

February 8, 1894.

Sir JOHN EVANS, K.C.B., D.C.L., LL.D., Vice-President and Treasurer, in the Chair.

A List of the Presents received was laid on the table, and thanks ordered for them.

The following Papers were read :—

- I. "Further Observations on the Organisation of the Fossil Plants of the Coal-Measures. Part I. *Calamites*, *Calamostachys*, and *Sphenophyllum*." By W. C. WILLIAMSON, LL.D., F.R.S., Emeritus Professor of Botany in the Owens College, Manchester, and D. H. SCOTT, M.A., Ph.D., F.L.S., F.G.S., Honorary Keeper of the Jodrell Laboratory, Royal Gardens, Kew. Received December 30, 1893.

(Abstract.)

I. *Calamites*.—The first part of the paper gives a detailed account of the vegetative structure of *Calamites*, on the basis of a renewed investigation, in which special attention has been directed to developmental questions.

The petrified specimens which have formed the chief material for our observations have their structure preserved in great perfection, and it has been possible to make a thorough study of their organisation at various stages of development.

The primary structure of the young stem, before growth in thickness has begun, bears a striking resemblance to that of *Equisetum*. The stem was jointed, with a whorl of leaves at each node. Although in the specimens showing structure the leaves have not been found in connexion with the stem, yet their position is evident, from that of the leaf-trace vascular bundles, the course of which can be clearly traced. Their distribution follows the same general lines as in *Equisetum*, but shows some additional complications.

In the internode, a single circle of collateral vascular bundles surrounds a relatively large pith, which is solid in some of the smallest twigs, but became fistular in all the larger stems.

In comparing the vegetative organs with those of *Equisetum*, it is evident that only the primary structure of *Calamites* can be taken into consideration.

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One important point to be decided was the nature of the canal, which in both genera accompanies each vascular bundle on its inner side. In *Equisetum* these canals, as is well known, mark the position of the first-formed tracheæ of the wood, which have become disorganised owing to the growth of the surrounding tissues.

We have now proved that the "internodal" canals of *Calamites* are of precisely the same nature. Here also the canals have been constantly found to contain the annular and spiral tracheæ of the protoxylem, which in longitudinal and oblique sections can be recognised with perfect distinctness.

At the nodes the canals are usually interrupted. The primary nodal xylem consists of a girdle of short, often reticulate, tracheæ, and closely resembles the corresponding structure in an *Equisetum*.

The foliar bundles pass out horizontally at the nodes. Their tracheæ are spiral, scalariform, or reticulated.

In many of the specimens the primary cortex is preserved. Its outer layers are usually more or less sclerotic, and in a few cases alternate hypodermal bands of sclerenchyma and parenchyma can be distinguished, as in many *Equiseta*.

On the whole, the primary structure of the stem of *Calamites* is substantially that of *Equisetum*.

In *Calamites*, however, secondary tissues were always added, and are only absent from the youngest branches. We have no evidence for the existence of any Calamite without secondary growth. The process, which went on essentially as in normal Dicotyledons, or Gymnosperms, has been observed at all stages. In the best-preserved specimens the cambium, with the thin-walled phloëm outside it, can be recognised.

The primary medullary rays separating the bundles are in some specimens prolonged, as parenchymatous tissue, through the secondary wood. In the type previously described as *Calamopitys* the principal rays consist of prosenchymatous cells, and the structure approaches that of *Calamodendron*.

In the majority of the typical stems of *Calamites* (= *Arthropitys* of Göppert) the principal rays become bridged over by interfascicular wood. In this case most of the radial series of parenchymatous elements die out towards the exterior, and are replaced by series of tracheæ. The exact manner in which this change takes place is discussed in the paper.

The wood consists of tracheæ, and of small secondary rays, the cells of which are usually upright. The tracheal elements appear not to be vessels, but tracheides; they may attain a length of 4 mm. The pits, which are bordered, are limited to the radial walls of the tracheæ, except in the most internal layers of the wood.

The innermost cells of the primary medullary rays underwent con-

siderable tangential dilatation, allowing of a certain increase in the diameter of the pith.

The cortical tissues attained a great thickness in the older stems, owing to the formation of abundant periderm. In one specimen the first origin of the periderm, by tangential divisions of the inner cortical cells, could be clearly traced.

A periderm-like layer was also formed on the surface of the diaphragms, cutting them off from the medullary cavity.

A number of specimens show the insertion of branches, on a relatively main axis. The branches were placed immediately above the node; often there were several in a whorl. Each branch usually lies between two of the leaf-trace bundles next below. The pith of the branch tapers towards the base, almost to a point, so that it is connected with the medulla of the parent stem by a narrow neck of tissue only. This gives rise to the characteristic conical form of those medullary casts which represent the pith-cavity of the basal portion of a branch.

In favourable specimens the continuity of the primary wood of the branch with that of the main stem can be demonstrated with certainty.

The branches were no doubt normal, not adventitious, appendages, and arose near the growing point. Subsequently both the base of the branch and the parent stem became coated by a common zone of secondary wood.

As the branch is traced, from below upwards, the diameter of the pith becomes larger, the number of the vascular bundles increases in the successive internodes, and the characteristic Calamitean structure is assumed. At a certain distance above the base the dimensions become approximately constant.

Many of the branches were abortive, or were at least cast off at an early age. This is proved by the fact that in many specimens the pith of the branch is enclosed towards the exterior by the secondary wood of the main stem.

From specimens shown to one of us by M. Renault, it appears that the roots, which were borne at or below the nodes, had the structure of *Astromyelon*. This fact necessitates a re-investigation of the fossils described under the latter name.

2. *Calamostachys*.—The homosporous *C. Binneyana* is first considered.

The morphology of the strobilus is well known. The axis bears alternate whorls of bracts and of sporangiophores. The bracts are coherent for a considerable distance from their base, forming the horizontal disc. Their free limbs turn vertically upwards, and extend at least as far as the second bracteal whorl above. The number of bracts in each whorl is about 12.

The sporangiophores are in verticils, placed midway between those of the bracts, and are usually about half as numerous in each whorl as the latter.

The sporangiophores are peltate, resembling those of *Equisetum*; each bears four sporangia on its lower surface, attached near the edge.

The structure of the axis of the strobilus has been studied in detail.

The central cylinder, or *stele* (which may be either obtusely triangular or quadrangular, as seen in transverse section), has a parenchymatous pith, of considerable relative size, around which are the collateral vascular bundles.

In the triquetrous form their number is 3 or 6; in the quadrangular type it is 4. The bundles are always placed at the projecting corners of the stele. On the inner side of each bundle is a gap, or irregular canal, in which the annular and spiral tracheæ of the protoxylem are contained.

The phloëm is very rarely preserved, but in one specimen could be clearly recognised.

The structure of the bundles, both in the internodes and nodes, is essentially similar to that of *Calamites*, the chief differences consisting in their small number and less definite canals.

In many of the axes a zone of secondary wood, of considerable thickness, was formed.

Vascular bundles pass out into each bract and sporangiophore.

In the latter the bundle forks twice, and each of the four branches runs out, through the peltate expansion, to the base of a sporangium.

The sporangial wall, as preserved, is usually a single layer of cells, which have their walls thickened in a manner resembling that of the "fibrous layer" of some anthers.

The spores are all of one kind. No trace of macrospores was found in any of the numerous strobili of this species which were examined.

The spores attain a diameter of about 0.09 mm. In some specimens they are isolated; in other sporangia they are still grouped in tetrads, each tetrad being enclosed within the wall of the mother-cell.

It is rare for all the four spores of a tetrad to be equally developed. As a rule, one or more of the sister-spores remained very much smaller than their neighbours, and were, to all appearance, abortive. The abortion of these spores must have allowed of an increased nutrition of the survivors, and thus have been of considerable physiological importance.

*Calamostachys Casheana*, Will., is the heterosporous species. Only two specimens are at present certainly known. The general morpho-

logy and anatomy of the strobilus are similar to, but not identical with, those of the homosporous *C. Binneyana*.

The macrosporangia and microsporangia were borne in the same strobilus, and in one case both kinds of sporangia were found on the same sporangiophore.

The diameter of the microspores is about 0.075 mm.; that of the macrospores is just three times as great.

In the macrosporangia, but never in the microsporangia, numerous abortive spores are constantly found. They are of variable size, but are always much smaller even than the microspores of the same plant. Their invariable presence in the macrosporangia, and equally constant absence from the microsporangia, leave little doubt that they were the abortive sister-cells of the macrospores.

These facts appear to throw some light on the origin of the phenomenon of heterospory in the genus *Calamostachys*. In *C. Binneyana* the abortion of certain sister-cells of the spores, involving the better nutrition of the survivors, had already begun, but still took place equally in all sporangia. In *C. Casheana* the same process, carried further in certain of the sporangia, rendered possible the development of specially favoured macrospores, which attained their relatively large size at the expense of their neighbours, which remained rudimentary. All analogy leads us to suppose that to these macrospores the formation of a female prothallus was entrusted. In the microsporangia no abortion appears to have taken place, and the spores attained a uniform small size.

The axis of the strobilus of *C. Casheana* has a well-marked zone of secondary wood, thus affording direct evidence of the occurrence of secondary growth in a heterosporous Cryptogam.

The affinities of *Calamostachys* are discussed at length. In neither of the species in question has the strobilus been found in connexion with vegetative organs. Other species however, e.g., *C. Ludwigi*, were borne on undoubtedly Calamarian stems.

The fructification of a true *Calamites* has been described in a previous memoir (Williamson, "Organisation of the Fossil Plants of the Coal-Measures, Part XIV," 'Phil. Trans.,' 1888). This strobilus differs from *Calamostachys* in the position of the sporangiophores, which were approximately axillary (instead of being placed in independent verticils, midway between those of the bracts), and also in the anatomy of the peduncle and axis, which was identical with that of the stem of a typical *Calamites*. To this fossil we now propose to give the name of *Calamites pedunculatus*.

The position of its sporangiophores is that characteristic of Weiss's genus *Palæostachya*.

The only certain fructification of a *Calamites* thus differs considerably from a *Calamostachys*. The differences, however, are not such

as to preclude a near relationship. A form described by M. Renault, under the name of *Bruckmannia Grand'Euryi*, unites the external morphology of a *Calamostachys* with the anatomy of a *Calamites*. It is therefore possible that the species of *Calamostachys* considered in this paper may have been borne on stems with Calamitean structure, but this cannot be proved until the strobili are found in actual continuity with the vegetative organs.

3. *Sphenophyllum*.—The habit of these plants is well known. The rather slender, jointed stem bore verticils of superposed leaves, the number of leaves in each verticil being some multiple of 3. The leaves were sometimes cuneate, sometimes dichotomously subdivided, sometimes linear.

The anatomy of several undoubted species of *Sphenophyllum* is now known, and there is no longer any doubt that some of the fossils described in previous memoirs under the name of *Asterophyllites* really belong to *Sphenophyllum*.

The first species described is *Sphenophyllum plurifoliatum* = *Asterophyllites sphenophylloides* of the former memoirs.

The number of leaves in each whorl was large, not less than 18. They were linear in form.

The axis is traversed by a solid vascular strand, triangular, as seen in transverse section, without any pith. The strand is triarch, with a group of narrow spiral and reticulate elements (protoxylem) at each angle. The primary wood of the stem was thus centripetal, and so far resembled that of most recent Lycopodiaceæ, with which, however, the genus has otherwise little in common.

Secondary growth in thickness took place constantly, and has been observed at every stage. The secondary wood consisted of radially arranged tracheæ (whether vessels or tracheides is doubtful) with strands of parenchyma between them. The longitudinal parenchymatous strands are connected by radially elongated cells, which, however, seldom form continuous medullary rays.

The cambium is excellently preserved in some specimens, a fact which removes all doubt as to the truly secondary character of the tissues in question.

The primary cortex and leaves were soon cast off by the formation of internal periderm. The older stems have a large amount of secondary tissue to the outside of the cambium. This is shown to consist partly of true phloëm, partly of internal peridermal layers, which in extreme cases formed a regular scale-bark.

A second species, *Sphenophyllum insigne* (= *Asterophyllites insignis*, Will.), is described. Its general anatomy agrees with that of the former species, apart from differences of detail. The most important structural peculiarity of *S. insigne* consists in the constant presence of continuous medullary rays in its secondary wood.

In the phloëm of this species large elements, closely resembling sieve tubes, are found.

The larger specimens, which have lost their primary cortex owing to the formation of periderm, have a very root-like transverse section. Some authors have therefore denied that they belong to *Sphenophyllum*, and have supposed that they are roots of some unknown plant. This is a mistake, for the large specimens have essentially the same structure as the smaller ones, which still retain the characteristic cortex and leaves of a *Sphenophyllum*. The intermediate conditions are also known.

Leaves had not been discovered in this species when the former account of its structure was given, in the earlier memoirs.

The recent researches of M. Zeiller have proved that the fructification previously described (Williamson, "Organisation, &c., Part XVIII," 'Phil. Trans.,' 1891) as *Bowmanites Dawsoni*, is that of a *Sphenophyllum*. In his specimens, strobili, agreeing in all respects with those of *Bowmanites*, are borne on the stems of the well known *Sphenophyllum cuneifolium*, Sternb. The fructification in question must therefore be transferred to the genus *Sphenophyllum*, and is here described under the name of *Sphenophyllum Dawsoni*.

The strobilus consists of an axis bearing numerous whorls of bracts, which are coherent for some distance from their base. The very long sporangiophores arise from the upper surface of the bracts, near their insertion, two sporangiophores corresponding to each bract. At the end of each sporangiophore a single sporangium is borne, which hangs down, parallel to the pedicel, somewhat resembling an anatropous ovule in position.

The axis of the strobilus is traversed by a triarch or hexarch vascular cylinder, essentially similar to that of the vegetative stem of *Sphenophyllum*. At every node vascular bundles are given off to the bracts. Each of these bundles, on entering the verticil of bracts, subdivides into three. The dorsal branch passes straight out into one of the free bracts. The two ventral branches of the bundle supply the two sporangiophores corresponding to the bract in question.

The bundle of the sporangiophore extends through its whole length, becoming thicker towards the apex, where it terminates at the base of the sporangium itself.

The cells of the sporangial wall are of great size near the base, and are very narrow at its opposite end, where dehiscence probably took place.

The spores are numerous in each sporangium, and are all of the same kind. There is at present no conclusive evidence for the existence of a heterosporous *Sphenophyllum*.

The morphological nature of the sporangiophore cannot be determined with certainty. The various possible views are stated in the

paper. For the present it seems best to regard this organ as simply a sporangium-pedicel, though there is no analogy among known Cryptogams for the presence of a vascular bundle in the stalk of a sporangium.

It appears that all species of *Sphenophyllum* in which the fructification is known, had essentially similar strobili, with pedicellate sporangia.

The genus *Sphenophyllum* cannot be placed in any existing family of Vascular Cryptogams. Anatomically there are some striking points of resemblance to Lycopodiaceæ, but the habit and fructification are totally different from anything in that order. *Sphenophyllum*, in fact, constitutes a group by itself, which is entirely unrepresented at the present epoch, and the affinities of which cannot be determined until additional forms have been discovered.

The paper is illustrated by numerous photographs from the actual preparations and specimens, and by a long series of camera-lucida drawings, executed by Mr. George Brebner.

II. "Researches on the Germination of the Pollen Grain and the Nutrition of the Pollen Tube." By J. REYNOLDS GREEN, M.A., B.Sc., Professor of Botany to the Pharmaceutical Society of Great Britain. Communicated by W. T. THISELTON DYER, F.R.S., C.M.G., C.I.E. Received January 2, 1894.

(From the Jodrell Laboratory, Royal Gardens, Kew.)

(Abstract.)

Many observers, especially Van Tieghem and Mangin, have established the fact that the growth of the pollen tube is a process of true germination, strictly comparable to that of the growth of the prothallus from the spore in the groups of Vascular Cryptogams. The germinative process is carried on at the expense of various reserve materials deposited partly in the pollen grain itself and partly in the conducting tissue of the style, down which the pollen tube makes its way.

The existence of certain enzymes in the pollen grain has also been proved by Van Tieghem and by Strasburger. The former has shown that when the pollen of several genera, especially *Crocus* and *Narcissus*, is cultivated in cane-sugar solutions, a certain amount of grape-sugar is produced in the culture, suggesting the presence of invertase; while the latter has shown similarly that certain pollens, when cultivated in starch paste, can liquefy it, with the formation of maltose.