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THE PTERIDOPHYTES OF THE ANCIENT WORLD

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I am happy to speak about pteridophytes because I like them. I grow all I can outdoors in my garden and I enjoy them as fossils. A pteridophyte fossil often tells you more about the whole plant than does any one specimen of a higher plant.

I will try to give you a general picture of the part played by pteridophytes in the world's vegetation through time, but this alas can only be of the fraction of the vegetation commonly preserved as fossils, mainly plants growing on low ground near the mouth of a river. I shall avoid burdening you with generic names and with the intricacies of morphology. And I shall not worry whether the pteridophytes are of the nature of a huge family, all descended from a common ancestor itself a pteridophyte or whether the major classes sprang from distinct algal ancestors. I take the pteridophytes as all the vascular plants that stand between two grades of reproductive evolution. At the bottom are plants producing similar, freely dispersed spores. At the top are plants with extreme heterospory, the single megaspore retained in a way that almost brings it within the definition of a seed. We have fossils at the top boundary whose classification as pteridophyte or gymnosperm can be debated but there is nothing near the bottom boundary for no alga, living or fossil, is at all suitable as a pteridophyte ancestor. Of course, ancestors can be imagined but in this lecture I keep to real things.

Many palaeobotanists hold that the first fossil pteriodphyte that they can accept is the little plant called *Cooksonia*. It occurs rather widely in rocks dating from just before the Devonian period at about 400 m years ago ; these rocks are placed at the end of the preceding period—the Silurian. I will give you a time scale of world history drawn as a clock, I have compiled it from well known publications, but frivolously, have made it more clock like. I start with an arbitrary zero and the 12 hours are 500 m year intervals and I take time forwards rather than looking back as do my source authors. You will see the fossil record, in the ordinary sense begins at just before 11 o'clock, and *Cooksonia* appears about 170 m years later.

There are indeed a very few older fossils that have been claimed as land plants but the evidence does not exclude their being animals. The time, 170 m years since the early Cambrian, would seem ample for algae to migrate from the sea to rivers and to land since they seem to do it rather easily today. But here I meet the uncertainty basic to Palaeobotany.

If you follow Harlan Banks who has done as much as anyone on early land plants you will hold that there were no land plants before the middle Silurian, in fact no land life. You will be in good company but there is another side and if you read a paper by Gray and Boucolt in Lethaia for 1977 you will find a vehement attack on Bank's views. The question is what do we make of the tiny scraps obtained by disintegrating rocks. Many look just like scraps from modern plants, pteridophyte or gymnosperm tracheids, spores like those of pteridophytes, pollen like those of gymnosperms and angiosperms, some like those of living genera. I fully accept the determinations but I am unsure about their origin and just refuse to accept a pollen grain from a living monocotyledon in the Cambrian. I am confident that it is out of place, but this does not affect other records, each should be judged on its merits, a thing I have neither the competence nor time to do. So I stand unsure of my facts right at the start of my lecture. I can and shall base my talk on *Cooksonia* as the start. I could give a very different lecture with plants of varied kinds waiting unseen like actors off-stage until their call came and then stepping onto the stage, a delta marsh, *Cooksonia* being meerly the first on stage. I keep this alternative in mind as a possibility and I make other choices but spare you details.

But even if we agree with Banks that something not much earlier than *Cooksonia* was the first land plant and before it the land was desert, a strange damp desert, we want to know why. Here the cosmologists come to our help, but since their conclusions differ I accept the one that gives a convenient model of the early earth. So we will take the earth model of Berkner and Marshall, 1965. They, as indeed others, give the early earth no free oxygen, but very gradually they make photosynthesis in the sea provide oxygen, at first all used in oxidising reduced materials, but then providing free oxygen in the waters when for the first time animals could become large enough and robust enough to form the earliest Cambrian fossils, and by 170 m years later the sea had given enough oxygen to the air to oxidise the rubbish on land. Finally in the Silurian there was free oxygen in the air and with it ozone was formed in the upper atmosphere and with that a screen from lethal ultraviolet light and with that a possibility for such life as wanted to emerge from the waters where they had been safely screened, to survive on land. Certainly a good many kinds of land life, animal as well as plant, first show themselves as fossils in Devonian time.

I return to *Cooksonia*, we know it poorly. But it is much like a far better known Devonian pteridophyte, *Rhynia* which you will find in text books. *Rhynia* has all that *Cooksonia* has and more information too and I will graft this information onto *Cooksonia*. *Rhynia* has a basal part creeping in the soil and bearing absorbative rhizoids, like root hairs. Its vascular core of tracheids has a sheath of delicate cells which may well be phloem. The cortex has intercellular air spaces and its outer part looks just like photosynthetic tissue. It had an epidermis and cuticle which made a complete cover apart from normal stomata. Its massive terminal sporangia had thick walls which look suited to open hygroscopically when dry and disperse the spores, completely normal looking pteridophyte spores.

After *Cooksonia*, it seems that new features in Devonian plants appeared one after another in quick succession. Plants with lateral sporangia and small lateral leaves appear and in some the leaf was below the sporangium just as in *Lycopodium*. Branching in *Cooksonia* was by equal dichotomy, but soon lateral branch systems of limited growth appear and their branching tends to be in one plane ; they are like large leaves. Secondary xylem appears and soon there are trees. Fertile branch apices become specialised as stalked sporangia and these may be associated in organised groups. The spores themselves, simple in the earlier plants, become specialised in form, and then in the same plant one finds some sporangia with normal spores, but others with fewer and larger ones. This begins to mark the doom of the pteridophytes for by the end of the Devonian a few plants were producing seeds, that is organs with a single large magaspore retained in the sporangium. I said doom, but it is doom of a special kind; the pteridophytes were producing advanced descendents which as seed-bearing trees were to replace them. Since to taxonomists these are gymnosperms, they are not pteridophytes, to the loss of that class.

I see Devonian vegetation, as the pteridophyte climax. They were of several classes but they were often hard to distinguish as befits ancestral forms. But by the end there were clearly lycopods, Equisetales with whorled parts, fern allies, and a group called the progymnosperms, which seem set apart by their name but as free sporing plants are clearly pteridophytes but with this distinction. Other pteridophyte families produced secondary xylem and seeds but those families later vanished. It seems likely that the progymnosperms were successful as the ancestors of later seed plants.

The noblest and best known of the progymnosperms is *Archaeopteris* which has the wood called *Callixylon*. Restorations make it a fine forest tree and it is easy to imagine its timber as an economically valuable softwood, unlike that of the tree lycopods and Equisetales. But its reproduction was surprisingly backward, the sporangia were all much alike, but some produced fewer and larger spores and its foliage was by no means fully organised as a horizontal leaf, it may be compared with the flat branch system of one of the cupressaceous conifers.

Professor Chaloner who has documented the appearance of fresh morphological features in pteridophytes through Devonian time has commented on our fascinating difficulty of classifying Devonian genera. It is good to classify, besides its convenience it displays awkward ignorance and may invite correction of error. If in the Devonian, pteridophytes were evolving rapidly from a very few progenitors we would not expect them to form well defined classes but to show resemblances to one another. The great families we meet later are clearly distinct because as we suppose, each is descended from a di - tinct early plant, one of the very few fortunate enough to have descendants living in a later era. He pointed out to me that it is hard to distinguish a progymnospeım from a fern, taken in the broad sense. If the possession of secondary xylem is the distinction then *Botrychium* though widely taken to be a fern qualifies as a living progymnosperm.

Both the successive arrival of new morphological features and the convergence or fusion of early pteridophyte classes are hard to explain on the idea that land plants were around long before the Devonian though only represented in the fossil record by dispersed microfossils. As I indicated, extreme supporters of this view consider that not only pteridophytes, but gymnosperms, even angiosperms were waiting off stage. I said 'hard to explain', I did not say 'impossible'. We have brains to get out of difficulty with and hard thought would provide some solution to that problem, possibly many solutions. But I will not give my thought to it because I have plenty of difficulties which I am sure are real.

Since as I said the Devonian marks the climax of pteridophytes the rest of time marks their decline, but still the pteridophytes fought back. Their early enemies were the Gymnosperms which as I suppose gradually captured the forests and extended their empire to all places where a tree could grow, but the pteridophytes were left in possession of the next layer. Then came the disastrous rise of the Angiosperms late in the Cretaceous. They eliminated the Gymnosperms from much of the worlds forests and but that may not have mattered to forest pteridophytes. But early in the Angiosperm conquest they produced aggressive herbs, the grasses were the worst, and these all but eliminated pteridophytes on unforested land. So now they must fit in where they get a chance, in the shade of damp forests, in temporary habitats like rock cracks and tree bark where their small spores in vast numbers help them to make an early start, but very rarely are they dominant plants in a good situation. But the story is not unrelieved decline.

In the Carboniferous there was one of those widespread climatic changes which I accept without understanding. Over large areas in the North at least, plants made phenomenally lush growth. As usual we mainly know them on deltas where land tended to sink beneath the sea and in shallow water the Equisetales were supreme and reached their highest development in size and morphological diversity. I see them as something like the giant bamboos of the tropics, but their secondary wood could have supported even taller plants. Just a few achieved seeds, but these highest members perished along with many less advanced.

On damp land, but perhaps seldom under water the *Lepidodendron* and *Sigillaria* trees were certainly dominant, there are a few places where stumps remain and they were crowded. I cannot compare them with anything because there is nothing I know like one. May be *Sigillaria* was slightly like a palm in its tall trunk, but not *Lepidodendron* which branched and its smaller shoots were like some conifer. But though tall trees they were more like giant herbs. The central wood was small, just enough to conduct water. Round it was a spongy cortex and then a hard and massive ring which was the trees sole support.

As far as I can see, *Lepidodendron* grew from a *Selaginella*-like megaspore almost to full stature, then it branched into progressively more slender branches and then it coned—and died and its fallen remains and especially its spore coats became the coal of Europe and N. America.

On land just slightly drier, I imagine ferns and pteridosperms in competition, under a canopy of *Lepidodendron* trees. But most of the drier land was already the territory of the gymnospermous Cordaitales, and then as the climate became drier of conifers.

This ends pteridophyte glory. Climates became drier and the tree lycopods vanished but where there were swamps the Equisetales still prevailed. But they were progressively reduced, that is to say the largest stems at each peirod are narrower than at the period before, but the smaller kinds continue, to this day.

I wonder why I suggest that gymnosperm trees became increasingly competent at growth in shallow water and as they did so they captured the territory of the larger Equisetales. In the early Mesozoic there are still some resembling *Calamites*, but their stems are less woody. There were at first very large kinds of *Equisetum* with reed-like stems that were not woody at all. I believe they conducted water through the protoxylem canals as does a modern species. And as time goes on the largest *Equisetum* stem of each period gets smaller—nearly 20 cm wide in early Mesozoic, then 10 cm, about 5 cm in the Cretaceous and now not much more than 1 cm. But throughout there were kinds with slender stems.

I should refer to the Southern half of the world, Gondwanaland, about which everyone here may know more than I. I merely say it offers another of the great climatic mysteries by having an enormously widespread ice age and then gymnosperm dominated vegetation, first of *Glossopteris*, then of *Dicroidium* which in their day provided great coal fields. There as in the North, the pteridophytes were in a subsidiary position.

In the North a desert climate prevailed over the part of the world I know in the later Palaeozoic and early Mesozoic and when I next see plants, at the outset of the Jurassic, it is a vegetation of varied gymnosperms, I imagine all of them trees or palm-like. Ferns and lycopods must have been very abundant in the undergrowth for fern leaf fragments and *Selaginella* megaspores are extremely common. Occasionally, I can imagine a plant association, of a particular conifer with a particular fern for I find their fragments together again and again.

As time goes on in the Jurassic there is again a drying of climate, but not to cause desert. Rather it would seem to be a seasonal drying as in N. Africa near the Mediterranean sea where there is a pleasantly cool and rainy season for a few months when plants grow and animals and men are happy and then several months of hot dry Hell. Much of the modern world has such a climate and wherever it prevails there is a terrible fire risk. Since nowadays there are people everywhere fires start often and the result is destruction or damage to the kinds of plant with permanent parts above ground, trees and shrubs and very great advantage to plants resting below ground, the herbs and especially grassy herbs. I had not mentioned ancient fire, but I believe it happened occasionally throughout the period when there was vegetation enough to burn and its cause was one that sometimes starts fire today, a lightening strike without accompanying rain. This is rare in England but I understand common in some Californian mountains. The evidence for fire is fossil charcoal, called fusain, a very common material in plant bearing rocks. I have met it in all the main floras I have studied.

But the earliest suggestion I know of an important effect of fire in favouring herbaceous pteridophytes is in the English Middle Jurassic. There is one species of fern, known as *Phlebopteris woodwardi* but I now suspect it would be right to include it in the living genus *Matonia*. Fragments of its leaves are common and almost all, well over 99% are preserved as fusain, but the ordinary form of a leaf compressed to a homogeneous film of coal, but preserved with every cell separate and still with an open cavity, as in wood charcoal. There are layers where charred bits of this fern and conifer wood charcoal are the only fossils and I suppose we see something like the ashes from a modern English heath fire. This is land which would become forest if left but it is burnt when dry enough, particularly in a dry period of winter when the dead leaves of the bracken fern *Pteridium* burn fiercely. This causes no harm to *Pteridium* but destroys its competitors.

This is unimportant in the Jurassic but I believe becomes very important in the English Lower Cretaceous where the vegetation suggests a more severe dry period, though the rains were enough to support forest. By far the most widespread fossils of a size you can see of the English Lower Cretaceous are charred fern leaf fragments. A peculiar fern called *Weichselia* predominates, but there is also a *Gleichenia* and a fern closely allied to *Matonia* ; *Weichselia* is a distant ally of *Matonia*. I did say the commonest fossils of a size you can see ; in fact the commonest fossils you can recognise microscopically are spores and pollen grains and the proportion of pteridophyte spores to pollen is high. Very commonly these charred leaf fragments occur without any charred wood at all as though they rather than trees fromed the vegetation of a district.

I picture the English Lower Cretaceous landscape as broad valleys and low hills, partly forested but partly clothed in herbaceous vegetation. In the lower Cretaceous when there were no Angiosperms known to us, the herbs had to be pteridophytes as indeed at previous periods. The open herbaceous vegetation was maintained and saved from becoming forest by being burnt every few years. I imagine a rather brief wet season when the ferns grew one or two metres tall and then as the long drought began they spored and their leaves withered but remained standing, the equivalent of a grassy savannah in its drought. The next rainy season began with high winds and electric storms. A dry lightening strike on the scorched fern leaves started fire, as it does today if there is no rain and the wind spread the fire widely. The fern plants did not suffer, their live rhizomes were safely below ground but any young gymnosperm trees were burnt off. And so there was a balance between forest and open vegetation, with the forest in the damper places, steep slopes and valleys but herbaceous ferns over much of the flatter land. It seems hard to think of ferns as the dominant plants of dry country but I feel sure that the reason why they show now so poorly in such vegetation is that the herbaceous grasses fill it more efficiently. Even today there are a few pteridophytes in dry regions and it is significant that they grow in the driest spots in these regions. In the Canadian prairie there is a small perennial *Selaginella* which is common on over-grazed land ; its short growth protects it from grazing and it endures the long freezing winter and then the very dry sunny summer. On the West Coast, in a better climate where the winter is mild and rainy, but the summer dry there is another *Selaginella* which grows on bare rocks and sometimes on house roofs ; it also just endures dessication like a moss. They escape competition but one day perhaps there will be an angiosperm that takes over these miserable habitats.

I will not attempt to deal with the fate of the pteridophytes in the Upper Cretaceous and Tertiary, once there were tree, shrub and herb angiosperms their position on land may have been much what it is today, fluctuating with climate.

But why are grasses more successful as Savannah plants than ferns and lycopods ? I do not know. This is only one of a large number of extinctions ; the most famous is the extinction of the dinosaurs and that is one that has caught the imagination of both scientific and popular writers. I cannot imagine the little mammals that were around at the time the dinosaurs vanished vanquishing them in battle, rather it seems that the dinosaurs vanished and rather later birds and then mammals took their place. The common statement that a class failed in competition with its successors is glib, but of course it may be right.

The replacement of the Mesozoic vegetation of gymnosperms and pteridophytes by one in which angiosperms was dominant was not quite sudden. We first meet angiosperms as rare pollen grains among hundreds of gymnosperms grains in the Lower Cretaceous. Then such pollen become common and then higher in the Cretaceous and a few million years after the early pollen you find leaves, seeds, woods, all parts of angiosperms. It is however sudden in relation to the very gradual changes that occurred through the Jurassic and Lower Cretaceous.

Any suggestion that a fern, such as a Cretaceous *Gleichenia* is a less efficient Savannah plant than some grass demands test by an experiment, but I have no idea how to frame the experiment. I have introduced many wild plants into my garden, pteridophytes and angiosperms. There is no general difference, some of each class fail altogether, some grow poorly, not liking my soil and climate but some are very vigorous and soon become a nuisance and this has no very obvious relation to the climate where I collected it. A *Dennstaedtia* has spread far too widely by rhizomes, it is North American ; certain small ferns from the west of England spread too widely by spores and those too must be treated as seeds. But both are in my garden where natural vegetation, perhaps oak trees and stinging nettles are suppressed by me.

I find it hard to be cheerful about the prospect for Pteridophytes in the future, man made world. Clearly the tropical rainforest may soon be represented only in herbaria and printed accounts, but of course there will be pleasant places made by man and they will be what our descendants will enjoy, but how many pteridophytes will be there ?

I end with an atom of hope. One form of land which is certainly not vanishing is the City suburb. I had a home in a suburb and grew ferns including the charming little *Cystopteris fragils* which is common on limestone in the damp West but is not native near London. Later I left and my garden was demolished. But then on a brief return, I saw on a neighbours wall where rather disgracefully water ran down from the roof, several vigorous young *Cystopteris* plants were established. The spores must have been blown two hundred metres ; it has colonised suburbia.