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*THE ORIGIN OF GYMNOSPERMS AND THE SEED HABIT.**

INTRODUCTORY.

THE most difficult as well as the most fascinating problem in connection with any group is its phylogeny. The data upon which we base opinions concerning phylogeny are never sufficient, but such opinions usually stimulate research and are necessary to progress. Any statement dealing with this problem is merely an expression of our knowledge of comparative morphology, and of our judgment concerning the phylogenetic importance of certain structures.

To my mind, the most conspicuous error in many schemes of phylogeny is the tendency to focus attention upon very few structures. It may be that the structures selected are the most significant, but the organism is a plexus of structures and must be considered in its totality. Very different structures have been laid hold of by the processes of evolution, and it may not be possible to relate the resulting forms properly upon the basis of any one or two structures. A conspicuous example is furnished by the liverworts, in which one line gave special attention to the structure of its gametophyte body, another to the form of its gametophyte body, a third to the struc-

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ture of its sporophyte body. Any attempt to relate these to one another upon the basis of a single structure, even so important a one as the sporogonium, is essentially misleading. But when we consider the totality of structure we are led to the opinion that these lines possibly diverged from an archetypal plexus in which there were gametophyte bodies as simple as that of Aneura and sporophyte bodies as simple as that of Riccia. Another illustration is the recent attempt of Arnoldi to associate Isoetes with Selaginella largely upon the basis of endosperm development, without regard to great diversities in habit and anatomical details. The association may be perfectly proper, but the reason given for it is inadequate.

In dealing with problems of phylogeny it is also important to remember that the origin of a prominent group of living forms from another group of living forms is extremely improbable. We can point out resemblances in structures which we have come to regard as essential, but this is not likely to mean the origin of the one group from the other. It may mean that the two groups can be traced to one, probably now extinct, which combined the characters now differentiated. Most living groups are best regarded as divergent rather than consecutive series.

But even this apparently sure ground has become very uncertain from the fact, becoming more and more apparent, that similar changes in structure, even very important ones, may have appeared independently in different lines. The response of organisms in structure to their environment is deeper seated than we were once inclined to believe, and testimony from the similarity of certain structures, when contradicted by the majority of other structures, argues feebly for recent community of origin. Such similarities in structure argue more for physiological conditions than for phylogeny. For instance, from the standpoint of evolution, the appearance of heterospory among the pteridophytes is one of the most important contributions to plant progress made by the group, but it is impossible to escape the conclusion that heterospory was attained independently by several lines. To put into the same genetic group all heterosporous pteridophytes would be regarded as a morphological absurdity. If heterospory appeared independently in several lines the same conclusion must be reached in reference to its natural outcome, the seed, and the polyphyletic origin of the spermatophytes becomes extremely probable.

This increases the perplexities of phylogeny, but it broadens its horizon and introduces another possibility. To continue the same illustration, in our search for the origin of seed-plants we have narrowed attention to the existing heterosporous pteridophytes, when some of the spermatophyte groups, as, for example, the gymnosperms, may represent an entirely distinct line in which heterospory and then the seed appeared, and may not be related directly to any existing heterosporous pteridophyte. In such a case we are permitted to look to some group of living homosporous pteridophytes as possibly containing the best living representatives of the group from which gymnosperms have been derived.

With all these possibilities in mind, I wish to discuss the phylogeny of the gymnosperms, not so much to reach a clear phylogeny as a clearer understanding of the complexity of the problem and the uncertainty of conclusions. This is a field in which no one can afford to be dogmatic.

THE ORIGIN OF GYMNOSPERMS.

From Hofmeister's classic researches to the discovery of gymnosperm spermatozoids by Hirase, Ikeno and Webber, the fact has become increasingly apparent that gymnosperms are very closely related to pteridophytes. It was natural, for a time, to regard gymnosperms as phylogenetically intermediate between pteridophytes and angiosperms, for it was not easy to believe that such a structure as the seed appeared in more than one genetic line; but it is probably not going too far to say that there is now no serious opposition to the view that the gymnosperm and angiosperm lines are genetically independent. However, such a discussion does not lie within the scope of this paper.

That gymnosperms have been derived from pteridophyte stock is hardly open to discussion; at least we must assume that this is true, or all attempts at phylogeny are useless. The first question which confronts us, therefore, is whether the very divergent gymnosperm lines have had a common origin in this pteridophyte stock or not. Was there a single group of archaic gymnosperms, derived from pteridophytes, which subsequently differentiated into distinct lines? The existing gymnosperm groups are so very diverse that one of two things seems evident: either they differentiated into divergent lines from a common gymnosperm stock in very ancient times, or they originated independently from the pteridophyte stock. From this discussion I wish to exclude the Gnetales, as we do not possess sufficient data concerning their early history, or concerning the morphology of the very dissimilar living forms, to justify any opinion as to their origin. They are such dissimilar fragments, living in such extreme conditions, that their origin is totally obscure. In some respects they are more cycad-like than conifer-like, but in most respects they are so unlike both that a separate origin seems possible. It may be even true that the three genera belong to groups of independent origin, which is certainly the easiest way of disposing of their differences; and their common characters of true vessels, the so-called perianth and elongated micropyle, may have been attained independently as readily as heterospory; but the combination of characters in common does not seem to justify such a disposition of them, and the three genera had better be regarded as of common derivation, wonderfully diversified by ancient separation, isolation and extreme conditions.

Approaching the subject from the historical standpoint, the group Cordaites seems to be the first with sufficient data to justify consideration. The structure of the vascular bundles, especially those of the leaves, is said to suggest those of conifers, cycads, Isoetes and Ophioglossum; and the sporophylls are organized into a strobilus, a character common to pteridophytes and gymnosperms. But such characters can be used only as cumulative testimony. In such evidences as we have of the structure of the male gametophyte, however, we obtain some valuable suggestions. Within the mature microspore there appears a considerable group of polygonal cells. In living groups of gymnosperms, so far as investigated, there is no such structure; and if we look to pteridophytes for suggestion we are constrained to believe that this group of cells is either prothallial or sperm mother cells. In either event, it would represent a condition of things much nearer pteridophytes than is shown by any living seed plant. In view of the discovery of spermatozoids in Cycas, Zamia and Ginkgo, taken in connection with the peculiar structure of the male gametophyte just described, I am of the opinion that the Cordaites also developed spermatozoids. With either hypothesis as to the nature of the cells developed within the microspore of Cordaites, in seeking for the pteridophyte origin of the group, we are led away from such heterosporous pteridophytes as now exist, for in them the male gametophyte is much more reduced than in Cordaites—in fact, more reduced than in most living cycads and conifers.

Additional testimony to the same effect is furnished by sections of the seeds of Cordaites. In addition to the remarkable nucellus beak, which probably has no phylogenetic significance, the large pollen chamber is a conspicuous feature. This is sometimes so extraordinarily large that it occupies the whole upper portion of the nucellus, and has been observed to contain numerous pollen grains. The pollen chamber is a well-known cycad feature, and seems to be associated with the early development of siphonogamy. By means of it, the tubular outgrowth from the antheridium wall is reduced to a minimum, and may coexist with spermatozoid development, as shown by Hirase, Ikeno and Webber.

The testimony all indicates that in Cordaites we have the beginnings of a siphonogamic line, brought about by the retention of the megaspore, which still develops its exine in Cordaites and some cycads.

As to the pteridophyte group from which the Cordaites were derived, data are not sufficient to make opinion other than a pure hypothesis. I think it is clear that such heterosporous pteridophytes as are living to-day must be set aside in this search, by the testimony of both of their gametophytes, especially the male. They stand for lines which have very much reduced the male gametophyte, have variously modified the female gametophyte, but have not developed siphonogamy by retaining the megaspore. It may be that the lycopod forms of the Carboniferous and earlier formations represent the pteridophyte plexus from which Cordaites were derived, but we know too little of their morphology to make any assertion. My judgment is that the Cordaites represent an independent heterosporous line, and that if they were associated in origin with the lycopod forms at all it was before the latter had developed heterospory, which seems never to have been extensively developed in the lycopod line until recent times.

I believe that we must regard either the ancient homosporous lycopod forms or the abundant Palæozoic Marattia forms as responsible for the origin of Cordaites, and my own inclination is toward their Marattia origin, perhaps for no better reason than that in such an origin I see more opportunity for the development of such a group as cycads; but such a view is further supported by the discovery that the spermatozoids of cycads, and their ally, the Ginkgo, are of the multiciliate type, and not biciliate, as in living lycopod forms. Just what stress should be laid upon this I do not know, but when opinion is fairly balanced it would seem to help to a decision. It seems satisfactory, therefore, to regard the origin of cycads as from the homosporous-eusporangiate plexus of Filicales, represented to-day most abundantly by Marattia and its allies. It would seem, further, that this has been brought about without the intervention of such Cordaites as we recognize, which, with probably similar origin, were developing a very different type of body, which finds its modern expression in the conifers. In the acknowledged Cordaites, therefore, I recognize a transition region between the homosporous-eusporangiate plexus of Filicales and the more modern conifer series; while in the cycads we have a line which continued more of the fern habit and structure, recognizable not merely in its foliage leaves and general port, but in its occasional vascular bundles of concentric type and its multiciliate spermatozoids. The Cordaites, however, must have included forms that we have not recognized as such, for it is only when they become differentiated from the fern habit that in the main we are able to distinguish them. This very fact of their sharp differentiation means that they had made a decided departure, and we are probably able to recognize only the most highly specialized forms. Of course, in what I have said I may have been using the name Cordaites in a much more inclusive sense than taxonomy would justify. As ordinarily defined I would see in them the first distinct beginnings of a type which afterwards gave rise to the conifers; as used in this paper they refer to a plexus of forms derived from the homosporous-eusporangiate Filicales which gave rise to both cycads and conifers as divergent lines, one retaining more nearly the fern habit and structure and culminating earlier, the other departing more widely from the habit and structure and culminating later. I believe that some Palæozoic forms now regarded as ferns will be found to be more closely related to the Cordaites. How many other lines arose from this large Cordaites plexus, as I have defined it, we have no means of knowing, but it seems to be responsible at least for all of the living gymnosperm forms.

It is important to obtain such historical evidence as we can in reference to the gymnosperm lines, restricted in this paper to the Cordaites, conifers and cycads. If a historical sequence can be established which conforms to the views expressed here as to the interrelationship of these lines the conclusion will have additional support. I need not apologize for the paucity of data furnished by paleobotanists. They have done what they could, and we are greatly in their debt. Morphologists recognize, however, that the structures usually preserved are not the most convincing as to relationships, and that nowhere are appearances more deceitful. While we have no sympathy with wild generalizations based upon fragmentary material, there is an increasing accumulation of data which furnishes a substantial foundation for some conclusions. It seems to be clear that during the Palæozoic there was an increasing display of gymnosperms. The fragments which bear this testimony became very abundant in the later periods of the Palæozoic, and are regarded, for the most part, as Cordaites. Associated with these forms is the great display of Marattia and its allies. A distinct type of leaf and of stem is attributed to each of these great groups, and when seeds or sporangia are associated with them the case seems clear enough, but apart from such association the uncertainty is profound. Intergrading forms between the two are to be expected, but with material so fragmentary and non-committal it would be a rare chance that would lead to its definite demonstration. In the Coal Measures the cycad type becomes apparent, but not prominent. This would seem to indicate either an early differentiation from the Cordaites plexus or a late differentiation from the Marattia plexus. I see no difficulty in the former view, as I see no advantage in multiplying the independent heterosporous and seed lines until forced to do so by incontrovertible evidence. The domination of cycads during the Mesozoic and their subsequent decline are well-known facts.

More suggestive, however, is the history of the conifers. It is generally stated that this line, in its modern expression, began during the Palæozoic, and that our modern genera have been recognized by stem and leaf anatomy. Such methods of determination we know to be untrustworthy, as there is the greatest possible amount of anatomical diversity even in contiguous regions of the same organ, much more in different organs and at different ages. In examining the claim that modern coniferous genera appeared during the Coal Measures, I find no evidence that seems to be worthy of serious consideration excepting that with reference to Ginkgo, and it is an interesting fact that Ginkgo is no longer regarded as a conifer. Long before the evidence of spermatozoids was discovered it seemed perfectly clear to me that Ginkgo was more cycad-like than conifer-like. In the light of our present knowledge the appearance of Ginkgo in association with the Carboniferous cycads seems natural enough. It is a matter of very secondary importance whether we are to regard it as an independent line or not. I am inclined to believe that, while during the Palæozoic heterospory and the seed were both attained, siphonogamy was in its beginnings, and that the spermatozoid habit was for the most part still continued in the seed line. There is no conclusive evidence, therefore, that any of our modern coniferous genera appeared during the Palæozoic, during which the Cordaites were the dominating seed plants. During the last Palæozoic periods undoubted conifers did appear, and in considerable abundance, and we may recognize the beginnings of distinct lines represented to-day by Abies and its allies, Taxodium and its allies, and Taxus and its allies, but the genera are not those of to-day. In the lower Mesozoic, however, modern araucarian and abietinous genera appear; and the Taxodium and Taxus lines become more distinct, but not modern until the later Mesozoic. At that time Cupressus forms also appear, but not of modern genera. Further details are not necessary, as the point to be made is that the conifer type was not recognizable until late in the Palæozoic, and then not in its modern expression. It certainly suggests a later departure from the Cordaites stock than do the cycads.

Another fact is interesting to note in connection with the evolution of the conifer forms. In existing conifers there is considerable variation in the development of the male gametophyte. In some forms, as the Abietineæ, the development of two or three prothallial cells, distinct from the large antheridial cell, is a well-known fact, an amount of prothallial development not shown by any other living heterosporous forms, even the heterosporous pteridophytes. In other forms, as Cupressineæ and Taxeæ, the reduction of the male gametophyte is greater, no sterile prothallial cells appearing, the whole structure being an antheridium, as in the angiosperms. Our historical evidence accords with this progressive reduction of the male gametophyte, the Taxus and Cupressus lines having attained modern expression after the Abies line; and back of the Abies line we find the Cordaites, with probably a still greater development of the sterile region of the male gametophyte indicated. To derive the Cordaites or Abies lines, with their two or three to many-celled sterile tissue of the male gametophyte, from such heterosporous lycopod forms as we know to-day, with their constantly more reduced male gametophytes, is not within the bounds of probability. Besides, the reduction of the male gametophyte seems to be so prompt a response to heterospory that its partially reduced condition in certain conifers, and probably in Cordaites, would seem to argue for their near derivation from some homosporous type.

The development of a suspensor in the lycopod forms has also suggested a genetic connection with gymnosperms, in which the suspensor development is so conspicuous. This organ, however, seems to have no morphological constancy. In gymnosperms it may be developed from a plate of cells formed in the oospore, as in most conifers; or from a mass of cells formed basally or parietally in the oospore, as in cycads; or from free cells formed within the oospore, as in Ephedra; or from the elongation of the oospore itself, as in Gnetum; or from the downward elongation of the archegonium, as in Welwitschia. The suspensor, therefore, seems to be a temporary organ of the embryo, of various morphological origin, intended to relate the embryo properly to its food supply, and not of phylogenetic significance.

The testimony of history and morphology seem to combine in pointing to a very generalized Palæozoic type as the origin of gymnosperms. This type is characterized by its advancement towards seed production rather than by its habit, which must have been extremely varied to have given rise to such types as cycads and conifers. The usually recognized Cordaites show but one tendency of a much more extensive group, for which the name Cordaites may be extended for convenience. Cordaites in this larger sense occur in such association with groups of homosporous eusporangiate Filicales, and approach them so much nearer in the important morphological structures mentioned than they do living heterosporous Filicales, that an independent heterosporous line is suggested. If such be the case, in the passage from the Marattia forms to the Cordaites forms both heterospory and the retention of the megaspore were attained, and probably siphonogamy begun.

THE SEED HABIT.

The evolution of heterospory seems simple enough. The physiological differentiation of the spores was complete when prothallia became persistently diœcious. This division of labor is to be expected in the case of two such distinct functions as the production of antheridia and archegonia. A prothallium producing both sex organs equally well may be regarded as in a state of equilibrium, an equilibrium which is disturbed by any conditions which favor the production of one sex organ rather than the other, in this case probably nutritive conditions. This disturbance of the equilibrium of a bisexual prothallium would certainly find an expression first in a diœcious tendency, and finally in a diœcious habit. With the habit once fixed the morphological differentiation of spores becomes inevitable, since the nutritive requirements of the two prothallia are so different. The evolution of heterospory seems to be one of the simplest of selective processes, with inequalities of nutrition to furnish the variations. From this point of view it would seem natural to expect that it may have been derived frequently from homospory.

The retention of the megaspore, however, does not seem to be so simple a problem. In a certain sense it is correlated with the reduction of the gametophyte, since retention would not seem practicable until reduction had proceeded far enough to make the gametophyte endosporic. Even greater reduction, however, is attained by the male gametophyte, but the spore is shed. It should be noted that even in the case of the microspore the male gametophyte is usually completely organized before pollination, but the fact remains that reduction does not compel retention. It has seemed to me that this phenomenon is to be explained by Bower's law of sterilization, developed in reference to the strobilus. This law certainly finds expression in the megasporangia of heterosporous pteridophytes, in which the sterilization of mother cells is conspicuous. This method of increasing the nutrition of the fertile cells is too common a phenomenon to need illustration; but it is a tendency that would seem very consistent with the development of megaspores, whose peculiar work holds so definite a relation to abundant nutrition. For this very reason high numbers of microspores may be continued, and a diminishing number of megaspores produced. This would reach its culmination in the production of but a single megaspore by a sporangium, and a proportionate increase in the size of the megaspore. With the development of a single spore imbedded in sterile tissue, shedding becomes not only mechanically difficult, but meaningless, since the necessity of scattering a brood of gametophytes, to avoid competition, has disappeared. It is further true that the development of such a spore involves nutritive supplies from numerous neighboring cells, and a certain amount of retention becomes necessary for this reason. Still further, the advantage to a single megaspore in being retained, thus securing more abundant outside nutrition during germination, would fix the habit if any selective process were at work. For these various reasons it would seem evident that when the sterilization of a megasporangium had reached its extreme limit, by organizing a single spore, retention is likely to follow sooner or later. If this line of reasoning be true the seed habit might have been developed in any heterosporous line.

With the retention of the megaspore pollination became necessary, but its gymnosperm expression differs in no way from the scattering of aërial spores in all the lower groups. The new feature demanded by the retention of the megaspore, therefore, was not the scattering of the microspores, but the development of siphonogamy. That the first retained megaspores were exposed to the microspores can hardly be doubted, and in such cases we now know that the spermatozoid habit must have been retained, and that no tube, or a very small protuberance of the antheridium wall, was needed to discharge the spermatozoids sufficiently near the oosphere. If chemotropism can explain the guidance of a pollen tube through much intervening tissue it would certainly be sufficient to cause the protrusion of an elastic antheridial wall. In the very few illustrations of Cordaites obtained, the megaspore is but slightly covered by sterile tissue at the bottom of a deep pollen chamber, and a very slight development of tube is necessary. The same condition is continued in the cycads, and thus the habit of siphonogamy may have been gradually built up. As siphonogamy developed, the gradual failure of the sperm mother cells to organize spermatozoids followed, and presently, almost exclusively now in gymnosperms, sperm mother cells are found to function directly as male gametes without further organization.

The secondary results which followed the retention of the megaspore were numerous. The well-known effect of fertilization upon adjacent tissues necessarily involved at least the sporangium, and the seed resulted. The presence of abundant available nutrition and favorable conditions induced the immediate germination of the oospore, which the development of a resistant tissue about the sporangium checked. As a consequence, the development of the embryo was thrown into two stages, the intra-seminal and the extra-seminal.

In the case of the angiosperms, however, another tendency was connected with the retention of the megaspore, namely, the tendency of the sporophyll to enclose the megasporangium, a tendency so evident in such pteridophytes as Isoetes and Marsilea that the direct pteridophyte origin of the group seems more natural than an origin from so specialized a type as the gymnosperms. Given the reduction of spore production to a single megaspore and the persistent enclosure of the sporangium by the sporophyll, and the angiosperm peculiarities follow. The profound effect of these conditions upon the germination of the megaspore is so remarkable, and the intergrading stages are so completely unknown, that there seems to be no clue to the sequence of changes. That an endosporic gametophyte might eliminate the archegonium seems evident, for the tendency is shown among gymnosperms by Gnetum, where oospheres are organized by free endosperm cells. That the reproductive region of the female gametophyte may be organized earlier than the nutritive region, when the gametophyte is supplied with outside nourishment by the retention of the megaspore, is hinted at among the heterosporous pteridophytes and gymnosperms. These tendencies have found full expression in the angiosperms, where archegonia have disappeared and the reproductive tissue of the female gametophyte is persistently organized before the nutritive tissue. Evidence as to the details of the evolution of this tendency is lacking and may not be in existence, but the tendency has certainly reached a remarkably definite expression. The unvaried appearance and movement of eight free nuclei or cells, and the remarkable fusion of two of them, represent habits so fixed through such an enormous group that they baffle explanation, and argue both for the monophyletic origin of angiosperms, and against their derivation from so divergent a line as gymnosperms.

The earlier evolution of the gymnosperm line is probably to be explained by ecological conditions. The body as a rule is organized to endure extreme conditions. It is certainly not a mesophytic type, and its evolution was certainly not in response to prevailing mesophytic conditions. On the contrary, the angiosperm type is essentially a mesophytic one, with great foliage display, and probably expanded in response to widely prevalent mesophytic conditions. This might explain the habit peculiarities of the two groups, but whether the more recondite morphological differences hold any relation to these or not is too obscure to permit even speculation.

SUMMARY.

1. A great Cordaites plexus, more extensive than the one usually included under that name, represented the characteristic Palæozoic seed plants.

2. It was probably derived from homosporous-eusporangiate Filicales, represented to-day most abundantly by the Marattia forms and their allies, and was the most common Palæozoic type of Filicales.

3. From it the gymnosperm lines, at least the cycads and conifers, were derived, the usually recognized Cordaites representing a transition stage towards conifers.

4. The frequent independent appearance of heterospory is to be expected, as it probably results from inequalities of nutrition in connection with the development of antheridia and archegonia.

5. The retention of the megaspore, resulting in the seed habit, follows the extreme sterilization of the megasporangium, which is attained with the organization of but one megaspore. With the development of a single megaspore imbedded in sterile tissue shedding becomes mechanically difficult, unnecessary, and even disadvantageous from the standpoint of nutrition.

6. The retention of the megaspore was followed by the development of seed coats, possibly through the well-known effect of fertilization upon adjacent tissues; by immediate germination of the oospore, on account of the favorable conditions and the abundant supply of available nutrition; and by the checking of the developing embryo by the mature seed structures, resulting in the characteristic intra-seminal and extra-seminal stages of germination.

7. The first retained megaspores were doubtless directly exposed to the microspores, and in Cordaites and cycads a pollen chamber of varying depth and extent is associated with the early stages of siphonogamy, with which the spermatozoid habit was more or less associated.

8. The pollination of gymnosperms is but a continuation of the ordinary method of dispersing aërial spores employed by cryptogams, the chief result of the retention of the megaspore upon the male gametophyte being the development of siphonogamy.

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