A missing link for seeds?

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IN the history of life on land, with the interplay between plants and animals that it records, it was plant evolution that set the pace. The first step in this process was the 'greening of the land' as terrestrial habitats were colonized by vascular plants; they made the land habitable for animal life by offering a shaded, moist environment with built-in primary productivity, into which first the arthropods and later the vertebrates came ashore. The second step was the evolution of the seed — a pre-packaged food parcel evolved as a store to give the plant embryo a start in life, but subsequently exploited by herbivores for their own nutrition. The discovery by Galtier and Rowe, reported on page 225 of this issue¹, of an entirely new type of early fossil seed in the Montagne Noire deposit in France, raises important and unexpected questions about the details of this major step in land-plant evolution.

During the past 20 years there have been many significant additions to the fossil evidence, providing a picture of the evolutionary stages leading up to the first seed^{2,3}. There is now a well-documented record⁴ of the spore-bearing ancestors (the Progymnospermopsida) which gave rise to the earliest gymnosperms. There is general agreement that these were the stock from which all living seed-bearing plants (both gymnosperms and angiosperms) ultimately arose. There are still disagreements about details, such as whether the seed evolved only once (monophyletically) or whether the seed appeared

independently more than once (polyphyletically) from different groups within the progymnosperms⁵.

The origin of the seed was an important breakthrough in land-plant reproductive strategies. Heterosporous plants of the late Devonian reduced the number of megaspores in each sporangium to culminate in a single, very large surviving

occupies an intermediate position between, say, the condition shown in *Bensonites* and *Archaeosperma* in the evolutionary series in Fig. 1.

Does this newly discovered fossil seed-precursor then represent a 'missing link' in seed evolution which survived into the early Carboniferous, after the appearance of true seeds with complex pollen-trapping structures? Or is it simply an immature stage of development which would eventually have formed some pollen-trapping structure like that seen in contemporaneous seeds of the early

Carboniferous? Of these two possible explanations, the latter must be rejected as the well-preserved tissue at the seed apex is very clearly mature. Some other pollination (or fertilization) strategy must have been involved, but what form it took can only be guessed at. Maybe this would-be seed simply fell into its swampy habitat and its egg was directly fertilized by sperm released into a surface water film. This would make the behaviour of

the whole structure more like the megaspore of a heterosporous plant, such as some of the living water ferns, rather than constituting a true seed. The further possibility exists that pollen was caught on the outer surface of the seed apex, rather as pollen lands on the stigma of flowering plants. A pollen tube could then have carried the sperm to the egg (siphonogamy), as in most living gymnosperms.

As with many fossil discoveries, Galtier and Rowe's seed-like body raises more questions than it answers. It certainly encourages re-thinking the question of seed monophyly, and may be seen to point to a polyphyletic origin. It is also a salutary reminder of how little is known about important details of early seed-plant fertilization processes, and how much the fossil record still undoubtedly holds. Further search for other early seeds in the Montagne Noire deposit, and others at the same or earlier horizons, will undoubtedly contribute further to our knowledge of this critical phase of land-plant evolution. □

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FIG. 1 A series of Devonian and Carboniferous megasporangia and seeds representing possible evolutionary stages in seed evolution, showing progressive reduction in megaspore number, and enclosure of the seed megaspore (from ref. 2).

megaspore forming the central structure of the earliest seeds⁶ of the end-Devonian/earliest Carboniferous (see Fig. 1). Then, instead of sexual reproduction involving motile sperm swimming through soil moisture to fertilize an egg in a megaspore lying on the ground (as in living *Selaginella*), the fertilization process was internalized. This gave plants greater independence from moisture in the environment in effecting their reproduction. Pollen borne on the wind was trapped by these early seeds, probably in an exuded moisture drop (as in living conifers), and drawn into a pollen chamber. This meant that the egg enclosed in the seed could be fertilized while still attached to the parent plant. The developing embryo could then be supplied with a food store before being shed, still inside the seed.

The discovery reported by Galtier and Rowe¹ of a new type of early seed-like structure in lower Carboniferous rocks (see Fig. 2) raises important questions about how the first seeds evolved. Hitherto, all known early fossil seeds show clear evidence of a fairly elaborate pollen-trapping mechanism at the seed apex (for example, *Cardiocarpus*), although their structure is in other respects significantly different from that of living gymnosperms. The seed-like body reported by Galtier and Rowe (which post-dates our earliest record of seeds only by a few million years) is surprising in having no pollen-trapping structure, or evident access for pollen to the female gametophyte. This is despite its preservation being remarkably good, in that it retains all the internal details of its cellular structure preserved three-dimensionally in silica. This fossil

FIG. 2 New primitive seed-like structure from the early Carboniferous of France — oblique transverse section through integument lobes. (Courtesy of J. Galtier.)

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