

The evolutionary history of flowering plants

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Abstract

In terms of species richness and important ecological roles, there are few biological groups that rival the success of flowering plants (Angiospermae). Angiosperm evolution has long been a topic of interest, with many attempts to clarify their phylogenetic relationships and timescale of evolution. However, despite this attention there remain many unsolved questions surrounding how and when flowers first appeared, and much of the angiosperm diversity remains to be quantified. Here, I review the evolutionary history of angiosperms, and how our understanding of this has changed over time. I begin by summarising the incredible morphological and genetic diversity of flowering plants, and the ways in which this can be studied using phylogenetic inference. I continue by discussing both the relationships between angiosperms and the other major lineages of seed plants, and the relationships between the main groups within angiosperms. In both cases, I outline how our knowledge has changed over time based on factors such as the different conclusions drawn from morphological and genetic data. I then discuss attempts to estimate the timescale of angiosperm evolution and the difficulties of doing so, including the apparent conflict between ages derived from fossil and molecular evidence. Finally, I propose future directions for angiosperm research to help clarify the evolutionary history of one of the most important groups of organisms on the planet.

Introduction

The diversity and interactions of life on Earth have long been of scientific interest. Quantifying biodiversity and the timescale over which it arose allows inferences about the biological history of the planet to be made, and can provide insight into how ecosystems might change in response to events such as climate change (Thuiller et al. 2011; Bellard et al. 2012). Flowering plants (angiosperms) have been of particular focus because of their important economic and cultural roles within society, as well as their ubiquity and importance within natural ecosystems. Specifically, angiosperms sequester large amounts of carbon from

the atmosphere, and act as primary producers of food for many animal groups, with their spread and appearance shaping habitat structure globally (Brodribb and Feild 2010; Magallón 2014). In addition, angiosperms have developed important mutualistic relationships with many groups of organisms, such as pollination interactions with insects, birds, and small mammals (van der Niet and Johnson 2012; Rosas-Guerrero et al. 2014).

However, to properly quantify the extent and impact of groups such as angiosperms, biological entities must first be recognised and described into distinct groups such as species, and, ideally, placed into higher-order classifications. The goal is to

recognise groups that contain only the descendants of a common evolutionary ancestor (monophyletic groups), which represent natural evolutionary groups.

For most of history, biological groups and the relationships between them have been recognised through observations of the form and structure of organisms. When these data are shared between two or more taxa after being inherited from their most recent common ancestor, they are known as synapomorphies. In addition to aiding the classification of extant taxa, these morphological data are also able to link extant and extinct diversity through comparison with the fossil record, which can suggest a timescale of evolution. However, morphological data often cannot reliably distinguish between competing taxonomic hypotheses because of a lack of informative characters, or can be misled by the independent evolution of similar traits in organisms that are not closely related (convergent evolution). Morphological data have been supplemented by molecular data since the inception of molecular phylogenetics in the mid-20th Century.

Molecular data typically comprise sequences of the nucleotides of DNA, or the amino acids that they encode. Each nucleotide or amino acid within a sequence represents a character that can be used for phylogenetic analysis. Therefore, molecular data sets can contain millions of characters for phylogenetic reconstruction, which makes such data sets especially useful for evaluating the taxonomic hypotheses that have been suggested by morphology. Analysis of molecular data is also useful for estimating the evolutionary timescale of organisms using molecular clocks (Lee and Ho 2016), especially for groups with poor fossil records.

Both morphological and molecular data have been used extensively to evaluate the

diversity of angiosperms. Angiosperms are among the most species-rich groups of organisms on the planet, and are by far the largest group of plants. The exact number of species is difficult to determine because of high amounts of taxonomic synonymy, and the fact that many species potentially remain to be discovered (Bebber et al. 2010; Pimm and Joppa 2015). Despite this, we can be fairly certain that there are at least 350,000 species of angiosperms, and probably *c.* 400,000 in total (Pimm and Joppa 2015). As expected in a group of this size, there is extreme variation in morphology, life history characteristics, and growth form. Angiosperms variously exist as herbaceous annuals, vines, lianas, shrubs or trees, and can be found growing in aquatic or terrestrial environments, or even growing on and/or parasitising other plants.

Similarly, there is large variation in genome size and content within angiosperms. For example, it is estimated that throughout their evolutionary history over 70% of angiosperms have had an increase in the number of copies of chromosomes contained within each cell (ploidy level) from the typical diploid state (Levin 2002). Most of the functions essential for growth and development are controlled by genes located within the cell nucleus, which are collectively known as the nuclear genome. *Paris japonica* Franch., a small herbaceous plant native to Japan, has the largest accurately measured genome known to science (Pellicer et al. 2010). At nearly 150 billion nucleotides, its octoploid genome is more than 50 times larger than the human genome, and nearly 2500 times larger than the smallest known plant nuclear genome of *Genlisea tuberosa* Rivadavia, Gonella & A.Fleischm., a carnivorous angiosperm from Brazil (Fleischmann et al. 2014).

Plant cells also contain specialised organelles known as chloroplasts and

mitochondria, which are responsible for the essential processes of photosynthesis and cellular respiration, respectively. Both of these organelles are predominantly uniparentally inherited and contain their own independent genomes, which is thought to be because of their origins as free-living organisms that were engulfed by early eukaryotic cells in separate endosymbiotic events (Sagan 1967; Schwartz and Dayhoff 1978). The chloroplast genome varies substantially among angiosperms, with the order of genes differing between groups, and with some genes being lost completely. For example, the chloroplast genome is drastically reduced in many parasitic plants, with many genes important for photosynthesis having been lost (Bungard 2004).

The mitochondrial genome of plants is more enigmatic, and is disproportionately less studied than the nuclear and chloroplast genomes. Plant mitochondrial genomes are large compared with animal mitochondrial genomes, and their content is highly dynamic, with many gene gains, losses, transfers, duplications and rearrangements, as well as a large proportion of repeated elements and introns (Kitazaki and Kubo 2010; Galtier 2011). Of direct importance for reconstructing the evolutionary history of plants is that the three genomes evolve at very different rates. The nuclear genome evolves at the highest rate, the chloroplast genome evolves at an intermediate rate, and, in contrast to its dynamic nature, the mitochondrial genome has by far the lowest evolutionary rate (Wolfe et al. 1987).

The global dominance of angiosperms indicates that they are ideally adapted to exist within many different habitats, and their great morphological and genomic variation suggests a history of varied selective pressures. This has long challenged those who have sought to quantify how such a

diverse group arose over a supposedly short period of time. Indeed, the traditional view is that angiosperms originated in the early Cretaceous. The subsequent appearance of fossils with highly diverse morphologies, over what was apparently an extremely rapid timescale, was famously described by Darwin as an “abominable mystery” in a letter to Joseph Hooker in 1879 (first published in Darwin and Seward 1903).

To understand fully the evolutionary history of angiosperms, their diversity needs to be characterised in a phylogenetic context. This approach indicates whether key traits for success are clade-specific, or have evolved multiple times in parallel. Additionally, incorporating temporal information into these analyses can allow inferences to be made about the environmental conditions that might have driven angiosperm diversification.

In this review, I begin by discussing our understanding of the relationships among the major seed plant lineages, and the importance of this for reconstructing the origin of flowers. I then discuss the relationships of the major lineages within Angiospermae, and examine estimates of the evolutionary timescale of angiosperms. I propose a number of the future directions that are likely to improve our understanding of the evolutionary history of angiosperms.

Higher relationships of angiosperms and the origin of flowers

Angiosperms are recognised as members of the superdivision Spermatophyta along with cycads, conifers, gnetophytes, and *Ginkgo*. The last four extant cone-bearing lineages are known as acrogymnosperms, whereas extant and extinct cone-bearing lineages combined are known as gymnosperms (Cantino et al. 2007). The five extant spermatophyte lineages are linked by the production of

seeds. Estimates of the number of seed plant species vary, but are consistently in the region of many hundred thousand species (Govaerts 2001; Scotland and Wortley 2003). Among other potential factors, the success of these lineages is perhaps due to the diversification of regulatory genes important for seed and floral development following ancient whole-genome duplication events along the lineages leading to seed plants and angiosperms (Jiao et al. 2011).

Angiosperms can be readily distinguished from gymnosperms through a suite of synapomorphies. These include the presence of flowers with at least one carpel, which develop into fruit (cf. the “naked” seeds of gymnosperms); stamens with two pairs of pollen sacs (cf. the larger, heavier corresponding organs of gymnosperms); a range of features of gametophyte structure and development, including drastically reduced male and female gametophytes compared with gymnosperms; and phloem tissue with sieve tubes and companion cells (cf. sieve cells without companion cells in gymnosperms) (Doyle and Donoghue 1986; Soltis and Soltis 2004). The production of endosperm through double fertilisation was previously considered to be a further synapomorphy of angiosperms, but this phenomenon has also been observed in some gnetophyte lineages (Friedman 1992; Carmichael and Friedman 1996).

Collectively, the synapomorphies of angiosperms are thought to be responsible for providing the evolutionary advantages that led to their global dominance, which coincided with a decline in gymnosperm diversity (Bond 1989). However, to reconstruct the evolution of these characters and evaluate their importance for angiosperm evolution, it is necessary to determine which lineage of seed plants is most closely related to angiosperms. The majority of earlier studies focused on

evaluating the seed plant phylogeny, including determining the sister lineage to angiosperms, using comparative morphology to assess homology of the reproductive and vegetative structures of the seed plant lineages (e.g., Doyle and Donoghue 1986).

One major hope was that determining the sister lineage to angiosperms might prove especially useful for inferring the origin and structure of the first flowers. Throughout the 20th century, the two main hypotheses for the origin of flowers were that they evolved from branched, unisexual reproductive structures found in most gymnosperms (“pseudanthial” theory, Wettstein 1907), or that flowers evolved from bisexual, flower-like structures, such as in the extinct group Bennettitales (“euanthial” theory, Arber and Parkin 1907). The inferred homology of morphological structures consistently suggested that gnetophytes were the extant sister lineage to angiosperms, with several potential close (non-angiosperm) fossil relatives. Specifically, various features of wood anatomy and flower-like structures seemed to suggest a close relationship between angiosperms, gnetophytes, and the extinct order Bennettitales, with this group being the sister lineage to the rest of the gymnosperms (Crane 1985; Doyle and Donoghue 1986). Therefore, based on the strength of morphological evidence, the euanthial theory was the most popular view in the 20th Century.

The acceptance of the euanthial theory, coupled with the predominance of Cretaceous *Magnolia*-like fossils at the time, led to suggestions that the ancestral flowers were similar to present-day magnolias. This implies that magnolias and their close relatives were some of the earliest-diverging angiosperm lineages (Endress 1987). However, most molecular phylogenetic studies from the 1990s onwards have

recovered different relationships between the extant seed plant lineages. The dominant theme in these modern studies is that all extant gymnosperm lineages form a monophyletic sister group to angiosperms (Chaw et al. 1997; Bowe et al. 2000; Chaw et al. 2000; Ruhfel et al. 2014; Wickett et al. 2014) (Figure 1). Particularly strong evidence has emerged for a close relationship between gnetophytes and conifers (Qiu et al. 1999; Winter et al. 1999). Indeed, the evidence seems to suggest that gnetophytes might even be nested within conifers and the sister group to Pinaceae (Bowe et al. 2000; Chaw et al. 2000; Zhong et al. 2010).

Overall, because none of the extant gymnosperm lineages is more closely related to angiosperms than to other gymnosperms, they cannot directly inform hypotheses on the homologies of angiosperm characters, or on the sequence of development of these characters (Doyle 2012). Therefore, while the relationships among the major seed plant lineages have been largely resolved, the structural origin of flowers, and the affinity of the earliest flowers to modern species, remains controversial. Progress in this area is likely to be achieved through improved understanding of the relationships among the major angiosperm groups.

Major relationships within Angiospermae

The major relationships within angiosperms have historically proved difficult to determine, and have long been in a state of flux. This has largely been due to differing ideas of the characters, initially morphological but later molecular, needed to reconstruct the angiosperm phylogeny. An early discovery was that flowering plants have either one or two embryonic leaves (Ray 1686–1704). While John Ray was the first to observe this dichotomy, he later

followed Marcello Malpighi in referring to these leaves as ‘cotyledons’. Accordingly, flowering plants with one cotyledon have subsequently been referred to as monocotyledons or ‘monocots’, and those with two cotyledons have been called dicotyledons or ‘dicots’.

Although the most widely known early classification scheme by Linnaeus was based solely on floral reproductive characters, the division into monocots and dicots has since been recognised as an important diagnostic feature to inform classification, with varying implications for the angiosperm phylogeny. A minority of early authors argued that some key morphological differences between monocots and dicots, such as vascular bundle anatomy, were irreconcilable with a monophyletic origin of angiosperms. Instead, these authors argued that angiosperms should be recognised as a polyphyletic group (= derived from more than one common evolutionary ancestor) (e.g., Meeuse 1972; Krassilov 1977). However, the predominant view was that angiosperms are monophyletic, and the division into monocots and dicots constitutes a natural split within flowering plants. This was echoed in many angiosperm classification systems developed in the 20th century, including the highly influential Takhtajan (1980) and Cronquist (1981) systems.

To infer the evolutionary relationships within monocots and dicots, many cladistic analyses were undertaken in the latter half of the 20th century using pollen, floral, and vegetative characters. This approach led to many informal subgroups being proposed. For example, Donoghue and Doyle (1989b) recognised five major groups of angiosperms, corresponding to Magnoliales, Laurales, Winteraceae-like plants, ‘paleoherbs’ (‘primitive’ herbaceous lineages including water lilies and *Amborella*), and

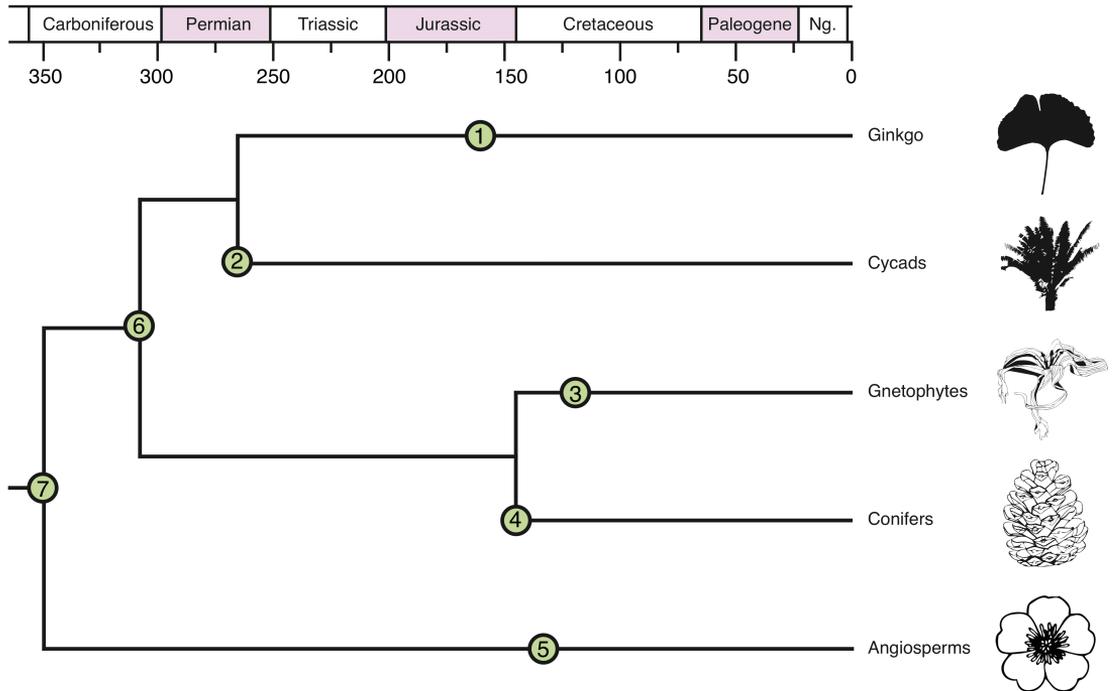


Figure 1: The relationships among seed plant lineages, scaled to geological time based on fossil ages. Numbers in green circles refer to the following: (1) oldest *Ginkgo* fossil (Yang et al. 2008); (2) oldest cycad fossil (Gao and Thomas 1989); (3) oldest gnetophyte fossil (Rydin et al. 2006); (4) oldest conifer fossils (Wieland 1935); (5) oldest angiosperm fossils (discussed in Doyle 2012); (6) oldest acrogymnosperm fossil ; (7) an estimated maximum age for crown-group seed plants (discussed in Magallón and Castillo 2009; Foster et al. 2016).

plants with tricolpate pollen. Although the constituent members of the subgroups varied across studies, the recognition of tricolpates as a monophyletic group was a consistent finding (e.g., Donoghue and Doyle 1989b; Donoghue and Doyle 1989a), leading to suggestions that dicots had multiple evolutionary origins (Endress et al. 2000; Endress 2002). Indeed, stratigraphical studies in which triaperturate pollen (tricolpate) fossils were consistently found to originate in younger sediments than both monocots and non-tricolpate dicots had already hinted that dicots did not form a

monophyletic group (Doyle 1969). Consequently, Doyle and Hotton (1991) chose to recognise tricolpates as distinct from the rest of the dicots, coining the term ‘eudicots’ for this group.

Taxonomic concepts for the major angiosperm groups have changed over time, which makes it difficult to chronicle concisely the changing opinions about the earliest-diverging angiosperms. For example, the group Magnoliidae now has a very different circumscription compared with the past, so statements in earlier studies regarding the relationships between

magnoliids and other groups might no longer be applicable. Nevertheless, it is clear that the most common view historically was that *Magnolia*-like flowers probably occupied a position at or near the root of the angiosperm phylogeny. However, there were other suggestions for the earliest-diverging angiosperm lineages, including Piperales+Chloranthales, several of the lineages in the formerly recognised paleoherb group, or even monocots (Burger 1977, 1981).

Attempts to clarify the relationships within the angiosperm phylogeny have since been greatly strengthened by the inclusion of molecular data. Some aspects of early classification schemes based on morphology have been strongly supported by molecular data (reviewed by Endress et al. 2000; Endress 2002). For example, the key concepts of the monophyly of angiosperms, monocots and eudicots, the polyphyly of dicots, and the position of magnoliids as an early diverging angiosperm lineage, were all further supported by molecular data (Endress et al. 2000). However, many molecular estimates of angiosperm evolutionary relationships have contradicted estimates based on morphological data. For example, molecular data have firmly resolved the family Hydatellaceae within Nymphaeales, rather than within Poales as former morphology-based studies had concluded (Saarela et al. 2007). Molecular data have also helped to clarify the extent of convergent evolution within angiosperms, such as C₄ photosynthesis evolving independently at least 60 times (Sage et al. 2011).

Arguably the most important finding from analyses of molecular data has been the rooting of the angiosperm phylogeny. Success was not immediate, with disagreements being found among the results of molecular analyses, depending on the

choice of molecular markers. An influential early attempt with molecular data to resolve the seed plant phylogeny and, necessarily, to determine the earliest-diverging angiosperm lineage, analysed sequences for the chloroplast *rbcL* gene from nearly 500 seed plant taxa using maximum parsimony (Chase et al. 1993). In this case, the widespread aquatic genus *Ceratophyllum* was found to be the sister lineage to all other flowering plants. However, this has subsequently been found to be an anomalous result seemingly unique to single-gene parsimony analyses of *rbcL*. A series of studies in 1999 found that the monotypic genus *Amborella* is strongly supported as being the sister lineage to all other flowering plants (Mathews and Donoghue 1999; Parkinson et al. 1999; Qiu et al. 1999; Soltis et al. 1999), and this finding has subsequently been supported by nearly all large multigene analyses (Moore et al. 2007; Soltis et al. 2011; but see Goremykin et al. 2013; Ruhfel et al. 2014; Wickett et al. 2014; Xi et al. 2014; Goremykin et al. 2015). These studies have also revealed that the base of the angiosperm phylogeny constitutes a grade of several successive lineages, originally referred to as the ANITA (*Amborella*/Nymphaeales/Illiciaceae-Trimeniaceae-*Austrobaileya*) grade, but now known as the ANA (*Amborella*/Nymphaeales/Austobaileales) grade.

The remaining ~99.95% of angiosperms are collectively referred to as Mesangiospermae. Within this group, five major lineages are recognised: Chloranthales, Magnoliidae, Ceratophyllales, monocots, and eudicots (clade names here are standardised to Cantino et al. 2007). Unfortunately, despite large increases in the amount of available genetic data and improved analytical techniques, the relationships among these mesangiosperm groups have remained uncertain (Figure 2). When analysing

chloroplast genome sequences, the most common finding is that eudicots + *Ceratophyllum* form the sister group to monocots, with these three lineages being the sister group to magnoliids + Chloranthales. Large nuclear DNA data sets, which have only become available in recent years, tend to resolve different relationships. For example, they have supported a sister relationship between eudicots and magnoliids + Chloranthales, with monocots being the sister group to these three lineages (Wickett et al. 2014). However, the number and choice of nuclear DNA markers can affect inferred relationships within Mesangiospermae. For example, analysis of a selection of 59 low-copy nuclear genes inferred a grouping of *Ceratophyllum* + Chloranthales and eudicots, with successive sister relationships to magnoliids and monocots (Zeng et al. 2014). Additionally, the choice of phylogeny reconstruction method can lead to the estimation of different topologies (Xi et al. 2014).

Nevertheless, despite conflicting topologies sometimes being inferred, we currently have an understanding of the angiosperm phylogeny that is greater than at any other time in history. The power of molecular data to resolve the historically challenging relationships among flowering plants is now well established. In response to the rapid advances in the field, a cosmopolitan consortium of researchers regularly collaborate to release timely summaries of the state of knowledge of the angiosperm phylogeny (see Angiosperm Phylogeny Group 1998, 2003, 2009, 2016). We now have a viable framework to allow fields related to phylogenetics to flourish and provide a greater understanding of the important evolutionary steps that have contributed to the overwhelming success of angiosperms, such as through evolutionary

developmental biology (evo-devo) studies (Preston and Hileman 2009). However, to gain a fuller understanding of the evolutionary history of angiosperms, it is necessary to know more than just the relationships among the major flowering plant groups; a reliable estimate of the angiosperm evolutionary timescale is also needed.

Evolutionary timescale of angiosperms

To understand how angiosperms came to dominance, including how the crucial morphological traits that led to their success first evolved, it is necessary to have some idea of the timescale of angiosperm evolution. Traditionally, the evolutionary timescale of organisms has been elucidated through study of the fossil record. In this approach, the first appearance of each taxon in the fossil record, as determined by morphology, provides an indication of when it first evolved. When considering the fossil record, it is important to distinguish between “crown” and “stem” groups. A crown group is the *least* inclusive monophyletic group that contains all extant members of a clade, as well as any extinct lineages that diverged after the most recent common ancestor of the clade (Magallón and Sanderson, 2001). In contrast, a stem group is the *most* inclusive monophyletic group that contains all extant members of a clade, as well as any extinct lineages that diverged from the lineage leading to the crown group (Magallón and Sanderson, 2001).

The fossil record of seed plants is ancient, with the oldest fossils of progymnosperms occurring in sediments from the Late Devonian, ~365 million years ago (Ma) (Fairon-Demaret and Scheckler 1987; Rothwell et al. 1989; Fairon-Demaret 1996). The fossil record of gymnosperms

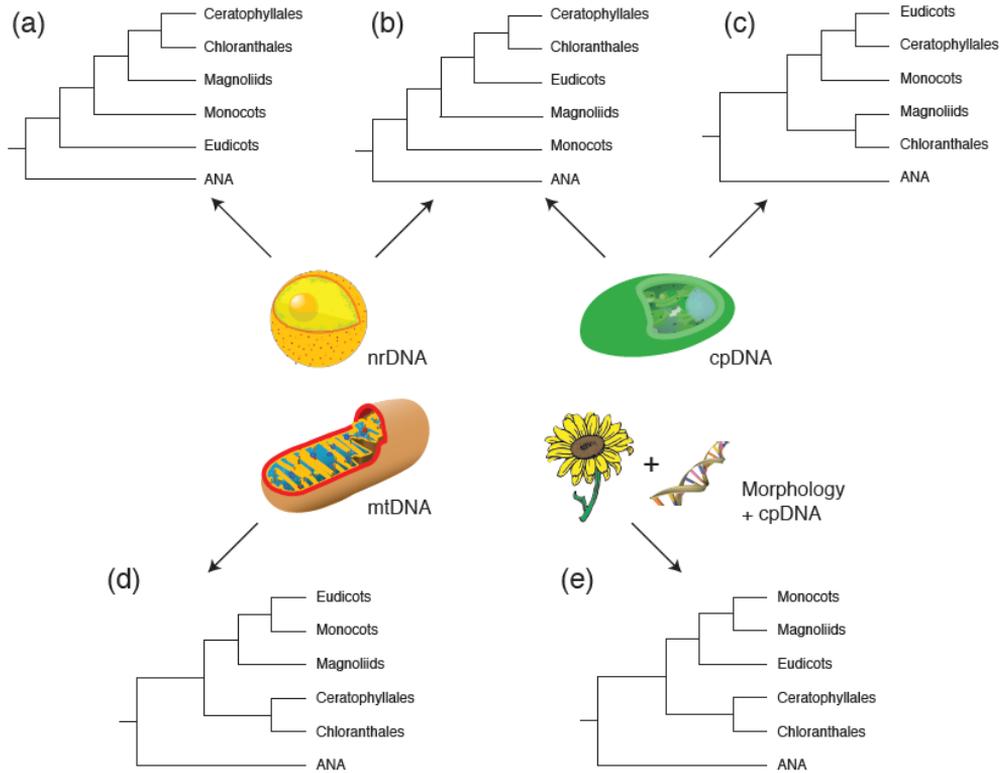


Figure 2: A comparison of several different estimates of the relationships among eudicots, magnoliids, monocots, Ceratophyllum, Chloranthales, and ANA-grade angiosperms, based on the comparison presented in Zeng et al. (2014). The different topologies represent findings from studies using nuclear DNA (nrDNA), chloroplast DNA (cpDNA), mitochondrial DNA (mtDNA), and a combination of morphological and molecular data. A sample of suitable references for the topologies are as follows: (a) Zhang et al. (2012); (b) Moore et al. (2011); Zeng et al. (2014); (c) Moore et al. (2007); Moore et al. (2010); Foster et al. (2016); (d) Qiu et al. (2010); (e) Endress and Doyle (2009).

is rich, with fossils becoming common from the Late Carboniferous to Early Triassic (Magallón 2014), and revealing an extinct diversity far greater than the extant diversity.

The oldest known fossil that can be confidently assigned to the stem group of angiosperms has suggested that angiosperms arose as early as 247.2–242.0 Ma (million years ago) (Hochuli and Feist-Burkhardt 2013). Accepted pollen fossils (microfossils) suggest that crown-group angiosperms first

Unfortunately,, the fossil record of angiosperms is not as extensive or informative.

appeared in the Valanginian to early Hauterivian (early Cretaceous, ~139.8–129.4 Ma), albeit in sparse amounts, with vast amounts of angiospermous microfossils occurring by the Barremian (~129.4–125 Ma) (Doyle 2012). There is a noticeable disparity in the number and presence of

fossils between lineages, particularly at the family level and below, with many excellent fossils being present for some groups but none for others (Magallón 2014).

While fossil data have traditionally provided the only source of information about the evolutionary timescale of major groups, molecular dating techniques provide a compelling alternative, especially for groups that lack fossils. In these approaches, evolutionary timescales can be estimated using phylogenetic methods based on molecular clocks. When the concept of the molecular clock was first proposed, evolutionary change was assumed to correlate linearly with time and to remain constant across lineages (“strict” molecular clock) (Zuckermandl and Pauling 1962). However, it has since become clear that strictly clocklike evolution is the exception, rather than the rule (Welch and Bromham 2005).

Rates of molecular evolution vary substantially across vascular plant lineages (Soltis et al. 2002), and are often strongly correlated with life history strategies. For example, substitution rates in herbaceous annual lineages of angiosperms are known to be substantially higher than in woody perennial plants (Smith and Donoghue 2008; Lanfear et al. 2013). Consequently, a variety of molecular clock models have been developed to account for evolutionary rate variation among lineages (Ho and Duchêne 2014). Fossil data are still intricately linked with these methods, because fossils are used to provide temporal information to calibrate the molecular clock, thereby providing absolute rather than relative ages of nodes. For example, in Bayesian analyses, temporal information is incorporated through calibrations priors, which can take the form of a variety of probability distributions (Ho and Phillips 2009). In the absence of fossils for a particular group being studied,

biogeographic events and rate estimates from other groups can be used as calibrations, but these are subject to a wide range of errors (Ho et al. 2015).

Collectively, molecular dating studies have yielded remarkably disparate estimates for the age of crown-group angiosperms (summarised in Bell et al. 2010; Magallón 2014; Foster et al. 2016). Inferred ages have ranged from the extreme values of 86 Ma (when considering only the 3rd codon positions of *rbcL*; Sanderson and Doyle 2001) to 332.6 Ma (Soltis et al. 2002). Most age estimates fall between 140 and 240 Ma, but this still represents a substantial amount of variation. Additionally, the earliest analyses found that crown-group angiosperms were considerably older than implied by the fossil record, in some cases by more than 100 million years (e.g. Martin et al. 1989). Smaller disparities between molecular and fossil estimates were obtained in later studies (e.g. Sanderson and Doyle 2001). However, some more recent estimates have tended to support a more protracted timescale for angiosperm evolution (e.g. Smith et al. 2010), echoing the results of the earliest molecular studies.

Progress in molecular dating can be characterised in terms of increasing methodological complexity and improving sampling of taxa and genes (Ho 2014). A persistent problem, however, has been the need for a trade-off between taxon sampling and gene sampling. Low gene sampling has been typical of studies of angiosperm evolution, albeit with some other exceptions, including the 12 mitochondrial genes analysed by Laroche et al. (1995), 58 chloroplast genes analysed by Goremkykin et al. (1997), 61 chloroplast genes analysed by Moore et al. (2007), and the 83 chloroplast genes analysed by Moore et al. (2010). However, most of these studies had sparse angiosperm taxon sampling. Among the few

other studies that have included more than 50 taxa, the largest number of genes sampled was five. The largest taxon samples have been those of Zanne et al. (2014), which used a staggering 32,223 species, and Magallón et al. (2015), which included 792 angiosperm taxa and one of the largest samples of fossil calibration points ever used. An exception to the above trade-off between taxon and gene sampling is the study by Foster et al. (2016), which analysed 76 chloroplast genes from 193 angiosperm taxa.

The most controversial aspect of angiosperm molecular dating studies has been an apparent incongruence between molecular estimates and those extrapolated purely from fossil occurrence data. Many modern molecular dating estimates without strongly informative temporal calibrations tend to suggest that angiosperms arose in the early to mid-Triassic (Figure 3) (Foster et al. 2016), which implies a considerable gap in the fossil record (Doyle 2012). This contradicts the claim that the evolutionary history of crown-group angiosperms is well represented in the fossil record (Magallón 2014), despite several lines of evidence supporting this suggestion: the gradual increase in abundance, diversity, and distribution of fossil angiosperms; the ordered progression of both morphological and functional diversification; and the agreement between the stratigraphic record and molecular data in the sequential appearance of angiosperm lineages.

If the fault lies instead with the molecular estimates, then it has been suggested that the substantial disparity between molecular and fossil-based estimates of the age of crown angiosperms might be a result of the choices of molecular markers, taxa, calibrations, or models of rate variation (Magallón 2014). Particular blame has been placed on the inability of molecular dating methods to account properly for non-representative

sampling of angiosperms and life history-associated rate heterogeneity (Beaulieu et al. 2015).

However, comprehensive investigations of the impact of models, priors, and gene sampling on Bayesian estimates of the angiosperm evolutionary timescale, using a genome-scale data set and numerous, widely distributed fossil calibrations, have still yielded remarkably robust estimates of a Triassic origin of angiosperms (Foster et al. 2016). This implies a long period of no angiosperm fossilisation, or that fossils of this age simply remain to be discovered (but see Wang et al. 2007; Gang et al. 2016).

Despite the disparate estimates for the origin of crown-group angiosperms, the timescale of evolution within this group is beginning to be understood with increased precision. Of particular note is that estimates for the origin of most modern angiosperm orders seem to be consistent regardless of the age inferred for the angiosperm crown group (Magallón et al. 2015; Foster et al. 2016). Ordinal diversification is most commonly estimated to have begun in the early Cretaceous, and is concentrated predominantly from this time through to the mid-Cretaceous (Magallón et al. 2015; Foster et al. 2016). Modern angiosperm families are estimated to have originated steadily from the early Cretaceous, with the peak of family genesis occurring from the late Cretaceous to the early Paleogene (Magallón et al. 2015). During this time, the supercontinent Pangaea largely completed its breakup into the continents of the present day. Concurrently, there were dramatic shifts in climate, with global temperatures and CO₂ levels far higher than in the present day (Hay and Floegel 2012). These changes, particularly in temperature, would have had significant impacts on the levels and efficiency of.

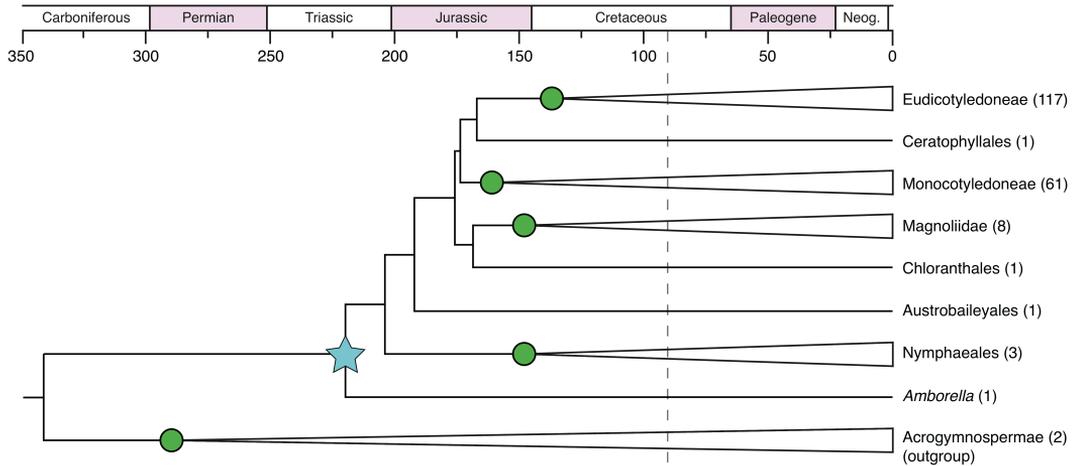


Figure 3: A recent estimate of the angiosperm evolutionary timescale, modified from Foster et al. (2016). Numbers in parentheses after taxon names refer to the number of taxa included from those groups in the study. Green circles indicate estimates of the crown age for lineages when more than one taxon has been included, and the blue star indicates the inferred age for the origin of crown-group angiosperms. The dashed line indicates the time by which all modern orders were inferred to have arisen.

photosynthesis (Ellis 2010; Hay and Floegel 2012). Selective pressures would have been high, ultimately influencing the evolution of angiosperms and, presumably, other taxa that interacted with them.

Concluding remarks and future directions

The substantial diversity and global dominance of flowering plants have puzzled and intrigued many researchers throughout history. The classification of angiosperms has long proved difficult because of the monumental size and such varied morphologies within this group. Subsequently, the key evolutionary innovations that first occurred to produce flowers, as well as the reasons for the overwhelming success of angiosperms, have historically been obscured. Therefore, it is reasonable to surmise that for most of

history, the relationship of angiosperms to other seed plants, the relationships within angiosperms, the timescale of angiosperm evolution, and the reasons for the relative success of angiosperms compared to gymnosperms were all largely unknown or not understood.

Thankfully, we have now made great progress in the quest to answer these questions. Work remains to identify potential stem-group relatives of seed plants, but we now have reliable estimates of the phylogeny of extant seed plants. However, the most widely accepted seed plant phylogeny suggests that no extant gymnosperm lineage preserves the evolutionary steps that led to the origin of the first flowers. Therefore, in some respects the resolution of the seed plant phylogeny has been somewhat of a disappointment for those wanting to reconstruct the

development of the flower (Doyle 2012). While this might be considered a setback, our greatly improved knowledge of the angiosperm phylogeny, including a strongly supported position for the root, allows increasingly sophisticated questions to be asked about angiosperm macroevolution (e.g., Turcotte et al. 2014; Zanne et al. 2014). Similarly, our modern estimates for the timescale of angiosperm evolution allow us to explore further the selective pressures that might have shaped the present-day distribution and diversity of flowering plants.

Despite our significant improvements in understanding the patterns and timescale of angiosperm evolution, the field is far from settled. The celebrated consistent, strongly supported phylogeny based on chloroplast markers is increasingly being recognised as only one estimate of the angiosperm phylogeny. The alternative phylogenies inferred through analysis of nuclear markers, and through the choice of phylogeny reconstruction methods, suggests that more work is needed to reconcile potentially conflicting evolutionary histories. Additionally, the controversy surrounding the age of flowering plants shows no signs of abating. Modern knowledge of the fossil record suggests that the rapid radiation of angiosperm lineages was not quite as explosive as implied by Darwin's "abominable mystery" proclamation, yet a new mystery is why molecular date estimates still generally far pre-date the oldest angiosperm fossils. It is unlikely that increasing the amount of genetic data will solve this problem (Foster et al. 2016); instead, increased sampling from underrepresented groups and methodological improvements in incorporating fossil data appear to be the way forward. The last point appears to be an especially promising avenue of research, with new methods being developed for the

simultaneous analysis of extant and extinct taxa (Ronquist et al. 2012; Gavryushkina et al. 2014; Heath et al. 2014). Overall, it is clear that our understanding of the evolutionary history of angiosperms has changed considerably over time, and we are now in an exciting new era of angiosperm research.

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