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PLANT RIDDLES IN THE ROCKS—THEIR CONTRIBUTION TO EVOLUTIONARY STUDIES

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IT is indeed a privilege to be here on this occasion when we honor the memory of two of the century's great botanists. I should like to offer a few informal words of tributes from my own brief but pleasant association with Professors Seward and Sahni. On his visit to the United States in 1948 Birbal Sahni spent several days at my University in St. Louis, sharing his knowledge and ideas with us; his interest in our research students and the generosity he displayed in discussing their problems with them will long be remembered. A memorable incident of my student days in England reflects the same helpful consideration that Professor Seward offered to junior colleagues embarking on a life-study of fossil plants. On several occasions, during vacations at Cambridge, I studied the fossil collections at the British Museum, working directly over a laboratory occupied by Professor Seward. One morning he brought in a specimen from the Mull Flora, apparently a liverwort, but the precise identification of which was giving him some trouble; to my surprise he asked for my opinion. I am not sure that I could have greatly aided him, but it was a gesture from which I derived considerable self-confidence at a time when it was rather badly needed.

The paleobotanical record at best offers us but fleeting glimpses of the landscapes of the past, yet so many remarkable discoveries have been made, particularly in the past half a century, that it is no longer possible for students of the modern flora to ignore the fossils. In particular, our concepts of evolutionary trends in the pteridophytic groups (the ferns and others that used to be known as their allies) and gymnospermous plants, have been profoundly altered.

One of the great contributions of the fossil record has been the revelation of plants, so unique by comparison with living ones, that their classification is uncertain or quite impossible. There are many isolated individuals as well as major groups that fall in this general category, which I refer to as "plant riddles". The question may be asked with good reason: "Why bother with plants whose affinities it is difficult to even guess at?" There are several reasons:

They tell of the great complexity of the plant kingdom and of how much has passed across the earth's landscapes in the last half a billion years.

As these unique, and at first isolated, bits of information accumulate, they complicate the task of understanding racial developments but lead us along paths that must inevitably be explored.

Finally, it is one of the great thrills of paleobotany to encounter a strange message from the past, perhaps undecipherable at first but quite clearly pointing the way into unfathomed depths of knowledge. It is not unlike the hope we entertain today that we may one day detect messages from other planets — these too must come out of the past and cover wholly new vistas of experience.

It is, therefore, my intention to consider certain of the plant riddles, to show how some have been fitted into an understandable pattern, and to suggest the significance of others even though their taxonomic position is still enigmatic. It may be emphasized that we are not dealing with mere curiosities; at least I shall try to avoid fossils that might be so regarded.

There has been a surge of interest in recent years in the problem of the age of our planet

earth and the way in which life became established on it. We are still a long way from understanding the ultimate beginnings but a landmark in this misty area of research, in which satisfactory evidence is so hard to come by, stands out in Tyler and Barghoorn's discovery of structurally preserved, apparently thallophytic, plant remains in a southern Ontario (Canada) chert which are dated as being 1700 millions of years old. Numerous presumed algae or alga-like structures have been reported from very ancient rocks but the Ontario fossils are structurally preserved and although they have not been precisely classified, they indicate quite clearly that plant life was established at that early date and had been for some time previously.

There is a long and perplexing gap between the point in time when these filamentous Ontario fossils lived and the establishment of woody plants on the land in late Silurian and early Devonian times. If we take the start of the Silurian as approximately 350 million years ago, the gap is in the vicinity of 1350 million years. Why were land vascular plants so slow in becoming established ? A few fragments of information have accumulated recently which begin to close the gap:

Several years ago Kryshtofovich described some spiny shoots under the name *Aldanophyton antiquissimum* from the Middle Cambrian of Siberia; these have been rather generally accepted as representing a lycopod but since sporangiate organs and vascular tissue are lacking no such precise classification is warranted.

Next, the reports of Indian and Soviet botanists of Cambrian spores, some of which are thought to represent vascular plants, are suggestive of a land flora at that time.

Perhaps the most convincing, if indirect, evidence that the lands were to some extent clothed in a low-growing vegetation in the earliest Paleozoic comes from the diversity of land plants that are now known to have existed in the Lower and Middle Devonian. The psilophytes have been the subject of much discussion in recent years and it is not necessary to review the subject in detail. The essential fact is that as our knowledge of the diversity of the Silurian and Devonian vascular plants expanded, it became apparent to many that they could not all be reasonably called psilophytes. If we start with *Rhynia* as a typical psilophyte, then what are we to do with fossils such as *Trimerophyton* with its trimerous branching; *Zosterophyllum*, *Bucheria* and others with their terminal spikes of sporangia; the strange *Gosslingia* from Wales with apparent sporangia scattered laterally along the branch system; and *Yarravia* from the Silurian of Australia with its terminal synangium.

There are even greater riddles than the diverse assemblage that, until recently, was gathered together in the Psilophytales; I refer to fossils such as *Nematothallus* and *Prototaxites*. It may well be that they are, as most botanists seem to believe, far off the paths that led to the dominant groups of vascular plants of the later Paleozoic. Yet these paths are so numerous and so devious that I hesitate to cast any evidence aside. There is some reason to regard *Nematothallus pseudovasculosa* as a really primitive vascular, or pre-vascular, plant; it is known from thalloid compressions up to about 6 cm. long and 4 or 5 cm. broad, although these apparently represent but fragments of the whole. It was covered by a cuticularized " epidermis " and contained tubes of two sizes as well as resistant spores. It is perhaps appropriate for me to insert a personal note here. Two years ago while studying the extensive Lower Devonian plant collections in the Brussels Natural History Museum I noted several specimens, identified as *Sporogonites exuberans*, attached to what I surmised was a thallus-like organ in life. *Sporogonites* is certainly in the problematical class and has had a controversial career. The sporangiate stalks were originally described by Professor Halle from Norway and, lacking any evidence of a vascular strand, were thought to be bryophytic. Later, influenced by certain features of the Rhynie plants, he considered the fossils as

being more correctly placed with the psilophytes. As to the Belgian specimens, there is no evidence of vascular tissue in either the sporangiate stalks or the thallus; they are however, deserving of more intensive study and additional collections might shed light on the form of the thallus. The plant may be classified tentatively as bryophytic, but it seems within the realm of possibility that better preserved specimens may show the thallus to be comparable in organization with the fossils described as *Nematothallus* in which case I would be inclined to regard the Belgian fossils as being a very primitive vascular plant.

Prototaxites is perhaps less convincing as a forerunner of true woody plants, and I am inclined to agree with most paleobotanists who have relegated it as a sort of dead-end alga. However, on a field trip following the Montreal Congress last summer we were shown a magnificient " log " nearly three feet in diameter in place in a cliff on Chaleur Bay. I recall a remark by one member of the party, a leading authority on Devonian floras, " this *must* have grown in an upright position ".

It seems evident that the diversity of form in these earlier members of the earth's vegetation indicates the presence of many evolutionary lines. The picture is more complex than it was a few decades ago, and it is safe to predict that it will become more so (yet correspondingly more fascinating). It is my own impression that we are only beginning to understand the early evolution of vascular plants and consequently the seeming taxonomic misfits should not be discarded, at least until the patterns of racial development become clearer.

There are several classic examples of fossil plants which, by virtue of their complexity, seem far out of place in the chronological scheme of things. One of the most vexing of these is *Cheirostrobus pettycurensis*, known from a single cone that was found in Lower Carboniferous rocks in southern Scotland more than 60 years ago. It has been generally accepted, and on good grounds, as belonging to the articulate group, to which the modern *Equisetum* belongs. The enigmatic nature of *Cheirostrobus* lies in the fact that it is much more complicated than the reproductive organs of the later Upper Carboniferous members of that great race of plants. The most logical explanation has been that the articulates were actually of earlier origin than was indicated by the scanty Devonian record. We are now finding evidence to confirm this suspicion and *Cheirostrobus* no longer stands in quite so isolated a position. Recently, Professor Suzanne Leclercq described the small cones of *Eviostachya*, an Upper Devonian articulate with very complex sporangiophores, and two years ago I had the pleasure of collaborating with her in a study of some Middle Devonian specimens of *Calamophyton* from eastern Belgium. The specimens that we studied were remarkably well preserved and proved to be much more complex than previous reports indicated for this genus. The riddle of *Cheirostrobus* thus seems to be partially unveiled; the articulate group was clearly a complex one prior to Lower Carboniferous times.

It may be well to note that not all plant riddles are of real significance; considerable caution must be used in interpreting problematical fossils. Some years ago an American paleobotanist described a new species of palm fruit; it was an ovoid structure with blunt ends and a shallow longitudinal groove around each face. A few years later another paleobotanist who harbored some suspicions of the identity of the specimen took the trouble to section it and found that it was composed of a mixture of clay and charcoal. He was able to demonstrate that it was part of a " Cape Cod firelighter " — a porous, absorbent ceramic object that is soaked in kerosene and used to ignite wood fires ! Had the original investigator taken the time to section the " fossil ", he probably would not have been led so far astray.

One of the most important assemblages of problematical fossil plants is the one we now refer to rather loosely as the coenopterid

ferns. As evidence of the taxonomical problem they present is the fact that almost every serious student of the group has put forward a different system of classification. I think it will be generally agreed that the coenopterids like the psilophytes include a very diverse group of plants, in size, structure, and in the habitats they occupied. Brief reference to a few examples makes this abundantly clear:

It is appropriate to cite *Botryopteris* first since it has been studied intensively by a member of your Institute and in my own laboratory. There is first some question as to how closely related the several species assigned to the genus may be but most important is the information that they afford on the evolution of the leaf, or perhaps I should say, on the differentiation of leaf and stem as distinct organs. Of special interest also are the great sporangial aggregates, some of them the size of a large plum — how were they borne on the plant and how were the spores shed ?

Dr. Surange's important discovery of heterospory in *Stauropteris burntislandica* has greatly influenced our thinking concerning the origin and complexity of the coenopterids. This plant from the Lower Carboniferous of Scotland, although apparently quite small, can hardly be called primitive. Does it represent a special line of early ferns or does it mean that the coenopterids are of more ancient origin than was previously suspected ?

Not the least interesting is *Biscalitheca musata* in which the sporangium wall is by far the most complex of any fern or fern-like plant.

As to their habitat some of the coenopterids appear to have been epiphytes, some scrambled over the surface of the ground, and quite recently a new species of *Tubicaulis* has been found in Illinois that is distinguished by the presence of aerenchymatous tissue in the cortex of the stem and petioles. This suggests a semi-aquatic habitat.

One could go on at some length but I believe enough has been said to reveal the diversity of form in these fossils and the problems of classification they pose. The coenopterids have been regarded by some botanists as transitional between the psilophytes and ferns while others have looked upon them as a specialized line of pteridophytes in their own right. There is probably truth in both viewpoints, for it is now evident that the plants we have assigned to the coenopterids constitute a very diverse asemblage. It seems safe to predict that we are beginning to get a glimpse of what was a great maze of pre-fern lines of evolution some of which were probably specialized dead-ends and others represent links in the stream of evolution leading to the ferns and possibly the pteridosperms.

Some especially interesting discoveries have been made in recent years which indicate that the gymnosperms, like the pteridophytes, are a diverse assemblage that originated along several quite distinct lines. There is a good deal of evidence to indicate that the pteridosperms and cordaites evolved quite independently of each other and Professor Harris has voiced the opinion that the Cycadales and Bennettitales are actually independent gymnosperm classes. We have here some of the most fascinating and I think important of all the plant riddles; brief consideration of a few reveals an increasingly complex pattern of evolution in the lower seed plants:

It is appropriate to cite first the Pentoxyleae, the justly famous symbol of the Sahni Institute. I find it difficult to correlate these fossils at all closely with any other gymnospermous group. Indeed, in 1948 Professor Sahni himself wrote of them as follows:

"Some discoveries in science help or appear to help, in the solution of the old outstanding problems; others — and these are perhaps the most interesting — seem to create new difficulties in our path. My object here is to draw attention to a recently recognized group of plants which defies classification and presents a new problem in our understanding of the evolution of Gymnosperms."

I am quite sure that we are all puzzled by the recent studies of *Glossopteris* and *Gangamopteris*. Until better preserved material is available, it seems pointless to speculate on the affinities of these plants; the available evidence, however, suggests that they are not only separate from other gymnospermous groups but that they may actually include several distinct types, the inter-relationships of which are problematical.

Two years ago I had an opportunity to see the type specimen of Professor Neuburg's *Vojnovskya paradoxa* at the Geological Institute in Moscow. This is a late Paleozoic plant; it was probably shrubby or arborescent, with rather large fan-shaped leaves and the fertile branches bore closely compacted microsporophylls (each with two pairs of sporangia) and scattered among them are apparent seed organs, each about 1 cm. long, bilaterally symmetrical and with a notched tip. This combination of characters is quite unlike that of any other plant and she has created the new order Vojnovskyales.

T. M. Harris has made two notable contributions recently which suggest unique gymnospermous groups: he has shown that the well-known and widely distributed *Czekanowskia* (long presumed to be ginkgophyte foliage) may have borne the curious fruiting capsules of *Leptostrobus*; among his many contributions stemming from studies of the Rhaetic Greenland plants he has shown that the distinctive microsporangiate organ *Hydropteridangium marsilioides* may have been borne on a plant with the cycad-like foliage known as *Ptilozamites nilssoni*. Much additional information is needed before the significance of these two examples can be accurately appraised but the unique nature of the reproductive organs suggests distinct plant groups.

It does not seem appropriate to close without some reference to the flowering plants and, indeed, we find here one of the most controversial of all our plant riddles. Four years ago R. W. Brown reported a fossil from the Triassic of Colorado consisting of a tapering stem tip bearing simple, elliptic, pleated leaves to which he gave the name *Sanmiguelia lewisi*. Most of the paleobotanists that I have talked with who have seen this fossil seem confident that Brown's identification as a palm is correct. If so, it is the most drammatic bit of evidence in support of the view that the angiosperms originated much earlier than their " sudden " appearance in the Cretaceous indicates.

In summary, it seems clear that the fossil record is telling us that the plant kingdom is of more complex organization than was formerly apparent. The paths of evolution have been numerous and a tremendous variety in plant form has come into being during the past two billion years. The extent of this diversity is in some measure made evident from the riddles — the problematical fossils that are difficult, or at the moment impossible, to fit into the known order of things. Undoubtedly, some of these are of greater significance than others but I urge that all be given a fair hearing.