

THIRTEENTH BIRBAL SAHNI MEMORIAL LECTURE

PLANTS, ANIMALS AND TIME

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I regard it as a great privilege to present the Sahni Memorial Lecture in this splendid new auditorium, which has only just been completed. It is a particular pleasure for me, but also a very humbling one, to reflect that the two men under whom I have studied palaeobotany, Professor Tom Harris of Reading and Professor Chester Arnold of Michigan, both in their time gave this Memorial Lecture.

I suppose that most people would say that the proper role of the palaeobotanist is to seek to reconstruct the plant life of time past in all its aspects. Over some 150 years in the development of our science, this has resulted in the accumulation of a vast body of information. Some of it is detailed, and well founded; some of it is of less secure quality. The very size of the palaeobotanical systematic "data store" has perhaps encouraged some to seek evidence of other aspects of past life, rather than simply adding to the store. One such line of research which has proved most rewarding in the last decade has been the study of palaeoecology. A particularly challenging aspect of this field is the extent of the interaction between plants and animals through time. What, if any, direct evidence do we have in the fossil record for their co-evolution? I want to briefly to explore this question.

In the entire fossil record of life, one thing is very clear. We have evidence of the existence of plants — or at least of aquatic autotrophic organisms long pre-dating by at least 1,000 million years any evidence of recognizable animal life (Barghoorn & Tyler, 1965). Perhaps the greatest evolutionary leap in the whole history of life was the migration from the aquatic into the terrestrial environment. Plants, which apparently arose in the aquatic setting, pioneered the colonization of the land. It is in the earliest records of plant life on land that we see the first hints of the interaction of

plant and animal life. In the Rhynie chert, a silicified peat deposit of Early Devonian age from Scotland, we have one of the first pictures of a terrestrial ecosystem (Tasch, 1957; Kevan *et al.*, 1975). Associated with structurally preserved remains of the vascular plants *Rhynia*, *Horneophyton* and *Asteroxylon* we have fragments of arthropods. Some, such as the freshwater "shrimp" *Lepidocaris*, were apparently aquatic. Others, such as the collembolan *Rhyniella*, the mite *Protacarus* and the trigonotarbid arachnids, were adapted for life on land. A number of reviews of this fossil ecosystem have been published in the last few years (Scott, 1980; Chaloner & MacDonald, 1980).

Two features of the Rhynie community are suggestive of plant-animal interaction. Firstly, empty sporangia of *Rhynia* have been found, containing several bodies of trigonotarbid arachnids (Kevan *et al.*, 1975). This may be simply a fortuitous association; or perhaps, more probably, the arachnids had entered the sporangia as a moist, protected microhabitat. The prey of this (probably zoophagous) arachnid, in the form of collembolans, might well have been inhabiting such sites within the bog surface litter, and the empty sporangia were a profitable feeding ground. Equally, the arachnids may have been spore eating. We have much more positive evidence of spore-eating in the Carboniferous (Scott, 1977; Scott *et al.*, in press). It seems that spore-eating may have been one of the earliest manifestations of phytophagy among land-adapted arthropods; perhaps the high protein and lipid content of spores made them a worthwhile food source for basically zoophagous organisms, when animal prey was unavailable. As Southwood (1973), discussing the evolution of insect feeding habits, says of the origin of plant-eating in that group: "The evolutionary path of the phytophagous insect has not been an

easy one; pollen feeding often seems to represent 'the first step' and feeding in or on foliage 'full success'. It is interesting that he makes this suggestion apparently solely on the basis of extant groups; for it is a proposition which is certainly consistent with the fossil evidence of spore eating appearing early in the fossil history of terrestrial arthropods.

A more direct hint of phytophagy in the Rhynie early Devonian community is the occurrence of lesions in the plant axes which evidently occurred in life, and show a "wound reaction" in the adjoining tissue (Kevan *et al.*, 1975). This indicates that the lesions were formed during the life of the plant, and that the plant survived the injury. These lesions characteristically extend to the phloem, and may represent the results of sap feeding by contemporaneous arthropods — possibly the arachnids.

When we come to the Carboniferous, there is much more extensive evidence of plant-eating by arthropods. Most notably, we have droppings (coprolites), attributed to arthropods, containing a diversity of spore exines (Scott & Taylor, 1983). Lepidodendrid spores, actually extracted from the gut of the Carboniferous insect *Eucaenus* (Scott *et al.*, in press) are perhaps the most direct possible evidence of Carboniferous spore-eating by insects.

Before leaving the topic of spore-eating, one particular aspect of it may be noted, since it bears on its role in subsequent plant/animal co-evolution. It may easily be shown (Chaloner, 1976) that spore-eating need not destroy the viability of all the spores; locusts, used in one experiment, only reduced the viability of spores fed to them by about 50 per cent. Such a relationship between plants and spore-eating insects would probably have had compensations for both parties. Even if the insect only digested the contents of say a half (or even three-quarters) of the spores consumed, their high nutritive value compared to, say, leaf tissue would have been very adequate compensation to the insect. The plant would at the same time have benefited by having at least the surviving spores transported well away from the parent plant and deposited (in a faecal pellet) in a moist, nutrient-rich site for germination. Such a site would be particularly suitable for the growth of subterranean (mycorrhizal)

gametophytes such as characterize many extant primitive spore-bearing plants (e.g. some *Lycopodium* spp., *Psilotum*).

A further feature of plant-animal co-evolution of mutual benefit is the development of fleshy seeds (and, in the angiosperms fruit), as a means of encouraging biotic seed-dispersal. The role of animals in the process is well documented for at least some of the few living gymnosperms (e.g. *Taxus*) which adopted this strategy. It is less clear, although eminently plausible, that even Palaeozoic gymnosperm seeds with this same "drupe syndrome" of a stony, inner structure surrounded by a soft fleshy one, may also have been showing an adaptation to biotic seed dispersal (Chaloner & Sheerin, 1981).

Scott and Taylor (1983) give very full documentation to the range of lesions seen in Carboniferous plant organs, which may reasonably be ascribed to some animal causal agent. Despite the diversity of such occurrences, surprisingly few are actually recorded in the literature. As those authors suggest, this may well be because of the inclination of palaeobotanists to avoid or ignore damaged specimens in their collecting, so that plant material damaged by phytophagous animals is seriously under-represented in our collections.

Evidence as to the role of different plant groups (and indeed different plant organs) as primary food sources through the rise of the terrestrial fauna of tetrapods — amphibians, reptiles and eventually mammals — is very inadequate. Swain (1978) has suggested the doubtless important role of various plant constituents, either distasteful or toxic, in discouraging predators. Inevitably, our picture of the evolution of such symptoms of plant-animal interaction — the so-called chemical warfare in the plant-animal struggle — is based almost solely on our knowledge of the biochemistry of living plants. The fossil record can contribute little in this direction, beyond evidence of the time of appearance of various plant and animal groups, and of such biochemically suggestive structures as glandular hairs (Scott & Taylor, 1983) and nectaries (Friis & Skarby, 1982).

The possible role of changing vegetation in the biology of (terrestrial) dinosaurs has probably had more than its fair share of attention, compared with other aspects of

plant-animal interactions. The displacement of gymnosperms by angiosperms, which is obviously a feature of the Late Cretaceous scene, has been implicated in dinosaur extinction in diverse ways by different authors. Swain (1978), says succinctly, "one fact stands out; the extinction of the dinosaurs (but not other mainly carnivorous small reptiles; crocodiles and snakes) is inversely related to the rise of the flowering plants". On the hand, Bakker (1978) turns the evidence the other way round, and suggests that a change in feeding strategy of herbivorous dinosaurs opened up ecological opportunities which triggered the diversification of the angiosperms. This particular field of plant-animal interaction seems to be strewn with conflicting interpretations of the evidence, and a corresponding multiplication of diverse working hypotheses!

The Cretaceous rise of the angiosperms must represent the major plant evolutionary event in which plant-animal co-evolution of the pollination process is most securely implicated. In the extant angiosperms, insects (and in a more limited way, birds and a few mammals) are deeply involved in their biotic pollination. Our knowledge of the extent of co-adaptation of angiosperms with animal pollinators (see e.g. Faegri & van der Pijl, 1979) is inevitably based largely on studies of living flowers. None the less, some progress has been made in linking fossil evidence of flower evolution with the appearance of relevant insect groups (Crepet, 1979).

Much less attention has been paid, at least by palaeobotanists, to the equally extensive involvement of mammals and birds, in particular, in the dispersal of angiosperms. The role of selection by fruit-feeding animals in the evolution of fleshy-fruited angiosperms is inescapable. The occurrence of many living angiosperm fruits and seeds with hooking devices to effect adhesion to mammals' hair is another obvious instance of such co-adaptation. But our supposition of the co-evolution involved in such plant adaptations is again based almost entirely on living plants, and direct fossil evidence of that type of plant-animal interaction is negligible.

The evidence for early insect spore-eating encourages the view that this must have been antecedent to gymnosperm pollen-

feeding by insects. Scott and Taylor (1983) renew the suggestion made by earlier authors that biotic pollination may have occurred in some Carboniferous pteridosperms. The evidence that the hermaphrodite Bennettitalean fructifications may have arisen in response to an insect pollination relationship has also recently gained ground.

The sequence of events leading to entomophily seems likely to have been:

1. Spore-eating by insects and ensuing spore dispersal in pteridophytes, which apparently occurred early in land plant evolution.

2. Since this probably pre-dated the evolution of the seed, pollen-eating is likely to have accompanied the rise of seed plants at least in some groups (see, for example, evidence of pollen-eating in the Mesozoic plant *Caytonia*, Harris, 1946).

3. An obvious step towards insect pollination would be effected by bringing the pollen and seed-bearing structures into juxtaposition. Only in this way would pollen-feeding (and scattering) predators, foraging for pollen, bring the compensation of "out-breeding" pollen into proximity with the ovule, in return for removal of "self" pollen. The assumption of a strong co-evolutionary link between a hermaphrodite flower and insect pollination is supported by the fact that among living wind-pollinated gymnosperms, pollen and seed-bearing structures are separate, either on the same plant (monoecy) or on separate plants (dioecy). The sole exception appears to be in some *Gnetum* species (Sporne, 1965).

4. The development of the hermaphrodite flower has made protection of the ovules (produced in limited numbers) an essential accompaniment to accessibility of the anthers to insect visitors, attracted by the opportunity for pollen feeding.

5. The evolution of zygomorphy, nectar secreting and storage structures, and the numerous complex behavioural relationships between insects and flowers must then have followed these early steps.

6. The fact that the many angiosperms which have reverted to wind pollination have frequently also reverted to separate male and female flowers (as in the sedges and in the wide range of catkin-bearing trees) is consistent with the suggestion made in (3) above.

Our picture of early flower structure has recently received a boost from the work of Dr E. M. Friis on charcoalfied flower buds of late Cretaceous age from Sweden (Friis & Skarby, 1982). Two interesting features in her work have relevance to the present theme. Her Saxifragalean flower, *Scandianthus*, shows in addition to all the essential flower parts, clear evidence of nectaries. This is perhaps the earliest occurrence in the fossil record of this particular tangible adaptation of the angiosperm flower to zoophily (presumably, entomophily). The other feature which emerges from the work of Friis (1983) on these Cretaceous fossils is that there were contemporaneous flowers, evidently of Juglandaceous affinity, with a reduced perianth, representing the early reversion to wind pollination which was eventually to culminate in the wind-pollinated amentiferous trees.

Crepet (1981) has reviewed the evidence for the early (Eocene and possibly Paleocene) adoption of wind pollination in the several catkin-bearing angiosperm families. It seems rather surprising that the angiosperms, having evolved the ingenious outbreeding potential represented by entomophily then abandoned it in certain groups relatively early in their evolutionary history. The grasses developed a parallel reversion to wind pollination, although in the context of a very different reproductive strategy from the Amentiferae. Pollen evidence suggests that, as in the dicots, this was an early feature of monocot evolution with grass-type pollen appearing in the Eocene (Muller, 1970).

The grasses seem to have combined this disengagement from insect pollination with the adoption of a different co-evolutionary relationship, involving grazing mammals. The grass vegetative strategy of keeping its growing point at or in the soil surface, coupled with leaf growth by basal (intercalary) meristems gave many members of that family a remarkable capacity to survive heavy grazing, seasonal aridity and even frequently recurring fire. By late Tertiary time, at least, the grasslands of the prairies and savana evidently supported extensive mammal populations. These, as a food source for early hunters may have helped to tempt them away from the forest environment.

The great American anthropologist and "human palaeontologist" Loren Eiseley,

has argued cogently for the close relationship between the rise of the angiosperms and that of the mammals. He expressed this idea in his characteristically graphic prose (Eiseley, 1958): "Flowers changed the face of the planet. Without them the world we know—even man himself—would never have existed. Francis Thompson, the English poet, once wrote that one could not pluck a flower without troubling a star. Intuitively he had sensed like a naturalist the enormous interlinked complexity of life. To-day we know that the appearance of the flowers contained also the equally mystifying emergence of man".

The early interaction of man and vegetation is very well documented, most particularly in the form of palynological evidence of forest clearance (by use of fire and axe), the spread of weeds favoured by arable and pastoral land use, and of the gradual appearance of the larger grass pollen characteristic of the cereals (for a readable general review, see Cole, 1967.) It is interesting that man's history came to be closely intertwined not so much with those "mainstream", entomophilous angiosperms, committed to their own co-evolution with the insects, but with the one group, the grasses, which had made such a success of reverting to wind pollination. The conventional picture of man's relationship with the cereals is one of control and manipulation by man. This has resulted in what is usually seen as the exploitation and modification of originally wild species to produce the high-yielding maize, wheat, barley, millets and rice on which such a large proportion of mankind now depends.

A less anthropocentric assessment of man's relationship with the cereals gives a very different picture. This might be best presented as a "fairy story", in which a grass plant, early in Pleistocene time, was confronted by a Fairy Godmother. (This is a figure dear to English children's folklore—she is, you will remember, able to grant three wishes.) The grass, competing with only limited success in the environment of expanding open habitats might have presented its plight to the Fairy Godmother as follows: "Firstly, when we produce our seed, much of it falls on compacted or dry ground, or in the shade of the forest. Our first wish is for something which would clear away the forests, and prepare and

irrigate the ground, so that our seedlings can develop successfully. Then, our young plants have to compete with other aggressive colonizers of open communities. So our second wish would be for something which would remove those competing herbs, and leave our seedlings to grow unimpeded. Finally, we would like to colonize new territory. Even our small wind-borne seed cannot cross oceans. Our third and final wish then, to achieve world-wide success, would be to have some mechanism which could gather up our seed and take it across the seas to other parts of the world”.

The Fairy Godmother might have replied: “You see that group of apes over there, chasing a mammoth? They are capable of fulfilling all three wishes for you. Their meat supply will run out eventually — they are destroying it pretty quickly. They will then find a substitute for it in your grain.

They will get addicted to eating your seeds, and will clear forests, plant huge areas of nothing but grass, which they will tend carefully, and will gather the seed and transport it all over the world for you. You will come to dominate huge areas of the world by thus enslaving these apes. Of course they will think that they have done it all — that they are manipulating you grasses, and exploiting you. As you well realize it is the other way round, and you will have tamed and harnessed this omnivorous ape, to achieve your own ecological success.”

Well, of course, all this came about. The end of this particular thread of the complex intertwining of the evolution of plants and animals has been that the grasses domesticated man. But we, with our usual egocentricity, prefer to see it the other way round,

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