

Review article

Progress in systematics and biogeography of Orchidaceae

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ABSTRACT

Orchidaceae are one of the largest families of angiosperms in terms of species richness. In the last decade, numerous studies have delved into reconstructing the phylogenetic framework of Orchidaceae, leveraging data from plastid, mitochondrial and nuclear sources. These studies have provided new insights into the systematics, diversification and biogeography of Orchidaceae, establishing a robust foundation for future research. Nevertheless, pronounced controversies persist regarding the precise placement of certain lineages within these phylogenetic frameworks. To address these discrepancies and deepen our understanding of the phylogenetic structure of Orchidaceae, we provide a comprehensive overview and analysis of phylogenetic studies focusing on contentious groups within Orchidaceae since 2015, delving into discussions on the underlying reasons for observed topological conflicts. We also provide a novel phylogenetic framework at the subtribal level. Furthermore, we examine the tempo and mode underlying orchid species diversity from the perspective of historical biogeography, highlighting factors contributing to extensive speciation. Ultimately, we delineate avenues for future research aimed at enhancing our understanding of Orchidaceae phylogeny and diversity.

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1. Introduction

Orchidaceae are among the largest families of angiosperms, encompassing over 700 genera and more than 30,000 species worldwide according to the Catalogue of Life (<https://www.catalogueoflife.org/>). The family is distributed across all continents except Antarctica and in extremely dry deserts (Fig. 1; Pridgeon et al., 2005; Chase et al., 2003; POWO, 2024). Many orchid taxa, such as *Cattleya*, *Cymbidium*, *Dendrobium*, and *Paphiopedilum*, play significant roles in horticulture, while species, such as *Cremastra appendicula*, *Dendrobium officinale*, and *Gastrodia elata*, possess vital medicinal value. All orchid species are listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) appendices I or II (<https://cites.org/>), highlighting their conservation importance. Orchidaceae exhibit a variety of habits and ecological

preferences, including terrestrial, epiphytic, climbing, and mycoheterotrophic lifestyles. This diverse array of characteristics represents an ideal case for the study of evolution and diversification (Jersakova et al., 2006; Lin et al., 2015; Kikuchi et al., 2020; Thompson et al., 2023).

Historically, orchid taxonomy has heavily relied on the morphology of reproductive organs, such as pollinia and the lip (Dressler, 1993). Numerous frameworks have attempted to trace orchid evolution from the “three fertile anthers group” of apostasioids (*Apostasia* and *Neuwiedia*) to the “two fertile anthers group” of cypripedioids (*Cypripedium*, *Mexipedium*, *Paphiopedilum*, *Phragmipedium*, and *Selenipedium*), followed by the monandrous orchids (Epidendroideae, Orchidoideae, and Spiranthoideae) (Pfitzer, 1887; Schlecter, 1926; Dressler and Dodson, 1960; Dressler, 1993). However, significant discrepancies often exist among various classification systems proposed on the basis of morphology (Pridgeon et al., 2005; Chase et al., 2003, 2015).

Molecular systematics has greatly revised the phylogenetic placement of many tribes and genera within Orchidaceae (Judd et al., 1993; Kocyan et al., 2004; Sosa, 2008; Raskoti et al., 2016). Phylogenetic analysis based on *rbcl* gene sequences

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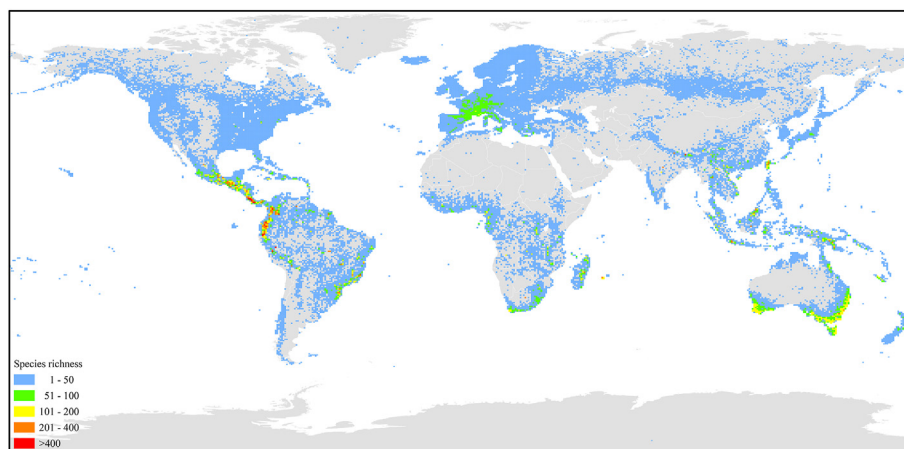


Fig. 1. Species richness of georeferenced records in Orchidaceae, based on data of GBIF (GBIF.org, 2024).

subdivide Orchidaceae into five major clades, subsequently recognized as five subfamilies in the widely-accepted classification system: Apostasioideae, Vanilloideae, Cyripedioideae, Orchidoideae, and Epidendroideae (Cameron et al., 1999; Chase et al., 2003). Further advances in sequencing technology have resulted in a comprehensive phylogenetic framework for Orchidaceae (Chase et al., 2015), although unresolved issues persist, particularly concerning relationships within and between tribes such as Cymbidieae, Epidendreae, and Vandaeae (Deng et al., 2015; Li et al., 2016, 2019b; Serna-Sanchez et al., 2021; Perez-Escobar et al., 2024; Zhang et al., 2023). Genomic data have generated numerous phylogenetic hypotheses and biogeographical inferences for Orchidaceae (Deng et al., 2015; Freudenstein and Chase, 2015; Givnish et al., 2015; Fernandez et al., 2019; Li et al., 2019b; Perez-Escobar et al., 2021, 2024; Serna-Sanchez et al., 2021; Zhang et al., 2023a, 2024), many of which have significantly clarified phylogenetic relationships within Orchidaceae. However, many previously recognized genera have been found to be non-monophyletic, leading to proposals for alternative generic delimitations (Zhang et al., 2015).

Orchid phylogenetics has also benefited from high-throughput sequencing technologies. Today, plant phylogenetic investigations routinely utilize organellar (plastid and mitochondria) genomic data and transcriptomic data (Wickett et al., 2014; Johnson et al., 2016; Bazinet et al., 2017; Unruh et al., 2018; Jin et al., 2021; Xia et al., 2022; Liu et al., 2023; Perez-Escobar et al., 2024; Zhang et al., 2023). For example, studies have shown that mitochondrial data is suitable for populations with diverse evolutionary rates, i.e., orchids (Ran et al., 2018; Guo et al., 2020; Stull et al., 2020). Although there are concerns that the transcriptomes of different tissues raise biases in phylogenetic inference, recent studies have demonstrated that lineage transcriptomics can be effectively employed for phylogenetic analysis as the results are only slightly affected by tissue type (Cheon et al., 2020).

The mechanisms underlying orchid diversity have long fascinated researchers. Previous work has examined net diversification rates and biogeography of genera, subtribes, and tribes within Orchidaceae (Micheneau et al., 2008; Guo et al., 2012; Givnish et al., 2016; Xiang et al., 2016; Perez-Escobar et al., 2017; Gamisch et al., 2021; Lai et al., 2021). Comprehensive studies of the biogeography and diversification of Orchidaceae require a robust phylogenetic framework, preferably resolved at the species level. However, efforts to resolve a phylogenetic framework of Orchidaceae at the genus level have been stymied by the pan-global distribution and exceptional diversity of the family (Givnish et al., 2016; Perez-Escobar et al., 2024).

In this review, we present a comprehensive synthesis of recent advances in phylogenetics, biogeography, and the mechanisms of diversification in Orchidaceae.

2. Phylogenetic research

Phylogenetic analyses based on plastid and nuclear genomes have advanced our understanding of orchid relationships at the subfamilial and tribal levels (Table 1; Unruh et al., 2018; Fernandez et al., 2019; Li et al., 2019b; Guo et al., 2020; Serna-Sanchez et al., 2021). Phylogenetic reconstructions based on chloroplast coding sequences (ptCDS) and mitochondrial coding sequences (mtCDS) have contrasted with previous studies based on morphology (Dressler and Dodson, 1960; Vermeulen, 1966; Garay, 1972; Dressler, 1981; Burns-Balogh and Funk, 1986; Berg et al., 2000; Chase et al., 2003), repositioning subfamilies Vanilloideae and Cyripedioideae (Li et al., 2019b), as well as designating Thaieae as a sister to the higher epidendroids (Xiang et al., 2012). However, recent research has also noted that phylogenetic trees based on nuclear data differ from those based on plastid data (Perez-Escobar et al., 2021).

Transcriptomic data have emerged as a source of information that can confirm fundamental phylogenetic relationships in Orchidaceae, but perhaps more importantly elucidate the evolution of traits within the family (Cheon et al., 2020; Guo et al., 2020, 2023). For example, studies have used transcription data of 315 single-copy orthologous genes to confirm that Orchidaceae consists of five subfamilies (Deng et al., 2015). In addition, transcriptomes have been used to explore the phylogenetic relationships of European *Ophrys* and *Gymnadenia*, focusing on investigating the deceptive pollination mechanism in orchids (Fernandez et al., 2019). Transcriptomic data has also been used to reconstruct orchid phylogeny in a study on the evolution of epiphytism across 610 orchid species (Zhang et al., 2023).

Here we provide a classification Orchidaceae based on research since 2015 (Fig. 2). At the family level, the classification aligns with the main taxonomic systems of Orchidaceae as outlined by Chase et al. (2015). No revisions have been made to subfamilies Apostasioideae, Vanilloideae, or Cyripedioideae. However, the placement of several groups remains controversial, e.g., Orchidinae, Goodyerinae, Angraecinae, Aeridinae, and Podochileae. Thus, in the following two sections, we focus only on progress in understanding subfamilies, tribes, and subtribes of Orchidoideae and Epidendroideae. Our summary highlights several controversial taxa proposed by Chase et al. (2015), and includes updated information on

Table 1
Phylogenetic analysis of Orchidaceae since 2015 and the statistics from Chase et al. (2015).

References	Subfamilies	Tribes	Subtribes	Species/genera	Datasets
Givnish et al. (2015)	5	18	22	39/39	75 plastid genes
Freudenstein and Chase (2015)	5	16	26	312/312	2 nuclear markers, 5 plastid markers, and 3 mitochondrial markers
Givnish et al. (2018)	5	14	27	54/43	77 plastid genes
Li et al. (2019b)	5	19	18	76/66	76 plastid genes and 38 mitochondrial genes
Kim et al. (2020)	5	15	13	124/61	79 plastid genes
Serna-Sanchez et al. (2021)	5	18	28	264/117	78 plastid genes
Perez-Escobar et al. (2021)	5	16	28	75/68	292 low-copy nuclear genes and 78 plastid genes
Wong and Peakall (2022)	5	13	21	69/48	633 nuclear genes
Zhang et al. (2023a)	5	19	42	437/297	1450 low-copy nuclear genes
Perez-Escobar et al. (2024)	5	17	40	448/285	610 to 1195 nuclear genes

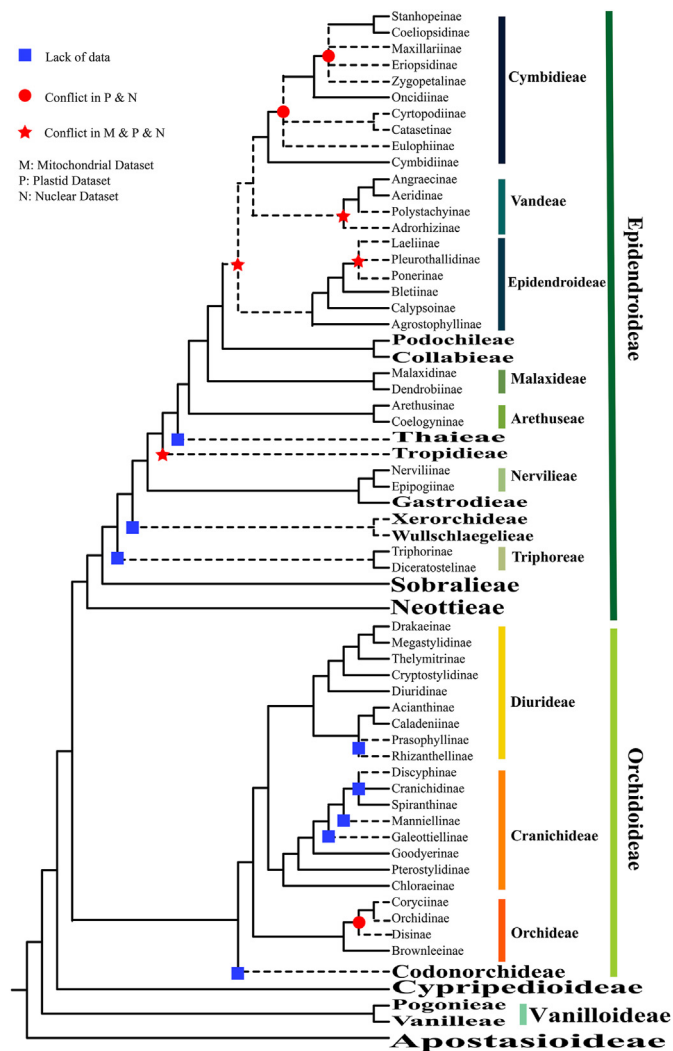


Fig. 2. A 'classification summary' tree for subfamilies, tribes, and subtribes of Orchidaceae. Dashed lines denote taxa with ambiguous phylogenetic positions. Conflicts of phylogenetic position in different datasets are marked in red color.

orchids genera and species numbers for referring the species number provided by POWO (2024; Appendix A).

2.1. Phylogeny within subfamily Orchidoideae

Orchidoideae comprises four tribes: Codonorchideae, Cranichideae, Diurideae, and Orchideae (Chase et al., 2015). Although few studies have been able to adequately sample Codonorchideae

(*Codonorchis* as the only constituent genus), we tentatively place the tribe as a sister group to the remaining tribes (Fig. 2) (Singer et al., 2018; Serna-Sanchez et al., 2021; Zhang et al., 2023).

The tribe Orchideae has been divided into four sub-tribes: Brownleeinae, Disinae, Coryciinae, and Orchidinae (Fig. 2). Brownleeinae is recognized as the first-diverging group, however, the relationships among Disinae, Coryciinae, and Orchidinae remain unclear due to limited sampling of Coryciinae (Serna-Sanchez et al., 2021; Zhang et al., 2023). In their phylogenetic analysis of the subtribe Orchidinae, Jin et al. (2017) recognized five genera in the Ponerorhchis alliance — *Hemipilia*, *Ponerorchis* s.l., *Sirindhornia*, *Shizhenia* and *Tsaiorchis* — and proposed conserving one, *Satyrium*. Here, we recognize *Ponerorchis* s.l. and *Hemipilia*. *Herminium* as currently delimited is expanded to include *Androcorys*, *Bhutanthera*, *Frigidorchis* and *Porolabium* (Raskoti et al., 2016; Raskoti, 2017). The generic delimitation of *Habenaria*, one of the largest genera in the Orchidaceae, remains intensely debated (Kurzweil and Weber, 1992; Batista et al., 2013; Chase et al., 2015; Jin et al., 2017; Ngugi et al., 2020). Limited sampling has stymied efforts to resolve this issue.

In tribe Cranichideae, subtribes Chloraeinae, Pterostylidinae and Goodyerinae have been confidently placed as successive sister groups to the remaining Cranichideae (Zhang et al., 2023; Perez-Escobar et al., 2024). All genera within subtribe Goodyerinae have been proposed to be monophyletic (Tu et al., 2021), except for *Goodyera* and *Hetaeria* (Chen et al., 2019; Smidt et al., 2021). Kim and Kim (2022) used 79 plastid-coding genes to determine the phylogenetic relationships of 18 *Goodyera* species. However, the phylogenetic relationships of *Goodyera* and *Hetaeria* remain unresolved (Chase et al., 2015; Hu et al., 2016; Chen et al., 2019; Smidt et al., 2021; Tu et al., 2021; Kim and Kim, 2022). Other subtribes within Cranichideae have also been limited by inadequate sampling, e.g., *Galeottillinae*, *Manniellinae*, and *Discyphinae*. This lack of sampling has made it challenging to verify the precise phylogenetic positions of these subtribes and has caused ambiguity in understanding *Spiranthisinae*, *Cranichidinae* and *Discyphinae* (Zhang et al., 2023; Perez-Escobar et al., 2024).

In tribe Diurideae, the branches of subtribes *Caladeniinae* and *Acianthinae* have been confidently identified as sister groups to each other. *Prasophyllinae* is the sister group to the clade comprising *Caladeniinae* and *Acianthinae* (Perez-Escobar et al., 2021; Zhang et al., 2023). The previously undetermined positions of *Megastylidinae*, *Thelymitrinae*, and *Drakaeinae* have been resolved, and *Thelymitrinae* was revealed as sister to (*Megastylidinae* + *Drakaeinae*) (Perez-Escobar et al., 2021; Serna-Sanchez et al., 2021; Zhang et al., 2023). *Diuridinae* and *Cryptostylidinae* are successive sisters to the branch of *Thelymitrinae* + (*Megastylidinae* + *Drakaeinae*) (Wong and Peakall, 2022; Zhang et al., 2023). To date, subtribe *Rhizanthellinae* has been inadequately sampled.

2.2. Phylogeny within subfamily Epidendroideae

There are 16 tribes in subfamily Epidendroideae: Neottieae, Sobralieae, Triphoreae, Xerorchideae, Wulfschlaegelieae, Gastrodieae, Nervilieae, Tropidieae, Thaeae, Arethuseae, Malaxideae, Podochileae, Collabieae, Vandaeae, Cymbidieae and Epidendreae. Neottieae, Sobralieae + Triphoreae, and Nervilieae + Tropidieae are successive sisters to the remaining Epidendroideae (Givnish et al., 2015; Zhang et al., 2023). Freudenstein and Chase (2015) suggested that Tropidieae is the sister group of Wulfschlaegelieae + Xerorchideae, and the Neottieae, Sobralieae, Tropidieae + (Wulfschlaegelieae + Xerorchideae), Triphoreae, and Nervilieae are successive sisters to the higher epidendroids. Givnish et al. (2018) placed Neottieae, Sobralieae, and Nervilieae + Tropidieae as successive sister groups of the remaining Epidendroideae. With the same placements of Neottieae and Sobralieae, Li et al. (2019b) positioned Nervilieae as the sister group to Gastrodieae using mitochondrial genes. Neottieae and Sobralieae are successive sisters to the remaining Epidendroideae (Kim et al., 2020; Perez-Escobar et al., 2024; Zhang et al., 2023), Gastrodieae and Nervilieae stably placed as sister groups to each other (Kim et al., 2020; Wong and Peakall, 2022; Perez-Escobar et al., 2024; Zhang et al., 2023), hence the interrelationships of these tribes are stable. The positions of Triphoreae, Tropidieae, and Thaeae have been debated due to sampling and datasets. It seems that Triphoreae, Gastrodieae + Nervilieae, Tropidieae, and Thaeae successively diverged along the backbone of Orchidaceae (Kim et al., 2020; Wong and Peakall, 2022; Zhang et al., 2023; Perez-Escobar et al., 2024). The phylogenetic positions of Xerorchideae and Wulfschlaegelieae, which both consist of difficult-to-sample single genera, are highly controversial (Freudenstein and Chase, 2015; Perez-Escobar et al., 2021, 2024; Zhang et al., 2023).

In the higher epidendroids, the relative phylogenetic positions of Arethuseae, Malaxideae, Podochileae, and Collabieae have been resolved (Givnish et al., 2015; Li et al., 2019b; Zhang et al., 2023; Perez-Escobar et al., 2024), although two alternative topologies for Vandaeae, Epidendreae, and Cymbidieae have emerged, even between similar datasets. One topology, based on mitochondrial and nuclear data, is Vandaeae + (Epidendreae + Cymbidieae) (Freudenstein and Chase, 2015; Li et al., 2019b; Perez-Escobar et al., 2021; Perez-Escobar et al., 2024; Zhang et al., 2023). An alternative topology based on transcriptome data or plastid genome data, and nuclear markers is Epidendreae + (Vandaeae + Cymbidieae) (Givnish et al., 2015, 2018; Serna-Sanchez et al., 2021; Wong and Peakall, 2022). Both topologies are strongly supported. In this paper, we adopt the Epidendreae + (Vandaeae + Cymbidieae) topology (Chase et al., 2015; Fig. 2). One reason why the relationships between these three tribes have been contentious is the complexity of phylogenetic relationships between subtribes within each tribe (Li et al., 2019b; Zhang et al., 2023; Perez-Escobar et al., 2024).

Generic delimitation has varied considerably in the tribe Arethuseae. Studies have determined that Arethuseae is a polyphyletic group (Goldman et al., 2001; Gravendeel et al., 2001; Chase et al., 2015, 2021; Huang et al., 2022a). Chase et al. (2021) combined 14 genera within the tribe (e.g., *Dendrochilum*, *Pholidota* and *Bulleyia* and others) into *Coelogyne*. Huang et al. (2022a) proposed a new genus, *Mengzia* to accommodate *Bletilla sinensis* based on molecular systematics and morphological characters. Nevertheless, owing to the low bootstrap values of some phylogenetic studies, relationships of the subtribe Coelogyneae require further investigation (Huang et al., 2022a).

The tribe Malaxideae consists of a large number of species and complex diversity of taxa. Although the phylogenetic relationships within the tribe have yet to be completely determined (Cameron,

2005; Chase et al., 2015), recent studies have made critical revisions. For example, Geiger (2023) placed the *Hippeophyllum* as the synonym of *Oberonia*. In addition, Li et al. (2020) proposed a new genus *Blepharoglossum*, subdivided from *Liparis*, based on morphological characters and molecular analysis.

In tribe Podochileae, *Eria* s.l. has been subdivided into 21 genera, including two newly recognized genera (Chase et al., 2015; Ng et al., 2018). In tribe Collabieae, morphological evidence and phylogenetic relationships within *Calanthe* have been used to expand *Calanthe* to include the species of *Cephalantheropsis*, *Gastrorchis*, *Phaius*, *Cyanorkis* and *Gastorkis* (Chase et al., 2020a, 2020b). This expansion has subsequently been supported by Zhou et al. (2023).

The relative positions of most of subtribes in Cymbidieae, such as Catasetinae, Cyrtopodiinae, Eulophiinae, Zygopetalinae, Eriopsidinae, and Maxillariinae, remain ambiguous. Freudenstein and Chase (2015) indicated that Eulophiinae is not monophyletic and that Catasetinae is nested within Eulophiinae. Givnish et al. (2015) suggested that Eulophiinae is sister to group containing Catasetinae and Cyrtopodiinae (Perez-Escobar et al., 2021; Zhang et al., 2023), whereas Serna-Sanchez et al. (2021) proposed that Cyrtopodiinae diverged earlier than Eulophiinae and Cyrtopodiinae was embedded within Catasetinae with low support. Molecular data support the placement of Eulophiinae as the common sister group of Catasetinae + Cyrtopodiinae (Perez-Escobar et al., 2024).

Previous studies suggested that subtribes Zygopetalinae, Eriopsidinae, and Maxillariinae diverged successively, and Maxillariinae diverged early in the Cymbidieae (Freudenstein and Chase, 2015; Givnish et al., 2015; Zhang et al., 2023). However, other studies suggested Zygopetalinae diverged early in the Cymbidieae (Perez-Escobar et al., 2021), and that Eriopsidinae is a younger group (Perez-Escobar et al., 2024). The phylogenetic placements of Cymbidiinae, Stanhopeinae, Coeliopsidinae, and Oncidiinae are not in dispute (Fig. 2).

Angraecinae and Aeridinae are monophyletic in Vandaeae, respectively, but the delimitation of Adrorrhizinae and Polystachyinae is currently speculative (Chase et al., 2015; Perez-Escobar et al., 2021; Serna-Sanchez et al., 2021; Zhang et al., 2023). Perez-Escobar et al. (2021) showed Polystachyinae diverged earlier, followed by Adrorrhizinae (Freudenstein and Chase, 2015; Perez-Escobar et al., 2024). Zhang et al. (2023) showed that the Adrorrhizinae diverged earlier, followed by Polystachyinae. In subtribe Aeridinae, Liu et al. (2020) proposed to combine *Vandopsis*, *Diploprora*, *Cleisostoma* and *Schoenorchis* into the *Cleisostoma*, and combine *Trichoglottis* into the *Gastrochilus*, and establish a new genus, *Cymbilabia*. In subtribe Angraecinae, Andriananjanantsoa et al. (2016) suggested that *Oeoniella* and *Sobennikoffia* are nested within *Angraecum*, however, there are many structural differences among them; therefore, we followed the earlier classification.

For tribe Epidendreae, the phylogenetic placements are less disputed, with the exception of Ponerinae, Laeliinae, and Pleurothallidinae. Pleurothallidinae is sister group to Laeliinae and Ponerinae with high support (Zhang et al., 2023; Perez-Escobar et al., 2024). Agrostophyllinae, Calypsoinae, and Blettiinae successively diverged in Epidendreae with high support (Fig. 2) (Perez-Escobar et al., 2021, 2024; Serna-Sanchez et al., 2021; Zhang et al., 2023). *Chysis* is temporarily treated as a member of Blettiinae, and *Coelia* was incorporated into Calypsoinae (Chase et al., 2015). However, more recently, *Coelia* and *Chysis* were recognized as distinct clades with relatively strong support (Zhang et al., 2023). *Risleya* falls within Calypsoinae on the basis of pCDS and mtCDS, instead of within Collabieae (Li et al., 2019b). We recommend broader sampling in the future to provide more robust phylogenetic outcomes.

3. Historical biogeography and molecular dating

The earliest divergence of monocots occurred between 185 and 139 Mya (million years ago, hereafter Mya; Kumar et al., 2017, 2022; Givnish et al., 2018; Li et al., 2019a; Shi et al., 2022). The Order Asparagales originated between 140 and 125 Mya (Givnish et al., 2018; Li et al., 2019a; Kumar et al., 2022). One early-diverging group within Asparagales included the Orchidaceae (Kumar et al., 2022). However, macrofossils of orchids remain scarce. Four fossils have been discovered, including two pollen fossils of Epidendroideae and subtribe Goodyerinae, as well as two leaf fossils of *Earina* and *Dendrobium* (Ramirez et al., 2007; Conran et al., 2009; Poinar and Rasmussen, 2017). The paucity of orchid fossils poses a further challenge to the study of temporal orchid evolution following the reconstruction of a phylogenetic framework (Givnish et al., 2016; Li et al., 2019b; Zhang et al., 2023).

Ramirez et al. (2007) inferred orchids originated during the Early Cretaceous between 76 and 84 Mya. More recent studies estimate that Orchidaceae originated between 76 and 132 Mya (Givnish et al., 2018; Li et al., 2019a; Shi et al., 2022; Zhang et al., 2023; Perez-Escobar et al., 2024). Although estimates of the age of Orchidaceae vary, these studies all suggest that orchids originated in the Cretaceous period and first diverged in the Late Cretaceous (Givnish et al., 2015, 2018; Serna-Sanchez et al., 2021), which supports the “ancient origin” of orchids. Some researchers have suggested that rapid diversification of orchids did not occur until the Cenozoic era (Givnish et al., 2015, 2018; Li et al., 2019b; Zhang et al., 2023). For example, the higher epidendroids have been shown to have diverged rapidly between 37.9 Mya and 30.8 Mya (Givnish et al., 2015). Zhang et al. (2023) indicated that most genera and species of orchids had recent origins less than 20 Mya. An additional study indicated that the majority of present-day orchid species diversity originated over the last 5 million years (Perez-Escobar et al., 2024).

Givnish et al. (2016) has proposed that the ancestor of extant orchids appeared in Australia ca. 120–102 Mya, and that repeated long- and short-distance dispersals have occurred throughout orchid history. Specifically, from Australia, Orchids spread to the Neotropics via Antarctica ca. 90 Mya, when vanilloid orchids diverged from the most recent common ancestor of orchids. Within vanilloids, both the Pogonieae and Vanilleae underwent long-distance dispersals, crossing the Pacific Ocean to New Caledonia between 64 and 59 Mya (Givnish et al., 2016). This hypothesis proposes that ancestors of Epidendroideae arose in the Neotropics ca. 64 Mya and the lower epidendroids then spread to Eurasia and Southeast Asia (Givnish et al., 2016).

An alternative biogeographical history of Orchidaceae proposes that Orchidaceae originated in Laurasia (Perez-Escobar et al., 2024). This proposal suggests that the most rapidly speciating lineages of Orchidaceae occurred in south-eastern Central America, e.g., *Epidendrum* and *Maxillaria*. In this scenario, Orchidoideae originated between 55 and 40 Mya as these plants dispersed from the Neotropics + Nearctic + Antarctic. Epidendroids were present in the Palearctic around 55–50 Mya, suggesting their earlier origin (Perez-Escobar et al., 2024).

The discrepancies between these two hypotheses can be attributed to two primary factors. One factor is that these studies used different datasets to construct phylogenetic frameworks of Orchidaceae. The phylogenetic framework of Australian origin of orchids is based on chloroplast genes (Givnish et al. (2016)), whereas the phylogenetic framework of the Laurasia origin is based on a nuclear dataset (Perez-Escobar et al., 2024). Evolutionary rates between organellar data and nuclear data are known to differ, potentially introducing biases into phylogenetic frameworks (Cheon et al., 2020; Guo et al., 2023). Another factor is the scope

and density of the sampling, which affects the accuracy of geographical history estimations (Givnish et al., 2016; Perez-Escobar et al., 2024).

Despite discrepancies between these two potential theories, both agree that the Neotropics (e.g., the Andes) have had profound effects on the spread and diversification of orchids (Givnish et al., 2016; Zizka, 2019; Perez-Escobar et al., 2022, 2024). Studies have shown that the Andes serve as both a key source and sink of Neotropical plant diversity (Perez-Escobar et al., 2022) and that the diversification of numerous Neotropical lineages has been significantly influenced by Andean uplift events (Perez-Escobar et al., 2017, 2022; Vitt et al., 2023). These uplift events rapidly alter topography within tropical climates, typically creating multiple microhabitats, potentially enhancing speciation rates and allowing islands within tropical mainland regions to foster higher evolutionary distinctness (Perez-Escobar et al., 2024; Vitt et al., 2023).

Phylogenetic studies of Orchidaceae genera have focused on biodiversity hotspots, elucidating orchid dispersal patterns and addressing challenges posed by species-rich taxa, e.g., *Bulbophyllum*, *Dendrobium*, and *Paphiopedilum* (Micheneau et al., 2008; Guo et al., 2012; Xiang et al., 2016; Perez-Escobar et al., 2017; Fernandez et al., 2019; Gamisch et al., 2021; Lai et al., 2021; Liu et al., 2023; Zhang et al., 2024). Xiang et al. (2016) indicated that Asian *Dendrobium* has been present in mainland Asia since the Oligocene and then spread to Malesia. Gamisch et al. (2021) proposed that *Bulbophyllum* dispersed from the Asian-Pacific region into Madagascar via a single long-distance dispersal event at ca. 12.9–7.0 Mya, or probably originated from similar habitats in the Asian-Pacific region. Tsai et al. (2020) explained that the taxa of *Paphiopedilum* in the Sundaland and Wallacea underwent repeated migration and isolation events between mainland south-eastern Asia and the Sunda Super Islands.

Several studies have examined how the biogeography of orchids in biodiversity hotspots is affected by mountain uplift events, e.g., *Calochilus* (Nargar et al., 2018), *Cymbidium* (Chen et al., 2024), *Cypripedium* (Liu et al., 2021; Szlachetko et al., 2021), *Holcoglossum* (Zhao et al., 2020), *Ornithocephalus* (Smidt et al., 2018), *Pabstiella* (Morales et al., 2021), *Pleione* (Wu et al., 2023). These studies have demonstrated that orchids have undergone multiple diversification and dispersal events (Lai et al., 2021; Thompson et al., 2023).

4. Diversification of Orchidaceae

Orchidaceae species, particularly their flowers and habitats, exhibit highly idiosyncratic features that appear to drive diversity. These features, which are either unique to this family or seldom found in other angiosperms, include epiphytism, CAM photosynthesis, and pollinia (Givnish et al., 2015; Zhang et al., 2023).

Epiphytic plants are integral components of numerous ecosystems, contributing greatly to global plant diversity (Ricogray and Thien, 1989; Spicer and Woods, 2022). Epiphytic orchid genera have been shown to contain more species than terrestrial genera (Gravendeel et al., 2004), and have higher speciation and extinction rates than do terrestrial orchids (Givnish et al., 2016; Zhang et al., 2023). The evolution of epiphytism in orchids coincides with rapid expansions of modern rainforests, posing the possibility that rainforests facilitated the transition from terrestrial to epiphytic habits (Zhang et al., 2023). Closed-canopy rainforest ecosystems provide ample ecological niches, e.g., trunks and branches of trees, with varying levels of sunlight and moisture (Nakamura et al., 2017; Spicer and Woods, 2022) that likely fostered epiphyte diversification. In addition, the higher fungal abundance and diversity that often characterize such habitats may have further contributed to high rates of epiphytic orchid diversity (Vance and Nadkarni, 1990; Cardelus et al., 2009).

More than 95% of epiphytic orchids descended from a single ancestor that became epiphytic at approximately 48.1–55.8 Mya, near the Paleocene-Eocene Thermal Maximum (Zhang et al., 2023). However, epiphytism may have evolved independently across several genera of Orchidaceae, underscoring its intricate evolutionary trajectory (Givnish et al., 2016; Zhang et al., 2023). Notably, epiphytic species are rare in Cyripedioideae and Orchidoideae. Epiphytes are entirely absent in Apostasioideae, and true epiphytes are absent in Vanilloideae, although there is debate regarding whether climbers such as most *Vanilla* species (Vanilloideae) should be considered epiphytes or hemiepiphytic (Chen et al., 2009; De Lima and Franco Pinheiro Moreira, 2022). Epiphytism was acquired no later than 35 Mya in Epidendroideae, but was subsequently lost at least three times (Givnish et al., 2015; Zhang et al., 2023). In Arethuseae, there were at least two independent acquisitions of epiphytism in Coelogyninae (Zhang et al., 2023).

Crassulacean acid metabolism (CAM) is a photosynthetic pathway that has evolved convergently in multiple plant lineages, especially in species inhabiting water-limited environments, such as hot semi-arid areas and tropical forests (Winter et al., 2021; Xue et al., 2023). Recent studies have indicated that the majority of epiphyte plants use the CAM pathway (Holtum et al., 2007), including bromeliads (Hermida-Carrera et al., 2020), pteridophytes (Silvera et al., 2010), and orchid species (Givnish et al., 2015; Zou et al., 2018; Gamisch et al., 2021; Hu et al., 2022; Zhang et al., 2022b). CAM photosynthesis, which has evolved at least four times within Orchidaceae, is thought to be a key innovation that has driven orchid diversity. Specifically, CAM photosynthesis has been linked to increased speciation and extinction in the higher epidendroids (Givnish et al., 2015, 2016).

Even in high-rainfall forests, CAM photosynthesis may confer selective advantages to tropical epiphytes without significantly affecting species diversity or diversification rates (Pierce et al., 2002; Gravendeel et al., 2004; Bone et al., 2015; Gamisch et al., 2021). Some researchers have argued CAM photosynthesis may lead to evolutionary dead-ends, noting that in certain lineages CAM photosynthesis may initially provide a short-term evolutionary advantage via speciation, but subsequently decrease net diversification rates (Ilgic and Busch, 2013; Gamisch et al., 2015; Hu et al., 2022). Although support for this hypothesis remains ambiguous, it challenges our prevailing assumption that CAM photosynthesis is a key innovation that drives diversity in tropical orchids.

Another innovation that has driven orchid diversity is pollinia. Pollinia is a single, cohesive mass of pollen, typically contained in a waxy body or other discrete compact unit found in members of Orchidaceae and Asclepiadaceae (Newton, 1984; Dressler, 1993; Johnson and Edwards, 2000). Pollinia evolved at least 64 Mya in Orchidoideae and Epidendroideae, transitioning from powdery to waxy. Research indicates that the evolution of pollinia significantly accelerated both speciation rates and extinction rates in Orchidaceae (Givnish et al., 2016).

The rate of diversification and morphological evolution varies in different groups of orchids. For example, previous research has identified increased rates of diversification in the orchidoids, including a second increase in the higher epidendroids, a further nested increase in Laeliinae + Pleurothallidinae + Ponerinae, and decreased rates of diversification in Agrostophyllinae + Calypsoinae (Givnish et al., 2015). An additional study has detected five increases and one decrease in diversification rate within Epidendroideae (Zhang et al., 2023). Although one increase in diversification is consistent between these studies, they differ on whether higher epidendroid diversification decreases at the node. Inconsistencies between these studies may be related to sampling sizes and the results of divergence time estimations (Zhang et al., 2023).

It is crucial to acknowledge that shifts in net diversification are scale-dependent. Taxon sampling in these studies is well suited to detect diversification shifts at tribal or subtribal levels within orchids, but may fail to identify such shifts within genera (Givnish et al., 2016; Zhang et al., 2023). A similar situation can be observed in families such as Asteraceae, Poaceae, and other families with a large number of species (Soreng et al., 2017; Zhang et al., 2021a; Huang et al., 2022b). Increased sampling density with a greater number of species is essential for a deeper understanding of the parallel evolution of life habits of orchids, notably at the species level (Givnish et al., 2016; Xiang et al., 2016; Guo et al., 2023). Given the challenges associated with sampling, it is critical to separately list species enrichment groups and hotspots for discussions on the mechanisms of orchid diversity. In recent years, numerous studies have contributed valuable information at the genus level, such as *Angraecum* (Andriananjamanantsoa et al., 2016), *Bulbophyllum* (Gamisch and Comes, 2019), *Cymbidium* (Chen et al., 2024), *Holcoglossum* (Zhao et al., 2020), *Pleione* (Wu et al., 2023), which to some extent support conclusions regarding the diversification of Orchidaceae.

5. Phylogenetic discrepancies between different datasets

Mounting genomic data has empowered scientists with an unprecedented ability to unravel the phylogenetic relationships between orchids and examine the mechanisms underlying their massive diversity. Each study consistently supports a similar backbone phylogeny for Orchidaceae, although some notable “hard conflicts” regarding specific groups persist. These topological discrepancies may arise from factors such as taxon sampling, idiosyncratic rates of evolution in some groups, or characteristics inherent to the datasets, such as variations in substitution rate. The major contributing factor to these conflicts in topologies lies in the conflicting sequencing techniques employed, comprising nuclear data, chloroplast data, and mitochondrial data (Niu et al., 2017; Li et al., 2019b; Serna-Sanchez et al., 2021; Zhang et al., 2023). Significant conflicts between plastid and mitochondrial trees can be attributed to several factors. These include the different substitution rates of these two genomes, intragenomic substitution rate heterogeneity of plastid substitution rate, and RNA editing in mitochondrial genomes (Petersen et al., 2006; Wicke et al., 2016; Edera et al., 2018; Dong et al., 2023). While RNA editing in mitochondrial genes is a common occurrence and has been considered a potential issue in phylogenetic reconstructions, extensive studies have concluded that it has no direct effect on reconstructions of phylogeny. Instead, RNA editing may increase variability at edited sites (Petersen et al., 2006; Qiu et al., 2010; Liu et al., 2014; Bell et al., 2020; Dong et al., 2023). Incongruities can also arise from sampling paralogous sequences and highly divergent substitution rates, which can result in long-branch attraction and biased results (Petersen et al., 2006; Edera et al., 2018).

Compared to plastid genes, mitochondrial genes are characterized by lower substitution rates and homoplasy levels, which render them particularly valuable for reconstructing relationships of fast-evolving or ancient groups (e.g., Nymphaeales; Qiu et al., 2010; Richardson et al., 2013; Zhu et al., 2014; Qu et al., 2022).

Transcriptome and plastid sequences produce fewer conflicts, with strong support across trees with multiple species and supermatrix analyses (Givnish et al., 2015; Kim et al., 2020; Perez-Escobar et al., 2024; Zhang et al., 2023). Discordances between plastid and nuclear gene trees at a few nodes highlight the complexity of plant genome evolution, including events such as hybridization, polyploidization, impulses of rapid speciation, and extinction (Guo et al., 2023). Importantly, transcriptomes are mainly a collection of coding gene sequences, therefore, the

informativeness of these sequences may be limited in rapidly differentiating species (Cheon et al., 2020; Guo et al., 2023; Leebens-Mack et al., 2019).

To date, 16 different complete orchid genomes have been published (Zhang et al., 2017, 2022a; Xu et al., 2021). These genomes indicate the orchids have undergone two whole-genome duplication (WGD) events, the most recent of which was shared by all orchids, whereas the older event was shared by most monocots (Van de Peer et al., 2017; Zhang et al., 2017). Changes within MADS-box gene classes, identified through these genomes, might have contributed to variations in labellum and pollinium morphology and accessory structures (Chao et al., 2018; Ai et al., 2021; Sun et al., 2021; Zhang et al., 2021b, 2021c).

These studies have elaborated on the evolutionary trajectory and divergence of orchids, leading to applications in various fields. For instance, they have facilitated the use of orchids in traditional Chinese medicine, and explored the heterotrophy of mycoheterotrophy and parasitic plants, or provided molecular evidence for partial endoreplication (Yuan et al., 2018; Hu et al., 2022; Jiang et al., 2022a, 2022b; Li et al., 2022).

6. Prospects

Genomic data and technological advances have profoundly enhanced our understanding of the phylogenetic relationships of orchids and facilitated more robust and reliable reconstructions of phylogenies. The phylogenetic relationships within taxa such as Xerorchideae and Wulfschlaegeliaceae are expected to be resolved soon through comprehensive sampling. Furthermore, the application of single-molecular sequencing and other advanced methodologies promise to unlock additional layers of complexity and refinement, albeit with accompanying challenges, thus propelling Orchidaceae phylogenetic reconstructions to unprecedented scientific rigor and depth.

Important challenges need to be addressed before a clearer view of orchid phylogeny emerges. Several groups exhibit discordant positions across different datasets (e.g., Epidendreae, Vandaeae, and Cymbidieae). Discrepancies in the phylogenetic positions of these groups will not be resolved by updating sequencing methods. Instead, the particularity of these taxa requires a more suitable approach and consideration of alternative interpretations of evolutionary relationships. Furthermore, despite notable progress, challenges still persist in topological analyses of clades where generic delimitation remains speculative (Aeridinae, Angraecinae, Arethuseae, Blettiinae, Goodyerinae, Malaxideae, Orchidinae, and Podochileae). The uneven sampling of biodiversity hotspots within Orchidaceae can be attributed to the extreme diversity and global distribution, coupled with practical limitations. This imbalance in sampling has led to gaps in the phylogenetic framework of Orchidaceae, particularly in regions with rich plant diversification. However, this scenario also underscores the immense potential value of orchids, highlighting the importance of further exploration and study, to better understand and harness the diverse and valuable traits within this botanical treasure trove.

The current state of phylogenomic inferences in Orchidaceae reveals a notable bias towards regions such as Europe, North America, and East Asia, with limited results from regions such as tropical Asia, Africa, and Latin America (Guo et al., 2023). This deficiency is particularly pronounced in narrow-ranged species in tropical countries, despite high species richness (Rudbeck et al., 2022). Additionally, many studies exhibit a restricted geographic and taxonomic scope, which can lead to excessive imbalanced sampling. Perez-Escobar et al. (2024) presented a novel hypothesis of biogeography of orchid plants, proving that taxon sampling depth and outgroups influence results. There is thus an urgent need

for global collaboration to undertake large-scale phylogenomic work in other plant lineages, as in the case of Fabaceae (Azani et al., 2017), Lamiaceae (Boachon et al., 2018), and Poaceae (Soreng et al., 2017, 2022); and *Carex* (Roalson et al., 2021). Achieving large-scale sampling efforts are vital to enhance scientific comprehension of lineage diversification with a large number of species, leveraging existing genomic data and increasing the scope of cooperation in research (Givnish et al., 2016; Hendriks et al., 2023; Thompson et al., 2023).

CRedit authorship contribution statement

Yajun Wang: Writing – original draft, Software, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Hanchen Wang:** Writing – review & editing. **Chao Ye:** Writing – review & editing, Visualization. **Zhiping Wang:** Data curation. **Chongbo Ma:** Writing – review & editing. **Dongliang Lin:** Writing – review & editing. **Xiaohua Jin:** Writing – review & editing, Supervision, Resources, Funding acquisition, Data curation, Conceptualization.

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Appendix A. Supplementary data

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