Mechanisms and milestones in the evolution of flowering plants

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Abstract. The evolutionary success of angiosperms is underpinned by a suite of genomic, developmental, anatomical, and ecological innovations that have enabled them to become the dominant plant group in most terrestrial ecosystems. This review synthesizes key mechanisms and milestones in angiosperm evolution, with a focus on polyploidy, developmental heterochrony, floral and fruit innovations, vascular adaptations, and mutualistic interactions. Whole-genome duplications (WGDs) have played a pivotal role in expanding gene regulatory networks and enabling morphological novelty. Floral diversification, driven by co-evolution with pollinators and regulated by MADS-box gene families, exemplifies the dynamic interplay between genetic architecture and ecological pressures. In parallel, the evolution of enclosed seeds and diverse fruit types facilitated reproductive success through enhanced protection and dispersal. Vascular and mechanical adaptations further supported ecological plasticity across variable habitats. Finally, symbiotic relationships, particularly mycorrhizal and nitrogen-fixing associations, have contributed to nutrient acquisition and speciation. The integration of phylogenomics, evo-devo, and ecological modeling provides a multidimensional framework to understand the complexity of angiosperm evolution and informs predictions under ongoing environmental change.

Key Words: angiosperm evolution, evo-devo, fruit and seed development, heterochrony, MADS-box genes, mycorrhiza, phylogenomics, pollination syndromes, vascular adaptation, whole-genome duplication.

Introduction. The evolution of plants showcases a variety of fascinating adaptations and transformations that illustrate their intricate relationship with the environment and the mechanisms that govern their development. This review aims to elucidate some key features of angiosperm evolution, particularly focusing on the genetic, anatomical, and ecological aspects while also providing a tabular representation of significant evolutionary events (Table 1).

Polyploidy and Genome Dynamics. Polyploidy, defined as the condition of having more than two complete sets of chromosomes, has been a significant driver of plant evolution. Many angiosperms have experienced whole-genome duplications (WGDs), which can lead to increased genetic variation and adaptability (Fischer et al 2014). Such duplications are hypothesized to play a crucial role in the evolutionary success of flowering plants (Leitch & Leitch 2012). Comparative analyses reveal that angiosperms often have larger and more dynamic genomes compared to other plant lineages, enhancing their adaptability to diverse ecological niches (Anderson et al 2011).

Heterochrony in Plant Development. Heterochrony, which refers to changes in the timing of developmental events, can significantly impact plant morphology and species diversity. For instance, the evolution of carpels and their structure is linked to shifts in developmental timing, facilitating diverse adaptations in reproductive strategies (Buendía-Monreal & Gillmor 2018; Remizowa & Sokoloff 2023). This phenomenon allows for the emergence of novel traits that can enhance reproductive success in varying environments, an example of which can be seen in the adaptability of the genus *Brassica* in response to drought conditions (O'Hara et al 2015).

Table 1

Selected plant evolutionary milestones

Event	Description	Reference
Whole-genome duplications (WGDs)	Major mechanism contributing to genetic diversity in angiosperms.	Leitch & Leitch (2012); Fischer et al (2014)
Heterochrony in carpels	Evolutionary shifts in timing affecting reproductive structures.	Buendía-Monreal & Gillmor (2018); Remizowa & Sokoloff (2023)
Climate change impact	Changes in local adaptations affecting survival strategies.	Li et al (2023)
Hybridization in island species	Evolution of genetic diversity in isolated populations.	López-Alvarado et al (2020)
Pollination syndromes	The co-evolution of floral traits and animal pollinators led to the emergence of distinct pollination syndromes (e.g., bees, birds, bats, wind, water).	Assis (2023)
Floral specialization	Development of specialized traits such as bilateral symmetry, nectar guides, and specific volatile compounds to attract target pollinators.	Zariman et al (2022)
Gene families in floral evolution	MADS-box transcription factors (e.g., APETALA, PISTILLATA, AGAMOUS) played key roles in floral organ patterning and identity.	Li et al (2022)
Pollination shifts (biotic to abiotic)	Shifts from biotic pollination (e.g., insects) to abiotic pollination (e.g., wind), often with a reduction in floral complexity.	Turchetto et al (2022)
Seed and fruit innovations	Angiosperms evolved enclosed seeds within fruits, providing selective advantages like increased embryo protection and enhanced dispersal.	Vandelook & Carta (2025)
MADS-box gene regulation in fruits	MADS-box genes (e.g., AGAMOUS, FRUITFULL, SHATTERPROOF) regulate fruit development, including tissue differentiation and maturation.	Becker & Theißen (2003)
Fleshy fruits and dispersal	Fleshy fruits evolved for endozoochory (animal dispersal), attracting frugivores with color, aroma, and nutritional rewards.	Parolin et al (2013)
Dry fruits and dispersal	Dry fruits (e.g., capsules, samaras) evolved for anemochory (wind dispersal) or autochory (self-dispersal).	Pijl (1969)
Seed evolution	Innovations in seed structure, such as reduced endosperm, double fertilization, and seed dormancy, enhance nutrient allocation and germination timing.	Linkies et al (2010)
Vessel element evolution	The development of vessel elements in xylem, with wider and shorter structures than tracheids, allowed for efficient water conduction.	Tung et al (2023)
Anatomical flexibility and leaf structure	Modular design of shoots and differentiated tissues (e.g., palisade and spongy mesophyll) enable efficient gas exchange, light capture, and water use.	Borsuk et al (2022)
Leaf venation patterns	Innovations in leaf venation, such as dense and reticulate networks, improve hydraulic efficiency and resilience.	Mander & Williams (2024)
Mechanical support	Evolution of fibers in xylem and phloem for	Zhang et al (2022b)

systems	mechanical strength, supporting vertical growth in trees and shrubs.	
Turgor-based support in herbaceous plants	Herbaceous plants use collenchyma and sclerenchyma tissues for mechanical strength and flexibility.	Coussement et al (2021)
MADS-box transcription factors in flower development	MADS-box genes regulate floral organ identity, contributing to floral diversity and novel pollination strategies.	Zhang et al (2024)
Gene duplication and evolutionary flexibility	Whole-genome duplications (WGDs) led to subfunctionalization and neofunctionalization, enabling new trait evolution.	Birchler & Yang (2022)
MicroRNAs and non-coding elements	MicroRNAs and non-coding regulatory elements modulate developmental timing, meristem identity, and organ morphogenesis.	Ma et al (2022)
Mycorrhizal symbioses	Mycorrhizal relationships, including arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM), enhance nutrient acquisition, particularly in nutrient-poor environments. Symbiotic systems, such as mycorrhizal and nitrogen-fixing interactions, enhance resource acquisition, stress tolerance, and speciation rates.	Păpuc & Bora (2023)

Ecological and Evolutionary Interactions. Plant evolution is closely tied to ecological dynamics, particularly in response to climate change and habitat fragmentation. For instance, studies show that local adaptations in certain alpine plants have induced evolutionary traps due to climate change, highlighting a paradox where adaptations to historical conditions may hinder species' survival in new environments Li et al (2023). Additionally, the unique evolutionary pathways in island biogeography, such as those observed in the endemic species of Centaurea in Sardinia, emphasize the role of geographical isolation in shaping genetic diversity through hybridization and reticulate evolution López-Alvarado et al (2020).

Evolution of Flowers and Pollination Syndromes. The origin and diversification of flowers represent one of the most consequential evolutionary innovations in angiosperms, facilitating their ecological dominance and extensive radiation. Flowers are not merely reproductive organs; they are complex structures whose morphological and biochemical traits have been shaped by intricate interactions with pollinators over millions of years. This co-evolution between angiosperms and animal pollinators is exemplified by the emergence of distinct pollination syndromes — predictable suites of floral traits that correspond to specific pollinator types (e.g., bees, birds, bats, wind, or water).

Early angiosperm flowers likely exhibited generalist features, accessible to a broad range of pollinators. Over time, selective pressures exerted by pollinators led to increasing floral specialization. For instance, the development of bilateral symmetry (zygomorphy), nectar guides, and specific volatile organic compounds enhanced reproductive efficiency by attracting targeted pollinators and reducing interspecific pollen transfer. The diversification of the Asteraceae and Orchidaceae, two of the largest angiosperm families, is tightly linked to such specialized interactions (Moreira-Hernández & Muchhala 2019).

Empirical evidence from phylogenetics and evo-devo studies has revealed that gene families such as MADS-box transcription factors (e.g., APETALA, PISTILLATA, AGAMOUS) played key roles in the patterning and identity of floral organs (Li et al 2022). Modifications in the expression domains and timing of these genes contributed to the emergence of novel floral forms adapted to specific pollination strategies.

Pollination syndrome evolution is not a linear process. Reversals and transitions are common. Shifts from biotic to abiotic pollination (e.g., from insect to wind pollination) have occurred multiple times, often in response to environmental constraints or pollinator scarcity. Such transitions are frequently accompanied by reductions in floral complexity, scent production, and nectar secretion (Ruchisansakun et al 2021).

Overall, the dynamic interplay between floral trait evolution and pollinator behavior underscores a central theme in angiosperm success: adaptive radiation through ecological interaction. Future research integrating molecular genetics, paleobotany, and ecological modeling will further elucidate how these syndromes originated and how they might shift under the pressures of ongoing environmental change.

Seed and Fruit Innovations. Among the defining features of angiosperms is the development of enclosed seeds within fruits — a key innovation that has had profound implications for their reproductive biology, dispersal strategies, and ecological success. Unlike gymnosperms, whose seeds are exposed on the surface of cones or other structures, angiosperms encase their ovules within a carpel, which matures into a fruit following fertilization (Proorocu & Kovacs 2003). This structural innovation enhances seed protection and facilitates complex dispersal mechanisms, including interactions with animals, wind, and water.

From an evolutionary perspective, the origin of the fruit represents a significant shift in plant reproductive strategy. It provided multiple selective advantages: increased embryo protection, controlled seed release, and enhanced dispersal efficiency. Fruit development is regulated by a coordinated expression of genetic networks—particularly involving MADS-box genes such as AGAMOUS, FRUITFULL, and SHATTERPROOF—which govern tissue differentiation and maturation processes (Becker & Theißen 2003).

Fruits have evolved into an extraordinary array of forms and functions. Fleshy fruits like berries and drupes are typically adapted for endozoochory (dispersal via ingestion by animals), relying on the attraction of frugivores through color, aroma, and nutritional rewards. In contrast, dry fruits such as capsules, samaras, and achenes often facilitate anemochory (wind dispersal) or autochory (self-dispersal mechanisms like ballistic ejection). These diversified morphologies reflect angiosperms' capacity to exploit a wide range of ecological niches and dispersal agents.

The evolution of the seed itself also underwent refinements in angiosperms. Features such as reduced endosperm in some taxa, double fertilization, and the development of seed dormancy mechanisms have increased the efficiency of nutrient allocation and timing of germination under variable environmental conditions. Such physiological and morphological innovations contribute to the establishment and persistence of angiosperms across diverse habitats.

Overall, the coordinated evolution of seeds and fruits exemplifies how structural and developmental complexity can be leveraged to achieve reproductive success. These innovations not only underpin the adaptive radiation of flowering plants but also continue to play a central role in shaping plant-animal interactions and ecosystem dynamics.

Vascular and Structural Adaptations. The evolutionary refinement of vascular and structural features in angiosperms has played a pivotal role in their ecological success and global diversification. Central to this success is the evolution of highly specialized water-conducting tissues, particularly the development of vessel elements in the xylem. Unlike the tracheids found in most non-angiosperm seed plants, vessel elements are wider, shorter, and more efficient at conducting water due to their perforation plates and large lumen diameters. This structural innovation allows for increased hydraulic conductivity, enabling angiosperms to support rapid growth and occupy a broader range of environmental conditions, including arid and seasonally dry habitats.

In addition to vascular improvements, angiosperms exhibit significant anatomical flexibility and architectural diversity. The modular design of their shoots and the presence of highly differentiated tissues — such as palisade and spongy mesophyll in leaves — allow for fine-tuned regulation of gas exchange, light capture, and water use efficiency. Moreover, innovations in leaf venation patterns, including dense and reticulate networks, contribute to improved redundancy and resilience against hydraulic failure.

Structural adaptations also include enhanced mechanical support systems. The evolution of fibers within the xylem and phloem strengthens the vascular tissue and supports vertical growth, contributing to the development of large trees and woody shrubs. In herbaceous angiosperms, turgor-based support mechanisms are complemented by collenchyma and sclerenchyma tissues, providing mechanical strength while maintaining flexibility.

The integration of vascular efficiency with reproductive and physiological traits enables angiosperms to synchronize water transport, transpiration, and photosynthesis with reproductive timing. This coordination is particularly evident in environments with pronounced seasonality or resource limitations.

Collectively, these vascular and structural adaptations have endowed angiosperms with superior ecological plasticity, allowing them to colonize diverse terrestrial ecosystems, from rainforests to deserts. The evolutionary refinement of vascular tissues, coupled with structural innovations at both the organ and cellular level, underscores the complex interplay between form and function that characterizes the evolutionary trajectory of flowering plants.

Molecular and Developmental Genetics (Evo-Devo). The field of evolutionary developmental biology (Evo-Devo) has provided critical insights into the molecular mechanisms underlying the diversification of angiosperm form and function. Central to this framework is the understanding that relatively small genetic changes, particularly in regulatory genes, can lead to significant morphological innovations that drive speciation and ecological adaptation.

One of the most influential discoveries in angiosperm Evo-Devo is the role of MADS-box transcription factors, a highly conserved family of genes involved in the regulation of floral organ identity. The classical ABC model of flower development, later expanded into the ABCDE model, describes how combinations of MADS-box gene expression domains specify the formation of sepals, petals, stamens, carpels, and ovules. For example, the coordinated action of APETALA1, APETALA3, PISTILLATA, AGAMOUS, and SEPALLATA genes underlies the development of floral whorls (Li et al 2022). Variations in the expression, duplication, or neofunctionalization of these genes are linked to the emergence of novel floral structures and pollination strategies.

Gene duplication events, particularly those following whole-genome duplications (WGDs), have played a major role in expanding developmental gene networks in angiosperms. These duplications allow for subfunctionalization or neofunctionalization, leading to evolutionary flexibility (Birchler & Yang 2022). For instance, paralogs of AGAMOUS have acquired new roles in fruit and ovule development in some lineages, contributing to trait innovation (Xiang et al 2024).

Beyond flower development, Evo-Devo studies have also revealed the importance of microRNAs and other non-coding regulatory elements in modulating developmental timing, meristem identity, and organ morphogenesis (Azad et al 2023). Regulatory changes, rather than coding sequence evolution, are increasingly recognized as major drivers of phenotypic diversification in plants (Azad et al 2023).

Furthermore, comparative studies between basal angiosperms (e.g., *Amborella* and Nymphaeales) and more derived lineages have shed light on ancestral developmental programs and the gradual emergence of complex floral architectures (Specht & Bartlett 2009). These findings suggest that the modularity and plasticity of genetic networks enabled the rapid radiation of angiosperms into diverse ecological niches.

In summary, the integration of molecular genetics with developmental biology has revealed how shifts in gene regulation and network architecture underpin the vast morphological diversity observed among flowering plants. Evo-Devo continues to be a powerful framework for uncovering the genetic basis of evolutionary novelty in angiosperms.

Rapid Radiation and Phylogenomic Insights. The evolutionary history of angiosperms is marked by a phenomenon of rapid radiation, a process in which multiple lineages diverged within a relatively short geological timeframe. Molecular clock estimates place the origin of crown-group angiosperms in the Early Cretaceous (~140–130 million years ago), followed by an explosive diversification that gave rise to the vast morphological and ecological diversity observed today (Benton et al 2022; Zhang et al

2025). This rapid evolutionary expansion, often referred to as the "abominable mystery" by Charles Darwin, remains one of the most intriguing questions in plant evolutionary biology.

Advances in phylogenomics—the application of genome-scale data to phylogenetic reconstruction—have significantly improved resolution of deep nodes within the angiosperm tree of life. High-throughput sequencing technologies, combined with refined models of molecular evolution, have enabled researchers to uncover relationships among major clades that were previously unresolved due to short internal branches and limited fossil calibration points (Benton et al 2022; Zhang et al 2025).

One of the major insights from phylogenomic analyses is the identification of ANA-grade lineages (*Amborella*, Nymphaeales, and Austrobaileyales) as early-diverging groups (Specht & Bartlett 2009). These taxa exhibit a mosaic of ancestral and derived traits, making them essential for understanding the morphological and genomic transitions that occurred early in angiosperm evolution. *Amborella trichopoda*, in particular, has become a model system for basal angiosperms due to its unique genomic architecture and lack of vessel elements in the xylem, traits that provide a living reference for the ancestral angiosperm condition (Carey et al 2024).

Phylogenomic studies have also revealed the pervasive role of whole-genome duplications (WGDs) in the evolutionary history of flowering plants (Almeida-Silva & Van de Peer 2023). These events are temporally correlated with major diversification bursts and are hypothesized to have provided the genetic raw material necessary for innovation and adaptation. Notably, a major WGD event (the so-called gamma triplication) is associated with the early diversification of core eudicots, one of the most species-rich groups of angiosperms (Chang et al 2022).

Despite these advances, several key relationships among early-diverging lineages remain contentious, largely due to incomplete lineage sorting, hybridization, and gene tree discordance. Integrative approaches combining nuclear, plastid, and mitochondrial data, along with improved fossil calibration and modeling of reticulate evolution, are essential to resolve these phylogenetic ambiguities.

In summary, phylogenomic research has dramatically reshaped our understanding of angiosperm diversification by illuminating the timing, tempo, and mechanisms underlying their early radiation. Continued exploration of genomic data from understudied and basal taxa will be critical for reconstructing a robust evolutionary framework and explaining the rapid rise of flowering plants to ecological dominance.

Mycorrhizal and Other Symbiotic Relationships. Symbiotic interactions have played a foundational role in the evolutionary history and ecological success of angiosperms (Păpuc & Bora 2023). Among the most critical of these are mycorrhizal associations, mutualistic relationships between plant roots and fungi that facilitate nutrient acquisition, particularly phosphorus and nitrogen, in exchange for plant-derived carbohydrates. These symbioses are widespread among angiosperms and are thought to have been a key innovation enabling colonization of nutrient-poor and marginal environments (Păpuc & Bora 2023).

There are two principal types of mycorrhizal associations in angiosperms: arbuscular mycorrhizae (AM), formed with Glomeromycota fungi, and ectomycorrhizae (ECM), formed primarily with Basidiomycota and Ascomycota fungi. AM associations are considered ancestral and are found in over 70% of extant angiosperm species (Zhang et al 2022a). They facilitate extensive nutrient exchange through intracellular structures called arbuscules, which increase surface area and metabolic interaction. ECM associations, while less common, are more specialized and typically occur in temperate and boreal forests. They involve the formation of a sheath around the root and intercellular hyphal networks (Hartig net), enhancing access to organic nutrients and contributing to the development of forest ecosystems.

In addition to mycorrhizae, angiosperms have evolved other significant mutualistic relationships, such as nitrogen-fixing symbioses with actinobacteria (Frankia) and alpha-proteobacteria (*Rhizobium* spp.) in root nodules. These associations, particularly common in Fabaceae and related families, provide a direct source of bioavailable nitrogen and are crucial in nitrogen-limited ecosystems. The evolution of these interactions involves complex signaling pathways, including the recognition of microbial Nod factors by plant receptor kinases, triggering nodule organogenesis and symbiosome formation.

Angiosperms also engage in above-ground symbioses, such as those with pollinators and seed dispersers, but certain specialized below-ground interactions are equally vital. For instance, mycoheterotrophic plants, which obtain carbon exclusively from fungal partners, have evolved multiple times independently within angiosperms. These represent extreme cases of symbiotic dependency and often involve co-evolutionary dynamics with specific fungal lineages.

From an evolutionary perspective, these symbiotic systems have not only enhanced resource acquisition and stress tolerance but have also likely influenced speciation rates, niche expansion, and biogeographical distribution. Genomic studies have begun to unravel the conserved and lineage-specific genes involved in symbiotic pathways, shedding light on how such complex interactions evolved and diversified across angiosperms.

In conclusion, mycorrhizal and other root-associated symbioses have been pivotal in shaping angiosperm evolution. Their roles in nutrient cycling, ecosystem function, and plant adaptation underscore the deep evolutionary integration between angiosperms and their microbial partners.

Conclusions. The evolution of angiosperms represents one of the most complex and consequential radiations in the history of life on Earth. This review has synthesized key mechanisms underlying their diversification, highlighting the integrative roles of polyploidy, heterochrony, floral evolution, and symbiotic interactions. Whole-genome duplications (WGDs) have served as engines of genomic innovation, fostering the emergence of novel traits through gene duplication and subfunctionalization. Simultaneously, changes in developmental timing and regulatory gene networks—particularly involving MADS-box transcription factors—have facilitated the evolution of diverse reproductive structures and strategies.

Ecological interactions, especially those related to pollination and seed dispersal, have exerted strong selective pressures that drove floral specialization and fruit diversity. These mutualisms not only increased reproductive efficiency but also contributed to the adaptive radiation of major angiosperm clades. Furthermore, the refinement of vascular architecture and mechanical support systems allowed angiosperms to thrive across a wide spectrum of environments, from xeric habitats to tropical rainforests.

Phylogenomic studies continue to shed light on early angiosperm diversification, yet unresolved phylogenetic relationships indicate the need for integrative approaches combining genomic, developmental, and fossil data. The evolutionary significance of mycorrhizal and other root symbioses—often underappreciated—emerges as another critical axis of angiosperm success, particularly in nutrient-poor and ecologically dynamic settings.

In sum, angiosperm evolution is best understood as the outcome of multiple interacting innovations—genomic, developmental, ecological, and symbiotic—each contributing to their unparalleled diversity and ecological dominance. Future work should prioritize underexplored basal lineages, integrate evo-devo with systems biology, and evaluate how ongoing environmental change may reshape evolutionary trajectories in flowering plants.

Conflict of Interest. The authors declare that there is no conflict of interest.

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