Fig. 1.—*Cycadeoidea marylandica*.

JOURNAL
OF THE
ROYAL MICROSCOPICAL SOCIETY.

APRIL, 1907.

TRANSACTIONS OF THE SOCIETY.

III.—*The President's Address: The Flowering Plants of the Mesozoic Age, in the Light of Recent Discoveries.*

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(Read January 16th, 1907.)

PLATES VI. TO IX.

THE subject which I have chosen for my address to-night relates to the Flora of a period very remote from the present day, though not so remote by far as periods of which I have had occasion to speak at previous meetings of the Society. We then referred to the plants of the Palæozoic period, embracing a vast range of time; the strata with which we were actually concerned were the Permian, the Carboniferous, and, in a lesser degree, the Devonian, of which the Flora is still imperfectly known. My remarks to-night relate to the plants of Mesozoic or Secondary age, ranging from the Trias, through the Jurassic, to the Cretaceous: the great period which bridges the gulf between the antique vegetation of Palæozoic days, and the essentially modern type of Flora which characterises the Tertiary formations.

EXPLANATION OF PLATE VI.

For figs. 1, 4, 5, and 6, I am indebted to the kindness of Dr. Wieland, who was so good as to send me proofs of illustrations from his book.

Fig. 1.—*Cycadeoidea marylandica*. The earliest described American fossil Cycad. From an original daguerrotype. Nearly thirty young fruits are marked in the present view by the groups of bract scars interpolated between the old leaf-bases. About one-fourth natural size. From Wieland's "American Fossil Cycads."

April 17th, 1907

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We all remember the general character of the Carboniferous forests, from which our conceptions of Palæozoic plant-life are chiefly drawn—their gigantic Lycopods and scarcely less gigantic Horsetails, together with the vast assemblage of plants with the habit of Ferns, the majority of which, however, as recent research has shown, were in reality seed-bearing forms, though not without Fern-affinities.* There were, in addition, trees of a far higher type of organisation, recalling, in their habit and the structure of their stems, some of the Coniferae of the Southern Hemisphere, though sufficiently distinct in other characters to constitute an order of their own—the Cordaiteae. Both they and the Fern-like Pteridosperms were Seed-plants, Spermatophytes. We have abundant evidence of the existence of Seed-plants in very early days, in fact, practically as far back in the Palæozoic as our records of terrestrial plants extend. To-night, however, I am going to speak of Flowering Plants, by which I do not mean the same thing as Seed-plants, though the two terms have often been used as synonymous. One of the results of the discoveries in Palæozoic Botany already mentioned has been to show that the seed-bearing and flower-bearing characters by no means coincide, for the fern-like Seed-plants of Palæozoic age were in no sense of the words Flowering Plants. The evidence shows that their seeds, like the fructification of ordinary Ferns, were borne on leaves differing but little from the vegetative fronds and not aggregated on any special axis as are the parts of a flower. The nearest and, indeed, the only analogy to be found among recent seed-plants, is in the female plant of *Cycas*, to which we shall return presently. The Mesozoic plants, however, with which we are concerned to-night were not only Seed-plants, but they bore their reproductive organs in a form which everyone would naturally describe as a flower. They were Flowering Plants in the full sense of the term, however different in other respects from the Flowering Plants of the present day.

The Mesozoic floras from the Upper Trias to the Lower Cretaceous maintain, on the whole, a very uniform character, widely different from that of the preceding Palæozoic vegetation. The Lycopodiaceous trees have disappeared; the gigantic Horsetails have given place to forms more like the Equiseta of our own day; the fern-like Seed-plants are no longer conspicuous, and the Cordaiteae are gone. True Ferns, on the other hand, are abundant, more so, no doubt, than in the earlier period; true Conifers, often much resembling recent genera, are now a dominant group; the family now represented by the Maidenhair tree (*Ginkgo*) is prevalent, but the most striking feature of the vegetation is the abundance, in all parts of the World, of plants belonging to the class of the Cycads, now so limited a group.

* See President's Address for 1905, "What were the Carboniferous Ferns?" this Journal, April 1905.

I will only refer to the Conifers in passing; they are of much interest to the botanist, who is naturally anxious to obtain evidence as to the relative antiquity of the various constituent families, but there is nothing sensational, as yet, about the Mesozoic Coniferæ, which, so far as our present very imperfect knowledge shows, did not differ in any very striking way from the Araucarias, Pines and Cypresses of our own time.

We will concentrate our attention on the Cycad-like plants, or Cycadophyta, to adopt the broader class-name, appropriately suggested by Professor Nathorst. The living Cycadaceæ, of which some account has been given on a previous occasion,* are, it will be remembered, quite a small family, embracing only nine genera, and, according to a recent estimate, about 100 species, inhabiting the tropical or sub-tropical regions of both the old and new worlds, but nowhere forming a dominant feature in the vegetation. Throughout the Mesozoic period, however, at least until the Upper Cretaceous is reached, plants with the habit and foliage of Cycads are extraordinarily abundant, in all regions from which secondary fossils have been obtained; they are as characteristic of Mesozoic vegetation as the Dicotyledons of our recent flora. In many cases the fossil leaves closely simulate those of living genera (*Zamiites*, *Dioonites*, *Cycadites*), others, such as *Otozamites* and *Anomozamites*, bear a more general resemblance to the Cycadean type of foliage. Trunks, described under the names of *Bucklandia*, *Fittonia*, and *Yatesia*, recall vividly those of living genera; in the first-named form an alternation of the scars of foliage and scale leaves has been traced such as is found in *Cycas* at the present day. The silicified stems, with structure preserved, confirm by their anatomical characters the Cycadean relationship indicated by the external features. Specimens of these various kinds are characteristic of the Mesozoic floras in all parts of the world, and there is thus a vast body of evidence for the abundance, during that period, of plants showing Cycadean characters.†

The most important point, however, in questions of affinity is the fructification. Throughout the recent Cycads this is of a simple type; in all the genera the staminate fructification is a cone, consisting of an axis densely beset with scales or sporophylls, each sporophyll bearing on its lower surface a number—often a very large number—of pollen-sacs, grouped, like the sporangia of a fern, in small sori. In eight out of the nine genera the female fructification is also strobiloid, each sporophyll bearing two marginal ovules. In the Mexican genus *Dioon* the scales of the cone are much expanded and have a somewhat foliaceous character. In *Cycas* itself, however, so far as the female plant is concerned, we

* See this Journal, 1905, p. 148.

† See A. C. Seward, Address to Botanical Section, British Association Report for 1903.

find a much more primitive arrangement; no cone at all is differentiated, but the carpels are borne directly on the main stem of the plant, in rosettes alternating with those of the vegetative leaves; thus there is no special reproductive axis, but the sporophylls spring from the axis of the plant as a whole, just as in an ordinary fern. The carpels themselves are lobed and extremely leaf-like, bearing as many as six ovules in many cases, though in one species the number is reduced to two. Thus in *Cycas* the seeds are borne on organs still obviously leaves, and nothing of the nature of a flower is differentiated. No other living seed-plant is so primitive as this, but the Cycads as a whole are undoubtedly the most primitive family of present-day Spermatophyta, as is most strikingly shown in their cryptogamic mode of fertilisation by means of spermatozoids, which they share with *Ginkgo* alone among Seed-plants.

When we go back to the Mesozoic age we might, on what one may call the elementary view of evolution, expect to find the Cycadophytes which were so abundant at that period, still simpler, and still nearer the cryptogamic condition than the members of the class which have come down to our own day. But this is by no means the case; there were, no doubt, a certain number of Cycads in Mesozoic times which were about on the same level of organisation as their living representatives, but the great majority, so far as the available evidence shows, attained a much higher organisation, at least in their reproductive arrangements, far surpassing any of the Gymnosperms now known to us. This is one of the many facts in palæontology which show that evolution is by no means the obvious progression from the simple to the complex which many people have imagined. Just as the Lycopods and the Horsetails

EXPLANATION OF PLATE VII.

- Fig. 2. *Bennettites Gibsonianus*. A. Diagram of the fructification in radial section. *rc*, receptacle; *br*, bracts, overlapping at the top of the fruit; *s*, seeds, seated on long pedicels, and each containing a dicotyledonous embryo; *p*, dilated ends of the interseminal scales (which should be more numerous) forming the "pericarp." B. Ramenta, like those of Ferns, in transverse section. $\times$ about 15 diam. C. Transverse section of a seed. *i*, the double-layered testa; *n*, membrane representing the nucellus; *ct*, the two cotyledons of the embryo, showing the young vascular bundles. $\times$ about 12 diam. D. Somewhat oblique longitudinal section, passing through the micropyle of a seed. *em*, radicle-end of embryo; *r*, apex of radicle; *e*, remains of endosperm(?); *m*, micropyle, obliquely cut; *i*, outer layer of testa; *p*, part of pericarp; *c, c*, crevices in pericarp, corresponding to the limits of the interseminal scales composing it. $\times$ 20 diam. From Scott's "Studies in Fossil Botany."
- „ 3. *Bennettites Gibsonianus*. Longitudinal section of seed, showing the dicotyledonous embryo. *c, c*, the two cotyledons; *a*, apex of plumule; *b*, radicle. $\times$ 12 diam. Photograph, from Scott's "Studies in Fossil Botany."

Fig. 2.—Bennettites Gibsonianus.

Fig. 3.—Bennettites Gibsonianus.

of the Coal Measures were not simpler, but far more complex than their successors, so the Cycadophyta of Mesozoic age were, on the whole, on a much higher level than the surviving family Cycadaceæ, which now represents them. The history of the vegetable kingdom, so far as its records are known, is the history of the ascendancy of a succession of dominant families, each of which attained at some definite period its maximum, both in extent and organisation, and then sank into comparative obscurity, or died out altogether, giving place to some other race, which, under changing conditions, was better able to assume the leading rôle. The Cycadophytes of the Mesozoic were, in their day (and it was a long one), a dominant group, almost as much so as the Dicotyledons are now, and they equipped themselves with a correspondingly high organisation, even rivalling the Angiospermous Flowering Plants (perhaps cadets of the same stock), which ultimately displaced them.

Among the Mesozoic Cycadophyta there were some, as already mentioned, which appear to have been essentially similar to our recent Cycads. The genus *Androstrobis*, for instance, appears to represent male cones not greatly differing from those of the living family. A good example from the Rhætic of Sweden has lately been described by Professor Nathorst,* and although the pollen-sacs do not quite agree with those of any recent Cycad, the author has no doubt of its affinity. Carpels much like those of the genus *Cycas* are also known from various Mesozoic horizons, and it is probable that this primitive type already existed as far back as the Triassic period. There is also evidence, though perhaps less convincing, for the presence of the type of the Zamieæ—the Cycads with seeds borne on definite cones—in Rhætic and Jurassic rocks. Thus we find, as we might expect, that the Cycadaceæ, as we know them at the present day, are themselves a very ancient race. I do not, however, propose to dwell on this line of descent, but will now pass on to those Mesozoic Cycadophyta which attained a higher level of organisation, giving them a better title to the name of “Flowering Plants” than any of their predecessors or contemporaries.

The genus *Bennettites* was founded by Carruthers in 1868 † for certain Cycadean stems, of Oolitic and Lower Cretaceous age, with fruits borne on secondary axes, not protruding beyond the bases of the petioles. The species on which, for many years, our knowledge of the group was principally based, is *Bennettites Gibsonianus*, of which a magnificently preserved specimen was discovered, just fifty years ago, in the Lower Greensand of Luccombe Chine, in the Isle of Wight. Some years later a second specimen was found in the same locality, but no others have as yet come to light. In

* “Beiträge z. Kenntniss einiger mesozoischen Cycadophyten.” Kongl. Svensk Vetensk. Akademiens Handlingar, xxxvi., 1902.

† “On Fossil Cycadean Stems from the Secondary Rocks of Britain. Trans. Linn. Soc. London, xxvi.

B. Gibsonianus, and other species, the external appearance of the stem was similar to that of many recent Cycads, its surface being completely invested by an armour of persistent leaf-bases. Anatomically, there is also a marked agreement, the chief distinction consisting in the simpler course, in the case of the fossil, of the vascular strands which pass out from the stem into the leaves. A striking feature is the presence, in great numbers, on the leaf-base and bracts, of flat, scaly hairs, of the same nature as the ramenta characteristic of Ferns (plate VII. fig. 2, B). Even in external appearance, however, a Bennettitean stem, if in the fruiting condition, differs conspicuously from that of any recent Cycad, in the presence of a number of short, lateral branches, like large buds, wedged in between the leaf-bases, and arising in their axils (see plate VI. fig. 1, from an American species). These bodies are the fructifications, the characteristic feature of the Bennettiteæ. In structure, as well as in position, they differ totally from any form of fructification met with in recent Cycads or other Gymnosperms. The short peduncle has the same anatomical structure as the main stem, on a small scale; it is remarkable, however, for the great development of the phloem, which much exceeds the wood in thickness. This unusual condition may be due to the fact that the crowded reproductive organs, and ultimately the seeds, made a great demand on the food supply, of nitrogenous and other assimilated material, which it is the special function of the phloem to convey.

The peduncle bears many spirally-arranged bracts, which completely inclose the fructification (see diagram, plate VII. fig. 2, A). The end of this peduncle expands into a convex receptacle, on which organs of two kinds are borne—the one fertile, the other sterile. The fertile appendages consist each of a long, slender pedicel, terminating in a single orthotropous seed, with the micropyle directed outwards. The seed-bearing pedicels are present in large numbers; the sterile appendages, or interseminal scales, are still more numerous. They form a dense packing between the seed-pedicels, and somewhat overtop the seeds themselves, expanding at their apices to form an almost continuous envelope, leaving only small perforations, into which the micropylar ends of the seeds are fitted. Towards the base of the receptacle the sterile scales are alone present (see diagram, plate VII. fig. 2, A). They form collectively a kind of pericarp, differing, however, from that of an angiospermous fruit in the presence of openings for the micropyles of the seeds. Both seed-pedicels and interseminal scales are each traversed by a single vascular strand, which in the former case terminates at the base of the seed itself. The whole complex fruit is enclosed in the mantle of overlapping bracts. In *Bennettites Gibsonianus* the fruits discovered are practically ripe, for each seed contains a large, dicotyledonous embryo, with somewhat fleshy cotyledons (see plate VII. fig. 3). The embryo almost

fills the seed, which was thus nearly if not quite exalbuminous—an unprecedented condition in a Gymnosperm. This plant, and a few of its immediate allies, afford the only instances, so far known, of the preservation of the embryo in a fossil seed.*

In the whole arrangement of the floral organs, the presence of a pericarp, and the character of the seed, the fructification differs entirely from anything known in Gymnosperms, and the inclusion of *Bennettites* in Saporta's Class "Pro-angiosperms," appeared justified on grounds of analogy, if not of affinity.

So far, however, nothing whatever was known of the staminate organs of these plants, and no one suspected that the fructifications already known were other than unisexual. Count Solms-Laubach, in conjunction with Professor Capellini, published in 1892 an elaborate investigation of the specimens of Bennettitæ preserved in the Italian museums. One of the fossils they examined is probably the most ancient palæontological specimen known, I mean historically speaking, for it was found placed as a decoration on an Etruscan tomb, having clearly been recognised as an object of value in pre-Roman days. This specimen (*Cycadeoidea etrusca*) was fruiting, and in one of the fructifications Count Solms-Laubach discovered bodies, interpreted as pollen-grains, lying in the spaces between the top of the ovuliferous column and the enveloping bracts. The preservation was too bad for anything to be ascertained as to the structure of the organs producing the pollen, though some remains of them were present, but the inference was drawn that in this species, and perhaps in other Bennettitæ, the stamens were borne in the same fructification with the ovules. The evidence was, however, too imperfect to appear decisive at the time. The detailed investigation by Professor Lignier of a magnificent specimen (*Bennettites Morieriei*) from the Oxfordian of Normandy,† demonstrated a structure agreeing in essentials with that of the Luccombe species, but brought no further information as to the male organs.

The complete elucidation of the subject was reserved for the American palæontologists, who possess a wealth of material for the investigation of Mesozoic Cycadophyta, far exceeding anything that Europe can show. No less than sixty species of silicified Cycadean trunks have now been described from the Mesozoic of America, ranging from the Upper Triassic to the Lower Cretaceous. Among the numerous localities, the most important are various places on the Rim of the Black Hills of Dakota and the Freezeout Hills of Wyoming (Upper Jurassic to Lower Cretaceous) and the Potomac beds (approximately of Wealden Age), Maryland. The

* Solms-Laubach, "On the Fructification of *Bennettites Gibsonianus*." English translation in Ann. of Bot., v. 1891.

† O. Lignier, "Végétaux Fossiles de Normandie"; "Structure et Affinités du *Bennettites Morieriei*." Caen, 1894.

Dakota and Wyoming districts have yielded forty-nine species, and the Maryland localities seven.

The specimens are often extremely numerous; thus the twenty-nine species from the Black Hills of South Dakota are represented by nearly 1000 more or less complete trunks. In fact, the Cycadophyta of the American Mesozoic are as important to the botanist as the gigantic Saurians (with which they are often associated) are to the zoologist.

Plate VI. fig. 1 represents the first American fossil Cycad ever discovered; it was found about 1860 in Maryland, between Baltimore and Washington, by the geologist, Philip Tyson, and well illustrates the external features of the group. A third of a century elapsed before any further discoveries were made, so the present magnificent material has been accumulated within quite a short period. The systematic arrangement of the specimens has been principally the work of Professor Lester Ward, while the morphological investigation has fallen to the share of Dr. Wieland, of Yale University, to whom the discoveries we have now to consider are due.

It may be mentioned, in passing, that the American palæobotanists use Buckland's generic name *Cycadeoidea* for plants which in Europe we should refer to Carruthers' genus *Bennettites*. Buckland's genus was founded on trunk-characters, while the diagnosis of *Bennettites* embraces the fructifications. In referring to Dr. Wieland's work I shall follow him in using the name *Cycadeoidea*, but it must be understood that this is synonymous, so far as we can tell, with *Bennettites*.

The richness of the American material enables us to form a good general idea of the habit of the family. The trunks were in no case very lofty—there seems to be no good evidence for a height of more than 10 or 12 feet, while the great majority of the stems were quite short. In some cases the stems are nearly spherical, and several are connected together, evidently as branches of one plant. In comparing these fossils with recent Cycads, we must, therefore, think of the short-stemmed genera, such as *Bowenia* or *Stangeria*, or at the most *Macrozamia*, rather than of tall plants like *Cycas* itself, some species of which are said to reach a height of 60 feet. In foliage and the external features of the trunk, there was on the whole the same general resemblance to modern Cycads which has already been noted, and the same striking dif-

EXPLANATION OF PLATE VIII.

- Fig. 4. *Cycadeoidea dacotensis*. Longitudinal section of flower. The centre is occupied by the long ovuliferous cone, on either side of which are seen parts of the compound stamens, with rows of synangia on their pinnæ. To the left, some of the bracts are well shown. $\times 3$ diam. Photograph, from Wieland's "American Fossil Cycads."

Fig. 4.—*Cycadeoidea dacotensis*.

Fig. 5.—*Cycadeoidea ingens*.

Fig. 6.—*Cycadeoidea ingens*.

ference in the presence of numerous lateral fructifications. In anatomical structure, the American species so far investigated agree wonderfully closely with the European species of *Bennettites*, but it must be remembered that the vast extent of the material will necessitate many years of arduous research before its investigation can be completed. During the eight years or so that Dr. Wieland has been at work, a marvellous amount has been accomplished. His results are embodied in a magnificent volume issued last August by the Carnegie Institution of Washington.* I will now go on at once to give a brief account of Dr. Wieland's discoveries elucidating the structure of the Bennettitean flower.

The male organs of the Bennettiteæ were first found in 1899, in the species *Cycadeoidea ingens*.† Two years later the important fact was established that the organs of both sexes occurred in the same fructification, the whole thus constituting a 'hermaphrodite,' or bisexual flower.‡ This discovery, though now of six years' standing, scarcely attracted the attention it deserved, until the publication of the full details within the last few months. Twenty-five trunks bearing bisexual flowers have now been investigated, belonging to seven American species. The conditions in *Cycadeoidea dacotensis*, one of the cases most fully investigated, are as follows. The whole fructification has a length of about 12 cm., and protrudes beyond the leaf-bases of the trunk. About half the length is occupied by the peduncle, the upper part of which bears 100 or more spirally arranged bracts, inclosing the essential organs. The centre is occupied by the ovuliferous cone, about 4 cm. in height, corresponding to the receptacle, with its seeds and other appendages, as shown in the diagram of *Bennettites Gibsonianus*, (plate VII. fig. 2, A). In *C. dacotensis*, however, the form of the central cone is much more pointed, and the stage of development far earlier, immature ovules taking the place of the ripe seeds of the more advanced European specimens (plate VIII. fig. 4).

* American Fossil Cycads. By G. R. Wieland, 1906.

† A Study of some American Fossil Cycads. Part I. The Male Flower of *Cycadeoidea*. Amer. Journ. Science, vii., 1899.

‡ Op. cit., Part IV. On the Microsporangiate Fructification of *Cycadeoidea*. Amer. Journ. Science, xi., 1901.

EXPLANATION OF PLATE IX.

- Fig. 5. *Cycadeoidea ingens*. Restoration of an expanded bisexual flower in longitudinal section, showing the central ovuliferous cone, the compound stamens bearing numerous synangia, and the surrounding bracts, hairy with ramenta. About half natural size. From Wieland's "American Fossil Cycads."
- „ 6. *Cycadeoidea ingens*. Plan of the bisexual flower, consisting of a central ovuliferous cone, an hypogynous whorl of compound stamens, united at the base, and a series of spirally inserted enveloping bracts, all shown diagrammatically on about the same scale as fig. 5, and as if pressed out flat. From Wieland's "American Fossil Cycads."

We have to do then, in this case, with an organ in the stage of a *flower*, as distinguished from the *fruit* previously described. The ovuliferous cone, or gynæcium, is completely surrounded by the hypogynous staminate disk, as Dr. Wieland calls it, springing from the rim of the receptacle at the base of the cone (see diagram, plate IX. fig. 5). The stamens are numerous (18–20 in *C. dacotensis*) and arranged in a whorl; their stalks are united to form a continuous sheath, which extends to about the level of the top of the gynæcium. Here they become free from each other; each stamen is a compound, pinnate sporophyll, about 10 cm. long altogether, and is folded inwards towards the gynæcium, the deflexed tip reaching down nearly to its base. The alternate pinnæ, of which there are about 20 pairs, are likewise bent inwards. The pinnæ, with the exception of those at the apex and base of the frond, which are sterile, bear the pollen-sacs in two rows, 10 in each row on the longest pinnæ. Thus the stamens are highly complex structures, resembling the fertile fronds of a fern, rather than the stamens to which we are accustomed in our modern Flowering Plants. The complexity, however, does not end here, for each pollen-sac is itself a compound structure containing two rows of loculi, 10 or more in each row. It thus constitutes a *synangium*, comparable to that of the Marattiaceous ferns, and especially the genus *Marattia*. The similarity to the fructification of such a species as *Marattia Kaulfussii* is, in fact, surprisingly close. It may be added that the vascular system of the stamens is a complex one, consisting of numerous bundles, as in the leaf of a highly organised fern or a Cycad.

It appears that all the specimens actually investigated were in the bud condition, the stamens being still infolded, as described above. Plate VIII. fig. 4 is from one of Dr. Wieland's sections, showing portions of the compound infolded stamens; from the comparison of a number of such sections the author was able to build up the whole construction of the flower. He presumes that the stamens eventually opened out, and the diagrams introduced in figs. 5 and 6 show them in the expanded condition. The ground-plan of the open flower, shown in plate IX. fig. 6, is based on *Cycadeoidea ingens*, a species in which a number of stamens is smaller than in *C. dacotensis*.

It is an interesting fact that in a large number of fructifications in the more mature, seed-bearing condition, Dr. Wieland was able to detect the remains of the staminate whorl seated on the rim of the receptacle. It thus appears that the hermaphrodite condition was general, if not universal, throughout the group, a conclusion which explains Count Solms-Laubach's early observation on *Cycadeoidea etrusca*. As the fruit matured the expanding gynæcium evidently encroached on, and ultimately filled, the space originally occupied by the staminate whorl (compare plate VII. fig. 2, A, with plate IX. fig. 5). Dr. Wieland is of opinion that the flowers must have been protandrous, the pollen being shed before the ovules

were ready for fertilisation. A more detailed knowledge of the condition of the ovules at various stages will be necessary in order to establish this conclusion.

The leading features in the organisation of the Bennettitean flower may be briefly recapitulated as follows: The centre is occupied by the gynæcium, seated on the convex receptacle, and consisting of numerous long-stalked ovules, imbedded among the interseminal scales. Surrounding this central body is the hypogynous whorl of stamens, fused below to form a tube, and expanding above into the pinnate sporophylls, bearing very numerous compound pollen-sacs or synangia, filled with pollen. The whole is surrounded by an envelope of spirally-arranged bracts springing from the upper part of the peduncle. The general arrangement of parts is manifestly just the same as in a typical angiospermous flower, with a central pistil, hypogynous stamens, and a perianth. The resemblance is further emphasised by the fact, long known, that the interseminal scales are confluent at their outer ends, to form a kind of pericarp or ovary-wall. When to these general features we add the practically exalbuminous character of the seed, with its highly organised, dicotyledonous embryo, the indications of affinity with the higher Flowering Plants become extremely significant. The comparison was drawn by Dr. Wieland in 1901, immediately on his discovery of the hermaphrodite flower. The Angiosperm which he specially selected for comparison was the Tulip-tree—*Liriodendron*. The elongated strobiloid fruit, with many carpels spirally arranged in the receptacle, no doubt suggests similarity, and, on general grounds, we should naturally look for analogies among the less specialised polypetalous Dicotyledons, such as Magnoliaceæ, in some of which the leaves of the perianth are spirally arranged. Analogies may also be found in our familiar Ranunculaceæ, such as *Anemone*, or, still better, the Globe-flower (*Trollius*), with its numerous sepals, or, again, in the Water-lilies (Nymphæaceæ). In certain respects, indeed, the Bennettitean flower was in advance of these simpler Dicotyledons, as seen in the arrangement of the stamens, which have abandoned the spiral phyllotaxis of the other organs to range themselves in a definite whorl, while at the same time their stalks are fused into a tube, thus becoming "monadelphous," as in the Mallows of our own flora.

The flower, with its great stamens, 10 cm. long in some species, must have been a striking object when it opened (plate IX. figs. 5 and 6). As, of course, we can know nothing of the coloration of the perianth and other parts, we cannot tell how brilliant its appearance may have been; the bright tints of the carpels and ovules in some recent Cycads, such as species of *Cycas* and *Encephalartos*, suggest the probability that the attractions of colour were not wanting to the more elaborate flowers of the older Cycadophyta; the possibility of a relation to the insect life of the period cannot

be ignored. It is not my intention to push further the comparison of the Bennettitean fructifications with the angiospermous flower; the deeply interesting questions which must suggest themselves to the mind of every botanist, as to how far these manifest analogies are likely to indicate an immediate affinity, will be fully discussed elsewhere by others. Enough has been said to show that the remarkable organs discovered by Dr. Wieland fully merit the name of "flower," in the same sense in which we apply it, in everyday language, to the flowers of our gardens and fields. I am inclined myself to believe that the comparison holds good from a morphological point of view also, but it may be fair to mention that some botanists have regarded each seed-bearing pedicel, with the adjacent interseminal scales, as itself constituting a flower, in which case the whole would, of course, be an inflorescence, comparable to the capitulum of the Compositæ. This interpretation, however, can scarcely be extended to the stamens, which are, to all appearance, seated directly on the receptacle. On the whole, I agree with Dr. Wieland that the simpler view of the whole fructification as a single axis, bearing fertile and sterile organs of a foliar nature, better corresponds to the facts and to the analogies with related groups. The homologies of the seed-pedicels and interseminal scales and especially their relations to the carpellary structures in Angiosperms, in any case present a difficult and fascinating problem to the morphologist.

As stress has been laid so far on the points of agreement with the flower of the Angiosperms, some reference must now be made to characters which indicate relations in other directions. The structure of the gynæcium renders it probable, if not certain, that the Bennettiteæ were still Gymnosperms as regards their mode of pollination, for the openings between the scales of the pericarp leave the micropyles of the seeds exposed (see pl. VII. fig. 2, A). One must therefore suppose that the pollen was received by the ovule directly, without the intervention of a stigma, so that functional Angiospermy had not yet been attained. This is, no doubt, a primitive condition, but it by no means excludes an affinity with Angiosperms. Just as in *Lagenostoma*, the seed of the Pteridosperm *Lyginodendron*, the beak of the nucellus was still the receptive organ for the pollen, in spite of the presence of an integument,* so, in the Bennettitean flower, the micropyle of the seed was still the receptive organ in spite of the presence of a pericarp. The integument in the one case and the pericarp in the other might be termed a "prophetic organ" in the only sense in which such organs exist, i.e. an organ which has not yet assumed all the functions to which it is destined.

The stamens, while by their arrangement and position they

* See Oliver and Scott, "On the Structure of the Palæozoic Seed *Lagenostoma Lomazi*," Phil. Trans. Roy. Soc., Series B., 197 (1904), p. 231.

suggest those of a typical Angiosperm, carry us back by their structure and form to the sporophylls of a Fern (see plate IX. figs. 5 and 6), so that the characters of the flower as a whole may almost be said to bridge the gulf between Cryptogams and the higher Flowering Plants. The fern-like characters, however, have probably come to the Bennettiteæ not directly from true Ferns, but through the intermediate group of the Palæozoic Pteridosperms. The fact that the pollen-grains are borne in compound pollen-sacs, or synangia, like those of the Marattiaceæ among Ferns, is one of great significance. I should not be disposed, however, to lay quite so much stress on this indication of Marattiaceous affinities as Dr. Wieland has done. The presence of synangia is probably to be explained by the relation of the Bennettiteæ to the Pteridosperms, to which, as we now know, certain of the supposed Marattiaceous fructifications of Palæozoic age really belonged. There can scarcely be a doubt that the Bennettiteæ trace their ancestry through the Pteridosperms and not directly from Filicinean forms, a conclusion in which Dr. Wieland appears to concur.* The true Marattiaceæ of the Palæozoic were probably a less extensive family than has been supposed, and, on present evidence, were less ancient than the Pteridosperms themselves, which we therefore cannot derive from them, though the two groups may have had a common origin. In spite, therefore, of the strikingly Marattiaceous character of the pollen-bearing synangia in Bennettiteæ, I cannot agree with Dr. Wieland in regarding the evidence for their descent from Marattiaceous Ferns as conclusive, but, so far as that particular family of Ferns is concerned, should not assume anything more than an indirect affinity.† None the less, it is impossible to emphasise too strongly the extraordinary combination of characters which the Bennettitean flower presents, uniting in itself features characteristic of the Angiosperms, the Gymnosperms, and the Ferns, and suggesting that the passage from the Filicineæ to the higher Flowering Plants may have been (comparatively speaking) a short cut. The complexity of this earliest known type of a true flower indicates the probability, as Dr. Wieland points out,‡ that the evolution of the Angiospermous flower was a process of reduction. There is thus no longer any presumption that the simplest forms among the flowers of Angiosperms are likely to be the most primitive. The tendency of the older morphologists to regard such flowers as reductions from a more perfect type appears fully justified by the discovery of the elaboration of floral structure attained by the Mesozoic Cycadophyta before the advent of the Angiosperms themselves.

* "American Fossil Cycads," p. 240.

† The general question of the relation of the early Seed-plants to Ferns is discussed in my article, "On the Present Position of Palæozoic Botany," *Progressus Rei Botanicæ*, Heft 1, 1906.

‡ "American Fossil Cycads," p. 143.