DOCTOR OF PHILOSOPHY

Studies in the flora of the Rhynie chert

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STUDIES IN THE FLORA OF THE RHYNIE CHERT

A THESIS

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Thanks are further due to every colleague who helped directly or indirectly in private talks.

I owe hearty thanks to my wife and colleague for her continuous help.

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Previous joint publications by the author

1. Said, H., Khalil, M. S., & El-Saadawy, W.
   The vegetative growth and reproduction of Egyptian Onions as influenced by pre-storage at different temperatures.
   Accepted for publication in the Ann; Agric. Sci. of the University of Ain Shams, Faculty of Agriculture, Cairo.
   On 16.7.1960.
2. Said, H., Khalil, M. S., & El-Saadawy, W.
   The metabolism of Egyptian Onions as influenced by pre-storage at different temperatures.
   Accepted for publication in the Ann; Agric. Sci. of the University of Ain Shams, Faculty of Agriculture, Cairo. On 14.2.1962.
3. Youssef, E., & El-Saadawy, W. (1963)
   The effects of 2,4-dichlorophenoxyacetic acid on the absorption and assimilation of Potassium nitrate by Radish root slices.
   J. Bot., U.A.R., Vol. VI, 61-74.
4. Youssef, E., & El-Saadawy, W. (1963)
   Respiration and nitrogen metabolism of Radish root slices as influenced by α-Naphthylacetic acid.
   J. Bot., U.A.R., Vol. VI, 75-84.

The first two publications are parts of my M.Sc. Thesis.
Copies of the latter two publications are enclosed in the back cover of the present Thesis.

ABSTRACT

This work is entirely concerned with the fossil flora of the Rhynie chert bed in Scotland. It falls into three main parts, in which more than 2500 peel-sections were studied.

In the first Part a good deal of information about the morphology of the stems and sporangia of Nothia aphylla is described. This plant was first thought to be "The probable fertile region of Asteroxylon mackiei" but was given the name Nothia aphylla by Lyon (1964) after his discovery of a more probable fertile region of Asteroxylon mackiei. In the conclusion it is suggested that Nothia aphylla should be classified in the family Zosterophyllaceae.

Part II describes two new Horneophyton lignieri fructifications with a more branched columella than previously known. Stomata are also described in the sporangial wall of Horneophyton.

In Part III the results obtained from the study of the vertical succession of plants in a new section (Trench No. 2A) are compared with those obtained previously (1917, 1921) by Kidston & Lang from their study of a vertical section in the original Trench No.1.

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PART III

PREFACE

It is nearly half a century since Kidston and Lang (1917 - 1921) published their well known papers on the fossil flora of the Chert Bed at Rhynie, Aberdeenshire, Scotland (Fig. 1). In their original work, Kidston and Lang described for the first time three extinct genera of primitive Tracheophytes with a total of four species; viz : Rhynia gwynne-vaughani, Rhynia major, Hornea lignieri and Asteroxylon mackiei, as well as various Thallophyta (Algae, Fungi, Bacteria and Nematophyton). Subsequently Barghoorn and Darrah (1938) showed that the name Hornea was invalid, because it was preoccupied by a living member of the Sapindaceae. These authors therefore proposed the genus Horneophyton for the Rhynie plant, by which name it is now known. Kidston and Lang described only the sporophytes of the four mentioned species. To this day gametophytes are not known with certainty, but Lyon (1957) has described germinating spores, while Merker (1958 - 61) and Pant (1960) have made interesting observations and suggestions about possible gametophytes. Lyon's germinating spores were found isolated in a small loose block of Rhynie chert. The spores produced small outgrowths which are supposed to represent early stages in the development of the gametophyte generation of certain Middle Devonian plants. Some of these germinating spores perhaps belong to Rhynia major.

Merker (1958 - 61) suggests that Rhynia rhizomes represent the gametophytic generation and that the aerial parts alone represent the sporophyte. He also believes that the swollen base of Horneophyton reasonably represents the gametophytic generation of this plant.

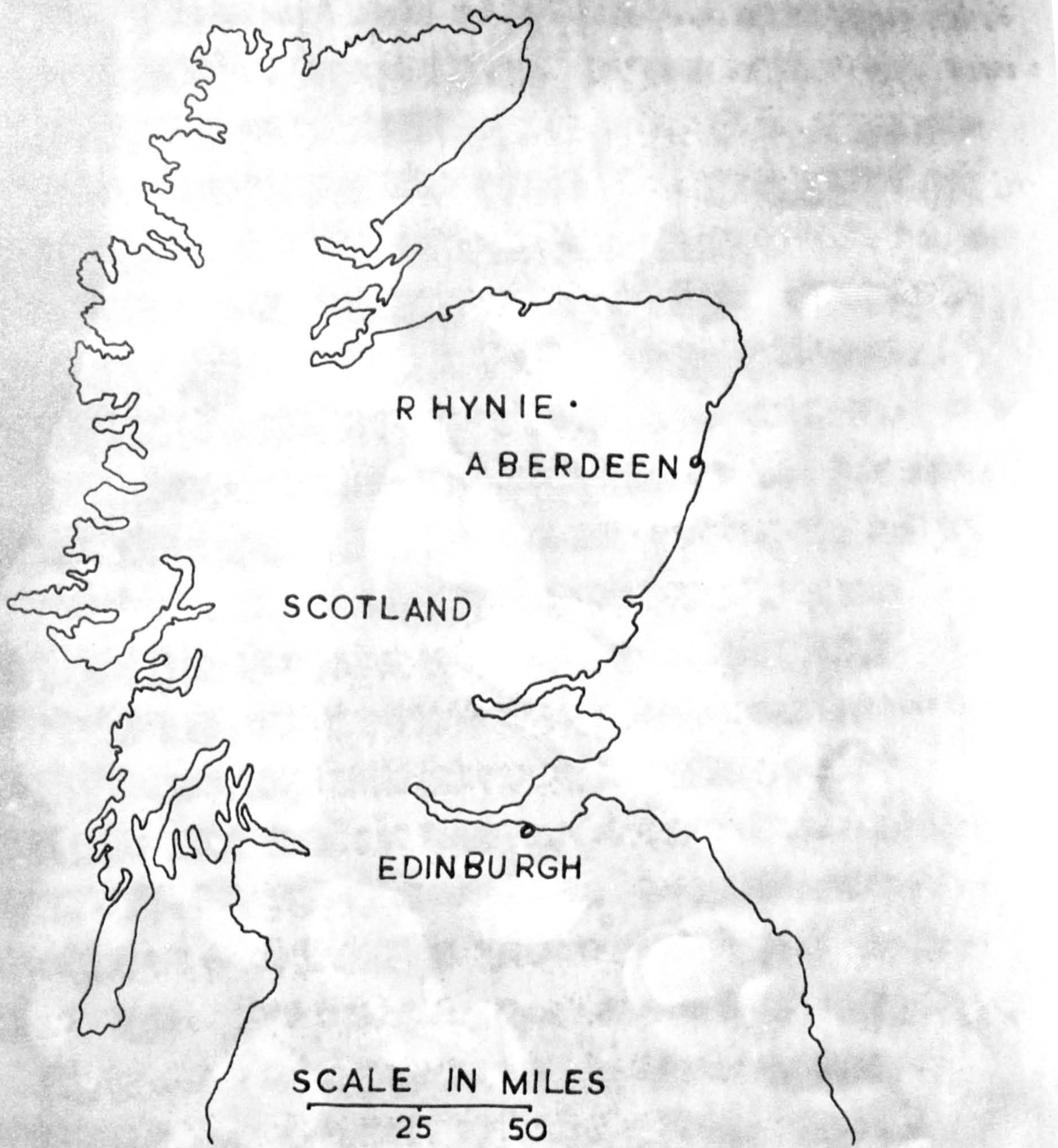


Fig. 1

On the other hand Pant (1960) suggests that the axes of Rhynia gwynne-vaughani are more likely to be gametophytic and that their hemispherical projections and adventitious branches possibly represent young sporophytes developing on these gametophytes.

Neither Merker nor Pant discovered convincing sex organs.

Although Kidston and Lang reconstructed the fertile parts of their four pteridophyte sporophytes, they were uncertain in the case of Asteroxylon mackiei because its sporangia were never found in organic connection with the stems of that plant; the final answer to this was left for future investigators. And indeed, quite recently, Lyon (1964) has described a fertile region from the Rhynie chert which is almost certainly that of Asteroxylon mackiei. Consequently he re-interpreted the previous "possible fertile region of Asteroxylon mackiei", discovered and described by Kidston and Lang (1920), as reproductive portions of an incompletely known, but quite distinct, plant for which he proposed the name Nothia aphylla.

The structure of most of these petrified plants is preserved in great perfection in many cases and Kidston and Lang (1917 - 21) gave a detailed description of almost every part of the sporophyte of each of these four plants. They classified Rhynia and Horneophyton as two related genera in one family, which they called Rhyniaceae. They suggested that Asteroxylon mackiei (until the uncertainty concerning its fertile region is settled) should be put together with Psilophyton princeps in another family to be called Asteroxylaceae, and they established an order of Pteridophyta to hold the two families and named it Psilophytales.

Beside the plants mentioned above the Rhynie chert deposit, up to the moment, has yielded a few more plants and also faunal remains; three blue-green Algae (Langiella scourfieldi, Kidstoniella fritschi, and Rhyniella vermiformis), Croft and George (1959), a nematophytalean (Nematoplexus rhyniensis), Lyon (1961 - 62), a Bryales capsule, Lemoigne (1966), some arachnid remains, Hirst (1923), some arthropod remains and Insecta, Hirst and Maulik (1926) and Tillyard (1928), a Crustacean, Scourfield (1926, 1940) and lung-books of a terrestial Arachnida, Claridge and Lyon (1961).

The age of the chert as Kidston and Lang reported (1917) was found to be "not younger than the Middle Division of the Old Red Sandstone of Scotland" (Middle Devonian). However, Walton (1959) stated without giving references, that recent stratigraphical work in the area has suggested that the chert may be of Lower, rather than of Middle Devonian age. Walton supported this suggestion on fossil plant evidence, namely, (1) the simplicity of the Rhynie chert plants compared to the many highly organized and more complex plants (e.g. Protopteridium, Halle (1936), Schizopodium davidi, Harris (1929), Calamophyton bicephalum, Leclercq and Andrews (1960), Hyenia elegans KrÄusel and Weyland (1926) .... etc.) found elsewhere in the Middle Devonian, and (2) the occurrence of a fragment of Nematophyton in the chert.

The present work deals with the flora of the Rhynie Chert and falls into three main parts. Part I is concerned with the structure and affinity of Lyon's incompletely known plant Nothia aphylla. Part II adds some details to the knowledge of the fertile parts of Horneophyton. Part III deals with the vertical distribution of plants in a new section in the

Rhynie Chert Deposit (Trench No. 2A) and its comparison with the findings of Kidston and Lang (1921) from their study of a vertical section in the original Trench No. 1 (see Fig. 1 of Part III).

PART I

ON THE STRUCTURE OF NOTHIA APHYLLA, LYON

INTRODUCTION.

Kidston and Lang (1920) described peculiar bare axes and small detached and apparently pear-shaped sporangia from two small blocks of chert which were found loose at Rhynie. They assigned both the axes and the sporangia to Asteroxylon mackiei as its possible sporangiophores and sporangia because they found them in close association with the vegetative remains of that plant, which apparently lacked a fertile region in organic connection. However, as already noted, Lyon (1964) has recently described a fertile region which is almost certainly that of Asteroxylon mackiei. Consequent upon this he re-interpreted the small leafless axes and the small sporangia mentioned above, as reproductive portions of an incompletely known, but quite distinct, type of plant for which he proposed the name Nothia aphylla.

The main findings of Kidston and Lang (1920) concerning "the possible fertile region of Asteroxylon mackiei", now Nothia aphylla, came entirely from two small blocks of chert. In one block, they found the small leafless axes associated with rhizomes, stems and leaves of Asteroxylon mackiei. In the other block, which they described as a bedded peat free from sand, they found the leafless axes together with the detached small sporangia, in association with stems and doubtful rhizomes of Asteroxylon mackiei and they found no trace of Rhynia or Horneophyton in this block.

In their diagnosis of Asteroxylon mackiei they stated the following, concerning its probable fertile region (now Nothia aphylla): "it consisted of slender, branched, leafless axes with peculiar structure and pear-shaped

sporangia about 1 mm. long; sporangia with epidermal layer thickened towards the summit, where regular dehiscence took place. Homosporous. Spores developed in tetrads, about 64 μ in diameter". They described and illustrated a good deal of that fertile region, but mainly the axes, because the several sporangia which they found, and of which they illustrated only a few, are more or less imperfect and decayed.

The following are the main features of the axes and the sporangia as reported by Kidston and Lang :-

The axes were of considerable length and branched by repeated dichotomy. The circular outline is only disturbed by contractions during preservation. The epidermis is more or less persistent, smooth and the outer walls of cells are distinctly thickened and covered with cuticle. Stomata with short guard cells and a small pore were found in the epidermis. The cortex is a uniform tissue of parenchymatous cells and is usually perished. The axis stele is either single or paired. The phloem is composed of narrow elongated thin-walled elements. In transverse sections the phloem tends to show small dark triangular markings at the junction of the cells. The phloem is usually collapsed. The xylem tracheids are narrow elongated tubes with pointed ends and brown walls; the thickening of the tracheids is lost or altered by decay and there is a wide range of tracheid diameter.

The arrangement of tissues in the steles of the axes exhibits the following remarkable variety :-

1 A single stele consisting of a solid core of xylem surrounded by phloem.

2 Presence of an island of phloem within the xylem strand.

3 The internal phloem may be continuous with the outer phloem making the cross section of the xylem horse-shoe shaped.

4 Presence of two xylem strands in a common mass of phloem.

5 Presence of two distinct steles within the same cortex.

They also found that some axes had stellate or triangular xylem, with small traces departing from the angles, and they mentioned that these specimens were in the immediate neighbourhood of the small sporangia.

The sporangia were imperfect and decayed and most probably borne on the peculiar axes described above. The sporangial wall is formed of the epidermis and a thick zone of thin-walled cells. The epidermal layer becomes thickened in the upper portion where dehiscence took place at the wider free end and in the immediate neighbourhood of the line of dehiscence the thickened epidermal cells become shallower. Thickening is restricted to the inner and lateral walls of the epidermal cells. There is no definite annulus. Sporangia appear to have been pear-shaped widening out from a thick stalk at the base. Spores were found inside the sporangia and free in the peat; their cuticularised wall is the only part remaining; it has a characteristic yellow colour and shows a trirediate marking.

The comparisons of the axes and the sporangia which Kidston and Lang made with other plants will be referred to in the discussion in Part I of this Thesis.

Since the publications of Kidston and Lang no further work has been done concerning the plant now called Nothia aphylla.

The present study, however, provides a lot more information regarding the structure of Nothia aphylla, particularly the sporangia, whose

connection with the leafless axes is also proved. Furthermore, some of Kidston's and Lang's (1920) figures can now be understood in the light of the new results. Nothia aphylla is compared with other early fossil pteridophytes and with certain living plants and its systematic position considered.

MATERIAL

The specimens forming the basis of the investigation described in Part I and Part II of this Thesis were kindly handed to me by Dr. A. G. Lyon, Botany Department, University College, Cardiff. They consist of 11 blocks of pure chert, carefully selected by Dr. Lyon from his Rhynie Chert collection, which he had accumulated from loose blocks in the locality over a period of more than 10 years.

The numbering of the blocks in Table No. 1 below refers to Dr. Lyon's collection. Dr. Lyon had already made 35 peel-sections from block No. 50 and 37 peels from block No. 56.

The blocks have a clear matrix, and thin dark bedding layers were seen in most of them, separating peat beds. A few sand grains and some little holes were met with in the blocks. Preservation of plant remains is sometimes quite good and there is not much difference in the degree of preservation of plants in all the blocks except in No. 86.

The following Table shows the plant remains that occur in the blocks and the number of peel-sections made from each block.

Table 1

Spg. = Sporangia

Block No.	N.sphylla axes	N.sphylla spg.	A.mackiei stems	A.mackiei spg.	Other plant remains	No. of peels made
50	+	+	-	-	A rhizome with rhizoids, probably of Horneophyton	145
56	+	+	+	-	Stems probably of Rhynia, one with necrosis A rhizome with rhizoids, probably of Rhynia	270
56a	+	+	+	-	Rhizomes probably of Asteroxylon	10
62	+	+	+	+		548
63	+	+	+	-		125
65	+	+	+	+		121
67	+	+	+	+	Rhizomes probably of Asteroxylon (some inside a leafy stem of Asteroxylon) A fragment of Asteroxylon transition region A few fertile specimens of Horneophyton One Rhynia sporangium (ill preserved) A few stems with necrosis .. Rhynia ..? A fragment of a Nematophyton.?	232
68	+	+	+	+	A fragment of Asteroxylon transition region	124
69	+	+	+	+	Rhizomes probably of Asteroxylon A fragment of a Nematophyton.?	132
69a	+	-	+	+	Rhizomes probably of Asteroxylon	21
86A	-	-	+	+		31
86B	-	-	+	+		31
89	+	+	+	-		36
91	+	+	+	-	Rhizomes probably of Asteroxylon	382

The sporangia here referred to Asteroxylon mackiei are of the type described by Lyon (1964), (see Figs. 309 and 310) and, of course, those referred to Nothia are of the type originally described by Kidston and Lang

(1920). 56a is a second face of block 56. 69a is a second face of block 69. Block 86 is in two pieces A and B. It is a small block (Plate 1, Figs. 10 and 11) containing fragments of Asteroxylon stems and sporangia only. In all the other 10 blocks, Nothia axes and sporangia were the main plant remains. Asteroxylon leafy stems, however, were occasionally met with in all the blocks except No. 50. A small number of Asteroxylon sporangia were found in 6 blocks out of the 10 containing Asteroxylon stems. Asteroxylon stems are usually ill preserved; the best being those in the small block No. 86. The other plant remains met with in the blocks and mentioned in the above table are rare. However, it is interesting to note that two of the Hornеophyton fertile specimens found in block No. 67 are rather peculiar, being of a large size and subdivided several times (see Part II, Figs. 1 and 2). Different fungal bodies were found in the tissues of Nothia axes and Asteroxylon stems, but a few were found in the matrix (Figs. 268 - 273).

Plate No. 1 shows a selected peel from every block to give an idea of the relative size of the peels made from the blocks.

The following is an account of the 11 blocks and the plant remains found in them :-

1 - Block No. 50. This was a small block (Plate 1, Fig. 2), about 1 cm. thick of which about 7 mm. was converted to peel-sections. Masses of decayed spores - most probably of Nothia - were met with in the clear matrix. Plant remains are fairly well preserved. The epidermis and the stele (xylem) of Nothia axes are usually persistent, the cortex has usually perished and the phloem is usually ill preserved. About 20

fragments of Nothia axes and more than 30 Nothia sporangia were counted. A rhizome with rhizoids probably of Horneophyton, was found at one edge of the block. No trace of Asteroxylon was found in the peat of this specimen.

2 - Block No. 56. This block was about 2 cm. thick. Of this, about 13.5 mm. was converted to peel-sections. This portion of the block which had been converted to serial peels contained more than 160 Nothia sporangia and about 20 fragments of axes. Preservation of Nothia remains is about the same as in the previous block. Three fragments of Asteroxylon leafy stems were found, all ill-preserved. Some rhizomes - probably belonging to Asteroxylon - were seen penetrating into the peat. A few stems, probably of Rhynia, were found, one of which had a necrosed area. One rhizome with rhizoids, probably of Rhynia was found at one edge of the block.

3 - Block No. 62. This block is completely converted to sections (548 peel-sections and one ground section). It was about 3 cm. thick. Preservation of Nothia remains is good; some axes have the cortex and the phloem more or less well preserved. The epidermis and the xylem are usually persistent. This block contained more than 30 fragments of Nothia axes and about 100 Nothia sporangia. Asteroxylon remains are ill-preserved; they are 5 fragments of leafy shoots and 8 sporangia. The widest axis of Nothia was found in this block (Fig. 76).

4 - Block No. 63. This was about 3 cm. thick, of which only about 6 mm. was converted to peel-sections. About 20 axes and 15 sporangia of Nothia were counted. The outlines of many axes are ill-defined. Three Asteroxylon stems were found; all are ill-preserved, except for two well-preserved stellate steles.

5 - Block No. 65. The thickness of this block was about 2 cm. Of this about 6 mm. was converted to serial peel-sections. One hundred or more fragments of Nothia axes and about 30 sporangia were counted. Preservation is fairly good. Asteroxylon remains are; 6 stems and 10 sporangia, all ill-preserved. One Asteroxylon transition region was found. A few stems, probably, of Rhynia were seen at one edge of the block.

6 - Block No. 67. This was the largest block (Plate 1, Fig. 7). Its thickness was about 3 cm., of which about 11.5 mm. was converted to sections. Preservation of Nothia remains is fairly good but Asteroxylon remains are poorly preserved. The plant remains met with are :

About 100 fragments of Nothia axes and at least 25 of its sporangia.

5 fragments of Asteroxylon leafy stems and 3 of its sporangia.

A few Asteroxylon transition regions with scale leaves.

Several rhizomes, most probably of Asteroxylon.

3 Horneophyton fertile specimens.

Some small stems, probably of Rhynia, one of which had a necrosed area, all found at one edge of the block.

One ill-preserved Rhynia sporangium.

Fragments of Nematophyton.?

7 - Block No. 68. This block was about 1 cm. thick, of which 6 mm. was converted to serial peels. Preservation of plant remains is fairly good. About 50 Nothia axes and 15 sporangia were counted. Masses of spores, probably of Nothia, were seen in the clear matrix. Four Asteroxylon sporangia and five of its leafy stems were found together with one transition region and a doubtful rhizome, all poorly preserved.

8 - Block No. 69. This block was about 3 cm. thick, of which 7.5 mm. was converted to peel-sections (from two faces of the block). Asteroxylon remains occupied most of the block. They are : 7 stems, 4 sporangia and several ? rhizomes. More than 20 Nothia axes were found. Nothia sporangia are quite few in number compared with other blocks and most of them were very small and ill-preserved. Spores, probably of Nothia, were seen scattered in the matrix and some are in masses. A fragment of ? Nematophyton was found.

9 - Block No. 86. This was the smallest block, about 1 cm. thick. It is in two pieces A and B. No trace of Nothia was found in its peat. Only 31 sections were made from each of the two pieces of the block. Five well-preserved Asteroxylon leafy stems were found, together with one sporangium. All tissues of the stems are fairly well-preserved.

10 - Block No. 89. Only 36 peel-sections were made from this small block. Plant remains are fairly well-preserved. More than 20 Nothia axes and about 15 Nothia sporangia were found, together with one stem of Asteroxylon.

11 - Block No. 91. This block, originally about 2 cm. thick, also is completely converted to serial sections (382 peel-sections and one ground section). A few ground sections were also made from small chips which came off from this block during grinding. Preservation is quite good. About 40 Nothia axes and more than 150 Nothia sporangia were found. Four ill-preserved Asteroxylon shoots were found, together with some doubtful rhizomes of Asteroxylon.

This account shows that may hundreds of Nothia axes and sporangia were found in the blocks. About 120 of these sporangia are shown on their axes (see reconstructions on Plate 24, Figs. 106 - 124).

Blocks No. 62 and 91 are the only two blocks which are completely converted to serial peel-sections. From these two blocks most of the reconstructions of Nothia were prepared. After making 548 peels from block No. 62 and 382 peels from block No. 91, these two blocks became thin and unsuitable for preparing more peels and a ground section was prepared from each of them. Other ground sections were also prepared from small bits of rock that inevitably came off from the blocks during the grinding. These small specimens were mounted on bifacial slides of the type described by Sims and Lyon (1963).

Although the ground-sections that were prepared are quite few in number, yet they are of interest and worth mentioning because they showed portions of Nothia sporangia in their entirety, as three-dimensional objects which could never be achieved by the very think peel-sections.

EXPLANATION OF PLATES

All Figs. are from untouched photographs (except line drawings).

All photographs are taken by reflected light from peels except when otherwise mentioned.

Detailed explanations are in text.

Plate 1

Selected peels from the eleven blocks. All Nat. size.

Fig. 2: Block No. 50, peel No. 100

Fig. 3: " " 56 " " 84.

Fig. 4: " " 62 " " 42.

Fig. 5: " " 63 " " 116.

Fig. 6: " " 65 " " 42.

Fig. 7: " " 67 " " 50.

Fig. 8: " " 68 " " 53.

Fig. 9: " " 69 " " 50.

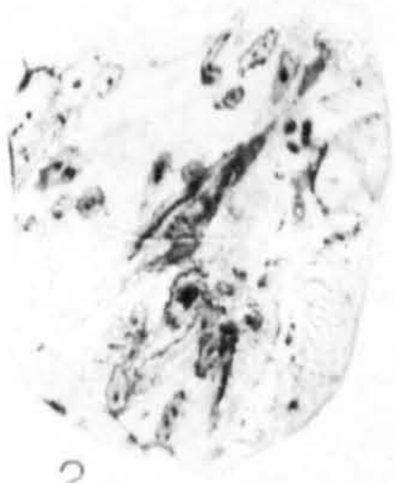
Fig. 10: " " 86A " " 13.

Fig. 11: " " 86B " " 28.

Fig. 12: " " 89 " " 23.

Fig. 13: " " 91 " " 98.

Plate 1



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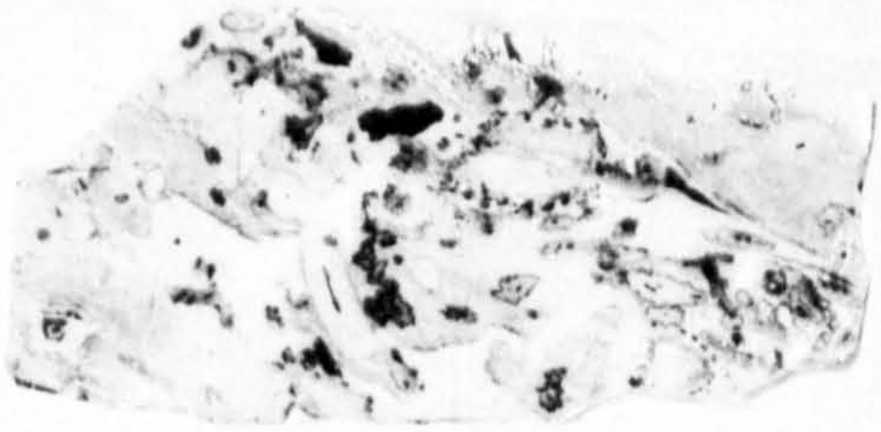

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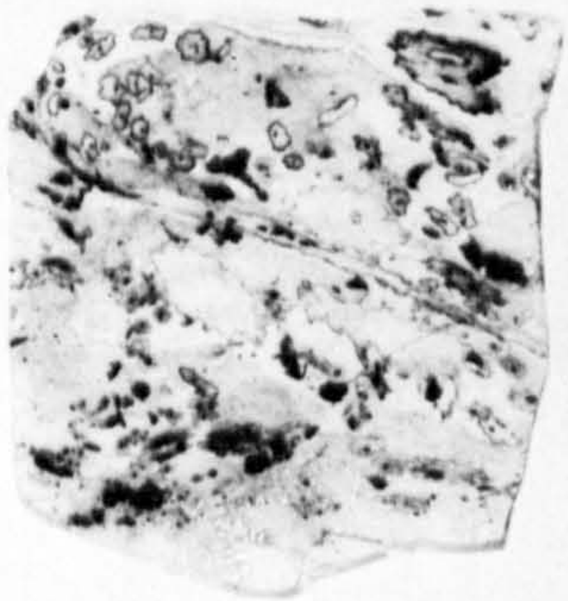

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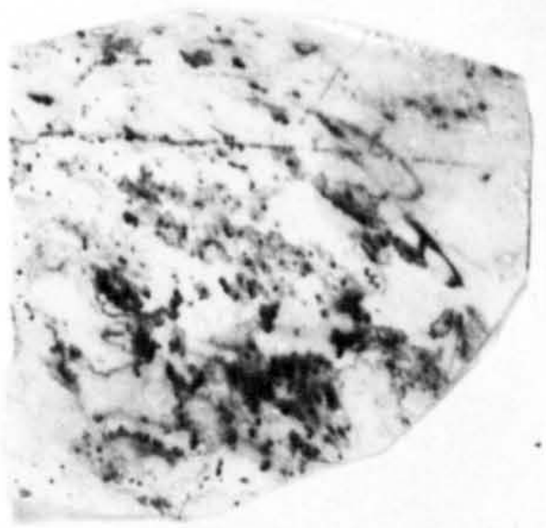

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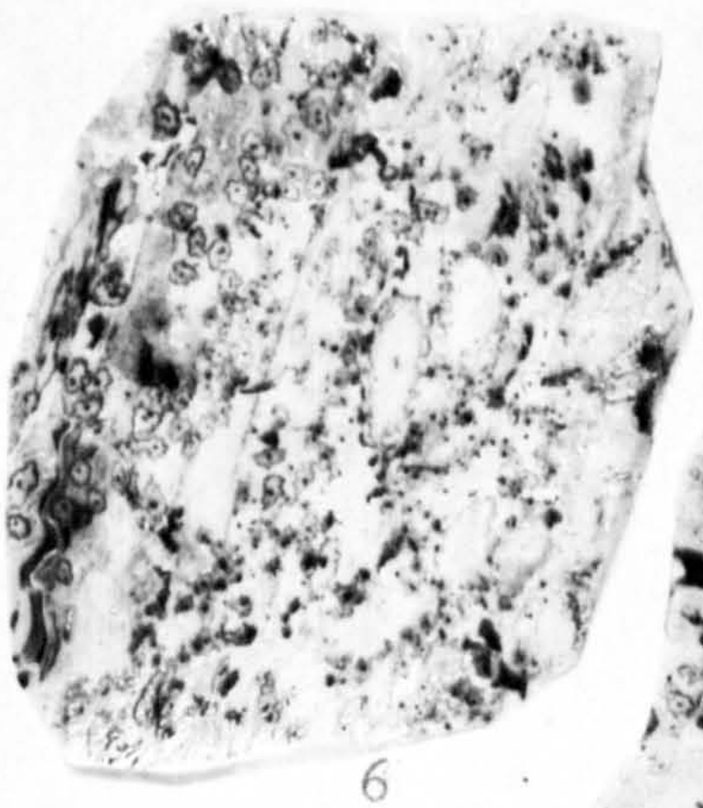

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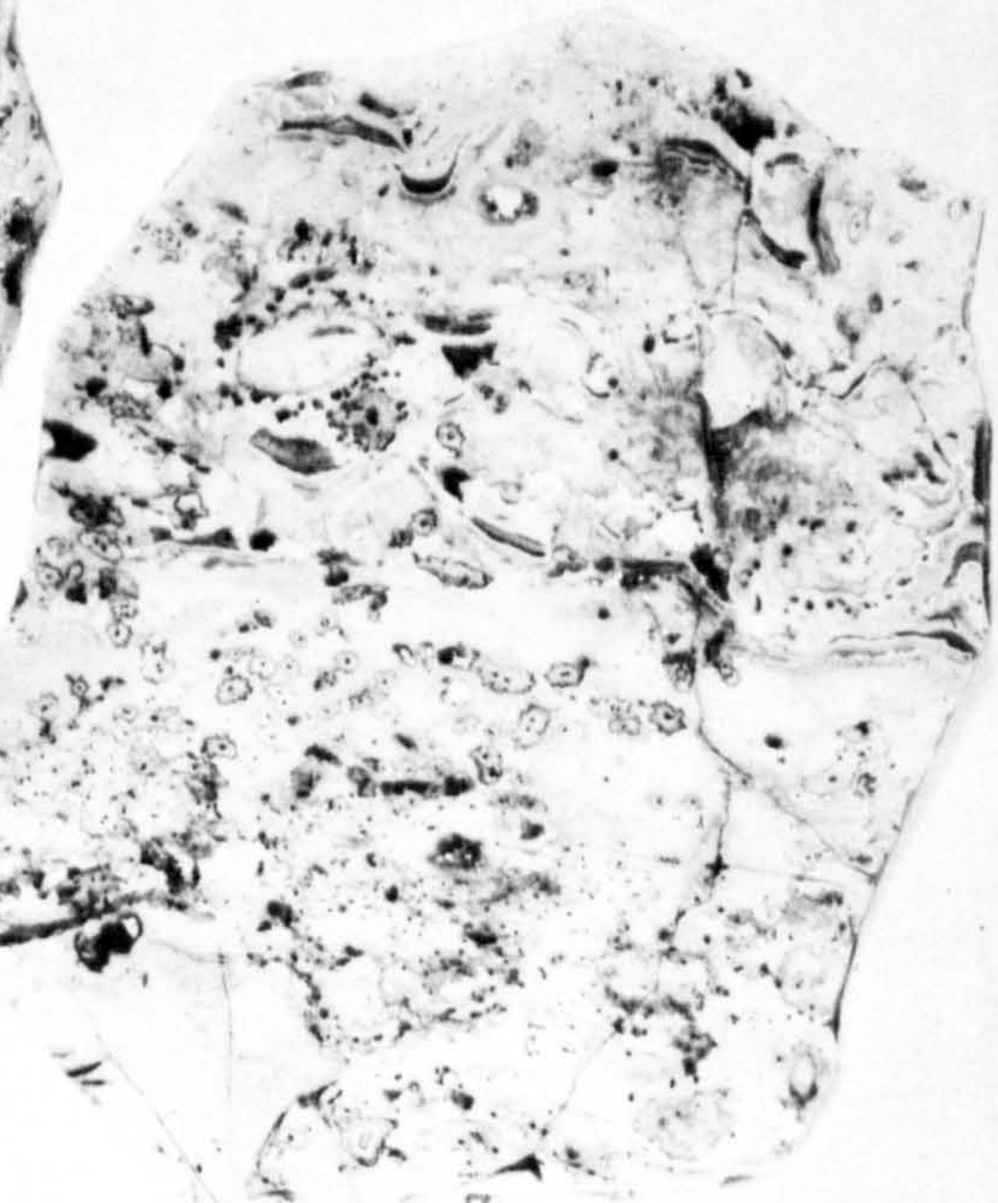

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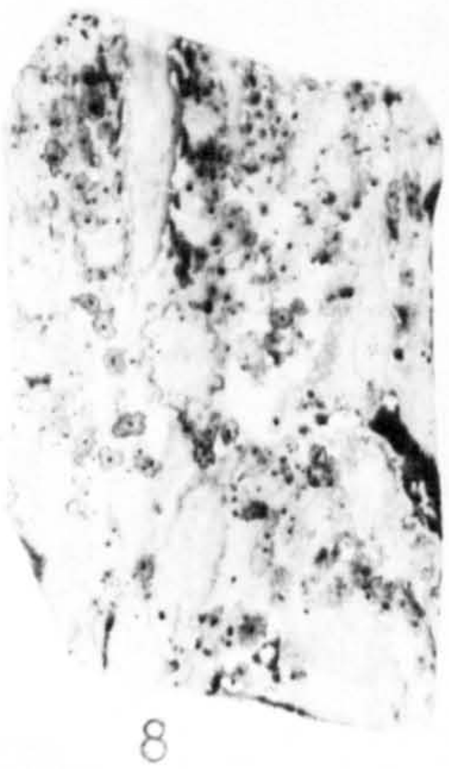

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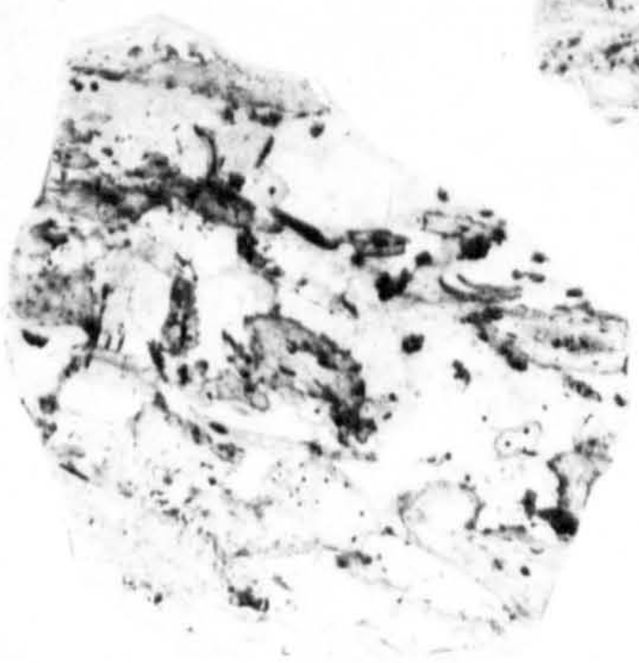

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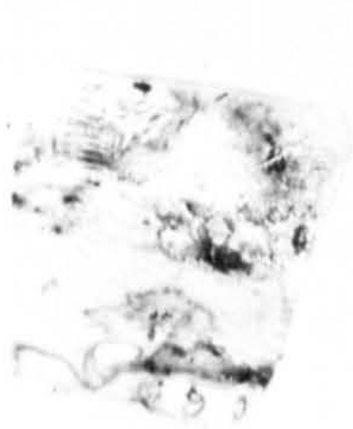

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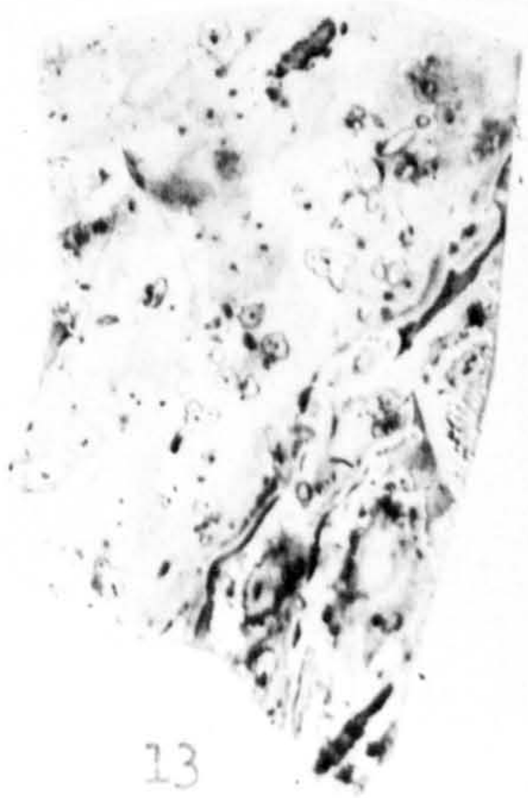

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METHODS

Preparation of peel-sections

The technique used for preparing peel-sections from the blocks is mainly that described by Joy, Willis and Lacey (1956) which is a modification of the peel-section method originally devised by Walton (1928). It is also developed from the somewhat similar technique of Sternberg and Belding (1942) for the preparation of fossil animal material.

The method involves the following stages :-

1. Preparation of the specimen. Each block was ground by hand with grade 80 carborundum powder (silicon carbide) and water on a ground-glass plate, until the required part was exposed. The exposed surface was washed carefully with water. The surface of the block except that to be examined, was covered with a protective coat (paraffin wax). This first stage was carried out only once for each block and was not repeated again.
2. Polishing. The exposed face was polished smooth using 600 grade carborundum powder as a fine abrasive with water on another ground-glass plate. The polished face was then dried.
3. Etching. This stage was carried out in a fume-cupboard with extreme care and using the appropriate equipment because it involved the use of the dangerous HF acid. The prepared specimen was placed with the smooth face uppermost and horizontal. This was achieved by placing the block on top of a piece of plasticine (placed in a polythene petri-dish), and levelling up using a spirit level which was placed over the

po polished face to make sure it is horizontal. Commercial HF (40%) was used for etching for about 3 to 4 minutes. Sufficient acid, to cover the face to be etched, was carefully poured on the polished face from a small plastic polythene bottle fitted with a dropper. Utmost care was taken so that the acid did not run off the polished surface.

4. Washing. The etched surface was washed free of acid in a gentle stream of running water, and care was taken not to touch the etched face.

5. Drying. The etched face was dried in dust-free air. This was accelerated by rinsing the face with a little acetone.

6. Preparation of the peel-section. The block was placed with the etched face uppermost and nearly horizontal. Sufficient acetone was added to moisten the surface and to form a small pool at one side. A piece of cellulose acetate sheet, 0.075 mm. (0.003 in.) thick and of appropriate size, was quickly and gently laid across the surface of the block, being first applied to the pool of acetone to avoid trapping air bubbles. When too much acetone remained under the sheet, it was quickly and gently smoothed down with the finger.

7. Drying of the preparation. The preparation was then set aside to dry in a dust-free place for about two hours at room temperature. Once the sheet has settled in position, the surface was not touched.

8. Peeling. The film or cellulose sheet with its embedded fossil material was then peeled off, by easing one edge of the film with a hard-back razor, then removing the whole film with careful steady pulling. When difficulty was sometimes experienced, the whole film

was shaved off with the hard-back razor blade.

The same face was polished again the the whole process repeated to make another peel and so on.

9. Mounting. Directly after peeling, the peel was trimmed with scissors and mounted on a plain paper-card using a piece of cellotape. The card was numbered. The mounted cards were stored in boxes of the card-index type.

10. Microscopic examination. The peels mounted on the cards were easily and conveniently examined by reflected light using a suitable microscope (Watson stereoscopic binocular microscope).

By this satisfactory and rapid cellulose peel technique more than 2,200 peels were prepared from the 11 blocks (see Table 1).

The distance between every two successive peels was found usually to be about 0.05 mm.

When remounting of any peel in Canada balsam was required (for microscopic examination by transmitted light or photographic purpose), the cellotape strip was carefully peeled off and the peel was removed for the purpose. However, most of the photographs in this Part and all those in Part II were taken by using reflected light, thus saving a lot of time which would have been required by the tedious remounting in balsam for examination by transmitted light. The only disadvantage of photography by reflected light from peels, is that when the part of the peels face to be photographed is not entirely smooth i.e. if wrinkles occurred in the surface of the peel during its drying before peeling for one reason or another, this might cause some difficulty in fine focusing of the object as a whole, as well as in achieving homogenity of the light reflected.

When holes of fissures were met with in the surface of any block they were filled before polishing with melted wax, which hardens quickly, causing no delay in the process. The projecting wax was removed by the hard-back razor and the block was ready for polishing.

Other materials besides the wax (such as durofix, widtite.) were tried for filling the holes but none had an advantage over the wax. They require quite a long time (over night or for one day) to become hard and the block ready for polishing, thus causing a considerable delay in the process of preparing the peel-sections. The fact that the wax filling has to be renewed every so often also holds for the other materials.

Construction of scale models

The method used here for constructing scale models is essentially that described by Lacey, Joy and Willis (1957).

Camera lucida drawings showing the outlines of the axes and the sporangia were prepared from successive peel-sections. Each drawing was protected with a think sheet of cellulose acetate, then a sheet of translucent dental wax about 1.25 mm. thick was laid over the drawing and the outlines of the latter were traced by cutting through the wax with a special wax cutting tool. The portions thus cut out were numbered, stacked in order (using pins $\frac{1}{2}$ in. and 1 in. long) and sealed together by means of a very fine gas flame from a glass capillary. Most of the pins were easily taken off during sealing. The distance between sections was corresponding in scale with the thickness of the wax used, i.e. the vertical scale of these wax models is the same as the horizontal scale, thus the constructed models are to scale in all dimensions.

Three models (see Plate 17) were constructed by this method.

Reconstruction of xylem and external morphology of Nothia

Microscopic measurements of the objects to be reconstructed, were taken from successive peels by means of a stage micrometer laid directly over the objects. The objects were reconstructed by converting the successive measurements to drawings on graph paper.

About 20 reconstructions of Nothia were prepared in this way. Most of the reconstructions are of fertile branches. The position of the sporangia and their arrangement on the axes are well shown. Xylem main strands and sporangial traces are also reconstructed.

NOTHIA, LYON, 1964

Synonym : Asteroxylon, Kidston and Lang, 1920, pro parte.

Type species of the genus : Nothia aphylla, Lyon, 1964.

Emended generic diagnosis :-

Small, slender, branched naked axes, up to 2.5 mm. in diameter bearing sporangia. Vascular strand protostelic; the xylem consisting of tracheids with no detectable pitting or differential thickening. Sporangia rather reniform, about 1.5 mm. long, 2.7 mm. wide and 1.2 mm. thick, eusporangiate, borne on adaxially recurved stalks. Dehiscence apical, by a long slit surrounded by thickened annulus-like cells. Spores produced in tetrads, about 65 μ in diameter and all of one kind.

NOTHIA APHYLLA, LYON, 1964

Synonym : Asteroxylon mackiei, Kidston and Lang, 1920, pro parte.

Specific diagnosis : that of the genus, since Nothia Lyon is monotypic.

DESCRIPTION OF SELECTED RECONSTRUCTED SPECIMENS

The following is a description of the 22 specimens reconstructed in the manner described on page 20. Most of the specimens come from block No. 91, some from block No. 62 and one from each of blocs No. 67, 69 and 56.

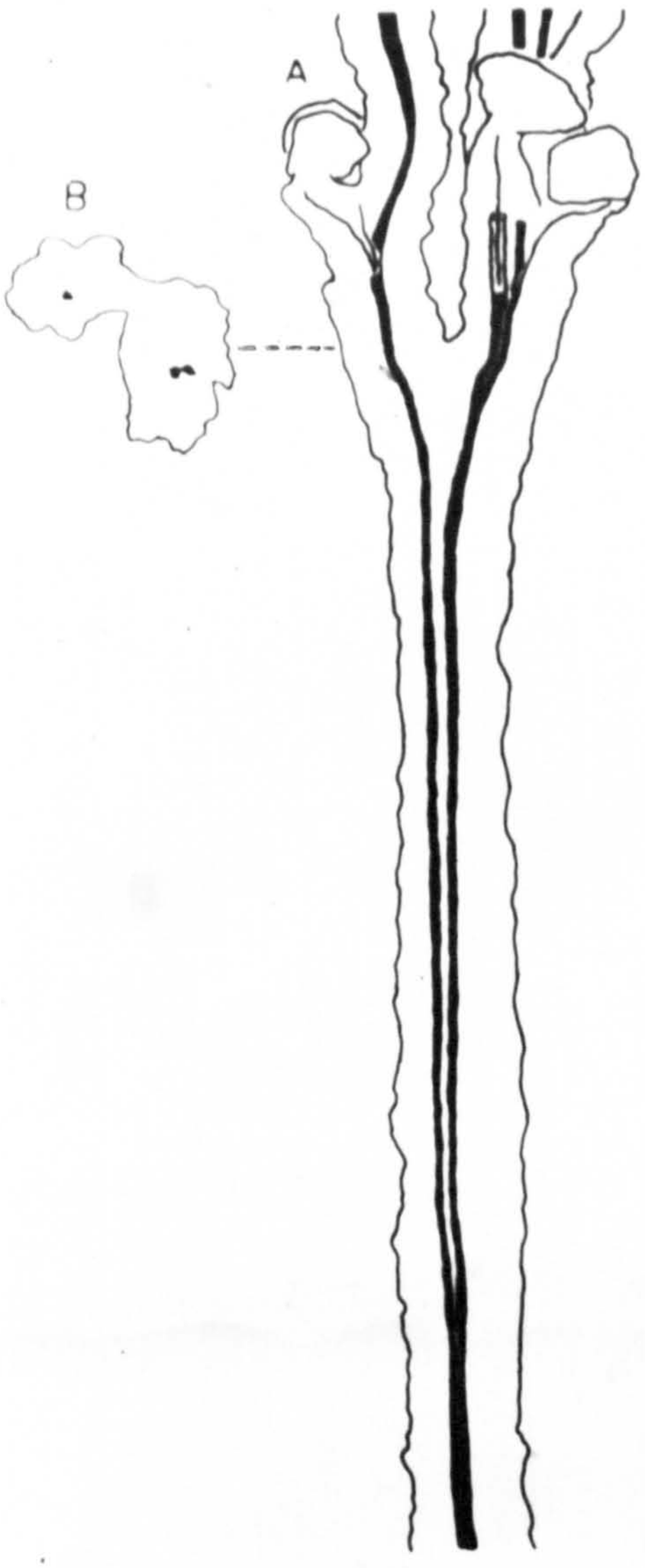
1. Figure 16 shows a reconstruction of a specimen about 1.8 cm. long. The main axis is about 1.5 mm. in diameter and each of its branches is under 1 mm. in diameter. Each branch bears one dehisced sporangium of average size. The trace of each sporangium departed from its branch-stele several millimeters before it enetered the stalk. This is

rather peculiar since sporangial traces usually depart only about 2.5 mm. before they enter the stalk. The stele of the right branch gives rise to a second trace slightly before its out end.

2. Figure 14-A shows a reconstruction of a branched axis, incomplete at both ends. The whole specimen is about 3 cm. long. The main axis is more than 2 cm. long and bears no sporangia. Each of the 2 branches bears a pair of dehisced sporangia. The main xylem of the axis divides into two strands a long distance (about 2 cm.) before its branching. The stele which entered the left branch remained undivided and gave rise to two sporangial traces at one and the same point. The two traces supplied the two sporangia borne on this branch. These two sporangia are borne at one level and very close to each other, as clearly shown in the transverse section (Fig. 15).

The stele which entered the right branch (which is larger in size than the left branch) divided into 2 steles as soon as it entered the branch (Fig. 14-B). Each of the two resulting steles gave rise to one sporangial trace to supply one of the two sporangia borne on this branch. The two sporangia are borne at almost the same level. A little higher one of the two steles of this branch gave rise to its second sporangial trace.

3. Figure 17A shows a reconstruction of a specimen about 1.8 cm. long. The main axis bears two short and close lateral branches on its lower part. A few millimeters above the level of the lateral branches, the single stele of the main axis divides into two steles in preparation for the branching of the axis. Each branch receives one of the two



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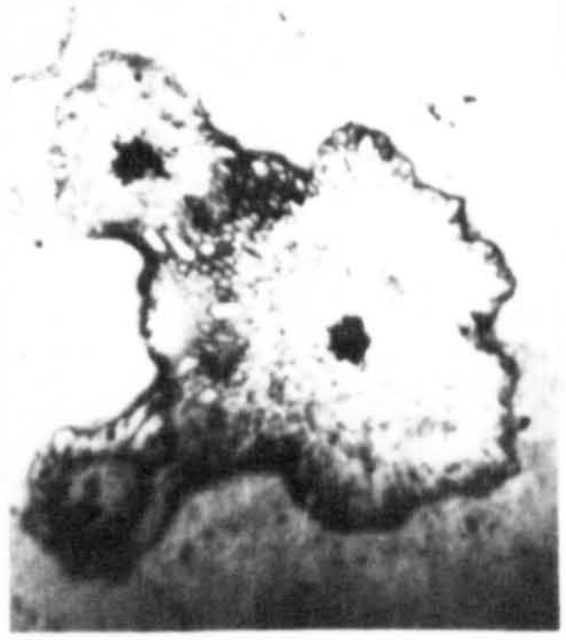

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Fig.14 : A- Reconstruction of a fertile specimen. Peels No.62/1-62/548. x 5.

B- Transverse section of the axis at the level shown by the interrupted line. Peel No.62/122. x 5.

Fig.15 : Transverse section of the left branch of the same specimen. Peel No.62/65. x 15.

Fig.16 : Reconstruction of a fertile fragment. Peels No.91/1-91/360. x 5.

steles. The right branch bears two dehisced sporangia and the vascular trace of a third one could be seen departing from the branch stele. The left branch does not bear sporangia on the portion reconstructed (which is only about 3 mm. long), but its seems to have borne sporangia a little higher, since a trace is seen to depart from the stele at the cut end of the branch. Figure 17B shows a transverse section in the axis and the two lateral branches. The xylem of the lower lateral branch is broken down to two portions. The axis and the two lateral branches have a curved shape in the transverse section, A narrow groove is seen opposite the slightly concave side of the xylem of the axis. The stele of the lower lateral branch divides into two steles near its tip. Figure 17C shows a transvers section in the axis just before dichotomous branching is complete. The stele of each branch is broken down to two portions.

4. Figures 18 and 19 show a reconstruction of a repeatedly branched axis. The specimen is just over 2 cm. long. The diameter at the lower part of the axis is about 2 mm., but it decreases gradually upwards, thus the diameter of each of the 8 upper slender branches is about 1 mm.

At the lower part of the specimen there are two steles, each of which enters a branch. The stele which entered the right branch divided directly into two steles and after a length of about 6 mm. one entered a lateral branch which is about 3 mm. long and has a diameter nearly the same as the main branch. After the separation of the lateral branch, the main branch continues with a single stele for about 3 mm. then its stele divides into two steles and again after

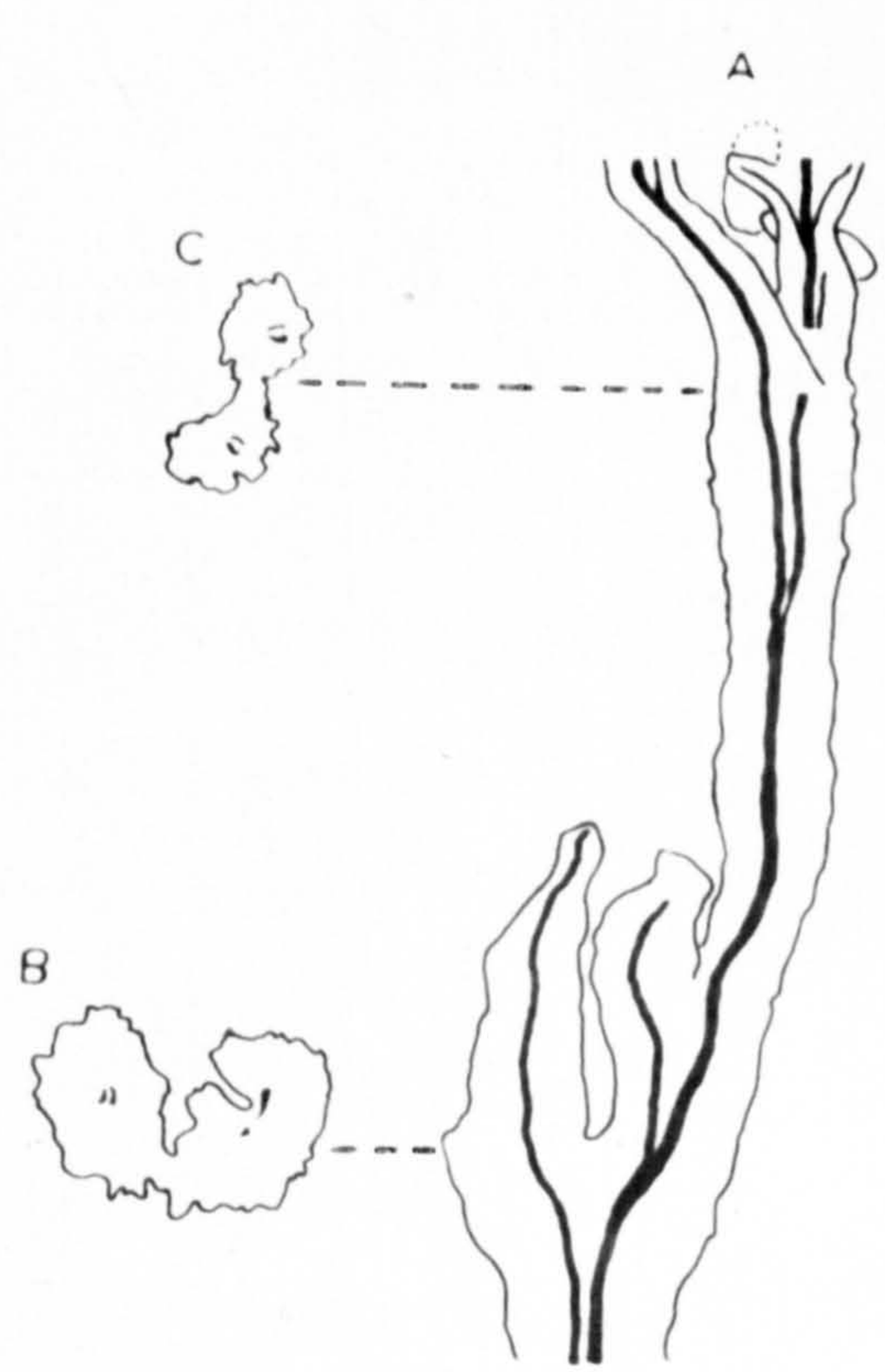


Fig.17 : A- Reconstruction of a branched axis. Peels No.62/1-62/354. x 5.

B & C- Transverse sections of the axis at different levels. Peels No.62/290 & 62/66. x 5.

1.5 mm. one of the two steles divides into two, thus the branch appears to have 3 steles, but only for a very short length (in fact it is the basal part of its 2 branches). The main branch then dichotomises and 2 of the 3 steles enter the left branch. The latter is very short and dichotomises directly into two slender branches; the right branch of this left pair bears no sporangia and its stele remains single and only one sporangial trace is seen to depart from the stele at the cut end of the branch. The left slender branch has its stele divided into two from the base of the branch and bears two sporangia.

The third of the 3 steles mentioned above enters the right branch and divides directly into two steles. This branch is about 5 mm. long and it dicotomises giving two slender branches. The right one bears 3 sporangia and at the cut end its stele is seen to give rise to a 4th trace. The left slender branch has a single stele and a sporangial trace is seen to depart from the stele and enters the basal part of a sporangium stalk.

Starting again from the lower part of the specimen; one of the two steles of the main axis enters the left branch and it divides into two steles just after it enters the branch. The branch has the double stele for a length of about 6 mm., then the branch dichotomises. Each branch receives one of the two steles; the left branch is about 7 mm. long and the right one is about a millimeter longer. The stele of the left branch divides directly into two, while that of the right branch divides into two after about 4 mm. The two branches dichotomise and two pairs of slender branches result.

18

19

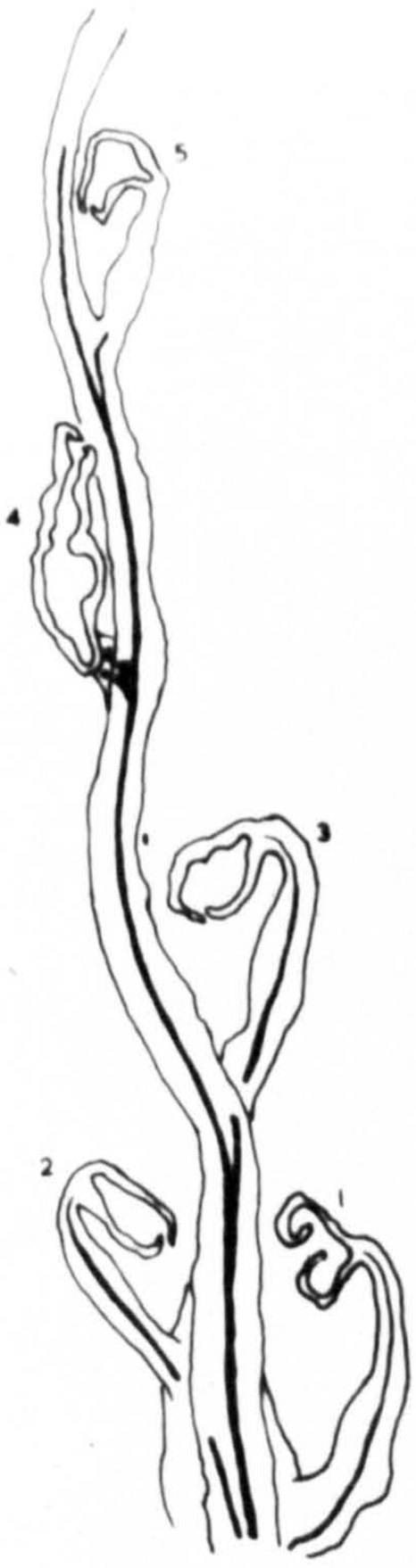
Fig.18 : Reconstruction of a repeatedly branched axis. Peels No.62/1-62/430. Nat.size.

Fig.19 : The same x 5.

The left branch of the right pair has a single stele and bears no sporangia, while the right branch has a double stele from its base and one sporangial trace is seen departing from each of the two steles.

The right branch of the left pair has a single stele and bears no sporangia while the left branch has also a single stele but it bears 5 sporangia and the basal parts of the stalks of the 6th, 7th and 8th sporangia are shown at the cut end of the branch. The arrangement of the sporangia on this branch is almost in a close spiral and not more than 3 sporangial traces could be seen in any one transverse section. All the 10 sporangia borne on the branches of this specimen were found to be dehisced. They are of a somewhat small size; about 1 mm. long, 2 mm. wide and 1 mm. thick.

5. Figure 20 shows a reconstruction of a fertile axis fragment. The axis and its 5 large sporangia are all shown in longitudinal section. A wax model of this specimen was prepared and is shown in Figs. 67 and 68. The axis is about 2.4 cm. long and is incomplete at both ends as well as the facing side and its lower part is peculiarly thick compared with the rest of the axis. The axis is not straight but curved opposite the position of the three upper sporangia. This specimen shows clearly the position of the stalk on the axis and its adaxial recurvature to the inside and the shape of the sporangia in longitudinal section which is almost pear-shaped. All the 5 sporangia are dehisced and it is clearly shown that the two halves of the sporangium overlap at the position of the dehiscence slit and the upper edge usually to the outside; this is well shown in sporangia No. 2, 3 and 5 of which sporangium No. 3 is shown in Fig. 21.



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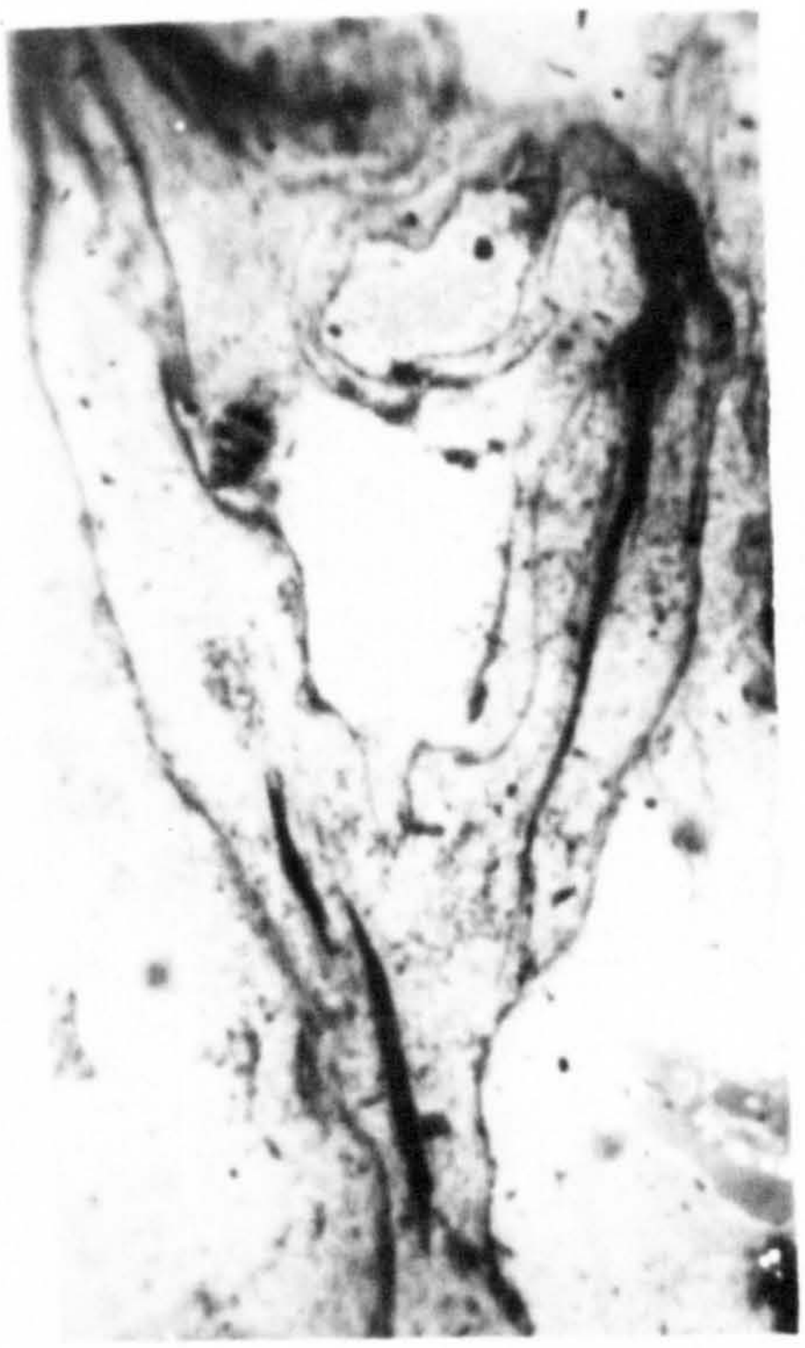

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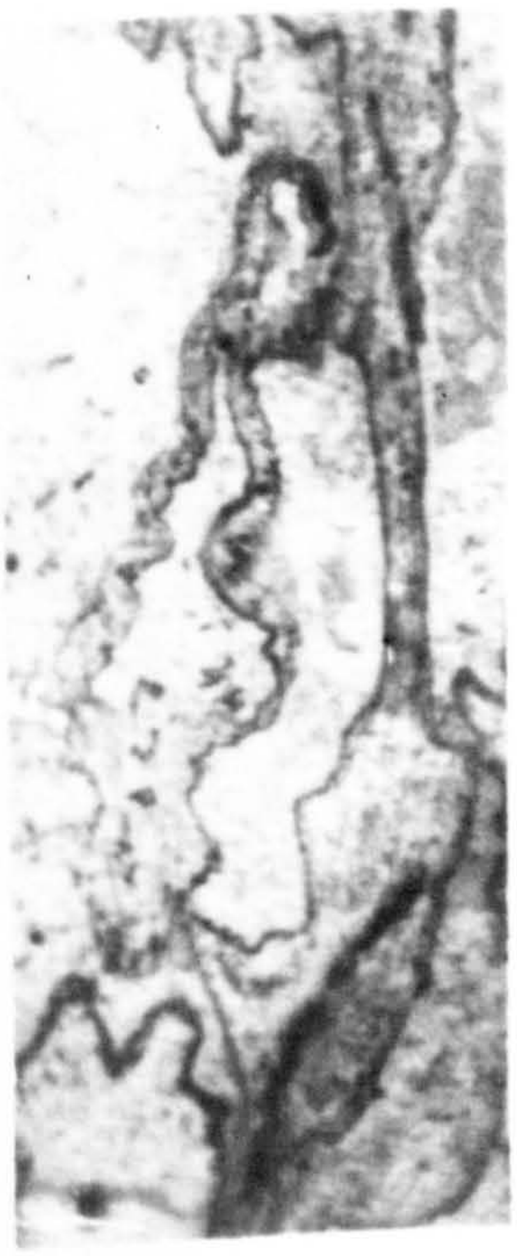

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Fig.20 : Reconstruction of a fertile axis. Peels No.56/2-56/100. x 5.

Fig.21 : Sporangium No.3 of the same axis. Peel No.56/17. x 15.

Fig.22 : Sporangium No.4 (two fused sporangia) of the same axis. Peel No.56/18. x 15.

Sporangium No. 4 is peculiar in its length; it was found that it is not one sporangium but two connected together, having one common spore cavity, but there are two slits of dehiscence, two vascular traces and two stalks connected together through out their short length. This double sporangium is shown in Fig. 22.

6. Figure 23A shows a reconstruction of a dichotomously branched fertile axis fragment. Sporangia are borne on the axis as well as on its two branches. There are 16 sporangia arranged at random on all sides of the axis and its two branches. The axis has a double stele and on branching each branch receives one stele from the main axis. Sporangia No. 3, 5 and 6 get their vascular supply from the stele at the left side in the reconstruction, while sporangia No. 4, 7 and 8 get their vascular supply from the other stele of the axis. This means that each stele gives a vascular supply only to the sporangia on its half-side of the axis. The traces of sporangia No. 1 and 2 are shown in the transverse section in Fig. 24. Whether trace No. 1 has departed from the left stele and trace No. 2 from the right stele is unknown because that section was at the end of the block.

Figure 23B shows a transverse section of the axis, 1 mm. before branching is complete. The stele of the left branch is shown with two traces quite close to it; they belong to sporangia No. 1 and 2 of the left branch. The stalk of sporangium No. 8 is shown in this section still in connection with the base of the right branch. The trace near the stele of the right branch belongs to sporangium No. 1 of this branch, while the trace of sporangium No. 2 of the same branch is shown about to depart from the stele.

23

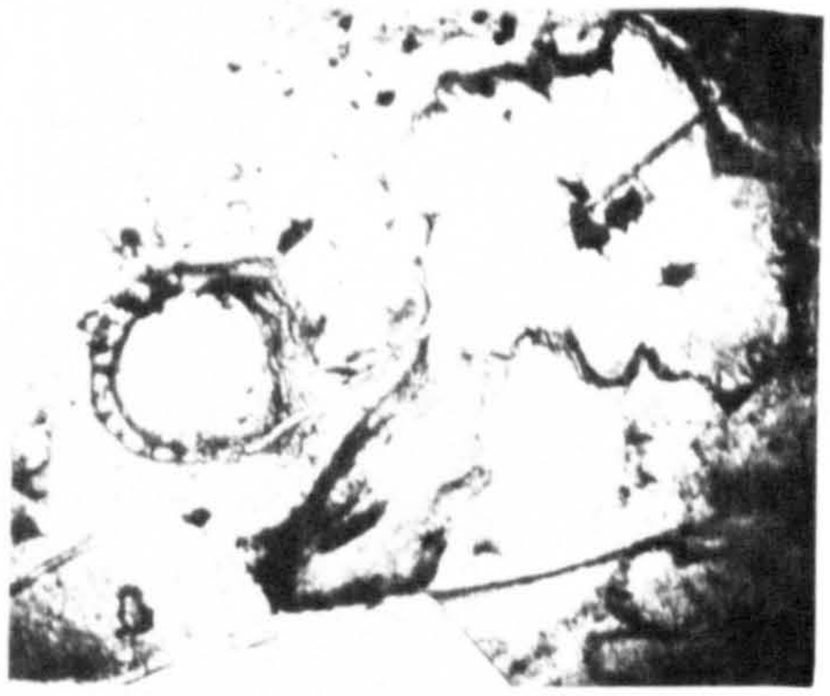

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Fig.23 : A- Reconstruction of a branched fertile axis. Peels No.91/1-91/382. x 5.

B- Transverse section of the axis. Peel No.91/100. x 5.

Fig.24 : Transverse section at the base of the same axis showing its two main xylem strands close together and the xylem strand of sporangium No.3 very close to one of them. The xylem strand of sporangium No.2 is a short distance to the right. Sporangium No.1 is seen near its stalk which is connected to the axis. Photo. by transmitted light. Ground section, slide No.91/376. x 15.

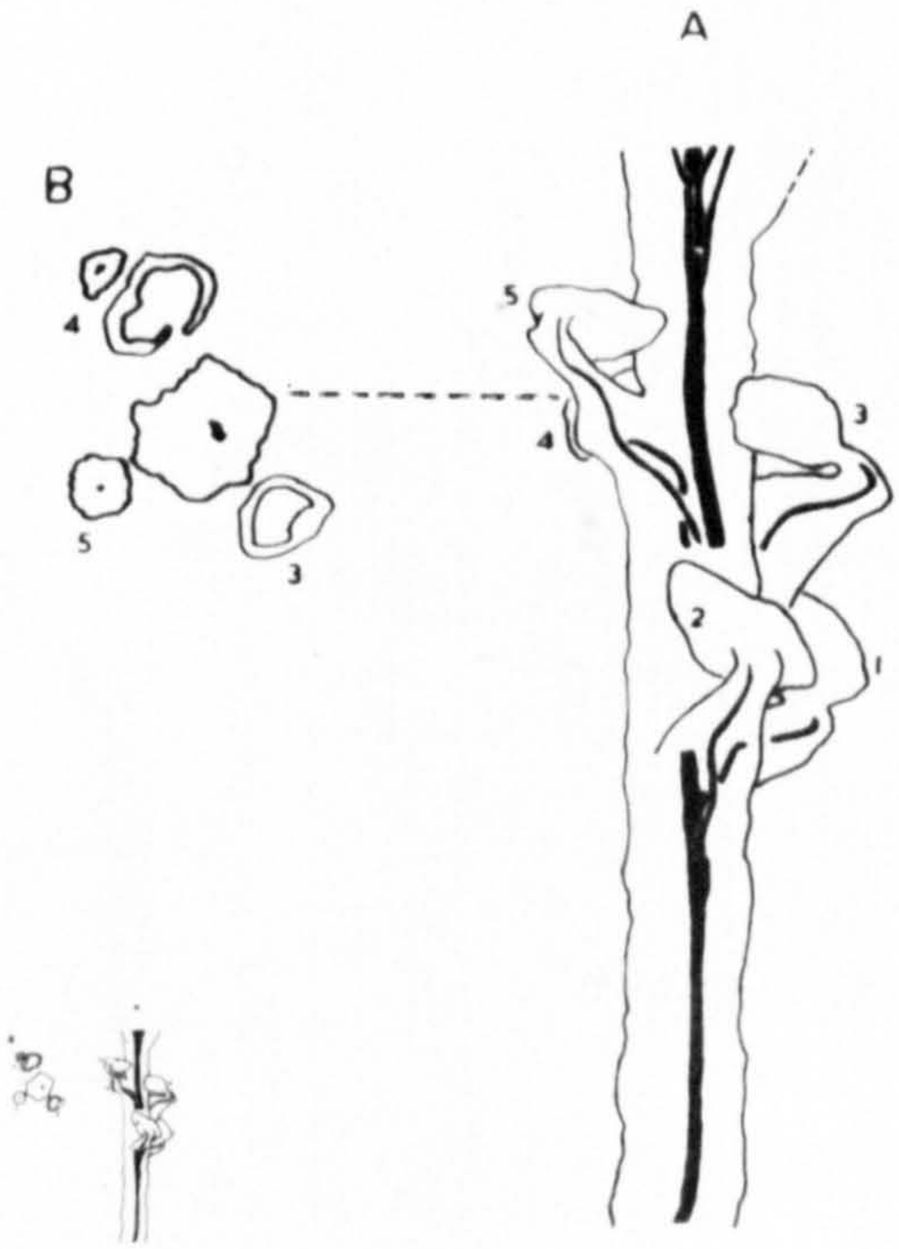
7. Figure 25 and 26A show a reconstruction of a fertile axis carrying 5 dehisced sporangia. The axis has a single stele. The two traces of sporangia No. 1 and 2 depart from the axis stele at almost one level. Sporangium No. 3 lies above the space between sporangium No. 1 and sporangium No. 2.

About 3 mm. above the departure of the first two traces the axis stele gives rise to 3 traces in a close spiral (Fig. 27). These 3 traces supply sporangia No. 3, 4 and 5. The 3 sporangia are borne at slightly different levels; thus sporangium No. 5 is only about 1 mm. higher than sporangium No. 3. In this fertile fragment no one of the 5 sporangia lies exactly above the other, as is shown in the reconstruction.

Figure 26B shows a transverse section of the axis and its single stele. The axis appears hexagonal in shape and is surrounded by sporangia No. 3, 4 and 5. The section passes through the upper part of sporangium No. 3, through sporangium No. 4 and its stalk and through the stalk of sporangium No. 5.

About 4.5 mm. above the departure of trace No. 5, the stele of the axis gives rise to another 3 sporangial traces, also in a close spiral but at alternating positions with the previous 3 traces as can be seen by comparing the transverse section shown in Fig. 27 with that in Fig. 28.

8. Figure 29 shows a reconstruction of a branched axis. The two branches are fertile bearing sporangia from their very base. The main axis has a double stele and each branch has a single stele. The right branch



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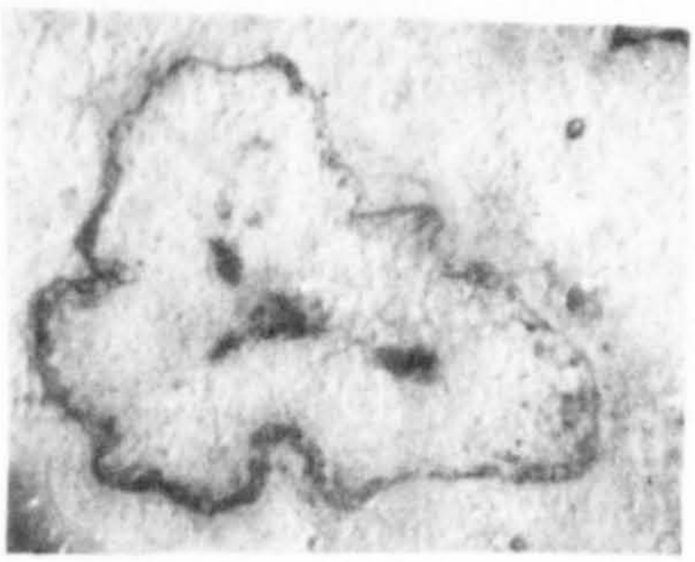

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Fig. 25 : Reconstruction of a fertile branch.Peels No.91/1-91/308. Nat. size.

Fig. 26 : A- The same x5.

B- Transverse section of the fertile branch.Peel No.91/70. x5.

Figs. 27&28 : Transverse sections of the same fertile branch at different levels.Peels No.91/115 & 91/5. x15.

bears 5 sporangia and the left one bears 3 sporangia. On the right branch sporangia No. 1 and 2 are borne at one level and a little higher come sporangia No. 3, 4 then 5; all the 3 are borne at different levels. The 5 sporangia are distributed on all sides of the branch i.e. no one of them lies above another. Their arrangement is very similar to the 5 sporangia of the previous specimen (Fig. 26A) with one difference, that is the upper 3 sporangia of the previous specimen are closer together (about to form a whorl).

Three more sporangial traces are shown to depart from the stele of the right branch, but unfortunately this was at the end of the block.

The left branch bears sporangia No. 1 and 2 at one level and sporangium No. 3 a few millimeters higher. Sporangium No. 3 in case of the right as well as the left branch is borne above the space between the first two sporangia. The stele of the left branch is seen to give rise to 3 more traces at the cut end of the branch.

9. Figure 30A shows a reconstruction of a fertile axis bearing 11 dehisced sporangia. The sporangia are arranged in the following variable manner:

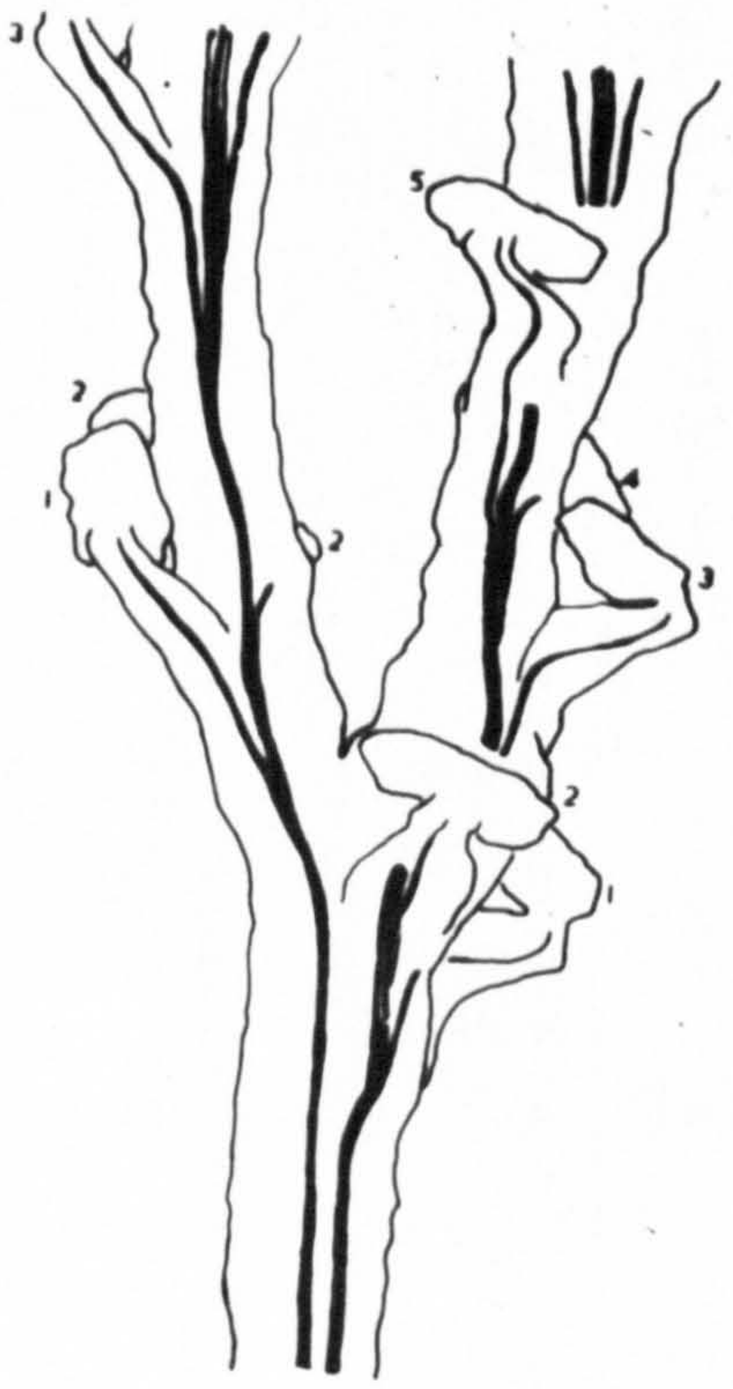
a - A single sporangium at one leve, like sporangia No. 3 and No. 4.

b - Two sporangia at almost the same level, as sporangia No. 1 and 2, sporangia No. 5 and 6, and finally sporangia No. 10 and 11.

c - Three sporangia at almost one level, like sporangia No. 7, 8 and 9.

The transvers section in Fig. 30B shows the axis with its single stele. The trace near the stele belongs to sporangium No. 3. The section passes through sporangium No. 2 and its stalk which is still connected to the axis as well as through sporangium No. 1.

Plate 8



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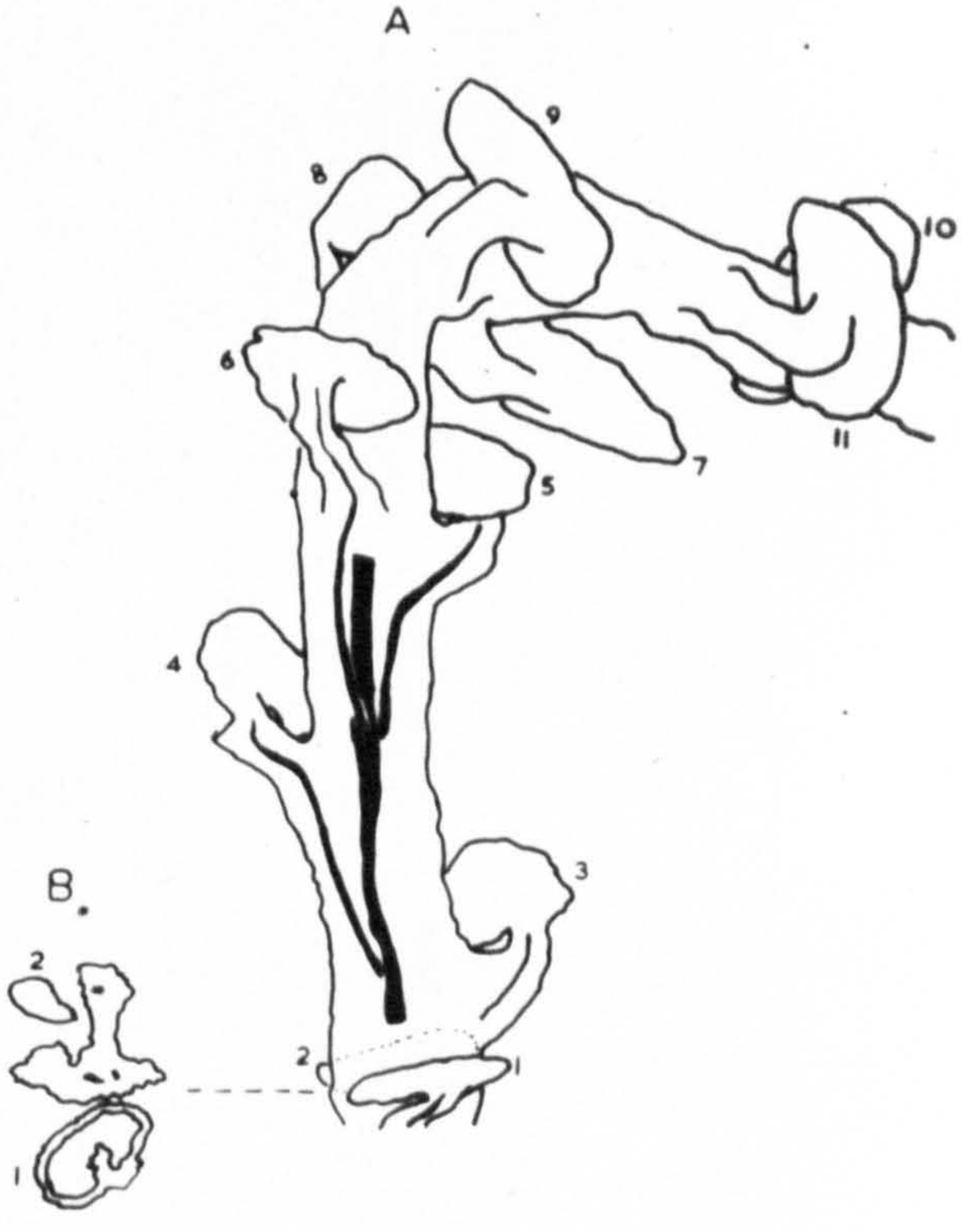

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Fig.29 : Reconstruction of a fertile specimen. Peels No.91/1-91/366. x 5.

Fig.30 : A- Reconstruction of a fertile branch. Note the comparatively small size of sporangia No.1 & 2. Peels No.91/46-91/382. x 5.

B- Transverse section at the base of the fertile branch. Peel No.91/370. x 5.

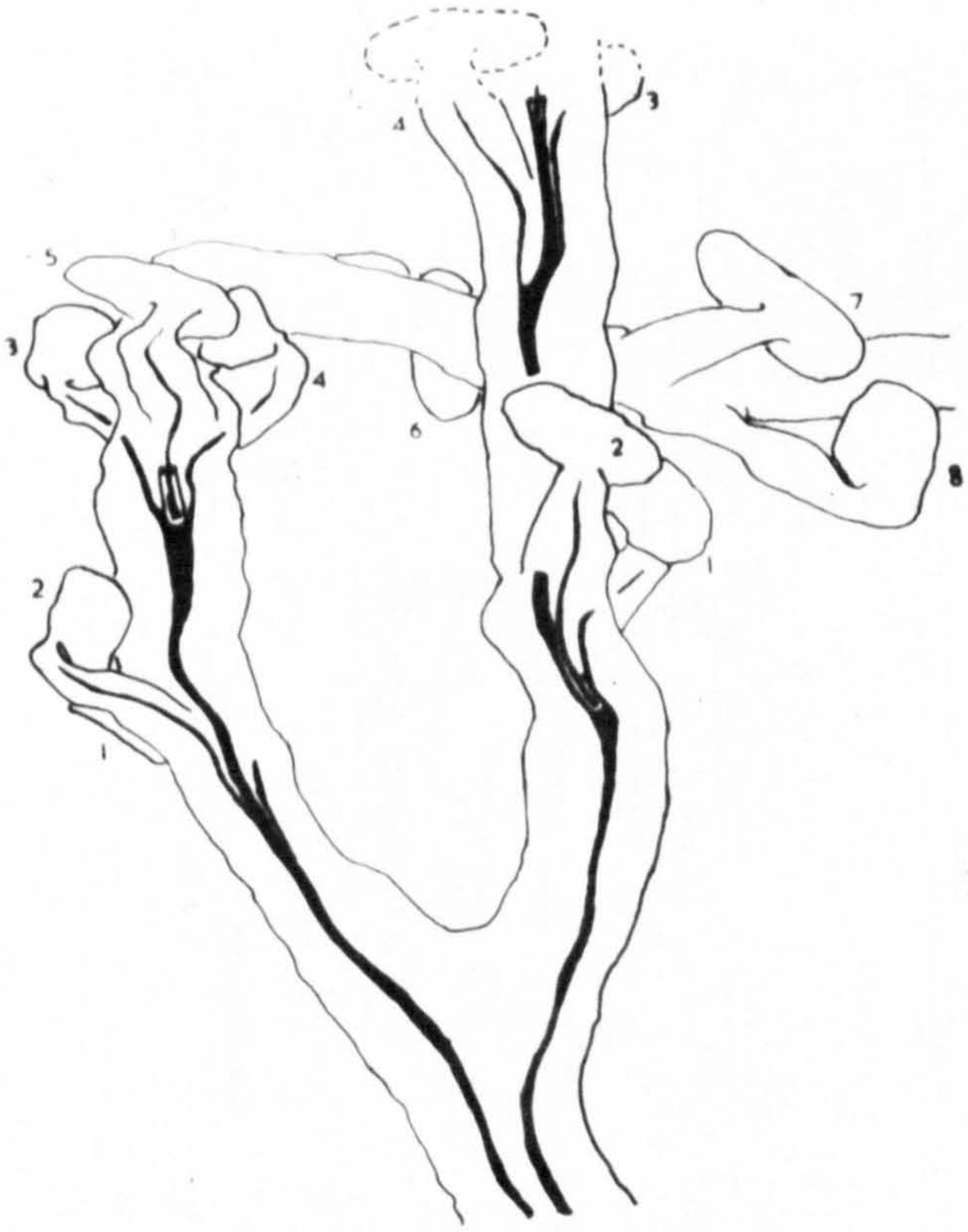
The sporangial traces were found to depart from all sides of the axis stele in accordance with the arrangement of the sporangia on the axis.

10. Figure 31 shows a reconstruction of the uppermost part of an axis with a double stele and its two fertile branches. Each branch has a single stele. The right branch is about 1.3 cm. long and bears 4 sporangia (sporangium No. 4 is restored as well as part of No. 3). The left branch is about 2.2 cm. long and bears 8 sporangia.

The right branch bears sporangia No. 1 and 2 at one level and about 6 mm. higher it bears the second pair of sporangia (No. 3 and 4). The second pair of sporangia alternate in position on the branch with the first pair, as can be seen by comparing the transverse sections shown in Fig. 32 and in Fig. 33. These two figures show that the vascular traces of the second pair of sporangia depart from the opposite direction to those of the first pair.

The left branch bears 2 sporangia at about the same level and on the outer side of the branch. About 4 mm. higher the branch bears a whorl of 3 sporangia, however 2 of them (No. 3 and 4) are slightly closer to each other than to the third one (No. 5). The traces of these 3 sporangia depart at exactly the same level from the angles of the stele which attains a triangular shape at this position (see Figs. 34 and 35). The branch is bent just above the position of the whorl and afterwards it bears sporangia No. 6, 7 and 8 at different levels. It must be mentioned that the part of the branch after the bend is ill-preserved.

Plate 9



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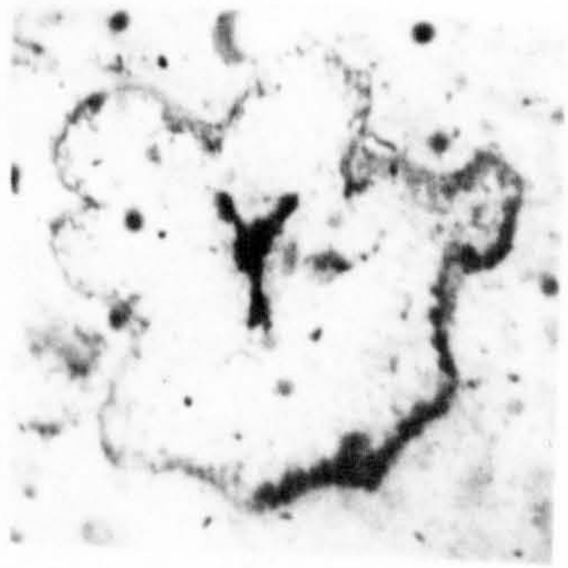

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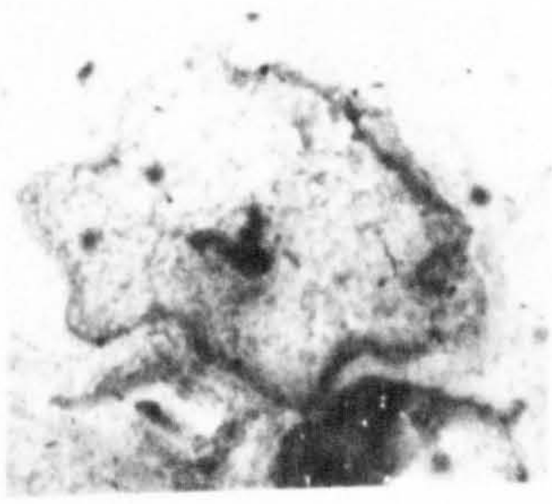

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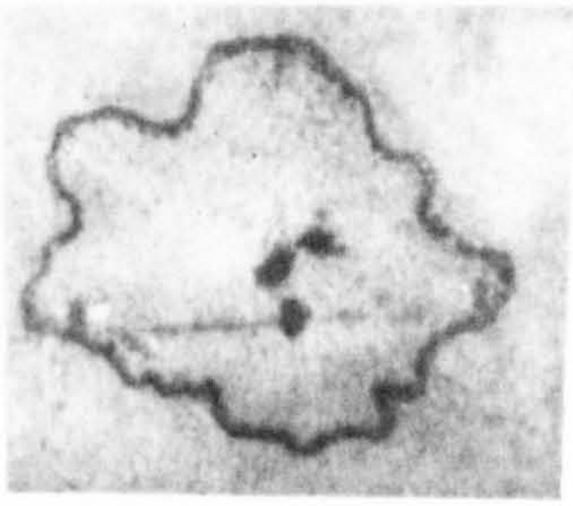

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Fig. 31 : Reconstruction of a fertile specimen. Peels No. 91/1-91/370. x5.

Figs. 32&33 : Transverse sections of the right branch at different levels. Peels No. 91/190 & 91/65. x15.

Figs. 34&35 : Transverse sections of the left branch showing the departure of the xylem strands of sporangia Nos. 3,4&5. Peels No. 91/128 & 91/122. x15.

11. Figure 36A shows a reconstruction of a fertile fragment about 1.6 cm. long. The axis has a single stele and bears 5 dehisced sporangia; 3 sporangia at almost one level and 2 at a higher level (about 5 mm. higher). The 3 sporangia are more or less confined to one side of the axis and the 2 upper sporangia are confined to the other side i.e. no one of the 5 sporangia lies above another. The two traces of sporangia No. 1 and 3 depart from the stele as one strand which directly divides into the two traces, while sporangium No. 2 gets its vascular trace directly and independently from the stele. The two traces of sporangia No. 1 and 3 form with the stele a more or less horse-shoe shape in cross section (Figs. 36B and 37). The stalk of sporangium No. 1 and that of sporangium No. 3 are very close at their base as clear in the transvers section shown in Fig. 36C.

After the departure of the traces of the first 3 sporangia the stele becomes rectangular in shape in transverse section and the traces of sporangia No. 4 and 5 depart from two neighbouring angles of the stele. The transverse section in Fig. 36D shows the axis stele and near to it is the trace of sporangium No. 5. The trace of sporangium No. 4 is within its stalk which is shown in an oblique longitudinal section and still connected to the axis. A third trace could be seen about to depart from the stele; this trace must have belonged to a 6th sporangium.

12. Figures 38 and 39 show a reconstruction of a fertile axis fragment about 1.8 cm. long and about 1.5 mm. in diameter. The 8 sporangia borne on this axis are all dehisced. Sporangia No. 1, 2 and 3 are

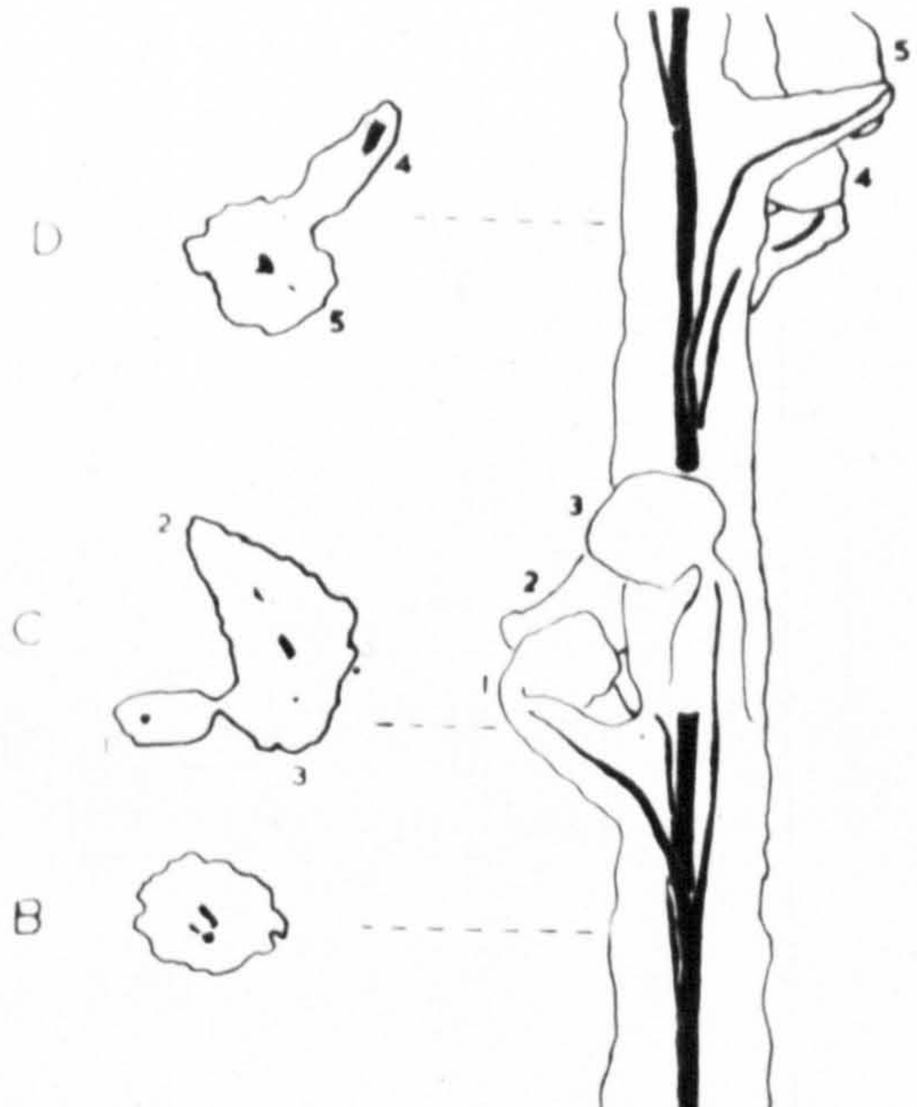

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Fig.36 : A- Reconstruction of a fertile fragment. Peels No.91/1-91/328. x 5.

B, C & D- Transverse sections of the axis at different levels. Peels No.91/260, 91/202 & 91/60. x 5.

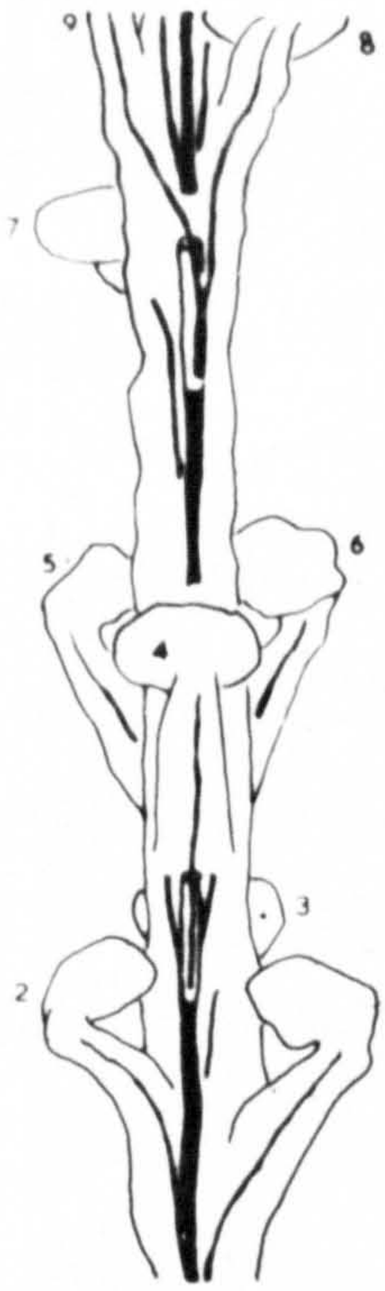
Fig.37 : Transverse section of the same axis at the same level as 36-B. Peel No.91/260. x 15.

arranged in a very close spiral so that they almost form a whorl. Their three traces depart from the stele at very short intervals (Fig. 40) and in accordance with the arrangement of the 3 sporangia i.e. the first trace to depart is that of sporangium No. 1, then 2, and finally 3.

Sporangia No. 4, 5 and 6 are arranged in the same manner as the first 3 sporangia but alternate with them in position on the axis, i.e. sporangium No. 4 lies above the space between sporangia No. 1 and 2 and sporangium No. 5 lies above the space between 2 and 3 and sporangium No. 6 lies above the space between No. 3 and 1. The traces of the 3 sporangia of the second whorl depart also at very short intervals from the stele and in accordance with the arrangement of their sporangia and alternating in position with the traces of the first whorl (Fig. 41).

About 5 mm. above the departure of trace No. 6, the axis stele gives rise to the trace of sporangium No. 7 and 2 mm. higher a vascular strand departs from the stele and divides into two traces; one supplies sporangium No. 8 and the other enters the stalk of sporangium No. 9. Before the separation of the two stalks of sporangia No. 8 and 9 from the axis, the stele of the latter gives rise to two traces (of the 10th and 11th sporangia) so that at this level 4 sporangial traces could be seen in one transverse section (Fig. 42).

This reconstruction shows clearly that the sporangia are generally arranged in a spiral manner, despite the fact that the first and second groups of 3 sporangia of the spiral are very close together so as to form 2 whorls. The first sporangium to lie exactly above sporangium No. 1 is sporangium No. 8.



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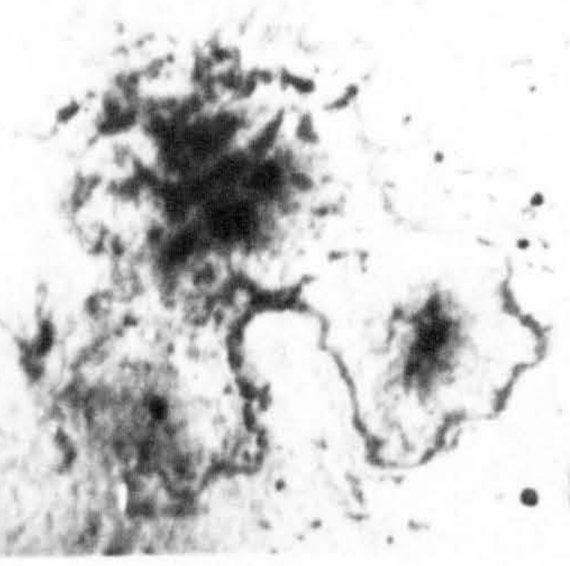

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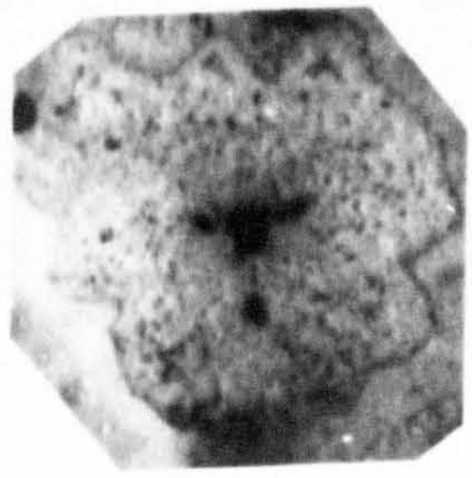

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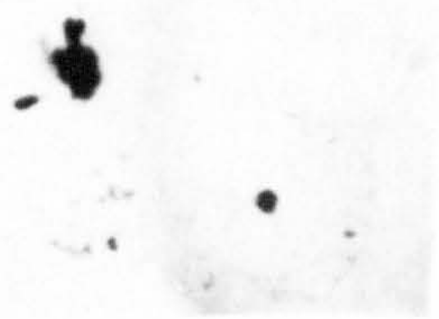

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Fig.38 : Reconstruction of a fertile fragment. Peels No.91/1-91/370. x 5.

Fig.39 : The same, Nat.size.

Figs. 40, 41 & 42 : Transverse sections of the same axis at different levels. Peels No.91/333, 91/259 & 91/32. x 15.

13. Figure 43A shows a reconstruction of a fertile axis bearing 13 dehisced sporangia. The fashion of the arrangement of the sporangia is a whorl of 3 sporangia followed by a single sporangium. This is repeated twice in the part of the axis reconstructed. The axis fragment is about 2.7 cm. long and has a single stele. Figure 43B shows a transverse section of the axis with its single stele and the trace of sporangium No. 4, it also shows sections of sporangia No. 1, 2 and 3.

Figure 43C shows a transverse section of the axis with its stele and the traces of sporangia No. 5, 6 and 7. The stalks of sporangia No. 6 and 7 are very close at their base as clear in the transverse section. The traces of sporangia No. 5, 6 and 7 depart from the stele at one level. The stele at that level is triangular in shape and the three traces depart from its angles. The traces No. 6 and 7 are closer to one another than to No. 5. A little higher the stele gives rise to the trace of sporangium No. 8, The stele then gives rise to two strands one of which supplies sporangium No. 9 and the other strand divides into two traces which supply sporangia No. 10 and 11. (Sporangium No. 11 is restored, as are parts of sporangia No. 9, 10 and 12).

The transverse section in Fig. 43D shows the axis stele and the four traces of sporangia No. 9, 10, 11 and 12. At this point the axis is bent as shown in the reconstruction. The upper part of this fertile fragment is incomplete; there is evidence that the stele divided into two strands which means that the axis must have branched higher up.

It is clear from the reconstruction that the position of the three sporangia of the middle whorl is different from those in the whorls above and below them.

Sporangium No. 4 is borne very close to the first whorl while sporangium No.8 is borne at equal distances from the second and the third whorls.

14. Figure 44A shows a reconstruction of a small frogment of a fertile branch ending in a pair of sporangia. The branch is about 1 cm. long and under 2 mm. in diameter and bears 4 dehisced sporangia of average size. The branch has a single stele which gives rise to a strand and this directly divides into two traces; one goes to sporangium No. 1 and the other to sporangium No. 2.

Figure 44B shows a transverse section of the branch with its single stele, and the trace close to it belongs to sporangium No. 2 and the trace far away belongs to sporangium No. 1. About 3 mm. above the departure of the strand the stele itself divides into two traces. These two traces end in the two terminal sporangia No. 3 and 4.

Figure 44C shows a transverse section of the branch with its stele in the action of division into the two final traces. The section cuts sporangium No. 2 longitudinally revealing its pear shape and the slit of dehiscence.

Figure 44D shows a transverse section of the stalks of the two terminal sporangia just before they are completely separated. Sporangium No. 4 is larger in size than sporangium No. 3.

43

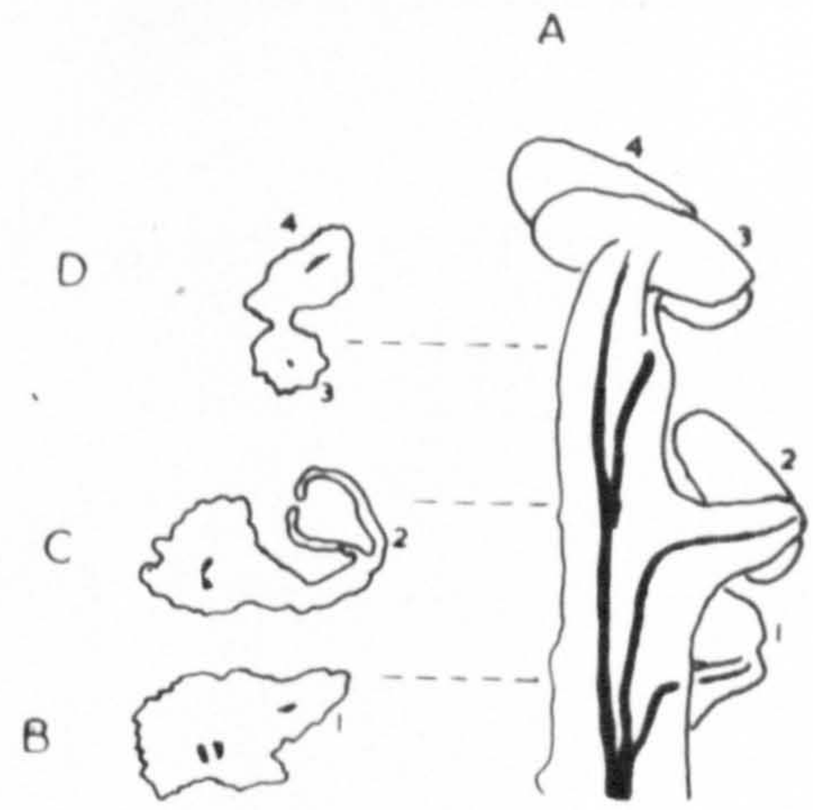

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Fig.43 : A- Reconstruction of a fertile axis. Peels No.91/1-91/376. x 5.

B, C & D- Transverse sections of the axis at different levels. Peels No.91/320, 91/200 & 91/24. x 5.

Fig.44 : A- Reconstruction of a fertile branch end. Peels No.91/132-91/324. x 5.

B, C & D- Transverse sections at different levels of the branch. Peels No.91/290, 91/238 & 91/192. x 5.

15. Figure 45A shows a reconstruction of a slender branch ending in 3 sporangia. The branch is about 1 cm. long and 1 mm. in diameter and it has a single stele (Fig. 45B). The stele becomes triangular in shape and divides into 3 traces (Fig. 45C); the first trace to depart supplies sporangium No. 1 and the other two traces separate from each other less than 1 mm. after the departure of the first trace and they supply sporangia No. 2 and 3.

Figure 45D shows transverse sections of the stalks of the 3 terminal sporangia; the stalks of sporangia No. 2 and 3 are about to be completely separated.

The size of the 3 sporangia is slightly below average and they are all dehisced.

16. Figure 46A shows a reconstruction of a fertile branch ending in 4 sporangia. The branch is about 7 mm. long and 1 mm. in diameter. The 4 sporangia are of a relatively small size and all are dehisced. The branch has a single stele (Fig. 46B). The stele gives rise to a trace which supplies sporangium No. 1 and about 1 mm. higher the stele divides into two strands one supplies sporangium No. 4 and the other divides into two traces to supply sporangia No. 2 and 3 (Figs. 46, C and D). The latter figure shows the relative positions of the 4 terminal sporangial stalks to one another.

17. Figure 47A shows a reconstruction of a fertile branch ending in a group of 5 sporangia. The branch is about 7 mm. long and just over 1 mm. in diameter and it has a single flattened stele (Fig. 47B). The stele divides into two strands; the left strand directly divides into two

traces (Fig. 47C) and these supply sporangia No. 1 and 2. The right strand divides after 1 mm. into 3 traces which supply sporangia No. 3, 4 and 5.

At the level of the transverse section in Fig. 47C the branch is curved as clearly shown in the figure.

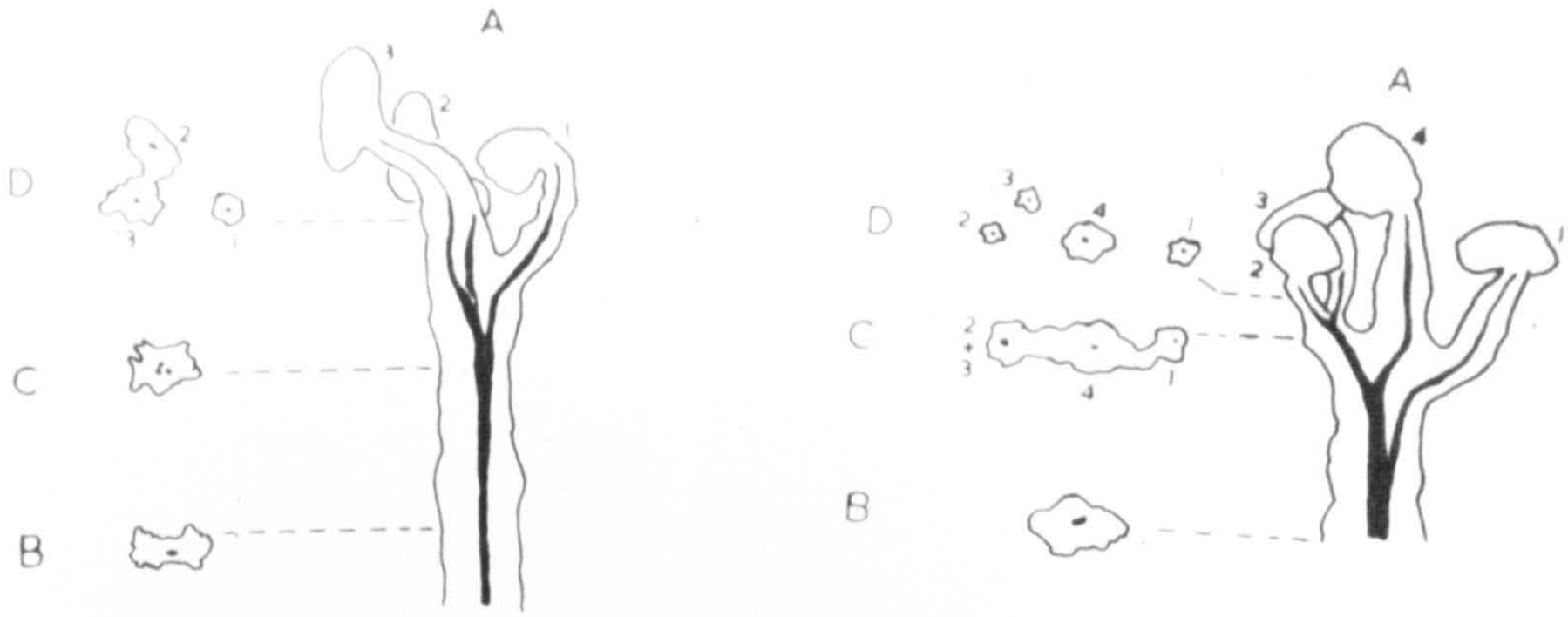
The size of each of the 5 sporangia is slightly below the average yet all are dehisced.

Figure 47D shows a transverse section of the stalks of sporangia No. 2, 3, 4 and 5 and an oblique longitudinal section of sporangium No. 1.

The 5 sporangia together form a cluster and their slits of dehiscence are on the inner side facing each other.

The 3 fertile branch ends reconstructed and shown in Figs. 45A, 46A and 47A were found in one and the same block (No. 91). They were very close to one another as shown in Fig. 48. Although there is no proof, it seems that they were converging a little bit below, but unfortunately there was no more of the block available.

18. Figure 49 shows a reconstruction of a slender branch ending is a fused pair of sporangia. The branch is about 1 cm. long and under 1.5 mm. in diameter. It has a single stele which is almost divided into two traces shortly before the end of the branch (Fig. 50). The upper part of the branch containing the two traces is in the form of two connected stalk#s (Fig. 51). The two connected stalks end in a connected or fused pair of sporangia, which has one common spore cavity and two slits of dehiscence as well shown in Fig. 52. There is doubt whether



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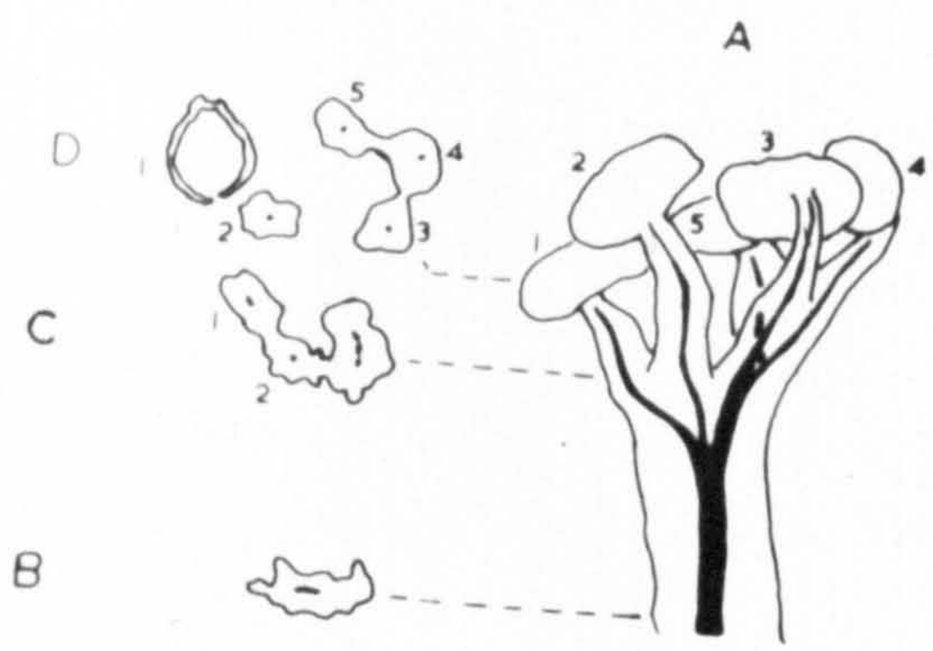

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Fig.45 : A- Reconstruction of a fertile branch end. Peels No.91/95-91/282. x 5.

B, C & D- Transverse sections of the branch. Peels No.91/254, 91/201 & 91/151. x 5.

Fig.46 : A- Reconstruction of a fertile branch end. Peels No.91/131-91/274. x 5.

B, C & D- Transverse sections of the branch. Peels No.91/274, 91/206 & 91/192. x 5.

Fig.47 : A- Reconstruction of a fertile branch end. Peels No.91/143-91/292. x 5.

B, C & D- Transverse sections of the branch. Peels No.91/288, 91/218 & 91/192. x 5.

Fig.48 : Reconstruction of the three fertile branches as they stood in the rock. Peels No.91/95-91/292. x 5.

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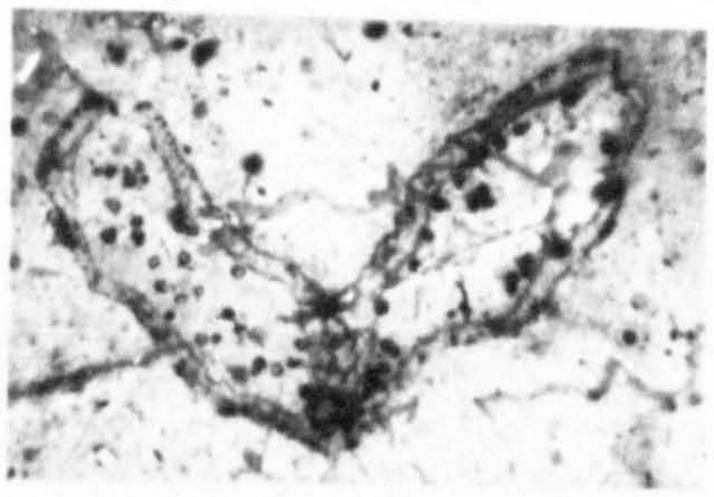

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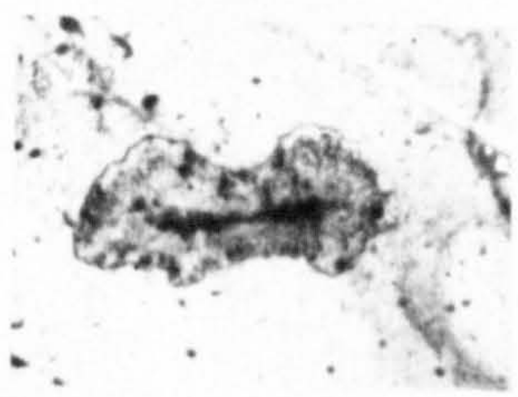

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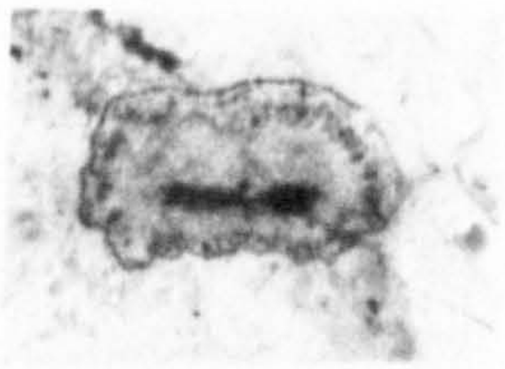

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Fig.49 : Reconstruction of a fertile branch end. Peels No.91/119-91/310. x 5.

Figs.50-52 : Transverse sections at different levels of the specimen. Peels No.91/192, 91/179 & 91/150. x 15.

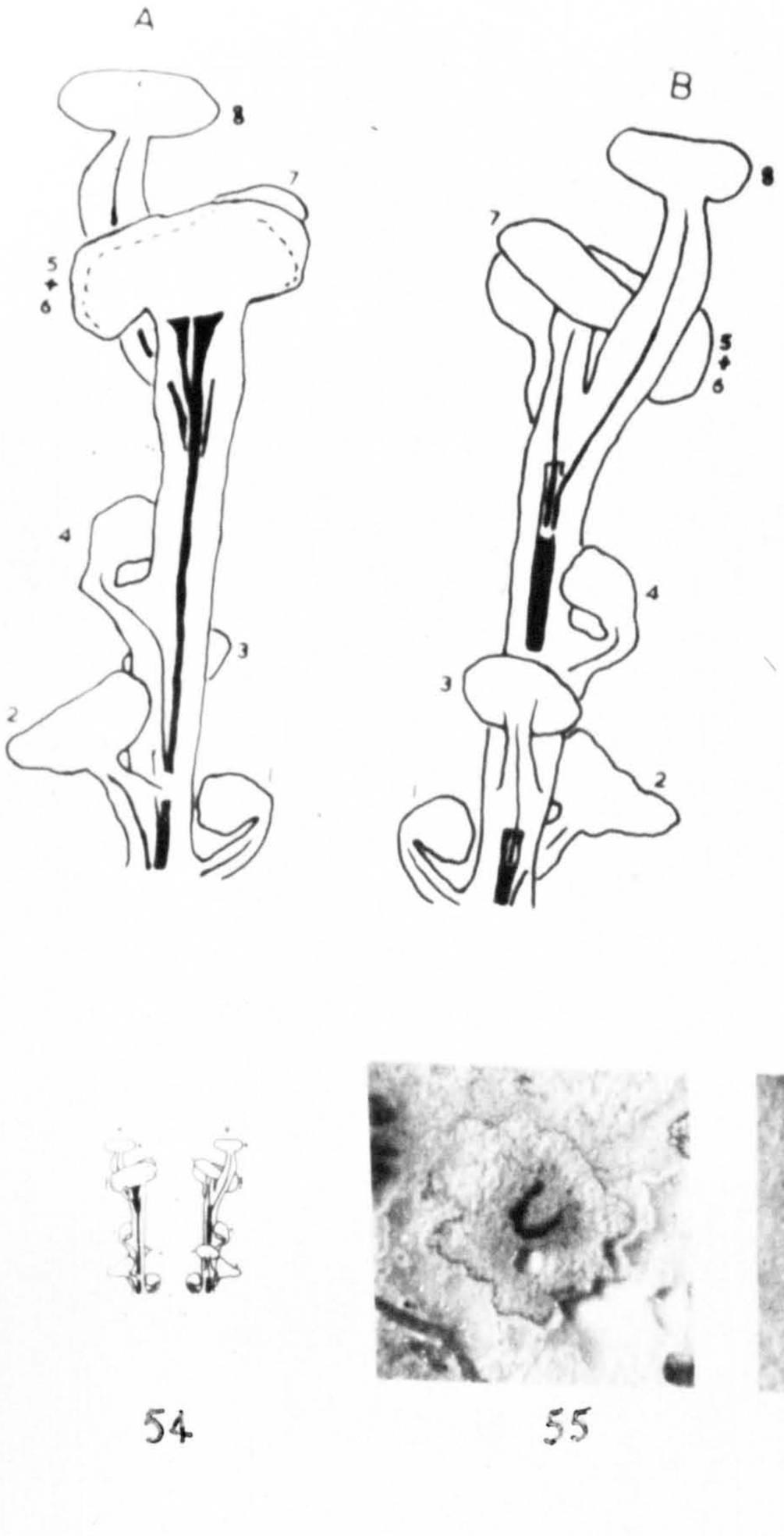
the two slits were or were not continuous, as preservation at the uppermost point is not good.

19. Figure 53A shows a reconstruction of a fertile axis about 1.5 cm. long and under 1.5 mm. in diameter. Fig. 53B is a reconstruction of the same specimen from the opposite side. Fig. 54 shows the same specimen in natural size. The axis bears 4 sporangia and terminates in another 4 sporangia, two of which are connected together. All the sporangia are dehisced. Sporangia No. 1, 2, 3 and 4 have different positions on the axis so that no one of them lies exactly above another. A few millimeters above the departure of trace No. 4 the xylem of the stele becomes horse-shoe shaped in cross section (Fig. 55). The xylem then divides into 2 strands one of which directly divides into 2 traces (Fig. 56). These 2 traces supply sporangia No. 7 and 8. The other strand divides after a while into 2 traces to supply the fused pair of sporangia No. 5 and 6 and the 4 traces could be seen in one transverse section (Fig. 57). The two fused sporangia have two connected stalks and these have two flattened traces (Fig. 58). The two fused sporangia have one common spore cavity and two slits of dehiscence (Fig. 59).

Several fragments of slender sterile axes typical of Nothia aphylla were met with in the blocks. Examples of these are shown in Figs. 60, 63 and 65.

Figures 61 and 62 show transverse sections of the specimen in Fig. 60.

Plate 15



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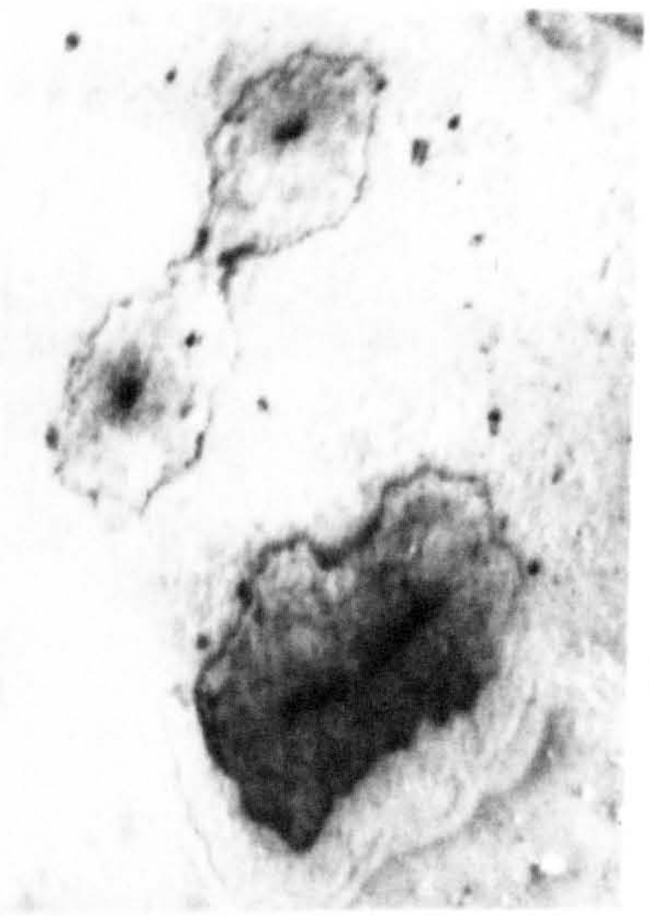

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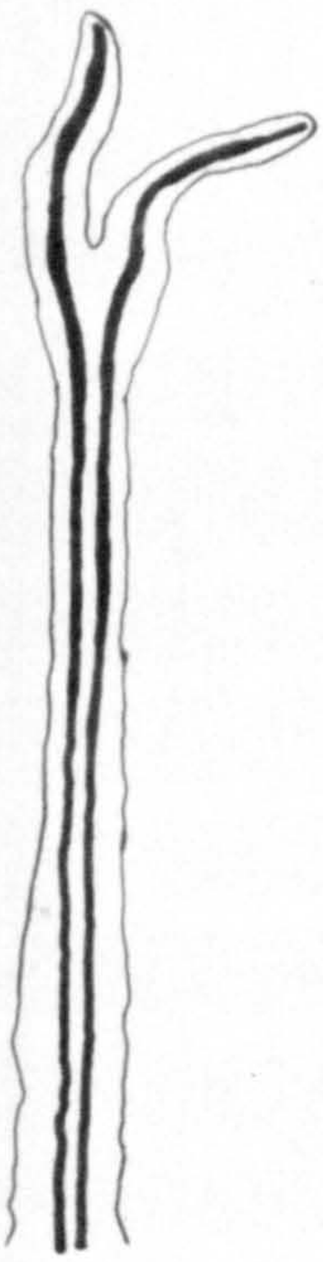
Fig. 53 :A&B- Reconstruction of a fertile branch from two opposite sides.
Peels No.91/62-91/360. x5.

Fig. 54 :The same , Nat. size.

Figs. 55-59 : Transverse sections at different levels of the fertile branch.
Peels No. 91/220, 91/214 , 91/173 , 91/165 &91/130. x15.

Some of the fine branchlets of the two specimens in Figs. 63 and 65 are recurved at their ends as shown in Figs. 64 and 66.

Whether these specimens belong to the shoot system of Nothia aphylla or to its root or underground system can not be stated. These specimens are generally ill-preserved.



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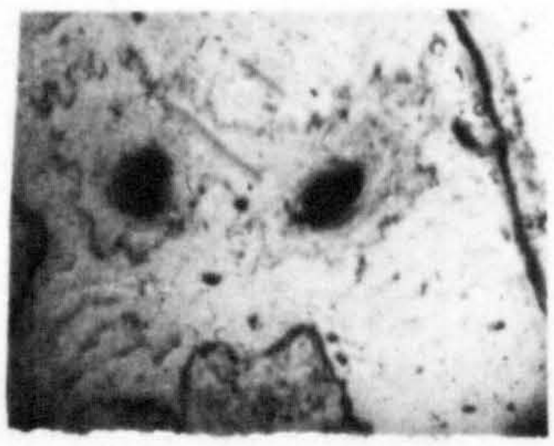

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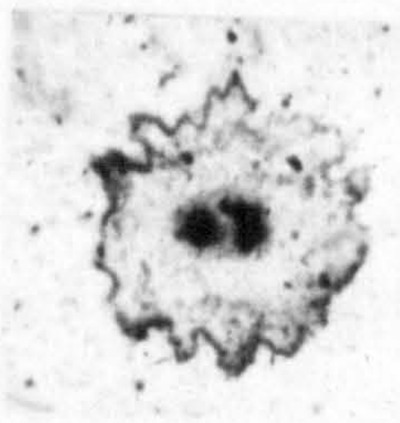

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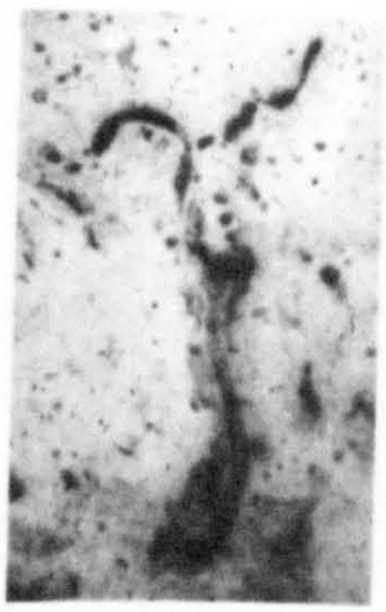

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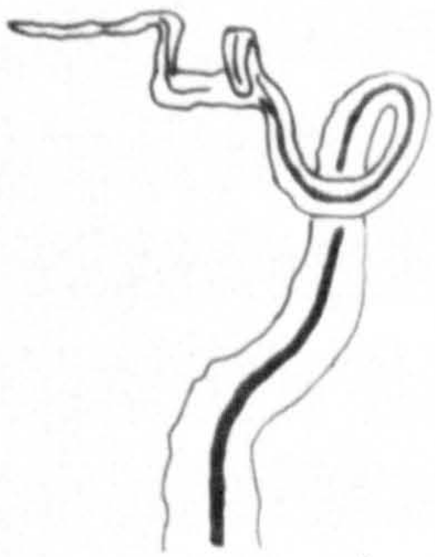

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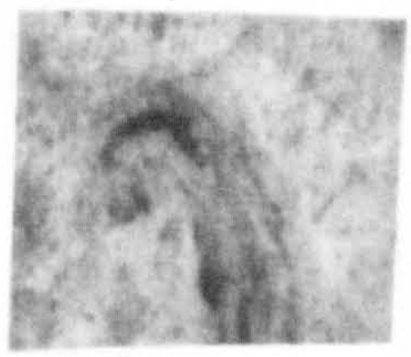

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Fig.60 : Reconstruction of a sterile specimen. Peels No.62/184-62/548. x 5.

Figs.61 & 62 : Transverse sections of the specimen. Peels No.62/501 & 62/260. x 15.

Fig.63 : Reconstruction of a sterile branch. Peels No.69/1-69/130. x 5.

Fig.64 : Fragment of the branch in longitudinal section. Peel No.69/111. x 15.

Fig.65 : Reconstruction of a fertile specimen. Peels No.67/1-67/160. x 5.

Fig.66 : Fragment of the specimen in longitudinal section. Peel No. 67/137. x 30.

DESCRIPTION OF THE WAX MODELS

Wax models of three specimens were prepared by the method described on page 19.

The first model is shown in Figs. 67 and 68. It is a model of a fertile fragment bearing 5 sporangia. One sporangium is in fact a fused pair of sporangia and this explains its peculiar appearance and its difference from the other 4 sporangia, as shown in the model. The specimen has already been described on pages 25 and 26. The wax model shows clearly the position of the sporangia on the axis, the adaxially recurved stalks, the pear-shape of the sporangia in longitudinal section and the overlapping of the two edges of each sporangium at the position of the dehiscence slit, the upper edge always to the outside. The 5 sporangia (including the double one) and the axis are all shown in longitudinal section. Figure 68 shows the side of the model opposite to that shown in Figure 67. The first sporangium from below (sporangium No. 1 in Fig. 20) is shown on its own in Fig. 71. However, this sporangium is incomplete at its left end.

The second wax model is shown in Fig. 72. It is a model of a branched axis. The left branch is not bearing sporangia while the right one bears 2 sporangia, one of which is incomplete. The two sporangia differ from other sporangia in the fact that their stalks are at right angles to the branch bearing them and their slit of dehiscence is longitudinal instead of transverse. Such examples of sporangia are uncommon and whether it is natural or due to displacement during growth or during preservation can not be stated.

The third model is shown in Figure 69. It is a model of two sporangia borne close together on an axis which is cut in a tangential longitudinal section. The stalks of the 2 sporangia are relatively short. The 2 sporangia are dehisced and the overlapping of the two edges at the dehiscence slit of each sporangium is well shown.

The opposite side of the model is shown in Fig. 70. A part of the long slit of dehiscence of the lower sporangium is shown facing the axis.

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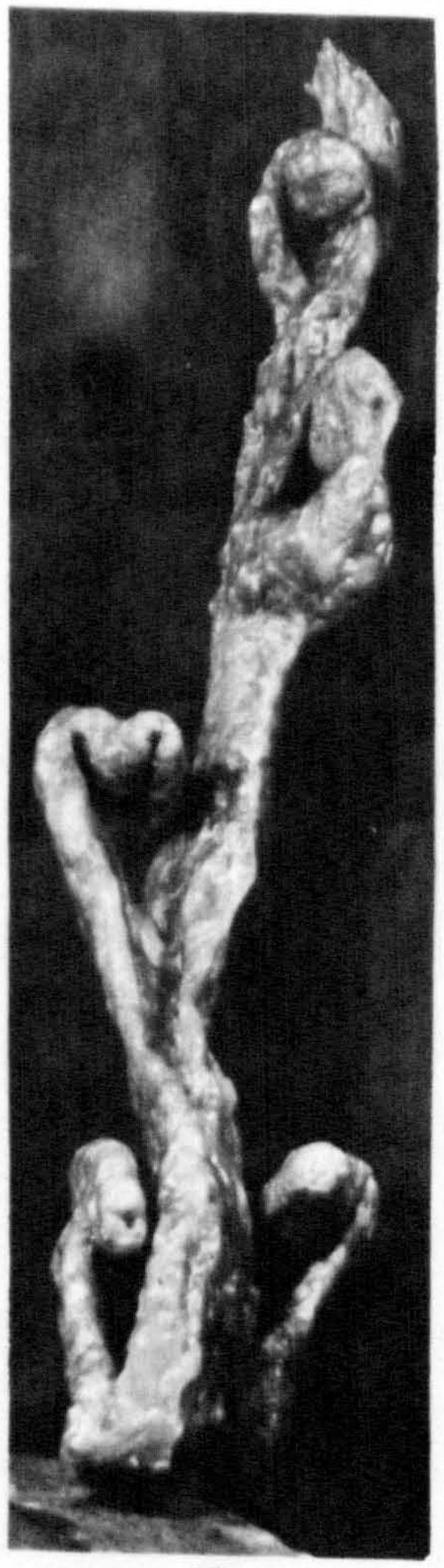

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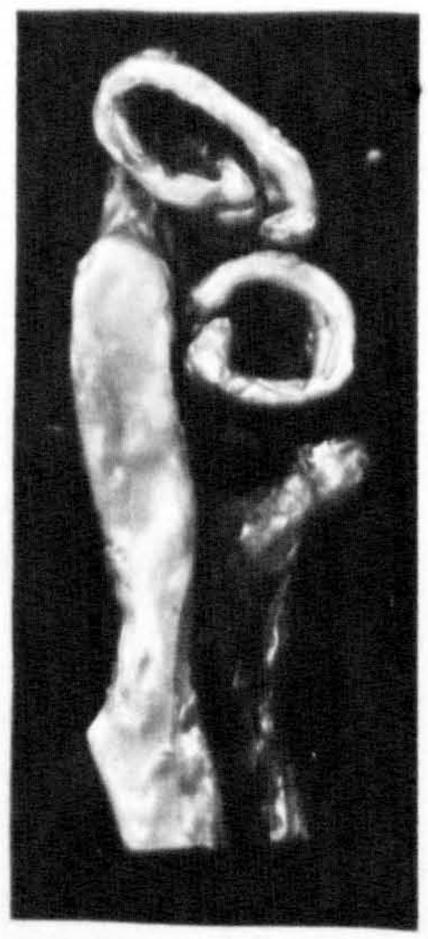

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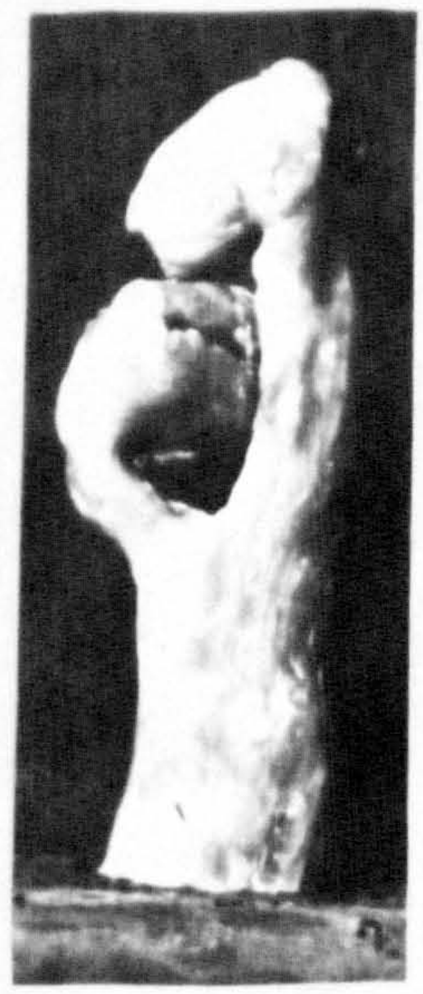

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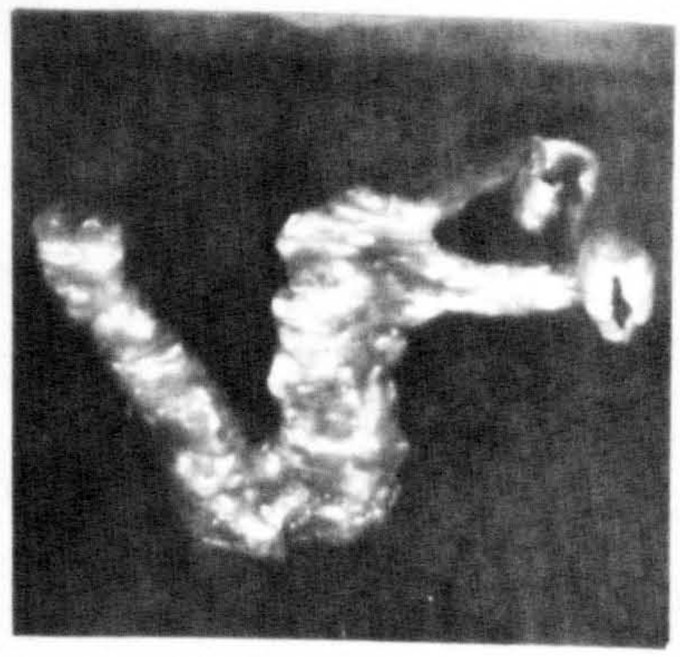

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Figs.67 & 68 : Wax model of a fertile specimen in two opposite sides. x 5.

Figs.69 & 70 : Two opposite sides of a wax model of an axis fragment bearing two sporangia. x 10.

Fig.71 : The lowermost sporangium of the model in Fig.67. x 10.

Fig.72 : Wax model of a branched axis. x 5.

GROSS MORPHOLOGY OF SHOOTS

The whole plant of Nothia aphylla is not yet known, so nothing can be said about its full size or general habit. All the knowledge concerning Nothia came from an enormous number of short fragments of its fertile region and from several fragments of its sterile branches. Nothing is known concerning other regions of the plant.

The general apperance of the axes and the sporangia in the peat is well shown in Figs. 73 - 75 on Plate 18.

The axes are slender leafless stems rarely exceeding a diameter of 2.5 mm. The widest axis (Fig. 76) has a mean diameter of about 5 mm. It is somewhat flattened which might be due to compression during preservation. This large axis branched and the dimensions of the two resulting branches (Fig. 77) are slightly less than those of the main axis.

The longest axis found, though incomplete at both ends, is just over 4 cm. (Fig. 78). The diameter of this axis is about 2 mm.

All axes were found incomplete at both upper and lower ends, but fortunately some fertile and a few sterile branch ends were met with in some of the blocks. Some of the fine ultimate branches of some sterile axes appear recurved at their ends (Plate 16, Figs. 63 - 66).

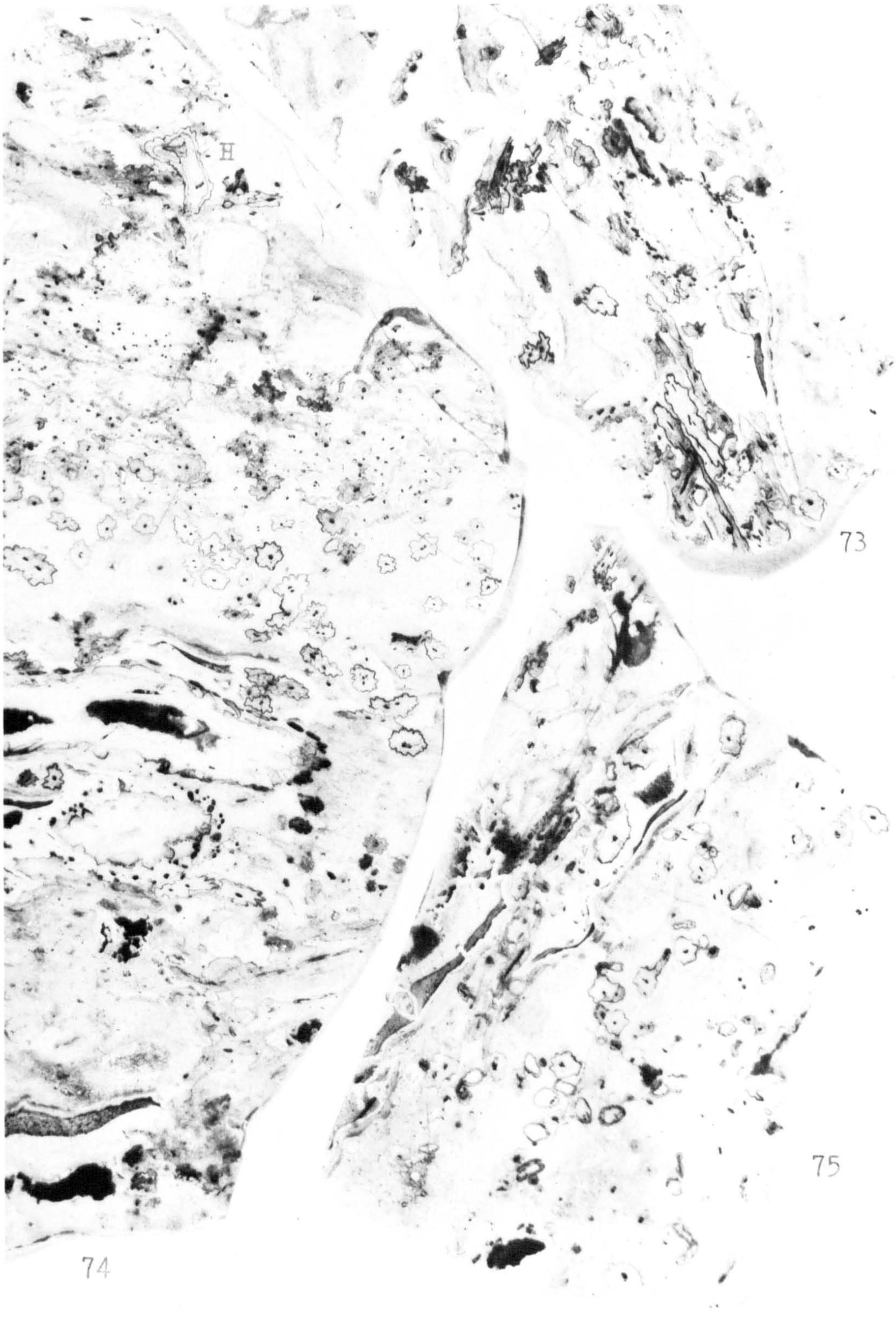
The outlines of the axes are always irregular as can be seen in all the transverse and longitudinal sections of the axes illustrated in this work. The ridges in the outlines of the axes are slightly raised parts, about .2 or .3 mm. high (Fig. 79) and usually have a stoma at their top (Figs. 80 - 82).

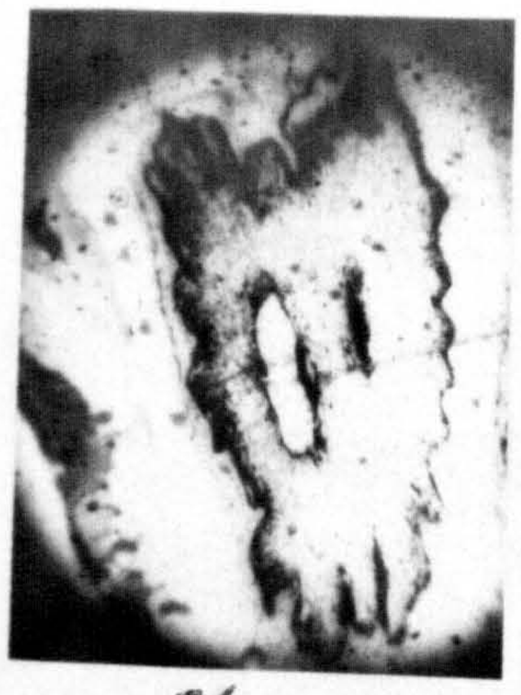
Fig. 73: Portion of peel No. 56/100 showing: Nothia axes, sporangia and Asteroxylon leafy stems. x2.

Fig. 74: Portion of peel No. 67/186 showing: Nothia axes, Asteroxylon stems and a large Horneophyton sporangium at H. x2.

Fig. 75: Peel No. 91/152 showing Nothia axes and about 20 of its sporangia. x2.

Plate 18





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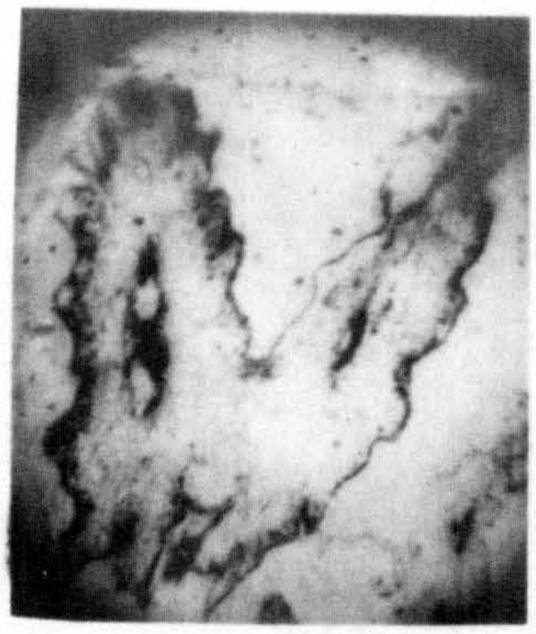

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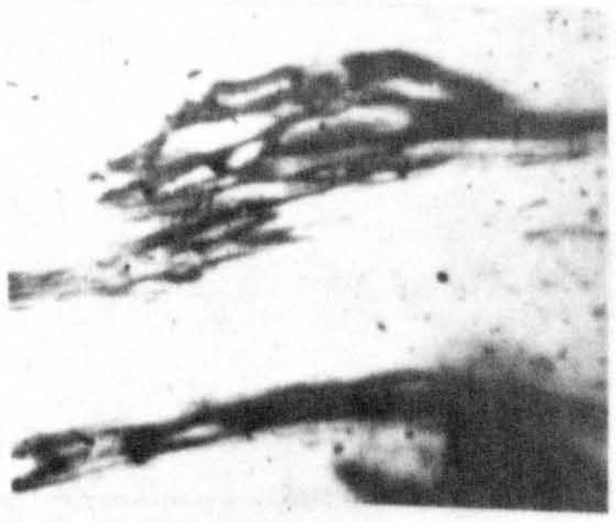

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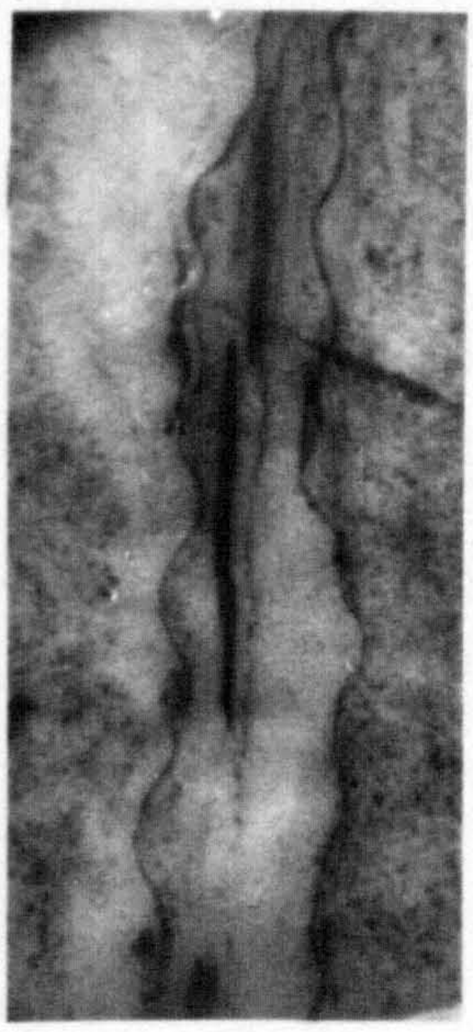

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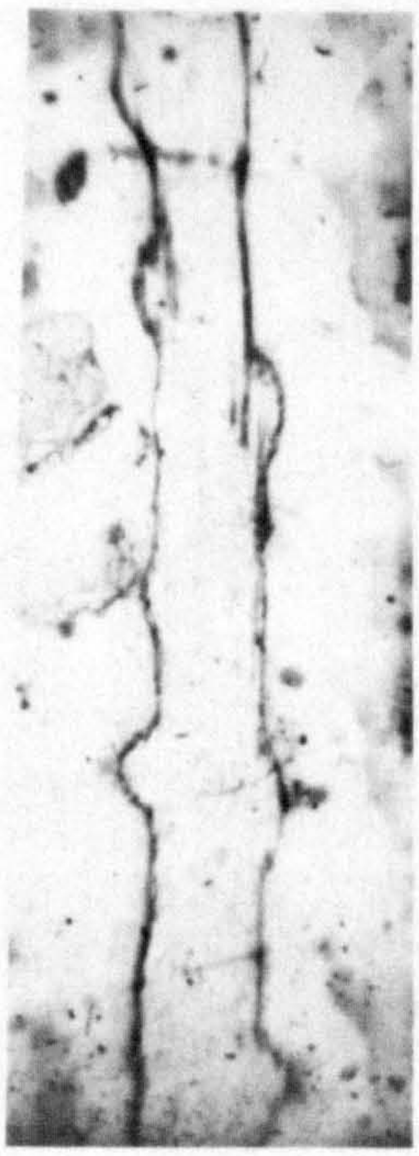

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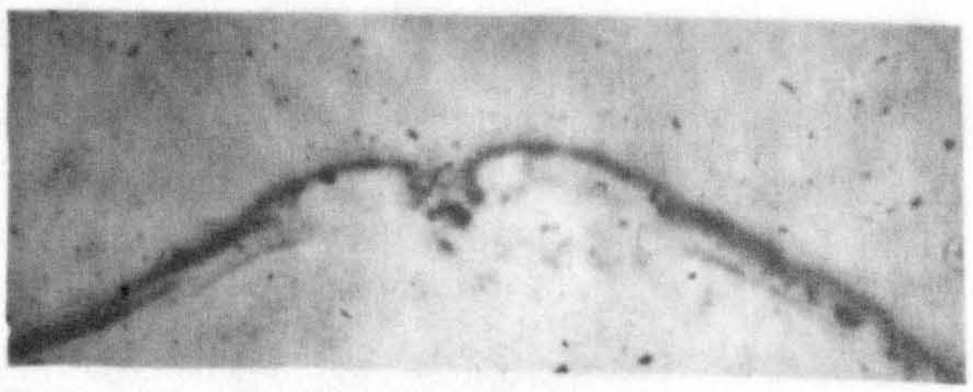

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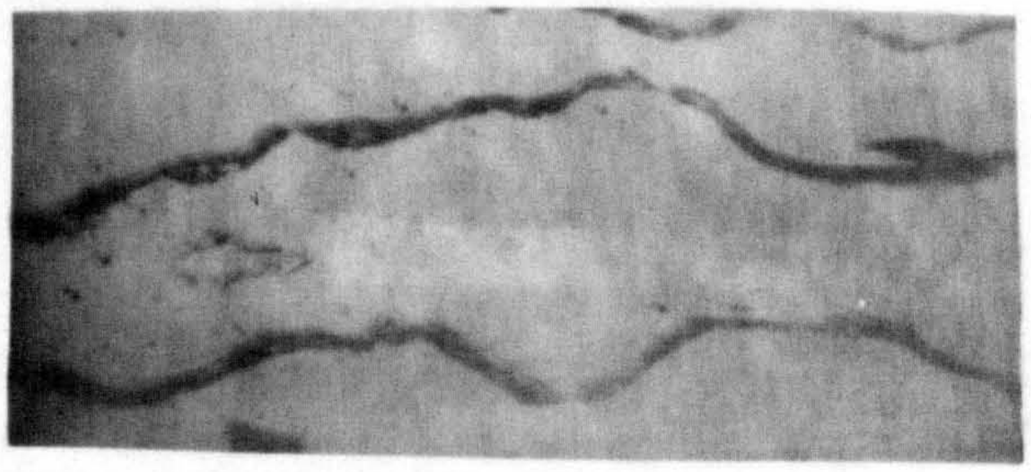

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Fig. 76 : Wide axis. Peel No.62/50 . x5 .

Fig. 77 : The same at the point of branching.Peel No.62/20. x5 .

Fig. 78 : Portion of the longest axis.Peel No.62/40. x10 .

Fig. 79 : T.L.S. of an axis showing several raised parts.Peel No.56/179. x10.

Fig. 80 : Surface view of a stoma at the top of a raised part of an axis. Peel No.56/142. x50 .

Figs. 81&82 : Position of stomata at the top of raised parts.Peels No. 62/112, x40 & 56/113, x20 .

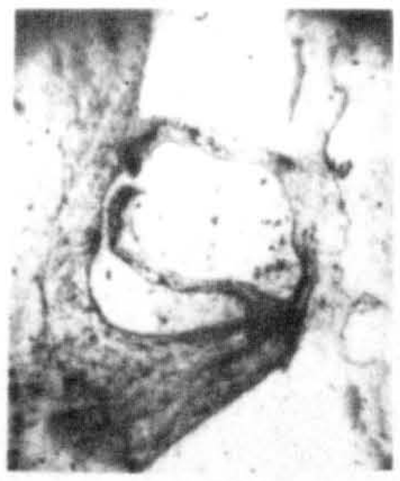
The axes appear to have been naturally twisting stems. The twisting was more conveniently studied in the long unbranched sterile fragments. Thus in one axis fragment it was found that 3 cm. of its length made only 3/4 of a circle. In another axis, 3 cm. of the axis length made only half a circle. However, it was not easy to detect twisting in most of the sterile fragments owing to their short length. In case of fertile fragments it was more difficult because the bases of the sporangial stalks obscured the twisting, if there was any.

Fertile axes and their branches bear many sporangia. The specimen shown in Fig. 43A, which is only about 2.5 cm. long, was found to bear 13 sporangia, though it is incomplete at both its upper and lower ends. Sporangia are borne on short special branches or stalks. Every stalk ends in a single sporangium. However, if a few cases, two stalks were found to be connected and in such cases the two connected stalks end in two fused sporangia, with one common spore cavity and two slits of dehiscence. Stalks vary in length from about 1 to 4 mm. (Figs. 83 - 85), the commonest length being about 2.5-3 mm. In cross sections stalks are almost rounded or slightly irregular (Fig. 87). Stalks are thick at their base having a diameter sometimes nearly the same as that of the axis bearing them (Figs. 84 and 86). However, stalks taper gradually upwards and at their distal ends they almost abruptly become very thin, incurve and end in the sporangium (Fig. 84). Although the junction point between a sporangium and its stalk is very slender yet not a single stalk was found with its sporangium detached. But some isolated sporangia were found in the blocks. The diameter of a stalk is generally just under 1 mm. The position of the stalk on the axis

is best shown in the longitudinal section of the fertile specimen in Fig. 84. It is clear in this figure that the stalk forms an acute angle with the axis bearing it. However, a few stalks were found to be almost perpendicular to the axis bearing them (Fig. 88). The stalks are adaxially recurved so that the long dehiscence slits of the sporangia are transverse and directed towards the main axis (Figs. 89 - 91). In a transverse section of a fertile axis passing through the apical part of a sporangium, the latter appears between its stalk and the axis (Figs. 89 and 92). In such a section the axis and the stalk are cut transversely while the sporangium itself is cut vertically. The long axis of a sporangium is usually horizontal, but in some cases it might be oblique or even vertical (Plate 17, Fig. 72). In the latter case the appearance of the sporangium in a transverse section of the axis is well shown in Fig. 93. The stalk is attached to the middle of the sporangium (Figs. 94 and 95) or sometimes slightly nearer to one end rather than to the other. Sporangia are more or less reniform and vary greatly in size but generally a sporangium is 1.5 mm. long x 2.7 mm. wide x 1.2 mm. thick. The smallest sporangia were found at the ends of slender fertile branches (Figs. 97 and 98). This, however, does not exclude the fact that sporangia of average size were found at fertile branch ends. Sporangia borne on slender branches are usually, but not always, smaller in size than sporangia borne on branches of larger diameters. The size of a fused pair of sporangia is almost double the size of a single sporangium (Plate 14, Fig. 52 and Plate 22, Fig. 96).

Branching of the axes

The axes branched by repeated dichotomy (Fig. 104). Unequal branching



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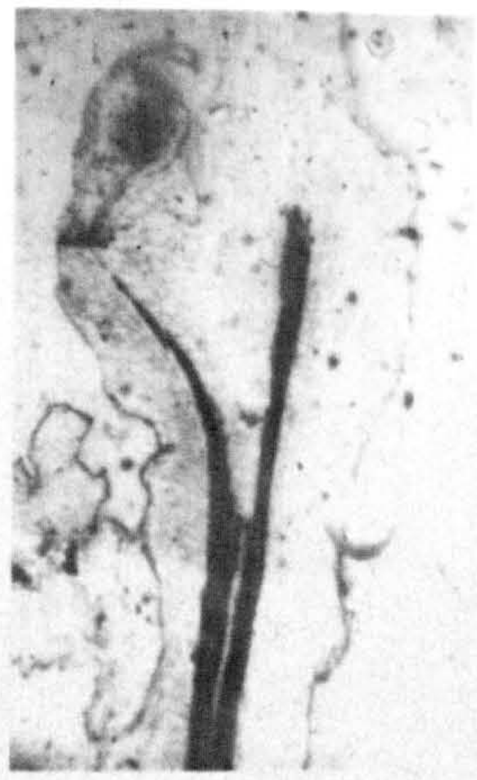

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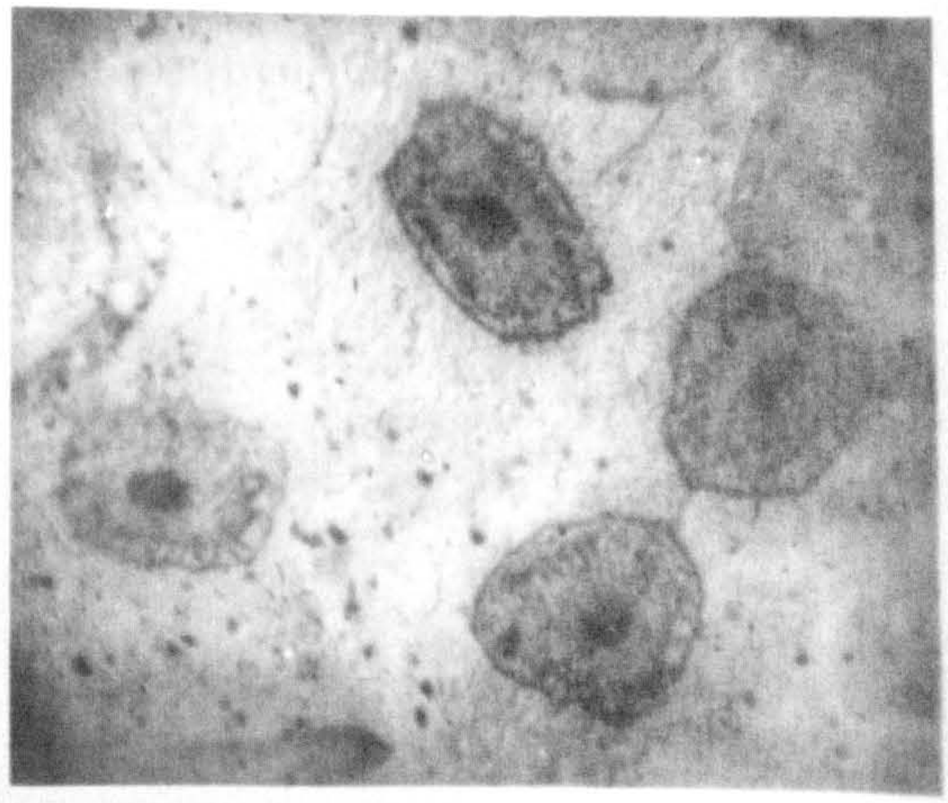

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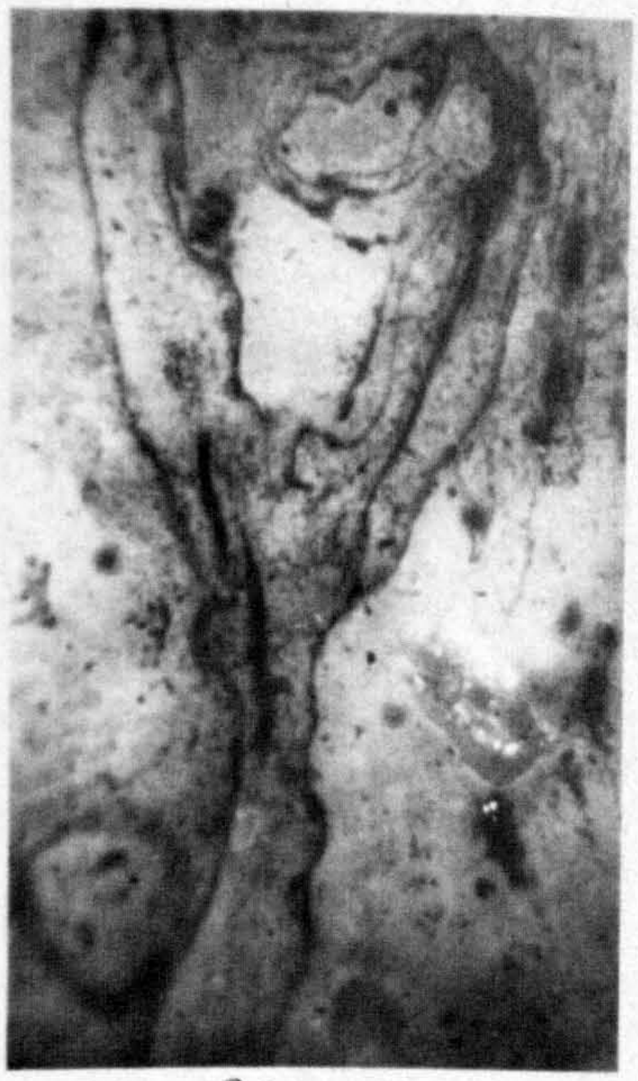

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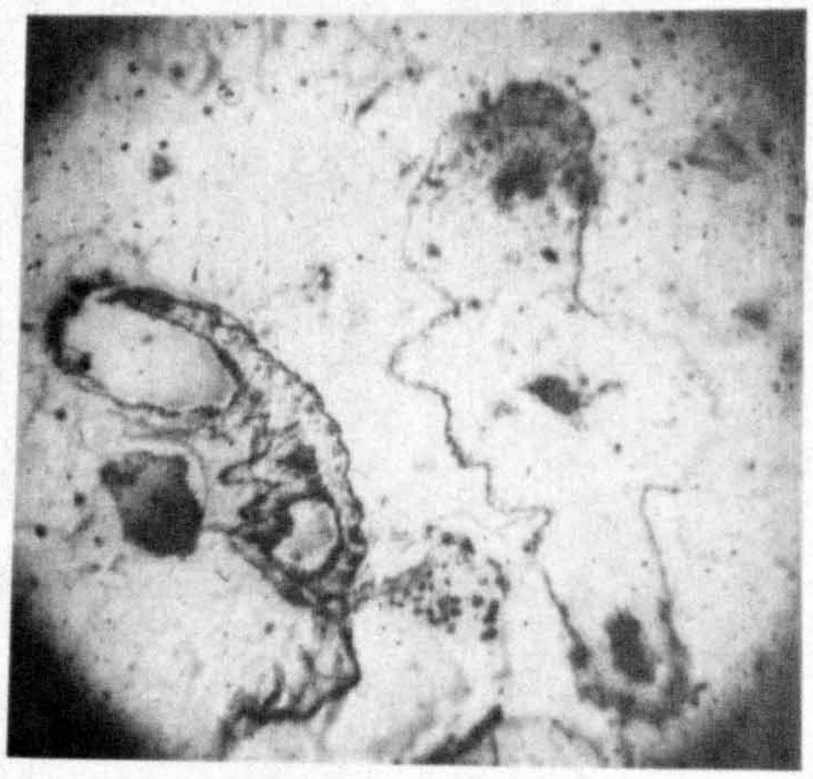

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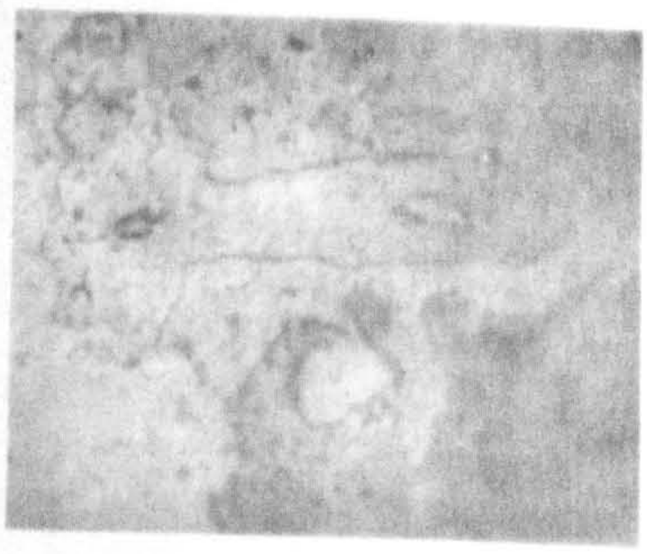

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Fig. 83 : Sporangium stalk about 1.5 mm. long. Peel No. 56/58. x10 .

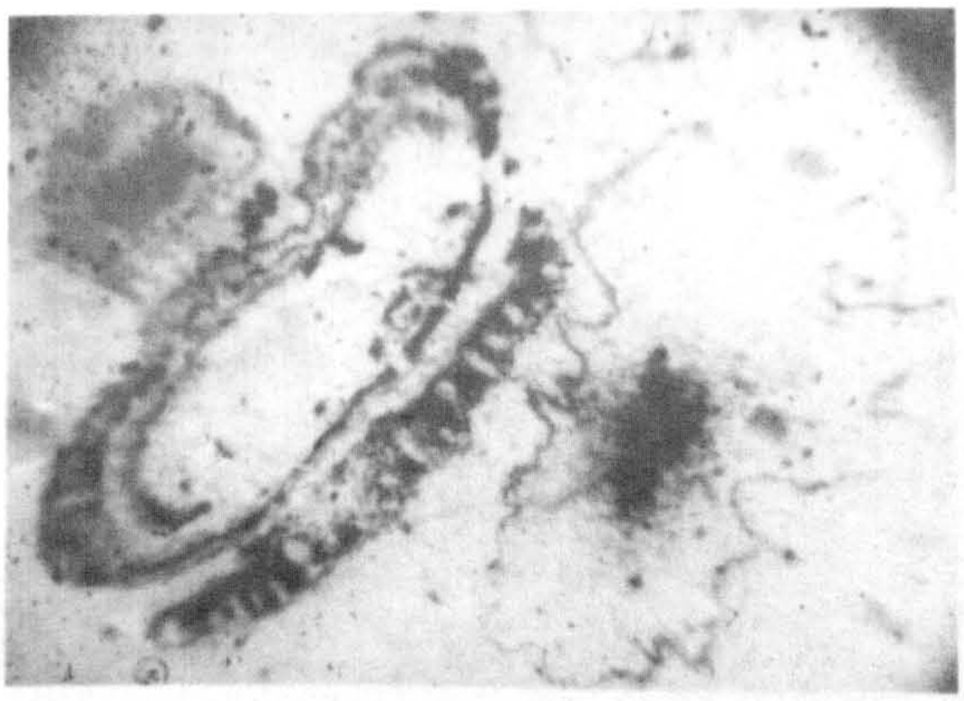
Fig. 84 : " " 4 mm. long . Peel No. 56/17. x10 .

Fig. 85 : " " under 1.5 mm. long. Peel No. 62/430. x10 .

Fig. 86 : Transverse section of a fertile specimen showing an axis bearing two opposite stalks. The sporangium at the left is cut in a vertical plane. Peel No. 91/332. x10 .

Fig. 87 : Four sporangial stalks in T.S. Peel No. 91/191. x20 .

Fig. 88 : T.S. of a fertile axis showing a perpindicular stalk. Peel No. 91/14. x10 .



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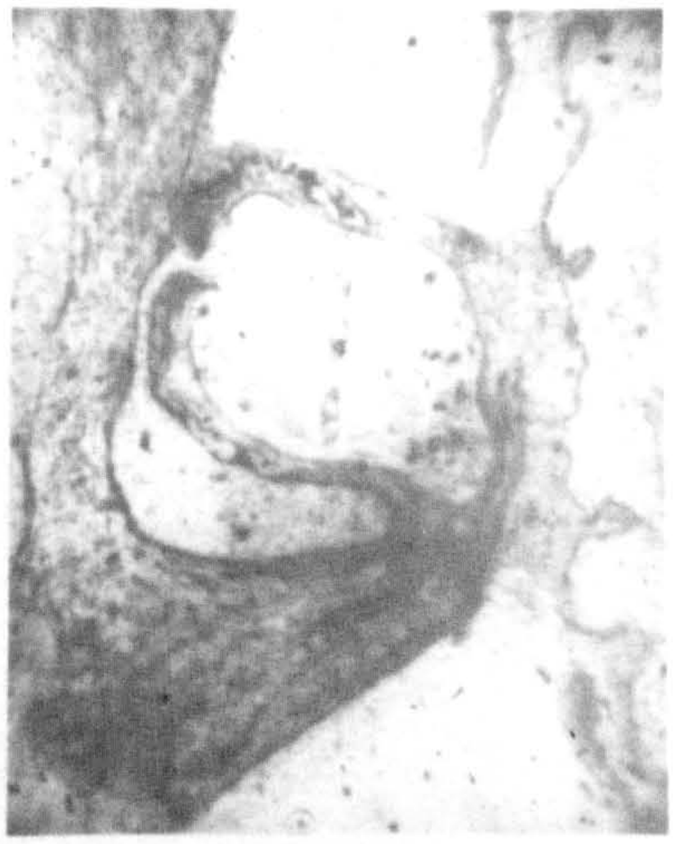

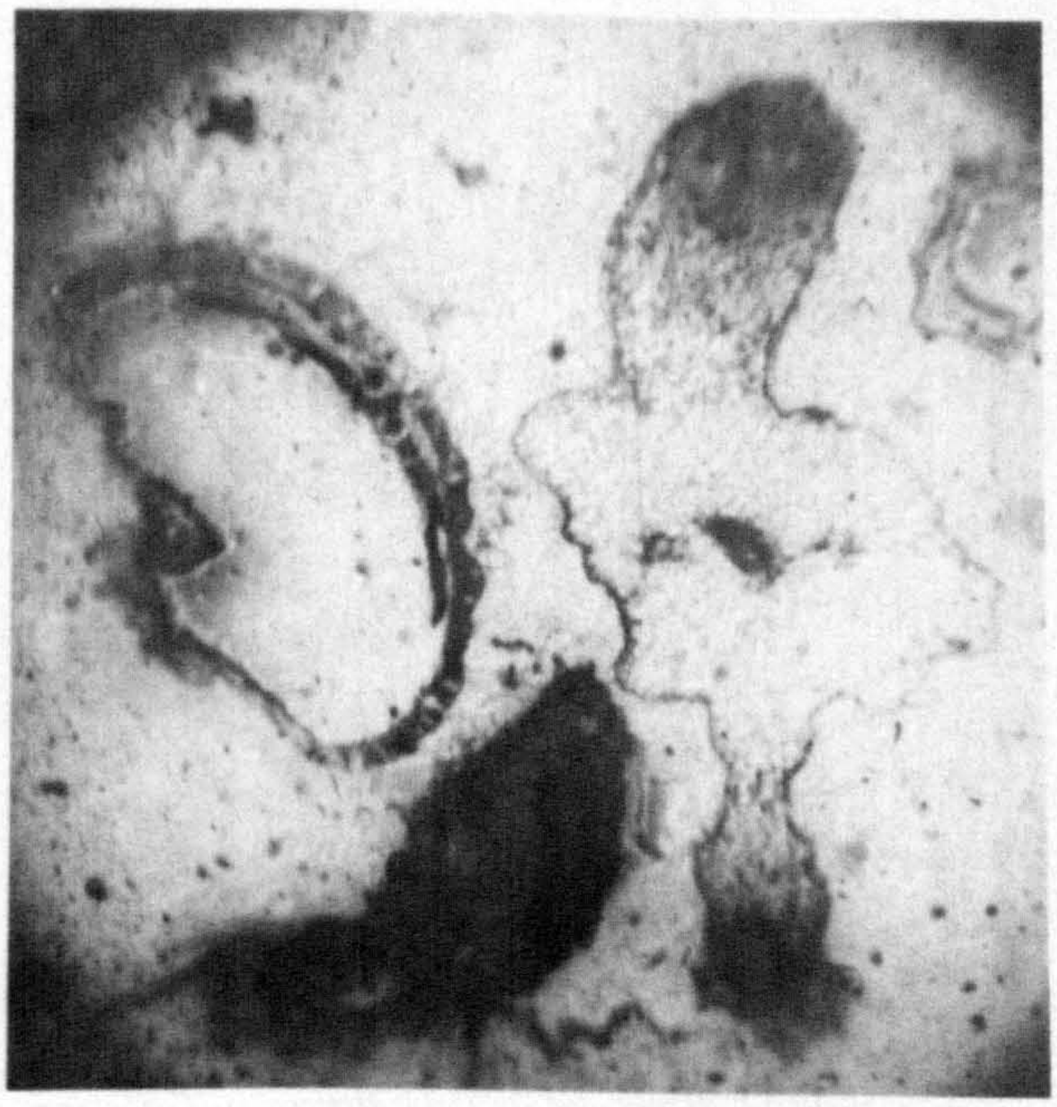

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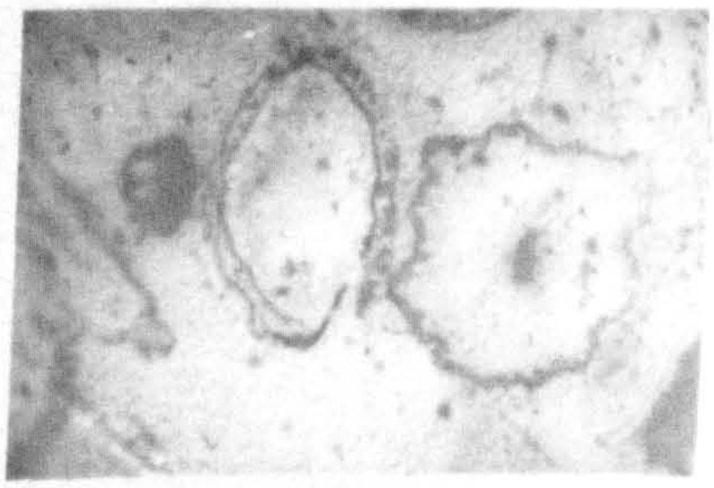


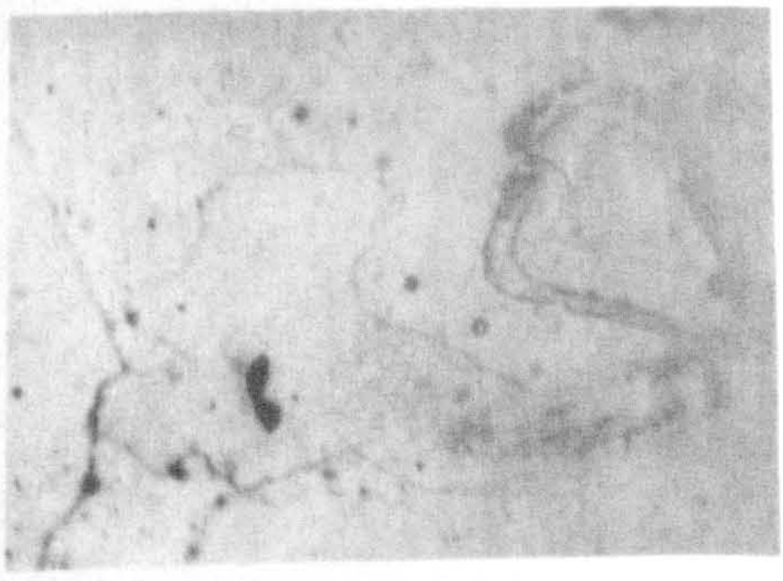


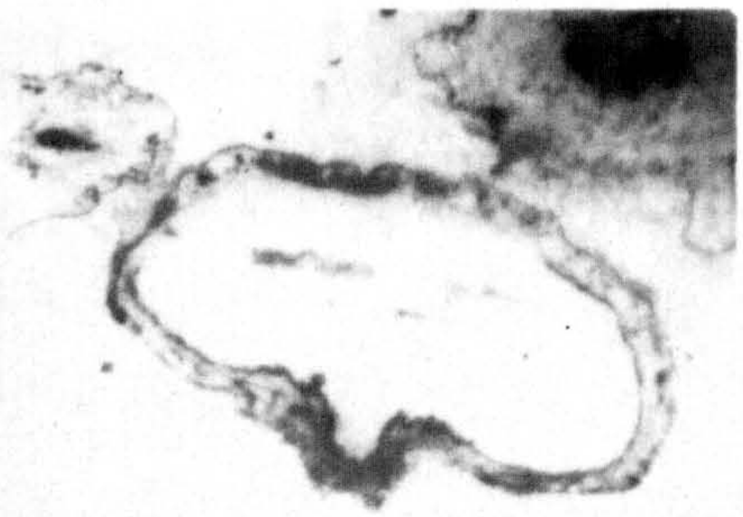
Fig. 89 : T.S. of a fertile axis.The sporangium is cut in a median vertical section and is seen between its stalk and axis.Peel No.91/152. x20 .

Fig. 90 : T.S. of a fertile axis bearing two opposite stalks.The sporangium is cut in a median vertical section. Peel No. 91/327. x15 .

Fig. 91 : L.S. of a sporangium showing dehiscence slit facing the axis. Peel No.56/58. x20 .

Fig. 92 : T.S. of a fertile specimen showing sporangium between its stalk and axis. Peel No.91/53. x10 .

Fig. 93 : T.S of a fertile axis . The oblicue sporangium is cut in L.S. Peel No.91/243. x15.



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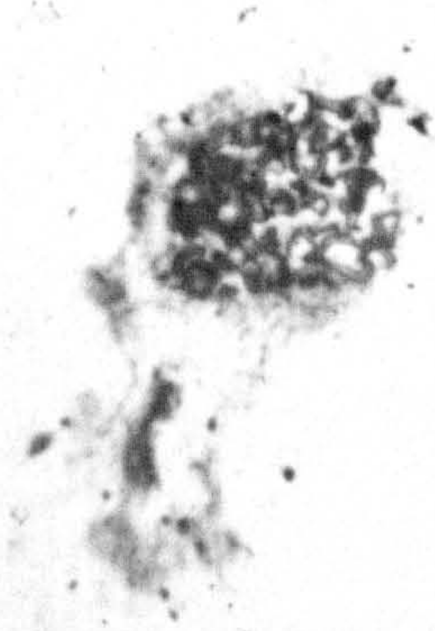

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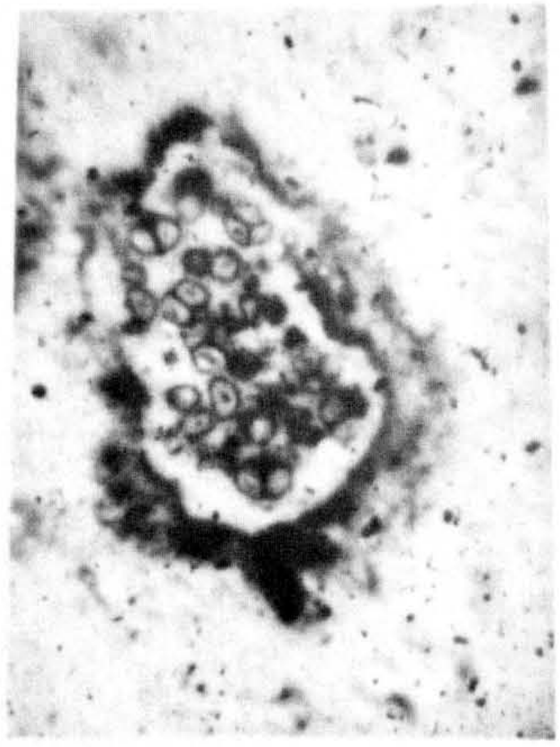

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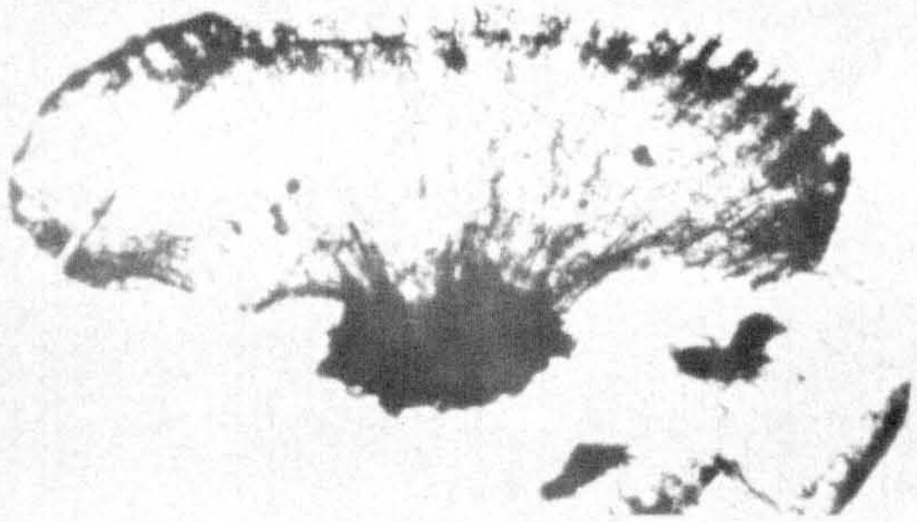

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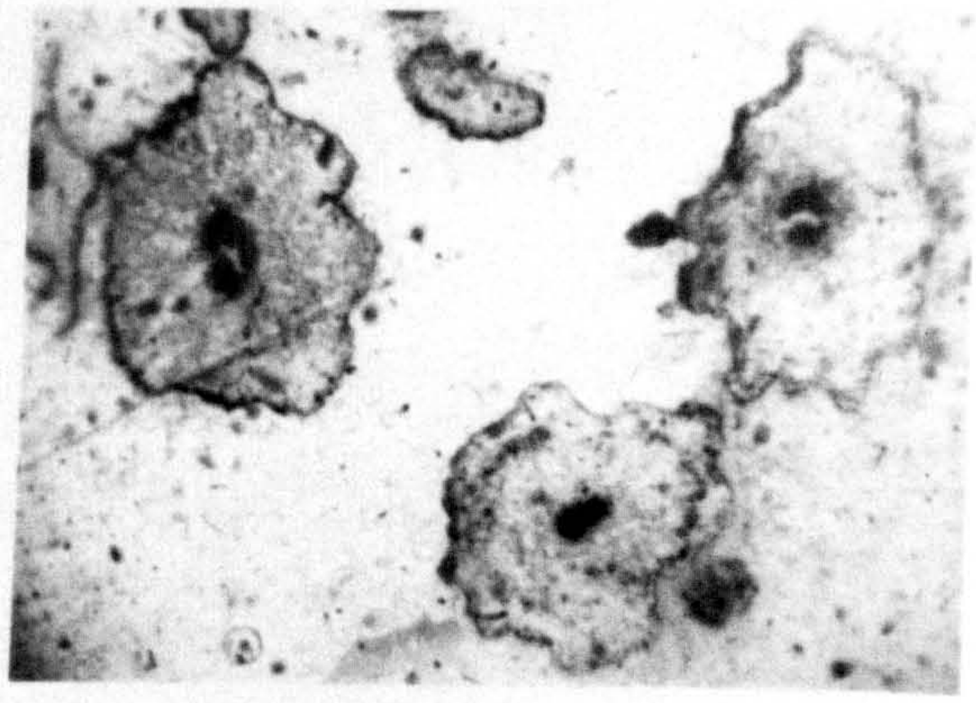

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Fig. 94 : Sporangium in vertical section.Peel No.91/173. x15 .

Fig. 95 : Vertical section passing through the wall of the sporangium. Photo by transmitted light.Ground section, slide No.91/377. x20.

Fig. 96 : Two fused sporangia.Peel No.62/317. x15 .

Fig. 97 : Small sporangium in L.S. Peel No.56/206. x50 .

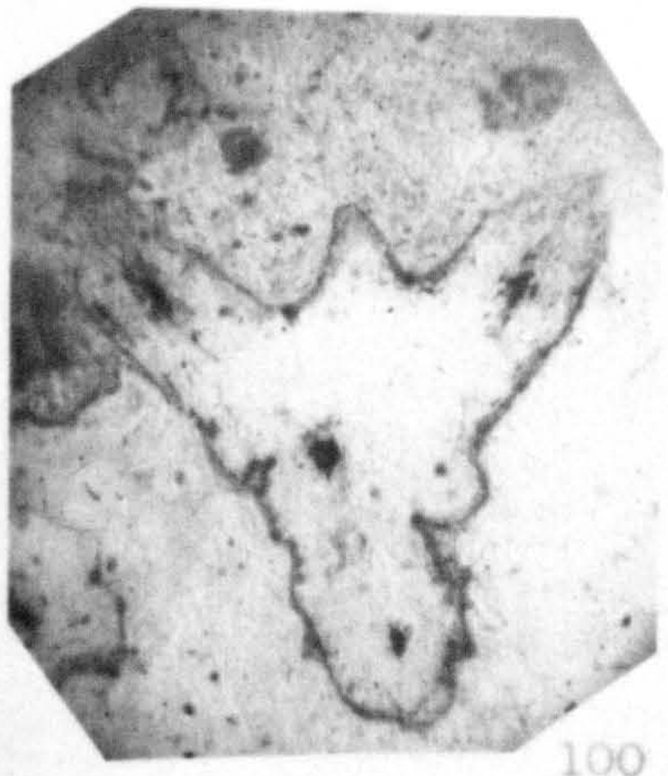
Fig. 98 : " " " " " Peel No.56/171. x50 .

Fig. 99 : T.S. of a specimen passing through the main axis (at right) and its two lateral branches (middle and left).Peel No.62/236. x15 .

was sometimes noticed (Figs. 103 and 105), as well as a few cases of lateral branching (Plate 22, Fig. 99). Branching is three-dimensional and is more frequent in the upper and more slender parts of the axis. It was observed (in the specimen on Plate 4, Fig. 19) that almost every dichotomous branching is at right angles to the previous and the following ones to it, i.e. if one dichotomy took place to the right and left, the following one will be to the back and front. But successive lateral branches are usually borne on one side of the axis and almost above one another. Most of the examples of lateral branches were found in block 62. The only 3 lateral branches reconstructed are shown on Plates 3 and 4, Figs. 17 and 19. The specimen shown in the first figure has two lateral branches, very close to each other and borne on one side of the axis and in the transverse section in Fig. 17B (Plate 3) they form with the axis a curved shape. In a second transverse section (Plate 22, Fig. 99) at about 2.5 mm. higher than the previous one, the position of the two lateral branches after their separation from the axis is well shown. Lateral branches are peculiar in that their diameter is almost the same as that of the main axis carrying them or even more (Fig. 99) yet their growth in length is very limited and the longest one found is less than 6 mm. long.

Arrangement of the sporangia on the axes

Many fertile specimens were examined and 19 of them were reconstructed. For the purpose of easy comparison they are all shown at a low magnification on Plate 24 (Figs. 106 - 124). These 19 fertile fragments carry between them more than 120 sporangia, the largest number being borne on the branched axis in Fig. 124. The sporangia are not crowded but fairly spaced on the



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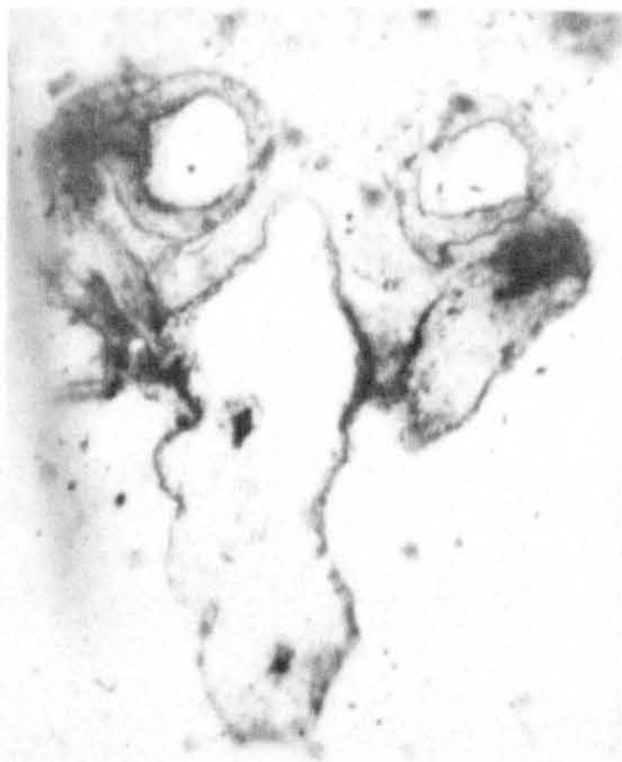

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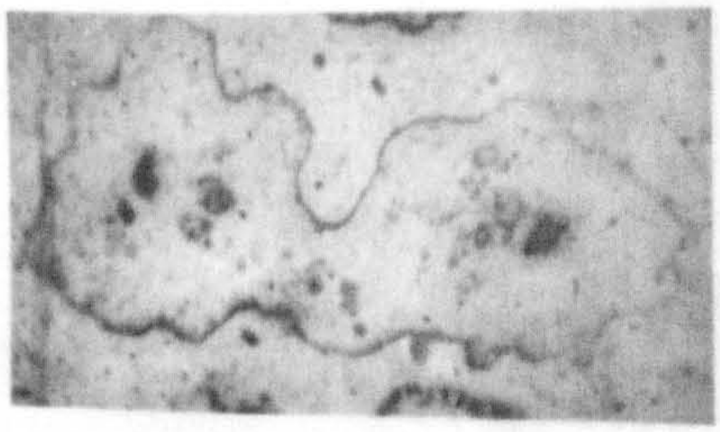

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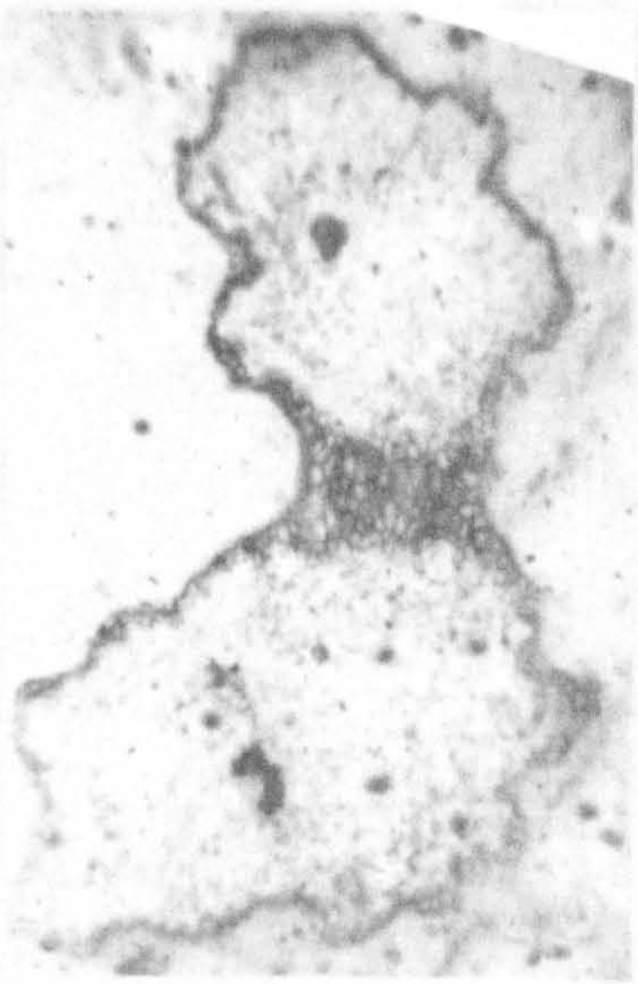

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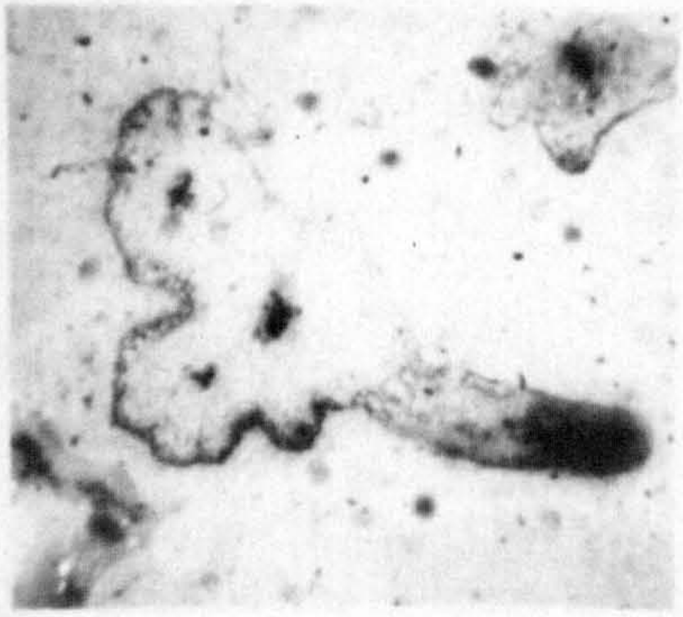

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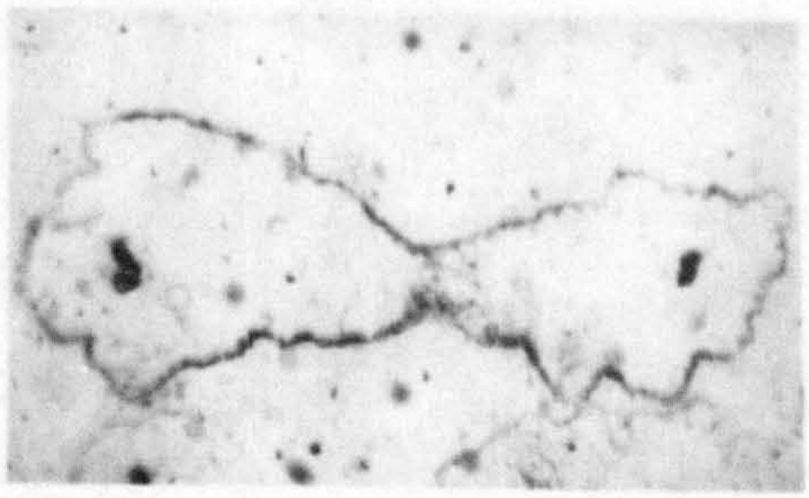

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Fig. 100 : T.S. of a fertile axis showing its stele and three sporangial traces. Peel No. 91/88. x10 .

Fig. 101 : T.S. of an axis. The sporangial stalk at the right is about to separate from the axis. Peel No. 91/95. x10 .

Fig. 102 : T.S. of an axis showing the separation of two sporangial stalks at the same level. Peel No. 91/80 . x10 .

Fig. 103 : T.S. of an axis showing unequal dichotomy. Peel No. 91/273. x10 .

Fig. 104 : Dichotomizing axis in T.S. Peel No. 91/199. x10 .

Fig. 105 : T.S. of an axis showing unequal branching. Peel No. 62/124. x15 .

axes and their branches. As shown in the reconstructions, they are stalked and borne laterally on the axes. Sporangia were found also to terminate branch ends.

The reconstructions show clearly the irregularity in the arrangement of the sporangia on the axes and their branches. The arrangement of the sporangia not only differs from one specimen to another but on one and the same specimen different patterns of sporangial arrangement are exhibited.

It must always be remembered that all the fertile specimens studied are incomplete at either the upper or the lower end or most usually at both. This makes it impossible to give a picture of the complete fertile region.

A general idea of the irregularity in the arrangement of the sporangia has already been given in the description of the specimens. However, the following are all the forms of sporangial arrangements discovered :-

1 - Sporangia arranged at random; on all the sides of the axis and its branches (Fig. 124).

2 - Sporangia arranged spirally on the axis. For example, those borne on the far left branch of the repeatedly branched specimen in Fig. 118.

Many fertile branches were found to start at their base with two sporangia borne at one level (Figs. 113 and 123). The specimen in the first figure and the right branch of the specimen in the second figure, each bears (after the first pair of sporangia) 3 spirally arranged sporangia.

3 - Sporangia arranged in whorls of three; a whorl might succeed a whorl (Fig. 117) or a single sporangium might be borne between every two successive whorls (Fig. 120). The single sporangium might be borne at equal distances from the two whorls (see sporangium No. 8 in Fig. 120), or

the single sporangium might be borne closer to one of the two whorls than to the other (see sporangium No. 4 in Fig. 120).

4 - Sporangia arranged differently on the axis; i.e. there is a mixture of patterns. At one level there might be borne a single sporangium, at another level a pair of opposite sporangia and at a third level a group or whorl of 3 sporangia (Fig. 121).

The specimen in Fig. 114 bears 5 sporangia; 3 of them are almost at one level, but they differ from whorls of other specimens in that they are confined to one side of the axis and the other 2 sporangia are confined to the opposite side.

It must be mentioned that the 3 sporangia of any whorl (in all the specimens studied) do not form an equal triangle around the axis, i.e. the 3 sporangia of a whorl are not equally spaced on the circumference of the axis; two of them are usually closer to each other than to the third one (Plate 23, Figs. 100 - 102).

The three sporangia of a whorl are usually borne at very slightly different levels (a very close spiral) or in some cases 2 of them are borne at exactly the same level and the third sporangium either very slightly lower (Fig. 101) or higher (Fig. 102) than them.

It has been noticed that the 3 sporangia of a whorl usually alternate in position on the axis with the 3 sporangia of the following whorl, this is best shown in the two successive whorls of the specimen in Fig. 117.

Fertile branches were found to end usually in 2 or 3 sporangia (Fig. 106 - 108). However, a group of 4 or 5 sporangia might terminate a fertile branch end (Figs. 109 - 11). In the case of the 5 terminal sporangia, they were arranged in a circle (Plate 36, Fig. 246) with their dehiscence slits to the inside facing one another.

As mentioned before, it happened sometimes that two sporangia were found to be connected together. Such fused sporangia might be borne latterally on the axis among other sporangia (Fig. 116) or terminally at branch ends (Figs. 106 and 111). The branch in the first figure ends in the two connected sporangia only while that in the second figure ends in two ordinary sporangia in addition to the fused pair.

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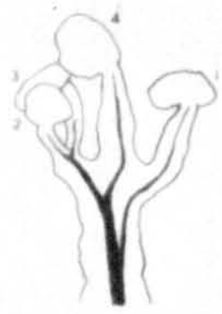

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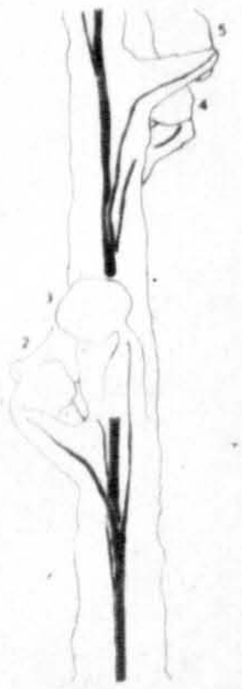

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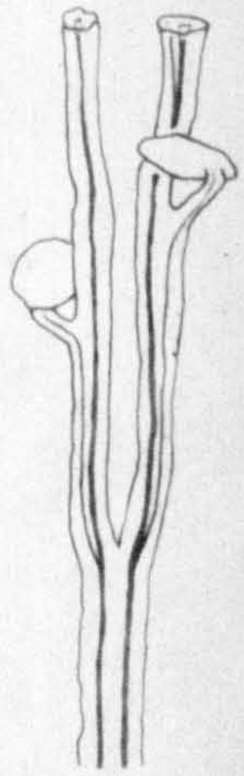

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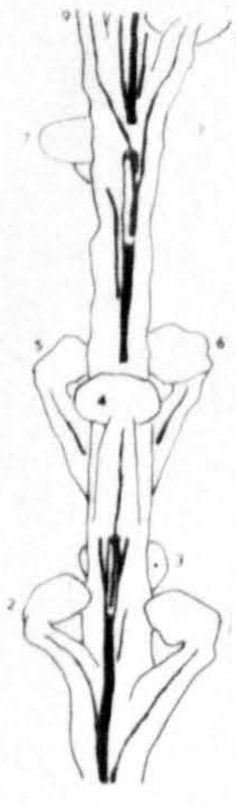

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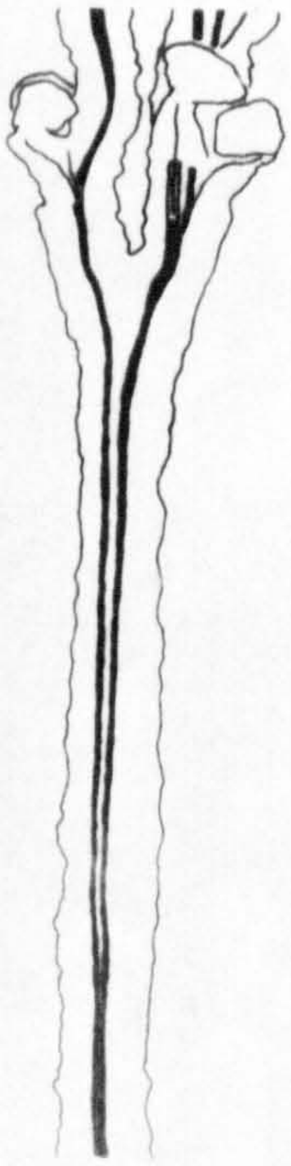

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Figs.106-124 : Reconstructions of 19 fertile specimens. All ; x 3.

MORPHOLOGY OF XYLEM

Xylem is usually the only persistent component of the stele. The axes (fertile or sterile) have a single or a paired protostele, but whenever there is a paired stele in an axis it is always found that the axis subsequently branches after a longer or shorter distance and each branch receives one of the two steles.

On entering a branch the stele may behave in a number of ways :-

1. The stele keeps single and in this case the branch does not branch again.

2. The stele divides into two directly on entering the branch or even just before entering the branch.

3. The stele keeps single for several millimeters then it divides into two, still a considerable distance before the branch branches again.

All these cases occured in the repeatedly branched axis shown in Fig. 118.

It was never found that an axis stele divided directly before branching of the axis (except in a few cases of lateral branching) but usually several millimeters before the branching.

The steles of two branches of an axis do not alway behave in the same way; the stele of one branch might divide directly on entering the branch while the stele of the other branch might keep undivided for several millimeters, though the two branches might be of equal size or one of them might be of a larger size than the other (Plate 23, Fig. 105) and in the latter case it is the larger branch that has its stele divided into two from the beginning.

In case of lateral branching also, the stele divides a long way before the branching of the axis occurs, except in a few cases when it was observed

that the division of the stele took place almost directly before the lateral branching occurred (Plate 24, Fig.112).

The division of the xylem into two strands as a preparation for the branching of the axis takes place in three different ways :-

1. (see Figures 125-131, 132-136 & 137-141). An island of phloem appears inside the solid core of xylem (Figs.126 & 132). The internal phloem increases in size and eventually becomes connected with the outer phloem on one side, thus making the xylem appear almost horse-shoe shaped in cross section (Figs.127, 133, 134 & 137). The horse-shoe shaped xylem eventually divides into two strands (Figs.128, 135 & 138). Slightly higher up in the axis, the two resulting strands appear like two small crescents with their concave sides facing each other (Figs. 136 & 139) or like two halves of a circle (Fig.129). However, still higher up the xylem strands no longer keep these shapes; they usually become almost round (Fig.130) like the original main strand. The two xylem strands travel upwards in a common investment of phloem for several millimeters, then the phloem divides and the two stelen are completely separated and this is directly followed by the dichotomy of the axis when each branch receives one of the two steles (Fig.131).

2. (see Figures 142-151). The second type of xylem division is most probably connected with lateral branching. It is similar in its beginning to the first type of xylem division described above but differs afterwards.

An island of phloem appears inside the solid core of xylem (Fig.142). The internal phloem increases in size and becomes connected with the

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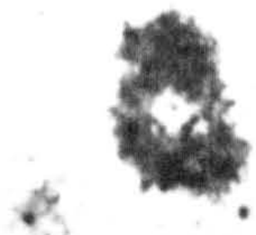

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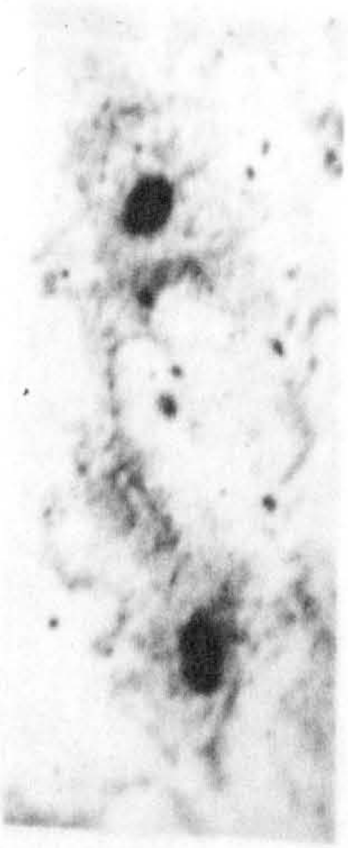

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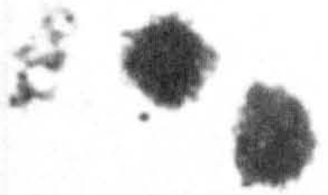

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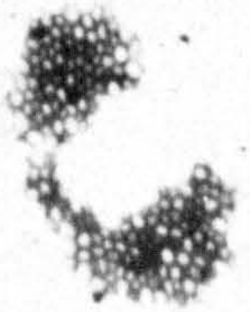

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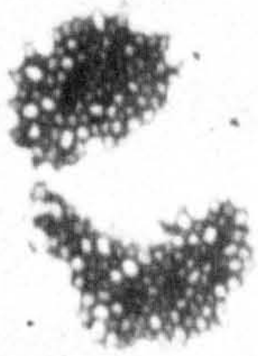

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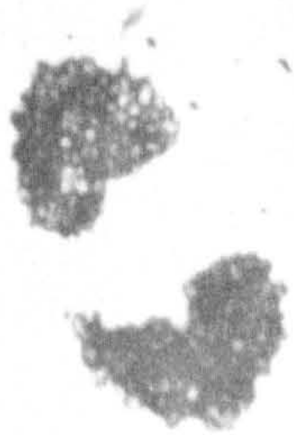

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Figs. 125-131 : A series of transverse sections of the main xyle of an axis showing its division into 2 strands. Peels No. 62/488, 62/403, 62/371, 62/339, 62/330, 62/300& 62/26. 125-130:x50, 131:x20 .

Figs. 132-136 : A series of transverse sections of an axis xylem showing its division into 2 strands. Peels No. 91/211, 91/185, 91/107, 91/65& 91/33. x50 .

Figs. 137-141 : A series of transverse sections of an axis xylem showing its division into two strands. Peels No. 91/315, 91/295, 91/217, 91/3 & 91/7. x50.

outer phloem and the xylem becomes almost horse-shoe shaped in transverse section (Figs.143 & 144). The xylem then becomes very wide and thin and almost semicircular in transverse section (Figs.145 & 146). A small branch strand separates from the xylem (Fig.147), moves out to a branch and at the same time another strand separates from the xylem in the same direction as the first one (Fig.148). The lateral branch (judging by the size of the xylem strand and the size of the branch and the fact that its xylem strand separated from the stele xylem directly before branching) then separates from the main axis (Fig.149). The branch strand moves out and enters the second lateral branch, which lies above the first branch, meanwhile a third strand has departed from the main xylem also in the same direction as the first and the second strands (Figs.150 & 151).

It was noticed that in case of lateral branching and while the main xylem is horse-shoe shaped or semicircular in cross section, the axis itself is curved and a narrow groove is seen opposite the concave side of the xylem (Figs.146 & 147).

3. (see Figures 152-155). The third type of xylem division in preparation for branching of the axis, is rather uncommon and is somewhat different from the two previously described types :

The solid core of xylem (Fig.152) becomes constricted at its centre as shown in Fig.153. The constriction increases until finally the xylem is split into two strands (Figs.154 & 155).

Different types of xylem division were found to occur in branches of one and the same axis (Figs.140 & 141).

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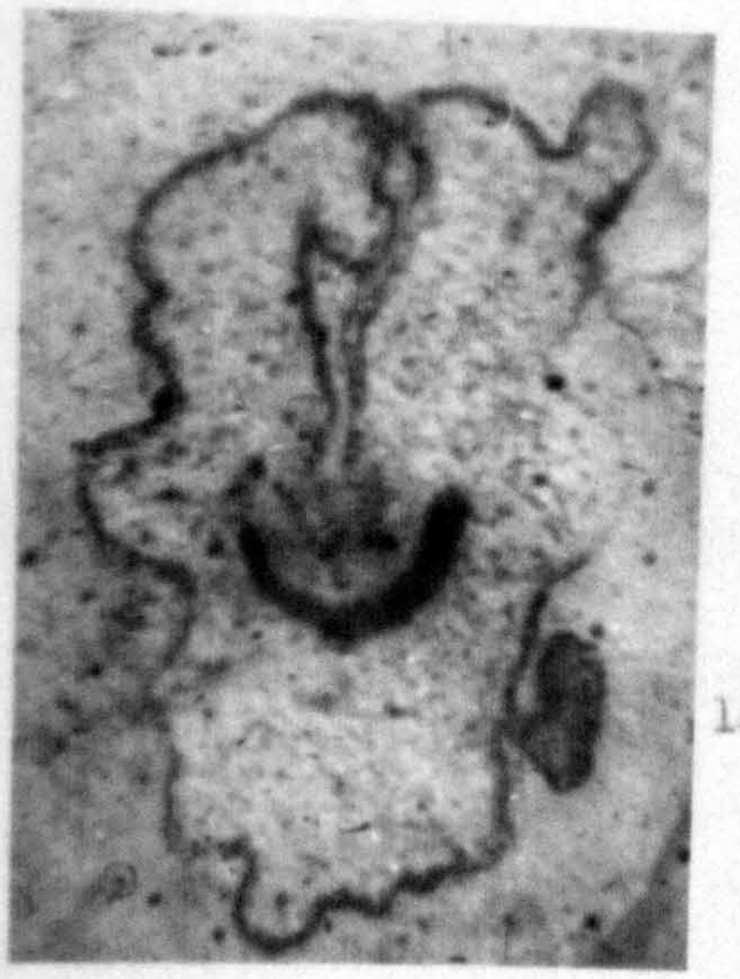

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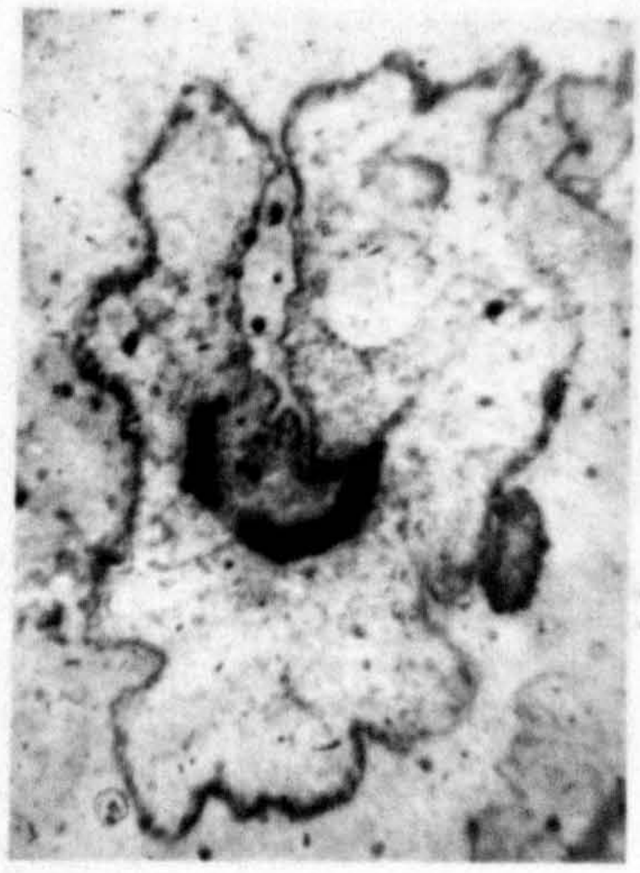

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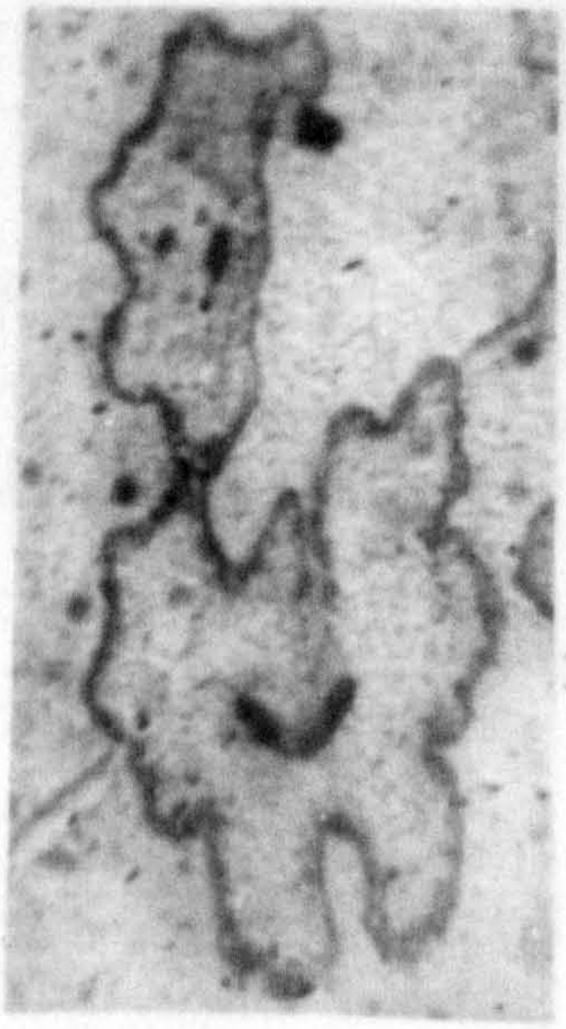

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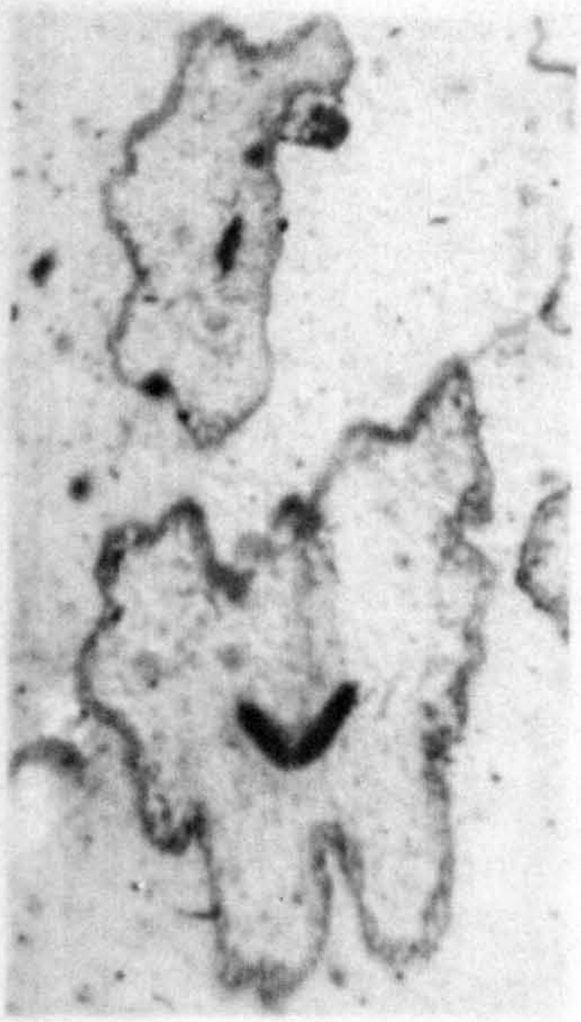

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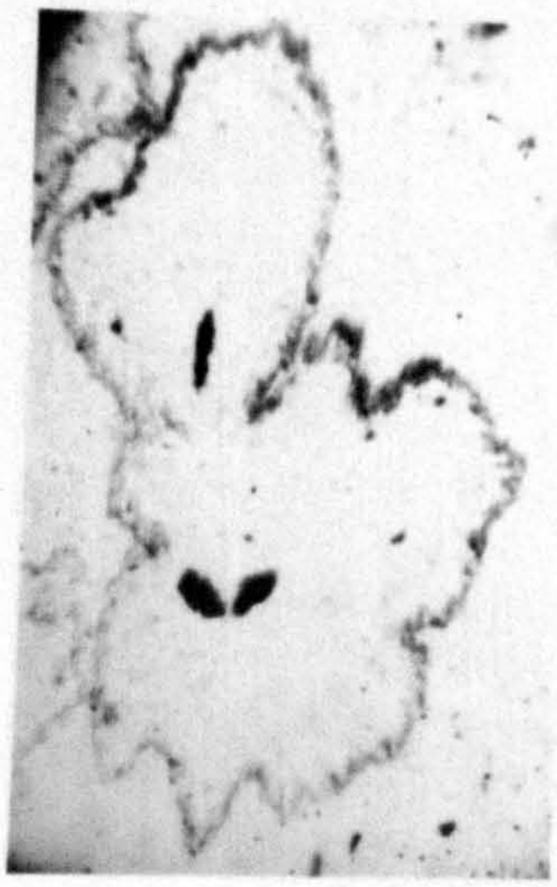

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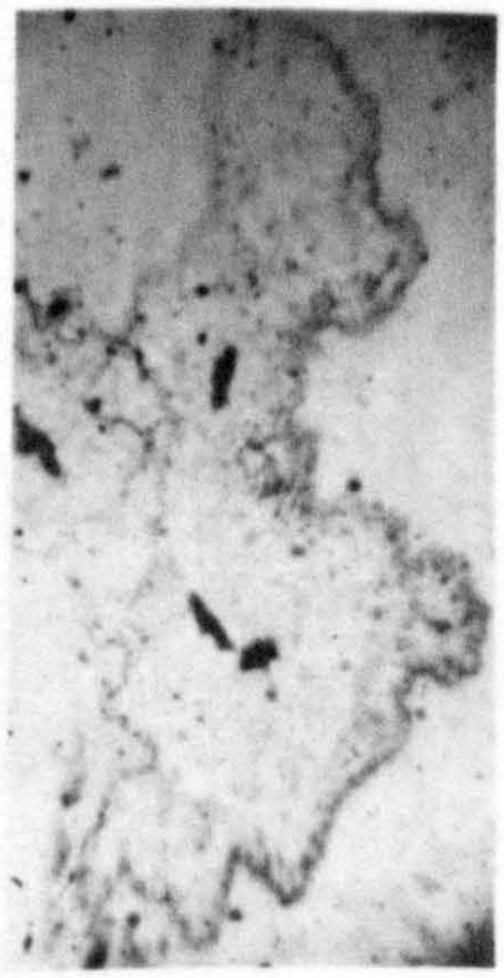

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Figs. 142-151 : A series of transverse sections of an axis showing the departure of 3 lateral branch-traces. Peels No. 62/364, 62/354, 62/340, 62/250, 62/250, 62/240, 62/161, 62/160, 62/28 & 62/1 . 142-145 : x50 , 146-151 : x20 .

Morphology of xylem in sporangial traces

The xylem strand of a sporangial trace usually starts as a small protrusion in the xylem of the axis stele. The xylem protrusion increases gradually in size and at the same time its connection with the stele xylem becomes thinner until it is completely separated. The xylem strand then travels slowly upwards through the stelar phloem and once it enters the axis cortex it moves rapidly through it to enter the stalk of the sporangium (Fig.156). The xylem strand of a sporangium trace vanishes at the base of the innermost layer of the sporangial wall (Fig.157). The xylem strand of a trace departs from the stele xylem usually about 2.5 mm. before it enters the stalk (Fig.156). In a cross section the xylem strand of a trace has no constant or characteristic shape. The xylem strand of a trace is usually smaller in size than the stele xylem from which it has departed but in some cases the xylem strand just after its departure from the stele xylem appears as big as the latter (Fig.186) which makes it difficult at such a stage to differentiate between the two.

Usually not more than 3 sporangial traces could be seen in one transverse section even when the fertile axis has a double stele (Fig. 160). However, in quite a few cases as many as 4 traces were seen in one transverse section (Figs.158 & 159). Other cases in which more than 3 sporangial traces could be seen in one cross section are : at the branching point of a fertile axis (Plate 6, Fig.23B) and at the end of a fertile branch terminating in more than 3 sporangia (Plates 35 & 36, Figs.239 & 242).

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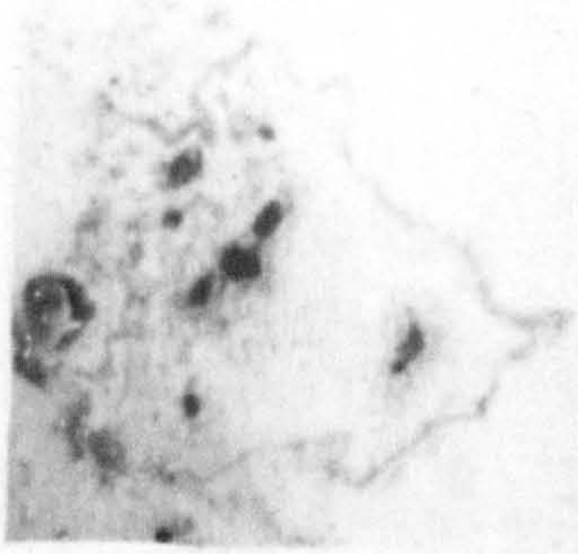

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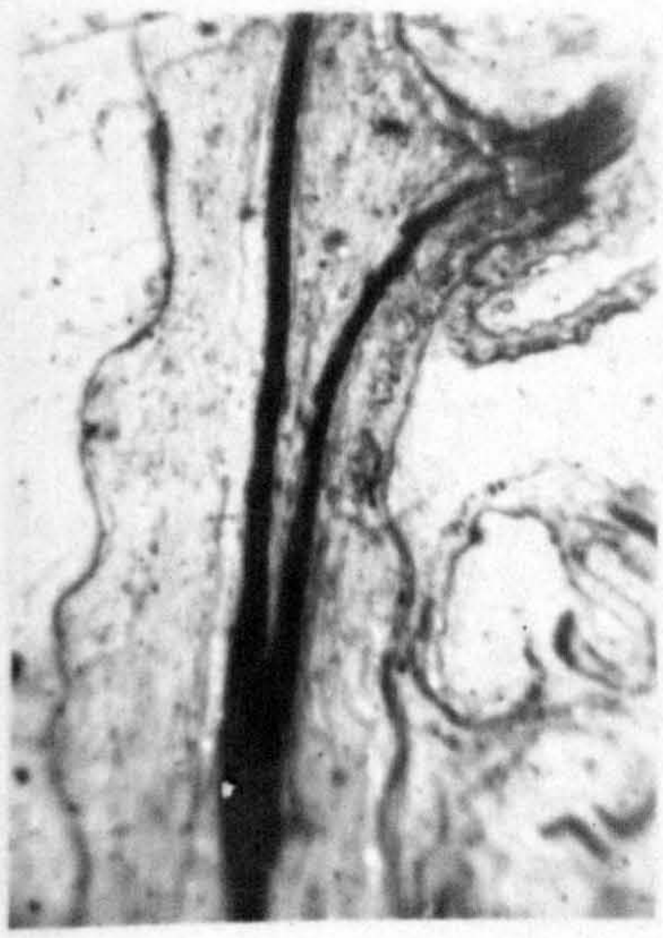

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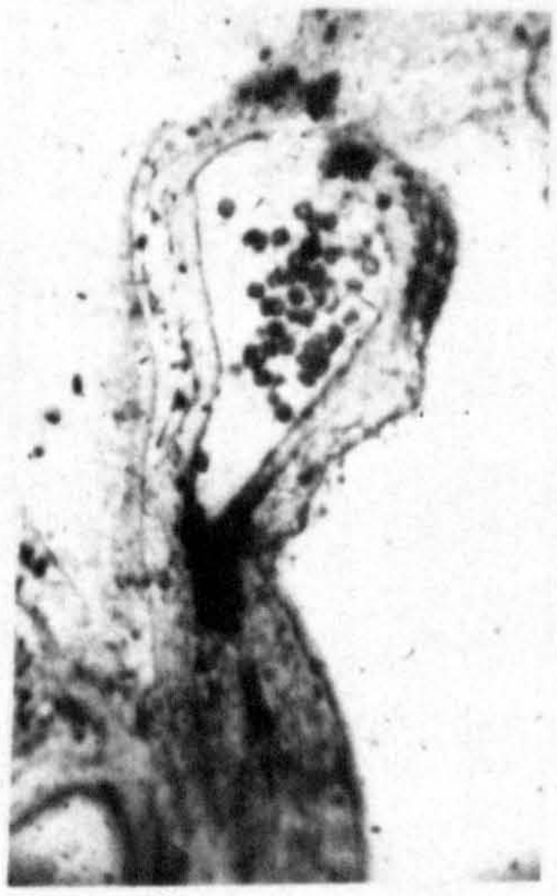

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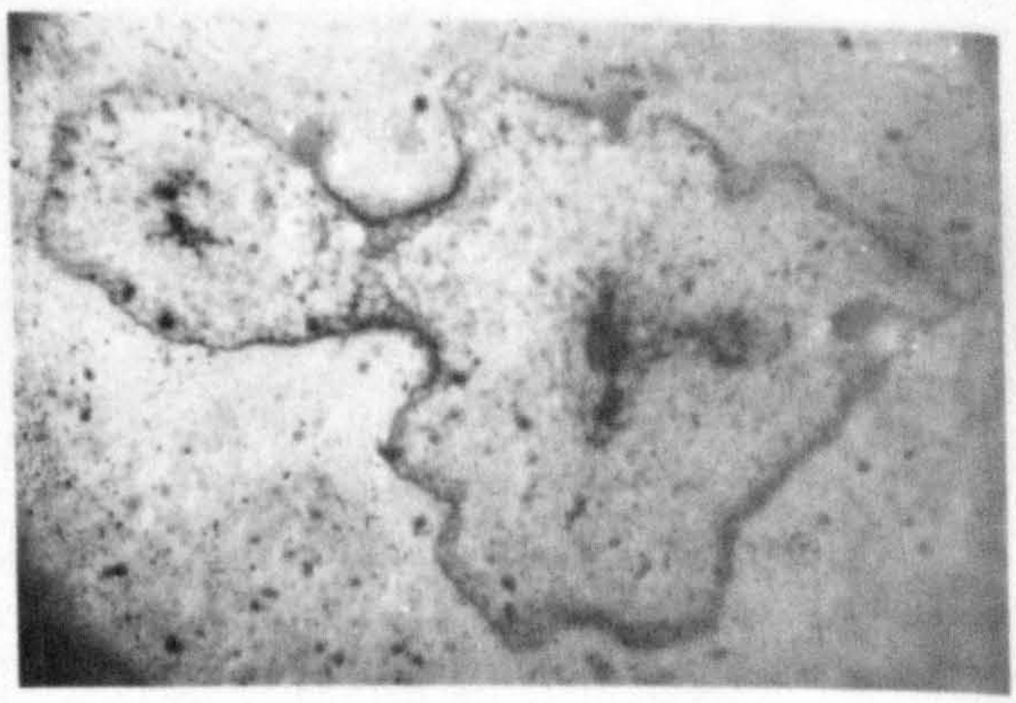

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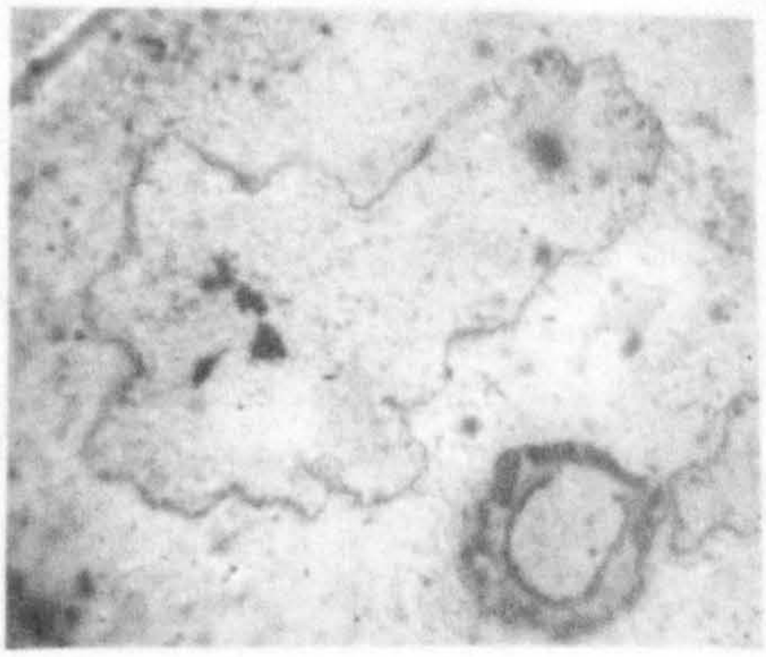

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Figs. 152-155 : A **series** of transverse sections of the main xylem of an axis showing its division into two strands. Peels No.62/214, 62/189, 62/184 & 62/171. x 50 .

Fig. 156 : Sporangial trace in L.S. Peel No.89/36. x15 .

Fig. 157 : Xylem strand ends at tapetum base.Peel No.56/58. x20 .

Fig. 158 : T.S. of an axis showing its main xylem and four sporangial traces.Peel No.91/37. x15 .

Fig. 159 : T.S. of a fertile axis showing its main xylem strand and four sporangial traces.Peel No.91/15. x20 .

Fig. 160 : T.S. of an axis showing two main xylem strands and three sporangial traces. Peel No.91/357 x15 .

The intervals at which xylem strands of sporangial traces depart from the stele xylem and their arrangement around it agree entirely with the intervals at which sporangia are borne on the axis and the way they are borne. If there are 3 sporangia at one level, then 3 xylem strands will depart from the stele xylem at one time. If the sporangia are spirally arranged on the axis then the xylem strands of their traces will depart from the stele xylem in a spiral manner. When there are 3 sporangia borne at slightly different levels on the axis, then the first trace to depart from the stele will supply the lowermost sporangium and the second trace to depart will supply the middle sporangium and the last trace will supply the uppermost sporangium on the axis. It must be mentioned that in some cases this regular relation might be altered, for example, the last xylem strand to depart from the stele might supply the lowermost sporangium on the axis and the first trace to depart might supply the middle sporangium. But it must also be remembered that the sporangia are borne at slightly different levels i.e. the distance between the uppermost and the lowermost sporangium might not exceed 1 mm.

Generally every sporangium receives the xylem strand of its trace directly and independently from the stele xylem but it happens sometimes that two sporangia are supplied by one xylem strand from the stele xylem which directly divides into two traces, and each sporangium receives one.

When one sporangium trace is departing from the axis stele, the xylem of the latter might be triangular or rectangular in shape in

cross section (Figs.161-166). The single trace usually departs from one of the angles of the main xylem (Figs.161 & 164). Sometimes in cross sections a single trace might be seen departing from one of the main xylem faces (Figs.163 & 166), this is due to the fact that other traces are starting to depart from the main xylem and this alters its shape.

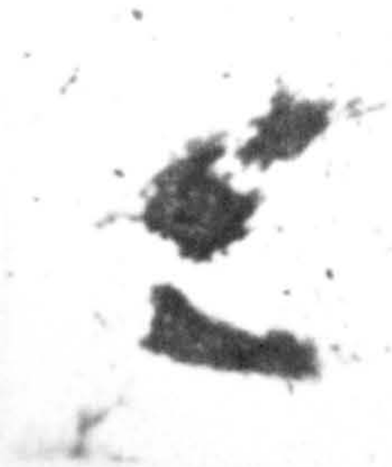
Although it is uncommon, the departure of a single trace might take place as follows :

An island of phloem appears in the solid core of xylem and quite close to its edge (Figs.167 & 168). The internal phloem rapidly joins the outer phloem (Fig.169). The internal phloem increases in size (Fig.170) until the single trace separates (Fig.171).

The departure of two sporangial traces from the axis stele at one level takes place in a number of ways :-

1. The stele xylem which is more or less rectangular in shape gives rise to two strands either from two opposite angles (Fig.172) or from two neighbouring angles (Figs.173-176).

2. The second type involves the formation of an island of phloem which becomes connected with the outer phloem. A big strand then separates from the stele xylem. This big strand divides after its separation from the main xylem into two sporangial traces or in many cases one sporangial trace separates from its sister trace before the latter has entirely separated from the main xylem (see Figs.177-182, 183-186 & 187-190).



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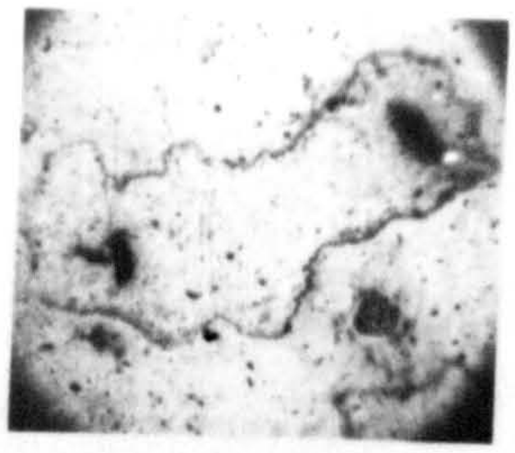

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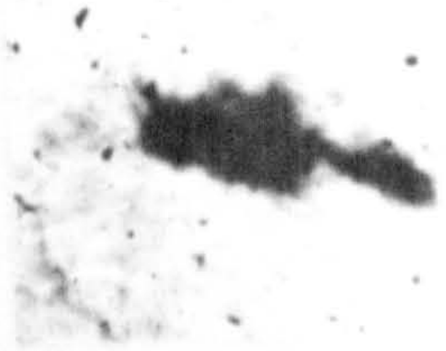

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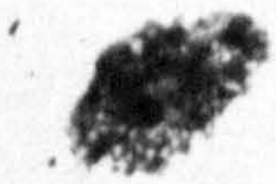

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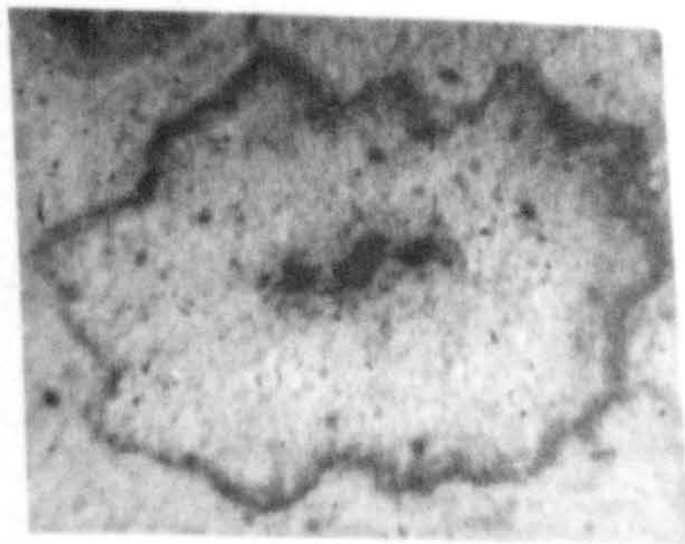

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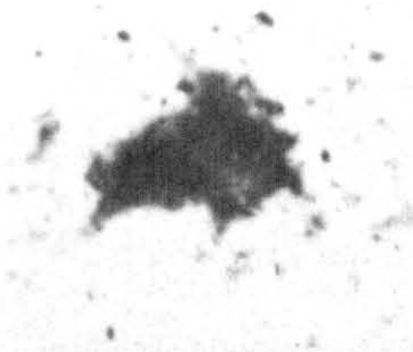
Fig. 161 : Transverse section of an axis stele showing two main xylem strands and one sporangial trace (upper). Peel NO. 62/94. x50 .

Figs. 162-166 : Transverse sections of different axes showing the departure of a single sporangial trace. Peels No. 91/331, 91/331, 91/152, 91/148 &91/143. 162 : x10, 163-166 : x50 .

Figs. 167-171 : A series of transverse sections of an axis stele showing the departure of a single sporangial trace. Peels No. 91/293, 91/288, 91/284, 91/267 & 91/261 . x 50 .

Fig. 172 : T.S. of an axis showing the departure of two sporangial traces from two opposite sides of the main xylem. Peel No. 91/37. x20 .



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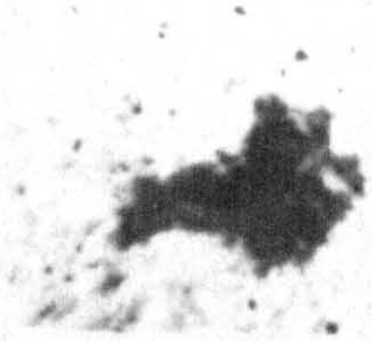

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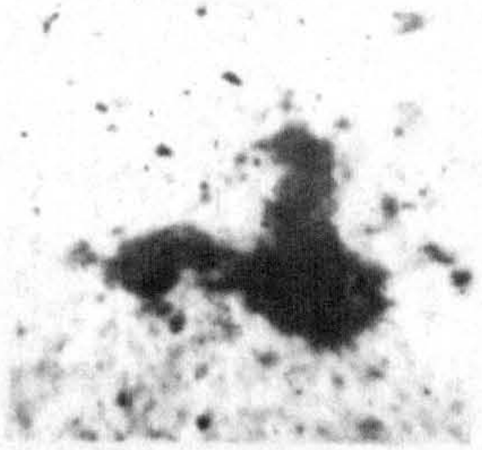

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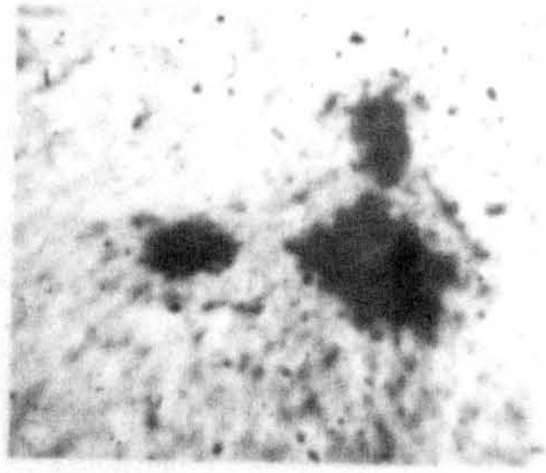

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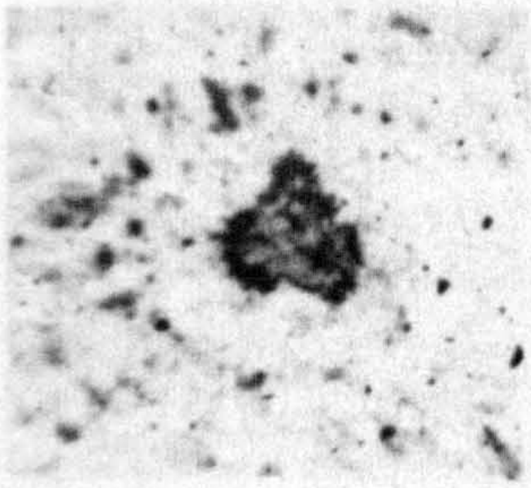

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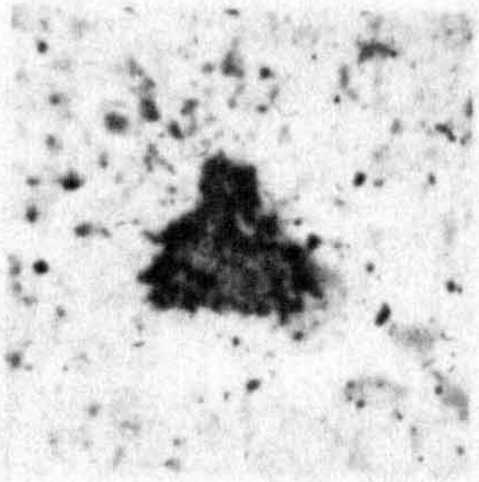

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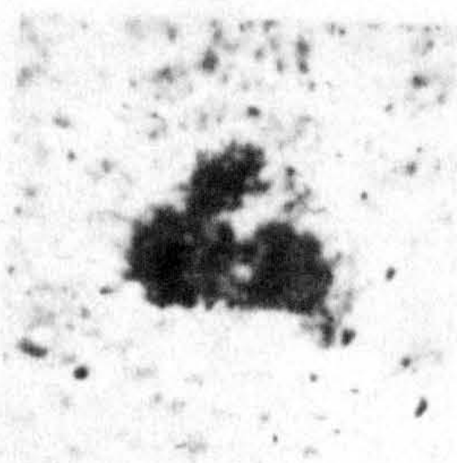

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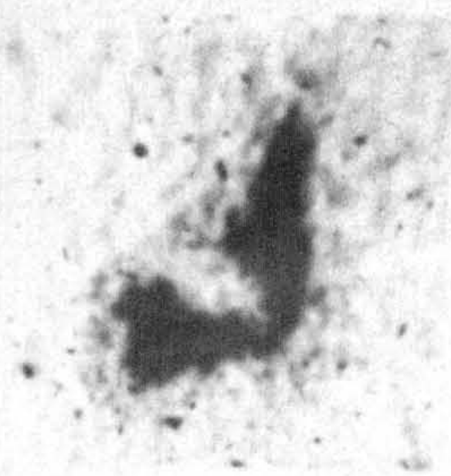

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Figs. 173-176 : A series of transverse sections of a stele xylem showing the departure of two sporangial traces.Peels No.91/103, 91/89, 91/64 & 91/55. x50 .

Figs. 177-182 : A series of transverse sections of an axis xylem showing the departure of two sporangial traces.Peels No.62/109, 62/101, 62/93, 62/92, 62/87 &62/85. x50.

Figs. 183-186 : A series of transverse sections of the main xylem of a fertile branch showing the departure of two sporangial traces . The main xylem is at the left.Peels No.91/324, 91/315, 91/310 & 91/308 . x50 .

3. When a fertile branch ends in two sporangia the stele of the branch ends by dividing into two traces. The division of the stele xylem into the two final traces takes place in almost the same manner as in stele division in preparation for axis dichotomy. This involves two different types :

a. The main xylem becomes constricted at its centre. The constriction deepens until the main xylem is divided into the two final traces (see Figs.191-195).

b. This type of division involves the formation of an island of phloem inside the solid xylem of the stele. The internal phloem becomes connected with the outer phloem and this is followed by the splitting of the stele xylem into the two final traces. However, in the example of this type of division, shown on Plate 31, Figs.196-202, the two final traces did not become entirely separated, although almost so, because the two terminal sporangia of this example were fused together. It must be noted that not all the connected pairs of sporangia have had partially joined xylem strands, for in other examples the two strands are clearly separated (Plate 35, Fig.240).

The maximum number of sporangial traces to depart at the same level from a fertile axis stele is never more than three. The 3 traces might separate from the main xylem at exactly the same level (Figs.203-207) or in a very close spiral succession of different paterns (Figs.208-210).

Generally the departure of 3 sporangial traces at the same level

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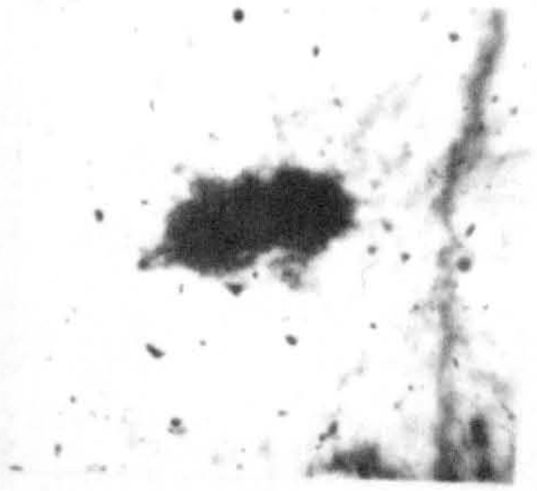
Figs. 187-190 : A series of transverse sections of an axis xylem showing the departure of two sporangial traces. Peels No. 91/271, 91/269, 91/264 & 91/250. x50 .

Figs. 191-195 : A series of transverse sections at the upper end of a fertile branch showing the division of its xylem into two final sporangial traces. Peels No. 91/258, 91/242, 91/237, 91/232 & 91/229. x50 .



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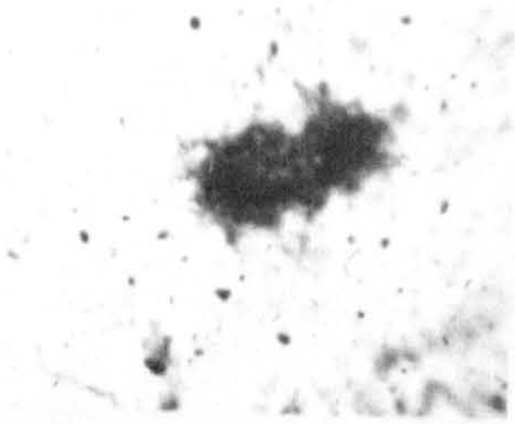

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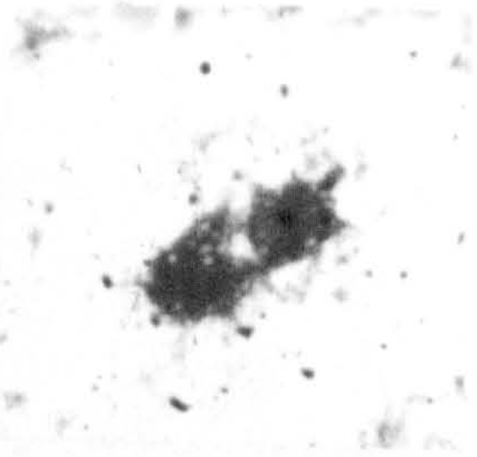

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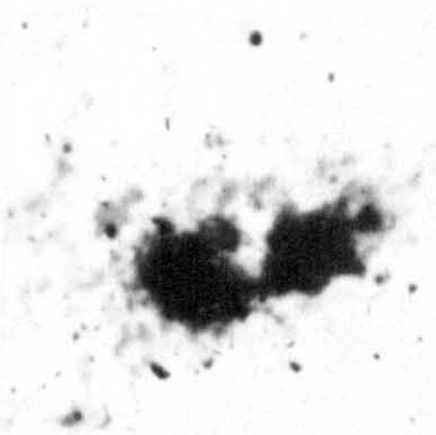

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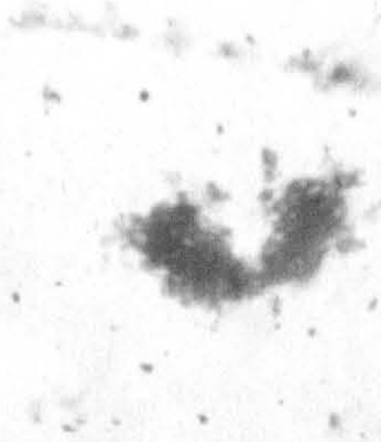

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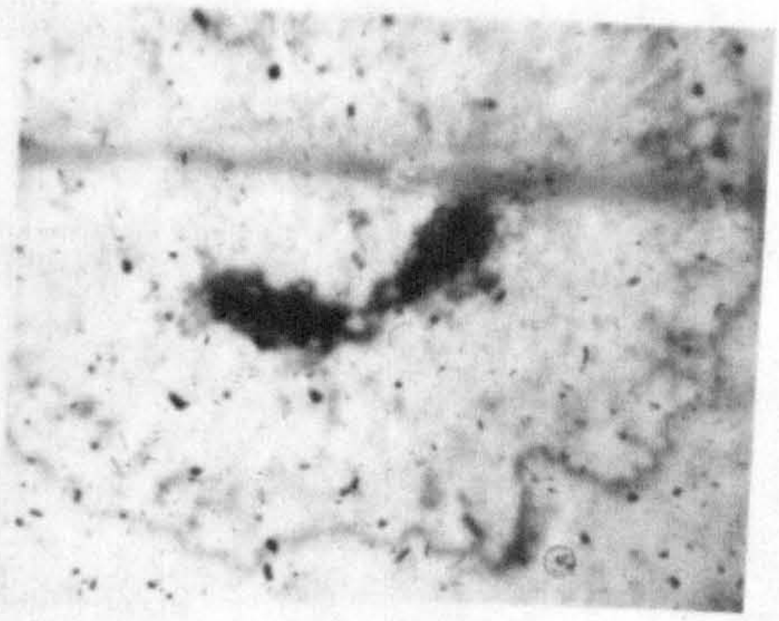

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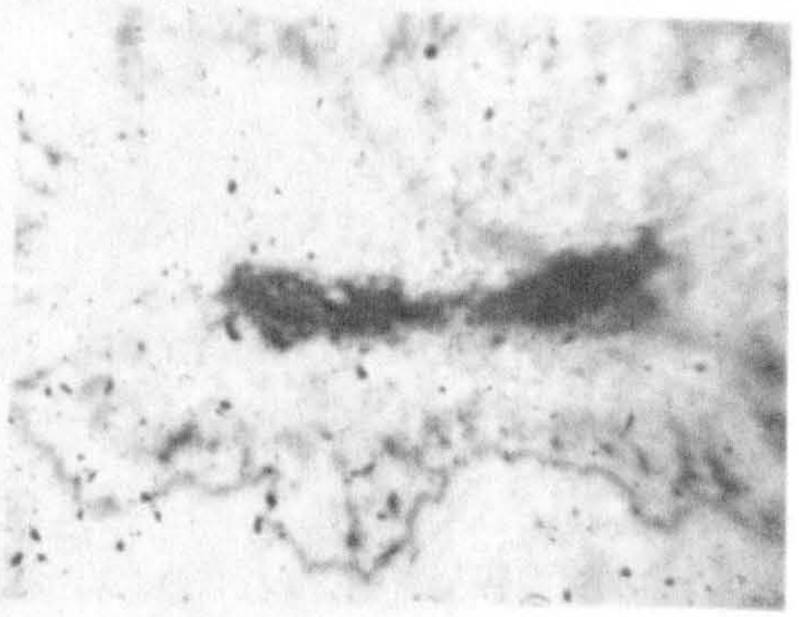


202

Figs. 196-202 : **A series** of transverse sections at the upper end of a **fertile branch** showing the division of its main xylem **into two final** sporangial traces; supplying a **fused pair of sporangia.** Peels No. 91/244, 91/231, 91/227, 91/224, 91/218, 91/207 & 91/195. x50 .

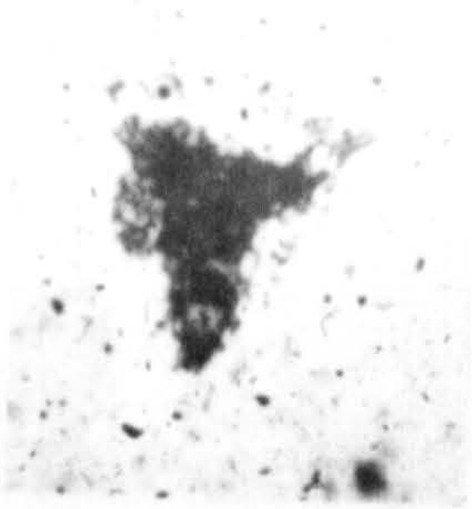
takes place in one of the following ways :

1. The three traces depart from the angles of the triangular stele xylem. In such a case the 3 xylem strands start as protrusions from the angles of the xylem. The traces increase in size and at the same time their connection with the stele xylem becomes thinner until they get separated (Figs.203-207).

2. In this type one sporangial strand separates from the main xylem by constriction and the separation of the other two sporangial strands (which are usually closer to each other) is achieved by the formation of an island of phloem between them and the main xylem, this island of phloem becomes connected with the outer phloem at 3 positions thus resulting in the separation of the two traces from the main xylem and from each other (see Figs.211-218).

3. When a fertile branch ends in 3 sporangia, then the division of the xylem of the branch stele into the 3 final traces takes place as follows :

The main xylem becomes triangular in shape in cross section (Fig.219). An island of phloem appears inside the xylem (Fig.220). The internal phloem increases in size (Fig.221) and then it joins the outer phloem at two positions thus bringing the separation of the first sporangial trace, at the same time the remaining portion of the main xylem becomes constricted at its centre (Fig.222). The constriction increases till the xylem splits into two final strands and the 3 final traces could be seen in one transverse section (Fig.223). The branch itself divides



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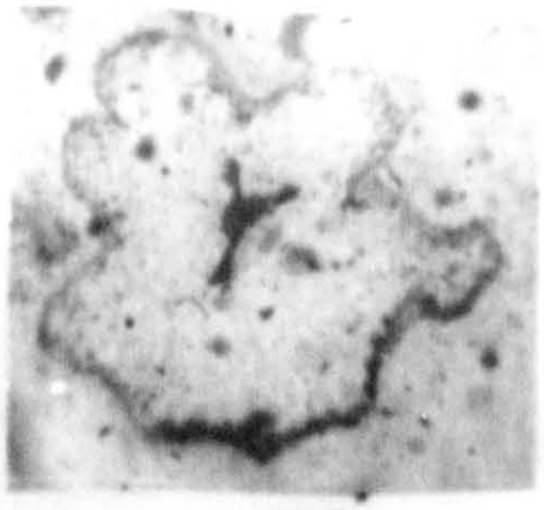

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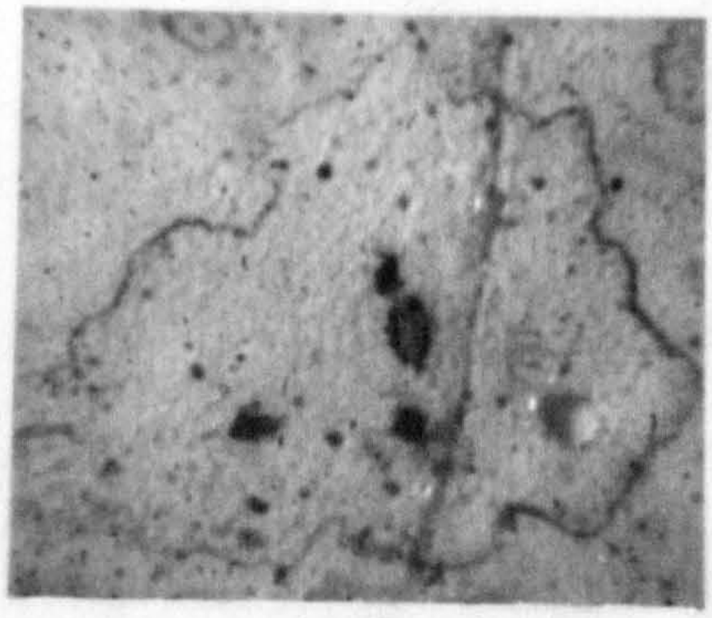

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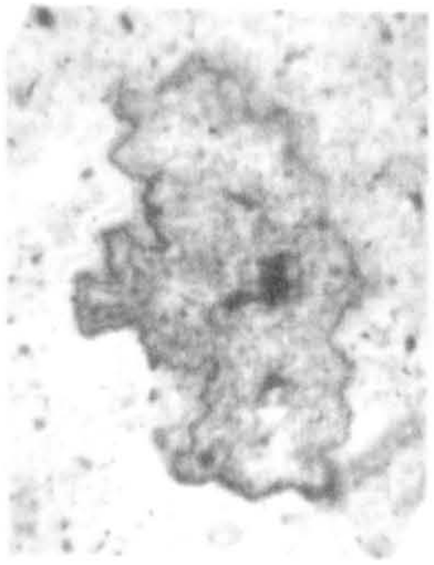

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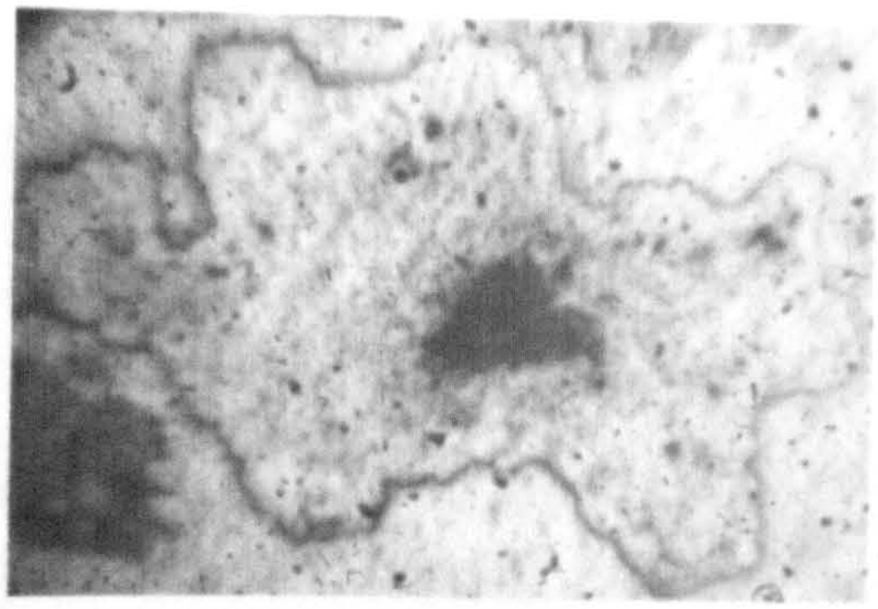
Figs.203-207 : **A series of transverse sections** of an axis showing the departure of three sporangial traces at the same level. Peels No.91/158, 91/136, 91/128, 91/122 & 91/115. 203 & 204 : x 50. 205-207 : x 15.

Figs.208-210 : **Transverse sections of fertile axes** showing different **patterns of departure of** 3 sporangial traces. Peels No. 91/221, 91/115 & 62/131. 208 : x20. 209 : x30. 210 : x20.

Figs.211-218 : **A series of transverse sections** of an axis stele showing **the departure of** 3 sporangial traces. Peels No.91/91, 91/72, 91/67, 91/62, 91/57, 91/50, 91/45 & 91/37. x 50.



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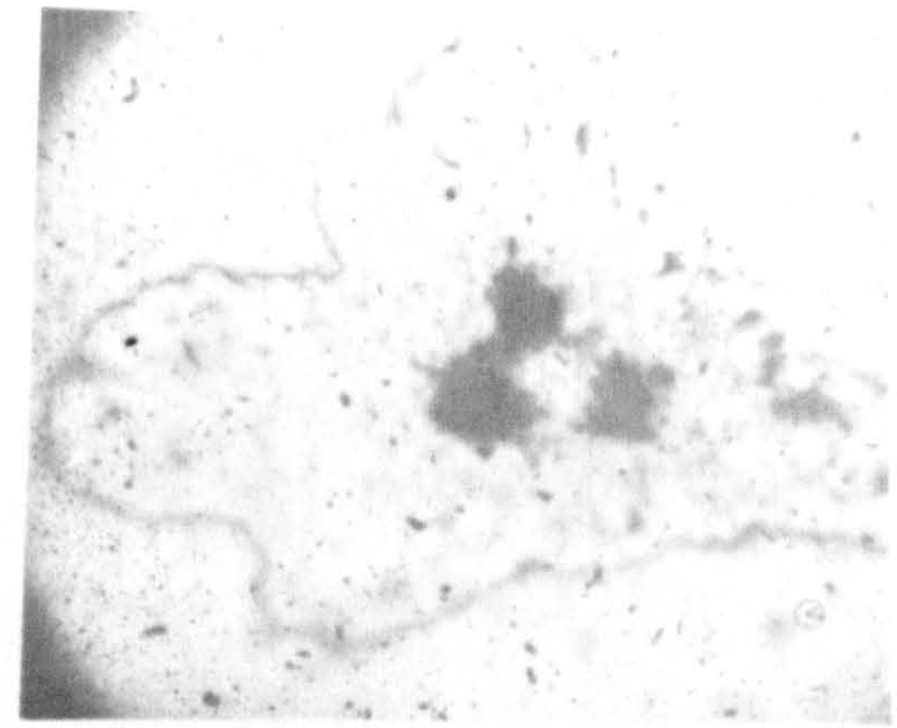

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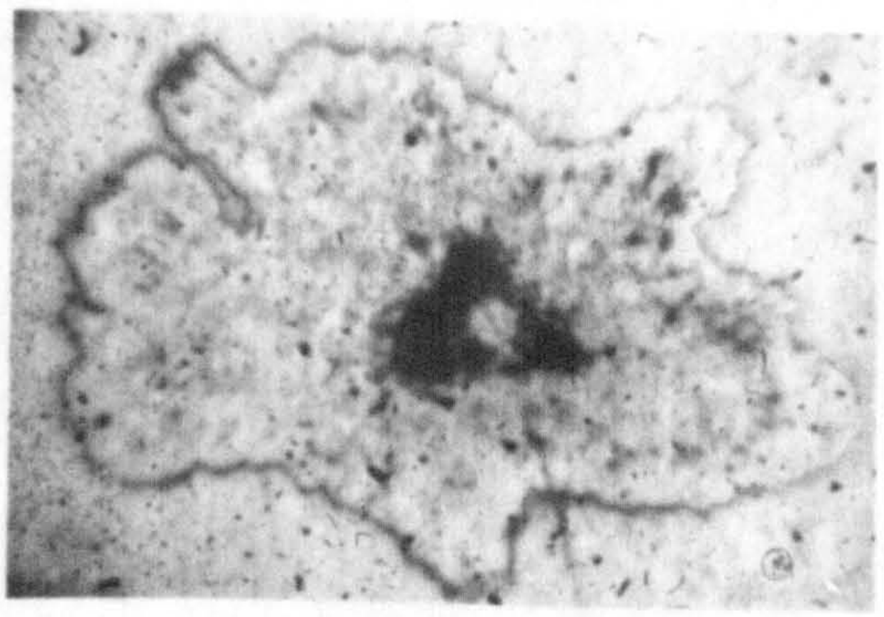

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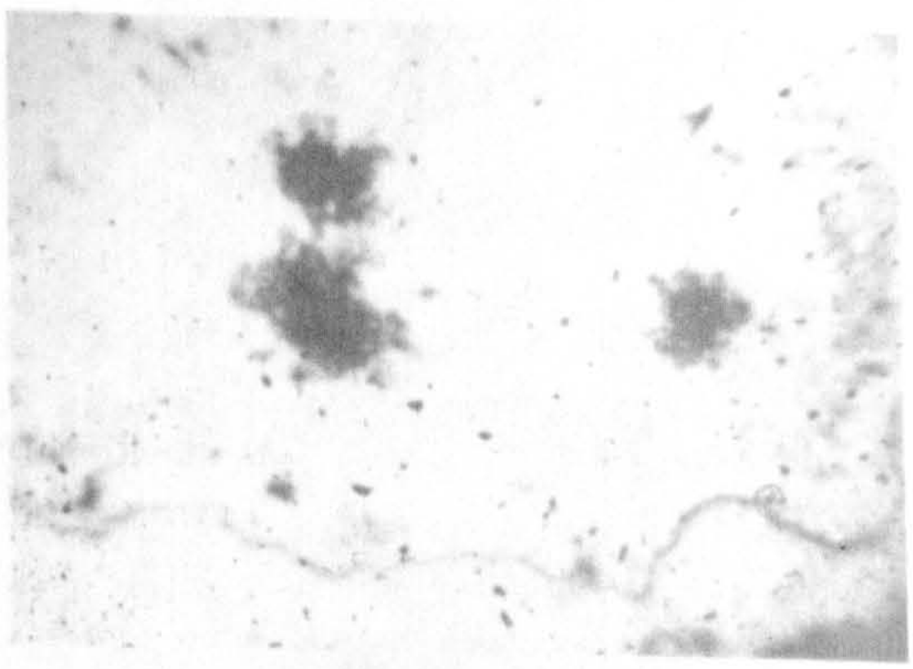

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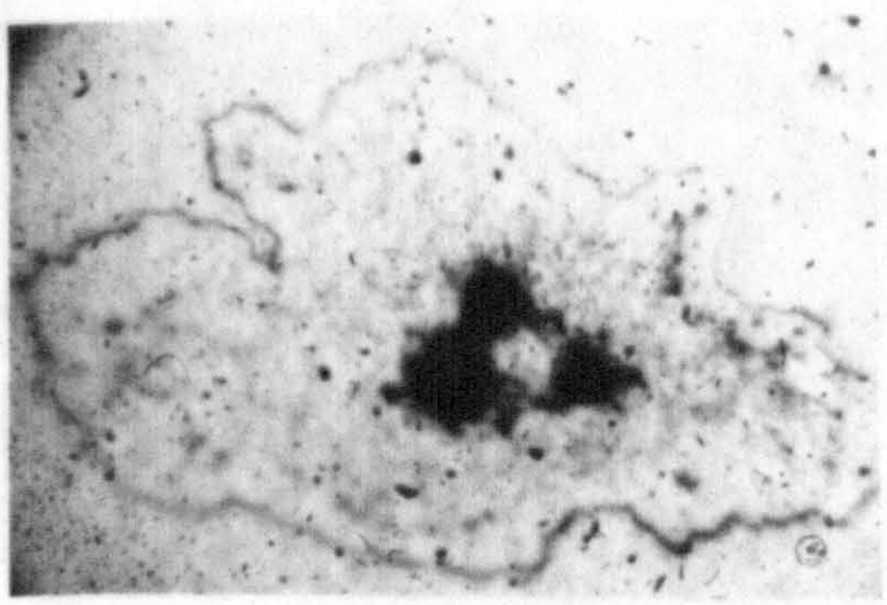

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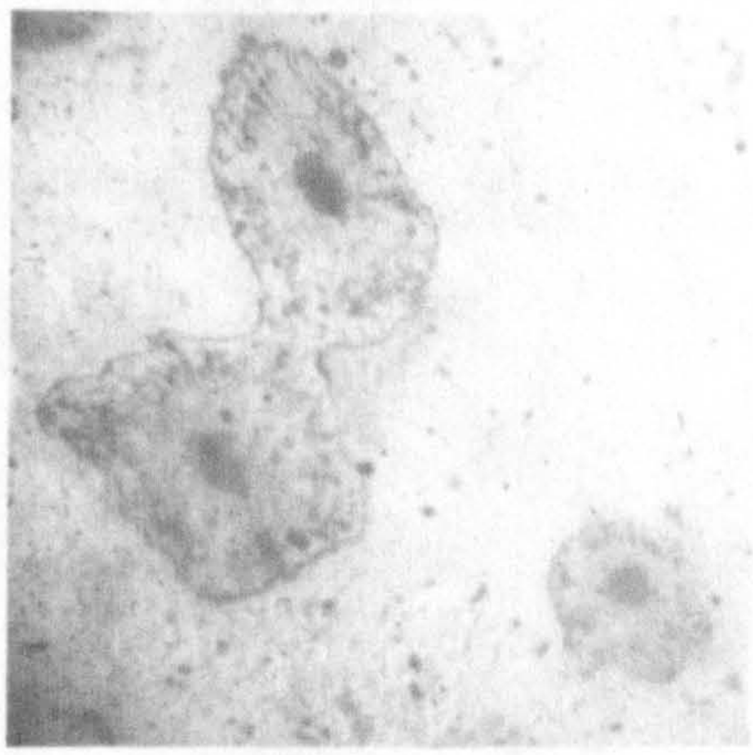

224

Figs. 219-224 :**A series of transverse sections** at the upper end of a fertile **branch showing** the division of its main xylem into 3 final **sporangial traces.** Perls No.91/218, 91/197, 91/194, 91/189. 91/176 & 91/151. x50 .

into 3 stalks, each of which receives one trace (Fig.224).

When a fertile branch ends in 4 sporangia, the division of the stele xylem into 4 strands takes place in either of the following ways :

1. An island of phloem forms inside the main xylem (Figs.225 & 226). The phloem island increases in size and eventually becomes connected with the outer phloem at two points, thus the first trace is separated (Fig.227). The remaining portion of the main xylem divides into two strands by constriction (Figs.228 & 229). In the latter figure there are 3 strands of which the one on the right is largest in size. The first stalk then separates (Fig.230) followed by the second stalk (Fig.231). The large xylem strand of the right stalk divides into two traces and this is followed by the division of the stalk itself into two very small stalks (Fig.232). The latter figure shows clearly that one division is at right angles to the other.

2. The second type involves some stages which are to some extent similar to the division of the stele of the axes in preparation for lateral branching described on pages 48 & 49.

An island of phloem appears inside the solid xylem which is more or less triangular in shape (Figs.233 & 234). The internal phloem increases in size and becomes connected with the outer phloem (Fig.235). The xylem becomes thin and almost semicircular in shape in cross section (Fig.236). The xylem then divides into two strands, one of which directly divides into two of the 4 final traces (Fig.237). At a slightly higher level the other strand divides into two final traces,

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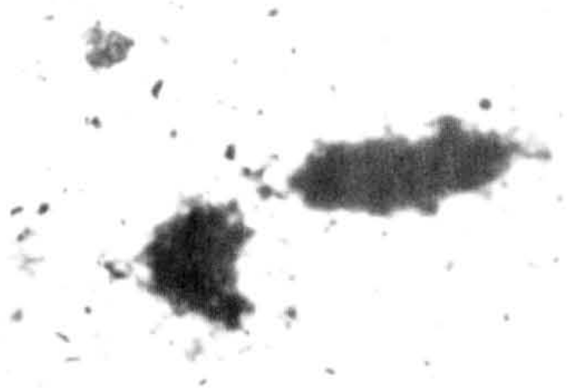

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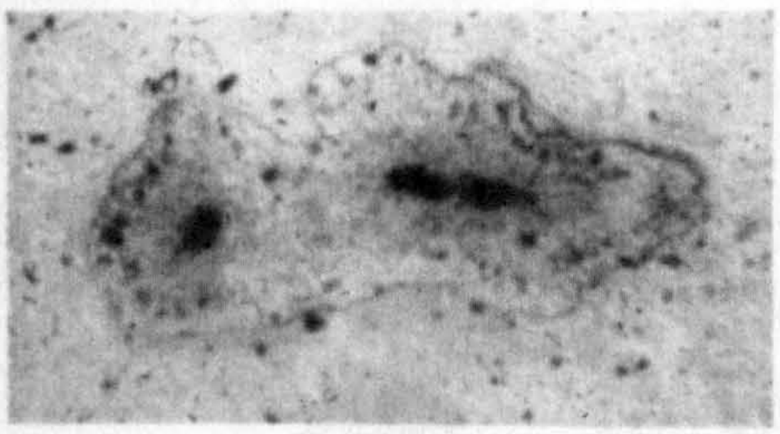

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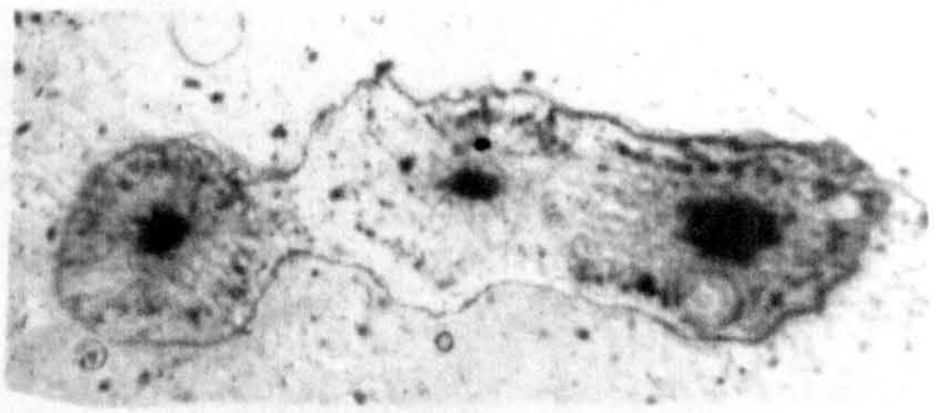

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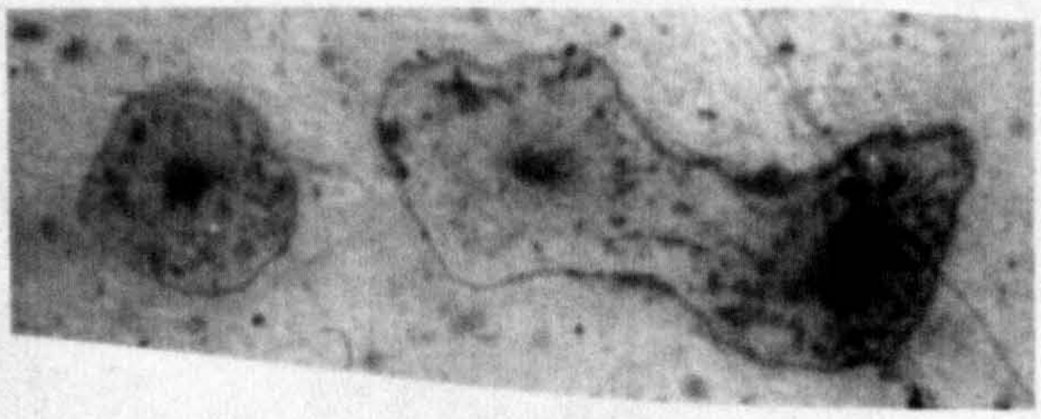

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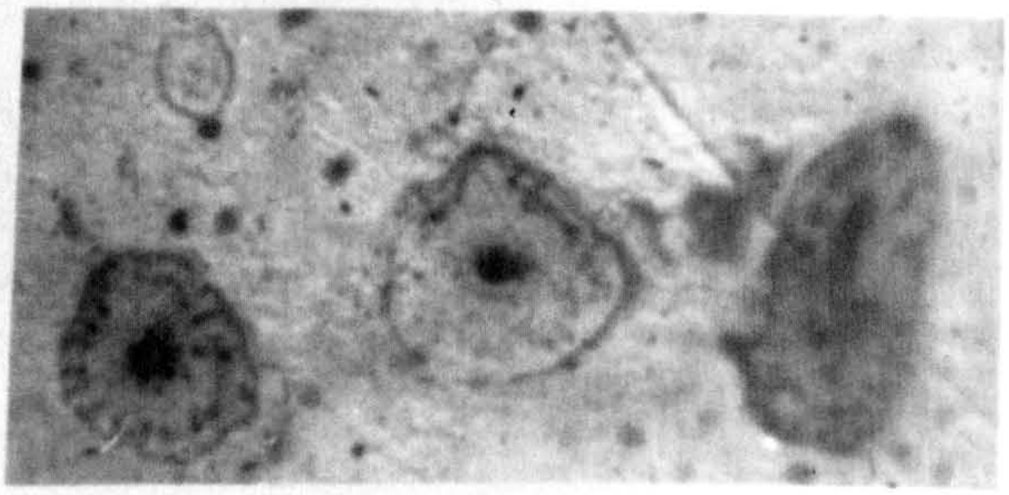

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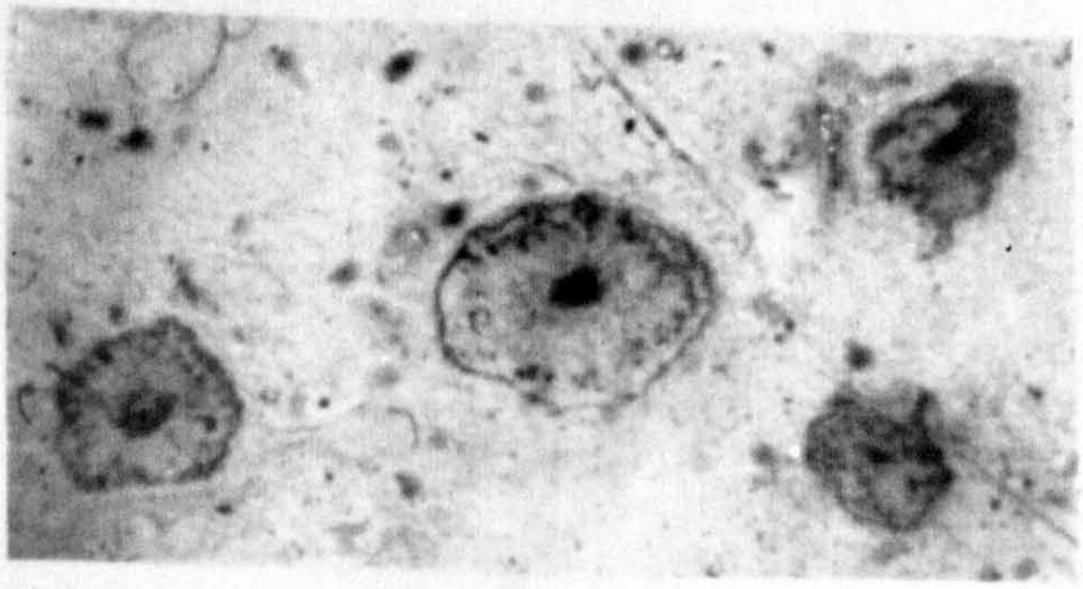
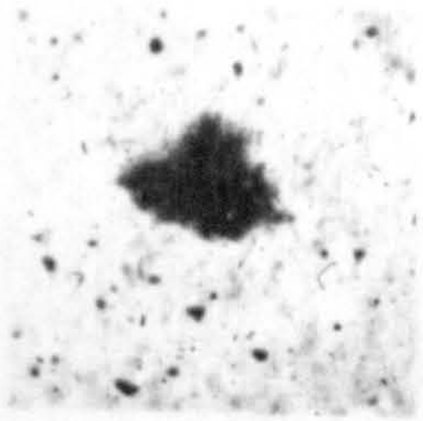


232

Figs. 225-232 : **A series of transverse sections of the upper part of a fertile branch showing the division of its main xylem into 4 final sporangial traces. Peels No.** 91/258, 91/240, 91/234, **91/218,** 91/208, 91/204, 91/201 & 91/192. 225-227 x50 , 228-232 : x20 .



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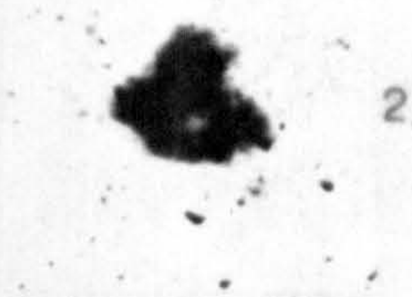

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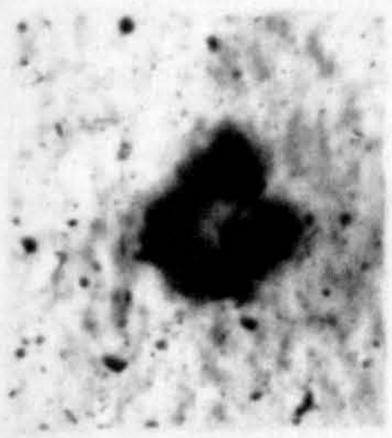

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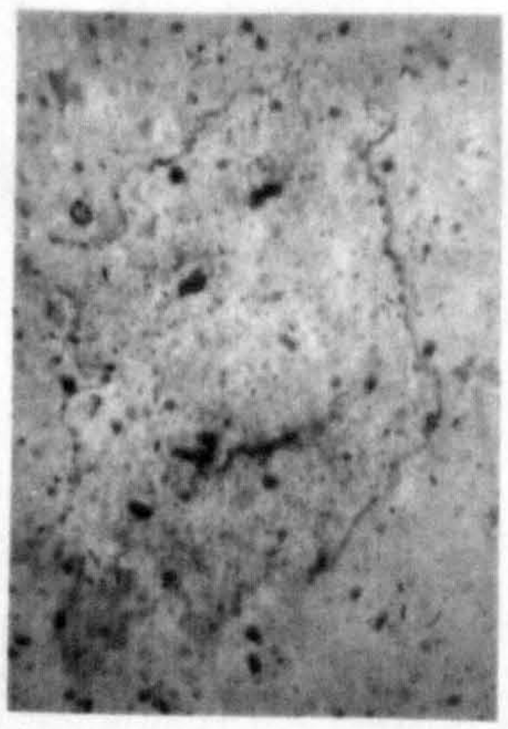

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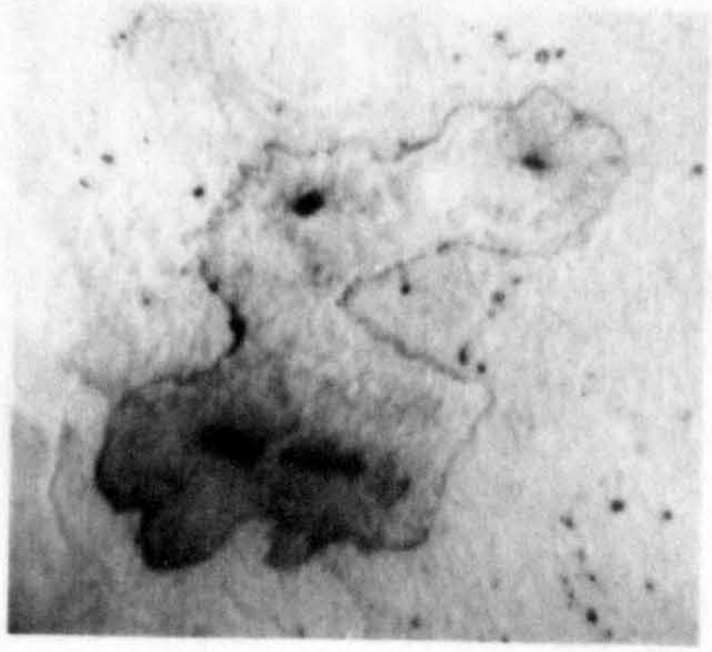

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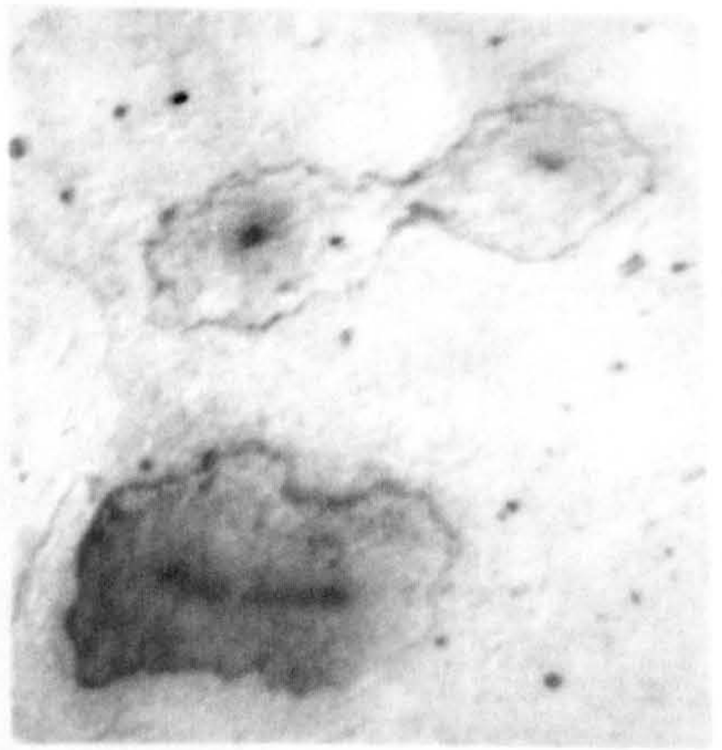

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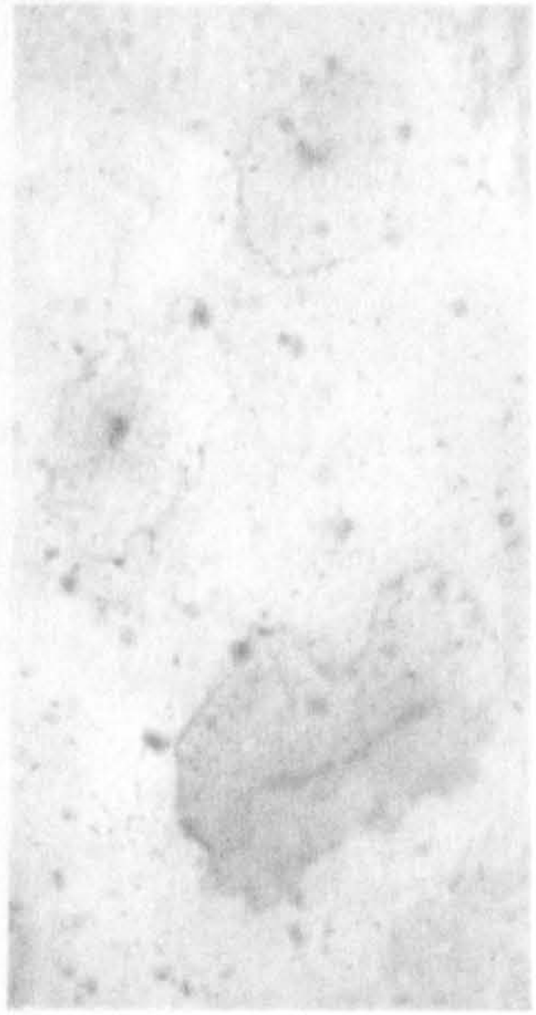

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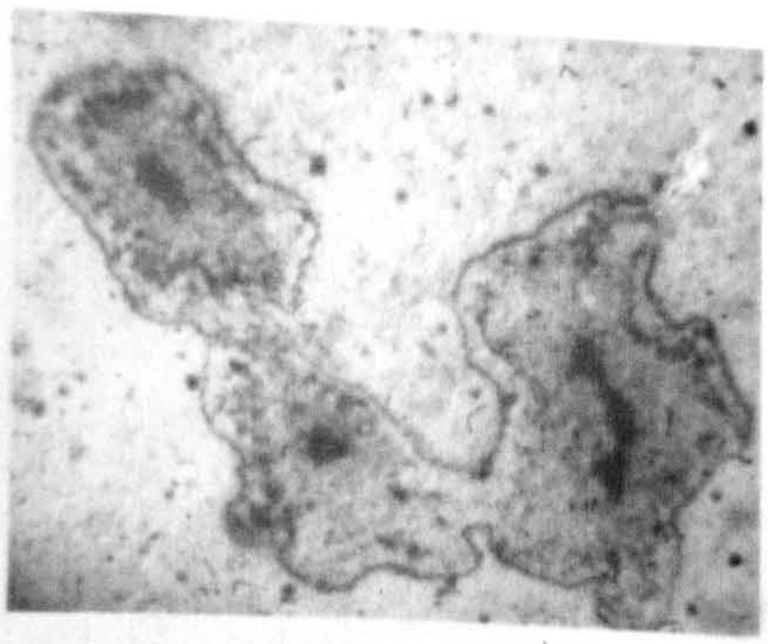
Figs. 233-241 : A series of transverse sections of the upper part of a fertile branch showing the division of its main xylem into four final sporangial traces. Peels No. 91/260, 91/251, 91/241, 91/220, 91/214, 91/188, 91/173, 91/165 & 91/162. 233-235 : x50 , 236-238 : x20 , 239-241 : x15 .

and at this stage the 4 final traces could be seen in one transverse section (Figs.238 & 239). Finally each trace supplies one sporangium (Figs.240 & 241). The two lower traces in Fig.241 supply a fused pair of sporangia, the two stalks of which are also fused.

When a fertile axis terminates in 5 sporangia, as the specimen reconstructed in Fig.110, on Plate 24, the division of the xylem of the axis stele into the 5 final traces takes place as follows :

An island of phloem appears inside the stele xylem. The internal phloem becomes connected with the outer phloem and then the xylem divides into two strands. One of the two strands divides into two traces by constriction, meanwhile the other strand starts to divide into 3 also by constriction (Fig.242). The first two stalks separate at one level while the traces of the 3 other sporangia have just separated (Figs.243 & 244). Figures 245 & 246 show the completion of the separation of the 3 other stalks and the arrangement of the 5 terminal stalks in a circular manner.

Plate 36



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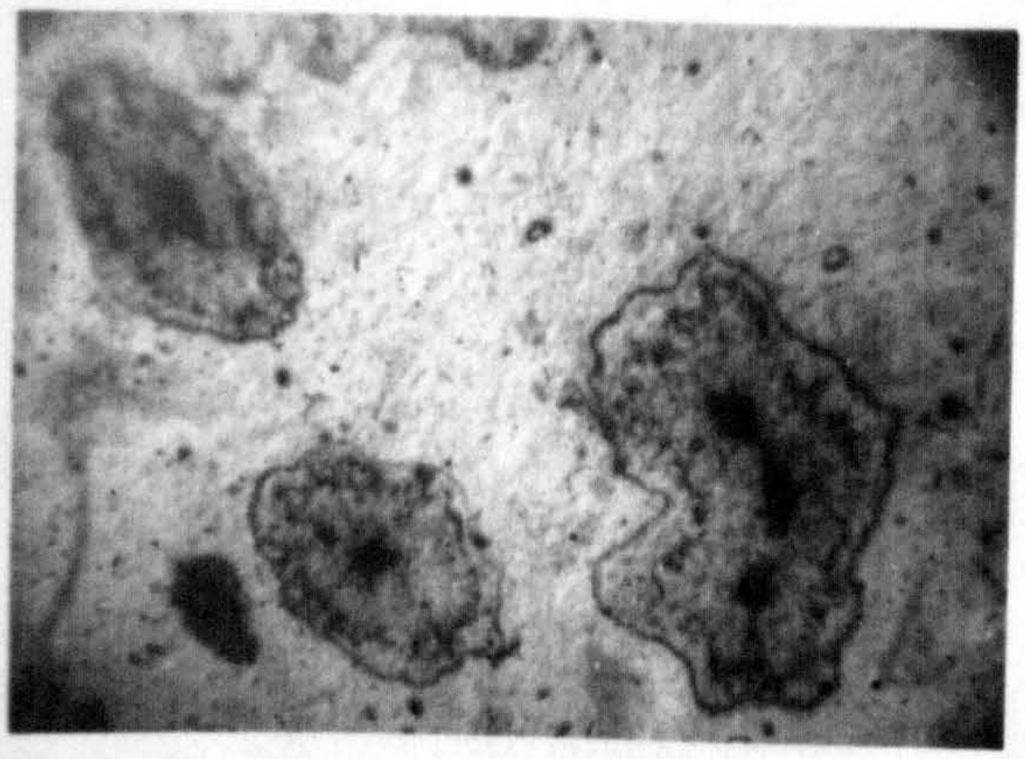

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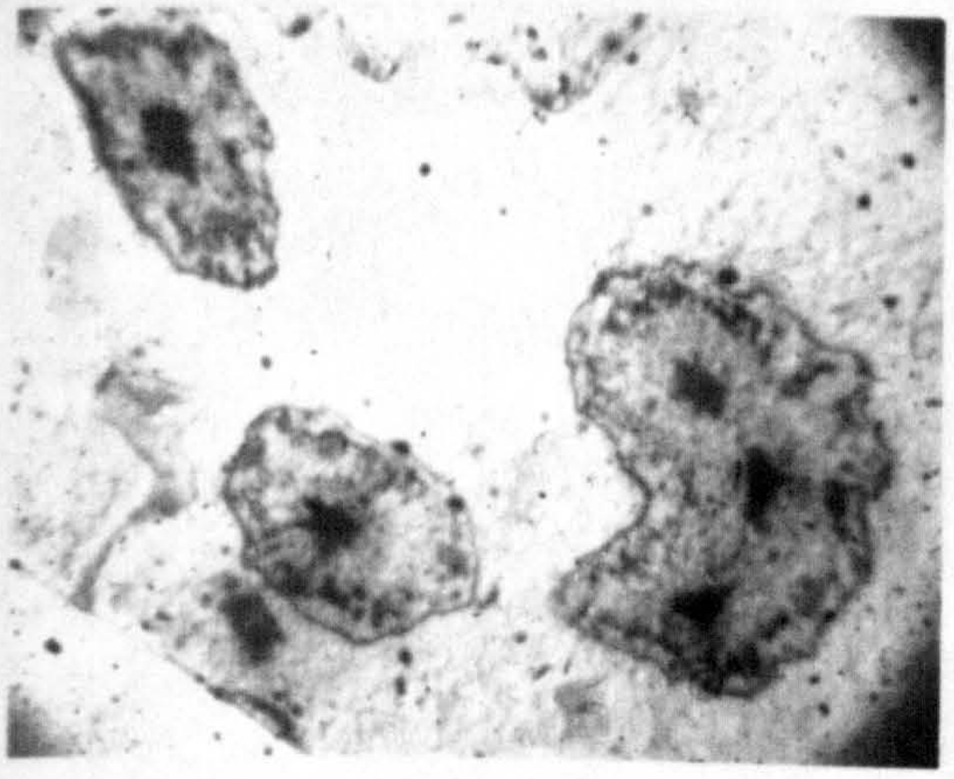

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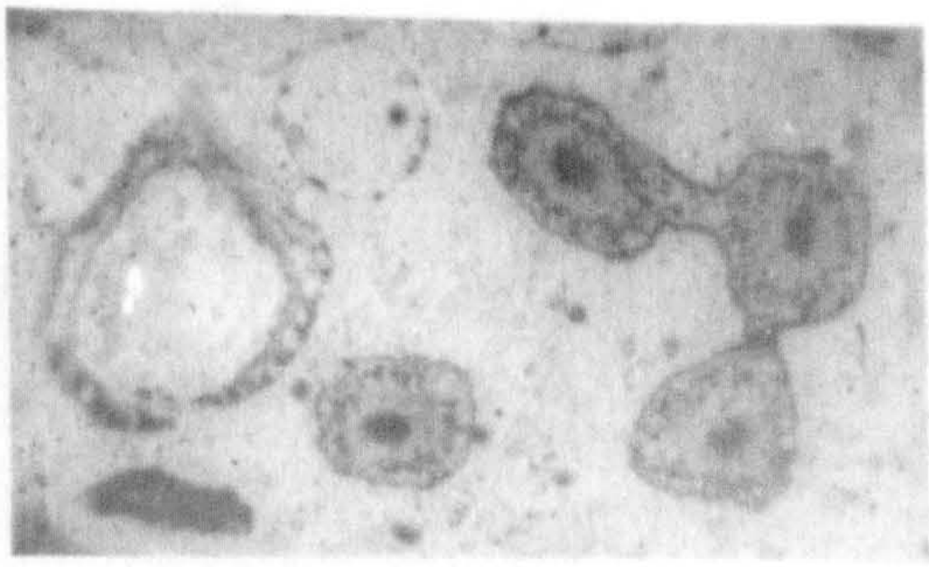

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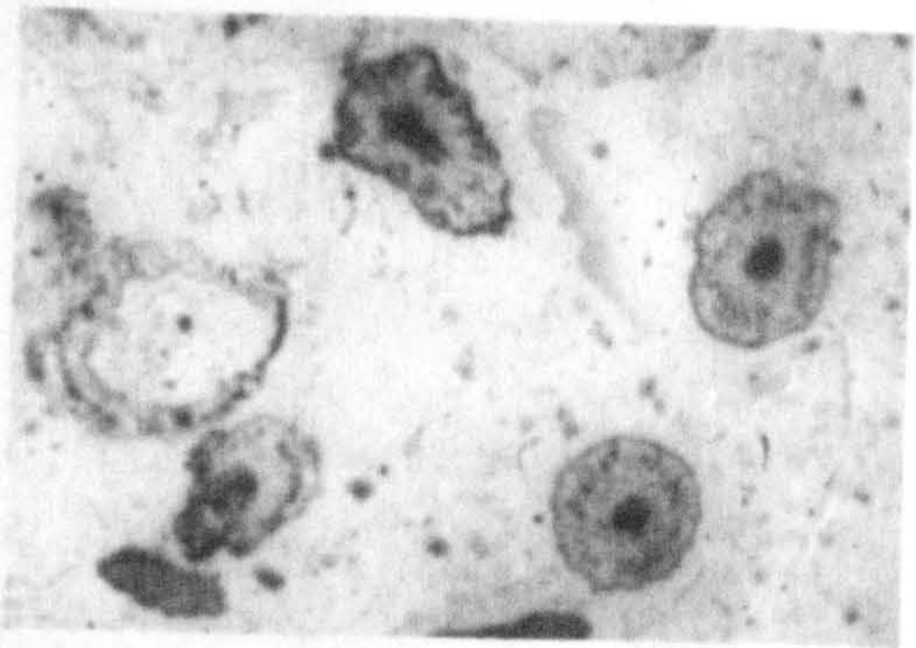

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Figs. 242-246 : A series of transverse sections of the upper part of a fertile branch terminating in a bunch of 5 sporangia. Peels No.91/218, 91/209, 91/205, 91/192 & 91/183.
242-244 : x20 , 245 & 246 : x15 .

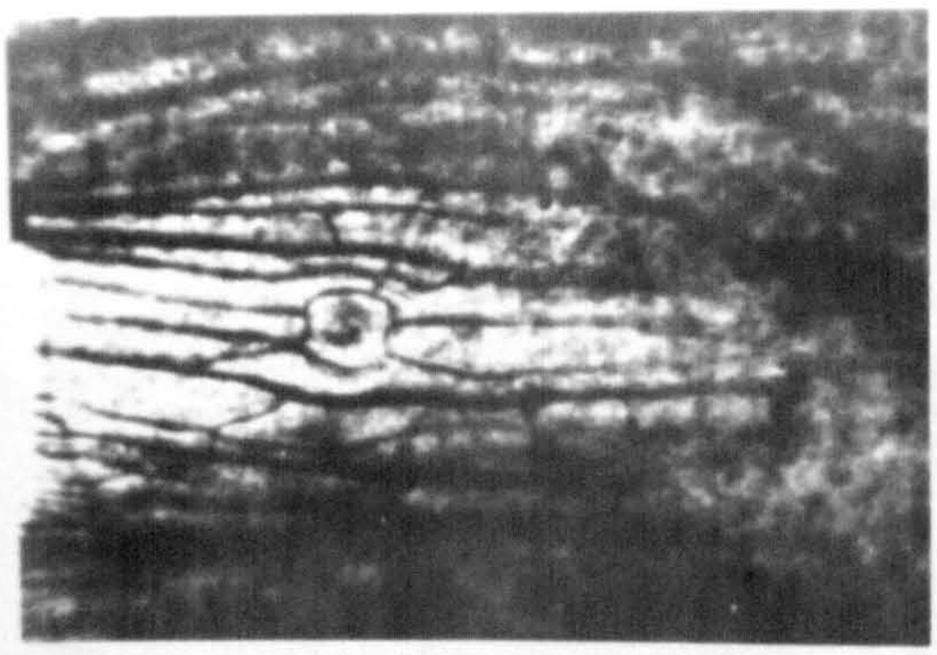
ANATOMY OF THE AXES

As far as histological details are concerned there is not much more information to add to what has already been reported by Kidston and Lang (1920), (see pages 6 & 7 of this Thesis).

The epidermis of the axes is composed of elongated cells, with transverse and oblique end walls and covered with cuticle. The epidermis cells are about 20-50 μ in width and vary in length from about 200 μ to about 500 μ. The appearance of the cells of the epidermis in transverse section and longitudinal section, as well as in surface view, is best shown in Figs.251, 252, 248, 247, 250 respectively.

Many stomata were seen in the epidermis (Figs.247, 250, 253-255). They are usually situated on the surface of raised parts of the axes (Figs.249, 255, 319 on Plates 37, 38, 47 respectively) and are always orientated in the same direction, parallel to the long axis of the stem. The average stoma measures about 100 x 80 μ. Some stomata have two equal axes, being round in shape; others are even broader (horizontally) than long (vertically). The epidermal cells around a stoma appear to be arranged in a regular manner (compare Figs.247, 250 & 255).

The epidermis of the axis is continuous with that of the stalk of the sporangium. The epidermal cells of the stalk are slightly shorter than those of the axis but longer than those of the sporangial epidermis. Stomata occur in the epidermis of the stalk (Figs.256 & 257).



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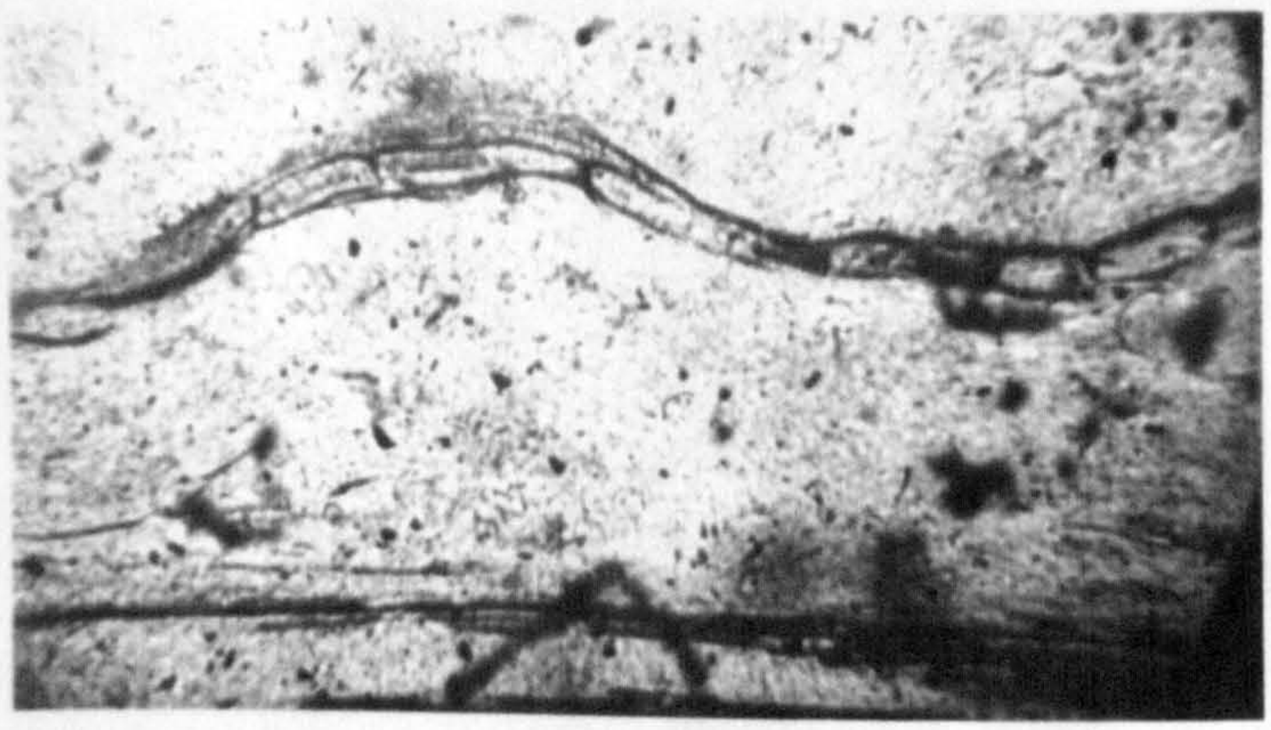

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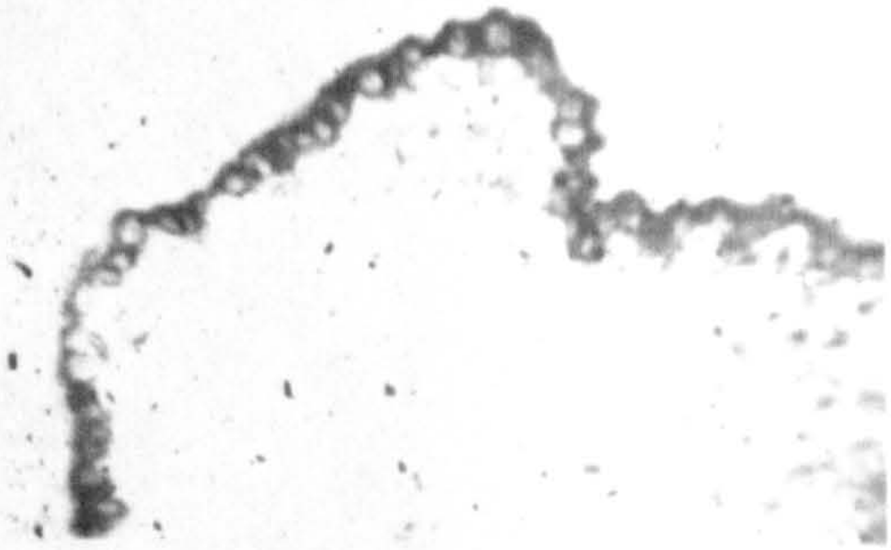

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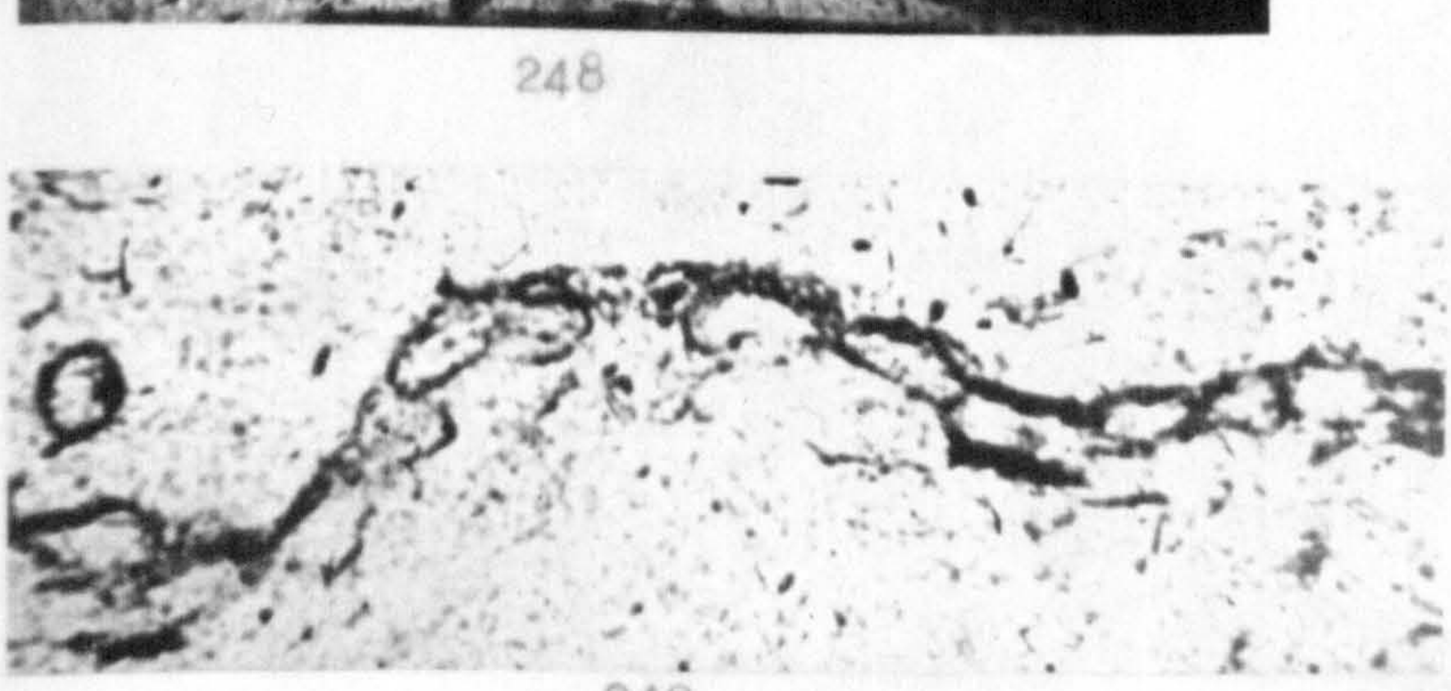

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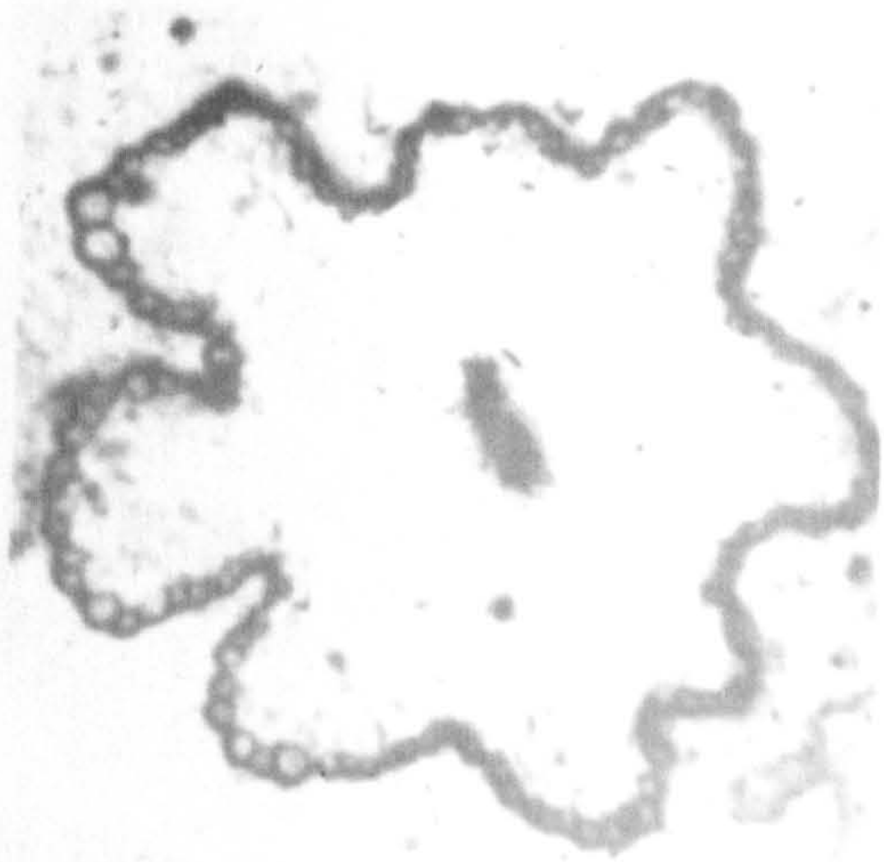

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Fig. 247 : Epidermis and stoma in surface view. Ppoto by transmitted light, Ground section , slide No.1. x70 .

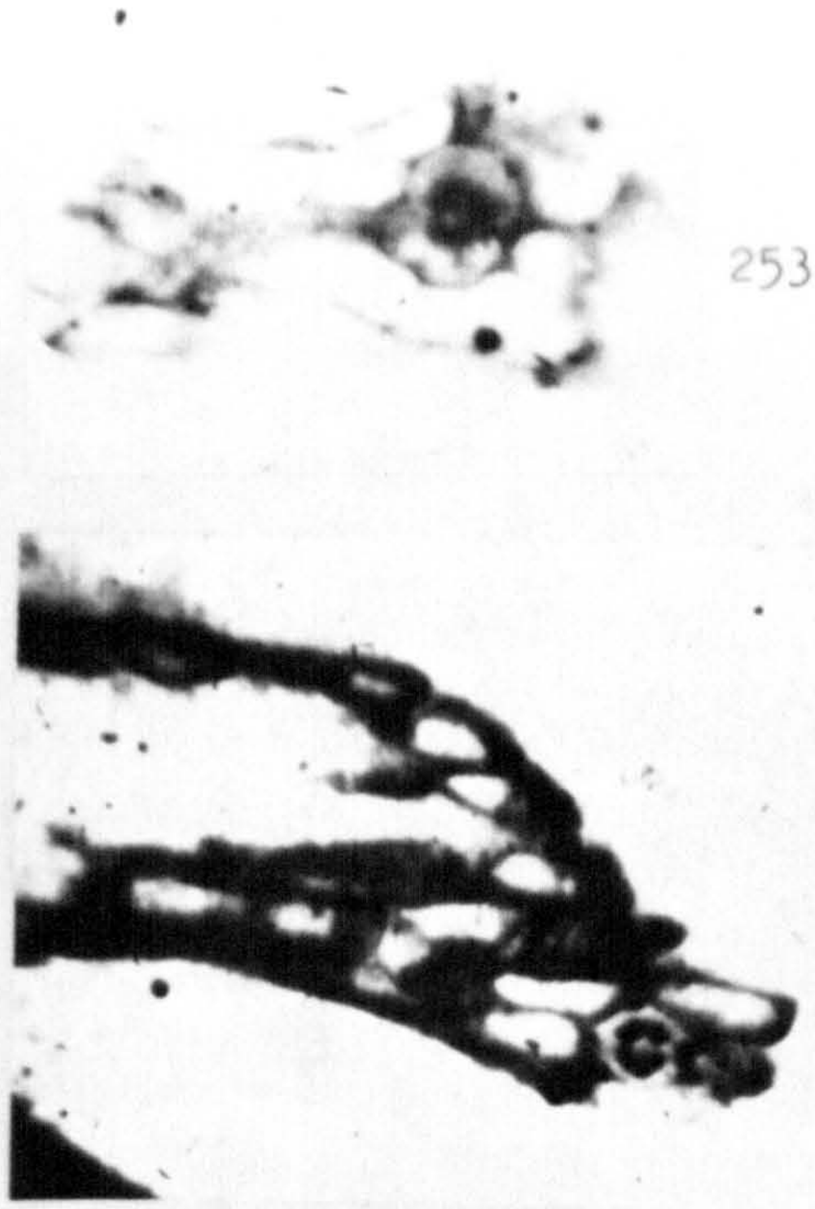
Fig. 248 : Epidermis in L.S. Photo by transmitted light. Peel-section slide NO.50/30 . x60 .

Fig. 249 : Stoma on a raised part of an axis. Photo by transmitted light. Peel-section slide No.50/30 . x100 .

Fig. 250 : Epidermis and stoma in surface view. Photo by transmitted light. Ground section slide No.1. x70 .

Fig. 251 : T.S. of an axis epidermis. Peel No.62/50. x50 .

Fig. 252 : T.S. of an axis showing epidermis. Peel No.67/25. x40 .



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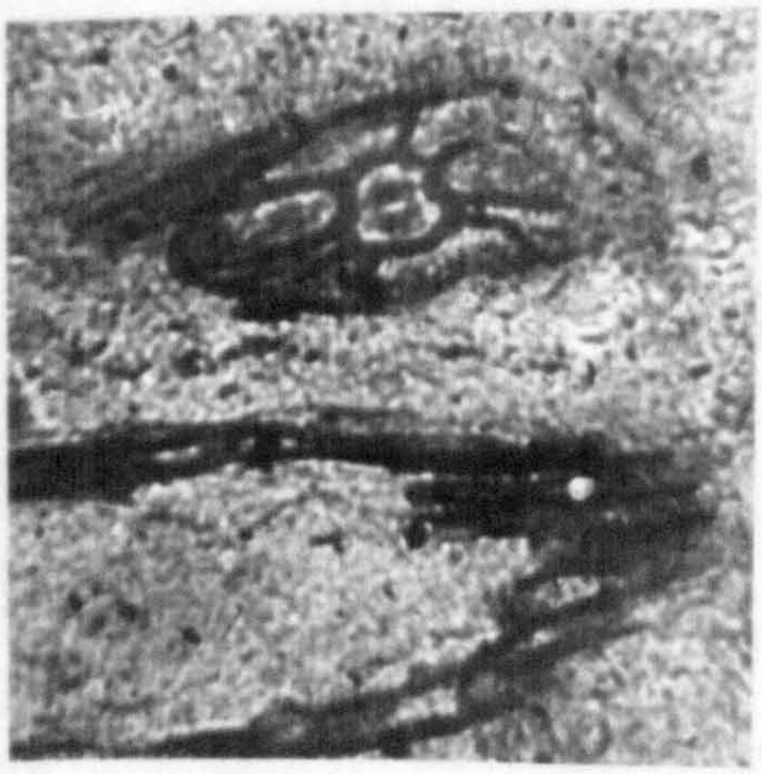

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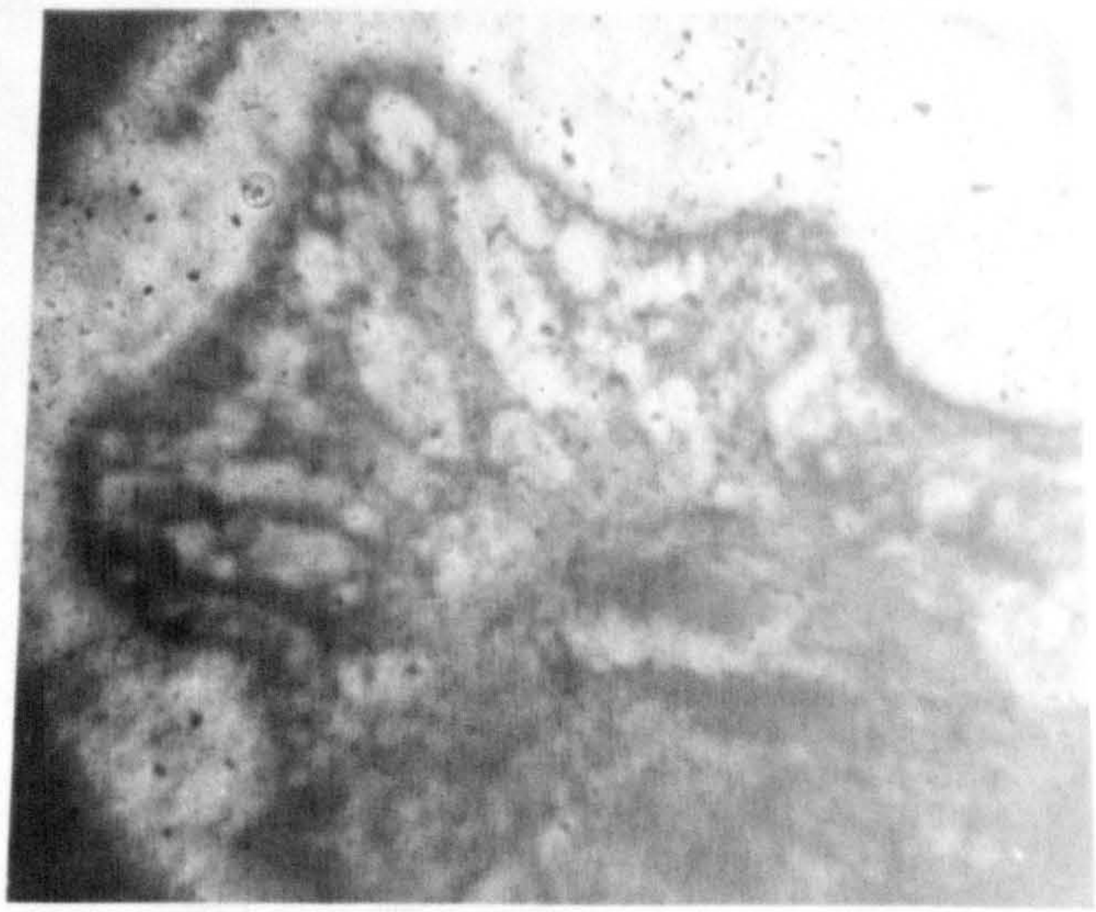

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Fig. 253 : Surface view of stoma of an axis. Peel No. 67/202. x100 .

Fig. 254 : " " " " " " " Peel No. 67/164. x80 .

Fig. 255 : Stoma on a raised part which is shaved off by the section. Peel No. 50/25 . x100 . Photo by transmitted light.

Fig. 256 : Stoma in the epidermis of a sporangial stalk. Photo by transmitted light. Ground section slide No. 1. x30 .

Fig. 257 : The same x100 . The dark patch represents the position of another stoma which is out of focus in this photo.

Fig. 258 : The cortex of an axis in T.S. Peel No. 62/8 . x30 .

Raised parts, similar to those of the axis, were met with in the stalks (Fig.275). In the cross sections of many stalks there are present several thin dark lines which extend from the surface of the epidermis to the outer layers of the cortex (Plate 39, Fig.262). On further examination some of them proved to be narrow cavities which give the impression that they were compressed stomatal chambers. These dark lines or narrow cavities are present also at the base of the stalks before they separated from the axis (Plate 39, Fig.260).

The cortex is usually perished but in a few axes it is slightly preserved as uniform parenchymatous cells. The cells of the outer layers of the cortex in some axes are of larger size and looser than those of the inner layers of the cortex. The outer layers of the cortex might even appear trabeculated (Plate 38, Fig.258). In the transverse section of the large axis in Fig.259, there seems to be a distinct outer cortex and an ill-preserved inner cortex. The outer cortex is formed of a few layers of rounded cells which are very loose beneath the epidermis. The cells have well marked dark walls. The zone of the inner cortex is thicker than that of the outer cortex but its cells are thin walled and ill-preserved.

In some axes, though not well-preserved, there is a faint demarcation between a narrow outer cortex and a wider inner cortex; these axes are usually relatively large in size. In one particular axis the whole cortex is not preserved but the colour of the sediment in position of the outer layers of the cortex is much darker than that in position of the inner layers (Plate 39, Fig.263).

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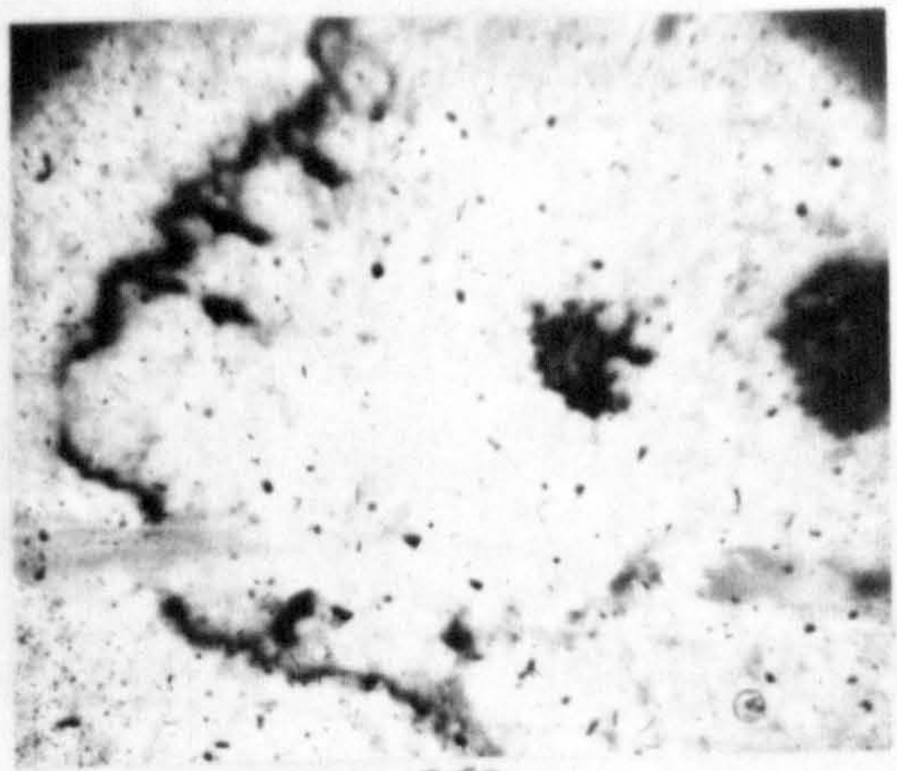

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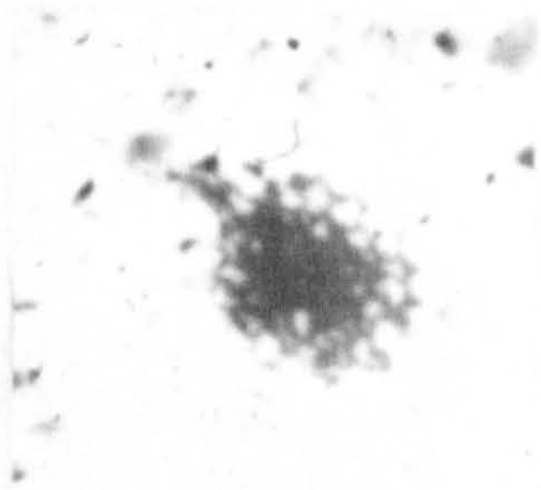

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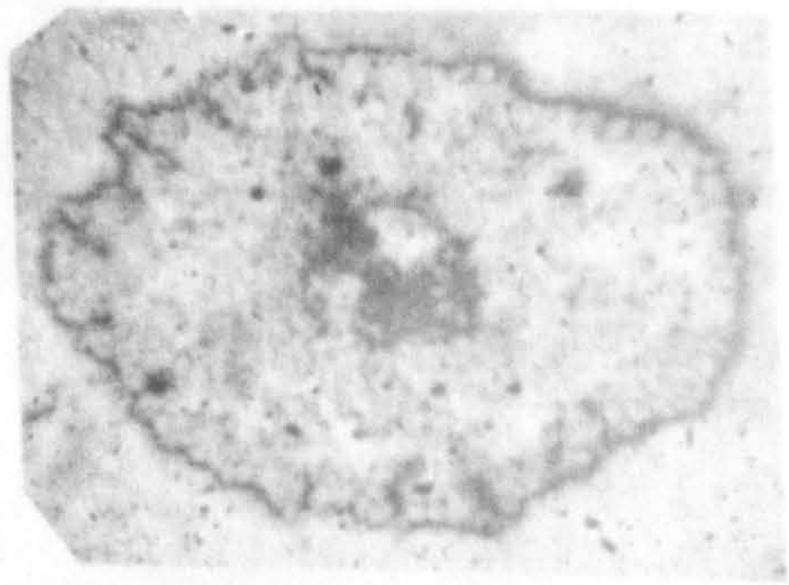

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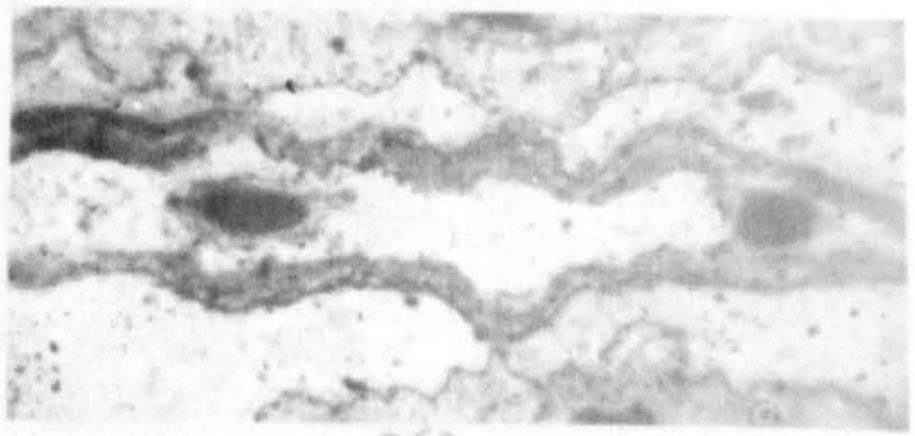

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Fig.259 : T.S. of an axis showing outer and inner cortex. Peel No. 62/47. x 50.

Fig.260 : Thin dark lines at stalk base. Peel No.91/195. x 50.

Fig.261 : T.S. of stalk xylem. Peel No.91/217. x 100.

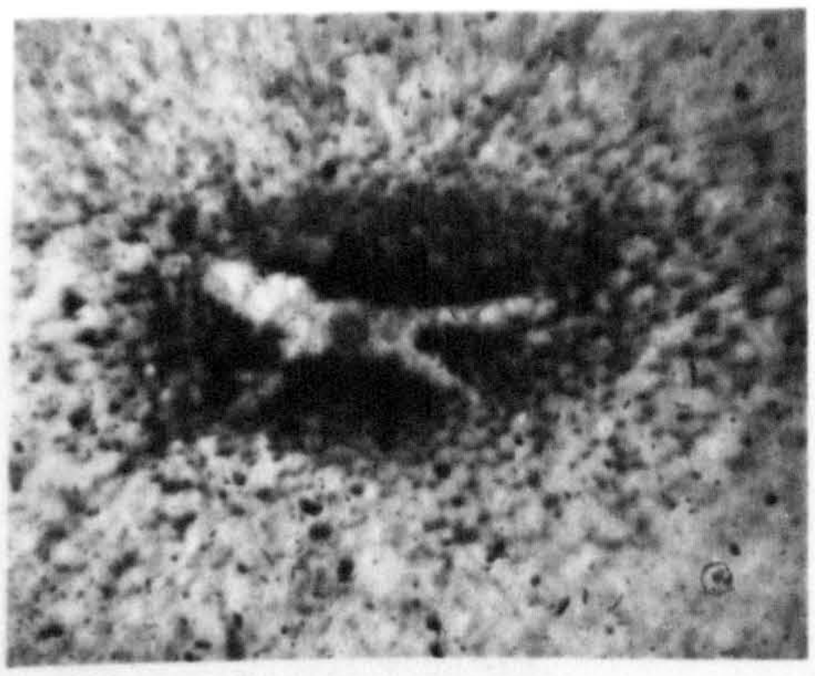
Fig.262 : Stalk in T.S. Peel No.91/5. x 50.

Fig.263 : Oblique T.S. of axis showing position of outer cortex. Peel No.62/368. x 20.

The stele is generally about .5 mm. in diameter of which the xylem is about .25 mm. The elongated thin-walled cells of the phloem are usually perished but in some axes they are slightly preserved (Plate 40, Figs.264-266). Xylem elements are narrow with no detectable thickening or pitting though carefully looked for in hundreds of specimens. The xylem strand is more or less 12 tracheids in thickness. Xylem strands of axes and stalks contain tracheids of different diameters varying from about 10 μ to about 30 μ. The narrower tracheids are usually in the centre of the xylem strand (Plate 25, Fig.135 & Plate 39, Fig.261). In many cases, however, the preservation of the xylem was too poor to allow more detailed investigation. The arrangement of the tissues in the steles of the axes which are preparing for branching or for giving off sporangial traces has already been described. The xylem of the stele was found in many cases to be broken down to two or more portions (Plate 40, Figs.264 & 265). These portions might unite again, rebreak and unite a number of times. This break down of the xylem is not accompanied by any corresponding changes in the outer tissues of the axis. In one block a few axes were found with fungal bodies preserved between the tracheids of the stele xylem (Figs.268 & 269). Although the appearance of the infected xylem in these figures agrees exactly with the features of broken down xylem yet it cannot be stated that the fungal bodies were the reason of the break down of the xylem because in the majority of the broken down xylem cases, no fungal bodies were found preserved between the portions of the split xylem. The tissue of the axis that was mostly invaded by

fungi is the cortex (Plate 41, Figs.271-273). These figures show different fungal bodies preserved in the cortex of some axes. Fungal bodies were also found in the cortex of some sporangial stalks as well as in the matrix of the blocks (Plate 40, Fig.270).

The internal anatomy of the stalk is not different from that of the axis and its branches (Plate 40, Fig.267). It was noticed that at the point of connection between a sporangium and its stalk, the latter abruptly becomes very thin for a length of about .5 mm. and the cells of the tissues of the stalk at this point are dark brown in colour (Plate 41, Figs.274-277).



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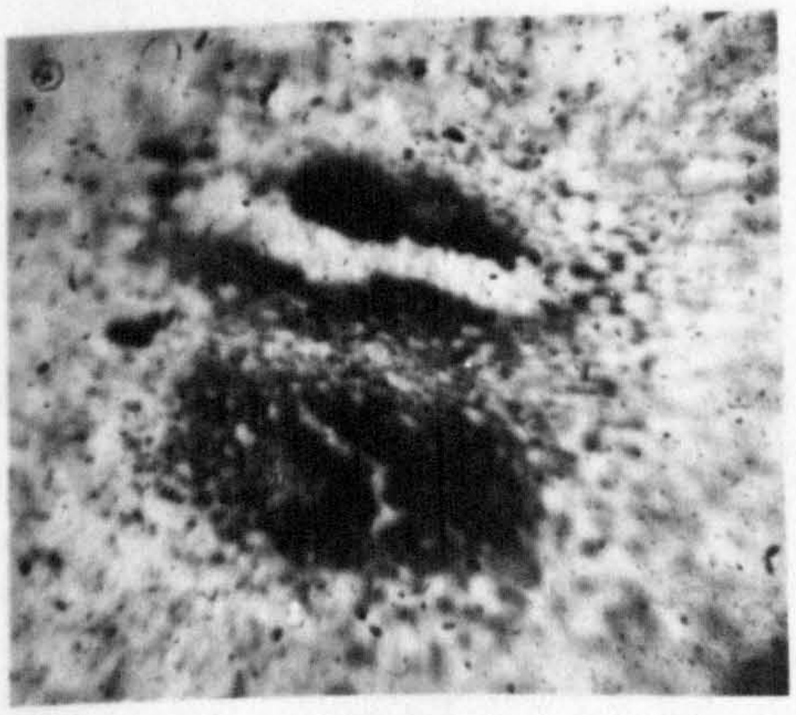

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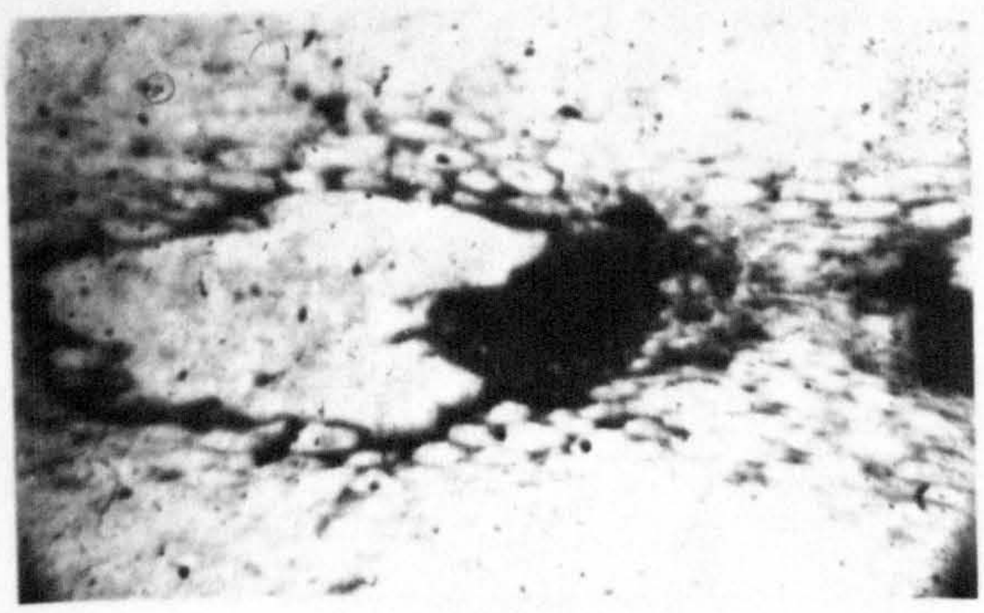

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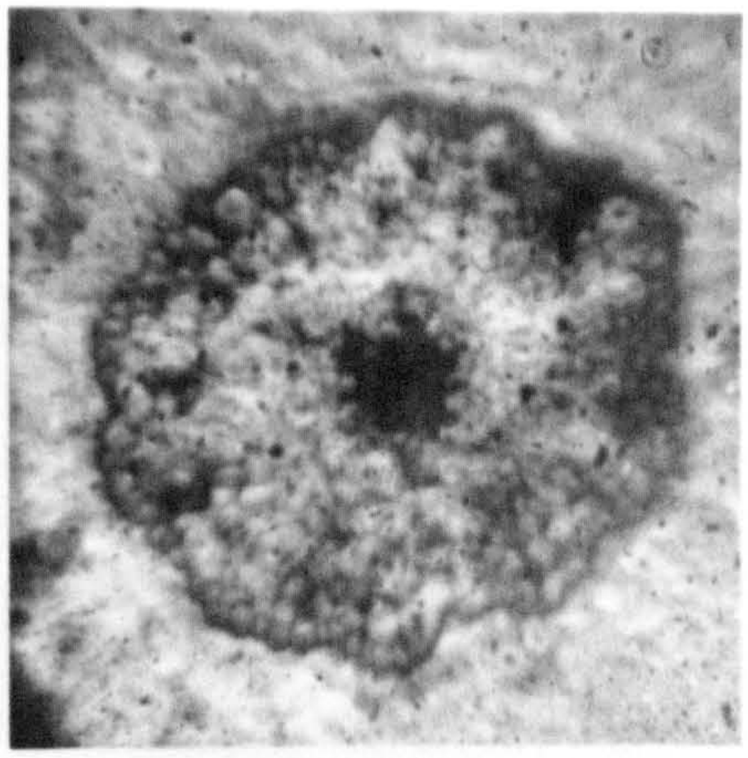

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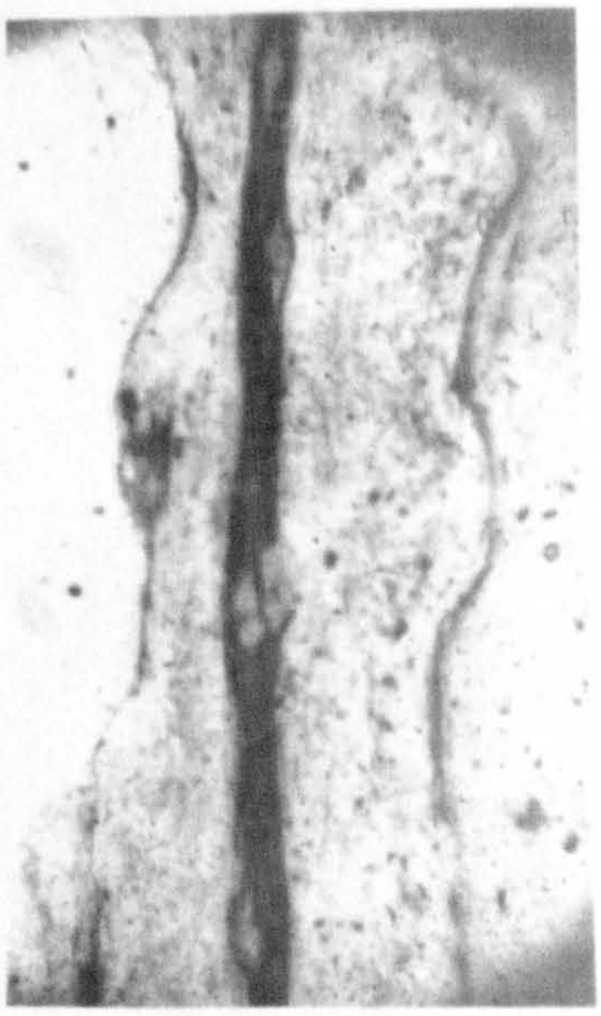

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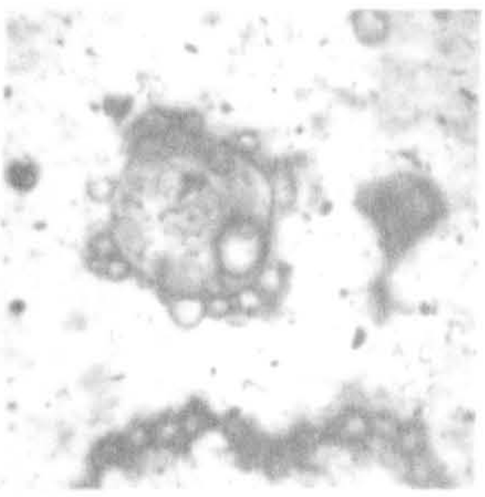

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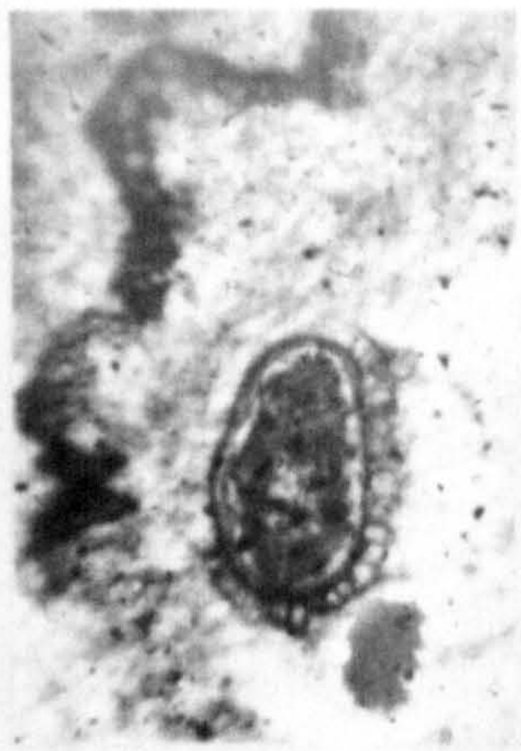
Figs. 264-266 : Transverse sections of axes showing phloem and broken down xylem. Peels No. 62/300, 62/354 & 62/8. x50 .

Fig. 267 : T.S. of sporangial stalk. Peel No. 91/68. x50 .

Figs. 268&269 : L.S. of axes showing fungal bodies between xylem elements. Peels No. 69/67; x10 , 69/84; x50 .

Fig. 270 : Fungal bodies in matrix. Peel No. 56/4. x50 .



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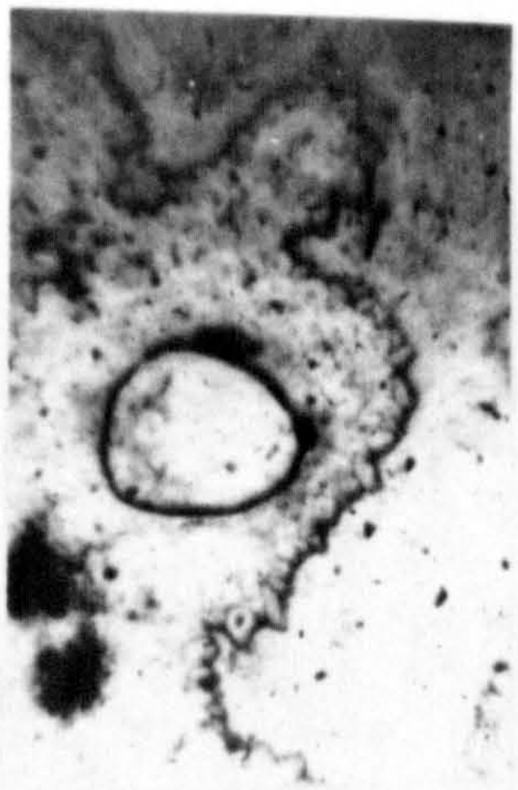

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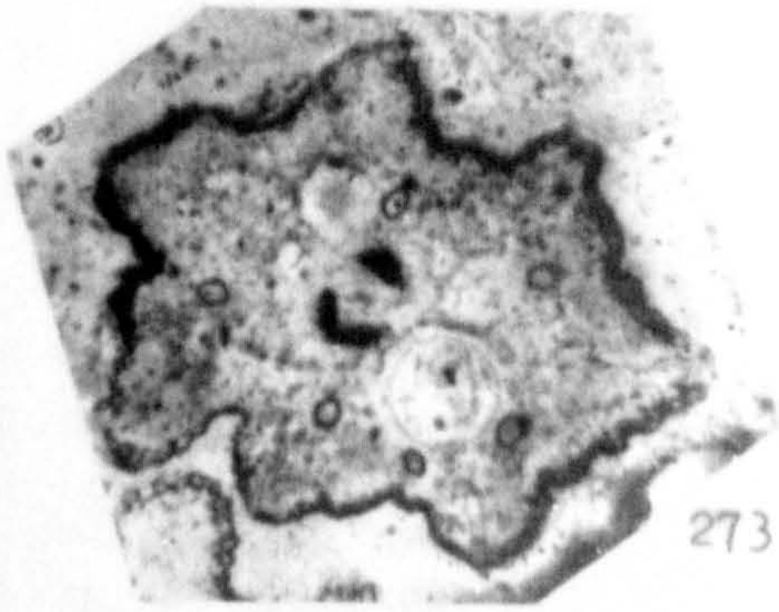

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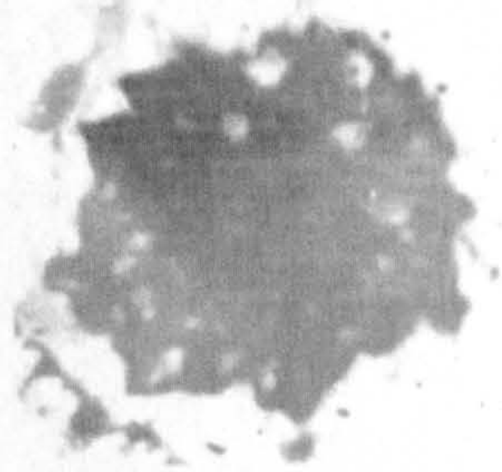

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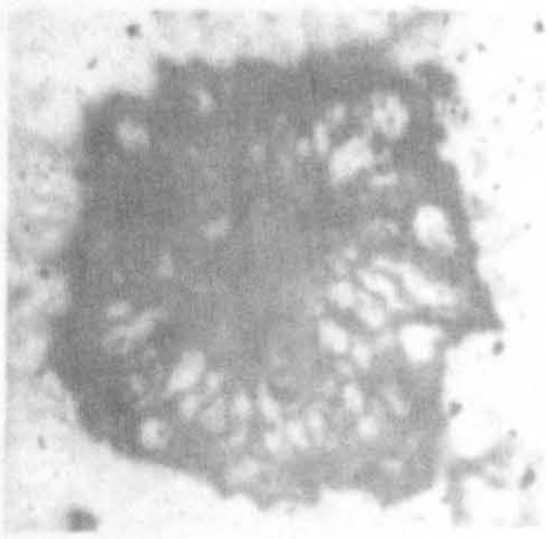

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Figs. 271-273 : Fungal bodies in axes cortex. Peels No. 67/5, 65/120 & 65/120. x50, x50 & x20 .

Fig. 274 : Thin dark connection between sporangium and its stalk as shown in L.S. Peel No. 50/2. Photo by transmitted light, x20 .

Fig. 275 : Raised part in stalk epidermis. Photo by transmitted light. Peel-section slide No. 50/3 . x50 .

Figs. 276&277 : Transverse sections of distal end of stalks showing dark colouration. Peels No. 67/112 & 67/110. x50 .

SPORANGIA AND SPORES

The stalked sporangia are borne both laterally and terminally on the fertile axes.

A general idea of the range in size of the sporangia can be gathered from the examples shown on Plates 21 & 22, Figs.91; 97, 98. The majority of dehisced sporangia are about 2.3-3.1 mm. wide, 1.2-1.8 mm. long and 1-1.4 mm. thick. Dehisced sporangia are sometimes very small; under 1 mm. in their three dimensions. Such very small sporangia were found at fine branch ends. Young immature sporangia were found also at fine branch ends but were too ill-preserved to be examined or described. The size of a connected pair of sporangia is almost twice that of an ordinary single sporangium.

The sporangium wall is about 4 or 5 layers thick and consists of an epidermis layer covered with cuticle, a zone of thin walled and usually ill-preserved cells about 2 or 3 layers thick and an innermost layer or tapetum which is usually persistent and dark in colour (Plate 42, Fig.279). The cell structure of the tapetal layer, however, is ill-preserved and it is in this layer that the xylem strand of the sporangium trace terminates (Plate 27, Fig.157).

Stomata were found in the epidermis of the sporangium wall. The appearance of the epidermal cells and the stomata in surface view is shown on Plate 43, Figs.285 & 289. The inner and lateral walls of the epidermal cells become thickened in the upper part of the sporangium (Plate 42, Figs.278 & 280; Plate 47, Fig.320) where dehiscence took

place at the apex by a long slit (Figs.282 & 283). The thickened annulus-like cells become shallower towards the line of dehiscence (Figs.278 & 280). The dehiscence slit extends throughout the whole width of the sporangium and also throughout most of its length on both sides (Plate 45, Fig.304). At both ends the slit apparently becomes slightly wider than elsewhere (Plate 42, Fig.281). The two edges of the sporangium overlap at the position of the dehiscence and the upper edge is always to the outside (Plate 42, Figs.279 & 280). It was found also that the upper edge is slightly longer than the inner one; which means that the line of dehiscence is not exactly in the middle of the sporangium tip but quite close to it. The dehiscence slit is surrounded by a continuous zone of annulus-like cells. This zone is several cells broad and has a darker colour than the rest of the epidermis (Plate 43, Figs.286 & 288).

Two diagramatic drawings of the sporangium, one in top view and the other in side view, are shown on Plate 47, Figs.312 & 318.

Numerous cavities about .1 mm. wide x .5 mm. long were found inside the sporangium wall (Plate 43, Fig.284; Plate 44, Figs.295 & 296). These cavities occur everywhere inside the wall, however, they are more distinct and abundant in the upper part of it. The cavities extend from the epidermis surface to the outer surface of the tapetal layer (Fig.296). The sporangium wall itself is about .15-.2 mm. thick. In some cases the two epidermal cells above a cavity are like two guard cells of a stoma and differ in shape from the neighbouring epidermal cells. Somewhat similar cavities were found occasionally beneath the

epidermis of some axes (Figs.293 & 294) and stalks (Figs.291 & 292). The figures suggest that these cavities are respiratory chambers. However, the abundance of these cavities in the sporangial wall, especially in the apical region with thick annulus-like cells makes this suggestion less probable in the case of the sporangia.

Irregularities in the surface of the sporangium are sometimes observed, especially in its lower part (Plate 42, Fig.279). Sporangia are more or less reniform. A median longitudinal section of a dehisced sproangium is usually pyriform (Figs.297 & 320). A vertical section through the apical part of a sporangium is reniform with the spore cavity bulged at the centre of the concave side where the sporangium joins its stalk (Plate 42, Fig.282).

Figure 311 on Plate 47 shows a diagramatic drawing of a sporangium in a median vertical section, transverse to the axis. All the longitudinal sections between points a and á in the diagram will appear pear shaped (Plate 47, Fig.315). All the longitudinal sections between points a and b or á and b́ will appear oval in shape (Plate 47, Fig.314) and longitudinal sections from point b or b́ to the end of the sporangium will be rounded in shape (Plate 47, Fig.313).

Three longitudinal sections in one and the same sporangium illustrating the pear, oval and rounded shapes are shown on Plate 45, Figs.297, 298 and 299 respectively.

Figure 317 shows a diagramatic drawing of a sporangium in a median longitudinal section at right angles to the axis. All vertical sections between points a and á will show the bulge of the cavity and

either one or two edges of the sporangium (Plate 42, Figs.282 & 283). Vertical sections in the sporangium from points a or á to the end of the sporangium will appear kidney shaped (Plate 45, Fig.305).

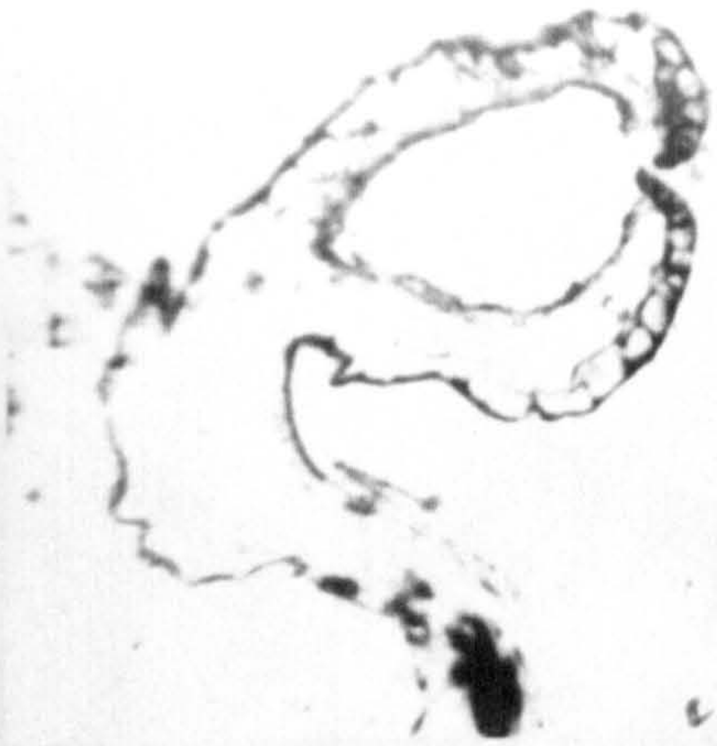
The appearance of the sporangium in cross sections at different levels is shown on Plate 45, Figs.300-303.

A small number of evidently undehisced sporangia were found to be reniform in all vertical sections including median ones i.e. they do not show the cavity bulge (Plate 43, Fig.290). In longitudinal sections, including median ones such sporangia always appear rounded (Figs.287 & 306). This is different from mature dehisced sporangia which are pyriform in median longitudinal sections. In the longitudinal sections of these undehisced sporangia, the apex is seen notched i.e. it has a longitudinal groove, lined by the dark thickened annulus-like cells which are shown to be continuous and the wall of the sporangium (though ill-preserved) at the dehiscence line is formed only of the thickened epidermal layer. This is clearly shown in longitudinal sections of dehisced sporangia (Figs.278 & 320). The undehisced sporangia are filled by spores, nearly all of them still in tetrads (Figs.290 & 306). These undehisced sporangia are of somewhat small size; under 2 mm. in width and about 1 mm. in length and thickness. However, it must be remembered that dehisced sporangia of smaller or similar size were also found (Plate 43, Fig.287).

The majority of dehisced sporangia were found empty. A minority were found containing a small number or a large number of spores some of which are still in tetrads (Figs.307 & 308).

Several thousands of spores were produced in each sporangium; 4 to 5 thousands were counted in some of them. However, small sporangia produced a small number of spores; 2000 spores or less were counted in some sporangia. In the very small sporangia the number of spores produced is much less; about 400 spores were counted in some of them.

Spores are about 65 μ in diameter irrespective of the size of the sporangium. Spores were found free in the matrix as well as inside the sporangia. The cuticularised walls of the spores are brown in colour in peel sections and slightly brighter in colour in ground sections. The wall is thin measuring about 3 μ in thickness. The triradiate marking as seen in the wall of some spores measures about 30-40 μ in length. Each spore has a convex outer wall and a three-sided inner face with a triradiate marking where it adjoined its sister cells in the tetrad. Spores exhibit some variation in size but on an average measure about 65 μ in diameter. The spores that were found free in the peat resemble those in the sporangia, but had increased slightly in size. No stages in the germination of the spore have been found. The smooth wall of the spore shows shallow reticulation. Some spores are illustrated on Plate 47, Fig.316.



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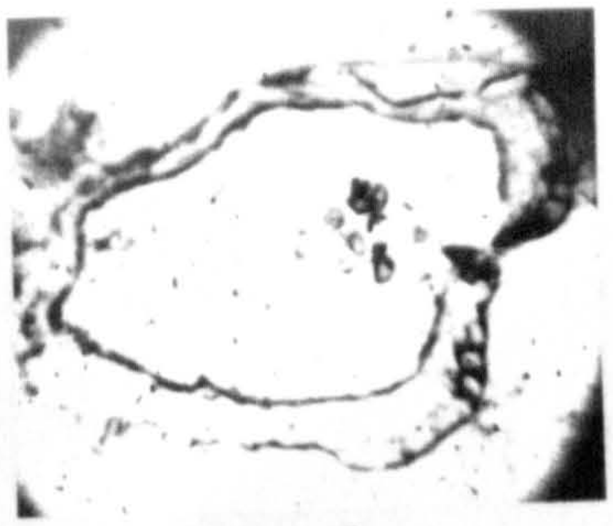

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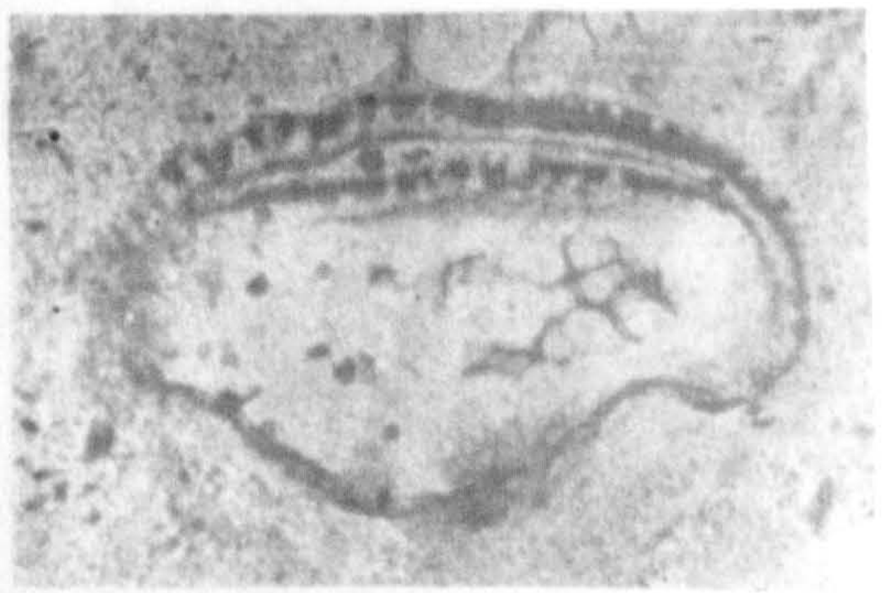

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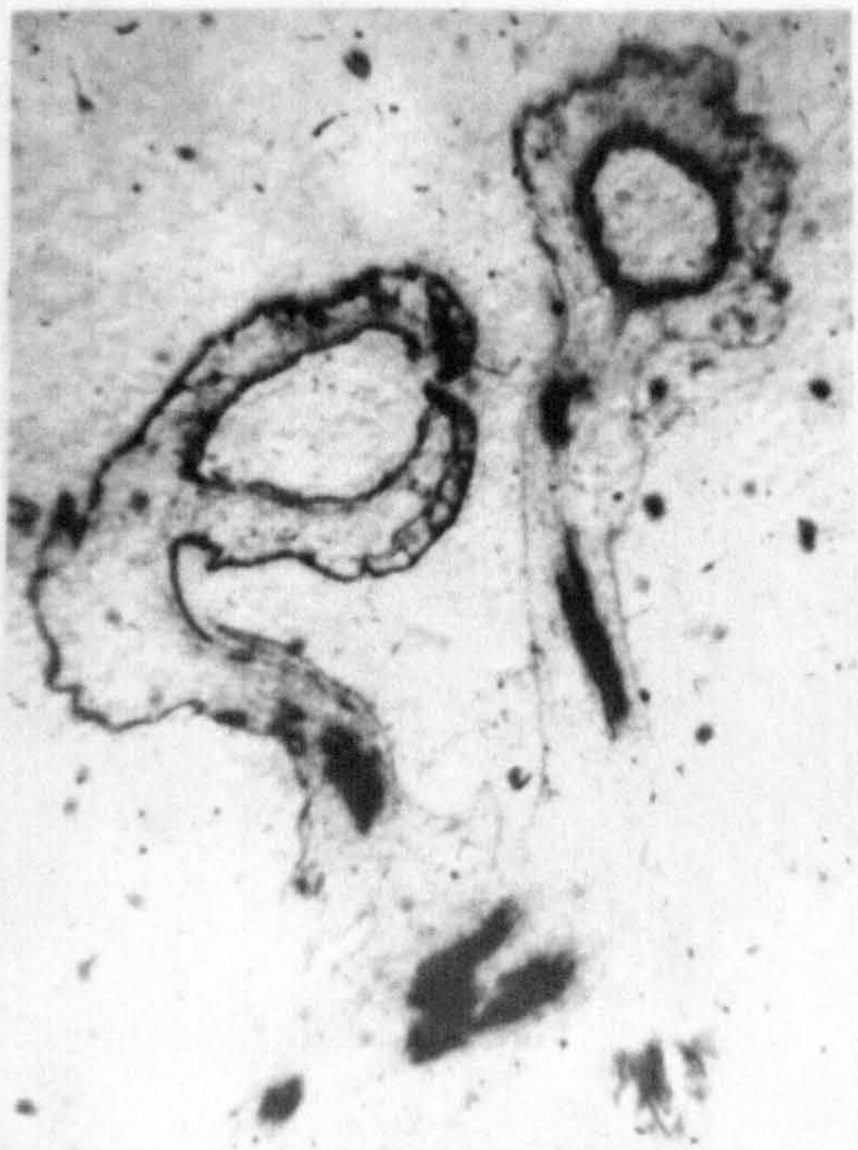

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Fig. 278 : Sporangium in L.S. Peel No.67/1. x40 .

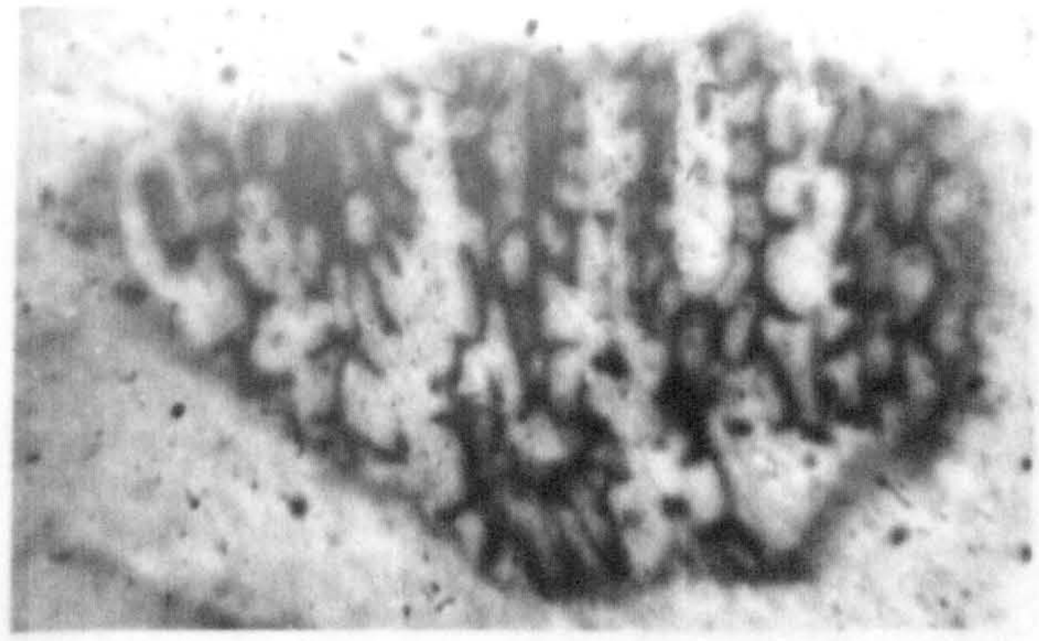
Fig. 279 : Two sporangia , the left of which is cut longitudinally and the other in oblique transverse section. Peel No.67/1. x30 .

Fig. 280 : Sporangium in L.S. Peel No.67/11. x30 .

Fig. 281 : End of dehiscence slit. Photo by transmitted light. Ground section slide No.1. x 30 .

Fig. 282 : Median vertical section of sporangium. Photo by transmitted light. Ground section slide No.91/377. x20 .

Fig. 283 : Median vertical section of sporangium. Peel No.91/100. x30 .



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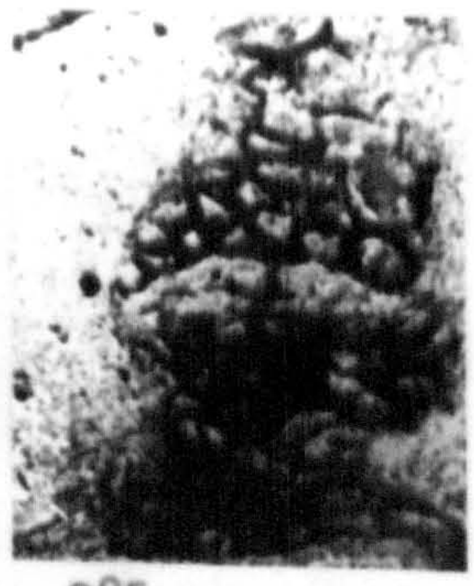

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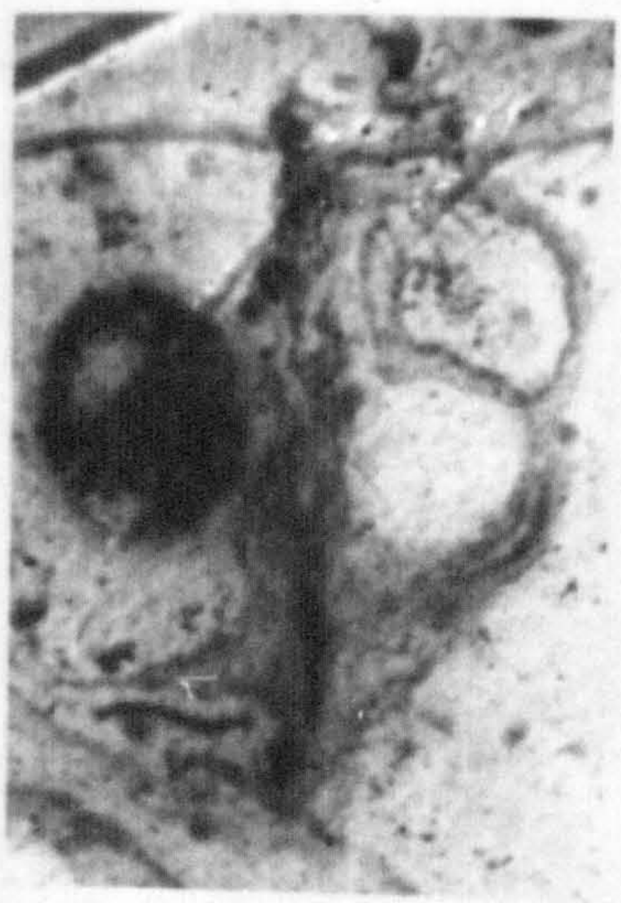

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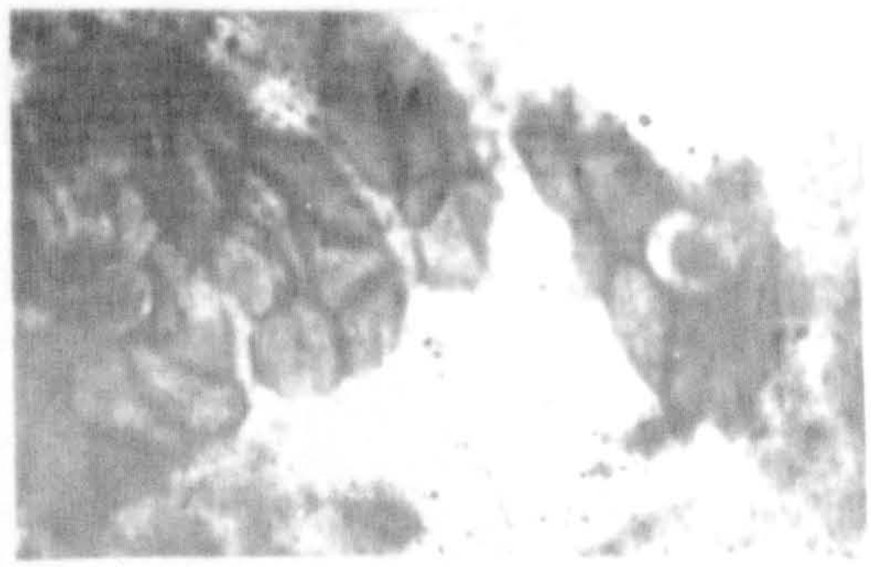

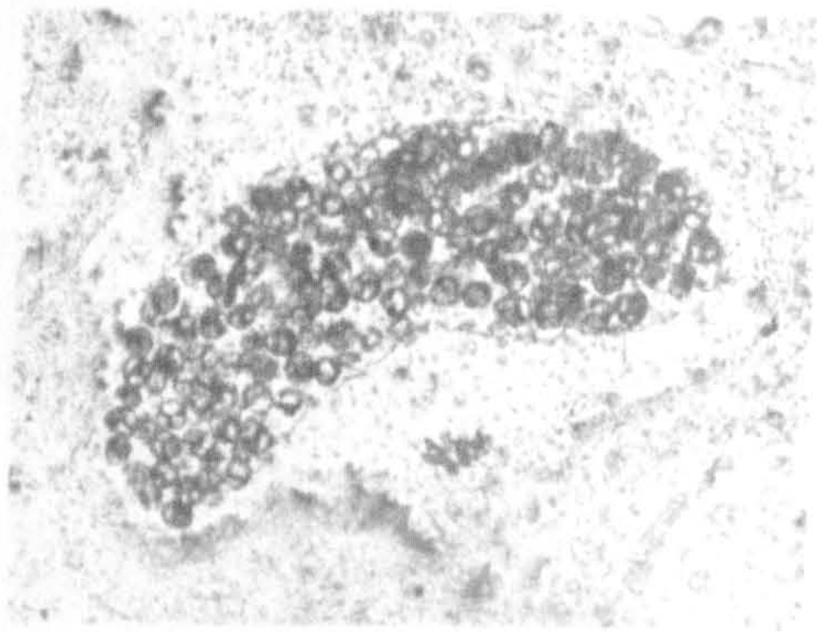

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Fig.284 : Section through sporangium wall parallel to epidermis, some cells of which are seen in surface view. Peel No.62/540. x 100.

Fig.285 : Stoma in sporangium epidermis; surface view. Peel No.62/24. x80.

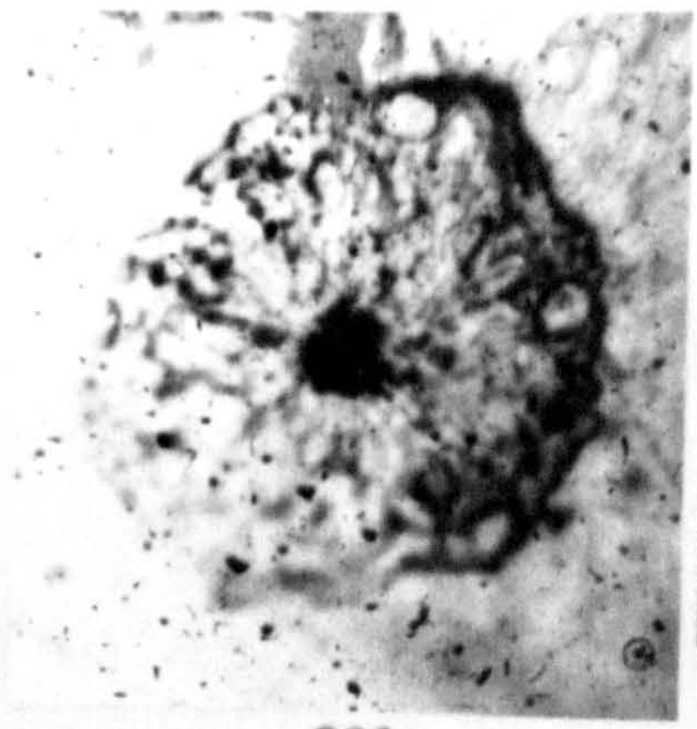
Fig.286 : Top view of sporangium showing dehiscence slit surrounded by annulus-like cells. Photo by transmitted light. Ground section slide No.91/377. x 50.

Fig.287 : Two small sporangia on a slender axis; the right sporangium is dehisced and empty while the left is undehisced and full of spores. Peel No.62/472. x 20.

Fig.288 : Sporangium. Photo by transmitted light. Ground section slide No.1. x 30.

Fig.289 : Sporangium epidermis with stoma in surface view. Photo by transmitted light. Ground section slide No.91/376. x 100.

Fig.290 : Median vertical section of undehisced sporangium full of spore tetrads. Photo by transmitted light. Peel No.67/63. x 30.



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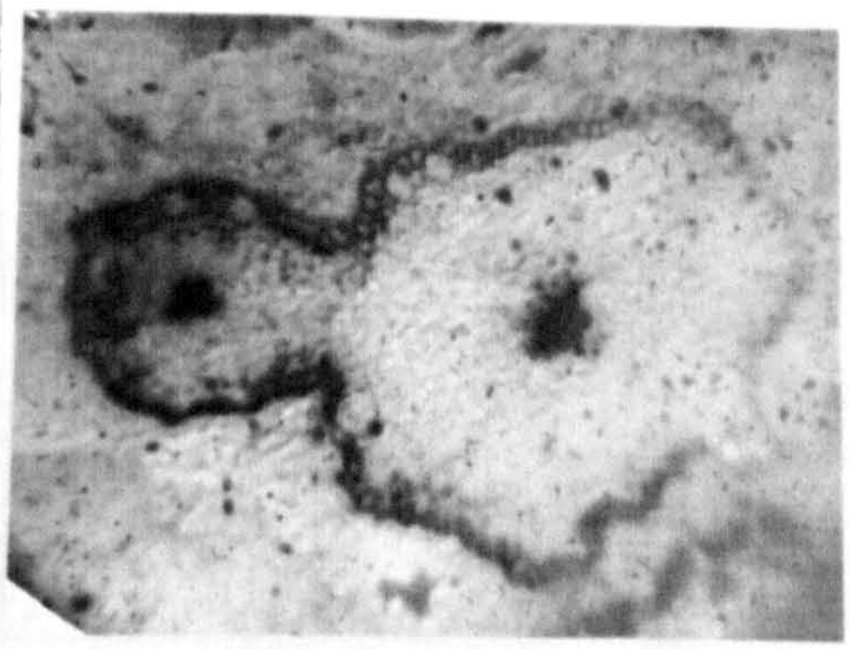

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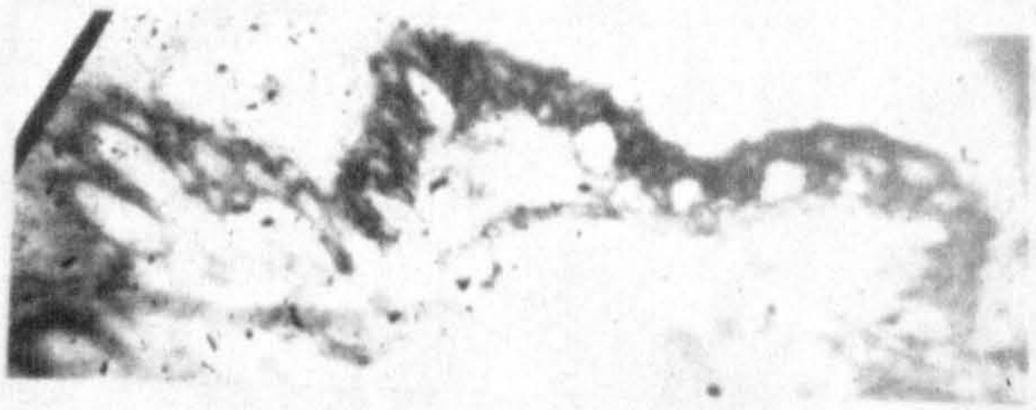

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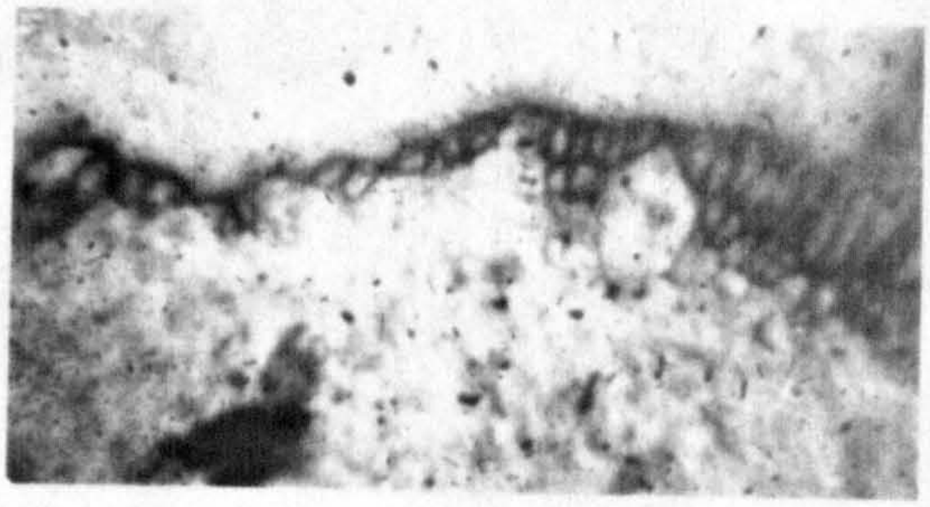

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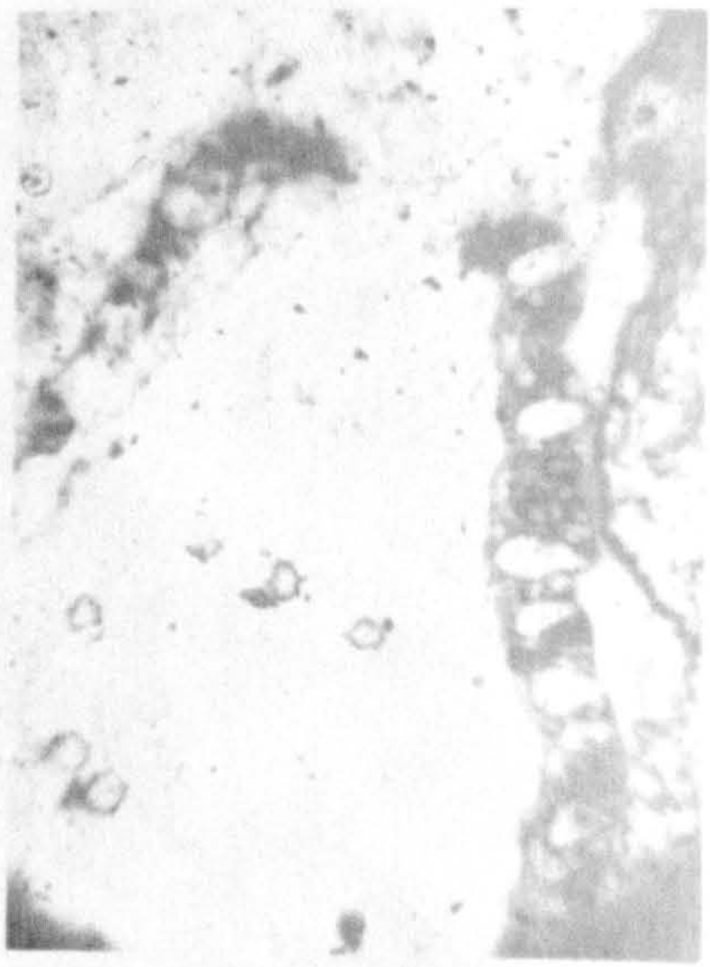
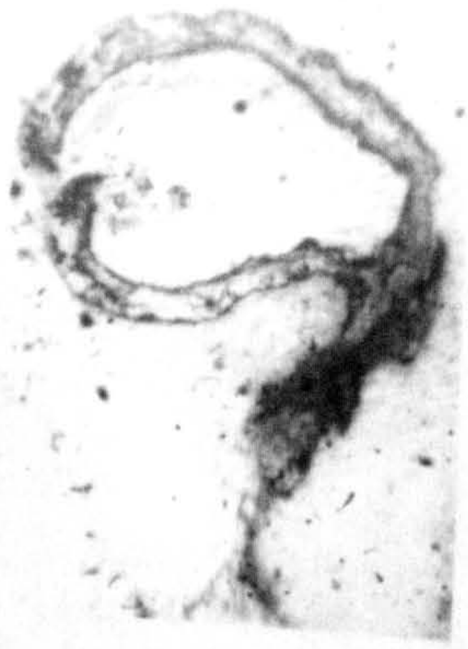


Fig.291 : Stalk epidermis showing cavities. Peel No.67/101. x 50.

Fig.292 : Cavities in the epidermis of axis and stalk. Peel No.91/74. x 20.

Figs.293 & 294 : Cavities in axes epidermis. Peels No.89/28, 62/122. x 50.

Figs.295 & 296 : Cavities in sporangium wall. Peels No.56/148 & 56/183. x 50.



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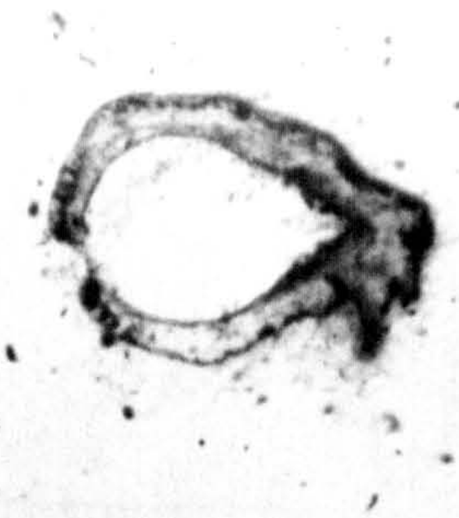

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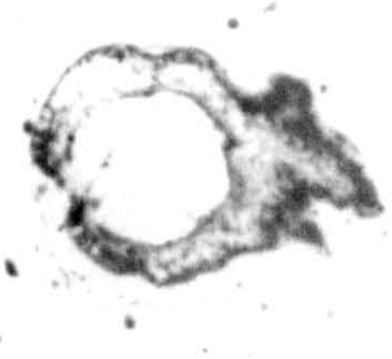

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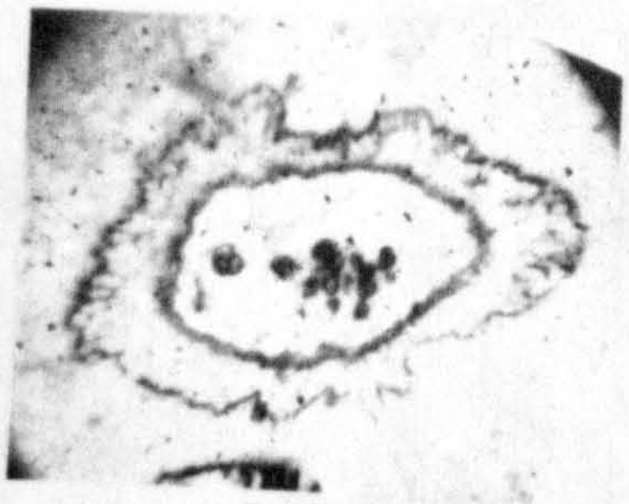

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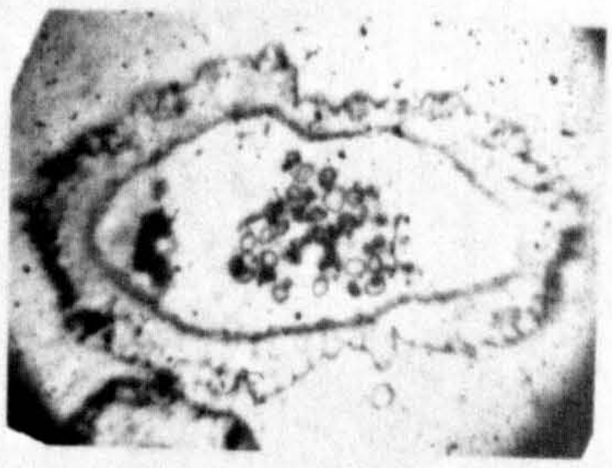

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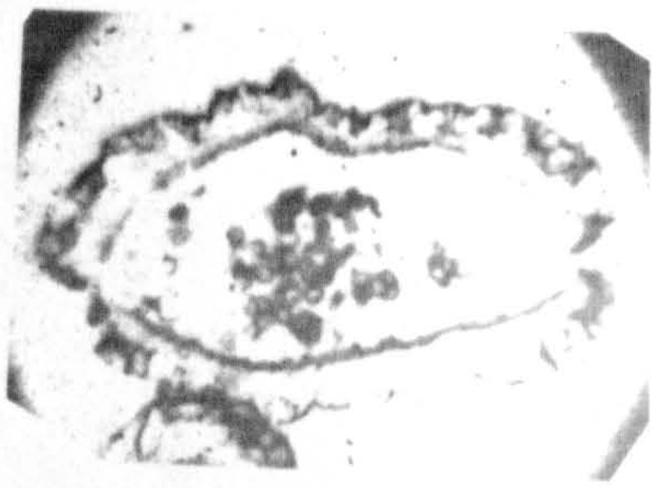

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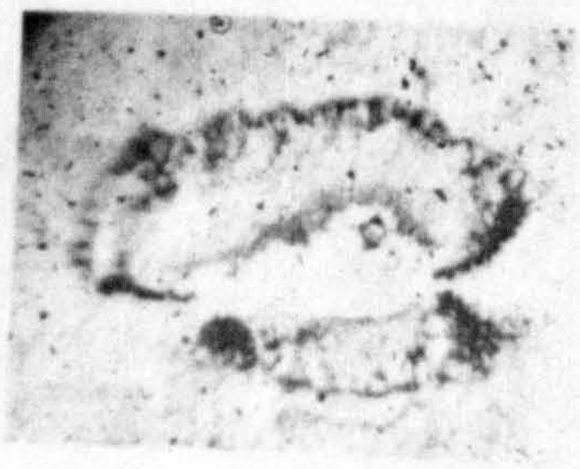

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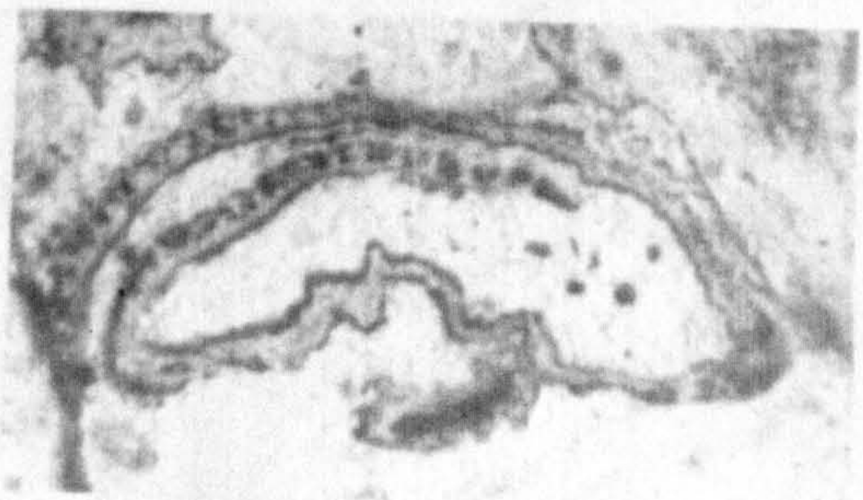

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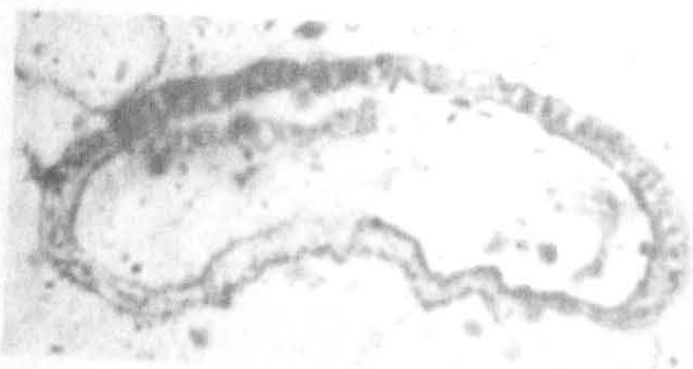

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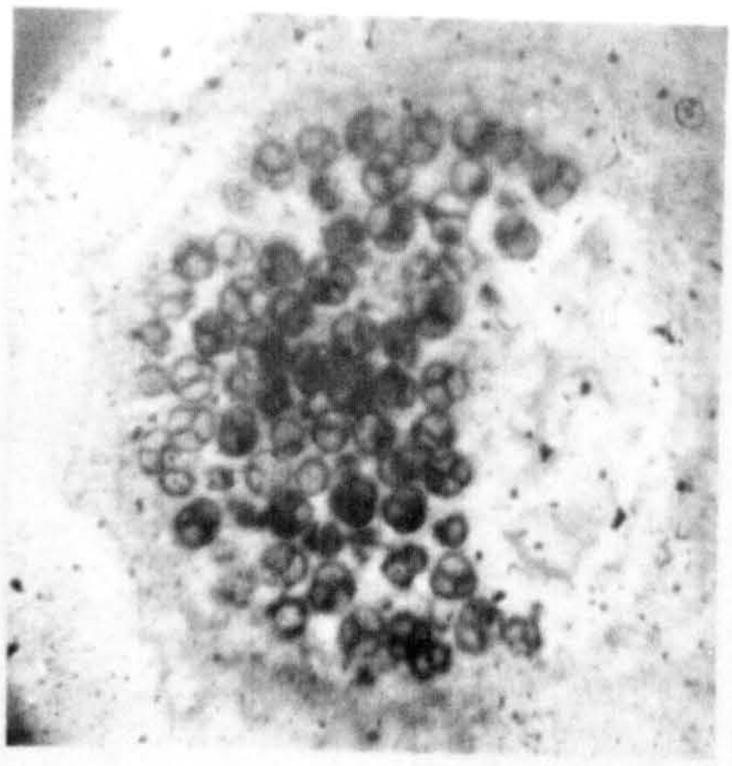
Figs.297-299 : Three longitudinal sections of one sporangium. Peels No.62/16, 62/22 & 62/24. x 20.

Figs.300-303 : Four transverse sections of one sporangium. Peels No. 67/5, 67/8, 67/11 & 67/19. x 30.

Fig.304 : Extended dehiscence slit. Peel No.62/546. x 20.

Fig.305 : Kidney-shaped sporangium in vertical section. Peel No.91/301. x 15.



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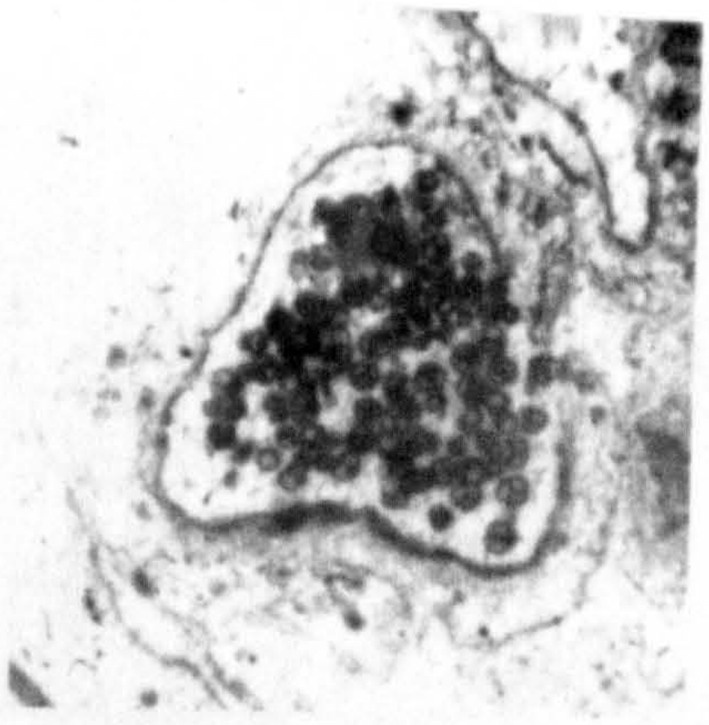

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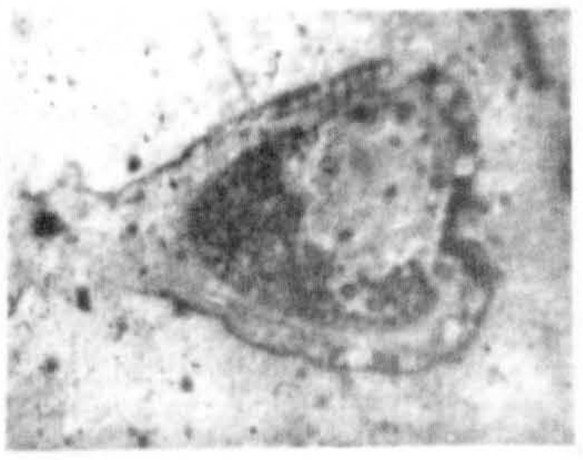

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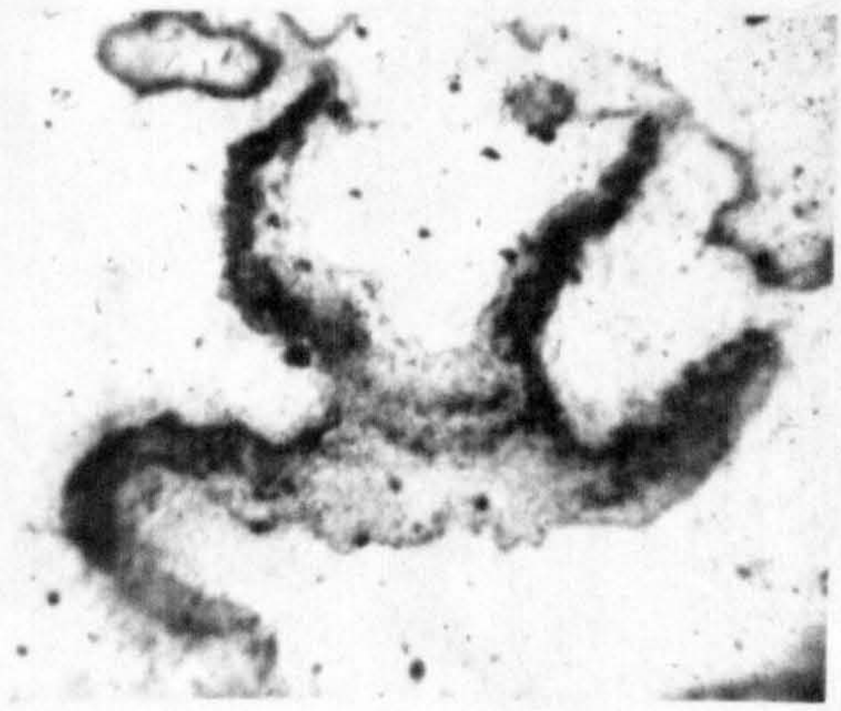

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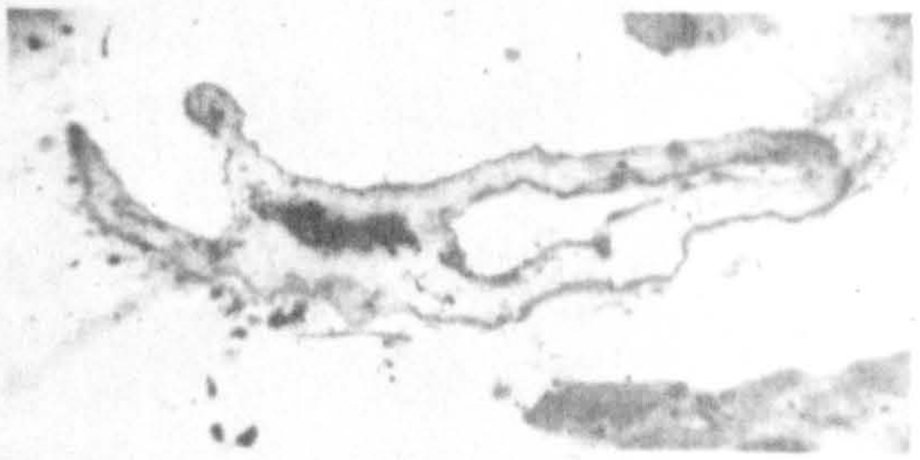

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Fig.306 : L.S. of undehisced sporangium showing round shape and spore tetrads. Peel No.62/258. x 50.

Fig.307 : L.S. of sporangium with many spore tetrads. Peel No.56/121.x30.

Fig.308 : L.S. of sporangium with not many spores left. Peel No.91/257. x 20.

Figs.309 & 310 : Two sporangia of Asteroxylon mackiei. Peels No.62/32, & 69/42. x 15 & x 10.

Fig. 311 : Median vertical section of sporangium. x c.15.

Fig. 312 : Top view of sporangium showing broad zone of annulus-like cells surrounding dehiscence slit. x c.15.

Fig. 313 : L.S. of sporangium. x c.15.

Fig. 314 : L.S. of sporangium. x c.15.

Fig. 315 : Median L.S. of sporangium. x c.15.

Fig. 316 : Some spores in different views. x c.140.

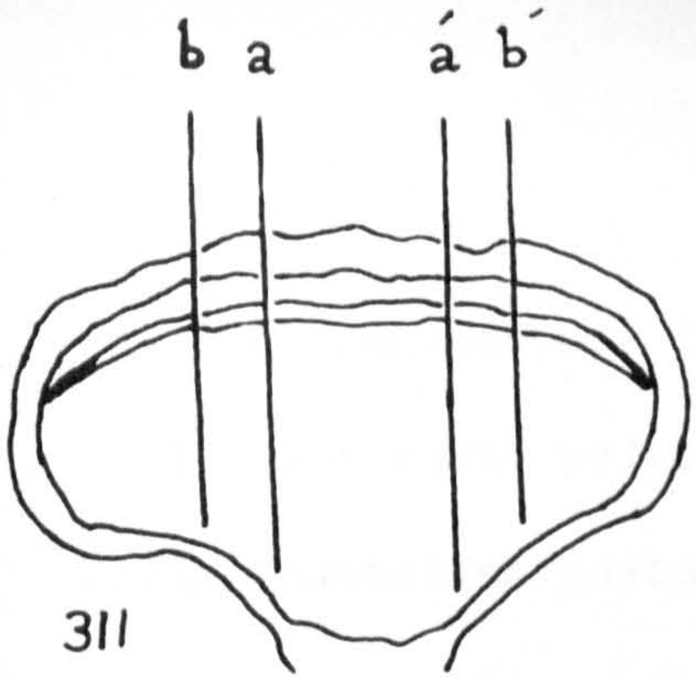
Fig. 317 : Median L.S. of sporangium. x c.15.

Fig. 318 : Side view of sporangium. x c.20.

Fig. 319 : Stoma on a raised part of an axis, based on Fig. 249. x 100.

Fig. 320 : Median L.S. of sporangium showing its pear-shape, broad zone of annulus-like cells at dehiscence position and the shape of these cells. x c.50.

PLATE 47



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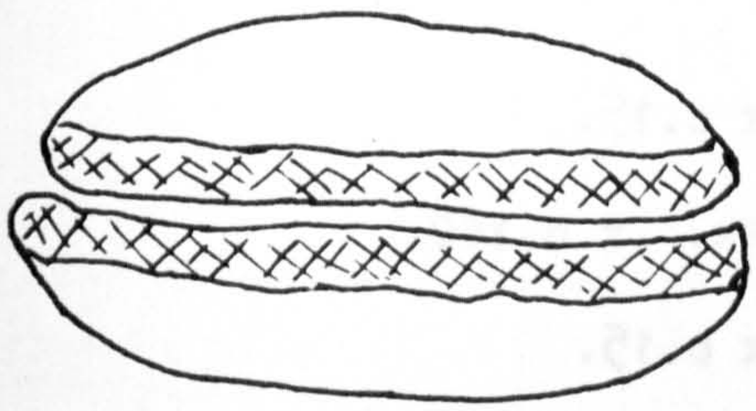
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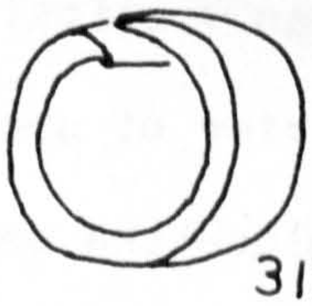
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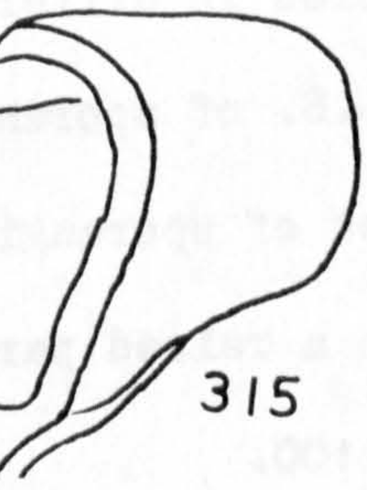
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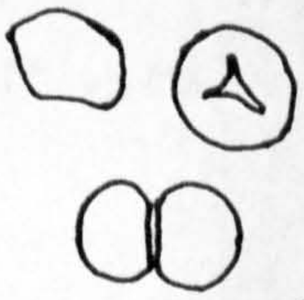
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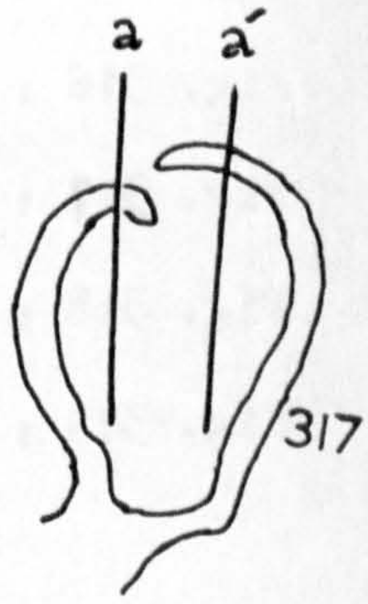

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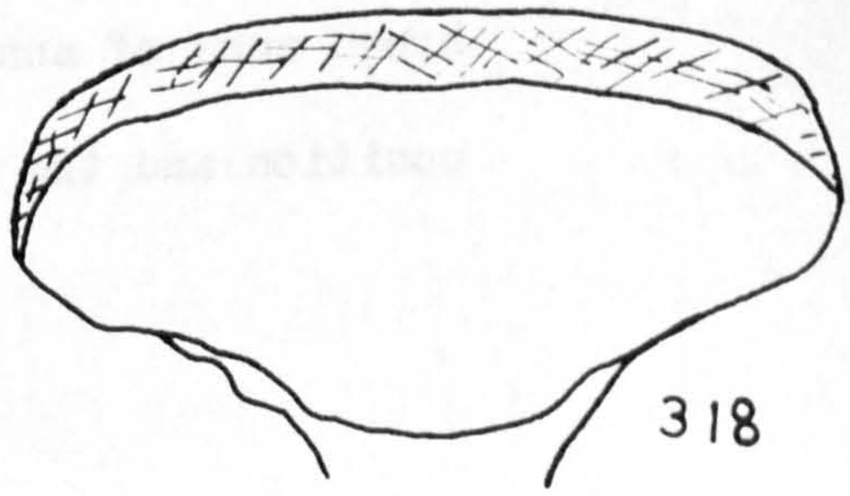
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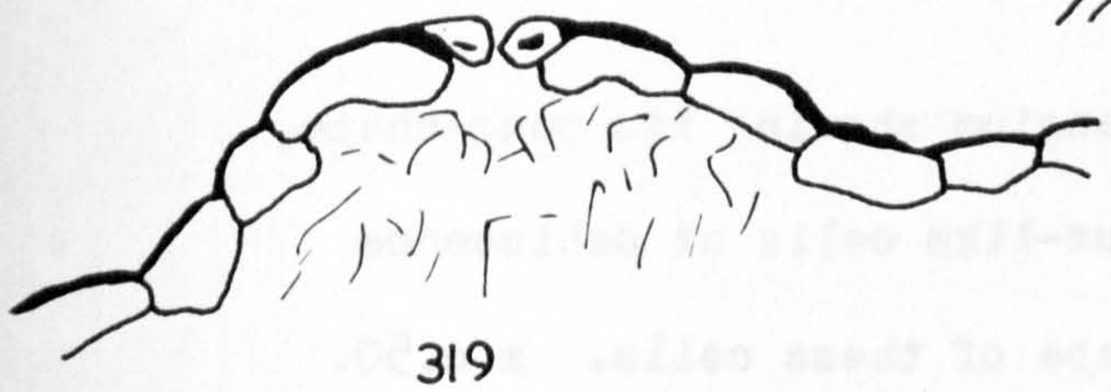
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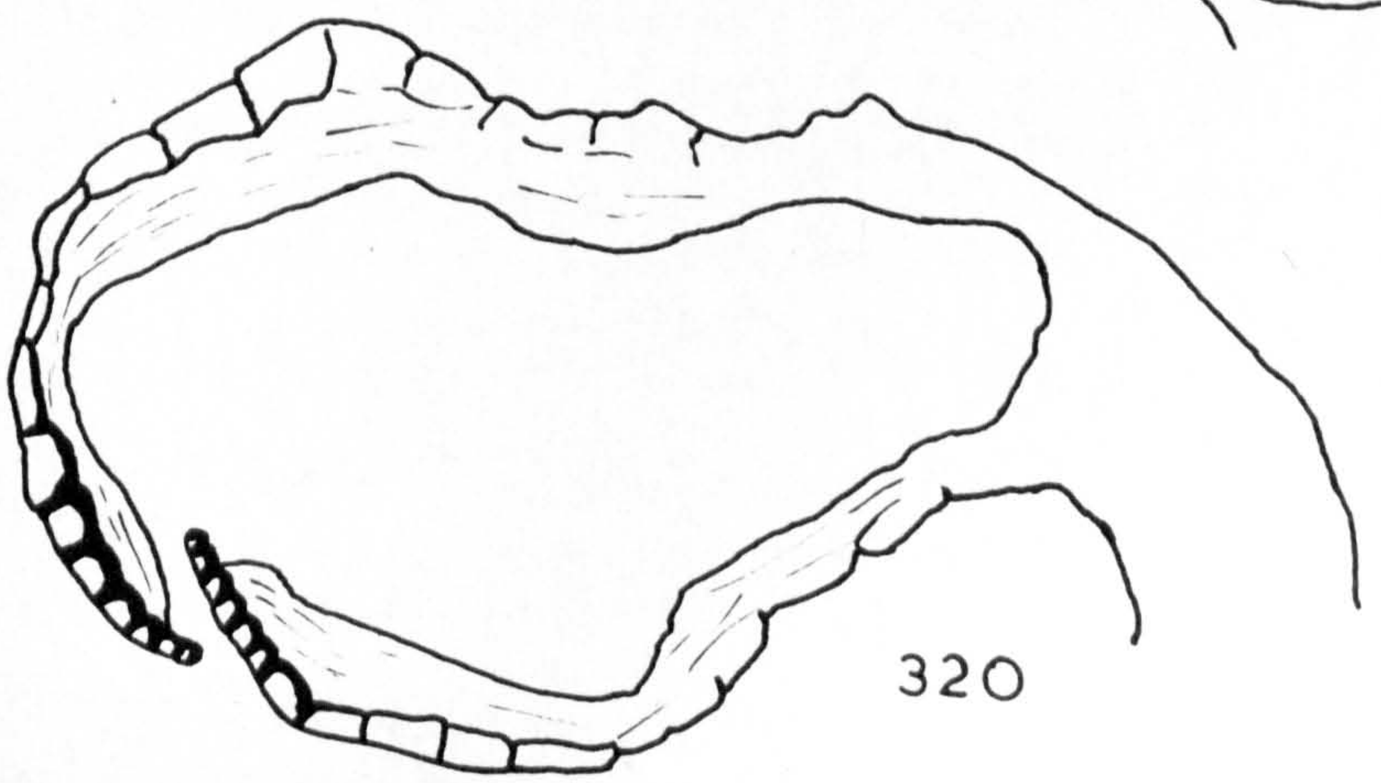
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COMPARISONS

The only part of Nothia aphylla known so far is the fertile region. Moreover, due to the fragmentary nature of the material, even the complete structure of this remains unknown, despite the large number of specimens available. This lack of knowledge of the vegetative parts of Nothia aphylla practically restricts its comparison with other plants to a consideration of their fertile region.

Comparisons will therefore be concerned with the structure of the axes, the way the sporangia are borne on the fertile axes and the structure of the sporangia and the spores.

As will be seen below, Nothia aphylla possesses characters which can be traced in living and extinct plants belonging to different groups in the plant kingdom.

For convenience, Nothia will be compared first with other members of the Rhynie chert flora, then with other fossil plants and finally with living plants. The comparisons will be followed by discussion and conclusion.

COMPARISON OF NOTHIA WITH OTHER MEMBERS OF THE RHYNIE CHERT FLORA

The axes.

In general structure Nothia axes resemble the stems of the Rhyniaceae and to some extent also the fine branches of Asteroxylon mackiei (except for the leaves); the similarity extends to the presence of an epidermis with stomata and covered with cuticle, cortex (inner

and outer) and a simple stele composed of a zone of phloem surrounding a central strand of solid xylem. The resemblance is greater to Horneophyton lignieri stems, specially in the manner and degree of preservation of the different tissues. Thus, whereas the stems of Rhynia are perfectly preserved, showing the fine details of their cellular structure and having an undisturbed entire circular outline, in Nothia and Horneophyton the epidermis is usually but not always well-preserved, the cortex is almost always perished, the phloem is sometimes preserved and showing dark triangular markings at the junction of the cells, the xylem is sometimes broken down (however, the appearance of broken down xylem in longitudinal section is different in the two plants) and there are always irregularities in the outlines of their stems, especially in Nothia. These similarities between Nothia and Horneophyton make them appear quite alike in transverse sections, specially when preservation is poor. In both plants the xylem is solid and composed of tracheids which exhibit a considerable range in diameter. Central tracheids are, always in Horneophyton and sometimes in Nothia, narrower than peripheral ones. In favourably-preserved specimens of Horneophyton the thickening of the tracheid walls was spiral or composed of irregularly connected rings. Usually, however, thickening was lost by decay (Kidston & Lang, 1920). In Nothia the thickening is always undetectable, though in transverse sections the xylem is sometimes beautifully preserved and shows clearly the outlines of its cells. This was also reported by Kidston & Lang (1920), who stated that thickening was altered or lost by decay. They

observed the same feature in the tracheids of Rhynia major, which they said readily perished and failed to show the type of thickening.

The epidermis layer of Nothia axes is usually persistent and of better preservation than that of Horneophyton stems. Stomata of Nothia are usually found on the raised parts on the axis surface. It has been proved (see Part II) that stomata are present on protrusions in the surface of Horneophyton sporangia, a fact which might also apply to the stems of that plant, since Kidston & Lang (1920) reported that the absence of stomata in Horneophyton stems might be due to the state of preservation of most of their material. In this connection it must be mentioned that Zimmermann (1927) described for the first time stomata in the epidermis of Horneophyton lignieri. The surface view of the stoma as illustrated by him is generally similar to that of Nothia stoma in surface view.

Nothia axes, so far as they are known, agree with the stems of Rhynia and Horneophyton in the absence of leaves and in this respect Nothia differs from Asteroxylon mackiei. Kidston & Lang (1920) stated that the circular outline of the leafless axes, now known as Nothia, is only disturbed by contractions during preservation. However, what attracts the attention is the presence of the stomata on raised parts in Nothia axes, on protrustions in the sporangial wall of Horneophyton lignieri and directly above some of the peculiar hemispherical projections on the stems of Rhynia gwynne-vaughani. Kidston & Lang (1920) believed at first, that the hemispherical projections of R.gwynne-vaughani could be regarded as affording a clue to the

leaves of Asteroxylon mackiei. But later they stated that the Rhyniaceae affords no clear indication as to the first origin of leaves. It is with great hesitation that one can say that some of the raised parts on the axes of Nothia (see Plate 19, Fig.79) might be regarded as an indication of the origin of microphylls or "enation" leaves in the sporophyte of the Pteridophytes. But since the stomata of the sporangial wall of Horneophyton lignieri were also found on tips of raised parts it would be more likely to think (though there is no evidence) that the vapours in the atmosphere (presence of geysers has been reported by Kidston & Lang) in which these plants lived might have been the reason for this peculiar relation between protrusions or projections and stomata in these plants. But this reason can not explain why these vapours did not have the same effect on Rhynia major and Asteroxylon mackiei. In the former the stomata are in the same level as the general surface of the epidermis and in the latter they are even depressed below the general surface.

The presence, sometimes, of narrow central tracheids surrounded by wider peripheral tracheids in the xylem of Nothia axes as well as in its sporangial traces finds similarities in the xylem of the stems of R.gwynne-vaughani, R.major, H.lignieri and in the leafe trace of Asteroxylon mackiei which was described as centrarch. The leaf trace of A.Mackiei differs in having true protoxylem and metaxylem elements.

The three-dimensional branching of Nothia axes is generally like that of the other members of the Rhynie chert Pteridophytes, especially that of Horneophyton as reconstructed by Kidston & Lang (1921); the

dichotomous branching being more frequently repeated in the upper regions of the plant and the stems diminishing in thickness as they subdivide. However, Nothia axes were more highly branched than Horneophyton stems.

The range in size of Nothia axes is exactly the same as for Horneophyton stems, but it should be remembered that nothing is known about the lower regions of Nothia. It evidently had a larger size for a single specimen has been found with a mean diameter of about 5 mm.

The structure of the epidermis of Nothia axes exhibits xerophytic features similar to the epidermis of the stems of Rhynia and Asteroxylon. There are, however, differences between them. The cuticle covering the epidermis of Nothia axes is much thinner compared to that covering the epidermis of the stems of Rhynia and Asteroxylon. The stomata of Nothia are situated on raised parts while those of Asteroxylon might have been depressed below the general surface of the epidermis. The stomata in the epidermis of A.mackiei, as illustrated by Edwards (1924), appear to be more numerous (about 8 or 10 per 1 mm^2) than those of N.aphylla (only about 3 per 1 mm^2). In this respect Nothia might be more comparable to Rhynia. The structure of the stomata of Nothia as seen in transverse sections is somewhat different from that of R.major and is distinct from that of A.mackiei. The stomata of the two latter plants were shown in transverse section by Zimmermann (1927). The difference in shape in surface view of Nothia stomata and those of Asteroxylon and R.gwynne-vaughani is not as pronounced as in

transverse section. The arrangement of the epidermal cells around the stoma of Nothia is different from that of Asteroxylon stoma. In Nothia and Asteroxylon the stomatal apparatus has one axis slightly longer than the other or the stoma is more or less rounded. However, those of Asteroxylon are of slightly smaller size. In Nothia, as well as in Asteroxylon, all the stomata are oriented in the same direction parallel to the long axis of the stem. The epidermal cells of Nothia axes are much longer than those of Asteroxylon stems, but there is a slight difference in width. The epidermal cells of Nothia differ from those of R.gwynne-vaughani and Asteroxylon in the absence of ridges.

Most of the Nothia specimens in every individual block were found parallel to each other and pointing in one direction. Since it is unlikely that such a large number of specimens could belong to a single branch system, it seems probable that they became preserved where they grew. This implies that Nothia had had a tufted growth, more or less like that of Rhynia species.

The fact that the stele xylem of Nothia axes divides into two strands a considerable distance before the axis itself branches accounts for the apparently large number of axes seen to have a double stele. However, Nothia should be regarded as monostelic.

Unfortunately no comparison could be made between the xylem morphology of Nothia and that of the other members of the Rhynie chert since that of the latter has never been described in detail.

The sporangia.

The comparison of Nothia sporangia with those of other plants involves the manner in which the sporangia are borne on the stems as well as their structure.

The manner in which Nothia sporangia are arranged on the axes and their branches is more advanced and complicated than the simple type exhibited by the Rhyniaceae. The extreme variability of the manner in which Nothia sporangia are borne on the axes offers a great difficulty when comparing it with other plants but at the same time makes possible comparisons with many types of plants. However, the various types of arrangement of Nothia sporangia can probably be derived from a basically dichotomously branched axis which by various means (unequal branching, overtopping, three-dimensional branching, condensation and fusion) formed in the same plant the following forms :

a. Spirally borne sporangia.

b. Whorled sporangia (pseudo-verticils).

c. Terminal bunches of 3 - 5 sporangia.

d. Irregular mixtures of a - c.

e. Occasionally fused sporangia.

This could be theoretically explained by line drawings in a manner not inconsistent with the derivation of a sympodial branch system from an isotomy as described and illustrated by Lam (1948) :

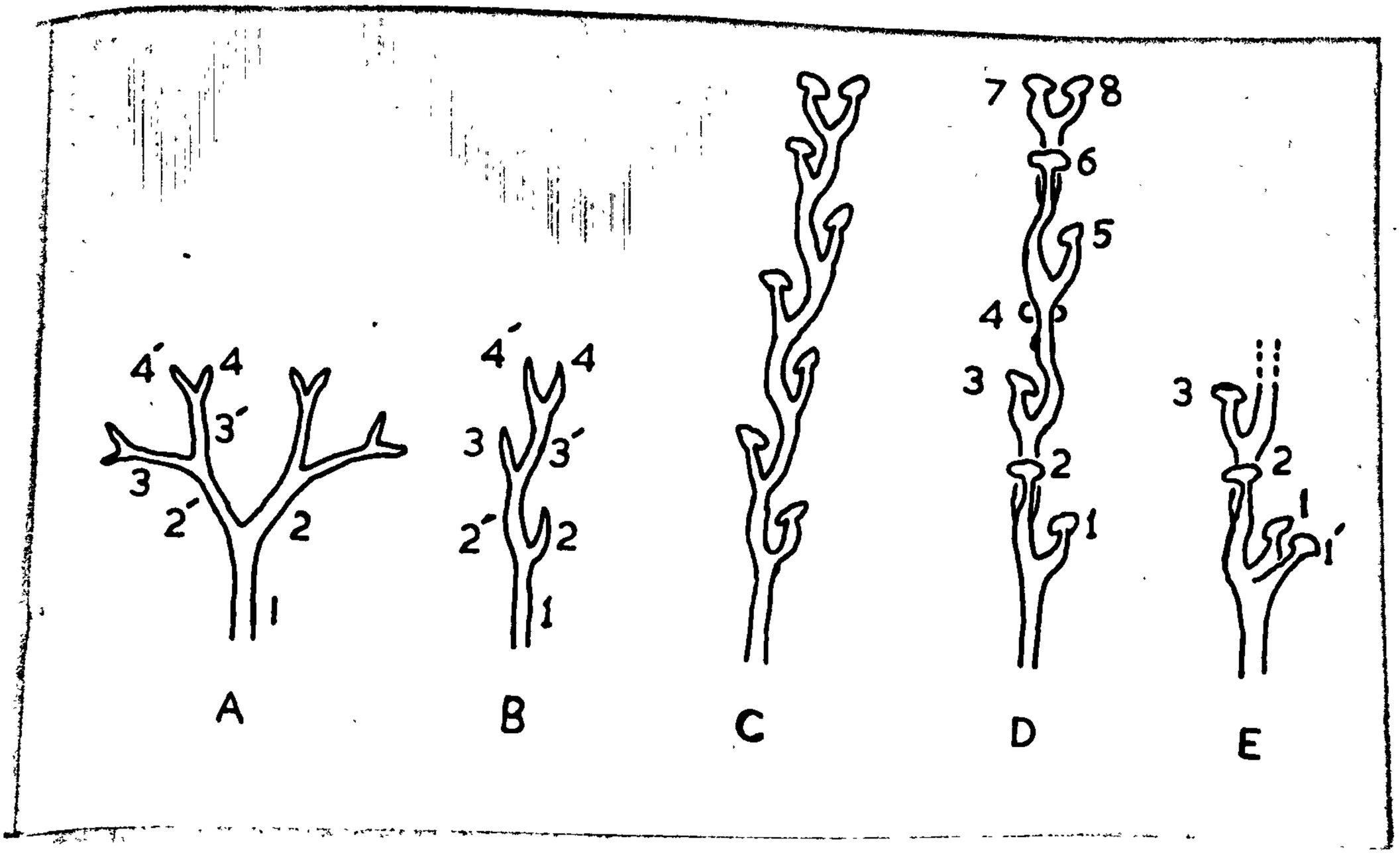

Figure A represents a typical primitive dichotomous branching system which by unequal branching leads to Fig.B. The latter by further growth in a dichotomous manner in which constant subordination of one branch and overtopping of the other leads to Fig.C, in which every subordinated branch terminates in a single sporangium, this could be said to form a raceme-like inflorescence. Figure D differs from Fig.C in that every dichotomy takes place at right angles to the one following it, and the result is a three-dimensional branch system, in which the sporangia are spirally arranged.

Sporangia Nos.1 and 1' in Fig.E might result from a rapid dichotomy which resembles an originally large branch system (branch No.2 in Fig.A). Sporangia Nos.1 and 1' help to explain the usual presence in Nothia of a pair of sporangia at one level and close together at the base of fertile branches (see Plate 24, Figs.119, 122, 123). However, a rapid dichotomy might occasionally occur higher up in the fertile shoot.

If by condensation of the spiral form E, sporangia Nos.2 & 3 were brought at one level then they will be alternating in position with sporangia Nos.1 & 1', a condition which is met with in Nothia as seen for example in the right branch of the specimen in Fig.122 on Plate 24.

By condensation from the spiral form (Fig.D), different forms might result :

a. Alternating pairs of sporangia might be obtained if every two successive sporangia were brought at one level (e.g. sporangium No.1 with 2 and 3 with 4 and so on). This is the same as just been mentioned above for Fig.E.

b. A group of 5 sporangia (e.g. 1-5) might form a crowded whorl in which the angles between the five sporangia encircling the axis will be equal i.e. 72^{o} each. This was never achieved in Nothia, though the specimen in Fig.113 on Plate 24 could be considered as a step towards the formation of such a whorl.

c. The four sporangia Nos.1-4 might form a whorl in which the angles between the sporangia of the whorl are equal, i.e. 90^{o} each, but this also was never achieved in Nothia though there was an approach to it as shown by the specimen in Fig.120 on Plate 24 (its sporangia Nos.1-4).

d. Sporangia Nos.1, 2 & 3 might form an asymmetric or pseudo-whorl in which one of the angles (the one between sporangia Nos.3 & 1) will be 180^{o} and the other two angles will be 90^{o} each.

Such whorls were exhibited by the fertile branches of Nothia;

however, the three sporangia were not at exactly the same level but in a very close spiral and only in a few whorls the three angles were 180°, 90° & 90°. For the majority of the whorls there was a slight tendency for the three sporangia of the whorl to spread and invade the wide angle as a step towards the formation of a symmetric whorl (in which each angle is 120°). This, however, was never quite achieved in Nothia. The range of the three angles was about 90-95°, 95-130° and 140-170°, the common average being 90°, 120° & 150°.

There is only one specimen (Plate 24, Fig.114) in which the wide angle was slightly more than 180°. In this whorl two of the sporangia might have resulted from a rapid dichotomy and by condensation became very close to the third one or such a whorl might have been the result of irregularities due to the transformation of one form of arrangement to another.

e. A bunch of 3, 4 or 5 terminal sporangia results if the condensation brings close together sporangia Nos.6-8, 5-8 or 4-8 respectively. These terminal sporangia will be arranged around a central space or cavity in almost the same manner in which they would have been arranged around the axis if they were not terminal. Thus, three terminal sporangia forms a triangle, four forms a square and five forms a circle. This more or less applies to the terminal sporangia of Nothia (see Plate 24, Figs.108-111).

The transformation of one form of arrangement to another very probably leads to irregularities such as :

1. Two sporangia might arise close together and at the same level.

Such two sporangia by condensation with a third one will form a whorl in which the two sporangia are at exactly one level while the third one is either at a slightly higher or lower level (according to its original position on the axis).

2. Two sporangia might arise very close together and at the same level or almost so that they develop united together from the very beginning resulting in a pair of fused sporangia.

3. Two sporangia might become borne at the same level and opposite each other (see Plate 24, Fig.121).

4. Further adaptations might occur to suit a new type of arrangement which can not be derived directly from the spiral form in Fig.D. As for example the two alternating whorls of the specimen shown in Fig.117 on Plate 24.

5. A mixture of spiral, whorled (of different patterns), opposite decussate, fused and randomly arranged sporangia might result from the transformation of one form to another or from uneven condensation or from condensation of an irregular spiral.

It is interesting to note here that some work has been done on the phyllotaxis of some species of Angiosperms, which, though far removed from Nothia is nevertheless worth mentioning in this respect.

Snow & Snow (1934) mentioned that Weisse (1894) showed that in a large number of species with whorled or decussate phyllotaxis, adventitious buds, whether produced normally or experimentally, often have spiral phyllotaxis. The two authors showed further (using Epilobium hirsutum) that a shoot which was already growing with normal

decussate phyllotaxis could be converted by an operation into one (or two) with spiral phyllotaxis. They showed also that as a result of their operation some of the plants developed peculiar positions of the subsequent leaves and that sometimes a pair of leaves arose joined and were nearly, or quite, at the same level and that such two leaves might be loosely or closely joined.

On the whole, the extreme variation in which Nothia sporangia are borne might suggest a morphologically unstable condition from which, theoretically, some of the more constant arrangements characteristic of other divisions of the Tracheophyta could be derived, as will be seen later.

For convenience in comparison with other plants, the fertile region of Nothia aphylla will be described as a terminal branched spike with variably arranged sporangia.

The terminal position of the sporangia of the Rhyniaceae is comparable to the sporangia terminating the spike of Nothia. The simplest is that of the genus Rhynia when branches terminate in a single sporangium. In Horneophyton, branches terminate either in a single sporangium or in a branched or lobed sporangium and the number of lobes in a single fructification ranges between two and five (as will be shown in Part II). In Nothia fertile branches end in a bunch of three to five sporangia or at least in a pair of sporangia (fused or separate) but not in a single sporangium. Thus the terminal sporangia of the spike of Nothia are more comparable to the terminal sporangia of Horneophyton than to those of Rhynia. If the branched

fructification of Horneophyton could be looked upon as more or less a synangium, in which each lobe represents a sporangium, then it follows that the number of terminal sporangia in both Nothia and Horneophyton is up to five, in the former the sporangia are usually separate and in the latter they are usually partially fused. However, in Nothia a pair of sporangia might be fused and also in Horneophyton sometimes two closely-placed sporangia are separate. But in the Rhyniaceae the sporangia are only terminal whereas in Nothia they are arranged in a terminal branched spike. Perhaps the Nothia specimen shown in Fig.106 on Plate 24 is the most comparable one to Rhynia and Horneophyton since the part of the axis below the terminal fused pair of sporangia did not bear sporangia for a length of at least 7 mm.

The lateral spirally-arranged sporangia of Nothia could be compared with those of Asteroxylon mackiei which are also lateral, but interspersed with veinless leaves, and their origin on the stem is likely to be more advanced than the subordinated dichotomies which have been postulated for Nothia. It is unknown whether the fertile shoots of Asteroxylon mackiei terminated in sporangia or whether the sporangia were restricted to isolated fertile regions in the leafy shoots.

The structure of the sporangium :

The size of Nothia sporangia is similar to that of Rhynia gwynne-vaughani and the single sporangium of Horneophyton lignieri but much smaller than that of Rhynia major and Asteroxylon mackiei.

Nothia sporangia, being reniform in shape, differ from the

cylindrical type characteristic of the Rhyniaceae and are more comparable to the somewhat reniform sporangia of Asteroxylon mackiei. It might be interesting to note here that the fused sporangia of Nothia give a greater resemblance in general appearance and in some transverse sections to the more or less reniform sporangia of Asteroxylon mackiei as described by Lyon (1964) than does a single sporangium.

The structure of the sporangial wall of Nothia sporangia is apparently more advanced than that of Rhynia and Horneophyton. The sporangium of Nothia being distinctly dehiscent (Horneophyton sporangia may be also, see Part II) and the dehiscence depending on the structure of the wall, where there is a broad zone of annulus-like cells surrounding an extended marginal slit, should be regarded as more advanced than the indehiscent sporangia of Rhynia. The wall of Nothia sporangia is less massive than that of Rhynia and Horneophyton. There is nothing in the nature of a columella in the sporangium of Nothia to permit comparison with Horneophyton columella. Stomata are present in the sporangial wall of Nothia (and Horneophyton, see Part II) but no stomata, so far, has been found in the sporangial wall of Rhynia. Nothin sporangia resemble those of Asteroxylon mackiei in the presence of an extended marginal slit and a vascularised stalk. However, the stalk of Nothia sporangia is different from that of Asteroxylon in construction and shape. There is nothing in the structure of the sporangial wall of Rhynia, Horneophyton and Asteroxylon to allow comparison with the peculiar cavities found in the wall of Nothia sporangia.

Regarding spores, those of Nothia being about 65 μ in diameter are of the same size as those of Rhynia major and larger than those of Rhynia gwynne-vaughani, Horneophyton lignieri and Asteroxylon mackiei.

It seems that the fertile region of Nothia could be compared more closely with other fossil fertile regions rather than those of the Rhynie Chert Pteridophytes.

COMPARISON OF NOTHIA WITH OTHER FOSSIL PLANTS

A. PSILOPSIDA

I Zosterophyllum :

Perhaps the fossil plant most similar to Nothia is the genus Zosterophyllum. It is a genus of wide geographical distribution, for it has been discovered in Scotland (Lang, 1927), Australia (Lang & Cookson, 1930), Germany (Krausel & Weyland, 1935), Wales (Croft & Lang, 1942), Belgium (Leclercq, 1942), France (Danzé-Corsin, 1956) and U.S.S.R. (Ananiev, 1960). It was found in Upper Silurian and Lower Devonian rocks. It comprises at least six species, each of which shows certain similarities to Nothia.

Croft & Lang (1942) divided the genus Zosterophyllum into two sections; Euzosterophyllum and Platyzosterophyllum. The former having its stalked sporangia radially arranged in its spike, while in the latter the sporangia are arranged in two vertical rows and the spikes are dorsiventral. However, all the species of the genus are similar to Nothia in that :

1. The axes are leafless.
2. The sporangia are more or less reniform and stalked.
3. Dehiscence is affected by an extended split which runs along the distal convex margin of the sporangium.
4. The sporangia are arranged in terminal spike-like fertile regions, the spikes being unbranched in case of Zosterophyllum and branched in case of Nothia. Concerning the fertile region of the genus Zosterophyllum Walton (1958) wrote "The fertile region may be regarded as a racemose branch system if we regard each sporangium as the terminal part of a short side branch the rest of which is represented by the stalk." The fertile region of Nothia could also be regarded in the same way.
5. The species involved in the section Euzosterophyllum are similar to Nothia in the radial arrangement of the sporangia on the fertile axes.

At the same time there are quite distinct differences between the two genera :

1. Nothia spikes are branched while those of Zosterophyllum are not.
2. The arrangement of the sporangia in the Euzosterophyllum section is spiral but in the Platyzosterophyllum section it is in dorsi-ventral spikes. The sporangia in Nothia are arranged spirally, randomly, opposite, in pseudo-verticils and the fertile branches end in two to five sporangia.
3. Fused pairs of sporangia are known in Nothia only.
4. Stomata were found in the sporangial wall of Nothia but, so far,

stomata are not known to occur in the sporangial wall of Zosterophyllum. However, this comparison may not be quite fair since Zosterophyllum is not yet known in a petrified condition.

Apart from general similarities and differences between Nothia and Zosterophyllum listed above, every species of the latter genus has its particular characters that approach or differ from Nothia.

A. Euzosterophyllum :

1. Z.myretonianum.

This species has been described by Lang (1927), Lang & Cookson (1930), Lele & Walton (1960-61) and Walton (1964). It is by far the most completely known member of the genus. It comes from the same horizon as Nothia; The Old Red Sandstone of Scotland, but, so far, the two plants have not been found together. The similarities which this species shows to Nothia are :

1. The axes are of about the same size.
2. A single strand of the main xylem supplies the sporangium, which is reniform in shape.
3. The main xylem strand is .2 or .25 mm. in diameter.
4. There is a slight difference in the range of the width of tracheids; 10-30 μ in Nothia and 15-40 μ in Z.myretonianum.
5. Two sporangia of Z.myretonianum were described (Lang, 1927) as being rather small and may have been more rudimentary than those in the upper region of the spike. A similar thing was observed regarding the two opposite and lowermost sporangia (Nos. 1 & 2) of the fertile specimen of Nothia shown in Fig.121 on Plate 24.

6. The elongated epidermal cells are oriented with their long axis parallel to the length of the stem. Stomata in both plants show the same orientation as the epidermal cells.
7. The arrangement of the sporangia in Z.myretonianum is spiral, however, sometimes two sporangia are almost opposite. Both types are represented in Nothia, together with other forms of arrangement.
8. In Z.myretonianum some of the sporangial stalks are curved and in the fertile specimen shown in Fig.15 (Lang, 1927) the position of some of the sporangia on the axis is similar to the distally recurved stalks of Nothia sporangia.
9. The spike of Z.myretonianum is loose compared to spikes of some other species of the genus, especially Z.australianum, and this makes it more comparable to Nothia than are the species with compact spikes.

There are, however, some pronounced differences between Nothia and Z.myretonianum. These are :

1. The stomata in the two plants are different in shape, structure and apparently also in numerical distribution.
2. The epidermal cells of Nothia are somewhat more elongate than those of Z.myretonianum.
3. The tracheids of Z.myretonianum had annular and a few spiral thickenings but in Nothia nothing is known of the thickening of the tracheids.
4. Branching in Nothia is more frequent in the upper region of the shoot while the reverse occurs in Z.myretonianum, where branching

is mainly restricted to the basal "confused region".

5. Spores are 25-30 μ in diameter in Z.myretonianum and about 65 μ in Nothia.

ii Z.australianum.

Described by Lang & Cookson (1930) and Cookson (1935, 1949) this species is known from the Upper Silurian and Lower Devonian rocks of Australia. Its sporangia were much larger than those of Nothia (more than twice as big). The sporangia are closely placed forming a strobilus which contrasts with the more lax spikes of Nothia. The sporangial stalks are of similar width and length in the two plants but in one specimen of Z.australianum the stalk was much longer than those of Nothia. In the two plants sporangia appear to be of the same size throughout the spike.

iii Z.cf.australianum.

This species is described by Croft & Lang (1942) from Lower Devonian rocks of South Wales. Its axes are somewhat wider than those of Nothia. The sporangia are much larger and more compact and were evidently spirally arranged in probably five vertical rows, a condition somewhat comparable to Nothia. The two plants are similar in that the cells composing the wall of the sporangium are elongate and radiate out from the base toward the curved distal margin.

iv Z.rhenanum.

This species is known from the Lower Devonian of Germany (Krausel & Weyland 1935). The sporangia are apparently larger than those of Nothia

but the spores are much smaller being 25-30 μ in diameter. The spikes are more compact than in Nothia. This species had a tufted growth like Nothia.

B. Platyzosterophyllum :

i Z.llanoveranum Croft & Lang (1942).

This species is of Lower Devonian age and comes from Monmouthshire. It probably had a tufted growth like Nothia. The axes are of about the same width as those of Nothia. The sporangial stalks in the two plants arise at more or less acute angles on the axis, and had the same width and range of length. In Z.llanoveranum the two rims of the sporangium are thick and appear to consist of elements elongated at right angles to the line of dehiscence itself and evidently differed structurally from the rest of the sporangial wall, a feature which is readily comparable to the broad zone of the thick annulus-like epidermal cells surrounding the line of dehiscence in Nothia sporangia. The reniform shape of the sporangia is very similar in the two plants, but the sporangia of this Zosterophyllum species are of a much larger size and are arranged in two lateral rows and not radial. Spores in the two plants are smooth walled, those of Nothia being somewhat larger in size.

ii Z.fertile Leclercq (1942).

This species is described from Lower Devonian rocks of Belgium. The sizes of the axes and the sporangia of this species are similar to those of Nothia. The sporangial stalks of this species are described as recurved so that the sporangia tend to point back toward

the axis; which is similar to the distally recurved stalks of the sporangia of Nothia. The tracheids in the two plants have similar diameters.

iii Z.(Platyzosterophyllum) sp.

This is another Lower Devonian plant from South Wales described by Croft & Lang (1942). Its sporangia nearly match those of Nothia in size and shape. In this species the sporangial stalks are curved so that the sporangia are turned upwards and inwards, they are thus directed towards the main axis or even slightly across one face of this: which is quite close to Nothia and also the previous species, Z.fertile.

If the recurved sterile tips on Plate 16 are correctly assigned to Nothia, which is very probable, then they could be compared to the circinately coiled tips of this species of Zosterophyllum.

iv Z.artesianum Danzé-Corsin (1956).

A Lower Devonian plant from France, of tufted growth and sporangia of similar size to those of Nothia.

II Bucheria

The genus Bucheria is of Lower Devonian age. A number of species is known, of which only two will be considered; B.ovata (Dorf, 1933) and B.longa (Hoeg, 1942).

Bucheria ovata.

Dorf (1933, 1934) described this plant from Lower Devonian rocks of Wyoming. The fertile spikes of this plant are usually compared to Platyzosterophyllum. The axes of B.ovata agree with those of Nothia in being leafless, spineless and of about the same width. Both plants

have their sporangia arranged in terminal spikes, but, the spikes of B. ovata differ from those of Nothia in that the sporangia are arranged in two series on one side of the axis i.e. the spikes are dorsi-ventral and not radial. B.ovata again differs from Nothia in that the sporangia are sessile and rounded in shape. The dehiscence of the sporangia is affected by a longitudinal median split extending from their central area to their pointed ends which is somewhat, but not very, different from the dehiscence of Nothia sporangia.

The slender (1 mm. wide) axis of B.longa bears numerous lateral organs each about 5 mm. long in spiral arrangement. If these organs prove to be sporangia then this species would agree with Nothia in the spiral arrangement of its sporangia.

III Cosslingia breconensis.

This is a lower Devonian plant described by Heard (1927) and Croft & Lang (1942) from the Old Red Sandstone of Wales (Senni Beds).

The axes of this plant agree with those of Nothia in width, in being leafless, and in the presence of a vascular tissue even in the extreme apical shoots. The tips are circinately coiled which might also prove correct for Nothia tips. However, the axes of Cosslingia differ from those of Nothia in that branching is always in one plane and in having bulges with hair-like structures. There are also differences between the phloem and xylem of the two plants. The presence of exarch protoxylem in Cosslingia contrasts with the presence of small central tracheids in Nothia. The surface view of the stomata

of Gosslingia as illustrated by Heard (1927), though the figure is not clear, indicates that it is apparently similar in shape and size to Nothia stomate. The sporangia of Gosslingia are reniform and very similar to those of Nothia in shape and size. In Gosslingia sporangium the dehiscence slit extends along the whole extent of the convex margin, which is the same as in Nothia sporangia. Moreover in Gosslingia the rim of the valves are often more strongly carbonized as though they had been thicker than the rest of the wall, which is directly comparable to what was found in Nothia sporangia. There are, however, marked differences in the arrangement of the sporangia; those of Gosslingia are borne laterally but not on special fertile branches, and every sporangium has a short thin stalk and lies with its long axis parallel to the branch bearing it and in the plane of the branch system which is quite different from the position of Nothia sporangia on the axes. The xylem tracheids of Nothia offer no positive features for comparison with the annular tracheids of Gosslingia or any other plant.

IV Cooksonia.

Lang (1937), Heard (1939), Croft & Lang (1942) and Obrhel (1962). This fossil is of Upper Silurian and Lower Devonian age (Downtonian of Britain and Upper Silurian of Bohemia). It is classified as a member of the family Rhyniaceae. The axes agree with those of Nothia more or less in width and in being leafless. The sporangia differ in shape in different species; they are hemispherical in C.hemisphaerica, more or less oval in Cooksonia sp. and much broader than long in C.pertoni.

The sporangia of the latter species are the closest in shape and size to those of Nothia, however, the sporangia in the genus Cooksonia attain much larger sizes than Nothia sporangia. The sporangia in Cooksonia terminate branches but are not arranged in spike-like fertile branches as in Nothia. The spores are much smaller than those of Nothia. Dehiscence is unknown in Cooksonia.

V Hedeia corymbosa.

This is a Psilophytalean fructification described by Cookson (1935) from the Upper Silurian of Australia. The fructification is composed of terminal branch system, most of the ultimate branches of which end in large elongate sporangia. The tips of the sporangia all come to about the same level, giving a corymbose appearance to the fructification as a whole. The fructification had a radial arrangement and therefore it is highly probable that the terminal branch systems were radial or cyclic structures. This cyclic structure can be closely compared with the terminal bunch of Nothia in which five sporangia are arranged in a circle. The resemblance is only in the cyclic structure of the two fructifications, and apart from this there are great differences between the two plants; (1) some of the sporangia of Hedeia are sessile and borne laterally on the inner side of a branch which itself ends sterile; nothing like this is known in Nothia. (2) The sporangia of Hedeia have a different structure and shape from those of Nothia which are, moreover, of a much smaller size. (3) Nothing in the nature of the branched fertile spike of Nothia occurs in Hedeia.

Cookson (1949) described some specimens from the Lower Devonian of Australia and referred to them as Hedeia cf.corymbosa. One of the specimens showed clearly the radial symmetry of its branch-system. She stated that five daughter-axes, at least, must have been terminally arranged around a central space and further subdivisions of these axes occurred by successive dichotomies at identical levels in one plane only. This construction is very similar to the terminal cluster of five sporangia in Nothia, the only difference being the branching of the five daughter-axes in case of Hedeia.

VI Yarravia.

A comparison is possible between the bunch of sporangia terminating the fertile branches of Nothia and the terminal fructifications of Y.oblonga and Y.subsphaerica, both from the Upper Silurian rocks of Australia (Lang & Cookson, 1935).

In Yarravia the synangium is usually composed of 3-5 sporangia and not more than six. The five terminal sporangia of Nothia are arranged in a circle surrounding a central space, which is also probable in the case of Yarravia as the authors reported. However, the difference is that the five sporangia of Nothia are separate while those of Yarravia are partially connected (they have free projecting tips) forming a synangium. The axes of Yarravia had a similar size to those of Nothia but the sporangia of the latter differ in shape and somewhat in size from the sporangia of the former, especially Y.subsphaerica, the sporangia of which were much larger.

Yarravia was discovered also in Lower Devonian rocks. Cookson (1949) described some specimens from the Lower Devonian of Australia under the name Y.cf.oblonga, while Danzé-Corsin (1956) described a new species from France.

VII Hostimella.

Halle (1916), Kräusel & Weyland (1923), Lang (1925) and Lang & Cookson (1926-27, 1930, 1935).

Hostimella had a wide geographical distribution and extends from Upper Silurian to Middle Devonian times. All the species of this genus agree with Nothia in having leafless axes of about the same width.

The sporangia of the Middle Devonian species H.globosa (Lang, 1925) are about the same size as those of Nothia but they are different in shape and are probably terminal but not in terminal spikes.

H.pinnata had terminal sporangia (Lang, 1925) but it is not readily comparable to Nothia.

A third species H.racemosa also of a Middle Devonian age (Lang, 1925) had a fructification like a raceme of sporangia. Compared to Nothia the sporangial stalks of H.racemosa are longer and the supposed sporangia (no spores obtained) are much larger in size.

Halle (1916) described a Lower Devonian species, the axes of which had all their ramifications in one plane. This is different from the three-dimensional branch system of Nothia.

VIII Dawsonites.

Halle (1916), Høeg (1935), Croft & Lang (1942) and Hueber (1964).

A genus of mainly Lower Devonian age but also occurs in Middle Devonian rocks. It had a world wide distribution (Canada, Norway, France, Britain) and is usually found in association with Psilophyton.

Dawsonites arcuatus was originally erroneously thought to be and even reconstructed as the fertile region of Psilophyton princeps by Dawson (1871, 1888), but later, Halle (1916) separated it from Psilophyton and considered it a distinct genus. A number of Dawsonites species has since been described, all of which are leafless but some are known to bear a few spines.

Dawsonites arcuatus is known from the Lower Devonian of Norway, (Halle, 1916) and the Lower Devonian of Wales, (Croft & Lang, 1942). The sporangia are terminal, pendant and somewhat larger in size than Nothia sporangia. They differ from Nothia sporangia in their fusiform shape, their structure and spore diameter.

Hueber (1964) described fertile specimens from Canada which he referred to as Cf.D.arcuatus. They had clusters of terminal fusiform sporangia which dehisced by a longitudinal slit. In Nothia the slit was transverse. Cf.D.arcuatus is regarded by Hueber as a fern ancestor.

D.ellenae was described by Høeg (1935) from the Middle Devonian of Norway. It is also regarded as a fern. Its shoots bear terminal clusters of sporangia which agree with Nothia sporangia in their reniform shape and in being stalked. The sterile shoots of D.ellenae bear small lateral appendages that end in circinately recurved tips which can be compared to the sterile recurved tips probably belonging to Nothia.

IX Psilophyton.

Dawson (1871, 1888), Halle (1916), Edwards (1924), Lang (1931, 1932), Krausel & Weyland (1938), Croft & Lang (1942) and Hueber (1964).

Under this devonian (Lower, Middle & Upper) genus a diverse group of fossil plants has been included (see Arnold 1941). One species (P.pubescens, Middle Devonian) has in its vascular bundle indications of problematical secondary thickening. The genus had a wide geographical distribution; Canada, Norway, Britain, Germany.

All the species had spinous stems and thus differ from the smooth, leafless axes of Nothia.

The large, globose, lateral, stalked sporangia of Psilophyton princeps, (Hueber, 1964) resemble those of Nothia in the presence of a distal extended slit, but they differ slightly in size and somewhat in shape.

Cf.Psilophyton princeps, as described by Croft & Lang (1942) and reconstructed by Leclercq (1954), had its short stalked oval sporangia borne laterally and in terminal spikes with double rows. These terminal spikes could be compared with the fertile region of Nothia but have many differences.

Halle (1916) stated that sister branches of P.princeps form a very acute angle with each other and are directed upwards nearly parallel to each other which is also the same in the case of Nothia branches (see Plate 24). The circinately curved branch tips of P.princeps (Dawson, 1888; Halle, 1916) might find similarities in Nothia.

From the investigations of cuticles of P.princeps by Edwards (1924) it is clear that this plant differs in the shape of its epidermal cells from Nothia. The latter has much longer cells which, however, are of similar width to those of the former. Some epidermal cells in both plants had oblique end walls. Stomata in the epidermis of P.princeps are more numerous than in Nothia. In the former according to Edwards (1924) there are about 4-9 stomata per 1 mm^2 However, in both plants the stomata are oriented in the same direction with their long axis vertical and parallel to the long axis of the stem. But the stomata are different in shape, size and structure in the two plants. In surface view the stomata of P.princeps are very different from those of Nothia, they measure about 70 x 30 µ, Edwards (1924), Lang (1932), (slightly different measurements were given by Huber & Crierson 1961) while Nothia stomata measure about 100 x 80 µ, with a type of thickening that is quite different from that of P.princeps stomata. Edwards (1924) stated that the number of epidermal cells around a stoma of P.princeps varies from 4-7 and with no definite arrangement and in some instances the cells appear very slightly below the general level of the epidermis. While in Nothia the stomata are usually situated on raised parts and the number of epidermal cells around a stoma is about 5-8, however, the cells around the stoma had a more or less definite arrangement.

Comparing the stomata of P.princeps with those of the Rhynie plants, Edwards (1924) stated that the narrower and longer appearance of the stomata of the former might be due to the difference in the

state of the stomata at the time of fossilisation.

There are some more differences between the epidermis of Nothia and that of P.princeps as, for example, the presence of possible hair bases and spine bases in the latter.

The following Devonian genera agree with Nothia in being leafless, but otherwise show little resemblance to it.

1. Taeniocrada (Halserites), a Lower Devonian genus described by Krausel & Weyland (1930) and Croft & Lang (1942). Its fertile region shows slight resemblance to Nothia.
2. Pectinophyton, a Lower Devonian fossil described from Western Siberia by Anniev (1957). The sporangia are aggregated into spike-like groups on lateral branches and the stalk is recurved around part of the sporangium. Pectinophyton was first described by Høeg (1935) from the Middle Devonian of Western Norway.
3. Sporogonites, a Lower Devonian genus described by; Halle (1916), Andrews (1958), Lang & Cookson (1930) and Croft & Lang (1942).
4. Hicklingia edwardi, a Middle Devonian plant described from the Old Red Sandstone of Scotland by Kidston & Lang (1923).
5. Enigmophyton (?) fructification. In 1942 Høeg described a new fossil plant from the Upper Middle Devonian (or lowermost Upper Devonian ?) of Spitsbergen which he named Enigmophyton superbum. He stated that the characteristic vegetative morphology of this plant is entirely different from all Psilophytes and it is also impossible to include it in any of the other known groups of vascular Cryptogams. What

is relevant here, is the type of fructification found in association, but not in organic connection with that plant and to which Høeg referred to as Enigmophyton (?) fructification. He stated that it is unreferable to any previously described type of fructification.

Nevertheless, his fructification has general external resemblance to that of Nothia, especially regarding size, manner of branching, length of the sporangium bearing appendages and perhaps also the manner of arrangement of these appendages. But there are also some basic differences as can be seen from Høeg's following description : The fructifications have the form of elongate spikes, borne on smooth axes which bifurcate just below the spore bearing region. Repeated bifurcation is seen, in at least, one case where the second bifurcation takes place within the fertile part. The axis below the sporophylls is entirely naked and smooth. The spike itself is generally 2-3 cm. long and consists of an axis bearing a great number of close-set sporophylls. It is somewhat uncertain how the sporophylls have actually been arranged on the axis. It is probable that the arrangement was not strictly bilateral, but spiral, or perhaps approximately verticillate but the axis is not articulate. Each sporophyll leaves the axes at about a right angle. The length of the sporophyll is 2 (-2.5) mm. All observations make it probable that there is only one sporangium on each sporophyll. It is placed on the upper side of the latter near the axis and looks like a bladder of somewhat variable shape. Micro and macrospores were found in different sporangia of one spike.

6. Dutoitia pulchra, an Early Devonian Psilophyte from South Africa, described by Høeg in 1930. Many of its stems have appendices in the shape of hemispherical protuberances or small spines. Sporangia, terminal obconical with flat tips.

Some Lower Devonian genera afford no grounds for comparison with Nothia. Examples are : Prototaxites (Nematophyton), Thallomia, Parka, Pachytheca (see Lang, 1937).

B. LYCOPSIDA

I Baragwanathia Longifolia.

This is an Australian fossil plant of Upper Silurian age (Lang & Cookson, 1935). Nothia sporangia being reniform are somewhat similar in shape and size to the reniform sporangia of Baragwanathia. Both plants had spirally arranged sporangia, but in Nothia the spiral form is sometimes irregular and mixed with other forms of arrangement. The sporangia of Baragwanathia were sessile on the stems with evident relation in psotion to leaves or perhaps were borne on the adaxial side of the leaves at their base. Contrary to that, Nothia sporangia are stalked and the fertile axes are leafless. Moreover Nothia sporangia are arranged in terminal spikes while those of Baragwanathia are apparently restricted to fertile zones on the leafy stems.

II Drepanophycus (=Arthrostigma).

Dawson (1871, 1888), Kidston (1895), Halle (1916), Cookson (1926), Krausel & Weyland (1935) and Croft & Lang (1942).

This is a Lower Devonian genus of world wide representation for it has been discovered in Canada, Scotland, Norway, China, Belgium, Germany, Australia and Wales. It is distinct from Nothia in many respects but there are some points that could allow for comparison.

Halle (1916) mentioned that the leaves of Arthrostigma gracile show a striking variation in their arrangement not only in different specimens but sometimes in one specimen, and the different arrangements which he found were; dense spiral, pseudo-verticillate and distant irregular. These leafe arrangements are apparently very much like the arrangements of Nothia sporangia. However, the number of Arthrostigma leaves in each pseudo-whorl is numerous compared to the number of Nothia sporangia per pseudo-whorl. The verticillate and spiral arrangements of A.gracile leaves had also been already mentioned by Dawson (1868).

Croft & Lang (1942) gave a description of Drepanophycus spinaeformis sporangia, which are larger in size and different in shape from those of Nothia; However, they stated that Krausel & Weyland (1935) described sporangia of Drepanophycus as being reniform and tangentially extended. They are therefore comparable to Nothia sporangia in shape but Drepanophycus sporangia are borne distally on fertile leaves.

The epidermal cells of Arthrostigma gracile have similar width to those of Nothia but they are much shorter. Stomata are more numerous in the epidermis of A.gracile than they are in Nothia. The surface view of the stomata of A.gracile as described by Lang (1932) is very similar to that of Nothia stomata. Lang stated that A.gracile stoma

has two strongly curved guard-cells encircling an area of relatively considerable size. The whole structure is as broad as long measuring about 75 μ in each direction. The pore was probably of considerable size but not as large as the area enclosed by the thickened ridges of the guard-cells which measures some 40 x 30 μ. Nothia stomata, especially those in Figs.285 & 289 on Plate 43 agree almost exactly with this description.

C. SPHENOPSIDA

This group of plants has extinct as well as extant members. The earliest sphenopsids are of Lower Devonian age. One of the main features of this group is that the sporangiophores are borne in whorls and in many forms these sporangiophores are recurved so that the terminal sporangia are directed towards the axis. This feature affords a comparison, though not a close one between Nothia and some members of the Sphenopsida. The sphenopsids are, however, rather complex, more advanced and quite distinct from Nothia.

The order Hyeniales is regarded as intermediate in evolution between the more primitive Psilophytales and the more advanced orders of the Sphenopsida, (Banks, 1960). The fact that in Nothia some of the sporangia approach the whorled condition and the number of sporangia in each whorl is always three and the stalks of the sporangia are distally recurved so that the sporangia face the axis; are reasons for comparing it with members of the order Hyeniales.

The simplest genus, Protohyenia, is of Lower Devonian age and in

one of its species, P.janovii (see Delevoryas 1962) there is a hint of a whorled arrangement of the appendages.

In Hyenia (Middle Devonian) the leaves are not exactly verticillate although more or less at the same level, and the tips of the fertile leaves are recurved so that the terminal sporangia are directed inwards, (Leclercq, 1940; Høeg, 1945).

Calamophyton bicephalum is of Middle Devonian age, and according to Leclercq & Andrews (1960) the leaves display a tendency towards a whorled arrangement and at least three and possibly as many as six sporangiophores are present in one whorl. In another species C.primaevum, also of Middle Devonian age (see Walton 1958 and Delevoryas 1962) there seems to be not more than three leaves in each whorl and the sporangiophores are recurved and forked; each usually with two sporangia.

In Pothocites strobili which belong to the order Calamitales and which are of Upper Devonian-Lower Carboniferous age (see Delevoryas 1962), whorls of sporangiophores with recurved sporangia are borne on the cone axis with no sterile bracts among the fertile appendages.

The genus Sphenophyllum (order Sphenophyllales) is of Upper Devonian, Carboniferous and Permian age (see Walton 1958). The leaves are attached to the nodes in whorls of six or multiples of three up to 18 or possibly more in some species. The end of each pedicel is curved so that the sporangium is borne in an anatropous manner and hangs over towards the axis.

Only the possible similarities between Kothia and the above mentioned members of the Sphenopsida have been considered, since it is unnecessary to discuss the many differences between them.

D. PTEROPSIDA

Coenopteridales.

There are not many features in common between Kothia and the members of this group of fern ancestors.

Protopteridium is one of the oldest members of the group; it occurs in the Upper level of the Lower Devonian age, (Halle, 1936). It combines features of Psilophytales with those of the Pterophyta. In this plant a presumably pluriseriate annulus exists on the sporangium which can be compared with the broad zone of annulus-like cells in Kothia sporangia. The construction of Protopteridium minutum by Halle (1936) shows that the terminal sporangia of this plant are borne on slender divisions of the branch system and the sporangia are usually in groups of two to six which is more or less comparable to the number of terminal sporangia of Kothia.

The broad zone of annulus-like cells of Kothia sporangia can be compared with the broad multiseriate annulus which runs the whole length on one side in the sporangia of Botryopteris globosa (see Darrah 1960). It can also be compared with similar multiseriate annuli as in the sporangia of Ankyropteris corrugata (see Darrah 1960), the sporangia of Botryopteris forensis and some other species of Botryopteris (see Walton 1958), the sporangia of Biscalitheca musata

(see Andrews 1961) and the sporangia of Zygopteris or Etapteris lacattei (see Halton 1958). The latter sporangia have a vertical annulus about 8 cells wide extending up two opposite sides and meeting at top and the transverse section of the sporangium is somewhat similar to the transverse section of a Nothia sporangium. However, Nothia sporangia differ in their shape, structure and arrangement from all the Coenopteridalean sporangia. The sporangia of Stauropteris oldhamia, which is of Upper Carboniferous age, (Scott 1905) and which Kidston & Lang (1920) thought to be closely similar to those of Nothia are in fact more different than similar to them; they are much smaller, exannulate, spherical in shape and with different structure. They are perhaps only similar to Nothia sporangia in the number of layers making up the sporangial wall.

The axes of Nothia, being leafless, might be compared with Arachnoxylon which is believed to be leafless (see Darrah 1960).

The stem of the Upper Carboniferous Apotropteris minuta is protostelic with small tracheids in the centre (see Delevoryas 1962).

COMPARISON WITH LIVING PLANTS

A. Psilotales.

In the Psilotales the aerial shoots may be leafless (see Smith 1955) and thus can be compared with the leafless axes of Nothia. However, the synangia of the Psilotales are always borne in relation to leaves. Smith (1955) mentioned that the application of the term synangia to the fused sporangia of Psilotales is misleading because the structure is not homologous with the synangia of marattiaceous ferns. Stages in early ontogeny show that there are separate sporangia and not one septate sporangium; this allows comparison between the two fused sporangia of Nothia and the diads of Tmesipteris or the triads of Psilotum.

Nothia and Psilotum agree in that the dichotomous branching is more frequent in the distal parts of the plant. In Psilotum (see Smith 1955) the epidermis is heavily cutinized and stomata are found chiefly in the grooves between longitudinal ridges of the stem, but in Nothia the stomata are chiefly found on the ridges of the axes. The fused sporangia of Psilotum, as illustrated by Bower (1935), are borne laterally on ultimate branches but sometimes also on a main branch which is comparable to the branched fertile region of Nothia, but in the latter the fertile branch itself ends in a number of sporangia.

In Nothia the number of sporangia in each whorl is either two or three which is comparable to the number of fused sporangia of

Tmesipteris and Psilotum, being two in the former and three in the latter.

B. Ophioglossales.

See Lang (1913), Bower (1935), Campbell (1939) and Smith (1955). The sporangia of Ophioglossum and Botrychium, though exannulate, open by a transverse slit, Nothia sporangia also did, but their slit is to the inner side facing the axis while that of Botrychium and Ophioglossum is to the outer side.

Nothia and Botrychium have leafless branched spikes, but with some clear differences. In Botrychium virginianum the wall of the ripe sporangium is 4-6 layers of cells in thickness which is not different from that of Nothia sporangia. The sporangia of Botrychium virginianum are stalked like Nothia sporangia but their stalks are thick and very short.

The presence of stomata in the sporangial wall of Nothia finds similarities in some species of Ophioglossum. The presence of stomata in the sporangial stalks and fertile axes of Nothia is comparable to stomata found in the sporangiophores of Ophioglossum vulgatum.

The xylem of Nothia and in Ophioglossales acquires a crescent-shape at certain stages or levels, but, as a result of different reasons in each of them (departure of leaf, branch or sporangial traces).

In Nothia the division of a single branch trace into two strands as soon as it enters the branch base can be compared with Botrychium lunaria where the single leaf-trace divides into two strands at the

base of the leaf, also with Ophioglossum lusitanicum where the primary bundle given off from the stele of the stem branches just after it enters the petiole.

C. Lycopodiaceae.

Lycopodium sporangia are stalked and always kidney-shaped when mature, dehiscence is affected by a transverse rupture of the sporangium apex along the line of the stomium and the sporangium wall consists regularly of three layers of cells (see Smith 1955).

Nothia sporangia agree with those of Lycopodium more or less in shape, in being stalked and in the position of the line of dehiscence, but obviously not in the mechanism of dehiscence since Nothia sporangia have a broad annulus-like zone surrounding the line of dehiscence. Nothia sporangia again differ from those of Lycopodium in the number of layers making the sporangial wall.

D. Anthocerotaceae.

Campbell (1924) stated that there are numerous resemblances between the sporophyte of Anthocerotaceae and that of the lower Pteridophytes. Nothia agrees with Anthoceros (see Campbell 1905) in the presence of stomata in the epidermis of their sporangial wall, but otherwise there is no close similarity between the two plants.

PHYLOGENETIC CONSIDERATIONS

In 1933 Halle described and reconstructed Carboniferous fossil fructifications of some Medulloseae, namely Whittleseya and Aulacotheca. These fructifications are terminal synangia consisting of a ring of long sporangia laterally fused to their tips to form a cup which was attached to the plant by a stalk. In Whittleseya the cup is formed of a large number of sporangia and has a wide opening but in Aulacotheca the opening is very narrow and the number of sporangia composing the synangium is small (9 as shown in his reconstruction). As to the origin of such Pteridospermalean synangia Halle's speculation was ".. the terminal sporangia of the Psilophytales and of some primitive ferns without laminae may be regarded as derived from spore producing tips of ordinary ultimate thallus or rachis-branches. In the case of a terminal tuft of sessile sporangia, as in some forms of Psilophyton, each sporangium would then represent an entire ultimate rachis-branch (telome) producing spores. Just as sterile rachis-branches (telomes) are generally supposed to have given rise to the lamina of a pinnule through lateral fusion in one plane (webbing), so a group of terminal sporangia in cyclic arrangement may produce through tangential fusion a spore bearing cupule-like structure." This speculation could be seen to have come almost true when we look at the fertile branch of Nothia which terminated in five separate sporangia that were arranged in a circle around a central space. In this connection, the terminal synangium of Yarravia described by Lang &

& Cookson (1935) should be mentioned. This synangium is composed of about five sporangia which are laterally connected but is more primitive than that of Aulacotheca because of the freely projecting tips of its sporangia. In Yarravia synangium the sporangia are probably arranged around a central space like Aulacotheca and Nothia. The synangia of Yarravia, which are composed of partially connected sporangia, though of older age than Nothia, could be regarded theoretically as an intermediate evolutionary step between the terminal cluster of five separate sporangia of Nothia and the entirely fused sporangia of the terminal synangia of the Whittleseyinae. The fact that Yarravia is of older age than Nothia does not exclude the possibility that the synangium of Yarravia has evolved from a terminal bunch of separate sporangia (similar to that of Nothia) which might have existed in older strata than that in which Yarravia itself was discovered. However, no suggestion whatsoever is made that one of these forms is directly derived from the other.

The sporangia of Nothia are similar to those of the genus Zosterophyllum in many respects. In Nothia, as well as in Euzosterophyllum, the sporangia are radially arranged. In Euzosterophyllum the arrangement is spiral, but sometimes two sporangia are borne almost opposite, which could be regarded as a whorl of two sporangia. The type of arrangement of Nothia sporangia could have been derived more or less directly from the spiral type of Zosterophyllum, since in Nothia the basic plan is also spiral and even in the whorls a very

condensed spiral arrangement could almost always be detected. The pseudo-whorls and the terminal clusters of Nothia sporangia could have been derived from the spiral form by condensation. If this be correct, then the fact that Zosterophyllum (one species of which occurs in the Lower Old Red Sandstone of Scotland) is contemporary with Nothia or of somewhat older age might account for the slight evolution or advance which Nothia has over Zosterophyllum and also for the irregularities in the arrangement of Nothia sporangia which could be regarded as still in the process of evolution or development that has not yet reached a stable uniform condition.

Walton (1958) mentions that in Silurian and Early Devonian times, Thallophytes and Pteridophytes constituted the vegetation of the Earth and that the presence of plants of an intermediate type such as Parka and Nematothallus and the marked thalloid form of many of the Pteridophytes suggests that during these early periods an important series of transformations were in progress.

This unstable morphological condition exhibited by the fertile region of Nothia allows for further theoretical speculations. Thus, as mentioned above, lateral fusion of the sporangia in the terminal clusters might have eventually evolved types as Yarravia and Aulacotheca synangia. The terminal fused pairs of Nothia sporangia could be regarded as a starting step in this direction, were they not a more chance result of the transformation of one form of sporangial arrangement to another as mentioned before on pages 75 and 76. However, if every

two sporangia of Kothia became fused, the result will be a fertile region rather similar to that of the living genus Tmesipteris. Furthermore if all the sporangia of Kothia became arranged in whorls and the three sporangia of every whorl became fused we could get a fertile region not unlike that of the extant Psilotum.

By further evolution Kothia might have lead (by condensation) to fertile regions in which all the sporangia are arranged in regular whorls; each whorl with three sporangia or six sporangia if every two successive whorls were brought to one level by condensation. Although no such fossil plant has been found as yet, this might be regarded as a primitive approach to the whorled sporangiophores of sphenopsid strobili; especially those in which no sterile leaves or bracts occur in the strobilus, as in Pothocites and the living Equisetum.

Although the sporangia of Kothia are somewhat Lycopod-like in their shape and line of dehiscence, yet no direct or even perhaps indirect derivation of the latter can be obtained from the former. Only if one could imagine that "enation" leaves or microphylls have emerged between the sporangia of Kothia, then only is it possible to derive a somewhat but not very similar condition to the probable fertile region of Asteroxylon mackiei described by Lyon (1964), which is regarded as having a Lycopod affinity.

DISCUSSION AND CONCLUSION

Current views on the Psilophytales :

It is necessary to review the Psilophytales as a whole, before proceeding to consider the position of Nothia aphylla within this Order.

The species Rhynia gwynne-vaughani, R.major, Horneophyton lignieri, Asteroxylon mackiei and Nothia aphylla are known only from the Rhynie locality. The genus Asteroxylon has a second species known from the Middle Devonian of Germany (Kräusel & Weyland, 1926). A supposed Horneophyton sp. was discovered also from the Middle Devonian of Germany by Kräusel & Weyland (1960).

In 1920 Kidston & Lang classified the Rhynie plants, Rhynia, Horneophyton, Asteroxylon and Psilophyton princeps as the typical members of the Order Psilophytales. However, recently it is becoming clear that the Rhynie deposit includes a diversified group of plants which are not all typical Psilophytales. Rhynia and Horneophyton are typical members of this Order whereas Asteroxylon with its laterally borne sporangia and Nothia with its peculiar branched fertile spikes show different affinities. Moreover a sixth vascular plant has been lately discovered from the Rhynie locality by Dr. Lyon (personal communication) which will naturally add to the diversity of the Rhynie fossil flora. This is in addition to the recently discovered bryophytic capsule referred to the Bryales by Lemoigne (1966).

When Kidston & Lang established the Order Psilophytales they included in it Rhynia, Horneophyton, Asteroxylon and Psilophyton princeps. Soon, however, this Order increased in size and diversity and became vaguely defined due to many new fossils being included in it, Chesters (1964) explains this situation of the Order in the following words "There appears to be a central core of plants forming the natural, somewhat narrowly defined group of Psilophytales, surrounded by others referable but with less confidence, to the group."

Høeg (1942) stated that the Psilophytes may be divided into two groups which at least at first sight differ very considerably from each other: those possessing spines or hairs, and those lacking such appendages. The typical members of the former group are Psilophyton, Asteroxylon, and Psilodendrion to which may be added Dutoitia and possibly Cosslingia. Spineless Psilophytes are Rhynia, Horneophyton, Taeniocrada, Zosterophyllum, Hicklingia, Sciadophyton and Pseudosporochnus. Pseudosporochnus is now regarded as a fern (Leclercq & Banks, 1959 & 1962).

Leclercq (1954) stated that "as far as the fructifications are concerned, two main types appear to loom out of the Psilophytalean fog; they are : (1) the sporangia borne at the end of the terminal naked branches including: Rhynia, Horneophyton, Hicklingia, Cooksonia, Dutoitia, Taeniocrada, Sporogonites, Dawsonites; and (2) specialized fertile branches consisting of loose terminal spikes with rows of erect sporangia including: Zosterophyllum, Cf.Psilophyton princeps, Bucheria.

Hueber (1964) similarly mentioned that there are two main lines

of development within the Order Psilophytales. The first with terminal sporangia which are fusiform and have a longitudinal dehiscence. The second with lateral sporangia which are globose or reniform with distal dehiscence.

Nothia aphylla being spineless, hairless and possessing terminal spikes of reniform sporangia may be added to the second group of Høeg, Leclercq and Hueber.

Nemejc (1960) divided the Psilopsida into three Classes; Horneophytineae, with one Order and two families, Psilophytineae, with eight Orders and eleven families and Asteroxylineae, with one Order and one family.

Concerning the affinities of the group Psilophytales as a whole there are several opposing opinions. While many botanists regard the Psilophytales as the starting point of all other groups of higher plants, others suggest a polyphyletic origin of land plants (Leclercq, 1954). Regarding Bryophytes, Takhtajan (1953) suggests that they may be reduced forms of Psilophytales, a view shared also by others (e.g. Richards, 1959). However, Campbell (1924) takes the reverse view, namely that the Psilophytales are developed or evolved from Bryophytic ancestors like Anthoceros. This latter view might be enforced by the recent discovery of a Bryales capsule in the Rhynie deposit (Lemoigne 1966), assuming that it is correctly assigned to the Bryales.

On the other hand, Nemejc (1960) takes quite a different view; he regards the Psilopsida as an intermediate plant phylum between the Bryophyta and all the Pteridophytic phyla, and that from the point of

view of phylogeney, Psilopsida is to be considered as parallel to all Pteridophytic types and that no direct relationship exists at all between the Psilopsida and Pteridophyta or Bryophyta. All features which the Psilopsida have in common either with the mosses or with the Pteridophytic types, can not be morphogenetically brought in direct connection with the same or similar features in these two phyla. They only present mere morphological convergences, i.e. features gained independently without any real relationship either to moss plants or to any Pteridophytic type.

Systematic position of Nothia aphylla.

Many botanists have pointed out that cytology (Anderson, 1937; Santapau, 1960), physiology (Gibb, 1958; Santapau 1960), embryology (Maheshwari, 1964), anatomy (Eames, 1953; Banks, 1965), palynology (Erdtman, 1964) etc., are important characters beside morphology as aids to plant taxonomy. Almost all these characters can be studied in a living plant; however, when dealing with a fossil plant many of them can never be revealed. This shows the difficulty of assigning a fossil plant to its appropriate position in the plant kingdom, especially if it is known only in a fragmentary condition. Sporne (1962) wrote "A fossil plant, even when properly reconstructed, is known only at the stage in its life-cycle at which it died. Other stages in its life-cycle, or in its development, may never be discovered. Yet, the classification of living organisms may (and indeed should) be based on all stages of the life-cycle."

Wagner (1959) pointed out; "single characters may be reliable and convenient for keys, but for phylogenetic research they must be used only in co-ordination with as many as possible other features."

Nothia aphylla, the subject of our present discussion, is known only as fragments of the mature fertile region of the sporophyte. Nothing is known regarding other regions or stages of development of the sporophyte; and the gametophyte generation is also completely unknown. However, the facts that are known about Nothia may serve as a useful key to its systematic position.

It is quite clear from the comparisons that Nothia aphylla is very closely related to the genus Zosterophyllum. Although the latter plant is more completely known than the former yet it is not known as a petrification which would have allowed for more close comparison between the two plants regarding histological details of the axes and the sporangia and the xylem morphology. The difference between Nothia and Zosterophyllum is mainly that the fertile region of the former is branched and that some of the sporangia approach the whorled condition in their arrangement on the axis. Nevertheless it seems that Nothia, as far as it is presently known, could find its place in the family Zosterophyllaceae. In this family sometimes Bucherin and Gosslingia are also included (Nemejc, 1960). Those two genera are also among those most closely comparable to Nothia.

PART II

ON THE SPORANGIA OF HORNEOPHYTON LIGNIERI (KIDSTON AND LANG) BARGHOORN AND DAURAH.

Horneophyton sporangia were described by Kidston and Land (1920) as terminal on ultimate branches, cylindrical, about 2 mm. long and about 1 or 2 mm. in diameter, indehiscent, with a thick wall composed of thickened epidermis, thin walled inner tissue, and persistent tapetal layer. A sterile columella composed of thin walled elongated cells extended from the base to near the top of the sporangium. Spores about 50 μ in diameter.

The same authors also mentioned that the sporangia evidently arose by the transformation of the tips of certain branches of the plant. When the apex was simple, a single sporangium resulted and when the apex was in a more or less advanced stage of division this was reflected in the subdivision of the sporangium and the lobing or branching of the columella. They also reported that such subdivided sporangia have a single cavity and that sometimes one of the two lobes of the columella might subdivide, i.e. the columella of a branched sporangium might be bilobed or trilobed.

During the course of the present investigation of Rhynie chert material, a number of new fertile specimens of Horneophyton lignieri were found. They agree with those described by Kidston and Lang in most features (e.g. wall structure and thickness, presence of a single sporangial cavity, spore size, etc..) but are of special interest in that they are larger and more branched than those described by Kidston

and Lang and the columella may have as many as 5 lobes.

The three specimens described below were found quite close to one another in block number 67.

In one of the three, the sporangia are filled by spores, many of them still in tetrads and agreeing well with those described by Kidston and Lang, but preservation is poor (Fig.15). The other two specimens are better preserved, but nearly empty. They are large and branched or subdivided a number of times.

Figure 1 Plate 1 shows a diagramatic drawing of one of the two branched fructifications in bottom view. This specimen has two main branches, each of which is subdivided. Thus the fructification has four subdivisions or sporangia and a similar number of columella lobes but one common sporangial cavity. Successive sections of the specimen at the levels A-H indicated in the diagram are shown in Figs. 3 - 10.

The stalk of the fructification is very slender; being under 1 mm. in diameter (Fig.6). The columella divides into two branches from its very beginning; the upper branch subdivides after a length of .5 mm. into two lobes (Fig.4) while the lower branch divides into two lobes after a length of about 2 mm. (Fig.9).

Figure 2 Plate 1 shows a diagramatic drawing of the second large branched fructification. This is even more highly branched than the one just described. It has three main branches, two of which are subdivided. Thus there are five subdivisions or sporangia of the fructification as well as five lobes of the sterile columella and a

single spore cavity. Successive sections of the whole structure at levels A-K as indicated in the diagram (Fig.2) are shown in Figs. 16-26.

The first three figures of this series show that the single stele of the stalk divides into three final traces; one of which departs about 1 mm. before the other two traces become separated from each other, thus representing two closely-placed dichotomies. The three traces enter the bases of the three main lobes of the columella as shown in the diagram, Figure 2.

The wall at the tip of each of the five subdivisions or sporangia is broad, somewhat concave and open or broken at the centre of these five concave tips (Figs.22-26 & 27-31). Kidston and Lang (1920) mentioned that Hornеophyton sporangia have broad flat tips, but the sporangia which they illustrated with flat tips were always filled by spores except one (see their Figs.66 & 67) which was empty and this also showed a break in the wall at its tip.

In the new fructification with four subdivisions (Plate 1, Fig.1) the wall is also broken at the end of its four subdivisions (Figs.3, 10 & 11-14).

There is no break anywhere else in the walls of the two fructifications except at the mentioned positions; that is in the middle of the concave broad tips of the subdivisions or sporangia. Small separated portions of the wall are sometimes found preserved near the break or inside the sporangium, as is clearly shown in some

of the figures on Plates 2 & 4.

It should be noted that the epidermal cells of the sporangium wall are usually more distinct and better preserved at the broad tips of the subdivisions where the break occurs rather than elsewhere (Figs.11-14, 27-31 & 37). Despite Kidston's and Lang's statement that the sporangia are indehiscent, it seems highly probable that there was a regular dehiscence in this position in Horneophyton, but it will be necessary to examine many more sporangia to determine whether this was really the case.

Several protrusions, such as those shown in Figs.32-34, were found in the surface of the two specimens. At the tip of some of these protrusions there are two tiny cells resembling guard cells which, unlike the rest of the epidermis, are covered with a very thin layer of cuticle (Figs.35 & 36). A small chamber is present beneath these cells which might suggest that these structures were of respiratory function or stomata. Kidston and Lang (1920) mentioned that "the sporangium wall shows irregularities in outline or projecting processes" which in their opinion "do not seem to be wholly accounted for by accidental contraction". However, Kidston and Lang (1920) also reported that they did not observe stomata in Horneophyton, but added that much weight cannot be attached to this negative result owing to the state of preservation of most of the material.

The present study proves that stomata were present in the sporangium wall of Horneophyton. Zimmermann (1927) had already observed stomata in the epidermis of Horneophyton stems.

Other features of the two large fructifications need not be mentioned since they agree exactly with Kidston's and Lang's (1920) descriptions.

DISCUSSION

A comprehensive discussion of Horneophyton Lignieri had already been given by Kidston and Lang (1920,1921). They stated that it is comparable to Hepaticae, Anthoceros, certain mosses, Sporogonites, some Pteridophytes, Psilotales and some Algae. No further mention of what they found and stated seems required.

Discussion here will be mainly concerned with the new information obtained. This includes; the presence of stomata in the sporangial wall, the possible dehiscence position and the nature of the fructification as a whole.

The presence of stomata in the epidermis of Horneophyton sporangia increases its similarity to Anthoceros and is also similar to Nothia and some species of Ophioglossum.

Regarding dehiscence Kidston and Lang (1920) stated that the thickened epidermis of Horneophyton sporangia seems to be an advance in specialisation, though apparently useless for dehiscence. But it was noticed in the two new specimens that the thickening and preservation of the epidermal cells at the top of all the nine sporangia are different and better than the rest of the epidermis. Also the presence of a slit or an opening at the top of the nine sporangia cannot easily be

considered as a mere coincidence. If spores were only dispersed by the decay of the sporangial wall, then the two new specimens should have been full of spores since their walls are fairly well-preserved.

The thickening of the epidermal cells at the top of Horneophyton sporangia is mainly on the outer walls and extends partly or entirely on the lateral walls while the inner walls are not thickened. This is quite similar to the type of thickening of the epidermis of Anthoceros capsule (see Smith 1955). It is highly probable that the zone of dehiscence in Horneophyton is also similar to that of Anthoceros. The type of thickening of Horneophyton sporangia contrasts with that found in the epidermis of Nothia sporangia where the inner and lateral walls are thickened but not the outer walls.

The fructification of Horneophyton with its branched columella has no parallel in Bryophytes or Pteridophytes. The compound structure of the fructification could be the result of several successive closely-placed dichotomies. This could be represented in simple line drawings, of the columella only, as follows :

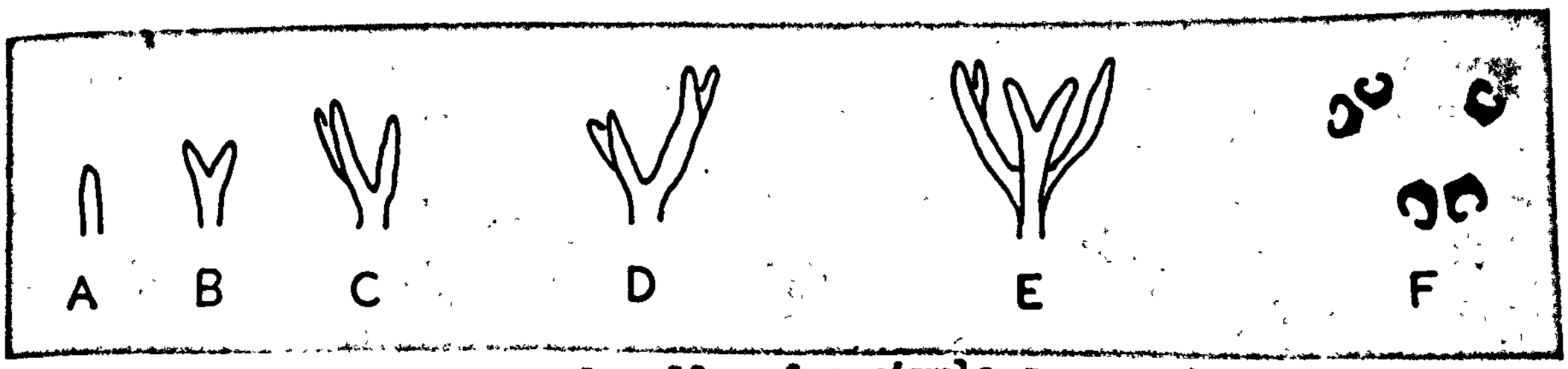

Fig.A represents a columella of a simple sporangium. In Fig.B one dichotomy results in a bilobed sporangium. A trilobed sporangium results from two dichotomies (Fig.C). Three dichotomies produce a four-lobed sporangium (Fig.D) and four dichotomies produce a five-lobed one (Fig.E). Figs.A-C represent sporangia described by Kidston and

Lang while Figs.D & E represent the two new specimens.

In the new fructification with five lobes, these are arranged in an asymmetric ring as shown in Fig.F, which represents a transverse section of the specimen at its upper part where the five lobes are no longer connected.

It could be seen that completely symmetrical repeated dichotomy could produce 2, 4, 6, 8, etc., subdivisions arranged in a ring.

It could be said also that these fructifications are in fact synangia in which a number of terminal sporangia, originally at one level or slightly different levels, became partially connected. The sporangia have free projecting tips and each one retains its lobe of columella and its slit of dehiscence but there is a continuous sporangial cavity.

A comparison is possible between the simple and compound sporangia or synangia of Horneophyton and the terminal sporangia of Nothia. In the latter the number of terminal sporangia ranges between two and five and when five they are arranged in a circle. In Horneophyton the sporangia which are only terminal range in number between 1 and 5 and also when five they are arranged more or less in a circle. In Nothia the sporangia are usually separate but sometimes two sporangia are fused having two vascular strands, two connected stalks, two dehiscence slits but one spore cavity. This is similar to the fused sporangia of Horneophyton where the number of dehiscence slits and columella lobes is equal to the number of the fused sporangia. There is also a number of vascular strands but only one sporangial cavity. In Horneophyton

it is known that sometimes two sporangia are borne close but separate at branch ends. It is probable that more than two sporangia were borne close and separate at fertile branch ends as known in Nothia.

Horneophyton compound fructifications can also be compared with the Upper Silurian - Lower Devonian synangia of Yarravia described by Lang & Cookson (1935), Cookson (1949) and Danze-Corsin (1956). In Yarravia the number of sporangia in the synangium ranges between three and five and is not more than six. The sporangia are also partially connected, having free projecting tips, and might have been arranged around a central space. The synangia of Yarravia and Horneophyton differ in that the sporangia of the former apparently have separate spore cavities but in the latter there is always a common sporangial cavity. Yarravia synangia are not known as petrification which limits the scope of comparison.

This leads to a comparison of Horneophyton with the Carboniferous synangia of Whittleseya and Aulacotheca described by Halle in 1933. These are terminal synangia consisting of a ring of long sporangia, laterally fused to their tips forming a cup. The synangium of Aulacotheca is composed of a small number of sporangia (9 shown in Halle's reconstruction) and the cup has a very narrow opening. But the sporangia of Aulacotheca, unlike those of Horneophyton, have separate spore cavities.

Another Upper Silurian-Lower Devonian fructification which is somewhat comparable to Horneophyton synangium-like fructification is that of Hedeia; described by Cookson in 1935 & 1949. In Hedeia the sporangia are terminal, large, elongate and radially arranged around a central space but the sporangia are separate and not by any means connected.

A comparison is also possible between the new Horneophyton fructification and the synangium Telangium scotti described by Benson (1904). This synangium has eight sporangial chambers arranged in two rows. The synangium is a little under 3 mm. in width and about 4 or 5 mm. long. The sporangia have free narrow apex. It is the similarity between Telangium scotti and the ovule Lagenostoma that made Benson (1904) suggest that "the seed is in fact a synangium in which all but one of the sporangia are sterile and form an integument to the one fertile sporangium which has become a megasporangium with one large megaspore". While Horneophyton fructifications are somewhat comparable to the synangium Telangium scotti, yet they offer no further support to Benson's theory.

The supposed Bryales capsule which has been recently (Lemoigne, 1966) discovered in the Rhynie Chert, bears certain similarities to the sporangium of Horneophyton. Both have columella and are very similar in general shape and size. The capsule differs from Horneophyton sporangium in its upper part where it has an operculum, also in the larger size of its spores (150 μ).

The synangia or fused sporangia (Smith 1955) of the Psilotales may also be mentioned as possibly comparable to the fused sporangia of Horneophyton.

EXPLANATION OF PLATES

All Figures are from untouched photographs except line drawings.

Detailed explanations are in text.

All photographs are taken by reflected light.

Plate 1

Fig. 1 : Diagrammatic reconstruction of Horneophyton fructification in bottom view showing stalk end in T.S., four lobes of columella and the supposed dehiscence position at the tip of the four subdivisions of the synangium. Peels No. 67/23-67/163. x 10.

Fig. 2 : Diagrammatic reconstruction of another Horneophyton fructification showing the division of the main xylem of the slender stalk into three final strands, the five branches of the columella and the five sporangia of the fructification, each with an opening at its tip. Peels No. 67/130-67/232. x 10.

Plate 1

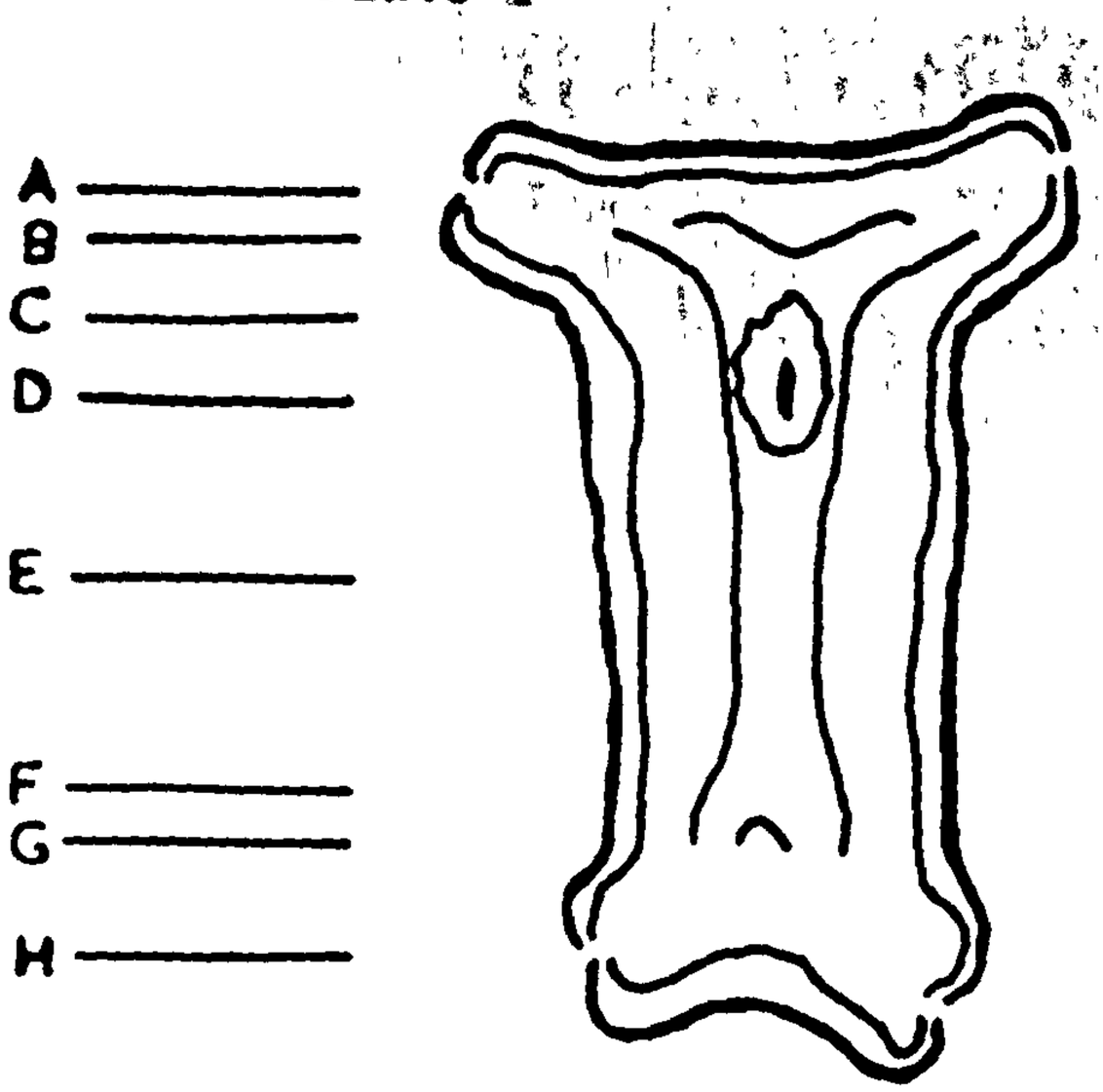

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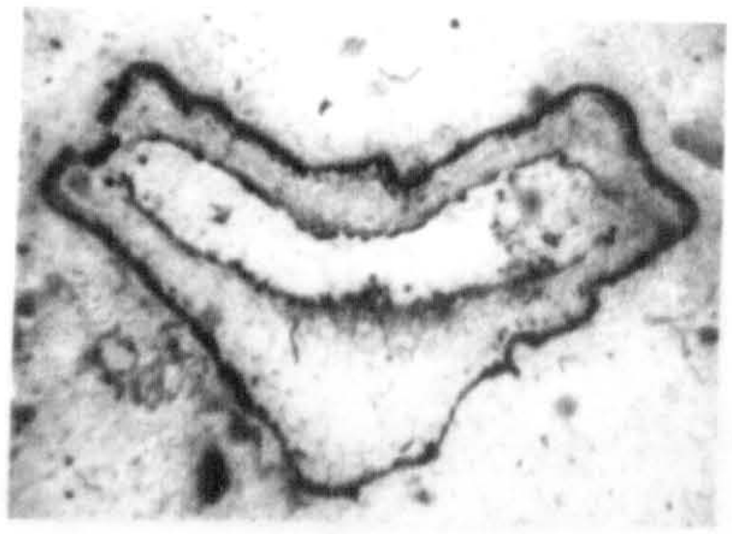
Plate 2

Figs. 3–10 : Sections of the specimen in Fig. 1 at the levels A–H. Peels No. 67/36, 67/43, 67/54, 67/66, 67/90, 67/120, 67/128 & 67/144. x 10.

Figs. 11–14: Sections of the synangium-like fructification in Fig. 1 showing an opening at the top of its four sporangia. Peels No. 67/36, 67/32, 67/144 & 67/157. x 20.

Fig. 15 : <u>Horneophyton</u> sporangium showing spores, some of them in tetrads. The wall of the sporangium is ill-preserved. Peel No. 67/169. x 50.



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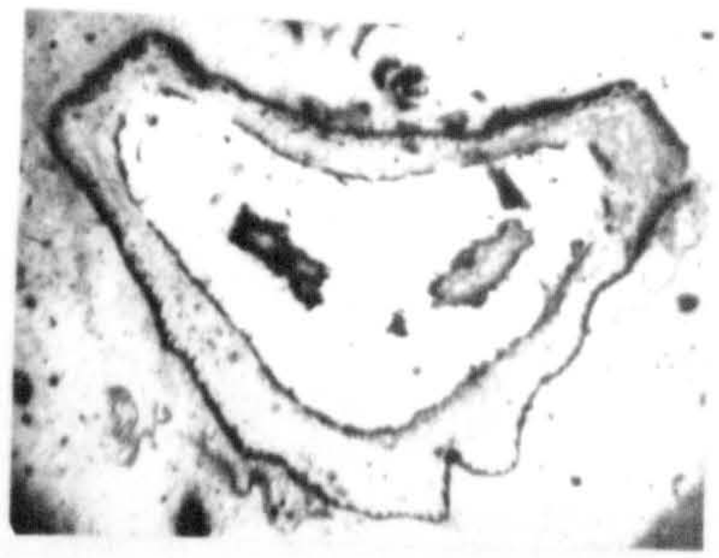

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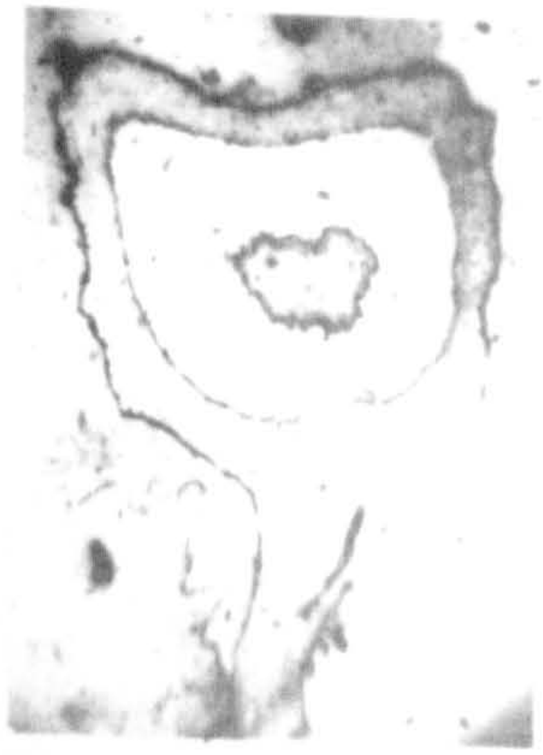

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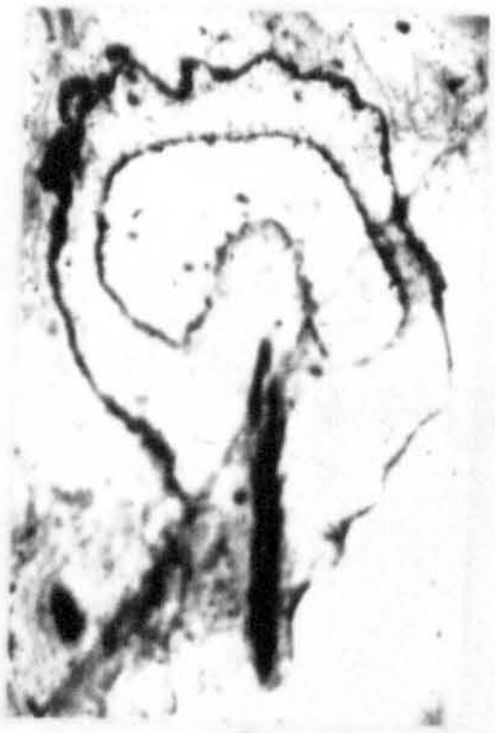

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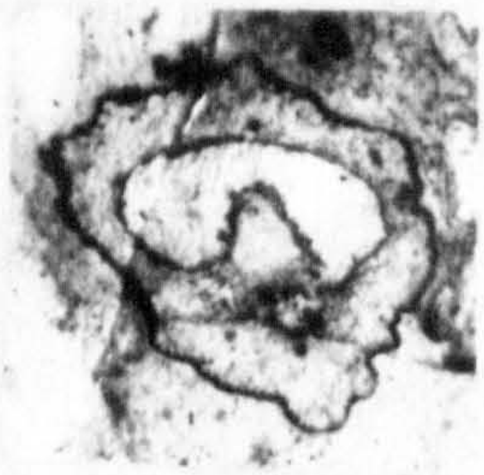

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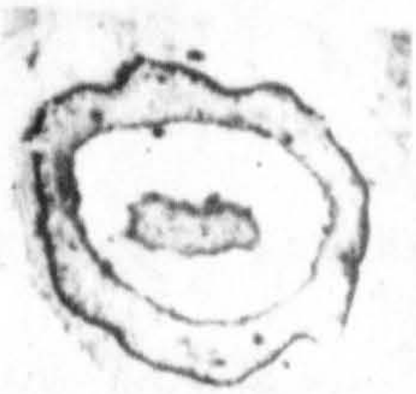

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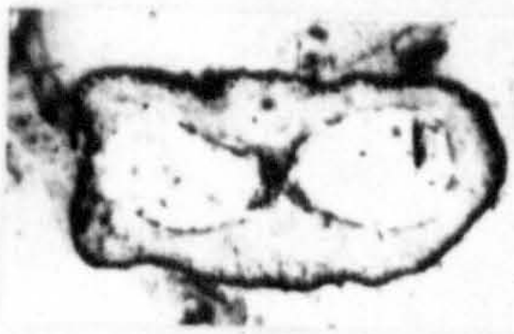

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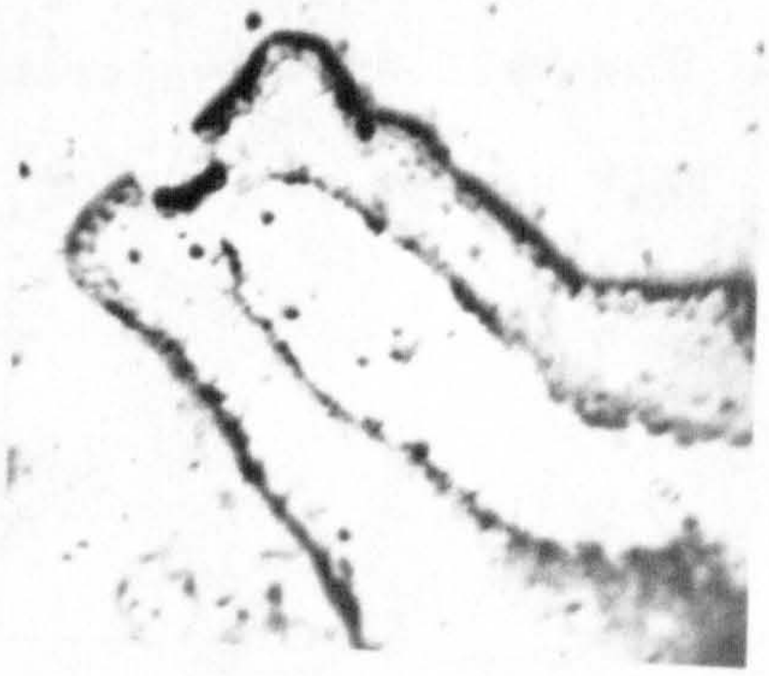

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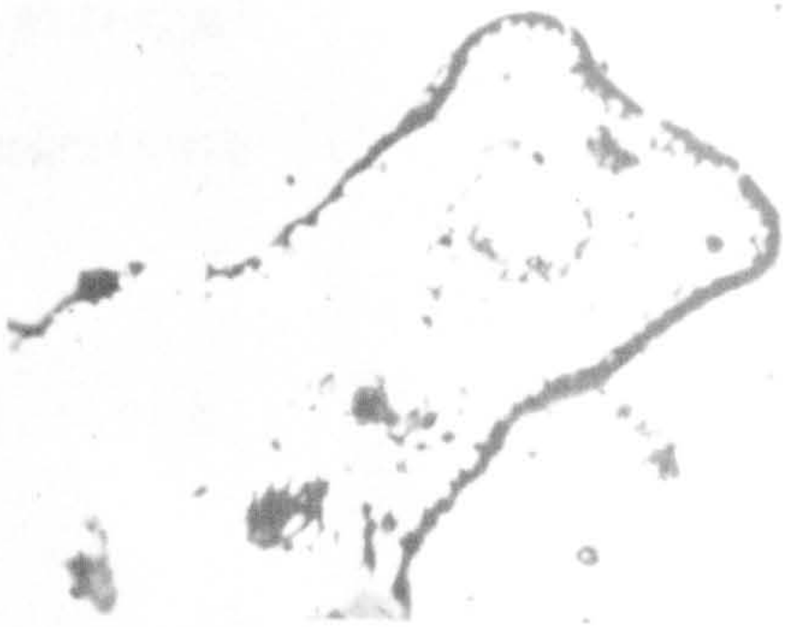

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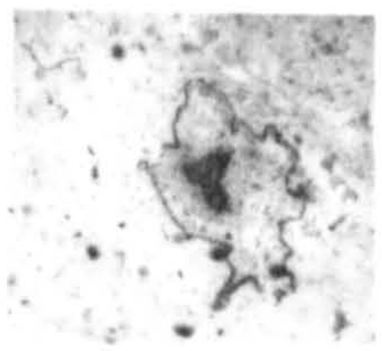
Plates 3 & 4

Figs. 16-26 : Sections at the levels A-K of the specimen in Fig. 2. Peels No. 67/140, 67/150, 67/172, 67/182, 67/186, 67/191, 67/194, 67/202, 67/206, 67/216 & 67/221. x 10.



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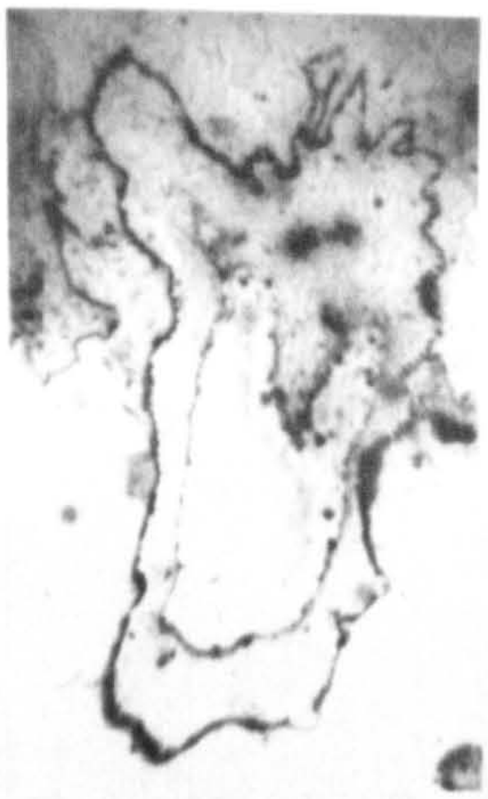

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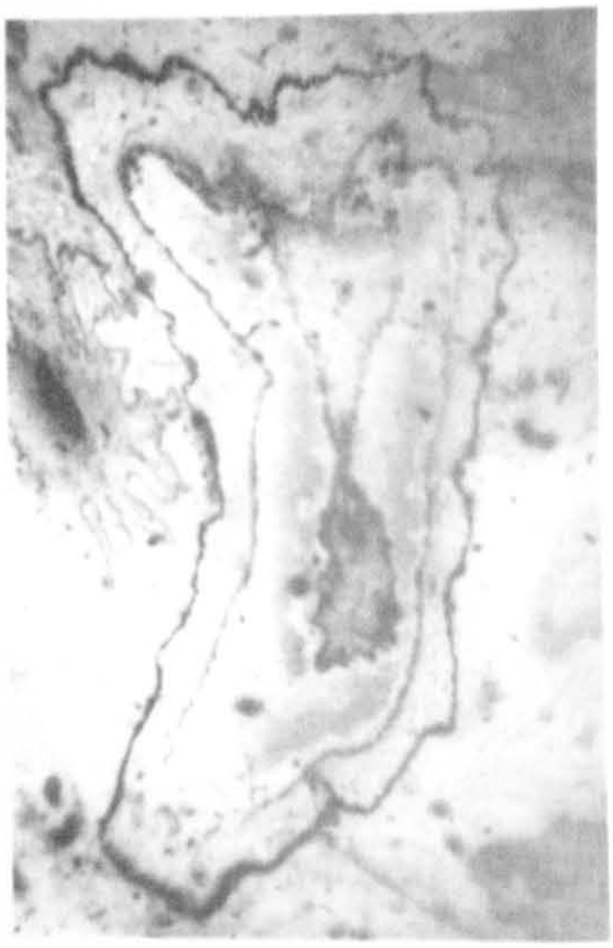

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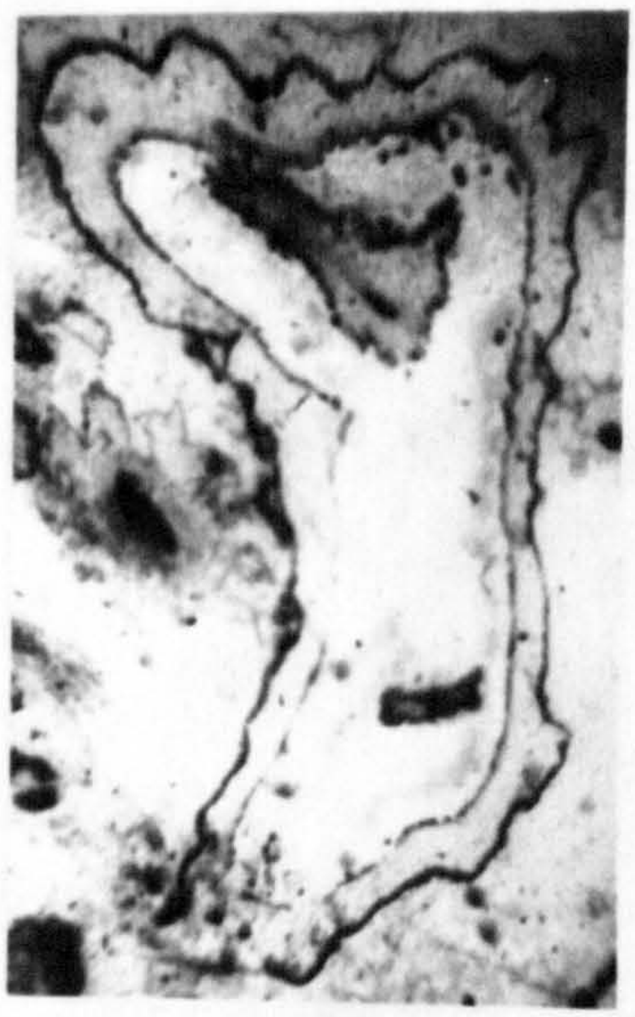

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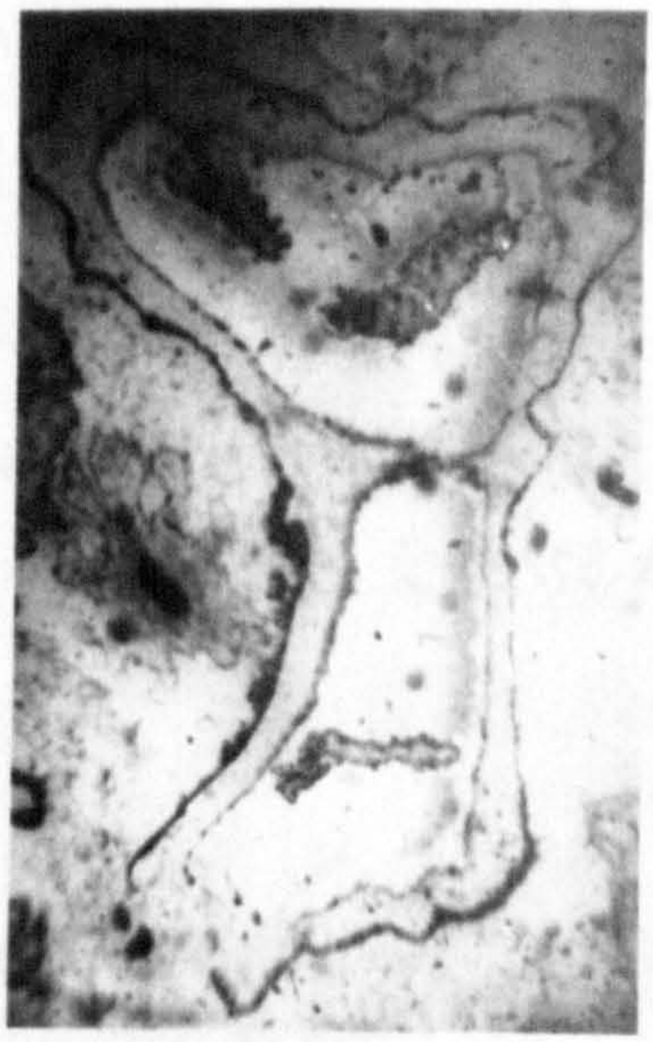

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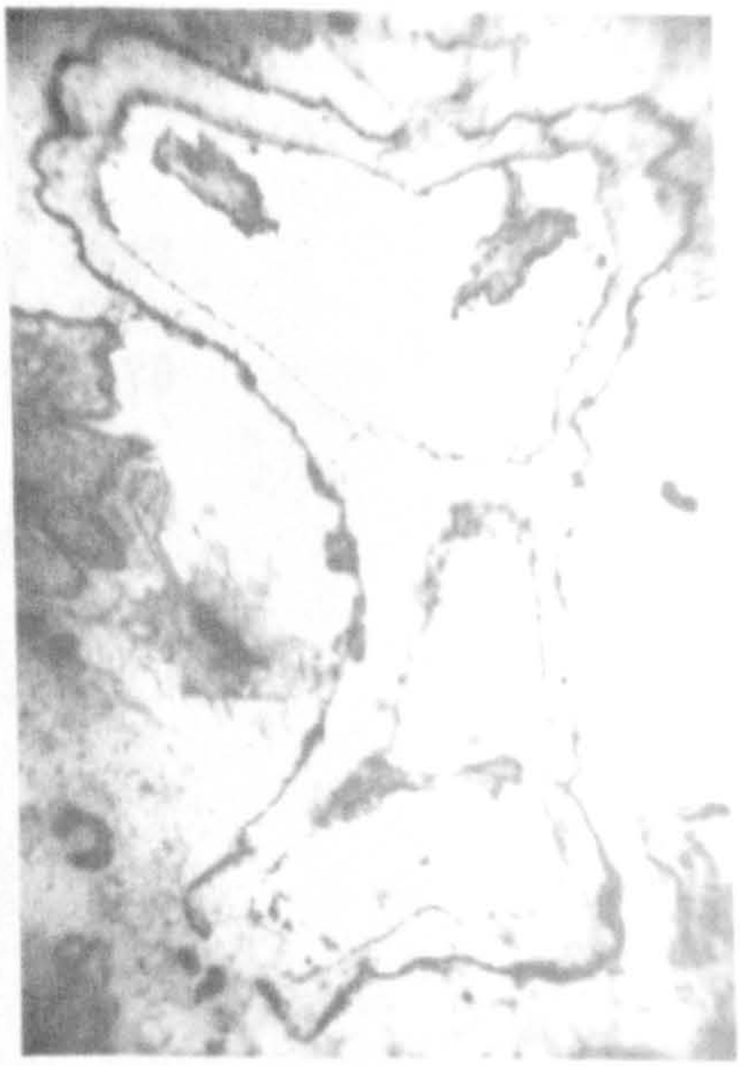

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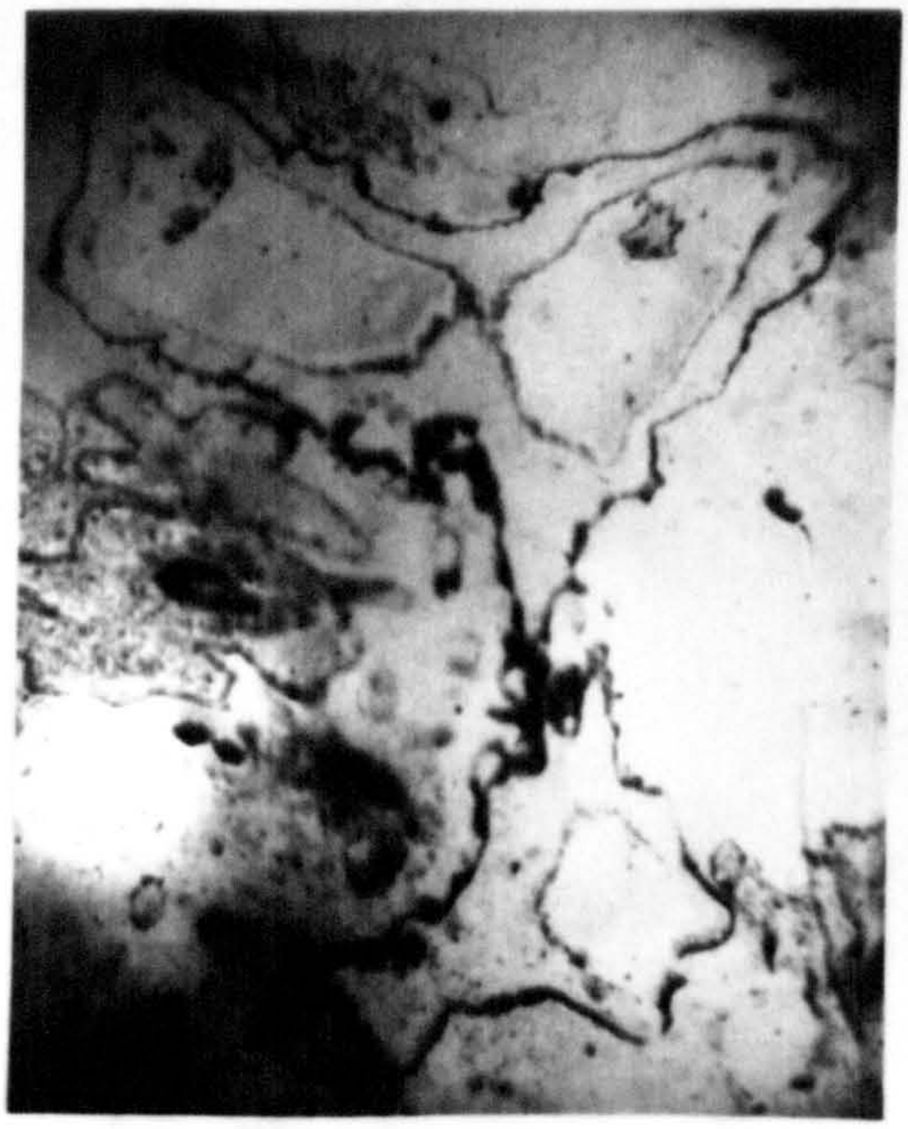

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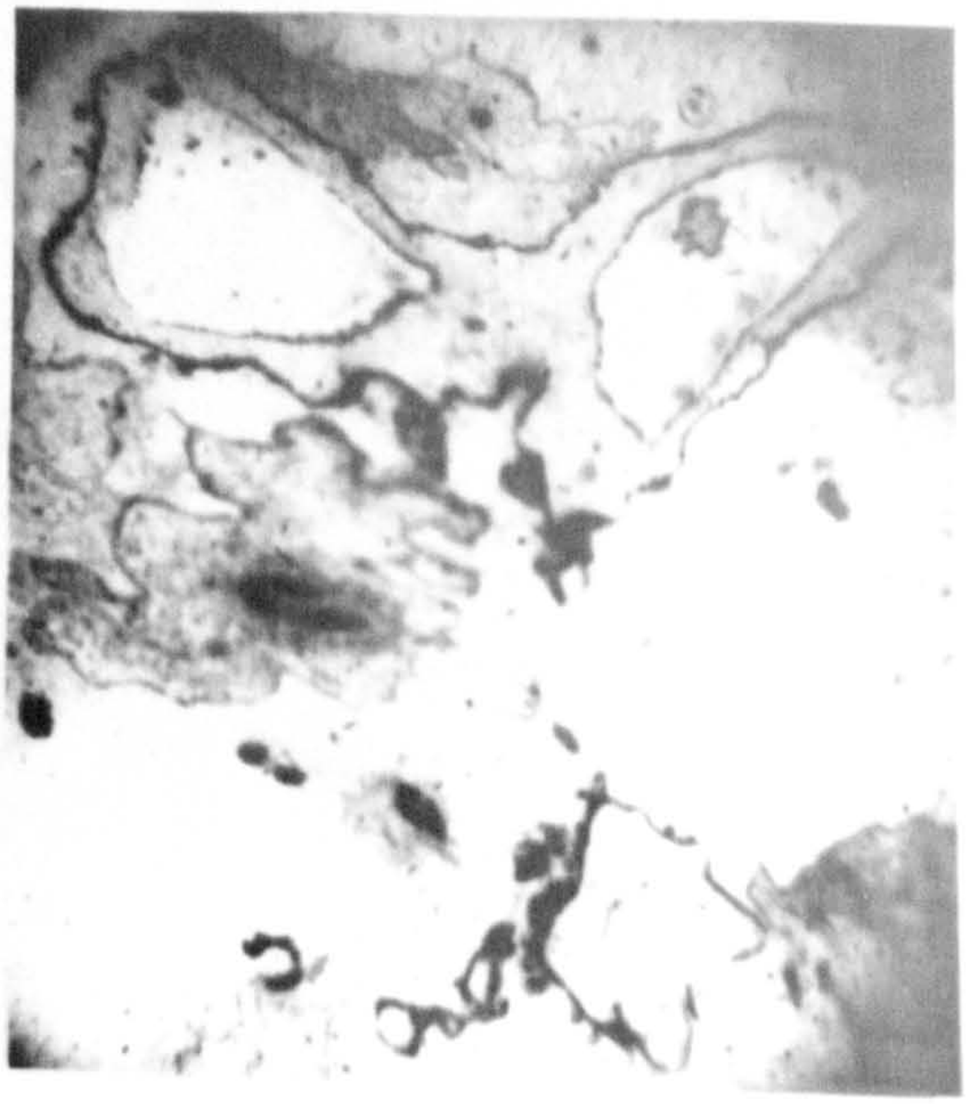

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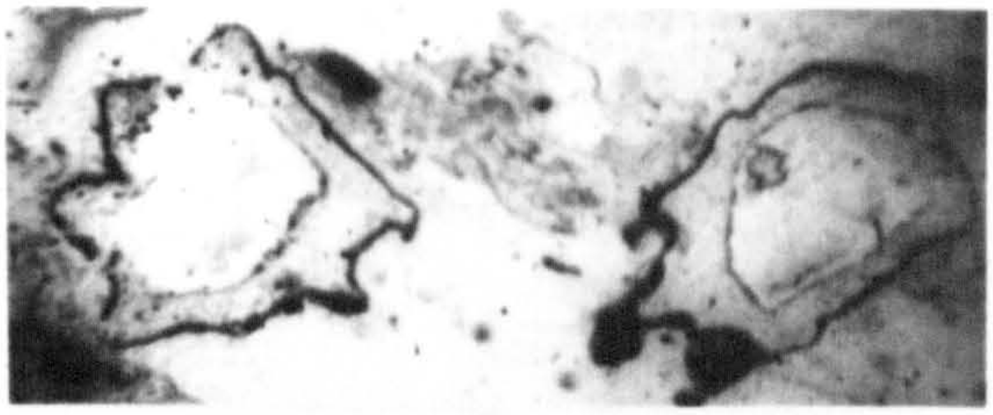
Plate 4

Figs. 27-31 : Sections of the synangium-like fructification in Fig. 2 showing an opening at the top of each of its five sporangia. Peels No. 67/212, 67/217, 67/221, 67/194 & 67/204. x 20.

Plate 4



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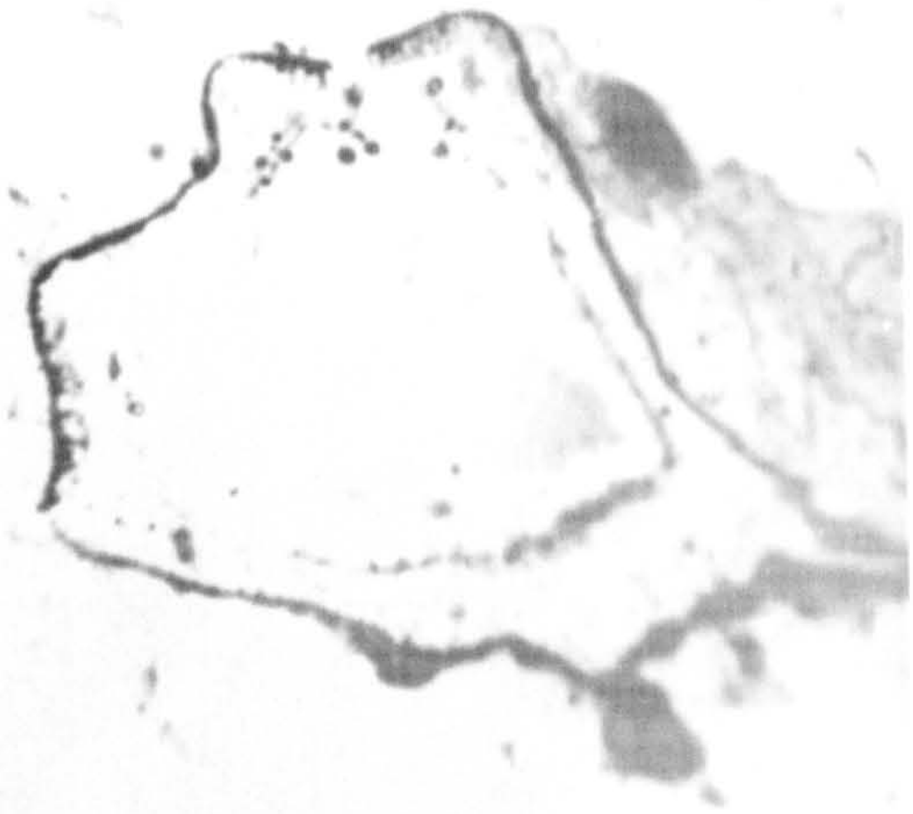

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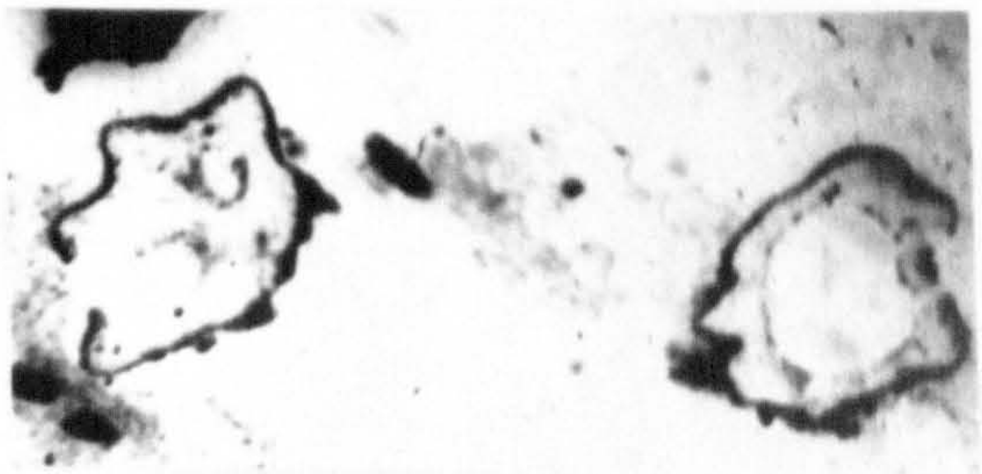

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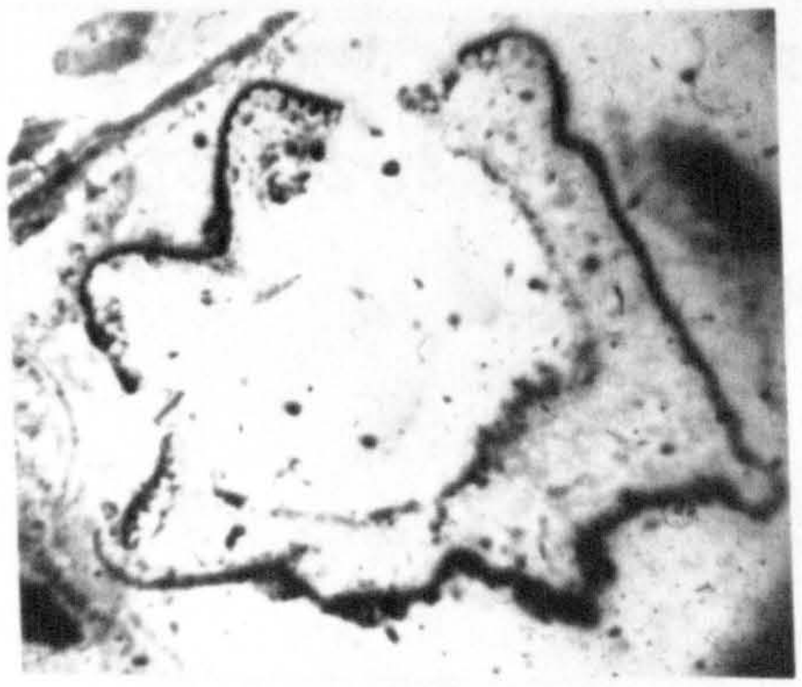

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Plate 5

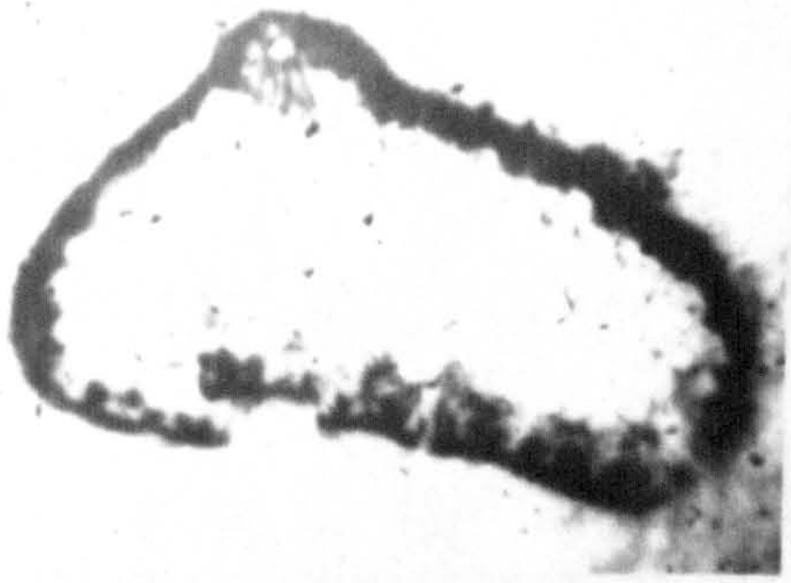
Fig. 32 : Portion of a sporangium showing a stoma at the top of a protrusion. Peel No. 67/27. x 50.

Fig. 33 : Transverse section of a sporangium showing protrusions in the wall. Peel No. 67/99. x 20.

Fig. 34 : Stoma at the top of a protrusion in a sporangium wall. Peel No. 67/125. x 50.

Figs. 35 & 36: The same. x 130.

Fig. 37 : The sporangium shown in Fig. 31, x 50. Peel No. 67/204.



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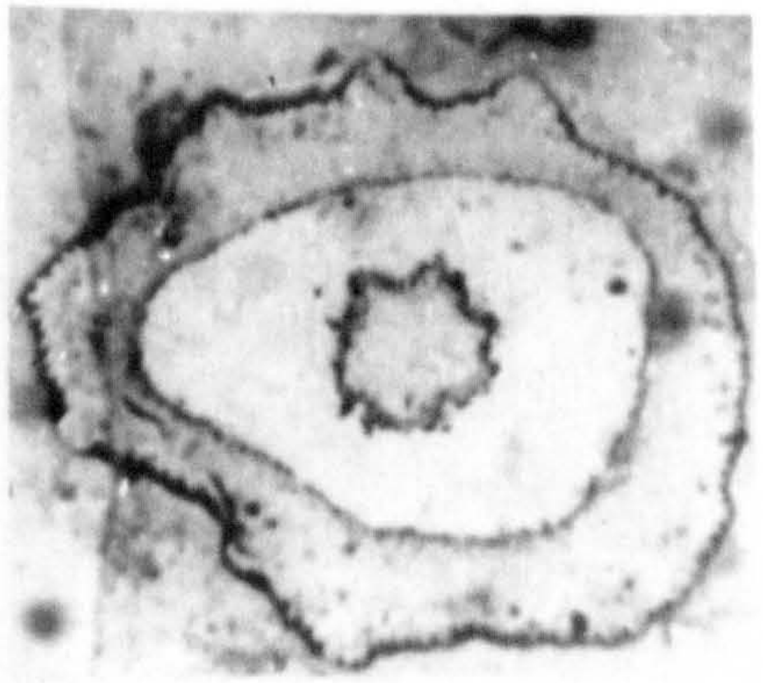

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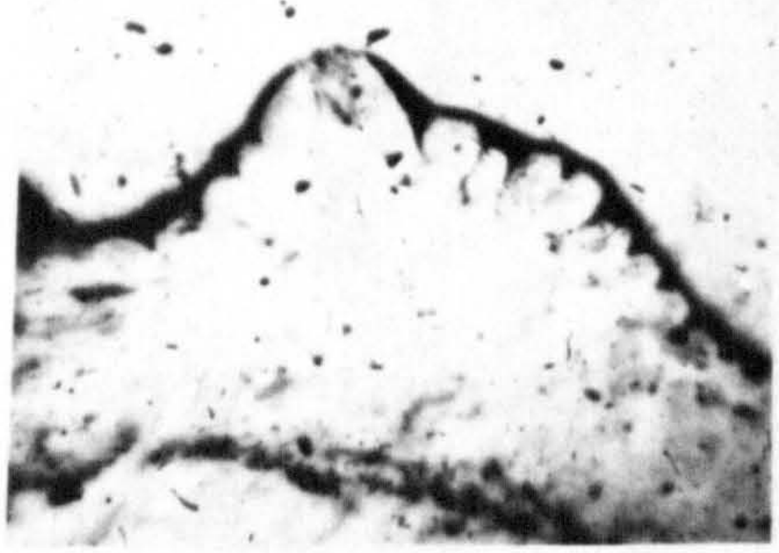

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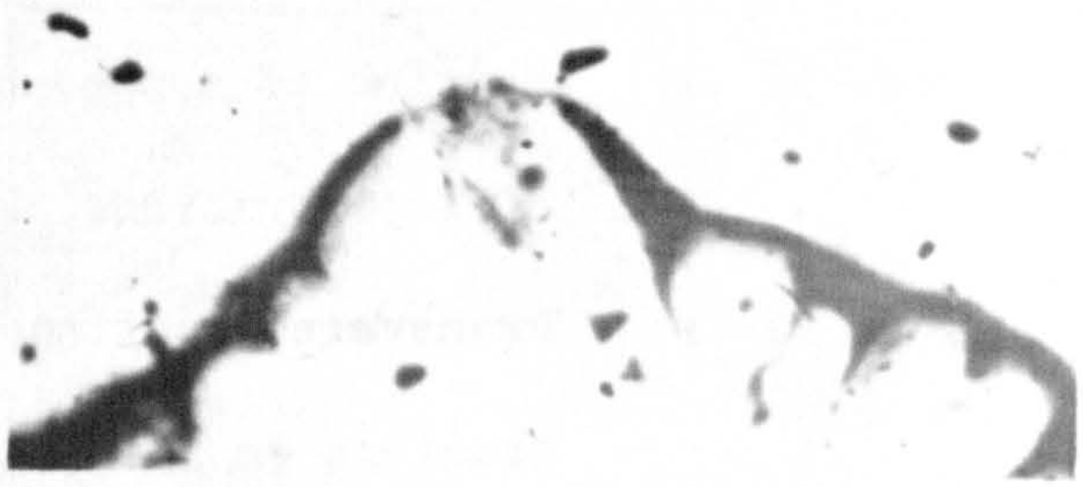

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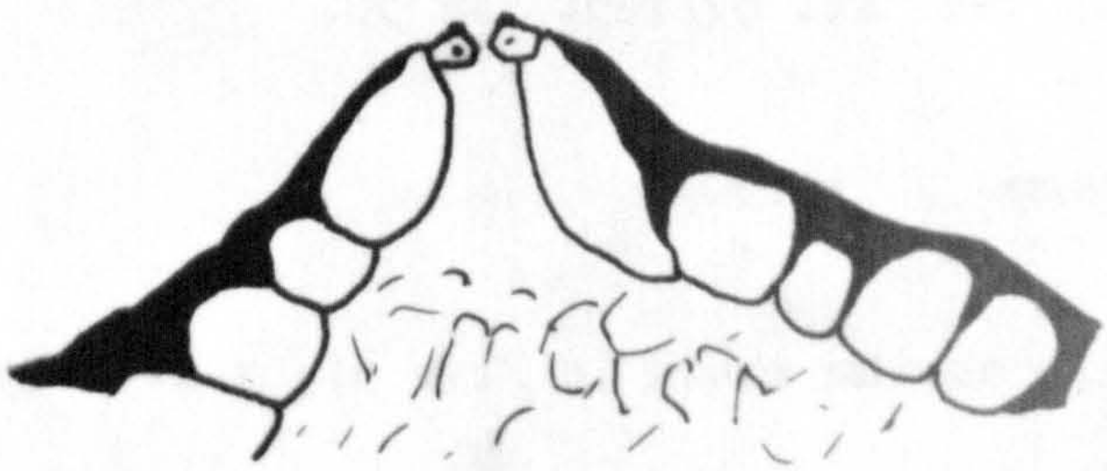

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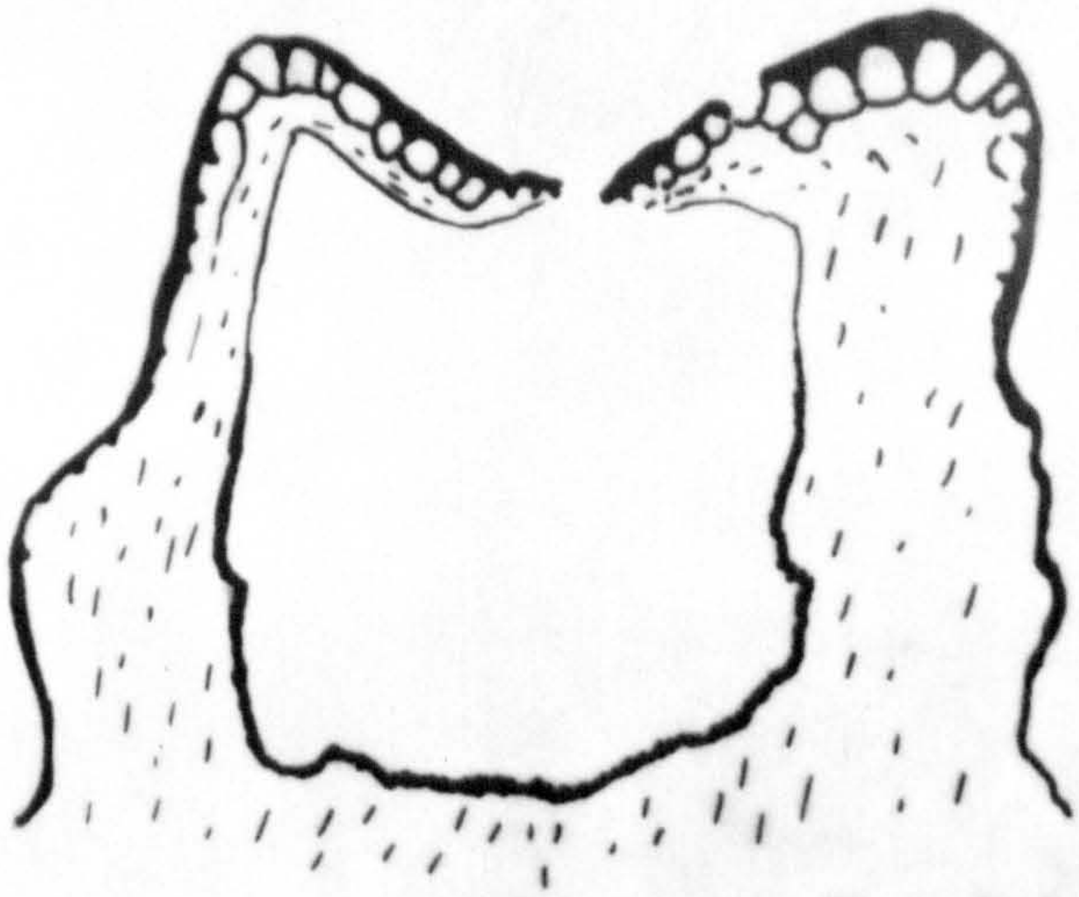

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Part III

ON THE VERTICAL DISTRIBUTION OF PLANTS IN A NEW SECTION OF THE RHYNIE DEPOSIT.

INTRODUCTION

Kidston & Lang (1917, 1921) studied the succession of the plants throughout a vertical section (Trench No.1) of the Rhynie bed. In their work they dealt with the succession of vascular plants (Rhynia, Horneophyton & Asteroxylon) as well as of lower plants (Fungi, Algae, Bacteria & Nematophyton).

Kidston & Lang considered the nature, conditions of accumulation and preservation of the Rhynie deposit in detail and made some speculations. They stated that the construction of Rhynia and Asteroxylon indicates a xerophytic condition. In the case of Horneophyton they stated that the absence of stomata perhaps indicates that this plant grew in shallow waters. Later, however, Zimmermann (1927) discovered stomata in the stems of Horneophyton and in Part II of this Thesis stomata were shown to occur in the sporangial wall as well. These facts suggest that this plant probably did not grow in a markedly different habitat from that of Asteroxylon, Rhynia and Nothia.

In his palaeoecological reevaluation of published evidence on the flora and fauna of the Rhynie chert, Paul Tasch (1957) discussed in detail geological aspects, as well as botanical and zoological ones, and their interrelations. He discussed the evidence and

speculations which Kidston & Lang (1921) put forward about the silicification of the peat, rejecting most of their suggestions. Basing his remarks on work done on living plants, Tasch stated that the xerophytic construction of the Rhynie plants must be rejected as insufficient to elucidate the chemical condition of the pre-peat soil. He discussed the story of the formation of the peat in great detail but that is beyond the scope of the present work which is only concerned with the succession of the vascular plants in a new vertical section of the Rhynie deposit.

Kidston & Lang (1921) also commented on the geology of the area. This, however, was more comprehensively considered in the Report of the British Association Committee (Horne et al., 1916). In this report an account of the geology of the area is given, as well as a summary of the geological work done on the Rhynie area by previous authors. The Report stated that the deposit belongs to the Old Red Sandstone. The map in Fig. 1 of the Committee's Report shows the position of twelve trenches (Nos. 1-12), the geological aspects of which are discussed in the report. The vertical section which Kidston & Lang studied comes from Trench No.1 of the Committee's Report.

The Trench No.1A on the map in Fig. 1 (Page 127) of the present work is roughly in the position of the original Trench No.1 which Kidston & Lang studied. A colour photograph of part of Trench No.1A is shown in Fig. 6 on Plate 2. The same map (Fig. 1) shows

also a second Trench, No.2A (see also Plates 1 and 2, Figs. 3, 4 & 5). This is roughly in the position of the original Trench No.2 mentioned in the Report of the Committee and it is the main subject of the present Part of this Thesis. In this Part the succession of the plants throughout a vertical section of the beds in Trench No.2A has been studied. The study is mainly concerned with the vascular plants (Rhynia, Horneophyton, Asteroxylon & Nothia); their remains, preservation and association. Dispersed spores have also been recorded. Thallophytes have not been included in this work, although it was observed that Fungi were abundant in the plant tissues in most of the sections. In samples lacking macroscopic plant remains showing structure, attempts have been made to study the spore content of the beds, as some indication of contemporary vegetation at the time of deposition.

The plan of ground showing the position of Trenches No.1A & 2A (Fig. 1) and the section showing the sequence of different kinds of strata in Trench No.2A (Fig. 2) were kindly supplied by Dr. A.G. Lyon.

The colour photographs shown on Plates 1 & 2 (Figs. 3-6) were kindly provided by Dr. W.S. Lacey who took them during a visit to the Rhynie locality in the summer of 1964.

In addition to the study of Trench No.2A, the present work includes also a brief account of the succession of the vascular plants in the lower beds (A" - D) at the south end of Trench No.1A (Fig.1). The results obtained from the study of these lower beds generally (but not exactly) confirm those found by Kidston & Lang.

PLAN OF GROUND AT RHYNIE, ABERDEENSHIRE

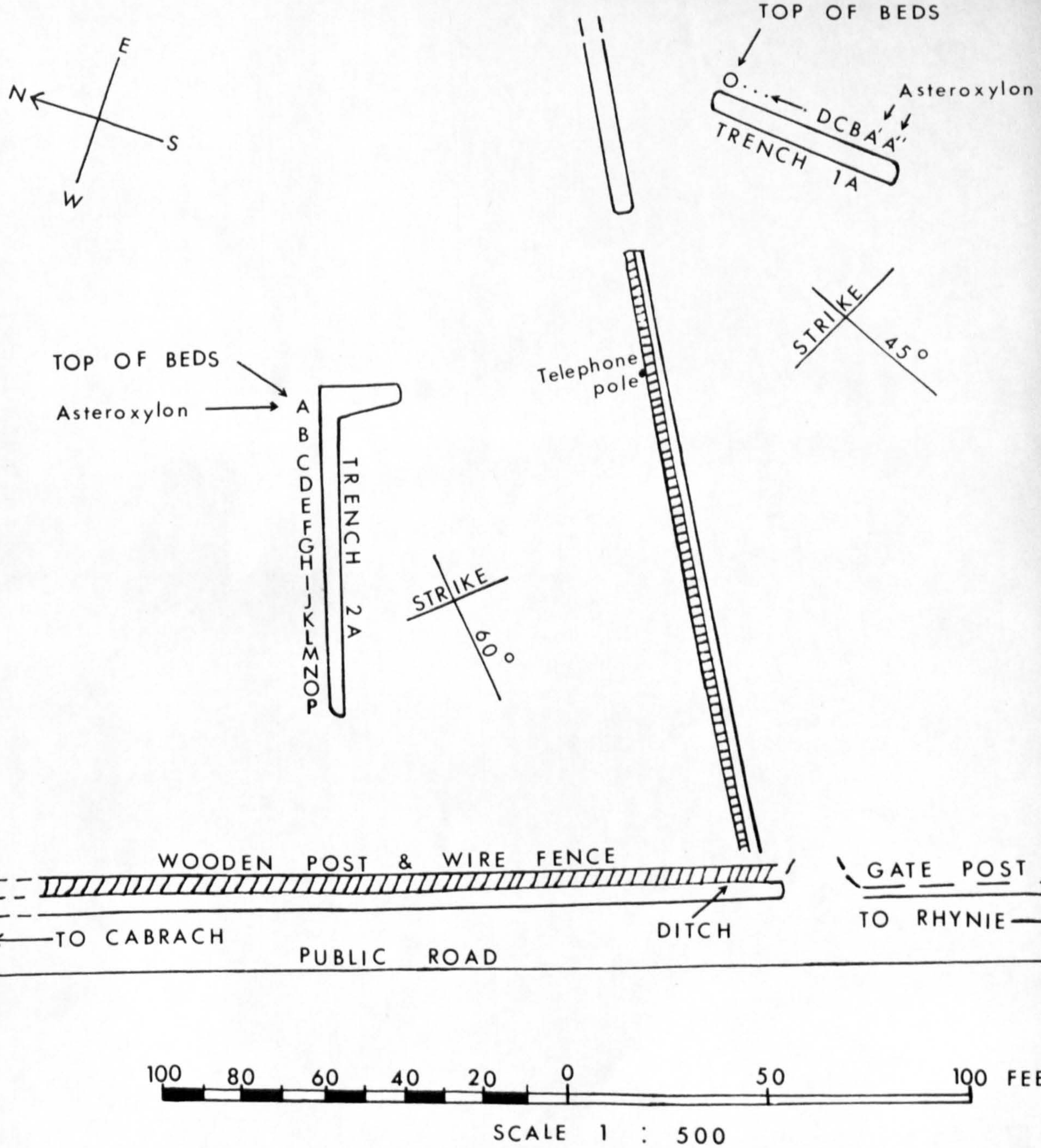

FIG. 1

Fig.2 : Section showing the sequence of different kinds of strata in Trench 2A.

TRENCH 2A

In situ : corrected thickness $14\frac{1}{2}$ ft.

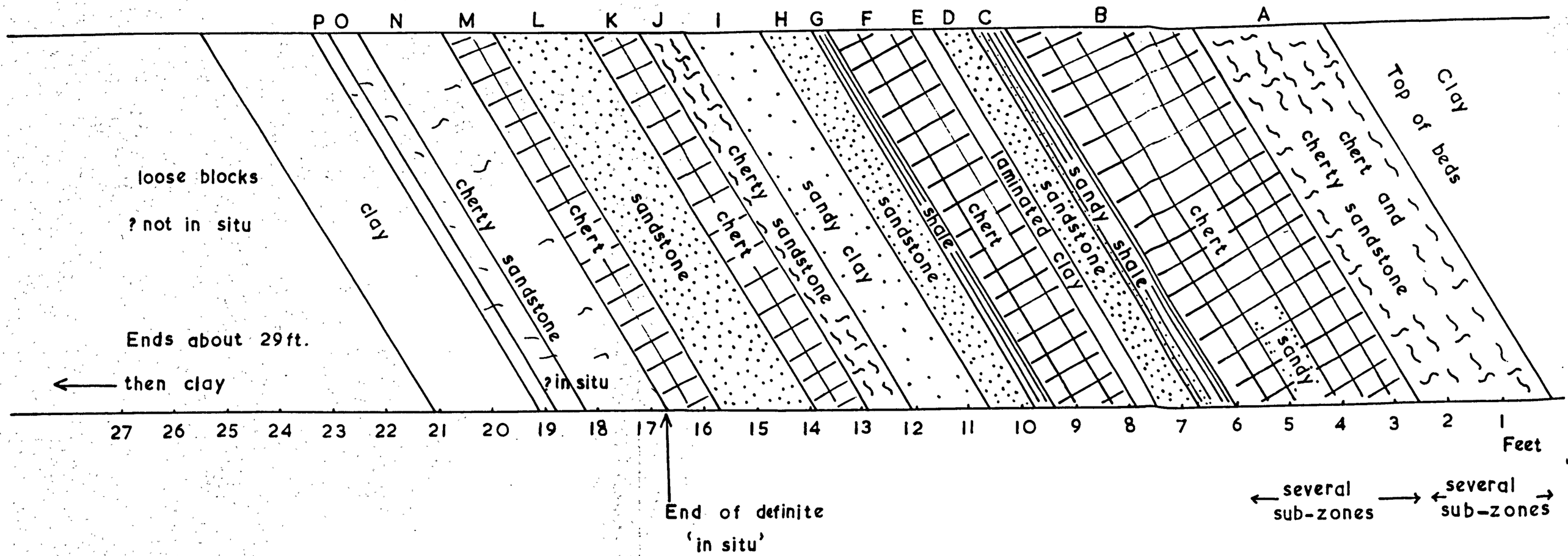

Plate 1

Fig.3 : Rhynie locality. General view: Noth mountain in background, line of Trench No.2A in foreground indicated by excavated material.

Fig.4 :

Trench No.2A.

Bottom of the beds.

Plate 2

Fig.5 :

Trench No.2A.

Top of the beds.

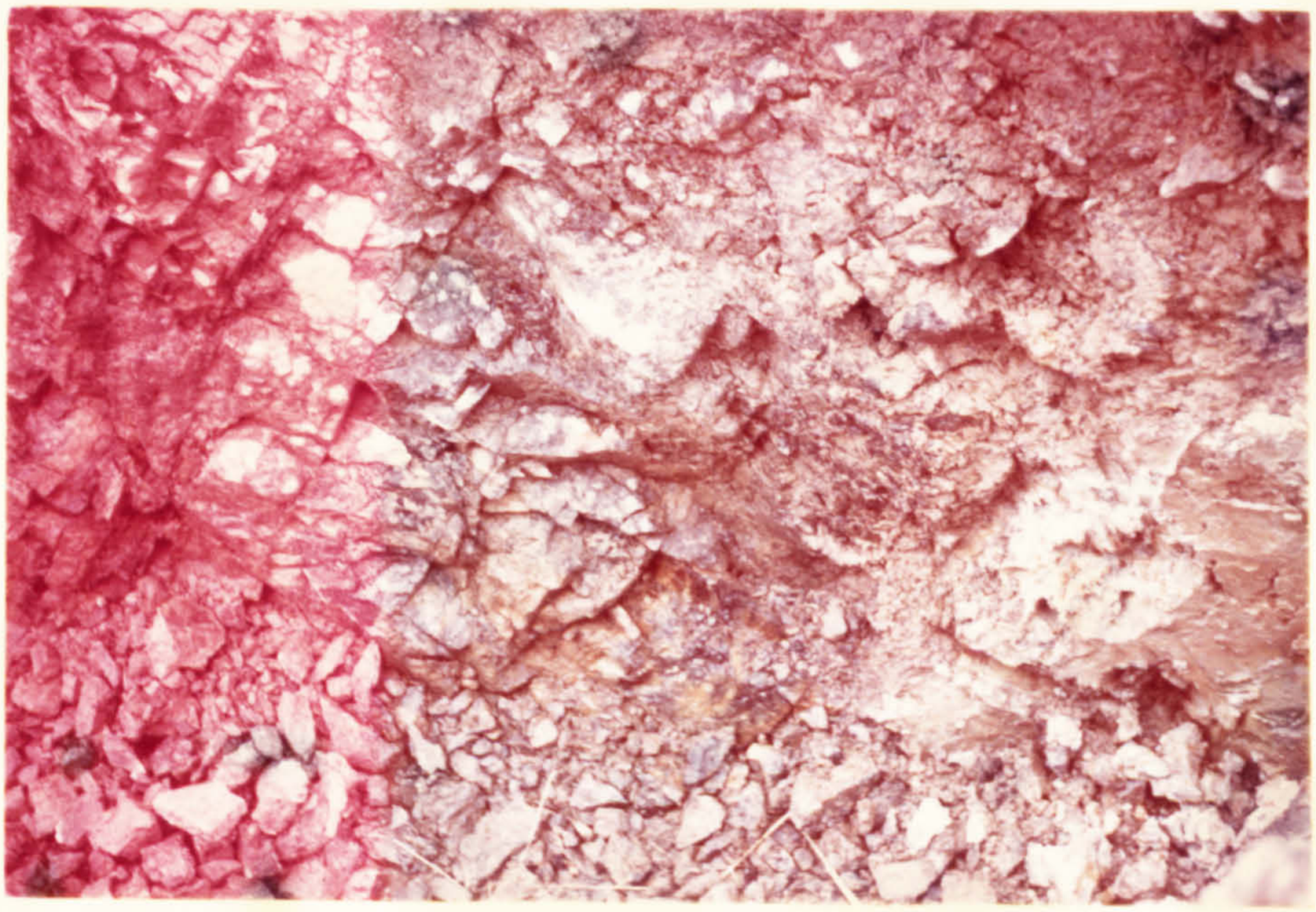

Fig.6 : Trench No.1A. General view of a chert band.

MATERIAL

The material used in the present study was collected by Dr. Lyon who kindly gave it to me for investigation. Both Dr. Lacey and I also visited the locality upon the occasion of the International Botanical Congress (Edinburgh 1964) and collected further samples.

The distribution, location and numbering of the 39 samples which represent a complete vertical section of the beds of Trench No.2A are shown in Table 1 and Fig.2 (see also colour photographs of this trench in Figs. 4 and 5).

Each sample consists of one or a number of blocks of varying sizes. 273 peel-sections were prepared from the blocks of all the samples, except 6 samples which were naturally unsuitable for preparing peels, being formed of clay or of brittle material. A number of slides was prepared from each of these 6 samples specially for spore investigation. The 6 samples are Nos. 1, C16, D17, E18, 036 & 39 (see Table 1).

The preservation of the plant remains depends to a great extent on the type of matrix in which they are imbedded, hence it varies tremendously in different samples or even in different blocks of one sample or furthermore at different points of one and the same block.

Beside the 39 samples of Trench No.2A, the material includes another 8 samples from the lower beds (A"-D) of Trench No.1A. 27 peel-sections were prepared from these samples (see Table 2).

METHODS

The three following methods were used in the investigation of the material:

1. Direct examination of the blocks

By simply moistening the surface of the block with water or etching it with HF acid (by immersing the whole block in the acid for a few minutes, then washing it with water) it was possible to recognize a good deal of the plant remains by naked eye. The blocks of all the samples were examined in this way. Asteroxylon stems and rhizomes, Rhynia stems and sporangia & Nothia axes were usually readily recognizable. Horneophyton remains were not easily recognized by this method, perhaps because its remains are usually ill-preserved. It was easy also to see if the different species were mixed or separated by bedding layers.

The observations obtained in this way were usually confirmed by microscopical examination of peel-sections prepared from the blocks.

2. Preparation of peel-sections

The method used for preparing peel-sections is that already described in the Methods in Part I of this Thesis.

It should be noted that the grinding of the great number of

the extremely hard blocks comprising the material studied in this Part was not done on a glass plate but on a power-driven grinding machine acquired by the Department of Botany at Bangor after the preparatory work for Parts I and II had been completed. This saved a good deal of my time and effort.

Peel-sections were prepared from all or some of the blocks of every sample and in many cases peels were prepared from more than one side of each block. Sometimes as many as five sides of one block were subjected to sectioning. The number of peel-sections prepared from each sample is shown in Table 1 for Trench No.2A and in Table 2 for Trench No.1A.

3. Preparation of slides for spore investigation

This was specially done for only 6 samples which were unsuitable for preparing peel-sections. They are samples No.1, 16, 17, 18, 36 and 39 (see Table 1).

About half a gram of the sample was put in a polythene tube. HF acid (40%) was added and the tube left for a few days in a fume-cupboard. The acid was decanted and the residue washed with distilled water several times until it became acid free. A few drops of each sample was mounted on a thin cover-glass and dried in a clean air, then mounted in Canada balsam on a glass slide. A number of slides was prepared from each sample (see Table 1). The slides were examined microscopically and the spores sizes re-

corded.

Although samples No. 1, 2 and 7 of Trench No.1A were unsuitable for peel preparation, they were not investigated for their spore content since this trench is only briefly considered.

VERTICAL DISTRIBUTION OF PLANTS IN TRENCH No.2A.

The results obtained, that is the plant remains identified in each sample and their degree of preservation, are all given in Table 1. The plants of each sample are arranged according to their relative abundance in the sample; the one mentioned first is the most abundant and the last is the least abundant. This also applies to dispersed spores.

Table 1 shows also the lettering of the beds (from A to P), the thickness of every bed and a brief description of its rock form (as given by Dr. Lyon). The number of samples collected from each bed is shown and, in thick beds, their relative depth is indicated.

The thickness of the section in situ is about 14½ feet, this extends from the top of the beds to bed M where definite in situ material ends. Section 2A stretches along the straight piece only of Trench 2A.

Table 1

Abbreviations:

R.m. = Rhynia major.

R.g-v. = Rhynia gwynne-vaughani.

H. = Horneophyton lignieri.

A. = Asteroxylon mackiei.

N. = Nothia aphylla.

Pres. = Preservation.

P = Poor, M = Moderate, G = Good & V = Very

Table 1

Bed	ft.	ins.		Sample No.	Plant remains	Pres.	No. of peels made
Top			clay	1.	spores 50 & 65 μ	VP	(4 slides)
				2. Extreme top of beds	R.m. & ? H.	P-M	15
A	1	10	chert & cherty sandstone	3. 9-16"	H., A. & R.m.	P-M	12
				4. 17"	H. & A.	P	10
				5. 18-23"	A., H., N. & R.m.	P-G	80
				6. 23½-26"	spores 50&70 μ	VP	10
				7. 29"	R.g-v. & R.m.	G	6
				8. 32"	R.g-v. & R.m.	G	7
			chert with	9. 36"	R.m.	P	5
B	3	2	thin sandy	10. 41"	R.m.	G	4
			layers	11. 48"	R.m.	VG	3
				12. 48-49½"	spores 65-80 μ	VP	6
				13. 50-54"	R.m.	G	8
				14. 58"	R.g-v. & R.m.	M-G	8
				15. B above C	R.m.	G	4
C	-	7	laminated sandy shale with carbonaceous partings	16.	spores 40, 65 & 50 μ	VP	(4 slides)

Table 1 (contd.)

Bed	ft.	ins.		Sample No.	Plant remains	Pres.	No. of peels made
D	-	7½	pale buff micaceous sandstone	17.	spores 40, 65-80 & 50 μ	VP	(3 slides)
E	-	4	laminated carbonaceous clay	18.	spores 40, 50 & 65 μ	VP	(3 slides)
				19. Just below E	R.m.	M-C	5
F	1	4	Bedded solid chert	20. Top	R.m.	M	4
				21. Middle	R.m.	M-VC	3
				22. Base	R.m.	M-C	5
G	-	2	Thin bedded shale	23.	spores 65 μ	VP	3
H	-	9	Micaceous sandstone	24.	spores 40, 50 & 60-70 μ	VP	6
I	1	3	Carbonaceous sandy clay with thin seams of shale	25.	spores 65 & 50 μ	VP	3
J	-	8	Bandy chert/ cherty sand-stone	26. Just below I	spores 50 & 70μ	P	3
				27.	R.m.	P-M	7
K	1	-	Chert	28. Top	R.m.	M-C	4
				29.	R.m.	C	3
				30.	R.m.	M	5

Table 1 (contd.)

Bed	ft.	ins.		Sample No.	Plant remains	Pres.	No. of peels made
L	1	5	Sandstone ?	31.	spores 65&50 μ	VP	4
			cherty	32.	? H.	VP	4
M	1	-	Chert	33. End of definite in situ	R.g-v. & H.	M-C	4
				34. ? in situ	H. & R.m.	M	6
N			Cherty sandstone	35. not in situ	H.	VP-P	18
O			(Clay-like)	36. not in situ	spores 50, 65 & 40 μ	VP	(3 slides)
P			Chert	37. not in situ	R.g-v. & R.m.	M-C	4
				38. not in situ	R.g-v. & R.m.	M-C	4
Base			Clay	39. not in situ	spores 50, 65 & 40 μ	VP	(3 slides)

DESCRIPTION OF THE 39 SAMPLES AND THEIR PLANT REMAINS

1. Clay unsuitable for peel preparation. No plant remains were found but a few decayed and compressed spores about 50 and 65 μ in diameter.

2. Several blocks with moderately preserved plant remains. Direct examination shows an abundance of R.major stems in all the blocks. In one block some small stems were seen which by sectioning proved also to belong to R.major. A rhizome with rhizoids and one decayed sporangium of R.major were spotted. Some stems show necrosis and fungal remains. Spores were found scattered in the matrix and measure about 60-90 μ . A spore mass was found composed of spores each about 65 μ in diameter, most probably of R.major. A few doubtful remains of Horneophyton were seen in the peels.

One decayed Horneophyton-like sporangium was found. This is about 5 mm. long x 3.5 mm. broad and has a slender stalk with an indication of a vascular strand. The space between the apparent columella and the ill-defined wall is filled by a tremendous number of small brown spores each about 15-20 μ in diameter, but no tetrads were seen. Mixed with these spores are tiny black objects each about 10 or 15 μ long and some of them give the impression that they are only carbonized portions of the walls of the brown spores.

3. One large block. Direct examination shows a layer of Asteroxylon stems with clear stellate steles of moderate preservation, the rest of the block being occupied by small stems and an occasional stem of R.major. By sectioning the small stems were found to belong to Horneophyton. Sporangia and spores of the latter are also present in relative abundance. R.major remains are a few stems and one

decayed sporangium. Spores scattered in the matrix are about 50 & 65 μ . Fungal remains are abundant. Horneophyton remains are poorly preserved.

4. One block with ill-preserved plant remains that were difficult to recognize by direct examination. Peel-sections proved the presence of Horneophyton stems and an occasional rhizome and a single Asteroxylon stem. Spores about 50 μ are scattered in the matrix. Fungal remains present.

5. Three blocks; two large ones and a small one. The latter by direct examination shows the presence of many small axes with irregular outlines. Some of them have double steles and are very similar to Nothia. Sectioning did not put this completely out of doubt since the preservation is rather poor. Some Asteroxylon rhizomes were met with and also fungal remains.

The second block has better preserved plant remains than the first. The remains are; several stems and some rhizomes of Asteroxylon, stems, rhizomes with rhizoids, sporangia with spores of Horneophyton and some Nothia axes. Fungal remains present.

In the third block plant preservation ranges between poor and good. Asteroxylon stems and rhizomes are frequent. Many decayed stems, rhizomes and sporangia of Horneophyton are present. Plenty of Nothia axes but no sporangia were found though a large number of

peels was made. A few stems and one sporangium of R.major were seen. Spores scattered and in masses 50 & 60 μ . Fungi present.

6. Several small blocks. Peel-sections showed much changed plant remains and many scattered and decayed spores about 50 & 70 μ .

7. One block with well-preserved plant remains. Direct examination shows pure growth of R.gwynne-vaughani stems on all sides of the block except one side where it is mixed with a few stems of R.major. More details seen in the peels are, necrosis in some Rhynia stems, the hemispherical bulges of R.gwynne-vaughani and fungal remains.

8. Two blocks with well-preserved Rhynia stems. Direct examination of the larger block shows that R.gwynne-vaughani stems occupy its half and the other half is occupied by R.major stems, with thin dark interrupted bedding layers in between. Peels add the presence of Fungi, necrosis and spores of about 50 & 70 μ diameters, in masses and scattered.

9. Two blocks with ill-preserved R.major stems. Spores in the matrix are much decayed and carbonized and about 65 μ in diameter. Fungal remains unfrequent.

10. Two blocks with well-preserved R.major stems. A few decayed

spores about 65 μ in diameter probably of R.major. Fungi present.

11. One block with pure growth of beautifully-preserved R.major stems. Spore mass in matrix each about 65 μ . Fungi present.

12. Four blocks with much altered plant remains. The scattered spores measure about 65-80 μ in diameter.

13. Five small blocks; all contain well-preserved R.major stems. Sporangia and rhizomes of the same species are occasionally met with. Necrosis and Fungi present.

14. Two blocks with well-preserved stems of both R.gwynne-vaughani and R.major, the former being more abundant. Fungi and necrosis seen.

15. Direct examination of the single large block of this sample shows R.major stems all over the sides of the block except at one small corner where some small stems were seen. These by sectioning proved to be also Rhynia but it was not possible to tell which species. Sections showed one empty sporangium of R.major, necrosis in some of its stems, and fungal remains. Spores were found in masses and scattered in the matrix and measure about 70 or 80 μ in diameter.

16. Laminated sandy shale, unsuitable for peel preparation. Spores

are present in large numbers but are decayed and disintegrated and measure about 40, 65 & 50 μ in diameter.

17. Micaceous sandstone unsuitable for preparing peels. Spores measure about 40, 65–80 & 50 μ in diameter.

18. Laminated carbonaceous clay unsuitable for preparing peel-sections. Spores measure about 40, 50 & 65 μ in diameter.

19. Five small blocks all containing fairly well-preserved R.major stems. A few R.major sporangia were found. Free spores measure about 50 μ & 65 μ in diameter. Necrosis and Fungi present.

20. One block containing moderately preserved R.major stems. Necrosis and Fungi not frequent.

21. Many small blocks. All contain R.major stems. Preservation ranges between moderate and very good. A single empty sporangium of R.major was spotted. Scattered spores measure about 65–75 μ in diameter. Fungi present.

22. Five blocks; all contain fairly well-preserved R.major stems. A mass of spores each about 65 μ in diameter perhaps of R.major. Necrosis and fungal remains present.

23. Brittle shale hardly suitable for peel preparation. Unrecognized plant remains, spores decayed and measure about 65 μ each.

24. Several blocks containing a large number of ill-preserved spores measuring about 40, 50 & 60–70 μ . No other plant remains were recognized.

25. The several blocks of this sample contain a large number of spores about 65 & 50 μ each. Preservation is very poor.

26. Plant remains are almost absent in the single block of this sample. Only a few spores were found, some measure about 50 μ and others about 70 μ .

27. The four blocks of this sample contain R.major stems. Preservation poor to moderate. Other plant remains are a mass of spores about 50 μ each and scattered spores measuring about 70–80 μ in diameter and fungal remains.

28. Two blocks containing fairly well-preserved R.major stems and some scattered spores measuring about 40, 50 & 70 μ in diameter. Necrosis and Fungi present.

29. The four blocks of this sample show a pure growth of well-preserved R.major stems. A few R.major sporangia and some scattered

spores were found in the matrix. Fungal remains visible by naked eye inside Rhynia stems.

30. Four blocks containing moderately-preserved R.major stems and an occasional sporangium of the same species. Spores in matrix measure about 65-70 μ in diameter. Fungi present.

31. One block with carbonized plant remains. Scattered spores measure about 65 μ & 50 μ .

32. Several blocks containing very poorly-preserved stems, probably of Horneophyton and some scattered spores about 55-60 μ each.

33. Several blocks with fairly well-preserved plant remains. R.gwynne-vaughani stems are present in most of the blocks. In one block some stems, rhizomes with rhizoids and sporangia of Horneophyton were found. Spores in the matrix measure about 40 & 50 μ in diameter. Necrosis and Fungi present.

34. Four small blocks with moderately-preserved plant remains. Horneophyton stems, sporangia and spores are present in abundance. R.major stems in smaller numbers. Fungi present.

35. Two blocks with well-preserved Horneophyton stems, sporangia and spores. Scattered spores measure about 40 & 65–80 μ . Little fungal remains present.

36. The material of this sample was unsuitable for preparing peels. Slides show a large number of decayed spores about 50, 65 & 40 μ in diameter.

37. One block with fairly well-preserved stems of both Rhynia species. There are two or three layers of R.gwynne-vaughani stems and one layer of R.major stems separated by thin bedding layers of dark colour. Scattered spores measure about 50 μ & 90 μ in diameter. Necrosis and Fungi present.

38. The several blocks of this sample are exactly the same as the previous sample in all respects.

39. Clay unsuitable for peel preparation. Slides show plenty of decayed spores about 50, 65 & 40 μ in diameter.

COMPARISON WITH KIDSTON'S & LANG'S VERTICAL SECTION IN TRENCH No.1

The difference in the total thickness of the beds exposed in the two trenches is great. The beds in Trench No.1 are only about 8 feet thick while those in Trench No.2A are about 14½ feet thick. This allows only for general comparison since with such a big difference in thickness it would be rather difficult to tell which beds, if any, in the two trenches exactly correspond.

Regarding plant remains, the two trenches agree in that R.major stems occur in almost all the plant-containing beds and in the beds where it is associated with other species it is usually dominated by them.

Horneophyton remains occur in the lower and upper beds ih the two trenches.

The difference between the two trenches, regarding plants, is mainly connected with the distribution of the remains of Asteroxylon and R.gwynne-vaughani.

In Trench No.1 Asteroxylon and R.gwynne-vaughani remains were found only in the lowermost beds exposed. This had been found by Kidston & Lang (1921) and is also confirmed by me (see Table 2) since I have examined a number of samples from the lower beds of Trench No.1A which is roughly in the position of Kidston's & Lang's original Trench No.1.

In Trench No.2A, Asteroxylon remains occur only in the uppermost

beds (A3, A4 & A5 in Table 1, page 135), a result which contrasts with that gained from the study of Trench No.1 or No.1A. In Trench No.2A R.gwynne-vaughani occurs in the lowermost beds (M33, P37 & P38) as in Trench No.1 but in addition R.gwynne-vaughani was found in some of the upper beds (B7, B8 & B14) of Trench No.2A (see Table 1).

One word remains to be said about the vertical distribution of plant remains in the lower beds (A", A' & B) of the two Trenches No.1 and No.1A. This is best shown in Table 2, which also includes the numbering of the samples of Trench No.1A and the number of peels made from each sample.

Table 2.

Abbreviations as in Table 1.

Bed	Trench No.1 (K & L) Plant remains	Trench No.1A (present work)		
		Plant remains	Sample No.	No. of peels made
D	Poorly-preserved R.m.	Poorly-preserved R.m.? Spores about 65-80 μ .	8	4
C	-	-	7	-
B	H., A. & R.m.	H. & R.m.	5 & 6	17
A'	-	A.& R.g-v.	4	3
A"	R.g-v., R.m., A. & H.	A. & R.g-v.	3	3
Clay below A"	-	-	2	-
Under clay	-	-	1	-

DISCUSSION AND CONCLUSION

Although Trench No.1A is supposed to be more or less in the same position of the original Trench No.1, yet there is some difference in the vertical distribution of plants. This suggests that the present samples must have come at somewhat different horizontal points from those studied by Kidston & Lang. This very probably indicates that at different points along one horizontal level of any one bed there could be an appreciable variation in the plant remains. Kidston & Lang (1921) also found that the succession of plants in blocks that come from the same level (and at no great distance) varies to some extent. It follows that the succession of plants in a vertical section of a trench (like that studied originally by Kidston & Lang and in the present thesis) is in reality too narrow a study. In order to have a far better idea about the vertical succession of plants in a trench, the vertical study should be accompanied by a wide horizontal study of every bed.

The differences between Trench No.1 and Trench No.2A in the distribution of the plants could be explained in the same way as mentioned above for the differences between Trench No.1 and Trench No.1A. That is, the vertical studies of plant distribution should also be accompanied by horizontal studies if one is to get more precise information about this Devonian landscape.

However, the presence of all the species in the lowermost beds of Trench No.1 and in the upper beds of Trench No.2A might mean that the latter beds are a natural extension of the former beds. What is more plausible is that they are distinct beds with similar vegetation, but the vegetation of each of them did not extend horizontally for a sufficient distance to make it appear in the other trench.

One could say also that since all the vascular species occur together in one or two beds, they or some of them, could be expected to occur together in some other beds of the deposit, if the examination of the beds was horizontally extended. This is supported to some extent by the results of the lower beds (A", A' & B) of Trenches No.1 and No.1A, by the presence of all spore types in several beds of Trench No.2A and by the presence of R.gwynne-vaughani in association with R.major in several samples of Trench 2A. This association between the two species of the genus Rhynia recalls Pant's (1960) suggestion that the axes of R.gwynne-vaughani are more likely to be gametophytic and that their hemispherical projections and adventitious branches possibly represent young sporophytes developing on these gametophytes.

The sole existence of R.major in the middle beds of the deposit in the two Trenches No.1 and No.2A might be changed or confirmed if horizontal studies were available. For example Kidston & Lang (1921) and also Tasch (1957) explained the arrest of the growth of R.gwynne-vaughani above the lowermost portion of bed A" in Trench

No.1 by the prevalence of new unfavourable conditions. But in the present investigation R.gwynne-vaughani was found in bed A' of Trench No.1A and at different levels of an upper bed (B) of Trench No.2A. This does not agree with their explanation or at least indicates that conditions were favourable for the growth of R.gwynne-vaughani at different levels of the deposit, i.e. favourable conditions were recurrent.

Nothia axes were found in sample No.5 only (see Table 1) and, although 80 sections were prepared, no Nothia sporangia were met with. It is worth mentioning that the degree of preservation of the Nothia axes in the blocks of this sample is quite different from and not as good as that of the Nothia remains found in the 10 blocks described in Part I of this Thesis. The former blocks are of cherty sandstone while the latter are of pure chert. This indicates that Nothia should occur at other points in the deposit in addition to the one from which sample No.5 comes. In fact, it has not yet been located in situ elsewhere.

The apparently complete absence of Nothia aphylla in the vertical section of Trench No.1 and of its sporangia in Trench No.2A and of the sporangia of Asteroxylon mackiei in the two vertical sections of Trenches No.1 and No.2A, although these mentioned plant remains were found in several loose blocks at the Rhynie area, indicates the insufficiency of the narrow vertical studies in showing the distribution of the plants and the importance of a horizontal study of the

different beds in the trenches. The same could also be said about the failure so far to find in the two trenches the sixth (as yet undescribed) vascular plant which has been recently discovered by Dr. Lyon in material collected from the Rhynie locality.

The samples which were unsuitable for preparing peel-sections were also very poor in plant remains. Even the cuticularized spores were mostly ill-preserved and broken. However, they all have smooth and thin walls and are thus characteristic of a Lower rather than of a Middle Devonian flora. Leclercq (1954) stated that Thomson (1952) has pointed out the sharp difference existing in the spore flora of the Lower and Middle Devonian rocks and that this is in conformity with the distinctive flora of these two geological horizons. Lower Devonian spores are simple, smooth, thin-walled, circular or elliptical, with or without triradiate markings. On the contrary, Middle Devonian spores might be with a dotted appearance, with short, long or hooked projections, or with a wing differently developed.

According to the sizes of the examined spores they could be referred to the vascular plants known to occur in the Rhynie deposit. The spores which are about 40 μ in diameter apparently belong to R.gwynne-vaughani and those measuring about 50 μ in diameter belong to Horneophyton and Asteroxylon. The spores which measure about 65 μ in diameter most probably belong to R.major and Nothia aphylla. Regarding the spores which were found to measure about 60, 70 or

80 μ in diameter or those described to range between 65 & 80 μ or 60 & 90 μ in diameter, it is possible that all or most of them also belong to the known Rhynie plants; however, the possibility that some or all of them belong to other unknown plants should not be excluded. It is due to the poor preservation of most of the spores and the fact that they lack clear distinguishing features that it was not possible to refer them with certainty to their parent plants.

However, no other markedly different types of spores were observed. For example, no elaborately ornamented spores or large megaspores were found; not even the large spores (150 μ) recently described by Lemoigne (1966). This negative evidence is not without some value, however, for it does suggest that the Rhynie area at the time of deposition of the peat beds supported a very sparse vegetation, limited to perhaps six taxa of vascular plants growing in temporary shallow pools, repeatedly appearing and disappearing, scattered over an otherwise barren landscape.

SUMMARY

The Rhynie Chert Deposit is situated about a quarter to half a mile to the west of the village of the Muir of Rhynie, Aberdeenshire, Scotland, United Kingdom. The fossil flora of this deposit has been the aim of the present study. The investigation of the collected material was mainly by the microscopic examination of the peel-sections prepared from the blocks.

The work was divided into three main parts:-

PART I

This Part dealt with the fertile region of *Nothia aphylla*, which is the only known region of the plant. 10 blocks of the collected material contained an enormous number of the petrified axes and sporangia of *Nothia*. More than 2200 peels were prepared from all the blocks. The microscopic examination of these peels and the reconstructions based on them gave the following new information:-

1. The sporangia are borne laterally and terminally on the axes and their branches.

2. The arrangement of the sporangia on the axes is extremely irregular, ranging from spiral to semi-verticillate. The number of terminal sporangia ranges from two to five, arranged in a circle around a central space.

3. The sporangia are more or less reniform in shape and

dehisced by an extended marginal slit.

4. Stomata are present in the epidermis of the stalk and sporangial wall.

5. Nothia sporangia are most similar to those of the genus Zosterophyllum; hence it is suggested that Nothia is to be included with Zosterophyllum in the family Zosterophyllaceae.

6. Many other details were discovered concerning the branching of the axes, xylem morphology of the axes and of the sporangial traces, the size of the sporangium and the structure of its wall.

7. In the peels of one block, two new Horneophyton fructifications were found, the study of which formed the basis of the second Part of the Thesis.

PART II

1. The two new fructifications are quite large in size. In one of them the columella has 4 lobes and in the other it has 5 lobes.

2. There is an opening or a break in the sporangial wall at the centre of the concave tops of each of the four sub-divisions of the first fructification and of the five sub-divisions of the second one, which is very suggestive of a dehiscence position.

3. Stomata were found to be present at the tips of protrusions in the sporangial wall.

PART III

1. The vertical succession of plants in a new section (Trench No.2A) of the Rhynie deposit has been obtained as the result of microscopic examination of 273 peel-sections and 20 slides prepared from 39 samples which represent a complete vertical section of all the beds of the trench.

2. A similar, but more brief, investigation was made of the lower beds of a second new Trench No.1A. The material consisted of only 8 samples. 27 peels were prepared from only 5 samples since the three remaining samples were not suitable for peel preparation.

3. For the first time Nothia axes have been located in situ at a certain level of one of the beds (A5) of Trench No.2A.

4. The results obtained from the study of the two new Trenches are compared with those previously obtained by Kidston & Lang (1917, 1921) from their study of the original Trench No.1 in the Rhynie deposit.

5. The similarities and differences between the succession of plants in the two trenches are discussed.

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موضوع البحث

دراسات عن النباتات المتحجرة فى منطقة رابنى Rhynie باسكتلاند Scotland

ملخص

يشتمل هذا البحث على دراسة نباتات حفرية عمرها حوالى ٤٠٠ مليون سنة . وتوجد الصخور التى تحتوى على هذه النباتات فى منطقة قريبة من قرية رابنى Rhynie فى إسكتلندة . وقد أمكن دراسة هذه النباتات المتحجرة والتى تحتفظ بكثير من شكلها الظاهرى وتركيبها الخلوى بواسطة عمل قطاعات رقيقة فى قطع الحجارة التى تحتوى على هذه النباتات وذلك بالطريقة التى وصفها Joy, Willis & Lacey (1956) سنة ١٩٥٦ . ولقد تم عمل ما يزيد عن ٢٥٠٠ قطاع بهذه الطريقة وفحصت بالميكروسكوب .

وينقسم هذا البحث إلى ثلاثة أجزاء رئيسية وهى :—

الجزء الأول :

ويتعلق بدراسة الشكل الظاهرى والتركيب التشريحى للحوافظ الجرثومية للنبات الحفرى "نوثيا أفيلا" *Nothia aphylla* وكيفية ترتيب هذه الحوافظ على الفروع وكذلك دراسة الشكل الظاهرى والتركيب التشريحى للفروع . ثم إقتراح بوضع هذا النبات فى إحدى عائلات النباتات الحفرية المنقرضة وهى العائلة Zosterophyllaceae .

الجزء الثانى :

ويتعلق بدراسة الشكل الظاهرى والتركيب التشريحى للحوافظ الجرثومية المتفرعة للنبات الحفرى المنقرض "هورنيوفيتن لينييرى" *Horneophyton lignieri* .

الجزء الثالث :

هذا الجزء عبارة عن دراسة التعاقب الرأسى للنباتات الزيدية المتحجرة المنقرضة وهى :

1. *Rhynia gwynne-vaughani*.
2. *Rhynia major*.
3. *Horneophyton lignieri*.
4. *Asteroxylon mackiei*.
5. *Nothia aphylla*.

وذلك فى قطاع أرضى جديد بمنطقة رابنى ومقارنته بالنتائج التى حصل عليها باحثان آخران هما Kidston & Lang من دراستهما التى قاما بها فى سنة ١٩٢١ لقطاع آخر فى نفس المنطقة .

دراسات عن النباتات المتحجرة فى منطقة راينى Rhynie

باسكتلندة Scotland

رسالة مقدمة إلى جامعة ويلز

من

وجيه السيد السعداوى

بكالوريوس فى العلوم مع مرتبة الشرف ١٩٥٦

ماجستير فى العلوم- القاهرة- ١٩٦٠

للحصول على

درجة دكتوراه الفلسفة فى العلوم

قسم النبات- كلية العلوم- بانجور - ويلز

يونيو ١٩٦٦

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THE EFFECTS OF 2,4-DICHLOROPHENOXYACETIC ACID ON THE ABSORPTION AND ASSIMILATION OF POTASSIUM NITRATE BY RADISH ROOT SLICES

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SUMMARY

Root slices supplied with potassium nitrate absorbed a good deal of their nitrate-N which mainly accumulated in the tissues, only a small portion being assimilated into peptides (rest-N) and proteins. Feeding with 2,4-D alone induced rapid assimilation of the initial nitrate-N into peptides (rest-N) and proteins. Root slices 'supplied with mixtures of nitrate and 2,4-D assimilated some of the inorganic-N into peptides (rest-N) and induced the formation of nitrite-N in the media. It is possible that 2,4-D when supplied with nitrate had activated an enzyme system at the cytoplasmic surface of radish root slices capable of reducing nitrate to nitrite.

Introduction

In a previous work (Said and Youssef 1955), the influence of 2,4-D on the respiration and nitrogen metabolism, as well as the effects of the auxin on the absorption and assimilation of organic nitrogen compounds have been clarified. To have a rather complete picture about the subject, the present work was planned to elucidate the effects of 2,4-D on the absorption and assimilation of inorganic nitrogen, namely potassium nitrate, by radish root slices.

Material and Methods

The experimental material used in this investigation was the root of *Raphanus sativus* var. *Aegyptiacus*. The preparation of the slices was carried out according to the procedure referred to by Said and Youssef (1955). Fourteen samples of fifteen grams each were prepared, kept in aerated running tap water for two days and washed several times with sterilized distilled water. Two samples were used for the determination

of the initial nitrogen content. The remaining samples were transferred to air-tight plant chambers each containing 400 ml of sterilized water or culture solution according to the following scheme:

No. of sample	Feeding medium (400 mls)
2	Distilled water.
2	0.050% 2,4-D (sodium salt)
2	0.007% KNO_3-N
2	0.014% KNO_3-N
2	0.007% KNO_3-N + 0.05% 2, 4-D
2	0.014% KNO_3-N + 0.05% 2, 4-D

Immediately after introducing the samples in their respective media, the latters were sampled and strong current of CO_2- free air was then bubbled through the experimental solution at a constant rate of four litres per chamber per hour. The plant chambers were kept at 25°C for a period of 48 hours during which the CO_2-output by the tissue slices as well as the nitrogen content of the various media were estimated at 24-hour-intervals. At the end of the experimental period, the samples were extracted and analysed for their contents of the various nitrogen fractions.

The methods used for the estimation of CO_2-output by the tissue samples and for the nitrogen analysis of the culture media and tissues were those referred to by Said and El-Shishiny (1944, 1947). Reduced iron was used with the tissue extracts and the media, to include nitrate and nitrite in the total soluble - nitrogen estimations as outlined by Pucher et al (1930). Nitrite-N was determined colorimetrically through the reaction with sulphanilic acid and α-naphthylamine to form a red azo dye (cf. Paech and Tracey 1956). Standard curve was constructed using sodium nitrite solutions. The"rest-N" fraction was determined by subtracting the sum of all the other soluble-nitrogen fractions from the total soluble-nitrogen. The results obtained from the duplicate samples were remarkably close and so only the mean values shall be discussed.

Experimental results
Analysis of the media

Table 1, shows the amounts of inorganic-N taken up by the root slices from the various culture media.

(TABLE 1)

Amounts of inorganic nitrogen absorbed by the radish root slices.
(Expressed as mg. N per 100 gm. original fresh weight of slices)

Culture-medium	Inorganic-N uptake in		
	1st 24 hours	2nd 24 hours	48 hours
0.007% KNO_3-N	63.40	12 3	75.7
0.014% KNO_3-N	78.40	4 2	82.6
0.007% KNO_3-N + 2, 4-D	0.00	23.0*	23.0
0.014% KNO_3-N + 2,4-D	0.00	31.6*	31.6

* These media revealed the presence of some nitrite-N, therefore these values represent the amount of inorganic-N absorbed, which may be nitrate-N, nitrite-N or mixture of both.

It is clear from this table that when radish root slices were fed with potassium nitrate alone, the rates of inorganic-N uptake were much higher in the first than in the second 24 hours of the experiment. Doubling the concentration of potassium nitrate in the media increased, but slightly the total inorganic-N uptake by the root slices; the increase was more pronounced after the first 24 hours of the experiment.

Addition of 2,4-D to the media containing potassium nitrate, strongly decreased the total uptake of inorganic-N. The uptake was somewhat higher from the media containing the high nitrate concentration than from media containing the low nitrate concentration. All the inorganic-N

absorption from the 2,4-D media took place in the second 24 hours of the experiment.

Analysis of the various media revealed the presence of some rest-N in all 2,4-D-containing media, the average values of which are recorded in table II.

(TABLE II)

Rest-N recovered in the culture media of radish root slices. (Expressed as mgm. N per 100 gm. original fresh weight)

Culture-medium	Amounts of rest-N recovered in		
	1st 24 hours	2nd 24 hours	48 hours
0.05% 2,4-D	3.58	13.83	17.41
0.007% KNO_3-N + 2,4-D	4.50	52.45	56.95
0.014% KNO_3-N + 2, 4-D	9.32	53.45	63.77

As shown in table II, most of the rest-N was found in the second 24 hours of the experiment. The presence of nitrate with 2,4-D stimulated the production of rest-N in the external media. Such production was slightly enhanced as the initial concentration of nitrate was doubled in the media.

Media containing nitrate with 2, 4-D showed, not only the presence of rest-N, but also the presence of small amounts of ammonia-N and considerable amounts of nitrite-N (Table III).

(TABLE III)

Nitrite-N and ammonia-N recovered in the culture media of radish root slices. (Expressed as mgm. N per 100 gm. original fresh weight)

Culture-medium	1st 24 hours		2nd 24 hours		48 hours	
	Ammonia -N	Nitrite -N	Ammonia -N	Nitrite -N	Ammonia -N	Nitrite -N
0.007% KNO_3-N+2, 4-D ..	1.78	—	2.30	67.89	4.08	67.89
0.014% KNO_3-N+2, 4-D ..	2.65	—	3.81	67.62	6.46	67.62

Ammonia-N was detected in the first and in the second 24 hours of the experiment, while the nitrite-N was produced in the second 24 hours only. While doublirg the concentration of nitrate in the media slightly stimulated the production of ammonia-N, it proved of no effect on the production of nitrite-N.

Analysis of the Tissues

Table IV shows the amounts of various nitrogen fractions of the initial as well as the differently treated radish root samples.

Behaviour of total soluble- and protein-N:

As shown in table IV, samples that were starved in distilled water for 48 hours, showed no change in their total soluble-, and protein-N contents.

Feeding with 2,4-D alone induced a great loss in the total soluble-N, the loss being partly built up into protein-N and partly excreted into the culture media.

Samples that were suspended in potassium nitrate media absorbed a good deal of the nitrate-N from their media (table I) and this caused increase in their total soluble-N and protein-N contents. The increase in the total soluble-N was much higher than the increase in the protein-N. Both fractions were slightly increased through doubling the concentration of nitrate in the external medium.

Feeding with mixtures of nitrate and 2,4-D induced maximum losses of total soluble-N and almost no change in protein-N contents. Such samples excreted considerable amounts of rest-N in their media.

It is necessary to mention here that all nitrate-N supplied to the slices could be accounted for by the analyses of the tissue and the medium, thus indicating no loss of nitrogen during the experimental period.

Behaviour of soluble - nitrogen fractions:

Nitrate- and rest-N:

Samples starved in distilled water showed no change in their nitrate and rest-N contents.

Feeding with 2,4-D alone induced rapid assimilation of the nitrate-N contents of the tissues into rest -N which, together with the rest-N initially present was partly built up into protein and partly accumulated in the tissue-medium systems.

(TABLE IV)

Analysis of the initial as well as the differently treated radish root slices for their contents of the different nitrogen fractions.

(Calculated as mg. N per 100 gm. original fresh weight)

Culture-medium	Ammonia-N	Amide-N	Amino-N	Nitrate-N	Rest-N	Total-soluble N	Protein-N	Total-N
Initials.	1.56	3.98	3.53	39.18	17.50	65 75	55.61	121.36
Distilled water	1.51	3.30	3.45	38.97	18.17	65.40	55.87	121.27
0.050% 2, 4-D	1.58	2.80	3.55	24.03	7.11	39.07	63 37	102.44
0.007% KNO_3-N	1.56	3.30	3.55	101.33	20 01	129.75	65.84	195.59
0.014% KNO_3-N	1.51	3.54	3 55	102.46	22 61	133.67	68.77	202.44
0.007% KNO_3-N + 2, 4-D	0.00	3.76	3.58	10.49	8 20	26.03	55 20	81.23
0.014% KNO_3-N + 2, 4-D	0.00	2.78	3.56	10.44	9 19	25.97	54 50	80.47

Samples suspended in potassium nitrate alone accumulated a good deal of the absorbed nitrate-N in their tissues, a portion of this nitrogen being assimilated into rest- and protein-N, particularly the latter. Doubling the concentration of nitrate in the media induced slight stimulation in nitrate-N assimilation and slight increase in protein-N formation.

Addition of 2,4-D to the nitrate media induced the formation of some nitrite-N in these media. In the meantime the root slices suspended in such media absorbed some inorganic-N from their media (cf. table 1). This inorganic-N may be nitrate-N, nitrite-N or a mixture of both. The absorbed inorganic-N together with some of the nitrate-N initially present in the tissue were converted into rest-N which together with some of the initial rest-N were excreted into the media.

The failure to detect any nitrite-N in these tissues, may suggest that the reduction of nitrate-N to nitrite-N might have occurred at the cytoplasmic surfaces of the slices, then some of the nitrite-N was absorbed by the tissues, where it was converted into rest-N. It may also be possible that the slices absorbed nitrate-N from the media, reduced it to nitrite-N inside the tissues, then part of the nitrite-N was built up into rest-N and the rest was excreted into the media. It is worthy to mention here that doubling the concentration of the nitrate-N in the medium induced slight stimulation in nitrate-N assimilated into rest-N; but showed no effect on the amount of nitrite-N produced. It seems therefore that the addition of 2,4-D to the media containing nitrate might activate an enzyme system capable of reducing nitrates to nitrites. The rate of nitrate ➡ nitrite conversion was more activated with 2,4-D than the rate of nitrite ➡ peptide formation, hence the accumulation of nitrite-N in the media. The presence of some ammonia-N in these media, was probably a result of nitrate reduction.

Ammonia-, Amide-, and Amino-N:

These three fractions hardly showed any change as a result of the various treatments.

Respiration of the Tissues

The mean values of the amounts of CO_2 given off by the differently treated radish root slices are represented graphically in figure 1 which shows that, feeding with 2,4-D alone stimulated the rate of respiration of the slices. Feeding with potassium nitrate again increased the rate of respiration of the slices well above that of the control samples. Doubling

the concentration of the nitrate seemed to have no significant effect on the total CO_2 production during the 48 hours of the experiment.

Addition of 2,4-D to the nitrate media, stimulated the rate of respiration of the slices to a level which is higher than that induced by 2,4-D or nitrate alone; the stimulatory effect being enhanced in the presence of high nitrate concentration.

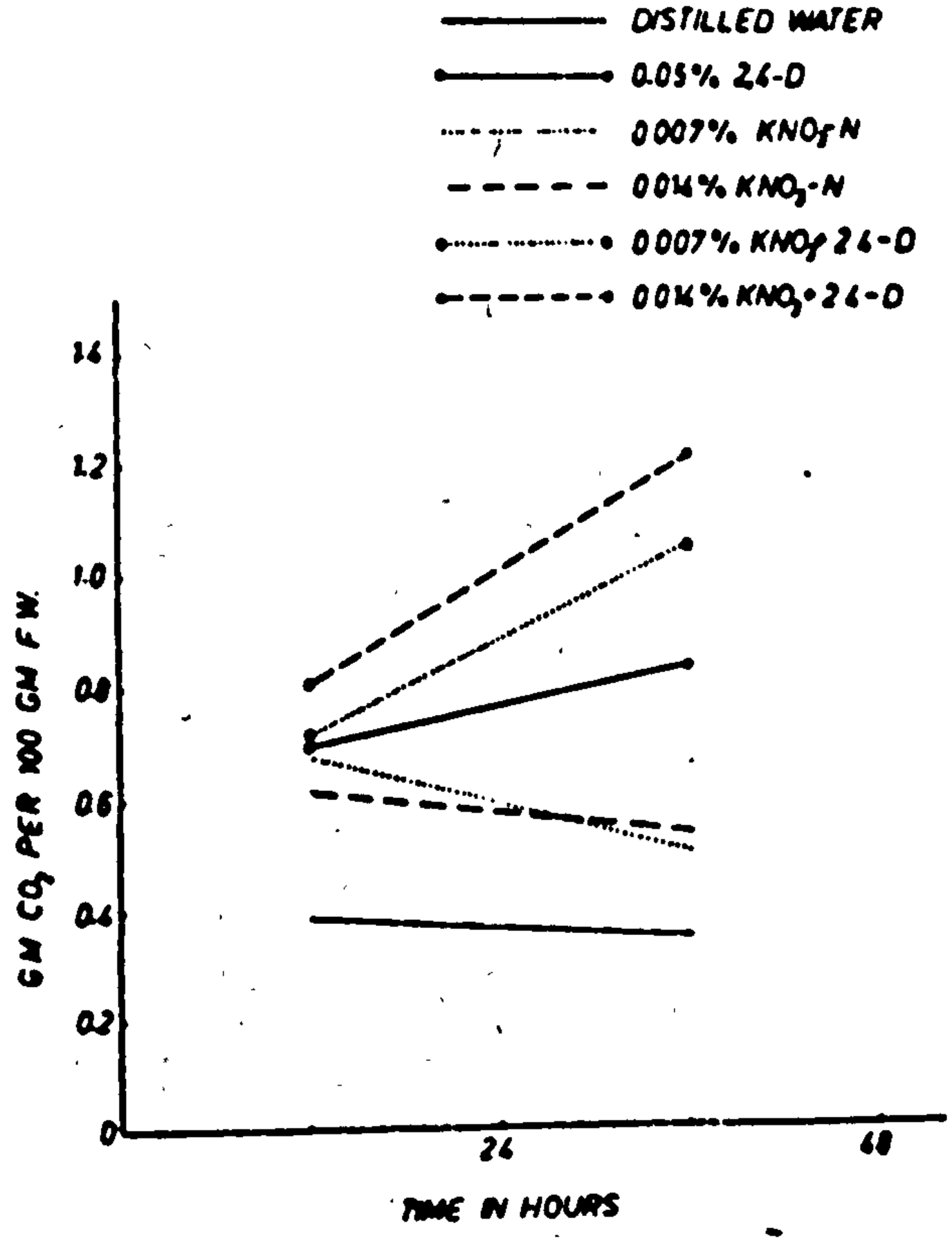

Fig. 1. — Carbon dioxide-output by the differently treated radish root slices (Expressed as g. CO_2 output/ 100 g. original fresh weight of slices).

Discussion

Nitrate-N assimilation in absence of 2,4-*D:*

The way in which nitrate-nitrogen is incorporated into organic nitrogen compounds of higher plants remains a matter of dispute. According to Prianischnikov (1931), Chibnall (1939) and others nitrate is reduced to nitrite and then ammonia before its assimilation. On the other hand, Burstrom (1945), is of the opinion that nitrate reduction may take

place in fungi and perhaps roots of higher plants, but in green leaves nitrate is not reduced to ammonia but rather combines with undetermined carbon-dioxide products prior to complete reduction. In the present work the radish root slices supplied with potassium nitrate alone, absorbed a good deal of nitrate-N from their media. The major part of the absorbed nitrate-N, was accumulated in the tissues, and a relatively small part was assimilated into peptides and proteins, no other nitrogen fraction was formed in the course of assimilation. These results are in complete agreement with those obtained by Said et al (1944, 1947, 1952). who suggest that the nitrate-N may be directly assimilated into peptides and proteins without necessarily passing through the classical reduction steps. If, however, nitrate was to be reduced before its assimilation, then the steps involved in the nitrate reduction and assimilation might have proceeded with equal rates, hence the absence of any intermediate product.

Nitrate-N assimilation in presence of 2,4-D*:*

Feeding radish root slices with 2,4-D alone stimulated the rapid assimilation of some of the initial nitrate-N content of the slices into peptide(rest) - and protein-N, thus confirming earlier results reported by Said and Youssef (1955).

Feeding the slices with 2,4-D and potassium nitrate mixtures induced rapid utilisation of nitrate-N into peptide (rest) and protein-N and revealed the presence of considerable amounts of nitrite-N in the media (table 3). It is possible that 2,4-D activated, in one way or the other, an enzyme system at the cytoplasmic surfaces of the slices which was capable of reducing nitrate to nitrite. Some of this nitrite-N gained entry in the tissues where it was converted into peptide-N. The rate of nitrate ⟶ nitrite conversion might have exceeded the rate of nitrite ⟶ peptide formation and hence the accumulation of nitrite-N in the media. Evidence in support of this assumption may be obtained from the failure to detect any nitrite-N in the tissues and also from the failure of radish slices to absorb nitrate-N during the first 24 hours of the experiment where reduction of nitrate to nitrite was not yet performed. In this connection, it may be mentioned that Burström (1945) stressed that, in wheat roots and fungal hyphae, reduction of nitrates appeared to take place at the surface of the cytoplasm. Said (1941), showed that invertase enzyme occurred at the cytoplasmic surfaces of radish root slices.

It may be also possible, though less probable, that the radish slices absorbed nitrate-N from the media and this nitrate-N was reduced inside the slices into nitrite-N part of which was converted into peptide (rest)-N, and the rest excreted into the media.

It is worthy of note here that these slices did not show any protein-N synthesis probably due to the presence of considerable amounts of nit-in the media.

It seems quite apparent from the work of several authors that 2,4-D alters the activity of the enzyme in an indirect fashion since in vivo and in vitro changes seldom agree. 2,4-D can lessen the effectiveness of naturally occurring inhibitors, or can increase or decrease vitamins and metallic ions for prosthetic or coenzyme function (Leucke et al 1949, Lo and Chem 1947). The results of the present work indicate that a nitrate reductase enzyme is possibly present at the cytoplasmic surfaces of the radish root slices together with a natural inhibitor, limiting or completely inhibiting the activity of the enzyme. 2-4-D may react with this inhibitor or may interfere with its formation.

Another possibility is that the enzyme may be present in a bound form and that 2,4-D liberated the enzyme from this inactive bound form. It is already reported by Veldstra and Booij (1949) and Söding (1953) that auxins are able to liberate bound enzymes from an adsorption complex in which it is maintained in an inactive form. In this connection, it is worthy to mention that Swanson and Shaw (1954) showed that 2,4-D can influence the ratio of oxidised to reduced nitrogen in plants, and they suggested that this may be achieved through the influence of 2,4-D on a nitrate reducing system.

It is interesting to mention that no loss of nitrogen was ever detected in any treatment of the present work, even where nitrite-N was formed. This result is not in agreement with the observations of Pearsall et al (1937) and Mothes (1938) who found that nitrites may react with amino acids resulting in the production of gaseous nitrogen. However Allison et al (1950, 1952) have shown that such a reaction is very slow or negligible at pH 5.3 or above. In the present investigation the initial amino-N content of the slices was very small, and the media containing nitrite-N were almost neutral.

Respiration of root slices:

Feeding with 2,4-D induced rapid stimulation of the rate of respiration of the root slices, thus confirming earlier work carried by Said

and Youssef (1955). Feeding with mixtures of nitrate and 2,4-D stimulated the rate of respiration to a level which was higher than that given by 2,4-D or nitrate alone. These higher stimulatory effects were associated with rapid nitrate assimilation into peptides (rest-N) and accumulation of nitrite in the media.

Acknowledgment

The authors wish to thank Professor H. Said for his illuminating discussions and criticisms.

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دراسة تاثير مادة ٢ : ٤ ــ د على امتصاص وتمثيل نترات البوتاسيوم بواسطة شرائح من جذور نبات الفجل

للدكتور الحسيني يوسف والسيد / وجيه السعداوى
قسم النبات ، كلية العلوم ، جامعة القاهـرة

عوملت شرائح من جذور نبات الفجل بغمسها فى محاليل تحتوى على مادة ٢:٤ــد أو نترات البوتاسيوم أو فى محلول منهما معا • ولقد اظهرت التجارب النتائج الآتية :

١) تمتص الشرائح كمية كبـيرة من نترات البوتاسيوم ، حيث يتراكم اغلبها داخل انســجة الشرائح بينمـا يتحـول القليل منهـا الى ببتيدات وبروتينات •

٢) أدت معاملة الشرائح بمحلول من مادة ٢:٤ــد الى سرعة تمثيـــل النترات الموجودة أصلا فى الشرائح الى ببتيدات وبروتينات

٣) عند معاملة الشرائح بمحلـــول من النترات ومادة ٢:٤ــد تحـول بعض النترات الى ببتيدات وتراكم بعضها فى المحلول الخارجى على هيئـة نيتريتات •

٤) أظهرت النتائج انه يبدو أن مادة ٢:٤ــد عنـد اعطائها للشرائح مع محلول نترات البوتاسيوم ، تنشط أنزيما خاصا على سطح السيتوبلازم للشرائح له القدرة على اختزال النترات الى النتريت •

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RESPIRATION AND NITROGEN METABOLISM OF RADISH ROOT SLICES AS INFLUENCED BY α-NAPHTHYLACETIC ACID

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SUMMARY

The effects of the sodium salt of NAA on respiration and nitrogen metabolism of radish root slices were studied. NAA seems to increase the permeability of the cell membranes. In concentrations of 25 p.p.m. or 50 p.p.m, NAA was found to stimulate slight protein synthesis. if present in relatively higher concentration (75 p.p.m. or 100 p.p.m) it induced protein hydrolysis, NAA stimulated the rate of respiratin of the radish slices, the stimulation being enhanced with increasing the auxin concentration.

Introduction

The basic knowledge of the effects of synthetic auxins on the metabolism of plants has, of course, a strong bearing on the intelligent application of these substances in applied fields. One of the most important synthetic auxins that has been of wide spread use in controling plant growth is α-naphthylacetic acid. The compound can induce fruit set (Stuivenberg, 1943), reduce fruit drop (Gardner et al, 1939, 1940), enhance fruit ripening (Stuivenberg 1946), induce root formation (Zimmerman and Wilcoxon 1935) and prevent sprouting of potato in storage (Guthrie 1939). From the bulk of literature we have at hand, only few workers have been interested to clarify the effects of such important synthetic auxin on the metabolism of plants (Mitchell et al, 1941; Hsiang, 1951; Hall and Khan, 1955).

The aim of the present work was to study the effects of the sodium salt of α-naphthylacetic acid on respiration and nitrogen metabolism of radish root slices.

Material and Methods

One mm. thick slices of *Raphanus sativus* var. *Aegyptiacus* roots were used in this investigation. Twelve samples of fifteen grams each were prepared according to the procedure described by Said and Youssef (1955). The samples were washed in aerated running tap water for two days in order to allow for the wound healing metabolism (cf. Said and El-Shishiny 1947). The samples were then washed several times with sterile distilled water and two of them were extracted and immediately analysed for their initial contents of the different nitrogen fractions. The remaining ten samples were transferred to air-tight chambers supplied with 400 mls each of sterile distilled water or sterile solutions of various concentrations of the sodium salt of α-naphthylacetic acid (NAA) as shown in the following scheme :

No. of samples	Medium, 400 mls
2	Distilled water
2	25 ppm NAA
2	50 ppm NAA
2	75 ppm NAA
2	100 ppm NAA

After introducing the samples in their respective media, a strong current of CO_2-free air was then bubbled through the experimental solution at a constant rate of four litres per chamber per hour. The plant chambers were kept at 25°C for a period of 48 hours, during which the CO_2-output by the tissue slices and also the nitrogen contents of the media were estimated at 24-hour intervals. At the expiry of the experimental period, the samples were drained, washed with distilled water and then analysed immediately for their nitrogen fractions.

The methods used for the determination of CO_2 outputs and the nitrogen fractions have been referred to in previous papers (Said and El-Shishiny 1944, 1947). The various nitrogen fractions determined in the water extracts of the slices were ammonia-, nitrate-, amide, amino-, and total soluble-nitrogen, the difference between the latter and the sum of the first four fractions gave the so called "Rest-nitrogen". The insoluble nitrogen (protein-N) was determined in the dried residue. Only the mean values will be presented in the tables, since results of duplicate samples were remarkably close.

Experimental Results

Analysis of the Media

The analysis of the media revealed the presence of different nitrogen fractions in all the media containing NAA; the distilled water media were free from any form of nitrogen. After the first 24 hours of the experiment, the NAA media contained only some rest-N, but by the end of the experimental period, some nitrate- and ammonia-N were detected in the media of 75 p.p.m. and 100 p.p.m. NAA; some amino-N being also found in the media of 100 p.p.m. NAA. The average values of the different nitrogen fractions recovered in the media during the 48 hours of the experiment are recorded in table 1. Since the root slices were not fed with any nitrogen compounds, it would be assumed that the nitrogen recovered in such media was excreted from the radish slices.

Examination of the total-N recovered in the media at the end of the experiment shows that slices treated with 25 ppm NAA revealed minimum excretion of nitrogen (amount=5.03 mg.). The excretion of nitrogen was strongly enhanced with increasing NAA concentration.

With regard to the rest-N recovered in the media, it is apparent from table 1, that the total excretion of rest-N was enhanced with increasing the concentration of NAA from 25 p.p.m. up to 75 p.p.m., but was maintained constant when the concentration was further raised to 100 p.p.m. As shown in table 2, the root slices treated with the latter concentration excreted most of their soluble nitrogen into the external media·

(TABLE I)

Nitrogen fractions recovered from the various media of radish root slices (Expressed as mg. per 100 g. original F.W. per 48 hours)

Culture medium	Nitrate-N	Ammonia-N	Amino-N	Rest-N	Total-N recovered
Dist. water	—	—	—	—	—
25 ppm NAA	—	—	—	5.03	5.03
50 ppm NAA	—	—	—	11.43	11.43
75 ppm NAA	18.02	1.82	—	24.35	44.19
100 ppm NAA	29.35	3.46	8.53	24.95	66.29

Analysis of the Tissues

The results of the analysis of the various tissue samples for their contents of the different nitrogen fractions are presented in table II.

Behaviour of total soluble- and protein-N:

As shown in Table II, the radish slices starved in distilled water showed no change in their total soluble- and protein-N-contents. All the tissue slices suspended in NAA - containing media showed loss in their total soluble-N, the loss of soluble-N being highly pronounced in case of 75 p.p.m. or 100 p.p.m. NAA. Tissue slices suspended in 25 p.p.m. or 50 p.p.m. NAA showed slight protein synthesis, while those suspended in 75 p.p.m. or 100 p.p.m. hydrolysed some of their initial protein-N. Hydrolysis of protein-N was stimulated when the concentration of NAA was raised from 75 p.p.m. to 100 p.p.m. In all samples, the loss in total-N of the tissues was more or less accounted for by the recovery of corresponding amount of nitrogen in the media.

(TABLE II) Analysis of the initial as well as the differently treated radish root slices for their contents of the different nitrogen fractions. (Calculated as mg. N per 100 g. original fresh weight)

Culture medium	Ammonia-N	Amide-N	Amino-N	Nitrate-N	Rest-N	Total soluble-N	Protein-N	Total-N
Initials	1.07	2.09	3.71	31.80	17.35	56.02	51.31	107.33
Dist. water	1.05	2.82	3.66	29.26	19.98	56.77	51.29	108.06
25 ppm NAA	1.08	2.79	3.70	28.94	13.62	50.13	54.51	104.64
50 ppm NAA	1.05	2.10	3 08	22.54	13.50	42.27	53.77	96.04
75 ppm NAA	—	2.30	3.71	4 39	8.27	18.67	44.15	62.82
100 ppm NAA	—	2.10	3 71	1.92	1.09	8.82	34.62	43.44

Behaviour of nitrate- and rest-N:

Table III shows the changes in the nitrate-N content of the tissue-medium system. Root slices suspended in aerated distilled water showed the disappearance of small amount of their nitrate-N, being apparently transformed into rest-N. Treatment with 25 ppm NAA did not show any effect on nitrate-N assimilation. 50 ppm NAA and 75 ppm NAA stimulated the assimilation of nirate-N almost to the same extent, the latter concentration induced the excretion of considerable amounts of nitrate-N into the media. Root slices that were treated with the highest concentration (100 p.p.m.) could hardly assimilate any of their initial nitrate-N, almost all of which being excreted (unutilised) into the external media. Whenever nitrate-N was assimilated by the root slices, it was converted into rest-N, which was either retained in the slices (slices in distilled water) or excreted into the culture media together with some of the initial rest-N of the slices. In some cases (slices treated with 25 p.p.m. or 50 p.p.m.) some of this rest-N was built up into protein.

(TABLE III)

Changes in the Nitrate-N contents of the tissue-medium systems (calculated as mg. N per 100 gm original fresh weight)

Culture medium	Initial content of nitrate-N	Nitrate-N remained in the tissue-medium systems			Nitrate-N assimilated
		tissue	medium	total	
Dist. water.....	31.80	29.26	0.00	29.26	2.54
25 ppm NAA	31.80	28.94	0.00	28.94	2.86
50 ppm NAA	31.80	22.54	0.00	22.54	9.26
75 ppm NAA	31.80	4.39	18.02	22.41	9.39
100 ppm NAA	31.80	1.92	29.35	31.27	0.53

Behaviour of ammonia-, amide- and amino-N:

These three fractions which were initially present in minute amounts in radish root slices, hardly showed any change through NAA treatments. However, some amino-N (amount=8.53 mg) and a small amount of ammonia-N (amount=3.46 mg) were found in the media of the samples

suspended in 100 p.p.m. NAA. These nitrogen fractions might have resulted from the protein hydrolysis in these samples.

Respiration of the Tissues

The mean values of the amounts of CO_2 given off by the differently treated radish root slices are recorded graphically in Figure 1. It is clear from this figure that the radish root slices that were respiring in aerated distilled water showed a low and steadily declining respiration rate during the experiment. Treatment with NAA apparently stimulated the rate of respiration of the root slices. The total CO_2 production t during the 48 hours of the experiment was increased with the increase in the NAA concentration. Raising the concentration of NAA from 50 ppm to 75 ppm did not have any effect on the rate of respiration during the first 24 hours. However during the second 24 hours, 75 p.p.m. NAA stimulated CO_2 production to a level which was significantly above that produced by 50 p.p.m. NAA. The rate of respiration of root slices treated with 100 p.p.m. NAA was lower in the first and higher in the second 24 hours than that of samples treated with any other NAA concentration.

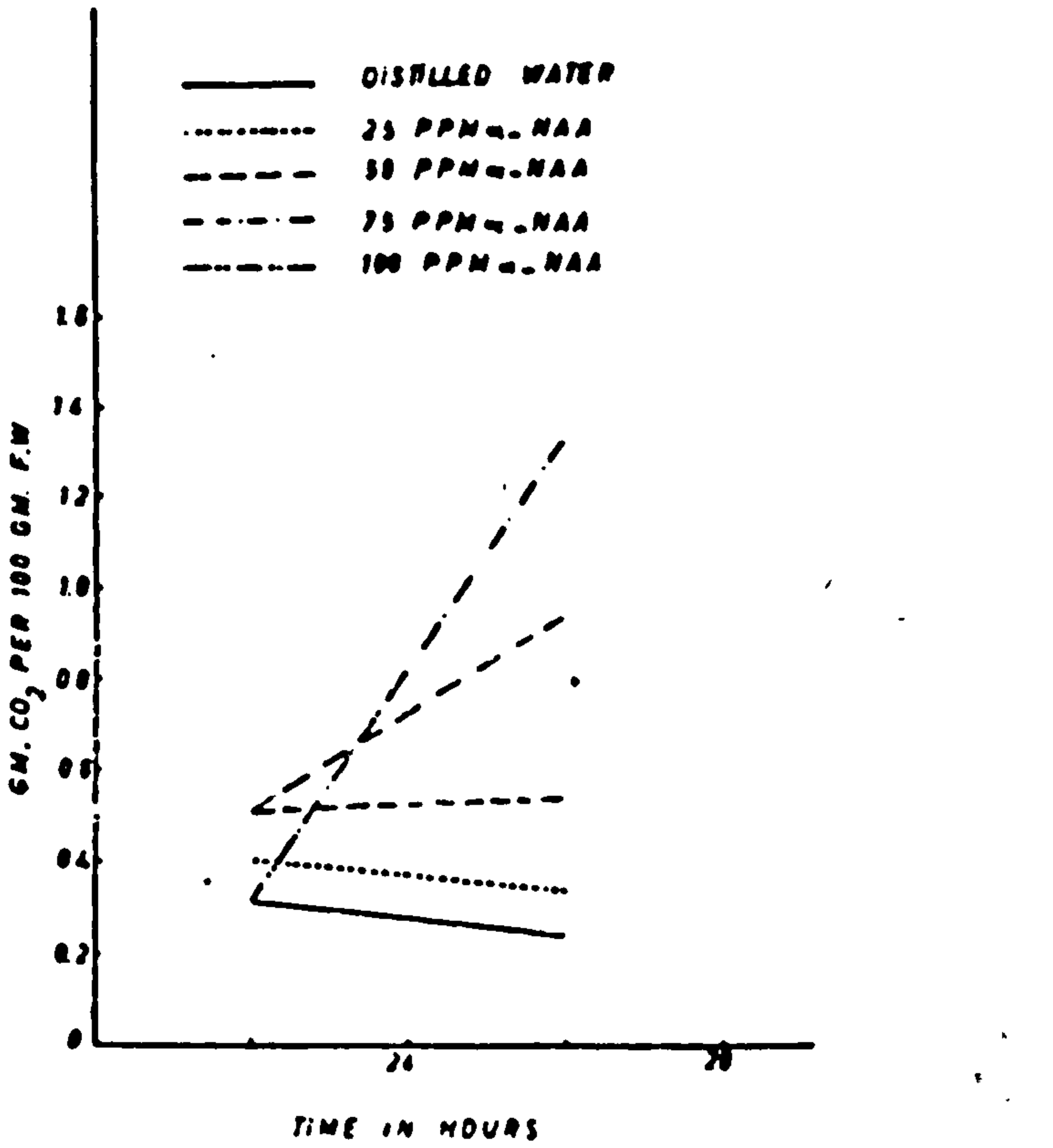

Fig. 1. — Carbon dioxide-output by the differently treated radish root slices. (Expressed as g. CO_2 output/100 g. original fresh weight of slices).

Discussion

It is clear from the present work, that NAA treatments induced excretion of soluble-N fractions from the radish root slices into the external media, the excretion was more pronounced in presence of higher concentrations of the auxin. This might be due to an increase in the permeability of cell membranes as a result of auxin treatment. In this connection, it may be mentioned that Veldstra and Booij (1949) showed that synthetic auxins (including NAA) in high concentrations undoubtedly increased the permeability of the cell membranes of beet root. However, Masuda (1953) indicated that lower concentrations of 3-indolylacetic acid increased the permeability of the membrane of onion-scale protoplasts, while higher concentrations decreased it.

The behaviour of the protein-N of the radish root slices towards NAA treatment depends on the concentration of the compound. Thus while 25 p.p.m. or 50 p.p.m. stimulated slight protein synthesis, relatively higher concentration (75 p.p.m. or 100 p.p.m.) induced protein hydrolysis. It is interesting to mention here that Northen (1942) has suggested that the essential action of auxins may be through hydrolysis of protein materials in the cells.

The results of the present investigation (table 3) also showed that the auxin can promote inhibit or have no effect on the nitrate-N assimilation by radish root slices. The nitrate -N was assimilated into rest-N, which together with the initial rest-N was excreted into the media or partly converted into proteins.

Feeding radish root slices with various concentrations of NAA stimulated their rates of respiration, the total CO_2 output was increased with increasing the auxin concentration. This result is in agreement with the findings of Hsiang (1951) who reported three-fold increase in the rate of respiration of orchid ovaries as a result of NAA treatment. The striking increase in the rate of respiration during the second 24 hours of the experiment in presence of 75 p.p.m. and 100 p.p.m. NAA, particularly in presence of the latter concentration, may be due to the high increase in the permeability of the cells induced by NAA at these concentrations. Such increase in the permeability may bring more respirable substrate in contact with the respiratory enzyme system. Moreover, the samples treated with such concentration (75 p.p.m. or 100 p.p.m.) showed some protein hydrolysis which might have activated the enzyme systems. Hand (1939) has already reported that protein dissociation can activate enzymes. Similar conclusion has been arrived at by Northen (1942), who added that if the

protein dissociation is carried out to the extreme, the stimulation effects upon enzymes in respiration would be reversed by dissociation of essential constituents from enzymes.

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دراسة تأثير مادة الفانفثالين حامض الخليك على التنفس والتحول النيتروجينى لشرائح من جذور نبات الفجل

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عوملت شرائح من جذور نبات الفجل بغمسها فى محاليل مختلفة التركيز من ملح الصوديوم لمادة الفانفثالين حامض الخليك وأظهرت التجارب النتائج الآتية :

١) يبدو أن المادة المستخدمة قد زادت من نفاذية الخلايا .

٢) فى حالة التركيزين ٠،٢٥، ٠٥ جزء من المليون أحدثت المادة زيـــادة طفيفة فى المحتوى البروتينى للخلايا ، أما التركيزان ٧٥ ، ١٠٠ جزء من المليون فقد أديا الى تحلل البروتينات .

٣) نشطت المادة معدل التنفس لشرائح جـذور الفجل ، كما أن زيادة تركيز المادة أدى الى زيادة فى نشاط معدل التنفس .