DOCTOR OF PHILOSOPHY

Studies on fossil plants of Karoo age from Central & Southern Africa

Williams, Peter

Award date:
1966

Awarding institution:
Bangor University

STUDIES ON FOSSIL PLANTS OF KARROO AGE FROM CENTRAL & SOUTHERN AFRICA

A THESIS SUBMITTED TO THE UNIVERSITY OF WALES

IN CANDIDATURE FOR THE DEGREE OF

PHILOSOPHIÆ DOCTOR

PETER WILLIAMS B.Sc. (WALES)

CONTAINS PULLOUTS

ABSTRACT

Approximately fifty specimens of compressions of Glossopteridean leaves, a stem, and several seeds or seed-like bodies, from the Transvaal and Southern Rhodesia, are described and compared with previously described species from India, Australia, Africa and Argentina.

In the genus Gangamopteris McCoy (1875), one existing species and one new species are described, and four further taxa are described but not named.

In the genus Glossopteris Brongniart (1828), two new species are described, three taxa are referred to or closely compared with existing species, and three further taxa are described but not named.

Fifty specimens of petrified wood from Rhodesia and South West Africa have been examined by means of petrological sections. Eight specimens are given specific designation, including two new species in the genus Dadoxylon Endlicher (1847) and one new species in the genus Rosembrioxylon Seward (1919).

A new genus, Helicoxylon, is proposed for wood previously placed in the genus Spiroxylon Walton (1925), and a second species is assigned to this new genus.

The stratigraphical value and possible evolutionary significance of these woods are discussed.

ACKNOWLEDGMENTS

I wish to express my thanks to Professor P. W. Richards, M.A., Sc. D., F.L.S., in whose department this work was carried out, and also to the Department of Scientific and Industrial Research, which provided me with a Research Studentship for three years and, throughout, has given me every assistance.

I am very grateful to Dr. W. S. Lacey, for introducing me to these problems and for his continued interest and encouragement during the preparation of this thesis.

Also, my sincere thanks are due to my wife, who has corrected the draft of the entire thesis, and who has helped in innumerable ways.

P. WILLIAMS

CONTENTS

PART I

THE STRATIGRAPHY OF THE KARROO SYSTEM IN CENTRAL AND SOUTHERN AFRICA

The Karroo beds are found in most parts of Africa south of the Sahara, and are composed of both volcanic and sedimentary rocks. The system is known from South West Africa and Angola in the west to Mozambique and Tanganyika in the east, and from Cape Province in the south to Uganda and the Congo in the north.

In the Kalahari desert region and in Portuguese East Africa, the more or less horizontal Karroo beds have been covered by younger Cretaceous and Tertiary deposits. Particularly to the west and to a lesser extent to the south and east of this region, considerable erosion has occurred, exposing the Karroo beds and some of the underlying rocks of the Cape and other older Systems. Thus in Southern Africa, outcrops of the Karroo System form a more or less continuous band following the coastline of the continent.

For convenience in description, A.L. du Toit (1954) arbitrarily divided the Karroo System into a Southern and Northern area, along a line through Windhoek in South West Africa to Pelfast in the Transvaal. It is in the Southern area, comprising the Cape of Good Hope, the Orange Free State, Natal, Basutoland, and parts of South West Africa and the Transvaal, that the System shows its greatest and most complete development. In this area are to be found the type localities after

which the four main subdivisions of the Karroo System are named. These are, in order of deposition, the Dwyka, Ecca, Beaufort and the Stormberg series (Table 1, Page 5). If these strata were all developed to their maximum in any one locality, they would give a total thickness of over 35,000 feet. Each Series is again subdivided, but in this case, the strata have been given different local names, depending on where the outcrops occur. The Southern facies shows a complete succession spanning parts of the Upper Palaeozoic and the Lower Mesozoic era, as recognised in the Northern Hemisphere. The basal Dwyka tillites and shales (which rest comfortably on the older glaciated rocks of the Cape System) are glacial deposits laid down during the time of the Upper Carboniferous Period of Europe, whilst the Stormberg Series is approximately equivalent in age to the Upper Triassic and Lower Jurassic Periods of Europe.

The deposits are almost entirely of Continental origin, but there are occasional incursions of marine deposits in South West Africa, which have proved to be of great importance in dating the adjacent non-marine beds, and in establishing correlations with the Gondwana beds of India, South America and Australia.

In the Northern area, which includes Rhodesia and Malawi (Nyasaland), Angola, Tanganyika, the Congo, Uganda and parts of the Transvaal, Bechuanaland and South West Africa, the Karroo System is not always complete. The Dwyka tillites are usually much reduced or absent, so that the Ecca beds may rest on rocks of pre-Karroo age. The Beaufort and Ecca Series may also be so reduced that the Stormberg

beds rest on Ecca or even earlier rocks.

Fossil plants are known from various sedimentary rocks throughout the whole of the Karroo Succession, commencing with the Glossopteris flora which extends from the Dwyka to the middle Beaufort series, and passing into a Dicroidium flora, which is more like the Mesozoic floras of the Northern Hemisphere, and which is found in the Upper Beaufort and the Stormberg Series.

In South Africa, knowledge of the succession of Karroo floras is due chiefly to the work of Zeiller (1896), Seward (1898 - 1919), Leslie (1921), Krausel (1956), Walton (1923, 1925), Thomas (1933, 1958) and Du Toit (1954). More recently, Plumstead (1952, 1956 a,b; 1958 a,b.) has added greatly to our knowledge of the Glossopteris flora as developed at Vereeniging, and has described an important series of Glossopteridean fructifications from this locality. Teixeira (1947 - 1954) has described the Glossopteris flora of Mozambique, whilst Pant (1958) and Høeg and Bose (1960) have described that of Tanganyika and the Congo respectively.

In Rhodesia and Malawi (Nyasaland) the main contributors to our knowledge of the fossil flora have been Molyneux (1903, 1909), Andrew and Bailey (1910), Lightfoot (1914, 1929), Utley (1957), Walton (1923, 1929, 1956), Bond (1952, 1955, 1962) and Lacey (1959 - 1961).

The subsequent parts of this thesis describe recent collections of fossil plant material from several localities in the Republic of South Africa, in Rhodesia and Malawi (Nyasaland), and in South West Africa (see map on Page 4).

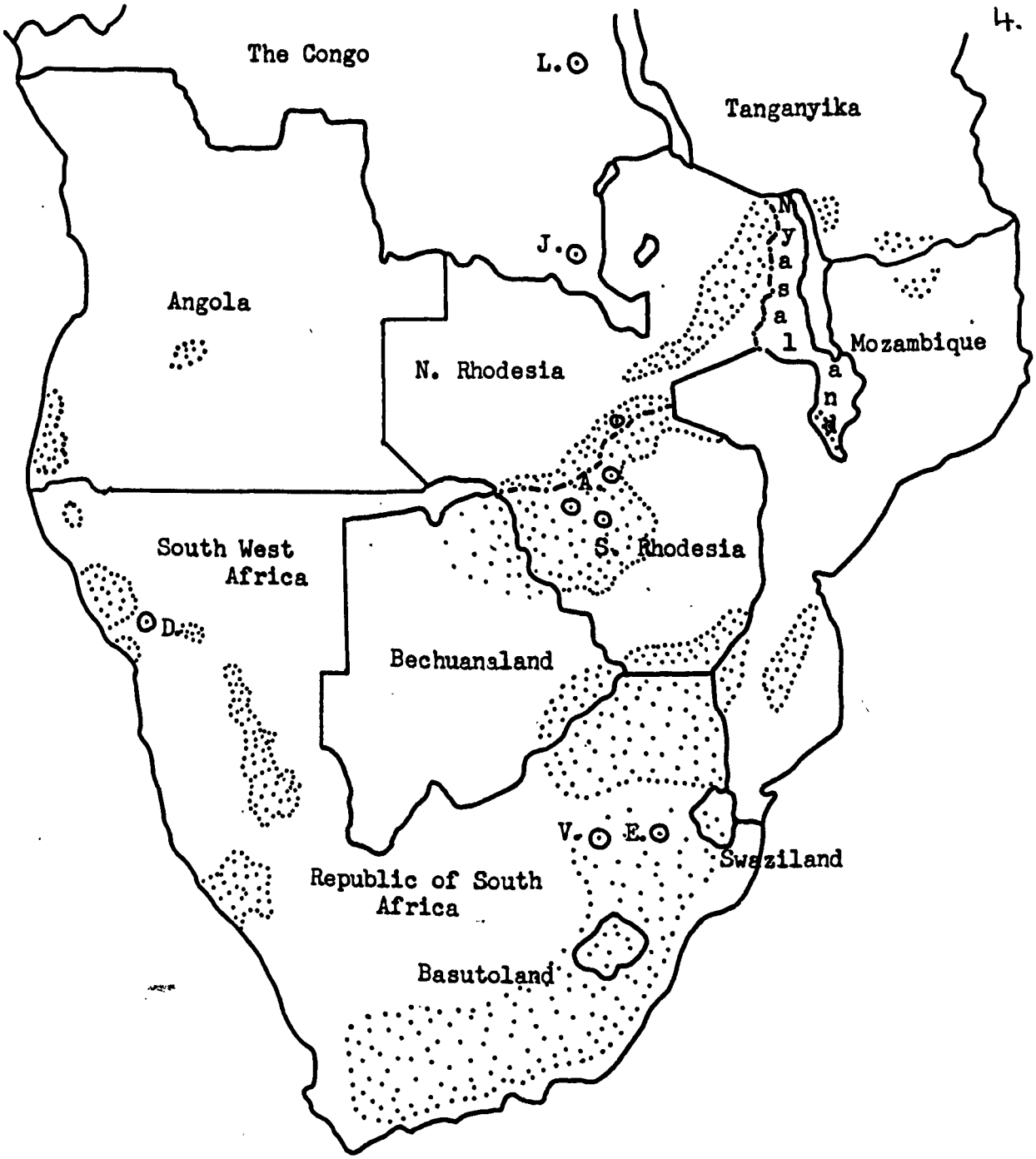


Fig. 1. Map to show the approximate distribution of some major Karroo Deposits in Central and Southern Africa, and the position of localities of particular interest.

Key: A. = Main collecting areas in Rhodesia. E. = Ermelo.
V. = Vereeniging (Plumstead) D. = Doroskrater (Krausel)
L. = Lukuga (Grambast) J. = Jadotville (Near Hoegand Bose's locality.)
Stippled areas = Karroo Deposits.

TABLE 1

The Karroo System in South Africa and Rhodesia

Series	Cape Province	Middle Zambesi Region	Approximate European Equivalents
Stormberg	Drakensberg Basalts.	Batoka Basalts	Jurassic
	Cave Sandstone	Forest Sandstone Pebbly Arkose	
	Red Beds		
	Molteno Beds	Fine Red Marly Sandstone Ripple-marked Flags Escarpment Grit	Upper Triassic
		Unconformity	
Beaufort	Upper	(Not Known)	
	Middle	(Not Known)	
	Lower	Upper Madumatisa Shales Middle Madumatisa Shales Lower Madumabisa Shales	Upper Permian
Ecca	Upper	Upper Wankie Sandstone	
	Middle	Wankie Coals and Shales	Lower Permian
	Lower	Lower Wankie Sandstone	
Dwyka	Upper Shales Glacial Boulder Beds	Glacial Boulder Beds and Varved Clays	Upper Carboniferous
	Lower Shales		

(after Lacey, 1961b)

PART II

CUTICLE STUDIES IN THE GLOSSOPTERIS FLORA OF THE TRANSVAAL, WITH A NOTE ON SOME FOSSIL PLANTS FROM SOUTHERN RHODESIA

C O N T E N T S.

PART II. CONTENTS (continued)

Source of the Transvaal Material.

The main work reported in Part II is the investigation of fossil plants from Bellevue Colliery, Ermelo, Transvaal, in the Republic of South Africa.

The specimens were taken from the roof shale immediately above the No. 3 coal seam at the Ermelo Colliery. This seam is the middle one of five, which together with the intervening shales are regarded as representing the Middle Ecca Series in the Transvaal. (A.L. du Toit, 1954. See Table 1, page 5, and Map (Text-Fig. 1) on page 4).

The collection was made by Dr. J. Townrow of the University of Tasmania, and sent to Dr. W. S. Lacey for examination. My thanks are due to the Management of the Bellevue Colliery for granting permission to collect the material, and to Dr. Townrow for making the collection available and agreeing to its being placed in my hands for investigation.

Description of Material and Specimens.

The Ermelo collection consists of twenty hand specimens of a dark grey, hard micaceous shale, in which parts of some fifty leaves, several stems and seed-like bodies are preserved as compressions.

According to Du Toit (1954) the only plants known hitherto from the Ermelo locality are Gangamopteris obovata (Carruthers) White, Cordaites (Noeggerathiopsis) hislopi (Bunb.) and Schenopteris sp. The opportunity to study a new collection was therefore, particularly attractive.

The results have proved to be of interest, not only in providing

several new records for the Republic of South Africa, but also in yielding well preserved cuticles. The study of these cuticles has provided additional information regarding the classification and identification of Gymnogramma and Cheilanthes leaves, and has resulted in the discovery of several species which were previously unknown.

Techniques Used in the Investigation of the Ryvale Collection.

(i) Macroscopic Examination

Most of the specimens were exposed with the aid of a variety of small cold chisels and a geological hammer. If a specimen was particularly delicate, or if this method was likely to damage neighbouring leaves, the overlying shale was removed by dissolving it in Hydrofluoric acid. A small wall of wax was built around the area of the rock to be removed, and filled with 40% Hydrofluoric acid. The acid was agitated with a camel-hair brush. Spent acid and debris was repeatedly washed away with distilled water and fresh acid was placed in the well, until the specimen was exposed to the extent desired. Occasionally the Kalton Canada balsam transfer method (for review of technique, see Lacey, 1953) was used to expose the obverse side of the specimen.

Detailed investigation of such features as the venation of the leaves required the use of strong oblique lighting or the immersion of the specimen in either water or xylol. The particular method employed depended on the state of preservation of the material being studied.

(ii) Preparation for Microscopic examination.

The techniques used in the subsequent examination were by and large those in common use in the study of carbonised compressions of leaves, the cuticles of which are still preserved.

(a) Removal of carbonaceous material from the rock by mechanical methods.

In some cases, the carbonaceous layer was in the form of large loose flakes, which could be easily detached from the rock by chipping the specimen with a small chisel or a needle. The cellulose pull method (Lang, 1926) was tried out on those specimens in which the carbonaceous layer adhered firmly to the rock, but the method was soon abandoned, as it invariably resulted in the cuticle breaking up into very small fragments.

(b) Chemical method of removing carbonaceous material from the rock.

The following method was used successfully to remove firmly adhering carbonaceous material from the shale. A chisel was used to remove from the specimen a small flake of rock with the carbonaceous layer still attached to it. The rock backing was then removed by dissolving it in hydrofluoric acid and/or a mixture of such mineral acids as nitric acid and hydrochloric acid. The chemical method proved to be the more satisfactory, as it yielded larger pieces of cuticle than the purely mechanical method, and was, therefore, preferred, unless it was particularly desired to keep the hand specimen unmarked. Even when the cuticle was chipped directly from the rock, it was found to be advantageous to treat the material with hydrofluoric acid, as this removed any grains of silica which adhered to the cuticle, and which sometimes obscured fine detail when the material was examined microscopically.

Treatment of Carbonaceous Remains following removal from Shale.

No matter which method was used to separate the carbonaceous material from the rock, the carbonaceous layer was partially oxidised in a solution of potassium chlorate in nitric acid (Schulze's solution). The remaining material was then transferred to a circular cover slip in a duralumin support (see below), washed with distilled water and then treated with dilute alkali. Dilute ammonia was found to be particularly effective, and the fact that it could be easily removed from the preparation by washing with distilled water or by gentle evaporation was a great advantage. The period of oxidation in Schulze's solution varied from about two hours to eight or ten days, and the subsequent treatment with alkali varied from a few seconds in very dilute ammonia to several days in 880 ammonia or 20% potash solution. The addition of a few drops of Ethyl alcohol to the alkali often seemed to make the tarry residues from the oxidation process pass more easily into solution. The time of each treatment varied from specimen to specimen (and indeed from one part of a leaf to another) and could be determined only by a process of trial and error. The application of alkali sometimes dissolved the tarry residue rapidly, and caused the cuticles which remained to float apart. More often, however, the cuticles had to be separated with fine needles. This operation was facilitated by the use of a pair of simple micro-manipulators (Fig.2a, page 13), which I designed and constructed with the assistance of Mr. J.O. Williams (Technician, Botany Department, University College, Bangor).

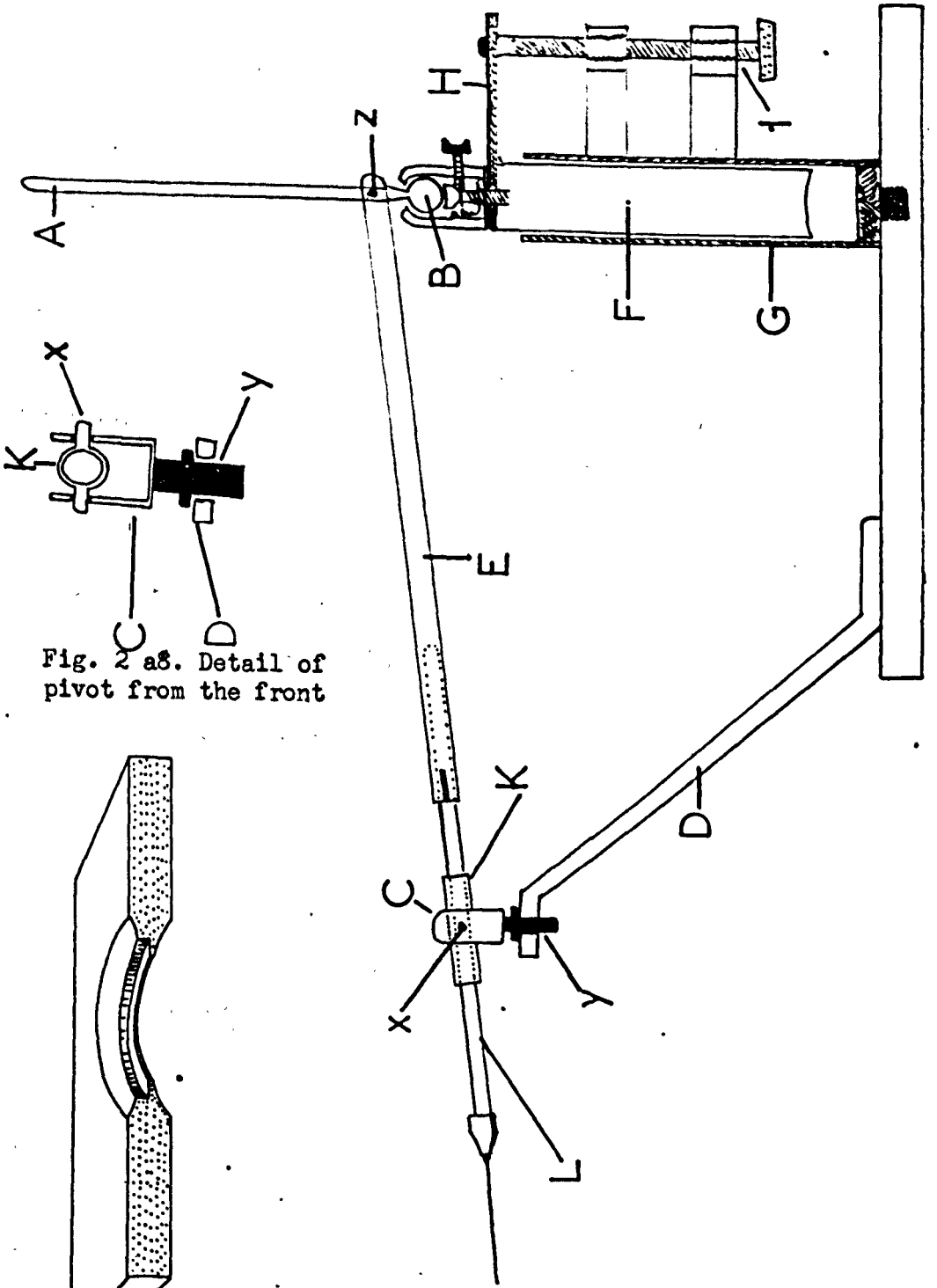


Fig. 2 a. Side view of Micromanipulator

Fig. 2a. Detail of pivot from the front

Fig. 2b. Section of Duralumin Support.

Movement of the needle in the horizontal plane is controlled by the joystick (A) which is attached to the ball and socket joint (B) and can, therefore, be moved in any direction. By placing the pivot (Z) as close as possible to (B) the movement transmitted from (A) through the brass tube (E) to the needle, is reduced by a ratio of approximately 20 : 1. The needle is held in a proprietary dissecting needle holder (L) which passes freely through the tube (K), but is held firmly in the split end of tube (E). The tube (K) can swing vertically about pivot (X) and horizontally about pivot (Y) (See side view Fig. 2a and end view Fig. 2a), so that movement of the needle in any direction is allowed for. Vertical movement of the needle is controlled by the vernier screw (I) which, through the connecting rod (H), moves the piston (F) up or down within the brass tube (C). The ball and socket joint assembly (B) is securely bolted to the top of the piston. The needle can be held in any desired position by tightening the screw of the ball and socket joint. The diagrams of this apparatus are not exactly to scale, and the various dimensions may be varied to suit the height of the microscope stage and the length of the operator's fore-arm.

The separated cuticles were then mounted (usually without staining) between two circular cover slips, using glycerine jelly as a mountant. The cover glasses were then sealed with shellac in a duralumin support, which allowed both sides of the preparation to be examined microscopically, using oil immersion objectives. Fig. (2b) on page 13 is a diagramatic median longitudinal section of one of these supports. The cover glasses

rest on the shelf (T). The duralumin is cut away above and below to allow the objectives to swing in and out freely.

Illustration.

Drawings

Both high and low magnification drawings were made with the aid of a camera lucida, to ensure that the proportions of the object were accurately reproduced and that a constant magnification was obtained. Very fine structures tend to be obscured by the camera lucida, and such details were added after the instrument was removed from the microscope. The original low and high power drawings were made with black indian ink on white cardboard at magnifications of 220 x and 2,200 x respectively. These were then photographed on Ilford N40 plates using ID13 as developer, and were finally printed on airmail paper at magnifications of 200 x and 650 x respectively.

Micro-photography.

The cuticles were photographed using an Exakta 35 mm camera. The camera lens was removed and the body clamped to the vertical tube of the microscope by a special adaptor. A x8 eyepiece and either a 10:1 or a 45:1 objective were used. The best film for this purpose was found to be "Ilford microneg", which has a very fine grain structure and produces a high degree of contrast, even with a fine grain developer such as Beutler's developer. The prints were made on airmail paper,

the final magnification being x 150 for the low power photographs and x 650 for the high power photographs.

Macro - photography

Photographs of the external features of the specimens were taken with the Exakta using microneg film, but in this case it was developed in "Ilford High Definition" developer. Unilateral daylight was used in the photography of whole specimens, as this gave perfectly even illumination overa large area. For photographs of fine detail, extension tubes were fitted to the camera, and strong lateral illumination was provided by a Beck spotlight. Prints were made on Airmail paper. Both Macro and Micro-photographs were mounted on white card to form plates, and these were re-photographed on Kodak B40 plates which were developed in Kodak D61a developer. Prints were then made on sheets of 10" x 8" Airmail paper. All this work was carried out by the author, but he wishes to acknowledge the advice, help and encouragement he received from Mr. Neville of the Mycology section of the Botany Department, University College of North Wales, Bangor.

Descriptive Terms.

In the following description of the cuticles of species of Gangamopteris and Glossopteris, it has been found convenient to use some terms in a sense not strictly applicable to recent plants. The cuticular pattern indicates the size and shape of the cells of the epidermis when seen in plan view. The term "cell" is used to describe

each unit of pattern which has been imposed on the cuticle by the underlying epidermal cell. It is readily admitted that in most cases no cellular structure is preserved, but the term has been used in this sense by many other workers in the field (Zeiller, 1896; Sahni, 1923; Hŕeg and Bose, 1960) and is easily understood. In describing the cell pattern it is often necessary to distinguish between those areas which were over the veins and those which lie between the veins. The terms "vein cell" or "cells over the veins", and the terms "mesh cell" or "cells of the mesh regions" are used respectively.

Epidermal cells are often papillate. The papillae may be of two types -

a) solid cuticular thickenings (Text fig. 22), and

b) hollow cellular outgrowths with or without additional cuticular thickenings, (Text fig. 31).

Salisbury (1927) has shown convincingly that it is desirable to use the stomatal index ($I = \frac{s}{e + s} \times 100$, where s = stomatal cells, e = epidermal cell per unit area) when comparing the stomatal distribution of different leaves or of the upper and lower surfaces of leaves, as this is less variable than the stomatal frequency, a value which depends largely on ecological conditions experienced during growth.

However, there is considerable inherent variation in the stomatal index of leaves of one species grown under the same conditions (e.g. according to Salisbury (1927) S.I. of Fagus sylvatica has a range of 7 - 27), and it is necessary to examine 200 or more leaves of each species and to employ statistical techniques before really useful

comparisons of S.I. can be made. This is clearly impossible in many investigations of fossil material, when only a few poorly preserved leaves are available. In spite of this it is usually possible to obtain some estimate of the relative abundance of stomates on the upper and lower surfaces of single leaves as equal sized pieces of both cuticles are usually obtained together from a particular part of a leaf. The ratio between the number of stomates on the upper and lower surfaces of a leaf may be called the "Stomatal ratio", and I have used this term in the comparison of several leaves in this Thesis.

SYSTEMATIC DESCRIPTIONS

The Genus Gangamopteris, McCoy 1875.

The specimen on which the genus Gangamopteris is founded was originally described by McCoy (1847) as Cyclopteris angustifolia. McCoy (1861) used the generic name Gangamopteris to describe the same frond, but did not publish either a specific or generic diagnosis until 1875.

Part of an amended diagnosis by Feistmantel (1879a) which was followed by Seward (1910b) is reproduced below.

"Leaves simple, sessile, varying in shape, obovate or spathulate, broadly lanceolate or rarely linear; the apex is usually blunt, but occasionally gradually tapered. In general appearance a Gangamopteris leaf is similar to that of Glossopteris indica, the chief difference being the absence of a mid-rib .....
.....The middle of the lamina, especially in the lower parts, is occupied by a few vertical veins, from which branches curve upwards and outwards towards the edge of the lamina. The secondary veins are connected by frequent anastomoses and agree very closely with those of Glossopteris. The lamina becomes narrower towards the base, which is either cuneate or ... slightly auriculate."

According to Arber (1905) the lower median veins are parallel and anastomosing.

The genus has a wide geographical distribution, having been found in the Antarctic, Australia, Central and Southern Africa, India and South America.

In all these areas, Gangamopteris is found only in the lower Gondwana deposits (i.e. those of Permo-Carboniferous age). It is represented in the Dwyka and Ecca Series in Central and Southern Africa (Table 1, page 5).

To date, some twenty species of Gangamopteris have been described by various authors, but the cuticle structure is known for only six of these (Srivastava, 1956; Høeg and Bose, 1960).

Gangamopteris sp.A.

Plate IC, Plate VIII A-D, Plate IX A & B, Text figures 3, 4, 5a & 8a.

Holotype. Specimen H.9.

Description.

This specimen is a broad, obovate leaf 12 cm. long and 6 cm. wide. A small part of the tip is missing and the state of preservation is poor (Plate IC). However, careful examination reveals that the central region of the lamina is occupied by eight to ten parallel and anastomosing veins spaced 1 - 1·5 mm. apart, from which the lateral veins curve out gently to meet the margin at an angle of 45° to the longitudinal axis; but in the upper part of the leaf the lateral veins bend rather sharply after leaving the central region, so that they meet the margin at an angle of from 80° - 90° to the longitudinal axis (Text fig. 8a). The lateral veins are spaced from 0·5 mm. to 0·75 mm. apart, and anastomose rarely to form long narrow meshes.

Cuticle.

The carbonaceous layer is very thin, and so badly worn that many parts of the specimen are completely denuded. The state of preservation of the cuticle taken from different parts of the leaf varied accordingly from very poor to excellent, as is shown in Plate VIII.

Upper Cuticle.

Cuticle taken from the region occupied by the median parallel

veins showed no differentiation into vein and mesh areas. All the cells are irregularly rectangular, approximately 60μ wide, from 60μ to 150μ long and with straight cell walls about 6μ thick (Plate VIII A). No stomates have been found in this region.

Preparations of cuticle obtained from other regions of the leaf showed similar arrangement of parallel-sided cells, and little differentiation between the vein and mesh areas (Plate VIII B & Text fig. 3).

The cells over the veins are mostly rectangular (Text fig.3 Plate VIII B) measuring approximately 50μ wide and from 100μ to 250μ long. The cell walls are straight and about 2μ thick. The mesh cells are almost identical to those over the veins, except that cells with oblique end walls and large hexagonal cells up to 350μ long and 75μ wide are more common in the mesh regions.

Stomates (Plate VIII B and IX A) are rare, and are only found scattered 550μ to 600μ apart, down the centre of the mesh regions. The stomates do not have a regular orientation and they are monocyclic. There may be four to six subsidiary cells, each measuring about 50μ by 75μ, [illegible] which are therefore appreciably smaller than the surrounding mesh cells.

In some cases, the position of the under-lying guard cells can be clearly seen, as shown in Text fig.3, but unfortunately. too few were well enough preserved to allow an accurate estimate of the size range to be obtained. The pairs of guard cells measured formed elliptical areas

from 40μ to 90μ long and from 30μ to 60μ wide. The stomatal pore varies in length from 35μ to 40μ.

Lower Cuticle.

The lower cuticle is thinner than the upper cuticle and the cells are smaller and more regularly arranged. In preparations taken from the median region it was not possible to distinguish between the vein and mesh regions. The cells are regularly rectangular, rarely distorted into elongated hexagons, 30μ to 40μ wide and 50μ to 90μ long (Plate VIII C.). The cell walls are straight and 1μ to 2μ thick.

Preparations taken from other parts of the lamina showed the cells over the veins to be rectangular, 30μ - 50μ wide and 50μ - 100μ long. The cells of the mesh regions are similar in size and shape, but oblique end walls are more common and many cells are isodiametric (Plate VIII D and Text fig. 5a).

The stomates are restricted to the mesh areas. Their orientation and distribution is irregular, and they are much more common than on the upper cuticle (Plate VIII D.).

There are from four to six subsidiary cells which are of about the same size as the surrounding mesh cells. The pair of guard cells lies beneath the subsidiary cells and forms a circular or an elliptical area between 60μ and 80μ across. The stomatal pore, therefore, lies at the bottom of a pit, and is from 30μ to 40μ long (Plate IX E., and Text fig.4).

Discussion and Comparison.

For discussion and comparison of Gangamopteris sp.A. with other species, see under Gangamopteris ermeloensis on page 45.

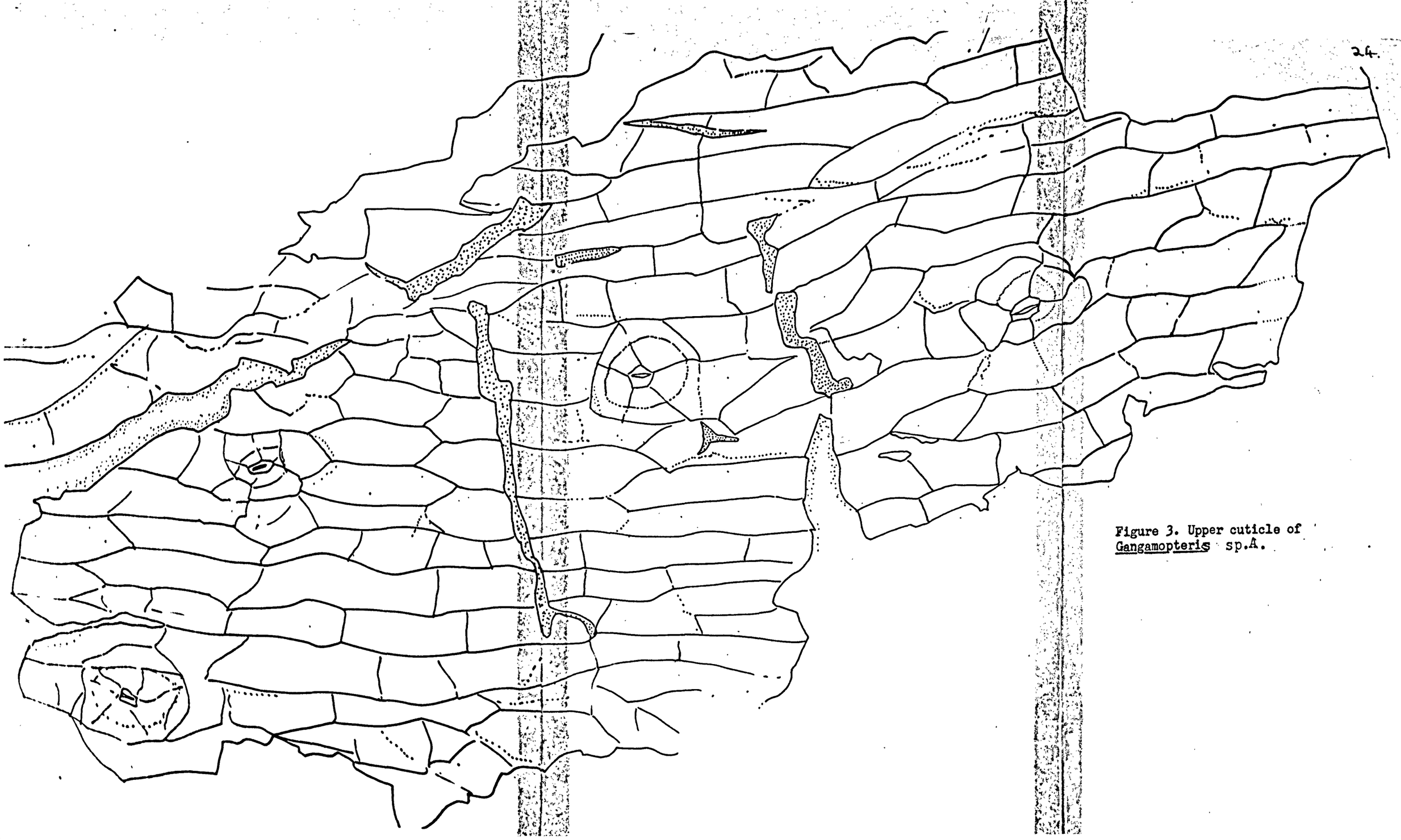


Figure 3. Upper cuticle of Gangamopteris sp.A.

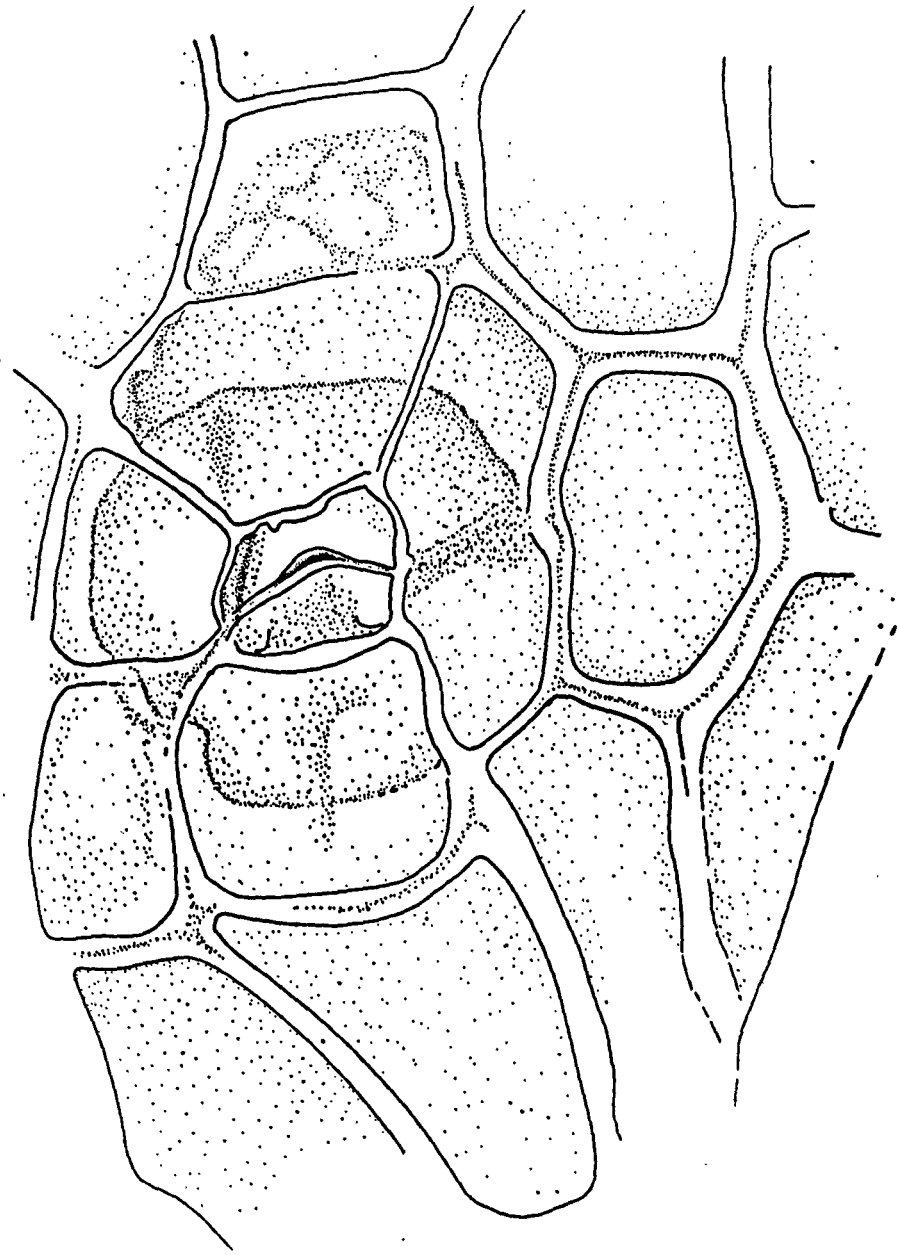


Figure 4. Gangamopteris sp. A.
Detail of stomate from the lower cuticle of the leaf.
(X 650)
Note the circular area of the guard cells and the rather small central pore.

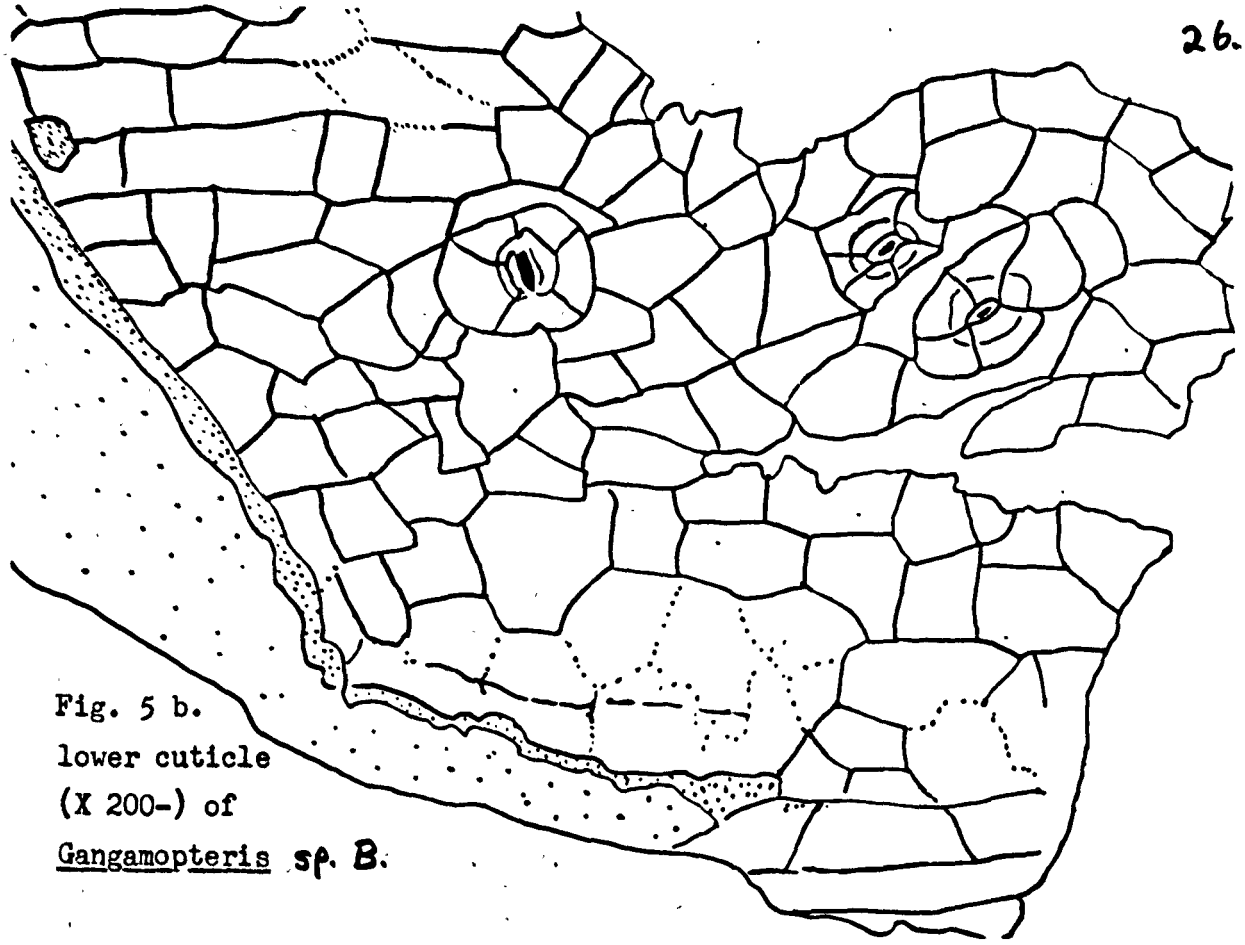
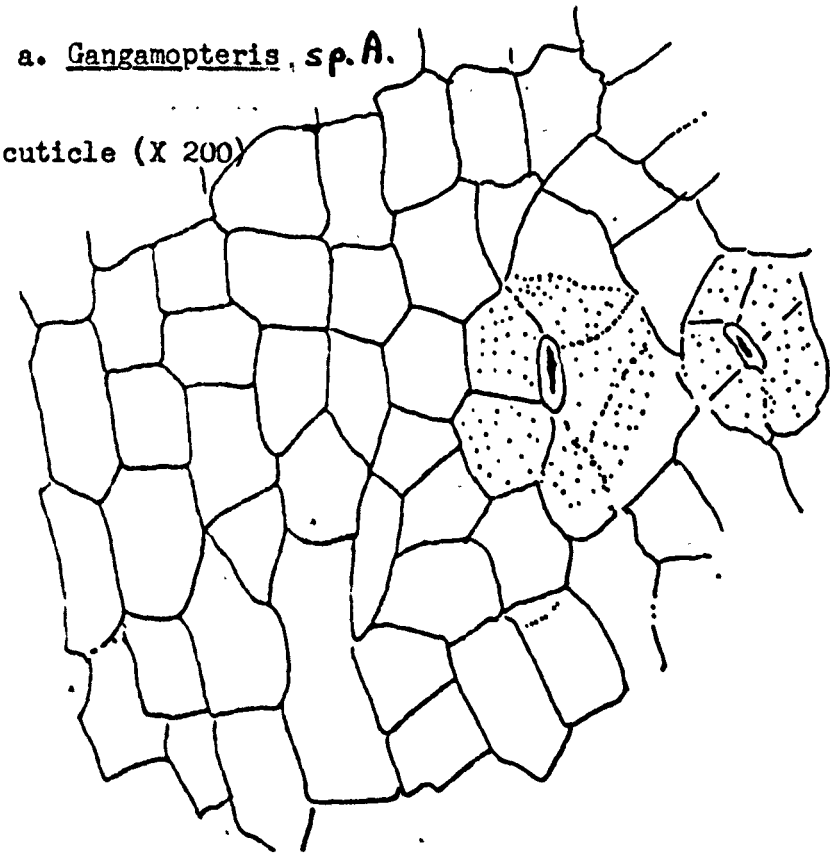


Fig. 5 b. lower cuticle (X 200-) of Gangamopteris sp. B.

Fig. 5 a. Gangamopteris sp. A.

lower cuticle (X 200)



Gangamopteris sp.B.

Plate I D, Plate IX C & D, Plate X A, Text figs. 5b, 6, 7, 8c.

Holotype. Specimen B.7d.

Description.

Specimen B.7d is apparently the basal portion of a leaf, and is 4 cm. long and 3·5 cm. wide. The state of preservation is good so that details of the venation can be clearly seen (Plate I D.).

There is a central band, approximately 12 mm. wide, which is occupied by eight to ten parallel and anastomosing veins. Lateral veins radiate from the base of the leaf and also arise as branches of the median veins. The lateral veins nearest the base curve out gently to meet the margin of the leaf at an angle of approximately 45° to the longitudinal axis. Further up, the lateral veins curve rather more sharply so that they reach the margin at an angle of 90° to the longitudinal axis, (Text fig. 8c and Plate I D.). Anastomoses are frequent, forming clear wide meshes from 0·5 mm. - 1·0 mm. wide and from 2·0 mm. to 8·0 mm. long.

Cuticle.

The cuticles are well preserved but tend to fragment along the line of the veins, so that only pieces about the same size as the meshes between the veins could be obtained.

Upper Cuticle.

The cells over the veins are usually rectangular in shape, or

elongated hexagons, measuring about 30μ wide and 90μ long. The cell walls are straight and from 2μ to 4μ thick. The veins are two or three cells wide (Text fig. 6).

The cells of the mesh regions are extremely irregular in both size and shape, ranging from more or less isodiametric square or polygonal cells, 40μ to 60μ across, to long, narrow polygonal cells 40μ wide and up to 160μ long (Text fig. 6 & Plate X A.).

The stomates are distributed irregularly within the mesh areas, but their orientation is usually with the long axis of the pore either at right angles to, or parallel to, the veins. (Text Fig.6.). This figure also shows that the stomates are either monocyclic or partly di-cyclic. There are usually five, but sometimes four or six subsidiary cells which are smaller than the other cells of the mesh area, measuring from 20μ to 30μ wide and from 30μ to 60μ long. The subsidiary cells are not papillate, but the walls which form the sides of the stomatal pit are heavily cutinised.

The guard cells lie beneath the subsidiary cells, and form a circular or elliptical area measuring from 40μ to 70μ across the long axis (Text figs. 6 & 7 and Plate IX C.). Text fig.7 and Plate IX C. also show the cutinised lips of the stomatal pore, which is about 30μ long.

Lower cuticle.

The lower cuticle is much thinner than the upper cuticle, and was rapidly "cleared" by the normal mounting medium, (glycerine jelly). The cuticle curled up when mounted in Euparol or Canada Balsam and was

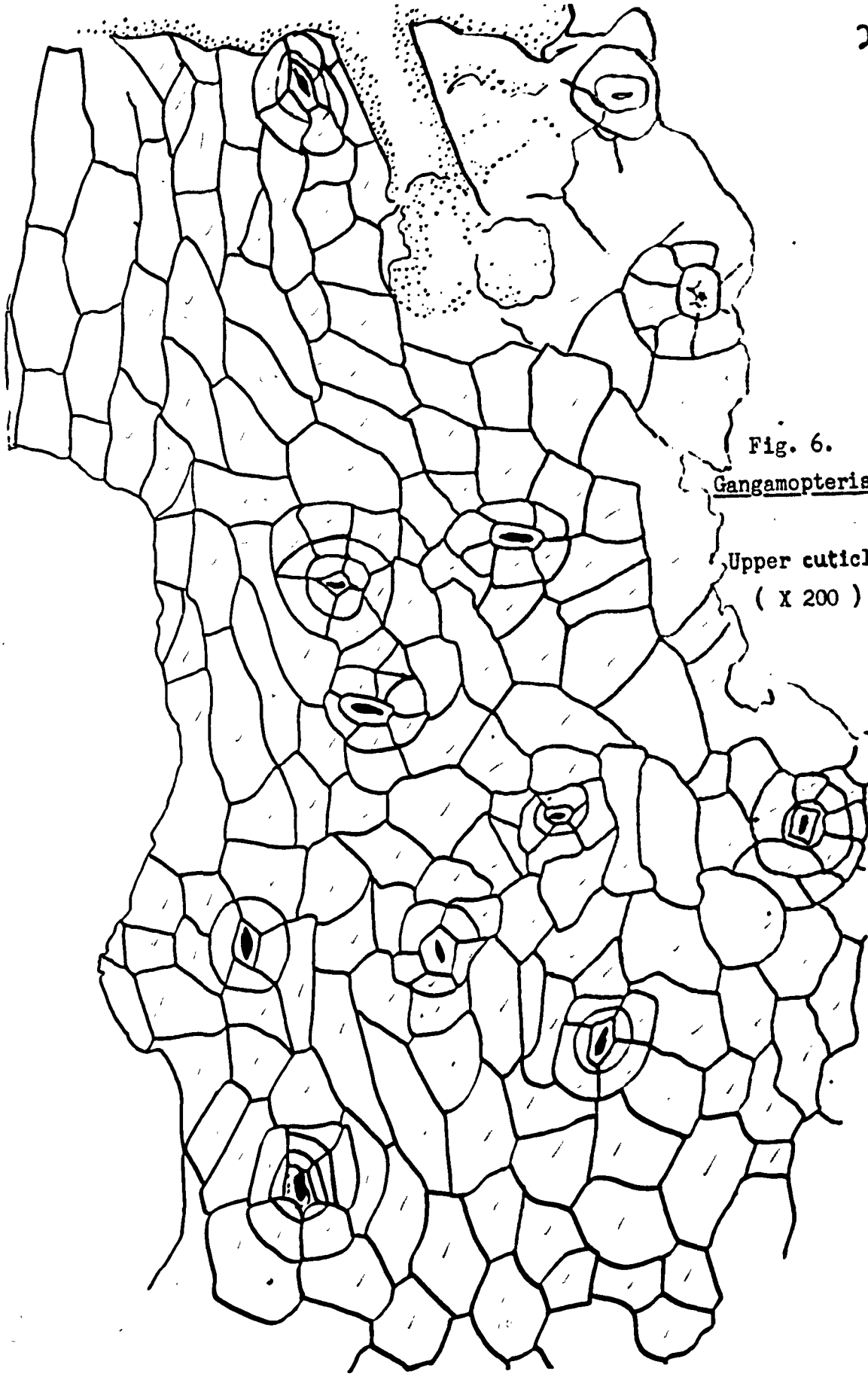


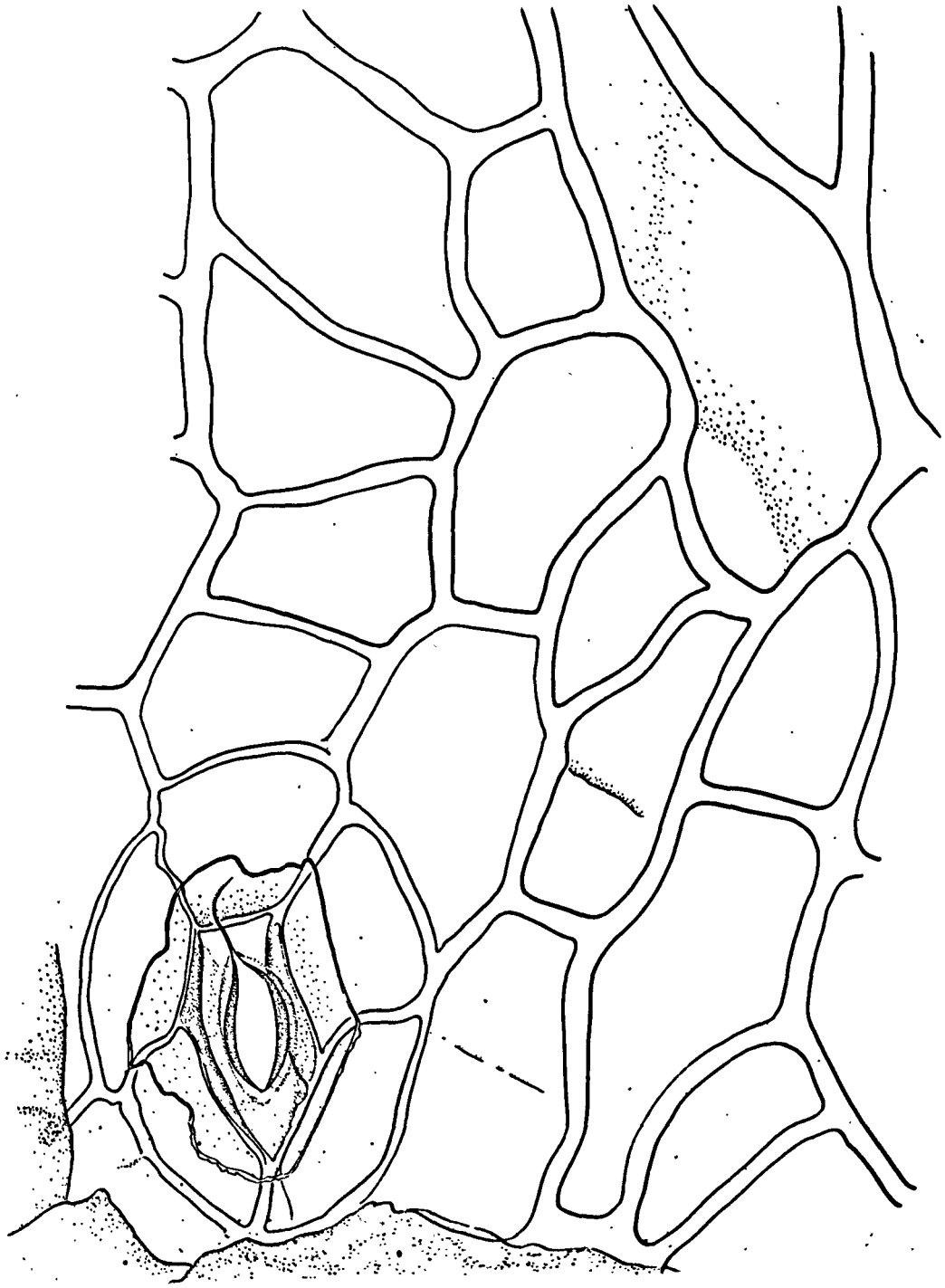
Fig. 6.
Gangamopteris sp. B.

Upper cuticle
(X 200)

Figure 7. Gangamopteris sp. B.

Detail of a single stomate and surrounding cells, from the upper cuticle of the leaf.

Note the well preserved guard cells and the cutinised lips of the pore, which are seen here from the inner surface of the cuticle.



for too delicate to unroll with needles. I was therefore unable to obtain a good photograph of the lower cuticle (Plate IX D.) but as is shown by comparing Text fig. 5b and Text fig.6, in the size and shape of the cells and in the distribution of the stomates, the upper and lower cuticles are practically identical.

Comparison and Discussion.

For discussion and comparison of Sphenopteris sp. B with other species, see under Sphenopteris arnoldensis on page 45 .

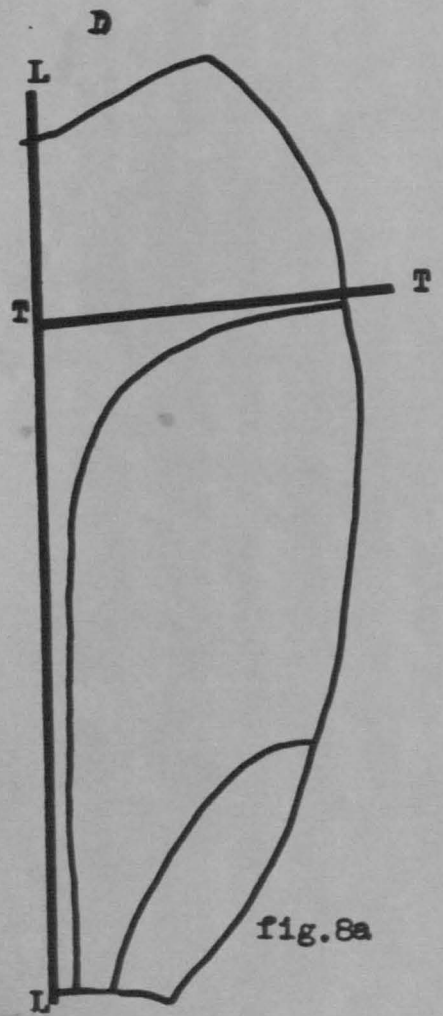


fig.8a

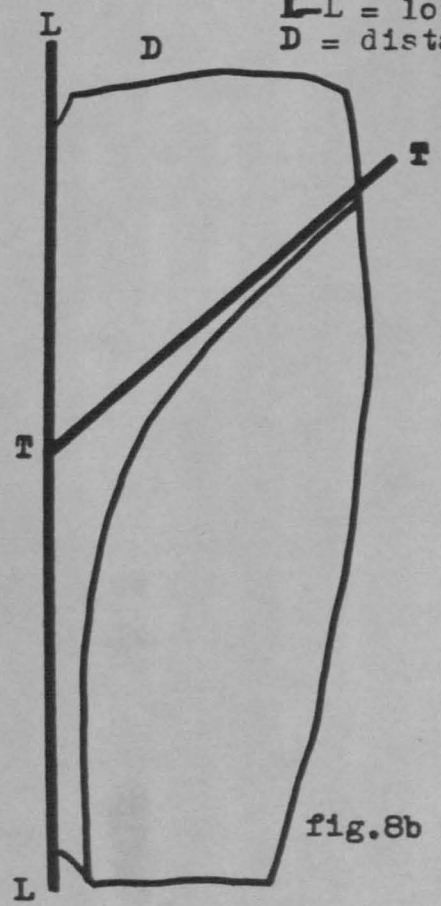


fig.8b

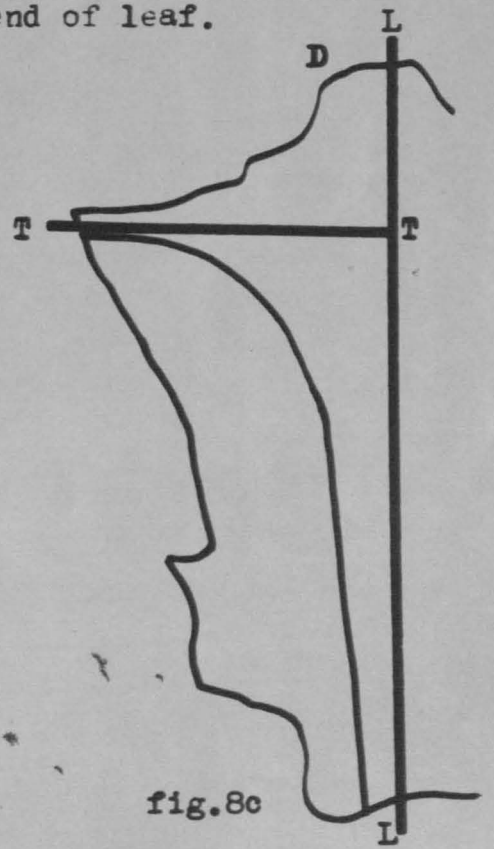


fig.8c

Key

T-T = line at a tangent to the veins at margin.
L-L = longitudinal axis of leaf.
D = distal end of leaf.

Fig.8.Diagrammatic representation of the vein curvature in a) Gangamopteris sp.A, b)Gangamopteris ermeloensis and c) Gangamopteris sp.B.

Ganzeropteris ermeloensis sp. nov.

Plate II A, B, E & F, Plate X B to D, Plate XI A to D, Plate XII A to D, Text figs. 8b, 9, 10, 11, 12, 13, 14 & 15

Holotype. Specimen H.7a. Figured Paratype. Specimen H. 14

Unfigured Paratypes. Specimens H.8c, H. 11d, H. 13c.

Diagnosis.

Macroscopic features.

Linear-lanceolate leaves with elliptic apices. Central region occupied by 8 - 10 parallel sporadically anastomosing veins which continue to within 5 mm. of the tip before fanning out. Lateral branches (0·1 - 0·3 mm. apart) arising from central veins at an acute angle and curving out gently to meet the edge of the lamina at an angle of 60° to the median axis, anastomosing infrequently to form long narrow meshes.

Microscopic features.

Upper cuticle thin, little difference between vein and mesh areas. Cells of vein areas more or less rectangular, 25μ - 50μ wide and up to 150μ long. Mesh cells 20μ - 40μ wide and 30μ - 80μ long, usually more or less rectangular but sometimes polygonal. Mesh areas 3 - 5 cells wide. Stomates 100μ to 300μ apart, pore parallel to the veins.

Lower Cuticle thin, vein and mesh areas clearly distinguishable. Vein cells more or less rectangular, elongated, 25μ to 60μ wide and 60μ to

160μ long. Cell walls straight and up to 5μ thick. Mesh cells irregularly polygonal, 30μ - 80μ wide and long. Mesh areas 5 - 12 cells wide. Stomates confined to mesh areas, distribution and orientation irregular. Subsidiary cells 4 - 7, irregular in shape, same size or smaller than mesh cells, usually faintly papillate, but not markedly overhanging the stomatal pit.

General description.

Specimen H.14 (Plate II, A, B.) is the largest and specimen H.7a (Plate II, E, F.) is the most complete of the leaves that have been assigned to this new species.

Specimen H.14 is incomplete. As is shown in Plate II A, most of one side of the leaf and its tip are missing. The base is attenuated and only one centimetre wide. The lamina expands gradually to its full width of 5 - 6 cm. (estimated) in a distance of 12·5 cm. The shape of the base suggests that the entire leaf was similar in shape to the smaller specimens listed above. Specimen H.7a (Plate II E, F.) is a linear-lanceolate leaf (17 cm. long, 2·5 cm. broad) narrowing smoothly to a small elliptic apex, and tapering gradually to a long narrow base.

In the basal part of all the specimens there is a shallow median groove which is occupied by several parallel anastomosing veins which run to within 2 mm. of the tip before they fan out. Lateral branches arise from the central veins at an acute angle and curve smoothly upwards and outwards to meet the edge of the lamina at an angle of 60° to the median veins. (Plate II B & F). The branches are

fine and crowded, anastomosing frequently to form narrow elongated meshes.

Cuticles.

Both cuticles are thin. Although the cuticle fragments obtained were small, there were sufficient pieces from different parts of the leaves for a complete picture of the whole to be built up.

Upper Cuticle.

The upper cuticle is in general rather poorly preserved. It varies greatly in thickness from one part of the leaf to another, but this seems to be the result of decay prior to fossilization or owing to damage sustained during the removal of the counterparts, rather than to any inherent variation. The cell pattern is very regular. Most of the cells are rectangular and there is little difference between the cells over the veins and those of the meshes. The latter are usually the smaller, and are also not so regular in shape. The vein cells are 25μ - 50μ wide and up to 150μ long, whilst the mesh cells are 20μ - 40μ wide and 30μ - 80μ long. The stomates are confined to the mesh areas and are spaced 100μ - 300μ apart depending on the size of the specimen (Text figs. 9a & 10b.). They are orientated with the pore parallel to the veins. The subsidiary cells are 4 - 7 in number and are 30μ - 50μ long. They are faintly papillate and overlap the guard cells so that the pore, which is 15μ - 20μ long, lies at the bottom of a shallow pit. The mouth of the pore is clearly marked by a thin ridge of cutin.

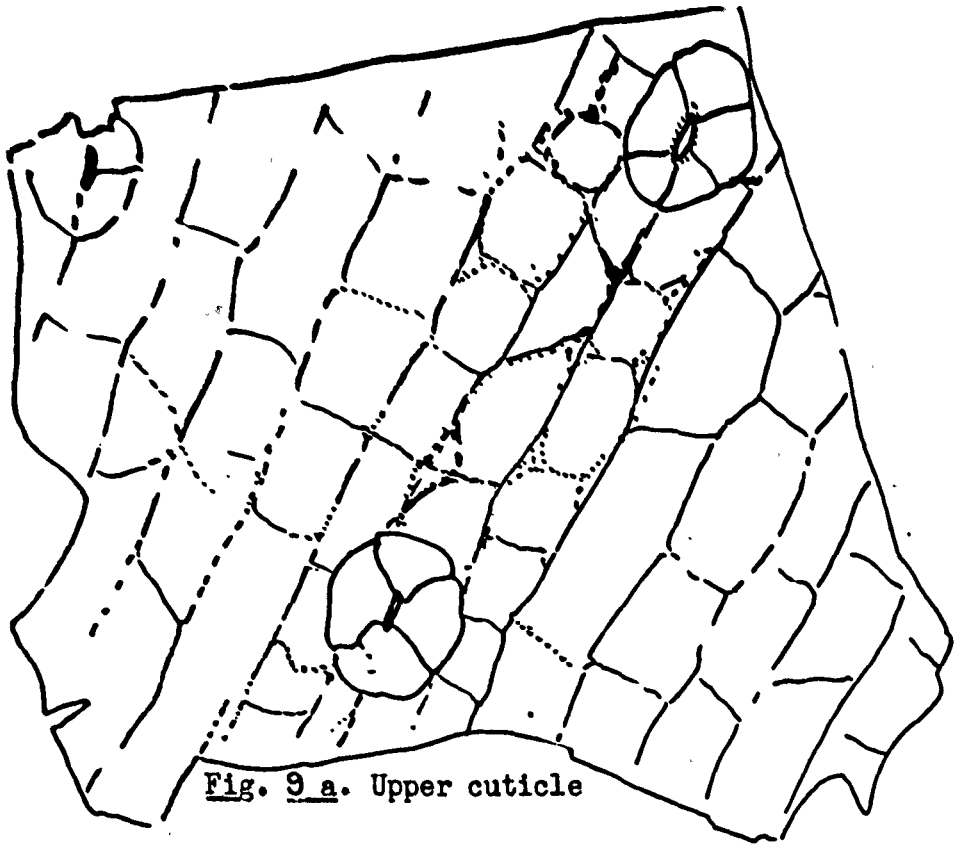


Fig. 9 a. Upper cuticle

Figure 9. Gangamopteris ermeloensis sp. nov.

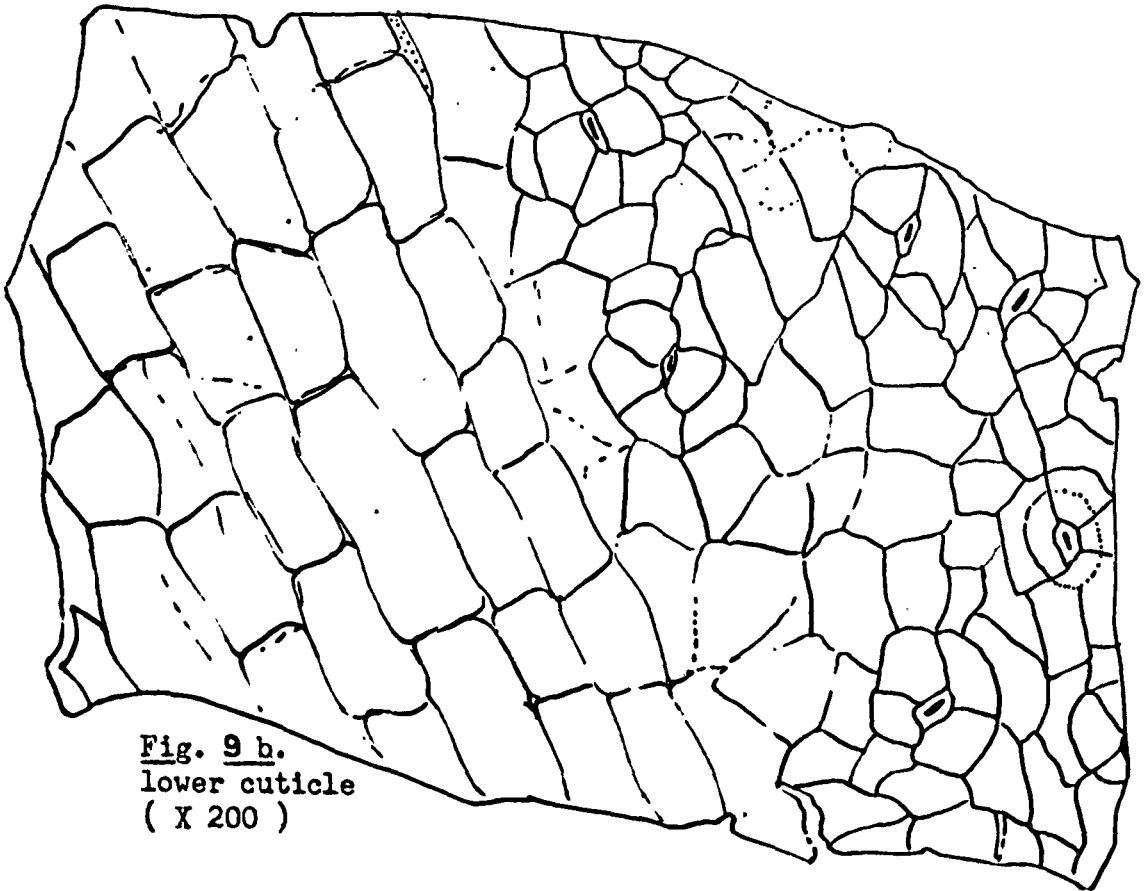


Fig. 9 b.
lower cuticle
(X 200)

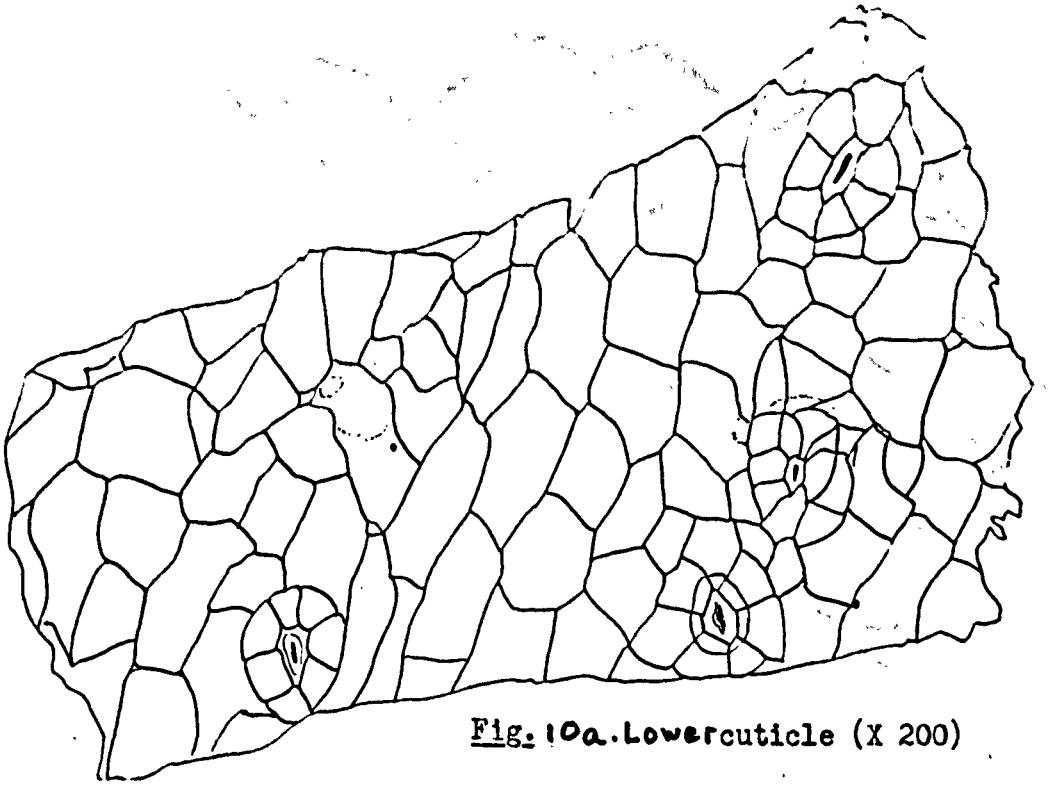
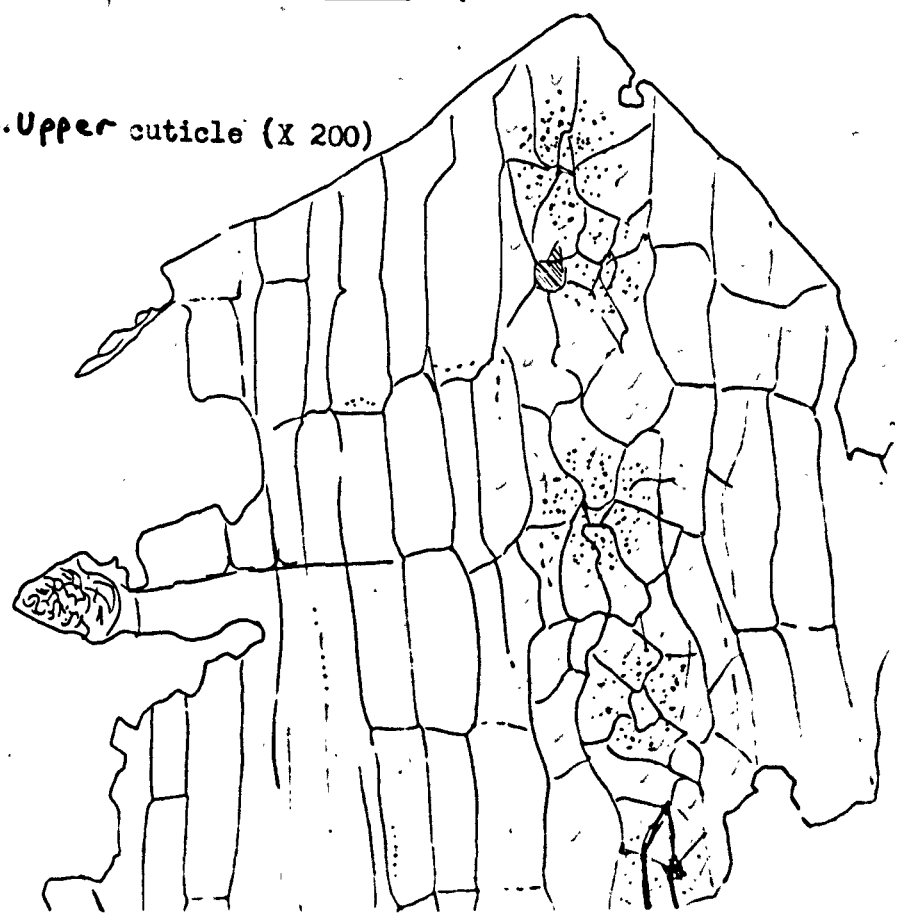


Fig. 10a. Lowercuticle (X 200)

Figure 10 Gangamopteris ermeloensis sp.nov.

Fig. 10b. Upper cuticle (X 200)



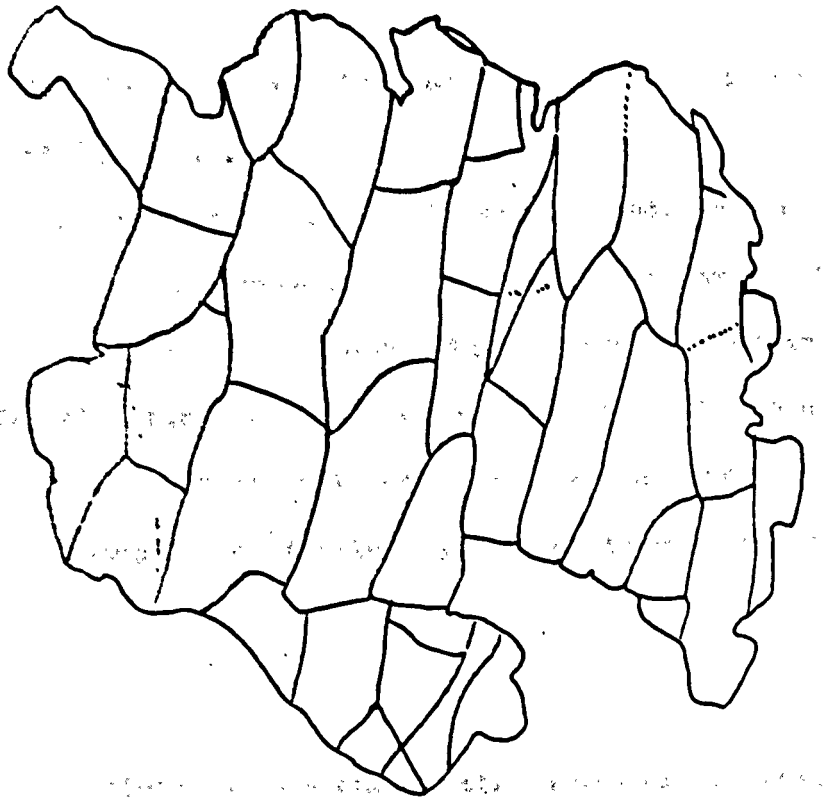


Fig.11a.Lower cuticle from the edge of the lamina.(X 200)

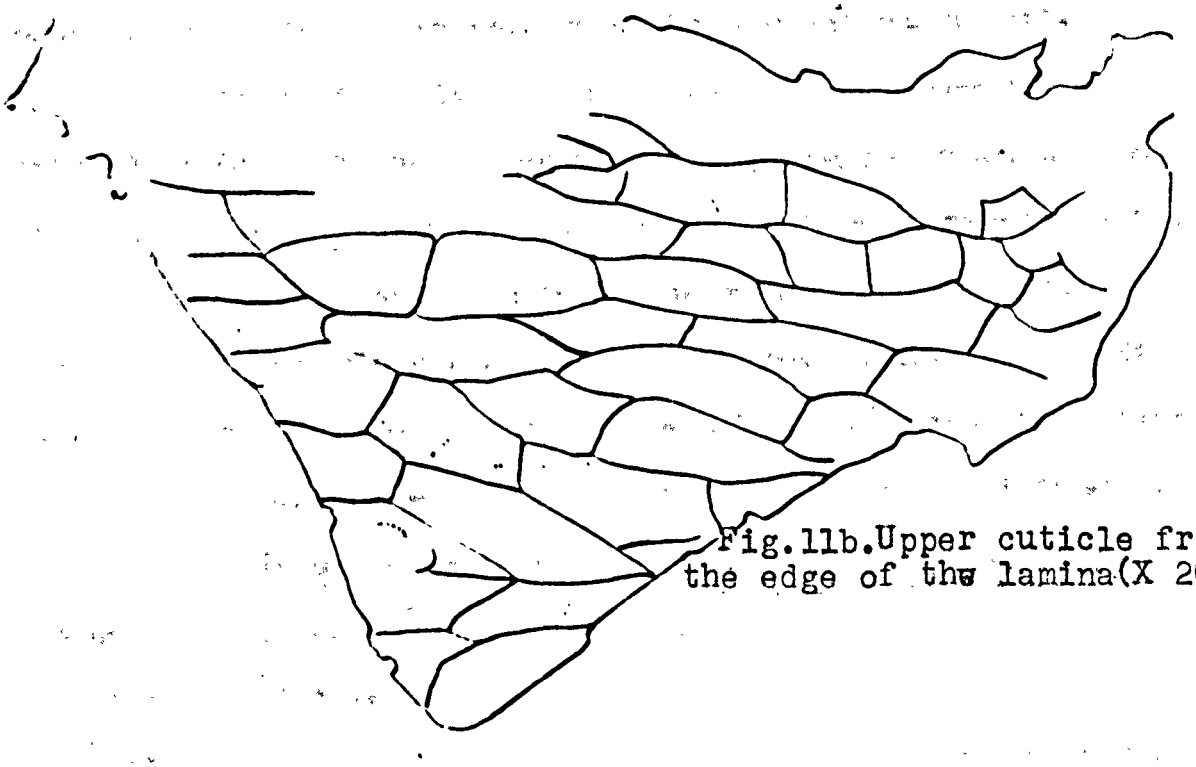


Fig.11b.Upper cuticle from the edge of the lamina(X 200)

Figure 11.Gangamopteris ermeloensis sp.nov.

The pair of guard cells forms an elliptical area with a mean diameter of about 50μ (Text fig. 12.).

The cell walls are straight or slightly curved, and are about 2μ thick. In fact the thickness of the cell walls appears to be directly related to the state of preservation of any particular piece of cuticle. In well preserved cuticle the cell walls show their maximum thickness, but they are extremely thin or even invisible in poorly preserved pieces. No stomates have been observed between the median veins.

Lower cuticle.

The lower cuticle is in a much better state of preservation than the upper cuticle, possibly because the lower cuticle has not been damaged during the separation of the part and counterpart.

The cells of the lamina show clear differentiation into vein and mesh areas. The cells over the veins are regularly arranged and are more or less rectangular or polygonal. There is some variation in the size of these cells, depending on the size of the specimen from which the cuticle was taken. Those from specimen H.14 (Text fig. 9b.) are 40μ - 60μ wide and 100μ - 160μ long, whereas those from specimen H.7a. are 25μ - 30μ wide and up to 150μ long (Text fig.10a.)

The mesh cells are irregularly polygonal, measuring between 30μ and 60μ across. They may be isodiametric or elongated parallel to the veins. The stomates are found in two broad bands running the full length of the leaf, one on either side of the median groove and

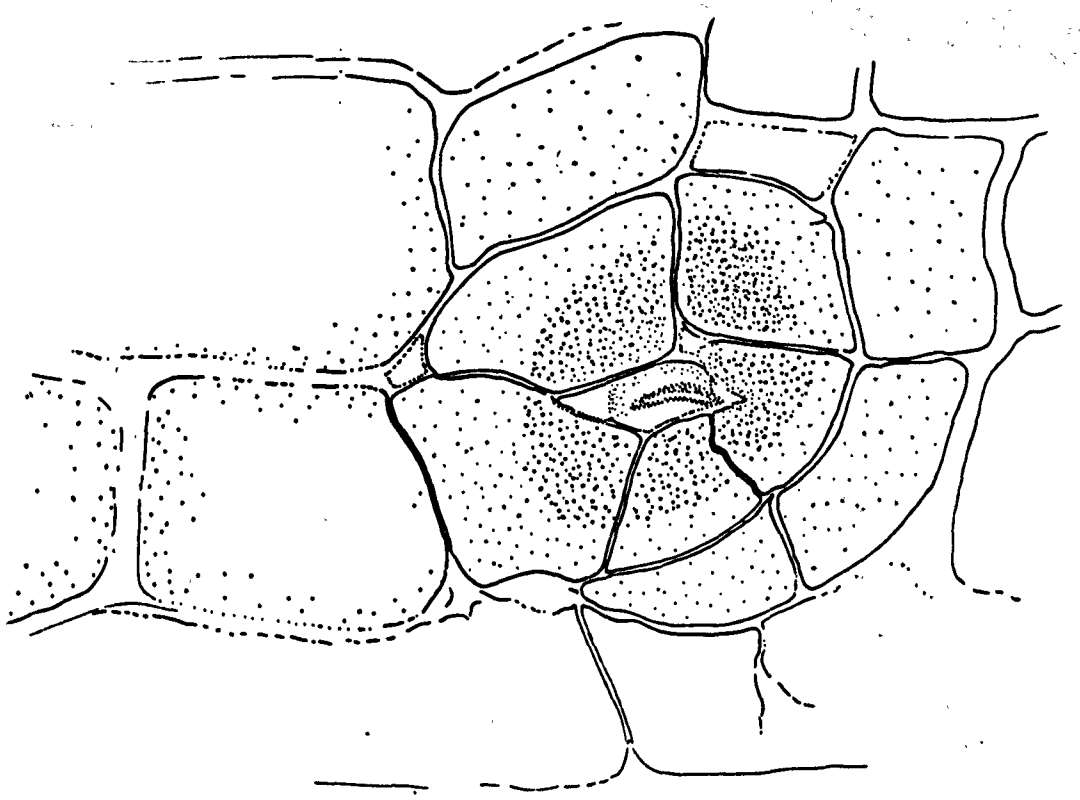
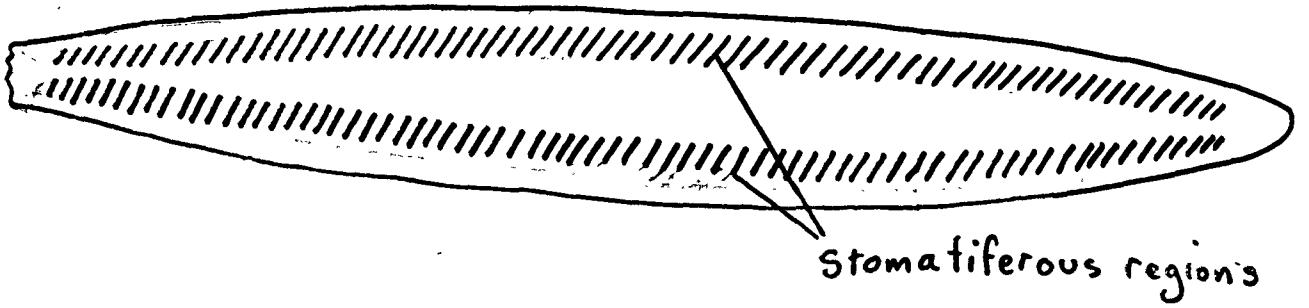


Figure 12a. Gangamopteris ermeloensis sp. nov.
A single stomate from the rather poorly preserved Upper cuticle. The cutinised lips of the pore can be seen and the area occupied by the guard cells is represented by the oval of dense stippling.

Fig. 12 b. Diagram showing approximate position of stomatiferous bands in G. ermeloensis



extending about two thirds of the way to the margin (Text fig. 12b.). The stomates are restricted to the mesh regions and are rather closer together than those of the upper cuticle, often being contiguous. The subsidiary cells are sometimes faintly papillate (Text figs. 13, 14) and are similar in size to, or somewhat smaller than, the adjacent cells of the mesh region. There are 4 - 7 subsidiary cells per stomate, which are monocyclic or partly dicyclic and overlap the guard cells (Text figs. 13 & 15.). The guard cells are 45μ - 60μ wide. They are well preserved and the cutinised lips of the stomatal pore can be clearly seen (Text figs. 13, 14, 15; Plate XI, B & C.).

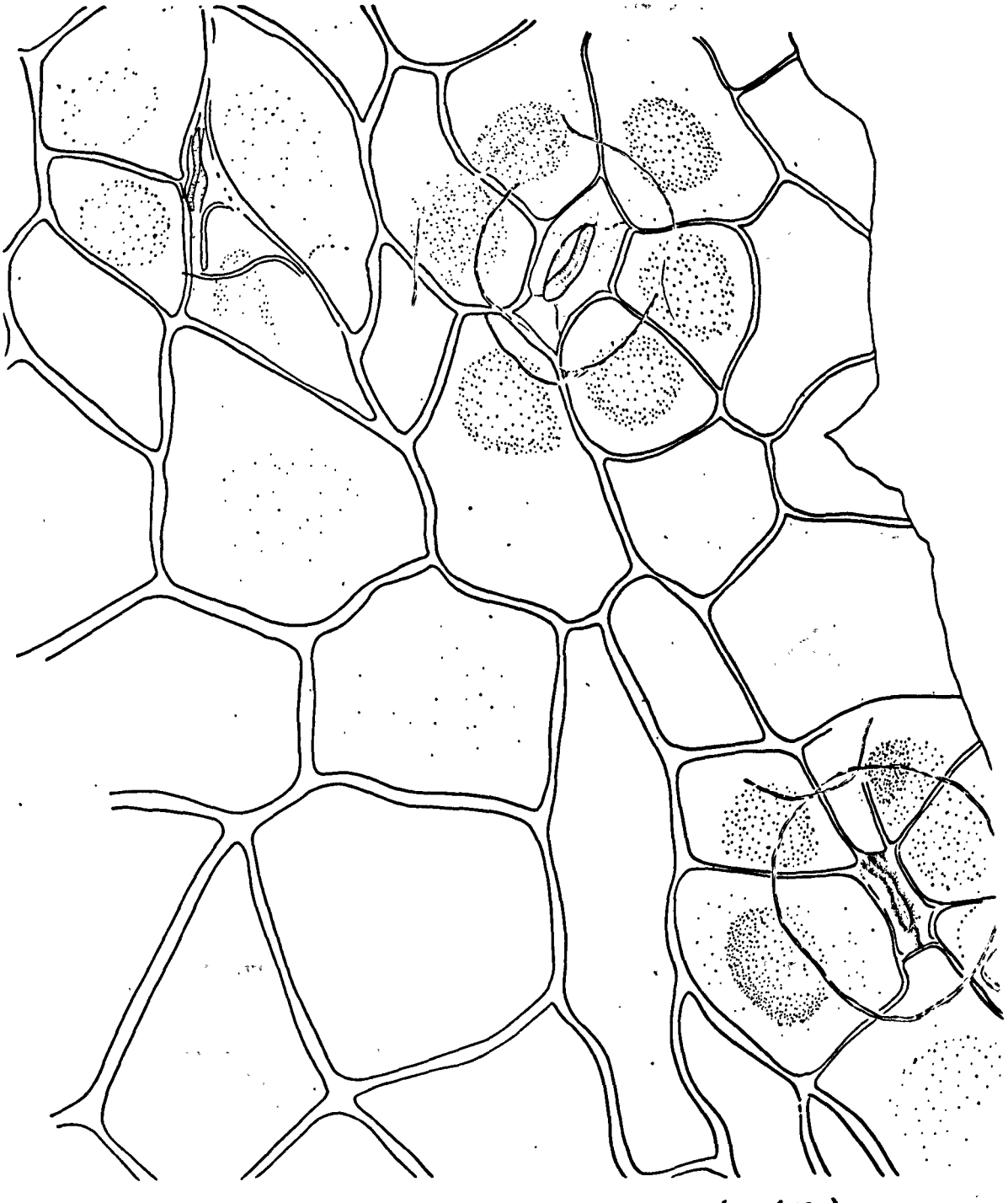


Fig.9. Gangamopteris ermeloensis sp. nov. (X 650)
Stomates from lower surface of leaf, with cutinised lips of the pore and pappilate subsidiary cells. Also traces of guard cells can be seen.

Figure 15. Gangamopteris ermeloensis sp.nov.
Stomate with five subsidiary cells. The outline of the guard cells and the thickened lining of the pore can be clearly seen. Viewed from the inner surface of the upper cuticle. (X 650)

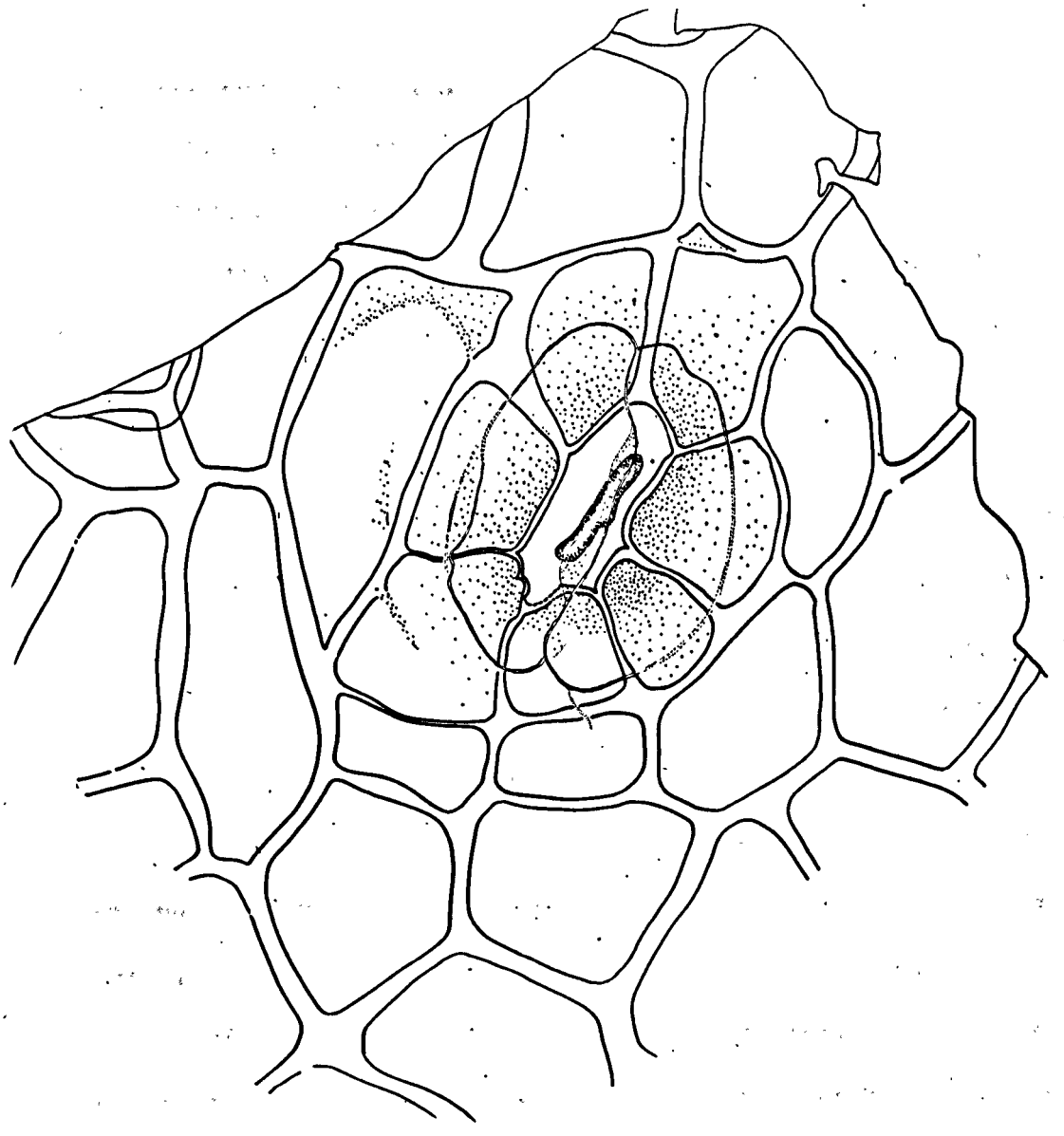


Figure 16. Gangamopteris ermeloensis sp.nov
Stomate with seven subsidiary cells. The fine structure of the guard cells and the stomatal pore is very well preserved. The subsidiary cells are thickened slightly on their inner edges, forming a broad, shallow pit. Viewed from the inner surface of the upper cuticle.(X 650)

Comparison and Discussion.

The leaves described so far show a striking similarity in the general nature of their cuticles, so that on this basis alone it is clear that they should all be placed in the same genus. Their venation, consisting of several, median, parallel, anastomosing veins and a network of lateral veins is typical of the genus Gangamopteris McCoy (1875). Owing to differences in their leaf shape, in the pattern of their lateral veins and in the detailed structure of their cuticles, I am by no means certain that they should all be placed in a single species. For this reason I have instituted a new species, Gangamopteris ermeleensis sp.nov. for some of the specimens and called two others Gangamopteris sp.A. and Gangamopteris sp.B.

To avoid needless repetition the three new taxa are compared with one another, and then each is compared with previously described species.

Both Gangamopteris sp.A. and Gangamopteris sp. B. are broad-based obovate leaves with 8-10 parallel anastomosing median veins. In both, the lateral veins arise at an acute angle, but soon bend sharply to meet the margin, at an angle of 90° to the longitudinal axis. Some are even reflexed. In these characters they differ from the specimens assigned to Gangamopteris ermeleensis, which have linear lanceolate narrow-based leaves, and in which the lateral veins curve out gently to meet the margin at an angle of 60° to the median axis. Gangamopteris sp.B has a vein pattern of relatively short broad meshes in contrast to the

long, narrow meshes of Ganganopteris erraloensis and Ganganopteris sp.A. In addition, Ganganopteris sp.B differs from Ganganopteris erraloensis in having almost identical upper and lower cuticles, whereas there is a clear difference between the upper and lower cuticles of the latter. The stomatal ratio (see page 18) of Ganganopteris erraloensis is about 1/2 and the stomates are confined to stomatiferous bands down each side of the leaf, whilst in Ganganopteris sp.B. the stomatal ratio is 1/1 and the stomates are most abundant between the median veins.

Ganganopteris sp.A differs from Ganganopteris erraloensis in having particularly large cells and widely spaced stomates on the upper cuticle, although the leaf is not particularly large.

Both Ganganopteris sp.A and Ganganopteris sp.B have stomates in which the subsidiary cells are not papillate, whilst they are frequently so in Ganganopteris erraloensis.

Ganganopteris sp.B differs from Ganganopteris sp.A in having shorter broader meshes and in having identical upper and lower cuticles. The stomatal ratio of Ganganopteris sp.B is 1/1 and that of Ganganopteris sp.A is 1/3. Stomates are common between the median veins of both cuticles of Ganganopteris sp.B, but they are absent from this region in Ganganopteris sp.A.

The differences and similarities in these three taxa are briefly summarised in Table 2 (pages 48 + 49).

If examination of further better-preserved specimens shows that the differences between these taxa are constant, it would support the erection of two new species; but if intermediate types were discovered

it might be necessary to merge all or any two of these taxa.

All three taxa can be distinguished from the specimens described by Srivastava (1956) and by Hoeg and Bose (1960), as Gangamopteris obovata, in which the stomates are restricted to the lower cuticle, Gangamopteris arnelensis also differs from Gangamopteris obovata in having a linear lanceolate leaf instead of an obovate leaf, and Gangamopteris spp. A. and B. differ in the arching of the lateral veins.

The macroscopic features of Gangamopteris sp.A and Gangamopteris sp.B are very similar to those of Gangamopteris castellanosii Archangelsky (1957, 1958), a species which has so far only been recorded from Argentina. Archangelsky (personal communication) agrees that these specimens are very close to Gangamopteris castellanosii since the arching of the lateral veins to meet the margin at an angle of 90° to the longitudinal axis is the main diagnostic feature of his species.

However, the type specimen of Gangamopteris castellanosii has no cuticular remains, so that if the separation of Gangamopteris sp.A and Gangamopteris sp.B is supported by later work, it would appear that the form species Gangamopteris castellanosii consists of at least two different species. It is, of course, impossible to say if either "A" or "B" is identical with Archangelsky's species.

The name Gangamopteris castellanosii must be retained for leaves which agree with the diagnosis given by Archangelsky (1957, 1958) and which do not have well preserved cuticles.

Leaves which agree with Archangelsky's diagnosis and which also have well preserved cuticles should be assigned to a different species,

Table No. 2. A COMPARISON OF THE MAIN FEATURES

CARBALLOPTERIS sp.A

Macroscopic features	Carballopteris arnaloensis.
Shape of leaf	Linear - lanceolate
Median veins	Curve out gently
Lateral veins	Curve out gently
Angle of veins at margin to longitudinal axis of leaf	60°
Shape of meshes	Long and narrow
Microscopic features	
Upper cuticle	
Marked difference between veins and meshes in median zone	-
Stomates in median zone	Present
Size of cells in median zone	25µ - 50µ x 150µ
Marked difference between veins and meshes of lamina	-
Size of cells of lamina	20µ - 40µ x 30µ - 80µ
Stomates, distribution and orientation.	In mesh areas, isolated, 100µ - 300µ apart. More parallel to the veins.
Number of subsidiary cells	4 - 7
Width of mesh areas	3 - 5 cells
Lower cuticle	
Marked difference between veins and meshes in median zone.	+
Stomates in median zone	Present
Stomates on lamina	Present
Stomatal arrangement	Numerous, in scattered groups
Papillate subsidiary cells	Present +
Stomatal ratio	1/2
Marked difference between upper and lower cuticles.	+

CF GANGAMOPTERIS HEXALOBOSIS sp. nov.

& GANGAMOPTERIS sp. B.

Gangamopteris sp.A	Gangamopteris sp. B
Obovate	Obovate
Tend more sharply	Tend more sharply
Tend more sharply	Tend more sharply
90°	90°
Long and narrow	Shorter and wider
-	+
Absent	Present
50μ - 75μ x 60μ - 150μ	30μ - 90μ x 40μ - 160μ
-	+
50μ - 75μ x 100μ - 350μ	40μ - 60μ x 40μ - 160μ
In mesh areas, isolated, 550μ - 600μ apart. Orientation irregular.	Numerous, in scattered groups within mesh area. Pore at right angles or parallel to veins.
4 - 6	4 - 6
8 - 10 cells	10 - 16 cells
-	+
Absent	Present
Present	Present
Few, in scattered groups	Numerous, in scattered groups
-	-
1/5	1/1
+	-

possibly to one described in this Thesis. This practice is supported by Pant (1958), by Høeg and Lone (1960) and by Archangelsky, (personal communication, 1962) and is in accordance with the recommendations of the International Code of Botanical Nomenclature. Recommendation P.H.6F states "Palaeobotanists should exercise great caution in applying to well preserved specimens names which have been originally attached to poorly preserved specimens or to specimens which have been inadequately described or figured."

The smaller specimens of Gangamopteris arraloensis bear a striking resemblance to the leaf described by Srivastava (1956) as Gangamopteris indica. The tip of Srivastava's specimen is not preserved, but the remainder (13 cm. long and 2·5 cm wide) is almost identical in shape to the corresponding portion of the present species. Srivastava's description of the lateral veins arising from the median veins and forming long, narrow meshes shows a leaf essentially the same as Gangamopteris arraloensis. The lower cuticles of these two species are almost identical, but Gangamopteris indica does not show such a wide range in the number of subsidiary cells as is found in Gangamopteris arraloensis and the subsidiary cells are never papillate. There are more striking differences between their upper cuticles, as that of Gangamopteris indica shows no difference between the vein and mesh areas and the cells are strictly rectangular and have thin sinuous walls. From their similarities it is clear that these species are closely related. In fact, varying ecological conditions could give rise to such differences as do occur within a single species, but they could equally

well be valid specific differences. (See General discussion, page 137). I do not think that there is sufficient evidence positively to identify the specimens described here as Ganganopteris arneloensis with Ganganopteris indica Srivastava, particularly as that species is founded on a single specimen. In the absence of positive evidence to the contrary, other authors have assumed that such differences are at a specific level, and not merely showing the existence of ecotypes within a species (Srivastava,1956; Pant, 1958). In these circumstances I feel it is justifiable to maintain two distinct species.

Apart from the obvious difference in leaf shape, both Ganganopteris sp.A and Ganganopteris sp.B can be easily distinguished from Ganganopteris indica as Srivastava's species has an upper cuticle showing rectangular cells with clearly sinuous walls.

As far as macroscopic features are concerned, Ganganopteris arneloensis also bears comparison with three species which have no well preserved cuticles.

Ganganopteris buriadica Feist (1879c) was first described as part of a pinnate frond, but Arber (1905) did not think that this was so. The leaf is more spatulate and its base is less attentuated than the present species. The lateral veins of Ganganopteris buriadica radiate from the base whilst those of Ganganopteris arneloensis arise as branches of the median veins and then curve out smoothly to the edge of the lamina.

The largest specimen of Ganganopteris arneloensis would certainly be placed in Ganganopteris kashmirensis Seward (Seward and Smith-Woodward, 1905), if its cuticle structure was not known.

The smaller specimens of Gangamopteris ermeloensis are rather more similar to Gangamopteris angustifolia McCoy (1847). McCoy's type specimen was redescribed by Arber (1905) and further specimens are figured by Archangelsky (1957). The margins of these leaves are parallel over the greater part of their length, and both Arber and Archangelsky attach great importance to an acute apex and a sharply contracted base as diagnostic characteristics of the species.

As the leaves placed in Gangamopteris ermeloensis do not have parallel margins, but do have well preserved cuticles, attenuated bases and, where present, an elliptical apex, these South African specimens cannot be referred to Gangamopteris angustifolia.

Gangamopteris obovata (Carruthers) D. White 1908

Plate I, A and B

Specimens. H.3a, H.8c, H.10, H.17.

Nomenclature.

In an article for the Geological Magazine, Carruthers (1869) figured a leaf from the Brazilian coal-fields, and called it Noeggerathia obovata sp.nov. His diagnosis was concise and clear; "Frond sessile flat, entire elongate obovate, attenuated towards the base; nerves dividing dichotomously". From his drawing there does not appear to be a mid-rib, but the central region is occupied by several parallel dichotomising veins.

Arber (1905) states that his examination of the type specimen revealed that the central and lateral veins anastomosed freely. This clearly shows that the specimen belongs to the genus Gangamopteris, and Arber suggested that it was probably the same species as many fronds described as Gangamopteris cyclopteroides by Feistmantel.

Carruthers' specimen is very similar in form to Gangamopteris cyclopteroides Feist., variety attenuata (Feist, 1886). This and many other varieties of Gangamopteris cyclopteroides described by Feistmantel, as well as Carruthers' Noeggerathia obovata, were all included in Arber's list of synonyms for the species Gangamopteris cyclopteroides (Arber 1905). White (1908) named his Brazilian leaves Gangamopteris obovata. Lundquist (1919) accepted White's determination, and considered

Gangamopteris cyclopteroides Feist., and Gangamopteris obovata (Carruthers) White to be synonyms. Dolianiti (1954) believed White's designation to be correct, although he admitted having used Gangamopteris cyclopteroides erroneously in previous papers.

According to the rules and recommendations of the International Code of Botanical Nomenclature (1956) the evidence available clearly shows that Gangamopteris obovata (Carruthers) D. White, is the correct designation of the leaves described as Gangamopteris cyclopteroides Feist.

General Description

Macroscopic features.

Specimen M.10 (Plate I A.) is incomplete. It consists of the central and right hand parts of the lamina, while most of the left side of the leaf and its tip are missing. The shape of the entire leaf would appear to be elliptic-obovate. The central part of the leaf is occupied by between five and ten parallel and anastomosing veins, which are 0·5 mm. to 0·75 mm. apart. From these, branches arise at an acute angle and curve out smoothly to the margin of the leaf. These veins anastomose frequently, forming long narrow meshes about 0·5 mm. wide and 12 mm. to 20 mm. long (Plat I B., specimen M.17).

Cuticles.

Although the carbonaceous layer was quite thick, only two specimens (specimens M.10 and M.17) yielded any cuticle at all, and in these cases the cuticle was so fragmentary and poorly preserved that only

occasional indications of cell outline were observed.

The cells appeared to be basically rectangular in shape, rather larger than those of the better preserved specimens described in this Thesis, and not unlike those described by Srivastava (1956) and by Hoeg and Bose (1960) from specimens called Gangamopteris cyclopteroides (G. obovata). No stomates were observed, but this is not surprising considering the size and the condition of the cuticle fragments obtained.

Comparison and Discussion.

As their cuticles were so badly preserved, only macroscopic features were considered in the identification of these specimens. Although incomplete, they seem to be identical with Gangamopteris cyclopteroides var. acuminata Feist (Plate 8a, fig. 5 of Feistmantel, 1886) and also very similar to the variety attenuata (Plate 13a fig.6 of Feistmantel, 1886). I am in fact unable to distinguish between those two varieties of Gangamopteris cyclopteroides as figured by Feistmantel in "The Fossil Flora of the Coalfields of Western Bengal" (1886). The sole distinguishing feature is the slightly longer leaf base of the variety attenuata so that the variety acuminata might even be an incomplete specimen of the variety attenuata.

Feistmantel's many varieties were merged by Arber (1905) as they were mostly founded on very small fragments which gave no clear idea of their form, and as they were in any case practically indistinguishable from each other.

As Carruthers' specific name clearly takes precedence over that

of Feistmantel, the present specimens are described as Gangamopteris obovata (Carruthers) White.

Macroscopically, Gangamopteris obovata can be distinguished from Gangamopteris castellanosii Archangelsky (1957a, 1959) and the specimens described here as Gangamopteris sp.A and sp.B as the lateral veins do not curve to meet the margin of the leaf at an angle of 90° to the longitudinal axis.

Gangamopteris obovata can also be distinguished from Gangamopteris ormeloemis (Page 33) on macroscopic features, as the latter has relatively long linear-lanceolate leaves with an elliptical tip.

Cardiopteris sp. C

Plate II C and D, Plate XII E, Plate XIII A - D, Text figs. 16a, 16b and 17

Specimen H.2a.

Description.

This specimen is a small fragment of a leaf, 1·5 cm. wide and 7·5 cm. long, which would hardly be worthy of description if the form of the venation and the cuticles were not well preserved.

The shape of the entire leaf cannot be determined from this specimen, but the base tapers gradually from about 3 cm. to 0·7 cm., in a distance of about 7·5 cm. (Plate II C.). From the base run six to eight widely spaced parallel veins, which anastomose infrequently. Lateral veins radiate from the base and also branch out from the median veins at an acute angle. As shown in Plate II D, the lateral veins curve out gently to meet the margin of the leaf at an angle of 30° to 45° to the median veins. Each vein may dichotomise once or twice, but anastomoses are rare, particularly near the base of the leaf.

Cuticles.

The carbonaceous layer broke into small fragments when removed from the specimen, so that it was not possible to obtain large pieces of cuticle.

Upper Cuticle.

The upper cuticle is moderately thick, and shows clearly the difference between the veins and meshes (Text fig. 16a) and the papillate nature of the majority of the cells (Plate XIII D). These illustrations also show that the cells over the veins are polygonal or rectangular and elongated along the veins. The longest walls are more or less parallel, straight, and about 2 μ thick. The cells are from 30μ to 50μ wide, and from 100μ to 150μ long.

The cells of the mesh regions are polygonal or quadrangular and may be isodiametric or elongated, measuring from 50μ to 100μ across (Text fig. 16a and Plate XIII D.). The cell walls are straight or slightly curved, (i.e. not sinuous) and they are about 2μ thick.

The stomates are confined to the mesh regions, and are arranged in one or more rows parallel to the veins (Text fig. 16a), the number of rows being dependent on the width of the mesh areas. The stomates are mono- or dicyclic, and the 4 - 6 subsidiary cells together form a more or less circular area 70μ to 100μ in diameter. The stomatal pit formed between the subsidiary cells is up to 60μ long, and is often heavily lined with cutin (Text fig. 17). The pore between the underlying guard cells is also heavily cutinised, and is about 20μ long. The subsidiary cells are invariably papillate and the cells of the veins and mesh areas are usually similarly marked or thickened (Plate XIII B & D). Where this is not clear, it appears to be due to poor preservation rather than to an original lack of papillae.

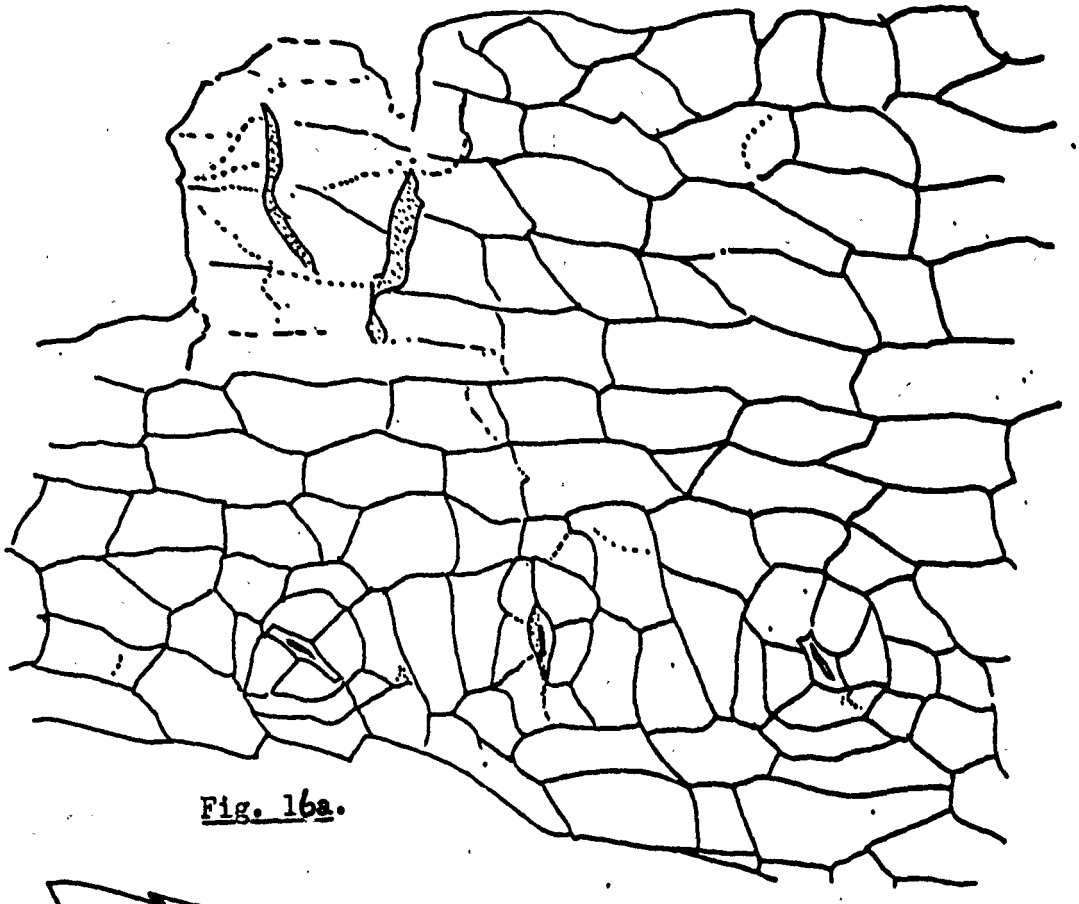


Fig. 16a.

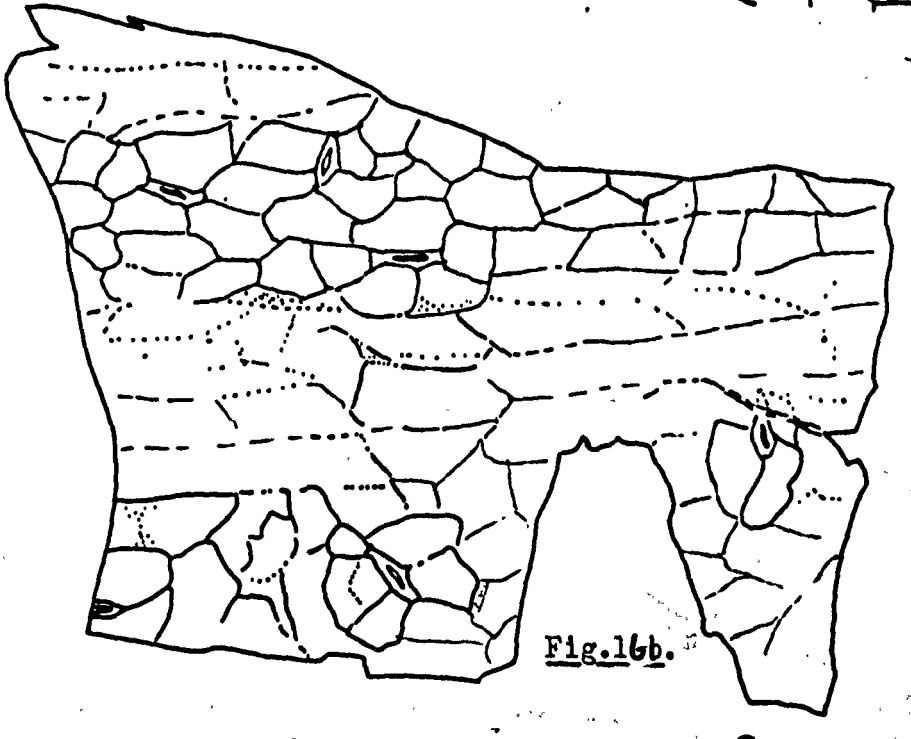


Fig.16b.

Figure 16. Gangamopteris [illegible] sp. C..
a) Upper cuticle . b) Lower cuticle.
(Both X 200)

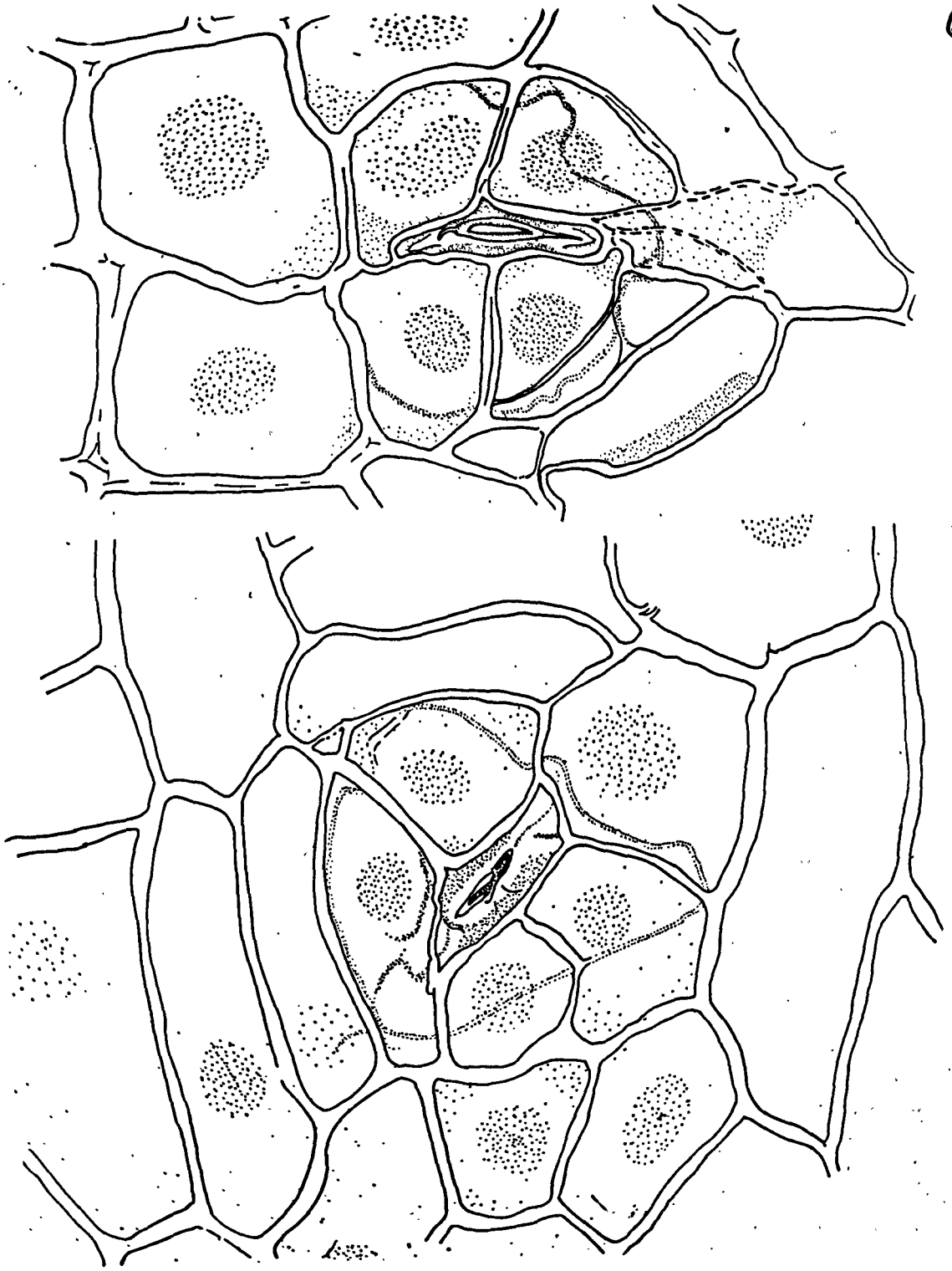


Figure 17. Gangamopteris sp. C. . . . Stomates from upper surface of leaf. Note elongated pit and pore, position of the guard cells and the papillae on the subsidiary and neighbouring cells. (X 650)

Lower Cuticle.

The lower cuticle is extremely thin, so that on many preparations the shape and size of the cells cannot be seen. However, from the portions of the cuticle which are well preserved, it is clear that the upper and lower cuticles are very similar with regard to the shape of the cells and in the form and distribution of the stomates (Plate XIII A & C, and Text fig. 16a & b). The cells over the veins have a maximum width of about 35μ, and a length of 70μ to 110μ. The cells of the meshes are also smaller than those of the upper cuticle and measure from 30μ to 70μ in each dimension (Text fig. 16).

A peculiar feature of the lower cuticle is that the rows of cells containing and including the stomates are more heavily cutinised (and therefore better preserved) than the other cells of the mesh regions or the cells over the veins (Plate XIII C and Text fig.16b). In contrast to the upper cuticle, only the subsidiary cells appear to be papillate.

Comparison and Discussion.

The specimen is really too small for comparison of its macroscopic features with those of other species to be worthwhile. The absence of a midrib and the presence of anastomoses excludes it from both Glossopteris and Palaeovittaria, but it should be noted that as anastomoses are so rare, the general appearance of specimen H2b is of a fragment of Palaeovittaria rather than Gangamopteris.

The cuticles of Gangamopteris sp.C closely resemble the lower

cuticle of Palaeovittaria kurzii, as described by Srivastava (1956), particularly in the shape of the stomatal pit. The presence of papillae on the subsidiary cells only of Palaeovittaria kurzii is similar to the condition found in the lower cuticle of Gangamopteris sp.C, but will serve to distinguish between the lower cuticle of Palaeovittaria and the upper cuticle of Gangamopteris sp.C. The upper cuticle of Palaeovittaria kurzii cannot be confused with any of these, as it consists solely of small, isodiametric, polygonal cells.

Glossopteris flexuosa, Srivastava (1956) has a similarly shaped stomatal pit, but in this case the cell walls are sinuous and the stomates are confined to the lower surface of the leaf.

Except for the complete absence of papillae, the lower cuticle of Glossopteris intermittens, Srivastava (1956) is very similar to both cuticles of the present specimen, and was considered by him to be very similar to Palaeovittaria kurzii. The regular arrangement of the cells on the upper surface of Glossopteris intermittens, which is devoid of stomates, is sufficient to distinguish between this species and Gangamopteris sp.C.

The form of the stomates is quite similar to those of Gangamopteris ermeloensis (Pages 42-44) but the abundant papillae and the peculiar variation in the thickness of the lower cuticle suggest that although poorly known, Gangamopteris sp.C. should be kept separate.

Thus it may be said that the cuticle structure of Gangamopteris sp.C does not fit clearly into any one of the well established genera Gangamopteris, Glossopteris or Palaeovittaria, but as it is so imperfectly known, I do not think it is wise to erect a new taxon.

Ganganopteris sp.D.

Plate VII E & F, Plate XXIII E & F, Plate XXIV D.

Specimen E.7a

This specimen is a small part of a leaf and is 5·3 cm. long with a maximum width of 2·1 cm. The veins radiate slightly from its basal end (Plate VII E) and occasionally dichotomise near the upper end (see Plate VII F).

Cuticle.

Maceration yielded only one cuticle, which was very well preserved. The cells are mostly rectangular, elongated parallel to the veins, 70μ to 80μ long and about 30μ wide (Plate XXIII F). Some of the cells are polygonal and about 50μ across (Plate XXIII E). These are more common in the mesh regions, but apart from the staining of the veins by tar residues there is no clear difference between the veins and the meshes. No stomates were seen, although the cuticle fragments prepared were large and well preserved. It is therefore more likely to be the upper cuticle than the lower cuticle.

Comparison and Discussion.

Without preparations of the stomatal apparatus, it is difficult to make any adequate comparison with previously described species. It is noteworthy that the cuticle is almost identical in the shape and size of the cells with that assigned by Høeg and Bose (1960) to Noeggerathiopsis hislopi. The description of the venation of that species also agrees

closely with the present specimen.

The general appearance of the cuticle is also very similar to the cuticles of Gondwanoptoris described in this Thesis and by Srivastava (1956), so the specimen is assigned provisionally to this genus.

THE GENUS GLOSSOPTERIS BRONGNIART 1828

The genus Glossopteris was instituted by Brongniart in 1828, when he described an Indian and an Australian leaf which he regarded as varieties of Glossopteris browniana(now called G. browni). I include here his diagnosis of these varieties and that of Glossopteris angustifolia as well as extracts translated from the description of these species given in Brongniart's original papers.

"Histoire des Végétaux Fossiles. By A. Brongniart. 1828. Page 22

GLOSSOPTERIS

Foliis simplicia, integerima, sublanceolata, basi sensim angustata, nervo medio valido apice evanescente percursa; nervulis obliquis arcuatis aequalibus, pluries dichotomis vel basi quandoque anastomosantibus et reticulatis.

GLOSSOPTERIS BROWNIANA (Page 223) Pl. 62.

G. foliis lanceolatis vel subspathulatis obtusis (1-2 pollicitus latis); nervo medio valido superne canaliculato; nervulis basi obliquis reticulatis, apice tantum simplicibus vel furcatis, marginique subperpendicularibus, vix obliquis.

Var. Australasica: foliis minoribus subspathulatis obtusis.

Var. Indica: foliis majoribus lanceolatis acutiusculis.

Abstract and translation from P. 224.

Fig. 2 is an Indian specimen, the middle portion of which is missing. It is much bigger and slightly different in shape from the

Australian specimens, but their structure is similar to such a degree that one cannot doubt that they both have the same sort of fructification and belong, therefore, to the same genus, above all when one observes equally great variations in size and shape in the impressions which are contained in the same pieces of Australian rock.

The single Indian specimen which I have drawn differs from those of the subspecies (a) (i.e. G.Prosnii) only in its bigger size, its more regularly lanceolate shape, and which appears as if it must end in a sharper point.

Glossopteris angustifolia. (P.224, Pl. 63, fig.1.)

G. Foliis angustis sublinearibus (sex-octo lineis latis); nervo medio valido plano; nervulis obliquis pluries dichotomis, basique rarius anastomosantibus.

Abst. and Trans. P.224

The single specimen I possess of this plant contains only leaves which are very incomplete, since both extremeties are missing in all, however, their linear shape, narrow and elongated, and their veins which are scarcely anastamosed at the base, distinguishes them from all the impressions so varied in size and shape, of the previous species (G.Brongniana), on the other hand, their general shape, the width of their mid-rib and the arrangement of their secondary veins, places them without any doubt in this genus (Glossopteris)."

The varieties australeaica and indica of G. Prosnii were raised to specific rank by Schimper (1869) and are now known as

G. brownii and G. indica respectively. Brongniart's original drawings were criticised by Bunbury, Feistmantel, Zeiller, Arber and others. In 1896 Zeiller published drawings of the venation of G. brownii, G.indica and G.angustifolia, which were stated to be accurate representations of the type specimens. Many species of Glossopteris were subsequently described by various authors (e.g. Feistmantel, Schimper, Bunbury, Lamm, Zeiller, Tenison-Woods, Etheridge and Seward), but this vast assemblage was reduced to only thirteen species by Arber (1905).

Several of these suppressed species have been resurrected by Srivastava (1956) on differences in cuticle structure. I do not support this practice, as in most cases the cuticles of the type specimens are not known. I believe that well preserved specimens with cuticles should be described under new specific names. This point is discussed in greater detail in the description of several species of Glossopteris and Gangamopteris by Høeg and Bose,(1960) and also in this Thesis.

The cuticles of twenty-one species of Glossopteris have been described by Zeiller (1896), Sahni (1923), Srivastava (1956), Pant (1958) and Høeg and Bose (1960). The cuticles of two new species and two existing species of Glossopteris are described in this Thesis, and two further species are described, but not named.

Glossopteris transvaalensis sp.nov

Plate III C, D, E, & F, Plate IV A to E, Plate XIV B, Plate XV A to D, Plate XVI A to D, Plate XVII A, Text figures 18 to 22.

Holotype. Specimen H.10a. Figured Paratypes, Specimens H.1, H.3b, H.19, H.11c, H.13b.

Unfigured Paratypes, Specimens H.3d, H.11i, H.7b.

Diagnosis

Macroscopic features.

Lanceolate-spathulate or linear leaves with attenuated base. Mid-rib strongly marked, up to 3 mm. wide. Lateral veins closely spaced, arising at an angle of 15^{0} - 20^{0} to the mid-rib and curving slightly to the margin, dichotomising once or twice. Anastomoses very rare, usually absent.

Microscopic features.

Upper cuticle thick, little or no difference between the veins and meshes. Cells rectangular/polygonal, thick-walled (10μ), 30μ-40μ wide and 30μ-120μ long. No stomates on this surface.

Lower cuticle thin, veins and meshes distinguishable. Vein cells rectangular/polygonal, 20μ-40μ wide and 50μ-120μ long. Mesh cells irregular, rectangular/polygonal, 20μ-40μ across, rarely papillate. Stomates confined to mesh areas, 5 - 6 rarely papillate subsidiary cells

(identical to normal mesh cells) overlying guard cells, which form an elliptical area approximately 40μ X 60μ. Stomatal pore about 20μ long, lips thinly cutinised, at the bottom of a pit, not overhung by subsidiary cells.

General description.

Nine specimens are assigned to this species, and this allows some estimate of the variation occurring within the species to be made. In seven of the specimens the leaf shape is lanceolate-spathulate, and the widest point (2-2·5 cm.) is about two-thirds of the length of the leaf from the base. From this point the leaf narrows gradually and evenly to the base, where the width is 0·5 to 0·7 cm. (Plate III C & F). In none of the leaves is the entire tip preserved, but in specimen H.7b the tip is clearly quite acute whilst that of specimen H.3b is much more obtuse. The actual specimens in my possession vary in length from 11 cm. to 13 cm., but the shape of the widest fragment suggests that it belongs to a leaf at least 20 cm. long.

Specimens H.11c and H.13f (Plate IV C, D & E) are relatively longer and narrower than the typical form of leaf. The first is an almost complete leaf from which one to two centimetres of the tip are missing. Most of the lamina is strictly linear in shape (11 mm. wide), but the base is very long and attenuated. It merges imperceptably with the lamina, but is mostly 5 mm. wide and slightly expanded at the point of attachment, giving the appearance of a distinct petiole. The whole leaf is 14·5 cm. long. Specimen H.13f is 9·5 cm. long and consists

largely of the basal part of a similar leaf.

Although there is some variation in the shape of the leaf, the form of the venation is remarkably constant. The mid-rib is strongly marked on the abaxial surface of the leaf where it is about 3 m.m. wide, but it is not so pronounced on the adaxial surface (Plate III C & E, Plate IV A & B). In both cases the mid-rib runs right through to the tip of the specimens. In the spathulate leaves the secondary veins leave the mid-rib at an angle of 20°, but curve immediately to an angle of 35-40° which is maintained right to the margin of the leaf. In the narrow-leaved forms the secondary veins leave the mid-rib at an angle of 15-20° and run straight out to the margin.

The secondary veins dichotomise once or twice, but anastomoses are extremely rare. They are, in fact, absent from most of the specimens, and those that do occur are very close to the mid-rib.

Table No. 3. Showing number of anastomosing veins in G.transvaalensis

Specimen	Vein density (vns./cm.)	Total No. of veins visible in specimen	Total No. of anastomoses observed
H.19	12/cm.	264	8
H.18	12/cm.	157	-
H.3b	25/cm.	460	-
H.7b	18/cm.	468	-
H.11i	10/cm.	150	2
H.1	13/cm.	208	-
H.3a	14/cm.	63	-
H.11c	14/cm.	84	-
H.13f	14/cm.	96	-

As shown in Table No.3., there is considerable variation in the vein density. The measurements were taken at the margin of the leaf and

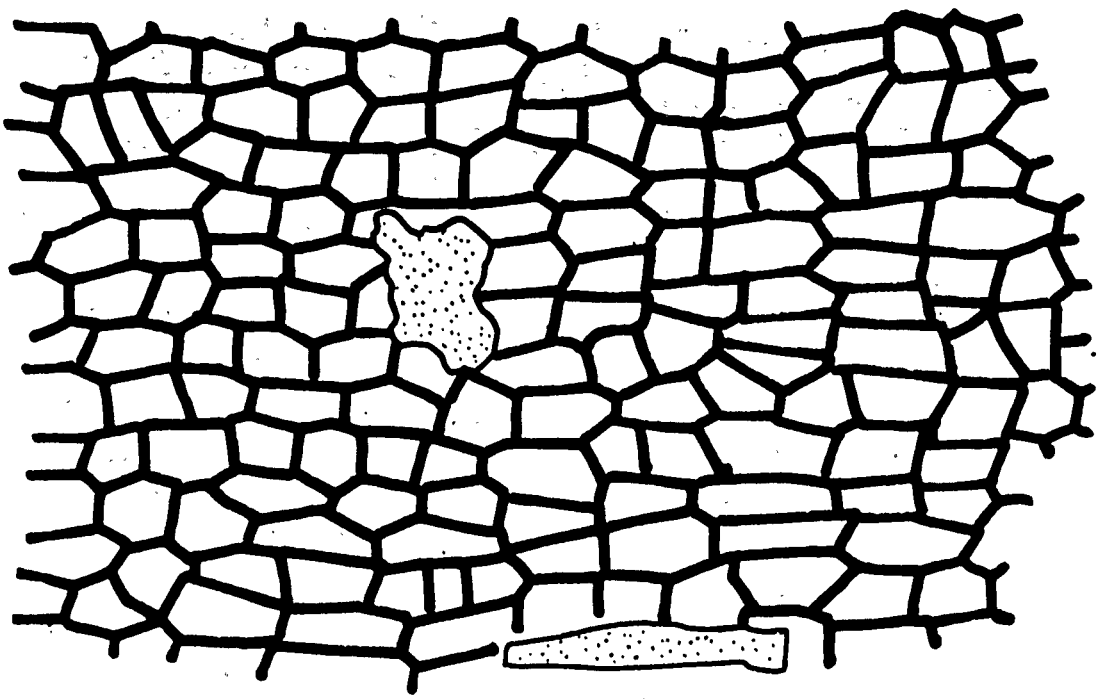
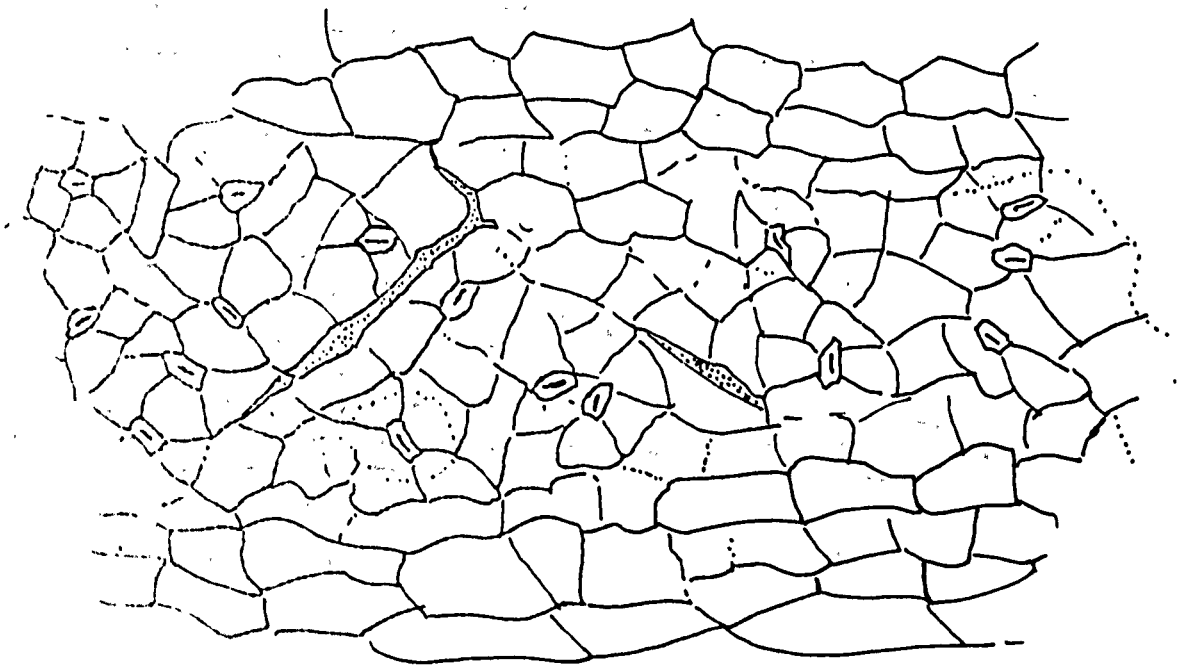


Figure 18a. Upper cuticle (X 200)

Figure 18. a & b, Glossopteris transvaalensis sp. nov.

Figure 18b. Lower cuticle (X 200)



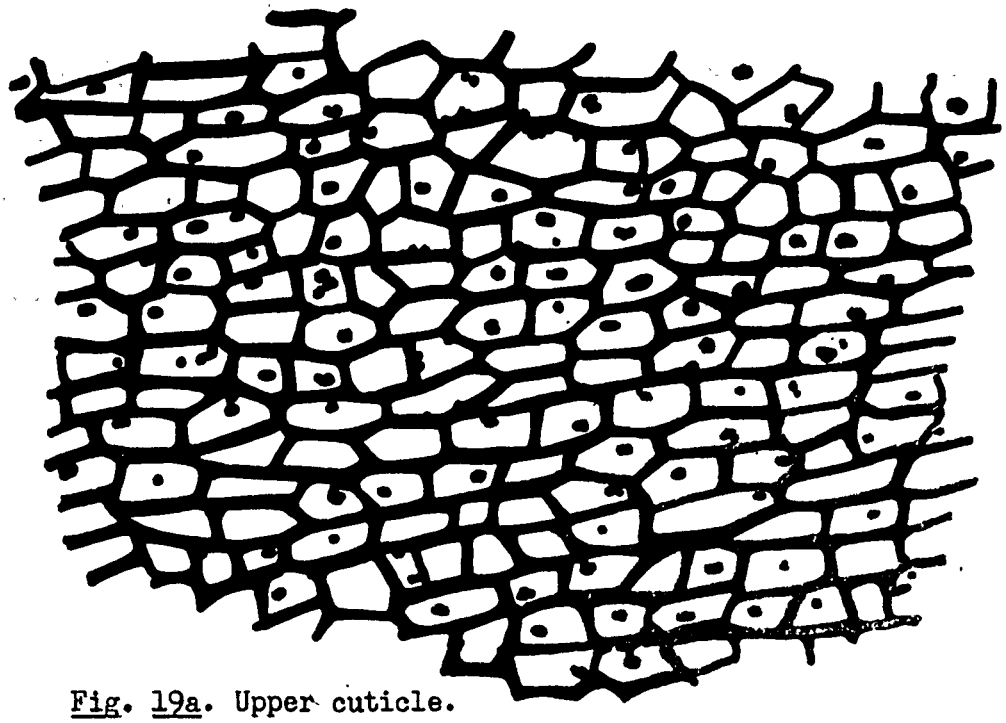


Fig. 19a. Upper cuticle.

Fig. 19b. Lower cuticle.

Figures 19 a & b, Glossopteris transvaalensis sp. nov.

(Both X 200)

are clearly affected both by the degree of dichotomy shown by the veins and by the angle at which they meet the margin of the leaf. In general it can be said that the veins are close together and parallel.

Microscopic features.

Upper Cuticle.

The upper cuticle is thick and shows little or no difference between the vein and mesh areas (Text figs 18a & 19a. Plate XV A,C). The cells are mostly rectangular or elongated polygons, 30μ - 40μ wide and 20μ - 120μ long, and lying parallel to the main axis of the leaf. The longitudinal walls are more or less parallel but the end walls may be at right angles to them, or oblique. The thickness of the cell walls is generally constant at about 10μ. No stomates are present on this cuticle. Papilla-like markings can be seen on some of the cells from the narrow leaved specimens. These marks may be centrally placed in the cell or attached to the cell wall.

Lower cuticle.

The lower cuticle is much thinner than the upper cuticle (Text fig. 19b. Plate XVI C), and the arrangement of the veins and meshes is clearly visible (Text figs. 18b & 19b. Plates XV B, D & XVI A). The cells over the veins are more or less rectangular, 50μ - 120μ long and 20μ - 40μ wide. The cell walls are straight, and those common to two vein cells are from 4μ to 6μ thick, and those between vein and mesh cells are 2μ - 3μ thick. All the cell walls are only 1μ - 2μ thick in the narrow leaved specimens. Each vein is 3 - 6 cells wide. Specimens

H.11c and H.13f also differ from the typical form of this species in that papillae may be present near the outer edge of the lamina, where there is a marginal vein running parallel to the edge of the leaf (Text fig.22, where part of the vein from near the torn edge of the lower cuticle from specimen H.13f is shown).

The cells of the mesh regions are irregular both in shape and arrangement. They may be more or less rectangular or polygonal, with dimensions in the order of 20µ - 40µ. The stomates are abundant but restricted to the mesh areas (Text figs. 18b & 19b). They are quite difficult to locate as the subsidiary cells are practically indistinguishable from the normal mesh cells (Plate XV D). There are five or six subsidiary cells which are rarely papillate (Text figs. 19b, 20 - 22. Plate XVI B,D). They overlap the guard cells, which form an elliptical area measuring about 60µ X 40µ. The pore apparently lies at the bottom of a shallow pit and is about 20µ long with thinly cutinised lips. (Text figs. 20 - 22. Plates XIV D, XVI B,D, XVII A).

Comparison and Discussion.

In the shape of the leaf and the mode of venation, the specimens described above are very similar to the forms of G.indica described by Plumstead (1952) and by Archangelsky (1957). Archangelsky (personal communication) states that G.indica (Schimper) sensu Plumstead, is characterised by having dichotomising veins with very few or no anastomoses. In her concept of G.indica, Plumstead (1952) also includes Glossopteris communtifolia var. taeniopteroides (Seward 1908) and G.indica

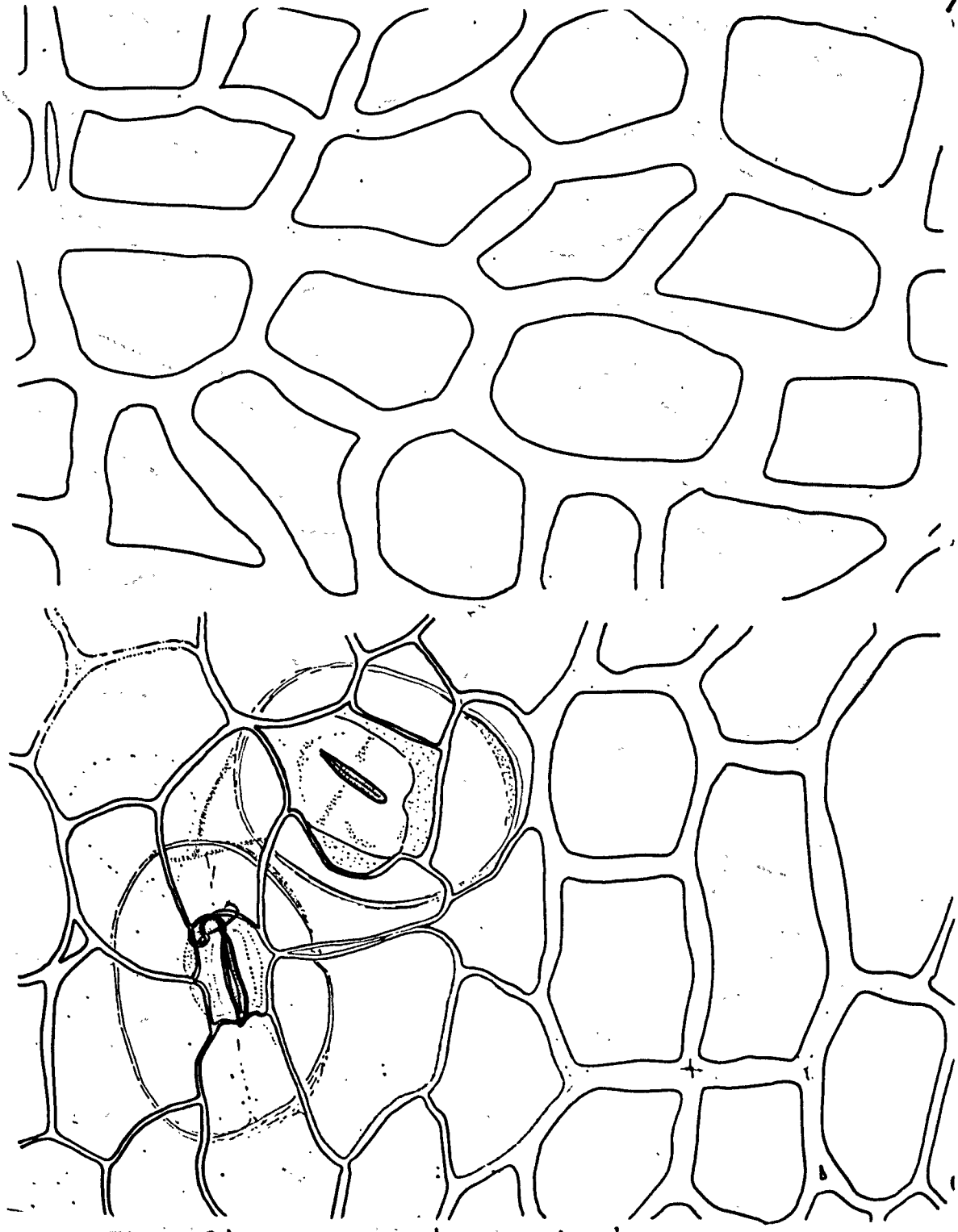


Figure 20 Glossopteris transvaalensis sp.nov.

Fig. 20a (top) Upper cuticle (X 650)

Fig. 20b.(bottom) Lower cuticle with two stomates, showing pore and guard cells. (X 650)

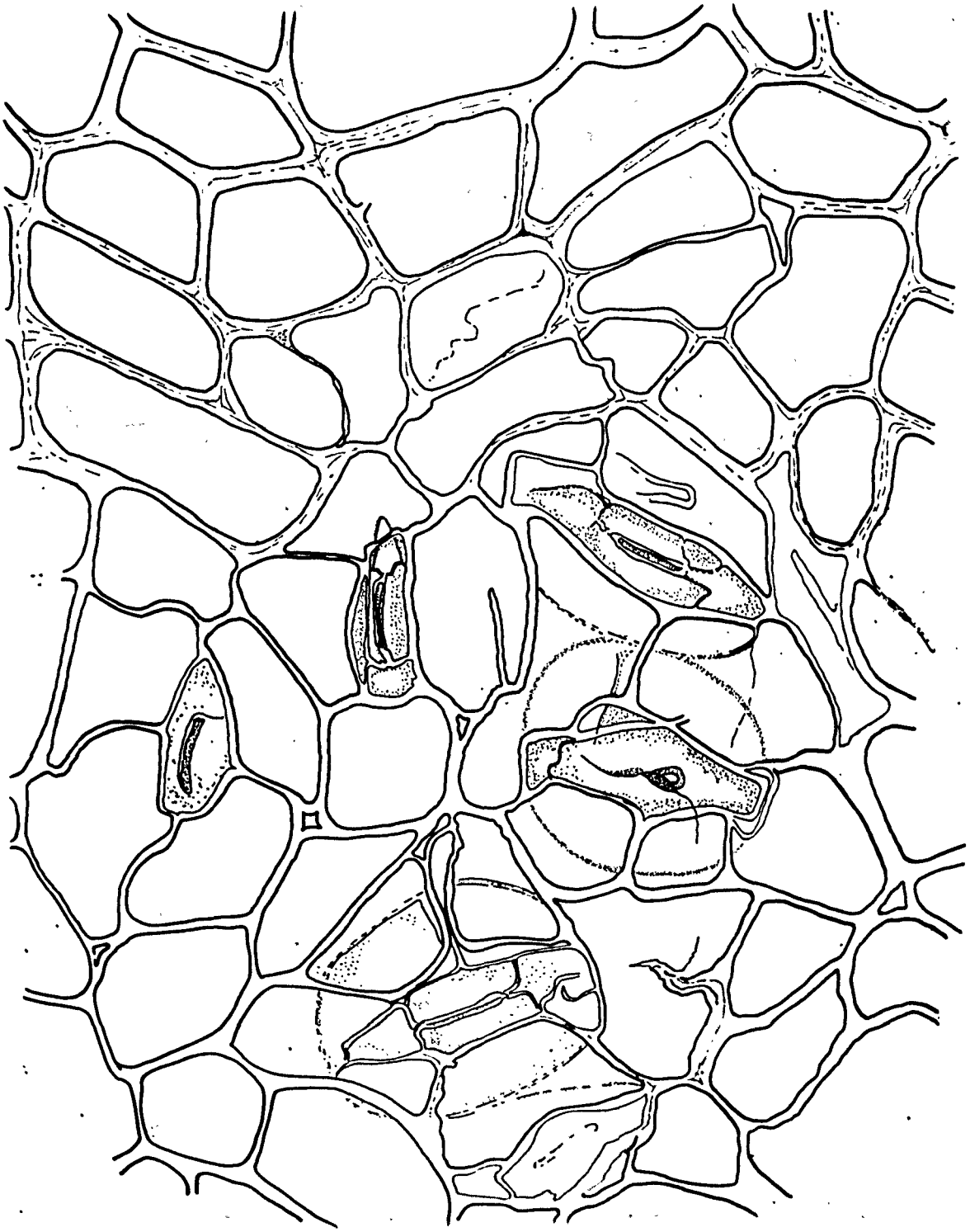


Figure 21. Glossopteris transvaalensis sp. nov. Lower cuticle from the mesh area, with group of contiguous stomates. Note the position of the guard cells, and, stomatal pore.

(X 650)

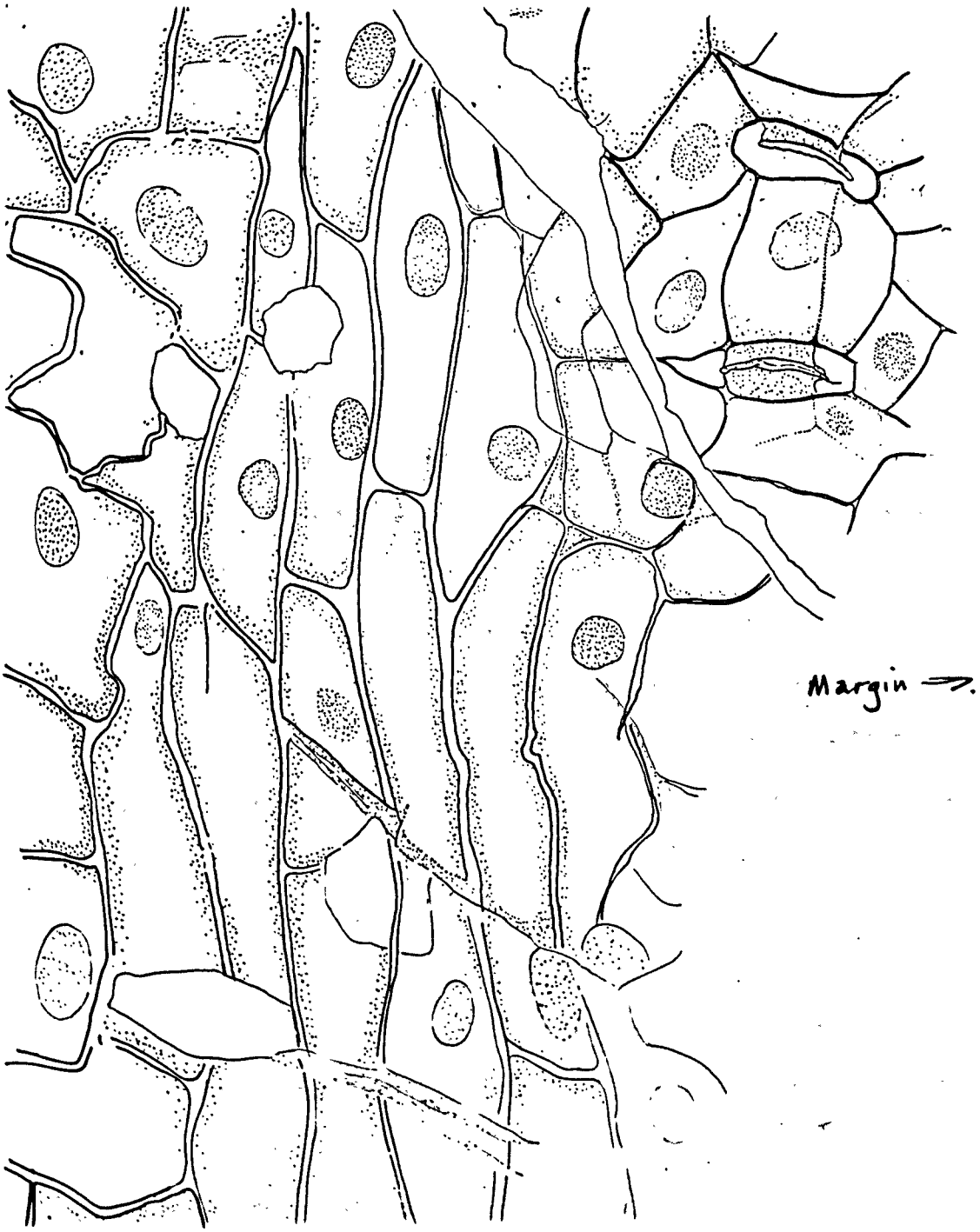


Figure 20. Glossopteris transvaalensis sp nov. Lower cuticle, showing vein-cells running parallel to the margin of the leaf. Note the papillae and the pair of contiguous stomates. (X 650)

var.wilsoni (Seward 1910b), as well as the type commonly known as G.indica, which was figured by Zeiller and which has numerous anastomoses. I have been fortunate in seeing Brongniart's original paper (1828); his description and drawings seem to be identical with the type described by Plumstead, by Archangelsky and by me.

This supports the inclusion of the "taenioptorid" type in the species G.indica.

However, Brongniart's drawings were criticised by Bunbury (1861), Feistmantel (1882), Zeiller (1896, 1902) and Arber (1905), on the grounds that they showed very few anastomoses. The discovery of so many specimens in South Africa and the Argentine, closely resembling Brongniart's original type, suggests that his drawings were, in fact, accurate, and the specimen figured by Zeiller may not have been Brongniart's type specimen. Alternatively, although this seems unlikely, Zeiller's drawings may have been inaccurate.

The cuticle studies of Glossopteris made by Sahni (1923), Srivastava (1956), Pant (1956), Upog and Rose (1960), and by me show that the "taenioptorid" type of leaf has a cuticle structure clearly different from those described from leaves of the normal "indica" type, in which the veins anastomose frequently. Some of the latter have been described under new specific names, as the cuticle of the type specimen of G.indica is not known. G.arberi, Srivastava (1956), G.calpodes, G.hispida, and G.fibrosa, Pant (1956), and G.jamottei Upog and Rose (1960) are examples of such species and all differ markedly in their cuticular and stomatal structures from leaves with a taenioptorid venation in the

Ermelo collection.

Although the specimen of Glossopteris taenioides described by Srivastava (1956) is incomplete, it compares closely in length and width with the narrow leaved specimens of Glossopteris transvaalensis. The mid-rib has the same width and the veins arise at a steep angle. However, the lateral veins anastomose frequently, unlike the dichotomising veins of Glossopteris transvaalensis. Also the upper cuticle of G.taenioides is not as thick as that of G.transvaalensis, and it clearly shows the pattern of the veins and meshes. The lower cuticles are more similar to each other, but stomates are rare in G.taenioides and the shape of the pit and pore differs from those of G.transvaalensis. Another similar elongated species with anastomosing veins is Glossopteris angustifolia Brongniart (1828). Cuticles described by Sahni (1923) from specimens assigned to this species, differ from those of G.transvaalensis in that both upper and lower cuticles are the same, having cells with very sinuous walls and stomatal subsidiary cells with strongly marked papillae.

It is suggested that in the light of the evidence obtained from cuticle studies, the leaves with dichotomising veins with few or no anastomoses, be separated from the type figured by Zeiller (1896) as Glossopteris indica. The former group seem generally to have a linear-spathulate leaf whilst the latter are more strictly lanceolate. It seems highly probable to me that the specimens described here are identical with those described by Plumstead (1952) as G.indica. This is supported by the great similarity in the shape of the leaf and in the

form of the venation, as well as by the fact that the localities in which they were found are only about 125 miles apart. However, this hypothesis cannot be proved until specimens with fructification and cuticular remains are discovered; the specimens described here have, therefore, been given a new specific name.

As has been stated, several new species have been erected as a result of the examination of the cuticle of leaves which otherwise agree in macroscopic features with Zeiller's description of G.indica. This shows clearly that the form species G.indica (Schimper) Zeiller is an aggregate species, if not, indeed, poly-generic in nature. The drawings by Zeiller of G.indica Schimper and G.brownii Schimper, are so alike in the form of the venation that it is suggested that these two forms be merged and referred to as G.brownii. G.indica should then be retained for the forms with taeniopterid venation, as described by Brongniart, Plumstead and Archangelsky. Specimens of either form with cuticular remains should be described under the appropriate specific name erected by Srivastava, by Hoeg and Bose or by myself; or a new specific name must be given, if the cuticle structure does not agree with that of any of these species.

Glossopteris africana sp.nov.

Plate IV F, Plate V A - C, Plate XVII B - D, Plate XVIII A - C,
Text figures 25 - 26.

Holotype. Specimen H.6a. Figured paratype. Specimen H.6a

Diagnosis.

Macroscopic features.

Lanceolate or linear lanceolate leaves with acute apices. Mid-rib persistent, 2·0 mm. at the base to 0·2 mm. wide at the tip. Lateral veins arise at an angle of 10° to 30° to the mid-rib changing to 40 - 65° within 2 - 5 mm. Veins anastomose frequently. Vein density 10 - 14 vns./cm. near the mid-rib, 20 - 25 vns./cm. at the margin.

Microscopic features.

Upper cuticle.

Thin, little difference between vein and mesh areas. Mesh cells 90μ - 120μ X 35μ - 50μ, vein cells 70μ - 180μ X 40μ - 50μ. Cell walls sinuous. 1 - 6 crenta per wall. No stomates present on this surface.

Lower cuticle.

Thin, clear difference between veins and meshes. Vein cells elongated rectangles, 60μ - 170μ X 20μ - 50μ with straight or sinuous

cell walls. Mesh cells elongated rectangles or isodiametric, up to 170μ long and 20μ - 60μ wide, cell walls sinuous, 1 - 6 crests per wall. Stomates confined to the mesh areas, usually orientated with pore parallel to or at right angles to the veins. Pore 18μ - 20μ long, in a shallow "I" shaped pit 30μ - 50μ long. Subsidiary cells 4 - 6, identical to normal mesh cells. Stomates numerous, rarely contiguous, irregularly distributed.

General description.

The two specimens assigned to this species differ slightly in shape and in vein density. Specimen H.6a (Plate IV F) is a typical lanceolate "indian" leaf, 16 cm. long and 4·0 cm. wide. The mid-rib appears as a shallow groove 2·0 mm. wide at the base, but narrowing to 0·2 mm. near the apex. The veins arise from the mid-rib at an angle of 10° - 15° anastomosing frequently (Plate V A). At approximately 0·5 cm. from the mid-rib the angle changes to 40° and the anastomoses are replaced by simple dichotomies.

Specimen H.8a is a more linear leaf of the "brownii" type, (Plate V B). Although the veins do not arise at such an acute angle and the vein density is slightly lower than in specimen H.6a, the general character of the vein pattern is the same in both specimens.

Table 4. Variation in vein density in Glossopteris africana.

	Vein density at mid-rib	Vein density at margin
Specimen H.6a	20 per cm.	14 per cm.
Specimen H.8a	21 per cm.	25 per cm.

Cuticles.

The cuticles from both surfaces were very thin, and those from the exposed surfaces of the leaves were apparently affected by weathering. This could account for the fact that the presumed upper cuticle was the thicker of the two obtained from specimen H.6a, but the thinner in specimen H.6a.

Upper cuticle.

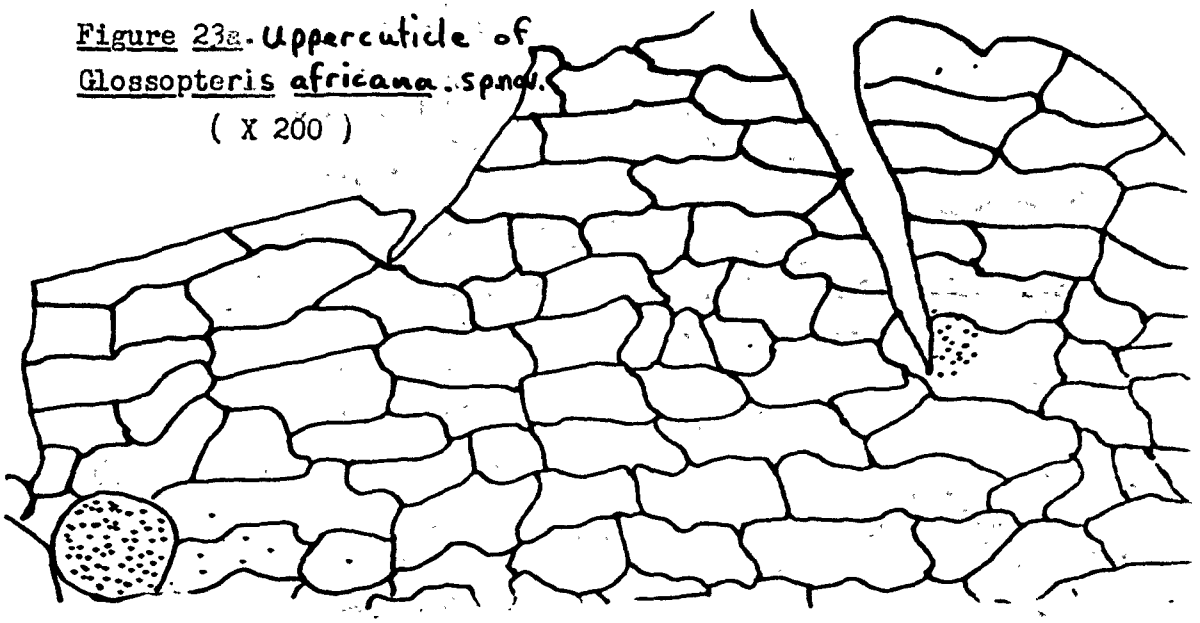
The cuticle preparations which showed no stomatal apparatus were assumed to be from the upper surface of the leaf.

These showed very little difference between the vein and mesh areas. The vein cells are 20µ - 50µ wide, 70µ - 100µ long and have almost straight or faintly sinuous cell walls with up to four crests per wall (Text fig.23a). The mesh cells show the same range in size, but tend to be broader in proportion to their length, than the vein cells. However, the preparations were fragmentary and poorly preserved so that it is not certain that this difference is a constant feature of the upper cuticle. The cells of specimen H.6a are slightly larger and more sinuously walled than those of specimen H.6a (cf. Text figs.23a & 24b). There is also a difference in the thickness of their cell walls, those of specimen H.6a being slightly thicker, but this might be due to variations in the quality of their preservation.

Lower cuticle.

Both specimens yielded cuticles with fairly well defined veins and with numerous stomates in the mesh regions. The cuticle from

Figure 23a. Uppercuticle of Glossopteris africana. sp.nov.
(X 200)



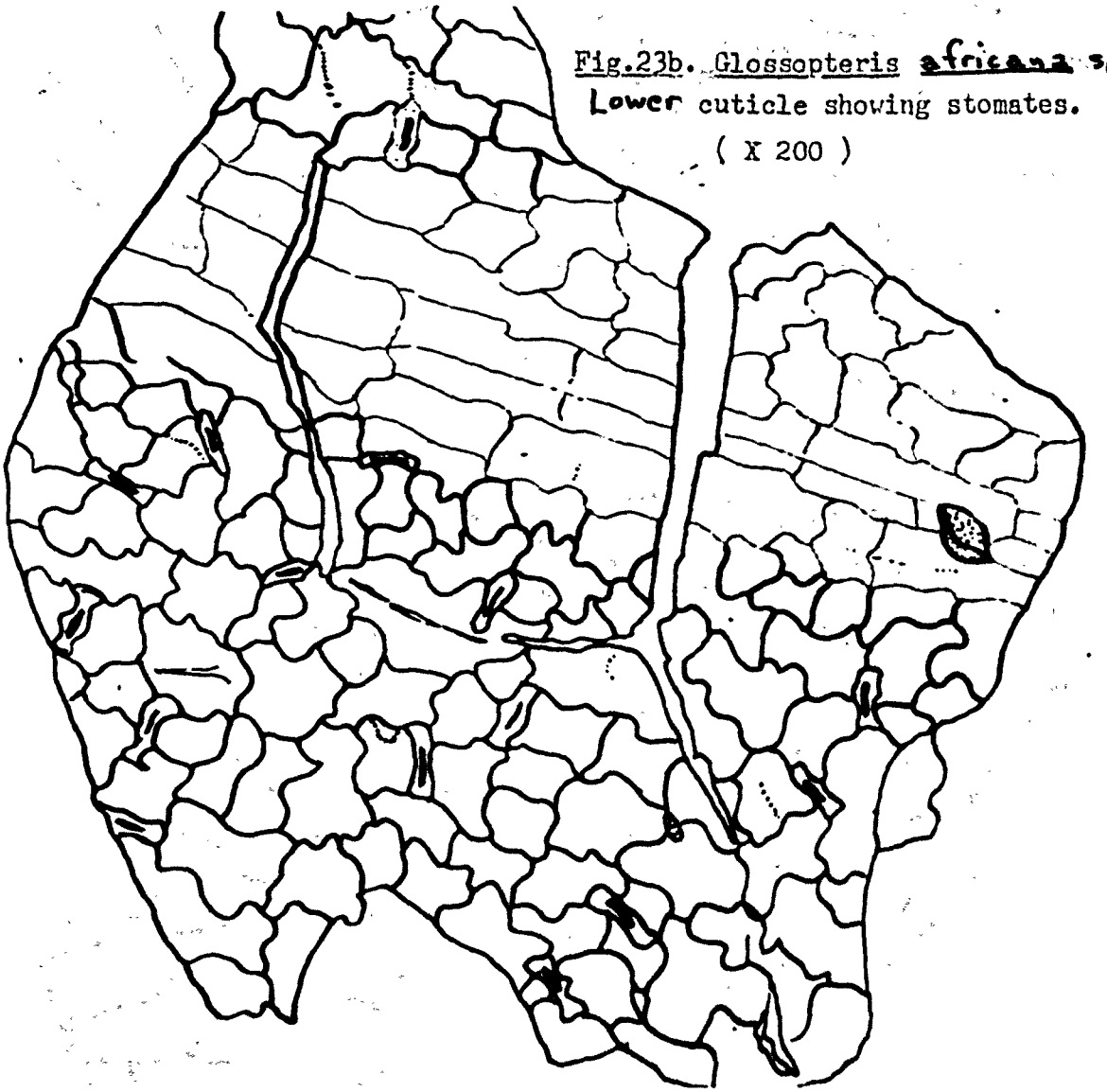


Fig.23b. Glossopteris africana sp.nov
Lower cuticle showing stomates.
(X 200)

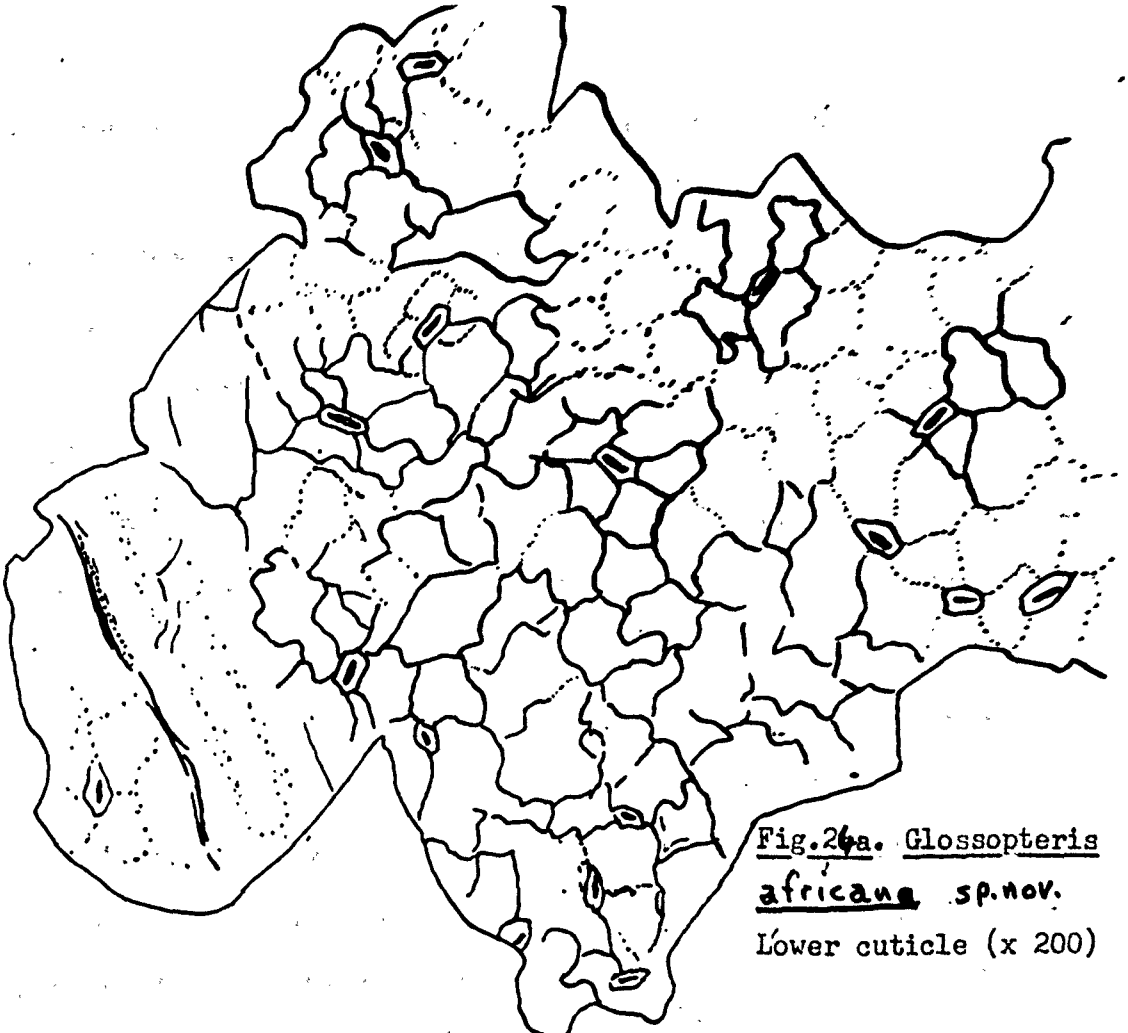
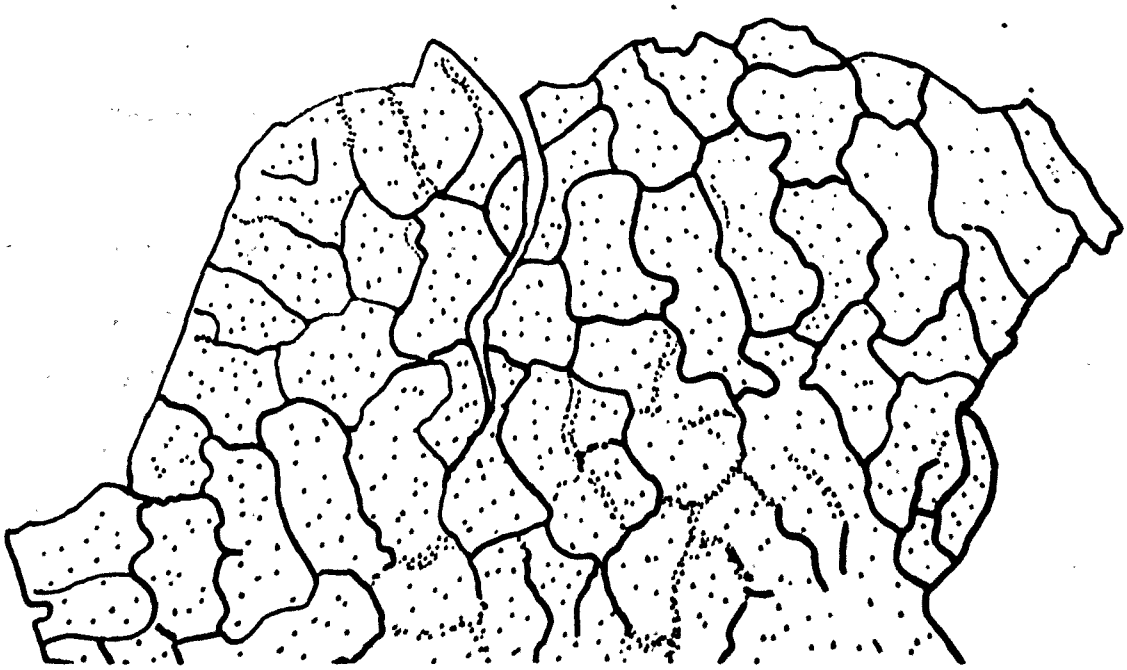


Fig. 26a. Glossopteris africana sp.nov.
Lower cuticle (x 200)

Fig. 26b. (below) Glossopteris africana. sp.nov.
Upper cuticle (X 200)



specimen E.8a is very poorly preserved, but sufficient detail remains to show that the size and shape of the cells and the distribution of the stomates is essentially the same in both specimens (Text figs.23b & 24a).

The cuticle over the mid-rib is relatively thick. The cells are elongated and lie parallel to the mid-rib. They are usually quadrangular or sometimes polygonal in shape, 110μ - 160μ long and 40μ - 50μ wide. The cell walls are generally straight and 1μ - 2μ thick.

The thinner cuticle from the lamina of specimen E.6a shows that the vein cells are elongated rectangles about 20μ wide and 60μ - 150μ long (Text fig.23b), with very thin, straight or faintly sinuous cell walls. The mesh cells adjacent to the veins are approximately the same size and shape as the vein cells, but the cell walls are more markedly sinuous. The longitudinal walls have from three to six crests per wall, whilst the transverse walls may be straight or have only one crest.

Towards the centre of the mesh region the cells are also basically rectangular, but a large proportion of the cells are more or less isodiametric, measuring 20μ - 60μ across and possessing one or two crests per wall. The stomates have 4 - 6 subsidiary cells which are indistinguishable from the neighbouring mesh cells. The stomatal pit is characteristically "I" shaped (Text fig.25) and is normally orientated with its longitudinal axis either parallel to or at right angles to the veins. The pit is about 50μ long and has bow-shaped polar walls. The

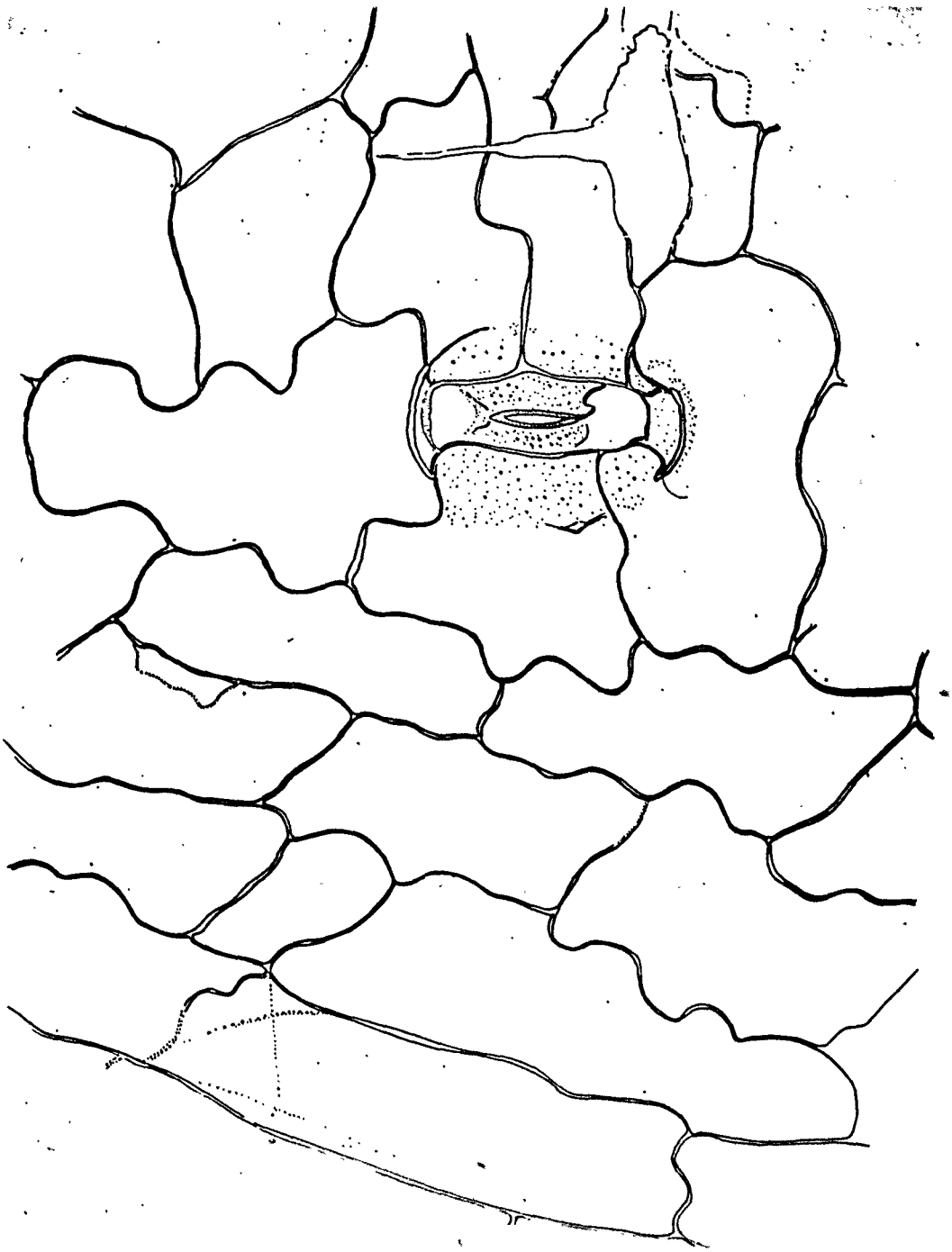


Figure 26. Glossopteris africana sp.nov.
Upper cuticle showing stomate in mesh area, and neighbouring vein-cells. (X 650)

Figure 26. Glossopteris africana.
Single stomate from the lower surface
of the leaf. (X 650)

pore is 18μ - 20μ long and is clearly marked by a cutinised rim about 2μ thick (Text figs. 25 & 26). In only a few cases can the guard cells be seen as a more or less circular area 50μ in diameter, lying beneath the subsidiary cells. The stomates are numerous, rarely contiguous, and there is no apparent pattern to their distribution.

Comparison and Discussion.

Glossopteris africana compares very closely with those forms of Glossopteris indica which have frequently anastomosing veins. The cuticles of neither of the type specimens of this species described by Brongniart (1828) and Schimper (1869), have been described, and that figured by Zeiller (1896) as belonging to Glossopteris indica was not adequately described.

At least three completely different types of cuticle have been described by Zeiller (1896), Srivastava (1956) and Egbg and Rose (1960), from leaves which appeared on macroscopic features, to be the same as Glossopteris indica Schimper. This suggests that the species based on macroscopic features only, may, in fact, be polyspecific or even polygeneric in nature. From this it is clear that the present specimens cannot be described under the name Glossopteris indica.

Although inadequately described, the cuticle studied by Zeiller (1896) is obviously different from that of Glossopteris africana, as it is very thick and has rectangular straight-sided cells.

On macroscopic features, Glossopteris Annottei, Egbg and Rose (1960) differs only slightly from the present species in having a

rounded leaf tip. Microscopically its cuticles differ in being thicker and having almost entirely straight walled cells, and in possessing stomates that are often arranged in contiguous groups. There is, however, quite a strong similarity in the shape of their stomatal pits, which are generally "I" shaped or dumb-bell shaped in both species. In this feature, both species are very similar to Glossopteris arberi Srivastava (1956). Glossopteris arberi is very similar to Glossopteris africana, but differs in having a thick upper cuticle which does not show the arrangement of the veins and meshes, and in which the cells are rectangular and papillate with thin highly sinuous walls (10 - 14 crests per longitudinal wall).

The macroscopic features of specimen K.Ca (Plate V B,C) are more similar to Glossopteris browniі Brongniart than to any other species. Particularly in the form of the network of the lateral veins, it is indistinguishable from the specimens of G.browniі Brongniart (para), as described by Feistmantel (1881 - 1886), Arber (1905), Seward (1910) and Srivastava (1956), differing from them only in having an acute rather than an obtuse or rounded tip. Srivastava's specimens yielded cuticles with straight cell walls and in which the subsidiary cells form a clear circular area around the stomatal pit.

Other Indian species which are macroscopically similar to the Glossopteris browniі-indica group are:-

1) Glossopteris angustifolia Brongniart as described by Sahni (1923).

2) Glossopteris retifera Feist. as described by Srivastava (1956).

3) Glossopteris sahnii Srivastava (1956)

The first may be distinguished from Glossopteris africana because the cell walls of the upper cuticle are much more highly sinuous, having 9 - 13 crests per wall. Also the cells of the lower cuticle are more regularly rectangular in shape than those of Glossopteris africana and the subsidiary cells are distinctly papillate.

Similarly, both cuticles of Glossopteris retifera show a strictly regular arrangement of rectangular cells, and the cell walls are finely sinuous or toothed. The stomates have six subsidiary cells which are much smaller than the neighbouring mesh cells and have very thin slightly sinuous walls.

The cuticles of Glossopteris nahnii are very thin, and the cells are irregular both in size and shape. The stomates are not preserved well enough for a useful comparison with those of Glossopteris africana to be made. The leaf of Glossopteris nahnii is much larger than that of Glossopteris africana, being well over 12 cm. wide. The mesh areas are about 10 mm. long and 3 mm. wide, and the veins arise from the mid-rib at right angles.

Pant (1958) has described two species of Glossopteris (G.hispida, G.colvadea) from Tanganyika which have macroscopic features very similar to some variation of Glossopteris indica, G.browniі and G.communis, and which have cuticles with sinuously walled cells. G.hispida Pant can be distinguished from G.africana as the cells of the upper cuticle have straight walls and their outer surfaces bear numerous minute papillae and are finely striated. The lower cuticle of G.hispida possesses trichomes and their damaged bases and the subsidiary cells of the stomates

are papillate.

The lower cuticle of G.colpodes Pant differs from that of G.africana in that the cells of the mesh regions have more highly sinuous walls (up to 16 crests per wall) and they are often marked by a median papilla. Both of the Tanganyika species differ from G.africana in having stomates with subsidiary cells bearing large hollow papillae which overhang the stomatal pit. The upper cuticle of G.colpodes has straight walled cells and has no stomates.

Srivastave (1956) has described the cuticles of Gangamopteris flexuosa which are very similar to those of Glossopteris africana and Glossopteris arberi Srivastava (1956). The stomates have the same "I" shaped pit as Glossopteris africana, but the cell walls are highly sinuous or toothed (upto 16 crests per wall). The cells of Gangamopteris flexuosa bear the scars of papillae similar to those shown by Glossopteris arberi, but this feature is not shown by Glossopteris africana.

Glossopteris cf. fibrosa Pant

Plate VI A - D, Plate VII A, Plate XIX A - D, Plate XX A - E,

Text figures 27 - 31.

Figured specimens. H.4, H.11a, H.16a, H. 16b.

Unfigured specimens. H.11f, H.11g, H.12a, H.13d.

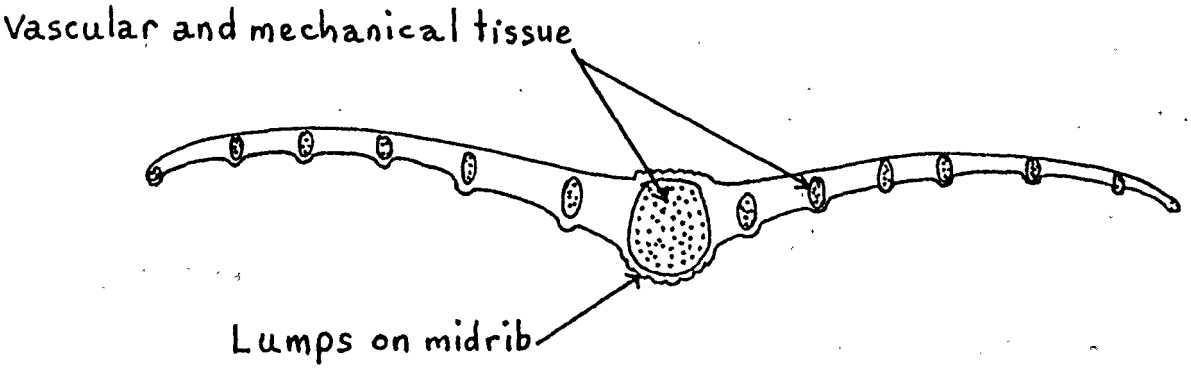
General description.

Macroscopic features.

The largest of these specimens (H.11a) has a maximum width of 5·0 cm., and a length of 30·0 cm., although at least 5·0 cm. of the tip are missing (Plate VII A). Specimen H.4 (Plate VI A, B) is also incomplete. It is 20·0 cm. long, and its maximum width of 6·0 cm suggests that the complete leaf was even larger than specimen H.11a. The smallest leaf is specimen H.16b, which is 14·0 cm. long and 2·3 cm wide. The other specimens are small fragments of large leaves (specimen H.16a, Plate VI C,D). The normal leaf shape appears to be lanceolate, the tip was probably acute and the lamina tapers gradually to the base (Plate VII A).

The mid-rib of specimen H.11a is 7·0 mm. wide at the base and 1·0 mm. wide at the tip. On the abaxial surface of the leaves, the mid-rib is strongly marked and convex (Plate VII A), whilst on the adaxial surface it is clearly marked, but less convex or flat. (Plate VI A, B, C). In most specimens, particularly in the basal part of the leaf, the mid-rib is covered with many small irregular lumps. The lamina

appears to have arched away from the mid-rib and curled slightly at the margin, as shown in Text figure 27.



Text figure 27. Diagramatic reconstruction of a Transverse Section of a leaf of Glossopteris cf.fibrosa Plant.

On both surfaces of the leaves the veins are strongly marked, appearing flat or slightly sunken on the adaxial surface (Plate VI A, B, C) and distinctly raised on the abaxial surface (Plate VI C,D). This suggests that the vascular and mechanical tissues in the veins were strongly developed, and resisted decay and compression during fossilization. The veins arise from the mid-rib at an angle of about 30°. Within approximately 0·5 cm. the angle changes to one of 40° - 70°. (See Table 5) and the veins then curve very gently or run more or less straight to the margin of the leaf. The meshes tend to be short and broad near the mid-rib, but become longer and narrower towards the margin (Plate VI). This is reflected in the vein density in the various regions of the leaves (Table 5). The range of size of the meshes varies with the

size of the leaf.

Cuticles.

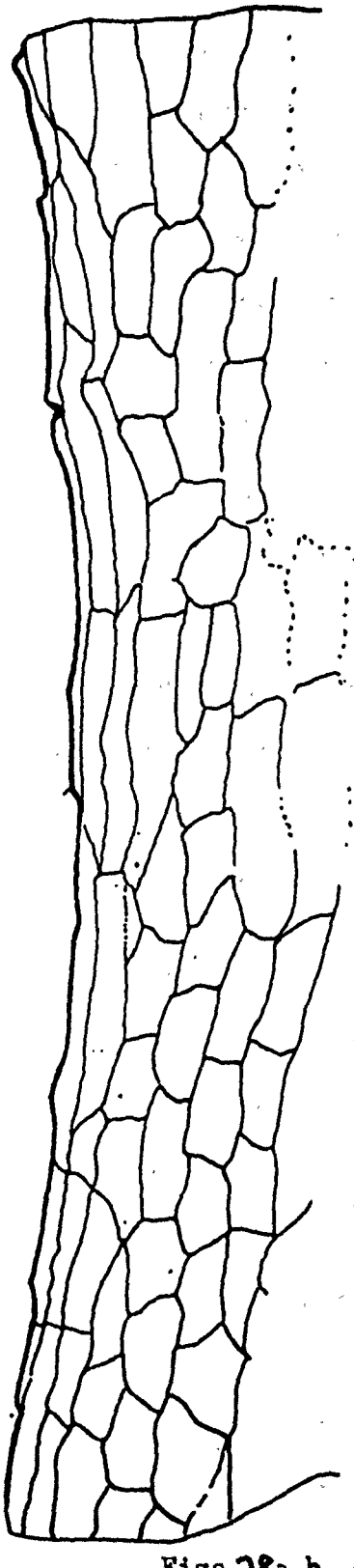
The preservation of the cuticles varies greatly from one part of the leaf to another, but some well preserved fragments have been obtained from each leaf. Both cuticles are moderately thick, and the upper cuticle is only slightly thicker than the lower.

Lower Cuticle.

In the region of the mid-rib, the cells are generally very regularly arranged in longitudinal files. The cells are quadrangular; 60μ - 80μ long; and 20μ - 30μ wide. The cell walls are straight and only about 2μ thick; the longitudinal walls are parallel, but the end walls of the cells are sometimes obliquo (Plate XX C. Text fig. 28b). In some preparations, the cells are polygonal, smaller than the rectangular cells of the rest of the mid-rib, and irregularly arranged (Plate XIX C. Text fig.28c). They coincide with the warts or lumps which have already been described on the mid-rib of some of the leaves. It is noteworthy that the cuticle in these regions is uncommonly well preserved, which suggests that the cells of the warts were more thickly cutinised than the normal cells of the mid-rib, or that the chemical composition of the cuticle rendered these cells less liable to decay.

The cuticle from the upper surface of the lamina does not show the arrangement of the veins and meshes very clearly (Text fig. 29b. Plate XIX A), but this is partly due to the fact that only small fragments of cuticle were obtained, which fails to reveal the pattern caused by

Fig. 28a. Upper cuticle from the edge of the leaf. (X 200)



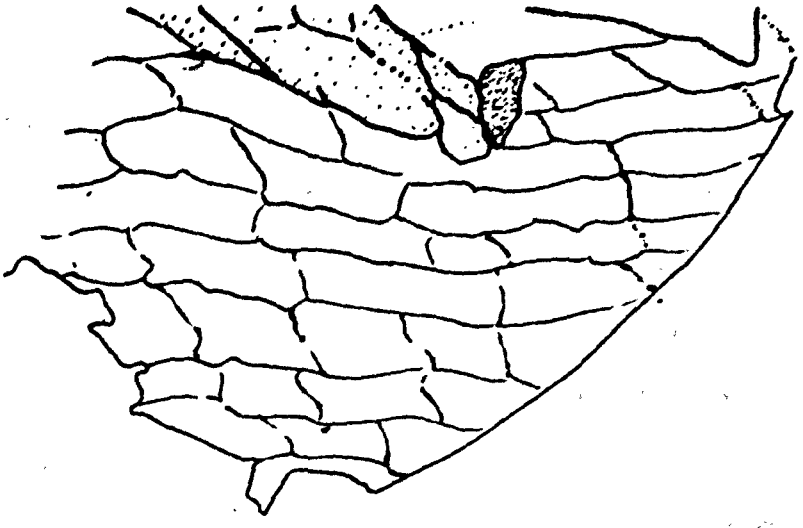


Fig. 28b. Upper cuticle, normal cells from the midrib. (X 200)

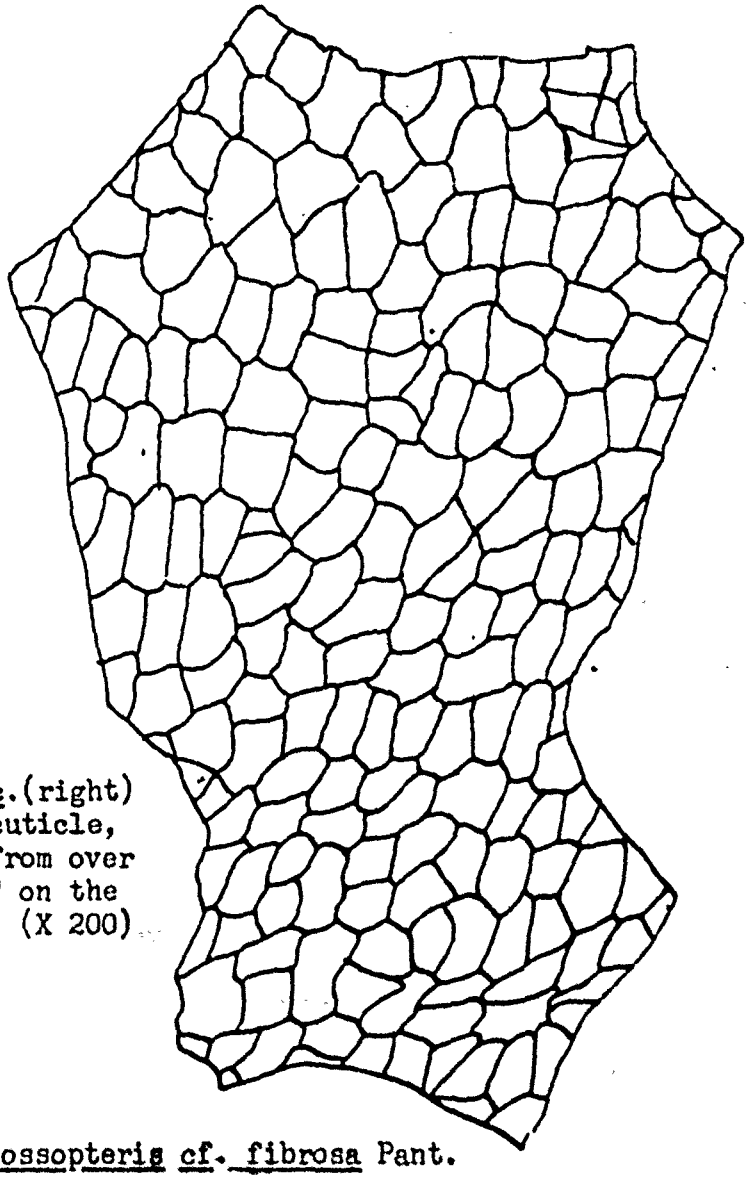


Fig. 28c. (right) Upper cuticle, cells from over "bumps" on the midrib. (X 200)

Figs. 28a, b, & c. Glossopteris cf. fibrosa Pant.

fairly wide meshes. In the mesh areas, the cells are arranged in rows parallel to the veins. The cells are more or less rectangular or polygonal, and may be isodiametric measuring about 40μ across, or slightly elongated measuring 30μ - 40μ wide and 50μ - 70μ long. Rarely, very short cells only about 10μ long, but of normal width, are interspersed with the normal cells (Plate XIX A, Text fig. 29b).

Over the veins the cells tend to be slightly longer and narrower than the cells of the mesh regions, but there is a variation in cell dimensions from 30μ - 60μ in length and from 30μ - 40μ in width.

The last 5 or 6 rows of cells at the edge of the leaf are similar to the cells of the mid-rib. They are clearly elongated parallel to the margin of the leaf, and they are more regularly arranged than the cells of the rest of the lamina. The cells are generally 60μ - 80μ long and 20μ - 30μ wide, but in the last row of cells some are over 200μ long, but only about 10μ wide. (Text fig. 28a, Plate XX E).

Lower Cuticle.

In the region of the mid-rib, the upper and lower cuticles are almost identical. However, the cells of the lower cuticle of the mid-rib often appear to have been compressed laterally, but this is undoubtedly due to the stresses which would arise when the prominent mid-rib was compressed during fossilisation (Walton 1936). The arrangement of the cells is quite uniform. They are more or less rectangular, 60μ - 80μ long and 20μ - 30μ wide. From leaves which have lumps on the lower as well as the upper surface of the mid-rib,

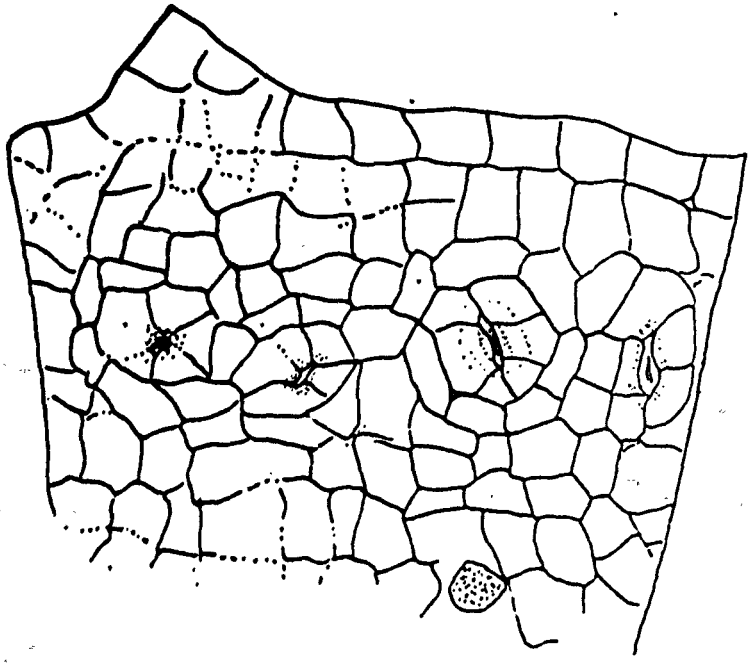


Fig. 29a. Glossopteris cf. fibrosa , Pant.
Lower cuticle of mesh region (X 200)

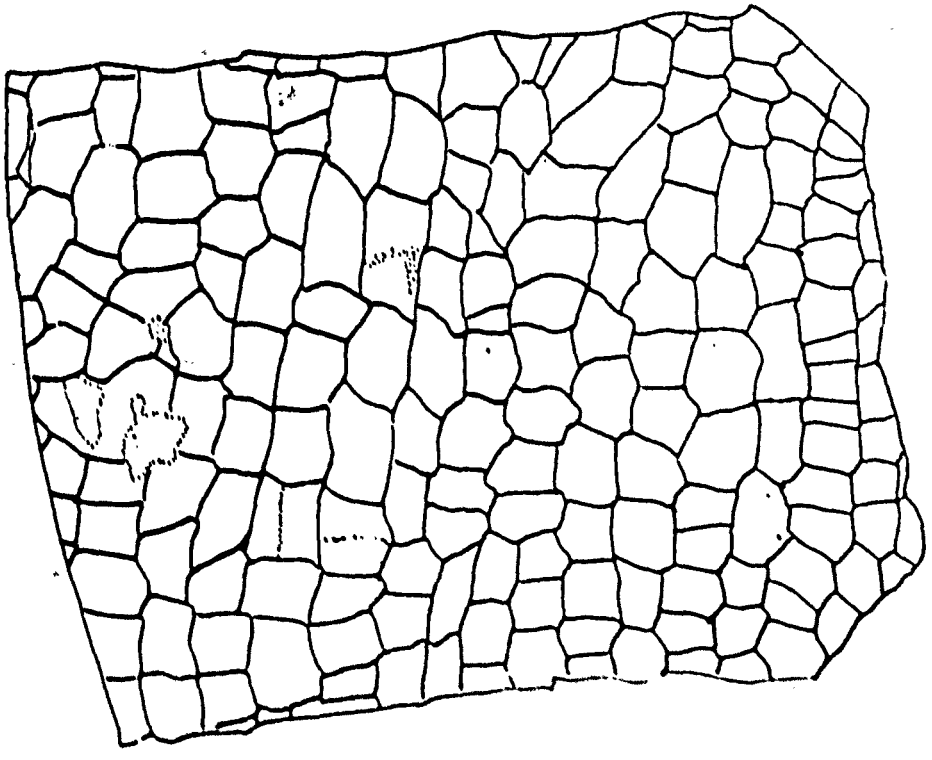


Fig. 29b. Glossopteris cf. fibrosa, Pant.
Upper cuticle from above 29a.
(X 200)

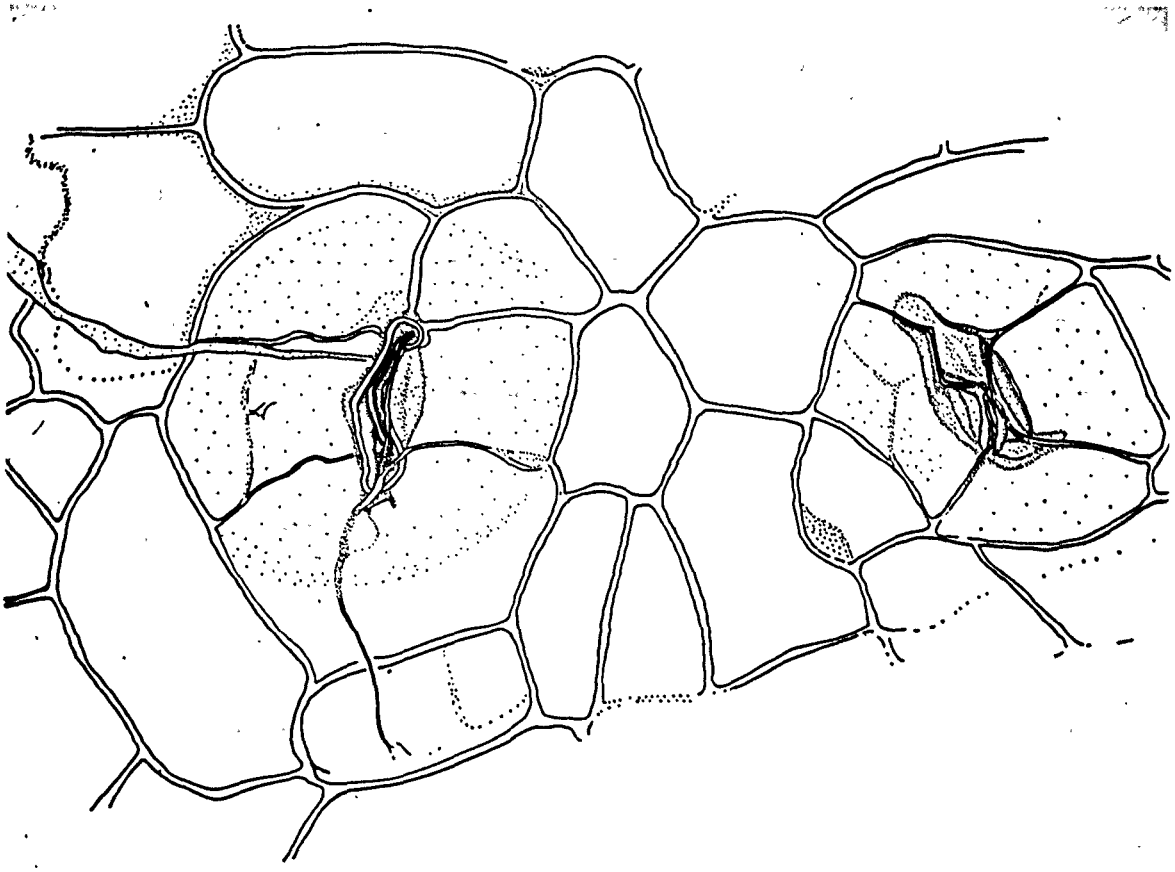


Fig. 30. Glossopteris cf. fibrosa Pant.
Stomates from the lower cuticle of Specimen H.16b. (X 650)

preparations showing small polygonal cells, similar to those observed from the warty regions of the upper cuticle, have been obtained (Plate XIX B). The lower and upper cuticles of the mid-rib may be distinguished by the fact that stomata occur, though only sporadically, on the former (Plate XX A).

The cells over the veins are regular in their arrangement and shape. They are basically rectangular, although occasionally the end walls are oblique, and are 45μ - 70μ long and 35μ - 45μ wide. The cells of the mesh regions may be quadrangular or polygonal, and isodiametric or elongated. They measure 25μ - 40μ wide and 20μ - 65μ long (Plate XIX B. Text fig. 29a).

The stomata, which are distributed in irregular groups, are occasionally monocyclic, but usually they are dicyclic (Text figs.30,31). The appearance of the stomata is very diverse, and depends on the state of preservation of the cuticle. The extent of this variation is shown in Text fig.31 and Plate XX A,B,D. No median papillae have been seen on any of the cells from either the upper or the lower cuticles.

Discussion and Comparison.

The external features of this assemblage of leaves are very similar (a) to those described by Feistmantel (1881,1886) as Glossopteris communis, (b) to the specimen described by Srivastava (1956) as G.communis and (c) to those described by Pant (1958) as G.hispida, G.fibrosa, G. colpodes and G.sp.A. The cuticle structure of Feistmantel's type specimen has not been described.

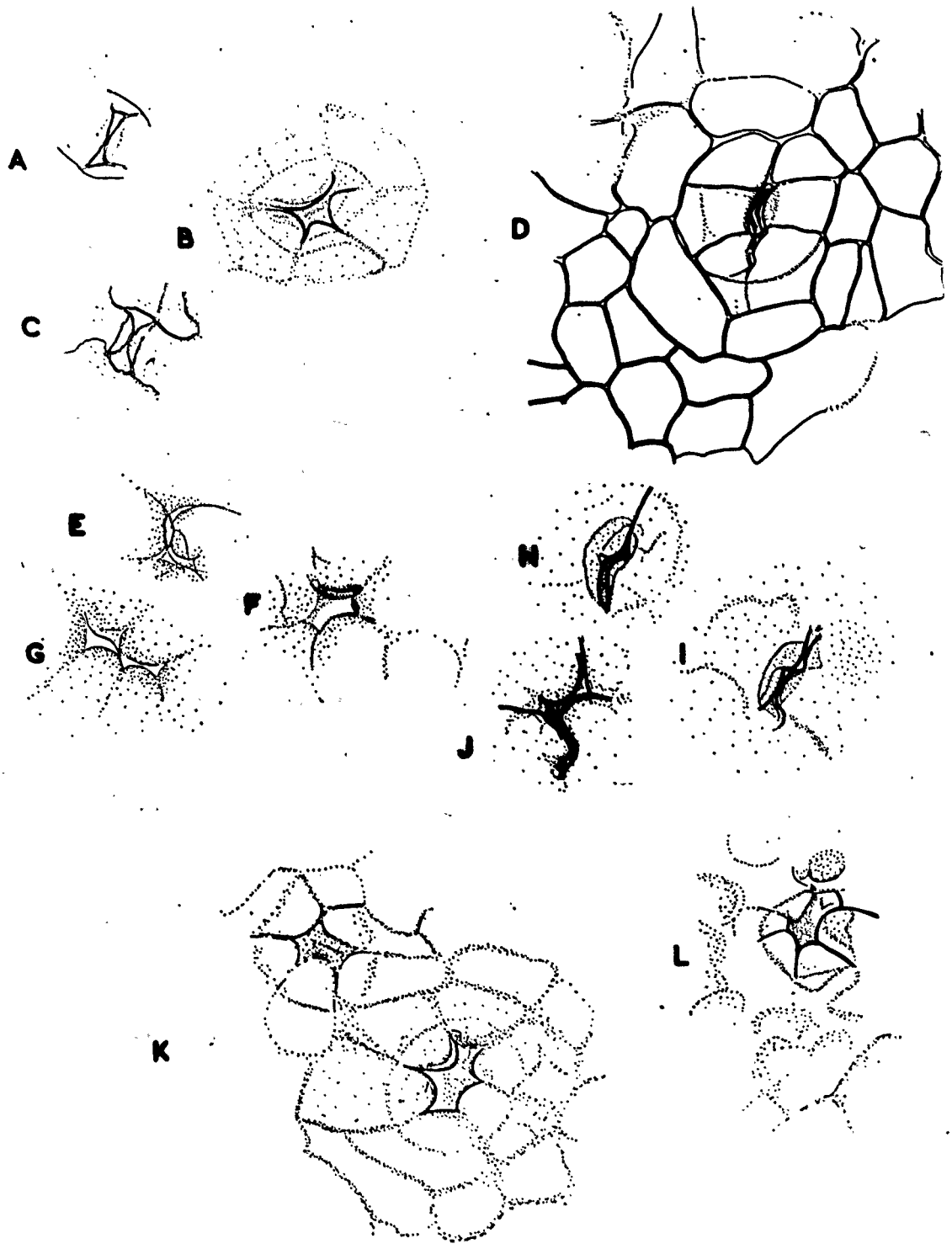


Fig.32. Showing the varied appearance of stomates from different parts of three specimens of Glossopteris cf. fibrosa Pant. Figs. A - D , Specimen H. 16b., E - I , Specimen H. 11a., and K - L , Specimen H. 4. (All X 390)

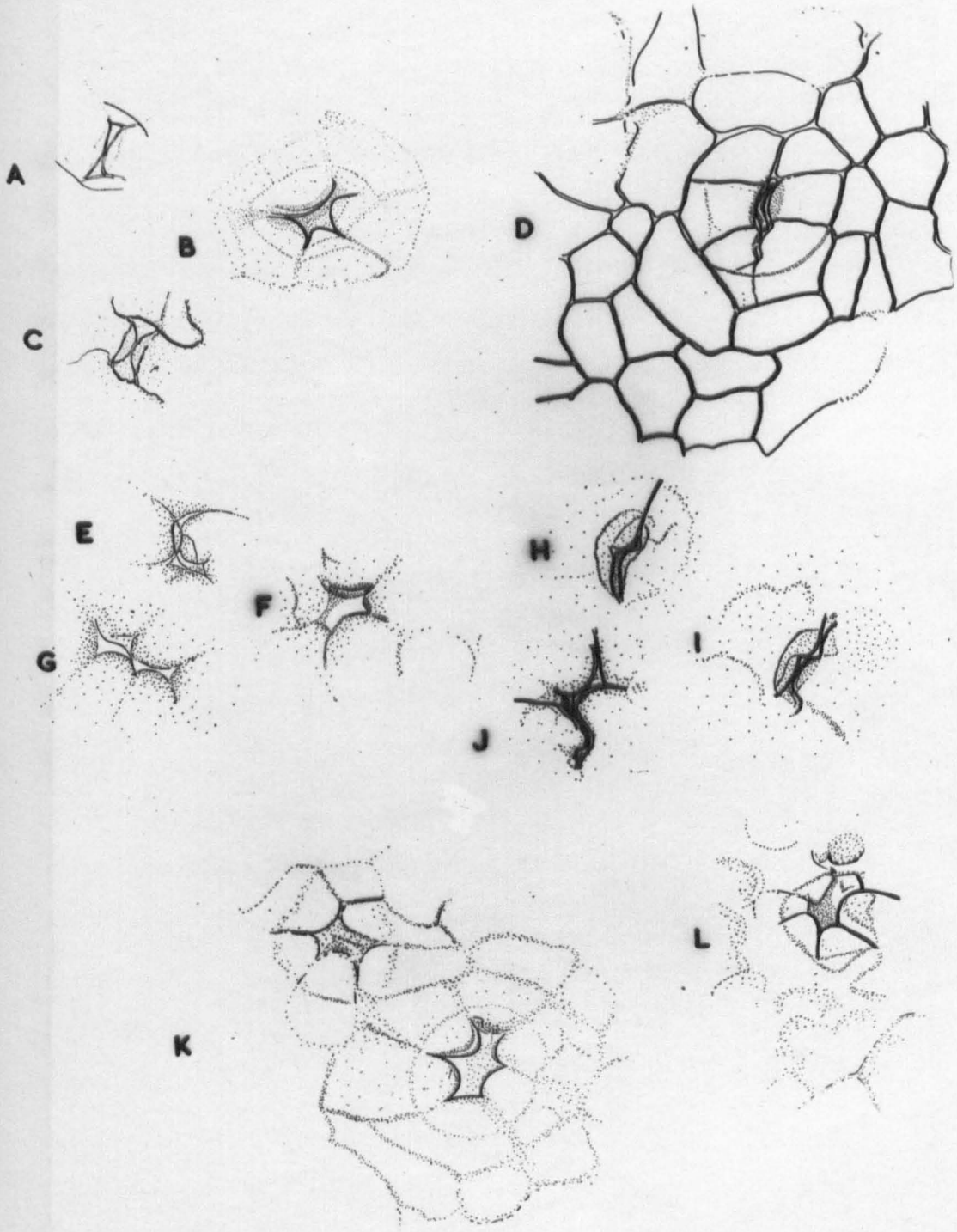


Fig.32. Showing the varied appearance of stomates from different parts of three specimens of Glossopteris cf. fibrosa Pant. Figs. A - D , Specimen H. 16b., E - I , Specimen H. 11a., and K - L , Specimen H. 4. (All X 390)

The cuticle of the specimen that Srivastava called Glossopteris communis is very similar to the present specimens in such features as cell size and shape. However, the veins and meshes are more easily distinguished, and the subsidiary cells of Glossopteris communis possess median papillae. They do not possess the large hollow papillae which overhange and protect the stomatal pore as in the present specimens. According to Srivastava (1956) Glossopteris communis has stomata on both surfaces of the leaf. Although none have been observed on the upper cuticle of the present specimens, the cuticles prepared were so fragmentary that it cannot be said categorically that no stomata are ever present on this surface. However, if they do occur, they must be rare and sporadic in distribution, and it does not seem likely that stomata are a normal feature of the upper cuticle of the present specimens.

Glossopteris hispida Pant (1958), although apparently identical to the present specimens in macroscopic features and in possessing stomata with overhanging papillae, may be distinguished from them, as the lower cuticle shows traces of numerous hairs, and the cell walls are sinuous. Glossopteris colpoden is almost identical with Glossopteris hispida, the only clear difference being the absence of hairs in the former species. The stomata of both species are monocylic.

Glossopteris fibrosa and Glossopteris sp.A of Pant (1958) are very similar to the present specimen, (a) in external features, (b) in the size, shape and arrangement of the cells, and (c) in the form of the stomates, which are mono or dicyclic, have tangentially elongated encircling cells, and have subsidiary cells with large, hollow papillae.

overhanging the stomatal pit. In both these species, the cells may bear a single median papillae, several small papillae, or longitudinal striations, whereas only the subsidiary cells of the present specimens are papillate.

One of the major diagnostic features of Glossopteris fibrosa is the presence of fibres between the veins. I have been unable to demonstrate whether or not similar fibres exist in the Ermelo specimens, so it is not possible to use this feature in their identification. The absence of papillae from the ordinary vein and mesh cells of the present specimens might be considered sufficient to separate them from Glossopteris fibrosa, but considering their great similarity in both microscopic and macroscopic features, I hesitate either to erect a new species or to identify them as the same until further work has clarified the situation. The Ermelo specimens are therefore referred to as Glossopteris cf. fibrosa Pant (1958). Table No. 5 (Page 104) comparing the macroscopic features of the leaves resembling Glossopteris fibrosa shows quite a large variation in such characters as vein angle and vein density, although the general character of the venation and the variation in the shape and size of the meshes is similar in all the specimens. In particular, Table No. 5 shows that the presence or absence of lumps or warts on the mid-rib is not a reliable diagnostic character.

Table No. 5

Macroscopic features of some leaves resembling Glossopteris fibrosa Pant

	H.4	H.11a	H.11f	H.12a	H.13d	H.16a	H.16b	I.2	H.13g
∠ of Vns. to mid-rib after 1cm.	70	40 - 50	50 - 60	45	45	45	45-50	65	60-70
No.vns./cm at base	11	12	??	??	14	??	14	17-18	16
Vns./cm mid-regn.1cm from mid-rib	16	12 - 14	13	??	??	??	16	20	20
Vns./cm mid-regn. nr. margin	22	22 - 24	20	??	??	??	22	36	34
Vns./cm tip 1 cm from mid-rib	20	20	??	??	??	??	22	??	??
Vns./cm tip nr. margin	27	25	??	20	20	20	--	--	??
Warts on mid-rib (+ or -)	--	++	++	++	++	--	++	--	++
Character of meshes and general remarks	Vns. leave mid-rib at ∠ of 45° but this changes to 70° within 1 cm. Meshes broad & short near mid-rib, but become longer and narrower towards edge of lamina. Identical with Pant's G.hispida-fibrosa-colpodes complex, on consideration of external features only.	Very similar to H.4, but inclination of veins to mid-rib more acute. Meshes wider at mid-rib than at margin of leaf. Differs from H.4 in possessing 'bumps' on mid-rib.	Small fragment of middle of a leaf, 2 cm wide and 6 cm long. Meshes fine, shows 'bumps' on mid-rib.	Fragment of large leaf near tip, 6cm long & 5 cm wide. Character of meshes same as H.11a. Bumps on mid-rib to within 2 cm of tip. This is unusual, as bumps are usually restricted to the basal portion of the leaf.	Small fragment of basal part of a leaf. Similar in all respects to specimen H.11a., including 'bumps' on mid-rib.	Fragment of large leaf from tip region, 10 cm long & 5 cm maximum width. ∠ of veins constant from mid-rib to margin of leaf, and same at basal end of specimen as at the tip. Shape and size of meshes constant, except at extreme tip, where they are slightly longer and narrower.	Small entire leaf, veins not strongly marked, upper surface exposed. Base asymmetric (c.f. G. fibrosa Pant). 'Bumps' show very faintly on mid-rib at extreme base. Note tip is unusually acute.	Small leaf from Sebungwe River, Southern Rhodesia. (Top of Lower Madumabisa Shales). Very similar to H.4. Has split down mid-rib. No cuticle preserved. (Glossopteris communis Feist).	Basal portion of small leaf, 7 cm. long, 2 cm. wide, almost parallel sided. Meshes clearly shown, similar to H.4., but shows 'bumps' on mid-rib. Slight cuticle differences suggest might not be the same species as other leaves (see text, page). Glossopteris sp.A.

Glossopteris formosa Srivastava (1956) has stomates which are very similar to those of the present specimens. They are mono- or di-cyclic, and have 4 - 7 subsidiary cells with large, hollow papillae overhanging the stomatal pore. The size and shape of the cells in the mid-rib region are quite similar in these two species, but the cell walls in Glossopteris formosa are 7 - 8 times as thick as those of Glossopteris cf. fibrosa.

The macroscopic features of the two species are quite dissimilar. Glossopteris formosa is a small narrow leaf and the veins leave the mid-rib at a very acute angle, which is maintained to the margin of the leaf. The veins anastomose to form large broad meshes very similar in character to those of Glossopteris retiformis.

Thus, as it stands, the evidence suggests that Glossopteris formosa and the present specimens are closely related, but the slight differences in cuticle structure, and the gross differences between their morphology suggest they are, in fact, two separate species, though of the same genus.

Glossopteris sp.A

Plate VII B, Plate XXI A - E, Text figures, 32 a - d. 33

Specimen : H.13g

General description.

Macroscopic features.

This specimen is a fragment from near the base of a small leaf (Plate VII B). It is 7 cm. long and has a maximum width of 2 cm. The angle of the veins and the character of the meshes are very similar to those characters as shown in the basal part of H.4, (Plate VI B) which has already been described as Glossopteris cf. fibrosa Feat. The meshes are smaller than those of H.4, and the vein density is consequently higher, but this may be due to the difference in size of the two leaves. The vein density and size of the meshes of H.13g are the same as in the Rhodesian specimen I 2 (page 133), a leaf of similar size. Specimen H.13g differs from both these other leaves in possessing clearly marked warts on the mid-rib. This specimen is included in the Table No.5 on page 104.

Microscopic features.

Cuticle.

The upper and lower cuticles of Glossopteris sp.A are easily distinguished owing to their different thicknesses. The upper cuticle is well preserved, but the lower cuticle is poorly preserved. Both are fragmentary.

Upper Cuticle.

The cells over the mid-rib are regularly arranged (Text fig.32c, Plate XXI C). They are mostly rectangular (some have oblique end walls) and are 80µ - 100µ long and about 30µ wide. The cells over the lamina are very similar, and there is little difference between the cells over the veins and those of the meshes (Text fig. 32d). The former are the same as the cells over the mid-rib, and the latter are shorter and broader, measuring about 60µ long and up to 40µ wide. They are arranged regularly parallel to the veins. The outer surface of all the cells is marked by numerous fine longitudinal striations or rows of very small papillae (Plate XXI A, B). The walls of the cells over the mid-rib and veins are about 4µ thick, while the walls of the mesh cells are only about 2µ thick. In all cases, the walls are straight and sometimes appear as broken lines.

Lower Cuticle.

The lower cuticle is very thin and poorly preserved (Text fig.30a,b. Plate XXI D). No information can be given regarding the differences in cuticle structure between the mid-rib, the veins and the mesh areas, as no preparations show any details of cell shape and size. Some fragments of cuticle show clearly well preserved stomates (Text figs. 32a, b and 35. Plate XXI B, D), but even in these preparations no cell walls can be seen between the stomates. It is assumed that these particular fragments come from the mesh areas of the lower cuticle. That they appear to be arranged in groups and that all members of one group are orientated in more or less

Fig. 32a.

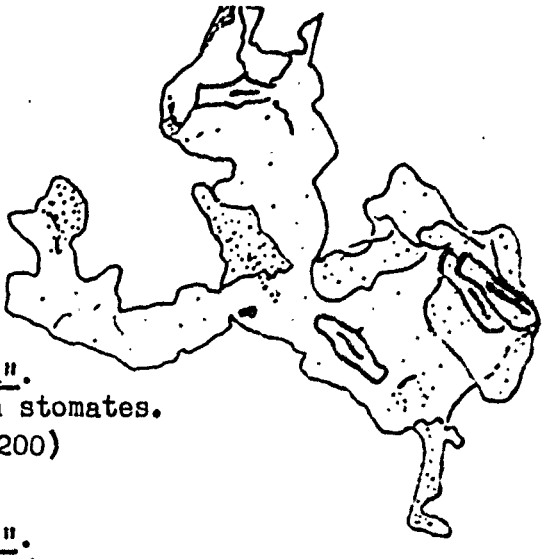


Fig. 32b.

Figs. 32a-b. Glossopteris sp. "A".
Fragments of lower cuticle with stomates.
(X 200)

Figs. 32c-d. Glossopteris sp. "A".
Fragments of upper cuticle. (X 200)

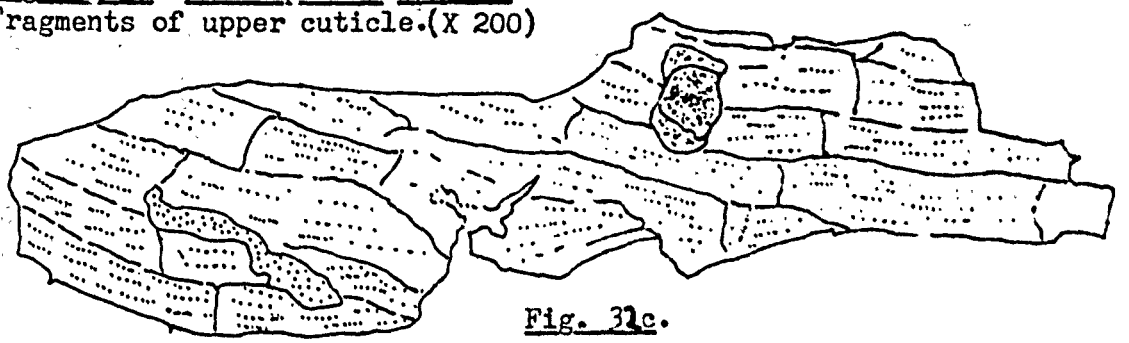


Fig. 32c.

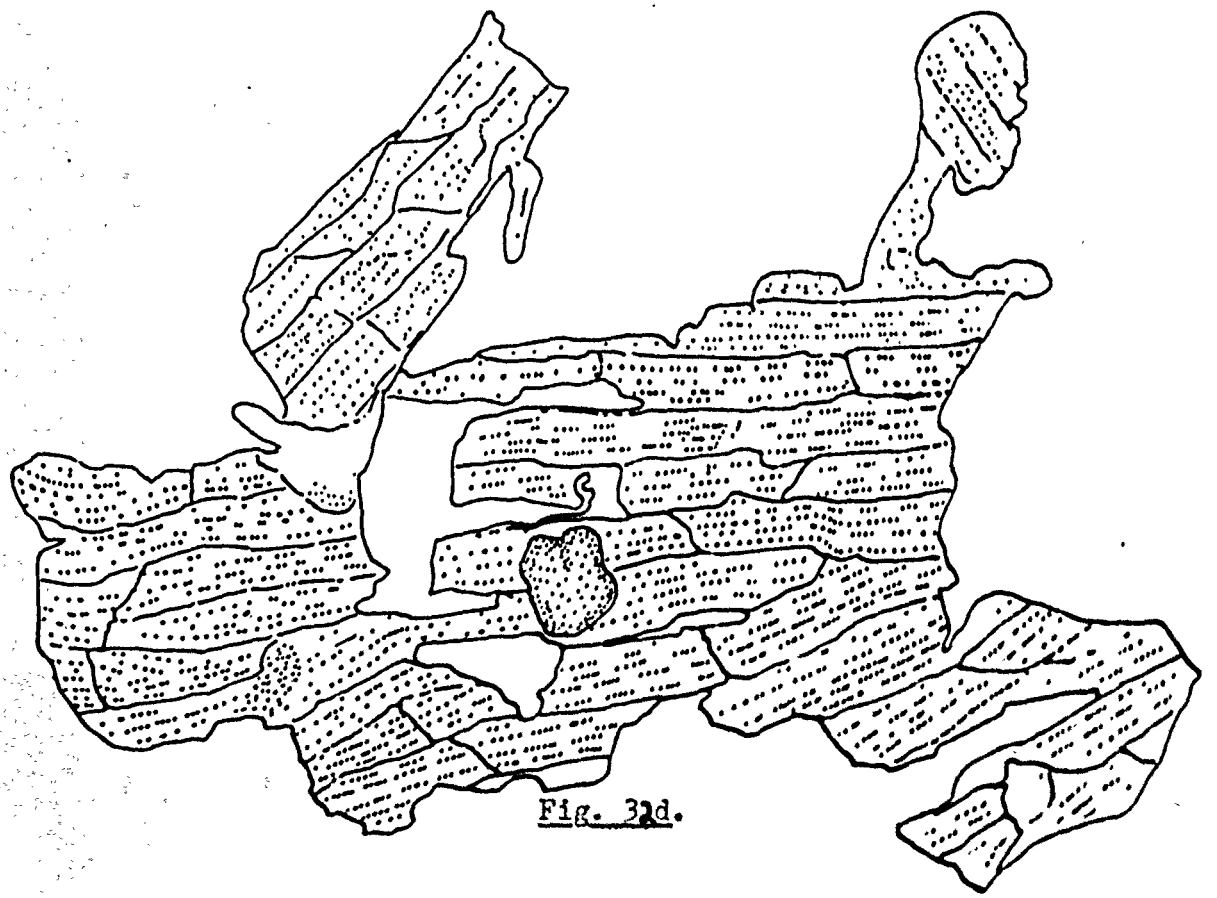


Fig. 32d.

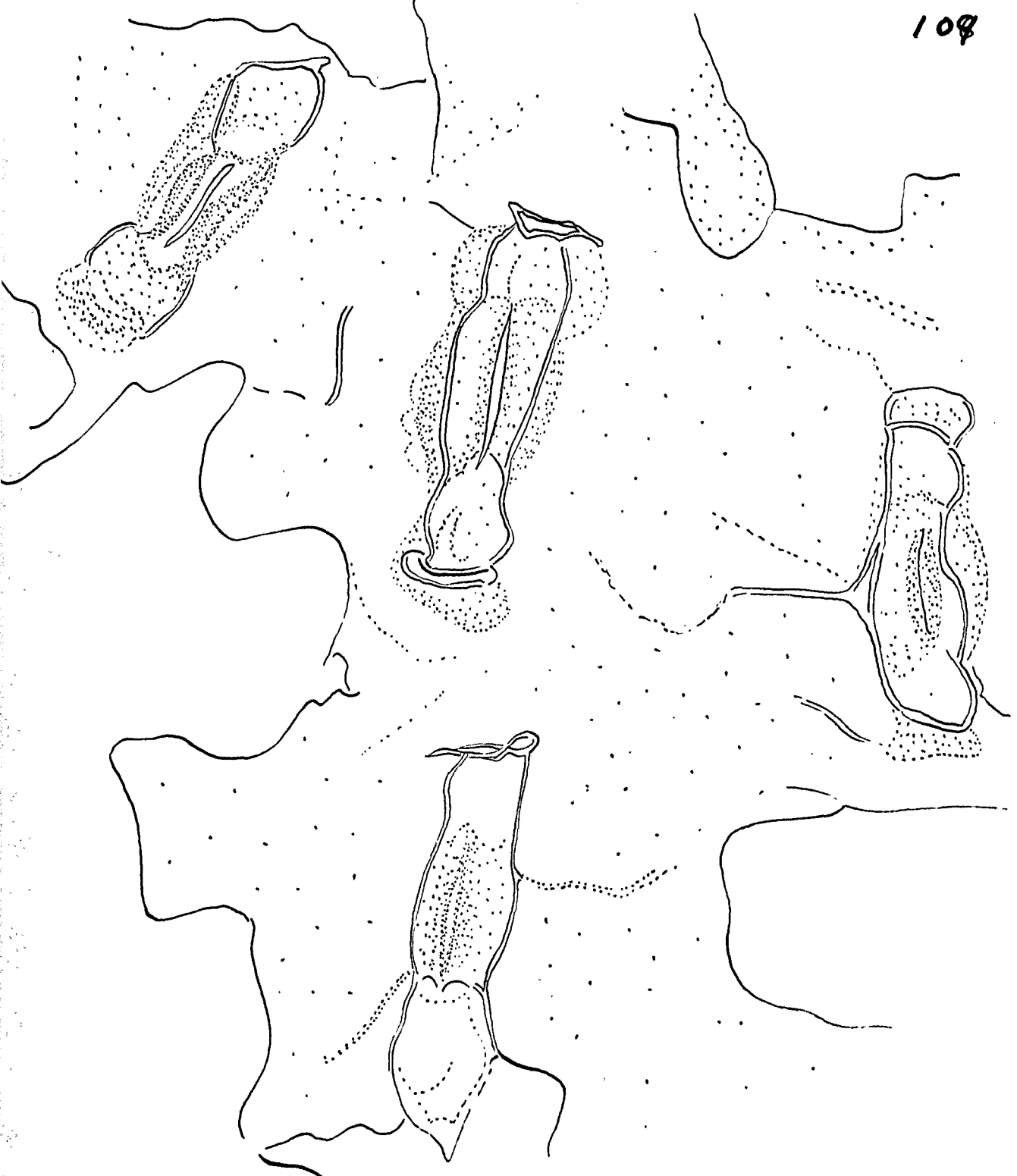


Figure 38. Glossopteris sp. "A". Lower cuticle with stomates.
(Tracing from original free-hand drawing, X 1300.)

the same direction, is all that can be said regarding the orientation and distribution of the stomata (Text fig.33).

The stomates are elongated. The pit which is dumb-bell shaped, is 60µ - 80µ long and 15µ - 20µ wide. The actual stomatal pore is 20µ - 30µ long. The lips of the pore are only slightly thickened, but the surface of some of the guard cells shows additional thickenings parallel to and on each side of the pore. These thickenings may be equivalent to the lignine lamellae described by Pant (1958) in his species of Glossopteris. The subsidiary cells appear to number between 4 and 6, and their inner walls seem to overhang the stomatal pit (Text fig. 33. Plate XXI B).

Comparison and Discussion.

In external features, and in the size and shape of the cells of the upper cuticle, N.13g is very similar, if not identical, to Glossopteris fibrosa Pant (1958). In both species, the cells of the upper cuticle bear many small papillae or longitudinal striations. The specimens already described here as Glossopteris cf.fibrosa are very similar in general character, but do not show papillae or striations on the cells of the upper cuticles.

Glossopteris sp.A differs from [redacted] Glossopteris fibrosa Pant and from the specimen here called Glossopteris cf.fibrosa, in that the stomata, which are confined to the lower surface, are much larger, and the pit is dumb-bell shaped. Also the subsidiary cells, although overhanging the stomatal pit, are not so clearly papillate as in the other two species. Unfortunately, the size and shape of the cells of

the lower cuticle are not known for this specimen.

Although this specimen is clearly different from any that has been previously described, the lower cuticle is not sufficiently well known to enable the author to erect another new species, so it will be referred to as Glossopteris sp.A.

Glossopteris Jamottai Upeg and Rose.

Plate XXII A - D, Plate XXIII A - C, Text figures 34 - 37.

Figured specimens. H.11b, H.13b, H.13c.

Unfigured specimens. H.7c, H.11j, H.13a

General description.

Macroscopic features.

Of the above specimens, only H.11b is complete. It is 10 cm long and has a maximum width of 1·5 cm (Plate VII A, a1 b. Text fig. 34). The other specimens range in width from 1·5 to 3 cm. in maximum width, the largest being H.13c.

The leaf shape is generally linear lanceolate. The tip is rounded, and the lamina narrows gradually to the base which is not petiolate. The mid-rib is strongly marked at the base, but becomes much more faint in the upper half of the leaf, although in some specimens it can be traced almost to the tip. It is prominent on the lower surface of the leaf, but forms a depression on the upper surface.

The lateral veins leave the mid-rib at an angle of about 25° and this gradually changes to one of 45° - 70°. The vein density over most of the lamina is 30 - 35 veins per cm, and the meshes are long and narrow (Text fig.34).

Cuticle.

Both cuticles are well preserved, though the lower one tends to

Fig.34b.

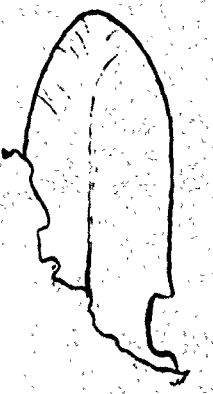


Fig.34a.

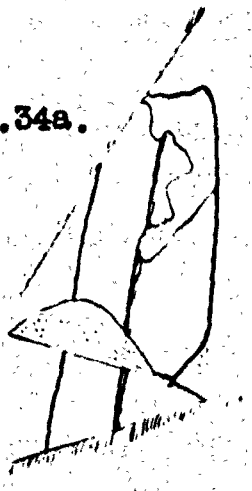


Fig.34c.

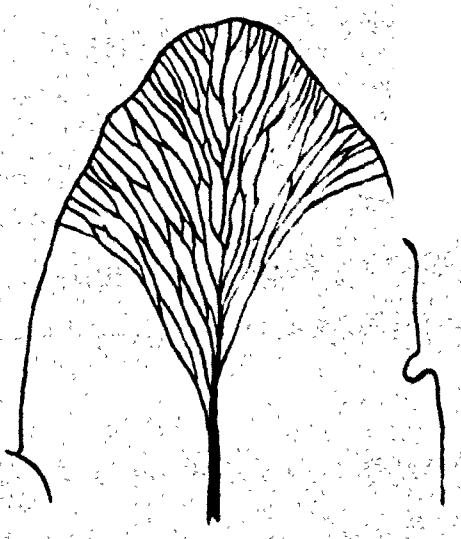


Fig.34. Diagrams to show the macroscopic features Glossopteris jamottei. a) Specimen 11b, X 1. b) Specimen 13b, tip of leaf, X 1. c) Detail of part of Specimen 13b, showing evanescent midrib and the nature of the venation.

be fragmentary. The upper and lower cuticles may be distinguished by their different thicknesses, by the general absence of stomata in the former, and by the difference between them in cell size.

Upper Cuticle.

The cells over the mid-rib are elongated and polygonal in shape. Normally the cells measure 30μ - 40μ long and 10μ - 15μ wide (Plate XXIII B). Exceptionally large cells may be 50μ long and 20μ wide. The cell walls are straight and 1μ - 2μ thick. The cells over the veins are long and narrow, measuring 100μ - 230μ long and approximately 35μ wide. They are arranged in longitudinal files; the lateral walls are more or less parallel, but the end walls are often oblique (Text figs. 35a, 36c). Over the meshes, the cells are arranged regularly in files parallel to the veins. The cells are more or less rectangular, and measure 40μ - 60μ wide and 45μ - 140μ long. The cell walls are straight or very slightly sinuous (Text.figs. 35b, 36a. Plate XXIII A), and are about 2μ thick. Near the mid-rib the cells tend to be smaller, and more or less isodiametric, and sometimes have clearly sinuous walls (this last feature may be due to distortion during fossilization) (Text fig. 36a, Plate XXIII B). Stomata are generally absent from the upper cuticle, but one preparation shows one isolated stomata (Text fig. 35b. Plates XXII C, XXIII A).

Lower Cuticle.

The cells over the mid-rib and veins are similar in size and shape to those of the upper cuticle (Text fig. 35c), but the cells of the mesh areas are smaller and not so regularly arranged. The mesh cells

are polygonal or rectangular in shape, and measure 50µ - 130µ long and 35µ - 60µ wide (Text Figs 35c, d. Plate XIII C). The stomates are monocyclic and are arranged in groups, but with no regular orientation. The subsidiary cells are exactly similar in size and shape to the other cells of the mesh region, and this makes it very difficult to locate the stomates (Plate XXII D, XIII C). The stomatal pit is 40µ - 60µ long and 15µ - 17µ wide and it is rectangular or dumb-bell shaped (Text fig. 37. Plate XXII A, B). The subsidiary cells overlap the guard cells which form an elliptical area 40µ across and 50µ long (Text fig.37). The stomatal pore itself is 15µ - 20µ long and has cutinised ridges on the lips.

Comparison and Discussion.

The description of the external features of this group of leaves might apply to any of the smaller forms of Glossopteris indica as described by Feiller, but for reasons already discussed, this specific epithet cannot be applied to leaves having well preserved cuticles. The external form is also particularly close to that of Glossopteris Amottai, as described by Lipeg and Rose (1960). The structure of the cuticles is also very similar in many points (e.g. the shape of the cells of both upper and lower cuticles and the form of the stomates), so that the Transvaal and Congo specimens are undoubtedly very closely related.

The rare occurrence of stomates on the upper cuticle and the possession of cells which sometimes have sinuous walls, are features which have only been observed in the Ermelo specimens. As the cuticles

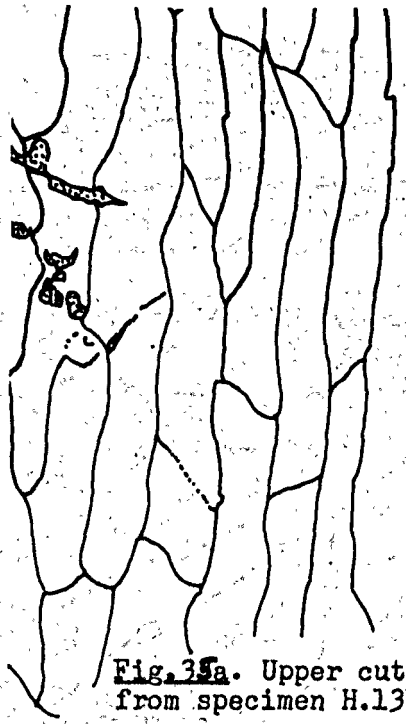


Fig.35a. Upper cuticle from specimen H.13b.

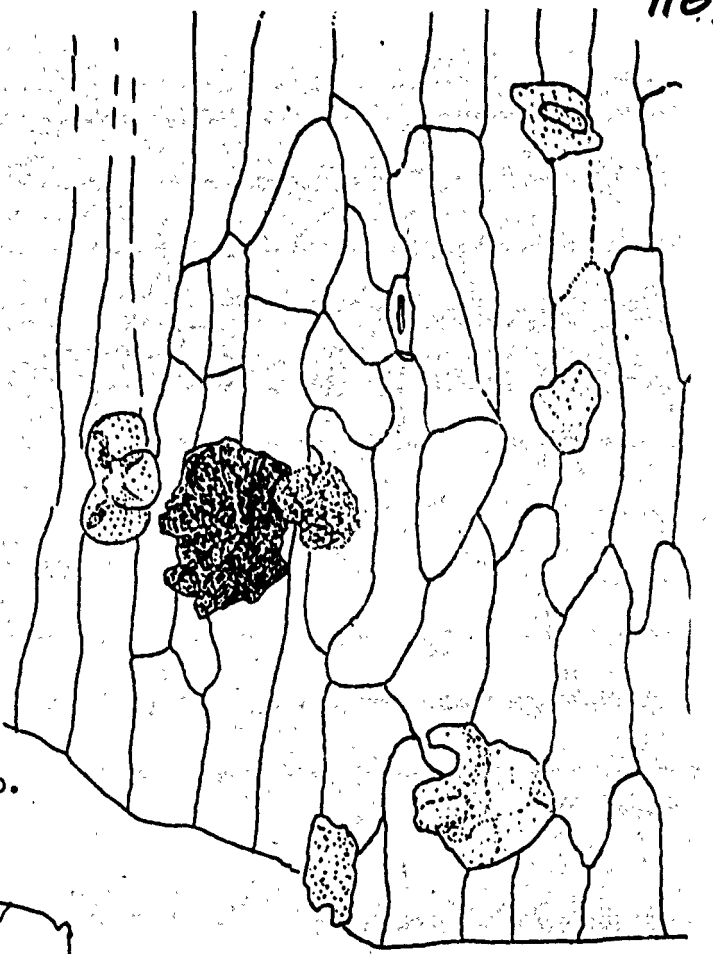


Fig.35b.(top right)Upper cuticle with stomate.H.13b.

Fig.35c.(bottom left) Lower cuticle from H.13e. Note stomates.

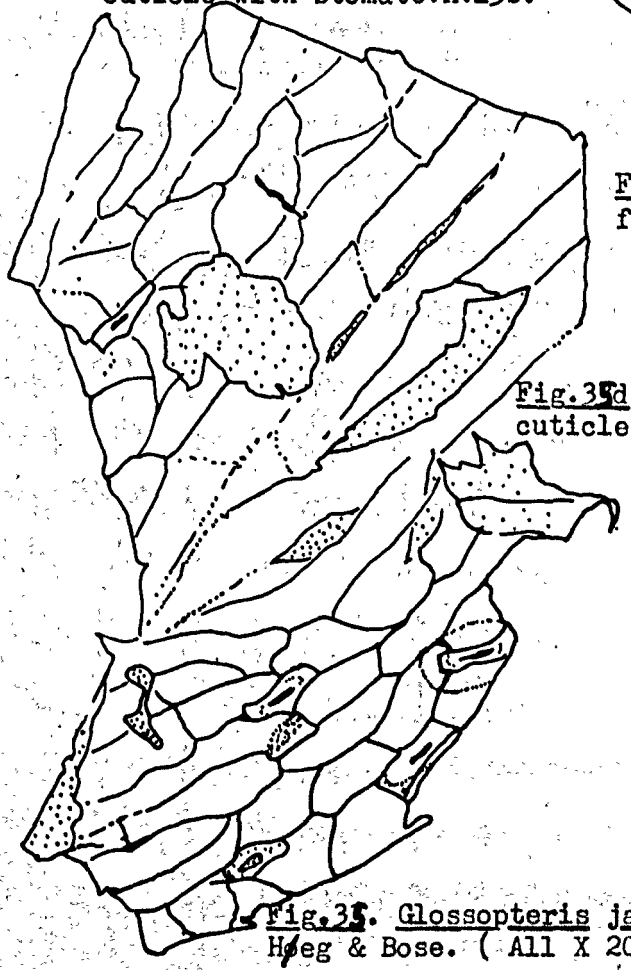


Fig.35d.(right)Lower cuticle from H.13e.

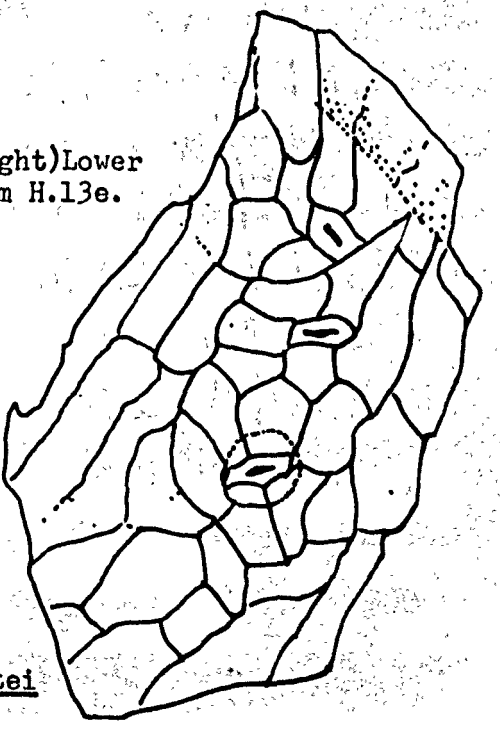


Fig.35. Glossopteris jamottei Høeg & Bose. (All X 200)

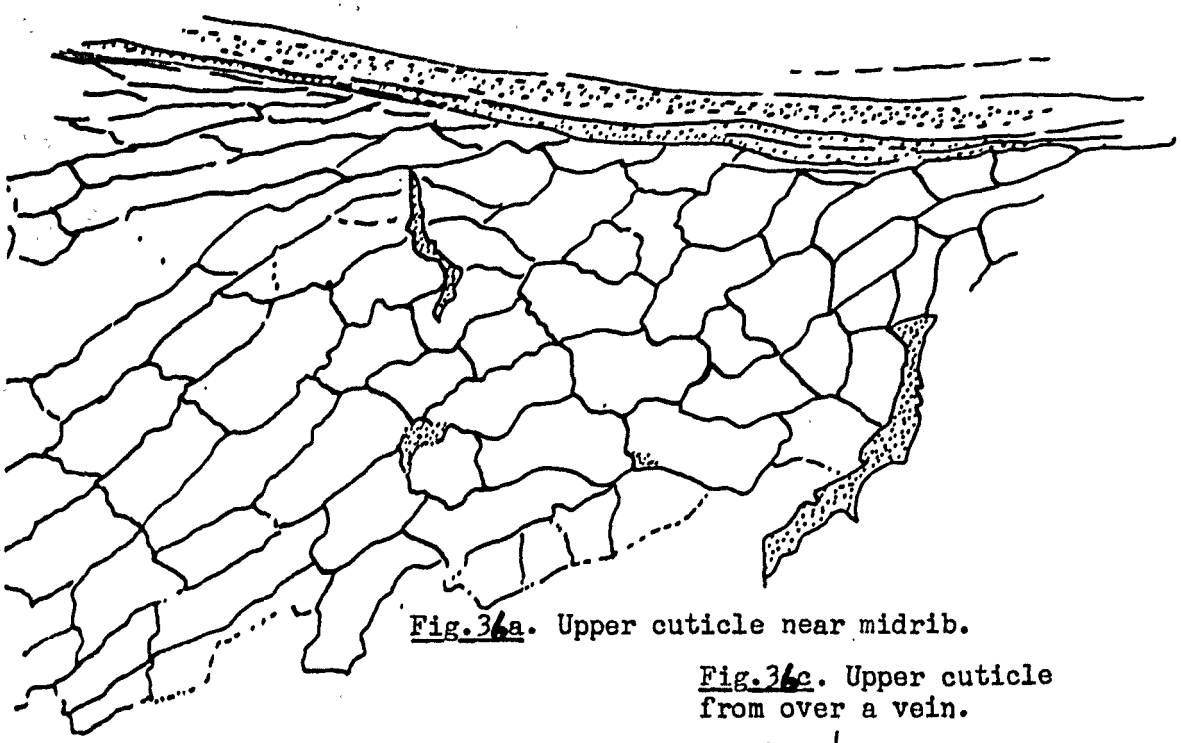
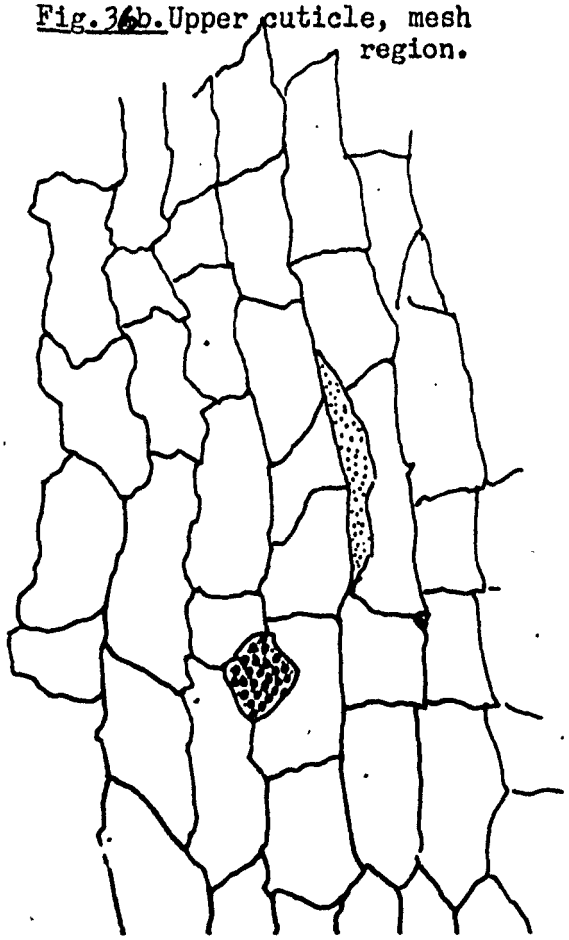


Fig.36a. Upper cuticle near midrib.

Fig.36c. Upper cuticle from over a vein.

Fig.36b. Upper cuticle, mesh region.



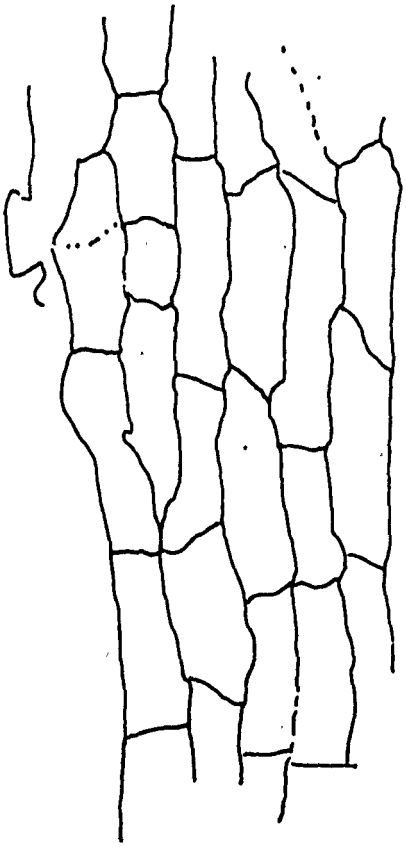


Fig.36a-c, Glossopteris jamottei Hoeg & Bose. All from H.11b. (X 200)

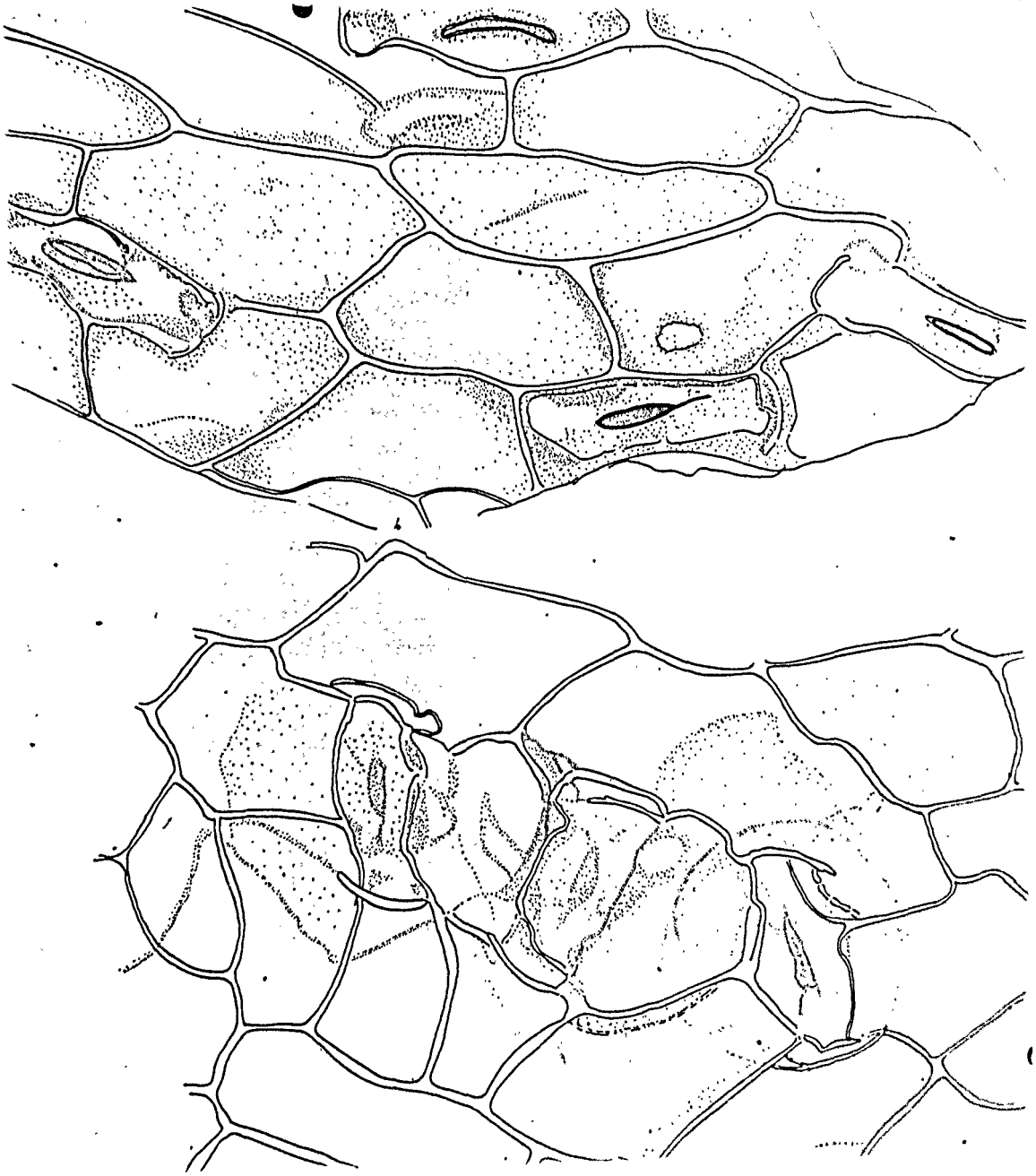


Figure 37. Glossopteris jamottei Høeg & Bose.
Fragments of the lower cuticle from specimen H.13e., showing stomates. All show the stomatal pore, and the outline of the guard cells can be seen, bottom right.
(X 650)

of the Congo specimens were very fragmentary, it is not surprising that these characters were not seen in the preparations examined by Hoeg and Bose, and it is doubtful if the erection of a new species (on these characters alone) could be justified. I, therefore, regard these features merely as an extension of our knowledge of Glossopteris Jamottei, and place the Ermelo specimens in this species.

It is worthy of note that in the size and shape of the stomates, and the more extreme examples of cells with sinuous walls, the cuticles of the Ermelo specimens of Glossopteris Jamottei bear a slight resemblance to those of Glossopteris angustifolia (Brong.) as described by Sahni (1923). The main differences are the absence of hairs or hair bases from the subsidiary cells of Glossopteris Jamottei and the fact that cell walls are only sometimes sinuous and then not so markedly as in Glossopteris angustifolia.

It is possible that some relationship exists between these species, but the discovery of further forms which are intermediate, both in the nature of the cuticle and in their external features, is required before this can be suggested more strongly.

In well preserved pieces of cuticle, the form of the stomates is similar to those of Glossopteris africana sp.nov (Page 81.). However, the cuticles of Glossopteris Jamottei are much thicker than those of Glossopteris africana and its lower cuticle has no sinuously walled cells. Even where such cells do occur (near the mid-rib of the upper cuticle), they are not so markedly sinuous as those of Glossopteris africana, and it is possible that the sinuosity is due to distortion as the cuticle was

folded and crushed in this region during fossilization. I do not think that they are sufficiently alike to be placed in the same species.

Indeterminable axis.

Plate V D, Plate XXIV E, Plate XVIII D, Text figure 38.

Specimen H.5

General description.

Macroscopic features.

The specimen is a small compressed axis, 14 cm long and 2 - 2·4 cm wide. The organic remains of the axis are present in the form of a coaley layer about 1·5 mm thick. The external form of the branch is quite well preserved, both on the surface of the carbonaceous layer and impressed on the underlying shale. The most obvious feature is the presence of a large number of lumps or swellings which are 1 - 3 mm in diameter and which are scattered irregularly over the surface of the branch. As these lumps are invariably associated with underlying nodules of pyrites, it is uncertain whether or not they are a feature of the living plant. The surface is also marked by numerous longitudinal ridges which may have been caused by fissuring of the bark of a tree or shrub, or by folding of the tissues under pressure during fossilization. (Plate V D).

Particularly where the shale beneath the coaley layer is exposed, several transverse scars are visible. The largest, at the base of the branch, is about 1 cm long and has a maximum width of about 1·5 mm. The scars are smaller and more closely spaced further along the branch. They are in staggered diagonal rows which suggests that they might have been

arranged in an irregular spiral on the branch before it was compressed during fossilization. This arrangement and the characteristic shape of the scars is shown in fig. E. Plate XXIV.

Microscopic features.

On maceration, the carbonaceous remains of the axis yielded a thin layer of cork-like material, 4 - 12 cells thick. (Text fig.39, Plate XVIII D).

Repeated attempts were made to discover the nature of the cells over the horizontal scars, using balsam transfer and cellulose pull methods, as well as ordinary maceration techniques, but they all proved unsuccessful.

Discussion and comparison.

The thickness of the axis, and the presence of a corky layer instead of a distinct epidermis, suggests that it had undergone some degree of secondary thickening. Thus it is probable that the specimen was the axis or a branch from a tree or a shrub.

The most interesting feature of the axis is the series of transverse scars shown in Plate XXIV E. It is possible that these marks are the remains of lenticels, and this is supported by their flattened lozenge shape with a median groove, which is very similar to the horizontal lenticels of some recent dicotyledenous trees, which I have examined, (Fagus sylvatica, Betula verrucosa, Crataegus monogyna and Ilex aquifolium.).

Transverse lenticels do not seem to be so common amongst the

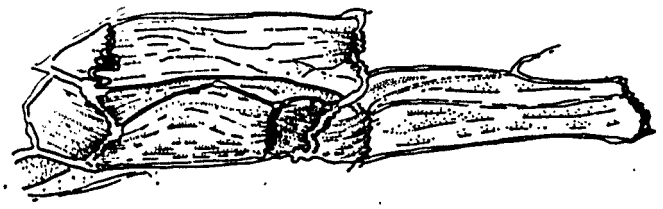


Fig.38a. cork cells in section

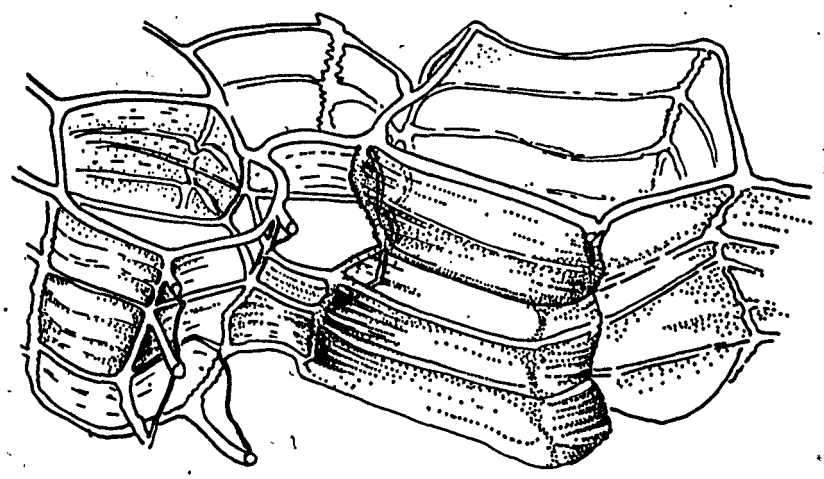


Fig.38b. 3-dimensional view of cork cells

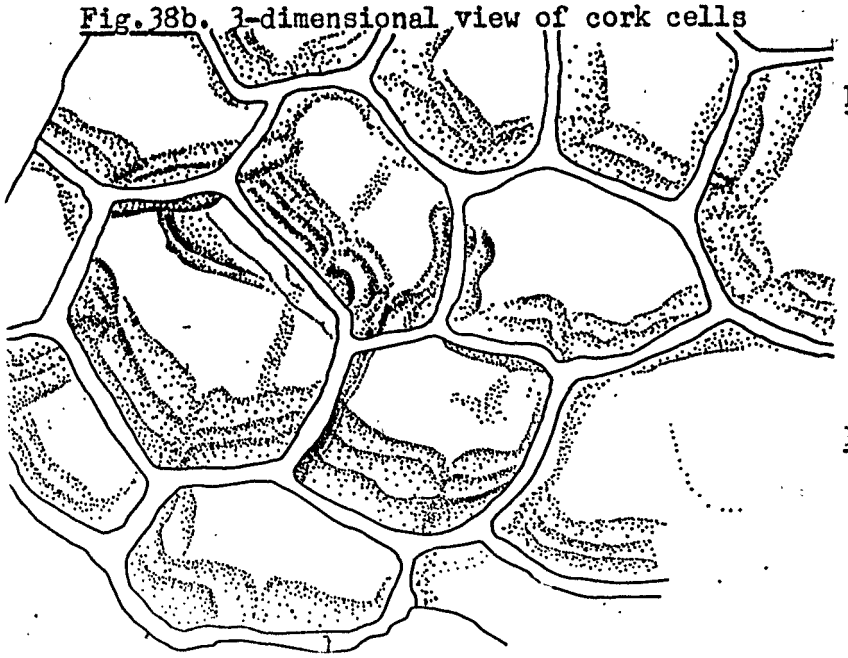


Fig.38c. Top 3-dimensional view of cork cells.

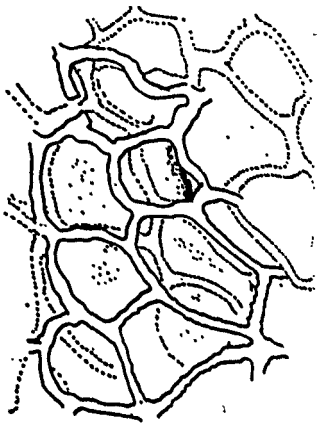


Fig.38d. Piece of cork before splitting.

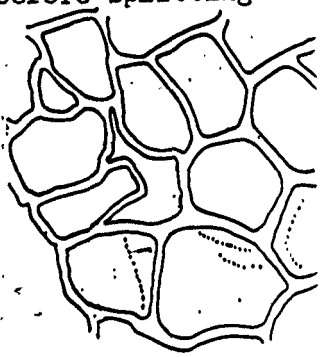


Fig.38e.

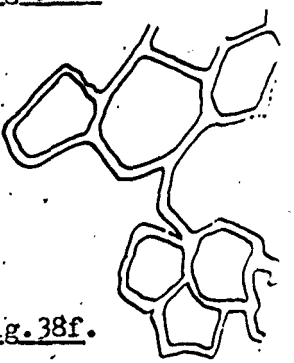


Fig.38f.

Fig.38g.

Figs.38e-g. Fragments obtained by splitting piece of cork shown in 38d.

Figures 38a-g. Cork cells from Indeterminable Branch.

gymnosperms. Jeffrey and Watmore (1926) described lenticel-like structures in the Abietineae, and compared them with the parichnos of the Lepidodendraceae. Their diagram of the "parichnos" in Pinus rigida (Page 633) is very similar to the scars shown in the present specimen. However, I have examined branches of several recent gymnosperms, but found no horizontal lenticel-like structures. The results of this investigation are given below.

1. Abies: Aerating tissue of cortex communicates with atmosphere through persistent leaf bases.

2. Araucaria: Vertical splitting of bark occurs, but no: lenticels are present. However, the persistent leaf bases and scars on older stems have a shape very similar to the fossil marks.

3. Cupressus: Vertical slits in bark occur opposite rays in wood. No definite lenticels with powdery corky tissue.

4. Ginkgo: Irregular vertical splits in bark - no true lenticels.

5. Juniperus: Aerating tissue connects with atmosphere through persistent leaf bases.

6. Larix europaea: No lenticels - only vertical splitting of bark.

7. Picea: Aerating tissue of cortex extends into persistent leaf bases.

8. Taxus: A single horizontal scar was seen, but this appeared to be the result of wounding.

Assuming that the axis is from a gymnospermous plant, the foregoing investigation does not support the hypothesis that the marks

are simple lenticels, as aerating tissue in the gymnosperms examined is associated with vertical splits in the bark, or with persistent leaf bases.

It is also possible that these horizontal marks are leaf scars. In this case, they must have been caused by the abscission of leaves with wide bases, such as Ganamopteris or Noeggerathiopsis, and the median groove can be considered as marking the point of entry into the cortex, of numerous leaf traces and/or aerating tissue.

In fact the marks bear a strong resemblance to the scars on an old trunk of Araucaria araucana, which are left by the rotting of the rather persistent leaves. In Araucaria, however, the scars are arranged in a close, regular spiral, and the irregular, if spiral arrangement of the marks on the present specimen, does not seem to support the hypothesis that they are, in fact, leaf scars.

On the evidence available, the marks could be either lenticels or leaf scars; both hypotheses are tenable.

Seed-like body (indet.)

Plate III A, B, Plate XIV A, B.

Specimen. H. 15

General description.

Macroscopic features.

The seed-like body described here is represented by both part and counterpart (Plate III A, B). It is a convex oval structure some 3·4 cm long and 1·9 cm. broad. Vein-like strands can be seen radiating from the base (Plate III A). Both part and counterpart have patches of carbonaceous material remaining.

Microscopic features.

One poor preparation of the cuticles has been obtained. Two distinct types are present. One is thick with straight or curved cell walls (Plate XIV B,A) and is mostly distorted due to lateral compression. The other is thin and has larger cells with thin sinuous walls (Plate XIV C, A).

Discussion and comparison.

On external features alone it is impossible to say whether the specimen is a large seed, or a small scale leaf of a gangamopterid type.

The sinuous-walled cells of the lower cuticle are unlike any described for a species of Gangamopteris in this Thesis, which would

suggest that the specimen does not belong to that genus. However, Srivastava (1956) has assigned several species with curved or sinuous walls to the genus Gensanopteris.

The cuticles described could equally well belong to a seed; but the fragments are so small and poorly preserved, that apart from confirming that the specimen is a fossilized plant structure, they add little to our knowledge.

The specimen is, therefore, referred to as:

Seed-like body (indet.).

A NOTE ON SOME FOSSIL PLANTS FROM SOUTHERN RHODESIA

INTRODUCTION

As well as the compressions from Ermelo, already described, I have been fortunate in being able to examine some compressions and impressions from the Sebungwe inlier, in the Sebungwe River Valley, Sebungwe District, Southern Rhodesia.

I am indebted to Dr. W. S. Lacey and Professor C. Bond for this material. In all there are six rock specimens bearing a variety of leaves and seeds. The specimens described here are numbered I.1 to I.3; unfortunately only the first yielded cuticles.

Specimen I.1 was not "in situ". It was collected in the bed of the Sebungwe River, a few hundred yards downstream from the outcrop of Lower Madumabisa Shale which yielded Specimen I.2.

Specimen I.3 came from an outcrop of Upper Madumabisa Shale of the Sebungwe River area, further downstream than the localities for I.1. and I.2.

Glossopteris sp.D

Plate VII C, D. Plate XXIV A, B, C.

Specimen I.1.

Age and Horizon. Probably Lower Madumabisa Shales; Lower Permian.

General description

Macroscopic features.

The rock is a dark grey, banded, micaceous shale, and on first examination this specimen appeared to be an impression of the basal part of a small linear leaf. It measured 6·6 cm long and had a maximum width of 1·5 cm. The venation was very poorly preserved, but the main veins were more or less parallel to the longitudinal axis, and in a few places irregular anastomoses could be seen (Plate VII D). The stippled areas on the drawing (Plate VII C) represent the very small fragments of carbonaceous material which remained adhering to the rock.

Cuticles.

After prolonged maceration, the carbonaceous remains yielded well preserved cuticles, which were identical in the shape and size of their cells and in the distribution of the stomata, but which differed greatly in thickness. The pattern of the veins which was but poorly shown by the hand specimen, was confirmed by the cuticles. This pattern is very similar to that shown on the lamina of Glossopteris

fibrous Plant and it is suggested that the specimen is not a small linear leaf, but a mere fragment of the lamina of a very much larger leaf. The narrow portion would appear to have been near the mid-rib of the leaf, whilst the broader "apex" was close to the margin of the leaf. Thus the whole leaf might have been as much as 12 cm broad, depending on the angle between the veins and mid-rib.

Upper Cuticle.

The upper cuticle is the thicker of the two and clearly shows the arrangement of the veins and the distribution of the stomata in irregular groups within the mesh areas (Plate XXIV A). The cells over the veins are more or less rectangular, measuring 100μ - 120μ long and about 20μ wide, and are arranged regularly with their long axis parallel to that of the vein (Plate XXIV B). The cells may be faintly papillate.

The cells of the mesh area are polygonal and are isodiametric, or elongated with the long axis parallel to the veins. They measure 30μ - 50μ wide and 40μ - 120μ long, and are all strongly marked with a median papilla (Plate XXIV A). The subsidiary cells of the stomates measure about 30μ - 40μ and are arranged in circles of 5, 6 or 7 around the stomatal pores and overlie the guard cells (Plate XXIV C). The exact dimensions of the guard cells could not be seen, but the stomatal apparatus, including the subsidiary cells, measures about 200μ across.

Lower Cuticle.

The lower cuticle is thinner than the upper, and consequently

details are not quite as well preserved. In all features, such as cell shape and size, in the distribution of the stomata and in the nature of the papillae, the two cuticles appear to be identical. In particular, the positions of the stomata on the upper surface always appear to coincide exactly with those on the lower surface.

Comparison and Discussion.

The specimen is so small and poorly preserved that little can be said regarding its external features. The form of the venation appears similar to that shown by many large Glossopteris leaves of the type of Glossopteris communis Feist, Glossopteris colpodes and Glossopteris hirsuta Pant (1958) and Glossopteris cf. fibrosa (Page of this paper).

Both upper and lower cuticles are very similar to the lower cuticles of Glossopteris fibrosa and Glossopteris sp.a. described by Pant but the upper cuticles of Pant's species do not possess stomata, and the cells do not have a single median papilla.

The lower cuticle of Glossopteris cf. fibrosa is also quite similar to that of the present specimen, but the cells are not so clearly papillate and the papillae of the guard cells are not so spur-like.

Both cuticles seem identical in all features to the isolated fragments described by Hoeg and Bose (1960) as Cuticle Type 57. Unfortunately they have no clue as to the external features of the leaf concerned.

From this it would seem that the cuticle almost certainly belongs to a leaf of the Glossopteris type, but it cannot be given a

specific name and is referred to as Glossopteris sp.B. The specimen is of particular interest, as it is the first fossil with cuticular remains to be described from Southern Rhodesia (Lacey, 1961b).

Glossopteris communis Feist (1881)

Specimen. I.2a

Age and Horizon. Probably from the top of the Lower Madumabisa Shales. Lower Permian.

General description.

Macroscopic features.

This is a fragment of a leaf, and is 6·5 cm. long with a maximum width of 4·0 cm. The mid-rib has been split about 2·5 cm. from the base. The shape of the leaf and the form of the venation are typical of the leaves described in this Thesis as Glossopteris cf. fibrosa Pant, and this specimen is included in Table No.5 on page 104 It is however referred to Feistmantel's species Glossopteris communis, as only macroscopic features are known.

Glossopteris sp.

Specimen I 2 f + g.

Age and Horizon: Probably from the top of the Lower Kadumadian Shales.

General description.

Macroscopic features

On the same block bearing the leaf described as Glossopteris communis are the impressions of two further fragments of leaves. Both are lanceolate-spathulate in shape; both have pronounced mid-rib, but the veins are not clearly shown. It appears to be the ab-axial surface of both leaves which is exposed. The largest is 13 cm long and has a maximum width of 3 cm. (both are incomplete). In general, the shape of these leaves is similar to those described here as Glossopteris cf. fibrosa, Pant, but as no cuticle was obtained from them, and the state of preservation was so poor, I hesitate to assign them to any species.

Samaropsis sp.

Specimens: I 2 b, c, d.

Age and Horizon: Probably from the top of the Lower Kadumabiss Shales.

General Description.

Macroscopic features.

On the same slab mentioned on the previous page are the impressions of three seeds, each about 2·5 cm. long and 1·5 cm broad. Each shows signs of possessing a narrow wing (2 mm. - 4 mm. broad) and apical or micropilar notch. Although there were some carbonaceous remains on the seeds, no cuticle was obtained. Because of their winged nature, I include them in the genus Samaropsis Goeppert, but because of their poor preservation, I am not prepared to place them in a species. There is, however, some similarity between these seeds and those described by Zeiller (1879) as Samaropsis millori.

Taeniopteris sp.

Specimen: I 5.

Age and Horizon: Upper Madumabisa Shales.

General description:

Macroscopic features:

This specimen is a piece of light grey shale, and bears the impression of a fragment of a large leaf. The fossil consists of fragments of only half a lead, from the mid-rib to the edge of the lamina.

The mid-rib is prominent and the veins, although faintly marked, can be seen leaving the mid-rib almost at an angle of 75°. They are widely spaced (about 0·8 - 1 mm. apart) and dichotomise about 0·75 cm. from the mid-rib.

Cuticles.

Although parts of the fossil possessed a pale brown layer, which was thought to be of organic origin, no preparations of cuticle were obtained.

Comparison and Discussion.

On external features, the specimen clearly belongs to the genus Taeniopteris, Brongniart, but owing to the lack of knowledge of the actual shape and size of the leaf, and of the cuticle structure, I cannot place them in a species.

General Discussion.

The work described in Part II of this Thesis has considerably increased our knowledge of the cuticle structure of Gangamopteris and Glossopteris leaves, but it may truthfully be said that the study has served to emphasise the difficulties of arranging a logical and natural classification of these types of leaves, rather than to clarify the situation.

Surange and Srivastava (1956) and Plumstead (1958a) have shown quite clearly that the division of the Glossopteridaae into only three genera (Gangamopteris, Glossopteris and Palaeovittaria) is an over-simplification of the situation, and is based on insufficient knowledge. The present study has stressed that it is unwise to attempt to erect a "natural" form of classification solely on the data which can be obtained from the macroscopic features of Glossopteridaan leaves, preserved as compressions and impressions.

The multiplicity of almost indistinguishable species which were erected by early workers, particularly Feistmantel, and which were later largely merged by Arber (1905) shows that the situation is complicated not only by lack of knowledge, but by differences between authors in quite subjective assessments of the relative importance of diagnostic characters.

Progress in the classification of the Glossopteridaae may be said to have taken place in three stages:-

1) work on macroscopic features of leaves only;

2) work on macroscopic features of leaves and cuticle studies;

3) work on the macroscopic features of leaves in organic connection with fructifications (but without knowledge of their cuticle structure).

It is only when these stages are combined that we can hope to achieve the understanding of these fascinating plants for which palaeobotanists are striving. This largely depends on the discovery of well preserved specimens with both fructifications and cuticles.

In spite of having no information regarding the nature of their fructifications, I have used the evidence afforded by their macroscopic and cuticular features to arrange the species described in this Thesis, in four groups, more or less in the manner followed by Surange and Srivastava (1956).

Group A.

All the specimens described under Gangamopteris.

Macroscopic features.

Lanceolate or obovate leaves, central region occupied by several parallel anastomosing veins. Lateral veins radiating from the base and arising from the median veins, anastomosing frequently.

Microscopic features.

Cuticles of medium thickness or thin, upper cuticle usually thicker than the lower. The cells over the veins are mostly more elongated than those of the mesh regions, otherwise there is little difference between them. All the cells are large and thin walled.

The stomates are large and have 4 - 7 subsidiary cells which are often papillate. They are usually monocyclic, but sometimes dicyclic. Stomates are found on both surfaces.

Group B.

Glossopteris transvaalensis sp.nov.

Macroscopic features.

Linear or linear lanceolate leaves with a thick mid-rib and steeply angled dichotomising veins. Anastomoses very rare or absent.

Microscopic features.

The upper cuticle is thick with rectangular or polygonal cells, not showing a clear difference between the veins and meshes, cell walls very thick. The lower cuticle is much thinner, and the veins and meshes are clearly shown. Stomates are confined to the mesh areas and each is sunk in a shallow pit.

Group C.

Glossopteris cf. fibrosa, Glossopteris communis Feist., Glossopteris sp.A., Glossopteris sp.B.

Macroscopic features.

Lanceolate leaves with a thick prominent mid-rib and clearly marked veins with numerous anastomoses.

Microscopic features.

Both cuticles of medium thickness, the upper normally being the thicker of the two. Veins and meshes fairly well marked, monocyclic or dicyclic stomates confined to the mesh areas of the lower cuticle. Subsidiary cells with large papillae overhanging the stomatal pore. Median papillae usually confined to the cells of the lower cuticle, but sometimes papillae are present on both surfaces.

Group D.

Glossopteris africana sp.nov., Glossopteris Jamottei Egbg and Boso.

Macroscopic features.

Lanceolate or linear lanceolate leaves with strongly marked mid-rib and anastomosing veins.

Microscopic features.

Cuticles medium thickness or thin. Veins and meshes fairly well marked, with sinuous or straight walled cells. Stomates with "I" shaped pit, normally confined to the mesh areas of the lower cuticle. Subsidiary cells identical to surrounding mesh cells.

The division of the Glossopterideae into six groups has been advocated by Surange and Srivastava (1956) on the basis of cuticle studies, and by Plumstead (1958) on fructifications.

A comparison of these systems with that given in the present study, does not yield a clear cut basis for classification, but the groupings proposed by the various authors, as set out in Table No.6, (P.143) show several possible correlations.

Possibly the most convincing is that between Group B (Williams), Groups I. Scutum and II. Hirsutum (Plumstead) and Group 3 and parts of groups 4 and 6 of Surange and Srivastava.

Note that Gangamopteris sp.B of Srivastava, included in Group 4 of Surange and Srivastava (1956), might, to judge from the original illustration (Plate 13, Figure 69), equally well be a species of Glossopteris.

The macroscopic features of the leaves bearing Lanceolatus (Group III of Plumstead) are similar to those of Group 2 (Surange and Srivastava) and Group C. (Williams), and to one specimen from Group 6 (Surange and Srivastava). The correlation between these last two groups is also supported by the general similarity of their cuticles.

There are rather less satisfactory grounds (on the basis of macroscopic features) for suggesting that a correlation between Groups V & VI of Plumstead, Group 1 of Surange & Srivastava, & group D(Williams). However, a relationship between group 1 of Surange & Srivastava, & group D of Williams, is again more strongly supported by an examination of their cuticles.

Cuticular evidence would suggest that there was also a correlation between on the one hand, Group 5 of Surange & Srivastava, & on the other, Groups 1(Surange & Srivastava) & D(Williams), although the first group consists entirely of Gangamopteris leaves, & the other two groups consist of Glossopteris leaves.

It is perhaps possible that these leaves of Group 5(Surange & Srivastava) forms a connecting link between the species of Glossopteris given in the table, & the species of Gangamopteris in group 4 Ottokaria, (Plumstead), part of group 4(Surange & Srivastava) & Group A (Williams). The last three groups seem to form quite a natural assemblage of broad leaved gangamopterids, with, so far as is known, rather similar cuticles.

As well as the difficulties involved in classification, table No.6 does appear to show the beginnings of a grouping of the Glossopterideae which is supported by three quite independent investigations.

As Plumstead(1958) states, a major difficulty in the erection of a satisfactory system of classification is the fact that many species are based on Feistmantel's original diagnoses & drawings, the latter often being misleading. It was for this reason that Arber(1905) was not more succesful in arranging a classification based on secondary

TABLE No. 6

Possible Correlations Between the Systems of Classification Suggested a) by Plumstead (1958) b) by Surange & Srivastava (1956) and c) in this Thesis.

Plumstead (1958)	Surange and Srivastava (1956)		Millions (this Thesis)
II. Hirsutum borne on :	Gangamopteris sp. B.	4	Group B.
Glossopteris indica *	Glossopteris taenioides	4	Glossopteris transvaalensis
&	Glossopteris taeniopteroides	4	
Glossopteris intermittens	Glossopteris intermittens	6	
I. Scutum borne on :			
Glossopteris damudica	Glossopteris damudica	6	
Glossopteris conspicua	Glossopteris conspicua	3	
Glossopteris decipiens	Glossopteris indica	3	
Glossopteris tortuosa			
Glossopteris brownii *			
III. Lanceolatus borne on:	Glossopteris brownii *	2	Group C.
Palaeovittaria kurzii *	Palaeovittaria kurzii *	6	
Glossopteris communis	Glossopteris communis	2	Glossopteris communis
Glossopteris retifera	Glossopteris formosa	2	Glossopteris cf. fibrosa
	Glossopteris stenoneura	2	Glossopteris sp.A
	Glossopteris divergens	2	Glossopteris sp.B
V. Cistella borne on :	Glossopteris retifera *	1	Group D.
Glossopteris stricta	Glossopteris arberi	1	Glossopteris africana
VI. Pluma borne on :	Glossopteris sahnii	1	Glossopteris jamottei
Glossopteris longicaulis	Glossopteris angustifolia	1	
	Gangamopteris indica	5	
	Gangamopteris buchani	5	
	Gangamopteris flexuosa	5	
	Gangamopteris sp.A.	5	
IV. Ottokaria borne on :			Group A.
Gangamopteris obovata	Gangamopteris obovata	4	Gangamopteris obovata
Gangamopteris turiadica			Gangamopteris ermaloensis
			Gangamopteris spp. A - D

(Note:- * denotes anomalus species, or more probably, different species which have been given the same specific name by different authors).

venation. Another source of error is the practice of using existing specific names for specimens with newly discovered cuticle structures, when the cuticle of the type specimen is not known. The present study has amply demonstrated that leaves with identical macroscopic features may have quite different cuticles.

It is, therefore, quite possible that a leaf with a fructification, described under a particular specific name by Plumstead, might, in fact, be quite unrelated to a leaf described under the same name by Srivastava. I feel that this might partly explain the lack of correlation between the systems proposed by Surange and Srivastava and by me on the one hand and by Plumstead on the other.

It is possible that too much importance has been attached to the diagnostic value of certain features of the cuticles. For example, the degree of sinuosity of the cell walls has been used as a "Key" character by many palaeobotanists. (Sahni, 1923; Srivastava, 1956; Pant, 1950), but it has been shown in living plants that this character is extremely variable, not only within the species, but on one plant, and is influenced by a number of environmental factors.

Watson (1942) shows that in Ivy leaves, the degree of waviness of the epidermal cell walls is affected directly by the rate of hardening of the cuticle, and that this is affected by the amount of illumination the leaf receives and by the humidity of the atmosphere. He shows that mature "Sun leaves" have relatively small cells with slightly sinuous walls, whereas the light and heavy shade leaves have larger cells with markedly sinuous walls. It was also demonstrated that young leaves

have very small straight-walled cells and that these grow and their walls become progressively more sinuous as the plant ages. The following interesting examples given by various authorities are quoted from Watson (1942).

Askenasy observed waviness in the epidermal cells of emergent leaves of Ranunculus aquatilis, but not in the submerged leaves.

Yapp, Moose and Rippel reported progressive degrease in waviness proceeding from the base of the plant to the tip. Numerous authors have confirmed the difference between sun and shade leaves.

Similarly, the presence or absence of stomata on one or both surfaces of the leaf is used as a "very important" diagnostic character; but this character is extremely variable within the species, as is shown by De Bary (1884). De Bary (Page 49) states that in species of Marsilea, Sagittaria, Polygonum, Callitriche, Myriophyllum, Nasturtium and Ranunculus, "where numerous stomata are found on surfaces developed in the air, corresponding surfaces developed under water have fewer stomata or none at all." In some species of Marsilea the stomata of the floating leaves are not depressed, whereas those of the aerial leaves are.

An interesting example of differences in the shape of the stomatal pits within species has been given by Larsen (1959) in his studies on diploid and tetraploid varieties of Cnobrychis Tommasinii and Cnobrychis Violaefolia. It is no doubt merely a coincidence that one of the forms described is very similar in shape to the stomatal pit of Glossopteris Africana, but it does serve as a warning that the reasons for differences

in cuticle structure are, as yet, imperfectly understood.

Some plants show gross differences in the shape of juvenile and mature forms of leaf. The well known case of Hedera helix will serve as one example, and Richards (1957) shows that many plants with leaves bearing long acuminate tips, known as drip tips, also have a mature leaf form with an obtuse or even indented tip. As species with drip tips are generally restricted to forests in hot moist regions, and also to the lower strata of such forests, Richards suggests that the success or failure of a leaf to develop a drip tip is controlled by temperature and humidity.

Undoubtedly fossil plants were subjected to similar variations in environmental conditions, and presumably they reacted to these differences in a way comparable to the reactions of present day plants.

It is, however, very difficult to take such variations into account in the examination of fossil plants. The only way to approach this is to examine a large number of specimens and to determine whether the character under investigation varies in a continuous or discontinuous manner. A continuous variation would suggest that the plants examined belonged to a single taxon, whereas discontinuous variation would suggest that more than one taxon was involved. This sort of analysis is particularly useful where differences between pre-supposed species or varieties are under investigation, and where more characters are very similar in the plants examined. A similar approach has been used by Townrow (1960) in his investigation of the Peltaspermaceae.

An example in this thesis where such an approach would have been

useful, if more specimens were available, is in the comparison between the specimen described as Glossopteris africana and Glossopteris arberi Srivastava (1956).

The shape of the cells and the form of the stomata are very similar in these two species, but the upper cuticle of Glossopteris arberi has more highly sinuous cells and the cells of the lower cuticle are papillate. The similarities suggest that the plants are closely related, and I feel that it is just possible that they come from different parts of the same plant, i.e. these differences might be variations between sun and shade leaves. As only a few specimens have been examined, it cannot be determined whether or not intermediate types exist, or if in fact these leaves are as closely related as suggested here. It is for this reason that the Ermelo specimens have been described under a different specific name.

In connection with this, I would like to refer back to the desirability of examining large numbers of specimens of a taxon. There is no justification for assuming that any single fossil is characteristic of a whole taxon, and indeed it is unlikely that this is so. In spite of this, many new specimens have been erected on inadequate knowledge of only one specimen. It would certainly be in the interests of scientific accuracy to limit the recognition of new species to those which are founded on the examination of an arbitrary minimum number of specimens. However, the advantages which would accrue from this procedure might well be outweighed by the difficulties which it introduces into questions of precedence of

nomenclature generally, and particularly in naming interesting but isolated specimens.

I fully realise that these criticisms apply to the present Thesis as well as to other published works.

SUMMARY TO PARTS I AND II

1) The distribution and Stratigraphy of Karroo deposits in Central and Southern Africa are briefly summarised.

2) The techniques used in the investigation are described.

3) The genera Gangamopteris McCoy and Glossopteris Brongniart are reviewed.

4) The macroscopic and cuticular structure of approximately fifty leaves, one stem and one seed-like body, which were preserved as compressions, were investigated. The macroscopic features only of a further four leaves and three seeds are described.

5) One new species, one existing species and four un-named species of Gangamopteris McCoy are described.

6) In the genus Glossopteris Brongniart, from the specimens yielding cuticles two new species and two existing species are described, a number of specimens are compared with an existing species, and a number of imperfectly known specimens are described but not assigned to a species. From the specimens without cuticles, one existing species is described, and some specimens are described but not placed in a species.

7) Some leaf fragments are placed in the genus Taeniopteris Brongniart, and some poorly preserved seeds are placed in the genus Samaropsis Goeppert.

8) A tentative correlation is suggested between the classification schemes for the Glossopteridsae proposed by Surange and Srivastava (1956), Plumstead (1956) and in the present Thesis.

APPENDIX

Fungal Spots.

Plate I B	Gangamopteris obovata
Plate II E, F	Gangamopteris ormeloensis
Plate III E, F	Glossopteris transvaalensis
Plate IV A, B	Glossopteris transvaalensis
Plate VI c, Text fig. 39	Glossopteris cf. fibrosa Pant

External Features.

Several leaves of different species of Gangamopteris and Glossopteris bear one or more raised marks on their adaxial surface. These are generally circular or ovoid in outline, with a diameter of approximately 1 - 2 mm, or irregularly elongated along the lateral veins of the leaf, and up to 5 mm. long. The structures have a markedly raised rim and are quite clearly an integral part of the coaly matrix of the fossil. It was quite impossible to remove them from the surface of the fossil, without removing the whole of the cuticular remains. In specimen H.18, Plate III F and Plate IV A + B, most of the bodies are arranged irregularly in bands more or less parallel to the mid-rib. In the other specimens, the marks are not so numerous, and their arrangement is random.

Microscopic examination.

Repeated attempts were made to determine the nature of these bodies by removing the coaly matrix from the rock and macerating it, as

previously described. In all but two cases, the cuticle from these regions dissolved or broke up into very fine fragments, although successful preparations were easily obtained from other parts of the leaf. This in itself suggests some change in leaf structure or cuticle at these points. In the remaining two preparations, the cuticle was very thin and fragile, but showed a few circular or ovoid patches about 150μ in diameter. One of these ovoid structures was associated with very thin-walled, branched tubes, 2μ - 5μ in diameter, (Text fig.39), which are probably fungal hyphae. On close examination, this ovoid structure appears to be an integral part of the epidermis. It seems likely that this structure is caused by a pathological reaction by the leaf to a fungal infection. Although the pieces of cuticle prepared are not large enough to show this, it is probable that the raised rim of the whole fungal spot is composed of many such warty regions, and that it also marks the region where the epidermis of the leaf has been ruptured by the hyphae. This type of host reaction is shown by many recent plants when infected by any one of a large variety of parasitic fungi.

Bunbury (1861), Feistmantel (1881), Arber (1905) and Sen (1955 a,b) have all described leaves of Gondwana plants bearing structures of the same size, shape and arrangement as those described above. They were regarded as form sori or Glossopteris fructifications by all these authors. Even a preliminary examination of the Ermelo material suggested strongly that the marks were due to attacks by fungi, rather than the presence of Glossopteris fruiting bodies. Garrett (1956) has suggested that the

pattern of sites of primary infection by epiphyllous fungi might be controlled by the distribution of spores by rain flowing along "run-off" channels. This hypothesis would certainly explain the peculiar mixture of randomness and regularity which is characteristic of the arrangement of these structures.

The suggestion that they are caused by fungi is greatly supported by the demonstration of their association with what are thought to be fine branched hyphae.

Potonié (1893), who also referred to Zeiller's illustrations (1892), suggested that this sort of mark was caused by an epiphyllous ascomycete. Seward (1898) agreed that they were probably fungal in nature, but criticised their assignment to the Ascomycetales on the grounds of insufficient evidence.

Plumstead (1958 a,b; 1962) working on Glossopteris from the Transvaal and from Antarctica, also described similar structures as fungal spots, but owing to the poor state of preservation of the material, was unable to support this by a microscopic examination of the cuticles of these leaves.

In view of the general irregularity in size, shape and distribution of the bodies described by the authors listed above, and by me, and of the fact that these bodies differ greatly in form from all the known fructifications of Glossopteris, Gangamopteris and Palaeovittaria, described by Plumstead (1952-62), Hamshaw Thomas (1950), Lacey (1959-61) and Higby (1960), it is extremely unlikely that they are Glossopteridean reproductive structures. It is highly probable that they are all, in fact, caused by a fungal infection. It is, of course, impossible to assign these fungi to any particular class.

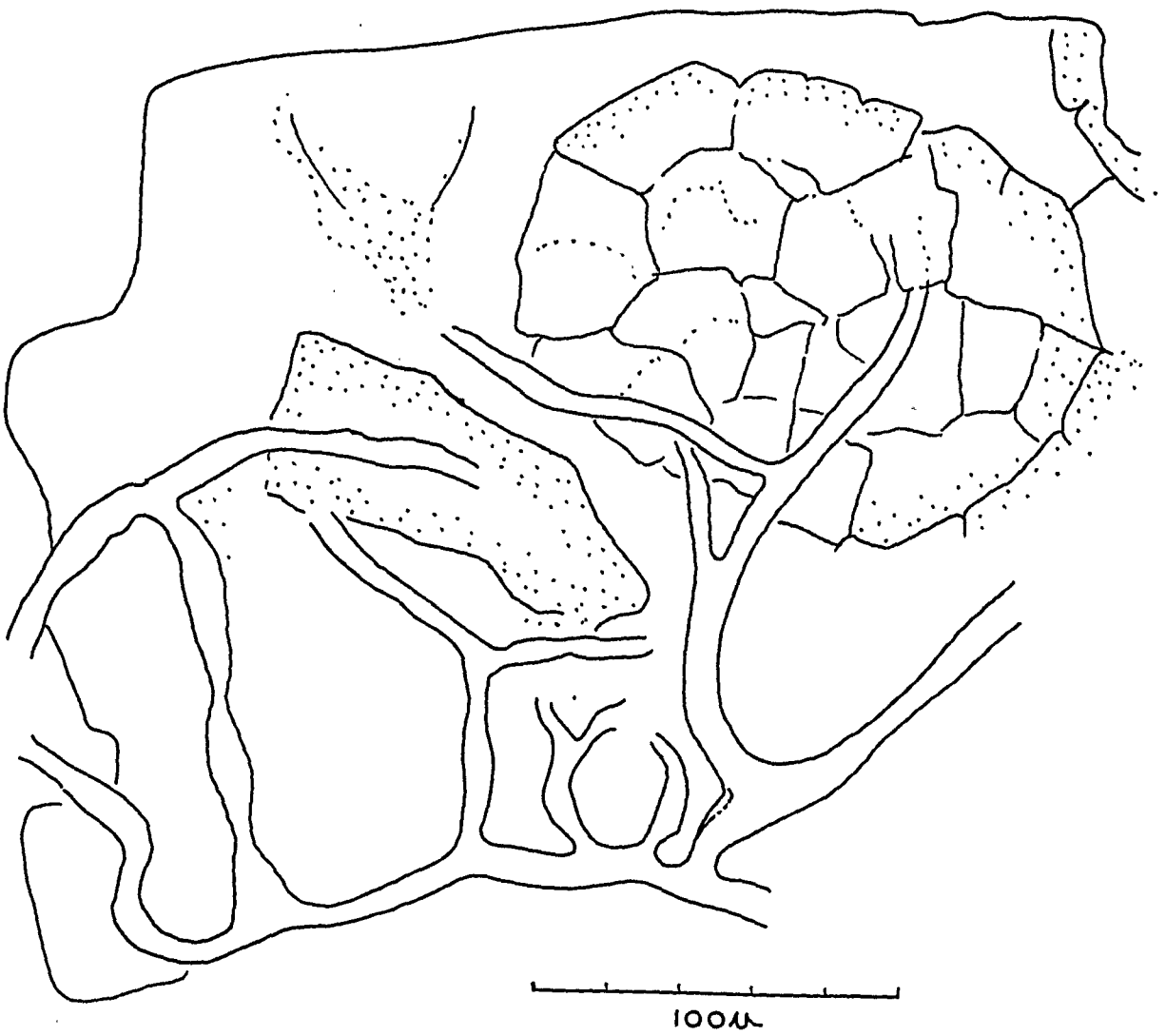


Figure 39. Diagram to show presumed fungal hyphae and cellular disorganisation from cuticle of specimen H. 18. (Glossopteris transvaalensis sp.nov.)

EXPLANATION of the PLATES

Plate I.

Fig. A. Gangamopteris obovata (Carr.) White.
Specimen H.10 (X 1.)

B. Gangamopteris obovata
Specimen H.17. (X2.)

C. Gangamopteris sp.A
Specimen H. 9 (X 1.)

D. Gangamopteris sp. B
Specimen H. 7d (X 2.)

Plate II.

Fig. A. Gangamopteris ermeloensis sp. nov.
Specimen H.14 (X 1.)

B. Gangamopteris ermeloensis sp. nov. (X 2.)

C. Gangamopteris sp. C. Specimen H. 2a. (X 1)

D. Gangamopteris sp. C. Specimen H. 2a. (X 2.)

E. Gangamopteris ermeloensis sp. nov. Specimen H. 7a (X 1.)

F. Gangamopteris ermeloensis sp. nov. Specimen H. 7a (X 2.)

Plate III.

Fig. A. Seed-like body (indet.) Specimen H.15 (X 2.)

B. Counter-part of Fig. A (X.2.)

C. Glossopteris transvaalensis sp. nov. Specimen H.19 (X 1.)

D. Glossopteris transvaalensis sp. nov. Specimen H.19 (X 2.)

E. Glossopteris transvaalensis sp.nov. Specimen H.3b (X 2.)

F. Glossopteris transvaalensis sp. nov. Specimen H.18 (X 1.)

Plate IV.

Fig. A. Glossopteris transvaalensis sp. nov. Specimen H.18 (X 2.)

B. Glossopteris transvaalensis sp.nov. Specimen H.18 (X.3)

C. Glossopteris transvaalensis sp. nov. Specimen H.11c (X 1.)

D. Glossopteris transvaalensis sp. nov. Specimen H.11c (X 2.)

E. Glossopteris transvaalensis sp. nov. Specimen H. 15 (X 1.)

F. Glossopteris africana sp. nov. Specimen H.6a (X ½.)

G. Glossopteris africana sp. nov. Specimen H.6a. (X 2.)

Plate V.

Fig. A. Glossopteris africana sp. nov. Detail of venation near mid-rib. Specimen H.6a (X 10.)

B. Glossopteris africana sp. nov. Specimen H.8a (X 1.)

C. Glossopteris africana sp. nov. Specimen H.8a (X 3.)

D. Indeterminable Branch. Specimen H.5. (X 1.)

Plate VI.

Fig. A. Glossopteris cf. fibrosa Pant. Specimen H.4. (X 1.) G. jamottei a t b

B. Glossopteris cf. fibrosa Pant. Specimen H.4. (X 2.)

C. Glossopteris cf. fibrosa Pant. Specimen H.16a (X 2.)

D. Glossopteris cf. fibrosa Pant. Specimen H.16a. (X 2.)

Plate VII.

Fig. A. Glossopteris cf. fibrosa Pant (Specimen H.11a.)

B. Glossopteris sp.A Specimen H.13 g (X2.)

C. Glossopteris sp.B Specimen I.1. (X 1.)

D. Glossopteris sp.B Detail of veins (X 10)

Plate VII

Fig. E. Gangamopteris sp.D Specimen H.7e. (X 1.)

F. Gangamopteris sp.D Specimen H.7e. (X 3.)

PLATE XIII

Fig. A. Gangamopteris sp.A. Upper cuticle from mid-rib region (X 150.)

B. Upper cuticle from the lamina, note stomate (X 150.)

C. Lower cuticle from the lamina, with stomates. (X 150)

D. Lower cuticle from the lamina, with stomates. (X 150.)

Plate IX.

Fig. A. Gangamopteris sp.A. Upper cuticle, Stomate. (X 650.)

B. Lower cuticle, stomate. (X 650)

C. Gangamopteris sp.B. Stomate from upper cuticle (X 650.)

D. Lower cuticle with stomates (X 150.)

Plate X.

Fig. A. Gangamopteris sp.B. Upper cuticle with stomates (X 150.)

B. Gangamopteris ormeloensis sp. nov. Lower cuticle, cells over median vein (X 150.)

C. Lower cuticle with stomates. (X 150.)

D. Upper cuticle, mesh and vein areas. (X 150.)

Plate XI

Fig. A. Gangamopteris ormeloensis sp.nov. Stomate from upper cuticle. Specimen H.14 (X 650.)

B. Stomate from lower cuticle. Specimen H. 14 (X 650.)

C. Stomate with 5 subsidiary cells. From the lower cuticle. Specimen H.7a. (X 650.)

Plate XI

Fig. D. Stomate with seven subsidiary cells, also from the lower cuticle. Specimen H.7a. (X 650.)

Plate XII

Fig. A. Gangamopteris ermeloensis sp.nov. Upper cuticle from middle region of leaf, showing stomates between the veins. (X 150.)

B. Lower cuticle from the same region, with stomates (X 150.)

C. Upper cuticle from the lamina, with stomates between the veins. (X 150.)

D. Upper cuticle from the outer edge of the lamina. (X 150.)

E. Gangamopteris sp.C. Lower cuticle with stomates (X 150.)

Plate XIII

Fig. A. Gangamopteris sp.C. Stomate from the lower cuticle (X 650.)

B. Stomate from the upper cuticle. (X 650.)

C. Lower cuticle with stomates (X 150.)

D. Upper cuticle with stomates, note papillate cells. (X 150.)

Plate XIV

Fig. A. Seed-like body (indet.). Cuticle fragments. (X 150.)

B. Seed-like body (indet.) Cuticle fragments. (X 150).

C. Seed-like body (indet.) Cuticle fragment (X 650.)

D. Glossopteris transvaalensis sp.nov. Stomate from the lower cuticle. (X 650.)

Plate XV.

Fig. A. Glossopteris transvaalensis sp.nov. Specimen H.18. Upper cuticle. (X 150.)

B. Glossopteris transvaalensis sp.nov. Specimen H.1. Lower cuticle, showing well marked vein cells. (X 150.)

Plate XV.

Fig. C. Glossopteris transvaalensis sp.nov. Upper cuticle. Note very thick cell walls and irregular papilla-like markings. Specimen H. 13f (X 150.)

D. Glossopteris transvaalensis sp.nov. Lower cuticle showing veins and mesh with stomates. Specimen H.11c (X 150.)

Plate XVI

Fig. A. Glossopteris transvaalensis sp.nov. Specimen H.13f. Lower cuticle showing veins and mesh areas. (X 150.).

B. Stomates and papillate cells, lower cuticle near edge of leaf of specimen H.11c. (X 650.)

C. Upper cuticle from specimen H.13f showing the great thickness of the cell walls and papilla-like markings. (X 650.)

D. Lower cuticle from the same specimen, showing stomate with papillate subsidiary cells. (X 650.)

Plate XVII

Fig. A. Glossopteris transvaalensis sp. nov. Stomates from lower cuticle of Specimen H.11c. (X 650.)

B. Glossopteris africana.sp.nov. Lower cuticle, showing sinuous cell walls and stomates in mesh region. Vein cells can be seen on extreme right. Specimen H.6a. (X 150.)

C. Stomate from lower cuticle of Specimen H.6a. (X 650.)

D. Stomate from lower cuticle of Specimen H.6a. (X 650.)

Plate XVIII.

Fig.A. Glossopteris africana sp.nov. Upper cuticle from Specimen H.8a. Note sinuous cell walls (X 150.)

B. Lower cuticle from the same specimen, showing stomates and sinuous cell walls. (X.150.)

C. Stomate from lower cuticle. (X 650.)

D. Indeterminable stem. Peridern, consisting of three or four layers of cells. (X 150.)

Plate XIX.

Fig. A. Glossopteris cf. fibrosa Pant. Upper cuticle from lamina of specimen H.16b. (X 150.)

B. Lower cuticle from the same preparation, showing stomates in the mesh region. (X 150.)

C. Upper cuticle of specimen H.11a., from a part of the mid-rib possessing "lumps". (X 150).

D. Lower cuticle from the same preparation. (X 150.)

Plate XX.

Fig. A. Glossopteris cf. fibrosa Pant. Stomate from lower cuticle of specimen H.4 (X 650.)

B. Stomate from lower cuticle of specimen H.16b., in a much better state of preservation than that shown in fig. A. (cf. Text fig.31.) (X 650.)

C. Glossopteris cf. fibrosa Pant. Lower cuticle of Specimen H.11a., from a region of the mid-rib where no lumps were present. The cells are long and have parallel side walls. (X 150.)

D. Mesh region from lamina of H.11a, showing numerous poorly preserved stomates. (X 150)

E. Upper cuticle from the edge of the same leaf. (X 150.)

Plate XXI

Fig. A. Glossopteris sp.A. Upper cuticle of specimen H.13g., showing "striae". (X 650.)

B. Stomate from lower cuticle of the same leaf. (X 650.)

C. Upper cuticle (X 150.)

D. Lower cuticle with stomates. (X 150.)

E. Upper cuticle (X 150.)

Plate XXII

Fig. A. Glossopteris Jamottei Hpeg and Rosa. Stomata from lower cuticle of specimen H.13a. (X.650.)

B. Stomata from lower cuticle of specimen H.13a. (X 650.)

C. Stomata from upper cuticle of specimen H.13b. (X 650.)

D. Lower cuticle of specimen H.13a. (X 150.)

Plate XXIII

Fig. A. Glossopteris Jamottei. Hpeg and Rosa. Upper cuticle of H.13b., showing single stomata. (X 150).

B. Cuticle from mid-rib of H.11b., showing some sinuously walled cells in the lamina near the mid-rib. (X 150.)

C. Lower cuticle from specimen H.13a, showing stomatas (X 150.)

D. Gangamopteris sp.D. Cuticle (X 150)

E. Gangamopteris sp.D. Cuticle (X 150.)

Plate XXIV.

Fig. A. Glossopteris sp.B. Upper cuticle with stomatas and papillate cells. (X 150.)

B. Upper cuticle showing clear vein and mesh areas (X 50.)

C. Stomata from upper cuticle. Note overhanging papillae of subsidiary cells, protecting the stomatal pit. (X 650).

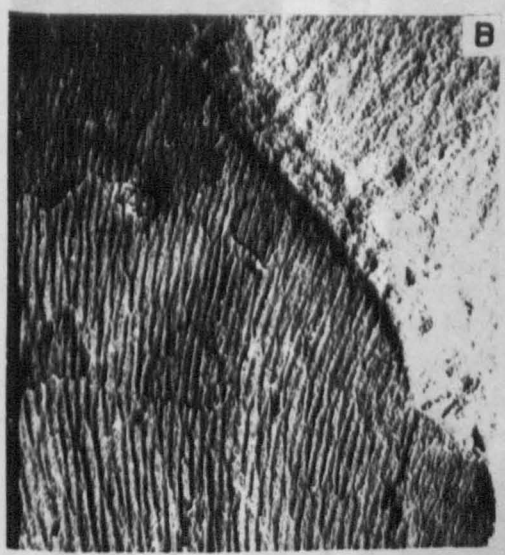
D. Gangamopteris sp.D Cuticle. (X 150.)

E. Indeterminable axis. Showing impression of horizontal scars in underlying shale. (X 1½.)

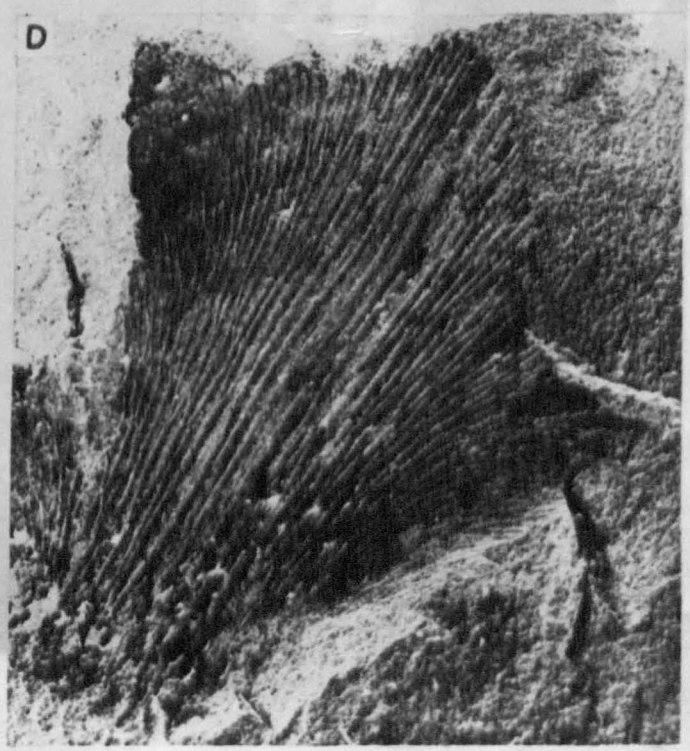
PLATE I

G. obovata
H 10 ×1

Gang.
sp. A
H9
×1

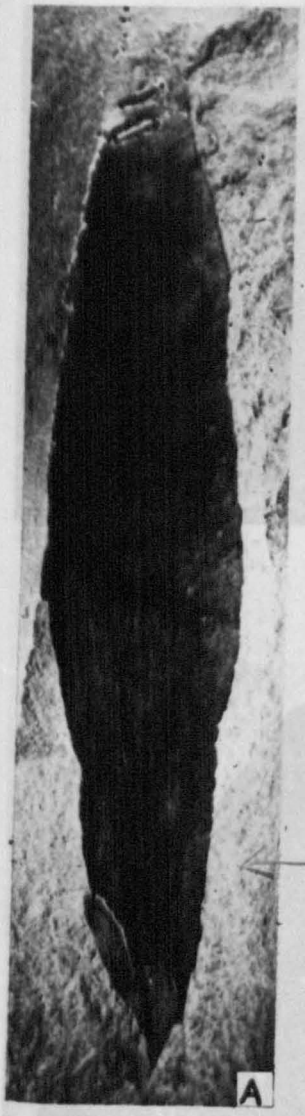


G. obovata
H 17 ×2



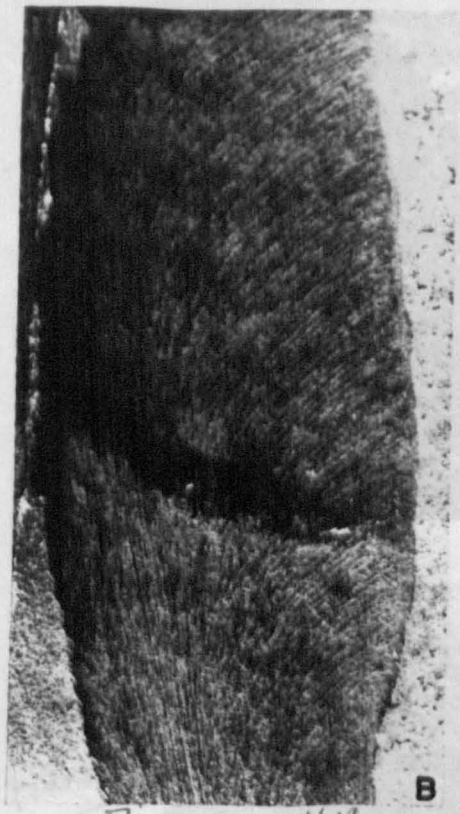
Gang sp. B. H7d ×2.

PLATE II



A

H14 ×1



B

H4 ×2

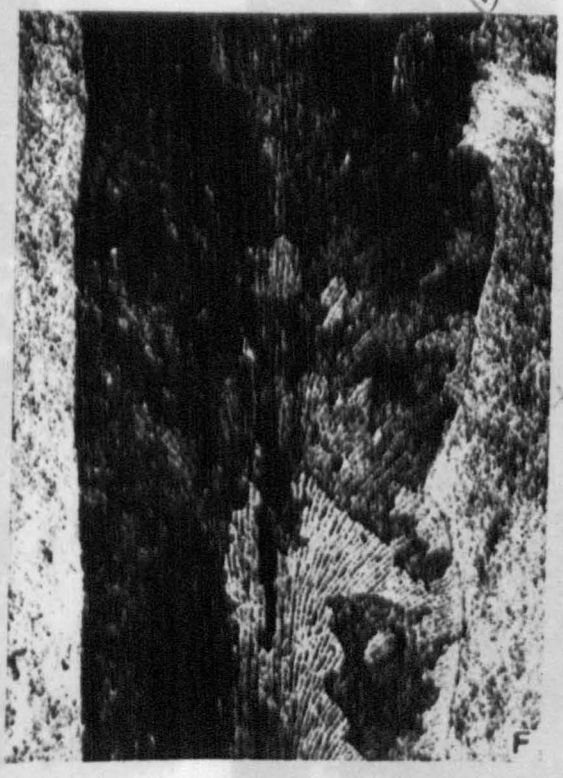
Gang. ermeloensis

×1

E

H 7a

×2.



F

C

H2a ×2.1

Gr. sp. C

D

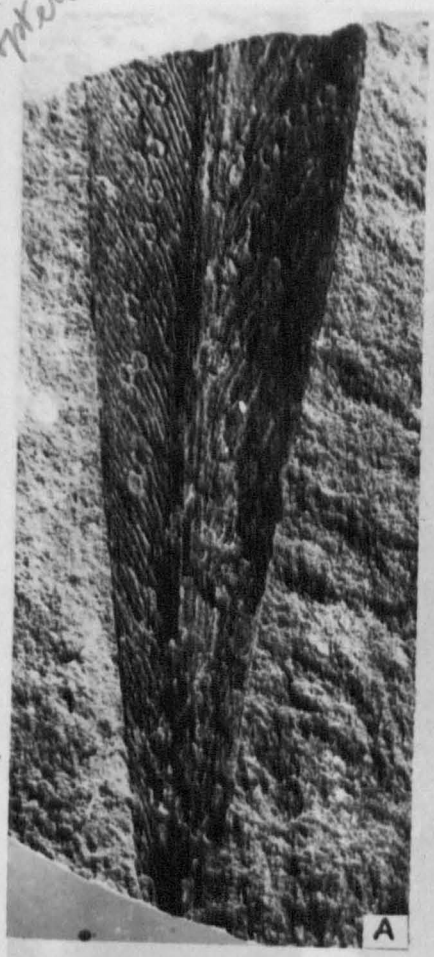
×2 H2a

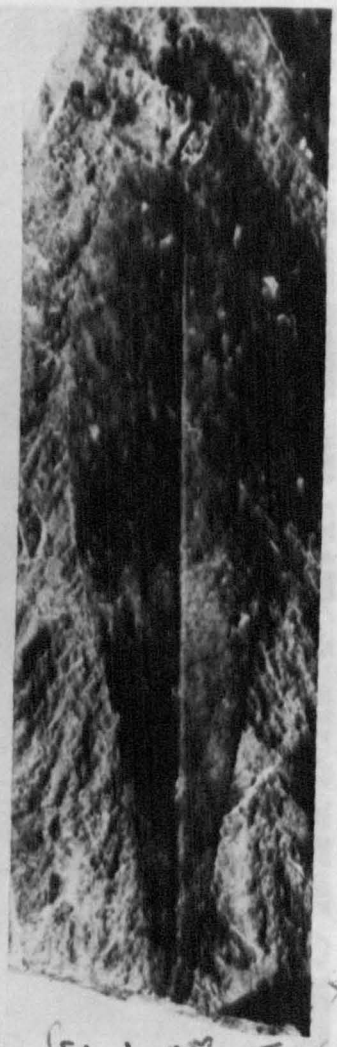
Gr. sp. C

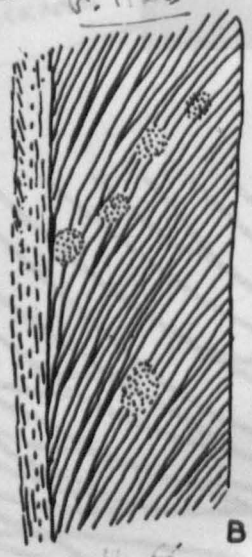
PLATE III


A
B
C
D
E
F
Scar-like body H15 ×2
all transvalen
H18 ×1
H19 ×1
×2 H19
cf. angustifolia var taeniopteroides
H3b ×2

PLATE IV







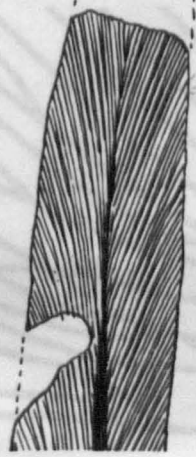
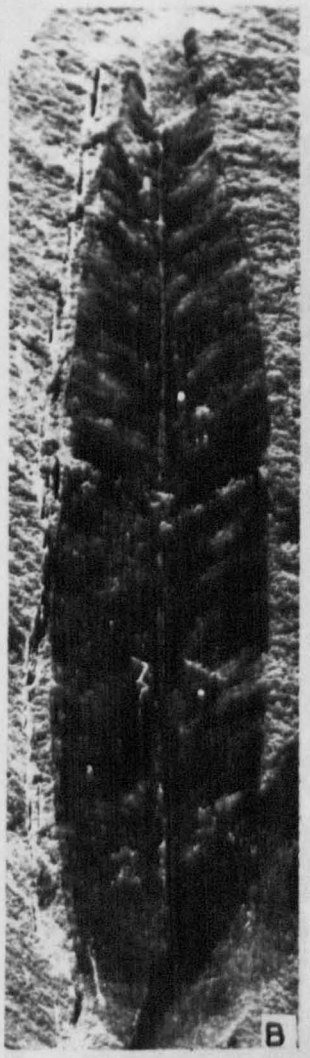
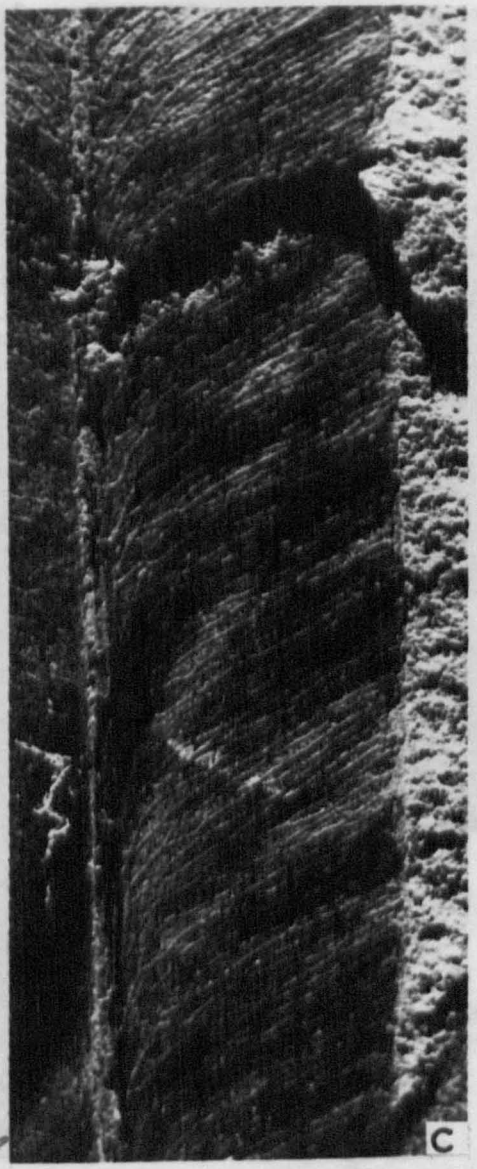


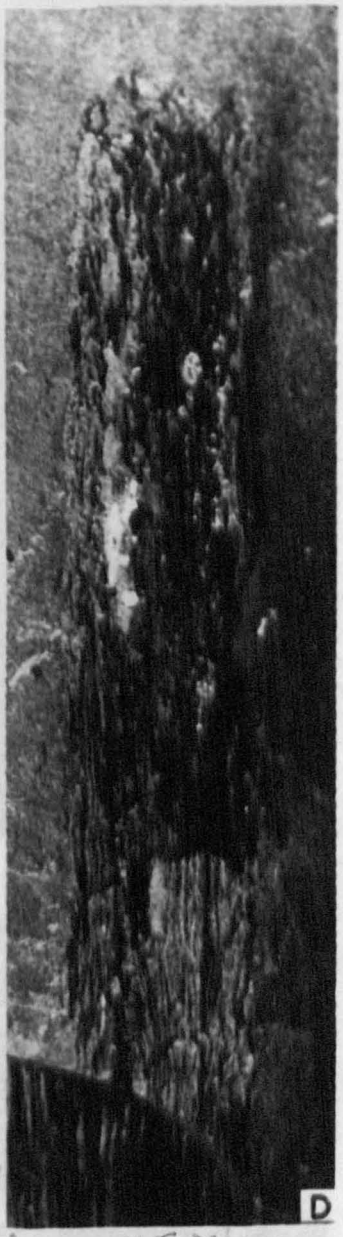
PLATE V



H 8a × 1
G. africanum



H 8a × 3



Branch H 5 × 1

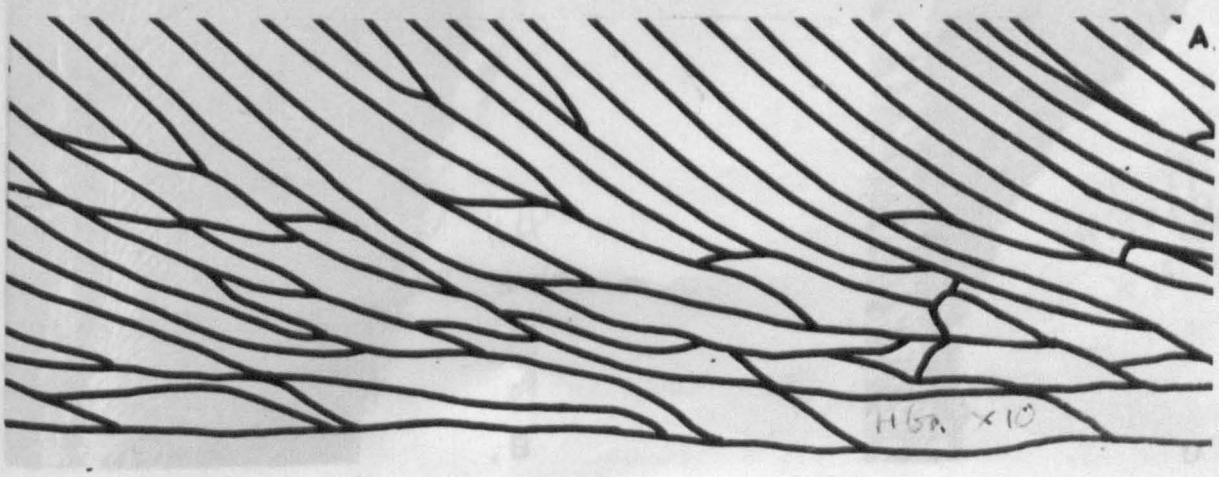
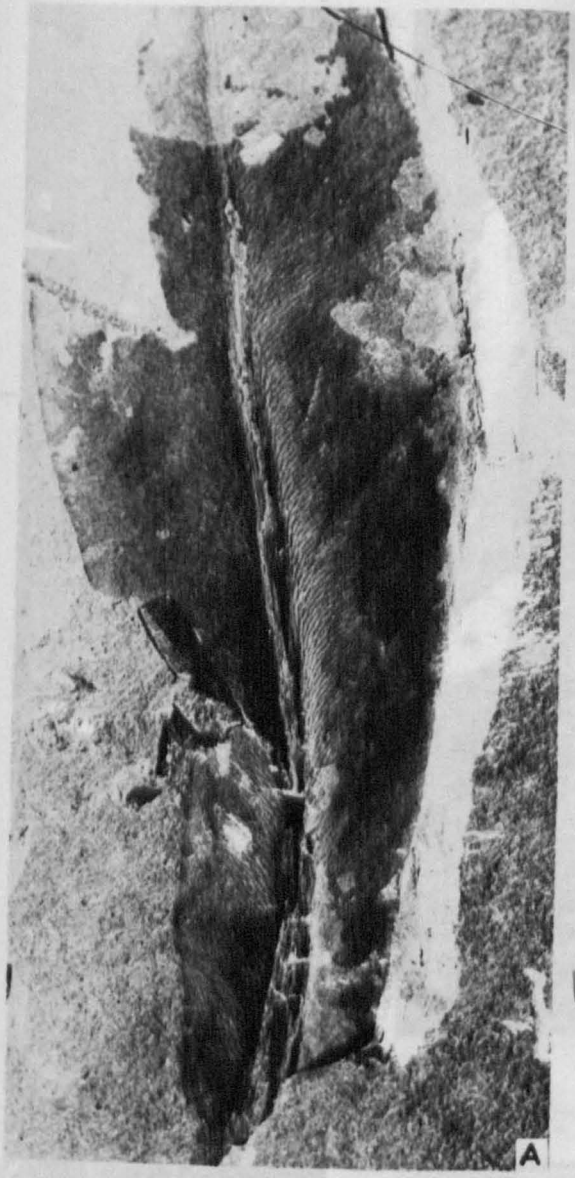
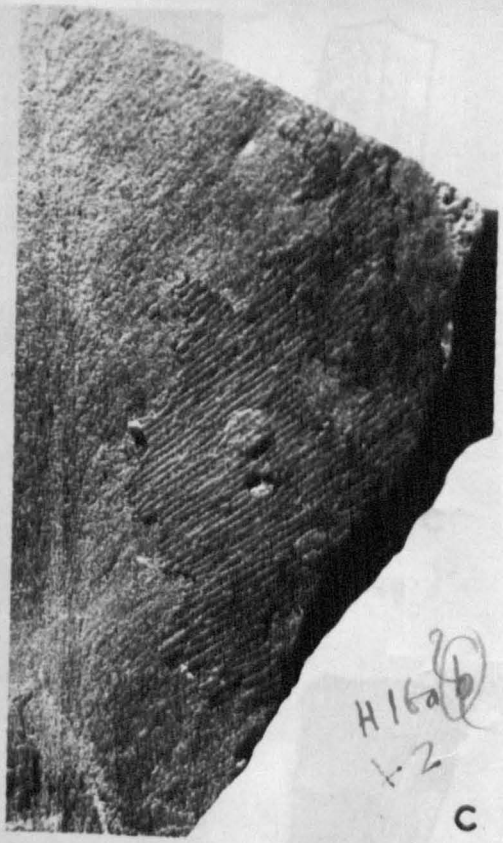


PLATE VI



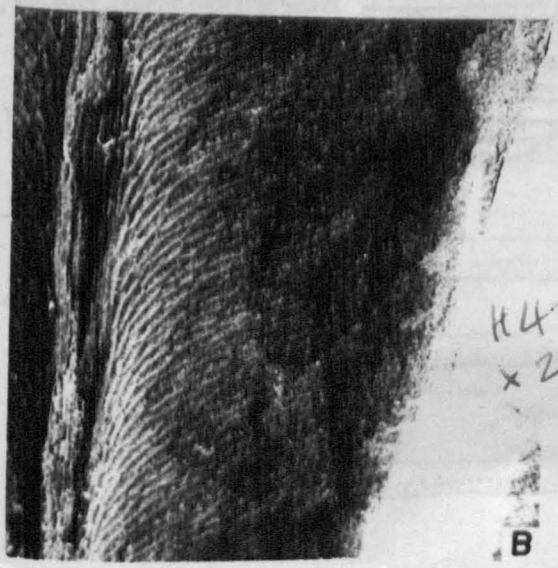
A

H4
×1
g. d. fibrosa
Post



H16a (b)
×2

C



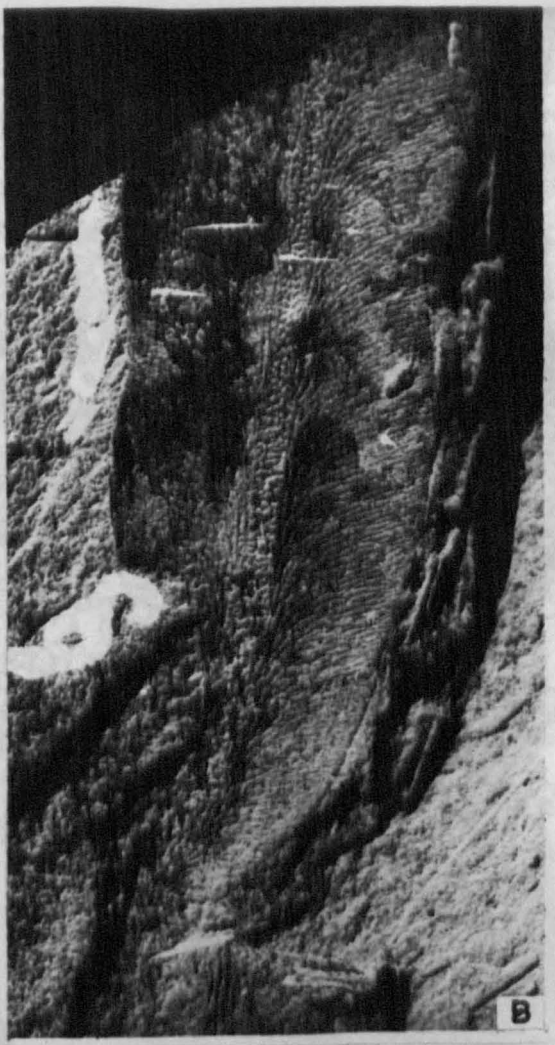
H4
×2

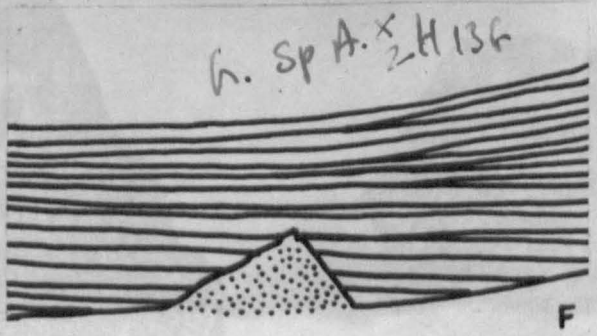
B

H16a (b)
×2

D

PLATE VII





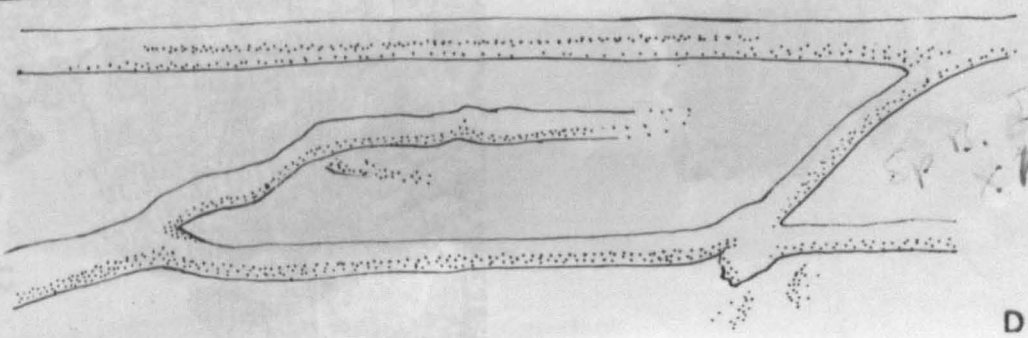
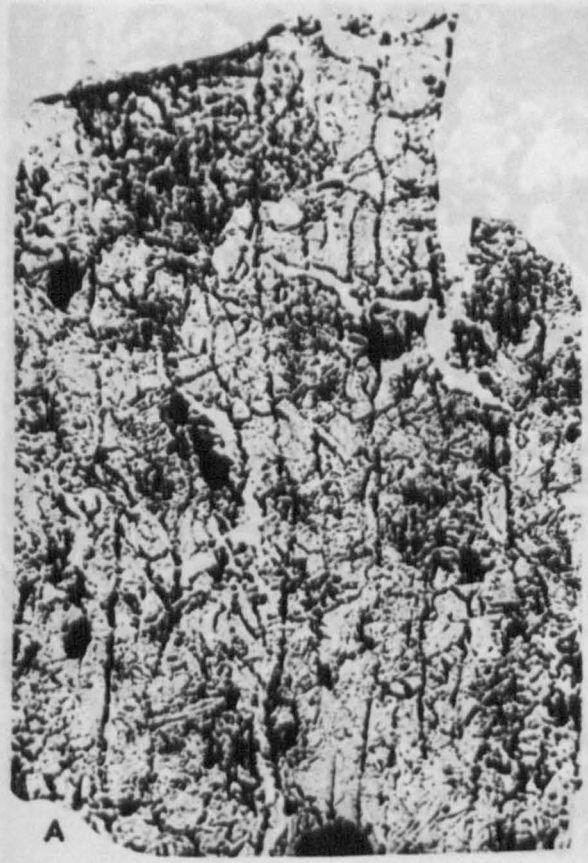


PLATE VIII

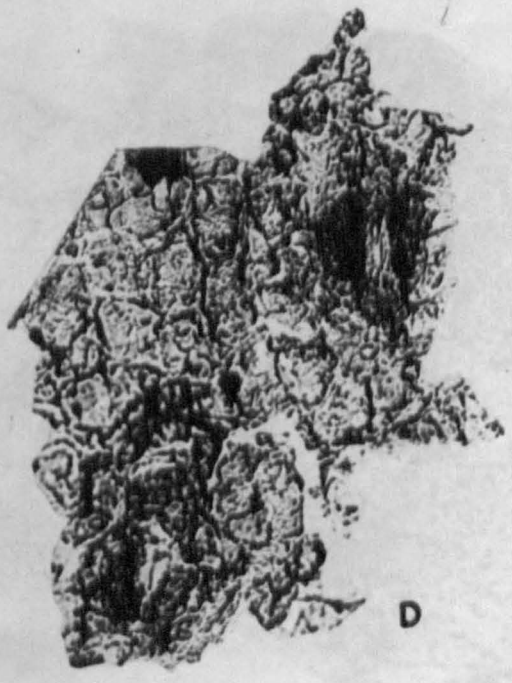


A

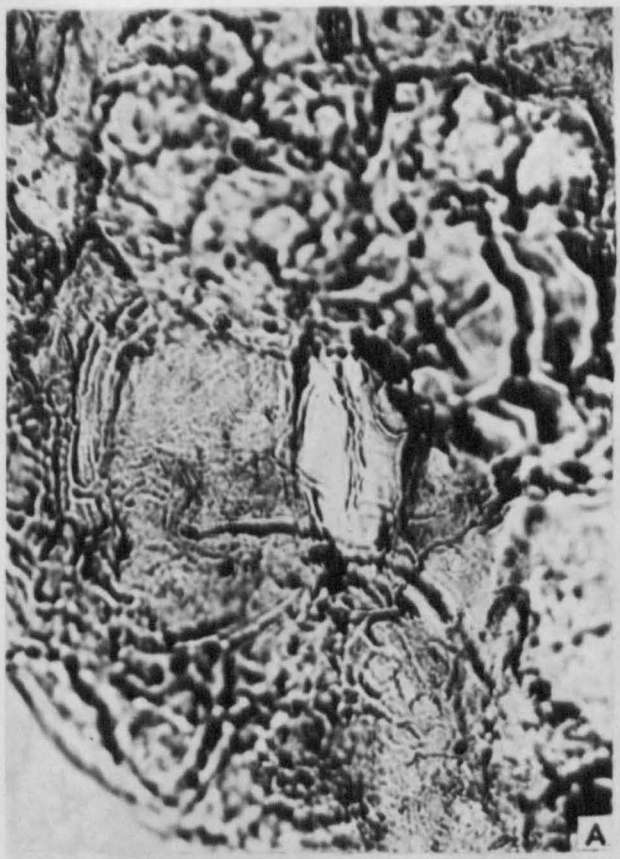
B

All Gang. sp. A

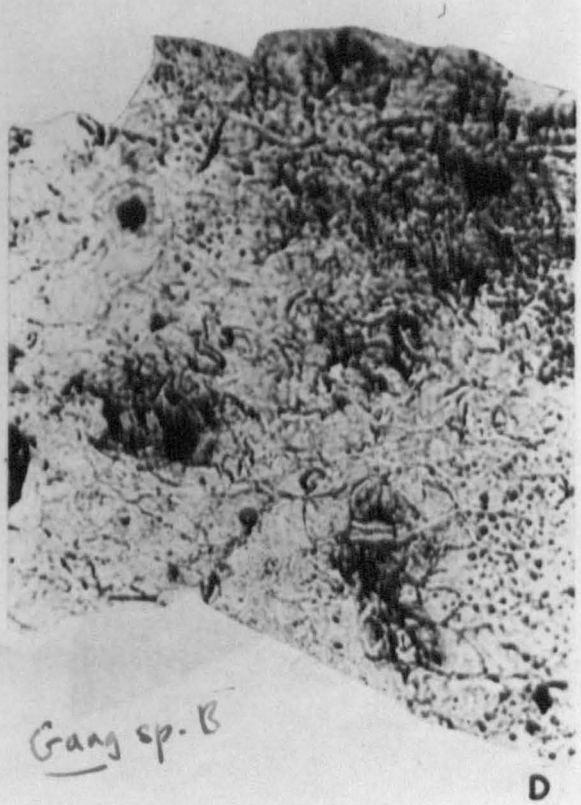
C



D

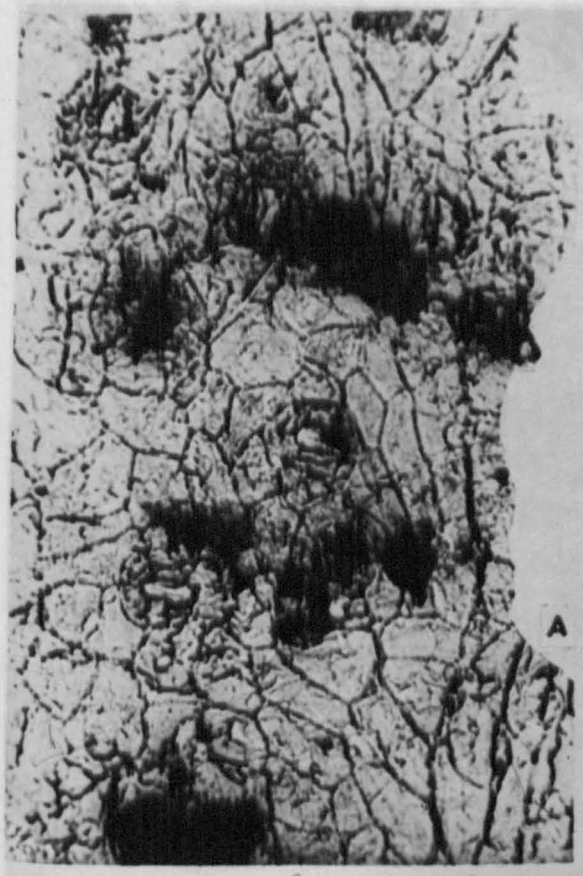


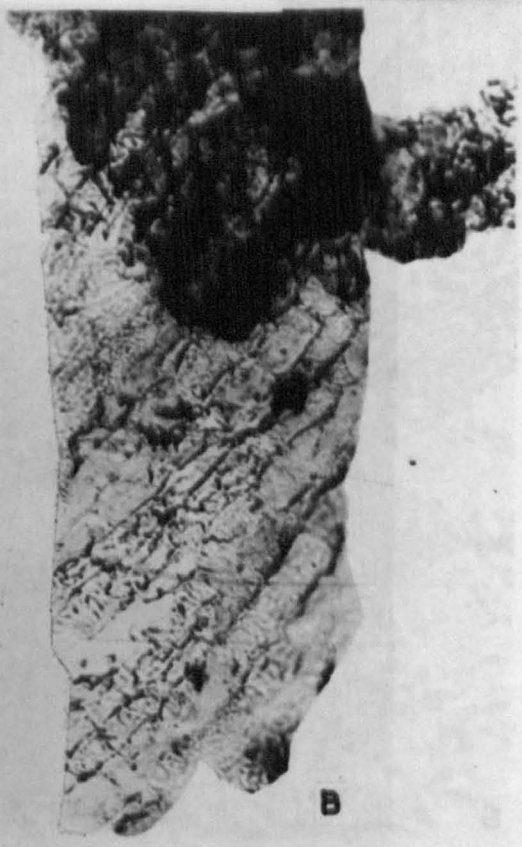
Gang. sp. A.



Gang sp. B

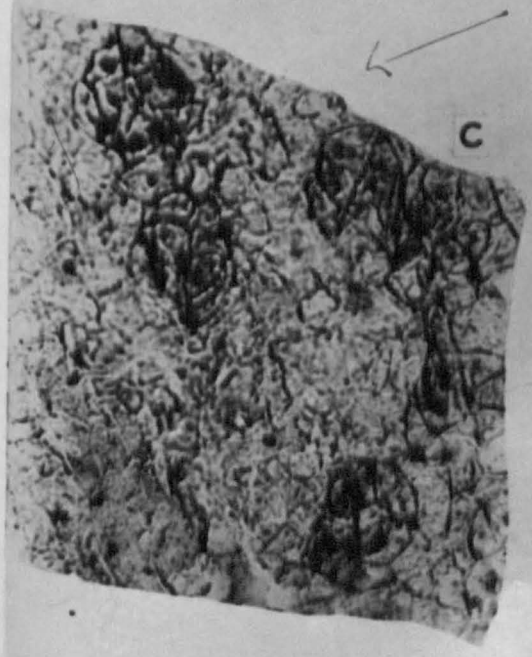
PLATE X





Gang. sp. B

Gang. ermeloensis



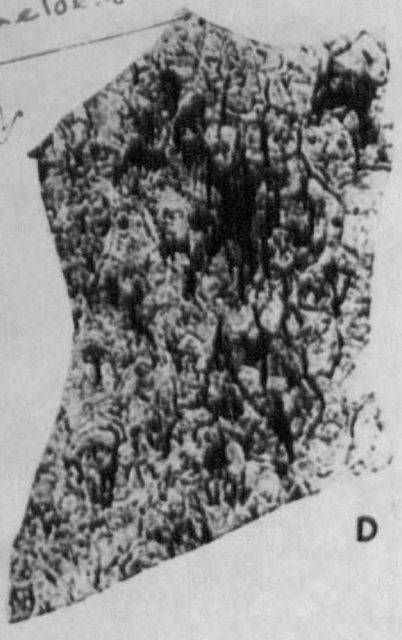
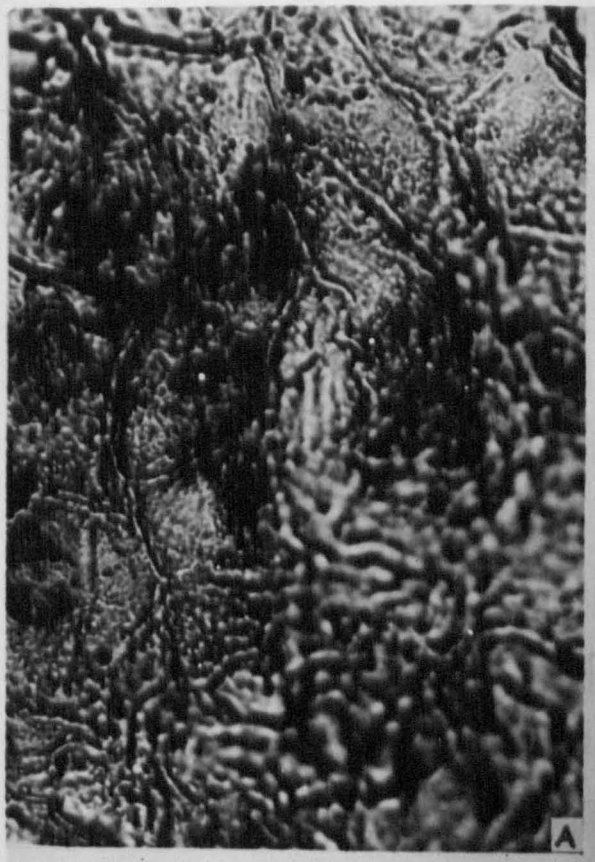
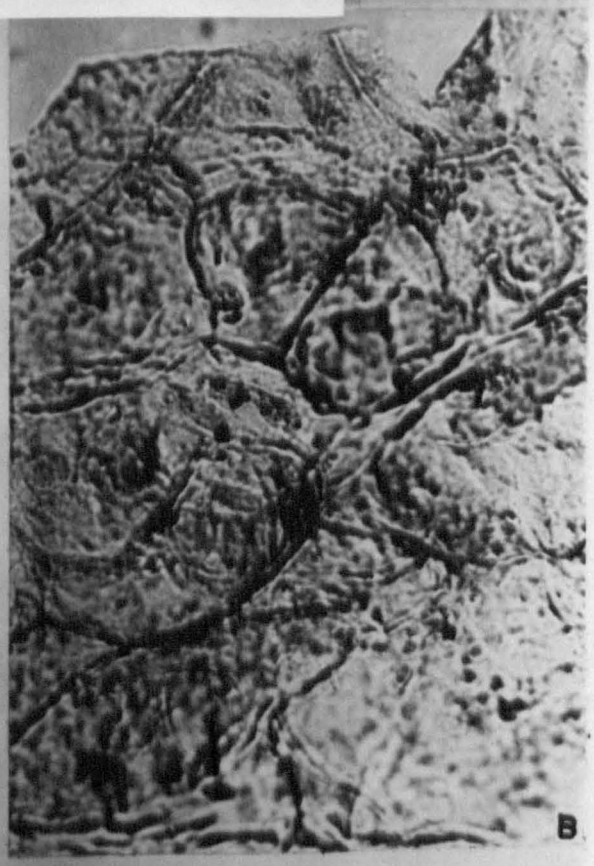


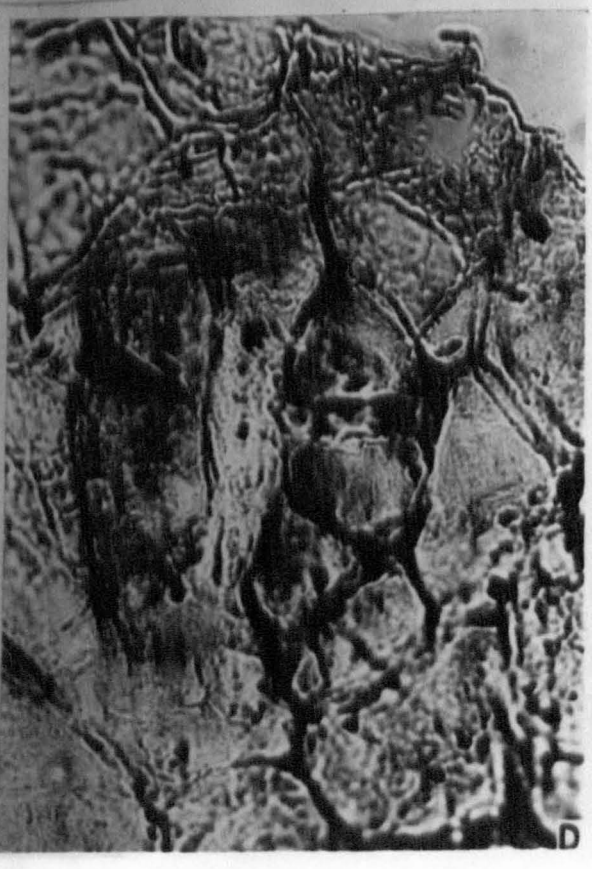
PLATE XI


A


B

All Gang- ermeloeasis


C


D

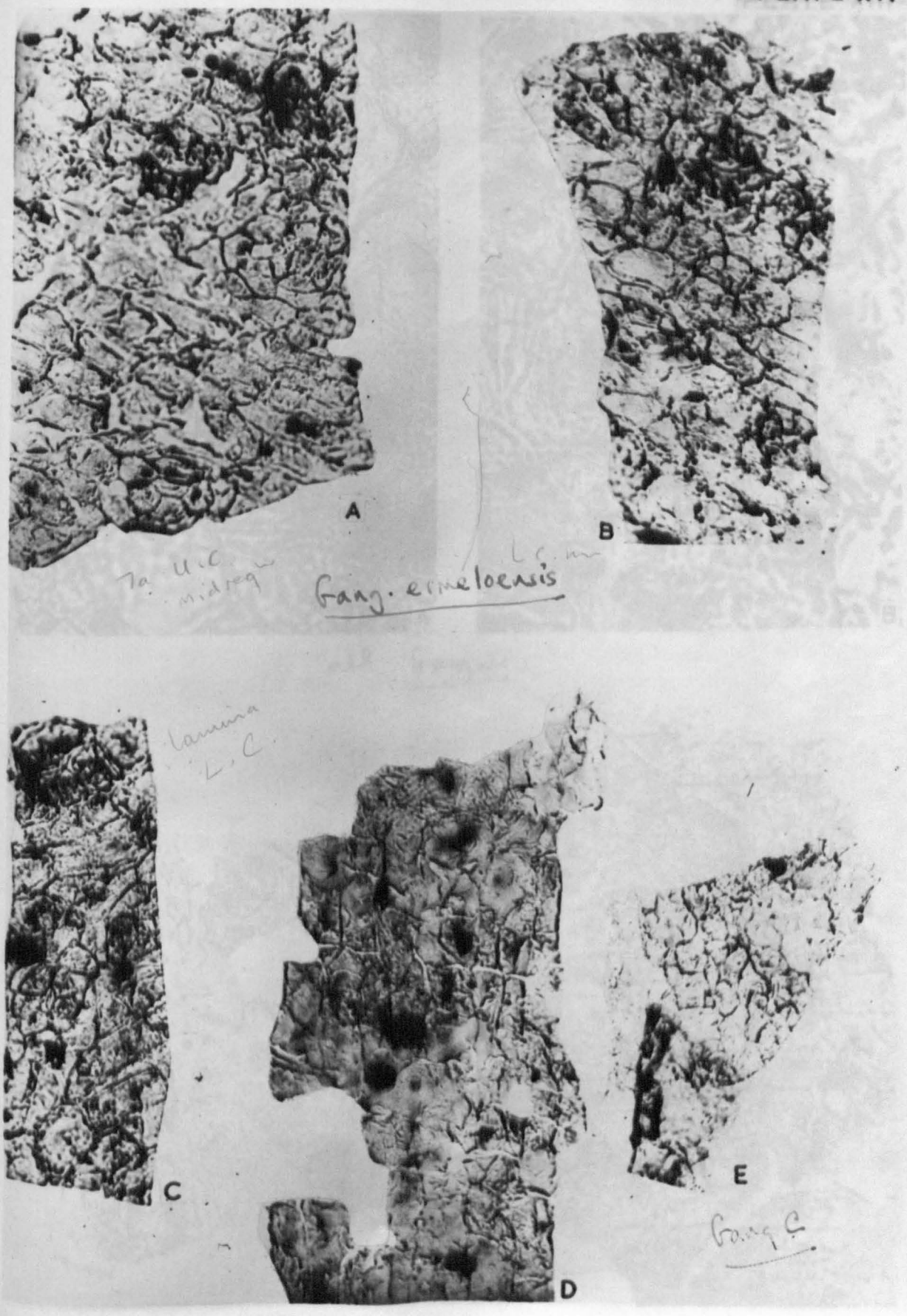
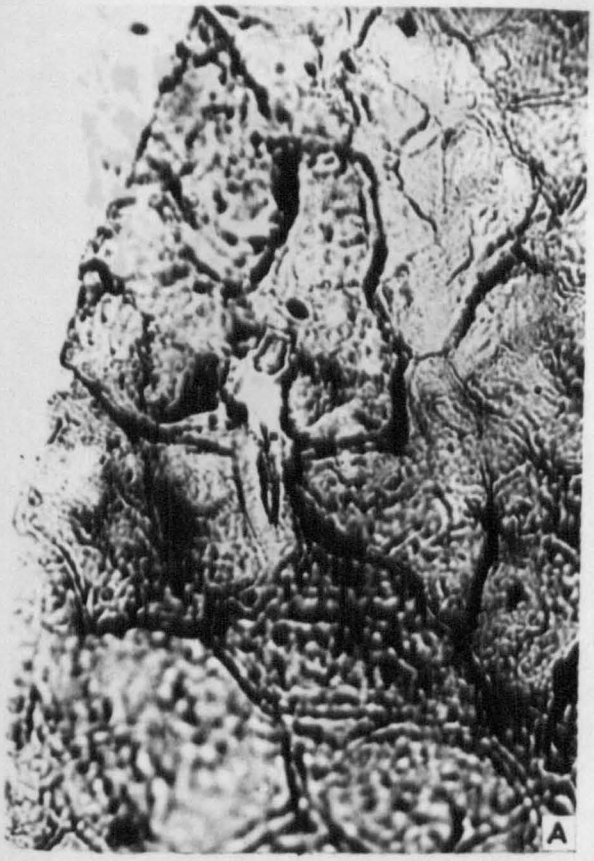
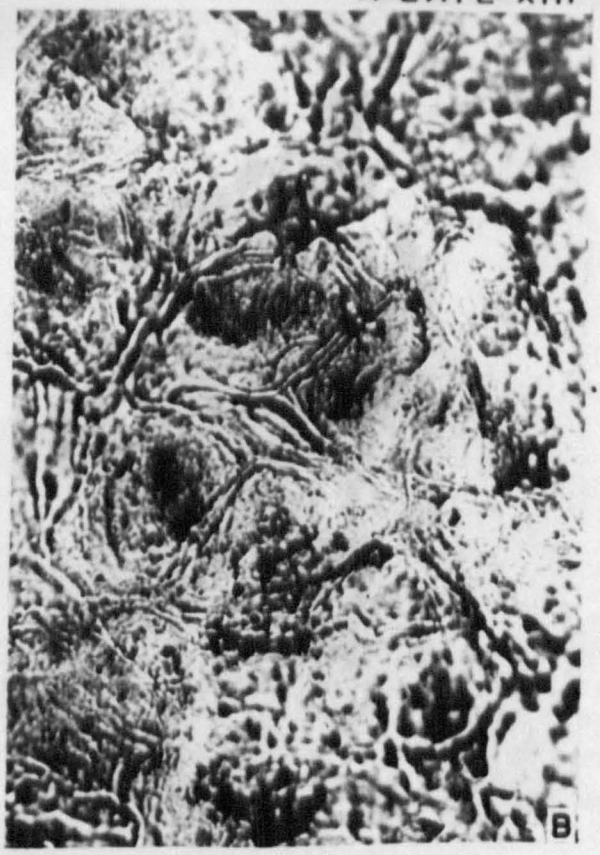

A
B
C
D
E

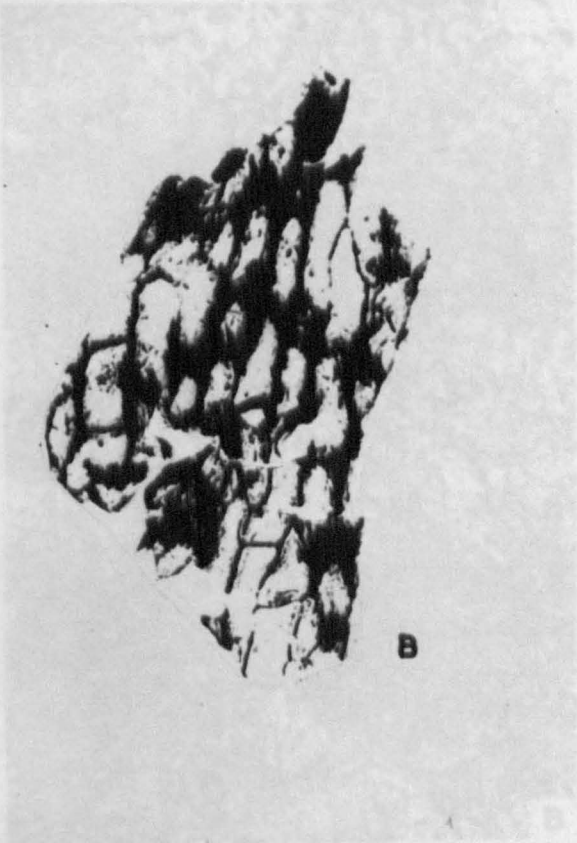
PLATE XIII

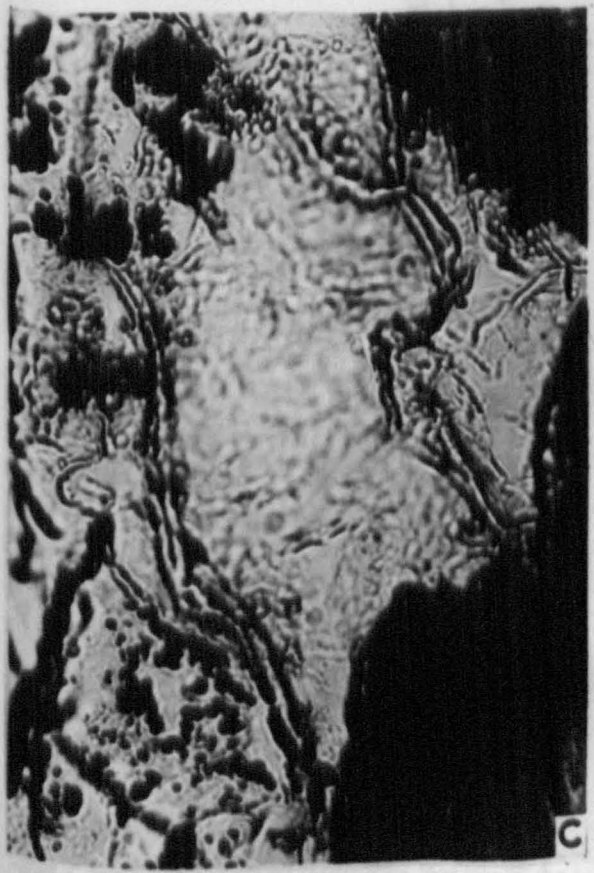




all Gang. C


A


B


C

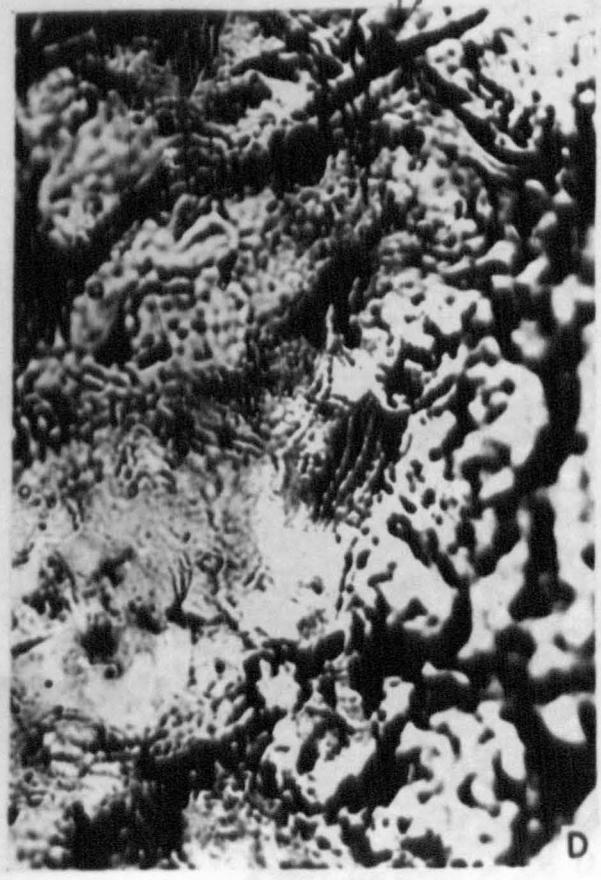
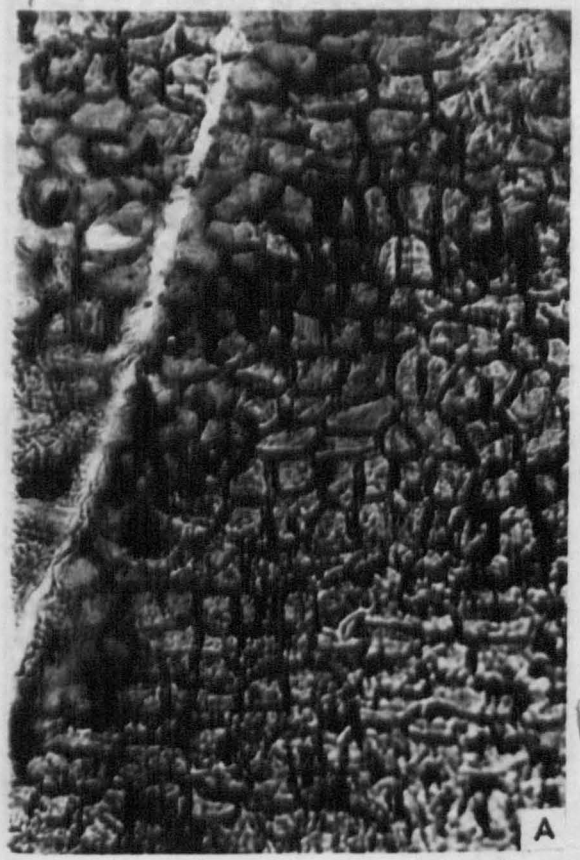
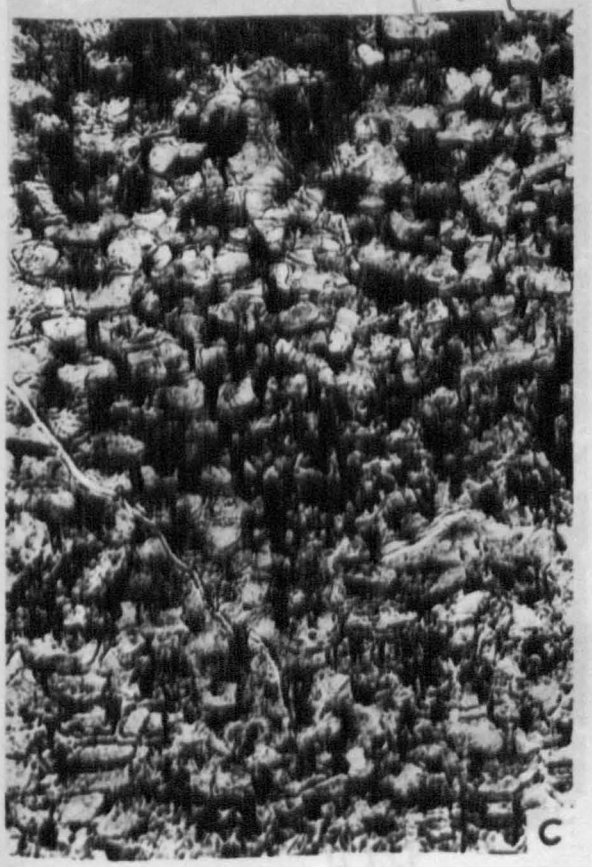

D

PLATE XV

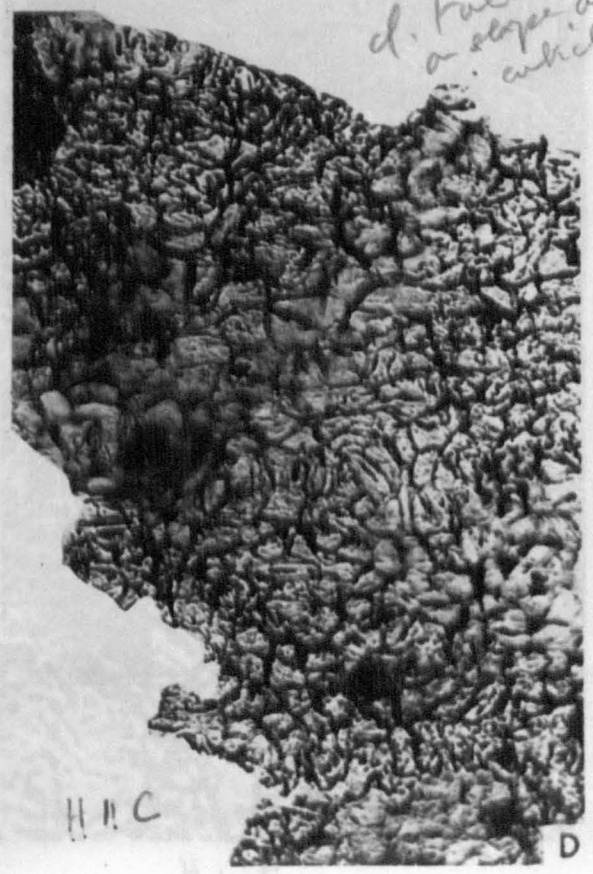


A

B

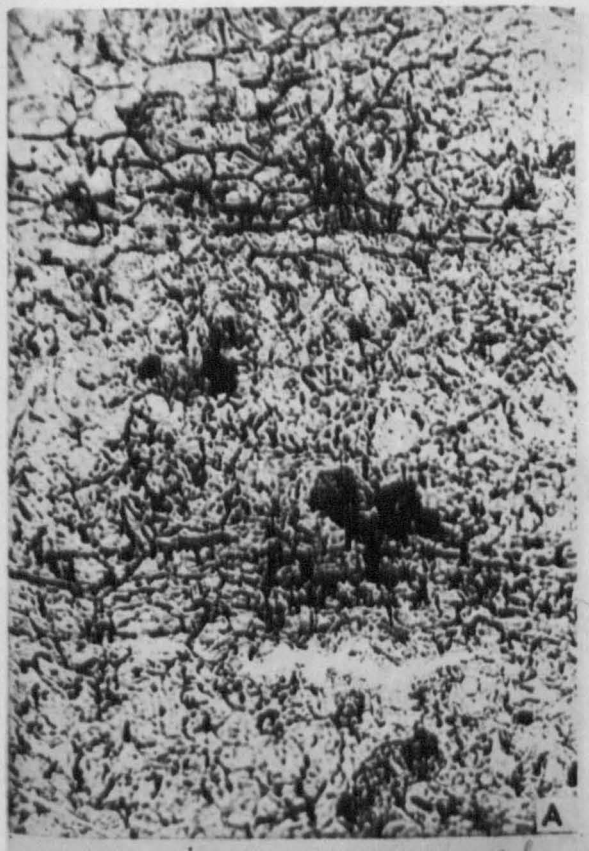


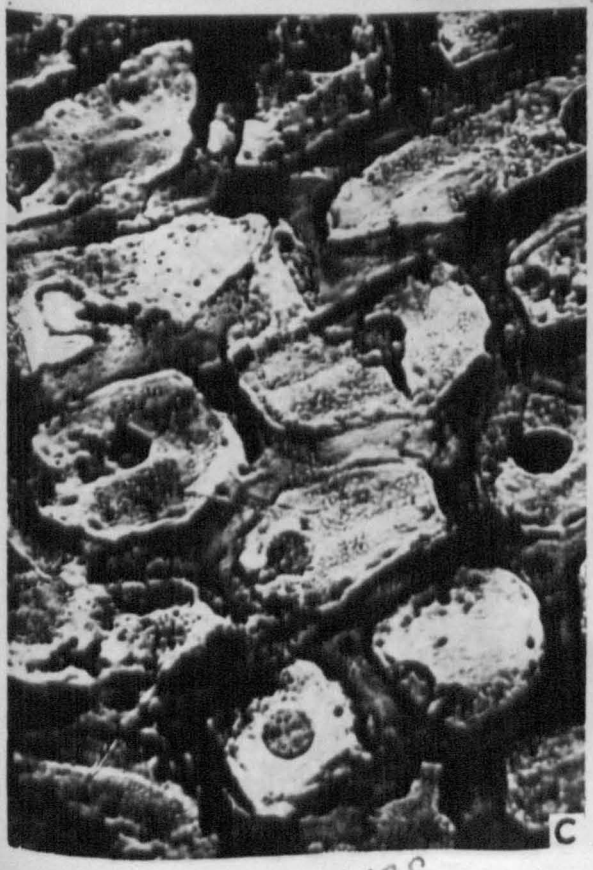
C



D

PLATE XVI





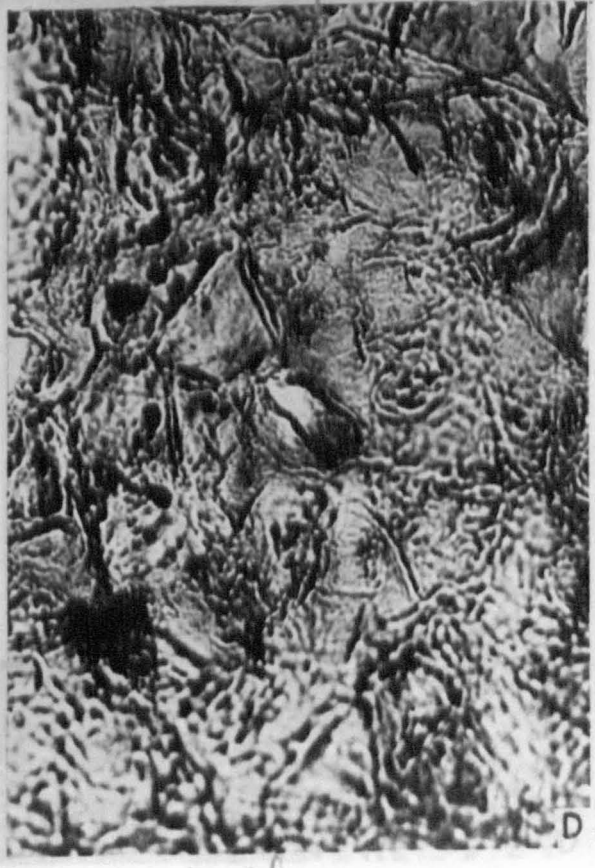


PLATE XVII

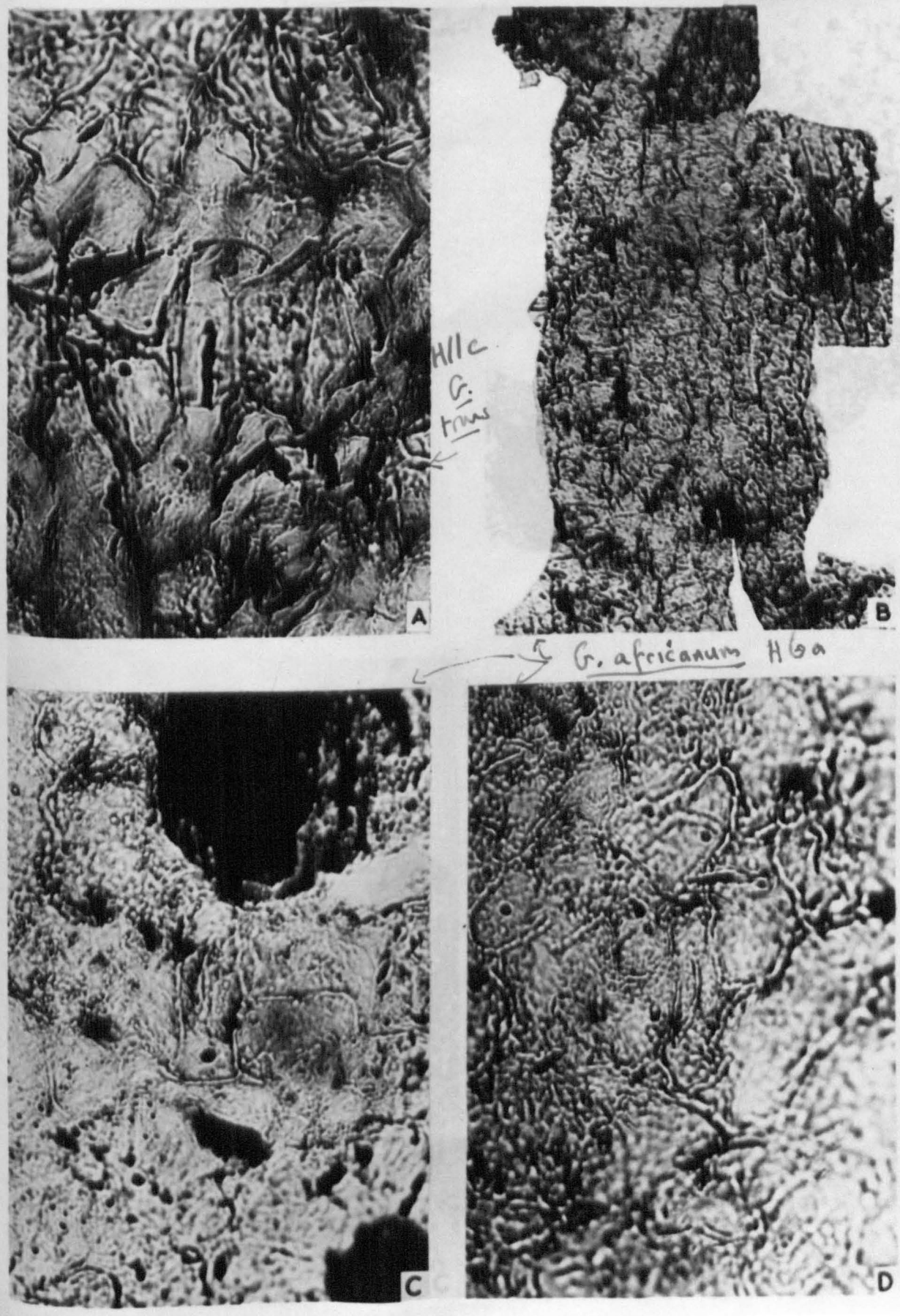
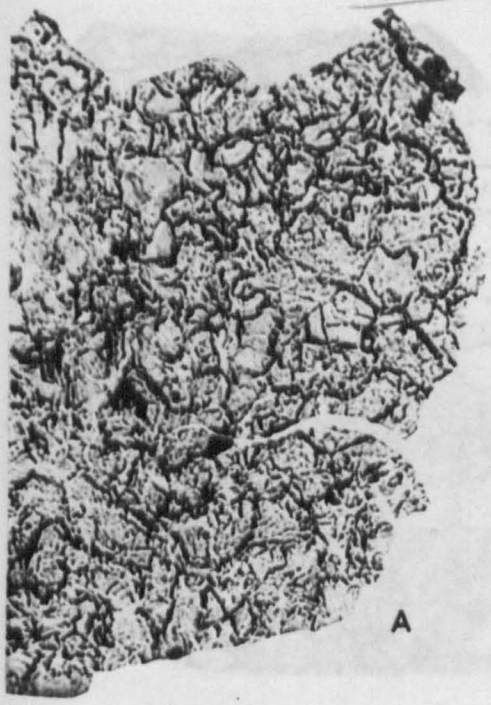
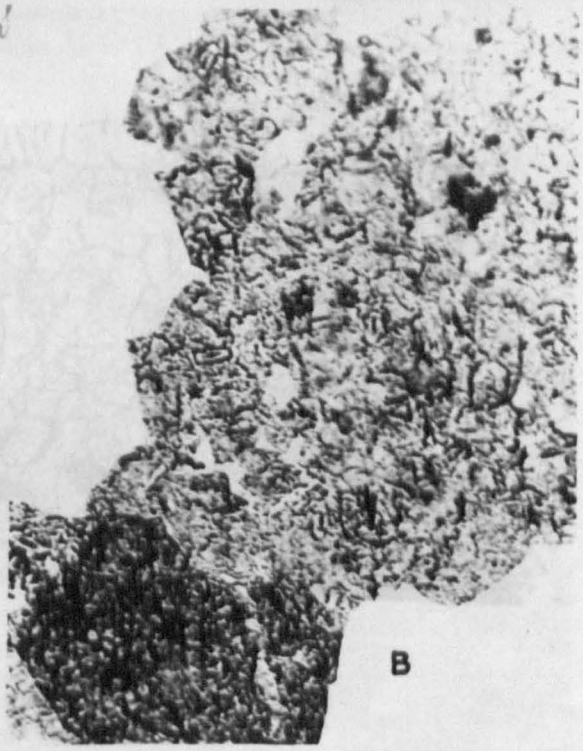


PLATE XVIII

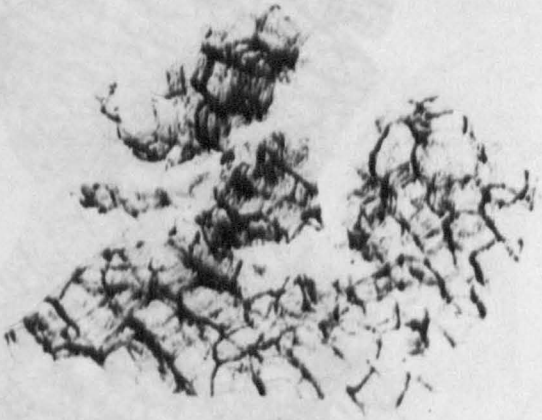


A



B

C

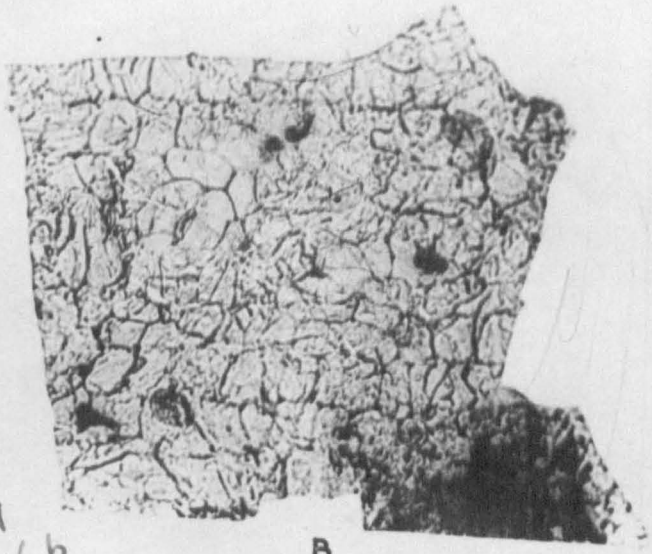


D

PLATE XIX

A

H 16b

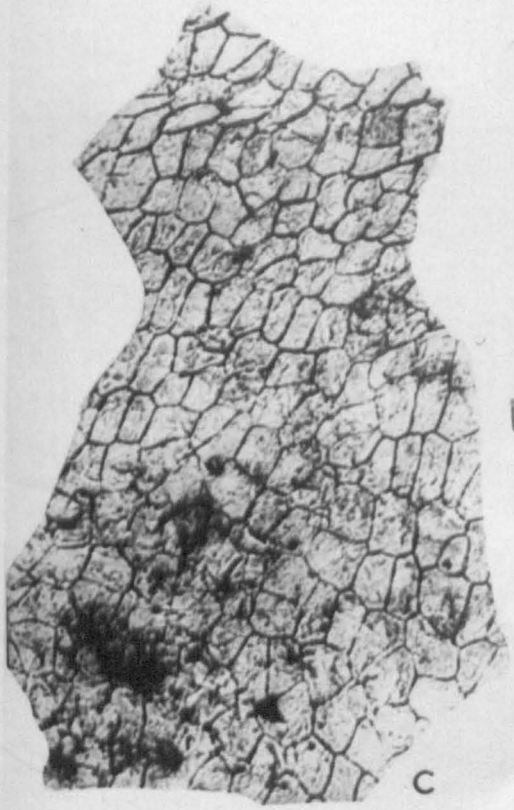


B

G. d. fibrm

~~H 16b~~

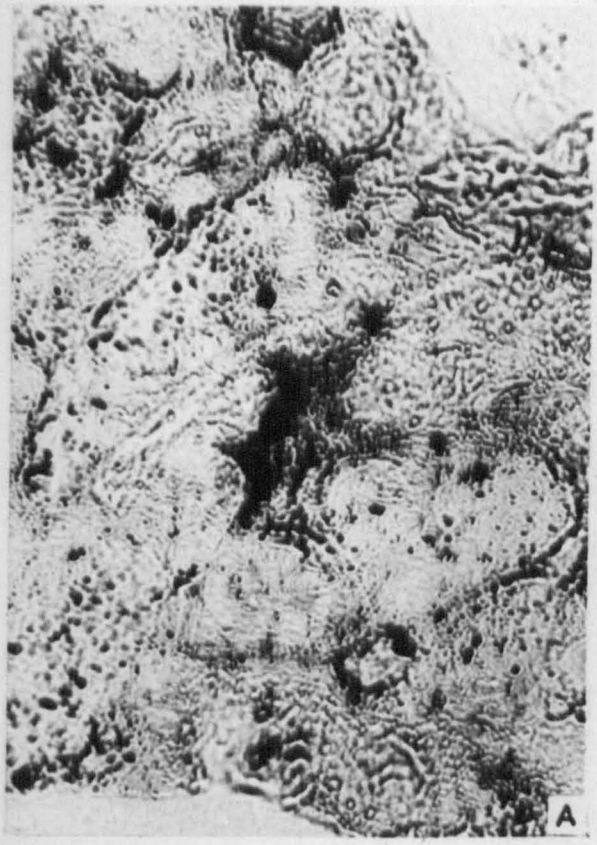
H 11a



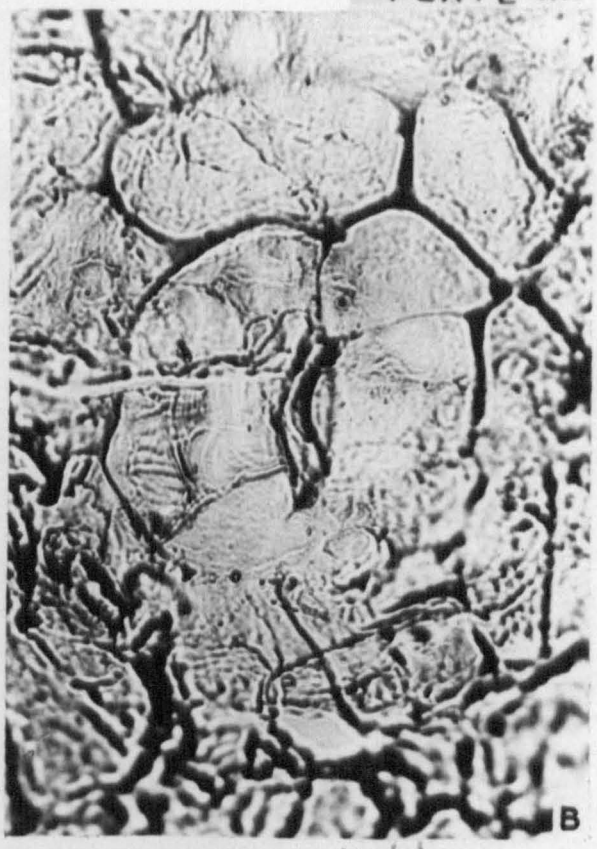
C

D

PLATE XX

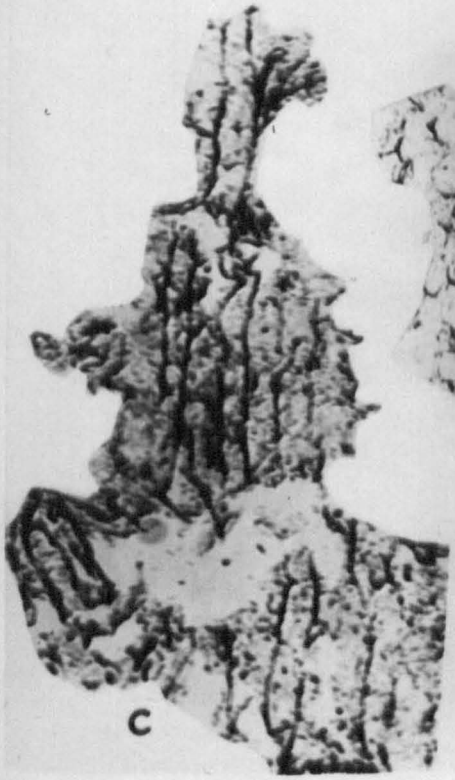


H4

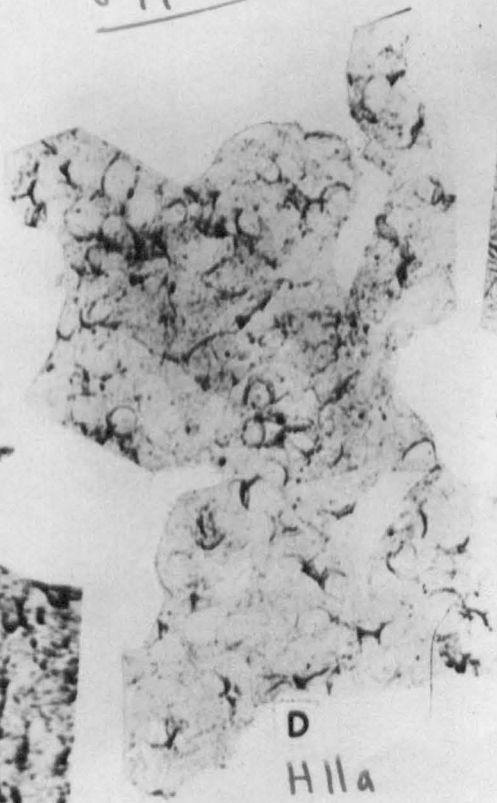


H16b

Gd. fibrosa.



~~H16b~~ H11a

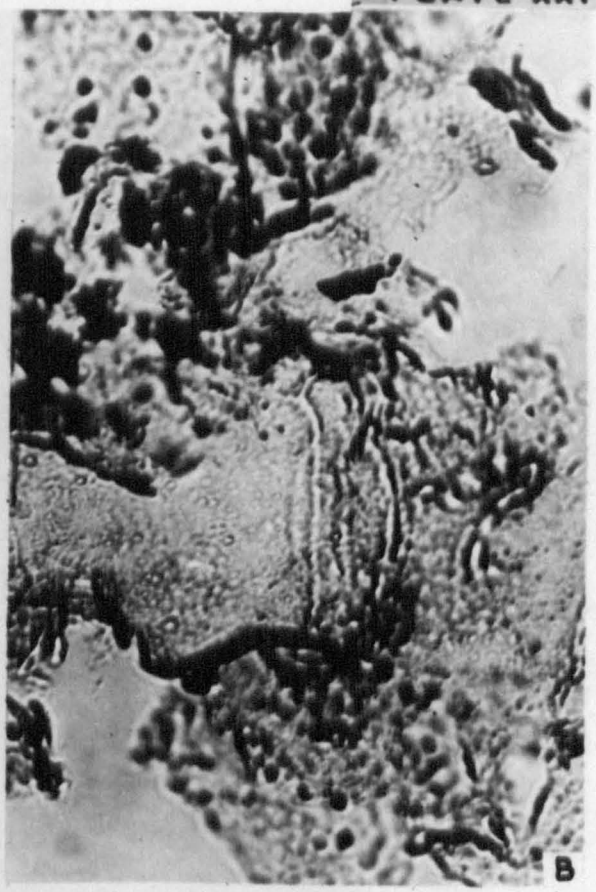


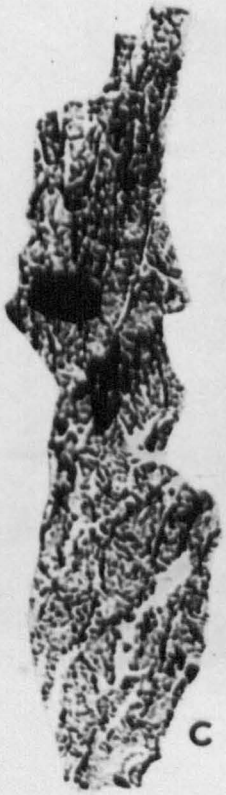
H11a

H11a

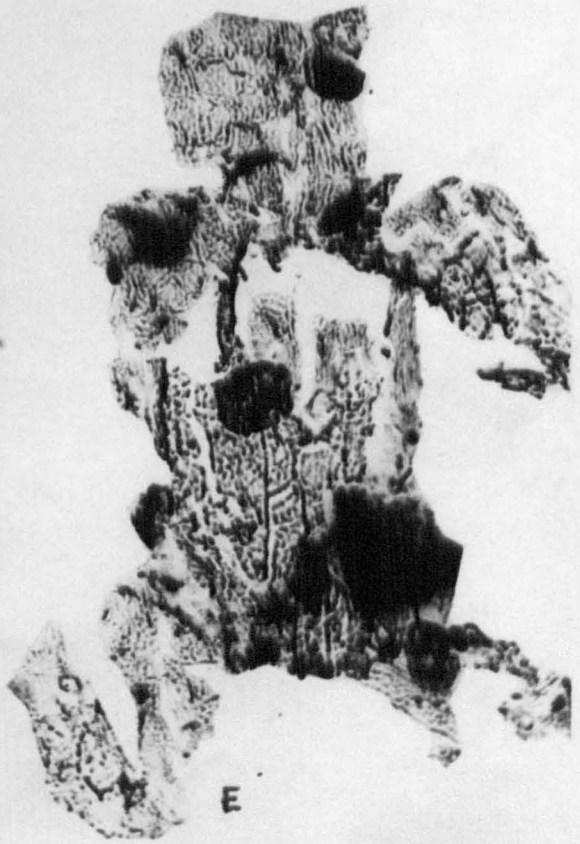
PLATE XXI


A


B


C


D


E

g. sp. A.

H. 13 g d. communis ✓

G. fumiter

PLATE XXII

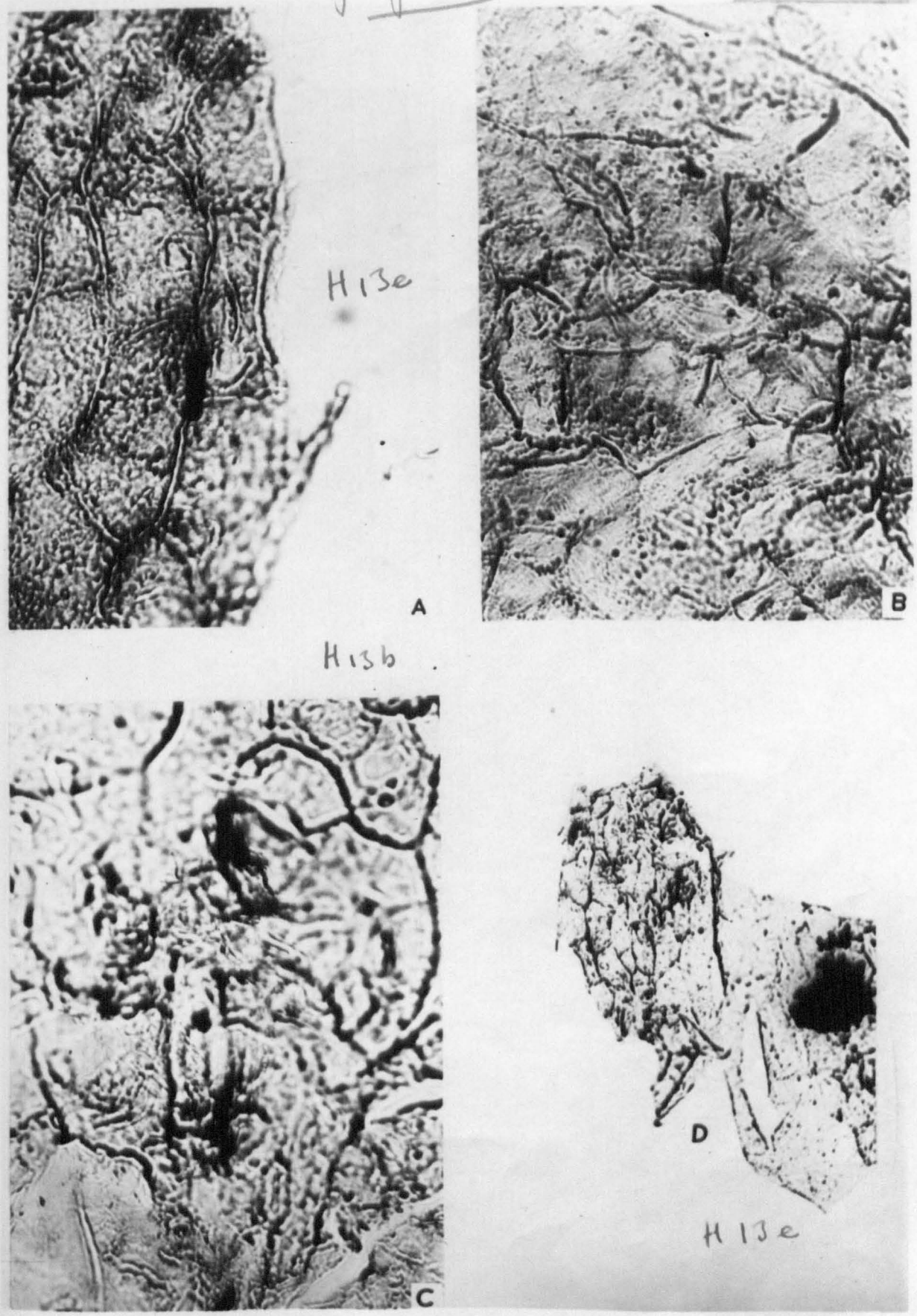
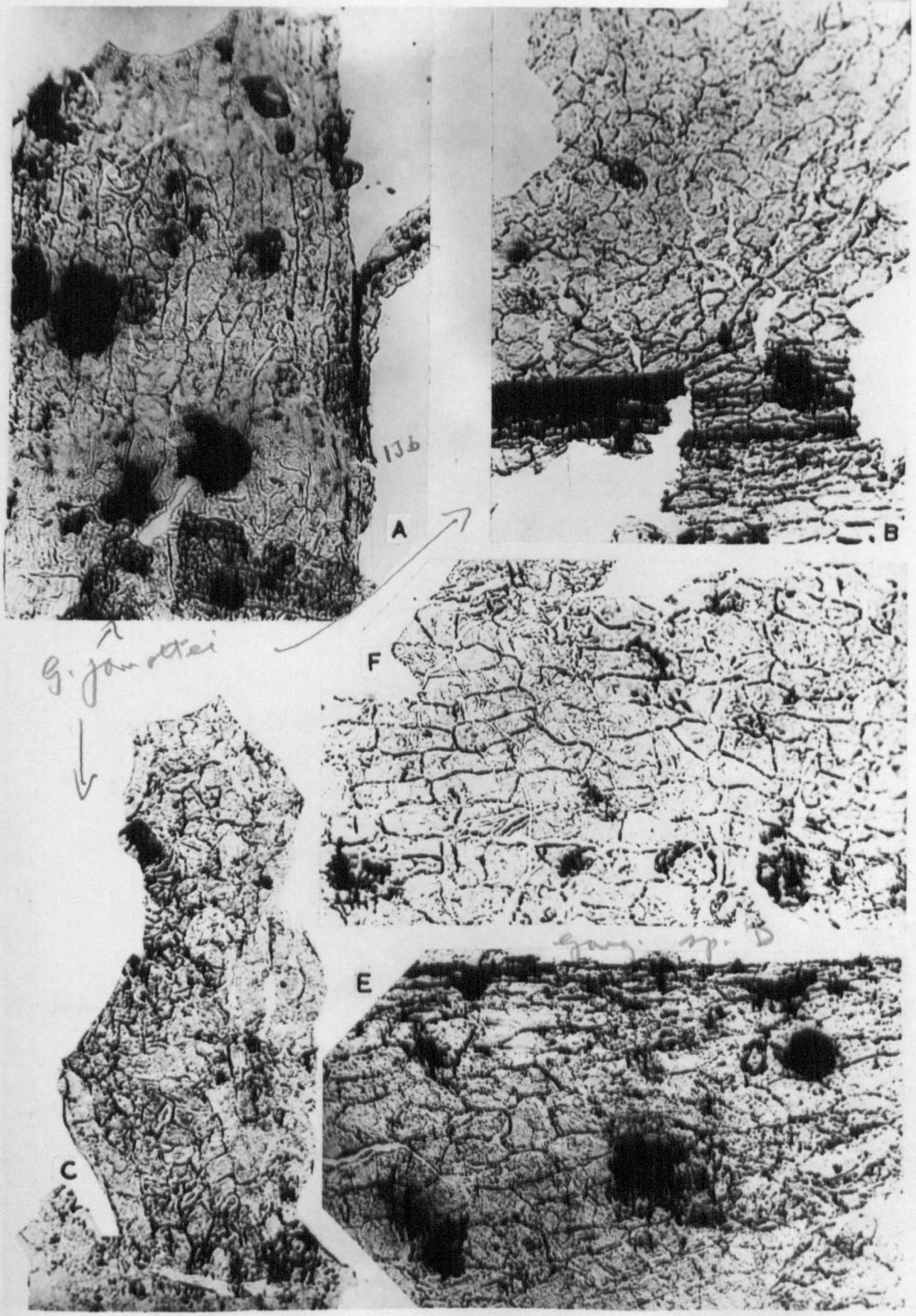


PLATE XXIII



PART III

PETRIFIED WOOD FROM RHODESIA AND SOUTH WEST AFRICA.

CONTENTS

SOURCE OF THE MATERIAL.

Nearly all the fossil woods described here have been collected from localities in Northern and Southern Rhodesia and are of Permian or Triassic age. An additional specimen from an unknown locality and horizon in South West Africa is also described.

The greater part of the collection was made by Dr. W. S. Lacey, of the Department of Botany, University College of North Wales, during a palaeobotanical expedition in Rhodesia and Malawi (Nyasaland). I am greatly indebted to Dr. Lacey for providing me with this material, and also to Professor Geoffrey Bond, Department of Geology, University College of Rhodesia and Malawi (Nyasaland) who subsequently sent additional specimens, (A4, G1-3 Table 1.) to Bangor, for me to examine.

DESCRIPTION OF THE COLLECTION.

The whole collection consists of fifty specimens from six localities in North and South Rhodesia and one in South West Africa. These have been grouped according to the locality. Each locality was given a letter for ease of identification, and each specimen within a group was given a code number. The specimens are catalogued as shown in the following table.

Table 1. Locality and age of specimens.

Card index no. of specimens.	Description of Locality	Horizon
A 4 *Helicoxylon Wallonii*	South West Africa (precise loc. not known)	Unknown (Possibly Permian or Triassic).
G 1 - G 3 *Mesembryoxylon gwaasense* *Dadoxylon bandii*	Locality 40 of Lacey (1961b) Headwater area of Gwave River 20 miles N.N.E. of Gokwe, S. Rhodesia	Probably Pebbly Arkose (Upper Triassic)
✓ F 1 - F 9	Locality 49 of Lacey (1961b) Fossil Forest, Chirundu-Kafue road, 10 miles west of Chirundu, N. Rhodesia	Escapment Grit or Pebbly Arkose (Upper Triassic)
✓ C 1 - C 7	Locality 42 of Lacey (1961b) Near Sai, Manyoni River Valley, Central Sebungwe, S. Rhodesia	Probably Escarpment Grit above basal conglomerate (Early part of Upper Triassic)
✓ B 1 - 7 *Dadoxylon bandii*	Locality 43 of Lacey (1961b) Dotsena Fossil Forest Wankie Game Reserve, S. Rhodesia	Probably Escarpment Grit above basal conglomerate (Early part of Upper Triassic)
✓ D 1 - 10 and E 1 - 10 *Dadoxylon A (cf niokii) sp. B*	Locality 9 of Lacey (1961b) Base of Chidoma Hill, 6 miles N.W. of Hadziwadzidos S. Rhodesia	Middle Madumabisa Shales (*Endothiodon* Zone) (Permian)
A 1, A 2, A 3 *Dadoxylon beughayi*	Locality 11 of Lacey (1961b) Near Gunyanka's old Kraal S. Rhodesia	Middle Madumabisa Shales (*Tapinocephalus* zone) (Permian)

The specimens ranged greatly in size, from 3 or 4 cubic centimetres, to large blocks measuring as much as 20 cm. x 10 cm. x 9·5 cm. They were all highly silicified, although some contained a fairly high proportion of carbonates (Series G 1 - C 7) and many of the harder specimens contained large veins of white quartz (Series B 1 - B 7; F 1 - F 9).

Iron staining was detectable in some of the specimens, and this may have played an important part in the preservation of the material (Wieland, 1941).

The best preserved specimens were highly silicified. They were whitish on the outside, owing to weathering, but broken or cut surfaces were brown to deep brown or black in colour. This was partly caused by the preserved material, but largely by iron staining of these tissues. The matrix between the cells was quite clear and transparent (Specimens A1 - A 4; G 1 - G 3). In these specimens, any lack of detail was due to decay before preservation was complete.

The "B" and "F" series were of even harder composition. The rock was hard and grey, almost granitic in appearance. The surface sparkled, and as the sections showed, thiswas due to the highly crystalline nature of the rock. This, together with the numerous intrusions of quartz, completely obscured all signs of cellular structure in many of these specimens.

However, the well preserved material has proved to be of considerable value in increasing our knowledge of the structure of fossil woods, particularly of the fine detail of the tracheidal and crossfield pits, and in evaluating the usefulness of various features as diagnostic characters. They have also shown that well preserved fossil woods can be of greater stratigraphical value than has been suggested previously (Warren, 1912; Walton, 1956).

It has been confirmed that woods with a mixture of features common to the Araucarineae and the Abietineae appear in large numbers in Gondwana deposits, much earlier than the similar woods (the Protopinaceae) in the Northern Hemisphere (Kräusel, 1919; Grambast, 1960).

Of the fifty specimens, only eight proved to be sufficiently well preserved to assign definitely to a species. Two new species of Dadoxylon and one of Mesembrioxylon are described. A new name, Helicoxylon is proposed for the specimen assigned by Walton (1925) to his genus Spiroxylon, since this name is preoccupied, (Hartig, 1848; Krausel and Range, 1928). In addition, a new species is assigned to Helicoxylon. Twelve specimens were preserved well enough to place them in a genus, and two others compared closely on macroscopic features, with one of the species described in this Thesis.

Summary of the Fossil Woods recorded from Rhodesia and Malawi (Nyasaland).

1) Fossil wood has been recorded from 29 localities in Karroo beds of all ages (Lacey, 1961b), but from very few of these have specific determinations been possible (Walton, 1956; Lacey, 1961b): e.g.

Rhexoxylon africanum, Bancroft (Walton 1923; 1956), from locality No. 57 (Lacey, 1961b).

Rhexoxylon sp. (Walton 1956) from localities 68, 69 and 75 (Lacey, 1961b).

Dadoxylon nicolii Seward (Dadoxylon arberi Seward) from locality 65 (Lacey 1961b).

Dadoxylon nicolii Seward (Determined by Edwards, 1937) locality 57 (Lacey 1961b).

Dadoxylon sclerosum Walton (1925) recorded by Edwards (1937) Locality 61 (Lacey 1961b).

2) The following species have been recorded during the present investigation:

Dadoxylon bourbovi sp. nov., from locality 11 (Lacey 1961b)

Dadoxylon bondii sp. nov. from localities 40 and 43 (Lacey 1961b)

Dadoxylon sp. A (Dadoxylon cf. nicolii Seward) from locality 9 (Lacey 1961b).

Dadoxylon sp.B from locality 9 (Lacey 1961b).

Mesembryoxylon swavense sp. nov. locality 40 (Lacey 1961b).

The specimen from South West Africa (A 4) has been described as Heliooxylon waltonii gen. et sp.nov.

Methods used in the investigation of the anatomy of the Petrified Woods.

At first, attempts were made to prepare sections from all the specimens by means of the cellulose peel method (Joy, Willis and Lacey, 1956).

This entailed cutting or grinding part of each specimen to obtain a perfectly flat surface, which was ground smooth using a medium grade carborundum powder and water, on a ground glass plate. Following a thorough washing with tap water for several minutes, the surface was polished with Grade "00" Aloxite and water on another glass plate. (Note that it is absolutely essential to avoid the contamination of these plates with a coarser grinding poser than that normally used). The polished surface was also washed thoroughly under a strong stream of tap water

for several minutes. The sides of the specimen were protected with wax, and the polished surface was placed in a shallow bath of hydrochloric acid (0·2N) for 30 minutes. As this clearly had no effect on the specimens, they were transferred to another bath containing 40% "Commercial Grade" hydrofluoric acid, for between one and twenty minutes.

This treatment was followed by a thorough, but gentle, wash under a tap, and the specimens were left to dry in a stream of warm air. (This can be hastened by the addition of a few ml. of alcohol after the final wash in water. The specimen was wedged with plasticene so that the etched surface was nearly horizontal, and this surface was then flooded with acetone. A thin film of cellulose acetate was applied to the acetone, great care being taken to exclude air bubbles, and to keep the film flat. The specimen was then left until the acetone had evaporated and the film of acetate was perfectly hard. This was peeled off carefully and mounted in Canada balsam for examination. All the specimens proved to have too little organic remains to yield usable peel sections. Specimen G 3 showed vague outlines of cells, and the position of the growth rings. However, even this was caused by a difference in the composition of the material in the region of the cell walls, and that occupying the cell cavities. The former was dissolved more rapidly than the latter, so thatthe cellulose film showed raised lines in the position of the cell walls. The information this revealed was little more than could be obtained from viewing the polished surface of the hand specimen with a hand lens.

This method was, therefore, abandoned in favour of cutting

petrological sections. The preliminary investigations were carried out in laboratories of the Nature Conservancy, Bangor, but more detailed work was carried out during two visits to the Geology department of the University College of Wales, Aberystwyth. My thanks are due to Dr. R. E. Hughes and to Mr. David Hall of the Nature Conservancy, for permission to use the rock cutting machine, and also to Professor Alan Wood, of the Geology Department, Aberystwyth, for permission to use the facilities in his department during extensive periods in November, 1960 and December, 1961. I am also extremely grateful to Mr. Gordon Rattray, Chief Technician in the Geology Department, Aberystwyth, for his kind interest in my work, and his advice on many points of petrological technique which resulted in a great improvement in the quality of the sections produced. In all, some 135 petrological sections were prepared, representing the expenditure of a good deal of time and labour.

Although the preparation of petrological sections is basically simple, it is laborious and requires great patience and attention to detail to produce the best results.

Normally, slices of rock are cut from the specimen in the desired plane, and one side of the slice is ground and polished using progressively finer grades of "Aloxite" on ground glass plates. As described previously, a thorough washing under a strong jet of water is required between stages, particularly after the last, as all traces of grinding compound must be removed before the slice is dried and fixed to a microscope slide; otherwise the sections will flake off. Adhesion is greatly improved if

the surface of the microscope slide is also lightly ground with grade "00" "Alozite".

The slice of rock and microscope slide are pre-heated to 70°C, and then the slice is fixed to the slide, polished face downwards, with a thermoplastic resin known as "Lakeside 70". This resin melts at 70°C, and boils at a few degrees higher, so than an electric hot plate with a variable thermostatic temperature control is essential for this process. "Lakeside 70" sets fairly rapidly at room temperature, and can be ground or cut within a few minutes.

It is advantageous to cut slices as thinly as possible, as this wastes less material, and saves a lot of time in hand grinding and polishing. However, the thickness of the slices cut depends entirely on the nature and hardness of the rock, and can only be determined by trial and error. About 1 mm. is the absolute minimum.

Friable material can be strengthened by boiling it in Canada balsam until it is thoroughly impregnated. On cooling, the Canada balsam solidifies, greatly strengthening the material. In addition, a microscope slide can be fixed to the polished surface of the specimen before each section is cut. This prevents the slice breaking into fragments as it is cut.

Once fixed to a slide, the slices can be roughly ground on a resin-bonded diamond wheel, but once again, the amount of material that can be removed in this manner depends on the nature of the rock; and great care is required at this stage if complete loss of the section is to be avoided.

When the mechanical grinding is complete, the section is further reduced in thickness with course grade "Aloxite" in water on a ground glass plate. I have found that a series of small circular motions is most efficient in this hand grinding, as it is important that each part of the glass receives equal wear, otherwise the surface soon becomes irregular, and is then useless for the preparation of sections. The section should be examined frequently to ensure that the section is not ground completely away. When some signs of cellular structure are visible, the slide is washed thoroughly and then polished on a second ground glass plate, observing all the precautions mentioned above. This stage is most laborious, but very important. Any time spent on polishing is amply rewarded by the increase in quality of the section. The section can then be flooded with Canada balsam in xylol and covered with a cover glass. Better results are obtained if the slide is heated to 50°C and solid balsam is melted on it. This method is less likely to produce bubbles under the cover glass at a later date, or to cause the section to come away from the slide. At first it was found more useful not to affix a permanent cover slip, as a more leisurely examination of the slide often revealed areas of great interest which would benefit from further polishing. For this type of examination, the slides were flooded with water or dilute glycerine. Permanent cover slips were affixed before the final photographs were taken.

The illustrations are prepared using the same materials and methods as described on page 15 . For sake of comparison, only four standard magnifications are used for the reproduction of photographs

showing microscopic features. Those selected are I) x 50; II) x 125; III) x 470 and IV) x 1,200. As far as possible, standard magnifications were used for each particular feature shown in the text figures, e.g. general transverse sections, tangential longitudinal sections and rays in radial section are all shown at x 125. The arrangement of tracheidal pits is shown at x 500, and details of tracheidal and crossfield pits in plan and section at x 1,100.

SYSTEMATIC DESCRIPTIONS.

The Genus Dadoxylon Endlicher 1847

The genus Dadoxylon is used for all specimens of fossilized gymnospermous secondary wood which have predominantly alternate or flattened and contiguous bordered pits on the tracheids, and which have no centripetal secondary wood or well preserved primary tissues (Endlicher, 1847; Seward, 1919; Krausel and Range, 1928; Walton, 1925, 1956; Vögellehner, 1964).

However, isolated specimens of normal centrifugal secondary wood of the Araucarian type have been described under a number of generic names besides Dadoxylon, e.g. Araucarites, Pinites, Cordaioxylon, Cordaites, Araucarioxylon.

Presl (1838) first applied the name Araucarites to impressions of branches and cones, so this name cannot be used for wood specimens which do not have organic connection with such branches or cones.

Pinites is a "nomen dubium" as it has been used by different authors for a variety of plant organs (Vogellehner, 1964).

In the absence of connected leaves or fructifications it is impossible to differentiate between wood of Dadoxylon, Cordaites, Cordaioxylon and Araucarioxylon. The separation of these genera solely on the grounds of geological age cannot be supported (Seward 1919). Cordaioxylon and Araucarioxylon are therefore regarded as synonyms of Dadoxylon Endlicher 1847 (Vogellehner 1964).

Dadoxylon is clearly an artificial genus and probably contains a

large number of different genera. This would account for the fact that woods of the Dadoxylon type have been described from rocks as old as the Middle Devonian (Lang 1929) right up to the present.

The Synonymy of Dadoxylon nicolii Seward 1917

In 1905, Arber described a specimen of secondary wood from Australia as Dadoxylon australe. Crié (1889) had already used the specific name "australe" for another species of Dadoxylon. This was pointed out by Seward (1917) who proposed the name Dadoxylon nicolii for Arber's specimen.

In 1919, Seward, without giving any reason, proposed yet another name Dadoxylon arberi for the same specimen. This was supported by Walton (1925) who suggested that the name Dadoxylon nicolii should be abandoned as Carruthers (1880) had already used the name Araucarioxylon nicolii. As Carruthers gave neither a description nor a figure of his specimen, Araucarioxylon nicolii is a nomen nudum.

Presumably for this reason, Walton (1956) reverted to the use of Dadoxylon nicolii Seward, for the species originally described by Arber (1905) as Dadoxylon australe.

Nadoxylon boughevi sp. nov.

(Plates I, II and III, Text figures 1 - 2)

Locality: Near Gunyanka's Kraal, Dusi River Valley, Southern Rhodesia (Locality II, Lacey 1961b).

Age and Horizon: Middle Madumabisa Shales, Tapinocephalus Zone.

Specimens: A1, A2 and A3 (Syntypes).

Diagnosis.

Secondary wood gymnospermous in appearance, homoxylic and pycnoxylic. Growth rings fairly wide, containing narrow but well marked zones of late wood. Tracheids averaging 2·55 mm. long. Pitting on radial walls of tracheids 1 - 4 seriate mostly "Araucarian", but pits are small and circular, not hexagonal where well preserved. Biseriate opposite pits and rims of Sanio rarely present, also possesses irregular isolated groups and separate, uniseriate pits. In section, pits like those of most modern conifers. Rays uniseriate or rarely partly biseriate, 1 - 66 cells high, mean value, 7·3 cells high. Ray cells thin walled, pitted, crossfield half-pits 2 - 6 per field, border circular, pore circular or an oblique slit.

Description.

The specimens are all segments of secondary wood, measuring approximately 7·5 cm. tangentially, 5·5 cm. radially and 5·5 cm. vertically. In transverse section (Plate 1A, Text fig. 1F) the tracheids are mostly

rectangular or sometimes hexagonal in shape, and are arranged in radial files. The tangential dimension of a file of cells is constant and varies between 15μ and 50μ, the average measurement being 27μ. The radial width of the early wood tracheids is approximately 40μ. There is normally a wide zone of these large tracheids in a growth ring, followed by a band of twenty or so slightly smaller cells measuring between 30μ and 35μ radially. There are then only 2 - 4 late wood tracheids which may each measure as little as 5μ radially. There is a great contrast between these cells and those of the succeeding early wood, so that the growth rings are well defined, even though the zone of late wood is so narrow.

Normally the growth rings are wide (6 - 7 mm), although near the edge of specimen A1 there is a very narrow ring measuring only 1 - 2 mm. across. The ~~medullary~~ rays are well marked, but the cells are often obscured by a heavy deposit of ferrous material.

In tangential section (Plate IB, Text fig. 1B) the rays are seen to be mainly uniseriate and sometimes biseriate in places. The general impression is that the rays are high, indeed, rays as much as 66 cells high have been seen, and in most sections 10% of the rays are over 20 cells high (See Appendix, page 262). The ray cells are very thin walled, approximately 27μ high and 12μ - 24μ wide. The sections are remarkable in that there are some rays in which the crossfield pits are shown in section. These are well shown in Plate III C and D and in Text fig. 2.c. From this it is clear that the pit in the tracheid is bordered, but the wall of the ray cell is not pitted. The tracheidal

pits are also well shown in section (Plate IIB and Plate IIID, also Text fig.2c). The form of the pit in section is typical of the recent Araucarineae. The middle lamella and primary wall can be seen. The torus is not well developed, consisting of a slight swelling of the primary wall. Isolated or biseriate and alternately arranged bordered pits, about 10μ in diameter, can be seen on the tangential wall of some of the tracheids (Text fig.2.c.). No xylem parenchyma (other than the ray cells) has been observed, and resin ducts or resin cells are entirely lacking. The ends of the tracheids taper gradually to quite a sharp point, and the mean tracheidal length was found to be 2·55 mm. (For method of determination of tracheid length, see Appendix, page). In radial section the ray cells vary from 50μ to 120μ, but mostly 60μ - 90μ long. No pits are present on the tangential walls of the ray cells.

There are 2 - 6 crossfield pits. In the early wood, these are circular with a diameter of 5μ - 6μ. The pore is central and also circular, measuring about 2μ - 3μ in diameter. In the late wood the pits are circular, 5μ - 6μ in diameter. The pore is broadly elliptical and oblique in the first of the late wood tracheids, but changes to a narrow oblique slit in the last row of the cells (Plate ID and Text fig. 2A and B).

The main tracheidal pits are small, 8μ - 12μ in diameter, with a central pore 2μ - 3μ in diameter. The borders are circular or oval in outline, occasionally with slightly flattened faces where they are contiguous. The pits vary considerably in arrangement, depending on the position of the tracheid in the growth ring. The tri- or even quadriseriate arrangement is the most common in the early wide tracheids, and in this case,

the pits are clearly alternate in the typical Dadoxylon fashion. In slightly narrower tracheids, the pits are arranged in one or two rows. Where they are biseriate, the pits are usually alternate, but the vertical rows of pits are often 3= or 4= apart. Sometimes the pits are oppositely arranged and bars of Sanio are present (Plate XIIA, B). Where the pits are uniseriate, they may be contiguous or distant, or arranged in pairs and occasional clusters of three or four pits. These different arrangements are shown in (Text fig. A - C.). Where the pits appear to be clearly hexagonal (Text fig. 1A) careful examination shows that the normal circular outline of the border has decayed revealing the limits of the primary pit field, which is hexagonal in shape.

Comparison and Discussion.

I have found great difficulty in comparing the specimens described above with the vast number of Gondwana fossil woods which have basically Araucarian features and which, for the most part, are poorly described and illustrated. However, of this number, I believe only the following bear a close comparison with Dadoxylon boughevi. These are:-

a) Dadoxylon nicolli Seward 1917 (as described by Walton 1925)

b) Dadoxylon pedroi Zeiller 1895

c) Dadoxylon butiense Rau 1934

d) Dadoxylon lukugense Grambast 1960

A comparison with Arber's original description (1905) of the type specimen of Dadoxylon nicolli, formerly known as Dadoxylon australe

and Dadoxylon arberi, would suggest that there is a little affinity with Dadoxylon boughevi, but Walton's more detailed examination (1925) brought out several features which show a similarity to this species. In both species the pits on the radial walls of the tracheids are 1 - 4 seriate mainly with typical Araucarian arrangement, but also with biseriate opposite pits and well isolated pits. Walton notes the presence of horizontal bars between some of the pits, but attributes them to the effects of decay. Similar marks are present in Dadoxylon boughevi, but I think they may well be true bars of Sanio. In both, the pits are 8μ - 12μ in diameter. There are, however, a number of differences which, taken together, are sufficient to separate them into two distinct species.

(1) The tangential walls of the tracheids of Dadoxylon boughevi are pitted, but those of Dadoxylon nicolii are not (Walton, 1925 page 3).

(2) Biseriate or partly biseriate rays appear to be more common in Dadoxylon nicolii than in Dadoxylon boughevi. The rays of Dadoxylon nicolii are 1 - 20 cells high and those of Dadoxylon boughevi are 1 - 61 cells high. Although height of ray is not normally taken to be a good diagnostic character, (indeed, I have shown that there is considerable variation within a single specimen, see Appendix, page 262), as 8 - 10% of the rays of Dadoxylon boughevi are over 20 cells high, this difference seems to be well outside the range of

variation for a single species (Phillips, 1948, Greenhaut,1960).

(3) There are only 2 - 6 crossfield pits in Dadoxylon boughoyi and 1 - 9 in Dadoxylon nicolii. Those of Dadoxylon boughoyi are bordered, whilst those of Dadoxylon nicolii are said to be simple.

(4) In radial section, the tracheidal pits are always circular in outline in the well preserved portions of Dadoxylon boughoyi, but contiguous hexagonal pits are the rule in the early wood of Dadoxylon nicolii.

(5) The ray cells measure only 50µ - 120µ tangentially in Dadoxylon boughoyi and 130µ - 240µ in Dadoxylon nicolii.

Dadoxylon pedroi is similar to Dadoxylon boughoyi in the extreme height of the rays, but differs in the fact that the tracheidal pits are clearly hexagonal, and at the most biseriate. Isolated pits are very rare, as are biseriate rays. The nature of the crossfield pits is not clearly shown. Pits are not present on the tangential walls of the tracheids.

Dadoxylon butiense also has high rays, but the tracheidal pits are slightly larger than those of Dadoxylon boughoyi. They are only exceptionally triseriate, and they are always very crowded and hexagonal. There are no tangential pits on the tracheids, and the rays are often tri-or even quadriseriate.

Similarly, Dadoxylon lukuense from the "assise de transition" in the Belgian Congo, has rays as many as 60 cells high, but the tracheidal pits are normally biseriate, only rarely triseriate, and

always very crowded and hexagonal, or flattened above and below. According to Cranbust (1960), the pores of the best preserved tracheids are elliptical, oblique, at an angle to those of the opposing tracheids, and possess a narrow border. In addition, the tangential section shows that the tracheids are much larger than those of Dadoxylon boughevi. They reach a maximum width of 90µ in the early wood and are normally between 35µ and 60µ in diameter.

Dadoxylon boughoyi is clearly different from these four species, and I think the evidence I have given supports the erection of a new species for this interesting fossil. I propose to name if after Professor Boughey formerly of the Botany Department, University College of Rhodesia and Nyasaland, Salisbury.

Possibly the most interesting feature of this new species is that it affords positive evidence in a species of Dadoxylon, that the ray cells are not pitted in the crossfield areas. This gives us another character which may be used in the classification of this difficult genus and lends support to the hypothesis that species of Dadoxylon have some relationship to the recent Araucarias. Also the shape of the tracheidal pits in section would seem to be of some taxonomic use, and this is brought out more strongly when they are compared with those of species described later in this Thesis.

Dadoylon bougheyi sp. nov.

Explanation of Text Figures 1A - F.

Fig. 1A R.L.S. Biseriate alternate pitting, with pit borders partly decayed. (X 500).

1B R.L.S. Triseriate alternating pits with well preserved circular borders. (X500).

1C R.L.S. Uniseriate and biseriate opposite pits with occasional isolated pits and small groups of pits. (X 500.-)

1D R.L.S. Ray cells and crossfield pitting. (X 375).

1E T.L.S. Partly biseriate ray and tracheid end walls. (X 375)

1F T.S. Transitional zone between late and early wood. (X 375).

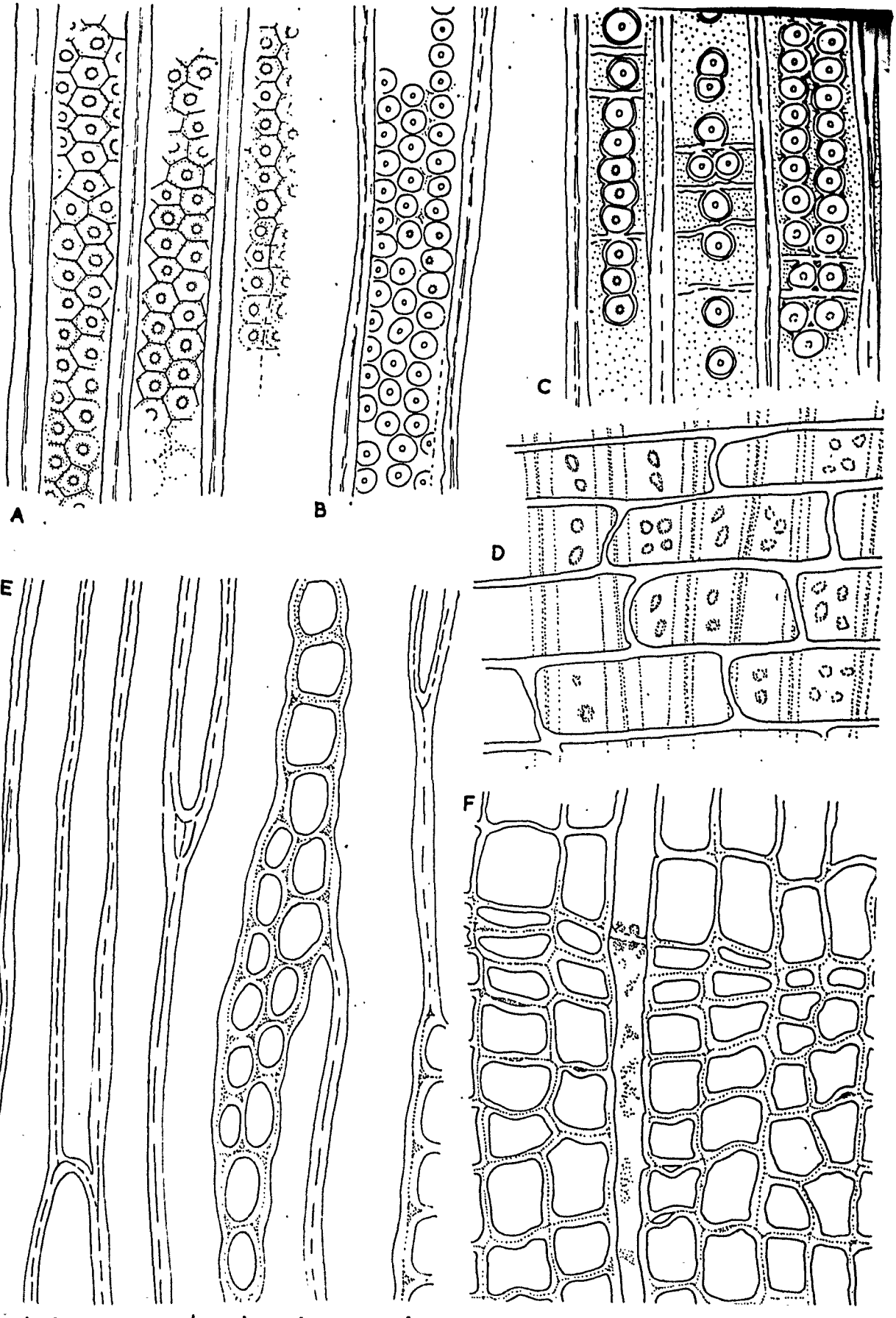
Dadoxylon bougheyi sp. nov

Explanation of Text Figures 2, A - C.

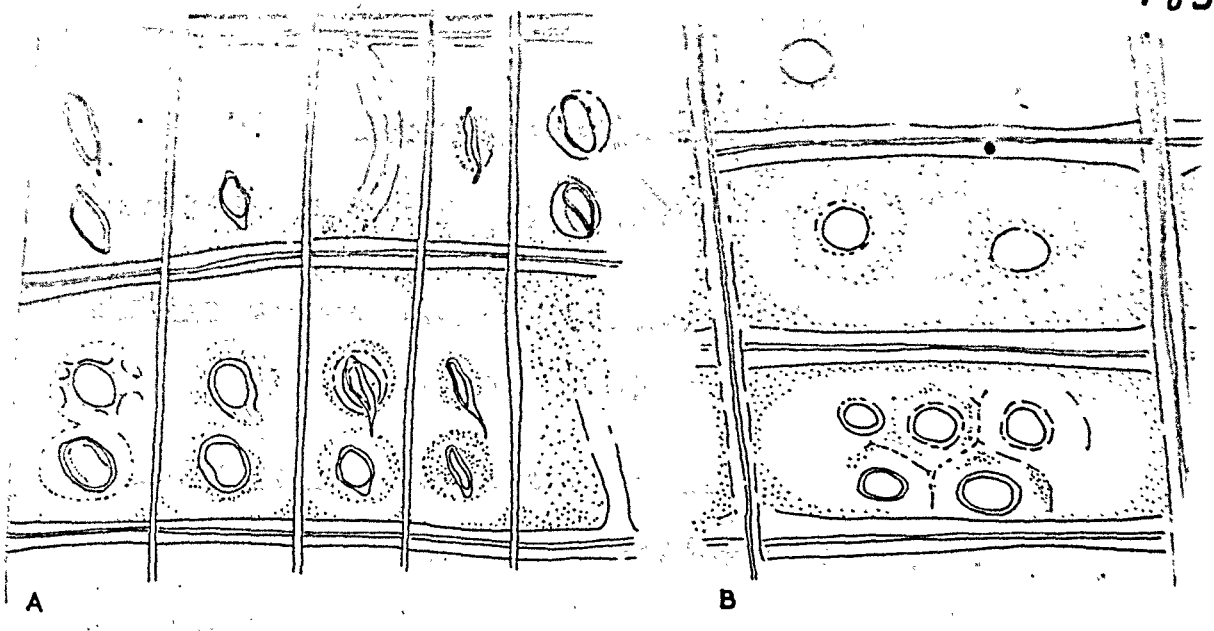
Fig. 2.A Crossfield pits in late wood. From R.L.S. (X 1,100)

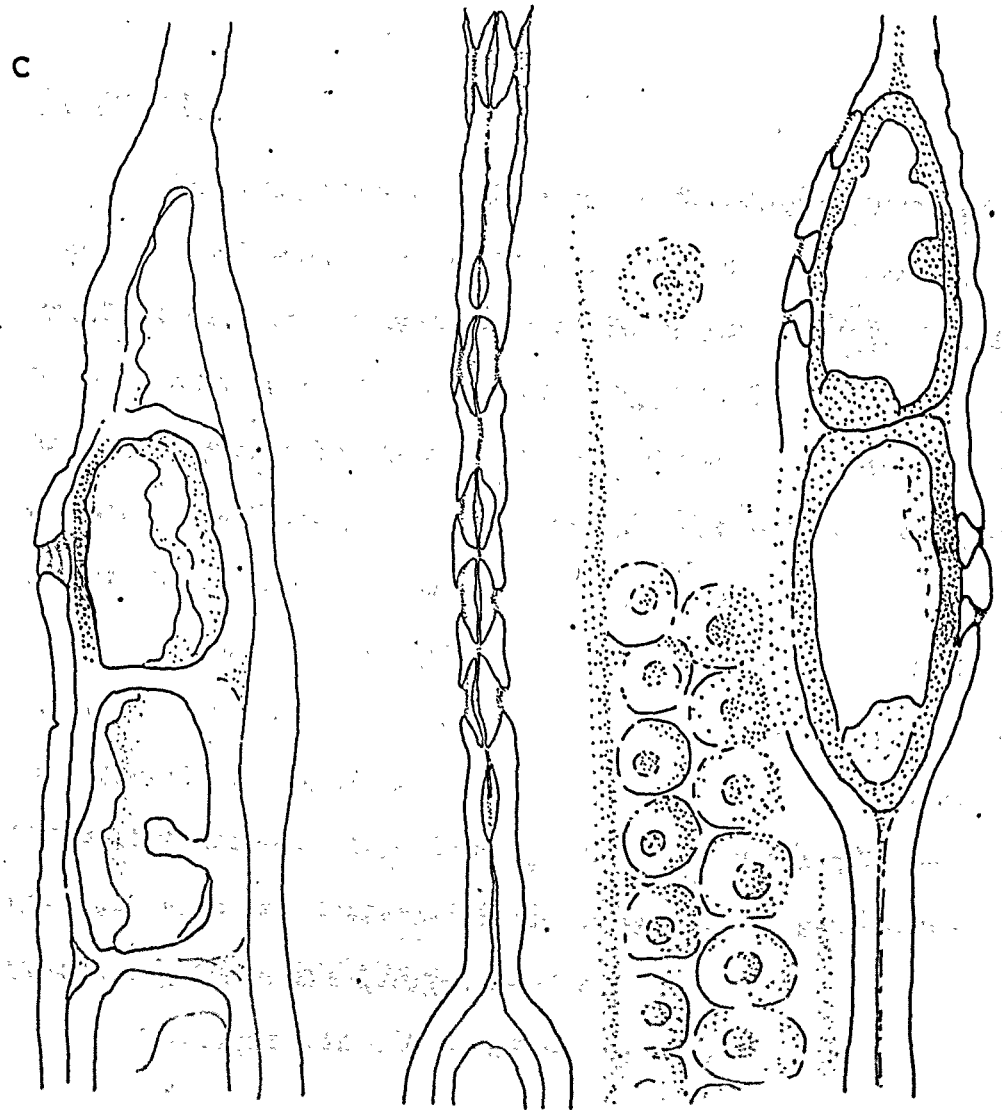
2.B Crossfield pits in early wood. From R.L.S. (X 1,100)

2.C. Tangential longitudinal section, showing crossfield pits and tracheidal pits in vertical section, and biseriate alternating pits on the tangential wall of one of the tracheids. (X 1,100).



Text.fig.1. Dadoxylon boughеyi sp.nov.





Text fig. 2. Dadoxylon boughevi sp.nov.

Dadoxylon sp.A (D. cf. nicolii Seward)

Plate IV A + B, Text figure 3 A - E.

Locality: Chidoma Hill, Southern Rhodesia.

Locality 9, Lacey 1961b)

Age and Horizon: Middle Madumabisa Shales,

(Endothiodon Zone) Upper Permian.

Specimens: D 1 - 10

Description:

The specimens are all well weathered fragments of silicified wood. The largest had a diameter of 10 cm. and was 7 cm. thick. The smallest were only 2 cm^3. The state of preservation was fair and would have been adequate for taxonomic purposes, if the tissues had not been greatly distorted by crushing (Plate IV A). Because of this, and the effect of weathering, I cannot assign this material with certainty to any known species. (Plate IV B) shows one of the best preserved regions.

In transverse section, the growth rings are quite distinct, although the tissues are badly crushed. Originally, the tracheids were clearly arranged in radial files, and were rectangular in outline. There were three or four rows of late wood tracheids, which contrasted strongly with the following early wood, but merged gradually with the preceeding tracheids (Text fig. 3 D + E).

The ray cells are thin-walled, with no pits in the tangential

walls. There are 2 - 4 pits in the crossfield, and these are circular to elliptical and appear to have a border, though they are not well enough preserved for one to be certain of this. The ray cells measure 55μ to 140μ, or more, radially (Text fig. 3 A).

Comparison and Discussion.

These specimens show considerable similarity to both Dadoxylon nicolii Seward and Dadoxylon bourbeyi. The pitting is similar to both, but the size of the tracheids, the proportions of the ray cells and the height of the rays seem more similar to the former than to the latter. With such difficult material it would be unwise to suggest a closer relationship, and I therefore designate these specimens as Dadoxylon sp A. (D. cf nicolii Seward).

Dadoxylon sp.A (D. cf. nicolii Seward)

Explanation of Text Figures 3, A - E.

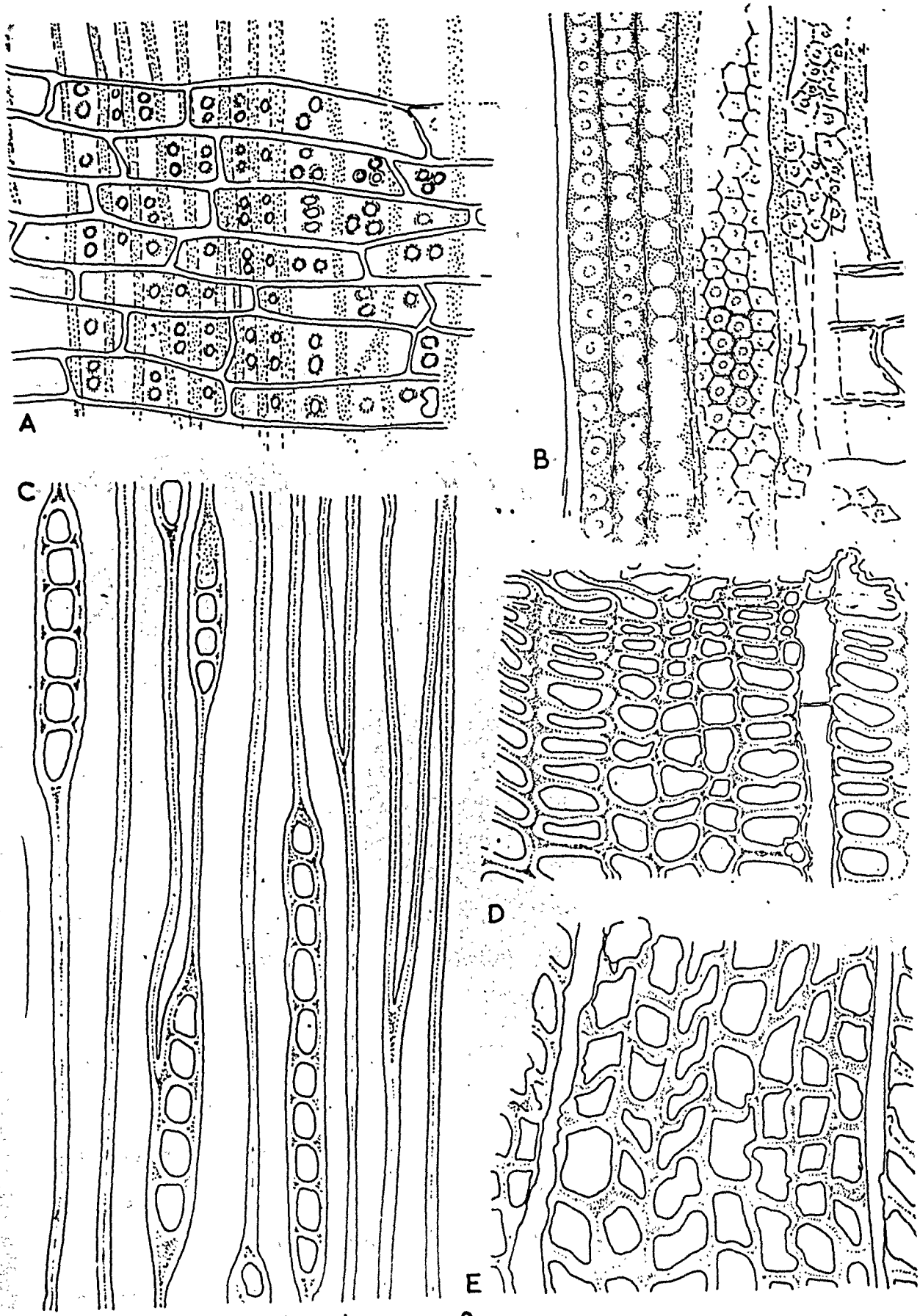
Fig. 3.A. R.L.S. (X 375.) Ray cells crossing zone of transition between late and early wood, showing differences in the shape and size of the crossfield pits.

Fig. 3.B. R.L.S. (X 500.) Uniseriate pits in the late wood and quadriseriate alternating pits in the early wood tracheids.

Fig. 3.C. T.L.S. (X 375.) Uniseriate rays and sharply pointed tracheid ends.

Fig. 3.D. T.S. Growth ring, transition from late to early wood. (X 375)

Fig. 3.E. T.S. showing relatively uncrushed tracheids from the middle of a growth ring, (X 375.)



Text fig.3. Dadoxylon sp. A,

Dadoxylon sp.B

Text figure 4.

Locality: Chidoma Hill, Southern Rhodesia
Locality 9, Lacey (1961b)

Age and Horizon: Middle Madumabisa Shales (Endothiodon Zone)
Upper Permian.

Specimens: E1 - 10

Description:

The series E consists of ten well-weathered small flakes of wood measuring between 2 x 5 x 1·5 cm. and 2 x 2 x 1 cm. One side of each was hard, smooth and coloured pale yellow or yellowish orange. The other side was fibrous in texture and black. The specimens had to be embedded in Canada balsam in order to obtain whole sections. The transverse section appeared to confirm my first impression that the specimens had been burnt on one side. Three distinct regions could be distinguished in the section. A black layer contained tracheids which were sufficiently well preserved for their rectangular outline and arrangement in radial files to be detected.

The cells in the next dark brown layer were completely disorganised; the walls had fragmented and no idea of the shape or arrangement of the cells could be obtained.

The last layer, yellow in colour, had been badly affected by weathering and crushing, but even so, the preservation of the cells was

again quite good, and the radial files of the cells could be seen. The specimens were too small to provide useful tangential longitudinal sections. The radial sections disintegrated, apart from the narrow strip of yellow rock, and here an odd patch of biseriate alternate pitting was discovered.

Comparison and Discussion.

The appearance of the cells in transverse section was quite similar to those of Podoxylon sp.A and the patch of alternate pitting seen in the R.L.S. enables me to suggest that the specimens are possibly a species of Podoxylon - no more can be said on this point.

I suggest the following as a possible explanation to account for the appearance of the transverse section:

1) The outer black layer had been very rapidly carbonised and the cells were, therefore, quite well preserved.

2) The next layer of cells were only partly charred, but subjected to intense heat and pressure, owing to the vapourisation of water inside the tracheids and combined in their wall structure. This would account for the bursting of the cells and the fragmentation of their walls.

3) The last zone would have been protected against the heat by the outer layers of wood, and consequently was not charred at all.

This hypothesis was tested by burning one side of a piece of Podocarpus milanjianus, a wood which was very similar in basic structure to this fossil wood. The burnt wood was then embedded in wax and

microtomed. On examination, the sections showed three distinct zones which had almost the identical appearance of those already described in the fossil.

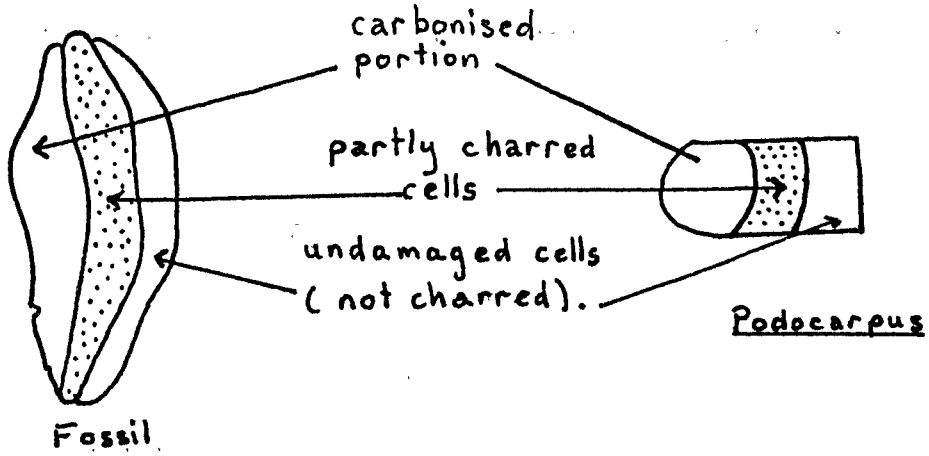


Fig. 4 To show zoning in burnt wood of Podocarpus and in fossil material.

As fragments of this type are found in fair quantities at Chidoma Hill, it seems reasonable to suggest that they are the result of a forest fire - in Permian times. The fragments were presumably burnt while in situ on the tree trunk and subsequently flaked off along the crack lines which arise when burnt wood contracts. (This can be seen by examining any partly burnt logs after a bonfire). It is interesting to note that the length : breadth ratio of the specimens described here falls between 1·0 and 1·5. This compares closely with those values found by Harris (1957, 1958) for fusain fragments belonging to Cheirolepis muensteri and experimentally burnt Pinus sylvestris wood.

This suggestion of a forest fire in Permian times is of some interest, but such an occurrence is not entirely unexpected. Harris (1958)

has already produced evidence from widely separate localities, of similar occurrences in Jurassic times.

Doubtless forest fires have been an important ecological factor in the past history of African vegetation, as they still are at the present day.

Dadoxylon bondii sp.nov.

Plate VIII C + D; Plate IXA- D; Plate X A - G, Text figures 5A - G; 6A - E and 7.

Locality: E1; Wankie Game Reserve, near Dotsema,
G2 + G3 20 miles W.N.W. of Gokwe, Southern Rhodesia.

Age and Horizon: E.1., ~~probably Escarpment grit~~ Pebbly Arkose; early part of upper Triassic.
G.2 + G.3 Upper Karroo, ~~probably~~ Pebbly Arkose, Upper Triassic.

Type specimen G.3. Paratypes E1, G2.

Diagnosis.

Secondary wood homoxylic, pycnoxylic, growth rings wide with very narrow well marked zones of late wood. Tracheids averaging 4·12 mm. long. Pitting on radial walls of all tracheids, uni- and biseriate, Araucarian pits present on tangential walls of late wood tracheids. Rays uniseriate, 1 - 17 cells high, mean value 4·3, ray cells thin walled, unpitted. Tracheids bear 2 - 10 half-bordered pits per crossfield - these are circular with an oblique elliptical pore. Wood contains spirally arranged complexes of leaf and shoot traces. Large branches when present ± whorled. Pits in young wood, (if present) small, unicseriate widely spaced.

Description:

Of the three specimens assigned to this species, two (G2, G3) show clearly a close spiral arrangement of groups of two or three small pits on the decorticated surface (Plate VIII C + D and Plate IX A, B).

Specimen G2 is 9 cm. long, and is from a tree trunk 9·5 cm. in diameter. In transverse section, the specimen is a little less than a semi-circle, but it appears to contain some of the pith. The scars on the surface are mostly double, or sometimes triple pits, but occasionally solitary larger scars (2 mm. in diameter) can be seen. Groups of pits are between 8 mm. and 10 mm. apart.

Specimen G 3 is only 4·5 cm. in diameter at the top, and 5·3 cm in diameter at the morphologically lower end. Triple, or more usually, double scars are abundant on the surface, but they are smaller and more closely spaced than those of the previous specimen. The spiral arrangement is equally clear, but the groups of scars are only 4 cm. or 4·5 mm. apart. In addition to these scars, the specimen bears the bases of five substantial branches, each being elliptical and measuring some 16 mm. x 24 mm. (Plate VIII, Plate IX A, B). As can be seen, these have a whorled, or at least a greatly compressed spiral arrangement.

Specimen B 1 is a piece of secondary wood measuring 5 cm. vertically, 6·5 cm. tangentially and a maximum of 4 cm. radially. No scars were visible on the external surface of the specimen, but these were clearly seen in the tangential sections. In this case, they are single or double traces. The spiral arrangement is quite clear, but the spacing is three times as great as in specimen G.2. (Horizontal

measurement between scars = 1 cm. in G.2. and 3 cm. in B.1.). From this we can calculate, (assuming an equal increase in circumference) that specimen B.1. came from a trunk which was, at this point, some 90 - 100 cm. in circumference and which, therefore, had a diameter of about 30 cm.

Transverse sections.

From a transverse section cut near the top of the specimen G.3, the pith was found to be oval in shape, measuring 1·0 mm. x 1.5mm. Six, or possibly seven growth rings were counted, these being 3 - 4 mm apart. At the base of the specimen the pith was 8 mm. in diameter. There appeared to be about a dozen primary xylem groups, but the preservation was too poor to be certain of this. Unfortunately, owing to the fragmentary nature of the rock, a complete transverse section of specimen G.3. could not be obtained. In a piece measuring 2 cm. radially, eleven quite definite growth rings were counted. They were mostly 2 - 3 mm. apart, but at one point, five quite clear continuous rings were counted within a space of 1·5 mm ! The growth rings in specimen B.1. were 2 - 3 mm. apart.

When the sections were examined microscopically, the preservation was found to be generally poor, except for scattered patches of well preserved cells. Sections from all three specimens showed the same features. The wood is very uniform in structure. The tracheids are hexagonal or rectangular in T.S. and are arranged in orderly radial files. Their walls are between 3μ and 4μ thick. Most of the cells are

isodiametric, measuring between 8μ and 40μ across. The growth rings are marked by a double row of cells, each of which measures 5μ - 10μ radially, and up to 40μ tangentially (Plate IX C, Text fig. 6 A). The rays are separated by 2 - 6 files of tracheids. No resin canals or xylem parenchyma cells were seen.

Tangential Sections.

From specimens B.1. and G.3, complete contiguous series of tangential longitudinal sections were obtained. From specimen G.2, the sections were taken from different parts of neighbouring segments of the stem in two groups, which overlapped to give a complete radial series. All the sections showed a diamond shaped pattern of transversely cut vascular bundles, as might be expected from the spirally arranged scars on the surface of the specimen. These traces were clearly visible to the unaided eye and their behaviour has been followed in some detail. All the traces arise as single concentric vascular bundles, not later than the end of the first year's growth. (G.3 T.L.S, No. 11, 10). These continue as such for some distance (G.2 T.L.S. No. 10, 8 and G.3. T.L.S. No. 9, 7). At this point, definite signs of multiple structure begin to appear (G.2. T.L.S. No. 7, 6 and G.3. T.L.S. No. 6, 5) and some of the bundles are noticeably larger than their neighbours. In G.2. T.L.S. No. 5, 4 and in G.3. T.L.S. No. 4, 3, 2, quite definite groups of two or three separate bundles can be seen, which mostly continue to the exterior unchanged, where their decay results in the formation of the characteristic pattern of scars. (Three stages in the development

of a "triple trace" are shown in Text figs. 6 C - E). In wood which is more than about 8 - 10 growth rings from the pith, still further developments may take place. (G.2. T.L.S. Nos 4 to 1). One of a group of traces may suddenly increase in size (up to 2 mm. in diameter). Its companion(s) may continue without change alongside. Sometimes they appear to peter out, or become absorbed into or obliterated by the largest bundle. Thus in the tangential sections of specimen B.1., most of the traces are single structures and are about 2 mm. in diameter.

Microscopically, the tangential sections were equally rewarding, although the patchiness of the preservation made it very difficult to find parts of sections showing important characters in the detail desired.

As can be seen in Plate IX D and Text fig. 6.B, the rays are uniseriate. They range in height from 1 - 17 cells, the average height in each of the specimens being for B.1., 4·437; for G.2, 4·106; and for G.3., 4·125 (See Appendix, page 165). The ray cells are extremely thin walled (1 - 1·5μ) and are very difficult to pick out where they are in contact with the tracheids. I have again found both tracheidal and crossfield pits in vertical section. Plate X F shows a vertical series of five of these crossfield pits. Plate X G shows only two pits, but the extreme thinness of the ray cell wall is well shown. In section, the mouth of the pit is 6μ or 7μ across. It very soon narrows to about 2μ. This width is maintained for 2μ, then the walls of the pore curve outwards to the inner mouth of the pore which is 3μ or 4μ across. Sometimes this last section of the pore seems to have been widened by decay, and this is shown in Text fig. 5 C. The wall of the ray cell is not perforated.

The tracheidal pit of the radial walls which are cut in section are not very well preserved (Text fig. 5 D), but they are probably identical in structure to the pits on the tangential walls of the tracheids, some better preserved examples of which are shown in (Plate X C and Text figs. 5 F, 7b). The plan view of the pits on the tangential walls of the tracheids and the uniseriate pits on their radial walls are identical, although the former are slightly smaller in diameter than the latter.

Radial Longitudinal Sections.

The pitting on the radial walls of the tracheids is generally uniseriate, the pits being contiguous and flattened above and below (Plate X B; Text fig. 5 E). They are large, (16μ in diameter) and the pore is central and circular (3 - 4μ in diameter). Particularly in the larger tracheids of the early wood the pits are often biseriate and alternate. The contiguous faces of the pit are flattened and the diameter of the pits is only 8 - 10μ. The pore is still circular and more or less centrally placed (Plate X D, Text fig. 5 E). In well preserved regions, the limit of the borders of both uniseriate and biseriate pits is marked by a distinct double ring (Plate X A + B). The radial longitudinal sections also show some of the pits on the tangential walls of the tracheids. In the pits shown in Plate X C and in Text fig. 7b there is a projection into the pit chamber from the wall of the tracheid on the left (T'). Careful focussing shows that the projection as seen in a section of the pits is in fact a complete ring of material near the outer rim of the pit chamber. It was at first thought that this might have some connection with the double rim of the pits seen on the

Dadoxylon bondii sp. nov.

Explanation of Text Figures 5. A - G.

Fig. 5.A R.L.S. (X 375.) Ray cells and crossfield pits.

Fig. 5.B R.L.S. (X 1,100.) Detail of crossfield pits.

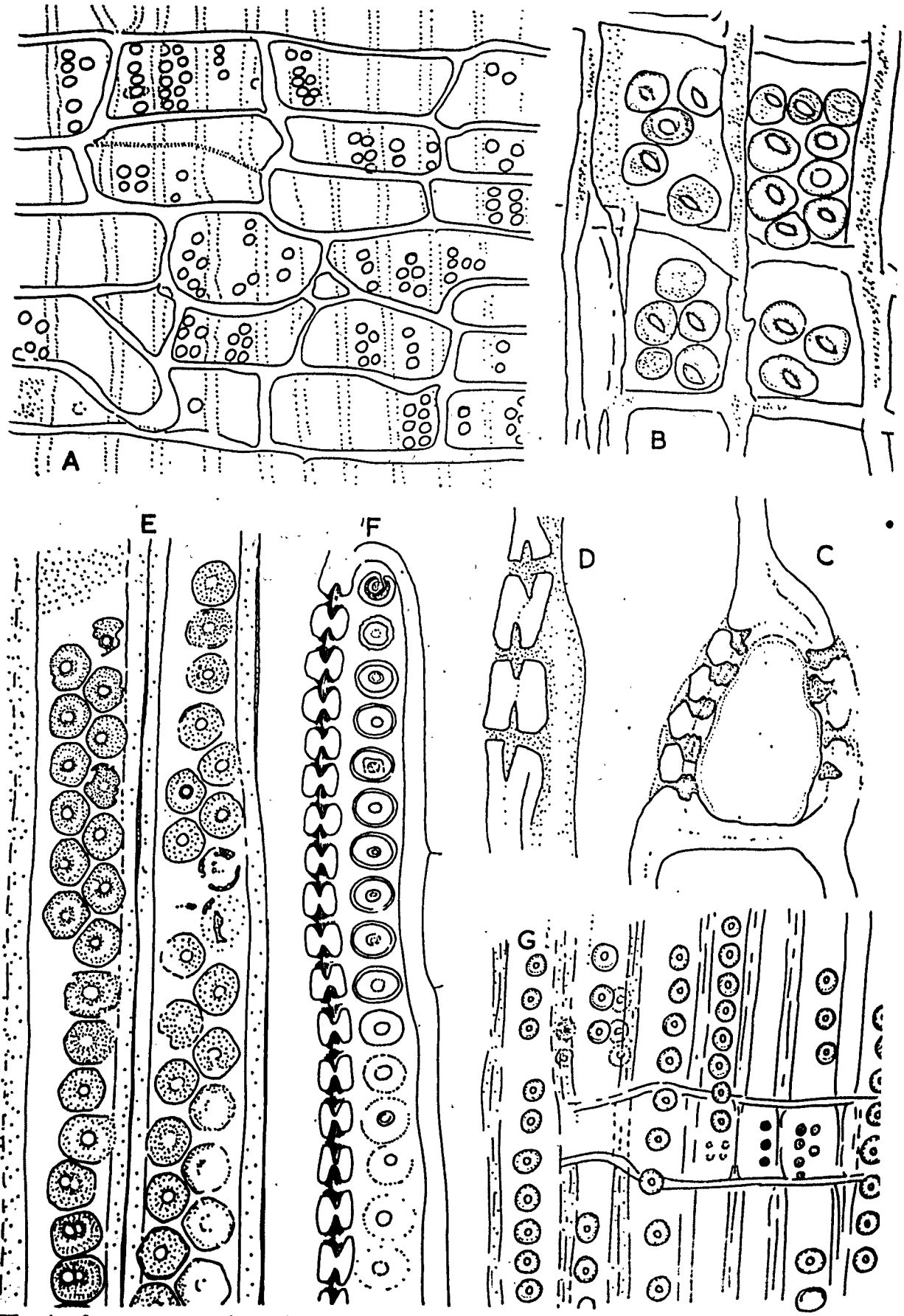
Fig. 5.C T.L.S. (X 1,100.) Vertical section through crossfield pits.

Fig. 5.D R.L.S. (X 1,100.) Vertical section through poorly preserved tracheidal bordered pits.

Fig. 5.E. R.L.S. (X 500.) Biseriate alternating pits, changing to uniseriate pitting.

Fig. 5.F. R.L.S. (X 500.) Uniseriate pitting (Note double rim.) Vertical section through bordered pits on tangential wall of tracheid.

Fig. 5.G. R.L.S. Branch (X 375)



Text fig 5. Dadoxylon bondii sp.nov.

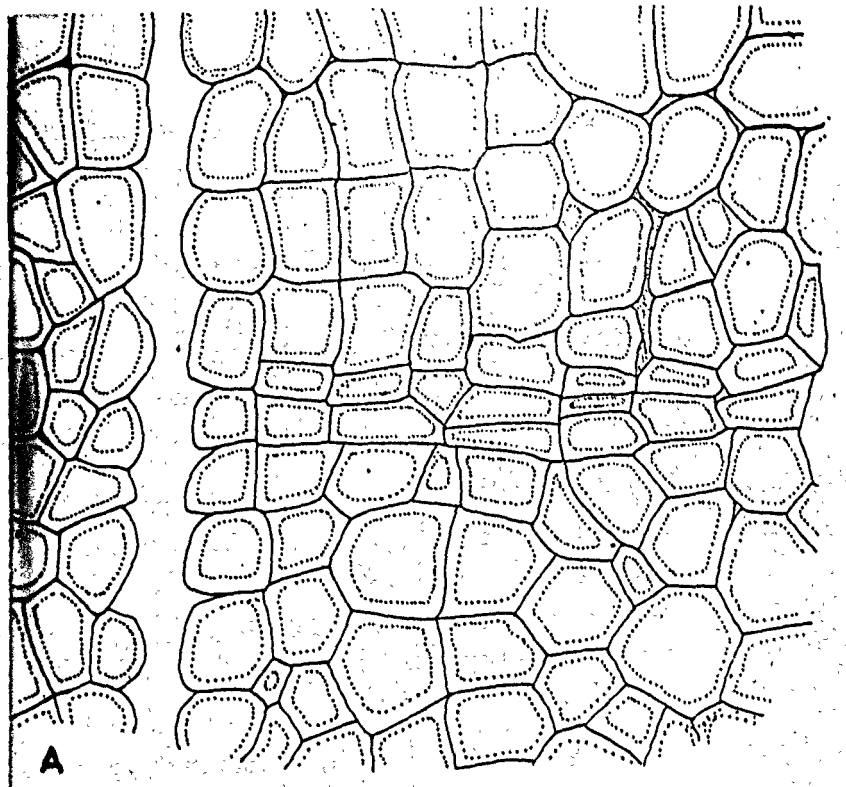
Dadoxylon bondii sp. nov.

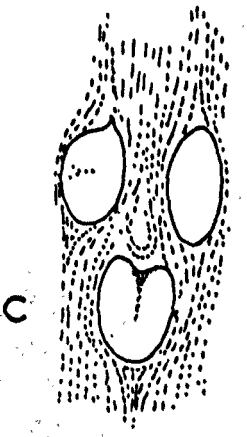
Explanation of Text Figures 6 A - E.

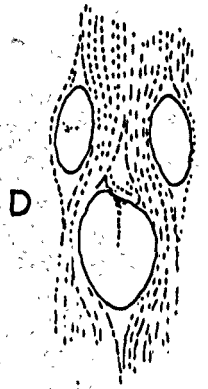
Fig. 6.A. T.S. (X 375.) through narrow zone of late wood.

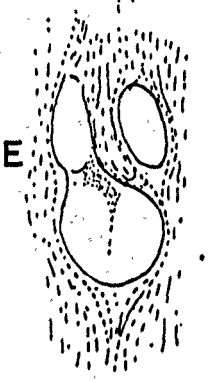
Fig. 6.B. T.L.S. (X 375.) Uniseriate rays and tracheid ends.

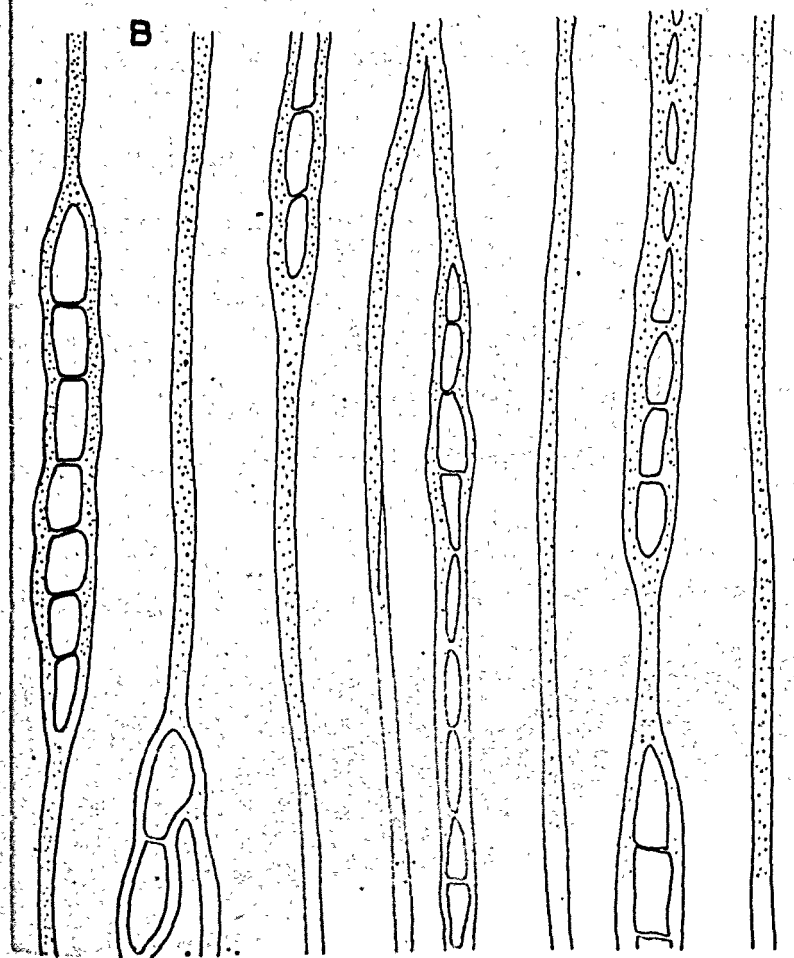
Fig. 6.C, D & E. Three stages in the fusion of members of a multiple leaf trace (X 50.)











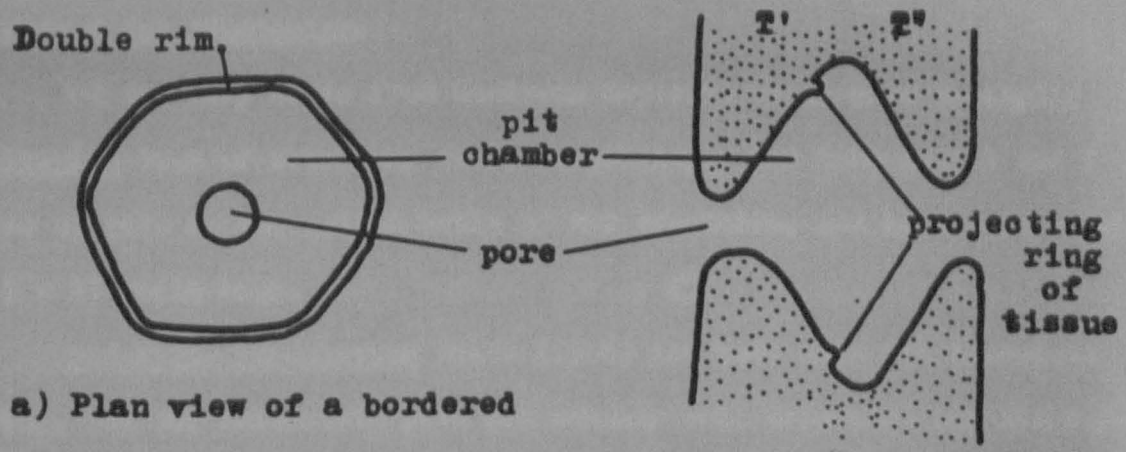
Text fig. 6. Dadoxylon bondii sp.nov.

radial walls of the tracheids, but the specimens are too poorly preserved to give further information. Also it should be noted that many recent Gymnosperms show a double rim to the border of their pits as seen in plan view, but they do not possess a ring of tissue in the pit chamber as shown in Plate X C (Phillips, 1948; Greguss, 1955; Harris; personal communication).

In this fossil the pits seen in sectional view do not appear to have a middle lamella and torus. In view of this it seems more likely that the ring of tissue is nothing more than the remains of the middle lamella which is displaced and largely decayed (Text.fig. 7 B). As shown in Plate X D, the ray cells are fairly short (60μ - 120μ radially) and tall (20μ to 40μ vertically). The walls are thin and no pits are present on the tangential or horizontal walls. The cross field pits (Plate X E, Text fig. 5 A, B) are elliptical or circular, with a clearly elliptical pore. The pore is oblique in the late wood, but almost horizontal in the earlier wood. The borders are 8μ or 10μ in diameter, and the pores measure approximately 3 - 3·5μ x 6 - 7μ. There are from 2 - 10 pits in the field.

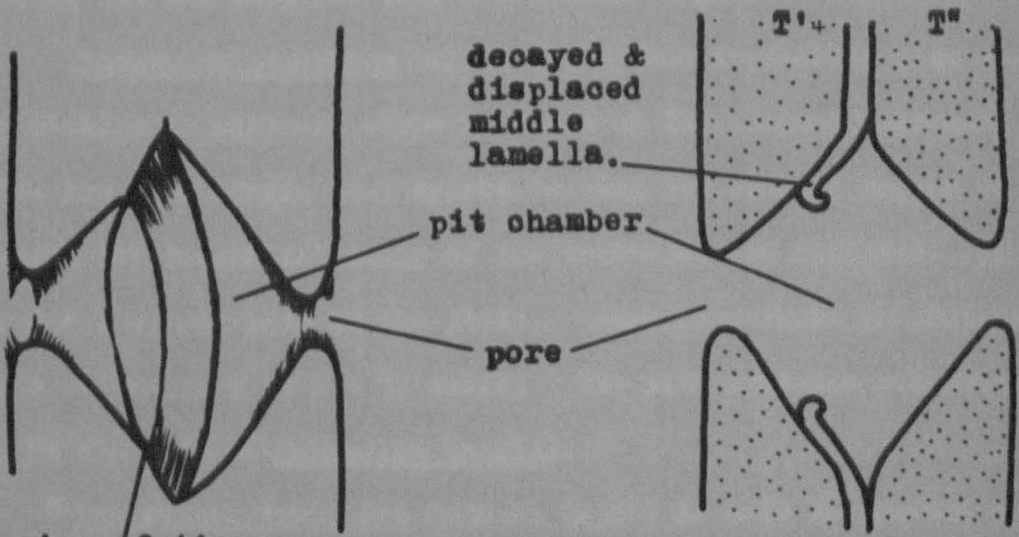
The young tissues of the branches of G.3. are in a slightly better state of preservation than are those of the main axis, but unfortunately, the actual primary wood and the pith are not preserved. The bordered pits on the tracheids of the branch are only 6μ - 7μ in diameter. They are circular uniseriate and mostly spaced between 4μ and 15μ apart. Sometimes they are as little as 1·5μ apart. (Text fig.5 C) The crossfield pits are very small (3μ in diameter) with a circular border and a broadly elliptical pore.

Dadoxylon bondii



a) Plan view of a bordered pit in the radial wall of a tracheid.

b) Section through a pit in tangential wall of tracheid



c) Diagram to show three - dimensional appearance of bordered pit seen obliquely

d)Diagram showing possible cause of projecting ring of material.

Fig.7. Diagrams to show the appearance of the bordered pits in plan view and in section(figs.a-c) and to explain the probable origin of the ring of material projecting into the pit chamber, (fig. d).

Comparison and Discussion.

Of the many woods from Gondwana deposits which have basically a Dadoxylon type of secondary wood, surprisingly few have only 1 and 2 series of pits on the radial walls of the tracheids, and have rays which are 1 - 17 cells high.

Dadoxylon murgularium White (1938) has both uni- and biseriate pitting, but the uniseriate pits are usually well separated and the rays may be biseriate and up to 30 cells high.

Dadoxylon indicum Holden (1917) has uni- and biseriate araucarian pitting, but the rays are only 2 - 7 cells high.

Dadoxylon scleronum Walton (1925) has tracheidal pits which are very similar in size and shape to those of the present specimen, and Walton has seen single leaf traces leaving the central region of the stem. However, the tangential walls of the tracheids are unpitted. There are only 1 - 4 simple pits in the field. Wound parenchyma is present, and the height of the rays is 1 - 35 cells. The pith contains scleroids (not seen in the pith of Dadoxylon kondii).

Kaokoxylon reuningii Krausel (1956) is said to possess uni- and biseriate pitting, and the uniseriate rays are 1 - 20 cells high. The pith again contains scleroids (Note Krausel includes Dadoxylon scleronum Walton, in Kaokoxylon) but Krausel's illustrations are too poor for any detailed comparison to be made.

Lobatoxylon Kaokense Krausel (1956) has tracheidal pits in one or two rows in the araucarian fashion. The rays are 1 - 15 cells high sometimes more. The crossfield pits are oval, but the number per field

is not given. (Note Krausel (1956) includes Dadoxylon pedroi Meiller in this new genus, which is based on the structure of the pith and primary tissues which are not preserved in Dadoxylon bondii).

Dadoxylon pedoi itself has pits in one or two rows, but the rays are often more than 50 cells high. Few of these species compare closely with Dadoxylon bondii and with those that appear as though they might be similar in structure, a detailed comparison is rendered impossible by a lack of adequate illustrations. In none of the above specimens has the arrangement, detailed structure and behaviour of leaf traces been described. These facts are, I think, sufficient to justify the erection of yet another new species of Dadoxylon. I therefore propose to name the species Dadoxylon bondii after Professor G. Bond of the Department of Geology, the University College of Rhodesia and Nyasaland, Salisbury, who sent the specimens to Bangor for investigation, and who has contributed greatly to our knowledge of the stratigraphical succession in Rhodesia.

The small size of the majority of the scars seen in sections from the various specimens of Dadoxylon bondii suggests that they are leaf traces. Persistent leaf traces of this nature are present in the Recent Araucarineae and are believed to be characteristic of this family (Thomson 1913; Seward 1919; Phillips 1948).

In Araucaria, however, the leaf trace leaves the secondary xylem and passes upwards through the phloem almost parallel to the surface, as a single bundle. It branches into three in the outer cortex. The median trace remains single, but the outer pair branch several times,

so that each has given rise to seven traces by the time they enter the base of the leaf (personal investigation).

In Agathis, the leaf trace leaves the perimedullary region as a double strand (Thomson 1913). Thus it seems that bifurcation or the splitting into three of the leaf trace is a common occurrence in the Araucarineae. In Dadoxylon bondii the splitting is irregular so that both double and triple bundles are found, though both arise as single structures.

It is possible that the larger traces which I have described in the older wood of Dadoxylon bondii have arisen because one of the group of bundles is supplying a bud (in the axil of the leaf) which has developed after a period of dormancy. This would necessitate an increase in the amount of vascular tissue supplying the bud, with the result seen in the tangential sections.

This mode of origin is clearly different from that of the main lateral branches in specimen 0.3. These have a large pith which is continuous with that of the main axis, and must have started to grow during the first year's growth of the axis.

The Genus Mesembrioxylon Seward 1919.

This genus was erected by Seward (1919, pages 173 and 203-212) to include fossil gymnospermous woods which combine features found in several recent genera, without implying that there was any relationship between the fossils and the genera of recent conifers.

In particular, Seward intended his new genus to replace the genera Podocarpoxylon Gothan, and Phyllocladoxylon Gothan, which not only imply a relationship with recent genera, but are, in practice, virtually indistinguishable.

The diagnosis given by Seward (1919) for Mesembrioxylon is very similar to that of Cupressinoxylon Goeppert. In both, the rays are usually uniseriate and pits are confined to the radial walls. The crossfield pitting in the summer wood is indistinguishable in these genera, and in the spring wood the pitting only differs in that the pores are oblique or vertical in Mesembrioxylon and horizontal in Cupressinoxylon. In both genera there may be several small pits in the field, or one or two large ones.

In Mesembrioxylon, xylem parenchyma is said to be present and scattered, but not so characteristic a feature as in Cupressinoxylon.

There are a number of other genera which are very similar to Mesembrioxylon.

Paracedroxylon Hinnot seems to be so similar that there can be little justification for maintaining it as a separate genus. The difference between them is the occasional presence of pitting on the horizontal and tangential walls of the ray cells in wounded regions,

and the restriction of vertical parenchyma to the same area. Seward (1919) states that the normal wood agrees most closely with Cupressinoxylon and Mesembrioxylon.

Some species of Cedroxylon Kraus, may have contiguous, flattened tracheidal pits, tracheids in the rays and resin canals confined to wounded regions. Xylem parenchyma, if present, is found only in late summer wood.

More recently, Kräusel (1949) has established a new genus, Circoporoxylon Kräusel, for secondary woods with simple, circular crossfield pits which are otherwise identical to Phyllocladoxylon or Podocarpoxylon (= Mesembrioxylon Sew). Kräusel has now placed a number of the species described by Seward (1919) under Mesembrioxylon, in his own genus Circoporoxylon.

When specimens possess bordered crossfield pits, it would seem to be correct to use the genus Mesembrioxylon, but considerable difficulty arises when the crossfield pits are badly affected by decay, when bordered pits may appear to be simple.

The genus Mesembrioxylon is of wide geographical distribution. The name means "Southern Wood", and many species have been described from the Antarctic, Australia (Seward, 1919) and India (Bhardwaj, 1953; Ramanujam, 1954; Sah, 1959). However, several species have been described also from the northern hemisphere, e.g. from Greenland, Poland, Austria and from Yorkshire and Bedfordshire in England (Seward, 1919).

The majority of the species are of Jurassic age, although Mesembrioxylon antarcticum Gothan and Mesembrioxylon müllori (Seward,1919)

are both of Tertiary age, and the species described in this Thesis (Mesembrioxylon gwavense) is from deposits of Upper Triassic age.

Mesembrioxylon gwavense sp.nov.

Plates IV C + D; V A - D; VI A - D; VII A - D; VIII A + B and Text figures 6 A - F.

Locality: Headwaters of Gwavo River, 20 miles W.N.W. of Gokwe, Southern Rhodesia.

Age and Horizon: Upper Karroo. Probably Pebbly Arkose. Upper Triassic.

Type Specimen: G.l.

Diagnosis.

Secondary wood homoxylic, pycnoxylic, late wood very difficult to detect, growth rings wide. Pits on radial walls of tracheids only; large, circular, uniseriate arrangement. Pits have characteristic "double wine glass" shape when viewed in section. Crossfield pits large, circular or oval, 2 - 4 per crossfield, border narrow. When seen in section, tracheidal portion of pit is as described for normal pits. Rays uniseriate, 1 - 23 cells high, mean value. Sparse vertical resin parenchyma. Wood surface shows large, circular scars - often accompanied by leaf traces.

Description.

Specimen G.l. is a magnificent piece of silicified tree trunk, 6 - 8 cm. in diameter and 12 - 14 cm long (Plate IV, C, D). The external appearance is quite striking as the whole surface is covered with closely spaced more or less circular scars, which are from 3 - 8 mm. in diameter.

These scars are spirally arranged and the distance between neighbouring scars is 3 - 10 mm. The polished surface of a transverse cut gave the impression that the specimen was very well preserved, and twelve growth rings, varying between 1·5 and 5·0 mm in width, were counted. On examination of a ground section under the microscope, the wood was found to be of very uniform structure. The limits of the growth rings were very difficult to pick out, as there is a gradual reduction in size of the tracheids from early to late wood. However, the transition from late wood to the following early wood is quite abrupt (Plate V A, C). Plate V D shows a double growth ring which was associated with a wound. This had been covered with callus and then overgrown by the succeeding years growth. The tracheids are thick-walled (about 8 - 12μ) and measure between 16μ and 32μ in diameter, the average size being about 20μ. The outline of all the cells was indistinct as evidently most of the organic material had been completely replaced by the invading minerals. This was borne out by an examination of the longitudinal sections.

The pith (4 - 5 mm in diameter) had mostly decayed before fossilization was complete, and the cavity was filled with extraneous material. Unfortunately, the remaining pith cells and the surrounding primary tissues have lost all signs of their original structure.

In tangential section, although the ray cells were quite well preserved, the walls of the tracheids were very indistinct (except where they were in contact with the rays) (Plate V D). The rays were uniseriate or very rarely partly biseriate, and ranged in height from 1 - 25 cells. However, only 3·5% of the rays were above 11 cells high (See Appendix, p.268.

The tangential sections also showed the tissues leading from the circular scars (Plate VI A + B). Typically there was a central pith region - 1 mm in diameter, then a narrow band of tracheids which had been cut transversely. These were surrounded by a band (1 - 1·5 mm across) of tracheids which were arranged radially about the centre of the pith cavity. They were interspersed with uniseriate rays 1 - 10 cells high (Plate VI B). It is evident that some of these tissues - particularly the pith and the outer band of tracheids, had decayed before silicification took place.

This arrangement of tissues is quite common in leaf traces and in short shoots and branches of many recent conifers; but compared with those I have examined (Abies alba, Araucaria araucana, Ginkgo biloba, Larix europaea, Picea sitchensis, Taxus baccata), the amount of tracheidal tissue cut transversely is rather small.

The size and shape of the scars on the outer surface of the specimen suggests more strongly that they are branch or short shoot scars, rather than leaf scars. This is supported by the fact that smaller traces - 0·1 mm - 0·5 mm in diameter - but of the same basic plan, are often found in close proximity to the larger ones. It is possible that these led to the leaves or scale leaves which subtended the buds giving rise to the branches. Sometimes fusion of these traces occurs. A number of large circular traces has been seen which contain two quite distinct bundles of vascular tissue (Plate VI A). I am as yet unable to suggest an explanation for this, although it should be noted that Ladell (1962) has described the occurrence of a leaf scale trace in Corsican pine,

which tends to fuse gradually with the leaf trace. Hill (1906) suggests that structures analogous to the parichnos of the Lepidodendraceae occur in some modern plants, but in this case the structure is parenchymatous rather than woody.

In spite of the poor preservation, some information has been obtained about the crossfield pits. In section (Plate VIII A, Text fig. 8 C) the tracheidal portion is quite clearly half bordered. The mouth of the pit is about 3μ in diameter, but there is a narrow waist about half that size, just before the wide opening of the lumen of the border, which is some 8μ in diameter. Unfortunately, I have not been able to make out the form of the pitting in the wall of the ray cell itself - or indeed to decide whether or not it is pitted at all. Pits have been seen which appear to be in the tangential walls of the tracheids (Plate VII A). From the same section (Plate VII D and Text fig. 8 B) it can be seen that the tracheid walls are very thick (12μ) and are pierced by bordered pits with a most characteristic shape. This might be described as like a pair of short stemmed wine glasses placed base to base! This is similar to the description already given for the half bordered pits in the crossfield, but in this case, the "vestibule" of the pit is at first some 6 or 7 μ in diameter. This narrows to a waist only 3 or 4 μ in diameter, and then expands to the full diameter of the border - some 11 or 12 μ. This is repeated (in mirror image) for the other half of the pit. The lumen of the border is about 4μ across. Neither middle lamella nor torus were seen, but their absence is unlikely to have been an original feature.

In the radial sections, most of the tracheids were so poorly

preserved that the relatively well preserved rays appeared to be "floating in space" (Plate VI D). The crossfield pits were easily picked out, there being 2, 3 or sometimes 4 large circular or oval pits (6 - 8μ in diameter) in each crossfield. They were mostly badly decayed and borders were rarely visible (Plate VII C, Text fig. 8 A). The horizontal and end walls of the ray cells did not appear to be pitted.

The pits on the radial walls of the tracheids are quite large (12μ in diameter) (Plate VII, A, B). They are circular or slightly flattened above and below, and are always uniseriate. They are normally spaced 1·5μ - 2μ apart. The pore is circular in outline and sometimes consists of two concentric rings. These are, no doubt, the wide mouth and the narrow waist of the pore which were seen in the tangential sections. In the late wood, the pore may be slit shaped and oblique (Text fig.8 E) and in this same region, large parenchyma cells with dark contents have been seen (Plate VIII B and Text fig. 8 E). These cells are very rare, and it is uncertain whether or not they are restricted to the late wood. No rims of Sanio were seen, but the preservation is so poor that their absence cannot be taken as a character of the living plant.

Comparison and Discussion.

The absence of well preserved primary tissues of Araucarian pitting from the tracheids, and of Abietineous pitting from the ray cells, together with the presence of vertical rows of parenchyma amongst the tracheids suggests that the specimen under discussion should be included in either Cupressinoxylon Goeppert (1850), or in Mesembrioxylon Seward (1919).

The latter would seem to be the more appropriate, as this Rhodesian specimen has only sparse xylem parenchyma, which is characteristically abundant in Cupressinoxylon. Apart from this, there appears to be little difference between these genera, and as we have no well preserved primary tissues, Mesembrioxylon is to be preferred as it does not suggest any close affinity with recent genera.

Paracedroxylon Sinnot (1909) is a genus which differs from Mesembrioxylon only in the presence of pits on the horizontal and tangential walls of the ray cells, in regions affected by wounding. How one differentiates between an unwounded specimen of Paracedroxylon and a species of Mesembrioxylon is not at all clear!

Cedroxylon Kraus is stated to differ from Cupressinoxylon in the scarcity or absence of vertical resin parenchyma from the wood, and in this feature it is similar to the present specimen. However, in Cedroxylon all the walls of the ray cells are pitted in the abietineous manner.

In the general structure of the wood, there is a number of species of Mesembrioxylon which show some similarity to Mesembrioxylon gwavense. Mesembrioxylon speciosum Ramanujam (1954) has uniseriate rays up to 18 cells high. The pits on the radial walls of the tracheids are similar in size and shape, but they are often contiguous. Double rows of opposite pits are quite common, and well defined bars of Sanio are present.

Coniferocaulon latisulcatum Sah (1959) would have been included in Mesembrioxylon if pith and primary tissues were not well preserved. It differs from Mesembrioxylon gwavense only in having shorter rays

(1 - 8 cells) and only 1 - 2 circular crossfield pits which have an oblique elliptical pore. Bhardwaj (1953) described a new species, Mesembrioxylon indicum, of Jurassic age from the Rajmahal Hills, Bihar. This wood differs in having widely spaced pits on the radial walls of the tracheids. The crossfield pits are large and there is only one per crossfield. The rays are only 1 - 5 cells high.

No previous description of any species of Mesembrioxylon contains a detailed account of the tracheidal and crossfield pits as seen in section. No species (to my knowledge) possess closely placed branches or short shoots as described here. Indeed, considering this last feature, Mesembrioxylon gwavense is more similar to Araucariopitys Jeffrey (1907) and Woodworthia Jeffrey (1910). Araucariopitys is of Middle Cretaceous age, and is described as showing the scars of short shoots on its decorticated surface. The wood structure shows a mixture of both Abietineous and Araucarian features. The tracheidal pits are often contiguous and flattened, but the pitting of the ray cells is abietineous. Vertical resin canals occur in wounded tissue, although not in normal regions. The short shoots, as shown in tangential section of the stem, are said to be accompanied by the trace of a subtending leaf. The main differences between this genus and Mesembrioxylon gwavense are 1) the Abietineous pitting of ray cells, 2) the presence of resin canals, 3) the predominance of Araucarian pitting on tracheids, 4) the occurrence of both alternate and opposite biseriate pitting.

Woodworthia (from the Triassic of Arizona) is of approximately the same age as Mesembrioxylon gwavense and also shows scars on the surface,

as in Araucarioxylon. The traces of these shoots sometimes branch deep in the wood (cf. Mesembrioxylon gwavense double trace, Plate VI A) a feature which Seward (1919) states has been recorded in Ginkgo. (Unfortunately, I have only been able to examine young wood of Ginkgo and the recent conifers mentioned previously (Page) and this feature was not seen). The sheet trace in Woodworthia was also accompanied by a leaf trace. As in Mesembrioxylon gwavense, the rays of Woodworthia arizonica Jeffrey (1910) are uniseriate (only 1 - 9 cells deep), and the ray cells are pitted only on the radial walls. Also the growth rings are not well defined and there are no resin canals. Thus it can be seen that these two species are very similar; in fact, they appear to differ only in the arrangement of the pitting on the radial walls of the tracheids, which is typically Araucarian in Woodworthia arizonica, but more or less separated and always uniseriate in Mesembrioxylon gwavense. Mesembrioxylon gwavense may be said to have certain Araucarian features, namely the slight flattening above and below of some of the tracheidal pits; the absence of abietinoous pitting from the ray cells, the absence of bars of Sanio (if this is an original feature) and the presence of persistent leaf traces, a feature which Lignier (see Seward, 1919, page 143) thought was of diagnostic importance.

Considering the great mixture of Araucarian and Abietineous characters which occur in many specimens of Permo-Carboniferous and Triassic Gondwanaland woods (Kräusel and Range 1920; Grambast 1952, 1954; and in this Thesis) I must confess that I am uncertain whether the feebly-developed Araucarian features of the present specimen, and its possession

of branch or shoot traces in the wood, are sufficient to merit its inclusion in Woodworthia; or, merely indicate that a relationship may exist between some members of Mesembrioxylon and Woodworthia. It must be remembered that Mesembrioxylon is an artificial genus, containing only secondary woods, many of which are probably not related at all.

Monsembrioxylon gwevanne sp. nov.

Explanation of Text Figures 8. A - F.

Fig. 8.A. R.L.S. (X 375.) Ray cells and crossfield pits.

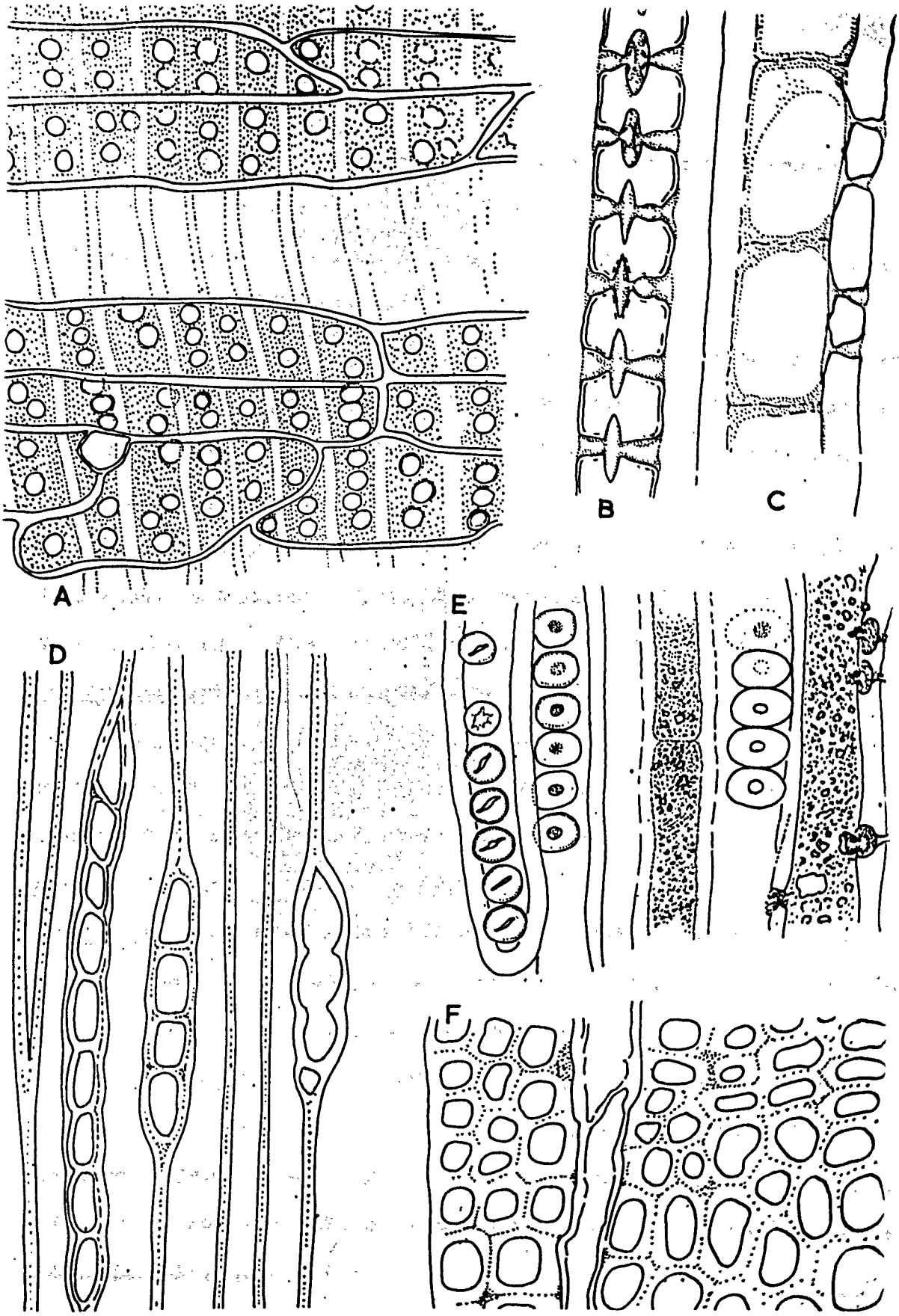
Fig. 8.B. Tracheidal pits in vertical section, showing "double wine-glass" shape of pores and borders (X 1,100.)

Fig. 8.C. T.L.S. vertical section through crossfield pits (X 1,100.)

Fig. 8.D. T.L.S. Uniseriate rays and tracheid ends (X 375.)

Fig. 8.E. R.L.S. Showing pits with slit shaped and circular pores. (X 500.).

Fig. 8.F. T.S. through ill-defined growth ring. (X 375.)



Text fig. 8. Mesembrioxylon gwavense sp.nov.

The Genus Helicoxylon Gen. nov.

In 1848, Hartig published a description of a specimen of fossil wood from the Brown-coal deposits of Germany. The tracheids bore uniseriate bordered pits and helicoid thickenings. He did not illustrate his rather brief description.

This would appear to be a valid publication, as article 36 of the International Code of Botanical Nomenclature, requiring an adequate description with illustrations only applies to species and taxa of lower rank published after 1912.

Presumably unaware of Hartig's paper, Walton (1925) described from South West Africa a specimen of secondary wood with helicoid thickenings, but with araucaroid pitting on the tracheids, as Spiroxylon africanum sp. et gen. nov.

Subsequently Krŭsel (in Krŭsel and Range, 1926) also working on South West African woods, erected a new genus Taxopitys to include wood which he thought was identical with Walton's, but which had well preserved primary tissues. Krŭsel also pointed out that the genus Spiroxylon should not be used for Walton's specimen as the name had already been used by Hartig. He did not, however, propose a new name for Walton's genus, although he did state that the specimen could not be included in Taxopitys, because no primary tissues were preserved.

I therefore propose the name Helicoxylon for woods having tertiary helicoid thickenings and araucarian pitting on the tracheids, but which do not have well preserved primary tissues. It will include ~~Spiroxylon africanum~~ Walton, 1925, a new species Helicoxylon waltonii

to be described below, and probably the Dadoxylon sp. from the Ecca of Natal described by Arber in 1910 (Walton, 1925).

According to Kräusel (1961), Shilkina (1960), has described a wood of carboniferous age from Eastern Siberia as Taxopitys sp. Kräusel comments that this specimen has no primary tissues, so that although it is otherwise similar to Taxopitys, it cannot be included in this genus. Although I have not read Shilkina's paper, it seems likely that his species could also be included in Helicoxylon.

Helicoxylon gen. nov.

Type species of the genus: Helicoxylon africanum (Walton, 1925)

Synonym: Spiroxylon africanum, Walton, 1925

Generic diagnosis:

Gymnospermous secondary wood without primary tissues. Homoxylic, no resin cells or canals. Growth zones visible macroscopically, wide, not easily seen microscopically. Tracheids thick walled with uni- or bi-seriate Araucarian pitting on radial walls, sometimes also present on the tangential walls. Tracheid walls additionally with 1 or 2 low pitched helical bands of tertiary thickening. 2 or more small crossfield pits, horizontal and tangential walls of ray cells not pitted. Rays mostly uniseriate.

Helicoxylon africanum (Walton, 1925) Comb. nov.

Plate II fig. 12, Plate III fig. 15 & 16 in Walton (1925).

Specific diagnosis:

Rays uni- or sometimes bi-seriate, 1 - 9 cells high, with 2 - 8 crossfield pits. Tracheids with 1 or 2 seriate Araucarian pits on radial walls, none on the tangential walls, and with a single or rarely double helix of tertiary thickening always passing between the pit borders.

Heliocoxylon waltonii sp. nov.

Plate XI, Plate XII. Text figure 9, A - H.

Locality: South West Africa (precise locality unknown).

Age and Horizon: Karroo deposits, horizon unknown.

Type Specimen: A 4.

Specific diagnosis.

Rays uniseriate, 1 - 37 cells high, mean height 8·04, 2 - 3 pits per crossfield. Average tracheid length 3·3 mm. Tracheids with 1 or 2 seriate Araucarian pitting on radial walls, and sometimes small 1-seriate bordered pits on tangential walls. In section, pits similar to most recent conifers.

Tracheid walls thick, bearing shallow double helix of tertiary thickening, which crosses border of tracheidal pits. Rims of Sanio present, but may be obscured by helicoid bands.

Description.

This specimen is a block of silicified wood measuring approximately 11 cm. in height and 8 x 9 cm. in cross section. The specimen is quite clearly part of a segment of the secondary wood of a tree trunk, which at this point measured not less than 20 cm., and possibly as much as 40 cm. in diameter. On the outside surface there is a large knot mark which itself is 6 cm. in diameter.

Owing to the extreme hardness of the specimen, the cutting of

sections proved to be very time consuming. For this reason, only one transverse and two each of the tangential and radial longitudinal sections could be cut. The preparation of a series of tangential longitudinal sections, which is desirable for a detailed investigation, had to be abandoned.

The preservation is on the whole good, and details of the shape of the cells and of tracheidal and crossfield pitting are clearly shown in the photographs on Plates XI and XII and in the Text fig. 9.

The polished transverse surface of the hand specimens appears to show quite clearly defined growth rings, between two and three centimetres apart, but under the microscope these are quite indistinguishable. There are bands of opaque ferrous material in the wood, but these are not continuous, and bear no relationship to growth rings.

The photograph, Plate XI A, shows a region extending over one of the apparent growth rings. Although the average size of the cells at the top and bottom of the photograph is greater than that of those in the central region, there is no sharply marked difference between late and early wood, as in the normal type of growth ring. In transverse section, the tracheids are rectangular or hexagonal, range from 20μ - 48μ in diameter, and are arranged in orderly radial files. The approximate average diameter of the tracheids is 30μ.

In tangential section, the rays are seen to be entirely uniseriate, (Plate XI B, Text fig. 9 G), and range in height from 1 to 37 thin walled cells, which measure approximately 16μ horizontally and 25μ vertically. The mean height of the rays (number of cells) estimated from a random count of

Helicoxylon waltonii sp. nov.

Explanation of Text Figures 9, A - H.

Fig. 9.A. R.L.S. (X 375.) Ray cells, thick walled tracheids and crossfield pits.

Fig. 9.B. R.L.S. (X 1,100.) Members of double helix of tertiary wall thickening crossing the borders of the tracheidal pits.

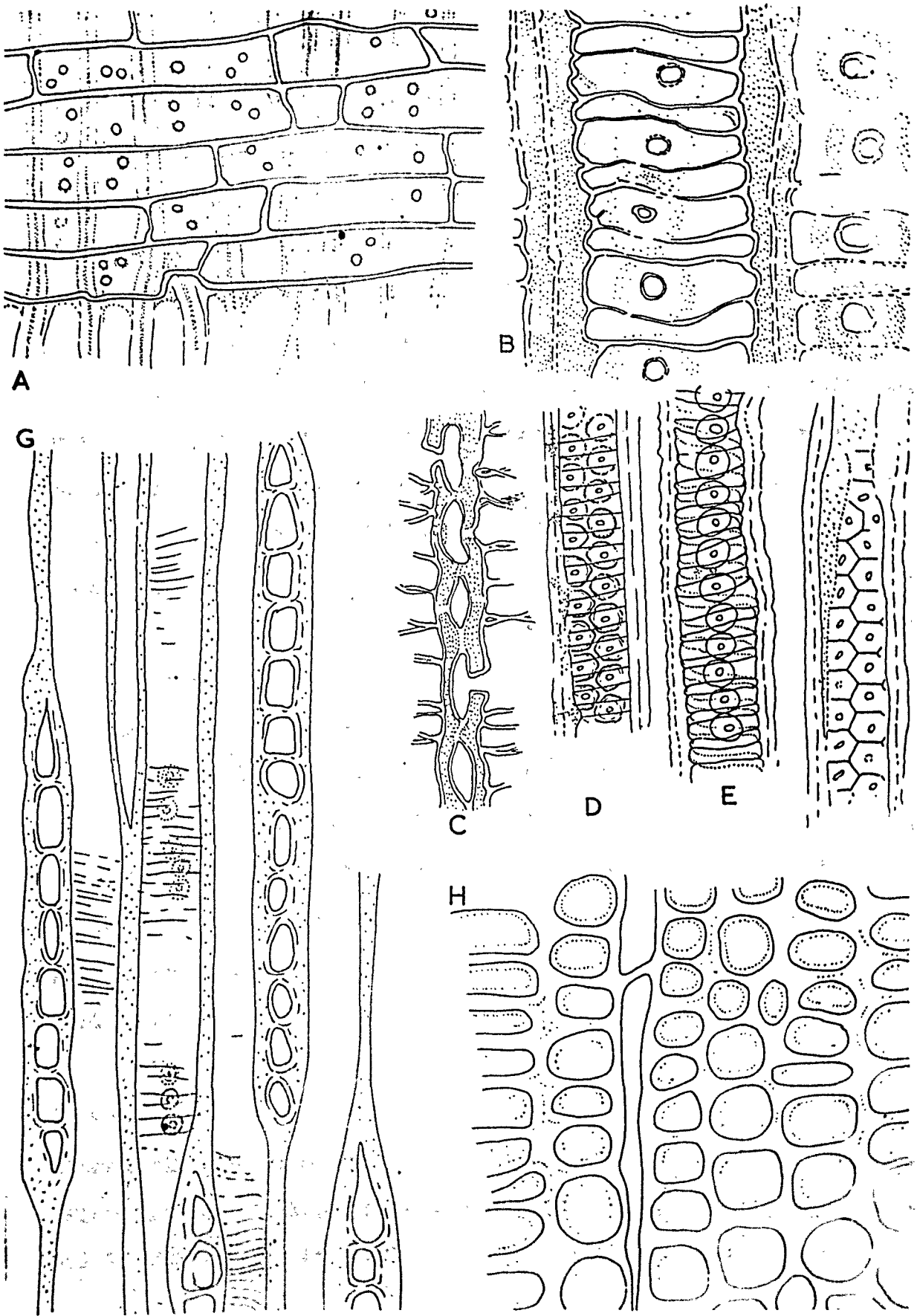
Fig. 9.C. T.L.S. (X 1,100.) Vertical section through bordered pits, also showing relative position of the double helix of tertiary wall thickening.

Fig. 9.D. R.L.S. (X 500.) Biseriate alternating pits and helicoid thickenings.

Fig. 9 E. R.L.S. (X 500.) Uniseriate pits and double helix of wall thickening, and further alternate biseriate pitting.

Fig.9 G. T.L.S. (X 375.) Uniseriate rays and tracheid end walls. Also showing small bordered pits on the tangential wall of one tracheid, and shallow double helices.

Fig. 9 H. T.S. Through region of "growth ring" which could be seen macroscopically. (X 375.)



Text fig. 9. Helicoxylon waltonii sp. nov.

200 rays from each tangential section, was 8·04 cells.

From the same sections, the mean tracheid length was found to be 3·35 mm. (see Appendix on page 261.) A few small bordered pits, between 7μ and 9μ in diameter, were observed on their tangential walls (Text fig.9 G). No pitting was observed on the tangential walls of the ray cells.

In both tangential and radial longitudinal sections, definite, more or less horizontal bands of thickening can be seen on the walls of the tracheids. In the radial sections (Plate XII C, D, E. Text figs. 9 B, D, E) these thickenings can be seen as an associated pair forming a shallow double helix, the members of which usually pass over the borders of the tracheidal pits, one each side of the pore, but not normally touching the actual edge of the pore. Where this does occur, the pores seem to have been enlarged by decay.

The tracheidal pits may be uniseriate or biseriate (Plate XII, A, B. Text fig. D, E). In the former case, the pits are contiguous, flattened above and below to a varying extent, so that their shape varies from circular to oval (Plate XII, C, D). The diameter of the pits is between 10μ and 15μ. The pore is centrally placed, round or oval in shape, and between 2μ and 3·5μ in diameter.

Where the pits are biseriate, they are alternate and hexagonal in shape. In some parts of the section, darker lines can be seen between the borders of the pits, forming a distinct hexagonal pattern. (Plate XII, B). These lines seem to mark the limit of the pit fields and in this respect at least are similar to rims of Sanio. The

pitting on one tracheid may change from the biseriate to the uniseriate arrangement, when the lines are continued and appear as very find rims of Sanio (Plate XII B), a feature which is absent from the recent Araucarinae. This same photograph also shows how the pores of the hexagonal pits can vary from circular to an almost vertical slit.

The helicoid thickenings are arranged in a characteristic manner in those tracheids with biseriate pitting. The members of the double helix always maintain the same position in relation to the borders and pores of the two rows of pits. Thus, one member of the double helix always passes above the pores of the pits on the left of a double row, but below the pores of the pits on the right, whilst the situation is reversed for the other memberof the double helix (Text fig. 9 D). Where the pits are uniseriate, one member of the helix seems always to cross the border above the pore of the pit, whilst the other always passes beneath the pore (Text fig. 9 E).

There are normally two, and rarely three, pits in the crossfield (Text fig. 9 A). The border is circular, and 4μ - 6μ in diameter. The pores are not well preserved, but Plate XI D shows them as being broadly elliptical and oblique.

The ray cells themselves can measure between 30μ and 90μ radially, although 80μ - 85μ is a more usual size. The cell walls are smooth, and only 1μ - 1½μ thick. The tangential walls are not pitted, and it is not certain whether the crossfield pits are present in the ray cell walls, or whether only the tracheids are pitted, as in Araucarineae.

Comparison and Discussion.

The definite helicoid thickenings on the tracheids of the secondary wood and typically araucarian pitting, form a quite distinctive combination of characters which strictly limit the number of fossil woods with which this specimen may be compared. Indeed, as far as I know, a Dadoxylon sp. (described by Arber in 1910), Helicoxylon (Spiroxylon) africanum Walton (1925), and Taxopitys africana Krausel and Range (1928) are the only previously described specimens which combine these features. All three are also from South West Africa. Arber's and Walton's specimens consist only of secondary wood, whereas Krausel's specimen also has the primary structures preserved.

I can find little difference between these specimens; and Krausel and Range (1928), in referring to the Dadoxylon sp of Arber state: "It appears, as far as we can say, considering the bad state of preservation of the wood, that this is the identical type of wood described by Walton, and it is now again available from the Doros Crater" (i.e. the locality of his own specimen - P.W.) "In fact, there is complete conformity in the construction of the secondary wood, and one would not hesitate to combine them if the primary structure were known". Because of this, Krausel left the first two as separate genera and species, and erected a new genus and species - Taxopitys africana - for his own specimen.

The specimens mentioned above and that described here differ in the structure of the secondary wood, as shown in the following table:-

Table II Comparison of Helicoxylon waltonii with similar species.

Helicoxylon waltonii sp. nov.	Helicoxylon africanum (Walton sp.) Helicoxylon (Dadoxylon) Arber sp. Taxopitys africana Krausel
Rays up to 21 cells high (137 of p226)	Rays up to 16 cells high
Helicoid thickenings always in double band	Helicoid thickenings single, sometimes bifurcating, rarely a true double band.
Helicoid thickenings pass over border of tracheidal pits, close to pore.	Helicoid thickenings pass between borders of pits.
Bordered pits on tangential walls of tracheids.	None mentioned — Walton — no pits on T. wall.
Alternate polygonal pits common	Not as common
2 or 3 crossfield pits	2 - 8 crossfield pits

As the primary tissues of the present specimen are not known, it must be included in the new genus Helicoxylon, and the difference between this and the previously described woods of a similar structure are quite sufficient to warrant the formation of a new species. It is named after Professor John Walton, who first described wood of this type from South West Africa.

If Shilkina's specimen (Shilkina, 1960) agrees closely with either Helicoxylon africanum or Helicoxylon waltonii, it must be described under the appropriate specific name, otherwise it may be necessary to erect a new species.

Creguns (1961) has described a new genus, Platyspiroxylon, which he believes is distinct from Taxopitys Krausel and Spiroxylon of Walton (1925), as the helicoid thickenings are much more coarse, and very

steeply inclined. Also, although the pitting is Araucarian, it is entirely uniseriate.

Helicoxylon waltonii is quite unlike any one living gymnosperm, but combines features of Araucaria and Cephalotaxus. The arrangement of the spirals is quite similar to that shown in Cephalotaxus, in which the spirals cross the border of the pit and may even be tangential to the pores (Gregus 1955), but this genus has no araucarian pitting. The pitting of Helicoxylon waltonii is quite typically araucarian.

Taxoxylon (Taxites) scalariformis (Goepp) is one of the few specimens assigned to this genus which have been shown to have true helicoid thickenings, but the tracheid pits are circular and separate, never at all araucarian. I must agree with those authors who have emphasised the need for distinguishing between true helices and the helicoid marks which are the result of the decomposition of wood (Seward, 1919; Walton, 1925; Kräusel and Range, 1928), and also between true helices and the helicoid cracks which are characteristic of compression wood in healthy trees. (Philips 1948). This last phenomenon is known as spiral checking. All the specimens of Helicoxylon and Taxopitys have been found in South West Africa, a relatively restricted geographical range. As so few specimens have been described, it is not unreasonable to suggest that the geological age range of this group may have been similarly restricted. Taxopitys africana is known to have come from beds above the Ecca, but certainly below the Stormberg series. This would place it somewhere in the Beaufort series, which range from Upper Permian to lower Triassic in age.

The Natal specimen formerly called Dadoxylon sp. by Arber in 1910 was from the Ecca beds, i.e. still older, being of lower Permian age. There would seem to be little evidence in support of Walton's statement (1925) that Heliocxylon africanum is not earlier than Mesozoic and is possibly of Tertiary age. Kräusel and Range (1928) also believe that the wood structure of Heliooxylon (Spiroxylon) africanum precludes a Cretaceous or Tertiary age. Comparison with the other South West African specimens suggests a Permian or early Triassic age.

The description of similar wood from the Carboniferous deposits of Siberia by Shilkina (1960) suggests that the present specimen could be as old as the Permo-carboniferous.

Cramblant (1960) has also expressed the opinion, which is supported by his work, that gymnospermous fossil wood showing a combination of characters usually found in separate conifer groups occurs earlier in the Southern Hemisphere (i.e. in the Upper Palaeozoic) than it does in the Northern Hemisphere. The placing of Heliocxylon in the Permian or Triassic rather than in the Tertiary fits in with this general principle.

Additional specimens from Rhodesia, not sufficiently preserved for full taxonomic treatment.

Specimens B 2 - 7

Locality: Deteema "Fossil Forest", Wankie Game Reserve.
Locality 43 of Lacey (1961b)

Age and Horizon: Probably Escarpment Grit, above basal conglomerate. Triassic.

All the specimens showed, externally, signs of grain structure and growth rings. They were hard grey pieces of rock, with some iron staining and a large number of quartz intrusions.

Specimens B 2 - 6 were all sectioned and one surface of specimen B 7 was polished. The transverse sections showed some signs of cellular structure in occasional patches, but the longitudinal sections were completely devoid of recognisable structures. This was mainly because of the crystalline nature of the rock and the fact that the greater part of the specimens consisted of pure white quartz. Specimen B 7 consisted of almost entirely this material. The vague outlines of the cells seen in transverse section were similar to those described in specimen B 1 (Rhodoxylon kondii, page 196) and the width of the growth rings was also in the order of 4 or 5 mm.

With certainty, all that can be said is that the specimens are of a poorly preserved fossil wood.

Specimen C 1.

Locality: Near Sai, in the Konyoni River Valley, Central Sobungwe. Locality 42 of Lacey (1961b)

Age and Horizon: Escarpment grit, above basal conglomerate.

This specimen is part of a small oval branch, with a greater diameter of 3·5 cm. Three subsidiary branch scars are shown (1 - 1·5 mm. in diameter) one laterally and two terminally situated. The last two are clear evidence of dichotomy, which suggests that the terminal meristem had been destroyed. Also, seven scars (2mm in diameter) and some smaller double and triple scars were seen, arranged in a spiral. In tangential longitudinal section, the arrangement and development of the two types of scar was found to be exactly the same as that described in the specimens of Pndoxylon bondii, and this was confirmed by the radial longitudinal sections C.1/RLS.1 and C.1/RLS.2.

In transverse section, the pith cavity was eccentrically placed and was surrounded by a large number of primary xylem groups (greater than 12, probably 20 - 25). Six growth rings were counted, between 3 and 5 mm. across. In all the sections, macroscopic features such as growth rings and leaf traces would be clearly seen, but under the microscope, no details of cellular organisation were visible; in fact, large parts of the section were quite glassy and clear.

Specimen C 3.

Locality - area and horizon as for C 1.

This specimen, a small piece of secondary wood measuring 2·0 cm x 1·7 cm. x 8·5 cm, shows scars of double and triple leaf traces and one large scar (2 cm. in diameter) on its outer surface. The arrangement of the scars is in a spiral as described for Padoxylon bondii and the previous specimen. Three growth rings were seen in the transverse section, but no cellular detail was seen.

In view of the great similarity in the arrangement of the leaf traces of Specimens C 1 and C 2 to that shown in Padoxylon bondii, it is not unlikely that they belong to the same species, although this cannot be confirmed by cellular structure. Sai and the Gwave River Area (their respective localities) are only some 10 miles apart. One specimen of Padoxylon bondii B 1, comes from the same bed as the "C" specimens (Escarpment grit). The "C" specimens are thought to be the Pebbly Arkose, but this is still of Upper Karroo, i.e. Upper Triassic age. (Note, there seems to be some confusion between the Escarpment Grit and the Pebbly Arkose in some localities (Lacey, 1961b) so it is possible that they are all of the same age)

Specimens C 5 - C 7

Locality, Area and Horizon: As for specimens C1 and C 2.

These specimens of secondary wood range in size from 4 cm. x 4 cm. x 1·5 cm. to 9 cm. x 5 cm. x 15 cm. No details of structure were found, except for occasional leaf or shoot traces.

Specimens F 1.- F 9.

Locality: Fossil Forest, 10 miles west of Chirundu on the Chirundu-Kafue Road, N. Rhodesia. Locality 49 of Lacey (1961b).

Horizon: Escarpment grit or possibly Pebbly Arkose.

Many large trunks are known in this locality (Lacey, 1961b, Plate 2, fig.2).

The specimens are fragments between 6 cm. x 3·5 cm. x 6·5 cm., and 20 cm. x 10 cm. x 9 cm. in size. The rock is hard, grey in colour, or stained deep red. The sections show that the rock is crystalline and contains a large amount of quartz, as described in the "B" series. The transverse section shows very widely spaced (average about 1 cm.), but rather indistinct growth rings. The cells are arranged in radial files, and appear to be of the normal gymnospermous type. The cell walls are indistinct and are rather thick (about 10μ). However, the crystalline nature of the rock obscured all signs of cellular structure in the longitudinal sections.

It is not possible to attempt any identification of specimens C 3 to C 7 and F 1 to F 9.

General Discussion.

Geographical and Stratigraphical Distribution.

Many species of wood have been assigned to Dadoxylon Endlicher, a genus of world wide distribution known from strata as old as the Devonian (Lang 1929). The species described in the present Thesis are of Permian and Triassic age. It has been stated (Warren 1912; Walton, 1956) that the genus is of no stratigraphical significance. However, Walton himself criticises Warren's suggestion that Dadoxylon nicolii has a particularly wide vertical distribution, and undoubtedly well preserved specimens of this species are only known from Perno-carboniferous strata. In fact, if Walton (1930) is correct in his belief that the Newcastle beds of Australia are of the same age as the Lower Beaufort beds of Cape Province, all the specimens of Dadoxylon nicolii so far described, are of closely similar age. Dadoxylon sp.A (cf. Dadoxylon nicolii described in this Thesis) is from the Middle Madumabisa Shales, which are also equivalent to the lower Beaufort beds of the Cape (Table 1, page 5 and Lacey 1961b).

Dadoxylon boughevi (page 176) is similar to Dadoxylon nicolii in the general character of the wood, and two other species, Dadoxylon lukugense Crembast (1960) and Dadoxylon pedroi Zeiller (1895) (=Lobatoxylon pedroi (Zeiller) Kräusel (1956) which closely resemble Dadoxylon boughevi in the general character of the wood structure, and in particular in possessing very high uniseriate rays, are of equivalent age.

The following table shows the country of origin and stratigraphical provenance of these and other similar species of Permo-Carboniferous age.

Table III

Dadoxylon species of Permo-carboniferous age

Species	Country of Origin	Horizon
Dadoxylon nicolii	Malawi (Nyasaland)	Coal shale group
Dadoxylon sp.A (D. cf. nicolii)	Southern Rhodesia	Middle Madumabisa Shales
Dadoxylon nicolii	Southern Rhodesia (Edwards 1957)	Lower Beaufort
Dadoxylon nicolii	Natal	Natal Coal Measures
Dadoxylon nicolii	Cape Province	Lower Beaufort
Dadoxylon nicolii	Australia	Newcastle Series
Dadoxylon bakeri (D. nicolii)	Falkland Islands	Permo-Carboniferous
Dadoxylon boughoyi sp.nov.	Southern Rhodesia	Middle Madumabisa Shales
Dadoxylon lukugaense	Congo	l'assise de transition (= Lower Beaufort)
Dadoxylon jedroi	Brazil	Tubarao (Permo-Carb.)

It is suggested that these species may be of some broad stratigraphical value. In referring to the specimens described in this Thesis, Bond (personal communication) states "While it is not usually difficult to decide whether an exposure belongs in Upper or Lower Karroo in the Zambezi Valley, the same may well not apply to places such as the Luangwa and the Luano, where facies differences may make discrimination difficult. Under these conditions, fossil woods might be extremely valuable."

The Triassic species, Dadoxylon bondii (page) which is characterised by a distinctive pattern of leaf traces, has drawn attention to a possible inaccuracy in the provisional dating of the exposures in localities 40 and 42 (Lacey 1961b). The exposures are some 10 miles apart, on opposite sides of the Charama Plateau, about 20 miles west of Gokwe. As the wood of Dadoxylon bondii is found at loc. 40 (the headwater area of the Gwave River) and wood which is probably the same species is found at Loc. 42 (near Sai, in the Manyoni River Valley) it is suggested that these localities lie in the same bed which is exposed on different sides of Charama hill. At the moment, it is not possible to determine the precise age, which is either Escarpment Grit or Pebbly Arkose.

Mesembrioxylon gwavense is also the same age as Dadoxylon bondii. Hitherto, woods of this type have been recorded from Jurassic to recent times, and so far the genus has not been of great stratigraphical value. Mesembrioxylon gwavense, however, is easily distinguished from all previously described species, and if it proves to be of restricted

vertical distribution, it will certainly be of some stratigraphical importance. That this is probably true, is supported by the fact that Woodworthia arizonica (Jeffrey 1910), a wood of very similar structure, is also restricted to the Triassic.

It has been established that woods from known horizons which have Araucarian pitting and helicoid tertiary thickenings on the tracheids, are of Permo-carboniferous to Triassic age. This suggests that the undated Heliconylon africanum and Heliconylon walkonii from South West Africa are of Permian or Triassic age, rather than Tertiary age as was suggested by Walton (1923).

The value of certain features as diagnostic characters.

The examples given here show clearly that accurate description and identification of specimens is essential. To increase the accuracy of determinations, it is necessary to take as many characters as possible into account, and it is not sufficient to rely solely on those characters which are conventionally accepted as being of taxonomic use. (This clearly applies most strongly to fossils in which the number of characters is often limited).

Thus I have found that ray height, which is not generally accepted as a character of importance, has proved to be most useful in distinguishing between certain taxa, particularly at the specific level. One of the objections which has been made to the use of ray height, as a diagnostic criterion, is its variability from one part of a specimen to another. Not only can this objection be overcome, but the variability

can be a useful additional character. In general, it may be said that ray height increases steadily with the age of the wood, until about the 20th year, when the proportion of rays of a given height remains roughly constant (Philips 1948). The ray-height data for specimens C.1. (Mesembrioxylon gwavense) and C.3 (Dadoxylon bondii) shows a gradual if erratic rise in mean ray-height from the tangential sections near the pith to those from the outer edge of the specimen (see Appendix, page). In all the other specimens from which sequences of contiguous sections have been prepared, there is considerable variation in mean ray-height from one section to another, but there is no steady increase or decrease from one end of the series to the other. This in itself suggests that the specimens were from wood over about 20 growth rings from the pith. In most cases this can be confirmed by consideration of the size of the specimen or of such features as the curvature of the growth rings.

If a histogram showing the percentage of rays of different heights plotted against ray height is prepared, the shape of the histogram is often quite characteristic of the species. This is well shown in the histograms drawn for the species described in this Thesis. For convenience in comparison, they are grouped together in the Appendix on page , and are not given in the descriptions of individual species.

The histograms of specimens C.2, C.3 and E.1. are almost identical in shape. This supports the conclusion reached on other grounds, that they all belong to the same species, i.e. Dadoxylon bondii.

On the other hand, the difference between this species and

Dadoxylon houghoyi is clearly emphasised by a comparison of their histograms.

It should be emphasised that ray height is only one character, and is not a panacea for the problems of fossil wood taxonomists.

I would like to draw attention to the method of measuring tracheid length in tangential sections of wood, described by Ladell (1959). [see Appendix, page 257].

In recent woods, Ladell has shown that this method is as accurate in obtaining the average length of cells obtained from a sample, as actually measuring the length of cells obtained from the macerated wood. To be used for this purpose, it is essential that the tangential sections should be accurately alligned in the vertical plane. Providing that this is so, there does not seem to be any appreciable error arising from the confusion of obliquely cut tracheids with true end walls.

Ladell's method has been used to determine the mean tracheid length in the species of fossil wood described in this thesis. I am sure that this method will be even more useful in the investigation of fossil woods which yield peel sections. In such cases it should be possible to locate accurately the position of each section within a growth ring (as it is in modern woods) and thus avoid errors which might arise from the actual variation of tracheid length within a growth ring. Chalk and Ortis (1961) and others have shown that tracheid length is greatest in late wood, and suggest the actual pattern of variation might be of use as a diagnostic character.

A character which has not been used (or even described in detail) previously, is the appearance of the tracheidal and crossfield pits when viewed in section. This character was very useful in this investigation. The preliminary investigation showed that the wood structure of specimens G.1., G.2., G.3., and B.1. was quite similar. The pits in plan view (radial section) were about the same size and shape, and only uniseriate pits had been seen in all the specimens. However, when viewed in section, the pits in specimen G.1. were clearly quite different in structure from those of the other specimens (compare Plate VII B and Plate X C) and further examination revealed other significant differences, such as the presence of alternate pitting in specimen G.1. and differences in the structure of the crossfield pits, which in general are similar to the normal tracheidal pits in section. As a result, the specimens were not all placed in the same species, indeed, the sum of all their differences was deemed sufficient to place them in separate genera.

Evolutionary and Systematic significance of Permo-Carboniferous and Triassic Woods.

The main feature of general interest is that in Dadoxylon boughevi we again have wood with a mixed structure (i.e. combining Araucarian and Abietinaeous pitting) occurring in beds of Permo-Carboniferous age. This phenomenon has already been commented upon by Crambast (1960) and is to be seen in Dadoxylon nicolii (Walton, 1925) in Dadoxylon bengalense (Holden, 1917) and in a Dadoxylon sp. described by Warren (1912).

Kräusel (1919) and Kokhold (1922) have assigned woods of a similar nature from the Northern Hemisphere to the Protopinaceae. In this case the woods are all of Mesozoic age and are particularly common in the Jurassic and Cretaceous periods. Bailey (1933) has demonstrated quite convincingly that the range of variation in the pitting of the Protopinaceae is, in fact, no greater than that found in many families of the recent Pinaceae. Crambast (1960) believes that as this mixed pitting is more strongly developed in the "conservative" root structures of recent conifers, it is a primitive character. Its occurrence in the Dadoxylon species and in the Protopinaceae is said to show that they are transitional groups between an ancient Araucarian stock and the more modern Abietineae.

This is supported to some extent by the description of Taxopitys (? Helicoxylon) from the Carboniferous (Shilkina, 1960), of Platyspiroxylon (Greguss, 1961) from the Permian and of Helicoxylon (this Thesis) probably from Permian or Triassic beds; all of which show a

mixture of Araucarian and Taxinean features, a combination which I have not come across in recent woods.

It seems possible that the evolution of these types took place much earlier in Gondwanaland than in the Northern Hemisphere. This early development of such a flora may well have been stimulated, as Grambast (1960) has said, by the seasonal variations in conditions which are believed to have occurred in this area during this age.

Personally, I think that the change from arctic glacial conditions in the Lower Dwyka times to the warm conditions of the Lower Beaufort is more likely to have brought about a steady evolutionary advance, than mere seasonal variations in climate.

As far as the actual taxonomic position of the species of Dadoxylon is concerned, the demonstration that in the region of the crossfield pits the ray cell walls are not perforated, would certainly support those who believe in a more or less direct link between Dadoxylon and the Araucarineae. However, the recent demonstration that Archaeopteris leaves are borne on stems with Callixylon type of wood (Beck, 1960, a, b, 1962) shows that speculation in this respect should stay very close to the available facts. All that can be said is that many species of Dadoxylon are extremely similar to the Recent Araucarineae in the structure of their secondary wood.

Palaeo-Ecology.

The presence of well defined growth rings in both Permian and Triassic woods certainly suggests that there were seasonal changes

during these times. As the growth rings are not noticeably abnormal, it is reasonable to suppose that these changes followed a yearly (annual) cycle. I would suggest that the extreme narrowness and abruptness of the late wood zone indicates a very sudden change in climate - such as would be produced in periods of drought, following a long period of warm moist conditions. This is supported by the uniform structure of the wood and the large size of the cells in the other parts of the growth ring. A more gradual slowing down of growth, and a correspondingly wider zone of late wood, would probably result from the onset of a cold season, unless this was unusually rapid.

The "drought season" hypothesis for the Permian is also supported by the occurrence of what is believed to be burnt wood in beds of this age. These have been interpreted as being formed as a result of a forest fire. As most natural outbreaks of forest fire seem to be caused by lightning without rain (Harris, 1957, 1958), the chances of a fire starting would be greatly increased if the timber, and particularly any litter or undergrowth was really dry, following a drought. This ties in well with the suggestions made by Bond (Bond, 1962; Lacey 1961b) which were based both on lithology and on the kind of fauna found in fresh water deposits of the Rhodesian Karroo.

Bond suggests that the climate changed fairly steadily from the arctic conditions indicated by the Dwyka, to hot dry conditions by the time of the Forest Sandstones. There is clear evidence of the periodic drying of lakes in the Middle Madumabisa shales, and Bond (personal communication) has suggested that pieces of wood lying in the shallows would easily become silicified. He also suggests that this

process is occurring in present day lakes in Central Africa, as the waters contain high percentages of calcium salts and silicates.

Although there were major wet periods (as indicated by the Moltano ripple-marked flags), conditions were almost certainly much drier and hotter in the time of the Pebbly Arkose and Escarpment grits, when the Triassic species described in this Thesis were growing.

The fact that the tracheid walls of the Triassic woods are much thicker than those of the Permian specimens might be interpreted as being of climatological significance. The similarity in the structure of the growth rings in the woods of both ages, suggests that there were probably sudden and severe periods of drought in the Triassic, as well as in the Permian.

Thick cell walls in more than one species might indicate great mechanical strength, or possibly the presence of a large amount of mucilaginous material in the tracheid walls. Either conditions might be taken as a xeromorphic character, indicating that conditions were even hotter and drier in parts of the Triassic than in the Permian.

This would be compatible with a climate more closely approaching that of the hot dry deserts of the Forest Sandstone age, and it would not be unreasonable to interpret the close series of growth rings observed in part of specimen G.3. (page 196) as resulting from a sequence of abnormally severe and prolonged periods of drought.

SUMMARY TO PART III

Fifty specimens of petrified wood from Rhodesia and South West Africa have been examined. Eight of these are assigned to definite species. Two new species of Dadoxylon Endlicher and one new species of Mesembrioxylon Seward, are described; for Walton's genus Spiroxylon (Walton, 1925) the new name Helicoxylon is proposed, and a new species is assigned to this genus. Twelve poorly preserved specimens are compared with species described in this Thesis and elsewhere. It is suggested that fossil woods of a "Mixed Wood Structure" (Crambant, 1960) have, on the whole, evolved earlier in the Southern than in the Northern Hemisphere, and that some of these woods may be of broad stratigraphical significance.

EXPLANATION OF TEN PLATES

Plate I.

Dadoxylon boughevi sp.nov.

Fig. A. Transverse section showing narrow zone of late wood.(X 125).

Fig. B. Tangential longitudinal Section.
Note the tall uniseriate rays. (X 125).

Fig. C. Radial longitudinal section showing crossfield pits in late and early wood (X 470) (Photograph mounted sideways).

Fig. D. Photograph of same region enlarged to X 1,200.

All figures from Specimen A.l.

Plate II

Dadoxylon boughevi sp.nov.

Fig. A. R.L.S. (X 470) Multiseriate alternate and opposite pitting.

Fig. B. T.L.S. Section through bordered pits in walls of tracheids (X 1,200)

Fig. C. R.L.S. (X 470) Biseriate opposite and alternate pitting and scattered groups of pits.

Fig. D. R.L.S. (X 470). Multiseriate, alternate pitting.

All figures from Specimen A.l.

Plate III

Dadoxylon boughevi sp.nov.

Figs. A & B. Biseriate opposite pits and bars of Sanio.
Note the isolated pit groups (X 1,200) (Specimen A.l.)

Figs. C & D. T. L. S. (X 1,200) Crossfield pits and Tracheidal pits in vertical section. (Specimen A.l.)

Plate IV.

Dadoxylon sp.A and Mesembrioxylon gwavense sp.nov.

Fig. A. Dadoxylon sp.A. Transverse section (X 125) showing crushing of tissues. (Specimen D.3)

Fig. B. T.S. of same specimen showing better preserved tissues near zone of late wood (X 125)

Fig. C. & D. Mesembrioxylon gwavense sp.nov. External features showing well marked circular scars. (X 1½) (Specimen C.1.).

Plate V.

Mesembrioxylon gwavense sp.nov.

Fig. A. T.S., showing wide, indistinct growth rings. (X 50)

Fig. B. Double zone of small tracheids associated with a wound (X 125.-)

Fig. C. "Normal late wood zone" (X 125).

All figures from Specimen C.1.

Plate VI.

Mesembrioxylon gwavense sp.nov.

Fig. A. T.L.S. showing T.S. through double branch trace (X 50.)

Fig. B. Single branch trace from the same section (X 50.)

Fig. C. R.L.S. showing tracheidal and crossfield pits. (X 125) (Plane turn sideways).

Fig. D. R.L.S. showing rays and crossfield pits. (X 125.)

All figures from Specimen C.1.

Plate VII

Mesembrioxylon awavense sp.nov.

Fig. A. Uniseriate trachoidal pits. (X 470.) From R.L.S.

Fig. B. R.L.S. (X 470.) Uniseriate trachoidal pits.

Fig. C. R.L.S. (X 470.) Ray cells and crossfield pits.

Fig. D. T.L.S. (X 1,200) Vertical section through trachoidal pits.

All figures from Specimen G.1.

Plate VIII

Mesembrioxylon awavense sp.nov. and Dadoxylon bondii sp.nov.

Fig. A. Mesembrioxylon awavense sp.nov. T.L.S. showing crossfield pits in section (X 1,200.) (Specimen G.1.)

Fig. B. R.L.S. Parenchyma cell with dark contents (X 1,200) (Specimen G.1.)

Fig. C. Dadoxylon bondii sp.nov. (X 2/3) showing spirally arranged scars. (Specimen G.2.)

Fig. D. Dadoxylon bondii sp.nov. (X 2/3) showing branch bases (Specimen G.3.)

Plate IX

Dadoxylon bondii sp.nov.

Figs. A & B. different views of Specimen G.3 (X 2/3) showing branch bases.

Fig. C. T.S. of Specimen G.5. showing narrow zone of late wood, and uniform structure of wood (X 125).

Fig. D. T.L.S. from same specimen (X 125)

Plate X

Dadoxylon bandii sp.nov.

Fig. A. R.L.S. (X 470.) Uniseriate pitting. Note double rim.

Fig. B. R.L.S. (X 470.) Biseriate alternate pitting.

Fig. C. Vertical section through tracheidal pits (X 1,200.) Note the difference in size between the two half-pits.

Fig. D. R.L.S. showing rays and tracheidal pitting (X 125.) (Photograph mounted sideways).

Fig. E. R.L.S. Detail of crossfield pits (X 1,200)

Fig. F. T.L.S. Vertical section through five crossfield pits. Note the extremely thin ray-cell walls (X 1,200.)

Fig. G. T.L.S. vertical section through two crossfield pits. Note that the wall of the ray-cell is not pitted. (X 1,200)

Figs. A to C from Specimen G.2.

Figs. D to G from Specimen G.3.

Plate XI

Heliconylon weltonii sp.nov.

Fig. A. T.S. (X 125.)

Fig. B. T.L.S. (X 125.) Note the tall uniseriate rays and the thick tracheid walls.

Fig. C. T.L.S. (X 50.) showing transverse cut through a leaf trace or a small branch trace.

Fig. D. R.L.S. (X 470.) Ray cells with poorly preserved crossfield pits.

All figures from Specimen A.4.

Plate XII.

Helicoxylon waltonii sp.nov.

Fig. A. R.L.S. (X 470.) Uniseriate tracheidal pits.

Fig. B. R.L.S. (X 470) Biseriate alternate pitting.

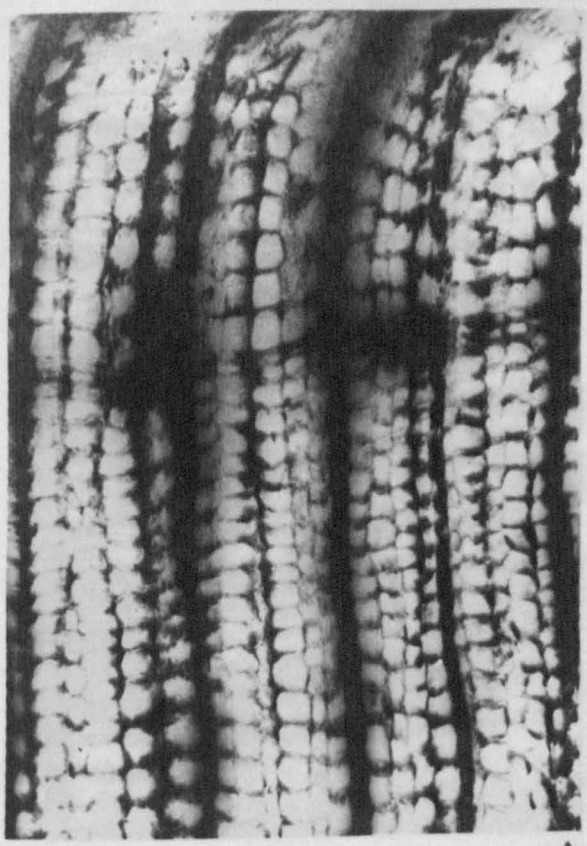
Fig. C. R.L.S. (X 470) Uniseriate pitting and helicoid tertiary thickening on tracheid walls.

Fig. D. R.L.S. (X 470.) Uniseriate pitting and a very clear double helix of tertiary wall thickening.

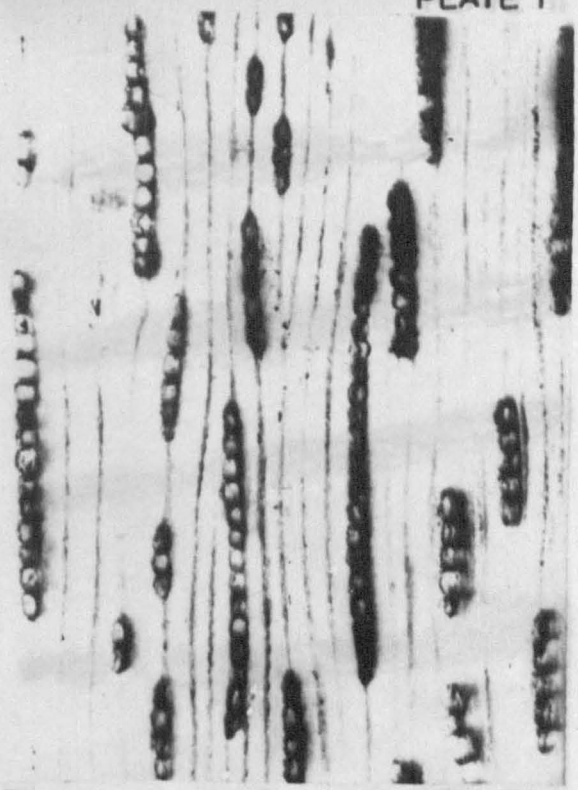
Fig. E. R.L.S. (X 470) Biseriate pitting and double helix of tertiary wall thickening. (Photograph mounted sideways).

All figures from Specimen A.4.

PLATE I

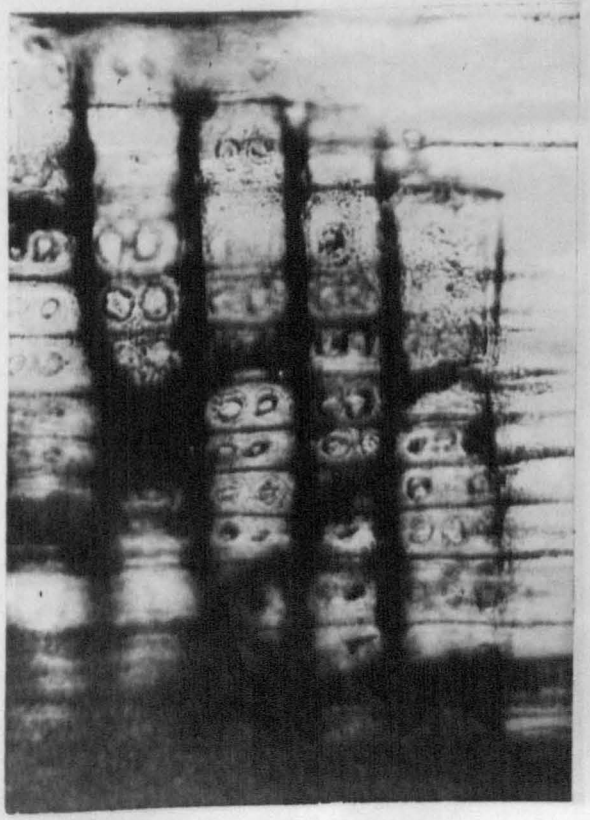


A



B

C



D

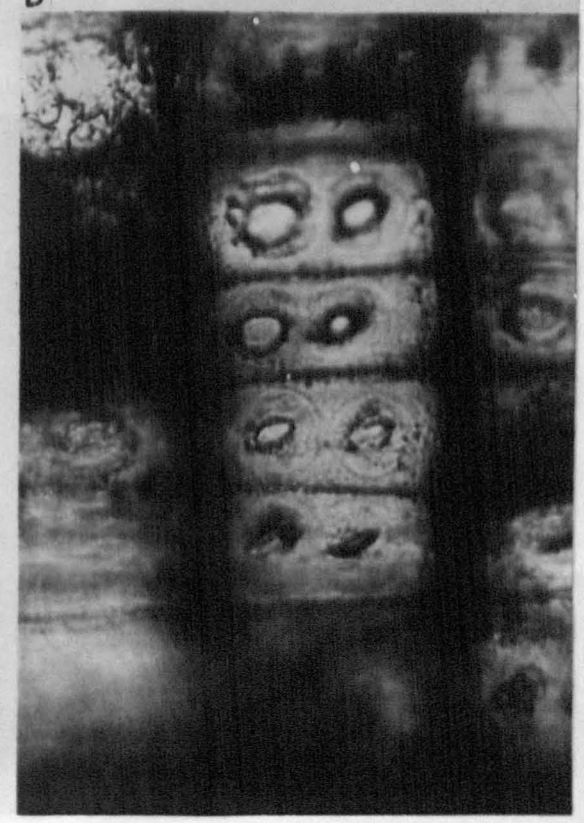
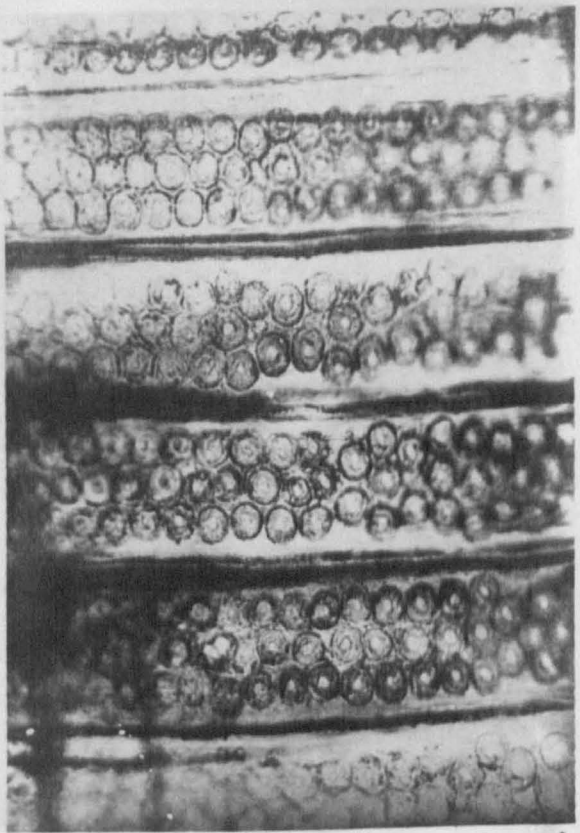
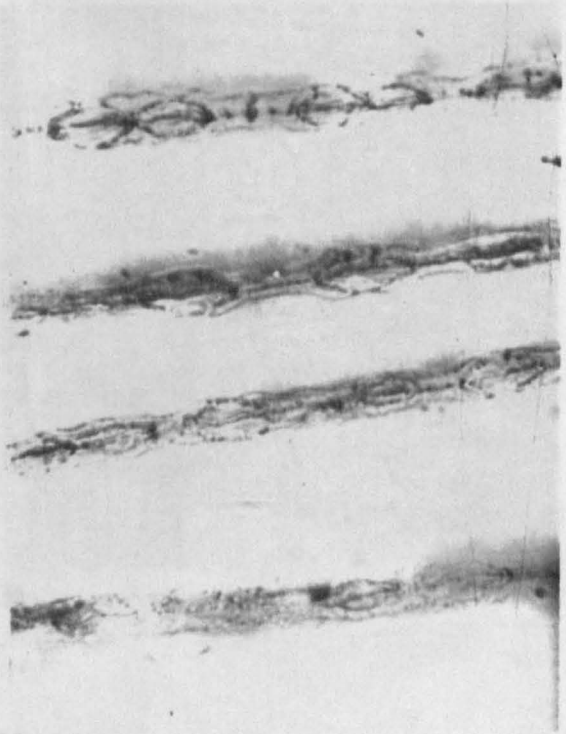


PLATE II

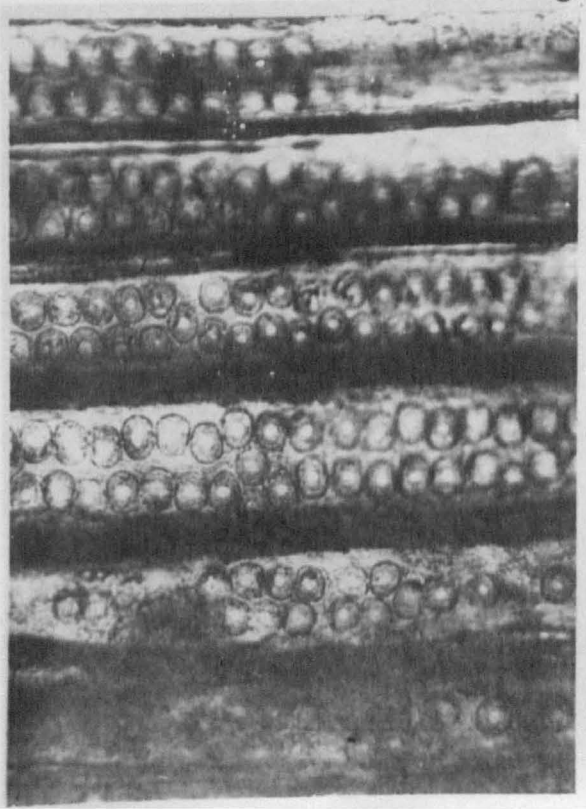


A



B

C



D

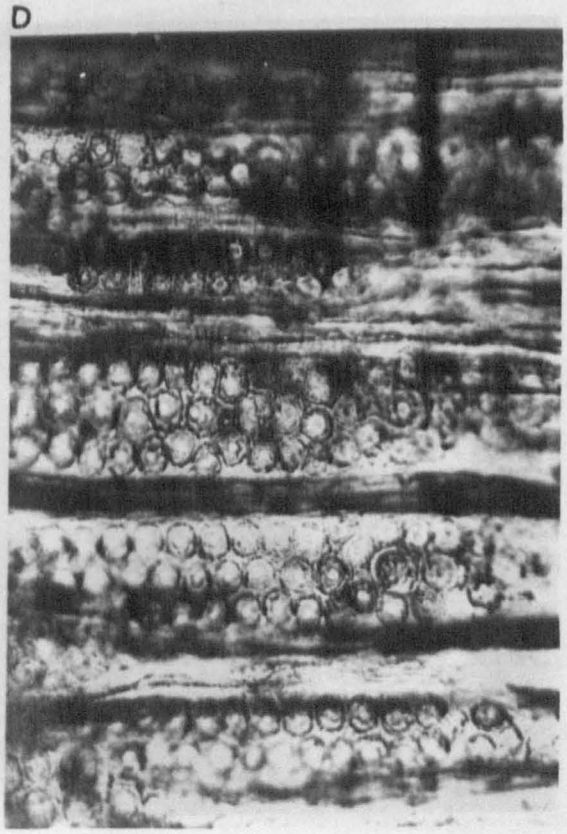
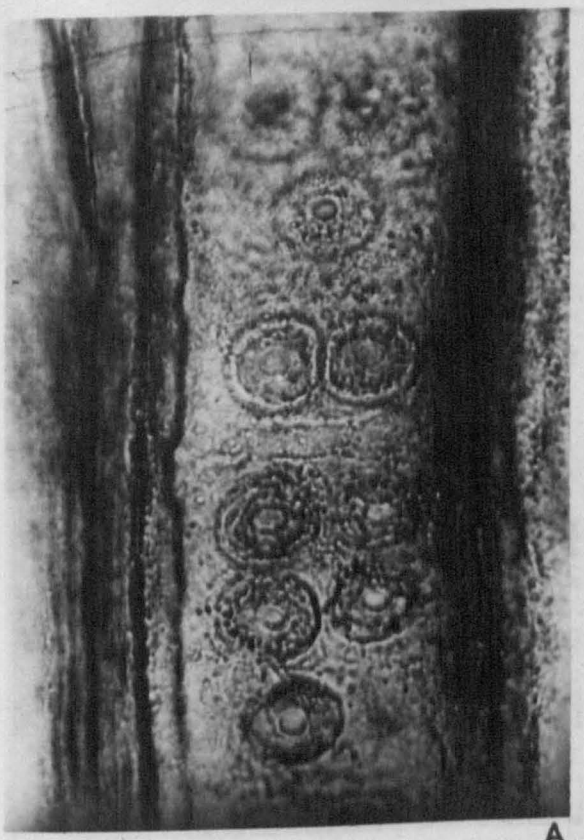
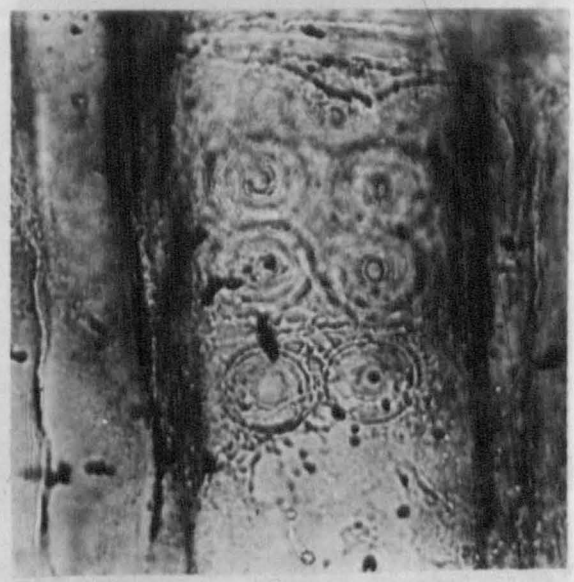


PLATE III.



A



B

C

D

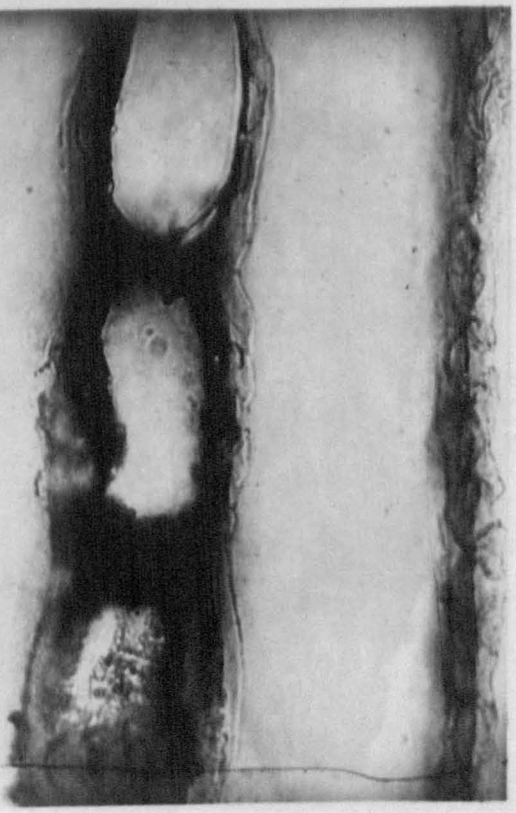
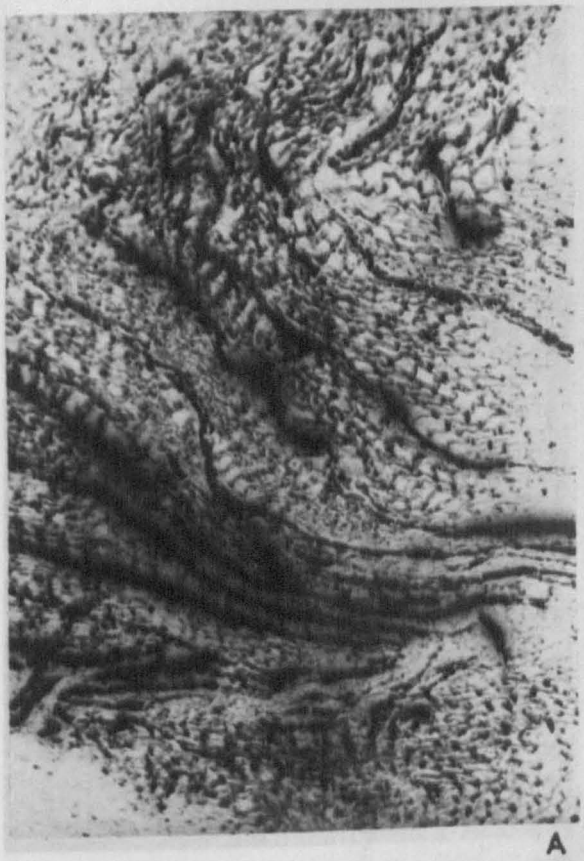
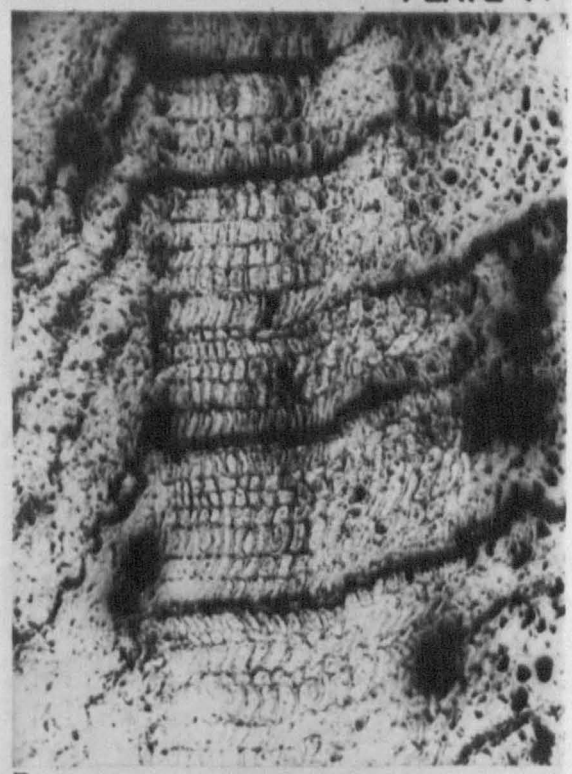


PLATE IV

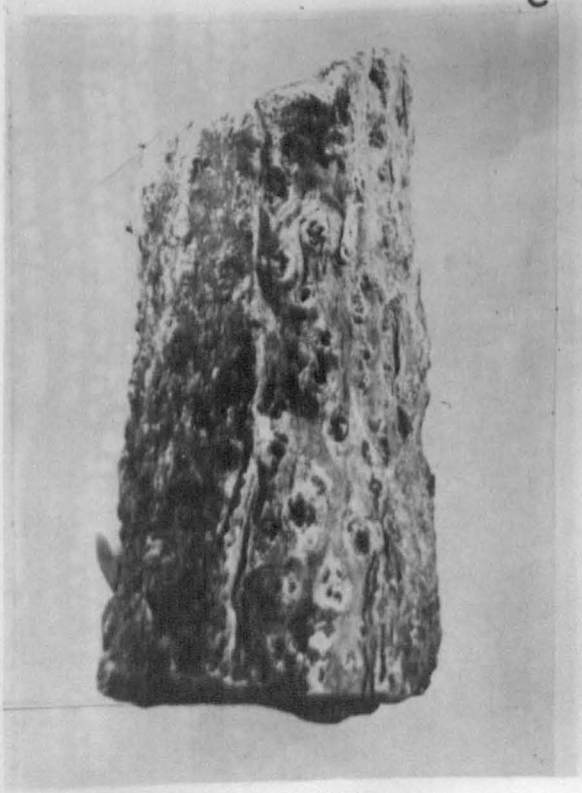


A



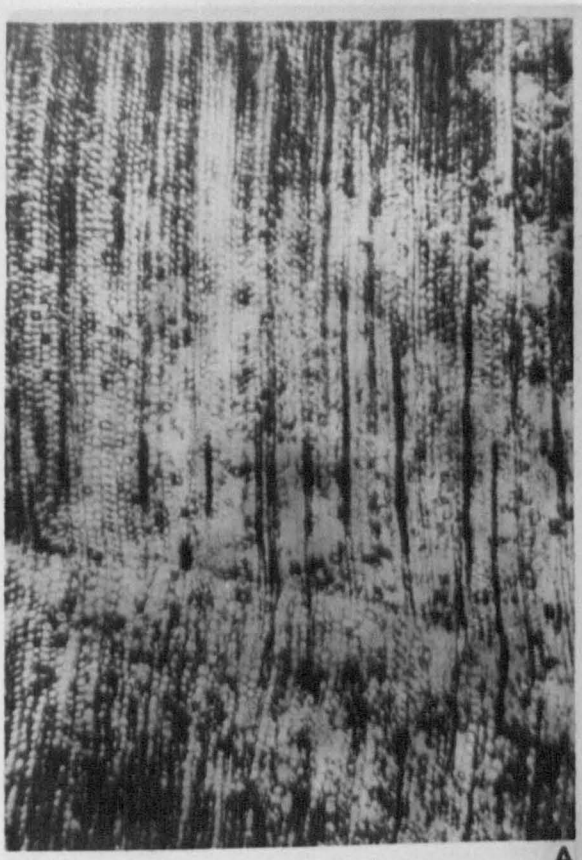
B

C

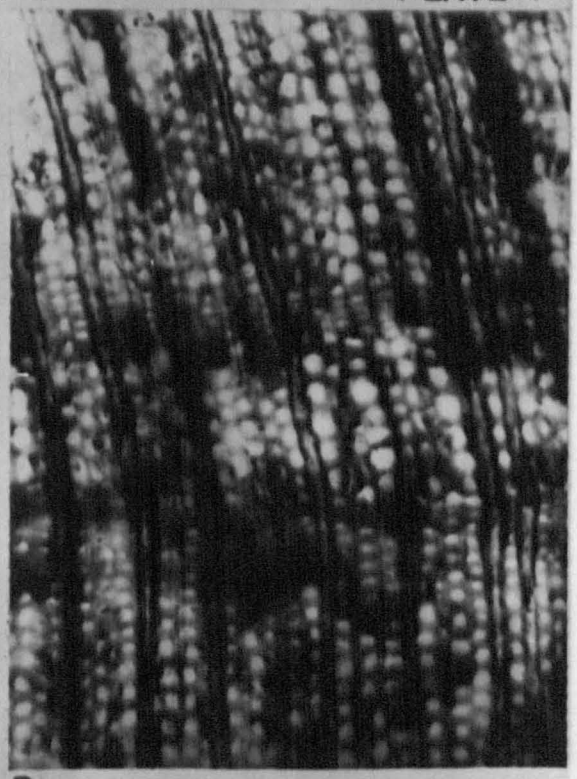


D

PLATE V

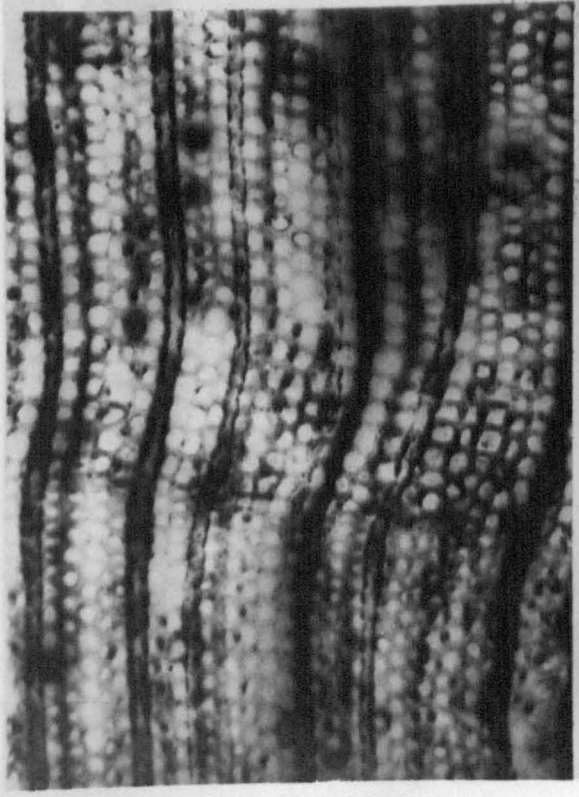


A



B

C



D

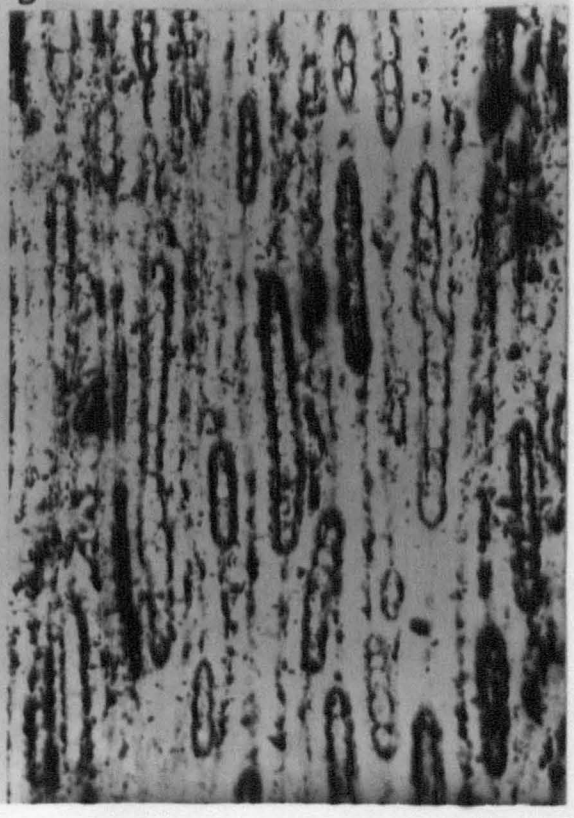
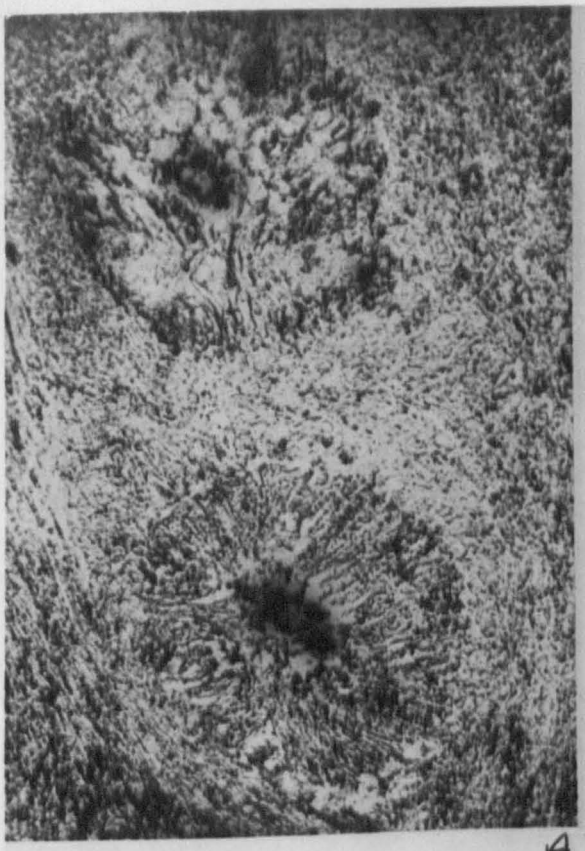


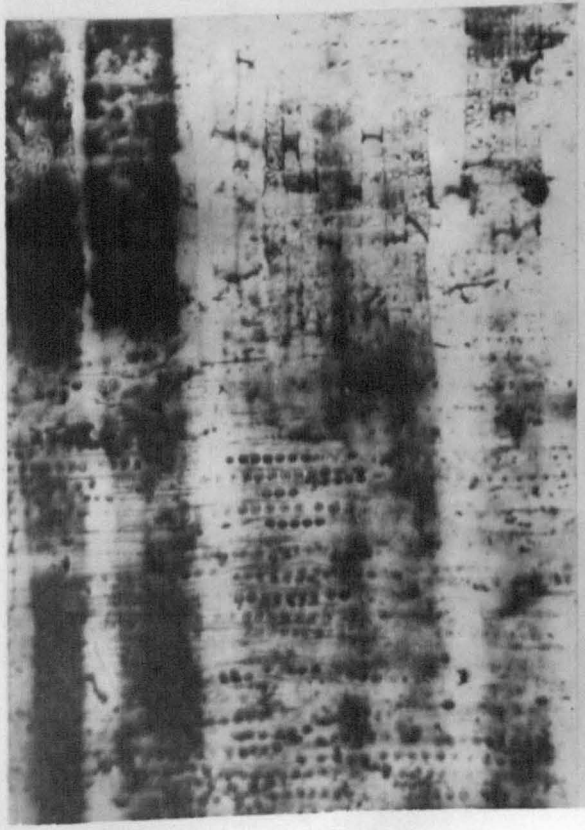
PLATE VI



A

B

C



D

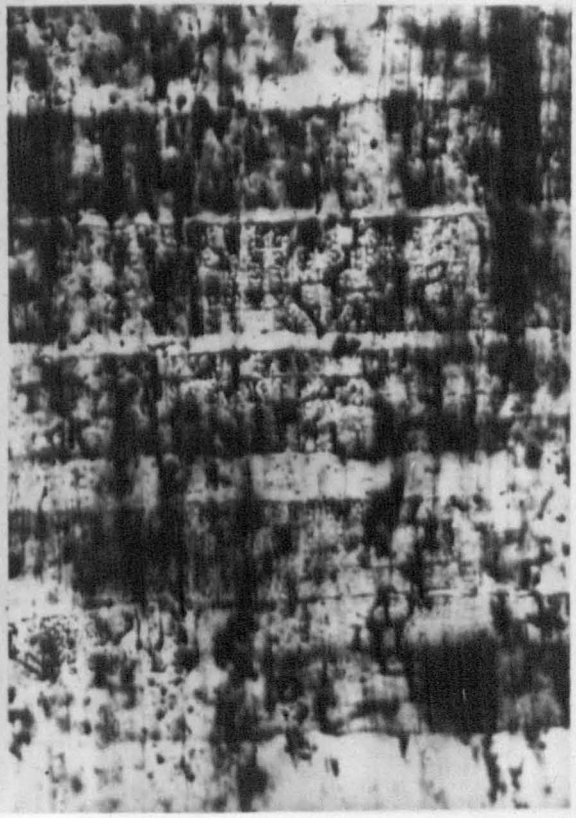
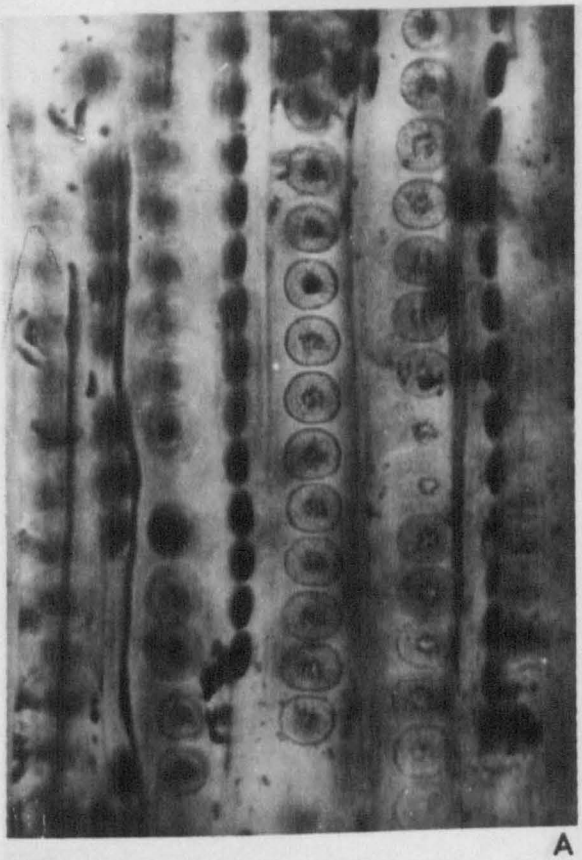
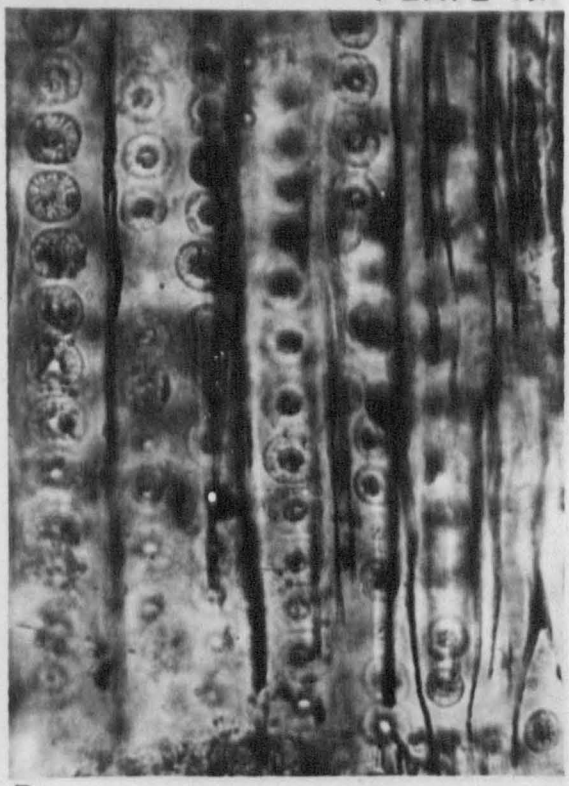


PLATE VII



A



B

C

D

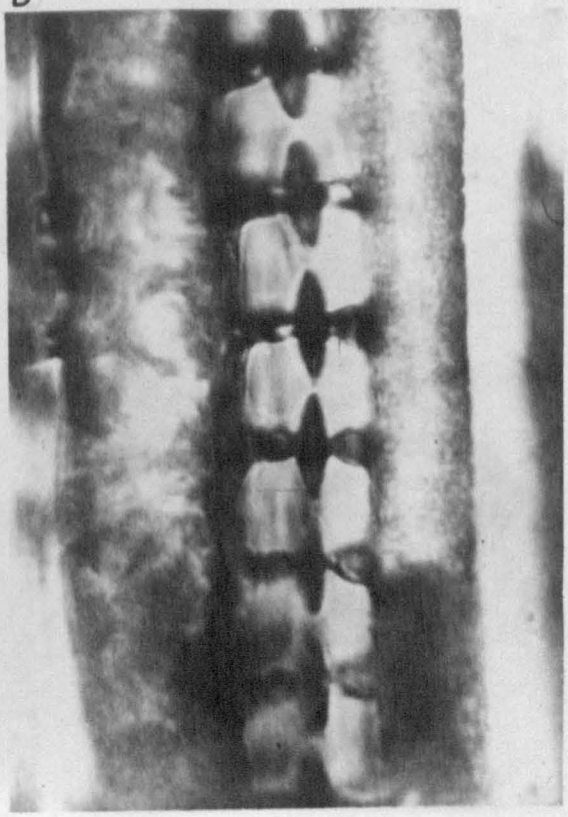
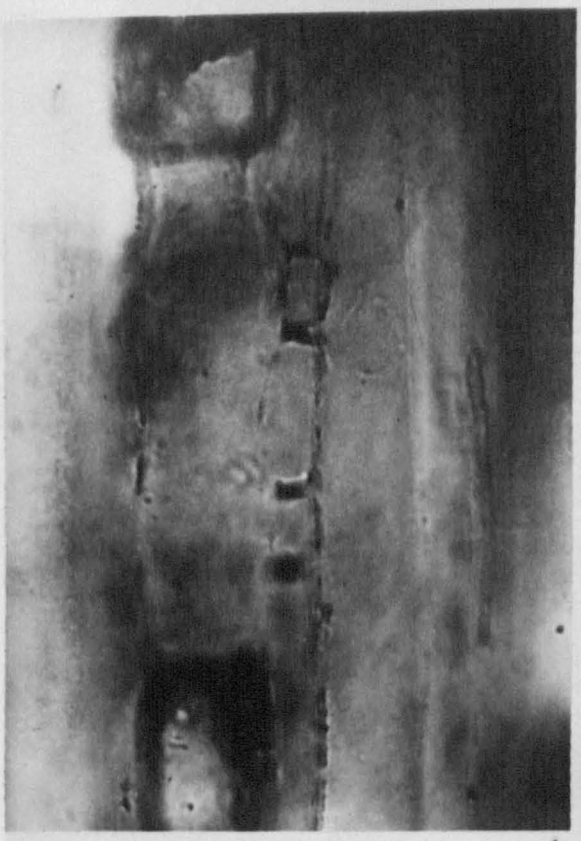


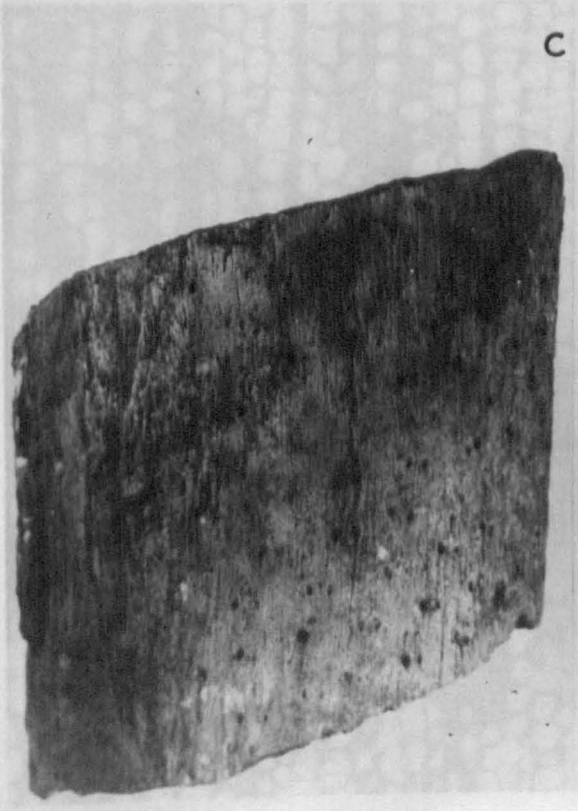
PLATE VIII



A

B

C



D

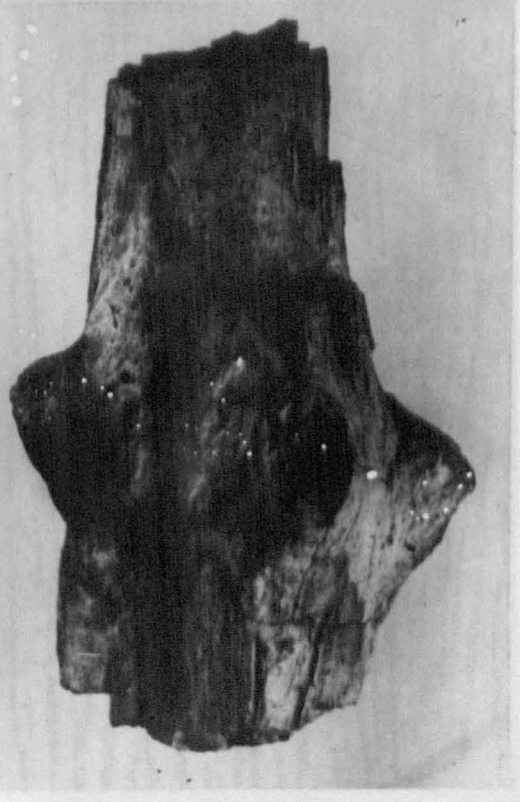


PLATE IX

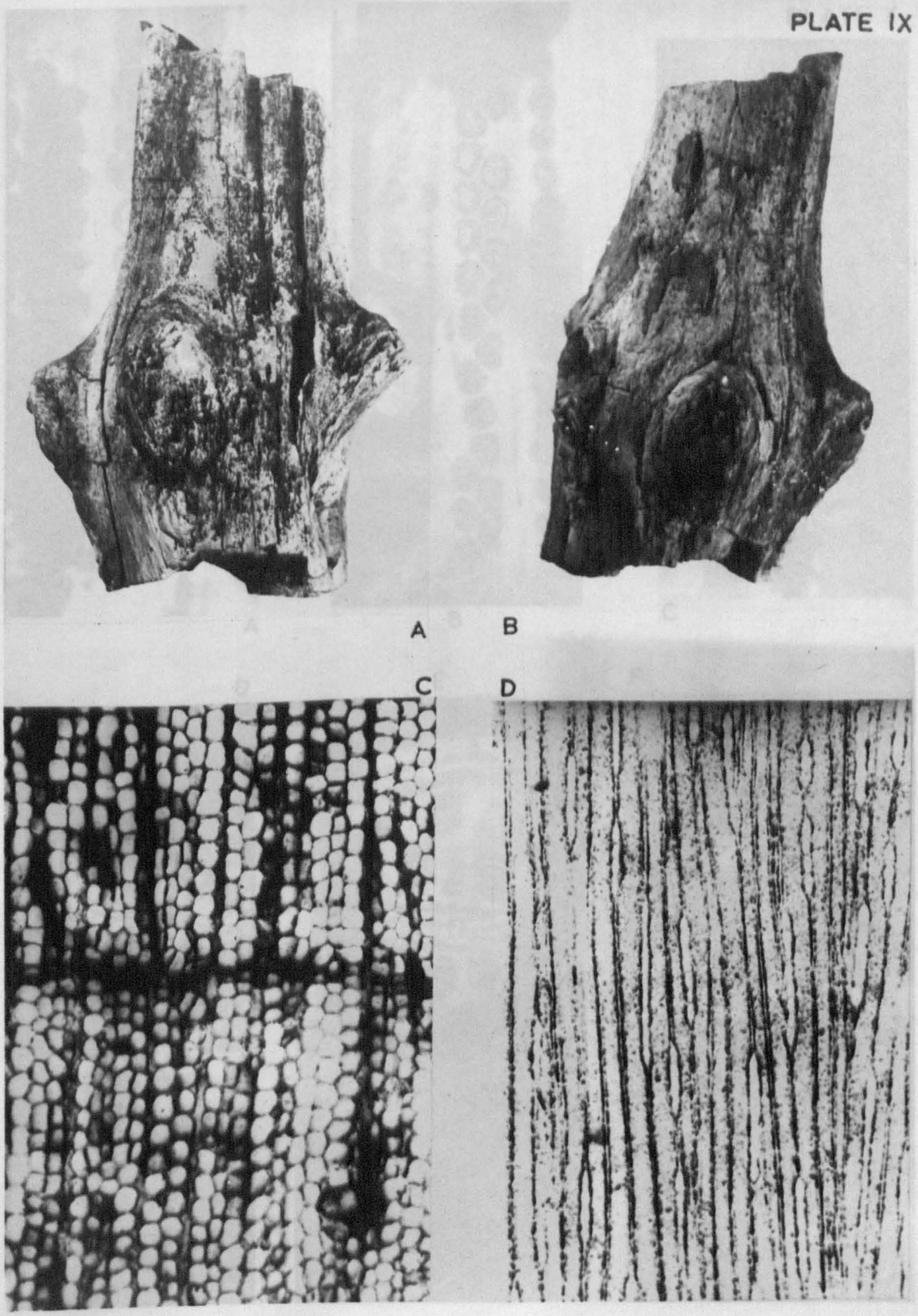
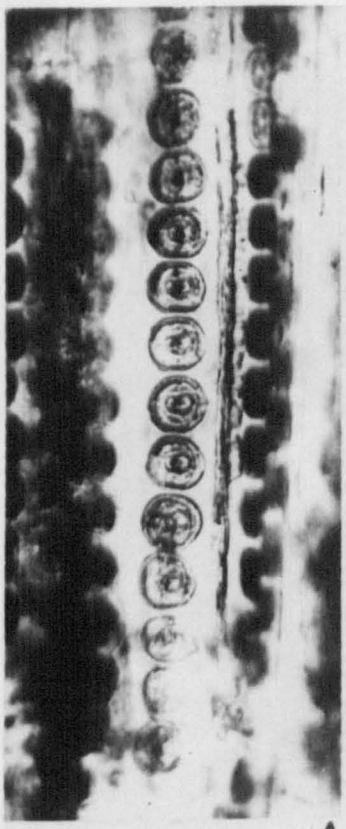
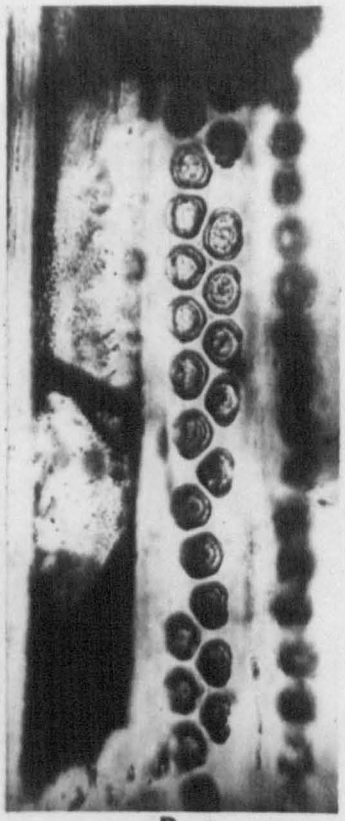


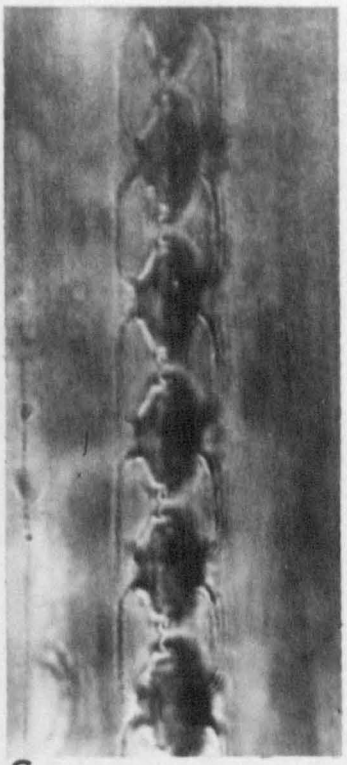
PLATE X



A

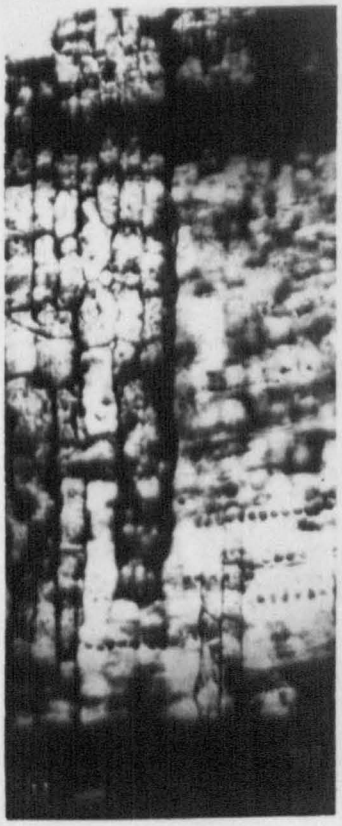


B



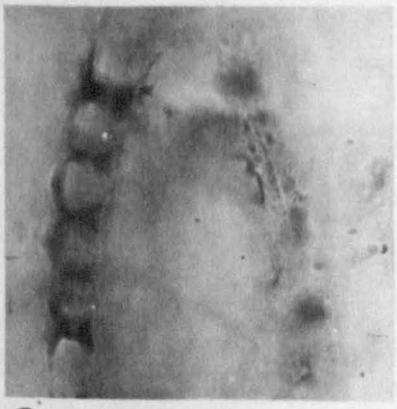
C

D



E

F



G

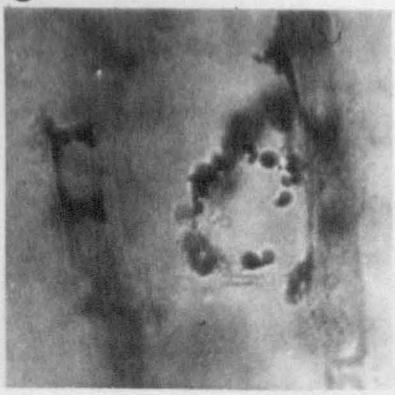
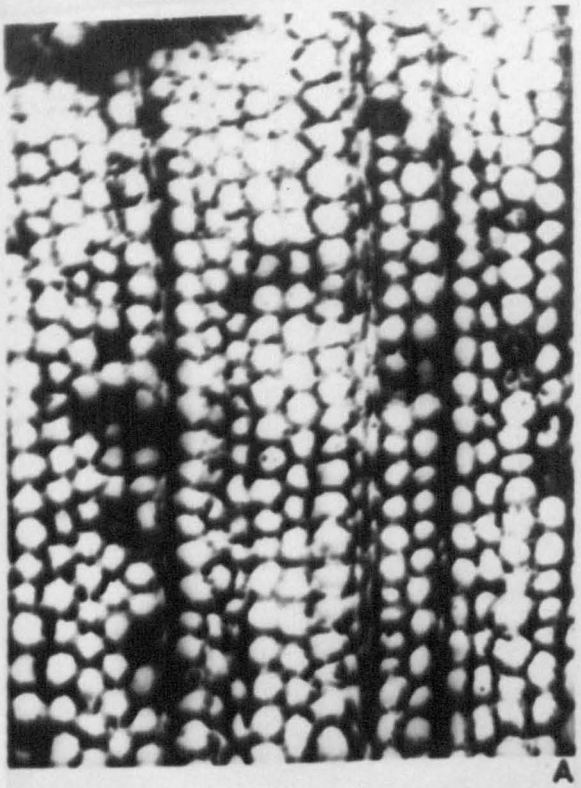
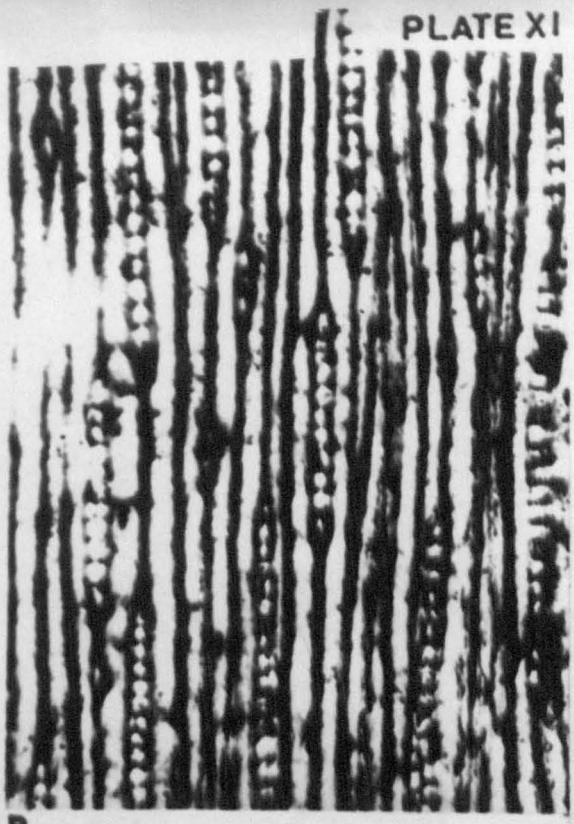


PLATE XI

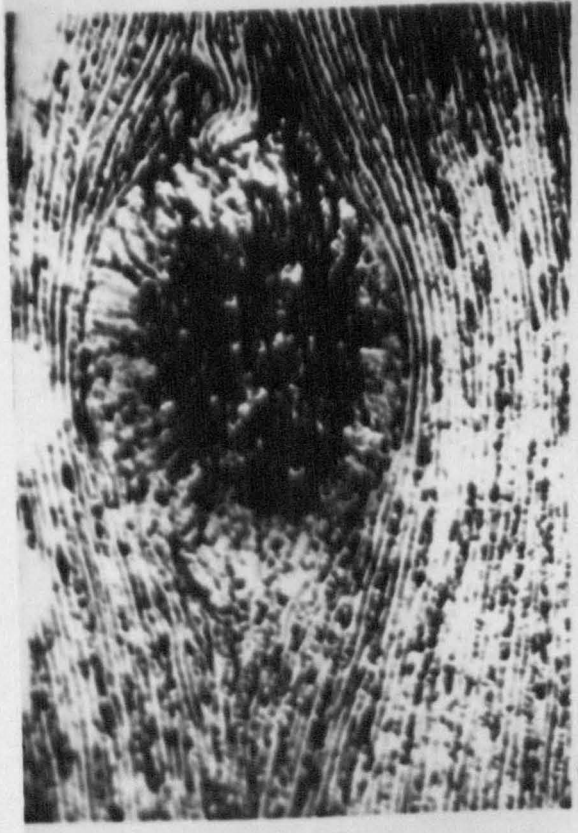


A



B

C



D

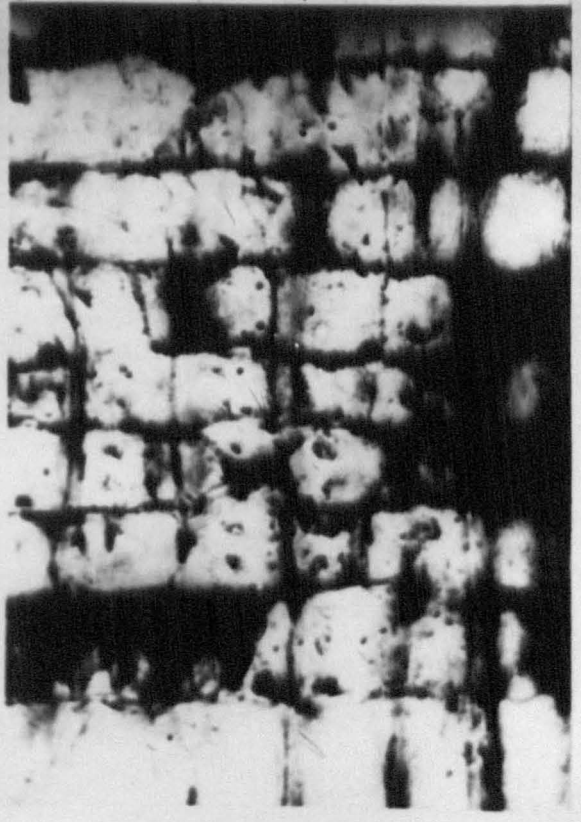
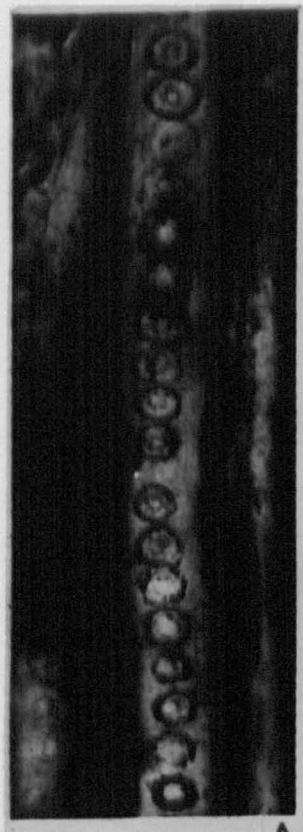
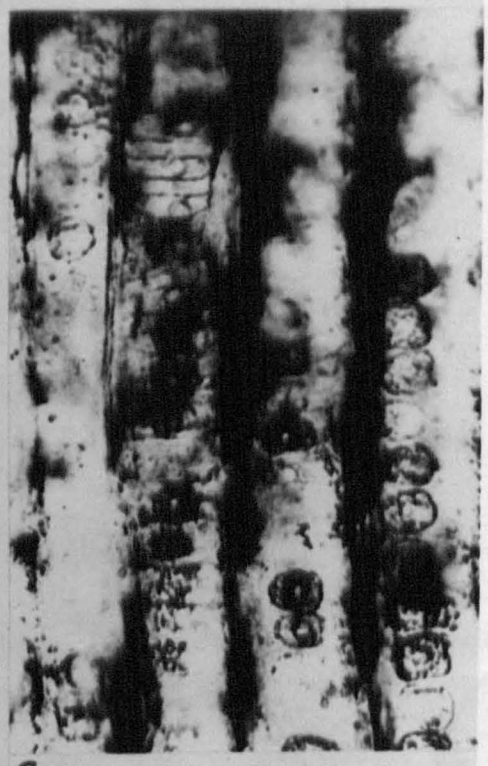


PLATE XII



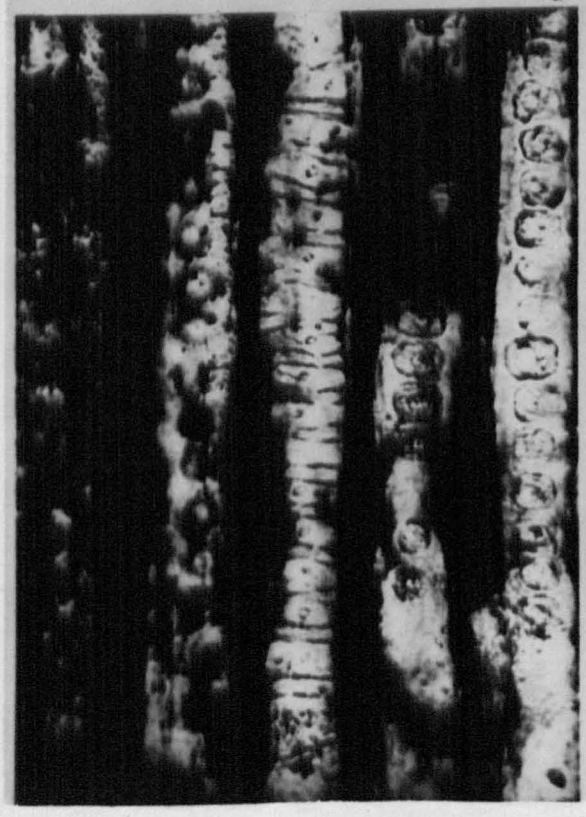
A

B



C

D



E

APPENDIX ON TRACHEID LENGTH AND RAY HEIGHT.

1) Tracheid Length

Ladell (1959) has described a method of obtaining an accurate estimate of the mean tracheid length within a specimen of wood, from a series of tangential longitudinal sections. It consists of counting the number of tracheid endings (cell tips) between a pair of arbitrarily spaced lines, which may be inscribed on a micrometer eye-piece, or on a screen on to which an image of the slide may be projected.

In this thesis, the first method was used and the lines measured on a stage micrometer scale were 0·5 mm. apart. The following formula was applied:

$$\text{Mean tracheid length} = \frac{\text{No. of cells} \times \text{distance between the lines}}{\text{No. of cell tips.}}$$

For further details of this method, Ladell's work should be consulted.

The results obtained during the investigation of these fossil woods are given in the following pages.

TRACHEID LENGTH COUNTS

Dadoxylon bouzhevi sp.nov.

Specimen A.l.

	T.L.S. 3	T.L.S.2	T.L.S. 1	T.L.S. 4
a)	5	1·66	1·66	1·25
b)	5	2·5	7·5	1·66
c)	2·5	1·25	2.5	2·5
d)	5	5	5	2.5
e)	1·25	1·66	2·5	1·66
f)	2.5	2·5	2·5	1·66
g)	1·66	1·25	1·66	1·66
h)	1·66	2·5	2·5	2·5
i)	2·5	1·25	5	1
j)	2·5	1·66	5	1.25
	2·957	2·123	3·082	1·764

Dadoxylon bougheyi sp.nov.

Specimen A.l. cont.

	T.L.S. 5	T.L.S. 7
a)	5	1·66
b)	1	2·5
c)	2·5	2·5
d)	5	1·66
e)	5	5
f)	1·66	2·5
g)	2·5	1·66
h)	2.5	2.5
i)	2·5	1·25
j)	2·5	2·5
	3·016	2·373

Average length of tracheid = 2·55 mm.

Dadoxylon bondii sp.nov.

Specimen G.3.

	T.L.S. 3	T.L.S. 4	T.L.S. 5	T.L.S. 6
a)	2·5	5	2.5	5
b)	5	5	5	5
c)	2·5	2·5	5	5
d)	2·5	5	5	2·5
e)	5	5	2·5	5
f)	2·5	5	5	5
g)	2·5	5	5	2·5
h)	5	2·5	5	5
i)	2·5	5	2·5	2·5
j)	5	5	5	5
	3·5	4·5	4·25	4·25

Average length of tracheid = 4·125 mm.

Heliocoxylon waltonii sp.nov.

Specimen A.4

	T. L. S. 1	T. L. S. 2
a)	1.25	2·5
b)	5	5
c)	5	1·66
d)	2·5	5
e)	2·5	2·5
f)	2·5	2·5
g)	5	5
h)	2·5	5
i)	1·66	2·5
j)	2·5	5
	3·041	3·666

Average length of tracheid = 3·3535 mm.

2. Data on variations in ray height in Tangential Longitudinal Section from Fossil Woods described in this Thesis.

Specimen A.2. Dadoxylon boughayi sp.nov.

No. of cells per ray.	No. of rays in T. L. S. No. : 1	2	3	4	5	6	7	8	9	Ray Total	%
1	5	3	9	9	7	1	5	5	1	45	5
2	19	25	25	20	24	27	23	9	15	206	22·8
3	14	9	11	11	14	9	11	12	18	109	12·1
4	12	11	12	10	5	8	12	15	6	91	10·1
5	7	10	6	14	8	6	9	9	6	75	8·33
6	6	4	6	5	1	7	7	9	9	54	6·0
7	3	9	4	1	5	9	5	8	13	57	6·4
8	2	3	2	8	3	2	4	6	5	35	3·88
9	7	5	4	2	3	2	2	4	3	32	3·55
10	1	4		2	4	5	2	1	2	21	2·33
11	3	1	2	2	1	1	4	4	1	19	2·11
12	5		4	1	1		3	2	2	18	2·0
13	2	3	1	1	2	2	3	1	3	18	2·0
14		1	2	1	2	2	4	1	4	17	1·88
15	3		1	3	5	2		1	1	16	1·77
16				3	2	2	1	2	1	11	1·22
17				1	3	2		2	1	9	1·0
18	3		4		3	2	1	2	2	17	1·88
19					1	3		2	2	11	1·22
20	3	2	1				1			4	0·44
21								1		1	0·11

cont. Specimen A.2. Dadoxylon boucheyi sp.nov.

No. of cells per ray	No. of rays in T. L. S. No. : 1	2	3	4	5	6	7	8	9	Ray Total	%
22	1	1	2	3	2					9	1·0
23	1	1				1	1			4	0·44
24	1	2	1	1				2	1	8	0·88
25	1	21	2					1		7	0·77
26		1							1	2	0·22
27		1					1			2	0·22
28		1		1	1	2				5	0·55
29											
30	1		1						1	3	0·33
31				1	1			1	1	4	0·44
32											
33	1					2	1			4	0·44
34									1	1	0·11
35											
36					1					1	0·11
37						1				1	0·11
38											
39											
40											
41											
42		1								1	0·11
43		1								1	0·11
48	1									1	
66					1					1	0·11

Specimen No.3 Dadoxylon sp. A

No. of cells per ray	No. of rays in T. L. S. No : 3	4	5	6	7	8	Total rays	%
1	1			1		3	5	1·17
2	3	1	8	5	4	5	26	6·11
3	5	3	10	7	11	8	44	10·35
4	11	4	12	16	14	23	80	18·82
5	8		10	18	14	7	57	13·41
6	19	5	10	13	17	14	78	18·35
7	11	1	9	10	10	7	48	11·29
8	7	3	6	5	5	8	34	8·00
9	9		9	3	6	9	36	8·47
10	9	3	5	4	5	4	30	7·05
11	6		4	5	2	5	22	5·17
12	3	1	3	4	5	2	16	3·76
13	2	1	6	2	1	2	14	3·29
14	1		2	1	1	1	6	1·41
15	3			1	2	2	8	1·88
16		1	1	3	1		6	1·41
17			1	1			2	0·47
18			1				1	0·235
19	1	1	1		1		4	0·941
20								
21	1		1	1			2	0·47
22					2		2	0·47
23			1		1		2	0·47
24		1					1	0·235
25								

Specimen O.3. *Dadoxylon bondii* sp.nov.

No. of cells per ray	No. of Rays in T. L. S. No. : 2	3	4	5	6	7	8	9	Ray Total	%
1	13		6	1	4	2	6	8	40	5
2	12	8	20	15	9	18	31	17	130	16·25
3	20	26	11	17	26	29	21	35	185	23·125
4	14	16	12	19	20	16	17	16	127	15·875
5	11	13	9	20	19	14	7	8	101	12·625
6	7	10	13	10	7	12	6	5	70	8.75
7	11	6	10	7	7	5	4	4	54	6·75
8	6	11	8	4	1	2	1	3	36	4·5
9	2	2	3	2	4	1	2	2	18	2·25
10	1	3	5	3	2	1	3	1	19	2·375
11	1	4	1	1			1		8	1·00
12	1	1					1	1	4	0·5
13	1								1	0·125
14				1		1			2	0·5
15										
16				1					1	0·125
17			1						1	0·125

Specimen G.2 — Dadoxylon bondii sp.nov.

No. of cells per ray	No. of rays in T. L. S. No. : 1	2	3	7	8	10	Ray Total	%
1	0	2	6	3	2	3	24	4·00
2	24	17	23	20	22	38	144	24·00
3	19	14	17	24	16	34	124	20·66
4	16	17	12	22	22	17	106	17·66
5	11	7	13	19	21	6	77	12·83
6	6	12	9	4	10	1	42	7·00
7	2	12	4	3	4	1	28	4·66
8	6	6	6	2	1		20	3·33
9	1	5	8	1	1		16	2·66
10	3	4	1		1		9	1·50
11	1						1	0·166
12	2	1	2				5	0·833
13		1					1	0·166
14	1	1					2	0·333
15								
16		1					1	0·166
17								

Specimen E.1. Dadoxylon hondii sp.nov.

No. of cells per ray	No. of rays in T. L. S. No.: 1	1A	2	2A	3	3A	4	Ray Total	%
1	1	2	2	1	2	1	7	16	2·285
2	13	11	19	14	20	15	18	100	14·285
3	16	25	27	23	17	21	19	148	21·142
4	19	21	17	16	26	23	20	141	20·142
5	15	18	21	18	17	17	13	119	17·00
6	9	8	13	14	10	10	11	82	11.714
7	6	8	4	6	7	7	4	42	6·00
8	4	4	4	5	2	3	4	26	3·714
9	6	2	1	2			2	15	2·142
10	3		1	1		1	1	7	1·00
11	2	11	1			1	1	6	0·999
12	2					1		3	0·429
13								2	0·299
14	2								0·299.

Specimen G.1. *Kaeoxylon rangense* sp.nov.

No. of cells per ray.	No. of rays in T. L. S. No. : 2	3	4	5	6	7	8	9	10	Total rays	%
1	1	2		3		3		2	2	13	1·44
2	13	17	12	13	21	10	15	25	20	146	16·2
3	13	15	12	16	6	22	11	14	22	131	14·5
4	12	11	11	17	22	17	20	21	15	146	16·2
5	16	14	15	12	14	17	16	15	14	133	14·7
6	11	12	11	11	9	11	17	7	8	-97	11·77
7	8	9	9	6	8	5	11	6	7	-69	7·66
8	1	4	7	4	5	6	2	6	6	-41	4·55
9	8	4	6	6	8	4	1	1		-38	4·22
10	5	2	4	6	3	1	3	1	2	-27	3·00
11	1	3	3	1	1		3	1	1	-14	1·55
12	4	1	4		1	1			2	- 9	1·00
13		1	1	1	1		1			- 5	0·55
14	2	2	1			1				- 6	0·66
15	2		1	2		1				- 6	0·60
16	1	1	2		1					- 5	0.55
17		1	1		1			1		- 3	0·33
18	1		1							- 2	0·22
19		1	1							- 2	0·22
20											
21	1									1	0·11
22											
23									1	1	0·11

Specimen A.4. *Heliooxylon waltonii* sp. nov

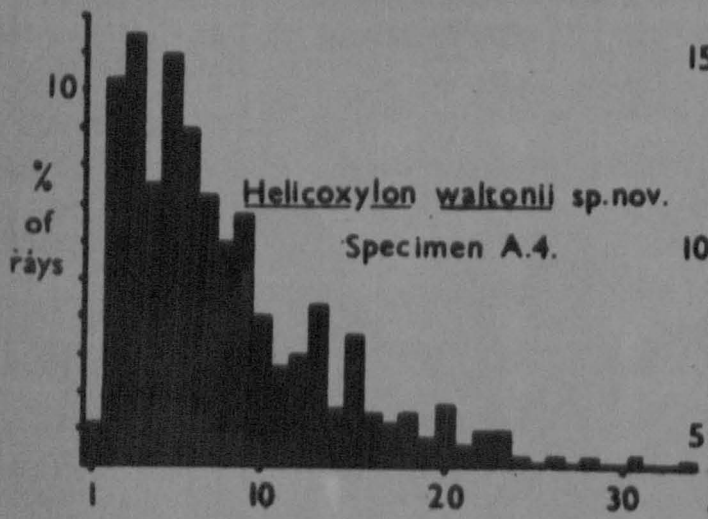
No. of cells per ray	Sections 1A	1B	2A	2B	Total Rays	%
1	2	2		1	5	1·25
2	10	12	8	11	41	10·25
3	11	12	12	11	46	11·5
4	5	12	7	6	30	7·5
5	11	14	13	6	44	11·0
6	9	5	9	13	36	9·0
7	5	7	10	7	29	7·25
8	5	6	6	7	24	6·0
9	8	4	7	8	27	6·75
10	6	4	4	2	16	4·0
11	3	2	3	3	11	2·75
12	3	5	1	3	12	3·0
13	6	3	3	5	17	4·25
14	1	2	2	1	6	1·5
15	3	2	4	5	14	3·5
16	1	1	2	2	6	1·5
17	1	1	2	1	5	1·25
18	1	1	1	3	6	1·5
19	1	1	1		3	0·75
20	2	2	3		7	1·75

Specimen A. 4. *Heliconylon waltonii* sp. nov. cont.

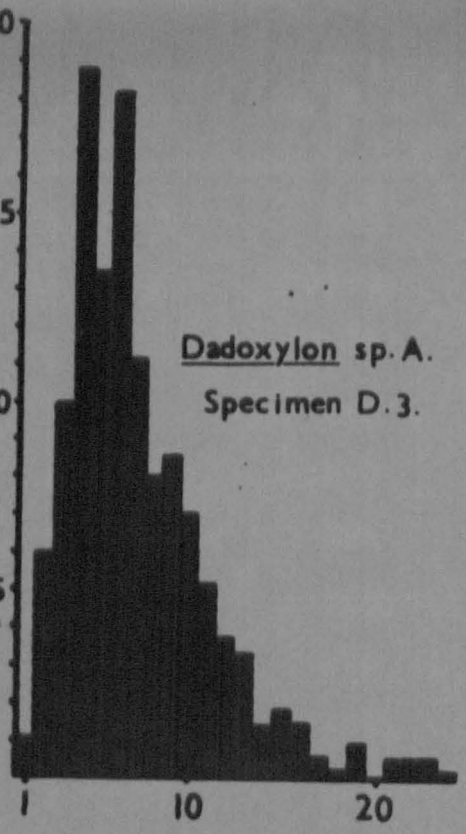
No. of cells per ray	Sections 1A	1b	2A	2B	Total rays	%
21		1		1	2	0·5
22	2		1	1	4	1
23	1			3	4	1
24	1				1	0·25
25						
26	1				1	0·25
27						
28					1	0·25
29						
30						
31					1	0·25
32						
33						
34						
35						
36						
37			1		1	0·25

PAGE NUMBERING AS ORIGINAL

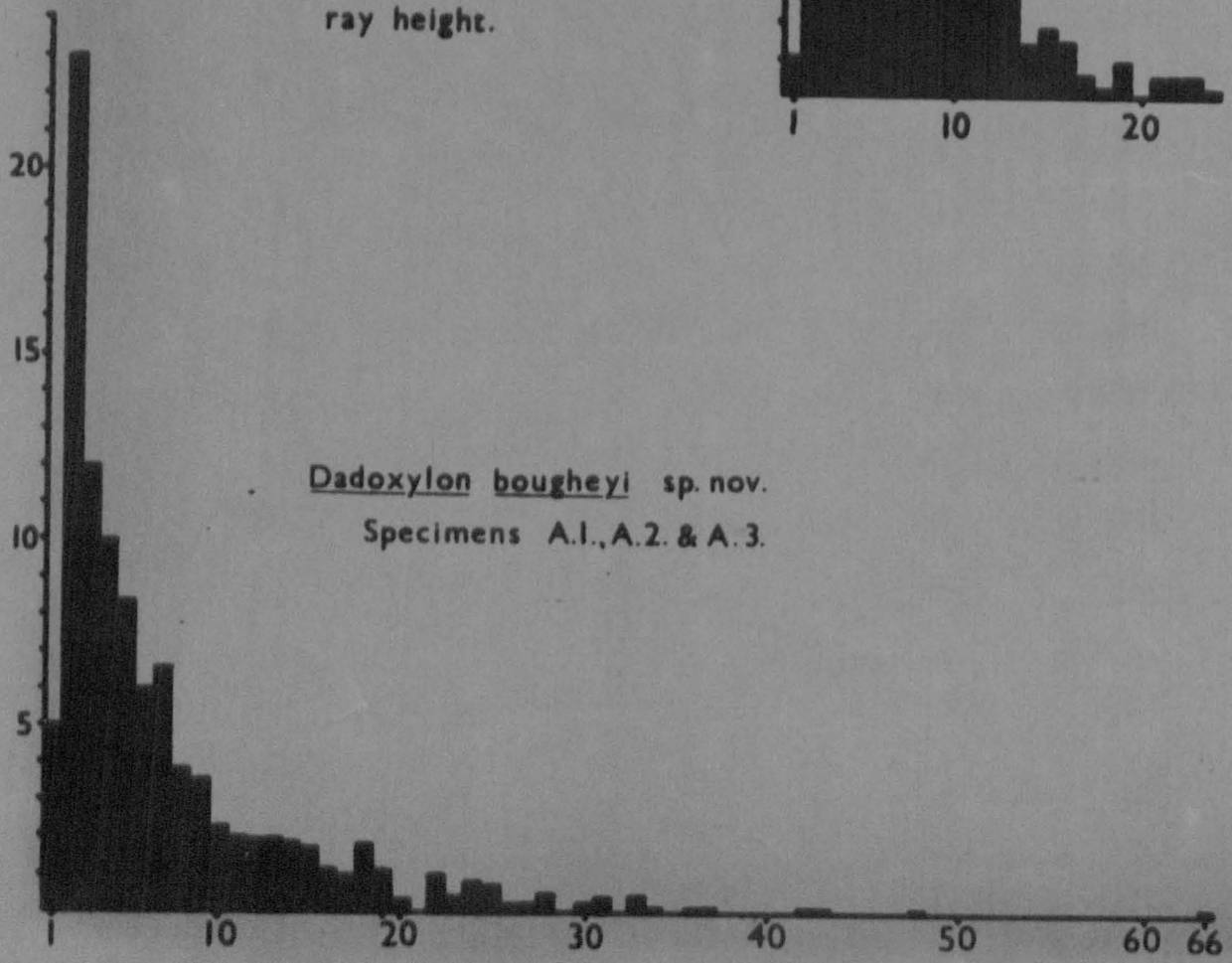
HISTOGRAMS SHOWING VARIATION IN RAY HEIGHT IN SPECIMENS OF FOSSIL WOOD.



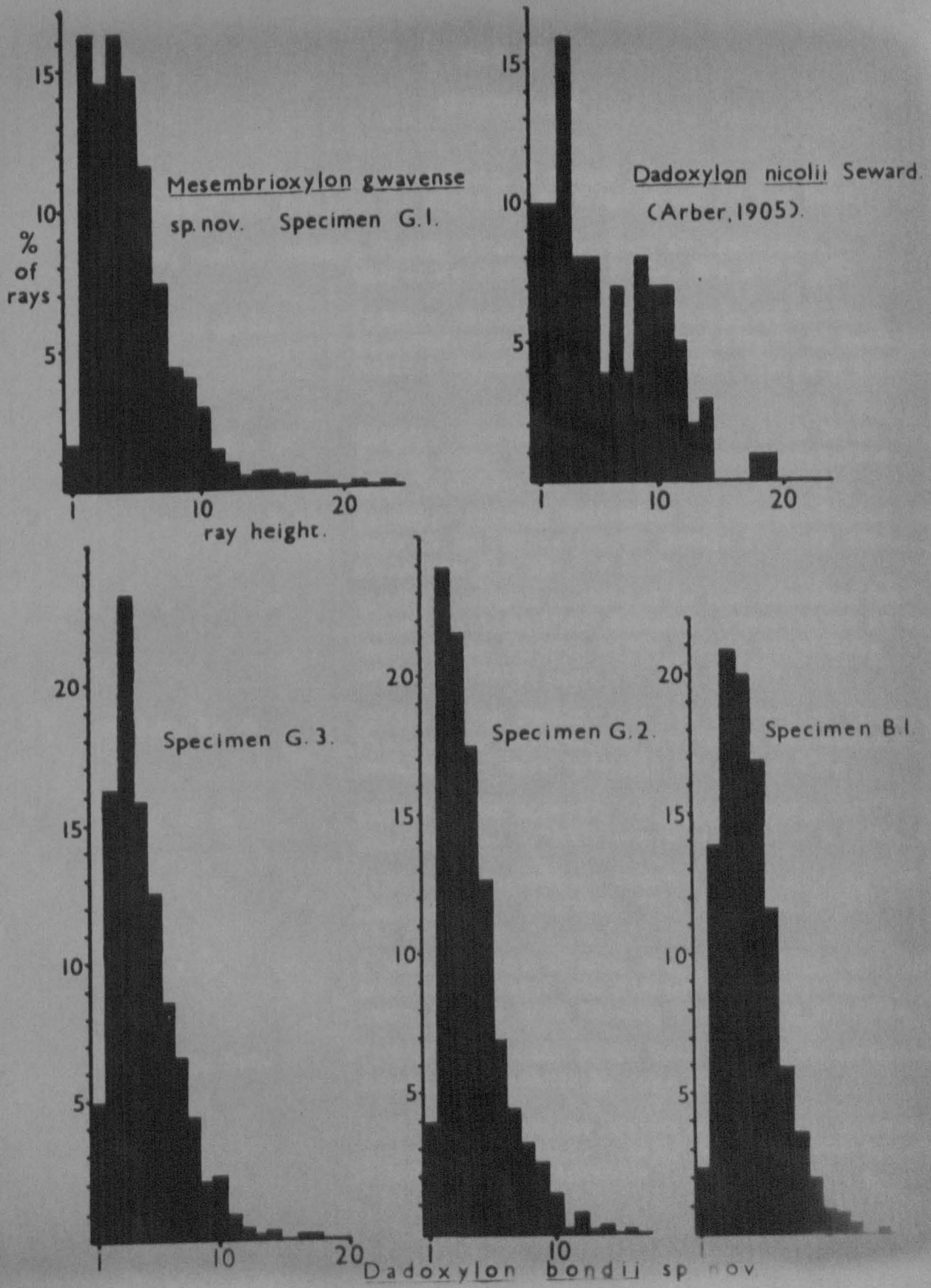
Helicoxylon waltonii sp.nov.
Specimen A.4.



Dadoxylon sp. A.
Specimen D.3.



Dadoxylon bougheyi sp. nov.
Specimens A.1., A.2. & A.3.


15
10
% of rays
5
1
10
20
ray height.
Mesembrioxylon gwavense sp. nov. Specimen G.1.
Dadoxylon nicolii Seward. (Arber, 1905).
Specimen G. 3.
Specimen G. 2.
Specimen B.1
Dadoxylon bondii sp nov

PART IV

BIBLIOGRAPHY

For the sake of completeness, a number of papers consulted by the writer are included in addition to those cited in the text.

Andrew, A.R. & Bailey, T.E.G. (1910). Geology of Nyasaland. Quart. J. Geol. Soc. Lond., 66, 169 - 251

Arber, E. A. N. (1905). Catalogue of fossil plants of the Glossopteris flora in the Department of Geology, British Museum Natural History, 255 pp., (London: H.M.S.O.)

Archangelsky, S. (1957). Las Glossopterideas Del Bajo de la Leona (Santa Cruz) Revista Geol. Asoc. Argentina. XII, 3. 1957. 135 - 164.

" " (1958). Estudio Geologico Y Palaeontologico Del Bajo de la Leona. (Santa Cruz). De Acta Geol. Lilloana. II. pp. 5 - 133.

" " (1960) Estudio Anatomico de dos Especies del Genero "Abietopitys" Krausel, Procedentes de la Serie Noura Lubecka Prov. Chubut Argentina. Acta Geol. Lilloana, III, pp. 331 - 338.

Bailey, I. W. (1933). The Cambium and its Derivative Tissues, VII., Problems in identifying the Woods of Mesozoic Coniferae. Ann. Bot. 47, pp. 145 - 157.

Beck, C. B. (1960). The identity of Archaeopteris & Callixylon. Brittonia, Vol. 12, No. 4 Oct., 1960.

" " " (1960b) Connections between Archaeopteris and Callixylon. Science, Vol. 131, No. 34/2. pp. 1524-25.

" " " (1962) Reconstructions of Archaeopteris and further considerations of its Phylogenetic position. Amer. Journ. Bot. Vol.49, No. 4. pp 373-382.

Bhardwaj, D.C. (1953). Jurassic Woods from the Rajmahal Hills, Bihar. Palaeobot. 2. pp. 59-69.

Bond, G. (1952). The Karroo System in Southern Rhodesia. Gondwana Symposium. (XIXe Congres- Geologique International. Algiers).

Bond, G. (1955) The Madumabisa (Karroo) Shales in the Middle Zambezi Region. Trans. Geol. Soc. S. Afr. 58 pp 71-99.

" " (1962) Past Climates of Central Africa. Oxford University Press. London.

Brongniart, A. (1828) Prodrome d'une Histoire des Végétaux Fossiles. viii + 223p Paris.

(1830) Histoire des Végétaux Fossiles 1,5. pp. 209-249 Paris.

Bunbury, C.J.F. (1861) Notes on a collection of fossil plants from Nagpur, Central India. Quart. J. Geol. Soc. Lond. 17. pp. 325-346.

Carruthers, W. (1869) On the plant remains from the Brazilian Coal beds, with remarks on the genus Flemingites. Geol. Mag. VI. p. 151.

" " (1880) In Etheridge, on a Collection of Fossil Plants from the Bowen River Coalfield, etc. Proc. Roy. Phys. Soc. Edin., 5, p.325.

Chalk, L & Ortiz, C.E. (1964) Variation in Tracheid Length. Forestry. 34. 2 pp. 119-124.

Crie, L. (1889) Beiträge zur Kenntniss der Fossilen Flora einiger Inseln des Südpacifischen und Indischen Oceans. Pal. Abhand. (Dames and Kayser) (N.F.), Bd.I Heft ii.

De Bary, A. Comparative Anatomy of the Phanerograms and Ferns. Oxford. Clarendon Press p. 659.

Dinwoodie, J.M. (1961) Tracheid and Fibre Length in Timber, a Review of Literature. Forestry. 24. 2. pp. 125-144.

Dixey, F. (1937) Geology of Part of the Upper Luangwa Valley, N.E. Rhodesia. Quart. J. Geol. Soc. Lond. 93 pp. 52-76.

Dolianiti, E. (1953) O Genero Glossopteris, (A Flora do Gondwana Inferior em Santa Catarina). Notas Serv. Geol. Brazil. 60. pp. 1 - 7.

" " (1954) O Genero Gangamopteris. Notas Serv. Geol. Brazil. 89. pp. 1 - 12.

" " (1954) O Genero Gangamopteris angustifolia & Gangamopteris Buriadica na Formacao Marica do Rio Grande do Sul. Notas Serv. Geol. Brazil. 87. pp 1 - 6.

Du Toit, A. L. (1954) The Geology of South Africa. Oliver & Boyd, Edin. x 611. pages.

Eckhold, W. (1922) Die Hoftüpel der rezenten und fossilen Koniferen. Jahrb. Preuss Geol. Landesanstalt 1921, 42, 1922.

Edwards, W.N. (1937). See Dixey, 1937.

Endlicher, S. (1847). Synopsis Coniferarum. Sangalli.

Esau, K. (1953) Plant Anatomy. x. 735p J. Wiley & Sons.

Etheridge, R. Jun. (1894) On the mode of attachment of the leaves, or caudex of Glossopteris, with remarks on the relation of the genus to its allies. Proc. Linn. Soc. New South Wales, Ser. 2. Vol. 9.

" " " (1903) The fructification of Shizoneura australis Eth. Fil. Rec. Geol. Surv. New South Wales. Vol. 7.

" " " (1918) The arrangement of the leaves in the Australian species of Noeggerathiopsis. Geol. Mag. N.S. VI, Vol5.

Feistmantel, O (1879a) Flora of the Talchir-Karharbari Beds. Mem. Surv. Ind. Ser. XII. Vol. 1.

" " (1879b) Outliers on the Madras Coast. Mem. Geol. Surv. Ind. Ser. II. Vol. 1, pat 4.

" " (1879c) The Fossil Flora of the Gondwana System (Lower Gondwanas). Mem. Geol. Surv. Ind. Pal. Ind. Ser. XII. Vol. III, pts. 1 - 3)

" " (1881) Flora of the Damuda and Panchet Divisions. Mem. Geol. Surv. Ind. Ser. II, XI, XII.

" " (1882) Fossil Flora of the South Rewah Gondwana Basin. Mem. Geol. Surv. Ind. Ser. XII Vol. 4, pt. 1.

" " (1886) The Fossil Flora of some of the Coal Fields in Eastern Bengal. Mem. Geol. Surv. Ind. Ser. XII. Vol 4. pt.2.

Gothan, W. (1905) Zur Apatomie lebender und fossilier Gymnospermenhölzer. Abh. K. Preuss. geol. Landes [N.F.] Heft XLIV. p.155.

Garrett, S.D. (1956) Lecture to the Cambridge Botanical School.

Geoppert, H.R. (1850) Monographie der fossilen Coniferen. Naturwerkundige Verhand. Holland. Maatschap. Wettenschappen Haarlem. Leiden.

Grambast, L. (1951) Tetraclinoxylon (Cupressinoxylon) bouroui nov. gen. nov. sp. Bois fossile du Chattien du Bassin de Paris. Extrait Bull. Soc. Geol. France 6° serie, I.

" " (1952) Sur la signification des structures généralisées chez les coniferales et la valeur des Protopinacées en tant que groupe. Extrait des Comptes-rendus des Séances de l'Académie des Sciences. 235 1533-1535.

" " (1954) Un Juniperoxylon Particulier dans L'Eocène Inferieur du Bassin de Paris. Achives Muséum (7°) 3. 1 - 24

" " (1960) Etude d'un Dadoxylon permien du Congo Belge et remarques sur les Dadoxylon Permo-carboniferes des Territoires à Flore de Gondwana. Annales du Musée Royal du Congo Belge. Tervuren.

Greguss, P. (1955) Identification of Living Gymnosperms on the Basis of Xylotomy. Budapest Akadomiai Kiado.

" " (1961) Permische Fossile Hölzer aus Ungarn. Palaeontographica Abt. B/109/Liefg. 5-6/131-146. Stuttgart, Nov. 1961.

Harris, T.M. (1957) A Liasso-Rhaetic Flora in South Wales. Proc. Roy. Soc. Lond. B. 147, 289-308.

" " " (1958). Forest Fire in the Mesozoic. J. Ecol. 46, pp. 447 - 453.

Hartig, T. (1848) Beiträge zur Geschichte der Pflanzen und zur Kenntnis der Norddeutschen Braunkohlenflora. Pot. Zeitung, Band 6, pp. 166-172.

Hill, T.G. (1906) On the presence of a Parichnos in recent plants. Ann. Bot. 20. pp. 267-273.

Høeg, O.A. & Bose, M.N. (1960). The Glossopteris Flora of the Belgian Congo. Annales du Musée Royal du Congo-Belge. (Sci. Geol.) 32. pp. 1 - 166

Holden, Ruth (1914) Cretaceous lignites from Cliffwood, New Jersey. Bot. Gaz. 58. p. 160.

" " (1917) On the anatomy of two Palaeozoic Stems from India. Ann. Bot., 31. p.p. 315-326.

International Code of Botanical Nomenclature (1956

Jeffrey, E. C. (1907) Araucariopitys, a new genus of araucarians. Bot. Gaz. vol. 44., p. 455

" " " (1910) A new araucarian genus from the Triassic. Proc. Boston Soc. Nat. Hist. 34. No. 9, p. 325

" " " (1917) The anatomy of woody plants. 1. vol. Chicago. University of Chicago Press. 1917

Jeffrey, E.C. & Hotmore, B.H. (1926). On the occurrence of Parichnos in certain Conifers. Ann. Bot. XL. pp. 799 - 811

Joy, K.W., Willis, A.K. and Lacey, W.S. (1956) A rapid cellulose peel method in palaeobotany. Ann. Bot. N.S. 20 pp. 635 - 7

Kräusel, R. (1919) Die fossilen Koniferenhölzer Palaeontögr. 62, 1919.

" " (1949) Die Fossilen Koniferenhölzer (unter Ausschluss von Araucarioxylon Kraus) II. Kritische Untersuchungen zur Diagnostic lebender und Fossiler Koniferen-Hölzer. Ibid., 89B: pp. 83 - 203.

" " (1956) Lianen aus den Karru-Schichten Süd Afrikas. Der Versteinertewald im Knokoveld, Sudwest Afrika Hoelzer aus den südlichen Gebeit der karru-schichten Sudwest Afrikas. Sonderdruck aus Senckenbergiana lethaea. Band. 37.

" " (1962) Trans Antarctic Expedition (1956) Scientific Report No. 9 (2) Geology. Fossil Floras of Antarctica. Appendix on Fossil Woods.

Kräusel, R & Dolianiti, E. (1958) Gymnospermenhölzer aus dem Palaeozoicum Brazilians. Palaeontogr. B. 104. pp. 115-137.

" " & Maithy, P.K. & Maheshwari, H.K. (1961) Gymnospermous wood with primary structures from Gondwana rocks. A review, Palaeobot. 10., Nos. 1 and 2 pp. 97 - 107.

" " & Range, P. (1928) Beitrage zur Kenntnis der Karrooformation Deutsch-Sudwest Africas. (Freuns. Geol. Land). Berlin, 1928.

Lacey, W. S. (1953) Methods in Palaeobotany. North Western Naturalist. June, 1953. pp. 234 - 249

" " " (1959a) Some aspects of Palaeoecology in the Karroo of Rhodesia and Nyasaland. Proc. Linn. Soc. 172.

" " " (1959b) The occurrence of presumed glossopteridian fructifications in Rhodesia and Nyasaland. Nature, London 184. 1592 - 93.

Lacey, W. S. (1961a) New Records of Fossil Plants in the Lower Karroo of Southern Rhodesia and Nyasaland. C.R. 4th. Carb. Congress, Harlem (1958) 2 pp-367 - 368.

" " " (1961b) Studies in the Karroo floras of Rhodesia and Nyasaland. Pt. 1. Proc. Transac. Rhodesian Sci. Assoc. 49. Pt. 1. pp. 26 - 53

Ladell, J.L. (1959) A new method of measuring tracheid length. Forestry, 32. No. 2. pp. 124-5

" " " (1962) Leaf scale traces in Corsican pine. Forestry 35, No. 1. p. 81-82.

Lang, W. H. (1926) A cellulose-film transfer method in the study of fossil plants. Ann. Bot. 40. No. 159.

" " " (1929) On fossil wood (Dadoxylon henrikei, n.sp.) and other plant remains from the clay slates of South Cornwall. Ann. Bot. 43. No. 172.

Larsen, K. (1955) Cytotaxonomical Studies on the Mediterranean Flora. Bot. Notiser. 108. pp 263 - 275

Leslie, T.N. (1921) Observations on some fossil plants from the permo-carboniferous of Vereeniging. Proc. Geol. Soc. S. Afr. 24. 19 - 31

Lightfoot, B. (1914) The Geology of the North-western part of the Wankie Coalfield. Bull. Geol. Surv. S. Rhod., 1, 4.

" " (1929) The Geology of the Central part of the Wankie Coalfield, Bull. Geol. Surv. S. Rhod., 19.

Linsbauer, K. (1930) Die Epidermis. Hand-buch der Pflanzenanatomie. Band 4. p.27

Lundquist, G. (1919) Fossile Pflanzen der Glossopteris Flora aus Brasilien. Kungl. Svenska Vetensk. Handl. Band.60. No. 3. p. 14 (Stockholm).

Monniero, J. (1944) Dadoxylon whitei sp. n. Bol. Fac. Fil. Sc. Ltr. Univ. Sao Paulo. 45 Geol. N.1. pp. 107-112 et. Revista Inst. Ad Lutz. 4. pp. 212-14.

" " (1946) Contribucao ao estudo de Dadoxylon nummulerium White. Dep. Nac. Produs. Min. Div. Geol. Minan Notas prelim. et estudos. No. 35. 1 - 6

McCoy, F. (1847) On the fossil botany and zoology of the rocks associated with the coal of Australia. Ann. & Mag. Nat. Hist. 20 pp. 145 - 297

" " (1861) Footnote to a commentary on "A communication made by the Rev. W. B. Clarke" &c. p. 96. Trans. Roy. Soc. Victoria, 5 (1860) p.107.

McCoy, F (1875) Prodromus of the Palaeontology of Victoria. Dec. 1. & 2. Geol. Surv. Victoria, Melbourne.

Molyneux, A.J.C. (1905) The sedimentary deposits of Southern Rhodesia. Quart. J. Geol. Soc. Lond. 59 pp 266-291

" " " " (1909) The Karroo System in Northern Rhodesia. Quart. J. Geol. Soc. Lond., 65, pp. 408 - 439.

Pant, D.D. (1958) The structure of some leaves and fructifications of the Glossopteris flora of Tanganyika. Bull. Brit. Mus. (Nat. Hist.). Geology 5. No. 4.

Phillips, E.W.J. (1948) Identification of Softwoods by their microscopic structure. Forest Products Research bulletin No. 22. H.M.S.O. Lond.

Plumstead, E.P. (1952) Descriptions of two new genera and six new species of fructification on Glossopteris leaves. Trans. Geol. Soc. South Afr. 55. 281 - 328

" " " (1956a) Bisexual fructifications born on Glossopteris leaves from South Africa. Palaeontographica B.100 1 - 25.

" " " (1956b) On Ottokeria, the fructification of Genamopteris. Trans. Geol. Soc. S. Afr. 59. 211-236

" " " (1958a) Further fructifications of the Glossopteridoae and a provisional classification based on them. Trans. Geol. Soc. S. Afr. 617.

" " " (1958b) The habit of growth of the Glossopteridoae. Trans. Geol. Soc. S. Afr. 61

" " " (1962) Permo-carboniferous Coal Measures of the Transvaal, South Africa, and example of contrasting stratigraphy in the Southern and Northern hemispheres. 4° Congres Avanc. Et. Stratigr. Carbonif. 2. 545 - 550.

" " " (1962) Transantarctic Expedition (1955-58). Scientific Report No. 9. (2). Geology Fossil Floras of Antarctica.

Potonié, H. (1893) Die Flora des Rothliegenden von Thuringen. Jahrb. k. Preuss. geol. Landesanst. 2.

Potonié, H. (1959) Taxonomy of fossil plants in the international code of botanical nomenclature, 1959. Palaeobot. 7. No. 1.

Presl, C.B. (1838) in Sternberg, K. Versuch Coognostich-botanischen Darstellung der Flora Vorwelt. 2. (7/8) 1 - 220.

Priestley, J.H. (1943) The cuticle in Angiosperms. Bot. Rev. 9 593-616.

Ramanujam, C.J.K. (1954) On some silicified woods from near Pondicherry. Palaeobot. 3 : 43-50.

Rau, W. (1934) Dadoxylon (Araucarioxylon) butiense n. sp. Ein beitrage zur entwicklung der holzstruktur der palaeozoischen koniferen Rio Grande do Sulo. Rev. Sudamer. Bot. 1, No. 6, pp. 1 - 4.

Richards, P.W. (1957) The Tropical Rain Forest. Univ. Press Cambridge.

Rigby, J.F. (1960) The discovery of Glossopteris fructifications in New South Wales. Aust. J. Sci., 23. 230.

Sah, S.C.D. (1959) Coniferocaulon latisulcatum sp. nov. from the Rajmahal Hills, Bihar. Palaeobot. 6. No.2.

Sahni, B. (1923) On the structure of the cuticle in Glossopteris nurustifolia (Brong). Rec. Geol. Surv. Ind. 54.

Sahni, B & Singh, T.C.N. (1926) On some specimens of Dadoxylon arberi from New South Wales and Queensland. J. Ind. Bot. Soc. 5. No. 111.

Salisbury, E.J. (1927) On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. Phil. Trans. Roy. Soc. Lond. B. 216. p.p. 1 - 65.

Schimper, W.P. (1869) Traité de Paléontologie Végétale. Paris. J.B. Baillière et Fils.

Scott, D. H. (1902) On the primary structure of certain palaeozoic fossils with the Dadoxylon type of wood. Trans. Roy. Soc. Edin. 40 pp 531 - 565.

Sen, J. (1955a) On some fructifications borne on Glossopteris leaves. Bot. Notiser. 108 pp 244-252.

" " (1955b) On a Glossopteris bearing scri-like structures. Nature, London 176. 742-3

Seward, A.C. (1898) Fossil plants vol. 1.

" " " (1908) On a collection of fossil plants from South Africa. Quart. J. Geol. Soc. Lond. 64. p. 83.

" " " (1910a) Antarctic Fossil Plants. British Antarctic "Terra Nova" Expedition. Brit. Mus. Geol. 1. No. 1.

" " " (1910b) Fossil Plants, vol.2.) Cambridge
" " " (1917) Fossil Plants, vol.3.) University
(1919) Fossil Plants, vol.14) Press.

Seward, A.C. & Ford, S. (1906) The araucarineae recent and extinct. Phil. trans. roy. soc. London. B.198.

Seward, A. C. & Leslie, T.H. (1908) Permo-carboniferous plants from Vereeniging. Quart. J. Geol. Soc. 64. p. 109

Seward, A.C. & Sahni, B. (1920) Indian Gondwana Plants. Mem. Geol. Surv. Ind. N.S. 7. No. 1.

Seward, A.C. & Smith-Woodward, A. (1905) Permo-carboniferous plants and vertebrates from Kashmir. Mem. Geol. Survey. Ind. N. S. 2. 2.

Shilkina, E.A. (1960) Wood of Cordaitalen (Taxopitys sp.nov.) from the Upper Carboniferous of Eastern Siberia. Palaeont. J. Acad. Sci. U.S.S.R. 3. p. 123-126. (original not seen. Quoted from Krausel, R. Maithy, P.K. and Mahashwari, H.K. 1961).

Sifton, H.B. (1957). Air-space tissue in plants. Bot. Rev. 23. (5). p. 168.

Sinnot, E.W. (1909) Paracedroxylon, a new type of araucarian wood. Rhodora 3. 129. p. 165.

" " " (1911) Some features of the anatomy of the foliar bundle. Bot. Gaz. 51. p. 258.

Srivastava, P.N. (1956) Studies in the Glossopteris Flora of India, 4; Glossopteris, Gangamopteris & Palaeovittaria from the Raniganj Coalfield. Palaeobot. Lucknow. 5, pp. 1 - 45.

Stopes, M.C. (1914) A new Araucarioxylon from New Zealand. Ann. Bot. 28. pp. 341 - 350.

" " " (1915) Cretaceous flora Pt. 2. Catalogue of Mesozoic Plants in Brit. Mus. (Nat. Hist.)

Surange, K.R. & Maithy, P.K. (1961) Studies in the Glossopteris flora of India. (13). Barakaroxylon, a new genus of petrified wood from the Lower Gondwanas of India. Palaeobot. 10. 1 & 2. pp. 108-113.

Surange, K.R. & Saxena, V.N. (1960) Dadoxylon barakaranense. sp. nov., from the Jharia Coalfield India. Palaeobot. 7. 1. pp. 1 - 5.

Surange, K.R. & Srivastava, P.N. (1956) Studies in the Glossopteris Flora of India, 5., Generic status of Glossopteris, Gangamopteris & Palaeovittaria. Palaeobot., Lucknow, 5. pp. 46-49.

Suryanarayana, K. (1955) Dadoxylon rajmahalense (Sahni) from the Coastal Gondwanas of India. Palaeobot. 4.

Teichert, C. (1952) A Brief History of the Gondwanaland Concept., and of the International Gonwana Commission. XIX^{O} Congres Geologique International.

Teixeira, C. (1947) Sobre a flora fossil do Karroo da regino de Tete (Mocambique) Estud. Geol. Palaeont. An.,2.

" " (1952) La flore fossile du Karroo de la Zambesie et la notion de Continent de Gondwana. C.R. 3rd Congr. Carb. Strat. & Geol. Heerlen, (1951) 2. pp. 627-630.

" " (1954) Fossil flora of the Karroo of the Zambesi Basin and the relation between Gondwanaland and Northern Territories. Proc. Pan. Indian Ocean. Sci. Congr. 100. pp. 82-83.

Tennison-Woods, J.E. (1883) On the fossil flora of the Coal deposits of Australia. Proc. Linn. Soc. N.S.W. 8. pp. 37-167.

Thomas, H.H. (1933) On some Pteridospermous plants from South Africa. Phil. Trans. Roy. Soc. B. 213. p. 302.

" " " (1950) Lidgettonia, a new type of fertile Glossopteris. Bull. Brit. Mus. (Nat. Hist.). Geol. 1 No. 5. Lond. 1950.

Thomson, R.B. (1913) On the comparative anatomy and affinities of the Araucarineae. Phil. Trans. Roy. Soc. 204. p.1.

Thomson, R.B. & Allin, A.E. (1912) Do the Abietineae extend to the Carboniferous? Bot. Gaz. 2. pt. 2. p.339.

Townrow, J.A. (1955) On some species of Phyllotheca. J.Roy. Soc. N.S.W. 89. pp. 39 - 64.

Townrow, J.A. (1960) The Peltaspermaceae, a pteridosperm family of Permian and Triassic age. Palaeontology, 3, pp. 333 - 361.

Varma, C.P. (1954). On two new species of Mesembrioxylon from the cretaceous rocks of the Trichinopoly District Madras, Palaeobot. 3. p. 97.

Vogellehner, D. (1964) Zur nomenklatur der fossilen holzgattung Dadoxylon Endlicher 1847. Taxon, Sept. 1964.13.7. pp. 233 - 237.

Walkom, A.B. (1930) A comparison of the fossil floras of Australia with those of South Africa. C.R. XV Session Internat. Geol. Congr. S. Afr. 2. Sect.3. pp. 161-168.

Walton, J. (1923) On Rhexoxylon, Bancroft. A triassic genus of plants exhibiting a liane type of vascular organisation. Phil. Transact. Roy. Soc. London. B 212.

" " (1925) On some South African fossil woods. Ann. S.Afr. Mus. 22.

" " (1929) The Fossil Flora of the Karroo System, Southern Rhodesia. Bull. Geol. Survey S.Rhod. 15, 62-75.

" " (1936) On the factors which influence the external form of fossil plants etc. Phil. Trans. Roy. Soc. London B.219.

" " (1956) Rhexoxylon africanum and Kadoxylon from the Lower Shire region of Nyasaland and Portuguese East Africa. Colonial Geol. Min. Res. 6. 2. pp. 159-168.

Warren, E. (1912) On some specimens of fossil woods in the Natal Museum. Ann. Natal Mus. 2. Pt. 3. p. 345.

Watson, R.W. (1942) The effect of cuticular hardening on the form of epidermal cells. New Phytol. 41. pp. 223-229.

Wetmore, R.H. (1926b) Organisation and significance of lenticels in dicotyledons. Pt. 2. Lenticels in relation to diffuse storage rays of woody stems. Bot. Gaz. 82. pp. 113-131.

White, D. (1908) Fossil Flora of Coal Measures of Brazil. Com. Est. Minas Carvao Brasil. Rel. final. Pt. III Rio de Janeiro.

Wienert, H.W. (1960) Techniques in the photography of fossilised plants. Contrib. Mus. Mich. 15. 6. pp. 125-132.

Wieland, G.R. (1941) The Carpathian-Black Hills cycadeoid parallel. Am. J. Sci. 239. pp. 523-532.

Zeiller, R. (1879) Note sur quelques fossiles du terrain Permien de la Correze. Bull. Soc. Géol. France, 8. p.196

Zeiller, R. (1892) Bassin Houiller et Permien de Brive. Etudes Gites Min. France. Paris.

Zeiller, R. (1895) Note sur la flore fossile des gisements houillers de Rio Grande do Sul (Brésil méridional) - Bull. Soc. Géol. Fr., (3°). 23, pp. 601 - 629.

" " (1896) Plates Fossiles des Environs de Johannesburg. Bull. Soc. Geol. France. Ser. 3. 24. pp. 368-369.

" " (1902) Observations sur quelques plantes fossiles des Lower Gondwanas. Mem. Geol. Surv. Ind. N.S. 2. Pt.1.

" " (1905) Observations sur quelques plantes fossiles des Lower Gondwanas. Mem. Geol. Surv. Ind. N.S. 2. Pts. 1.