than he otherwise could. If the trouble is in the bone, the nervous system or the kidney, a piece of the stomach usually tells us nothing. The microscope or the culture tube can show us only what is present and for assistance they must be used in conjunction with other information or to verify or refute suspicion. This means, therefore, that men who are to become practitioners must be trained in the knowledge of specific etiology, the newer pathology and therapeutics, *in addition to and not as a substitute* for the training in thorough systems of physical examination and in close observation of signs and symptoms in diagnosis and treatment. This not only increases the responsibilities of our teachers, but also demands that technical professional knowledge shall be grafted upon well-trained and noble men. There is no other profession where accuracy, correct interpretation and application are of greater significance than they are in this, yet there is no other where men are elevated to positions of responsibility with so little real preparation. We seem to have forgotten that in the acquisition of knowledge and the coming into an understanding of a profession, the element of time and the discipline of routine work and research are as essential as they are in a science like chemistry or physics.

I have dwelt somewhat at length upon the difficulties in bringing into action men who will meet the demands, improve the opportunities and fulfill the responsibilities of the veterinary profession. If these difficulties are analyzed, it will be found that they are temporary and incident to the transition stage of our knowledge, methods of instruction and the newer conception of the important work of the veterinarian. These all point clearly to the opportunity for veterinary service equal to that of any other occupation or profession. The watchword of to-day is the prevention of disease quite as much as its cure and when this dual purpose becomes fully recognized the necessary means will be forthcoming. While there is much to be accomplished, while our problems are difficult and our burdens sometimes seem greater than we can bear, my voice has proved a recreant servant if any tones of doubt, or fear of ultimate victory, have marred this discussion. There are many reasons to believe that the time will soon come when there will be an American system of veterinary education, laws and practise that will take first place in the world-wide effort to secure the highest possible efficiency in veterinary service.

Veranus A. Moore

THE BRITISH ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE

ADDRESS TO THE BOTANICAL SECTION[1]

Greatly as I prize the honor done me by the Council of the British Association in electing me to the office of President of the Botanical Section, my gratification has been heightened by the knowledge that the meetings of this section would be graced by the presence of the distinguished group of Continental and American botanists who have just taken part in the International Phytogeographical Excursion to the British Isles.

I am sure that I am voicing the unanimous feeling of the section in offering them a hearty welcome to our deliberations, and, in conveying to them our sense of the honor they have done us by their acceptance of the invitation of this association, I would like to express our hope that by their participation in our proceedings they will help us to promote the advancement of botanical science, for which purpose we are met together.

[1] Portsmouth, 1911.

In view of these special circumstances under which we forgather, it may seem inappropriate if I deal, as I shall be doing, in my presidential address mainly with fossil plants, with the study of which I have been for some time occupied; but I need hardly assure our visitors that, while we entertain some feelings of satisfaction at the contributions made during the past half century towards our knowledge of extinct flora of Britain, yet, as the later sittings of this section will show, and as they have no doubt realized during their peregrinations through this country, our botanical sympathies and energies are by no means limited to this branch of botanical study. Moreover, I hope during the course of my address to point out the ecological interest which is afforded by certain aspects of paleobotany.

On the sure foundations laid by my revered predecessor, the late Professor Williamson, so vast a superstructure has been erected by the active work of numerous investigators that I must limit myself in this address to exploring only certain of its recesses, and I shall consequently confine myself to some aspects of paleobotany which have either not been dealt with in those able expositions of the subject given to this section by previous occupants of this presidential chair, or which may be said to have passed since then into a period of mutation.

The great attractiveness of paleobotany, and the very general interest which has been evinced in botanical circles in the progress of recent investigations into the structure of fossil plants, are due to the light they have thrown upon the relationship and the evolution of various groups of existing plants. It was the lasting achievement of Williamson to have shown, with the active cooperation of many working-men naturalists from the Lancashire and Yorkshire coal-fields, that the structure of the coal-measure plants from these districts can be studied in microscopic preparations as effectively as has been the case with recent plants since the days of Grew and Malpighi. Indeed, had Sachs lived to continue his marvelous historical account of the rise of botanical knowledge up to the years 1880 or 1890, he would undoubtedly have drawn attention to the remarkable growth of our knowledge of extinct plants gained by Binney and Williamson from the plant remains in the calcareous nodules of English coal-seams, and by Renault from the siliceous pebbles of Autun. We are not likely to forget the pioneer work of these veterans, though since then investigations of similar concretions from the coal deposits of this and other countries have been undertaken by numerous workers and have revealed further secrets from that vast store of information which lies buried at our feet.

The possibilities of impression material had indeed been practically exhausted in 1870, and further advance could only come from new methods of attacking the problems that still remained to be solved. The most striking recent instance of the insufficiency of the evidence of external features alone was Professor Oliver's demonstration of the seed-bearing nature of certain fern-like plants, based on microscopical comparison of the structure of the cupule of *Lagenostoma*, with the fronds of *Lyginodendron*, after which discovery confirmatory evidence speedily came to hand from numerous plant impressions examined by Kidston, Zeiller, and other observers.

Undoubtedly in the hands of a less competent and far-sighted observer than Williamson, the new means of investigation might have proved as misleading as the old method had been in many instances. Indeed, as is well known, the recognition in the sections of *Calamites* and *Sigillarias* of the presence of secondary wood had caused Brongniart to place these plants among conifers, owing to his belief that no vascular cryptogams exhibited exogenous growth in thickness. It required all Williamson's eloquence and pugnacity to convert both British and French paleobotanists to his views, ultimately accepted with such handsome acknowledgment by *Grand' Eury,* one of his antagonists, in his "Géologie et Paleontologie du Bassin Houiller du Gard."

It is curious that Grand' Eury refers in his introduction to the discovery of traces of secondary growth in *Ophioglossum,* and not to that of *Isoëtes,* a plant much more nearly related, as we now believe, to the Lepidodendraceæ, and the structure of which had been so thoroughly investigated by Hofmeister. Williamson, it is true, refers to the secondary growth in the stem of *Isoëtes* in his memoir on *Stigmaria,* but compares it with the periderm-forming cambium of that plant, and does not therefore recognize any agreement in the secondary growth of these two plants.

Adopting von Mohl's interpretation of the root-bearing base of the *Isoëtes* plant as a "caudex descendens," Williamson instituted a morphological comparison between the latter and the branching *Stigmaria,* and came to the conclusion that they were homologous structures, a view which, as we heard at Sheffield, is supported by Dr. Lang on the strength of a reexamination of the anatomy of the stock of *Isoëtes.* If we do not accept Williamson's interpretation of the Stigmarian axis as a downward prolongation of caulome nature, the question remains open whether this underground structure represented a leafless modification of a normal leaf-bearing axis as is known in the leafless rhizomes of *Neottia* and other saprophytic plants, or whether the Stigmarian axes were morphological entities of peculiar character. Grand' Eury, in comparing them with the rhizomes of *Psilotum,* accepted the former alternative and, apart from morphological considerations, was led to this view by the fact that he had observed aerial stems arising in many instances, as buds on the horizontal branches of *Stigmaria.* Confirmation of this mode of growth is still required, but it is quite conceivable that there may have been a mode of vegetative reproduction in the *Stigmariæ* analogous with that of *Ophioglossum.*[2]

The alternative interpretation of the Stigmarian axes as special morphological entities has received weighty support from Scott and Bower, who consider them comparable to the rhizophores of *Selaginella,* which, as is well known, may either be root-bearers, or under certain circumstances become transformed into leafy shoots. This peculiarity has led Goebel to regard them as special members, somewhat intermediate between stems and roots. But though they might therefore be regarded as of a primitive nature, the rhizophores of the Selaginellaceæ seem such specialized structures that I incline to agree with Bower that, as far as their correspondence with *Selaginella* is concerned, the Stigmarian axes would agree most closely with the basal knot formed on the hypocotyl of *Selaginella spinulosa.* Seeing, however, that the nearest living representative of the Lepidodendraceæ is in all

[2] It is of interest in this connection to note that Potonié has recently put forward the suggestion that many of these vertical outgrowths from the more or less horizontal Stigmarian axes, some of which, as figured and described by Goldenberg, taper off rapidly to a point, without any trace of ramification, may be comparable with the conical "knees" of *Taxodium,* and represent woody pneumatophores so common in the swamp cypress and other swamp-inhabiting trees.

probability *Isoëtes,* which Bower has aptly summarized as like " a partially differentiated *Lepidostrobus* seated upon a Lepidodendroid base," we must inevitably consider the root-bearing base of *Isoëtes* as homologous with the branching axes of *Stigmaria,* whatever their morphological nature may have been, and perhaps we shall be on the safest ground if we consider them both as different expressions of the continued growth of the lower region of the plant, which appears to have been a primary feature in the morphology of both these members of the Lycopodiales.

The somewhat considerable difference in external appearance between the homologous organs of these two plants may be considered bridged over by the somewhat reduced axes of *Stigmariopsis* and by the still more contracted base of the Mesozoic *Pleuromoia,* which, in spite of its very different fructification, we may unhesitatingly compare with *Isoëtes* as far as its root-bearing axis is concerned.

I was inclined at one time to seek an analogy for the Stigmarian axis in that interesting primitive structure, the protocorm of *Phylloglossum,* and of embryo Lycopods; but I now consider that the resemblances are largely superficial, and do not rest upon any satisfactory anatomical correspondence.

One of the features which has caused some divergence of opinion in the past as to the morphology of the Stigmarian axis has been the definite quincuncial arrangement and the apparent exogenous origin of the roots borne on these underground organs. Schimper, indeed, considered these two features so characteristic of foliar organs that he suggested that these so-called "appendices" might possibly be metamorphosed leaves. Not quite satisfied with this view, Renault endeavored to establish the existence of two types of lateral organs on the Stigmarian axis, true roots with a triarch arrangement of wood and root-like leaves of monarch type. Williamson, however, clearly showed that the apparent triarch arrangement was really due to the presence at two angles of the metaxylem of the first tracheids of secondary wood, and reasserted the existence of only one type of appendicular organs, agreeing so closely, both in structure and in their orientation to the axis, on which they were borne, with the roots of *Isoëtes* that it would be impossible to deny the root nature of the Stigmarian "appendices" without applying the same treatment to the roots of *Isoëtes.*

Still, so distinguished a paleobotanist as Solms Laubach, after a careful weighing of all the available evidence, continued to uphold Schimper's view of the foliar nature of these outgrowths, both in his "Paleophytologie" and in his memoir on *Stigmariopsis,* in which he stated that he was in complete agreement with Grand' Eury's conclusion: "Que ces organes sont indistinctement des rhizomes et que les Sigillaires n'avaient pas de racines réelles, ainsi que *Psilotum.*" Indeed, in reviewing the account I gave of the occurrence of a special system of spiral tracheids in the outer cortex of the Stigmarian rootlets, Count Solms drew attention to their similarity to the transfusion tissue of Lepidodendroid leaves, and asserted that we have here a further indication of the former foliar nature of these rootlets. Personally, I still adhere to the belief, expressed at the time, that these peripheral cortical tracheids represent a special development required by a plant with an aquatic monarch root of the *Isoëtes* type and a large development of aerial evaporating surface. The fact that the lateral outgrowths from the Stigmarian axis have been generally considered to be exogenous is not a valid argument against their root nature, as the same origin is ascribed to the roots of *Phylloglossum* and to those produced on the rhizophores of *Selaginella*. Probably, indeed, as Bower points out in his masterly exposition of the "Origin of a Land Flora," in dealing with the Lycopodiales, "the root in its inception would, like the stem of these plants, be exogenous." According to the "recapitulation theory," indeed, the exogenous formation of the roots in the embryo of certain Lycopods, as well as of the first root of *Isoëtes* and the first root of the Filicales, might be regarded as the retention of a more primitive character in these particular organs. The roots of *Stigmaria*, even if exogenous, might therefore merely represent a more ancestral stage. This difference between the roots of *Isoëtes* and the rootlets of *Stigmaria* may, however, be more apparent than real, for my colleague, Dr. Lang, has drawn my attention to the fact that there appear to be in *Stigmaria* remnants of a small-celled tissue on the outside of what has generally been taken to be the superficial layer of the Stigmarian axis, and a careful investigation of this point inclines me to agree with him that very probably the Stigmarian rootlets were actually formed like those of *Isoëtes*, somewhat below the surface layer, which, after the emergence of the rootlets, became partially disorganized. Should this surmise prove correct when apices of *Stigmaria* showing structure come to light, the last real difference between the rootlets of *Isoëtes* and the rootlets of *Stigmaria* will have disappeared, and the view for which Professor Williamson so strongly contended will be finally established.

While a careful comparison of *Isoëtes* with the extinct Lycopodiaceous plants may be taken to finally settle its systematic position, the Psilotaceæ have been somewhat disturbed by such comparisons. Placed formerly without much hesitation in the phylum Lycopodiales, certain features in their organization, such as the dichotomy of their sporophylls, and the structure of their fructification generally have suggested affinity with that interesting group of extinct plants, the Sphenophyllales. Their actual inclusion in this group by Thomas and by Bower may seem, perhaps, somewhat hazardous, considering the differences existing between the Psilotaceæ and *Sphenophyllum;* and the more cautious attitude of Seward, in setting up a separate group for these forms, seems on the whole more satisfactory than forcing these aberrant relatives of the Lycopods into the somewhat Procrustean bed of Sphenophyllales, which necessitates the minimizing of such important differences as the dichotomous branching of the axis and the alternate arrangement of their leaves, though the latter character allows, it is true, of some bridging over. But, even adopting this more cautious attitude, the study of the Sphenophyllales has been of great help in coming to a clearer understanding of certain morphological peculiarities of the Psilotaceæ, quite apart from the flood of light which this synthetic group of Sphenophyllales has thrown upon the relationship of the Lycopodiales to the Equisetales.

More far-reaching in its bearing on the relationships of existing plants has been the study of those interesting fern-like plants which seem to show in their vegetative organs a structure possessing both fern-like and Cycadian affinities. Full of interest as these so-called Cycadofilices were in their vegetative organization, they were destined to rivet on themselves the attention of all botanists by the discovery of their fructifications. No chapter in the recent history of paleobotany is more thrilling than the discovery, by the patient and thorough researches of Professor Oliver, of the connection between *Lyginodendron* and the well-known paleozoic seed, *Lagenostoma*. With Dr. Scott as sponsor, this new and startling revelation met with ready acceptance, and, thanks to the indefatigable energies of paleobotanists, no fossil fern seemed at one time safe from possible inclusion among the Pteridospermæ.

The infectious enthusiasm with which the discovery of the seed-bearing habit of the Lyginodendreæ and the Medullosæ was greeted carried all before it, and we in England, particularly, have perhaps not looked carefully enough into the foundations upon which rested the theory that these groups form the "missing links" between the ferns and cycads. A criticism against the wholesale acceptance of this view has been put forward by Professor Chodat,[3] of Geneva, that distinguished and versatile botanist, whom we have on several occasions had the pleasure of welcoming in our midst. Couched throughout in friendly and courteous language, and full of admiration for the work of those who were concerned in the establishment of the group of Cycadofilices, now termed Pteridospermæ, Professor Chodat suggests that English paleobotanists have not sufficiently appreciated the work of Bertrand and Corneille[4] on the fibro-vascular system of existing ferns, and have not revised, in the light of the researches of these French investigators, the interpretation given to the arrangement of the primary vascular tissues of *Lyginodendron*. In Chodat's opinion the structure of the primary groups of wood found in the stem and in the double leaf-trace of this plant is not directly comparable with the arrangement found in the petiole of existing Cycads. In the latter the bulk of the metaxylem is centripetal, while we have in addition a varying amount of small-celled centrifugal wood towards the outside of the protoxylem, and though separated from it by a group of parenchymatous cells, the bundle may be conveniently described as mesarch. In *Lyginodendron*, and the same applies to *Heterangium*, the primary bundles of the stem appear at first sight to be mesarch too, but in Chodat's opinion, if I understand him correctly, the metaxylem is exclusively centrifugal in its development, but, widening out and bending inwards again, in form of the Greek letter ω, the two extremities of the metaxylem are united on the inside of the protoxylem, forming an arrangement described by Bertrand and Corneille in the case of several fern petioles under the name of "un divergeant fermé."

Several details of structure, such as the type of pitting of the metaxylem elements and the separation of the protoxylem from the adaxial elements of metaxylem by parenchymatous cells, confirm Chodat in his view that the primary bundles of *Lyginodendron* are not really mesarch, and that the stem of *Lyginodendron* is essentially Filicinean in nature. Chodat cites other characters, such as the presence of sclerized elements in the pith, and the absence of mucilage ducts, in support of his view of the purely filicinean affinities of the Lyginodendreæ. The presence of secondary thickening in *Lyginodendron* he regards not as indicative of Cycadian affinity, but merely as another instance of secondary growth in an extinct Cryptogam, taking up very much the position of

[3] Chodat, R., "Les Ptéropsides des temps paléozoïques," *Archives des Sciences physiques et naturelles*, Genève, Tome XXVI., 1908.

[4] Bertrand, C. E., and Corneille, F., "Etude sur quelques characteristiques de la structure des filicinées actuelles," *Travaux et mémoires de l'Université de Lille*, 1902.

Williamson in his earlier controversy with French botanists with regard to the secondary thickening of *Calamites* and Lepidodendreæ. Chodat is also at variance with Kidston and Miss Benson as to the nature of the microspores borne on the fronds of *Lyginodendron* or *Lyginopteris,* as he prefers to call this plant. He certainly figures some very fern-like sporangia, attached to the fronds of *Lyginodendron,* but any one who has worked with the very fragmentary and somewhat disorganized material contained in our nodules knows how difficult it is to be absolutely certain of structural continuity. Neverthless, a reinvestigation of the whole question of the microsporangia of *Lyginodendron* seems to me clearly called for by the publication of Chodat's figures.

As regards the seed-bearing habit of *Lyginodendron,* Chodat adopts wholeheartedly Oliver's correlation of *Lagenostoma* with the fronds of *Lyginodendron,* but would regard the seed, apparently devoid of endosperm at the time of pollination, as a somewhat specialized macrosporic development, of more complex structure, but analogous in its nature to the seed-like organ exhibited by *Lepidocarpon* in another phylum of the Pteridophyta. "In any case," he concludes, "the origin and the biology of this kind of seed must have been very different from those of the seeds of the Gymnosperms."

This contention, based mainly on the tardy development of the endosperm in *Lagenostoma,* is the least weighty part of Chodat's criticism, for it has never been asserted that the seeds were identical with those of existing Cycads. We know that the seed-habit was adopted by various groups of Vascular Cryptogams, and it is revealed in fossil plants in various stages of evolution, so that it may be readily presented to us at a special stage of its evolution in *Lyginodendron.* Moreover, we must remember that in so highly organized a Gymnosperm as *Pinus,* the macrospore itself is not fully developed at the time of pollination. Though not suggesting this as a primitive feature in the case of the pine, we can well imagine how, by a gradual process of "anticipation," the prothallus might become established before pollination in any group of primitive seed-bearing plants. There are other more specialized rather than primitive features in the complex structure of *Lagenostoma* which might with much more reason be invoked, to show that the seed of *Lyginodendron* does not form a step in the series of forms leading to the Cycadian ovule.

But leaving this point out of consideration, Chodat brings forward some strong reasons for his conclusions that the Lyginodendreæ were plants possessing stems of purely fern-like structure, increasing in thickness by means of a cambium, that their foliage was of filicinean structure, but provided with two kinds of sporangia, microsporangia similar to those of Leptosporangiate ferns, and macrosporangia of specialized type, containing a single macrospore. This group, therefore, Chodat regards as a highly specialized group of ferns, which, he considers, shows no particular connection with the Cycads, and which may have formed the end in a series of highly differentiated members of the Filicineæ.

Of the Medullosæ, on the other hand, Chodat takes a very different view. Both in the structure of their primary and secondary growth, as well as in their polystely, he sees close affinity of these forms to the Cycads, borne out by smaller secondary features, such as the presence of mucilage ducts, and the simple form of pollen-chamber. Chodat considers the agreement of the Medullosæ with the Cycadaceæ to be so close that he regards them as Protocycadeæ, the fern-like habit being restricted to the position of the sporangia on the vegetative fronds. *Medullosa,* therefore, would be only one link in the chain connecting the Cycads with the Filicales, and a link very near the Cycadian end of that chain. Other forms more closely connected with the Filicinean phylum are still to be sought.

In bringing Professor Chodat's views to your notice, I do not wish to urge their acceptance, but his criticism seems to me sufficiently weighty to demand a careful reconsideration of the structure and affinities of the Lyginodendreæ, which, whatever may be their ultimate position in our scheme of classification, will continue in the future, as they have done in the past, to command the attention of all botanists interested in the evolution of plant life.

If the whole-heartedness with which we in England received the theory of the Cycadian affinity of *Lyginodendron* has laid us open to friendly criticism, I am afraid some of us may be accused of exceeding the speed-limit in our rapid acceptance of the Cycadoidean ancestry of the Angiosperms. Ever since Wieland put forth the suggestion in his elaborate monograph of the "American Fossil Cycads" that "further reduction and specialization of parts in some such generalized type, like the bisporangiate strobilus of *Cycadoidea,* could result in a bisexual angiospermous flower," speculation as to the steps by which the evolution might have been brought about has been rife, and Hallier in Germany and Arber and Parkin in England have put forward definite schemes giving probable lines of descent. Arber and Parkin in their criticism and detailed suggestions connect phylogenetically with the Bennettitales, the Ranales, as primitive Angiosperms, and displace from this position the Amentales and Piperales, which were regarded by Engler as probably more closely related to the Proangiosperms. Of course, the resemblance between the amphisporangiate, or, as I should prefer to call it, the heterosporangiate "strobilus" of *Cycadoidea,* and the flower, say, of *Magnolia* is very striking, and the knowledge we have gained of the structure and organization of the Bennettitales certainly invites the belief in a possible descent of the Angiosperms from this branch of the great Cycadian plexus; but the ease with which the flower of the Ranales can in some respects be fitted on to the "flower" of *Cycadoidea* raises suspicion. Critics of the Arber-Parkin hypothesis may possibly incline to the view that "truth is often stranger than fiction," and that the real descent of the Angiosperms may have been much less direct than that put forward in these recent hypotheses. The particular view of the morphology of the intraseminal scales and seed pedicles adopted by Arber and Parkin is, as they admit, not the only interpretation that can be put upon these structures, and the views on this point will probably remain as various as are those of the female cone of *Pinus.* Even if we regard the ovulate portion of the Cycadoidean "flower" as a gynecium, and not as an inflorescence, we are bound to admit, as do Arber and Parkin, that it is highly modified from the pro-anthostrobilus type with a series of carpels bearing marginal ovules. *Cycadoidea* was evidently a highly specialized form, and may well have been the last stage in a series of extinct plants.

Arber's very sharp separation of mono- and amphisporangiate Pteridosperms does not seem to me quite justified. Amphisporangiate forms may have been preserved, or may have arisen anew in various groups of Pteridosperms or in their descendants. Heterospory, we know, originated independently in at least three of the great phyla of vascular Cryptogams, and originally, no doubt, the same strobilus contained both macro- and microsporangia, as was the case in *Calamostachys Casheana,* in the strobili of most Lepidodendraceæ, and as is still the case in the strobili of *Selaginella* and in *Isoëtes.* Even in the existing heterosporous Filicineæ, micro- and macrospores are found on the same leaf and on the same sorus; and though in the higher Cryptogamia and the lower Phanerogamia there may have been a tendency to an iso-sporangiate condition, yet, as the two kinds of spores are obviously homologous in origin, nothing is more natural than an occasional reversion to a heterosporangiate fructification. Thus in the group of Gymnosperms we have many instances of the occurrence of so-called androgynous cones. In 1891, at the meeting of the British Association in Leeds, I described such amphisporangiate cones which occurred regularly on a *Pinus Thunbergii* in the Royal Gardens of Kew, and only this spring I was able to gather several hermaphrodite cones of *Larix Europea.* They have, of course, been observed and described by many authors for a variety of Gymnosperms. What more likely than that many extinct Gymnosperms may have developed heterosporangiate fructifications? It is not necessary, therefore, to fix on one group of ancestors for the origin of all existing Angiosperms. Indeed, the great variety of forms, both of vegetative and reproductive organs, which we meet with in the Angiosperms, not only to-day, but even in the Cretaceous period, in which they first made their appearance, warrants, I think, the belief in a polyphyletic origin of this highest order of plants. It is no doubt true, as Wieland points out "that the plexus to which *Cycadoidea* belonged, as is the case in every highly organized plant type, presented members of infinite variety," and, indeed, so far as the vegetative organization goes, we know already, through the labors of Nathorst, of such a remarkable form as *Wielandiella angustifolia,* while Wieland has shown us a further type in his Mexican *Williamsonia.* Nevertheless, these diverse forms all agree in the structure of their gynecium, the particular organ which is not so easy to bring into line with that of the Angiosperms.

I am quite alive to, though somewhat sceptical of, the possibility of a direct descent of the Ranales from the Cycadoideæ, but my hesitation in accepting Arber and Parkin's view of the ancestry of the Angiosperms is enhanced by the consideration that it seems almost more difficult to derive some of the apparently primitive Angiosperms from the Ranales, than the latter from Cycadoidea. Indeed, this common origin of Angiosperms from the Ranalian plexus will, I feel sure, prove the stumbling-block to any general acceptance of the Arber-Parkin theory. It is easy enough to assume that all Angiosperms with the unisexual flowers have been derived by degeneration or specialization from forms with hermaphrodite flowers of the primitive Ranalian type, but unfortunately some of these degenerate forms possess certain characters which appear to me to be undoubtedly primitive.

It is difficult for those who accept Bower's view of the gradual sterilization of sporogenous tissue not to regard the many-celled archesporium in the ovules of *Casuarina* and of the *Amentales* as a primitive character, and though, as Coulter and Chamberlain point out, this feature is manifested by several members of the Ranunculaceæ and Rosaceæ, as well as by a few isolated Gamopetalæ, its very widespread occurrence in the Amentales seems to indicate its more general retention in this group of plants, and does not agree readily with the theory that these unisexual orders are highly specialized plants, with much-reduced flowers. The possession of a multicellular archesporium is, however, not the only primitive character exhibited by some of the unisexual orders of the Archichlamydeæ. Miss Kershaw[5] has shown, in her investigation of the structure and development of the ovule of *Myrica,* that in this genus, which possesses a single erect ovule, the integument is entirely free from the nucellus, and is provided with well-developed vascular bundles, in both of which features it resembles very closely the paleozoic seed *Trigonocarpus.* The same features were shown, moreover, by Dr. Benson[6] and Miss Welsford to occur in the ovules of *Juglans regia* and in a few allied genera, such as *Morus* and *Urtica.* Also in a large number of Amentales with anatropous ovules (*Quercus, Corylus, Castanea,* etc.), Miss Kershaw has demonstrated the occurrence of a well-developed integumentary vascular supply. No doubt a further search may reveal the occurrence of this feature in some other dicotyledonous ovules, but in the meantime it seems difficult to believe that such a primitive vascular system, which the Amentales share with the older Gymnosperms, would have been retained in the catkin-bearing group, if it had undergone far-reaching floral differentiation, while it had disappeared from the plants which in other respects remained primitive. It would be still more difficult to imagine that it had arisen in the Amentales subsequently to their specialization.

There are other structural characters and general morphological considerations, which I have not time to deal with, which underlie the belief in the primitiveness of the Amentales and some allied cohorts, and I trust they will be set forth in detail by a better systematist than I can claim to be. My object in bringing the matter forward at all is to point out some of the difficulties which prevent me from accepting a monophyletic origin of the Dicotyledons through the Ranalian plexus.

One of these difficulties lies in the relationship of the Gnetales to the Dicotyledons. Arber and Parkin have recently made the attempt to gain a clearer insight into the affinities of this somewhat puzzling group by applying to it the "strobilus theory[7] of Angiospermous descent." The peculiar structure of the flowers of *Welwitschia* lends itself particularly well to a comparison with those of *Cycadoidea,* and a good case can no doubt be made out for a hemiangiospermous ancestry of this member of the Gnetaceæ, and by reduction the other members, in many respects simpler, might be derived from a similar ancestor, though probably, as far as *Ephedra* and *Gnetum* are concerned, an equally good, if not better, comparison might be made with *Cordaites.* But even supposing we admit the possibility of a derivation of the Gnetales from an amphisporangiate Pteridosperm, I think the Amentales merit quite as much as the Gnetales to be considered as having taken their origin separately from the Hemiangiospermæ, and not from the Ranalian plexus. I find this view has been put forward also by Lignier[8] in his attempt to reconstruct the phylogenetic history of the Angiosperms, and I feel strongly that

[5] *Annals of Botany,* Vol. XXIII., 1909.

[6] *Ibid.*

[7] Arber, E. A. N., and Parkin, J., "Studies on the Evolution of Angiosperms," "The Relationship of the Angiosperms to the Gnetales," *Annals of Botany,* Vol. XXII., 1908.

[8] Lignier, O., "Essai sur l'Evolution morphologique du Règne vegetal," *Bull. de la Soc. Linnéenne de Normandie,* 6 sér., 3 vol., 1909, reimprimé février, 1911.

such a polyphyletic descent, whether from the more specialized anthrostrobilate Pteridospermæ or from several groups of a more primitive Cycado-Cordaitean plexus, is more in accordance with the early differentiation of the Cretaceous Angiosperms, and with the essential differences existing now in the orders grouped together as Archichlamydeæ.

Attempts at reconstructing the phylogeny of the Angiosperms are bound to be at the present time largely speculative, but we may possibly be on the threshold of the discovery of more certain records of the past history of the higher Spermaphyta, since Dr. Marie Stopes has commenced to publish her investigations of the cretaceous fossil plants collected in Japan, and Professor Jeffrey has been fortunate enough to discover cretaceous plant-remains showing structure in America. The former have already provided us with details of an interesting Angiospermic flower, and if the latter have so far only yielded Gymnosperms, we may at all events learn something of the primitive forms of these plants, the origin of which is still as problematical as is that of the Angiosperms.

I trust that the criticisms I have made of the theory put forward by Messrs. Arber and Parkin will not be taken as a want of appreciation on my part of the service they have done in formulating a working hypothesis, but merely as an expression of my desire to walk circumspectly in the very alluring paths by which they have sought to explore the primeval forest, and not to emulate those rapid but hazardous flights which have become so fashionable of late.

While the description of new and often intermediate forms of vegetation has aroused such wide-spread and general interest in paleobotany, other and more special aspects of the subject have not been without their devotees, and have proved of considerable importance. Morphological anatomy has gained many new points of view, and our knowledge of the evolution of the stele owes much to a careful comparison of recent and fossil forms, even when these investigations have produced conflicting interpretations and divergent views.

Another promising line of paleobotanical research lies in the direction of investigations of the plant tissues from the physiological and biological points of view. Happily, the vegetable cell-wall is of much greater toughness than that of animal cells, and in consequence the petrified plant-remains found in the calcareous nodules are often so excellently preserved that we can not only study the lignified and corky tissues, but also the more delicate parenchymatous cells. Even root-tips, endosperm and germinating fern-spores are often so little altered by fossilization that their cells can be as easily studied as if the sections had been cut from fresh material. It is this excellence of preservation which has enabled us to gain so complete a knowledge of the anatomy of paleozoic plants, and since the detailed structure of plant organs is often an index of the physical conditions under which the plants grew, we are able to form some opinion as to the habitat of the coal-measure plants. Though a beginning has already been made in this direction by various authors, we have as yet only touched the fringe of the subject, and, as Scott points out in the concluding paragraph of his admirable "Studies," the biology and ecology of fossil plants offer a wide and promising field of research. Such studies are all the more promising, as we now have material from such widely separated localities as the Lancashire coalfield, Westphalia, Moravia and the Donetz Basin in Russia.

Now that it has been definitely shown by

Stopes and Watson that the remains of plants are sometimes continuous through adjacent coal-balls, we may safely accept their conclusion that these calcareous concretions were in the main formed *in situ,* and that the plant-remains they contain represent samples of the vegetable débris of which the coal-seam consists. We have in these petrifactions, therefore, an epitome, more or less fragmentary, of the vegetation existing in paleozoic times on the area occupied by the coal seam, and the Stigmarian roots in the underclay, as well as other considerations, lead us to believe that the seam more frequently represents the remains of the coal-measure forest carbonized *in situ.* While this seems to be the more usual formation of coal-seams, it is obvious from the microscopic investigations of coal made by Bertrand, and as has recently been so clearly set forth by Arber in his "Manual on the Natural History of Coal," that in the case of bogheads and cannels the seam represents metamorphosed sapropelic deposits of lacustrine origin. In other cases, again, considerations of the nature of the coal and the adjacent rocks may incline us to the belief that some, at any rate, of the deposits of coal may be due to material drifted into large lake-basins by river agency.

Broadly speaking, however, and particularly when dealing with the seams from which most of our petrified plant-remains have been collected, we may consider the coal as the accumulated material of paleozoic forests metamorphosed *in situ.* What, then, were the physical and climatic conditions of these primeval forests? The prevalence of wide air-spaces in the cortical tissues of young Calamitean roots, as indeed their earlier name Myriophylloides indicates, leads us to believe that, as in the case of many of their existing relatives, they were rooted under water or in water-logged soil. We gather the same from the structure of *Stigmaria,* while the narrow xerophytic character of the leaves at any rate of the tree-like *Calamites* and *Lepidodendra* closely resembles the modifications met with in our marsh plants. It has been suggested by several authors that the xerophytic character of the foliage of many of our coal-measure plants may be due to the fact that they inhabited a salt marsh. A closer examination of the foliage, however, of such plants as *Lepidodendron* and *Sigillaria* does not reveal the characteristic succulency associated with the foliage of most Halophytes, and in view of the absence of such water-storing parenchyma, the well-developed transfusion-cells of the Lepidodendreæ can only be taken to be a xerophytic modification such as is met with in recent Conifers.

The specialization of the tissues indeed is only such as is quite in keeping with the xerophytic nature of marsh plants. Moreover, the particular group of Equisetales are quite typical of fresh water, and we should expect that if their ancestors had been Halophytes, some, at any rate, at the present day would have retained this mode of life. Nor have we at the present time any halophytic Lycopodiales, while *Isoëtes,* the nearest relative to the *Lepidodendra,* is an aquatic or sub-aquatic form associated with fresh water.

Among the Filicales, *Acrostichum aureum* seems to be the only halophytic form, inhabiting as it does the swamps of the Ceylon littoral,[9] and though, as Miss Thomas has pointed out, its root structure is in close agreement with that of many paleozoic plants, its frond shows considerable deviation from that of *Lyginodendron* or *Medullosa,* both of which plants, as

[9] Tansley, A. G., and Fritsch, "The Flora of the Ceylon Littoral," *New Phytologist,* Vol. IV., 1905.

Pteridosperms, are on a higher plane of evolution, and might therefore be expected to show a more highly differentiated type of leaf. But on the contrary these coal-measure plants show a more typically Filicinean character, both as regards the finely dissected lamina and also in the more delicate texture of the foliage compared with the specialized organization of the frond of *Acrostichum aureum,* described by Miss Thomas.

Nor is it necessary to call to aid the salinity of the marsh to explain the excellent preservation of the tissues of the plant-remains in the so-called coal-balls, in view of the well-known power of humic compounds to retard the decay of vegetable tissues. In addition to these arguments, I might draw attention to the presence of certain fungi among the petrified débris, as more likely to be found in fresh water than in marine conditions. *Peronosporites,* so common in the decaying Lepidodendroid wood, and the *Urophlyctis*-like parasite of Stigmarian rootlets, seem to me to support the fresh-water nature of the swamp; just as the occurrence of the mycorhiza, described by Osborn, in the roots of *Cordaites* seems to indicate the presence of a peaty substratum for the growth of that plant. Potonié also refers to the occasional occurrence of Myriapoda and fresh-water shells as indicative of the fresh-water origin of at least many of the coal deposits, and a common feature of the petrified remains of coal-measure plants is the occurrence of the excrements of some wood-boring larvæ in the passages tunneled by these paleozoic organisms through the wood of various stems.

A strong argument in favor of the brackish nature of these swamps would be supplied by the definite identification of *Traquairia* or *Sporocarpon* as Radiolaria, though we must remember that certain marine Cœlenterata find their way up into the Norfolk Broads, the fresh-water Medusæ are by no means unknown in different parts of the tropics. Of course, if the coal-measure swamps were estuarine or originated in fresh-water lagoons near the sea, they may have been liable from time to time to invasions of salt water, sufficient to account for the presence of occasional marine animals, but without constituting a halophytic plant association.

Potonié, who has made so close a study of the formation of coal, and who supports the theory of its fresh-water origin, considered for a long time the comparison between the coal-measure swamp and the cypress swamps of North America, as the nearest but at the same time a somewhat remote analogy, more particularly as he believed that the nature of the coal-measure vegetation required a tropical and also a moister climate than obtains in the southern states of North America. Though, in view of the great development of Pteridophytic vegetation in countries like New Zealand, I think Potonié possibly exaggerates the temperature factor, he is probably right in assuming a fairly warm climate for the coal-measure forest. The difficulty, so far, has been to account for the great thickness of humic or peaty deposits which must have accumulated for the formation of our coal-seams, in view of the fact that extensive peat formation is generally associated with a low temperature. In the tropics, peat may be deposited at high altitudes, where there is low temperature and high rainfall, but it is generally supposed that the rate of decomposition of vegetable remains is so active that lowland peat-formation was out of the question. Dr. Koorders, however, has observed a peat-producing forest in the extensive plain on the east side of Sumatra, about a hundred miles from the coast. This swamp-forest has been recently reexplored at the instance of Professor Potonié, and he finds it to agree closely with the vegetative peculiarities which he considers must have been presented by the vegetation of the coal-measure forest. A typical "Sumpflachmoor," this highly interesting tropical swamp has produced a deposit of peat amounting in some places to thirty feet in thickness. The peat itself consists mainly of the remains of the Angiospermic vegetation of which the forest is made up, including pollen-grains and occasional fungal filaments; the preservative power, which has enabled this accumulation of débris to take place, being due to the peaty water which is seen above the roots of the bulk of the vegetation. The latter consists mainly of dicotyledonous trees belonging to various natural orders, and they mostly show such special adaptations as breathing roots (pneumatophores) and often buttress roots. With the exception of a tree-fern, Pteridophyta, Liverworts and Mosses, and, indeed, all herbaceous vegetation, are poorly represented in this swamp, though high up in the branches of the trees there are a fair number of epiphytes, and at the edge of the swamp-forest lianes, belonging particularly to the palms, play an important part in the vegetation. The water, partly on account of its peaty nature, partly owing to the intense shade, is almost devoid of algæ, and none of these organisms were found in the peat itself. The interesting account given by Potonié of this tropical peat-formation is very suggestive when certain features, as, for example, the absence or relative paucity of certain of the lower groups of plants, such as algæ and Bryophyta, in the peat, are compared with the plant-remains in some of our coal-seams. Replacing the now dominant Angiosperms by their Pteridophytic representatives in paleozoic times, we have a very close parallel in the two formations.

Another interesting question arises when we consider the great variety of types of vegetation met with among the plant-remains of the coal-seams. For in addition to the limnophilous *Calamites* and Lepidodendraceæ mentioned above, the coal-balls abound with the remains of representatives of the Filicales, the Pteridospermæ and the Cordaitaceæ. Were these also members of this swamp vegetation, or have their remains been carried by wind or water from surrounding areas? With regard to some plant-remains, namely, those found exclusively in the roof nodules, the latter was undoubtedly the case; for we have ample evidence, both in their preservation and their mode of occurrence, that they have drifted into the region of the coal-measure swamp after its submergence below the sea. This would apply to such plants as *Tubicaulis Sutcliffii* (Stopes), *Sutcliffa insignis* (Scott), *Cycadoxylon robustum* and *Poroxylon Sutcliffii* and other forms, the remains of which have so far not been observed in the coal-seam itself. These plants represent a vegetation of non-aquatic type, and may be taken to have grown on the land areas surrounding the paleozoic swamps. But, on the other hand, we have remains of many non-aquatic plants in the coal-seam itself, closely associated with fragments of typical marsh-plants. How can their juxtaposition be explained?

The advance of our knowledge of ecology points, I think, to a solution of this difficulty. No feature of this fascinating study, which has of late gained so prominent a place in botanical investigation, is more interesting than to trace out the succession of plant associations within the same area, noting the ever-changing conditions which the development of each association brings about. If we follow with Schroeter the gradual development of a lacustrine vegetation from the reed-swamp through the marsh (or Flachmoor) to a peat-moor (Hochmoor), we see how one plant association makes place in its turn for another. May not the mixture of various types of vegetation which we meet with in the petrifactions of our coal-seam represent the transition from the open Calamitean or Lepidodendroid swamp to a fen or marsh with plentiful peat-formation, due to the gradual filling up of the stagnant water with plant-remains? Thus in places, at any rate, a transition from aquatic to more terrestrial types of vegetation would take place, while the tree-like forms rooted in the deeper water would continue to flourish. The coal-measure swamp in this stage would differ from the tropical swamp of Kooders by a more abundant undergrowth of herbaceous and climbing plants, rooted in damp humus and passing off gradually into drier peat. Such an undergrowth of Cryptogamic types, mainly Filicinean or Pteridospermic, would have admirable conditions for luxuriant development, apart from the provision of a suitable substratum for its roots, owing to the narrow xerophytic nature of the foliage on the canopy of the trees under which it grew.

Here, too, we see the explanation of the striking difference between the microphyllous and arborescent *Calamites* and Lepidodendraceæ, and the large ombrophile foliage of the Filicineæ and Pteridosperms, which spread out their shade-leaves under the cover of marsh xerophytes, in exactly the same way as Professor Yapp has so admirably depicted for recent plants in his account of the "Stratification in the Vegetation of a Marsh."

The development of a mesophytic vegetation in the shelter of the marsh xerophytes makes it unnecessary to postulate an obscuration of the intense sunlight by vapors, as was done by Unger and Saporta for the Carboniferous period. The assumption of a variety of conditions of plant life within the same area helps materially to clear up the difficulties presented by the somewhat incongruous occurrences met with in the petrified plant-remains. The presence of fragments of *Cordaites,* mixed with those of *Calamites* and *Lepidodendra,* in the coal-balls can not always be explained either by a drift theory, or by conceiving the fragments to be wind-borne; but, given an area of retrogressive peat above the ordinary water-level, and even so xerophytic a plant as *Cordaites* might well establish itself there, its mycorhiza-containing roots being well adapted for growth in drier peat. The curious occurrence of more or less concentric rings in the secondary wood of the stem and roots of *Cordaites* may represent a response probably not to annual variations of climate, but to abnormal periods of drought, which would affect the upper-peat layers, but not the water-logged soil in which were rooted the *Calamites* and *Lepidodendra.*

If, as I suspect, we had in the peat deposit of the coal-seam a succession of associations, we ought to find its growth and history recorded by the sequence of the plant-remains, very much as Mr. Lewis has discovered with such signal success in our Scottish peat-bogs. That some differences occur in the plant-remains building up a seam can be noted by a microscopic examination of the coal itself, in which, as Mr. Lomax tells me, the spores of *Lepidodendra* occur in definite bands. But no systematic attempt has as yet been made to investigate from this point of view the seams charged with petrified plant débris. Before the Shore pit, which was reopened last summer through the renewed generosity of Mr. Sutcliffe, was finally closed down, I obtained two series of nodules, ranging from the floor to the roof of the seam, and have had these cut for detailed examination. I should not, however, like to make any generalizations from these isolated series, but intend, during the coming winter, to investigate in the same manner further series taken from large blocks of nodules, which have been removed bodily so as to retain the position they occupied in the seam. Though at present the data are only fragmentary, there seems to be some indication that the plant-remains are not without some relation to their position in the seam. Of course, Stigmarian rootlets are ubiquitous, and in the nodules of the lower part of the seam predominant, but other plant-remains appear to be more frequently found at one level of the seam than another. The problem, however, is very involved, and it has become apparent that it is as important to study the fine débris in which the larger fragments are embedded as the distribution of these latter. Moreover, attention must be paid to the stage of decomposition presented by the particles forming the matrix of the nodule, as this varies in the lower and upper parts of a seam, very much as in a peat-bed we can distinguish the lighter-colored fibrous peat from the darker layers at the base of a peat-cutting. Mr. Lomax, who has so unique an experience of these coal-balls, informs me that he can tell whether a nodule is from the top or bottom of the seam by the lighter or darker color of the matrix. The importance of applying the methods which have been so successful in elucidating the history of modern peat-deposits to the investigation of the coal-seam will be clearly appreciated both by paleobotanists and ecologists, and this particular problem offers a striking illustration of the interdependence of various branches of botanical investigation. It is fortunate indeed that the two fields of work, paleobotany and plant ecology, though they have been subjected to fairly intensive cultivation, have not become exclusively the domain of specialists. The strength and progress of modern botany have been due to the close collaboration of workers engaged in different branches of botanical science, and the fact that British ecologists have combined to attack a series of the problems from very diverse points of view leads one to hope that, with a continuance of that intimate cooperation which has characterized their work so far, and with the added stimulus of the friendly visit of our distinguished colleagues from abroad, considerable progress may be expected in the future in this branch of botanical study. Privileged as I have been to assist at the deliberations of the British ecologists, without as yet having taken any active part in their work, I feel myself at liberty to point with appreciation to the excellent beginning they have made of a botanical survey of Great Britain and Ireland, as well as to the more detailed investigations of special associations and formations, such as the woodlands, the moorlands, the fens, the broads, salt marshes and shingle beaches. I am glad to think that our foreign visitors have been able to see these interesting types of vegetation under the guidance of those who have made a special study of these subjects.

The importance to ecologists of an up-to-date critical flora was dwelt upon by my predecessor in this presidential chair, and this obvious need may be regarded as a further illustration of the interrelationship of the various aspects of botanical science. Though it has been obvious to all that the swing of the pendulum has been for a long time away from pure systematic botany, I am convinced that the great development of plant ecology, of which we have many indications, will not merely lessen the momentum of the swinging pendulum, but will draw the latter back towards a renewed and critical study of the British flora. That a revival of interest in systematic botany will come through the labors of those who are engaged in survey work and other forms of ecological study, is foreshadowed by the fact that Dr. Moss has undertaken to edit a "New British Flora," which will, I believe, largely fulfill the objects put forward by Professor Trail in his presidential address. I trust, however, that in addition to the ecologists, those botanists who are interested in genetics will contribute their share towards the completion of our knowledge of critical species, varieties and hybrids, all of which offer such intricate problems alike to the systematist and to the student of genetics.

De Vries prefaced his lectures on "Species and Varieties, their Origin by Mutation," by the pregnant sentence: "The origin of species is an object of experimental investigation," and this is equally true of the study of the real and presumptive hybrids of our British flora, which may be investigated either synthetically or, when fertile, also analytically, as in some cases their offspring show striking Mendelian segregation. Some good work has already been accomplished in this direction, but more remains to be done, and we have here an important and useful sphere of work for the energies of many skilled plant-breeders.

I would, therefore, like to plead for intimate collaboration between all botanists, hopeful that, as progress in the past has come through the labors of men of wide sympathies, so in the future, when studies are bound to become more specialized, there will be no narrowing of interests, but that the various problems which have to be solved will be attacked from all points of view, the morphological, the physiological, the ecological and the systematic. Thus by united efforts and close cooperation of botanists of all schools and of all countries we shall gain the power to surmount the difficulties with which our science is still confronted.

F. E. Weiss

WORK AT THE MARINE BIOLOGICAL STATION OF SAN DIEGO DURING THE SUMMER OF 1911

Because a majority of the station's staff are still holding college positions and hence can be at La Jolla only during vacation time, the summer months are the most active of the year. This disadvantage must continue until the income is sufficient to maintain operations at sea and a considerable part of the work in the laboratory throughout the year.

On the biological side the most important event of the year is the final issuance of Mr. E. L. Michael's "Classification and Vertical Distribution of the Chætognatha of the San Diego Region" (Univ. Calif. Public. Zoology, Vol. 8, No. 3, 165 pp.). In this the author not only records all the species so far taken in these waters and subjects the description and taxonomy of the group to a critical examination, but deals quantitatively with the large amount of data collected during the five years from 1904 to 1909.

The aim of the ecological aspect of the investigation was to ascertain the facts concerning the distribution, seasonal and vertical, of the organisms, and to see how far these are correlatable with and hence dependent upon the environmental factors of light, and of temperature and density of the water. Efforts were limited to these three environmental factors simply because the scope of the station's work up to this time has not made it possible to extend the hydrographic observations beyond these.

While it is impossible to summarize here