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The origins of flowering plants and insect pollination

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One line summary: New research draws conflicting conclusions about the timing of the origin of flowering plants, with profound implications for understanding how and when interactions with pollinators evolved.

Main text

For more than a century there has been a fascination with the surprisingly rapid rise and early diversity of flowering plants (angiosperms). Darwin famously described the seemingly explosive diversification of angiosperms as an “abominable mystery”, and debates still rage about the origin and the processes driving angiosperm speciation. Dating the origin of angiosperms was traditionally the prerogative of palaeobotanists that read the fossil record of plants, but with DNA sequencing becoming increasingly sophisticated and accessible, molecular dating methods have come to the table. Many angiosperm fossils can be dated to the Early Cretaceous [~145 million years ago (Mya)], which has led palaeobotanists to reason that they originated during that era. Nowadays, it is increasingly recognised that angiosperms are probably older than the oldest fossils, but how much older remains controversial. Dating the origin of angiosperms is not only important from a strict botanical point of view, but it is also key to understanding the origin and evolution of those animals that act as pollinators, in particular insects such as bees, butterflies, moths and flies, as well as vertebrates such as hummingbirds.

Recent papers highlight the disparity of molecular and palaeontological timescales and draw conflicting conclusions as to the timing of angiosperm diversification (Figure 1). Based on gene sequences from 2881 chloroplast genomes belonging to species from 85% of living flowering plants, time calibrated using 62 fossils, one study (*1*) dated the origin of angiosperms to the Late Triassic (>200 Mya). This is ~70 My (roughly the equivalent of the Jurassic) before the earliest accepted angiosperm fossils. They further suggest that major radiations occurred in the Late Jurassic and Early Cretaceous. By contrast, an overview of palaeobotanical evidence (*2*) refutes a substantive pre-Cretaceous diversification, with only some specific clades (such as water lilies) perhaps originating during the Late Jurassic. They argue that the sequential appearance of different types of fossils and morphological characters render major earlier diversification events unlikely, supporting previous studies (*3*, *4*). Although the idea that angiosperms arose around the beginning of the Cretaceous may seem hard to reconcile with the rapid increase in morphological diversity observed during that interval, it is not impossible if the Cretaceous radiation occurred rapidly.

Both palaeontological records and molecular analyses have their strengths and weaknesses. The strength of fossils is that they can provide information on past form, function and clade richness, and indirectly provide information on speciation and extinction. Fossils are particularly useful when they harbour intermediate structures or combinations of characters that no longer exist, which can provide insightful examples that help reconstructing the course of evolutionary events. However, the interpretation of fossils can be subjective and controversial, because important features of these plants may not be preserved and often palaeontologists are working with two-dimensional and compressed remains. In addition, the absence of evidence is no evidence of absence, and it is known that the fossil record can be incomplete or biased, because some taxa may be less likely to fossilise. For example, specific ecologies or habitats will influence the likelihood of whole plant fossilisation, though pollen is a useful exception as it can generally survive more extreme conditions. Furthermore, anchoring a fossil to a specific time period relies on accurately dating the strata in which it was found, which can also be problematical, although the error margin caused by this factor is usually rather small. It is important to keep in mind that there can be a considerable lag between time of origin and the earliest recognisable fossil, because fossils generally appear when a taxon has existed for some time and in relatively high frequencies, a phenomenon known as the Signor-Lipps effect. Additionally, molecular analyses are built on hard-to-estimate variables, such as the distribution of mutation rates across taxa and time. Variation in branch lengths – which inevitably occurs in datasets with many species – frequently leads to overestimation of age (*5*, *6*). Indeed, molecular analyses often push origin dates back in time, including the older lineages, but whether this is a methodological error remains unclear.

One of the hallmarks of angiosperms is their relationship with animal pollinators, especially insects. As with plants, the diversification of insects is a field with many uncertainties. The origin of several important orders of flower-visiting insects (e.g., Coleoptera, Diptera, Hymenoptera and Lepidoptera) lies in the Permian/Triassic (Figure 1) with marked radiations in the Cretaceous, which is frequently mentioned to coincide with the main angiosperm radiation (*7*). However, the timing of the origin of flower-visiting insects is debated. For example, for Lepidoptera (butterflies and moths), a Late Triassic radiation has been suggested based on fossil evidence (*8*), but a recent study using transcriptomes covering nearly all Lepidoptera superfamilies dated the origin even further back (*9*). Although butterfly diversification may be triggered more by host plant chemistry than by floral diversity – which need not be correlated – given the importance of butterflies and moths for angiosperm reproduction, their diversification is important in understanding plant-pollinator interactions.

Notwithstanding that the timing of the origin of angiosperms remains debated, if angiosperms arose before the Jurassic, this has profound implications for understanding how insect pollination evolved. There is little doubt that insect pollination accelerated the angiosperm radiation; however, which factor triggered what evolutionary event becomes more complex given the latest findings. It was long considered that wind pollination in early-diverging nonflowering seed plants (gymnosperms) was replaced by animal pollination in angiosperms, and that this switch to animal pollination led to angiosperm diversification, but this seems an oversimplification (*10*). Many now-extinct gymnosperms (e.g. Bennettitales) were insect-pollinated, and angiosperms could have either evolved directly from insect-pollinated gymnosperms or from wind-pollinated gymnosperms in such a way that they co-opted insects that were servicing gymnosperms in the same community. Conversely, if the earlier Triassic origin of angiosperms is correct, some gymnosperms may have co-opted insects as pollinators from early angiosperms. It seems unlikely, however, that this latter process was important in the grand scheme of angiosperm evolution, because even if they occurred at this earlier period, angiosperms were not a dominant plant group in the Jurassic. By contrast, Bennettitales were ecologically dominant plants in Late Triassic to Jurassic floras, arguing that the transition to insect pollination in angiosperms came via these gymnosperm groups. These possibilities are more complex than the standard progress from primitive wind to advanced insect pollination scenarios. They hint at a richer ecological milieu of more complex interactions between species than had previously been appreciated, including insect groups that are currently much less important as pollinators, such as scorpionflies (*Mecoptera*) (*12*).

The timing of flowering plant origins also provides a minimum age for the evolution of their most prominent feature – flowers. Insect pollination in many extant gymnosperms (e.g., cycads, *Ephedra*, *Gnetum*) is facilitated mainly by scent, rather than visual attraction. If the same was true of the extinct gymnosperms, which is plausible, then the increasing importance of visual-based cues to attract pollinators in angiosperms could be one of the defining features of angiosperm evolution and their success. Further, if floral structures predate some speciose orders of flower-visiting insects, perhaps flower features have shaped trait evolution in these large insect groups. There are clear examples of co-evolution of specific floral and pollinator characteristics in some systems, e.g., floral tube and pollinator tongue length (*12*).

What about more general floral features such as colour and scent? For example, did floral colour and scent evolve to match pollinator vision and olfaction, or vice versa, or did signal production and detection evolve synchronously? The basic principles of colour vision in insects, such as the possession of three types of photoreceptors (ultraviolet, blue, green), seem to predate flowers regardless of whether they arose during the Triassic or later (*13*). Colour vision is also used for key behaviours such as mate and predator detection and finding oviposition sites, together indicating that the evolution of colour vision is unlikely to be driven by flower colours. A similar ancestral origin of olfaction compared to scent production was documented in a group of plants pollinated by scarab beetles (*14*), where odour reception by pollinators predates production of the signal by plants. However, behavioural aspects of olfaction or colour vision, such as innate colour preferences that shape foraging behaviour in various insect groups (*15*), may have evolved later, in response to floral signals. All of this depends on the timing of the evolution of flowering plants, and the order of the evolution of insect pollination. If insect pollinated gymnosperms predate angiosperms, for example, then it may be possible to trace the origin of these visual and olfactory traits to long-extinct clades of plants that once dominated terrestrial floras.

Future palaeontological discoveries will undoubtedly unveil additional fossils, and the use of complementary sequencing approaches and more sophisticated evolutionary models will help to mitigate the limitations imposed by the rampant polyploidy in plants that frequently hinders analysing nuclear genes. Whether Darwin's question about the timing of flowering plant evolution and radiation will ever be answered remains a mystery, but clearly this question including its ecological implications for understanding insect pollination, are very complicated.

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Figure 1. Evolution of angiosperms based on molecular and fossil evidence.

Fossil and molecular evidence draw conflicting conclusions about the timing of the origin of flowering plants. Fossil evidence suggests flowering plants arose near the beginning of the Cretaceous, but molecular analyses date the origin much earlier, in the Triassic.

Evolution of angiosperms according to molecular and fossil evidence

Fossil and molecular evidence lead to conflicting conclusions about the timing of the origin of flowering plants. Fossil evidence suggests that flowering plants arose near the beginning of the Cretaceous, but molecular analyses date the origin much earlier, in the Triassic.