

A FAMOUS ISLE OF WIGHT FOSSIL PLANT.

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The Isle of Wight has long been classic ground to the geologist, for the succession of the upper Secondary and Tertiary strata is shown there almost with the clearness of a diagram. The geological structure of the island consists essentially of an anticline with its corresponding syncline. The anticlinal axis or line of elevation—the crest of the wave—runs roughly from Sandown on the South-East, to Brook Point on the South-West coast; at these places the oldest rocks are brought to the surface, and are exposed, owing to denudation having removed the strata which once lay over them. These oldest rocks are of Wealden age. The exposure of the Wealden, however, does not extend right across the island but is limited to the neighbourhood of the respective coasts and is interrupted inland by a tract of country in which the Wealden is still overlaid by the Lower Greensand formation.

On either side of the anticline the strata succeed each other in regular upward sequence—Lower Greensand, Gault, Upper Greensand, Chalk, and then to the North, the Tertiaries of the syncline, or hollow of the wave. The southern syncline is under the sea, and on this side nothing is shown newer than the Chalk.

The northern ridge of Chalk, marking the division between anticline and syncline, forms the great range of downs which extends through the whole length of the island, from Culver Cliff on the East to the Needles on the West; the southern

Chalk forms the mass of still loftier downs from Shanklin to St. Catherine's.

Many of the beds in the Isle of Wight are extraordinarily rich in fossils: the Tertiaries of Whitecliff Bay, Headon Hill and Hamstead Cliffs are specially famous and constantly visited by geologists. Here, however, we are only concerned with the older strata, the Wealden and the Lower Greensand.

The Wealden is exposed, on the South-East coast, for about a mile northwards from Sandown, and for nearly six miles on the South-West coast, from Compton Bay to near Atherfield Point.¹ The latter exposure is much the more important geologically, as well as the more extensive, and has become famous from the numerous bones of gigantic reptiles, *Iguanodon*, *Plesiosaurus* and *Ichthyosaurus* among others, which it has yielded. The oldest Wealden beds are exposed at Brook Point, well known to the fossil botanist for the "Pine Raft," a great accumulation of fossil trunks of coniferous trees, lying prone on the rocks and laid bare at low spring tides. No doubt they formed part of a vast mass of drift-wood, such as is found at the present day off the mouths of great rivers.² The Wealden was a freshwater formation, deposited under the waters of an immense river. Hence, as one should expect, it is rich in fossil plants, which once grew on the banks of the river or in the marshes bordering it. The Wealden is in fact one of the very best formations for the fossil remains of an extinct vegetation.

So far as our own part of the world is concerned, the Wealden Flora has proved to be entirely of an early type, such as had prevailed throughout the preceding epoch. The Sub-Kingdom of the Angiosperms, the ordinary flowering plants,

¹ For recent accounts of Isle of Wight Geology see R. S. Herries, in "Geology in the Field," Chap. xviii. p. 414, 1910, and G. W. Colenutt, in Morey's "Guide to the Natural History of the Isle of Wight," p. 1, 1909.

² For a striking illustration of this, see Seward, "Links with the Past," Cambridge, 1911, Fig. 7.

which now dominate the vegetation of the land is, so far as we know, entirely unrepresented. Such plants had probably begun to appear as early as this in other regions, but in the Wealden rocks of England and the neighbouring parts of Europe we find only families like the Ferns, the Horsetails, the Conifers, and other groups not so familiar, to which we shall refer immediately.

After the Wealden period, the land through which the great river had flowed became sunk beneath the waters of the sea, but at first only a shallow sea. The Lower Greensand, so extensively developed in the southern part of the Isle of Wight, was a marine deposit, immediately succeeding, without a break, the freshwater beds of the Wealden.³ In the period represented by the Lower Greensand the old families of plants were still dominant, but they were no longer alone; the representatives of a higher and more modern type of vegetation begin to appear.

The fossil to which the title of this article specially refers, belongs to the Lower Greensand: it represents one of the ancient families of plants still flourishing at the time, but destined in the next age to give way to more modern competitors.

Our plant was found at Luccomb Chine, one of those beautiful cliff-valleys which are so characteristic of the southern shores of the island. The spot lies a mile or more to the South of Shanklin, and just where the picturesque scenery of the Landslip begins. Here, in 1856 or thereabouts, the first specimen was discovered by Mr. Thomas F. Gibson, after whom the species was named by Mr. Carruthers *Bennettites Gibsonianus*.⁴ The fossil is a short thick stem elliptical in section: in the principal specimen the long

³ Both are included by geologists in the Neocomian.

⁴ The genus *Bennettites* is named after J. J. Bennett, Keeper of the Botanical Department of the British Museum, from 1858-1870.

diameter is 11 inches and the short $6\frac{1}{2}$ inches. The external surface is completely clothed by the persistent bases of the leaves. Plate i. gives an idea of the external configuration. It does not, however, show (except at the sides) the actual rough outside surface, but a section a little inside the surface and parallel to it, so that the arrangement and form of the leaf-bases come out clearly. It will be noticed that each leaf-base is lozenge-shaped, with the greater diameter horizontal. The dots shown on some of the leaf-bases are the cut ends of the vascular strands which supplied the leaf, and are of the same nature as the marks we see on the scar left by the fall of the leaf, in a Horse Chestnut or other deciduous tree.

Wedged in here and there, among the bases of the leaves, are very peculiar organs (two are shown near the top of the figure in Plate i.) resembling at first sight large buds. These have turned out to be the fruits of the plant, enclosing the numerous seeds (Plate iii.). They are the most remarkable feature of the fossil and we shall have much to say about them.

A tranverse section across the stem is shown in Plate ii. We see from this that the leaf-bases are of considerable length, forming collectively a thick, protective armour round the stem. Here again, the fruits are met with among the bases of the leaves: one of them, cut lengthwise and shaped like a pear, is seen to the right of the figure.

The stem itself contains a fairly thick zone of wood, enclosing a large pith (dark in the Figure). From the wood numerous vascular strands pass out to the leaf-bases, while others enter the fruits.

The whole is wonderfully well preserved; it is not, like so many specimens of fossil plants, a mere *cast*, but a true *petrification*, the mineral substance (here chiefly Calcium Phosphate) having completely permeated all the tissues and preserved them almost perfectly, except at certain points

where the presence of Iron Pyrites interferes. The remarkable excellence of the general preservation has made it possible to study the structure in detail under the microscope, by means of thin sections, and though this has not, even yet, been completely carried out, we know enough to determine the relationships of the plant.

Our figures of *Bennettites Gibsonianus* are taken from the type specimen in the British Museum, (Natural History). A second specimen was found by Dr. Leeson, of Bonchurch, a little later.

Before considering our Luccomb fossil more in detail, we must shortly refer to an allied species, also from the Isle of Wight, which shows some parts of the structure even better than *B. Gibsonianus*. This is *B. Saxbyanus*, found long before the Luccomb plant and described in 1851 by the great Robert Brown—"botanicorum facile princeps"—under the name *Cycadites Saxbyanus*. It is said to be of an older geological date than the Luccomb plant, for it is described as coming from the Wealden beds of Brook Point. Though not so good for the fruits as Gibson's species, the structure of the stem is shown with even greater clearness. Plates iv. and v. illustrate the specimen of this plant exhibited at the British Museum (Natural History). Plate iv. represents a transverse, Plate v. a median longitudinal section. The dimensions are not very different from those of the former species, but one of the specimens was as much as 19 inches long, showing that the stem must have been rather taller than in many members of the family.

The pith is larger and the zone of wood narrower than in the Luccomb stem. The wood has a lax structure, interrupted by large medullary rays, and is altogether poorly developed considering the size of the stem. The vascular strands, shaped, as seen in transverse section, like a horseshoe (Plate iv.) are very plainly shown; on their way out from the wood

to the leaves; their origin and course have been accurately traced by Carruthers. A single strand leaves the wood to supply each leaf, dividing up repeatedly to form the numerous strands which enter the leaf-base.⁵

It is a curious fact that the relationship of *Bennettites* to plants now living has been discovered solely through the characters of the vegetative organs—the stem and leaves. The reproductive organs, usually assumed to be the important features in classification, have thrown no light on the question, for they are totally unlike those of any plants now to be found on the face of the earth.

The form of the stem, the armour of leaf-bases, the structure of the stem and leaf-bases, especially that of the wood and vascular strands, and, in other species where the leaves are preserved, the form and structure of the leaf itself, show so many points of close agreement with the living family Cycadaceæ, as to leave no doubt in the mind of any botanist that there is a real relationship between the recent and fossil groups. We cannot go into details here, but may point out that, except for the fruits, the Plates i. and ii. might almost be taken from a recent Cycad.

But what are Cycads? The family is very little known, except to botanists, though its members are usually large and handsome plants. They are distantly related to the familiar Conifers, but totally different in appearance, and externally more like Palms, with which they really have nothing to do. A fine collection of Cycads can be seen in the Palm-house at Kew. The most striking feature of the plants is their foliage. The great compound leaves, usually pinnate, have suggested the deceptive comparison with Palms, while

⁵ A third Isle of Wight species, *B. maximus*, is mentioned by Carruthers, and is about to be more fully described by Dr. Marie C. Stopes, who tells me that it had a trunk 30 centimetres (a foot) in diameter, and a wood cylinder only 2 millimetres thick.

nothing can be more unlike the "needles" of Conifers, with which there is yet a true affinity. In some the stem is tall, and the Cycad becomes a tree, 30, 40, or even it is said, 60 feet in height. Such arborescent forms are found in the Cuban *Microcycas*, in a Mexican *Dioon*, and in an Australian *Cycas*, among others. More often, however, the stem remains short, forming a low sturdy column, or, in some cases, scarcely rising above the ground. Columnar stems are found, for example, in the South African *Encephalartos*, and the Australian *Macrozamia*, while very short stocks occur in the fern-like *Stangeria* from Natal, and in *Bowenia* from Queensland, remarkable for its twice-pinnate leaves.

In many Cycads the stem is clothed in a persistent armour, formed of the bases of the leaves after the leaves themselves have been shed, exactly as in our Isle of Wight fossils. Like these, too, the stem has a large pith, and often a very meagre zone of wood. In fact, as already mentioned, the structure of the vegetative parts of the fossil plants can be matched in almost every point among living Cycads.

The usual fructification of the Cycads is a cone, comparable, in a general way, to that of the Coniferae. The sexes are always separated on distinct plants. The male fructification is in all cases a cone, often of large size, reaching 20 inches in length in some species. The axis of the cone bears a large number of flat scales (the stamens) each with numerous pollen-sacs on its lower surface. In eight out of the nine genera the female plant also bears cones, much like those of the male, but in this case bearing the seeds, two on each scale. *Cycas* itself, the genus which gives its name to the family, is quite peculiar, for here the female plant does not form a cone at all, but produces on its main stem, alternately with the green leaves, rosettes of leaf-like fertile scales or carpels, bearing from two to six seeds each. No other living plant has so primi-

tive an arrangement, but throughout the family the fructification is of a simple kind.*

To return to our Isle of Wight fossil plants, the most surprising point about them is that while as regards stem and leaves they were essentially Cycads, in fructification they differed entirely from that family and were on a far higher level. The Luccomb fossil is of the greatest historical interest, for it was the first plant in which the structure of this extinct type of fructification was made out, though more recently there have been vast additions to our knowledge from other sources. Carruthers in 1868 first explained in their main features the reproductive structures of *Bennettites Gibsonianus*: the details were further elucidated twenty years later by a distinguished German botanist, Count Solms-Laubach, who likewise worked at the Luccomb specimens.⁶ The fruits, as we have seen, are closely surrounded by the bases of the leaves (Plates i. and ii.): a fruit is often placed immediately above a leaf, suggesting that it was borne in the axil of the latter, as flowers so often are. The fruit is a pear-shaped body which may be as much as two inches in extreme length (Plate iii.). Its protected position amongst the surrounding leaf-bases may help to account for the good preservation. The fruit is seated on a short, thick stalk, bearing, in its upper part, a large number of simple leaves or bracts, which overlap each other and completely close in over the top of the fruit, giving the whole its bud-like appearance. (Plate iii. and Text-figure 1A). The stalk expands at the top into a hemispherical cushion or receptacle, on which the essential organs of the fruit are inserted. From the

* A good illustrated account of recent Cycads will be found in Coulter and Chamberlain's "Morphology of Gymnosperms," 1910.

⁶ Carruthers, on Fossil Cycadean Stems from the Secondary Rocks of Britain. Trans. Linnean Society, Vol. xxvi., 1870 (read in 1868). Solms-Laubach, on the Fructification of *Bennettites Gibsonianus*. Annals of Botany, Vol. v., 1891.

convex surface of the receptacle there spring a large number of slender rods or pedicels, each of which bears at its upper end a single erect seed. (Text-figure 1A). As seen in a longitudinal section of the fruit, the seed-pedicels have a fan-like arrangement, diverging towards the outer surface. Between and around the seed-pedicels are sterile organs, the interseminal scales, which fill up all the available space. These are important because they collectively form the wall of the fruit. Each interseminal scale expands at its end, and the expanded portions coalesce, so as to form a practically continuous shell, leaving only minute apertures into which the tips of the seeds fit tightly. The wall of the fruit thus constituted is in its turn enclosed by the overlapping bracts.

The narrow passage (micropyle), through which fertilization was no doubt effected at an earlier stage, is at the top of each seed, where it projects through the wall of the fruit. (Text-figure 1A, s). The most remarkable feature of the seeds is the presence in each of a large, dicotyledonous embryo, practically filling up the whole of the space inside the seed-coat. The two thick seed-leaves or cotyledons of the embryo are shown, cut across, in Text-figure 1B. *Bennettites Gibsonianus* and a few of its nearest relations are the only fossil plants in which the embryo has been found preserved.

Another remarkable point is that the embryo occupies the whole interior of the seed. In modern Cycads and Conifers the embryo is comparatively small, most of the space being occupied by a food-tissue (endosperm) which in *Bennettites* is almost, if not entirely, absent.

The remarkable structure that we have now described is clearly a ripe fruit, as shown by the presence of fully-formed embryos in the seeds. From the Isle of Wight specimens and others like them nothing could be gleaned as to the earlier condition, when the fruit was still a flower, nor as to the nature of the stamens. On these points information came

to us at a later date from America, where fossil plants of the *Bennettites* family are extraordinarily abundant in the Jurassic and Lower Cretaceous rocks of Maryland, Dakota and Wyoming. It was Dr. Wieland's classic investigations that first revealed the structure of the *flower* as distinguished from the *fruit* of *Bennettites* and its allies.⁷ To complete our story we must say a few words about his results, for there is no doubt that the flower of our Luccomb plant was essentially the same as that of the American specimens, though it happens so far to have only been found in the ripe, fruiting stage. The general features of the American plants, of which about 60 species have been described, agree with those of the English fossils; the fructifications are borne in the same position, between the leaf-bases, and have essentially the same structure, but fortunately they were fossilized in many cases while still young, as *flowers* instead of as *fruits*.

In the specimen of the flower figured in longitudinal section (Text-figure 2) the central receptacle is taller and more conical than in the Luccomb plant; it bears great numbers of small, immature seeds, or rather *ovules*.

But the most striking feature of the flower is the presence of the large and complex stamens, arranged in a ring round the central receptacle, and numbering from 10 to 20 in different species.

They are compound pinnate leaves, almost like the fronds of some of the Ferns, and bear great numbers of pollen-sacs on their leaflets. Each pollen-sac is divided into compartments, in which the pollen-grains are contained.

In the condition in which they are actually found in the fossils, the stamens are always infolded, bending inwards and downwards till their tips nearly reach the base of the receptacle (Text-figure 2). On the other hand, the restoration in Text-figure 3 shows the flower as it would appear if fully

⁷ Wieland, "American Fossil Cycads," Carnegie Institution, 1906.

expanded, when seen from above. This gives a good idea of the complicated structure, especially of the stamens.

No doubt the flowers of our Luccomb plant and other English species had the same organisation, but were fossilized too late to show the stamens, which had already been shed. In some cases the bases of the old stamens are actually found in the fruit, forming a ridge just below the receptacle.

We see then that the plants of the extinct family Bennettitæ had bisexual (hermaphrodite) flowers, with the parts arranged in the same way as in the ordinary modern flower—the bracts on the outside answering to the perianth, next the circle of stamens, and finally the seed-bearing part or pistil in the middle of the flower. The nearest comparison is with flowers like the *Magnolia*, or in a less degree the *Anemone*. But at the same time, the form and structure both of the stamens and "pistil" are extremely different from anything we find among the Flowering Plants of our own period; the stamens, indeed, rather remind us of the fertile fronds of certain Ferns.

We have in fact, in *Bennettites* and its allies, the beginnings of a flower; but all its possibilities were still far from being realised. For example, the ovules appear to have received their pollen directly as in modern Cycads and Conifers, and not through the intervention of a stigma and style, as in the higher Flowering Plants (Angiosperms).

The family represented by *Bennettites* may, however, fairly be called the forerunners of the Flowering Plants. As we have seen, it was a very extensive family in the Secondary Period; but after all, the Bennettitæ were only one special group of a great class. Another important family, that of the *Williamsonias*,⁸ is known from the Jurassic rocks of Yorkshire, Sweden, Mexico and India. They had

⁸ So named by Carruthers after the great palæobotanist, W. C. Williamson, who described the first specimens.

much in common with the Bennettiteæ, but differed from them in their slender stems, with well-developed wood, and in the details of the flower. Their flowers were often of great size, resembling the flower-heads of an Artichoke in external aspect. In some of them the sexes were, it appears, separate, in different flowers if not on distinct plants. There was much variety in this family, which, like its relations the Bennettiteæ, had the foliage of the Cycads.⁹ In the Secondary Period (as far up as the Lower Cretaceous) the so-called Cycads, or rather Cycadophytes, to use a wider name, were the dominant features of the world's vegetation. Of the land plants, from one-half to one-third were Cycadophytes; this group played almost as great a part then as the Dicotyledons do now, though the existing Cycads are now limited to a few tropical or sub-tropical forms.

The great majority of this vast class were of the *Bennettites* or *Williamsonia* type, differing totally, as regards their reproductive apparatus, from the little family of living Cycadaceæ, and much in advance of them. It is true that Cycads of the simpler kind, like the modern representatives, also existed in Secondary times, but only to a small extent, the species never, perhaps, having been much more numerous than they are now.

The existence of the vast extinct class of "Flowering Cycads" as we may call them, the highly organised race which anticipated, if it did not give rise to, the Flowering Plants of our own period, was first revealed by the discovery of the Lucomb Chine fossil. It would be difficult to cite another instance in which one plant has played so important a rôle in advancing our knowledge of the history and evolution of the Vegetable Kingdom.¹⁰

⁹ See Wieland, on the Williamsonian Tribe, *American Journal of Science*, vol. xxxii., 1911.

¹⁰ A fuller account of the Secondary Cycadophytes will be found in the writer's "Studies in Fossil Botany," 2nd edition, 1909, pp. 555-604.

Bennettites Gibsonianus, however, is by no means the only fossil plant which the Lower Greensand of Luccomb has yielded. I cannot better conclude this article than by quoting a paragraph, kindly written for this purpose by Dr. Marie C. Stopes, who has an intimate personal acquaintance with the treasures of these plant-bearing deposits:—

“The series of the beds of the Lower Greensand, so admirably described by Fitton, Forbes and other early writers, is well displayed in section in the cliffs near Luccomb. Here the dip of the bed brings successive members of the series to view, and just at Luccomb Chine itself the best plant-bearing strata, with the coarse sandy matrix, dark with glauconite grains, is so placed as to be within reach of the shore and thus to enable the fossil-hunter to collect pieces of wood and other plant fossils *in situ*, as well as to find numerous scattered pieces among the wave-washed pebbles.

“These beds represent a marine deposit. At the time they were accumulated what is now the East of the Isle of Wight was under the sea, but not very far from a land which appears to have been well covered by an interesting mixed flora. From this flora only fragments reach us, but they are enough to indicate the nature of the more recently evolved and vital competitors of *Bennettites*. From what appears to have been the very bed in which *Bennettites* was found, branches of Cupressinean trees (Cypresses) have turned up, beautifully petrified. On this spot I picked out of the rock, a few feet above the stream, a fragment of foliage of a new fossil *Sequoia* closely allied to the still-living giant American trees. Living also at the same time were various Abietineæ (Fir-trees) some genera now extinct, and some amazingly like the living *Pinus*, which are the oldest of their type to show the characteristic structure of the wood which is so salient a feature of *Pinus* to-day. In the same forests were grown Angiosperms of remarkably modern type, as we can tell from the woody branches of Dicotyledons which drifted into the same deposit as *Bennettites* both in the Isle of Wight and in Kent. For, though the first and most important, the Isle of Wight is not the only place in England where *Bennettites* has been found in the Lower Greensand—that period of transition and the entry on the scene of the newer types which hold the field to-day; in the region now called Kent, and then also under sea-water, drifted together great logs of woody Angiosperms and another species of *Bennettites*. Of the herbaceous contemporaries humbly nestled round the massive *Bennettites* we know nothing, except that they must have been of the meek which inherit the earth.

“Nor is it surprising that we know nothing of the smaller and more delicate plants when we remember that the rocks which provide the remains of this flora are all marine and the plants must have drifted some distance before being overwhelmed and entombed.”

DESCRIPTION OF THE PLATES.

Plate i.—*Bennettites Gibsonianus*.

Side-view of the stem, seen in section through the region of the leaf-bases. Several fruits are present, two of which, at the top of the figure, are clearly seen. The left-hand fruit shows the seeds (white); the right-hand one is cut through the stalk. About half natural size.

Plate ii.—Transverse section of the stem showing pith, wood, cortex and leaf-bases. On the right a pear-shaped fruit is shown, cut longitudinally. About half natural size.

Plate iii.—Fruit in longitudinal section. The light oval bodies are the seeds. About natural size.

The above are from photographs of the type specimen in the collections of the British Museum (Natural History). They were kindly taken for me by Mr. G. A. Rendle, son of the Keeper of Botany, Dr. A. B. Rendle, F.R.S.

Plate iv.—*Bennettites Saxbyanus*.

Transverse section of the stem, showing the large pith, the narrow zone of wood, the vascular strands, the cortex, and the leaf-bases. About half natural size.

Plate v.—Longitudinal section of the upper part of the same specimen. The leaf-bases are particularly well shown.

Plates iv. and v. are from photographs of the type specimen in the British Museum, taken by the kind permission of the Keeper of Geology, Dr. A. Smith Woodward, F.R.S.

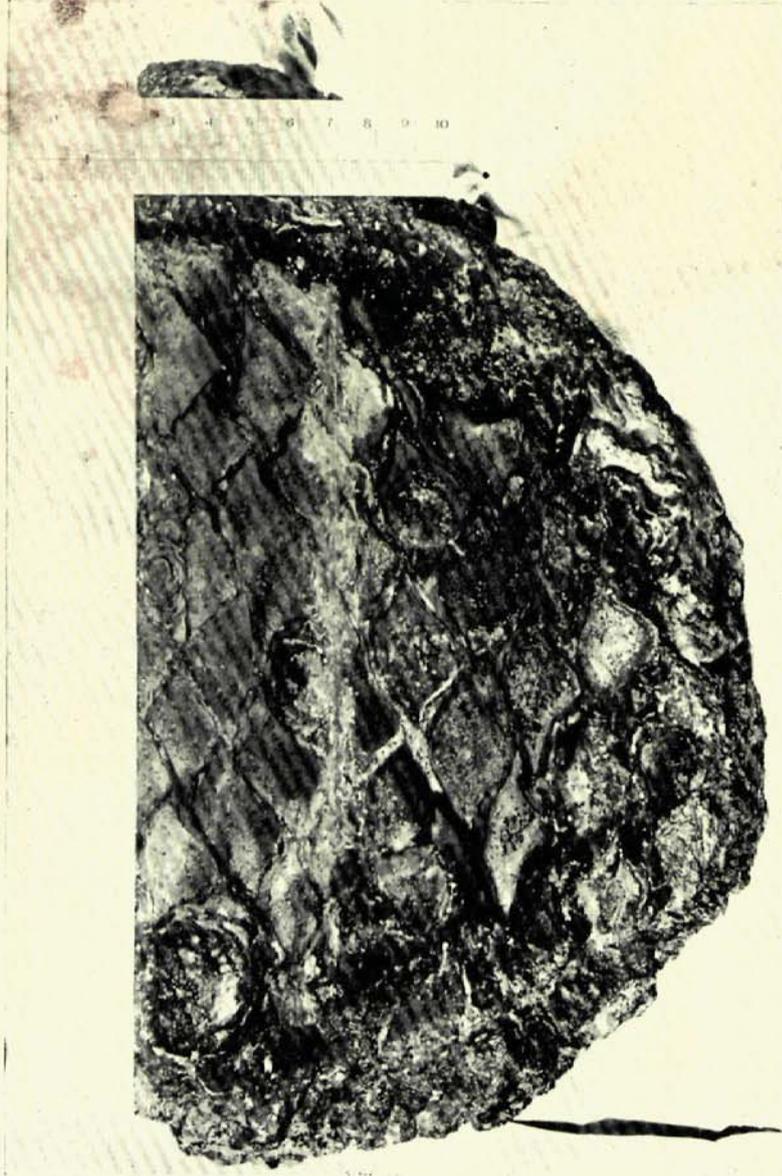


PLATE I. BENNETTITES GIBSONIANUS.



PLATE II. BENNETTITES GIBSONIANUS.

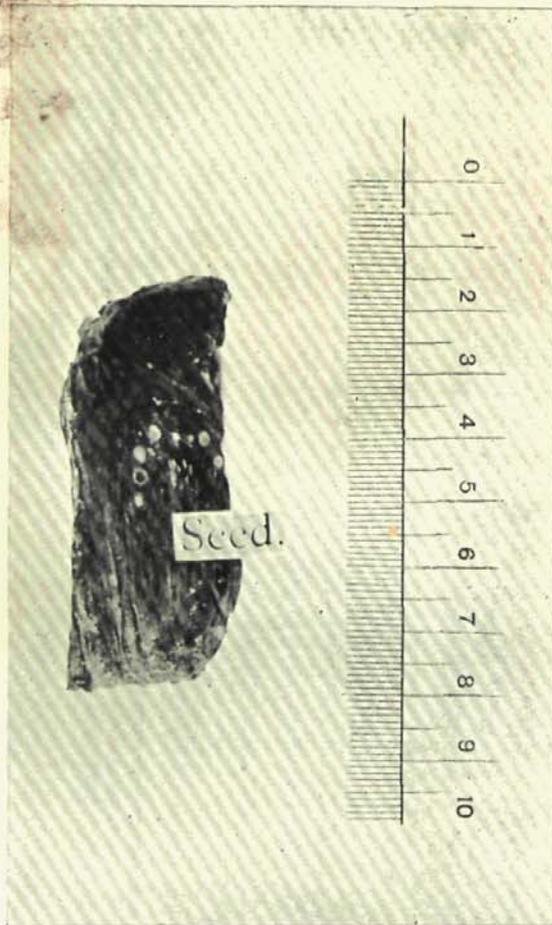


PLATE III. BENNETTITES GIBSONIANUS.

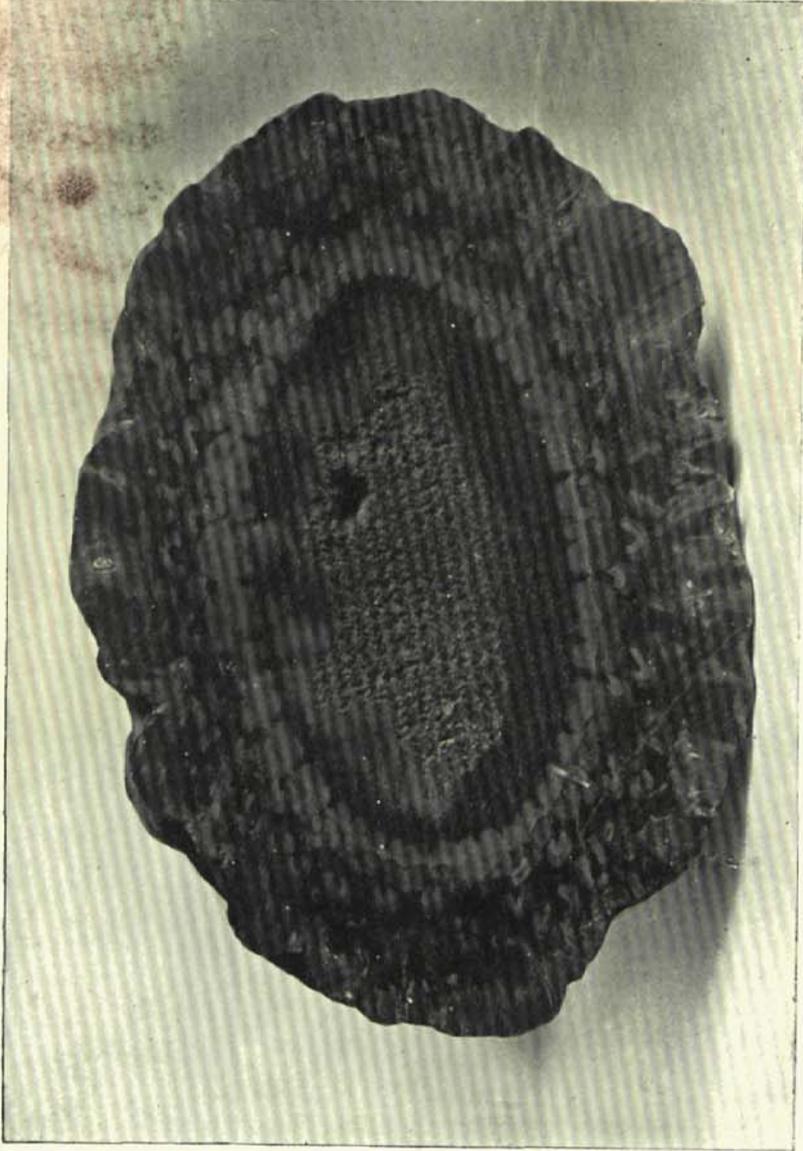
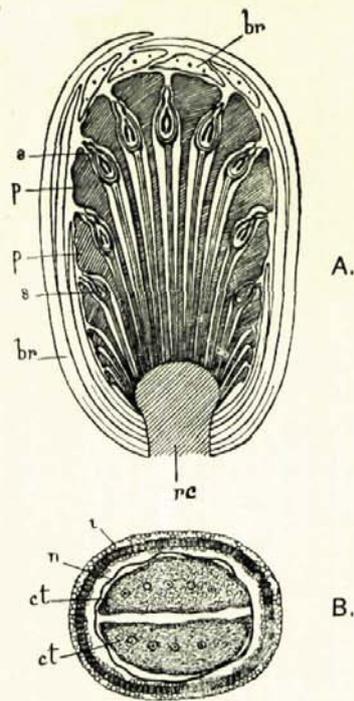


PLATE IV. BENNETTITES SAXHYANUS.



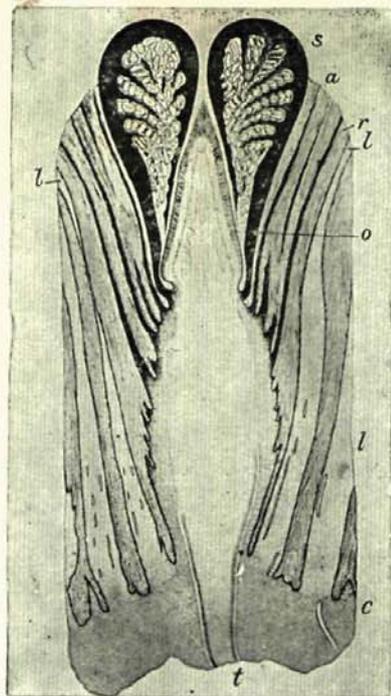
PLATE V. BENNETTITES SAXBYANUS.



Text Fig. 1. Bennettites Gibsonianus.

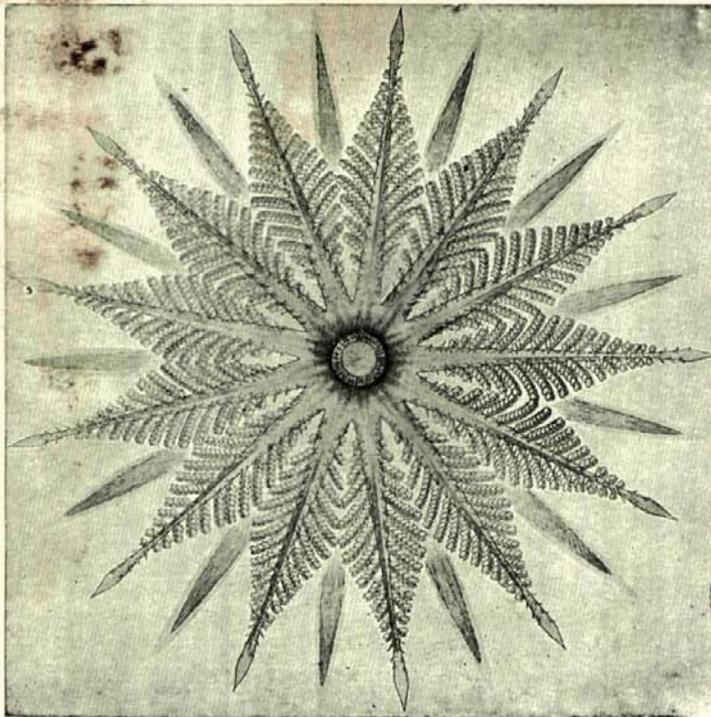
A. Diagram of the fruit in longitudinal section. *br.*, bracts, overlapping at the top; *s.*, seeds, on long pedicels (in each seed the dicotyledonous embryo is indicated); *p.*, interseminal scales (more numerous in reality) dilated above, to form collectively the wall of the fruit; *rc.*, receptacle.

B. Transverse section of a seed. *i.*, the seed-coat; *n.*, remains of nucellus; *ct.*, the two cotyledons of the embryo, cut across, each containing several vascular strands. Magnified about 12 times.



Text Fig. 2. *Bennettites dacotensis*.

Median longitudinal section of a bisexual flower. *t.*, base of the flower-stalk, which ends above in the conical, ovule-bearing receptacle, *o.*; *s.*, the large compound incurved stamens, with their numerous pollen-sacs; *a.-r.*, bracts (incomplete); *l.*, leaf-bases of the main stem; *c.*, cortex of the main stem. About two-thirds natural size. From Wieland.



Text Fig. 3. *Bennettites ingens*.

Open flower seen from above, showing the central ovule-bearing receptacle, the circle of 13 compound stamens, bearing pollen-sacs on their leaflets, and the hairy bracts. About half natural size. From Wieland.