THE LIVING CYCADS AND THE PHYLOGENY OF SEED PLANTS[1]

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Phylogeny is a big word and it can be made to cover most of the problems of relationship. Among the phylogenetic problems of a group, two always stand out prominently: "What has been its origin?" and "Has it left any progeny?"

In the cycads these two problems are not equally difficult, for the origin can be traced back, with more or less certainty, to the ferns; but whether they have left any progeny is doubtful. However, if we stick close to the living cycads, it seems safe to claim that none of the nine genera has left any progeny or is likely to have any descendants. Like the higher members of the Cycadofilicales and Bennettitales, they are the last of their race; and if there should be another epoch succeeding the present, just as the present succeeded the Mesozoic, the Cycadales would become extinct, just as the Bennettitales became extinct.

First let us consider the less difficult problem, the origin of the cycads.

Just how far back the cycads extend, is a question which could be answered only by complete geological evidence; but what we know of available structures shows that the line goes back farther than any fossils yet discovered would indicate.

A morphologist must depend largely upon comparative morphology in studying relationships, tracing each structure, geologically, from its earliest appearance, and tracing the ontogeny wherever material is available.

The graphic method will illustrate clearly some of the principal features in the comparative morphology of cycads and at the same time will indicate their geological distribution (Plate VI).

A very prevalent fern habit—a crown of pinnate leaves at the top of an unbranched stem—has been retained by the cycad line, with remarkable tenacity, from their earliest appearance up to the living forms. The armor of persistent leaf bases is another character which can be traced from the Paleozoic up to the living forms. The large pith, comparatively scanty zone of wood, and large cortex are features common to the living cycads, Bennettitales, and Cycadofilicales (Plate VI).

If these three features—the crown of pinnate leaves, the unbranched stem with its armor of leaf bases, and the topography of a transverse section of the stem—were the only features worth considering, there could be little

[1] Invitation address read before the joint session of Section G, A. A. A. S., the Botanical Society of America, and the American Phytopathological Society, in the symposium on the "Phylogeny of Seed Plants," at St. Louis, December 30, 1919.

objection to putting the entire Cycadophyte phylum into one family. But when one turns to the reproductive structures, it is evident that the ancestral stock, the Cycadofilicales, has either differentiated into two lines, or has given rise to the Bennettitales, which, very soon, gave rise to the Cycadales.

The spore-bearing structures of the Cycadofilicales may be represented diagrammatically: In the center, a crown of much reduced leaves, bearing seeds; just outside these, a crown of reduced leaves—but not so much reduced—bearing microsporangia. But in none of the Paleozoic forms, the Cycadofilicales, is either of these two crowns of reduced spore-bearing leaves compacted into cones. This feature marks the Cycadofilicales, for in the succeeding forms one or both of these crowns of reduced leaves become compacted into cones (Plate VI).

The Bennettitales and Cycadales are best separated from each other by the fact that, in the former, the microsporophylls have not yet been compacted into cones; while in the Cycadales the microsporophylls form closely compacted cones. In both groups, the ovulate structures form cones, except in the genus Cycas.

The microsporophyll is easily traced, not only from the Paleozoic Cycadofilicales, but even from the ferns, up to the living cycads. It was the close resemblance of this microsporophyll to the spore-bearing leaves of Marattiaceous ferns, as well as the close resemblance in vegetative leaves, that led to the earlier geologists to call the Carboniferous "The Age of Ferns."

Throughout the series, the microsporangia are borne on the margin or on the under (abaxial) side of more or less reduced leaves. In the Bennettitales the microsporophylls, while much smaller than the foliage leaves, still show the pinnate character, with no tendency toward becoming compacted into cones. In the Cycadales, the pinnate character has been lost entirely and, in every genus, the compact cone stage has been reached. But the resemblance to a leaf is still seen in the prevailing distribution of the sori into two groups, representing the two series of pinnae, one on each side of a midrib (Plate VI).

The structure of the individual microsporangium has changed very little since the phylum was differentiated from the ferns. It would be interesting to compare the contents of pollen grains of Carboniferous, Mesozoic, and living forms; but no satisfactory fossil material has been sectioned. It seems safe to say that there were no pollen tubes in the carboniferous forms. Engler's term *Siphonogamia* would not include these early seed plants. The small size of the pollen grains, together with the absence of the pollen-tube habit, would indicate that the sperms were very small and that germination and the development of sperms took place very rapidly, as in our living heterosporous ferns.

The immense size of the sperms in the living cycads is an example of giantism which—so paleozoologists tell us—indicates that the phylum has reached its limit and is ready for extinction.

The megasporophyll of Cycas is of the greatest importance in tracing relationships, for it is essentially identical with the megasporophyll of the Paleozoic genus Pecopteris; while in the living cycads, a series of genera like Cycas, Dioon, Macrozamia, and Encephalartos shows the gradual reduction of the individual sporophyll and, at the same time, shows how a loose crown of sporophylls has been compacted into a cone (Plate VI).

This megasporophyll of Cycas is so different from any yet described in the Bennettitales that we think it is safe to claim that the Cycadales have not come from any forms like Cycadeoidea, or from any others with such reduced seed-bearing structures. While we should recognize the phenomenon known as atavism, or reversion, we believe it could appear only after a rather limited time. We can easily believe that a Pecopteris-like megasporophyll has persisted from the Paleozoic up to the present time; but we could not believe that the megasporophyll of Cycadeoidea, if reduced from a Pecopteris type, could—after millions of years—revert to the Pecopteris type, and so give rise to a megasporophyll like that of Cycas. We might believe in spontaneous generation and in the special creation of species, but not in that.

Consequently, if the Cycadales are a branch from the Bennettitales, the point of union is so far back that it becomes a question of arbitrary definition rather than a question of fact whether there has been a main stock with an early branch, or whether there have been simply two lines coming independently from the Cycadofilicales.

This seems to me to answer the question, "What was the origin of the living Cycads?" as far as it can be answered in the present state of our knowledge. If Professor Wieland would give us three big books on the Cycadales of the Triassic, Jurassic, and Cretaceous, like his three big books on the Bennettitales, we could state facts instead of spinning theories.

In tracing the plane body, with its stem, leaves, and spore-producing structures, from the Paleozoic up to the living cycads, the record is fairly complete, and there is not a very serious danger of mistakes; but in tracing the origin of the seed the Cycadophyte line has afforded little evidence, for the seeds—as far as they have been described—are almost as highly developed in the Paleozoic as they are today. In this line, they must have come from heterosporous ferns. But, until some one finds and sections a convincing series in heterosporous ferns, or in some more primitive members of the Cycadofilicales than any yet discovered, we must base our theories of the origin of the seed upon the behavior of living heterosporous forms which have not quite reached the seed stage.

What is the answer to the second question, "Have the Cycads left any progeny?"

Something has left some progeny; for an abundant progeny, both Angiosperm and Gymnosperm, is very visible and very much alive. What groups could have been responsible for this progeny?

If we consider only the nine genera of living cycads, as we know them today, the answer is easy: they are not responsible; they are the last of their race, restricted in geographical distribution, restricted in numbers, and struggling for their very existence.

To some this may seem like too positive a statement; but if it should be challenged, we should ask, "To what could the cycads have given rise?" The only possibilities are the Cordaitales, Ginkgoales, Coniferales, Gnetales, and the Angiosperms.

The Cordaitales, as the ancestral stock of the Coniferophyte line, might be expected to show resemblances, if any were to be found; but in habit they are very different from the Cycadophytes. They are the forest types, while the Cycadophytes bore somewhat the same relation to them that the ferns of today bear to the forests in which they occur. The leaves are prevailingly simple, contrasting sharply with the prevailing pinnate or twice pinnate leaves of the Cycadophytes. Not enough is known of spore-producing members in the Cordaitales, to make safe comparisons, but the Cordaitales certainly had well-developed cones; so that, in this feature, they had progressed far beyond the Cycadofilicales. The fact that the cones were compound, while those developed later in the Cycadophyte line were simple, would indicate that the Cordaitales were from a different stock. We believe the available evidence indicates that the Cordaitales have come directly from the Pteridophytes; but whether they have come from the fern section or from the lycopod section is a problem in the solution of which morphological characters of still undetermined value are balanced against each other.

In the Ginkgoales, the pollen-tube structures, with the two motile sperms, present a startling resemblance to the corresponding structures in the cycads, even to the blepharoplasts developing into spiral ciliated bands, the peculiar behavior of the persistent prothallial cell, and the haustorial habit of the pollen tube. The extensive free nuclear period in the development of an embryo with two cotyledons is common to the cycads and Ginkgo; but here the resemblance ceases. The plant body and the strobili make relationship seem impossible. As far as the Mesozoic cycads are known, they afford no better Ginkgo resemblances.

In my opinion the Bennettitales are no more nearly related, although I once tried to compare the long-stalked ovules of Ginkgo with the ovulate strobilus of the Cycadeoidea type.

Even if we go back to the Paleozoic Cycadofilicales, it seems no easier to establish a relationship. Besides, the Ginkgoales can be accounted for quite naturally as an offshoot from ancient Cordaitales stock.

A relationship with any of the Coniferales would be even more difficult to establish. Corresponding structures are too contradictory. The large pinnate leaves of the Cycadophyte line do not compare well with the small, entire leaves of the Coniferophytes; nor does the unbranched trunk of the former compare well with the profusely branched trunk of the pines and Ginkgo.

In trying to provide progeny for the Cycadophytes, some have cast a hopeful eye upon the Gnetales, because the staminate flower of Welwitschia has a sterile ovule and thus presents a bisporangiate condition in which a vivid imagination might see some resemblance to the bisporangiate strobili of the Bennettitales. But my imagination is too weak to see more than a superficial resemblance, even in this feature; while a comparison of the stems of the two phyla, the comparison of pinnate leaves with simple leaves, and of simple strobili with compound strobili, seems impossible.

Could the Cycadophytes have given rise to the Angiosperms?

For the living cycads, we should answer with a positive *no*. This conclusion cannot be escaped, if we compare the haustorial pollen tube and its contents with the sperm-carrying pollen tube of the Angiosperms. The large, ciliated, highly differentiated sperms of the cycads are headed for extinction rather than for evolution into the comparatively simple structures of the Angiosperms. The extensive free nuclear period in the development of the cycad embryo does not compare well with the total lack of such a period in the Angiosperms. However, reductions in the free nuclear period are not entirely impossible.

It is true that the general habit of the cycad, with its unbranched stem and crown of pinnate leaves which form an armor of leaf bases, is so strongly suggestive of palms that the layman calls Encephalartos the "Bread palm," Dioon the "Dolores palm," Cycas the "Sago palm," etc. But the resemblance is superficial. A section of the palm stem shows an advanced monocotyl condition, and the flower is truly monocotyl. It may seem like begging the question to say that the Monocotyls have come from the Dicotyls, but we believe this has been proved as definitely as anything is likely to be proved in relationships.

The resemblance between the Bennettitales and the Angiosperms is about the same; but here an attempt has been made to reconcile the floral structures. The resemblance pointed out was between the Bennettitales flower and a sympetalous flower. Our objection here would be along the same line: the sympetalous condition is a modification of the polypetalous, and the Sympetalae, like the Monocots, have come from the Archichlamydeae.

In the Cycadofilicales we are nearer the source of things, but the discrepancies keep becoming greater and greater and indicate that we are on the wrong trail. Like the hasty student, trying to pigeon-hole *Eryngium yuccaefolium* among the Monocots, we need to go back and make a fresh start.

We have tried to show that the Cycadophytes have come from the ferns, by way of the Cycadofilicales directly or as an early branch from the Bennettitales; and we have also tried to show that they have not given rise to any other seed plants.

This might seem like a logical place to stop, for we have tried to answer

our two questions: "What was the origin of the cycads?" and "Have the cycads left any progeny?"

But it would emphasize the answer to the second question if we could show that the visible progeny could be referred to some other ancestry. In case of murder, the victim constitutes a concrete fact to be accounted for. The defendant may claim he didn't do it; but it adds weight to his claim if he can cast suspicion on some one else.

So let us ask another question: "Could some other group have given rise to the Coniferophytes and the Angiosperms"? We shall consider the two groups separately.

If the Coniferophytes have not come from Cycadophytes, they must have come from the ferns or from the lycopods. This is a problem, in the discussion of which leaf gaps are balanced against leaves, pinnate leaves against simple leaves, and abaxial sporangia against adaxial. I believe the evidence is sufficient to establish a Pteridophyte origin; but the comparative claims of ferns and lycopods do not appear the same to me as they did several years ago.

As far as the seed is concerned, some of the Paleozoic lycopods, like some of their living descendants, had progressed so far that their megasporangia are separated from seeds by arbitrary definitions rather than by facts.

We separate the Gymnosperms from the Angiosperms by the ovules on open carpels and ovules enclosed in an ovary; and the distinction is good and very useful in a taxonomic key; but rigid definitions may harden our ideas and may prevent us from getting an unbiased view of the facts.

In most Angiosperms, except epigynous forms, the ovules appear on open carpels, the closed ovary developing later. In cases like the Ranunculaceae, the integuments of the ovule appear and the embryo sac is well started while the carpel is just as open as in any Gymnosperm. In the Amentiferae, the ovules are well started before the carpels close; and in Podophyllum, sometimes the carpels do not close at all, the ovules being borne on perfectly open carpels, as in the Gymnosperms.

In considering this whole subject, we must remember that the extinct forms which have been preserved are mostly woody, especially in the Mesozoic. Has there been an extensive herbaceous flora which has disappeared? Have we lost herbaceous Gymnosperms which may have given rise to herbaceous Angiosperms? And could such herbaceous Angiosperms have given rise to the woody Angiosperms which became prominent in the Cretaceous?

Unless such an herbaceous flora has arisen and disappeared, it is necessary to derive the Cretaceous Angiosperms from woody forms; and this means from more or less well known Cycadophytes or Coniferophytes. Such attempts have been made. We have already paid some attention to the claims of the Cycadophyte line.

In looking for the origin of the Angiosperms, the claims of the Coniferales

and the Gnetales may be considered separately, although they have much in common.

Familiar representatives of the Coniferales show more resemblances and fewer contradictions. The plant body is similar, and the internal structure of the stem often shows striking resemblances. The catkins of the Amentiferae may not differ much, morphologically, from some of the cones of the Coniferales; the pollen-tube structures of Angiosperms could be derived from those of Coniferales, and the embryogeny could be reconciled. The leaves are harder to reconcile, but leaves are very susceptible to environment.

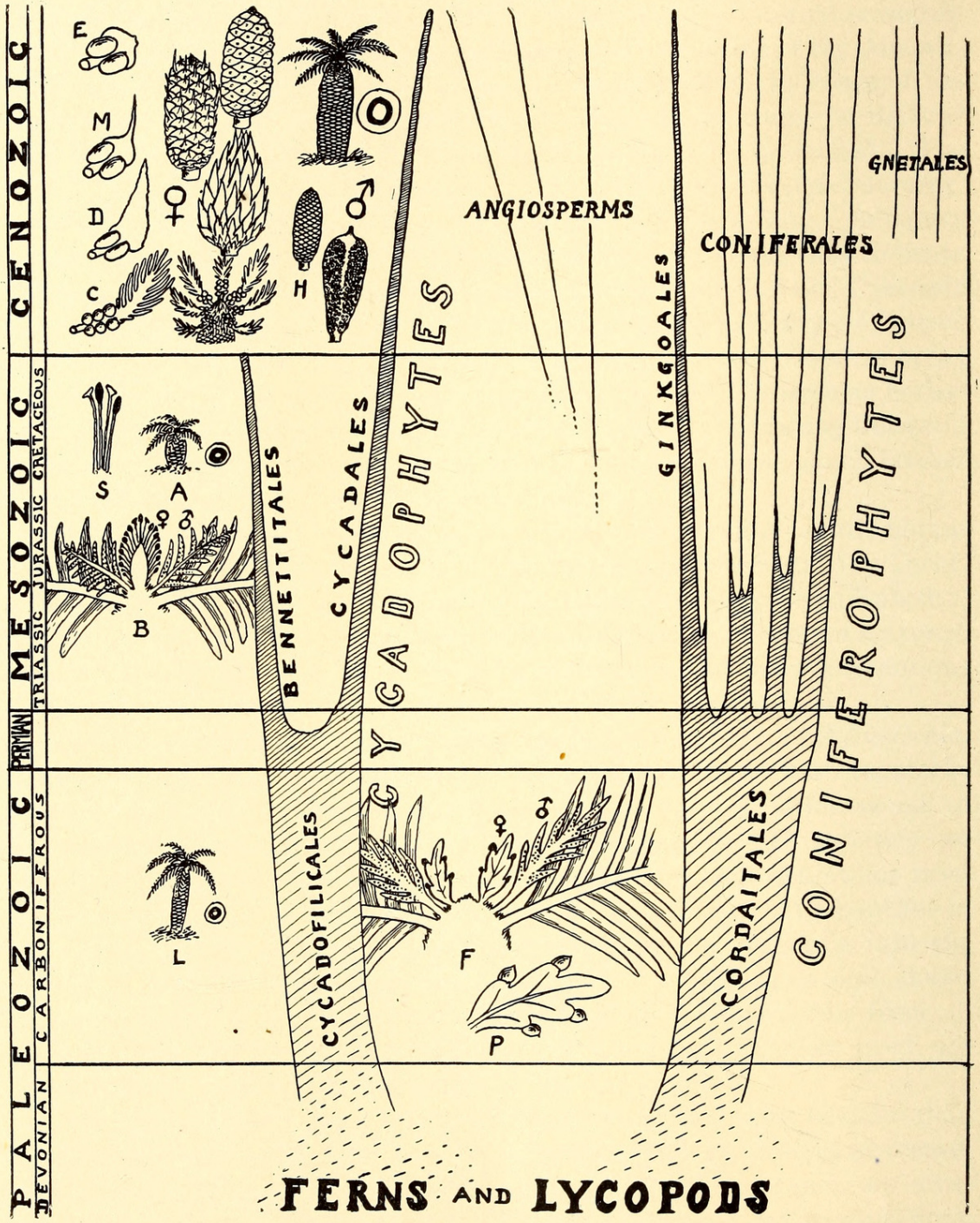
While these resemblances would not induce us to claim any Coniferales yet described as the ancestors of the Angiosperms, we believe they indicate the direction of the trail. We should remember that most of our Paleozoic and Mesozoic material is woody, and that there is a possibility—I believe there is a strong probability—that a great herbaceous vegetation has failed to be preserved, or, at least, has not yet been discovered. In such an herbaceous vegetation, leading up to woody forms, I believe the missing links will be secured, and that the Angiosperms will be found to extend much farther back than any available records have indicated.

The Gnetales show some striking Angiosperm characters. Most botanists, looking at the habit and leaves of *Gnetum Gnemon*, would call it a Dicot, and the histology of the stem continues the Dicot impression. In Ephedra, the habit, the strobili, and the spermatogenesis show Angiosperm features. It is so evident that the leaves have been reduced from more pretentious structures, that they need not constitute any objection.

In this connection, the less said about the leaves and habit of *Welwitschia*, the better; but its flowers, especially the staminate flower with its sterile ovule, would pass for Angiosperm flowers. The only objection seems to be that definition relating to open and closed carpels. Fortunately we have reached a stage in botanical development at which definitions need not interfere with research; for we do not put the Liliaceous Agapanthus in the Dicots simply because it has two cotyledons; or Nelumbo into the Monocots because it has only one cotyledon. So the open and closed carpel need not be absolute marks separating all Gymnosperms from all Angiosperms, and the presence of one condition or the other need not interfere with research into the origin of the Angiosperms.

It is easy to be humorous and to say that an ancestor must be older than the offspring, and that, therefore, the Gnetales, with no geological record, could not qualify as progenitors of anything. But here, again, we must remember the possibility, or probability, of an extinct herbaceous flora, which, very late in its history, developed a few woody members. Earlier in its history, it may have given rise to herbaceous Gnetales and to primitive Angiosperms, which developed into the woody forms of the Cretaceous.

We have tried to show that the Cycadophytes have come from the ferns and that they have not left any progeny, outside of the Cycadophyte line;



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and we have tried to emphasize the second claim by showing that the Coniferophytes and Angiosperms—the undoubted progeny of something—can be referred to another ancestry.

EXPLANATION OF PLATE VI

Diagram illustrating some features of the Cycadophytes and Coniferophytes.

At the bottom: *L*, a diagrammatic representation of a member of the Cycadofilicales, with a transverse section of the stem at the right; *F*, an idealistic view of spore-producing members; *P*, pinnule of *Pecopteris* with seeds on the margin.

In the middle: *A*, habit of one of the Bennettitales with section of stem; *B*, bisporangiate strobilus; *S*, two seeds on long stalks and two scales.

At the top: habit of a living cycad; *C*, sporophyll of *Cycas* with crown of sporophylls at the right; *D*, *Dioon;* *M*, *Macrozamia;* *E*, *Encephalartos;* each with corresponding cones at right; *H*, male cone with a single sporophyll below. All very diagrammatic.