AN INTRODUCTION TO THE STUDY OF FOSSIL PLANTS
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BY

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PREFACE TO FIRST EDITION

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. Duerden, Dr. H. Godwin, Professor T. G. Halle, Professor T. M. Harris, Professor O. A. Høeg, Professor W. H. Lang, Professor Suzanne Leclercq, Mrs. L. Macfarlane, Professor N. W. Radforth, Dr. J. B. Simpson, and Dr. J. Weir: to them I express my cordial thanks.

My thanks are also due to the Controller, H.M. Stationery Office, for permission to use the photograph illustrated in the
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frontispiece. Permission was kindly granted by the following societies and publishers to reproduce figures from their publications: the Royal Society of London (Figs. 1, 4, 56, 69, 113, 114, 116), the Royal Society of Edinburgh (Figs. 2, 23, 24, 26, 61, 61b, 61c, 86, 110, 111), the Manchester Lit. and Phil. Society (Fig. 125), The Annals of Botany (Fig. 3), Macmillan & Co. (Figs. 6, 11, 32, 33, 36, 88, 117, 127, 130), Cambridge University Press (Fig. 108).

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.

PREFACE TO SECOND EDITION

Since this book first appeared in print in May 1940 a great deal of additional information about fossil plants has been published in various scientific journals. For reasons of economy it has been impossible to introduce more than a very small fraction of this into a book of this size. I have also attempted to restrict the types of fossil plants to as few as possible. However, some additional information has become available since 1940 which supplements our knowledge about those that were originally selected, and this has been added to the previous descriptions.

One of the most important developments during the last twenty years is the result of the discovery of an almost unlimited source of coal-balls, containing petrified plants, in coal seams in the United States. This has stimulated there a wide interest in Palaeobotany and there are more than two hundred workers in the palaeobotanical field in that country alone.
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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
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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
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<th>GEOLOGICAL PERIODS</th>
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<td>Present Day</td>
<td>0</td>
</tr>
<tr>
<td>Quaternary</td>
<td>Post-Glacial</td>
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<td>Tertiary</td>
<td>Pliocene</td>
</tr>
<tr>
<td></td>
<td>Miocene</td>
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<td></td>
<td>Oligocene</td>
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<td></td>
<td>Eocene</td>
</tr>
<tr>
<td></td>
<td>(About 11,000 years B.C.)</td>
</tr>
<tr>
<td>Triassic</td>
<td>Angiosperms dominant</td>
</tr>
<tr>
<td>Jurassic</td>
<td>Gymnosperms and</td>
</tr>
<tr>
<td></td>
<td>Pteridophytes dominant</td>
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<tr>
<td>Rhaetic</td>
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<td>Permian</td>
<td>Upper</td>
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<td>Carboniferous</td>
<td>Lower</td>
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<td>Upper</td>
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<td>Devonian</td>
<td>Lower</td>
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<tr>
<td></td>
<td>Upper</td>
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<td>Middle</td>
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<td></td>
<td>Lower</td>
</tr>
<tr>
<td>Silurian</td>
<td>Early records of</td>
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<td></td>
<td>land plants</td>
</tr>
<tr>
<td>Ordovician</td>
<td>Algae</td>
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<tr>
<td>Cambrian</td>
<td>Algae</td>
</tr>
<tr>
<td>Precambrian</td>
<td>Upper</td>
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<tr>
<td></td>
<td>Lower</td>
</tr>
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<td>Traces Algae?</td>
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TABLE A
(Adapted from A. Holmes, 1947)

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 native only 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
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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 Cruciferæ 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 Cruciferæ 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 Cruciferæ 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,
INTRODUCTION

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. Calymnatotheca Honinghausi 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.

**APPROXIMATE GEOLOGICAL RANGES OF THE PRINCIPAL PHYLA OF PLANTS**

<table>
<thead>
<tr>
<th>Present Day</th>
<th>Tertiary</th>
<th>Cretaceous</th>
<th>Jurassic</th>
<th>Rhaetic</th>
<th>Triassic</th>
<th>Permian</th>
<th>Carboniferous</th>
<th>Devonian</th>
<th>Silurian</th>
<th>Ordovician</th>
<th>Cambrian</th>
</tr>
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</table>

- **Bacteria**
- **Myxophyceae**
- **Rhodophyceae**
- **Chlorophyceae**
- **Fungi**
- **Phytophaga**
- **Pteridophyta**
- **Lycophyta**
- **Pteridospermae**
- **Gymnospermae**
- **Coniferales**
- **Cycadiales**
- **Bennettitales**
- **Angiospermae**
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 move-
ments. 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 sedi-
ment at its sides, but the vertical pressure caused a vertical com-
pression 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 con-
verted 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 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).³

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

³ A name followed by a date refers to the Literature at the end.
METHODS OF INVESTIGATION

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. 47, 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 internal structure. 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.
METHODS OF INVESTIGATION

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 NaClO₃. 1 c.c. of conc. H₂SO₄ 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. H₂SO₄ 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. 150) 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. 137) 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 KCIO₃ 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. Petrifications.—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
METHODS OF INVESTIGATION

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 petrifications 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.

Petrifications 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 petrifications 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
THE STUDY OF FOSSIL PLANTS

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.

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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
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THALLOPHYTA AND BRYOPHYTA

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 Palaeo- porella, 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, Dasyaporella, and Cyclorimus 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.\(^1\)

Other representatives of the Dasycladaceae are found in rocks

\(^1\) A detailed account of these fossil Algae will be found in Hirmer's Handbuch der Paläobotanik.
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 *Dactyloporella* 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 Estonia.

**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 *Perimnestre*. 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*. 
THE STUDY OF FOSSIL PLANTS

**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. The recent discovery of fructifications almost certainly of an Ascomycete indicate the existence of Higher Fungi in the Upper Carboniferous.

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
THALLOPHYTA AND BRYOPHYTA

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 *Proto-
taxites* or *Nematophyton* has 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 *Prototaxies* 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 *Prototaxies*, 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.

*Parha.*—Among the plants found in Lower Devonian and Upper Silurian (Downtonian) rocks is one to which the name *Parha 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 μ 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).
THE STUDY OF FOSSIL PLANTS

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

![Diagram](image)

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

found in plants which are exposed to the atmosphere for prolonged periods and are characters which we associate with land plants.

*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. Willui* (Fig. 3, A) the thallus
must have been constructed much as in the living \textit{Aneura}. In both occasional tufts of rhizoids are found. In \textit{H. lobatus} (Fig. 3, D) the thallus has lateral leaf-like expansions, one cell in thickness, placed alternately on each side. \textit{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 \textit{Treubia}. \textit{Hepaticites metzgerioides} (Fig. 3, C) is closely comparable to the living \textit{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 \textit{Hepaticites glebosus} similar in form to \textit{Hepaticites lobatus} but larger in size in Rhaetic rocks in East Greenland. He has also discovered that \textit{Naioedita lancealata} 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 \textit{Riella} than with any other existing Liverwort.

\textit{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.
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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 Mono-graptus, 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 vegetative shoots. The sporangia were about 2 mm. broad and
Fig. 4.—Baragwanatha longifolia L. & C.A. Portions of shoots with remains of leaves, vascular column shown at A.—B. Apex of a shoot with leaves and sporangia.—C. Peel section from a vascular column showing tracheids with thin annular thickenings. × 150.—D. Peel section from a sporangium shown in B 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.
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 Baragwanatha 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 Lycopsods but the structure of the tracheids differs very markedly from that found in any living Pteridophyte, and in this feature Baragwanatha 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 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 region may be regarded as a racemose branch system if we regard each sporangium as the terminal part of a short side branch the rest of which is represented by the stalk. 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 not later than Middle and probably of Lower Old Red Sandstone (Lower Devonian) age on the Muir of Rhyne 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 meristematic 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

*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-
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.

In sections of the aerial stems (Fig. 8) a distinct cutinised
EARLY VASCULAR PLANTS

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.

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

**Fig. 9.—Rhynia major. Longitudinal section of a sporangium. The sporangium contains thousands of spores. = 6·5. Kidston Col. 2393.**
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 prob-
able of the nature of a water-conducting sheath similar in func-
tion 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*.

*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

![Diagram of Asteroxylon Mackiei](image)

![Diagram of Hornea Lignieri](image)

Fig. 11.—(1) Reconstruction of Asteroxylon. \( \times \frac{1}{3} \).—(2) Reconstruction of Hornea. \( \times \frac{1}{4} \). After Kidston and Lang. From D. H. Scott's *Extinct Plants and Problems of Evolution* (Macmillan & Co. Ltd., London).

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.
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

![Figure 12](image.png)

Fig. 12.—*Rhynia Ligustri*. 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.

this transformation took place shortly after the apex of the stem forked, the result was a forked sporangium.

*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 pre-
sumably 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 Baragwanatha. 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.

Thuraphyton.—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.

Asterosxylon.—This genus, represented by two Middle Devonian species Asterosxylon 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
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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.](image-url)
to be long tracheids for the most part with spiral thickening, though occasionally the thickening is in the form of rings, par-

Fig. 14.—*Asterosylon 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.—*Asterosylon Mackiei*. Tracheids seen in longitudinal section. The second tracheid from the right is a very slender protoxylem element. × 210. After Kidston and Lang.

ticularly in the smaller elements of the protoxylem. The phloem extends as a thin layer all round the xylem but attains its
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 9 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 Machiei* has been detected in the Rhynie chert, *Asteroxylon elberfeldense* bore almost leafless slender ultimate branches.

*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 repre-
resents 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 Protoperidium 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 tetraads 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 Parkia 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.

Thanks to the activity of collectors in recent years, considerable and important additions have been made to our knowledge of Devonian plants, and special reference may be made to the rich floras found in Svalbard (Spitsbergen) (Høeg, 1942). These are of special interest in view of the high latitude of Svalbard and the arctic conditions which prevail there today. Many discoveries are being made in the Devonian strata of the United States and we are becoming better acquainted with the extent and composition of North American Devonian floras.

A most remarkable Upper Devonian fern, Rhacophyton zygo-
pteraides, has recently been described by Dr. S. Leclercq of Liège, who has been able to reconstruct practically the entire external form of the plant (Leclercq, 1951). She has also been able, by special techniques, to reveal some of its internal anatomy. It is evidently related, although perhaps distantly, to some of the Carboniferous ferns (p. 93).
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 Isoetes, 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 Jurassic, Triassic, Cretaceous, and later ages.

The Lycopodiales may be classified as follows:

LYCOPODIALES

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

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

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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 Lycopsids 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 Lycopsids 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 imigesi*. 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.**—Stigmatic tree-base of Upper Carboniferous age. After Williamson.

Stigmatic 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

![Figure 19: Stigmaria fœcident. Branch of a Stigmarian bane. 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 appendages; r, appendages. ½ nat. size. Hunterian Museum, Glasgow Univ. J. W. Photo.](image)

and bear numerous evenly spaced appendages (Fig. 19) evidently produced in acropetal succession in the manner of leaves at a stem apex.

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 to the appendages 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 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 appendages.

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

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**Fig. 20.** Transverse section of a Stigmarian branch. × ½. x, wood; c, middle cortex; pd, secondary periderm; c', primary cortex; c", hypodermal tissue; rt, appendage base. Photo by Boodle.
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 appendages 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 found in close association with

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**Fig. 21.** *Stigmaria ferrisii*. A. Section of an appendage. × 16. After Scott. B. Section of another type. *par.*, outer cortex; *i.e.*, 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.
LYCOPODIALES

Lepidophloios Wunschianus 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 appendages in young Stigmariae are slightly endogenous, originating below a few layers of the outer cortex. In mature Stigmariae these outer cortical layers have disappeared and the appendages appear to be exogenous. What are here called appendages have usually been called roots or rootlets, the use of the non-committal term appendage has been made as a result of recent discoveries which make it doubtful that they are morphologically equivalent to roots. The appendages exhibit dichotomous branching. Their surface is smooth and no hairs have been detected on them. 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 Isotetes. 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 appendage 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.

Stigmaria bacupennis, Scott and Lang.—The type of Stigmaria to which this name was given has been found in European coalballs. It differs from Stigmaria ficoides in having, instead of a parenchymatous pith or pith cavity, a mixed tissue consisting of very small tracheids and parenchyma. There are also larger gaps in the secondary wood where the traces to the appendages pass through it. Dr. Duerden (1951), at a meeting of the British
Association, described a specimen of a plant which bears an
exact resemblance to *Stigmaria bacupensis* in the structure of the
vascular system and cortex and in the slightly endogenous origin
of regularly spaced appendages (Fig. 21a). He has very kindly
permitted me to illustrate their structure here.

It is in the structure of the appendages that Dr. Duerden's
specimen differs from all other known *Stigmariae*.

The appendages are slightly endogenous and bear small leaves
(Fig. 21a) each of which has a ligule attached to its adaxial surface

![Diagram of Stigmaria cf. bacupensis](image)

**Fig. 21a.—** *Stigmaria cf. bacupensis*. A. Transverse section of an appendage and some of its leaves.—B. Longitudinal section of one of the leaves with its ligule. *o.c.*, outer cortex; *i.e.*, inner trabecular cortex; *v*, vascular strand; *L*, Leaf; *l*, ligule. A and B × 80. Photo by Dr. H. Duerden.

near the base. No vascular strand is present in the leaf and no
stomata have been discovered. Since an examination of a con-
siderable number of specimens of *Stigmaria bacupensis* of both
English and Belgian origin has failed to show any trace of these
leafy appendages we are faced with three possibilities. The first
is that we are dealing with a hitherto undiscovered species of
plant; the second, that possibly *Stigmaria bacupensis* bore in cer-
tain regions of its Stigmarian system leafy appendages. It is pos-
sible perhaps that in the early formed part of the young plant these
leafy appendages formed a supplementary photosynthetic system.
The third possibility is that exposure to light might induce the
LYCOPODIALES

production of leafy instead of normal appendages. The absence of stomata suggests that if this third possibility is right the *Stigma* "maria" branch had grown out of the forest litter into a pool or water channel. Whichever of these suggestions is correct it is clear that the Stigmarian appendage is not an organ which can be described simply as a root. This, considered in conjunction with the other

un-rootlike peculiarities of *Stigmariaceae*, suggests clearly that in the Lycopodiales there is not such a clear-cut morphological distinction between shoot and root as exists in other vascular plants. We have a comparable situation in *Selaginella* where, as Dr. S. Williams has shown, the meristems which normally produce the typical leafless rhizophores may be induced by removal of the adjoining stem meristems, to produce leafy shoots.

Of the trunks which possessed Stigmarian bases those of the
genus *Lepidophloios* are the best known. In the Calceiferous Sand-
stone series (Lower Carboniferous) of Scotland several examples have been found. A transverse section of *Lepidophloios Wüns-
chianus* 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 meristematic 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.

![Image of a fossil plant](image)

**Fig. 23.—*Lepidophloios Wünschianus*. Transverse section of the trunk found at Dalmeny in West Lothian, Scotland. p, pith; s₁, primary xylem; s₂, secondary xylem; c, fissured secondary cortex. 1/2 nat. size. After Seward and Hill, 1900.**

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 tracheids and those of the secondary wood are very long and have scalariform thickenings. The medullary rays are small and
Fig. 24.—*Lepidophloios* Wiss. 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, 1835.
Fig. 16. Lepidodendron Hueneiense. A. Transverse section of part of the main stem, x 0. B. Part of the peripheral part of a similar branch, x 0.1. m, medullary parenchyma; n, primary wood; k, leaf trace system; l, secondary tissue of leaf trace. After Williams, T.H.E. 1935.
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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).

A considerable number of different species have been recognised among the examples of petrified branches belonging to the two genera Lepidodendrois and Lepidodendron. They differ from one another in many respects. The list below gives some of

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<th>Lower Carboniferous</th>
<th>Primary Wood</th>
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<tr>
<td>Lepidodendron pettycorensis&lt;br&gt;Vislethius&lt;br&gt;Rhodiummense&lt;br&gt;brevifolium</td>
<td>Solid&lt;br&gt;Medullated&lt;br&gt;Solid&lt;br&gt;Medullated</td>
<td>Present&lt;br&gt;Absent&lt;br&gt;Present&lt;br&gt;Absent</td>
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<tr>
<td>Lepidophloios Scottii&lt;br&gt;Harcourtii</td>
<td><strong>&lt;br&gt;</strong></td>
<td><strong>&lt;br&gt;</strong></td>
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<tr>
<td>Upper Carboniferous</td>
<td>Medullated&lt;br&gt;Mixed pith&lt;br&gt;Medullated</td>
<td>Present&lt;br&gt;Absent</td>
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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.
LYCOPODIALES

Bothrodendrostromus.—There is a most remarkable similarity between the sporophylls of Bothrodendrostromus and some forms

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Fig. 31.—Graphical representations of the spore contents of two northern England coal-seams at a series of localities in the coal-field. A-E₂, the types of spore whose frequencies are represented by the heights of the black columns. Adapted from Raistrick and Simpson, 1933.

Fig. 32.—Longitudinal section of sporophyll and sporangium of A, Bothrodendron natureum, after Scott and Lyon; l.g., ligule; B, Selaginella apus, from Bower, Primitive Land Plants, 1935 (Macmillan & Co. Ltd., London).

of Selaginella (Fig. 32, A and B). The female prothallus bulged out of the spore to a greater extent than in Lepidostrobus.
Fig. 37.—A, B. Lepidocarpon Wildianum. Transverse sections of two sporophylls. x 15. From D. H. Scott's Extinct Plants and Problems of Evolution (Macmillan & Co. Ltd., London). C. Lepidocarpon Lomasii. 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.
Lycopodiales

Lepidocarpon 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 indus-
ium which almost completely enclosed the sporangium, leaving
but a narrow opening along the top of the sporangium (Fig. 33).
This sporophyll may be compared with a seed, the megaspore and
the sporangium corresponding to the embryo sac and nucellus,
while the indusium with its slit-like aperture corresponds to an
integument and micropyle. We do not know, however, whether
the microspores effected fertilisation on the tree or whether this
event occurred on the ground after the sporophyll became de-
tached from the strobilus. No trace of an embryo has been found
as yet. It is clear, therefore, that in one group of these extinct
Lycopods the evolution of a seed from a heterosporous condi-
tion 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. Sigillaria was heterosporous. In Mazo-
carpon, which was probably borne by Sigillaria, the megasporan-
gium (Fig. 35, A, B) had a large columnella 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).

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 evenly spaced appendages (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 on the abaxial side of the sporophyll
Fig. 34.—Sigillaria tepeleta. Specimen showing parts of three layers of the cortical tissues. ep, external surface with vertical rows of leaf scars; e₁, periderm layer; e₂, cortical layer below periderm. After Schimper.

Fig. 35.—Masocarpon. 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, basally-shaped extension of sporangium wall; k, part of sporophyll below sporangium; sm, part of sporangium wall; mg, megaspore; pr, probasulus. After Benson.
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.*

**FIG. 36.** *Pleuromeia Sternbergi.* Base of plant showing the four rhizophoric lobes. Above on the stem may be seen leaf scars. 2/5 nat. size. After Bischof. From Bower’s *Primitive Land Plants* (Macmillan & Co. Ltd., London).

**FIG. 37.** *Nathorstiana arbores.* Reconstruction of plant. After Mägdefrau, 1932.

The whole plant bears some resemblance to an elongated *Isoëtes.* In the Cretaceous we find a plant called *Nathorstiana* (Mägdefrau, 1932), which was only about 12 cm. in height (Fig. 37). The shoot
resembled Isoëtes while the base had dichotomously forked appendages borne in a regular succession. There seems little doubt that the arborescent Lycops of the Palaeozoic and Pleuromeia, Nathorstiana, Isoëtes, form a series in which there is a progressive reduction in size and in which the basal 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 "roota" 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 (sporophylla) 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 sporangioles. 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:

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) Protocalamites*
   c. Equisitaceae
      (Permian—Present day) ...................................... *Phyllotheca, Schizoneura*,
      *Equisites, 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 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 whors 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 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
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; Wandia, B. Rhodesia. After Walton, 1929.—C. *S. sino-euroum*. Leafy shoot showing flat arrangement and two large and one small pairs of leaves. Permian, Shantai, 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.
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 struc-
ture. 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 forma-
tion 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 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

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. x about 50. J. W. Photo. Katschm
Slide Coll. 1907.
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. insignis* 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, forming sharp points in those species with segmented or dentate leaves (e.g. *S. cuneifolium*).
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; ε, phloem; d, e, cortex; g, h, leaves; j, leaf trace; l, base of leaf; m, t axillary bud.—D. Transverse section of a small piece of secondary wood from another specimen. × 60. ε, 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.
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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 Sphenophyllostachyta and Bowmannites have been given to these fructifications.

![Diagram of Sphenophyllum sp.](image)

**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*) Dawson.—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 sporangium 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 Sphenophyliean. 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 sinusous 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 Sphenophylloideae.

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 ventral lobe of a sporophyll, the fertile appendage with the two
sterile appendages being considered as a sporophyll divided into
a fertile dorsal lobe and a bifurcating dorsal lobe. It would appear

![Diagram](image)

**Fig. 48.—*Sphenophyllum* fertile, Scott. Reconstruction of part of a strobilus by
Dr. Suzanne Leclercq. 1a, one of the fertile appendages with the heads of
the sporangiophores removed; hfa, base of stalk of fertile appendage; sa, sterile
appendages; sp, sporangiophore with two sporangia.

more likely that the two sterile appendages, judging from their
vascular strands, are lateral to the fertile part, although in de-
velopment they have been displaced in an abaxial direction. The
sporophyll cannot therefore be regarded as divided into a dorsal
and ventral lobe.

While well-defined strobili are found in the genus *Sphen-
ophyllum*, 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 to-
gether as are their equivalents the bracts in *S. Davisoni*. From the
stem immediately above the leaf 1 to 3 slender pedicels project
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close to the surface of the leaf, and each bears at its extremity a group of four pendulous sporangia (Fig. 49).

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 Scotland. It compares with *Sphenophyllum fertile* in having superposed whorls of sporophylls, some branches of which are fertile and others sterile. The stele is stellate in section with about twelve protoxylems. The vascular supply to the sporophyll is divided...
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into two lateral and a central bundle (Fig. 52), the two lateral bundles passing out into sterile appendages. The central bundle

Fig. 51.—Chiasmastrobas pectiniformis. Part of a longitudinal section. 4, peltate sporangiophores; 1, sterile appendages. x 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, Chiasmastrobas, 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.

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 are sterile and assume an abaxial position and the distal pinnae fertile and assume an adaxial 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. 33.—A. Calamites Göpperti. Imprint of external surface of a stem showing about twelve leaf-bearing nodes and parts of two branch whorls. ¥ nat. size. After Kidston and Jongmans, 1915.—B. Calamites undulatus. Compression of a stem. x, external surface; y, ridged pitch cast; u, v, nodes. a, b, branch-scars.

= §. 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.

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*.
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 multisieriate 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.

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
ARTICULATALES—II

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 in 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 vein has
Fig. 56.—*Annularia Jungmani*. Part of a branch showing characteristic leaf-mosaic. Nat. size.

Fig. 57.—*Annularia sphemicylindrica*. Part of a leaf-whorl. One leaf shows the pointed tip and two show the terminal expansion of the vein. × 15. Transfer preparation. Walton Coll. 403.
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 

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

In _Calamostachys Casheana_ heterosporpy 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 *Sphenophylostachys* 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*.

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. 78), 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

![Figure 61: Asterocalamites Göppertii A. Transverse section through internode showing one primary strand on inner face of secondary wood. The carinal canal is filled with tyloses. Glasgow Univ. F.S.C. 233. x 76.—B. Transverse section through node, showing the development of centripetal metaxylem. Glasgow Univ. F.S.C. 237. x 60. cx, centripetal xylem; par, parenchyma; px, pectostylem; ss, secondary xylem.](image)

*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*).

A petrified example of *Asterocalamites Göppertii* Solms. (Walton, 1949) shows us that the stem in the internodes (Fig. 61, A) had the same structure as that of *Calamites* except in the pitting of the secondary tracheids, which in *Asterocalamites* have multi-seriate closely packed bordered pits with oblique slit-like pores. It is at the nodes, however, that we find the most important difference. Unlike *Calamites* in which no centripetal metaxylem occurs anywhere in the stem, we find a very considerable development of centripetal metaxylem at the node (Fig. 61, B) and the
carinal canal is absent. This metaxylem consists exclusively of large scalariform tracheids. The leaf-traces are linked with the protoxylem and centrifugal metaxylem and pass horizontally through the secondary wood.

The fertile parts of *Asterocalamites* are terminal parts of the stems and branches, and appear as if one or more of the internodes at the extremity of the shoot were covered with crowded sporangiophores. In other words, the terminal fertile part of the shoot or strobilus is interrupted at wide intervals by whorls of leaves similar to those on the vegetative parts of the shoot. No bracts are present among the sporangiophores unless we regard these intercalary leaf whorls as such. The sporangiophores and the leaf whorls are in vertical series, *i.e.* superposed, and the sporangiophores are in whorls. Each sporangiophore bears four sporangia. Since our knowledge of these fructifications is based on compressions, we know nothing of their internal structure, but the cone *Protocalamostachys* to be described below was probably closely similar.

*Protocalamites pettycurensis.*—This Lower Carboniferous type of Equisetalean stem has primary bundles with carinal canals as in *Calamites* but with well-developed centripetal metaxylem not only at the nodes but throughout the internodes as well (Fig. 61a). In the upper part of the Lower Carboniferous a number of species of Calamitean stems occur in the form of compressions in which there is a mixture of alternation and superposition of the bundles at the nodes. To these types the generic name *Mesocalamites* has
been given as they may be regarded as intermediate between *Asterocalamites* and *Calamites* as regards the arrangement of the bundles at the node.

According to one investigator of the structure of the node of *Protocalamites* alternation occurs, but others have reported the presence of the superposed arrangement.

*Protocalamostachys*.—In the vegetable debris found inside the hollow fossil trees from Arran, two fragments of a strobilus named

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**Fig. 61b.**—*Protocalamostachys*. Diagrammatic reconstruction of axis of strobilus. 
*Ep*., epidermis; *Par*., medullary parenchyma; *Pr*., pith cavity; *Sp*., 1–9 bases of sporangiophores. × 15.

*Protocalamostachys* have been found (Walton, 1949, p. 729). The axis of the strobilus has six primary bundles with centripetal metaxylem, and if it were not for the presence of sporangiophores would be identified as a stem of *Protocalamites*.

The series of stems *Protocalamites*, *Asterocalamites*, *Calamites*, and *Equisetum*, as regards the structure of their primary xylem, suggests that in the evolution of the group there has been a progressive reduction in the centripetal metaxylem, and it is conceivable that the forerunners of the group had a solid protostele with exarch protoxylems. It is possible, however, that the fertile parts of *Asterocalamites*, like the nodal region of its vegetative shoot, had bundles with centripetal xylem; in which case *Protocalamostachys* may prove to be merely a petrified fragment of strobilus of *Asterocalamites*. The sporangiophores are situated
opposite the bundles from which they receive a vascular supply and are in vertical series. Since some of the vertical sporangio-
phore series have sporangiophores which fork at the base (Fig. 61b), there are more vertical series of sporangiophores than there are bundles in the axis. The sporangiophores are arranged in superposed whorls and no bract or leaf whorls have been found, among them. However, as only a small piece of strobilus was found it is possible that the fertile region was like that of *Asterocalamites* with occasional whorls of leaves.

Each sporangiophore divides at its distal end into four slender pedicels, each containing a slender strand of tracheids, which curve over through 180° and are directed toward the axis of the strobilus (Fig. 61c). Each of the four pedicels bears an elongated sporangium of the *Calamostachys* type. The fibrous layer which forms the wall of the sporangium extends for some distance down the surface of the pedicel.

The sporangiophore bears some resemblance to that of *Calamophyton* (Fig. 38). Its form suggests that the peltate sporangio-
phore of the Calamitaceae and Equisetaceae is derived from a forking sporophyll similar to that of *Calamophyton* and that the peltate head is formed by webbing of the sporangial pedicels.

**Equisetaceae.**—In the Mesozoic Era the Equisetineae are represented by the genera *Phyllotheca* and *Schizoneura* and
Equisetites. 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 close resemblance to Equisetum have been found in strata ranging from the Carboniferous to the Tertiary: to these the name Equisetites is given.

The presence of secondary xylem in the Carboniferous Lycopodiaceae and Articulatae is one of the features in which they differ from present-day representatives of these groups with the exception of Isoëtes.

Secondary wood is also found in several Devonian genera which are probably Pteridophytes. Protopitys, a Lower Carboniferous genus, attained arborescent dimensions with trunks with wood over a foot thick. The wood is almost entirely secondary and has been assumed until recently to belong to a gymnospermous plant. The recent discovery of a fertile branch (Walton, J., 1957. On Protopitys, etc. Trans. R. Soc. Edin. vol. 63) with much-divided sporophylls on which the sporangia differ in the size of spore they contain indicates that Protopitys had pteridophytic reproduction and was not a seed-plant. The Protopityales would seem therefore to occupy a position between the Ferns and the Pteridosperms.
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.

Rhacophyton (see p. 40) has been cited as a representative of the Ferns, and is no doubt related to the Coenopteridinae of the Carboniferous (Leclercq, 1951).

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 STUDY OF FOSSIL PLANTS

The Filicales may be classified as follows:

1. Coenopteridinae
   a. Cladoxyloideae
   b. Stauropteridinae
   c. Zygopteridinae
   d. Botryopteridinae
2. Marattiinae
3. Osmundaceae
4. Schizaeaceae
5. Gleicheniaceae
6. Matoniaceae
7. Dicksoniaceae and Cyathaceae
8. Dipteridaceae
9. Polypodiaceae

1. Coenopteridinae. 2. Cladoxyloideae (genera—Asteropterus, Cladoxylon).—Our knowledge of this group is based on petrified stems from Lower Carboniferous beds in Europe (see Bertrand, 1915). The stems of some, e.g. Asteropterus (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.—Asteropterus nothobrachies. 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

1 In this list only the more important divisions which include fossil forms of Pretertiary age are given.
FILICALES—I

Fig. 63.—Cladoxylon radiatum. Diagram of part of stem T, with the base of lateral branch. F. = about 24. 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 *Astropteris* 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 *Cladoxylloides* and their attribution to the Ferns is based on the anatomy of their stems and petioles.

b. *Stauropteridaceae* (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 serial parts consist of repeatedly branching rachides. 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 rachides 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 rachides and may be repeated on the third-order rachides (Fig. 67). The later rachides, however, have their laterals in two rows as in the common type of pinnate leaf. The ultimate rachides 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.

_Steuropteris_ was for a long time thought to be homosporous, but recently Dr. K. R. Surange has found that appendages of the plant which were thought to be glands are in fact megasporangia.

The microsporangia (Fig. 68, A, B) are of the massive eusporangiate type and are exannulate. Dehiscence was apical. Examples of sporangia have been found in which the spores had germinated.
and produced rhizoids. The spores are 32-40 μ in diameter and were produced in tetrads.

Rina Scott (1908) had proved that peculiar structures named *Bensonites fusiformis* were in fact borne on parts of *Stauropteris burntislandica*, and she considered them to be glands. *Bensonites* is a spindle-shaped object 1.3 mm. long and 0.42 mm. wide at the middle, borne on a slender pedicel from 0.06-0.12 mm. thick (Fig. 67a). A slender strand of scalariform tracheids traverses the pedicel and extends through the centre of the uniform parenchyma to a distance of about two-thirds from the base. The epidermis consists of tabular cells and extends to the distal end. At the distal end and occupying about a third of the length is a cavity, oval in shape, which projects down into the parenchyma, but its upper part appears to be covered by the epidermis alone. This cavity contains rounded objects which she evidently regarded as the remains of glandular tissue, although it had been suggested to her that these were megaspores. Recent investigations by Dr.
Surange have established that they are indeed megaspores, and judging from their size there were probably as many as four present. Some show the mark of the tetrad. The presence of vascular tissue in the parenchymatous mass suggests that the latter is an expanded cortical region of the pedicel.

Stauropteris stands rather apart from the other ferns grouped in the Coenopteridinae. The vascular supply, consisting as it does in some rachides of a central solid mass of tracheids with exarch protoxylems, resembles that of a lycopod stele. The metaxylem tracheids are all scalariform. The heterosporous state occurs in Archaeopteris latifolia, a fern of Upper Devonian age (Arnold, 1947, p. 176), as well as in Stauropteris. We have evidence, therefore, that heterospory in Filicales is not a recent development.

c. Zygopteroidae (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 rachides were circinnately coiled. The frond, however, had no pinnae or flattened lamina apart from the aphlebiae.

The stem in section (Fig. 69) is seen to have a nearly cylindrical protoxyle 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.
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 protoxylen 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 *Botrychoxyton 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.

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.

![Fig. 72.—Etapertis 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. x 9.](image)

and the trace becomes H-shaped with four protoxylemas. 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 *Etapertis* has been given (Fig. 72). Each pair of laterals then passes into a secondary rachis on which two series of flattened aphanlebiae are borne. The frond may therefore be described as being bipinnate. Professor Sahni has thus been able to demonstrate that *Zygopteris*, *Botrychioxylon*, and *Etapertis* 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 *Etapertis* fronds) are borne in bunches on small rachides (Fig. 73). 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. westphalensis*. The sporangia of these ancient Ferns compare with the sporangia of the Rhyniaceae in

![Diagram](image)

**Fig. 73.—*Elapteris Lavoaei*. 1. Four sporangia on a rachis (a). × 1. 2. Two sporangia, one in median section, the other showing the thick cell (*c*) of the annulus down one side. × 2. 3. Section through annulus. × 5. Transverse sections of sporangia. × 20. After Reno.[u]

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 *Marattia-rum* synangia. Individually, however, they resemble the sporangia of *Zygopteris*. Two Lower Carboniferous Fern genera, *Metacleysydropis* and *Diplolabia*, have peltiæ 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

Assumed primitive type

A

![Clepsydropsis](image)

B

![Bibroplectania](image)

D

![Diploplana Ramen](image)

E

![Eisreplichri Scotti](image)

F

![Eisreplichri Scotti](image)

G

![Eisreplichri Scotti](image)

H

![Dineuron](image)

I

![Dineuron](image)

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

11 cm. The stele was of the *Ankyropterus Gray* 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 *Zygopterus* where there are two protoxylems.
THE STUDY OF FOSSIL PLANTS

In the Zygopteridae 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-Zygopteras-Metaclepsydropsis* group the stele tends to become simplified but the petiolar trace becomes more complex.

d. *Botryopteridae* (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 Zygopteridae, 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 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, Lt²) face towards the stele, further out face laterally (Lt¹).

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. The fronds, which therefore must have had the appearance of the more familiar type of Fern frond, were also circinately coiled when young. The sporangia were borne on some of the slender
rachides 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*.

![Diagram of transverse sectional view of the xylem in the petioles of various Botryopteroidae. The protoxylems are represented in black; the metaxylems are shaded. They are all shown with the adaxial surface uppermost.](image)

Other genera of Botryopteroidae 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 Zygopteroidae and Botryopteroidae. The subsequent forking of the pinna traces is orientated to the plane of symmetry of the petiole as in the Zygopteroidae. It is thus possible that the Zygopteroidae and Botryopteroidae 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 Botryopteroidae. 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 Coenopteridinae and is remarkable in view of the relative simplicity of the vascular organisation of the group. 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 Botryopterideae.
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 Pteridosperma. 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. Olivieri, 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 Cysteaceous 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
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.

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 *Toleda*, 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 *Osmondopsis* 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

![Diagram of leaf trace](image)

Fig. 83.—*Thunnopteris Schlechtendallii*. 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. Metaxylen is shaded and the protoxylen is black. Roughly = 3 nat. size. After Kidston and Gwynne-Vaughan, 1907.

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.

The Permian genera differ principally from those of later age
in having a solid protostele. The centre of the axis contains short thick tracheids 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*, *Zaleskya*, *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*.

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. sidegateensis* (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. Cernieri*, 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 *Gramnatopteris Baldaufi* (Sahni, 1932) has a stele intermediate in character between those of *Ankyropteris* and the Permian Osmundaceae. Its petiolar bundle, which is in

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**Fig. 85.** *Senftenbergia planus*, Artis sp. Parts of three primary pinnae of a tri-pinnate frond. = about 1/4 nat. size. After Seott.

the form of a straight bar as seen in section in some species, is also intermediate in form. Both the Osmundaceae and the Coenopteridinae have large sporangia so that we have several reasons for supposing that these two groups may have had a common origin.

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 tri-pinnate 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 *Dactylothece*, 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 Seftraubergia. A. Sporangium of *S. plumosa* isolated by transfer and maceration. ×125.—
B. Apex of sporangium of *S. plumeiformis*, 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 *Anemia* 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 *Chamiitheca* (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. Undoubtedly 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: *Campopteris*, Keuper and Rhaetic; *Thaumatopteris*, Keuper and Jurassic; *Dictyophyllum*, Keuper—Lower Jurassic; *Clathropteris*, Rhaetic and Jurassic; *Hauwmanna*, 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:
LYGINOPTERIDAE

This important group of vascular plants belongs to the Sperma-
phyta (seed plants) but its members bear some obvious resem-
bances 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 Ferna. It is
likely that the Pteridospermae were in existence in the Upper
Devonian but the evidence is scanty. As the result of investiga-
tions 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 Pterido-
spermae was used to suggest the combination of Fern and seed-
plant characters.

Calymmatolecha 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.

*The Stems* (*Lyginopteris oldhamia*).—Many beautifully preserved petrifications 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

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*Fig. 87.* *Calymmatotheca Höninghausi*. Stem with the bases of six petioles. Broken lines indicate petioles arising on the far side of stem. 1/2 nat. size. Upper Carboniferous, Kilwinning, Scotland. Hunterian Museum, Ph. 1691.
Fig. 88.—*Lyginopteris aldhamia*. Transverse section of stem. $\times 2$. $R$, base of a root; $t. t$, 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 aldhamia*. Part of a transverse section of a stem. $x^2$, secondary wood; $r$, medullary rays; $x$ and $x'$, primary wood; $p_x$, protoxylem; $p$, pith; $t. t.$, secretory cell. $\times 100$. 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.

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 circinately 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
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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).

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

cells with dark contents, possibly of the nature of a secretion. Scott has pointed out that the outer cortex bears a close

Fig. 92.—_Logipteris oldhamia._ Transverse section petiole. hy, cortical bands of sclerenchyma; v.b., boundary of vascular bundle; ph, phloem; x, xylem. × about 35. After Williamson and Senet.

Fig. 93.—_Kolaxylon Hauheri._ Root of _Logipteris oldhamia_ in transverse section. rt, lateral roots; ps, one of the seven protostyles; x, centripetal metaxylem; xx, secondary xylem; ph, phloem; i.e. and o.e., inner and outer cortex. × 24. After Scott.
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

Fig. 94.—Calyptrothea Höningshain. A. Seed cupule on end of slender rachis. both cupule and rachis are covered with glandular hairs. × 3.—B. Seed cupule containing seed. × 5. 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.

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.

The seeds were borne singly in cupules (Fig. 94) on the ends of slender rachides (Jongmans, 1930), and there is evidence to
prove that these rachides were attached to fronds which also bore pinnules of the ordinary sterile type. Like the stem and leaves, the slender cupule-bearing rachides 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 stalk 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.

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

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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 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 *Calyymmatotheca 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.

*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 forking 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 *Diplomama 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.

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 (*o.c*), 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.

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.

![Diagram of Heterangium](image)

Fig. 101.—Heterangium Gristii. A. Part of a transverse section.—B. Longitudinal section cut through the corresponding tissues. pk, phloem; x', secondary xylem; x', centrifugal metaxylem; x and xex, centripetal metaxylem; px, protostele; 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 Monotyledonous 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 so attained a size comparable to that of some living Conifers.

**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 that that they are parts of the same plant. This seed, *Trigonocarpus Parkinsonii* (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 inclusions 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 *Medulloideae*. A good deal of confusion has been caused in the past from the superficial resemblance of these pollen-producing fructifications to seeds or seed capsules. Professor Halle has shown that these fructifications may be divided on structural grounds into

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**Fig. 104.** *Medulloso 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; it., leaf traces; o.c., cortex with fibres; pd, periderm; r, adventitious root; an, accessory vascular strands. Slightly reduced. After Scott.

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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 *Potomieinae*, 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* (*Whittlesea* 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 *Whittlesea* the cup has a wide opening but in *Aulacotheca*, which for many years was regarded

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

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**Fig. 106.**—*Medullana stellata*. A. *Medullana stellata*. Stem with several small steles and one large outer tubular stele. x ½ nat. size.—B. *Medullana Solmsi*. Stem with two concentric rings of steles. ½ nat. size. X', inner secondary xylem of outer stele; X'', outer secondary xylem of outer stele. The primary xylem, including protoxylems, is shown in black. A, after Cotta; B, after Weber and Steensel.

as a seed, the opening is very narrow. In *Potonia* the long sporangia are separately attached to the inside of a cup of sterile tissue. The spores of *Potonia* (length 70 μ) are smaller than those of the *Whittleseyineae* and rounder. In *Doloreotheca* the synangium
Fig. 107. *Neuropteris heterophylloides*, Port of a frond with fructification. = 2.5.
Coal-measures, Staffordshire. After Hall, 1933.

Fig. 108. *Trigonocarpus Parkinna*. A. Longitudinal section of seed. — B. Transverse section near apex. — C. Transverse section across middle. — D. Transverse section of *Trigonocarpus shorensis*. *Sa*, sarcotesta; *Sc*, silhouette (in black); *m*, micropyle; *t*, inner fleshy layer of testa; *f*, tracheidal disc; *Ps*, pollen chamber; *W*, 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 like those of Whittleseya (Schopf 1947, p. 698).

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.

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 Aulacothea type.

Further evidence in favour of this theory is provided by a large cupular fructification to which the name Calathospermum scoticum
is given. A number of specimens was found in beds of Lower Carboniferous age in Scotland (Walton, 1949). *Calathospermum* may be described as a large cupule with six segments which are free for over three-quarters of their length (Fig. 110). Each segment has from four to six vascular strands. The stalk has a horse-shoe shaped vascular strand and the stalk in most specimens is slightly bent just below the cupule so that it is not in line with the central axis of the cupule. Some specimens must have contained over sixty ovules. The ovules have slender elongated pedicels which are attached either to the margins of the lower parts of the cupular segments (Fig. 110, B) or to the base of the cupule. Their placentation may therefore be described as parietal and free central. The integument of the ovule is prolonged into nine slender processes (Fig. 111, A and B). The surface of the ovule and pedicel bears fine-pointed hairs. The prothallial cavity is lined by a fine membrane, presumably the megaspore membrane, and is surmounted by a domed pollen chamber from which a narrow tube projects upwards where it is surrounded by the
nine integumental processes. The flask-shaped structure, salpynx and pollen chamber, is called the lagenostome. The majority of specimens of *Calathospermum* contain no ovules but contain large numbers of terete pedicels which bear fine pointed hairs on their surface. They extend right up to the top of the cupule.

It may be assumed that these cupules represent a final state in which the pedicels have reached their full length and have extruded the ovules for pollination or the seeds for dispersal.

![Diagram](image)

**FIG. 111.—** *Calathospermum sectinum.* A. Longitudinal oblique section of a young cupule showing parts of six ovules and their terminal processes. × 5·7. Glasgow Univ. Hunterian Museum. Ph. 2392.—B. An ovule in another cupule. × 5·7. Hunterian Museum. Ph. 2396. c, segment of cupule; lo, pollen chamber; S, attachment of a pedicel to base of cupule; sa, part of nucellus tube (salpynx).

The structure of the cupular segments which have fibrous tissue to the inside and rather bulky thin parenchymatous tissue to the outside, suggests that under dry conditions the parenchymatous tissue would shrink and cause the segments to bend outwards and expose the ovules, while in moist conditions the segments would close together. This may have functioned as a mechanism for protecting the ovules from rain and ensuring that they were only exposed when pollination by wind-borne pollen could be effected. The integumentary processes would probably assist as a pappus in wind dispersal of the seeds.

*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 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 syngnium of the _Potoniea_ or _Dolerotheca_ type. If the segments of the cupule were fertile a _Whittlesey_ or _Aulacotheca_ type of syngnium would be produced.

The late Professor W. T. Gordon (1941) has described a similar ovule under the name _Salpingostoma dasu_ (Fig. 111a, A) which differs from the ovule in _Calathospermum_ in having six integumentary processes and a felted mass of very fine hairs between the nucellar tube (salpynx) and the processes. The pedicle of the _Salpingostoma_ ovule like the cupule of _Calathospermum_ has a crescentic vascular strand.

_Calathospermum_ is one of the earliest type of cupule and seed of which the internal structure is known. A reduction in ovule number from some such type of cupule may have led to the evolution of _Gnetopsis_, a cupule of Upper Carboniferous age which contains three or four plumed seeds (Renault). _Lagenostoma_ and other single-ovuled cupules may represent a still later stage in reduction.

The form of the vascular strand in the pedicel of the _Salpingostoma_ ovule and in the stalk of _Calathospermum_ cupule and the presence of vascular strands in the integument processes, as well as in the cupules, point to a morphological similarity of cupule and integument. The form of the vascular strand is like that of the petiole of a leaf with dorsiventral organisation in spite of

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_Fig. 111a._—Pteridosperm Ovules. A, _Salpingostoma_; long, section through ovule and integumental processes. X 2 approx. — B, C, D, E, apical parts of ovules of B, _Physoestoma_; C, _Connostoma_; D, _Lagenostoma_; E, _Sphaerostoma_. B - E X 15. Adapted from Gordon, 1941.
the fact that cupules and integuments appear to have a radial symmetry. It suggests that integument and cupule have been evolved from a frond or part of a frond (Fig. 111b) and this seems to support Professor Halle’s theory (p. 139).

The formation of the micropyle varies considerably in the Pteridosperms (Fig. 111a). Salpingostoma and Calathospermum are probably the earliest known types. The summit of the nucellus or sporangium bears a projecting part known as the nucellar cone (see Fig. 111a, A) or lagenostome. In most ovules with this

structure the inner tissue of this cone has disappeared leaving a cavity, the pollen chamber.

In the Salpingostoma type this cavity has a long narrow tubular part, the salpynx, and the whole lagenostome has the form of an empty long-necked flask (Fig. 111a, A). In most of the later forms a salpynx is not formed, but in Physostoma there is a rudimentary one. The pollen chamber itself is recognisable in all and in Lagenostoma and Sphaerostoma part of the central tissue of the nucellar cone persists as a plug of tissue in the middle of the pollen chamber. The integument also exhibits a range of structure. In Salpingostoma the integument consists of a number of free processes and there is nothing that can be called a micropyle. Where, however, the integument closes as a complete sheath round the megasporangium as in Conostoma (Fig. 111a, C) and Trigono-carpus (Fig. 108) the narrow passage left between the megasporangium and the exterior of the integument constitutes the micropyle as in modern Gymnosperms and Angiosperms. Evidently
during the time that has elapsed since the earlier part of the Carboniferous there has been a general tendency for the megasporangium or nucellus to become almost completely enclosed by the integument. The integuments of these palaeozoic ovules have a well-developed vascular supply in contrast to what is found in the ovules of most present-day Gymnosperms and Angiosperms. There are, however, a few natural orders of Angiosperms in which vascular strands are present in the integuments.

From a comparison between the vascular anatomy of Lyginopteris, Heterangium, and Medullosa it is clear that they have several important features in common. Besides Calymmatopteris, Neuropterus, 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 Perm-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).

Mesozoic Pteridosperms.—In the genera *Thinnfeldia*, *Dicrodium*, *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 Pteridospermidae 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 Liassic-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 ovules were borne on each head but only one appears to have attained maturity.

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 fructifica-

**Fig. 114.**—**Corytostamnaceae.** A. *Stenopteris.* A frond. ½ nat. size.—B. *Umkomasia Muirhami.* Inflorescence. Nat. size.—C. *Umkomasia Muirhami.* Cupule with seed and projecting micropyle. × 5.—D. *Pterochus africanaus.* Part of microsporophyll. × 1.5. All after Thomas, 1933.

**Corytostamnaceae** (genera—*Dicroidium, Stenopteris, Umkomasia, Pilophorosperma, Spermacodon, Pterochus*).—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 axis 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 Pterichus.

Pterichus (Fig. 114), which, judging from cuticular structure, is probably the microsporophyll of one of the preceding form-genera of the Corystospermaeae, 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 Corystospermaeae compare with the Peltaspermaeae 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 Pteridospermae.
CHAPTER XII

MESOZOIC PTERIDOSPERMAE—II:
CAYTONIALES

(Genera—Sagenopteris, Grisithoria, 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 Grisithoria. 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 en-
closed (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 Sewardii*, 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
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 nearly closed 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 Grisbrook type of megasporophyll to a single cupule would produce something comparable to an Angiosperm carpel. The quadrilocular syxangia 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 approach to Angiospermy in the Pteridosperm line may be regarded as an achievement comparable to the near 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 the Caytoniales were the ancestral

Fig. 116.—Fruktifications of Caytoniales. A. Megasporophyll of Grisebrook. Nat. size.—B. One seed-bearing cupule of Grisebrook. x 8.—C. Longitudinal section of cupule and seeds of Caytonia. x 3.5.—D. Part of microsporophyll of Caytonanthus. x 3.5.—E. Part of a single anther showing the four lobes. x 8.
All after Thomas, 1933.
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 centripetal 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 *Poroxyton* (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
of these stems show structural affinities with the Pteridospermae 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.

*Fructifications of Cordaites.*—The fructifications were borne
CORDAITALES

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 polleri-bearing parts or the ovules.

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 x 50 μ in length. The bud may therefore be regarded as a staminate flower bearing sterile scales and stamens.
Fig. 121.—Cordaites laevii. 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.—Cordaites Penjoni. A. Longitudinal section of a staminate "flower", x 0.3. B. Stamens enlarged. a, axis; b, bract; c, filament of stamen; d, pollen sacs. After Renault.
Cordaitales

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.

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.

Fig. 123.—Cordaitanthus Grand'Enry. A. Longitudinal section through part of a "flower" showing part of the axis, some bracts, and one ovule. a, axis; b, bracts; c, integument; n, nucellus; cp, pollen-chamber; g, canal of pollen chamber. x 24.—B. Canal of pollen chamber enlarged. g, cells of canal; o, canal; p, p', pollen-grains; es, outer membrane of grain; in, cells of male prothallus. x 150. —C. Pollen showing prothallus cells within. After Renault.
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 Ptygmophyllum 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
GINKGOALES AND CONIFERALES

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 (Harris, 1951).

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.

*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*.

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**Fig. 125.** Cone Scale of *Pseudovoltzia*. A. An outline drawing of the ventral surface of the scale. 1, 2, the two small lobes; 3, 4, 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.
*exelsa* 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.

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, Metasequoia,* 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. Williamsoniaceae. Flowers borne on relatively slender stems or pedicels and fully exposed.
   Genera—Wielandiella; Williamsoniella, Williamsonia.

   Genus—Cycadeoides (= Bennettites).

1. Williamsoniaceae. 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 Anomosamites 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. § 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 Tuetiopteris type and three flowers. About § 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, B, and C from Zimmerman; after Thomas.
BENNETTITALES AND CYCADALES

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. 167). 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, Otomezamites, 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.

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 gynoeceum 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. **Bennettitaceae. Cycadeoides** (= *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, how-

![Image of Cycadeoides](image-url)

**Fig. 130.**—*Cycadeoides columnae*. 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-C 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).

ever, 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 petrifications, some of them of almost complete plants, which were found in Jurassic or Cretaceous strata in Dakota, U.S.A., and described by Wieland (1906).

The trunks (Fig. 130), unlike those of the Williamsoniaceae, are usually short and thick and bear a very close resemblance to
Macrobotamia 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 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. 133). 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 Cycada but the cuticular structure is quite different.

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 *Cyco-deoidea* 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. dacotenx*. 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 Pteridospersms.

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 Williamsoniae. 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. albicans, 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-
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.

Relationships of the Bennettitales to other Groups.—There is no doubt of the close relationship of the Williamsoniceae to the Bennettitaeae. 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 Bennettitaeae 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 Cycadaeae 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 Cycadaeae 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.
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<td>Grand Canal</td>
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<td>Ganges</td>
<td>Taj Mahal</td>
</tr>
<tr>
<td>Europe</td>
<td>Rhine</td>
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</tr>
<tr>
<td>USA</td>
<td>Mississippi</td>
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</tr>
<tr>
<td>Canada</td>
<td>St. Lawrence</td>
<td>CN Tower</td>
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**Notes:**
- The table lists key geographical features and historical landmarks from selected regions around the world.
- Each entry includes a major river, a notable structure, and a significant historical monument or cultural site.

**Table C**

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<tr>
<td>Great Britain</td>
<td>Thames, London Eye</td>
</tr>
<tr>
<td>China</td>
<td>Great Wall, Forbidden City</td>
</tr>
</tbody>
</table>

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**Other Regions:**
- Middle East: Suez Canal, Great Pyramid of Giza
- South America: Amazon River, Machu Picchu
- Africa: Nile River, Pyramids of Egypt
- Australia: Great Barrier Reef, Sydney Opera House
- Japan: Mt. Fuji, Tokyo Tower
- Russia: Volga River, St. Isaac's Cathedral

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**Acknowledgments:**
This table was compiled with data from various sources including travel guides, historical accounts, and cultural heritage sites.
CHAPTER XVI
ANGIOSPERMAE

The Angiospermae 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 Angiospermae 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 on p. 6) 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.

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

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**Fig. 138.—** Fossil Angiosperms. A. *Sabalites Ungerii*, an Upper Cretaceous Palm from Texas, ¼ nat. size. After Dorf, 1930.—B. Pollen grain cf. *Nelumbium* Jurassic, Sutherland, side view.—C. Similar grain polar view. B and C after Simpson; both x 1000.—D. *Betula nova*. Leaf from peat of Glacial age, Cambridgeshire. Perithecia of two types of fungi are present on the leaf. x 11.
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 was 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 distinguished 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 Aprian 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 Archichlamydaceous families, and in particular the Nymphaeaceae and Magnoliaceae, in the earliest floras containing Angiosperms suggests that the simple Ranalian 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 earliest record of Monocotyledons assuming a dominant rôle in the vegetation of an area are afforded by grass fruits found at several horizons in the Miocene and Pliocene in the western part of the United States (M. K. Elias, 1942). In that part of the world we find evidence that the widespread subtropical and warm temperate forests which during the latter part of the Cretaceous and in the early Tertiary covered the lowland areas, which are now deserts or semi-deserts, were gradually replaced by dry subtropical forest, scrub, and chaparral. These in turn were succeeded by grassland and scrub which became extensive during the late Tertiary. It is suggested that the Angiosperms which at present occupy these desert areas were probably slowly evolved by natural selection from those constituents in the Early Tertiary forests on which the increasing aridity of the area had a selective action (Axelrod, 1950). There is evidence that many of the other deserts in the world have had a similar history. It is interesting to note that the appearance of these grasslands in North America and the rapid evolution of the modern horse during the late Tertiary are related phenomena.

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

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.

4 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.

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.

At Ardnamurchan and Mull in Scotland, Simpson (1936) records lignite seams with rich pollen floras at two Tertiary horizons. The earlier of these, the Ardnamurchan seam, is exposed below the first of the lava outpourings of the extensive basaltic plateau of this region and is believed by him (1951) to be of Oligocene age. The later, Mull seams, are associated with a sedimentary intercalation within the lava succession, some hundreds of feet above its base. These lignites are believed to be of late Miocene or even early Pliocene age.

Dr. Simpson's full results are not yet published, but he has kindly provided the information contained in the following paragraphs.

"The Ardnamurchan floral list comprises angiosperms only, and includes the following genera: *Aponogeton, Casuarina, Balanops, Fagraea, Lambertia, Petrophila, Alnus, Engelhardtia, Haloragis, Euryale, Nelumbo, Larix, Magnolia, Menispermum, Buchhania, Corylopsis, Dicorypha, Eustigma, and Platanus.*

The Mull list is longer and in contrast it contains gymnosperms as well as angiosperms. The genera recognised include: *Ginkgo, Cedrus, Cryptomeria, Cunninghamia, Metasequoia, Picea, Pinus, Podocarpus, Pseudolarix, Taxodium, Aponogeton, Dryandra, Lambertia, Petrophila, Alnus, Corylus, Planera, Morus, Haloragis, Acer, Sapindus, Eucypelaea, Buchhania, Corylopsis, Hamamelis, Platanus, Eucalyptus, Cornus, Castanea,* and *Quercus.*

The results agree with those of other British workers in showing how profoundly these Tertiary floras differ from the present-day flora of north-west Europe. Not only did they contain floriastic
elements—East Asian, North American, Australian, and South African—now vanished from Europe, a feature most interesting in itself, but, what is probably of greater significance, there occurred in some families a grouping together of genera themselves now widely dispersed. Thus in the Ardnamurchan flora the Proteaceae were represented by genera now exclusively Australian and exclusively South African, and in the Hamamelidaceae Dicoryphe, whose habitat is now Madagascar, is associated with various East Asian genera of the family. It is also unquestionable in the case of wide-ranging genera such as Acer, Alnus, and Cornus that the fossil species are most closely related to living Asiatic and American species. Both the Ardnamurchan and Mull floras, viewed as wholes, suggest widely different climatic conditions, particularly conditions of temperature, from what now prevail in this latitude (56° N.). It is suggested that the nearest natural habitat of these floras now would be Portugal, Spain, and Northern Africa, that is to say, at least 20° of latitude nearer the Equator.

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.

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 today.

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
FLORAS AND CLIMATES OF THE PAST

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 annular 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. One of the most interesting theories is that propounded by Wegener to explain 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 separated 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.

Another theory is offered by the astrophysicists (Hoyle, 1950, pp. 54-60). Part of the radiation we receive from the Sun is produced by the impact on its surface of interstellar material in gaseous form attracted to it by gravity. The rate of supply of gases to the solar surface depends on the relative speed of the Sun and the interstellar material. The Sun’s speed through the gases must be changing continuously owing to disturbances such as eddies and vortices in the gas. The slower the Sun is moving relatively to the gas the greater will be the rate of absorption and radiation. This increase in radiation would increase the cloudiness of the polar regions on Earth and this in turn would result in a
raising of the winter temperature. This theory would offer a
reasonable explanation not only of the more luxuriant vegetation
in the polar regions in the past history of the Earth but also of the
glacial periods which have occurred.

Perhaps the most important characteristic of living organisms
is adaptation by natural selection to the conditions under which
they live. From our studies of the fossil plants of the Silurian and
Devonian we get a clear impression of simplicity in organisation
in comparison with that of many living plants. Many exhibit a
thalloid form with no differentiation into leaf, root, and stem,
and it is not until we come to the latter part of the Devonian that
we encounter plants with the extensive flat photosynthetic sur-
faces presented by the leaves or fronds of the majority of later
plants. Professor F. O. Bower has repeatedly emphasised that
in the Pteridophyta at any rate there seem to have been evolu-
tionary changes leading to progressively greater adaptation to
existence on land.

One of the most striking general transformations that has
occurred is the increasing degree of protection afforded to
the sporangium, especially the megasporangium. The exposed
massive terminal sporangia exhibited by many of the Silurian
and Devonian plants and well illustrated in Rhynia are succeeded
in later periods by smaller thinner-walled sporangia which are
protected during their early development in various ways. In the
Lower Carboniferous Salpingostoma or Calathospermum the
megasporangium is found surrounded by partially concrescent
structures which form a sheath round its base.

The summit of the megasporangium is exposed and the
micropyle so characteristic of Gymnosperms and Angiosperms
was evidently formed by the almost complete closing in of the
integuments. This stage was also attained in the Carboniferous
and is shown in Trigonocarpus and other seeds of the same
period. Finally there was the evolution of Angiospermy with
complete enclosure of the ovules.

These changes are undoubtedly related to the advantages of
greater protection of the megaspore and its contents, especially
the embryo which develops on the parent plant. In Angiosperms
insect pollination and the production of succulent and other types
of fruit probably followed and led to greater efficiency in the use
of pollen and in wider dispersal of the seed. It is the Angiosperms
that have become the dominant plants in the modern world and
they are the plants which show such wide range of adaptability to various terrestrial environments.

While undoubtedly the evolution of plants has been largely influenced by the climates and physical geography of the Earth’s surface affecting the action of natural selection, we must not forget that the vegetation has itself had an important affect in modifying the physical environment. The formation of calcareous reefs, the stabilisation of mud and sand surfaces, the control of drainage and the rôle of forests as water retainers and their influence on atmospheric humidity are all instances of this. Dr. Julian Huxley (1951) writes:

“Life in its entirety is seen as another name for the process of biological evolution. That process automatically results from self-reproducing but self-varying living matter interacting with its physical and biological environment, through the indirect intermediation of natural selection. It is irreversible, and constantly produces novelty and increasing variety. Like other processes, it takes a definite time to run its course—rather over a thousand million years, to be as precise as is at present possible.

In transforming itself, life also transforms its environment, even its inorganic environment. The rocks of the earth’s crust, its covering of soil, the composition of its atmosphere, the distribution of temperature and pressure and moisture over its surface—these and much else are different because of biological evolution.

If asked to name the most significant characteristic of the process of evolution by natural selection, I would say the fact that it steadily reveals new possibilities inherent in living matter. The upper limit attained by life in respect of complexity, of knowledge of and control over environment, of independence of external change, of individuality (or more correctly individuation), of internal harmony of parts and many other properties, have constantly risen during geological time.”
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