NINETEENTH
SIR ALBERT CHARLES SEWARD MEMORIAL LECTURE
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THE STRANGE BENNETTITALES

BY
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TOM M. HARRIS

WHEN I was asked to give the Seward lecture I felt moved and I feel, moved now. You all know Seward's name as a great Palaeobotanist of the past but there must be many here who never met him. To those of us who were with him he was much more than a great scholar; he was a strong and cheerful fellow of warm good nature and intensely loyal. I loved him as my Professor and teacher, as Professor Sahni had loved him, just a few years before me.

I chose the Bennettitales for this lecture for several reasons. One is that Birbal Sahni wrote a distinguished paper on an Indian Bennettitalean forty years ago. He wrote distingushed papers on many subjects and in some announced startling discoveries. This paper on *Williamsonia sewardiana* was not startling but on the contrary gave us comfort. We had some general ideas about the plant that bore a certain kind of flower and a very abundant kind of leaf but our ideas were full of doubt. He gave us peace and unequivocal knowledge.

Then I think the Bennettitales are very strongly represented in the Indian Jurassic, more strongly than in either of the two northern floras on which I have mainly worked. In both of these I have spent about a fifth of my time on them and this is more than on any other family, but in India the fraction might be a third. It might be even more because your Indian Jurassic gives a wonderful opportunity by providing petrifactions, almost unique at their age. A good deal has been learnt from them and I am sure that more remains but that the work will be heavy and difficult. The reward will be what the worker deserves and will depend on his patience and deep understanding.

I call the Bennettitales strange because to me they do seem strange. I do not doubt that their strangeness is largely unreal and arises from confusion in my mind. There is not one kind that we know as fully as we have a right to know a fossil and of course we lack what can only be known by the study of a live plant. Instead we have incomplete information about several and scraps about hundreds. I am sure that if Nature had been kind and had spared us just one member of the class as she did for the Ginkgoales much of the mystery would never have been thought of. This survivor would be a plant so much studied that it might seem staid, almost dull. But we have no such plant; we know the Bennettitales as flourishing in the Middle Triassic and throughout the Jurassic and into the early or Middle Cretaceous and then suddenly and dramatically vanishing. Their known span is about 100 million years and during this time they were of major importance, at least in the fraction of the worlds vegetation that is known to us.

Part of their strangeness was created over a century ago when they were wrongly taken as fossil Cycads and though now corrected the error still haunts us. After all, we called the Mesozoic the Age of Cycads to balance those who called it the Age of Dinosaurs and a strong phrase holds the mind. Its effect was enhanced by the many Cycad names in the literature, you will find some dozen beginning *Cycado* — or *Cycadeo* — and nearly all of these genera that have been again studied are now anything but Cycads

Many are Bennettitales, some are conifers. These should not mislead. We all know that a scientific name is just a name, a mere word without implications. But so many scientific names do convey sensible and useful meanings that those that suggest wrong meanings mislead us.

I think particularly of *Cycadeoidea* a name rather older than *Bennettites* which is a synonym. Some prefer to call the class Cycadeoideales and wish that the rules of nomenclature required us to do so, but they do not. I keep to the old Bennettitales which is still more the familiar name for the class.

The class only became generally accepted in the early years of the present century but it might have been recognized may years earlier. There were Yorkshire amateur naturalists who knew about the flowers we now call *Williamsonis gigas* and in 1822 two of them figured a flower along with leaves which they regarded as belonging to the same plant. However, their account was so artless and unsophisticated that I suppose that no one outside their own circle was impressed. They thought the flower like the artichoke Cynara and it does indeed resemble it in many ways. Also in 1822 Williamson was taken by his father to collect 'Zamia heads.' Young Williamson was then six years old and does not say what he thought about the fossils but his father, a gardener must have been very familiar with artichokes which were then grown as a crop. These naturalists had little enough scientific knowledge of Botany and had no reason to be troubled by a Zamia plant producing an artichoke but there were many better informed Botanists who rejected the idea at once. They had not seen the field evidence; these worthy amateurs had no skill in presenting a hypothesis in a scientific paper and the idea was at once unlikely, to say the least. Later Williamson the son was educated as a Botanist and in due course became a Professor and must have learnt about living Cycads. However this did not divert him for he already knew about his fossils. He wrote a series of notes and short papers on this fossil culminating in a long one at the Linnean Society in 1871 At the same meeting Carruthers named the whole plant *Williamsonia gigas* after the father and the son. It was only then that the plant began to be widely accepted as a real thing and some continued to struggle against it. But it is pleasant to record that the great Brongniart was one of those who had been convinced by the specimens collected by the Yorkshiremen and even those who remained vigorously of the opinion that the Williamsonia flowers had nothing to do with the associated leaves conducted their disagreement courteously. If there is a moral in this it is perhaps that occasionally in science innocence is better than knowledge.

Though several contributed to the establishment of the Bennettitales, I think it was Nathorst who did most by his study of the cuticles of the Yorkshire flowers. Even Nathorst thought it advisable to link the Bennettitales and Cycads in a single class the Cycadophyta with which were included also a good many unplaced leaves. As I see it the Cycadophyta is not so much a class as a broad cloak which decently covers these two classes and all unplaced Mesozoic leaves which are of pinnate construction and are thought to be Gymnospermous. As such leaves become placed its practical value lessens.

As I see them the Bennettitales are distinguished from all other plants by certain definite characters particularly their gynaedium and the details of their stomata. It is true that similar stomata do occur in other plants particularly angiosperms but their leaves are otherwise different. Other Bennettitalean organs may have distinguishing characters but I think they would be harder to define and perhaps also less secure. Inevitably there are many fossils which are not known to show these characters but which are linked with the Bennettitales for more or less convincing evidence and so it must be with fossils.

The gynaecium perplexes me for several reasons and I will mention one which may seem trivial. Their seeds are often remarkably small for a Gymnosperm but were produced in very large numbers. In several species they were minute, no larger than a hair chopped into short lengths. Other kinds have seeds rather larger, about the size shape of uncooked rice grains. I can only think of two both rather early, where they are as large as sunflower seeds.

Tiny seeds are met in plants of various kinds of vegetation but today they are notably common in weeds of cultivation and plants which grow in open places where the seedling does not have to struggle in competition. If a plant needing open ground is to find its opportunity its seeds must be produced in great numbers and widely dispersed. You do find small seeded plants which cannot be called weeds, like the epiphytic orchids but these start in a kind of open place. Even some large forest trees like the poplars have tiny seeds but I think these start in clear spots in forests. The plants of established, closed vegetation, particularly the trees of high forest mostly have large seeds with considerable reserves that support the seedling till its leaves are above the ground floor.

Were the Bennettitales weedy plants? I doubt it and for reasons I shall give, I suspect many were forest trees. And were their seeds efficiently dispersed as would fit small seeds? — it is not at all obvious now. The tough armour round the gynaecium seems all against dispersal.

I will refer to the gynaecia I know best, those of *Ptilophyllum pecten* described well over a century ago and still to be found commonly in a classic Yorkshire locality. This gynaecium is round and reminds me of a litchee fruit in size and in the little swellings that mark its tough armour, though these swellings are of completely different Botanical nature, and instead of one large seed it contains a few hundred tiny ones.

You do occasionally find complete and intact gynaecia, detached as a rule but occasionally on stems These though prize specimens are plainly biological failures for they cannot have given rise to a fresh plant.

Far more commonly you find old denuded gynaecia, just the core with harder parts at its two ends and often too there are sheets of the detached armour, corresponding to bits of discarded rind of a litchee. But what I do not find is scattered seeds and they should be common. If they were a hundred times commoner than the bits of gynaecium they should be on every slab of rock. Now I must not build much on my inability to find a fossil even though I have sometimes looked hard. Still if I may build something, let me suggest that the gynaecium, also like a litchee, was delicious and some animal ate it, discarding the tough rind and stringy core. If it were delicious the edible part would be the soft stalks of the interseminal scales. I hope I may one day find fossil dung packed with these seeds as I have done occasionally for the Caytonia seeds, but cetainly I never have found one and till I do my suggestion has no support.

I am sure if I could have lived in the Jurassic along with this plant this would never have seemed a problem. No British gardener who grows strawberries would consider it a problem whether the birds ate his fruit, he knows they do and finding strawberry seedlings growing all over the place he never calls it a problem whether the birds distribute the strawberry seeds; on the contrary his problems are how to prevent these things happening.

The gynaecium was surrounded by stiff bracts as Williamson knew 150 years ago, sometimes these bracts persist as in *Williamsonia gigas* making it look like an artichoke but more often they fall off. These detached bracts are poorly characterized and show a considerable range of structure in a single flower. These facts are easy to understand but they make study tiresome. But in addition these floral bracts do present some little problems.

One is that the thicker bracts — the outer ones I think, corresponding to the edible outer bracts of an artichoke are mostly crossed by conspicuous wrinkles often marking out little squares. The thin inner bracts are smooth. Everyone is agreed that these wrinkles arose post mortem through decay and compression — and I have always subscribed to this. But when I wrote the text of this lecture, I felt ashamed of this empty opinion. Artichoke bracts are available and there is mud in plenty let me make a fossil and produce wrinkles.

At first I had no success but later I had a good deal more than I expected.

In my first experiment I took cooked artichoke scales because these are easily separated from the parenchymatous tissue at the base of the inflorescence, but before cooking this parenchma is almost as hard as wood. I failed to produce any of the peculiar wrinkles of *Cycadolepis* when these were rotted.

In the second attempt I dissected out fresh scales, and put these to rot and to assist I added some liquefied carrot tissue attacked by the Bacterium called *carotovorus*, a considerable pest in my garden. It rots many sorts of plant tissues by dissolving the substance of the middle lamella between cells. These scales were rapidly attacked and the whole of the edible parenchyma, just beneath the upper epidermis was liquid when the harder tissues, the epidermis and the sheet of fibres just above the lower epidermis remained intact. Mud entered the cavity just as it often does beneath the upper epidermis of *Cycadolepis*, but at this stage there were no wrinkles. However, wrinkles were easily generated by causing the tissues to shrink, drying does this and drying at higher temperatures causes progressively greater shrinkage. The most impressive results were obtained by putting the rotted scale between flat stones and baking it at about 400°C., the separate upper epidermis is strongly wrinkled but the lower epidermis which is still bound to the fibres remains smooth. At this temperature all parts have shrunk but the, detached epidermis rather more and it has only about 70% of its original length. The whole scale is black and looks exactly like a typical *Cycadolepis*.

I will consider what is the use and what are the limitations of such an experiment in a few minutes when I tell you about a second experimentally produced imitation of a fossil.

In the artichoke the outer bracts or scales are green but the thin inner ones are pale. In some other flower heads of Compositae the papery scales are brightly coloured and make the attractive flowers we call everlastings. Could they have been so in the Bennettitales? I think the outer ones were green for they have a liberal supply of stomata and stomata go very much with green tissues, but the papery inner ones have scarcely any stomata. What colour they had I do not know but they certainly could have made a large and handsome flower if they spread widely at pollination time and carried a load of pigment.

But were these flowers insect pollinated? Certainly there were flying insects in the Jurassic and no doubt these would visit flowers if they found it worth while. There are no special nectar secreting organs in the female flower but I see a possibility in the young ovules. These are continued to the gynaecium surface by little tubes the micropyles, and if the ovules secreted a sugary solution the whole surface would become sweet and sticky, inviting an insect to lick it clean. Certainly pollen arrived and was drawn down the micropyles, no doubt by the absorbtion of pollination drops as in many other plants. You can easily demonstrate pollen grains in the fossil seeds.

The pollen producing organs the androecium, also have their strange features. They are often large and rather fleshy but their substance is far less tough than that of most of the female flower. In particular their cuticles are delicate. This could be easily understood if the male flowers or the male parts of a bisexual flower fell off as soon as they had performed their function of offering pollen. On the other hand parts of the female flower would be needed for months as a protection for the developing seeds.

The male flowers and their pollen producing organs have a range of form and organization which astonishes me: the female flowers are almost standard. I am sure they will be the delight of those who will eventually produce a classification of the whole Bennettitalean plants. What their variety means I do not know and I do not intend in this lecture to talk about varied plant structure.

But I will refer to some points of biological interest. one of them arising through mistaken interpretation.

For about fifty years our text books have illustrated the pollen producing organs of Cycadeoidea. These were studied by Wieland from some rather unevenly preserved American petrified flowers In part their structure was shown with great beauty but in part it was thoroughly bad because the fleshy tissues had rotted. Wieland restored them as microsporophylls branching in the manner of a fern leaf and spreading at pollination time to make a handsome flower. It is easy to see from his photographs how he reached this conclusion. But it was wrong and his error was embodied in some superb Museum models in glass.

Recently Delevoryas has again studied Wieland's sections as well as fresh ones. It is now clear that the pollen producing part of the flower was a solid structure which did not divide into fern-leaf segments, and in fact never opened to expose its pollen but must have shed the pollen inwardly and then fallen off as a whole. Pollen must have covered the young gynaecium very thickly. Again the photographs support Delevoryas's conclusion and it would have been possible for anyone looking at Wielands, photographs to say — ' but surely his explanation is wrong '. No one but Delevoryas did so. I understand that it is hard to decide whether the little gynaecium under the pollen producing mass ever grew into the large seed bearing one which we know at the ripe stage. I find it easier to imagine this small organ as an abortive gynaecium, perhaps on a purely male plant and its function was to present pollen — for transport by insects I suppose — to functional female flowers.

Let me make it plain, I do not at all deride Wieland's work. If you are bold in palaeobotany you are sure, sooner or later to fall into considerable error. Wieland was bold and here made an error which was later corrected. Had he been cautious I suppose he would have got nowhere and that is much worse. I may mention that I fell into error in describing a certain Bennettitalean male organ but I was luckier. No one as far as I know took it up and before long I realized and corrected it myself. Wieland's error was important in that it gave a wrong idea about Cycadeoidea and to some extent about the whole class. Although Cycadeoidea is among the last of the Bennettitales its microsporophyll seemed to us or at any rate to me, as very nearly my ideal of what the primitive Bennettitalean should have. Now I can say simply, I have no idea what is the primitive type but I am sure Cycaeoidea is one of the most specialized.

I have referred to the female flowers of *Ptilophyllum pecten* from a classic Yorkshire locality. The male flower found there also has its strange features. Nathorst displayed its organization sixty years ago so well that no one has been able to add much to his account. He showed that its stiff rays bore pollen sacs that easily fell off and that in the centre of the flower where these rays unite there are bodies like the pollen sacs but rather smaller and these do not fall off. Very reasonably he called them abortive pollen sacs. They contain no pollen but when you prepare them they yield much resinous matter in shreds more or less united into a solid network.

Nothing useful had been made of their organization but I imagined the solid internal residue might have been produced by chemical changes in oily contents to a solid and stable resin. I now suggest as a result of some experiments that it is more likely to be produced by the modification of cell proteins, perhaps together with tannin.

I macerated various plant tissues including oily seeds and a number of nectaries in the usual way for preparing cuticles and found no encouraging indications from the cell contents. But then I tried a trick which is hard to defend except that it seems work—I gently baked these plant organs, initially in a domestic oven, at temperatures between 300°C and 400°C The tissues darken but they are far from being charcoal, that is elemental carbon at such temperatures, but are modified organic materials. The cuticle can still be isolated. What interested me was that the cell contents of the nectar-secreting cells of various nectaries had now become considerably resistant to ordinary maceration—Schultz's mixture followed by ammonia, while cellulose and lignine walls dissolve as usual I got my best results with the large nectaries on the leaf stalks of *Ricinus* and here the secreting cells are packed with dense protoplasm and also with red anthocyan which on death combines with the proteins and stains them. I cannot say if it helps stabilize them, but as a tannin it may do. I may add that these cells are very rich in protein but have only small amounts of carbohydrate and very little oil indeed.

What possible justification is there for baking these plant organs?. It is certain that the Yorkshire fossils and most others deposited in wet muds never met such temperatures for millions of years after they were deposited. The only justification is that it quickly produces effects that seem to simulate the chemical and physical changes occuring very slowly in normal preservation, the processes called diagenesis. Simulated diagenesis is a phrase that makes a casual exercise sound better. I have used baking before. Years ago I was perplexed by the preservation of internal casts of the stone cells of Caytonia seeds – and these casts resist Schultz's solution almost as well as cuticles, but they are not chemically the same as cuticle for unlike it they subsequently dissolve in glycerine. After a good deal of experimentation I succeeded in producing similar internal casts of stone cells from cokernut shells when I first baked them and then macerated them.

I think it fair to say that I have given a little support even if only by doubtful analogy to my idea that these organs which Nathorst rightly called abortive pollen sacs may also be functional nectaries that attracted pollinating insects. It is indeed possible that they were functionless, but I think truly functionless organs are not common in plants, on the contrary if you look with willingness to see, the organ which had been thought functionless and vestigial does perform a vital biological function but one that is different from its ancestral function. But that is not to say that they had the particular function of nectaries.

You have heard me tell of two experiments in which I have tried to produce something with the characteristics of a fossil plant organ, and this is as near as I can get to an experiment in paleobotany. Both involved baking, an unnatural process. It is important that I should not adopt my findings as discoveries, but should view them in a detached way, and this I find easy to do. They are just the sort of exercise a rather brash young research student might think of, carry out without my knowledge and then surprise me with the result. I am sure the first thing I would do would be to laugh, and then having found that he had only spent a very few days of his time on each, I would mildly suggest he should try to think of other such experiments — but only ones which might cost him just two or three days' labour

I must not omit the leaves which, as usual, are by far the commonest organs found fossil. They seem strange in entirely different ways. Nature has been strangely kind to Palaeobotanists. She has endowed them with a good thick cuticle which shows specific characters remarkably well and also with a family character which differentiates them from other Gymnosperms. This family character is the well known arrangement of subsidiary cells next the guard cells, an arrangement that is nearly always easy to recognize. I can think of no comparable gift of Nature to the Taxonomist — a gift which as far as I can see we have done nothing to deserve — so I look on it with certain amount of suspicion but it has never been proved to have misled us and till it is proved unsafe I certainly shall use it. Then the Palaeobotanists of today have been remarkably lucky in the wisdom of the men of the past. They recognized that the leaves were just leaves and made a classification suitable for leaves and did not deceive themselves in supposing that they were classifying whole plants. The Bennettitalean leaves could be arranged in a continuous but elaborately branched series and as far as I can see this series could have been arbitrarily chopped up into units to be called genera in more than one way and the number of these genra could have been small or large, even a hundred. In fact they made just a few, eight and one or two others used occasionally. Each of these eight has boundary problems where authors disagree particularly with species whose leaves differ considerably between their tops, middles and bottoms. If we had a hundred genera, boundary problems would be apalling as they are in the Conifers.

I will turn to the stems and that leads me at once to the problem — what did a Bennettitalean look like while it was growing the in what sort of vegetation did it grow?

Here the genus Cycadeoidea has dominated our ideas and several people have reconstructed landscapes with Cycadeoidea growing fresh and green. Now as far as I can see their pictures of Cycadeoidea (apart from the flowers) cannot fail to be accurate, but I feel doubtful about their setting. I see Cycadeoidea as looking very like theC ycad Encephalartos, and growing, not in a lush forest but in rather stunted and dry looking savannah. Savannah of today is covered with grass or grassy sedges and these were plainly not around the Cycadeoidea trunks but there could have been a low scrub of Conifers and herbaceous pteridophytes. The vegetation of the uppermost Jurassic and Lower Cretaceous when the Cycadeoideas were flourishing gives me the impression of more aridity than does the more lush vegetation of the Lower and Middle Jurassic; (I speak chiefly of N. W. Europe). Now as far as I have seen it, savannah is not merely controlled by a climate which is dry for some months of the year; it is controlled to a large extent by fire in the dry season and without fire, most savannah changes to a dry form of high forest. Because of fire today, every year forest is being replaced by savannah and the savannah is turning into thin impoverished grassland. Could Cycadeoidea have been a plant of fire savannah as Encephalartos is where I have seen it ? It is possible for fire occurred and in some places was frequent long before there were men. It would be worth looking for evidence, a scorched surface on Cycadeoidea trunks and fossil charcoal or fusain round about.

I think the older Bennettitaleans were very different from Cycadeoidea and we have been given pictures of two rather different sorts of plant. There are ones looking like palm and also like woody shrubs. For the first we have Williamson's old drawing of *Williamsonia gigas* and Sahni's of *Williamsonia sewardiana* made a century later. Both have stems just a few centimetres thick and they are really very similar, particularly if we made Williamson's look less stiff. I know that some of the stems of his plant were not straight but curved gently. What we do not know is whether the stems arose, perhaps as a single plant from the ground or perhaps branched below, nor do we know how tall they were. I prefer to imagine them as growing like one of the slender palms which branch at ground level and only grow a few metres high. Such plants should make a convincing thicket on the bank of a deltaic river and provide plenty of material to be preserved as fossils.

The second kind of plant was restored by Nathorst in 1909 for *Wielandiella* and by Thomas in 1915 for *Williamsoniella*. Both have leafy stems a centimetre thick and their leaves and also their flowers are smaller than those of *Williamsonia gigas*. The leaves fall off leaving a clean scar. The stems of both branch freely by one or usually two buds growing out below the flower. Both were considered as shrubby plants, I suppose on the idea that the parts known and drawn in the restorations represented most of the plant. But they could have been the end branches of large trees.

More recently I drew a restoration of the common Yorkshire species of Ptilophyllum, *P. pecten* and *P. pectiniodes* as branches of trees and here I had some evidence though less than I wanted. Along with the leafy and flower bearing stems a centimetre thick there are rather larger stems with only leaf scars and then a series of thicker and thicker stems and finally great broken slabs of bark many centimetres wide which must have come from large trees. The surface changes as the stems enlarge, leaf scars are no longer seen but lenticels are formed in a characteristic pattern. I pieced them together as a series but I lack supporting microscopic evidence. Unfortunately the stem cuticle is lost early and replaced by a cork which is seen only as little round cells without much specific character. So it may be all wrong.

If *Ptilophyllum pecten* was a tree the other two with very similar branches could also be trees and trees form and can dominate a forest. I picture them as making forests on the flat but moderately dry land beyond the river banks and here competing on equal terms with Conifers and Ginkgos. This would explain the enormous local abundance of their leaves, often by far the commonest things in the river mud that became the deltaic rocks. This may as I said be wrong and you may find it nonsensical. But to me it is less nonsensical than seeing them as an undergrowth under a high forest of Ginkgos or Conifers when their leaves are presently to be preserved in far greater abundance. In Yorkshire, Conifers and Ginkgos do sometimes dominate a plant bed hut Bennettitalean leaves do so more often.

The things I have told you about are ones which happen to interest me as problems, another man could give you an entirely different set of problems. They interest me as problems because there is a ceriain conflict of suggestions from different lines of thought. But they all refer to matters which are potentially soluble because in their day they were matters of fact. For example *Ptilophyllum pecten* **was** a tall forest tree — or it was something else; its flowers were pollinated by insects attracted by bright colours and nectar or they were pollinated in some other way; its seeds were distributed by an animal that ate the ripe fruit, or again in some other way.

But there is another set of problems which I would not be able to answer with certainty even if I lived in the Jurassic along with the Bennettitaleans. I refer to what was their origin, what are their nearest relatives and why were they presently to vanish dramatically? — other Gymnosperm families did not vanish suddenly but gradually lost ground. These problems are fair subjects for speculation in a lecture or for scientific fantasy but are beyond the scope of this particular lecture.

I will now end with some general remarks which might indeed have made my introduction. Some of you I am sure had been hoping for solid and even important new facts but what I have given must seem as thin as air and I am not penitent.

What I have tried to do is to give these very dead fossils vestiges of life. Once they were very much alive and solved the problems a live organism must solve. If I have made lots of surmise, I have at least kept the uncertainty of surmise before you. If my surmise proves wrong, then I hope research will soon establish fact and my surmise will be forgotten and if rerearch establishes it as right, my surmise will at once be valueless and forgotten. But I do hope you will remember in your own research that all fossils were once alive even if after sincere and devoted effort you can give them no life at all but only detailed anatomy or formal classification. Your failure may be unavoidable and wholly excusable but failure it will be.

I really think a lecture should deal with suggestions, feelings for things and with principles. If you want fact go to the printed page and if the writer chose his words carefully, read him carefully. The lecture is less like a text book than a sermon and a sermon should, I take it, be concerned with morals.