Tracing the history of angiosperm systematics through Liliales and Asparagales

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Abstract The field of systematics is central to how we understand, classify, and discuss organisms and their evolution. Systematics directly or indirectly touches every branch of biology. Over the last 50 years, methods in the field have been continually reshaped by advancing technologies, transitioning from primarily relying on morphological data to utilizing genomic-scale data sets. As the methods systematists use have changed, so too has our understanding of deep evolutionary relationships among flowering plants. In this primer, we illustrate advances in systematic methods using two closely related botanical orders, Liliales and Asparagales. Members of these orders were once both considered part of the same family, Liliaceae. Molecular data steered us towards a more refined understanding, validating the decision to split Liliaceae into several currently recognized orders including Liliales and Asparagales. In early molecular studies primarily using chloroplast data, Liliales was most closely related to the group containing Asparagales and another lineage, commelinids. Over the past decade, the increasing availability of large-scale nuclear data across non-model plants has made possible several studies that demonstrate a direct sister clade relationship between Liliales and Asparagales. Here, we summarize the history of angiosperm systematics and demonstrate how advances in theory and practice have shaped the relative placements of Liliales and Asparagales in the monocot phylogeny. We further discuss the impact of a sister relationship among Liliales and Asparagales on our understanding of monocot trait evolution, and the implications of current and advancing methodologies for the future of plant systematics.

Background

Understanding the plant tree of life is one of the major research areas of the botanical sciences (*e.g.*, Baker et al., 2022). Between cutting-edge global collaborations (Chase et al., 1993; APG IV, 2016; Cheng et al., 2018; Givnish et al., 2018; Zuntini et al., 2024), increasing availability of genome-scale genetic data (Cheng et al., 2018; One Thousand Plant Transcriptomes Initiative, 2019), and ever-improving methods of analysis (Cheng et al., 2018; Baker et al., 2022), researchers have made great strides towards a unified hypothesis of plant evolutionary history. Given the central importance of DNA in modern-day **systematics**, it is hard to believe that **molecular systematics** was only developed in the last 50 years (Mayr, 1974). So, how did we get to where we are today? Here, we will provide an overview of the history of plant systematics and explore how this history shaped current thinking and methods. To examine these questions, we will follow two groups of monocots now prescribed as Liliales and Asparagales. As the methods and theory of systematics changed, so did our understanding of the relationships between these important lineages.

Introduction to the Monocot Phylogeny

Monocots—vital to ecosystem stability and human well being—make up about 20–25% of angiosperm species diversity (60,000–85,000 species; Givnish et al., 2010; Timilsena et al., 2022). Notable monocots include grasses (wheat, rice, bamboo), bananas, cardamom, pineapple, and palms (Palmaceae; Zeng et al., 2014; Timilsena et al., 2022). Several **morphological characters** are shared by most or all monocots including a single cotyledon, floral parts in groups of three (Fig. 1c, 1d, 1k, 1l), parallel leaf venation (Fig. 1g, 1o), and a lack of the vascular cambium needed to form woody tissue (Chase, 2004).

Within monocots, those that possess two whorls of tepals were historically recognized as a distinct group called the petaloid monocots (Zomlefer, 1999; Johansen and Frederikson, 2006). This group includes the modern **taxonomic** orders Asparagales, Dioscoreales, and Liliales, with some exceptions (Judd, 1997; Seberg et al., 2012). The history of two of these closely related orders, Liliales and Asparagales, has been particularly fraught with taxonomic and phylogenetic instability. Liliales contains several important horticultural plants including lilies (Fig. 1l) and tulips (Vinnersten and Bremer, 2001), and Asparagales contains crop plants such as onions and vanilla and ornamental plants like orchids (Seberg et al., 2012; Wang et al., 2024). Difficulties grouping petaloid monocots have frustrated botanists for well over a century (Lindley, 1853; Cronquist, 1981), and, in the three decades since the first molecular phylogenetic studies of monocots, the relative placements of Liliales and Asparagales have often been an obstacle to a consistent, well-supported monocot phylogeny (Chase et al., 2000; Chase, 2004; Petersen et al., 2006; Givnish et al., 2010,

Figure 1: Morphological features of Asparagales (left, orange) and Liliales (right, blue). (a) *Allium douglasii* bulb (b) *Brodiaea coronaria* seeds (c) *Sisyrinchium californicum* flower (d) *Hippeastrum striatum* flower (e) *Ornithogalum umbellatum* ovary (f) *Allium constrictum* inflorescence (g) *Maianthemum stellatum* leaves and flowers (h) *Gasteria tukhelensis* leaves (i) *Bomarea obovata* rhizome and root tubers (j) *Lilium columbianum* seeds (k) *Bomarea* sp. flower (l) *Lilium michiganense* flower (m) *Calochortus longebarbatus* ovary (n) *Xerophyllum tenax* inflorescence (o) *Streptopus amplexifolius* leaves and fruit (p) *Bomarea obovata* tepal with basal nectary. Photos by Gabriel Campbell, Gerald D. Carr, Robert L. Carr, Emily Humphreys, and Carrie Tribble.

2018; Timilsena et al., 2022). In particular, hypotheses about how these orders are related to commelinids, a major group of monocots containing grasses and palms, have changed over time (Chase et al., 2006; Zuntini et al., 2024). The challenges systematists face in placing Liliales and Asparagales, and the advances that helped provide clarity, exemplify trends in systematics history.

The Goals of Systematics

Systematics is a broad field with two components: taxonomy—grouping, describing, and naming organisms (Box 1; Turner et al., 2013), and **phylogenetics**—hypothesizing evolutionary relationships (Rouhan and Gaudeul, 2021; Society of Systematic Biologists, 2024). In short, "systematics is the study of biological

diversity and its origins" (Society of Systematic Biologists, 2024).

In systematics, how best to create a useful, stable, and informative taxonomy remains a major topic of debate (The Angiosperm Phylogeny Group, 1998; International Commission on Zoological Nomenclature, 1999; Turland et al., 2018; Cantino et al., 2020; Laurin, 2024). Most systematists agree that named taxonomic divisions should both reflect phylogenetic relationships and be practical for describing and discussing organisms (The Angiosperm Phylogeny Group, 1998). Overwhelmingly, when defining taxonomic groups at the species-level and above, scientists strive for **monophyly** in classification, where groups of organisms comprise an ancestor and all of its descendants (The Angiosperm Phylogeny Group, 1998; Hörandl, 2006; Laurin, 2024). It is important to note that while taxonomy aims to *reflect* something true about nature, taxonomy itself is a human construct; monocots could be divided into one order or twenty, and nothing would have changed about our understanding of the evolutionary relationships in the group.

To reconstruct evolutionary relationships through phylogenetics, systematists identify characters that provide evidence of evolutionary history. When looking at any **character state** shared by two taxa, it needs to be determined whether it is shared through descent from a common ancestor and, thus, evidence of phylogenetic relationship, or whether it has evolved independently in each taxon. Shared character states that independently evolve in different lineages can introduce **phylogenetic noise**, which is similarity that could appear to be informative, but conflicts with the true pattern of evolutionary divergence (Townsend et al., 2012). It is similar to a radio signal with static; a little static is okay, but when the static gets to be too much the message cannot come through. Selecting characters that change at an appropriate rate for a group of interest and increasing the number of independent characters analyzed can help maximize the information available for phylogenetic inference (Givnish and Sytsma, 1997; Townsend et al., 2012; Mishler, 2014; Givnish et al., 2018). Other challenges to phylogenetic reconstruction include interruptions in strict ancestor-decedent relationships through processes such as **hybrid speciation**, **introgression**, or **horizontal gene transfer** (See Box 2: Glossary, Mishler, 2014). Convergence can also mask true evolutionary relationships as it leads to shared character states without shared evolutionary history (Patterson and Givnish, 2002; Givnish et al., 2006). Many of these complications have likely impacted our ability to understand the relationship between Liliales and Asparagales (discussed further below in "Why do trees disagree?"). Phylogenies represent hypotheses of evolutionary relationships and can change with new information and techniques. Careful choice of methods and an appreciation for the complexity of evolutionary processes help mitigate error.

Systematics before DNA

A Brief History of Taxonomy

Throughout history, people have categorized living things (Laurin, 2024). Predating written language, taxonomy arose more than 5600 years ago (Rouhan and Gaudeul, 2021). Given the vastness of life on Earth, grouping organisms through taxonomy is foundational to communication (Haider, 2018). Concepts so fundamental as to be commonplace, such as ”plants,” ”grass,” or even ”humans,” are in fact taxonomic groupings. These groupings form some of the building blocks of thought, shaping not only the way the natural world is communicated about, but also how it is understood.

Modern plant taxonomy derives from the revival of Greek thinking during the Renaissance (Rouhan and Gaudeul, 2021; Laurin, 2024). It was during this time that monocots were first named by British botanist John Ray (1627–1705) who recognized the single cotyledon as an important unifying characteristic (Ray, 1682, 1696, 1703). The most influential taxonomic system of this period was created by Swedish naturalist Carolus Linnaeus (1707-1778) (Linnaeus, 1753a,b). Linnaeus' system grouped plants based on reproductive structures, reflecting the shift towards relying on plant characteristics (*e.g.*, anatomy, morphology) to inform taxonomy instead of plant uses (*e.g.*, food, medicine) (Rouhan and Gaudeul, 2021; Laurin, 2024). Like many early taxonomists, Linnaeus' goal was to describe groups he believed were created by the Christian god (Sloan, 1972; Mishler, 2014; Rouhan and Gaudeul, 2021). Linnaeus divided plants into hierarchical ranks and popularized binomial nomenclature, forming the foundation of the nomenclatural system most widely used in botany today (Turland et al., 2018; Rouhan and Gaudeul, 2021). Still, Linnaeus' classification is quite divergent from our current understanding of relationships; he placed several members of Liliales and Asparagales together in his group Hexandria monogynia (six stamens, one pistil), but also much more distantly related groups such as *Berberis* (Ranunculales) and *Richardia* (Gentianales) (Linnaeus, 1753a).

Box 1

Here, we focus on the history of western scientific plant taxonomy which traces its roots to Greek botanical traditions (Laurin, 2024). It is important to note that there are many other taxonomies used for plants around the world (Turner et al., 2013). These plant taxonomies reflect extensive collective knowledge of the natural world. Many incorporate distinctions between plants based on plant traits and/or the role that plants play in the lives of the people who use the taxonomy. These taxonomies are highly practical and complex, while largely serving a different purpose from the taxonomy we describe throughout this article.

A major shift in taxonomic thinking began in the late 1850s when the work of Alfred R. Wallace (1823-1913) and Charles Darwin (1809-1882) introduced the theory of evolution (Wallace, 1855; Darwin, 1859; Lloyd et al., 2010). For the first time, shared morphology was seen not simply as a basis for describing "natural" groupings, but as a reflection of **homology** and common ancestry (Sloan, 1972; Mayr, 1974; Judd et al., 1999; Rouhan and Gaudeul, 2021). Despite this shift in understanding, the process of classification remained functionally the same for nearly a century as methods for investigating evolutionary history had yet to be developed (Endersby, 2009; Laurin, 2024).

Theory and Methods of Phylogenetic Analysis

The mid-20th century saw innovation in systematics. **Cladistics**, a new conceptual framework, led to one of the most influential theoretical and practical shifts in the history of the field (Williams and Ebach, 2014). Cladistics originated as a theory of classification in which organisms are grouped by common descent inferred from **synapomorphies** (Mayr, 1974; Mishler, 2014). Cladistics holds two distinct but interconnected goals: reconstruct phylogenetic relationships and use the resulting groupings as the basis of taxonomy (Mayr, 1974). Our modern understanding of cladistics derives from the work of German entomologist, Willi Hennig, whose book *Phylogenetic Systematics* (Fig 2.) popularized phylogenetics as the foundational reference system of systematics and biology as a whole (Hennig, 1950, 1966). While methodological advances have continued, the "Hennigian revolution" of the 1970s and 1980s forever changed the discipline of systematics (Mishler, 2014).

In parallel, the practicality of inferring evolutionary relationships greatly expanded with increasing computational power (Sneath and Sokal, 1962; Williams and Ebach, 2014; Laurin, 2024). This facilitated an early implementation of cladistic theory: **parsimony analyses**, which improved researchers' ability to infer phylogenetic relationships (Laurin, 2024). Parsimony centers around the idea that the tree that requires the fewest character state changes best represents evolutionary history. This method relies on knowledge of whether character states are ancestral or derived, as only derived character states are phylogenetically informative (Mayr, 1974). Over time, proponents of parsimony came to be called "cladists". An alternative approach to phylogenetic inference, **model-based analyses**, boasted meaningful innovations, such as the ability to consider the variation in the rates at which character states change (Laurin, 2024). For example, the DNA of annual plants tends to accumulate nucleotide substitutions more quickly than perennial plants (Gaut et al., 2011). Parsimony would treat nucleotide substitutions in both as equally likely, whereas model-based analyses allow for more flexibility. Furthermore, model-based analyses consider the probability of reversals (for example, nucleotide A transitions to C, and then back to A), which are effectively

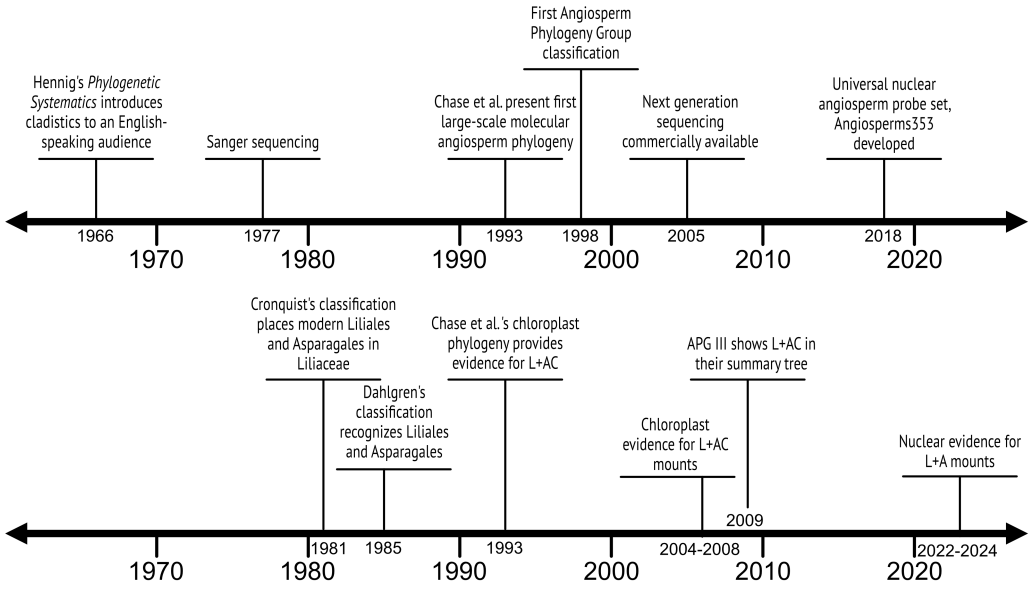

Figure 2: (top) Major events in the recent history of plant systematics. (bottom) Major events in our recent understanding of the relative placements of Liliales and Asparagales. There have been two main hypotheses for the patterns of relationships among these lineages: L+AC (Liliales sister to Asparagales + commelinids) and L+A (Liliales + Asparagales). See the text for additional primary literature supporting these hypotheses.

ignored by parsimony analyses. Overall, if there is complexity in the underlying evolutionary process, parsimony will likely fail (Yang, 1996). Model-based analyses—which are more computationally intensive to run than parsimony—include maximum likelihood and Bayesian methods which incorporate statistical models that aid in development of phylogenetic hypotheses (Laurin, 2024). Like parsimony, these methods can be applied to both morphological data and the molecular data most popular today.

Pre-molecular Understanding of Petaloid Monocots Relationships

Within petaloid monocots, taxonomic relationships remained poorly understood and hotly debated through much of the 19th and 20th century. Though at times split, disagreement and uncertainty led to much of the group being treated as a single family, Liliaceae, by multiple authors for over a century (Lindley, 1853; Engler and Prantl, 1889; Hutchinson, 1959; Cronquist, 1981; Zomlefer, 1999). Speaking on Liliaceae *sensu lato*, Lindley (1853) wrote, "there are few great groups of plants which have been more neglected by the exact botanist or which stand more in need of his patient attention." Lindley (1853) opted to treat the group as one family, fearing there was too little information to confidently subdivide it. His sentiment is strikingly similar to that of Cronquist (1981) more than a century later, who also noted the great amount of work to be done in Liliaceae and defined the family broadly in his treatment due to a lack of convincing evidence

for subdivision (Fig. 2).

Cronquist's 1981 treatment had an important place in plant systematics. Over a decade later, his dicot circumscriptions were used by Chase et al. (1993) in, what was at the time, the largest cladistic analysis of plants to have been conducted (Fig. 2). Notably, though, Chase et al. (1993) used the monocot circumscription of Dahlgren et al. (1985), *not* Cronquist (1981). The work of Dahlgren et al. (1985) represented a major step forward in angiosperm taxonomy as it was one of the first large-scale treatments to extensively incorporate emerging cladistic analyses. This approach overturned many established understandings of deep monocot relationships which had put greater emphasis on qualitative notions of similarity and assumptions about which character states might be "advanced" (Takhtadzhian, 1958; Cronquist, 1981; Dahlgren et al., 1985). Dahlgren et al. (1985) treated petaloid monocots, including genera that Cronquist (1981) had placed in one *family* just four years earlier, as multiple taxonomic *orders* including Liliales and Asparagales (Fig. 2). In drawing distinction between the morphologically similar Liliales and Asparagales, Dahlgren et al. (1985) built on the work of Huber (1969) and referenced several morphological differences. These included succulence in some Asparagales, spotted tepals in many Liliales, and differing nectary placement in the two orders, among others (Fig. 1). One important synapomorphy he noted for most Asparagales is a phytomelan layer in the seed coat which gives Asparagales seeds a shiny black appearance (Fig. 1b; Dahlgren et al., 1985; Zomlefer, 1999). The classification of Dahlgren et al., complete with the major changes in the circumscription of petaloid monocots, was widely accepted and remained highly influential as systematics transitioned towards molecular phylogenetics (Duvall et al., 1993a; Chase, 1995; APG II, 2003). Future molecular analyses reveled Dahlgren et al. (1985) misplaced several monocot families perhaps due to convergent evolution (Chase et al., 1993; Duvall et al., 1993a; Givnish et al., 2018). Still, Seberg et al. (2012) asserts that Dahlgren et al. (1985) "may be considered the starting point of modern systematics of the monocotyledons."

Diverse Sources of Evidence in Phylogenetic Analysis

While morphology and anatomy were the primary sources of systematic data during the early- and mid-20th century, botanists also turned to the fossil record, secondary plant chemistry, chromosome number and structure, and more as they tried to interpret relationships (Dahlgren, 1983; Dahlgren et al., 1985; Gandolfo et al., 2000; Soltis et al., 2009). Fossils provided early evidence that monocots were descended from plants with two seed leaves (cotyledons), rendering the traditional group dicots non-monophyletic (Dahlgren et al., 1985). Fossils were also included as tips in some early cladistic analyses of monocots (Gandolfo et al., 2000). Serological data, which reflects the similarity of proteins (Boyden, 1936), showed that

Asparagus may be most closely related to other members of Asparagales and less closely related to members of Liliales (Dahlgren, 1983), potentially supporting the split of Cronquist (1981)'s Liliaceae. Chemical analyses, while they provided little decisive evidence of evolutionary history, were comparatively revealing in Liliales and Asparagales as these orders contain many unusual chemicals (Kite et al., 2000). For example, colchicine alkaloids are common in the family Colchiaceaeae (Liliales), but uncommon outside of it (Kite et al., 2000). These indicators of phylogenetic relationships were gradually replaced by direct comparison of macromolecules such as DNA, RNA, and proteins (See Early molecular understanding, Zuckerkandl and Pauling, 1965; Soltis et al., 2009). Although, by the late 1970s, higher order relationships among flowering plants had become largely stable, these relationships were not to remain certain for long (The Angiosperm Phylogeny Group, 1998).

Early molecular understanding

Transforming molecular phylogenetics from a theoretical ambition to a practical reality required methodological innovation. Early molecular techniques included RNA sequencing (Holley et al., 1965; Cedergren et al., 1972), indirect inference of genetic relatedness though amino acid sequence data (Mayr, 1974; Martin et al., 1983) and comparison of DNA fragmentation patterns (Palmer and Zamir, 1982). Above all else, the development of **Sanger sequencing** revolutionized molecular systematics (Fig. 2; Sanger and Coulson, 1975; Sanger et al., 1977; Graham and Hill, 2001; Barrett et al., 2016). Sanger sequencing made DNA sequencing practical and reliable for the first time. The power of Sanger sequencing was magnified by the development of polymerase chain reaction (PCR), which allows a small quantity of genetic material to be amplified into the millions of copies of a region of interest commonly needed for Sanger sequencing (Mullis et al., 1986).

By the 1990s, DNA-based systematic methods were generally quicker to complete than traditional, largely morphological methods and required less training to implement (Mishler, 2014). Importantly, DNA data introduced a vast swath of new, independent characters for analysis (Soltis et al., 2009). It was suggested (Givnish and Sytsma, 1997) and later demonstrated (Givnish et al., 2018) that increasing the number of independent characters greatly improves phylogenic resolution and support. Among these molecular characters, inferring homology was often straightforward (Soltis et al., 2009). Moreover, DNA data was seen as more objective than other characters used in systematics (Chase et al., 1993), and molecular phylogenetics was held in esteem as being at the cutting-edge of science (Mishler, 2014). Still, both molecular and non-molecular phylogenetic techniques (such as chemistry and morphology) were in frequent use and

were sometimes analyzed together (Chase, 1995; Soltis et al., 2000; Stevenson et al., 2000). Chase (1995) took care to clarify that in taxonomic studies, molecular and morphological data are best as complements, and they hoped the results of their molecular work on monocots would spur future morphological examination. Still, given the benefits of molecular phylogenetics, morphological and chemical analyses were quickly overshadowed (Kite et al., 2000; Soltis et al., 2009; Mishler, 2014).

Between the 1990s and 2010s, botanical systematists primarily used data from chloroplast genes, as well as a small number of genes that code for ribosomal RNA in their phylogenetic analyses (Chase et al., 1993; Givnish et al., 2005; Graham et al., 2006; Givnish et al., 2010). There are several advantages to chloroplast data that contributed to its widespread use: compared to nuclear DNA, the chloroplast genome is small in size, it accumulates genetic change slowly which can reduce false signal, it is relatively structurally consistent, it is less likely to reflect **incomplete lineage sorting** (ILS), and there are large amounts of chloroplast DNA in green plant cells (Davis et al., 1998, 2014; Naciri and Linder, 2015; Goncalves et al., 2019; Do et al., 2020). Analyses informed by a small number of chloroplast genes were crucial in advancing our understanding angiosperm evolutionary relationships towards a greater consensus (Chase et al., 1993; Savolainen et al., 2000). Until recently, chloroplast data was the greatest contributor to our understanding of the angiosperm phylogeny (Goncalves et al., 2019; Li et al., 2019; Zuntini et al., 2024).

Most of the initial molecular phylogenetic investigations that included Liliales and Asparagales used chloroplast data and analyzed a limited number of gene regions (Chase et al., 1993; Duvall et al., 1993b,a; Davis, 1995; Nadot et al., 1995; Davis et al., 1998; Källersjö et al., 1998; Givnish et al., 1999; Chase et al., 2000; Fuse and Tamura, 2000; Savolainen et al., 2000; Soltis et al., 2000). Out of these early studies, a pattern began to emerge. Despite the close relationship of Liliales and Asparagales in morphological phylogenies (Chase et al., 1995; Stevenson et al., 2000), analyses conducted with primarily chloroplast data indicated that Asparagales may be more closely related to commelinids than Liliales (Fig. 3a) (Chase et al., 1993; Duvall et al., 1993b,a; Chase et al., 1995; Davis, 1995; Davis et al., 1998; Chase et al., 2000; Fuse and Tamura, 2000; Savolainen et al., 2000; Soltis et al., 2000). This pattern was also found in Soltis et al. (1997) using a nuclear region. By 2000, this set of relationships was considered a general trend (Chase et al., 2000), but a high degree of uncertainty was still acknowledged as relationships among Liliales and Asparagales were still commonly unresolved or very weakly supported (Nadot et al., 1995; Fuse and Tamura, 2000; Savolainen et al., 2000; Soltis et al., 2000). For example, multiple studies recovered a consensus tree in which Asparagales and Liliales were part of a large **polytomy** (Chase, 1995; Soltis et al., 2000). An alternative set of relationships was also recovered from plastid trees where Liliales and Asparagales were sister lineages (L+A.; Fig. 3b); this result was more in line with the traditional morphological understanding, though these

findings had little statistical support (Givnish et al., 1999; Savolainen et al., 2000) .

In 1998, among the buzz of molecular phylogenetic research, a collaborative group of experts, the Angiosperm Phylogeny Group (APG), published their first classification of flowering plants (Fig. 2; The Angiosperm Phylogeny Group, 1998). This classification was designed to remedy the tension between **authority-based plant classifications** (Cronquist, 1981; Thorne, 1992; Takhtadzhian, 1997) and the new **consensus understanding** of the angiosperm phylogeny (APG II, 2003). Where authority-based classifications represented the informed opinion of experienced taxonomists, the APG classification was derived from explicit, repeatable analyses of primarily molecular data (The Angiosperm Phylogeny Group, 1998). In the decades since, the APG treatment and subsequent updates have come to be widely regarded as a preeminent authority on the standardized understanding of angiosperm relationships (Chase et al., 2006; Seberg et al., 2012; Zeng et al., 2014). Both APG I and II summary trees resolved Liliales, Asparagales, Dioscoreales, Pandanales, and commelinids as a polytomy (The Angiosperm Phylogeny Group, 1998; APG II, 2003), further highlighting the historical lack of resolution in petaloid monocot relationships.

The new millennium ushered in the first whole plant nuclear genome (Arabidopsis Genome Initiative, 2000; Soltis et al., 2009). Despite advances in computing and sequencing, the chloroplast genome continued to be the primary source of DNA used to study deep angiosperm relationships due to its relative abundance within plant tissues and its sequencing reliability (Davis et al., 2014). From 2000 to 2010, multiple phylogenetic studies used primarily chloroplast data and found moderate to high support for Liliales as sister to a clade comprised of Asparagales and Commelinids (L+AC; Figs. 2 and 3; Tamura et al., 2004; Chase et al., 2006; Graham et al., 2006; Pires et al., 2006; Qiu et al., 2006; Saarela et al., 2008). Still, some studies incorporating chloroplast data that were published during this time recovered a variety of disparate relationships among petaloid monocots and commelinids, accompanied by low or no support (Davis et al., 2004; Givnish et al., 2005); generally, these analyses included fewer gene regions. A more limited set of analyses turned to mitochondrial DNA for a source of genetic characters independent from the widely-used chloroplast genome. These analyses overwhelmingly failed to recover L+AC, instead providing support for various alternate relationships (Davis et al., 1998; Petersen et al., 2006; Qiu et al., 2006, 2010). Despite conflicting signals among mitochondrial trees and a heavy reliance on chloroplast data for strong evidence supporting L+AC, APG III presented this set of relationships in their summary tree in 2009 (Fig. 2; APG III, 2009). To all the world, petaloid monocots were a polytomy no more.

Why do Trees Disagree?

As molecular phylogenetic evidence mounted, most deep relationships in the angiosperm phylogeny stabilized across studies using different data sources and methods (Timilsena et al., 2022; Zuntini et al., 2024). However, a few deep relationships, such as the one between Liliales and Asparagales, remained inconsistently or poorly supported (Li et al., 2021; Zuntini et al., 2024). There are many reasons why uncertainties may persist including **long branch attraction**, difficulties selecting appropriate evolutionary models, too few independent characters, biased or insufficient taxon sampling, and incorrect identification of homology often amplified by convergence (Patterson and Givnish, 2002; Heath et al., 2008; Zeng et al., 2014; Givnish et al., 2018; Doyle, 2022; Zuntini et al., 2024). As a further complication, the major angiosperm lineages, as well as Liliales and Asparagales, are likely the result of **rapid radiations** (Timilsena et al., 2022; Zuntini et al., 2024). When speciation occurs quickly, genetic change between lineages has little time to accumulate. As a result, the genomic signal uniting groups can be very weak (Soltis et al., 1997), making it difficult to confidently reconstruct phylogenetic relationships.

Our understanding of the relationships among major angiosperm lineages has been influenced by the heavy reliance on chloroplast sequence data for phylogenetic inference (Davis et al., 2014). Each of the three plant genomes, chloroplast, mitochondrial, and nuclear, and different genes or regions within each, may have their own, distinct evolutionary history (Tyszka et al., 2023). These unique evolutionary histories can diverge from one another or the evolution of the species as a whole (Doyle, 1992, 2022). When a segment of DNA (a "gene") is used to build a phylogenetic tree, the resulting **gene tree** represents the evolutionary history of only that segment, which may not fully represent the history of diversification (*i.e.*, the **species tree**) (Doyle, 1992). When divergent relationships are recovered across gene tree(s) and a species tree, this is termed **phylogenetic incongruence** (Doyle, 1992; Goncalves et al., 2019). Many factors may lead to incongruence, including introgression, incomplete lineage sorting (ILS) (Timilsena et al., 2022), and **gene duplication** (Doyle, 1992). Some of these phenomena are more likely to impact lineages that emerged from rapid radiation (Koblmüller et al., 2010; Slovák et al., 2023). Using multiple genes for phylogenetic analysis and/or combining organellar data with nuclear data may reduce the impact of these drivers of incongruence by providing multiple, independent indicators of evolutionary history (Doyle, 1992, 2022). This was recognized early on. As far back as 1995, Chase (1995) emphasized that nuclear data in addition to chloroplast data would be needed to understand relationships among higher-level monocots.

Analyses using multiple regions from an organellar genome are more likely to produce gene trees that are inconsistent with the species tree than those built using multiple nuclear regions (Doyle, 1992, 2022).

This is because organellar DNA is most often maternally inherited (McCauley, 2013; Davis et al., 2014), and because it acts much more like a single evolutionary unit than nuclear DNA (Doyle, 2022). As such, a whole chloroplast genome may contain a limited amount of independent evolutionary evidence. Analyses based on many chloroplast regions can have high levels of support (Givnish et al., 2018), but this could be because the singular chloroplast provides strong and consistent support of relationships, not necessarily because it reflects the "true" history of speciation (Doyle, 2022). It is also possible for chloroplast or mitochondrial genomes to be transmitted between species though **organelle capture** (Stegemann et al., 2012). This means that the chloroplast genome of a modern plant could have a weak relationship to patterns of speciation. As discussed above, major improvements in our understanding of the angiosperm phylogeny were and still are deeply rooted in chloroplast sequence data (Goncalves et al., 2019; Li et al., 2019), and these data present distinct benefits, including being less influenced by ILS (Naciri and Linder, 2015). In general, patterns of relationships based on chloroplast data have been concordant with those derived from nuclear analyses (Timilsena et al., 2022; Zuntini et al., 2024). Still, understanding the propensity of chloroplast data to generate gene tree-species tree incongruence provides important context for understanding discordance between chloroplast and nuclear phylogenies, particularly in lineages that diversified rapidly, such as Liliales and Asparagales.

Recent molecular understanding

Just as Sanger sequencing had done decades before, **next-generation sequencing** (NGS) changed the scale of molecular phylogenetics (Fig. 2; Givnish et al., 2010; Godden et al., 2012; Barrett et al., 2016; Givnish et al., 2018). Introduced in the mid-2000s (Margulies et al., 2005; Soltis et al., 2009; Egan et al., 2012), NGS allowed the number of analyzed genomic regions to drastically increase and greatly reduced the cost and time of sequencing (Margulies et al., 2005; Egan et al., 2012; Godden et al., 2012; Steele et al., 2012; Barrett et al., 2016). In NGS, large numbers of genomic fragments are sequenced simultaneously. By 2010, NGS had made it not only possible to sequence whole plastid genomes, but routine (Soltis et al., 2009; Givnish et al., 2010).

In parallel with increases in the scale of molecular data available, there have been steady advances in computing power and software for phylogenetic analyses. As it is the least computationally intensive, many early analyses used parsimony methods (*e.g.*, Chase et al., 1993; Soltis et al., 1997; Givnish et al., 1999). As time went on, more studies came to employ maximum likelihood approaches (*e.g.*, Duvall et al., 1993b; Givnish et al., 2010; Wickett et al., 2014; Givnish et al., 2016, 2018), and computationally intensive

Box 2 Glossary

Authority-based classification. A classification based on the informed opinion of an experienced taxonomist.

Character. A trait or characteristic used for phylogenetic or taxonomic inference.

Character state. A particular form taken on by a trait or characteristic.

Cladistics. A conceptual framework that posits that phylogenetics should be the foundational reference system of biology. Now used primarily to refer to parsimony-based phylogenetics.

Consensus-based classification. A data-driven classification created collaboratively by a diverse group of expert systematists.

Gene duplication. The duplication of a genomic region. Results in two or more copies of the original gene which can take on independent evolutionary trajectories.

Gene tree. A phylogenetic tree that represents relationships for a gene.

Homology. Similarity due to shared evolutionary history.

Horizontal gene transfer. Transfer of genetic material from one organism to another through any mode other than reproduction.

Hybrid speciation. Speciation resulting from hybridization.

Incomplete lineage sorting. A phenomenon in which multiple character states are passed down from a variable ancestral population to a variable descendent population, complicating the search for phylogenetic signal.

Introgression. Hybridization between taxa and subsequent backcrossing resulting in the transfer of genetic material from one taxon to another.

Long branch attraction. A phenomenon in which long branches are more likely to group together in a phylogenetic tree regardless of evolutionary history.

Model-based analyses. Methods for inferring phylogenetic relationships based on a model of evolution. These methods allow for variation in the rates of character state changes.

Molecular systematics. DNA-based systematics.

Monophyletic. A group of organisms comprised of an ancestor and all of its descendants.

Morphology. Gross characteristics of physical structures.

Next-generation sequencing. Methods for sequencing many regions in parallel.

Organelle capture. A phenomenon in which an organelle, but not the nucleus, transfers from one organism to another.

Parsimony analyses. A method of estimating phylogenetic trees that minimizes the number of character state changes needed to explain the data.

Phylogenetic incongruence. Disagreement in hypothesized evolutionary relationships between different phylogenetic trees.

Phylogenetic noise. Information that could appear to be phylogenetically informative but is not a result of shared evolutionary history.

Phylogenetics. The field devoted to the study of evolutionary history.

Polytomy. A set of unresolved phylogenetic relationships represented in a phylogeny by more than two branches sharing a node.

Rapid radiation. A burst of speciation occurring over a short period of time.

Sanger sequencing. The first scalable method of DNA sequencing. Provided the basis of early molecular phylogenetic understanding.

Species tree. A phylogenetic tree that represents relationships among species.

Synapomorphy. A shared, derived trait.

Systematics. A branch of evolutionary biology dedicated to grouping, describing, and naming organisms (taxonomy) based on evolutionary history (phylogenetics)

Taxonomy. The field devoted to grouping, describing, and naming organisms.

Topology. The pattern of relationships depicted by a phylogenetic tree.

Bayesian analyses became more common and were used across increasingly large data sets (*e.g.*, Hilu et al., 2003; Kim et al., 2013; Wickett et al., 2014; Do et al., 2020). It is not uncommon for analyses to incorporate multiple analytical methods (parsimony, maximum likelihood, Bayesian), which may support incongruent

topologies.

Amidst this backdrop of hope and growth, assembling a comprehensive plant tree of life came to be seen as practical and achievable (Soltis et al., 2009; Givnish et al., 2010). In 2010, the Monocot Assembling the Tree of Life project was announced (Givnish et al., 2010), which sought to develop a fully resolved phylogeny of monocots by greatly increasing sampling of plastid and nuclear gene regions, including by investing heavily in sequencing whole plastid genomes. A landmark publication out of this project provided the most robust support to date for the L+AC relationship using whole plastid data (Givnish et al., 2018). Simultaneously, the European monocot initiative worked to sequence two plastid regions for all $\sim$2400 genera in the monocotyledons (Givnish et al., 2010), and the 1000 Plants Initiative aimed to sequence 1000 transcriptomes across all green plants (One Thousand Plant Transcriptomes Initiative, 2019). Continuing the tradition of large collaborations in botanical systematics (*e.g.*, Chase et al., 1993), these projects and others worked to increase the breadth, depth, and variety of monocot DNA sequenced.

As the number of regions analyzed grew dramatically throughout the 2010s, chloroplast phylogenies continued to find strong evidence for L+AC (Soltis et al., 2011). This general set of relationships was recovered with moderate or high support across analyses using NGS (Givnish et al., 2010, 2016, 2018; Gitzendanner et al., 2018; Lam et al., 2018; Li et al., 2019), though analytical method sometimes impacted the **topology** recovered (*e.g.*, Ruhfel et al., 2014). Given this evidence, the most recent APG publication, APG IV, maintained L+AC on their summary tree (APG IV, 2016).

At the same time, spurred by NGS and increasing computational capacity, large analyses of nuclear DNA quickly increased in feasibility and popularity (Davis et al., 2014). In these analyses, an alternate pattern of petaloid monocot relationships repeatedly emerged. While some analyses in the early 2010s found low support and inconsistent relationships among petaloid monocots and commelinids using nuclear data (Morton, 2011; Wickett et al., 2014), later studies using large nuclear data sets have consistently recovered L+A with moderate to high support (Fig. 2; Zeng et al., 2014; Baker et al., 2022; Timilsena et al., 2022, 2023; Zuntini et al., 2024; Liang et al., 2025). The placement of Liliales and Asparagales was repeatedly found to be the largest discordance in major relationships within monocots between plastid and nuclear derived phylogenies (Timilsena et al., 2022, 2023).

With continued improvements in sampling and sequencing, what has long been a trend seems to be a well-supported pattern: chloroplast data tends to resolve L+AC and nuclear data tends to resolve L+A (Fig. 3). Recent analyses that rely solely on chloroplast DNA continue to find strong support for L+AC (Do et al., 2020; Li et al., 2021), suggesting that for Liliales and Asparagales, the difference in topologies truly rests with different signals across genomes, not methodological differences between older and newer studies.

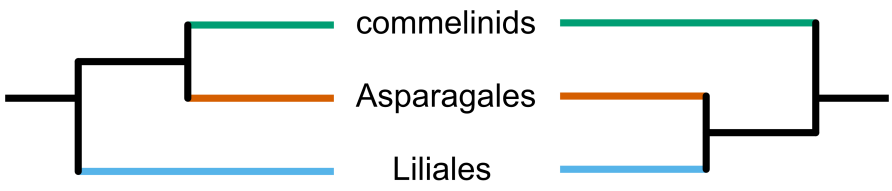

Figure 3: (left) Understanding of Liliales, Asparagales, and commelinid evolutionary relationships derived from chloroplast data. (right) Understanding of Liliales, Asparagales, and commelinid evolutionary relationships derived from nuclear data. The body of literature supporting these two hypotheses is summarized throughout the text.

Given that large nuclear analyses encompass many more regions with independent evolutionary histories than large chloroplast analyses (Doyle, 1992), it seems likely that L+A best represents the species tree. In retrospect, there is evidence our understanding of the relationships among Liliales, Asparagales, and commelinids was not fully settled even before large nuclear analyses became feasible. Alternate topologies were repeatedly recovered from mitochondrial DNA (Davis et al., 1998; Petersen et al., 2006; Qiu et al., 2006, 2010), and a persistent portion of chloroplast analyses recovered low or no support for the relationships among these lineages though these were often based on a limited number of genes (*e.g.*, Hilu et al., 2003; Givnish et al., 2005). Our shifting understanding of the relationship between Liliales and Asparagales demonstrates the impact of sampling and analytical methods on tree topologies, especially for lineages that rapidly diverged. With increasing sampling, new types of data being analyzed, and new phylogenetic methods continuing to be developed, our understanding of evolutionary relationships may change as the tree of life continues to be refined and stabilized.

Implications of a Sister Relationship between Liliales and Asparagales

Changes in accepted phylogenetic relationships often have important implications for trait evolution. This is evident as we reinterpret the history of Liliales and Asparagales evolution. If we understand the relationship among Liliales and Asparagales to be L+AC, it seems as though the long-recognized morphological similarity of the two orders (Cronquist, 1981; Seberg et al., 2012; Givnish et al., 2016) might best be attributed to shared common ancestry deeper in the monocot phylogeny and shared traits being conserved over time. Understanding the relationship as L+A, on the other hand, suggests these morphological similarities may in fact be synapomorphies or evidence of uniquely shared genetic architecture. For example, floral forms in Liliales and Asparagales are often strikingly similar (Dahlgren et al., 1985). Most members of both orders

have two whorls of similar tepals, distinct perianth segments, 6 stamens, and superior 3-locular ovaries (Cronquist, 1981; Hitchcock and Cronquist, 2018). These similarities are exemplified when comparing the striped Barbados lily (Asparagales, Fig. 1d) and Michigan lily (Liliales, Fig. 1l). Moreover, members of both families typically have underground storage organs such as bulbs, corms, or rhizomes (Asparagales, Fig. 1a; Liliales, Fig. 1i; Cronquist, 1981; Hitchcock and Cronquist, 2018). It it possible that high-level molecular mechanisms shared due to evolutionary history may facilitate similar morphology in both orders, making them more likely to evolve similar forms. A sister relationship between Liliales and Asparagales invites this hypothesis and many more.

This new understanding also shapes how we look back on the taxonomic history of Liliales and Asparagales. Morphological similarity between the orders led to members of modern Liliales and Asparagales being prescribed as part of the same family as recently as the 1981 (Cronquist, 1981). Despite the strong morphological affinity between Liliales and Asparagales, for two decades molecular evidence led us towards the conclusion that Asparagales was sister to the more morphologically divergent commelinids. Notably, as nuclear data refines our understanding, it seems that the relationship between the two orders is actually more similar to that indicated by the morphological classification of Liliaceae *sensu lato* than the relationship suggested by early molecular phylogenetic work. This full-circle understanding is a testament to the careful work of morphological systematists, the importance of multiple modes of evidence including morphology, and the non-linear nature of the scientific process as we work towards consensus.

Botanical phylogenetic methods today

Throughout the history of systematics there has been a continual effort to consider a greater number and diversity of characters in phylogenetic inference. We now appear to be entering the age of whole nuclear phylogenetics. In 2025, the first whole annotated nuclear genomes became available for Liliales (Liang et al., 2025). Several whole nuclear genomes have likewise been published for economically important members of Asparagales (Hao et al., 2023).

DNA data revolutionized phylogenetic reconstruction, but DNA can only be used to consider extant plants found today. Recently, there has been a focus on integrating molecular and morphological data from extant species with morphological and temporal data from fossils to model evolutionary history in a process called total evidence dating (Zhang et al., 2016; Gavryushkina and Zhang, 2020). As fossil evidence and morphological characters informed much early systematic work (Cronquist, 1981; Gandolfo et al., 2000; Hamilton, 2014), the renewed appreciation for the value of these data alongside molecular evidence repre-

sents an integration of old and new understanding.

Today, a wealth of collaborative initiatives seek to infer the angiosperm phylogeny at never-before-seen genomic and taxonomic scales. The success of the 1000 Plants Initiative lead to the launch of the 10,000 Plants Genome Sequencing Project which seeks to construct annotated reference genomes for every genus of land plant (Cheng et al., 2018). Similarly the Plant and Fungal Tree of Life Project (PAFTOL) aims to sequence one member of every angiosperm genus (Baker et al., 2022). Instead of sequencing whole genomes, PAFTOL researchers are focusing on 353 nuclear regions dubbed "Angiosperms353" regions (Fig. 2; Johnson et al., 2018; Baker et al., 2022). PAFTOL recently reached a major milestone with the publication of Zuntini et al. (2024), which used the Angiosperms353 regions to construct an angiosperm phylogeny with fifteen times the taxonomic sampling of previous phylogenies that used similar methods. This phylogeny supported L+A (Zuntini et al., 2024). Pursuit of a fully-resolved tree of life extends far beyond plants. Announced in 2018, The Earth BioGenome Project aims to sequence the genomes of all eukaryotic species over 10 years (Lewin et al., 2018). Although Lewin et al. acknowledge the project's goal is a "moonshot for biology", they emphasize that methodological advances make such a goal achievable for the first time. Efforts such as these require a massive amount of collaboration, bringing together scientists from around the world and from every branch of evolutionary biology. Fueled by ever advancing systematic methods and an insatiable hope for the future, systematists work to understand the complex history of life on earth.

Conclusion

In a relatively short period of time, we have transitioned from single region molecular phylogenetics (Chase et al., 1993) to sampling hundreds to thousands of regions for thousands of species (Zuntini et al., 2024) and are working towards even loftier goals (Cheng et al., 2018; Lewin et al., 2018; Baker et al., 2022). The molecular phylogenetic era has led to well established relationships among the major lineages of angiosperms and greater phylogenic clarity across all taxa and all scales of life (Soltis et al., 2009). Still, some relationships remain uncertain. Broad, unbiased sampling, consideration of multiple independent sources of phylogenetic evidence, and an appreciation for how past methodologies shape current thinking will be instrumental as we continue to deepen our understanding of phylogenetic relationships in an ever-changing scientific landscape.

Acknowledgments

We thank Thomas J. Givnish and an anonymous reviewer for suggesting valuable revisions, Richard Olmstead, Chiara Smythies, Alan Li, Peter Ricci, Hayden Wright, and Fanya Yuan for their thoughtful feedback on an early version of the manuscript, and Gabriel Campbell, Gerald D. Carr, Robert L. Carr, Sophie Zhang, and the University of Washington Biology Greenhouse and Medicinal Herb Garden providing photographs/collections to photograph. EAH was supported, in part, by funding from the the ARCS Foundation.

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