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Chloroplast phylogenomics further supports the placement of *Hyssopus* within *Dracocephalum* (Lamiaceae: Nepetinae)

Ibrokhimjon Ergashov[1], Farkhodjon Mingboev[1,2], Dilfuza Akhmedova[3], Mohidabonu Masodiqova[3], Murodjon Holikulov[3], Giyos Buxorov[4], Elyor Ortikov[5], Malika Shavkatjonova[6], Ziyoviddin Yusupov[*1]

1 Institute of Botany, Academy of Sciences of Uzbekistan, Tashkent, Uzbekistan
2 University of Chinese Academy of Sciences, Beijing, China
3 Faculty of Natural Sciences, Fergana State University, Fergana, Uzbekistan
4 Turan University, Karshi, Uzbekistan
5 Faculty of Humanities and Pedagogy, Turan International University, Namangan, Uzbekistan
6 Jizzakh State Pedagogical University, Jizzakh, Uzbekistan

I. Ergashov: https://orcid.org/0000-0002-0991-1076
F. Mingboev: https://orcid.org/0009-0005-6285-1091
D. Akhmedova: https://orcid.org/0009-0001-6158-2516
M. Masodiqova: https://orcid.org/0009-0000-1703-1848
M. Holikulov: https://orcid.org/0009-0000-0881-2319
G. Buxorov: https://orcid.org/orcid.org/0009-0000-7540-9896
E. Ortiqov: https://orcid.org/0000-0002-1677-3273
Z. Yusupov: https://orcid.org/0000-0003-2278-542X

Corresponding author: Ziyoviddin Yusupov
E-mail: yusupov@mail.kib.ac.cn

Abstract

Background and aims – *Dracocephalum nuratavicum*, *D. komarovii*, and *D. seravschanicum* are narrowly distributed species from Uzbekistan that have not previously been included in plastome-based phylogenetic studies of *Dracocephalum*. This study aimed to assemble and compare their complete chloroplast genomes and to test the placement of *Hyssopus* within *Dracocephalum*.

Material and methods – Complete chloroplast genomes were generated for three Uzbek species using high-throughput sequencing. Comparative plastome analyses were carried out using accessions representing *Dracocephalum* and related taxa, and phylogenetic relationships were reconstructed from complete chloroplast genome sequences with maximum likelihood analyses.

Key results – The plastomes ranged from 149,819 to 151,181 base pairs and showed the typical quadripartite structure with 133 genes. Overall genome structure and gene content were highly conserved across the sampled taxa. Several highly variable regions were detected, especially

in the intervals *psbD–rps16* and *trnR*-ACG–*rrn16*. Phylogenetic analyses placed *D. nuratavicum*, *D. komarovii*, and *D. seravschanicum* within well-supported *Dracocephalum* lineages. *Hyssopus officinalis* and *H. cuspidatus* were nested within the *Dracocephalum* clade.

Conclusion – The newly generated plastomes provide the first genomic evidence for the phylogenetic placement of three poorly studied Uzbek species and further support the inclusion of *Hyssopus* within *Dracocephalum*. These results improve the taxonomic framework of the group and provide useful genomic resources for future systematic and conservation studies.

Keywords: chloroplast genome, comparative genomics, *Dracocephalum*, *Hyssopus*, Lamiaceae, molecular markers, phylogenomics, systematics, taxonomy, Uzbekistan.

INTRODUCTION

The genus *Dracocephalum L.* (Lamiaceae), commonly known as dragonhead, comprises approximately 70–80 recognized species, the majority of which are distributed across temperate Eurasia, with one species each occurring in North America and North Africa (Chen et al. 2022; Sheidai et al. 2024). These herbaceous or subshrub plants exhibit notable morphological diversity and occupy a broad range of ecological habitats, including alpine meadows, rocky slopes, and steppe-desert zones (Chen et al. 2022; Abdullaeva et al. 2019).

Central Asia, particularly Uzbekistan represents a center of species richness and endemism for the genus, with 14 species currently recorded, including *Dracocephalum nuratavicum*, a narrowly endemic taxon confined to the Nuratau Mountains (Abdullaeva et al. 2019). Although its presence has been botanically documented, *D. nuratavicum* has remained genetically uncharacterized, and its evolutionary position within the genus is unresolved.

Several *Dracocephalum* species, such as *D. moldavica*, *D. kotschyi*, and *D. heterophyllum*, are valued for their aromatic and medicinal properties and have demonstrated antimicrobial, antioxidant, and pharmacological potential. Their applications range from traditional medicine to food preservation and pharmaceutical formulations (Șimea et al. 2024; Koohdar and Sheidai 2019; Sonboli et al. 2011; Fu et al. 2022).

With the advent of next-generation sequencing, plastome-based analyses have become a key tool in plant systematics. Chloroplast genomes typically exhibit a conserved quadripartite structure—comprising a large single-copy (LSC) region, a small single-copy (SSC) region, and two inverted repeats (IRs)—and encode core genes involved in photosynthesis and gene expression (Ergashov et al. 2026a). Due to their uniparental inheritance, low recombination rates, and moderate sequence divergence, plastomes are widely used in studies of phylogeny, population genetics, and molecular taxonomy (Huang et al. 2020; Nyamgerel et al. 2025; Zhang et al. 2024; Fu et al. 2022; Ergashov et al. 2025b; Alieva et al. 2025; Dekhkonov et al. 2025; Ergashov et al. 2026b).

Complete plastome sequences are now available for several *Dracocephalum* species, including *D. moldavica* (Huang et al. 2020), *D. ruyschiana* (Nyamgerel et al. 2025), *D. rupestre* (Han et al. 2023), *D. argunense* and *D. integrifolium* (Zhang et al. 2024), and *D. heterophyllum* (Fu et al. 2022). These studies have revealed high structural conservation, while also identifying informative lineage-specific variations in simple sequence repeats (SSRs), codon usage, and hypervariable loci such as *ycf1*, *ycf2*, and *trnT–psbD* (Fu et al. 2022; Huang et al. 2020; Ergashov et al. 2025a; Ergashov et al. 2026c).

Phylogenetic reconstructions based on plastid genomes have also highlighted the non-monophyly of *Dracocephalum* unless it includes the genera *Hyssopus* and *Lallemantia*, both of which are embedded within the broader *Dracocephalum* clade according to nuclear and plastid data (Chen et al. 2022; Koohdar and Sheidai 2019). The genus is hypothesized to have originated in Central and West Asia and southern Siberia, with subsequent dispersals into the Qinghai-Tibetan Plateau (QTP) during the Pliocene, likely driven by climatic aridification and tectonic uplift (Chen et al. 2022; Sheidai et al. 2024; Rakhmataliev et al. 2025).

Despite the expanding genomic database, species such as *D. nuratavicum*, *D. komarovii*, and *D. seravschanicum* remain unsequenced and have been excluded from phylogenomic comparisons. In this study, we present the first complete chloroplast genomes of *D. nuratavicum*, *D. komarovii*, and *D. seravschanicum*, assembled using high-throughput sequencing technologies (Fig. 1).

In addition, we conducted a comparative plastome analysis of 29 accessions representing 14 congeneric species to assess gene content, sequence divergence, and genome structure.

Furthermore, we reconstructed a plastome-based phylogenetic tree to determine the evolutionary positions of *D. nuratavicum*, *D. komarovii*, and *D. seravschanicum* within the genus *Dracocephalum*, and to examine broader phylogenetic relationships.

By providing novel genomic data for narrowly distributed endemic species, this study enhances our understanding of plastome evolution, species diversification, and taxonomy in the genus *Dracocephalum*, particularly within the floristically rich yet genomically understudied regions of Central Asia.

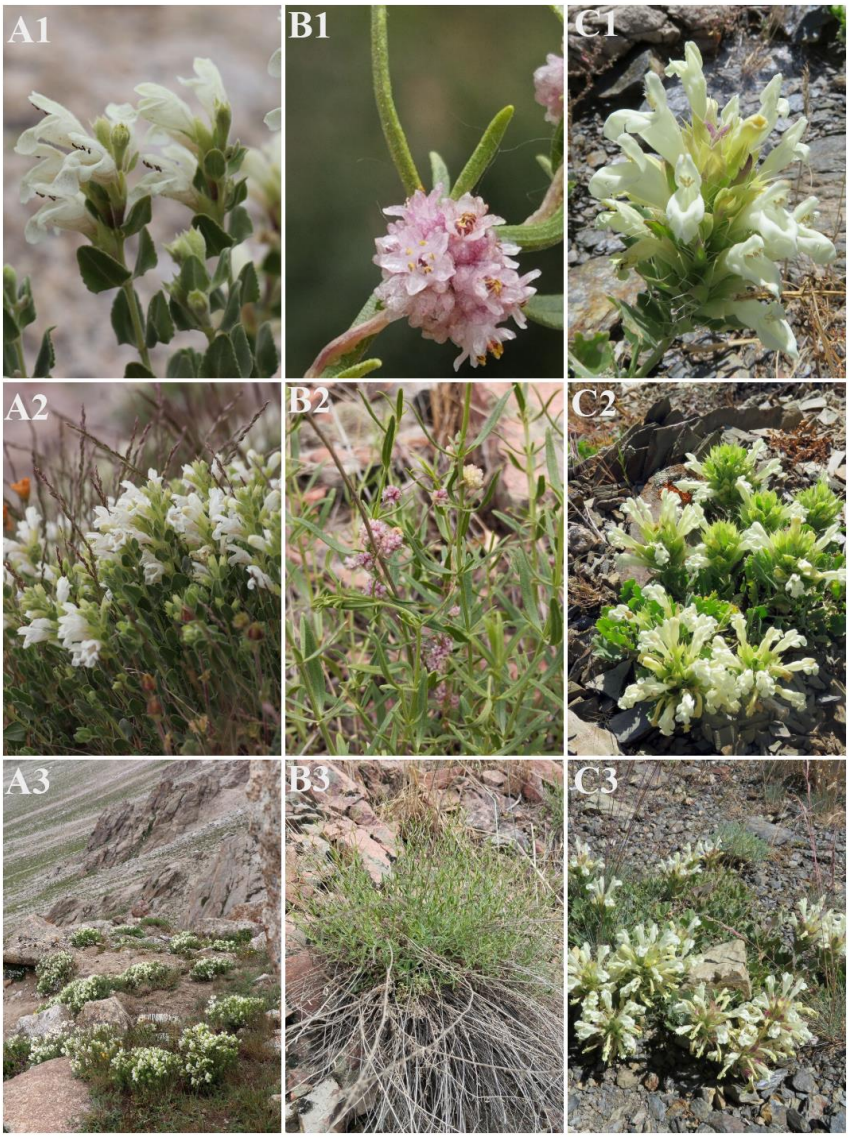

Figure 1. Flowering individuals and natural habitats of three *Dracocephalum* species in Uzbekistan. (A1–A3) *Dracocephalum komarovii*—flowering plants (background: flowering Chamaenerion angustifolium and fruiting Carex tianschanica). Ugam–Chatkal National Park, Maidantal Range, upper Tekeshsai Valley, Tekesh Glacier moraine, Tashkent Region, Uzbekistan (photo by Natalia Beshko). (B1–B3) *Dracocephalum seravschanicum* —flowering plants. Ohangaron District, Tashkent Region, Uzbekistan (photo by Boburbek Karimov). (C1–C3) *Dracocephalum nuratavicum* —flowering plants. Nuratau Range, Nurata Nature Reserve, Khayatsai tract, rocky slope, Uzbekistan (photo by Natalia Beshko).

MATERIAL AND METHODS

Fresh leaf samples of *D. nuratavicum*, *D. komarovii*, and *D. seravschanicum* were collected from wild populations in their natural habitats in Jizzakh Region, Ohangaron District of Tashkent Region, and the Ugam–Chatkal National Park (Maidantal Range, upper Tekeshsai Valley) in Tashkent Region, Uzbekistan, in June 2024.

Species identification was carried out by N. Beshko and B. Karimov at the National Herbarium of Uzbekistan, and representative voucher specimens were deposited in the TASH Herbarium.

The collected materials were immediately dried in silica gel and stored at room temperature until DNA extraction.

Genomic DNA was isolated from leaf tissues using a modified cetyltrimethylammonium bromide (CTAB) method (Doyle and Doyle 1987), adhering to the manufacturer's protocol. High-throughput sequencing was performed using the Illumina NovaSeq 6000 platform, generating 150 bp paired-end reads. Raw reads were filtered to remove low-quality reads and adapter sequences using Trimmomatic v0.39 (Bolger et al. 2014). Clean reads were mapped and assembled de novo using GetOrganelle v1.7.5 pipeline (Jin et al. 2020). The assembled chloroplast genomes were annotated with Geneious Prime v2025.1.2 software (Tillich et al. 2017), using the chloroplast genomes of *D. ruyschiana* (PQ963003) as a reference. Annotations then were manually checked in Geneious Prime v2025.1.2 to ensure accuracy. The final annotated chloroplast genome maps were visualized using OGDRAW (Greiner et al. 2019).

The boundaries of the large single copy (LSC), small single copy (SSC), and inverted repeat (IR) regions across the chloroplast genomes of 12 Dracocephalum species were identified and compared. Boundary shifts at junctions JLB(LSC/IRb), JSB (SSC/IRb), JSA (SSC/IRa), and JLA (IRa/LSC) were determined and visualized. These comparative analyses were carried out using IR scope (Amiryousefi et al. 2018) and manual alignment in Geneious Prime v2025.1.2 (Fig. 3). To identify nucleotide variability across the chloroplast genomes, multiple sequence alignments of complete genomes were performed using MAFFT v7.471 (Katoh and Standley, 2013). The aligned sequences were used to compute nucleotide diversity (π) using DnaSP v6.12.03 (Rozas et al. 2017). A sliding window analysis was conducted with a window length of 800 bp and a step size of 200 bp to detect highly variable regions. These hypervariable regions are potential molecular markers for phylogenetic and barcoding studies.

Phylogenetic relationships were reconstructed using complete chloroplast genome sequences of *Dracocephalum* and closely related genera (*Nepeta*, *Lycopus*) within the subtribe Nepetinae. The inclusion of *Hyssopus* species within *Dracocephalum* was critically tested with this framework, based on recent plastid phylogenomic evidence (Zhang et al. 2021). Sequence alignment was performed using MAFFT v7.520 (Katoh and Standley 2013). Phylogenetic trees were constructed using RAxML v8.2.12 (Stamatakis 2014) under the GTRGAMMA substitution model with 1,000 bootstrap replicates to the support for the inferred relationship. *Lycopus lucidus* and *Nepeta hemsleyana* were used as outgroup taxa.

RESULTS

The complete chloroplast genomes of 14 species of the genus *Dracocephalum*, including the reclassified *Hyssopus cuspidatus H. officinalis*, *H. seravschanicum*, and *H. komarovii* were successfully assembled and analyzed. These genomes exhibited the typical quadripartite structure, consisting of a large single-copy (LSC) region, a small single-copy (SSC) region, and two inverted repeats (IRa and IRb) (Fig. 2). The overall genome sizes ranged from 149,819 bp in *D. moldavica* (MT457747) to 151,181 bp in *D. rupestre* (NC_068682), placing them within the expected range for Lamiaceae plastomes. The LSC region varied between 81,527 and 82,581 bp, while the SSC ranged from 17,160 to 17,730 bp. The IR regions were highly conserved, generally spanning 25,318–25,636 bp each (Fig. 3). All plastid genomes analyzed contained a total of 133 genes, comprising 88 protein-coding genes, 37 transfer RNA (tRNA)

genes, and 8 ribosomal RNA (rRNA) genes. The gene content and structural arrangement were largely conserved among the species. As expected, gene duplications were primarily found within the inverted repeat (IR) regions, particularly involving the rRNA operons (*rrn16*, *rrn23*, *rrn4.5*, and *rrn5*) and several protein-coding genes such as *rpl2*, *ndhB*, and *ycf2* (Table S1).

The sliding window analysis of nucleotide diversity (π) across the chloroplast genomes of *Dracocephalum* species revealed that π values ranged from 0.001 to 0.05 (Fig. 4). Most genomic regions exhibited a high level of variability, with π values generally not exceeding 0.045.

Relatively high diversity peaks were detected in the regions between 5,000–8,000 bp and 28,000–29,000 bp. In addition, a pronounced and continuous increase in nucleotide diversity was observed between approximately 113,000 bp and 134,000 bp, where π values exceeded 0.04 and reached a maximum of 0.045. However, low variability was recorded in the regions spanning 89,000–111,000 bp and 136,000–157,000 bp.

Relatively high nucleotide diversity was observed in the *psbD–rps16*, *psbM–psbC*, *ycf3–ndhK*, *ycf4–psbJ*, *psaC–ndhA*, and *trnR-ACG–rrn16* regions. In particular, a sharp increase in nucleotide diversity was detected in the *psbD–rps16* and *trnR-ACG–rrn16* intervals, indicating that these regions are highly polymorphic. In contrast, π values declined sharply and stabilized at low levels in the central and terminal regions of the genome.

Overall, these results indicate that certain intergenic spacers and gene regions within the chloroplast genome exhibit high variability, highlighting their potential importance for the development of molecular markers and for phylogenetic studies (Fig. 4).

A maximum likelihood phylogenetic tree was generated based on the complete chloroplast genome sequences of *Dracocephalum* and its closely related genera (Table S2). The resulting topology divided the taxa into two well-supported major clades. Clade 1 included three accessions of *D. rupestre* and two accessions each of *D. psammophilum*, *D. cuspidatus*, *D. seravschanicum* and *D. officinalis*, while *Lycopus lucidus* and several *Nepeta hemsleyana* accessions formed an outgroup. Clade 2 contained the remaining *Dracocephalum* species, including *D. ruyschiana*, forming the distinct clade, two accessions of *D. taliense*, tree accessions of *D. tanguticum*, *D. nuratavicum*, *D. komarovii*, three accessions of *D. heterophyllum*, *D. fragile*, two accessions of. *D. palmatum*, and four accessions of *D. moldavica*. Notably, *D. nuratavicum* was positioned within Clade 2 forming the distinct subclade, clustering with four accessions of *D. heterophyllum*. Bootstrap support values for most internal nodes were high (100), with one branch of accessions belonging to *D. rupestre* receiving minumum support, indicating overall strong resolution across the plastome-based phylogeny.

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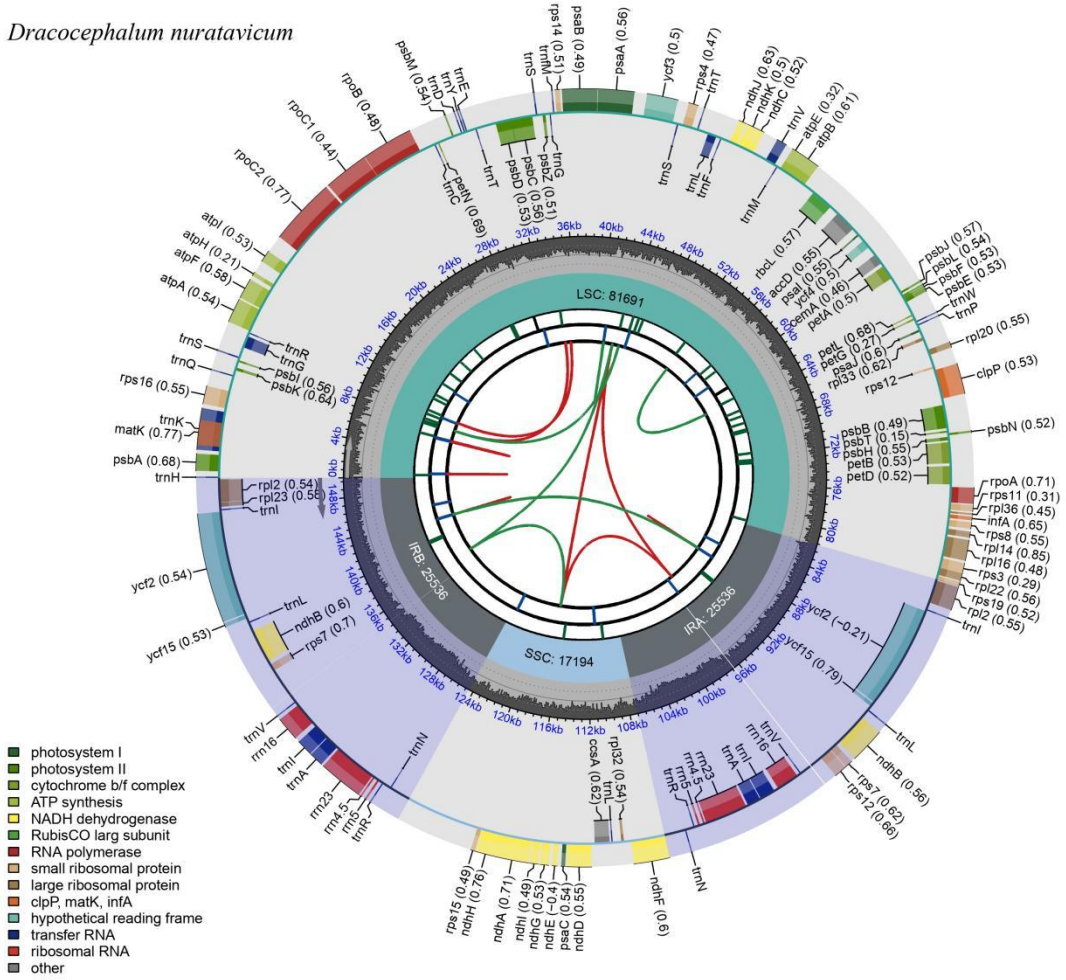

Figure 2. Chloroplast genome map of species within the genus *Dracocephalum*. Genes located within the circle are transcribed in a clockwise direction, while those outside the circle are transcribed counterclockwise. The inner dark grey circle indicates the GC content, while the light grey circle represents the AT content.

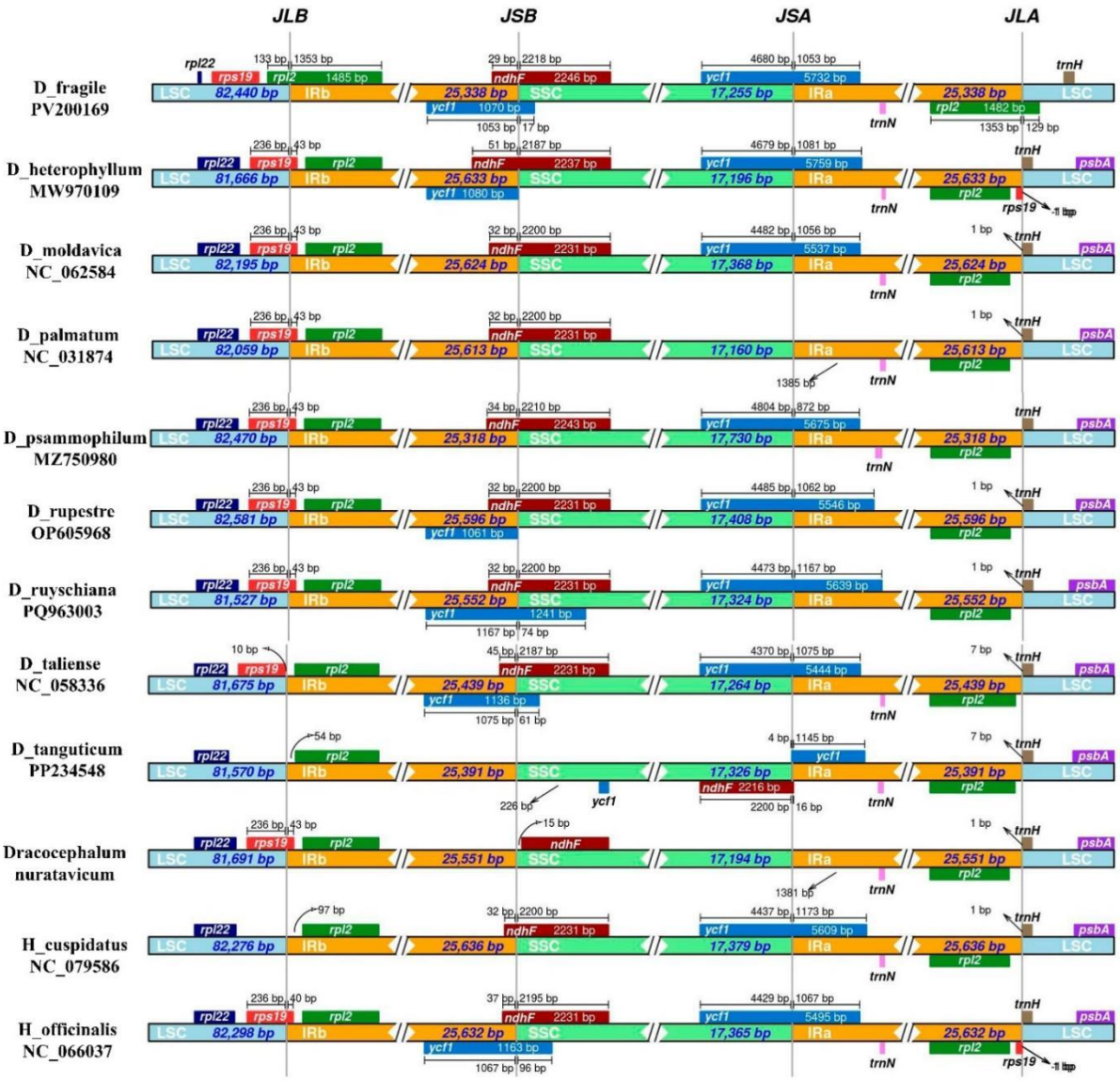

Figure 3. Comparative analysis of the LSC, IR and SSC boundary regions in the 17 chloroplast genomes of the genus *Dracocephalum*. The JLB represents the junction of LSC and IRb, JSB indicates the junction of SSC and IRb, JSA denotes the junction of SSC and IRa, and JLA signifies the junction of LSC and IRa.

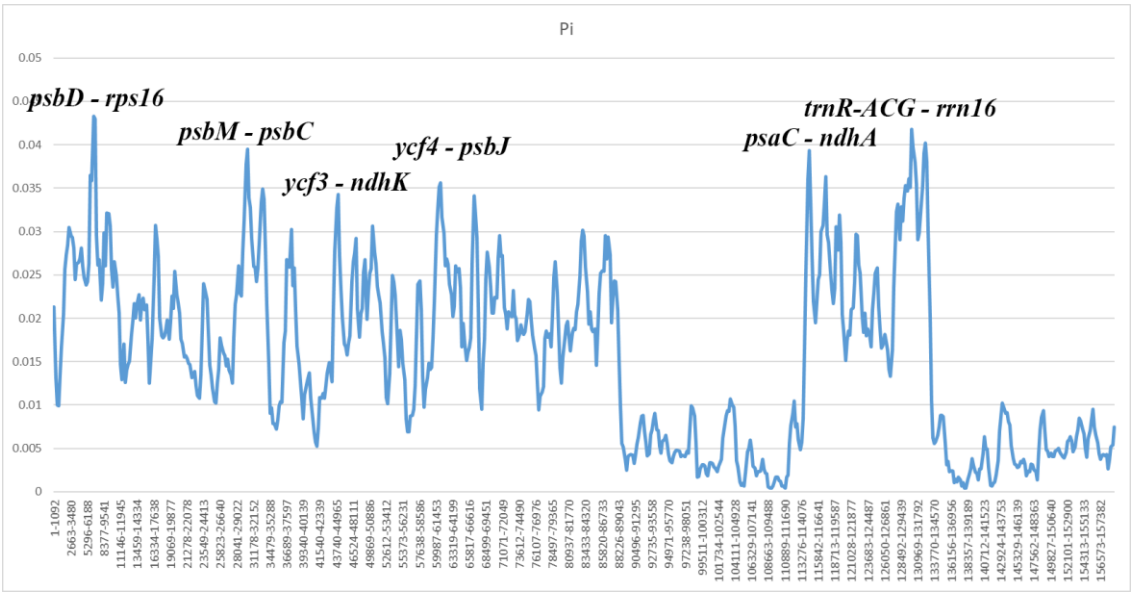

Figure 4. Nucleotide variability (Pi value) across the *Dracocephalum* genus genomes, displayed using a sliding window approach (window size: 800 bp, step size: 200 bp).

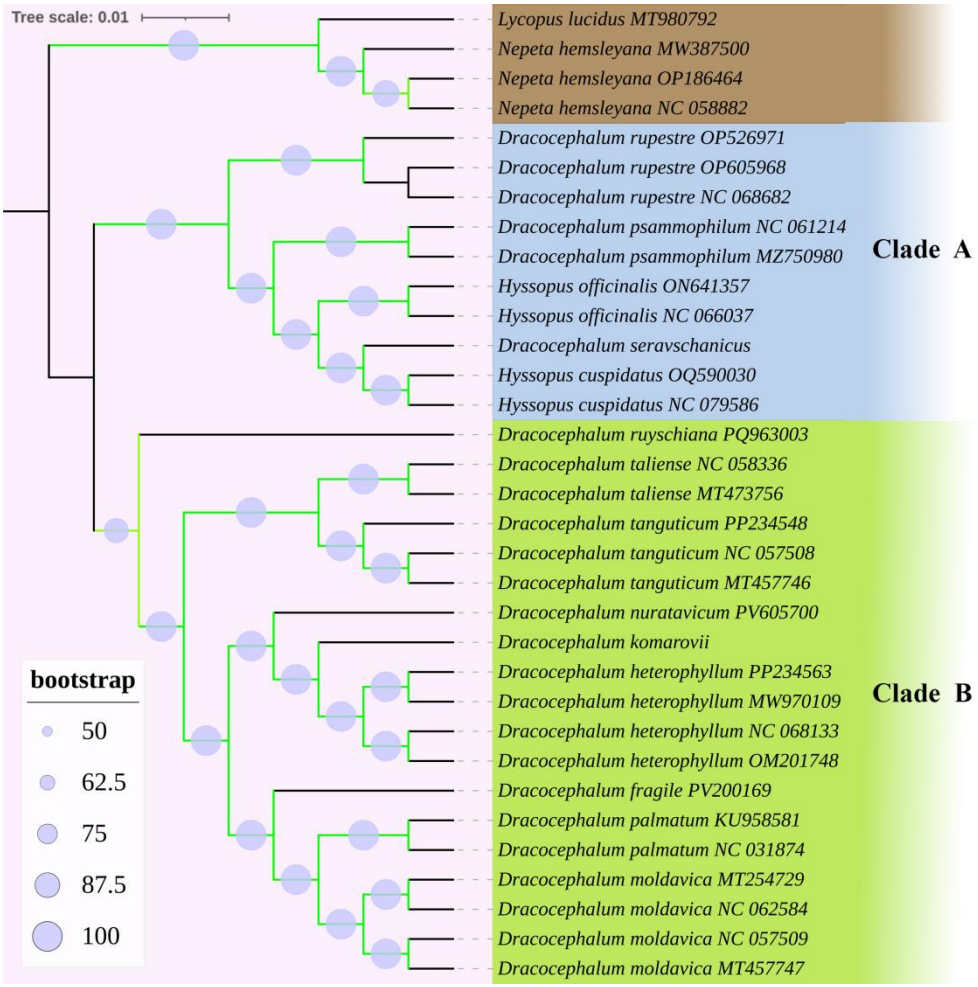

Figure 5. Phylogenetic tree of *Dracocephalum* species constructed from the complete chloroplast genome using maximum likelihood (ML) analysis. Bootstrap support values are shown at the nodes.

DISCUSSION

The present study offers new insights into plastome evolution and phylogenetic relationships within the genus *Dracocephalum*, highlighted by the first chloroplast genome characterization of *D. nuratavicum, D. komarovii*, and *D. seravschanicum*, a narrowly endemic species from Uzbekistan. The plastome of *D. nuratavicum, D. komarovii*, and *D. seravschanicum* exhibit the typical quadripartite organization seen across Lamiaceae, and shares conserved gene content and structural features with previously published genomes of *D. moldavica*, *D. ruyschiana*, *D. heterophyllum*, *D. palmatum*, and *D. argunense* (Nyamgerel et al. 2025; Fu et al. 2022; Zhang et al. 2024; Han et al. 2023).

Plastome length among sampled species ranged from 149,819 to 151,181 bp, primarily reflecting differences in the lengths of the large single-copy (LSC) and small single-copy (SSC) regions, while the inverted repeat (IR) regions remained comparatively conserved. These observations align with previous findings in *Dracocephalum*, where IR expansion or contraction contributes minimally to genome size variation (Fu et al. 2022, Zhang et al. 2024). All examined plastomes encoded 88 protein-coding genes, 37 tRNA genes, and 8 *rRNA* genes, supporting prior reports of plastome stability across the genus (Huang et al. 2020; Fu et al. 2022; Yusupov et al. 2022; Tojiboeva et al. 2025; Nikitina et al. 2025).

Sliding window analysis of nucleotide diversity revealed several regions of elevated sequence variation, with the highest levels observed within the SSC region. Variable loci included genes such as *ycf1*, *rps15*, *ndhH*, *ndhA*, *ndhI*, *ndhG*, *ndhE*, *psaC*, *ndhD*, *ccsA*, and *ndhF*, as well as adjacent intergenic spacers. The most pronounced diversity peak was located in the intergenic spacer between *trnL-UAG* and *ndhF*, a hotspot previously reported in other Lamiaceae plastomes (Fu et al. 2022; Simea et al. 2024; Khassanov et al. 2023; Kurbaniyazova et al. 2026). These hypervariable regions may serve as promising targets for *DNA* barcoding, species delimitation, and population-level studies within *Dracocephalum*.

To assess both intra- and interspecific variation, we included multiple accessions for several species particularly *D. heterophyllum, D. moldavica*, and *D. rupestre*. This allowed us to examine phylogenetic consistency within species and to detect potential cryptic diversity or population divergence. Most species formed monophyletic clades with high bootstrap support, reflecting strong plastome-level genetic stability. Notably, four accessions of *D. heterophyllum* clustered tightly with *D. nuratavicum*, forming a distinct and well-supported subclade within the second major lineage. This suggests a close evolutionary relationship between the two species, possibly reflecting shared ecological adaptation or geographic origin (Chen et al. 2022). In contrast, accessions of *D. rupestre* exhibited some topological variation, with one branch receiving lower support. This discordance could reflect population-level divergence, recent speciation, or limited resolution of plastid markers in closely related taxa (Fu et al. 2022; Nyamgerel et al. 2025).

Given the historical debate over the taxonomic circumscription of *Dracocephalum*, we included plastomes of *Hyssopus officinalis* and *H. cuspidatus* to test their phylogenetic positions. Both taxa were nested within the primary *Dracocephalum* clade, reinforcing previous suggestions that *Hyssopus* is not phylogenetically distinct from *Dracocephalum* (Chen et al. 2022; Koohdar and Sheidai 2019). Unfortunately, due to the unavailability of complete plastome sequences for *Lallemantia* species in GenBank and other repositories, we

were unable to include this genus in our plastome dataset. However, prior studies based on nuclear and plastid markers have consistently demonstrated that *Dracocephalum*, *Hyssopus*, and *Lallemantia* form a single monophyletic lineage (Chen et al. 2022; Sheidai et al. 2024). As such, there is increasing support for treating *Hyssopus* and *Lallemantia* as taxonomic synonyms under *Dracocephalum*, probably this might require formal revision following plastome-level confirmation.

Finally, *D. nuratavicum, D. komarovii*, and *D. seravschanicum* were consistently placed within Clade 2**.** *D. nuratavicum* and *D. komarovii* formed a closely related phylogenetic group with *D. heterophyllum*, whereas *D. seravschanicum* showed a close evolutionary relationship with *Hyssopus cuspidatus*. These relationships were reliably supported by high bootstrap values.

These results provide the first genomic evidence for determining the taxonomic positions of poorly studied endemic species from Central Asia.

The inclusion of these species in the present study enriched the developing plastome database of the genus *Dracocephalum*, enhanced our understanding of evolutionary diversity and phylogeographic patterns, and made an important contribution to the development of future conservation strategies for the region's floristic endemism.

CONCLUSION

This study presents the first complete chloroplast genomes of *D. nuratavicum*, *D. komarovii*, and *D. seravschanicum*, narrowly endemic species from Uzbekistan, and expands the comparative plastome dataset for the genus *Dracocephalum*. The plastomes of *D. nuratavicum, D. komarovii*, and *D. seravschanicum* exhibit conserved structural organization and gene content consistent with other *Dracocephalum* species, yet contain lineage-specific variations in highly divergent regions of the SSC, particularly between *psbD–rps16* and *trnR-ACG–rrn16*. Sliding window analysis identified these regions as potential hotspots for marker development.

Phylogenetic analysis based on whole chloroplast genomes resolved *D. nuratavicum, D. komarovii*, and *D. seravschanicum* within a well-supported clade alongside multiple accessions of *D. heterophyllum* and *Hyssopus cuspidatus*, confirming their close evolutionary affinity. The inclusion of multiple accessions per species further reinforced plastome-level genetic stability within most lineages and highlighted minor topological variability in *D. rupestre*. The incorporation of *Hyssopus* species into the plastome tree supports previous findings that *Hyssopus* is embedded within *Dracocephalum* s.l., however, conclusions regarding monophyly remain tentative due to the lack of complete plastome data for *Lallemantia*.

Overall, this work strengthens the molecular framework for species delimitation, phylogenetic inference, and taxonomic revision within *Dracocephalum*, and contributes valuable genomic resources for future evolutionary and conservation studies of the Central Asian flora.

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Table S1. Annotated list of genes present in the chloroplast genomes of *Dracocephalum* species.

Category	Group of Gene	Gene Name
Gene for photosynthesis	Subunits of photosystem I	*psaA*, *psaB*, *psaC*, *psaJ*, *psaI*
	Subunits of photosystem II	*psbA*, *psbB*, *psbC*, *psbD*, *psbE*, *psbF*, *psbH*, *psbI*, *psbJ*, *psbK*, *psbL*, *psbM*, *psbN*, *psbT*, *psbZ*
	Subunits of NADH dehydrogenase	*ndhA*, *ndhB* (2×), *ndhC*, *ndhD*, *ndhE*, *ndhF*, *ndhG*, *ndhH*, *ndhI*, *ndhJ*, *ndhK*
	Subunits of cytochrome b/f complex	*petA*, *petB*, *petD*
	Subunits of ATP synthase	*atpA*, *atpB*, *atpE*, *atpF*[1], *atpH*, *atpI*
	Large subunit of rubisco	*rbcL*
Self-replication	Proteins of large ribosomal subunit	*rpl2*[1] (2×), *rpl14*, *rpl16*[1], *rpl20*, *rpl22*, *rpl23*, *rpl32*, *rpl33*, *rpl36*
	Proteins of small ribosomal subunit	*rps2*, *rps3*, *rps4*, *rps7* (2×), *rps8*, *rps11*, *rps12* (2×), *rps14*, *rps15*, *rps16*[1], *rps18*, *rps19*
	Ribosomal RNA	*rrn4.5* (2×), *rrn5* (2×), *rrn16* (2×), *rrn23* (2×)
	DNA-dependent RNA polymerase	*rpoA*, *rpoB*, *rpoC1*[1], *rpoC2*
	Transfer RNA	*trnA-UGC*[1] (2×), *trnC-GCA*, *trnD-GUC*, *trnE-UUC*, *trnF-GAA*, *trnG-GCC*, *trnG-UCC*[1], *trnH-GUG*, *trnI-CAU* (2×), *trnI-GAU*[1] (2×), *trnK-UUU*[1],

		trnL-CAA (2×), trnL-UAG, trnL-UAA[1]*, trnM-CAU, trnN-GUU (2×), trnP-UGG, trnQ-UUG, trnR-ACG (2×), trnR-UCU, trnS-GCU, trnS-GGA, trnS-UGA, trnT-CGU, trnT-UGU, trnV-GAC (2×), trnV-UAC*[1]*, trnW-CCA, trnY-GUA*
Biosynthesis	Maturase	*matK*
	Protease	*clpP*[2]
	Envelope membrane protein	*cemA*
	Subunit Acetyl-CoA carboxylase	*accD*
	C-type cytochrome synthesis gene	*ccsA*
	Translation initiation factor	*infA*
Unknown	Conserved open reading frame	*ycf1 (2×), ycf2 (2×), ycf3*[2]*, ycf4, ycf15 (2×)*

Note: [1] Gene containing a single intron; [2] Gene containing two introns; (2×) indicates duplicated genes.

Table S2. NCBI accession numbers of the species of the genus *Dracocephalum* and outgroups. New sequenced accessions was given in bold in this study. NCBI numbers in bold means newly sequenced samples for this study.

№	Species name	NCBI numbers
1	*Dracocephalum fragile*	PV200169
2	*Dracocephalum heterophyllum*	MW970109
3	*Dracocephalum heterophyllum*	NC_068133
4	*Dracocephalum heterophyllum*	OM201748
5	*Dracocephalum heterophyllum*	PP234563
6	*Dracocephalum moldavica*	MT254729
7	*Dracocephalum moldavica*	MT457747
8	*Dracocephalum moldavica*	NC_057509
9	*Dracocephalum moldavica*	NC_062584
10	*Dracocephalum palmatum*	KU958581
11	*Dracocephalum palmatu*	NC_031874
12	*Dracocephalum psammophilum*	MZ750980
13	*Dracocephalum psammophilum*	NC_061214
14	*Dracocephalum rupestre*	OP526971
15	*Dracocephalum rupestre*	NC_068682

16	*Dracocephalum rupestre*	OP526971
17	*Dracocephalum ruyschiana*	OP605968
18	*Dracocephalum taliense*	MT473756
19	*Dracocephalum taliense*	NC_058336
20	*Dracocephalum tanguticum*	MT457746
21	*Dracocephalum tanguticum*	NC_057508
22	*Dracocephalum tanguticum*	PP234548
23	***Dracocephalum nuratavicum***	**PV605700**
24	***Dracocephalum komarovii***	**PX928789**
25	***Dracocephalum seravschanicum***	**PX929666**
26	*Hyssopus cuspidatus*	NC_079586
27	*Hyssopus cuspidatus*	OQ590030
28	*Hyssopus officinalis*	NC_066037
29	*Hyssopus officinalis*	ON641357
30	*Lycopus lucidus*	MT980792
31	*Nepeta hemsleyana*	MW387500
32	*Nepeta hemsleyana*	NC_058882
33	*Nepeta hemsleyana*	OP186464