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INSIGHTS

PERSPECTIVES

EVOLUTION

The origins of flowering plants and pollinators

New research raises questions about when flowering plants and their pollinators evolved

By **Casper J. van der Kooi¹** and **Jeff Ollerton²**

For more than a century there has been a fascination with the surprisingly rapid rise and early diversity of flowering plants (angiosperms). Darwin described the seemingly explosive diversification of angiosperms as an “abominable mys-

tery,” and debates continue about the origin and processes driving angiosperm speciation. Dating the origin of angiosperms was traditionally the prerogative of paleobotanists who read the fossil record of plants, but with DNA sequencing becoming increasingly sophisticated, molecular dating methods have come to the table. Many angiosperm fossils

can be dated to the Early Cretaceous (~135 million years ago), which has led paleobotanists to reason that they originated during that era. It is now increasingly recognized that angiosperms are probably older than the oldest fossils, but how much older remains controversial. When angiosperms originated is key to understanding the origin and evolu-

The aquatic angiosperm *Archaeofructus liaoningensis* is one of the earliest fossil angiosperms to have been identified so far.

the Late Triassic, >200 million years ago. This is ~70 million years (roughly the equivalent of the Jurassic) before the earliest accepted angiosperm fossils. This study further suggests that major radiations (species diversification) occurred in the Late Jurassic and Early Cretaceous, ~165 to 100 million years ago. By contrast, an overview of paleobotanical evidence (2) refutes a substantive pre-Cretaceous diversification, with only some specific clades (such as water lilies) perhaps originating during the Late Jurassic. The sequential appearance of different types of fossils and morphological characteristics is proposed to 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 paleontological 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 harbor intermediate structures or combinations of characters that no longer exist, which can provide insightful examples that help to reconstruct 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 must be inferred from two-dimensional compressed remains.

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 fossilize. For example, specific ecologies or habitats will influence the likelihood of whole-plant fossilization, although pollen is a useful exception because it can generally survive more extreme conditions. Furthermore, anchoring a fossil to a specific time period relies on accurately dating the stratum in which it was found, which can also be problematic, although the error margin caused by this factor is usually small. It is important to keep in mind that there can be a considerable lag between time of origin and the earliest recognizable 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.

Molecular analyses are built on hard-to-estimate variables, such as the distribution

of mutation rates across taxa and time. Variation in divergence times—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 or Triassic (300 to 200 million years ago) with marked periods of diversification 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 on the basis of fossil evidence (8), but a recent study using transcriptomes covering nearly all Lepidoptera superfamilies dated the origin even further back, during the Carboniferous (~300 million years ago) (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 non-flowering 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 evolved either 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

tion of pollinators, particularly insects such as bees, butterflies, moths, and flies.

Recent reports highlight the disparity of molecular and paleontological time scales and draw conflicting conclusions about the timing of angiosperm diversification (see the figure). On the basis of gene sequences from 2881 chloroplast genomes belonging to species from 85% of living flowering-plant families, time-calibrated using 62 fossils, one study (1) dated the origin of angiosperms to

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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.

the 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 and other early seed plants were ecologically dominant in Late Triassic to Jurassic floras, indicating that the transition to insect pollination in angiosperms arose through these gymnosperm groups. These possibilities are more complex than the standard scenarios that envisioned a progression from primitive wind pollination to advanced insect pollination. 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) (11).

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 by visual attraction. The same may have been true of the extinct gymnosperms, but because scent does not fossilize, it may be impossible to ever know. However, if the reproductive structures of these extinct gymnosperms functioned in a manner similar to their living relatives, with odor predominating, then the increasing importance of visual-based cues to attract pollinators in angiosperms could be one of the defining features of angiosperm evolution and success. Further, if floral structures predate some speciose orders of flower-visiting in-

sects, perhaps flower features have shaped trait evolution in these large insect groups.

There are clear examples of coevolution of specific floral and pollinator morphological characteristics in some systems, such as floral tube length and pollinator tongue length (12). What about floral features such as color and scent? For example, perhaps floral color and scent evolved to match pollinator vision and olfaction, or vice versa. Alternatively, signal production may have evolved synchronously with detection. The basic principles of color 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). Because color vision is also used for key behaviors such as detecting potential mates and predators and finding oviposition (egg-laying) sites, the evolution of color vision is unlikely to be driven by flower colors.

A similar ancestral origin of olfaction compared to scent production was documented in a group of plants pollinated by scarab beetles (14), where odor reception by pollinators predates production of the scent signal by plants. However, behavioral aspects of olfaction or color vision, such as innate color preferences that shape foraging behavior 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 as well as the order of evolutionary events that led to 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 paleontological discoveries will undoubtedly reveal 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 analysis of 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 and its ecological implications for understanding insect pollination are complicated. ■

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