

## THE FOSSIL CYCADS

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ABSTRACT. The fossils considered are those in which attribution of one organ to the Cycadales (in the strict sense) is supported by the evidence from a different organ believed to be of the same plant. It thus deals with *Palaeocycas*+*Bjuvia*; *Androstrobus prisma*+*Pseudoclenis lanei*; *Androstrobus* spp.+*Beania* spp.+*Nilssonia* spp. Two classic fossil Cycads, *Cycadospadix* and *Dioonitocarpidium*, are considered not fully convincing. The kind of evidence needed is mentioned and the need is urged for assembling separate fossil organs into further synthetic plants.

THE Recent Cycads are a small family of Gymnospermous seed plants, scattered through the tropics of the world and of no particular economic importance but very familiar to botanists. Many of them look like squat palms. The 'fossil cycads' are a large and very indefinite assemblage of all sorts of plant organs, but nearly all of them of Mesozoic age. To some authors they comprise about a hundred genera and a few thousand species, in fact almost everything ever called a fossil cycad, irrespective of present views. Many are rather more discriminating than this and, in this address, I shall limit myself extremely to those fossils which not only have every appearance of being truly Cycadean but in which this appearance is strongly supported by a second line of evidence.

Botanists agree that the Cycads ought to be found fossil. All their organs, stem, leaf, male and female organs are large, robust, and strongly characterized and as it seems well suited to be preserved and then to be recognized. And we have long been impressed by their archaic features; one such is fertilization by spermatozoids, but there are half a dozen others and they look as though they had persisted without change from very early times. Cycads are so archaic that had they been extinct and only known fossil, it would have been a very easy thing to point a moral. And so when a century or more ago leaves just like modern Cycad leaves were found in vast numbers in the Mesozoic rocks, and also a fair number of similar stems, and even a few suitable reproductive organs, everybody gladly recognized them as Cycadean and some people even called the Mesozoic the Age of Cycads. The literature was filled with generic names recalling those of Cycads. Gradually, however, this simple picture became complicated and confused. Certain plants called fossil Cycads and with very suitable looking stems and leaves proved to have totally different reproductive organs, and for these another class, the Bennettitales, was established. We now think that a good deal more than half of the fossils, formerly called Mesozoic Cycads, belong to the Bennettitales but the proportion is uncertain. A few have been proved to have Bennettitalean reproductive organs; a much larger number are linked with these few by some special character, for instance, the epidermal structure of the leaf. Others in which the structure is unknown are just vaguely associated. On the other hand, a minute number of fossil Cycads have been proved to be Cycadean in the strict sense (the ones considered here) and a moderate number are associated with them on more or less impressive evidence. A very considerable number of the fossils originally proposed as fossil Cycads are still uninvestigated and of unknown affinity.

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It is partly conservatism which makes some of us continue to call the Bennettiales fossil Cycads even though we do not think they have anything to do with them, but partly a reaction to imperfect knowledge. We have the small group of the definite fossil Cycads, the moderate-sized group of definite Bennettiales, and associated with each is a large penumbra of less and less clearly attached fossils. We use our terms today in such various ways that we must cause real confusion. There are all varieties of opinion between those who regard the Bennettiales as so remote that they may as well be called unrelated (this is my position) and those who, while recognizing that they are quite different in some organs, feel that other organs are so similar that they must be related through a not very distant common ancestor. A term has been created which I find repugnant, but it is generally used and I freely admit it has its usefulness; this is Cycadophyte. It was intended to cover Recent and fossil true Cycads, the fossil Bennettiales and fossils not yet clearly placed in either family. It has been found a conveniently broad filing space to accommodate several other Mesozoic genera. Some of these like *Caytonia* and *Pentoxylon* are rather fully known and they will not fit well into any plant class. Of course, when they are pushed in here, they broaden the Cycadophytes still further and, as far as I can see, the fossil Cycadophyte is just a short name for any Mesozoic plant with a leaf constructed on a more or less pinnate plan, without regard to the other organs of the same plant! The trouble with such a word is that people *will* regard it as a natural class and proceed from that to make mistakes.

In the early days it was inevitable that isolated plant organs alone were considered, and those that looked Cycadean were considered Cycadean. It was when the plants began to be put together that it became plain that the whole plant would not fit fully into the Cycad mould. This directs our attention to one of the main differences in outlook between fossil botanists with botanical outlook and plant morphologists working on modern plants. With modern plants you may consider a particular organ or even just a small part of it, but you never forget that it belongs to a certain whole plant. With fossils you take what you have, that is some isolated organs, and you engage in thoughts about them without having any whole plant at all, though you may create one as a hypothesis. This sort of thought has always fascinated the fossil botanist and no doubt always will, but it is very dangerous and I think he could have used his mind to better advantage. As I shall emphasize at the end of the address, botanical progress depends on working towards a whole plant.

#### THE CASE OF *PALAEOCYCAS*

The first fossil Cycad I shall accept on my restricted definition is *Palaeocycas integer*, described by Florin in 1933. It is not a complete plant but it has two important organs, the foliage leaf called *Bjuvia simplex* and the seed-bearing organ or megasporophyll to which the name *P. integer* properly applies. In fact both organs had been described fifty years earlier from the Rhaetic of Sweden and Florin was revising old specimens, but if you compare the first treatment with the second you will see the second is over twenty times longer and possibly twenty times as laborious. This gives one reason why such work is rare. Florin gives a spirited reconstruction of *Palaeocycas*; it consists of two known fossils synthesized on the basis of the recent genus *Cycas*: it is perfectly clear what is fact and what surmise. Florin could, had he wished, have used a different model; for instance the tropical Ginger family, which happens to have leaves looking very like those

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of *Palaeocycas*, could provide several alternative models, though they might be less attractive botanically since we believe these fossils are unrelated to the Gingers.

There is another difficulty. Not one of the specimens of megasporophyll figured still bears its seeds. It is true that the stalk shows bulges which look as though they were the points where large seeds were borne, and I can only say that if I had been studying the specimen, I would have assumed that it did bear seeds in the way Florin showed. But until seeds are seen, let us always remember that this is an assumption.

Accepting then that the organ is a seed-bearing megasporophyll, what is the evidence that this and the leaf, which has been described under an entirely different name, belong to the same plant? And then when we have the evidence that they are correctly put together, what is the evidence that the whole plant is a Cycad?

The organs are found separately and most of the specimens are broken. The evidence for attributing them to one species is only circumstantial; no specimen suggests continuity. There is, in the first place, the evidence of association. The fossils are preserved in a deltaic deposit full of fossil plants and in such a deposit association of fossil organs shows that they were produced at the same time and in nearly the same place. It is the more suggestive because the leaf is an uncommon fossil, having only two Swedish localities and the megasporophyll is rare, occurring in one of the leaf localities. Reproductive organs in general are so much rarer than leaves that when in a flora preserved near where it grew, you find several specimens of a reproductive organ, you have a right to expect to find the appropriate leaf with them. Still there are many other species of leaves also associated.

Then there is the evidence of agreement in structure. The only part of which we have information is the cuticle of the epidermis, but this is excellently preserved and open to study at high magnification. By numerous preliminary studies, Florin showed, as others had done less systematically, that certain features of the epidermis tend to run through all the organs of a plant. This is specially true of the stoma. We may add that when a part happens to be green and rather leaf-like, it often has rather close resemblance to the cuticle of the leaf. The cuticle can have family characters running through all the organs and it can also have specific characters which act even if obscurely as a specific label for the various organs.

Florin showed that there was extremely close agreement between the leaf cuticle and that of the expanded lamina of the megasporophyll. There are also points of agreement between the stalks of the two organs. He examined all the associated leaves of other species and found that all of them differed more or less; so there is no rival leaf to claim the megasporophyll. We will take it that the two organs of *Palaeocycas* are rightly attributed to one plant (though always bearing in mind that there is an element of risk in this assumption); what then is the evidence that it is a true Cycad? In fact there is no living Cycad with a leaf just like the fossil but the essential architecture is similar so the difference is not too disturbing. The structure of the stomata is exactly similar and somewhat special to this family, so the leaf fits well enough. The megasporophyll is more like that of *Cycas* than anything else known to us on earth (but again we bear in mind the reservation that it has not yet been proved to bear *Cycas*-like seeds).

What has happened is that instead of the knowledge of two separate bits of fossil plants, we have the much more impressive coherent knowledge of the pair, with certain reservations it is true but not ones that I would let worry me. What should we now do?

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Plainly we need more; we should look for further circumstantial evidence bearing on the question whether the two organs belong together; for instance, we might search the second leaf bearing locality for associated megasporophylls. And then there are great gaps in our botanical knowledge. It is probably too much to hope that we could find the real stem so as to replace Florin's hypothesis by fact; and too much to hope that, if we do find it, we might learn how the leaves and megasporophylls were borne in relation to one another. There is a better hope that with further collecting we might find megasporophylls still bearing seeds and that such specimens might reveal a good deal of their seed structure as it has done in another fossil Cycad. It is not too much to hope that we might find the pollen-bearing organs.

The mine which yielded *Palaeocycas* has long been closed, so the only hope is that it is eventually found in another locality. Florin's material was collected nearly a century ago by men who may have been acute and discriminating and the work of such men is not to be despised; but it really is a matter of luck if they found and preserved the precise kind of specimen which was needed to make progress in the laboratory a century later.

If such progress were made, what result would we expect? Probably the circumstantial evidence for putting the organs together might be reinforced. Probably what we managed to learn about the seed, or the male organs, would fully confirm Florin's Cycad idea; but it is at least conceivable that they might prove utterly different and force us to look at *Palaeocycas* in an entirely new light. Even if it were spoilt as a fossil Cycad, it would become a still stranger and more interesting plant.

#### CYCADOSPADIX AND DIOONITOCARPIDIUM

I next take *Cycadospadix* which for a century has figured in botanical textbooks as one of the best-established representatives of the fossil Cycads. The classic specimens are a dozen isolated fossils scattered in marine Liassic rocks. No doubt they had floated far out to sea and with such fossils association tells you very little. It really looks exactly like a *Cycas* megasporophyll and everyone accepted it as that, though no seed is known attached. I for one would never have doubted it but for one accident. When collecting in the Greenland Rhaetic, I found fossils looking like *Cycadospadix* and which I naturally determined as a species of *Cycadospadix*; a new one as it happened. Then in the course of ordinary routine, I examined the cuticle of my *Cycadospadix* and I was surprised to find that it had all the characters of the Bennettitales and was sharply different from that of any true Cycad. In fact, I convinced myself that my fossils were not seed-bearing megasporophylls at all, but sterile scale leaves; very probably belonging to the flower of a certain one of the associated Bennettitalean leaves.

The original specimens of *Cycadospadix* seem never to have been examined very closely and we certainly know nothing of their fine structure. The nearest thing to a full reinvestigation I know is a pencil note by my own teacher, A. C. Seward, to the effect that the original figures were rather restored and that the specimens did not show clear seed stalks in the way the figures suggested. I hope someone examines *Cycadospadix* critically; I would not be surprised if it proved to be exactly what it has always been supposed to be, but then it might be a sterile scale leaf like my Greenland fossil. *Cycadospadix* certainly does not come into my category of Cycad-like organs supported by a second line of evidence; it is not even as firmly in the category of organs which are clearly Cycad-like just on their own merits as I once thought.

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It is only right to mention that Florin, while accepting my fossil as a Bennettitalean scale leaf, decided that it had nothing to do with the other species of *Cycadospadix* and gave it a new generic name. He may be right, but no one can be sure without looking again at the original specimens. The position of another famous fossil Cycad, *Dioonitocarpidium*, is better, but as it seems to me not very secure. *Dioonitocarpidium* has a few rare species from the Keuper of central and eastern Europe (Lilienstern 1928; Kräusel 1949, 1953). It is primarily the name of a seed-bearing megasporophyll, but a certain leaf has been attributed to it; thus like *Palaeocycas* it has two organs. Also like *Palaeocycas*, it is the subject of a spirited restoration, the stem and megasporophyll being built on to the stem of *Dioon*, the Recent Cycad genus from which it takes its name.

The evidence is, however, much less massive. The leaf is attributed to the megasporophyll on the evidence of association which is said to be impressive, but this time it is not yet supported by anatomical agreement. Then in *Palaeocycas* there was the slightly disconcerting fact that the seeds were missing; here there is the disconcerting fact that, though they are present, they are not quite right or so I feel. The sterile end of the megasporophyll fits very well into the general picture of a *Cycas* or *Dioon* megasporophyll, but the more important fertile end does not fit in well. The bodies at the base are compared with *Cycas* or *Dioon* seeds, but such seeds ought to project and instead they are sunken. In some of the figures the sunken bodies do indeed look like seeds but in others they look more complicated, as though they were sacs enclosing small seeds. These doubts are tiresome for *Dioonitocarpidium* may be just what it is supposed to be and a few solid facts might dispel them all, but without solid facts the doubts remain and it is a duty to retain them.

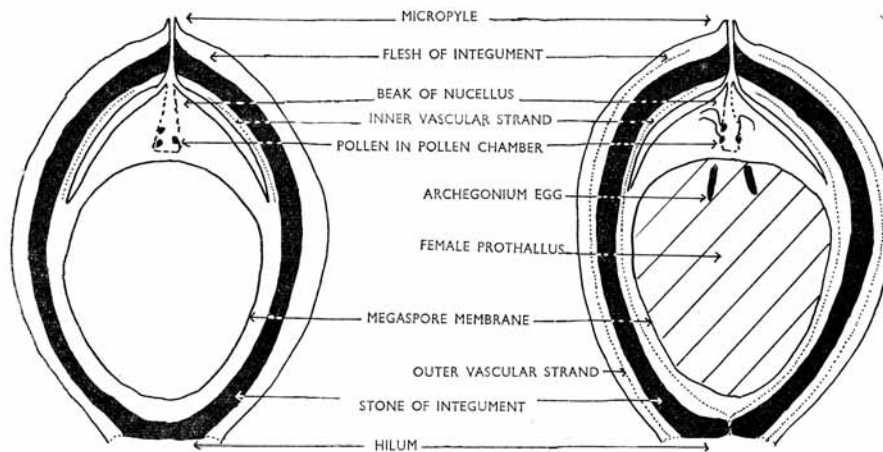
Here solid facts means in the first place microscopic details and we have none at all, and I do not know whether the material is preserved in a way which provides any. When we have such facts, we should be able to relate the leaf and megasporophyll in much the same way as Florin did for *Palaeocycas*. We should also be able to learn about the basal bodies of the megasporophyll; are they in truth simple seeds as supposed or something quite different? If they are quite different, *Dioonitocarpidium* might well disappear from the Cycad alliance.

#### BEANIA

The next Cycad I take is again synthetic and this time having four important organs—the leaf, the female cone, the seed, and the male cone—it is the most complete. The great gap is the stem (see Harris 1941, Thomas and Harris 1960). The leaf is called *Nilssonia*, a large genus with species occurring in most floras from the Rhaetic to the Middle Cretaceous, sometimes in great abundance. It is again a fairly large leaf of basically pinnate construction as in the Recent Cycads, but it looks rather unlike any Recent Cycad and it was formerly not thought to be specially close to them. For one thing, the lamina is attached to the very top of the midrib instead of being towards the sides, and for another the lamina is rather differently segmented and often divided so irregularly as to look pathological. Recent Cycad leaves delight formal gardeners by their regularity. Then the cuticle, though of Cycad type, is thinner than usual.

*Beania*, the female cone, was described from excellent specimens a century ago; in fact the first figure dates from 1835 and Carruthers's account that gave the name in 1869 was sensible and compared it properly with a Cycad cone, but after that progress

was arrested and only very gradually did different people contribute crumbs of information from much less good specimens, mostly isolated seeds of half a dozen species. The final synthesis for which I was responsible in 1941 was thus largely a compilation. The reason why Carruthers's account was not fully accepted was in the first place the cone, although fundamentally like certain Cycad cones, does not look like one, being far less compact, and secondly that he did not give any considerable supporting details. It was just one of many hopeful comparisons and the fact that it happened to be supportable failed to convince until that evidence appeared. I give a restoration of the type species



TEXT-FIG. 1. Left, diagram of seed of *Beania gracilis* showing parts so far demonstrated by maceration. Right, generalized diagram of a Recent Cycad seed.

of *Beania* which differs only slightly from the best specimens, so excellent are they. Several Cycad genera have cones like this except that they are compact; in fact, the *Beania* fruit is only technically a cone, it is more like a loose bunch of dates on their stalk.

It is surprising how much structure a compressed seed will reveal when subjected to the ordinary method of destructive maceration; that is to say, slow and uneven destruction which can be stopped when you will. The *Beania* seed (text-fig. 1) shows four distinct cuticles and, with ordinary care, these can be seen in their relative positions. Underneath the outermost cuticle there is a partly disorganized tissue in which scattered fibres occur; and this clearly corresponds to the more or less edible flesh of a Cycad seed, and inside that is a compact woody layer, corresponding to the hard stone. All these layers can be matched fully in Recent Cycad seeds (text-fig. 1).

This is all routine study and ordinary comparison, but I must make a confession. When you have found out all you can hope to see and have interpreted all visible things in a satisfactory way, however sensible it may be to stop, you make a great mistake if you do so. Several times I have gone on blindly, just macerating further seeds without any plan and presently new information appears, perhaps in the twentieth seed, or as with some *Caytonia* seeds after a few hundreds. For some reason occasional specimens

are rather differently preserved and show a feature clearly that is usually so obscure as to be missed. With the *Beania* seed some of this information could have been hoped for, but as it happens is seldom available. For instance, in a cavity at the top of one of the inner cuticles called the nucellus, I was able to find pollen grains. They are just where they would be expected in a Cycad seed some time after pollination and they have burst widely, again as expected, so that although the rather fantastic method of pollen development of a Cycad has not been fully observed in *Beania*, the limited facts are fully consistent with it.

The other observation is of an unpredictable sort. In a few macerated seeds, tiny woody strands are seen sticking to the inner cuticle of the integument (that is inside the stone of the seed). Such strands occur in exactly this position in Recent Cycads but it is not to be expected that they would be seen in *Beania* because they ordinarily decay readily and, even if they do not, maceration destroys them. Here maceration reveals them. It seems that they are casts of tracheids, some sort of resinous matter has impregnated the tracheid walls and showed up their characteristic cast. Need I say the supply of *Beania* seeds gave out before I learnt any more?

I was lucky to have a series of *Beania* cones of various sizes, some of my collecting but most collected by Dr. Hamshaw Thomas nearly fifty years ago. It seems that the *Beania* plant like many plants today shed a lot of its fruits at early stages. When this happens, it is convenient for the fossil botanist because the abortive specimens provide him with a series of young stages reflecting the normal course of development more or less perfectly. The fact these young cones are loose shows that the *Beania* cone is loose all its life, and not like the cones of some plants which are at first compact but later on become loose through the elongation of the cone axis; this elongation making it easier for the seeds to be shed. In the female cones of Recent Cycads, the cone is compact almost all its life. It elongates a little just at pollination time when the scales draw apart leaving small gaps which admit pollen to the seeds, but then it becomes hard and compact again and it remains compact until it is ripe when the cone again elongates a little, making it easier for the animals that eat and distribute the seeds to tear it open. The difference is only one of proportions but it is considerable. Anyone familiar with fir cones would call the female cone of the Recent Cycad, *Encephalartos*, for example, a 'cone', but he would hardly call the *Beania* cone a 'cone' at all. He might rather compare it with a number of dates or currants on their stalk, and I suggest that it has a flexible stalk and hung from a tree branch instead of being borne stiffly erect on a stalk which raises it above the crown of leaves.

The male cones of this plant which are certain species of the old composite genus *Androstrobus* were only recognized recently. This is not so much because it is rare as because it makes an untidy fossil. Anyone who has collected plants where they are abundant as in a coal-measure tip will have been forced to select the best. You reject duplicates and you reject the innumerable black bits that mean nothing and you go on rejecting them until one forces itself on your attention as a definite thing. These particular male cones reveal a good deal of structure and show half a dozen features characteristic of Cycad male cones. They differ in two. They have no stalks, but the Recent cones are always borne on stout erect stalks which raise them clear of the leaf crown. They seem to have been less substantial than the Recent cones, and indeed flimsy. I suggest they hung as catkins from tree branches just like the female cones.

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The seed of *Beania* is known attached to its cone, but the other organs are all found separately and they have been assembled in the usual way, on the evidence of association and on the evidence of agreement in structure. The first suggestion came from Nathorst early this century who noticed the association of certain seeds with *Nilssonia* leaves and then several others noticed similar association for various different species. It was Hamshaw Thomas who first pointed out that there was some structural resemblance between *Beania* and *Nilssonia*; and since then both association and agreement in structure have been noted repeatedly for several species in rocks of different stages of the Rhaetic and Jurassic. The structural agreement is most impressive for two Yorkshire species where each has its own specific characters running like a label through the suite of organs. There are a few bits of clinching evidence which are pleasing, though not important; for instance, the same kind of pollen occurs in the male cone as in the seed though that in the seed has germinated.

*Proposed reconstruction.* I have been slightly unsympathetic about the imaginary stems given by others to their restored Cycads, so it is only decent that I should offer one for their criticism (text-fig. 2). We can be sure the stem was fairly thick, I mean at least 2 cm., because the leaf base is broad; it was also bare and not covered with the bases of dead leaves like most of the Cycads. This again we know because the leaf base was cut off cleanly like the leaves of ordinary dicotyledon trees. In fact, the modern Cycad is unlikely to offer a good model. Instead I take a Dicotyledon tree with thick stems and large lanceolate leaves; the African Shea Butter tree *Butyrospermum* would do, and there are many others. The leaves are borne on the young apical parts of the stems and behind them are the hanging fruits; we will not follow our model farther since they are botanically unrelated. I believe it differs in another respect; the Shea butter grows in dry country but I think *Nilssonia* must, from its local abundance, have been a dominant tree of the Deltaic swamps or else of the river banks. So far as I know, modern Cycads never dominate such places.

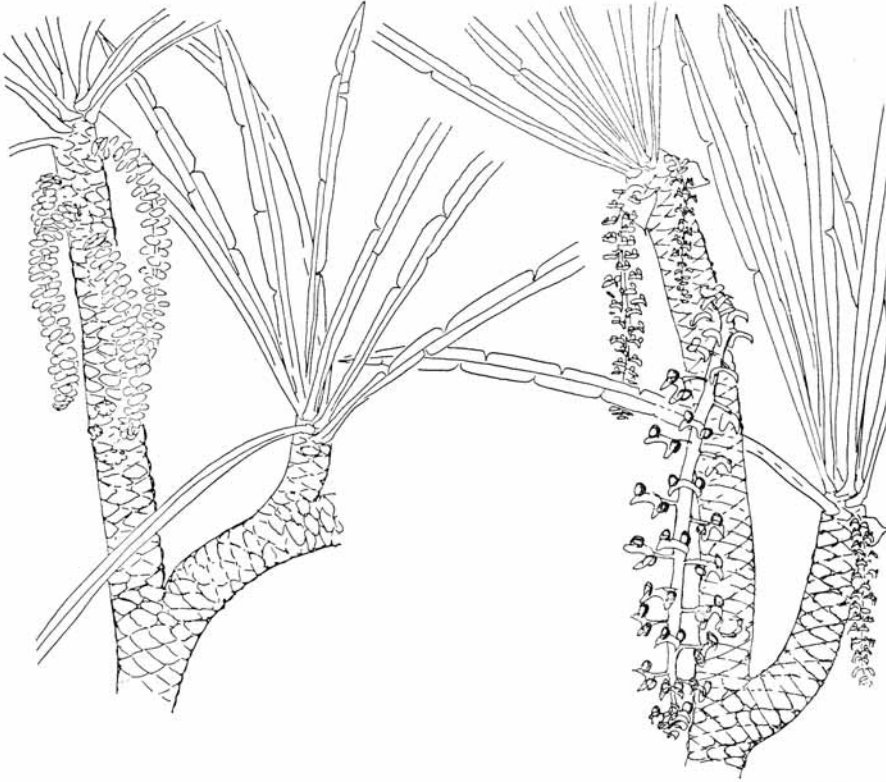
#### OTHER CASES AND SUMMARY

The final fossil Cycad, which qualifies for inclusion here, is one just described by Thomas and myself. This is the assembly of a leaf and a male cone, and each organ shows Cycad characters. The leaf is *Pseudoctenis lanei* and the male cone *Androstrobus prisma* and as usual they are put together on the evidence of association, in three Yorkshire localities, and on agreement in cuticle structure. In one respect it proves a little disappointing: it shows nothing at all new. The leaf looks exactly like the leaf of several Recent Cycads and agrees very well too in cuticle; and the rather massive male cone could be matched by a bit of the male cone of almost any Cycad. In the absence of any further information, it would be ridiculous to assert that the whole plant agreed with these living Cycads, but it could well be that it does.

There are indeed a great many leaves and some other fossils which have been classified as Cycads in the strict sense and on grounds which I would regard as reasonable. Some look very like the Recent plants, others are rather obviously different and the evidence that they are Cycadean is usually a Cycad-like stoma. Fossil leaves must be described even though nothing more is known about the plant, and they need classification if only for convenience, whether they are known merely from the coarsest facts of gross form,



or with fine microscopic details. It does not matter much if the classification is right, so long as it is reasonably stable and widely accepted. Indeed the improved classification, which results from microscopic study, is chiefly improved in being more nearly botanically correct; to those who will not bother to use a microscope it must be a perfect nuisance.



TEXT-FIG. 2. Restoration of plant bearing *Nilssonia tenuinervis* and *Androstrobus womnacotti* (left) and young and old cones of *Beania mamayi* (right). The stem is imaginary.

A good many genera of leaves seemed so convincingly like living Cycads when first described that they were named after them, but curiously enough most of these have proved to belong to the Bennettitales. The genera about which we now feel more confident (I think of those mentioned here and also such leaves as *Ctenis*) are not specially similar in gross form, though they agree well in fine structure. But such confidence about an isolated leaf merely means that the limited evidence we have points in a certain way and, even though many agree about it, the position remains the same. Are such leaves as *Ctenis* truly Cycadean?, this means are their undiscovered reproductive

organs and stem sufficiently Cycadean to be fitted into the general Cycad mould? I expect some will, but I sincerely hope they will not all, or else we should have reached the stage in Mesozoic Palaeobotany when no surprises remain.

I will now summarize. The fossil Cycads consist of a good many genera of isolated organs classified on more or less good evidence as Cycadales, a very few genera with two known organs and one genus with more than two organs. If we are right in our synthesis of these plants with two or more organs, and also right in our present classification of, say, half of the isolated organs (and I think it unreasonable to hope for more), then we can say that by Jurassic times the family had probably completed its evolution. It looks as though what happened since was the progressive extinction of important genera and with extinction the impoverishment of the whole family. The nine genera living today are usually placed in two subfamilies, one with *Cycas*, the other with the remaining eight. Both subfamilies were then differentiated, but there was also *Nilssonia* which is worthy of a subfamily of its own; there is nothing to suggest whether there are or are not other subfamilies. The known Jurassic genera are no more primitive than the living ones and they do not help at all in linking the Cycadales with any other family, and for this link one looks first at the Pteridosperms. If we are to find progressive evolution it must be before the Jurassic.

#### GENERAL CONCLUSIONS

Then I have some general points. I chose the Cycads to illustrate the aims of fossil botany today, but other families would have served instead.

The first point is that in fossil botany we have very broken knowledge. We have separate bits of knowledge about a very large number of separate bits of plants. These separate bits are the ones to which the fossil botanist gives names. Until recently the great majority were the names of leaf species, but now there is an uncontrolled flood of pollen-grain species. I have described quite a number of these one-organ species myself and they are useful and necessary, but their use is almost entirely for the geologist, chiefly as potential zone fossils. Botanically, they are not much good at all. To be sure they are classified, say as Cycads, and when classified are used as evidence that the Cycad family was represented at that time. Then their classification being accepted, morphologists consider them and use them as stages of evolution; but is the classification right? I am now sure that something like nine-tenths of the genera made by the older authors, who gave names implying Cycad affinity, are either mistakenly applied or very doubtful. Why should the ones that I put out hopefully and with an equal feeling of confidence prove right?

My second general point is that the great botanical need is to put together plants out of these organ species. Even a plant with only two known organs is of immensely greater value than the organs taken separately, and after this every item of additional information enhances the value of the whole. In the end, as we approach the whole plant, we get a thing which we can discuss in just the same way as the morphologist discusses his plants: he may consider single organs but he has the whole plant firmly in the background. To be sure there is a drawback; the synthesized fossil plant is the product of an argument based on circumstantial evidence and there is a risk of error. But as fossil botanists know, they have the risk of error always with them.

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My third point is that such work as a rule needs special material as well as special laboratory procedure. A preliminary collection *may* give you just what you want; but more likely it just offers a suggestion. It is the same with a collection made by someone else, perhaps years ago. It seldom happens that an early collector knew what specimen I should want to answer my problem today. All too often the missing key specimen is a small and unattractive fossil organ. Then if you want to use the evidence of association, you must go into the field and look and not rely on an uninformed collector. In fact, you must collect, work in the laboratory, and then go back into the field and collect selectively. There was still the tradition a few years ago that the fossil botanist should find his material in a Museum where it had been contributed by a professional collector, and I remember twenty years ago being advised by an old man that to try to collect for myself was a great mistake. Then, of course, the fossil botanist must be willing to do a good deal of hard work in the laboratory and to study the specimens minutely. Some may find this a drawback, but I have always found it the most interesting and rewarding part of my job.

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