ANGIOSPERM PHYLOGENY

Evolution in hidden forests

Christopher J. Cleal

PALAEONTOLOGICAL evidence now suggests that flowering plants (angiosperms) may have evolved first in the middle Mesozoic, possibly the late Jurassic, then radiated into different groups in the late Cretaceous. There have, however, remained lingering doubts about the quality of the early angiosperm fossil record. Do the fossils really reflect the early evolution of angiosperms as a whole, or are they just the remains of a group of species which happened to favour lowland habitats? To try to resolve this problem, Martin, Gierl and Saedler have applied the 'molecular clock' principle to nine extant angiosperms, representing six subclasses of both dicotyledons and monocotyledons. These authors report their rather startling results on page 46 of this issue[1].

The pattern of divergence of the lineages represented by these nine species is perhaps not surprising. The oldest divergence is of the monocot and dicot lines, followed later by the concurrent divergence of the five dicot subclasses. The primary division of the angiosperms into monocots and dicots is widely recognized, and the early divergence into these two lineages lends support to this. But the timing of these divergences is more problematic: the monocot–dicot divergence is thought to have occurred in the Carboniferous (319 ± 35 million years ago), and the dicot subclass divergence in the Permian (276 ± 33 million years ago). But this is about 150 million years before the earliest indisputable angiosperms appear in the fossil record.

Martin, Gierl and Saedler point out that, at face value, these results suggest that the angiosperms have a long pre-Cretaceous history, as has been argued by Axelrod[2]. If this is true, there must have been an angiosperm homeland — a hypothetical 'upland' area where the group first appeared, perhaps in the Triassic or Permian, but where it would not be preserved in the fossil record. Angiosperms are supposed to have evolved in these hidden forests for a considerable time, until the Cretaceous, when they developed characters that made them pre-adapted to lowland habitats. Only then were they able to make their appearance in the fossil record. This view has recently become unpopular, mainly through the work of Hickey and Doyle[3] and Doyle[4], who have demonstrated an apparently plausible phylogeny for early angiosperms in the Cretaceous fossil record. But it is surely something of a coincidence that, of all the terrestrial habitats that were available, the flowering plants just happened to appear first in lowland, sediment-accumulating areas.

I suspect that the truth lies somewhere in between: angiosperms probably did evolve in so-called 'upland' areas, where fossils were unlikely to be preserved[5], but not as long ago as the Triassic or Permian. It seems unlikely that the flowering plants, which are today so environmentally adaptable, took 100 million years to occupy the lowlands. There are more problems if the first appearance of the angiosperms was in the Carboniferous; not only is there an extra 50 million years or so, during which angiosperms were unable to descend to the lowlands, to account for, but where were the angiosperm ancestors? They are widely believed to have been among the Mesozoic seed-plants, such as the bennettites and corystosperms[6], but there is no unequivocal evidence that these groups existed before the Triassic. Is it necessary again to postulate a long 'upland' history for these groups? Perhaps Long's hypothesis[7] needs to be re-examined. Long suggested that angiosperm ancestors would be found among Lower Carboniferous pteridosperms, but subsequent cladistic analyses do not support this idea[6,8].

Martin *et al.* alternatively suggest that their results may reflect a polyphyletic origin for the angiosperms. The postulated dates of divergence are those of the most recent common ancestor and, if angiospermy arose along several distinct lineages, this common ancestor need not itself be an angiosperm. Several authors have argued for angiosperm polyphyly[9,10], but the presence of unique characters in the group, including double fertilization, provides a strong argument in favour of monophyly[6,8]. It is difficult (but not impossible) to see how these characters all appeared independently in several lineages.

Martin *et al.* provide a thought-provoking study, but the marked discrepancies between their results and the fossil record make it essential that their method is robust. As a geologist, I am unqualified to enter into such a debate, but, if I understand the argument of Martin *et al.* correctly, the dating of the divergences depends on a constant rate of change in nucleotide sequences over long periods of time. I wonder about the validity of this argument, and even how it could ever be tested, other than by comparisons with the fossil record? The molecular clock was clearly ticking in the angiosperms, but was it keeping the right time? □

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ANGIOGENESIS

Successful growth of tumours

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THE successful growth of tumours is dependent on the process of vascularization (angiogenesis), but it is not known how these processes are related to each other. On page 58 of this issue[1], however, Folkman *et al.* clearly confirm that there is a correlation between the presence of factors that stimulate tumour growth and angiogenesis. Furthermore, Rastinejad *et al.*[2] have discovered a previously unknown inhibitor of angiogenesis which seems to be produced by cells when they are capable of expressing an active cancer-suppressor gene. The loss of this inhibitor activity occurs concomitantly with expression of both angiogenesis and tumorigenesis[2].

In their studies reported in this issue, Folkman *et al.*[1] examined genetically engineered mice expressing an oncogene in the beta cells of the pancreatic islets. As a consequence, these cells demonstrate a heritable capacity to proceed through the steps of tumorigenesis — from normal to hyperplastic to neoplastic. Folkman *et al.* find that in some isolated hyperplastic islets *in vitro*, angiogenic activity appears before the neoplastic transformation, suggesting that these hyperplastic islets induce angiogenesis by secretion of angiogenic molecules. Similar activity would presumably occur when hyperplastic islets become vascularized *in vivo* at a frequency correlated with incidence of tumour formation.

Folkman *et al.* interpret their results to imply that the angiogenic capability expressed by a given islet cell develops because of changes in the hyperplastic islets during the pre-neoplastic period, presumably after they have become committed to progressing to neoplastically transformed cells. In particular, Folkman *et al.* say that their data indicate a correlation between angiogenesis and the start of vascularization that precedes tumour formation (or that may be partly responsible for the transition from hyperplasia to