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EARLY RECORDS OF ANIMAL AND PLANT INTERACTION

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ABSTRACT

The paper presents a brief account of animal and plant interactions during the Palaeozoic times. Possible lines of future research in this, hitherto neglected area in our country are also suggested.

It is well known that feeding was the primary interaction between plants and animals and later there were many by-products of this relationship which were useful to plants as well as to animals. The early history of these relationships has just begun to be deciphered and I shall attempt to present some of the highlights of these researches. The Mesozoic and post Mesozoic history of plant-animal interactions has its parallel in present day relationships of plants and animals and therefore I shall generally leave it out.

DEVONIAN

Kevan, Chaloner & Saville (1975) have pointed out that it is highly probable that the first land plants developed close interactions with arthropods and fungi. Undoubted evidence for this comes from the Rhynie Chert. In these rocks some of the early land plants are closely associated with arthropods and fungi. The fungi may have been saprophytes or mycorrhizic. This was indeed an ecosystem where arthropods may have been eating plant parts and the lesions reported by Kidston & Lang (1921) on the Rhynie plants, which they thought were caused by poisonous gases, may have been caused by the associated arthropods. The callus formation seen in the wounds of such plants suggests injury in life. Later the arthropods may have started eating the protein rich spores of these plants and disseminating them. Kevan *et al.* point out that a majority of arachnids in the Rhynie Chert are preserved as fragments within the sporangia of *Rhynia major* and they may have entered the sporangia either to feed on animals living there or to eat up the food rich spores of the plant.

Perhaps the first records of insects could also be deemed to be dating back to the late Devonian where Rodendorf (1961) found the remains of what appears to be a movable wing of an insect *Eopterum devonicum*. He also described another late Devonian fossil *Eopteridium*. Subsequently he himself assigned these fossils to Crustacea although Kevan *et al.* (1975) continue to hold that they may still prove to be the remains of insects. If we leave out these doubtful late Devonian records of insects we are left with the first undoubted winged insects which appeared in the Carboniferous about 50 million years later as described by Reik (1970) and Crowson *et al.* (1967).

Kevan *et al.* (1975) have correlated the appearances of ornamentation of spores with their being dispersed by animals particularly arthropods and insects. They point out that the origin of land arthropods and insects and ornamented spores took place almost simultaneously. They also think that an ornamented spore wall could not have been a purposeless innovation since much energy is involved in developing it. As far as I can see, it obviously strengthens the wall against swelling of the spore by imbibition and prevents the bursting of spore wall at points other than those which are designed for the purpose like the tetrad marks, colpae, germ poes, etc. Wall sculpture may also give greater bouyancy in water by engulfing air between the ornamentations. It may also be helpful in air dispersal by offering greater resistance to wind currents and may even increase the chances of dispersal by small animals by sticking to them, since it is well known that ornamentations help in attaching spores to animal bodies. Moreover, wall ornamentations like spines, baculae and strengthening bars can also help in protecting spores from feeding animals and such spores can even pass out undigested (Proctor, 1972). Chaloner (1976) experimentally fed *Pteridium* spores to locusts and found that this reduced their viability only by 50% after they passed out in the faecal pellets. The spores of *Isoetes* have a silicious coat which may be helping in their protection from enzymes contained in the alimentary canals of earthworms and other feeding animals (see Duthie, 1929, Pant & Srivastava, 1962).

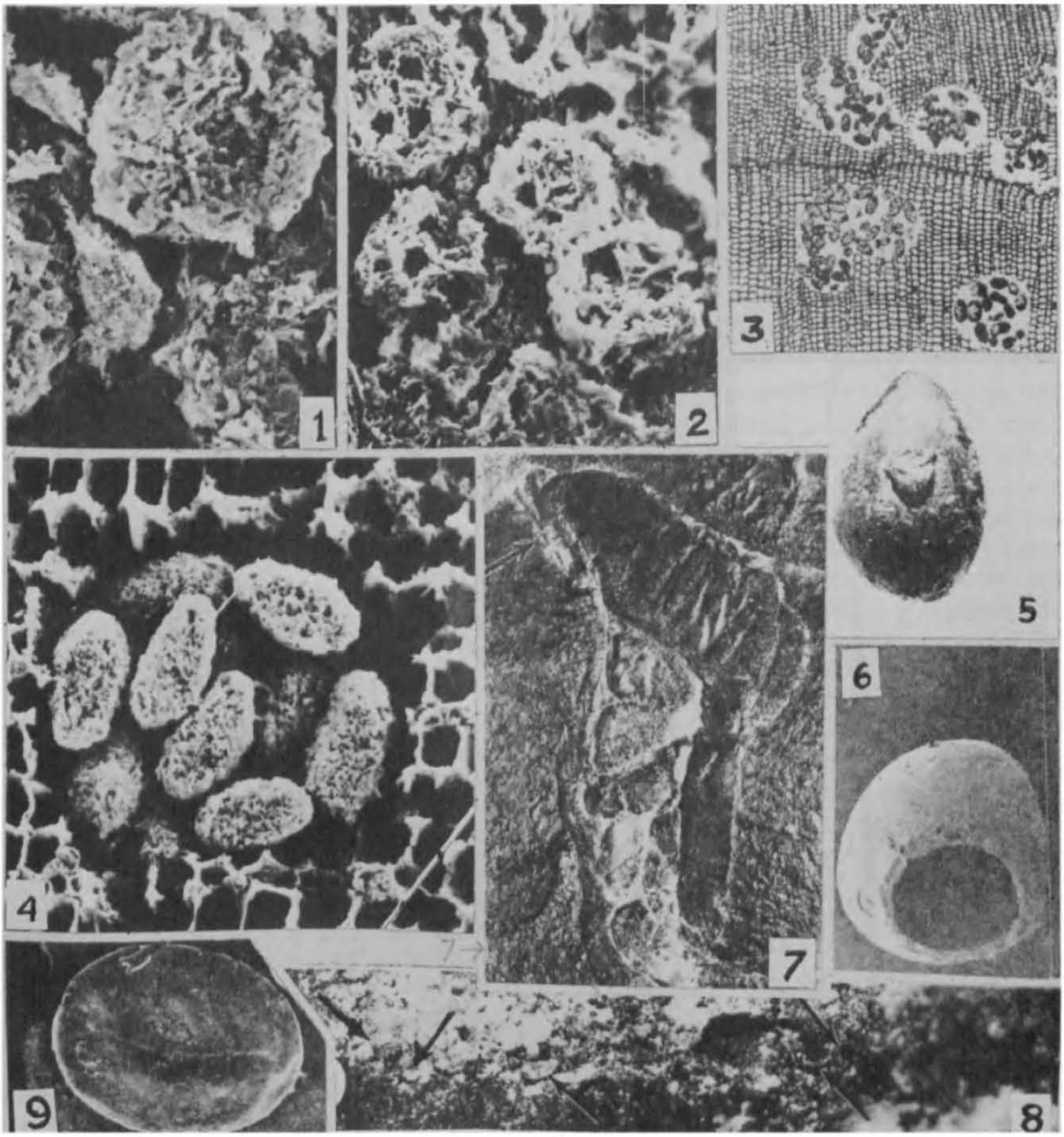
CARBONIFEROUS

We mentioned earlier the connection between plants and animals in connection with the possible spore eating arachnids in the Devonian but more positive evidence of such animal plant relationships comes from the carboniferous and more especially from the Upper Carboniferous (Scott & Taylor, 1983, also Text fig. F).

Spore eating and pollination must have been one of the earliest byproducts of these associations. As early as 1903 when Oliver & Scott described the possible connection between *Lagenostoma, Lyginopteris* and *Sphenopteris,* in one of his letters to Scott, Hooker had suggested the possible role of glands in attracting insects for pollination (Andrews, 1980). In recent years Chaloner (1970) has suspected that some of the spines of *Psilophyton* may have been glandular and these may have served for the protection of the high held sporangia from crawling arachnids. Alternatively they may have served to attract them.

From the Upper Devonian onwards arborescent habit enabled plants to hold their sporangia at heights which became inaccessible for crawling animals to reach but during the Carboniferous this was soon overcome by flying insects.

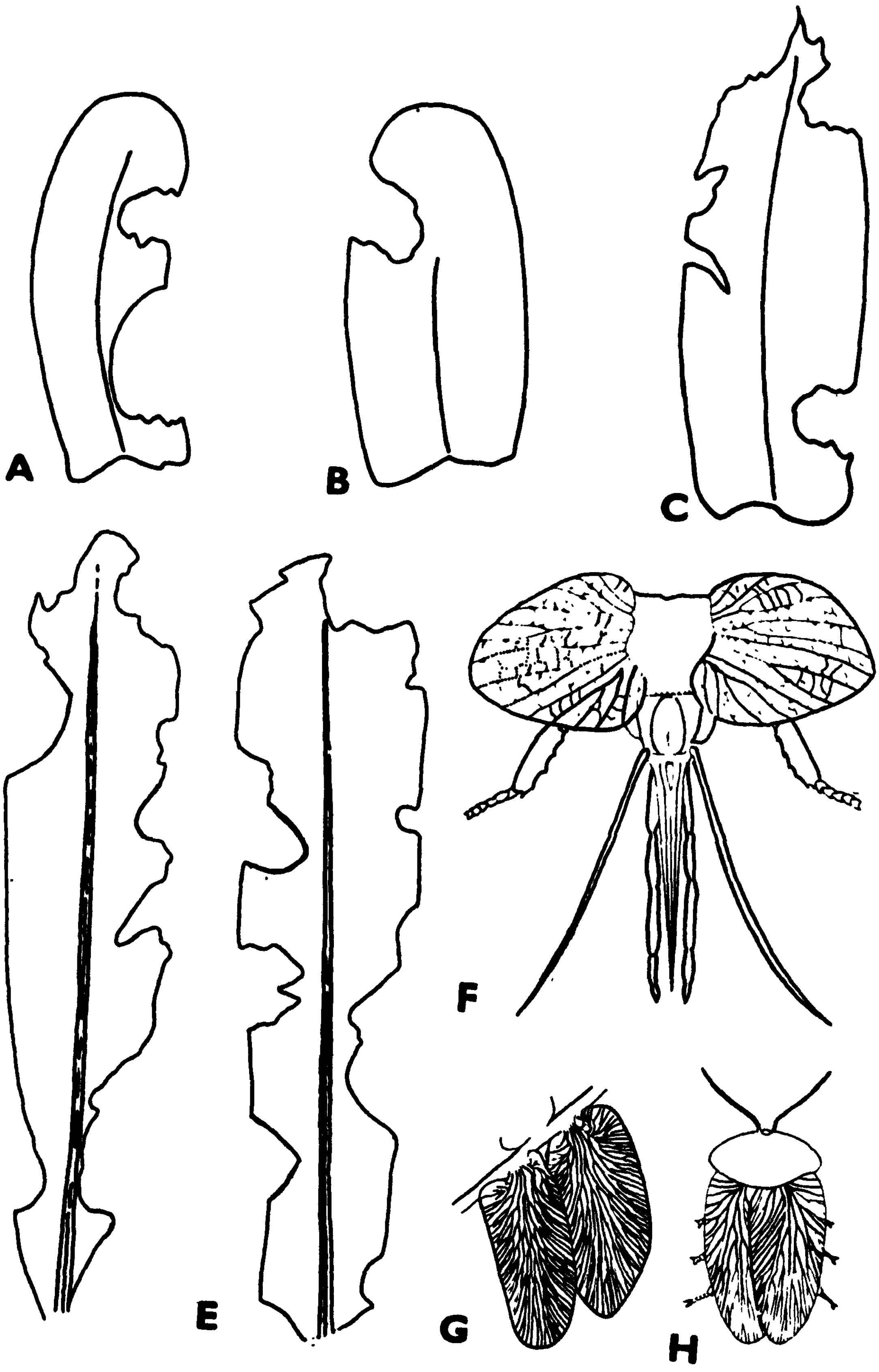
Commencing on the ecosystems of the coal age Scott & Taylor (1983) point out that the forest floor of that period was much like present day forest floors. Coprolites described by Scott (1977), Baxendale (1979), Cichan & Taylor (1982), Rothwell & Scott (1983), Scott & Taylor (1983) and Taylor & Scott (1983) lying freely or in wood borings inside coal balls (Plate, figs. 1-4) suggest that the ground below the forest canopy at that time of Upper Carboniferous age abounded, as now, in phytophagous mites, collembola, cockroches, centipedes and millipedes, since such coprolites resemble those of these animals. Chewed leaf remains, bored seeds (Plate, fig. 5), megaspores (see Plate, fig. 6) and pollen of seed ferns which have been found on the bodies of insects or spores of lepidodendroids and *Monoletes* pollen contained in the gut of *Eucaenus* (Plate, figs. 7-9), a



PLATE

(All figs after Scott & Taylor, 1983)

Plate Figs 1-9 1 Coprolites from Lower-Middle Pennsylvanian age of Eastern Kentucky 1 Details of morphology, × 600. 2. Small coprolites within the lumen of a tracheid, × 150 3. Section of *Premnoxylon* wood showing several coprolite burrows (Lower-Middle Pennsylvanian 1 9× 27 4. A burrow in *Premnoxylon* wood filled with frass pellets. × 300 5 Sandstone cast of *Trigonocarpus* with plug representing hole in original seed coat. × 1.5. 6 *Setosisporites praetextus* megaspore with hole × 16 7. Leg segment of *Arthropleura* from the Mazon Creek area. Arrow indicates position of *Monoletes* pollen, × 1. 8. Details of Fig 7 showing *Monoletes* pollen grains (arrow) on *Arthropleura*. × 38 9. *Monoletes* pollen grain extracted from leg segment illustrated in Fig 7 × 100.



Text. fig. 1. A–E, Fossil foliage presumably damaged by insects, A–C, Pinnules of *Neuropteris scheuchzeri*, × 1 · D, E, leaves of *Glossopteris*, × 1. F, suggested reconstruction of the head and prothorax of *Stenodictya lobata*, × ca 4. G, H, suggested example of mimicry between pinnules of *Odontopteris callosa* and a cockroach, *Phylomylacris vitteri*. (A–C, F–H after Scott & Taylor, 1983, D, E, after Plumstead, 1963).

Mazon Creek Carboniferous insect (see Scott & Taylor, 1983 and Chaloner, 1984), as well as those inside the intestine of a Lower Cretaceous saw fly (see Krassilov & Rasinitsyn, 1982) suggest that sporivory or pollenivory and dispersal by insects had become important from the Carboniferous onwards. At present some of the above mentioned animals feed on living tissue of plants but others consume dead litter. Collembola (spring tails) which date back to the Devonian can be eating living plants, dead litter or may even be saprophagous. Wounded stems of *Calamites, Psaronius* and other plants have been reported by Scott (1977). Cichan & Taylor (1982) have reported abundant coprolites in the borings of wood of *Premnoylon* (Plate, figs. 3, 4).

However, the most common insects of the Carboniferous seem to have been cockroaches. Present day cockroaches dwell in the forest litter but others live under the bark. They are saprophagous or possibly phytophagous. The Orthoptera (grass hoppers and crickets) are mainly phytophagous but some wingless forms live in the ground litter. This must have been so even during the Carboniferous when such insects had come into existence. *Neuropteris* leaves seemingly damaged by insects with their bite marks have been commonly recognized (Text. fig. A-C). Plumstead (1963) has described insect eaten leaves of *Glossopteris* during the Permian (Text. fig. D, E).

Another group of animals which must have inhabited the Carboniferous soil was the annelids. As at present, they must have drawn nourishment from the humus rich soil of the Carboniferous forests. It has been found that at present they can sometimes help in the dispersal of spores like those of *Isoetes* (see Duthie, 1929, Pant & Srivastava, 1962) and they may have similarly dispersed resistant spores and propagules of Carboniferous plants.

Strategies involved in plant and animal interactions

Standing on the side of plants, I consider these under three headings:

(1) Defensive devices.
(2) Attractive devices.
(3) Offensive or insectivorous devices.

1. *Defensive devices:* Thick coats and sculputured spores were developed as early as Devonian. The hard protective coats of seeds with thick stony layers were obviously developed to protect the contained gametophytes and embryos. Hairs and spines particularly the glandular ones, gummosis and latex have similarly protected plants from animal attacks. Also mentionable here are chemical defences evolved by plants to protect themselves from herbivory. Certain caterpillars feeding on cycads have 3 glucosidase in their digestive tracts which breaks, oxyglucosidase to MAM which should kill them but they attach a glucose to it forming a more stable cycasin. The cycasin is stored and not excreted. The caterpillar is poisonous to animals eating it (Teak, 1967). However, such chemical defences presently are difficult to decipher from the fossil record [although the work of Niklas (1976), Niklas & Chaloner (1976), Niklas & Gensel (1976) and others on palaeobiochemistry suggests that such determinations may be possible in future]. It is, however, possible that such strategies, as the present day ferns and gymnosperms exhibit, have had their beginnings in the Devonian and Carboniferous times when these groups may have originated. Mimicry like that of *Odantopteris* leaves and insect wings (Text fig. G, H) may have also served for protection on either side (see Scott & Taylor, 1983).

2. *Attractive devices:* These include colours, scent, nectar, mimicry and fleshy parts like fruits and fleshy seeds which have been utilized by plants for attraction

in their pollination and dispersal by animals. The intricate mimicry of *Ophrys musciflora* flowers and other species involves the imitation of the females of *Campscolia ciliata* and other moths not only in appearance but also in their metallic lustre, scent and colour. An association of this kind seems to be a culmination of such relationships between plants and animals.

3. *Offensive or insectivorous devices:* These are developed by carnivorous plants which attract insects to trap them or actively suck them into. the pitchers of *Utricularia*. It is imagined that the devices of offering food for attracting insects for pollination may have been partly diverted in these plants for trapping them for insectivory.

Topics for future research in India

With the above introduction to early records of animal and plant interactions it seems necessary to mention a few connected areas of research which we could take up in this country. One of the neglected areas of research in India is the study of fossil insect remains. These are abundant in some beds of Rajasthan but they have to be studied as parts of an ecosystem with the plants with which they occur associated. Another neglected area is the recognition of insect remains in the *Glossopteris* bearing rocks of India (and of other Gondwana countries). The forest floor of that period could not have been entirely lacking in fossils of insects as Rayner & Conventry (1985) have recently shown. We have to look for such remains which may have been mistaken for plant parts since we too have found some insect wing-like remains in the *Glossopteris* bearing shales at Handappa. A third area is the search for insect coprolites and their comparative study with faecal pellets of living insect and other animals. Harris (1946) described coprolites containing pollen and cuticles of *Caytonia*. He experimented with a goat, a hen and a dog to find out whether such parts come out undigested in the faecal pellets. Lately Pant, Nautiyal & Chaturvedi (1981) have found a butterfly caterpillar *(Euchrysops pandava)* which eats modern *Cycas* leaves and these authors have shown that its faecal pellets contain the remains of cuticles of leaves and other remains of *Cycas*. Unpublished results of my laboratory show that the faecal pellets of the larvae of *Philosamia ricini* contain remains of the leaf cuticles and pollen grains of *Ricinus communis* on which they feed. All this work indicates that the coprolites of *Caytonia* may have belonged to an insect caterpillar. It is reasonable to believe that the plants of the Glossopteris flora of India and other parts of Gondwanaland were living in conditions which were quite like those of the coal forming Carboniferous forests of Europe and N. America and therefore it is quite possible that the plant animal interactions in the coal forming Gondwana forests may have been similar. Accordingly if we try to look for the fossil evidence of such interactions in our Lower Gondwana strata it should yield positive results.

In fact, there seems to be an urgent need of a reorientation of our entire outlook on fossil plants wherein we need to incorporate palaeoecology and taphonomy in comparison with similar work on living plants. Most palaeobotanists have hitherto confined their studies to individual aspects of fossil plants in complete isolation and without looking at associated animal remains for plant animal interactions and without interpreting our results in the light of comparable aspects of living ecosystems. Indeed our approach in palaeobotany requires a complete paradigm shift where the emphasis should henceforth be on holistic studies which try to understand the interrelatedness of fossil plants, nay the entire fossil floras and contemporary animals as they lived in their surrounding environment in comparison with similar holistic studies of present day plants and animals.

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