LECTURE

Hayfever in the Palaeozoic: reproductive strategies of lycophytes

Summary of lecture presented to the Society on Saturday 10th March 2001 by Dr Alan Hemsley, of Cardiff University.

The Lycopodiopsida (club mosses) arose in the late Silurian and early Devonian and, like other plant groups, began to diversify as part of the adaptive process of terrestrialisation. Like all early land plants, the club mosses reproduced by the dispersal of spores that were small in size and easily distributed by air currents (Burrows, 1975). Although probably not allergenic, the shear volume of small spores produced by Palaeozoic land plants was impressive. These spores were part of a reproductive cycle that arose as a result of the alternation of generations (diploid and haploid) presumably inherited from algal ancestors. Simply, mature diploid club moss plants (sporophytes) would produce haploid spores that germinated to give diminutive haploid plants (gametophytes) which in turn would produce male and female reproductive apparatus. Male structures (antheridia) would produce sperm that would swim in a film of water to the female eggs (archegonia) where they would then fuse to form a zygote (diploid again). This would then grow into a new club moss plant (sporophyte) to repeat the process. We can be confident that these plants followed this sequence because it is exactly how living pteridophytes such as ferns, horsetails and surviving club mosses reproduce today.

Reproduction by small spores is efficient as demonstrated by the abundance of living pteridophytes despite a wealth of competition from seed plants. However, pteridophytes such as club mosses are restricted in their possible habitats by the requirement of that film of water for the swimming sperm during reproduction. Inevitably, as land plants flourished through the Palaeozoic, so competitive evolution led to the exploration of possible means by which the pteridophytic mode of reproduction could bypass the need for abundant substrate moisture. The first major development to escape constraint was heterospory.

Heterosporous pteridophytes produce two types of spore; small male spores much the same size as ordinary wind dispersed spores (30-80 mm), and large female spores that may reach 2 mm or more in diameter. These spore types give rise directly to sperm in the case of the male while the large female spores split open along predefined lines of weakness to expose archegonia within. Although this process still requires a water film for sperm transit, many other features of the pteridophyte reproductive cycle have been minimised. In both the male and female, the gametophyte plant is largely retained within the protective coat of the spores and only the sperm has to brave the external environment. The female megaspores (Fig. 1a and b) are large because they contain food reserves for the rapid development of young sporophytes once their eggs are fertilised. This helps to speed up the reproductive process. Thirdly, there are many examples where we find the small spores of a club moss species attached to the outer coating of megaspores of the same species. This method, by which females carry males with them, must surely assist in the likelihood of fertilisation and minimise the distance over which the sperm must swim to achieve this. It is the adaptations of the spore coatings for small spore capture and the dispersal of the megaspore that made these large spores a particular nasal and skin irritant.

Heterosporous club mosses were abundant in the Carboniferous and at this time, many forms had evolved that had attained tree-like proportions. These produced a rain of both small spores and megaspores. Tree club mosses was able to disperse spores over a greater distance but some forms produced wing-like modifications of their coatings that enabled them to travel even greater distances. The flange-like wings effectively reduced their density and the speed with which they fell.

Other megaspore types (e.g. Lagenicula) may have evolved to achieve minimal dispersal. These were spiny with an aerodynamic extension to the apex of the spore. They perhaps fell directly to the ground beneath the parent plants that grew in dense dark swamp forests. This would have been a useful strategy where the parent was monocarpic (it died after spore production) since the death of the parent would provide a gap in the canopy and an increase in the available light immediately above the sporelings. These monocarpic tree club mosses posed additional airborne irritation besides their spiny megaspores. With these and other club mosses, spores were produced in small packets (sporangia) which were borne in association with a scale-like leaf. These scale leaves were usually aggregated into cones borne at the ends of branches. Once the spores were shed from the sporangia, the cones would have disintegrated, releasing the sharp scales to fall to the ground.

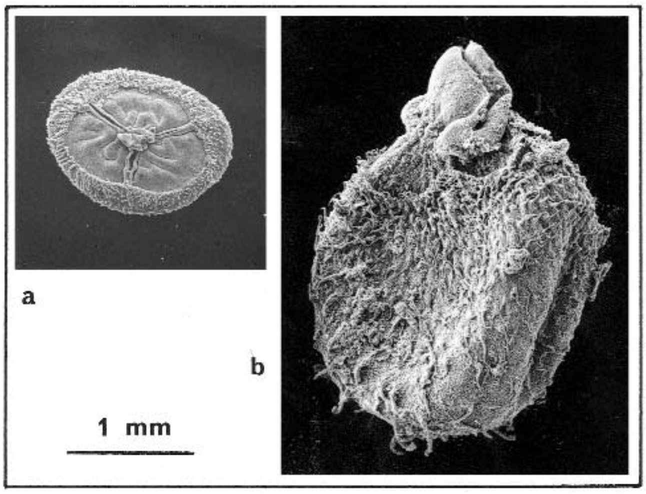

Figure 1. a) *Setosisporites brevispinosus*, a typical Carboniferous club moss megaspore. b) *Lagenicula crassiaculeata*, one of a number of species of megaspore produced by tree club mosses.

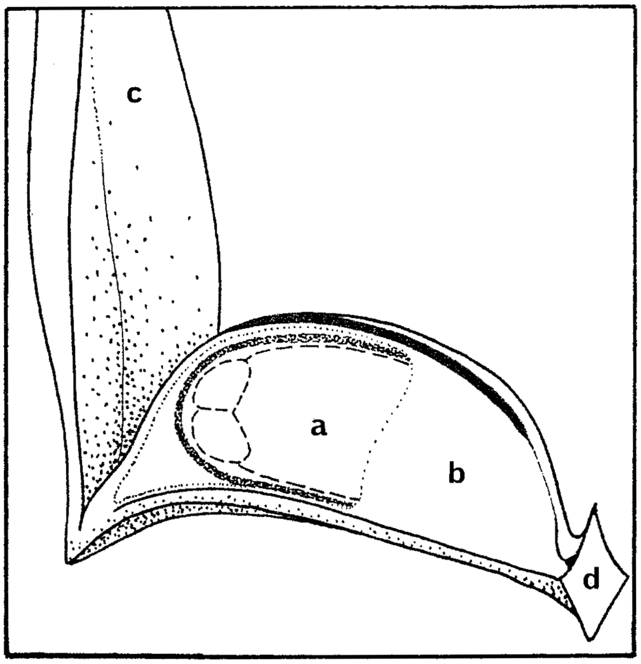

Figure 2. The Lepidocarpon reproductive unit, consisting of a megaspore within a sporangium (a) enclosed by extensions of the scale-like leaf (b) that also extended as a wing-like projection (c) beyond the sporangium. These were attached to a central axis at (d).

All of these megaspore-bearing plants, despite their abundant success (they form much of the plant material constituting the Carboniferous coal measures), were still restricted by the requirement of a water film for the passage of sperm to egg. One form of tree club moss, however, adopted a more extreme strategy. The cone known as Lepidocarpon was unusual in that the sporangia within only contained one functional megaspore of enormous size (up to 11 mm). Furthermore, the sporangium was enclosed almost completely by two extensions of the associated scale-like leaf (Thomas, 1981). This unit (Fig. 2) was therefore dispersed in its entirety; scale, sporangium and spore all together. One reason for this may have been that the attached scale could have aided dispersal by acting in much the same way as the wing of a sycamore seed. Laboratory experiments utilising models of 'lepidocarps' suggest that this was indeed a factor and also demonstrated how dangerous these sharp-scaled falling units would have been (Habgood et al., 1998). However, the most important function of the enclosing scale may have been to selectively collect male spores for fertilisation of the female, directly from air currents.

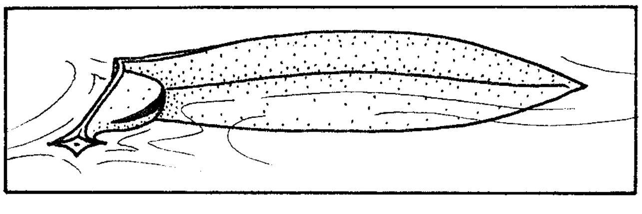

Figure 3. The floating position of 'lepidocarps', on their sides, where the slit along the top permitted fertilisation from spores and sperm at the water meniscus.

If this were the case, then Lepidocarpon behaved in the same way as seed plants that capture pollen from the air flow to fertilise an ovule (Crane, 1986). This method of male spore capture and delivery directly to the archegonia of the female spore eliminated the need for a film of water and thus enabled Lepidocarpon and its descendants to colonise drier habitats along with the seed plants that had already established a foothold in these areas.

Sadly, however, it seems that 'lepidocarps' were not fertilised by male spores captured from the air whilst they were still attached to their cones. Instead, they appear to have been even more reliant upon water fertilisation than some of the conventional megaspores. Laboratory experiments suggest that, following dispersal, 'lepidocarps' floated on the surface of local water bodies in such a way that the small opening left between the enclosing leaf scale extensions was in the perfect orientation to collect male spores and sperm from the water meniscus where they too had been shed or released (Habgood *et al.*, 1998, Fig. 3). This method of fertilisation matches our understanding of Carboniferous swamp ecology, but rather diminishes the status of Lepidocarpon as the club moss that almost became a seed plant.

There can be little doubt that, during the Carboniferous, the club mosses achieved a startling degree of diversity and that 'Lepidocarpon' is an advanced reproductive structure that crowned this age of pteridophyte exuberance. The seed plants, however, were already exploring drier habitats with their sophisticated pollination mechanisms and would go on through the Mesozoic to become the dominant land plants. None the less, in the dark swamp forests of the Palaeozoic, the club mosses thrived and to have ventured into such places (if one could) without a face mask and robust head protection would have been unwise indeed.

The author thanks Prof. Barry Thomas and Dr Kate Habgood for their assistance in laboratory experiments involving 'lepidocarps'.

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