

Research paper

Worldwide phylogeny and integrative taxonomy of *Clematis*: Insights from phylogenomics

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ABSTRACT

The genus *Clematis* (Ranunculaceae) comprises over 300 species with remarkable morphological and ecological diversity worldwide. Despite its horticultural, medicinal, and ecological importance, a well-resolved phylogeny and coherent infrageneric classification are still lacking. Here, we reconstruct a robust phylogeny for *Clematis* using a phylogenomic approach and revise its infrageneric taxonomy. We incorporated 198 samples representing 151 species, two subspecies, and 12 varieties, covering all subgenera and most sections worldwide, obtained from both fresh and herbarium material. Nuclear single nucleotide polymorphisms (SNPs) and complete plastid genomes were assembled for phylogenetic analyses. We also prepared a nuclear ribosomal ITS (nrITS) dataset comprising 171 species, two subspecies, and 12 varieties (217 samples) to include as many species as possible for phylogenetic inference. Phylogenies based on plastid genomes and nrITS exhibited limited resolution and modest support, highlighting challenges in resolving certain relationships. Nuclear SNP analyses yielded a robust phylogenetic tree with 22 well-supported clades corresponding to 22 sections, with most previously recognized subgenera and sections not recovered as monophyletic. Ancestral state reconstruction of 12 key morphological characters revealed multiple independent origins of character states. This study presents the first comprehensive sectional classification for *Clematis* based on robust phylogenomic evidence, redefines morphological characteristics for each section, and resolves long-standing taxonomic ambiguities. Our results establish a framework for future studies on the evolution, ecology, and horticultural potential of this globally significant genus.

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1. Introduction

Reconstructing a reliable phylogenetic framework for plant groups with rapid species radiation remains one of the most significant challenges in exploring the tree of life (Morales-Briones et al., 2021; Chen et al., 2023). Yet, this endeavor holds great value for advancing our understanding of the evolution and classification of these diverse groups, which is crucial for economic, ecological, and conservation efforts (Jiao et al., 2023). The first

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major hurdle lies in achieving comprehensive sampling, particularly for widely distributed groups. Additionally, selecting suitable molecular markers—both informative and sufficient for robust phylogenetic reconstruction—poses another key challenge. In this context, integrative taxonomic approaches, combining multidisciplinary data, are essential for resolving complex evolutionary relationships and improving the accuracy of species delimitation in rapidly radiating lineages.

The conventional approach to molecular phylogenetics, which relies on Sanger sequencing method, frequently struggles to produce a well-resolved phylogenetic framework for species-rich genera (e.g., Liu et al., 2006; Xie et al., 2011). Furthermore, the issue of cytonuclear conflict, frequently observed in groups undergoing rapid radiation, have complicated phylogenetic analysis. The last two decades have seen a significant transformation in molecular phylogenetics due to the emergence of cost-effective high-throughput sequencing (HTS) technologies, increased computational capabilities, and sophisticated analytical tools, thereby making phylogenomics a dynamic field of study (Escudero et al., 2020). Phylogenomics has revolutionized the field by providing advanced methods for creating large datasets and novel strategies for constructing phylogenetic trees, which serve as effective instruments for clarifying the phylogenetic relationships of rapidly radiating groups (Kandziora et al., 2022; Chen et al., 2025; Xu et al., 2025).

Clematis L. is one of the few cosmopolitan genera in the Ranunculaceae family, comprising about 240–350 species (Tamura, 1987, 1995; Johnson, 1997; Grey-Wilson, 2000; Wang and Li, 2005b). The genus comprises mostly vigorous, woody, deciduous/evergreen vines or lianas, rarely with erect perennial herbs and shrubs distributed widely, spanning habitats ranging from tropical to sub-arctic areas. *Clematis* shows a considerable diversity in the temperate and subtropical regions of the Northern Hemisphere, especially in eastern Asia (Fig. 1), where about half of the species occur (Wang and Li, 2005b). Many *Clematis* species are of great ornamental value, known for their vibrant flowers and versatility in landscaping. They are also extremely popular among gardeners for their ease of cultivation and breed through hybridization (Johnson, 1997; Grey-Wilson, 2000; Toomey and Leeds,

2001). Some species, such as *C. chinensis* Osbeck, *C. armandi* Franch., and *C. intricata* Bunge, have also been used as traditional medicinal plants (Chang et al., 1980). The young shoots of certain species, e.g., *C. hexapetala* Pall. and *C. brevicaudata* DC., can be eaten as wild vegetables in northern China. Several shrubby species, such as *C. fruticosa* Turcz., *C. tomentella* (Maxim.) W.T. Wang & L.Q. Li, and *C. nannophylla* Maxim., are used to stabilize dunes as sand-binding vegetation preventing the spread of desertification (Li et al., 2020). The values of *Clematis* species have aroused interest in its taxonomy and in many other fields, such as horticulture, phytochemistry, pharmacology, and ecology. An updated comprehensive taxonomy of *Clematis*, based on a robust phylogenetic framework, would undoubtedly facilitate its optimal utilization.

The genus *Clematis* was first described by Linnaeus (1753) and initially included nine species. In the same publication, Linnaeus also established another genus *Atragene* L. which contained four species. Later taxonomists conducted extensive studies on the delimitation of the *Clematis* genus (de Candolle, 1818; Kuntze, 1885; Prantl, 1888; Spach, 1839). In Ranunculaceae, the characteristics of *Clematis* were traditionally considered to include the R (*Ranunculus* L.) type chromosome, predominantly climbing (rarely erect) stems, opposite leaves, actinomorphic monopetalous flowers, valvate sepals, indehiscent fruit, and achenes with a long plumose tail (Tamura, 1995). Nonetheless, these characters are not essentially diagnostic for *Clematis*. Several small genera, such as *Archiclematis* (Tamura) Tamura, *Naravelia* DC., and *Clematopsis* Bojer ex Hutch., were morphologically related to or merged with *Clematis* (Tamura, 1995; Johnson, 1997; Wang and Li, 2005b).

Within *Clematis*, infrageneric groups, such as subgenera and sections, were gradually proposed by different taxonomists (de Candolle, 1818; Spach, 1839; Kuntze, 1885; Prantl, 1888; Tamura, 1955, 1956, 1967, 1987, 1995; Snoeijer, 1992; Johnson, 1997; Grey-Wilson, 2000; Wang and Li, 2005b). They were accepted or partly revised by later taxonomists based on their respective studies on the *Clematis* species from a certain region. Many taxonomists have studied *Clematis* by using diverse morphological features, including habit (vine or liana, shrub, subshrub, or perennial herb), seedling morphology (seedling leaf alternate or

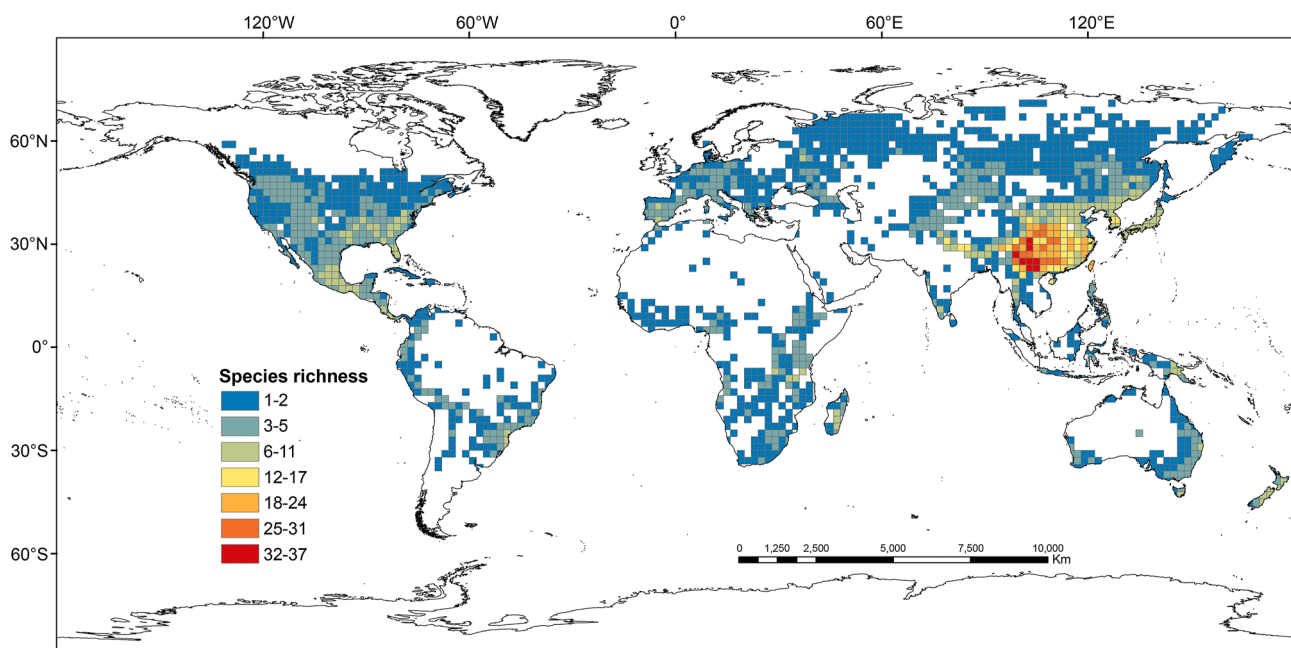


Fig. 1. Species richness of georeferenced records in *Clematis*, based on taxonomic revision of Wang and Li (2005b).

opposite), leaf type (simple or various compound), inflorescence (terminal or axillary; pedunculate, bibracteate, or several-flowered cymes), flower sexuality (bisexual or unisexual), aestivation of sepals (imbricate or valvate), sepal orientation (spreading, ascending, or erect), petal presence or absence, filament indumentum (glabrous, hairy filaments, or hairy filaments and anthers), pollen morphology (tricolpate, pantoporate or pantocolpate), elongation of persistent styles, and fruit size and shape of fruits (see Wang and Li, 2005b).

Classifying *Clematis* has proven to be challenging due to significant morphological variation both among and within its species. Nevertheless, due to the immense horticultural value of *Clematis*, it has attracted significant attention from researchers. Over the past 40 years, at least six comprehensive classification systems of *Clematis* have been published, including three species-level monographs (Tamura, 1987, 1995; Snoeijer, 1992; Johnson, 1997; Grey-Wilson, 2000; Wang and Li, 2005b). However, all these classification systems differ in their delimitation of the genus and its infrageneric classification (e.g., Prantl, 1888; Tamura, 1987, 1995; Johnson, 1997; Grey-Wilson, 2000; Wang and Li, 2005b; Table 1), reflecting the complexity and different characters prioritized by each author.

For instance, there are notable differences between the two most influential classification systems in *Clematis* taxonomy, Tamura (1995) and Wang and Li (2005b), regarding both the delimitation of the genus and the circumscription of its subgenera and sections. The two classification systems show agreement in their definitions of sect. *Cheiroopsis* DC., sect. *Tubulosae* Decne., sect. *Atragene* (L.) DC., sect. *Viticella* DC., sect. *Pseudanemone* Prantl, and sect. *Pterocarpa* Tamura. Both classifications similarly treated *Naravelia* as distinct genus from *Clematis*. However, Tamura (1995) segregated *C. alternata* Kitam. & Tamura as *Archiclematis*, while Wang and Li (2005b) retained it in *Clematis* subg. *Viorna* (Pers.) Gray sect. *Archiclematis*. There are major differences between the two classifications in the definitions of many other sections. For example, Tamura (1995) included all shrubby *Clematis* under sect. *Fruticella* Tamura, while Wang and Li (2005a, b) restricted their classification to those with yellow flowers. Tamura (1995) delineated sect. *Meclatis* (Spach) Tamura, which is effectively the same as the integration of sect. *Meclatis* (Spach) Baill. and sect. *Brachiatae* Snoeijer as defined by Wang and Li (2005b). In Wang and Li's (2005b) classification, sect. *Aspidanthera* Spach is equivalent to the combination of sect. *Aspidanthera* and sect. *Lasiantha* Tamura, as treated by Tamura (1995). Moreover, according to Wang and Li (2005b), the definition of sect. *Clematis* encompasses sect. *Clematis*, sect. *Flammula* DC., and sect. *Angustifoliae* (Tamura) Serov as delineated by Tamura (1995). The definition of sect. *Viorna* (Reichb.) Prantl, as defined by Wang and Li (2005b), is also much broader and includes sect. *Campanella* Tamura, sect. *Bebaeanthera* Edgew., and subg. *Viorna* (Pers.) Gray as classified by Tamura (1995). Finally, there is a monotypic sect. *Atragenopsis* Boiss. in Wang and Li (2005b) that is not present in Tamura (1995). These differences reflect varying interpretations among authors regarding the evolution of morphological characters in *Clematis*, yet they have caused some challenges in applied fields. While numerous systematic analyses have explored the morphology, anatomy, palynology, and cytology of *Clematis* (e.g., Tobe, 1974, 1980a, 1980b, 1980c, 1980d; Essig, 1991; Zhang, 1991; Yano, 1993; Yang and Moore, 1999; Shi and Li 2003; Xie and Li, 2012; Cheng et al., 2016), the information derived from these studies does not sufficiently support the classification of this large genus, particularly at the sectional level.

Previous molecular phylogenetic studies relying on nuclear ribosomal DNA (nrDNA), plastid segments, and complete plastome sequences, have successfully resolved several issues, including the

delineation of the genus *Clematis* and the identification of its sister groups (Miikeda et al., 2006; Xie et al., 2011; Zhang et al., 2015; Lehtonen et al., 2016; Jiang et al., 2017; He et al., 2021). However, these previous studies have not succeeded in obtaining a robust phylogenetic framework of *Clematis*, and the significant issue of cytonuclear discordance continues to be inadequately explained. The phylogeny obtained from nrDNA fragments does not provide enough information to resolve the relationships within *Clematis*, and the investigation of plastid regions and genomes has led to confusing phylogenetic relationships within the genus (He et al., 2021). Xiao et al. (2022) proposed a novel approach to derive nuclear SNP sequences through the alignment of genome skimming data against a reference draft genome of *Clematis*. The results from the nuclear SNP data analyses established a *Clematis* phylogeny with a much better resolution than that of the nrDNA sequences and a more plausible explanation than the plastome sequences. Using this method, Lyu et al. (2023) elucidated the species relationships of sect. *Tubulosae* and its close relatives in *Clematis*. Both studies focused mainly on *Clematis* species native to East Asia, and did not cover the full range of species from around the world. As of now, a taxonomic revision of the genus *Clematis*, based on a comprehensively sampled and well-resolved phylogenetic framework, is urgently warranted.

In this study, we employed a genome-skimming sequencing method to obtain the plastid genome sequence (He et al., 2021) and nuclear SNP data (Xiao et al., 2022; Lyu et al., 2023) from both silica-gel dried and herbarium materials of *Clematis*. We further expanded our sampling scheme within the genus by using nrITS regions obtained from genome-skimming data and resources from GenBank. This study aims to (1) reconstruct the phylogenetic framework of *Clematis* based on a worldwide representative sampling scheme with genomic data, with a particular focus on the nuclear genome; (2) investigate evolutionary patterns of key morphological characters of the genus; and (3) update the infrageneric taxonomy of *Clematis* for the first time based on an integrative approach incorporating morphological and phylogenomic data. This study will provide a solid foundation for future systematic and evolutionary studies on *Clematis*, allowing us to delve into its immense value. Our results also highlight the necessity of utilizing phylogenomic data to re-establish a taxonomic framework for mega-diverse plant groups, especially those with contentious relationships as revealed by prior molecular phylogenetic studies that relied on a narrow set of molecular markers.

2. Materials and methods

2.1. Plant taxon sampling

In this study, we implemented a sampling scheme that encompasses the entire spectrum of morphological diversity, geographical distribution, and a wide array of infrageneric groups following the classifications of Tamura (1995) and Wang and Li (2005b). Our taxon sampling comprised 198 ingroup samples representing 151 species, two subspecies, and 12 varieties, including 107 newly generated genome skimming datasets and 91 obtained from previous studies. The sampling of our genome skimming data represents all known subgenera and most of the sectional groups within *Clematis* according to previous taxonomic treatments (Table 1). Our sampling strategically included the type species of as many published sections as possible (only types of sect. *Pseudanemone* and sect. *Atragenopsis* were not available) to ensure the nomenclatural stability of our proposed taxonomic treatment. Known hybrid taxa, such as *C. takedana* Makino (Makino, 1907) and *C. pinnata* Maxim. (Lyu et al., 2021), were not included in this study. In addition, we obtained nrITS data for 20

Table 1
Genome skimming and nrITS data sampling in this study corresponding to three important *Clematis* classification systems.

Tamura (1995)	Estimated species number	Genome skimming	ITS	Johnson (1997)	Estimated species number	Genome skimming	ITS	Wang and Li (2005b)	Estimated species number	Genome skimming	ITS
		Samples /Species	Samples /Species			Samples /Species	Samples /Species			Samples /Species	Samples /Species
<i>Clematis</i> L.				<i>Clematis</i> L.				<i>Clematis</i> L.			
Subg. 1. <i>Campanella</i> Tamura				Sect. 1. <i>Archiclematis</i> 1		1/1	1/1	Subg. 1. <i>Cheiropsis</i> Peterm.			
Sect. 1. <i>Campanella</i> 40	33/27	34/28		Sect. 2. <i>Pseudanemone</i> Prantl	19	1/1	1/1	Sect. 1. <i>Cheiropsis</i> DC.	23	16/12	15/12
Sect. 2. <i>Tubulosae</i> Decne.	8	14/7	14/7	Sect. 3. <i>Novae-zeelandiae</i> M. Johnson	11	1/1	3/3	Subg. 2. <i>Clematis</i> Keener & Dennis			
Sect. 3. <i>Bebaeanthera</i> Edgew.	4	3/3	3/3	Sect. 4. <i>Atragene</i> (L.) DC.	18	8/4	9/5	Sect. 1. <i>Clematis</i>	74	45/36	48/39
Sect. 4. <i>Atragene</i> (L.) DC.	9	8/4	9/5	Sect. 5. <i>Naravelia</i> (DC.) Prantl	7	4/3	5/4	Sect. 2. <i>Aspidanthera</i> Spach	73	12/12	19/19
Sect. 5. <i>Meclatis</i> (Spach) Tamura	20	20/14	23/17	Sect. 6. <i>Tubulosae</i> Decne.	8	14/7	14/7	Sect. 3. <i>Brachiatae</i> Snoeijer	24	8/5	9/6
Sect. 6. <i>Pseudanemone</i> Prantl	25	1/1	1/1	Sect. 7. <i>Connatae</i> (Kohne) M. Johnson	47	33/27	34/28	Sect. 4. <i>Pseudanemone</i> Prantl	16	1/1	1/1
Subg. 2. <i>Viorna</i> (Pers.) Gray	21	9/8	14/13	Sect. 8. <i>Meclatis</i> (Spach) Tamura	14	12/9	13/10	Sect. 5. <i>Meclatis</i> (Spach) Baill.	13	12/9	13/10
Subg. 3. <i>Clematis</i> Keener & Dennis				Sect. 9. <i>Bebaeanthera</i> Edgew.	4	3/3	3/3	Sect. 6. <i>Fruticella</i> Tamura	5	13/5	13/5
Sect. 1. <i>Clematis</i>	30	21/17	21/18	Sect. 10. <i>Cheiropsis</i> DC.	10	11/9	11/9	Sect. 7. <i>Naraveliopsis</i> Hand.-Mazz.	21	9/8	9/8
Sect. 2. <i>Cheiropsis</i> DC.	13	12/9	12/9	Sect. 11. <i>Clematis</i>	70	34/27	37/31	Sect. 8. <i>Pterocarpa</i> Tamura	1	1/1	1/1
Sect. 3. <i>Naraveliopsis</i> Hand.-Mazz.	13	8/7	8/7	Sect. 12. <i>Lasiantha</i> Tamura	2	1/1	1/1	Sect. 9. <i>Viticella</i> (Dill. ex Moench) DC.	11	8/8	8/8
Sect. 4. <i>Aspidanthera</i> Spach	51	9/9	16/16	Sect. 13. <i>Aspidanthera</i> Spach	14	3/3	6/6	Sect. 10. <i>Tubulosae</i> Decne.	7	14/7	14/7
Sect. 5. <i>Lasiantha</i> Tamura	2	1/1	1/1	Sect. 14. <i>Naraveliopsis</i> Hand.-Mazz.	21	9/8	9/8	Subg. 3. <i>Viorna</i> (Pers.) Gray			
Subg. 4. <i>Flammula</i> (DC.) Peterm.				Sect. 15. <i>Viorna</i> (Reichb.) Prantl	24	9/8	14/13	Sect. 1. <i>Viorna</i> (Reichb.) Prantl	71	45/38	51/44
Sect. 1. <i>Flammula</i> DC.	25	19/16	20/17	Sect. 16. <i>Flammula</i> DC.	34	24/19	25/20	Sect. 2. <i>Archiclematis</i> Tamura	1	1/1	1/1
Sect. 2. <i>Angustifoliae</i> (Tamura) Serov	1	2/1	2/1	Sect. 17. <i>Pterocarpa</i> Tamura	1	1/1	1/1	Subg. 4. <i>Atragene</i> Torr. & Gray			
Sect. 3. <i>Fruticella</i> Tamura	7	18/8	19/9	Sect. 18. <i>Fruticella</i> Tamura	9	18/8	19/9	Sect. 1. <i>Atrogenopsis</i> Boiss.	1	0	0
Sect. 4. <i>Viticella</i> (Dill. ex Moench) DC.	10	8/8	8/8	Sect. 19. <i>Viticella</i> (Dill. ex Moench) DC.	11	8/8	8/8	Sect. 2. <i>Atragene</i> (L.) DC.	14	8/4	9/5
Sect. 5. <i>Pterocarpa</i> Tamura	1	1/1	1/1	Undetermined		3/3	3/3	<i>Naravelia</i> DC.	/	4/3	5/4
<i>Archiclematis</i> Tamura	1	1/1	1/1					Undetermined		1/1	1/1
<i>Naravelia</i> DC.	7	5/4	6/5								
Undetermined		5/5	5/5								

Clematis species from GenBank (<https://www.ncbi.nlm.nih.gov/>) to incorporate a wider species sampling scheme. In total, 217 samples of 171 species, two subspecies and 12 varieties of *Clematis* were included in our nrITS dataset (Table 1) representing all the subgenera and sections of the genus according to Tamura (1995) and Johnson (1997). Most of the newly sequenced samples were collected from the field, while 15 samples came from herbarium specimens from the Herbarium of Institute of Botany and Kunming Institute of Botany, the Chinese Academy of Sciences (PE and KUN; herbarium code follows Thiers, 2021). Based on previous

phylogenetic studies (Zhang et al., 2015; Jiang et al., 2017), we designated *Anemoclema glaucifolium* (Franch.) W.T. Wang as the outgroup. Information on vouchers, SRA accession numbers, and GenBank accession numbers are provided in Table S1.

2.2. DNA extraction and sequencing

For the newly sequenced samples, total genomic DNA was extracted from silica gel-dried leaf tissues using a genomic DNA extraction kit (Tiangen Biotech Co. Ltd., Beijing, China). The

genomic DNA from the herbarium specimen samples was extracted by using a modified Cetyltrimethylammonium Bromide (CTAB) protocol, following the method described by Li et al. (2013). Subsequently, the isolated DNA samples were sent to BerryGenomics (Beijing, China) for DNA library construction and next-generation genomic sequencing (NGS). Paired-end libraries of 2×150 bp were constructed and sequenced using the Illumina NovaSeq 6000 platform (Illumina, San Diego, California, USA). Each sample yielded approximately 6 Gbp raw data. The data underwent a filtering process where adapters and low-quality sequences were eliminated using the FASTX-Toolkit (http://hannonlab.cshl.edu/fastx_toolkit).

2.3. Plastome, nrITS, and nuclear SNP assembly

Assembly of plastid genomes and nrITS sequences adhered to the protocol of Xiao et al. (2022) and Lyu et al. (2023). The Map function in Geneious Prime v.2020 (Kearse et al., 2012) and the reference sequences (MG675223.1 and MH710901.1) were used to filter out plastid and nrDNA reads. Subsequently, the *De Novo* Assemble function of Geneious Prime v.2020 was applied with a low sensitivity setting to compile the complete plastid genome and the nrDNA sequences. We then bridged gaps by applying 20 iterations of Fine Tuning in Geneious Prime v.2020 whenever it was required. Complete plastid genomes were annotated and the downstream analyses were carried out using PlastidHub (Zhang et al., 2025). The assembled nrDNA sequences were annotated by Geneious Prime.

We obtained nuclear SNP sequences from genome skimming data. Our previous published paper (Xiao et al., 2022) provided a comprehensive explanation of the SNP data and the processes used for its assembly, focusing primarily on strategies for genome partitioning and addressing methodological challenges in the phylogenetic analysis of *Clematis*. This method is essentially based on the nuclear SNP calling approach proposed by Olofsson et al. (2019), and this method has already been applied to other super-diverse angiosperm taxa (Jiao et al., 2023). However, the genus *Clematis* possesses an exceptionally large genome (exceeding 7Gb, Xiao et al., 2022), and currently lacks high-quality whole-genome reference data. Consequently, our preliminary studies involved extensive foundational work in data mining and processing (Xiao et al., 2022; Lyu et al., 2023).

We employed high-depth genome data of *Clematis brevicaudata* (Xiao et al., 2022) and used the GATB pipeline with GATB-Minia (<https://github.com/GATB/gatb-minia-pipeline>) to assemble a draft genome (Drezen et al., 2014). We then utilized RepeatMasker v.4.0.9 (Chen, 2004) to discard repetitive and low-coverage regions. To further improve the quality of the reference genome, we used Geneious Prime v.2020, aligning genome skimming data from five *Clematis* species (*C. leschenaultiana* DC., *C. repens* Finet & Gagnep., *C. songorica* Bunge, *C. tibetana* Kuntze, and *C. viridis* (W.T. Wang & M.C. Chang) W.T. Wang) with the draft genome. We applied the script “low_seq_del.py” (https://github.com/Jhe1004/low_seq_del, accessed on 1 June 2025) to eliminate regions that did not match with any of the five samples, resulting in the acquisition of a *Clematis* reference genome. Genome skimming data of each species was mapped to this reference genome to generate the SNP dataset.

Xiao et al. (2022) evaluated two bioinformatic pipelines, GATK and Geneious, for SNP sequence assembly and systematically compared different missing data parameter settings for *Clematis*. Here, we employed both strategies to assemble the nuclear SNP dataset, adopting the optimal missing-data parameters recommended by Xiao et al. (2022). The Geneious pipeline applied the Map to Reference function in Geneious Prime v.2020 (Kearse et al.,

2012) to align the genome skimming data from each sample with the reference genome, and then used the Generate Consensus Sequence function to generate sequence file for each sample. The GATK pipeline used BWA-MEM v.0.7.1 (Li, 2013) to map each genome skimming data to the reference genome. Subsequently, we used the HaplotypeCaller function of GATK v.4.2.5 (McKenna et al., 2010) to call variants and generated “vcf” files. We filtered and deleted the site that met any of the following three criteria: (1) coverage less than 4, (2) site quality score less than 20, and (3) heterozygous. Finally, we converted the “vcf” file into a “fasta” file using the Python script “gvcf2fasta.py” (<https://github.com/Jhe1004/gvcf2fasta>).

2.4. Phylogenetic analysis

Plastid genome sequences were aligned using MAFFT v.7.3 (Katoh and Standley, 2013) with default parameters, while preserving a single inverted repeat (IR) region. We used a Python script (https://github.com/Hejian151004/get_homology) to eliminate ambiguous alignment regions that had 20% or higher missing data. nrITS sequences were extracted from nrDNA sequences according to the annotation. Subsequently, nrITS sequences obtained from GenBank were merged into this dataset. Sequences were aligned with MAFFT v.7.3 (Katoh and Standley, 2013) using default settings, followed by manual adjustments.

For plastid genome and nrITS datasets, phylogenetic analyses were performed by both the Maximum Likelihood (ML) and Bayesian Inference (BI) methods. Evaluation of the best nucleotide substitution models was conducted using the Akaike information criterion in jModelTest v.2.1.4 (Darriba et al., 2012). ML analyses for both datasets were conducted using RAxML v.8.2.12 (Stamatakis, 2014) with the GTR + I + G model, and bootstrap values were calculated after running 1000 replicates. BI analyses were performed using MrBayes v.3.2.3 (Ronquist et al., 2012) with the GTR + I + G model for the plastid genome data. Markov chain Monte Carlo (MCMC) simulated were executed for 2,000,000 generations, sampling trees every 100 generations. The first 25% of the trees were eliminated as burn-in, while the remaining trees contributed to generate the consensus tree.

To eliminate invariant sites from the nuclear SNP datasets generated by Geneious and GATK pipelines, we used SNP-sites v.2.5.1 (Page et al., 2016). Afterward, we deleted aligned columns from the Geneious dataset that had over 5% of the missing data, while for the GATK dataset, we set the threshold at 40% according to Xiao et al. (2022) and Lyu et al. (2023). The difference in missing data thresholds stems from the fact that GATK's SNP filtering criteria are substantially more stringent than those of the Geneious pipeline, yielding only about one-quarter as many SNPs. If the missing data threshold is set too strictly under these circumstances, it would result in retaining too few SNP loci for phylogenetic tree construction. Maximum likelihood analyses were conducted using RAxML v.8.2.12 (Stamatakis, 2014), with the “ASC_GTRGAMMA” model along with 1000 bootstrap replicates. To illustrate the discordance between nuclear and chloroplast phylogenies, the cophylo function in the R package *phytools* (Revell, 2012) was used for visualization.

2.5. Ancestral character reconstruction

Ancestral character states were optimized on the nuclear SNP (Geneious pipeline) phylogenetic tree of *Clematis*. For this analysis, we selected 12 key morphological characters that represent the most important classification features (Table 2). All the characters are discrete, and character states were coded from our observations on living or herbarium specimens (BJFC, BM, E, IBSC, K, KUN,

LE, NAS, P, PE, US, herbarium code follows Thiers, 2021), the taxonomic revisions (Tamura, 1995; Johnson, 1997; Wang and Li, 2005a, 2005b, b; Wang, 2002, 2003, 2004a, b, c, 2006a; Wang and Xie, 2007; Yang et al., 2009), and other related studies (Essig, 1991; Tamura, 1980; Xie and Li, 2012; Cheng et al., 2016). Character states and scores for all species are presented in Table S2. The ancestral states of the 12 characters were reconstructed using the Bayesian Binary Method (BBM), which was implemented in RASP v.4.2 (Yu et al., 2020). BBM analysis was performed using the ML tree, with 10 MCMC chains run for 5,000,000 generations, sampling every 1000 generations and discarding the first 20% as burn-in.

3. Results

3.1. Characteristics of the plastid genome, nrITS, and nuclear SNP datasets

The newly sequenced plastid genomes displayed identical gene numbers and organization patterns across all examined *Clematis* species. The lengths of complete plastid genomes of the 107 newly sequenced *Clematis* ranged from 159,294 bp for *C. texensis* Buckley to 159,846 bp for *C. mauritiana* Lam. The percentage of GC content ranged from 37.8% to 38.0%. Large single copy (LSC) regions varied in length from 79,111 bp in *C. fengii* W.T. Wang to 79,589 bp in *C. insidiosa* Baill. Inverted repeat (IR) regions ranged between 31,017 bp for *C. montana* var. *glabrescens* (H. F. Comber) W.T. Wang & M.C. Chang to 31,252 bp for *C. mauritiana*. Small single copy (SSC) regions ranged from 17,748 bp in *C. yui* W.T. Wang to 18,178 bp in *C. aristata* R. Br. ex Ker Gawl. The plastid genomes of *Clematis* comprise a total of 112 distinct genes, including 79 genes responsible for encoding proteins, 29 genes for transfer RNAs, and four genes for ribosomal RNAs (Table S3). The aligned plastome matrix ultimately reached 128,319 bp in length, with the incorporation of only one IR region.

The nrITS data matrix comprises 218 samples, making it the largest dataset available for this genus. The ITS1 region measures between 160 and 198 bp, while the 5.8S rDNA region ranges from 161 to 162 bp, and the ITS2 region spans 220 to 277 bp (Table S4). The aligned length of the nrITS region is 573 bp, of which 201 bp (36.8%) are variable and 161 bp (28.1%) are parsimony informative. GenBank accession numbers of all the newly generated plastome and nrDNA sequences are presented in Table S1.

The assembly of the draft and reference genomes for *Clematis* was completed in our prior study (Xiao et al., 2022). We obtained a 7.81 Gbp draft genome, which was too large for downstream analysis. To reduce its size, we first excluded repetitive regions using RepeatMasker v.4.0.9 (Chen, 2004), then removed low-

coverage regions by mapping genome skimming data from five distantly related *Clematis* species (see Xiao et al., 2022) via Geneious Prime v.2020 (Kearse et al., 2012) and deleting unmatched regions using “low_seq_del.py” (https://github.com/jhe1004/low_seq_del). The final reference genome size was 616 Mbp (the draft and reference genome are available online, <https://doi.org/10.5281/zenodo.17103951>). Using this reference, we aligned the genome skimming data of each sample to extract the SNP data. Ultimately, we generated data matrices of 2,165,371 bp through the Geneious pipeline, with missing data proportions fluctuating between 0.1% and 64.4% across different samples. The GATK pipeline produced a matrix of 455,374 bp, with missing data percentages ranging from 19.8% to 84.3%.

3.2. Phylogenetic inference

Analysis of the complete plastid genome dataset resulted in a generally well-defined phylogenetic structure for *Clematis*, yet nearly all major clades encompass a wide variety of species, and the subgenera and sections proposed by previous taxonomists, such as Tamura (1995), Johnson (1997), and Wang and Li (2005b), did not receive sufficient support. For example, species from sect. *Tubulosae* and sect. *Clematis* grouped together, and cannot be clearly separated (Fig. 2 and Fig. S1). Species from the broadly defined sect. *Viorna* (sensu Wang and Li, 2005b) are scattered across many major lineages of the genus. Furthermore, the phylogenetic relationships inferred from the plastid genome differ markedly from those obtained through the nuclear SNP analyses (Fig. 2).

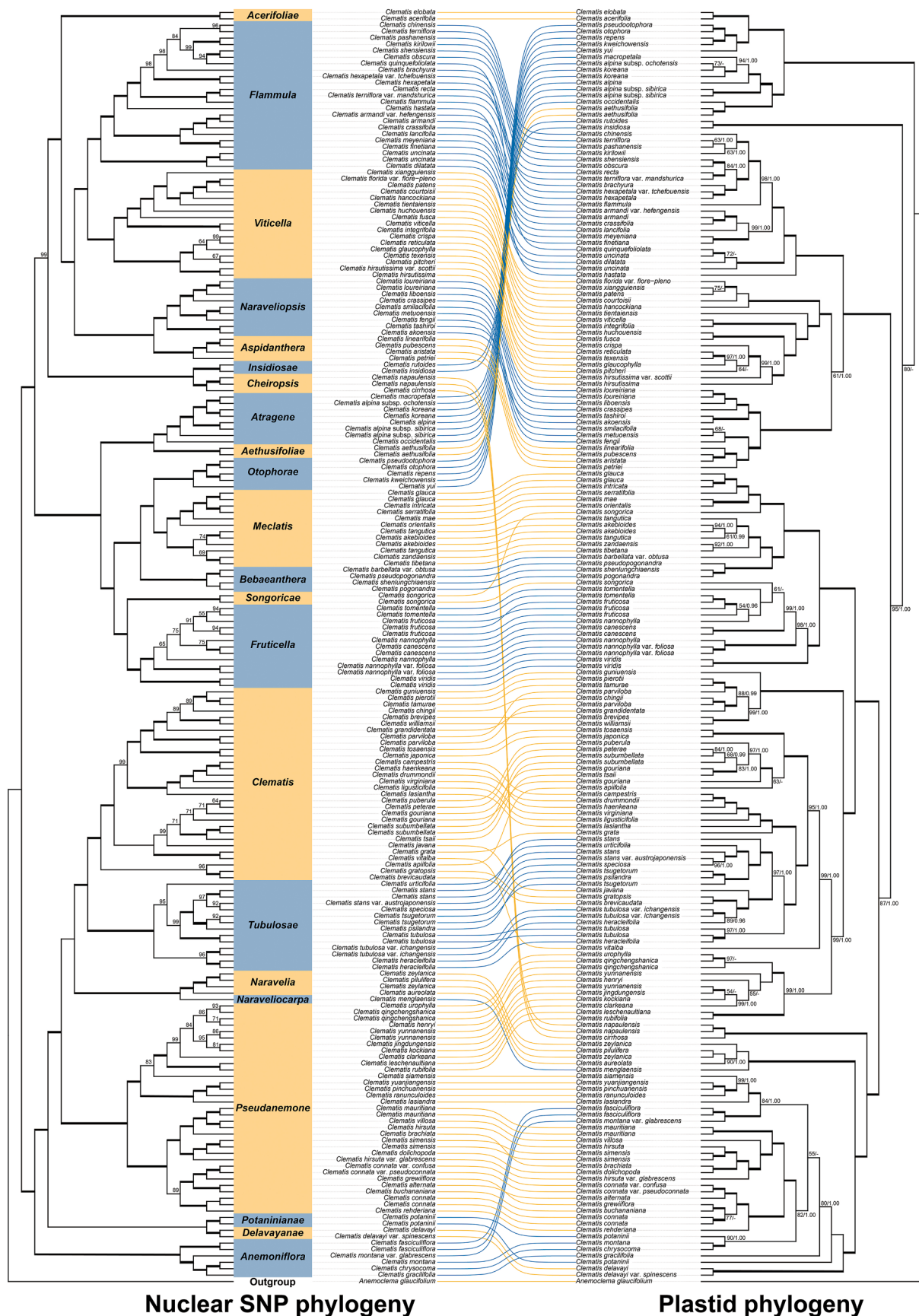
Phylogenetic relationships inferred from the nrITS dataset showed low resolution and support (Fig. S2), being only partially consistent with the nuclear SNP phylogeny. However, the nrITS dataset still holds reference value due to its significantly expanded sampling coverage. Particularly for the unisexual taxa distributed in Australia, the nrITS data sampling has been substantially improved, providing valuable insights for delimiting sect. *Aspidanthera*.

The phylogenetic trees inferred from nuclear SNPs using the Geneious pipeline (Fig. 3) and the GATK pipeline (Fig. S3) showed a high degree of agreement, with the Geneious method producing a more robust phylogeny than the GATK approach. These two methodologies differ in only one key aspect in their topologies. The Geneious method identified the sect. *Clematis* clade (clade 8) and the sect. *Tubulosae* clade (clade 7) as distinct clades, yet the GATK method grouped them together into a single clade. In both approaches, the *Naravelia* group (clade 6) exhibits a long branch due to a higher percentage of missing data. The elimination of this clade does not alter the phylogenetic structure of *Clematis*.

Table 2
Key morphological characters and their states of *Clematis* and *Anemoclema* in this study.

No.	Character	Character states and their scores
1	Seedling morphology	(A) Type I; (B) Type II ^a
2	Sepals	(A) Spreading; (B) Ascending; (C) Erect
3	Filaments	(A) Hairy; (B) Glabrous
4	Flower sexuality	(A) Bisexual; (B) Polygamous; (C) Unisexual
5	Habit	(A) Vine; (B) Erect herb; (C) Shrub
6	Leaves on mature individuals	(A) Alternate; (B) Opposite; (C) All basal
7	Leaflet margin	(A) Dentate; (B) Entire
8	Flower arrangement	(A) Solitary; (B) Fasciculate; (C) Cyme
9	Petals	(A) Absent; (B) Present
10	Staminodes	(A) Absent; (B) Present
11	Pollen grains	(A) Tricolpate; (B) Pantocolpate; (C) Pantoporate
12	Connectives	(A) Not elongate; (B) Elongate

^a According to Essig (1991), Tamura (1995), and Cheng et al. (2016).



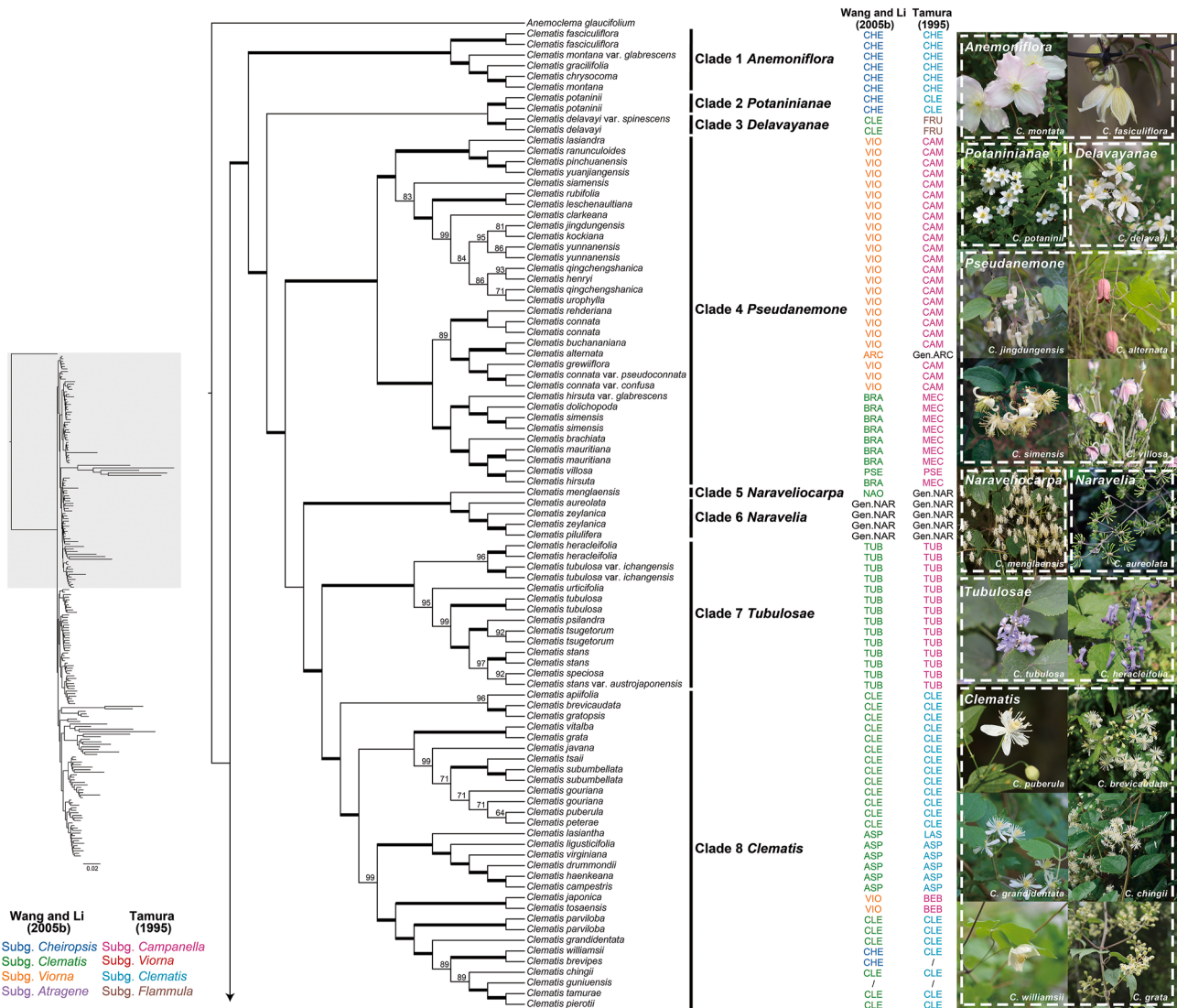


Fig. 3. Maximum likelihood phylogenetic tree obtained from the alignment of nuclear single nucleotide polymorphisms (SNPs). A phylogram showing branch lengths is presented left below. Bootstrap support (BS) values below 100 are indicated along branches, and bold branches mark fully supported. Representative species of each section in the new classification are shown on the right. The subgeneric classifications of Wang and Li (2005b) and Tamura (1995) are marked in color, and sectional classifications are abbreviated as follows: sect. *Atragene* (ATR), sect. *Archiclematis* (ARC), sect. *Aspidanthera* (ASP), sect. *Angustifoliae* (ANG), sect. *Campanella* (CAM), sect. *Cheiropsis* (CHE), sect. *Clematis* (CLE), sect. *Fruticella* (FRU), sect. *Flammula* (FLA), sect. *Lasiantha* (LAS), sect. *Meclatis* (MEC), sect. *Naraveliopsis* (NAO), sect. *Naravelia* (NAR), sect. *Pseudanemone* (PSE), sect. *Tubulosae* (TUB), sect. *Vioria* (VIO), sect. *Viticella* (VIT).

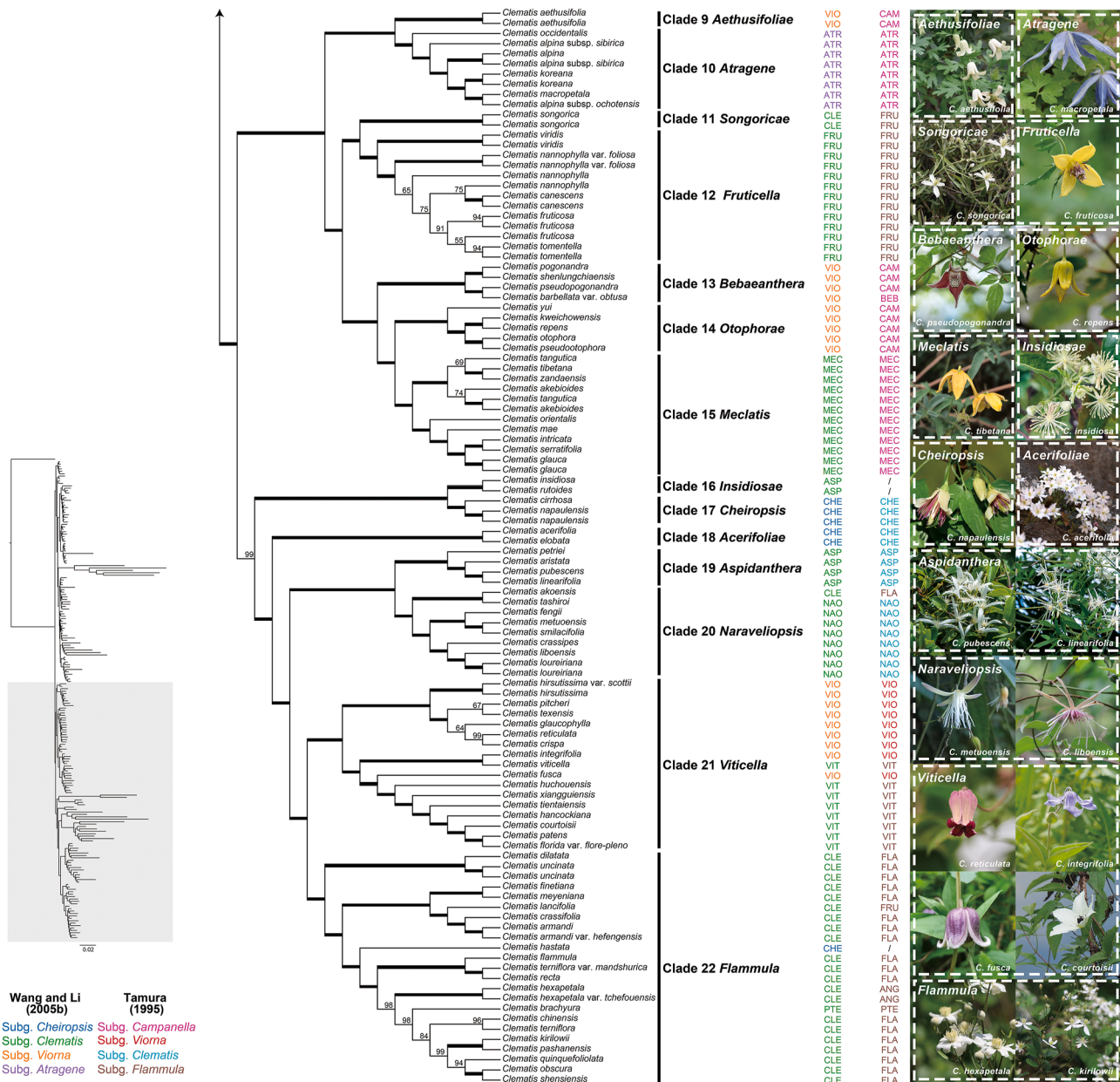
Therefore, we retained the *Naravelia* clade (clade 6) for our examination. Because the Geneious pipeline generated more SNP data and higher resolved phylogeny of *Clematis* than the GATK pipeline, the phylogenetic framework derived from the Geneious pipeline (Fig. 3) served as the basis for discussion and taxonomic revision (also see Xiao et al., 2022; Lyu et al., 2023).

Our analyses do not support all subgenera established by previous taxonomists (Tamura, 1995; Wang and Li, 2005b), apart from subg. *Atragene* Torr. & Gray (Wang and Li, 2005b) (Fig. 3). Moreover, our phylogenomic analysis does not support all previously proposed morphologically-defined monotypic sections. Section *Archiclematis* (Johnson, 1997; Wang and Li, 2005b; or the genus *Archiclematis* by Tamura, 1995) resides in clade 4, and both sect. *Pterocarpa* (Tamura, 1995; Johnson, 1997; Wang and Li, 2005b) and sect. *Angustifoliae* are nested within clade 22. Only a few sections, including sect. *Atragene* (Tamura, 1995; Wang and Li, 2005b; Yang

et al., 2009), sect. *Fruticella* (Wang and Li 2005a, b), and sect. *Meclatis* (Wang and Li, 2005b) are monophyletic, whereas most other sections have been shown to be polyphyletic.

By integrating morphological characteristics and geographical distribution, we identified 22 highly supported clades in *Clematis*. One large clade was formed within the genus by clades 1 through 8, while another was formed by clades 9 through 22 (Fig. 3). Here, we summarize the 22 clades of *Clematis* based on the two most important previous infrageneric classifications (Tamura, 1995; Wang and Li, 2005b). All relationships referenced in the following findings are fully supported, and any exceptions are explicitly noted.

Clade 1 consists of the species from sect. *Cheiropsis* (Tamura, 1995; Wang and Li, 2005b) that are distributed from Taiwan (China) to the western Himalayas. The clade does not include species that were formerly placed in sect. *Cheiropsis*, such as



C. acerifolia Maxim., *C. williamsii* A. Gray, *C. brevipes* Rehd., *C. potaninii* Maxim., *C. cirrhosa* L., *C. napaulensis* DC., and *C. hastata* Finet & Gagnep.

Clade 2 contains one species, *C. potaninii* from southwestern China. It was previously considered to be a member of sect. *Cheiropsis* by Wang and Li (2005b) or sect. *Clematis* (Tamura, 1995).

Clade 3 together with clade 2 are sister to clades 4–8. This clade is also represented by a single species, *C. delavayi* Franch., a shrub that was considered to be a member of sect. *Fruticella* by (Tamura, 1995). In Wang and Li's (2005b) classification, this species was classified in to sect. *Clematis* according to its floral characters (white flower with spreading sepals and glabrous stamens).

Clade 4 comprises a large group of species from sect. *Campanella* (sensu Tamura, 1995), sect. *Brachiatae* (sensu Wang, 2004b; also, Wang and Li, 2005b), sect. *Pseudanemone* (Wang, 2004c; also, Wang and Li, 2005b), and sect. *Archiclematis* (sensu Wang and Li, 2005b). However, this clade does not include some species that

were previously categorized within sect. *Campanella*, including but not limited to *C. aethusifolia* Turcz., *C. pogonandra* Maxim., and *C. repens*.

Clade 5 includes a single species, *C. menglaensis* M.C. Chang, from tropical Asia. This species has been considered to be a member of sect. *Naraveliopsis* Hand.-Mazz. (Chang et al., 1980; Wang and Li, 2005b; Wang, 2006b). However, our analysis places it as sister to clade 6.

Clade 6 includes species from sect. *Naravelia*, a group considered by many taxonomists as a distinct genus (Tamura, 1987, 1995; Wang and Li, 2005b). This group of species features leaf tendrils and petals that produce nectar, with a distribution concentrated in tropical areas of Asia.

Clade 7 is sister to clade 8 and encompasses species from sect. *Tubulosae*. The members of this clade correspond to subsect. *Tubulosae* (Decne.) W.T. Wang of sect. *Tubulosae* in Wang and Xie (2007) as well as Wang and Li (2005b). This clade is also roughly

consistent with sect. *Tubulosae* as defined by Tamura (1995), except that Tamura's (1995) sect. *Tubulosae* included some hybrid taxa which were excluded in this study.

Clade 8 encompasses sect. *Clematis* (sensu Tamura, 1995) distributed in Eurasia, along with unisexual species found in both North and South America, as well as *C. williamsii* and *C. brevipes*, which were formerly classified under sect. *Cheiropsis* (sensu Wang, 2002; as well as Wang and Li, 2005b), in addition to species belonging to sect. *Bebaeanthera* from Japan (sensu Tamura, 1995).

Clade 9 is sister to clade 10. It includes only one species from sect. *Campanella* (sensu Tamura, 1995), *C. aethusifolia*, in north-eastern Asia, which has yellow bell-shaped flowers and 2–4 pin-natisect leaves. In Wang and Li's (2005b) classification, this species was placed in sect. *Viorna*, subsect. *Connatae* Koehne, ser. *Aethu-sifoliae* Tamura.

Clade 10 comprises species from sect. *Atragene* (Tamura, 1995; Wang and Li, 2005b; Yang et al., 2009), which are distributed mainly in the frigid regions of Eurasia and North America. These plants possess petaloid staminodes, making them important hor-ticultural species.

Clade 11 is sister to clade 12 and consists of only one species, *C. songorica*. This species is a shrub with white, plate-shaped flowers found in central Asia. Tamura (1995) classified this spe-cies in sect. *Fruticella* based on its shrubby habit, whereas Wang and Li (2005b) grouped it into sect. *Clematis* based on its floral characters (white flower with spreading sepals and glabrous stamens).

Clade 12 comprises species from sect. *Fruticella* (sensu Wang and Li, 2005a). Species in this section are also shrubs, but with yellow bell-shaped flowers. We separate clades 11 and 12 as distinct groups because clade 12 originates from a hybridization event involving the progenitors of clade 11 and clade 14 (He, 2022). In Tamura's (1995) system, the species of clade 12 also belong to sect. *Fruticella*. However, Tamura's (1995) circumscription of sect. *Fruticella* additionally included some white-flowered shrub spe-cies, such as *C. delavayi* and *C. songorica*.

Clade 13 is sister to clades 14 and 15. Four species in this clade are from sect. *Bebaeanthera* and sect. *Campanella* (sensu Tamura, 1995) and have ternate to bi-ternate leaves and bell-shaped (purple or purplish yellow) flowers. In Wang and Li (2005b), these species belong to sect. *Viorna*, subsect. *Connatae*, ser. *Pogo-nandrae* W.T. Wang (*C. pogonandra* Maxim. and *C. shenlungchiaensis* M.Y. Fang) and subsect. *Bebaeanthera* (Edgew.) W.T. Wang (*C. barbellata* Edgew. and *C. pseudopogonandra* Finet & Gagnep.).

Clade 14 also comprises species from sect. *Campanella* (sensu Tamura, 1995). Species in this clade have yellow bell-shaped flowers with hairs on both filaments and anthers. In Wang and Li's (2005b) classification, species of this clade were included in sect. *Viorna*, subsect. *Connatae*, ser. *Connatae* Rehd. & Wils.

Clade 15 comprises species from sect. *Meclatis* (sensu Wang and Li, 2005a). In Tamura's (1995) classification, the species included in Clade 15 also belong to sect. *Meclatis*. However, Tamura's (1995) circumscription of sect. *Meclatis* additionally encompassed numerous African taxa (sect. *Brachiatae* sensu Wang and Li, 2005b), which in the present study were resolved within Clade 4.

Clade 16 includes two unisexual species from Madagascar. It is sister clade to clade 17. These two species were formerly classified as members of sect. *Aspidanthera* in both Tamura (1995) and Wang and Li (2005b).

Clade 17 encompasses two species from sect. *Cheiropsis* (Tamura, 1995), characterized by their remarkable bracts that are fused together into a cup form. In Wang and Li's (2005b) classi-fication, they placed these two species in a distinct subsect. *Cir-rhosae* Prantl, within sect. *Cheiropsis*.

Clade 18 includes two rare and endangered species, *C. acerifolia* and *C. elobata* (S.X. Yan) S.X. Yan & L. Xie, both of which inhabit the cliffs of the Taihang Mountains in northern China (Yan et al., 2016). Based on their inflorescence and floral characteristics, previous taxonomists often placed them in sect. *Cheiropsis* (Tamura, 1995; Johnson, 1997). Wang and Li (2005b) also included them in sect. *Cheiropsis*, treating them as subsect. *Acerifoliae* W.T. Wang.

Clade 19 comprises unisexual species from Australia and New Zealand. Previous classifications placed these species within sect. *Aspidanthera* according to their unisexual flowers (Tamura, 1995; Wang and Li, 2005b).

Clade 20 is sister to clade 19 and encompasses species of sect. *Naraveliopsis* (Tamura, 1995) from tropical Asia. In addition, *C. akoensis* Hayata, previously classified into sect. *Clematis* (Wang and Li, 2005b), also nested into this clade. However, *C. menglaensis*, included in sect. *Naraveliopsis* by Wang and Li (2005b), is not clustered in this clade but sister to clade 6.

Clade 21 and clade 22 form a larger clade, encompassing *Clematis* species characterized by the type II seedling morphology (Essig, 1991). Clade 21 includes species of sect. *Viorna* (sensu Tamura, 1995) and sect. *Viticella* (sensu Tamura, 1995; Wang and Li, 2005b), which have highly distinct floral traits. However, spe-cies of these two sections did not form two distinct subclades.

Clade 22 basically represents sect. *Flammula* (sensu Tamura, 1995). In addition, previously recognized monotypic sections, such as sect. *Pterocarpa* (Wang and Li, 2005b) and sect. *Angusti-foliae* (Tamura, 1995), are nested within this clade. An erect shrub species, *C. lancifolia* Bureau & Franch. (sect. *Clematis* in Wang and Li, 2005b), is also nested into this clade.

3.3. Morphological character evolution in *Clematis*

Ancestral character state reconstructions were carried out by using the ML tree inferred from the nuclear SNP alignments through the Geneious pipeline. Our ancestral character recon-struction showed that the ancestral states of *Clematis* (at crown node of the genus) include climbing habit, type I seedling, opposite leaves, serrate or dentate leaves, cymes, bisexual flowers, spreading sepals, no petals, no staminodes, glabrous filaments, tricolpate pollen, and no elongated connectives. Some character-istics emphasized by previous taxonomists have evolved multiple times in the genus, e.g., shrub habit (Tamura, 1995), unisexual flower (Tamura, 1995; Wang and Li, 2005b), fascicle flower (Tamura, 1995; Wang and Li, 2005b), spreading or erect sepals (Tamura, 1995), and glabrous or hairy filaments (Tamura, 1995) (Figs. 4–6).

4. Discussion

4.1. Phylogeny of *Clematis*

This study utilized SNPs from the nuclear genome to elucidate the phylogenetic relationships among *Clematis* species worldwide, while also providing the most extensive datasets of plastid ge-nomes and nrITS for this genus. During the Sanger sequencing era, nrITS emerged as one of the most widely utilized nuclear DNA fragments, proving particularly effective for systematic and taxo-nomic studies across numerous plant groups (China Plant BOL Group et al., 2011). However, nrITS provides insufficient phyloge-netic information to resolve relationships within the genus *Clematis*, particularly at deeper nodes where major clades show low support values (Fig. S2). Although limited in resolution, the expanded nrITS dataset in this study, particularly with increased sampling of Australian *Clematis* species, still contributes to a better understanding of phylogenetic relationships within the genus. In

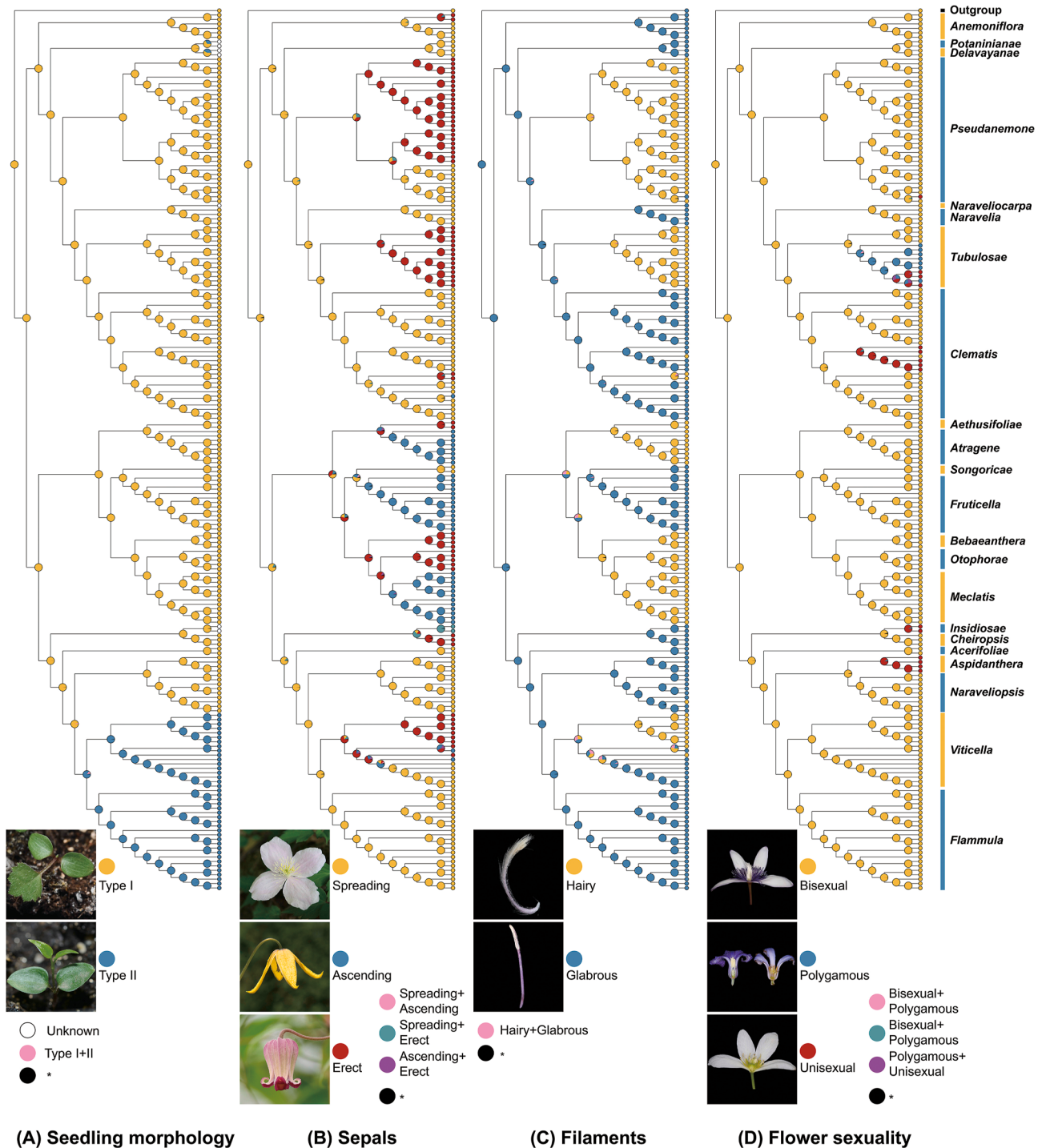


Fig. 4. Evolution of four key morphological characters in *Clematis* estimated by RASP v.4.2 (Yu et al., 2020) using the BBM method based on the nuclear SNP phylogeny. (A) Seedling morphology; (B) Sepals; (C) Filaments; (D) Flower sexuality. Colors of dots on the nodes and branches indicate the character states and their probabilities.

the nrITS phylogeny (Fig. S2), the expanded sampling of Australasian unisexual taxa formed a clade sister to *Naraveliopsis*, a relationship consistent with nuclear SNP data (Fig. 3). This congruence provides stronger evidence for delimiting sect. *Aspidanthera*.

The plastome phylogeny (Fig. S1) demonstrates significantly higher resolution compared to nrITS. However, substantial conflicts exist between the plastid and nuclear gene trees (Fig. 2). Previous studies suggested that such cytonuclear discordance in *Clematis* likely results from extensive interspecific hybridization

coupled with severe incomplete lineage sorting (ILS) (Lyu et al., 2021, 2023; Xiao et al., 2022). When cytonuclear discordance occurs, the nuclear gene tree often reflects the true evolutionary relationships among species more accurately than the plastid gene tree (Liu et al., 2022). This is because plastid genomes are uniparentally inherited and may undergo chloroplast capture due to hybridization and backcrossing events, causing their phylogenies to often misrepresent actual species relationships. Our previous studies have also shown that molecular markers

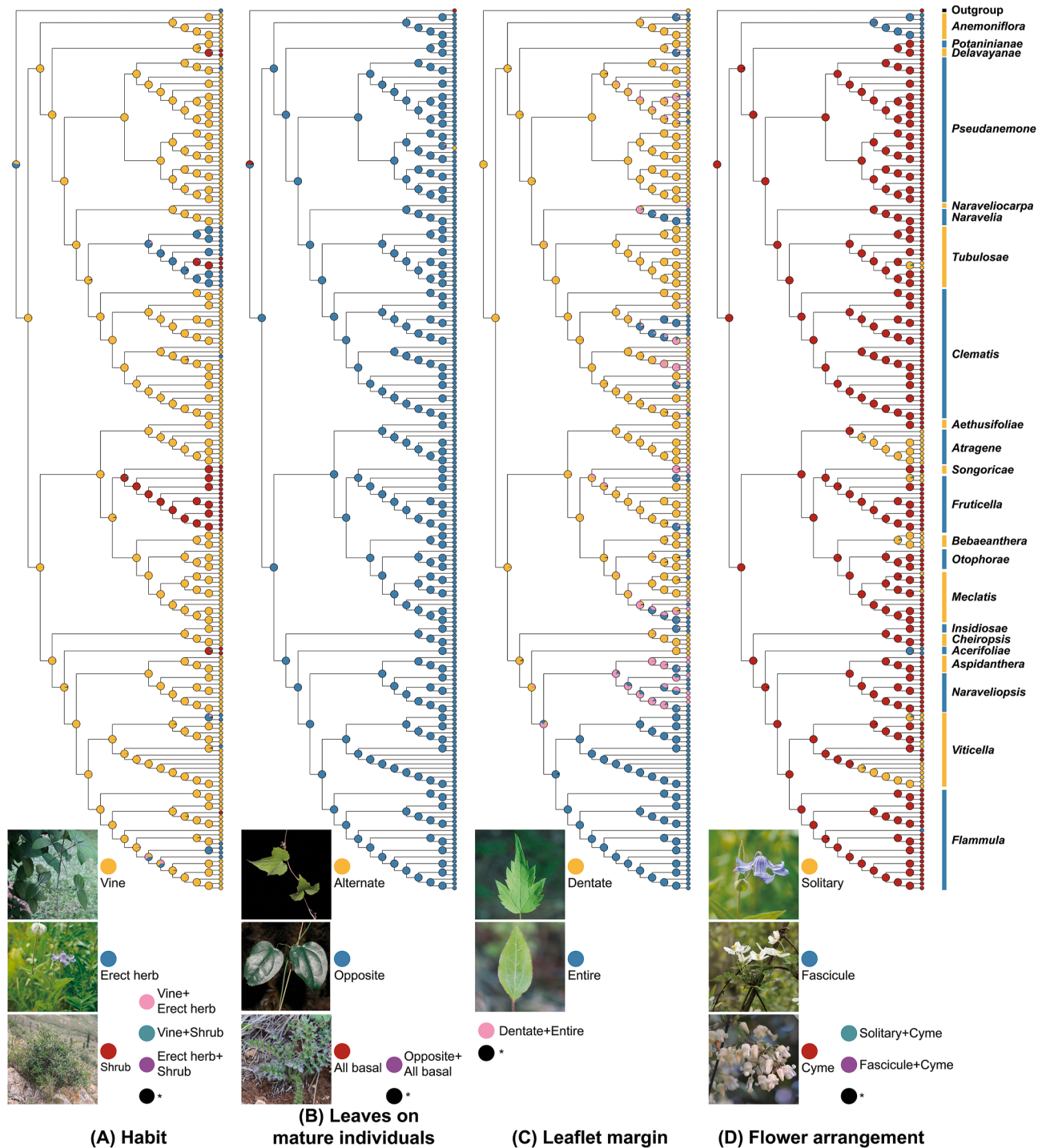


Fig. 5. Evolution of four key morphological characters in *Clematis* estimated by RASP v.4.2 (Yu et al., 2020) using the BBM method based on the nuclear SNP phylogeny. (A) Habit; (B) Leaves of mature individuals; (C) Leaflet margin; (D) Flower arrangement.

from the nuclear genome are more reliable than those from plastids when determining the phylogenetic relationships within *Clematis* (Lyu et al., 2021, 2023; He, 2022; Xiao et al., 2022). This fact is evidenced by the fact that (1) conspecific monophyly in nuclear trees contrasting with plastid-based polyphyly (e.g., in sect. *Clematis*, sect. *Tubulosae*, and sect. *Fruticella*, He et al., 2021; He, 2022; Lyu et al., 2021, 2023), (2) several cytonuclear discordant species occupy more phylogenetically plausible positions (morphologically justified) in the nuclear gene tree (e.g.,

C. brevicaudata, *C. gratopsis* W.T. Wang, *C. javana* DC., and *C. songorica*, He et al., 2021; Xiao et al., 2022; Lyu et al., 2023; and this study), and (3) strong congruence between SNP-based and transcriptome-derived nuclear phylogenies (Xiao et al., 2022; He, 2022). The value of plastid genomes lies in their ability to reveal historical hybridization events when cytonuclear discordance occurs. A species' position in the plastid tree may indicate past hybridization and help infer the approximate process of introgression.

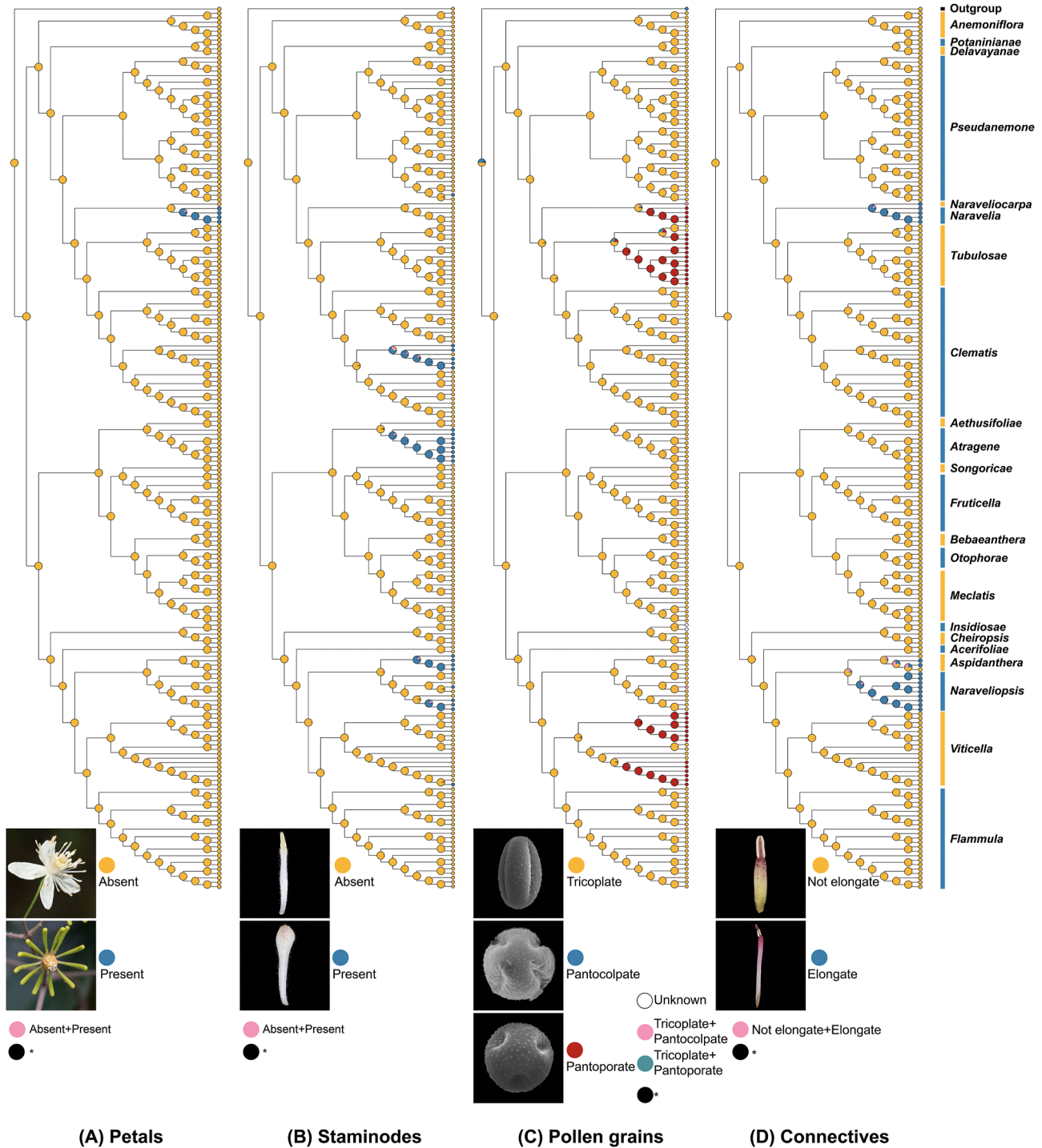


Fig. 6. Evolution of four key morphological characters in *Clematis* estimated by RASP v.4.2 (Yu et al., 2020) using the BBM method based on the nuclear SNP phylogeny. (A) Petals; (B) Stamens; (C) Pollen grains; (D) Connectives.

In this study, when cytonuclear discordance occurred, the nuclear SNP phylogeny still better reflected the phylogenetic relationships among species. For instance, in sect. *Clematis*, species, including *C. brevicaudata*, *C. gratopsis*, and *C. javana*, were clustered within the sect. *Tubulosae* clade in the plastome tree, whereas they grouped robustly with other sect. *Clematis* members in the nuclear SNP phylogeny (Fig. 2). This pattern suggests that although frequent hybridization occurred between sect. *Clematis* and sect. *Tubulosae* (as evidenced by Lyu

et al., 2021, 2023), nuclear SNP data nevertheless accurately reflect morphological and taxonomic relationships. The same situation occurred in *C. songorica*. Two different individuals of *C. songorica* clustered in different clades in the plastome phylogeny, whereas in the nuclear SNP tree they formed a clade sister to sect. *Fruticella* (Fig. 2). For these reasons, we discuss the phylogenetic relationship within the genus and revise its infrageneric taxonomy according to the results of nuclear SNP analysis.

In line with previous studies (Miikeda et al., 2006; Xie et al., 2011; Lehtonen et al., 2016; Jiang et al., 2017; He et al., 2021), our phylogenomic analysis provided evidence for the most broadly defined *Clematis* (Johnson, 1997). It is essential to integrate all previously recognized small genera of the subtribe Clematidinae, such as *Archiclematis*, *Naravelia*, and *Clematopsis*, into the genus *Clematis*. The early branching lineages of *Clematis* displayed notably short branch lengths, which implies that the genus underwent a rapid species radiation in the early stages of its evolutionary diversification.

4.2. Infrageneric taxonomy of *Clematis*

The genus *Clematis* has commonly been classified into no more than 20 sections, with some classifications merging them into a small number of subgenera (Tamura, 1987, 1995; Johnson, 1997; Wang and Li, 2005b). However, the classifications of these subgenera and sections proposed by different authors often show some inconsistencies. For example, sect. *Viorna* and sect. *Clematis* defined by Wang and Li (2005b) are much broader than those defined by Tamura (1995) and Johnson (1997). These discrepancies among classification systems stem from differing interpretations among authors regarding the evolutionary patterns of morphological characters in *Clematis*. A robust and well-sampled molecular phylogeny will provide a framework for evaluating these historical taxonomic treatments. Previous molecular studies have revealed significant conflicts between phylogenies and the classifications of *Clematis* (Miikeda et al., 2006; Xie et al., 2011; Lehtonen et al., 2016). The primary factor contributing to this issue is that those studies did not provide enough phylogenetic information because they used a limited set of molecular markers or predominantly relied on plastid markers. Our current analyses of the nuclear SNP data provide a higher resolution phylogenetic framework for *Clematis* that is more consistent with morphological variations.

Compared to existing classification systems, our nuclear SNP analysis fully supported three sections within the genus: sect. *Atragene* (sensu Tamura, 1995; Wang and Li, 2005b), sect. *Fruticella* (sensu Wang and Li, 2005b), and sect. *Meclatis* (sensu Wang and Li, 2005b). Three sections, sect. *Tubulosae* (sensu Tamura, 1995; Wang and Li, 2005b), sect. *Naraveliopsis* (sensu Tamura, 1995; Wang and Li, 2005b), and sect. *Naravelia* (sensu Johnson, 1997), are largely supported. Sect. *Tubulosae* should be redefined by excluding two hybrid taxa, *C. pinnata* and *C. takedana*, according to our previous studies (Lyu et al., 2021, 2023). In clade 20 (Fig. 3), species of sect. *Naraveliopsis* grouped with *C. akoensis*, which was classified into sect. *Clematis* (sensu Wang and Li, 2005b) or sect. *Flammula* (sensu Tamura, 1995). Sect. *Naravelia* (Johnson, 1997) needs to be redefined after the exclusion of *C. eichleri* (*C. menglaensis*) (Tamura, 1986; Johnson, 1997).

In addition to the six sections mentioned above, our phylogenomic analysis showed that many other large sections are either polyphyletic or paraphyletic. For example, the following sections are highly heterogeneous polyphyletic: sect. *Cheiroopsis* (sensu Tamura, 1995; Wang and Li, 2005b), sect. *Viorna* (sensu Wang and Li, 2005b), sect. *Campanella* (sensu Tamura, 1995), sect. *Clematis* (sensu Wang and Li, 2005b), sect. *Fruticella* (sensu Tamura, 1995), sect. *Meclatis* (sensu Tamura, 1995), and sect. *Aspidanthera* (sensu Tamura, 1995; Wang and Li, 2005b). Sect. *Viorna* (sensu Tamura, 1995) and sect. *Viticella* are paraphyletic groups and mixed together with each other in clade 21 (Fig. 3). Morphologically distinctive monotypic sections, such as sect. *Angustifoliae* (sensu Tamura, 1995), sect. *Pterocarpa* (sensu Tamura, 1995; Johnson, 1997; Wang and Li, 2005b), and sect. *Archiclematis* (sensu Johnson, 1997; Wang and Li, 2005b), are not supported by

the nuclear SNP data. They are all nested within larger clades. The above-mentioned problems with these classification systems lie in their overemphasis on certain morphological characteristics while neglecting overall phenotypic similarity and geographic distribution patterns. For instance, the placement of *C. acerifolia* in sect. *Cheiroopsis* (Tamura, 1995; Wang and Li, 2005b), based solely on floral positioning, is problematic, as it conflicts with both its overall morphological characteristics and distribution patterns. The classification of *C. aethusifolia* in sect. *Campanella* (Tamura, 1995; Johnson, 1997), based solely on erect sepals and pubescent stamens, is also biogeographically problematic. Similarly, the inclusion of all dioecious species worldwide in sect. *Aspidanthera* (Wang, 2004a; Wang and Li, 2005b) and all shrubby species in sect. *Fruticella* (sensu Tamura, 1995) has resulted in artificial taxonomic groupings. Therefore, the nuclear SNP data in this study provide a powerful tool for re-evaluating the morphology, geographic distribution, and evolution of *Clematis*, while enabling critical assessment of previous classification systems.

The phylogenetic positions of some controversial or recently published species have been further confirmed. Previous authors often placed *Clematis williamsii*, *C. brevipes*, *C. acerifolia*, and *C. hastata* into sect. *Cheiroopsis* according to the position of their flowers (Tamura, 1995; Wang, 1998; Wang and Bartholomew, 2001; Wang, 2002; Wang and Li, 2005b). However, morphological and phylogenetic analysis indicate that those species are not close relatives of *C. montana* Buch.-Ham. ex DC. Moreover, *C. potaninii* was considered to belong to sect. *Cheiroopsis* (Wang, 2002) or sect. *Clematis* (Tamura, 1995; Johnson, 1997), but it forms a separate clade. As for recently published species, although the authors suggested that *C. guniuensis* W.Y. Ni, R.B. Wang & S.B. Zhou may be a member of sect. *Viticella* (Wang et al., 2019), our phylogenomic analysis suggests that this species is a member of sect. *Clematis*. From a morphological perspective, this phylogenetic position is undoubtedly correct. The dentate leaves of *C. guniuensis* clearly show closer affinity with species in sect. *Clematis* than with the entire-leaved members of sect. *Viticella*. *Clematis aethusifolia* (clade 9) was often classified under sect. *Campanella* (Tamura, 1995) or sect. *Viorna* (Wang and Li, 2005b). However, this species showed a position sister to sect. *Atragene* (clade 10). Species of both clades are mainly distributed in the cold areas of northern Asia with some species of sect. *Atragene* extending to Europe and North America. Our phylogenomic analysis indicates that it is essential to revise the infrageneric classification of *Clematis* to align with the newly established phylogenetic framework. New sections need to be established, and existing sections need to be re-circumscribed or reinstated (see below).

4.3. Morphological character evolution within *Clematis*

The phylogenetic analysis based on the nuclear SNP data indicates that the 12 key morphological characters of *Clematis* (e.g., growth form, flower shape, and the presence or absence of filament hairs) exhibit complex evolutionary trajectories within the genus (Figs. 4–6). Similar results have been reported by a range of previous studies (Miikeda et al., 2006; Xie et al., 2011; Lehtonen et al., 2016; He et al., 2021; Xiao et al., 2022). Any classification approach that relies predominantly on one or a few key morphological characters for delineating subgenera or sections in *Clematis* risks creating artificial groupings. These issues are well demonstrated by several previously recognized artificial taxa, including the genus *Archiclematis*, as well as sect. *Cheiroopsis* (Tamura, 1995; Wang and Li, 2005b), sect. *Fruticella* (Tamura, 1995), and sect. *Aspidanthera* (Wang, 2004a; Wang and Li, 2005b). That is why any attempt to divide *Clematis* into subgenera (such as Tamura, 1995) based on a few key characters is unacceptable (Fig. 3).

Of all the 12 key characters, seedling morphology, recognized by Tamura (1987) as the most important character of *Clematis* classification, holds potential for interpreting the evolutionary relationships within the genus (Fig. 4). Our results suggest that Type II seedling likely represents a derived state within the genus, whereas Type I seedlings appear to represent the ancestral state. However, the morphological characteristics of *Clematis* seedlings have not been thoroughly observed and recorded, leading to a significant gap in knowledge regarding this trait, which remains ambiguous or even unknown for many species within *Clematis*, as pointed out by Cheng et al. (2016) and He et al. (2021). Therefore, comprehensively recording and reevaluating the morphological characteristics of *Clematis* seedlings is crucial.

The remarkable morphological complexity in *Clematis*, characterized by repeated evolutionary transitions in most character states (Figs. 4–6), necessitates caution against basing infrageneric classifications on limited morphological characters. Our nuclear gene tree demonstrates that despite high intra-clade morphological variability (excluding single-species clades), most clades maintain distinct geographic distribution patterns (Table 3) consistent with broader angiosperm biogeography. Our phylogenomic analysis would prevent taxonomically implausible groupings such as placing the *C. montana* group and *C. acerifolia* in the same section, which would otherwise imply an improbable disjunct distribution between the Taihang Mountains and the Himalaya-Hengduan Mountains region. Our morphological analysis underscores the importance of adopting an integrative taxonomic approach that holistically considers both overall phenotypic similarity and biogeographic coherence in future classifications.

4.4. Revised sectional taxonomy of *Clematis*

Our phylogenetic analysis indicates that existing infrageneric classification systems fail to accurately depict phylogenetic relationships in *Clematis*. Utilizing the 22-clade phylogenetic framework inferred from our nuclear SNP data, we can update the infrageneric taxonomy of *Clematis*. In this study, the 22 major clades receive sectional designations without further grouping them into subgenera due to a lack of clear morphological support. A thorough examination of the morphological features of the sections is outlined in Table 3. This study focuses on the infrageneric taxonomy framework of *Clematis*, thus omitting detailed taxonomic discussions. Acknowledging the significant challenges in conducting integrative taxonomic research on *Clematis*, a genus known for its vast species diversity and large genome size, this study presents a recommended workflow (Fig. 7 and detailed in Appendix 1) aimed at assisting the study of other complex taxa with similarly large genomes.

Taxonomic treatments:

Clematis L., Sp. Pl. 1: 543. 1753. Type (chosen by Britton and Brown, 1913): *C. vitalba* L. (铁线莲属)

Woody or herbaceous vines, rarely erect shrubs, subshrubs, or perennial herbs. Leaves opposite, rarely alternate, simple or compound, rarely with leaf tendrils. Flowers in cymes, sometimes solitary. Flowers bisexual, unisexual, or rarely polygamous. Sepals 4–8, petaloid, spreading, ascending, or erect, often valvate in bud. Petals absent or rarely present. Stamens numerous, sometimes outer ones sterile and becoming linear or petaloid stamens. Carpels many, ovaries with one pendulous ovule. Style persistent, elongated after anthesis, rarely slightly or not elongated. Achenes usually bilaterally compressed, persistent style usually plumose.

The genus *Clematis* comprises 300–350 species, classified into 22 sections. It is widely distributed throughout the world, with the exception of Antarctica.

1. ***Clematis* sect. *Anemoniflora*** Loudon, Encycl. Trees and Shrubs 15. 1869. ≡ *Clematis* subsect. *Montanae* Schneid., Ill. Handb. Laubh. 290. 1906. ≡ *Clematis* sect. *Montanae* (Schneid.) Grey-Wilson, *Clematis* 75. 2000. Type: *C. montana* Buch.-Ham. ex DC. (绣球藤组)

= *Clematis* sect. *Fasciculiflorae* (Tamura) Grey-Wilson, *Clematis* 94. 2000. ≡ *Clematis* ser. *Fasciculiflorae* Tamura in Acta Phytotax. Geobot. 16 (3): 8. 1956. Type: *C. fasciculiflora* Franch.

Woody vines. Type I seedling leaves. Cauline leaves opposite. Leaves ternate, rarely pinnate, leaflet margin usually dentate. Flowers bisexual, often large, 1–3-many arising from axillary bud of old branch, pedicellate only. Sepals four, spreading, or rarely erect, white or pink. Stamens glabrous. Pollen tricolpate.

Distribution: Comprising ca. 13 species, distributed from Taiwan (China) to the western Himalayas.

Etymology: The Chinese name of this section is derived from the Chinese name of its type species, *C. montana*, which is “绣球藤” (Xiùqiúténg).

Notes: The flowers of this group are often clustered in the leaf axils of old branches, leading to their placement in sect. *Cheiropsis* in previous classification systems (Tamura, 1995; Johnson, 1997; Grey-Wilson, 2000; Wang, 2002; Wang and Li, 2005b). However, the traditionally defined sect. *Cheiropsis* is clearly a polyphyletic group as shown by many previous studies (Xie et al., 2011; Lehtonen et al., 2016; He et al., 2021; Xiao et al., 2022), and should be separated. The plants within sect. *Anemoniflora* are not closely related to *C. acerifolia* (a cliff-dwelling species from northern China), *C. cirrhosa* (a European species), or the taxonomically contentious *C. potaninii* and *C. brevipes*.

Species in sect. *Anemoniflora* typically have trifoliate leaves and large, spreading sepals, though some exhibit pinnate leaves and erect sepals. All species have glabrous stamens, type I seedlings, and tricolpate pollen grains. Furthermore, they share a continuous distribution range in the mountainous regions of southern to southwestern China and adjacent countries. Plants of this section hold significant horticultural value.

2. ***Clematis* sect. *Potaniniana*** (Johnson) J.M. Xiao & L. Xie, **stat. nov.** ≡ *Clematis* subsect. *Potaniniana* M. Johnson, Släktet *Clematis* 410. 1997, p.p. excl. *C. trichotoma* Nakai. Type: *C. potaninii* Maxim. (美花铁线莲组)

Woody vines. Seedling unknown. Cauline leaves opposite, usually bipinnate, leaflets dentate. Cymes axillary on the leaf axils of hornotinous branch, often 1–3-flowered. Flowers bisexual, large. Sepals often six, spreading, white. Stamens glabrous. Pollen tricolpate.

Distribution: One species (*C. potaninii*) in southwestern China.

Etymology: The Chinese name of this section is derived from the Chinese name of its type species, *Clematis potaninii*, which is “美花铁线莲” (Měihuā tièxiànlián).

Notes: The taxonomic status of *Clematis potaninii* has long been controversial. This species is morphologically distinct from members of sect. *Anemoniflora*, exhibiting bipinnately compound leaves and typically six sepals. In traditional classifications, it was often placed in sect. *Cheiropsis* based on its floral arrangement (axillary flower clusters) (Wang, 2002; Wang and Li, 2005b). However, some taxonomists argue for its inclusion in sect. *Clematis* (Johnson, 1997) due to other shared floral characteristics, further complicating its systematic placement.

Phylogenetic results from this study demonstrate that *Clematis potaninii* is not closely related to sect. *Anemoniflora*, sect. *Cheiropsis*, or sect. *Clematis*. Even its proposed sister-group relationship with *C. delavayi* lacks strong statistical support, rendering this

Table 3
Summary of morphological characters and distribution of each *Clematis* section.

Section	Seedling morphology	Sepals	Filaments	Flower sexuality	Habit	Leaves on mature individuals	Leaflet margin	Flower arrangement	Petals	Staminodes	Pollen grains	Connectives	Distribution
<i>Anemoniflora</i>	Type I	Spreading, rarely erect	Glabrous	Bisexual	Vines	Opposite	Dentate	Fascicule	Absent	Absent	Tricolpate	Not elongate	Taiwan (China) westward to the western Himalayas
<i>Potantinianae</i>	Unknown	Spreading	Glabrous	Bisexual	Vines	Opposite	Dentate	Cyme	Absent	Absent	Tricolpate	Not elongate	Southwestern China
<i>Delavayanae</i>	Unknown	Spreading	Glabrous	Bisexual	Shrubs	Opposite	Entire	Cyme	Absent	Absent	Tricolpate	Not elongate	Southwestern China
<i>Pseudanemone</i>	Type I	Erect or spreading	Hairy	Bisexual	Vines, subshrubs or erect herbs	Opposite, rarely alternate	Dentate, rarely entire	Cyme, rarely solitary	Absent	Absent	Tricolpate	Not elongate	Western China, Japan, southeastern Asia, south Asia, Africa
<i>Naraveliocarpa</i>	Unknown	Spreading	Glabrous	Bisexual	Vines	Opposite	Entire	Cyme	Absent	Absent	Tricolpate or pantocolpate	Elongate	Southern China and Thailand
<i>Naravelia</i>	Type I	Spreading	Glabrous	Bisexual	Vines	Opposite	Entire (dentate when young)	Cyme	Present	Absent	Pantoporate	Elongate	Tropical Asia
<i>Tubulosae</i>	Type I	Erect	Hairy	Polygamous, bisexual or unisexual	Erect herbs or subshrubs	Opposite	Dentate	Cyme, rarely solitary	Absent	Absent	Pantoporate, rarely tricolpate	Not elongate	Eastern Asia
<i>Clematis</i>	Type I	Spreading, rarely ascending or erect	Glabrous, rarely hairy	Bisexual or unisexual	Vines	Opposite	Dentate, rarely entire	Cyme, rarely solitary	Absent	Absent or present	Tricolpate	Not elongate	Eurasian, Africa and Americas
<i>Aethusifoliae</i>	Type I	Erect	Hairy	Bisexual	Vines	Opposite	Entire or dentate	Cyme	Absent	Absent	Tricolpate	Not elongate	Northeastern Asia
<i>Atragene</i>	Type I	Ascending	Hairy	Bisexual	Vines	Opposite	Dentate or serrate	Solitary	Absent	Present	Tricolpate	Not elongate	North Eurasia and America
<i>Songoricae</i>	Unknown	Spreading	Glabrous	Bisexual	Shrubs	Opposite	Dentate or entire	Cyme	Absent	Absent	Tricolpate	Not elongate	Central Asia
<i>Fruticella</i>	Type I	Ascending	Glabrous	Bisexual	Shrubs	Opposite	Dentate or entire	Cyme, rarely solitary	Absent	Absent	Tricolpate	Not elongate	Loess Plateau, Gobi Desert of Mongolia, and northeastern Hengduan Mountains
<i>Bebaeanthera</i>	Type I	Erect	Hairy	Bisexual	Vines	Opposite	Dentate or entire	Solitary	Absent	Absent	Tricolpate	Not elongate	Himalaya
<i>Otophorae</i>	Type I	Erect	Hairy	Bisexual	Vines	Opposite	Serrate or entire	Cyme or solitary	Absent	Absent	Tricolpate	Not elongate	Southeastern, central, and southwestern China
<i>Meclatis</i>	Type I	Ascending	Hairy	Bisexual	Vines	Opposite	Dentate or entire or serrate	Cyme or solitary	Absent	Absent	Tricolpate	Not elongate	Central and northern China, western Asia and eastern Europe
<i>Insidiosae</i>	Unknown	Spreading or erect	Glabrous	Unisexual	Vines	Opposite	Entire	Cyme	Absent	Absent	Unknown	Not elongate	Madagascar
<i>Cheiropsis</i>	Type I	Erect	Glabrous	Bisexual	Vines	Opposite	Dentate, or entire	Fascicule	Absent	Absent	Tricolpate	Not elongate	Southwestern China, the Himalayas, Mediterranean region
<i>Acerifoliae</i>	Type I	Spreading	Glabrous	Bisexual	Shrubs	Opposite	Dentate	Fascicule	Absent	Absent	Tricolpate	Not elongate	Taihang Mountains in northern China
<i>Aspidanthera</i>	Type I	Spreading	Glabrous	Unisexual	Vines	Opposite	Entire or dentate	Cyme	Absent	Absent	Tricolpate	Elongate or not elongate	Australia, New Zealand, tropical Pacific islands
<i>Naraveliopsis</i>	Type I	Spreading	Glabrous, rarely hairy	Bisexual, rarely unisexual	Vines	Opposite	Entire, rarely dentate	Cyme	Absent	Absent or present	Tricolpate or pantocolpate	Elongate	Tropical Asia
<i>Viticella</i>	Type II	Spreading or erect	Glabrous or hairy	Bisexual	Vines or erect herbs	Opposite	Entire	Solitary or cyme	Absent	Absent, rarely present	Pantoporate or tricolpate	Not elongate	Eurasian and North America
<i>Flammula</i>	Type II	Spreading	Glabrous	Bisexual	Vines, rarely erect herbs or shrubs	Opposite	Entire	Cyme	Absent	Absent	Tricolpate	Not elongate	Asia, Europe, Africa

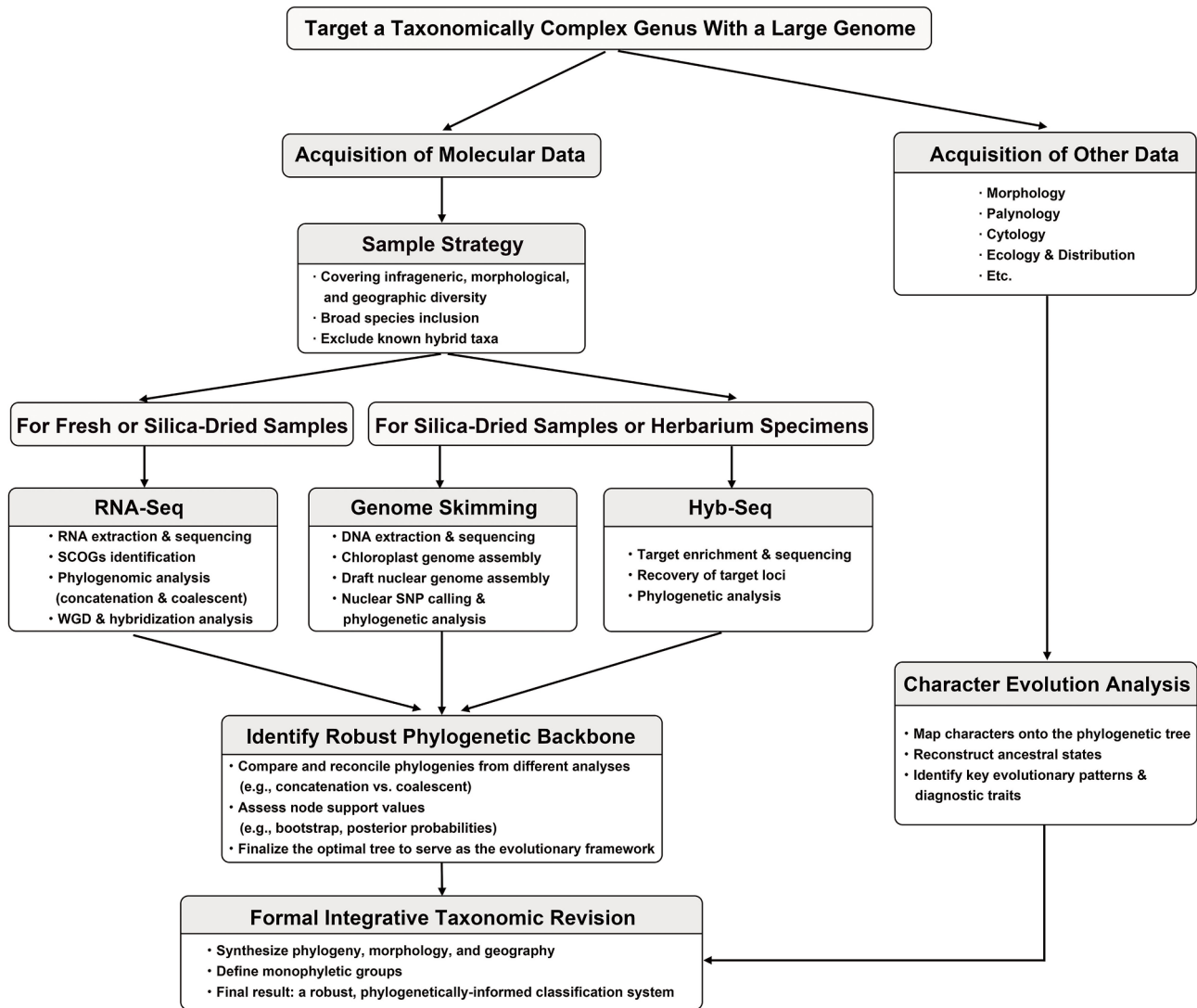


Fig. 7. A suggested workflow for integrative taxonomic study of genus with great species diversity and large genome size.

species phylogenetically isolated within the genus. Given its distinct position, we propose elevating it to sectional rank in *Clematis*.

3. *Clematis* sect. ***Delavayanae*** J.M. Xiao & L. Xie **sect. nov.** Type: *C. delavayi* Franch. (银叶铁线莲组)

Diagnosis: Sect. *Delavayanae* is closely related to sect. *Potani-nianae* but differs significantly in being an erect shrub, as well as having once-pinnate leaves and terminal cymes.

Small shrubs. Seedling unknown (likely type I). Cauline leaves opposite. Leaves pinnate, leaflets small. Cymes terminal. Flower white, bisexual. Sepals 4–6, spreading. Stamens glabrous. Pollen tricolpate.

Distribution: One species (*C. delavayi*) in hot-dry valleys of the southern parts of the Hengduan Mountains.

Etymology: The scientific name of this section is based on the specific epithet of its type species, “delavayi.” The Chinese name of this section is derived from the Chinese name of its type species, *C. delavayi*, which is “银叶铁线莲” (Yínyè tièxiànlíán).

Notes: *Clematis delavayi* is another taxonomically contentious species within the genus. This species exhibits highly distinctive

morphological and ecological characteristics: it grows as an erect shrub with small, pinnately compound leaves featuring silvery-white undersides, and produces white flowers with spreading sepals. Endemic to the dry-hot valleys of the Hengduan Mountains in southwestern China, *C. delavayi* represents a rare xerophytic adaptation within the genus.

In previous classifications, some taxonomists placed *Clematis delavayi* in sect. *Fruticella* based on its shrubby habit (Tamura, 1995; Johnson, 1997), while Wang and Li (2005a, b) assigned it to sect. *Clematis* according to its floral characteristics. He et al. (2021) revealed through plastid genome analysis that *C. delavayi* does not belong to sect. *Fruticella*, yet it also shows no close relationship with species in sect. *Clematis*. Our study further demonstrates that *C. delavayi* occupies a phylogenetically isolated position within the genus. Therefore, we propose establishing a new section to accommodate this ecologically and morphologically distinct species.

4. *Clematis* sect. ***Pseudanemone*** Prantl in Bot. Jahrb. 9: 257. 1888. ≡ *Clematopsis* Bojer ex Hutch. in Bull. Misc. Inform. Kew 1920: 12. 1920. Type (chosen by Tamura, 1995): *C. pimpinellifolia* Hook. (茴芹铁线莲组)

= *Clematis* sect. *Archiclematis* Tamura in Sci. Rep. Osaka Univ. 4: 45. 1955. = *Archiclematis* (Tamura) Tamura in Sci. Rep. Osaka Univ. 16 (2): 31. 1967. Type: *C. alternata* Kitam. & Tamura.

= *Clematis* sect. *Campanella* Tamura in Acta Phytotax. Geobot. 38: 38. 1987, p.p. Type: *C. lasiandra* Maxim.

= *Clematis* sect. *Connatae* (Koehne) M. Johnson, Klematis 287. 1997. = *Clematis* subsect. *Connatae* Koehne, Deuts. Dendr. 158. 1893. Type: *C. connata* DC.

= *Clematis* sect. *Brachiatae* Snoeijer in *Clematis* 1992: 12. 1992. Type: *C. brachiata* Thunb.

Vines, subshrubs or erect herbs. Type I seedling leaves. Mature cauline leaves opposite or rarely alternate, simple or compound, leaflets often dentate. Flowers bisexual. Cymes 1-many flowered. Sepals erect or spreading. Stamens pubescent. Pollen tricolpate.

Distribution: Comprising ca. 68 species, widely distributed in southern and western China, Japan, southeastern Asia, southern Asia, Africa, and Madagascar.

Etymology: This clade encompasses the type species of several morphological sections, including sect. *Campanella*, sect. *Archiclematis*, sect. *Brachiatae*, and sect. *Pseudanemone*. Following the principle of nomenclatural priority, the earliest published section name *Pseudanemone* has been retained for this group.

Notes: This lineage represents one of the largest and most compositionally complex clades within *Clematis*, encompassing species distributed from southern and southwestern China across South Asia to the African continent. The most important component of this section comprises species of sect. *Campanella* (sensu Tamura, 1995, p.p.) from southwestern China, characterized by their type I seedlings, campanulate flowers, and pubescent stamens. Phylogenetic analyses place *C. alternata*, the sole species in the genus exhibiting alternate leaf arrangement in mature plants, firmly within this clade, confirming that its distinctive foliar morphology provides neither sufficient evidence to maintain it as a separate genus nor adequate justification for sectional recognition, a conclusion supported by both earlier molecular studies and our current genomic data (Miikeda et al., 2006; Xie et al., 2011; Lehtonen et al., 2016; He et al., 2021). Two African groups, sect. *Brachiatae* (sensu Wang, 2004b) and sect. *Pseudanemone* (sensu Wang, 2004c), are also embedded within this clade (Clade 4, Fig. 3), revealing a distinct biogeographic pattern. The southwestern Chinese taxa form a large paraphyletic assemblage at the base of the clade, while the African lineages are derived from one of the East Asian lineages, clearly indicating their late-derived status. The species in this section are generally characterized by type I seedling leaves, often with serrate leaf margins, and flowers with erect sepals forming a campanulate shape (at least in early flowering stage), along with pubescent stamen filaments.

5. *Clematis* sect. *Naraveliocarpa* Tamura in Acta Phytotax. Geobot. 51: 127. 2001. Type: *C. eichleri* (Tamura) Tamura (= *C. menglaensis* M.C. Chang) (勐腊铁线莲组)

Woody vines. Seedling unknown. Cauline leaves opposite. Leaves pinnate or bipinnate, leaflets entire. Flowers bisexual. Cymes axillary or terminal, almost panicle-like. Sepals four, caducous. Stamens glabrous, anthers with connective projections. Achenes fusiform, often twisted. Pollen tricolpate or pantocolpate.

Distribution: One species (*C. menglaensis*) in southern China and Thailand.

Etymology: The scientific name of this section is from Tamura (2001). The Chinese name of this section is derived from the Chinese name of its type species, *C. menglaensis*, which is “勐腊铁线莲” (Měnglǎ tiěxiànlián).

Notes: Chang et al. (1980) published and classified *C. menglaensis* into sect. *Naraveliopsis*. Tamura (1986) described a

Thai species under the genus *Naravelia* as *N. eichleri*. Later, he transferred (Tamura, 2001) this species to *Clematis* (as *C. eichleri*) and established sect. *Naraveliocarpa* to accommodate it. However, Wang and Li (2005b) and Wang (2006) subsequently proposed that *C. eichleri* and *C. menglaensis* represent the same taxonomic entity. They synonymized *C. eichleri* and maintained the species within sect. *Naraveliopsis*, where *C. menglaensis* had previously been classified by Chang et al. (1980). Interestingly, Johnson (1997) did not notice that *C. eichleri* is the same species as *C. menglaensis*, and he recorded *C. menglaensis* under sect. *Naraveliopsis*, and recorded *C. eichleri* under sect. *Naravelia*.

In this study, we obtained plant material of *Clematis menglaensis* from southern Yunnan Province. Our phylogenetic analyses support Tamura's (2001) hypothesis that this species shows closer affinity to sect. *Naravelia* than to sect. *Naraveliopsis*. Given that this species forms a sister clade to sect. *Naravelia*, we retain the sect. *Naraveliocarpa* proposed by Tamura (2001) to demonstrate its special phylogenetic position.

6. *Clematis* sect. *Naravelia* (DC.) Prantl in Bot. Jahrb. 9: 261. 1888. = *Naravelia* DC. Syst. Nat. 1: 167. 1818, nom. et orth. cons. Type: *C. zeylanica* (L.) Poir. (锡兰莲组)

Woody vines. Type I seedling leaves. Cauline leaves opposite. Compound leaves with tendrils, leaflets entire and dentate when young. Flowers bisexual. Cymes paniculate, terminal to axillary. Sepals four. Petals present, linear to clavate. Stamens glabrous, connectives distinctly project. Achenes fusiform, often twisted. Pollen pantoporate.

Distribution: Comprising ca. six species, distributed in tropical Asia.

Etymology: The Chinese name of this section is derived from the Chinese name of its type species, *C. zeylanica*, which is “锡兰莲” (Xílán lián).

Notes: The plants of sect. *Naravelia* exhibit highly distinctive morphological features, including tendril-bearing leaves and flowers with club-shaped, nectariferous petals, which clearly differentiate them from all other members of *Clematis*. Due to these unique characteristics, most taxonomists have historically treated this group as a separate genus (Tamura, 1995; Grey-Wilson, 2000; Wang and Li, 2005b). Molecular phylogenetic studies have consistently demonstrated that this group is embedded within the genus *Clematis* and should not be treated as a separate genus (Miikeda et al., 2006; Xie et al., 2011; Lehtonen et al., 2016; Jiang et al., 2017; He et al., 2021; Xiao et al., 2022). In our study, *Naravelia* species form a distinct clade within *Clematis*, leading us to recognize them at the sectional rank.

7. *Clematis* sect. *Tubulosae* Decne. in Nouv. Arch. Mus. Hist. Nat. Paris, ser. 2, 4: 203. 1881; Type (chosen by Eichler, 1958): *C. heracleifolia* DC. (大叶铁线莲组)

Erect perennial herbs or subshrubs. Type I seedling leaves. Cauline leaves opposite, ternate, leaflets dentate. Flowers polygamous, bisexual or unisexual, in many-flowered panicle-like cymes or rarely solitary. Sepals four, erect, often blue or purple. Stamens pilose. Pollen pantoporate, rarely tricolpate.

Distribution: Comprising seven species, *C. heracleifolia*, *C. psilandra* Kitag., *C. stans* Siebold & Zucc., *C. tubulosa* Turcz., *C. tsugetorum* Ohwi, *C. speciosa* (Makino) Makino, and *C. urticifolia* Nakai ex Kitag., distributed in East Asia.

Etymology: The Chinese name of this section is derived from the Chinese name of its type species, *C. heracleifolia*, which is “大叶铁线莲” (Dà yè tiěxiànlián).

Notes: Sect. *Tubulosae*, endemic to East Asia, exhibits highly distinctive morphology within the genus, characterized by its unique combination of erect herbaceous or subshrubby habit, trifoliolate leaves, tubular-campanulate flowers with erect (often blue) sepals, and conspicuously pubescent stamen filaments. This suite of morphological traits clearly differentiates sect. *Tubulosae* from its close relative sect. *Clematis* (sensu Tamura, 1995), which is characterized by climbing habit, 1–2-pinnately or 1–2-ternately compound leaves, white flowers with spreading sepals, and glabrous filaments. However, frequent interspecific hybridization occurs between these two groups. Our previous studies showed that some F1 hybrids (such as *C. pinnata* and *C. tartarinowii* Maxim.) have even been mistakenly described as “species” in the past, contributing to taxonomic confusion within the genus (Lyu et al., 2021, 2023). Unlike hybrid-origin species, F1 hybrid individuals fail to form monophyletic groups in both chloroplast and nuclear genomic trees (Lyu et al., 2021). In contrast, stabilized hybrid species establish consistent mating populations. While their individuals may not cluster together in plastid phylogenies due to differential organelle inheritance, they typically form cohesive clades with proper phylogenetic positioning in nuclear gene trees (Lyu et al., 2023). For this reason, we excluded tested F1 hybrids from our analysis and also exclude subsect. *Pinnatae* (W.T. Wang) W.T. Wang (sensu Wang and Li, 2005b; Wang and Xie, 2007) from sect. *Tubulosae*.

8. ***Clematis* sect. *Clematis*.** Type: *C. vitalba* L. (钝萼铁线莲组)

= *Clematis* sect. *Lasiantha* Tamura in Sci. Rep. Osaka Univ. 16 (2): 34. 1967. Type: *C. lasiantha* Nutt.

Woody vines. Type I seedling leaves. Cauline leaves opposite, once or twice ternate or pinnate, leaflets often dentate. Flowers bisexual or unisexual, often small. Cymes often many-flowered, often arising from leaf axils of hornotinous branch, or rarely from axillary buds of old branch. Sepals four, spreading, rarely ascending or erect. Stamens glabrous, or rarely hairy. Pollen tricolpate.

Distribution: Comprising ca. 67 species widely distributed in Eurasia, Africa, and Americas.

Etymology: The inclusion of *C. vitalba* L. (the type species of the genus) within this clade necessitates its designation as sect. *Clematis*. This section's Chinese name is based on *C. peterae* Hand.-Mazz. (钝萼铁线莲, Dùn'è tièxiànlián), a characteristic species widely distributed across China.

Notes: This section represents another large and compositionally complex lineage within *Clematis*, exhibiting remarkable morphological diversity and challenging taxonomic boundaries. The inclusion of New World dioecious species (often placed into sect. *Aspidanthera* and sect. *Lasiantha*, sensu Tamura, 1995) in this section is morphologically justified by their striking similarity to Eurasian sect. *Clematis* members. The taxonomically controversial species *C. brevipes* and *C. williamsii* also cluster within this clade, resolving long-standing uncertainties about their phylogenetic placement (Miikeda et al., 2006; Huang et al., 2024).

However, the inclusion of *Clematis tosaensis* Makino and *C. japonica* Thunb. within this clade presents a surprising result. Morphologically, these species have traditionally been classified in sect. *Bebaeanthera* (sensu Tamura, 1995), characterized by their erect sepals, campanulate flowers, and pubescent stamens, features that distinguish them from other members of this section. Nonetheless, both plastid and nuclear gene trees consistently found them closely related to species from sect. *Clematis*. Based on this result, we provisionally reassign these species to sect. *Clematis*, while acknowledging that further studies are needed to

fully resolve this discrepancy and understand the evolutionary implications of their morphological variations.

9. ***Clematis* sect. *Aethusifoliae*** (Tamura) Serov in Bot. Zhurn. 73 (12): 1739. 1988. = *Clematis* ser. *Aethusifoliae* Tamura in Acta Phytotax. Geobot. 16: 79. 1956. Type: *C. aethusifolia* Turcz. (芹叶铁线莲组)

Perennial herbaceous vines. Type I seedling leaves (Cheng et al., 2016). Cauline leaves opposite, 1–2–4 pinnatisect, margin entire or 1-denticulate. Flowers bisexual. Cymes axillary or terminal. Flowers yellow, bell-shaped. Sepals four, erect. Stamen filaments sparsely puberulous. Pollen tricolpate.

Distribution: Comprising only one species, distributed in northern and northeastern Asia.

Etymology: The Chinese name of this section is derived from its type species, *Clematis aethusifolia*, known as “芹叶铁线莲” (Qínyè tièxiànlián).

Notes: Traditionally, *Clematis aethusifolia* has been classified in sect. *Campanella* (sensu Tamura, 1995) based on floral characteristics, despite its markedly divergent leaf morphology and geographical distribution compared to other members of this section. Previous molecular phylogenetic studies have consistently revealed its isolated phylogenetic position within the genus (Xie et al., 2011; He et al., 2021). Our current study demonstrates that *C. aethusifolia* forms a sister group relationship with the circum-boreal sect. *Atragene*, which is distributed across Eurasia and North America (Yang et al., 2009). However, given the profound morphological disparity between *C. aethusifolia* and sect. *Atragene* species, we propose recognizing it as a distinct monotypic section (sect. *Aethusifoliae*), reflecting its unique evolutionary trajectory within *Clematis*.

10. ***Clematis* sect. *Atragene*** (L.) DC., Reg. Veg. Syst. Nat. 1: 165. 1818. = *Atragene* L., Sp. Pl. 1: 542. 1753. Type (chosen by Britton and Brown, 1913; affirmed by Green in Sprague et al., Nom. Prop. Brit. Bot. 163. 1929): *Atragene alpina* L. [= *C. alpina* (L.) Mill.]. (长瓣铁线莲组)

Woody vines. Type I seedling leaves. Cauline leaves opposite, ternate or biternate, leaflets dentate. Flowers bisexual, solitary and terminal, often arising from an axillary bud of old branch. Sepals ascending. Stamen filaments pubescent. Outer stamens sterile, petal-like. Pollen tricolpate.

Distribution: Comprising ca. nine species, distributed in cold and temperate areas of the northern hemisphere.

Etymology: This section's Chinese name is based on *Clematis macropetala* Ledeb. (长瓣铁线莲, Chángbàn tièxiànlián), a characteristic species widely distributed in northern China.

Notes: The circumscription of this section aligns with traditional taxonomic concepts (Tamura, 1995; Wang and Li, 2005b; Yang et al., 2009), encompassing extremely cold-tolerant *Clematis* species distributed across northern Eurasia and North America (Pringle, 1971) that are characterized by their petaloid staminodes.

11. ***Clematis* sect. *Songoricae*** (Serov) J.M. Xiao & L. Xie, stat. nov. = *Clematis* ser. *Songoricae* Serov in Bot. Zhurn. 73 (12): 1739. 1988. Type: *C. songorica* Bunge (准噶尔铁线莲组)

Shrubs or subshrubs. Seedling unknown. Cauline leaves opposite, simple, linear to lanceolate, sparsely denticulate to entire. Flowers bisexual. Cymes terminal. Flowers white. Sepals 4–6, spreading. Stamens glabrous. Pollen tricolpate.

Distribution: One species, distributed in central Asia.

Etymology: The Chinese name of this section is derived from its type species *Clematis songorica*, known as “准噶尔铁线莲” (Zhūngǎ’ěr tiěxiànlíán) in Chinese.

Notes: *Clematis songorica* represents another taxonomically challenging species, exhibiting conflicting morphological and molecular phylogenetic signals that have long complicated its systematic placement (Tamura, 1995; Wang and Li, 2005b; He et al., 2021). Due to its shrubby growth habit, *C. songorica* has conventionally been classified within sect. *Fruticella* (Chang et al., 1980; Snoeijer, 1992; Tamura, 1995; Johnson, 1997; Grey-Wilson, 2000). However, Wang and Li (2005a, b) argued that the floral morphology of *C. songorica* aligns more closely with that of sect. *Clematis*, thereby challenging its traditional placement in sect. *Fruticella*.

Subsequent molecular phylogenetic analyses have revealed a complex evolutionary history of *Clematis songorica*, demonstrating incongruent placements between plastid and nrDNA trees (He et al., 2021). Although clearly not allied with sect. *Clematis*, the species shows discordant phylogenetic signals, being embedded within sect. *Fruticella* (sensu Wang and Li, 2005a, b) in plastid genome phylogenies while forming a sister clade to this section in nrDNA trees. Our expanded sampling of shrubby *Clematis* species and subsequent phylogenomic analysis using single-copy orthologous genes extracted from transcriptome data revealed that the entire sect. *Fruticella* originated through hybridization, with *C. songorica* being identified as one of its parental species (He, 2022). These findings not only clarify the controversial systematic position of *C. songorica* but also provide novel insights into the hybrid relationship among *Clematis* lineages. Our nuclear SNP data consistently place *C. songorica* outside of sect. *Fruticella*, corroborating findings from our previous studies. Based on comprehensive evidence from both current and prior studies (He et al., 2021; He, 2022), we propose recognizing *C. songorica* at the sectional rank as sect. *Songoricae*, reflecting its phylogenetically distinct position within the genus.

12. ***Clematis* sect. *Fruticella*** Tamura in Sci. Rep. Osaka Univ. 16 (2): 34. 1967. Type: *C. fruticosa* Turcz. (灌木铁线莲组)

Small shrubs. Type I seedling. Cauline leaves opposite, simple, undivided or pinnatilobed to pinnatisect, at margin dentate or entire. Flowers bisexual, in terminal cymes, rarely solitarily arising from the apexes of axillary branchlets. Flowers yellow. Sepals ascending, narrowly dilated along margin after anthesis. Stamen filaments glabrous. Pollen tricolpate.

Distribution: Comprising five species, *Clematis fruticosa*, *C. viridis*, *C. nannophylla*, *C. canescens* (Turcz.) W.T. Wang & M.C. Chang, and *C. tomentella*, distributed in the Loess Plateau, Gobi Desert of Mongolia, and the dry-hot valleys of the northeastern parts of the Hengduan Mountains.

Etymology: The Chinese name of this section is derived from its type species *Clematis fruticosa*, known as “灌木铁线莲” (Guànmù tiěxiànlíán) in Chinese.

Notes: Based on the aforementioned previous studies we have discussed, we now circumscribe *Clematis* sect. *Fruticella* in accordance with Wang and Li (2005a, b), which comprises erect shrubby taxa distributed in northern China characterized by yellow campanulate flowers and glabrous stamens.

13. ***Clematis* sect. *Bebaeanthera*** Edgew. in Trans. Linn. Soc. London 20: 25. 1851. $\equiv$ *Clematis* subsect. *Bebaeanthera* (Edgew.) W.T. Wang in Acta Phytotax. Sin. 39: 16. 2001. Type: *C. barbellata* Edgew. (西南铁线莲组)

$\equiv$ *Clematis* ser. *Pogonandrae* W.T. Wang in Acta Phytotax. Sin. 36 (2): 170. 1998. Type: *C. pogonandra* Maxim.

Woody vines. Type I seedling. Cauline leaves opposite, ternate or biternate, at margin entire or dentate. Flowers bisexual, yellow or purple, bell-shaped, solitary arising from leaf axils of hornotinous branch or from axillary bud of old branch, pedicellate only, with pedunculate and bracts wanting. Sepals four, erect, thick. Filaments and anthers hairy. Pollen tricolpate.

Distribution: About six species, distributed in Hengduan Mountains and Eastern Himalayas.

Etymology: The Chinese name of this section is derived from *C. pseudopogonandra* (西南铁线莲, Xīnán tiěxiànlíán), a common species distributed in southwestern China.

Notes: In this study, our circumscription of sect. *Bebaeanthera* differs from previous taxonomic treatment (Tamura, 1995) by excluding the Japanese species *C. japonica* and *C. tosaensis*, while incorporating ser. *Pogonandrae* W.T. Wang as defined by Wang (1998). The species in this section are primarily characterized by their axillary solitary flowers and pubescent anthers.

14. ***Clematis* sect. *Otophorae*** J.M. Xiao & L. Xie sect. nov. Type: *C. otophora* Franch. ex Finet & Gagnep. (宽柄铁线莲组)

Diagnosis: Sect. *Otophorae* resembles sect. *Bebaeanthera* but can be distinguished by its leaf morphology and inflorescence structure. Sect. *Otophorae* often has simple or ternate serrate leaves, produces 1–3-flowered cymes with bracts and peduncles from young branches, whereas sect. *Bebaeanthera* often bears ternate to biternate leaves with entire or dentate margin, and solitary flowers from leaf axils of hornotinous branch or from axillary bud of old branch.

Woody vines. Type I seedling. Cauline leaves opposite, simple or ternate, at margin often serrate. Flowers bisexual, yellow, bell-shaped. Cymes axillary, 1–3 flowered, bibracteate. Sepals four, erect, thick. Filaments and anthers hairy. Pollen tricolpate.

Distribution: Comprising five species, *C. yui*, *C. otophora* Franch. ex Finet & Gagnep., *C. pseudootophora* M.Y. Fang, *C. kweichowensis* C. Pei, and *C. repens*, distributed in southeastern, central, and southwestern China.

Etymology: This section's scientific name, sect. *Otophorae*, originates from the species epithet of its type “otophora.” The Chinese name of this section is derived from its type species *C. otophora*, known as “宽柄铁线莲” (Kuānbǐng tiěxiànlíán) in Chinese.

Notes: This group of plants closely resembles sect. *Bebaeanthera* in sharing identical floral characteristics, particularly the presence of pubescent filaments and anthers. Traditionally, this group was classified within sect. *Campanella* (sensu Tamura, 1995). However, multiple molecular phylogenetic studies (Xie et al., 2011; He et al., 2021; Xiao et al., 2022) have consistently demonstrated that these plants, with pubescent filaments and anthers, are phylogenetically distant from sect. *Campanella* members, which only exhibit pubescent filaments. Our earlier phylogenomic study utilizing transcriptome data and the HyDe method revealed that

sect. *Fruticella* originated through hybridization between *C. songorica* and the ancestor of sect. *Otophorae* (He, 2022). This genomic evidence explains both the morphological intermediacy of sect. *Fruticella* taxa and their phylogenetic discordance in prior analyses. In this study, we formally recognize this group of plants as a new section, sect. *Otophorae*.

15. **Clematis** sect. **Meclatis** (Spach) Baill., Hist. Pl. 1: 57. 1867. ≡ *Meclatis* Spach, Hist. Nat. Veg. Phan. 7: 272. 1839. Type (chosen by Tamura, 1987): *Meclatis orientalis* (L.) Spach (= *C. orientalis* L.). (黄花铁线莲组)

Woody vines, rarely dwarf shrubs. Type I seedling. Cauline leaves opposite, 1–2 ternate or pinnate, leaflets dentate or entire. Flowers bisexual, in few to many-flowered cymes, rarely solitary. Sepals four, yellow or purple, ascending. Stamen filaments hairy. Pollen tricolpate.

Distribution: Comprising ca. 14 species, distributed in central and northern China, western Asia to eastern Europe.

Etymology: This section's Chinese name is based on *Clematis intricata* (黄花铁线莲, Huánghuā tiěxiànlíán), a characteristic species in this section with a wide distribution across northern China.

Notes: The delimitation of *Clematis* sect. *Meclatis* in this study is consistent with that of Wang and Li (2005b) and Wang (2006a). This group of plants is characterized by yellow, broadly campanulate flowers and pubescent filaments. Tamura (1995) defined sect. *Meclatis* in a broader sense, including plants from the African sect. *Brachiatae* (sensu Wang, 2004b). However, the results of this study indicate that these African plants should not be classified under sect. *Meclatis*.

16. **Clematis** sect. **Insidiosae** (W.T. Wang) J.M. Xiao & L. Xie, stat. nov. ≡ *Clematis* ser. *Insidiosae* W.T. Wang in Acta Phytotax. Sin. 38 (6): 513. 2000. Type: *C. insidiosa* Baill.

Woody vines. Seedling unknown. Cauline leaves opposite, 1–3 pinnate, leaflets entire. Cymes arising from leaf axils of hornotinous branch. Flowers unisexual. Sepals of staminate flower spreading and those of pistillate flower erect. Stamen filaments glabrous. Staminodes absent in pistillate flowers. Pollen unknown.

Distribution: Comprising two species (*C. rutoides* W.T. Wang and *C. insidiosa*), distributed in Madagascar.

Etymology: Since this plant group is endemic to Madagascar with no natural distribution in China, no Chinese name was assigned in this study.

Notes: The plants of this section are dioecious. Previously, dioecious taxa were often placed in sect. *Aspidanthera* (Tamura, 1995; Wang and Li, 2005b). However, multiple molecular phylogenetic studies (Xie et al., 2011; Lehtonen et al., 2016; He et al., 2021) have shown that these dioecious groups, distributed across the Americas, Australia, and Africa, form a polyphyletic assemblage and cannot be classified into a single section. Wang (2000, 2004a) and Wang and Li (2005b) established subsect. *Insidiosae* W.T. Wang under sect. *Aspidanthera*, which included the two Madagascar-endemic species of Clade 16 (Fig. 3) in this study. In our molecular phylogeny, these two species form a sister clade to the narrowly defined sect. *Cheiroopsis* distributed in southern Eurasia. Given that these two species are dioecious with sexually dimorphic flowers and are endemic to Madagascar, markedly distinct from the narrowly defined sect. *Cheiroopsis*, we elevate subsect. *Insidiosae* to sectional rank (sect. *Insidiosae*).

17. **Clematis** sect. **Cheiroopsis** DC., Reg. Veg. Syst. Nat. 1: 162. 1818. ≡ *Cheiroopsis* (DC.) Bercht. & J. Presl, Prir. Rostlin 1 Ranuncul. 11. 1823. ≡ *Clematis* subsect. *Cirrhosae* Prantl in

Bot. Jahrb. 9: 259. 1888. Type (chosen by Tamura, 1955): *C. cirrhosa* L. (合苞铁线莲组)

Woody vines. Type I seedling leaves. Cauline leaves opposite, simple to ternate, at margin dentate. Flowers bisexual. Cymes involucrate, rarely bibracteate, 1–3 flowered arising from axillary bud of old branch. Sepals four, petaloid, nearly erect. Stamens glabrous. Pollen tricolpate.

Distribution: Comprising two species (*C. cirrhosa* and *C. napaulensis*), distributed in southwestern China, the Himalayas and Mediterranean region.

Etymology: The Chinese name of this section derives from its only species distributed in China, *C. napaulensis*, known as “合苞铁线莲” (Hébāo tiěxiànlíán).

Notes: Molecular phylogenetic studies (Xie et al., 2011; He et al., 2021; Xiao et al., 2022, and this study) revealed that the traditionally defined sect. *Cheiroopsis* is polyphyletic (Tamura, 1995; Wang, 2002; Wang and Li, 2005b). After removing unrelated species, only two species remain in sect. *Cheiroopsis*: the type species of this section, *C. cirrhosa* (distributed in Europe), and *C. napaulensis* (found in the Himalayan region).

18. **Clematis** sect. **Acerifoliae** (W.T. Wang) J.M. Xiao & L. Xie, stat. nov. ≡ *Clematis* subsect. *Acerifoliae* W.T. Wang in Acta Phytotax. Sin. 36 (2): 161. 1998. Type: *C. acerifolia* Maxim. (槭叶铁线莲组)

Small shrubs. Type I seedling. Cauline leaves opposite. Leaves simple, palmately 5-lobed or not lobed, at margin dentate. Flowers bisexual, with leaves arising from an axillary bud of uppermost leaf. Flowers white or pink. Sepals 5–8, spreading. Stamen filaments glabrous. Pollen tricolpate.

Distribution: Comprising two species (*Clematis acerifolia* and *C. elobata*), distributed on the cliffs of southern and northern Taihang Mountains.

Etymology: The Chinese name of this section is derived from its type species, *Clematis acerifolia*, known as “槭叶铁线莲” (Qìyè tiěxiànlíán).

Notes: This section includes two cliff-dwelling species endemic to the Taihang Mountains in northern China: *C. acerifolia* and *C. elobata*. Although morphologically similar, these species are separated by over 400 km and exhibit significant genetic divergence (Yan et al., 2016). Previous classification systems placed this group within the broadly defined sect. *Cheiroopsis* (Wang, 2002; Wang and Li, 2005b), but molecular phylogenetic studies have never supported this placement (Xie et al., 2011; He et al., 2021; Xiao et al., 2022). Given their phylogenetically isolated position within the genus, we propose recognizing them as a distinct section in this study.

19. **Clematis** sect. **Aspidanthera** Spach, Hist. Nat. Veg. Phan. 7: 283. 1839. Type: *C. aristata* R. Br. ex Ker Gawl. (单性铁线莲组)

= *Clematis* sect. *Novae-zeelandiae* M. Johnson, Klematis 159. 1997. Type: *C. paniculata* Gmelin.

Woody or herbaceous vines, rarely erect subshrubs. Type I seedling. Cauline leaves opposite, compound, rarely simple. Leaflets entire or dentate. Flowers unisexual, usually dioecious. Sepals 4–8, spreading, often white, in some species linear. Stamens glabrous, connectives distinctly projected or not projected. Staminodes present. Pollen tricolpate.

Distribution: Comprising ca. 34 species, distributed in Australia, New Zealand, and tropical Asia.

Etymology: The Chinese name of this section, “单性铁线莲组” (Dānxìng tiěxiànlíán zǔ), is derived from the dioecious nature

shared by all species within this section. The term “单性” (dānxìng) refers to their unisexual/dioecious reproductive system.

Notes: The previously defined sect. *Aspidanthera* was also a highly heterogeneous group that encompassed most dioecious taxa within the genus (Tamura, 1995; Wang, 2004a; Wang and Li, 2005b). Molecular phylogenetic studies have progressively clarified its delimitation. Our results demonstrate that the dioecious taxa distributed in Australia and tropical Asia–Pacific islands form a monophyletic clade. Based on these findings, we propose a revised circumscription of sect. *Aspidanthera* in this study.

20. ***Clematis* sect. *Naraveliopsis*** Hand.-Mazz. in Acta Hort. Gotob. 13: 219. 1939. Type (chosen by Eichler, 1958): *C. smilacifolia* Wall. (菝葜叶铁线莲组)

Woody vines. Type I seedling. Cauline leaves opposite, simple, ternate, pinnate, biternate or bipinnate. Leaflets entire, rarely dentate. Cymes axillary, rarely terminal. Flowers bisexual, rarely unisexual. Sepals spreading, often thick. Stamens glabrous, rarely hairy, sometimes outermost stamens transformed into linear staminodes, anthers with conspicuous connective projections or rarely with minutely projection. Pollen tricolpate or pantocolpate.

Distribution: Comprising ca. 13 species, distributed in tropical Asia.

Etymology: The Chinese name of this section is derived from its type species, *Clematis smilacifolia* Wall., known as “菝葜叶铁线莲” (Bāqiā yè tièxiànlíán).

Notes: Sect. *Naraveliopsis* represents one of the few tropical-distributed groups within *Clematis*. Our study generally maintains the traditional circumscription of sect. *Naraveliopsis* (Wang and Li, 2005b; Wang, 2006b), with the exception of transferring *C. menglaensis* back to the resurrected sect. *Naraveliocarpa*. However, *C. akoensis* (distributed in Taiwan, China), previously classified in sect. *Clematis* (sensu Wang and Li, 2005b), was resolved within sect. *Naraveliopsis* in our analysis. Geographically and in terms of vegetative morphology (particularly leaf characters), *C. akoensis* shows remarkable similarity to *C. tashiroi* Maxim. (another species in sect. *Naraveliopsis* in Taiwan, China). However, its floral morphology differs significantly from sect. *Naraveliopsis* members, notably lacking the prominently protruding connectives on the anthers, a key diagnostic feature of this section. Given the congruent placement of *C. akoensis* in both plastid and nuclear gene trees, we provisionally assign it to sect. *Naraveliopsis* in this study, pending further investigation.

21. ***Clematis* sect. *Viticella*** (Dill. ex Moench) DC., Reg. Veg. Syst. Nat. 1: 160. 1818. ≡ *Viticella* Dill. ex Moench, Method. 296. 1794. Type: *Viticella deltoidea* Moench (= *C. viticella* L.) (铁线莲组)

= *Clematis* sect. *Viorna* (Pers.) Prantl in Bot. Jahrb. Syst. 9(3): 258. 1888, p.p. ≡ *Atragene* subg. *Viorna* Pers. in Syn. Pl. 2: 98. 1807. ≡ *Viorna* (Pers.) Reichenb., Handb. Nat. Pfl.-Syst. 277. 1837. ≡ *Clematis* subg. *Viorna* (Pers.) Gray, Syn. Fl. N. Amer. 1 (1): 5. 1895. Type: *C. viorna* L.

Woody or perennial herbaceous vines, or rarely erect herb. Type II seedling. Cauline leaves opposite, simple, once or twice ternate or pinnate, leaflets entire. Flowers bisexual, sometimes large, in axillary cymes or solitary, terminal. Sepals 4–8, spreading or erect, usually dilated. Stamen filaments glabrous or hairy, rarely transformed into petaloid staminodes. Achenes large, compressed. Pollen pantoporate or tricolpate.

Distribution: Comprising ca. 35 species, distributed in temperate zones of the northern hemisphere.

Etymology: The Chinese name of this section follows the conventional use in Flora Reipublicae Popularis Sinicae (Fang, 1980) and Wang (2007).

Notes: The sect. *Viticella* as circumscribed in this study encompasses not only the traditionally defined members but also the subg. *Viorna* sensu Tamura (1995). These two groups share several vegetative characteristics, including frequently fleshy fibrous roots, type II seedlings, often entire leaves, and large flattened achenes. However, they differ markedly in floral morphology: the traditional sect. *Viticella* exhibits spreading sepals and glabrous filaments, whereas subg. *Viorna* (sensu Tamura, 1995) is characterized by erect sepals and pubescent filaments. Molecular phylogenetic studies have demonstrated that these two groups form a clade but without clear separation. The Eurasian-distributed species of subg. *Viorna* are nested within sect. *Viticella* (which is exclusively Eurasian in distribution). Therefore, we propose to merge them into a single section in this study.

22. ***Clematis* sect. *Flammula*** DC., Reg. Veg. Syst. Nat. 1: 133, 1818. Type: *C. flammula* L. (威灵仙组)

= *Clematis* sect. *Angustifoliae* (Tamura) Serov in Bot. Zhurn. 73 (12): 1740. 1988. ≡ *Clematis* subsect. *Angustifoliae* Tamura in Sci. Rep. Osaka Univ. 4: 55. 1955. Type: *C. hexapetala* Pall.

= *Clematis* sect. *Pterocarpa* Tamura in Sci. Rep. Osaka Univ. 4: 50. 1955. Type: *C. brachyura* Maxim.

Woody or herbaceous vines, rarely erect herb or shrubs. Type II seedling. Cauline leaves opposite, once or twice ternate or pinnate, leaflets entire. Flowers bisexual. Cymes terminal or axillary, few to many-flowered. Sepals often white, spreading. Stamen filaments glabrous. Pollen tricolpate.

Distribution: Comprising ca. 37 species, distributed in Eurasia.

Etymology: The Chinese name of this section is derived from *Clematis chinensis* (威灵仙, Wēilíngxiān) in this section, a renowned medicinal species native to China.

Notes: This represents another section in the genus *Clematis* with relatively complex composition. Some monotypic sections, including sect. *Angustifoliae* (sensu Tamura, 1995) and sect. *Pterocarpa*, were nested within this clade. Additionally, *C. lancifolia*, a species with previously controversial taxonomic placement (He et al., 2021), also clustered within this group. Nevertheless, the group exhibits well-defined shared characteristics: Type II seedling morphology, entire leaves, often small white flowers with spreading sepals, and glabrous filaments.

Undetermined groups: sect. *Atrageneopsis* (Wang and Li, 2005b) is a monotypic section (*C. robertsiana* Aitch. & Hemsl.) distributed in Pakistan. It is morphologically similar to sect. *Atragene* but without petal-like staminodes. This study did not acquire the sample of this species. For these reasons, we recorded this section as an undetermined group here.

5. Conclusions

Clematis is a large, taxonomically difficult genus in the buttercup family with a worldwide distribution. Many different classification systems have been published during the long taxonomic history of *Clematis*. Previous molecular phylogenetic studies faced challenges due to inadequate sampling and insufficient information from limited molecular markers, resulting in many unresolved phylogenetic relationships within the genus. This study utilized nuclear SNPs, complete plastid genome sequences, and nrITS datasets, implementing an expanded sampling strategy to reconstruct the phylogeny of *Clematis*. Although the plastid

genome and nrITS data did not generate a well-resolved phylogeny of *Clematis*, the nuclear SNP data provide a phylogenetic framework with higher resolution and that better corresponds to morphological classifications.

The analysis of nuclear SNP data produced a well-resolved phylogenetic tree for the genus, consisting of 22 clearly defined clades that correspond to 22 sections. Most of the subgenera and sections established by previous taxonomists are not fully supported by our phylogenetic analysis. The analysis of morphological character evolution showed that different states of these characters often originated independently multiple times. This study presents a revised infrageneric classification for the genus, with the 22 recognized sections reflecting the new phylogenetic framework, of which three (sect. *Atragene*, sect. *Fruticella* sensu Wang and Li, 2005b, sect. *Meclatis* sensu Wang and Li, 2005b) are consistent with the previous classification, two (sect. *Dela-vayanae* and sect. *Otophorae*) are herein newly described, ten (sect. *Pseudanemone*, sect. *Tubulosae*, sect. *Bebaeanthera*, sect. *Clematis*, sect. *Cheiroopsis*, sect. *Aspidanthera*, sect. *Viticella*, sect. *Flammula*, sect. *Naravelia* and sect. *Naraveliopsis*) have been re-circumscribed, three (sect. *Anemoniflora*, sect. *Naraveliocarpa*, and sect. *Aethusifoliae*) have been reinstated, and four, including sect. *Acerifoliae* (stat. nov.), sect. *Insidiosae* (stat. nov.), sect. *Songoricaricae* (stat. nov.), and sect. *Potaniniana* (stat. nov.), are newly combined. This study proposes, for the first time, a new framework for sectional classification based on phylogenetic analysis, the results of which will provide important references for further in-depth studies on horticulture, breeding, and systematics of *Clematis*.

CRedit authorship contribution statement

Jia-Min Xiao: Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Ming-Yang Li:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Jun Wen:** Writing – review & editing. **Radosław Puchałka:** Writing – review & editing. **Huan-Yu Wu:** Investigation. **Wen-He Li:** Investigation. **Zi-Yi Li:** Investigation. **Bo-Wen Liu:** Investigation. **Yue-Xin Luo:** Investigation. **Ru-Dan Lyu:** Investigation. **Le-Le Lin:** Investigation, **Jian He:** Methodology, Conceptualization, Supervision. **Jin Cheng:** Resources. **Lei Xie:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Liang-Qian Li:** Resources, Conceptualization.

Data availability statement

The sequenced data have been deposited in the NCBI SRA database under BioProject PRJNA1226155. Sequence alignments, phylogenetic trees and reference genome of this study are openly available in the Science Data Bank at <https://doi.org/10.57760/sciencedb.j00143.00118>.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pld.2025.11.004>.

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