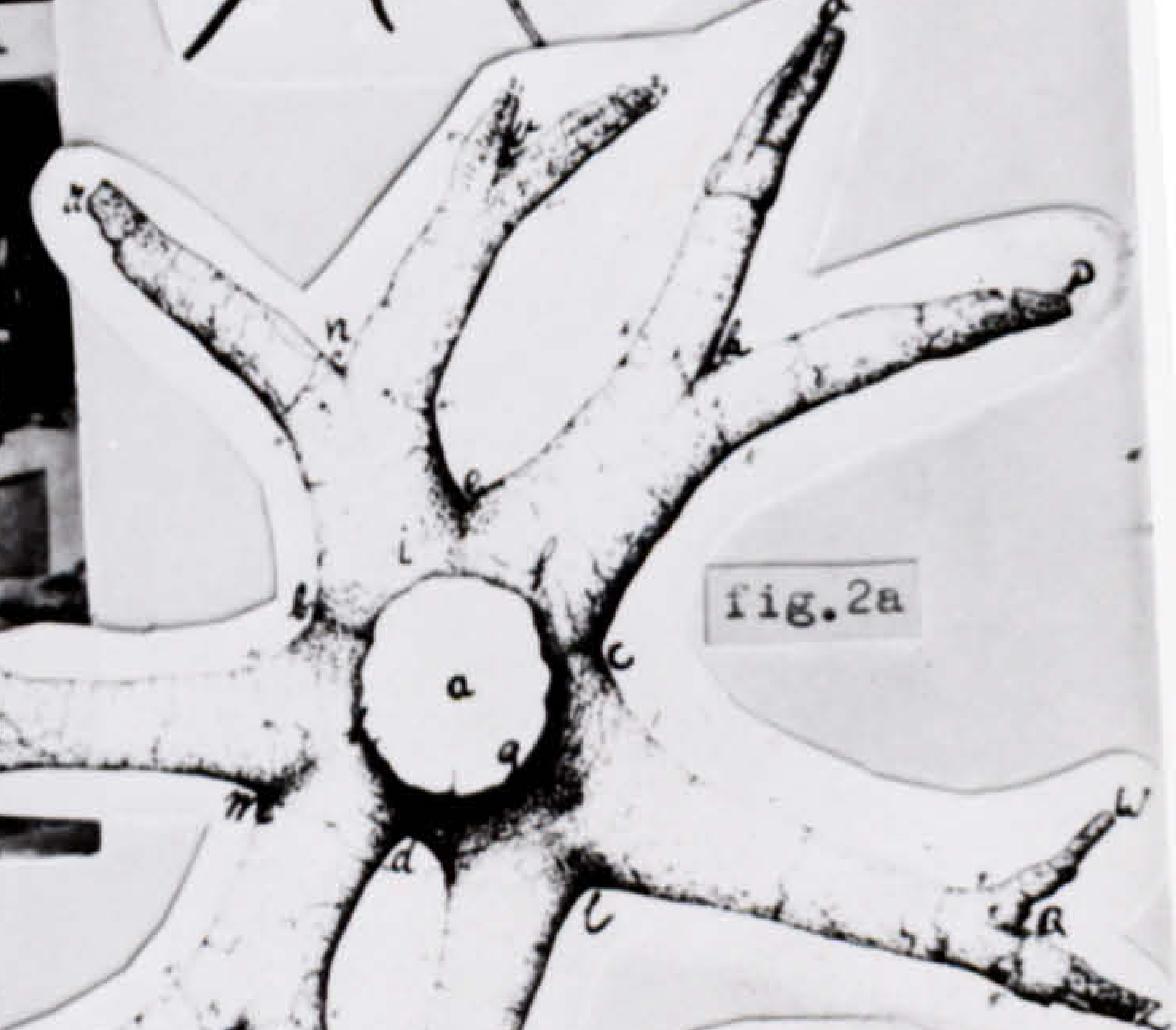


fig.2a

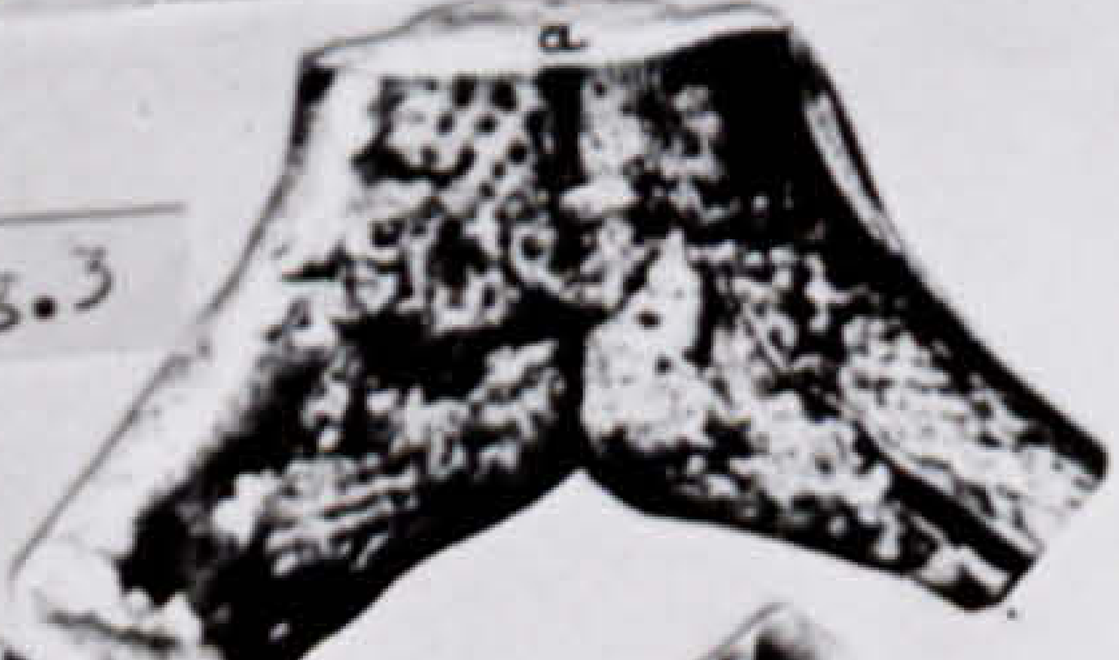


fig.3

fig.3a

fig.6

fig.4

fig.5

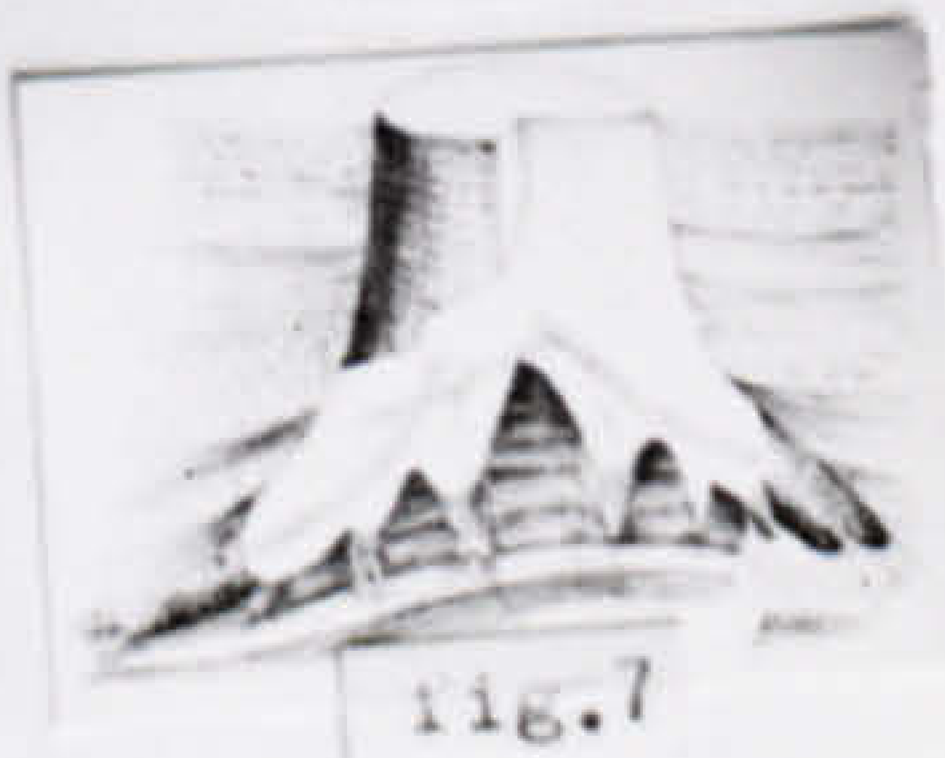


fig.7

Plate II

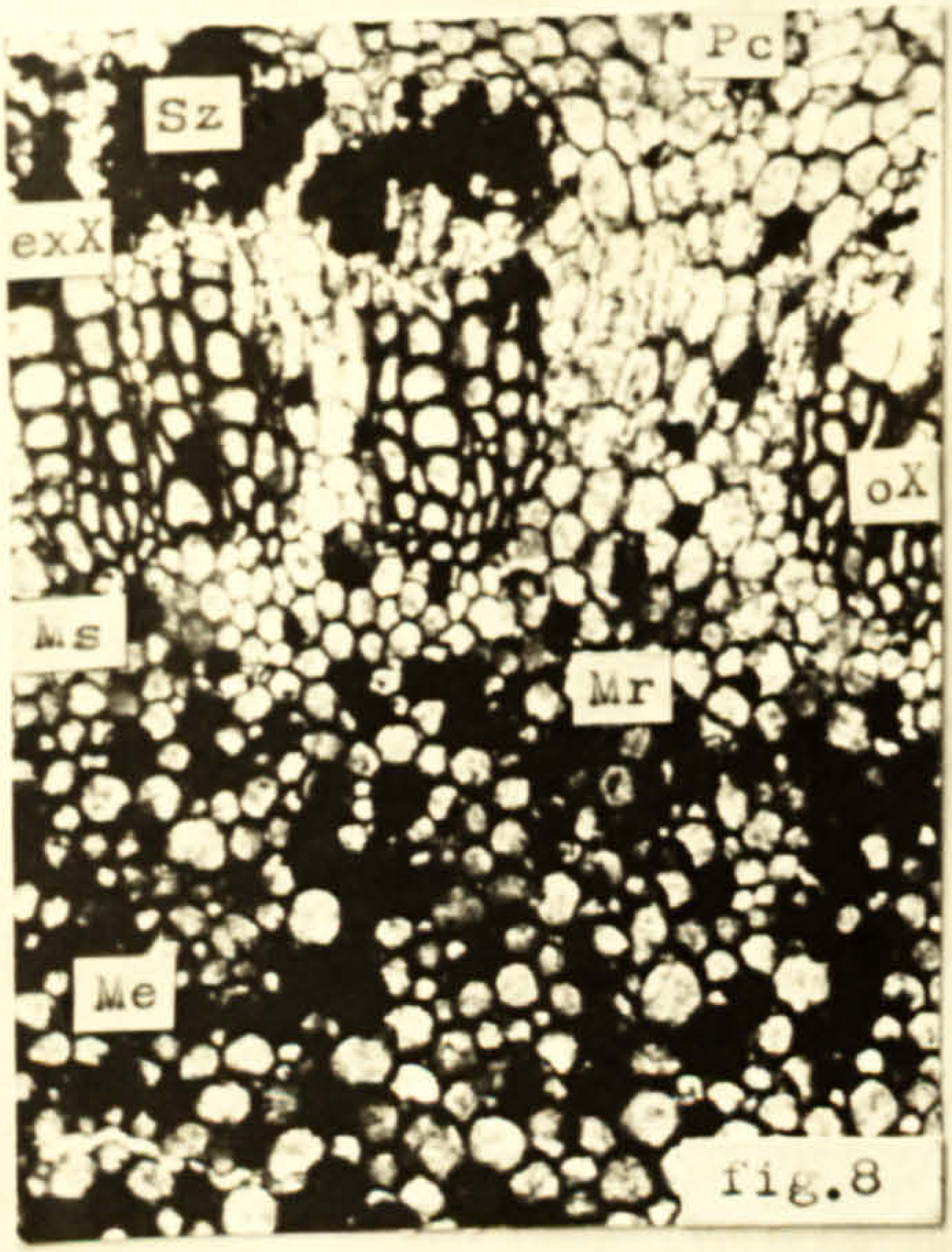


fig.8

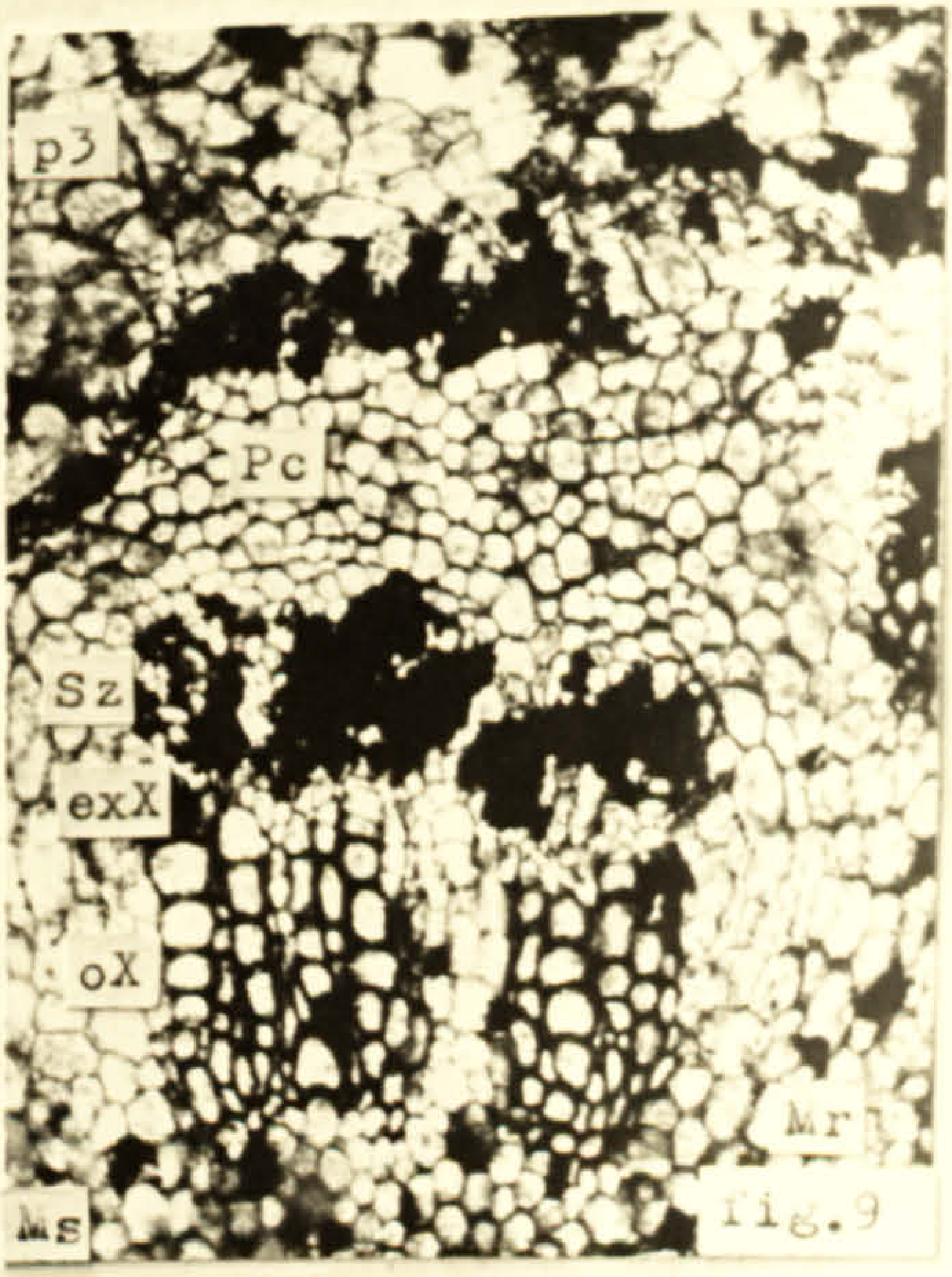


fig.9

fig.10

fig.11

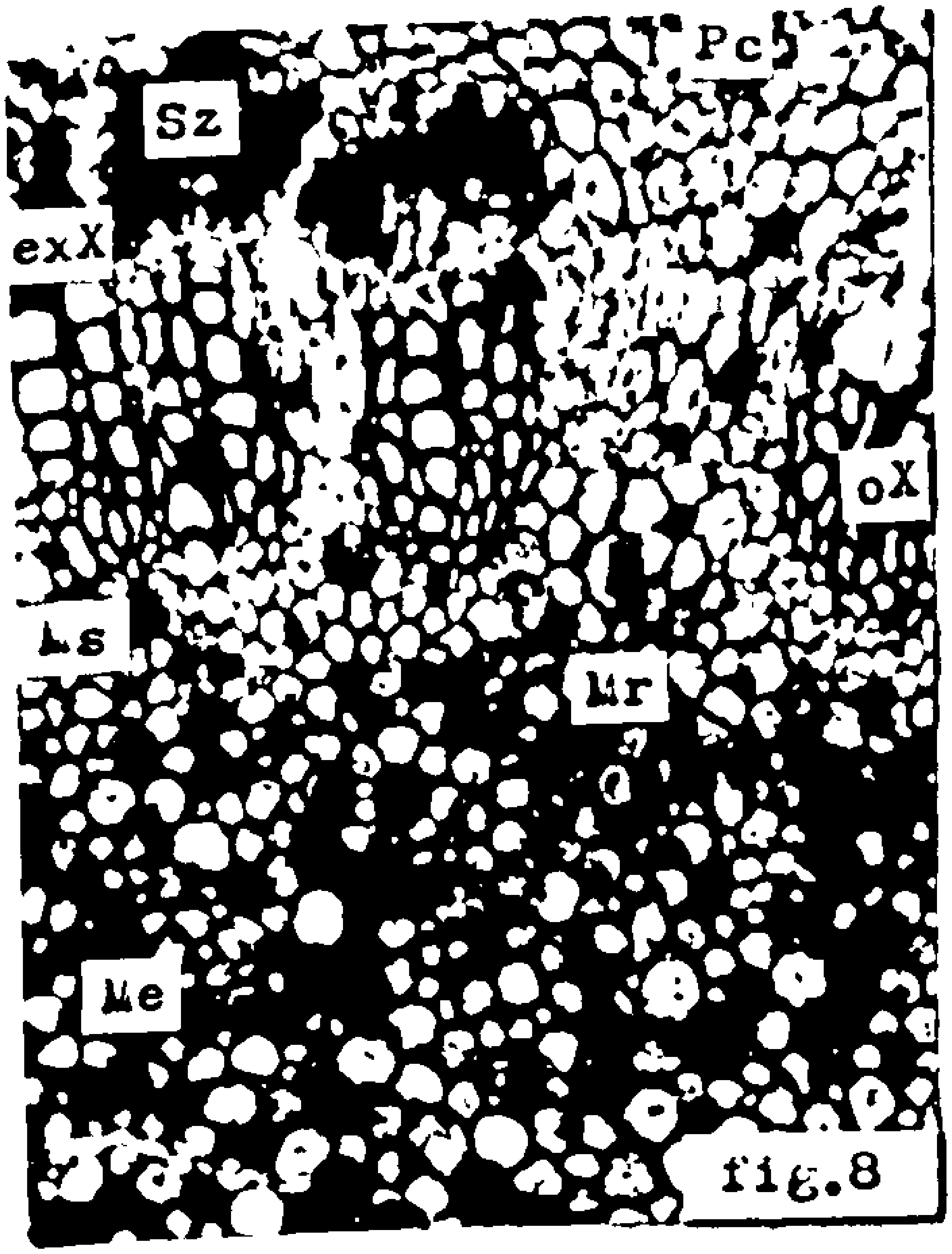


fig.8

fig.9

fig.10

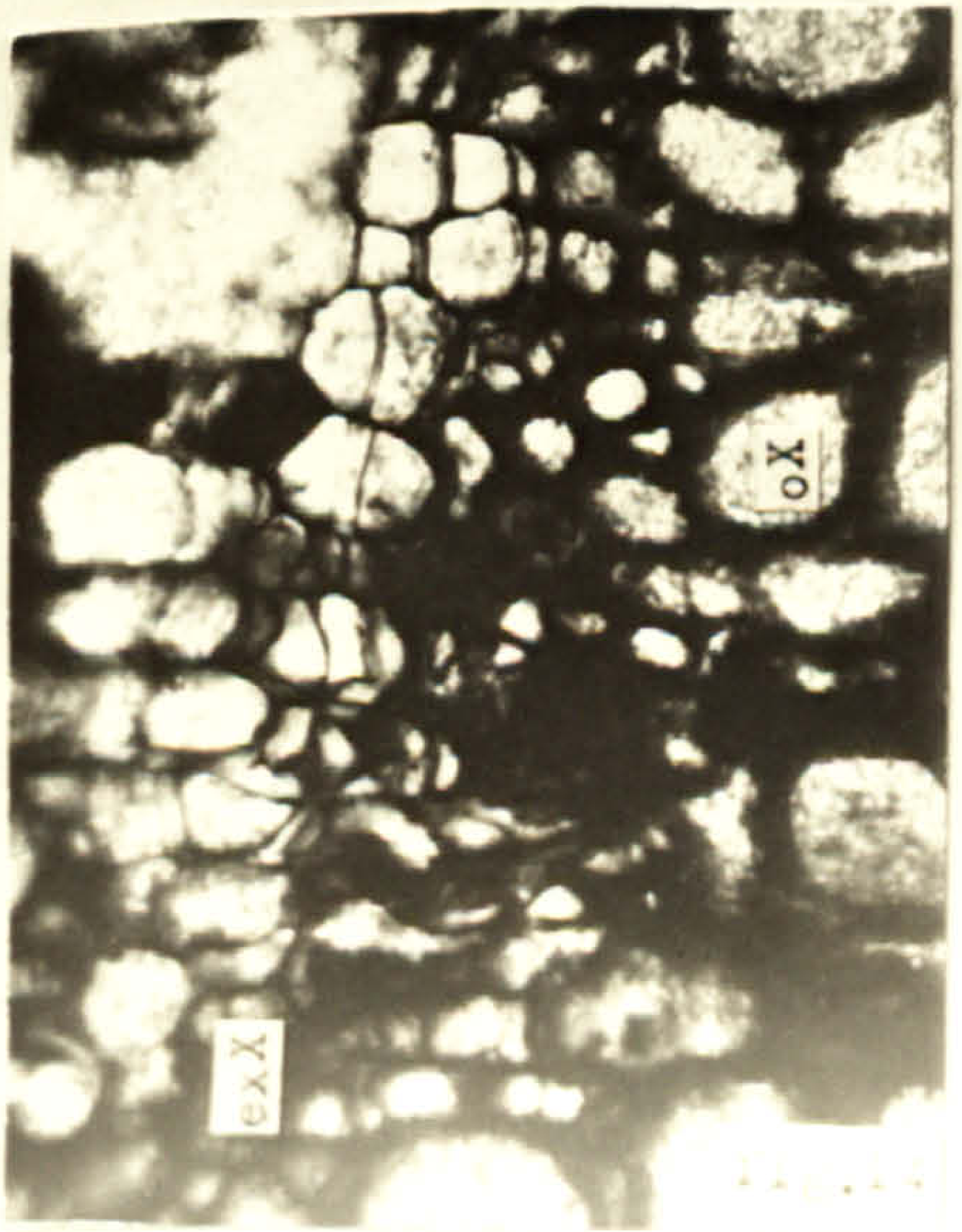
fig.

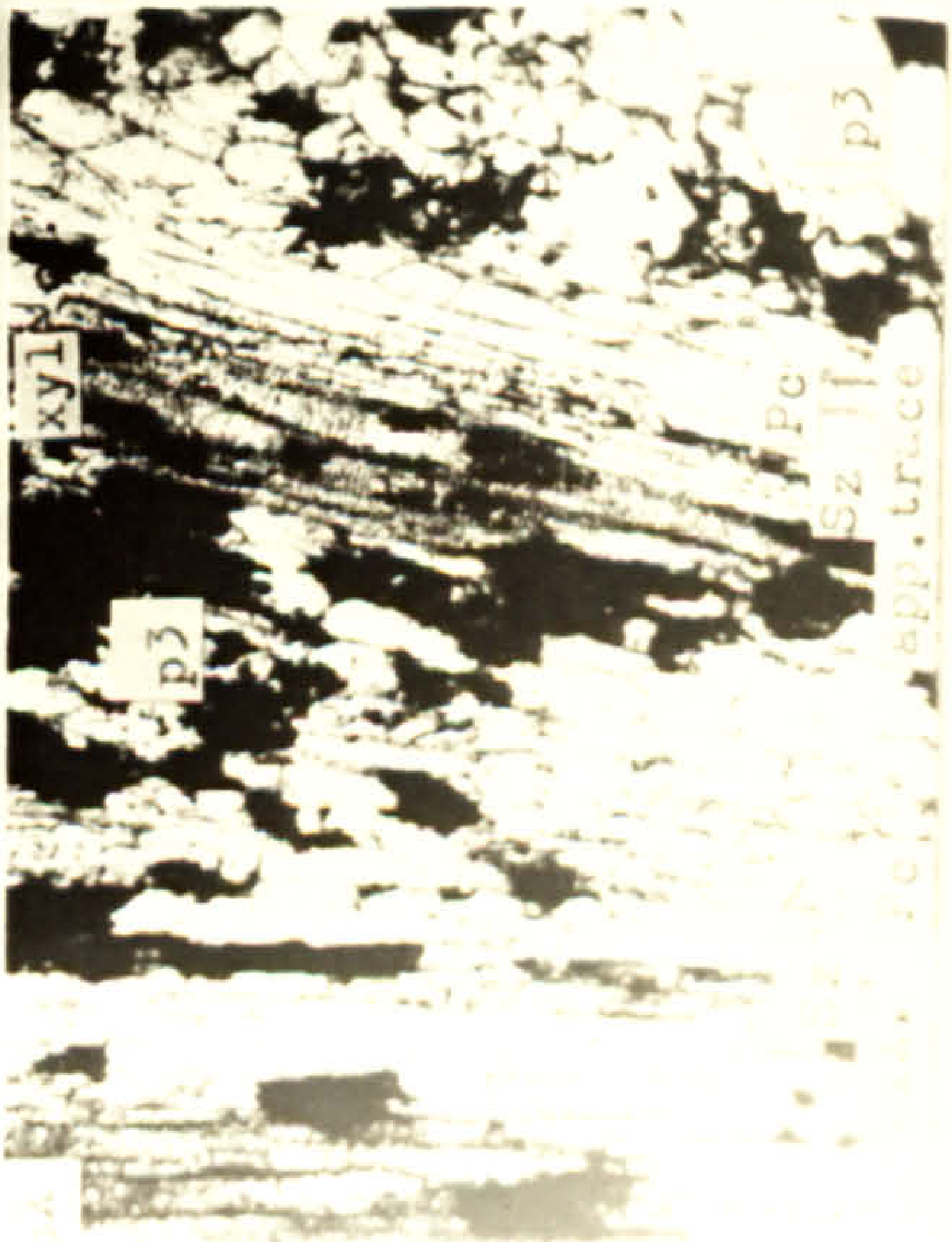

app.trace
p3
Pc
Pc
Sz
exX
oX

fig.12


F
M
Pc
Vs
M

fig.13


oX
exX


p3
xyl
Pc
Sz
app.trace
p3

Plate

fig.12

fig.13

Plate IV

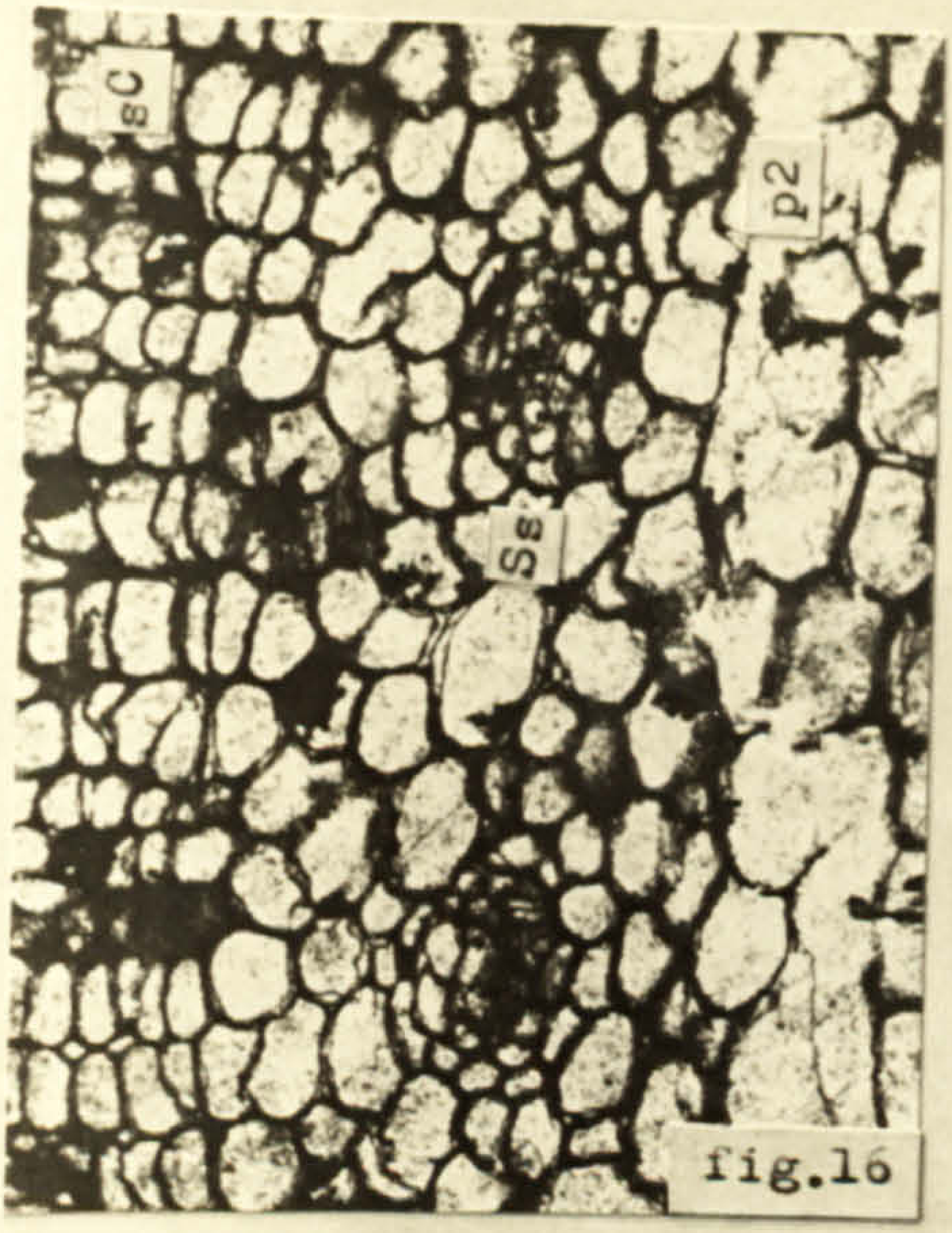


fig.16

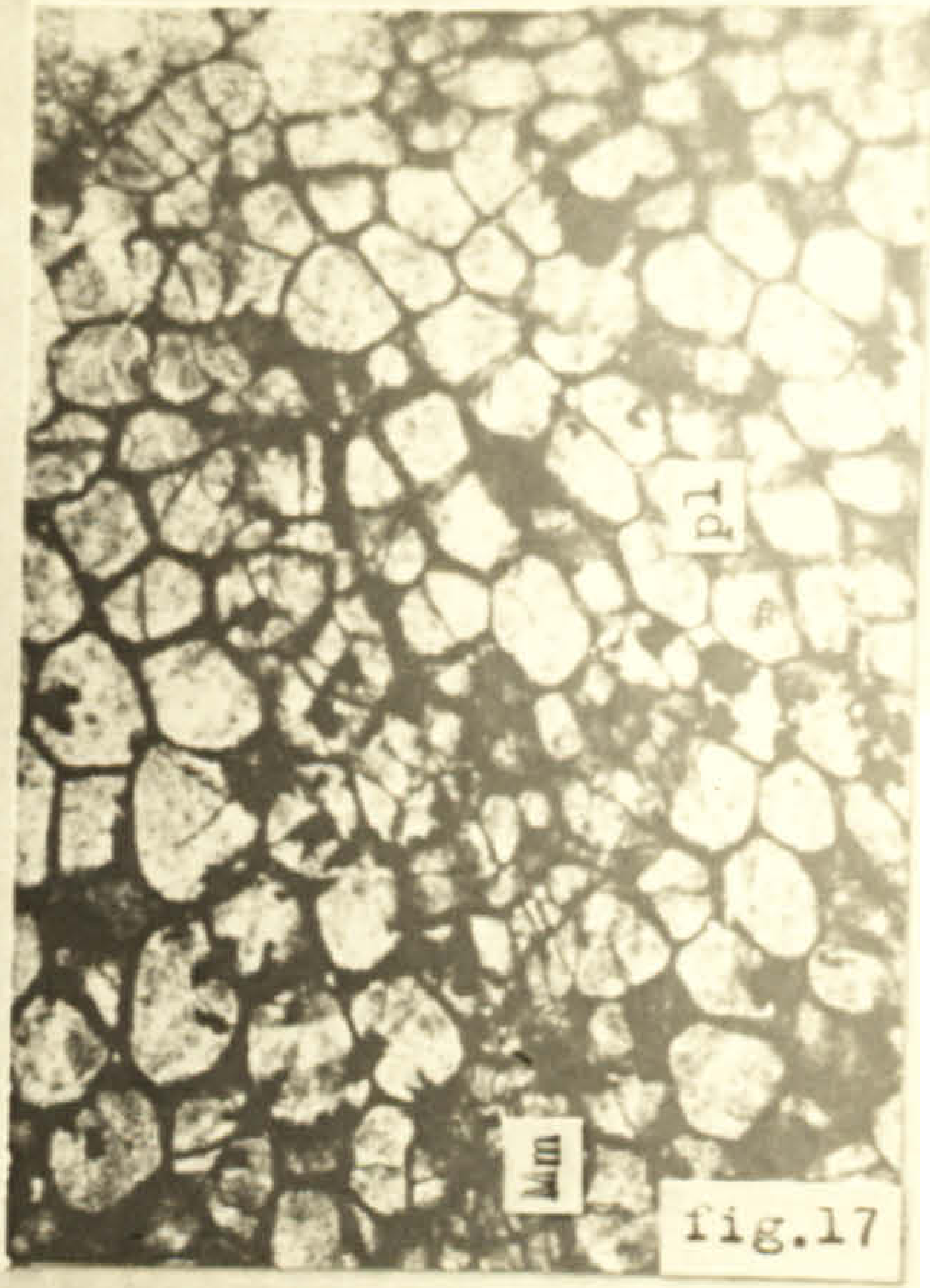


fig.17

fig.18

fig.19

Plate IV

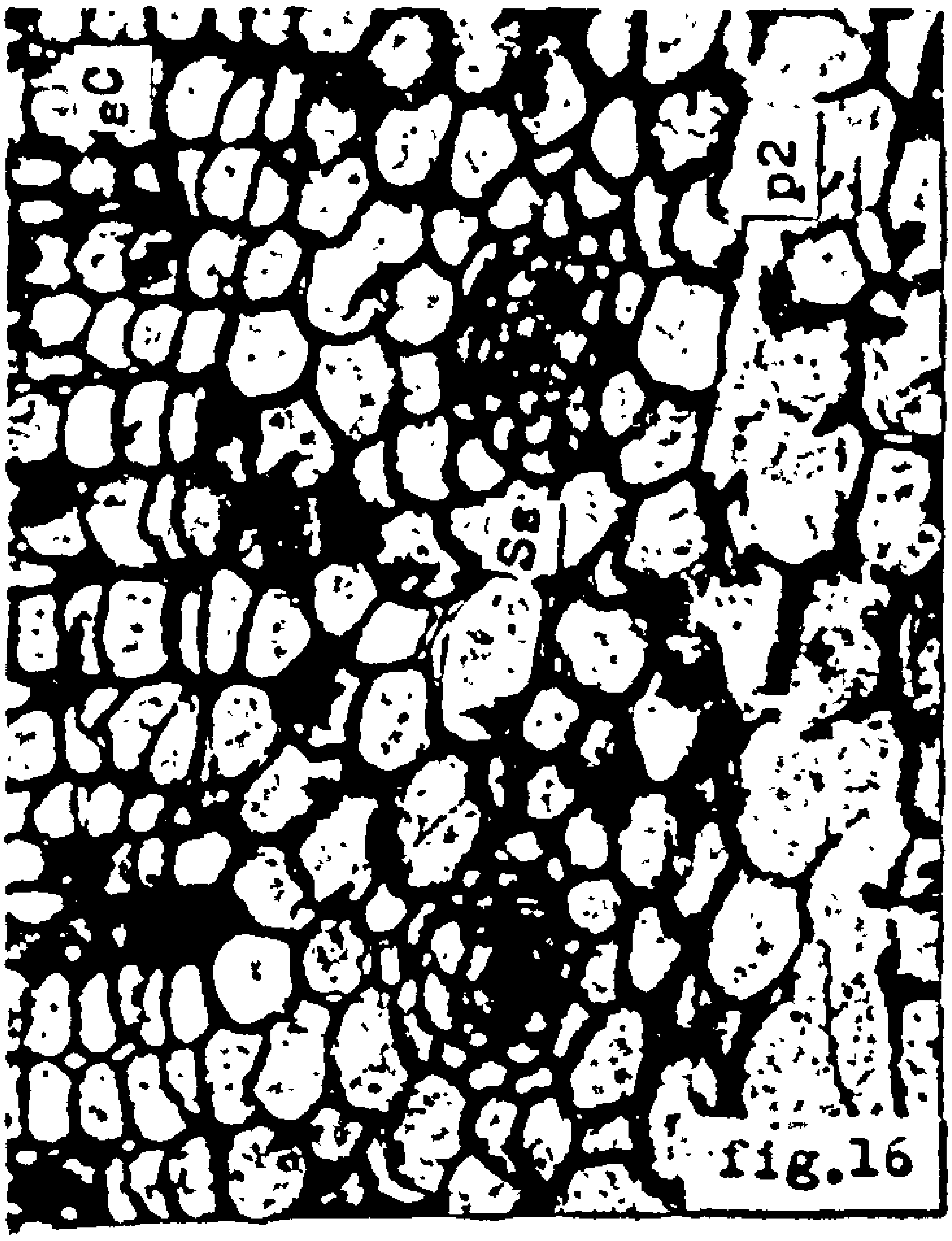


fig.16

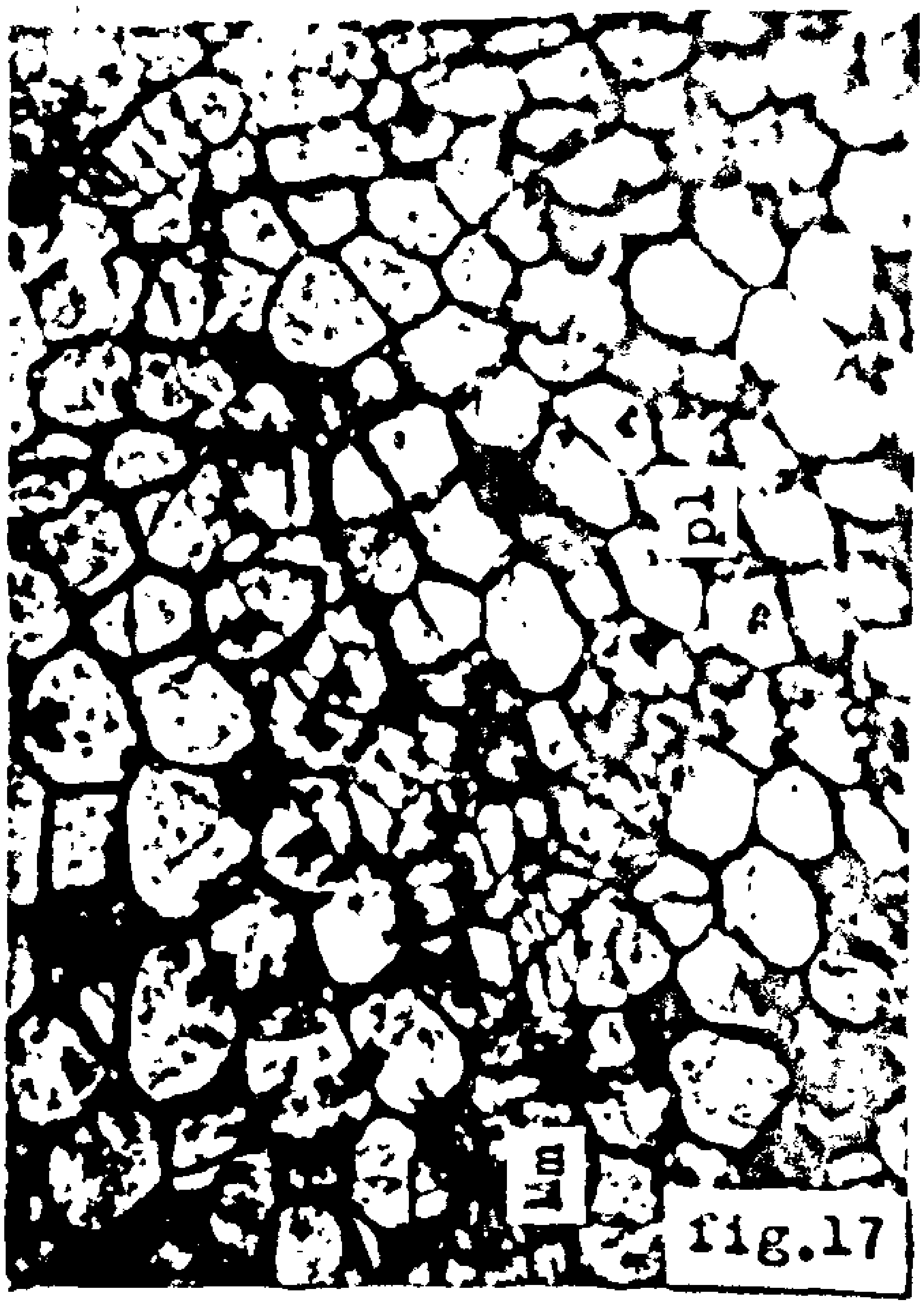


fig.17

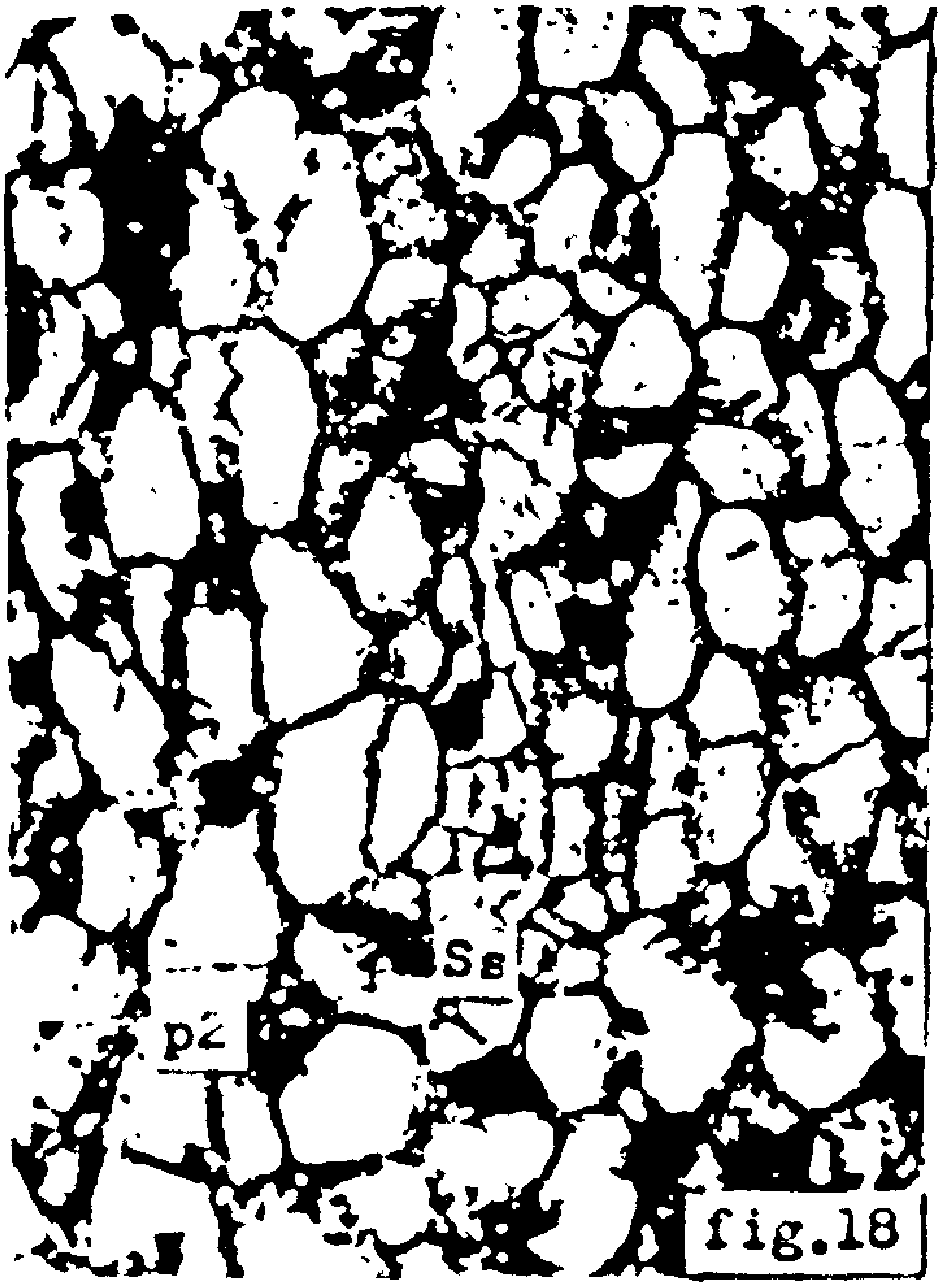


fig.18

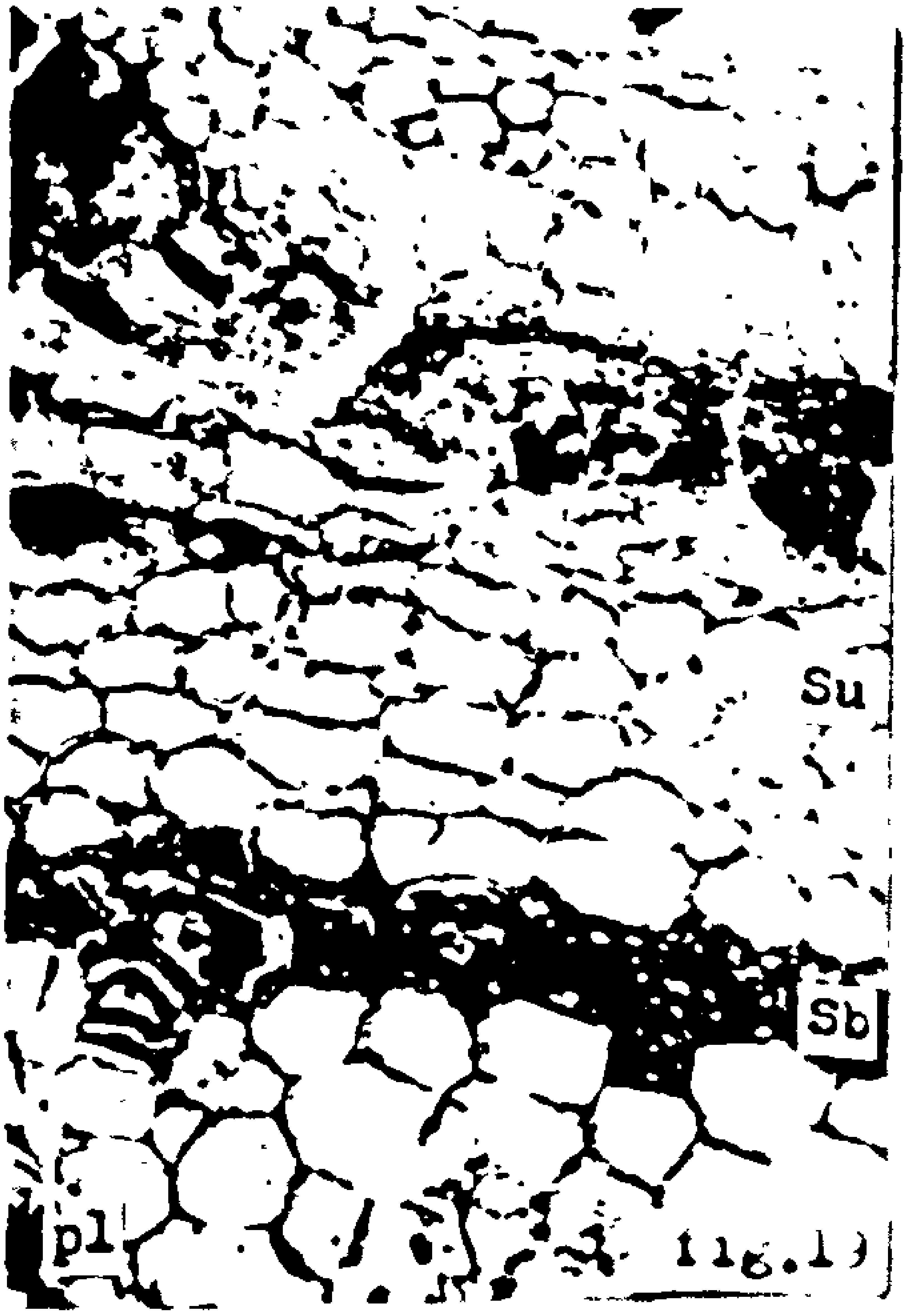


fig.19

Plate V

fig.20

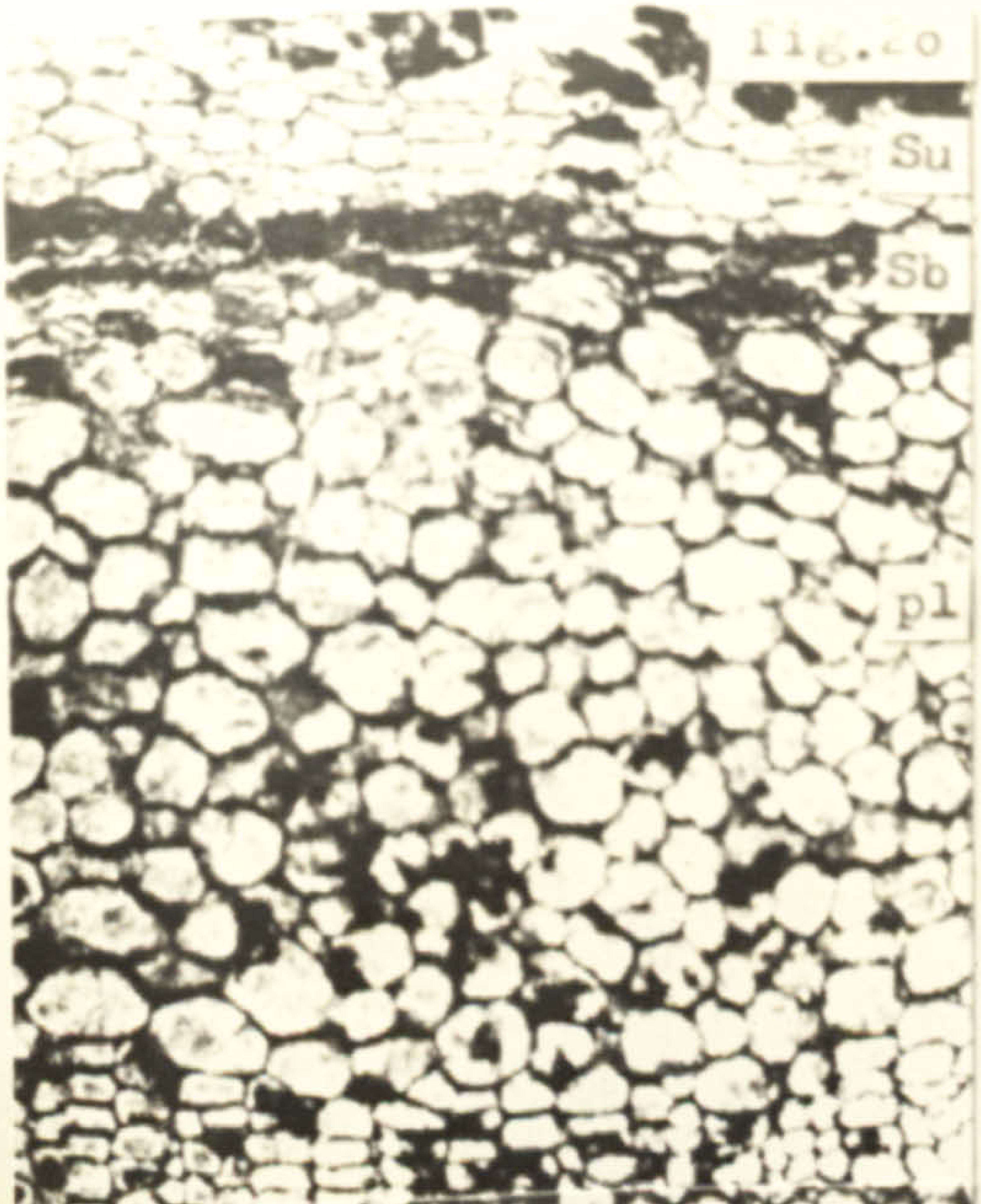


fig.20a

fig.21

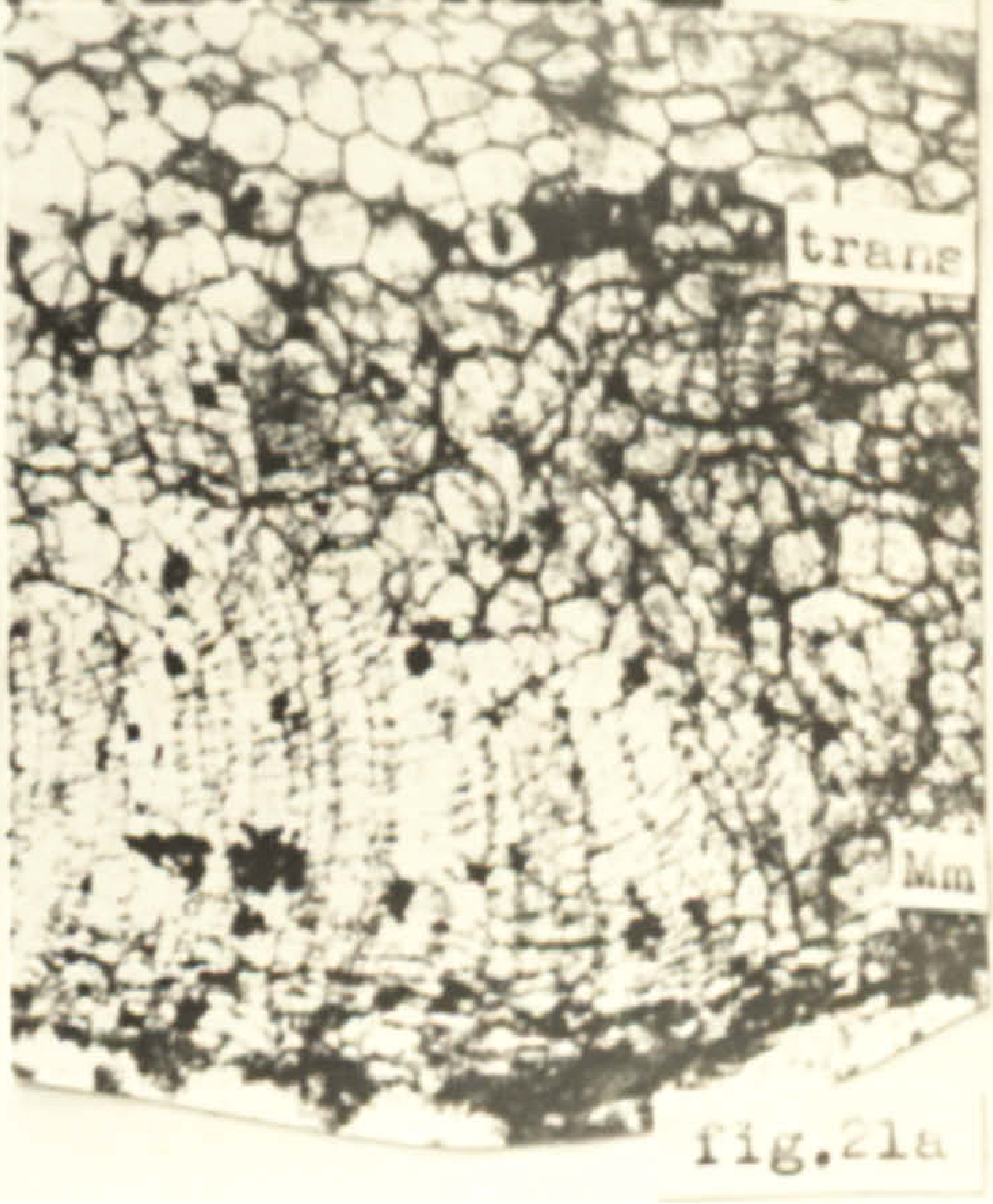


fig.21a

fig.20a

fig.21a

Plate VI


fig.22


fig.23

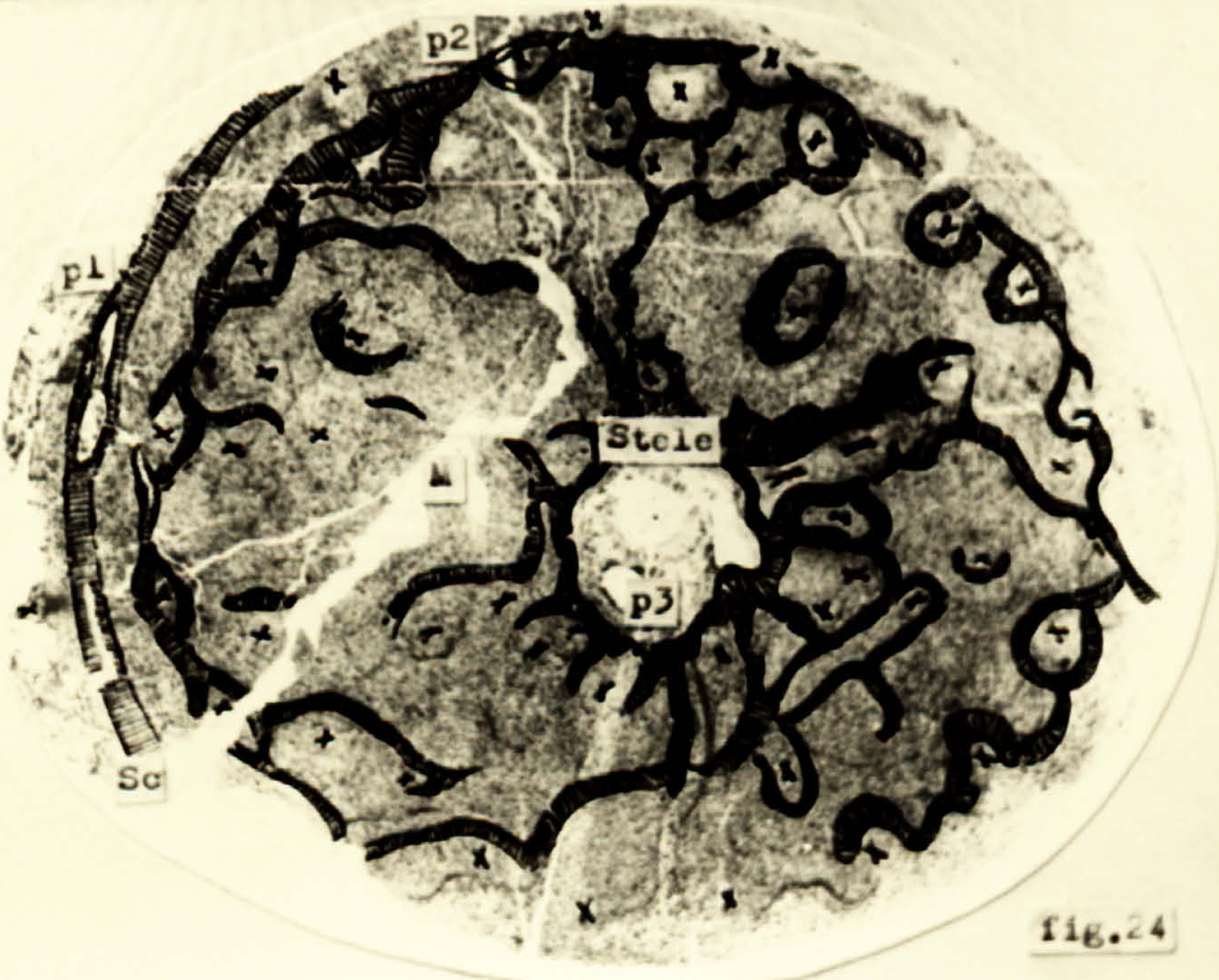


fig.24

fig.22

fig.23

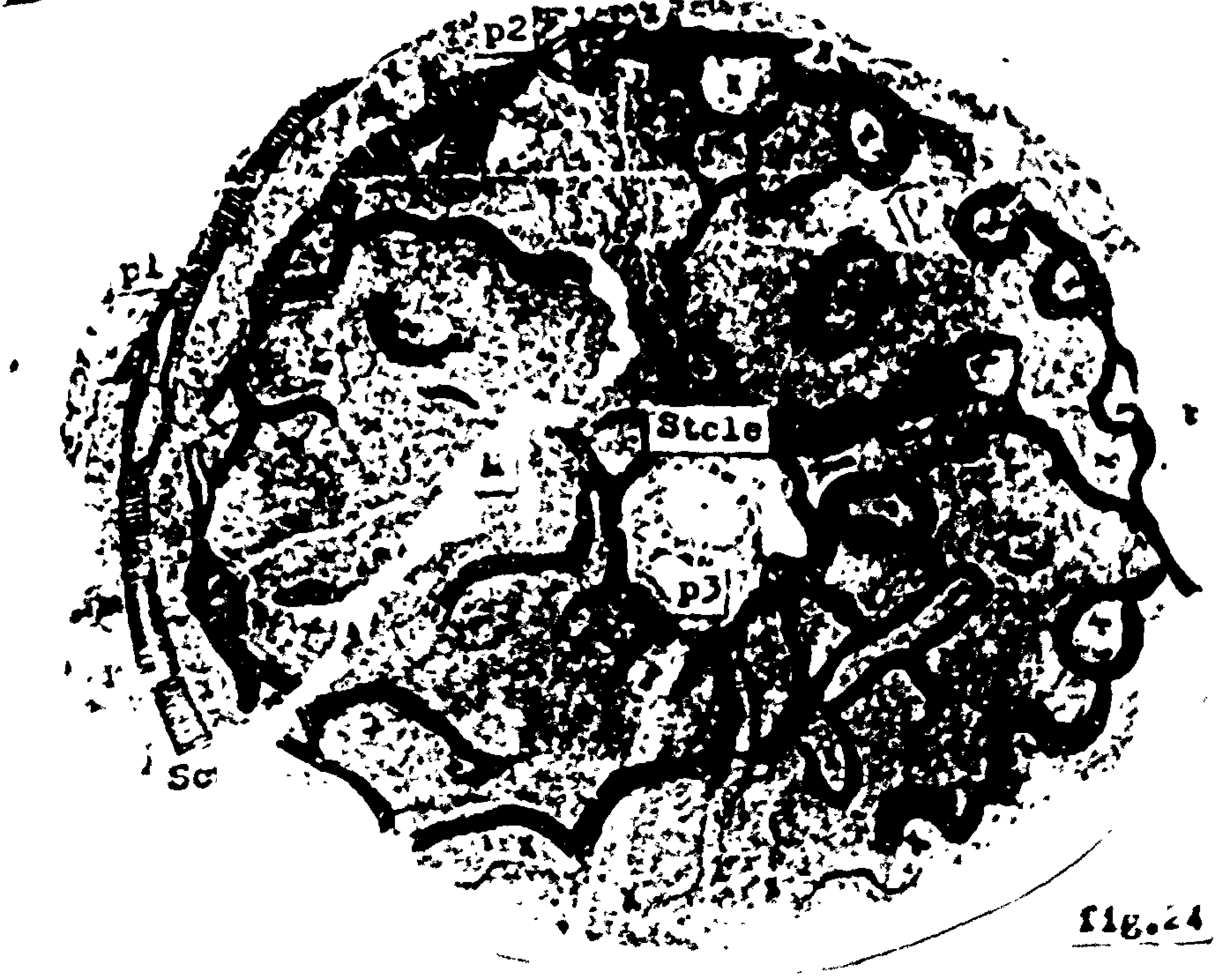


fig.24

Plate VII

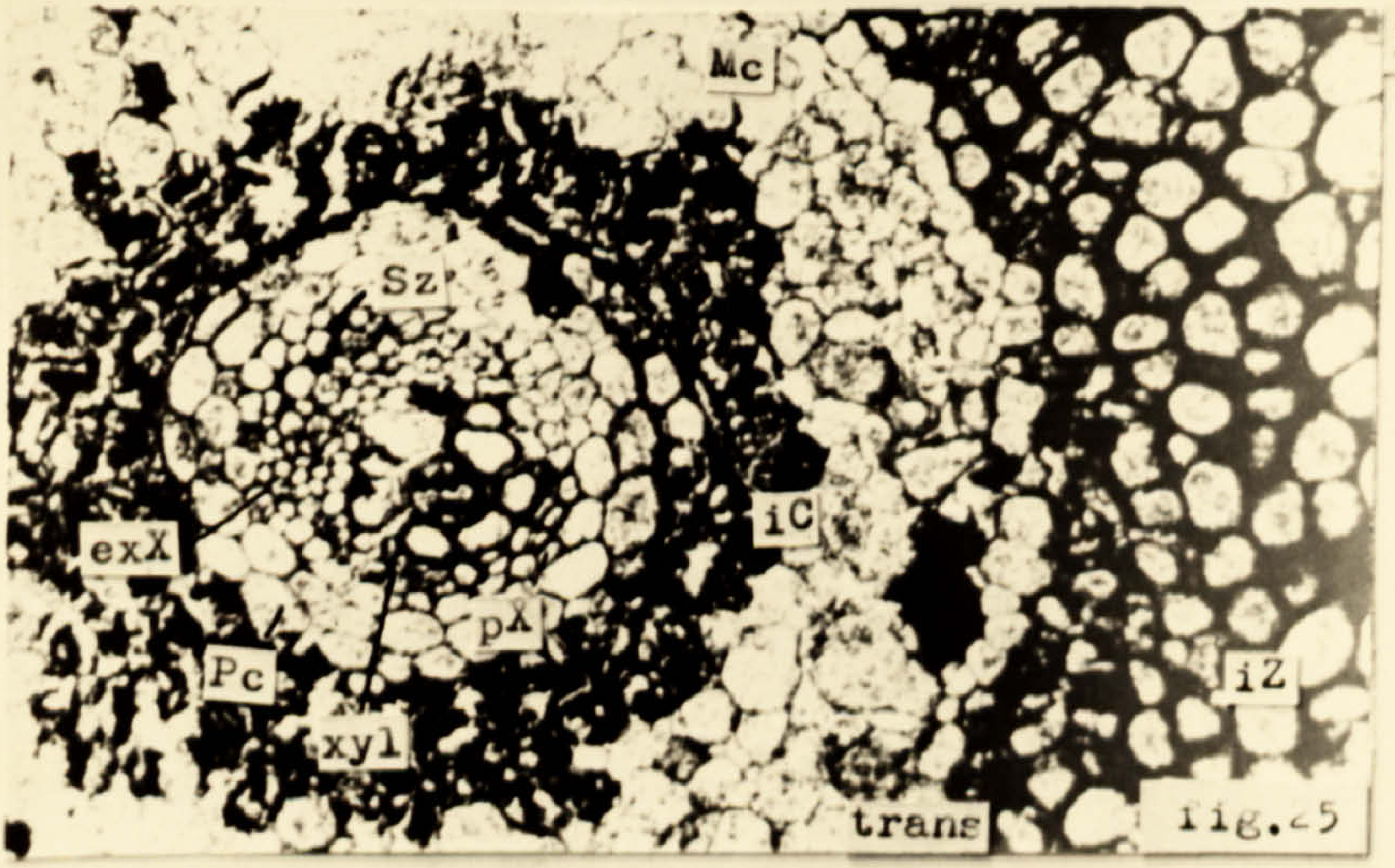


fig.25

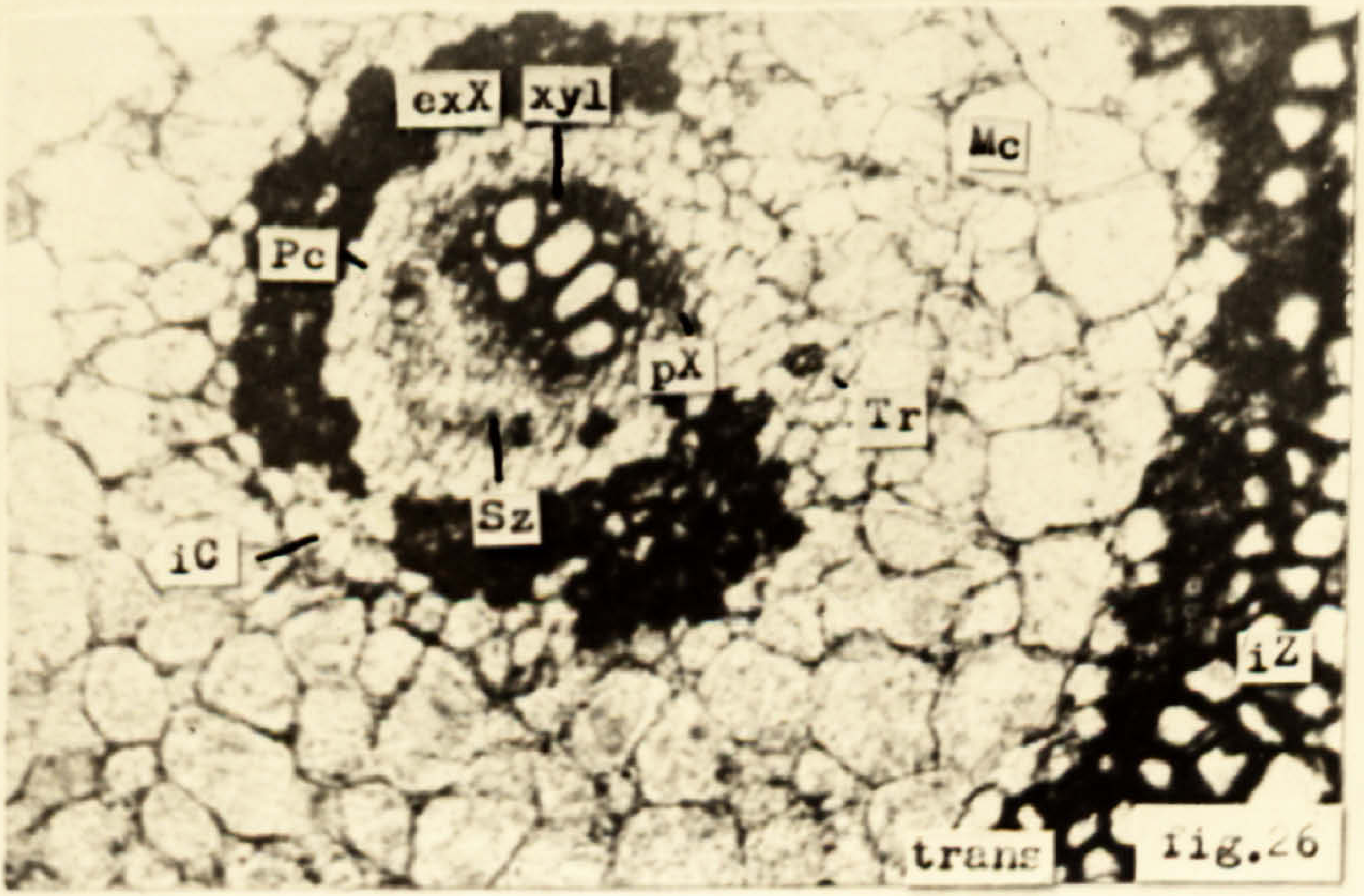


fig.26

fig.25

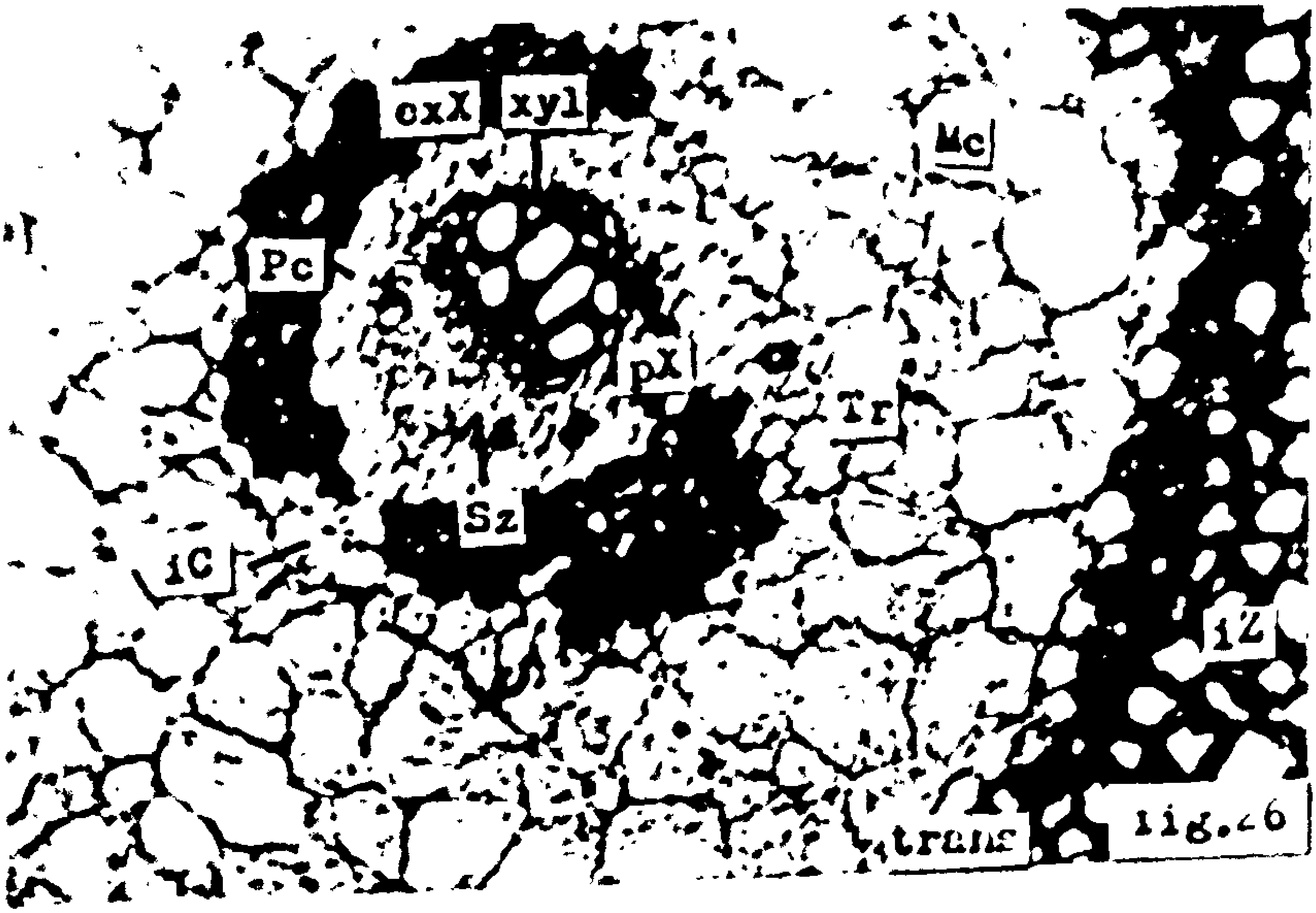


fig.26

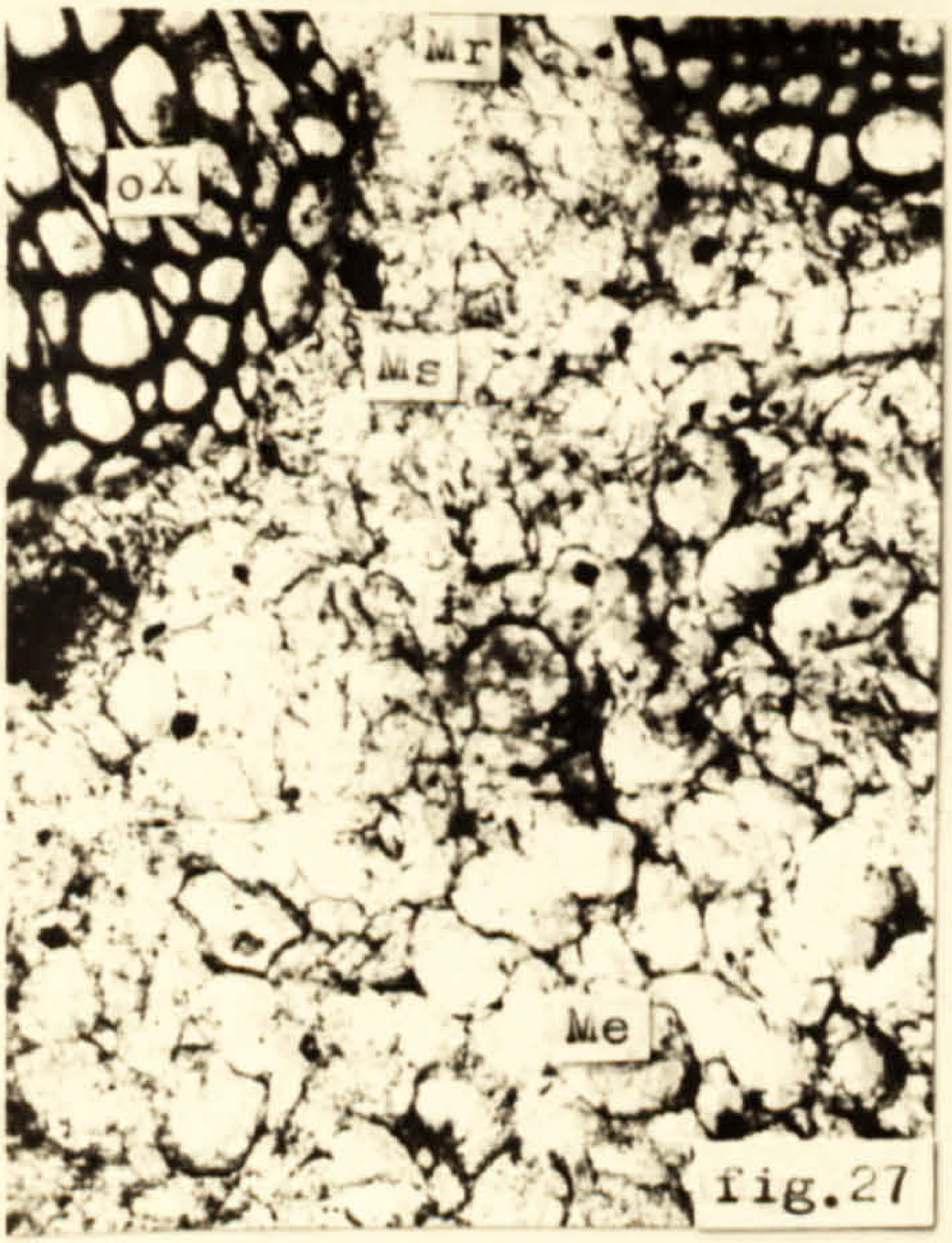


fig.27

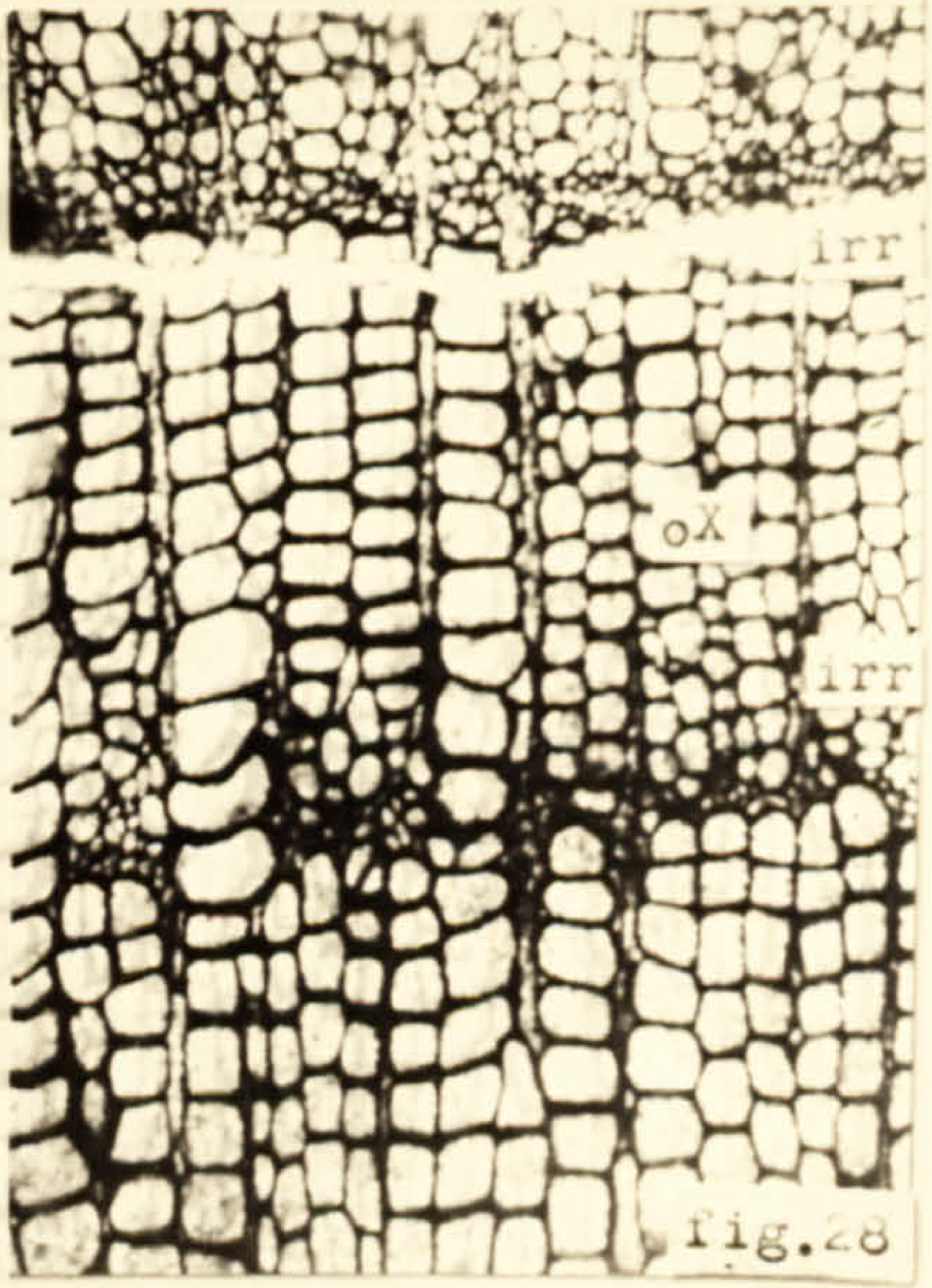


fig.28

fig.29

fig.30

Plate VIII

fig.27

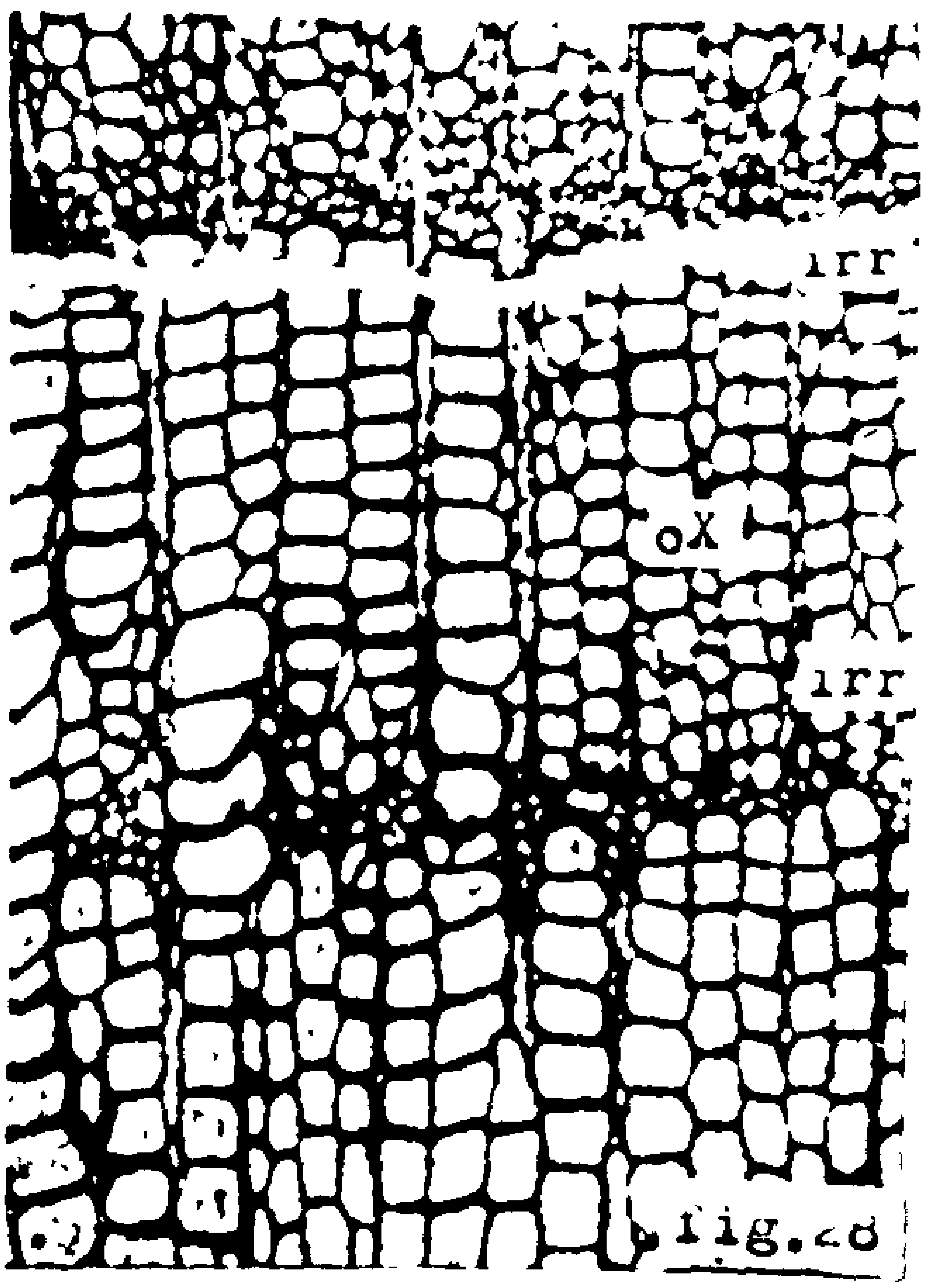


fig.28

fig.29

Plate IX

fig.31

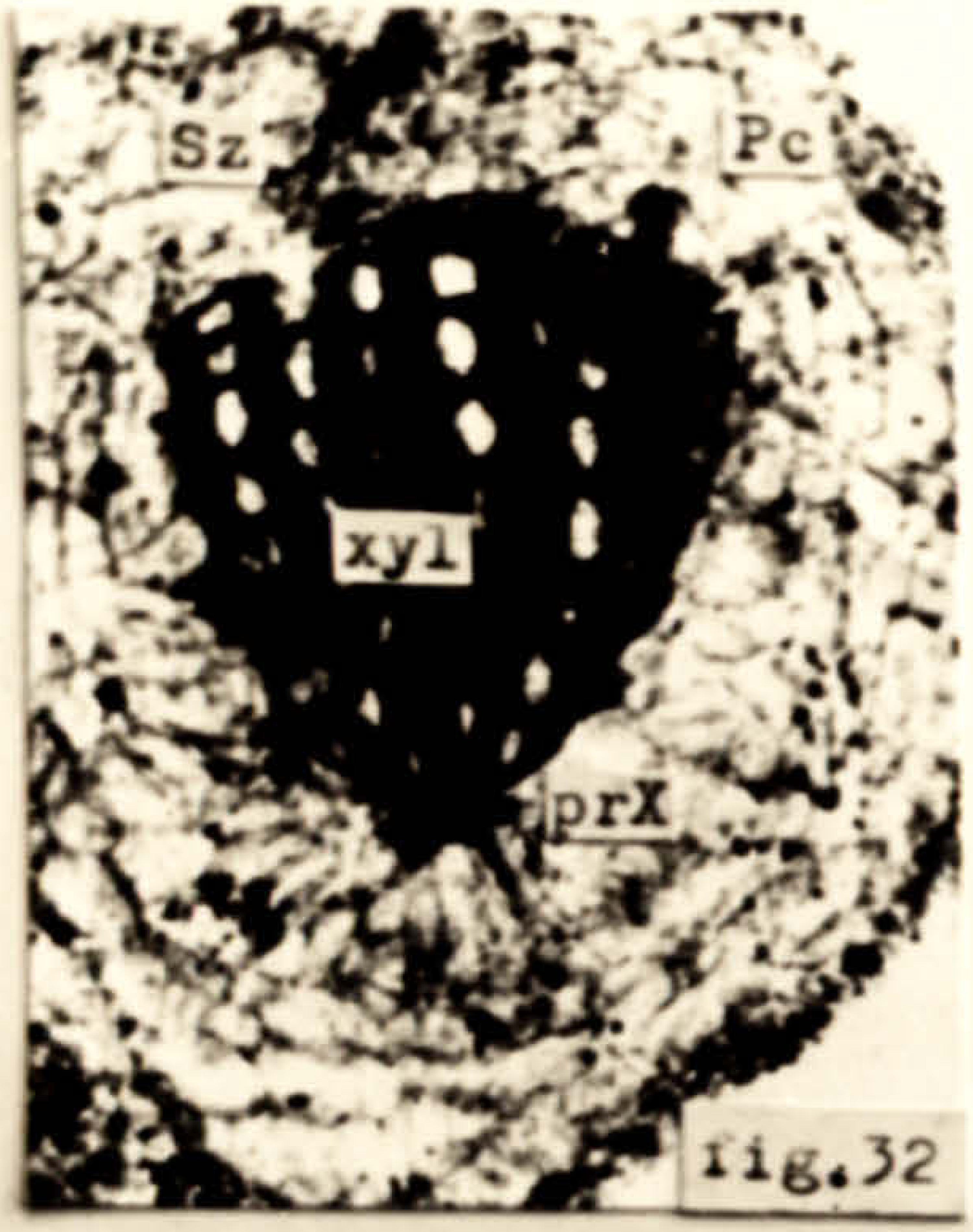


fig.32

fig.33

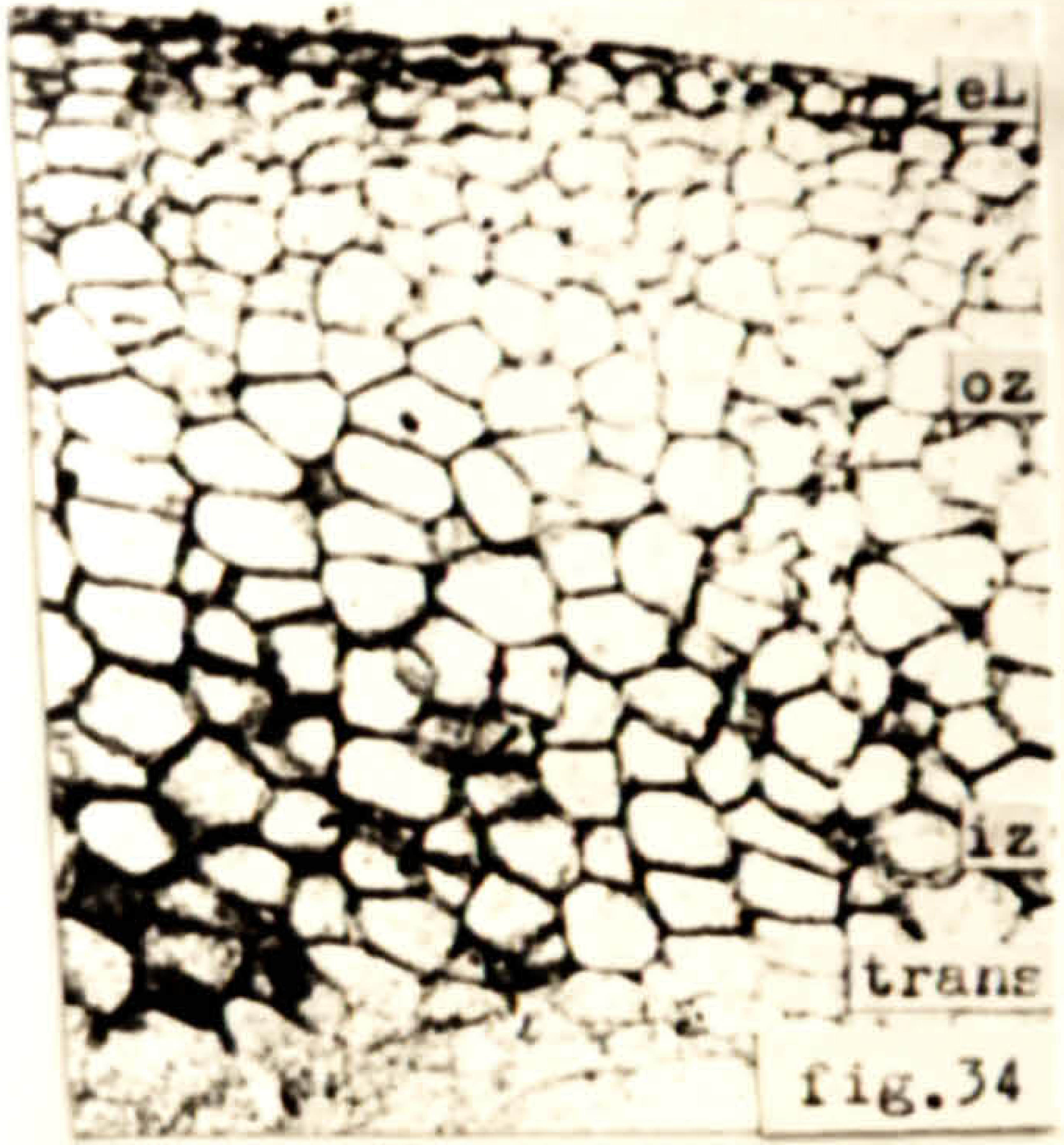


fig.34

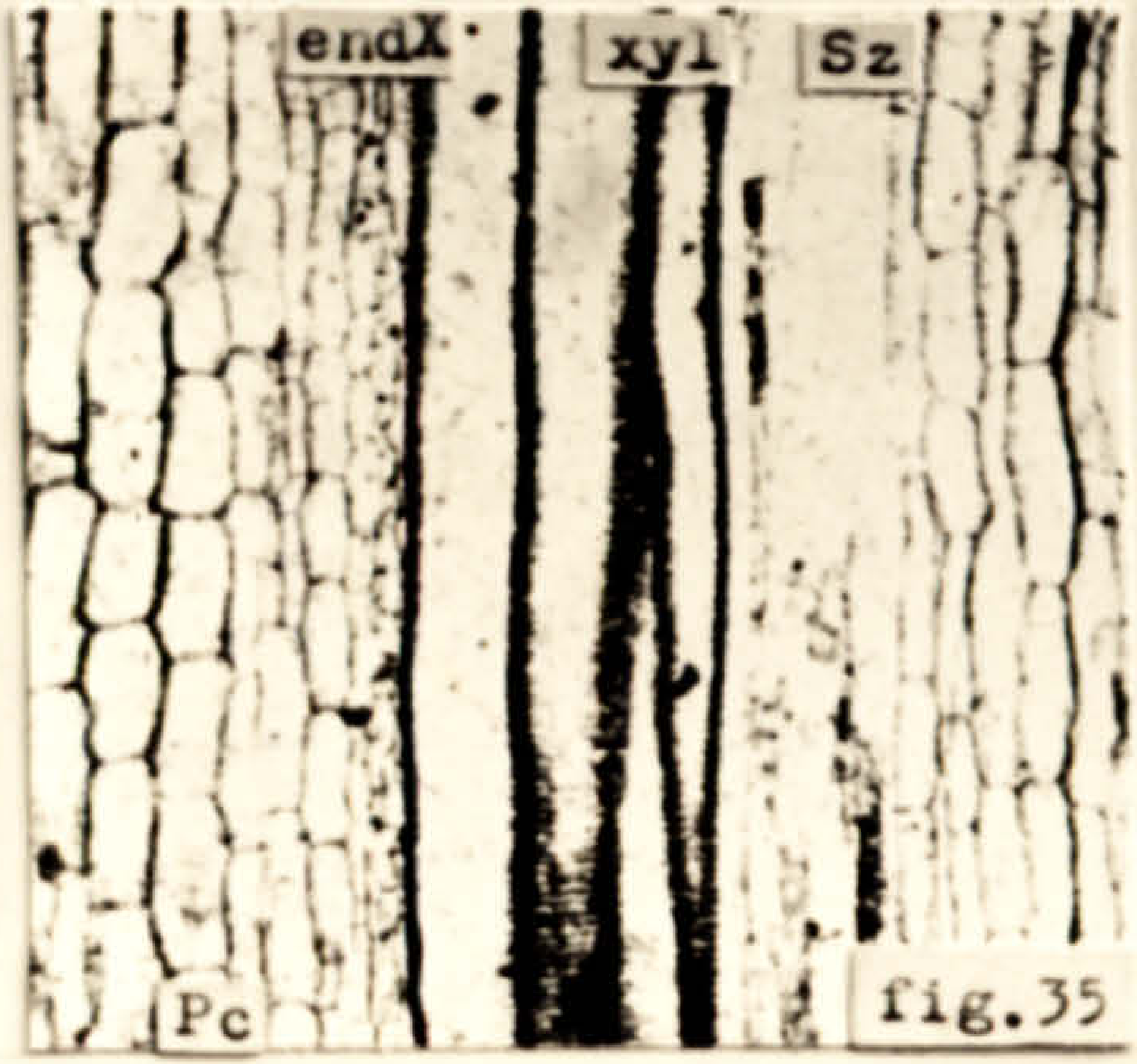


fig.35


fig.36

Plate IX

fig.31

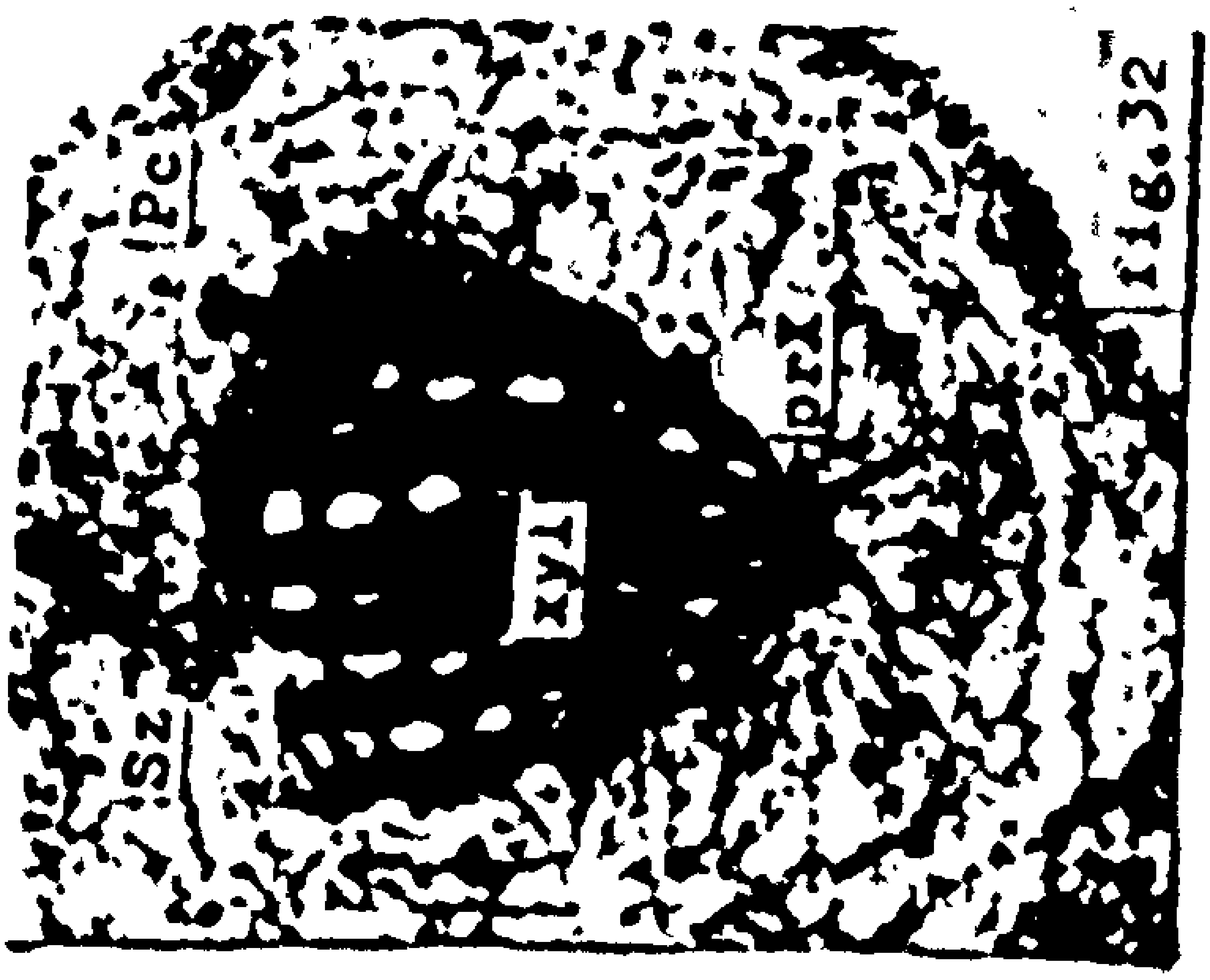


fig.32

fig.33

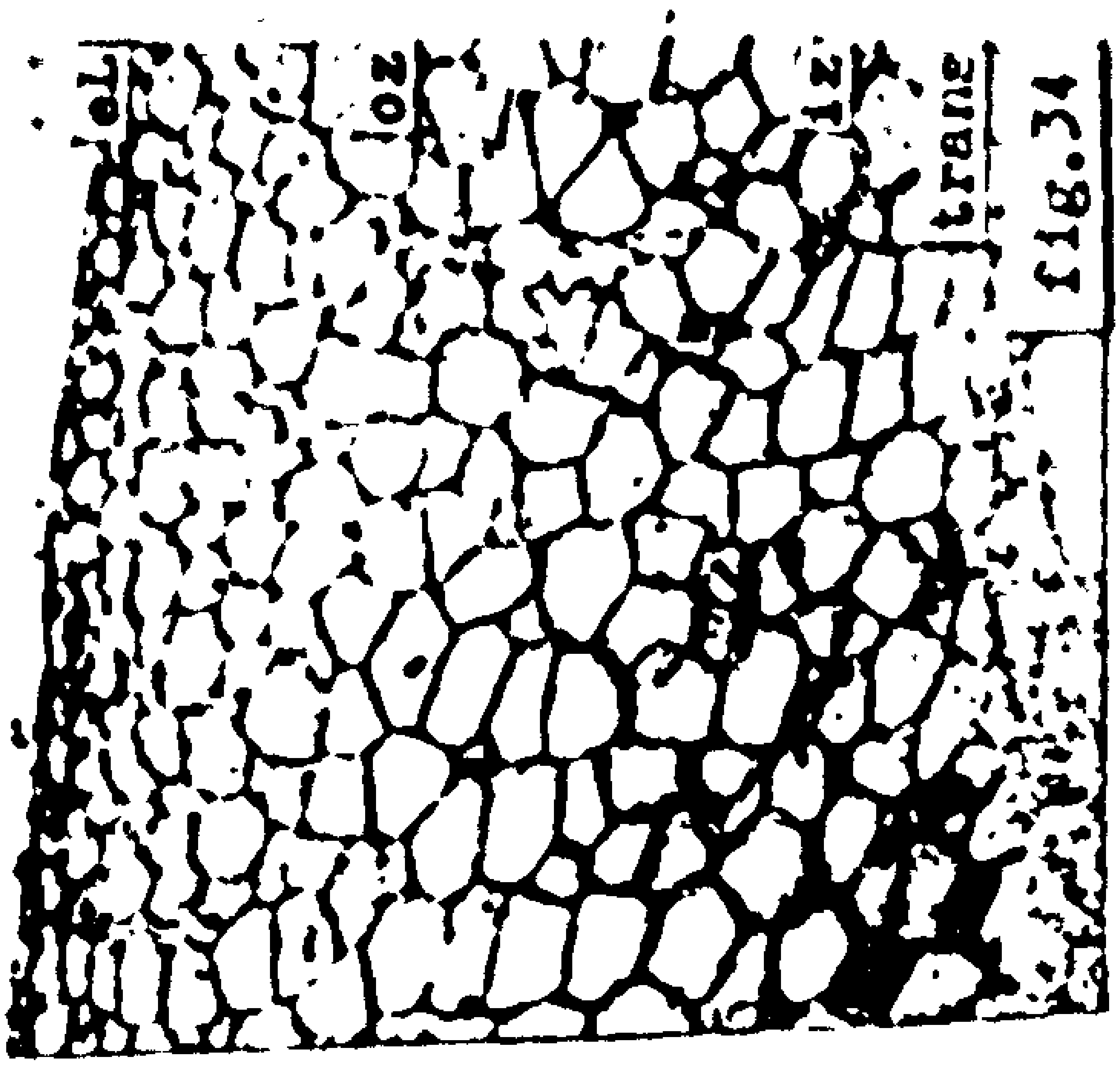


fig.34

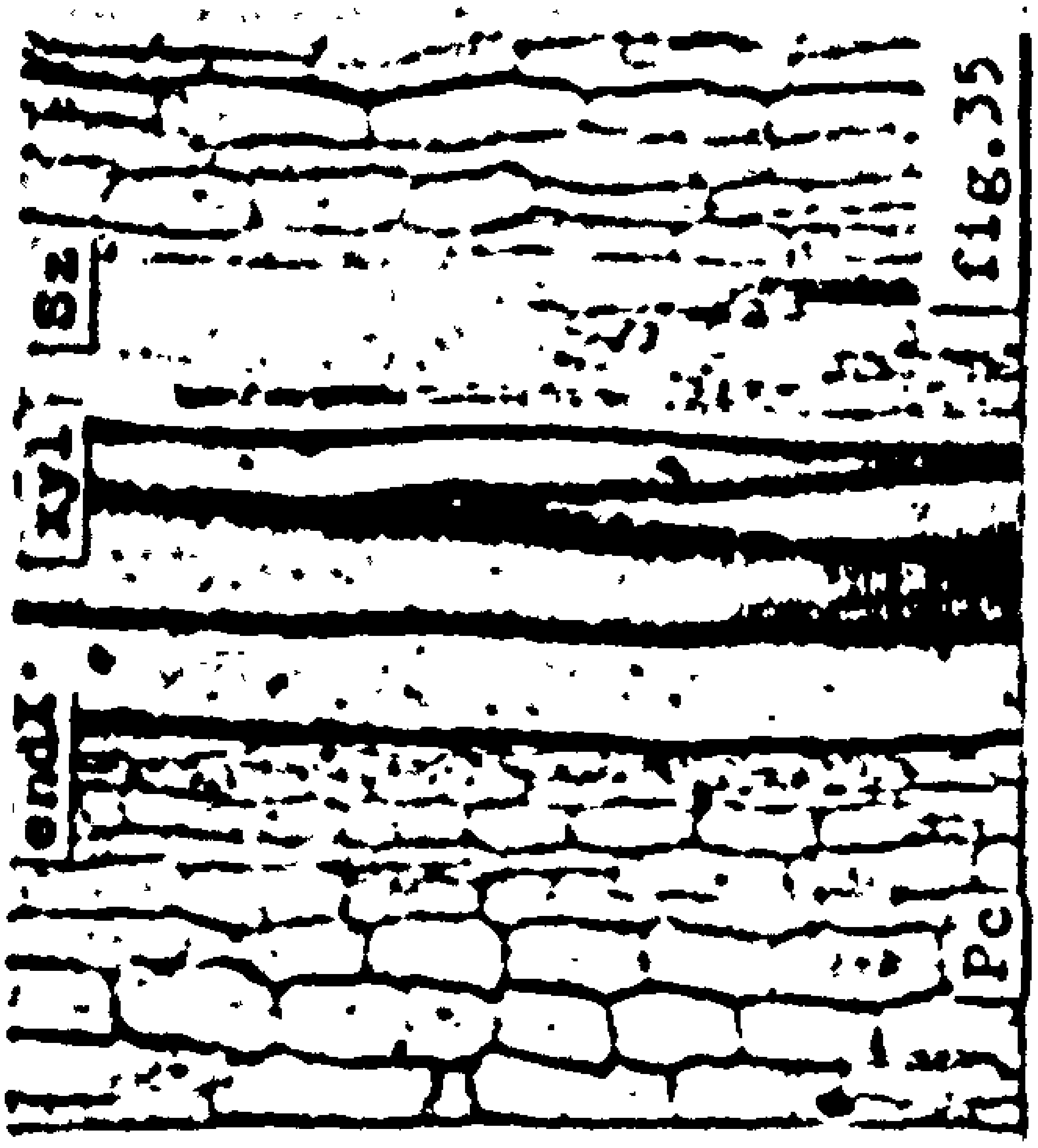


fig.35

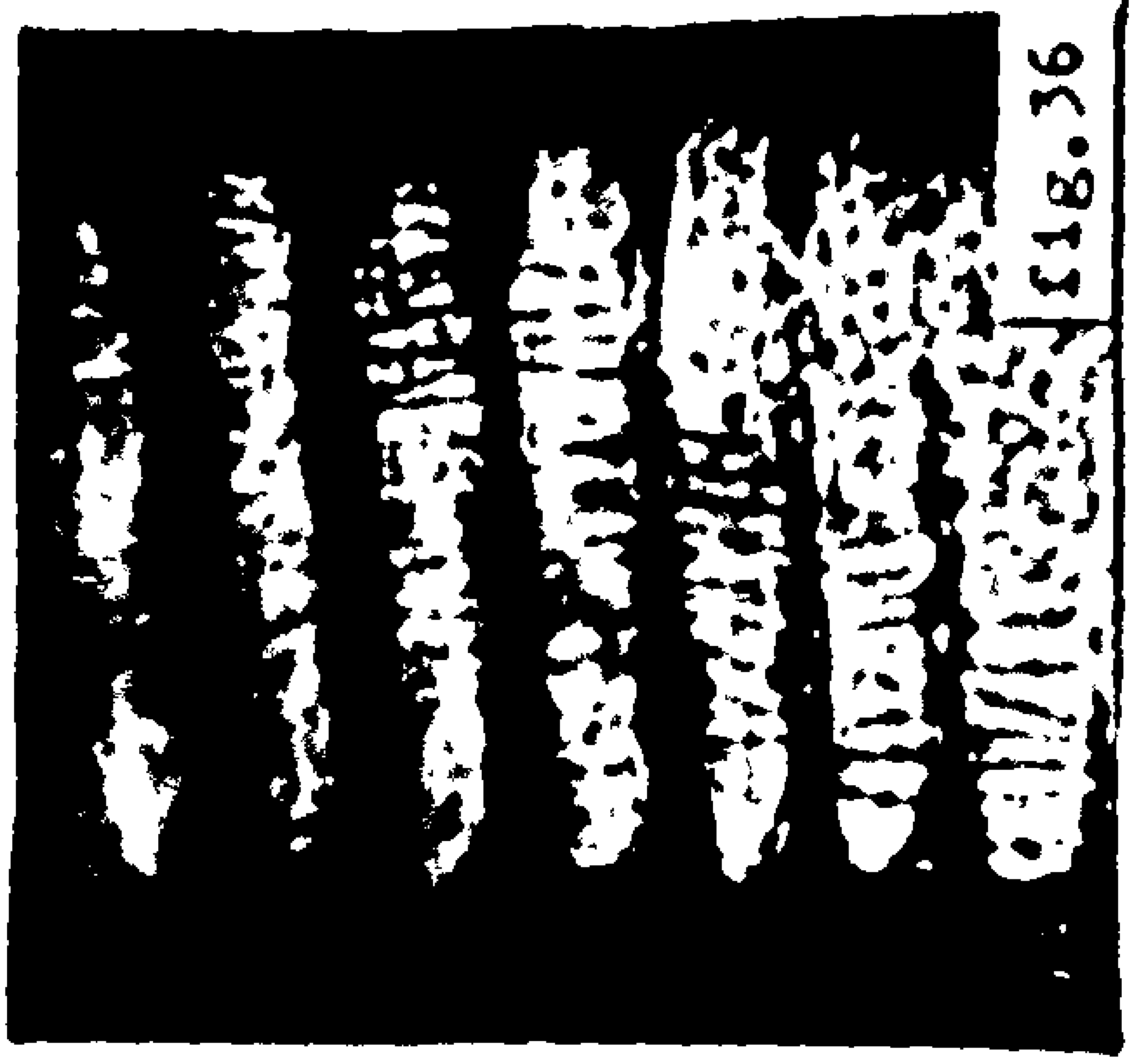


fig.36

Plate X

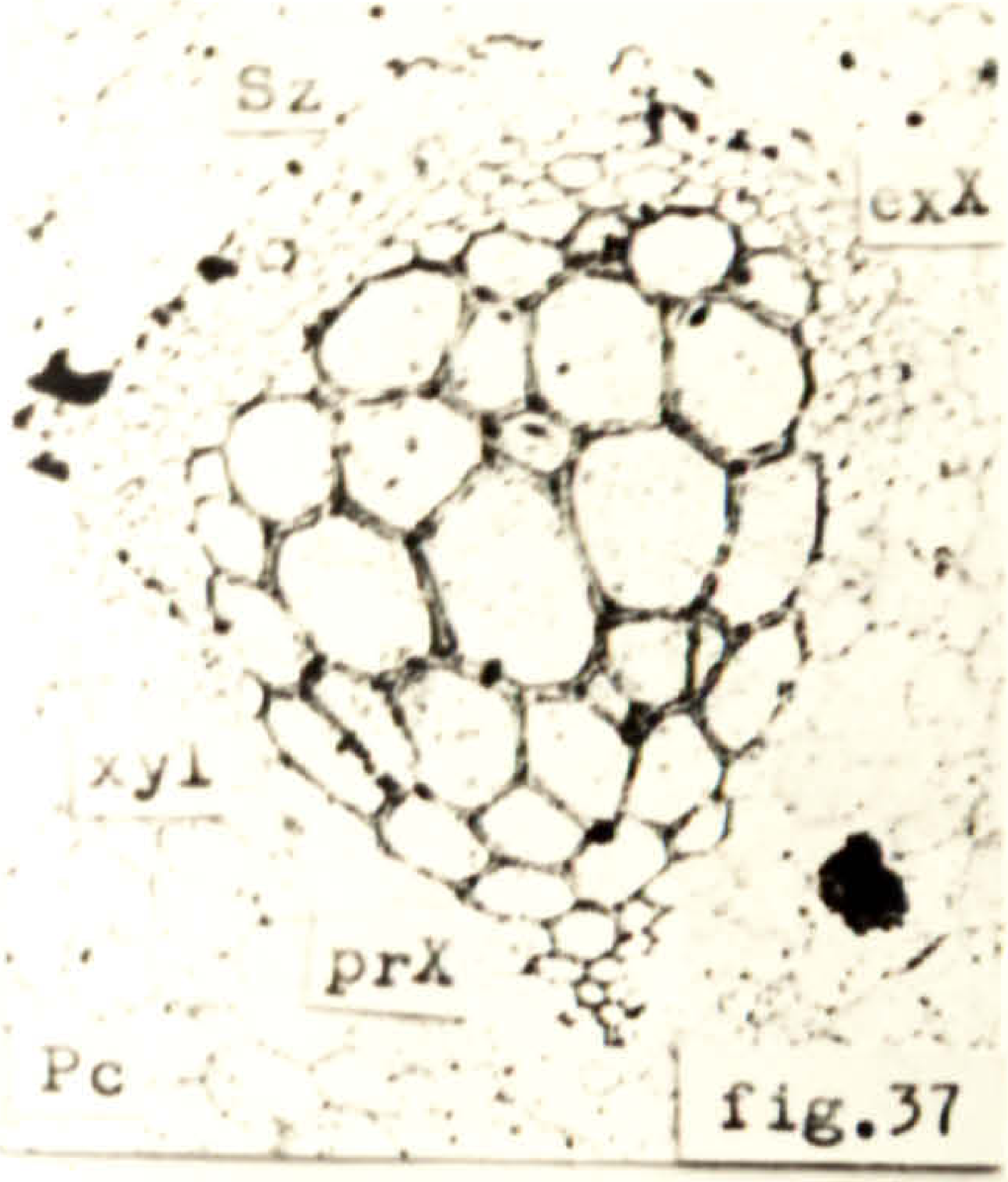


fig.37

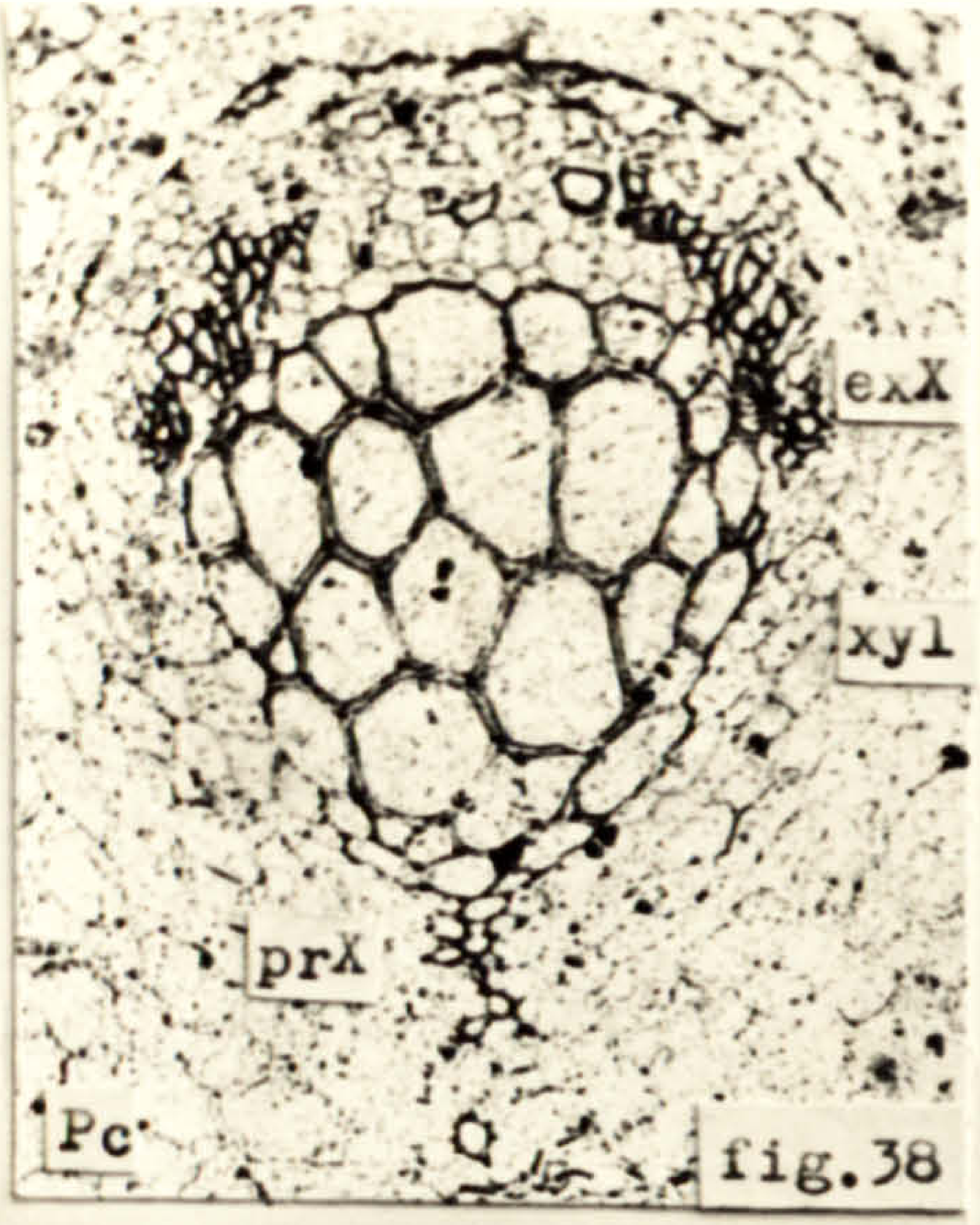


fig.38

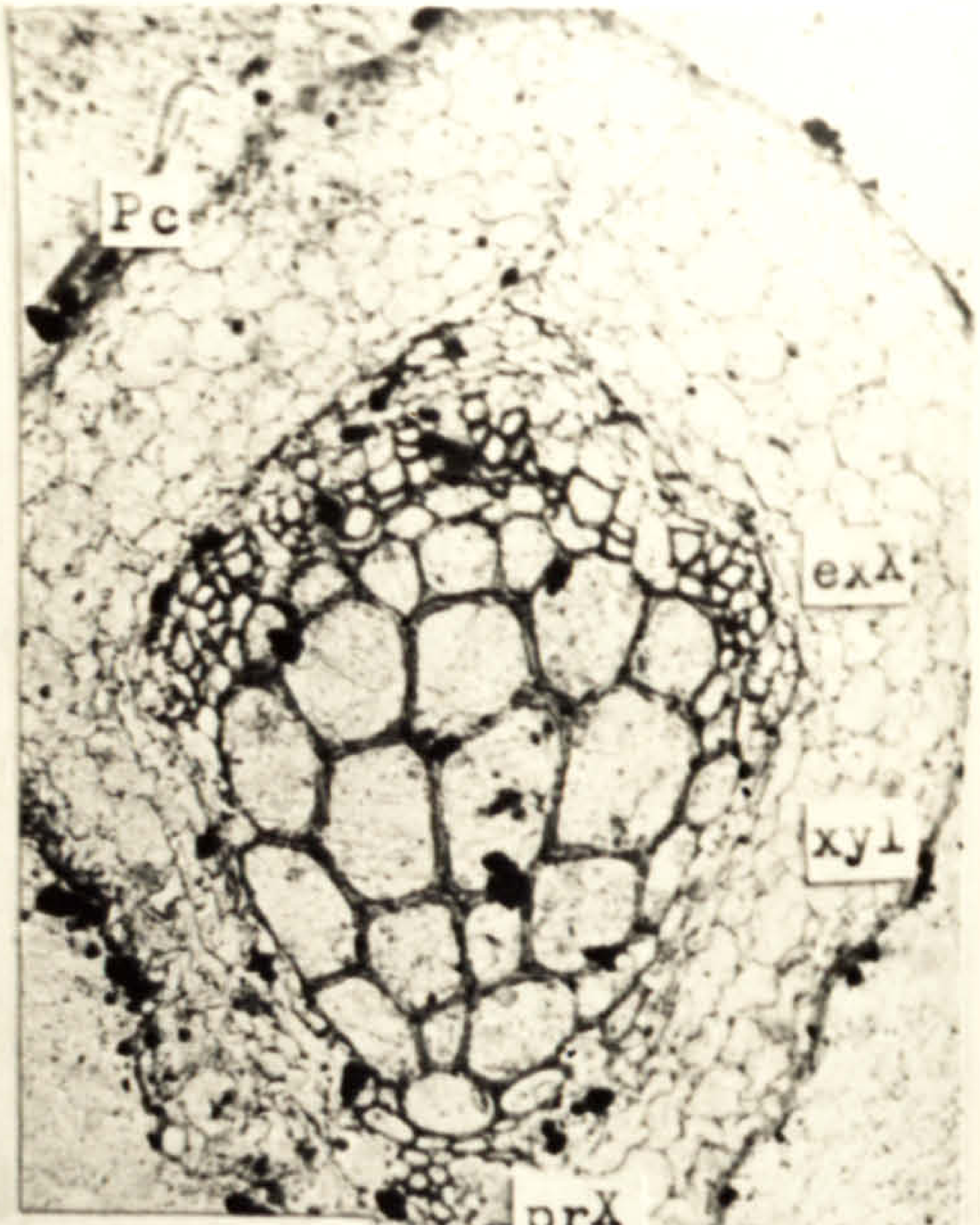


fig.39

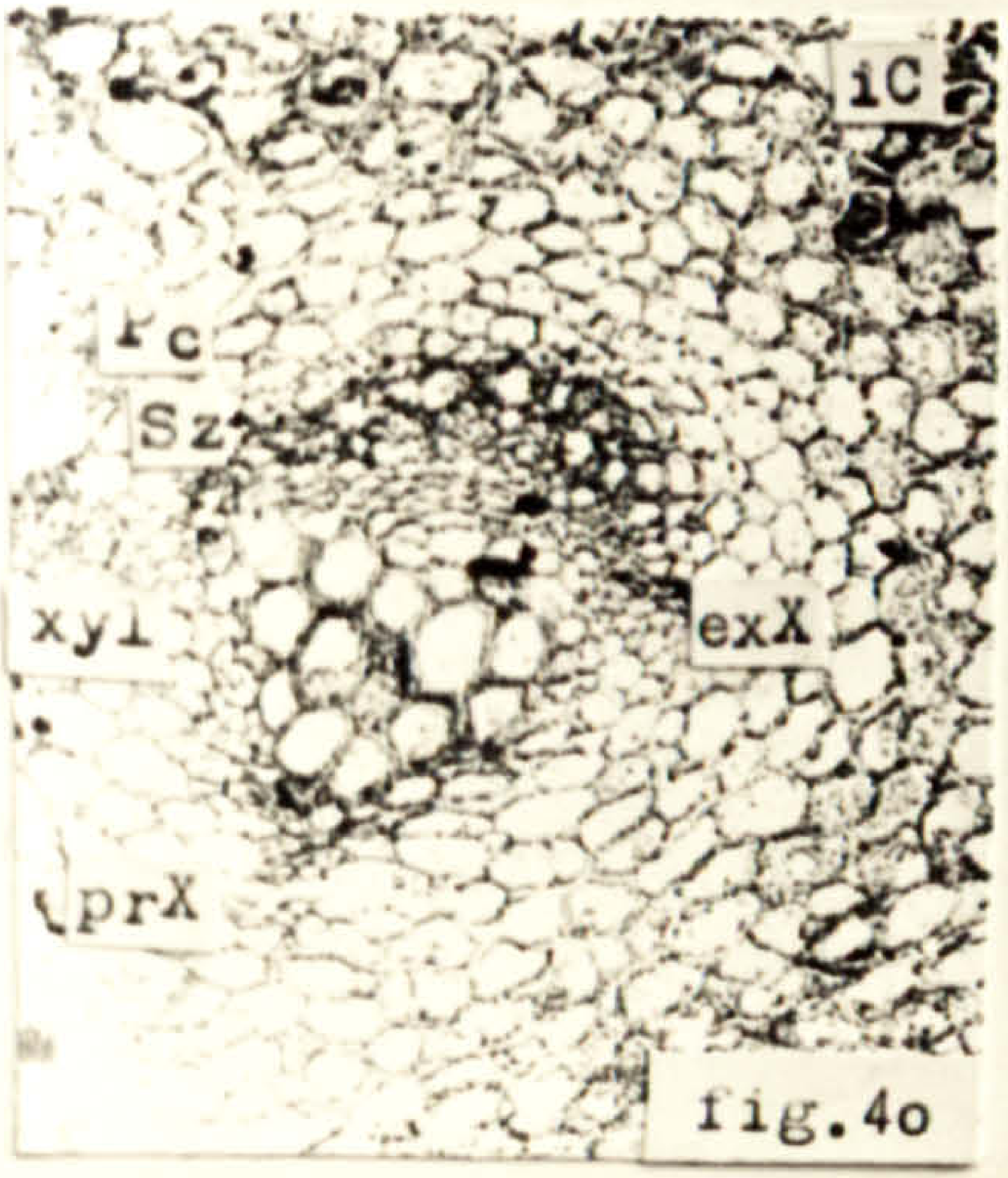


fig.4o

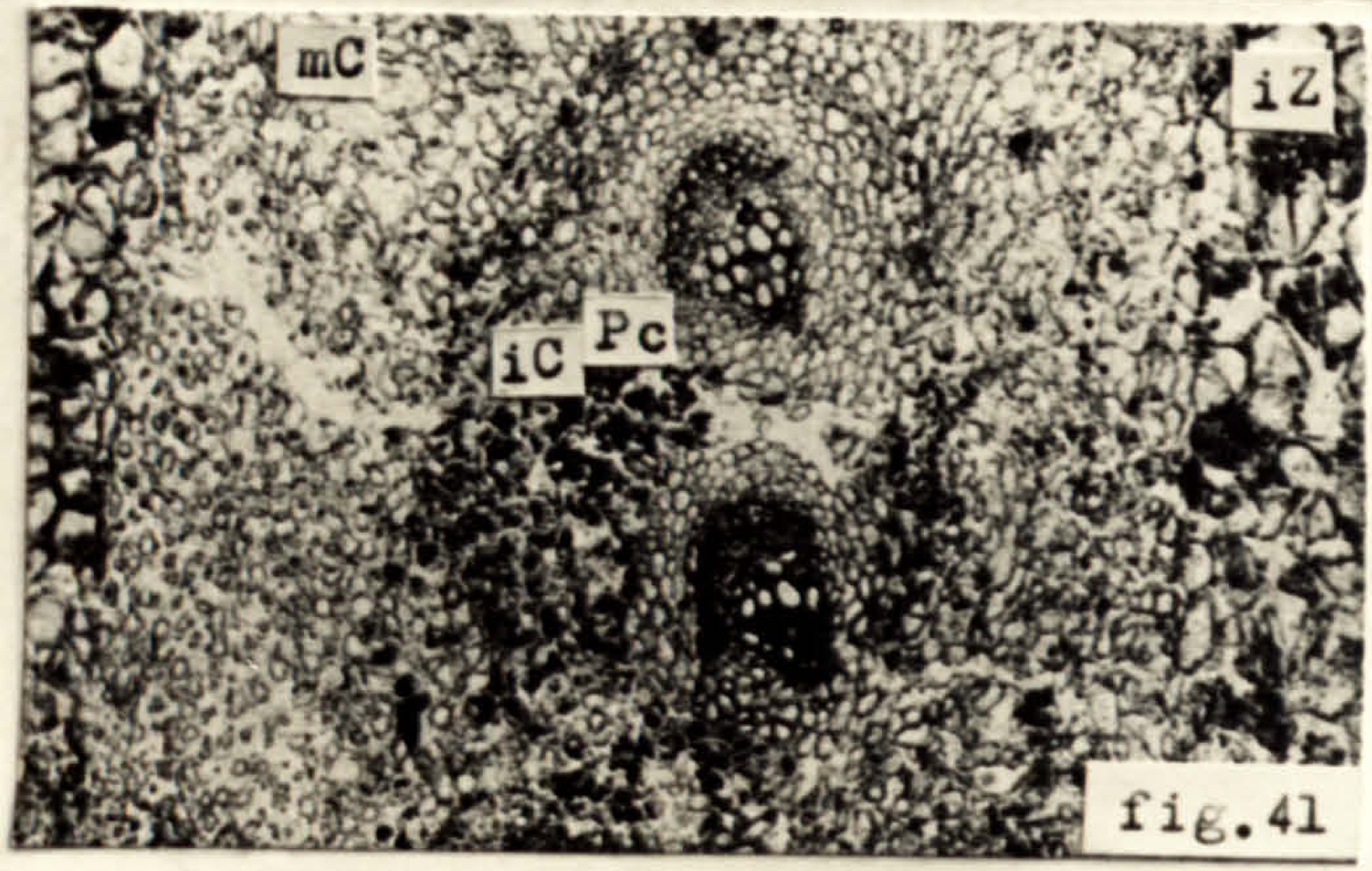


fig.41

Plate X


fig.39

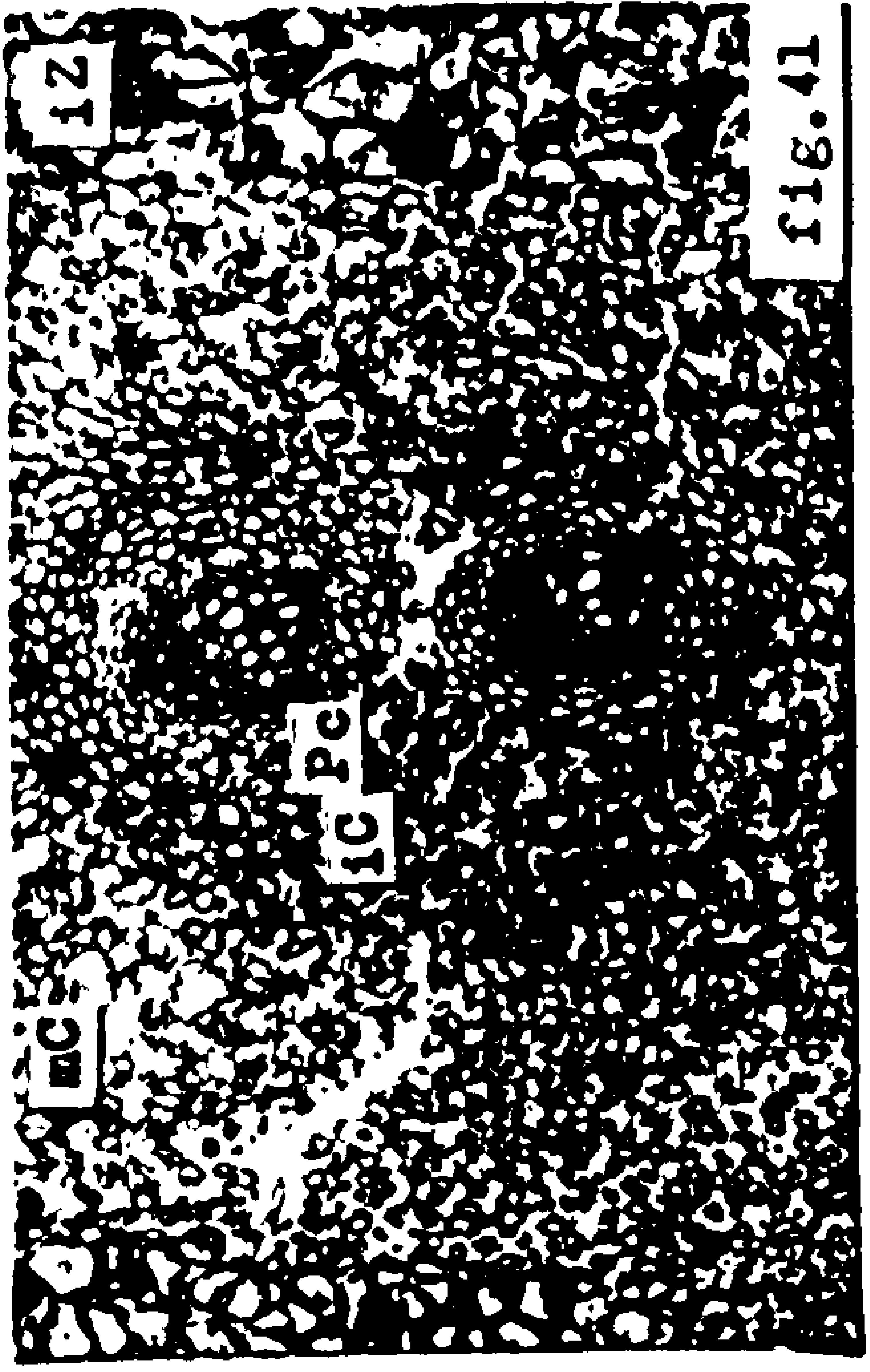


fig.41

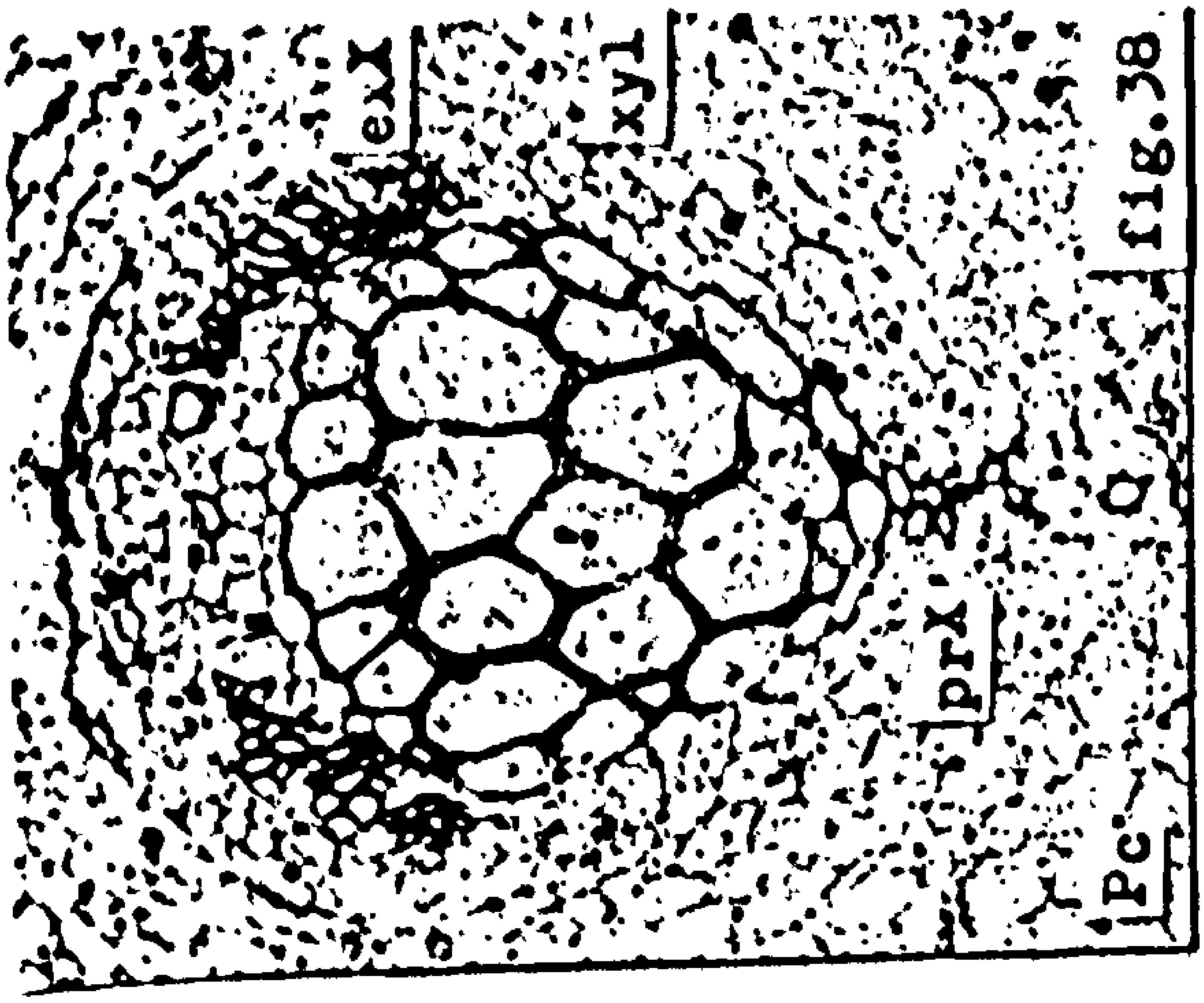


fig.38


fig.40

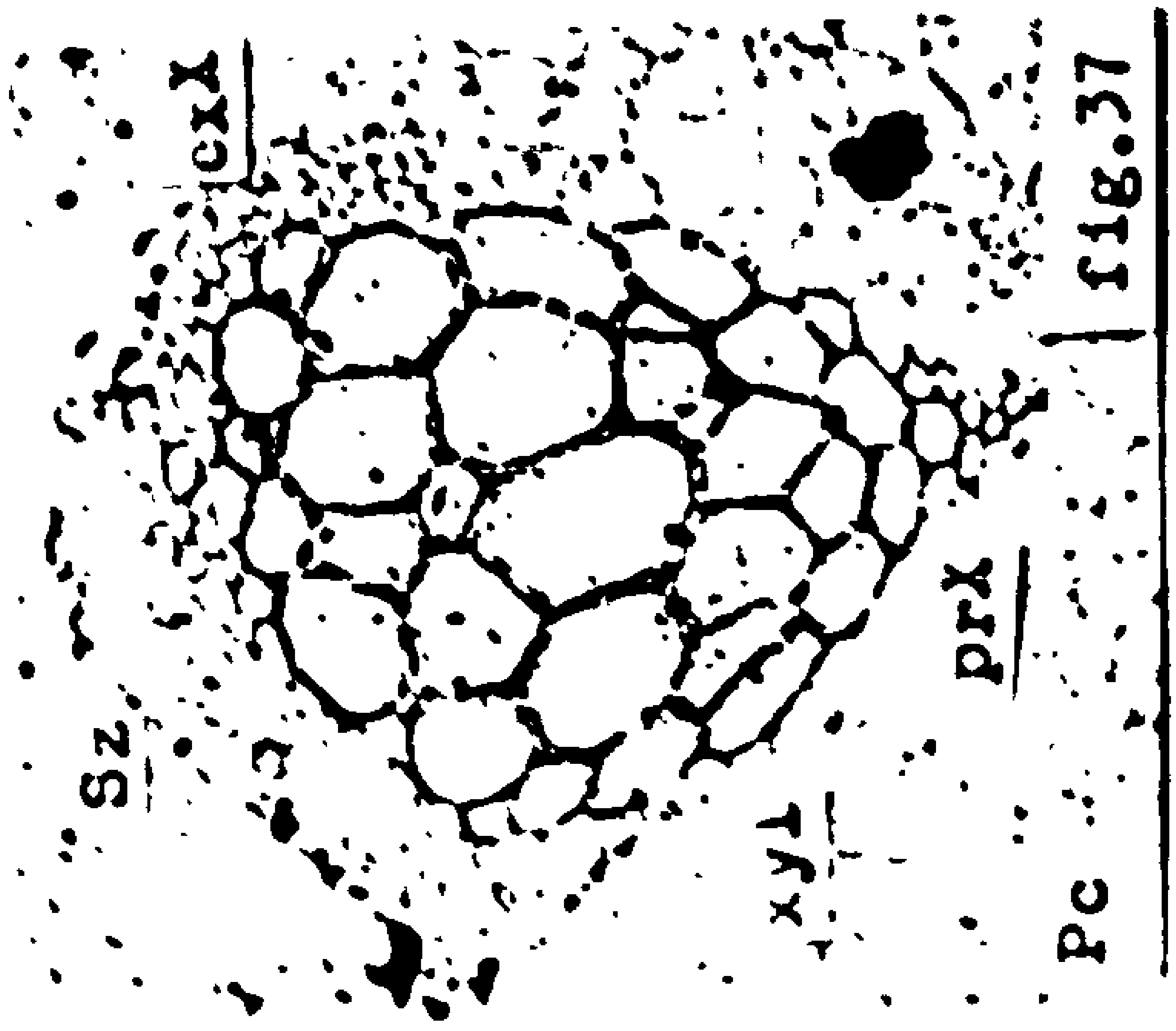


fig.37

Plate XI

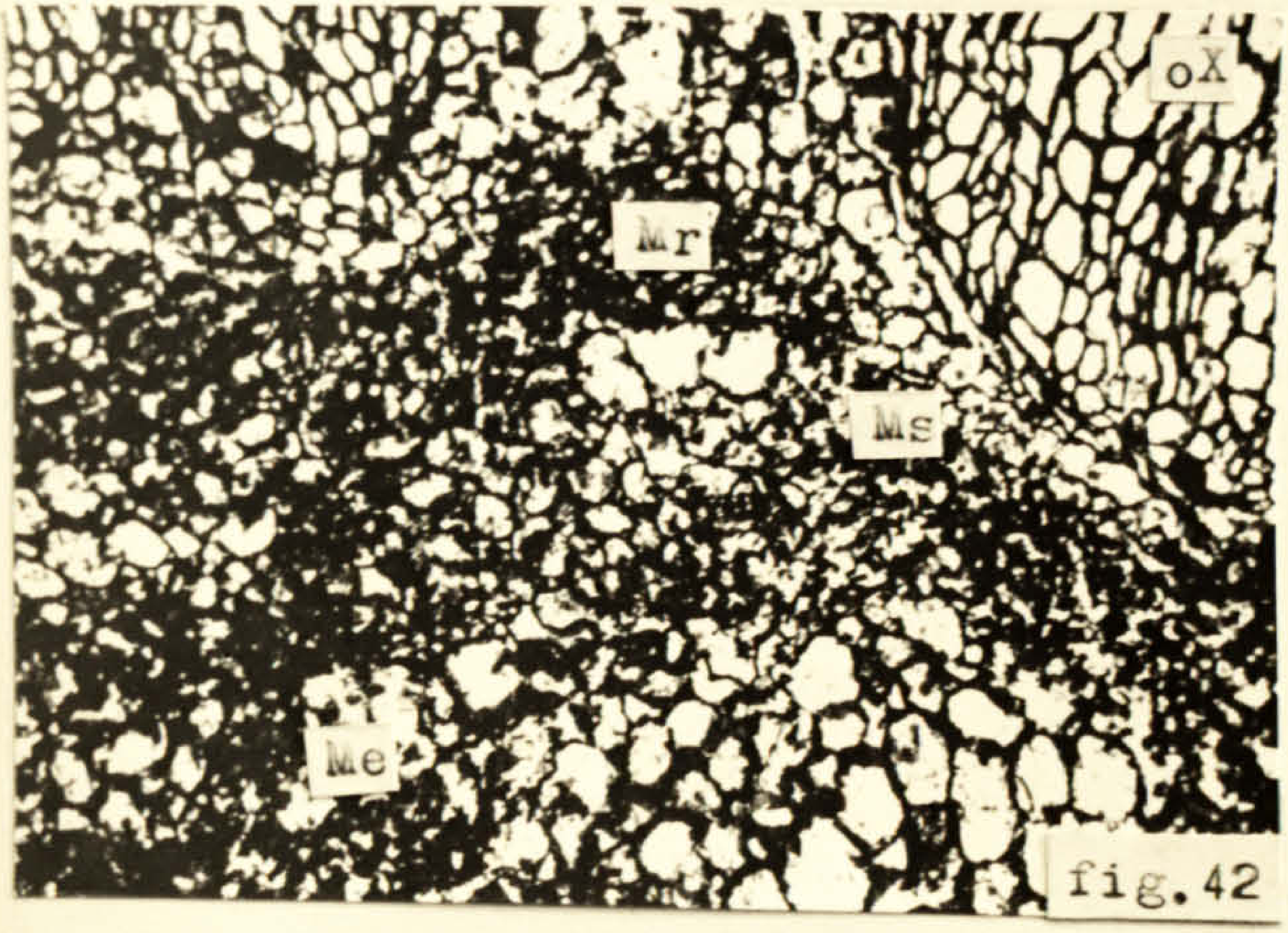


fig.42

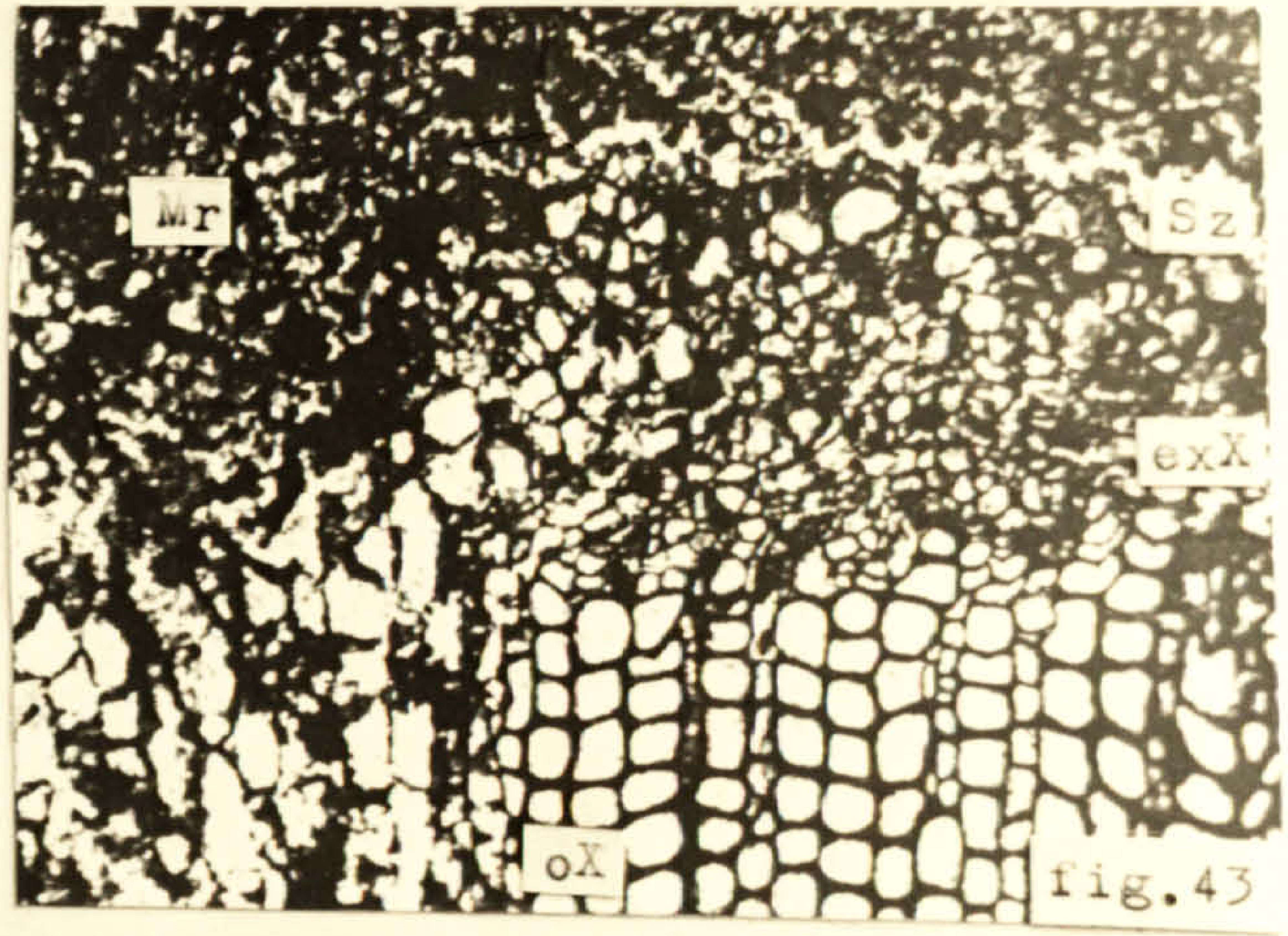


fig.43

fig.44

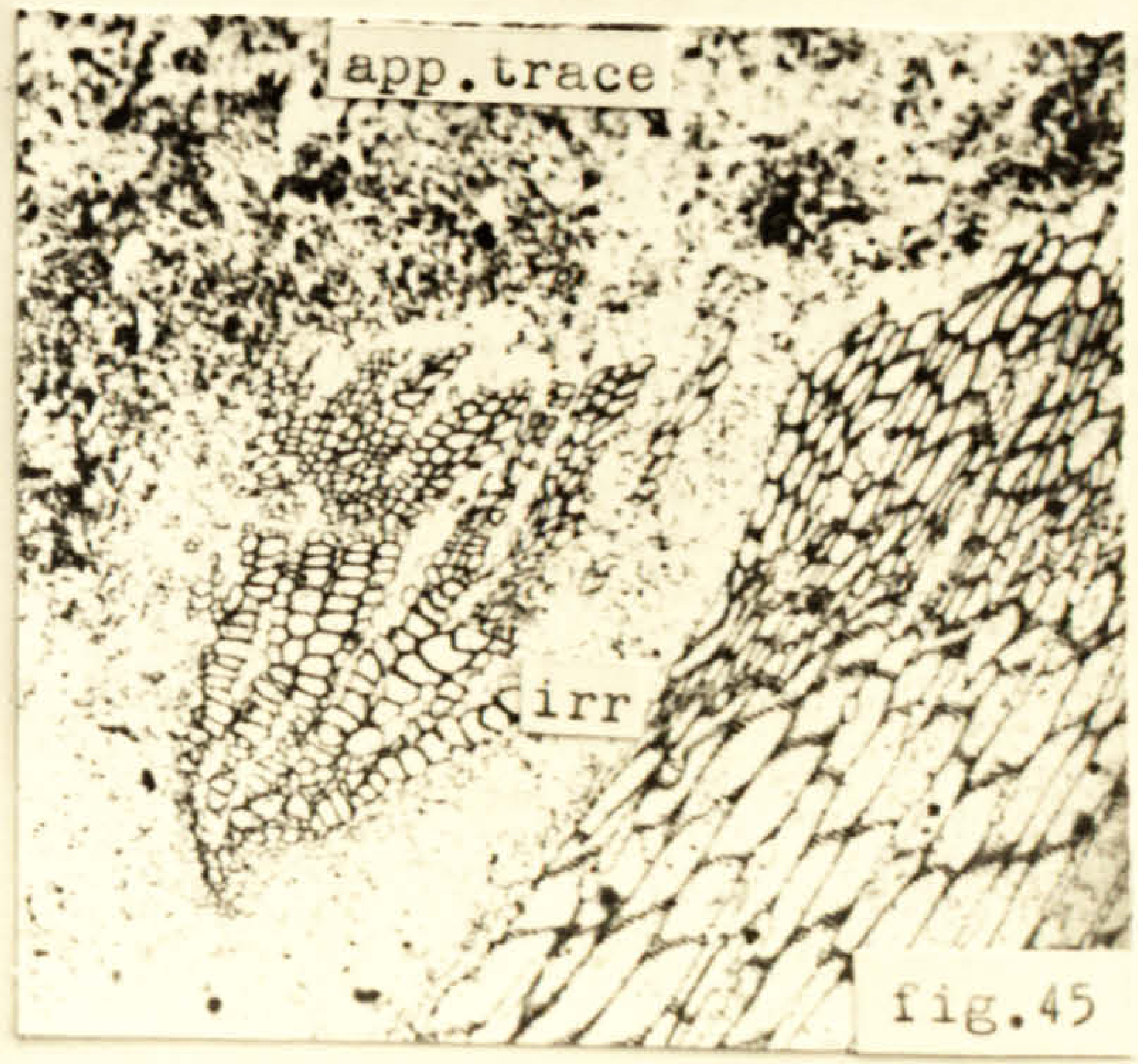


fig.45

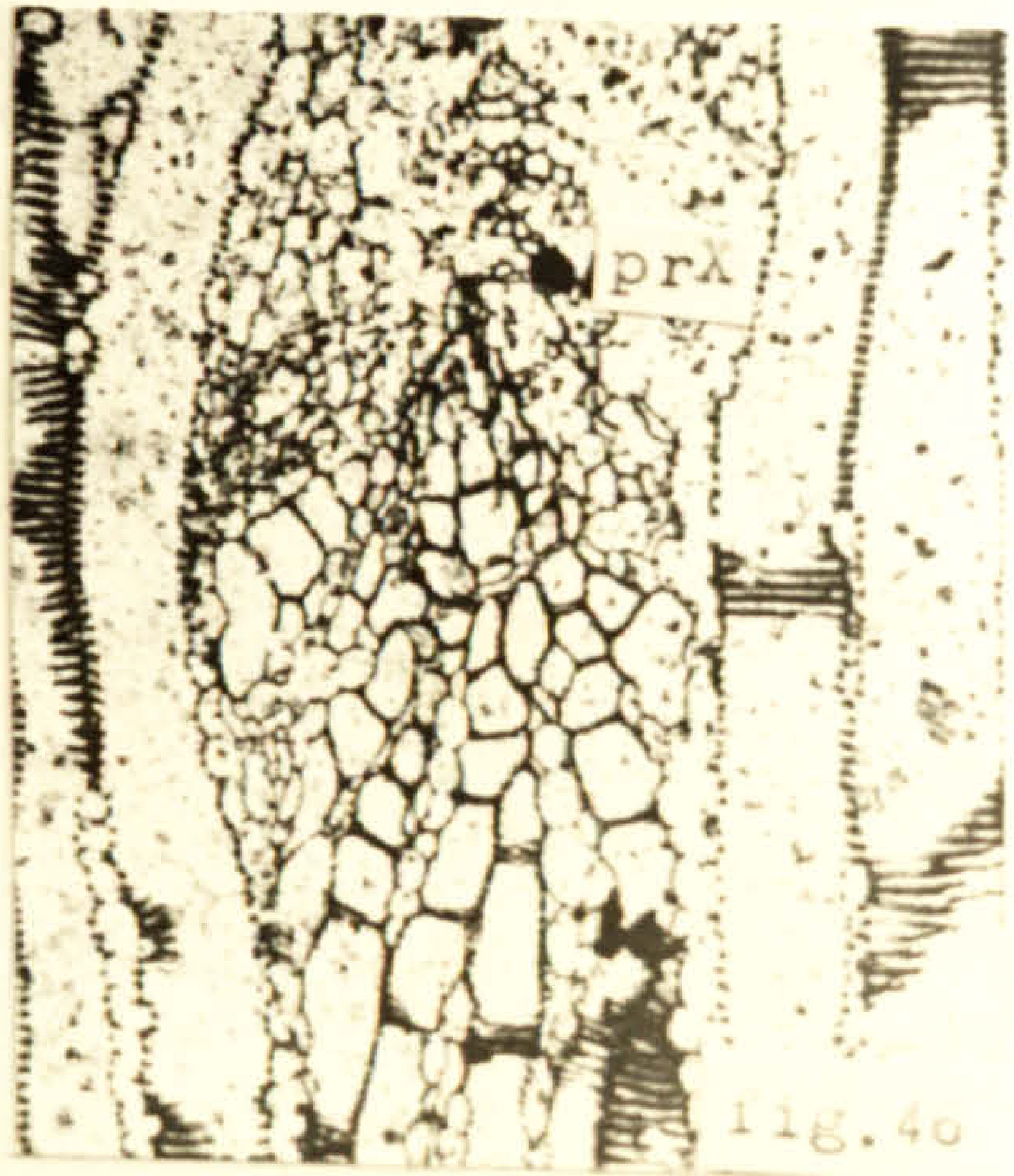


fig.46

fig.42

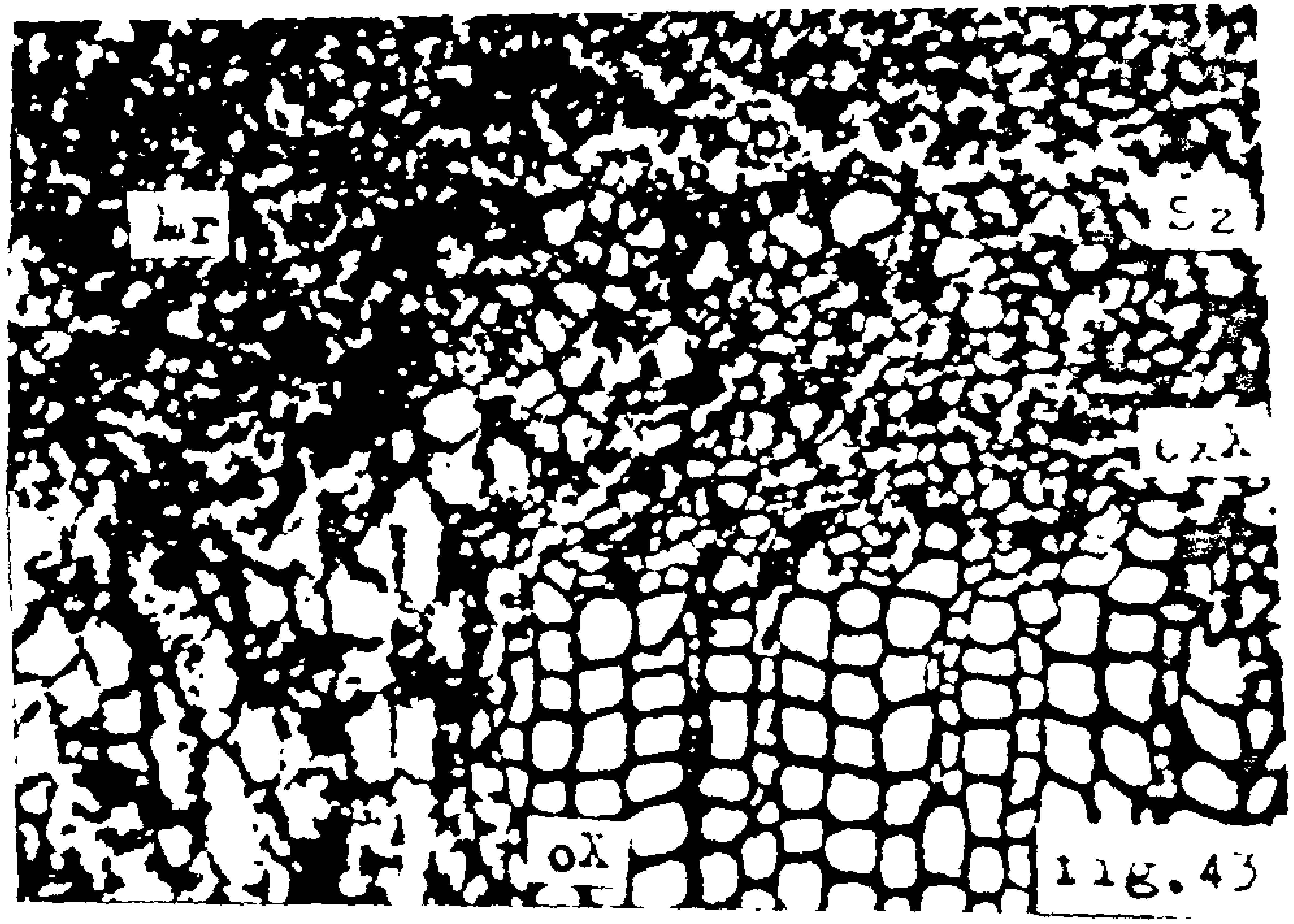


fig.43

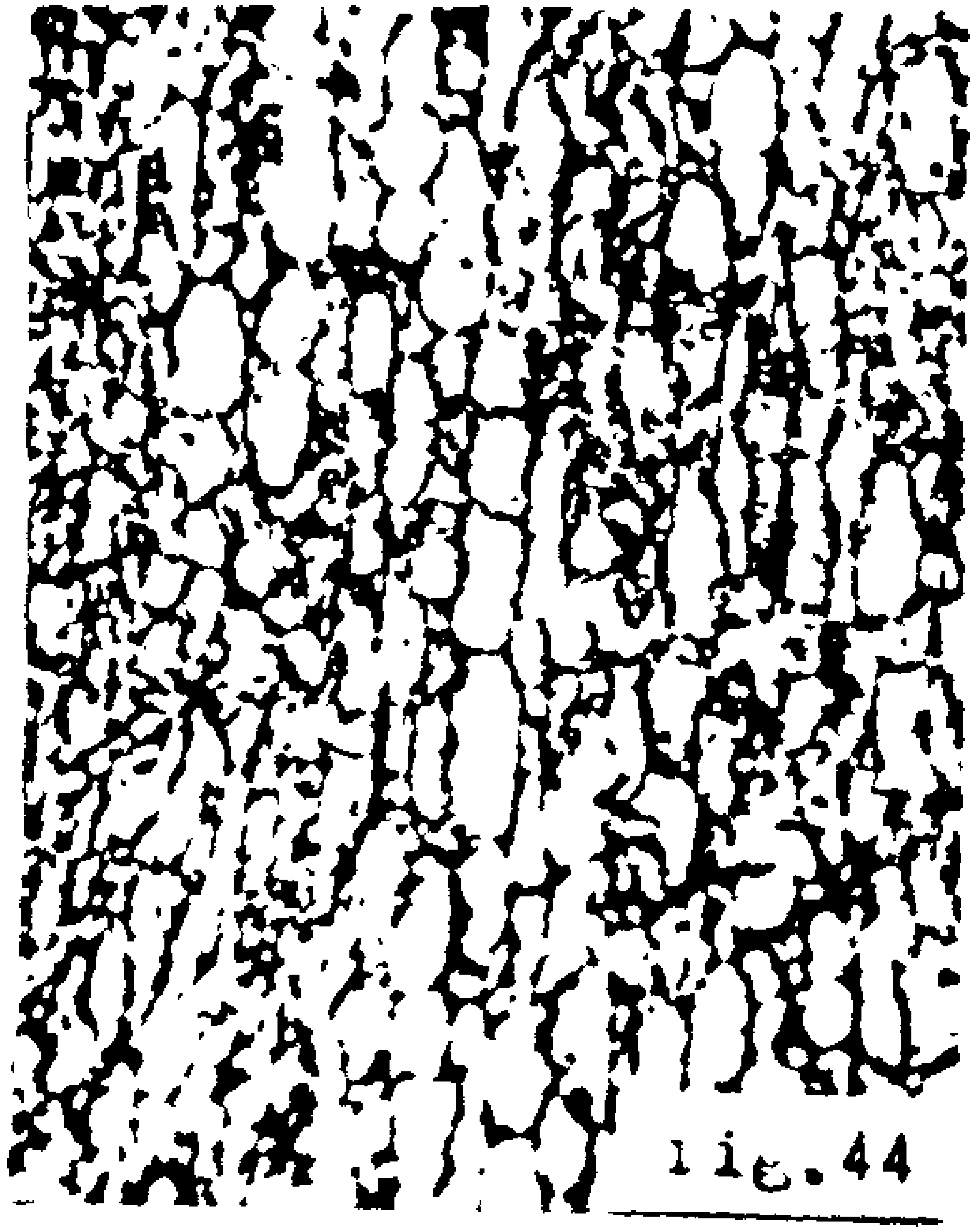


fig.44

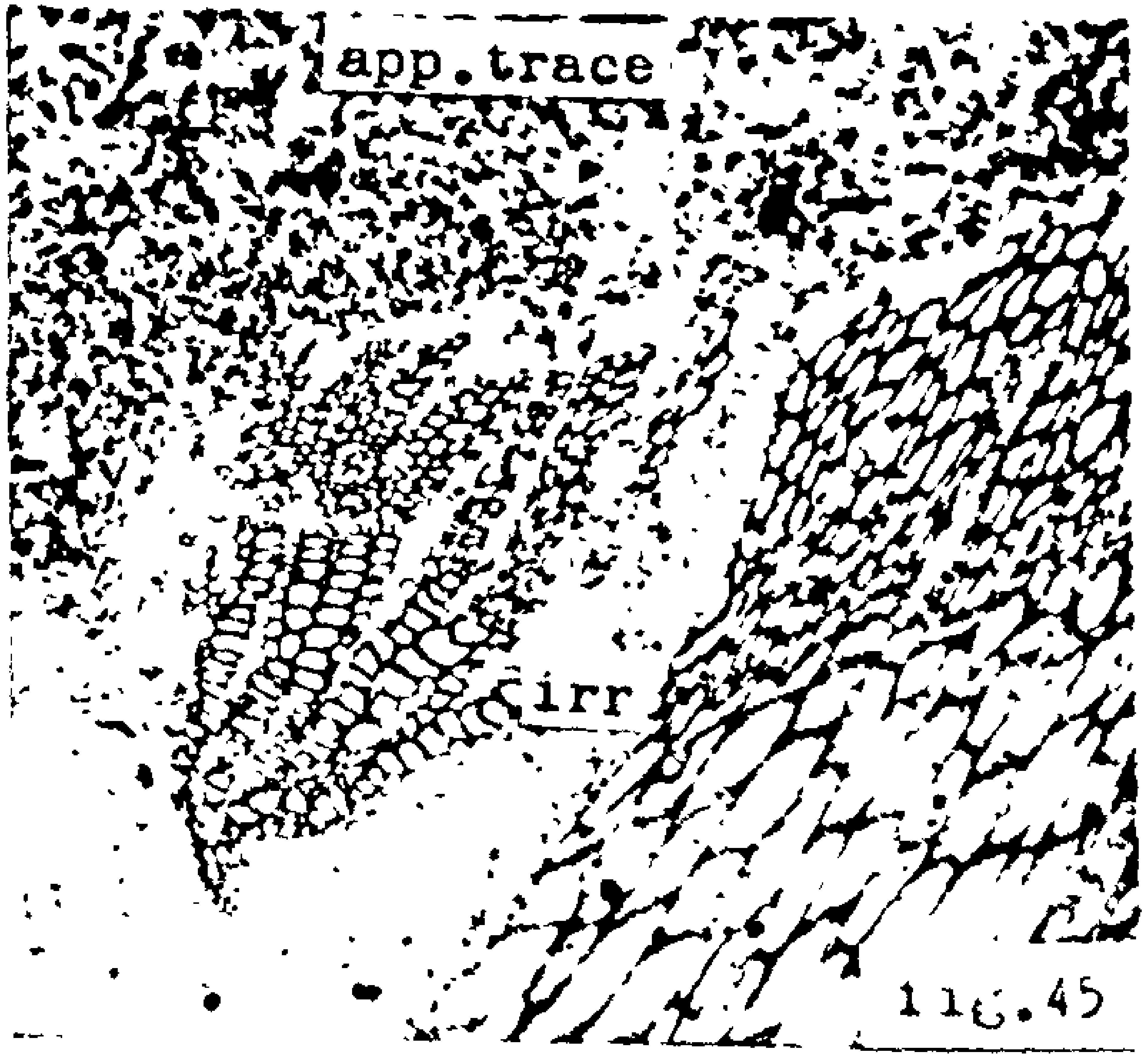


fig.45

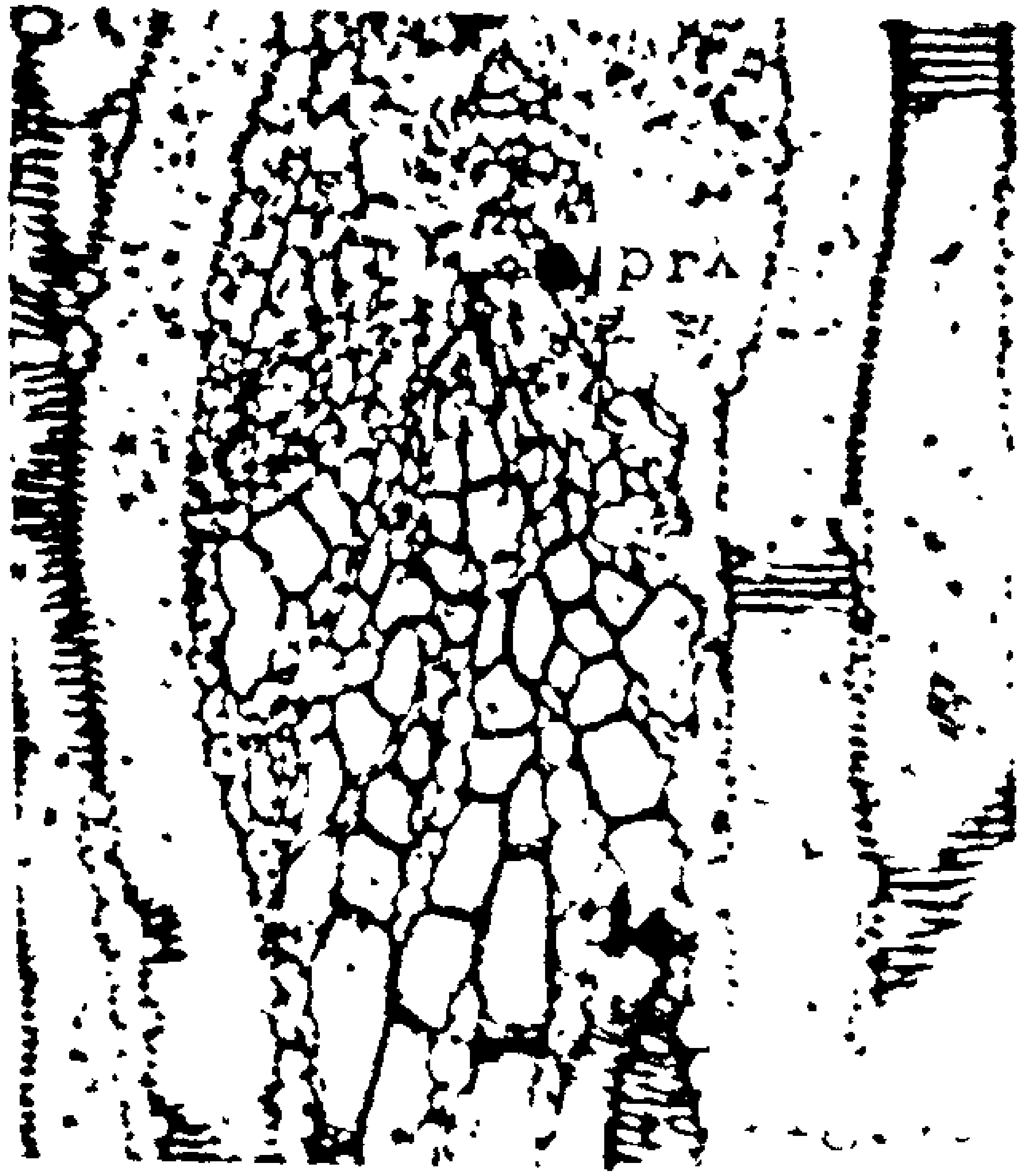


Plate XII

fig.47

fig.48

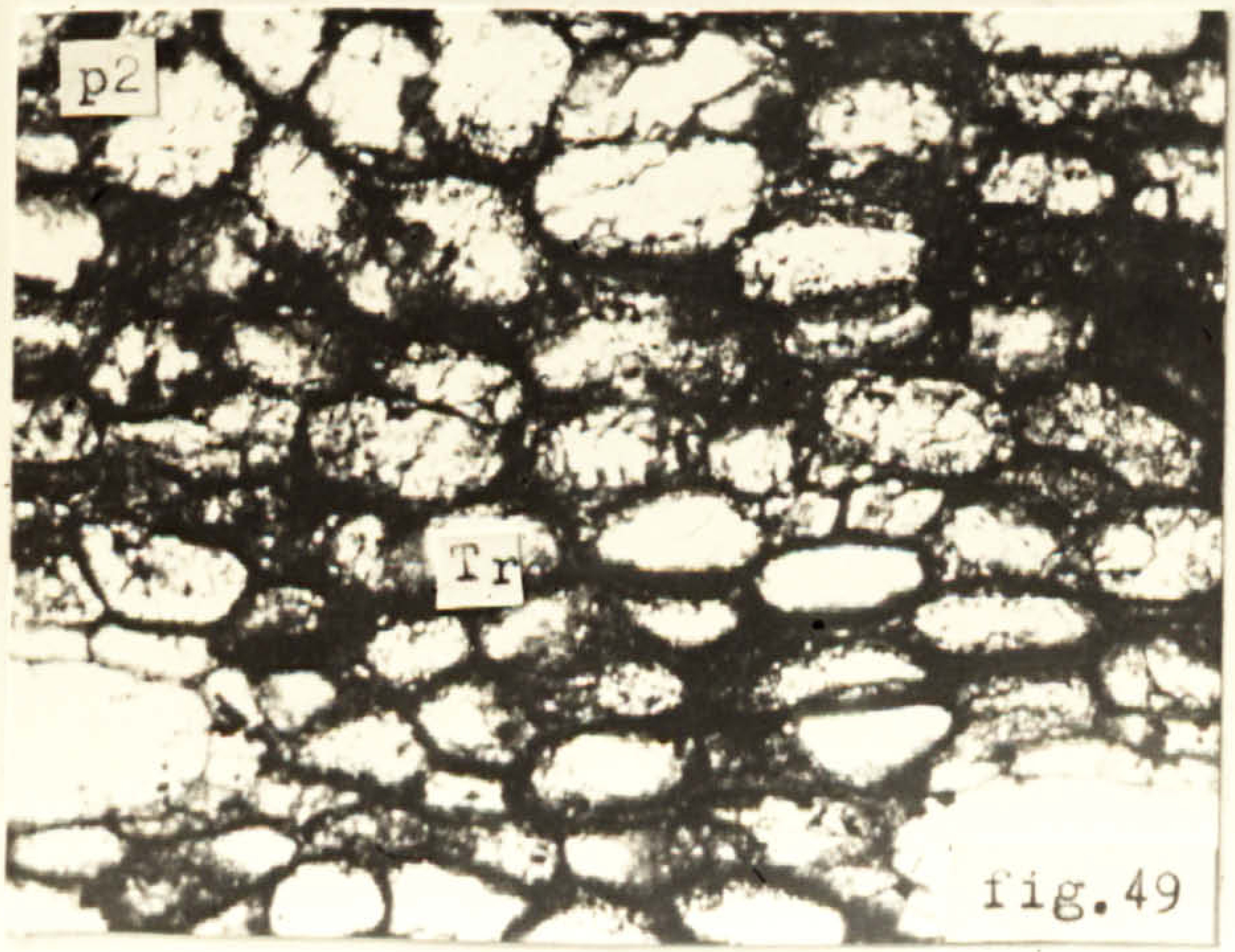


fig.49

fig.5o

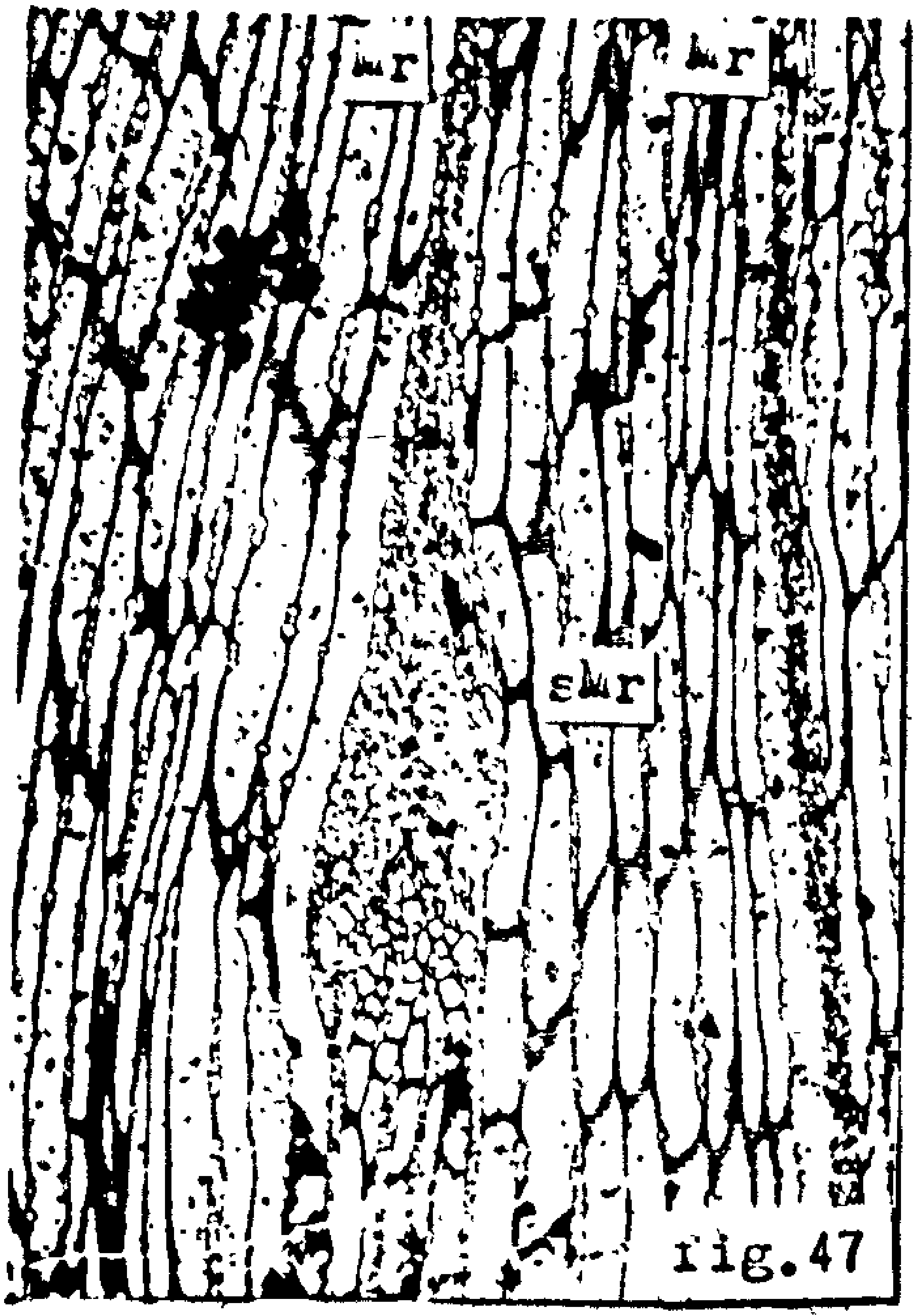


fig.47

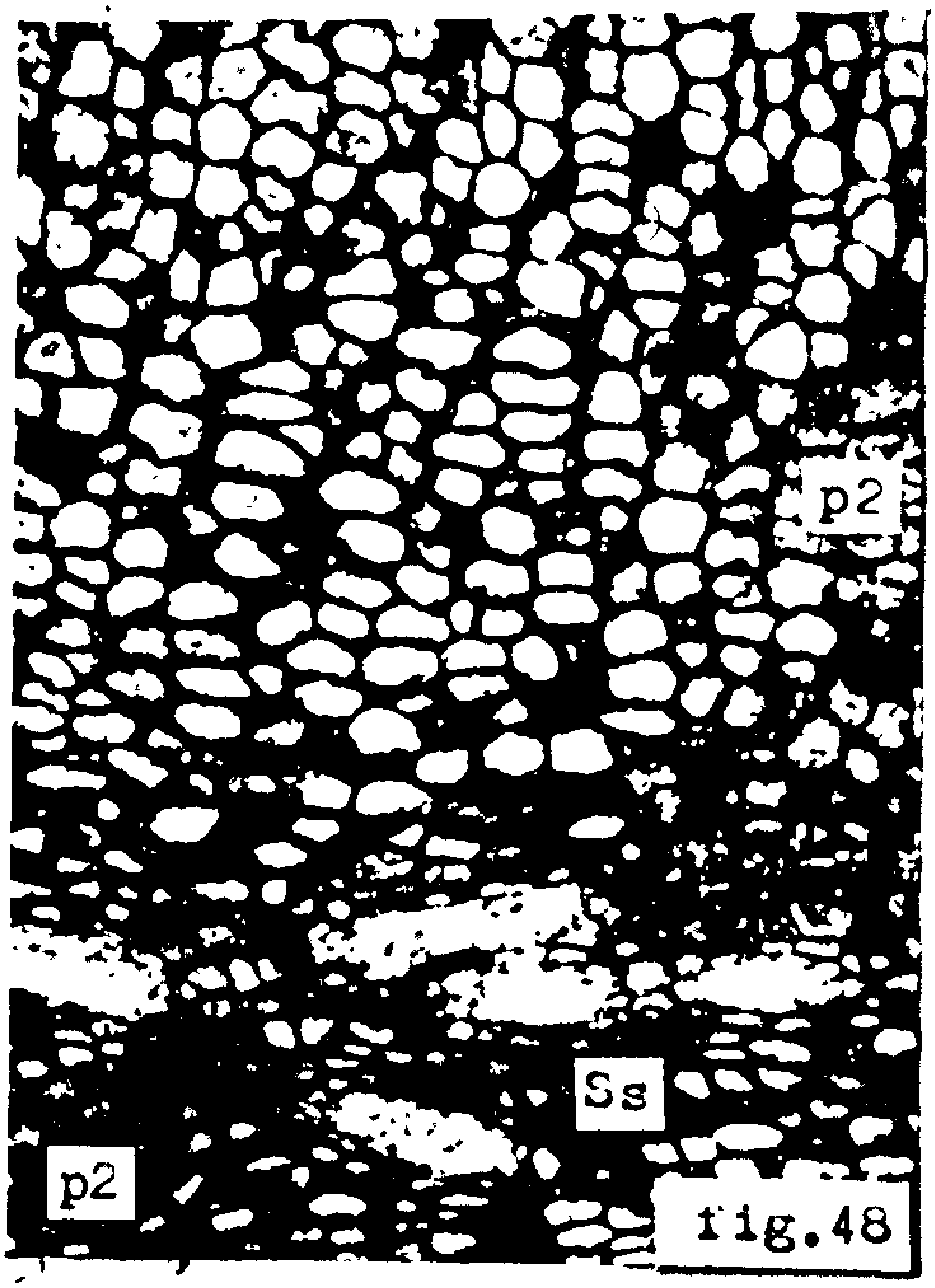


fig.48

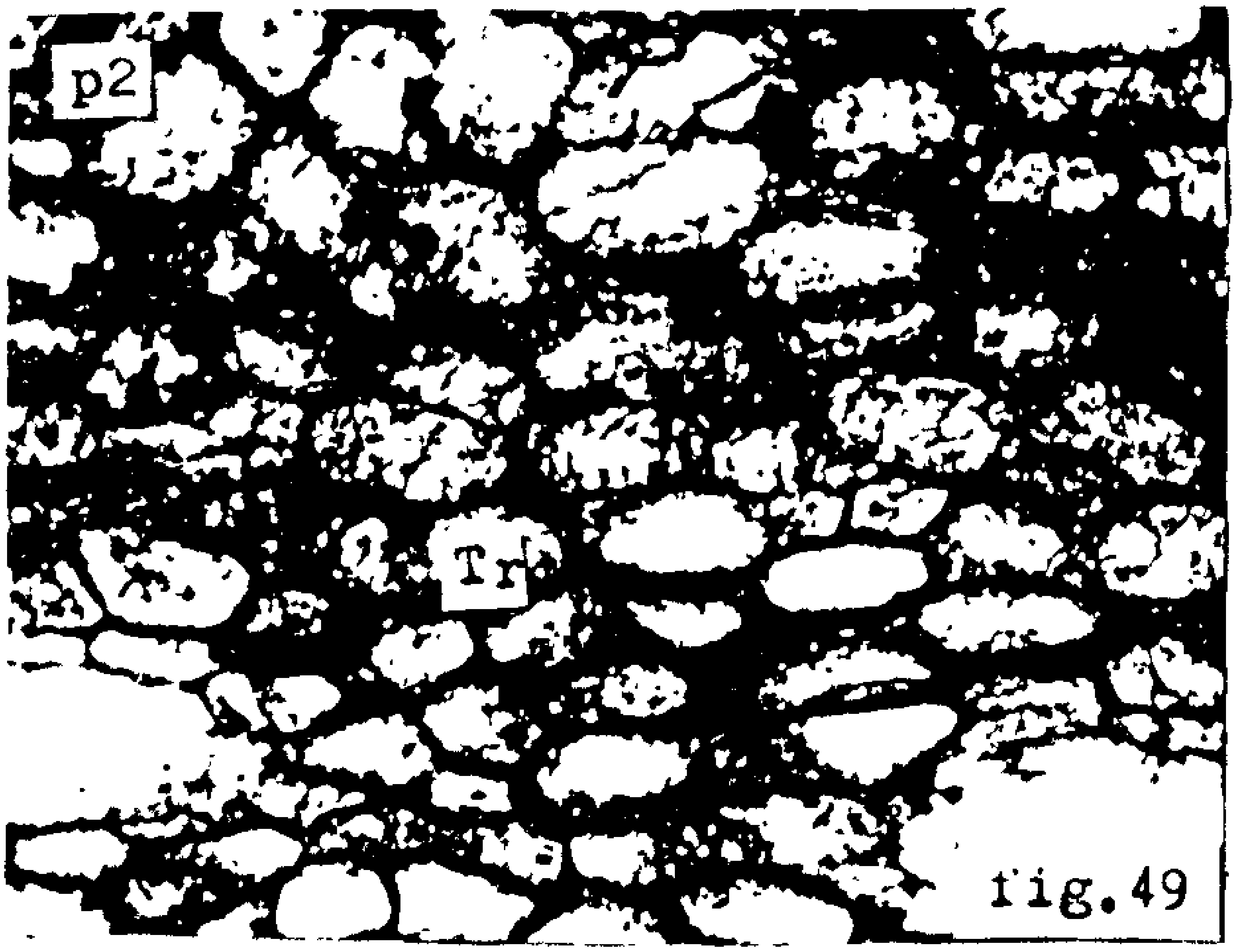


fig.49

fig.5o

Plate XIII

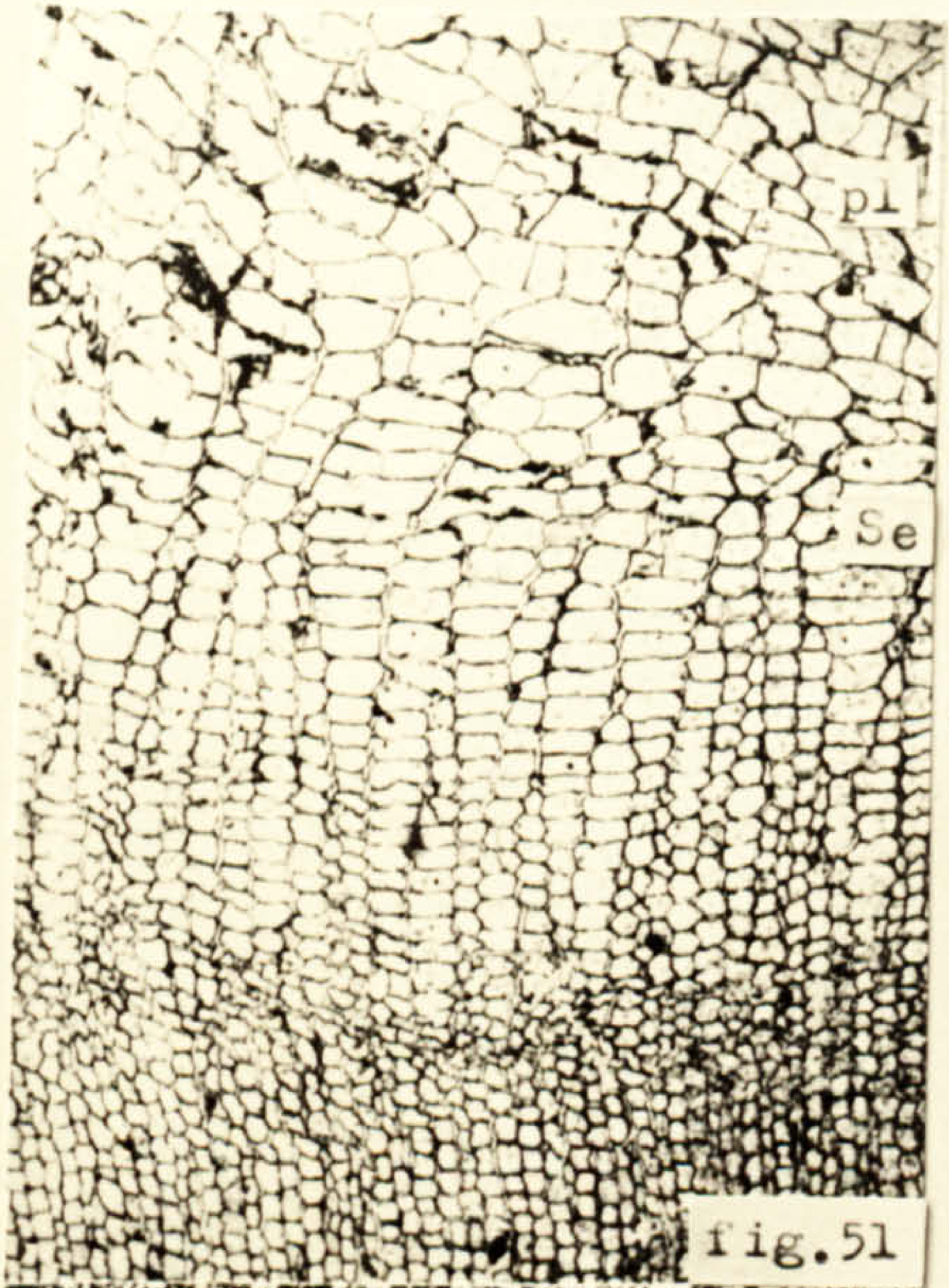


fig.51

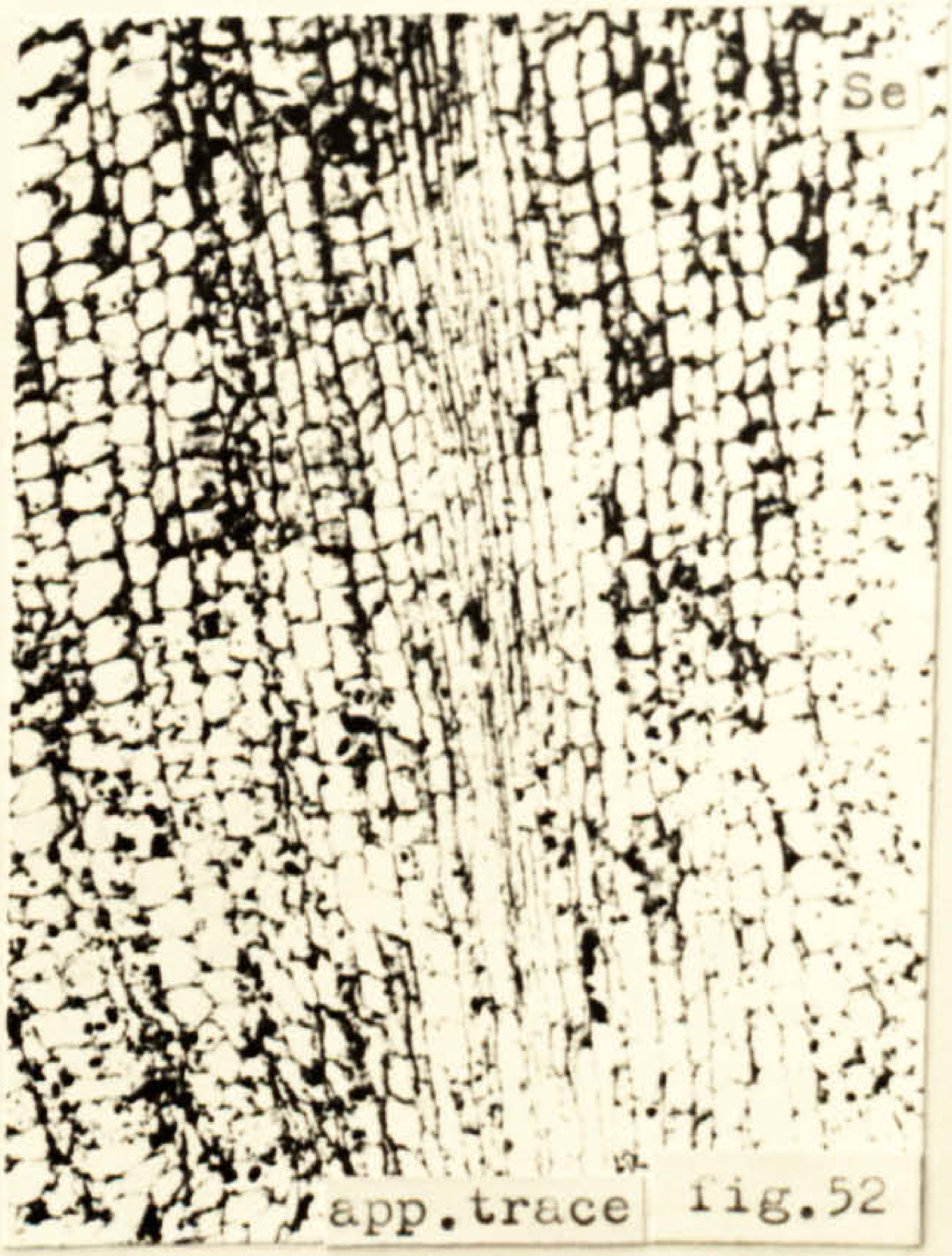


fig.52

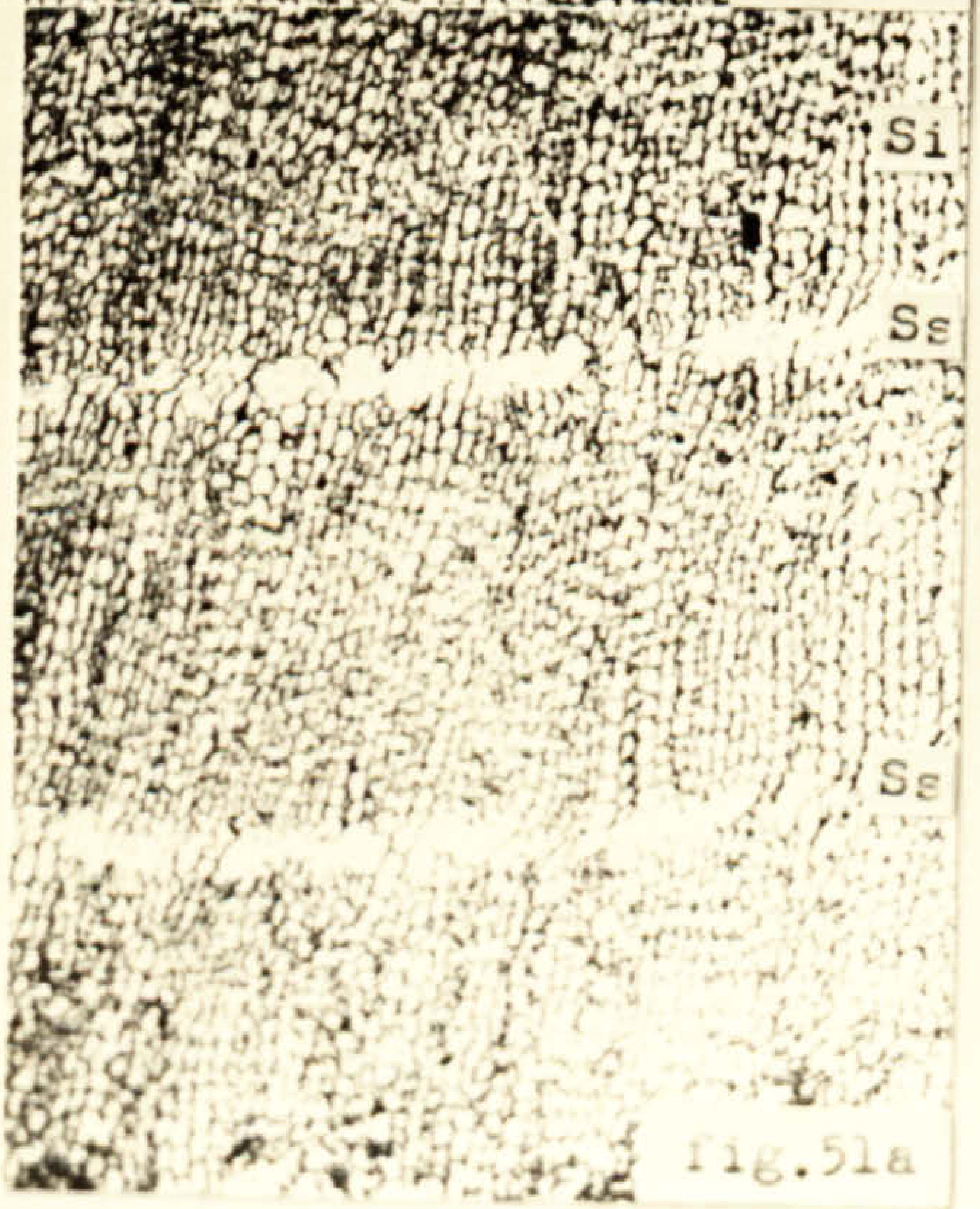


fig.51a

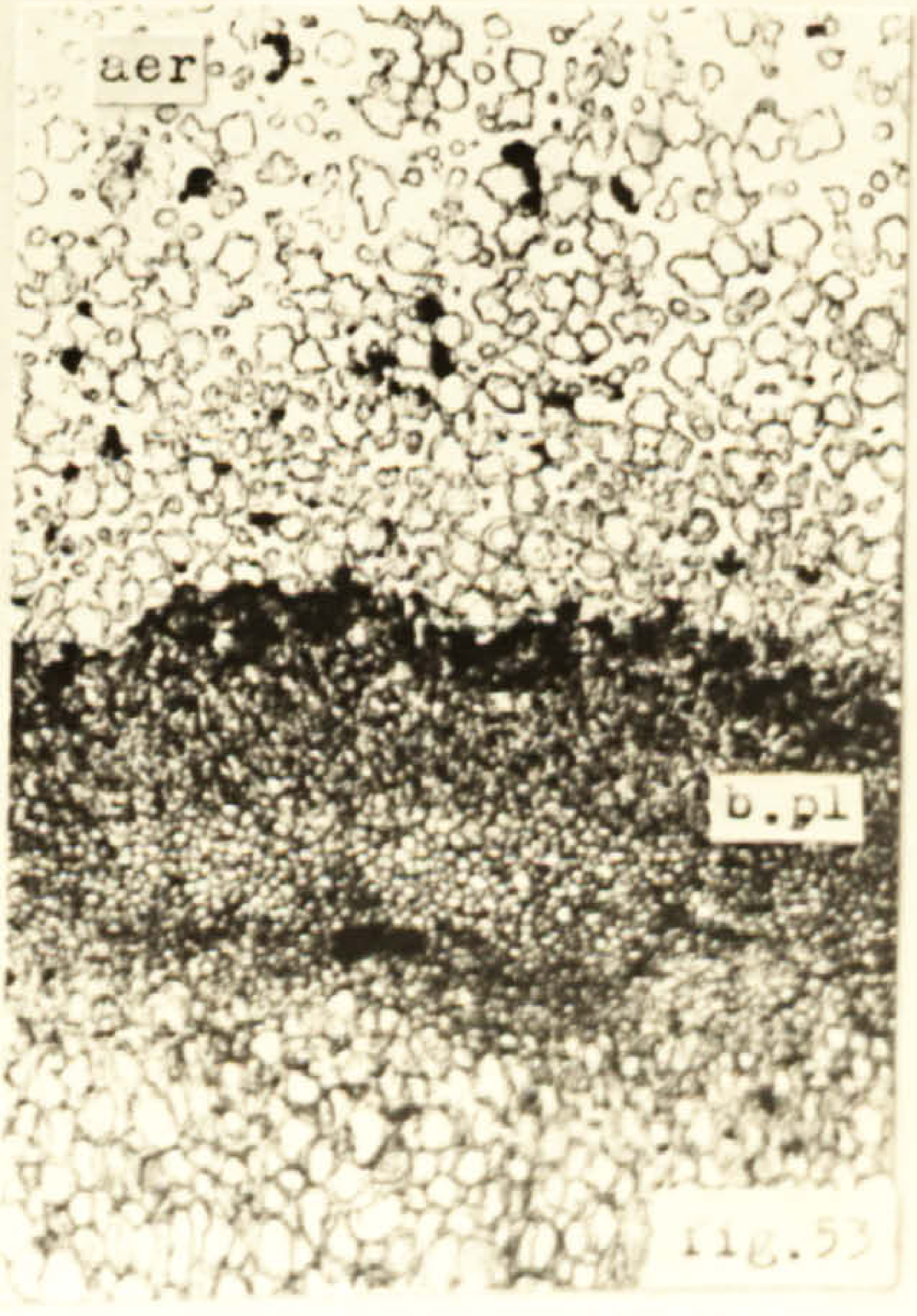


fig.53

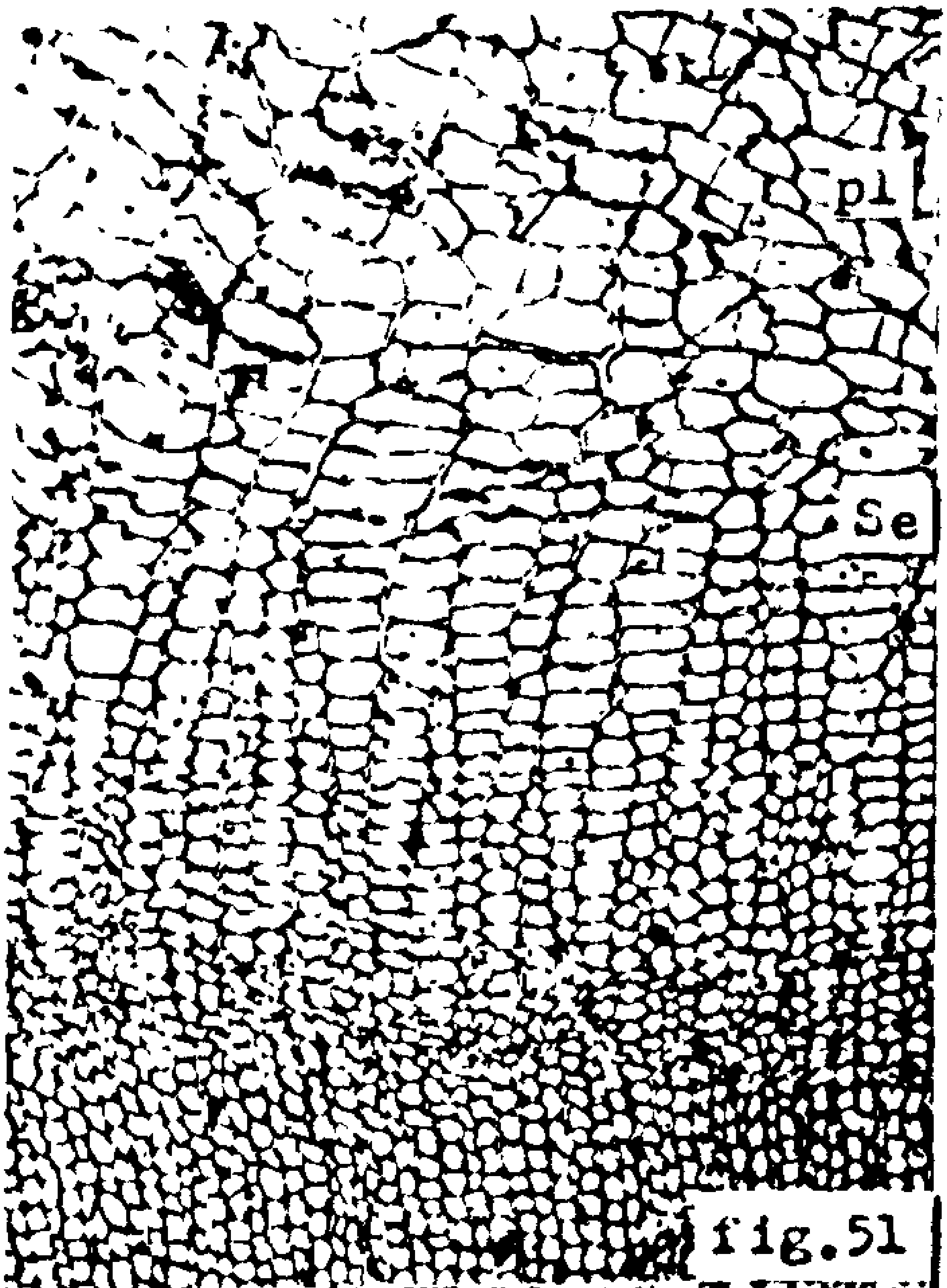


fig.51

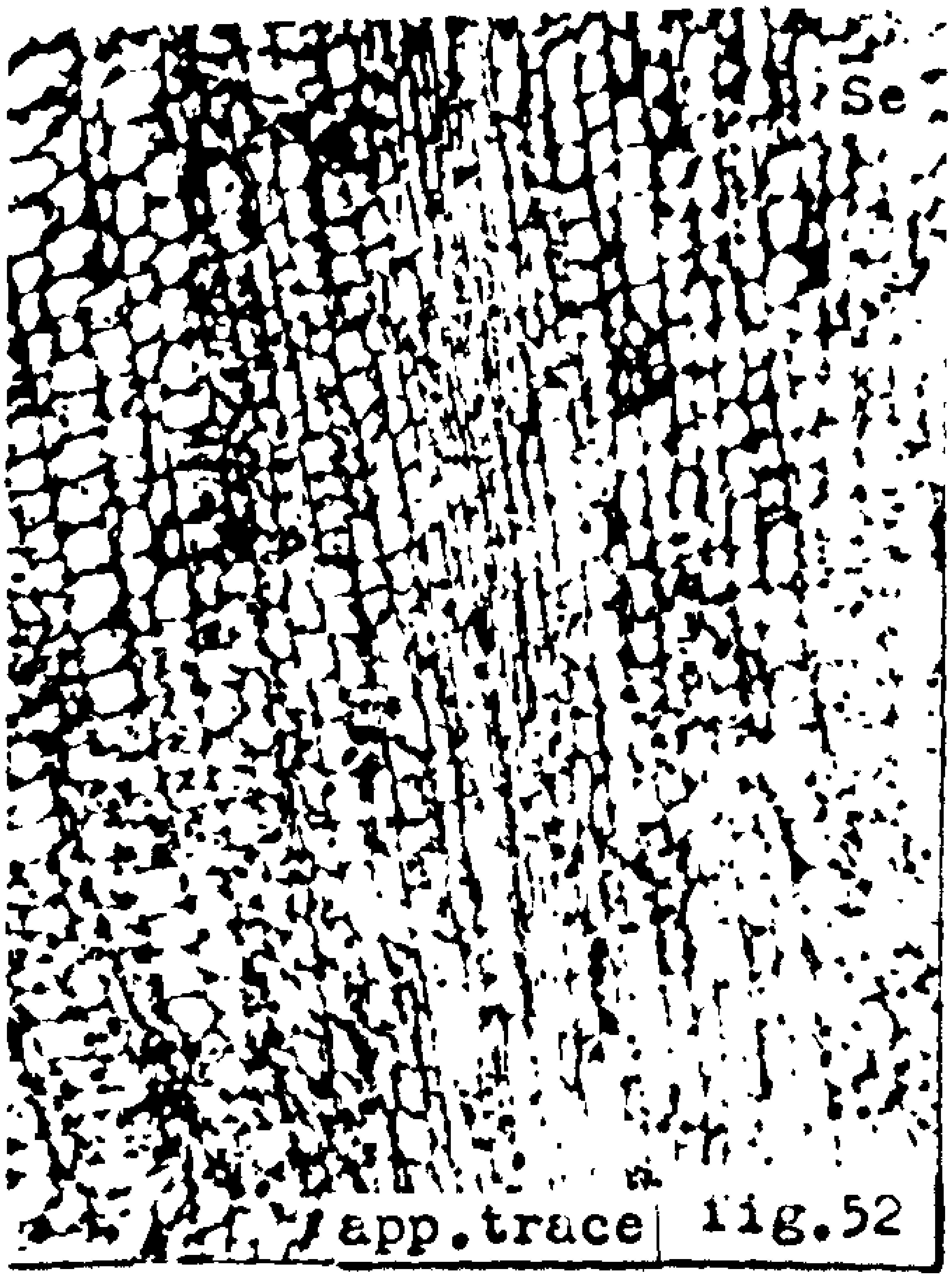


fig.52

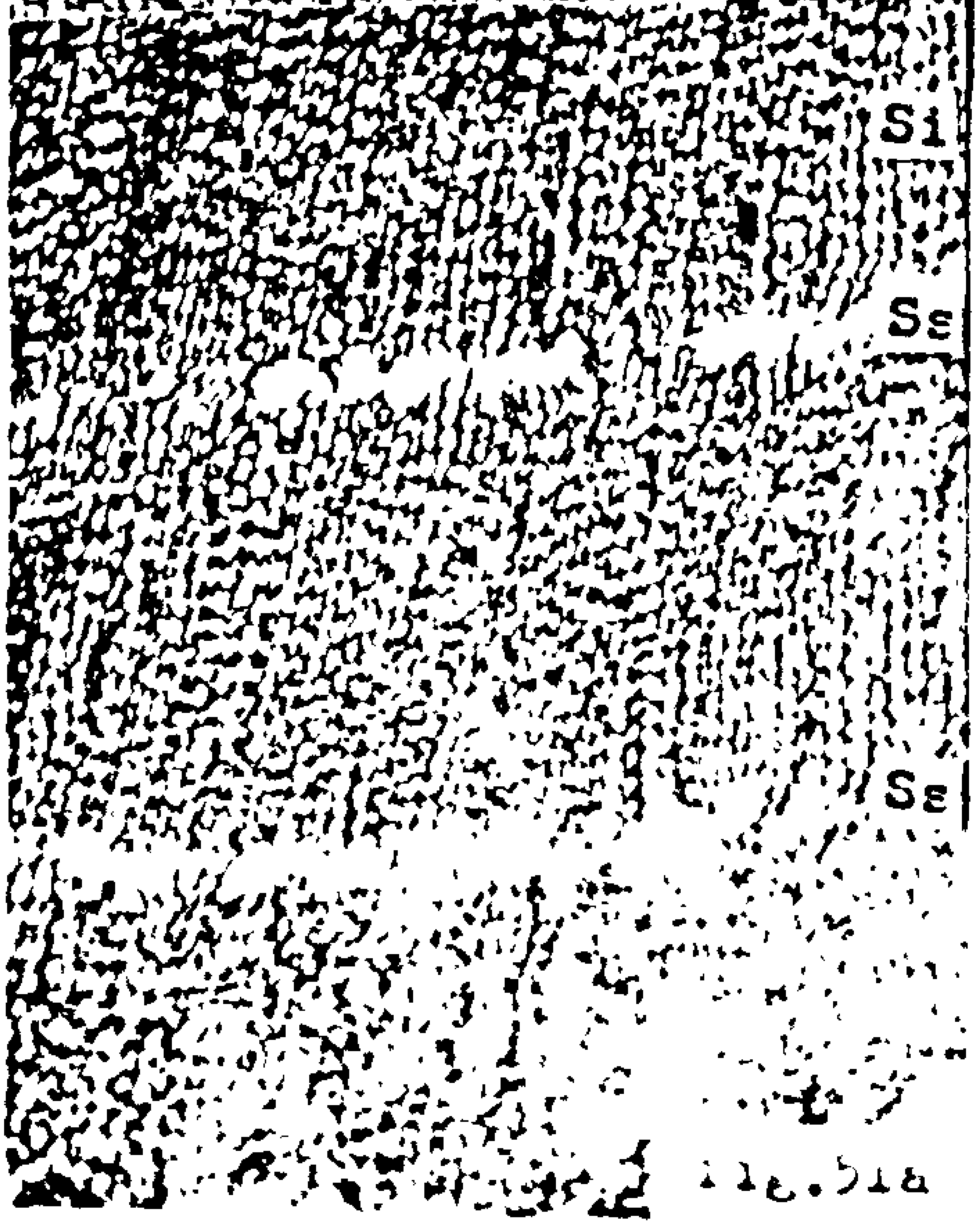
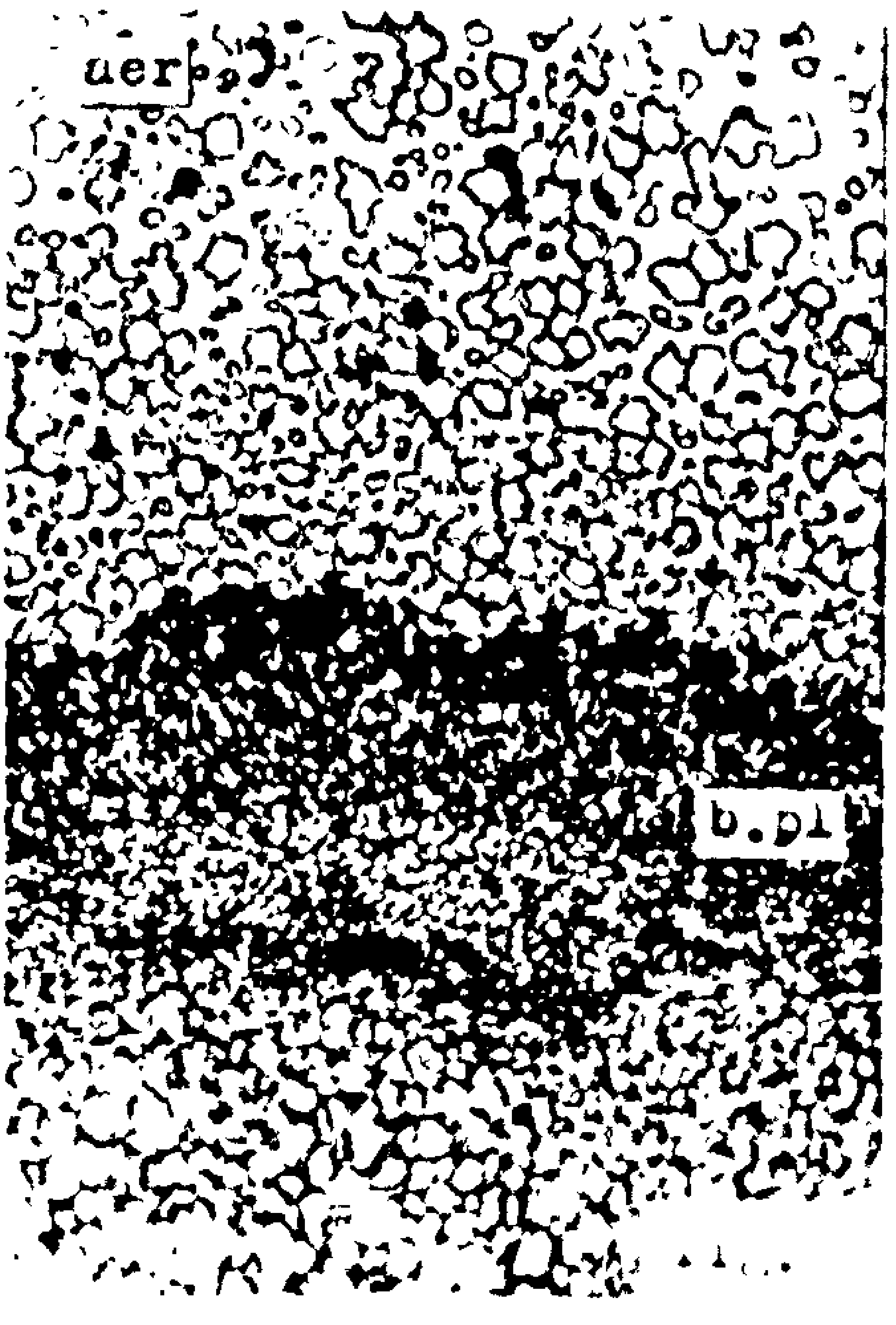


fig.51a



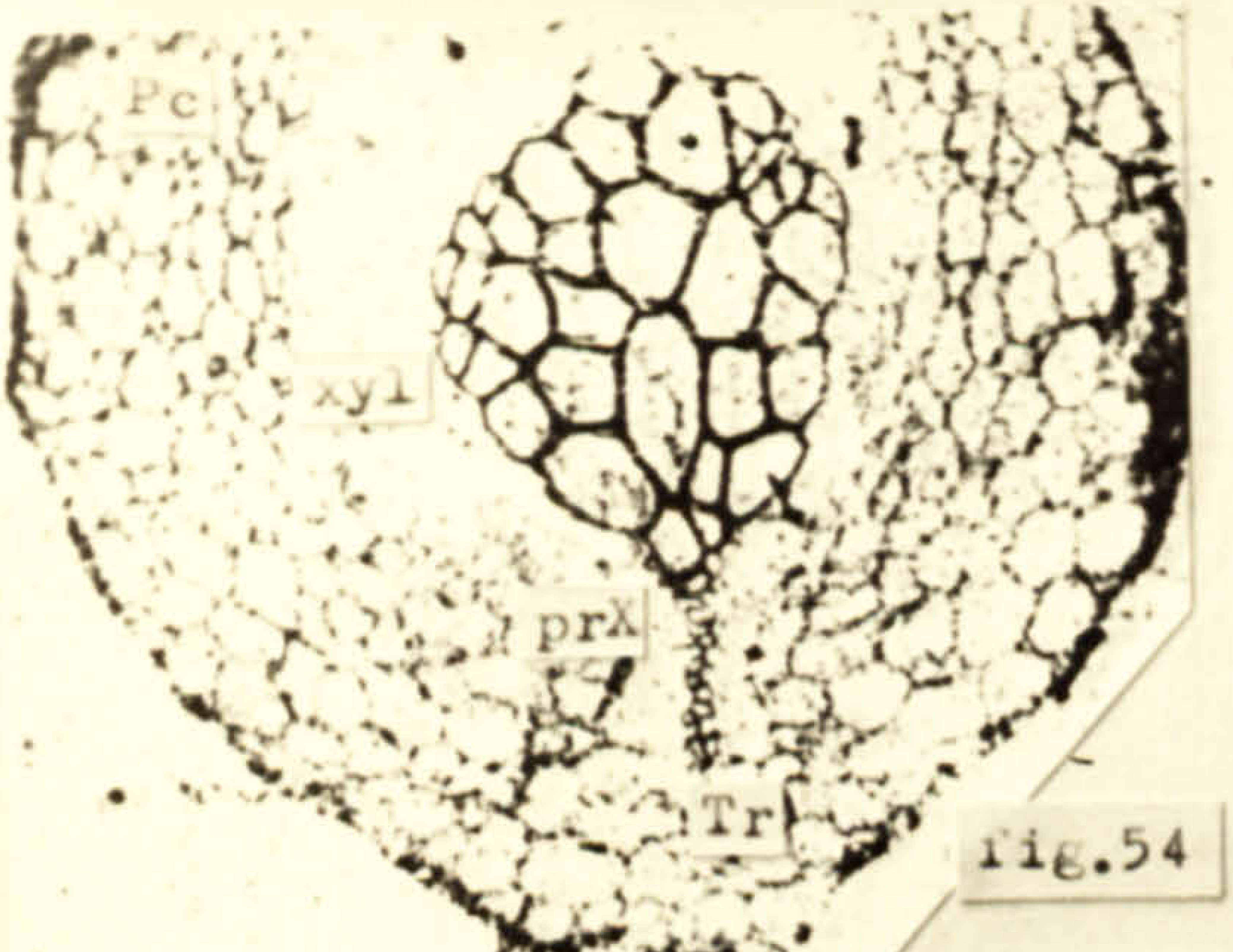


fig.54

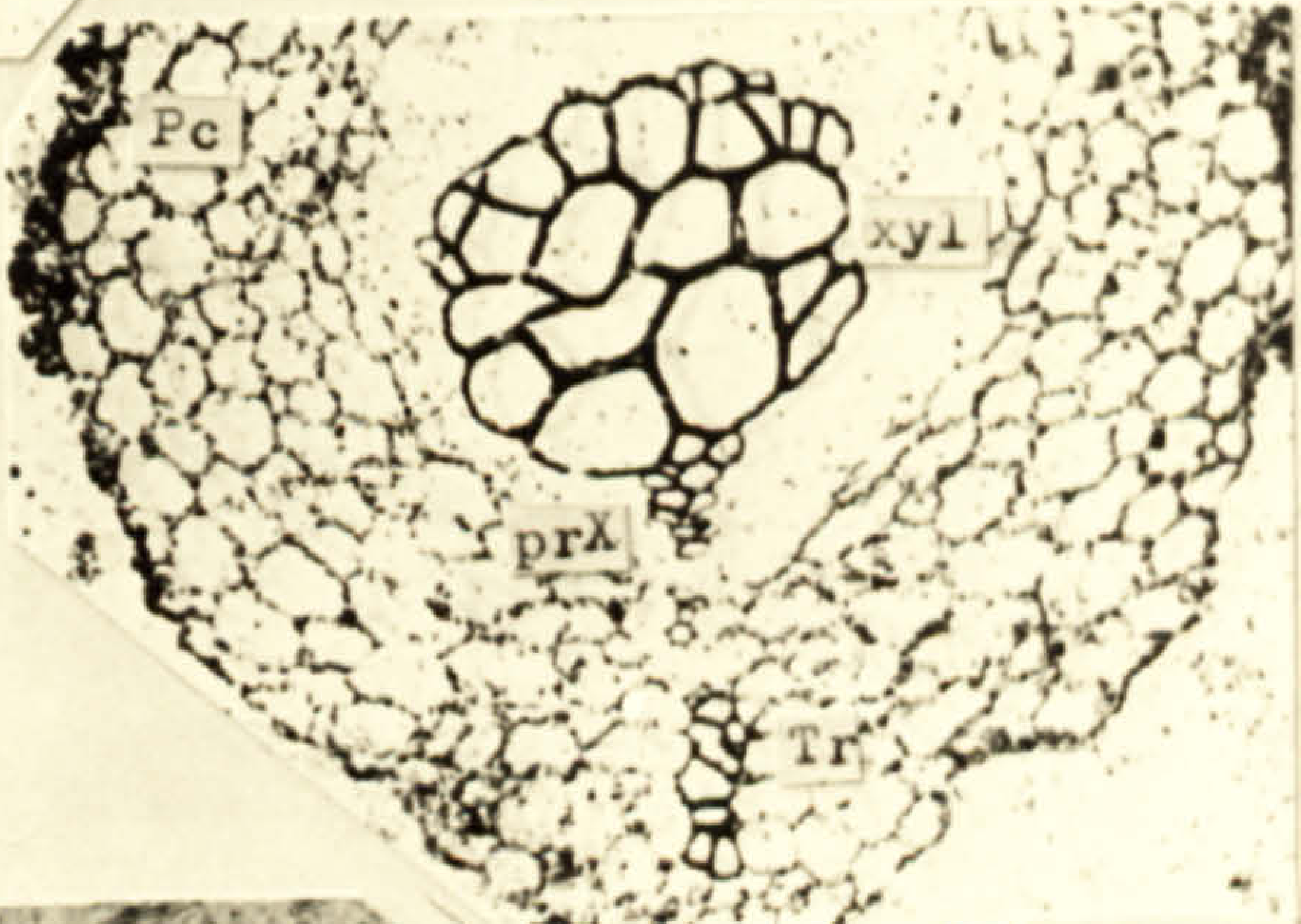


fig.55

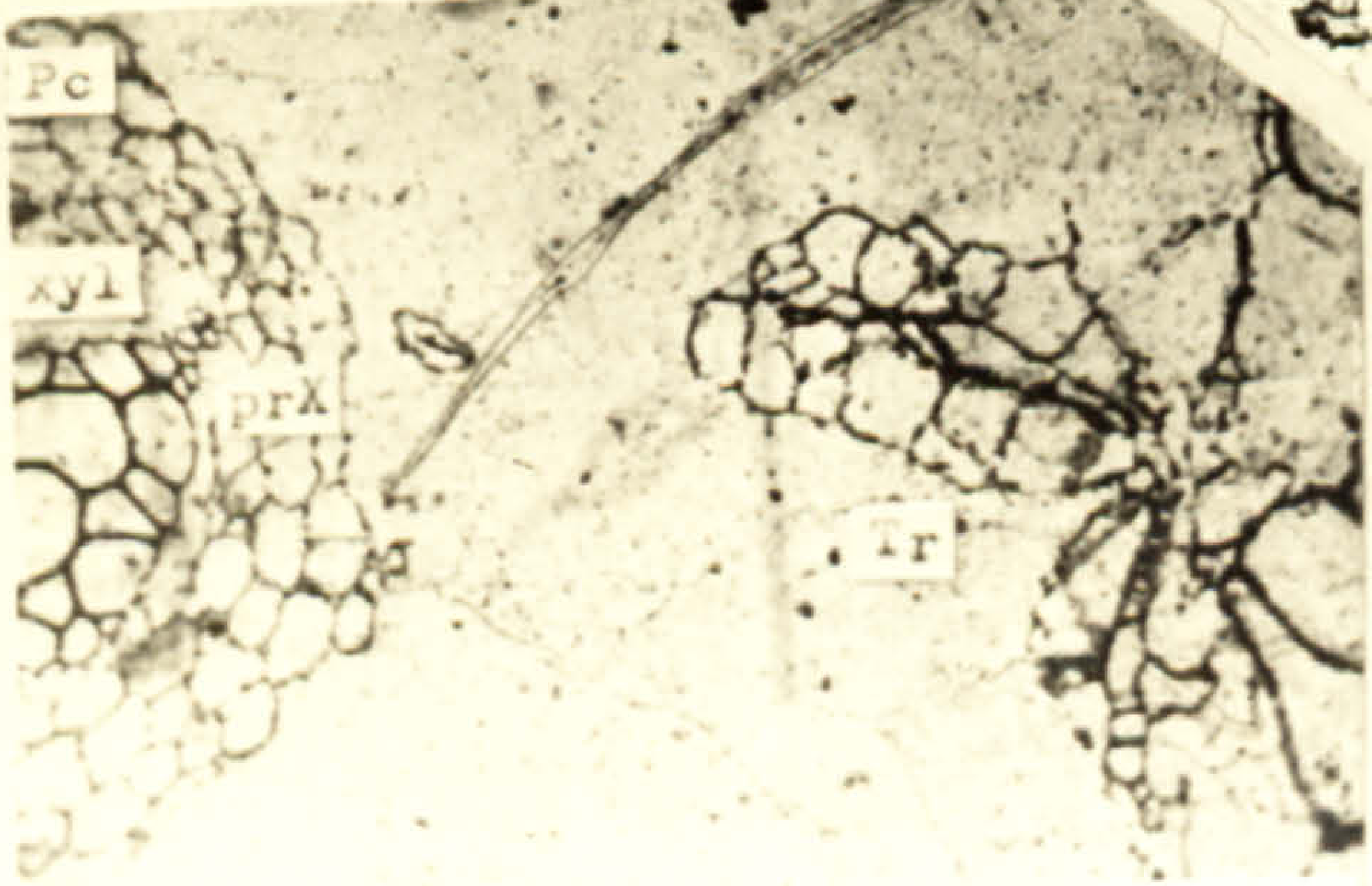


fig.56

fig.54

fig.55

fig.57

fig.58

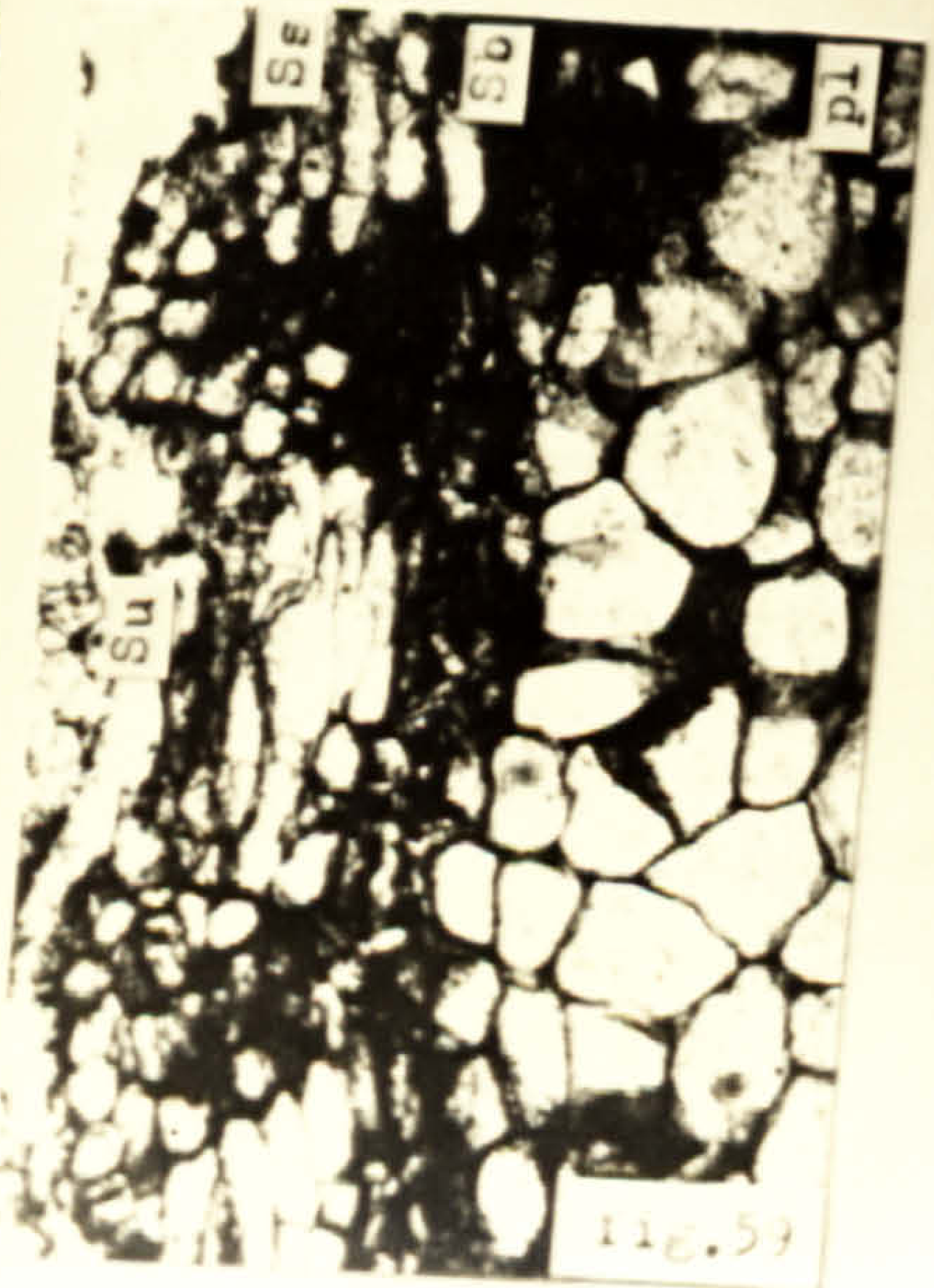


fig.59

fig.60

fig.57

fig.58

fig.59

fig.60

Plate XVI

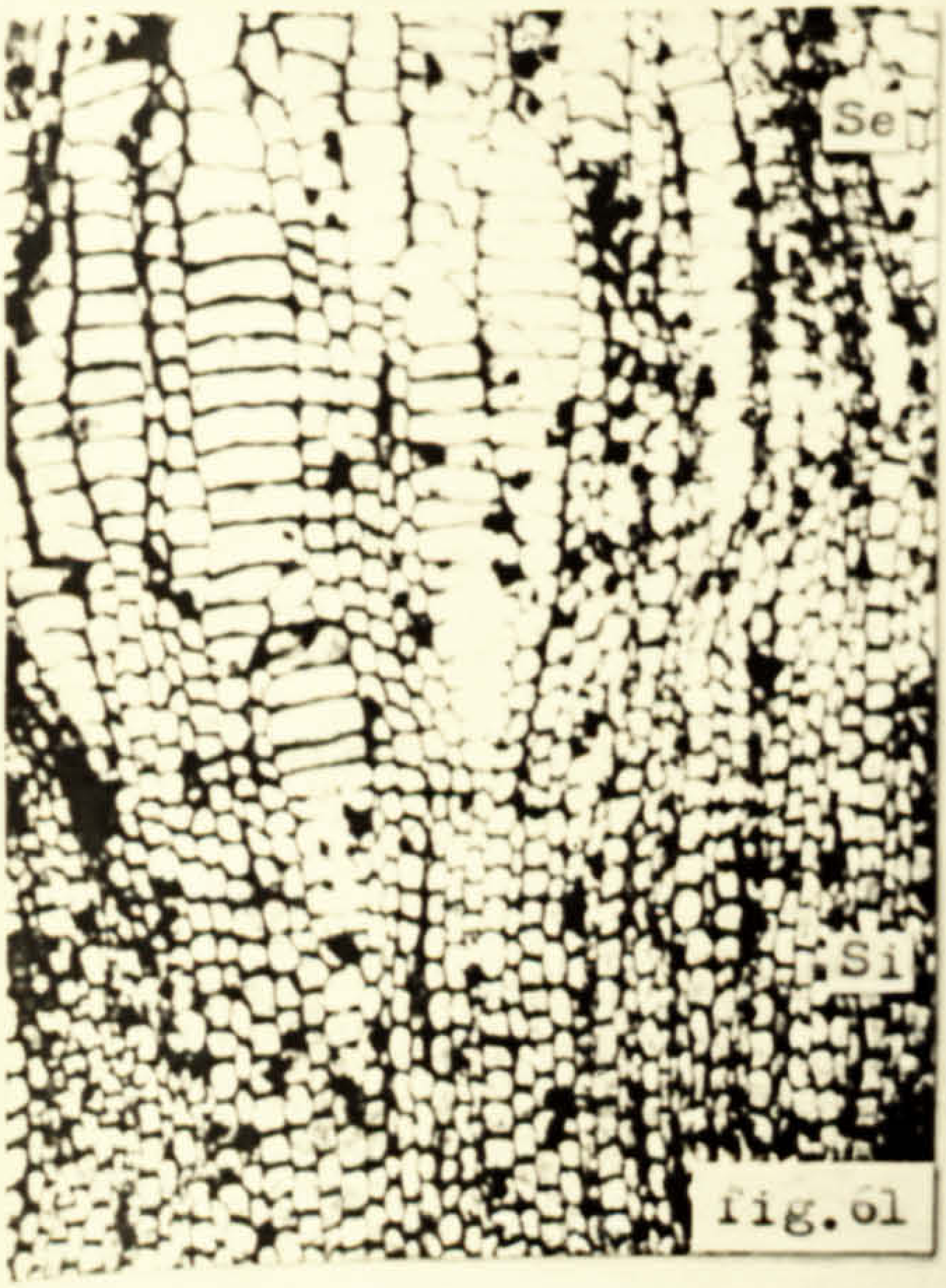


fig.61

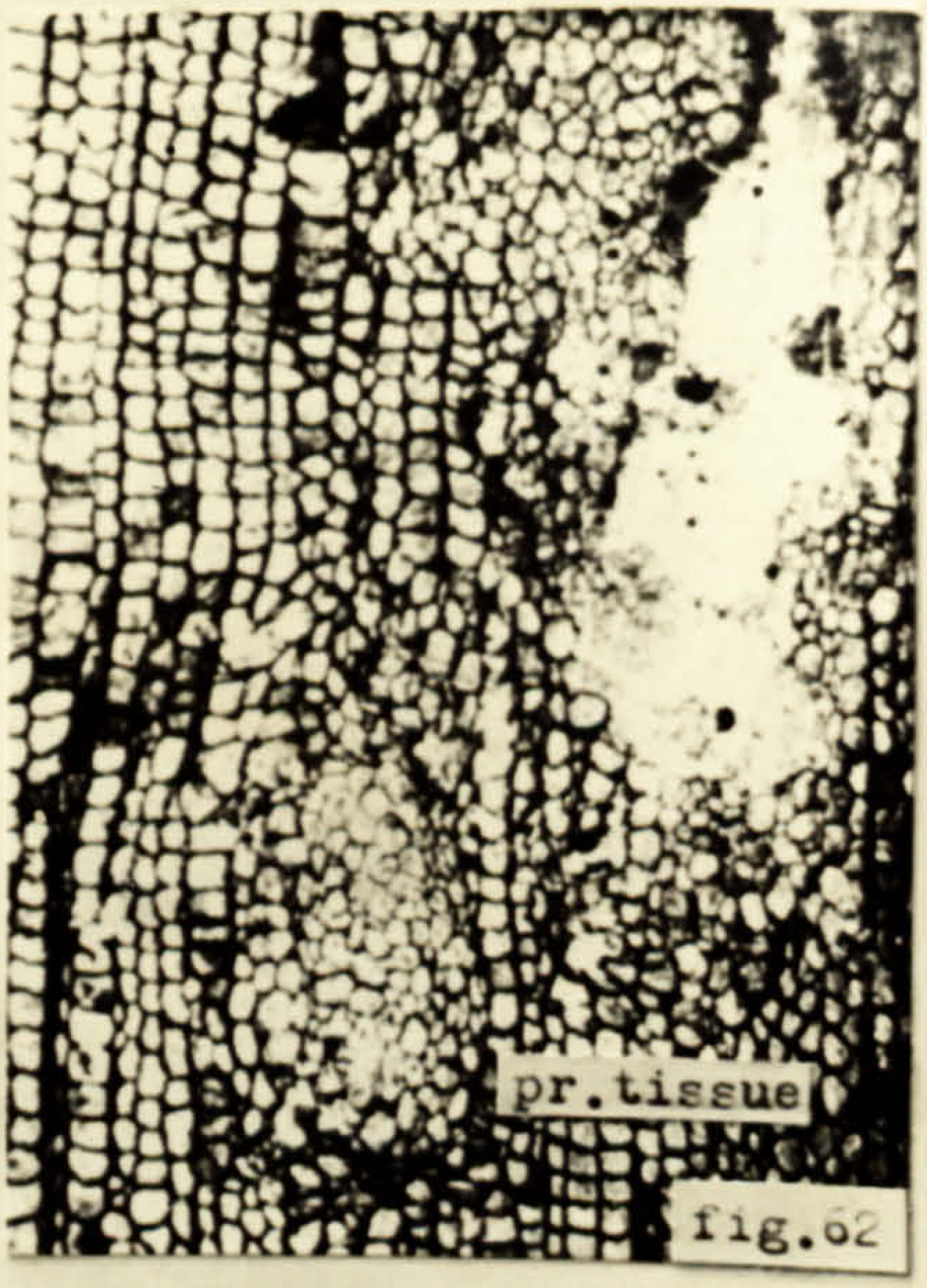


fig.62

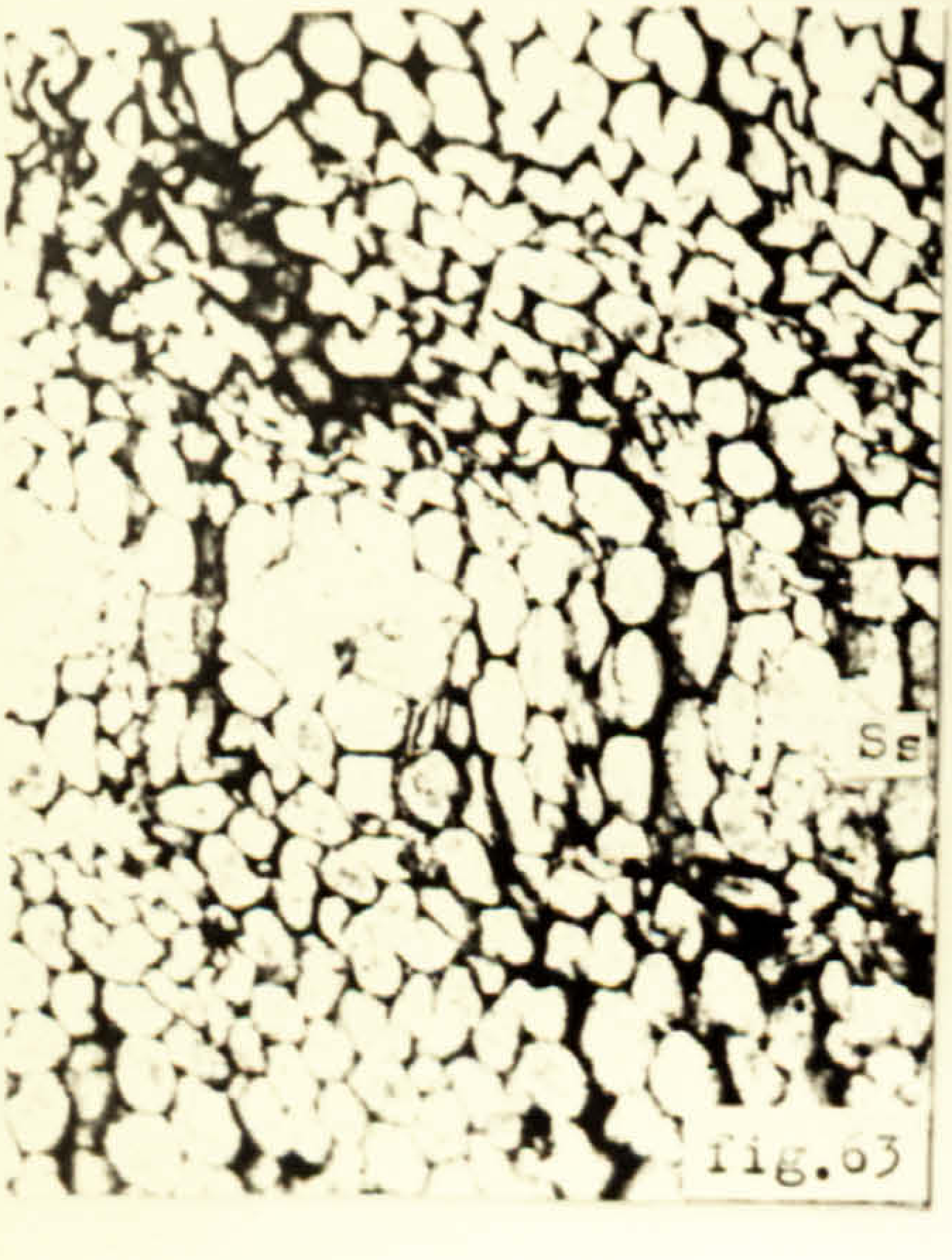


fig.63

fig.64

Plate XII

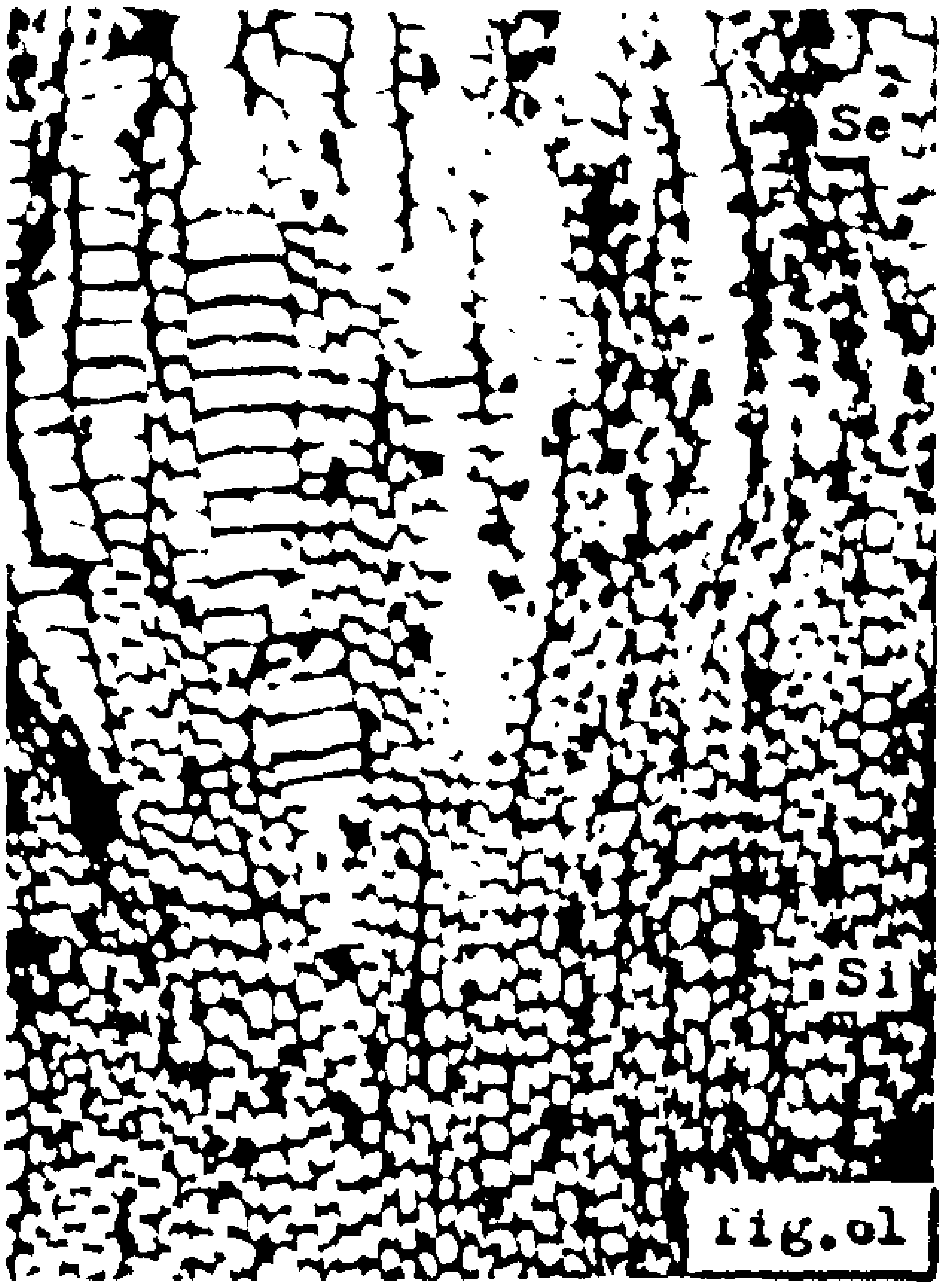


fig.01

fig.02

fig.03

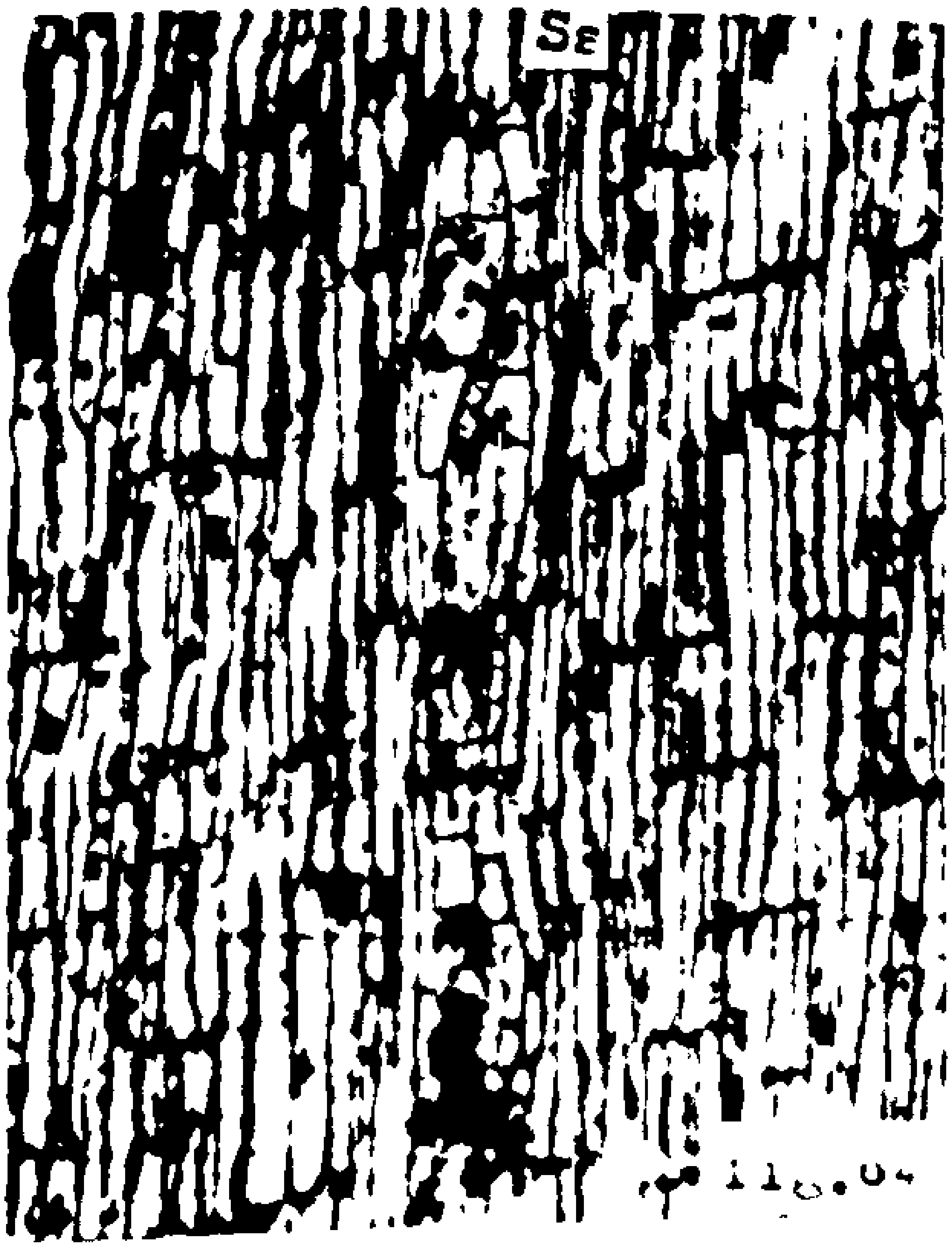


fig.04

Plate XVII

fig.65

fig.66

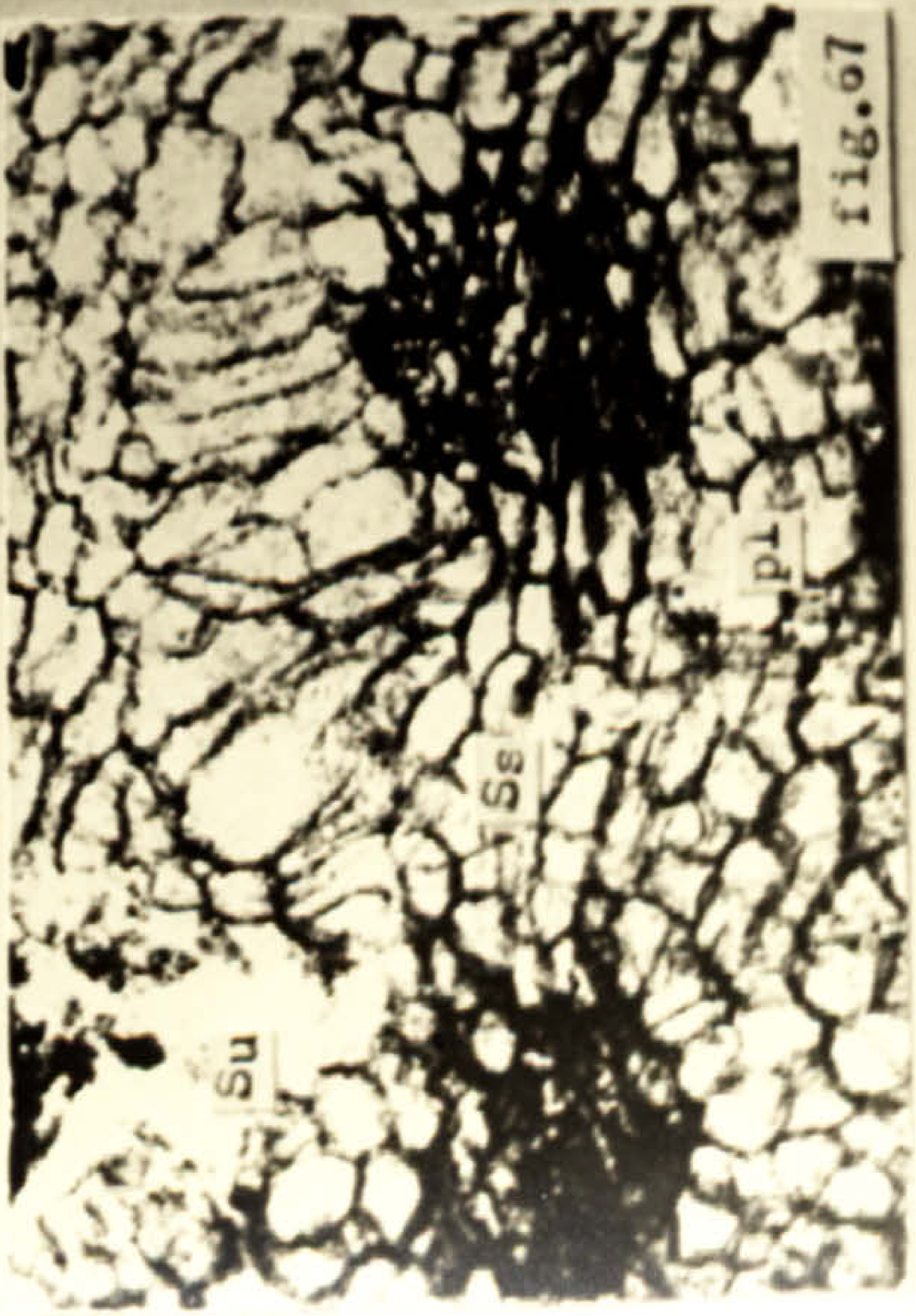


fig.67

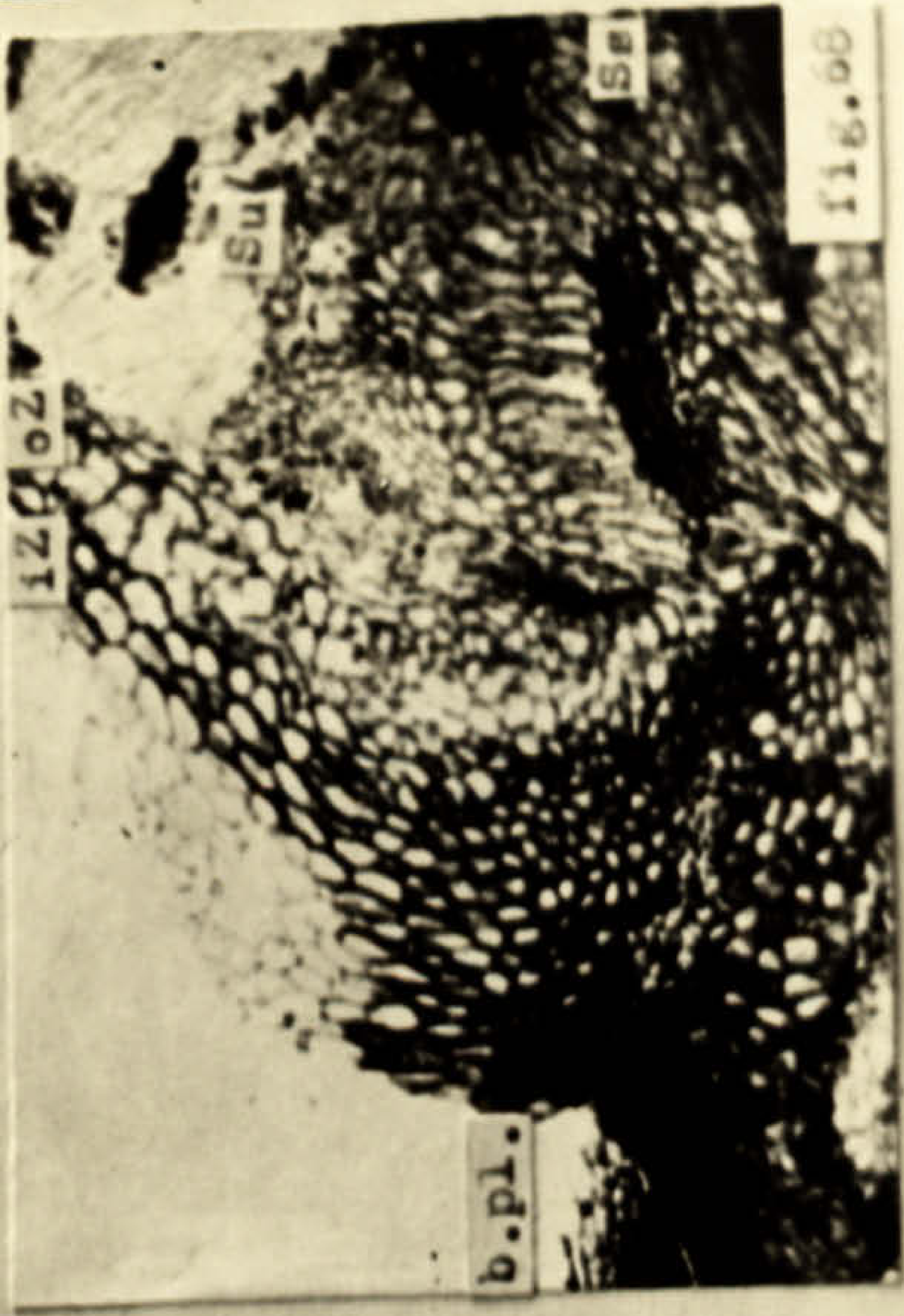


fig.68

Plate XVII

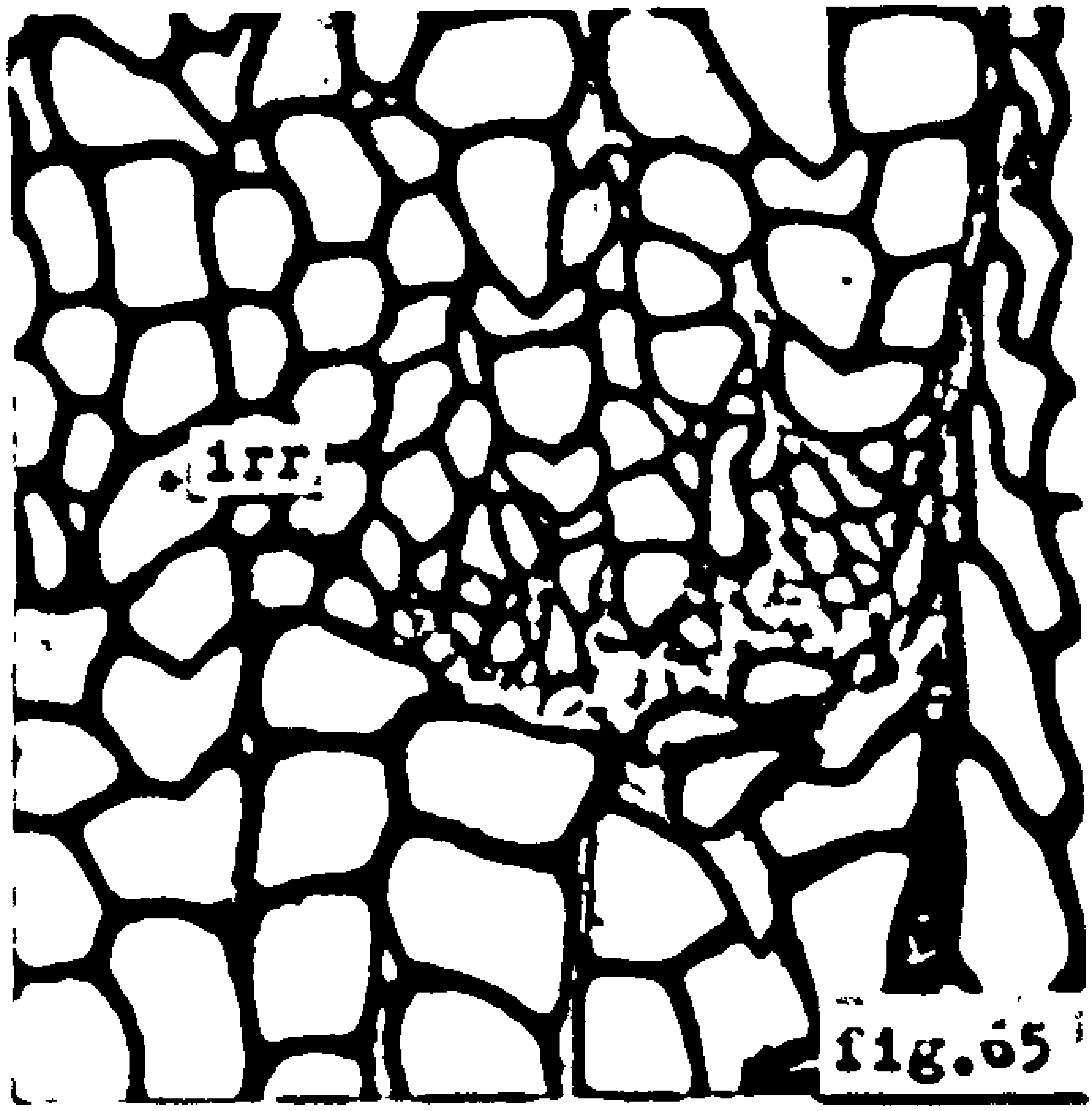


fig.65

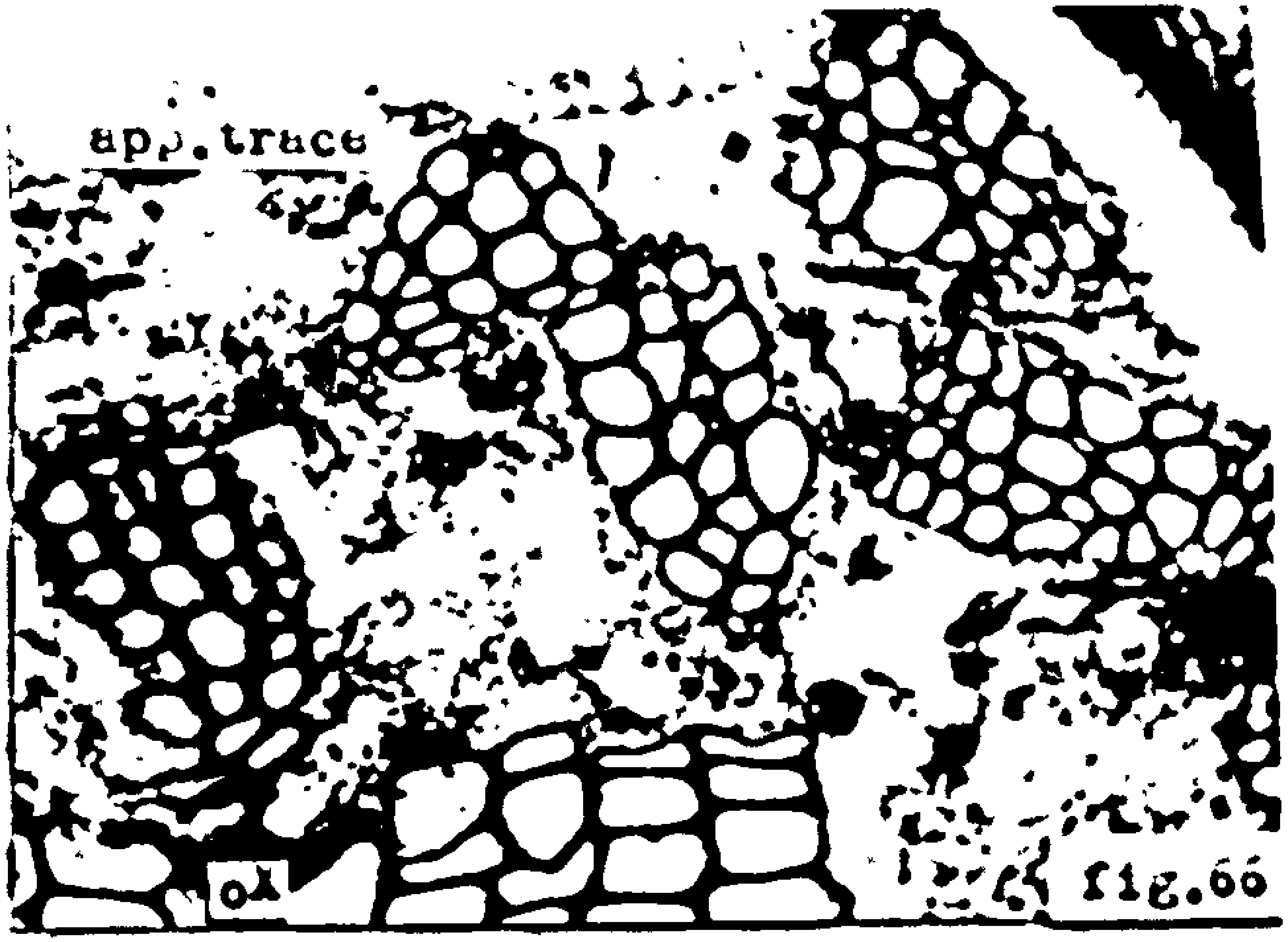


fig.66

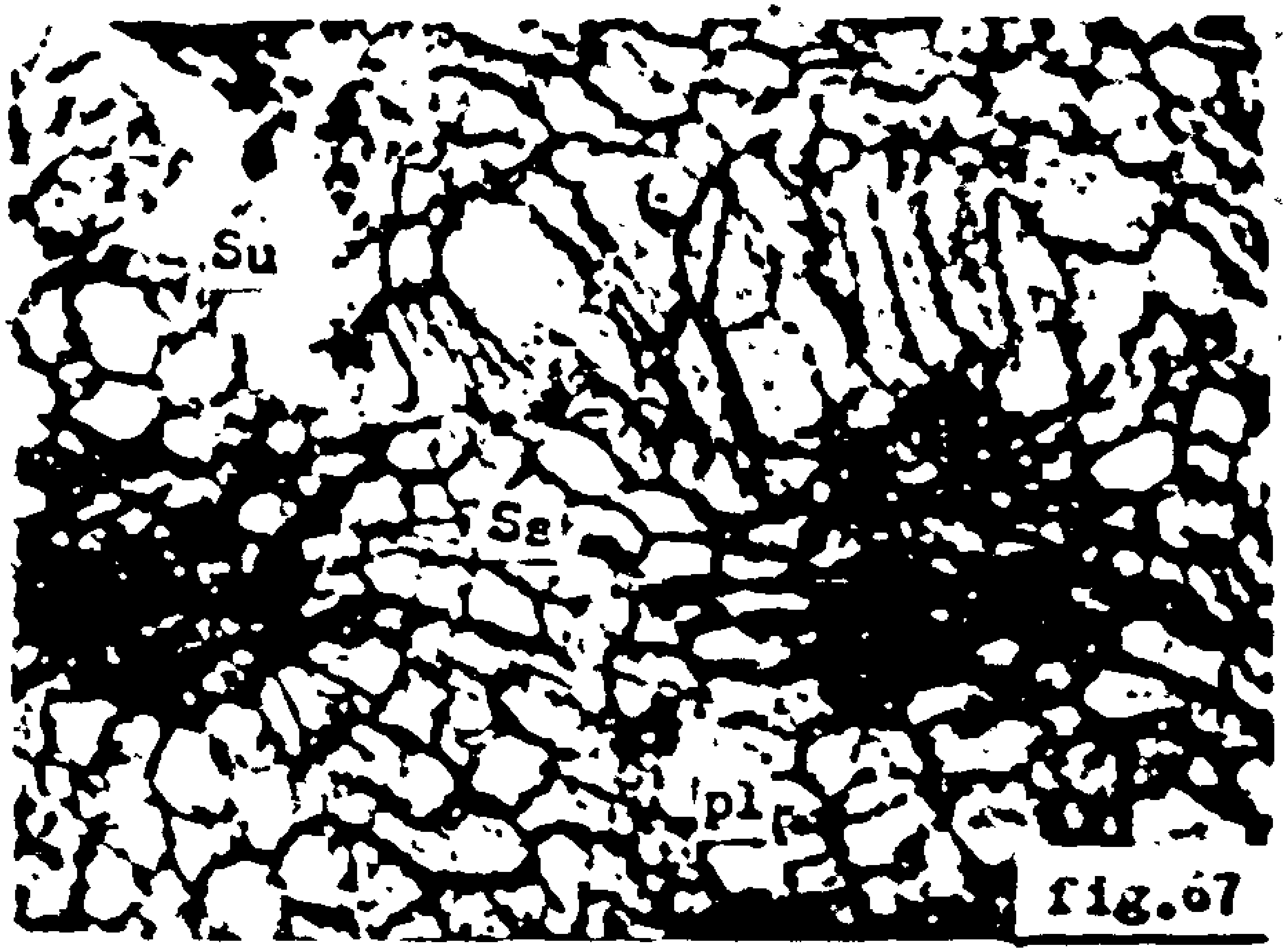


fig.67

fig.68

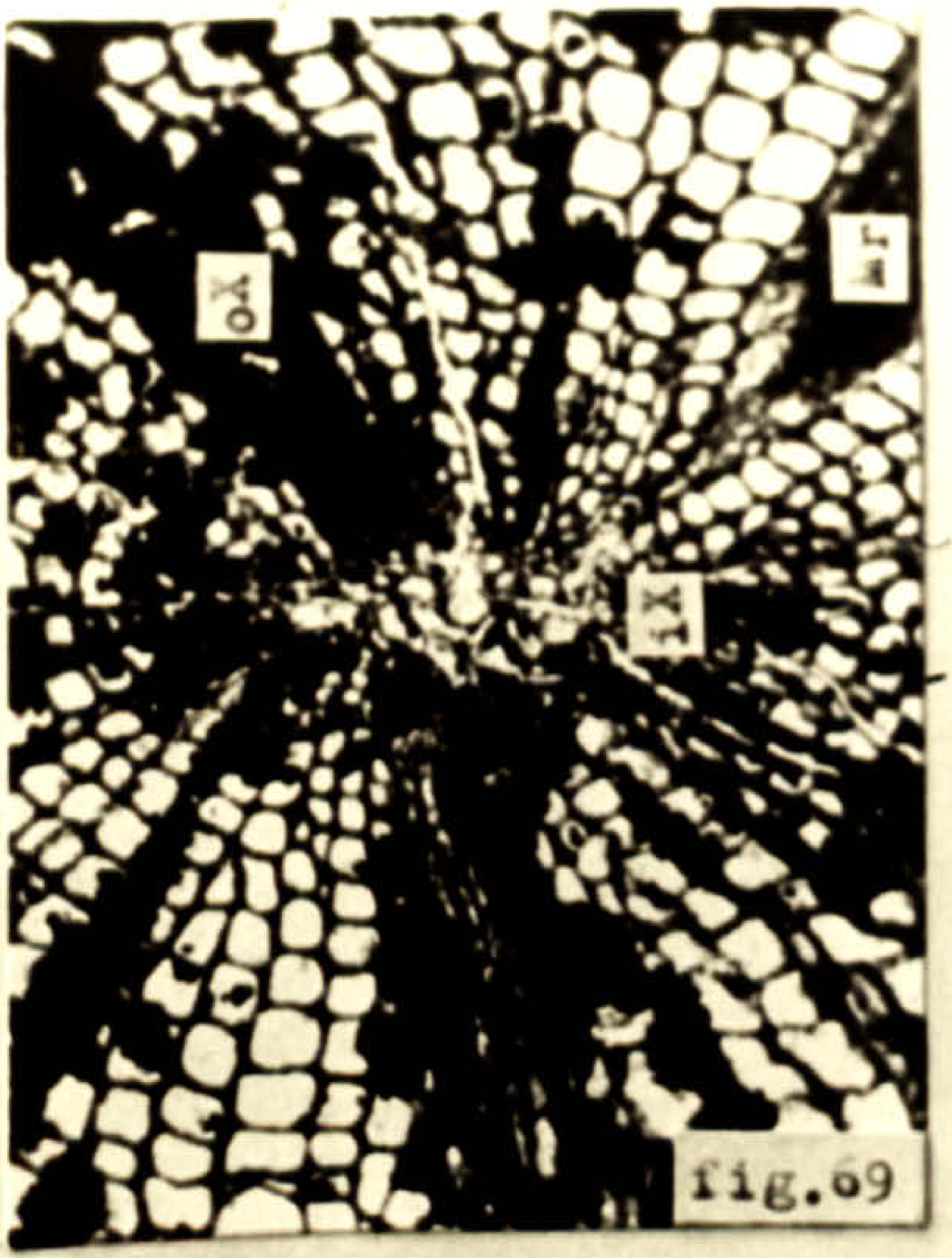


fig.69

fig.7o

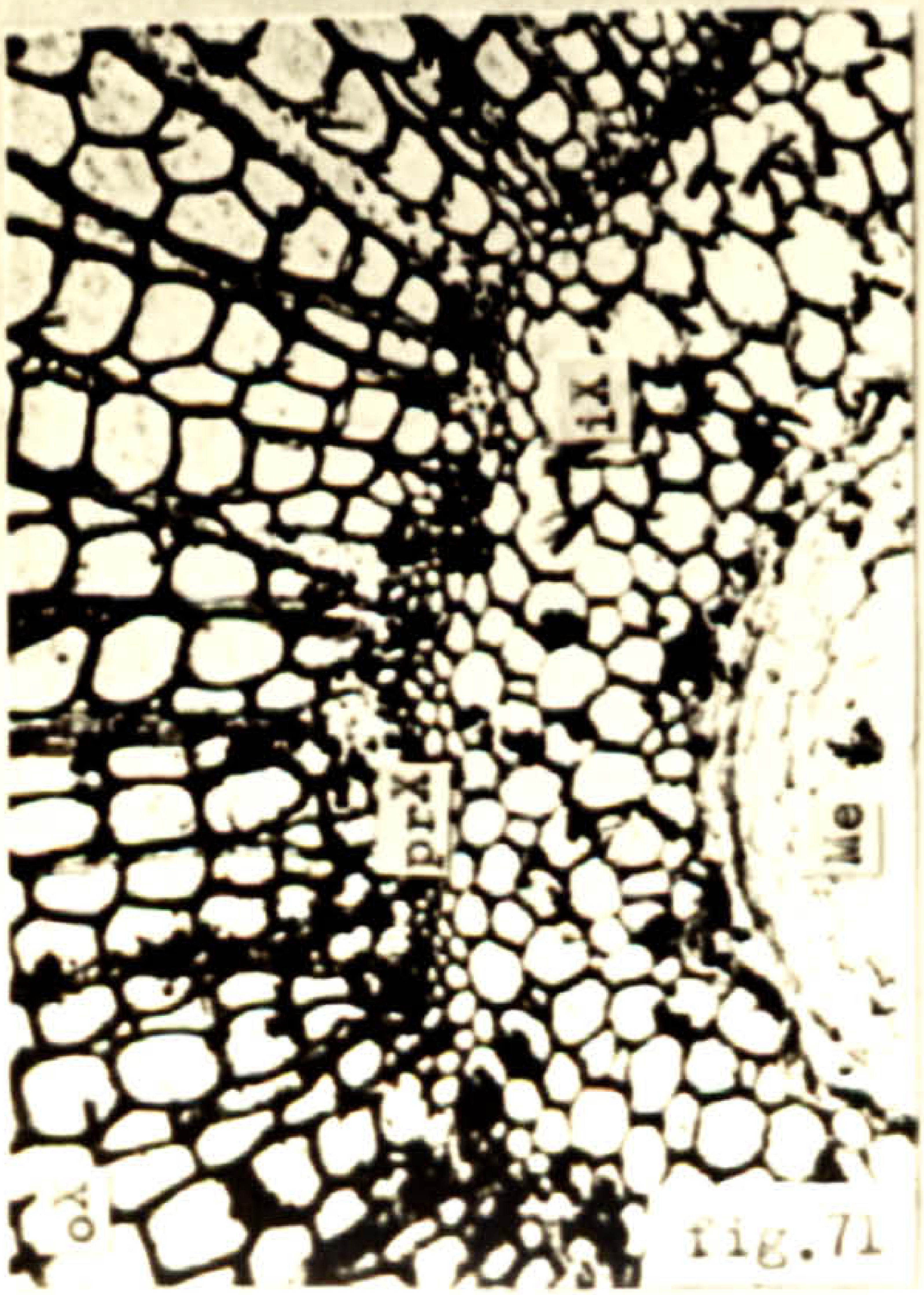
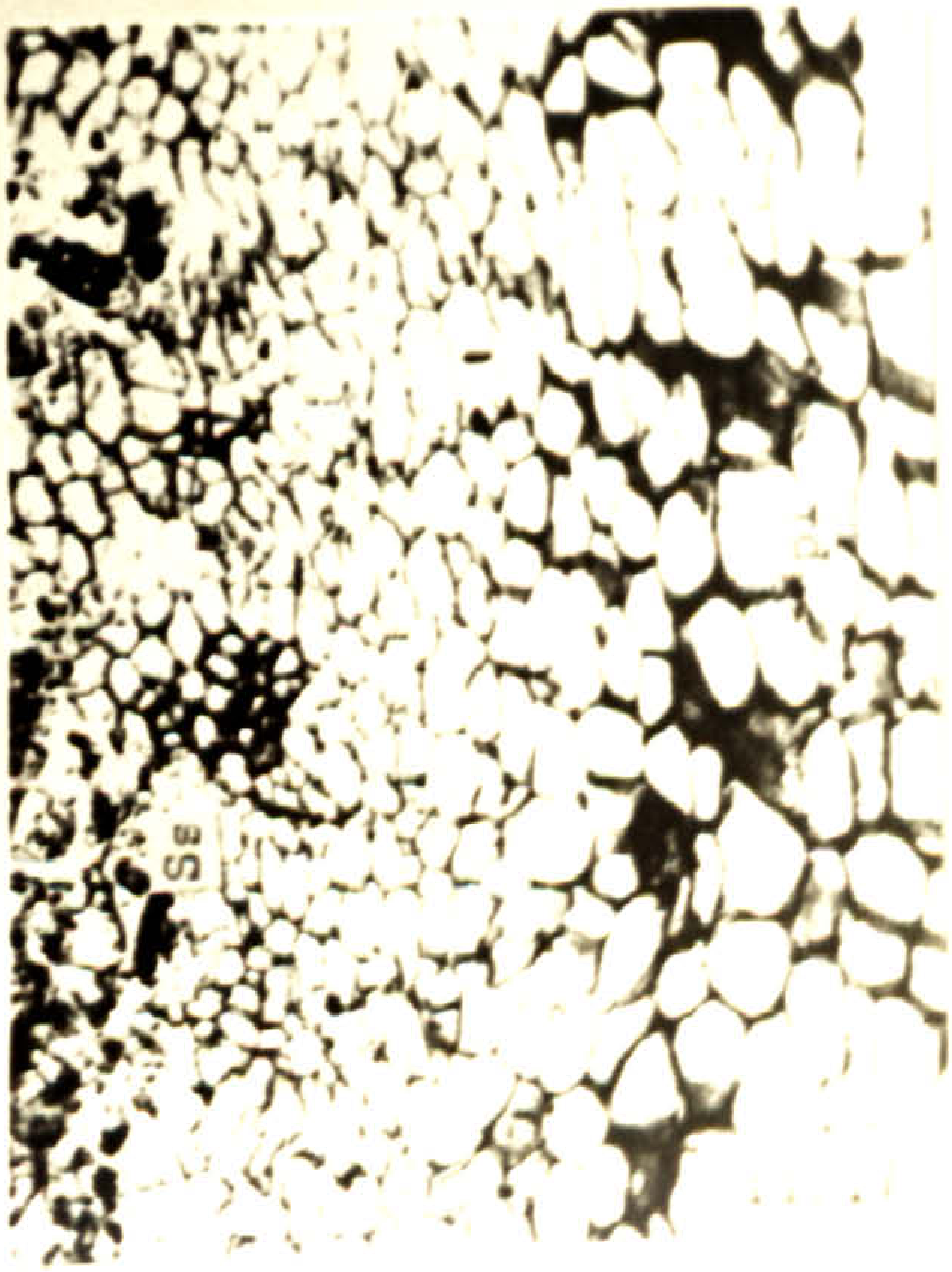


fig.71



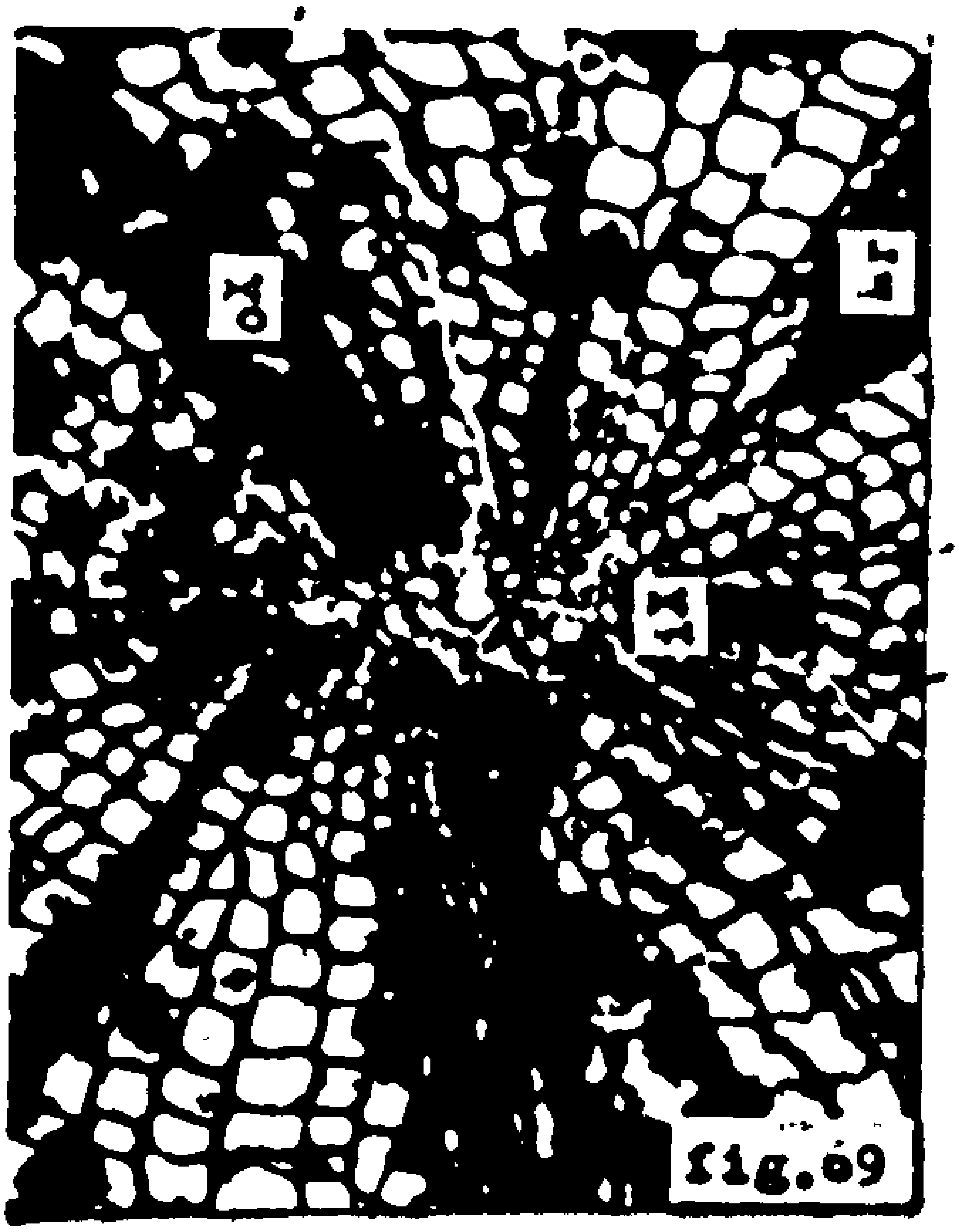


fig.69

fig.70

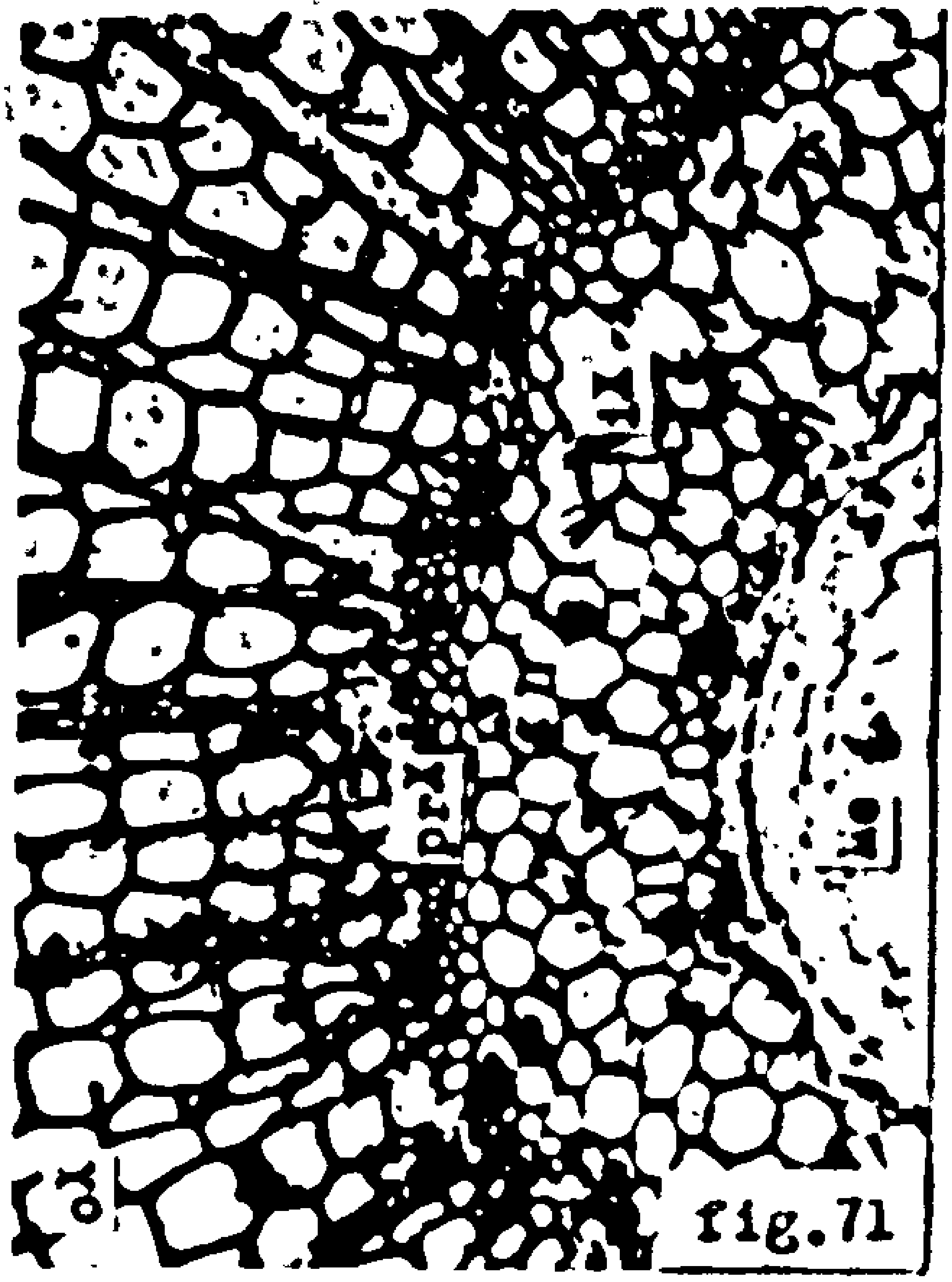
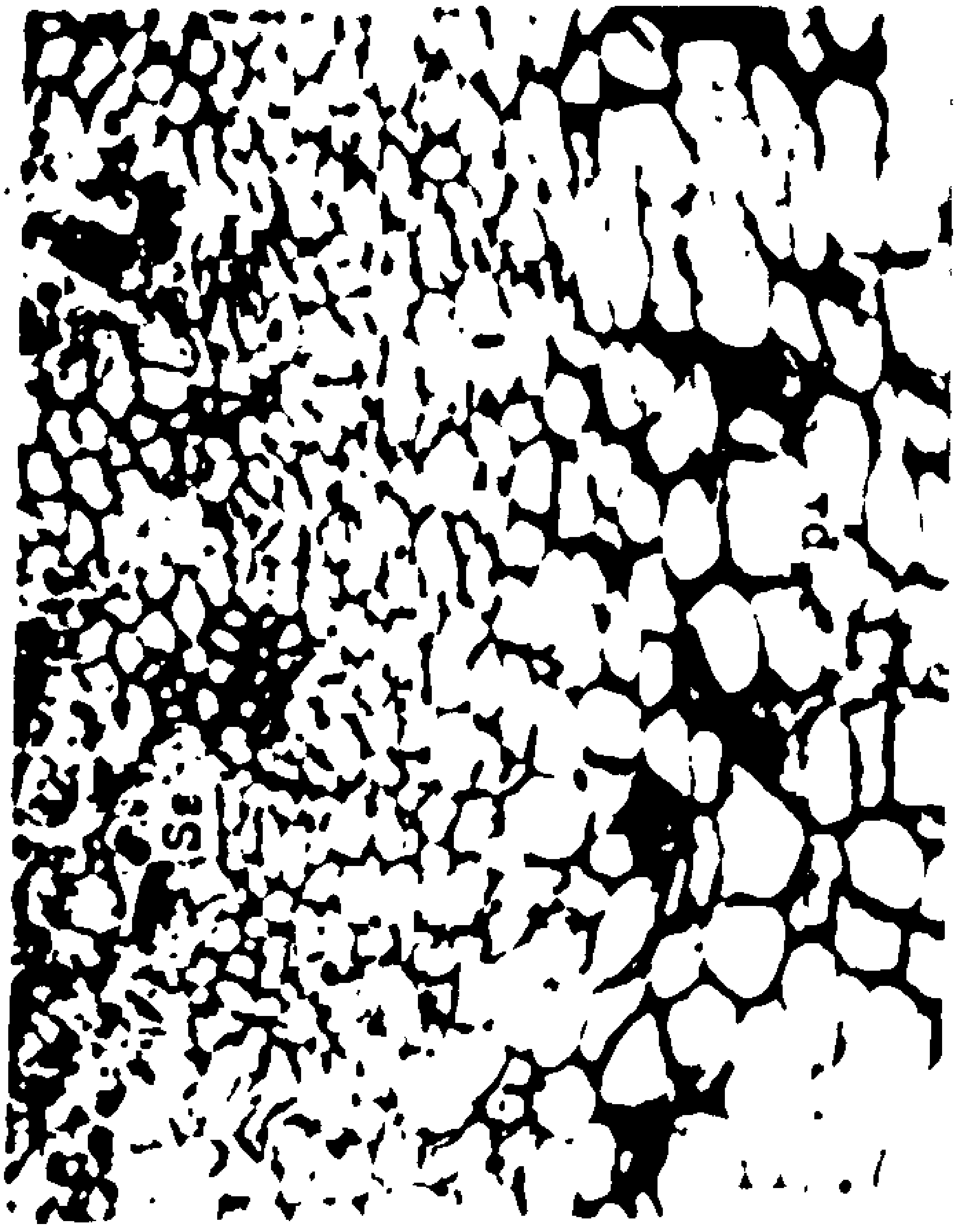


fig.71



[illegible]

Plate XIX

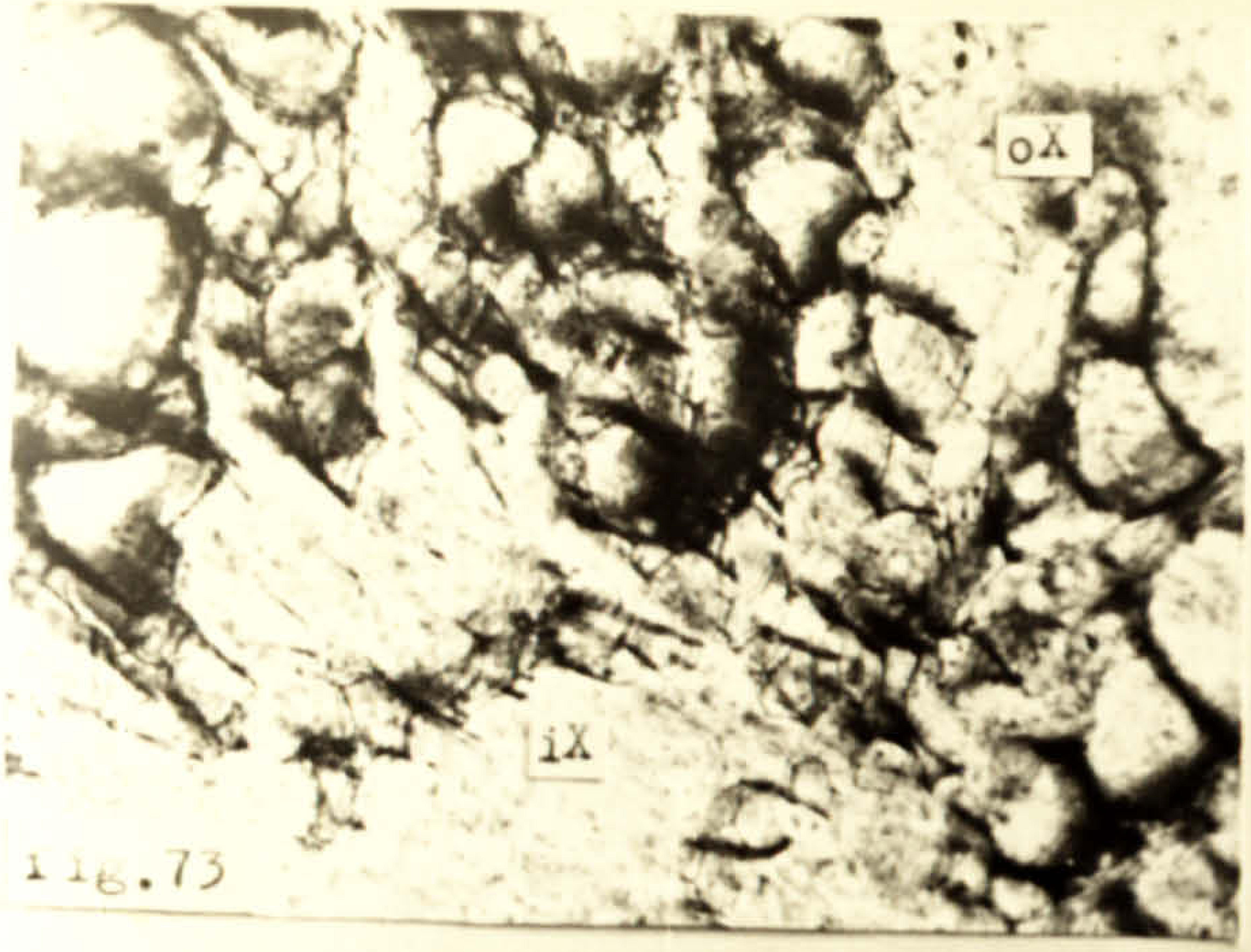


fig.73

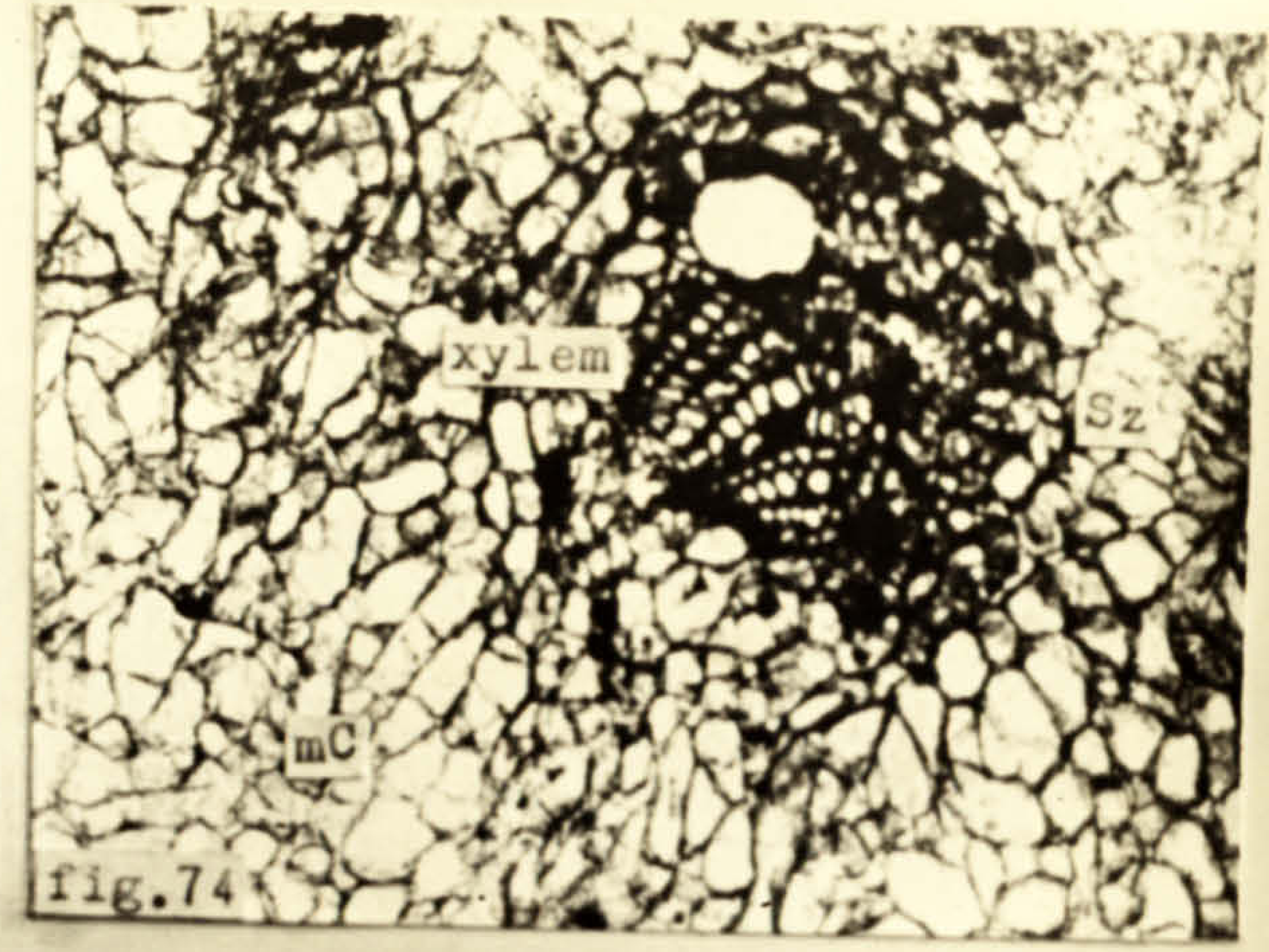


fig.74

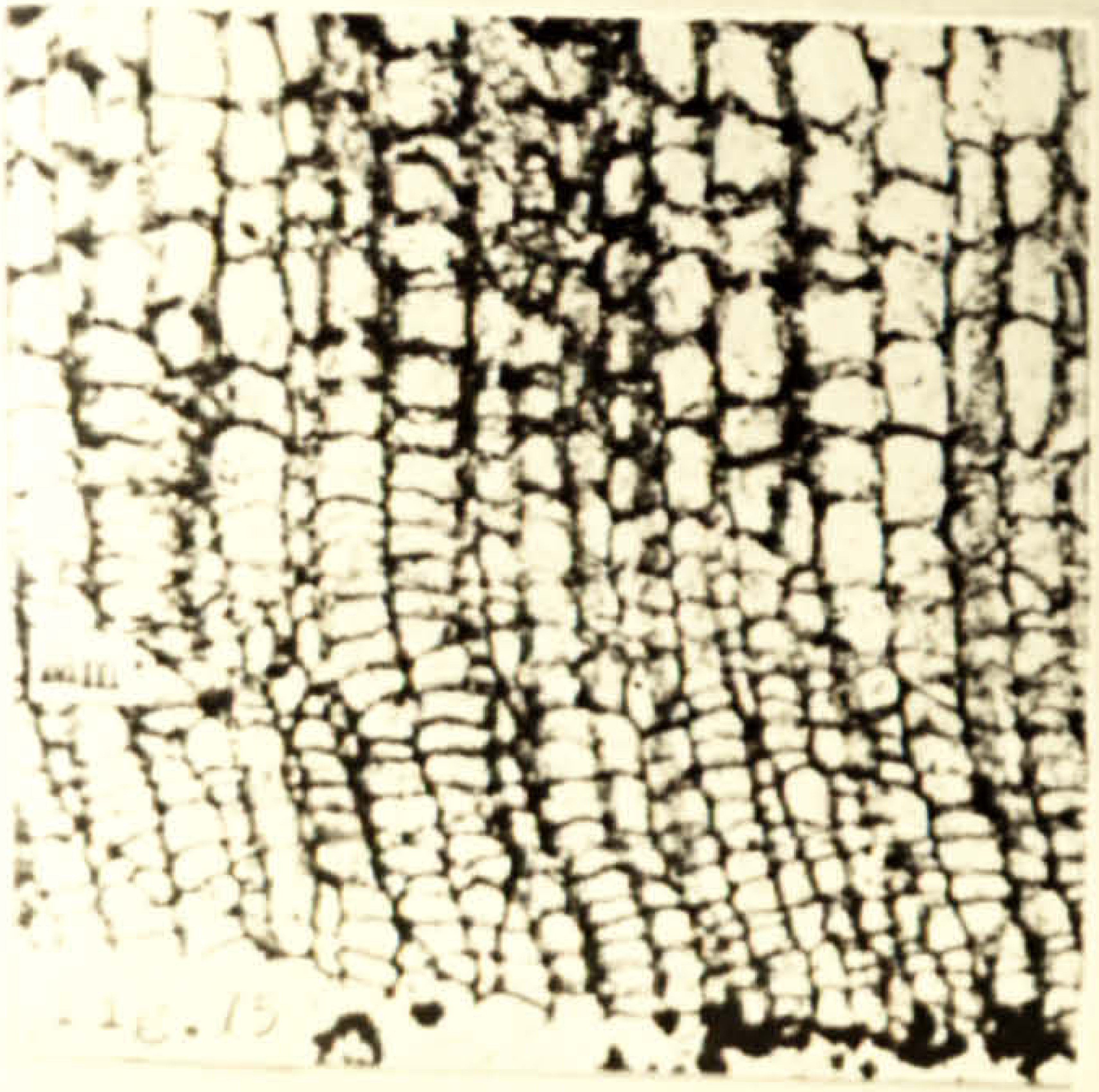


fig.75

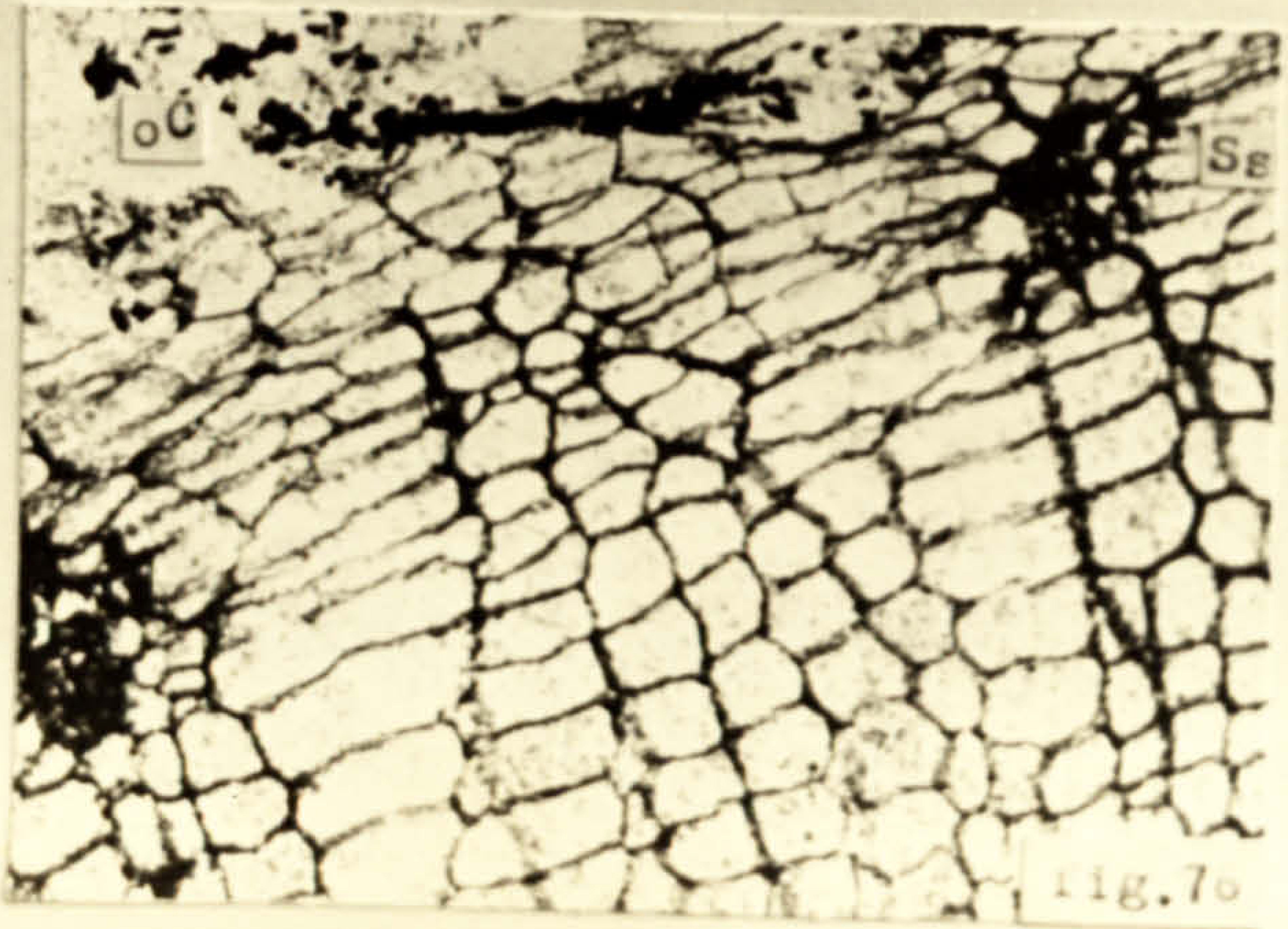


fig.76

Plate XIX

fig.75

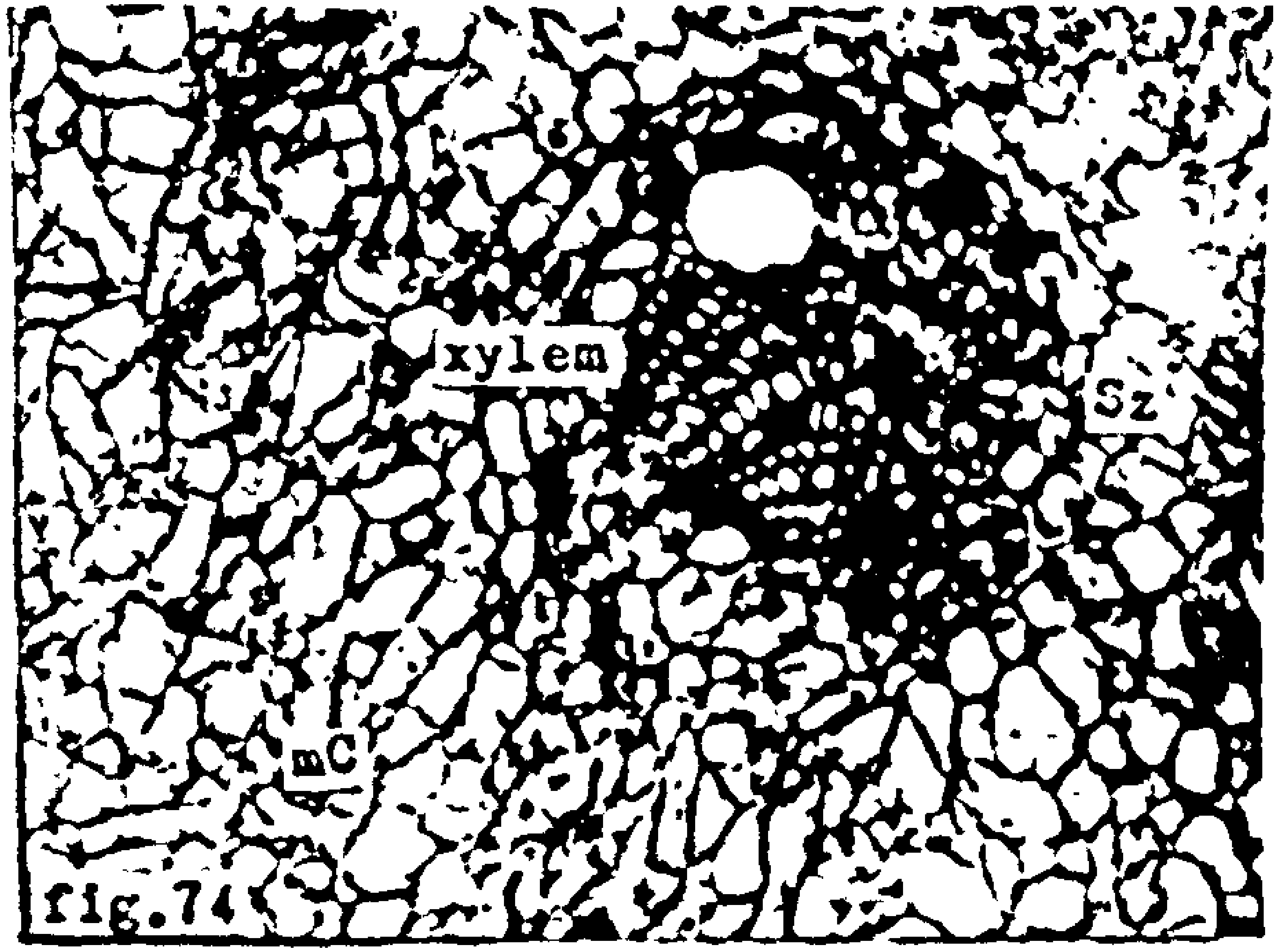


fig.74

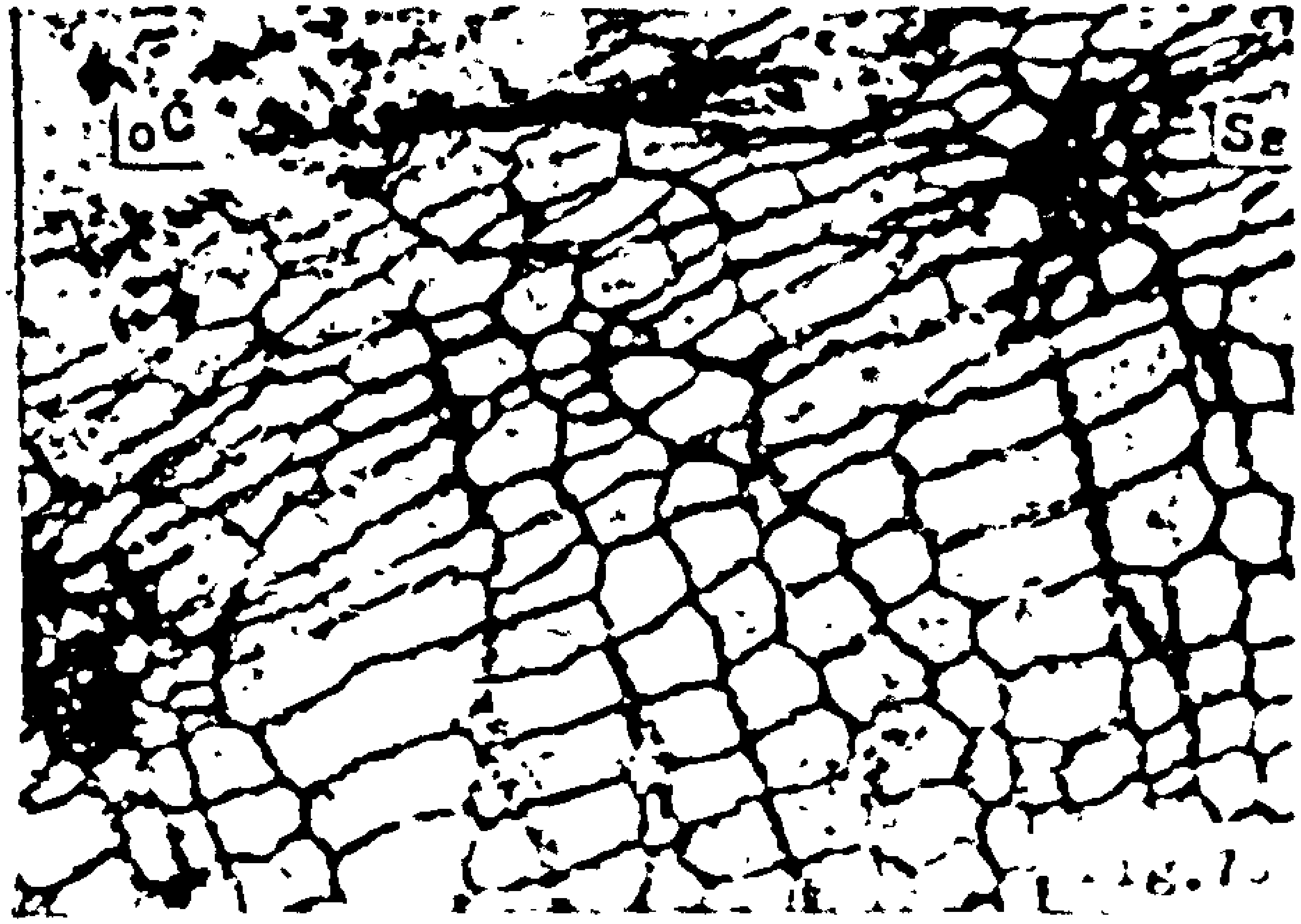


fig.7

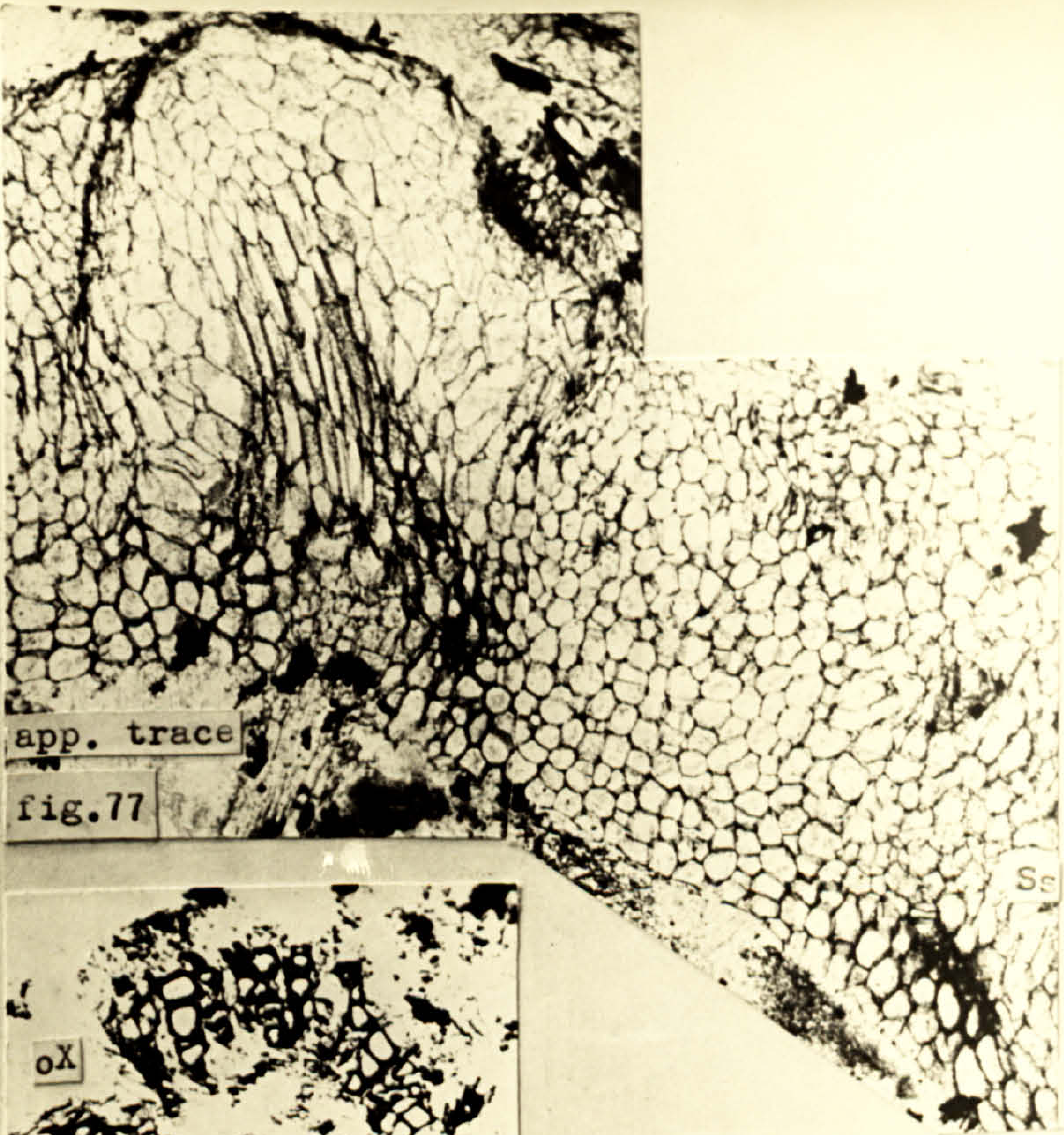


fig.77

fig.77a

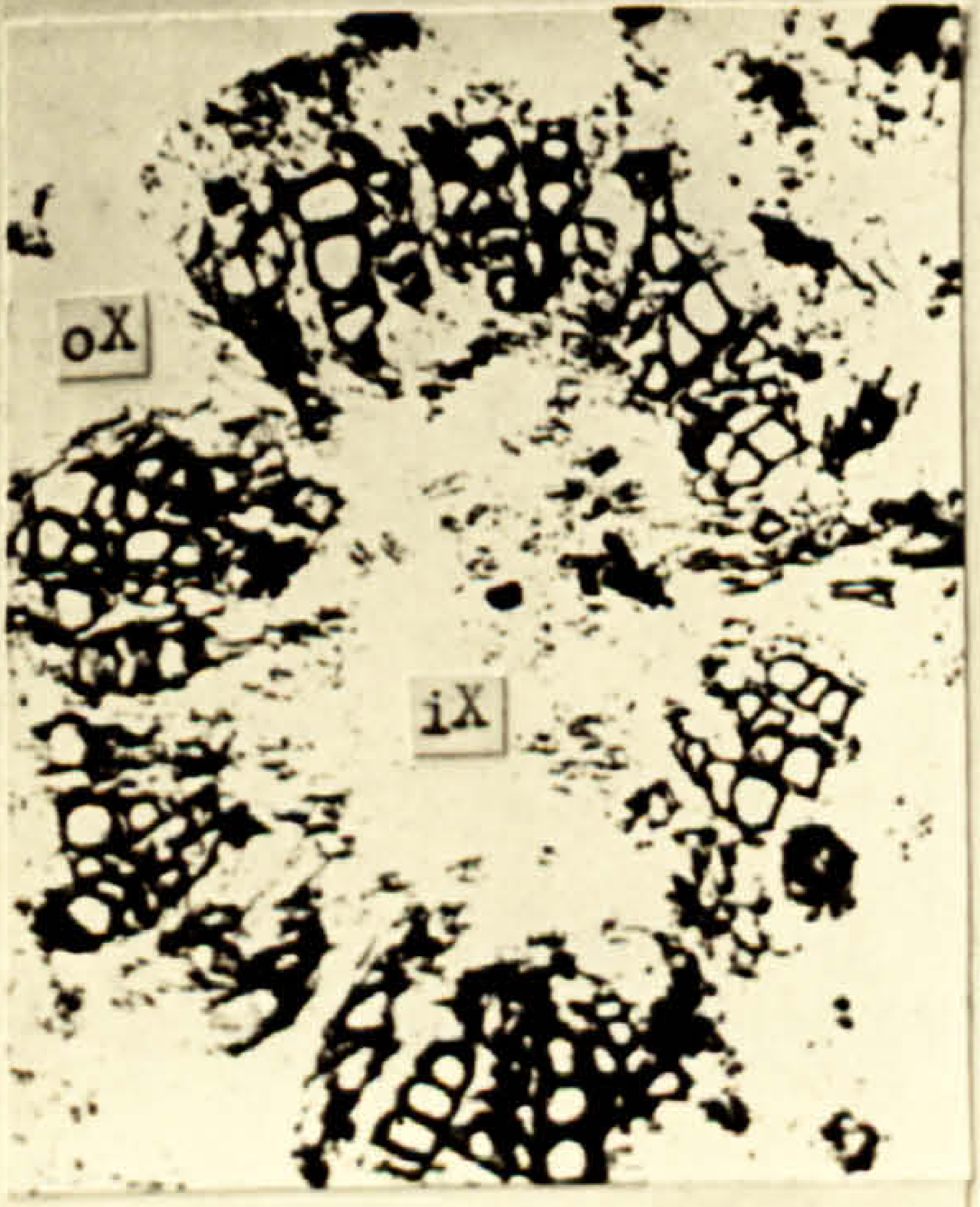


fig.78

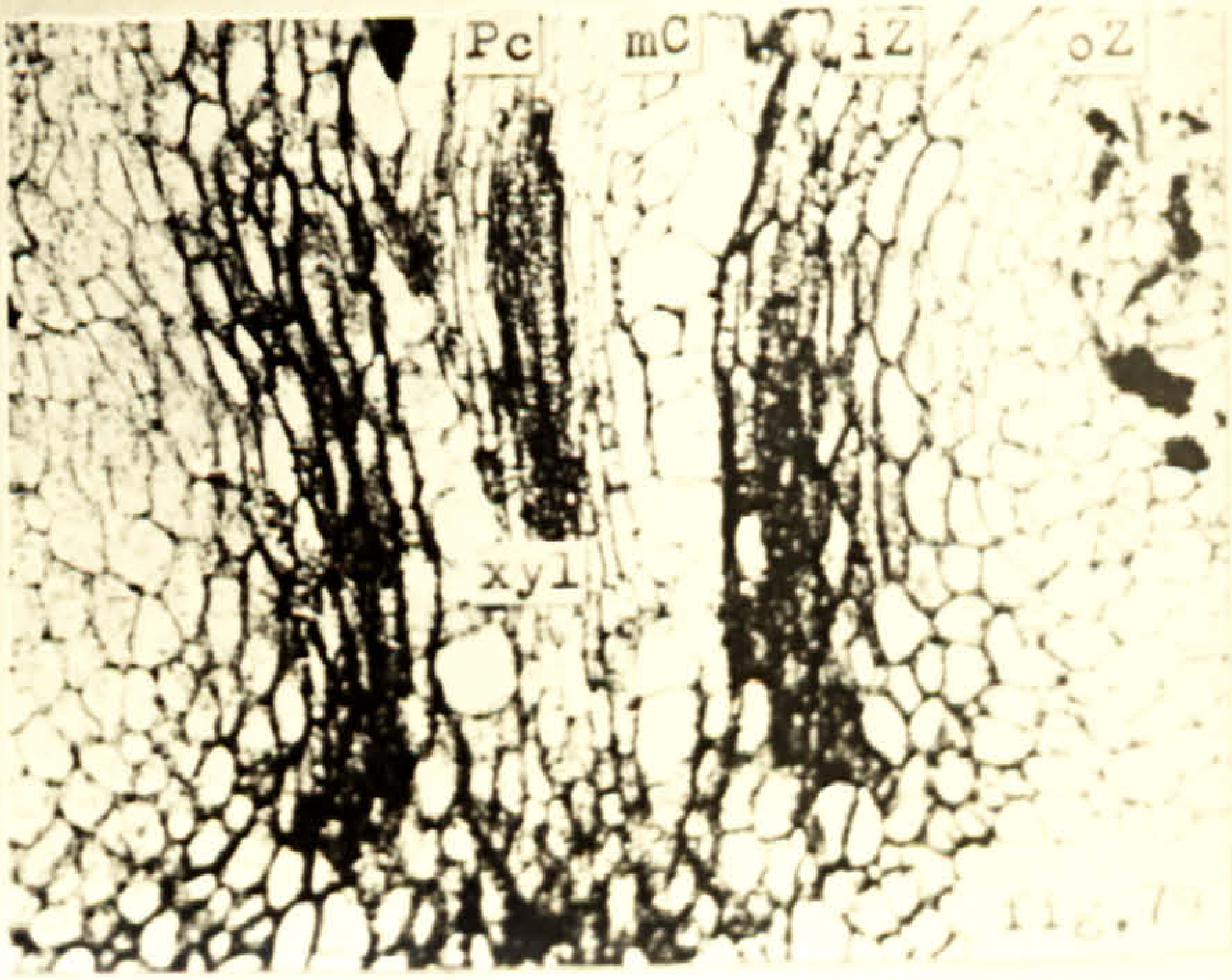


fig.79

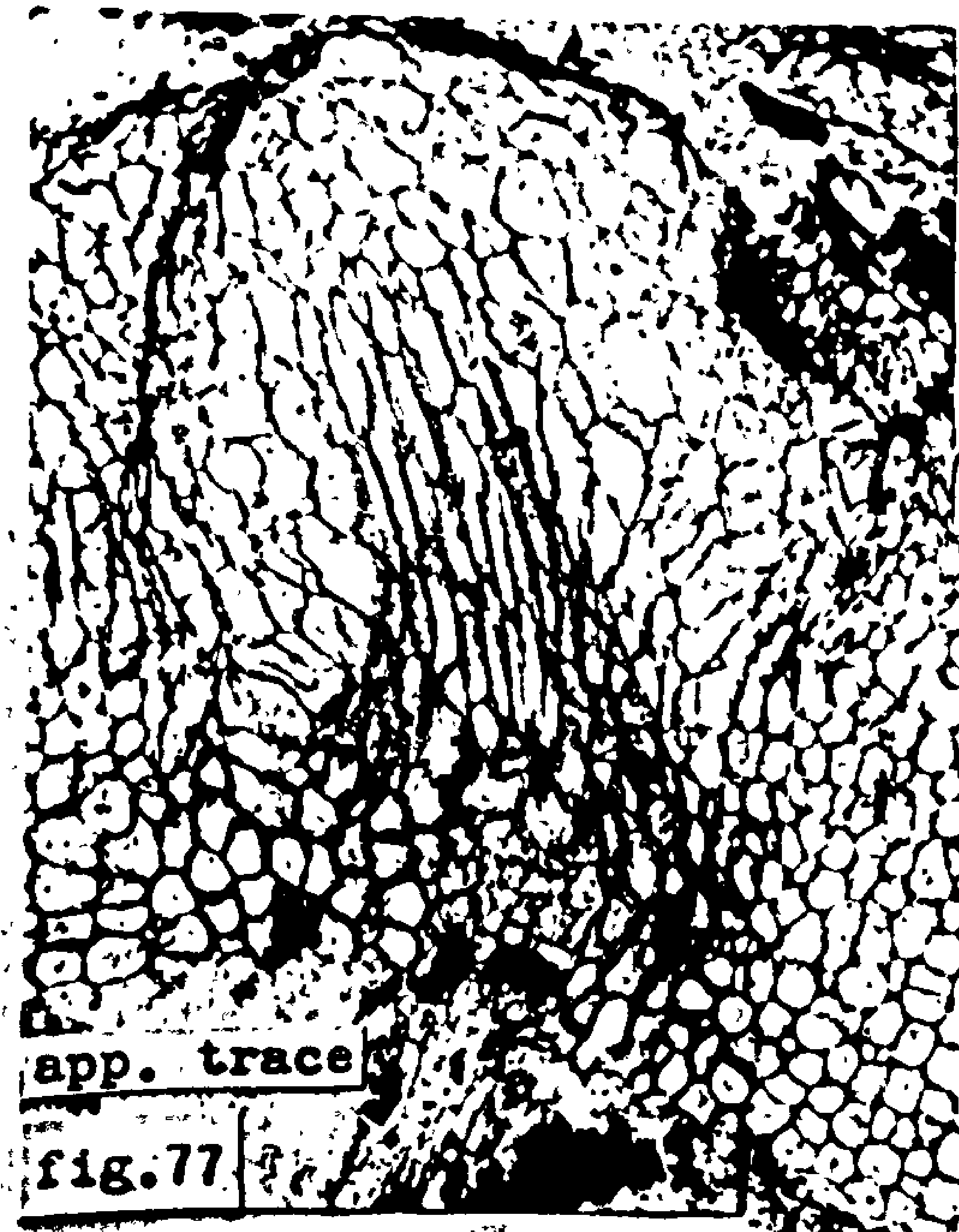


fig.77

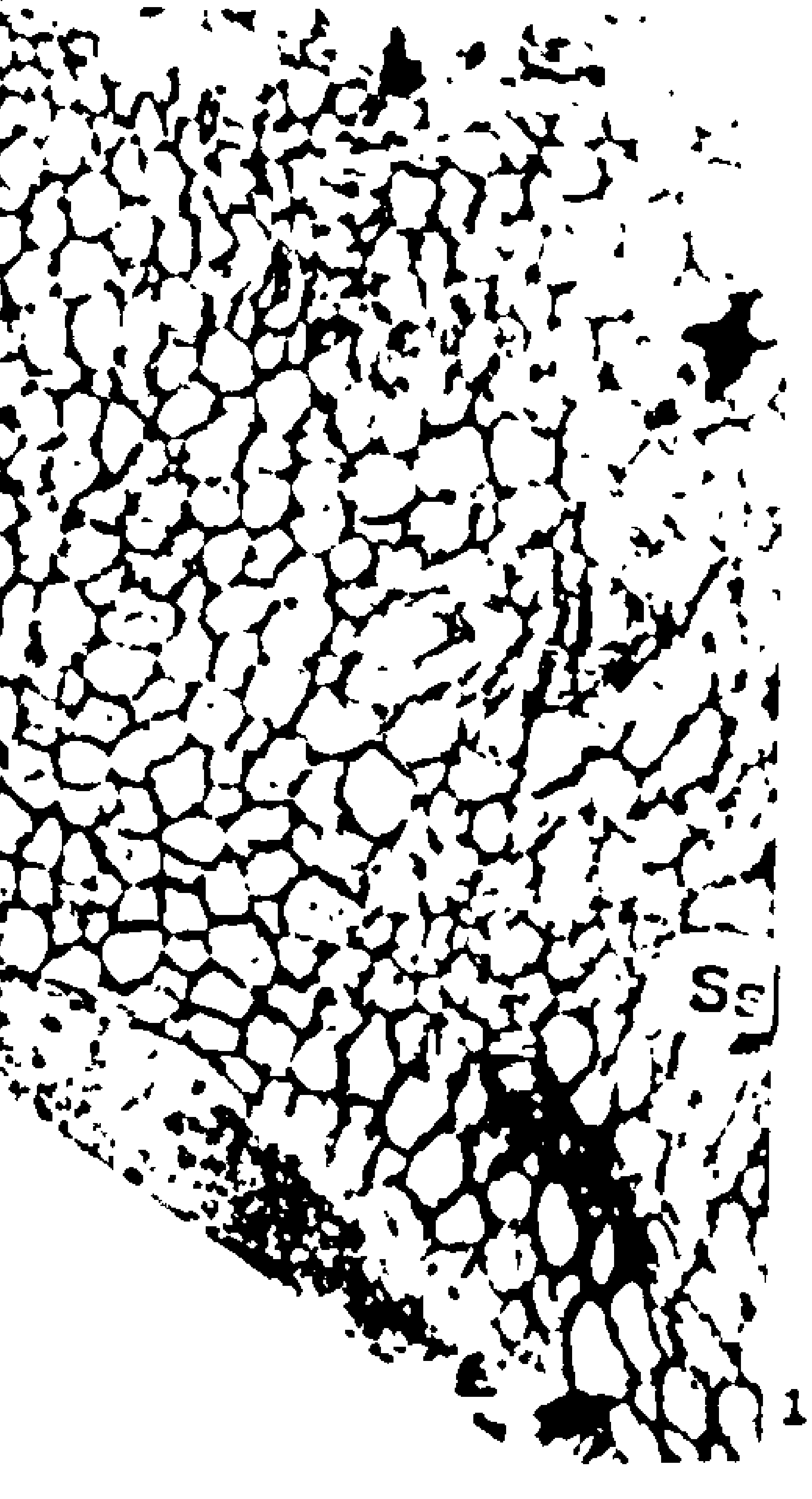


fig.77a

fig.78

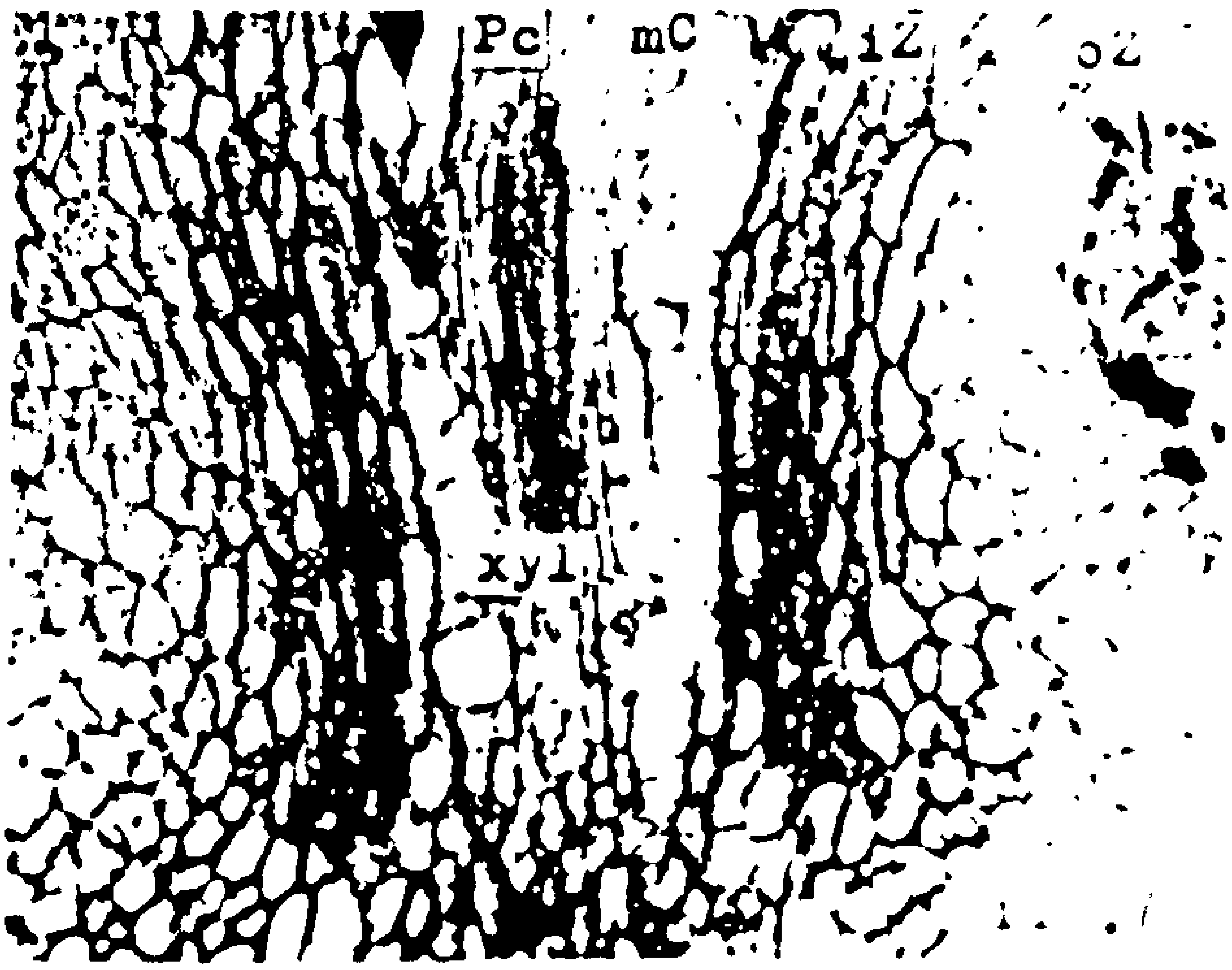


Plate XXI

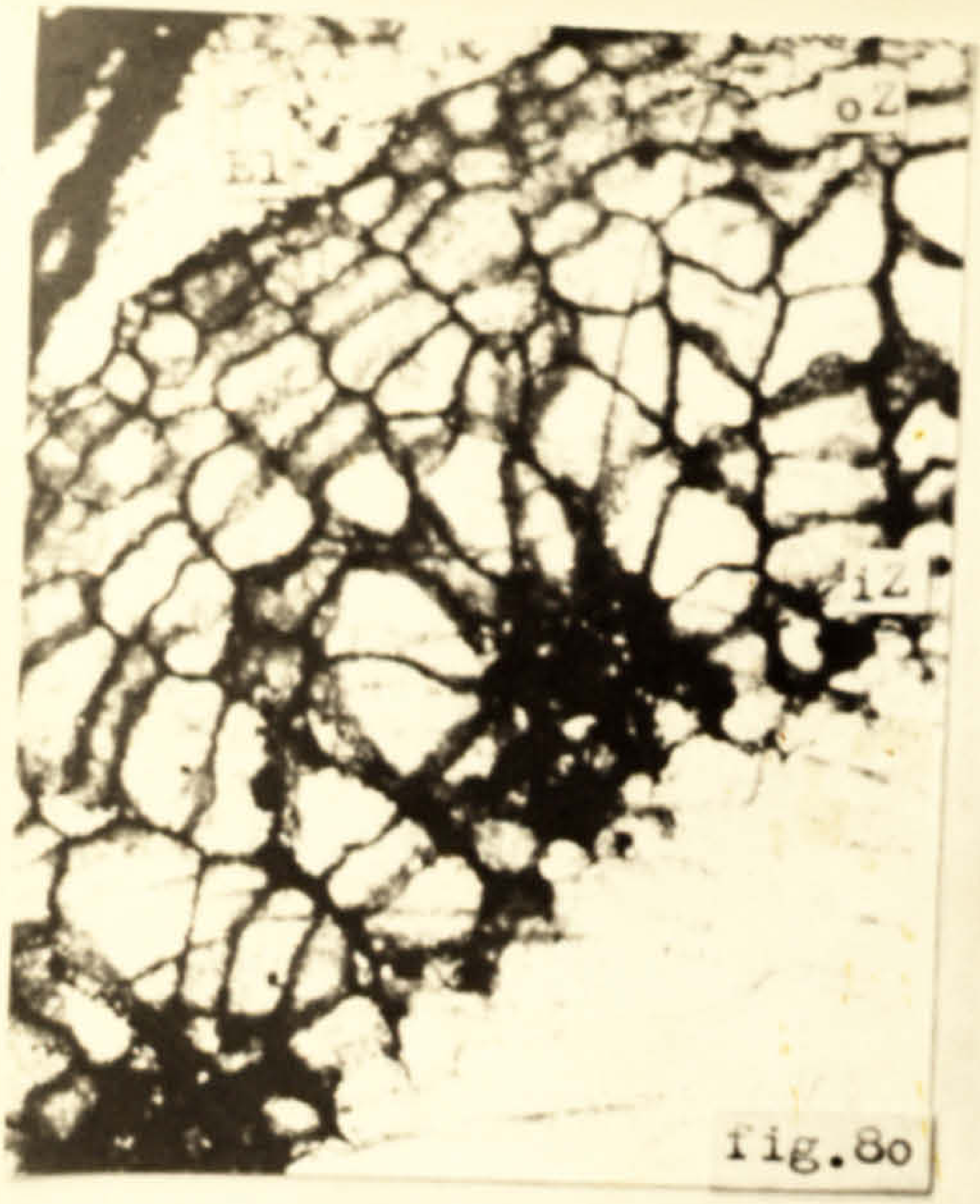


fig.8o

fig.81

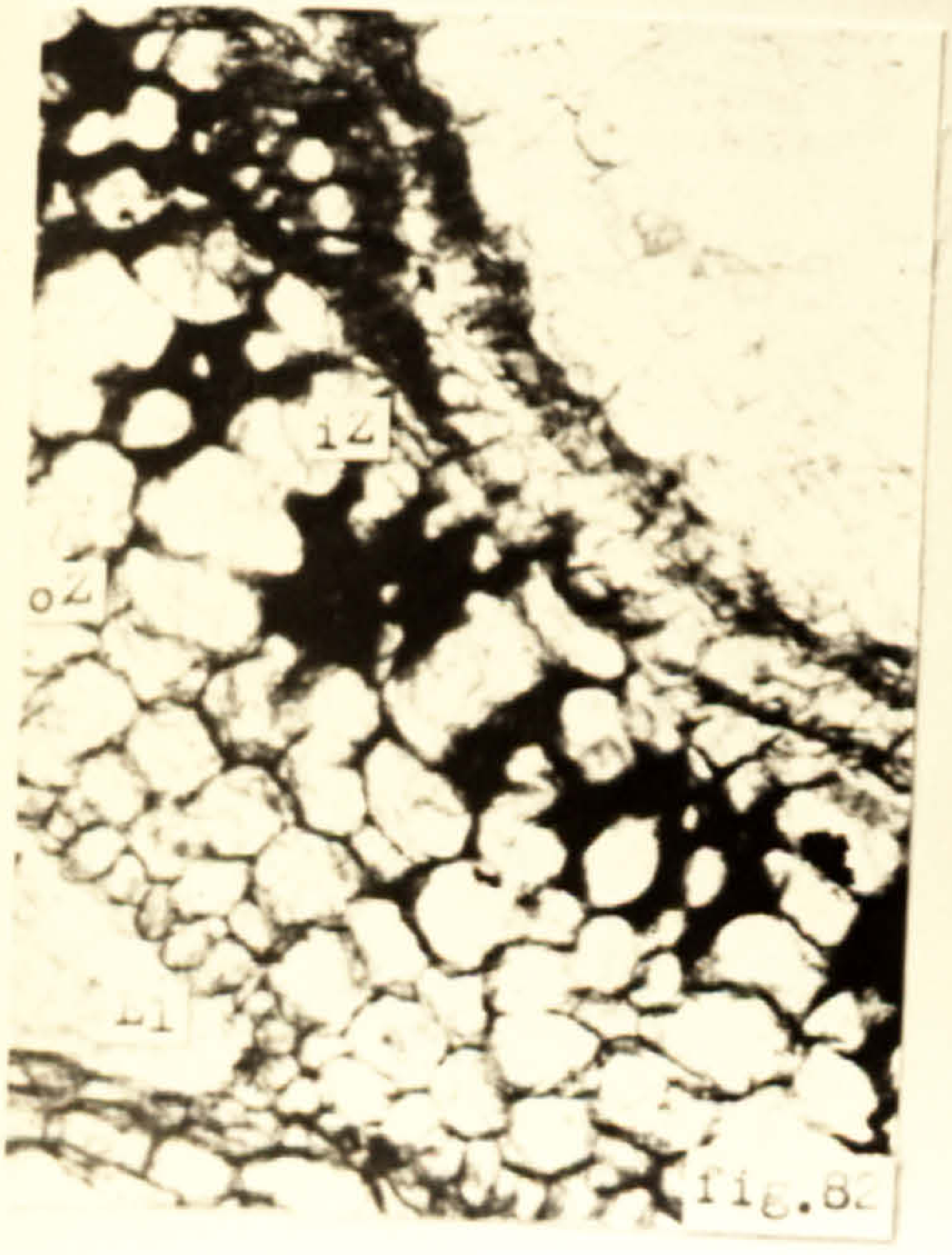


fig.82

fig.83

fig.80

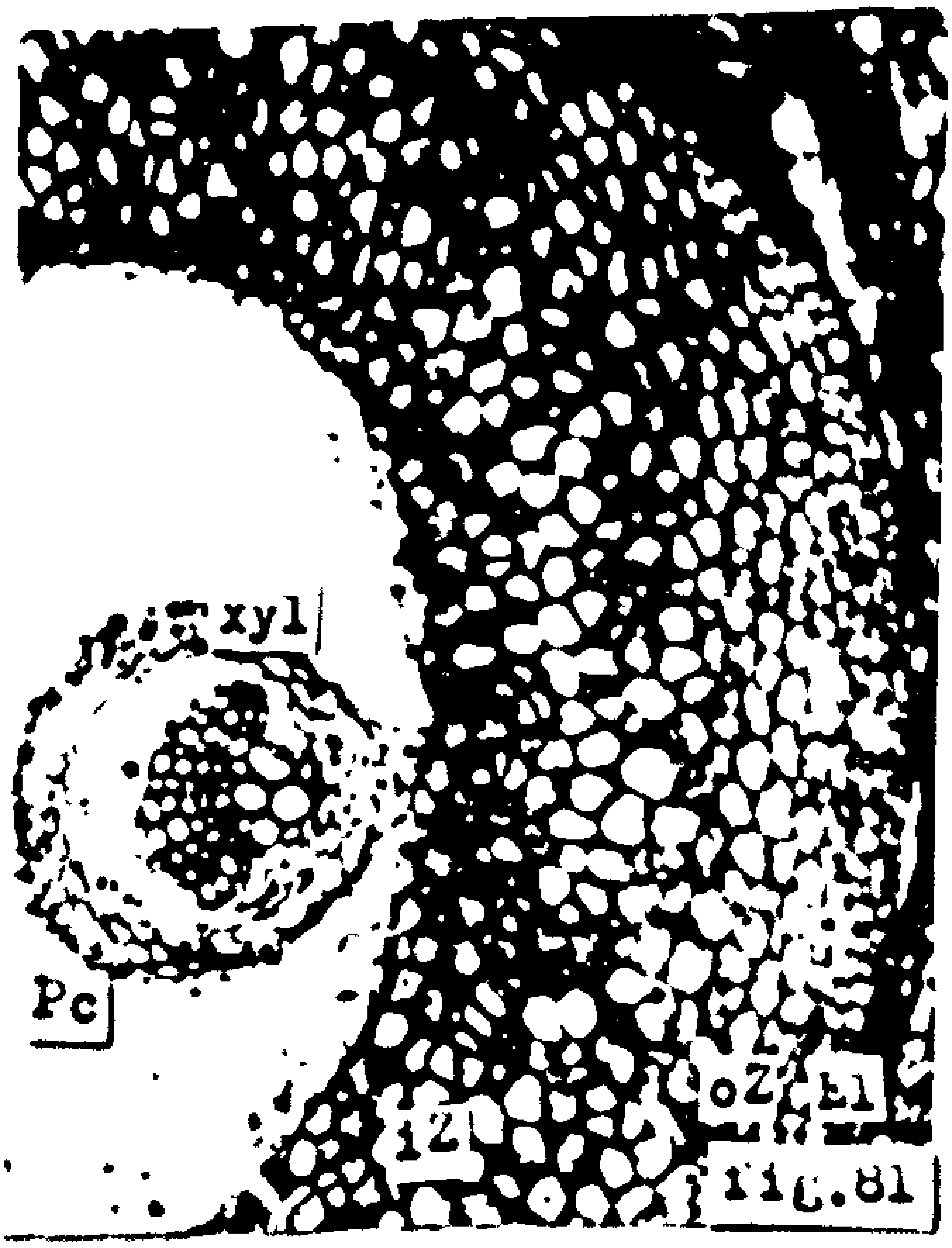


fig.81

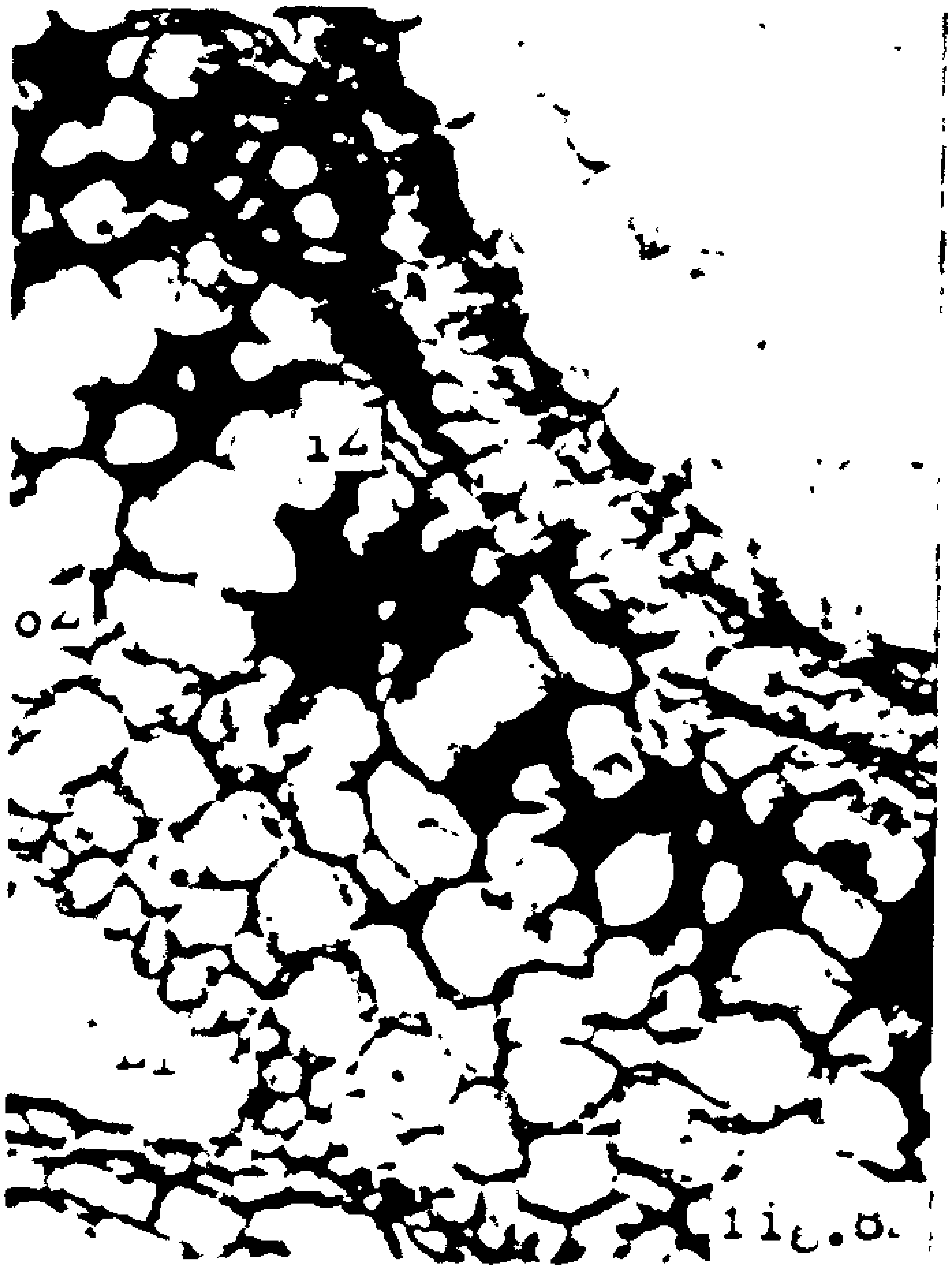


fig.8

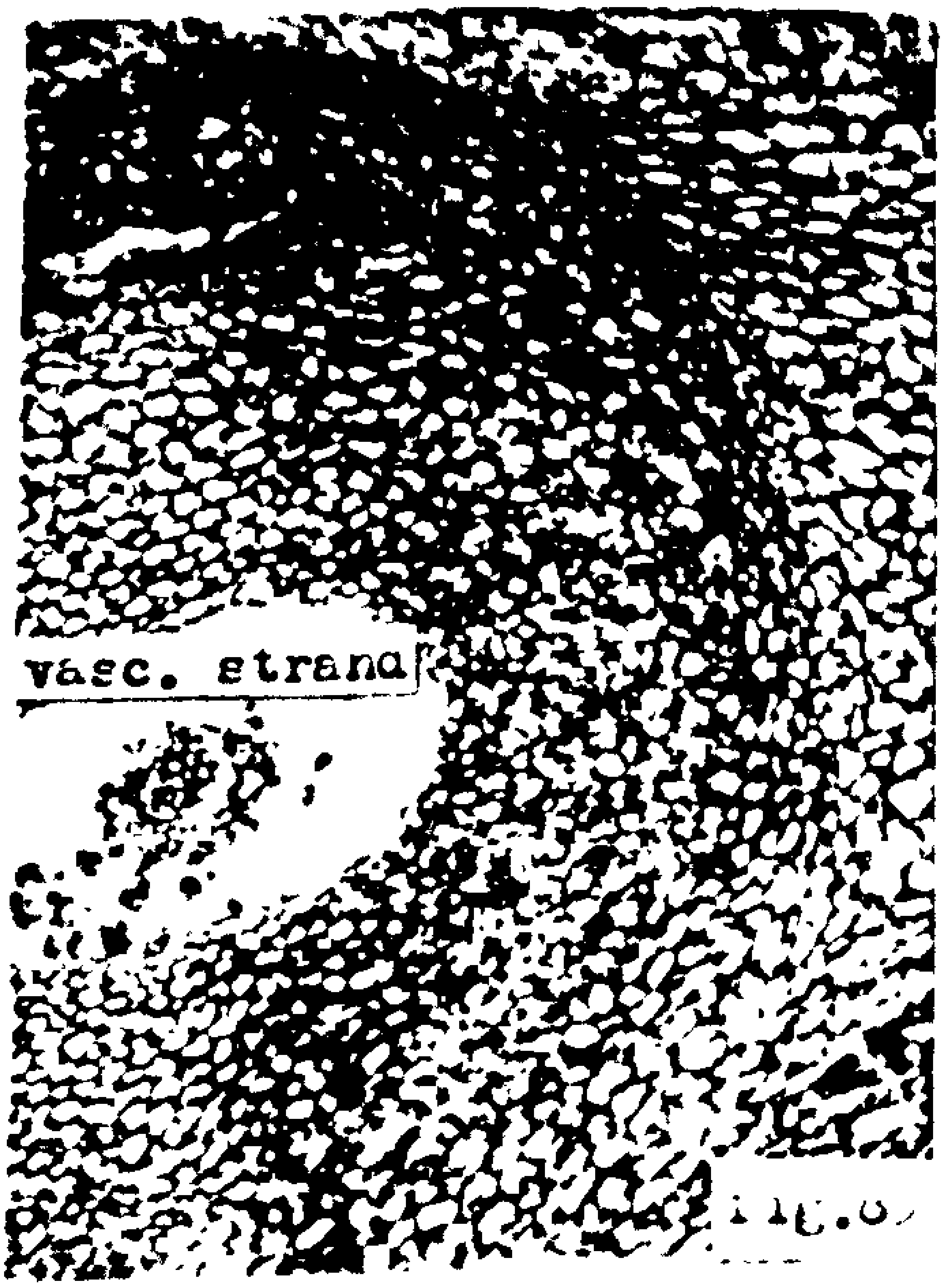


fig.8

Plate XXII

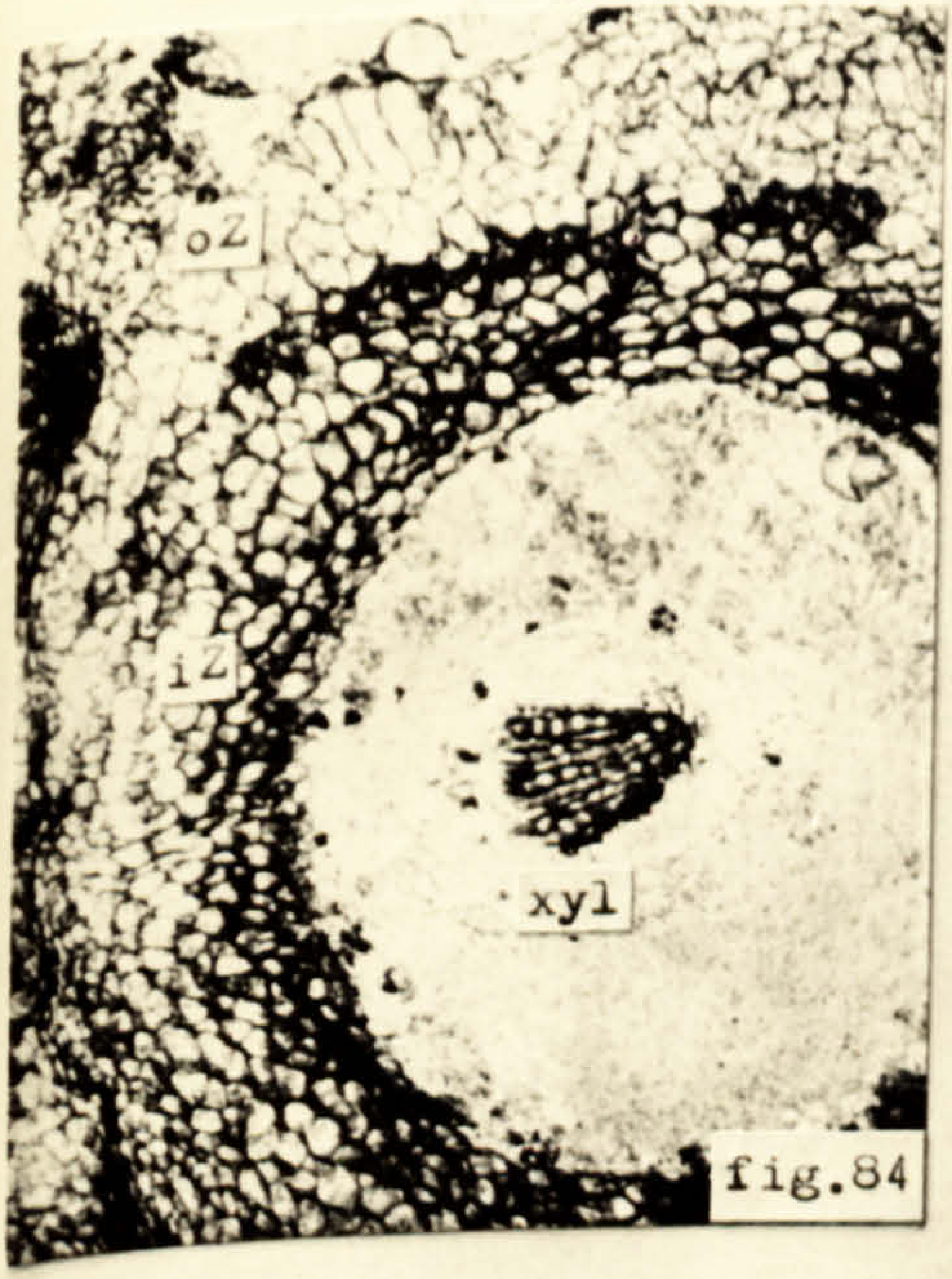


fig.84

fig.85

fig.86

fig.87

Plate XXII

fig.84

fig.85

fig.86

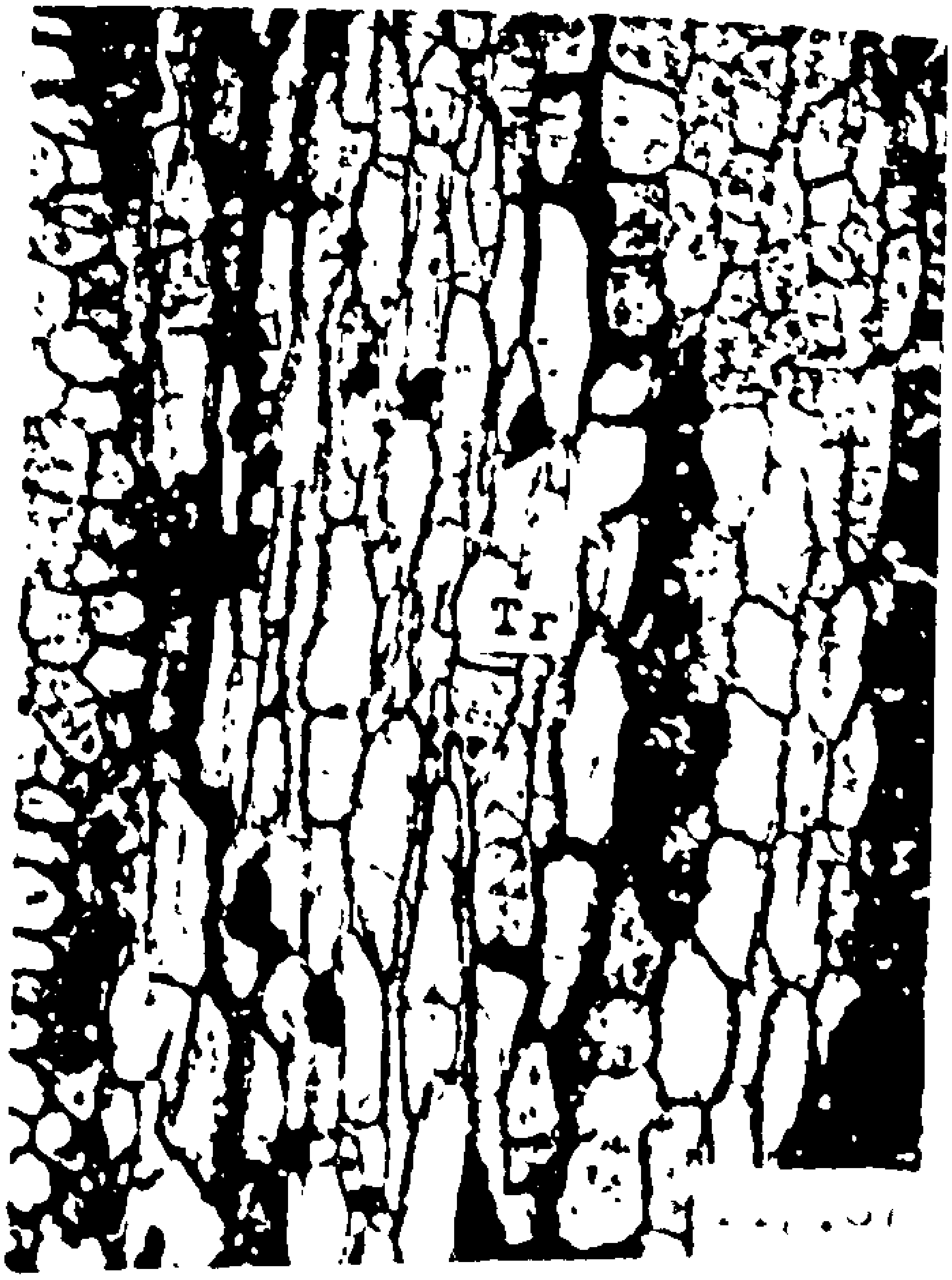


fig.87

Plate XXIII

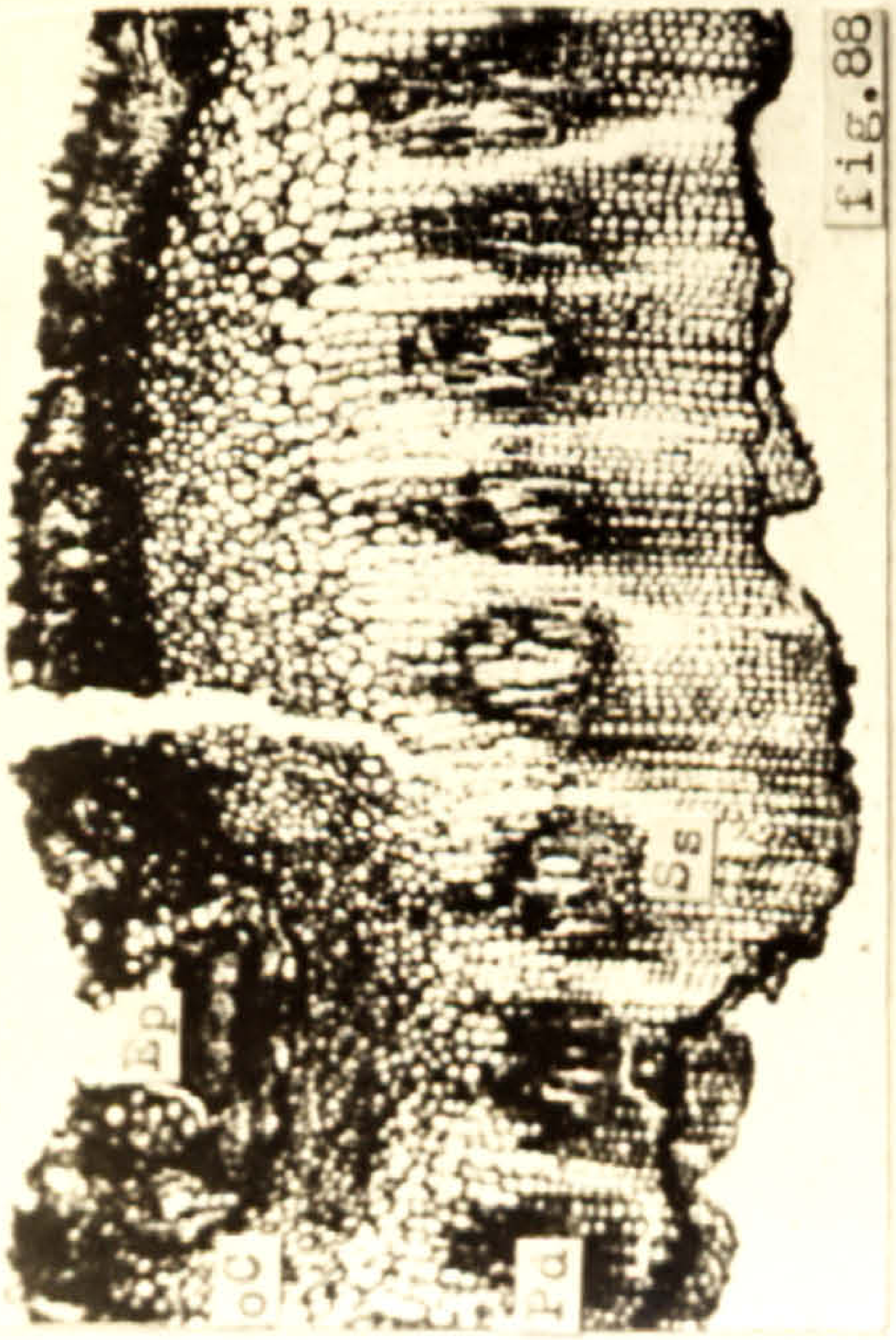


fig.88

88

fig.89

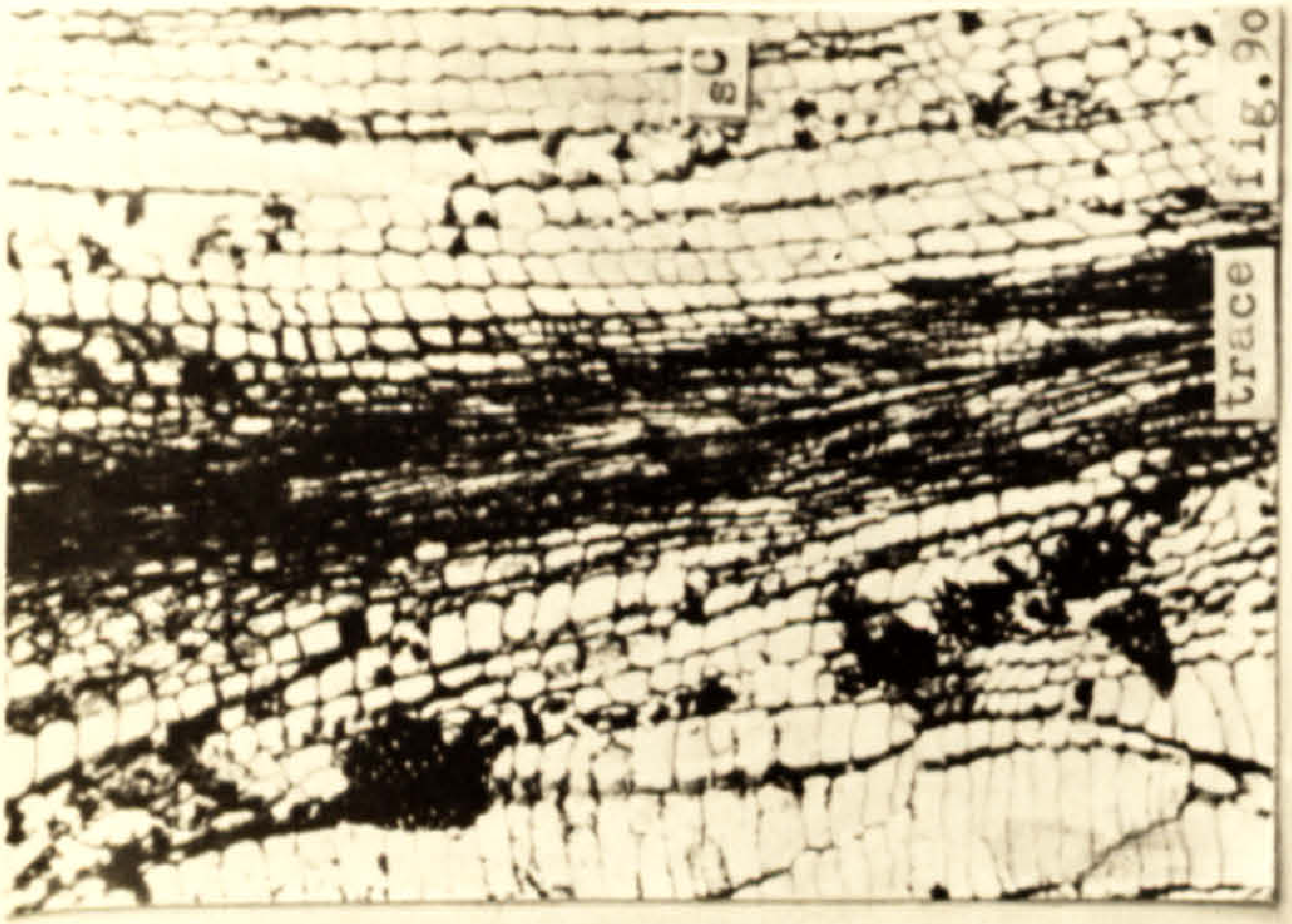


fig.90

90


fig.90


fig.88

88


fig.89

Plate XXIV

fig.91

91

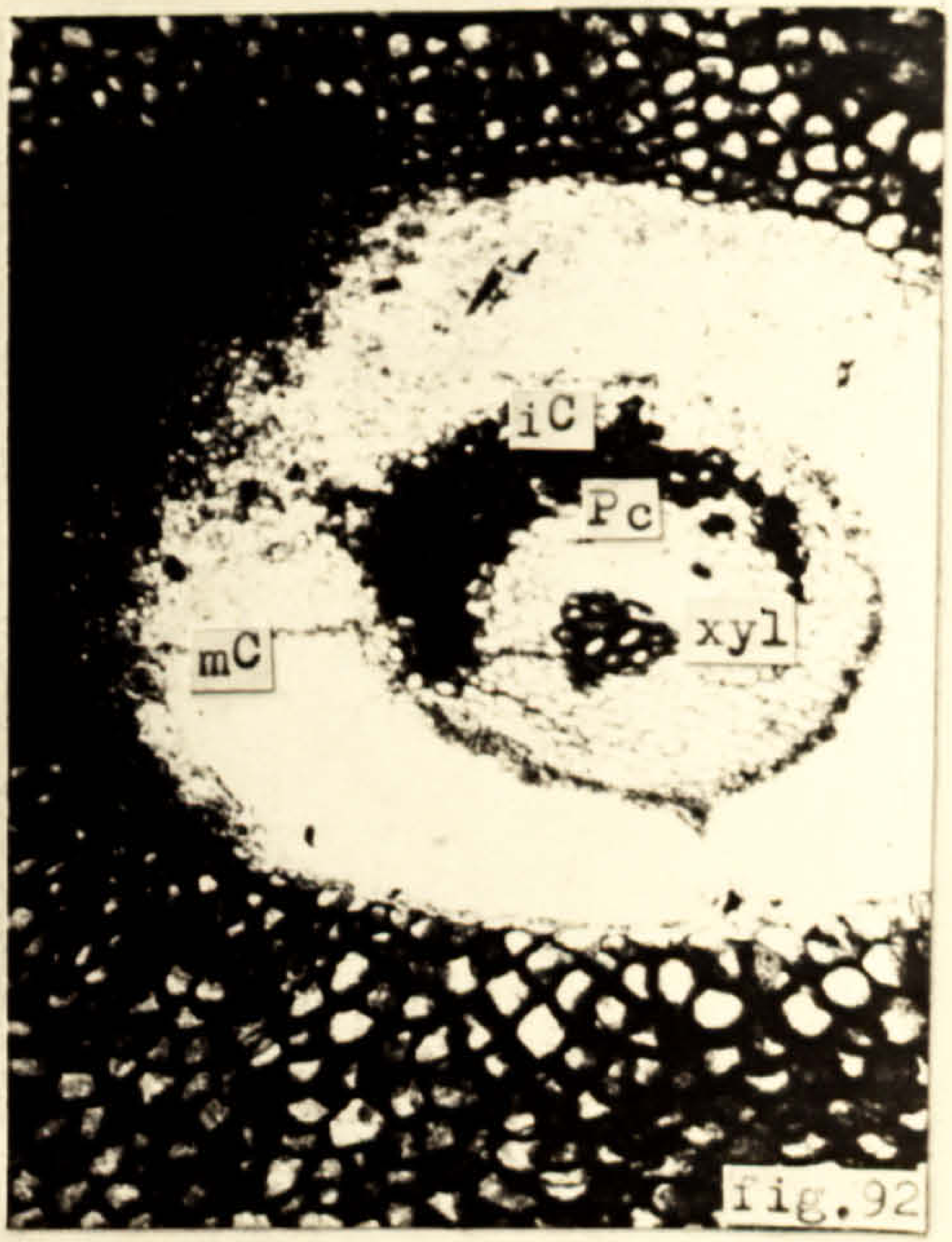


fig.92

92

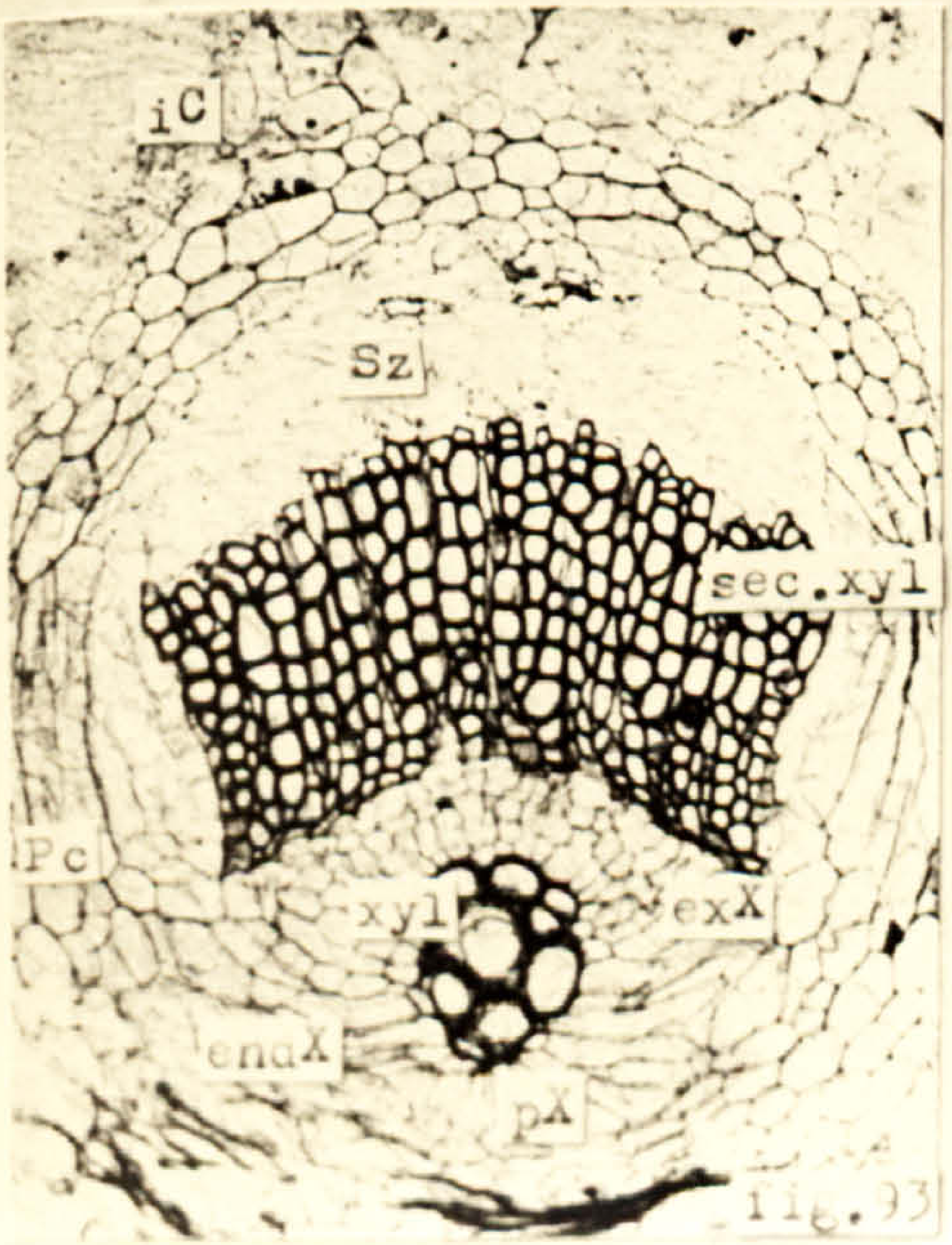


fig.93

fig.94

fig.91

91

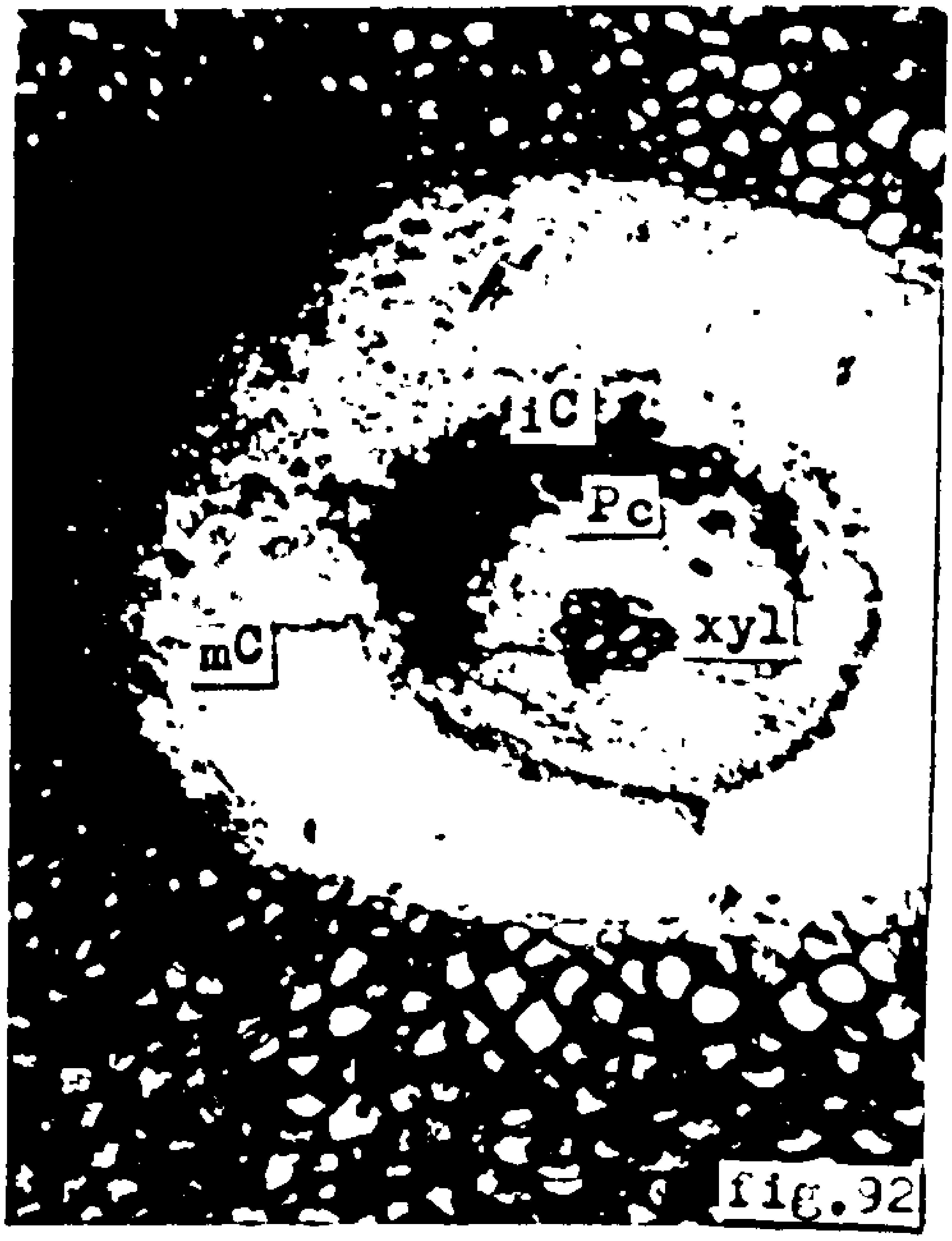


fig.92

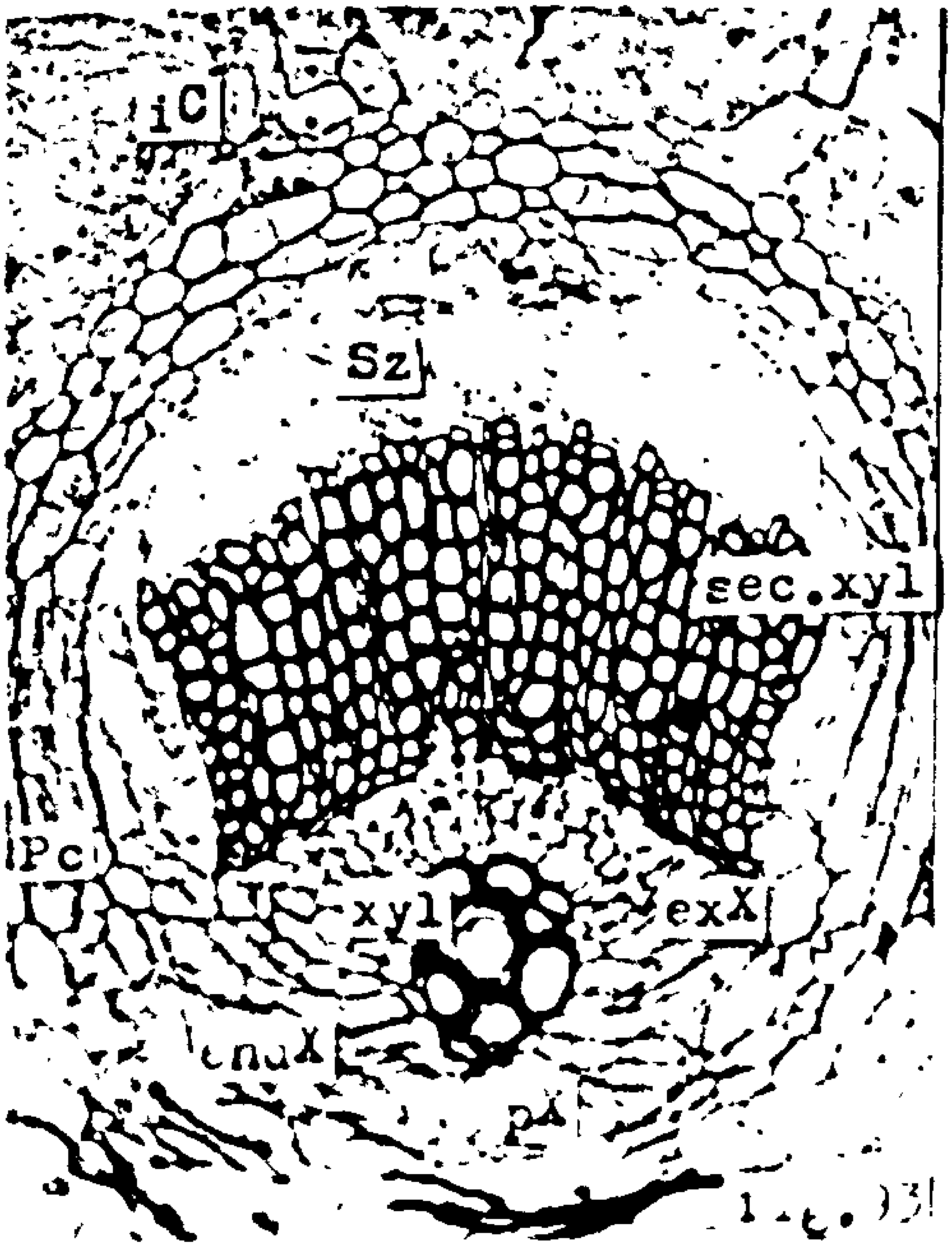


fig.93

fig.94