On the Origin of Angiosperms. By E. A. NEWELL ARBER, M.A., F.L.S.,
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(With 4 Text-figures.)

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INTRODUCTION.

THE recent progress in our ideas as regards the phylogeny of the Gymnosperms,
and more especially of the present day Cycads, led us, in 1903, to begin an
enquiry into the origin of Angiosperms. During the last three years we have
devoted considerable attention to the living members of this group, for it was
thought that the attack could be best begun by taking as broad a survey as

possible of their varied types of fructification, with a view to determining which among them exhibit features that strike us as being of a more or less primitive nature. Having completed this study, we have endeavoured to test the accuracy of our conclusions by an appeal to such evidence as is presented by fossil botany. The result has been that our previously ascertained notions, as to the constitution of the flowers of comparatively primitive members of the group, have been found to agree to a remarkable extent with the facts presented by the fructifications of some, now well-known, Mesozoic fossils. So close is this agreement, that the phylogeny of the Angiosperms in its broad outlines seems to us to be sufficiently clear to permit of the construction of a working hypothesis towards its solution.

It appears to us that although the direct ancestors of the Angiosperms are as yet unknown in the fossil state, this line of descent can now be traced back to the great group of Mesozoic Cycadophyta, and to a hypothetical race of plants nearly related to the Bennettiteæ. There would seem to be good reasons to connect the Cycadophyta themselves with the Fern-like Spermophytes, or Pteridosperms, of the Palæozoic period, and thus the Angiosperms, on our hypothesis, can be derived ultimately from an as yet unknown, fern-like ancestor, existing at a very early geological period.

In this connection the publication of Wieland's full account of the 'American Fossil Cycads' has furnished us with data with regard to the Mesozoic Cycadophyta which, until recently, we did not possess, and to the author of this magnificent volume we would gratefully express our indebtedness for the material which he has placed at our disposal.

We have from the first recognized that what is called the problem of the origin of Angiosperms is in reality a plexus of problems. In addition to the evolution of the flower, there is the puzzling type of Angiospermous foliage, and many other questions to be explained in connection with this group. At the time when we commenced a consideration of this subject, there could hardly be said to be a clue to the mystery in which these matters were shrouded. In presenting this, the first definite hypothesis with regard to the phylogeny of the race, we are aware that many of the main points of our argument are devoid of novelty. Others, notably Hallier, have already brought forward arguments or facts, of which we have made free use in this attempt to fashion our theory.

The subject is a large one, and the present communication is to be regarded as a brief *résumé* of a discussion which we hope to elaborate more completely elsewhere. For the present we have contented ourselves with a statement of the main features of the problem, and its solution, with brief evidence in support of our views.

We would take this opportunity of expressing our sincere thanks to Dr. D. H. Scott, F.R.S., for many suggestions during the past three years, and for the interest he has taken in the progress of the work.

HISTORICAL.

The great race of plants, commonly referred to as the " Flowering Plants," differ so obviously from the rest of the Vegetable Kingdom, that they were recognized, comparatively early in the history of botanical study, as forming a distinct group, and for a long time attention was almost entirely concentrated on them.

The stamens and carpels were soon identified as the male and female organs respectively, and by the close of the 17th century Camerarius had shown that reproduction by means of seeds depends on the male element, the pollen, reaching the receptive part, or stigma, of the female organ ; though what exactly happens in the process of fertilization remained mere guesswork until many years later. This establishment of the sexual theory of reproduction in Flowering Plants led to the subdivision of the Vegetable Kingdom, by Brongniart in 1843, into two great groups, the Phanerogams and the Cryptogams, the latter still being incorrectly regarded as devoid of sex, and as possessing a ' cryptic ' type of reproduction.

The researches of Robert Brown led to the distinction of Gymnosperms as opposed to Angiosperms, though for many years the former were commonly looked upon as a detached group or appendage of the Dicotyledons, with the consequence that the terminology of the *flower* came to be applied to their very different kind of fructification. Hofmeister's classical researches, published in the years 1849 and 1851, completely broke down the barrier separating the Phanerogams from the Cryptogams ; in fact these terms were no longer applicable in their original sense, for their meaning had become reversed, since the Flowering Plant was found to be more ' cryptogamic ' as regards its manner of sexual reproduction than the Fern. The alternation of generations, so clear in the Pteridophytes, was shown to be also present in both Gymnosperms and Angiosperms. The male and female prothalli of the heterosporous Vascular Cryptogams had their very reduced representatives in the pollen-grain and embryo-sac respectively of the Phanerogams.

These discoveries, followed so closely by the publication of Darwin's ' Origin of Species,' gave a great impetus to the evolutionary hypothesis as applied to plants, and a great stimulus to phylogenetic speculations.

Though the various parts of the embryo-sac of the Conifer could be interpreted in terms of the female prothallus of a heterosporous Pteridophyte, investigations of the corresponding organ of the true Flowering Plant (either Monocotyledon or Dicotyledon) failed to show any such clear homologies. In other words the gap that originally existed between the Phanerogams and Vascular Cryptogams was now bridged, and in its place there appeared a wide gulf between the Conifers and true Flowering Plants, or more exactly between the Gymnosperms as a whole and the Angiosperms.

The subsequent tendency of various lines of research, until quite recently, has been on the one hand to draw closer together the ties of relationship existing between Gymnosperms and Pteridophytes, and on the other hand to increase the isolation of the Angiosperms. For instance, one of the most important embryological facts, recently brought to light, linking together the Gymnosperms and the Pteridophytes, is the formation of antherozoids in the pollen-tubes of *Cycas* and *Ginkgo*.

Much work has been done on the embryo-sac of Angiosperms, primarily with the hope of throwing light on the question of its homologies, and the line of descent of the group. Practically every Angiospermous family, which is of interest phylogenetically, has now been examined, including quite recently the Magnoliaceæ *. The outcome of the whole of this vast investigation has merely emphasized the great difference which exists between the Angiospermous and Gymnospermous embryo-sacs, and in addition the great similarity between those of the Dicotyledons and the Monocotyledons. Variations do occur, but these appear to us to be points of detail rather than of fundamental importance. In fact they are of such a kind that it is uncertain whether they should be best regarded as primitive or as recently acquired. This is particularly true of the antipodals, a group of cells more variable perhaps than any of the other constituents of the embryo-sac. Though the net result of these studies has so far not enabled us to bridge the gap between the Angiospermous and Gymnospermous embryo-sacs, yet additional discoveries of great interest have been made, *e. g.* double fertilization and chalazogamy. The former seems to increase rather than to diminish the difficulty of explaining the Angiospermous embryo-sac and especially its endosperm in terms of the fern-prothallus, or the female gametophyte of the Gymnosperm.

Turning now to palæobotanical work, the main result has been the same. Remarkable fossils have been found connecting the Gymnosperms more closely with the Ferns, but anything of a like nature bearing on the Angiosperms has remained hidden. The rocks have been singularly silent as regards the origin of the latter group, now predominant in the vegetation of the world.

The existing Cycads, and less clearly the Conifers, have been linked up with the Ferns by means of the anatomical investigations of certain Palæozoic petrified stems possessing fern-like characters, known as the Cycadofilices, and by the discovery of the seeds and male fronds of these plants. The old idea of connecting the Gymnosperms with the Lycopods is now no longer tenable, at any rate so far as the Cycads are concerned. The Angiosperms, on the other hand, have been considered to have sprung from the Ferns; yet no work on the existing Filices has shown any direct connection between the two groups. It is true that *Isoetes* † has been brought forward as revealing in the mode of origin of its stem, root, and first leaf, as well as in its adult

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* Strasburger (1905).   † Campbell (1891) pp. 253–254.

vegetative features, points of close resemblance to certain Monocotyledons, but to build a relationship upon such slight evidence appears to us hardly worthy of serious consideration. In fact Campbell himself says * : "There is, however, an immense interval between the flower of the simplest angiosperm and the sporophylls of *Isoetes*, and it would be rash to assume a relationship unless more evidence can be produced on the side of the angiosperms to warrant this."

It is generally held that when we first meet with fossil Angiosperms in the Mesozoic rocks, the leaf-impressions closely resemble those of existing genera. Whence they sprang has hitherto remained a complete mystery.

Saporta and Marion †, some twenty years ago, in their work entitled L'Évolution du Règne végétal,' brought into use the term Proangiosperms for a hypothetical group of extinct plants which gave rise to the modern Monocotyledons and Dicotyledons. They went even further, and included such fossils as *Williamsonia* among the members of this group. These suggestions we think were particularly happy, considering the material then at their disposal. In the main palæobotanical science at the present time supports them.

A brief reference must be made to the supposed connection between the Angiosperms and the Gnetaceæ. Of all the existing Gymnosperms, this particular group has long been considered to show the largest number of features in common with the true Flowering Plants. Attempts, however, to establish a clear relationship have not met with much success.

Lotsy ‡, from an embryological study of *Gnetum*, came to the following conclusions. The group appears to be of very ancient origin, it probably arose independently of the other Gymnosperms direct from the heterosporous Pteridophytes, and, moreover, has not given rise to any single Angiosperm.

Lignier §, more recently, from a general examination of the Gnetacean fructifications, also decides against any direct relationship. He says that such a complex inflorescence as that possessed by the Gnetaceæ cannot be held to show any affinity between this group and the simplest Angiospermous flower. Hence he concludes that the Gnetaceæ are not intermediate between the Gymnosperms and Angiosperms.

Miss Benson ‖, on the other hand, since the publication of these two memoirs, has endeavoured to bring the floral morphology of this group into line with that of the Angiosperm. She suggests that the suppression of the internodes in the inflorescence of *Gnetum* may have been carried still further, so that the whole is reduced to a conical torus, that is to a structure resembling the receptacle of a flower like *Liriodendron*. This seems a complicated, and hardly justifiable hypothesis, for there is no evidence to

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* (1901) p. 254.   † Saporta & Marion (1885).
‡ Lotsy (1899).   § Lignier (1903²).
‖ Benson (1904).

show that such simple flowers as those possessed by the Magnoliaceæ are in reality compound structures, i. e., very compressed inflorescences. Everything points in the other direction, namely that the sporophylls (stamens and carpels) are borne directly on the main axis of the floral shoot.

Hallier *, quite recently, has suggested a possible connection between the Gnetaceæ and the Loranthaceæ. Though agreeing in the main with his phylogenetic views respecting the Flowering Plants as a whole, we are inclined to regard this as a somewhat rash, though ingenious speculation ; especially because it necessitates, as he admits, the nucellus of *Gnetum* being regarded, not as a single ovule, but as a placenta bearing several ovules.

Finally, then, we may conclude that the study of the Gnetaceæ does not, and does not seem likely to, help us in understanding the phylogeny of existing Angiosperms. It would appear more probable that a knowledge of the descent of the latter, obtained from other sources, will itself shed light on the relationships of the former.

From a discussion on the vascular structure of seedlings, at the last meeting of the British Association at York †, the inference may be drawn that some help will be forthcoming from this line of study towards solving the problem of the origin of the Angiosperms. So far, the examination of the " transition " phenomena in seedlings has led Mr. Tansley and Miss Thomas to regard the simple type met with in the Dicotyledons, and most of the Coniferæ, as derived by reduction from the more complicated one found in the Cycads and the Araucarieæ.

Thus, by way of summary, it may be said that no definite theory, as regards the origin of the Angiosperms, has up to the present been elaborated. The views put forward from time to time have been more of the nature of casual suggestions. The problem has not yet been separately treated as a whole, in all its bearings. The morphologist has perhaps hitherto inclined only to a comparison between living members of the race, with neglect of the fossil evidence. The palæobotanist, in approaching the subject, does not appear to have arrived at any clear conception of what may be considered the primitive features of living Angiosperms.

In concluding this section of the paper, it is interesting to note that this unsolved problem has its parallel in the Animal Kingdom. The origin of the highest group, the Mammalia, still remains largely problematical.

PRINCIPLES OF EVOLUTION.

Before discussing what we regard as the primitive forms of the various organs of the Angiospermeæ, we would emphasize briefly certain principles connected with evolution to which we attach considerable importance when attempting to trace the phylogeny of living or extinct races.

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* Hallier (1905).   † Anonymous (1906) p. 182.

The Law of Corresponding Stages in Evolution.

If we study the stages in evolution reached by the different organs of a seed-plant at any one period, we shall find that they are dissimilar. Some are obviously more highly evolved than others. Corresponding stages in the evolution of the various members of a seed-plant are not contemporaneous in point of time. Conversely, at any one period in geological time, one organ or set of organs will be found to have reached a far higher stage of evolution than another.

The study of fossil botany has afforded numerous instances of the truth of this principle. The foliage of the Pteridospermeæ, as also the habit of the stem, is essentially fern-like, though the female organ is a seed. The male organs (*Crossotheca*) of *Lyginodendron* are obviously far less highly evolved than the female (*Lagenostoma*). The former is essentially a simple fern-like fructification, the latter a highly evolved seed.

Or, again, to turn to the Bennettiteæ, the Mesozoic descendants of the Pteridospermeæ, the microsporophylls are still essentially fern-like fronds, while the megasporophylls are of an extremely advanced type. The trunk habit of these plants also shows scarcely any modification as compared with that of a Palæozoic tree-fern.

Or to turn to recent plants. The fern-like foliage of the Cycad *Stangeria* is associated with highly-evolved strobili. Again, the female sporophyll of *Cycas* is more primitive than the male, and its fern-like origin is still traceable.

Other instances might be quoted *, but the above may suffice. It follows from this law that there was never in existence such a plant as a really primitive Angiosperm, in the sense that all its organs were equally of a primitive nature. On the contrary, the earliest Angiosperms were no doubt characterised by possessing some members much more highly evolved than others. There is reason to believe that the Angiosperms were derived from other seed-plants, but that the seed, in itself a highly evolved structure, originated at a much more remote period.

We believe that the application of this principle will be found to be of great service in such considerations as the present. At a later stage (p. 70) we propose to demonstrate by its aid the probability that the earlier Angiosperms still retained the megaphyllous foliage of their ancestors ; a supposition which will explain several puzzling facts.

Homoplasy.

It is well recognised that one of the great difficulties to be faced in attempting to trace the phylogeny of living groups lies in the tendency to error, arising from laying stress on certain features as indicative of close

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* See Wieland (1906) p. 244, who has also discussed this law.

relationship, which are more probably simple expressions of parallelism of development. Sometimes the issue is so obscured by numerous instances of homoplasy, that it is difficult to arrive at any sure conclusion. The broad question of the phylogeny of Angiosperms, however, seems to us to be remarkably free from embarrassment in this respect.

Mutation.

While we regard the course of evolution as for the most part a slow and gradual process of variation, we are prepared to admit that, now and again, abrupt and discontinuous phases * occur. The same conclusion holds in regard to theories connected with inorganic evolution. Catastrophism has been replaced by uniformitarianism, which in turn is succeeded by a theory, which admits that, at certain periods, the forces of nature may have been working at a greater intensity than they are to-day.

There is a bare possibility that mutation may have been concerned with the evolution of the Angiosperms themselves, for the suddenness with which this group rises to the position of a dominant type in the flora of the Cretaceous and Tertiary periods is perhaps difficult to explain on any other hypothesis, unless we accept the theory of the imperfection of the geological record in this instance.

One of the great difficulties which arises from our still highly imperfect knowledge of the Mesozoic floras is that at present, in the great majority of instances, we are familiar only with the foliage of these plants. Among such leaf impressions, the absence of any conspicuous intermediate forms combining features common to the Angiosperms and any other group is remarkable, and this evidence, though not perhaps of great importance, may admit the possibility of mutation rather than of gradual variation (see p. 71). On the other hand, too free a use of this principle is not to be favoured, else there is a distinct danger that mutation may become the last resort of the phylogenetically destitute.

PRIMITIVE FEATURES AMONG LIVING ANGIOSPERMS.

The Strobilus Theory of the Angiospermous Fructification.

The basis of our theory as to the nature of a typical Angiospermous flower is that such a fructification consists essentially of a strobilus or cone †. We regard the simpler, unisexual flowers, including apetalous forms, as derived from a amphisporangiate ‡ strobilus by reduction. The term " flower " has

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* De Vries (1901, 1905).   † Coulter & Chamberlain (1904) p. 9.

‡ The terms " bisporangiate " and " ambisporangiate " have been used by Wieland and other authors. We regard these terms as open to objection, and propose to adopt " amphisporangiate " in their place, as the antithesis of " monosporangiate."

been used in a great variety of senses *. We would, however, restrict its application to the Angiosperms alone, since it was from these plants that the idea expressed by the word originally arose. In our opinion extra-seminal pollination, in which the carpel or carpels play the chief part in the pollen collection, is the essential feature of a hermaphrodite, or female flower. We regard a flower as typical when it possesses both micro- and megasporangia, as well as a perianth which in many cases has an attractive function.

A flower, on our view, is a *special form* of a type of strobilus, which is common both to the Angiosperms and to certain Mesozoic plants, and which may be termed an *anthostrobilus*. The anthostrobilus of hypothetical Mesozoic ancestors of the Angiosperms, and of their supposed near relatives the Bennettiteæ, differed from the flower of the Angiosperm in certain important respects, especially in the presence of direct pollination, in which the megasporophyll played no part. It may perhaps be useful to distinguish it as a *Pro-anthostrobilus*, and the Flower proper, a term here restricted, as an *Eu-anthostrobilus*.

Anthostrobilus
{
Pro-anthostrobilus of Mesozoic Ancestors and Bennettiteæ.

Eu-anthostrobilus (Flower) of Angiospermeæ.

The necessity for these new terms arises from the fact that the word " flower " has been applied in many different senses, for instance even to the strobili of the Coniferales. Also because, as we hope to show here, the Angiosperms are descended from Mesozoic ancestors nearly related to a group of fossil plants, whose fructification is now well known, and indeed has been, though as we think inaccurately, termed a flower.

We shall discuss at some length at a later stage the evidence for the derivation of the Eu-anthostrobilus from the Pro-anthostrobilus—types of cones which we believe represent different stages in the evolution of the fructification of one and the same line of descent.

The strobilus or cone is of course a very ancient type of fructification, common to many distinct, and only very remotely related lines of descent. Other forms of strobili were borne by plants which flourished at a very much earlier period in geological time than the anthostrobilate races discussed here. The anthostrobilus is distinct from any of these, and it is, in all probability, the newest modification or creation of the strobilate form of fructification, in point of geological time. It differs from all other strobili in that it is typically amphisporangiate, by the megasporophylls being invariably aggregated on the axis of the strobilus above the microsporophylls (*i. e.* nearer the apex of the cone), and by the presence of a distinct perianth, below the fertile sporophylls, whose function is apparently wholly, or partly, of a protective nature. In

* Coulter & Chamberlain (1904) p. 9.

other words, the protective office, which in the strobili of many Pteridophyta is performed by the aggregate of the fertile sporophylls themselves, is, in the anthostrobilus, localised towards the base of the cone, and performed by sterile members. In order to bring out more clearly the essential features of the anthostrobilus, we may compare it briefly with a heterosporous cone of an ancient type, such as that of *Lepidodendron Hibbertianus*, Binney *, from the Lower Carboniferous of Scotland.

	L. Hibbertianus, Binn.	*Anthostrobilus.*
Elongated axis	cylindrical.	more or less conical.
Megasporophylls situated	basally as regards the microsporophylls.	apically as regards the microsporophylls.
Protective function performed by	distal extremities of both types of fertile sporophylls.	sterile, basal, leaf-like organs.

ENGLER'S THEORY.

The Strobilus Theory of the nature of the typical Angiospermous flower is not by any means a new one †, though it differs *in toto* from that generally accepted by systematists at the present time. According to current notions, widely but not universally adhered to, the primitive type of Angiospermous fructification is to be sought for among the unisexual Apetalæ, which, on our view, are forms reduced from amphisporangiate strobili, in each case possessing a perianth.

This prevailing opinion, for which Engler ‡ is largely responsible, has been too readily accepted § as a self-apparent axiom, before careful examination of its truth has been made.

In a recent authoritative discussion of this question, Coulter and Chamberlain ‖ state that as a consequence of the now " discarded doctrine of metamorphosis . . . . it has been a very prevalent conception, therefore, that flowers of simpler structure than the assumed type are reduced forms. There are certain cases in which this seems clear . . . . but the vast majority of simpler flowers are better regarded as primitive than as reduced forms."

On the other hand there have not been wanting others ¶, especially Hallier **,

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* ;See Scott (1900) p. 162, fig. 65.
† Coulter & Chamberlain (1904) pp. 9 & 10.
‡ Engler (1897) p. 358.   § Chamberlain (1897).
‖ Coulter & Chamberlain (1904) p. 10.
¶ Henslow (1893[1]) p. 485; Čelakovský (1897).
** Hallier (1901[1], 1901[2], 1903, 1905).

who have already upheld the view maintained here. Goebel *, in particular, regards the amphisporangiate condition as primitive, and the monosporangiate as derived from it.

It will be necessary here to examine somewhat at length the evidence for the assumption that certain naked flowers may be regarded as primitive, and the consequent corollary that their near relatives, with insignificant perianth, are derived from them.

The main departure of Engler's and Eichler's systems of classification from that of Bentham and Hooker consists in the abolition of the large group Monochlamydeæ or Incompletæ, and the distribution of its families among the Polypetalæ, making one large series, the Archichlamydeæ or Choripetalæ ; without question a move in the right direction. At the same time both Engler and Eichler cease to regard the Ranales (Polycarpicæ) as the starting point of existing Dicotyledons. They commence their systems with plants possessing flowers composed of few parts, especially the Piperaceæ and its near allies, and also with the Amentiferous families. Their scheme of classification then gradually advances from plants with naked flowers to others possessing an insignificant sepaloid perianth, and finally to such orders as the Caryophyllaceæ with a well-marked calyx and a conspicuous corolla. From this point of view, the gradual evolution and differentiation of a perianth can be traced in a general way.

Three objections of considerable weight can be advanced against this theory. In the first place, it must be assumed that the perianth is evolved *de novo,* and is an organ *sui generis.* Secondly, in many of the groups regarded as primitive, *e. g.,* Piperales, Amentiferæ, and Pandanales, the inflorescence is a sharply defined and often a highly complicated structure. Lastly, such a theory has so far proved barren from a phylogenetic standpoint, especially when the attempt is made to bring into line evidence derived from the study of fossil plants.

We may now briefly examine the cohorts which Engler regards as showing primitive features.

Piperales.

This cohort is placed first in Engler and Prantl's system, and includes four orders, of which only the Piperaceæ is well represented by the species of two genera *Piper* and *Peperomia.* A survey of its members suggests that its flowers are fashioned, for the most part, on the trimerous plan, with two whorls of stamens and three carpels. No one would argue that a species of *Piper* with only two stamens has preceded one with six, nor that one with three carpels has been derived from an ancestor with a single carpel. Nor is it to be supposed that a genus like *Chloranthus,* with a single tepal, has given rise to one

* Goebel (1905) p. 528.

like *Lacistema*, with a complete perianth whorl. It is much more natural to suppose that the other members of the whorl have been aborted, and that such genera as *Piper* and *Peperomia* have been evolved by further reduction, during which the perianth has disappeared altogether. In the monotypic genus *Lactoris*, placed by Engler in the Ranales, but by Bentham and Hooker, among others, in the Piperaceæ, can be found a synthetic type linking these two cohorts together *.

Thus, in our opinion, the more obvious and plausible view is that the Piperales branched off, probably at an early period, from the Ranales, and, as in the case of many other Angiosperms, have suffered considerable reduction in the individual flower, so much so that in many instances they have lost their perianth. This line of evolution appears to have progressed side by side with a tendency to aggregate the flowers into dense spikes ; the bracts assuming more and more the functions originally performed by the perianth. In a few of the Piperales the grouping of the flowers has advanced a stage further. In the Peppers of the section *Potomorpha* the spikes are arranged in umbels. Such compound inflorescences surely are hardly characteristic of "plants of low organisation" †.

Both the recent studies of the seed-development of the Piperales by Johnson ‡, and of the seedling-structure by T. G. Hill §, have led these authors to conclude that this is not to be regarded as a primitive cohort.

Amentiferæ.

The term Amentiferæ is used here, for the sake of convenience, to include those families of trees characterized by unisexual flowers—or at least the male flowers—crowded together into very dense and definite inflorescences known as catkins ; a type of inflorescence which is shed entire, and thus functions largely as a single flower. In some families, *e. g.*, those included in Engler's cohort Fagales, the catkin is of a highly complex and compressed nature—a feature hardly suggestive of primitiveness, but rather of a reduction in the component parts. In such, a suppression of the perianth might naturally be expected.

Salicaceæ.—This family consists of two genera only, *Salix* and *Populus*, the one entomophilous, the other anemophilous. Divergency of opinion exists as to whether the entomophilous habit of *Salix*—an almost unique occurrence amongst the Amentiferæ — is to be regarded as a primitive feature, or one derived from a Poplar-like ancestor by a change in the method of pollination.

Chamberlain ‖, from an embryological study, concluded that the genus

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* Hallier (1901²).   † Willis (1904) p. 515.   ‡ Johnson (1905).
§ Hill, T. G. (1906).   ‖ Chamberlain (1897).

Salix is primitively unisexual, diœcious, and naked. Robertson [*], on general grounds, considers *Populus* the more recent genus.

On the other hand, the opposite view has been maintained, and has quite recently received strong support from Haines' [†] descriptions of two new species of Indian Poplars. One of these, *Populus glauca*, Haines, frequently possesses hermaphrodite flowers with an undoubted perianth.

To us it appears to be the more reasonable view to regard *Populus* as the older genus, and *Salix* as derived from a Poplar-like ancestor at a more recent period. On this view, *Populus glauca* has retained more primitive features than the other species, and thus departs less from the ancestral type, while the entomophily of *Salix* is but a recently acquired character. It also implies the derivation of a flower such as that of *Salix*, which has only two stamens and never more than two carpels, by reduction from a plant like *Populus*, possessing many stamens and sometimes more than two carpels. At the same time, we regard *Populus* itself as not primitively anemophilous, but derived originally, with the other Amentiferous families, from entomophilous ancestors.

Another fact to be taken into consideration in this connection is that, at the present day, the genus *Salix* is largely represented by species, whereas *Populus* contains comparatively few. The former thus appears to be a plastic up-grade type, as is further emphasized by the ill-defined nature of many of its species. The re-adoption of entomophily has possibly been the saving of the Willows.

Casuarina.—For those who uphold the view that some of the present day Angiosperms without perianth are primitively naked, this genus has been perhaps the most promising. In several features it strongly suggests the retention of archaic structures. Attempts have been made to separate it entirely from the rest of the Dicotyledons. Treub's [‡] suggestion, based on the initial discovery of chalazogamy, broke down when the fact was ascertained that many of the Amentiferæ, as well as other groups, also exhibit this mode of fertilization. On the other hand, Engler [§] regards *Casuarina*, which he places in a new cohort Verticillatæ, as the most primitive of Dicotyledons, from the fact that many megaspores are found within the nucellus. In the light, however, of recent research this conclusion is by no means justified, for Chamberlain [||] finds that more than one megaspore occasionally occurs in *Salix*. Still more recently Shoemaker [¶] has shown that in *Hamamelis* several megaspores are found. Frye's [**] study of the embryo-sac of this genus has demonstrated that it is quite of the usual type, and does not differ as regards

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[*] Robertson (1904).   [†] Haines (1906).
[‡] Treub (1891).   [§] Engler (1897) p. 362.   [||] Chamberlain (1897).
[¶] Shoemaker (1905); see also Coulter & Chamberlain (1904) p. 242.
[**] Frye (1903).

the presence of antipodals, or the time of endosperm formation, from that of other Dicotyledons, as Treub supposed. It has been further suggested, within the last year, on embryological evidence, that *Casuarina* is closely related to *Carpinus*, and may be placed within the Betulaceæ as a group of equivalent rank with the Coryleæ [*].

Consequently, on such arguments as have been brought forward, we fail to find conclusive evidence that the flower of *Casuarina* is essentially of a primitive nature. Nor does the position of the group now appear to be isolated.

Fagales.—The perianth of the female flower, when present, is superior and somewhat gamophyllous. These are not likely to be the characters of a primitive perianth. Besides, the syncarpous inferior ovary does away with any idea of primitiveness as regards the whole flower. The inflorescence is also especially complicated. Similar considerations apply equally to the Juglandales.

We are inclined to adopt Hallier's [†] view, that this group can be connected with the Hamamelidaceæ, and thus with ancestors possessing hermaphrodite flowers and biseriate perianths. On this supposition, the perianth of the Fagales may probably be regarded as a survival of the calyx, the corolla having disappeared completely.

Monocotyledons.

Among the Monocotyledons we find certain genera which may very possibly be ancient types, without, or with a only very insignificant perianth. Hence the question arises whether these plants were originally without such an envelope.

Pandanales.—To this group, regarded as among the most primitive by Engler [‡], and also by Coulter and Chamberlain [§], we think the same arguments apply as in the case of the Piperales and Amentiferous families. The inflorescence is of a very dense and sharply defined nature. In the Pandanaceæ the individual flowers are difficult to make out, bracts and bracteoles being absent. It seems much more probable that in this case the perianth of the individual flowers, as well as the bracts and bracteoles of the inflorescence, have totally disappeared, and the internodes of the floral axis become greatly reduced, with the result that the individual flowers, especially the male, have become so merged together that they can hardly be distinguished from one another. Consequently we are inclined to think that the Pandanaceæ branched off at some early period from the main line of the Monocotyledonous descent, and are thus capable of being derived from an ancestor with hermaphrodite flowers and a well-developed perianth.

Araceæ.—In the interpretation of the Araceous flower we are in general agreement with Engler. He regards those members of the family with few

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[*] Benson, Sanday & Berridge (1906) p. 43.   [†] Hallier (1903).
[‡] Engler (1897) p. 360.   [§] Coulter & Chamberlain (1904) p. 228.

floral parts as reduced. Here the gradation from hermaphrodite flowers with a complete perianth to unisexual naked types presents all stages of reduction. At the same time we can trace the evolution of a complicated inflorescence. The attractive function of the perianth in a less highly evolved genus, such as *Acorus*, is transferred in many of the higher members to the spathe, which may become petaloid and envelop the whole inflorescence. In fact the inflorescence practically comes to function as a single flower.

Here we find our opponents adopting the very views which we, in common with Hallier and others, urge as applicable to all such cases where naked flowers are aggregated in dense inflorescences. If *Acorus* and its near allies were non-existent, would this interpretation of the family have met with equal acceptance ? Because these stages cannot be so easily traced in other groups such as the Piperales and Amentiferæ, the absence of a perianth in these flowers has been too readily accepted as a primitive feature.

Though Engler regards the hermaphrodite flowers of a genus like *Acorus* as the most primitive types in the order, Campbell *, on the other hand, has decided that the unisexual flower, with a single carpel and a solitary basal ovule, e. g., *Spathicarpa, Aglaonema*, and *Nephthytis*, is really the least highly evolved. This conclusion, based on embryological considerations, appears to us to rest on far too slender evidence, especially in view of the fact that no general agreement exists as to which features presented by a study of the embryo-sac may be regarded as primitive.

THE PRIMITIVE FORM OF THE ORGANS OF THE EU-ANTHOSTROBILUS OR FLOWER.

We have seen that Engler and others regard certain orders, where the flowers are devoid of perianth and often unisexual, as the more primitive members of both existing Dicotyledons and Monocotyledons. But it must not be overlooked that Engler's Theory, like the Strobilus Theory discussed here, is but a working hypothesis, the truth of which is to be sought for in its application. The, at present, prevailing view has the merit of simplicity. We start with something simple, and from it derive the more complicated types of flowers, possessing a biseriate perianth, and at the same time the hermaphrodite or amphisporangiate condition. But its application as a working hypothesis does not assist us in our search for a clue to the phylogeny of the Angiosperms as a whole. Nor does it help to bring this group into line with any of those now known to us in the fossil state. On the other hand, the Strobilus Theory, which postulates that the monosporangiate Apetalæ were derived by reduction from an amphisporangiate strobilus possessing a distinct perianth, leads us back naturally to a great group of Mesozoic plants, the Bennettiteæ, which afford the key to the ancestry of the race in question.

* Campbell (1905).

In trying to arrive at some conclusion with regard to the primitive form of
the various organs of the Angiospermous strobilus, we have found it helpful to
endeavour to conceive a mental picture of a flower in which all the members
were alike primitive. We, however, by no means wish to infer that such a
flower ever existed, for, as we have pointed out above (p. 35), this would be
contrary to the general trend of evolution, since corresponding stages in the
differentiation of the various organs of a seed-plant, at any one point of time, are

Fig. 1.
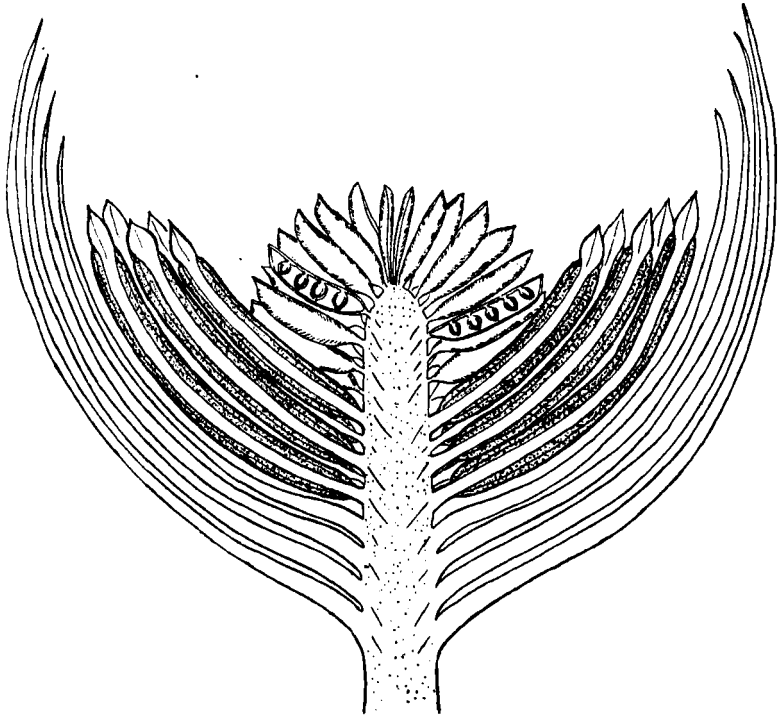
An Angiospermous strobilus or flower in which the perianth, microsporophylls and mega-
sporophylls, two of the latter being shown in longitudinal section, are represented as if
in the primitive condition. This cone is entirely imaginary, and in all probability
never existed.

dissimilar. Such a strobilus (see fig. 1) would consist of a large, elongated,
conical axis bearing megasporophylls above and microsporophylls below.
At the base of the cone, a well marked perianth would be found, con-
sisting of sterile, leaf-like members, affording protection to the cone as a
whole, and playing some part in the mechanism for insuring cross-fertilisation
by adding to its conspicuousness. All the organs of the cone would be of
large size, numerous or indefinite in number, and spirally arranged. The
cone would be solitary, borne either terminally or axillary.

The gynæceum would consist of an indefinite number of carpels forming apocarpous, monocarpellary ovaries, each containing several ovules, with marginal placentation. There would be no style. The stigmatic surface would be more or less confined to the apex of the carpel, and would probably be of a sticky nature, or the apex of the carpel may have remained slightly open, as in the modern *Reseda*. The ovule would be orthotropous, with two integuments. The carpel would dehisce by the ventral suture, and the seeds be distributed by simply falling from the carpel, or being shaken out of it by the wind. The embryo would germinate within a short period after fertilisation, and would possess two epigeal cotyledons.

The andrœcium would comprise an indefinite number of stamens, with long anthers. The filaments would be short, and the connective produced beyond the anther as a slight expansion.

The perianth would consist of numerous, spirally arranged members, either all similar in form, colour, etc., or somewhat differentiated, with an inner petaloid series serving both as an attractive and protective organ.

The mode of fertilisation would be by means of entomophily, the pollen-collecting mechanism being performed by the carpels

It will thus be seen that we regard polypetaly, hypogyny, and apocarpy * as primitive conditions, antecedent in point of time to the more highly evolved states, in which cohesion and adhesion of similar or dissimilar organs is to be found.

As we have pointed out, there is no reason to believe that any Angiosperm with a complete assemblage of primitive floral characters is to be found to-day, nor indeed that such a flower ever existed. On the other hand, there are many Angiospermous flowers which retain one or more primitive features. According to our view, the greatest number are exhibited in the families Magnoliaceæ, Ranunculaceæ, Nymphæaceæ and Calycanthaceæ, amongst Dicotyledons ; and Alismaceæ, Butomaceæ and Palmaceæ, among Mono-cotyledons.

Magnoliaceæ.

In this family we find an elongated receptacle, bearing an indefinite number of stamens and carpels, which are spirally arranged. The form of the stamen, with its long and broad connective, continued below as a very short filament and above as a sterile apex, is also a primitive feature. The perianth of the members of the two tribes Schizandreæ and Illicieæ consists of many tepals, spirally arranged. In the tribe Magnolieæ however, it is cyclic, and sometimes in three definite whorls ; a stage obviously derived from the preceding. In the allied Anonaceæ this arrangement is generally characteristic.

* See also Bessey (1897).

Certain members of this alliance also retain a primitive feature in the homoxylous character of the wood, e. g., *Drimys*, *Tetracentron*, and *Trochodendron* *. This family has already been instanced by Hallier † and others as showing a comparatively large number of primitive characters. The recent study by Strasburger ‡ of the embryo-sac of *Drimys* has shown, however, that it practically does not depart from the stereotyped form common to nearly all Angiosperms.

Ranunculaceæ.

Some members of this family present primitive features in the form of the receptacle and perianth, as well as in the fact that the numerous stamens and carpels are spirally arranged. The perianth of this group is also in many cases of a primitive nature, though often petaloid and sometimes clearly differentiated into calyx and corolla. In addition, honey-leaves, the homologues of fertile microsporophylls, may be present.

Nymphæaceæ.

In the members of this family, especially in the genus *Nelumbium*, we find numerous stamens of a similar form to those of the Magnoliaceæ, as well as certain features in connection with the perianth, which we regard as fairly primitive.

Calycanthaceæ.

The numerous, spirally arranged stamens and carpels, and the large number of perianth members may be regarded as primitive features.

MONOCOTYLEDONS.

Alismaceæ and Butomaceæ.

In some members of these closely-allied families the stamens are indefinite in number, and the carpels numerous and apocarpous, features which, from our point of view, may be regarded as primitive.

Palmaceæ.

In this large family, in many instances, the unbranched habit § and the free carpels are primitive features.

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* Harms (1897).   † Hallier (1903).

‡ Strasburger (1905).   § See Morris (1893).

The Megasporophylls and Megasporangia.

The dictum of Goethe that the carpel is a fertile leaf, more or less modified, has stood unshaken, and there appear to be such ample evidences of its truth that it need not be considered further here. Among the Angiosperms, the condition of apocarpy seems to us to be primitive. The spiral arrangement of the monocarpellary ovaries on a long receptacle, a state of affairs which still survives in the Magnoliaceæ, and in certain other members of the Ranales, may be regarded as a primitive feature of the flower. From this we derive, by suppression of the internodes, the whorled arrangement so characteristic of the great majority of Angiosperms, and often common to all parts of the strobilus. We regard the verticillate grouping as due partly to a tendency to cohesion and adhesion, which has always been marked among the Angiosperms, and partly to a proneness to a dissimilarity in the size and shape of the different organs of the strobilus. The fact that the protective function is, in this type of cone, relegated to sterile members at the base may also have had some bearing on the question ; more efficient protection being perhaps afforded where the axis is reduced in length, and the various organs arranged in whorls. The result has thus been a tendency to a horizontal rather than a vertical distribution of the organs.

There are numerous instances shown by many families, *e. g.*, Ranunculaceæ, Crassulaceæ, and Rosaceæ, of how syncarpy has arisen from apocarpy. In the great majority of the Angiosperms there has been a distinct bias in this direction, with various modifications, the significance of which is to be sought for in the fruits. Bi- and multicarpellary ovaries have been the result.

We regard the carpel as a megasporophyll, present in the ancestor of the Angiosperms as an open leaf, bearing several ovules on its margins, and not unlike the megasporophyll of *Cycas*. With the shifting of the pollen collection from the seed itself to the carpel, it became possible for the latter, both to afford more efficient protection to the developing seeds, by completely closing over them, and also, at the same time, to fulfil its new duties as a pollen receiver, by adopting some mechanism for the purpose at the apex. The necessity for some protection for the ovule is well seen in *Bennettites*, where, however, it is effected in a totally different manner. The style, probably non-existent at first, may be looked upon as a later adaptation, connected with the perfection of the method of insuring cross-fertilisation. The stigmatic surface was, in the early stages, simply a localised portion of the carpel, adapted possibly by some sticky secretion for the collection of pollen.

It need hardly be mentioned that we are in agreement with Bessey *, and other recent writers, in deriving all syncarpous ovaries from apocarpous

* Bessey (1897).

ancestors, and all inferior ovaries from ancestors in which these organs were
superior.

The ovule in the primitive Angiosperms was orthotropous. This view is
also that commonly held *. From this primitive type were derived the
campylotropous and anatropous types.

We are inclined to regard the primitive carpel as multi-ovulate †. There
is, however, a constant tendency to reduction in the number of ovules among
monocarpellary ovaries. This is especially well seen in an order such as
Ranunculaceæ. The significance is to be found in the fruits, which commonly
become indehiscent and one-seeded, i. e., achenes.

The Microsporophylls and Microsporangia.

The type of microsporophyll and microsporangium, found almost throughout
the living Angiosperms, is a very constant one on the whole, and this indicates
that these are organs which have become fixed, although in many cases there is a
strong tendency in the direction of abortion, suppression, or transformation.
We regard the stamen as a sporophyll, equivalent to the modified foliar organ,
which can be shown to have existed in the case of the Pteridospermeæ
or Palæozoic ancestor. This sporophyll bears two synangia, each, in some
respects, similar to the male organ of a Pteridosperm, e. g., *Crossotheca*.
The synangial view of the stamen is by no means a new one, but hitherto
no attempt has been made to link it with an ancestor, also possessing
this type of microsporangium. We shall endeavour to show at a later stage
(pp. 67, 68) that such a view is tenable.

Among living Angiosperms, we regard the andrœcium as primitive in such
an order as the Magnoliaceæ, especially as regards the spiral arrangement,
the indefinite number, and the form of the microsporophylls and microspor-
angia. The shortness of the filament, the length of the connective, and its
continuation beyond the anther as a sterile tip, are important features in this
connection. We are thus in general agreement with Hallier ‡ as regards
the microsporophylls of Angiosperms. From such a type of stamen, later
stages in evolution have involved modifications of the connective and
filament, resulting in the basifixed and versatile types of anther.

The Perianth.

It has been already shown that Angiospermous flowers without a perianth,
or those in which this organ is insignificant, occur in plants possessing dense
inflorescences. Solitary naked flowers, with many stamens and carpels, are
almost unknown to us. In consequence of these two facts, we believe that

* Coulter & Chamberlain (1904) p. 57.   † Prantl (1888).   ‡ Hallier (1903).

all existing Angiosperms are descended from forms with a conspicuous perianth, and that, in those plants where it is not present, its absence is due to abortion. We are thus inclined to postulate for the group a primitive perianth, which was completely differentiated, from the sporophylls on the one hand, and from the foliage leaves on the other, before the existing Angiosperms came into being. Hence we can hardly seek for its origin among their present-day representatives. At the same time we agree that the modern perianth may have, in certain instances, acquired additional members, either from above by the sterilisation of microsporophylls, or from below by the modification of foliar organs.

On this supposition, let us endeavour to arrive at some idea, from a study of living forms, of what may have been the characters of this primitive perianth, possessed by the immediate ancestors of the existing Angiosperms. Naturally we turn first to the Ranales, for in this group of families, as we have already seen, a number of primitive features appear to be retained in the androecium and gynæceum. The special points presented by the Ranalian perianth as a whole, which strike us as primitive, are the inconstant number and spiral arrangement of its members, as well as the absence of a marked separation into calyx and corolla. The perianth of the Magnoliaceæ is of special interest from this point of view, as showing transitions towards a definite number of tepals, arranged in whorls, and a differentation into a calyx and corolla. In *Illicium*, there is a gradual passage from sepaloid to petaloid tepals. In *Drimys*, the distinction between the protective and attractive parts of the perianth is more marked, though they are still spirally arranged. In *Magnolia*, and its close allies, the perianth tends to assume a cyclic arrangement, and the tepals become reduced to a definite number. *M. grandiflora*, L., and *M. stellata*, Maxim., for example, have as many as thirteen perianth members, all much alike. In *M. Yulan*, Desf., they are reduced to nine, arranged in three fairly similar whorls. *M. obovata*, Thunb., and *M. glauca*, Linn., have likewise the same number, but the three outer ones are quite small. The tendency then in this family may be said to be towards a definite perianth, comprised in three whorls. Such a floral envelope, in which as a rule the outer whorl is sepaloid and the two inner petaloid, is a constant feature of the closely allied, but more highly evolved family, the Anonaceæ.

The Ranunculaceæ are perhaps the next most interesting Ranalian family from this point of view, but the perianth here, on the whole, appears to be hardly so primitive, and is complicated by the occurrence of the so-called "honey-leaves," which we regard, in agreement with Prantl [*], as recent modifications of some of the outer stamens. We should be inclined to view

[*] Prantl (1888).

the many-leaved floral envelope of *Trollius*, with its spirally arranged and largely petaloid members, as a primitive perianth.

Without going into further details as regards the Ranales, we believe their perianth can be best explained on the assumption that their ancestors possessed one composed of an indefinite number of members spirally arranged, of which the outer were sepaloid and the inner petaloid, but with no marked separation between the two. Since we regard the Ranales as the most primitive group, we should expect the immediate ancestors of the Angiosperms, as a whole, to have possessed this type of perianth.

Without attempting to follow fully the evolution of the perianth in the higher cohorts of the Dicotyledons, a few tentative remarks here may not be out of place. It might be inferred from the above hypothesis of a primitive perianth, partly sepaloid and partly petaloid, that we would consequently derive the floral envelopes of the higher Polypetalæ and the Gamopetalæ by a marked separation of the sepaloid and petaloid members into two distinct, usually pentamerous whorls, corresponding respectively to the calyx and corolla of these sub-classes. This of course is a possible, and besides a simple view, but there may be other explanations, which appear equally plausible. A. P. De Candolle long ago suggested that all floral leaves are derived from the sterilisation of sporophylls. Čelakovský *, from an exhaustive study of the perianth, finally came to the same conclusion. For the petals, at any rate, this view is supported by the Ranunculaceæ, where the evolution of a "corolla" of honey-leaves, by a modification of stamens, can be traced.

A third origin of the biseriate perianth occurs to us, on the supposition of a primitive floral envelope. The latter may have become wholly petaloid, and persisted as the corolla, whereas the calyx may have been a new structure, derived from foliage leaves.

In the Ranales we believe it is possible to trace the origin of a double perianth in conformity with each of these three theories. As regards the first method—viz., the differentiation of the original simple perianth into a definite calyx and corolla,—the flowers of *Drimys*, and of members of the Anonaceæ, may be instanced. As regards the second, the direct origin of the corolla from stamens may be followed in *Ranunculus*; and with respect to the third—viz., a calyx derived from below through a modification of foliage leaves, or, their direct homologues, bracts,—attention may be drawn to *Anemone Hepatica*, Linn., *Pæonia*, and genera of Dilleniaceæ †.

In fact, the Ranales may be considered an experimental group so far as the formation of a distinct calyx and corolla is concerned, some members progressing in one direction, and some in another.

* Čelakovský (1897) Part II. p. 46.
† Placed in the Cohort Ranales by Bentham and Hooker.

FOSSIL EVIDENCE.

In the foregoing pages we have emphasized certain features exhibited by living Angiosperms, which appear to us to be of a more or less primitive nature. We may now turn to fossil botany to inquire whether we can there gather any evidence of a race of plants, which combines any of these peculiarities.

There occur in the Mesozoic rocks a large number of fossils, which in many respects have much in common with the living Cycads. These plant-remains have been often spoken of as Mesozoic Cycads, and the idea has to some extent become ingrained that, whatever else they may have been, they were essentially Cycads. This conclusion, we believe, is incorrect. It partly arises from the fact that these fossils were for many years, and are perhaps even now, best known to us by impressions of their detached fronds, which are admittedly of the same general type as those of modern Cycads.

Even Wieland * in his quite recent work, in many respects the most important which has ever been done in this direction, has labelled his book 'American Fossil Cycads,' and speaks of the extremely interesting members of the genus *Cycadeoidea* as Cycads. This conclusion we hold to be incorrect, and one which is liable to give rise to a false impression as to the nature of these fossils, many of which we regard as standing nearer to the Angiosperms than to any other group.

For some years past, it has become more and more fully realised, in certain directions, that, among this great plexus of Mesozoic fossils, there were many which could not be called Cycads in the sense that we apply the term to the living plants. It was for this reason that Nathorst †, in 1902, proposed the name Cycadophyta, as a general and non-committal designation for this extensive Mesozoic plexus.

It has also become clear that this group was complex. It includes some plants which were true Gymnosperms, and so nearly allied to the modern Cycads, that, in all probability, they may be regarded as the ancestors of that race. These true Gymnosperms naturally fall within the group Cycadales. As illustrations, we may mention the fact that the type of female fructification exhibited by the living genus *Cycas* is apparently an ancient one. Several examples ‡ of carpellary leaves like those of *Cycas*, in some cases even with seeds attached, are known in the fossil state from rocks of different ages §. Also strobilate fructifications, similar to those of other genera of living Cycads, have been described ‖.

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* Wieland (1906) Chapter IX.   † Nathorst (1902) p. 3.
‡ Nathorst (1902) p. 6, pl. 1. fig. 11.   § Solms-Laubach (1891) p. 86.
‖ Seward (1895) p. 109, pl. 9. figs. 1–4 ; Nathorst (1902) p. 5, pl. 1. figs. 1–4.

THE BENNETTITEÆ.

Apart from such fossils as may well be included within the term Cycadales, there are others, differing *in toto* as regards the type of fructification. During the last thirty-six years we have gradually come to know more of these Mesozoic plants. The earliest account of their structure relates to *Williamsonia gigas*, described by Williamson *, in 1870. This was followed immediately by the important work of Carruthers † on *Bennettites* and other genera, also founded on British material. Solms-Laubach ‡, some years later, added considerably to our knowledge of this group, from British and Italian specimens of the latter genus. Lignier § has also contributed further information with regard to *Williamsonia* and *Bennettites*, from French material.

From these researches it has become clear that neither of these genera can be regarded as members of the Cycadales, but must be placed in a new group of ordinal rank, the Bennettiteæ ‖.

But by far the fullest, and from our point of view the most important work, which has been carried out on these fossils, is that of Wieland ¶ on the magnificent material of *Bennettites (Cycadeoidea)* ** collected from the Jurassic and Cretaceous rocks of the United States. The earlier, preliminary papers †† of this author have now been supplemented by a complete account, published in the sumptuously illustrated volume, entitled ' American Fossil Cycads,' which appeared last autumn. It is to this work that we are specially indebted for the first adequate description of the amphisporangiate strobilus of the genus, as well as for much further information on the subject of the habit and structure of these fossils. Wieland's work has also cleared up many points which were left obscure by the British, French, and Italian material, earlier examined.

This study of the American Bennettiteæ has further emphasized the fact that not only did there exist a great abundance and variety of Cycad-like Mesozoic plants, which cannot be included in the Cycadales, but that some of them warranted the distinction of being regarded as more closely related to the Angiosperms than to Gymnosperms. In fact the Mesozoic Bennettiteæ, as we now know them, appear to afford the long sought for clue to the phylogeny of the Angiosperms, especially on our view of the primitive features of the flower, already discussed.

    * Williamson (1870).   † Carruthers (1870).
    ‡ Solms-Laubach (1890) ; Capellini and Solms-Laubach (1891).
    § Lignier (1894, 1901, 1903¹, 1904).
    ‖ This term is now employed in a much wider sense than that originally intended by Carruthers. Engler (1897) pp. 5, 341, adopts the derivative Bennettitales.
    ¶ Wieland (1906).
    ** We regard these generic names as synonymous, though we express no opinion as to priority.   †† Wieland (1899, 1901).

It is only proposed here to recapitulate briefly the main points in the morphology of the fructification of *Bennettites*. For a full account the reader is referred to Wieland's excellently illustrated monograph.

The structure of the strobilus is illustrated by figs. 2 & 3 taken from Wieland's book *. As Dr. Scott † has pointed out, it is evident that "in approaching this subject we must divest our minds of all preconceptions drawn from a knowledge of existing Cycadean cones."

Fig. 2.

Diagrammatic sketch of a longitudinal section through the amphisporangiate cone of *Bennettites* (*Cycadeoidea*) *dacotensis*, Ward. About natural size. (After Wieland.)

The species, which may be regarded as typical from our point of view, is *Bennettites* (*Cycadeoidea*) *dacotensis*, Ward, from the Black Hills of South Dakota. As is invariably the case in this genus, the fructifications are borne laterally, wedged-in between the persistent leaf-bases of the stem. In all the examples, so far obtained, the cone is quite mature, and has reached the fruiting stage.

* Wieland (1906) text-figs. 87 & 88 on pp. 164-5.
† Scott (1900) p. 454.

The strobilus, which has a length of about 12 cm., consists of an elongated conical axis, bearing several series of bract-like structures below,-ibetween which is packed a copious ramentum. Above these bract-like organs, recognised in figs. 2 and 3 by their hairy surface, and attached to the axis in a hypogynous manner, is a structure known as the " disc,"-formed by the basal cohesion of 18–20 bipinnate fronds, the male sporophylls. In fig. 2, one of the latter is seen in the incurved condition, and the other, asiexpanded
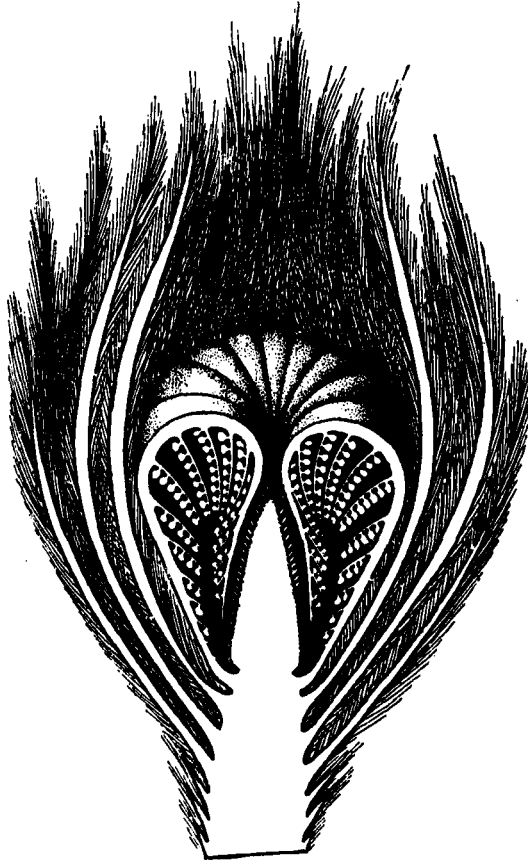
Fig. 3.

Restoration of a longitudinal section through the amphisporangiate strobilus of *Bennettites* (*Cycadeoidea*). About natural size. (After Wieland.)

when fully mature. In fig. 3 several of the microsporophylls are indicated in the unexpanded state. The bipinnate frond bears many, very reduced pinnules, each supporting two sessile synangia. The microsporophyll is bent inwards in the young state, for about a third of its length, and the secondary rhachides are folded inwards in pairs, lying in the plane of the primary rhachis.

At the apical portion of the strobilus, at a later stage when the

microsporophylls have been shed, a large number of orthotropous seeds are found, mounted on long pedicels, arising directly from the axis. The seeds contain dicotyledonous embryos. Between the seeds, a still larger number of somewhat club-shaped organs, known as the interseminal scales, occur, also attached directly to the receptacle. Distally these scales are all coherent by their apical margins, thus completely covering in the seeds, leaving, however, an orifice directly above each seed, through which the micropylar tube projects. Thus, in the fruiting stage, the interseminal scales form a complete investment or pericarp, and the whole of the macrosporangiate portion of the cone appears to be of the nature of a single fruit. In figs. 2 and 3, the scale is too small to show the young seeds and interseminal scales clearly. Their position, however, lining the apical portion of the axis, is indicated.

Further points in relation to the structure of the fructification of *Bennettites* will be discussed subsequently. We will, however, only add here that Wieland's elucidation of the amphisporangiate cone of *Bennettites* has incidentally extended our knowledge of the earlier described genus *Williamsonia*, in which the fructifications are borne on long peduncles, among the leaves forming the crown at the apex of the stem. It is possible that *Williamsonia*, in these features, is more primitive than *Bennettites*.

Previous Interpretations of the Bennettitean Strobilus.

Before beginning a discussion of the origin of the Angiospermeæ from ancestors nearly related to the Bennettiteæ, we would endeavour to make it clear that we do not consider any known member of the latter group to be exactly on the main line along which the Angiosperms have advanced. They, however, diverge so slightly, that we believe there is now little difficulty in perceiving how the Angiosperms may have originated.

We may commence by considering the interpretations which have been arrived at with regard to the strobili of the known members of the group. In thus reviewing some of the earlier work, it must be remembered that, until recently, the evidence has been very incomplete.

It is curious in this connection to find that in one of the earliest descriptions of the strobili of *Williamsonia*, read by Yates [*] before the Yorkshire Philosophical Society in 1847, the fructification was interpreted as consisting of " a number of scales, resembling sepals, petals, or perhaps dilated stamens, all growing from the top of the fruit-stalk, and overlapping one another." Yates also points out how very different this cone is, both externally and internally, from the flowers of the Cycads.

Williamson [†], working with very incomplete material of the genus *Williamsonia*, distinguished two types of fructification as male and female, which he compared with the cones of living Cycads. Although we know now that this

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[*] Yates (1855) p. 40.   [†] Williamson (1870) p. 672.

was not a correct conclusion, it was hardly to be expected that a closer approximation to the truth would then have been possible.

Carruthers [*], discussing the cone of *Bennettites* in relation to those of the living Cycadeæ, states that " the points of difference are more obvious than those in which they agree. . . . . The fossil is truly gymnospermous, the pollen having access to the embryo-sac through the tubular openings in the covering of the seed, and not through a style developed from an investing carpellary organ. The most remarkable difference is to be found in the compound fruit of the fossil. . . . . . It must be considered to hold the same relation to the other Cycadeæ that *Taxus*, with its succulent, cup-shaped pericarp, does to the cone-bearing Coniferæ."

Saporta [†] regarded the fructification of *Williamsonia* as the fruit of a primitive Monocotyledon, and more especially as belonging to a member of the Pandanaceæ. The same author [‡], in conjunction with Marion, recognised in the interseminal scales the homologues of carpels, and concluded that the inflorescence is similar to a spadix, bearing unisexual flowers, found in certain Monocotyledons.

Solms - Laubach [§], when discussing the fructification of *Bennettites Gibsonianus*, Carruth., in 1890, states that its closest affinities among living plants are with the Cycadeæ, though he is not altogether disinclined to accept Saporta's argument that the genus may be found to show analogies in the direction of the Angiosperms. The same author also outlines three hypotheses as to the homologies of the female portion of the strobilus. Either the seed-pedicels and interseminal scales are all carpels, the one fertile and the other sterile ; or the scales are of the nature of shoots without leaves, and the pedicels shoots ending in a flower reduced to a single ovule ; or, again, the scales are leaves subtending uniovulate shoots. On the whole he inclines to the last of these interpretations.

Similarly, Lignier [||], in describing the structure of *B. Morierei*, Sap. & Mar., in 1894, concluded that, so far as the female cone is concerned, it is of the nature of an inflorescence, the bracts and interseminal scales being the leaves of the main axis, the seed-pedicels being fertile leaves which belong to unifoliate buds of a higher order. He regards the group as descended from ancestors common to the Cycadeæ, but not from the Cycads themselves, and further suggests that eventually the Bennettiteæ and Cordaitales may be found to have a greater affinity than is at present supposed.

In March 1899, Wieland [¶] described, for the first time, the male flower of *Bennettites* (*Cycadeoidea*) *ingens*, Ward, and showed that it differed entirely from the male cones of the living Cycads. However, as the author [**] sub-

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[*] Carruthers (1870) p. 698.   [†] Saporta (1875) p. 56.

[‡] Saporta & Marion (1881) p. 1187 ; Saporta (1891) p. 88.

[§] Solms-Laubach (1890) pp. 830, 832, 843.   [||] Lignier (1894) pp. 69 & 73.

[¶] Wieland (1899) p. 224.   [**] Wieland (1901 and 1906).

sequently pointed out, this strobilus is really amphisporangiate, a fact which was not then recognised. In this later communication, Wieland calls attention to the resemblance of this fructification to that of the Angiosperms on the one hand, and to that of the Cycadofilices on the other.

Dr. Scott, in his ' Studies in Fossil Botany ' *, sums up the views with regard to the homologies of the Bennettitean cone. He says, " that the axis of the inflorescence is a modified branch of the stem is clear, the enveloping bracts are obviously modified leaves or leaf-bases (*B. Morierei*), and likewise present no difficulty. We might well compare them to the scale-leaves, in which the young cone of an ordinary Cycad is enwrapped." With regard to the seed-pedicels and interseminal scales, " the simplest view, then, would be to regard them as modified leaves, the fertile pedicels being the sporophylls, and the interseminal scales representing either abortive sporophylls or a special kind of bract. But we might also interpret both organs as reduced shoots, or might limit this view to the seed-pedicels, continuing to regard the interseminal scales as bracts, comparable to the paleae found among the florets on the receptacle of some Compositæ."

It must be remembered that, when these views were expressed, our knowledge of the Bennettiteæ was much less advanced than it is at the present time, thanks to the researches of Wieland.

In a later paper, Lignier † adheres to his interpretation of the nature of the female strobilus of the Bennettiteæ, mentioned above, and discusses the morphological value of the cone of *Bennettites (Cycadeoidea) ingens*. He suggests that the male portion may be of the nature of a flower, that is to say, composed of staminiferous fronds borne on the main axis, though the female is an inflorescence. He also criticises Wieland's comparison of this strobilus with that of the Cycadeæ and Angiosperms. He appears to derive the latter from the Cordaitales ‡. In a later note the same author § discusses the morphology of the interseminal scales.

We now pass to consider the interpretation given by Wieland, who alone has so far had before him the complete evidence of the strobili of the American Bennettiteæ. That author ‖ describes the amphisporangiate axis as a flower homologous with that of an Angiosperm. He speaks of it as follows:— " The flower or strobilus as thus borne on a short and heavy peduncle consists in a terminal ovulate cone surrounded by an hypogynous staminate disc and an outer series of enveloping bracts, followed by the old leaf-bases of the armor " ¶. Comparing this cone with the flower of the Angiosperms, the same author ** concludes :—" It appears that organization into a disc

* Scott (1900) pp. 475–76.
‡ Lignier (1903¹) diagram on p. 49.
‖ Wieland (1906) Chapter VII. & p. 143.
¶ Wieland (1906) p. 165, also p. 235.
† Lignier (1903¹) p. 44.
§ Lignier (1904).
** Wieland (1906) p. 230, also p. 79.

preceded by spirally arranged bracts with the subsequent prolongation of the main floral axis, either as that of a simple terminal cone (or an inflorescence), is, in later geological time, mainly an angiospermous juxtaposition, although it may yet prove that its seemingly isolated occurrence in gymnosperms is largely due to an imperfectly known and understood fossil record."

Discussing the evolution of the Bennettiteæ, contrasted with the Cycads, he says *:—" In the one case the much greater change went on in the mega-sporophylls, and there was evolved a form of true flower exactly suggestive of the types of change in reproductive organs that resulted in the angiosperms. In the other" [the Cycads] " both types of sporophylls were seized upon and carried forward through the same stages of reduction, save for that single, wonderful, and marvelous survival from the Paleozoic, that analogue of the staminate frond, the carpophyll of *Cycas*."

The present Interpretation of the Fructification of the Bennettiteæ.

Having briefly reviewed previous opinions as to the homologies of the Bennettitean cone, we may pass on to state our own interpretation, which differs considerably from nearly all those previously advocated. According to our view, this cone is a simple strobilus, and not an inflor-escence. Its parts are homologous with the carpels, stamens, and perianth of a typical, amphisporangiate, Angiospermous flower. In other words, the simple cone of the Bennettiteæ is an anthostrobilus (see p. 37), differing from the anthostrobilus of the Angiosperm in several important features, especially in the presence of a seminal pollen-collecting mechanism, and in the form of the microsporophylls. Such a fructification may be distinguished as a pro-anthostrobilus (p. 37).

It will readily be seen that this interpretation has all the merit of simplicity. Yet, like most theories, it has certain difficulties peculiar to itself, which will be discussed here. We propose to show that it is possible to institute a very close comparison between the eu-anthostrobilus of the Angiosperm and the pro-anthostrobilus of the Bennettiteæ. Further, the agreement between these two types of anthostrobili is so close that the conclusion that the Angiosperms sprang from Mesozoic ancestors, nearly related to the Bennettiteæ, is rendered extremely probable.

On the view that the pro-anthostrobilus is a simple cone, the term " bract " can no longer be applied to the outer, enveloping, foliar organs. On our interpretation, these constitute a primitive perianth, and are of the nature of sterile leaf-members. The male organs, the 10–20 bipinnate, Marattiaceous-like fronds, are collectively homologous with the androecium of the Angio-sperms, the stamens of the latter being derived from them by reduction. The position of the microsporophylls on the axis, with regard to the other

* Wieland (1906) p. 66.

organs of the strobilus, is similar to that of the androecium of a typical
Angiospermous flower, and, with the exception of *Welwitschia*, *is peculiar
to this line of descent*. The female organs consist of seeds, mounted
on long pedicels, and interseminal scales. We regard the latter as homologous
with the carpels of the Angiosperms, despite the fact that they subtend, and
do not bear the seed-pedicels. The obvious difficulty which arises from this
fact will be discussed later (p. 66). It is this feature, interpreted on the
axioms of rigid morphology, which has hitherto biased opinion in favour of
interpreting the ovulate portion of the pro-anthostrobilus as an inflorescence.
On our view, the carpels of the Bennettiteæ are to a certain degree syncarpous,
and this represents a stage in evolution antecedent, in this case, to the method
of enclosing the seeds by the infolding of the carpels on themselves. We
regard this feature especially as one in which the known Bennettiteæ depart
from the direct line of descent of the Angiospermeæ. In their basal cohesion
and cyclic arrangement, the male organs show a like early departure.

We regard the fructifications of the Bennettiteæ as having been essentially
amphisporangiate, though we recognise the possibility that in this group, as in
their descendants the Angiospermeæ, there has been a strong and constant
tendency to reduction to the monosporangiate condition, with the corollary of
the monoecious and dioecious states. This view has been emphasized so
admirably, and at such length by Wieland *, that it is unnecessary to do more
than add the following quotation :—" The condition in the great majority
of the cones thus far examined is such that one is forced to the conclusion
that all the known Cycadeoideæ are descended from bisporangiate forms, and
that of all the considerable number of fruits of *Cycadeoidea* and *Bennettites
Gibsonianus* or allied species, far the larger portion were actually bisporangiate
and discophorous." We may add, in discussing this point, that it must be
remembered, that in the majority of the known cones of the Bennettiteæ, the
fruits are more or less mature, and often possess a well-developed embryo.
At such a stage the microsporophylls would most likely have died down, or,
as Wieland expresses it, " wilted," or have been shed altogether, as that
author has pointed out at some length. Remnants of the " hypogynous disc,"
formed by the basal cohesion of the 10–20 microsporophylls, usually remain
as sole evidence of the amphisporangiate nature of the cone, except in some
25 known cases, including *Bennettites* (*Cycadeoidea*) *Jenneyana*, Ward,
B. (*C.*) *ingens*, Ward, *B.* (*C.*) *dacotensis*, Ward, where these organs are
preserved. Even in *Williamsonia*, such " discs " have been long known,
though their precise nature has only recently been explained by Wieland's
work.

That the fructification of the Bennettiteæ presents features recalling those
of the Angiosperms has been already pointed out by previous authors.

* Wieland (1906) p. 114, also pp. 130, 137, 169, 174, 184.

Saporta *, in 1871, referred *Williamsonia* to the Monocotyledons on the supposed similarity of the female portion of the strobilus to the fruit of certain Pandanaceæ. In subsequent memoirs this author †, in conjunction with Marion, included the genus in a new class, the Proangiospermeæ, or primitive Angiosperms. Although the evidence for this attribution was then very imperfect, and the deduction by no means warranted or strictly accurate, yet Saporta, in our opinion, was perfectly correct in his happy guess as to the near affinities of this Mesozoic fossil.

In 1880, Nathorst ‡ came to the conclusion that the supposed fruits of the Bennettiteæ really represented parasitic plants analogous to the Balanophoraceæ.

Solms-Laubach's § conclusions have been already mentioned (p. 56). In the English translation (1891) of his 'Fossil Botany,' the following passage occurs :—" It is possible that the seed-stalks may prove to be carpophylls of a peculiar kind ; in that case we should be obliged to separate the Bennettiteæ altogether from the Cycadeæ, and to regard them as an intermediate group between Gymnosperms and Angiosperms."

Dr. Scott ‖ remarked in his 'Studies,' published in 1900, that the fruit of *Bennettites* "comes very near to being angiospermous," but "only in the sense that the seeds were enclosed within a coherent pericarp." The same author concluded that " the Bennettiteæ may well be called pro-angiosperms, to use Saporta's name, if by that we simply mean to indicate plants with a near approach to angiospermous structure, without implying any relationship to the Class Angiosperms as now existing. On the present evidence such a relationship is altogether improbable."

It must, however, be pointed out that it was only in 1901, or, more strictly speaking, during the last year, that the full evidence as to the fructification of *Bennettites* has become available, and consequently these conclusions, founded on imperfect material, could not be other than provisional.

Wieland ¶ in 1901, when describing in a preliminary note the amphisporangiate strobilus of *Bennettites*, emphasized the following suggestion, made in a previous communication : " While the staminate disk surrounding the ovulate axis of *Cycadeoidea* indicates primarily an evolution terminating, so far as now possible to trace, in the Gymnosperms, the juxtaposition of parts is exceedingly suggestive of the possibility, if not the manner as well, of angiosperm development directly from pteridophytic forms. For in these strobili the sporophylls are organized into a flower, ... foreshadowing distinctly the characteristic angiospermous arrangement of stamens inserted on a shortened axis about an ovulate center, apical and sometimes strobilar as seen in *Liriodendron*."

* Saporta (1875) p. 56.

† Saporta & Marion (1885) vol. i. p. 246, and Saporta (1891) p. 87.

‡ Nathorst (1880).   § Solms-Laubach (1891) p. 97.

‖ Scott (1900) pp. 462, 477, & 478, also p. 523.   ¶ Wieland (1901) p. 426.

In 1903, Lignier * criticised Wieland's views with regard to the possible relationship of the amphisporangiate strobilus of *Bennettites* to the Angiosperms, and rejected this theory on the ground that the fructification could not be correctly interpreted as a simple cone.

Of more importance are the opinions expressed by Wieland † in presenting the full evidence with regard to the fructification of *Bennettites,* recently published. He concludes that " it would be most extraordinary if at the present day the angiosperm line of descent could be laid down, except on the broadest lines. It would be most extraordinary, we say, if a mere half-dozen well-understood great plant types scattered over vast periods of time, and representing but a few of a vast array of unknown evolutionary steps, should be exactly the ones enabling us to say, for instance, that certain lines (Cycadofilices) led into the Cycadales and Ginkgoales, and sent off a branch which yielded Cycadeoidean stock *first,* then the Cordaitales, or *vice versa,* and that from these latter the angiosperms sprang." This author ‡ also expresses his conviction that primitive seed-ferns gave rise " to such types as the Mesozoic *Cycadeoideæ,* and, as I believe, at much the same time or a little later than these the early angiosperms."

He defends § the analogy which he previously suggested between the Cycadeoidean flower and that of *Liriodendron.* He says : " Also, in the case of the sole remote type of which we have now gained a fortuitous knowledge, striking analogies to living angiosperms are suggested, no difference whether, laying histological structure somewhat aside, we fasten our attention upon one set of characters and *Liriodendron* be called to mind, or upon another with the result that the male and female catkins of Amentaceæ first suggest themselves, or upon a third set that call to mind some other hint of characters that must have been present in the countless members of a great proangiosperm complex, just as the monocotyl *Pandanus* thus suggested itself to Saporta. We should not ask too much of isolated evidence, nor yet be content with a scant interpretation of highly suggestive facts."

Further he adds ‖ : " For the purposes of broader generalization, fern-like fronds upon which were doubtless borne the pollen of *Lyginodendron,* the staminate fronds of *Cycadeoidea* of true Marattiacean type, the mega- and microsporophylls of *Cycas,* the stamens of *Cordaites* and *Ginkgo,* and finally of *Ricinus* and *Liriodendron,* all belong to a series." The same author ¶ also points out other analogies between the Bennettiteæ (Cycadeoideæ) and the Angiosperms.

It will be seen from this short *résumé* of previous opinion that, so far as the full structure of the cone of the Bennettiteæ has been disclosed, there

* Lignier (1903¹) p. 45. † Wieland (1906) pp. 243–44.
‡ Wieland (1906) p. 243. § Wieland (1906) p. 245.
‖ Wieland (1906) *ibid.* ¶ Wieland (1906) pp. 66, 79, 123, 143.

have already been recognised, on many sides, indications of Angiospermous affinity, and thus support is afforded to the theory maintained here.

Only one discussion of the affinities of the Bennettitean strobilus has appeared, so far as we are aware, since Wieland's full results were disclosed last autumn. Professor Oliver *, in a short paper on this subject, has stated some of the main points of the argument, to which we had arrived independently. He says : " We now come to the question of the morphological interpretation of this fructification, whether it is to be regarded as 'an axis beset with sporophylls,' i. e. a flower, or whether, on the other hand, it is really a much more complex-structure, i. e. an inflorescence or branch-system showing extreme reduction. . . . . . The view taken by Dr. Wieland, that we have here a hermaphrodite flower, will meet with very general agreement. Looked at broadly and having regard to the pteridospermous affinities of the Bennettiteæ this interpretation seems irresistible. To take the other view and read a ' cyathium ' into its structure seems to verge on the gratuitous."

The same author adds : " Whatever else one may think of this flower it cannot be regarded as that of a quite typical Angiosperm. . . . . Its great interest and value seem to be that whilst just missing the Angiosperm it shows how close the Cycad line could come to realising it. It is indeed the key to the Angiosperms ; when that is recognised the rest is easy . . . . It is possible, no doubt, though it seems almost incredible, that a flower with perianth, stamens, and gynæceum in proper relative position as in *Cycadeoidea* should have been produced except in a line very closely related to that which led to the Angiosperms."
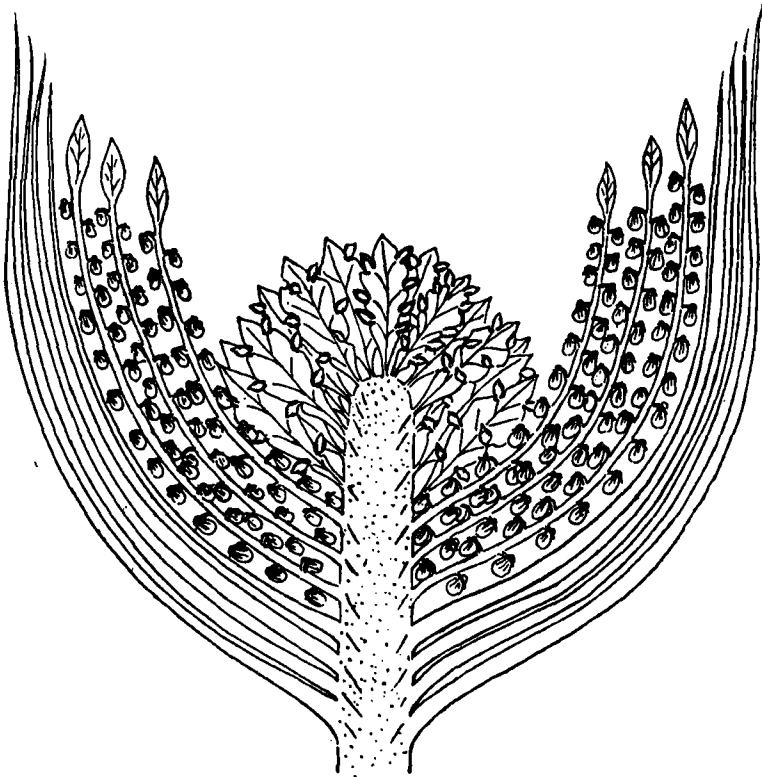
THE HEMIANGIOSPERMEÆ.

According to our view, the Tertiary and Recent Angiosperms are directly descended from a group of Mesozoic plants to which we apply the new term *Hemiangiospermeæ*. This group at present is entirely hypothetical. Nothing is known as to the fructification of any of its members, but we believe that its cone approximated so closely to the pro-anthostrobilus of the Bennettiteæ, that the latter, although somewhat removed from the direct line of descent, demonstrates emphatically the type of strobilus which gave rise to the eu-anthostrobilus, or flower of the Angiospermeæ. This cone (fig. 4), like that of the closely related Bennettiteæ †, was an anthostrobilus of the pro-anthostro-biloid type. It was also essentially a Gymnospermic fructification, the pollen collection being performed by the ovule itself. Yet it agreed with the typical flower of the Angiosperm on the one hand, and with the strobilus of the Bennettiteæ on the other, in the juxtaposition of the mega- and micro-sporophylls, a feature which is peculiar to the cones of this line of descent,

* Oliver (1906) pp. 239–40.
† Hallier (1901 ¹) p. 105, (1905) p. 154

as well as in the possession of a primitive perianth.   It differed from
the Bennettitean strobilus in that the megasporangia were seated on the
margins of the carpels, the homologues of the interseminal scales, which were
free from one another and not united at the apex.   Also the microsporophylls
were spirally arranged, and perhaps more reduced than those of that group.
Such a strobilus would be all but Angiospermic, were it not that the task of pollen
collection was still performed by the ovule, and that it lacked the precise form

Fig. 4.

The pro-anthostrobilus of the hypothetical Hemiangiospermeæ.   Diagrammatic
representation of a longitudinal section through the cone, showing perianth,
microsporophylls and megasporophylls.

of microsporophyll which is termed a stamen.   The general form of mega-
sporophyll would correspond more closely with that of the living genus *Cycas*,
than with the corresponding structures presented by the known Bennettiteæ.
That this assumption is a natural one may be inferred from the known
antiquity, and frequent occurrence of such a type of megasporophyll in the
ancient rocks *.

* See Solms-Laubach (1891) p. 86.

The fact that such a cone appears to be wholly unknown at present should not militate against the theory, if we bear in mind that the total number of Mesozoic fructifications of Gymnospermous affinity at present discovered is extremely small, as Wieland has emphatically pointed out in the passages quoted above.

It might be asked why we have not adopted Saporta's * term, Proangiospermeæ, if some such name is really required. It must, however, be remembered that this name was given to fossils, which were regarded as primitive Angiosperms, combining characters common to both Dicotyledons and Monocotyledons, whereas the hypothetical forms, which we are discussing, were the ancestors of these primitive Angiosperms, and were *Gymnosperms.* Further we do not agree that the Bennettiteæ, in the light of the recent researches of Wieland, can be referred to the Proangiospermeæ † of Saporta, as the latter author concluded, for the same reason that their mode of fertilization was essentially Gymnospermic ‡.

THE ORIGIN OF THE ANGIOSPERMEÆ.

We may now proceed to outline the steps by which the typical strobilus of the Angiospermeæ was evolved from that of the hypothetical Hemiangiospermeæ. We have already (pp. 44–45) indicated what we regard as the primitive form of the various organs which compose the flower.

The amphisporangiate cone of the Bennettiteæ was identical, so far as the juxtaposition of the mega- and microsporophylls is concerned, not only with that of the Hemiangiospermeæ, but also with that of the Angiosperms themselves. The hypogynous arrangement of the parts, as in the Bennettiteæ, was also a primitive feature of the Angiosperms, from which the perigynous and epigynous states have been more recently evolved, as indeed has been pointed out by several writers §.

In the cone of the Bennettiteæ, all the organs are spirally arranged with the exception of the microsporophylls. In the cyclic grouping of the latter, these plants may be regarded as showing evidences of an early departure from the main line of descent of the Angiosperms. In the strobilus of the hypothetical Hemiangiospermeæ, the organs were all arranged spirally (see fig. 4), and this primitive feature is still to be found preserved to some extent

* Saporta & Marion (1885) vol. i. pp. 220 & 222.

† This term is also open to the objection that many fossils have been included under it, the nature or affinities of which are wholly doubtful.

‡ The term 'Angiocycad,' provisionally suggested by Oliver (1906) p. 240, does not appear to us to be free from objections, for we regard the fructification of this ancestor as, in the first place, Gymnospermic, and, in the second, very far removed from that of the living Cycad.

§ Coulter & Chamberlin (1904) p. 13.

among Angiosperms, as for instance among certain members of the Magno-liaceæ. With the Angiosperms generally, just as with the Bennettiteæ, there has been a constant tendency, by suppression of internodes, to derive a cyclic arrangement of the parts of the cone from the primitive spiral type.

The first step in the immediate evolution of the Angiosperms was the transference of the pollen-collecting mechanism from the ovule to the carpel or carpels, with consequent localisation of the stigmatic surface. It was this act which called the Angiosperms into being, as we shall endeavour to emphasize more fully at a later stage in this consideration.

We may therefore first consider the gynæceum.

The Gynæceum.

We regard the Bennettiteæ, so far as the megasporophylls of the cone are concerned, as departing considerably from the main line of descent of the Angiospermeæ. The orthotropous ovule or seed, enveloped by what was probably a single integument *, may be regarded as a fairly primitive structure. In the anthostrobilus of the Angiospermeæ, the primitive condition of the ovule was undoubtedly orthotropous, and probably there was a distinct funicle, a feature which may, or may not, be homologous with the seed-pedicel of the Bennettiteæ. The origin of the second integument does not appear to us to present any great difficulty. It is absent in many living Angiosperms, especially among the Gamopetalæ, and several members of the Ranunculaceæ, an order which we regard as having retained a comparatively large number of primitive features in the strobilus †. Moreover, we regard an integument as a structure which may arise *de novo*, and one without close homologies among those plants which do not bear seeds. That this is the case is evident in such a seed as that of the Palæozoic Lycopod, *Lepidocarpon* ‡, and in certain arils found among living Angiosperms.

The seeds of the Bennettiteæ show a close approximation to those of the Angiosperms in the fact that the embryo of *Bennettites*, and presumably of the Hemiangiospermeæ, possesses two cotyledons, and that, unlike the Cycads, and in all probability the Pteridosperms, these seeds germinated after a comparatively short resting period, both of which we regard as primitive features among the Angiospermeæ.

The structure of the unfertilised ovule of the Bennettiteæ is still practically unknown, for in all the specimens examined so far, the ovule has apparently already become a mature seed. We are, therefore, ignorant of the precise anatomy of the micropylar end of the ovule. Did it possess a pollen chamber, comparable to that of *Lagenostoma*, or was the pollen-collecting mechanism confined to the micropylar region of the integuments? On this point

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* Wieland (1906) p. 234. † Prantl (1888).
‡ Scott (1901) p. 317.

Wieland * gives no clear information. But the fact that the integument, enclosing the micropyle, is produced † beyond the united outer surfaces of the interseminal scales for some 2 mm., or, as Wieland describes it, "projects stigma-like a little beyond the pericarp," seems to show that the latter, whatever their homologies may be, played no part in the pollen-collecting mechanism, a duty no doubt performed by the ovule itself. This also lends probability to the view that pollination was effected by means of anemophily. These points appear to us to be of great importance, since we regard the likelihood that, in the Bennettiteæ and the Hemiangiospermeæ, the pollen-collecting office was performed by the ovule itself (as in the Coniferales and the Pteridospermeæ), and the additional probability that the microspores were brought into position, as it were, by the wind, as being two features eminently characteristic of these groups, as opposed to the Angiosperms.

With regard to the precise homologies of the seed-pedicels and interseminal scales of the Bennettitean fructification, there are already several theories in the field. Lignier's conclusions have been mentioned (p. 56) and Wieland's ‡ views will be found discussed at length in the IXth Chapter of his book. We do not intend to pursue the matter at length here. On our view, the homologues of the interseminal scales of the Bennettiteæ in the cone of the Hemiangiospermeæ were simple carpellary leaves, bearing several ovules on their margins, much like the megasporophylls of the living genus *Cycas*. We conceive that the ancestors of the Bennettiteæ themselves also possessed this type of sporophyll, though in *Bennettites* this structure has become highly modified, perhaps even divided ; for there is a possibility that the seed-pedicels may, in part, represent a lobe of the carpellary leaf. Also the megasporophylls, or portions of them, have become united to form the pericarp of the fruit. In these features we recognise clearly that the strobilus of the Bennettiteæ departs considerably from the lines along which the Angiospermeæ have descended. The evolution of the pericarp of the Bennettiteæ represents one path of advance, and one wholly gymnospermic. On the other hand, the Angiospermeæ, with their closed carpels, form another line of descent, called into being by the adoption of the entomophilous habit, in conjunction with a shifting of the mechanism for pollen-collection from the megaspore itself to the closed megasporophylls.

Since the adoption of entomophily, by means of closed carpels, as the mode of fertilisation, evolution has taken place in many different directions, and thus the great cohorts, families, and orders of Angiosperms have been called into being. Among the more important changes have been reduction and suppression in the number of the floral members, leading in extreme cases to the monœcious and diœcious conditions, often, as we have pointed

* Wieland (1906) p. 122, fig. 63.   † Wieland (1906) pp. 121, 234.
‡ Wieland (1906) p. 230, &c.

out, correlated with increased complexity of the inflorescence ; the general replacement of the spiral by the cyclic arrangement in the parts of the flower ; cohesion and adhesion, especially the evolution of the perigynous and epigynous states from the primitive hypogyny * ; and alterations in symmetry †, notably the evolution of zygomorphic structures. Further in many cases there has been a return to the primitive anemophilous habit, often accompanied by diclinism, and complicated inflorescences.

The Andrœcium.

Perhaps the most striking contrast between the pro-anthostrobilus and the flower or eu-anthostrobilus, is to be found in the nature of the microsporophylls. In the Bennettiteæ, these are bipinnate ‡ fronds of the fern type, coherent at the base, bearing greatly reduced pinnules, which in turn bear synangia. The connection between such organs and the andrœcium of the Angiosperms is not at first sight obvious. If, however, we compare parallel stages in the evolution of the andrœcium and the gynæceum, we may perhaps arrive at a clearer insight on this point.

The seed itself is an exceedingly ancient organ, dating back far beyond the period at which we first became acquainted with fossil plants. In other words, it was a highly evolved structure at a very remote period in geological time. The seed of the Pteridosperms, the earliest stage in the line of descent under discussion with which we are at present familiar, was long antecedent to the evolution of the stamen. The male organs of the Pteridosperms, so far as we have been able to recognise them, were simple synangia-like structures, not dissimilar to those of the Eusporangiate Ferns in certain particulars, and were borne on fern-like fronds. In another Palæozoic group, the Cordaitales, an organ, in some respects closely similar in organisation to a stamen, existed contemporaneously with the fern-like male organ of the Pteridospermeæ, but this line of descent, on our view, has, at the most, only a remote connection with that discussed here. Thus we find that an organ in some respects like a stamen was in existence in the Palæozoic period, although in the Angiosperm line of descent it was not evolved until quite late in geological time.

The fructifications of the Pteridospermeæ, both male and female, were borne in a lax manner, on fronds similar in structure to the sterile fronds, or on leaves in which the lamina was more or less greatly reduced. There is no indication, in any known member of the group, that there was any attempt to aggregate either the male or female fructifications in the form of a strobilus or cone.

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* Coulter & Chamberlain (1904) p. 13.　　　　† Coulter & Chamberlain (1904) p. 15.

‡ Wieland (1906) p. 165, &c., describes the microsporophylls as " once pinnate." They are, however, obviously bipinnate.

In the case of the Bennettiteæ, however, the Mesozoic descendants of this group, we find both the male and female organs aggregated into an amphisporangiate strobilus, and further that the megasporophylls are of a highly advanced type, and have undergone great reduction, as well as possibly other extreme modifications. The stage reached in the evolution of the microsporophylls is obviously greatly behind that of the megasporophylls. They show hardly any marked advance beyond the condition of affairs met with in the Pteridospermeæ. The microsporophylls are still essentially compound, fertile fronds. Any progress in evolution is confined to the synangium, which is still the dominant type of male fructification. and perhaps more highly evolved in the Bennettiteæ than in any known Pteridosperms. The stamen, *per se*, is quite a recent innovation, so far as this line of descent is concerned. But the adoption of entomophily, by means of closed carpels, which in the ultimate analysis will, we believe, be found to be the real influence which called the Angiosperms into being, no doubt involved considerable modification in other parts of the flower, and among these the male organs. The incoming of this type of pollination, thereby effecting an immense saving in the amount of pollen production necessary to ensure cross-fertilization (see p. 74), seems to have been the signal for considerable reduction in the male fronds of the pro-anthostrobilus. Eventually a much simpler structure has been evolved, consisting of a sporangiophore bearing two synangia.

Although we regard the microsporophyll of the Angiosperms as derived originally from a highly branched organ, by reduction, there would seem to be very few cases among living members of the group in which a survival of this ancient feature can be traced. It is just possible that such may occur among the Myrtaceæ, e. g., *Calothamnus*, and possibly also in *Ricinus*, where the stamens are pinnately branched, but in the Polypetalous orders, such as Capparidaceæ, Dilleniaceæ, Resedaceæ, Hypericaceæ, Cistaceæ, Malvaceæ, &c., in which so-called branched or divided stamens are found, this phenomenon is of a different nature *, and has no direct bearing on this discussion. On the other hand, it is admitted that the gap between the male organs of the Bennettiteæ and the Angiosperms is a big one, and that we are not at present able to trace the various stages in the reduction of the microsporophyll.

The Perianth.

The Bennettitean cone possesses a basal, spirally arranged series of sterile, leaf-like organs, which form an integral part of the strobilus. We imagine that the pro-anthostrobilus of the Hemiangiospermeæ also possessed this feature, which we interpret as an undifferentiated, primitive perianth. With the assumption of entomophily, and the consequent evolution of the Angio-

* Goebel (1905) p. 535.

spermeæ proper, concomitant changes' in the form and function of the primitive perianth may well have taken place. To the original protective function of this organ would be added an attractive office, in connection with the entomophilous habit. The changes involved may have affected the perianth as a whole, or only the higher series of its members. While we may suppose that, in some cases, the primitive perianth became differentiated in this way into an outer series the calyx, and an inner series the corolla, it is unlikely that all corollas, or, for that matter, all calyces have originated in this manner. The study of the homologies of the members of the floral envelopes among living Angiosperms is a very difficult one, as we have already pointed out (p. 50). In some cases, e. g., *Nymphæa*, the petals may be modified stamens, *i. e.* degraded fertile sporophylls, as Grant Allen * long ago suggested. In others, foliar structures, not originally forming an integral portion of the cone, may have come to function as a calyx. A well-known example occurs in the case of the involucre of *Anemone Hepatica*, L.†.

While therefore, we reserve for the present a fuller discussion of the homologies of the various types of floral envelopes found among living Angiosperms, we may conclude that at least a part of the modern perianth was derived originally from the ancient primitive perianth of the Hemiangiosperms.

The Angiospermous Type of Foliage.

If our view is correct that the eu-anthostrobilus or flower of the Angiospermeæ has been evolved from the pro-anthostrobilus of an unknown ancestor, allied to the Bennettiteæ, then we may imagine that this evolution would be correlated with a marked change in the habit of the whole plant, especially as regards the branching and leaf-form. We believe, however, that this latter modification took place at a considerably later geological period than the evolution of the flower. In other words, we conceive that the earlier Angiosperms may have retained, for the most part, the unbranched habit, and also the Cycadean type of foliage of their ancestors, for some considerable time after the fructification had become a typical eu-anthostrobilus or flower.

One of the most difficult of the lesser problems which make up the plexus of problems, which we call the origin of Angiosperms, refers to the evolution of the typical form of Angiospermous foliage. The leaves of this group are greatly varied both in form and size, but the majority of them exhibit certain peculiarities of shape and nervation, which, though hard to define, readily permit us to recognise at sight the affinities of such plants, even when we have only their detached foliage to guide us.

* Allen (1882) p. 11.   † Goebel (1905) p. 550.

What, then, is the origin of this type of foliage ?   We believe the solution
to the question is to be sought for in a study of the branch-habit.
Wieland* has shown clearly that the Bennettiteæ possessed stems of restricted
vertical growth, either unbranched or branched only to a limited extent.
The same also seems to have been true of the Pteridospermeæ, their ancestors.
On the other hand, one of the great characteristics of the Angiosperms, as a
whole, is their free branching, whether of the monopodial or the sympodial system.
With this change in habit was probably correlated a general alteration in the
character of the foliar organs.   The Pteridospermeæ, with their unbranched,
or tree-fern-like habit, obtained a considerable assimilatory surface by means
of very large leaves.   Probably, for mechanical reasons, the increase in the
size of the leaf as a whole would have to be accompanied by much subdivision
of the lamina.   Hence the highly compound fronds of the Palæozoic period.
The large, but simpler foliage of the Bennettiteæ, and of the Cycadophyta
generally, can easily be derived from this type of leaf, and is likewise corre-
lated with a non-branched or feebly branched habit.   The association of
megaphylly and a simple stem is found in certain living Angiosperms,
e. g., the Palms, where it may perhaps be regarded as an ancient
feature.

Thus in the Angiosperms as a class, free branching and small leaves have
been substituted for a simple unbranched habit and large leaves.   One can
readily understand how, as the tendency to branching increased, the necessity
for microphylly would arise and smaller foliage be evolved.   In the one case
branching takes place, as it were, in the leaf, in the other, in the stem.
Both represent efficiency from a physiological standpoint attained by
different methods.

The theory that the origin of the Angiospermous type of branching and
consequently the prevailing leaf-form, took place some considerable time after
the evolution of the primitive flower is in harmony with the axiom (see p. 35)
that corresponding stages in the evolution of the various organs of a seed-
plant are not reached contemporaneously.   It also explains certain facts
which have hitherto been regarded as highly mysterious.   When we attempt
to summarise the existing data relative to the first appearance of Angiosperms
in Neocomian rocks, we are led to three remarkable conclusions.   In the
first place, the Angiosperms appear to arise very abruptly or suddenly.   In the
second, judging by their detached leaf-impressions, our sole evidence at present,
they belong to highly evolved, and still existing natural orders.   There
appears to be nothing primitive about these early forms.   In the third place,
from their first incoming, they are the dominant types in the vegetation of
the Cretaceous and Tertiary periods.

* Wieland (1906) Chapter II.

These conclusions are easily explained on the supposition that the earlier Angiosperms still retained the Cycad-like type of foliage of their ancestors ; and as our knowledge of the Mesozoic floras is in great part, if not almost entirely, derived from detached leaf-impressions, and not from fructifications, it is not surprising that we have been puzzled by the facts as presented by the geological record. The so-called " sudden appearance " of the Angiosperms in Neocomian times may have no significance as regards the phylogeny of the group, but may well express the fact, that this group, already highly evolved and diversified, then assumed the free-branching habit and consequent microphylly. This hypothesis also explains why this race appears to be dominant over other groups even in the Neocomian period, for the subsidiary incoming stage of the life-line would be masked by the retention of the Cycad-type of foliage.

But, apart from these considerations, the great problem remains as to how the microphyllous foliage of the Angiosperms was derived from the Cycadean type. On this point we are at present unable to offer any suggestion unless we call mutation to our aid (see p. 36). So far we are not aware that fossil botany has afforded evidence of transitions from the type of foliage peculiar to any Mesozoic group to that of the Angiosperms.

THE ORIGIN OF MONOCOTYLEDONS.

It is still a matter of keen debate whether the Dicotyledons or the Monocotyledons are geologically the older group. The arguments are derived, partly from our knowledge of their living members, and partly from a study of fossil impressions. But it may be doubted whether either of these lines of attack afford sufficient data at present to settle the question quite beyond doubt.

Some [*] have regarded the Dicotyledons as derived from the Monocotyledons, while others[†], including Hallier[‡], hold the converse, in some cases with the reservation that the Monocotyledons branched off from the main Angiospermous line, i. e. Dicotyledons, at a very early period. With the latter view we entirely agree.

So far as the fossil evidence is concerned, we doubt if it is possible to show that either group is really more ancient than the other. We agree with the opinion, now generally held, that the earliest fossil remains, which in the present state of our knowledge we can recognise as clearly belonging to the

[*] Lyon (1901, 1905).
[†] Sargant (1903), Mottier (1905), Chrysler (1906), Plowman (1906).
[‡] Hallier (1905).

Angiosperms, are those of the Neocomian (Lower Cretaceous) of Portugal and the United States.   In these rocks, what appear to be Dicotyledonous and Monocotyledonous leaf-impressions occur together.   There have, of course, been many attempts to show that Monocotyledonous leaves are to be found in Mesozoic sediments of pre-Cretaceous age, or even in the Palæozoic. None of these, however, appear to us to afford trustworthy evidence, and in many cases such fossils have been already claimed as members of other groups, such as the Cycadophyta and Cordaitales.

It seems evident that the earlier Angiospermous fossils afford practically no help in attempting to trace the ancestry of the race.   Such plant remains consist almost entirely of detached leaf-impressions, which furnish little or no trustworthy evidence, beyond the fact that they are of undoubted Angiospermous origin.   In the Tertiary rocks, seeds and fruits, also detached, occur on certain horizons, but impressions of flowers are almost unknown, or at least extremely rare.   On the other hand, petrified woods, showing the typical structure of Dicotyledons and Monocotyledons, especially Palms, are found in the Upper Cretaceous and Tertiary formations.   These fossils are usually of considerable size, but on the whole hardly advance our ideas in respect to the phylogeny of the group.

On the other hand, the Bennettiteæ, the near relatives of the hypothetical Hemiangiospermeæ, afford some evidence in this connection.   As was first pointed out by Solms-Laubach some years ago, the embryo of *Bennettites* has two cotyledons.   We imagine that the Hemiangiospermeæ also possessed two cotyledons, and that the Dicotyledonous type was thus more primitive than the Monocotyledonous.

Turning to the living Monocotyledons, we regard this race as one which has become largely specialised, in part to a geophilous, and in part to a hydrophilous [*] habit.   The best explanation of the monocotyledonous embryo is, in our opinion, that put forward by Miss Sargant [†].   We consider that it is more than probable that the single cotyledon of Monocots, and also of some Dicots, is due to the fusion of the two cotyledons originally present, in response to the geophilous habit.

During the course of evolution there would seem to have been considerable "play upon," or modification of, every unit of the flower.   And this appears to us to be true also of the embryo.   Late, or far from primitive adaptations are to be found among embryos, just as among flowers.   The cotyledonary tubes of some Ranunculaceæ and other families, and the division of labour exhibited by the cotyledons of certain geophilous Peperomias, recently described by Mr. A. W. Hill [‡], appear to us to be cases in point.

In regarding the Angiosperms as a whole as monophyletic, we are in

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[*] Gardner (1883), Henslow (1893) p. 527.   [†] Sargant (1903, 1904, 1905).
[‡] Hill, A. W. (1906).

agreement with Hallier * and Bessey † among others, though the contrary view has been recently upheld by Coulter and Chamberlain ‡. In our opinion, the similarity to be found between the general structure of the amphisporangiate strobili of both Monocotyledons and Dicotyledons, especially in those cases which we regard as preserving primitive features, and the general identity exhibited by the gametophytes, is almost conclusive in this respect. The supposition that such resemblances are due to homoplasy, as Coulter and Chamberlain assert, does not appeal to us, for the chances of such complete parallelism of long duration must be almost infinitely small.

Some evidence also has been recently brought forward to show that the polycotylous embryo may have been derived from a dicotyledonous ancestor, by the splitting of the two seed-leaves §. This, in conjunction with the fact that *Bennettites*, as also *Ginkgo* and living Cycads, possess two cotyledons, inclines us to the view that the dicotylous condition was a primitive feature of the great majority, if not all Spermophyta.

ENTOMOPHILY.

We have already indicated that, on our view, it was a radical change in the method of cross-fertilisation which called the Angiosperms into existence. It is not perhaps safe to assume that the Bennettiteæ, or still more the Hemiangiospermeæ, were wholly anemophilous, though we think there is a strong probability that such was the general method of pollination. At first we may imagine that such insects as visited the Mesozoic ancestors would be attracted to the male sporophylls for the sake of the pollen. In such amphisporangiate strobili as those of the Hemiangiosperms, cross-fertilisation would be likely to result occasionally through insect visitors, owing to the close proximity of male and female sporophylls. In a monosporangiate strobilus, however, the male cones would probably alone be visited, hence there would be no tendency to cross-fertilisation. Consequently the evolution of entomophily may be expected to have arisen in anthostrobiloid plants. In the case of the Angiosperms such primitive entomophily was preserved, and rendered permanent by a transference of the pollen-collecting mechanism from the ovule itself to the carpel or megasporophyll, and by the closure of this organ.

Such a view is in accordance with that expressed by Robertson ‖. The question, however, remains as to why this change in the manner of fertilisation should have necessitated the infolding and union of the carpels. Robertson has recently asked this question, at the same time pointing out that a single ovule could hardly be pollinated any better, and that more than one could not be fertilised as well by the anemophilous method. It might,

* Hallier (1901², 1905). † Bessey (1897).
‡ Coulter & Chamberlain (1904) p. 283. § Hill & de Fraine (1906).
‖ Robertson (1904).

however, be argued that the closed condition would be as effective for wind pollination as the open carpel. A definite, receptive part of the closed sporophyll could catch the pollen wafted by wind as easily as the ovule of an open one. True, but on the supposition of a multiovulate carpel, the closed state would not be so effective for anemophily, since the chances are that insufficient pollen would reach the stigmatic surface to fertilise all the ovules. By entomophily, on the other hand, large masses of pollen, sufficient for the fertilisation of all the ovules, would be deposited on the carpel, as the result of a single visit. This view is borne out by the fact that most anemophilous Angiosperms have uniovulate carpels.

There is this further consideration that, by the closing in of the carpel, more efficient protection is afforded to the developing ovules and seeds, and at the same time the chance of their being pollinated is increased by the localisation of the collection mechanism. The insect has only to leave the pollen on one part of the carpel, whereas to fertilise each ovule of a multiovulate open carpel it must be deposited on or near each ovule.

Though agreeing so far with Robertson, we part company with him when he suggests that honey, and not pollen, first attracted insects to flowers. The converse seems to us the more probable, and besides offers a better explanation of how entomophily arose. Otherwise how are we to account for the evolution of floral nectaries? The secretion of honey previous to insect visitation does not appear likely. Afterwards, of course, the plant would gain by substituting this cheaper food-material in the place of pollen. It could then exercise considerable economy in the production of the latter, quite apart from the fact that entomophily in itself is less wasteful in this respect than anemophily. It is unnecessary here to trace further the evolution of the Angiospermous flower under insect influence. This study belongs to a special branch of botany, the main results of which are general knowledge.

While we regard the entomophilous condition as a primitive feature among Angiosperms *, there are numerous instances in which a return to the older, anemophilous habit has, more recently, taken place. These are frequently associated with the more extreme cases of reduction from the amphisporangiate to the monosporangiate condition, accompanied by suppression, often complete, of the perianth. Against the view that such anemophilous plants are primitive may be urged the fact that the inflorescence is almost invariably of a dense, complicated type, while the style, and especially the stigma, are obviously highly evolved structures, fashioned on the same plan as pertains in entomophilous flowers.

* Henslow (1893²) p. 266; Wallace (1889) pp. 323–4.

GENERAL CONCLUSIONS AND SUMMARY.

From a general survey of existing Angiosperms, we have arrived at the conclusion that the Apetalous orders without perianth, such as the Piperales, Amentiferous families, and Pandanales, cannot be regarded as primitive Angiosperms. We thus dissent entirely from the current view, advocated especially by Engler. Engler's theory is criticised on three grounds. Firstly it presupposes that the perianth must arise *de novo*, and be an organ *sui generis*. On the contrary, we surmise that the perianth is an ancient structure, present in the fructification of the immediate ancestors of the Angiosperms. In the second place, the so-called primitive flowers of the above orders are invariably accompanied by a complicated and highly-evolved inflorescence, which we are unable to regard as a primitive character. Thirdly, such a theory is phylogenetically sterile, for, while it has the merit of simplicity, it does not afford any clue to the ancestry of the group, nor does it tend to bring the living Angiosperms into line with the fossil plants of the past. On our view, the primitive and typical Angiospermous fructification is a special form of amphisporangiate cone, distinguished by the peculiar juxtaposition of the mega- and microsporophylls, and by possessing a well-marked perianth. A strobilus exhibiting these features we term an *Anthostrobilus*. The word "flower," which in our opinion should be restricted to the Angio· sperms, is used in a great variety of senses. The flower of members of this group is regarded as a special form of the Anthostrobilus, and may be distinguished as an *Eu-anthostrobilus*, of which the distinctive features are the presence of the special type of microsporophyll termed a stamen, and of closed carpels. On our view, however, an earlier form of Anthostrobilus is to be found among Gymnosperms, where, however, the megasporophylls are not closed, and the microsporophylls have not the form which can be called stamens. We designate this latter type a *Pro-anthostrobilus*. This is the form of cone possessed by the Mesozoic Bennettiteæ, and also we believe by the hypothetical, direct ancestors of the Angiosperms, or, as we here term them, the *Hemiangiospermeæ*.

On the strobilus theory of the primitive Angiospermous fructification, we find, when we turn to the fossil evidence, that it is possible to trace the descent of living Angiosperms in its broad outlines. The direct ancestors of this group (the Hemiangiospermeæ) are unknown as yet in the fossil state But on this theory we recognise in the Pro-anthostrobilus of the Mesozoic Bennettiteæ, which we regard as closely related to the Hemiangiospermeæ, features which enable us to restore in some measure the missing fructification of the ancestor. We are helped in this task by what we have termed the law of corresponding stages in evolution, which states that equivalent stages in the evolution of the different organs of one and the same seed-plant are not contemporaneous in point of time. This has proved

especially valuable in the consideration of the origin of the Angiospermous
type of leaf, which we suggest was initiated by a change in the branch habit.

We regard the Angiosperms as essentially a monophyletic group, the
Monocotyledons having branched off from the Dicotyledonous stock at an
early period, probably from the Ranalian plexus. In both these groups
entomophily was a primitive feature. We consider that the change, from the
assumed generally anemophilous habit of the Mesozoic Hemiangiospermeæ,
and the Bennettiteæ, to entomophily, by means of a shifting of the pollen-
collecting mechanism from the megasporangium to the megasporophyll, and
the consequent formation of an ovary, has supplied the "motive force,"
which not only called the Angiosperms into existence, but laid the foundation
of their future prosperity.

If these conclusions have weight, then it is now possible to trace back the
line of descent of the Angiosperms to a very early geological period. This
may be shown in tabular form as follows :—

|		
5. Angiospermeæ	{	Mesozoic and Tertiary (Recent),— Eu-anthostrobilateæ.
4. Hemiangiospermeæ .... (unknown fossils).	}	Mesozoic,—Pro-anthostrobilateæ.
3. Pteridospermeæ .... 2. Heterosporous Fern-like Ancestor. 1. Homosporous Fern-like Ancestor..	}	Palæozoic,—Non-strobilate Ancestors.

Numbers 1, 2, and 4 are unknown fossils, but the key to numbers 1 and 2
is given by the Pteridospermeæ (No. 3), and to number 4 by the Bennettiteæ.
Numbers 3, 4, and 5 were Spermophytes.

Such a theory of descent will permit us to venture rather further afield.

In both the homo- and heterosporous, primitive, fern-like ancestors, there
is every reason to believe that the sporophylls were arranged in a lax manner,
and not aggregated into definite strobili. This condition still remained a
feature of the fern-like seed-plants, or Pteridospermeæ. From this Palæ-
ozoic plexus, however, strobilate lines of descent were probably evolved
in Mesozoic times by two distinct methods. In the one, like sporophylls
were aggregated into monosporangiate cones. In the other, both male and
female sporophylls were massed in one amphisporangiate strobilus, the
sporophylls however, for a time at least, retaining their primitive, fern-like
form, as is clearly seen in the male organs of the Bennettiteæ. The mono-
sporangiate Strobilateæ led to the modern Cycads. This conclusion receives
support from the fact that, in the genus *Cycas* itself, only the male sporophylls
are aggregated into cones. The female may be regarded as having remained
more or less in their ancestral condition, especially with regard to their
distribution on the axis. Such a case would be difficult to explain on the

supposition that, in the modern Cycads, the monosporangiate condition was originally derived from a amphisporangiate strobilus. On the other hand, the amphisporangiate Strobilateæ gave rise to other groups, such as the Bennettiteæ and the Angiosperms, in the manner indicated in the following table :—

TABLE OF ANGIOSPERMOUS RELATIONSHIPS.
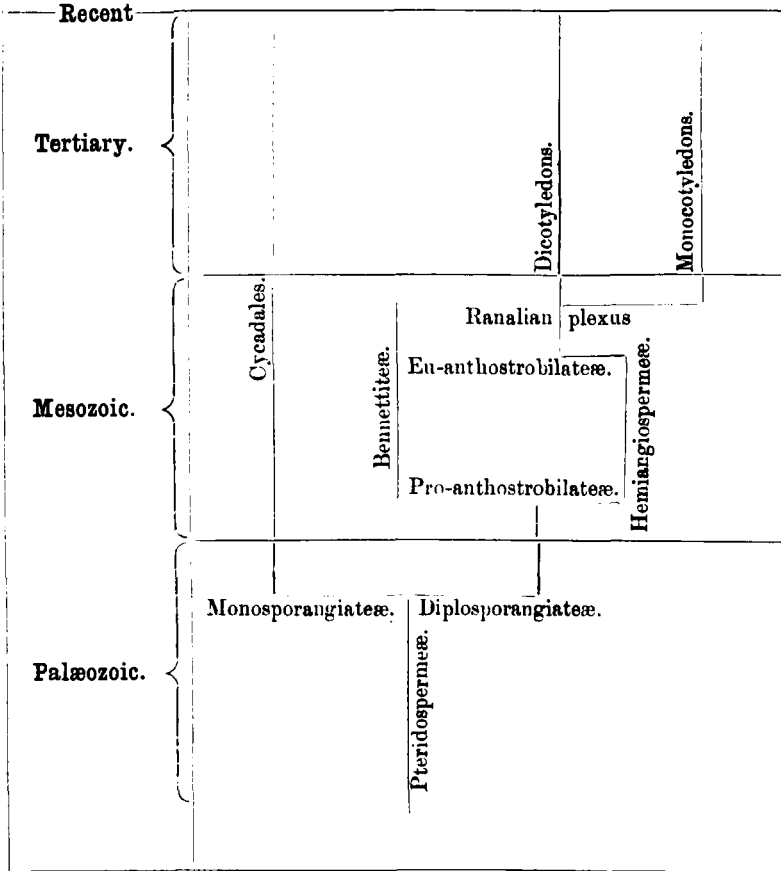
BIBLIOGRAPHY.

ALLEN, G. (1882).—The Colours of Flowers. (Nature Ser.) London, 1882.

ANONYMOUS (1906).—Discussion on the Vascular Structure of Seedlings. *New Phytologist*, vol. v. 1906, p. 182.

BENSON, M. (1904).—The Origin of Flowering Plants. *New Phytologist*, vol. iii. 1904, p. 49.

BENSON, M., SANDAY, E., & BERRIDGE, E. (1906).—Contributions to the Embryology of the Amentiferæ. Part II. *Carpinus Betulus. Trans. Linn. Soc. London*, 2nd ser. *Bot.* vol. vii. pt. 3, 1906, p. 37.

BESSEY, C. E. (1897).—Phylogeny and Taxonomy of the Angiosperms. *Bot. Gaz.* vol. xxiv. 1897, p. 145.

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bcdefgCAMPBELL, D. H. (1891).—Contributions to the Life-History of *Isoetes*. *Ann. of Bot.*
vol. v. 1891, p. 231.

—— (1905).—Studies on the Araceæ. III. *Ann. of Bot.* vol. xix. 1905, p. 329.

CAPELLINI, G., & SOLMS-LAUBACH, H., GRAF ZU (1891).—I Tronchi di Bennettitee dei
musei italiani. *Mem. R. Accad. Sci. Inst. Bologna*, Ser. 5, vol. ii. 1891, p. 161.

CARRUTHERS, W. (1870).—On Fossil Cycadean Stems from the Secondary Rocks of Britain.
Trans. Linn. Soc. London, vol. xxvi. 1870, p. 675.

ČELAKOVSKÝ, L. J. (1897).—Ueber den phylogenetischen Entwicklungsgang der Blüthe und
über den Ursprung der Blumenkrone. I. Theil. *Sitzungs. k. Böhm. Gesell. Wiss.*
(*M.-N. Cl.*), vol. for 1896, xl. 1897; II. Theil. *Ibid.* vol. for 1900, iii. 1901.

CHAMBERLAIN, C. J. (1897).—Contributions to the Life History of *Salix*. *Bot. Gaz.*
vol. xxiii. 1897, p. 147.

CHRYSLER, M. A. (1906).—The Nodes of Grasses. *Bot. Gaz.* vol. xli. 1906, p. 1.

COULTER, J. M., and CHAMBERLAIN, C. J. (1904).—Morphology of Angiosperms. London
and New York, 1904.

ENGLER, A. (1897), in ENGLER & PRANTL : Die natürlichen Pflanzenfamilien. Nachtrag :
Parts II.-IV. Leipzig, 1897.

FRYE, T. C. (1903).—The Embryo-Sac of *Casuarina stricta*. *Bot. Gaz.* vol. xxxvi. 1903,
p. 101.

GARDNER, W. (1883).—On the Physiological Significance of Water-Glands and Nectaries.
Proc. Camb. Phil. Soc. vol. v. part 1, 1883, p. 35.

GOEBEL, K. (1905).—Organography of Plants. Part II. Special Organography. (English
Edition) Oxford, 1905.

HAINES, H. H. (1906).—On two new Species of *Populus* from Darjeeling. *Journ. Linn. Soc.
London, Bot.* vol. xxxvii. 1906, p. 407.

HALLIER, H. (1901¹).—Beiträge zur Morphogenie der Sporophylle und des Trophophylls in
Beziehung zur Phylogenie der Kormophyten. *Jahrb. Hamburg. Wissen. Anstalt*,
Beih. 3, vol. xix. 1901, p. 1.

—— (1901²).—Ueber die Verwandtschaftsverhältnisse der Tubifloren und Ebenalen, den
polyphyletischen Ursprung der Sympetalen und Apetalen und die Anordnung der
Angiospermen überhaupt. *Abhandl. Naturw. Verein Hamburg*, vol. xvi. 1901,
p. 1.

—— (1903).—Über den Umfang, die Gliederung und die Verwandtschaft der Familie
der Hamamelidaceen. *Beiheft. Bot. Centralb.* vol. xiv. 1903, p. 247.

—— (1905).—Provisional Scheme of the Natural (Phylogenetic) System of Flowering
Plants. *New Phytologist*, vol. iv. p. 151, 1905. See also *Ber. Deutsch. Bot. Gesell.*
vol. xxiii. 1905, p. 85.

HARMS, H. (1897).—Ueber die Stellung der Gattung *Tetracentron* Oliv., und die Familie
der Trochodendraceen. *Ber. Deutsch. Bot. Gesell.* vol. xv. 1897, p. 350.

HENSLOW, G. (1893¹).—A Theoretical Origin of Endogens from Exogens through Self-
Adaptation to an Aquatic Habit. *Journ. Linn. Soc. London, Bot.* vol. xxix. 1893,
p. 485.

—— (1893²).—The Origin of Floral Structures through Insect and other Agencies.
2nd Edit. *Intern. Scient. Ser.* vol. lxiv. London, 1893.

HILL, A. W. (1906).—The Morphology and Seedling Structure of the Geophilous Species of
Peperomia, together with some Views on the Origin of Monocotyledons. *Ann. of
Bot.* vol. xx. 1906, p. 395.

HILL, T. G. (1906).—On the Seedling-Structure of certain Piperales. *Ann. of Bot.* vol. xx.
1906, p. 161.

HILL, T. G., and DE FRAINE, E. (1906).—On the Seedling-Structure of Gymnosperms.
Ann. of Bot. vol. xx. 1906, p. 471.

JOHNSON, D. S. (1905).—Seed Development in the Piperales and its bearing on the Relationship of the Order. *Johns Hopkins Univ. Circ.* No. 178 (N.S. No. 5), 1905, p. 28.

LEWIS, C. E. (1904).—Studies on some anomalous Dicotyledonous plants. *Bot. Gaz.* vol. xxxvii. 1904, p. 127.

LIGNIER, O. (1894).—Végétaux fossiles de Normandie. Structure et Affinités du *Bennettites Morierei*, Sap. & Mar. (sp.). *Mém. Soc. Linn. Normandie*, vol. xviii. 1894, p. 1.

—— (1901).—Végétaux fossiles de Normandie. III. Étude anatomique du *Cycadeoidea micromyela*, Mor. *Mém. Soc. Linn. Normandie*, vol. xx. 1901, p. 331.

—— (1903[1]).—Le Fruit du *Williamsonia gigas* Carr., et les Bennettitales. *Mém. Soc. Linn. Normandie*, vol. xxi. 1903, p. 19.

—— (1903[2]).—La Fleur des Gnétacées est-elle intermédiaire entre celle des Gymnospermes et celle des Angiospermes ? *Bull. Soc. Linn. Normandie*, Ser. 5, vol. vii. 1903, p. 55.

—— (1904).—Notes complémentaires sur la structure du *Bennettites Morierei* Sap. et Mar. *Bull. Soc. Linn. Normandie*, Ser. 5, vol. viii. 1904, p. 3.

LOTSY, J. (1899).—Contributions to the Life-History of the genus *Gnetum*. *Ann. Jard. Bot. Buitenzorg*, vol. xvi. (Ser. 2, vol. i.) 1899, p. 46.

LYON, H. L. (1901).—Observations on the Embryogeny of *Nelumbo*. *Minnesota Botanica Studies*, vol. 2. No. xxxviii. 1901, p. 643.

—— (1905).—The Embryo of the Angiosperms. *Amer. Nat.* vol. xxxix. 1905, p. 13.

MORRIS, D. (1893).—On the Phenomena concerned in the Production of Forked and Branched Palms. *Journ. Linn. Soc. London, Bot.* vol. xxix. 1893, p 281.

MOTTIER, D. M. (1905).—The Embryology of some Anomalous Dictyledons. *Ann. of Bot.* vol. xix. 1905, p. 447.

NATHORST, A. G. (1880).—Några anmärkningar om *Williamsonia*, Carruthers. *Öfvers. k. Vetenskaps-Akad. Förhandl.* vol. xxxvii. No. 9, 1880, p. 33.

—— (1902).—Beiträge zur Kenntnis einiger Mesozoischen Cycadophyten. *K. Svens. Vetensk.-Akad. Handl.* vol. xxxvi. No. 4, 1902.

OLIVER, F. W. (1906).—Pteridosperms and Angiosperms. *New Phytologist*, vol. v. No. 10, 1906, p. 232.

PLOWMAN, A. B. (1906).—The Comparative Anatomy and Phylogeny of the Cyperaceæ. *Ann. of Bot.* vol. xx. 1906, p. 1.

PRANTL, K. (1888).—Beiträge zur Morphologie und Systematik der Ranunculaceen. *Engler's Bot. Jahrb.* vol. ix. 1888, p. 225.

ROBERTSON, C. (1904).—The Structure of the Flowers and the Mode of Pollination of the Primitive Angiosperms. *Bot. Gaz.* vol. xxxvii. 1904, p. 294.

SAPORTA, GASTON DE (1875).—Paléontologie française. 2e Séries—Végétaux. Plantes Jurassiques. Vol. II. Cycadées. Paris, 1875.

—— (1891).—Paléontologie française. 2e Séries—Végétaux. Plantes Jurassiques. Vol. IV. Types Proangiospermiques, etc. Paris, 1891.

SAPORTA, G. DE, and MARION, A. F. (1881).—Sur les genres *Williamsonia* Carruth. et *Goniolina* d'Orb. *Compt. Rend. Acad. Sci.* vol. xciv. 1881, pp. 1185 & 1268.

—— —— (1885).—L'Évolution du Règne végétal. Les Phanérogames. Vol. I. Paris, 1885.

SARGANT, E. (1903).—A Theory of the Origin of Monocotyledons founded on the Structure of their Seedlings. *Ann. of Bot.* vol. xvii. 1903, p. 1.

—— (1904).—The Evolution of Monocotyledons. *Bot. Gaz.* vol. xxxvii. 1904, p. 325.

—— (1905).—The Early History of Angiosperms. *Bot. Gaz.* vol. xxxix. 1905, p. 420.

SCHAFFNER, J. H. (1897).—The Development of the Stamens and Carpels of *Typha latifolia*. *Bot. Gaz.* vol. xxiv. 1897, p. 93.

Scott, D. H. (1900).—Studies in Fossil Botany. London, 1900.

—— (1901).—On the Structure and Affinities of Fossil Plants from the Palæozoic Rocks.—IV. The Seed-like Fructification of *Lepidocarpon*, a genus of Lycopodiaceous cones from the Carboniferous Formation. *Phil. Trans. Roy. Soc.* Ser. B, vol. 194, 1901, p. 291.

Seward, A. C. (1895).—The Wealden Flora.—Part II. Gymnospermæ. Catalogue of the Mesozoic Plants in the British Museum (Nat. Hist.), London, 1895.

Shoemaker, D. N. (1905).—On the Development of *Hamamelis virginiana*. *Bot. Gaz.* vol. xxxix. 1905, p. 248.

Solms-Laubach, H., Graf zu (1890).—Ueber die Fructification von *Bennettites Gibsonianus* Carr. *Bot. Zeit.* for 1890, pp. 789, 805, 821, 843. Translation in *Ann. of Bot.* vol. v. 1891, p. 419.

—— (1891).—Fossil Botany. (Engl. Trans.) Oxford, 1891.

Strasburger, E. (1905).—Die Samenanlage von *Drimys Winteri* und die Endospermbildung bei Angiospermen. *Flora*, vol. xcv. 1905, p. 215.

Treub, M. (1891).—Sur les Casuarinées et leur place dans le système naturel. *Ann. Jard. Bot. Buitenzorg*, vol. x. 1891, p. 145.

Wallace, A. R. (1889).—Darwinism. London, 1889.

Wieland, G. R. (1899).—A Study of some American Fossil Cycads. Parts I.-III. *Amer. Journ. Sci.* Ser. 4, vol. vii. 1899, pp. 219, 305, 383.

—— (1901).—A Study of some American Fossil Cycads. Pt. IV. On the Microsporangiate Fructification of *Cycadeoidea*. *Amer. Journ. Sci.* Ser. 4, vol. xi. 1901, p. 423.

—— (1906).—American Fossil Cycads. Washington, 1906.

Williamson, W. C. (1870).—Contributions towards the History of *Zamia gigas* Lindl. & Hutt. *Trans. Linn. Soc. London*, vol. xxvi. 1870, p. 663.

Willis, J. C. (1904).—A Manual and Dictionary of the Flowering Plants and Ferns. 2nd Edit. Cambridge, 1904.

Vries, H. de (1901).—Die Mutationstheorie. Vols. I-II. Leipzig, 1901-03.

—— (1905).—Species and Varieties. Their Origin by Mutation. London, 1905.

Yates, J. (1855).—Notice of *Zamia gigas*, a fossil plant occurring on the N.E. coast of Yorkshire. *Proc. Yorkshire Phil. Soc.* (read 1847), 1855, p. 37.