Extinct plants and problems of evolution : founded on a course of public lectures delivered at the University college of Wales, Aberystwyth, in 1922 / by Dukinfield Henry Scott ; with 63 figures and a frontispiece.

EXTINCT PLANTS AND PROBLEMS OF EVOLUTION

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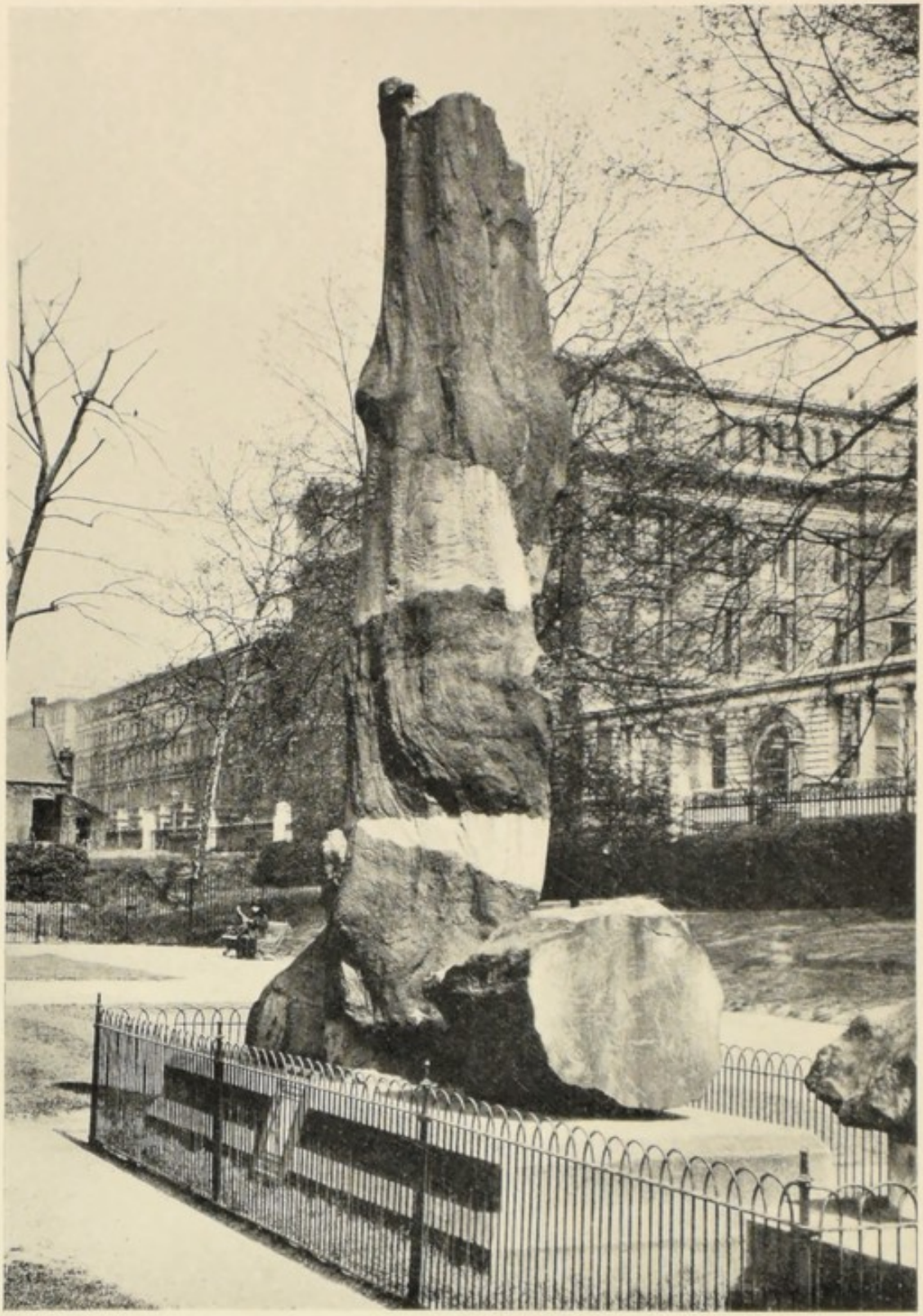

Frontispiece [*Photo by H. G. Herring, N.H. Museum, London*

Pitys Withami, the Craigleith Tree. Main trunk and detached portion; in the garden of the British Museum (Natural History). See p. 150.

EXTINCT PLANTS AND PROBLEMS OF EVOLUTION

Founded on a Course of Public Lectures delivered at the University College of Wales, Aberystwyth, in 1922

BY

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"STUDIES IN FOSSIL BOTANY," "AN INTRODUCTION TO STRUCTURAL BOTANY," ETC.

WITH 63 FIGURES AND A FRONTISPIECE

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TO

CERTAIN NAMELESS BENEFACTORS
OF LEARNING,

WHO ENDOWED THE COURSES OF PUBLIC LECTURES IN THE
UNIVERSITY COLLEGE OF WALES, ABERYSTWYTH,
THIS BOOK IS DEDICATED

PREFACE

THE lectures on which this book is based were addressed to a general audience, by no means wholly botanical. In rewriting the text for publication my aim has been to maintain the original character of the course, and to treat the subject in a way intelligible to a wider circle than that of botanical students.

The investigation of extinct plants has made great progress of late years; it is a matter of interest to consider the bearing of the results so far attained on the Theory of Descent and the problems involved in it.

The first chapter of the book is introductory and contains a brief discussion of some current problems of Evolution and of the present position of Darwinism. In the succeeding chapters the geological history of the Plant-kingdom is sketched, in broad outline, in its relation to evolutionary questions. The method adopted is to trace rapidly the succession of past Floras, beginning with the most recent, and working back, step by step, to the earliest known beginnings of a land-vegetation. In conclusion, the general results of the survey are indicated, as bearing on the problems of Evolution stated in the first chapter.

The interest of the subject at the present time lies rather in the questions raised than in the solutions already reached. The greatest problems regarding the evolution of the plant-world remain open; attention is specially directed to these outstanding questions. Though we cannot, as yet, get very far with our theoretical conclusions, the ancient plants are in themselves well worth our study

and their attractions are enhanced by the mystery which still hangs around their origin.

References in the footnotes are given in an abbreviated form (*e.g.* " Osborn, 1913 "). The detailed references will be found in an alphabetical list at the end of the book.

The illustrations are from various sources. I am much indebted to colleagues (mentioned under the figures in question) who have supplied the originals. Special attention may be called to the fine restoration of *Neuropteris heterophylla* (Fig. 33) drawn by Miss Janet Robertson and lent by Prof. T. G. Hill.

A large number of the cuts have been drawn or redrawn by Mr. G. T. Gwilliam, F.R.A.S., whose initials only appear in the case of his more original drawings. Many of the new photographs were taken by Mr. W. Tams.

My wife, Mrs. D. H. Scott, F.L.S., has undertaken the preparation of the Index.

To all these collaborators I desire to render my thanks.

D. H. Scott.

October 26, 1923.

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EXTINCT PLANTS AND PROBLEMS OF EVOLUTION

CHAPTER I

INTRODUCTORY. SOME CURRENT PROBLEMS OF EVOLUTION. POSITION OF DARWINISM. BEARING OF FOSSIL BOTANY ON THE QUESTIONS AT ISSUE.

A NATURALIST of my generation has a certain advantage in being able to remember the early days when Darwinism was still young, and had as yet by no means become popular. One can recall how, some fifty years ago, there were some otherwise intelligent families where the name of Darwin was almost like a bad word, which one did not care to utter, lest it should shock one's elders. One hardly dared to bring the "Origin of Species" into the house, and even such a harmless book as the "Fertilisation of Orchids" was rendered suspect by the name of the author.

Even ten years later, I remember hearing a lecture by a worthy Nonconformist divine, in which Darwinism was dismissed as "the offspring of the sin-diseased brain."

But all this time the theory was rapidly winning its way; we witnessed its complete success, and all but universal acceptance by scientific men, while among the general public it became the fashion, and was warmly defended even by theologians, some of whom, perhaps, had once been among its bitterest opponents. There is a story that Prof. Huxley, after listening to a strong, pro-evolutionary sermon, said to a scientific friend who was with

him, "Why, these gentlemen will soon be burning us for not going far enough!"

And so the victorious career of the Darwinian doctrine went on, till most of us entertained the comfortable thought that the main problem of the origin of living forms had really been solved and that only the details needed filling in. But, even then, there were some that doubted.

The term "Darwinism" has the authority of Wallace, the fellow-originator of the theory, who in 1889 published a brilliant exposition of the doctrine, under the title "Darwinism." What, then, is really meant by this word, so universally used, but not so universally understood? Many people who loosely employ the word "Darwinism" no doubt imagine that it is essentially the same thing as Evolution. In reality, of course, the idea of evolution is immensely older than the time of Darwin. We all know that Lamarck, at the beginning of the nineteenth century, was a confirmed evolutionist. So was Erasmus Darwin, grandfather of Charles, a little earlier. We find the doctrine foreshadowed in Buffon, half a century before, though in those days he had the fear of the Church before his eyes and found it necessary to guard his words.

The idea of evolution has been traced back to quite early days of Greek philosophy. Prof. H. J. Rose, of Aberystwyth, has called my attention to the following passage quoted from Anaximander, who died about 545 B.C.: "He says, moreover, that in the beginning man originated from animals of a different species, because the other animals soon are able to get their food, but man alone needs long nursing; wherefore being what he is he could not otherwise have survived originally."

In so far as this old philosopher believed in the origin of man from other animals, he may be called an evolutionist, but, as Osborn [1] points out, the more closely we examine his

[1] Osborn, 1913, p. 33.

theories, the less they seem to resemble modern ideas. It is, of course, quite inadmissible to try to read the ideas of modern science into the speculations of ancient philosophers.

Empedocles (495–435 B.C.) has been called "the father of the Evolution idea," for he appears to have maintained, that he himself had formerly existed as a bush, a bird and a fish. It is probable, however, that his ideas had more in common with the metempsychosis of Pythagoras and the Easterns, than with any scientific conceptions of later days. At the same time, Empedocles and his followers have some claim on the interest of botanists, for they had a good deal to say about plants; they imagined "that plant life came first and animal life developed only after a long series of trials." [1] They were fond of comparing plants with animals, and held that the former, like the latter, possessed a "soul."

Some of the early writers may seem to have had an idea of something like natural selection, for they speak of the extinction of monstrous forms, and the survival only of more normal creations. But it seems that what they had in view was really the disappearance of the mythical Centaurs, Chimæras and so on.

Xenophanes (576–480 B.C.) is said to have been the first to recognise fossils as remains of once living animals. This was a real advance in science, and of much more value than guesses at something which we can interpret as a sort of Evolution.

Anaxagoras (500–428 B.C.) seems to have had some idea of design in Nature and thus to have been the father of the school which we associate with the name of Paley. It has rightly been pointed out that the doctrine of design was a necessary step in biology, for it implied a recognition of adaptation.

Aristotle (384–322 B.C.) was, of course, on quite a different level from any of his predecessors. As Osborn says, "he,

[1] Osborn, *l.c.*, p. 37.

by the force of his own genius, created Natural History." He himself fully realised that he was making altogether a fresh start. From his extensive studies of animal forms, he was led to the conception of a genetic chain, stretching from the polyp up to man, and may perhaps be called the first evolutionist. In fact, his single-chain theory held the field, among all who adopted evolutionary ideas, up to the beginning of the nineteenth century.[1]

Among later writers, the poet Lucretius (99–55 B.C.) (Epicurean) in some passages expresses quite modern-sounding ideas about living things. For example, he pointed out how, while wild animals are preserved by their strength, speed, or cunning, domesticated animals owe their preservation to their utility to man.[2]

Cicero (106–43 B.C.), on the other hand (a Stoic), took a more crudely teleological view, holding that living creatures exist for the sake of man. It appears that Cicero to a considerable extent anticipated Paley's famous argument from design.[3]

Lucretius further had the thoroughly scientific conception of a succession of dominant races; as one form decays and languishes from age, another emerges and takes its place.

It is interesting to see that the free speculation of the Greeks and their Roman disciples survived to a certain extent among the early Fathers of the Church, especially Augustine (354–430 A.D.), who, it has been said, " distinctly rejected Special Creation in favour of a doctrine which, without any violence to language, we may call a theory of Evolution." [4] It was not till much later times that the doctrine of special creation became a dogma of orthodoxy and at the same time a principle of conservative science.[5]

[1] See Osborn, *l.c.*, p. 44.
[2] Lucretius, " De Rerum Naturâ," v, 853 *et seq.*
[3] Cicero, " De Naturâ Deorum." [4] Osborn, *l.c.*, p. 72.
[5] For classical references I am much indebted to both Prof. H. J. Rose and Mr. F. Escombe and desire to express my warm thanks, only regretting that it has been impossible to do any justice to the subject within the limits of this little book.

Thus Evolution, or the Theory of Descent, though the most important, is by no means the most characteristic feature of Darwinism. The foundation of the Darwinian doctrine was laid by the joint papers of Darwin and Wallace, communicated to the Linnean Society by Lyell and Hooker on July 1st, 1858, under the title, "On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties by Natural Means of Selection." The essential point of the theory is the "Origin of Species by Natural Selection or the preservation of favoured races in the struggle for life," the "favoured races" being, of course, those varieties which happen to be best adapted to the prevailing conditions. This was the theory which for a long time dominated biological thought, though there were always some rival hypotheses in the field. Samuel Butler, for example, was a famous writer (though more literary than scientific) who never accepted Darwinism and had a theory of his own, brilliantly set forth in his books "Unconscious Memory," "Luck or Cunning," and others.

Prof. Bateson in 1894,[1] in his book "Materials for the Study of Variation," showed how far we were from having solved the problem of Specific Difference, and while not opposing the theory of the origin of species by means of Natural Selection, pointed out how baseless were many of the assumptions commonly made by Darwinians, on such matters as heredity, reversion, and supposed continuous variation.

In spite, however, of such doubts and criticisms, Darwinism still continued to prevail, and dominated Biology, especially in this country and in Germany, up to the year 1900, which may be taken as the critical period in its history.

A few years previously the able work of Weismann on the continuity of the germ-plasm had greatly strengthened the extreme Darwinian position, in so far as it tended to

[1] Bateson, 1894.

show that all inheritable variation must arise in the germ-cells, and thus be uninfluenced by the direct action of the external environment on the individual. This excluded the Lamarckian factor of the inheritance of acquired characters, which Darwin himself had always recognised as an adjunct to his main theory. Weismann, in 1893, published an essay under the title, "The All-sufficiency of Natural Selection," which we may regard as marking the zenith of Neo-Darwinian speculation.[1]

The work of Darwin and Wallace was, indeed, completely, and we believe finally, successful in establishing once for all the doctrine of evolution, or the origin of organic forms by descent with modification. Major Leonard Darwin has recently put on record a remark once made in conversation by his father: "After all, evolution is the great thing, not natural selection."[2] That is true, and the greatest work Darwin did was to teach the world to believe in evolution. This, so far as one is able to say it of any scientific theory, is a permanent acquisition. It was to a great extent the specially Darwinian theory of natural selection which, by supplying a *vera causa*, convinced people of the truth of evolution. As Weismann said, it was through the theory of selection that the doctrine of development was first firmly established. At the same time Darwin's skilful marshalling of the general evidence for evolution no doubt contributed to his success. He and Wallace may be said to have brought the whole question out of the domain of speculation into that of science.

A year or two ago I was called on to give an address to the Botanical Section of the British Association, and on that occasion I ventured to speak of the Darwinian period as past; I think that statement was justified; we do not, of course, mean by it that we are likely to give up our belief in evolution; that is not in question. What we do mean

[1] Weismann, 1889 and 1893. [2] Leonard Darwin, 1921.

is that the special Darwin-Wallace theory of the origin of species by variation and natural selection is seriously shaken. This change dates from the year 1900. It was the Austrian monk Mendel, already long dead, who brought about the revolution.

Mendel's work had been done a whole generation before the time of which we are speaking; in fact it was not much later than Darwin's, for the "Origin of Species" came out in 1859 and Mendel's "Experiments in Plant-hybridisation" about 1865. But his conclusions attracted no attention whatever at the time. The distinguished German botanist Nägeli was a correspondent of Mendel's and knew what he was doing, but he seems never to have realised in the least the importance of the results attained.

Mendel was born in 1822, entered the Königskloster at Brünn in 1843, became Prelate of the monastery in 1868, and died in 1884. His scientific work, much of which remained unpublished, belongs to the period 1856–1872. His later years were taken up by somewhat trying monastic business, and his health failed. It was not till 1900, sixteen years after his death, that his work, published in the *Proceedings* of the Brünn Natural History Society, was rediscovered independently, by De Vries in Holland, Correns in Germany, and Tschermak in Austria. Then at last justice was done to the able investigations and sound conclusions of the clear-headed Austrian abbot.[1]

The main points of Mendelism are now familiar. Mendel's crossing experiments were carried out in the monastery garden, and the most important were made with different races of the garden pea (*Pisum sativum*). Here we need only recall the simplest possible example. There are tall peas averaging about six feet in height, and dwarf peas about one foot high. Mendel crossed these races and raised the seeds. It might have been expected that he would have obtained some intermediate form, but this was

[1] Bateson, 1909.

not the case. The whole of the first generation (F1) resulting from the cross consisted of tall peas, at least equal in stature to the tall parent. Then Mendel self-fertilised the F1 plants, and the second generation (F2) was found to be made up of both tall and dwarf plants, in the proportion of three talls to one dwarf. Here tallness was the dominant character and dwarfness the recessive, to use Mendel's own terms. Further breeding showed that of the three talls one (on the average) bred true, giving talls only; while the remaining two-thirds segregated out again in the same proportion as before. On the other hand, *all* the dwarfs bred true. When both factors are present in the cross only the dominant shows itself in the offspring—hence the impure (mixed) individuals appear like the pure dominants. Where only the one character is represented (*i. e.* where the race is pure) of course only that one can show itself. Hence *all* the recessives (dwarfs) breed true, for the recessive character can only show itself if the dominant factor is absent. Only one-third of the F1 plants showing the dominant character (tallness) breed true, because they alone contain the dominant to the exclusion of the recessive factor; the remaining two-thirds are mixed, containing both factors, and therefore segregate on breeding in the same way as the preceding (F1) generation.

Mendel made many other experiments, crossing races of Peas which differed in the form of the seed, the colour of the seed-coat, the colour of the cotyledons inside the seed, and so on, and in all cases the result was the same—one of the two alternative characters proved to be dominant, the other recessive, and segregation in the second and succeeding generations took place in the same proportions as in the first example we have chosen.

Naturally, it often happened that the plants crossed differed in more than one character, *e. g.* in the shape or colour of the seed, as well as in the stature of the plant.

In such cases, which are the rule in practice, different combinations result in the successive generations, according to the dominant or recessive nature of the characters in question.

Mendel's theoretical interpretation of his results has been expressed by Punnett in the following words: "He conceived of the gametes [sexual cells] as bearers of something capable of giving rise to the characters of the plant, but he regarded any individual gamete as being able to carry one and one only of any alternative pair of characters. A given gamete could carry tallness or dwarfness, but not both. The two were mutually exclusive so far as the gamete was concerned. It must be pure for one or the other of such a pair, and the conception of the purity of the gametes is the most essential part of Mendel's theory." [1]

On this simple foundation the great modern science of Genetics has been built, by the labours of a large number of investigators, among whom our countryman Bateson is one of the chief. Many complications have been found, and various subsidiary hypotheses have had to be called in to interpret them, but the original Mendelian conclusions form the basis of the whole structure.

It has been quite truly said that Mendelism is a theory of Heredity, not of Evolution; but it has had a profound influence on evolutionary ideas, and has in fact changed the whole outlook. This it has done, in the first place, by bringing in experiment, as the main method of investigation. It was a just reproach of Bateson's against the Darwinians that they had, on the whole, neglected experiment. To a considerable extent Darwin's theory was based on the unconscious experiments of breeders and cultivators in raising new forms of domestic animals and field or garden plants. Darwin relied very much on their results, but there was rarely any trustworthy record to show how they had been obtained. Mendel showed the way to scientific

[1] Punnett, 1912, p. 18.

experimenting; its results, so far, have not been favourable to Darwinism.

Mendelian experiment has established the existence of definite unit characters which do not appear to be subject to change. This result is opposed to the Darwinian idea of the gradual accumulation of minute differences, under the influence of Natural Selection. As Bateson has recently said: "The central tenet of Darwinism that species are merely the culmination of varietal differences such as we find contemporaneously occurring, is not easily reconcilable with the new knowledge." [1] In fact, the origin and nature of species, which Darwinians thought had been satisfactorily explained, are now seen to remain utterly mysterious.[2] In particular, the old crux of the sterility of inter-specific hybrids still baffles the geneticist; he finds no clue in his experiments to the origin of this very general characteristic of natural species.

Thus the great growth of our knowledge of genetic constitution, derived from Mendelian experiment, so far from clearing up the question of the origin of species, has only shown that our old Darwinian conceptions are unproven, and that all is again in the melting-pot.

Partly as the result of Mendelism, partly from other causes, the idea of variation, as Darwinians understood it, is discredited, or at least our ignorance of it shown up. Darwin believed that variation was an obvious truth. He found, as he thought, variations in abundance, everywhere available for the making of new species. As a matter of fact, the position is by no means so favourable.

The small variations which are so common, and on which the Darwinian tended to rely, as the material for natural selection to work on, have turned out for the most part to be mere fluctuations, oscillating about a mean, and therefore incapable of giving rise to any permanent new forms. Such fluctuating variations appear to depend on some

[1] Bateson, 1922. [2] *Ibid.*

action of the environment on the individual, and not to indicate differences in the germ-cells.

Again, every botanist was familiar with species which were supposed to be highly variable, the varieties often being well marked, and such as might well represent nascent species. The Whitlow Grass (*Erophila verna*), the little Crucifer which grows on old walls, is a familiar example of a common plant with very numerous " varieties." It appears, however, that we are not justified in calling such forms " varieties." The view now commonly accepted, in accordance with Jordan's conclusions from his cultures many years ago, is that they are fixed and constant " elementary species," the origin of which is as unknown as that of the larger units, the Linnean species, of which they form part.

Recent genetic work, however, as Dr. Lotsy kindly informs me, is throwing a new light on the supposed " micro-species " of *Erophila*. It now appears that many of these forms are apogamous races, *i. e.* races in which the seed develops without fertilisation and that they owe their constancy to the loss of sexuality. In cases where a cross has been effected, the offspring, in the second generation, may become apogamous. If these phenomena should prove to be general, it would follow that the " elementary species " are not species at all, but neither are they varieties in Darwin's sense; they are merely non-sexual races.

Thirdly, there are the " mutations " of De Vries. The eminent Dutch botanist thought that he had found the true origin of species in the occasional occurrence of relatively sudden changes, which he called Mutations. Such " permanent and transmissible variations " were chiefly observed by him in an Evening Primrose, *Oenothera Lamarckiana*, which he investigated. He was the first to point out the essential distinction between the fluctuational variations already referred to and actual genetic variations or mutations. But the true interpretation of

De Vries' own results is open to much doubt; as Bateson has recently said: "We see novel forms appearing, but there are no new species of *Oenothera*, nor are the parents which produce them pure or homozygous forms." [1]

Hence the De Vriesian mutations have been interpreted as Mendelian segregations, the result of a previous cross. The changes, however, do not seem to admit of so simple an explanation; distinct mutations really occur, but they appear to be of a very peculiar kind. The remarkable changes observed have proved, in many cases, to be correlated with irregularities in the number of the chromosomes, those constituents of the nucleus which appear to be the transmitters of hereditary characters. Normally, the number of chromosomes is constant for each species, becoming reduced to half before fertilisation and again restored to the full number when the nuclei of the sexual cells unite. Now in the mutant *Oenothera lata*, which has been obtained from several different "species" of the genus, the number of chromosomes is fifteen, while in the parents it is only fourteen. A chromosome has entered the wrong nucleus, and so the normal distribution is upset. The form *lata* has various peculiarities, among which "almost completely sterile anthers" are included. Thus the mutant would not have much chance of survival in real life. In other cases, the typical number of chromosomes is doubled, as in *Oenothera gigas*, a form abnormally large in all its parts. We may agree with Dr. Ruggles Gates, the chief investigator of mutation in this country, that the origin of species by doubling of chromosomes is not likely to have been a common occurrence in Nature.[2]

One gets, in fact, the impression that to a certain extent "Mutation" is concerned in the origin of monstrosities rather than the evolution of species. It may be, as Dr. Gates suggests, "that even mutational monstrosities have

[1] *Homozygous*, formed from two sexual cells both bearing the same characters; therefore not a cross. [2] Gates, 1909, p. 547, and 1920.

played their part in the production of species." [1] Still, one can scarcely accept mutation, in the present state of our knowledge, as a very promising kind of variation from an evolutionary point of view.

Thus it appears, on a general survey, that we are still surprisingly ignorant of variation as a source of new species. Dr. Lotsy, in 1916, went so far as to say : " The perplexity of the subject . . . is caused, in my opinion, by the simple fact that inheritable variability does not exist." [2]

How then, on such a view, is evolution possible? Dr. Lotsy replies : " For hereditable variability read segregation." Segregation is the separation, in the sexual cells, of the two factors of an alternative pair; *e. g.* we saw, in the case of Mendel's tall and dwarf Peas, how the factors for tallness and dwarfness segregated in the offspring of the cross. From an evolutionary point of view, segregation is the isolation by crossing of a race pure for some particular character.

Segregation and crossing bring about an infinite reshuffling of characters or rather factors. The reshuffling of characters, however, could give us nothing new. Out of the tall and dwarf Peas one gets nothing but talls and dwarfs in certain proportions; we must assume that here there is a single factor for each character. Where this is not the case, the character depending on more than one factor, other combinations become possible and quite new forms may result from crossing. For example, there is the famous case of crossing two white Sweet Peas which gave, in F1, a purple-flowered offspring—the " Purple Invincible." In the next generation segregation takes place, but various coloured strains, including the " Purple Invincible," are persistent. That colour is produced from whiteness in such cases is due to the fact that two factors (at least) are concerned in the development of colour, determining the formation of two chemical bodies

[1] Gates, 1920, p. 216. [2] Lotsy, 1916, p. 41.

which must react on one another to form the pigment. In each parent only one of these factors is present.

Many such cases are known to Mendelians. To take a striking instance. Dr. Lotsy crossed two quite normal petaloid forms of Campion (*Lychnis* [1]), and produced an entirely novel type which had no petals at all! This startling result shows how great a transformation, rarely paralleled in the genus, may be effected simply by crossing. It appears, however, that these apetalous Campions were sterile, so, like many "mutations," they would not have much chance in Nature.

Dr. Lotsy further crossed a great many forms of *Antirrhinum* (Snapdragon) with surprising results. Some of the forms obtained had flowers quite unlike a typical *Antirrhinum;* thus on crossing *A. glutinosum* with a red form of the familiar *A. majus*, in the F2 generation, "several remarkable forms occurred, in one the sepals were coloured and petaloid, another showed several spur-like excrescences at the lower lip of the flower, and some had flowers astonishingly different from those of the parent-species, resembling more a *Rhinanthus* [Yellow Rattle] than an *Antirrhinum* and of a type entirely unknown hitherto within this latter genus." [2]

No doubt anyone seeing for the first time Dr. Lotsy's wonderful collection of forms obtained solely by crossing would be impressed by them as splendid material for the origination of species. And Dr. Lotsy himself does, in fact, hold that the origin of species is effected by hybridisation; "the cause of evolution lies in the interaction of two gametes of different constitution." [3] Species (in the ordinary, Linnean sense) owe their origin to the occasional possibility of a cross, and their persistence to the bars to intercrossing.[4]

Other authorities, however, do not agree with Dr.

[1] The Campions are placed in the genus *Melandrium* by Continental botanists.

[2] Lotsy, 1916, p. 128. [3] *l.c.*, p. 65. [4] *l.c.*, p. 99.

Lotsy in rejecting inheritable variation. The difference turns partly on the meaning attached to "variation," which seems sometimes to be used to include segregation. Thus Prof. Bateson, in his recent address at Toronto, said: "Then came the Mendelian clue. We saw the varieties arising. Segregation maintained their identity." [1] But the only varieties that the Mendelian sees arising, in the ordinary course of his experiments, are the product of crosses. The author adds: "Plenty of the Mendelian combinations would in Nature pass the scrutiny of even an exacting systematist and be given 'specific rank.' In the light of such facts the origin of species was no doubt a similar phenomenon." So far this is all in agreement with Dr. Lotsy's theory, but the lecturer was speaking of the position when Mendelism was young, and points out that by now "Faith has given place to agnosticism."

Variation, however, other than by segregation, is recognised. Prof. Bateson tells us that "we have no difficulty in finding evidence of variation by loss. Examples abound, but variations by addition are rarities, even if there are any which must be so accounted." [2] Whether any evolution is possible by the continued loss of factors may well be doubted. To Dr. Lotsy and to many others "evolution by a process of repeated losses is inconceivable." [3] On the other hand, it has been held that the course of evolution may conceivably be represented by "an unpacking of an original complex which contained within itself the whole range of diversity which living things present." This tremendous assumption, which has been said to make a greater demand on our faith than any doctrine in any theology, has been ingeniously defended by Mrs. Arber in her recent excellent book on "Water Plants." The passage is too long to quote, but the gist of it lies in the sentence: "Every evolutionist must suppose that, as the descendants of the primæval speck of protoplasm multiplied and

[1] Bateson, 1921, p. 2. [2] *l.c.*, p. 4. [3] Lotsy, 1916, p. 166.

advanced along diverse lines of development, what they gained in specialisation they lost in plasticity." [1] Thus the supposed loss of Mendelian factors is identified with the admitted loss of potentialities, as organisms become specialised. It may be questioned, however, whether the dropping of factors would not involve a loss of specialisation just as much as a loss of potentialities.

At any rate, it must be admitted that our present knowledge of variation is not such as to throw any clear light on the origin of species. It does not, of course, follow that inheritable variation of an effective kind does not occur; probably Dr. Lotsy goes too far in denying its existence. Experiment has done a great deal, but we must not expect too much from it. Sometimes we must look beyond the seed-frame and the breeding-pen; we cannot expect to reconstruct Evolution even in the best-equipped experimental garden.

In the meantime, Dr. Lotsy's theory of Evolution by Crossing demands serious consideration. It is open indeed to the obvious criticism that if species arise by crossing, there must be something to cross. How did the original forms which first crossed spring into existence? That seems an unanswerable question, unless we assume the variation which Dr. Lotsy denies. Evidently the crossing theory does not explain everything—no theory does. Yet it seems probable enough that crossing may have really played an important part, though not the sole *rôle*, in the origin of species. Occasional small mutations, followed by repeated interbreeding, might well give a vast variety of new forms.

As I have pointed out on another occasion,[2] the theory of the origin of species by crossing, if confirmed, would throw great light on the significance of sexual reproduction. The precise value of sexuality in Evolution has been much disputed by biologists; some have held that it encouraged

[1] Arber, A., 1920, p. 334.

[2] Scott, 1921.

variation, others that it tended to maintain stability. On the crossing hypothesis, the importance of the sexual process at once becomes evident, for races endowed with sexuality would alone be capable of crossing and so of giving rise to a sufficiency of new forms to meet the inevitable changes in the environment. Hence the organisms which we find surviving would naturally be, for the most part, those which are sexually reproduced. Probably this is not the whole truth, but at any rate the crossing theory of evolution helps to render the prevalence of a sexual process intelligible.

I may be permitted to quote, from the address already cited, a passage dealing with another aspect of the theory of evolution by crossing. "Again . . . the crossing theory might be helpful to the evolutionary morphologist, for breeding is open to unlimited experiment, and we might hope to learn what kinds of change in organisms are to be expected. For example, the *Lychnis* experiment shows how easily a petaloid race may become apetalous. Such results might ultimately be a great help in unravelling the course of evolution in the past. We should gain an idea of the transformations which might actually have taken place, excluding those which were out of the question. At present all speculation on the nature of past changes is in the air, for variation itself is only an hypothesis, and we have to decide, quite arbitrarily, what kind of variations we think may probably have occurred in the course of descent." [1]

This sanguine idea, that the Mendelian might, on the crossing theory, be able to tell us what sort of changes were likely to have taken place in the past, receives no support from Dr. Lotsy himself. On the contrary, he declares that "Phylogeny, *i. e.* reconstruction of what has happened in the past, is no science, but a product of fantastic speculations." [2] Why this pessimistic attitude in

[1] Scott, 1921, p. 2.

[2] Lotsy, 1916, p. 140.

an author who has himself published several large volumes on the phylogeny of plants? As he says: "Nobody cares to destroy his own efforts." The explanation may be given in Dr. Lotsy's own words: ". . . we know that evolution proceeds forwards, sidewards, and backwards, along the meshes of a net, so that it is absolutely hopeless to choose out of the many ways, in which one can draw a broken line on such a netting, the one along which evolution has proceeded."

In other words, he is so staggered at the results of crossing experiments, and especially at his own results in obtaining the extraordinary forms (*e. g.* in *Lychnis* and *Antirrhinum*) already referred to, that he fancies that anything may have happened, we cannot tell what. I have even heard it suggested that two Early Devonian plants, the one of unprecedented simplicity, leafless and rootless, the other a highly organised "Coniferous tree," or at least a probable Gymnosperm, might have been segregates from the same cross! Of course this is merely farcical—if you can believe that you can believe anything. It is very doubtful even whether results like Dr. Lotsy's ever occur in Nature, or can be perpetuated if they do occur. In a broad sense, the old doctrine that "like breeds like" still holds good, and this is the one basis on which any attempts to trace descent can be founded. Like Dr. Lotsy, I have become sceptical of late as to most phylogenetic reconstructions, but one need not go so far as he does: in "dim outline," at all events, we may still hope to catch glimpses of the course of evolution.

So much for the still obscure subject of variation. We may next ask, How does it stand with Darwin and Wallace's distinctive theory of natural selection, the essence of Darwinism? That all new forms, however they may arise, have to pass the ordeal of selection is evident—the unfit are certainly weeded out. So much is admitted by everybody, but the modern tendency is to recognise

natural selection only as a "negative force"—it has even been set aside as a "truism." No one, however, who has really understood Darwin and Wallace's theory can be content to dismiss Natural Selection in this offhand way. The doctrine may be true or false; a "truism" it certainly is not. It was not the obvious extinction of the unfit, but the repeated selection of the more fit, with consequent exact adaptation, which was the point of Darwin and Wallace's theory, that the origin of species is by natural selection.

Yet it is true that the only weapon of natural selection is extinction. It can do no more than eliminate the less fit. Its efficacy depends on the strictness with which this elimination is carried out. Artificial selection is not quite on a par, for man can do more; he can cultivate the fit.

Is it possible for a process of elimination to produce positive results? It may be so. Let us take as an illustration a sculptor at work. All he can do is to chisel off chips of marble from his block—he can do nothing more than eliminate the bits that he does not want. Of course, the modern critic might say, he can produce no positive result in this negative way. But he does—he produces the statue. So perhaps it may be possible for natural selection, by constantly removing the less fit, ultimately to produce the fit. It all depends on the fineness with which the process works. Hence the predilection of Darwinians for minute variations.

The special merit of Darwin and Wallace's theory was that it appeared to give a natural explanation of adaptation. As Sir William Thiselton-Dyer said, Darwin "swept in the whole of Paley's teleology, simply dispensing with the supernatural explanation."[1] All Darwinians have been excessively keen on adaptation. A great sign of the reaction against Darwinism is the prevailing tendency to despise teleology and belittle adaptation. One con-

[1] Linnean Society, 1908, p. 37.

stantly comes across this peculiarity in modern biological work. No doubt the anti-adaptation movement is in part a reaction against the too facile assumption, on the part of some Darwinians, of unproved utility in all sorts of biological characters. It has been justly said that there is no limit to the discovery of such hypothetical adaptations except in the fertility of the discoverer's imagination. But this criticism does not in the least affect the manifest fact that adaptiveness is, on a broad view, the main feature of living organisation.

The Darwinian, in fact, possessed, in his theory of natural selection, an admirable means of accounting for adaptation; consequently he made the most of it and sought for adaptation everywhere. The Mendelian, on the other hand, has no such theory; to him all characters, useful or useless, are alike (unless they are actually lethal, so as to put an end to his experiments). Hence he tends, as far as possible, to ignore adaptation. The former tendency was perhaps the more healthy of the two.

There are two questions about natural selection: does it explain adaptation? and does it explain the origin of species? We have seen that theoretically it accounts for the former. But there are difficulties even here. Where, to go back to our illustration, are the sculptor's chips? Do the unfit, the errors, really exist? Probably they do, to some extent, but it is difficult to find evidence in Nature. Selection no doubt takes place, but is it adaptive? We may think of the Parable of the Sower: some of the seeds fell by the wayside, others in stony places, others among thorns; only that which fell on the good ground yielded fruit. Here there is plenty of selection, but it is by the chances of the environment, and survival has nothing to do with the merits of the seeds or seedlings. Undoubtedly a vast amount of the selection that goes on is of this fortuitous, non-adaptive kind, and can in no way help to improve the race.

It is true that among crowded seedlings there is a certain amount of true selection, apart from accidents of position. Certain seedlings survive on their merits, but their superiority over their fellows seems to be of the kind which we vaguely call "constitutional." I am not aware of any direct evidence for survival owing to better structural characters, and it is structural characters with which we are chiefly concerned. The survival of the fittest, it has been said, often means no more than the survival of the survivors.

Here again it is our ignorance of inheritable variation which prevents us from judging of the efficacy of natural selection. Adaptations abound everywhere, but we do not see them arising. In this connection we may well echo Bateson's recent appeal for more co-operation between the Field-naturalist and the Geneticist.

The other question, the significance of natural selection in the origin of species, is closely connected with the adaptation problem. Darwin, as we all know, was convinced that it "has been the most important, but not the exclusive means of modification." [1] On this point Bateson's remarks in his Toronto address may be quoted: "The survival of the fittest was a plausible account of evolution in broad outline, but failed in application to specific difference. The Darwinian philosophy convinced us that every species must 'make good' in Nature if it is to survive, but no one could tell how the differences—often very sharply fixed—which we recognise as specific, do in fact enable the species to make good. The claims of natural selection as the chief factor in the determination of species have consequently been discredited." [2]

Thus the non-utility of specific characters is the point on which Natural Selection, as a theory of the origin of species, is believed to fail. It may account for the origin of adaptations, but in so far as specific characters are non-

[1] "Origin of Species," p. 4. [2] Bateson, 1921, p. 4.

adaptive, it cannot explain them. It is no doubt true that in a large proportion of cases the utility of the features which we use in the diagnosis of species is not proven. And we must beware of assuming a hypothetical adaptiveness for which there is no evidence.

Some writers go further, and assign a very wide range to non-adaptive characters. Dr. Willis wrote a paper "On the Lack of Adaptation in the Tristichaceæ and Podostemaceæ." [1] These families, commonly grouped together as Podostemads, include many extraordinary plants, living on the rocks in tropical streams and cataracts. They are flowering plants, perhaps allied to the Saxifrages, but so strangely modified in their vegetative parts that most of them resemble Lichens, Liverworts or Mosses, rather than Dicotyledons. In some the secondary shoots, in others the main stems, become flattened out into a thallus,[2] which may adhere closely to the rock. In many others it is the root which assumes the form of a thallus, of strange and varied shapes, and bears the flowering shoots; if the root is thalloid, the stem is not, and *vice versâ*.

Dr. Willis says of these plants: "The whole of the extraordinary morphological changes through which they have gone are without any adaptational significance whatever. . . . In spite of the great variety of form and structure, it is impossible to say that any one form is better suited to the conditions of life than any other." [3]

I make no criticism on these remarks; Dr. Willis has perhaps a better knowledge of these strange plants than any other living botanist, and his opinion is of great weight.

At the same time, it may be pointed out that nothing is more difficult than to determine what characters enable a species to "make good"; the same end, as every naturalist knows, is attained by very various means. The common

[1] Willis, 1914.

[2] *I. e.* an organ not differentiated into stem and leaf, resembling a Lichen or a simple Liverwort.

[3] Willis, 1914, p. 546.

Nipplewort (*Lapsana communis*) gets on very well without a pappus, but it would be rash to say that the pappus of other Compositæ had no adaptational significance.

While the Darwinian, as we have seen, laid stress wholly on function, *i. e.* on adaptation, the modern tendency is to take what is sometimes called the mechanical view of organisation. To clear the ground of a possible misconception, we may say at once that to call an organism a "mechanism," though true, is no explanation. A mechanism is "a system of mutually adapted parts working together as in a machine."[1] Paley in his time (and Cicero before him!) took the view that a living thing is a mechanism, but for him what required explanation was the adaptation of the parts.

The mechanical point of view is different. It is well explained by Prof. J. H. Priestley in the introduction to his "Physiological Studies in Plant Anatomy." He says: "It is true that, theoretically, natural selection may explain the existence of any useful working mechanism, but the mere demonstration of usefulness tends to draw a veil over the way in which the mechanism comes into being, and any real explanation of the structure must wait until its development has been traced and interpreted in terms of physico-chemical causation."[2]

Prof. Priestley is here speaking of the ontogeny, the development of structure in the individual plant. Clearly there is room for both methods of research, the mechanical and the functional. The steam engine is a mechanism; we can equally well inquire how the parts were made, and what purposes they serve. The former is Prof. Priestley's line of investigation; the latter that of Haberlandt, in his well-known book on "Physiological Plant Anatomy," and of the Darwinian School generally. Both are equally valuable and necessary.

It is, however, the application of the mechanical principle

[1] Concise Oxford Dictionary.

[2] Priestley, 1922, p. 58.

to evolution which chiefly concerns us here. Prof. D'Arcy Thompson, who is a great exponent of this principle, chiefly on the zoological side, finds, in mathematical considerations "a proof that variation has proceeded on definite and orderly lines, that a comprehensive 'law of growth' has pervaded the whole structure in its integrity, and that some more or less simple and recognisable system of forces has been at work." [1]

If Dr. Lotsy should be right, and we have here for "variation" to read "segregation," this would accord well with the "orderliness" of the process, for segregation, working with definite unit-characters, must give more orderly results than the variation of the Darwinian was likely to afford. However that may be, it seems to be extremely probable that evolutionary changes tend to take place in determinate directions, rather than in a merely indefinite manner.

Even allowing the utmost scope to natural selection, it is evident that the favourable changes available for selection have been different on different lines; each line has pursued its own course, controlled, no doubt, by selection, but directed by internal causes. In this sense, a mechanical theory of evolution may well be justified, though we are still much in the dark as to the determining factors.

The question of the inheritance of "acquired characters," *i. e.* of such modifications as are produced in the body (*soma*) of the individual in response to the environment, has been discussed *ad nauseam*. Experiments are constantly brought forward to prove such inheritance, and they are as regularly discredited, or shown to admit of other interpretations. It would be futile to enter on such controversies here. It may be said at once that the inheritance of mutilations is not the point. If mutilations were inherited there would probably be no normal organisms left in the world by this time! Experiment of the crude,

[1] D'Arcy Thompson, 1915, p. 862.

mutilating kind has no bearing on the real question.[1] What is done to the plant is surely not inherited; what the plant does for itself, in reacting to the conditions of life, may perhaps be.

That changes in the environment induce changes in the organism is, of course, perfectly obvious; it is the commonest and best-known form of "variation" if we call it by that name. My old friend, Prof. George Henslow, has written book after book on the subject, and has had no difficulty whatever in proving that plants respond in the most varied and striking ways to the action of the environment. For example, if you water Wallflowers with salt water, you can make them succulent, like sea-side plants. Characters thus produced in the individual by special conditions are often closely similar to those which in other plants are more or less fixed and hereditary; this establishes a certain presumption that long-continued action of the environment may in time produce hereditable modifications. But there is still a lack of proof and the question is an involved one, because other causes, such as segregation and selection, must also play their part.

The most interesting form in which the doctrine of acquired characters has been maintained is that of inherited memory, so ably advocated by Hering, Samuel Butler,[2] and others, and defended by Sir Francis Darwin in his Presidential Address to the British Association in 1908.[3] The idea that heredity may be due to unconscious memory, the "mnemic" theory, as it is called, has been applied to plants, especially by the last-named author. "Plants must be classed with animals as regards their manner of reaction to stimuli." "The fact that stimuli are not momentary in effect, but leave a trace of themselves on the organism is in fact the physical basis of the pheno-

[1] Some readers may be amused to compare Bernard Shaw, in "Back to Methuselah," p. xlix, "Three Blind Mice."

[2] Butler, 1910. [3] F. Darwin, 1908.

mena grouped under memory in its widest sense as indicating that action is regulated by past experience." Thus the plant, like the animal, can and does form habits, as shown by the rhythm of the day and night movements of leaves, which still go on even when the plant is kept in darkness. Sir Francis Darwin adds : " My view is that the rhythm of ontogeny is actually and literally a habit." Thus the heredity which determines the development of a new generation from the ovum is identified with the " memory" which leads the individual organism to form a habit.

This ingenious theory, to which it is impossible to do justice in our brief summary, will be found expounded with great literary skill in the works of Samuel Butler already referred to. It evidently involves the assumption that the lasting impressions (" engrams ") made by appropriate stimuli on the individual can be transmitted in some way through the germ-cells. " Under the influence of Weismann's conception of continuity of the germ-plasm, the very possibility of acquired characters or impressed modifications being inherited was denied." [1] In more recent days some geneticists have taken the negative view just as strongly. Dr. Gates, however, points out that too much emphasis has been laid on the supposed segregation between germ-cells and somatic cells, a distinction which can scarcely be said to exist in plants. We do not know it to be impossible that such a transmission of impressions or engrams as is postulated by the mnemic theory may take place, and the conception is an attractive one. But at present it is all pure hypothesis, and only very extended cultural experiments carried on through many generations, and supported by field observations, can be expected to throw any further light on the long-disputed problem.

Another question which has been much discussed is that of the supposed distinction between morphological

[1] Gates, 1920, p. 235.

and adaptive characters. Personally, I do not believe that any such distinction exists, but we may inquire what it means. The famous German botanist, Nägeli, said that he did not know among plants a morphological modification which could be explained on utilitarian principles. What is a "morphological modification" or character? Darwin himself, who admitted the distinction to some extent, cited as examples "The arrangement of the leaves, the divisions of the flower or of the ovarium, the position of the ovules." [1] Generally we may say that "morphological characters" are those which distinguish the larger groups of organisms; features, that is, which were presumably evolved long ago and have become the common property of whole families or classes.

On a previous occasion I was at some pains to show that certain "typical morphological characters, on which the distinction of great classes of plants is based, were adaptive in origin, and even that their constancy is due to their functional importance." [2] This applied in particular to the pollen-tube and the seed, which were considered in relation to fossil evidence, as will be shown later in the present book.

The argument in the main holds good, but the phrase "adaptive in origin" may be open to criticism. If, as now seems probable, evolutionary changes follow a determinate course, the origin of new structures is prescribed by internal causes, though they may be perpetuated and shaped by natural selection. This consideration, however, involves no distinction of two sorts of characters; all alike have to pass through the mill of selection, and those which prove most useful are likely to be those which will persist, and become the features characteristic of extensive races. It is only trivial characters which can escape becoming adaptive.

[1] Darwin, "Origin of Species," p. 176.
[2] "Darwin and Modern Science," 1909, p. 218.

As Sir Francis Darwin well says: "The essence of morphology (in the better and more precise sense) is descent; thus we say that a pollen-grain is morphologically a microspore.[1] And this very example serves to show the falseness of Nägeli's view, since a pollen-grain is an adaptation to aerial as opposed to aquatic fertilisation." [2]

It is true that characters such as whorled or alternate leaves, parietal or axile position of the ovules, are probably not in themselves adaptive. We cannot suppose that the one arrangement has necessarily any advantage over the other. Phyllotaxis, for example, may have been inherited from remote ancestors, living under conditions totally different from those to which their living representatives are adjusted. But such characters, whatever their origin, have come to be parts of a well-adjusted mechanism, for assimilation or fertilisation, or seed-dispersal, as the case may be. The whole has become adaptive, though the ground-plan may once have been determined by unknown internal factors.

Dr. Guppy has recently proposed a theory of plant-evolution which has something in common with the ideas just discussed, though his point of view is quite original. Dr. Guppy does not believe in a regular and continuous course of evolution. In the history of the Flowering Plants, with which alone he is concerned, he distinguishes sharply between two principal eras. "(1) The era that witnessed the rise of the great families, a period of relatively uniform conditions. (2) The era that witnessed the differentiation of these family types in response to the differentiation of the climatic and other conditions." [3]

In the first era, instability prevailed: "It was an age of mutations, free and unchecked, and an age of uniformity of conditions." [4] As Dr. Guppy reminds us, the era of

[1] The small spore which, in *Selaginella*, and some other Higher Cryptogams, produces the male organ, and ultimately the free-swimming spermatozoids.
[2] "More Letters," vol. II, p. 376, footnote.
[3] Guppy, 1919, p. 471. [4] *Ibid.*, p. 472.

world-wide floras began to pass away after the Cretaceous age.[1] The second period, in which we are still living, is that of variation and natural selection. A theory based on existing conditions can only, we are told, apply to this second era. At the most, only the " abnormal side of plant-life " in the present age can be used to elucidate the earlier period. Dr. Guppy finds such an illustration in " the account by Dr. Willis [referred to above] of the extreme uniformity of conditions in which the Podostemaceæ and Tristichaceæ live in mountain torrents and rushing streams around the tropics, a description of a state of things approaching the primæval state as far as uniformity is concerned. . . ." What one is concerned with here is the association of extreme uniformity of conditions with extreme instability of type.[2]

Such a case is quite exceptional in the present era. It was only in the first period, now long past, that, as Dr. Guppy believes, free mutation, under uniform conditions of life, went on unchecked.

This distinction of two widely different eras in evolution involves some surprising conclusions. Dr. Guppy holds that, in considering evolution, we must pass from the family to the species, not from the species to the family, as is usual. Thus he regards the origin of families (in his first era) as quite a different process from the subsequent origin of species. He even objects to employing the terms " genus " and " species " when speaking of an age different in almost every respect from the present one.[3] " The age that witnessed the rise of the great families and the age that witnessed their subsequent differentiation are things apart, and cannot be dealt with by the same method."

This is evidently a question on which the fossil history alone can throw light. If there were really two quite different eras of evolution, if the great families sprang at once into existence during the first period, we must find

[1] See below, Chap. II. [2] Guppy, 1919, p. 443. [3] *Ibid.*, p. 457.

some evidence of such striking phenomena in the records of the older floras. At the present moment I will only point out that at the time when the Angiosperms (to which Dr. Guppy confines his attention) were still in his first era, other classes (such as the Conifers and Cycads) were already in the full swing of "differentiation," with plenty of genera and species. Thus the differentiation stage of one group was the origination age of another, and therefore the distinction, if it existed, cannot have depended on the conditions of the time. We shall see more fully later on how the fossil evidence bears on Dr. Guppy's hypothesis.

Two distinguished French palæobotanists, now deceased, Grand'Eury and Zeiller, were led, chiefly by their extensive observations of the older fossil floras, to the belief that the change from one species to another was not gradual, but sudden. Zeiller went further, and held that the idea of mutation, of discontinuous evolutionary series, should be extended to groups of a higher order than species. He said that this discontinuity was shown, whatever the rank of the groups examined.[1] In this extreme form, the doctrine of mutation, or rather of saltation, to some extent foreshadowed Dr. Guppy's idea of the origin of families *de novo*, during his first era of evolution. The French authorities, however, seem to have intended their conclusions to apply generally to all periods. Consequently they are open to the criticism that such violent changes as those which Zeiller appears to have had in view are not known to occur among recent organisms. This question has, in fact, already been considered (p. 18).

The subject of the present book is "Extinct Plants and Problems of Evolution." We have now passed in rapid review some of the current problems of evolution, and may next briefly consider what light is likely to be thrown on them by the evidence of Fossil Botany.

[1] Zeiller, 1907, pp. 21–23.

As we have already seen, such evidence has a direct and perhaps decisive bearing on such a question as the existence of two distinct eras of evolution. Dr. Guppy's hypothesis must stand or fall by the verdict of the geological record. So too with the opinion of Zeiller that new groups of plants arose by sudden saltations. This view was based on palæobotanical evidence and must be judged by the same testimony. This also applies to Grand'-Eury's more moderate doctrine of specific mutations; to criticise this conclusion, however, would require a more detailed survey of fossil species than is possible in a general course.

The question of the supposed distinction between morphological and adaptive characters, though not dependent on fossil evidence, may receive fresh light from this source. And still more, the mechanical principle, the theory that evolution has followed certain determinate directions, as opposed to indefinite variation, must look for confirmation chiefly to the records of past changes.

In connection with all these problems, the question of the adaptation of the organs of plants in remote periods is clearly of the first importance. From such evidence we may judge whether, at any past epoch, the conditions of life were as exacting as at present, the struggle for life as acute, and natural selection as rigorous. Much can be done in this direction; the proof of close and exact adaptation is clear enough at all periods for which adequate data are available. This is a subject which will be constantly before us in considering the organisation of ancient plants.

And finally, the "great thing," as Darwin called it, Evolution itself, forms of necessity our main theme.[1]

[1] Some account of Dr. J. C. Willis's well-known theory of "Age and Area," expounded in his book under that title, might naturally be looked for in this chapter. Dr. Willis's statistical deductions, however, while they have an important bearing on evolution, constitute primarily a theory of distribution, and as such lie beyond the scope of the present book.

CHAPTER II

THE RECENT FLORA. THE VEGETATION OF THE TERTIARY PERIOD. THE CRETACEOUS TRANSFORMATION. THE OLDEST KNOWN FLOWERING PLANTS.

We have so far been concerned with quite general questions connected with the doctrine of evolution and the present position of the Darwinian theory. It appears that the evidence of Fossil Botany has a direct bearing on some of the problems before us. We have now to survey this evidence and to trace, in outline, the general course of the past history of plants as at present known to us.

In this survey I propose to start from the recent Flora and work back. This order seems on the whole the best for a course like the present one. It is true that there is a certain awkwardness in thus turning history upside down and narrating events in the opposite order to that in which they occurred. It would not be very easy to write a History of England, from the present day, say, to the time of William the Conqueror! Still, the method of working backwards has one great advantage for our purpose; it enables us to start with things that everybody knows, whereas, if we tried to begin at the beginning, we should have to start with things that very few people know, namely, the Early Devonian plants. So we will make the Flora now living our point of departure.

To give any adequate account of the groups of existing plants and their characters, would be to write a small Text-book of Botany. This is clearly out of the question here, so I must be content to remind the reader of the

existence of these groups and the sorts of plants which they contain.

The main divisions of the Vegetable Kingdom may be shown, in the form of a table, thus:

- Seed-plants
  - Angiosperms
    - Dicotyledons
    - Monocotyledons
  - Gymnosperms
    - Conifers
    - Maidenhair Trees
    - Cycads
- Spore-plants
  - Higher
    - Ferns and allies
    - Mosses and allies
  - Lower
    - Algæ
    - Fungi

The broad distinction between Seed-plants and Spore-plants is easy to grasp. The Seed-plants are reproduced by complex bodies, the seeds, sometimes of large size, and always made up of various tissues; usually the seed contains an embryo, the rudiment of the young plant.

Spore-plants, on the other hand, are reproduced by extremely simple bodies, the spores, always minute, and usually consisting only of a single cell.

The two divisions of the Seed-plants, the Angiosperms and the Gymnosperms, are extremely different and have a very different geological history, the former being, on present evidence, the youngest, and the latter one of the oldest of the groups of land-plants. The Angiosperms, having their seeds in a closed seed-vessel, and fertilised through the mediation of a stigma and style, are the true Flowering Plants, and are obviously the dominant group at the present day. They include all our important food-plants, and, of course, all our garden flowers and wild flowers.

The two classes of Flowering Plants, Dicotyledons and Monocotyledons, are not fundamentally so very different

from each other, though as a rule easily distinguished. The technical distinction is based on the presence of a pair of seed-leaves in the former, and of a single seed-leaf in the latter class, the seed-leaves being simply the first leaves of the seedling. Further, the Dicotyledons generally show growth in thickness of the stem and root by means of a cambium, while in most Monocotyledons this is not the case, though a peculiar form of secondary thickening occurs in the Dragon-trees and a few other woody types. There are some other distinctive characters, but these are the most important.

The Dicotyledons are the more numerous, but the Monocotyledons the more important to man, as they include the Cereals and Grasses generally. All our native forest trees (in so far as they are not Conifers) are Dicotyledons, and so are most of the great flowering families, such as the Compositæ, the Leguminosæ, the Umbelliferæ, the Labiatæ, and very many more. The Monocotyledons include (besides the Grasses) the Palms, the Orchids, the Lilies, the Rushes, and other families.

When we come to the Gymnosperms, characterised by their naked seeds, not in a closed seed-vessel, though commonly in a cone, and fertilised directly without the intervention of a style or stigma, we are really in a different world, for we have reached an immensely ancient type of structure, differing in most points of importance from the up-to-date Angiosperms. The reproductive processes are profoundly different, and the anatomy, as a rule, is of another type.

Among the Gymnosperms, the Conifers (Firs, Cypresses, Big Trees of California, Yews, etc.) are well known to everybody, as important timber trees in the forest and as "specimen trees" in our gardens.

The family of the Maidenhair Tree is in a very different position, for it is only represented in the living Flora by a single species, *Ginkgo biloba*, a beautiful tree with leaves

like magnified leaflets of the Maidenhair Fern. There is some doubt whether this species is actually known in the wild state; to a great extent it has been preserved from extinction by the piety of the Buddhists, who grow it as a sacred tree in the precincts of their temples, in China and Japan. The Maidenhair Tree is the last survivor of a group of Gymnosperms of considerable importance in long-past geological times.

Then we come to the Cycads, a family little known except to botanists or travellers in warm countries. A magnificent collection of these plants will be found at Kew, chiefly in the Palm-house. This group is of the utmost interest to students of Fossil Botany, as we shall see. At present it is represented by nine genera, with perhaps 100 species, distributed over the tropical and sub-tropical regions of both hemispheres. The Cycads often bear a superficial resemblance to Palms, and are sometimes called by the absurd name of Sago-palms; really they have nothing to do with the true Palms, and their sago is not of much account. For the most part the Cycads bear cones; they are fine, handsome plants, and we shall have a great deal more to say about them in the next chapter.[1]

Among the Spore-plants, we come first to the Ferns and their allies, the Horsetails and the Club-mosses. These are the highest of the Spore-plants, and are called the Vascular Cryptogams, because they agree with the Seed-plants in possessing a vascular system, *i. e.* strands of wood and bast, tissues specially adapted to the conduction of water and of food-substances.

The Ferns are popular plants, familiar to everybody, and need no description. In their life-history they present a typical instance of "alternation of generations,"

[1] I pass over yet another group of Gymnosperms, the Gnetaceæ, which, though of great botanical interest, have no known fossil representatives, and so do not concern us here.

for we all know that if one sows the spores of a Fern, it is not a Fern that comes up. What grows from the spore is a totally different organism, a little flat, green thallus, like one of the lower Liverworts. On this plantlet, called the prothallus, the sexual organs are borne. Fertilisation takes place, by means of actively swimming male-cells, the spermatozoids, and then, from the embryo thus formed, a new Fern arises. Thus, in normal cases, the asexual generation represented by the Fern-plant alternates regularly with the sexual generation, represented by the prothallus.

It is the same with the Horsetails. These plants, with their jointed stems, whorled branches, and reduced, sheathing leaves, are as different as possible from the Ferns in habit, but they have a similar life-history. Their fructifications, however, are in definite cones. The group is now a small one, consisting of a single genus, *Equisetum*, with about twenty-five species. This family, like that of the Cycads, is chiefly of interest to the fossil botanist, for allied plants played a great part in the past history of the world.

The Club-mosses, or Lycopods, are a far more important group in the recent Flora, including several genera and some 600 or 700 species. The popular name "Club-mosses" does not, of course, imply any affinity to the true Mosses, a totally different class of plants, but merely indicates the outward appearance of the best-known Lycopods.

We must distinguish between the Lycopodiaceæ (*Lycopodium* and *Phylloglossum*) and the Selaginellaceæ (*Selaginella* and *Isoëtes*). The former are plants with forked stems and relatively small leaves, resembling large mosses in habit. The life-history is on the same general lines as that of Ferns, but the prothallus is usually of a more solid build and often subterranean. The Selaginellaceæ, on the other hand, are heterosporous, having spores

of two kinds, small and large. The former (the microspores) are numerous. On germination, a male organ (antheridium) is formed, producing the spermatozoids. The prothallus is almost wholly suppressed. The large spores (megaspores) are few in comparison; each produces a somewhat massive prothallus, which, however, never becomes free from the spore, and on this the female organs (archegonia) are borne. Thus we find in the Selaginellaceæ a much higher differentiation than in the Spore-plants hitherto mentioned. The microspore and megaspore are comparable to the pollen-grain and embryo-sac of the Seed-plants.[1]

In habit, *Selaginella*, species of which are commonly grown in greenhouses, bears a general resemblance to *Lycopodium*, with which it is sometimes confused. The genus *Isoëtes* (Quillwort) is quite different, the plants, usually aquatic or amphibious, having stunted stems, bearing long, quill-like leaves.

The Lycopod group, though still considerable, was of vastly greater importance in Palæozoic times, when it constituted one of the dominant classes in the forests of the Coal-period. The Club-moss line can be traced back to the days of the earliest known Flora of the Land.[2]

We now leave the Vascular Cryptogams and come to the Mosses. The true Mosses are pretty little plants, growing everywhere, on walls, trees, and among turf. Here the generations are reversed, as compared with the Fern-type, for the little leafy plant itself bears the sexual organs. The result of fertilisation is the development of the stalked fruit or capsule in which the spores are formed. Thus the fruit is here the asexual generation.

[1] In a peculiar group of Ferns (the Water-ferns or Hydropterideæ) there is a similar differentiation which goes even further, for only a single megaspore in the megasporangium comes to maturity.

[2] The small family of the Psilotaceæ, epiphytes of the Tropics and Southern Hemisphere, is often included under Lycopods. The plants are highly peculiar, but in their life-history show a general agreement with *Lycopodium*.

It will be noticed that in the Mosses the two generations are permanently attached to each other, so that the alternation of distinct phases is less obvious than among the Ferns and their allies.

The Liverworts are allied to the Mosses, and have the same life-history, but in many of them there is no differentiation between stem and leaf, the whole plant constituting a flat, green thallus.

It is only of recent years that the Moss group has begun to have much interest for the fossil botanist. In the last chapter we shall see that some of the oldest known Land-plants have some features in common with the Bryophytes.

The Lower Spore-plants, as we have called them, are often known as the Thallophytes, on the assumption that they show no distinction between stem and leaf. This, however, does not always hold good, for some of the Seaweeds have quite definite leaves, *e. g.* the Gulf-weed (*Sargassum*), which covers hundreds of thousands of square miles in the mid-Atlantic, forming the "Sargasso Sea." In fact many of the Algæ are in this respect on a higher level than many of the Liverworts.

The Algæ cover an immense range of structure, from little unicellular plants up to the highly organised Seaweeds, such as the great Oarweeds (*Laminaria*) of our own coasts and the gigantic *Macrocystis* of the Pacific. The recent work of Prof. Lloyd Williams of Aberystwyth has shown how much there is to be learnt from the life-histories of even the most familiar forms. The Algæ are essentially aquatic; many are fresh-water plants, others, and those the most numerous and the highest, inhabit the sea. They are the oldest of all plants, extending far back beyond the beginnings of a Land Flora, and were probably the source from which all other plants sprang. I need say no more, for space does not allow of our including the fossil history of the Algæ in this book, though we shall have to allude to them again when we come to the earliest land-plants.

The Fungi are a vast group, parasitic on living plants and animals or saprophytic on their dead remains. They are more important to man than the Algæ; not so much from some of them, such as mushrooms and truffles, being nice to eat, but rather in a disagreeable way, as causing many of the worst diseases of our field crops and garden plants. The Fungi are again a very ancient group; the remains of the Early Devonian land-plants simply swarm with Fungi. But here too we are getting beyond the scope of our present inquiry.

We will now enter on our main work, and endeavour to trace something of the past history of the plant world in its bearing on evolutionary questions. We will begin at the top, that is, with the fossil plants which lived nearest to our own time, and work downwards to the older Floras. We shall have to confine our attention to the higher groups, and shall dwell especially on the history of the highest of all, the Seed-plants, in so far as evidence is available.

Most people have some idea of the succession of geological strata. The following table will serve to recall the main periods from which fossils are known.

Tertiary or Cænozoic.	Pleistocene.
	Pliocene.
	Miocene.
	Oligocene.
	Eocene.
Mesozoic	Cretaceous.
	Jurassic.
	Triassic.
Palæozoic.	Permian.
	Carboniferous.
	Devonian.
	Silurian.
	Ordovician.
	Cambrian.

Without going into the vexed question of geological dates, it will be understood that a duration of very many (perhaps several hundred) million years is covered, even if we go back no further than the Devonian, which is practically our limit in the present course.

Generally speaking, the thickness of the strata, and consequently the time which it took to deposit them, increases as we go downwards. Thus the Mesozoic Period covered a much longer time than the Tertiary, and the Palæozoic a far longer time than the Mesozoic.

For the botanist, there are three critical points in the long succession, points where a transformation in the character of the Flora took place, or appears, with our imperfect knowledge, to have taken place. The latest transformation was during the Cretaceous Period, when our modern type of Flora first became dominant. The next older was at the close of the Palæozoic era, in or just after the Permian, when the Mesozoic Flora began to replace the ancient vegetation of the Coal-Forests. The third and oldest transformation took place about the middle of the Devonian Period, when the highly organised Flora of the later Palæozoic succeeded the simple types which are now known to have flourished in Early Devonian times. These great changes in the *facies* of the vegetation are real enough, but no doubt the actual origin of the incoming Flora was in each case much earlier than our existing records show.

There was undoubtedly another and yet earlier transformation, the most important of all, when the original vegetation of the sea first invaded and occupied the land. But of this profound change we have as yet only a theoretical conception, though recent discoveries have brought us face to face with the problem.

We now return to our starting-point, and inquire what the plants were like which immediately preceded the Flora of our own day. The answer is perhaps somewhat dis-

appointing; for a long way back, though the geographical distribution of plants varied greatly, we find little evidence of any great change in the plants themselves. Our present leading types of plants extend back right through the Tertiary Period, to the Upper Cretaceous, and in a few cases even further down still.

In the latest deposits, the Pleistocene, sometimes distinguished as the Quaternary, and extending from the Glacial Period onwards, all the genera and most of the species are recent. Many familiar plants, such as *Dryas octopetala*, *Azalea procumbens*, *Saxifraga oppositifolia*, with White Birch, Aspen, and Dwarf Willows are met with in these beds.

Even the pre-glacial, Pliocene Flora, which flourished just before the cold of the Glacial Epoch set in, was surprisingly like our present one. In a paper by Mr. and Mrs. Clement Reid on the pre-glacial Flora of Britain, 147 species are enumerated, and of these all but about thirty are referred to species still growing in this country. "The Flora was driven out by the cold of the Glacial Epoch and came back little altered." Very many of our commonest plants are represented, such as Creeping Buttercup, Dog Violet, Chickweed, Maple, Blackberry, Wild Parsnip, Coltsfoot, Thistles, Woody Nightshade, Water Mint, Oak, Beech, Yew, Scotch Fir, Water Plantain, Water Soldier, and the Common Reed, with plenty more.[1]

There were, however, a few exotics also, among them the Water Chestnut (*Trapa natans*) and the Spruce (*Picea excelsa*). The interest of the later fossil records lies much more in distribution than in evolution. The work of the late Mr. Clement Reid, continued by Mrs. Reid, has added immensely to our knowledge of the Pleistocene and Pliocene plants, chiefly by means of the careful comparative study of fruits and seeds, which have proved to afford most valuable characters for the determination of species.

[1] C. and E. M. Reid, 1908.

In a Middle Pliocene Flora (older, therefore, than that referred to above) from the County of Durham, Mrs. Reid calls attention to " the presence of so many species belonging to the Chinese-North-American Association." [1] They include a Japanese Hornbeam, three North American Hawthorns, Chinese and Japanese Brambles, a North American Nettle, etc. And these exotic forms occur side by side with many common British species. We cannot go into the subject of distribution here, but the migrations of plants must always be borne in mind, as they greatly complicate questions of descent.

A certain number of extinct species are recorded from the older Pliocene Flora. We may hope, in the future, to see some light thrown on the evolution of recent species, by the study of the later fossil remains, but at present Palæobotany is far behind Animal Palæontology in this respect.

Going further back into the Tertiaries, the post-Eocene Flora generally was much like that of the present day, apart from some very remarkable changes of distribution. Thus from the Miocene back to the Eocene, Palms flourished in our latitudes, and much further North. Fruits of a Palm (*Nipadites*) are common in the Bournemouth cliffs, of Upper Eocene age.

The fossil history of the Flowering Plants shows no sign of a beginning, for, with few exceptions, all the specimens known can be referred to families still existing. It may, however, be pointed out that the attribution to recent families is not always free from doubt. Remains of Angiospermous plants are extremely abundant from the Tertiaries and the Upper Cretaceous, but the majority of the specimens are leaves only. As a rule, impressions of leaves are an unsafe guide to affinity. For example, the leaves of the Mesozoic " Cycads," as we shall see, are so like those of recent Cycadaceæ, that they would

[1] E. M. Reid, 1920, p. 109.

undoubtedly be referred to the same family, if we had not further evidence, from fructification and structure, to prove that most of them belonged to a quite distinct, though distantly related, group. In like manner, some of the Palæozoic "Fern-fronds" were actually attributed by leading botanists to living genera, but we have now learnt that these very fronds were those of seed-bearing plants, and not of Ferns at all. Thus, where only the evidence of leaves is available, we must be careful how we accept references of fossil plants to recent families.

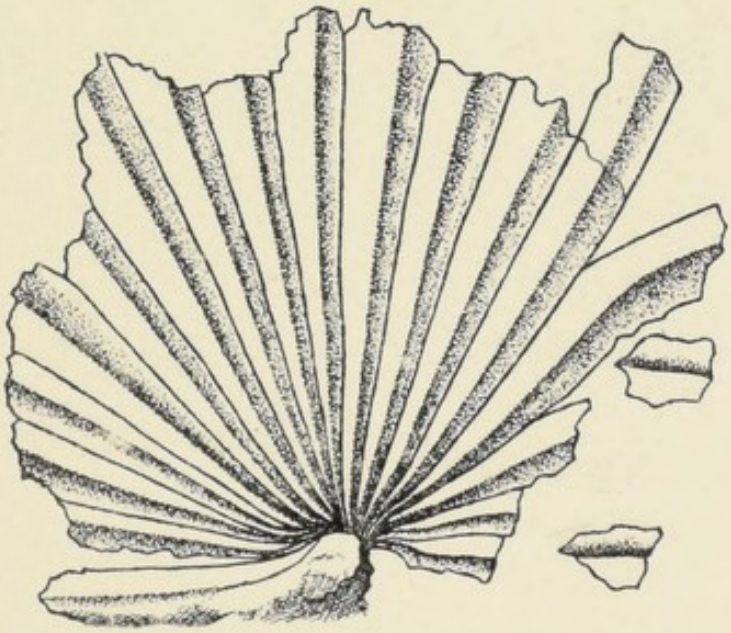

FIG. 1.—*Chamærops helvetica.* Palm leaf from the Oligocene of Saxony. From Gothan (after Friedrich).

The record shows no time-limit between Monocotyledons and Dicotyledons, and throws no light on the possible derivation of the one class from the other. Both extend back far into the Cretaceous, and throughout the whole time the Dicotyledons appear more numerous than the Monocotyledons, as they are at the present day.

As it is neither practicable nor expedient to attempt any full account of fossil Angiosperms in the present book, it will suffice to pick out a few leading families which have a geological history long enough to be of interest.

Beginning with the Monocotyledons, we may first glance

at the Palms, a noble race, the "Principes" of Engler, which have, as becomes them, an ancient family history, going far back into the Cretaceous. A fossil Coconut, recognisable by the familiar three holes in the shell, is recorded from the Lower Cenomanian, about the same as our Upper Greensand, of France, so that by that time Palms much like the living forms had already appeared.

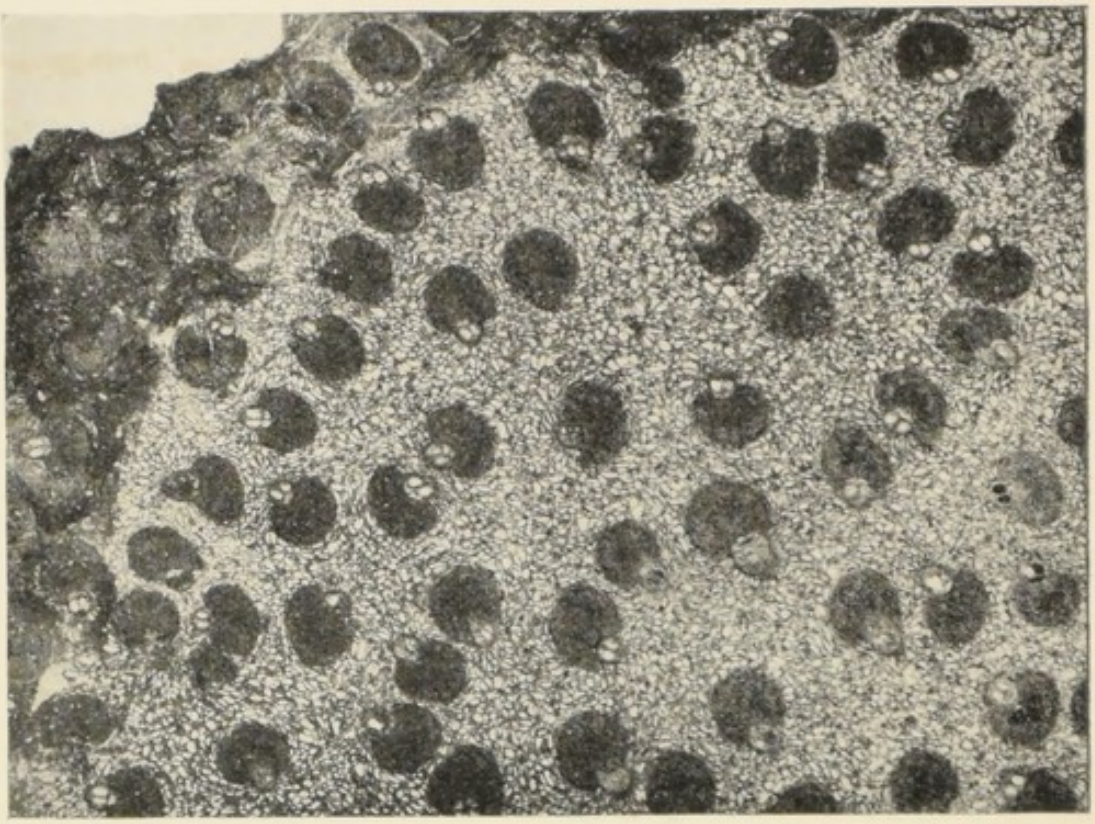

FIG. 2.—*Palmoxylon cheyennense*. Transverse section of Palm Wood from the Upper Cretaceous of Dakota, U.S.A. (× about 7.) Scott Collection, 3088.
From a photograph by Mr. W. Tams.

Palm-leaves, so characteristic as to leave little room for doubt, are common throughout the Tertiaries, and back to the Cretaceous. The fan-shaped type is the commoner. The example figured is a *Chamærops* from the Oligocene, representing the genus to which the Dwarf Palm, the only recent European member of the family, belongs. (Fig. 1.)

Palm wood is often found in a petrified state, with the structure beautifully preserved. The section figured (Fig. 2) is from a specimen of Upper Cretaceous age, from

the Black Hills Rim of Dakota. It shows the typical vascular bundles, each with a great strand of fibres and large vessels, embedded in a loose ground-tissue. In some of these bundles the double phloëm, common in recent Palms, is easily recognised. Thus, even in detail, the structure of Cretaceous Palms was quite modern. The early development of this great and advanced Monocotyledonous family shows how far we must be from tracing the Flowering Plants to their origin.

The evidence for the occurrence of Grasses as fossils is often unsatisfactory, for the leaves attributed to them may belong to other groups. The Reeds, however, are well attested as far back as the Upper Cretaceous of Greenland and North America, their rhizomes and stems being sufficiently characteristic for determination.

The well-known aquatic family of the Bur-Reeds (*Sparganium*) goes back to the Cretaceous, as witnessed by fruits as well as by leaves.

Among the Liliaceæ, Dragon Trees (*Dracæna*) and other arborescent forms are found in various Tertiary beds. The climbing genus, *Smilax*, occurs, if the evidence of the leaves is to be trusted, as far back as the Upper Cretaceous of Bohemia.

Perhaps the most interesting Monocotyledonous fossil is the petrified flower, *Cretovarium japonicum*, of which a number of specimens were discovered by Dr. Marie C. Stopes and Prof. Fujii, in Upper Cretaceous beds in Japan. This is among the oldest known fossil Angiospermous flowers, and appears to be the only one with the structure preserved. A transverse section is shown in Fig. 3. The trilocular ovary is well preserved and remains of the perianth are present. Other specimens show something of the ovules contained in the loculi. The flower was of a Liliaceous type and may well have belonged to that family.[1]

We have only chosen a few examples, but enough has

[1] Stopes and Fujii, 1910. Stopes, 1910.

been said to show that very diverse families of Monocotyledons were already present, in their typical form, well back in the Cretaceous Period.

Passing on to the Dicotyledons, it may be noted that polypetalous and apetalous families are better represented in the fossil record than the higher group, Sympetalæ. This seems theoretically correct, but we must be careful how we accept the evidence. The Apetalæ, and, in a lesser degree, the Polypetalæ, are rich in trees and shrubs, compared with the Sympetalæ, which consist very largely

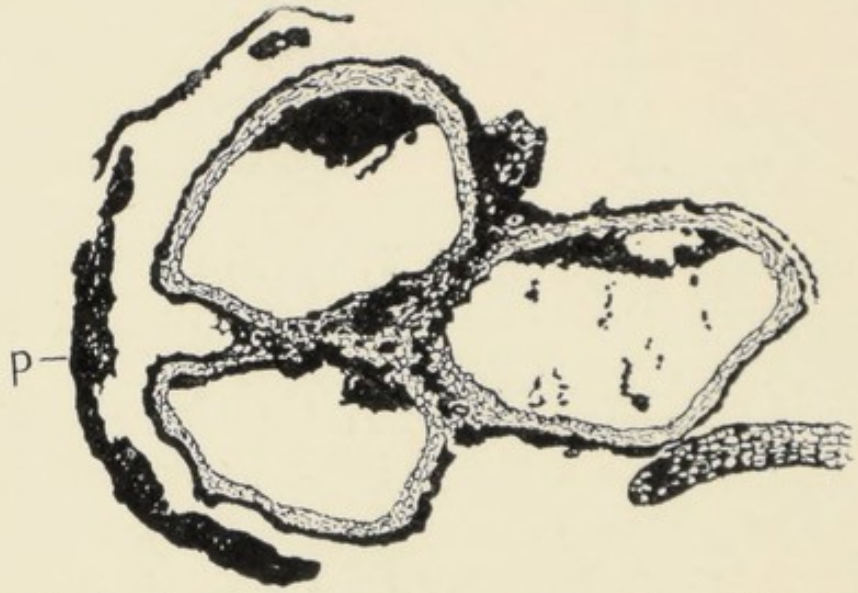

FIG. 3.—*Cretovarium japonicum*. Transverse section of flower (no doubt Monocotyledonous) showing the trilocular ovary and part of the perianth (*p*). From the Upper Cretaceous of Japan. (× about 25.)
After Stopes and Fujii.

of herbaceous plants. Now it is chiefly the remains of trees and shrubs that are preserved in the fossil state. This is not surprising. If one walks through a wood in winter one finds the ground covered with the fallen leaves, mixed with the fruits, of the trees, while but little trace of the herbaceous undergrowth is met with, when its season is over. Hence it appears that trees and shrubs have always had a better chance of leaving their remains behind them than herbaceous plants, and this may account for the greater abundance of apetalous and polypetalous Dicotyledons among fossils, without assuming that this

fact has any evolutionary significance. Indeed the little that we do know of fossil Sympetalæ suggests that this sub-class also had a long history in past ages.

Taking a few leading families as examples, we may begin with the Salicaceæ. Willows and Poplars are among the oldest known Angiosperms, going back to the Middle Cretaceous.[1] Catkins, fruits and seeds, as well as leaves, attest their early appearance. According to Laurent, it is always the types of warm climates, foreign to Europe, which are the oldest. The Bog Myrtles (family Myricaceæ) seem to be of equal antiquity.

It is interesting to note that a stem with structure preserved, from the Upper Cretaceous of Japan, is referred by Dr. Stopes and Prof. Fujii to the Saururaceæ, a small family allied to the Peppers.

Another ancient family is that of the Walnuts, which are recorded from the Cenomanian and extend all through the Tertiaries.

Birches and Alders are mainly known from the Eocene, but the Beech goes back to the Cretaceous of Dakota and Saxony, the latter of Cenomanian age. The well-known beech-mast, in its various forms, lent itself readily to fossil preservation, and affords a certain means of determination.

Great numbers of fossil Oaks have been described, but mainly on the evidence of the leaves. They are said to appear as far back as the Middle Cretaceous of North America. On the other hand, the Elms do not seem to have been traced beyond the Tertiary.

Among the Moraceæ the now tropical Breadfruit (*Artocarpus*) has, curiously enough, been found in the Cretaceous (Cenomanian) of Greenland, a fact which brings home to us the vast difference in geographical distribution between those days and our own. The specimen figured (*A. Dick-*

[1] The Gault is commonly included in the Upper Cretaceous by English geologists, but others place it in the Lower. I have therefore spoken of the Middle Cretaceous to indicate an age roughly corresponding to the Gault. Few Angiospermous fossils are older than this.

soni) shows quite clearly the characteristic compound fruit and the almost equally distinctive leaf (Fig. 4).

A great deal used at one time to be said of the fossil occurrence in Europe and the North of the now Australian and South African family Proteaceæ. The evidence, however, has not stood examination and it is probable that the few genuine fossil Proteaceæ are limited to Australia.

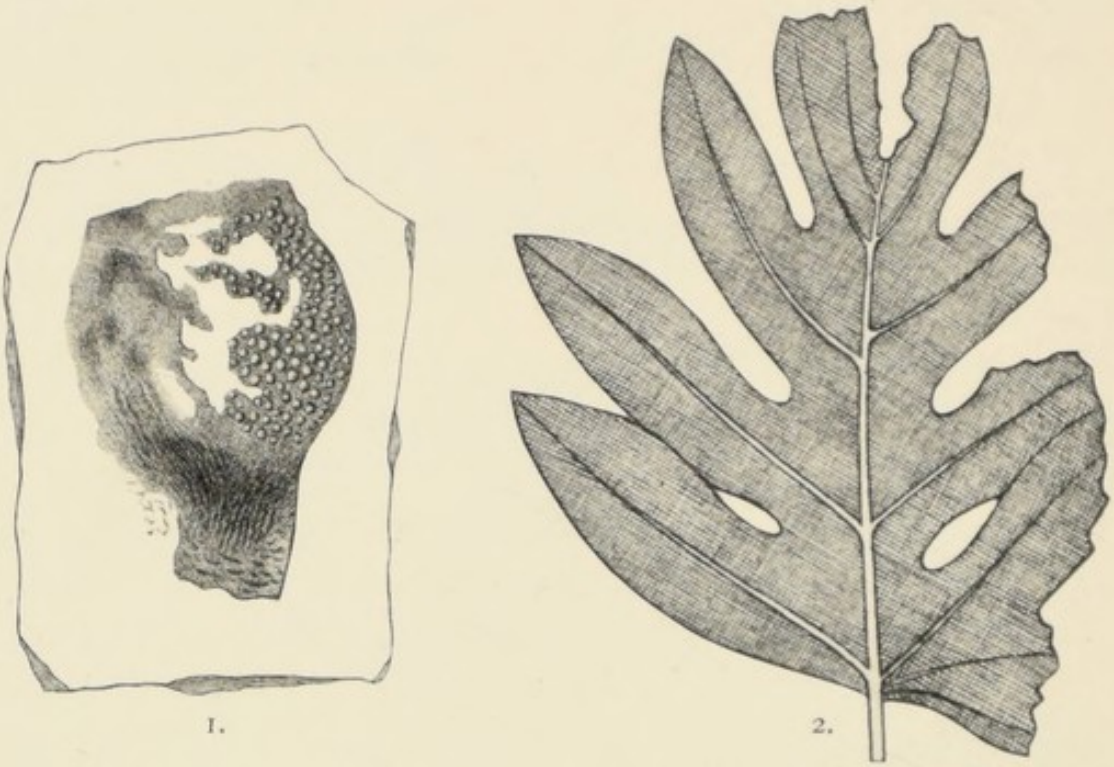

FIG. 4.—*Artocarpus Dicksoni*. 1. Compound fruit ($\frac{2}{3}$ of natural size). 2. Leaf ($\frac{1}{3}$ of natural size). From the Cenomanian (Upper Cretaceous) of Greenland.
From Gothan (after Nathorst).

The family of the Waterlilies (Nymphæaceæ) has a long fossil history, rhizomes, fruits, and seeds, in addition to leaves, furnishing good means of identification. The Lotus (*Nelumbo*) has been recognised in the Upper Cretaceous of North America, Greenland, and Europe. The non-European genus *Brasenia*, or a similar form, is recorded from the older Cretaceous rocks of Portugal; *Nymphæa* and *Nuphar* are known in beds of Tertiary age.

The Magnoliaceæ are rich in supposed fossil representa-

tives. Various species of *Magnolia* have been recorded, going back, both in North America and Europe, to the Middle Cretaceous. The Tulip Tree (*Liriodendron*) appears to be of like antiquity. While the Tertiary records are sometimes confirmed by the presence of fruits, the earlier occurrence of these plants is too often indicated by leaves only, evidence which has sometimes proved deceptive.

The Ranunculaceæ have no very ancient records, unless the doubtful genus *Dewalquea*, with pedate leaves like a Hellebore, was really of that affinity. *Dewalquea* is an Upper Cretaceous and Eocene plant, which has also been referred to the Ivy family (Araliaceæ).

The true Laurels (Lauraceæ) are well attested as an old family. *Sassafras* is said to be the earliest representative; it is recorded, from an horizon equivalent to our Gault, in North America. As Dr. Berry says: "Like all genera which are monotypic in the existing Flora, *Sassafras* has a most interesting geological history." [1] He adds that the most ancient forms are three species of late Lower Cretaceous (Gault) age from the Maryland-Virginia area, and a fourth species of like antiquity from Portugal. "The Upper Cretaceous shows an extensive development of Sassafras-like forms in Europe, Greenland, and America." The peculiar lobed leaves of *Sassafras* appear to be sufficiently characteristic for determination in many cases, though some are doubtful. Other genera of Lauraceæ, including *Cinnamomum* and *Laurus*, are also recorded from Cretaceous beds in various parts of the world.

The Witch Hazels (Hamamelidaceæ) likewise appear to be ancient. *Liquidambar*, well known as a living plant for its fine autumn colouring, appears in the Cenomanian of North America, and a genus closely allied to *Hamamelis* itself is recorded from a similar horizon.

The Plane Tree family (Platanaceæ) is undoubtedly

[1] Berry, 1911, p. 484.

an old group, its presence in Cretaceous deposits being proved by the occurrence of flowers and fruits, besides leaves. The well-known globular catkins are preserved in specimens from the Cretaceous of Bohemia. The extinct genus *Credneria*, of Cretaceous age, is now regarded as probably, in part at least, related to the Planes. Prof. Seward, among fossils which he collected in Greenland in the summer of 1921, has a Cretaceous specimen showing on one side of the slab a Dicotyledonous leaf, like that of a Plane, and on the other the leaf of one of the old Cycads—a striking case of the meeting of the modern and ancient Floras.

The geological history of the Maples has been traced with much care. Leaves and fruits of *Acer* are recorded from the Middle Cretaceous of America, and species occur throughout the Tertiaries. The allied Sapindaceæ also appear to go back to the Cretaceous; the genus *Sapindopsis* is well represented in the Patapsco (Gault) formation of Maryland. The affinity, however, is scarcely beyond doubt.

Of the great family Leguminosæ numerous fossil representatives have been recorded, but mostly on somewhat questionable evidence. A few, however, including the Bladder-Senna (*Colutea*) have been recognised in Cretaceous deposits.

The Vines (Vitaceæ) have not been identified with certainty before the Tertiary era. The same is true of the Lime Tree family (Tiliaceæ), the fruits of which, with the adherent bract, are particularly easy to recognise where they occur.

Among the Myrtaceæ, it is interesting to find that the presence of the Australian Gum-trees (*Eucalyptus*) in Europe in Cretaceous times is well attested. The specimen figured, showing a shoot bearing both flowers and leaves, is from the Cenomanian of Bohemia (Fig. 5).

We now come to the Sympetalæ, considered to be the

highest group of Dicotyledons. As already pointed out, their fossil record is somewhat scanty. In the Ebony order (Ebenaceæ) the genus *Diospyros* has been traced back, apparently on good evidence, through the whole Tertiary era to the Cretaceous of Africa, North America, and Greenland, a striking fact in ancient distribution.

FIG. 5.—*Eucalyptus angustus.* Shoot, bearing leaves and flowers. From the Cenomanian of Bohemia.
After Gothan.

Among the Oleaceæ the Ash (*Fraxinus*) has apparently the longest fossil history, for leaves attributed to the genus appear in the Upper Cretaceous of Greenland.

The Dogbanes (Apocynaceæ), an advanced family of Sympetalæ, appear to go back a long way, for the Oleander genus (*Nerium*) is represented by the characteristic leaves

in the Upper Cretaceous of Westphalia, while flowers are also present in the Lower Eocene of Paris.

The Caprifoliaceæ are another ancient group; the genus *Viburnum*, to which our familiar Guelder Rose and Wayfaring Tree belong, is represented by leaves, flowers, and fruits, and appears in the Cretaceous of Greenland and North America.

Those few examples of the earliest records appear to show that the Sympetalæ go back as far as most other Dicotyledons, though, for reasons already given, their remains are not so frequent.

In fact, if we judge by present evidence, it would not be surprising to find that by about the middle of the Cretaceous Period the Angiosperms generally were developed very much as they are now, so far as the families and even some of the genera are concerned. Their distribution, however, was totally different, for in Cretaceous times there was one, fairly uniform, world-wide Flora, which gradually, during the Tertiary era, became marked out into floral districts, as we see at present.

If we now inquire, What is the evidence for the presence of Angiosperms in still older formations? we find that the chief records are in the form of petrified stems, of Lower Cretaceous age.

Fossil wood of Angiosperms is frequent, but apart from Palm-woods, already mentioned, is seldom of Cretaceous age. In the very interesting petrified Flora from Japan, described by Stopes and Fujii, about one-third of the species are Angiosperms, and most of them are fossil stems. This Flora is of Upper Cretaceous age. Besides *Sauuropsis*, a probable ally of the Peppers, already referred to, there are four Dicotyledonous woods, *Jugloxylon*, resembling Walnut-wood, *Populocaulis*, a stem agreeing most closely in structure with that of the Poplars, *Fagoxylon*, apparently very near the Beech, and *Sabiocaulis*, referred provisionally to the Sabiaceæ, a small order allied to the

Sapindaceæ.[1] These fossils are of great interest, but do not carry back the groups concerned further than had already been inferred from other evidence.

The oldest fossil Dicotyledons are from our own country, and appear to be all of Lower Greensand age. Dr. Marie Stopes, to whom our knowledge of these fossils is due, distinguishes five genera, each with a single species. The interesting point is that they are all quite distinct, and all of typically Dicotyledonous structure, with nothing primitive about them. Thus at this early period the Dicotyledons, so far as anatomy is concerned, were already highly differentiated in various directions, as they are at present.

Thus in *Cantia arborescens*, from the Folkestone Beds, near Ightham, Kent, the wood has a small quantity of fibre-tracheides and parenchyma, with an enormous number of small isolated vessels, 30–50 μ in diameter; their pits are round, oval, or scalariform. The medullary rays are numerous and uniseriate. This wood has been compared with that of the Birch family, the Magnoliaceæ and *Viburnum ;* its affinities are undetermined.

On the other hand, *Woburnia porosa* (Fig. 6), from the Lower Greensand of Bedfordshire, has excessively large vessels, 350 μ in diameter; they are very numerous, and have small, oval pits. There is much wood-parenchyma, and the medullary rays are mostly many cells wide and of considerable height. The structure agrees with that of the Dipterocarpaceæ, a tropical family of fine timber trees.

Sabulia Scottii, another Bedfordshire fossil, is quite different again. Here the ground-mass of the wood is made up of thick-walled fibres, with scattered vessels of rather small size, 25–70 μ in diameter. The inconspicuous medullary rays are either uniseriate or only two or three cells wide. The affinities of the plant are unknown, but

[1] Stopes and Fujii, 1910.

" every detail of its structure is characteristic of the higher woody Dicotyledons."

In *Hythia Elgari*, from the Hythe Beds near Maidstone, the wood consists of fibre-tracheides, parenchyma, and isolated vessels, 50–70 μ in diameter; the pits are round, merging into the scalariform type. The numerous medullary rays are multiseriate; some of them very broad and

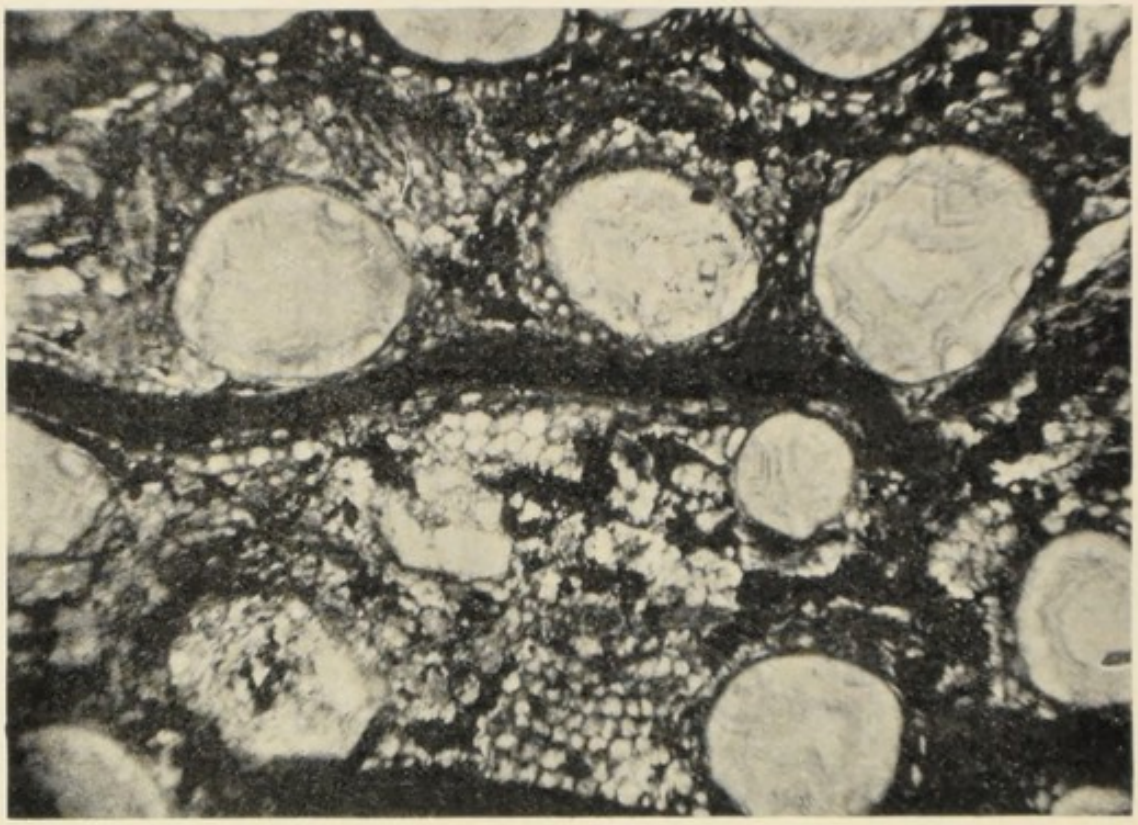

Fig. 6.—*Woburnia porosa*. Transverse section of wood, showing the very large vessels, medullary rays, etc. (Highly magnified.) From the Lower Greensand of Bedfordshire.
From a photograph by Dr. Marie C. Stopes.

conspicuous. Some possible affinity with the Beech type is suggested.

Aptiana radiata (Fig. 7) is believed, from the nature of the matrix in which it occurs, to come from Luccomb Chine, in the Isle of Wight. This locality, if confirmed, would be very interesting, for the Lower Greensand of Luccomb Chine has yielded one of the most famous of the old-world Cycads, *Bennettites Gibsonianus*, and it would be a very striking fact if plants of such different

Floras occurred side by side. The wood of *Aptiana* consists of fibre-tracheides and isolated small vessels, 20–40 μ in diameter. The majority of the pits on the vessels are scalariform. Both multiseriate and uniseriate medullary rays are present, and the rays generally are a conspicuous feature. *Aptiana* is exceptional in having the phloëm preserved; it consists of hard bast and soft bast

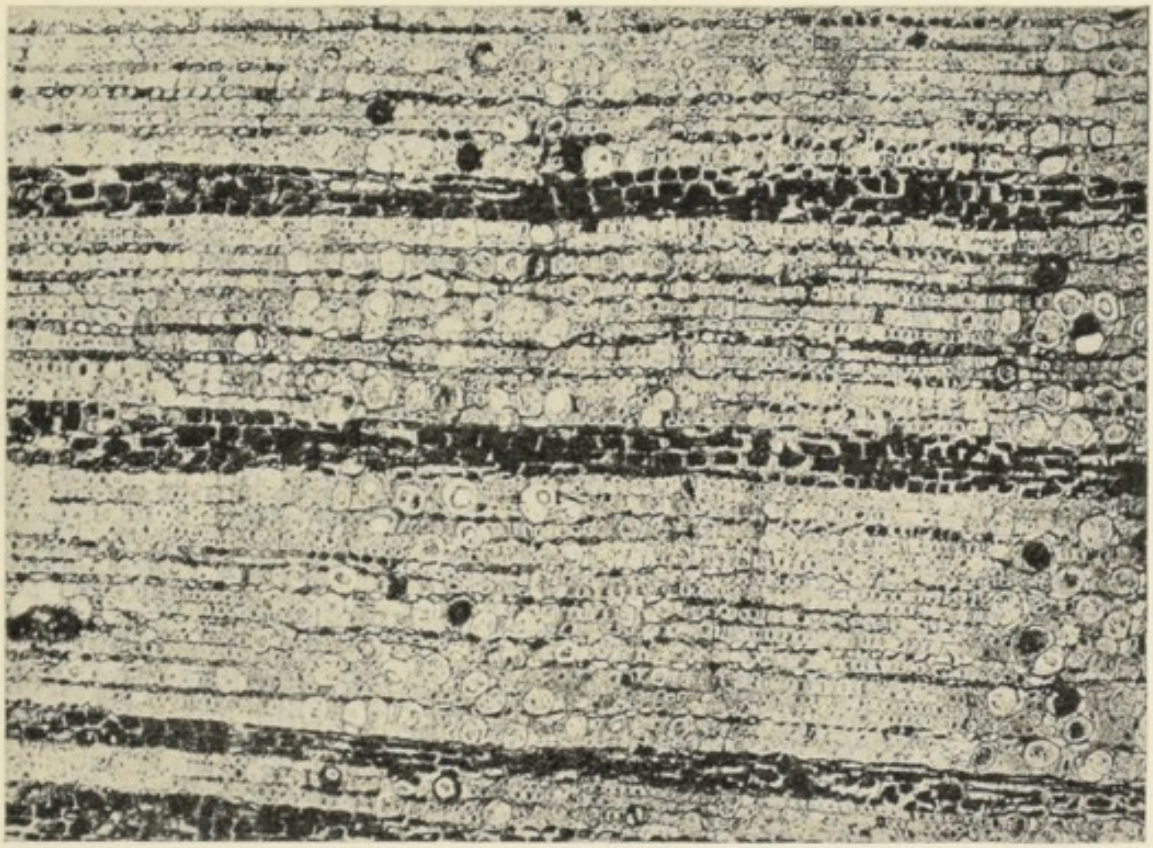

FIG. 7.—*Aptiana radiata*, transverse section of wood, showing the small vessels, multiseriate medullary rays, etc. (On the same scale as Fig. 6, for comparison.) From the Lower Greensand, probably of Luccomb Chine, Isle of Wight.
From a photograph by Dr. Marie C. Stopes.

in irregular alternating patches, as in many recent Dicotyledons. While Dr. Stopes does not venture to refer the genus to any special family, two Dutch writers, Profs. Janssonius and Moll, have confidently placed it in the recent order Ternstrœmiaceæ, to which Tea and the Camellia belong. However this may be, the attribution shows that the structure of this ancient fossil is of an essentially modern type.

I have omitted details, though perhaps too much has already been said for the non-botanical reader. My object is to show that these earliest known remains of Dicotyledons prove clearly that the class had already, in Lower Cretaceous times, attained a high and characteristic development in various directions. It is evident that the really early evolutionary stages of the Dicotyledons (and doubtless of the Angiosperms as a whole) must have been traversed in periods long previous to those from which their first recognisable traces have come down to us.

There is little to be said here of supposed remains of Angiosperms older than the Cretaceous Period. A leaf from the Stonesfield Slate (Great Oolite) described by Prof. Seward, has all the appearance of a simple, ovate leaf of a Dicotyledon, but the specimens are too isolated for any conclusion to be based upon them as yet.[1]

Some very remarkable fossils of somewhat greater antiquity have been discovered by Mr. H. H. Thomas in the Inferior Oolite (Middle Jurassic) of the Yorkshire coast. No full description has yet been published, so no details can be given. The " specimens consist of small branches of stalked fruits which are inverted and show traces of what may be a stigma. . . . Each fruit contains about eight small seeds, covered with a double fibrous integument."[2] Two genera, *Caytonia* and *Gristhorpia*, are distinguished. They are regarded as constituting a group of Angiosperms of which there are no living representatives. The specimens, which look something like fossil bunches of currants, certainly suggest Angiospermous fruits, but no opinion as to their true affinities can be formed till the investigation, which is being conducted with elaborate care, is completed. The discovery promises to prove of great interest.

[1] Seward, 1904, p. 152, Pl. XI (*Phyllites*).
[2] H. H. Thomas, 1921.

Apart from these rare and isolated indications, we may say that Angiosperms are unknown before the Cretaceous. They seem to appear suddenly, in their full strength, like Athene sprung from the brain of Zeus. We know nothing of their evolution. I do not go so far as to say that we have absolutely no light on the question, for I am one of those who are inclined to think that some of the old extinct Mesozoic types, to be described in the next chapter, show so much analogy with the true Flowering Plants as to suggest a certain degree of affinity. But as to primitive representatives of the Angiosperms themselves, we have as yet no evidence at all. Possibly Mr. Thomas's strange fruits may eventually put us on the track.

We have now traced back the modern period of plant-life to its birth—apparent, however, not real. The great transformation of the Flora takes place, as I have said, in the Cretaceous Period. The Upper Cretaceous vegetation was mostly modern,[1] the Lower mostly ancient.

So far we have been dealing with plants of quite familiar types, with little or nothing peculiar about them. From this point onwards, as we descend to earlier strata, we lose the Flowering Plants which we know so well, and find ourselves in a strange world, a world occupied by Gymnosperms and Cryptogams—a rich Flora enough, but unfamiliar in aspect, with races dominant which are now subordinate, or of which we see little or nothing in the present Flora. The next chapter will be devoted to this ancient vegetation, typical of the Mesozoic Era.

[1] For summaries of the fossil history of Angiosperms, see Schenk, 1890; Laurent, 1907; Menzel (in Gothan), 1921.

CHAPTER III

THE FLORAS OF THE MESOZOIC AGE. THE CYCADS: THEIR SIGNIFICANCE AND GEOLOGICAL HISTORY. THE MESOZOIC CYCADOPHYTES A VARIED AND DOMINANT CLASS. ANALOGIES WITH THE FLOWERING PLANTS

We have now reached the ancient and characteristic Flora of the Mesozoic Age. The great botanical transformations do not usually coincide with the limits of the great geological Eras. As we have already seen, the modern period, the reign of the Angiosperms, extends well back into the Mesozoic Era, as far as the Middle Cretaceous, and a little further. Its real beginnings, of which we know nothing, must lie much further back still.

In sketching the outlines of history during the modern period, we have confined our observations to the Flowering Plants, for they are the most interesting. If space had allowed of our dealing with other groups, such as the Gymnosperms or the Ferns, there would only have been the same story to tell—great changes of distribution, with little evidence of evolution.

Now we come to a critical point in plant-history. The typical Mesozoic Flora, as we may call it, was totally different, so far at least as the dominant races are concerned, from the modern type of vegetation. Broadly speaking, the *facies* of the Mesozoic Flora was fairly uniform, from the Lower Cretaceous back as far as the Trias—at least the same great groups prevailed all through that immense period, though changes of course occurred. Thus the Age of the characteristic Mesozoic vegetation is, on the whole, just as definite a botanical period as the modern era extending from the Cretaceous to our own day.

The Mesozoic botanical period has been called the Age of Gymnosperms; the dominant groups were Conifers, Cycads and Maidenhair Trees. Besides these, the Higher Cryptogams were well represented. There were great numbers of Ferns, belonging for the most part to rather unusual families, that is to say, to families not very familiar to us at the present day. There were also a good many Horsetails, and as we go further back we find them becoming gigantic in stature and different in other respects from the Horsetails as we know them now. Not very much is known about the Club-mosses of the Mesozoic—some of them were probably on a grander scale than the modern kinds.

In this chapter we will concentrate our attention on the Cycads (in a very wide sense) as on the whole the most important and interesting of the leading Mesozoic races. They are of great interest in themselves, for it is impressive to find that a class now insignificant in extent then dominated the world; and they are further of special significance because the Mesozoic Cycads, so called, constitute the one extinct group which shows any analogy with the higher Flowering Plants of modern times.

The abundance of the Mesozoic plants, which we call in a general sense Cycads, is very remarkable. I once ventured on an estimate that in those days, out of all the land-plants, one in every three was a Cycad. Dr. Wieland, the greatest living authority on the subject, thinks that this was not going far enough, and reckons that, taking the average of the Mesozoic Floras, two out of every five land-plants were Cycads.—A similar proportion in the recent Flora would give some 40,000 odd species, instead of the bare 100 which actually exist.

These Mesozoic Cycads represent in the Plant Kingdom the Deinosaurs and their allies in the Animal world—not quite so monstrous or startling to look at, but equally characteristic. But just as the great reptiles of that age

belonged, for the most part, to families now extinct, so it was with the Mesozoic Cycads. Very few of them were of the same family as our little surviving group of Cycadaceæ.

We must, however, say a little more about the living family before we go on to the fossils. Our modern Cycads are quite a small body, with a comparatively slight range of structure. Of the nine genera, one, *Cycas*, is common to Asia and Australia; two (*Macrozamia* and *Bowenia*) are peculiar to Australia; two (*Encephalartos* and *Stangeria*) are African, and the remaining four (*Zamia*, *Dioon*, *Ceratozamia* and *Microcycas*) are American, *Zamia* being the only genus with at all a wide distribution on that Continent. All belong to warm countries; *Cycas* extends as far North as Japan and *Stangeria* as far South as the Cape.

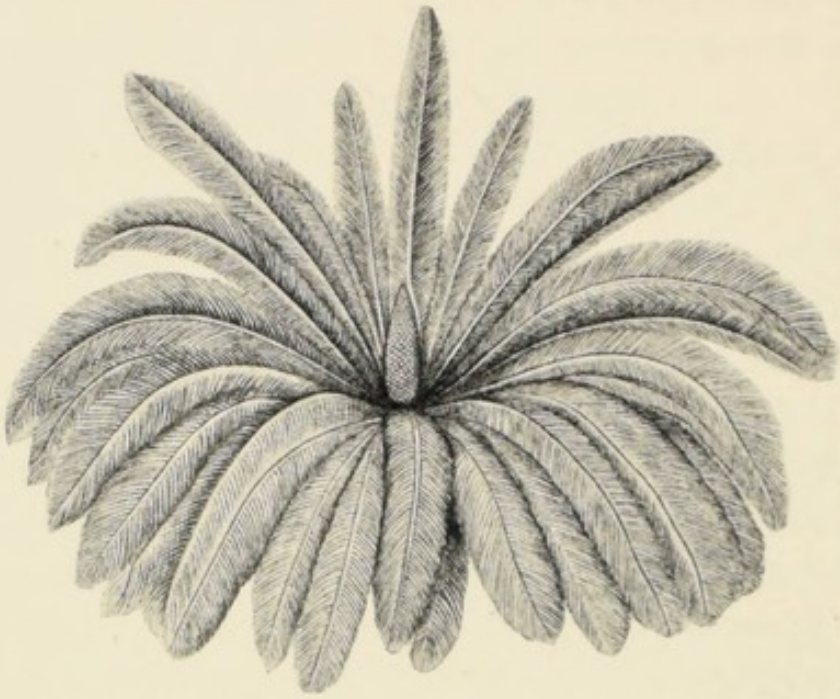

Fig. 8.—*Cycas revoluta*. Male plant, bearing a single terminal cone. From a specimen at Kew (G.T.G.).

The recent Cycads have, for the most part, a fairly uniform habit, characterised by the fine foliage; the large compound leaves are usually of the simply pinnate type (Figs. 8 and 9). In the Australian genus *Bowenia* they are bipinnate, and in a species of *Cycas* from Annam (*C.*

Micholitzii) the leaflets are twice forked; such cases, however, are exceptional.

The genus *Cycas* is peculiar in having only a single vein (the midrib) in each leaflet, while all the other Cycads have numerous, forking veins; in *Stangeria* a midrib is differentiated, from which the lateral strands branch off. The foliage of *Stangeria* is remarkable for its fern-like character; this is so striking that the plant, when first brought to Europe, was actually described as a Fern, of the genus *Lomaria*, until it coned and thus revealed its true nature. This deceptive resemblance is worth noting, as we shall find when we come to the fern-like Seed-plants of the Palæozoic.

The stem of Cycadaceæ may either be dwarf and subterranean, as, for example, in *Stangeria* and *Bowenia*, or erect and columnar, as in *Cycas* itself, *Dioon*, *Microcycas*, and some species of *Encephalartos* and *Macrozamia*. In a few cases the columnar stem may reach a considerable height. The tallest of all Cycads, according to Prof. Chamberlain, who has travelled over a great part of the world to visit the Cycads in their native haunts, is a species of *Macrozamia*, *M. Hopei*, of Northern Queensland, which occasionally reaches a height of 60 feet. The Mexican species, *Dioon spinulosum*, has been known to attain 50 feet, while the Cuban *Microcycas* (inappropriately named) sometimes exceeds 30 feet. Species of *Cycas* may rise to a stature of a little over 20 feet.

Cycads live to a great age. In many species the stem remains clothed throughout life in an armour formed of the old leaf-bases (Fig. 9) and with their help, and a knowledge of the rate of production of new leaves, the age of the plant may be calculated. By this method it has been estimated that a *Dioon* with a trunk not more than a foot in diameter and 6 feet in height may have reached an age of 1000 years.[1]

[1] Chamberlain, 1919, pp. 69, 70.

Branching occurs not infrequently, but is often spurious, the development of the branch being due to wounding;

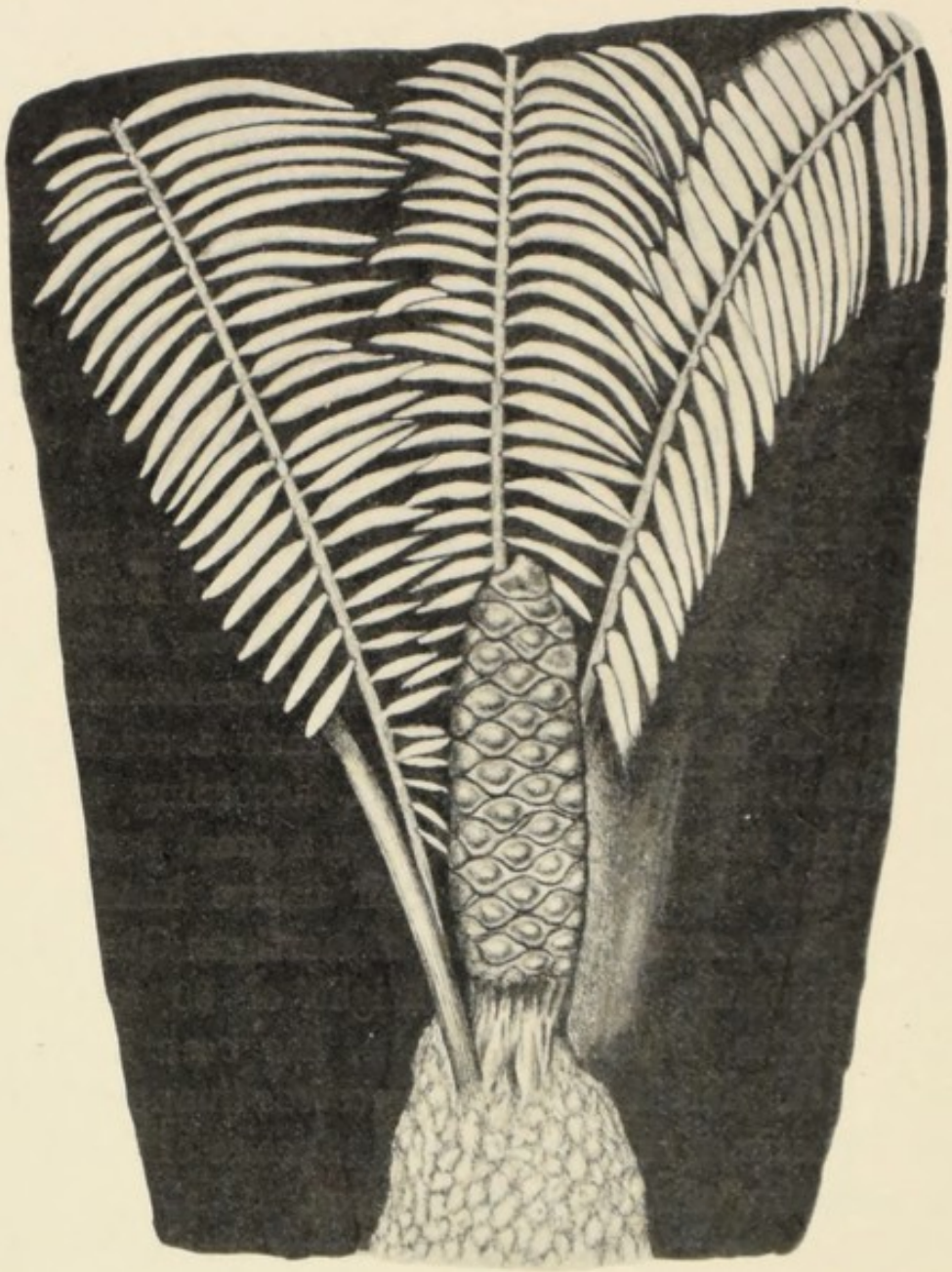

FIG. 9.—*Encephalartos villosus*. Female plant, bearing a single terminal cone. Some of the leaves have been removed.
From a specimen at Kew (G.T.G.).

or branching may be simulated by "the germination of seeds in the nest formed by the crown of leaves." [1]

The living Cycads are always diœcious, that is to say, the sexes are separate, the plants being either male or

[1] *l.c.*, p. 74.

female. With the exception of the female plant of *Cycas*, the fructification is always in the form of cones (Figs. 8 and 9), often of immense size, but simpler in construction than those of most Coniferæ. The cones of the two sexes are, as a rule, externally similar, except in dimensions; the female are the larger; thus in *Microcycas*, the male cone is about a foot long while the female cone, in extreme cases, reaches 3 feet. If it is true that a single female

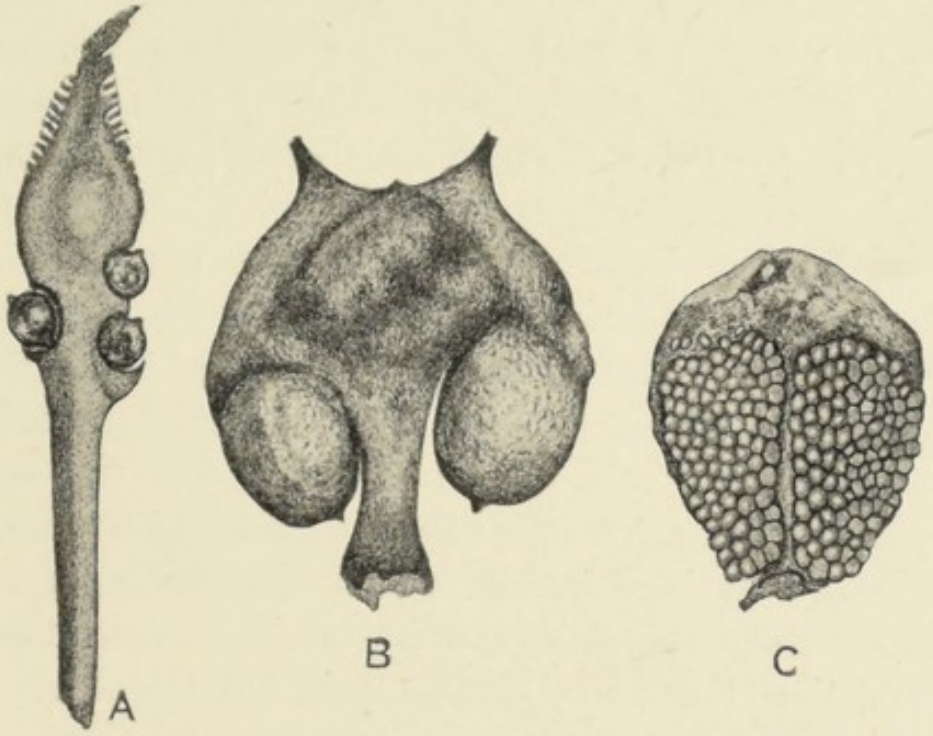

FIG. 10.—Sporophylls of Cycadaceæ. (A) *Cycas circinalis*; carpel, bearing three ovules (reduced). (B) *Ceratozamia Migueliana*; carpel, bearing two ovules (slightly enlarged). (C) *Macrozamia Fraseri*; stamen, lower surface, bearing numerous, crowded pollen-sacs (slightly enlarged). (G.T.G.)

cone of an *Encephalartos* weighed 90 lb., it must have rivalled the most monstrous prize Marrow in bulk!

Each cone is usually developed from the terminal bud of the stem, though in some cases the position is said to be lateral. The cone has a stout stalk, and the fertile part bears closely-packed scales, of large size, the stamens or carpels, as the case may be. They vary in form in the different genera, and it is on these characters that the generic distinctions are largely based.

Taking the male fructification first, each sporophyll

(stamen) bears, on its under surface, a large number (amounting to about a thousand in some cases) of round pollen-sacs. An example, from a *Macrozamia*, is shown in Fig. 10, C. The pollen-sacs are in two masses, on either side of the median line, and are further arranged in small groups, which have been compared to the sori of sporangia in a Fern, though this grouping is not evident in the mature condition. The sacs dehisce, and emit the numerous pollen-grains, the packing of the stamens becoming somewhat loosened at the time to allow of the escape of the pollen.

Leaving *Cycas* out of consideration for the moment, the sporophylls (carpels) of the female cone usually resemble the male sporophylls of the same species in form, though they are larger. Each carpel bears two ovules or seeds, inserted on the margin of the enlarged distal end, and lying one on each side of the stalk (see Fig. 10, B, from a *Ceratozamia*); the seeds grow very large in some forms, and may be as big as a plum or bigger. The ripe seed, in fact, is not unlike a plum, for it has a fleshy outer envelope, and a stone inside, within which the endosperm (and ultimately the embryo) is contained. We must remember, however, that the drupe-like body in the Cycads is not a fruit at all, but just a seed.

We must now return to *Cycas*, which, though the type-genus of the Order, is really its most exceptional member. We have already seen that the venation is quite peculiar. The male cone, however, is constructed on the same lines as in all the other genera (see Fig. 8); it is the female fructification which is remarkable. No cone is formed; the carpels, like any other leaves, are borne directly on the main stem of the plant, forming rosettes, which are preceded and again succeeded by the ordinary vegetative leaves. The female *Cycas* is the only living Seed-plant which has neither flower nor cone; this condition, as we shall see, was common among the early Seed-plants of the Palæozoic.

The carpels, thus borne with the leaves on the main stem, are themselves leaf-like, and are often most conspicuous objects. Thus in *Cycas revoluta*, the commonest species in cultivation, the carpel is a large, deeply cut, woolly organ, about 9 inches long, bearing half a dozen marginal seeds on the two sides of the lower, stalk-like portion. The orange-coloured carpels, contrasting with the scarlet seeds, present a striking appearance. The example figured, from *C. circinalis*, is of a somewhat simpler form; in this specimen only three seeds are present (Fig. 10, A). The carpels of *Cycas* are the most leaf-like sporophylls known among living Seed-plants.

The seed or ovule has a single coat or integument, which becomes differentiated into the fleshy and stony layers above mentioned. We cannot go into the details of its structure and development, but one point must be mentioned. Like all Gymnosperms, Cycads are pollinated directly, *i. e.* the pollen falls on or is conveyed to the ovule itself; there is no stigma or style. In Cycads and in the Maidenhair Tree, but in no other living Gymnosperms, there is a special receptacle prepared for the pollen; this is called the pollen-chamber, a cavity formed in the apex of the nucellus or central body of the ovule. In this flask-like hollow, the pollen-grains are received, and here they germinate. The pollen is caught in a drop of fluid secreted by the cells of the pollen-chamber, and as the drop evaporates, the grains are drawn down into the cavity below.

The pollen-chamber was discovered and its function clearly demonstrated by our countryman, William Griffith, in an Indian species of *Cycas*. The exact date of his observations is, I believe, unknown; it lay between the years 1832 and 1845. Two of his original figures, only published in 1852, seven years after his death, are reproduced in our Fig. 11, A and B. They show clearly the general structure of the *Cycas* ovule and in particular the

deep and narrow pollen-chamber, filled in its upper part with the pollen-grains.[1]

The presence of a pollen-chamber in Cycads and *Ginkgo* is correlated with the method of fertilisation in these plants. These Seed-plants are fertilised, like Cryptogams, by actively swimming ciliated spermatozoids, as was first discovered in 1896–7 by the Japanese botanists, Hirase and Ikeno. A pollen-tube is formed, but it remains compara-

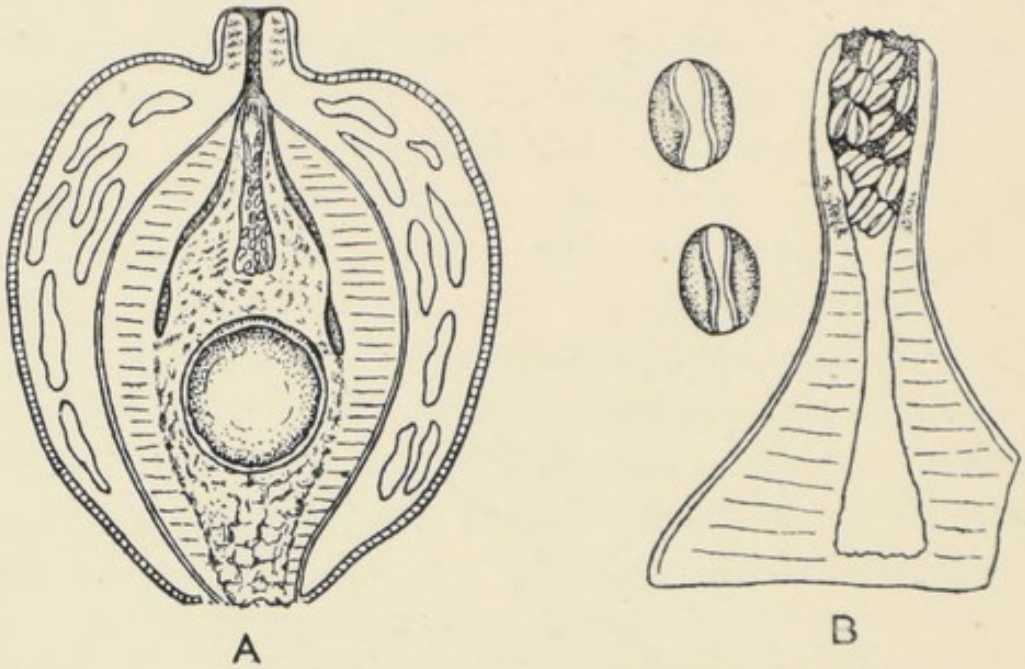

FIG. 11.—*Cycas* sp., Griffith's figures. (A) Median section of ovule, showing integument, micropyle, nucellus, embryo-sac, and pollen-chamber, forming a deep cavity in the upper part of the nucellus. (B) Enlarged section of pollen-chamber, showing numerous pollen-grains in the upper part of the cavity. Two pollen-grains on the left, further enlarged. These are the earliest figures showing the pollen-chamber.

tively short and serves partly as an anchoring organ, though its growth is sufficient to bring the spermatozoids (two of which are, as a rule, formed in each tube) nearer to their goal. The final stage of their journey to the eggs is accomplished by their own movements, as they swim in the fluid discharged from the distended pollen-tubes when they burst. Thus the receptacle provided by the pollen-chamber ensures the reception of the pollen at a spot within easy reach of the female cells, without the

[1] Griffith, 1852.

necessity for the growth of a long pollen-tube, while at the same time the necessary moisture is supplied from the tubes.

The importance of the pollen-chamber from our present point of view lies in the fact that, though so exceptional among recent Seed-plants, it was of general occurrence in seeds of the Palæozoic Age. In fact, the Cycad type of seed was the prevalent one in those early days; no doubt fertilisation by spermatozoids was then the rule among seed-bearing plants. But here we are anticipating. Our immediate concern is with the history of the Cycad class during Mesozoic times.[1]

The fossil Cycads of the Mesozoic Era are a new revelation to botanists who only know the surviving family. In a general sense, we may call them "Cycads," but very few indeed would find a place in the Order Cycadaceæ, as it now exists. There are some such cases among fossils, but they are very rare. One or two instances may be given.

The carpels of *Cycas* are very characteristic organs, and have been recognised several times in Mesozoic Rocks. Perhaps the oldest record is Nathorst's *Cycadospadix integer*, from the Rhætic (uppermost Triassic) of Sweden. This fossil much resembles in form and size the carpel of some recent *Cycas ;* there are protrusions on either side of the stalk, which probably mark the places where the seeds were borne. A more famous example is the *Cycadospadix Hennoquei* of Saporta, from the Lower Lias of Metz. Here the lamina of the carpel is fringed with narrow segments, as in some recent forms of *Cycas*, while in Nathorst's species it is entire. In Saporta and Marion's figure of *C. Hennoquei*,

[1] An excellent account of the whole process of fertilisation in Cycads will be found in Chamberlain's little book, "The Living Cycads," 1919, already cited. A general description of the recent Cycadaceæ, adapted to the needs of fossil-botanists, is given in Seward's "Fossil Plants," Vol. III, Chap. xxviii, 1917.

often reproduced, a seed is shown attached on one side of the stalk. This would be fairly conclusive as to the nature of the fossil, but recently some doubt has been cast on the presence of the seed; it may have been "restored" in the drawing. In any case, the seed-scars, one on each side, are evident. *Cycas*-like leaves are associated with the fossil, and there is not much doubt as to its being a carpel of the *Cycas* type.

A certain number of fossil cones, resembling the male or female strobili of Cycadaceæ, have been referred to that family, but the evidence is usually open to doubt. Some of them in all probability really belonged to Cycads, but the preservation is hardly ever good enough to prove it. The supposed female cones are commonly called *Zamiostrobus*, and the male ones *Androstrobus*. One of the best examples of the latter genus is Seward's *A. Nathorsti*, from the Wealden of Sussex. The cone bears numerous, more or less triangular scales; on the basal surface of some of the scales there are regularly arranged, depressed prints, supposed to mark the position of the pollen-sacs. The evidence, however, is not conclusive.

On the whole, the remains of true Cycadaceæ, of the modern type, are scanty in Mesozoic deposits. Still the records, such as they are, appear to show that the family is an extremely ancient one, though it seems never to have occupied a very important place in the Flora of the world. It will be noticed that the evidence is stronger for the early existence of the genus *Cycas*, than for that of the rest of the family. *Cycas* is perhaps the most striking example of the survival, down to our own day, of a really ancient and possibly primitive type of Seed-plant. The Maidenhair Tree may be equally ancient, but is more specialised.

The most important point, however, is this: the vast majority of the Mesozoic Cycads, as we call them, were not Cycadaceæ, in the sense of modern Botany, at all, but

belonged to quite diverse and wholly extinct families. That there was a certain affinity between the dominant Mesozoic Cycads and the surviving family is undeniable. It is, however, chiefly indicated by the vegetative structure; the reproductive organs, on which we are accustomed in matters of classification to lay the chief stress, were totally different in the two groups. Hence it is desirable to have a more general name to cover such widely divergent, though still related, groups; Nathorst's name, Cycadophyta, answers the purpose satisfactorily.

We have now to inquire what were the leading features of the dominant Cycadophyta of the Mesozoic Era.

The prevalent Mesozoic Cycads, as at present known, may be regarded as constituting one great class. It may be convenient to speak of them as the Cycadeoids, in contrast to the surviving family Cycadaceæ. If we search the records of the rocks in downward order, we first meet with Cycadeoids in the Middle Cretaceous: the Gault. Thus they decidedly overlapped the Angiosperms; as we have already seen, there was a certain period during which the old and the new races were flourishing side by side. In the Lower Greensand and Wealden the Cycadeoids are very numerous; they were abundant all through Jurassic times, and perhaps at their maximum in the Lias. In the Rhætic age they were already extremely abundant; they may be called a dominant race as far back as the Keuper (Upper Trias). Below that their remains are scanty, but they no doubt overlap, to a certain extent, the relics of a still older Flora, to which we shall come in due time.

Within the compass of the great Cycadeoid class we may distinguish two main tribes, which may be called the Bennettiteans and the Williamsonians. In outward aspect, and to a great extent in vegetative structure, the Bennettiteans were much like ordinary modern Cycads. Their foliage was almost the same; they usually had rather short, stout trunks. The Williamsonians tended to

have longer, more slender stems, often much branched, and were, generally speaking, less like the living family. Both tribes alike differed altogether from the recent Cycadaceæ in all their reproductive arrangements.

Broadly speaking, the stumpy Bennettiteans are the later, the more slender Williamsonians the earlier group in geological history. We will take the Bennettiteans first, both because we meet with them first, in our descending series, and because they are the more thoroughly known of the two tribes.

The stature of the Bennettitean Cycad was short, even compared with that of many recent Cycadaceæ. The height of the trunk, judging from the specimens described, seems rarely to have much exceeded 4 feet. On the other hand, the trunk is often of great thickness, reaching, in some species, a diameter of 20 inches or more. Some stems are nearly globular, while others are actually shorter than broad, as in the "Crows' Nests" of the Portland quarries.

In external aspect the Bennettitean trunk was much like that of a living Cycad, such as *Macrozamia* or *Encephalartos*, for an armour of leaf-bases clothed the surface. The leaves themselves were also completely Cycadaceous, of the usual simply pinnate type. In certain cases they are found preserved, still folded, in the terminal bud of the stem. Their structure proves to be all but identical with that of the ordinary leaves of those recent Cycads in which the leaflets have many parallel veins. The structure of the stem itself was also much like the usual modern type, with a large pith and a woody zone of moderate thickness. In some anatomical details the Bennettitean stem was somewhat simpler than that of the surviving family.

The outward appearance of a short Bennettitean trunk is shown in Fig. 12. The important feature is the presence, among the leaf-bases, of large, bud-like rosettes, each with

a central axis surrounded by the bases of bracts. These rosettes are the fructifications; it is characteristic of the Bennettiteæ that they were always borne laterally, in between the leaves, and probably in an axillary position. The presence of these bodies, embedded in the armour of

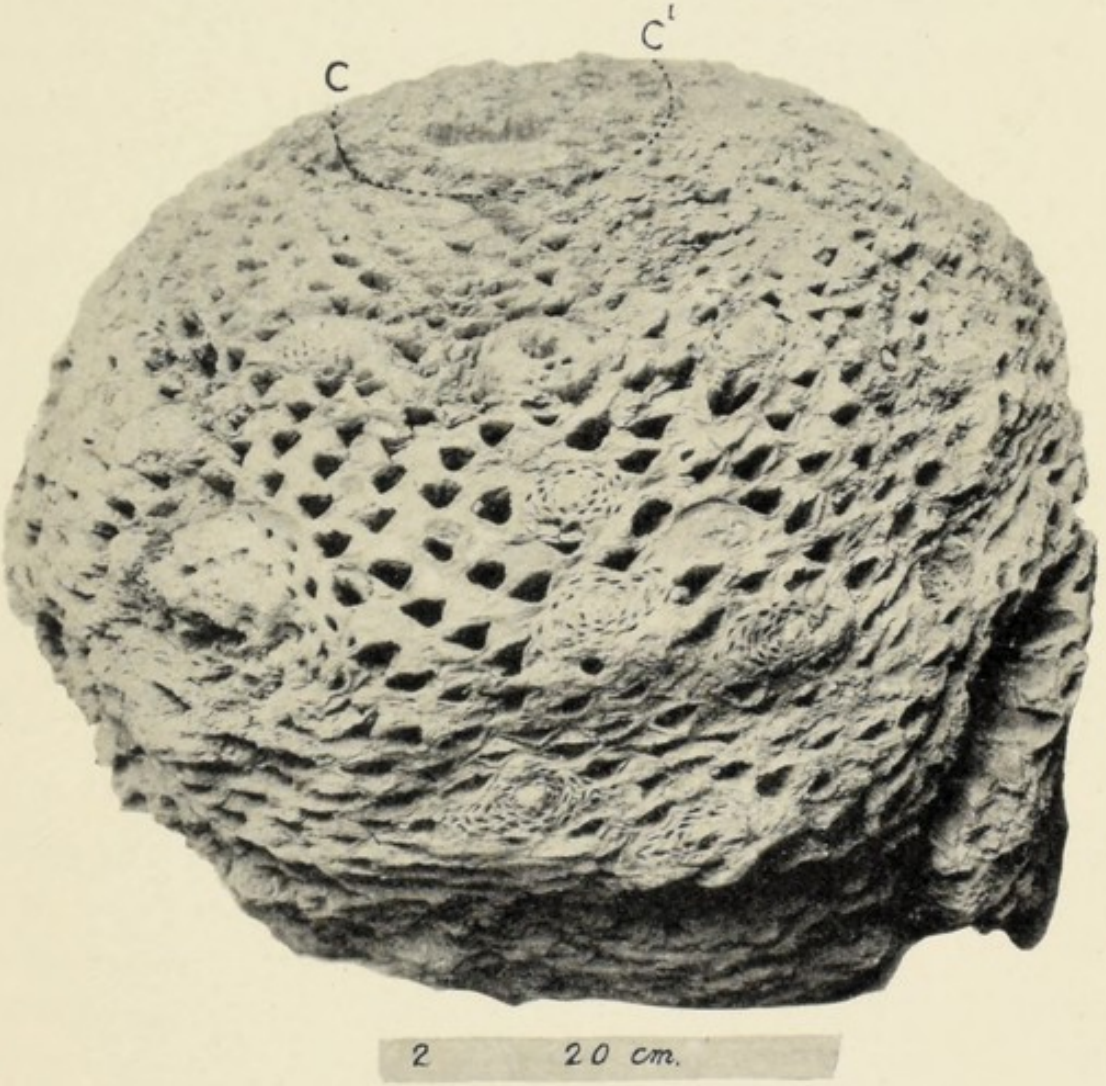

FIG. 12.—*Cycadeoidea colossalis*. Short stem complete, showing the leaf-bases and the rosette-like fructifications. C—C¹, position of emergent crown of fronds. The stem was about 19 inches in diameter.
From a photograph supplied by Dr. Wieland.

leaf-bases, at once proves that the stem is that of a Bennettitean and not of a member of the Cycadaceæ. The position of the fructifications is, however, a character of the Tribe Bennettiteæ, and not of the whole Cycadeoid class, for in the Williamsonian Tribe, as we shall see, other conditions prevailed.

Branching of the stem was not uncommon; in several species clusters of stems, no doubt formed as branches on a common stock, have been observed.

Another characteristic feature is the presence of great numbers of scales or ramenta, in which the leaf-bases and indeed all the organs are closely packed. These ramenta are flat structures, from one to several cells in thickness, and show a clear analogy with the chaffy paleæ or ramenta on the fronds of Ferns. They are not known in recent Cycads, which only have ordinary, filiform hairs.

We have now to return to the fructifications, which are the really distinctive organs, marking out the Cycadeoids as a class by themselves. So far as the Tribe Bennettiteæ is concerned, the reproductive organisation is fairly uniform; when we come to the Williamsonians we shall find somewhat greater variety. Our knowledge of the fructification, now tolerably advanced though scarcely complete, has been built up by the researches of various observers, among whom Carruthers, Solms-Laubach, Lignier, and above all Wieland, are the chief.

Carruthers led the way by his masterly elucidation of the fruits of the famous Isle of Wight species, *Bennettites Gibsonianus*; Solms-Laubach followed this up; he was the first to recognise the embryo, besides comparing a number of other species, chiefly Italian; Lignier worked out all the details in a beautifully preserved French fossil, *B. Morierei*, and lastly Wieland, with the magnificent American material at his disposal, was the first to demonstrate the structure of the flower as distinguished from the fruit; by his extensive comparative investigations he has placed our knowledge on a broad basis, and in his later works has done much to establish the true relations between the Bennettitean and Williamsonian Tribes.[1]

[1] Carruthers, 1870; Solms-Laubach, 1891; Capellini and Solms-Laubach, 1892; Lignier, 1894; Wieland, 1906, 1916; Wieland's two large volumes on American Fossil Cycads are magnificently illustrated.

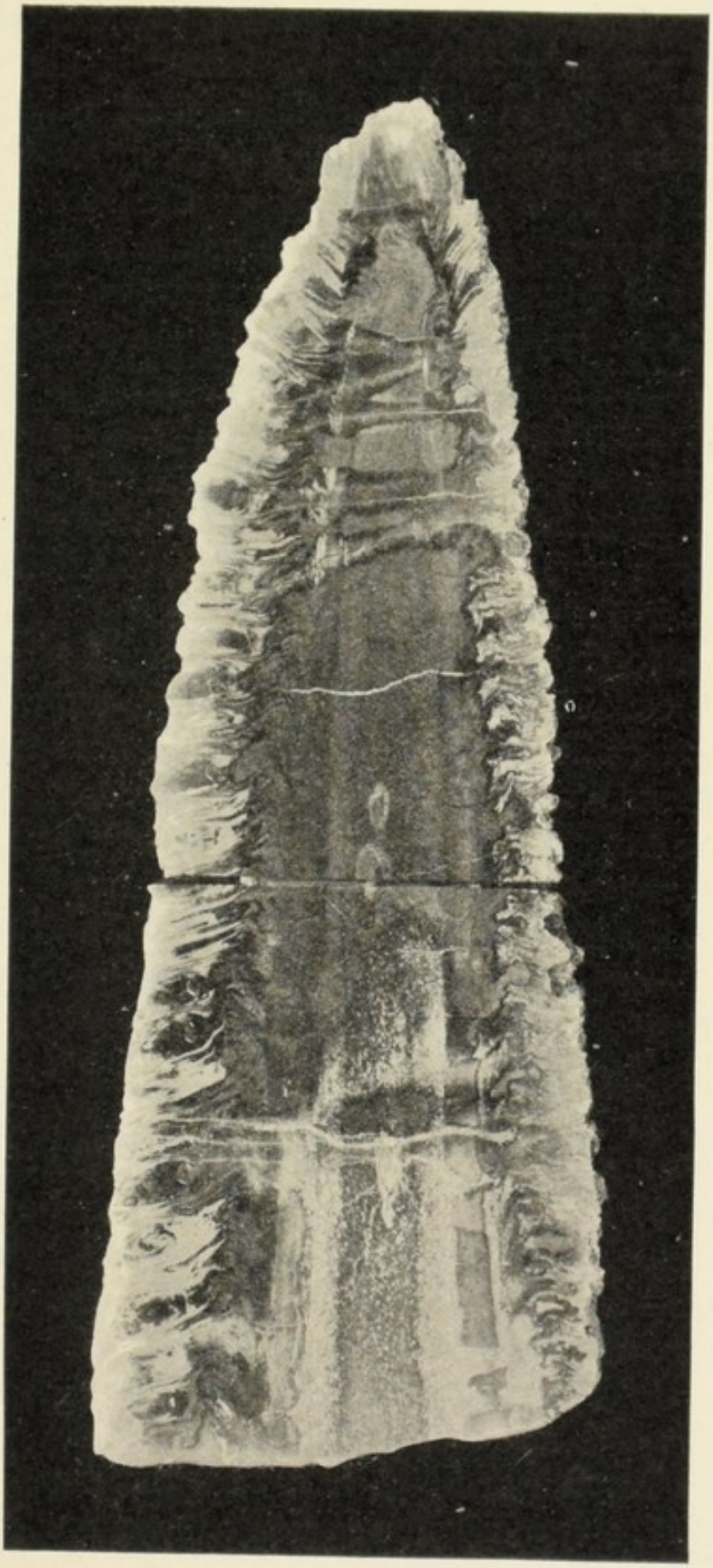

FIG. 13.—*Cycadeoidea Dartoni.* The Hermosa Cycad. Upper part of stem, cut longitudinally, showing the axis and leaf-bases, with numerous fruits embedded among them. This specimen was over 20 inches in height. From a photograph supplied by Dr. Wieland.

We have spoken of the Bennettitean fructification as a *flower* and not as a cone, for the former is the natural term to apply to an organ which in most respects has more in common with the familiar Angiospermous flower than with the cone of Cycadaceæ or Coniferæ. At the same time, we must remember that we are dealing with a wholly extinct type of reproductive apparatus, not directly comparable to anything met with in the recent Flora, though significant analogies may be traced.

The American Cycadeoids, from the Upper Jurassic and Lower Cretaceous of Dakota, Wyoming, and Maryland, are extremely numerous—over 1000 specimens are known, referred to a number of species, all of which now find their place in the one genus *Cycadeoidea*.[1]

In order to give a definite idea of what a Cycadeoid in the fertile condition was like, we may take the wonderful fossil known as the Hermosa Cycadeoid (*C. Dartoni*). This was found as an isolated specimen near Hermosa, in South Dakota, and appears to be of Lower Cretaceous age.

The upper part of the stem, including the apical bud, is preserved, the length being a little over half a metre; the full height was probably about a metre (Fig. 13). The preservation is almost perfect throughout. The most remarkable feature of the fossil is that more than 500 fructifications are present in the part preserved, one for nearly every leaf-axil. The great majority of the fruits are perfect; they are in the ripe condition, and every one of the seeds, of which there are many in each fruit, contains an embryo—an astonishing fact in a fossil plant, though other species of Bennettiteæ show the same. The observation that the whole stem, so far as preserved, is covered throughout with ripe fruits (except a few that were abortive) leads Dr. Wieland to believe that this plant, as well as some other Cycadeoids, was *monocarpic*, fruiting once only in its lifetime and then dying down. The same

[1] Buckland's name. *Bennettites*, Carruthers, is synonymous.

phenomenon is well known in certain Palms and Bamboos among recent plants.

We may now turn our attention to the details of the fructifications, remembering that in this specimen they were already ripe fruits and not " flowers." The fruits in

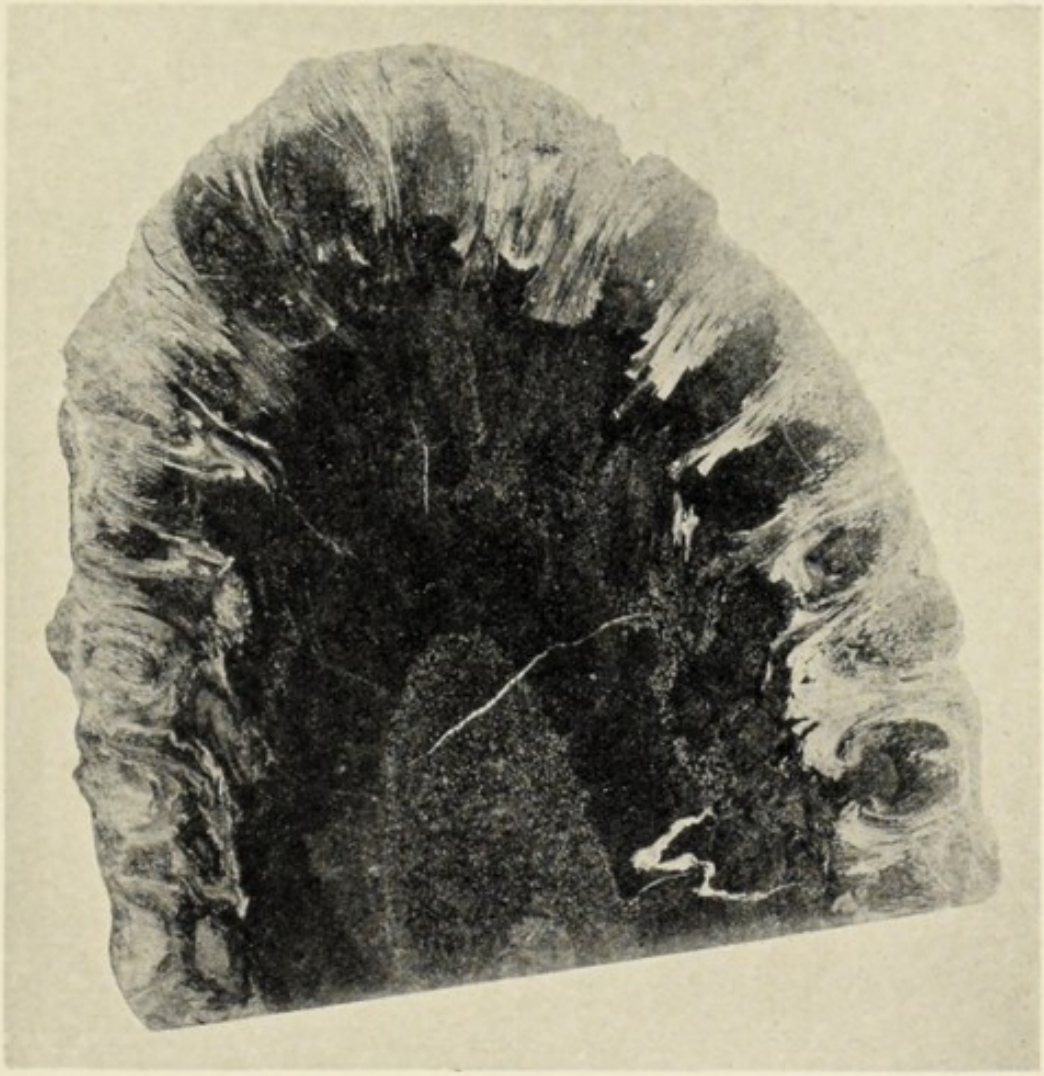

FIG. 14.—*Cycadeoidea Dartoni.* Transverse section of stem, showing the axis, with its pith and wood and very numerous fruits in the outer armour. Half natural size.
From a photograph supplied by Dr. Wieland.

the Hermosa Cycad were rather small compared with those of some other species, measuring from 2 to 3 cm. in length, with a diameter of 1·5 cm. or less. Each fruit is borne on a short, stout stalk from 1 to 2 cm. long (Fig. 14), and is enclosed in an envelope of bracts, springing from the upper part of the peduncle, and overlapping the

top of the fruit (Figs. 15, 16). The stalk or peduncle terminates in a hemispherical cushion or receptacle, on which the organs constituting the essential part of the fruit are borne.

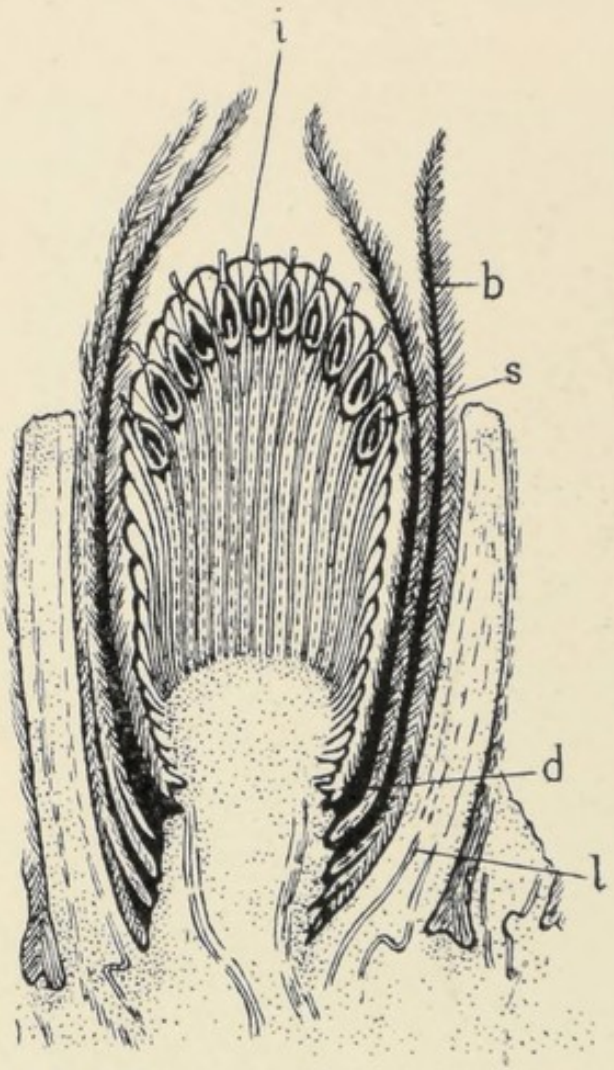

FIG. 15.—*Cycadeoidea Wielandi*. Somewhat diagrammatic longitudinal section of a ripe fruit. *l*, Leaf-base, *d*, position of hypogynous whorl of stamens, now shed; *b*, hairy bracts; *s*, seeds; in each the dicotyledonous embryo is shown; *i*, interseminal scales, enlarged at the tips, to form the pericarp.
After Wieland.

These organs are of two kinds. There are numerous long and slender pedicels, each terminating in an erect seed, with the micropyle directed outwards (Figs. 15, 16). Between the seed-stalks are still more numerous sterile appendages, the "interseminal scales." Up to the level of the seeds the interseminal organs are filiform and extremely slender (see Figs. 16, 17), but at the upper end they expand greatly; their massive heads fit together and form collectively an almost continuous envelope (the pericarp of Carruthers) enclosing the seeds, except where the micropyles pass through and reach the surface (Figs. 15, 16). Thus a strongly constructed fruit was formed, comparable to that of an Angiosperm, but arrived at in quite a different way.

In an Angiospermous fruit, as we all know, the carpels

themselves form the pericarp.[1] In the Cycadeoids this is not the case; the carpels are represented only by the pedicels of the seeds; the enclosure of the fruit was effected by a quite distinct set of organs, the interseminal scales. Further, the enclosure is never complete, for the pericarp is penetrated by the micropyles of the seeds. We have, in fact, in the Cycadeoids, a type of fruit highly developed

FIG. 16.—*Cycadeoidea Dartoni*. Upper part of fruit, in longitudinal section, showing the seeds on their pedicels, with the linterseminal scales between them. In some of the seeds the micropyle is cearly seen. (× 5.) From a photograph supplied by Dr. Wieland.

on its own lines, but quite distinct from any fruit known among living plants.

The fruits of the Bennettiteans have long been known. They were first discovered in the famous Isle of Wight fossil, *Bennettites Gibsonianus*, described by Carruthers in 1870. The original specimen, though not on the same grand scale as the Hermosa Cycad, was equal to it in preservation and long afforded the basis of our knowledge. Essentially, the structure is the same.

The most interesting point about the seeds is that the

[1] I leave out of consideration the case of the inferior ovary, which has no bearing on the present question.

embryo is so often preserved. I believe there is no other group of fossil plants in which this is the case. The embryo is large and practically fills the seed-cavity; whether a little endosperm may have remained is doubtful

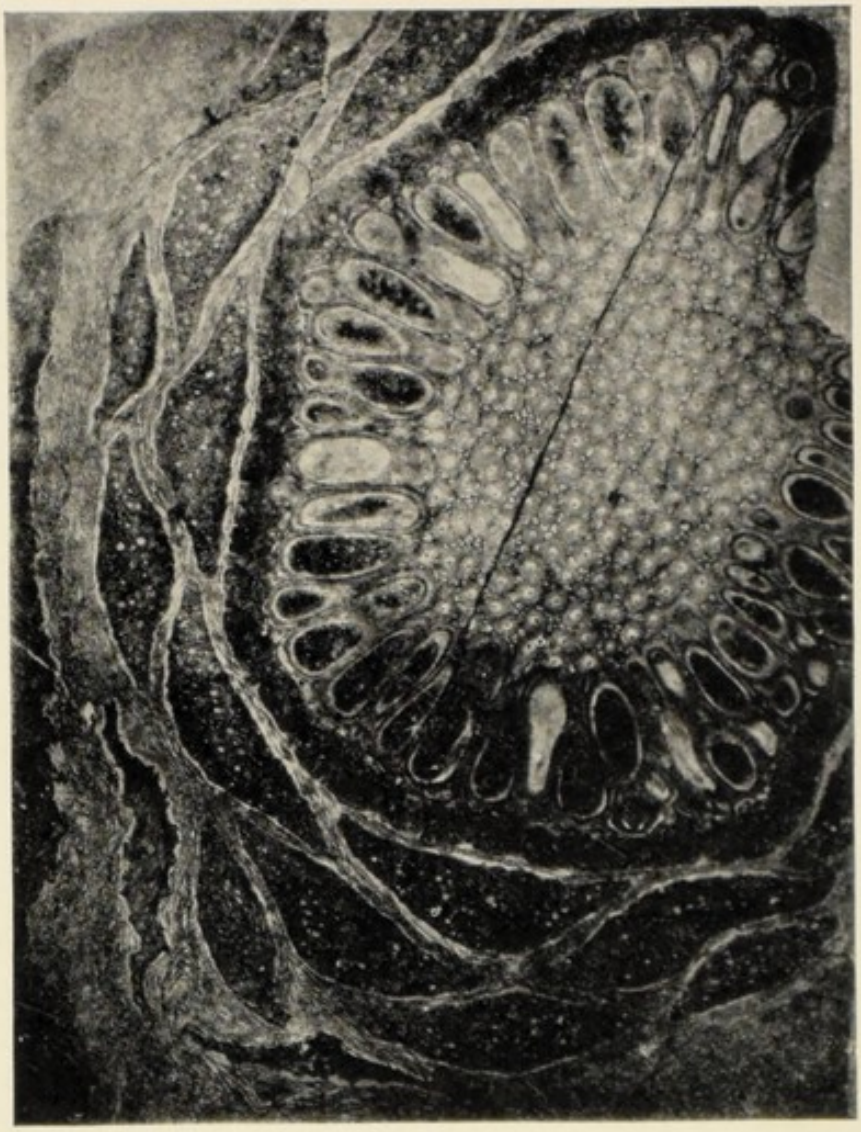

FIG. 17.—*Cycadeoidea Dartoni*. Transverse section of fruit, showing the surrounding bracts, the pericarp, formed of the enlarged interseminal scales, the seeds, and in the middle the crowded pedicels of the upper seeds and interseminal scales. (× 5.)
From a photograph by Dr. Wieland.

—anyhow it was so little that the seed, in the language of recent systematic botany, may be called exalbuminous. The seed and embryo figured are from the Isle of Wight species, *B. Gibsonianus* (Fig. 18). The radicle (young root) of the embryo is turned, as usual, towards the micropyle;

at the other end are the two massive seed-leaves, for the Bennettitean embryo, like that of recent Cycads, was dicotyledonous. The modern Cycadaceæ, however, like other Gymnosperms, have a large endosperm in the ripe seed; its absence or insignificant amount in the Ben-

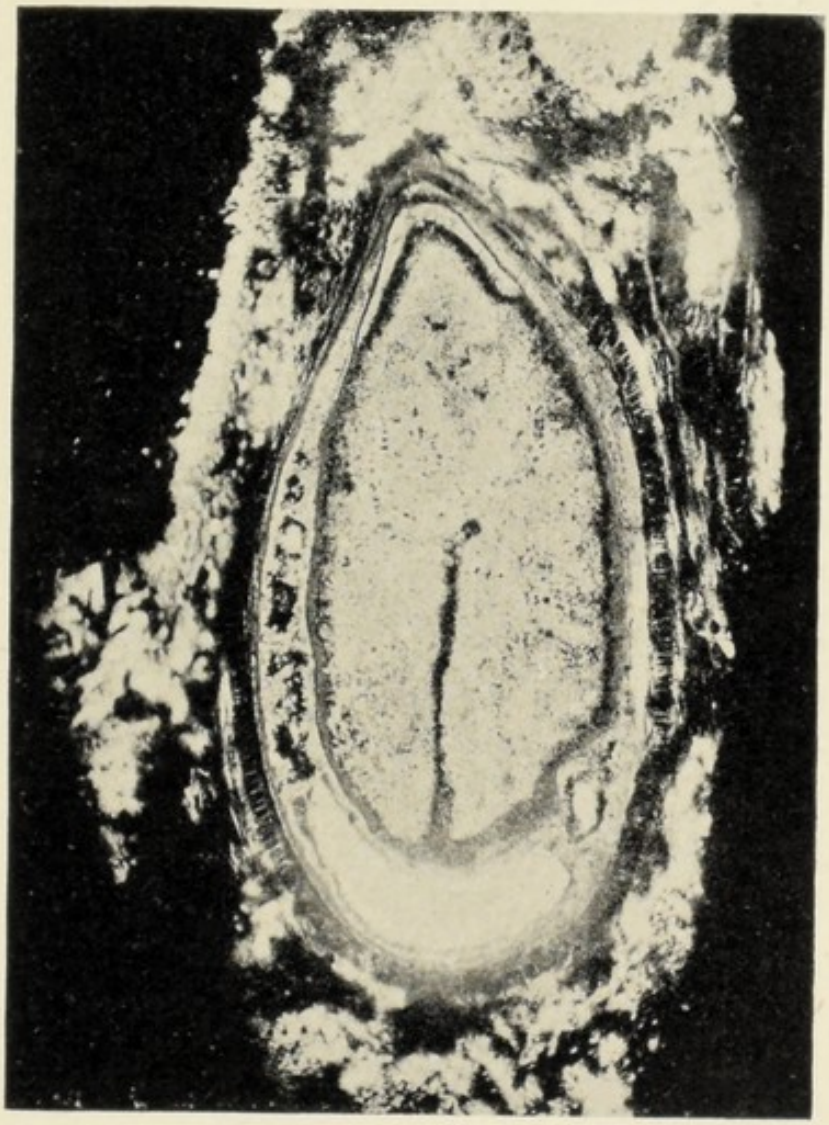

FIG. 18.—*Bennettites Gibsonianus*. Longitudinal section of seed, showing testa, and the large dicotyledonous embryo, with the radicle directed upwards. (× 19.) Scott Collection 351.
From a photograph by Mr. W. Tams.

nettiteæ is a most peculiar feature, only paralleled among the Angiosperms.

We have so far considered the ripe fruit, which was the stage at which the Bennettitean fructification was first observed. It was many years later that Dr. Wieland, in the American material, was able to demonstrate the

organisation of the flower, with all its organs still present. In all known cases the Bennettitean flower was bisexual, or hermaphrodite, to use the old term. The arrangement of the parts was the same as in all bisexual flowers of Angiosperms; the analogy is closest with flowers of the *Magnolia* type.

A number of examples of Bennettitean fructifications at the flower stage have been observed by Dr. Wieland. They belong to various species, but on the whole the main features of the organisation are uniform throughout. The whole flower is surrounded by numerous bracts, which, as we have already seen, are persistent in the ripe fruit. The bracts may perhaps be compared to the perianth of those Angiospermous flowers in which there is no distinction of calyx and corolla and the perianth leaves are spirally arranged.

The stamens, which Dr. Wieland was the first to observe, are inserted round the base of the receptacle, below the ovule-bearing region; they are thus "hypogynous," as in Ranunculaceæ and other families of De Candolle's Thalamifloræ. The stamens are extraordinary organs, quite different from any stamen known in a living plant. Their number ranges from about 10 to 20 in different species; they are in one whorl, and their basal portions are fused together into a tube or disk, like the "monadelphous" stamens of a mallow. Higher up, the stamens become free—they are large and compound leaves of the pinnate type, and so far resemble the vegetative foliage. Each pinna or leaflet bears very numerous pollen-sacs, in two rows (Fig. 19).

The pollen-sacs are themselves complex structures, for each is divided into a number (20–30) of compartments or loculi, forming a double row. In the loculi the pollen-grains are contained (Fig. 20). These compound pollen-sacs have been compared to the compound sporangia (synangia) of certain tropical Ferns (Marattiaceæ), and

the analogy is certainly a close one. There seems to be little doubt that the compound structure in the case of these Ferns is due to the fusion of sporangia, and the same interpretation may be extended to the compound pollen-sacs of the Cycadeoids, but it must not be forgotten that here we are comparing groups which are very wide apart.

The stamens are very large. In the case of *Cycadeoidea dacotensis* Dr. Wieland estimates their length, if straightened out, at 10 cm. As a matter of fact they are always found folded, in a simply circinate manner, their tips curving over towards the central receptacle (Fig. 19). This, no doubt, was their position in the bud; an open flower has never been observed, so far as I am aware, in the Bennettiteæ, though, as we shall see, the open condition is often found in the flowers of the Williamsonian Tribe.

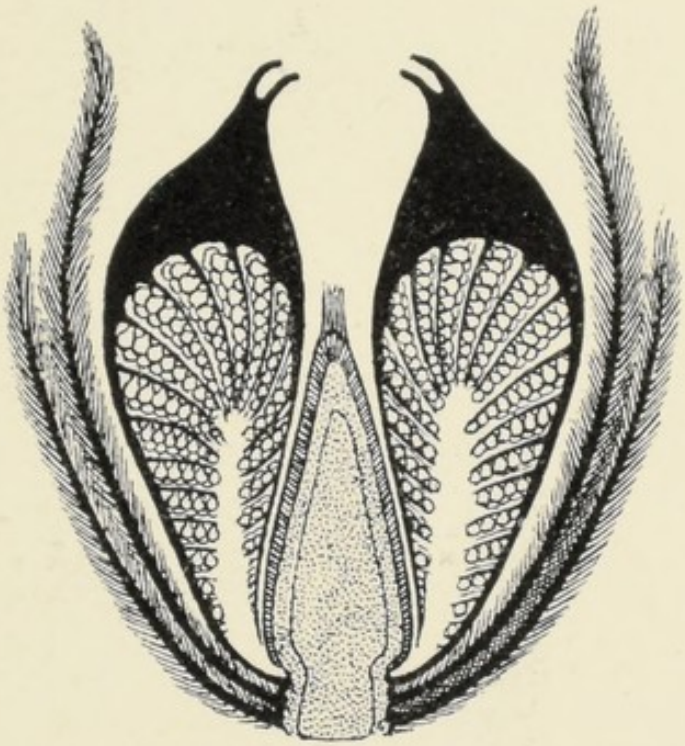

FIG. 19.—*Cycadeoidea dacotensis*. Restoration of flower, in longitudinal section. On the outside are the hairy bracts. Then come the great incurved stamens, with numerous pinnæ bearing the pollen-sacs. Their curved summits are shown enormously thickened, with appendages, as indicated by recent observations of Dr. Wieland. In the middle is the conical ovuliferous receptacle, with a sterile tuft at the apex.

Reconstructed, from various figures of Dr. Wieland's. (G.T.G.)

Considering that each of the 10–20 compound stamens bore several hundred large pollen-sacs, the total output of pollen, per flower, must have been enormous. This suggests wind-pollination rather than self-pollination or entomophily, but these are questions which can hardly

be settled when we are dealing with fossil plants so remote from any living family.

In the centre of the flower is the receptacle, covered with the ovules and interseminal scales. At the flower

Fig. 20.—*Cycadeoidea dacotensis.* Longitudinal section of flower, showing the bracts, on the outside, the lower parts of the stamens (cf. Fig. 19), with numerous compound-pollen-sacs, and the conical receptacle in the middle, bearing immature ovules and scales. (× 2.)
From a photograph supplied by Dr. Wieland.

stage these organs are naturally little developed as compared with the ripe, fruiting condition; the thickness of the ovulate zone is barely one-tenth of what it would be in the mature, seed-bearing stage. It is not surprising that the delicate tissues are imperfectly preserved, and

that we know little as yet of the structure of the ovule at the time of pollination.

In many species (such as *C. dacotensis*), the receptacle is conical and elongated, not short and rounded as in the Hermosa Cycad and our *Bennettites Gibsonianus*. In the case of the conical receptacle there is usually a tuft of sterile scales at the summit of the cone, the fertile region being thus limited to the sides (Fig. 19).

There is little else to note in the way of variations of structure. In a flower referred to *C. colossalis*, Dr. Wieland finds a somewhat peculiar organisation. The stamens are winged at the back, the wings (two to each stamen) forming collectively a spire or dome at the top of the whole flower; [1] at the same time, the part of the stamen bearing the pollen-sacs is much reduced. The fertile ovuliferous zone of the central receptacle is also short, and the sterile apex unusually long. This seems to be the only Bennettitean flower at present known to show any marked peculiarities, though doubtless other variants on the general plan may be expected to present themselves in the future.

Bennettitean flowers are scarce among European fossils, and none have been found worthy to compare with the fine American examples. This is rather a curious accident, for some European specimens of the *fruit*, e. g. *Bennettites Gibsonianus* and *B. Morierei*, have always held their own with the best.

Among the few European flowering specimens, one only, discovered by Dr. Marie Stopes, is known from our own country. The plant in question was named *Bennettites maximus* by Carruthers; the one specimen, a fine trunk, comes from the Lower Greensand of Shanklin in the Isle of Wight.[2] The numerous fructifications are at a very young stage, flower-buds rather than flowers, and the

[1] It is possible, as Dr. Wieland points out, that this feature may have been common to other species (cf. Fig. 19).

[2] Stopes, 1918, p. 432.

structure was difficult to make out. The peduncle and bracts were already fairly well developed, but the fertile region was still very rudimentary. Traces of the stamens, or of the strands supplying them, have been observed, but the most interesting point is that very young ovules, in some cases showing the integument, are present. The ovules appear sessile, neither pedicels nor interseminal scales having yet been developed. These somewhat obscure buds are all we have to show in Britain, at present, in the way of bisexual Bennettitean flowers.

The absence of stamens in ripe fruits like those of *Bennettites Gibsonianus* of course affords no presumption whatever against their presence at the flowering stage. We do not expect, even in living plants, to see much of the stamens when the fruit is mature. In several cases Dr. Wieland was fortunate enough to find recognisable remains of the old staminate disk at the base of ripe and partly ripe fruits. That such traces cannot always be detected need cause no surprise. The positive evidence so far appears to be entirely in favour of the conclusion that all known Bennettitean flowers were bisexual, for all flowers observed have both male and female organs; it is only at the fruiting stage that the stamens have sometimes left no trace.

Dr. Wieland, however, has raised the question whether, in some cases, the flowers may not have been functionally monœcious, *i. e.* unisexual, by abortion of one or the other of the essential organs. He believes that he has found a clear case of the kind in *Cycadeoidea Jenneyana*, and suspects others. In the species mentioned, two fructifications are compared; he finds a bisexual flower with thirteen stamens, bearing nearly mature pollen-sacs, while the ovulate zone of the receptacle is so little developed as to suggest abortion. On the same stem he has observed a "relatively mature ovulate cone," much larger than the former, with seeds, pedicels, and interseminal scales all

well developed, while the hypogynous disk line of intersertion appears as if completely grown over. "It is in fact very improbable that any earlier borne basal disk [of stamens] could have reached even a minor development." [1]

It is quite possible that Dr. Wieland's interpretation is right, and that in some cases functional monœcism actually occurred, but personally I am not convinced by the evidence. The two fructifications in question are obviously at very different stages of development, and it seems not unlikely that the differences between them may merely be due to age. The question is evidently a difficult one to settle in fossil specimens, and must, I think, be left open.

In any case, all the evidence goes to show that in the Bennettitean flower both sexual organs were constantly present, even if not in all cases functional.

We have mentioned that the Gault is the latest horizon at which Cycadeoids have been found, the only exception being the imperfectly known Texan species, *Cycadeoidea Uddeni*, which appears to be somewhat later. One of the most remarkable fossils of this family is a fruit from the Gault of Folkestone, found by Mr. G. Walton and described by Dr. Marie Stopes.

Only a fragment of the fruit was found, but what there is of it is perfectly preserved. It must have been much larger than any other known fruit of this group. The size can be calculated from the curvature of the surface in the part found. The diameter cannot have been less than 70 mm., and may probably have been as much as 120 mm. In other words, the fruit was certainly as big as an orange, and may have been as big as a melon. Other Bennettitean fruits do not much exceed 30 mm. in diameter, so the Folkestone species was altogether exceptional in size; in form the fruit was rather flat and dome-shaped. It is named

[1] Wieland, 1916, p. 40.

Bennettites albianus, from its occurring in the Albian or Gault.

The number of seeds was enormous, compared with that in other Bennettitean fruits. Two hundred and fifty were counted in a transverse section of the fragment, and Dr. Stopes estimates that the total number must have run into thousands. The fruit had an extremely solid construction; the pericarp formed a strong, continuous shell, for the heads of the interseminal scales were firmly fused to each other and to the micropyle-tubes of the seeds, while the micropyle-openings were plugged up. The tissues are of the toughest kind, like those in the stone of a modern fruit. Without going into details, we may say that the Folkestone fossil is altogether the most elaborate and perfect, as well as the largest, of all Cycadeoid fruits. It represents the extreme development known to us of this type of seed-vessel.

Dr. Stopes has pointed out that in Gault times the Cycadeoids were rapidly approaching extinction: "hence it is extraordinarily interesting to find a species growing at that time which produced by far the largest and most elaborate cone on record in the family; it is obvious and tempting to compare this with the giant and elaborate forms which appear in so many groups of animals shortly before their final extinction." [1]

Dr. Stopes warns us that we do not yet know enough to judge whether such a comparison is legitimate, but certainly the idea that the great fruit of the Folkestone Cycadeoid represents the last and crowning effort of a splendid but doomed race cannot but appeal to the scientific imagination.

The important discoveries which we have briefly recorded, revealing the remarkable and complex structure of the flowers and fruits of the Bennettiteans, naturally led us,

[1] Stopes, 1918, p. 391.

for a time, to think of this Tribe as the dominant race of Mesozoic Cycads. Their wide distribution and richness in specific forms strengthened this idea. But on considering the whole of the evidence (not all of it new) we are compelled to take a different view. Dr. Wieland, to whom, more than to any other individual, our present knowledge of the Bennettitean Cycads is due, has taught us to moderate our estimate of their relative importance. They may represent the culmination of the Cycadeoid stock, but they were not its main line.

We have already noticed the remarkable uniformity, both in vegetative and reproductive organisation, of the whole Bennettitean Tribe. As Dr. Wieland says: "The narrow structural range of the silicified trunks, well-nigh expressible in the terms of a single genus, is only what might be hypothesised from the features of a single species like *Cycadeoidea dacotensis* were it the only known form. These are then the stereotyped terminal forms of a side branch from a great plastic and dominant precursor race, unquestionably including the vast bulk of Cycadophytan vegetation from the earliest Triassic to mid-Cretaceous times." [1] He further remarks that the robust stems of the Bennettiteans, "with thin wood, an immense medulla, and heavy, persistent armor, are exceptional to the point of abnormality." [2]

Thus the Bennettiteæ, like the existing Cycads, are "relegated to a lateral position." [3] What, then, was "the great plastic and dominant precursor race," of which this advanced and specialised family, however important, was only an offshoot? It is represented by the Williamsonian Tribe, a varied and extensive group, which includes, generally speaking, the more ancient members of the Cycadeoid phylum.

The Williamsonian Cycads have been known much longer than the Bennettiteæ. Williamson, as far back as 1847,

[1] Wieland, 1916, p. 178. [2] *l.c.*, p. 191. [3] *l.c.*, p. 225.

published a paper on a plant which was then called *Zamia gigas*. He described it more fully in 1870; it was named *Williamsonia gigas* by Carruthers, and is now the type of the Williamsonian Tribe. Williamson's general reconstruction of the plant, with a fairly tall stem, pinnate leaves like those of a *Zamia*, and large, stalked fructifications resembling Globe Artichokes, has proved to be correct. The details, however, of Williamson's specimens are very difficult to interpret, and clearer ideas can be obtained from other examples.

We will first consider the genus *Williamsonia* itself, of which many species have been described. In the habit of the plant and the stalked fructifications the genus appears to have been very different from the Bennettiteæ, but the foliage, of the ordinary pinnate Cycad type, was similar, though the leaves were usually smaller. The fructifications are, in a general sense, of the same type as in the later group, but there is more variety.

The Williamsonian Tribe, especially in the earlier Mesozoic times, attained an immense development all over the world. Williamsonias are abundant in the Jurassic strata of Yorkshire, where they were first discovered, and also occur in Scotland. Many specimens are recorded from India; they are found in Greenland, and are extraordinarily abundant in the Lias of Mexico. Dr. Wieland, not content with the magnificent Cycadeoids of his own country, made an expedition to Mexico, and spent a long time collecting fossils in the province of Oaxaca. It was there that he was led by his discoveries to realise the full importance of the Williamsonian Cycads. The Liassic Flora of the province is wonderfully rich, and 70 per cent. of the species are Cycads. Fourteen new species are referred to *Williamsonia*.[1]

Abundant as is the material, it suffers from one great disadvantage as compared with the Bennettitean fossils.

[1] Wieland, 1914; 1916.

The latter are commonly preserved in a petrified condition, usually silicified, so that the structure, often in every detail, is preserved. This is very rarely the case with the Williamsonian specimens. As a rule, they are preserved only as impressions or casts, in which the external features are well shown, but little of the internal structure can be traced. There is therefore much more difficulty in determining the essential characters of the Williamsonian Cycads than in the case of their Bennettitean allies.

The Williamsonian stem, according to Dr. Wieland, had, as a rule, a fairly dense and compact woody zone (comparable to that of a Conifer) and was normally slender and branching. Our knowledge of the stem is based on fragmentary specimens, and therefore unsatisfactory. There is evidence that various stems described under the name *Bucklandia* really belonged to Williamsonias. They are often clothed with the bases of the leaves, but are much more slender than those of the Bennettiteans, commonly about 4 inches or less in diameter. Branching specimens have occasionally been found.

In a few cases the internal structure has been preserved. In Williamsonian stems from the Jurassic of India, there is a fairly large pith, surrounded by a compact zone of wood, with narrow medullary rays.[1] The structure of the wood is thus very different from that in most Bennettitean or recent Cycadaceous stems. A long, slender stem is shown among the foliage and flowers in Fig. 21.

The foliage of *Williamsonia*, as already mentioned, was of the usual Cycad type, the pinnate leaves having numerous leaflets (Fig. 21). Various genera have been distinguished according to the variations in the form of the leaf, but these differences are of little importance. The foliage shown in Fig. 21, in association with *Williamsonia* flowers, is placed in the form-genus *Otozamites*. It is an unfortunate

[1] Bancroft, 1913. For a full account of the Williamsonias, see Seward, 1917; also Wieland, 1916.

necessity in fossil botany to give separate names to different organs, which may have belonged to the same plant, but are not usually found in connection. In some favourable

FIG. 21.—Mexican *Williamsonia*, showing flowers, foliage, and branched stem, as exposed on a slab of Liassic rock. (Reduced.)
From a photograph supplied by Dr. Wieland.

cases, however, fronds as well as flowering shoots are found attached to the stem, so that all doubt is removed. This is the case with *Williamsonia gigas*, where the leaves were named *Zamites*.

The flowers of *Williamsonia* were often very large; a flower-bud, described by Wieland, was $4\frac{3}{4}$ inches in diameter. They are still imperfectly known, but enough has been established to prove the general affinity with the Bennettitean Tribe. The flower, when complete, was here also surrounded by bracts, but in many specimens they have been lost. The two sexes are very commonly found separate, and it is generally held that in many species the flowers were unisexual, though perhaps this has never been strictly proved.

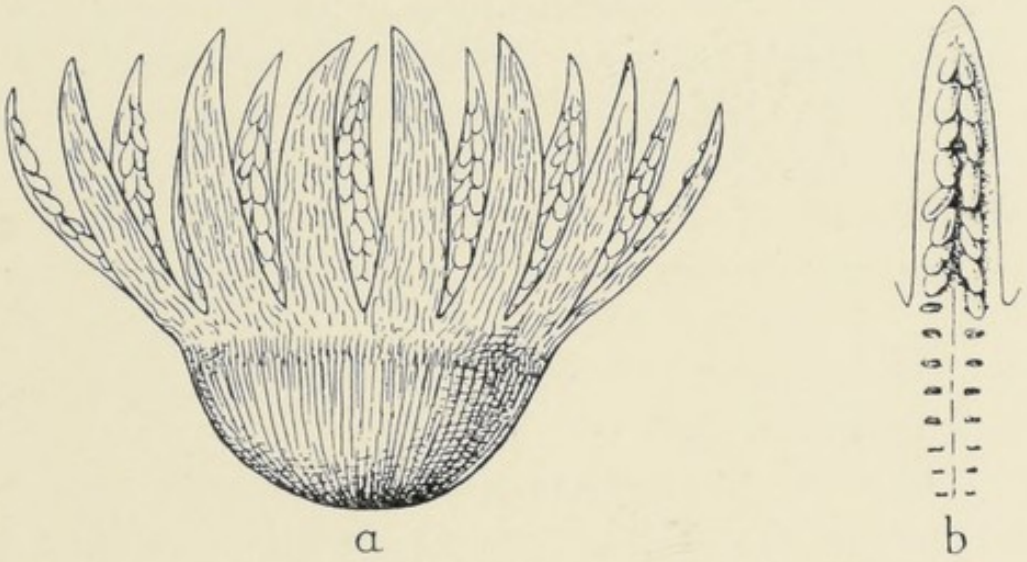

FIG. 22.—*Williamsonia whitbiensis*. *a*. Restoration of male flower, showing the whorl of stamens, united below, and bearing pollen-sacs on their free limbs. *b*. A single stamen, seen from above, showing the simple structure, with a double row of pollen-sacs.
After Nathorst.

An example of a male flower, or at least of one in which only the stamens are present, may be taken from a Yorkshire species (*W. spectabilis*) discovered by Nathorst. No bracts are shown: only the stamens are preserved. They are fused at the base into a cup or disk, as in the Bennettiteæ. The free limbs of the stamens are curved inwards, and bear two rows of slender leaflets, said to be given off, not from the edges, but from the midrib of the sporophyll. The pollen-sacs are borne on the slender pinnæ. Thus there is a general agreement with the staminate apparatus of a Bennettitean flower.

In other flowers referred to *Williamsonia* the arrangement is simpler. Thus in *W. whitbiensis*, another Yorkshire plant, while the general form of the so-called male flower is similar to that in the last species, the limbs of the stamens are quite simple and undivided, each bearing two rows of pollen-sacs on its inner surface (Fig. 22). Essentially the same condition is shown in the El Consuelo Cycad (*Williamsonia mexicana*), one of Wieland's discoveries. The diagrams, taken from that author, shown in Fig. 23 illustrate the difference. In A the arrangement in such a flower as *Cycadeoidea dacotensis* is represented; it would also serve in essentials for *Williamsonia spectabilis*. Here the stamens, united into a disk below, are pinnate above, and each pinna bears two rows of pollen-sacs; they are also indicated on the midribs of the disk below, for which there is some evidence. In B, the *W. mexicana* type is shown. In this the stamens, united as before, are simple, each bearing directly two rows of pollen-sacs, which again extend downwards on the fused portion.

A comparative simplicity of the staminate apparatus seems rather characteristic of the Williamsonian Tribe. It was a tempting idea to suppose that the compound stamen of the Bennettiteans, with its innumerable pollen-sacs, was a primitive type of microsporophyll, comparable to the fertile frond of a Fern. But we are hardly justified in such an assumption, for among the older Cycadeoids, the Williamsonians, simpler stamens are frequent. They may, of course, have arisen by reduction, but it may equally well be that the more complex forms of stamen arose by elaboration from the simpler.

An example of a probably bisexual flower of *Williamsonia* from the Yorkshire coast has been described by Wieland, who has identified the central ovulate cone, surrounded by parts of the staminate fronds.[1]

Otherwise, the specimens show the organs of one sex

[1] Wieland, 1916, p. 204, Fig. 80, D.

only. Some male examples have already been described. A number of female fructifications have been recorded, especially by Nathorst and Wieland; as a rule, they are at an advanced stage—fruits rather than flowers. Dr. Wieland says that in none of the forms from Oaxaca can it be determined whether an hypogynous staminate

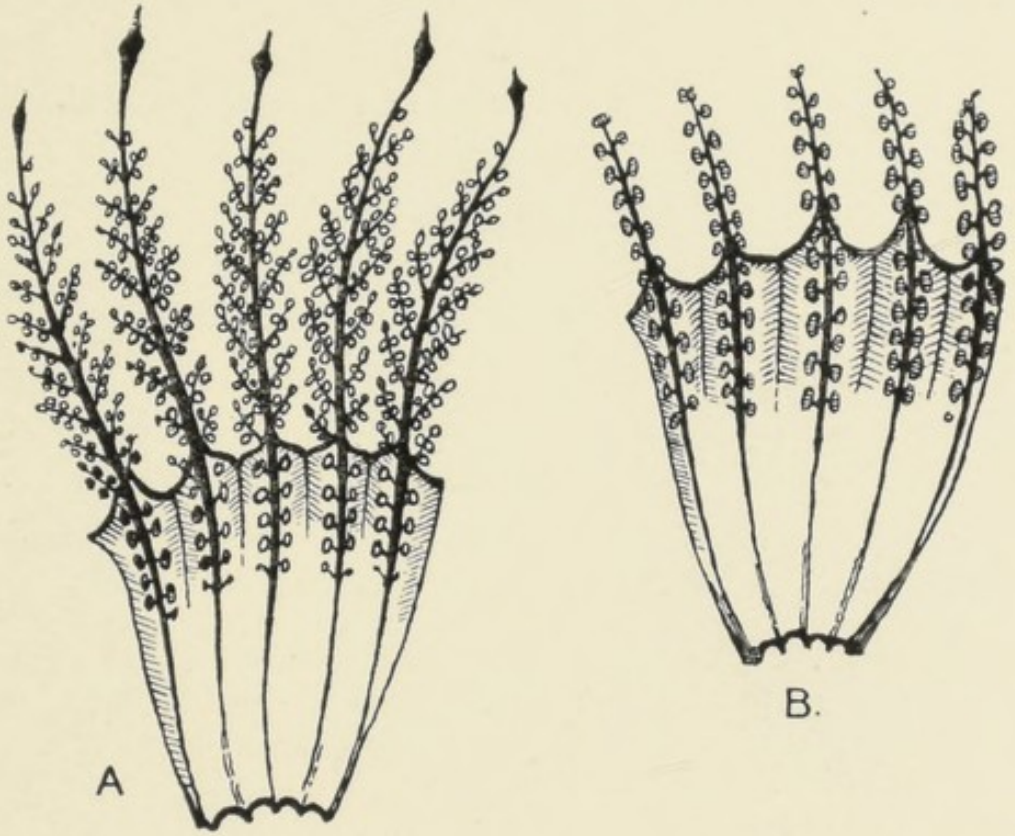

FIG. 23.—(A) *Cycadeoidea*. Diagram of staminate whorl, showing the continuous disk below, and the pinnate free limbs bearing pollen-sacs on the pinnæ. The tips are sterile. (B) *Williamsonia mexicana*. Similar diagram, showing the simple stamens, bearing the pollen-sacs directly on the main stalk.
After Wieland.

disk was present or not. The same uncertainty extends to other cases. The fruits, at the stage usually found, may well have lost their stamens, and, conversely, we can hardly feel sure that a young ovulate receptacle may not have been present in flowers described as male. The question of bisexuality must therefore be left open; in one case, however, to be mentioned presently, there seems to be a strong presumption in favour of the unisexual condition.

The female apparatus of *Williamsonia* was evidently of the same type as in the Bennettiteæ, often with a sterile apex, and in some species with a sterile zone at the base. The interseminal scales, surrounding the micropyles of the seeds, have been clearly observed in various cases; the arrangement agrees completely with that already described in the Bennettitean Cycads. The fruits are in some cases still surrounded by bracts, while in others they are without any.

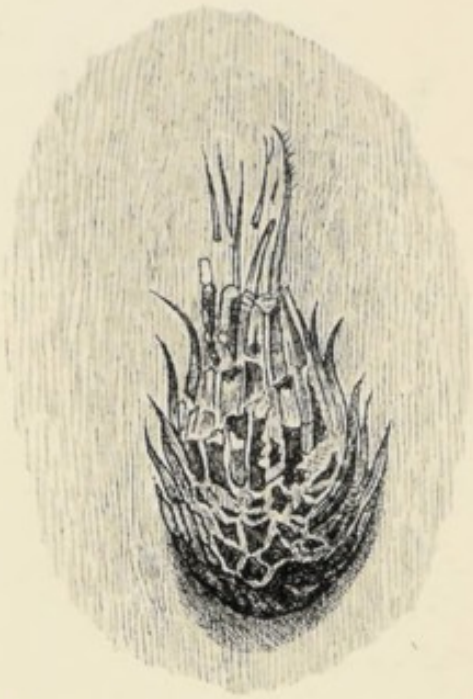

Fig. 24.—*Williamsonia scotica*. External view of fructification, showing the overlapping bracts, toothed at their ends. About half natural size.
After Hugh Miller.

Probably the most interesting specimen of the female flower of a *Williamsonia* is one described by Prof. Seward, under the name *W. scotica*; it is the only example in a petrified condition, with structure preserved. The specimen was originally discovered by Hugh Miller, who gave an excellent figure (see Fig. 24) and description of its external aspect.[1] It came from Eathie, in Cromarty, and was described by Miller as of Liassic age, but is now believed to be later, probably Upper Jurassic. Prof. Seward has thoroughly investigated the structure.[2]

The cone (to use Miller's term) is 11 cm. long by 6 cm. greatest diameter, and is clothed in slender, tapering bracts, some of which show minute denticulations near the tip. They are covered with ordinary filamentous hairs, like those of recent Cycads, not with flat scales like the Bennettiteæ—a point of some interest. The central recep-

[1] Miller, 1857, p. 480.
[2] Seward, 1912 and 1917, p. 449.

tacle is coated with a thin layer (only 2 mm. in thickness) of ovules and interseminal scales. The small size of these organs indicates at once that the flower was young. It is, in fact, the best example we have, in any Cycadeoid, of the female fructification at an early stage. The short-stalked ovules and the sterile scales are somewhat similar

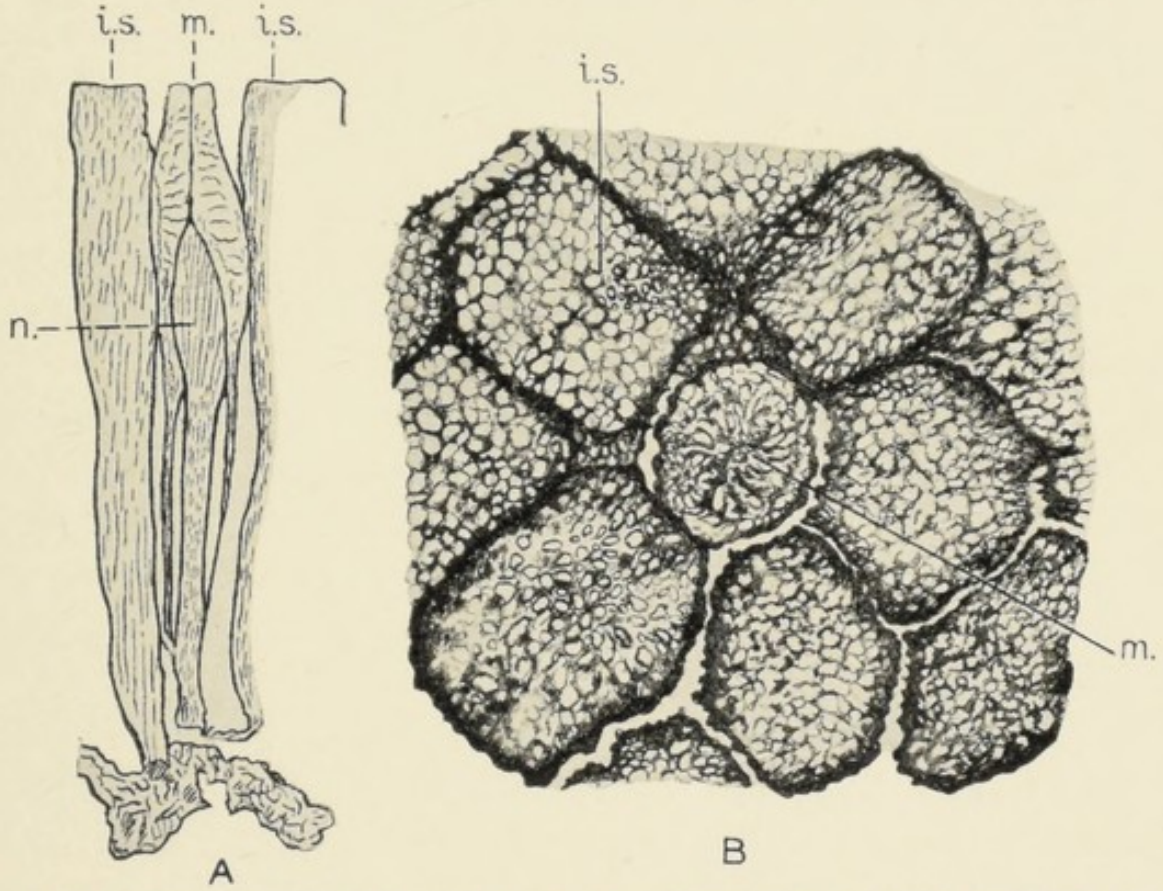

FIG. 25.—*Williamsonia scotica.* (A) Section of part of fruit, showing an ovule, with the adjacent interseminal scales (*i.s.*) in longitudinal section; *m*, micropyle; *n*, nucellus of ovule. (× about 35.) (B) Tangential section of part of fruit, showing the micropylar end of a seed (*m*), surrounded by interseminal scales (*i.s.*). (× about 100.)
After Seward.

in general form and dimensions, the scales being a little the larger (Fig. 25, A). Each ovule, as seen in transverse section, was surrounded by a rosette of five or six interseminal scales (Fig. 25, B).

In the ovule the nucellus, or central body, is clearly shown (Fig. 25, A), surmounted by a long micropyle with a narrow opening. No differentiation has been detected in the tissue of the nucellus; presumably the embryo-sac

was not yet developed. The woolly bracts, completely enclosing the flower, suggest that it was not yet ready for pollination. Thus the stage was a very early one, though not quite so early as in Dr. Stopes's flower-buds of *Bennettites maximus*.

No trace whatever of male organs could be found. As Prof. Seward points out, the immaturity of the ovules renders it improbable that, if the fructification had been bisexual, the stamens would already have been shed. We may therefore fairly take this specimen as a genuine example of a unisexual (female) Williamsonian flower. And, no doubt, the recognition of one such clear case heightens the probability of unisexuality in other cases, where the evidence is more doubtful.

Some account may next be given of two genera, *Williamsoniella* and *Wielandiella*, which appear to belong to the Williamsonian Tribe, though they stand a little apart from the genus *Williamsonia*, and have recently been placed by Dr. Wieland in a family of their own, the Microfloræ.[1]

Williamsoniella coronata, the best-known species of this genus, was discovered by Mr. H. H. Thomas, in Middle Jurassic beds on the Yorkshire coast. Flower-buds and mature flowers, as well as their detached parts, were found. Foliage and stems, referred to the same plant, were also present.

The flowers are comparatively small (a little over an inch in diameter) and borne on long stalks (Fig. 26). There are no bracts, the flower consisting of a whorl of 12–16 free stamens, surrounding the ovulate receptacle. The stamens are quite simple, and each bears about six pollen-sacs in two rows, on the upper surface. The sacs appear to have been partitioned, as in other Cycadeoids.

The female receptacle bore numerous (apparently sessile) ovules, with the usual interseminal scales among them.

[1] Wieland, 1919.

In the open flower the long micropyles project between the scales. The receptacle ended above in a conspicuous sterile column, or corona.

Thus the flower of *Williamsoniella* was bisexual. It is remarkable for the very simple stamens, not united into a disk.

The narrow, simple leaves, known as *Taeniopteris*, are closely associated with the flowers, and appear from details of their structure to have belonged to the same plant; slender forked stems, less than an inch in diameter, are also associated; there is evidence from the leaf-scars that they bore the *Taeniopteris* leaves. All these organs are referred, on good if not conclusive grounds, to *Williamsoniella*, and Mr. Thomas has accordingly given a restoration of the habit of the plant. While the flowers are clearly of the Cycadeoid type, the foliage and mode of growth attributed to the plant are totally unlike those of any Cycad.[1]

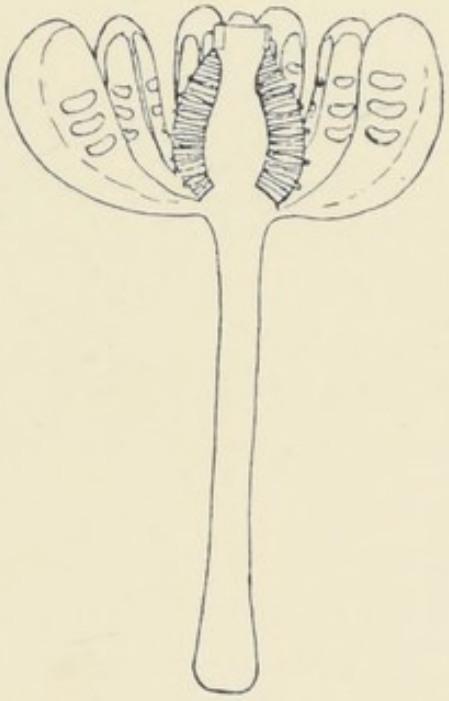

FIG. 26.—*Williamsoniella coronata*. Flower, showing the simple stamens with their pollen-sacs, and the central ovuliferous cone, surmounted by the corona. After Hamshaw Thomas.

The somewhat similar genus *Wielandiella* had previously been described by Nathorst; it is more ancient than Mr. Thomas's plant, as it comes from the Rhætic of Sweden. It is, in fact, one of the oldest Cycadeoids known. The flowers are on about the same scale as in *Williamsoniella* and, as in that genus, are bisexual. The stamens, however, are somewhat obscure, and perhaps incompletely preserved; they form a low ring round the base of the female receptacle, and pollen has been obtained

[1] Thomas, 1915; Seward, 1917, p. 467.

from them. The female organs, when present, are of the usual Cycadeoid character, the micropyles of the seeds, with the interseminal scales, being quite well preserved. The flower, when complete, is surrounded by bracts.

In the case of *Wielandiella*, the fructifications have been found attached to the stem, which was rather more slender than in *Williamsoniella*. The flowers were borne at the forks (Fig. 27). The leaves appear to have been in clusters,

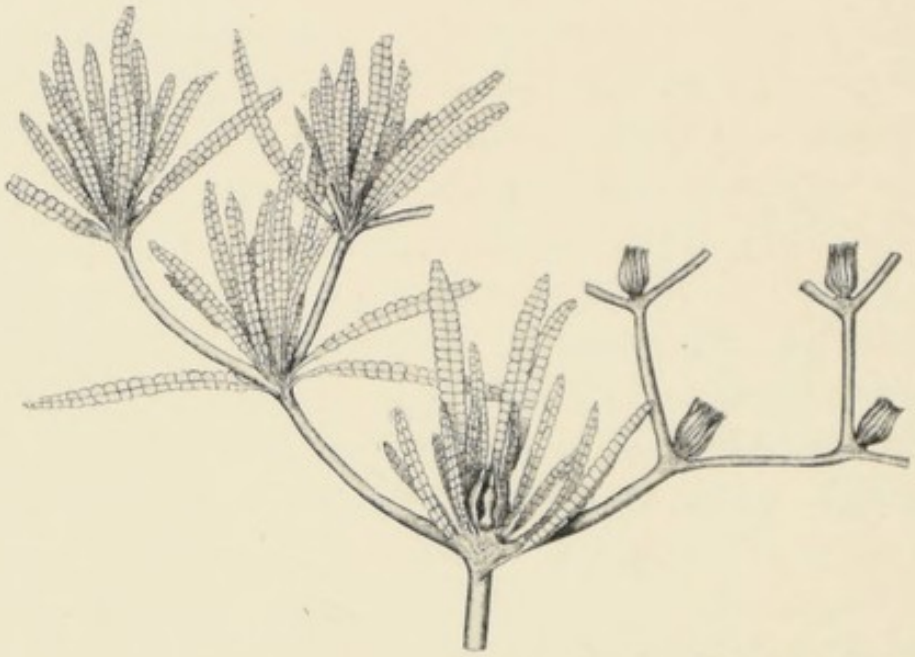

FIG. 27.—*Wielandiella angustifolia*. Restoration, showing the slender forked stem, the segmented leaves and several flowers. The central flower shows the female receptacle exposed.
After Nathorst.

just below the forks of the stem. They have not been found in connection, but the associated leaves are small, narrow fronds about 3 inches long, cut into pinnately arranged segments (*Anomozamites minor*), (Fig. 27).[1]

Both the genera just described depart widely from our conception of a Cycad. Yet the structure of the flowers, and especially of the female organs, shows beyond doubt that we are dealing with plants of the Cycadeoid class. Thus one objection to the idea of a certain relation between the Cycadeoids and the Angiosperms is removed. As long

[1] Nathorst, 1909; Seward, 1917, p. 463.

as we only knew the thick-stemmed Bennettiteans, so entirely Cycadean in habit and foliage, the difference from any of the usual Angiospermous types might seem insurmountable. But the Microfloræ show us that plants of Cycadeoid affinity, including some of the most ancient, may possess a habit quite consistent with Angiospermous relationships. Dr. Wieland has pointed out that stems such as that of *Wielandiella* and that attributed to *Williamsoniella* may well be compared with those of the Magnolias among Dicotyledons. It has already been mentioned that the Magnoliaceous flower has some analogies with that of the Cycadeoids.

We see, then, that the more ancient forms of the Cycadeoids were the more generalised and the less tied down to the narrow Cycadean scheme. This fact, it is true, lands us in a difficulty, for the more specialised Bennettiteans are altogether Cycad-like in habit and to a great extent in vegetative structure; and yet in their organs of fructification no plants could be more different from the living Cycadaceæ. It seems impossible to believe that there is any direct affinity between the later Mesozoic Cycadeoids, with their elaborate bisexual flowers, and the recent Cycads with their simple unisexual cones or still simpler stem-borne carpels (*Cycas*). One must, I think, suppose that the external and anatomical resemblances between these diverse families are due, in part at least, to convergence, favoured perhaps by the controlling influence of a similar environment.

To return to the question of Angiospermous relationship. On what characters is the suggestion based? The chief ground, no doubt, is the general organisation of the flower; where the Cycadeoid fructification is bisexual and complete, it presents the same arrangement of organs as an equally perfect flower of an Angiosperm. On the outside are the bracts, which may serve very well as a perianth, such as that of *Calycanthus* or some Magnolias; then we

come to the whorl of stamens, hypogynously inserted, as in the simpler Angiosperms; lastly, in the centre of the flower stands the gynæceum or ovule-bearing axis, answering to the pistil of a Flowering Plant.

Another point is the formation of a closed fruit with a firm pericarp; for example, in such an extreme case as Dr. Stopes's Gault specimen we have a perfection of fruit-structure equal to anything in modern Flowering Plants.

Lastly, we may mention the exalbuminous or practically exalbuminous seeds—a character quite unknown among Gymnosperms, but familiar in many families of Angiosperms.

It is true that when we begin to look into details resemblances vanish and diversities appear. The stamens are never really like those of an Angiosperm, though somewhat less unlike in the simpler and older Williamsonians than in the elaborate and later Bennettiteans.

The ovulate apparatus, as already pointed out, is totally different in the two classes. There are no recognisable carpels in the Cycadeoids and no interseminal scales in the Angiosperms. Here there is no approximation whatever. The gynæceum of the Cycadeoids has essentially the same structure throughout, while the enclosure of the ovules by the carpels is universal in Angiosperms.

It may further be pointed out that the peculiar arrangement in the Cycadeoids allowed the micropyles of the ovules to reach the surface, so that they were freely exposed and could receive the pollen directly. The presumption is that the mode of fertilisation was still purely Gymnospermous, in spite of the simulation of a closed Angiospermous fruit.

In the face of these facts it is impossible to derive the Angiosperms from the Cycadeoids as at present known to us, and probably no one would attempt to do so. The hypothesis of an affinity between the two groups was

suggested, and has always been maintained, by Wieland, and was worked out as a matured theory by Arber and Parkin in their well-known essay on the " Origin of Angiosperms." [1] On their view the Angiosperms are descended from a hypothetical group of Mesozoic plants to which they applied the name Hemi-angiospermeæ. They believed that the fructification of this group approximated so closely to the flower of the Bennettiteæ that the latter, though somewhat removed from the direct line of descent, demonstrates emphatically the type of strobilus which gave rise to the flower of the Angiospermeæ.

It is interesting to note that Arber and Parkin's hypothetical reconstruction of the flower of a Hemi-angiosperm [2] agrees almost exactly, as regards the structure of the stamens, with the subsequently discovered *Williamsonia mexicana* of Wieland (see above, Fig. 23). Thus the investigation of the old Williamsonian Tribe has actually done something towards confirming a theory based essentially on a knowledge of the later Bennettiteæ.

But we are still a very long way from tracing the ancestry of the Angiosperms. That there are striking analogies between the great modern sub-kingdom and the once dominant Cycadeoids of the Mesozoic is undeniable. It is also true that the analogies become accentuated if we take into consideration the older and more generalised Williamsonians rather than the later and specialised Bennettiteans. On the Angiospermous side, it is with such families as the Magnoliaceæ and other Ranales that analogies can best be traced. But, after all, a wide gap remains. We cannot be certain that there is anything more than a parallel development; even so, the fact that the flower, using the word in its natural sense, was already a feature of the leading Mesozoic race, is in itself of great interest.

[1] Arber and Parkin, 1907. I understand that a re-statement of the theory, in the light of recent work, is being published by the surviving author, Mr. Parkin. (Parkin, 1923.)

[2] *l.c.*, p. 63.

But it may be that a real affinity exists; that the Cycadeoids and the Angiosperms are branches of a common stock, and that the former deserve the name of Pro-Angiosperms which Saporta, perhaps with prophetic insight, long ago gave them.

CHAPTER IV

THE PERMIAN TRANSFORMATION. THE CARBONIFEROUS FLORA IN RELATION TO THAT OF THE MESOZOIC AGE. PROFOUND CHANGES. EXTINCT GROUPS. THE "SEED-FERNS" AND THE TRUE FERNS.

We have now worked back to the beginning of the Mesozoic Age. But before we leave it, we may call to mind that there were many other groups of Land-plants flourishing in Mesozoic times, besides the great class of the Cycadophytes on which we have concentrated our attention. The Cryptogams—Ferns, Horsetails, and Club-mosses—have already been referred to. The two former groups, especially, would prove of great interest, if we had the space to give them which they deserve.

The Mesozoic Age, however, is justly called the "Era of Gymnosperms." Besides the Cycads, there were in those days very many Conifers overspreading the world, and a considerable number of Maidenhair Trees or their relations. This last group is of much interest, from the fact, already mentioned, that it is now represented by a solitary surviving species. The zenith of the Maidenhair Trees (Ginkgophyta) was attained in the Jurassic. At that period, various species are found which cannot be distinguished from the recent genus *Ginkgo*, while there were also others, with more divided leaves and some further differences, indicating distinct genera.

Our knowledge is for the most part limited to the leaves, though in a few cases fructifications are preserved. In some of these, both pollen-sacs and seeds were more

numerous than in the recent plant, in which there are normally two pollen-sacs to the stamen and two seeds on the peduncle. The group is clearly as old as the Cycadophyta, perhaps older, but our knowledge of it is far less satisfactory.

The Mesozoic Conifers were abundant and varied, the families of the "Big Trees" (*Sequoia* or *Wellingtonia*) the Cypresses and the Araucarians being prominent, while the Firs (Abietineæ) were also well represented, especially in the Jurassic. So far, however, little light has been thrown on the evolution of the class. In fact, while most botanists accept the Araucarians as the oldest and most "primitive" of the Conifers, there is an important school in America, headed by Prof. Jeffrey, who boldly maintain that this position belongs to the Abietineæ, and that the Araucarians were derived from them! Forms of an apparently intermediate character, occurring in Cretaceous rocks, have been interpreted in both senses. Under these circumstances it is wisest in a popular book like the present to say no more. As regards antiquity, Conifers no doubt go back as far as the Cycadophyta—how much further we do not know.

We have now reached the second period of transformation in our descending course. Just as we passed from the modern Flora of Flowering Plants to the strange vegetation of the Mesozoic, characterised above all by the dominance of Cycadophyta, so now we have to go back to a still more ancient Flora, which has little enough in common with that of the Mesozoic Age.

As we have already found, the great botanical transformations do not necessarily correspond to the main geological divisions. The modern type of Flora became dominant during the Cretaceous, and in like manner, according to Prof. Gothan, the typical Mesozoic Flora goes back as far as the Upper Permian, thus encroaching somewhat on the Palæozoic Age. While in the upper beds, corresponding to

our Magnesian Limestone, the vegetation has already a Mesozoic character, owing to the prevalence of Conifers and Maidenhair Trees or their allies, the shales and sands of the Lower Permian contain a Flora essentially of a Carboniferous *facies*. Thus, to use Gothan's terms, the change from the "Palæophyticum" to the "Mesophyticum" took place in the middle of the Permian Formation, while the Animal fossils, on which the geological periods are based, changed later. It is probable, however, that the change in vegetation was not simultaneous in all parts of the world.

We may here deal with the Permo-Carboniferous Flora collectively, as there is so much in common between the vegetation of the Lower Permian and that of the Upper Carboniferous.

The first question which will occur to us is, What trace do we find, in this older Flora, of the great Cycadophyte class which played so important a part in Secondary times? The answer is, that we find very little. In the upper beds of the Permo-Carboniferous we meet with a few Cycad-like fronds and with one or two fructifications which may have belonged to some kind of Cycadophyte. But when we get a little lower down in the Carboniferous rocks, we lose these Cycad-like forms entirely. The case of the Conifers is much the same; in the uppermost beds we find some fairly typical representatives of the Conifer class, apparently of Araucarian affinity. But as we descend to earlier horizons, we no longer meet with anything which can be certainly referred to Coniferæ. The Maidenhair Trees also become few and doubtful.

There is, in fact, on the whole, a sharp break between the typical Mesozoic and the typical Palæozoic Floras. A leading authority has recently gone so far as to suggest that there may have been no direct connection between the two, though no doubt there was a certain amount of overlapping (see p. 213).

What, then, were the dominant groups of the typical Upper Carboniferous Flora? The vegetation was extraordinarily rich, and indeed the Coal-Flora is better known to the world at large than any other age of fossil plants. We will first take the Seed-plants, which were already strongly represented, though the period used to be called "the Age of Cryptogams."

Among the Carboniferous Spermophytes the most prominent family in stature was that of the Cordaiteæ, an extinct race of Gymnospermous forest trees, named after the distinguished palæobotanist, Corda. They have characters in common with all the three main groups of later Gymnosperms—Conifers, Maidenhair Trees, and Cycads, but their habit was peculiar to themselves. They may have had some survivors in the older Mesozoic Floras, but were essentially a Palæozoic family.

There was, further, the important class of the Pteridosperms, or, in more popular language, "Seed-Ferns," a most remarkable group of plants with the habit of Ferns, but bearing highly organised seeds on their fronds. The Pteridosperms were so Fern-like in appearance that, until the present century, they were almost always classed as Ferns. It is probable that a majority of the well-known fern-fronds, so-called, of the Carboniferous, belonged in reality to this ancient race of seed-bearing plants.

Passing on to the Cryptogams, it must be admitted that the Carboniferous period was truly the "Age of Spore-plants" in the sense that the Higher Cryptogams then attained a development which has never since been equalled. Among them, the true Ferns, though not so prominent as we once supposed, were actually an important and varied group. Many were Tree-ferns, not, however, of the same families as the Tree-ferns of the present day, but constituting an extinct group, related to the tropical Marattiaceæ. Besides these, there were many highly peculiar Ferns, which differed widely from any of the

living families, and have been grouped under the name Primofilices.

As is well known to all, the Club-mosses (Lycopods) of the Carboniferous attained an extraordinary development, one great family, the Lepidodendreæ, growing into huge trees, which must have formed a principal constituent of the swampy forests of the Coal Measures. Contemporary with these gigantic forms, however, there were also little herbaceous Club-mosses, quite comparable to our living Selaginellas.

In like manner, the Horsetails, represented by the Calamites, developed to a surprising extent, attaining the stature of large trees and showing, in all respects, a far higher organisation than their modest successors in our own day.

Finally we meet with a wholly extinct Carboniferous family, known only to fossil-botanists. Naturally, these plants have no popular name; we may call them the Sphenophylls. They were comparatively small plants, many of them probably climbers, with whorled leaves like the Horsetails, to which they seem to have been in some degree related. They are among the most graceful, and in some respects the most highly organised, of the Palæozoic Cryptogams.

The groups just enumerated constituted, essentially, the higher Land-Flora of the Lower Permian and Upper Carboniferous times. The Lower Carboniferous plants will be dealt with later. We will concentrate our attention on the Seed-plants of the period, the Cordaiteans and the Seed-Ferns, for they have a special interest for us, in relation to the later Floras, already considered.

Among the Gymnosperms, the Cordaiteans were tall trees, comparable in stature to most of our familiar Conifers, but different from them in habit. They had lofty, branched stems, and bore large, simple leaves, sometimes a yard in

FIG. 28.—Restoration of various Cordaiteæ. The tall trees on the left are typical *Cordaites*; the lower one next these is a *Dorycordaites*, and the one to the right of this, with narrow leaves, is a *Poacordaites*. The smaller plant on the left is a *Dicranophyllum*.

From Grand'Eury.

length (see Fig. 28, reproducing Grand'Eury's fine restoration of various trees of this family). Most of the Conifers have small leaves, very often of the sharp, narrow kind, which we call "needles." There are, however, a few which have

FIG. 29.—*Agathis robusta*. Leafy shoot, to compare with the foliage of *Cordaites*. Reduced.
After Baker and Smith, "Pines of Australia."

fairly large leaves, as in some of the Araucarians of the Southern Hemisphere. A good example is the foliage of the Queensland Kauri (*Agathis robusta*), with leaves 4–5 inches long by over an inch broad (Fig. 29). This is probably as good an analogy as we can find, among living trees, for the Cordaitean habit.

The Cordaiteæ may be described as intermediate in organisation between the true Conifers and the Maidenhair Trees, while, as already mentioned, they had some points in common with Cycads. Thus the group affords evidence of the inter-relationship of all the chief Gymnospermous types (leaving the Gnetaceæ out of consideration).

The structure of all the organs of the Cordaitean trees is known, in certain instances, owing to the important work of Grand'Eury and Renault, in the seventies of the last century.[1] Since then the additions to our knowledge have been comparatively small.

The stem is remarkable for the large pith, far more extensive than in any Conifer, and rather comparable in size to that of a Cycad. It was, however, peculiar in usually being "discoid," *i. e.* consisting of a series of transverse diaphragms or disks with empty spaces between them. A similar structure is met with in the Walnut and a few other recent plants.

The structure of the wood, at least in the genus *Cordaites*, was very much the same as in the Araucarian Conifers of the present day. It was a dense wood, with narrow medullary rays and the tracheides (water-conducting elements) had two or more rows of bordered pits on their radial walls. The spiral tracheides, as in recent Gymnosperms generally, were situated on the extreme inner edge of the woody zone.

A genus, named *Mesoxylon*, represented by several species in the Lower Coal Measures, is distinguished by having strands of primary wood on the inner side of the main zone. These strands were developed from without inwards (centripetally), while the rest of the wood was, as usual, developed from within outwards (centrifugally). These primary wood-strands, though not very conspicuous in *Mesoxylon*, are of considerable interest, for they are a very ancient feature, and serve to link on the Cordaiteæ

[1] Grand'Eury, 1877; Renault, 1879.

to other early races of plants. In a related genus, *Poroxylon*, the primary strands are decidedly more prominent than in *Mesoxylon*.

It is unnecessary to go into further anatomical details of the stem, but it may be mentioned that the bast (phloëm) appears to have been as highly developed as in recent Conifers.

As a rule, the leaf-trace or vascular system supplying the leaf itself, was a double strand, a feature characteristic of the recent Maidenhair Tree.

The leaves were highly organised (Figs. 30, 31); in some respects the structure of the whole leaf in the Cordaiteæ was like that of a single leaflet of the frond in

FIG. 30.—*Mesoxylon*, sp. Complete transverse section of small leaf, showing the girder-like construction, with a vascular bundle in each compartment formed by the mechanical tissue. Slightly magnified.
From a section in the Scott Collection.

those Cycads which have parallel veins; the vascular strands have the same peculiar structure in both groups. The leaves are also remarkable for their perfect mechanical construction, adapted to resist bending strains. The tough fibrous strands, on which mechanical strength depends, are, as a rule, concentrated on the upper and lower surfaces of the leaf, thus corresponding to the "flanges" of a T-girder, while the less resistant tissues between represent the "web." It is interesting to note that the construction of the leaves of this extinct race of Gymnosperms was, from an engineering point of view, on the same lines as that of the similar leaves of certain Monocotyledons at the present day. Thus, when the conditions were identical, the adaptations of Palæozoic plants were the same as those of plants of similar habit now living.

The fructifications of the Cordaiteæ were, like the rest of the structure, highly organised. They were in the form

of small catkins, borne on special fertile branches, the whole constituting an "inflorescence" (Fig. 32). The male and female catkins are externally very much alike. Both consist of a stout axis bearing spirally-arranged bracts. In the male catkins, the stamens are borne among the upper bracts. Each stamen has a stalk, surmounted by several long, upright pollen-sacs. There is some resemblance to the stamens of those fossil Maidenhair Trees in which the pollen-sacs were somewhat numerous.

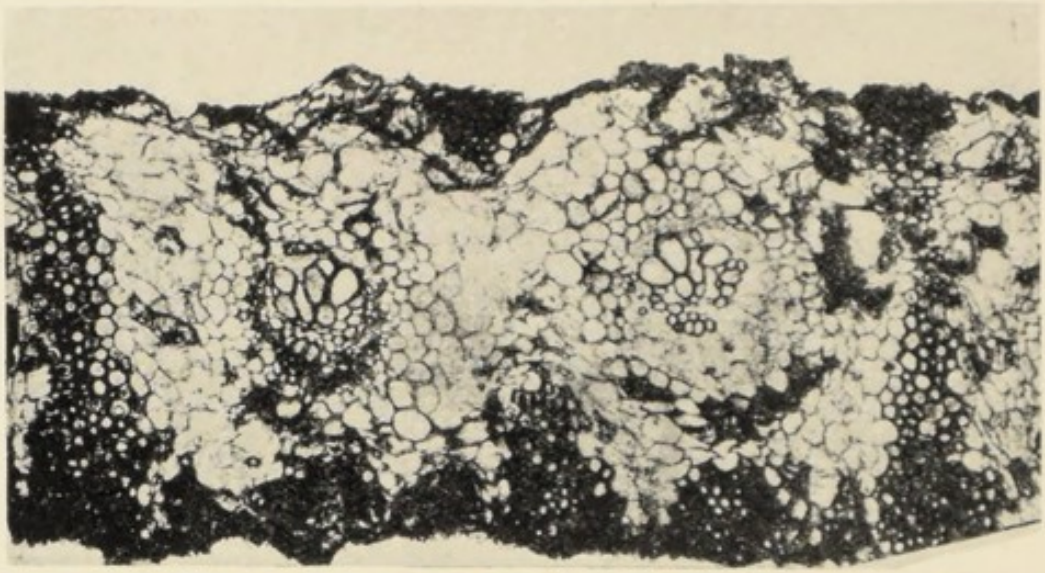

FIG. 31.—*Mesoxylon*, sp. Part of leaf in transverse section, more highly magnified. Two vascular bundles are shown. On the lower, and to a less extent on the upper surface, are strands of mechanical fibres, which also form vertical partitions. From a section in the Scott Collection.
Photographed by Mr. W. Tams.

The female catkins bore a few ovules, each seated on a short stalk in the axil of a bract. Most of the bracts, however, were barren. The ovule and the ripe seed bear, in various respects, a striking resemblance to those of living Cycads. The pollen-chamber, in which the pollen-grains are often found, is a constant feature. The pollen-grains are divided up into a number of cells, and in all probability produced motile spermatozoids, as in the Cycads and the Maidenhair Tree of our own day.

The fructifications, considered as a whole, cannot be directly compared with those of any living Gymnosperm.

They are totally different from the simple cones of the recent Cycads, and the catkins are unlike anything found in the Maidenhair Tree. A comparison with the cones of some Coniferæ is perhaps less remote, but, apart from other details, the sterility of most of the bracts in the Cordaitean

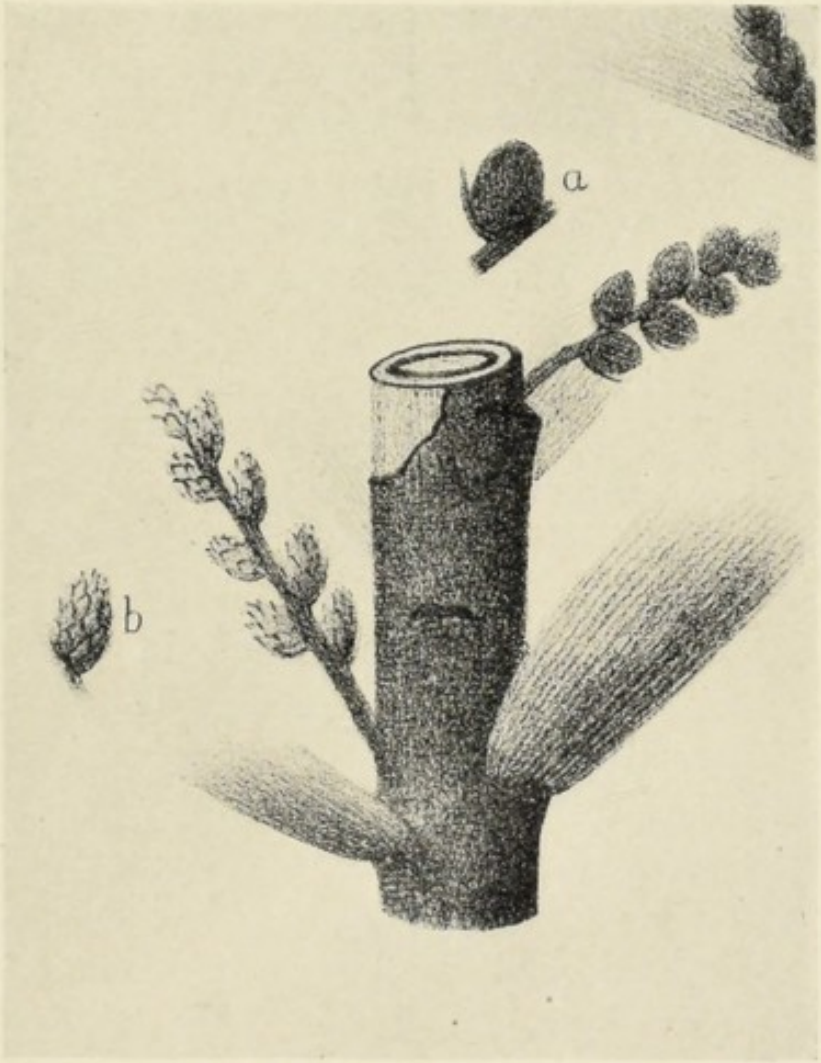

Fig. 32.—*Cordaites lævis.* Part of stem, bearing leaves and two inflorescences. The catkins on the upper inflorescence are female and on the lower male. *a*, Female, *b*, male catkin, enlarged.
From Grand'Eury.

catkin is a peculiar feature. Nor is any close comparison possible with the highly specialised flowers and fruits of the Mesozoic Cycadeoids.

The Cordaiteæ and their immediate allies no doubt constituted, in their day, an advanced race of Gymnosperms, retaining perhaps some relatively primitive features, but

highly modified in certain directions. At the same time, it may be well to remember that our knowledge of Cordaitean fructifications is still limited to few examples. *Mesoxylon*, in which the general structure of the fertile shoots is known, appears to have differed little from *Cordaites*. In *Poroxylon*, a genus somewhat further from the type, the fructification is not known with certainty, but the seed and inflorescence doubtfully attributed to it are not essentially different from those of *Cordaites*.

The Cordaiteans, as we have seen, were an advanced group, peculiar in many ways, but approximately of as high a grade of organisation as the recent families of Gymnosperms. We now come to a class of plants on a different footing, highly organised it is true, in their own way, but presenting certain characters which may fairly be called "primitive," as compared with those of other Spermophytes.

The group in question is that of the Pteridosperms or "Seed Ferns." They were first called by that name in 1903, which was also, in a sense, the date of their discovery. At one time they were mixed up with the true Ferns; if you look at the older lists of Carboniferous plants, you will find that almost exactly half the species were referred to Ferns—the period, if this estimate had been a true one, might well have been called the "Age of Ferns." As already said, we now have reason to believe that most of the so-called Ferns of the Carboniferous were really seed-bearing plants, of Fern-like habit.

The resemblance to true Ferns is so close that it once deceived the best botanists. Even Sir Joseph Hooker, writing about 1848, believed that the genus *Pteris*, to which the Bracken Fern belongs, was represented in the Carboniferous Formation. The particular "Fern" which seemed to him so nearly akin to the Bracken is now known not to have been a Fern at all, but a Pteridosperm.

Long before the year 1903 there were some palæobotanists who had their suspicions as to some of these supposed Ferns. The Austrian Stur, in 1883, pointed out that certain important genera, based on the fronds, had never been found to bear any fern-fructification, and therefore could not have been Ferns, but must have belonged to some other group. Stur's scepticism has been completely justified by the event.

The way in which the discovery came about was this. There is a Carboniferous plant, now known as *Lyginopteris oldhamia*, with the foliage of a *Sphenopteris*, something like that of a recent *Asplenium* or *Davallia* (Fig. 35). The structure of all the vegetative organs—stem, leaf, and root—was well known before 1903, mainly through the work of Williamson. The anatomical evidence was enough to show that the plant was not simply a Fern, but in some of its characters rather approached the Cycads. The reproductive organs, however, were still unknown.

The leaves and stems of *L. oldhamia* were known to bear very characteristic glands, each stalked, with a spherical head. Now there were certain seeds known at that time, recorded by Williamson, though without any published description, which were sometimes found in association with the *Lyginopteris*. The seed (*Lagenostoma Lomaxi*) is enclosed in a cupule, like the husk of a hazelnut on a small scale. This husk was found by Prof. F. W. Oliver to bear glands identical in structure with those of the *Lyginopteris*, and unknown in any other plant. He at once inferred that this seed could have belonged to no other plant than *Lyginopteris oldhamia*.

Further investigation, in which I was privileged to take part, brought to light other points of close agreement between the stalk and cupule of the seed and the frond of the *Lyginopteris*. This was the first evidence which established, on grounds of comparative anatomy, that a Carboniferous plant with wholly Fern-like foliage never-

FIG. 33.—*Neuropteris heterophylla.* Restoration. The upper figure shows the foliage with some leaves expanded and others still circinately coiled. The two lower figures on the left show seeds borne on the fronds, that to the right shows a young frond.

From drawings by Miss Janet Robertson. Figure lent by T. G. Hill, F.L.S.

theless bore seeds. Thus *Lyginopteris oldhamia* was the first Pteridosperm to be recognised.[1]

In this case, the proof, though conclusive enough, was indirect. Very shortly afterwards, however, Dr. Kidston obtained direct evidence in a member of a totally different genus, *Neuropteris heterophylla* (Fig. 33). Here he found the seeds actually borne on the fronds, which in this plant somewhat resemble those of the Royal Fern, *Osmunda*. The *Neuropteris* seeds are large, of the size of a fine filbert; the stalks on which they were supported still bore the characteristic leaflets of the species, like those of the sterile frond. Here the proof was complete, though the internal structure was not preserved.[2]

In the same year, the American palæobotanist, David White, discovered, at an horizon corresponding to our Millstone Grit, the seeds of yet another "Carboniferous Fern," *Aneimites* (or *Adiantites*) *fertilis*. This was again quite a different type; the fronds are rather like those of a Maidenhair Fern, and the little flat, winged seeds are borne directly upon them (Fig. 34).[3] Other species of the genus were also found with seeds.

In the following year, 1903, a further striking discovery was made by the distinguished French investigator, Grand'-Eury. In *Pecopteris Pluckeneti*, a plant with a somewhat Bracken-like frond, he found seeds in hundreds, borne on the ordinary foliage; the seeds are small and winged, and it is an interesting point that they so closely resemble the seeds of one of the Cordaiteæ that the two can scarcely be distinguished when found apart from the parent plants. Grand'Eury's specimens of *Pecopteris Pluckeneti* came from the Upper Coal Measures of France.

Grand'Eury's discovery was perhaps the most impressive of all, for up to that time not the slightest suspicion had attached to the genus *Pecopteris*, which was universally

[1] Oliver and Scott, 1904. A preliminary statement appeared in 1903.
[2] Kidston, 1904. [3] White, 1904.

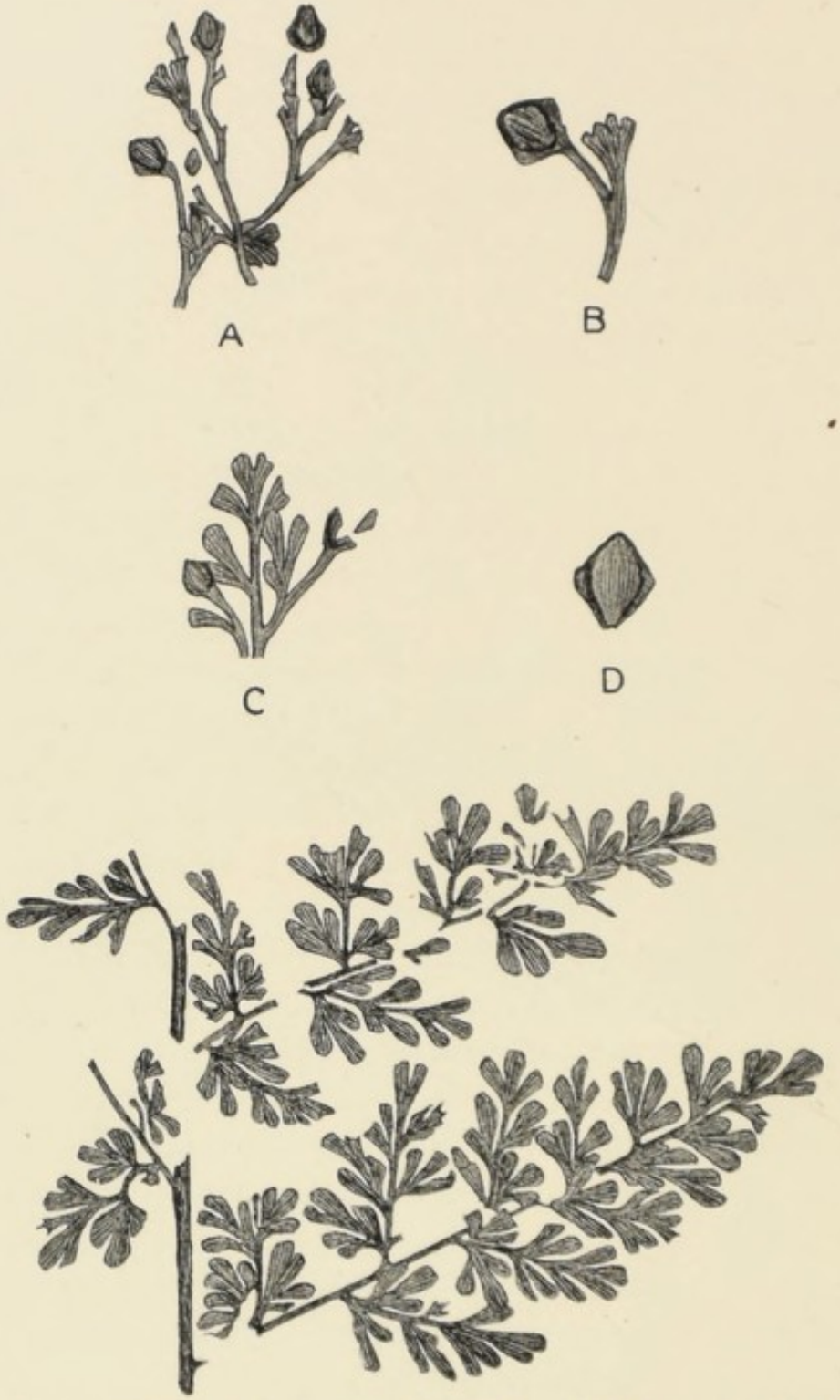

FIG. 34.—*Aneimites fertilis*. Part of frond. (A) Part of rachis, bearing seeds and reduced leaflets. (B) Seed and leaflet (× 2). (C) Fragment of frond bearing a seed on the left. (D) Seed (× 2).
After David White.

accepted as belonging to the true Ferns. It is now clear that plants of this Bracken-like habit were of quite diverse natures, certain species of *Pecopteris* being true Ferns, with some affinity to the surviving tropical family Marattiaceæ, while others were seed-bearing plants of a wholly extinct race.

FIG. 35.—*Lyginopteris oldhamia.* Restoration. The stem, rooted below, bears a vegetative frond in the middle; the frond on the left bears the pollen-sacs on peltate leaflets (*Crossotheca*); that on the right bears seeds (*Lagenostoma*). The forked bases of two other fronds are shown. (A) Two cupulate seeds on rachis with numerous glands. (B) Peltate leaflets, bearing pollen-sacs; both enlarged. Note the contemporary Dragon-fly.
G.T.G., after Mrs. D. H. Scott.

Other instances of a direct connection between seeds and Fern-like fronds have since come to light, and in numerous cases indirect evidence, partly from association, partly from comparative structure, goes to show that a large

proportion of the apparent Ferns of Carboniferous times were really Seed-plants of the Pteridosperm class.

The structure of the "Seed Ferns" does not admit of a

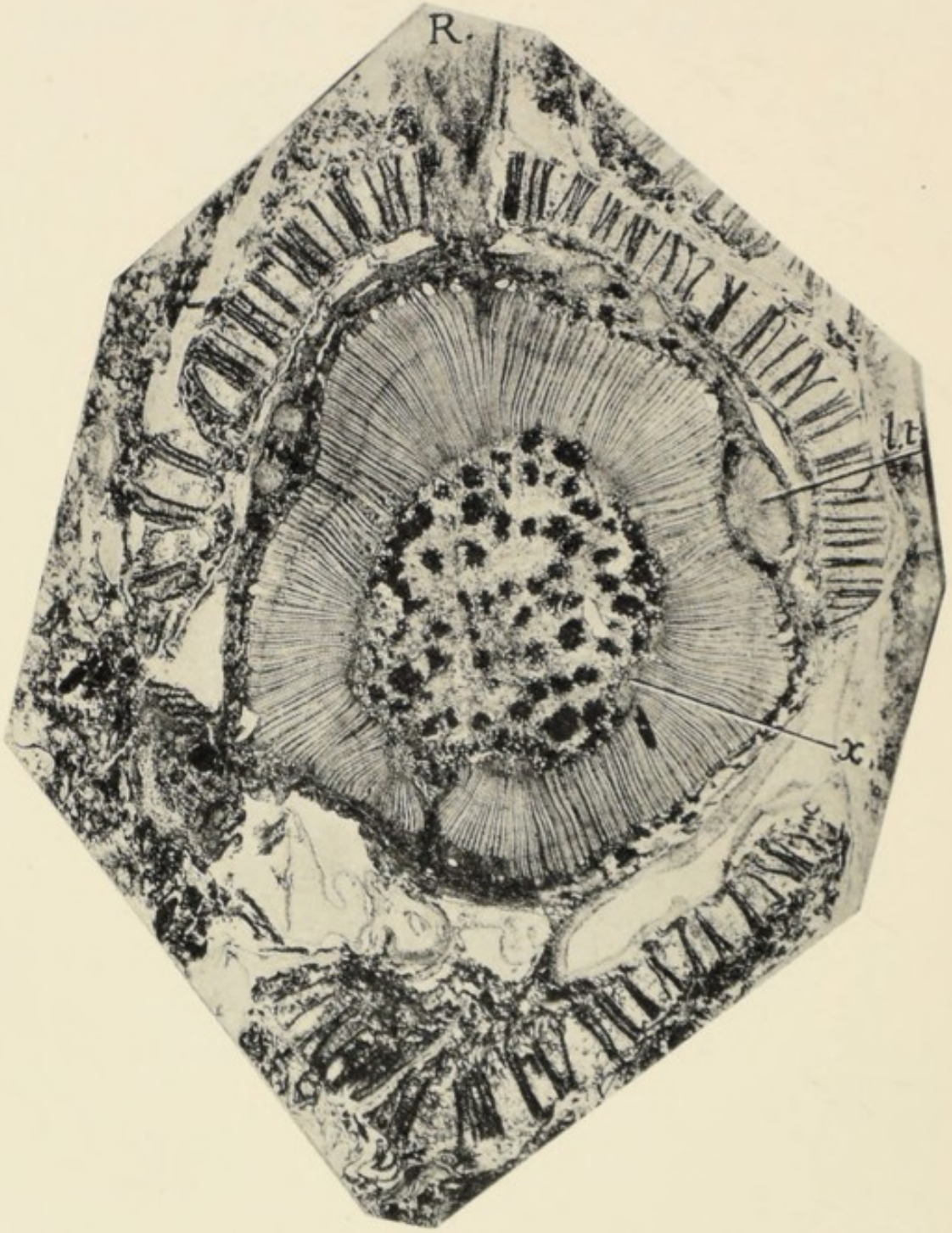

Fig. 36.—*Lyginopteris oldhamia*. Transverse section of large stem; the pith contains many dark sclerotic nests. *x*, One of the strands of primary wood at the edge of the pith. Then come the broad zone of secondary wood, and the phloëm; *l.t.* one of the outgoing leaf-traces. The outer cortex consists of alternating radial bands of hard and soft tissue: R, base of a root. (× 2½.) Scott Collection 648.

From a photograph by Mr. L. A. Boodle.

rapid description, for it varied greatly, both as regards the seeds and the vegetative organs, in the different families referred to this class. Here we must be content with one or two examples, and may begin with *Lyginopteris oldhamia*, now almost the best known of fossil plants.

The stem was long and comparatively slender, not exceeding 4 cm. in diameter. The plant may not improbably have been a climber, for the spines on frond and stem would have enabled it to cling to its stronger neighbours. Internally, the stem has a fairly large pith, surrounded by several strands of primary wood, considerably more developed than is usual in Cordaiteæ (Fig. 36). These primary strands are continuous with the leaf-traces, each of which divides into two before entering the base of the frond, though the two strands usually reunite in the petiole.

Outside the primary strands there is a zone of secondary wood and bast, with wide medullary rays. The pitting of the tracheides is similar to that in the Cordaiteæ, but the vertical rows of pits are usually more numerous. The delicate tissue of the bast or phloëm is often perfectly preserved. The outer cortex was strengthened by a network of fibrous strands, affording mechanical support to the stem. This arrangement, under various modifications, was very common among the plants of the period.

The roots were "adventitious," springing from the stem. In primary structure and secondary growth the root is quite similar to Dicotyledonous or Gymnospermous roots at the present day (Fig. 37). As it happens, the resemblance is closer to the roots of some Dicotyledons than to those of Gymnosperms, but the absence of vessels in the wood of course shows that the true affinities were with the latter class.

There is a little point connected with the roots and rootlets of *Lyginopteris* which has a distinct bearing on the affinities of the plant. In the small rootlets, the primary wood is what botanists call "*diarch*," *i. e.* it forms, as seen

in transverse section, a little plate of tracheides, corresponding to a diameter of the vascular cylinder. The French botanist, van Tieghem, showed that where a

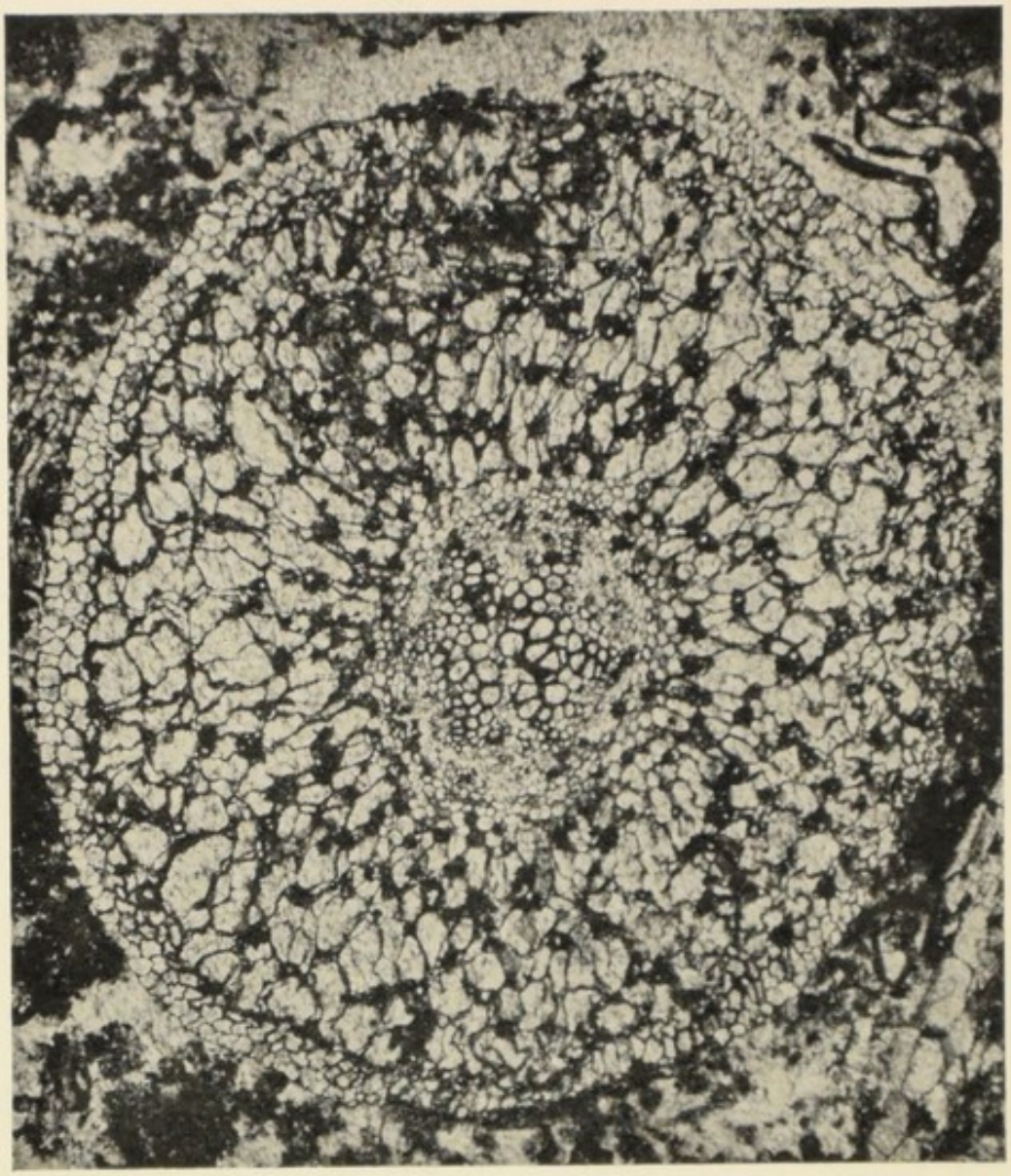

Fig. 37.—*Lyginopteris oldhamia.*—Transverse section of young root before secondary thickening. In the stele the hexarch xylem and the phloëm-groups between its arms, are clearly shown. The inner cortex is loosely constructed, while the external zone consists of two or three layers of closely fitting cells. (× about 30.) Scott Collection 2083.
From a photograph by Mr. W. Tams.

diarch rootlet is attached to the main root, its wood-plate is *parallel* to the axis of the root, in the Spermophyta, but at *right angles* to it, in Vascular Cryptogams. Prof. Weiss, of Manchester, has found that in the roots of *Lyginopteris* the position is *parallel*. Hence, in this small

but definite character *Lyginopteris* shows itself a true Phanerogam.

We now return to the frond, which, as we have seen, was large, highly compound, and altogether Fern-like (Fig. 35). If *Lyginopteris* were living now it would no doubt be a very popular decorative plant in our Fern-houses, though it was no more a Fern than the so-called

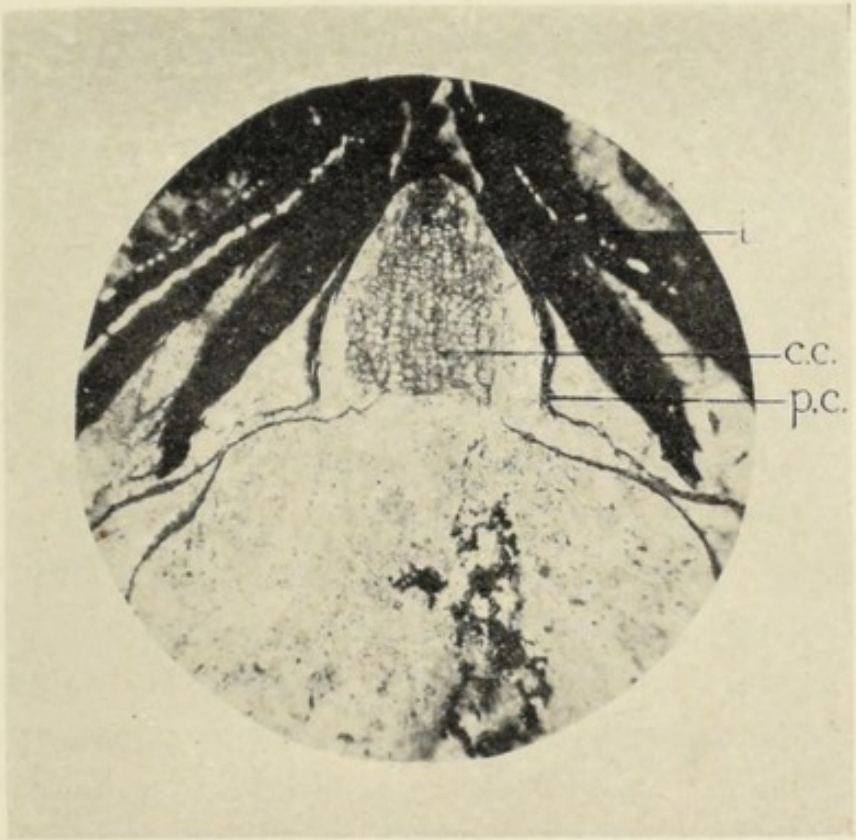

FIG. 38.—*Lagenostoma ovoides*. Closely allied to the seed of *Lyginopteris*. Longitudinal section of upper part of seed. *i*, Integument, forming canopy; *p.c.*, wall of pollen-chamber; *c.c.*, central column of pollen-chamber.
From a slide in the collection of the Botanical Department, University College of Wales, Aberystwyth. Photograph supplied by Prof. Lloyd Williams.

"Asparagus Fern" of the present-day gardener. A remarkable feature of the frond was that the main stalk or rachis was forked, the whole leaf thus being divided into two similar halves. A single vascular strand traversed each successive branch of the rachis, dividing up to form the veins in each of the leaflets, which were rather thick and fleshy. Their structure was very much what we should expect to find in such leaflets among living plants.

It was on the fronds that the seeds were borne. From the analogy of similar seeds found as impressions and still in position, it is probable that the fertile parts of the frond were naked, the rachis being without leaflets in the seed-bearing region.

We already know that the seed was surrounded by a cupule or husk, studded with the glands which played so important a part in the identification of the organ (Fig. 35, A). The cupule was a complex structure, with its own vascular system.

The seed itself was very elaborately organised. It was a barrel-shaped body, of small size, little exceeding 5 mm. in length and 4 mm. in greatest diameter. The highly-differentiated seed-coat is traversed by about nine vascular strands, which terminate in the chambers of the "canopy" surrounding the micropyle. The whole was no doubt an apparatus for the supply of water, probably to serve as a "drop-mechanism," such as ensures fertilisation in many recent Gymnosperms, and perhaps also providing a swimming-bath for the spermatozoids.

The seed-coat was closely united to the nucellus, or central body of the seed, except at the upper end. The nucellus was provided at its summit with a pollen-chamber, comparable to that of recent Cycads (cf. Fig. 11, p. 66), but more complex. The pollen-chamber in *Lagenostoma* was partly occupied by a central column of tissue, so that the actual space available for the reception of the pollen-grains was limited to the crevice between the central column and the external wall of the chamber (Fig. 38). The pollen-grains are sometimes found in the annular space; the arrangement probably served to bring them accurately to a position immediately above the archegonia (female organs) which were to be fertilised.

The seed, in possessing a pollen-chamber and a highly developed vascular system, was evidently of the Cycad type. All Palæozoic seeds, so far as the structure is

known, agree in these characters, however different in other respects; some were much more like those of recent Cycads than *Lagenostoma* was. It is highly probable, if not certain, that they further resembled Cycads and the Maidenhair Tree in being fertilised by means of active spermatozoids. The whole organisation of the seeds and the multicellular structure of the pollen-grains favour this view, though the actual detection of the spermatozoids themselves is a doubtful matter in fossil material. Renault, however, from the structure of the pollen-grains found in some of his palæozoic seeds, inferred the presence of spermatozoids, ten years before they were discovered in living Cycads and the Maidenhair Tree.

The general remarks just made apply to the seeds of Cordaiteæ as well as of Pteridosperms—in fact we know of no constant distinction between the seeds of the two groups; this agreement is strong evidence of affinity.

Though many Palæozoic seeds are known with structure preserved, it is remarkable that in none of them has an embryo ever been found, however good the preservation. It will be remembered that in the seeds of the Mesozoic Cycadeoids the embryo is often a conspicuous feature. Its absence, so far, in Palæozoic seeds is unexplained, but we find an analogy in recent Cycads. In this family, the embryo is often quite undeveloped at the time when the seed is ripe, and may not be recognisable for a year afterwards, and then only when the seed is sown. Similar conditions may have prevailed generally among Palæozoic Seed-plants.

Some of the seeds of Carboniferous times were of great size and complexity. The seeds named *Pachytesta* were as big as a duck's egg, with an immensely thick and highly organised seed-coat. Such seeds must have been of the utmost value for the protection and nutrition of the embryo-plant, whenever it developed. *Pachytesta* is believed to have belonged to one of the Seed-Ferns,

though there is no actual proof. Most of the seeds of the period are found detached, and cannot be referred with certainty to the parent plants.

It has already been mentioned that the seeds of *Lyginopteris* appear to have been borne on a naked rachis, *i. e.* on a part of the frond somewhat specialised as compared with the barren vegetative portion. In other Pteridosperms, however, there was little or no modification. In species of *Neuropteris* (Fig. 33), in *Aneimites* (Fig. 34), and in *Pecopteris Pluckeneti* the rachis which bore the seeds also bore leaflets of the normal form, either quite unchanged or somewhat reduced. Thus it was characteristic of the Pteridosperms that their seeds were produced, like the sporangia in most Ferns, on the leaves themselves; so far as we know there were no special sporophylls. This is the character which justifies us in speaking of the "Seed-Ferns" as relatively primitive Spermophytes, though their seeds in themselves were highly developed.

The only relic of this Pteridospermous feature to be found among living plants is in the genus *Cycas*, where, as we have seen, the carpels are still leaf-like organs, borne directly on the main stem. It is not suggested that *Cycas* has any specially near relation to the Seed-Ferns, but in the way its seeds are borne there is undoubtedly a certain analogy.

The fine and artistic restoration of *Neuropteris heterophylla*, reproduced in Fig. 33, gives a clear impression of the foliage, both vegetative and fertile, of a typical Pteridosperm. The Neuropterid family was very distinct from that of *Lyginopteris*, already considered. The fronds were of immense size, with petioles 5 inches or more in diameter, and repeatedly divided, with large leaflets (Fig. 33). The stems were in proportion; indeed some of these plants must have been good-sized trees.

The seeds, as we have seen, were borne on the fronds. The internal structure of the seed is not known in *Neuro-*

pteris, but somewhat similar seeds (*Trigonocarpus*) in all probability belonged to the allied genus *Alethopteris*, and in their case the structure is well preserved. There was a fleshy outer coat, enclosing a stony shell, just as in Cycad seeds at the present day, and the details agree nearly, though not, of course, exactly, with those in the recent family. The Cycadaceous seeds are evidently of a very ancient type, and the same applies to the seeds of the Maidenhair Tree.

The anatomy of all parts of the plant is now known in

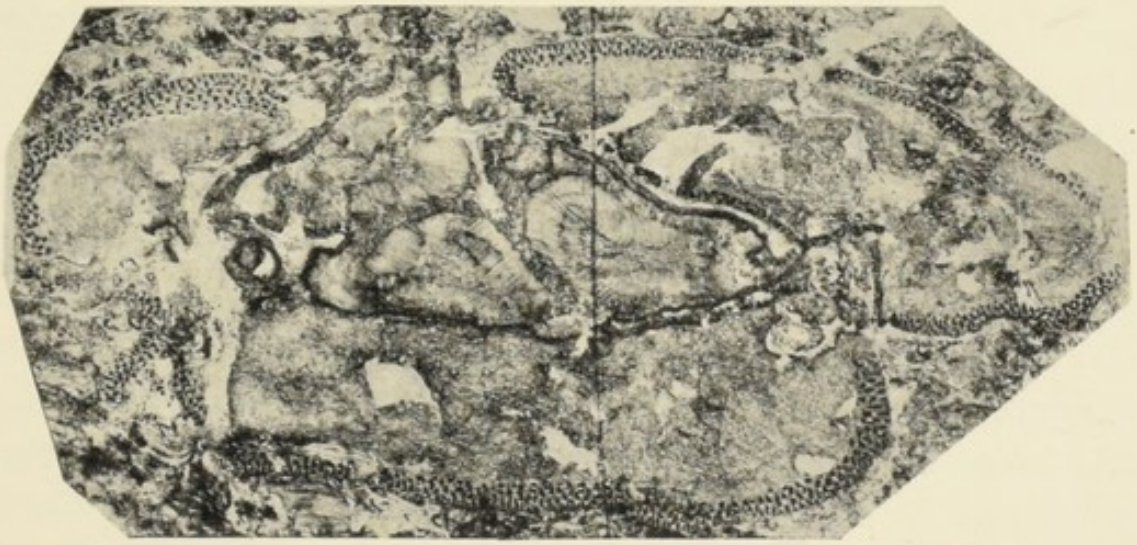

FIG. 39.—*Medullosa anglica*. Transverse section of stem with three leaf-bases attached. In the middle are the three steles, each with secondary thickening. About natural size.
From a photograph by Mr. L. A. Boodle.

certain of the Neuropterids. The stems, when their structure is preserved, are placed in the genus *Medullosa*, and the family, from an anatomical point of view, is known as the Medulloseæ. The reason for this double naming is that in many cases we know the external form without the structure, or the structure without the form, though they have been correlated in certain favourable instances.

Medullosa, of which a number of species are known, had an extremely complex structure, scarcely paralleled among recent plants. We may find some analogy among the Ferns. In the majority of Ferns of our own times,

the stem contains several distinct vascular cylinders or steles. In *Medullosa* we likewise find a polystelic structure, with the additional peculiarity that each of the vascular cylinders grew in thickness on its own account, forming new wood and bast all round it, by means of a cambium. This seems a very unpractical arrangement, for it is evident that, as this secondary growth went on, the steles, growing larger and larger within a confined space, must have got in each other's way. In fact, under such circumstances, only a limited amount of new growth was possible. We see this condition in the simplest species, such as *Medullosa anglica* from our own Lower Coal Measures (Fig. 39). Here there are usually three steles, all of approximately the same size.

In some of the more complex Continental species of later (Permian) age, the difficulty was to a certain extent got over, for the outer steles formed a more or less continuous ring, and secondary growth was greatest on the external side, where there was nothing to hinder it, while the inner steles and the inner side of the outer ring only increased to a limited extent. This plan seems to have answered very well, for stems of the Permian *Medullosa stellata* are known over a foot and a half in thickness, though without the cortex. In these extreme cases, however, new rings of wood and bast, outside the original system of steles, aided in swelling the bulk. What is of interest to us here is the fact that the stems of these ancient " Seed-Ferns " attained a complexity of structure which we should seek in vain among plants of the present day, except perhaps in some tropical climbers. The eccentricities of Lianes are, however, related to the peculiar scandent habit; there is no proof that the Medulloseæ were climbers, nor is their structure really comparable to the anomalies of Liane anatomy.

Dr. David White has pointed out the significance of the strange types of stem met with in Palæozoic times : " It

is as though Nature were at the Carboniferous moment in the midst of a series of amazing engineering experiments, most of which were either buried deep in Palæozoic oblivion, or permitted to survive only as vestigial relics and atavistic ghosts." [1]

We must not go further into anatomical detail, but it is a fact of interest that the petiole and rachis of the leaf in the Medulloseæ had much in common structurally with the corresponding parts of the Cycadaceæ, with which, as we have seen, the seeds also agree. On the other hand, there is little anatomical evidence for any relation to the Ferns. Though the Medulloseæ, like so many of the latter class, were usually polystelic, the resemblance in this respect is somewhat superficial, for the relation of the steles to the leaf-traces was quite different in the two groups.

We have already learnt something concerning the seeds of the Pteridosperms, and have seen that pollen-grains are often found caught in their pollen-chambers. What, then, was the nature of the male fructifications (microsporangia) in which these pollen-grains were produced? Our information on this point is not so complete as we could wish, but evidence is gradually accumulating. Dr. Kidston, in 1906, discovered the pollen-sacs borne on portions of a frond referred to *Lyginopteris oldhamia*. They were produced on special little fertile leaflets, of oval form, and hung down from the lower surface, the whole suggesting an epaulet with its fringe (Fig. 35, B). Fructifications of this kind had long been known, under the name of *Crossotheca*, and used to be referred to supposed Marattiaceous Ferns.[2]

Dr. Kidston finds that the pollen-sacs on the fertile pinnule were six or seven in number, and that each was bilocular, the two compartments containing the pollen-

[1] White, 1905, p. 389. [2] Kidston, 1906.

FIG. 40.—Restoration of Carboniferous Ferns and Pteridosperms. The tall trees are true Ferns; at the base of the stems the *Psaronius* root-zone is shown. The smaller Fern-like plants are nearly all Pteridosperms. After Grand'Eury.

grains. The preservation was not such as to admit of any detailed study of the structure. Bilocular sporangia, however, also occur with structure preserved, and are probably of the same nature as Dr. Kidston's specimens.

In some of the Neuropterideæ the fertile disks or leaflets are much larger than in the *Crossotheca* type; they bore the pollen-sacs, but the details of structure are still obscure, for the specimens are found as carbonaceous impressions, and not as petrifactions, which alone show the internal organisation.

There is a considerable general resemblance between the male fructifications of the Pteridosperms and the spore-bearing organs of some Carboniferous plants referred to the true Ferns. If, however, the bilocular structure occurring in pollen-sacs of the former group should turn out to be general, a definite distinction would be established.

We must now leave the Pteridosperms (though we shall return to them when we come to the Lower Carboniferous Flora) and say something about their contemporaries, the true Cryptogamic Ferns. They were quite an important body in Upper Carboniferous times, though their apparent numbers have been so much thinned by transfers to the "Seed-Ferns." They fall for the most part into two main divisions, the Tree-Ferns and the Early Ferns or Primofilices.

The Palæozoic Tree-Ferns (Fig. 40) were no doubt quite equal in stature to the tallest plants of this habit at the present day, but they did not belong to the same families. As already mentioned, the nearest affinities of the extinct Tree-Ferns seem to have been with the modern Marattiaceæ, a family which no longer assumes the tree-habit, though it includes some very fine Ferns.

The fossil group agrees with the recent one chiefly in the characters of the fructification and in the general anatomical structure. In both families, the sporangia are often

united together to form a compound spore-fruit or synangium. In both, the stem has, as a rule, a complex structure, with numerous vascular bands (steles) often in concentric circles (see Fig. 41). Most of the Palæozoic

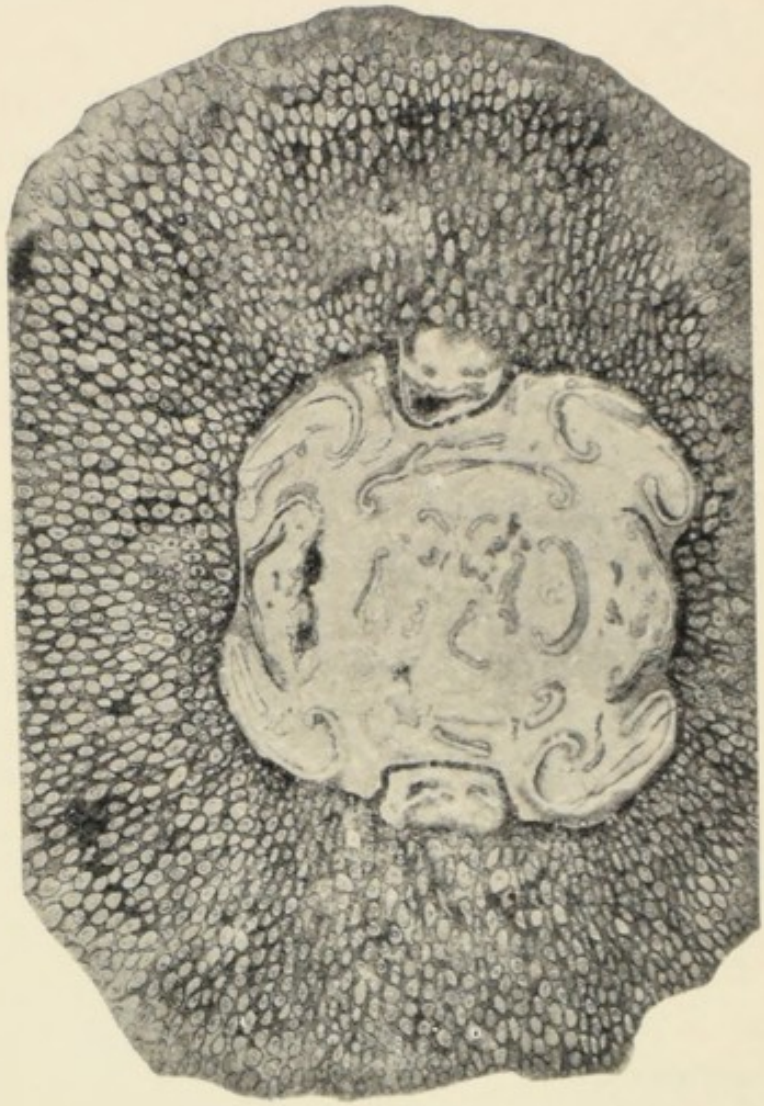

Fig. 41.—*Psaronius brasiliensis*. Transverse section of stem, with surrounding zone of roots. In the stem, the numerous curved steles are shown. The leaf-traces spring from the four sides of the square stem, while the adventitious roots are supplied from the peripheral steles at the corners. Not quite half natural size.
After E. A. N. Arber; from a specimen in the British Museum Collection.

Tree-Ferns come from the Upper Coal Measures or the Permian. In an older species, from the British Lower Coal Measures, the structure of the stem was comparatively simple.

The stems, when the structure is preserved, are placed in the genus *Psaronius*. They have been popularly

known much longer than most fossil plants, for the stems when cut and polished make decorative objects, which used to be called "Starling-stones," from their markings. The technical name *Psaronius* has the same meaning. In all cases, the true stem was enveloped in a thick mantle of crowded roots, growing down from the stem, and closely felted together in a dense mass of hairs, produced partly by the stem, but mostly by the roots themselves. This feature is peculiar to the fossil family.

On the whole we may safely say that the *Psaronius* Tree-Ferns, with their usually elaborate anatomy, their felted roots, and their often compound fructifications, were on quite as high a level as the most advanced living Ferns. We know little of their history, for they are scarcely found in rocks older than the Upper Carboniferous, where they form a definite and practically isolated family, though some of their relations appear to have come down to our own times in the form of the Marattiaceæ of tropical and sub-tropical lands.

While the Tree-Ferns of the Palæozoic are fairly comparable with some of our recent Ferns, the other great contemporary group, the Primofilices, or Early Ferns, as we may call them, was much more peculiar. The Primofilices are so named because they are regarded as the Ferns characteristic of the Primary rocks; they go back much further than the Upper Carboniferous Flora which we are now considering. Thus the name has been translated "Early Ferns."

So far as we know, they were comparatively small plants, though one of them has been given the dignity of a "fair-sized Tree-Fern." They varied much in habit, for some had long creeping rhizomes, while others had short, stout, upright stems, crowded with leaf-bases. The anatomy throughout (confining our remarks to the well-known families) was on much simpler lines than that of the *Psaronius* group, for there was always a single

vascular cylinder, though in some representatives it assumed a remarkable stellate form, in transverse section, and was not necessarily simple in detailed structure.

The foliage was the most remarkable feature. There are only a few cases in which any actual lamina has been observed. In most species, we know of nothing beyond a branched rachis, not, however, quite destitute of appendages, for it often bore small scale-leaves or "aphlebiæ," as they are called, which, curiously enough, also occur on the stem.

In the extensive and peculiar family of the Zygopterids the leaves had an unusual construction. In some of them there were two rows of pinnæ, one on each side of the main rachis, as in ordinary leaves, but the pinnæ, instead of lying in the same plane as the principal axis, were oriented at right angles to it. Many Zygopterids, however, went much beyond this, for they had two rows of pinnæ on each side—four rows in all. Such arrangements are quite unknown in recent Fern-fronds, or indeed in any leaves. In the genus *Stauropteris*, the most remarkable of all, this four-fold pinnation was repeated in successive ramifications of the frond. Lignier compared the ordinary arrangement to a *palisade*, the quadriseriate pinnation of many Zygopterids, to a *hedge*, and the repeated four-fold ramification of *Stauropteris* to a *bush*. The habit of such leaves must have been quite peculiar, and quite unlike anything which we associate with Ferns at the present day. Unfortunately, we have very little information as to the outward aspect of the Zygopterid fronds, our knowledge being mainly dependent on anatomical evidence.

The sporangia of the Primofilices are well known in certain cases. They were often borne on the ends of the branches of a naked rachis. In some cases they were large sacs, with an annulus two or more cells in width, not uniseriate as in most recent Ferns. In other cases, there was no annulus at all, as in *Stauropteris*. In this

genus germinating spores have been observed, by special good fortune, inside the sporangium, and it is interesting to find that the early stages of germination were just the same as in Fern-spores at the present day. This removes all doubt that in such cases we are dealing with true Ferns, however peculiar in some of their characters.

In a genus called *Anachoropteris* it has lately been proved that the fructification was a compound spore-fruit or synangium, such as we find so often in Marattiaceæ and their fossil allies. This discovery goes to show that there may have been some relation between plants referred to the Primofilices and Ferns of the higher, *Psaronius*, type.

It should be borne in mind that the term " Early Ferns " (Primofilices) is intended to cover an extensive and varied group of plants. Only a few families are at all thoroughly known, and all that has been said relates to examples taken from these particular families.

As regards affinities, it has been suggested that some of the best-known races of Primofilices were related to the Royal Ferns (Osmundaceæ) and the Adder's Tongues (Ophioglossaceæ). The geological history of the former family has been traced back by Kidston and Gwynne-Vaughan to the Permian, and it is remarkable that the oldest known Osmundaceous stems approach very nearly in their structure to some of the stems of the Zygopterids of the Carboniferous. On the other hand, nothing is known of the fossil history of the Adder's Tongues, and the evidence for their relationship to some of the Primofilices rests on comparison between the latter and the living family. In the absence of any connecting links, such an inference must always be hazardous, though in this case it is supported by arguments drawn both from the vegetative anatomy and from the sporangia.

There can be little doubt, however, that many of the Primofilices were specialised races, with characters peculiar to themselves, thus representing an extinct stock, having

no direct connection with the main line of evolution of the Fern series.[1]

The question now arises, What relation, if any, was there between the "Seed-Ferns" of the Carboniferous Flora and the true Ferns? The two great groups ran a parallel course during long ages, for we shall find both well represented in rocks much older than those with which we are concerned in the present chapter. We have already seen how strikingly close was the resemblance between them in habit—close enough to have deceived the best botanists until the clue was found. After the Pteridosperms had been recognised as seed-bearing plants, many of us were still so obsessed by their Fern-like characters as to believe that they were really modified Ferns—Ferns which had become Spermophytes. We then thought that the "Seed-Ferns" had actually been derived from the true Ferns, and consequently that most, if not all, of the great groups of Seed-plants traced their origin, through the Pteridosperms, back to the Cryptogamic Ferns themselves.

This interpretation of the facts must now, I think, be abandoned. It was a tempting theory, for all botanists had long been accustomed to assume that the Seed-plants had come from the Vascular Cryptogams, and the discovery of the "Seed-Ferns" seemed to reveal to us the particular class of Cryptogams from which they had sprung.

The hypothesis of a direct relation between the Pteridosperms and the Ferns was supported by arguments drawn from habit, anatomy, and the nature of the pollen-bearing organs. We have already dealt with the habit; all botanists know that similar habit is often quite deceptive. We need only remind the reader of the striking likeness between the succulent Euphorbias of the Old World and the giant Cacti of the New, so impressively illustrated by

[1] For illustrations of the structure of Primofilices, see Scott, "Studies in Fossil Botany," Vol. I., 3rd. ed., chap. ix.

the great plants of each group grown in the houses at Kew. Of course, the two are totally unrelated—the resemblance is solely due to adaptation to similar conditions of life in desert regions. A She Oak (*Casuarina*), an *Ephedra*, and an *Equisetum* are much alike in habit, with their jointed stems and rudimentary leaves; yet they belong to three different main divisions of the Vegetable Kingdom. Instances might be multiplied *ad infinitum*—habit by itself is no guide to affinity.

The conditions prevailing in Carboniferous times may perhaps be sufficient to account for the similar external habit of Ferns and Pteridosperms; the plants of both groups may quite probably have formed the undergrowth of the damp Coal Forests, in which the overshadowing canopy was supplied by the taller trees, giant Lycopods and Calamites, and the lofty Cordaiteans.

As regards the argument from anatomy, it was mainly based on a comparison between some of the Palæozoic Pteridosperms and recent Ferns. For example, the young stem of *Lyginopteris*, before secondary growth set in, had a structure something like that of an *Osmunda* at the present day. Another genus, *Heterangium*, allied to *Lyginopteris*, has been compared, in its young stage, with the stem of some recent Gleichenias. Such comparisons, however, can obviously only yield analogies; no one will suppose that there is any affinity between the fossil and recent genera compared, or that any Fern now living is at all likely to represent the ancestors of Palæozoic Seed-plants.

It is much more important to inquire whether the Palæozoic Ferns and the "Seed-Ferns" of the same period show any approach to each other in structural characters. The answer, as it appears to me, must be decidedly in the negative. There was a great range of structure both in the Ferns and the Pteridosperms of the Carboniferous Age, but in no case do the two groups

converge. The simplest of the true Ferns (e. g. *Botryopteris*) are anatomically quite unlike the simplest of the Pteridosperms (e. g. *Heterangium*). The more complex representatives of the two groups have evidently gone ahead on their own independent lines.

It is true that there are families on both sides which have several vascular cylinders in the stem, but otherwise there is no resemblance between them. The polystely of *Psaronius* is like that of other highly complex Ferns, while the polystely of *Medullosa* is essentially different, the gaps between the steles having no relation to the leaves. The elements of the wood are of quite distinct types in the two families. We may recall in this connection the fact that we have polystelic Dicotyledons at the present day, in species of *Gunnera* and *Primula* (*e. g.* the *Auricula*).

A detailed comparison, though well worth carrying through, would take us much too far here, but it may safely be said that the comparative anatomy of the ancient Ferns and "Seed-Ferns" lends no support to the belief that the one class was derived from the other.

When we compare the reproductive organs of the two groups, we are faced by the fact that it is often difficult to distinguish between the pollen-sacs of a Pteridosperm and the sporangia of a true Cryptogamic Fern of the same period (see above, p. 131). Thus *Crossotheca*, until Dr. Kidston identified one of its species as the male fructification of *Lyginopteris*, was accepted quite readily as the spore-bearing apparatus of some of the Marattiaceous Ferns. It must be remembered, however, that we might well be in the same difficulty with the microsporophylls (stamens) of the Mesozoic Cycadeoids, if they were found by themselves, and yet the Cycadeoids are obviously too advanced to have any direct relation to the Ferns. At present our knowledge of the pollen-bearing organs of the Pteridosperms is somewhat scanty, and it would be rash to draw any conclusion from resemblances which may be accidental and superficial.

As regards the seeds, it is hardly necessary to point out that they are far too advanced to admit of any comparison with the sporangia of Ferns or other Cryptogams. Some of the most complicated seeds known are of Palæozoic age and referable, sometimes with certainty, sometimes with high probability, to the Pteridosperms. It would be difficult to name any vegetable object less like a Fern-sporangium than the seed *Trigonocarpus* or *Pachytesta*.

The seed, in fact, may be said to have reached its zenith of complexity in Carboniferous times; subsequent changes have been, on the whole, in the direction of simplification, owing, no doubt, in great measure to the original functions of the seed having been partly taken over by other organs, such as the fruit. Modern Cycads and the Maidenhair Tree alone retain in essentials the old, complex type of seed.

On the whole of the evidence, the Pteridosperms show much less sign of any near relation to the true Ferns than was once supposed. We shall have to return to the subject when we consider the Flora of still older rocks, but it is well to explain at this stage that the Fern-like Seed-plants of the Palæozoic and the contemporary Cryptogamic Ferns are best regarded as distinct and in some respects parallel series, and that there are no sufficient grounds for believing that the one race was ever derived from the other.[1] As Dr. Kidston pointed out in 1906: "It seems to be highly improbable that the Cycadofilices [Pteridosperms] could have descended from plants to which the name of 'Fern,' as understood in recent botany, can be applied."

Another question, of no less interest, is that of the relation of the "Seed-Ferns" to the Cycadophyta of the Mesozoic Age and our own time. In this direction there

[1] A discussion of the question by the present writer will be found in "Aberystwyth Studies," Vol. IV, under the title "The Origin of the Seed-Plants (Spermophyta)."

seems to be a strong case for genetic relationship, though this view is not universally accepted.

There are various points which the Pteridosperms have in common with the Cycadophytes. The features which first suggested a relation, before the seeds were discovered, were anatomical. We have already called attention to the significance of centripetal wood, developed from without inwards, as an ancient character, contrasting with the centrifugal wood, developed from within outwards, which is the only wood existing in the stems and leaves of most Seed-plants now living. Of course, in all *roots* the primary wood is centripetal, so we are not concerned with them. Otherwise practically the only instances of centripetal wood among living Seed-plants are in Cycads; chiefly in their foliar bundles, where it is highly developed, but sometimes also in the peduncles of the cones, which are stem-structures.

In the Pteridosperms, centripetal wood was very general, forming in most cases an important feature in the stem, as well as in the leaf. We can trace its gradual reduction in the stem until it came to be relegated to the leaf only.[1]

This is the case in some of the Cordaiteans, which were in this respect on a level with recent Cycads, while other members of the family, as we have seen, retained some centripetal wood in the stem. The Cordaiteans were not, of course, on the road to Cycads, but in certain ways show a parallel development.

Another, less important, point, in which most of the Pteridosperms approach the Cycads is the structure of the secondary wood, with its multiseriate bordered pits and wide medullary rays. In the latter respect the Cordaiteans diverge, for their wood was generally dense with narrow rays, like that of Araucarian Conifers.

[1] Scott, 1902.

The anatomical characters of the Mesozoic Cycadeoids were in general, though not always, on the same lines as those of the recent Cycadaceæ. So far as anatomy is concerned, there is no special difficulty in connecting them with the Palæozoic Pteridosperms, though in other respects the relation, as we shall see, is very obscure. It has already been mentioned that the petiole and leaf of the Medulloseæ, in particular, had much in common with those organs in recent Cycads and Mesozoic Cycadeoids, as shown by the numerous bundles entering the leaf, and by the centripetal wood of these strands. The comparative stem-structure, however, presents considerable difficulties in this case.

Much the most important evidence of consanguinity between Pteridosperms and Cycads is, however, derived from the seed. All known Palæozoic seeds, whether referred to "Seed-Ferns" or Cordaiteans, were, broadly speaking, built on the Cycad plan, for all, so far as investigated, possessed a pollen-chamber and a highly developed vascular system. In certain groups the resemblance is specially close. Thus in the *Trigonocarpus* type of seed, no doubt borne by the Neuropterid Pteridosperms, there was an outer, fleshy, and an inner, stony, coat, a double vascular system, and the usual pollen-chamber. In all these points there is close agreement with the modern Cycadaceous seed, though some differences of detail can, of course, be detected. It is difficult to believe that such resemblances can be accidental. It is far more natural to suppose that the Cycads, and to a lesser extent the Maidenhair Tree, have retained a Palæozoic type of seed, which has come down to them from their remote ancestors.

It is unnecessary here to speculate on the question of the particular family of Pteridosperms with which the later Cycads may have been most nearly connected. The seeds of some of the Neuropterids or Medulloseæ appear

the most Cycad-like, but it does not by any means follow that the stems of the hypothetical ancestors of the Cycads had the complex structure of *Medullosa*.[1]

We know of more seeds than plants from Carboniferous rocks, and it is quite possible that stems may then have existed with a single stele, but bearing Cycad-like seeds, and perhaps Neuropterid fronds. We have, in fact, some evidence for the possibility of such a combination of characters in the Medullosean genus *Sutcliffia*.[2]

It is interesting to find that, so far as the seed-characters are concerned, the Pteridosperms approach the recent Cycads rather than the more typically Mesozoic Cycadeoids. It must be remembered, however, that true Cycadaceæ are not limited to modern Floras, but appear to go back, at any rate, as far as the Rhætic, while Cycad-like fronds occur also in the Permocarboniferous rocks. The line of the true Cycads may have branched off from the Pteridosperms during later Palæozoic times. As regards the Cycadeoids, we have no clue. Their complex flowers and fruits and simplified seeds show no relation to anything known to us in the Palæozoic Floras, though their vegetative characters prove that they too were Cycadophytes.

The position of the Cordaiteans is different again. They have points in common both with the Pteridosperms and the Cycads, but clearly constituted a distinct, though related, race. There is no reason to suppose that they had any connection with the Cycadophytes of later ages, but it is highly probable that they were akin to the Maidenhair Trees and also to the Conifers. With the former they are connected by the characters of their fructifications, with the latter by their anatomical structure; the Cordaitean wood, as already mentioned, is almost identical with that of an Araucarian Conifer. It is not at all likely that the known Cordaiteæ were the direct ancestors of

[1] On this subject, see de Fraine, 1912; and Seward, 1917, p. 155.
[2] Scott, 1906 and 1923; de Fraine, 1912.

either family, but they may well have been near the line of their descent.

In this brief discussion we have assumed the probability that the Palæozoic Seed-plants were, in some way or other, the progenitors of the Seed-plants of succeeding ages. In this general form such an assumption seems evidently justified. Recently, however, a distinguished authority has warned us that the relationship between the two ages (Palæozoic and Mesozoic) may not be as close as it is usual to assume, and that plant-life, viewed as a whole, may best be represented by separate and independent lines of evolution, or disconnected chains which were never united.[1] Certainly the transformation from the Palæozoic to the Mesozoic Flora strikes us as abrupt, especially in the Northern Hemisphere. We will not, however, pursue the general question any further here, but will leave it for somewhat fuller discussion in the concluding chapter.

In the meantime, the conclusion at which we have provisionally arrived is this: that the Cycadophyta of the Mesozoic and later periods were probably derived from the great plexus of Pteridosperms or "Seed-Ferns" which overspread the world in Carboniferous times, while the Conifers and Maidenhair Trees may trace their origin to the same stock to which the Palæozoic Cordaitean trees belonged. This stock evidently had relations with the Pteridosperms themselves, but the closeness of these relations can only be discussed in connection with evidence supplied by the older Palæozoic Floras, which will be considered in later pages.

[1] Seward, 1922, pp. 231, 238.

CHAPTER V

LYCOPODS, HORSETAILS AND SPHENOPHYLLS. THE LOWER CARBONIFEROUS FLORA. EXTINCT FAMILIES. ABSENCE OF SOME FAMILIAR TYPES. THE UPPER DEVONIAN FLORA. HIGH ORGANISATION OF THESE ANCIENT PLANTS

In the last chapter we gave a sketch of the land vegetation of the Permian and Upper Carboniferous Periods, directing our attention chiefly to the seed-bearing plants, and to the true Ferns. The Upper Carboniferous includes the whole of the Coal Measures, with the Millstone Grit below them. There is sometimes a risk of confusing the Lower Coal Measures with the Lower Carboniferous. The former simply constitute a subdivision of the Upper Carboniferous, while the latter is a distinct and more ancient main division.

Before leaving the Upper Carboniferous, however, a word more must be said about the other groups of Cryptogams, which were then prevalent. This is not a manual of Fossil Botany, and there will be no attempt to describe all the classes of plants mentioned, but one or two points are of direct interest to us in this brief survey of evolutionary data and problems.

The first point to be emphasised as regards the Lycopods is that Carboniferous members of this class were, generally speaking, heterosporous, like *Selaginella* and *Isoëtes* at the present day. There may have been, and probably were, exceptions, but no absolutely certain case of a homosporous Lycopod of that period is known. On the other

hand, the evidence for the presence of the two kinds of spore, microspores and megaspores, of extremely different dimensions, is everywhere abundant. Thus the Carboniferous Lycopods were, as a rule, on the highest modern level of their class as regards reproductive arrangements.

Some of them, however, and this is the point of chief

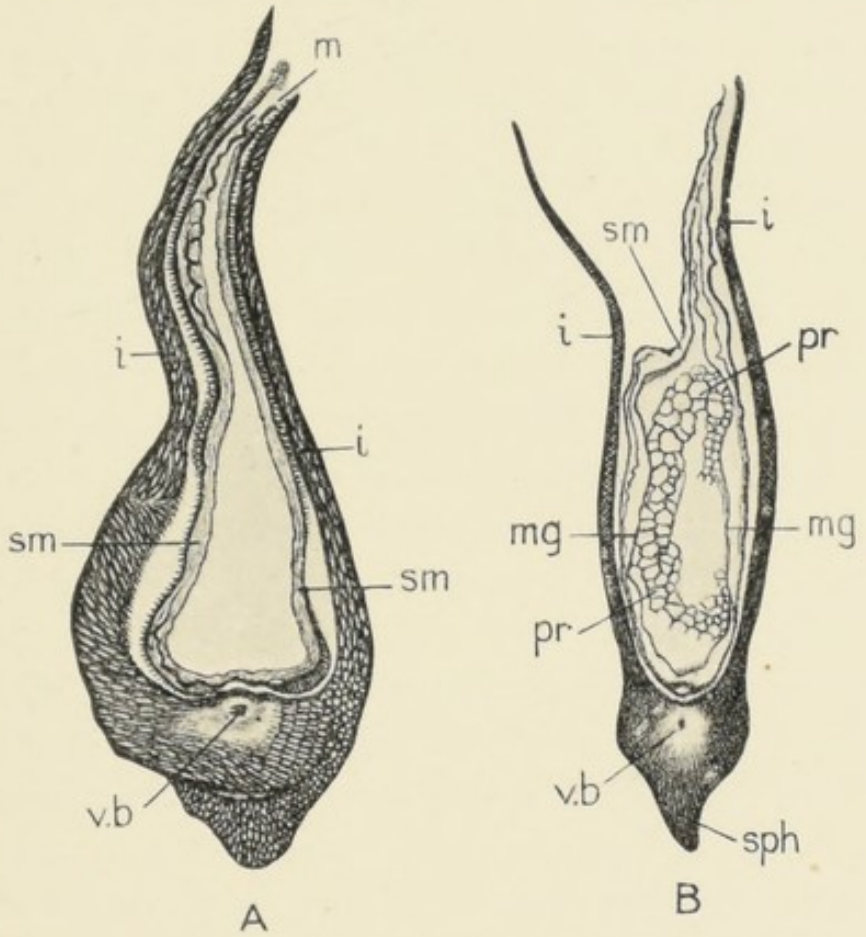

FIG. 42.—*Lepidocarpon Wildianum.* (A) Seed-like body, cut transversely to the bract. *i*, Integument; *v.b.*, vascular bundle of bract; *sm*, wall of sporangium; *m*, micropyle. (× 19.) Scott Collection 1105. (B) Similar section to show prothallus. *sph*, Bract; *mg*, membrane of megaspore; *pr*, prothallus partly preserved. The micropyle is accidentally sprung open. Other lettering as in A. (× 15.) Scott Collection 1070 (G.T.G.).

interest to us, went far beyond any of their recent relations, and developed on their own lines a kind of seed. This state of things was first discovered in *Lepidocarpon*, a genus which no doubt belonged to the Lepidodendreæ; this family of trees included a large proportion of the giant Club-mosses of that period. In *Lepidocarpon*, a single megaspore only came to maturity in the sporangium,

occupying practically all the available space, and in fact constituting an embryo-sac like that of true seeds (Fig. 42, A). It was never shed as a spore, but remained permanently enclosed in the sporangium-wall. In the meantime, an envelope grew up around the sporangium, simulating the integument of an ovule, and closed it in, except for a narrow crevice along the top. Thus the structure of a seed was very closely imitated. The prothallus in the embryo-sac is sometimes preserved (Fig. 42, B).

The reproductive bodies of *Lepidocarpon*, while much resembling seeds, differed in certain important respects from true seeds, such as those of the Pteridosperms or Cordaiteans. The " seed " in *Lepidocarpon* was not shed separately, but the whole bract was detached with it. The micropyle was not tubular, but had the form of a long slit. Lastly, the " seed " had no vascular system of its own. The only vascular strand was that of the bract.

The other " seed "-bearing genus of Lycopods, *Miadesmia*, was a little delicate plant, perhaps growing as an epiphyte, on some of its arborescent allies. Here the reproductive body was somewhat more seed-like than in *Lepidocarpon*. The " seed " was of a roundish form and the small micropyle was directed towards the free end of the bract. The organ looks quite like a seed, but here also the whole bract was detached, its broad blade serving, no doubt, as a wing to the " seed." Neither was there any vascular system apart from that of the bract.

These organs are of great interest, as showing that some of the Lycopods of Palæozoic age made an attempt to rival the contemporary Seed-plants by producing bodies serving the purpose of seeds. These devices were, no doubt, quite efficient, but do not seem to have persisted for long. The main lines of Spermophytes, with which the rival Lycopod seed-bearers had nothing to do, held

their own, and the effort to compete with them on their own ground was soon given up.

We have already mentioned that *Miadesmia* was a little herbaceous plant, probably something like a living *Selaginella*. The latter group was well represented in Carboniferous times. Some of the species placed in the fossil genus *Selaginellites* scarcely differed from the modern *Selaginella*. They were all heterosporous, and in some there were only four megaspores in the sporangium, just as in the recent genus. Other species were more peculiar, with as many as twenty megaspores in each sporangium.

It is evident that, side by side with the gigantic Lepidodendrons and Sigillarias of the Coal Period, small herbaceous Club-mosses, of the modern type, had already started; we should even be justified in saying that the genus *Selaginella* itself goes back to the Carboniferous Age. But it is remarkable that all these plants, so far as they are known, had two kinds of spores. The simpler type of *Lycopodium* has not yet revealed itself in the Carboniferous Flora. The average level of the Lycopods of the Coal Age was altogether far higher than that of the same group in our own time.

Although we have used the popular name " Horsetails " to include the great Calamites of the Carboniferous Period, it must be pointed out that these ancient plants differed very considerably from the recent family, and were probably not on the direct line of their descent. Not only were the leaves better developed and the vascular system more complex, but the cones were differently and more elaborately constructed. It was the rule in the fructifications of the Calamites that sterile whorls of bracts were present among the fertile whorls of sporangium-bearing organs. In the recent *Equisetum*, of course, the fertile whorls are alone represented. In the ancient cones the sterile and fertile whorls were usually equal in number

and alternate, though there were many variations and complications in their arrangement.

Another point of special interest is that, while all living Horsetails bear one kind of spore only, like Ferns, a few of the Carboniferous Calamites are known to have been heterosporous, the microspores and megaspores having been formed in different sporangia of the same cone. Thus, the Carboniferous representatives of the Horsetails, like the corresponding Club-moss allies, were in every respect more highly organised than their modest successors in the living Flora.

We have little space to spare for the Sphenophylls, though they claim great interest as a wholly extinct race of plants, scarcely known after the Palæozoic Era. Their leaves, like those of the Horsetails, were in whorls; the two classes are often grouped together under the common name of Articulatæ. The leaves themselves were typically wedge-shaped, but often filiform and sometimes forked. While the Calamites, like the modern Horsetails, had a large pith in the stem, the Sphenophylls possessed a perfectly solid wood, reaching to the centre of the axis. The primary wood was developed centripetally, but was succeeded by a zone of centrifugal secondary wood, with corresponding layers of bast. Secondary growth in thickness was, in fact, of very general occurrence among the Vascular Cryptogams of Carboniferous age.

The cones were usually complex structures, with sterile bracts as well as sporangium-bearing organs, though in certain cases no special cone was differentiated. The sporangiophores commonly appear as definite appendages of the bracts, whereas in Calamarian cones the two are often separated. There is no clear proof of heterospory within the group, which, so far as the Upper Carboniferous forms are concerned, was a fairly homogeneous one, consisting throughout of slender plants, of no great

size; very possibly, as Prof. Seward has suggested, they may have supported themselves by climbing on the stems of their more robust neighbours. While a certain affinity with the Horsetails is well established, the Sphenophylls show no clear indications of relationship in other directions.

The Lower Carboniferous Flora

The passage from the Upper to the Lower Carboniferous Flora is not, of course, one of our great transformations; it is a minor transition, but yet an important one

The Lower Carboniferous, as developed in Great Britain, includes the Mountain Limestone, so conspicuous in the great range of the Mendip Hills in Somerset, and the Calciferous Sandstone Series of Scotland, an important formation in the south of that country. The latter belongs to the older part of the Lower Carboniferous and "graduates downward insensibly into the Upper Old Red Sandstone" (Geikie). The Calciferous Sandstones are peculiarly rich in remains of fossil plants, which have in places given rise to important seams of coal, worked commercially in various parts of the south of Scotland. We must not suppose that workable coal is by any means limited to what are technically called the "Coal Measures."

The Lower Carboniferous is commonly spoken of by Continental geologists as the "Culm." They have adopted this English term (though somewhat inaccurately), and where one finds the "Culm Flora" mentioned by a Continental authority, it is always the Lower Carboniferous Flora that is meant.

The Lower Carboniferous Flora is of great interest; though of the same general character as the Upper, it differs in detail and in some important points. It is even more completely and typically Palæozoic, for all traces of such comparatively modern classes as the Cycads and

true Conifers are here absent, while the Ferns, and indeed all the groups, are a little more archaic, though not necessarily any more primitive, for the Lower Carboniferous plants were on a very high grade of development.

Dr. Kidston, who is our greatest authority on both the Upper and Lower Carboniferous Flora, and has had special opportunities of studying the latter, states that there is not a single species common to the two. More fundamental distinctions, moreover, are not lacking.

The Cordaiteans, those great forest trees, with catkins and long leaves, which formed so striking a feature in the Upper Carboniferous Flora, are very poorly represented in the older formation, and little or nothing is known about them. One often meets in the literature with exaggerated statements as to the age of this family. It was essentially an Upper Carboniferous race, and though it doubtless already had allies in older Floras, the Cordaiteæ themselves are scarcely found.

There was, however, another important family of Gymnospermous trees characteristic of the Lower Carboniferous and extending still further back in geological time. Readers who have visited the Natural History Museum at South Kensington will no doubt have noticed, in the Museum Garden, a great fossil trunk set up (see Frontispiece). This belongs to the famous Craigleith Tree, found in a quarry near Edinburgh in 1826; it was the first member of the family to be described. The type genus is named *Pitys*, and the Craigleith Tree is called *Pitys Withami*, after Witham, of Lartington, who first recorded it in 1829, and who was the first investigator of the microscopic structure of fossil plants.[1]

The *Pitys* stems had a characteristic structure. The pith was large, and scattered in it, either round the outer margin or throughout its substance, there were numerous little strands of primary wood; the more external of the

[1] Witham, 1833.

strands passed out as leaf-traces. The secondary zone had wide medullary rays, very wide indeed in some species, while the water-conducting elements had the usual Araucarian pitting on their radial, and occasionally on their tangential, walls. We knew little more of the structure than this until Dr. W. T. Gordon took up the investigation quite recently. He worked especially at stems found

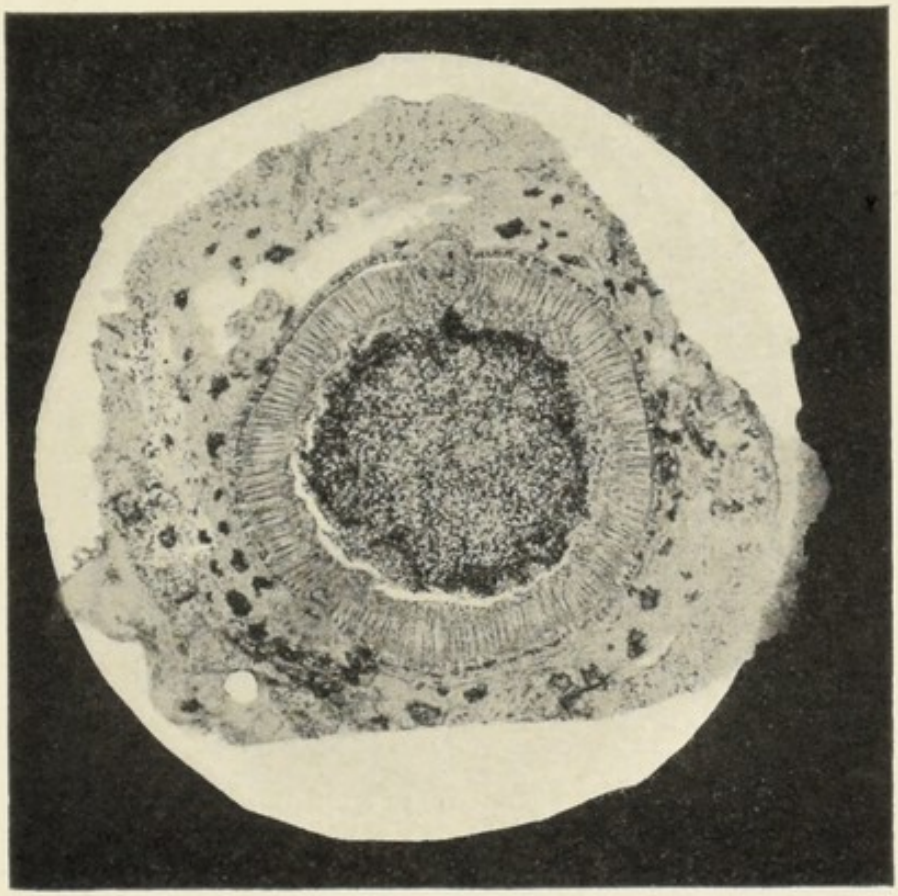

FIG. 43.—*Pitys Dayi*. Transverse section of stem, showing pith, wood, and cortex. Leaf-traces are passing out through the wood and cortex, dividing up as they go. (× about 3.)
From a photograph by Prof. W. T. Gordon.

embedded in the rocks on the shore at Gullane, on the south coast of the Firth of Forth. He succeeded in finding specimens, not only with the cortex preserved (Fig. 43), but even with the leaves attached. The foliage turns out to have been quite peculiar, bearing no resemblance either to the large, flat leaves of the Cordaiteans, or to the much-divided fronds of the Pteridosperms. The leaves or petioles of *Pitys* were of a tapering, pointed

shape, more like stout Pine-needles than anything else. They were, however, more complex than Pine-needles internally, for each leaf was traversed by several vascular strands (Fig. 44), produced by the subdivision of the

Fig. 44.—*Pitys Dayi*. Transverse section of leaves or petioles. In two, the structure is well shown, with three or four vascular strands, arranged in a V and embedded in ground-tissue. The cortex has a strong mechanical construction. (× about 12.)
From a photograph by Prof. W. T. Gordon.

single leaf-trace. There is no sign of a lamina. Dr. Gordon suspects an affinity with the Araucarian tribe of Conifers. We are still awaiting the publication of his results in full.[1]

It is evident that the *Pitys* family constituted a distinct

[1] See Gordon, quoted in Scott, 1923, p. 256.

race, quite separate from the Upper Carboniferous Cordaiteans. Unfortunately, we know nothing of the fructification; from the whole organisation, however, we can scarcely doubt that *Pitys* and its allies were Gymnospermous Seed-plants.

A good many seeds are known from the Lower Carbon-

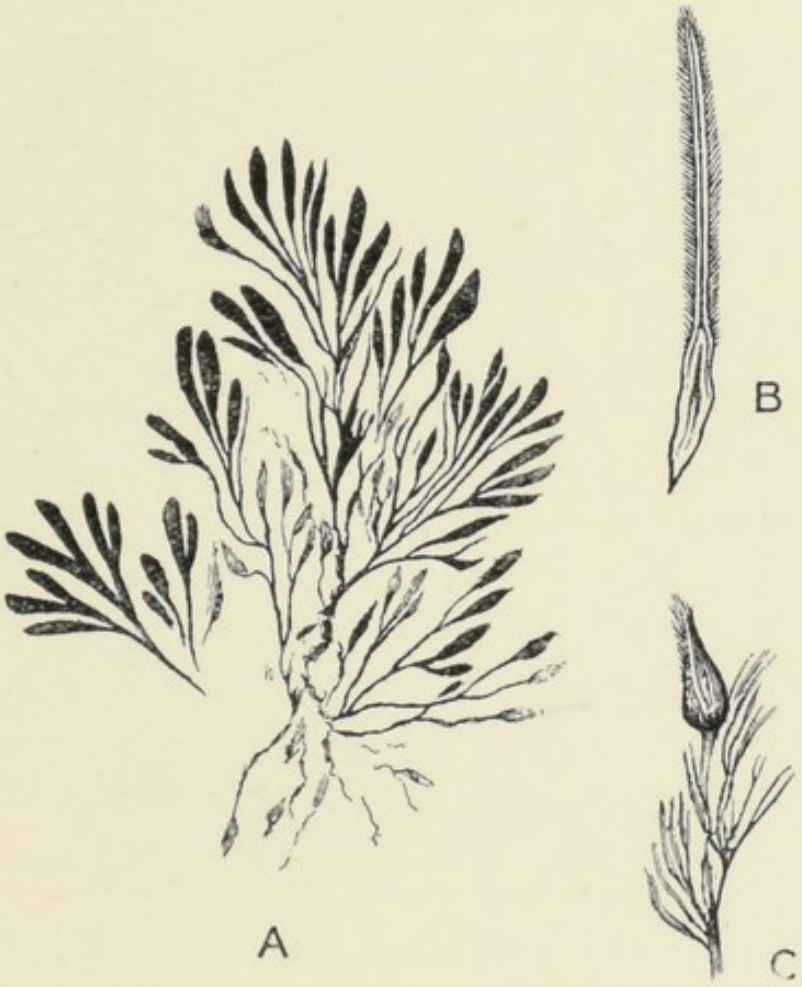

FIG. 45.—(A) *Sphenopteridium Norbergi*, part of Fern-like frond. (B) *Thysanotesta sagittula*, seed, with long beak bearing a pappus of hairs. (C) Seed (incomplete), in connection with part of the *Sphenopteridium* frond. After Nathorst.

iferous, though there are only a few with structure preserved. It is possible that some of the seeds may have belonged to the *Pitys* family, but as to this there is no evidence. Where there are grounds for attributing the seeds to the plants which bore them, it is the Pteridosperms that are indicated. Prof. Nathorst described a

specimen in which a small seed is seen in connection with a finely divided, Fern-like frond (a *Sphenopteridium*). The seed in question (*Thysanotesta sagittula*) is a remarkable one, for it bore a long beak, more than an inch in length, which was densely clothed with hairs. The whole arrangement may be called a pappus, analogous to that of our familiar Composites, and no doubt serving the same function, namely, to ensure the seeds being scattered by the wind (Fig. 45).

There are other cases in which the connection of seeds with Fern-like foliage is suggested; on the whole there can be no doubt that the Seed-Ferns were quite as strongly represented in the Lower Carboniferous Flora as in that of the Upper beds.

The evidence is very largely from anatomical structure. It has already been pointed out that, even before the first discovery of the seed of a Pteridosperm, we had indications from the anatomy, which warned us that not all the Fern-like plants of the Carboniferous could be true Ferns. Now we are in a position to go further; when we find a certain type of structure in a Palæozoic plant, we feel justified in referring it, with some confidence, to the Pteridosperms, even though the seed is still undiscovered.

It would take us too far to explain fully here the nature of the anatomical characters by which we think Pteridosperms may be recognised. There is always a great development of primary wood, sometimes forming distinct bundles round the pith, sometimes a continuous zone in which the pith is enclosed, and in other cases again extending, as a solid, woody cylinder, to the centre, so that there is no pith at all. Or, as we saw in the case of *Medullosa*, there may be several such cylinders in the stem. Surrounding the primary wood we always find, if the stage is sufficiently advanced, a zone of secondary wood and bast, formed, in the usual way, by a cambium.

The leaf-traces are relatively large (for the foliage to be supplied was extensive). It may be added that the water-conducting elements (tracheides) usually have the form of pitting which we call Araucarian, *i. e.* the pits are in several rows, bordered, and mostly limited to the radial walls.

Now there are no fewer than six known families of Lower

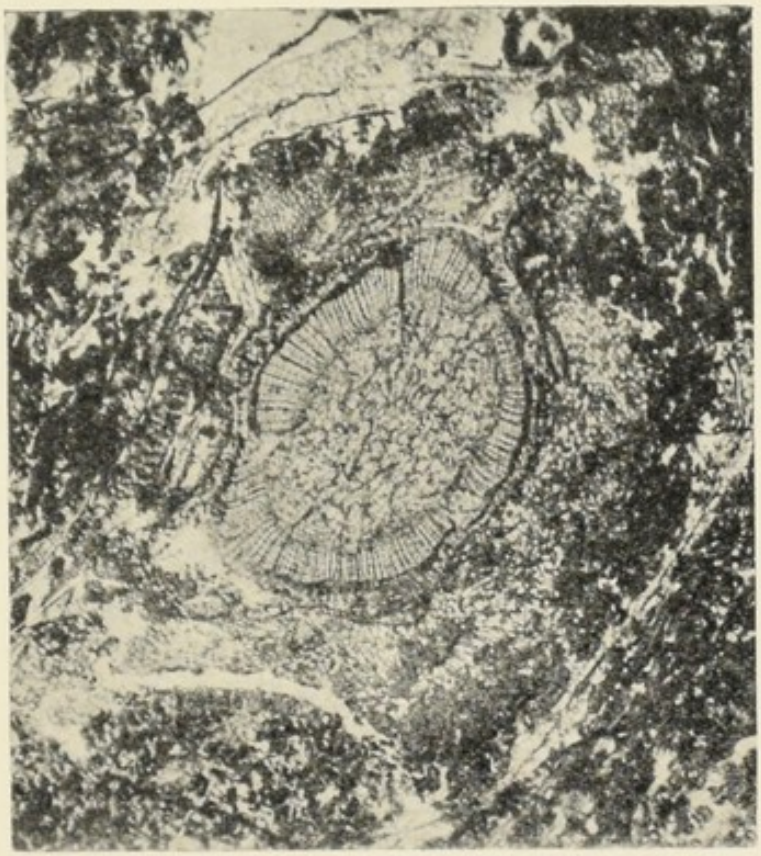

FIG. 46.—*Heterangium Grievii*. Transverse section of stem showing the protostele, with primary and secondary wood, pericycle, and cortex. A leaf-trace is just departing from the stele. Scott Collection 1016. (× about 7.) From a photograph.

Carboniferous age which, from anatomical characters, almost certainly belonged to the Pteridosperms, though differing widely among themselves. In only one of these families have we any evidence as to the seed. This is in the case of the genus *Heterangium*, a near ally of *Lyginopteris*. Species of the genus occur both in the Upper and Lower Carboniferous. The Lower Carboniferous species, *H. Grievii*, is one of the best known of

fossil plants. The foliage is found in the form of impressions; it was of the *Sphenopteris* type; the fronds were finely divided, with narrow leaflets, something like those of some modern Aspleniums.

Anatomically, the great characteristic of *Heterangium* is that it had no pith, the primary wood occupying all the central part of the stem (Fig. 46). The near relationship to *Lyginopteris* has been confirmed by the discoveries of the Austrian palæobotanist, Dr. Kubart, who has observed, in the coal balls of Upper Silesia, stems of Millstone Grit age (*i. e.* from the lower part of the Upper Carboniferous) which show a certain transition from the *Heterangium* to the *Lyginopteris* type of structure. There is a *Heterangium* with more cellular tissue than usual among the primary wood, and a species of *Lyginopteris* with a few tracheides persisting in the pith. Thus it appears that the *Lyginopteris* stem-structure may have been derived from that of *Heterangium* by successive reductions in the central part of the primary wood.

The stems and leaf-stalks of *Heterangium Grievii* are among the commonest petrifactions in the well-known locality at Pettycur, on the north shore of the Firth of Forth. The bed in which they occur belongs to the Calciferous Sandstone Series. Roots are also present, so the vegetative structure of the plant is pretty completely known. Apart from the solid wood (the vascular cylinder of the stem constituting what is called a *protostele*), the organisation agrees closely with that of *Lyginopteris*, and the two genera are therefore placed in the same family.

Dr. Margaret Benson has described in detail a seed, already recorded by Williamson, which is so closely associated with *H. Grievii* as to leave little doubt of its belonging to that plant, though direct proof of connection may not be fully established. The seed in question (*Sphærostoma ovale*) is excellently preserved, and has a complex structure of the same type as the seed of *Lygino-*

pteris, but differing in detail. There was a husk or cupule closely investing the seed. Both cupule and integument had its own vascular system. The micropyle had a very characteristic frilled structure, and there was a highly-organised pollen-chamber at the apex of the nucellus. Dr. Benson has endeavoured to find out how the mechanism worked; she believes that the pollen-chamber opened to receive the pollen-grains, and then closed up tightly again, the wall of the chamber shutting down on the low central column (Fig. 47). It is evident that this ancient seed was on a very high grade of organisation.

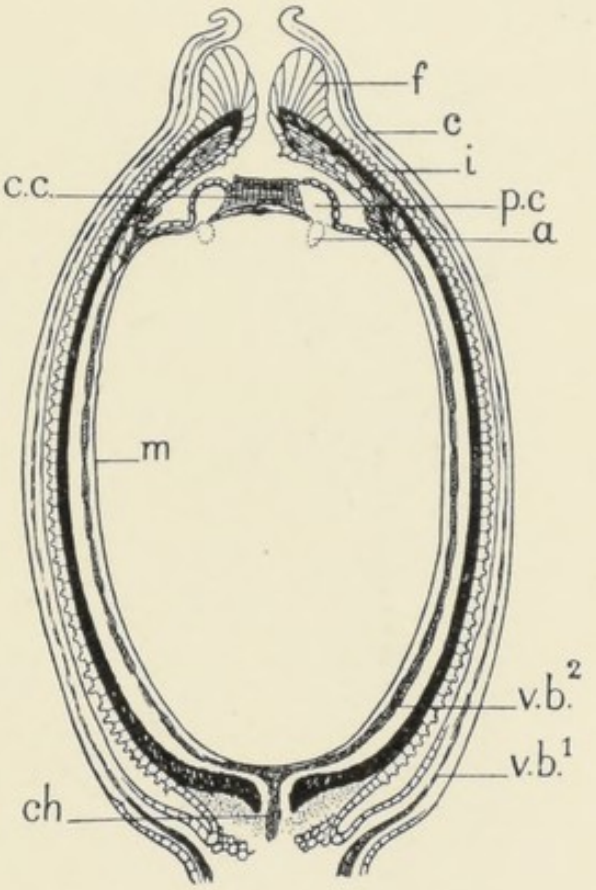

FIG. 47.—*Sphærostoma ovale*, the probable seed of *Heterangium Grievii*. Diagrammatic median section: *c*, cupule; *f*, frill at top of integument, *i*; *p.c.* pollen chamber; *c.c.*, its central column; *a*, indication of archegonia; *m*, membrane of megaspore; *v.b.*¹, vascular bundles of cupule; *v.b.*², those of integument; *ch*, main strand at chalaza. After Benson.

As we have seen, the family Lyginopterideæ was common to the Upper and Lower Carboniferous. The other five families mentioned above were all, so far as we know, peculiar to the Lower. Thus there was a remarkable wealth of forms in those days among plants which, in their structure, show clear evidence of Pteridosperm affinity. It is a pity we do not know more about them. The stem-structure is well enough preserved, but we have little knowledge of the foliage, and none of the fructification.

Without going into detail, it will be worth while to attempt a brief sketch of the structure in these families, so as to give some idea of the variety they show.

One family is founded on the genus *Rhetinangium*, another of the Pettycur fossils, discovered by Dr. Gordon. Only the one species, *R. Arberi*, is known at present. The stem-structure bears a general resemblance to that of *Heterangium* (Fig. 48). Here also the vascular system formed a protostele. The leaf-traces, however, were quite

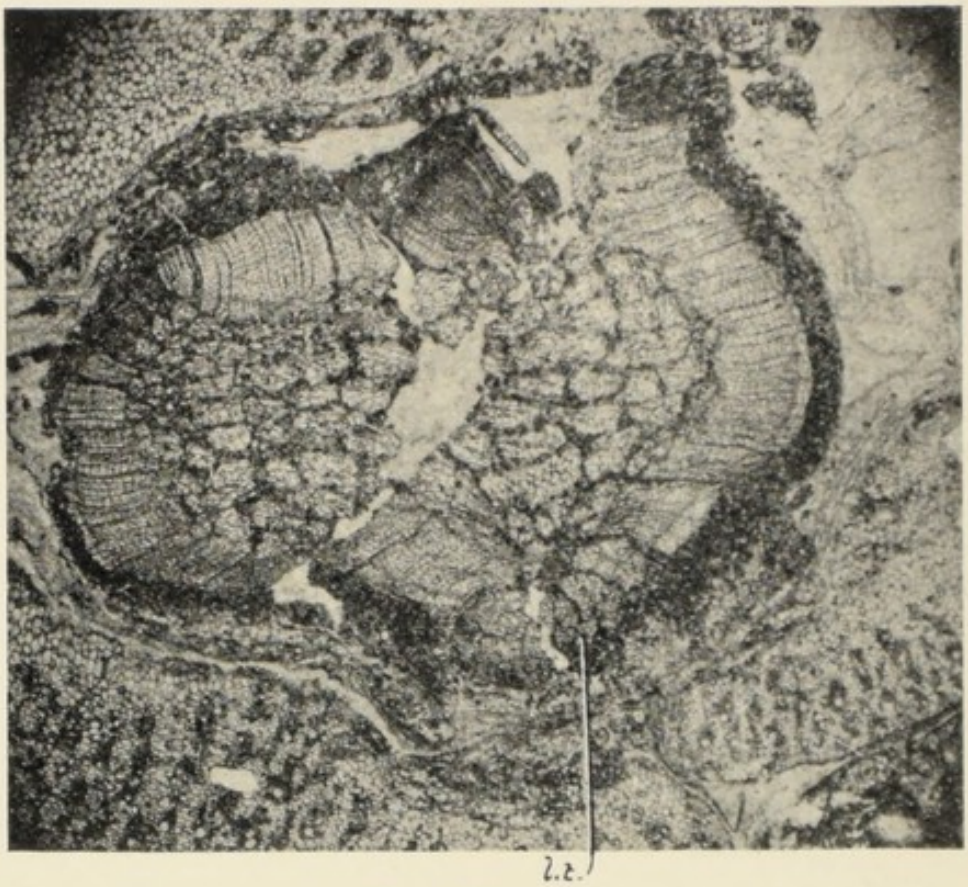

FIG. 48.—*Rhetinangium Arberi*. Transverse section, showing stele, with primary and secondary wood and part of cortex. *l.t.*, Compound leaf-trace, passing out from the stele. (× about 8.)
From a photograph by Prof. W. T. Gordon.

peculiar and unlike those of any other plant. While the trace supplying each leaf was in *Heterangium Grievii* a simple strand, in *Rhetinangium* it was a complex body, of considerable breadth, representing a number of strands fused together laterally, the whole forming an irregular corrugated band. The same structure was maintained, with little change, in the petiole and the branches of the rachis. The foliage was, no doubt, compound, but we

have no details of its form. There are other differences between *Heterangium* and *Rhetinangium*, but we have called attention to the most striking. The family seems evidently allied to the Lyginopterideæ, through *Heterangium*.

The family of which *Calamopitys* is the type-genus was a rather extensive one, for a number of species are known, from our own country, Central Germany, and the United States. This group also shows some affinity to the

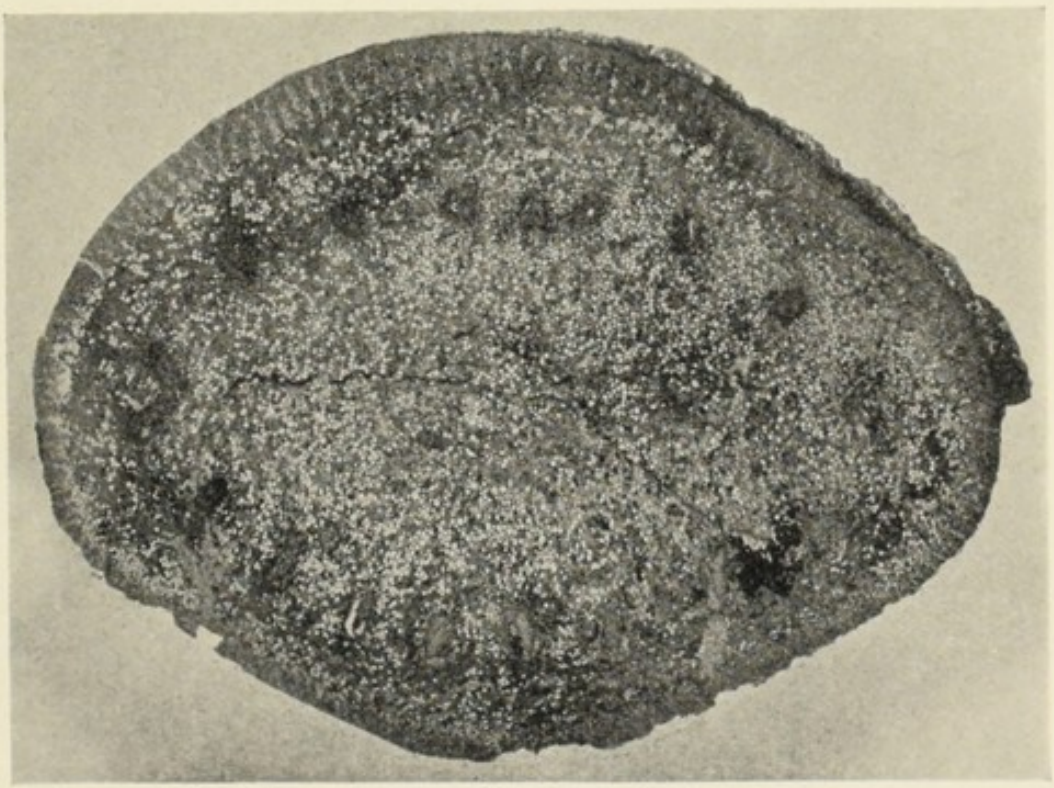

FIG. 49.—*Kalymma*, the petiole of a *Calamopitys*. Transverse section, showing the ring of numerous vascular strands, and the strongly constructed outer cortex. (× about 2.) Scott Collection 3046.
From a photograph by Mr. W. Tams.

Lyginopterideæ. There was a definite pith, surrounded by a ring of rather large strands of primary wood (cf. Fig. 50). In some of the species, however, there were tracheides scattered throughout the pith, which was thus what is termed a "mixed" one, a survival, it appears, of the protostele. In other cases the pith was of the ordinary cellular structure throughout.

The great distinction from the *Lyginopteris* family is in the structure of the petiole, known in three species of

Calamopitys; it was a large, complex organ, traversed by a great number of distinct vascular strands, arising from the subdivision of a single leaf-trace (Fig. 49). The leaves were no doubt compound, but here also we have no clue to the actual form of the frond. In *Calamopitys*

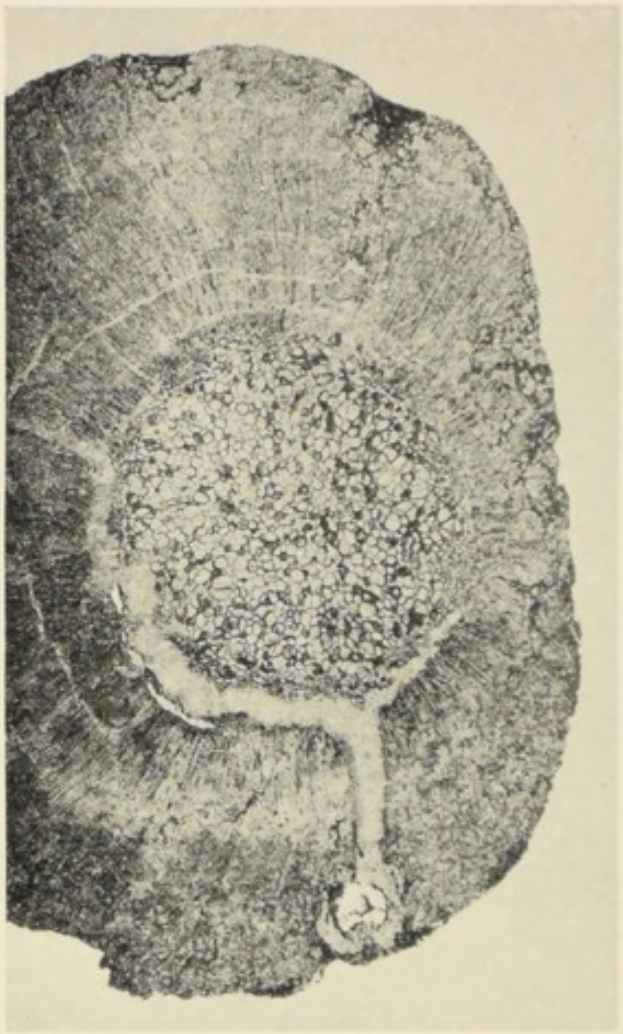

FIG. 50.—*Bilignea solida.* Transverse section of stem (wood only), showing the central mass of tracheides, the scattered leaf-trace strands at the outer margin of this, and the surrounding zone of dense secondary wood. Out-going leaf-traces are seen in the wood. The section is like that of a *Calamopitys* of the Eristophyton group, only in the latter there is a true pith. (× about 7.)

From a section in Dr. Kidston's collection, photographed by him.

proper, the secondary wood was usually rather lax, with wide medullary rays; in *Eristophyton* (if, following Dr. Zalessky, we make a separate genus of it) the wood was dense, with narrow rays, much like that of the Cordaiteans of a later time.

Dr. Kidston has recently discovered a new and remarkable genus of the *Calamopitys* family. He has named it *Bilignea ;* there are two species, from localities in the south of Scotland. The peculiarity of the genus is that the whole of the pith is replaced by a central column of short tracheides, serving apparently for the storage of water (Fig. 50). In other respects, the structure is like that of *Eristophyton*, the most advanced genus of the group. It is therefore suggested that the peculiar central column of wood may have been derived from a pre-existing pith, rather than directly from a protostele.

Calamopitys and its allies were evidently large plants. Some of the petioles of *C. americana* were $2\frac{1}{2}$ inches in diameter. Probably we are dealing with a family of trees, though their main trunks are still unknown or unrecognised. There is evidence that the group already existed in Upper Devonian times.

The next family is represented by Dr. Kidston's genus *Stenomyelon*, with two species, both from the valley of the Tweed. The type is quite an isolated one (Fig. 51). The primary wood has a bluntly triangular form, as seen in transverse section. It was not perfectly solid, for the mass is usually divided into three by thin bands of cellular tissue, the "narrow pith" of the generic name. The whole is surrounded by a zone of secondary wood, with rather wide rays in one species and narrow ones in the other. The cortex had the strong mechanical construction, effected by a system of fibrous bands, usual in plants of this class.

From each corner of the primary wood in succession a large leaf-trace was given off, single at first, but soon dividing up into a great number of strands, which passed through the cortex and supplied the petioles. Thus each leaf received numerous vascular bundles, as in *Calamopitys*. There are some indications of a thick leaf-blade, perhaps simple.

Stenomyelon shows no obvious affinity to any of the other families, but, on account of the petiolar structure, may provisionally be placed next the *Calamopitys* group.

S. tuedianum, the type species, has a remarkable history.

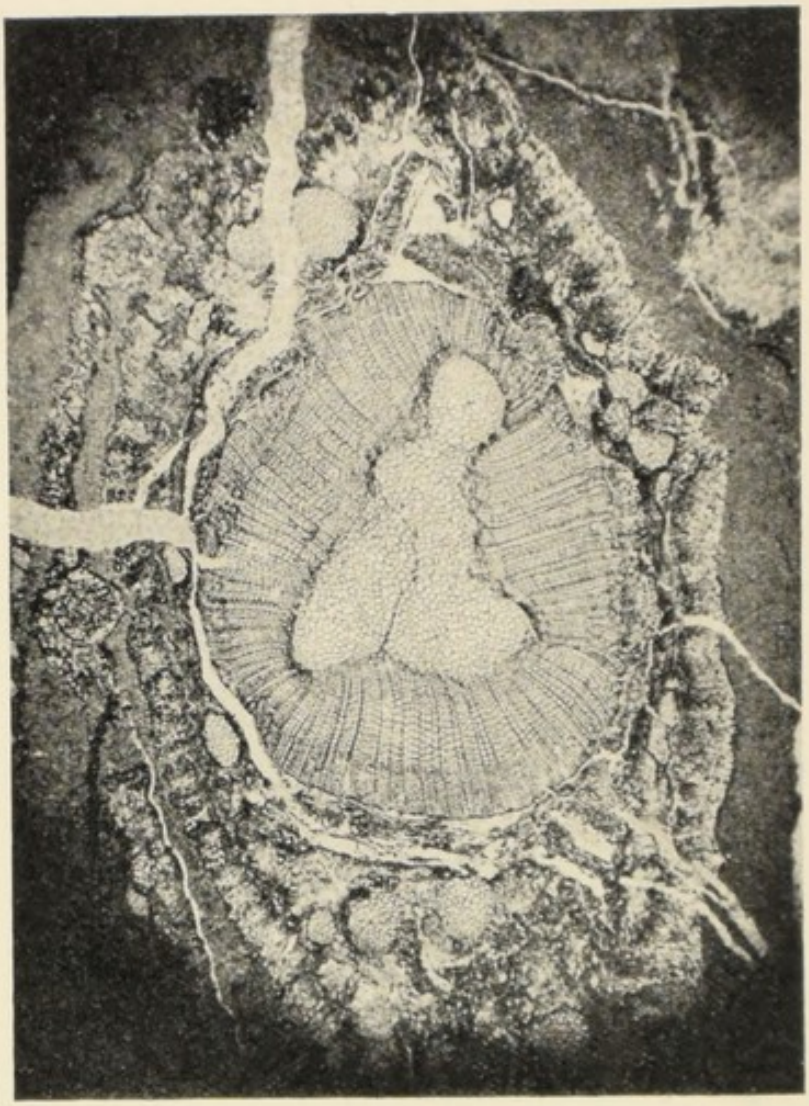

Fig. 51.—*Stenomyelon tuedianum*. Transverse section of stem, showing the almost solid primary wood, with the "narrow pith," the secondary wood, and part of the cortex. A leaf-trace strand is just departing from the stele, and others, in course of division, are seen in the cortex. (× 5½.) Scott Collection 2758.

From a photograph by Mr. W. Tams.

It was originally discovered by the geologist Matheson in the fifties of the last century. He called it the "Tweed Mill fossil," [1] from the place where it was found. The original sections were incomplete, and only allowed of the conjecture that the plant was probably a Pteridosperm.

[1] There are others; *e.g.* one of Witham's trees, *Pitys primæva*.

Dr. Kidston naturally wanted to know more about it. He noticed that the specimens were in a peculiar dark-coloured matrix, which he recognised as belonging to a particular bed of the Lower Carboniferous as shown on the Tweed. He went to the locality, Norham Bridge, and there, among the stones thrown up in making a drain by the roadside, he recognised the matrix and found among the fragments a magnificent specimen of the plant sought. Thus, with other specimens to help, Dr. Kidston, in conjunction with the late Prof. Gwynne-Vaughan, was able to give a full description of this remarkable fossil.

The two remaining families stand a little apart from the rest. *Protopitys* is a remarkable genus, represented at present by a single species from the Lower Carboniferous of Falkenberg in Silesia, where it is a common fossil. Dr. Kidston has another species from the Yoredale rocks of Yorkshire, but it is still undescribed.

Protopitys Buchiana, the Silesian species, was a large plant, attaining the girth, at any rate, of a good-sized tree. One of the stems, though probably without its bark, was almost a foot and a half thick. The structure was in every respect peculiar. The leaves, as shown by their bases, were in two alternating rows, one row on each side of the stem, as in the Traveller's Tree (*Ravenala*) of Madagascar at the present day.

The anatomy of the stem reflects the distichous arrangement of the foliage. There was an elliptical pith, with the long axis in the plane of the leaf-bases. The pith was surrounded by a zone of primary wood, thin at the sides, but much thickened at the ends of the ellipse (Fig. 52). From each end alternately a massive leaf-trace was given off, which divided into two as it entered the base of the leaf. Each new leaf-trace was formed by the junction and fusion of two opposite enlargements of the woody zone.

The secondary wood, often of great thickness, is remarkable for the multitude of very small medullary rays, and for the pitting on the tracheides. The pits were not, as a rule, of the rounded or hexagonal form usual in Pteridosperms, but transversely elongated, approaching the ladder-like (scalariform) sculpturing of most Fern-tracheides.

These details are mentioned here to emphasise the

FIG. 52.—*Protopitys Buchiana*. Transverse section of stem, showing the oval pith, with a narrow band of primary wood at the sides, and a massive leaf-trace strand at each end. The leaf-trace at *a* is further out than that at *b*. Part of the secondary wood is shown, and some fragments of cortex. (× about 6.) Solms Collection 239*a*.
From a photograph by Mr. W. Tams.

fact that *Protopitys* stands alone. There is no other known Pteridosperm at all like it. The nearest approach in habit was in some of the Carboniferous Tree-Ferns, where the leaves were likewise in two rows, but here the anatomy was totally different. We put *Protopitys* in the Pteridosperms because there is nowhere else to put it. It is no doubt more akin to them than to any other known group, but it is far more isolated than any of the types previously described. Our knowledge of the

structure of this extraordinary plant is chiefly due to the work of the late Count Solms-Laubach.

The last family, of which *Cladoxylon* is the type, is even more remarkable than *Protopitys*. It is a group that has long been known, for a number of forms were described by the Austrian botanist, Unger, as early as 1856. The vascular system of the stem consisted of numerous steles, each forming its own secondary zone of wood and bast. So far the *Cladoxylon* family resembles the Upper Carboniferous Medulloseæ, but a detailed examination reveals so many differences that an affinity between the two groups seems improbable. The Medulloseæ themselves are not known to be represented in the Lower Carboniferous.

Most of the specimens of the *Cladoxylon* family come from Central Germany; only one species is British, *Cladoxylon Kidstoni*, described by Solms-Laubach from a Berwickshire specimen in Dr. Kidston's collection.

The steles are usually elongated in transverse section, straight in some species, curved in others (Fig. 53). It is a very general rule that the long axis of the steles is radial to the stem, whereas in *Medullosa* such elongated steles are placed tangentially. The wood of each stele, whether primary or secondary, consists of elements with elongated scalariform pits, whereas in *Medullosa*, as in other Pteridosperms with the exception of *Protopitys*, they are of the round, Araucarian type. In *Cladoxylon*, the secondary wood is traversed by little medullary rays something like those of *Protopitys*, but in *Völkelia*, a genus from Falkenberg in Silesia, there are no rays at all.

The structure of the petiole and rachis has now been ascertained in certain species of *Cladoxylon*. Like the stem, the petiole was polystelic, the vascular system consisting of several bands of wood surrounded by bast. This, again, is totally different from the petiole-structure of *Medullosa* with its numerous small bundles, like those of a Cycad. It seems evident that the *Cladoxylon* group

was quite unrelated to the later family, and probably more primitive. Prof. Paul Bertrand, who knows more than anybody else about the somewhat mysterious *Cladoxylon* race, thinks they were probably Phanerogams, while at the same time he calls attention to the slight differentiation between stem and petiole. This suggests that the Cladoxylons may represent a specially early

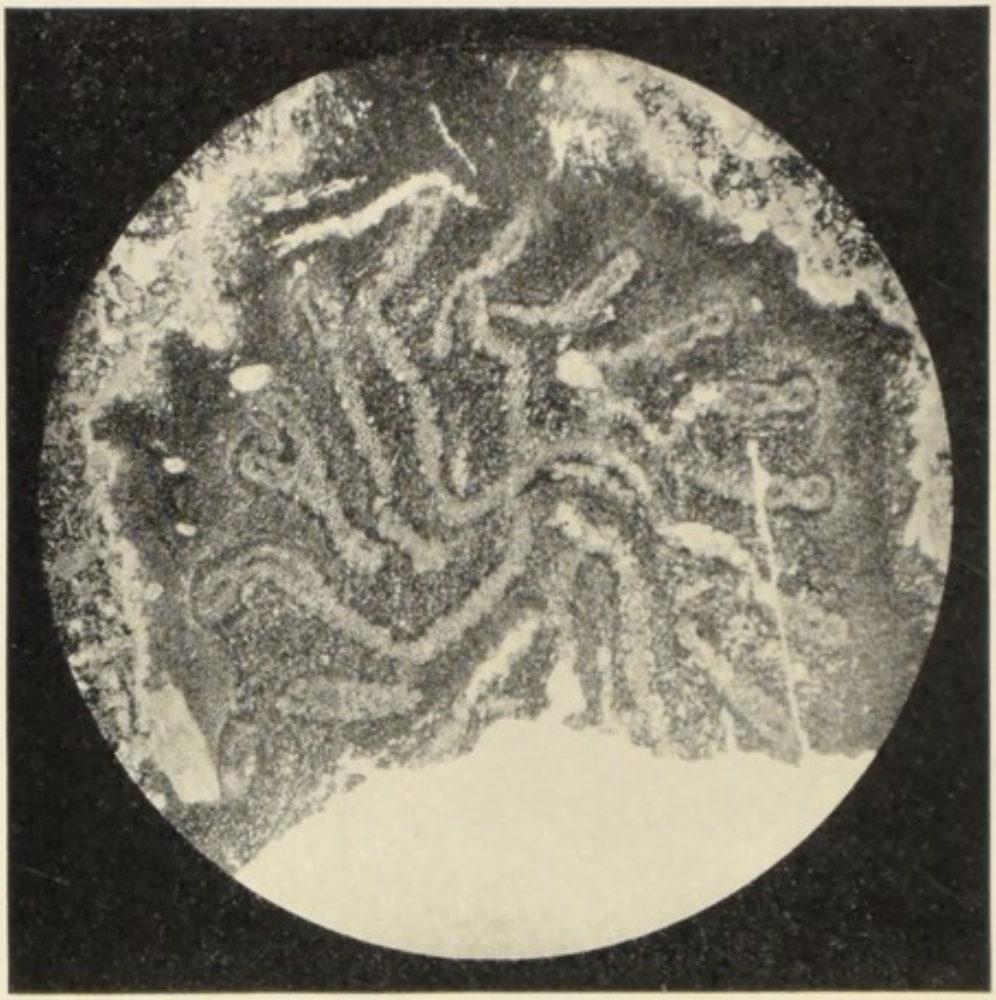

FIG. 53.—*Cladoxylon mirabile*. Transverse section of a young stem before secondary thickening, showing the numerous curved steles, with protoxylem-groups near their outer ends. (× about 14.) Berlin Collection 73.
From a photograph by Prof. Paul Bertrand.

race of seed-bearing plants, but our knowledge is too incomplete for any certain conclusion to be drawn.

There is some slight and doubtful evidence as to the nature of the foliage in *Völkelia*, for, associated with the stems, fragments were found bearing the remains of Fern-like fronds, with small leaflets; in fact, the plant

was named *Sphenopteris refracta* when first discovered. We cannot be certain that the foliage really belonged to the *Völkelia* stems, but it is not improbable, and if this was the case we should know that one at least of the Cladoxyleæ had a Fern-like habit.

Glancing back at the six families we have briefly surveyed, we know that the Lyginopterideæ were seed-bearing plants—Pteridosperms. There seems no reasonable doubt that the three succeeding families, represented by *Rhetinangium*, *Stenomyelon*, and *Calamopitys*, were of the same general nature: there are so many points of structure in common. Some botanists have even suspected that *Eristophyton*, distinguished from *Calamopitys* by its denser wood, may be related to the more advanced race of the Cordaiteans.

The two families last considered, represented by *Protopitys* and *Cladoxylon*, seem to be somewhat remote from the rest. Though they still have more in common with the Pteridosperms than with any other known stock, they are so peculiar in various respects that they may probably belong to distinct races, otherwise unknown, and perhaps only distantly connected with the Pteridosperms which we regard as typical.

From the number of distinct structural types, sometimes represented only by one or two species, it is evident that we are dealing with scattered relics of what was in reality an extensive and varied class of Palæozoic plants.

Our knowledge of the Lower Carboniferous Pteridosperms, though necessarily imperfect, is in some respects more satisfactory than our records of the contemporary true Ferns. Fern-like fronds are indeed extremely common in the Lower Carboniferous strata, but we seldom have any certain criterion by which we can distinguish between true Ferns and "Seed-Ferns." There seems to be as yet scarcely any evidence for the presence of the

Marattiaceous Tree-Ferns in the Lower Carboniferous Flora. They may have been there, but if so we cannot recognise them with any certainty.

Prof. Zeiller, in 1906, said the question might be raised whether Ferns really existed at the epoch of the "Culm" and the Devonian. Although he thought they were not entirely absent, he regarded them as then altogether subordinate to the Pteridosperms. As a matter of fact, we have conclusive evidence for the presence of true Ferns in the Lower Carboniferous, in the form of specimens with structure preserved. Practically all such specimens, at present known, belong to the Primofilices, that strange early race of which we have already spoken in considering the Upper Carboniferous Flora.

The Zygopterid family was as well represented in the Lower as in the Upper Carboniferous Age, and as highly organised. The old genus *Clepsydropsis*, which appears to go back to the Upper Devonian, while simple in the structure of its petiole, turns out to have possessed a stem of a high type with a complex vascular system of the stellate form, like that of the most advanced Upper Carboniferous genera.

Clepsydropsis had the simpler form of leaf-organisation, with one row of pinnæ on each side of the rachis. The other Lower Carboniferous Zygopterids, however, show the peculiar quadriseriate arrangement of the leaflets, which seems so unfamiliar to the student of recent plants. Thus the most striking feature of the Zygopterids was already manifested and even predominant at the earlier period. *Stauropteris*, where the bush-form of the frond is so marked, has a Lower Carboniferous species.

As regards fructifications, the older species of *Stauropteris* is associated with spore-sacs of the same simple kind as those belonging to the Coal Measure form. In a fructification attributed with much probability to *Diplolabis*, a Lower Carboniferous genus, the sporangia are

grouped, several together, on a common pedicel, though not fused to one another.

The family of the Botryopterids is at present represented in the Lower Carboniferous only by a single species, *Botryopteris antiqua*, of Kidston. It was a small plant with a very simple structure, differing little from the Coal Measure forms, though much less advanced than Renault's somewhat later species. The fructifications, which in all probability belonged to *B. antiqua*, consisted of small sporangia, with an annulus of two rows of cells, just as in the Coal Measure species.

Botryopteris, at least in the older species, is so simple a type of Fern that it might quite conceivably have had an evolutionary future before it. In other words, we may imagine that this group had some relation to the later developments of the Fern stock.

The case of the Zygopterids is different. They appear to have been already so specialised a family, on lines different from those of any Ferns of succeeding periods, that they could hardly have led on to the latter. They are best regarded as a characteristic Palæozoic group, representing in some respects a high development of the Fern phylum at that period, but lying apart from the main line of Filicinean evolution.

We may return for a moment to the question of the relation of the Pteridosperms to the true Ferns. If there were any approximation between them we might expect to find better indications of it as we go back further in geological time. No such approach, however, is to be detected among the Fern-like plants of the Lower Carboniferous. We find, as we already found in the later Carboniferous Flora, great difficulty in distinguishing the fronds of the one group from those of the other. That, however, is a mere matter of habit, already sufficiently dealt with.

Anatomically there is no approximation. Among the Lower Carboniferous Ferns, the simplest structure we find is that of *Botryopteris*, while among Pteridosperms we may take *Heterangium* as anatomically the simplest. Each had a protostele, *i. e.* a single vascular cylinder with no pith, the primary wood extending to the centre. In *Botryopteris*, the primary wood was nothing but a solid mass of tracheides. In *Heterangium*, it was sharply differentiated into a network of mingled tracheides and cellular tissue. The tracheides themselves were quite differently pitted in the two genera. Neither is there any resemblance in the structure of the leaf-trace. We cannot go into details here, but it may safely be stated that there is nothing in common between the simplest Fern of the period and the simplest Pteridosperm, beyond the fact that both had a protostele. That type of structure, of course, occurs in many groups, and is in itself no evidence of relationship.

It need hardly be added that if the seed *Sphærostoma* is rightly attributed to *Heterangium*, that genus was already an advanced Spermophyte, far removed from any Cryptogamic stock. At present, in fact, we know of no really simple Pteridosperm.

A few words may now be said as to the position of the other main races of land-plants in Lower Carboniferous times.

The Lycopods (see Fig. 54) were already richly developed, and on a very high level, though the characteristic Upper Carboniferous genus *Sigillaria* was but scantily represented in the older Flora. The structure is well known in many cases, and it is interesting to find that in several Lower Carboniferous species of *Lepidodendron* there was a solid wood, without any pith. This protostelic structure seems to have been the more primitive type in the group, though there is little enough in the rest of the structure

to suggest primitiveness. Secondary thickening, by means of cambium, was the rule, though there may have been some exceptions.

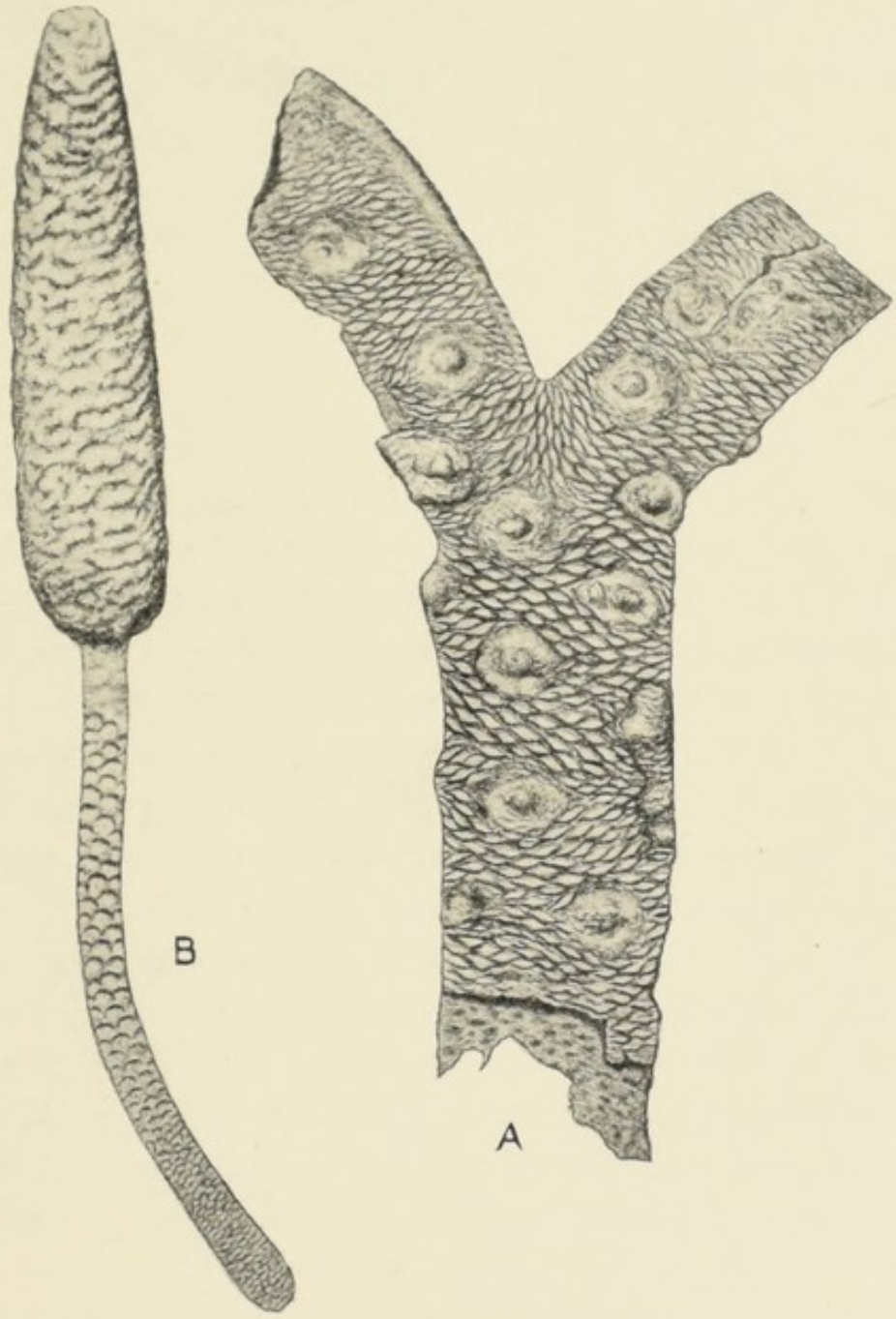

FIG. 54.—*Lepidophloios scoticus.* (A) Forked stem, covered with the bases of leaves and the scars of deciduous branches, about one-third of natural size. (B) Stalked cone of the same, about natural size.
After Kidston.

As regards the fructification, the Lower Carboniferous Club-mosses were as highly developed as their successors. All known forms were heterosporous in the highest degree,

the differentiation between the two kinds of spore being extremely marked. The seed-like bodies of *Lepidocarpon* are represented by a Lower Carboniferous species from the Pettycur beds (see Fig. 42), as well as by other examples.

The prothallus is sometimes well preserved both in the "seeds" and in the ordinary megaspores. Among the latter, Dr. Gordon has described, in the case of *Lepidostrobus Veltheimianus*, a perfectly typical archegonium (female organ) agreeing exactly with that of heterosporous Lycopods still living.

Among the allies of the Horsetails, the best-known Lower Carboniferous genus is *Archæocalamites*, remarkable for its leaves, which were long and often repeatedly forked, and thus very different from the rudimentary foliage we are accustomed to meet with in Horsetails of the modern kind. As we have already seen, the Upper Carboniferous Calamites were in this respect intermediate between the two extremes.

The fructifications associated with *Archæocalamites*, and probably belonging to it, are in some respects more like those of the modern *Equisetum* than the cones of the later Calamites. Sterile bract-whorls were few, or even perhaps absent altogether in some cases; whereas, as already shown, the Upper Carboniferous cones of this group had the bracts highly developed, the sterile and fertile whorls being usually equal in number and alternating regularly. Our knowledge of Lower Carboniferous Calamite cones is, however, decidedly limited, and it is highly probable that the *Calamostachys* type may have already existed.

The anatomy of *Archæocalamites* was quite of the usual Calamitean character. In another genus, however, called *Protocalamites*, primary wood, centripetally developed, was present in the stem, thus offering some analogy with

the Sphenophylls, in which the primary wood is an important feature.

This is the last we shall see of the Horsetail race, for, curiously enough, we know of no clear evidence for its presence in older formations. Yet the Calamites were so advanced in Lower Carboniferous times that they obviously had a long history behind them, and the absence of Devonian examples can only be due to the imperfection of the geological record.

The Sphenophylls of the Lower Carboniferous were highly developed, and in the genus *Cheirostrobus* reached their zenith. *Sphenophyllum* itself was at that period chiefly remarkable for the narrow, forked leaves; the more typical wedge-shaped foliage seems to have been a later development. The anatomical structure, known in the case of *S. insigne*, from the Pettycur locality and also from Central Germany, was of the same general type as in Upper Carboniferous species, but seems to have been rather less specialised.

Cheirostrobus, the most remarkable of the Sphenophylls and very different from the type-genus, is only known by the cone and its stalk, for, unfortunately, the vegetative part of the plant has not been identified. The specimens come from the famous Pettycur bed. The cone was a large one, about an inch and a half in diameter; we do not know the full length, which, at any rate, exceeded 4 inches. In structure it is the most complex Cryptogamic fructification known, either fossil or recent.

The axis bore crowded whorls of compound sporophylls,[1] about a dozen in a whorl. Each sporophyll consisted of six segments, three above and three below. The three upper segments were fertile; each had a peltate head and bore four sporangia. The three lower segments were

[1] The term sporophyll is used for a leaf which, directly or indirectly, bears the sporangia.

sterile bracts, which overlapped the heads of the fertile organs and all fitted together with the utmost precision, the sporangia thus being most efficiently protected until the time arrived to shed the spores. So far as observed, the spores were all of one kind. For details, the text-books must be consulted; all that is necessary here is to emphasise the elaboration and perfection of the mechanism of this ancient spore-fruit.

From the arrangement of the parts and the anatomical structure of the axis and sporophylls and of the sporangia themselves, an affinity with the Sphenophylls is evident, while at the same time there are certain points in common with the Calamites. *Cheirostrobus* is placed in the class Sphenophyllales, in a family of its own. While its general relationships are clear, the plant is an isolated type; it indicates that the Sphenophyll group, if more completely known, would prove to present a great range of structure.

The Sphenophylls and Calamites of the Lower Carboniferous decidedly confirm the conclusion already suggested by their later representatives, that the two groups are related, and may be regarded as branches of one main phylum, the Articulatæ.

The Lower Carboniferous Flora, of which we have now completed our rapid survey, is in some respects the most interesting of all the Fossil Floras. It is comparatively well known, and shows the Palæozoic Plant-World practically at its highest development, still in the freshness of youth, and as yet quite untouched, so far as we know, by any tendency to modern innovations!

The Upper Devonian Flora

We now come to a still older Flora, that of the Upper Devonian period, or the Upper Old Red Sandstone, as it is called in Scotland. We are making no great step at this point, for some palæobotanists treat the Lower

Carboniferous and the Upper Devonian Flora as one. No doubt there is a marked likeness between them; unfortunately, our knowledge of the Upper Devonian plants is as yet by no means on a par with that of their immediate successors.

We are now getting a long way back in our retracing of geological history, but we still find the plants very

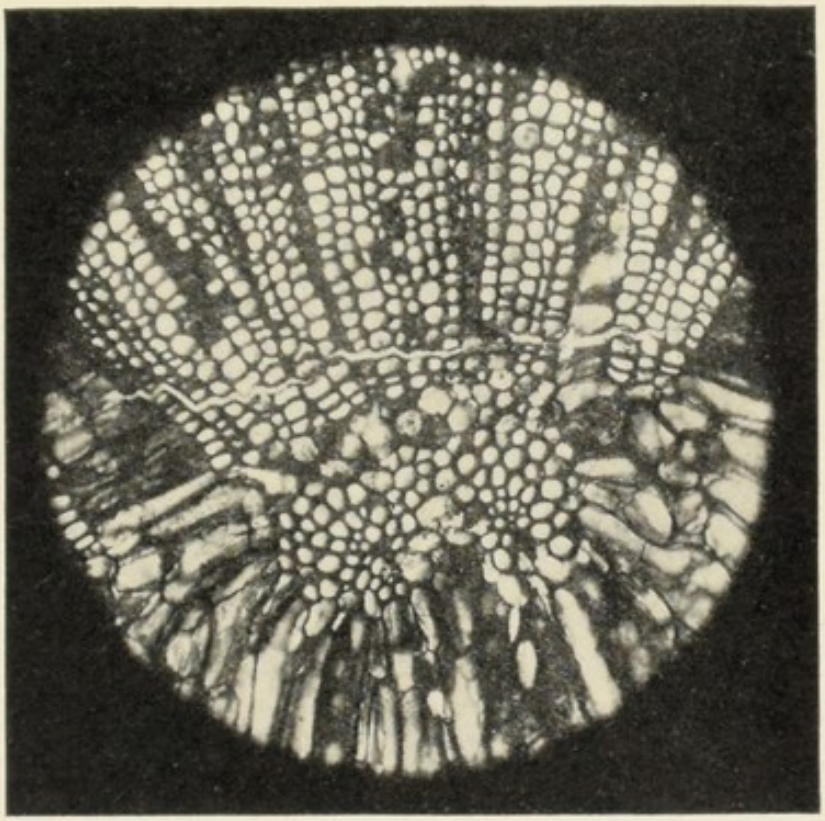

FIG. 55.—*Callixylon Trifilievi.* Small part of transverse section, showing a few cells of the pith, a double strand of primary wood, and the corresponding arc of secondary wood. (× 50.)
From a photograph by Dr. Zalessky.

highly organised. Seed-plants, Ferns, Club-mosses, Sphenophylls, and their allies are all represented and all well advanced on their several lines. A few more primitive-looking forms may be met with, the survivors of a yet more ancient vegetation.

The evidence for the presence of Seed-plants in the Upper Devonian, though practically conclusive, is indirect, for actual seeds of that age are still unknown or too obscure to be relied on. There are, however, some beautifully

preserved stems, with an advanced Gymnospermous type of structure.

The genus *Callixylon*, founded by Dr. Zalessky on a species from the Upper Devonian of the Donetz Basin, in South Russia, is remarkable for its high organisation. The small strands of primary wood, round the pith, and some other details, indicate that it belonged to the *Pitys* family (Fig. 55). The secondary wood has the usual

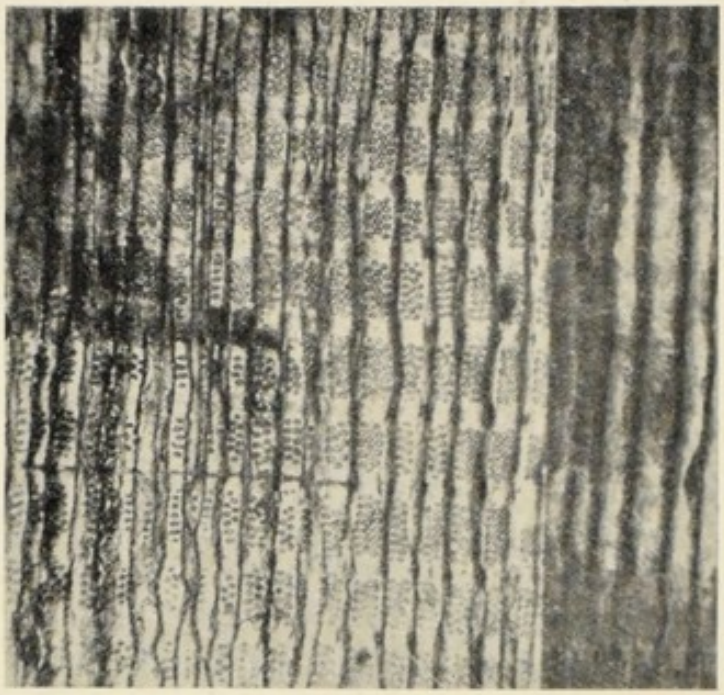

FIG. 56.—*Callixylon Oweni*. Radial section of secondary wood, showing the bordered pits grouped in definite areas on the walls of the tracheides, the pitted areas ranged in radial series. (× about 70.)
After Elkins and Wieland.

Araucarian structure, but with a marked peculiarity. The bordered pits are not distributed uniformly over the radial walls of the tracheides, but are aggregated in definite groups with bare spaces between them. These groups of pits are arranged in regular radial series, so that the longitudinal section is marked out in alternating pitted and pitless bands (Fig. 56). The structure was thus more elaborate than that of most living Conifers.

Other species of *Callixylon* are known from similar horizons in North America. The genus, as shown by its

relation to *Pitys*, was evidently not a Pteridosperm, but a member of a higher race.

The Pteridosperms themselves were probably well represented, but, as usual, where only impressions of fronds are available, we cannot distinguish them from true Ferns. There is at present very little structural evidence. The genus *Calamopitys* is known, not only from the Lower Carboniferous Waverley Shale of the United States, but also from the underlying Genessee beds, of Upper Devonian age. So far as we can tell, there seems to have been no important difference between the earlier and later specimens.

Few examples of fossil plants are more familiar to the general public than the magnificent Fern-like fronds of *Archæopteris*, especially the type-species, *A. hibernica*, from Kiltorkan, in Co. Kilkenny, Ireland. The frond is of large size, much divided, with leaflets something like those of a Maidenhair Fern, but more robust. The fructification, or rather *a* fructification, is known. It consisted of clusters of spindle-shaped sporangia or pollen-sacs, borne on fertile leaflets of the frond. We do not know what was the true nature of these organs. They may either have been Cryptogamic sporangia, or a male fructification. No seeds have been found, but they may have existed, and thus we are left in doubt whether these fine plants were "Seed-Ferns" or true Cryptogamic Ferns.

The same doubt applies to other Fern-like plants of the same period. The Fern-habit was well represented, but the true affinities of the plants showing it cannot yet be determined.

We have, however, direct evidence, from structural specimens, of the presence of true Ferns in the Upper Devonian period. We have already referred to the genus *Clepsydropsis*, one of the Primofilices. The Australian specimens, in which the stem was first discovered, were found in rocks referred to the Upper Devonian.

There is, further, the genus *Asteropteris*, discovered many years ago by Sir William Dawson in the Upper Devonian of the State of New York. The vascular system of the stem, recently reinvestigated by Prof. Paul Bertrand, was stellate in transverse section, and both this fact and the structure of the leaf-traces indicate that the plant was an early representative of the Zygopterid family. Thus these peculiar early Ferns were already well established in Upper Devonian times.

Going on to other groups, the Club-mosses were very vigorous at this period. A genus called *Bothrodendron*, distinguished by the very small leaf-scars on the surface of the stem, is characteristic. The Irish species, *B. Kiltorkense*, a large plant, is pretty completely known, so far as its outward aspect is concerned, for stem, root-stock, leaves, and cones have all been found. The cones were short, thick bodies, almost of the size of a hen's egg. They had very long bracts, but the interesting point is that they bore two kinds of spores. Thus the higher type of Lycopod was already flourishing.

Dr. Zalessky has recently described an Upper Devonian *Lepidodendron*, from the Donetz basin, with structure preserved. It is interesting to note that the wood was solid, with no pith, a form of anatomy frequent, as we have seen, in Lower Carboniferous Lycopods. In Dr. Zalessky's specimens, no secondary wood had been formed, but of course we cannot be sure that it was always absent.

On the whole, we have no reason to assume that the Upper Devonian Lycopods were of a lower grade than their successors in the Lower Carboniferous.

The Horsetail race, strangely enough, appears to be unrepresented, but this, as already pointed out, is no doubt due to deficiencies in our knowledge rather than in the Flora of the period.

Other Articulatæ, however, were present; *Sphenophyllum* was represented by species with narrow, filiform

leaves, like those of the Lower Carboniferous forms. A plant, something like a *Sphenophyllum*, but without the characteristic swollen nodes, was found by the late Prof. Nathorst in rocks of Middle Devonian age. It may well have been a precursor of the true Sphenophylls of succeeding periods. It is named *Hyenia sphenophylloides.*

FIG. 57.—*Pseudobornia ursina.* Branch, bearing the whorled leaves, which are highly compound.
After Nathorst.

Prof. Nathorst discovered in the Upper Devonian of Bear Island, in the Arctic Ocean, a very curious and isolated type of Articulatæ, which he named *Pseudobornia.* This plant had jointed stems, like a Calamite, and whorled leaves, usually four in a whorl. The leaf was doubly compound; it was forked in a palmate manner, and each

fork was cut into narrow segments. In fact, the leaves were so much divided that they were at one time described as Fern-fronds (Fig. 57).

The cones are also known; they were of considerable length; Nathorst believed that some of the sporangia borne on the bracts contained megaspores. This strange and complex plant represents a wholly extinct race, of which we can say no more than that it belonged to the phylum of the Articulatæ.

Lastly, it may be mentioned that leaves, described under the name *Psygmophyllum*, bearing some resemblance to those of the Maidenhair Tree, are found in Upper Devonian strata. We have no clue to their affinities. Possibly they may represent the foliage of some unknown race of Seed-plants.

In the Upper Devonian, imperfect though our knowledge may be, we are still for the most part among highly organised plants, often showing clear affinity with known groups, though sometimes more isolated. At the next, and final, stage of our descent through the rocks we shall enter on another world of plants, wholly unfamiliar to the student of recent Botany.

CHAPTER VI

THE EARLY DEVONIAN, THE AGE OF THE OLDEST KNOWN LAND FLORA. PLANTS FOR THE MOST PART SIMPLE, BUT HIGHER TYPES PRESENT ALSO

THE RHYNIE DISCOVERIES; STRANGE AND SIMPLE PLANTS, NOT REFERABLE TO ANY EXISTING CLASS. THE QUESTION OF THE ORIGINAL TRANSMIGRATION FROM SEA TO LAND

BEARING OF EVIDENCE FROM FOSSIL PLANTS ON EVOLUTIONARY PROBLEMS

We have now got down to the Early Devonian, the Age of the oldest Land Flora of which we have any adequate knowledge. The change from the Upper to the Early Devonian period is the last and oldest of our great transformations, so far as they are known to us. A still greater and earlier change—the transmigration from Sea to Land—undoubtedly occurred, but *how* it occurred is necessarily a matter of hypothesis.

The Middle and Lower Devonian Floras, so far as we know, were similar in general character, and we may treat them together. In the main, the plants of this early period, of which we are only now beginning to have any satisfactory knowledge, were of simple and unfamiliar types. But there is evidence that among these archaic forms some plants of far higher organisation were already present. The most famous of these, now known as *Palæopitys Milleri*, was discovered nearly eighty years ago by the great Scottish geologist, Hugh Miller, who was deeply impressed by the revelation of so advanced

a type at so low an horizon. It may be of interest to quote his own words, from his book "Footprints of the Creator"; written as a counterblast to that famous work of a pre-Darwinian evolutionist, "The Vestiges of Creation." Miller's book was originally published in 1847, the "Vestiges" three years earlier.

The author is picturing the researches of the geologist into the remote past under the image of a voyage of exploration into uncharted seas. He says: "Our voyage, like that of the old fabulous navigators of five centuries ago, terminates on the sea in a thick darkness, beyond which there lies no shore and there dawns no light. And it is in the middle of this vast ocean, just where the last zone of the Old Red leans against the first zone of the Silurian, that we have succeeded in discovering a solitary island unseen before—a shrub-bearing land, much enveloped in fog, but with hills that at least look green in the distance. There are patches of floating seaweed much comminuted by the surf all around it; and on one projecting headland we see clear through our glasses a cone-bearing tree." [1]

In these days, people no longer record their discoveries in such poetic language! Miller added: "This certainly is not the sort of arrangement demanded by the exigencies of the development hypothesis." For that very reason the discovery, no doubt, appealed more to him than it did to his successors in the Darwinian period. The sections were redescribed by McNab in 1870, without figures; [2] (Miller's own figures are rather vague), [3] and nothing more has been done till now, when a full investigation has just been completed. [4]

Hugh Miller somewhat exaggerated the age of his

[1] Hugh Miller, "Footprints of the Creator," edition of 1861, p. 198.
[2] McNab, 1870. This author is responsible for the name.
[3] Miller, *l.c.*, p. 194.
[4] Kidston and Lang, 1923. Their results have now been published. After reading the paper, I see no reason to alter what is said in the text, though the authors are more cautious.

"cone-bearing tree"; it is now assigned to the Middle and not the Lower Old Red Sandstone (Devonian). It may still prove to be the oldest known Gymnosperm. I have had the opportunity of examining some sections of what is no doubt the same species (kindly sent by Dr. Kidston). The structure appeared to me to be that of a well-organised Gymnospermous stem, if we use the term "Gymnospermous" to cover the possibility that the plant may have been a Pteridosperm. At any rate, it represents a very advanced type of anatomy.

Having recorded the presence of this high form in the Early Devonian Flora, we may now go on to consider the remarkable plants specially characteristic of that age, and distinguished on the whole by their surprising simplicity of form and structure.

Among these plants, one of the first to be recorded was Sir William Dawson's *Psilophyton*. The type-species, *P. princeps*, was discovered by him in the Lower Devonian of Gaspé, Canada, in 1859, and has since been recognised in beds of various Devonian horizons, in many countries, such as the United States, Scotland, Norway, Germany and Belgium.

We now have every reason to accept Dawson's account of his plant as substantially correct, but for a long time it was received with little favour by botanists. It is not so many years since a doubt was expressed by a high authority whether it was worth while to keep up the genus *Psilophyton* at all, so little was thought of it then. Now, however, recent discoveries have so largely confirmed Dawson's results that *Psilophyton* has become the type of a newly-recognised Class of vascular plants, the Psilophytales of Kidston and Lang, and must rank as one of the most important of fossil plants. It is the old story of "the stone which the builders rejected!"

Psilophyton will best be considered after we have spoken

of the Rhynie discoveries, which have thrown much light on its nature. Our present accurate knowledge of some of the simple Early Devonian plants is essentially due to the investigation of the Rhynie chert-bed. The locality is in Aberdeenshire, and the bed was discovered by the geologist Dr. Mackie in 1913. The plants have been thoroughly worked out, with singular skill and judgment, by Dr. Kidston and Prof. Lang, whose results are recorded in their remarkable series of memoirs.[1]

The chert-bed, which is not later than of Middle Old Red Sandstone age, is of considerable interest in itself. It represents an ancient, fossilised peat-bed, or rather series of peat-beds; the successive layers of peat, crowded with organic remains, are separated by sandy layers. It belongs to an active volcanic period, and it is highly probable that the silica-containing water, which from time to time overflowed the peat-bed, and caused the petrifaction, was emitted by hot springs or geysers.

The plants, during life, may have suffered somewhat from the volcanic surroundings, for the investigators are inclined to attribute certain wounds which the specimens bear to heat. The conditions, however, were extremely favourable for preservation after death; the plants, in many cases, are still found standing upright, as they grew, and both external form and inner structure are well exhibited. Thus these relics of an ancient land-flora have come to be some of the best known of all fossil plants. We must bear in mind, however, that we are dealing with a limited and very special Flora, the vegetation of an old peat-bed, growing under conditions not by any means advantageous, and therefore not necessarily to be taken as typical of the plant-life of the period.

The species of vascular plants from Rhynie at present known are four in number, grouped in three genera—*Rhynia*, named after the locality, *Hornea*, named in

[1] Kidston and Lang, 1917–1921.

honour of the former distinguished head of the Scottish Geological Survey, and *Asteroxylon*, which means "star-wood." *Rhynia* and *Hornea* are placed together in

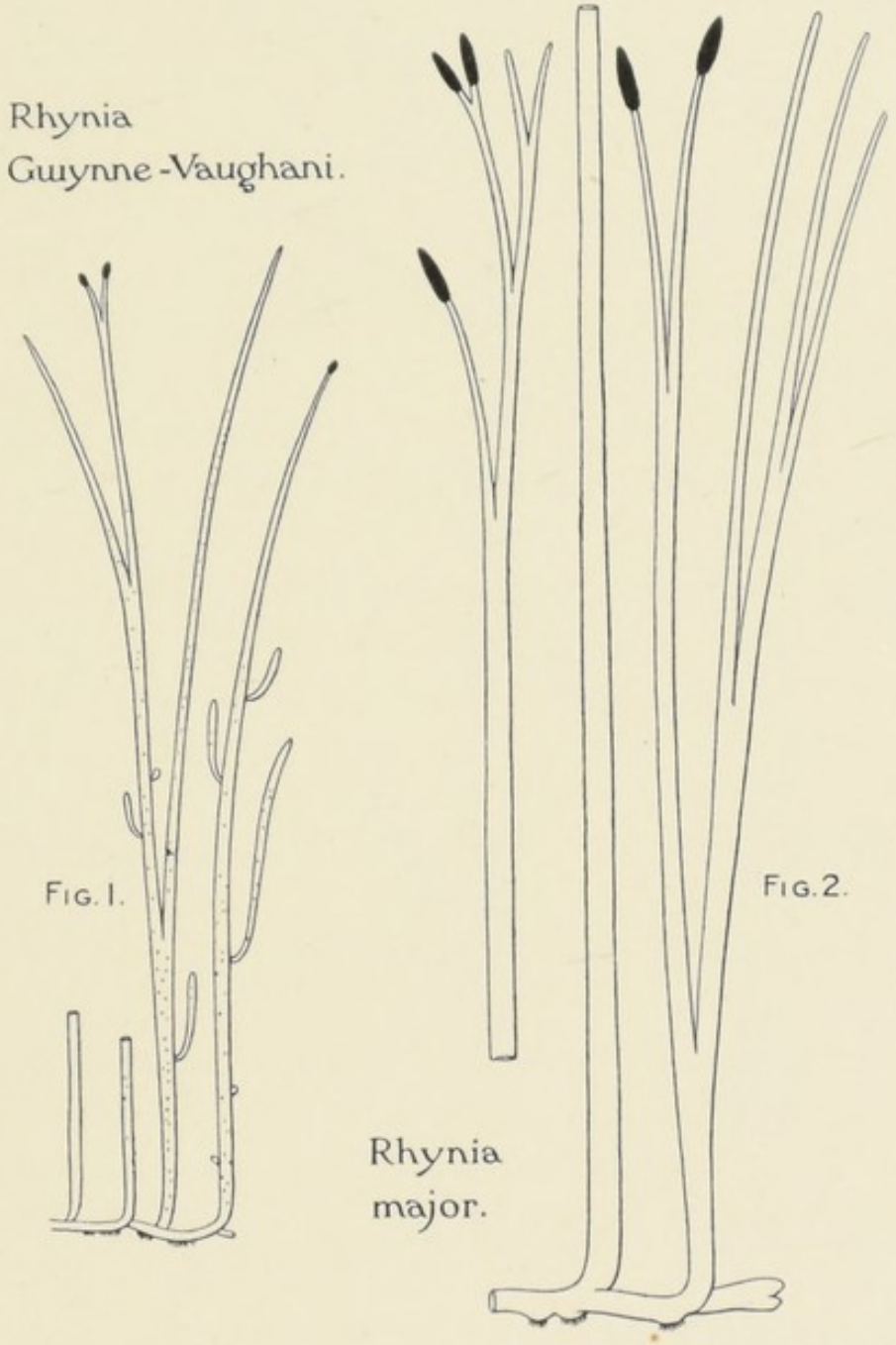

Fig. 58.—Restorations of Rhynie Plants. Fig. 1: *Rhynia Gwynne-Vaughani;* shows creeping, hairy rhizome, forked aërial stems, adventitious branches, dots indicating the hemispherical outgrowths, and terminal sporangia. Fig. 2: *R. major;* shows the simpler organisation, without adventitious branches or outgrowths. Reduced.
From Kidston and Lang.

the family Rhyniaceæ, and are the simplest of any known vascular plants. *Asteroxylon* was more advanced, and will be considered later (Figs. 58 and 59).

There are two species of *Rhynia*, *R. Gwynne-Vaughani*, named after that able Welsh botanist, the late Prof.

Fig. 59.—Restorations of Rhynie Plants. Fig. 3: *Hornea Lignieri*; shows the tuberous, hairy rhizome, the forked aërial stems and the terminal sporogonia, some of which are themselves forked. Fig. 4: *Asteroxylon Mackiei*; shows the creeping, hairless rhizome, the transitional region, and the branched, leafy, aërial stems. On the right, above, a supposed fertile shoot, bearing small terminal sporangia, is indicated, but detached. Reduced.
From Kidston and Lang.

D. T. Gwynne-Vaughan, and *R. major*. The larger species was somewhat the simpler of the two.

Rhynia major was a wholly leafless and rootless plant. It had an underground stem or rhizome, from which the vertical aërial shoots arose; the rhizome bore absorbent hairs, but there is no sign of any differentiated root. Both the creeping rhizome and the upright stem branched by forking—no appendages of any kind were present on the stem. The slender, cylindrical, branched stem may, with perfect justice, be described as a thallus, quite comparable to that of many familiar seaweeds (Fig. 58). The plant attained a height of eight inches or more. At the ends of some of the aërial branches, large spore-sacs, nearly half an inch long, were borne.

But, strangely simple as the plant was in its external configuration, the structure shows that *Rhynia* was of vascular status and manifestly adapted to land-life. Both rhizome and stem were traversed by a slender vascular strand, with wood in the middle and a delicate tissue, regarded as phloëm, on the outside (Fig. 60). The tracheides are of the annular kind, such as are usually found in the first-formed part of the wood in ordinary plants.

The epidermis of the aërial stem bore stomata of perfectly typical structure, but few in number. Thus the plant, possessing both "breathing pores" and conducting tissue, was fully equipped for life in the air, as distinguished from the submerged existence of seaweeds.

R. Gwynne-Vaughani was, in two respects, somewhat more complex than its larger relative. In the first place, the stem, instead of being perfectly smooth, bore a number of hemispherical outgrowths (Fig. 60). They have been regarded as rudimentary leaves, but the later observations of Kidston and Lang throw great doubt on this interpretation, for it appears that the outgrowths were only developed late in life, usually as new formations beneath the stomata, and thus formed no part of the original organisation of the plant.

However that may be, the outgrowths became of great importance in certain cases, for they were often the seat of formation of additional branches, quite apart from the normal forking of the stem. This is the second and more important point in which *R. Gwynne-Vaughani* differed

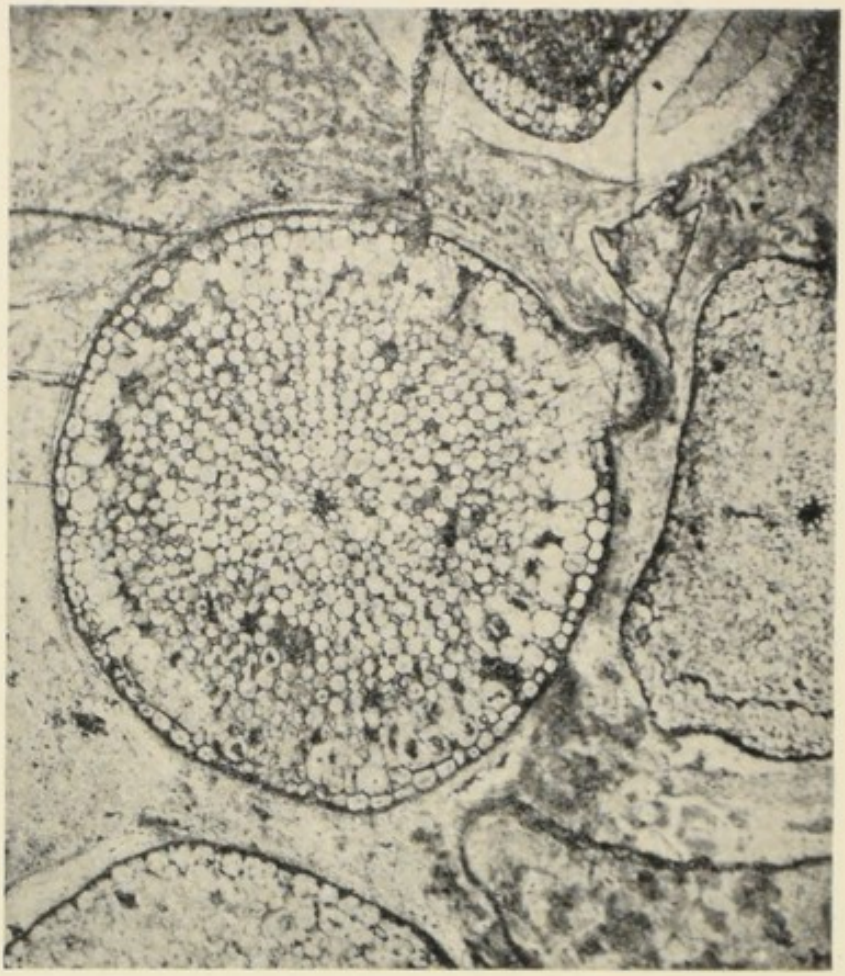

FIG. 60.—*Rhynia Gwynne-Vaughani*. Transverse section of stem, showing the minute central vascular strand, the radially seriated inner cortex, the large-celled outer cortex, and the epidermis. On the right, a hemispherical outgrowth is shown. (× about 25.) Scott Collection 3133.
From a photograph by Mr. W. Tams.

from *R. major*. The extra, or adventitious, branches thus formed were usually without any vascular connection with the main stem; they often became detached, affording a ready means of vegetative propagation.

Apart from the two points just mentioned, the two species of *Rhynia* agree in everything except size.

Passing on to the reproductive organs, the spore-sacs

or sporangia were borne, as we have seen, on the ends of the finer branches of the stem or thallus. The sporangium had a fairly complex wall, several cells thick, and contained a great number of spores (Fig. 61); they

FIG. 61.—*Rhynia major*. Transverse section (somewhat oblique) of sporangium. The palisade layer of the wall is well shown on one side, and in the cavity are many spores. (× about 14.) Scott Collection 3130. From a photograph by Mr. W. Tams.

are so well preserved that the spore-membrane must have had the same tough, resistant nature as in the spores of the higher Cryptogams now living. This is evidence that the spores were adapted to dispersal in the air; they are quite unlike the delicate reproductive bodies of sea-weeds. The spores are often found still grouped in fours,

showing that they were developed in the same way as in Ferns or Mosses at the present day. So far as observed, all the spores were of one kind.

The next genus, *Hornea* (Fig. 59, 3), was just as simple a plant as *Rhynia major*, but on a smaller scale. The chief peculiarity of its vegetative structure is that the rhizome, instead of being stem-like, was thick and tuberous; it has been compared to the protocorm formed, at an embryonic stage, in the development of some of the Club-mosses. The anatomy of the stem was essentially like that of *Rhynia*.

The chief interest of *Hornea* lies in the fructification, which was remarkable in more ways than one. The spore-sacs terminated certain branches of the stem; their wall was very little differentiated; in fact the spore-sacs were simply the ends of branches, enlarged to contain the spores; often the sporangium itself is forked just like an ordinary branch. This is the first point of interest, for it shows that in these old and simple plants the sporangium was not a distinct organ, but just the end of a branch, modified for spore-bearing purposes.

The other interesting feature in the spore-sac of *Hornea* is that it contained a central column of sterile tissue, over-arched by the dome-shaped spore-bearing layer (Fig. 62). This is exactly the arrangement found in the capsule of the Bog Moss (*Sphagnum*) and a few other Mosses at the present day. This feature has strongly suggested that *Hornea* and its allies, though vascular plants, may have had some affinity with the Moss stock.

In another fossil, from Norway, of Lower Devonian age, described by Dr. Halle, the same structure is found, while the form of the whole fruit is much more Moss-like than in *Hornea*. Taking the two plants, *Hornea* and Halle's *Sporogonites*, together, we cannot help recognising a certain analogy, to say the least of it, between these early Vascular Plants and the Mosses. This is a point

of considerable interest, for previously the fossil record had thrown no light at all on the history of the Bryophytes.

The Rhyniaceæ, simple as they are, show such a remarkable combination of characters that they have been

FIG. 62.—*Hornea Lignieri.* Longitudinal section of sporogonium. *w*, Wall of sporogonium at the apex; *s*, spore-bearing zone with numerous spores; *c*, sterile columella, over-arched by the spore-bearing zone. (× about 20.) Scott Collection 3136.

From a photograph by Mr. W. Tams.

placed by different botanists in three of the great subkingdoms of plants. Kidston and Lang, whom I have followed, assign them to the Pteridophytes, because the spore-bearing generation was a vascular plant; my late friend, Dr. Newell Arber, in whose time only *Rhynia*

had been described, referred the genus to Thallophytes, on the ground of its undifferentiated, thalloid stem; the family has also been included under Bryophytes, on account of the characters we have just been discussing presented by *Hornea* and *Sporogonites*. This is a very extraordinary position and shows that the Rhyniaceæ are a unique race of plants.

It is possible to interpret the family as a synthetic group, related to both the Vascular Cryptogams and the Bryophytes, while still retaining some of the characters of an original Algal stock. Such a conclusion is justified on the facts actually known, but, on the other hand, we can scarcely feel quite certain that the remarkable simplicity of the Rhyniaceæ was wholly primitive. The peat habitat, as already pointed out, was not a very favourable one, and it is possible that plants growing under such conditions may have already undergone a certain amount of reduction. However that may be, the fact remains that the Rhyniaceæ are the simplest and among the most ancient of land-plants known to us.

The third Rhynie genus, *Asteroxylon*, was a very different sort of plant from the Rhyniaceæ and much more advanced; in fact, in outward appearance it must have been something like a Club-moss (Fig. 59, 4). *A. Mackiei*, the only known species, was a fairly large plant, with a main stem sometimes over a centimetre in diameter. It was clothed with small, simple leaves (Figs. 59, 4 and 63) and branched freely, both laterally and by forking. The underground parts consisted of a branched rhizome, like that of *Rhynia*, but bearing no hairs. Although a leafy plant, *Asteroxylon* was entirely without any differentiated root.

While the rhizome had the same simple anatomy as a stem of *Rhynia*, the structure of the aërial stem in *Asteroxylon* was much more complex. The wood of the large stele was stellate, in transverse section, with long, forking

rays (Fig. 63, *t.s.*); this was surrounded by a continuous zone of phloëm. Leaf-traces were given off; a trace

FIG. 63.—*Asteroxylon Mackiei.*—Stems in longitudinal and transverse section. *l.s.–l.s*, Stem in longitudinal section, bearing a number of leaves. The round bodies in the lower part are fungus-spores. *t.s*, stem in transverse section, showing the stellate wood, and the trabecular layer of the cortex. Other transverse sections also shown. (× about 6.) Scott Collection 3139. From a photograph by Mr. W. Tams.

entered the base of each leaf, but got no further, the blade thus being left without any vascular supply. In this respect, *Asteroxylon* was rather rudimentary, as is

also shown by the want of any proper roots. A third point, suggestive of a somewhat primitive simplicity, is the structure of the wood. Though well developed, it was little differentiated, for all the tracheides alike were of the spiral type.

It is unfortunate that the evidence as to the reproductive organs of *Asteroxylon* is less satisfactory than in the case of *Rhynia* and *Hornea*, for the fructifications attributed to the plant have never been found in connection with it. Peculiar naked branches, quite different in structure from the vegetative stem, have been found in close association with some specimens; and again, associated with these doubtful branches, sporangia have been observed (Fig. 59, 4.) They are widely different from those of the Rhyniaceæ, and rather resemble the spore-sacs of certain Carboniferous Ferns. For example, the sporangia occurring with *Asteroxylon* had a definite dehiscence, like Fern-sporangia, while no such provision exists in the spore-sacs of the Rhyniaceæ.

I cannot undertake to say whether the reproductive organs provisionally assigned to *Asteroxylon* really belonged to the plant or not. It looks as if they did, but there is no proof.

The uncertainty as to the reproductive organs of *Asteroxylon* leaves the affinities of the plant quite doubtful. In habit and anatomy there are decided resemblances to the Lycopods and also to the family Psilotaceæ, a small group of tropical and sub-tropical epiphytes, only known in the recent Flora. If, however, we assign the supposed fertile branches and sporangia to *Asteroxylon*, we must recognise an approach to the Ferns also, and the plant assumes a most surprising synthetic character.

It may be mentioned that Kidston and Lang are inclined to identify *Asteroxylon* with *Thursophyton*, a Middle Devonian genus (resembling a Club-moss) otherwise only known in the form of impressions. Previous writers,

however, have attributed to species of *Thursophyton* fructifications of a Lycopodiaceous nature, totally different from the supposed reproductive organs of *Asteroxylon*. Thus the whole question remains in a difficult position, and can only be solved when further facts come to light.

In the meantime, *Asteroxylon* is placed in the Psilophytales; though on a much higher grade of organisation than the Rhyniaceæ, a relatively primitive position is indicated by the points already mentioned—the absence of roots, the imperfect vascular supply of the leaves, and the want of differentiation in the tracheides.

We must now return for a moment to the old genus *Psilophyton*, which clearly has much in common with the newly-discovered Rhynie fossils. *Psilophyton* bears a certain resemblance to *Asteroxylon*, for the main stem bore spines, which have been compared to the leaves of the latter genus. The nature, however, of the spines is doubtful.

Dawson pieced together his more or less fragmentary specimens, and gave a restoration of the plant, which may now be accepted as probably, on the whole, correct. He pictured his *Psilophyton princeps* as having upright, forked stems, of somewhat slender proportions, springing from a creeping rhizome. The stouter stems bore the little spines already mentioned, but the upper, fertile branches were usually naked. The tips of the young branches were curled in a circinate manner, like the budding fronds of a Fern—a curious point, which is well attested.

The spines, scarcely equal in length to the diameter of the stem, seem hardly worthy of the name of "leaves," but comparison with other Devonian plants, such as *Arthrostigma*, in which similar spines are more developed, tends to confirm their foliar nature. Arber compared them to the hemispherical outgrowths of *Rhynia Gwynne-*

Vaughani; the latter, however, are not known to assume the spine-like form.

The fructification of *Psilophyton* was in the form of long, oval spore-sacs borne, often in pairs, on the ends of the finer branches. They bear a considerable external resemblance to the sporangia of *Rhynia*.

There is some evidence as to the anatomy of *Psilophyton*. Dawson described and figured sections of the "rhizoma"; they show an almost exact agreement with the stem-structure of *Rhynia*, but it must be remembered that the rhizome of *Asteroxylon* was of the same simple type of anatomy. Sometimes specimens of *Psilophyton*, preserved as impressions, have the epidermis intact, and in such cases, according to unpublished observations by Mr. W. N. Edwards, stomata are found, as in *Rhynia*, but more numerous.

Psilophyton has been made the type of the class Psilophytales, and there can be no doubt as to its general affinity with the petrified plants of the Rhynie chert-bed. Whether it was more nearly allied to *Rhynia* or to *Asteroxylon* is, however, an open question. Arber identified *Psilophyton* and *Rhynia*, regarding the latter as simply the petrified condition of the former. On the other hand, Kidston and Lang not only consider these two genera as distinct, but separate *Psilophyton* from the Rhyniaceæ and put it provisionally in the same family with *Asteroxylon*. The latter view assumes that the spines of *Psilophyton* are leaves, comparable to those of *Asteroxylon*. Further, the spineless fertile branches of *Psilophyton* are compared to the supposed fertile branches, without leaves, attributed to *Asteroxylon*. This comparison is, of course, of doubtful value, as continuity has not been proved in the case of *Asteroxylon*. We must be content to recognise the fact that *Psilophyton* was a real plant, not a myth or a chimæra, as some have fancied, and that it had a definite relation to the vascular plants

of Rhynie. There is some evidence that *Psilophyton* goes back to the Silurian.

Besides the four representatives of the Psilophytales above described, a great many plants of lower rank were found at Rhynie, chiefly fossil Fungi, of which a remarkably fine collection was obtained. There were also a certain number of Algæ. The most remarkable association is with a plant of a genus long known by the name of *Nematophycus* (otherwise *Nematophyton*). The genus is represented in Silurian as well as in Devonian rocks; in some cases the plants were of gigantic size, the stem reaching, it is said, a yard in thickness. The structure is an elaborate system of interwoven filaments, much like what we find in many Algæ, such as the Laminarias or the larger Siphoneæ. The plants have therefore for many years been accepted by most botanists as Algæ. At the present day such great Algæ are only known as seaweeds.

Now if *Nematophycus* was really a marine Alga, it is an extraordinary thing to find it in an inland peat-bed like that of Rhynie, which geologists tell us was far away from the sea (perhaps 200 miles or so) in Early Devonian times. It is, however, quite possible, as Kidston and Lang point out, that the species of *Nematophycus* generally were marsh plants rather than seaweeds. This does not diminish the mystery, for in later times such plants, of a high Algal type, are totally unknown in any terrestrial habitat. The species of *Fucus* which are able to make themselves at home among the herbage of salt-marshes by the sea can scarcely be considered as a case in point. The association of *Nematophycus* with vascular land-plants in an inland locality suggests an unexpected degree of adaptability in the higher Algæ of those days.

There are a number of Early Devonian land-plants

known as impressions, but with little or no evidence as to structure. They were of various habits. Two or three may be mentioned.

Arthrostigma, a Lower Devonian plant, of wide distribution, was much like a big *Psilophyton*, with thick stems, sometimes over an inch in diameter, occasionally branched, and studded with large, hooked spines. The stem contained a vascular strand, and the vein sometimes detected in the spines was probably of the same nature.

Thursophyton, already mentioned, looked like a Club-moss, and was originally described as a *Lycopodites ;* until the question of its fructification has been cleared up, it is useless to speculate on its affinities.

Pseudosporochnus, from Bohemia, had a thick, somewhat bulbous stem, dividing up above into numerous fine branches. Its appearance is remarkably like that of an Alga, but the stem is known to be vascular.

In the Early Devonian Flora there is no satisfactory evidence for the presence of Ferns, in the ordinary sense of the word. Branched stalks, which might represent the naked rachis of a frond, have often been described, but in no case is there any sign of a lamina. The old idea, that the preservation was at fault, hardly holds good, for, as Halle points out, this supposition amounts to arguing in a circle, since bad preservation is only assumed because a lamina is absent ! It is, of course, possible that some of these naked branch-systems may have really belonged to Ferns, comparable, for example, to the Carboniferous *Stauropteris*, in which the rachis was actually without any lamina. But it is practically impossible to distinguish such supposed fronds, when only preserved as impressions, from a branched thallus such as that of a *Rhynia* or a *Psilophyton*, especially when we remember that circinate vernation occurred in the latter.

It is a curious point that we have such inadequate evidence for the existence of Ferns in Early Devonian

times, while, as Hugh Miller's discovery showed, plants of a much higher grade, very probably of Gymnospermous affinities, were already represented.[1]

The Transmigration

We have referred more than once to the great Transmigration from Sea to Land which the plant-kingdom must at some time or other have accomplished. How far may we regard the simplest vascular plants of the Early Devonian, for example the Rhyniaceæ, as in any degree representing the original transmigrants which first invaded the land from the sea? Dr. Church, in his able essay on "Thalassiophyta and the Subaërial Transmigration,"[2] written without any reference to fossil evidence, imagines the transmigration to have taken place at an immensely earlier period than the Devonian. If the event happened once for all, he is probably right in this. Still it is not impossible that some of the plants living in Early Devonian days may have retained transmigrant characters; the Alga-like habit of the Rhyniaceæ and a few other plants of the period makes such a supposition a tempting one. But, as already pointed out, we do not know for certain that the simplicity of these plants was altogether primitive.

Dr. Church gives a vivid picture of the transmigration as he conceives it to have happened. He imagines a universal ocean, covering the whole face of the earth. Probably most geologists will not agree with this hypothesis. He supposes this ocean first peopled with swarms of minute, free-swimming organisms—this was the Plankton stage. Then as the sea-bottom began to rise in places, the stage of mere plankton was in time succeeded by the "Benthic" stage, the period of rooted seaweeds. This went on for ages, and the seaweeds attained a very high grade of organisation. Lastly, as the land began to emerge

[1] On other Devonian plants, see Arber, "Devonian Floras," 1921.
[2] A. H. Church, 1919.

from the waters, the marine vegetation became in part converted into a terrestrial Flora.

If, on the other hand, the universal ocean never existed, the conditions of transmigration would have been very different. We may suppose that in an age previous to the appearance of Life the surface of the globe was thrown into folds; the sea would then have filled the hollows, while the ridges formed the continents, and sea and land would be equally old.

Under such circumstances the transmigration might have started at any time, as soon as the plants themselves were ready for the venture; it might also, when once initiated, have gone on continuously over long periods. The invasion would no doubt have been checked in time, when the land was fully occupied, for any newly emerging areas would then have been more easily peopled from the existing Land Flora than by fresh transmigrants from the sea.

To return to Dr. Church's views. Believing that the land was colonised by an already highly developed marine vegetation, he holds that the greater part of the differentiation shown by the higher land-plants had already been attained among the ancient seaweeds from which they sprang. Stem and leaf were already marked out as distinct organs; roots, in the form of hold-fasts, had appeared, while conducting strands (though only of the nature of phloëm) already formed part of the internal equipment. The life-history, too, is believed to have already shown the alternation of generations so characteristic of the higher plants.

All these features are such as we find at the present day among the more advanced of the existing seaweeds. It is not supposed, however, that the ancestors of the land-plants belonged to any of the surviving marine families.

When the transmigration occurred, the organs already differentiated merely required, on Dr. Church's hypothesis,

to become adapted to subaërial conditions. In particular, the transpiration-stream had to be set going by the provision of a water-conducting tissue (wood) and also of stomata; the roots, which had served only for fixation, were now required to take on the new function of absorption; the spores, hitherto fitted only for transport by water, now needed a resistant cell-wall to equip them for the changes and chances of dispersal by air.

It will be noticed that the Devonian Rhyniaceæ were in some ways actually simpler plants than Dr. Church's transmigrant Algæ are supposed to have been. They possessed, indeed, water-conducting strands and stomata, and their spores were adapted for transport by air; on the other hand, they were without leaves or differentiated roots.

Against the theory of the origin of land-plants from highly organised transmigrant Algæ, it has been urged that such plants, already elaborately adapted to the conditions of marine life, would have been too specialised to adopt an entirely new mode of existence on dry land. It is suggested that lower organisms would presumably have proved more adaptable, and that the Land Flora may have made a fresh start from humble beginnings, and have differentiated, on the land itself, the organs fitted for land conditions.

All this is pure speculation; the chief fact on which we have to rely is that some of the Early Devonian land-plants, though vascular, are much like seaweeds in their external characters. The Rhynie discoveries, so far as they go, tend to support, in a general way, the view that the vascular plants came from fairly high Algæ.

Closely connected with this subject is the important question whether the different races of vascular plants sprang from one ancestral stock already vascular, or had an independent origin from different lines of marine vegetation.

On the whole, one is impressed by the independence of the various phyla of vascular plants, all through the geological record. The Lycopods nowhere show any approach to the other lines of Pteridophyta, though it is possible that they may become merged in the Psilophytales, as we trace them back to the older Devonian. The Sphenophylls and Horsetails are doubtless related, and may well be branches of one phylum, but the Articulatæ as a whole remain perfectly distinct throughout. All we know of the beginning of the Ferns is that in Early Devonian times there were plants with a naked branched rachis, possibly the precursor of the Fern-frond. The so-called "Seed-Ferns," on present evidence, appear as a quite independent phylum, which never joins the true Ferns, unless it be in some very early stock, comparable to the Psilophytales. It seems certain that the higher Palæozoic Gymnosperms (Cordaitales) had a definite affinity with the Seed-Ferns, but at present we know nothing of a common ancestry.

Thus a polyphyletic theory of the distinct origin of, at least, the main phyla, Lycopods, Articulatæ, Ferns, and perhaps the Seed-plants is evidently quite tenable. At the same time, our knowledge of the oldest Land Flora, in spite of the great progress in recent years, is still so limited that we cannot be certain that there may not have been a common initial group of vascular plants, from which all the later lines diverged. This monophyletic hypothesis is maintained by Halle, with special reference to the lines of the Lycopods and the Ferns.

He suggests that *Psilophyton Goldschmidtii*, a species described by him, in which the lateral branches are rather sharply differentiated from the main axis, may represent an intermediate stage between a mere branched thallus and a stem bearing fronds. This is in accordance with Lignier's hypothesis of the thalloid origin of the leaf in the Fern series. Halle also reminds us that "the circinate vernation

of the Fern-fronds is paralleled in the branches of *Psilophyton princeps*." He thus recognises a possible relation of the *Psilophyton* group to Ferns on the one hand, as well as to Lycopods on the other, and points out that "from this point of view the whole pteridophytic stock would be monophyletic, Lycopsida and Pteropsida being derived from a common form already vascular." [1]

Kidston and Lang concur, generally, in Halle's monophyletic view. They tell us that "the geological age and succession of the Early Devonian plants are, on the whole, consistent with the origin of various groups of vascular Cryptogams from a common source." [2] In a later memoir they maintain this opinion, while pointing out that the evidence is not such as to establish it beyond question.[3] The Bryophytic features shown in the Rhyniaceæ and in *Sporogonites* further suggest "the convergence of Pteridophyta and Bryophyta backwards towards an Algal stock." [4]

On the other hand, the polyphyletic theory is also well represented. Dr. Arber, in his "Devonian Floras," maintained that the Sphenopsida (Articulatæ), Pteropsida and Lycopsida were three distinct lines of descent, each derived from Thallophytic Algæ of a distinct type. Arber took an original view of the little group Psilotales, which he regarded as "a quite independent race, also of Algal origin, which appeared on the scene long after the other races . . . possibly in Mesozoic times or even later." [5] This would make four separate lines altogether.

Dr. Church, without reference to the fossil evidence, arrives at a highly polyphyletic conception of the course of evolution. He believes that "all the main lines of what is now Land Flora must have been differentiated in the Benthic Epoch of the sea (*i. e.* as Algal lines)"; and

[1] Halle, 1916, p. 39.
[2] Kidston and Lang, Part III, 1920, p. 673.
[3] *Ibid.*, Part IV, 1921, p. 843.
[4] *Ibid.*, Part III, 1920, p. 675.
[5] Arber, 1921, pp. 72, 87.

he even adds that possibly "existing groups of Land Flora may trace back their special line of progression to the flagellated life of the sea, wholly independently of one another." [1] He applies this extreme view especially to the phyla of the Lycopods and Ferns. Thus, on Dr. Church's hypothesis, not only did land-plants generally attain their morphological differentiation before the trans-migration, but each phylum may have run through the whole course of its evolution independently, from the original plankton phase onwards.

We have clearly not yet got the data necessary to enable us to decide between the monophyletic and poly-phyletic theories. On the one hand, the geological history seems to emphasise the distinctness of the main phyla; on the other, the revelation of the existence in Early Devonian times of a surprisingly simple race of vascular plants may favour the idea of a common origin on land.

Another consideration is the agreement among the existing Pteridophyta in many important points of mor-phology and structure. Among characters common to all the recent phyla (however diverse otherwise) are: the alternation of generations, with the asexual sporophyte as the predominant partner; the mode of development of the spores; the structure and development of the sexual organs; the histology (though not the grosser anatomy) of the vascular system, and the structure of the stomata. Such community of organisation may well be regarded as indicating a common origin from a stock already adapted to land conditions.

Dr. Church, however, attaches little importance to reproductive processes as evidence of systematic affinity. He considers these phenomena rather as inevitable phases which every phylum must pass through. He says: "The greatest fallacy of Classification in the nineteenth century has been to mistake a 'reproductive phase' for indication

[1] Church, 1919, p. 41.

of affinity. Broader lines of affinity are expressed more clearly in somatic equipment. . . . Newer reproductive phases are progressive and follow an inevitable 'sequence,' in all phyla the same." [1]

The "inevitable sequence" may, it seems, hold good for some somatic characters also, as, for example, for the wonderfully conservative stomata. Thus we cannot tell how far the characters in question are marks of affinity and how far they simply indicate a like response to like conditions. Hence the fundamental question of the single or multiple origin of the races of vascular plants must still be left open.

We have already considered the Moss-like characters shown by *Hornea* and *Sporogonites*, and have referred to the opinion that the Rhyniaceæ should be classed as Bryophyta. Kidston and Lang have pointed out that the three phyla, Pteridophyta, Bryophyta, and Algæ, are undoubtedly brought nearer together by the Rhynie discoveries. Prof. Bower says on this point: "Long ago it was remarked that the widest gap in the sequence of plants was that between the Bryophytes and the Pteridophytes. It is within this gap that the newly-discovered fossils take their natural place, acting as synthetic links, and drawing together more closely the whole sequence of land-living, sporangium-bearing plants." [2]

Among the Rhynie fossils it is *Hornea* which shows clear indications of Bryophytic affinity, but when this is granted it is easy to extend the conclusion to *Rhynia* also; in fact, the relation of the two genera is so obvious that we cannot avoid doing so. In the case of *Sporogonites*, our knowledge is limited to the capsule and stalk. As Halle points out, we do not know whether the fossil represents a theca and seta, like that of a Moss, or merely the fertile part of a branched stem or thallus, such as we

[1] Church, 1919, p. 43.

[2] Bower, 1920, p. 9.

find in *Psilophyton* and the Rhyniaceæ. This will prove an important point, if it can ever be decided, for on it may turn the question whether true Bryophytes existed or not in Early Devonian times.

In *Hornea*, at any rate, the sporogonia were borne on the branches of a vascular thallus. It is the first case of the kind known, and various interpretations are possible. We may suppose that the Moss-like structure of the fructification is merely a parallel development, without phylogenetic significance. If, on the other hand, we assume that a real affinity to the Bryophytes is indicated, at least two hypotheses are open to us. We may consider that a plant like *Hornea* was either on the up-grade or the down-grade of evolution.

According to the old "antithetic" theory, the sporophyte was an intercalated generation, developed by the elaboration, in the course of evolution, of the zygote or fertilised egg-cell. On this view, the simpler forms of the Bryophytic sporogonium were supposed to represent, more or less closely, the earlier stages of elaboration. The seta was a later product, and the rooted stem of the Pteridophytes a much later one still.

Those who adopt this theory might regard a plant like *Hornea* as being on the up-grade of development, from a simple, Bryophyte-like stage towards the Pteridophytic type of sporophyte. The unbranched seta of the Bryophyte would, on this hypothesis, have already become elaborated into a branched stem or thallus, bearing many sporogonia, though differentiated roots had not yet appeared.

The alternative view, long ago maintained by Haberlandt, is that the Moss-sporophyte owes its origin to reduction from some higher type. The difficulty has always been to see what it could have been reduced from. *Hornea* may perhaps supply a clue. We may suppose that such a plant was already on the down-grade, and might

by further reduction and condensation have led on to the simple sporophyte of the Bryophytic series. In other words, *Hornea* (and no doubt *Rhynia* also) might be called a Bryophyte which still retained the branched thallus and numerous spore-sacs of an ancestral stock.

We may imagine either that this assumed ancestral stock was an early and generalised race of Pteridophytes, or that it belonged to the Algæ. On the latter supposition, the Bryophytes and Pteridophytes would have run a distinct course from the first, as required by the general polyphyletic theory, discussed above.

On the whole, the hypothesis of reduction from an Algal stock seems somewhat the most probable. It accords best with the Alga-like habit of the Rhyniaceæ, and with the imperfect differentiation of the sporogonia in *Hornea*. That the spore-sacs should be but little modified from branch-endings seems natural enough if the plants came from Algæ, but would be hard to explain if they were derived from Bryophytes, in which we are accustomed to meet with a well-defined sporogonium. At present, however, our data are still but few, and the safest plan is to recognise the presence of Bryophytic features without committing ourselves to any phylogenetic interpretation.

Later Stages of Evolution

A like caution is needed when we come to consider the more advanced stages of evolution. The subject bristles with difficulties, and no certainty is attainable. We have already seen that, on a review of the whole evidence, the former belief in the origin of the Pteridosperms (and through them of the Seed-plants generally) from Ferns must be given up. We have no reason to believe that Ferns, as botanists understand the name, are any older than the Pteridosperms themselves; the points in common between the two groups now appear to be homoplastic, and not indicative of the descent of the one from the

other. Thus the origin of the Seed-plants is still an unsolved problem.

We may suppose that the Spermophytes had a common origin with the Ferns from some early stock, perhaps no more advanced than the Rhyniaceæ. But that is pure conjecture. All that we know is that plants with an anatomical structure suggesting Gymnospermous affinities already existed in Middle Devonian times, and were therefore about contemporary with the simplest known land-plants as found at Rhynie. For all we know, the Seed-plants may be as ancient as any Vascular Cryptogams.

It is evident that our present conception of the immense antiquity of the Spermophyta must reopen the whole question of the origin of the seed-habit. It has been held, since the classical days of Hofmeister, that the Seed-plants must have been derived from heterosporous Vascular Cryptogams. This may be the case, but it now seems certain that they did not come from any known heterosporous group, or from anything at all similar. The unknown ancestors may not have belonged to the Vascular Cryptogams at all, in the ordinary sense of the term. Thus the knowledge gained from the investigation of the geological history of plants, far from solving our problems, in this case rather opens up new ones, or reopens questions we had thought settled. At the same time, we may congratulate ourselves that a new life is thus breathed into the dry bones of the established morphology.

Another question is whether the Seed-plants, whatever their origin may have been, all belonged to one stock. If this was so, we should naturally fix on the "Seed-Ferns," the most primitive known Spermophytes, as most nearly representing the common source. At the same time, we must admit that we have no proof, as yet, that the Pteridosperms are any more ancient than the Cordaitales. In the Upper Devonian the latter are represented by the

very highly organised *Callixylon*, an ally of *Pitys*. Our knowledge of Pteridosperms of the same age is rather vague, though no one will doubt that they existed. In the Early Devonian we have *Palæopitys Milleri*, which may have belonged to some group of Gymnospermous affinity. The recent researches now published do not help to determine its more exact position.

There is a good deal in common between Pteridosperms and Cordaitales. So far as the anatomy is concerned, the older (and some of the later) members of the latter class have strands of centripetal wood in the stem, strongly suggestive of the characteristic structure of the *Lyginopteris* and *Calamopitys* families among the Pteridosperms. But the most important point is the organisation of the seed, which appears to be essentially the same in the Cordaiteæ and certain of the Pteridosperms. For these reasons, it seems fairly clear that there is a real affinity between the two classes.

This conclusion has, however, been disputed by some recent authors. Among those who have discussed the question are Prof. Chamberlain, Dr. Margaret Benson, and Prof. Sahni. Prof. Chamberlain regards the Cycadophytes and Coniferophytes, as he calls them, as two distinct lines, the former commencing with the Pteridosperms, the latter with the Cordaitales. He derives the Pteridosperms from Ferns, in accordance with the view then current, but leaves the origin of the Cordaitales an open question; he considers their cone-structure as a bar to any near relationship with the Pteridosperm and Cycad stock.[1]

Prof. Sahni divides the Gymnosperms (in the widest sense) into two groups, the Phyllosperms, with the seeds borne on leaves, and the Stachyosperms, with seeds borne on the stem.[2] The former include the Pteridosperms and

[1] Chamberlain, 1920.

[2] This character is dependent on the assumption that the seed in these plants is immediately borne on a reduced axillary shoot. It is quite possible, however, that the seed may be really *leaf-borne* in both divisions.

Cycads, the latter the Cordaitales, Conifers, and Maidenhair Trees.[1] He admits the probability of a common origin of the two divisions from a megaphyllous stock, but lays stress on the marked differences and the absence of intermediate forms.

Besides the main distinction drawn from the fructifications, Prof. Sahni attaches importance to the great diversity in the leaves of the two series. The difference between the compound frond of a Pteridosperm and the simple leaf of a *Cordaites* is no doubt striking, but is it any greater than the difference between the foliage of a Hemlock and a Hare's-ear within the family Umbelliferæ? Neither does the leaf of a Maidenhair Tree differ more from the frond of the Pteridosperm *Aneimites* than *Adiantum reniforme* from *Adiantum Capillus-Veneris*. Leaf-characters (apart from anatomy) are very inconstant and of little taxonomic value.

The difference in the way the seeds are borne in the two divisions is undoubtedly extreme, and there is as yet nothing to bridge the gap. Our knowledge of the fructification of Palæozoic Stachyosperms is, however, limited to the narrow *Cordaites* type.

Dr. Margaret Benson accepts Prof. Sahni's two main lines of Gymnosperms, but goes much further than he, and regards them as totally distinct.[2] She, too, relies on leaf-characters as well as on those of the reproductive apparatus, and even associates the Stachyosperms with the Sphenopsida, while the Phyllosperms are grouped with the Ferns. It is suggested that "possibly if we knew the history of the Cycad seed we could show that the resemblance to a Stachyosperm seed is the result of relatively recent convergence."[3] As we have seen, however, the Cycad type of seed was common to Cordaitales and Pteridosperms in Palæozoic times.

Without entering further into controversy, the opinion

[1] Sahni, 1920, p. 297. [2] Benson, 1921. [3] *l.c.*, p. 87.

may be expressed that on the ground both of anatomical structure and seed-characters, a real relation between Pteridosperms and Cordaitales is well established. On the anatomical side, besides the gradation in the primary structure already mentioned, there is the fairly close agreement in the character of the tracheides. In a group like the *Eristophyton* section of *Calamopitys*, the anatomical features of the two lines are so nearly balanced that the affinity of the plants is still disputed.

That the seeds of Cordaiteans and Pteridosperms are often indistinguishable is a fact already emphasised. The difficulty of conceiving a transition from the seed-bearing fronds of the latter to the cones or catkins of the former is no doubt great, but we must bear in mind that the Cycads are generally admitted to have come from the Pteridosperms, and most of the Cycads have well-defined cones. Those of the Cordaitales may be more complex, but that is a question which would carry us too far into debatable regions of morphology.

Assuming that the Pteridosperms and the Cordaitales were related, we cannot be certain what was the nature of the relation. We have no proof at present that the whole body of the Seed-plants passed through the Fern-like phase represented by the Pteridosperms. We may, however, hold, on the available evidence, that the two lines had a common origin.

Most botanists are now agreed that the origin both of the Conifers and the Maidenhair Trees is to be sought among the Cordaitales. We need not discuss the theory, once strongly held, but no longer very seriously maintained, that the Conifers sprang from Lycopods. We can, however, only derive them from the Cordaitales in the most general sense. There are no grounds for tracing them from the special family Cordaiteæ, which in fructification and especially in seed-characters were very different from the Conifers. We have, in fact, no evidence as to

any particular family from which the great modern group may have arisen. Perhaps Dr. Gordon's suggestion of an affinity between the ancient *Pitys* race and the Araucarians may afford a clue.

On the other hand, the Maidenhair Trees, in their seeds, fructifications, and general habit, show a nearer relation to the Cordaiteæ themselves, and may have sprung from some not very remote source.

Since the discovery of the Pteridosperms it has generally been recognised that the Cycadophyta were descended from this great plexus of relatively primitive Seed-plants. Before that time, the French School used to derive the Cycads from the *Sigillaria* group. The view now current seems well established. The female *Cycas*, with its frond-like, stem-borne carpels, is still almost a Pteridosperm! The foliage in some recent Cycads recalls that of the "Seed-Ferns," and there are some anatomical points of agreement.

There is evidence that Cycadophyta already existed in the later Palæozoic times; stems are known with a structure somewhat intermediate between the *Lyginopteris* type of Pteridosperm and some of the Cycads. We cannot, however, asume that this was the line of descent, for in some other respects the Medulloseæ (Neuropterideæ) may have stronger claims to relationship with the Cycadophytes.

It is a curious fact that the Cycadaceæ themselves appear to have more in common with the Palæozoic stock than the Mesozoic Cycadeoids. It does not seem difficult to imagine how the true Cycads may have come from the "Seed-Ferns"; in fact, no other origin is so probable. The Cycadeoids, on the other hand, present great difficulty in their fructifications. There is nothing known among Pteridosperms to foreshadow in any degree the flowers of the Mesozoic race.

The stamens of the Cycadeoids are, it is true, sometimes quite frond-like and at least offer an analogy with the pollen-bearing fronds of the "Seed-Ferns." The

gynæceum, however, is so wholly remote from the simple Pteridosperm arrangement that no comparison is possible, without the most extreme assumptions of reduction. While in Pteridosperms the seed was borne on a little-modified pinna of the ordinary frond, in Cycadeoids there is no evident female sporophyll at all; each seed is borne at the summit of a mere stalk, of quite doubtful homology, while the interseminal scales are equally inexplicable. Further, the seed itself is so modified, in relation to the development of the complex fruit, as to have little in common with the widespread seed-type of Palæozoic Gymnosperms and the true Cycads. Here we are face to face with an apparent gap in evolution which no amount of hypothesis will serve to fill until we have gained more knowledge. It is true that the vegetative organisation of most Cycadeoids bears so manifest a relation to that of the Cycadaceæ that we are naturally led to assume a like origin for the two lines. But we must bear in mind that it is just the older Cycadeoids, the Williamsonians, which show in some of their members the widest departure from the prevailing Cycadean type. This point has already been considered in Chapter III.

It must be admitted that the argument for a Pteridosperm origin is much stronger in the case of the Cycadaceæ than in that of the Cycadeoids. But it must hold good for both groups, if we are justified in associating the two under Cycadophyta.

It has been pointed out in Chapter IV that there is a sharp break between the Palæozoic and Mesozoic Floras. We cannot fairly discuss the relation between plants of the two periods without taking note of views recently expressed by an eminent palæobotanist, Prof. Seward. If the conclusions which he suggests were justified, it would be futile to seek for any genetic relation between Palæozoic and Mesozoic land-plants.

The question is discussed in Prof. Seward's Hooker Lecture for 1922.[1] The subject of the lecture is the Mesozoic Ferns and their distribution. The author's more general conclusions, though applying immediately to the Ferns, must hold good, if established, for other classes of land-plants.

Prof. Seward says: "It is not my aim to connect the Mesozoic records with the Palæozoic; between the two there appears to be a wide gulf"; "the relationship between the two ages may not be as close as it is usual to assume. In the latter part of the Triassic period we seem to pass with remarkable suddenness to a new phase of plant evolution; one cycle is completed and another has begun."[2]

Further on he becomes more explicit: "The opinion may be hazarded, rash though it is, that the selected representatives of Mesozoic Ferns mentioned to-day are not directly connected by descent with Palæozoic ancestors."[3] His representatives include the most prominent Mesozoic families of Ferns, so that the view suggested implies that, so far as the Ferns are concerned, there was no evolutionary connection between the plants of the two ages.

The following passage expresses the author's somewhat revolutionary ideas in their most general application: "As new lands emerged from the sea, new lines of evolution may have been inaugurated; the transmigration of marine plants which Dr. Church conceives as a single act may have been recurrent. It may be that we shall never piece together the links in the chain of life, not because the missing parts elude our search, but because the unfolding of terrestrial life in all its phases cannot be compared to a single chain. Continuity in some degree there must have been, but it is conceivable that plant-life viewed as

[1] Seward, 1922. The full title runs: "A study in Contrasts; the Present and Past Distribution of certain Ferns."

[2] *l.c.*, p. 231.

[3] *l.c.*, p. 237.

a whole may best be represented by separate and independent lines of evolution, or disconnected chains which were never united, each being initiated by some revolution in the organic world." [1]

From this statement it is clear that the author's theory is intended to apply to the Mesozoic Flora generally, and not merely to certain families of Ferns. The suggestion evidently is that at the beginning of the Mesozoic Age new lines of plant-evolution started fresh out of the sea. Hence the Mesozoic land-plants would have had no genetic connection with the Palæozoic land-plants, but would form disconnected chains, which began from new starting-points, owing their origin to recurrent transmigration from sea to land.

Thus the continuity, which Prof. Seward recognises as necessary, would only have been maintained through the repeated intervention of marine plants—presumably Algæ. Between the land-plants as such there was no continuity from one period to the other. One is reminded of Dr. Arber's suggestion that the Psilotales may have had a late and independent origin from Mesozoic Algæ; Prof. Seward's hypothesis, however, is not limited to any special group, but is applicable to the whole Land Flora.

The bold suggestion of Prof. Seward is, I think, to be welcomed. It brings home to us the fact that the evolution of plants, so far as the record shows, does not present a uniform progression, but rather a series of diverse periods of vegetation, each with a character of its own.

As Prof. Seward says in a later address: "Persistence of type, and from time to time the apparently sudden influx of new types, rather than a steady progressive development, are among the outstanding features of the history of plant-evolution." [2] And at the same time we are compelled to face the conviction that we really know

[1] *l.c.*, pp. 237–238. [2] Seward, 1923, p. lxxx.

very little of evolutionary history. We may exhaust our ingenuity in trying to derive Mesozoic land-plants from their Palæozoic predecessors, and then we are told, on good authority, that there may very likely be no connection at all between them! This is, at any rate, a wholesome check on speculation.

But, all the same, Prof. Seward's suggestion scarcely seems credible. If we suppose that the Mesozoic Land Flora, or any considerable part of it, arose from a new transmigration of marine plants, we may surely expect to find among the Mesozoic vegetation some sign of the invaders, in the form of relatively primitive, Alga-like types, comparable, let us say, to the Devonian Psilophytales. So far as I am aware, nothing of the kind has ever been observed. The Mesozoic land-plants have nothing primitive about them; they show no sign whatever of a fresh start. On the contrary, they are, according to our standards, more advanced than the Palæozoic groups with which we compare them. That there is a gap is evident, but the apparent break of continuity strikes one as suggesting a sudden jump ahead, rather than a fresh start from below.

Prof. Seward lays great stress on the prevalence of arid, desert conditions in Triassic times. Here the clue may indeed be found. The marked change in the environment may well have proved unfavourable to the great races which had hitherto been dominant, and may have given the opportunity to somewhat divergent groups, previously in the background, to "increase and multiply and replenish the earth."

In this sense there may have been fresh starting-points among the land-plants themselves, but at present there seems to be no evidence for a renewed invasion from the sea.

The question of a possible relation between the Mesozoic

Cycadophytes and the Angiosperms has been sufficiently discussed in Chapter III. That the true Flowering Plants may have sprung from a common source with the flowering Cycadeoids is at least a tenable hypothesis. At the same time, it is quite possible that the problem may prove more complex than we thought; in particular, we may have to reckon with Mr. Hamshaw Thomas's strange and apparently advanced fruits from the Middle Jurassic, mentioned in Chapter II.

We will not pursue further questions of phylogeny, for a discussion of the probable lines of evolution of other groups, such as the Cryptogams, from the Palæozoic onwards would involve too much botanical detail for a course like the present. On a general survey, it is clear that while an evolutionary sequence, in a broad sense, is unmistakable in the records of the past, our knowledge is still far too fragmentary to admit of the construction of anything like a genealogical tree for the vegetable kingdom.

Some Problems of Evolution

There were some special problems connected with Evolution to which we referred in Chapter I; we may now briefly consider how far the evidence from extinct plants has a bearing on these questions.

With reference to Dr. Guppy's theory that there have been two distinct eras of evolution, the era of origination and the era of differentiation, we must bear in mind that he was only concerned with the Angiosperms. As we have seen, most of the Angiospermous families already existed by Upper Cretaceous times, if not earlier. Therefore the period of origination of new types, on Dr. Guppy's view, must have preceded that time. We know nothing whatever of the origin of the Angiospermous families, so the field is open to speculation.

But as already pointed out, during the Mesozoic ages, when the Angiosperms were presumably in course of

evolution, the world was overspread with Cycads, Conifers, and Ferns; there is no doubt that these dominant groups were rich in species, and well in the "differentiation" stage, at a time when the Flowering Plants were, *ex hypothesi*, still in the stage of origination or mutation. And if we went still further back, we should find the same state of things—Palæozoic Pteridosperms, Ferns, Lycopods, etc., differentiating into hosts of species, at a time when the Cycadophytes and Conifers were, apparently, only beginning.

It thus seems impossible to doubt that the "differentiation" of species (Dr. Guppy's second stage) has gone on at every period, in one group or another. Consequently it could not have been dependent on the special conditions prevailing at any particular time.

Whether there was really any such sharp distinction between the differentiation of the smaller groups and the origination of the larger, as Dr. Guppy supposes, remains an open question. No doubt in each phylum the evolution of new types went on more actively at some periods than at others. But the new types may have themselves come from small beginnings, and some of the merely specific novelties of the later differentiation may conceivably prove to be the starting-points of new phyla. We really know nothing about the matter.

There seems to be no reason why important morphological changes should not be initiated as specific characters. Instances may easily be found. The differentiation of special sporophylls is an important step. Yet in a genus like *Osmunda*, we find distinct fertile fronds in some species and not in others, and, further, both conditions occur in forms of the same species (*O. regalis*).

The strobilus is another similar morphological feature of admitted importance. But in the genus *Lycopodium*, as everybody knows, there are species with a well-marked strobilus, while in others there is no such differentiation.

the fertile and sterile regions being quite alike. The same differences appear to have existed within the Palæozoic genus *Selaginellites*.

Heterospory, again, is of undoubted morphological importance. Yet we find some species of *Calamostachys* heterosporous, while in most of the species, otherwise quite similar, all the spores were still of one kind.

While, as Prof. Bateson has reminded us, we are still ignorant of the mode of origin of new species, it seems hardly worth while to postulate some different unknown origin for the larger groups. All the same, Dr. Guppy's theory serves a useful purpose, for it suggests a comparison of successive geological periods, with reference both to their fertility in new types and their richness in species. This should prove an interesting line of investigation.

Grand'Eury's ideas on the mutation of species among fossil plants are summed up in the following lines, which have been freely translated: "The permanence of species and the rapid transitions which nevertheless connect them among themselves suggest the idea that their mutations have acted in the manner of metamorphoses, or even perhaps, in opposition to the well-known axiom, by leaps, certain consecutive forms presenting different characters between which the mind can conceive no middle term; the cases of sudden changes are by no means rare." [1]

Grand'Eury had worked for a quarter of a century on the Flora of the French coalfields, and possessed an unrivalled knowledge of the plants as they occur *in situ*. Hence his opinions deserve the utmost respect, especially when we consider that he began, as he tells us, with the contrary idea of a continuous variation. It would be out of place to attempt any serious criticism here, nor is the present writer in a position to undertake such a task.

[1] Grand'Eury, 1906, p. 4.

It need only be pointed out that the succession of species in a continuous series of beds, does not necessarily represent the course of their evolution. What we actually find may rather be the result of migration, and the origin of the new species may have taken place elsewhere.

Further, if we admit Grand'Eury's conclusions, we may remember that the distinctions between Carboniferous species are not, as a rule, so very marked, and indeed are often difficult, for those who are not specialists, to recognise. Such moderate mutations as Grand'Eury believed in are by no means beyond credit, and would not very seriously affect our conception of evolution.

On the other hand, Zeiller's belief that discontinuity is shown, whatever the rank of the groups examined, involves the suggestion of a sudden origin for families or classes, a change altogether without analogy in the present order of things. On this question, it may be appropriate to quote some words of Darwin's:

"There are, however, some who still think that species have suddenly given birth, through quite unexplained means, to new and totally different forms; but, as I have attempted to show, weighty evidence can be opposed to the admission of great and abrupt modifications. Under a scientific point of view, and as leading to further investigation, but little advantage is gained by believing that new forms are suddenly developed in an inexplicable manner from old and widely different forms, over the old belief in the creation of species from the dust of the earth." [1]

I believe that this powerful statement still holds good. The only justification for the theory of violent saltations is to explain apparent breaks in the continuity of evolution—such gaps are frequent enough, as all must

[1] Darwin, "Origin of Species," 6th edition, p. 424. 1878.

acknowledge. But really the assumption of sudden saltations is no explanation, for there is no evidence for such violent changes except the existence of gaps in the record. If such evidence proves anything, it proves too much. Take, for example, the oldest indubitable Angiosperms, namely, the highly organised Dicotyledonous woods from the Lower Greensand. They are wholly unconnected with any known type of plant which went before. Yet it would be quite absurd to suppose that such typical members of the highest class of plants could have sprung, by some sudden saltation, from any of the preceding groups. Zeiller himself would have been the last to imagine anything so unreasonable.

Zeiller, however. as already stated, maintained that discontinuity was shown at all grades and whatever might be the rank of the groups examined.[1] He spoke, as Prof. Seward has since spoken, of "discontinuous chains,"[2] but while the latter author explains their want of continuity by the hypothesis of fresh incursions from the sea, Zeiller regarded it as evidence of evolution by leaps.

The only safe assumption appears to be this: that discontinuity proves nothing except our ignorance. There are gaps in the record which no conceivable saltation could have bridged, and thus the supposed explanation leaves us in the lurch just where our difficulty is greatest.

The question of morphological characters may be considered in connection with that of adaptation. There can be no doubt that plants, as far back as the Upper Devonian, were just as adaptive in their organisation as those of the existing Flora, though in certain respects adapted to different conditions. Potonié's idea that some of the Carboniferous plants showed imperfect adaptation to mechanical strains has been shown to be baseless:

[1] Zeiller, 1907, p. 21.

[2] *Ibid.*, 1909, p. 656.

Potonié failed to realise that in many Palæozoic stems and petioles mechanical stability depended on the peripheral fibrous system and not on the relatively weak central column of wood. The latter was no doubt mainly adapted to the conducting functions.[1]

Attention has already been called to the very perfect mechanical adaptation of the Cordaitean type of leaf. If Schwendener, who first worked out in detail the engineering principles on which the stems and leaves of Monocotyledons are constructed, had applied the same methods to the leaves of these Palæozoic trees he would, no doubt, have found equally good illustrations of his laws.

We are still unable to explain completely the conducting mechanism of the wood in living plants. It is worth pointing out, however, that one of the most highly differentiated wood-structures among Gymnosperms is found in the Upper Devonian *Callixylon*, with its neatly localised pitted areas on the tracheid-walls. It has been said that this ancient wood is as perfect as that of *Pinus*, though on different lines.

Among more special adaptations, one may recall the pappus of the Lower Carboniferous seed *Thysanotesta*, the pollen-chamber and elaborate system of water-supply in Palæozoic seeds generally and the sheltering of the stomata in the hair-clothed furrows of a *Lepidodendron* leaf.

It is unnecessary, however, to labour the argument for adaptation in ancient plants; the whole structure, as briefly sketched in the preceding pages, is a manifest mechanism, or system of mechanisms, just as in recent plants, only adjusted to the conditions of the time. The position is precisely the same whether we are dealing with members of the living Flora, or with Carboniferous vegetation.[2]

[1] Scott, 1909, p. 4.

[2] For an interesting discussion of adaptation in a still older race, the calcareous Siphoneæ (Algæ), see Julius Pia, 1922.

The case, however, may be different when we get back (if we ever do) to the beginning of a new phase of plant-life. Can we say that the Rhynie plants were as well adapted as their successors? They all did without roots, and *Rhynia* and *Hornea* dispensed with leaves also. The case of the two organs is not quite parallel, for the branches of the rhizome no doubt answered the purpose of roots, though not differentiated as such, while leaves, in the Rhyniaceæ, were absent altogether.

If we assume that the Rhyniaceæ represent in some degree the organisation of the original transmigrants from the sea, we may suppose that they had not yet fully adapted themselves to the new subaërial conditions, and still showed the imperfect mechanism which one might perhaps expect in Algæ which had taken to the land. That they were sufficiently well adapted for practical purposes is obvious from the fact of their existence, but they may still have been at a rudimentary grade of organisation.

The Rhynie plants were peat-dwellers, and possibly their modest habitat may have enabled them to flourish, in spite of an inadequate equipment. In other localities, as we know, plants of an infinitely higher organisation were already in the field. Of course we cannot be certain that we have really run down, in the Rhyniaceæ, a case of primitive imperfection; the plants may already have suffered reduction, in response to the local conditions, and this appears the more probable when we reflect that among the Algæ themselves there are plants with quite well-differentiated leaves (e. g. *Sargassum*). But at any rate we must admit the possibility, or even certainty, that when plants first invaded the land their adaptation to the new conditions would naturally have been imperfect compared with subsequent attainments.

How, then, does it stand with the question of "morphological characters"? It may be doubted whether Fossil

Botany is in a position to throw much light on the subject. We are seldom so fortunate as to be allowed to assist at the first origin of an important morphological feature, and only important features concern us here, for trivial specific differences lie outside our subject. In spite of all the growth of our knowledge, we are still quite ignorant of the origin of such organs as the flower or the seed.

In the Lycopod phylum, it is true, seed-like bodies appear among plants not otherwise differing from the ordinary representatives of the group; these bodies, however, seem to have nothing to do with the true seeds of the Spermophyta. Such as they are, they are evidently adaptive structures, and afford no support to the idea that the seed is to be classed as a morphological character.

As we have seen above, important morphological differentiations, such as the specialised sporophyll, the strobilus, and heterospory, may occur, as specific characters, in certain genera, whether recent or fossil. In the cases of *Osmunda* and *Lycopodium*, the differentiation may be of relatively recent origin, for in the former both conditions occur within the limits of a single Linnean species, while in the latter there are transitional forms between the undifferentiated fertile shoot and the definite strobilus. In such cases the morphological advance, in its first stages, can have been of little or no functional importance, and may perhaps be reckoned as a non-adaptive morphological character.

In the more striking case of heterospory, appearing within the Palæozoic genus *Calamostachys* (and possibly in other Calamarian genera), we have what looks like a sudden advance, presumably of considerable adaptive significance. But it is not at all certain that we have really got the first stages. If, as has been suggested, the abortion of certain spores (met with in homosporous species) favoured the development of certain survivors into megaspores, the first origin of heterospory in this family may

have been accidental, *i. e.* independent of functional value. Of course, by "accidental" we mean due to more or less unknown internal causes, so that, in other words, we may say that an important adaptive differentiation may have started as a merely morphological character.

Better examples, however, of such characters are found in certain features common to extensive groups of plants. Thus throughout the long series of the Articulatæ, from their first known beginnings in the Middle Devonian down to our own day, the whorled leaves have been a constant feature. The infinite play of adaptation has left the ground-plan untouched from first to last.

So, too, with the microphyllous character of the Lycopods. This runs essentially all through this great phylum, whether we consider a minute *Selaginella* or a gigantic *Lepidodendron* tree. The leaves are a mechanism; the stem is a mechanism; and so is the plant as a whole. But the general design and scheme of the machine were laid down, once for all, ages ago, and have never been departed from. In this sense we may speak of "morphological characters," though every organ of the plant is adaptive.

Facts such as those just referred to would also seem to illustrate the doctrine of the mechanical morphologists, "that variation [whatever we may understand by this term] has proceeded on definite and orderly lines." The changes during the long course of evolution of the Articulatæ, however great they have been, have never affected the underlying verticillate scheme, but have all been on lines consistent with the ground-plan. So too with the microphylly of the Lycopod stock. We may regard this constancy as evidence of a definite orderliness in the evolution of these lines.

Of course it is not the same characters which are constant in every group. In the Ferns, for example, though

megaphylly prevails, this is often departed from. Again, phyllotaxis, so constant in the Articulatæ, is variable among the Lycopods, whorled and spiral arrangements occurring in nearly-related species.

It is often difficult or even impossible to decide whether the constancy of a particular character throughout a large group is due to internal causes or to the controlling action of natural selection. The seed, once established, preserves a considerable degree of uniformity throughout wide classes, such as the Cycads (apart from the Mesozoic Cycadeoids), the Conifers, and even the Angiosperms. The constancy is more marked, in each group, in the details of development than in the mature structure. So too with various other organs, such as the archegonium and antheridium, the annulate sporangium, or the Angiospermous stamen. All follow very similar lines throughout extensive groups. In all such cases we may have to do with a certain rigidity, inherent in the race, restricting, in certain directions, the amplitude, and determining the lines of change.

But it is equally allowable to suppose that in such cases, where we are concerned with organs essential to the continued existence of the race, their constancy is due to their functional value, that such organs are kept fairly constant, because any change in their essential features would impair their efficiency, and thus endanger the survival of the race. It is quite impossible to decide whether the mechanical or the selectional factor has played the greater part in determining such lines of evolution.

The title of the present book is "Extinct Plants and Problems of Evolution." The feeling with which one concludes this brief survey is that we know a good deal about extinct plants, but not enough, as yet, to throw much light on the problems of their evolution. New

discoveries constantly raise new questions and seldom solve those which were already before our minds.

I may venture, however, to maintain that a consideration of all the evidence, which, in brief outline, we have had before us, while not favouring any exaggerated Darwinian ideas such as the so-called "omnipotence of Natural Selection," yet is, on the whole, favourable to the old, truly Darwinian conception of an orderly and gradual evolution without sudden and inexplicable leaps, an evolution in harmony with the uniformitarian principles established by Lyell.

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