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THE ORIGIN OF THE CYCADS[1]

The widest gap in the evolution of plants used to be the one between the ferns and seed plants; but the researches of the past thirty years have bridged the gap so completely that the two groups are now separated only by the artificial definitions of the taxonomist.

The Cycadofilicales, which our British friends prefer to call the Pteridosperms, are the bridge. They looked like ferns and were naturally mistaken for ferns; and there is no doubt that their immediate ancestors were heterosporous ferns which had gradually developed the seed habit.

The forms already discovered have seeds much larger than the sporangia of any known heterosporous fern and almost as highly developed as those of the living Gymnosperms; but when the more primitive members shall have been discovered, we predict that the seeds will be comparatively small, developing from small ovules, containing still smaller female gametophytes, which will have little free nuclear division, or even none at all.

But the forms already discovered have the characters necessary to qualify them as the ancestors of the rest of the cycadophyte line; that is, the "fossil cycads" of the Mesozoic, more precisely known as the Bennettitales, and the living cycads, the Cycadales.

That the Paleozoic Cycadofilicales have given rise to the Mesozoic Bennettitales, or "fossil cycads," is practically certain. Researches upon the Paleozoic forms, especially by British botanists, and the magnificent researches of Wieland upon the Mesozoic Bennettitales have established this connection beyond any reasonable doubt. These Bennettitales were called "fossil cycads" because they were supposed to be the ancestors of the living cycads.

The living cycads, with one family, nine genera and about one hundred species, form a natural assemblage; but their geographic distribution, as well as their morphological characters, make it evident that the various genera have been separated for a long time, perhaps during most of the Mesozoic.

Dioon, with three species, is probably confined to Mexico.

Ceratozamia, with two species, may also be confined to Mexico. It has been reported beyond the

[1] Address of the vice-president and chairman of Section G—Botanical Sciences—American Association for the Advancement of Science, Washington, D. C., December, 1924.

southern boundary but, so far as I have been able to find out, there is no evidence that the plants were growing wild.

Microcycas is even more restricted, being confined to Cuba.

Zamia, with more than a third of the species of the whole family, has a wider range, the numerous species being scattered from Florida, Mexico and the West Indies, down the Andes to Chili.

These four genera are confined to the western hemisphere; and all except *Zamia,* and even most of its species, lie north of the equator.

The other five genera belong to the Oriental tropics. Encephalartos, with sixteen species, is confined to South Africa. *Encephalartos latifrons* may be the slowest growing of all the cycads. It is found only in the extreme southern part of South Africa.

Encephalartos caffer has the largest cone ever developed by any plant; fifty pounds is a common weight and ninety-three pounds has been reached. *Encephalartos Altensteinii* is the most popular species in cultivation.

Stangeria, with only one species, is also confined to South Africa. It is not surprising that it was classed with the ferns until the cones were discovered.

Macrozamia, with sixteen species, is confined to Australia. Some of the species, like *M. spiralis,* have subterranean stems; while others, like *M. Moorei,* have well-developed trunks.

Bowenia, with only two species, is even more restricted in its range, having been found only in the northeastern part of Australia.

The eighteen species of *Cycas,* the remaining genus, are scattered from Japan down through the various islands to New South Wales in Australia.

So all the oriental genera, except *Cycas,* are south of the equator. All the living genera are tropical or subtropical, and no genus is common to the eastern and western hemisphere.

However, in the Mesozoic, the geographical distribution was probably more extensive; and it is suggestive to note that the fossil Zamites of South Africa might very well pass for the impression of a living leaf of a Mexican *Dioon edule.*

What could have been the origin of this group, now so scattered and limited in distribution?

Many years ago, a noted botanist, in a paper on nuclear and cell division, said that the achromatic structures came from the nucleus or from the cytoplasm or, possibly from both. Thus, no matter what might be proved in the future, he was in position to claim priority.

Similarly, in case of the cycads, it may be that every extinct race of plants has been called upon, at one time or another, to function as their ancestor. Consequently, it would be impossible to suggest an entirely new origin, unless some entirely new race of fossil plants should be discovered.

We believe it safe to assume that the cycads could not have come from the lycopods or from any group with lycopod affinities; or even from any group in the Coniferophyte phylum. The cycads must have come directly or indirectly from the ferns. There are three possibilities: They may have come directly from the Filicales, or they may have come from the Cycadofilicales or they may have come from the Bennettitales.

In regard to the Filicales, or ferns, little need be said. During the Devonian, especially the upper Devonian, heterospory must have been developing with increasing frequency; for some ferns had already reached the seed condition before the end of that period; and during the Carboniferous, the seed ferns, the Cycadofilicales, may have outnumbered the true ferns. During the transition from homospory to heterospory and from heterospory to the seed condition, the leaf and stem remained practically unchanged, so that it was very natural to mistake these early seed plants for ferns.

The transition must have been gradual and it doubtless followed the line indicated by the ontogeny of the living heterosporous ferns. As megaspores became larger and larger, development would proceed farther and farther before the spores were shed; until, finally, a time would come when the megaspores would not fall out from the sporangium. Then, by definition, the sporangium with its contained megaspore would be a seed, and the plant would belong to the Gymnosperms.

That the Bennettitales have come from these fern-like Gymnosperms of the Paleozoic can hardly be questioned; but whether the living cycads have come directly from the same source, or have arisen later from the Bennettitales, possibly from some very low and still undiscovered members of that order, may still be a subject for discussion. We believe that the living cycads have come, like the Bennettitales, directly from the Cycadofilicales, the fern-like Gymnosperms of the Paleozoic.

Of course, whole plants of these Carboniferous forms, with roots, stem, leaves, stamens and seeds all in place, have never been discovered and we do not even hope to see them: but the parts have been found separately —a leaf attached to its stem, a seed still attached to a leaf—so that we are able to reconstruct the plant with reasonable accuracy, and to refer loose seeds to the proper plant, just as one refers a hickory nut or a chestnut to the tree from which it came. Putting various well-known parts together, we can reconstruct a hypothetical ancestor which could have given rise to both the Bennettitales and the Cycadales. A female sporophyll of the Pecopteris type, with male sporophylls, foliage leaves and trunk of types so common that they caused the Carboniferous to be called the "Age of Ferns," will serve for a start.

Beginning with such a hypothetical, but very possible and even probable ancestor, both the Bennettitales and Cycadales could be developed.

The pinnate leaves of the fern has been retained throughout the entire phylum. It is more than doubtful whether the three orders can be distinguished by the leaves. The leaf impressions of some of the Mexican Bennettitales, like *Ptilophyllum acutifolium* and *Pterozamites angustifolium,* so thoroughly described and illustrated in Wieland's "Flora Liassica," can hardly be distinguished from *Dioon,* which now flourishes in southern Mexico: and the leaf impressions of the African Zamites, as already indicated, also bear a close resemblance to the leaf of *Dioon,* although neither *Dioon* nor any other cycad with a similar leaf is now living in Africa.

The stem throughout the phylum has a large pith, scanty zone of wood, a fairly large cortex and, with exceptions, an armor of leaf bases.

The histological structures should not be overlooked. In the Cycadofilicales the stem is, prevailingly, a mesarch siphonostele; while in both the Bennettitales and the Cycadales it has advanced to the endarch condition, with the mesarch condition still appearing in the seedlings of Cycadales and, probably, in those of the Bennettitales as well.

In the Cycadofilicales the wood, in most cases, is composed of tracheids with bordered pits, a condition more advanced than that in the ferns, which are characterized by scalariform tracheids. Since ferns scarcely ever get beyond the scalariform tracheid stage, we should expect to find the lowest members of the Cycadofilicales characterized by scalariform tracheids. Since the wood of the Bennettitales is composed almost exclusively of scalariform tracheids, the order must have come from forms lower than the known forms of Cycadofilicales, which have already reached the pitted tracheid stage.

Most of the Cycadales have reached the pitted tracheid stage of development, although the scalariform tracheid is still prevalent in the metaxylem; and in the fern-like *Stangeria* the scalariform tracheid is still retained even in the secondary wood.

On the whole, the vegetative structures of the Bennettitales and Cycadales show an advance over those of the Cycadofilicales; and the evidence seems conclusive that the Bennettitales have come from the Carboniferous Cycadofilicales. But whether the Cycadales have come from the Bennettitales, or have come directly from the Cycadofilicales, is a question which could not be answered by the vegetative structures; at least could not be answered without an intensive study of the vegetative structures of all three orders.

But when we turn to the reproductive structures, the evidence is more decisive, in our opinion conclusive, that the Cycadales have not come from the Bennettitales, not even from the lowest members of this order, but have come directly from the Cycadofilicales.

None of the Carboniferous Gymnosperms of this phylum had attained the cone condition. The leaves bearing male sporangia and those bearing female sporangia were still in loose crowns, bearing more or less resemblance to the crowns of vegetative leaves, but were becoming reduced in size and there was a strong tendency to simplify the outline, just as we see both of these tendencies in the spore-bearing leaves of many of our living ferns. Naturally, the original axis would persist throughout the life of the plant, for the crowns of spore-bearing leaves would fall off just like crowns of foliage leaves.

The Bennettitales would develop naturally from such an ancestor. A progressive reduction of the lateral pinnae of the female sporophyll would finally result in the production of a single seed on a slender stalk, with no trace of leaflets along the sides. As the sporophylls became smaller, they became more numerous and became compacted into a tight cone. Many of the sporophylls lost not only the lateral pinnae, but even the seed at the top, becoming entirely sterile and functioning only as protective structures.

The male sporophylls were much less modified. Even in the most advanced members of the Bennettitales they continued to appear in loose crowns and retained more or less of the characters of the pinnate leaves.

The origin of the Bennettitales from the Cycadofilicales is so obvious that, as far as we know, it is not disputed. There might be different views as to the mode of origin, but hardly as to the origin itself.

In our opinion, it is even more obvious that the Cycadales also have come from the Cycadofilicales. In this case, the upper part of the female sporophyll has become sterile, while the lateral ovules have persisted. *Cycadospadix Hennoquei,* in the Lias, shows this type; but this ancient sporophyll had already diverged farther from the foliage leaf than has the living *Cycas revoluta.* A still wider divergence is shown by *Cycadospadix Milleryensis,* in the Permian, which shows the type of cone we should anticipate if the living *Cycas tonkinensis* should group its crown of sporophylls into a cone. Since this type is more advanced than the preceding, the Cycas type must have been differentiated very early, probably in the Carboniferous. We believe that these sporophylls belong to the Cycadales, and that from this point there has been a reduction of the pinnate leafy top, while the ovules remained lateral.

If the Cycadales have come from the Bennettitales, the connection would have to be between the lower members of both groups; but even in the Triassic, and probably much earlier, the Bennettitales had already lost their lateral pinnae and had become established in the terminal ovule habit. As far as age is concerned, one order seems to be as old as the other.

My friend, the late Samuel Williston, used to say that, phylogenetically speaking, when a tooth is lost, it is lost for good. We accept as a fundamental principle, proved by paleontologists, especially vertebrate paleontologists, that when a structure has been lost during phylogeny, it can not be regained. The horse of to-day will never regain the toes it kept losing during the Oligocene, Miocene, Pleiocene and Pleistocene. The phenomenon known as reversion, or atavism, is effective over too short a period to be of much interest to the vertebrate paleontologist or the paleobotanist. The horse of to-day does not revert to a five-toed race of horses; and, in accordance with the same fundamental principle, we believe that the female sporophyll of the Bennettitales, having lost its lateral pinnae, lateral ovules and leafy top, could not have given rise to the primitive sporophyll of the Cycadales, in which these lost characters are dominant.

If the case is proved for the female sporophyll of the Cycas type, it is proved for the whole group; for within the living members of the Cycadales, the development of the compact cone from a loose crown of sporophylls can be traced with confidence.

In the genus *Cycas* itself, the various species show a reduction of the pinnate, leafy top, and the ovules become reduced to a single pair which characterizes all the other genera. In *Dioon edule* the female sporophylls have lost practically all the pinnate character, but still retain something of the topography of the foliage leaf, and they are grouped into a loose cone, which looks as if it might proliferate; for even compact, staminate cones sometimes show a little proliferation.

In other genera the reduction becomes more and more pronounced. In *Macrozamia* the midrib of the sporophyll persists as a long spine, with occasional traces of the lateral pinnae; in *Ceratozamia,* two of the lateral pinnae remain as strong spines; in *Encephalartos* both midrib and pinnae have been lost, although there are traces of lateral pinnae in some species. In the highest genera, like *Zamia,* even such occasional slight traces of pinnae have disappeared, and only its origin and nature entitle the ovule-bearing structure to be called a sporophyll.

We believe the evidence shows that the Cycadales are not a branch from the Bennettitales, but that they have arisen directly from the Cycadofilicales. The Cycas type was probably differentiated during the latter part of the Carboniferous, and some of its forms soon advanced to the cone type, while others remained at the Cycas level and are represented to-day by the genus *Cycas.* However, it is not necessary to assume that all the genera with the female sporophylls in cones were differentiated at such an early period; for cones like those of *Dioon* and *Stangeria* might very well have been developed from the *Cycas* type at a much later period.

The strongest objection to our contention is the scarcity of fossils in the Mesozoic, which can be referred, positively, to the Cycadales. Throughout the period there are leaves to which the Cycadales have as good a claim as the Bennettitales. The cycad leaf is tough and leathery and well suited to preservation; but the female sporophylls of the Cycas type, and all cones, soon decay, so that the chances for their preservation are slight. The condition is very different from that in the Bennettitales, whose well-protected cones are in a very favorable position for preservation.

The scarcity of fossils, especially any scarcity in the Cretaceous and Tertiary, is not such a strong objection, when we remember that living cycads are all tropical and subtropical, and that more than half belong to the southern hemisphere; while fossils have been hunted and studied principally in the university zone of the northern hemisphere. And the objection is weakened still further when we remember that probably more than half of our knowledge of the Bennettitales has come from the enthusiastic researches of one man. Wieland goes to a new place, and we have the "Flora Liassica." And now the text-books can say that the lower Mesozoic of southern Mexico is very rich in fossils of the lower Bennettitales.

If four or five Wielands should search for fossils throughout the Carboniferous, Permian, Mesozoic and Tertiary, in both the northern and southern hemispheres, our knowledge of the facts would not long remain so fragmentary. We should have facts instead of inferences.

We have confined ourselves almost entirely to a discussion of the macroscopic structures. In the living cycads the microscopic details are fairly well known: the microscopic structure of the sporophyte, the development of the gametophytes, with the details of oogenesis, spermatogenesis, fertilization and embryogeny, have been described rather thoroughly in some forms and have been outlined in others. The swimming sperm, a fern character, is still retained by all the living genera; but the development of the archegonium is more advanced than in *Pinus*. The embryogeny is more primitive than in any known forms of the Coniferophyte phylum. While these features are of great importance in deciding the interrelationships of the living genera, they could not have much value in determining the origin of the cycads, unless we could learn corresponding details of Mesozoic and Paleozoic forms. What some of these details must have been, we can hazard a guess. The seeds of the living cycads are large, some of them reaching six centimeters in length. In such a seed, the female gametophyte is large, with large archegonia, the pollen tubes are long and there is an extensive free nuclear period in the embryogeny. No Mesozoic seeds in either Cycadales or the Bennettitales even approached the size of the seeds of some species of *Cycas* and *Macrozamia*. Consequently the female gametophyte must have been smaller, with smaller archegonia and probably a shorter free nuclear period in the embryogeny. The pollen tube must have been shorter and may have contained many sperms. In the Bennettitales, with their very small seeds, the female gametophyte must have been very small, with little free nuclear division, extremely small archegonia and, perhaps, no free nuclear stage in the embryo. Pollen tubes were either very short or entirely lacking. In the Paleozoic Cycadofilicales, with many of the seeds smaller than those of the Bennettitales, there were no pollen tubes, and in the earliest seeds the conditions could not have been much more advanced than in some of the living species of *Selaginella*. While these structures may seem visionary, they are about what we should expect to find, as we go from large seeds to smaller and smaller ones, if the same kind of differences which we see in the larger and smaller seeds of the living cycads are continued in the still smaller and smaller seeds of the Mesozoic and Paleozoic forms of the same phylum.

While we believe that microscopic details, if available, would be of even greater value than the macroscopic in tracing relationships, we feel certain that the facts already known prove that the Cycadales have come from the Cycadofilicales and that the differentiation of the two groups may have occurred long before the end of the Carboniferous.

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"AGE AND AREA" IN RELATION TO EXTINCTION

THERE are few generalizations in regard to the geographical distribution of species which have aroused so much interest and elicited so much criticism as the theory of Age and Area of Dr. J. C. Willis. I think it must be admitted that the laborious statistical researches of this investigator have established a fairly definite relation between the number of related endemic species in a given region and the areas which the several species occupy. Willis finds that species of wide distribution are relatively few in number; species whose range is less wide are more numerous, and species which are much restricted in area are most numerous of all. According to the Age and Area theory the "wides" are on the average the oldest species, the small area species being in general those of recent origin which have not had time to spread widely. Dr. Willis believes that under normal conditions species extend their range very slowly, and hence if a species has a wide distribution it must have been in existence for a great length of time. In a very broad and general way this contention is probably right. It is not entirely evident, however, that the species of narrow range are nearly all young, although Dr. Willis has advanced many arguments against the common view that they are species approaching extinction. In general, and so far as is permitted by barriers, the range of a species, according to Willis, is determined not by natural selection or any other agency making for adaptation, but in a more or less "mechanical" way as the result of mere age. "The real difference," he tells us, "between the old view of dispersal and that given by Age and Area is that under the latter we regard *almost all* species as in process of extending their areas of dispersal, not some as extending their areas and as many or more contracting theirs. The exceptions to this—the real relics—are comparatively few and far between, forming perhaps 1 to 2 per cent. of the total of species of very restricted area."[1]

The idea that species are almost all on the spread, and that the process of extension goes on in a "mechanical" fashion leads Willis to set little store by the struggle for existence and selective survival as factors in the distribution of life. "The struggle for existence," he tells us, "can no longer be regarded as an important determining cause in evolution." It acts most strongly in species that are "just commencing." "If they can not succeed in this first struggle they will simply die out and leave no trace. But if they do succeed, they may be looked upon as estab-

[1] "Age and Area," Cambridge, 1922.