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VIEWS OF HIGHER SEED PLANT DESCENT SINCE 1879[1]

By Dr. G. R. WIELAND

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IN the year 1876 the celebrated Thomas Henry Huxley visited at Yale my old preceptor, O. C. Marsh, finding intense interest in the new collections of vertebrate fossils from the Tertiary of the west. In the "Life and Letters of Huxley," edited by his son, Leonard, there are given full references to the sojourn in New Haven. In Huxley's opinion there was no European collection of mammalian fossils quite equal to that then assembled by Marsh. Its glory was in the fossil horses. For the first time, said Huxley, a series of fossil species leading into a living type had been brought to light.

Those were brilliant days in biology. The "Origin of Species" and the "Descent of Man" had appeared but a few years before. In the closing paragraphs of the "Descent" Darwin had paid fine tribute to the genius of Haeckel, who "had confirmed nearly all his own conclusions." But as yet the lore of fossil plants had not reached the distinctiveness first seen in the invertebrate and then in the vertebrate records. Much was indeed known about fossil plants, going back to those patriarchs of paleobotany, Brongniart, Goeppert and Williamson. In 1868, too, William Carruthers had brought out a splendid account of the fossil cycadean stems from the secondary rocks of Britain, including histologic study of the utterly isolated and singular seed cone of *Bennettites Gibsonianus* from the Isle of Wight, while two years after came Williamson's later notes on the "History of *Zamia gigas*." But the "scaly heads and collars" of the Yorkshire coast still remained "Williamson's riddle," while Carruthers, perhaps too much impressed by the utter singularity of the mature cycadeoid cone structure, is credited with the thought that

[1] Opening address at the eastern meeting of the Botanical Society of America at Dartmouth, June 25.

it was very unlikely that fossils would ever feature the events in plant descent much more closely than they already had.

How little could then be discerned of higher seed plant descent in older plant records is told in few words by Joseph Dalton Hooker in a letter to Arber, lately quoted by Hutchinson:

> With regard to your queries respecting the primitive type of angiospermous plants, that subject has never been far from my mind for upwards of half a century, during which period I have failed to grasp a feature in the morphology, physiology or geographical distribution of angiosperms that gave much color to whatever speculations I may have indulged in respecting it. I do not share Engler's views as expressed in his classification and writings. The classification is neither better nor worse in the abstract than DeCandolle's (so-called), and is far more troublesome to apply for practical purposes.

The passage is quoted in full as direct testimony to the fact that while the artificial plant systems have always held near to certain larger outlines that must have some relation one way or the other to true evolutionary series, any accord as to the starting-point is very recent. Darwin could well say in 1879 that the origin of the angiosperms was an "abominable mystery," and except for the fact that Ginkgo could be called "a living Cordaite," the origin of the gymnosperms was nearly as mysterious. Whether the fact was very consciously in the minds of botanists or not, some discovery of new types of fructification leading into gymnosperms, or from them toward angiosperms, could alone lead to bettered ideas of higher plant descent. What could be inferred from the isolated records of stem structure or foliage could only adumbrate, without defining, the general course of change in the successive canopies.

A first rift in the veil of mystery resting over not merely angiosperm but more or less all higher seed plant descent seemed to come as if by chance, though not from an entirely unsuspected group—the cycads. That flowers and cones must go back to carpels was long noted, but that some marvelously composite type might suddenly flash into full view, as did the flower of *Cycadeoidea ingens* in 1899, was not quite foreseen. From that year on, down to this evening, discovery illuminating the course of phylogenetic change in seed plants has so outrun even well-placed theory that he must be a modest botanist indeed who would admit that the plant record has contributed less to ideas of the greater evolutionary course than either the invertebrate or vertebrate records.

Continuing the recital, it is recalled that the very first of the short papers on cycadeoid fructification was sent to A. G. Nathorst. He had had in hand certain late Triassic plants from Skone which seemed of very debatable relationship. As it happened, too, Nathorst had collected Williamsonians at Cloughton Wyke in that dark year of 1879! Cone structure in his types being so generalized, however, and the fact that the Williamsonians belonged to a great tribe of flowering gymnosperms remaining as yet hidden, instead of a single, there now seemed to be two "riddles." There were made, it is true, various suggestions of angiosperm analogies, although always from indirect or insufficient view-points. But as soon as a related petrified form appeared in the foreground, the situation cleared. Study could now be successfully extended to the casts and imprints.

Nathorst could now see what to look for in his material. He later said, as he showed me his finely elaborated collections, "While it should have been possible to reach exactitude from the beginning, without your discovery of the petrified flowers I much doubt if I would ever have found the incentive to restudy of the Williamsonians, or have gained ideas of how to proceed."

We may, then, at this point briefly sum up the fossil discoveries bearing on higher seed plant evolution:

I. The flower of *Cycadeoidea* indicated that the "complete flower" with bracts, sepals, petals, stamens and a central seed cone was old and of varied form. It suggested great possibilities of variation in emplacement, and in fusion and number of parts, with long courses of both giantism and reduction. The stamens, as old as Marattia, were astonishing.

II. *Wielandiella* is either a "missing link" or a plain ordinary early member of the Magnoliales. It might well be such. Discovery of the staminate features and wood structure is awaited, but the habitus is so distinctly that of a Magnolia that Gothan says the type is "at least as significant in the plant as *Archaeopteryx* is in the animal world." In 1901 Coulter[2] and Chamberlain could say that the cycadeoid fructification mainly indicated transitions between pteridophytes and gymnosperms, without as much suggestion of angiosperms "as living gymnosperms had already given." That was then the fair statement to make, although but a single year later the restudy of *"Anomozamites"* thus brought into view a type which solely because of its reduced seed cones could be considered as related to cycadeoids at all—a type now to be regarded as more angiospermous than gymnospermous, if floral plan and vegetative habitus combined signify anything in descent.

III. *Seed ferns.*—In 1903, only a year after Nathorst's first restudy of the Skone fossils, Oliver and Scott announced the discovery of the seed-bearing quasifern, *Lyginopteris.* Since then many extensions

[2] John M. Coulter, "Relations of Paleobotany to Botany," *Amer. Nat.*, vol. XLVI, 1912.

of knowledge of the "seed ferns" have been made. But as in the cycadeoids and the *Wielandiella* series, some of the most important features are yet to determine. Pencil in hand, many hypothetical Pteridosperms may be sketched. Somewhere near or within this group it may be believed the simplest of anthostrobili were developed—plants bearing staminate fronds below, and ovulate above, or tending to do so, and then gradually organizing the two types of sporophylls on axes of limited growth; or in part becoming dioecious, and organizing cones of both sexes, after the manner of cycads. If there was an upward course from Selaginella it is still undiscernible.

IV. *Vegetative features of the older gymnosperms.*—There is no need here to single out the many studies of the past thirty or forty years which have brought into view the fact that the Devonian, Carboniferous and the Permian were periods of extremely varied stem structure in the older seed-bearing plants. Besides the varied types of Cordaites running well back into the Devonian with the remarkable cosmopolitan genus Callixylon, there may be merely mentioned the transitional Heterangium and the many so-called Medullosan types. And then there is to note the Rhetinangium, Kalymma of our own Kentucky Devonian, Bilignea, Stenomyelon, Protopitys, which Scott says bore its leaves in two alternating rows, one row on each side of the stem as in the "Traveler's Tree" of Madagascar, and the even more remarkable Cladoxylon series of stems. Finally, too, the restoration of the Upper mid-Devonian Eospermatopteris as studied at the State Hall at Albany by Winifred Goldring has a fine value, and can not fall short of a virtual reality. This type may be an early Medullosan.

V. The investigation of the Cretaceous coniferous lignites of Kreischerville, Long Island, in 1909 by Hollick and Jeffrey must be given a high place in paleobotanic records, not alone because of the accurate descriptions of significant stem types, but also because this was really the first successful study of such lignites. Nathorst had led the way, but here a further refinement of method was made. Ever since, the possibility of similar studies of lignites containing the older angiosperm stem structures has seemed near, seems only to await some fortunate observation of Triassic or older lignites.

VI. *American coal balls.*—By "coal balls" is usually meant petrified parts of lesser coal seams, mainly calcitic. Often, preservation is exquisite, and there is the great advantage of occurrence of varied types in the closest association—the disadvantage of an exceeding difficulty of study because of this very fact. The well-oriented thin section with respect to the given stems, foliage or fruits in the mass of plants is not entirely fortuitous, though nearly so in the case of lesser seeds or leaves. After determination of the position of stems or cones of fair size, with care, the oriented section may often be cut. But final study and elaboration thus require a familiarity with both occurrence in the field and slow accumulation of reference types.

The year 1855 was momentous in the history of paleobotany for the description of the Trigonocarpon seeds from "certain limestone nodules enclosed in seams of bituminous coal" by Joseph Dalton Hooker and Edward William Binney. But quite thirty years passed before the investigation of the English "coal balls" could be said to be well under way.

By some lapsus, fatality, inadvertence or inattention on the part of geologists or botanists, it was not until 1923 that Professor Noé, sixty-eight years after the Trigonocarpon sectioning by Hooker and Binney, secured the first American coal balls and successfully began their observation, collection and study at the University of Chicago. Since then, many determinations have been made. How far paleobotanists may extend discovery of critical structures preserved in the coal balls is still somewhat uncertain. The coal-ball record, being so much that of shore levels and lines, may prove in the longer course of study to be too one-sided, with but scant evidence of more plastic inland, plateau and mountain vegetation. Nevertheless, it is certain that the coal-ball plants are a great and alluring field in which many significant discoveries must yet be made. It may be that the Mississippian and Pennsylvanian coal balls come too early in time to yield indisputable progenitors of the angiosperms, but I am one of those who believe that a real step forward was made when it was suggested that it will not do to call old stems pteridospermous too generally, and that from somewhere within the Medullosan assemblage the monocots were possibly derived. Strange, if the Medullosans all went down to an utter extinction too soon for any of them to have made initial change toward strobilar or floral organization.

VII. *Conifer antiquity.*—The necessity for going through the collections of fossil plants for the purpose of restudying the little known or problematic conifers by improved methods has been recognized for some time, and has now had for several years the attention of Dr. Florin, of the Natural History Museum at Stockholm, where repose the splendid Nathorst collections. Both Abietineans and Araucarians go back to the Carboniferous, with the former more abundant and varied than perhaps expected. Furthermore, John Walton has recently confirmed such results by the description of a Voltzia obtained

from a boring in the Carboniferous. As the result of careful development it appears that the Voltzia lax cone unit consists in a median and several lateral sporophylls subtended by a large protecting bract. Once more the best explanation is that of a short axillary shoot of a kind easily undergoing simplification.

A negative result bearing on the age of the conifers merits citation here. In my collections from the Como of both the Black and the Freeze Out Hills are certain conifer stems associated with the Dinosaurs and the Cycads, sometimes of singularly fine preservation. One of these stems from the northeastern Black Hills was some time ago turned over to Dr. H. J. Lutz, of the Yale Forestry School, for sectioning and study. It is of course specifically new, and conveniently set in the rather comprehensive fossil genus Cupressinoxylon. But the wood structure as preserved in all detail, if found in a living form, would be referred to either the genus Cupressus, or else to Juniperus. These genera, therefore, unless undergoing some recent specific development, have so far as wood structure goes undergone almost negligible change since the close of Jurassic time. Dr. Lutz's study will shortly be published. Several related species have been sectioned, awaiting close study.

My own studies of the Patagonia cones from the Cerro Cuadrado also show the present-day coniferous types to go far back, but have the further interest of bringing to light cone types intermediate between Abietineans and Araucarians.

VIII. *Caytonia.*—The discovery of the singular angiospermous fruit called Caytonia by Hamshaw-Thomas brings to view an unexpected Jurassic type by very careful methods of study. The significance of Caytonia lies partly in the lively expectation of further such discoveries, partly in the suggestion of somewhat of primitiveness in the carpellary type. Were it certain that the accompanying foliage really was of the Sagenopteris type, the fact would be important in gaining further ideas of Jurassic leaf change and the several modes of origin of the net venation.

Having enumerated in more or less casual manner some of the outstanding discoveries or courses of discovery which have signally influenced views of seed plant descent in more recent years, it is easier to note present-day views. Apropos of the monocots it is seen that the view of a dicot derivation is generally accepted. It is pointed out that the Ranunculaceae are the most primitive herbaceous dicotyledons. No one can dispute that view now. A tree peony (*Paeonia moutan*) is a very instructive plant. Bessey in his synopsis of plant phyla, moreover, placed the Alismales at the base of the monocots—that being the very group that can be cited as next related to the Ranunculaceae. When, then, did separation occur? When it was suggested a few years ago that the monocots may have split off from other anthophyta as far back as Carboniferous time it was rather hotly urged by some that that could not be, because all medullosans must be seed ferns. That could not be!

Why not? Seeds with two cotyledons, in view of their splendid and varied development in the Cycadeoids, with presence in Araucarians, must be very old. Vessels may be very old too. If they could arise in a simply explained manner in the dicot lines, they could also appear in monocot lines. A direct derivation of monocot stem types from the Lyginodendron-Heterangium complex is not an iron-bound impossibility. With stem and leaf plasticity granted for the medullosans, in them as well as in other pteridosperms, primitive types of flowers, proanthostrobili, could arise.

A few old, even prejudiced, views should here be set aside, or at least proved out. Monocot origin can no longer be viewed as simply as when dicot stem, foliage and floral features were believed post-Jurassic. The single Jurassic angiosperm stem described by Kraeusel proves once more how slender fossil evidence may long remain. Palms, too, are old looking in the sense that they have changed long and much. They are, when it comes to fruiting, facile branchers. Denial that Medullosans could run into floral types or be closely related to the primitive stocks of flowering plants is the same as saying that was impossible to seed ferns in general. The larger outlines of stem morphology and stem history make monocot descent from within or near the medullosans a very distinct possibility.

A few years ago the hiatus between pteridosperms and early magnolias seemed impassable. There was no visible tie-up in stem structure or fructification. That the great tracheids of Lyginopteris might account for the origin of vessels is still omitted from consideration. Vessels and net venation are thought to have come rather late in angiosperm history. None the less, later consideration of Wielandiella greatly affects all the view-points. The general fact that origins are being pushed back so far greatly favors diphyletic views.

The idea of monophyletic origin of the angiosperms has been more carefully considered by Ethel Sargant[3] than by any one else. Without reviewing in detail the argument she presents, it is here urged only that after all it is determination of the appearance of

[3]Ethel Sargant, "Reconstruction of a Race of Primitive Angiosperms," *Ann. Bot.*, vol. XXII, 1908.

organs in geologic time which it is sought to determine. Like megaphylly and microphylly, the terms mono-, di- and polyphyly too readily become vague in the course of discussion.

The question of the monophyly or polyphyly of the monocots and of the dicots finds analogy in that of the conifers. There it is the singularly clear Stephanie Herzfeld,[4] who has given an excellent résumé of the view for the unity of the greater conifer phylum. Eames had reached similar exact views. Jeffrey has contended that Araucarians are descended from Abietineans. And I have for the present convinced myself from the study of those marvelous Cerro Cuadrado cones of Patagonia that the existing conifers are a unit—with Araucaria in some respects (wood and foliage) primitive, but taking cones and all, the most specialized conifer. Earlier I thought differently, partly because I did not understand the cone structure very well, partly because not admitting that Araucaria was without old features or of Mesozoic origin. That was about the view of Seward too.

Let this point be emphasized. In the Paleobotany of to-day and of to-morrow, the fruitful promising fields of research lie in the gymnosperms, ancient and modern. There is the discernible, greater record—the older angiosperm record as yet depending so much on chance discovery. Almost any field of fossil plant research could of course be said to depend on casual discovery of new materials in the field, but in the attempt to gain bettered views of higher seed-plant development the gymnosperms, including the cycadeoids, seem to present the open way. Especially the plants of Rhetic-Oolitic time are far too little known.

It has been just noted that the conifers, while discrete since Carboniferous time, now appear to be a homogeneous group. Also, as distinctly as any "find" that has turned up, the Voltzia subtending bract and sporophylls of Walton seem to indicate the widespread occurrence in old conifer days of a fairly complex axillary shoot, correspondent to a spur shoot but which could also have a relation to a terminal crown. The order of these axes and how they related themselves to the earliest true flowering types can not yet be clear. But evolutionary faith leads to the idea of some very simple relation. The later history of the conifers then becomes a rather open book. The inflorescence theory holds. There is mainly needed to avoid dulling the sharp edge of the new discoveries by failure to consider both age and structure together —appearance in time. Stephanie Herzfeld says:

> I hold it safer, in attempting to prove or disprove the inflorescence theory, to discontinue the attempt to homologize the flowers of both sexes. There are instances where the female flowers are organized into more complicated inflorescences than the male, or *vice versa*, while examples of like order of the flowers of both sexes occur.
>
> Hence the explanation for these variations must be sought for in the history of the phylum. If the conifers were derived from a Torreya-like ancestry, bearing cones with the single flowers inserted on an axis of the third order, as is the case in Torreya to-day, and if the staminate flowers had a similar composition and insertion, then it would not be singular that in the course of later development instances arose in which the staminate inflorescence was simplified (Cupressus, Cunninghamia), more than the ovulate, and other instances in which the reverse took place (Taxodium distichum, Podocarpus macrophylla), or finally those cases in which both sexes have simplified in the same manner (Pinus, Larix, Cryptomeria, Taxus).

The theory of conifer derivation would seem clear if, long ago, following great variation in the pteridosperms with varied phases of monoecism, dioecism and finally fruiting axes of limited growth from megaphyllous types down to minute, there was a period of Cordaite, lax-cone conifer or hemiconifer and varied cycadeoid vegetation, antecedent in close to equal degree to Ginkgos, to specialized conifers, and also to the existing flowering plants, that is, gnetaleans and angiosperms. Those generalized types would, of course, disappear; only the specializing types would come down. The Carboniferous and Permian then would have been the period during which the compact cone conifers and the truer flowering plants, ancient and modern, arose; for the Cycadeoidae flowers must be looked upon as holdover types from the older days of seed plants, though grown much specialized. So too, Gnetum.

Then all seed plants would once have been very much related to each other, with later evolution following two great lines—coniferous and floral. The conifers are now utterly specialized. In them all but the merest recessive traces of the primitive amphisporangiate fruiting shoot are lost and the highest degree of forest specialization in both foliage and flowers has been reached. *Per contra,* the floral types are still plastic, in the emplacement of fruiting organs still primitive; but cosmopolitan, reaching into every environment, they run by way of carpellary fusions and reductions more and more into varied or specialized types easy to recognize as such.

In such a sense the forest canopy would always have presented a certain unity from the most ancient days, would always have been in a condition of unstable equilibrium, or better put, always in a state of response to the changing geologic environment. Conifers would seem older than angiosperms only in the sense that they more rigidly changed. If such a

[4] Stephanie Herzfeld, "Die weibliche Koniferenblüthe," *Oesterreichischen Botanisches Zeitschr.*, 1914.

broadened view does not have in it much of actuality, then theory becomes complex. Then it is too utterly difficult to understand how it is that the best students so often reach the view that the conifer bract and scale are the end results of a leaf or bract, and an axillary shoot. Certainly the short shoot view of bract and scale is a simple view. It relates the cone to the flower in fairly understandable manner; it explains Voltzia as the modified form of the older fertile shoot, and easily undergoing further reduction. It leaves the conifers related to other seed plants in somewhat the same manner as the ungulates are found apposed to other mammalians as the result of digit reduction.

CEREMONY ATTENDING THE OPENING OF DOWN HOUSE, THE HOME OF CHARLES DARWIN

By Dr. JOSEPH LEIDY, II

PHILADELPHIA

THE formal opening of Down House as a public memorial took place on June 7 in the presence of a large and distinguished party as the guests of the president, Sir William Bragg, and officers of the British Association.

Dr. Joseph Leidy, II, represented the American Association for the Advancement of Science; Dr. Edward B. Poulton, of Oxford, and Dr. Henry Fairfield Osborn, president, represented the American Museum of Natural History. The ceremony was attended by upwards of four hundred members of the British Association, friends and representatives of other scientific societies.

Down House lies in the midst of beautiful gardens and orchards in the Kentish Downs, about fifteen miles from London Bridge.

The ceremony was held on the lawn under the presidency of Sir William Bragg, at whose invitation Mr. Buckston Browne formally presented the house into the keeping of the British Association. In the course of a brief address he said that Darwin, like Shakespeare, required no monument. But it might be permitted to them to treasure, preserve and keep sacred always the house that sheltered Darwin—the things in it that he had handled and the grounds he had walked upon. It was this which he (Mr. Buckston Browne) was extraordinarily privileged to accomplish, assisted by Major Leonard Darwin, the surviving son of Darwin, and other members of the Darwin family.

Sir William Bragg thanked Mr. Buckston Browne for his national gift, and accepted it on behalf of the association.

The principal address was delivered by Sir Arthur Keith, F.R.S., on "Science and Sentiment."

Thanks to the munificence of Mr. Buckston Browne we are to-day able to throw open to all the world the home of an English gentleman, Charles Darwin. Henceforth it becomes a national possession entrusted to the care of the British Association for the Advancement of Science. Its rescue was made just in time. In another generation Darwin's home would have gone the way that all human homes go sooner or later; wide-spread decay had set in and Greater London, spreading into Kent, would have eaten up this retreat from which Darwin spoke to the great world of his day.

All danger of such a fate overtaking one of the historical homes of England is now past. Mr. Browne has not only made Down House a national gift; he has repaired it, inside and out, top and bottom; at great personal pains and expense he has restored the chief rooms of the house to the state they were in when Darwin occupied them; thanks to the generosity of the Darwin family and to their ever-ready cooperation, he has been able to place in their appropriate niches pieces of furniture actually used by Darwin and to exhibit personal relics of the great naturalist. Further, he has secured his gift against the ravages of time by an ample endowment for maintenance. Thus to-day a dream which some have dreamt has come suddenly and unexpectedly true. In this little area of the chalky uplands of Kent the nineteenth century will continue to bloom and remain an oasis where our successors, worn with the cares of centuries, may repair for refreshment and inspiration.

Why should this desirable home be withdrawn from active service in the community and be dedicated to an altogether special purpose? It is because there is here enshrined the personality of a great man. Darwin's home is one which we are justly proud to claim as English and which we are convinced our children's children will value as we do. I have no doubt they would have held this generation blameworthy if it had made no effort to save it for them. Our distant successors, I am sure, will be proud of it not so much perhaps on account of the books which were composed and written within its walls but rather, I suspect, because of the personality of the man who wrote them. In the ultimate scale of reckoning, men will always place goodness above greatness; Darwin's was both good and great. It is right that we should stress now this personal aspect of Darwin's life, for the character of no man has been so wilfully travestied in his own century as well as in ours. He was an English gentleman. We have the best of reasons for believing he came of a stock which has lived for more than three thousand years