AN INTRODUCTION TO THE STUDY OF
FOSSIL PLANTS

THE FOSSIL GROVE, VICTORIA PARK, GLASGOW

Stumps of Lepidodendroid trees of Lower Carboniferous Age are seen in their positions of growth. The fossils are natural sandstone casts of the original trees.

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AN INTRODUCTION TO THE STUDY OF
FOSSIL PLANTS

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PREFACE

In writing about fossil plants within the limit of a small volume a somewhat arbitrary selection of types has to be made from the abundant material described in the literature of the subject. As far as possible I have restricted myself to types of which not only the vegetative but also the reproductive organs are at least in part known. I hope that this book will encourage students to make use of such more comprehensive works as Seward's *Fossil Plants* and *Plant Life through the Ages*, and Hirmer's *Handbuch der Paläobotanik* to widen their outlook on the subject.

This book is intended for students who have completed at least a year's course of study in Botany at a British or American College or University. I hope that those who use it will be encouraged to examine actual specimens and sections of fossil plants, for most botanical departments are provided with at least small collections. To appreciate the value of the evidence provided by fossils it is essential that the student should handle examples and know something about their nature, origin, and the methods used in their investigation. An opportunity of collecting specimens in a quarry or coal-bing always stimulates the interest of the student.

While a small part of the subject-matter in this book is new, by far the greater part is based on the work of others, and to them I gratefully acknowledge my indebtedness. Many of the illustrations are borrowed from Scott's *Studies in Fossil Botany*, a book from which I have learned much. Acknowledgment is made in the text of the sources of information and illustration. Among those who have kindly helped by giving me photographs and useful advice are: Dr. H. Godwin, Professor T. G. Halle, Professor T. M. Harris, Dr. O. A. Høeg, Dr. W. J. Jongmans, Professor W. H. Lang, Dr. Suzanne Leclercq, Mrs. L. Macfarlane, Dr. Murray Macgregor, Dr. N. W. Radforth, Dr. J. B. Simpson, Professor A. E. Trueman, and Dr. J. Weir: to them I express my cordial thanks.

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To Sir Albert Seward and Dr. Hamshaw Thomas who introduced me to the study of fossil plants, and to my wife who gave me much help in the preparation of the text, I owe a special debt of gratitude.

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INTRODUCTION

THE geologist is able to place in chronological order an immense series of past incidents in the history of the Earth, incidents which have recorded themselves as structural features in the rocks which constitute the crust. During the course of geological time, ever since a solid crust of rock was formed by the cooling of the originally molten mass, the agents of denudation have been continuously weathering it and breaking it up into mineral particles. These have been distributed and deposited as sediment in the form of sand and clay in the sea or in lakes. There is clear evidence that, owing to the stresses and strains developed in the solid crust, large depressions and elevations have been formed at various epochs in the geological past. In the depressions so formed seas or lakes appeared, on the bottoms of which the debris produced by denudation has collected. Sometimes the sinking of part of the crust has continued for very long periods and as a result very thick deposits of sediment have accumulated. These deposits are as a rule variable in character: when deposited in shallow water or near the land, they would consist of the coarser particles along with plant and animal fragments; in deeper water in the sea they would consist of fine-grained sediments with the remains of deep-water animals. In fresh-water lakes and estuaries large quantities of vegetable material might be expected.

In course of time these sediments might be buried to still greater depths and owing to the pressure and the higher temperature be changed into sandstone and shale, forming what are known as sedimentary rocks. Interbedded between deposits of sedimentary rocks are sometimes found beds of limestone containing fossil corals and coralline Algae which represent the buried remains of once living coral reefs, or layers of lava and volcanic ashes indicating periods of vulcanicity. We may find buried vegetation in the form of forests which have been converted into coal.

While sedimentation was proceeding, and sedimentation has been in progress since denudation of the original crust started, a record has thus been kept not only of many geological phenomena but also of contemporary life. Along with the sediments there were deposited and buried the remains of plants and animals which, as the sediment in course of time changed to rock, have been changed in chemical composition and to a certain extent in shape, and are now found as fossils in the rock.

From their studies of the sedimentary deposits found in widely separated parts of the Earth's surface geologists have been able to construct a fairly complete record of sedimentation from very early times, and what is more important from our point of view, they have thus been able to draw up in chronological order a pageant of plant and animal life which, though incomplete, is of great historical significance to the biologist.

It is now possible by analysing radioactive minerals to find out their age and therefore the age of that part of the series of sedimentary rocks in which they were found. The periods into which the sedimentary succession is arbitrarily divided are shown in Table A, with the age in millions of years where that has been determined. From the vertical distribution of a fossil species in the succession of sedimentary rocks we may draw an approximate idea as to how long the species has existed in sufficient abundance to give us a chance of finding its fossil remains when we examine the limited number of samples of rock that may be available. To take an example, there is a well-known group of fossil animals probably related to the Coelenterates called Graptolites which from the fossil evidence appeared first in the Cambrian and were evidently abundant in Ordovician and Silurian seas, yet we find no trace of them in rocks of Devonian or later ages or at the present day. During the Jurassic and the earlier part of the Cretaceous periods we have abundant evidence of the existence of a group of Gymnospermous plants, the Bennettitales. There are no traces of this group in the Carboniferous or earlier periods or later than the Cretaceous. We may reasonably deduce that the group came into existence not long before the Triassic and became extinct before the Tertiary. It must be remembered, however, that the apparent absence of a particular group of plants in the rocks of a geological period is not conclusive proof that they were not in existence then; circumstances may have been unfavourable for their preservation or they may have formed such a small proportion of the total bulk of the vegetation that the chance of finding a trace of them is

Geological Periods				Age in millions of years
	Present Day			0
Cainozoic	Quaternary	Post-Glacial Glacial	(About 11,000 years B.C.)	
	Tertiary	Pliocene Miocene Oligocene Eocene	Angiosperms dominant	70
Mesozoic	Cretaceous	Upper Lower	Gymnosperms and Pteridophytes dominant	
	Jurassic	Upper Middle Lower		
	Rhaetic			
	Triassic			
Palaeozoic	Permian	Upper Lower	Pteridophytes dominant Gymnosperms	
	Carboniferous	Upper Lower		350
	Devonian	Upper Middle Lower		380
	Silurian		Earliest records of land plants	
	Ordovician		Algae	
	Cambrian		Algae	
	Precambrian	Upper Lower	Traces ? Algae	700 1500

TABLE A

remote. Relatives of *Ginkgo biloba* (the Maiden-hair Tree), judging from fossils that have been found, were abundant in the Jurassic, Cretaceous, and Tertiary periods. The living representative, which is probably only native in parts of China, exists in such small numbers at the present day that the likelihood of anyone in future ages finding traces of it in sediments which had accumulated at the present time would be very small indeed and the erroneous assumption might be made that it was extinct.

The study of fossil plants not only gives us an insight into the history and past geographical distribution of existing groups of plants but also introduces us to many extinct types. The present distribution of human racial types and cultures would be quite enigmatical if we had no historical explanation. We have been able to find some explanation of the distribution of the existing European and American floras by studying the fossil plants found in deposits formed during the Tertiary period and the succeeding Glacial age: we cannot explain their distribution in terms of existing geographical and ecological features alone.

It is a striking fact that the numerous species of living Angiosperms fall seemingly naturally into fairly definite groups or genera which in turn may be grouped into Families or Natural Orders. The species and genera which constitute the Cruciferae appear to be related because they exhibit the same type of floral construction, but we also find that they produce similar chemical substances in their secretions and, what is still more significant, have a similar nuclear construction. The transmission of hereditary characters is intimately related to the structure and behaviour of those parts of the nucleus which are called chromosomes, and cytological investigations, when taken in conjunction with the mode of inheritance of characters, indicate that some inherited characters are borne in parts of the chromosomes. In the Cruciferae the chromosomes in the nucleus of each cell are relatively small in size and there is evidently some significant relationship between the chromosome numbers which are characteristic of the different species. Cytological investigations have indicated that in the Cruciferae we have a set of species and genera that are genetically related. Some species have been derived from others by changes related to alterations in the chromosome number brought about by natural hybridisation or by other means, and similar cytological relationships have been observed in other families.

If we consider next the Angiosperms as a group of families it seems probable that these families are themselves related, though very distantly compared to the degree of relationship between closely related species in a family or genus. The larger divisions of the Plant Kingdom—Angiosperms, Gymnosperms, Pteridophytes, Bryophytes, and Thallophytes—appear to be so distinct that any genetic relationship seems incredibly remote, and yet it is difficult to believe that they are completely distinct lines of descent or evolution. Comparative morphology, particularly of such reproductive structures as the archegonium and embryosac, has revealed certain fundamental resemblances between some of these major groups and we are tempted to believe that some, at any rate, are related by having a common ancestry remote though it undoubtedly was.

It has been the aim of palaeobotanists to look for evidence which may help to establish the ancestral connection between these groups, but so far it cannot be said that the search has met with much success. The information gained from a study of fossil plants has added to our knowledge of the Thallophytes, Pteridophytes, and Gymnosperms a very large number of extinct types, and has given us valuable information about the relative antiquity of these and other groups.

Having drawn up the order of succession in the sedimentary rocks of the plant and animal life of the past, the geologist is in a position to make use of that knowledge to determine the position in the sedimentary series of a group of rocks of which the position in the succession is unknown by means of the fossils included in them. Thus if the geologist finds in the rocks which he is investigating species of fossil plants which have hitherto only been found in rocks of Lower Devonian age, he is justified in coming to the conclusion that the rocks which he is investigating are also of that age. This principle has been used extensively in correlating the seams of coal in a single coal-field or even in widely separated coal-fields. Some fossil plant species are of very restricted vertical range in the rocks and these species are of special value to the geologist. *Calymmatotheca Höninghausi* and certain associated species are found restricted to certain strata with coal-seams in Yorkshire, Lancashire, South Wales, Belgium, Holland, France, Germany, Czechoslovakia, and North America. We may assume that this indicates the existence of a flora which was fairly widespread during a certain part of the Carboniferous period, and that the rocks in which this assemblage is found are approximately contemporaneous. If specimens of a species of fossil plant were found in rock samples taken from a known depth in a bore-hole sunk in the neighbourhood of a coal-field in which the same species of plant was found in strata associated with certain seams of coal, the geologist would be justified in assuming that the same set of coal-seams was being penetrated by the bore, and that if a shaft were sunk profitable results might follow.

In Table A, p. 3, are given the divisions of the sedimentary succession. The Upper Silurian marks the first appearance of fossils of land plants. The sudden appearance and rapid rise to dominance of the Angiosperms in the Cretaceous is one of the most surprising features of plant history. The development of the Angiospermic entomophilous flowers must have been correlated with the development of certain classes of insect. The remains of mammals make their first appearance in the Triassic period, while the earliest known remains of man are probably more recent than the Tertiary.

CHAPTER I

ON THE NATURE OF FOSSIL PLANTS AND THE METHODS USED IN INVESTIGATING THEM

MOST fossil plants have been produced during sedimentation by the burial in mud or sand of fragments of plants. This has usually happened in lakes or estuaries or in regions where the land surface was slowly subsiding owing to geological movements. Occasionally plants are found buried in volcanic ash or encrusted with calcium carbonate.

Fossil plants may be classified as follows:

1. *Compressions.*—This is the type most commonly found in sedimentary deposits. As the sediment accumulated over the plant fragments its increasing weight caused any air and water contained in the tissues to be pressed out and displaced upwards between the particles of the overlying sediment. The plant was prevented from squashing or spreading out laterally by the sediment at its sides but the vertical pressure caused a vertical compression of the plant and the sediment and the plant in the fossil condition is found to be almost completely flattened. It is not, however, quite flat, although its vertical measurements have been very considerably reduced. Thus a cylindrical mass of uniform plant tissue buried with its long axis horizontal would be converted under such conditions to a form in which the transverse section, which was originally circular, would have the form of a narrow ellipse with its shortest axis vertical (see Fig. 1).

The sedimentary material in which the plant is buried also undergoes vertical compression. A layer of mud, consisting of a large proportion of water and vegetable particles, will contract to a fraction of its original thickness as the water is displaced from it. If therefore a hollow stem is filled with mud the resulting cast of the cavity will be elliptical in section. Mud containing sand will undergo less compression and a pure sand will contract very little, a sandstone pith-cast being usually almost circular in section. Taking into consideration the compressibility of plant substance and the material in which it has been buried it is possible to estimate the resulting form attained by a plant fragment of

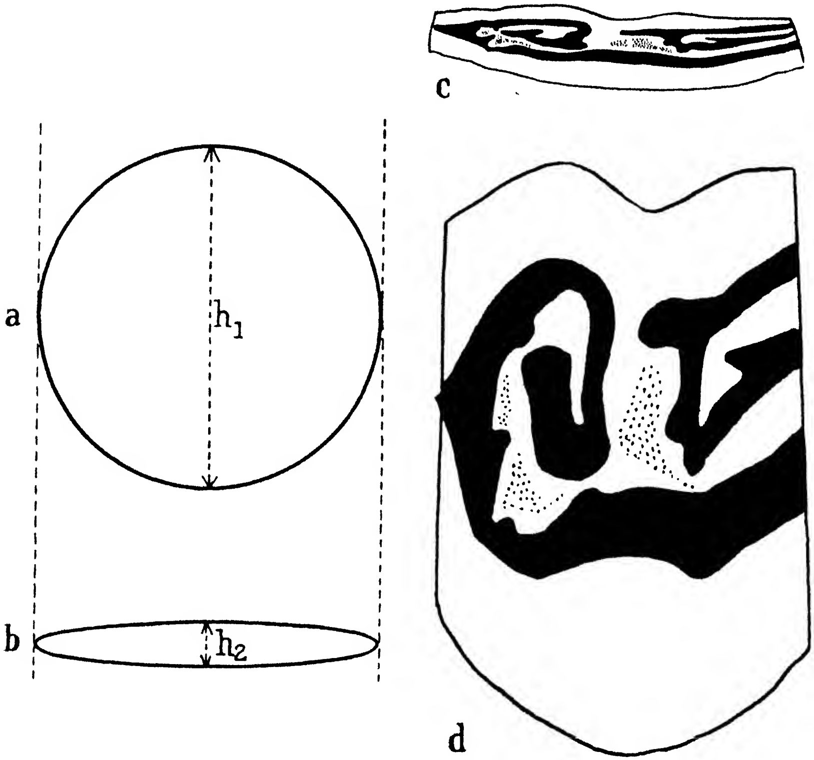

FIG. 1.—Vertical Compression. *a*, *b*. Diagrams to illustrate the change in shape of a mass of sediment or plant tissue, circular in section, subject to a simple vertical compression. The horizontal dimensions do not change but vertical dimensions are all reduced to ⅛.—*c*. Section of a lignitised *Gleichenia*-rachis from the Cretaceous of Greenland. Xylem is in black.—*d*. Figure obtained by enlarging vertical dimension in *c* by 8. This figure bears a close resemblance to the cross section of the rachis of a living *Gleichenia*. (See Seward, 1926.)

more complex shape when it is surrounded by sediment and subjected to compression. The position of the plant structure has also an important effect in determining the resulting form of the compression (Walton, 1936).[1]

In course of time the organic substance of the plant, consisting principally of cellulose and lignin, became converted into coal, the carbohydrate substances having changed into hydrocarbons, but the cuticles and spore coats may remain almost unchanged in

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[1] A name followed by a date refers to the Literature at the end.

character. Cutin appears to be exceedingly resistant to change, and it is possible to separate cuticles which have many of their original properties from fossil plants from rocks as early as the Devonian.

While these changes have been occurring in the buried plant fragments the surrounding sediment has been consolidated into hard rock. Sand has been converted into sandstone and mud into shale. On splitting open a block of sandstone or shale we may find a fossil plant inside. The rock tends to split parallel to the layering of the original sediment. As a rule, when a fossil plant is exposed in this way, part of the coaly layer representing the original plant adheres to the rock on one side of the split and some to the other side. Usually a leaf is not equally smooth on both surfaces. The abaxial stomatiferous surface is rougher than the non-stomatiferous surface, and as a result practically the whole substance of the fossil remains adhering to the rock surface which was in contact with the stomatiferous surface of the leaf. The smooth adaxial surface merely leaves an *impression* on the other rock surface. The *compression* therefore shows us the original silhouette or outline of the plant but we cannot as a rule tell from the fossil the original thickness of the specimen (Walton, 1936). Much valuable information may be got from the most unpromising-looking material. If first of all the coaly layer representing the plant is *transferred* from the rock to a transparent base it is possible to examine both surfaces. A fossil plant transfer is made in the following way (Walton, 1923). The fragment of rock with the fossil on it is cemented to a glass slide with hot fused Canada balsam so that the fossil faces the glass and is only separated from it by a layer of balsam. If necessary some of the excess rock is then ground away from the back of the specimen by rubbing it on a glass plate with some carborundum powder and water. Care must be taken not to grind down too near to the fossil. The back of the rock is slightly moistened and the whole slide and specimen are given a complete coat by dipping them several times into hot paraffin wax. The wax when hard is cut away from the rock so that the rock is exposed but the glass slide is completely covered with the wax. The whole preparation is then put into a bath of hydrofluoric acid. The acid dissolves the silica in the rock, which is converted into mud, and the fossil is left adhering to the balsam on the slide. The surface of the fossil which is now exposed is that which was in contact with the rock, and as the rock has been removed by solution the surface is almost perfect and undamaged. Features such as hairs and sporangia (see Fig. 113, A) may be found still adhering in their original positions. When a rock is split open to reveal a fossil the surface exposed is as a rule damaged in the process of splitting. This method of exposing an undamaged surface is one of the chief advantages of the Transfer Method. If the specimen is given a coating of a cellulose acetate solution before fixing to the slide with balsam, the balsam, after the rock has been removed, may be dissolved away and the specimen is obtained mounted on a cellulose acetate film (Lang, 1926).

In fossil plant *transfers* (*e.g.* Figs. 41, 57) structural features such as the course of the veins, the nature of the vascular elements, and the structure of the epidermis may sometimes be observed. When the carbonaceous matter of the transferred plant fragment is opaque to the eye infra-red photographs may reveal details of structure (Walton, 1935 a). It is sometimes possible to isolate the cuticular membranes of a leaf or stem fragment by digesting in strong nitric acid mixed with potassium chlorate and then washing away the oxidised products with dilute potassium hydroxide or ammonia. If the treatment has been sufficient only the cuticle will remain as a transparent membrane on which the epidermal cell outlines and the stomata are usually clearly visible (Fig. 137). The spores from a single sporangium may be extracted in this way and even counted (Radforth, 1938). The cuticularised membranes of the integument, micropylar tube and megaspore in a fossil seed may be rendered visible by similar methods.

By *bulk maceration* with hydrofluoric acid or other suitable reagents large fragments or even complete organs of fossil plants may be freed from the rock for microscopic investigation (Harris, 1926).

Peat, Lignite, and Coal are compressions of masses of plant material. In peat the plant fragments are least changed in shape and chemical composition, while in coal the fragments are so altered that the mass appears in parts homogeneous. Lignite is intermediate in character.

Peat may often be pulled into pieces and separate fragments of the constituent plants isolated (Fig. 138, D). The mineral matter in peat may be removed by treatment with hydrofluoric acid and the softened mass impregnated with wax and sectioned on a microtome.

Of recent years much work has been done on the pollen found in peat. Various methods have been used in its extraction. Erdtman (1934 and 1936) and Godwin (1934) are prominent among those who have contributed improvements in the methods commonly used. Dr. Godwin has kindly allowed me to describe the method which he now uses.

From 2 to 3 gm. of wet peat are broken up in 20 c.c. 10 per cent KOH in a boiling tube. This is fitted with a condenser and kept at 100° C. for 1 to 12 hours. This treatment disintegrates the peat. Distilled water is then added and the contents of the tube stirred up. The mixture is then centrifuged at 2000-3000 r.p.m. for 3 to 4 minutes and the solution is poured off. The residue is again mixed with distilled water and centrifuged. If the residue is then mixed with water and examined in a shallow dish, seeds and other macroscopic remains may be picked out. To the residue is then added 8 c.c. glacial acetic acid and 4·5 c.c. of a 50 per cent solution of $NaClO_3$. 1 c.c. of conc. H_2SO_4 is then added drop by drop with careful shaking. The mixture is left for 12 hours with occasional stirring. The residue is washed with distilled water and centrifuged twice. This process removes the lignified material. The cellulosic compounds are then removed by treating the residue with 10 c.c. glacial acetic acid and 1 c.c. conc. H_2SO_4 for ½ hour at 100° C. The residue, which now consists of spores, pollen grains, and fragments of cuticle, is thoroughly washed and centrifuged two or three times. Finally the residue is mixed with twice its bulk of glycerine jelly (with Safranin), mixed thoroughly, spread on slides, and covered with large cover-slips. The pollen may now be examined under the microscope and counted.

Jeffrey (Hollick and Jeffrey, 1909) treated lignitic remains of Cretaceous Conifers with 1-3 per cent caustic soda for several days and then removed the mineral matter by treatment with hydrofluoric acid. The softened mass was then impregnated with celloidin and sectioned (Fig. 126). Thomas (1925) softened compressions of *Caytonia*-fruits of Jurassic age (p. 140) by boiling in alcoholic potash for up to five weeks and then demineralising in hydrofluoric acid. The softened fruits were then imbedded in celloidin and sectioned. The sections were then treated with various reagents to bring out the structure.

Halle (1933) used similar methods for the much harder compressions of some Carboniferous fructifications (p. 130) but carried them out in closed gun-metal vessels under high pressures.

The investigation of the structure of coal is now almost a distinct branch of scientific research. Polished surfaces of the coal may be examined with different methods of lighting or the polished surface may be etched with a saturated solution of chromic acid with a little sulphuric acid (Seyler, 1925), which reveals some of the cellular construction of the plant constituents. Another method is to scorch the surface with a flame to assist in revealing structure. Coal may be cut into slices so thin that they are translucent. In such sections spores and cuticles may be visible and even a certain amount of cellular structure. The spores may be extracted from coal by breaking the coal up into a coarse powder which is digested with a mixture of 3 parts $KClO_3$ and 20 parts pure nitric acid (Raistrick, 1934). The residue may then be washed with water and then treated with 10 per cent KOH. The residue will consist of spores and small fragments of cuticle.

2. *Incrustations and Casts.*—An incrustation may be described as an external mould of a plant usually in some incompressible material such as sandstone, ironstone, or tufa which undergoes very little subsequent compression. As a rule the plant substance has disappeared and a cavity has been left which has the form of the original plant. Sometimes this cavity is subsequently filled up with mineral matter which thus forms a *cast* of the original plant. The surrounding material, the mould, forms the *incrustation.* Casts of the pith cavities of hollow stems are sometimes found (Fig. 53, B, y) which have resulted from the entry of sand or mud into the hollow stem. In the course of time this filling material is converted into an internal mould of the hollow stem.

3. *Petrifactions.*—It has sometimes happened that before vertical pressure has come into play plant fragments have been saturated with water containing mineral substances in solution. The mineral substances have gradually separated out from solution in the tissues and the water has been displaced so that finally the tissues and cells have a complete filling of solid material and the whole forms a solid incompressible mass. Such a fossil is termed a petrifaction. The petrifying minerals impregnate the tissues in much the same way as the paraffin wax used in impregnating living plant tissues before sectioning on a microtome. In both cases the impregnating material takes the place of the air

and water present in the tissues and cells. Calcium, magnesium, and iron carbonates, iron-pyrites, and silica are perhaps the commonest petrifying minerals.

After this stage of petrifaction the solid parts of the plant, such as the cell-wall substances, undergo the same process of conversion to coal as in the compression type of fossil, but frequently further changes may occur and the organic substances may be removed by such processes as oxidation or perhaps hydrogenation and the space they occupied filled with more inorganic material, so that eventually the fossil may contain no organic material. Such petrifactions are actually elaborate internal casts of the cells and when examined in thin sections may show the form of each cell in great perfection of detail.

Petrifactions may be cut into thin slices which are ground down until they are so thin that they are translucent and the cellular framework of the tissues may be observed. In a few instances protoplasmic structures are preserved. It is for this reason that petrifactions are of exceptional value to the palaeobotanist.

The petrifaction is sawed through by means of a rotating disc of metal, the edge of which is charged with diamond dust or carborundum powder (Kräusel, 1929). The flat cut surface is ground smooth on a glass plate with carborundum powder and then cemented to a glass slide. Another cut is then made with the saw close to the slide so that a thin slice of the petrifaction is left sticking to the slide. This slice is then ground down on a glass plate with fine carborundum powder until it is so thin that it is translucent and the cellular structure of the fossil plant can be seen (examples of such sections are illustrated in Figs. 9, 42, 82). If the petrifaction is friable it must be impregnated with shellac, Canada balsam, or some synthetic resin before sectioning. The section is finally covered with Canada balsam and a cover-slip.

This method of preparing thin sections is one that requires skill (Weatherhead, 1938) and for many purposes sections prepared by the *Peel-section* method are quite satisfactory. In this method (Walton, 1928) a flat surface is cut or ground in the direction the sections are required. This surface is then ground smooth and then etched with a suitable acid. This removes a thin film of the rock or petrifying material but does not affect the coaly plant substances forming the walls, which therefore project slightly above the etched surface. A solution of some cellulose ester is then poured over the surface where it is allowed to dry. The projecting walls are thus imbedded in the cellulose film. This is then stripped off the surface and mounted in balsam under a cover-slip. It furnishes a very thin section of the fossil plant (*e.g.* Figs. 22, 24). By repetition of this process a large series of sections of a small object such as a seed may be made. By the section *cutting* method only two or three sections could be made from an object of the same size.

Further information about the technique of palaeobotanical research will be found in Kräusel's *Paläobotanische Untersuchungsmethoden* and Seitz and Gothan's *Paläontologisches Prakticum.* For information about coal and coal-seams the student is advised to consult Raistrick and Marshall (1939), *The Nature and Origin of Coal and Coal Seams.*

CHAPTER II

THALLOPHYTA AND BRYOPHYTA

THALLOPHYTA.—The Algae, Bacteria, Fungi and Lichens exhibit a great variety of types of construction ranging from microscopic unicellular organisms to large plants in which there is a certain amount of differentiation into tissues. Some consist of separate filaments, while there are others such as the larger Fungi and Algae, in which the plant body is built up of closely packed cellular filaments or hyphae. In the study of fossil plants the most readily observed differences, apart from their methods of reproduction, between the Thallophyta and the Vascular Plants (Pteridophyta, Gymnospermae, and Angiospermae) are the absence in the Thallophyta of a cuticle, stomata, and lignified water-conducting tissue. There are exceptions: the submerged parts of aquatic Angiosperms have no cuticle or stomata and have very reduced vascular tissues in which there may be no lignification. The majority of Thallophyta are only able to grow in water or in a saturated atmosphere, but there are the Lichens, that large group of composite organisms built up of Algae and fungi, some of which are extreme xerophytes.

It is usually possible to determine whether a cuticle is present or not in a fossil plant (p. 10), and as the cuticle is exceedingly resistant to decay, the absence of a cuticle may be an indication that the organism is a Thallophyte, and if in addition there is no evidence of vascular tissues it may be assumed with greater confidence that the organism is a Thallophyte. Confirmatory evidence afforded by the nature of the reproductive structures is always desirable.

Bacteria.—There are many records of discoveries in rocks, some as old as the Precambrian, of microscopic bodies which have been claimed as fossil Bacteria. They have usually been found in rocks which have been formed of deposits of calcium

TABLE B

APPROXIMATE RELATIONSHIPS OF PALAEOZOIC PLANT-BEARING ROCKS IN EUROPE AND AMERICA

Europe				North America		Britain	
				West Virginia	Pennsylvania		
Permian				Permian		Permian	
Carboniferous	Upper	(Stephanian) Westphalian	E D C	Dunkard Monongahela Conemaugh Allegheny	Monongahela Conemaugh Allegheny	Upper Westphalian (Morganian)	Radstockian Staffordian
			B A	Kanawha New River Pocahontas	↑ Pottsville ↓	Lower Westphalian (Ammanian)	incl. "Yorkian" and "Lanarkian"
		Namurian		↓		Millstone Grit Upper Limestone Group Limestone Coal Group	
	Lower			Mississippian (incl. Pocono Series)		Lower Limestone Group Calciferous Sandstone Series: Oil Shale Group Calciferous Sandstone Series: Cementstone Group	
Devonian	Upper			Conewango and Chemung, Genesee Shales		Upper Old Red Sandstone	
	Middle			Catskill, Ludlowville, Gaspe Sandstone		Middle Old Red Sandstone	
	Lower			Bear Tooth Butte (Wyoming)		Lower Old Red Sandstone	
Silurian				Silurian		Silurian	
Ordovician				Ordovician		Ordovician	
Cambrian				Cambrian		Cambrian	

carbonate, iron compounds, or silica. The association of these microscopic structures with such mineral substances is highly suggestive that they actually represent Bacteria, for at the present day Bacteria are often found to be agents in the precipitation of such deposits. The recognition of Bacteria depends so much on their physiological activities and so little on their external form that the identification of small particles with Bacteria even though they may consist of carbon compounds must be always highly speculative. In rocks of the Devonian period (see Table A, p. 3) and up to the present day it is equally difficult to prove the existence of fossil Bacteria although we believe that they must have been in existence. Small Bacteria-like particles are often found associated with fossil plants which have obviously suffered decay before fossilisation, and it is impossible to imagine the Earth which we know was clothed with vegetation from Silurian times onward without agents of decay. There must have been, we imagine, some means by which the organic compounds in the dead plants and animals were converted into carbon dioxide and nitrogen compounds which could be utilised by the living.

Myxophyceae (Blue-green Algae).—We are afforded satisfactory evidence of the existence of this group in the Palaeozoic by several fossils one of which, the Middle Devonian *Archaeothrix oscillatoriformis* (Kidston and Lang, 1921), may be closely compared in form and cellular dimensions with the living genus *Oscillatoria*.

Pachytheca.—Small spherical bodies from 2 to 5 mm. in diameter are found in Upper Silurian (Downtonian) and Devonian rocks (Kidston and Lang, 1924). These fossils, to which the name *Pachytheca* is given, have a central core consisting of loosely spaced interlacing tubes and an outer zone of closely packed straight tubes which extend from the core normally to the surface. Inside these outer tubes are fine cellular filaments which run the length of the tubes and then extend slightly beyond into what was probably a gelatinous sheath which surrounded the colony.

Several genera of living Blue-green Algae consist of cellular filaments of similar dimension to those of *Pachytheca* enclosed in tubular gelatinous sheaths, and it is with the Blue-green Algae among living plants that *Pachytheca* may be most closely compared, although in the absence of information about protoplasmic cell structure we cannot come to a definite conclusion. Some investigators deny the vegetable nature of this fossil.

Chlorophyceae (Green Algae).—In the past just as they do at the present day Algae played an important rôle in the building up of Calcareous reefs in the sea. There are two groups of living Algae having representatives which secrete calcium carbonate, the Siphonales (Chlorophyceae) and the Rhodophyceae (Red Algae). The fossil algae *Dimorphosiphon* (Fig. 2, A) and *Palaeoporella*, which are found in limestones of Ordovician age, are closely comparable in thallus organisation with the living genus *Halimeda*. There were also present in Ordovician times algae to which the names *Rhabdoporella*, *Dasyporella*, and *Cyclocrinus* are given which are obviously closely related to the living verticillate Siphonales included in the family Dasycladaceae. We are probably justified in supposing that conditions in the Ordovician oceans were similar to those of the present day.[1]

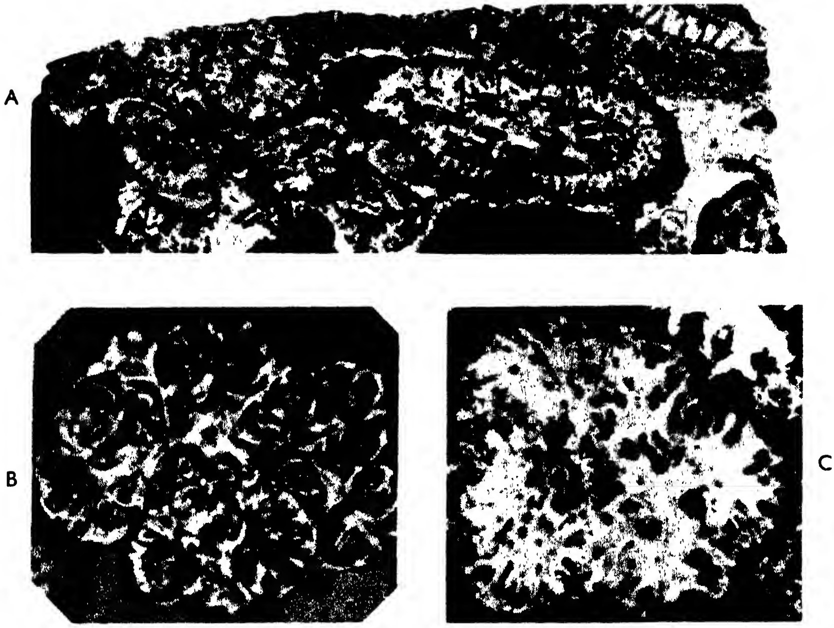

Fig. 2.—A. *Dimorphosiphon rectangulare*, Høeg. Slice of Middle Ordovician Limestone from Norway showing sections of the thallus of what is the oldest known member of the *Codiaceae*. × 5 nat. size. After Høeg.—B. Colony of the living *Botryococcus Braunii*. × 1000.—C. Colonies of *Reinschia* in a section of algal coal (Torbanite) from Scotland. × 300. After Blackburn and Temperley, 1936.

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[1] A detailed account of these fossil Algae will be found in Hirmer's ***Handbuch der Paläobotanik***.

Other representatives of the Dasycladaceae are found in rocks of later geological periods, *Mizzia* from the Permian, *Diplopora*, *Macroporella*, and several other genera from the Triassic, *Triploporella* from the Jurassic, *Neomeris* from the Cretaceous, and *Dactylopora* and many others from the Tertiary.

There are combustible deposits known as boghead coals found in Carboniferous rocks in Scotland, Pennsylvania, and New South Wales composed largely of fossil Algae, which must have been very like the living alga *Botryococcus Braunii* (Fig. 2, B) in structure. The cells, which had thick gelatinous walls, were grouped in small, roughly spherical colonies (Fig. 2, C). Early investigators recognised two types to which the names *Reinschia* and *Pila* were given, but already in 1898 Sir Albert Seward was of the opinion that they were different forms of the same organism and recent investigations (Blackburn and Temperley, 1936) have confirmed his opinion. Extensive rubbery deposits called Coorongite, formed by one of the living species of *Botryococcus*, are found on the shores of some Australian lakes, and as much as 69 per cent of this rubbery material consists of oil, most of which consists of hydrocarbon compounds. This living Alga forms large quantities of oil which accumulates in the gelatinous investments of the cells. One of the most important characters of boghead coals is the large amount of hydrocarbon oils which may be distilled from them. We must conclude that *Pila* and *Reinschia* represent the fossil remains of an Alga which, if not specifically identical with the living *Botryococcus Braunii*, had colonies of the same form and, like it, produced large quantities of oil as a metabolic product. Considerable deposits of a combustible material called Kuckersite, consisting of compressed colonies of an Alga, are found in Silurian strata in Esthonia.

Charales.—This peculiar group of freshwater Algae contains a number of forms which secrete a covering of calcium carbonate over the surface of their thallus. Examples of the group are found in Cretaceous and later periods. The oospores which have a very characteristic sculpturing and are called gyrogonites are probably the commonest form of Charalean fossil. Professor Harris (1939) has recently given some very full descriptions of some Jurassic species belonging to the genera *Clavator* and *Perimneste*. Kidston and Lang (1921) discovered fragments of a plant in the Rhynie chert which they named *Palaeonitella* on account of its close resemblance in vegetative features to the living Charalean genus *Nitella*.

Diatomales (Diatoms).—The oldest satisfactory evidence of the existence of Diatoms comes from the Jurassic. The siliceous cell walls of living Diatoms which are so resistant to the action of strong acids are not, so it seems, preserved for long as fossils, for water, particularly water with an alkaline reaction, dissolves silica, and as a result small particles of silica may disappear relatively rapidly. It has been observed that in certain parts of the sea bottom the upper layers of mud may contain large numbers of diatoms while a few inches below the surface of the mud few traces of diatoms can be found. Their absence in the lower layers is supposed to be due to the solution of the silica in their walls.

Phaeophyceae (Brown Algae).—There is no conclusive evidence for supposing that Phaeophyceae existed before the Jurassic. *Nematophyton*, a thallophyte of tree-like dimensions from Silurian rocks, has sometimes been compared with the stipes of some of the larger Brown Seaweeds, but the differences are far too great for us to assume any phyletic relationship.

Rhodophyceae (Red Algae).—*Solenopora*, a widely spread type of reef-building alga which ranges from the Ordovician to the Jurassic, bears many points of resemblance in vegetative structure to the living *Lithothamnion* which appears to succeed it as reef-builder from the Cretaceous to the present day. Unfortunately no reproductive organs have as yet been found on *Solenopora* so that its relationship to the Rhodophyceae cannot be regarded as conclusively proved. There is, however, satisfactory evidence of the existence of the group in the Cretaceous.

Fungi.—The tissues of the vascular plants fossilised in the Middle Devonian chert found at Rhynie in Aberdeenshire (see p. 28) are frequently found to be riddled with fungal hyphae, some of which bear vesicles, sporangia, and thick-walled cysts. Only very rarely are cross walls visible. They are probably the remains of Phycomycetous fungi. No indubitable evidence of the existence of the Higher Fungi is found in rocks earlier than the Cretaceous.

Fungal hyphae are frequently found in fossil plants of all ages from the Devonian onward, but it is usually impossible to decide whether they are parasitic or saprophytic; most are probably saprophytic. The almost constant occurrence of fungal hyphae in the rootlets of *Cordaites*, a Carboniferous Gymnosperm, appears to afford substantial evidence that the relationship between a higher plant and a fungus which we term mycorrhiza had been established by then. The large fructifications of the Higher Fungi decay so readily compared with the cutinised membranes and lignified tissues of the Vascular Plants that it is perhaps not surprising that they are so rarely found fossilised.

Thallophyta which cannot be classified with any Living Groups.—Investigations of fragmentary plant remains from Silurian and Devonian rocks have shown that there were in existence in those times thalloid plants which possessed characters not found in any living Thallophyta. The fossil remains, to which the name *Prototaxites* or *Nematophyton* have been given, are fragments of large stems, some of which must have been a metre in diameter. The whole stem consists of interlacing tubes. There are large tubes which tend to run parallel to the axis and small tubes which form a felted mass between them. At the surface of the axis the tubes are ranged at right angles to the surface. The structure is reminiscent of the organisation of the stipes of the larger Brown Algae.

In the Downtonian beds of the Silurian *Prototaxites* is usually found associated with irregular-shaped flattened carbonised fragments in some of which Professor Lang (1937) has demonstrated a most peculiar combination of characters. These fragments, to which he has given the name *Nematothallus*, consist in part of branching tubes of two sizes as in *Prototaxites*, but here some, at any rate, of the larger tubes contained annular thickenings and the surface of the plant fragment was covered with a resistant cuticle. In addition spores which probably had a cutinised wall and were formed in tetrads are found imbedded in the tubular tissue.

Parka.—Among the plants found in Lower Devonian and Upper Silurian (Downtonian) rocks is one to which the name *Parka decipiens* has been given. The plant appears to have had the form of a flat thallus roughly circular in outline and probably increased in size by the activities of a marginal growing region as in the living *Cutleria*. The plants vary in size from about 5 mm. to 7 cm. across. The surface is frequently covered with flattened disc-shaped structures (2 mm. in diameter) which consist of numerous cutinised spores (28-34 mm. in diameter); there is no evidence, however, that the spores were formed in tetrads. The thallus is not built up of tubes as in *Nematothallus* but appears to have been of a parenchymatous nature (Lang, 1937).

We have evidence therefore that in the latter part of the Silurian period there were in existence undoubted Algae and plants which, while thalloid in form like the Algae, differed from them in possessing cuticle and cutinised spores, some indeed possessing tubular elements with annular thickenings in their thallus. These characters which are not those of the Algae are usually found in plants which are exposed to the atmosphere for prolonged periods and are characters which we associate with land plants.

FIG. 3.—Upper Carboniferous Liverworts. A. *Hepaticites Willsii* (× 10).—B. *H. Kidstoni* (× 20).—C. *H. metzgerioides* (× 20).—D. *H. lobatus* (× 20). These specimens were obtained by digesting shale with hydrofluoric acid. Walton Collection. Walton, 1925, 1928.

Bryophyta. Hepaticae (Liverworts).—The oldest fossil Liverworts are some which have been found in the Upper Carboniferous coal-measures in England. Numerous small fragments of the gametophytes have been found but so far no reproductive organs or sporophytes. Four types of thallus construction are found. In *Hepaticites Langi* and *H. Willsii* (Fig. 3, A) the thallus must have been constructed much as in the living *Aneura*. In both occasional tufts of rhizoids are found. In *H. lobatus* (Fig. 3, D) the thallus has lateral leaf-like expansions, one cell in thickness, placed alternately on each side. *Hepaticites Kidstoni* (Fig. 3, B) has a more complicated leafy form. Opposite each lateral lobe there is on the axis a smaller lobe which, together with its accompanying lateral lobe, possibly represented the development from one segment of the apical cell. In the organisation of its leafy shoot it may be compared fairly closely with the living Malayan Liverwort *Treubia*. *Hepaticites metzgerioides* (Fig. 3, C) is closely comparable to the living *Metzgeria*. Its ribbon-shaped dichotomously forking thallus had a central midrib region in which there were elongated cells. The wings of the thallus were one cell in thickness but the midrib with the elongated cells must have been about four cells in thickness.

The features exhibited by these Carboniferous Liverworts may all be matched in the living Anacrogynous Jungermanniales. There is no evidence of the presence of other groups such as the Acrogynous Jungermanniales or the Marchantiales. It is noteworthy too that they are all of small dimensions compared with the living forms with which they most nearly compare. Professor Harris (1931) has discovered a liverwort *Hepaticites glebosus* similar in form to *Hepaticites lobatus* but larger in size in Rhaetic rocks in West Greenland. He has also discovered that *Naiadita lanceolata* from the Rhaetic in the Bristol area (Harris, 1938), which at first was thought to be a Monocotyledon and more recently a Lycopod, is actually a Liverwort. The plant consists of an axis bearing leaves and rhizoids. There are gemma cups bearing multicellular discoid gemmae on the ends of some of the branches. Archegonia are borne along the axis. The sporogonia are spherical, the seta of the sporogonium is short or absent. Spore tetrads are present in the sporogonia but no elaters have been observed. From the associated fossils it is probable that it was a submerged aquatic. Professor Harris is of the opinion that it may be compared more closely with *Riella* than with any other existing Liverwort.

Musci (Mosses).—While Tertiary deposits have furnished ample evidence of the existence of Mosses belonging to the same genera and probably species as those existing now, older records are remarkably rare and throw practically no light on the history of the Mosses. In the Carboniferous two traces have been found. One consists of a compression of small leafy shoots which externally resemble those of a large moss such as *Polytrichum*, the other a small petrified shoot bearing rhizoids with oblique cross-walls. These rhizoids with oblique walls afford the only reliable evidence of the existence of Mosses in Pretertiary rocks.

CHAPTER III

EARLY VASCULAR PLANTS—SILURIAN AND LOWER AND MIDDLE DEVONIAN

If fossil plants are found which possess cuticle, stomata, or lignified vascular tissue we may justifiably infer that they were land plants. The oldest fossil plants which show such structures are some which have been found in Silurian rocks in Australia. That they are of Silurian age is established by the presence, on the same blocks on which the plants are found, of examples of *Monograptus*, a genus of Graptolites characteristic of undoubted Silurian strata elsewhere.

Baragwanathia.—Professor Lang and Dr. Cookson (1935), who have recently investigated these Australian fossils, distinguish several types. *Baragwanathia longifolia* (Fig. 4) had stems or branches which varied from 4 to 65 mm. in thickness, bearing closely set and probably spirally disposed leaves. The leaves were slender, 0·5 to 1 mm. in width and up to 40 mm. in length. They seem to have been of a flexible nature and possessed a slender central vascular strand which contained tracheids. The stems branched dichotomously but some show relatively slender lateral branches which may possibly be interpreted as roots or rhizomatous branches. The stems and branches contained a central vascular column which, in one partially petrified specimen, is seen in transverse section to have its xylem in the form of an irregularly rayed star. In longitudinal sections the wood is seen to be constructed of elongated tracheid elements with tapering ends and thickened internally with rings (Fig. 4, C). The vascular strands of some of the leaves may be traced following an oblique course down through the cortex of the stem to the tracheids of its vascular column.

Some of the shoots were fertile (Fig. 4, B) but apart from the presence of sporangia do not appear to differ from the purely

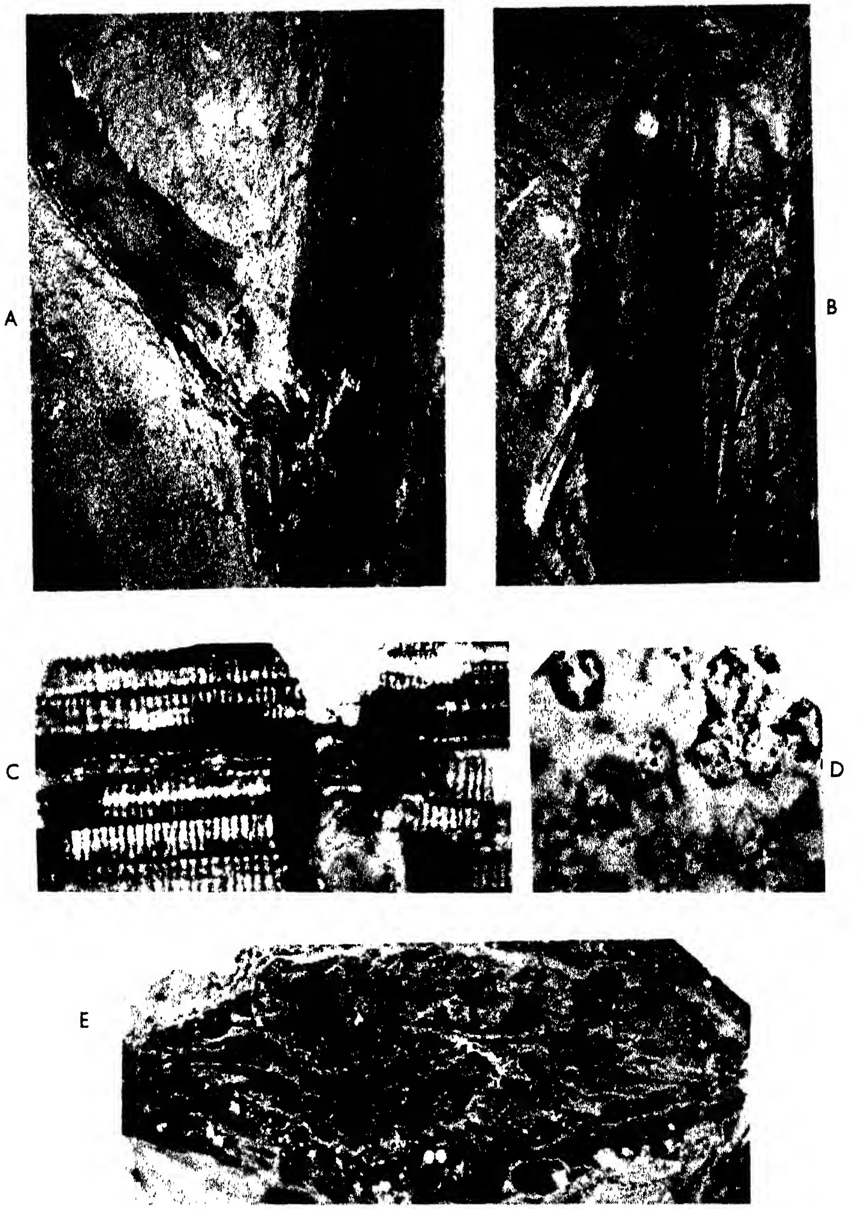

Fig. 4.—*Baragwanathia longifolia*, L. & C. A. Portions of shoots with remains of leaves, vascular column shown at *s*.—B. Apex of a shoot with leaves and sporangia (*s*).—C. Peel section from a vascular column showing tracheids with thin annular thickenings. × 150.—D. Peel section from a sporangium shown in C with spores. × 200.—E. Polished surface cut at right angles through a vascular column. The lighter areas towards the centre represent the xylem. × 12·5. From the Silurian of Victoria, Australia. After Lang and Cookson, 1935.

vegetative shoots. The sporangia were about 2 mm. broad and approximately spherical. It is probable that each sporangium was attached near the base of a leaf or on the stem close to the adaxial surface of a leaf. The sporangia contained spores slightly oval in form which measure about 50 μ in diameter (Fig. 4, D). From the size of the spore and the fact that they seem to have been all of the same size, one would suppose that the plant was homosporous.

We may visualise *Baragwanathia* as a plant somewhat similar to *Lycopodium* in habit and in the position in which its sporangia were placed. The nature of the xylem column is not unlike that found in some living Lycopods but the structure of the tracheids differs very markedly from that found in any living Pteridophyte, and in this feature *Baragwanathia* compares more closely with some of the other land plants found in the Early Devonian period.

Zosterophyllum.—This genus is represented in the Australian Silurian Flora (Lang and Cookson, 1930) but had also a world-wide distribution in the Devonian period. It has been found in Lower Devonian rocks in Scotland, Germany, and in the Devonian of Perry, Maine, U.S.A. Usually only small fragments of the plants are found, but Professor Lang has described what may be a complete plant or group of plants in which several erect branches rise from an irregular tangled mass of branches. Some of the branches in this tangled region fork in a characteristic manner (Fig. 5, A) and are probably to be regarded as the rhizomatous part of the plant. The whole plant consisted apparently of cylindrical leafless stems covered with a cuticularised epidermis. The erect branches forked dichotomously

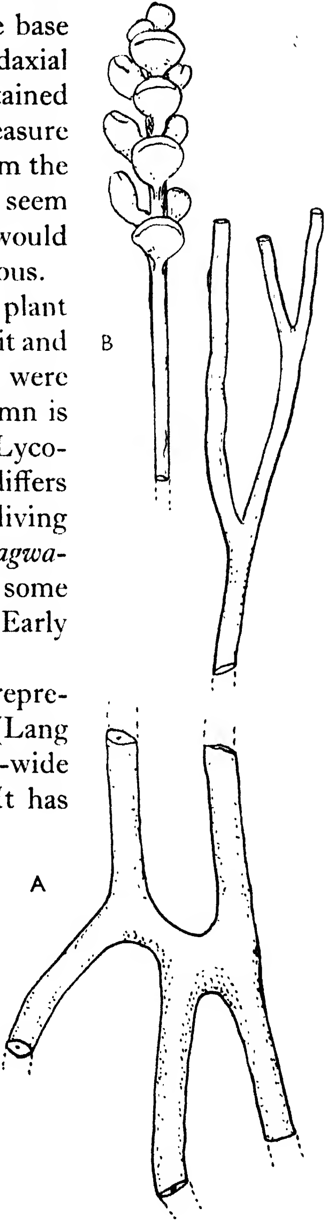

FIG. 5.—Reconstruction of *Zosterophyllum*. A. Rhizomatous basal part.—B. Apex of aerial shoot with sporangia. × about 2.

or occasionally bore lateral branches. The branches were about 2 mm. in diameter with a vascular strand 0·25 mm. in diameter in which tracheids with annular thickenings similar to those in *Baragwanathia* may be detected.

Some of the erect shoots bear racemes of large kidney-shaped, stalked sporangia (Fig. 5, B) containing spores with a diameter of about 75 μ. The dehiscence of the sporangium was effected by a tangential split across the top as in the sporangium of *Lycopodium*. Judging from the shape of some of the fossil remains the sporangia had walls which were several cells in thickness, and the stalk of each sporangium contained a strand of tracheids.

In *Zosterophyllum* we observe a combination of characters of exceptional interest. The plant shows no differentiation into stem, leaf, and root and may therefore be said to have a thalloid form. The fertile regium may be regarded as a racemose branch system if we regard each sporangium as the terminal part of a short side branch the rest of which is represented by the stalk. In spite of its thalloid form there can be no doubt that it was an inhabitant of the land in view of the existence of cuticle and tracheids, which undoubtedly functioned as water channels and were probably lignified.

Among the fossil plants of Lower Devonian age discovered at Bear Tooth Butte, Wyoming, U.S.A., and described by Dr. Erling Dorf (1934), are some fructifications named *Bucheria ovata* which consist of massive sporangia arranged in two series on one side of a smooth axis. The one-sided arrangement of the sporangia contrasts with the radial arrangement in *Zosterophyllum* but the close similarity in the size and shape of the sporangia suggests that *Bucheria* and *Zosterophyllum* are closely related forms.

Psilophytales.—In 1913 silicified plant remains were found in beds of Middle Old Red Sandstone (Middle Devonian) age on the Muir of Rhynie in Aberdeenshire in Scotland. The plants had evidently formed a peaty mass and were preserved in their positions of growth. Preservation had been effected by waters containing silica derived from some volcanic source. The preservation of the plants is so perfect that in some instances meristemmatic tissues are found in which structures undoubtedly representing nuclei and other cell contents are visible. Dr. Kidston and Professor Lang (1917–21), who investigated these fossils, found it possible to reconstruct with an extraordinary degree of completeness four species of vascular plants which formed the principal constituents of the peat, *Rhynia Gwynne-Vaughani*, *Rhynia major*, *Hornea Lignieri*, *Asteroxylon Mackiei*.

Rhynia Gwynne-Vaughani (Fig. 6) was a small herbaceous plant, possibly about 18 cm. high, consisting of slender cylindrical aerial stems and branches rising from a basal rhizomatous part which was buried in the peaty mass formed of the dead remains of other plants of the same kind. There is not much difference in structure between the rhizomatous part and the aerial shoots but tufts of rhizoids are found on the under sides of the former. The aerial shoots branched dichotomously and varied from 1 to 3 mm. in diameter; they were covered with a cuticularised epidermis and bore rather widely spaced stomata. Small hemi-

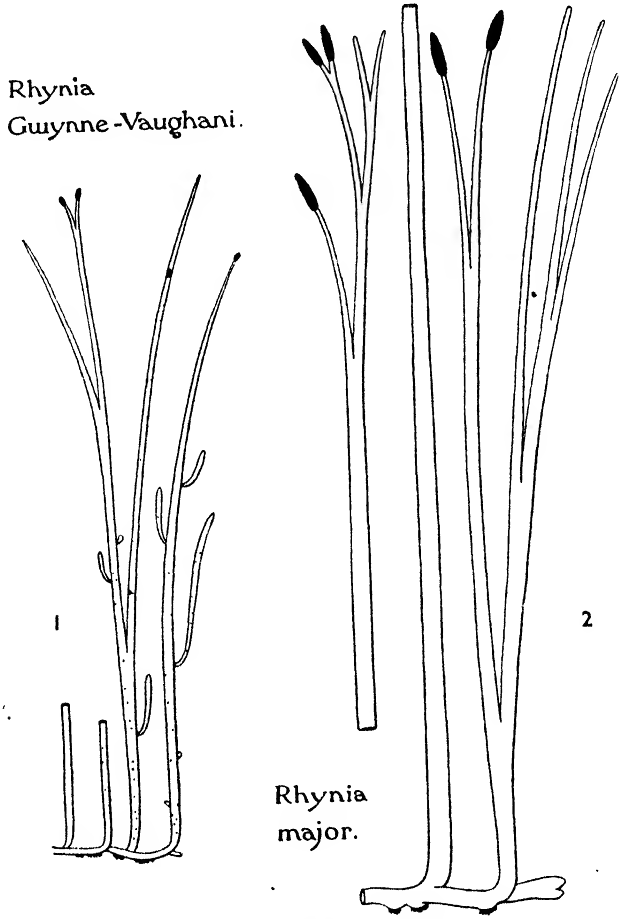

FIG. 6.—(1) Reconstruction of *Rhynia Gwynne-Vaughani*.—(2) Reconstruction of *Rhynia major*. About ½ nat. size. After Kidston and Lang. From D. H. Scott's *Extinct Plants and Problems of Evolution* (Macmillan & Co. Ltd., London).

spherical swellings are found on most of the stems and branches (Fig. 7). These swellings sometimes produced rhizoids and sometimes, it seems, developed into adventitious branches. There is no vascular tissue between the swellings and the vascular tissue of the stem, nor between the adventitious branches and the stem on which they were produced. The development of adventitious branches may have provided a means of vegetative propagation.

FIG. 7.—*Rhynia Gwynne-Vaughani.* Surface view of a stem showing the epidermis and some of the small hemispherical bulges. × 14. After Kidston and Lang.

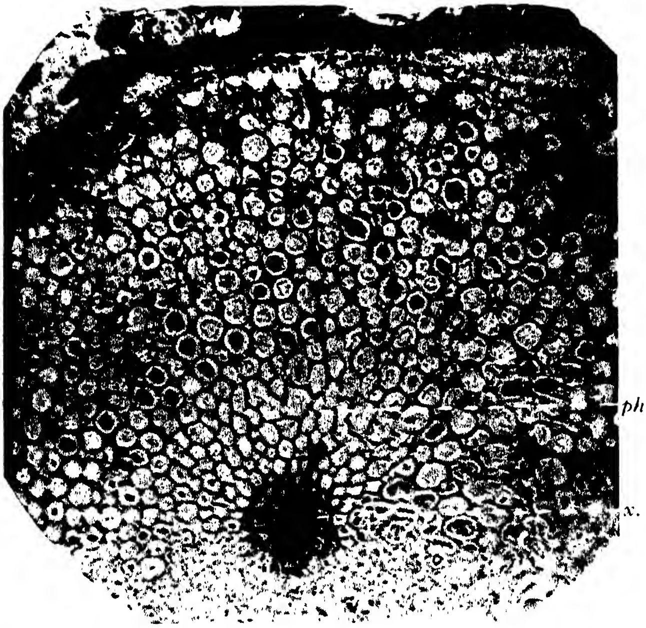

FIG. 8.—*Rhynia Gwynne-Vaughani.* Part of a transverse section of a stem. *ph.*, phloem tissue; *x.*, xylem. × 60. After Kidston and Lang.

In sections of the aerial stems (Fig. 8) a distinct cutinised epidermal layer is seen occasionally interrupted where a stoma occurs. The outer cortex consisted of large parenchymatous cells rather larger than the cells of the epidermis or inner cortex. The outer cortex appears to have represented a hypoderm. The inner cortex contains many intercellular spaces which communicated through gaps in the hypoderm with the substomatal spaces. The inner cortex was probably the region in which most of the photosynthetic activity took place. In the centre of the stem is a cylindrical strand consisting of nothing but tracheids, which in longitudinal sections are seen to have annular and occasionally traces of spiral thickening. Sometimes, but not always, the tracheids in the centre of the strand are smaller in diameter than those around them, which suggests that the differentiation of the xylem was endarch. The tissue lying between the xylem and the inner cortex consists of thin-walled cells which appear to have contained but little substance. There are no intercellular spaces between them and in longitudinal sections they are seen to be elongated cells with oblique end-walls: they are evidently part of the stelar tissue and probably functioned as phloem. There is no evidence of the existence of sieve plates or pores and in this respect the tissue differs from the phloem of living Pteridophytes. In the rhizome there was less distinction between an outer and inner cortex and the xylem strand consisted of fewer tracheids.

FIG. 9.—*Rhynia major*. Longitudinal section of a sporangium. The sporangium contains thousands of spores. × 6·5. Kidston Col. 2393.

Large sporangia were borne singly on the ends of some of the aerial branches. The length of the sporangium was about 3 mm., the breadth 1·5 mm., and it was approximately cylindrical in shape. They were similar in construction to the still larger sporangia of *Rhynia major* (Figs. 9 and 10). The wall consisted of three distinct layers of cells, a fairly stout epidermis, a layer about three cells deep of thin-walled cells, and an inner layer of usually well-preserved cells. In the opinion of Dr. Kidston and Professor Lang this inner layer of the sporangium wall was probably of the nature of a water-conducting sheath similar in function to the tracheidal sheath found in some fossil sporangia, although characteristic tracheidal thickenings are not visible in its cells. The sporangium produced tetrads of cuticularised spores each about 40 μ in diameter.

Rhynia major was a similar plant of somewhat greater stature probably attaining a height of about 50 cm. (Fig. 6). The stems were twice as thick and there was a more distinct group of small tracheids in the centre of the xylem. The sporangia were about four times the length and twice the thickness and the spores one and a half times the diameter of those in *R. Gwynne-Vaughani*. No adventitious branches or cortical bulges have been observed on *R. major*.

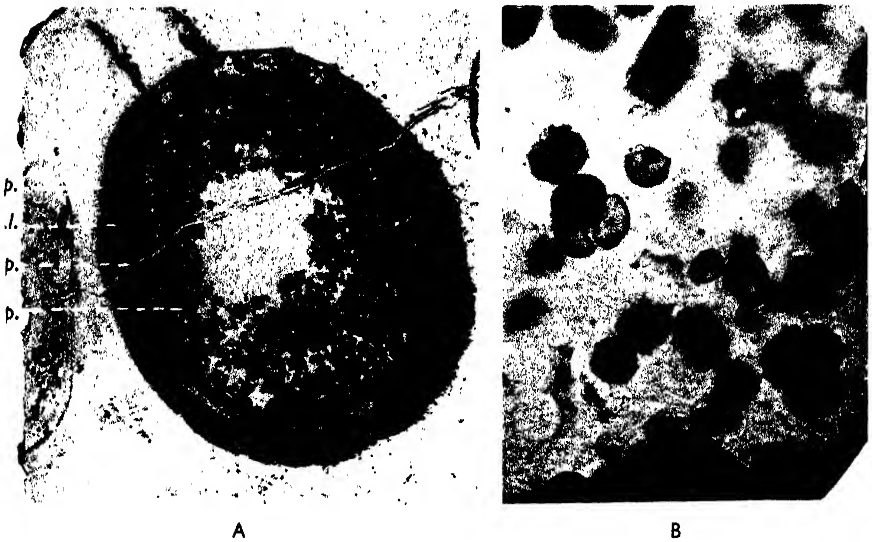

FIG. 10.—A. *Rhynia major*. Transverse section of a sporangium. *ep.*, thick-walled epidermis; *m.l.*, middle layer of wall; *tap.*, "tapetum"; *sp.*, spores. × 14. After Kidston and Lang.—B. Spores in a sporangium. Some are still associated in tetrads. × 160. After Kidston and Lang.

Hornea Lignieri (Fig. 11), another vascular plant from Rhynie, a smaller plant than *Rhynia*, was similar in the external form of its aerial shoots. The aerial stems, which did not exceed 2 mm. in diameter, were upward growths from tuberous rhizomes, which bore abundant rhizoids on their lower surfaces. If traced downward from the aerial stem, the xylem of the vascular cylinder is found to terminate in the upper part of the tuberous rhizome in a group of approximately isodiametric cells, the walls of which have the same colour as the tracheids, in contrast to the other cells of the rhizome which appear to have been parenchymatous. There is no vascular tissue in the rhizome itself. One piece of rhizome could evidently give rise to more than one aerial shoot, but there was no vascular connection between such shoots.

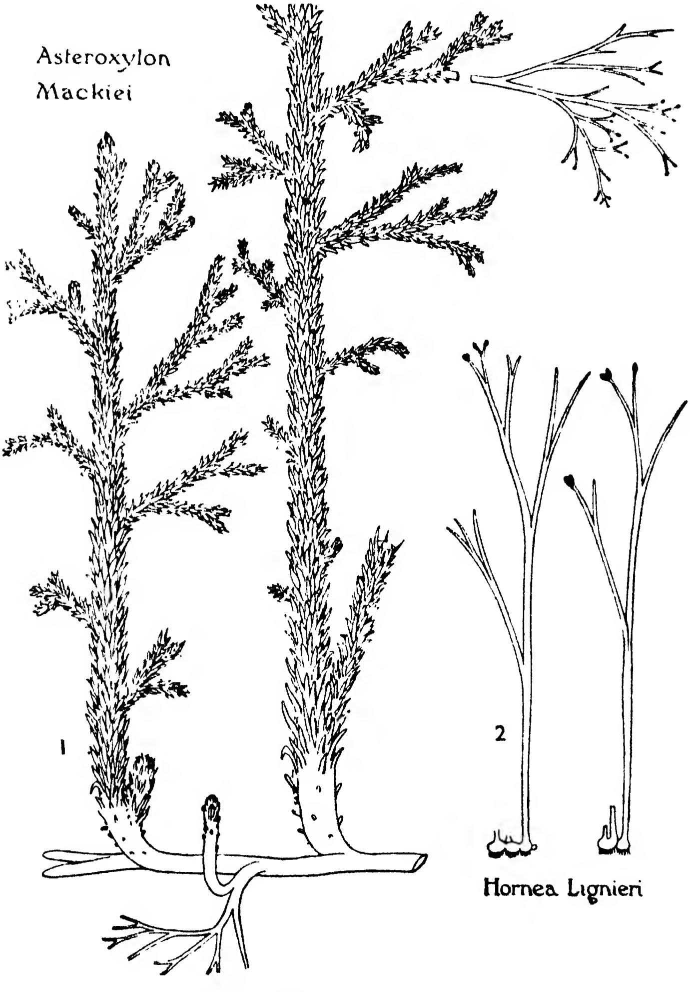

FIG. 11.—(1) Reconstruction of *Hornea*. × ½.—(2) Reconstruction of *Asteroxylon*. × ⅓. After Kidston and Lang. From D. H. Scott's *Extinct Plants and Problems of Evolution* (Macmillan & Co. Ltd., London).

The sporangia (Fig. 12) were terminal as in *Rhynia* but differed in one important respect. All the tissue inside the sporangium wall was not transformed into spores, for rising from the base of the sporangial cavity there is a columella of slender elongated cells which is continuous with the phloem of the stem below. The spore tissue surrounded the columella and extended over its top. Examples have been found of forked sporangia and in these the columella is also forked (Fig. 12). The spores (50 μ in diameter) were formed in tetrads. It would seem that the sporangia arose by transformation of the ends of certain branches, and if this transformation took place shortly after the apex of the stem forked, the result was a forked sporangium.

FIG. 12.—*Hornea Lignieri*. Longitudinal section of two sporangia (sm¹ and sm²), that on the left is forked. The columella may be seen extending upwards in the midst of the spore mass. × 12. After Kidston and Lang.

Psilophyton.—In 1859 Sir J. W. Dawson described some fossil plants which had been found in Lower Devonian rocks at Gaspé in Canada and later gave a reconstruction based on the evidence afforded by the fossils of a plant which he named *Psilophyton princeps*. Examples of this plant have been found in rocks of the same age in Norway and Scotland, and recently a very closely related species, *Psilophyton wyomingense*, has been found at Bear Tooth Butte, Wyoming, U.S.A. (Dorf, E., 1934) in Lower Devonian rocks. The essential correctness of Dawson's reconstruction has been supported by recent investigators. *Psilophyton princeps* is a plant in habit somewhat similar to *Rhynia* with branching cylindrical stems, the lower parts smooth and presumably subterranean, the upper parts clothed with small spines. The stems varied in diameter from 1 to 7 mm. and the spines, which were abundant on the lower parts of the aerial stem and few and widely separated on the ultimate branches of the stem, varied from 0.5 to 2.5 mm. in length. It has been shown that the surface of the stem and spines was covered with cuticularised epidermis. Stomata were present on the surface of the stem but not on the spines, most of which appear to have had a small ovoid swelling of a glandular nature at the tip. The stems had a vascular column which contained tracheids with annular thickenings similar to those in *Baragwanathia.* There is no evidence of vascular tissue in the spines, which appear to have been glandular emergences and not primarily photosynthetic organs.

The sporangia, which were terminal on the branches, vary in size from 4 to 6.5 mm. in length and 1 to 2 mm. in width. The wall was at least two-layered. There was an outer stout epidermis and an inner layer which may be compared with the peculiar inner layer of the *Rhynia* sporangium. The spores which are found inside many of the sporangia vary from 60 to 100 μ in diameter and from their shape it is evident that they were formed in tetrads.

Thursophyton.—Our knowledge of this Middle Devonian genus is scanty. It seems to have been constructed on much the same plan as *Psilophyton*, but the structures which correspond in position to the spines in *Psilophyton* were flattened tangentially and more leaf-like, although no vascular tissue has as yet been detected in them.

Asteroxylon.—This genus, represented by two Middle Devonian species *Asteroxylon Mackiei* (Fig. 11) from Rhynie, Aberdeenshire, and *A. elberfeldense* from the valley of the Rhine, is similar in external morphology to *Psilophyton.* The internal structure of *A. Mackiei* is beautifully preserved. The reconstruction gives an idea of its external morphology. The rhizomes were smooth and bore slender branches which no doubt functioned as roots. They had a central strand of spirally thickened tracheids surrounded by zone of thin-walled vertically elongated cells with pointed or oblique ends. They were therefore not unlike the stems of *Rhynia* in general construction. There is a transition region between the smooth rhizomatous part and the aerial leafy shoots. On the transition region there are some small scales without any trace of a vascular strand developed in relation to them. On the aerial parts, however, a vascular strand is present in connection with the xylem of the shoot which extends upwards through the cortex as far as the base of each leaf into which, however, it does not extend. The leaves were slightly dorsiventral and oval in section. Like the surface of the shoot, the epidermis of the leaf was cutinised and bore stomata. The stem (Fig. 13) contains a strand of xylem in the form of a deeply fluted column which in section appears as a multi-rayed star. The tracheids of which the xylem is entirely composed are slightly smaller at the ends of the rays (Fig. 14). The leaf traces were attached to the ridges of the xylem column and are visible as small black spots opposite the ends of the rays in the transverse section of the stem. In longitudinal section (Fig. 15) the tracheids of the xylem are seen

FIG. 13.—*Asteroxylon Mackiei*. Transverse section of stem and leaves. The stem is cut just below a fork and the two stellate columns of xylem are seen in the centre. Leaf traces (black) are seen in the cortex but the leaves are seen to have no vascular tissue. × 7. After Kidston and Lang.

to be long tracheids for the most part with spiral thickening, though occasionally the thickening is in the form of rings, particularly in the smaller elements of the protoxylem. The phloem extends as a thin layer all round the xylem but attains its

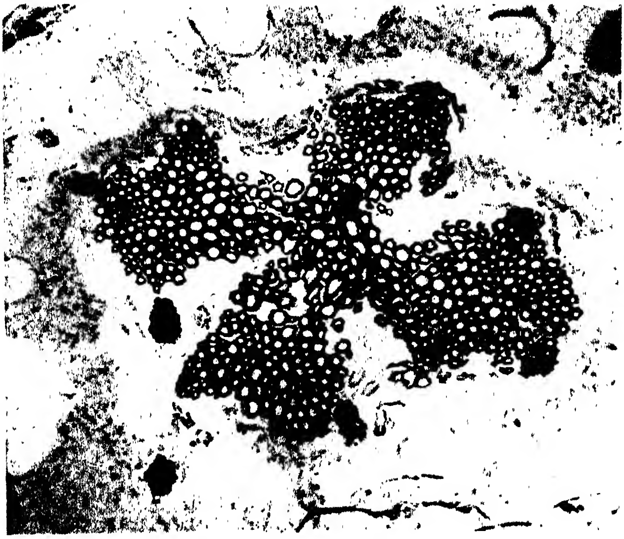

FIG. 14.—*Asteroxylon Mackiei*. Transverse section of the vascular column showing departure of leaf traces from the ends of the xylem rays. × 33. After Kidston and Lang.

FIG. 15.—*Asteroxylon Mackiei*. Tracheids seen in longitudinal section. The second tracheid from the right is a very slender protoxylem element. × 210. After Kidston and Lang.

maximum development in the bays between the rays of xylem. In some specimens there are indications that an ill-defined endodermis was present.

Sporangia have been found in the Rhynie chert which are probably those of *Asteroxylon*. The available evidence, which is not conclusive proof, suggests that these sporangia were borne on slender dichotomously forked leafless branches which formed the extremities of some of the leafy shoots. The sporangium was pear-shaped, narrowing at the base, where it was attached to a relatively stout stalk. The sporangium was about 1 mm. in length and had a wall of more than two cells in thickness. The spores, which were formed in tetrads, were about 64 μ in diameter. The sporangium dehisced at the end. While no evidence of the attachment of these smooth branches to leafy ones of *Asteroxylon Mackiei* has been detected in the Rhynie chert, *Asteroxylon elberfeldense* bore almost leafless slender ultimate branches.

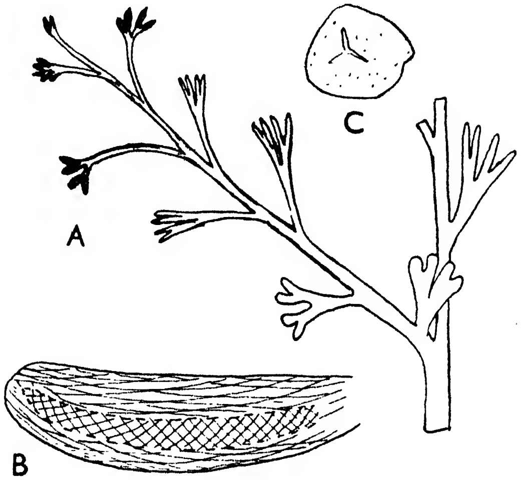

FIG. 16.—*Protopteridium minutum*. A. Part of a branching axis bearing sporangia and flattened leaf-like divisions. × 2.—B. Sporangium (diagrammatic). × 25.—C. Spore showing triradiate ridge. × 250. Adapted from Halle, 1936.

Protopteridium.—This genus has been found in the Middle Devonian of Bohemia and China (Halle, 1936). In the Chinese species *P. minutum* (Fig. 16) the aerial shoots consist of sympodially branched axes with dichotomously forked lateral branches. Some of the smaller branches were flattened in form and bear a close resemblance to leaflets or pinnules and the whole branching system resembles a fern frond. It is possible that this plant represents an evolutionary stage in the development of a flattened photosynthetic lamina with branching veins, such as is found in the fronds or leaves of Upper Devonian and later plants, by a webbing together of branches, from the cylindrical branch systems characteristic of the Rhyniaceae and many other Silurian and Early Devonian Plants.

The sporangia are borne on the ends of slender divisions of the branching system as in the Rhyniaceae. In contrast to the Rhyniaceae the sporangium (Fig. 16, B) has a band of cells different from those which form the greater part of the wall which extends longitudinally down one side. It is not clear whether this band represents an annulus or a line of dehiscence.

If *Protopteridium* is a Fern certainly some of its characteristics are very reminiscent of the Rhyniaceae.

The land-flora of the Silurian and Lower and Middle Devonian consisted, as far as we can judge, of plants which produced cutinised spores in tetrads and had cuticles and lignified vascular tissue. It was a flora of Pteridophytes which were none of them heterosporous as far as we know. The seed had not been evolved and we have no decisive evidence that true roots existed. Where leaves are found they are of the small, microphyllous type and there is no evidence that these Pteridophytes had evolved structures homologous with the fronds of Ferns. The structure of the xylem elements differs from that of any living Pteridophytes.

We can recognise two main types in this early land-flora. In *Baragwanathia* and *Drepanophycus* (*Arthrostigma*) (Kräusel and Weyland, 1935), the plants resemble Lycopods in external appearance and the sporangium is borne on or near the upper surface of the leaf base. In the other type seen in *Zosterophyllum*, *Psilophyton*, and the Rhynie genera the sporangia are borne terminally on branches of the stems. *Asteroxylon* and a few others approach the Lycopod type in the form of the shoot with its small leaf-like appendages, but many have a thalloid form with no distinction into leaf, stem, and root.

Among living plants the Psilotales show the greatest resemblance to this latter type in vegetative structure.

In the Psilotales the sporangia are grouped in synangia, a condition which is not characteristic of these early plants but which is found in a simple form in the forked sporangia of *Hornea*. It is interesting in this connection to note that fructifications called *Yarravia* (Lang and Cookson, 1935) found in association with *Baragwanathia* consist of three terminal sporangia closely joined together. The Psilotales have no roots.

Thus in the Silurian and Early Devonian, Thallophytes and Pteridophytes constituted the vegetation of the Earth. The presence of plants of an intermediate type such as *Parka* and *Nematothallus* and the marked thalloid form of many of the Pteridophytes suggests that during these early periods an important series of transformations were in progress. It would seem that from plants with predominantly thallophyte characteristics land-living Pteridophytes were being evolved.

CHAPTER IV

LYCOPODIALES

A COMPARISON has been drawn (p. 27) between *Baragwanathia* and the living genus *Lycopodium*. It is possible that the former may be an early representative of the *Lycopodium*-phylum, but if so, the intervening history of the phylum is very scanty. On the other hand the other important genera of the group, *Selaginella* and *Isoëtes*, are obviously the remaining members of a phylum which played a conspicuous rôle during Carboniferous times and of which we have undoubted traces in the Triassic and the Cretaceous.

The Lycopodiales may be classified as follows :

LYCOPODIALES

A. Eligulatae (Homosporeae)
  I. Lycopodiaceae
    1. *Spencerites* (Carboniferous)
    2. *Lycopodites* (Carboniferous, Rhaetic)
    3. *Lycopodium*
    4. *Phylloglossum*

B. Ligulatae (Heterosporeae)
  I. Lepidodendraceae
    1. *Lepidodendron* (Carboniferous)
    2. *Lepidophloios* ,,
  II. Lepidocarpaceae
    1. *Lepidocarpon* (Carboniferous)
  III. Miadesmiaceae
    1. *Miadesmia* (Carboniferous)
  IV. Bothrodendraceae
    1. *Bothrodendron* (Carboniferous, ? Devonian)
  V. Sigillariaceae
    1. *Sigillaria* (Carboniferous, Permian)

VI. Isoëtaceae
  1. *Pleuromeia* (Triassic)
  2. *Nathorstiana* (Cretaceous)
  3. *Isoëtes*
VII. Selaginellaceae
  1. *Selaginellites* (Carboniferous)
  2. *Selaginella*

In all instances in which the evidence is complete ligulate forms are found to be heterosporous and eligulate plants homosporous, but it is difficult to make sure whether or not a ligule is present on fossil plants preserved as compressions.

The Devonian genus *Cyclostigma* and the Carboniferous *Pinacodendron* are known to be heterosporous but ligules have not as yet been detected on them. The systematic position of such forms as *Archaeosigillaria*, *Omphalophloios*, *Ulodendron*, *Asolanus* is also uncertain.

A. ELIGULATAE.—Apart from the Silurian *Baragwanathia* which bears a close resemblance to the genus *Lycopodium* in external morphology but differs in the structure of its tracheids, the only reliable evidence for the existence of this division of the Lycopods in the Palaeozoic is afforded by a cone called *Spencerites*. This Upper Carboniferous strobilus (Fig. 17) bears a close resemblance to the strobilus of *Lycopodium cernuum*.

The spores of *Spencerites* differ very considerably from those of *Lycopodium*. They have a conspicuous wing extending round the equator of the spore and the wing is hollow and inflated. The spores are large (140 μ in diameter). The relatively large size of the spore and the fact that no smaller type of spore is found have led to the assumption that the plant was homosporous. The fossil is well preserved as a petrifaction and it is clear that there is no ligule.

The term *Lycopodites* has been applied to some imperfectly known fossils of herbaceous plants of the Lycopod habit which appear to be homosporous but which are only known in the form of compressions.

B. LIGULATAE.—While the living ligulate Lycopods are all small herbaceous plants the majority of the known fossil Ligulatae were large trees. In the rocks of the Carboniferous period fossil tree-stumps are frequently found which have a characteristic formation of their root-bearing region (Fig. 18). This type of tree base is called *Stigmaria* and it is known that several distinct genera, *Lepidophloios*, *Lepidodendron*, *Bothrodendron*, and *Sigillaria*, had bases of this type. Tree-stumps of this kind are sometimes found in large groups which suggests that they were the dominant plants in some of the extinct forests (Frontispiece).

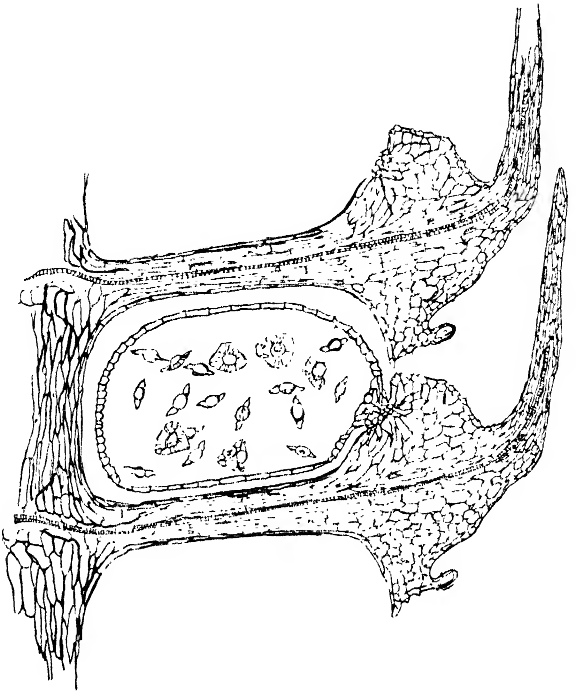

FIG. 17.—*Spencerites insignis*. Reconstruction of a longitudinal radial section of part of a strobilus showing two sporophylls. Winged spores are shown in the sporangium. After Miss Berridge.

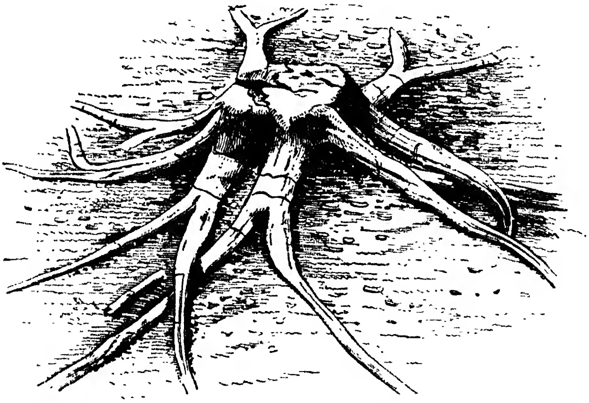

FIG. 18.—Stigmarian tree-base of Upper Carboniferous age. After Williamson.

Stigmarian bases are also found in large numbers projecting from the lower surfaces of coal-seams into the underlying rock, indicating that the trees whose debris went to form the coal were for the most part arborescent Lycopods.

Each *Stigmaria* consists of four main arms which spread outward and downward from the trunk (Fig. 18), each dividing almost at once by a dichotomous forking. These branches underwent further dichotomies and in some cases they have been found to extend for a distance of nearly 40 feet from the base of the trunk. The ultimate branches vary from about 4 to 10 cm. in diameter and bear numerous evenly spaced roots (Fig. 19). The roots were evidently produced in acropetal succession in the manner of leaves at a stem apex.

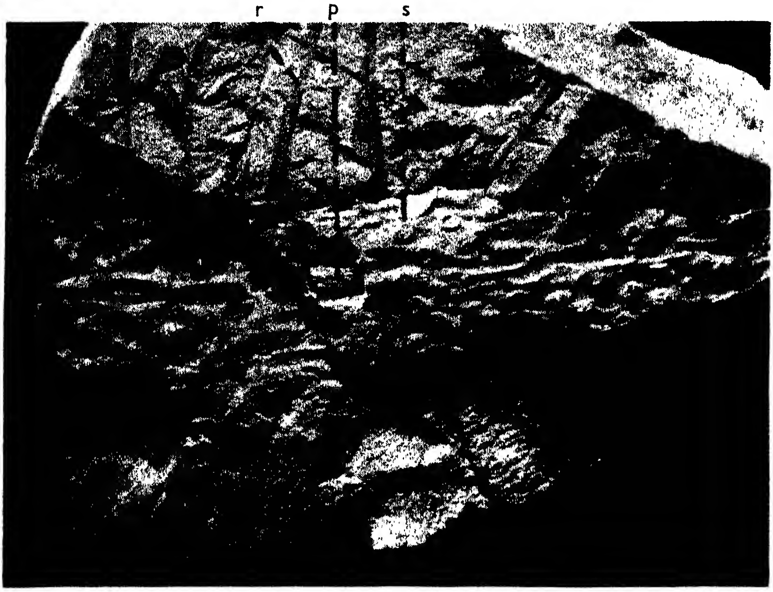

FIG. 19.—*Stigmaria ficoides*. Branch of a Stigmarian base. The cavity originally occupied by the inner cortical tissues is filled with shale which has also formed a pith cast, *p*, of the vascular cylinder; *s*, surface of branch with places of attachment of roots; *r*, roots. ½ nat. size. Hunterian Museum, Glasgow Univ. J. W. Photo.

In the commonest type of *Stigmaria* there is a central pith or pith cavity (Fig. 20) surrounded by a ring of vascular bundles. The protoxylems are next to the pith and consist of spiral tracheids. They are succeeded by scalariform tracheids which are radially seriated. The vascular strands, which supply the roots, extend through the wood from the protoxylems and each is accompanied on its side facing the apex by a medullary ray of thin-walled tissue. The woody cylinder is thus perforated at regular intervals by these medullary rays. The root strands then curve towards the apex and pass up through the phloem for some distance. In mature Stigmarian axes the traces are rarely encountered in the middle cortex, which has only been found preserved in a few examples. In the narrow outer cortex they follow a slightly ascending course and then enter the roots.

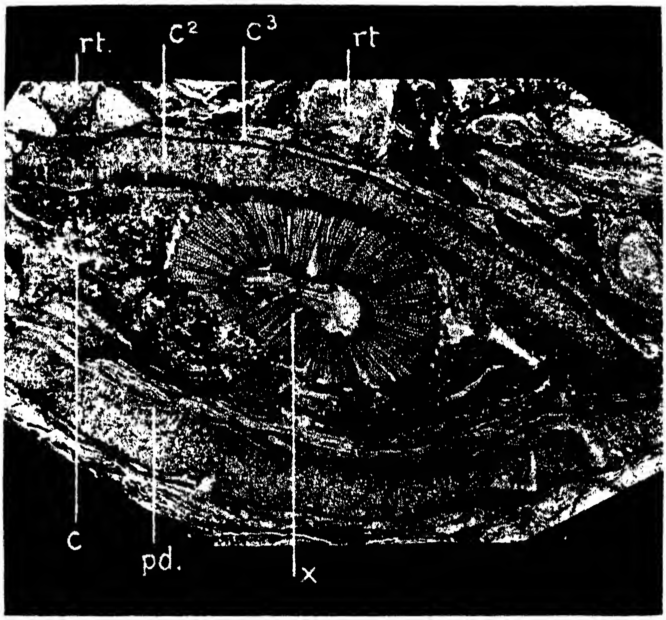

FIG. 20.—Transverse section of a Stigmarian branch. × $3\frac{1}{2}$. *x*, wood; *c*, middle cortex; *pd.*, secondary periderm; c^2, primary cortex; c^3, hypodermal tissue; *rt.*, root base. Photo by Boodle.

In 1891 Hick described, at first under the name *Tylophora* and then *Xenophyton*, a fossil plant which Professor Weiss has shown to be in all probability the Stigmarian axis of *Lepidophloios fuliginosus*. The specimen represents a part near the growing point and affords us an excellent opportunity of examining a Stigmarian axis in its young condition. There is much less secondary wood than is usually found in *Stigmaria*, the cambium is preserved in places, and the peculiar type of phloem characteristic of *Lepidophloios* is well preserved. There is a narrow inner cortex of thin-walled parenchyma. The middle cortex consists of parenchyma in which many of the cells are in filaments closely packed together and somewhat resembling a fungal tissue. The outer cortex is parenchymatous and of firmer construction. The inner part of the outer cortex consists of cells which, by tangential divisions, have formed a thick zone of secondary cortex. There does not appear to be a definite cambial layer, the secondary tissue being produced by repeated tangential divisions of all the cells. This tissue is the conspicuous part of the cortex of mature Stigmarian axes and usually has the remains of the outer tissues and the root bases present on its outer side. In the young axis, however, in the specimen described by Hick and Weiss, numerous irregular bands of secondary cortex were formed throughout the hyphal middle cortex, and in the mature Stigmarian axes

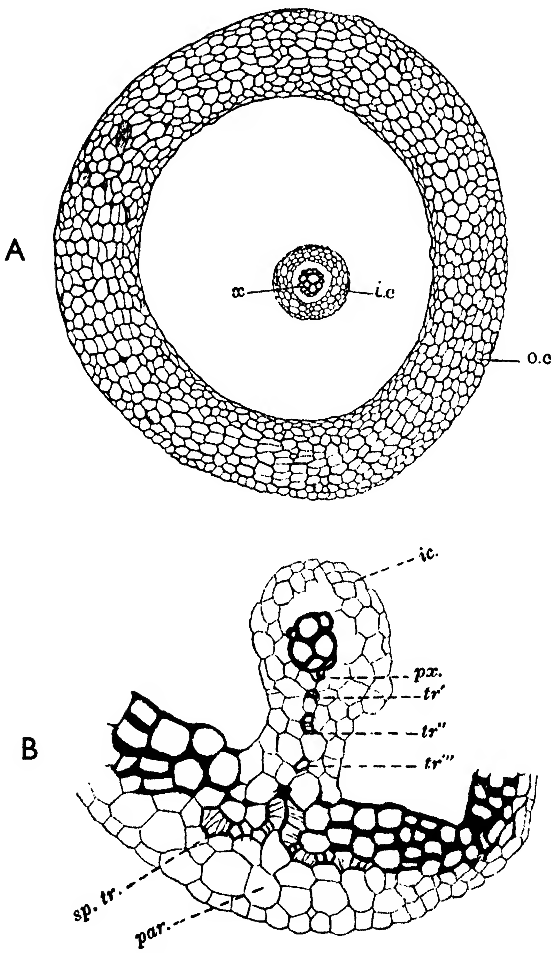

FIG. 21.—*Stigmaria ficoides*. A. Transverse section of a root. × 16. After Scott.—B. Part of another type of root. *par.*, outer cortex; *i.c.*, inner cortex; *x*, xylem; *px.*, protoxylem; tr', tr'', tr''', sections of accessory strands traversing flange. *sp. tr.*, sheath of tracheids in outer cortex. × 67. After Weiss.

found in close association with *Lepidophloios Wünschianus* in Arran a very large part of the middle cortex consists of radially seriated tissue and there are only traces of the hyphal tissue. This suggests that the hyphal tissue was gradually transformed into radially seriated tissue by the repeated tangential division of its constituent cells.

Professor Lang has shown that the roots in young examples of *Stigmaria* are slightly endogenous, originating below a few layers of the outer cortex. In mature *Stigmarieae* this outer tissue has usually disappeared and the roots appear to be exogenous.

The roots which exhibit dichotomous branching are evenly spaced over the surface of the Stigmarian branch. The outer surface of the root was smooth and on no Stigmarian roots have root hairs been observed. The outer cortex consists of parenchyma and is usually well preserved (Fig. 21). There are sometimes traces of tracheidal cells on its inner surface. The middle cortex is represented by a space as in the root of *Isoëtes.* In the middle of this space the vascular strand is seen to be surrounded by a narrow sheath of parenchyma, presumably the inner cortex. The xylem, which is wedge-shaped in section, has a single protoxylem and sometimes a small amount of radially seriated tracheids on the far side of the metaxylem from the protoxylem where the phloem is found. Small strands of narrow tracheids are sometimes found extending from the protoxylem across the middle cortical space to the inner surface of the outer cortex where they link up with the lining of short tracheids which is sometimes found there. These small strands are surrounded by a sheath of parenchyma (Fig. 22) and served as a channel of communication between the vascular tissue and the outer cortex. In some types of Stigmarian root a flange of parenchyma joins the vascular strand along its whole length to the outer cortex (Fig. 21, B) and the accessory strands of tracheids traverse this bridge.

At the base of the root where it is attached to the Stigmarian axis there is sometimes stellate parenchyma forming the middle cortex. In an Australian species of *Isoëtes* Dr. S. Williams has found that throughout the root the middle cortex consists of stellate cells.

Of the trunks which possessed Stigmarian bases those of the genus *Lepidophloios* are the best known. In the Calciferous Sandstone series (Lower Carboniferous) of Scotland several examples have been found. A transverse section of *Lepidophloios*

Wünschianus from Dalmeny in West Lothian is shown in Fig. 23. It has a deeply fissured bark formed of secondary cortical tissues. This tissue, which was developed by meristemmatic activity in the outer cortex, consists of elongated cells with very thick radial walls (Fig. 24, D) and formed a very strong sheath round the axis. Inside this tissue which gave the trunk its rigidity and strength there is a zone of large-celled parenchyma, the inner part of the outer cortex. The middle and inner parts of the cortex are not preserved. The stele or vascular column is very small in comparison with the total diameter of the trunk. In the section of the stele illustrated (Fig. 23), the pith consists of hyphal parenchyma with a central gap. The primary xylem is in the form of a ring with the protoxylems on the outside. The protoxylems appear as small projections in a transverse section. The large metaxylem

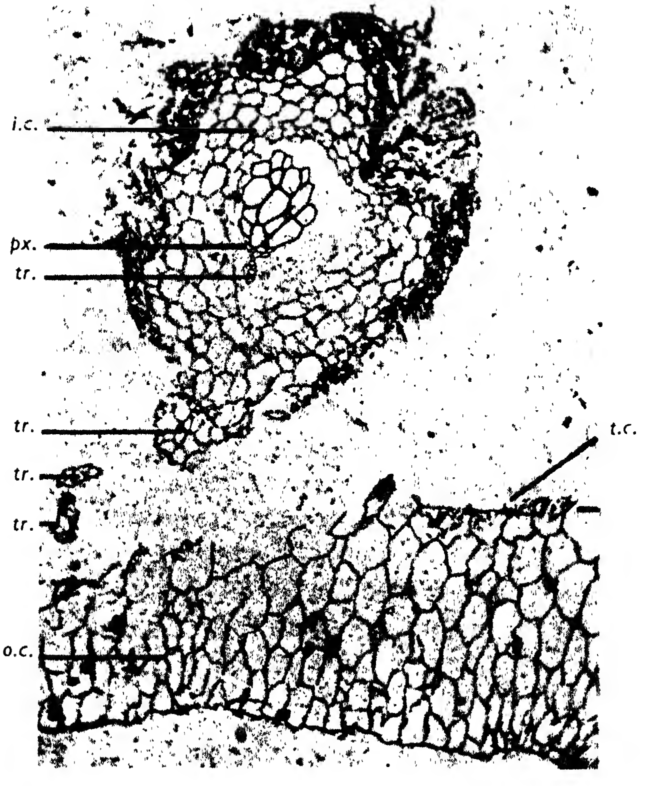

FIG. 22.—*Stigmaria ficoides*. Part of a transverse section of a root probably belonging to *Lepidophloios Wünschianus*. Lower Carboniferous, Arran, Scotland. *o.c.*, outer cortex; *px.*, protoxylem of root; *i.c.*, inner cortex; *tr.*, trabeculae with tracheids in their centres; *t.c.*, tracheidal cells. J. W. Coll. Slide 608.

tracheids and those of the secondary wood are very long and have scalariform thickenings. The medullary rays are small and consist of small cells with spiral or scalariform thickenings. The wood apparently contained no living cells in the mature condition. No example is known of a trunk in which the diameter of the wood exceeded 80 mm.

Outside the secondary xylem are radially seriated thin-walled cells but these are rarely preserved. They are not cambial cells and they are quite short. Outside this tissue, which is only found in trunks, there is a peculiar tissue to which the name "secretory tissue" has been given. It consists of wide thin-walled cells with small cells with dense contents between them (Fig. 27, A). In longitudinal sections it is evident that vertical rows of the large cells formed ducts by the absorption of the horizontal walls (Fig. 27, B).

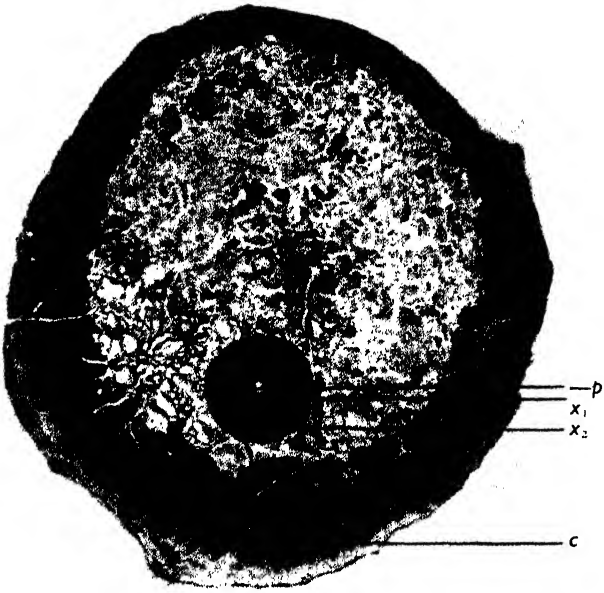

FIG. 23.—*Lepidophloios Wünschianus*. Transverse section of the trunk found at Dalmeny in West Lothian, Scotland. *p*, pith; x_1, primary xylem; x_2, secondary xylem; *c*, fissured secondary cortex. ⅓ nat. size. After Seward and Hill, 1900.

In some petrified stumps of *Lepidophloios Wünschianus* found in Lower Carboniferous strata on Arran in the Clyde (Walton 1935), it has been found that the stele varied in structure a different levels in the trunk. Near the base the primary wo

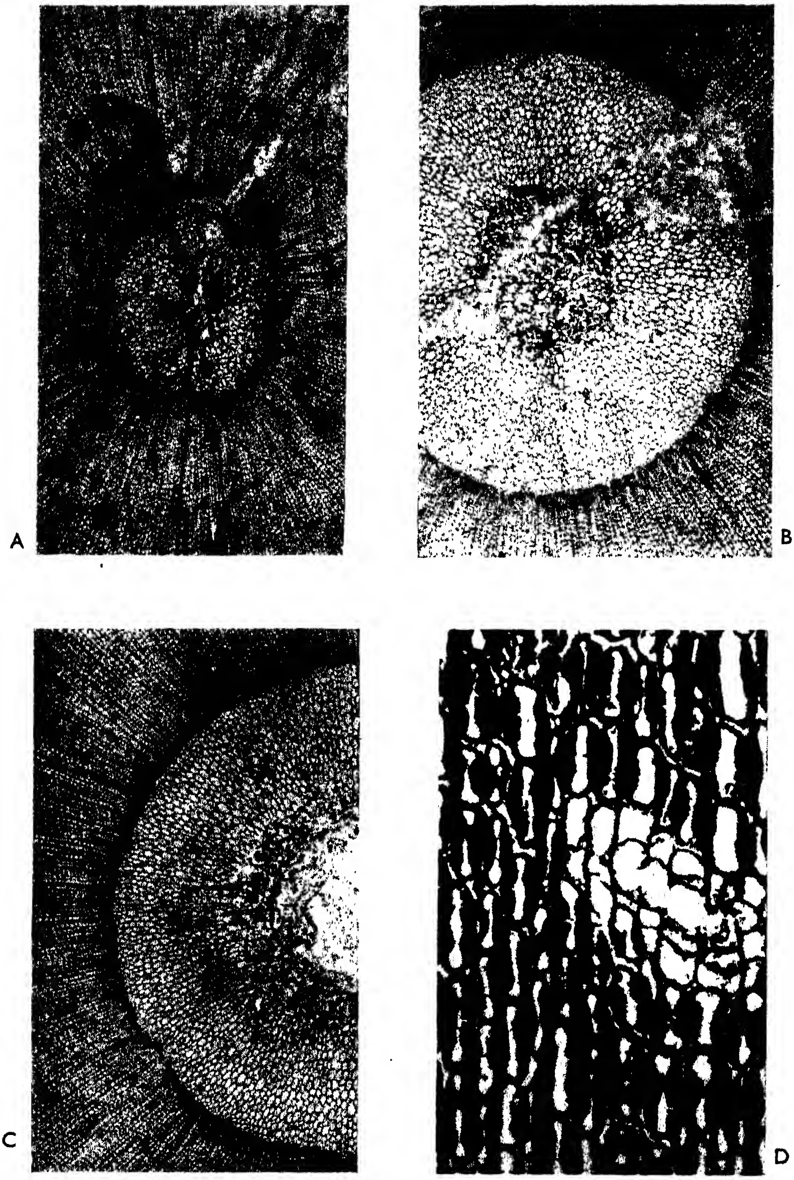

FIG. 24.—*Lepidophloios Wünschianus*. A, B, C. Sections of the stele of the trunk. All × 6. A, from near the base, showing solid primary core surrounded by secondary wood; B, higher up trunk, with hyphal medulla in centre of primary wood; C, still higher up, with cavity in medulla.—D. Section of cortical fibrous tissue. × 200. Walton, 1935.

consists of a slender solid core of tracheids (Fig. 24, A), about 2 mm. in diameter, surrounded by a thick development of secondary wood. Further up the trunk the primary wood increases in diameter and a pith of hyphal cells is found (Fig. 24, B). Still higher a cavity appears in the pith, and the primary wood forms a wide tube up to 26.5 mm. in diameter with correspondingly less secondary wood (Fig. 24, C). It is to be noted that the total diameter of the wood is practically constant throughout the length of the trunk. In one trunk the total diameter of the wood at the base is 73 mm. and the primary 5.5 mm., while higher up, where the total diameter is 63 mm., the diameter of the primary is 15 mm.

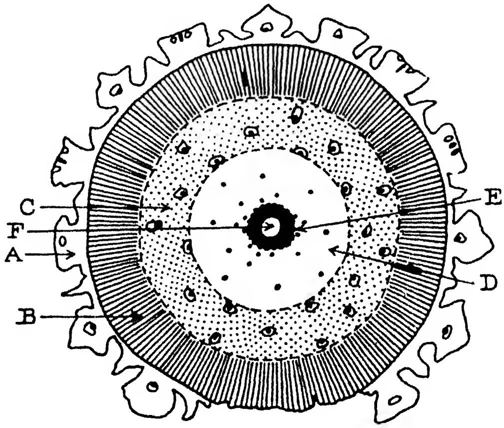

Fig. 25.—*Lepidophloios Wünschianus.* Diagram of a transverse section of a branch. × ⅓. *A*, outer cortex and leaf bases; *B*, secondary cortical fibres; *C*, inner part of outer cortex; *D*, inner cortex; *E*, primary xylem; *F*, pith.

These facts suggest that the tree developed from a small plant with a small solid stele of primary xylem which, as the plant grew, was supplemented by the addition of radially arranged tracheids. As the plant increased in size and vigour the apical meristem increased in size and a larger primary stele was built up.

In the branches of *Lepidophloios Wünschianus*, which closely resemble those of *Lepidophloios Harcourtii* described by Witham over a hundred years ago, there is no secondary wood (Fig. 25). The branch owed its rigidity to cortical fibres similar to those found in the cortex of the trunk. The primary xylem in the larger branches has a pith (Fig. 26, A) but the smaller branches have a solid stele (Fig. 27) similar to that found at the base of the trunk. The xylem is all centripetal and the protoxylems are on the

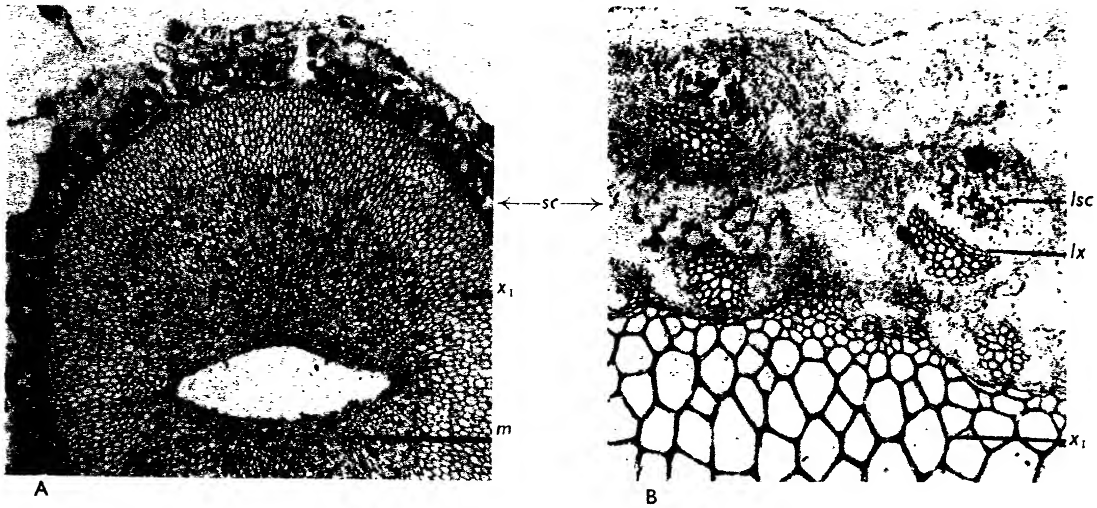

FIG. 26.—*Lepidophloios Wünschianus*. A. Transverse section of part of the stele of a branch. × 6.—B. Part of the periphery of the stele of a similar branch. × 41. *m*, medullary parenchyma; x_1, primary wood; *lx*, leaf-trace xylem; *sc*, secretory tissue; *lsc*, secretory tissue of leaf trace. After Walton, T.R.S.E., 1935.

outside. The projecting points of small tracheids, which appear round the periphery of the wood in a transverse section, are sections of an anastomosing series of ridges.

The leaf traces are attached to the surface of the primary wood between the ridges (Fig. 26, B). As they pass the secretory tissue (Fig. 26, *lsc*) a strand of the latter accompanies each trace on its abaxial side. The leaf trace passes across the space representing the soft cortical tissues, which have usually disappeared, and enters the firm outer cortex, where a strand of soft tissue accompanies each trace on its abaxial side. This part of the trace represents an extension of the soft inner cortical tissues.

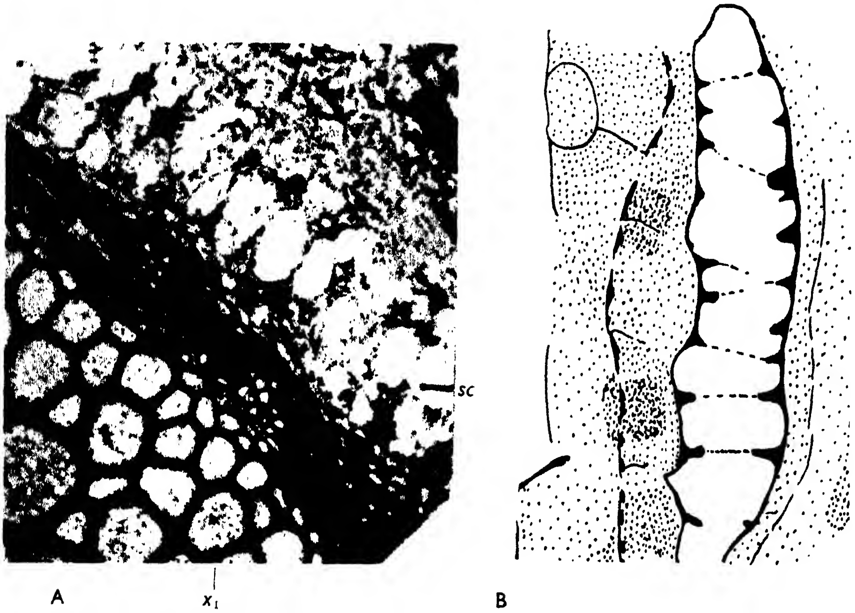

FIG. 27.—*Lepidophloios* sp. A. Transverse section of a small twig. × 65. *sc*, secretory tissue; x_1, outer part of primary xylem.—B. Drawing of element of secretory tissue in longitudinal section. × about 100. Sections in Royal Scot. Mus., Edin. Photo and drawing by Mrs. L. Macfarlane.

As the leaf trace enters the base of the leaf this strand of delicate tissue divides into two strands (parichnos strands) which diverge and then curve upward until they come to lie one on each side of the leaf trace. When the leaf is cut off by the absciss layer the parichnos strands appear on the surface of the leaf scar as small marks on each side of the vascular strand (Fig. 28, C). In some species of *Lepidodendron* (Fig. 28, B) there may be seen on the persistent leaf base just below the leaf scar two small depressions on the surface. These have been produced by the collapse of a tissue with well-developed intercellular spaces which lies between the surface of the leaf base and the two parichnos strands underneath. These two depressions were formerly thought to be due to the parichnos strands bending outwards and passing close beneath the surface before they attained the leaf scar.

The base of each leaf bore a ligule as in *Selaginella*, but in these extinct types it is deeply sunk in a pit. The ligule was left behind when the leaf fell off and the presence of the ligular pit may be seen on the persistent base of the leaf just above the scar (Fig. 28).

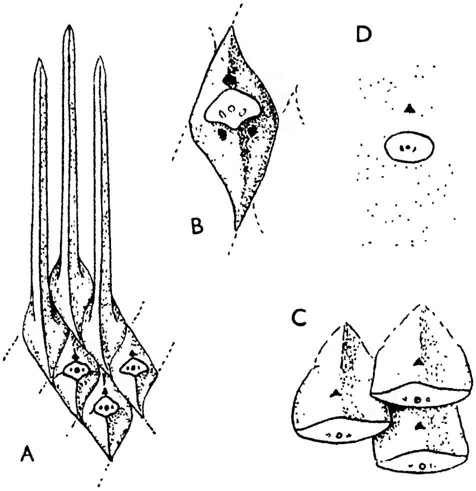

FIG. 28.—A. Diagrammatic representation of part of the surface of a young twig of an arborescent Lycopod, showing three leaves in attachment and the scars left by the fall of three others. The other figures represent the changes in form of the persistent leaf bases in B, Lepidodendron; C, Lepidophloios; D, Bothrodendron.

A considerable number of different species have been recognised among the examples of petrified branches belonging to the two genera *Lepidophloios* and *Lepidodendron*. They differ from one another in many respects. The following list gives some of the species with information about their wood. It is clear that many of them differ from *Lepidophloios Wünschianus* in having secondary wood in their branches. *Lepidodendron selaginoides* (= *L. vasculare*) is remarkable in having a mixture of parenchyma and small tracheids in the medulla.

It is clear that the solid stele must be regarded as primitive; it is found in what is presumably the sporeling part of *L. Wünschianus* and in the ultimate branches of probably all the others.

	Primary Wood	Secondary Wood
LOWER CARBONIFEROUS—		
Lepidodendron pettycurense	Solid	Present
,, *Veltheimii*	Medullated	,,
,, *Rhodumnense*	Solid	Absent
,, *brevifolium*	Medullated	Present
Lepidophloios Scottii	,,	Absent
,, *Harcourtii*	,,	,,
UPPER CARBONIFEROUS—		
Lepidophloios fuliginosus	Medullated	Present
Lepidodendron selaginoides	Mixed pith	,,
,, *Hickii*	Medullated	Absent

The leaves of the fossil Lycopods are simple lanceolate or linear with a single median vein. They are arranged in some complex spiral phyllotaxy. The leafy branches must have borne some resemblance to those of the living species of *Araucaria*. The leaves on the trunks and main branches were, as a rule, much larger and longer than those on the ultimate branches, which bore small, stiff, sometimes falcate, leaves.

Trunks and branches are frequently found from which all the leaves had fallen leaving a characteristic pattern formed by the persistent leaf bases (Fig. 28, A–D). The different genera of the Lepidodendraceae have characteristic patterns, but in all of them the young shoots bore closely crowded leaves and the lozenge-shaped leaf bases completely covered the surface of the branch (Fig. 28, A). In *Lepidodendron* (B) the leaf bases expanded after the fall of the leaf but did not alter much in shape. In *Lepidophloios* (C) the leaf base drooped downwards and the branch appears to be covered with overlapping scales. In *Bothrodendron* (D), a closely allied genus, the growth-expansion of the branch caused a flattening out of the leaf cushions so that the leaf scar appears to be flush with the surface and the ligular pit appears to be on the branch above it.

Lepidostrobus and Bothrodendrostrobus.—These names are given to the strobili ("cones") of the Lepidodendraceae—*Lepidostrobus* to those of *Lepidophloios* and *Lepidodendron*, and *Bothrodendrostrobus* to those of *Bothrodendron*. They were similar in shap to *Picea* cones and varied from about 5 cm. long and 1 cm. w to over 40 cm. long and 3.5 cm. wide.[1] In *Lepidophloios*, *Bo dendron*, and probably in some *Lepidodendrons* the

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[1] Specimen in the Botanical Department, Glas

borne on slender side branches attached to the larger branches. In many *Lepidodendrons*, however, they were attached to the ends of the smallest branches.

The strobili compare very closely with those of *Selaginella* but in *Lepidodendron* the sporangium was much longer in proportion, reaching in some instances a length of 17 mm. It was attached for its whole length along the top of the base of the sporophyll (Fig. 29). Its wall consisted of a single layer of palisade-like cells.

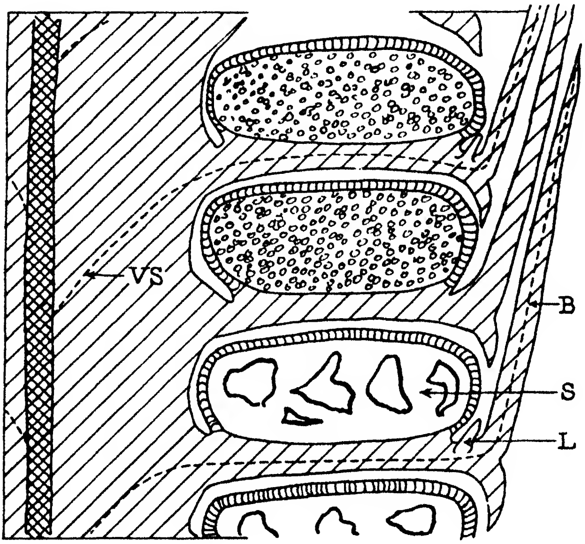


FIG. 29.—*Lepidostrobus*. Longitudinal section of part of a cone represented diagrammatically. Two sporophylls are seen in median section. Two microsporangia are seen at the top and two at the bottom of the part shown. *VS*, vascular strand; *B*, blade of sporophyll; *S*, sporangial cavity; *L*, ligule. About 12 times nat. size.

In some species the strobili produced only one kind of spore but in others both microspores and megaspores are found in the same cone, with the sporangia containing the megaspores at the base. As in *Selaginella* (Fig. 32, B) the ligule is placed between the end of the sporangium and the upturned part of the blade of the sporophyll.

The microspores vary from 0.02 to 0.03 mm. in diameter, while the megaspores, which are much larger, vary from 0.5 to .0 mm. in diameter. The remains of the prothallus and arche-
nium have been found in some megaspores (Fig. 30), a proof
se similarity in method of reproduction between these
s and the living *Selaginella* and *Isoëtes*.

spores from an arborescent lycopod must have been prodigious. They collected in large numbers on the forest floor and presumably fertilisation and the development of the young sporelings took place there. Coal which consists of the remains of forest vegetation usually contains large numbers of spores, many of which came from these Lycopods. Both kind of spore show great variety in form and ornamentation. If an analysis is made of the spore population in a coal-seam, a graph may be constructed showing the relative quantities of the different kinds of microspores (Fig. 31). A similar graph is usually obtained if the same seam is analysed in a different part of the coal-field, but a different seam will show quite a distinct form of graph, resulting from different proportions between the constituent types of spore. Such analyses are of great value to the geologist in the identification and correlation of coal-seams, even in areas where the strata are much disturbed by faulting.

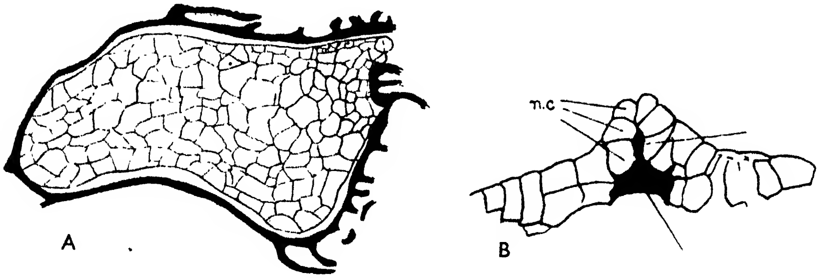


Fig 30.—*Lepidostrobus Veltheimianus*. A. Section of a megaspore containing prothallial tissue. × 50.—B. Longitudinal section through the archegonium of another prothallus. *nc*, neck cells × 275. After Scott.

Bothrodendrostrobus.—There is a most remarkable similarity between the sporophylls of *Bothrodendrostrobus* and some forms of *Selaginella* (Fig. 32, A and B). The female prothallus bulged out of the spore to a greater extent than in *Lepidostrobus.*

Lepidodocarpon and Miadesmia.—In some strobili to which the name *Lepidocarpon* has been given each sporangium produced one large megaspore, presumably by the abortion of all but one member of a single tetrad. This spore was not liberated from the sporangium. The sides of the sporophyll formed a sheath or indusium which almost completely enclosed the sporangium, leaving but a narrow opening along the top of the sporangiur (Fig. 33). This sporophyll may be compared with a seed, megaspore and the sporangium corresponding to the embr and nucellus, while the indusium with its slit-like apertur sponds to an integument and micropyle. We do not kr ever, whether the microspores effected fertilisation on the tree or whether this event occurred on the ground after the sporophyll

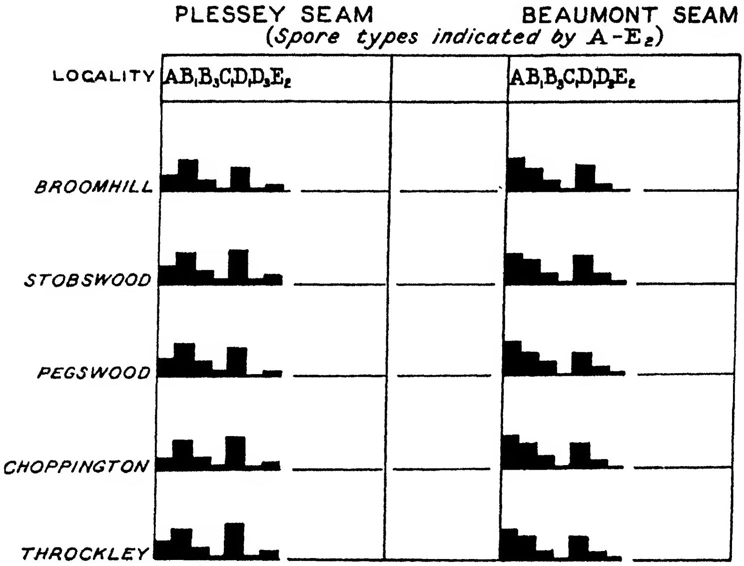
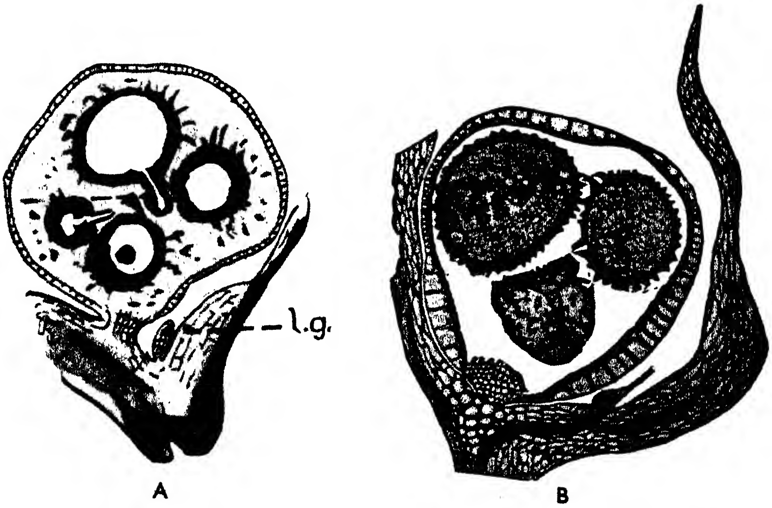


FIG. 31.—Graphical representations of the spore contents of two North of England coal-seams at a series of localities in the coal-field. A–E_2, the types of spore whose frequencies are represented by the heights of the black columns. Adapted from Raistrick and Simpson, 1933.



. 32.—Longitudinal section of sporophyll and sporangium of A, *Bothrodendron* *undum*, after Scott and Lyon; *lg*, ligule; B, *Selaginella apus*, from Bower, *imitive Land Plants*, 1935 (Macmillan & Co. Ltd., London).

detached from the strobilus. No trace of an embryo has d as yet. It is clear therefore that in one group of these

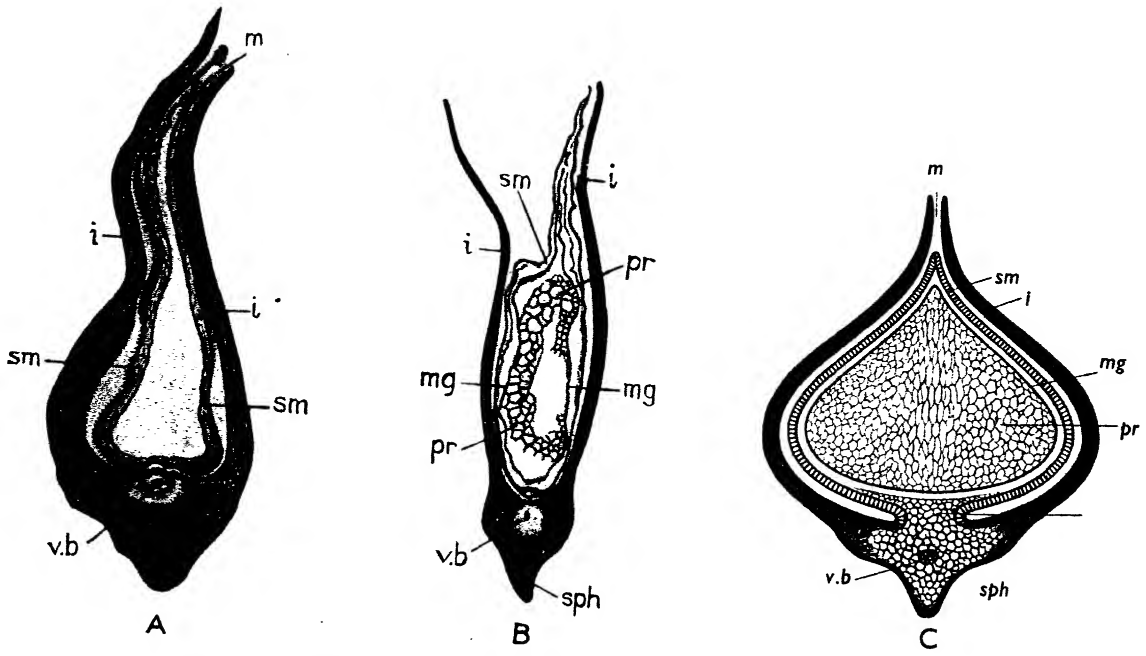


FIG. 33.—A, B. *Lepidocarpon Wildianum*. Transverse sections of two sporophylls. × 15. From D. H. Scott's *Extinct Plants and Problems of Evolution* (Macmillan & Co. Ltd., London).—C. *Lepidocarpon Lomaxi*. Transverse section of sporophyll (diagrammatic). *sph*, sporophyll below sporangium; *v.b*, vascular bundle; *i*, integument or indusium; *sm*, wall of sporangium; *m*, micropyle; *mg*, megaspore membrane; *pr*, prothallus. After Scott.

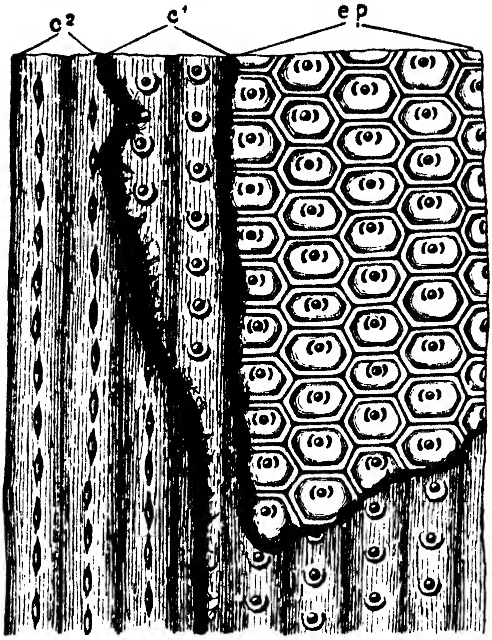


FIG. 34.—*Sigillaria tesselata.* Specimen showing parts of three layers of the cortical tissues. *ep*, external surface with vertical rows of leaf scars; c^1, periderm layer; c^2, cortical layer below periderm. After Schimper.

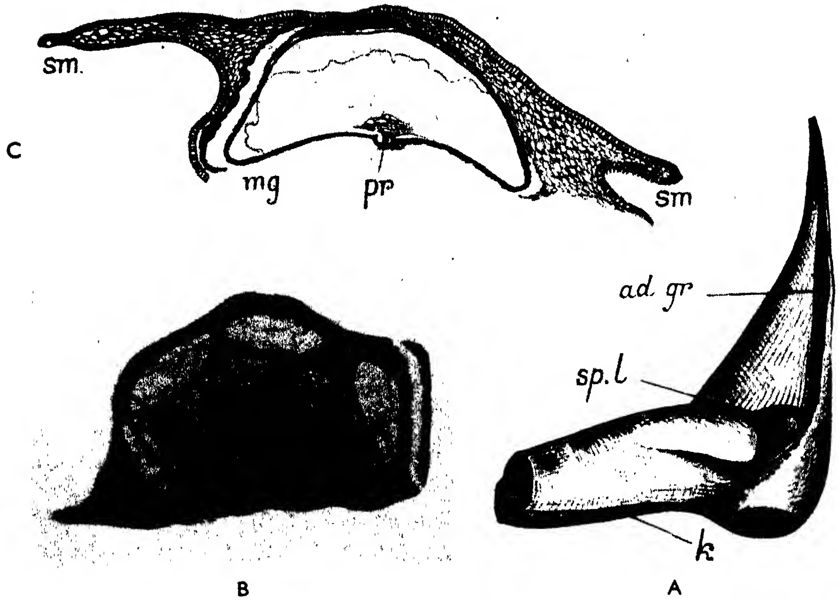


FIG. 35.—*Mazocarpon.* A. Reconstruction of a sporophyll. × 6.—B. Transverse section showing four megaspores.—C. Detached megaspore with adherent fragment of sporangium wall. *ad gr*, adaxial groove of sporophyll; *sp. l*, basin-shaped extension of sporangium wall; *k*, part of sporophyll below sporangium; *sm*, part of sporangium wall; *mg*, megaspore; *pr*, prothallus. After Scott.

extinct Lycopods the evolution of a seed from a heterosporous condition was nearly attained.

In *Miadesmia*, which was a small, possibly herbaceous plant, the sporophyll is even more seed-like.

Sigillaria.—Sigillaria stands somewhat apart from the types already described. The Sigillariae, of which a large number of species are known, had stigmarioid bases and tall straight trunks. Judging from the available evidence they were, however, rarely branched. In most species the leaf bases formed vertical lines on the trunk, which had as a result a ribbed appearance (Fig. 34). The leaves were long and grass-like, attaining in some instances a length of as much as a metre. The strobili were heterosporous. In *Mazocarpon*, which was probably borne by *Sigillaria*, the megasporangium (Fig. 35, A, B) had a large columella of sterile tissue around which the eight megaspores were situated. There is evidence that the megaspores broke away with part of the sporangium wall adhering to them (Fig. 35, C).

FIG. 36.—*Pleuromeia Sternbergi*. Base of plant showing the four root-bearing lobes. Above on the stem may be seen leaf scars. $\frac{2}{3}$ nat. size. After Bischof. From Bower's *Primitive Land Plants* (Macmillan & Co. Ltd., London).

Mesozoic Lycopodiales.—By the end of the Permian period the arborescent Lycopods had become practically extinct. In the Trias the only plant which may be attributed to the same group is *Pleuromeia*, which attained a height of about one metre. It had a four-lobed base, which bore roots in a regular arrangement (Fig. 36) as in *Stigmaria*, and the stem was unbranched and bore linear leaves. The apex of the stem was fertile and bore round scale-like sporophylls, each with a single large sporangium. The sporangium has been described as being in the abaxial side of the sporophyll but the evidence is not conclusive. It was probably on the adaxial surface but bulged outwards in the base of the leaf as in *Isoëtes*. The whole plant bears some resemblance to an elongated *Isoëtes*. In the Cretaceous we find a plant called

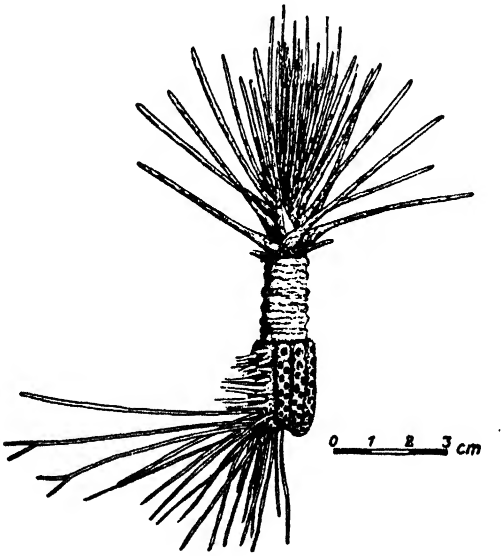


Fig. 37.—*Nathorstiana arborea*. Reconstruction of plant. After Mägdefrau, 1932.

Nathorstiana (Mägdefrau, 1932), which was only about 12 cm. in height (Fig. 37). The shoot resembled *Isoëtes* while the root-bearing region had dichotomously forked roots borne in a regular succession. There seems little doubt that the arborescent Lycopods of the Palaeozoic and *Pleuromeia*, *Nathorstiana*, *Isoëtes*, form a series in which there is a progressive reduction in size and in which the root-bearing region becomes simplified in external form. It must be remembered, however, as Professor Lang has pointed out, that the meristems in the grooves and not the lobes of *Isoëtes* correspond to the growing points of the Stigmarian branches and the lobes of *Pleuromeia*. In *Selaginella spinulosa* roots are produced in a definite order from the basal knot, which may therefore be compared with the rhizophoric regions in these fossil plants (see Weiss, 1932).

CHAPTER V

ARTICULATALES—I: PROTOARTICULATINEAE AND SPHENOPHYLLINEAE

FROM the Devonian period up to and including the present day we have evidence of the existence of land plants in which the shoot has a distinctly jointed appearance and the leaves, usually small in relation to the axis, are borne in whorls at the joints which represent the nodes of the axis. In some the sporangia are borne on structures (sporophylls) which may from their position be interpreted as leaves or parts of leaves, while in others, as in the living genus *Equisetum*, the sporangia are borne on stalked structures which may be termed sporangiophores. These, from the fact that their position on the axis appears to differ from that of the leaves, cannot be interpreted so readily as fertile leaves.

The Articulatales have been classified by Professor Hirmer (1927) as follows, although some of the less important groups have been omitted here:

	Representative genera
1. Protoarticulatineae (Devonian)	*Calamophyton*, *Hyenia* ✓
2. Sphenophyllineae (Devonian and Carboniferous)	*Sphenophyllum*,✓ *Cheirostrobus*
3. Equisetineae	
a. Calamitaceae (Carboniferous, Permian)	*Calamites*, etc.✓
b. Asterocalamitaceae (Lower Carboniferous)	*Asterocalamites* (*Archaeocalamites*)
c. Equisetaceae (Permian–Present day)	*Phyllotheca*, *Schizoneura*, *Equisetites*, *Equisetum*

1. **Protoarticulatineae.** *Calamophyton primaevum* (Fig. 38).—Fossil plants with jointed stems and small dichotomously forked leaves were discovered in 1925 by Kräusel and Weyland in the Middle Devonian rocks of West Germany. The leaves, which are small and forked at the apex, are attached to the stems in whorls at the joints. There do not seem to have been more than three leaves in each whorl. Some of the shoots of *Calamophyton* bear small stalks, which, like the leaves, are attached at the nodes and are forked at the apex. A sporangium is borne on each division. These sporangium-bearing structures may be regarded as fertile leaves or sporophylls. Sometimes the shanks of the fork at the apex of the sporophyll are very short and the sporangia

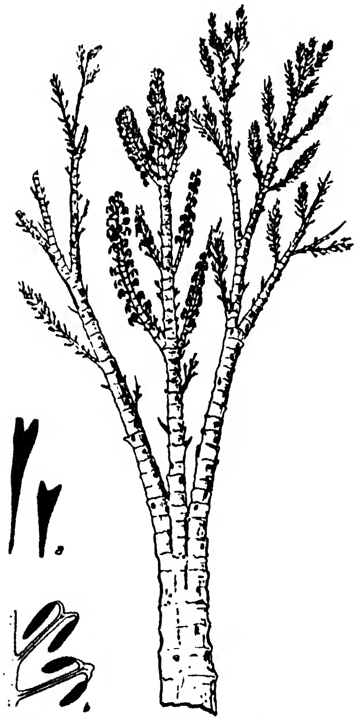


Fig. 38.—*Calamophyton primaevum.* Reconstruction after Kräusel and Weyland. *a*, leaf; *b*, sporophyll. ¼ nat. size.

Fig. 39.—*Sphenophyllum cuneifolium.* Branching stem. Branch *a* bears a cone and some foliage at the base. Branch *b* bears whorls of normal leaves. A small part of another branch is shown with narrow linear leaves. After Stur.

appear to be situated on a small knob at the end of the stalk of the sporophyll.

The small branches are seen in transverse section to have what appears to be a three-cornered pith, and in longitudinal sections reticulate and scalariform tracheids are visible. Kräusel and Weyland are of the opinion that the greater diameter of the major branches indicate that secondary tissues were developed.

Hyenia elegans, another genus of the same geological age and from the same district, is a plant of somewhat similar habit but differing from *Calamophyton* in having repeatedly forked leaves and a correspondingly larger number of sporangia on each sporophyll.

2. SPHENOPHYLLINEAE. *Sphenophyllum*.—The genus *Sphenophyllum* occurs in Upper Devonian rocks but attained its maximum development in the Carboniferous and Permian periods. There is some doubt about its existence in the Triassic period. Our knowledge of the genus is based principally on material found in the Carboniferous and Permian coal-measures of Europe.

Vegetative Parts.—From a study of compressions such as those shown in Fig. 39 it is evident that the species were herbaceous or shrubby in habit. The stems, which do not exceed about a centimetre in diameter, are distinctly jointed, and are usually longitudinally ridged. The leaves are attached to the nodes in whorls of six or multiples of three up to eighteen or possibly more in some species. The leaves vary in the genus from slender forking leaves of the *Calamophyton* or *Hyenia* type to cuneate leaves with a dentate or entire distal margin (Figs. 40, 41). While in many species the leaves of a whorl all stood out at the same angle to the axis giving a radial symmetry, in some species, particularly those of Permian age, the leaves are so orientated with reference to the axis that their laminae are extended in a plane parallel to the axis, so that the shoot is dorsiventral and the leaves form a flat mosaic (Fig. 40, B). The two leaves on the upper side of the shoot are bent over abaxially so that they lie parallel to and over the internode below, and are often smaller in size than the other leaves in the whorl. In other species (e.g. *S. cuneifolium*, Fig. 39) some parts of the shoot bear slender forking leaves instead of the usual cuneate leaves which are found elsewhere on the shoot. It is possible that this heterophyllous

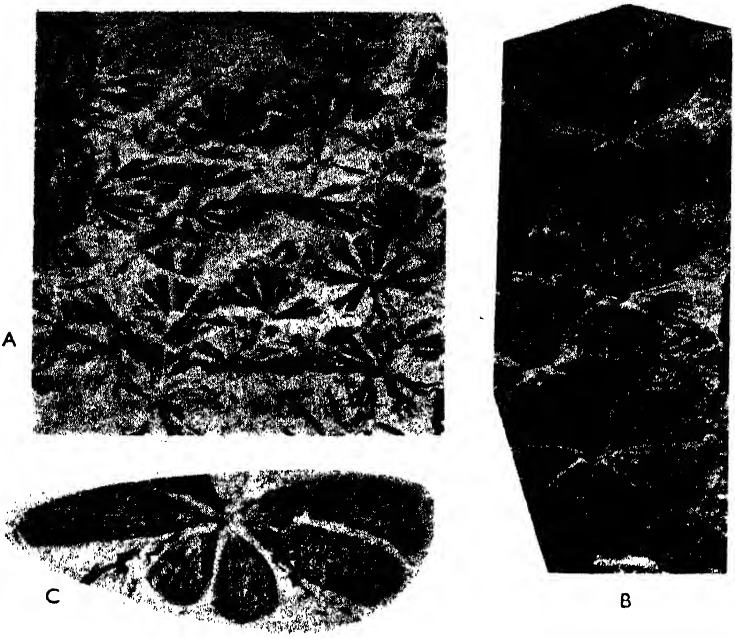


FIG. 40.—A. *Sphenophyllum cuneifolium* (var. *saxifragaefolium*). Compressions of leaf shoots. Westphalian, Yorkshire. Nat. size. Photo by Hemingway.—B. *S. oblongifolium.* Leafy shoot showing flat arrangement of the leaves. Upper Carboniferous or Lower Permian; Wankie, S. Rhodesia. After Walton, 1929. —C. *S. sino-coreanum.* Leaf whorl showing flat arrangement and two large and one small pairs of leaves. Permian, Shansi, China. Nat. size. After Halle.

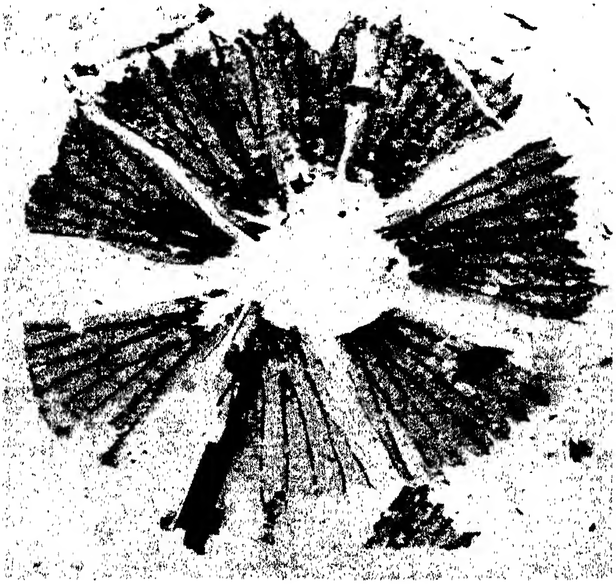


FIG. 41.—*Sphenophyllum cuneifolium.* Transfer of a compression of a leaf whorl showing the excurrent veins at the tips of the segments. Westphalian Series, Wales. × 6. J. Walton Coll. 204.

condition may be comparable to what is found in the Conifers, where juvenile and adult types of foliage are found on the same plant; or it is possible that the upright shoots had the slender forking type of leaf while the lateral branches had the cuneate type. In *Sphenophyllum* the leaves in a whorl did not alternate with those in the whorl below but were superposed.

Numerous petrifactions of *Sphenophyllum* shoots, strobili, and roots have been found in coal balls from the Upper Carboniferous coal-measures, and from a study of these we get information about their internal structure. The stems of *S. plurifoliatum*, which bore foliage of the *S. myriophyllum* type, are seen in transverse section to have a triangular central strand of primary wood (Fig. 42) and the differentiation of this wood was centripetal, the protoxylem occupying the three angles. There was no pith. The stem of *Sphenophyllum* is thus remarkably like a root in its vascular structure. The primary wood consists entirely of tracheids, of which those of the protoxylem are spiral and those of the metaxylem scalariform or pitted. Cambial activity has resulted in the formation of a single row of secondary tracheids on the sides of the primary, and in this example the primary and secondary tracheids are separated by xylem parenchyma. Stems

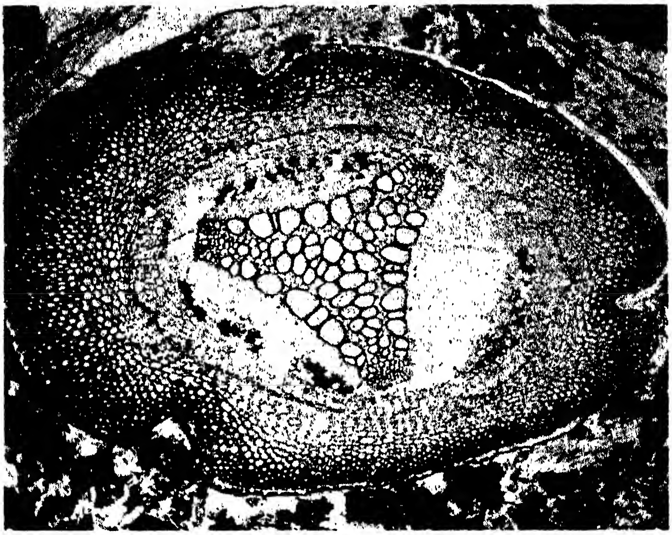


FIG. 42.—*Sphenophyllum plurifoliatum*. Transverse section of stem just below node showing triangular form of primary wood with a protoxylem at each corner and a single row of secondary tracheids along the sides. The primary phloem contains some cells with dark inclusions. × about 30. J. W. Photo. Kidston Slide Coll. 1907.

have been found with only primary xylem and they are assumed to be young stems, but in most stems there is evidence of cambial activity. The triangular primary strand is surrounded by secondary tracheids which were at first laid down on the three sides of the primary strand, giving rise to a cylindrical core of xylem, which then expanded uniformly by the activity of the cambium as in the root of a Dicotyledon.

Traces of cambium are sometimes found immediately outside the secondary xylem and these are succeeded by tissues which represent the phloem. Outside the phloem, presumably in the pericycle and cortex, there is usually a phellogen, which gave rise to cork. In some old stems it is clear that later cork layers were formed from deeper-seated tissues. The inner part of the cortex is parenchymatous and the outer cortex and the epidermis consist of thick-walled or sclerenchymatous tissue. In the older stems the cortex was sloughed off and the cork formed the covering tissue of the stem.

The secondary wood consisted of radially seriated tracheids, which have small crowded pits on their radial walls and a few scattered pits on their tangential walls. At the corners of the tracheids are very small, vertically elongated thin-walled cells (Figs. 43, D and 44), which, with similar cells forming the slender medullary rays, constituted a connected system of wood parenchyma. In *S. insigne* from the Lower Carboniferous the vertical strands of parenchyma are not represented and there are simple medullary rays.

At the nodes the xylem of the leaf trace extends from the protoxylem into the cortex, where it divides in a horizontal plane into the several strands which pass into the leaf bases (Fig. 43). In *S. plurifoliatum* each leaf was supplied with one strand but in other species there are two strands. The vascular supply of the leaf gave rise by repeated divisions to the veins which spread through the lamina and its segments. The fact that the leaves at a node were in multiples of three may be correlated with the triarch structure of the primary wood. The leaf, as Renault has shown, was bounded by a thick-walled epidermis on the adaxial surface and a thinner-walled stomatiferous epidermis on the abaxial face. The cells of the epidermis have sinuous anticlinal walls and are fitted together like pieces of a jigsaw-puzzle. The veins which lie in the middle of the mesophyll have accompanying strands of fibres which extend into the segments of the leaf,

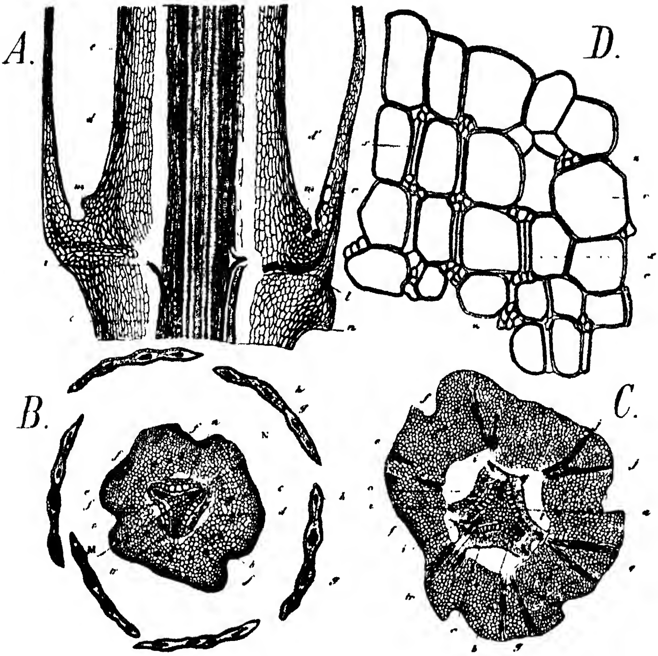


FIG. 43.—*Sphenophyllum quadrifidum*. A. Median longitudinal section through a node cut in the plane of *MN* in B.—B. Transverse section of the same stem above the node showing the six leaves in section.—C. Transverse section through the node with the forking showing leaf traces. A, B, C × 9. *a*, *b*, primary wood; *c*, secondary wood; c^1, phloem; *d*, *e*, cortex; *g*, *h*, leaves; *j*, leaf trace; *l*, base of leaf; *m*, ? axillary bud.—D. Transverse section of a small piece of secondary wood from another specimen. × 60. *c*, tracheids; *x*, parenchyma (medullary ray tissue). After Renault.

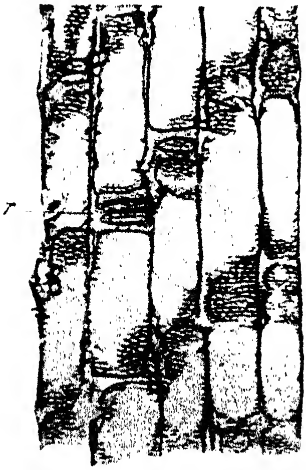


FIG. 44.—***Sphenophyllum plurifoliatum*. Radial longitudinal section of secondary wood showing tracheids and medullary ray parenchyma at *r*. After Scott.**

forming sharp points in those species with segmented or dentate leaves (e.g. *S. cuneifolium*).

The roots which were borne at the nodes had a small diarch or rarely triarch stele with secondary wood (Fig. 45). The cortex differs from that of the stem in having large thin-walled cells, but it is closely similar to the stem in vascular construction.

Fructifications.—Great variety is shown in the fructifications known to belong to plants which have the *Sphenophyllum* type of stem or shoot. The generic terms *Sphenophyllostachys* and *Bowmanites* have been given to these fructifications.

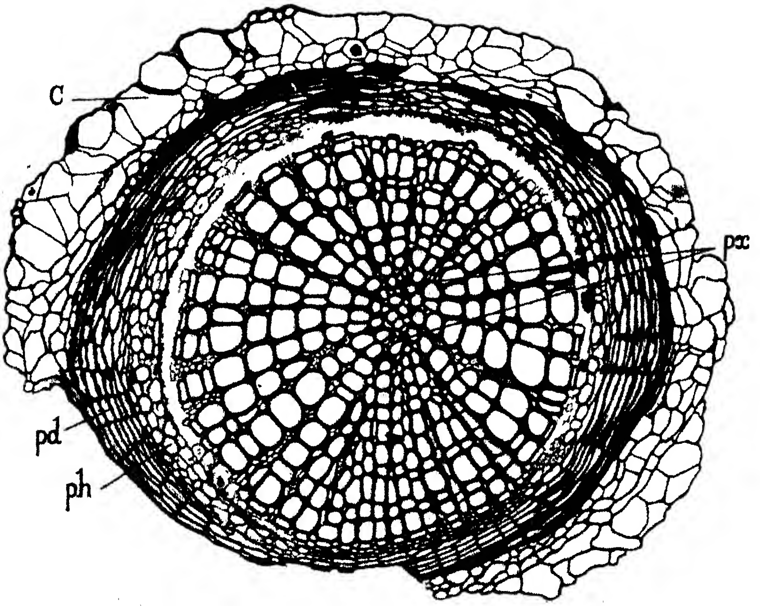


FIG. 45.—*Sphenophyllum* sp. Transverse section of root. *px*, protoxylem; *ph*, phloem; *pd*, periderm; *C*, large cells of outer cortex. × about 30. After Scott.

Sphenophyllum (*Sphenophyllostachys*) *Dawsoni.*—These complex strobili are known to have been borne by stems which had the *S. plurifoliatum* structure. The strobili (Fig. 46) were about half an inch in diameter and several inches in length and appear to have been borne on the ends of the branches. Each strobilus is built up of a series of whorls of leaf-like bracts, which are fused together for about half their length so that each whorl forms a cup round the axis of the strobilus (Fig. 47). The upper halves of the bracts overlap the whorls immediately above so that the surface of the strobilus is covered by a scaly mantle. Each bract had a median vascular bundle. It is not known with certainty whether the bracts of successive whorls were superposed or whether they alternated. The number of bracts in a whorl varied from 14 to 20. Attached to the axis immediately above the bracts in each whorl is a whorl of slender pedicels, each of which terminated in a sporangium. These pedicels are about twice as numerous as the bracts and are of various lengths. Each pedicel is attached for a considerable portion of its length to the surface of the cup formed by the basal part of the bracts. In some strobili the sporangia form two circular series concentric with the axis of the strobilus; in others there are three such series. The end of each pedicel is curved so that the sporangium is borne in an anatropous manner and hangs over towards the axis. The pedicel has a vascular strand which extends from the strobilus stalk up to the base of the sporangium. The wall of the mature sporangiun

FIG. 46.—*Sphenophyllostachys Dawsoni* (forma β). Oblique longitudinal section of a strobilus. *A*, *B*, *C*, *D*, and *E*, bract-whorls. Photo by Lomax. After Scott.

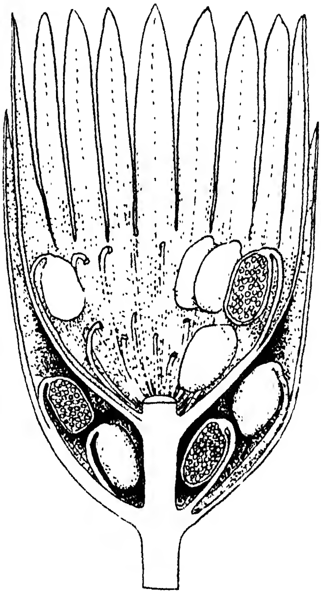


FIG. 47.—*Sphenophyllostachys Dawsoni.* Diagrammatic drawing of part of a strobilus cut lengthwise. The halves of two bract-whorls and some of the sporangia are shown. × 9.

consists of a layer of cells with fibrous thickenings, which are more developed on the inner and anticlinal walls so that the sporangium wall resembles in structure, and probably in function, the fibrous hypoderm in a Liliaceous anther. The wall split along one side on dehiscence. The spores (about 90 μ in diameter) bear spines connected by ridges on their surface. While there is some small variation in size among the spores, all the species of *Sphenophyllum* so far discovered appear to have been homosporous.

Bowmanites Römeri.—Although no vegetative parts have been found connected with it, this strobilus, which was found in Carboniferous rocks near Cracow, has obvious claims to be regarded as *Sphenophyllean.* In general construction the strobilus resembles that form of *S. Dawsoni* strobilus in which there are three concentric rings of sporangia on each bract-whorl. The bracts in a whorl, like the foliage leaves of *Sphenophyllum*, were superposed over those of the whorl below. The principal difference is in the presence of two sporangia on the end of each pedicel, which had a correspondingly larger apical knob. The wall of the sporangium is several cells in thickness in contrast to that of *S. Dawsoni*, which, except at the base, is one cell in thickness at maturity. The spores agree very closely in their ornamentation with those of *S. Dawsoni.* Solms-Laubach, in his description of the only known specimen, shows that the epidermal cells of the upper part of the pedicel had sinuous walls. The author has found that the epidermis of *S. cuneifolium* and *S. majus* is constructed of the same type of cell, a fact which gives supporting evidence in favour of attributing *Bowmanites Römeri* to the Sphenophylleae.

Sphenophyllum fertile.—Only the strobilus of this plant is known (Fig. 48) but the triangular form of the section of the triarch or hexarch primary wood is perhaps sufficient evidence to prove its relationship to *Sphenophyllum.* The appendages of the strobilus are arranged in whorls and were superposed in position like the leaves on vegetative shoots of *Sphenophyllum.* The appendages are of two kinds (Leclercq, 1935, 1936). In the whorl there are six adaxially inclined stalks, each of which, at a point about half way between the axis and the periphery of the strobilus, gave rise to from 14 to 18 slender pedicels. Each pedicel bore two sporangia. The pedicel with its two sporangia closely resembles the corresponding structure in *Bowmanites Römeri.*

The other type of appendage arises from the node at a slightly lower level than the fertile stalks. They arise in pairs one on each side of the base of each fertile stalk. They are directed in an abaxial direction and extend unbranched to the periphery of the strobilus in the form of straight slender stalks. Each possesses a vascular strand which, when traced back to the axis, joins on to the side of the strand which supplies the fertile appendage (Fig. 52, A). They have been described as the two branches of a dorsal lobe of a sporophyll, the fertile appendage with the two sterile appendages being considered as a sporophyll divided into a fertile ventral lobe and a bifurcating dorsal lobe. It would appear more likely that the two sterile appendages, judging from their vascular strands, are lateral to the fertile part, although in development they have been displaced in an abaxial direction. The sporophyll cannot therefore be regarded as divided into a dorsal and ventral lobe.

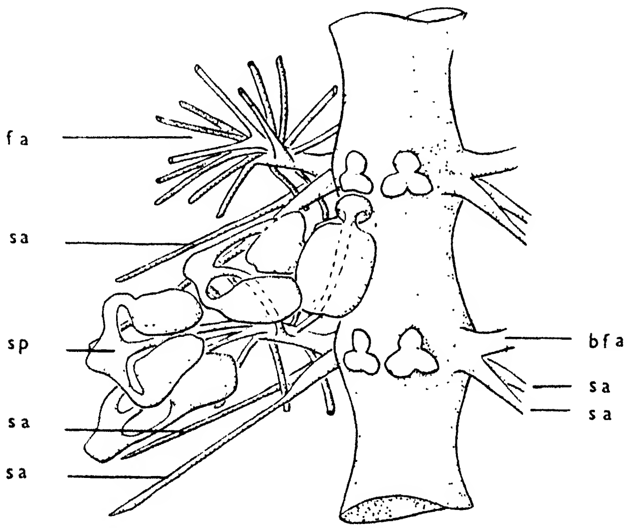


FIG. 48.—*Sphenophyllum fertile*, Scott. Reconstruction of part of a strobilus by Dr. Suzanne Leclercq. *fa*, one of the fertile appendages with the heads of the sporangiophores removed; *bfa*, base of stalk of fertile appendage; *sa*, sterile appendages; *sp*, sporangiophore with two sporangia.

While well-defined strobili are found in the genus *Sphenophyllum*, several species do not show the same sharp distinction between reproductive and foliage shoots. In *Sphenophyllum majus* (Fig. 49) fertile parts of the shoot are intercalated between parts that bear only foliage, and there is little difference between bract and leaf. A fertile whorl consists of a set of leaves which subtend pedicels bearing sporangia. The fertile leaves are not fused together as are their equivalents the bracts in *S. Dawsoni*. From the stem immediately above the leaf 1 to 3 slender pedicels project close to the surface of the leaf, and each bears at its extremity a group of four pendulous sporangia (Fig. 49).

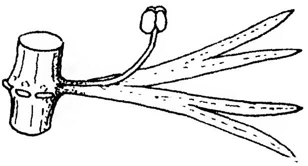


FIG. 49.—*Sphenophyllum majus*. Diagrammatic drawing to show the relation between a fertile leaf and the sporangiophore. The latter bears four sporangia.

In *S. trichomatosum*, which has slender dichotomously forked foliage leaves, the simple fertile leaves bear a single sporangium apparently on the upper surface near the axil.

Cheirostrobus pettycurensis (Figs. 50, 51) is a strobilus of very complex construction of which a few specimens have been discovered in the Lower Carboniferous rocks at Pettycur in

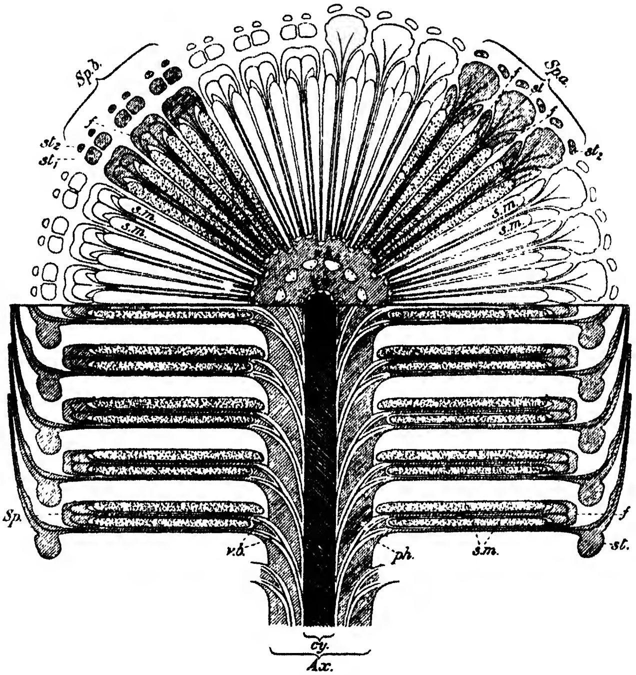


FIG. 50.—*Cheirostrobus*. Diagrammatic representation of a cone. The top part represents half of a transverse section; the lower part, a radial longitudinal section. Parts of six sporophylls are seen in the transverse section. *Sp.a.*, section cutting through sterile appendages; *Sp.b.*, section cutting through sporangiophores. In the longitudinal section *Sp.* is a longitudinal section of one sporophyll; *f*, sporangiophore; *st.*, sterile appendage; *s.m.*, sporangia; *v.b.*, vascular bundle; *cy.*, stele; and *Ax.*, axis of cone. × 2. After Scott.

Scotland. It compares with *Sphenophyllum fertile* in having superposed whorls of sporophylls, some branches of which

FIG. 51. *Cheirostrobus pettycurensis*. Part of a longitudinal section. *s*, peltate sporangiophores; *l*, sterile appendages. × about 10. After Scott.

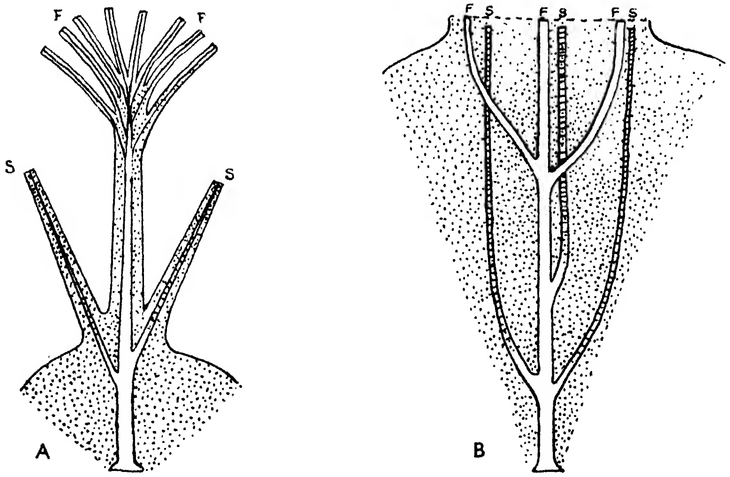


FIG. 52.—Diagrams to illustrate the course of the vascular tissue in the compound sporophylls of A, *Sphenophyllum fertile* and B, *Cheirostrobus*, viewed from the adaxial faces. *S*, *S*, stalks of sterile divisions; *F*, *F*, stalks of sporangiophores. The areas marked with dots are the cortical regions of the cone axis and sporophylls.

are fertile and others sterile. The stele is stellate in section with about twelve protoxylems. The vascular supply to the sporophyll is divided into two lateral and a central bundle (Fig. 52), the two lateral bundles passing out into sterile appendages. The central bundle a little farther out branched into two. The smaller of the two branches passed out between the two bundles which supplied the two sterile appendages and provided the vascular tissue to a third sterile appendage. The central bundle then divided into three bundles, each of which supplied a pedicel with a peltate head, to which four sporangia are attached. Each sterile appendage consisted of the slender pedicel terminating in a peltate scale which was deeply bifid. The relationship between the fertile and sterile parts of the sporophylls is shown in Fig. 52. When the vascular systems supplying the sporophylls of *Sphenophyllum fertile* and *Cheirostrobus* are compared a striking similarity is apparent. They may both be interpreted as derivatives of pinnate sporophylls; in *Cheirostrobus* three and in *S. fertile* two of the basal pinnae being sterile and assuming a dorsal position and the distal pinnae fertile and assuming a ventral position.

The structure of the sporangium wall and the spores compares closely with the corresponding parts of strobili which are known to have belonged to plants with *Sphenophyllum*-type of vegetative shoots. There are good reasons, therefore, for believing that *Cheirostrobus* belonged to a plant closely related to *Sphenophyllum*.

CHAPTER VI

ARTICULATALES—II: EQUISETINEAE

3. EQUISETINEAE.—In the Equisetineae are included with the living *Equisetum* a large number of extinct Pteridophytes which reveal in their morphology many striking resemblances to the living genus. These resemblances are so close that there seems little doubt that this grouping is justified and that the fossil and living forms are phylogenetically related.

CALAMITACEAE.—Of frequent occurrence in the rocks of the Carboniferous coal-measures are fragments of jointed stems bearing whorls of small simple leaves and reproductive strobili. From a study of very large numbers of examples it has become evident that these fragments belonged to plants which, while having many of the outstanding peculiarities of *Equisetum*, must have had the stature and something of the habit of large Bamboos. The diameter of the pith alone in one stem has been found to be at least 30 cm. and some of the stems must have attained a height of at least 30 metres.

The classification and naming of these fossils presents in forcible fashion one of the difficulties which face the student of fossil plants. It is found to be convenient to give what are called form-generic names to the various parts of these plants. Thus the stems and principal branches are called *Calamites*, the roots *Myriophyllites* and *Astromyelon*, the foliage twigs *Annularia*, *Asterophyllites*, *Annulariopsis*, etc., and the strobili *Calamostachys*, *Palaeostachya*, *Macrostachya*, etc. It may happen later that a specimen is found in which a species of *Calamitean* stem and a species of *Annularia* (foliage) are found in connection, showing that they are parts of the same plant, but this does not exclude the possibility that other species of Calamitean stems bore the same type of foliage. Occasionally it is possible to reconstruct a complete type of plant from collected evidence. It is known, for example, that *Calamites multiramis* bore foliage of the *Annularia* *stellata* type and strobili of the *Calamostachys tuberculata* type; but such opportunities of synthesis are rare. The species grouped in a form-genus may prove to belong to several different genera based on the form of the strobili, and if we were to adopt the system of classification used for living plants we would use the form of the reproductive structures as our basis of classification.

FIG. 53.—A. *Calamites Goepperti*. Impression of external surface of a stem showing about twelve leaf-bearing nodes and parts of two branch whorls. ½ nat. size. After Kidston and Jongmans, 1915.—B. *Calamites undulatus*. Compression of a stem. *x*, external surface; *y*, ridged pith cast; *n*, *n*, nodes. *b*, *b*, branch-scars. × ⅔. Hunterian Museum, Glasgow Univ., Pb. 1825.

Form-genera such as *Annularia* may therefore be regarded as provisional genera for the inclusion of species which in most instances have never been found with reproductive structures connected to them.

Calamites.—Fortunately petrifactions as well as compressions and casts are available for the study of these stems and branches. The structure of the internode of the young Calamitean stem in the primary condition is remarkably like that of *Equisetum*. There is a wide pith cavity (Fig. 54) enclosed by parenchymatous tissue in which lies a ring of vascular bundles. The spiral and annular elements of the protoxylem in each bundle are next to the pith, but owing to the development of a carinal canal, as in *Equisetum*, they are disrupted and fragments are found adhering to the sides of the canal. The protoxylem is immediately succeeded by centrifugal metaxylem, surrounded externally by cambial and phloem tissues, which, owing to their delicate nature, are rarely preserved. In well-preserved examples the sieve tubes are seen to have sieve plates on their sides and to resemble the type of sieve tube found in *Equisetum* and the Ferns. The cortical tissues call for no special attention but in a few species in which the surface is ribbed the ribs are found to consist of cortical strands of sclerenchyma.

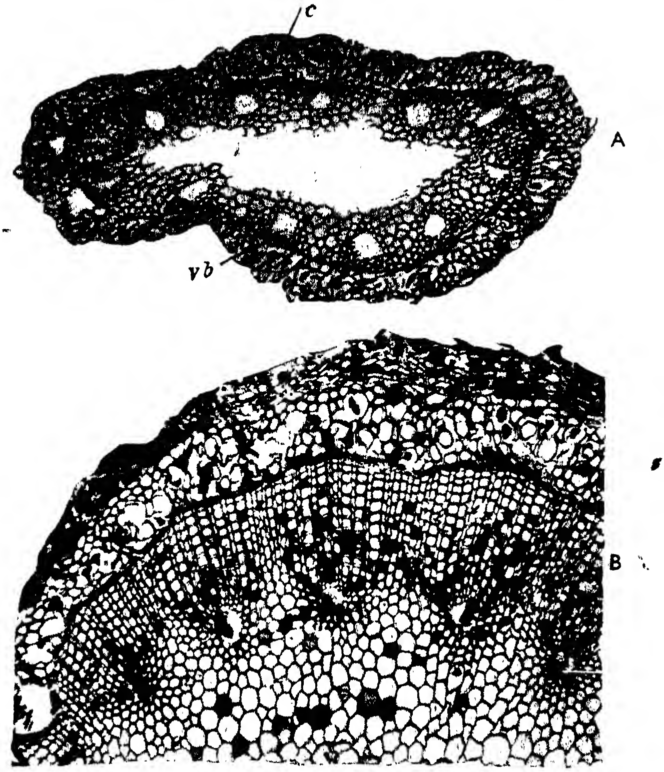


FIG. 54.—*Calamites* sp. A. Young stem in section. Showing pith cavity, pith, ring of protoxylem canals, and cortex (*c*). × about 40.—B. Similar stem showing well-preserved pith and secondary wood. After Scott.

At the nodes the leaf traces are found to be continuous with the internodal bundles from below and the internodal bundles are linked by anastomoses of metaxylem just as in *Equisetum*. In some *Calamites*, however, the arrangement at the node is less regular (Fig. 55) and more complicated, for the number of leaves in the whorl is less than the number of bundles in the internode below. The branches are attached immediately above the node between two leaf traces as in *Equisetum*, and the roots at or just below the level of the node between two internodal bundles.

Unlike *Equisetum* the Calamitean stem (Fig. 54, B) has secondary wood consisting of radially seriated tracheids with scalariform or multiseriate oval pits. Occasionally the tracheids are septate. The medullary rays are formed of thin-walled cells elongated in a vertical direction. In the older stems periderm was formed in the cortex and this has been observed to have attained a thickness of at least 5 cm.

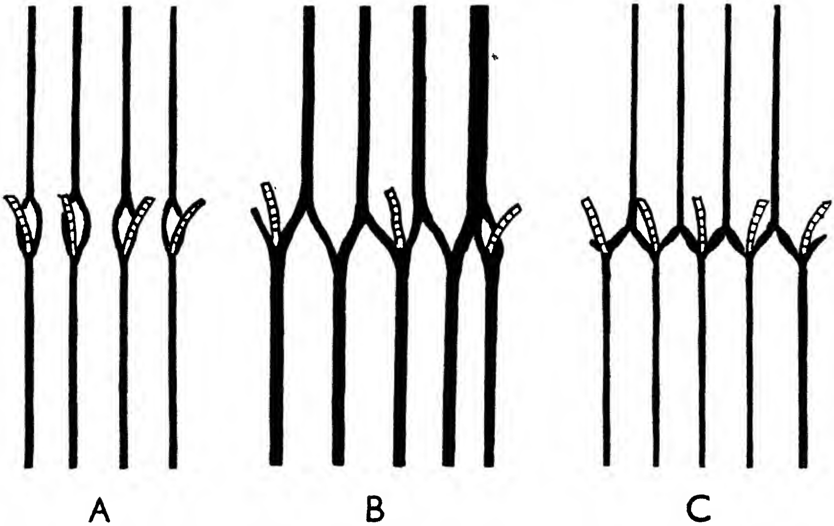


FIG. 55.—Diagrams to illustrate the relation between the internodal bundles and the leaf traces in A, *Asterocalamites*, B, *Calamites*, and C, *Equisetum*.

From a study of compressions of large fragments of stem the order of the branching has been observed. In some species the branches were in crowded whorls but only a small proportion of the nodes bore branches (Fig. 53); in other species a larger number of nodes produced branches and there were fewer branches at each node. The specific identification of Calamitean stems is largely based on the arrangement of the branches. The surface of the stem was sometimes smooth or furnished with transverse wrinklings. In most instances a longitudinal ribbing is evident, but this is usually not an original surface feature but is due to the entry into the pith cavity of sand or mud, which made an internal cast of the pith cavity and bore the impress of the vascular strands which usually projected slightly into the cavity. This cast tends to show through the flattened remains of the tissues of the stem and causes them to appear ribbed. In Fig. 53, B, the wrinkled surface of the stem is seen in one part of the specimen and in another the pith cast, where the superficial parts have been removed.

The roots are variable in size and structure. The smaller roots have a diarch to tetrarch stele of primary wood with secondary wood around it. Apart from the secondary wood they closely resemble the large roots of *Equisetum limosum*, which grow vertically downwards from some of the nodes of the horizontal rhizomes. These *Equisetum* roots have from three to six protoxylems and, like the Calamite roots, have a "double endodermis" and large lacunae formed of schizogenous spaces between the rows of radially arranged inner cortical cells. The larger Calamitean roots had as many as eighteen protoxylem groups and a wide pith cavity, and only with difficulty can be distinguished from stems with secondary wood, when the centripetal primary wood and the cortex are not preserved.

It is highly probable that in *Calamites* as in *Equisetum* there were branch meristems at the nodes which could either develop into lateral branches or remain dormant, and from the base of these meristems single roots or bunches of roots could originate.

The leaves, which were borne on the main stems and branches, are simple and linear. Sometimes as many as sixty were borne in one whorl, and in some instances the bases of the leaves were fused to form a narrow sheath round the node. On the ultimate branches the leaves as a rule are different in form from those on the main stems and branches. In some species of *Asterophyllites* the leaves on the lower order branches were arranged in radial symmetry round the node; in others, e.g. *Asterophyllites equisetiformis* and in the genus *Annularia* (Fig. 56), the leaves were so arranged that they formed a flat mosaic as in *Sphenophyllum*. The leaves of *Asterophyllites* are long and slender while those of *Annularia* are as a rule broader and show greater variety of form (Walton, 1936). In *Annularia sphenophylloides* (Fig. 57) the leaves are spatulate with a sharp point at the end, and the vein, which is single as in all other Calamitean leaves, has a distended part near the tip of the leaf. This swelling of the vein was probably related to hydathodic activity. In some species of *Equisetum* the

FIG. 56.—*Annularia Jongmansi.* Part of a branch showing characteristic leaf-mosaic Nat. size.

FIG. 57.—*Annularia sphenophylloides.* Part of a leaf-whorl. One leaf shows the pointed tip and two show the terminal expansion of the vein. × 13. Transfer preparation. Walton Coll. 403.

vein has a slightly expanded end and water exudes in droplets from the end of the leaf. In *A. fimbriata* the margins of the leaf are fringed with hairs and inrolled. It has been shown that the guard cells of the stomata have cuticular ridges as in *Equisetum.*

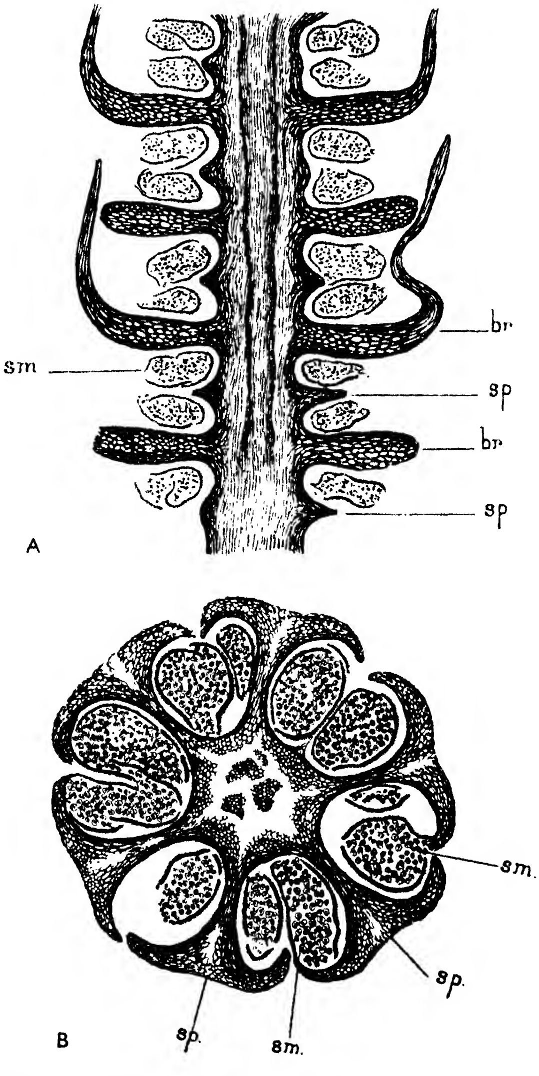


FIG. 58.—*Calamostachys Binneyana.* A. Longitudinal section of a cone showing four whorls of bract sheaths. (*br.*) Two of the four sporangia and part of the base of each sporangiophore are shown. × 8.—B. Transverse section of a cone through a whorl of sporangiophores (*sp.*). Sporangia are shown attached to the edge of the sporangiophores at *sm.* × 16. After Scott.

Calamostachys.—The characteristic sporangium-bearing organ in the Calamitaceae is called a sporangiophore (Figs. 58, 59).

consists as in *Equisetum* of a peltate scale but it bears only four sporangia, which are attached to the edge of the scale and lie beneath the scale and parallel to the stalk. A vascular strand is present in the stalk, and in the scale it branches into four, each of which passes to the base of a sporangium. The wall of the sporangium is one cell thick and the cell walls have fibrous thickenings as in *Sphenophyllum*. The spores (diam. 90 μ) were produced in tetrads inside the mother-cell membrane. The fully formed spores in *Calamostachys Binneyana* are all of the same size.

The sporangiophores formed part of a strobilus (Fig. 58) which consisted of alternating whorls of sporangiophores and sterile bracts. The sterile bracts were fused at the base to form a cup as in *Sphenophyllum*. The morphology of the strobilus is complicated, for while the sporangiophores of successive whorls are superposed the bracts of successive whorls are alternate with one another. The vascular axis consists in some strobili of three bundles forming a triangular-shaped stele; in others there are four pairs forming a quadrangular stele. In the triangular type the bundles are often double.

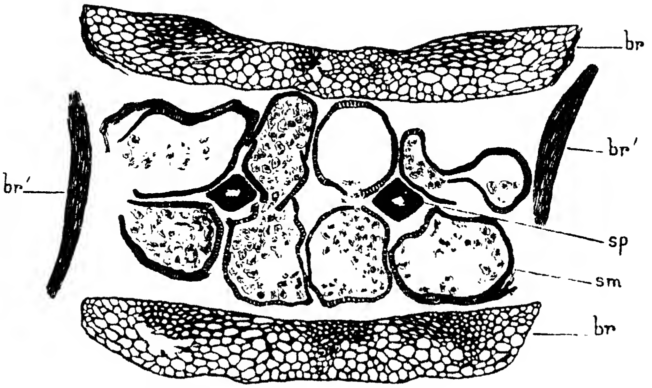


FIG. 59.—*Calamostachys Binneyana*. Tangential section cutting across the middle of two sporangiophores and their four sporangia and the bases of two bract sheaths (*br.*). *br*^{1}., free parts of bracts from a lower sheath; *sp.*, sporophyll stalks; *sm.*, sporangium. × about 25. After Scott.

In *Calamostachys Casheana* heterospory has been observed; some sporangia produced large numbers of small spores while other sporangia of the same size produced a smaller number of larger spores. The small spores are about one quarter the diameter of the larger ones.

Palaeostachya.—In *Palaeostachya* (Fig. 60) the whorl of sporangiophores arises close to the whorl of bracts below. The bracts are twice as numerous as the sporangiophores. The general form of the strobilus is therefore not unlike *Sphenophyllostachys Römeri* except that there is only one ring of sporangiophores and each of the latter have four instead of two sporangia.

In *Palaeostachya* the vascular supply to each sporangiophore is attached to the vascular axis of the strobilus at the same level as the supplies to the bracts of the whorl below. There is thus structural evidence for believing that the sporangiophores are fertile parts of sporophylls whose sterile parts form the bract-whorl and a comparison is obvious with *Sphenophyllum.*

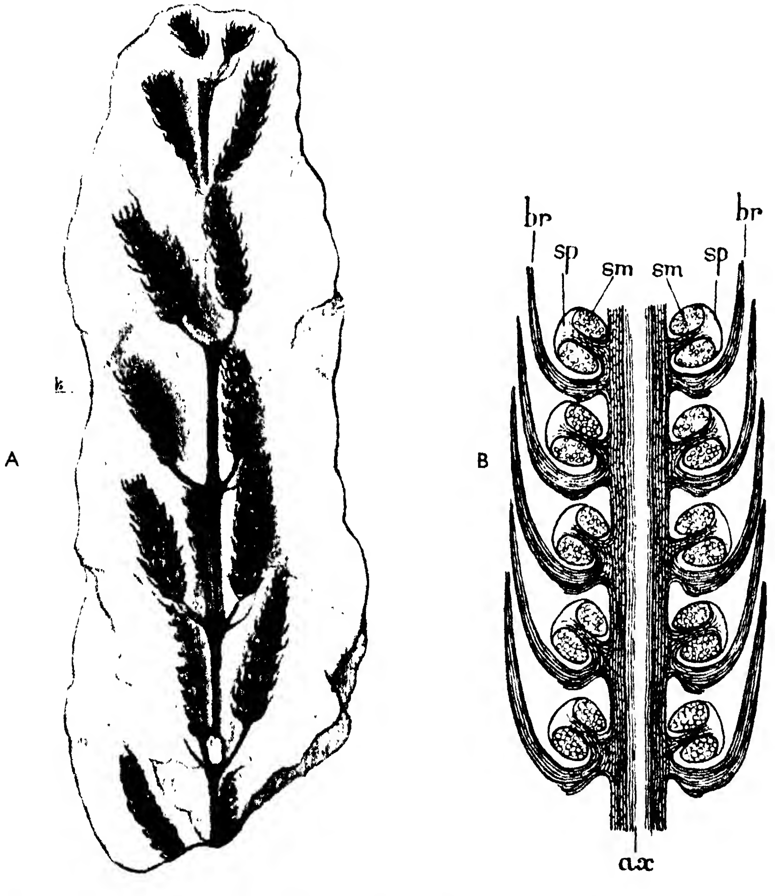


Fig. 60.—*Palaeostachya.* A. *Palaeostachya pedunculata* branch-bearing cones. After Williamson.—B. *Palaeostachya* sp. Longitudinal section of part of a cone. *br*, bract; *sp*, sporangiophore; *sm*, sporangium. After Renault.

Professor Hirmer has put forward a theory in which the strobili of *Sphenophyllum* and *Calamites* are regarded as being built up of compound sporophylls. Each sporophyll is divided into a dorsal and ventral lobe. The ventral or upper lobes are fertile and are the sporangiophores; the dorsal are sterile and are the bracts. From anatomical considerations, to which I have referred in connection with *Sphenophyllum* (p. 76), I am inclined to regard these strobili as built up of pinnate sporophylls, the proximal pinnae being sterile and deflexed in development into a dorsal position and the distal being fertile and assuming the ventral position. In *Equisetum* the sporangiophore would, from this point of view, be regarded as a single undivided sporophyll.

ASTEROCALAMITACEAE. The Lower Carboniferous genus *Asterocalamites* (= *Archaeocalamites*) differs from *Calamites* in that the vascular bundles of successive internodes are continuous across the node (Fig. 55) and do not alternate as in Calamites, and the leaves are several times dichotomously forked (cf. Calamophyton). The sporangiophores are peltate with four sporangia and are arranged in superimposed whorls with an occasional whorl of leaves. There are no specialised leaves in the form of bracts. In this respect the strobilus bears considerable resemblance to that of *Equisetum*.

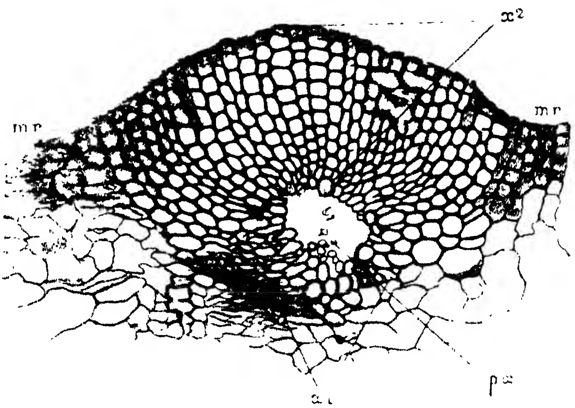


FIG. 61.—*Protocalamites pettycurensis*. Transverse section of a vascular bundle in an internode. x^2, secondary wood; *px*, protoxylem canal; x_1, centripetal primary wood; *mr*, medullary rays. × about 60. After Scott.

Mesocalamites.—There are a number of Lower Carboniferous species which differ from the typical Upper Carboniferous types in that the vascular bundles in successive internodes sometimes alternate but are more often superposed and thus appear to run straight through the node. In some petrified examples of this type there is a small amount of centripetal xylem in the stem bundles.

Protocalamites.—Some petrified examples of Calamitacean stems (Fig. 61) from the Lower Carboniferous of Scotland, to which the name *Protocalamites pettycurensis* is given, have a pronounced development of centripetal metaxylem on the pith side of the protoxylem cavity. This may be regarded as an indication that the *Equisetum* type of vascular construction has been derived from a solid protostele similar to that found in *Sphenophyllum.* It is probable that *Protocalamites* is part of a *Mesocalamites,* for some investigators have found evidence of alternation of the bundle at the node while others find evidence of superposition.

EQUISETACEAE.—In the Mesozoic Era the Equisetineae are represented by the genera *Phyllotheca* and *Schizoneura.* Our knowledge of them is based on the study of compressions. In *Schizoneura* the leaves in a whorl are joined laterally to form a flat lamina. This condition may be compared to an *Equisetum* leaf-sheath which had been split down one side and spread out flat. The remains of plants with a closer resemblance to *Equisetum* have been found in strata ranging from the Carboniferous to the Tertiary: to these the name *Equisetites* is given.

CHAPTER VII

FILICALES—I: COENOPTERIDINEAE

PLANTS with leaves like fern-fronds existed from the Devonian period to the present day but experience has taught us that we cannot determine the affinity of a plant from the form of its leaf alone. We have definite information that a very large number of extinct plants which had fern-like leaves produced seeds and were therefore not members of the Filicales. Of the many forms of such leaves found in the Permian and Carboniferous rocks some have been proved to be true Ferns, others to belong to the Pteridosperms, an extinct group of seed plants, while there is a large residue about whose relationships nothing is yet known with certainty. It is, however, clear that both Ferns and Pteridosperms were important constituents of the vegetation of the Earth from Lower Carboniferous times down to the Permian. After the Permian the Pteridosperms appear to have diminished in importance and to have become extinct before the end of the Jurassic, while the Ferns retained an important position during the Jurassic and then became less important in succeeding times.

Protopteridium (see p. 38) has been cited as a possible representative of the Ferns, but unfortunately we have no knowledge of its internal structure.

The Lower Carboniferous and later periods offer ample evidence of the existence of true Ferns. The Carboniferous Ferns were for the most part of types now extinct and of unfamiliar aspect. From a study of some indubitable Ferns from the Carboniferous we are led to believe that some older and less completely known fossils, the Cladoxyloideae from the Upper Devonian and Lower Carboniferous, were also Ferns. These will be described first, although without the evidence furnished by fossils of later periods we should have insufficient evidence for that belief.

The Filicales may be classified as follows:[1]

1. Coenopteridineae
    - a. *Cladoxyloideae*
    - b. *Stauropteroideae*
    - c. *Zygopteroideae*
    - d. *Botryopteroideae*
2. Marattiineae
3. Osmundaceae
4. Schizaeaceae
5. Gleicheniaceae
6. Matoniaceae
7. Dicksoniaceae *and* Cyatheaceae
8. Dipteridaceae
9. Polypodiaceae

1. COENOPTERIDINEAE. a. *Cladoxyloideae* (genera—*Asteropteris*, *Cladoxylon*).—Our knowledge of this group is based on petrified stems from Lower Carboniferous beds in Europe (see Bertrand, 1935). The stems of some, e.g. *Asteropteris* (Upper Devonian) (Fig. 62) and *Cladoxylon radiatum* (Lower Carboniferous) (Fig. 64), had elaborate steles stellate in section, but in others it appears as if the central part of the stele was imperfectly developed, resulting in a system of disconnected rays of xylem surrounded by phloem with only occasional anastomoses at the centre. The protoxylems were situated near the outer extremities of the rays. In some of the Cladoxyloideae the xylem is all clearly primary, but in others the main bulk of the xylem of the ray is radially seriated and has the appearance of secondary xylem. Radial seriation of the cells of a tissue does not necessarily imply secondary growth from a cambium, because it may be observed in the xylem in the petioles and midribs of many leaves and in cortical tissues in water plants. It may be due to general tangential division in the meristem before even the protoxylem is lignified.

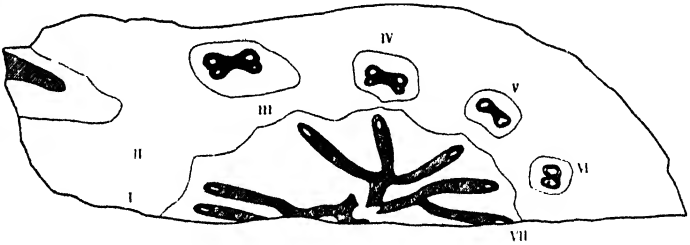


FIG. 62.—*Asteropteris noveboracensis*. Transverse section of part of a stem showing part of stellate stele and several leaf traces. × 3. After Bertrand.

Lateral branches were produced by these stems and in the process several adjoining rays of the stele were involved (Fig. 63). In some forms the branches resembled the stem in the radial symmetry of their vascular tissues; in others the branch has a

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[1] In this list only the more important divisions which include fossil forms of Pretertiary age are given.

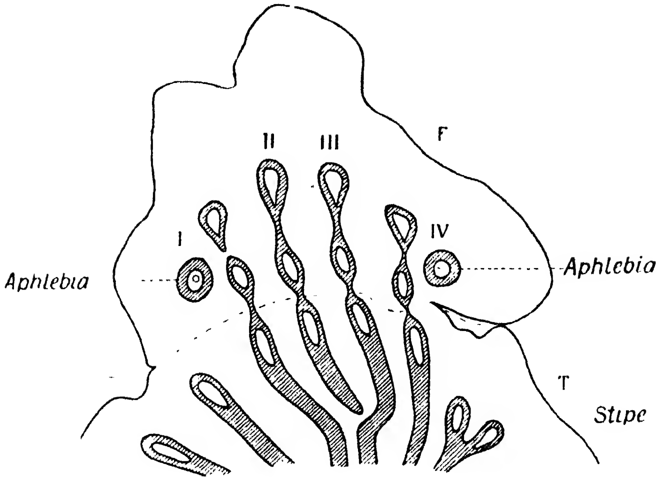

FIG. 63.—*Cladoxylon radiatum.* Diagram of part of stem T, with the base of lateral branch, F. × about 14. After Bertrand.

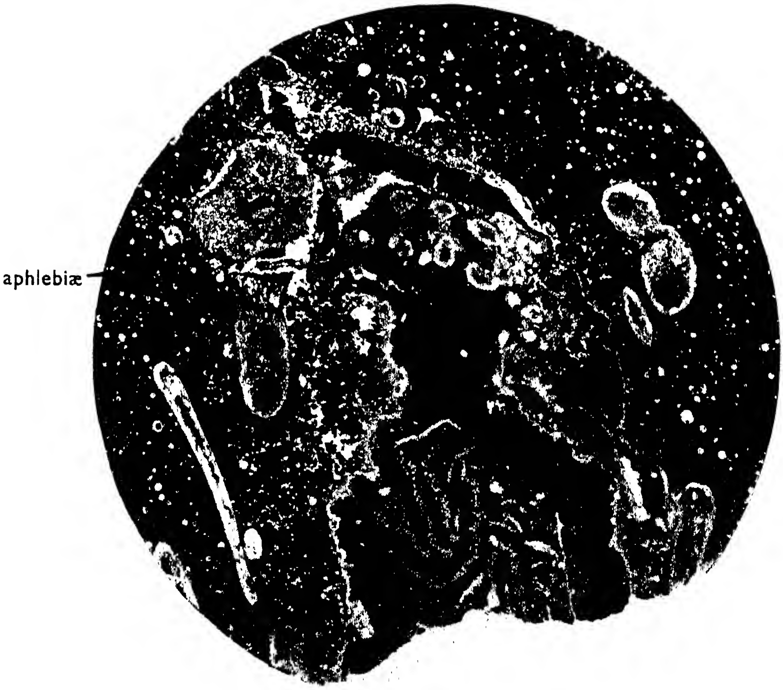

FIG. 64.—*Cladoxylon radiatum.* Section of stem at foot of figure with immediately above it a branch with about eight vascular strands. The branch is still connected to the stem by dark tissue. On either side of the branch are forking aphlebiae. × 7. After Bertrand.

bilateral symmetry. In *Asteropteris* each ray of the stele gave rise to a tangentially elongated leaf trace which had above its point of origin two protoxylems. This type of leaf trace is characteristic of the petiole bases of many of the undoubted Ferns of Palaeozoic age: it has also been found in *Cladoxylon*. Further out the leaf trace has four protoxylems (Fig. 62) and the leaf bore in all probability four ranks of appendages. Nothing is known of the fructifications of the *Cladoxyloideae* and their attribution to the Ferns is based on the anatomy of their stems and petioles.

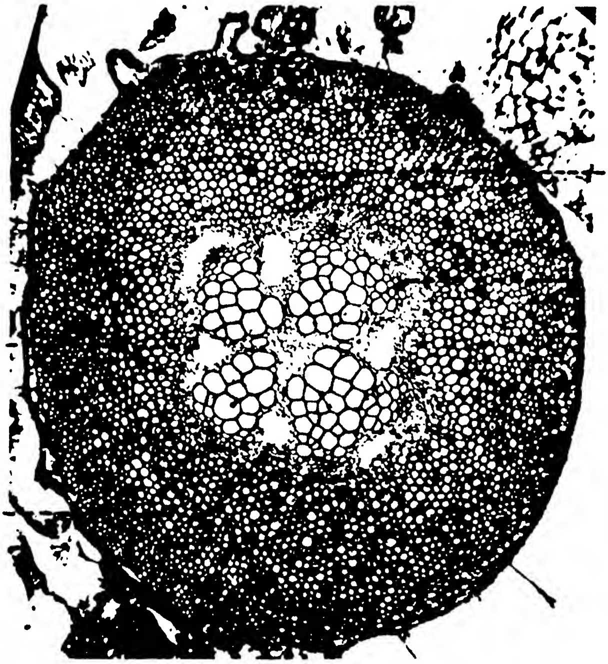

FIG. 65.—*Stauropteris oldhamia*. Transverse section of a rachis. Each of the four strands of metaxylem has a protoxylem. The two strands on the right have each produced a second protoxylem which will pass out into the lateral branch of the rachis situated on the right at a higher level than this section. After Bertrand.

b. *Stauropteroideae* (genus—*Stauropteris*).—In this genus there are two species, one of Upper and the other of Lower Carboniferous age. The main stem of the plant has not yet been discovered. The aerial parts consist of repeatedly branching rachises. No trace of a leaf lamina has been found, although many well-preserved examples of the ultimate branches of the rachis have been examined. The sporangia were borne terminally on the slender branches. The vascular supply of the largest rachises consists of four strands of centripetal metaxylem (Fig. 65), which may be separate or joined together. The whole rachis has a nearly radial symmetry, but the sieve tubes, some of which are found in the angles between the xylem, are more abundant on two opposite sides of the xylem. These two sides were probably the anterior and posterior faces of the rachis. Lateral branches of the rachis are given off in pairs alternately from the lateral faces of the main rachis (Fig. 66). Each pair of branches is subtended by a pair of stipular outgrowths (aphlebiae).

The vascular system of each lateral repeats in form that of the main rachis. The same four-ranked arrangement of laterals is found on these secondary rachises and may be repeated on the third-order rachises (Fig. 67). The later rachises, however, have their laterals in two rows as in the common type of pinnate leaf. The ultimate rachises terminate in sporangia and possess a single strand of tracheids. The outer cortical tissues of the rachis is thin-walled parenchyma and was probably photosynthetic.

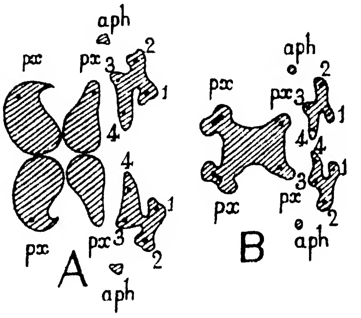

FIG. 66. — *Stauropteris oldhamia.* Diagram to show A, the vascular arrangements between a rachis and a pair of its branches; B, those between secondary and tertiary. The black dots represent protoxylems (*px*); *aph*, aphlebia traces. After Bertrand.

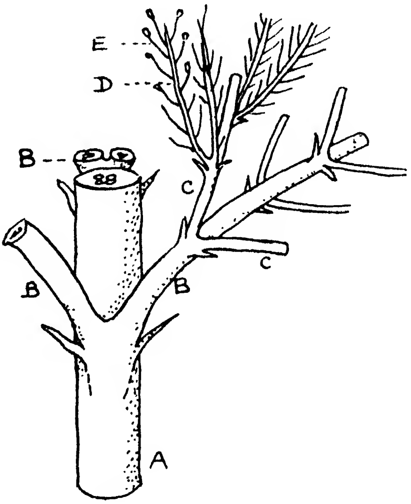

FIG. 67. — *Stauropteris oldhamia.* Diagrammatic drawing to illustrate the successive orders of branching, *B*, *C*, *D*, *E*, of the rachis *A*.

The sporangia (Fig. 68) are of the massive Eusporangiate type. The sporangium has a terminal stomium but there is no annulus. That the plant is a fern is proved by examples of sporangia in which the spores have germinated and produced rhizoids. The spores are 32-40 μ in diameter and were produced in tetrads.

c. Zygopteroideae (genera—*Ankyropteris*, *Zygopteris*, etc.).—

Ankyropteris. As the result of investigations by Williamson in 1876 and Holden in 1930 we have been given a fairly complete idea of the vegetative parts of this genus of small Ferns whose fragmentary remains are found in the coal-balls of Lancashire and Yorkshire. The Fern, to which the name *Ankyropteris corrugata* is given, had a prostrate hairy rhizome about 2 cm. in diameter, which forked dichotomously and bore stiff scales (aphlebiae), fronds, and roots. There was a row of petioles on each side of the rhizome, those on one side alternating with those on the other. The petioles were dichotomously branched and bore a row of aphlebiae on each side and numerous hairs. The tips of the rachises were circinnately coiled. The frond, however, had no pinnae or flattened lamina apart from the aphlebiae.

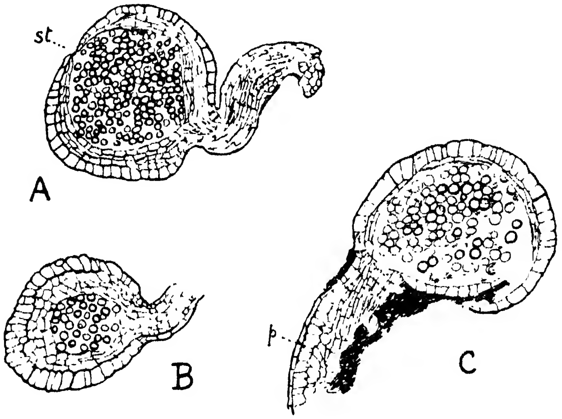

FIG. 68.—*Stauropteris oldhamia*. Three sporangia. A and C. Longitudinal sections. —B. Tangential section. *st*, stomium; *p*, palisade tissue in rachis. Drawing by R. Scott.

The stem in section (Fig. 69) is seen to have a nearly cylindrical protostele with a central core of parenchyma and small tracheids. The protoxylems are near the surface of this inner tissue, which is surrounded by a zone of large metaxylem tracheids. The xylem is surrounded by phloem. The cortex is parenchymatous and there is a poorly developed sub-epidermal periderm. The vascular supply to each petiole arises as a bulge on the xylem. The xylem of the leaf trace at first contains two lateral and one median strand of parenchyma and small tracheids which are connected with the similar tissue in the centre of the stele. In *A. corrugata* the median protoxylem fades out at a slightly higher level in the cortex but in *A. Grayi*, another Upper

Carboniferous species, it continues as the protoxylem of an axillary branch. In *A. corrugata* there is no axillary branching and the median protoxylem of the trace is probably vestigial.

In the petiole the two protoxylems with their associated parenchyma become much extended so that the petiolar strand becomes H-shaped (Fig. 69, C). The vascular supply to an aphlebia arises from the narrow band of tracheids flanking the protoxylem, and the plane of symmetry of the aphlebia is at right angles to that of the petiole which bears it.

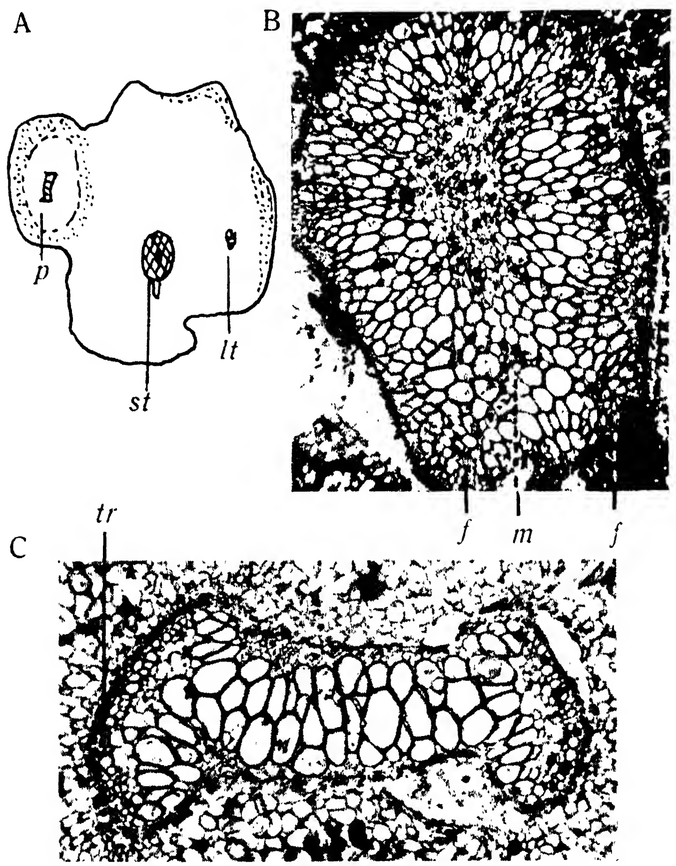

FIG. 69.—*Ankyropteris corrugata*. A. Transverse section of stem. × 2.— B. Vascular cylinder. × 25.—C. Petiolar strand. × 35. *p*, petiole; *st*, vascular cylinder; *lt*, leaf trace; *f*, *f*, the two lateral and, *m*, the median protoxylems of a leaf trace cut below the level of its separation from the vascular cylinder; *tr*, loop of tracheids enclosing protoxylem parenchyma. A, after Williamson; B, C, after Holden, 1930.

A. Grayi differs from *A. corrugata* in having a phyllotaxy with closely set petioles and radial symmetry. The stele is stellate in section. The projections are the base of the petiolar strands. The smaller tracheids which form the core are scalariform and are continuous with the protoxylem elements, which are found in the centres of the projecting arms of the stele. The petiolar strand before attaining the characteristic H-shape gives off a cylindrical branch, which supplies an axillary shoot.

Ankyropteris westphaliensis, of which only the petiole is known (Fig. 70), has a vascular strand in which the xylem has the form

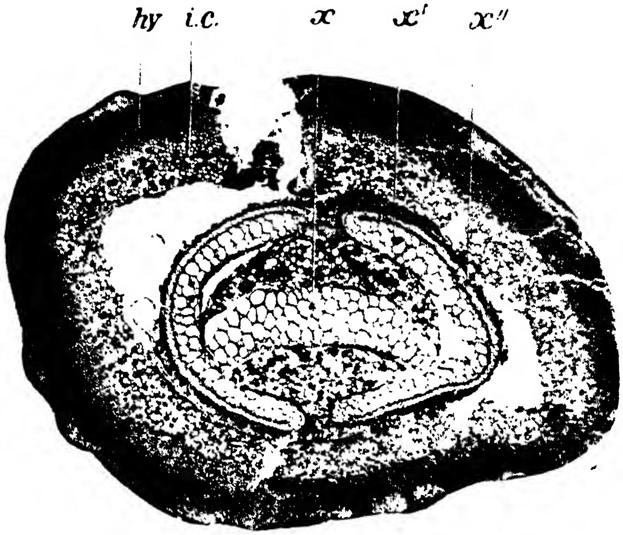

FIG. 70.—*Ankyropteris westphaliensis.* Transverse section of a petiole. x, middle band of xylem; x', lateral bands of metaxylem (antennae); x'', narrow band of small tracheids. The protoxylem lies between x' and x''. *hy*, outer cortical sclerenchyma; *i.c.*, inner cortex. Photo by Boodle.

of a double anchor. As in *A. corrugata* it bore two series of laterals, one on each side. The vascular supply to each lateral arises as part of the narrow band of small tracheids bounding the protoxylems on each side of the petiolar strand.

Zygopteris. Zygopteris primaria is a Permian Tree-Fern, which was incompletely described by Cotta in 1832 and more recently investigated by Sahni (1932). The slender stem (diam. 1.5 cm.) bore petioles arranged in a close 3/8 phyllotaxy. The stem and petiole bases were imbedded in a mass of adventitious roots and the whole mass must have ~~formed~~ a false trunk of at least 20 cm. in diameter. The xylem cylinder has a central core of small scalariform tracheids and parenchyma with projections corresponding to the points of attachment of the petioles. The xylem which surrounds the core is all radially seriated and consists of scalariform and multiperforate tracheids. The cortex is parenchymatous. Scott (1912) described under the name *Botrychioxylon paradoxum* (Fig. 71) a stem which is identical in structure with the stem of *Zygopteris*. The cortical cells in Scott's stem are radially seriated as well as the tracheids of the xylem. This again supports the view that the radial seriation of the tracheids does not indicate that they were formed from a definite cambium.

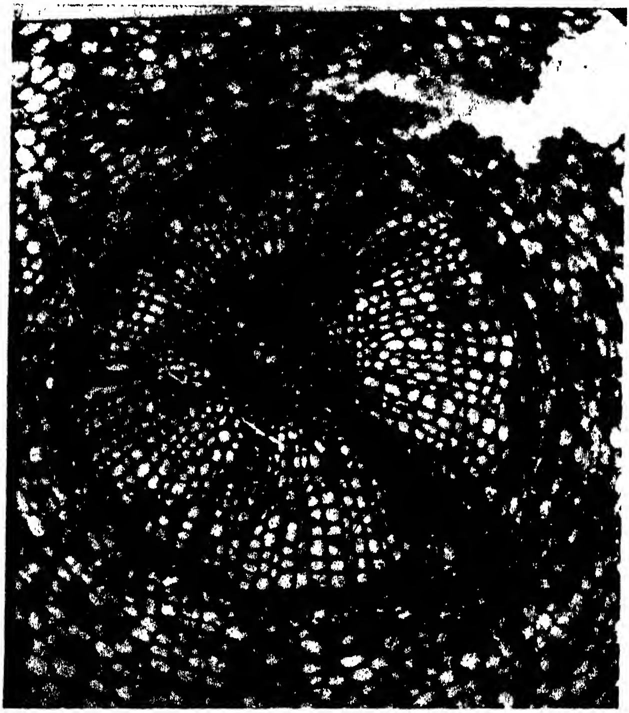

FIG. 71.—*Zygopteris* sp. (*Botrychioxylon paradoxum*). Transverse section of stele and inner cortex. There is a small mixed pith in the middle. The metaxylem and inner cortical cells are radially seriated. × 35. Photo by Boodle.

The petiolar strand in both *Zygopteris* and *Botrychioxylon* consists at the base of radially seriated tracheids with a single central protoxylem. The protoxylem divides tangentially into two. The radially seriated tracheids are replaced by ordinary metaxylem and the trace becomes H-shaped with four protoxylems. Pairs of lateral strands are given off alternately from the two sides of the petiolar strand, each pair anastomosing almost immediately and then separating again into two. This fusion of the pairs of lateral strands is characteristic of petioles to which the name *Etapteris* has been given (Fig. 72). Each pair of laterals then passes into a secondary rachis on which two series of flattened aphlebiae are borne. The frond may therefore be described as being bipinnate. Professor Sahni has thus been able to demonstrate that *Zygopteris*, *Botrychioxylon*, and *Etapteris* are parts of the same species of Tree-Fern, or at any rate parts of closely related species.

The sporangia of *Zygopteris* (they have been found attached to *Etapteris* fronds) are borne in bunches on small rachises (Fig. 73).

FIG. 72.—*Etapteris Scotti*. Transverse section of petiole. On the left the double leaf trace is seen entering the base of a lateral pair of pinnae. On the other side of the main bundle the combined pinna trace is seen pressed against the inner cortex. × 9.

The wall of the sporangium is at least two cells thick and there is a vertical annulus about eight cells wide of thick-walled cells extending up two opposite sides and meeting at the top. The spores (diam. 80 μ) are of the usual tetrahedral Fern type. Similar sporangia have been found associated with the remains of *Ankyropteris corrugata* and *A. westphaliensis*. The sporangia of these ancient Ferns compare with the sporangia of the Rhyniaceae in the massive construction of the wall and in their terminal position on the plant.

In *Corynepteris* the sporangia form compact groups of five or six closely resembling *Marattiaceous* synangia. Individually, however, they resemble the sporangia of *Zygopteris*. Two Lower Carboniferous Fern genera, *Metaclepsydropsis* and *Diplolabis*, have petioles and steles of much the same form as *Zygopteris* and are evidently closely related genera (Fig. 74).

Clepsydropsis.—This genus is of Lower Carboniferous, and possibly late Devonian, age. *Clepsydropsis australis* from New South Wales (Sahni, 1928) was a Tree-Fern. The leaves were closely crowded and the "trunk" attained a diameter of at least 11 cm. The stele was of the *Ankyropteris Grayi* type—a five-rayed star with blunt points. The inner zone of xylem consisted of mixed tracheids and parenchyma. The petiole had a trace in the form of a tangentially elongated bar with two protoxylems, one at each end, with peripheral loops of metaxylem. The trace therefore resembles the basal part of the petiolar strand of *Zygopteris* where there are two protoxylems.

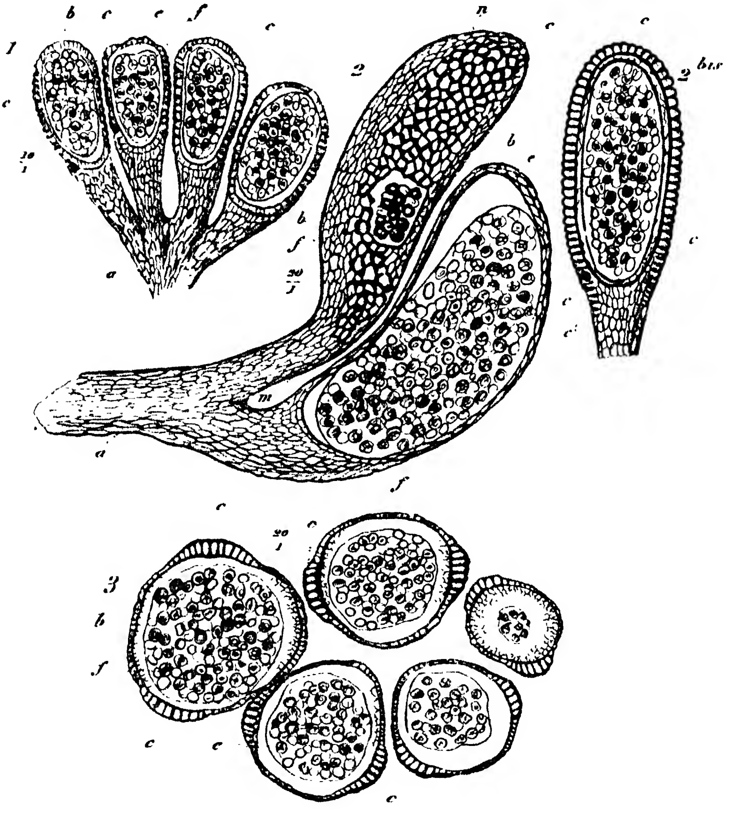

FIG. 73.—*Etapteris Lacattei.* 1. Four sporangia on a rachis (*a*). × 10.—2. Two sporangia, one in median section, the other showing the thick cells (*c*) of the annulus down one side.—2 *bis*. Section through annulus.—3. Transverse sections of sporangia. *c*, annulus. × 20. After Renault.

In the Zygopteroideae we have a group of plants which have many features in common but evolution in the group has followed various lines; in some, e.g. *Asteropteris*, *Clepsydropsis*, and *Asterochlaena*, the stele has become elaborate while the petiolar strand (Fig. 74) has remained relatively simple. In the *Ankyropteris-Zygopteris-Metaclepsydropsis* group the stele tends to become simplified but the petiolar trace becomes more complex.

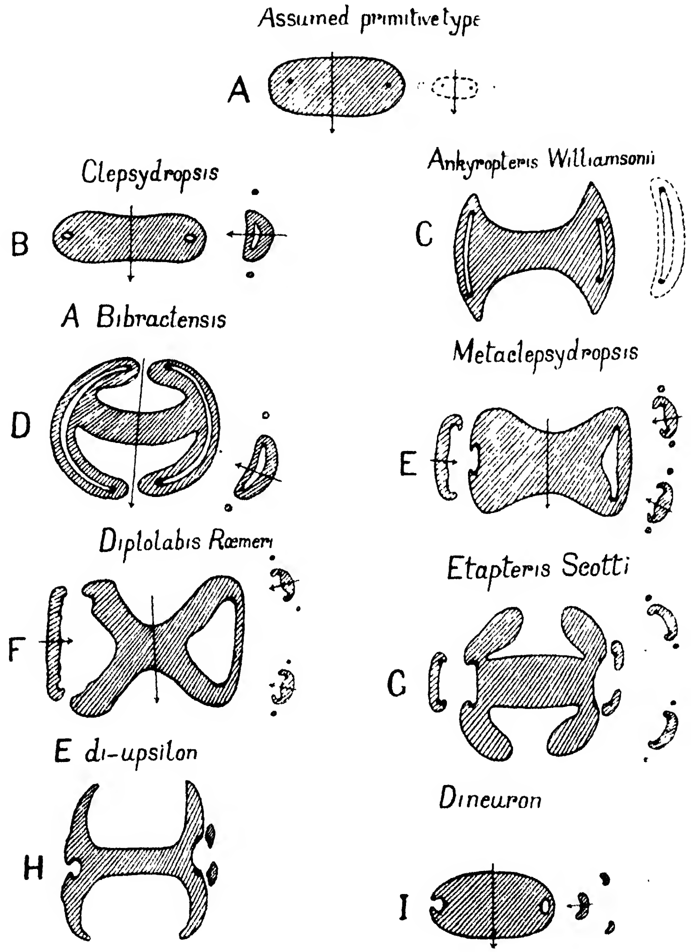

FIG. 74.—Diagrams to show the form of the petiolar bundles in the Zygopteroideae. The adaxial side is uppermost in each case. After Kidston and Gwynne-Vaughan.

d. *Botryopteroideae* (genera—*Botryopteris*, *Grammatopteris*, *Anachoropteris*).—In this group of Carboniferous and Permian Ferns the stem is protostelic and the lateral branches of the petiole face the same way as the petiole, as in most modern Ferns, in contrast to the arrangement in the Zygopteroideae, where the plane of symmetry of the lateral is at right angles to that of the petiole (cf. Figs. 74, 78).

Botryopteris. About ten species of *Botryopteris* have been described from Carboniferous and Permian rocks. The oldest and simplest in structure is *Botryopteris antiqua* from the Lower Carboniferous. The stele consists of a solid strand of primary wood with one to four protoxylems grouped near its centre. These protoxylems are continuous with the protoxylems in the petioles. The petiolar strand may have but one protoxylem.

In *B. cylindrica* (Fig. 75), found in coal-balls of Westphalian age in Lancashire and Yorkshire, the stem, which occasionally forked dichotomously or sometimes unequally, is a little over 2 mm. in diameter with petioles at intervals of about 3 cm. The petioles are nearly as thick as the stem. The plant had probably a creeping or decumbent habit. Roots of the usual Fern type were borne on the stem. The rachis of the petiole was branched but no pinnules with flattened lamina have been found connected to it. The stele, which consists of a solid strand of metaxylem, has in some examples a single median protoxylem but more usually from 2 to 5 situated near the centre. The metaxylem consists of scalariform and multiseriate pitted tracheids and was surrounded by phloem. The leaf trace is mesarch in the stem but in the base of the petiole it has centrifugal wood alone. The

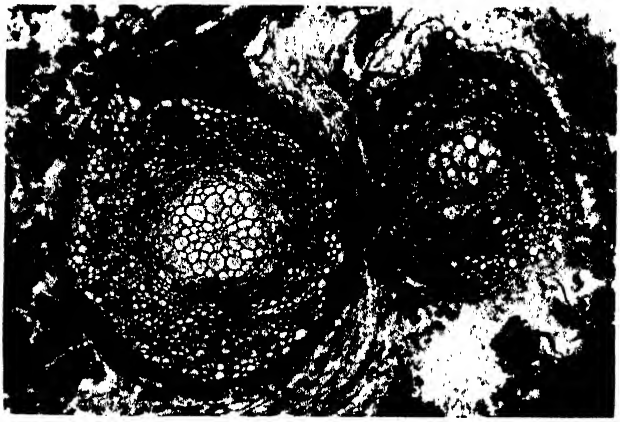

FIG. 75.—*Botryopteris cylindrica.* Transverse section of stem and petiole (right). There are two or three protoxylems in the centre of the stem and two close together on the lower, originally adaxial side of the petiole. × about 24. From Scott.

petiolar trace has either two protoxylems, or only one as in *B. antiqua*.

In the slightly more complex species *B. ramosa* (Fig. 76), which is also of Westphalian age, the petioles are arranged in a 2/5 phyllotaxis and the petiole has three protoxylems. It will be noted that the protoxylems, which at first (Fig. 76, l.t^2) face towards the stele, further out face laterally (l.t^1).

In the Permian species *B. forensis* (Fig. 78) the petiole has a more elaborate form and the smaller divisions of the rachis of the frond bore pinnules with a somewhat fleshy, lobed lamina.

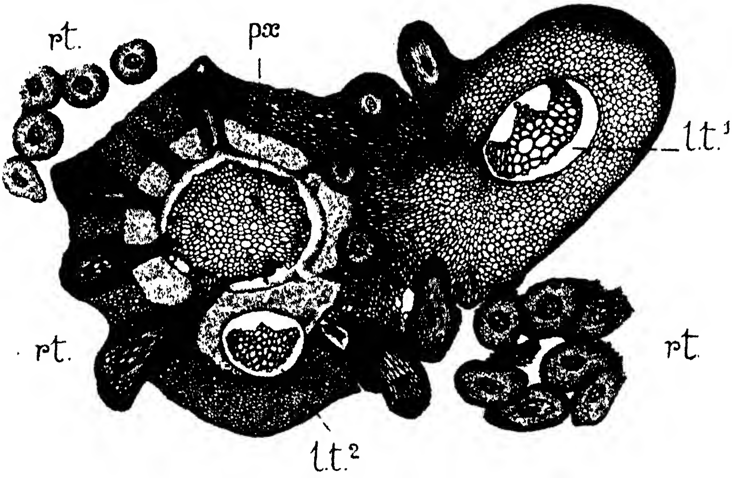

FIG. 76.—*Botryopteris ramosa*. Transverse section of stem, petiole bases (*l.t.*) and roots (*rt.*). × 8. From Scott.

The fronds, which therefore must have had the appearance of the more familiar type of Fern frond, were also circinnately coiled when young. The sporangia were borne on some of the slender rachises of the frond. The sporangia (Fig. 77) are pear-shaped and shortly stalked and they varied from 2 to 1.5 mm. in length and from 1 to 0.7 mm. in diameter. The annulus was restricted to one side of the sporangium and consisted of a wide band of thick-walled cells. The spores are of the usual Fern type. Similar sporangia have been found associated with *B. hirsuta*, *B. ramosa*, and *B. cylindrica*.

Other genera of Botryopteroideae are known. *Tubicaulis* (Westphalian and Permian) was a small tree with a diameter of about 20 cm. *Tubicaulis* is in some respects intermediate in character between the Zygopteroideae and Botryopteroideae. The subsequent forking of the pinna traces is orientated to the plane of symmetry of the petiole as in the Zygopteroideae. It is thus possible that the Zygopteroideae and Botryopteroideae have had a common origin.

Anachoropteris. This genus, containing about a dozen species based on the form of the petiole, is of Westphalian and Permian ages. The petiolar strand in the simpler forms is like that of *Tubicaulis* (Fig. 78). The lateral pinnae are orientated as in the rest of the Botryopteroideae. The fructification according to Kubart consists of synangia borne on the incurved margins of the pinnules of the fronds. Each synangium consists of four sporangia. This is the most complex type of fructification found in the Coenopteridineae and is remarkable in view of the relative simplicity of the vascular organisation of the group.

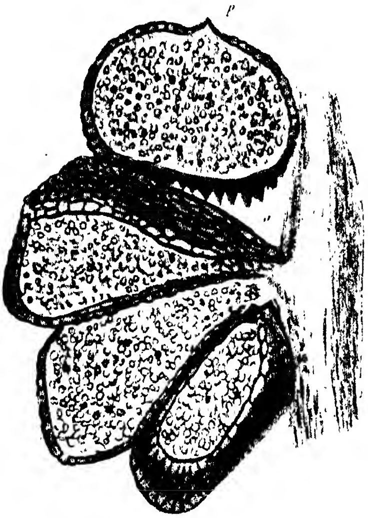

Fig. 77.—*Botryopteris forensis.* Group of sporangia. The top sporangium is cut transversely and shows section of the multiseriate annulus at *o*. *p*, section of line of dehiscence. × 35. After Renault.

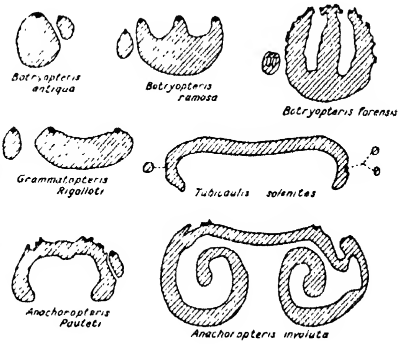

Fig. 78.—Diagrams of the transverse sectional view of the xylem in the petioles of various Botryopteroideae. The protoxylems are represented in black; the metaxylem is shaded. They are all shown with the adaxial surface uppermost.

The student is advised to consult the memoir by Corsin (1937) if detailed information is required about the structure of the stems and petioles of the Botryopteroideae.

CHAPTER VIII

FILICALES—II: MARATTIINEAE TO POLYPODIACEAE

2. MARATTIINEAE.—From two different sources we get evidence of the existence of Marattiineae in the Palaeozoic period, from fertile fronds and from stems. A considerable number of large Fern-like fronds, for reasons which will be given in a later chapter, belong to a group of seed plants called the Pteridosperms. There are, however, a number of types of frond included in the form-genus *Pecopteris*, which in the fertile condition are found to have their sporangia in groups or synangia which bear a close resemblance to those found in the living Marattiaceae.

In *Scolecopteris* the leaves are large multipinnate fronds such as are borne on Tree-Ferns, and in the sterile condition they are called *Pecopteris*. In *Scolecopteris polymorpha* the sporangia are grouped in fours in circular synangia. Each sporangium is elongated and tapers to a fine point. They are fused at the base to a short stalk which has a vascular strand. The synangia are arranged in two rows, one on each side of the abaxial surface of the pinnule (Fig. 79). The sporangia probably dehisced by a small slit near the apex facing the centre of the synangium. In *Scolecopteris elegans* the sporangia are smaller and are fused together at the base as in some of the living Marattiaceae. These synangia are like those of the living genus *Christensenia* but they are stalked as in some species of *Marattia*. Scott and Holden (1933) have given a good description of the vegetative structure of another species, *S. Oliveri*, and have shown that both hairs and scales are present on the leaves. Scales are an advanced type of appendage in the Ferns and it is somewhat surprising to find them on a Palaeozoic Fern. *Scolecopteris* is one among several Carboniferous and Permian plants which, on similar grounds, may be regarded as Marattiaceous.

Petrified stems, to which the name *Psaronius* is given, are found in Upper Carboniferous and Permian strata. They were the stems of plants with the habit of Tree-Ferns. In a transverse section of *Psaronius brasiliensis*, a South American, probably Permian, species, the structure (Fig. 80) is seen to be remarkably like that of a living Cyatheaceous Tree-Fern in general construction, for the main bulk of the "trunk" consists of a thick mantle of adventitious roots which arise from the surface of the true stem. The roots in structure are like those of the Marattiaceae and have a rather massive stele with five or six exarch protoxylems. The surfaces of the roots near to the stem and the surface of the stem itself are covered with a dense mass of filamentous hairs, which form a compact tissue between the roots (Fig. 81, A). This tissue must have added considerably to the rigidity of the "trunk". The stem has an outer zone of sclerenchyma enclosing an extensive parenchymatous region in which the vascular tissues are embedded. The vascular tissue, like that

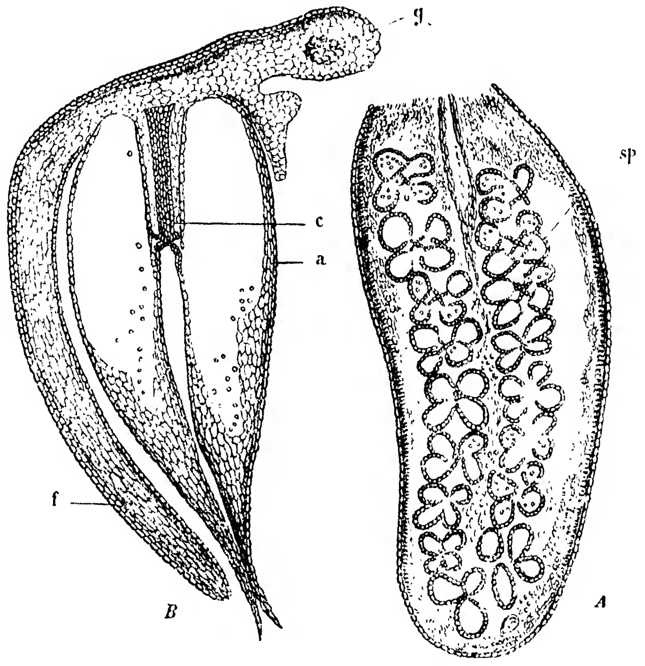

FIG. 79.—*Scolecopteris polymorpha*. A. Abaxial surface of pinnule with two rows of synangia each consisting of three or four sporangia *sp*. × about 8.—B. Longitudinal section of synangium and part of leaf. *g*, vascular bundle of pinnule; *f*, incurved edge of pinnule; *a*, wall of sporangium; *c*, receptacle to which the bases of the sporangia are fused. After Renault.

of the Marattiaceae, e.g. *Angiopteris*, consists of a large number of strands forming a complex polycyclic dictyostele (Bower, 1926). The vascular strands or meristeles have a concentric structure with xylem surrounded by phloem (Fig. 81, B). The leaves are arranged in *P. brasiliensis* in four vertical rows on the stem and the arrangement is nearly decussate. The opposite pairs were, however, not quite on the same level. The petiolar bundles, F_1 and F_2, were crescentic. There are four main peripheral steles, P_1, P_2, P_3, P_4, which alternate in position with the rows of leaves and gave rise to the roots. The petiolar strands

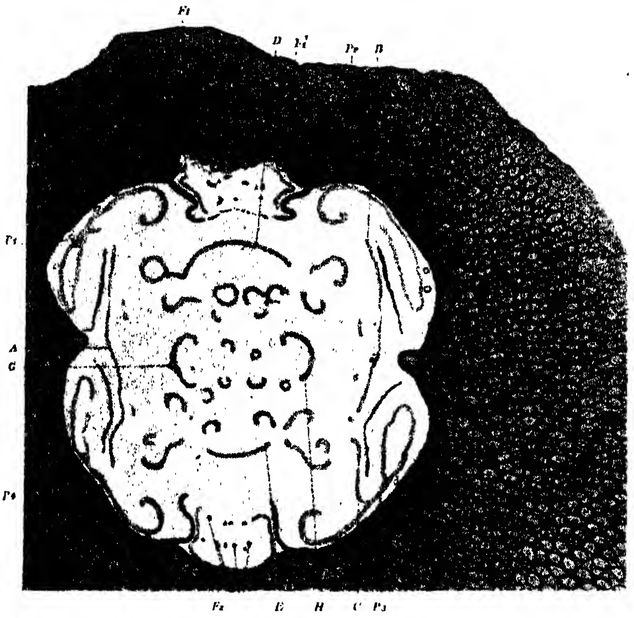

FIG. 80.—*Psaronius brasiliensis*. Transverse section of "trunk". The true stem is seen surrounded by the thick mantle of adventitious roots. For detailed description see text. ½ nat. size. After Zeiller.

separate from "reparatory" strands, which are in nearly opposite pairs, A-B, D-E, and H-G. Anastomoses occur between the reparatory and peripheral strands when the former are about to pass out into the petiole. The inner series of strands or steles also anastomose.

Some species of *Psaronius* have a simpler construction with two vertical rows of leaves, and others have numerous vertical series of leaves with a still more complicated vascular anatomy. This vascular complexity is paralleled in other groups of Ferns and, as Professor Bower has emphasised, is related to the large size of the plant (Bower, 1926, p. 108). The structure of some of

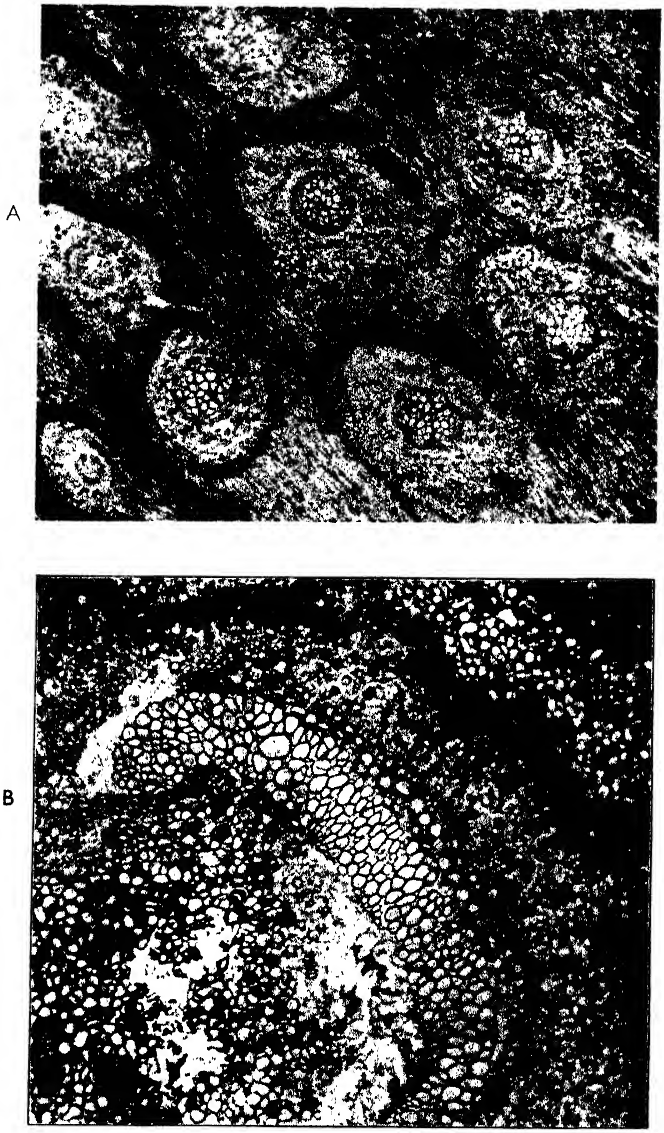

FIG. 81.—A. *Psaronius* sp. Section showing transverse sections of roots with filamentous tissue between. × about 7.—B. *Psaronius Renaulti*. Section of a solenostelic stem. Part of the stele is shown. The protoxylems are at the inner edge of the xylem. × 13. After Scott.

the other types is described in Hirmer's *Handbuch der Paläobotanik*, where a fuller account of the fossil Filicales will be found.

The frequent association of the *Pecopteris* type of leaf with species of *Psaronius* suggests that they were parts of the same type of plant, and supports the view that in the Permian and, to a lesser degree, in the Upper Carboniferous Marattiaceous Tree-Ferns were an important part of the vegetation.

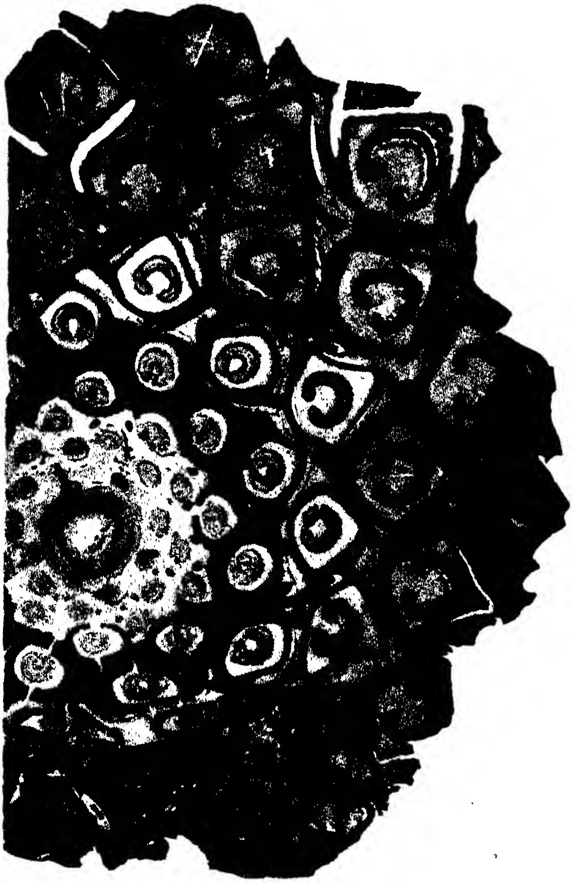

FIG. 82.—*Thamnopteris Schlectendalii.* Transverse section of stem with persistent leaf bases. Note stele surrounded by leaf traces in a parenchymatous cortex, zone of dark sclerenchymatous cortex and sections of petioles with crescentic strands. Approx. nat. size. After Kidston and Gwynne-Vaughan.

3. OSMUNDACEAE.—The Osmundaceae have had a long history and wide geographical distribution in the past. In the Mesozoic, particularly in the Rhaetic and Jurassic, the family was quite an important constituent of the flora. Fertile and sterile fronds are found which compare closely with those of the living *Todea*, and to such the name *Todites* has been given. The

fertile fronds bear their sporangia as in *Todea* but the sporangia are smaller and the whole apex of the sporangium consists of thickened cells. The dehiscence slit runs vertically. In *Osmundopsis* the sporangia are distributed as in *Osmunda* but the sporangia are more like those of *Todea.* Some of the Osmundaceae from the Rhaetic of Greenland (Harris, 1931) afford excellent examples of fronds and sporangia preserved in the form of compressions.

The most interesting fossil Osmundaceae are petrified stem and leaf bases from various geological horizons from the Permian to the Tertiary. They have been described in detail by Kidston and Gwynne-Vaughan (1907–14). They all agree in having closely crowded leaves with persistent leaf bases. The roots, which arose from the stem or leaf bases endogenously, are similar to those of *Osmunda* in structure. The structure of the leaf trace is very uniform throughout the group (Figs. 82, 83), and is a very characteristic feature. Since the publication by Kidston and Gwynne-Vaughan of their memoir, other Permian genera have been discovered.

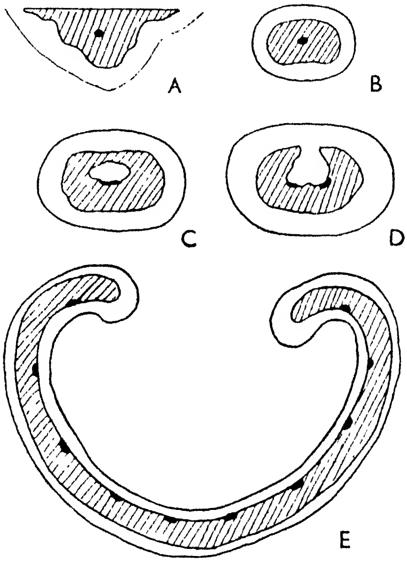

FIG. 83.—*Thamnopteris Schlectendalii.* Diagrams to show the form of the leaf trace. A. Trace separating from surface of stele.—E, Form of trace in petiole.—B, C, D. Structure at successively higher levels between A and E. Metaxylem is shaded and the protoxylems are black. Roughly × 5 nat. size. After Kidston and Gwynne-Vaughan, 1907.

The Permian genera differ principally from those of later age in having a solid protostele. The centre of the axis contains short thick traceids while the outer xylem (Fig. 84) consists of long tracheids and is connected with the leaf traces. The best known are *Petcheropteris* (Zalessky, 1931), *Thamnopteris*, *Zalesskya*, *Chasmopteris* (Zalessky, 1931). Even in these Palaeozoic genera the crescentic petiolar bundle with several adaxial protoxylems is remarkable for its similarity to that of the living *Osmunda.*

Fig. 84.—*Thamnopteris Schlechtendalii.* Part of stele in transverse section. *c.x.*, central xylem; *o.x.*, outer xylem; *x.sh*, conjunctive tissue; *ph*, phloem. A leaf trace is seen forming a projection from the *o.x.* at the top of figure. × 13. After Kidston and Gwynne-Vaughan.

In the Mesozoic representatives referred to the genus *Osmundites* some, e.g. *O. Kolbei* from the Cretaceous, have retained the solid protostelic condition in the form of a mixture of tracheids and parenchyma. In others the central region contains no tracheids and a parenchymatous medulla is found. In those of more recent age the outer xylem is interrupted by a gap where a leaf trace leaves the stele. In *O. skidegatensis* (Cretaceous) there is phloem on the inner side of the xylem, which is connected through the leaf gaps with the outer phloem, while in *O. Carnieri*, which is of doubtful age, the stele is broken up completely and the stem is truly polystelic. There is no doubt that these fossils are closely related to the living Osmundaceae.

The Permian Fern *Grammatopteris Baldaufi* (Sahni, 1932) has a stele intermediate in character between those of *Ankyropteris* and the Permian Osmundaceae. Its petiolar bundle, which is in the form of a straight bar as seen in section in some species, is also intermediate in form. Both the Osmundaceae and Coenopteroideae have large sporangia so that we have several reasons for supposing that these two groups may have had a common origin.

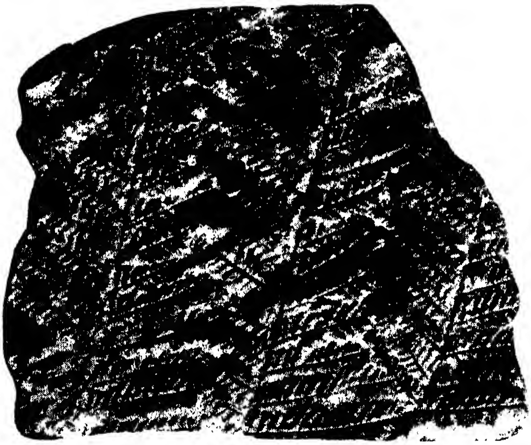

FIG. 85.—*Senftenbergia plumosa*, Artis sp. Parts of three primary pinnae of a tripinnate frond. × about ½ nat. size. After Scott.

4. SCHIZAEACEAE.—The earliest record of Schizaeaceous Ferns until recently was *Senftenbergia* from the Upper Carboniferous. The sporangia of this genus were borne in two rows on the abaxial surface of a tripinnate frond, and the annulus of the sporangium consisted of an apical cap of thick-walled cells as in the living *Schizaea*.

Dr. N. Radforth (1938, 1939) has recently shown that the genus *Dactylotheca*, which was described as having an exannulate sporangium, has in fact the same type of sporangium as *Senftenbergia* and may no longer be regarded as a distinct genus. One species, *Senftenbergia Sturi*, occurs in the Upper part of the

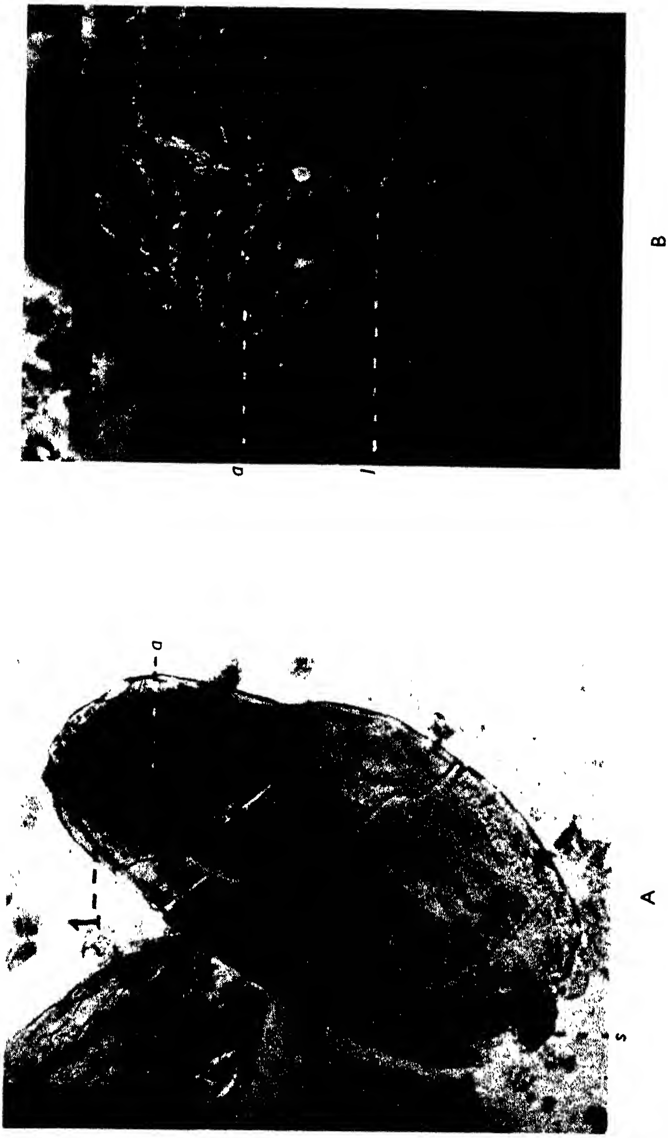

Fig. 86.—Sporangia of *Senftenbergia*. A. Sporangium of *S. plumosa* isolated by transfer and maceration. × 125.—B. Apex of sporangium of *S. pennaeformis*, from a transfer. × 100. *s*, stalk; *a*, annulus; *l*, line of dehiscence. After Radforth, 1938, 1939.

Lower Carboniferous and the other species occur in the Upper Carboniferous. By careful treatment of compressions, Dr. Radforth has shown that the sporangium (Fig. 86) was very like that of *Aneimia* and was in all the species he investigated attached to the incurved margin of the pinnule by a short stalk. The large fronds are tripinnate (Fig. 85) and must have been borne on a plant the size of a Tree-Fern. It is likely therefore that the living Schizaeaceae constitute the reduced relics of a group which was in the Palaeozoic of large stature and an important constituent of the flora. Nothing is known about the stems of the fossil Schizaeaceae.

5. GLEICHENIACEAE.—The sporangia of *Oligocarpia*, a genus of Westphalian age found in Europe and China, and those of *Chansitheca* (Halle, 1927), from the Permian of China, bear a close resemblance to those of *Gleichenia* and like them are arranged in compact sori. Without the application of maceration methods it is difficult to determine with certainty the nature of the annulus. These two forms are only to be included provisionally in the Gleicheniaceae. Undoubted species of *Gleichenia* are found in Cretaceous rocks in Europe, Spitsbergen, Greenland, Patagonia, and the Argentine.

6. MATONIACEAE.—The Matoniaceae appear to have been abundant in the Rhaetic, Jurassic, and Lower Cretaceous. The family is represented by the genera *Laccopteris* and *Matonidium*.

7. DICKSONIACEAE and CYATHEACEAE.—The fossil examples of these two groups add nothing to our knowledge of their morphology. What evidence there is suggests that they may have existed as early as the Jurassic.

8. DIPTERIDACEAE.—This family, which is represented by the single living genus *Dipteris*, was of importance in the Mesozoic (Oishi and Yamasita, 1936). The following are the more important genera: *Camptopteris*, Keuper and Rhaetic; *Thaumatopteris*, Keuper and Jurassic; *Dictyophyllum*, Keuper—Lower Jurassic; *Clathropteris*, Rhaetic and Jurassic; *Hausmannia*, Rhaetic to Upper Cretaceous.

9. POLYPODIACEAE.—The Polypodiaceae have left scanty records of their existence and do not appear to have existed before the Cretaceous period.

For a general review of the relationship of the fossil and living Pteridophytes, the reader is advised to consult *The Ferns* and *Primitive Land Plants*, by Professor Bower.

CHAPTER IX

PALAEOZOIC PTERIDOSPERMAE—I: LYGINOPTERIDEAE

THIS important group of vascular plants belongs to the Spermaphyta (seed plants) but its members bear some obvious resemblances to the Filicales, particularly in the shape of their large, usually multipinnate, leaves and in the venation of the leaflets (Kidston, 1925, p. 16). The leaves are very common fossils in the Carboniferous coal-measures but it was not until about 1883 that any doubt was thrown on their relationship to the Ferns. It is likely that the Pteridosperms were in existence in the Upper Devonian but the evidence is scanty. As the result of investigations of the petrified plants in the coal-balls found in the Upper Carboniferous coal-measures in Yorkshire and Lancashire and in the Lower Carboniferous in Scotland, the structure of a number of examples of the group is comparatively well known. They seem to be intermediate in some structural characters between Ferns and Gymnosperms. Some of their Fern-like fronds have been found with seeds attached to them and the name Pteridospermae was used to suggest the combination of Fern and seed-plant characters.

Calymmatotheca Höninghausi.—This Pteridosperm is found in Westphalian rocks in several of the British and European and North American coal-fields, and will be described before the earlier Lower Carboniferous forms as our information about it is more complete. For many years the leaves, stems, roots, and seeds were known but it was not realised until much later that they were parts of the same plant. The parts were discovered and named in the following order:

Leaves:	*Sphenopteris Höninghausi* Brongniart, 1828
Stems:	*Lyginopteris oldhamia* Binney, 1866
Petioles:	*Rachiopteris aspera* Williamson, 1874

Roots: *Kaloxylon Hookeri* Williamson, 1876
Seeds: *Lagenostoma Lomaxi* (Williamson MS.) Oliver and Scott, 1903

In 1929 Dr. Jongmans proved that the seeds were borne in cupules of the type called *Calymmatotheca*, and according to the rules which govern the naming of fossil plants the plant as a whole must be called *Calymmatotheca Höninghausi*. The pollen-producing organ is the only part of the plant that has not yet been identified.

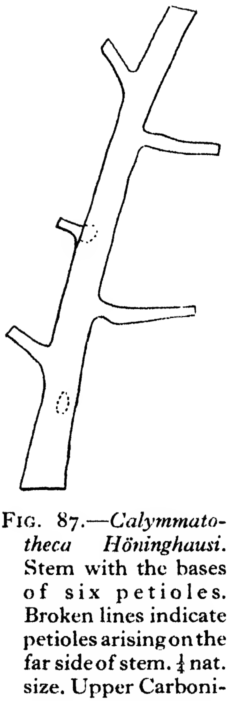

FIG. 87.—*Calymmatotheca Höninghausi*. Stem with the bases of six petioles. Broken lines indicate petioles arising on the far side of stem. ¼ nat. size. Upper Carboniferous, Kilwinning, Scotland. Hunterian Museum, Pb. 1651.

The Stems (*Lyginopteris oldhamia*).—Many beautifully preserved petrifactions and large compressions of stems have been found. They were long and relatively slender, ranging from 2 to 40 mm. in diameter. In a few examples branching occurs and in one specimen the branch is axillary. It is doubtful, however, if this was a constant feature. The leaves were arranged in a 2/5 phyllotaxy (Fig. 87). The stem contained a central pith (Fig. 88) containing numerous rounded masses of thick-walled cells comparable to the stone cells in the skin of a pear. Around the margin of the pith are the primary xylem strands arranged in a ring. Each strand contains a protoxylem element (Fig. 89). Differentiation of the metaxylem started centrifugally from the protoxylem and then extended round towards the centre of the axis until the protoxylem and a small strand of parenchyma were enclosed by the metaxylem. The primary wood is therefore in the form of mesarch strands. Surrounding the primary strands, which consist of large tracheids with crowded bordered pits on all their walls, there is in most stems a considerable development of secondary wood. These tracheids differ from those in the metaxylem in their smaller size and in absence of pits on the tangential walls. Sometimes, as in the section figured, there are large medullary rays alternating with the primary strands and through these rays the leaf traces passed. In other stems the wood formed a complete cylinder with no conspicuous rays. The cambium is situated on the outside of the secondary wood and secondary

FIG. 88.—*Lyginopteris oldhamia.* Transverse section of stem. × 2½. *R*, base of a root; *l.t.*, leaf trace; *x*, one of the strands of primary xylem. From D. H. Scott's *Extinct Plants and Problems of Evolution* (Macmillan & Co. Ltd., London).

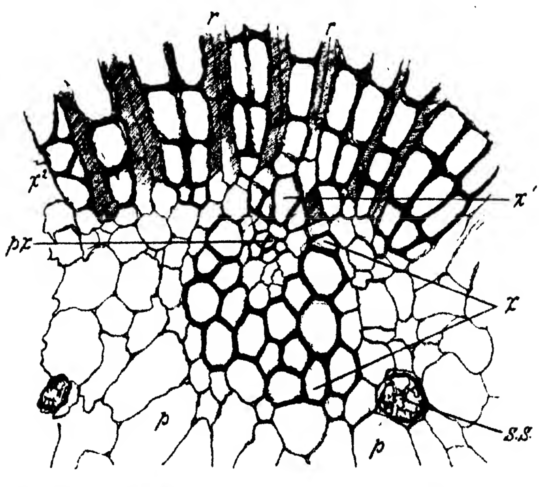

FIG. 89.—*Lyginopteris oldhamia.* Part of a transverse section of a stem. x^2, secondary wood; *r*, medullary rays; *x* and x^1, primary wood; *px*, protoxylem; *p*, pith; *s.s.*, secretory cell. × 100. After Scott.

phloem was formed to the outside of it. The pericycle has short cells with occasional groups of stone cells. The outer part of the pericycle included a periderm cambium.

The inner cortex is usually poorly preserved but appears to have consisted of large-celled parenchyma. In the outer cortex are radially extended bands of fibres. These bands anastomosed and formed a strong reticulum, which gave rigidity to the stem. In transverse section they resemble the Roman numerals on a clock-face.

FIG. 90.—*Lyginopteris Höninghausi.* Stalked gland showing glandular tissue at the apex. × about 60. After Oliver and Scott.

The surface of the stem bore glands (Fig. 90). In the formation of these structures the outer part of the cortex as well as the epidermis was involved. The head of the gland was spherical and contained a small-celled tissue, which was probably active in forming some secretion. Some of the glands were stalked and others were sessile.

Each leaf contained in the base of its petiole two strands. If we follow inwards these two strands we find that they pass across the cortex and then bend and pass steeply down through the pericycle and phloem region for about five internodes. They then pass into the secondary wood region where each has some secondary wood on its abaxial side. Here the two strands fuse together and the single strand enters the outer part of the pith, where it bends to the right and joins one of the circum-medullary strands. There are five circum-medullary strands to which the leaf traces are attached corresponding to the five vertical rows of leaves on the stem. In a transverse section of the stem these five strands and a number of leaf traces which have not yet fused with them will be seen in the region round the pith.

The leaves were large, in some cases attaining a length of at least 50 cm. (Fig. 91). They were circinnately rolled like the young fronds of a Fern. The petiole, which has a somewhat swollen base, forked about half-way up the frond into two equal arms. The primary pinnae are arranged up the sides of the petiole below the fork as well as above. The secondary pinnae bore two alternating rows of small-lobed pinnules. The whole of the frond including the surfaces of the pinnules bears hairs and glands.

In the base of the petiole the two vascular strands join together if they are traced upwards in the petiole and a V-shaped bundle is found at higher levels (Fig. 92).

Fig. 91.—*Sphenopteris Höninghausi.* Middle region of a frond showing the dichotomy of the main rachis. $\frac{3}{8}$ nat. size. After Potonie.

The roots were adventitious and emerged from the stem among the leaves. In some instances roots have been found above the level of branches. The largest roots have a diameter of about 7 mm. and each produced large numbers of smaller lateral roots. In section (Fig. 93) the root is seen to have a number of protoxylems, each of which has an accompanying development of centripetal metaxylem. Secondary wood is present. The cortex is of special interest: the inner zone of large cells contains many

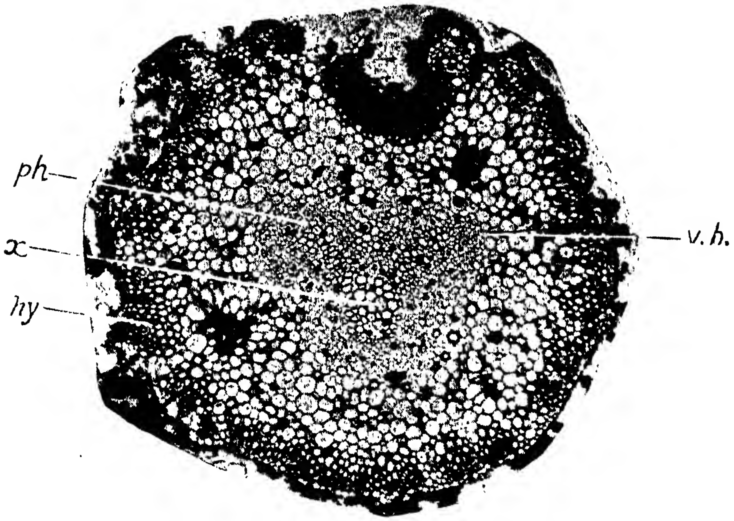

FIG. 92.—*Lyginopteris oldhamia*. Transverse section petiole. *hy*, cortical bands of sclerenchyma; *v.b.*, boundary of vascular bundle; *ph*, phloem; *x*, xylem. × about 35. After Williamson and Scott.

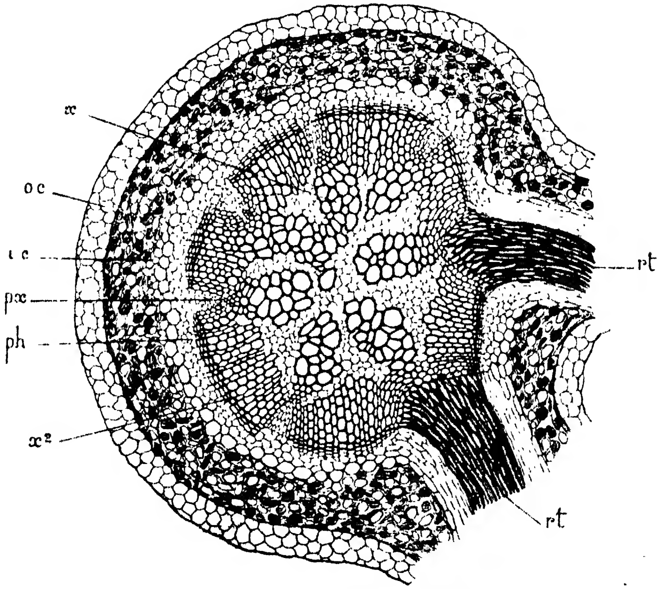

FIG. 93.—*Kaloxylon Hookeri*. Root of *Lyginopteris oldhamia* in transverse section. *rt*, lateral roots; *px*, one of the seven protoxylems; *x*, centripetal metaxylem; x^2, secondary xylem; *ph*, phloem; *i.c*, and *o.c*, inner and outer cortex. × 24. After Scott.

cells with dark contents, possibly of the nature of a secretion. Scott has pointed out that the outer cortex bears a close resemblance to the velamen of an orchid root. In the small lateral roots there are two protoxylems, and Professor Weiss has discovered that these two protoxylems lie in the same plane as the axis of the parent root. This is the arrangement found in the Phanerogams and it differs from that in the Pteridophytes in which the two protoxylem strands of a lateral root are found to lie in a plane which intersects that of the main root at right angles.

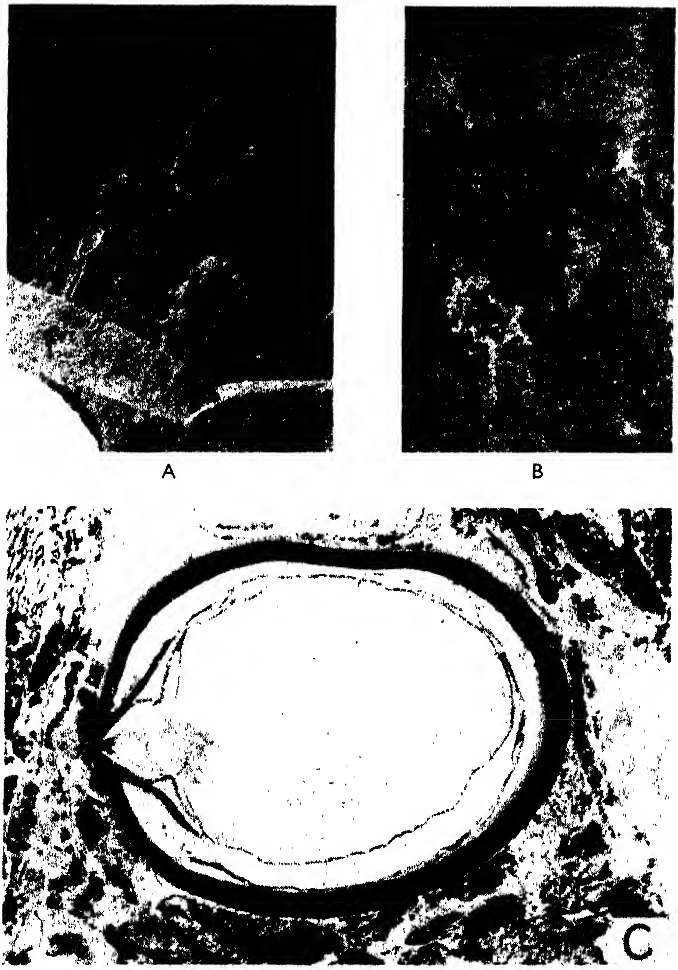

FIG. 94.—*Calymmatotheca Höninghausi*. A. Seed cupule on end of slender rachis: both cupule and rachis are covered with glandular hairs. × 3.—B. Seed cupule containing seed. × 3. A and B from Upper Carboniferous, Holland. After Jongmans, 1930.—C. Longitudinal section of a petrified seed. × 12. Upper Carboniferous, England. Kidston Slide Coll. No. 609.

The seeds were borne singly in cupules (Fig. 94) on the ends of slender rachises (Jongmans, 1930), and there is evidence to prove that these rachises were attached to fronds which also bore pinnules of the ordinary sterile type. Like the stem and leaves, the slender cupule-bearing rachises and the cupules themselves are studded with glands and hairs. The cupules and seeds are known in a petrified condition.

The vascular bundle in the rachis has a single xylem strand with a central protoxylem. On entering the base of the cupule about ten vascular strands pass out laterally into the cupule. These strands occasionally divide higher up. The cupule is deeply lobed and the edges and outer surfaces of the lobes are studded with glands similar to those found on the frond and stem.

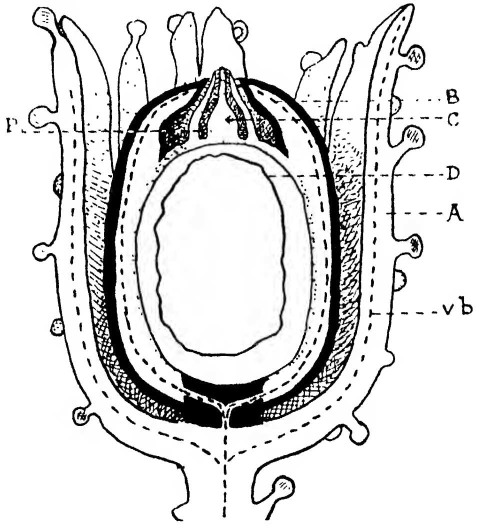

FIG. 95.—*Lagenostoma Lomaxi.* Diagrammatic reconstruction of the seed and cupule. *A*, cupule with glands; *B*, upper part of integument with outer thick-walled zone (black) and an inner soft zone with vascular bundles (broken lines); *C*, nucellar column; *D*, megaspore membrane; *vb*, vascular strands; *P*, pollen chamber. × 8.

The seed is orthotropous (Figs. 94, C, and 95). The integument has a palisade layer of cells which possibly, as in the seeds of many existing plants, secreted mucilage. The rest of the integument consists of an outer thick-walled layer and an inner zone of soft tissue in which about nine vascular bundles are situated. These bundles are given off from the bundle which enters the base of the seed. At the top the integument is divided into nine parts, each of which contains a bundle surrounded by soft tissue. From a comparison with other types of seed it is clear that these nine parts are equivalent to nine lobes, but in this seed the lobes are not separated from one another and form a continuous sheath round the micropyle.

The most striking feature is the elaborate form of the top of the nucellus (sporangium). In the mature seed a cone of tissue forms the apex of the nucellus and the outer layer of this cone separates from the sides forming a pollen chamber. Pollen grains are found in this narrow space between the superficial loosened layer and the rest of the nucellar cone. The pollen grains were no doubt drawn in to the cavity by the contraction of a drop of liquid, which in so many living Gymnosperms projects from the micropyle at the time of pollination. The large central space in the seed contains the megaspore, of which as a rule only the membrane is preserved. A well-preserved portion of the prothallus has been found in one seed (Fig. 96) but as yet no trace

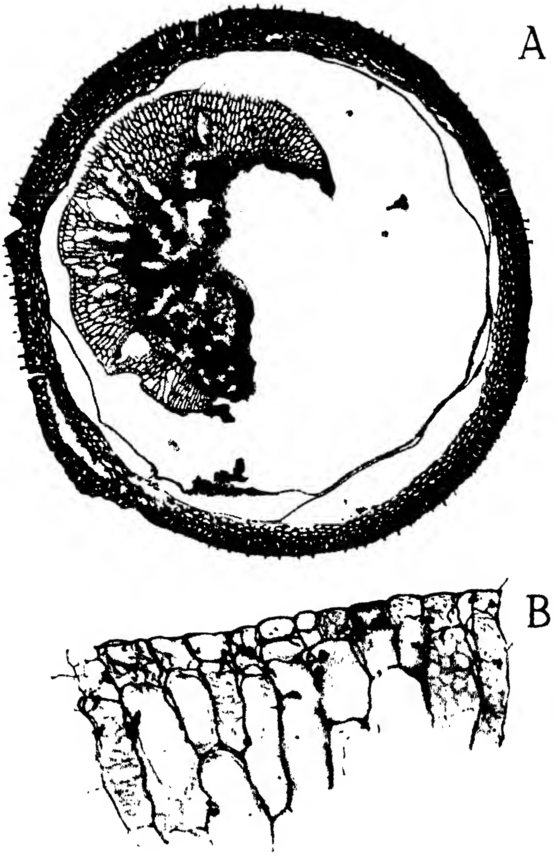

FIG. 96.—*Lagenostoma Lomaxi*. A. Transverse section of seed. The integument, remains of nucellus and megaspore membrane, and part of the prothallus. × 18.—B. Outer tissues of the prothallus. × about 190. After R. C. McLean.

of an embryo. It is probable that there was a ring of archegonia at the top of the prothallus immediately below the pollen chamber.

There is no doubt that the seed is borne on part of a leaf and

FIG. 97.—*Crossotheca Kidstoni.* Fragment of a fertile frond in an ironstone nodule. At the top the long sporangia pendent from the peltate pinnules are shown. × 3. Photo by Kidston.

it seems likely that the cupule, if not the integument as well, represents a group of modified pinnules. The structure of the seed is, however, very advanced and is completely gymnospermous in character.

The pollen-producing parts of *Calymmatotheca Höninghausi* have not been as yet discovered. A frond now called *Crossotheca Kidstoni* was at one time thought to be its pollen-bearing frond. This frond, found at a somewhat higher geological horizon, is closely similar to the frond of *Calymmatotheca Höninghausi* and it is probable that eventually the latter will be found to bear pollen-bearing structures like it.

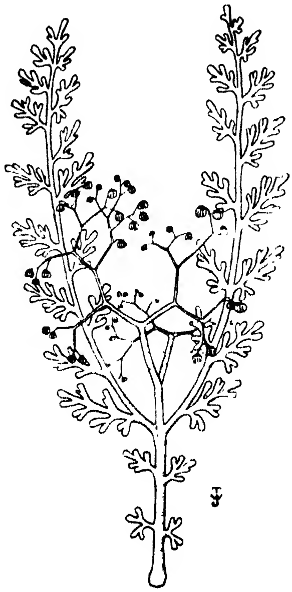

FIG. 98.—*Diplopteridium teilianum.* Reconstruction of a complete frond with fructifications of the *Telangium* type. About ⅓ nat. size. Walton, 1931.

Crossotheca Kidstoni (Fig. 97) has fertile pinnules which are in the form of small, almost peltate oval structures. They are traversed by a vein which branches in the rather thick lamina. From one surface project six bilocular sporangia. Each bilocular sporangium ends in a sharp point, is about 3 mm. long and 1.5 mm. in diameter at its widest part, and has no annulus.

Similar sporangia are found in other Carboniferous plants. In a form known as *Telangium* the bilocular sporangia are closely grouped together in synangia borne on small peltate discs. The frond of *Diplopteridium* (Fig. 98), which bore synangia of the *Telangium* type, forks into two equal parts as in many Pteridosperm fronds. The synangial discs are borne on a slender rachis with wide-angled forkings which is attached in the angle of the main fork of the frond. Most specimens of *Diplopteridium* have no fertile rachis in this position but a few have been found with a short stump in the angle of the main fork. This stump may represent an aborted fructification. Fronds with a forked main rachis are frequent in the Carboniferous. It is possible that their pollen-bearing parts were placed as in *Diplopteridium* but became detached before the vegetative part of the frond matured. This might account for the fact that pollen-bearing fructifications have never been found connected to the frond of *Calymmatotheca*, *Heterangium*, or any other Pteridosperms in which the frond forks in this manner.

Heterangium.—This genus, which occurs in Upper and Lower Carboniferous beds, is closely related structurally to *Calymmatotheca Höninghausi*. *Heterangium Grievii*, the oldest and best known species, is of Lower Carboniferous age and has been found in the form of compressions and petrifactions. Several other species are known, some of them intermediate in character between *H. Grievii* and *Calymmatotheca Höninghausi.*

Heterangium Grievii.—This plant was similar in habit to *Calymmatotheca Höninghausi.* The largest stems are 4 cm. in diameter and only one branching specimen is known (Fig. 99). The leaves were similar in general form, the rachis forking into two equal parts in the middle, but there were no lateral pinnae below the fork. The foliage has usually been called *Diplotmema adiantoides* and, judging from the number of specimens that have been found, the plant must have been abundant towards the close of the Lower Carboniferous.

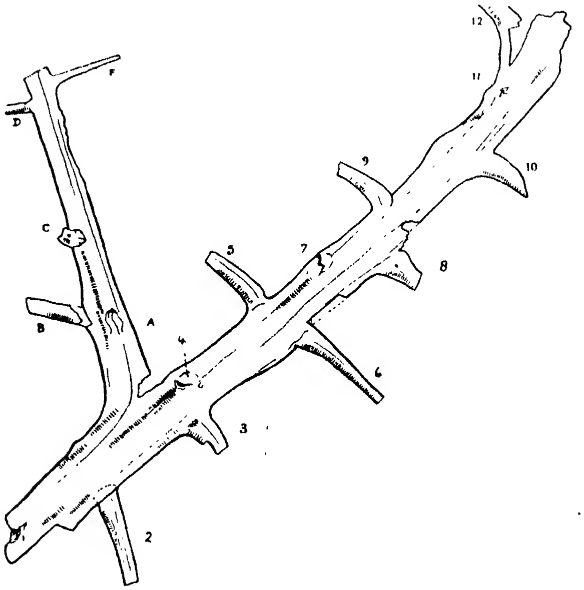

FIG. 99.—*Diplotmema adiantoides* (=compressions of *Heterangium* stems and foliage). Outline drawing of branching stem showing 17 petiole bases (1-12 on main axis and *A-E* on lateral branch). Petioles 7, 11, *A*, and possibly 1, are attached to the far side of the axis. Nat. size. Upper Limestone group, Carboniferous, Cuthill, East Lothian. Hunterian Museum, Glasgow Univ., Pb. 1810.

The stem has ridges formed by the decurrent bases of the leaves. In section (Fig. 100) the outer cortex is seen to contain small longitudinal ribs of sclerenchyma (*oc*), which in compressions of the stem show through as coarse longitudinal striations. The wide inner part of the cortex consists for the most part of parenchyma, but embedded in it are series of horizontal plates of stone cells. In compressions these show through the surface as transverse ridges. These ridges are a characteristic feature of the compressions of both stems and fronds.

The vascular column consists of a central mass in which there are numerous strands of tracheids separated by bands of parenchyma. The primary strands (Fig. 101), which are situated in the peripheral part, have the same structure as those of *Calymmatotheca Höninghausi*. In *Heterangium* there is thus a solid stele of tracheids mixed with parenchyma in contrast to the medullated type in *Calymmatotheca*. In *Heterangium* the leaf trace as it leaves the stele contains one protoxylem, which divides into two almost at once, but the strand as a whole does not divide into two separate strands. The leaf is therefore supplied by a single strand.

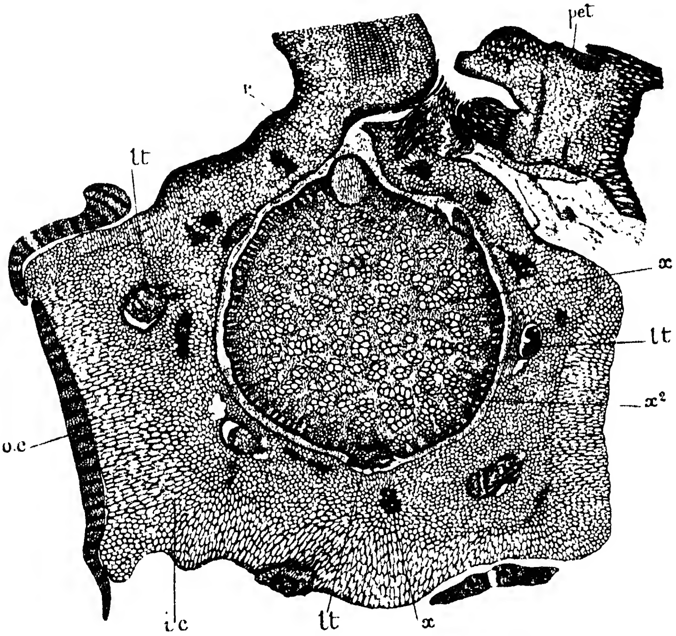

FIG. 100.—*Heterangium Grievii*. Transverse section of stem. *x*, central mass of primary wood consisting of tracheids and parenchyma; *o.c*, outer cortex with fibres; *i.c*, inner cortex with plates of stone cells and leaf traces (*l.t.*); x^2, thin layer of secondary wood. The base of a petiole is shown at *pet.* and a root at *r*. × about 5. After Scott.

The roots are usually provided with three protoxylems but the small roots may have only two.

The fructifications are not known but a seed called *Sphaerostoma ovale* is commonly found associated with the remains of

Heterangium. This seed bears a general resemblance to *Lagenostoma* and is quite likely the seed of *Heterangium.*

The plant evidently compares closely with *Calymmatotheca* but is simpler and more primitive in construction. In some of the other species of *Heterangium* there is a much greater proportion of parenchyma in the centre of the stele showing an approximation to the condition in *Calymmatotheca.*

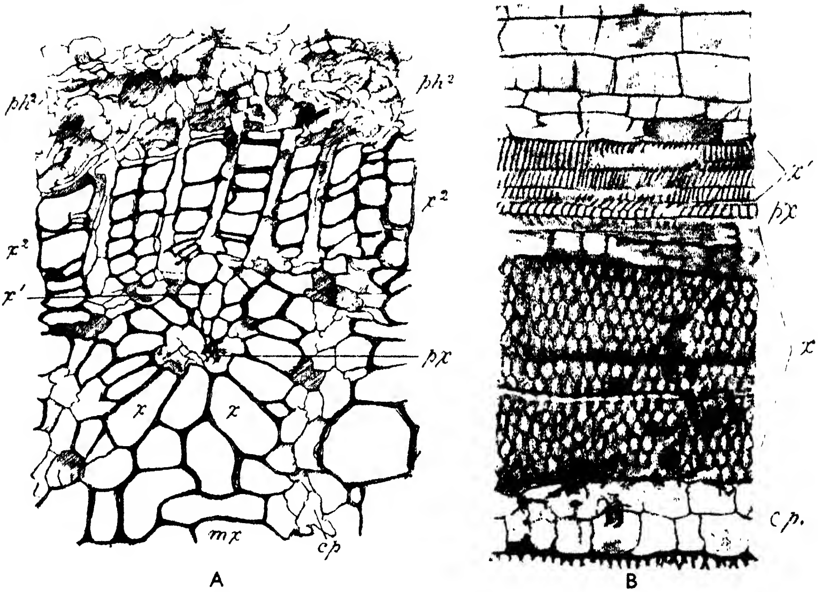

Fig. 101.—*Heterangium Grievii.* A. Part of a transverse section.—B. Longitudinal section cut through the corresponding tissues. ph^2, phloem; x^2, secondary xylem; x^1, centrifugal metaxylem; *x* and *mx*, centripetal metaxylem; *px*, protoxylem; *cp*, xylem parenchyma. × 135. After Williamson and Scott.

In *Heterangium* the central mass of the stele consists of tracheids and parenchyma, but in *Tetrastichia* a newly described Lower Carboniferous genus (Gordon, 1938) which, judging from its structure, is a Pteridosperm, the stele in section appears as a four-rayed solid mass of tracheids. The facts support the theory that in the Pteridosperms, as in so many other groups of vascular plants, there has been evolution from a solid to a medullated type of stele.

CHAPTER X

PALAEOZOIC PTERIDOSPERMAE—II: MEDULLOSEAE

AMONG the many types of Fern-like frond found in the Carboniferous and Permian there are two, *Alethopteris* and *Neuropteris*, which are very abundant. The fronds were large and compound, bi-, tri-, or sometimes quadripinnate in construction, with a length in some of 1 metre or perhaps more. The pinnules have an open Fern-like venation (Fig. 102).

The stems which bore this type of foliage are known in the form of compressions and petrifactions. The leaves were arranged in a 2/5 phyllotaxy. One of these stems, *Medullosa anglica*, which bore the *Alethopteris* type of leaf, has a complex type of vascular anatomy. An idea of its external form is given by compressions (Fig. 103). In section the stem, which attained a diameter of about 8 cm., is seen to contain three steles (Fig. 104), each closely similar to the single stele of *Heterangium*. The stem may therefore be said to be polystelic. The steles occasionally anastomose. The leaf traces are given off from the outer sides of the steles. Each leaf trace is at first concentric in structure with primary wood in the centre surrounded by secondary wood and phloem. Further out in the cortex there is no secondary wood and it divides up to form a large number of small collateral bundles (Fig. 105), each consisting of a strand of centripetal xylem with a strand of phloem. These bundles pass into the large leaf bases which cover the stem and thence into the petioles. The outer cortex of the leaf bases and petioles contains numerous slender strands of fibres, which cause the coarse striations seen on the surface of the compressions. With its numerous small vascular bundles the petiole bears a close resemblance to a Monocotyledonous stem and has indeed been mistaken for such.

Several other species of *Medullosa* have been discovered in the Permian and some of these had large upright trunks with concentric rings of steles (Fig. 106). As a result of this arrangement the secondary wood, which was formed on the outer sides of the steles, formed a complete cylinder. Such a stem could undergo continuous secondary thickening and some attained a size comparable to that of some living Conifers.

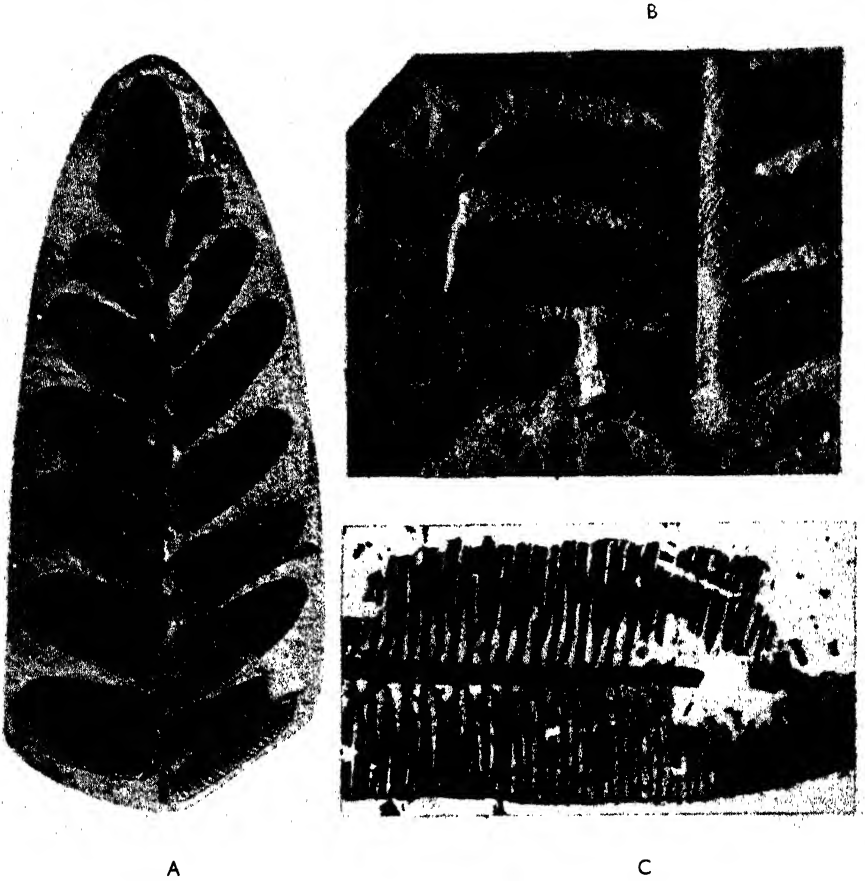

FIG. 102.—Leaves of Medulloseae. A. *Neuropteris Nikolausi*. Secondary pinna of a large frond. Sarre Coal-field, France. × 2.—B. *Alethopteris lonchitifolia*. Part of a secondary pinna. Sarre Coal-field, France. × 3.—C. Transfer of a fragment of *Alethopteris* to show venation of a pinnule. × 6. J. W. Coll. 33. A and B after Bertrand, 1932.

Fructifications of the Medulloseae.—Large seed-like bodies have been found attached to the fronds of *Alethopteris* and *Neuropteris* (Fig. 107). It is clear that in some instances these are seeds. Large seeds are frequently found associated with *Medullosa* in petrifactions and with *Alethopteris* in compressions and there is little doubt but that they are parts of the same plant. This seed, *Trigonocarpus Parkinsoni* (Fig. 108), had in its integument a thick fleshy outer region or sarcotesta, and a hard inner region or sclerotesta.

This sclerotesta was in three parts (Fig. 108, B), and in compressions, where the sarcotesta is compressed to a thin layer or in incrustations of the seeds from which the sarcotesta had been removed by decay, the seed appears to have three ridges. The pollen chamber has a complex form as in *Lagenostoma*.

A considerable number of fructifications are known which from circumstantial evidence are regarded as the pollen-producing organs of the Medulloseae. A good deal of confusion has been caused in the past from the superficial resemblance of these pollen-producing fructifications to seeds or seed cupules. Professor Halle has shown that these fructifications may be divided on structural grounds into

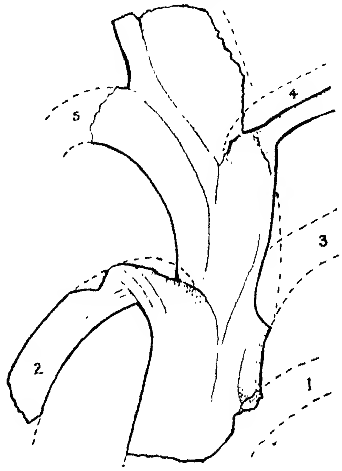

FIG. 103.—*Medullosa* sp. Outline drawing of a compression showing the stem with the bases of five petioles, 1-5. ⅓ nat. size. Westphalian Series, Alloa, Scotland. Hunterian Mus. Pb. 1811.

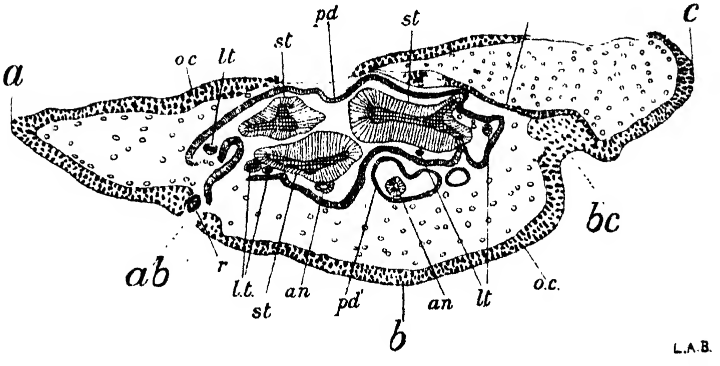

FIG. 104.—*Medullosa anglica*. Diagrammatic transverse section of stem with three leaf bases *a*, *b*, *c*. *ab* and *bc*, positions of next leaf bases higher up; *st*, steles; *l.t.*, leaf traces; *o.c.*, cortex with fibres; *pd*, periderm; *r*, adventitious root; *an*, accessory vascular strands. Slightly reduced. After Scott.

two groups: the *Whittleseyinae*, which are probably the pollen organs of plants bearing either *Alethopteris* fronds or fronds of the *Neuropteris* (imparipinnate) type, and the *Potonieineae*, which belonged to plants with the *Neuropteris* (paripinnate) type of leaf. These fructifications are only known in the state of compressions but Professor Halle (1933) removed from the rock portions which he softened and then sectioned. From the sections he was able to reconstruct the form of the fructifications (Fig. 109). These fructifications, or synangia as they may be called, consisted in the *Whittleseyineae* (*Whittleseya* and *Aulacotheca*) of a ring of long sporangia fused together to form a cup, which was attached to the plant by a stalk. The spores are large (250 μ in length) and have a broad groove down one side. In *Whittleseya* the cup has a wide opening but in *Aulacotheca*, which for many years was regarded as a seed, the opening is very narrow. In *Potoniea* the long sporangia are separately attached to the inside of a cup of sterile tissue. The spores of *Potoniea* (length 70 μ) are smaller than those of the *Whittleseyineae* and rounder. In *Dolerotheca* the synangium

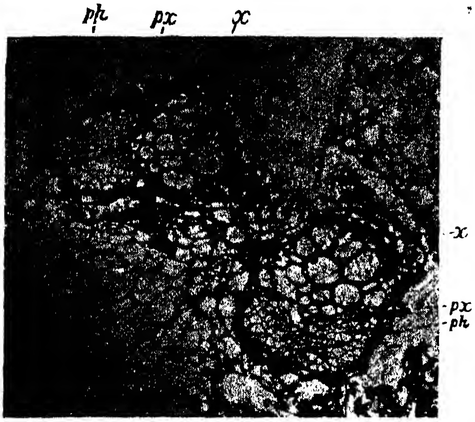

FIG. 105.—*Medullosa anglica.* Two leaf-trace bundles, in outer cortex of stem. *ph*, phloem *px*, protoxylem; *x*, centripetal xylem. × 35. After Scott.

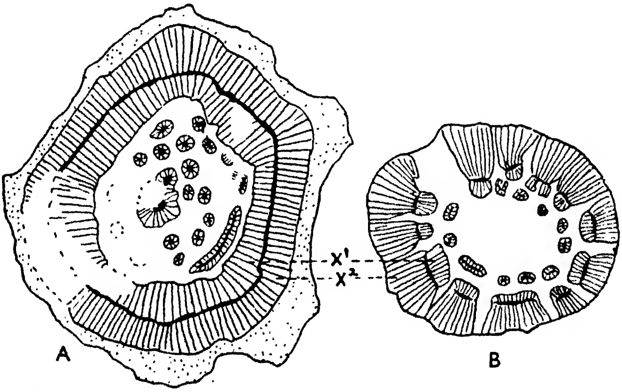

FIG. 106.—Medullosa stems. A. *Medullosa stellata.* Stem with several small steles and one large outer tubular stele. × ½ nat. size.—B. *Medullosa Solmsi.* Stem with two concentric rings of steles. ½ nat. size. X^1, inner secondary xylem of outer stele; X^2, outer secondary xylem of outer stele. The primary xylem, including protoxylems, is shown in black. A, after Cotta; B, after Weber and Sterzel.

FIG. 107.—*Neuropteris heterophylla*. Part of a frond with seed. × 2.5. Coal-measures, Staffordshire. After Halle, 1933.

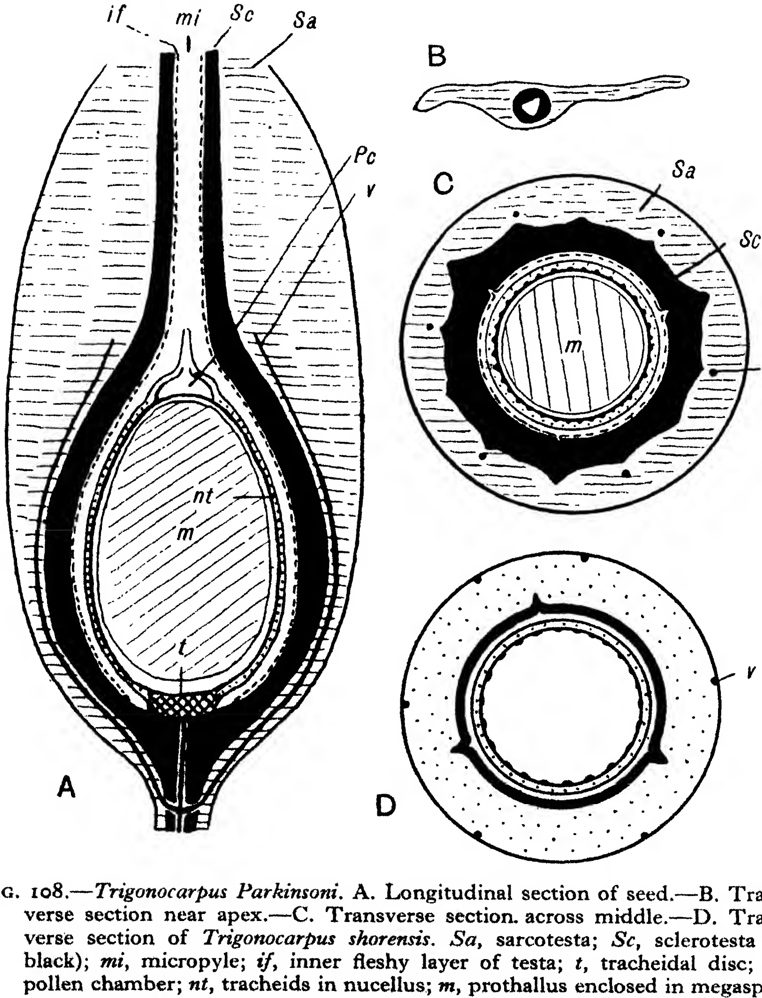

FIG. 108.—*Trigonocarpus Parkinsoni*. A. Longitudinal section of seed.—B. Transverse section near apex.—C. Transverse section across middle.—D. Transverse section of *Trigonocarpus shorensis*. *Sa*, sarcotesta; *Sc*, sclerotesta (in black); *mi*, micropyle; *if*, inner fleshy layer of testa; *t*, tracheidal disc; *Pc*, pollen chamber; *nt*, tracheids in nucellus; *m*, prothallus enclosed in megaspore membrane; *v*, vascular strand. A, C, after Scott; B, after Wild; D, after Salisbury. From Seward's *The Fossil Plants*, vol. iii. (C.U.P.).

has a similar form to that of *Potoniea* but the sporangia are embedded in a loose tissue and only their tops project. The spores are of the same type as those of *Whittleseya.*

Professor Halle (1939, p. 66) suggests that seed cupules and pollen-synangia of the Palaeozoic Pteridosperms are morphologically equivalent structures. They show radial symmetry although the evidence suggests that they are all borne on leaves.

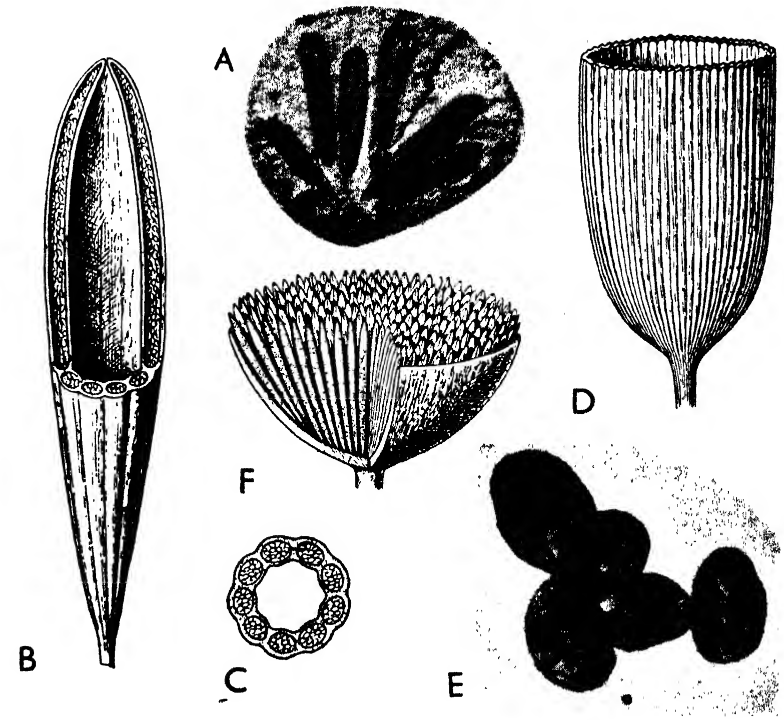

FIG. 109.—*Pteridosperm synangia.* A. *Aulacotheca Hemingwayi.* Group of synangia. ¾ nat. size.—B. *Aulacotheca oblonga.* Reconstruction of synangium with part removed.—C. Transverse section of synangium shown in B.—D. Reconstruction of synangium of *Whittleseya elegans.* About nat. size.—E. Spores of *Whittleseya.* × 56.—F. Reconstruction of synangium of *Potoniea adiantiformis.* × 2¼. All after Halle, 1933.

He supposes that they are formed by the inrolling of part of a leaf consisting of several pinnules, sterile in the case of a cupule but with long terminal sporangia in the case of a synangium (Fig. 111). This theory accounts very well for cupules, integuments, and synangia of the *Whittleseya* and *Aulacotheca* type.

Further evidence in favour of this theory is provided by a recently discovered fructification to which the name *Calathospermum scoticum* is given. A number of specimens was found in beds of volcanic origin in the Kilpatrick Hills in Scotland. The beds are of Lower Carboniferous age. *Calathospermum* may be described as a large radially symmetrical stalked cupule with six segments (Fig. 110). The largest specimens are about 6 cm. long and 3 cm. in diameter at the widest part. Each segment has from four to six vascular strands, which unite at the base of the cupule. The stalk has a crescentic vascular strand, which suggests that it is part of a leaf rachis. In several of the specimens there are a number of stalked seeds attached to the base and lower part of the cupule inside. The stalks of the outer seeds are attached to the edges of the segments of the cupule and may therefore be regarded as marginal. Each of the enclosed seeds has a pollen chamber surmounted by a nucellar tube somewhat similar to that of *Trigonocarpus*. The integument, however, has numerous vascular strands, which pass out into long narrow projections. There are usually nine of these projections to each seed. Comparison may be made with *Lagenostoma* in which there are nine lobes at the apex of the integument.

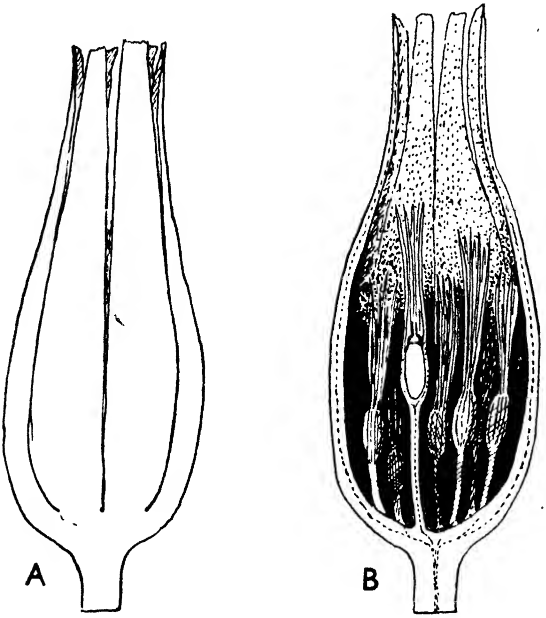

FIG. 110.—*Calathospermum scoticum*. A. External view of a cupule. About nat. size.—B. Cupule cut lengthwise to show enclosed seeds. About nat. size.

In the majority of cupules which have been sectioned there are no seeds but only long vascular stalks extending to the top of the cupule. The ends of these stalks appear to be shrivelled. These facts suggest that the seeds were extruded at a later stage in their development from the cupule by the elongation of their stalks.

Calathospermum may be taken as an ancestral type from which we may imagine other types of fructification to have arisen. If the number of seeds were to be reduced to three or four, a cupule and seeds similar to the Upper Carboniferous *Gnetopsis* would result. If only one seed were developed, a cupule and seed not unlike *Lagenostoma* would be formed. If in the place of stalked ovules long microsporangia were formed, we would have a synangium of the *Potoniea* or *Dolerotheca* type. If the segments of the cupule were fertile a *Whittleseya* or *Aulacotheca* type of synangium would be produced.

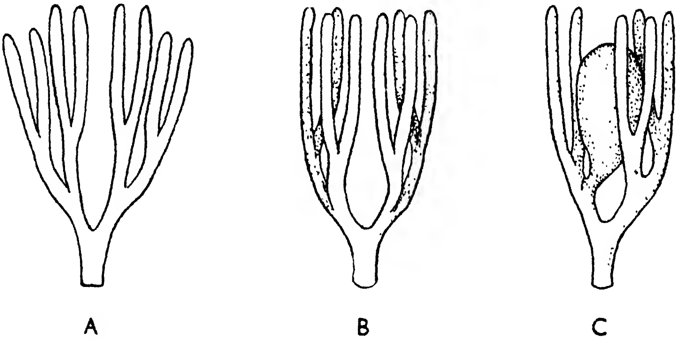

Fig. 111.—Diagram to illustrate the theory of the evolution of a cupule or microsporocarp, B, and an ovule, C, from a part of a segmented leaf, A. Concrescence of the segments in B would give rise to a cupule or, if fertile, to a fructification like *Whittleseya*. In C one of the segments bears a megasporangium, and concrescence would result in an ovule.

From a comparison between the vascular anatomy of *Lyginopteris*, *Heterangium*, and *Medullosa* it is clear that they have several important features in common. Besides *Calymmatotheca*, *Neuropteris*, and *Alethopteris*, which are known to be Pteridosperms from the fact that they have been either found to bear seeds or belong to the stems mentioned above, there are other Fern-like fronds which are also probably Pteridospermous. Several Sphenopteris and Pecopteris types of fronds have been found with seeds attached to them. The form-genera *Mariopteris*, *Lonchopteris*, *Odontopteris*, and *Callipteris* (a Permian genus) are also probably the leaves of Pteridosperms. *Callipteris*, like several other Permian fronds, has a relatively thick cuticle, a feature which is found in many of the Mesozoic Pteridosperms.

CHAPTER XI

THE GLOSSOPTERIS FLORA AND MESOZOIC PTERIDOSPERMAE—I

THE Lower Carboniferous floras which are found in Europe, North and South America, Greenland, Spitsbergen, and Australia are very much alike in composition. The Upper Carboniferous and Lower Permian floras of North America and Europe are again alike in character with many of the same or closely related species. Our knowledge of the flora of the Upper Carboniferous of these two regions, which probably grew under warm conditions, is based largely on the fossils found in their extensive coal-measures.

The Upper Carboniferous and Lower Permian of India, Australia, South Africa, South America, and Antarctica have, however, a completely different flora from that of the North American and European areas, and there is in these southerly parts of the world clear evidence of an extensive glaciation known as the Permo-Carboniferous Ice age. Closely succeeding these glacial beds, and in South Africa actually interbedded with them, are strata which contain a flora in which the most abundant fossils are leaves which have been named *Gangamopteris* and *Glossopteris*. *Gangamopteris* is found in the lower beds and *Glossopteris* in the higher beds of the series. This flora is frequently called the Glossopteris Flora. *Gangamopteris* and *Glossopteris* are tongue-shaped leaves with reticulate venation. In *Glossopteris* there is usually a fairly definite midrib (Fig. 112). In *Gangamopteris* the central veins are more widely spaced but in both the lateral veins form a reticulum. The stems (*Vertebraria*), to which in a few cases the leaves have been found attached, possessed secondary wood with multiseriate pitted tracheids and parenchymatous medullary rays (Walton and Wilson, 1932). Small seeds are often found associated with the leaves and it is probable that *Glossopteris* and *Vertebraria* are parts of seed plants.

The remarkable difference between the Glossopteris Flora and the contemporary flora of Europe and North America and the almost constant relation of the former to evidence of glacial conditions has led to the view that the Glossopteris Flora grew in a cold climate. In Rhodesia a mixture of the two floras has been found (Walton, 1929).

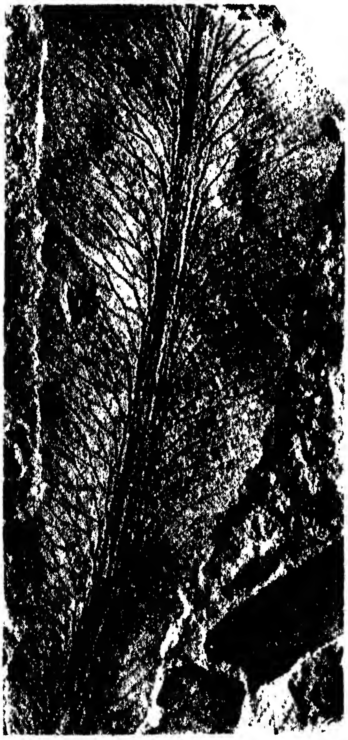

FIG. 112.—*Glossopteris Browniana.* Middle part of an *impression* of a tongue-shaped leaf. × 2. After Walton, 1929.

MESOZOIC PTERIDOSPERMS.—In the genera *Thinnfeldia*, *Dicroidium*, *Pachypteris*, and *Lepidopteris* are included a number of types of leaves of Triassic, Rhaetic, and Jurassic age which, although Fern-like in outline, have cuticles which show that they are not true Ferns. Some of these have been proved to belong to seed plants which may be placed provisionally in the Pteridospermae until more is known of their structure.

Peltaspermaceae.—*Lepidopteris*, a Rhaetic and Triassic genus, has bipinnate fronds similar in general form to the fronds of some of the Palaeozoic Pteridosperms. They were, however, smaller (Fig. 113, C), rarely exceeding 30 cm. in length. Associated with *Lepidopteris* leaves in beds of Liasso-Rhaetic age in East Greenland, Professor Harris (1932) has discovered microsporophylls and peculiar peltate seed-bearing structures which in their cuticular structure resemble them closely. It is clear that they are parts of the same kind of plant. The microsporophylls (Fig. 113, A) have a main rachis with alternate left- and right-hand branches. Each branch is forked into several smaller branches all of which, however, do not lie in the plane of the main axis and its laterals. The ultimate branches bear two short rows of pollen sacs at their ends. The pollen sac is about 2 mm. long and 1 mm. wide and apparently dehisced by a longitudinal slit along one side. The pollen grains are oval and about 30 μ long.

The seeds are borne on the lower surface of a peltate structure. They were ovate and about 7 mm. long. The testa is prolonged into a curved beak, which formed the micropylar canal. Oval pollen grains similar to those found in the microsporangia are found inside the nucellus, which must therefore have had some form of pollen chamber. In Natal Dr. Hamshaw Thomas has found *Lepidopteris natalensis* fronds associated with a fructification with the same cuticular structure. The peltate heads, of somewhat similar form to those from Greenland, are arranged spirally on a slender axis (Fig. 113, B). Several seeds were borne on each head but only one appears to have attained maturity.

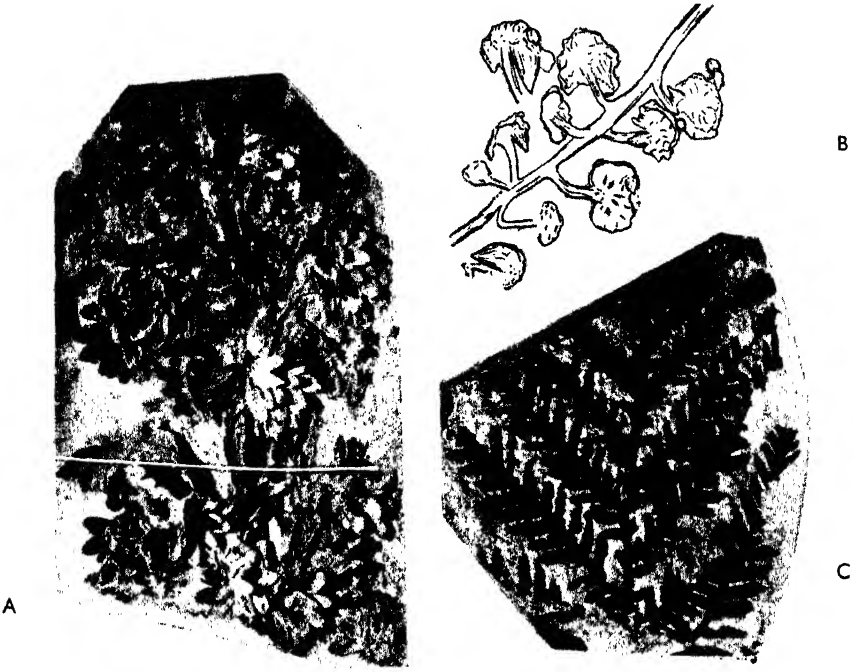

FIG. 113.—*Lepidopteris*. A. Transfer of part of microsporophyll of *L. ottonis*. × 2.—B. Seed-bearing part of *L. natalensis*. × 2.—C. Part of leaf of *L. ottonis*. About ¾ nat. size. A and C after Harris (1932); B after Thomas (1933).

In the form of the leaves and the microsporophyll *Lepidopteris* shows a general resemblance to the Pteridosperms. The radial arrangement of the peltate heads on an axis suggests a comparison with the seed cone of a Cycad and the peltate heads may be compared with everted cupules. Radial construction is characteristic of stems and not often found in leaves or sporophylls. If this seed-bearing fructification is axial it is different from anything hitherto found in the Pteridosperms. The seed cupules of the Pteridosperms, judging from their relation to the rest of the plant, were borne on fronds or leaves. It may be argued, however, that the leaves of all megaphyllous plants are merely just specialised branches of an ancestral thallus, in which case the seed fructification of *Lepidopteris* and the seed-bearing frond of the other Pteridosperms may be morphologically comparable.

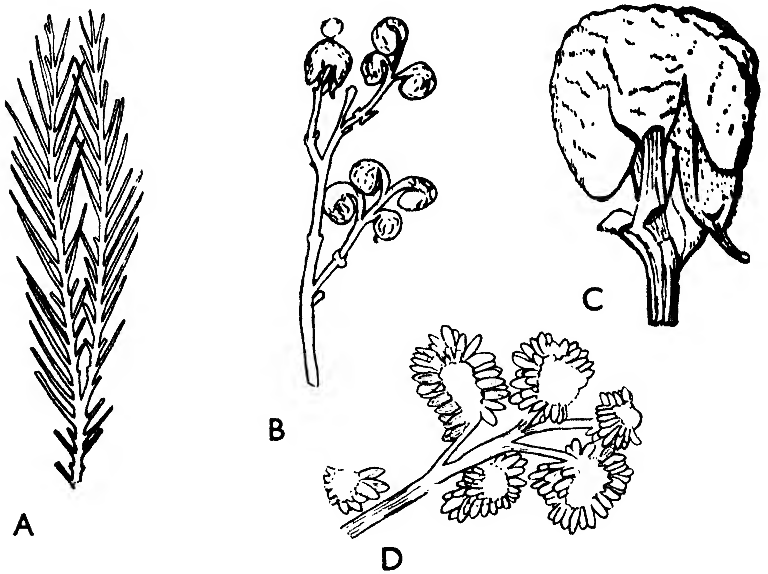

FIG. 114.—*Corystospermaceae*. A. Stenopteris. A frond. ½ nat. size.—B. *Umkomasia Macleani*. Inflorescence. Nat. size.—C. *Umkomasia Macleani*. Cupule with seed and projecting micropyle. × 5.—D. *Pteruchus africanus*. Part of microsporophyll. × 1·5. All after Thomas, 1933.

Corystospermaceae (genera—*Dicroidium*, *Stenopteris*, *Umkomasia*, *Pilophorosperma*, *Spermacodon*, *Pteruchus*).—Our knowledge of this family is due to Dr. Thomas (1933), who has described fructifications and leaves from Triassic beds in Natal. It is clear from a comparison of the cuticular and stomatal structure that leaves and fructification are parts of the same or closely allied species.

The leaves belong to the form-genera *Dicroidium* and *Stenopteris* (Fig. 114) and are Pteridospermous in character.

Umkomasia. This is an inflorescence consisting of an axis (Fig. 114) bearing occasional opposite pairs of small bracts. The lateral branches are in one plane and arise in the axils of bracts. The distal part of each branch forks into smaller branches which terminate in recurved cupules. The cupule is divided by two clefts which lie on opposite sides of the cupule in the plane of the axis. Each cupule contains a seed which has a long curved micropyle. In the closely related *Pilophorosperma*, of which eight species have been found, the cupule has only one cleft at the side of the stalk. In the third genus, *Spermacodon*, some of the branches are spirally arranged on the inflorescence axis. Pollen grains have been found in the nucellus of a detached seed belonging to one of these genera. This pollen is like that found in associated pollen-bearing fructifications which Dr. Thomas has named *Pteruchus*.

Pteruchus (Fig. 114), which, judging from cuticular structure, is probably the microsporophyll of one of the preceding form-genera of the Corystospermaceae, bears terminal expansions on which the pollen sacs are borne. If these fructifications had been found in the Carboniferous they would probably have been called *Crossotheca* so closely do they resemble that form-genus in general features. The pollen sacs vary from 1 to 4 mm. in length. The pollen is quite different from any other type of known Pteridosperm pollen. Each grain has a central cell with a hemispherical bladder-like extension of the wall on each side. The grain is therefore somewhat like a pollen grain of the Pine but the bladders are on exactly opposite sides of the grain.

In the curved form of the micropyle the Corystospermaceae compare with the Peltaspermaceae and the peculiar type of pollen is also found in the Caytoniales, a group of Jurassic seed plants of which an account will be given next. In the form of associated leaf and microsporophyll they compare most closely with the Palaeozoic Pteridosperms.

CHAPTER XII

MESOZOIC PTERIDOSPERMAE—II: CAYTONIALES

(GENERA—*Sagenopteris*, *Gristhorpia*, *Caytonia*, *Caytonanthus*)

IN the year 1925 Dr. Hamshaw Thomas brought to the attention of botanists a group of seed plants from the Jurassic of Yorkshire which presents some remarkable features. From constancy of association and similarity of cuticular structure he was able to show that certain leaves, microsporophylls, and seed-bearing organs belonged to one and the same type of plant. The material found was all in the form of compressions but by chemical treatment the coaly material of the fruits was softened and microtome sections were cut. A great deal of microscopical detail was visible. The leaves, which had been known previously by the name *Sagenopteris Phillipsi* (Fig. 115), are compound. The leaflets, which are lanceolate and vary from 2 to 6 cm. in length, are borne palmately in a group of from 3 to 6 at the upper end of a slender petiole. The venation of the leaflet is reticulate.

The microsporophylls (Fig. 116), called *Caytonanthus* (=*Antholithus*) *Arberi*, were pinnately branched, and judging from the cuticular structure were dorsiventral. The lateral branches are short and repeatedly and irregularly forked, the ultimate divisions each bearing several synangia. Each synangium has four loculi or pollen sacs, which contained winged pollen grains (Fig. 115, F) of the same form as those found in *Pteruchus*.

The same kind of pollen grain has been found adherent to the stigmatic region of certain seed-bearing fructifications to which Dr. Thomas gave the name *Gristhorpia*. The axis of this fructification is pinnately branched (Fig. 116, A) and shows the same indications of dorsiventrality as *Caytonanthus*. It may therefore be regarded as a megasporophyll. Each branch terminates in a small nearly spherical body which may be regarded as a recurved cupule, which is so recurved that the seeds are completely enclosed (Fig. 116, B, C). There is, however, a small flap of tissue close to the stalk which no doubt represents the free edge of the cupule. The flap surrounds a small depression. The cupule contained from 10 to 12 seeds which were orthotropous and presumably attached to the inside of the fleshy cupule. Sections reveal the fact that there was no free opening to the outside, although there might have been one at an earlier stage of development. Pollen grains are found on the flap, which was therefore of the nature of a stigma. A closely allied type of megasporophyll, *Caytonia Sewardi*, was also found by Dr. Thomas. In it the seeds were borne in two parallel rows inside the cupule. In another species, *C. Thomasi*, from Greenland, Professor Harris (1933) has shown that the pollen reached the micropyles of the

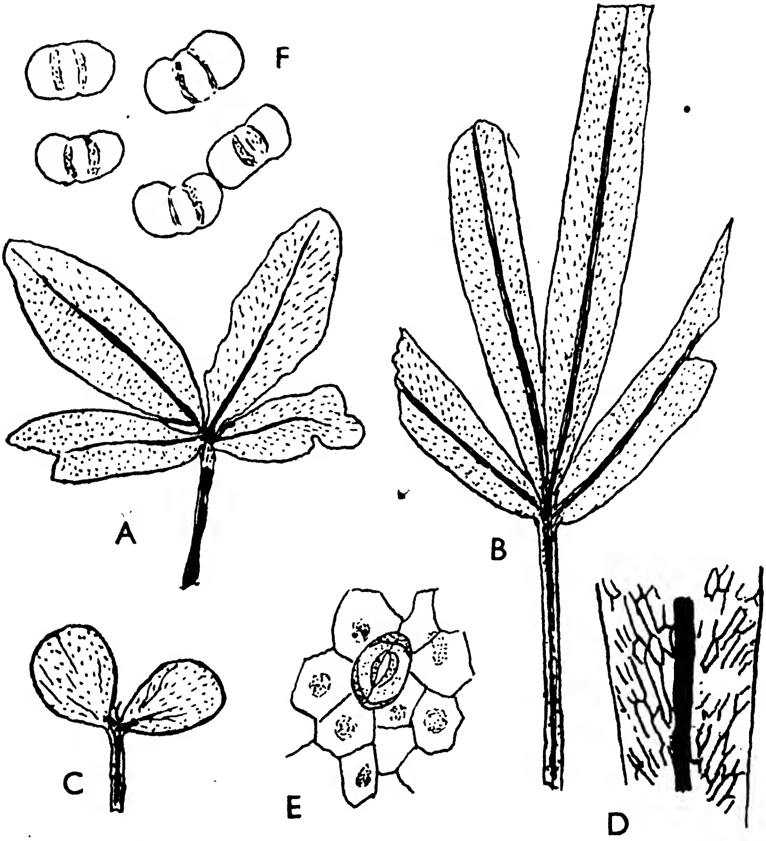

FIG. 115.—Foliage and Pollen of Caytoniales. A, B, C. *Sagenopteris Phillipsi*. ⅔ nat. size.—D. Part of leaf to show venation. × about 3.—E. Piece of cuticle with stoma of *Sagenopteris Hallei*. × about 130.—F. Pollen grains from *Caytonanthus*. × 300. A, B, C after Seward ; D after Thomas; E, F after Harris.

seeds so that there must have been open channels from the flap down to the seeds inside the cupule.

Perhaps the most interesting feature in some species of the Caytoniales is the closed form of the cupule. This condition is nearly comparable to what is found in the Angiosperm ovary, where the pollen is deposited on a stigma and fertilisation is effected by the growth of the pollen tube through the tissues of the carpels. It has been suggested that the Caytoniales may represent a starting point from which the evolution of the Angiosperms started. The reduction of the *Gristhorpia* type of megasporophyll to a single cupule would produce something comparable to an Angiosperm carpel. The quadrilocular synangia of *Caytonanthus* are comparable to anthers and the form of the leaf is not unlike that of some Dicotyledons. Whatever may be the relationship of the Caytoniales to the Angiosperms, there is no doubt that they are closely allied to the Pteridosperms. This attainment of Angiospermy in the Pteridosperm line may be regarded as an achievement comparable in importance to the attainment of the seed habit in the Lycopodiales. It is not generally accepted that any group of the Gymnosperms were derived from the Lycopodiales and it may be regarded as doubtful that

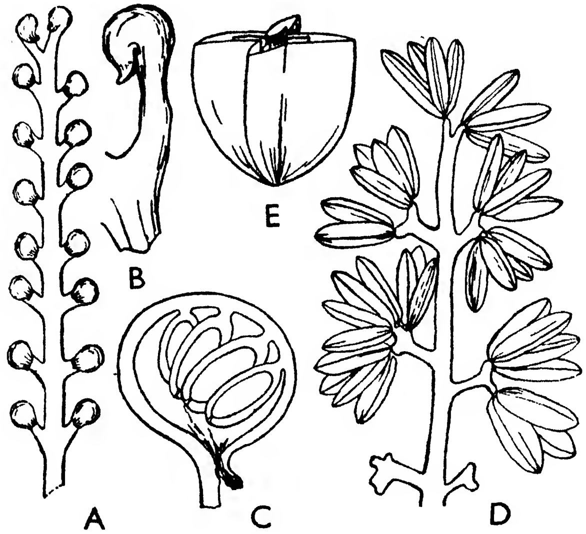

FIG. 116.—Fructifications of Caytoniales. A. Megasporophyll of *Gristhorpia*. Nat. size.—B. One seed-bearing cupule of *Gristhorpia*. × 8.—C. Longitudinal section of cupule and seeds of *Caytonia*. × 3·5.—D. Part of microsporophyll of *Caytonanthus*. × 2·5.—E. Part of a single anther showing the four lobes. × 8. All after Thomas, 1925.

the Caytoniales were the ancestral group from which the Angiosperms originated. However, there is no doubt that among the Pteridosperms, Bennettitaleans, and Caytoniales, which are no doubt interrelated groups, we can pick out features from which an Angiosperm might theoretically be constructed. Our knowledge of Carboniferous and Mesozoic seed plants is very meagre and at present discussion of the origin of the Angiosperms can only be highly speculative.

CHAPTER XIII

CORDAITALES

THIS group of Gymnosperms appears to have existed from about the close of the Lower Carboniferous and to have persisted into the Permian and perhaps even into the Triassic. The best known genus, *Cordaites*, was an important constituent of some of the Upper Carboniferous forests.

Cordaites.—Under this name are included remains of probably a large number of species which show a general similarity in the form of leaf and vascular anatomy.

The plants which are included in this genus were trees, some attaining a height of 30 metres (Fig. 117). The trunks were columnar and bore a crown of branches to which long strap-shaped leaves were attached. The leaves in some species are as much as 15 cm. broad and more than 1 metre in length. In others the leaves were much narrower. The veins are closely set and parallel, giving the leaf a distinctly Monocotyledonous appearance. In a transverse section of the leaf (Fig. 118) each vein is seen to have a single protoxylem with some centripetal metaxylem. Separated from the protoxylem on its abaxial by some parenchyma are a few small tracheids which represent centrifugal metaxylem. The lamina is strengthened by longitudinal ribs of sclerenchyma. In some species the vein is situated in a rib of sclerenchyma which extends from one epidermis to the other. As regards its mechanical construction and position of the mesophyll the Cordaites leaf bears a close resemblance to the leaves of many grasses, but the construction of the xylem is like that of a Cycad, having both centripetal and centrifugal elements.

The stem (Fig. 119), which is attributed to the genus *Cordaites*, is closely comparable with that of a living Conifer. The pith, which is relatively large, is however discoid, being split up by transverse lens-shaped cavities (Fig. 120). The wood is entirely centrifugal with the protoxylems situated next to the pith. It consists of multiseriate pitted tracheids and parenchymatous medullary rays and is thus Araucarian in type. The leaf traces as in *Ginkgo* are double strands.

A large number of fossil stems with a general resemblance to the Conifer type of construction are known. In them the main bulk of the xylem is secondary. *Mesoxylon*, an Upper Carboniferous species closely allied to Cordaites, has a small amount of centripetal metaxylem between the protoxylems and the pith. *Mesoxylon* is otherwise closely similar to *Cordaites*. In *Poroxylon* (Permian) the primary strands of wood are remarkably like those of *Lyginopteris* but the leaves are of the *Cordaites* type. There is an interesting series of forms all of which may be gymnospermous plants which have the Cordaitean type of secondary wood. In *Palaeopitys* (Kidston and Lang, 1923) from the Middle Devonian there is a solid primary stele with no pith, while in Callixylon (Arnold, 1931) and Calamopitys (Scott, 1923; Read, 1937) from the Upper Devonian, and Pitys (Gordon, 1935) and Protopitys (Scott, 1923) from the Lower Carboniferous, the primary strands which have mesarch structure form an important part of the conducting system. Some

FIG. 117.—Restoration of some Cordaiteae. After Grand'Eury, from Scott. From D. H. Scott's *Extinct Plants and Problems of Evolution* (Macmillan).

of these stems show structural affinities with the Pteridosperms on the one hand and with the Cordaitales on the other.

The roots of Cordaites, which have been called *Amyelon*, are usually diarch or triarch and closely resemble those of living Conifers. The smaller roots are sometimes found to contain an endotrophic mycorrhiza.

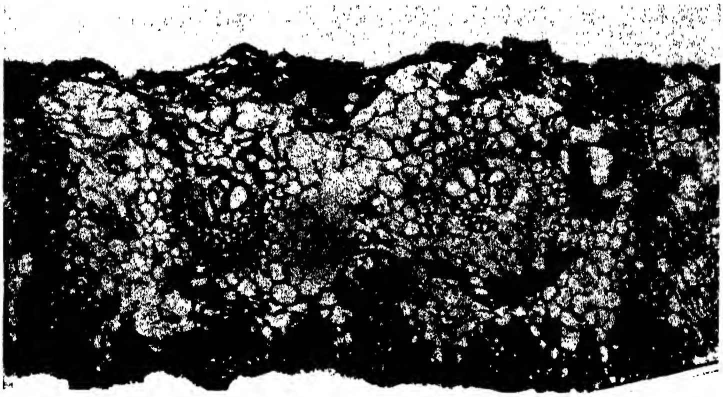

FIG. 118.—Section of a Cordaitean Leaf (*Mesoxylon*). The adaxial epidermis is uppermost. The protoxylem is near the centre of the xylem strand; above it are some large centripetal xylem elements, while below it are a few small centrifugal xylem tracheids. × 60. After Scott. From D. H. Scott's *Extinct Plants and Problems of Evolution* (Macmillan).

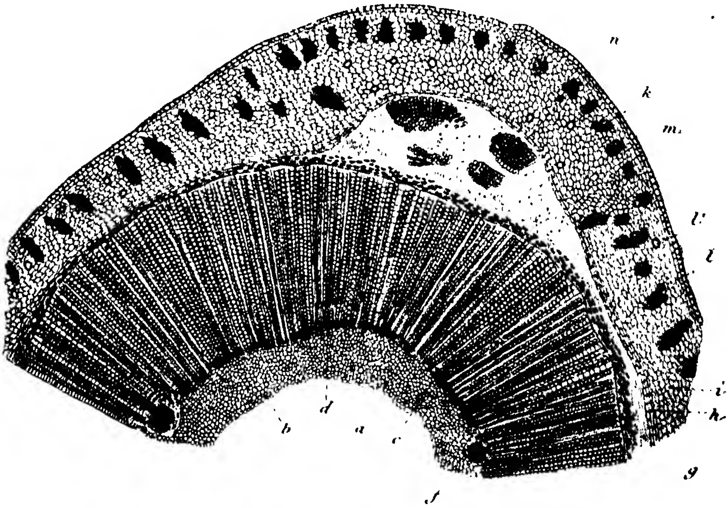

FIG. 119.—Young *Cordaites* Stem. *a*, cavity in pith; *b*, pith tissue; *c*, inner edge of secondary wood; *d*, secondary wood; *f*, primary xylem strand; *g*, phloem; *h*, layer of periderm; *i*, cortex; *l*, gum canals; *k*, strands of fibres; *n*, one of the two leaf-trace strands; *m*, epidermis. × 10. After Renault.

Fructifications of Cordaites.—The fructifications were borne on slender lateral branches (Fig. 121). Each slender branch bore a series of bud-like structures. Petrified examples of these bud-like structures have been sectioned and are found to contain either the pollen-bearing parts or the ovules (Darrah, 1940).

The microsporangia or pollen sacs are borne on slender stalks which are attached to the axis of the bud, which bears in addition a number of overlapping scales (Fig. 122). The stalks are attached to the axis in positions which suggest that they are morphologically comparable to the scales and may therefore be regarded as sporophylls. Each stalk, and there are several in each bud, bears distally one to possibly six sporangia, which split longitudinally and liberated large oval pollen grains (90 × 50 μ) in length. The bud may therefore be regarded as a staminate flower bearing sterile scales and stamens.

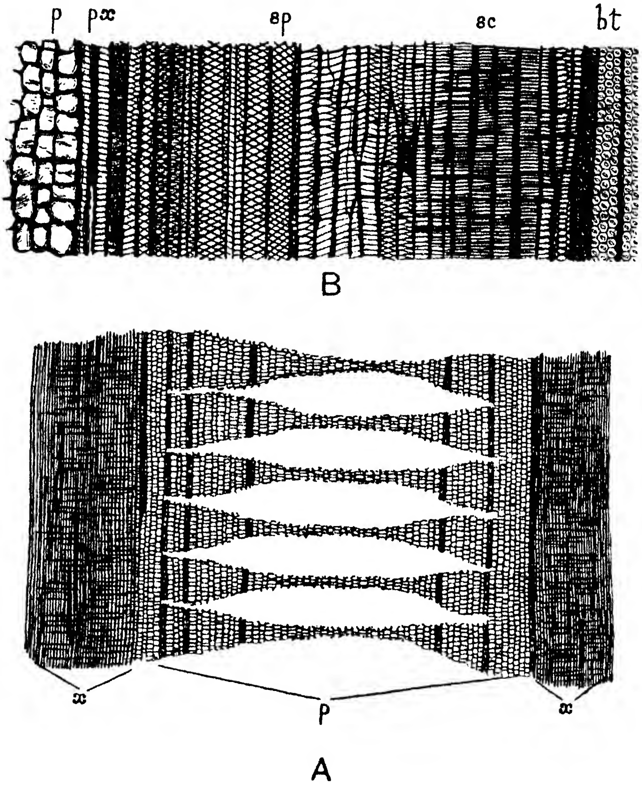

FIG. 120.—*Cordaites Brandlingii*. A. Radial section of pith *p* and wood (*x*). × about 7.—B. Part of a similar section enlarged. *p*, pith; *px*, protoxylem with narrow spiral tracheids; *sp*, metaxylem with large spiral tracheids; *sc*, scalariform tracheids; *bt*, secondary tracheids with multiseriate bordered pits. × 95. From Scott.

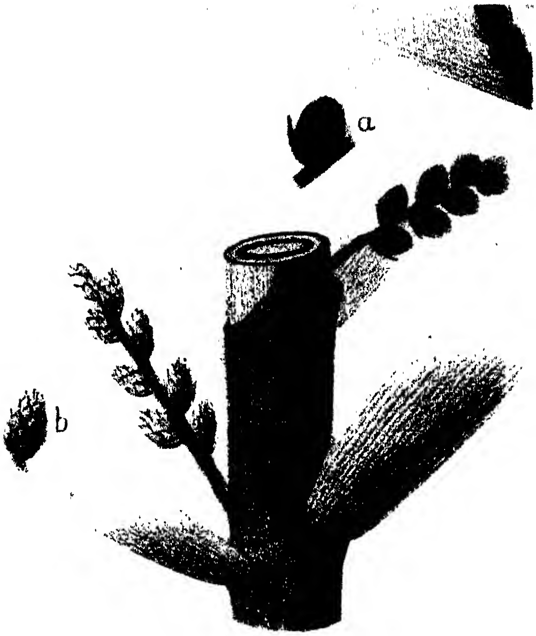

FIG. 121.—*Cordaites laevis.* Stem with bases of leaves and two inflorescences. *a*, staminate "flower"; *b*, ovulate "Flower" enlarged. After Grand'Eury. From D. H. Scott's *Extinct Plants and Problems of Evolution* (Macmillan).

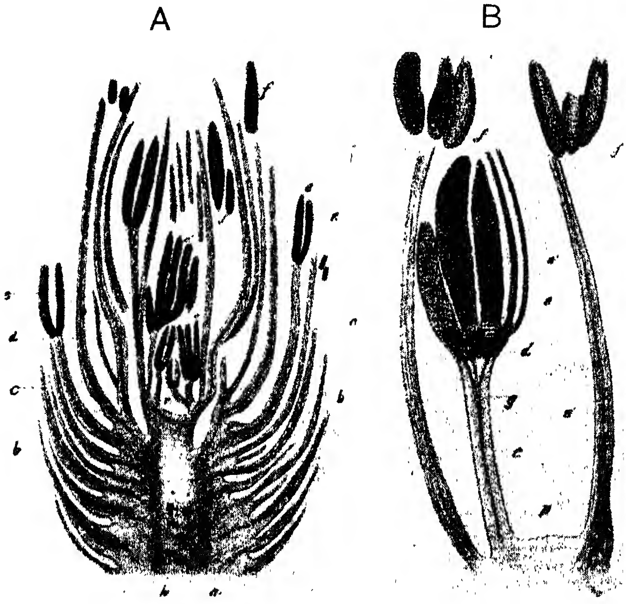

FIG. 122.—***Cordaianthus Penjoni.*** **A. Longitudinal section of a staminate "flower". × 6·5.—B. Stamens enlarged.** ***a*, axis; *b*, bracts; *c*, filament of stamen; *e*, pollen sacs. After Renault.**

The ovulate flower (Fig. 123) bore ovules on short stalks in corresponding places to the stamens in the staminate flower.

Renault, who first described these flowers, thought that the ovule was situated in the axil of a scale. This has been subsequently found to be incorrect. The ovule is flattened in a tangential direction. The integument is thick and became differentiated into an outer fleshy and an inner hard layer. The nucellus has a sunken pollen chamber surmounted by a funnel-like neck in which the large pollen grains are sometimes found lodged. Each pollen grain contains a number of cells which probably represent an antheridium. The structure of the nucellus suggests that the grains did not produce a pollen tube but that they produced motile sperms (Florin, 1936). It seems likely that *Cordaites* was, in its method of fertilisation, intermediate between the Pteridophyta and Cycads, where a pollen tube and motile sperms are found.

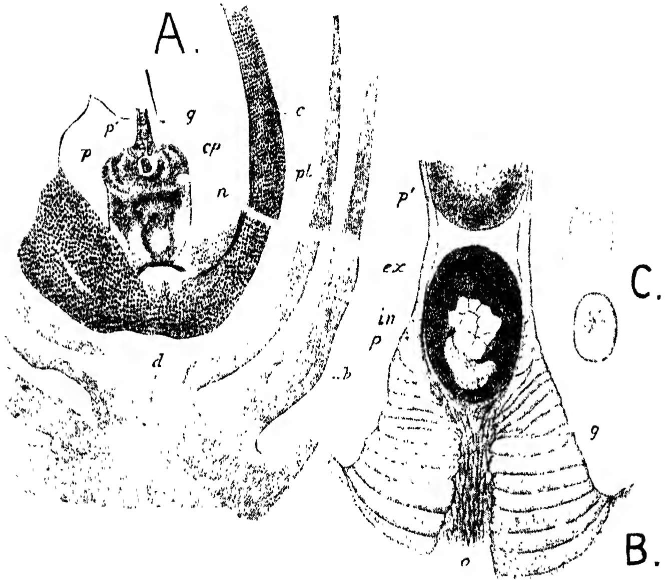

FIG. 123.—*Cordaianthus Grand'Euryi.* A. Longitudinal section through part of a "flower" showing part of the axis, some bracts, and one ovule. *d*, axis; *b*, bracts; *c*, integument; *n*, nucellus; *cp*, pollen-chamber; *g*, canal of pollen chamber, × 24.—B. Canal of pollen chamber enlarged. *g*, cells of canal; *o*, canal; *p*, *p'*, pollen-grains; *ex*, outer membrane of grain; *in*, cells of male prothallus. × 150. —C. Pollen showing prothallus cells within. After Renault.

In its structure and method of reproduction Cordaites exhibits some features which suggest a relationship to the Pteridosperms and others which are distinctly Cycadean in character.

CHAPTER XIV

GINKGOALES AND CONIFERALES

A. GINKGOALES.—The Ginkgoales to which the Maidenhair Tree (*Ginkgo biloba*) belongs became an important group during the Triassic and Rhaetic. It is possible that some of the fossil leaves included in the Palaeozoic genus *Psygmophyllum* may be Ginkgoalean but there is no doubt that the Mesozoic *Ginkgoites* and *Baiera* (Fig. 124) are leaves of plants closely related to the living *Ginkgo*. *Baiera* is like a somewhat deeply divided *Ginkgo* leaf and

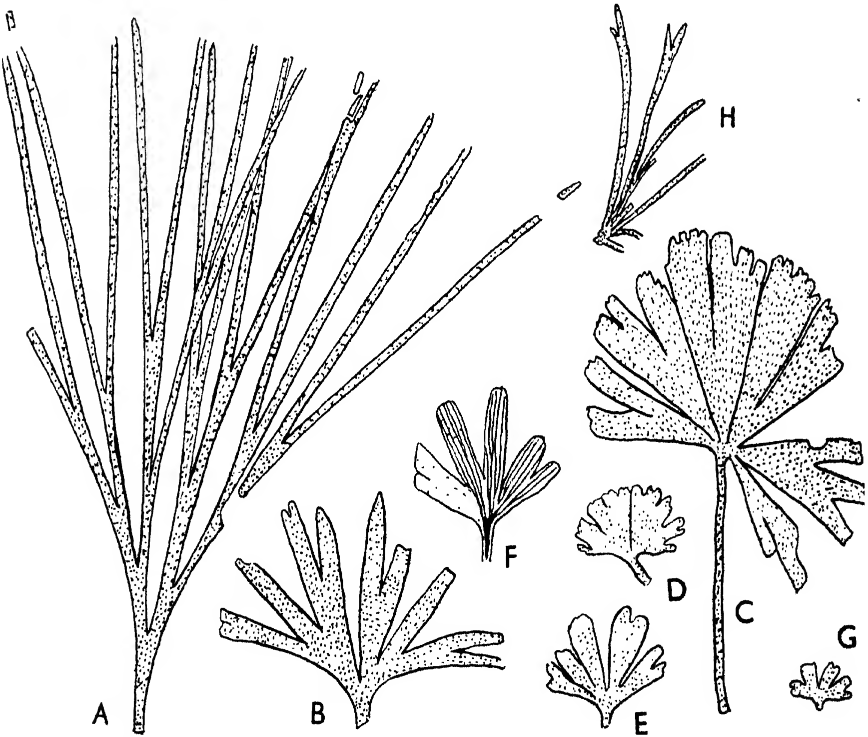

FIG. 124.—Ginkgoalean leaves from the Rhaetic of E. Greenland. A. *Baiera spectabilis*.—B. *Ginkgoites taeniata*.—C, D, E, F, and G. *Ginkgoites acosmia*.—H. Spur shoot of *Hartzia tenuis*. All ⅔ nat. size. After Harris, 1935.

is common in Rhaetic rocks. *Ginkgoites* is more like the living type. Many species of *Ginkgoites* and *Baiera* have been described but it is a remarkable fact that almost as wide a range of leaf-form may be found on a single individual of *Ginkgo*. The cuticular and stomatal structure of these genera is closely comparable with that of *Ginkgo* and in some species of Ginkgoites there are secretory sacs between the veins as in the living species. In *Czekanowskia*, *Hartzia* (Fig. 124, H), and *Phoenicopsis*, the leaves are simple and linear and only occasionally forked but like *Ginkgo* were borne on shoots of limited growth.

No satisfactory information is available about the fructifications of the fossil Ginkgoales.

B. CONIFERALES.—It is only possible to make a very brief reference to this large and important group of Gymnosperms which, from the close of the Carboniferous, has played an increasingly important part in the vegetation of the Earth. Two Palaeozoic species will be briefly described because they throw some light on the morphology of the "cone" of the Abietineae and other existing groups.

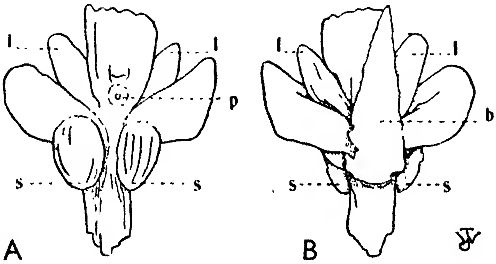

FIG. 125.—Cone Scale of *Pseudovoltzia*. A. An outline drawing of the ventral surface of the scale. *l*, *l*, the two small lobes; *s*, *s*, the seeds; *p*, scar of attachment of a third seed.—B. An outline drawing of the dorsal surface of the scale shown in A, showing the bract scale *b*. The other lettering as in A. Both drawings twice nat. size. Walton, 1928.

Walchia, an Upper Carboniferous and Permian genus, bears a close resemblance to *Araucaria excelsa* in its habit and foliage. According to Dr. Florin, the cone had spirally arranged bifurcate bracts, and short axillary shoots, with spirally arranged scales. Some of these scales bore flat (platyspermic) seeds like those of *Cordaites*. The cone therefore corresponds to the slender branch with buds which forms the inflorescence of *Cordaites*. The staminate cones of *Walchia* produced pollen similar to that of Cordaites (Florin, 1929).

In *Pseudovoltzia*, which also bore a resemblance to *Araucaria* *excelsa* in its foliage, the ovulate cones bore simple pointed bracts (Fig. 125) in the axils of which we find a relatively large five-lobed scale. At the base of the scale on either side there is a seed. There seems little reason to doubt that the five-lobed scale represents a flattened axillary branch. A further reduction in this axillary lobed scale would result in a structure with the same general form as the seed scale in *Pinus*.

The series *Cordaites*, *Walchia*, *Pseudovoltzia*, *Pinus* suggests therefore very clearly that the seed scale of the Pine and allied Conifers represents a reduced axillary branch.

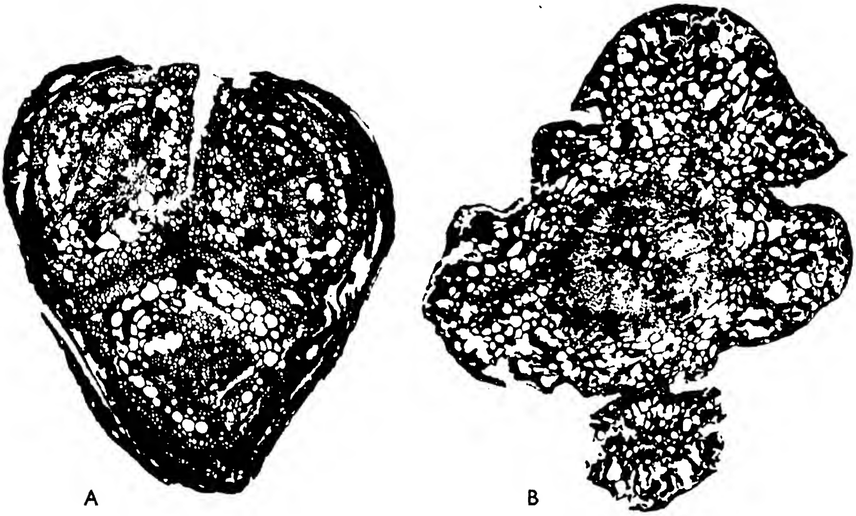

FIG. 126.—Conifers from Cretaceous Lignite; Raritan Formation, New York, U.S.A. *Microtome Sections of softened lignite*. A. *Pinus triphylla*. Transverse section of three leaves surrounded by scales of spur shoot. × 40.—B. *Widdringtonites Reichii*. Transverse section of twig with leaf bases. × 40. A and B are from Hollick and Jeffrey.

During the Mesozoic there existed many types of Conifer and among them are precursors of most of the living forms. In the Tertiary, with the exception of the Gnetales and Cycadales, most of the living families and genera of Gymnosperms have been detected. The present restricted geographical distribution of such genera as *Araucaria*, *Sciadopitys*, *Sequoia*, and *Ginkgo*, which during Cretaceous and Tertiary times were widespread over the world, suggests that these genera may be in process of extinction.

For detailed information about fossil Conifers the student should consult Seward's *Fossil Plants*, vol. iv., and *Plant Life through the Ages*.

CHAPTER XV

BENNETTITALES AND CYCADALES

A. BENNETTITALES. During the Mesozoic period Ferns and Conifers which had risen to an important position during the Palaeozoic increased in numbers and importance. The Lycopods, which were dominant during the greater part of the Palaeozoic, are of minor importance in the Mesozoic. During the Mesozoic, from the Triassic to the close of the Lower Cretaceous, by far the most important group of Gymnosperm appears to have been the Bennettitales. From the somewhat Cycad-like form of their fronds and the short stems covered with an armour of persistent leaf bases found in some genera, this group has been placed by some in the Cycadophyta. The Mesozoic has even been termed the Age of Cycads. This is wrong, for as we shall see the more important features of the group show that they are not at all closely related to the Cycads. It is true that representatives of the Cycadales are found in the Mesozoic but they evidently represent a relatively unimportant part of the vegetation.

BENNETTITALES

1. *Williamsonieae.* Flowers borne on relatively slender stems or pedicels and fully exposed.
   Genera—*Wielandiella; Williamsoniella, Williamsonia.*
2. *Bennettiteae.* Flowers on short pedicels deeply sunk among persistent leaf bases on relatively short thick trunks.
   Genus—Cycadeoidea (= *Bennettites*).

1. WILLIAMSONIEAE. *Wielandiella.*—A reconstruction of the shoot of this Rhaetic genus is given in Fig. 127. The leaves are attached in a spiral at the upper end of each part of the branching system round the base of the terminal flower. Further branching is produced in a dichasial manner from among these leaves. The leaves are of the type which has been called *Anomozamites* and are pinnate with several parallel veins in each pinna.

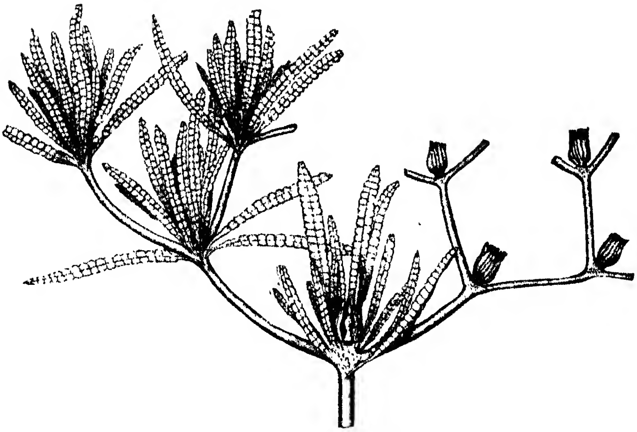

FIG. 127.—*Wielandiella angustifolia*. Reconstruction. The club-shaped floral axis is exposed in the flower above the main fork. The leaves have been removed from the right-hand branches. $\frac{1}{6}$ nat. size. From D. H. Scott's *Extinct Plants and Problems of Evolution* (Macmillan). After Nathorst.

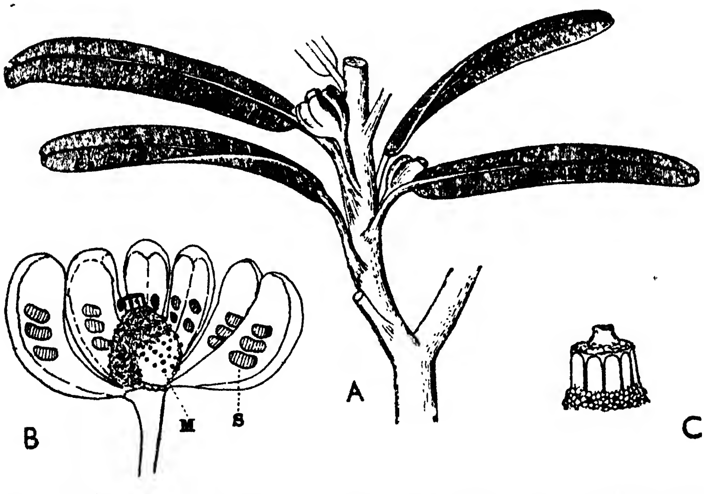

FIG. 128.—*Williamsoniella coronata*. A. Shoot with leaves of the *Taeniopteris* type and three flowers. About $\frac{2}{3}$ nat. size.—B. Flower with some stamens removed to show central axis with mass of interseminal scales forming a surface through which the micropyles (*M*) project.—*S*, synangium. About × 2.—C. Short sterile column at top of floral axis. A and C from Zimmerman; B after Thomas.

The flower, which is about the size of a *Ranunculus* flower, consists of a whorl of bracts enclosing a club-shaped axis, on which are found large numbers of small stalked ovules or seeds. The seeds are separated from one another by numerous peltate scales. The micropyles of the ovules project slightly beyond the surface formed by the heads of the scales. The structure of the seeds and these interseminal scales is better known in the petrified examples of the Bennettiteae and will be described later (p. 160). The gynoecium is, however, very uniform in structure in both divisions of the Bennettitales.

From a study of specimens from the Rhaetic of Greenland Professor Harris (1932) has concluded that the flowers which had a functional gynoecium had no pollen-producing parts. Other examples of flowers have been found in which there is a ring of synangia containing pollen at the base of the floral axis above the bracts. The flowers were therefore unisexual. No petrifactions of *Wielandiella* have been found and nothing is known about its vegetative anatomy. The cuticles of the leaves, however, have been isolated and the stomatal apparatus has a characteristic and complex form. This type of stoma is found in all the Bennettitales and differs from that of other Gymnosperms (Florin, 1931).

Williamsoniella.—*Williamsoniella* (Fig. 128), a Jurassic genus (Thomas, 1915), has a similar habit to *Wielandiella* and again our knowledge of the plant is based on compressions. The leaves of an entire form called *Taeniopteris* were arranged spirally on the stem. The flowers were bisexual. There are no floral bracts but at the base of the flower is a whorl of stamens (microsporophylls). Each stamen consists of a thick blade with a median ridge on its adaxial side, on the two sides of which pollen-producing synangia are attached (Fig. 128, B). Each synangium contained several distinct masses of pollen.

The middle part of the floral axis bore stalked seeds and interseminal scales as in *Wielandiella.* The extremity of the axis formed a short column with a number of flat facets corresponding to the number of the stamens. It is supposed that in the young unopened condition the ends of the stamens fitted tightly against these facets.

Williamsonia.—This genus has been recorded from the Upper Triassic and Rhaetic but is more abundant in the Jurassic. It differed from the preceding genera in having stouter columnar stems with closely placed pinnate leaves (Fig. 129). In appearance the plant resembled Cycas. The leaves resembled those of Zamia and left a rhomboidal abscission scar on the stem. Several types of leaf are found associated with *Williamsonia* flowers. They are of the Zamites, Otozamites, and Ptilophyllum types.

In form and structure the leaves and stem of *Williamsonia* (Sahni, 1932) closely resemble those of Cycads. The stem has a thick covering of persistent leaf bases. The pith is surrounded by endarch protoxylems and the wood is almost all secondary. Unlike the Cycads, however, the wood has less medullary ray tissue and the tracheids have multiseriate bordered pits. This type of secondary wood is more like that found in the Coniferales.

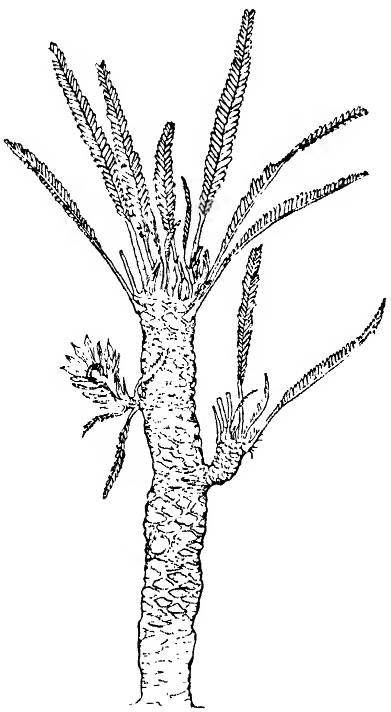

FIG. 129.—*Williamsonia Sewardiana.* Reconstruction. The trunks in this species attained a height of probably less than two metres. After Sahni, 1932.

The flowers were large (about 12 cm. in diameter in some examples) and were borne on long pedicels. The flower consisted of a large number of spirally arranged bracts which were arranged round the base of the floral axis. As in *Wielandiella* and *Williamsoniella*, the sides of the axis were covered in the middle region with ovules and interseminal scales. The apex of the axis was sterile. The androecium consisted of a whorl of pinnate or simple sporophylls joined at the base to form a cup. It is uncertain whether the flower was unisexual or not, for the staminal cups are found separate.

The group shows considerable uniformity in the type of gynoecium but the androecia show a wide range in form. It is probable that the pinnate sporophylls that are found in some forms of *Williamsonia* exhibit the primitive type as they are most leaf-like. If this is true, then we may regard the series, *Williamsonia*, *Williamsoniella*, *Wielandiella*, as representing a reduction series. In *Wielandiella* the androecium is reduced to a ring of synangia round the base of the floral axis.

2. Bennettiteae. *Cycadeoidea* (=*Bennettites*).-- This genus includes a number of species which bear a most remarkable resemblance in their trunks and leaves to those living Cycads which have short thick trunks. Their flowers and fruit are, however, quite different from anything found in the Cycadales, and presumably the same type of trunk and leaf has evolved separately in the two groups. Our knowledge of the genus is based principally on a large number of petrifactions, some of them of almost complete plants, which were found in Jurassic or Cretaceous strata in Dacota, U.S.A., and described by Wieland (1906).

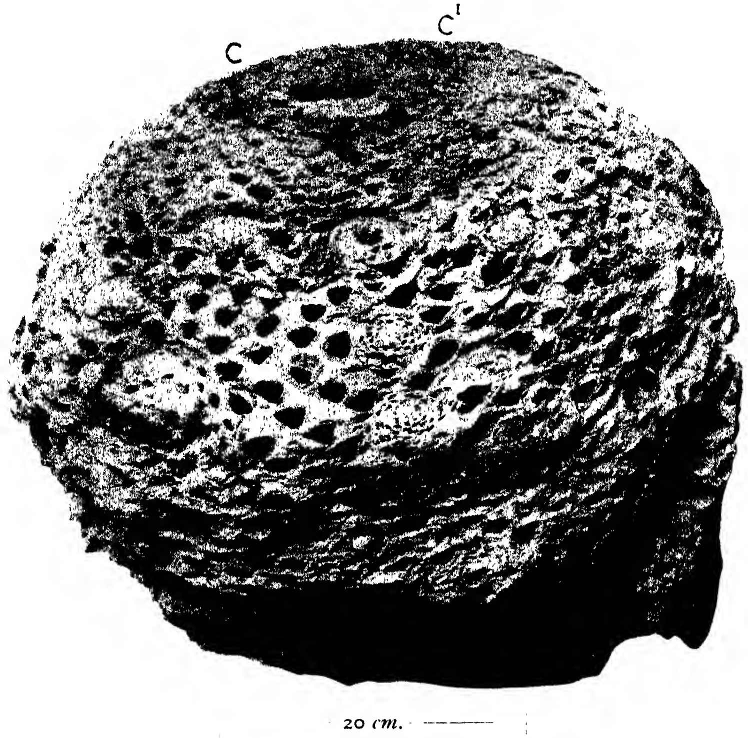

Fig. 130.—*Cycadeoidea colossalis*. Showing complete almost spherical stem. The leaf bases are weathered out and appear as triangular cavities. A large number of flowers are seen among the leaf bases. The area C–C¹ includes the apex and the positions of the last season's leaves. From Scott after Wieland. From D. H. Scott's *Extinct Plants and Problems of Evolution* (Macmillan).

The trunks (Fig. 130), unlike those of the Williamsonieae, are usually short and thick and bear a very close resemblance to

Macrozamia and *Encephalartos* in the form of trunk and in the closely packed persistent leaf bases with which they are covered (Fig. 131). The leaves, which have been found in the young

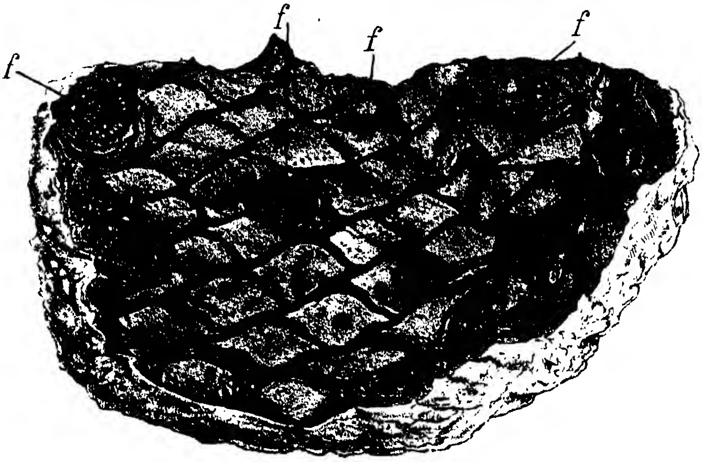

FIG. 131.—*Bennettites Gibsonianus.* Tangential section through leaf bases and flowers. The vascular bundles in the petiole bases appear as black dots. *f, f,* flowers. From Scott after Carruthers.

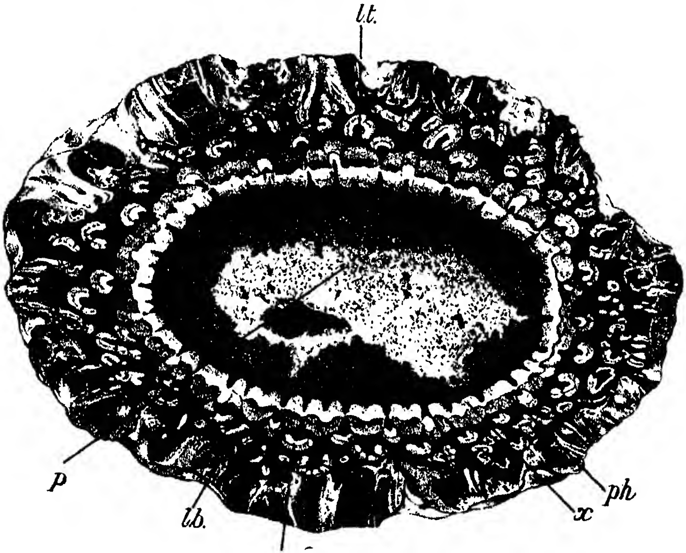

FIG. 132.—*Bennettites Saxbyanus.* Transverse section of trunk. *p,* pith; *x,* xylem; *ph,* phloem; *l.t.,* leaf traces in cortex. They divide repeatedly before entering petioles. *l.b.,* leaf bases. Reduced. From Scott after Carruthers.

condition round the apical bud, are pinnate and the leaflets have several parallel veins. Structurally the stems resemble those of the living Cycads in having a large pith surrounded by a ring of vascular bundles with entirely centrifugal xylem (Fig. 132). The structure of the wood, however, consists of scalariform pitted tracheids, and the leaf traces, instead of passing half-way round the stele before passing into the petioles, pass out directly. The bases of the leaves are covered with a clothing of scales which fill the interspaces between the leaf bases. The internal structure of the leaves differs in no important respect from that of the living Cycads but the cuticular structure is quite different.

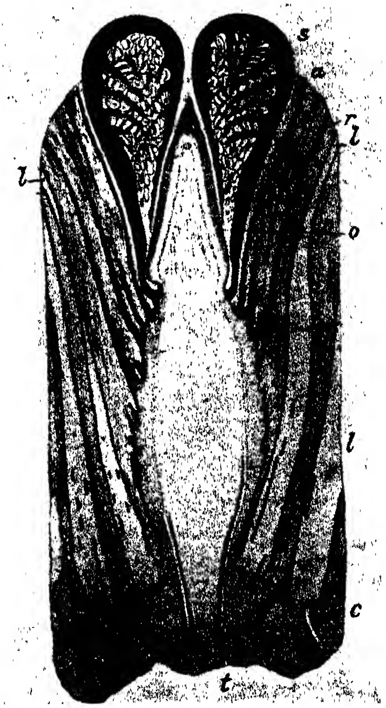

Fig. 133.—*Cycadeoidea dacotensis*. Longitudinal section of a flower. Reconstructed from sections from several similar flowers. *s*, unexpanded microsporophylls; *a*, surface of trunk formed by broken-off bracts and leaves (*l*); *r*, clothing of scales between bracts; *c*, cortex of trunk; *t*, vascular bundles supplying peduncle. *o*, ovules and interseminal scales. ⅔ nat. size. From Scott after Wieland.

The flowers are situated in the axils of the leaves and are almost completely sunk in the armour of leaf bases. The flowers were produced in very large numbers. One example of a *Cycadeoidea* is known on which there were 500 flowers in the fruiting condition on a piece of stem 50 cm. long. The flowers varied in size from about 2 cm. long and 1·5 cm. in diameter in *C. Dartoni* to 8 cm. long and 3 cm. in diameter in *C. dacotensis*. In the latter species the flower (Fig. 133) consisted of a floral axis about

8 cm. in length with between a hundred and a hundred and fifty bracts arranged in spiral order on the lower two-thirds of its length. Above the bracts there is a whorl of stamens fused at the base and forming a cup-shaped androecium similar to that of *Williamsonia*. Each stamen is pinnately branched and each pinna bears a double row of purse-shaped structures (Figs. 134, 135) containing sporangia and similar in form to the synangia of *Marattia*.

Professor Harris is of the opinion that the purse-shaped structure is equivalent to a pinnule folded along the midrib with sporangia on each side. It is therefore not equivalent to a true synangium of the Marattiaceous type, which consists of a group of fused sporangia on the surface of the leaf. The pollen grains (length 68 μ) are oval and have a broad longitudinal groove resembling in this respect the grains found in some Pteridosperms.

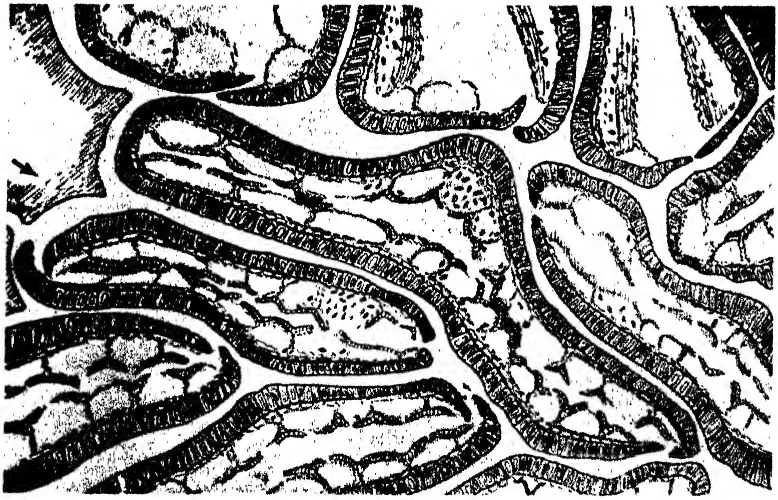

FIG. 134.—*Cycadeoidea dacotensis*. Transverse section through microsporophyll (see arrow) and several folded pinnules containing sporangia. × about 25. From Scott after Wieland.

Above the level of the staminal whorl the floral axis is conical and is completely covered by ovules (or seeds) and interseminal scales. The gynoecium is therefore like that of the Williamsonieae. The micropyles of the ovules project slightly above the surface formed of the closely packed heads of the interseminal scales (Fig. 136, B). The angiospermic condition of enclosed seeds is therefore very nearly attained. The seed of *C. albianus*, a species from the lower part of the Upper Cretaceous at Folkestone in England, has a slender pedicel, with a central strand of vascular tissue, surrounded by an outer tissue of tubular cells which have grown up and formed a cup-like investment round the seed (Fig. 136, A). The testa of the seed is separated from the sheath of tubular cells by a layer of cells, the "deliquescent layer", which was apparently of a transitory nature. The integument has an outer layer of square thick-walled cells, a middle layer of thick-walled fibrous cells, and an inner layer of thin-

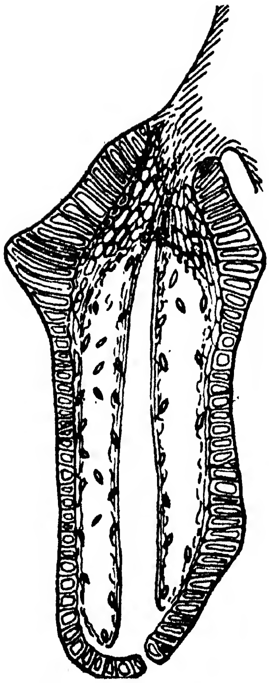

FIG. 135.—*Cycadeoidea dacotensis.* Longitudinal section of one of the folded pinnules bearing sporangia. The palisade tissue of the pinnule is seen to enclose the thin-walled sporangia. × 40. From Scott after Wieland.

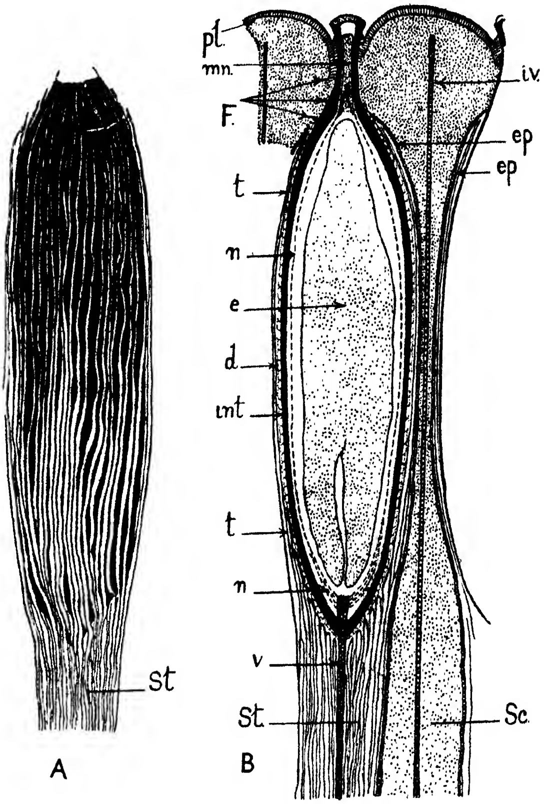

FIG. 136.—*Bennettites albianus.* A. Reconstruction of external appearance of a seed.—B. Longitudinal section of seed and two of the surrounding interseminal scales. × 17. *St*, sheath of tubular cells on stalk and seed; *pl*, epidermis; *F*, micropylar tube fused to scales here; *mn*, apex of nucellus (*n*); *iv*, vascular bundle in scale; *ep*, epidermis of scale; *t*, tubular cells of sheath; *d*, deliquescent layer; *Sc*, stalk of interseminal scale; *e*, embryo; *v*, vascular strand. From Scott after Stopes.

walled cells. The nucellus fills the integument and is fused with it up to near the base of the micropylar tube, where it is free and projects into the micropyle as a conical plug. A pollen chamber is present in the base of the conical plug. The embryo, which has its radicle directed towards the micropyle, has two equal-sized cotyledons and a rather massive hypocotyl.

It appears that in most Cycadeoideae the flower was protandrous, the stamens maturing before the gynoecium. In flowers in the young condition the stamens may be mature while the ovules are poorly developed and in flowers in which seeds are present only traces of a staminal whorl may be seen. Some investigators believe that these traces represent an undeveloped androecium and that the flowers were unisexual. It is certainly difficult to decide finally whether the structure in the position of the androecium is an undeveloped structure or whether it is the relic of a caducous functional androecium.

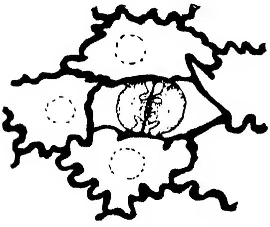

FIG. 137. — *Dictyozamites Johnstrupi.* Drawing of a small piece of a Bennettitalean cuticle showing a stoma with a few epidermal cells. × 325. After Florin, 1931.

Relationships of the Bennettitales to other Groups.—There is no doubt of the close relationship of the Williamsonieae to the Bennettiteae. They have the same type of floral construction and their leaves, though showing a certain range in form, have the same type of peculiar stomatal structure. The form of stem in the Bennettiteae is remarkably like that of some of the living Cycadales. The leaves too are of similar form and structure but the cuticular and stomatal structure (Fig. 137) is quite different from that found in any other group of vascular plants. The beaked nucellus and pollen chamber are not unlike the corresponding structures in some of the Pteridospermae, Cordaitales, and in the living Cycadaceae and Ginkgo. To the Cordaitales they bear some resemblance in the form of the ovuliferous flower, which in both groups consists of a short axis bearing a mixture of sterile and fertile appendages.

On these grounds we are probably justified in believing that the Cordaitales, Coniferales, Ginkgoales, Bennettitales, and Cycadales are fairly distinct groups of equal rank, all showing some features in common with the Pteridosperms from which they have possibly all evolved (Thomas, H. H., 1939, p. 50).

B. Cycadales.—Little is known of the early history of the Cycadales. It is obvious from what is known about the Bennettitales that leaves and stems that resemble those of living Cycads in several respects but not in cuticular structure belonged to plants which, if we rely on the evidence of reproductive organs, were not related to the Cycads at all. Probably the majority of Cycad-like leaves which are found in the Mesozoic rocks have the Bennettitalean type of stomatal and cuticular structure.

There are, however, reproductive structures of Triassic age which may possibly be Cycadalean. *Dioonitocarpidium* (Lilienstern, 1928) is a pinnate leaf about 20 cm. in length with two seeds borne one on each side of the base. It has therefore some resemblance to the sporophyll of Cycas and at the same time resembles the cone scales of the other Cycadaceae in having two seeds. There is a Rhaetic fructification known as *Cycadocarpidium* which appears to consist of a leaf-like sporophyll with two basal seeds, but Professor Harris (1935) has shown that the weight of evidence is in favour of regarding it as part of the fruit of Podozamites and that in all probability the plant was a Conifer. Similar doubts have been expressed about other fossils which had at one time been thought to be Cycadalean. There is no reliable record of fossil Cycadales in later geological periods and the geological history of the living Cycads is a complete mystery.

TABLE C

		GREAT BRITAIN	UNITED STATES	OTHER REGIONS	
QUATERNARY		Peat, Alluvium, Glacial Deposits			
TERTIARY	Pliocene	Cromer Forest Bed	Citronelle Form. (Ala., Miss., La.)	Brit. Columbia, France, Holland	
	Miocene	. .	Florissant (Col.)	Oeningen (Switz.) Brown Coal (Germ.)	
	Oligocene	Bovey Tracey (Devon.) Bembridge (I. of W.)	Bridge Creek (Ore.)	Baltic Amber Deposits	
	Eocene	Sheppey, Bournemouth, Mull (Scot.), Ireland	Wilcox and Claiborne Flora (Ala.) Latah Form. (Wash.)	Arctic Regions incl. W. Greenland and Spitsbergen	
CRETACEOUS	Upper	Chalk (Marine) Upper Gault	Laramie Form. (Wyo.) Tuscaloosa Form. (Ala.) Dacota Flora (Kan. Neb.) Raritan Form. (Mass., N.J.)	Argentina, Patagonia	
	Lower	Albian Aptian (Lower Greensand) Neocomian, Wealden	*Potomac Formations* Patapsco (Md., Va.) Arundel ,, ,, Patuxent ,, ,,	Bernissart (Belg.), W. Greenland, Peru, etc.	
JURASSIC		Estuarine Ser. (Yorks) Sutherland (Scotland)	Arizona, Black Hills (Dak.), Oregon	Almost world-wide	
RHAETIC		*Naiadita* Bed (Som., Worcs, War.)	. .	Germany, Sweden, E. Greenland, Tonkin, Japan	
TRIASSIC		Keuper Ser. (Worcs) Bunter Ser.	Richmond Coal-field (Va.) Petrified Forest (Ariz.)	Keuper Series, Europe Bunter Series, Europe	GLOSSOPTERIS FLORA in Antarctica, Australia, S. Africa, India, Mexico, S. America
PERMIAN		Zechstein (Hilton Plant Beds, Manchester Marls) Rothliegende	Hermit Shale Flora (Ariz.) *Gigantopteris* Flora (Texas)	Kusnezk Flora (Siberia) *Gigantopteris* Flora (Shansi, China)	

CHAPTER XVI

ANGIOSPERMAE

THE Angiosperms make their appearance as a conspicuous part of the world's flora in Lower Cretaceous times (Table C) and their sudden rise to dominance by the end of the Cretaceous is one of the most striking phenomena in the geological history of plants. Judging from the enormous number of Angiosperm species which now exist, the rate of evolution of the group during the Cretaceous and Tertiary must have been exceptionally rapid. This rise to dominance of the Angiosperms was associated with a decline in the importance of several other important groups. The Bennettitales appear to have suffered complete extinction. The older groups were apparently unable to compete successfully with these vigorous newcomers in the struggle for living room.

The types of Angiosperm found in the Lower Cretaceous can be referred to living families or even genera and there is no evidence of primitive types. They show no features which are not found in living Angiosperms nor do they show features which suggest any closer a relationship to any of the groups which have been already described.

The earliest indubitable Angiosperm remains (Table D, p. 172) are pollen grains found by Dr. Simpson (1937) of Edinburgh, in coal of Jurassic age from Brora in Scotland. There are, however, a few examples of leaves resembling those of Dicotyledons which are worthy of mention. Professor Harris (1932) discovered some leaves, to which he gave the name *Furcula*, in Rhaetic rocks in Greenland and the impression of what appears to be a dicotyledonous leaf has been found in Jurassic rocks at Stonesfield in England.

The Brora pollen grains (Fig. 138, B, C) are unlike any found in earlier rocks. One type is a pollen with three grooves, one smaller than the others, which gave the pollen a trilobed form with one lobe slightly smaller than the others (Fig. 138, B, C). This form of grain is characteristic of the Nymphaeaceae and is almost indistinguishable from that found in *Nelumbium*. A second type of grain compares very closely with the pollen of *Castalia*. It seems unlikely that this elaborate type of pollen was evolved in more than one group of plants.

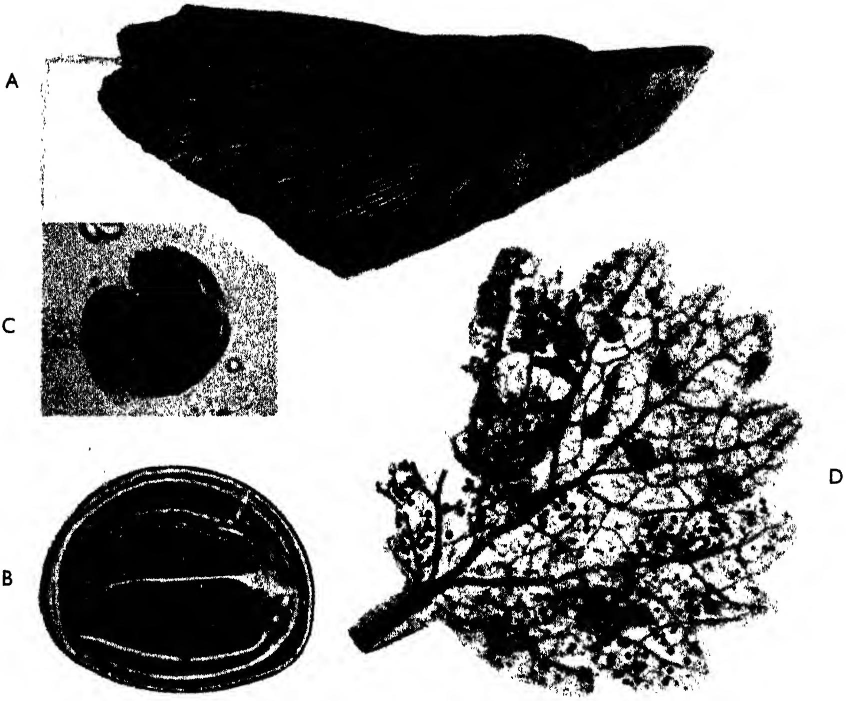

FIG. 138.—Fossil Angiosperms. A. *Sabalites Ungeri*, an Upper Cretaceous Palm from Texas. $\frac{1}{12}$ nat. size. After Dorf, 1939.—B. Pollen grain cf. *Nelumbium* Jurassic, Sutherland, side view.—C. Similar grain polar view. B and C after Simpson; both × 1000.—D. *Betula nana*. Leaf from peat of Glacial age, Cambridgeshire. Perithecia of two types of fungi are present on the leaf. × 11.

It has been found that pollen of elaborate form or ornamentation is a reliable means of identifying living genera or species. They certainly afford more reliable evidence than that afforded by leaf form. A great many Cretaceous and Tertiary fossil Angiosperm leaves have been given names which imply a relationship to existing families and genera, although it is well known that quite widely separate groups have leaves of almost the same form and that leaves on a single individual may show considerable variation. It is perhaps comforting to find that in a recent investigation of the pollen in coal of Tertiary age from Mull in Scotland, Dr. Simpson has been able to identify some of the same families and genera which previous investigators identified by means of leaf impressions found in associated sediments.

A very early Cretaceous flora containing Angiosperm leaves is also found in the North in Greenland. Sir Albert Seward is of the opinion that the Pteridophytes, Bennettitales, Ginkgoales, and Coniferales in this flora are representatives of the Jurassic flora which spread northward and became associated with the Angiosperms which had possibly evolved in the Arctic continent. In 1890 Nathorst described leaves and fragments of inflorescences of *Artocarpus* (Bread-Fruit Tree) found in these Greenland beds and his identification has been confirmed by later observers. Sir Albert distinguishes among the numerous types leaves of the following families: Fagaceae, Moraceae, Menispermaceae, Magnoliaceae, and Lauraceae. These are all Archichlamydeous families. The Liliaceae are represented by a leaf similar to *Smilax*.

In the Aptian of England petrified dicotyledonous wood has been found which resembles that of the living Dipterocarpaceae.

In the Cretaceous of Maryland and Virginia, U.S.A., the Lower Cretaceous is divided in ascending order into the Patuxent, Arundel, and Patapsco formations (see Table C). The Patuxent flora, like that of the Wealden of Europe, is predominantly Jurassic in composition and only a few imperfect specimens of Angiosperm leaves have been found in it. The Patapsco flora contains about 30 types of Angiosperm leaves while the Upper Cretaceous, which overlies the Patapsco, has a flora consisting mainly of Angiosperms, Conifers, and Ferns: the Bennettitales have become extinct.

The fact that practically all of the Angiosperm fossils in these Cretaceous beds are the leaves of trees may be due to accidents of preservation, although on theoretical grounds botanists regard the arborescent type of Angiosperm as probably the primitive type. If we examine the dead leaves which accumulate in ditches and pools where they might in course of time become buried in mud and converted into fossils, we will find that most of them belong to trees. The leaves of herbs generally shrivel and decay without becoming detached from the plant and are less likely to be preserved as fossils.

The fossil Angiosperms do not yield any information about the ancestry of the group beyond what is already provided by living representatives. The presence of almost exclusively Archichlamydeous families, and in particular the Nymphaeaceae and Magnoliaceae, in the earliest floras containing Angiosperms suggests that the simple Ranalean type of floral construction may be primitive. But it also suggests that the type of flower found in the Fagaceae, often regarded as a reduced type, had an early origin.

The fossil Angiosperms throw no light whatever on the relation between the Monocotyledons and the Dicotyledons, and it is clear that the origin of the Angiosperms must be much further back in geological time. We may perhaps eventually find traces of ancestral types in the Early Mesozoic or even in the Palaeozoic. From our brief survey of the flora of the Palaeozoic it is clear that the Pteridosperms afford the most likely source; but of primitive Angiosperms we know nothing.

CHAPTER XVII

A BRIEF REVIEW OF FLORAS AND CLIMATES OF THE PAST[1]

If a botanist were given a collection of living plants without being told from what part of the world they came, he might, if he could identify them, be able to tell something about the conditions and climate in which they grew. To be able to do this, however, he would require a considerable knowledge of the geographical distribution and climatic requirements of the species represented in the collection. His task would not be easy and his estimate of climate would only be approximate because many species can adapt themselves to a wide range of climate. For example, *Ginkgo*, which we know from fossil evidence to have been widely distributed in the Tertiary, is now only native in China, although it is a hardy plant and can be grown successfully in a wide range of climates. Its present distribution is evidently not determined by climatic conditions alone. Even closely related species differ very considerably in their requirements. Some species of *Lycopodium* exist in North Temperate sub-Alpine conditions while other closely related species are restricted to the Tropics.

The relation of plants to climate is obviously very complex. We can only make a very rough estimate of the climate even from collections of living species. Fortunately there are a considerable number of plants which are only found in certain climatic regions, although they may be found in many parts of the world, and we know from experience that they will not grow under different climatic conditions. In practice it would be possible to determine whether a collection of living plants came from a Cold, Temperate, or Tropical region.

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[1] For a comprehensive and authoritative account of fossil floras and a full discussion of the problem of climates the student is advised to consult Seward's *Plant Life through the Ages.*

We may apply this method to the study of fossil floras, and since the later fossil floras contain plants most like those of the present it is reasonable to work backwards into the past to the earlier periods when the flora consisted of unfamiliar types, whose reactions to climatic conditions cannot now be observed.

Quaternary Period (Table C).—Fossil plants found in Quaternary deposits are mostly specifically identical with living species. The peat deposits which are found covering extensive areas in the Northern Hemisphere were formed in post-Glacial times and are still accumulating. Peat consists of only slightly altered plant fragments and may contain considerable numbers of pollen grains. These were not necessarily produced by the plants which formed the peat and they are not fully representative of the flora because some kinds of pollen are not preserved under the conditions of peat formation. The most important and interesting is the pollen of anemophilous trees many of which grew in the country round about and were not usually rooted in the peat. This pollen may be extracted (see p. 11) and identified and counted and a pollen diagram of the peat deposit constructed. Such a diagram may be used in the same way as the spore diagrams used in the comparison of coal-seams. Many interesting facts regarding the history of peat deposits have been discovered by this method. Relics of prehistoric civilisations are sometimes found in peat and it is possible to find out something of the nature of the climate and flora which existed in the regions in which we find traces of prehistoric man.

During the Ice age which preceded the peat deposits large areas of Europe and North America were covered by ice and the form of the land surface still bears evidence of its action. Round the limits of the ice Arctic plants grew and there were probably isolated patches of vegetation on the high peaks or nunataks which projected above the ice, as in Spitsbergen and Greenland at the present day. The remains of these plants are sometimes found in the deposits which formed just beyond the limit of the ice. Near Cambridge in England thin beds of peat are found in which there are the remains of such plants as *Betula nana* (Fig. 138, D) and *Dryas octopetala* and a similar flora has been found at Bovey Tracey on the South Coast.

Tertiary Period.—In North America and Japan the floras which are found in Pliocene deposits (Table C) consist of many of the species still found living in those countries. There appears to have been but little change since then in the flora and presumably also in the climate. In Europe the species which are found in the youngest Pliocene are for the most part still found in Europe, and the Ice age, though temporarily changing the flora, has had little lasting effect on the flora as a whole. In the Early Pliocene in Europe, however, the flora contained a large number of species which are now found in the Himalayas, China and Japan, and North America. It is clear that during the Pliocene a number of species and genera which ranged all round the Northern Hemisphere in early Pliocene times became more restricted in distribution. Climatic fluctuations may have caused this change.

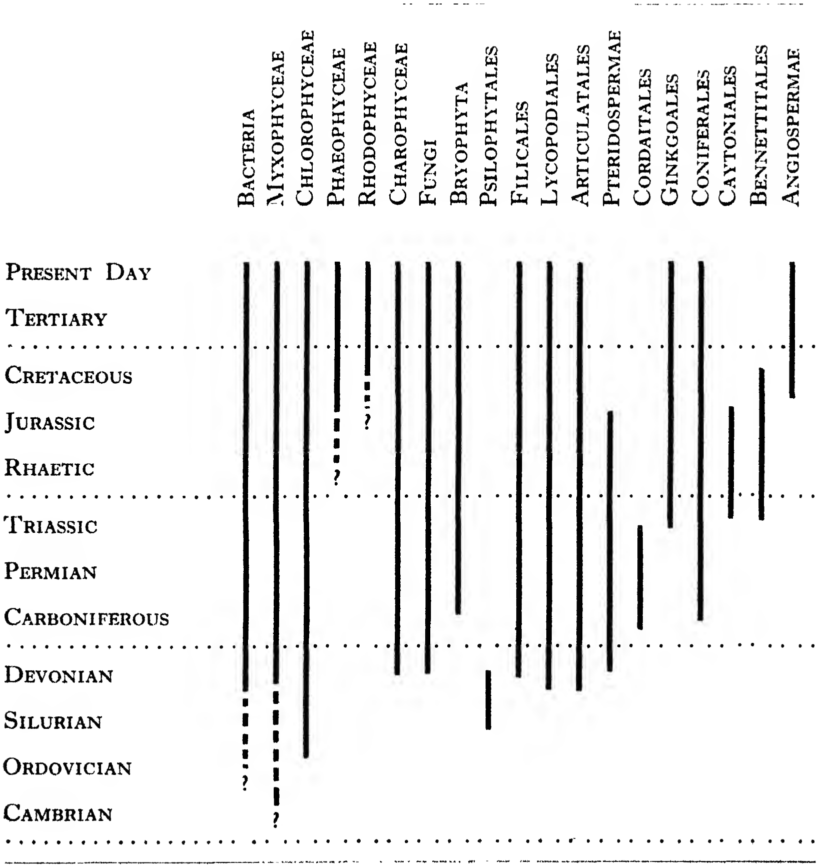
In the Miocene and Oligocene in Europe and North America we have evidence from the composition of the floras that the climate was warm to subtropical. The best known Miocene floras are those found at Florissant (Col.) and at Oeningen in Switzerland. In the rich Oligocene flora from Bembridge in the Isle of Wight (Reid and Chandler, 1926) it is noteworthy that 89 per cent of the flora consists of species and genera which are most closely related to those now found in existing American and Eastern Asiatic floras. A species of the Water Fern *Azolla* has been found in the Bembridge beds which is intermediate in character between the species now found in America and Australia and those found in Africa, Ceylon, and Japan. Conifers are represented by *Pinus*, *Cupressus*, and *Araucaria*. The Baltic amber, which contains beautifully mummified fragments of plants and insects, is of Oligocene age. The climate must have been warm, temperate, or subtropical.

In Mull in Scotland beds of Eocene age have furnished a rich flora. The identifications of the plants have been based not only on leaves but also on the pollen found in thin coal-seams (Simpson, 1936). The flora consists of representatives of the following genera: *Engelhardtia*, *Alnus*, *Corylus*, *Planera*, *Magnolia*, *Bucklandia*, *Corylopsis*, *Fortunearia*, *Loropetalum*, *Dicoryphe*, *Distylium*, *Ginkgo*, *Pinus*, *Cedrus*, *Abies*, *Podocarpus*, and others. Most of the species compare closely with species of existing Eastern Asiatic floras but some others to species now found in Africa and North America. An important example of an Eocene flora, the Wilcox Flora, is found in Alabama. Other floras are known from the Arctic regions including Spitsbergen and Greenland. The climate of the Eocene was evidently warm.

The London Clay Flora, which is found in the London basin, in Essex, Hampshire, and elsewhere in the South-East of England, has been described in an important monograph by Reid and Chandler (1933). The identification of most of the species which are listed is based on fruits and seeds which are partially preserved in pyrites and which when split open reveal a considerable amount of structure so that close comparisons with living forms are possible. The conclusions reached were that the flora was mainly that of a tropical rain forest closely allied in floristic composition to the existing Indo-Malayan flora.

TABLE D

APPROXIMATE GEOLOGICAL RANGES OF THE PRINCIPAL PHYLA OF PLANTS



Earlier Periods.—One may make a less reliable estimate of the climate which prevailed in Cretaceous times because the species and many of the genera are different. In the Cretaceous flora of Greenland we find leaves resembling such genera as *Platanus*, *Cinnamomum*, *Ocotea*, *Dalbergia*, *Magnolia*, and *Artocarpus*. This assemblage suggests the existence of tropical conditions; a striking contrast to the climatic conditions of Greenland to-day.

In the Jurassic and Rhaetic the composition of the flora appears to have been fairly uniform all over the world, including such regions as Greenland, Spitsbergen, North America, Mexico, Europe, India, Japan, Australia, and New Zealand. The climate was at least a warm and moist one judging from the types of Fern which formed important constituents of the flora. With the exception of the pollen in the Jurassic coal from Brora (see p. 165) there are no records of Angiosperms which we can use as tests of climate. The heavily cuticularised leaves of the Bennettitales and some of the Conifers suggest that the temperatures may have been high. The Cycadeoideae, judging from the form of their trunks and structure of their leaves, might well have been xerophytes.

The study of Palaeozoic plants yields much interesting information about the morphology of large numbers of extinct types, and in some instances structural peculiarities may reveal something about the conditions under which the plants grew. But such suggestions are not reliable. We know, for instance, that the peculiar features of xerophytic plants, such as sunken stomata and thick cuticles, are by no means restricted to plants which grow in arid climates. Some have speculated as to the nature of the climate which prevailed during the formation of the Upper Carboniferous coal-measures. There are those who point out that the secondary wood of petrified plants found in the coal-measures of Europe and North America shows no development of annual rings, a feature often found in tropical plants but by no means restricted to them. Wood of approximately the same geological age from those regions where the Glossopteris flora existed shows definite annual rings, and we have other reasons for believing that the Glossopteris flora was subject to a cold climate. On the other hand it has been pointed out that peaty masses such as those which were converted into coal-seams are rarely formed under tropical conditions.

We may, it is true, be able to deduce the ecological conditions under which some of the plants grew. The Carboniferous Calamites, for example, are so similar in construction to the living

Horsetails that we may be sure that they grew in wet or waterlogged soil, an inference which is supported by geological evidence. We are no doubt right in assuming that the climate of the Carboniferous was between temperate and tropical. A remarkable feature of Palaeozoic and later floras is their geographical distribution. The fossil floras which are found in circumpolar regions do not provide evidence that conditions of growth were less favourable there. There have been enormous glaciations in the past but on the whole there is no evidence to show that the climate of the world as a whole has changed either for warmer or for colder. There has undoubtedly been an extraordinary change in the distribution of climates. It has been suggested (Brooks, 1922) that, by a different arrangement of ocean basins and currents, Arctic regions might have been given much warmer climates. Sir Albert Seward (1931, p. 536) has suggested that plants may have responded differently to climatic conditions in the past and points to the adaptability of many species to altered conditions. The most promising theory is that propounded by Wegener in explanation of the shapes of the continental masses. The continental masses are supposed to rest on plastic foundations and during geological time to have been moving about on the surface of the Earth. Wegener supposed that at one time the present continental masses were united in a single immense continent which became broken up and the parts became separated from one another. Some consider that this theory explains the wide separation of the areas in which the Glossopteris flora and traces of the Permo-Carboniferous glaciation have been found. Professor Sahni (1936) regards the close proximity of the Glossopteris flora in India with the distinct flora containing the Fern-like plant *Gigantopteris* in China as evidence of a drifting together of previously separate areas. The ocean basin which originally separated them was, he supposes, crumpled into folds and formed the Himalayas.

The land masses which are now in the Arctic and Antarctic regions were possibly nearer the Equator when they bore the vegetation which has left its relics in their rocks. There is no doubt that large pieces of the crust of the Earth have been moved hundreds of miles by geological movements, but we have no knowledge of forces in the Earth large enough to move continents: such forces and movements are beyond the range of our experience.

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