



## Correspondence

Integrating high-volume molecular and morphological data into the evolutionary studies of *Allium*

The genus *Allium* (Amaryllidaceae), which includes economically important plants such as onions, garlic, and leeks, is one of the most species-rich and diverse genera of monocotyledon plants in the Northern Hemisphere (Govaerts et al., 2021), with approximately 1000 species. The evolution of *Allium* is characterized by ecological diversification, with most species preferring open, sunny and fairly dry habitats, although others are adapted to forests, European subalpine grasslands and moist subalpine environments, Himalayan alpine steppes, Central Asian alpine mountains, gravel fields along riverbanks, and even saline environments (Fritsch and Friesen, 2002). *Allium* species are widely distributed, however, nowhere is their radiation more magnificent than in the region that extends from the Mediterranean to Central and Southwest Asia, as well as within North America (Fritsch and Abbasi, 2013), each of which harbors several hundred endemic species.

Studies on the evolutionary history of *Allium* species (e.g., Friesen et al., 2006; Li et al., 2010; Hauenschild et al., 2017; Han et al., 2019; Xie et al., 2020) have identified three evolutionary lineages (Li et al., 2010) consisting of 15 subgenera: the subgenera *Nectaroscordum*, *Amerallium* and *Microscordum*; the subgenera *Caloscordum*, *Anguinum*, *Vvedenskyia*, *Porphyroprason* and *Melanocrommyum*, most of which, excluding *Anguinum*, are endemic to eastern and central Asia, as well as the Mediterranean; and the subgenera *Butomissa*, *Cyathophora*, *Rhizirideum*, *Allium*, *Cepa*, *Polyprason* and *Reticulobulbosa*, which comprise 60% of *Allium* species. Despite this progress, few studies have been able to generate a reliable *Allium* phylogeny that is consistently resolved and strongly supported. This limitation has made it difficult to estimate divergence times, propose biogeographical histories and identify macroevolutionary patterns within *Allium*.

Several factors may explain why research has failed to elucidate phylogenetic relationships within *Allium*. *Allium* is a species-rich, cosmopolitan genus, in which hybridization and polyploidization is common between species (Han et al., 2019; Li et al., 2021b). These factors have led to complex morphological and genetic parallels between species. Although the advent of phylogenomics has shed light on the phylogenetic relationships of numerous organisms, few studies have successfully used this approach with *Allium*, as the large genome size (> 7.6 Gb, <https://cvalues.science.kew.org>) and high heterozygosity of *Allium* species (Sun et al., 2020; Liao et al., 2022) result in low mapping rates that require high computational power. In addition, several *Allium* lineages have undergone recent evolutionary radiations, leading to extensive morphological and genetic polymorphisms, consequently magnifying the

challenges of reconstructing a well-resolved phylogeny for the genus (e.g., Friesen et al., 2006, 2021; Li et al., 2010, 2016, 2021a, 2021b; Seregin et al., 2015; Herden et al., 2016; Sinitayna et al., 2016; Xie et al., 2020). Thus, many questions remain concerning *Allium* taxonomy and evolutionary history.

In this issue, two papers on *Allium* may exemplify how to solve some of these long-standing puzzles. Jang et al., 2023 examine flower characteristics to provide key taxonomic information for *Allium* species delimitation. Flower morphology is one of the major traits used to assess *Allium* taxonomy, however, no studies have documented its taxonomic importance and systematic significance. This study provides a research paradigm for how to use morphological traits to assess *Allium* species taxonomy along a phylogenetic tree. Using this framework, the major traits of subgenera and sections, as well as their species, can be circumscribed in future work when combined with more morphological traits. Moreover, using detailed morphological traits, interspecific hybrids may also be discriminated from the parent species and excluded in subsequent phylogenetic analyses. Consequently, when a strongly supported and well-resolved phylogeny of *Allium* is provided, character evolution can be further studied. Phylogeny-based trait evolution is often plagued by genome-wide gene-tree discordance (GTD). Previous studies have indicated that individual plastome fragments typically do not provide satisfactory resolution within *Allium* (Friesen et al., 2006; Li et al., 2010). Although complete plastomes have been widely used to resolve phylogenetic relationships within some *Allium* lineages (e.g., Xie et al., 2020; Cheng et al., 2022; Yang et al., 2023), the value of this approach is limited when reconstructing plastome phylogenies of multiple species (Xie et al., 2020). These limitations are exacerbated at both deep and shallow nodes where incomplete lineage sorting (ILS) and cross-species introgression are likely to have occurred. One solution to these problems is the use of transcriptome data, which has been shown to produce reliable phylogenies (Cheon et al., 2020). In this issue, Zhang et al., 2023 use this phylotranscriptomic approach to produce a strongly-supported species tree for the *Allium* subg. *Cyathophora*. However, a high GTD was found across the genomes of subg. *Cyathophora*, as well as the discrepant topologies between the species tree based on these transcriptome data and chloroplast genome tree. Coalescence simulation illustrates that these discrepancies within *Allium* subg. *Cyathophora* are a product of ILS, indicating that hemiplasy accounts for interspecific trait transitions along the species tree. Ultimately, this robust phylogeny lays a solid foundation for ongoing work on the generic classification of the subgenera

Peer review under responsibility of Editorial Office of Plant Diversity.

<https://doi.org/10.1016/j.pld.2023.12.002>

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and sections of *Allium* that will allow analyses of character evolution, biogeography and spatiotemporal evolution.

### Author contribution

**King-Jin He:** Conceptualization, Data curation, Writing – original draft, Writing – review & editing.

### Declaration of competing interest

No conflict of interest.

### Acknowledgements

This research was supported by the National Natural Science Foundation of China (Grant Nos. 32100180, 32070221, 32170209, 31270241).

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1 December 2023

Available online 14 December 2023