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RESEARCH ARTICLE

Complete chloroplast genomes and phylogenetic positions of species of the genus *Ziziphora* (*Lamiaceae*) from Uzbekistan

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Abstract. Species of the genus *Ziziphora* (*Lamiaceae*) are valuable medicinal and economically significant plants in the flora of Uzbekistan. Due to morphological similarities among species, accurate identification has been challenging. This study presents the first comprehensive analysis of the complete chloroplast genomes of species of *Ziziphora* native to Uzbekistan. Comparative analysis revealed genome size variation, conserved circular structures, and differences in nucleotide compositions. Each genome contains 131 genes, 86 of which are protein-coding and mainly associated with photosynthesis and plastid function. A relatively low GC (~37.8%) content is characteristic of chloroplast DNA compared to nuclear genomes of *Ziziphora* species. Phylogenetic analyses based on whole chloroplast genomes and selected variable markers positioned *Ziziphora* species as a distinct monophyletic lineage within the tribe *Mentheae* of the subfamily *Nepetoideae*. The results support the use of chloroplast DNA as a reliable marker in molecular phylogenetic taxonomy and evolutionary studies. This research contributes essential insights into the genetic structure, evolutionary history, and taxonomic placement of taxa of *Ziziphora*, providing a valuable foundation for conservation strategies.

Keywords: chloroplast genome, genetic structure, genome size variation, *Lamiaceae*, molecular taxonomy, phylogenetic analysis, taxonomic placement, *Ziziphora*

Introduction

The genus *Ziziphora* L. (*Lamiaceae* Martinov, subfamily *Nepetoideae* Burnett, tribe *Mentheae* Dumort.) comprises aromatic and medicinal plants of significant therapeutic and economic value, particularly prominent in the traditional medicine systems of Central Asia and the Middle East. Globally, the genus currently encompasses 14 species (POWO, 2025–onward), which predominantly thrive in open, xerophytic environments. *Ziziphora* species are resilient to arid and semi-arid conditions, making them adaptable to diverse ecological zones. Central Asia, particularly Uzbekistan, serves as a

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biodiversity hotspot and a probable center of origin for this genus, with seven species identified within the region: *Z. capitata* L., *Z. clinopodioides* Lam., *Z. pamiroalaica* Juz. (≡ *Z. clinopodioides* subsp. *pamiroalaica* (Juz.) Sennikov & Lazkov), *Z. persica* Bunge, *Z. suffruticosa* Pazij & Vved., *Z. tenuior* L., and *Z. pedicellata* Pazij & Vved. These species are distributed mainly across the foothill and mountainous zones of the Tien Shan, Pamir-Alai, and Western Tien Shan ranges, predominantly inhabiting dry, rocky slopes and montane environments.

Despite their ecological importance, accurate identification of *Ziziphora* species has been a considerable challenge due to their morphological similarities. Traditionally, species identification relied heavily on external traits and characters, such as leaf morphology, inflorescence structures, calyx shape, and even habitat preferences (Vvedensky, 1961; Tulyaganova, 1978). However, these methods often lead to misidentifications, as many species exhibit similar characters and their variability.

To overcome traditional taxonomic challenges, molecular techniques, particularly phylogenetic analysis using DNA nucleotide sequences, have been employed as more reliable methods for precise species identification. This approach is essential for accurately distinguishing species, supporting biodiversity conservation, and ensuring the sustainable use of these plants in various applications (Mirzayeva, 2023; Alieva et al., 2025; Dekhkonov et al., 2025; Ergashov et al., 2025). Moreover, the selection of appropriate molecular markers is crucial for advancing our understanding of relationships and evolutionary history of *Ziziphora* species.

Species of *Ziziphora* are components of the Irano-Turanian floristic region, which is known for its rich diversity and endemism, particularly among selected taxonomic groups of aromatic and medicinal plants. The genus' adaptability spans from mesic conditions in the western part of its total geographic range to more extreme xeric environments in Central Asia. Phylogenetic studies suggest that the diversification of *Ziziphora* is linked to orogenic events and climatic changes during the Miocene and Pliocene epochs of the Neogene. For instance, *Z. clinopodioides* (or a similar species) has been traced back to about 5–10 million years ago in the mountainous regions of northern Iran (Tabaripour et al., 2020).

In addition to their ecological and taxonomic significance, *Ziziphora* species have substantial economic and therapeutic value. They are widely utilized in traditional medicine for their sedative, antiseptic, carminative, and expectorant properties (Zhaparkulova, 2022; Abduraimov et al., 2023). *Ziziphora* essential oils, extracted from the aerial parts of these plants, contain bioactive compounds such as pulegone (40–89%), limonene, menthone, and caryophyllene, which exhibit various biological activities, including antibacterial, antifungal, and insecticidal effects (Olennikov, 2016; Šmejkal et al., 2016; Mohammadhosseini, 2017; Azimi et al., 2021). These oils hold great promise for pharmaceutical, industrial, and agricultural applications.

This study focuses on the comparative analysis of chloroplast genomes of the *Ziziphora* species found in Uzbekistan. We examine the genome size and structure, nucleotide diversity, and construct a phylogenetic tree based on chloroplast genome data to clarify species relationships and enhance our understanding of the genus' evolutionary history. Our findings will contribute to the ongoing efforts to accurately identify *Ziziphora* species and to explore their potential for conservation and industrial use.

Materials and Methods

Sampling

The objects of this research were five key species: *Ziziphora clinopodioides*, *Z. pamiroalaica*, *Z. pedicellata*, *Z. persica*, and *Z. tenuior* collected in Uzbekistan (Table 1, Fig. 1). Voucher herbarium specimens have been deposited at the National Herbarium of Uzbekistan (TASH), offering a valuable resource for further studies on plant systematics, phylogeny, and molecular evolution.

DNA extraction, library construction, and genome sequencing

Leaf tissues from *Ziziphora* species were used for genomic DNA extraction, utilizing the Tiangen kit according to the protocol provided by the manufacturer. For sequencing library preparation, the NEB kit was employed, which involved fragmenting the DNA into smaller pieces of around 350 base pairs, followed by the attachment of sequencing adapters and PCR amplification. The libraries were purified after preparation, and their quality was assessed using the Agilent 5400 system, with concentrations measured to ensure optimal quality.

These high-quality libraries were then sequenced using an Illumina platform at Novogene Bioinformatics Technology Co., a specialized sequencing

Table 1. **Information on the collected specimens of species of *Ziziphora***

Species	Length (bp)	ID number in GenBank	Locality in Uzbekistan, coordinates, altitude, date
Ziziphora tenuior L.	151 610	PV116305	Surkhandarya Province, Baysun District, 38°03'03"N, 67°26'42"E, 868 m, 1 June 2024
Z. persica Bunge	151 693	PV138185	Surkhandarya Province, Hissar Ridge, 38°33'35"N, 67°36'00"E, 1476 m, 26 May 2024
Z. pedicellata Pazij & Vved.	151 750	PV138187	Southwestern Pamir-Alay, Kugitang Ridge, stony slope, 38°34'17"N, 67°54'31"E, 1291 m, 9 July 2024
Z. pamiroalaica Juz.	151 725	PV138186	Pamir-Alay, Khoja-Gurgur-ata Mountains, 38°26'20"N, 67°28'04"E, 1864 m, 11 July 2024
Z. clinopodioides Lam.	151 728	PV116304	Urgut District, Zarafshan Ridge, 39°18'05"N, 66°54'43"E, 1618 m, 2 June 2024

Fig. 1. Habits of the studied species of *Ziziphora*. A: *Z. pedicellata*; B: *Z. persica*; C: *Z. tenuior*; D: *Z. pamiroalaica*; E: *Z. clinopodioides* (photos by S. Mirzayeva)

provider. The raw sequencing data underwent quality control to remove any unreliable reads, ensuring the accuracy of the dataset. The clean, high-quality reads were assembled into chloroplast genomes using the NOVOPlasty tool (Dierckxsens et al., 2017). For gene annotation, the chloroplast genome of *Clinopodium barosmum* (W.W. Sm.) Bräuchler & Heubl (≡ *Calamintha barosma* W.W. Sm. ≡ *Micromeria barosma* (W.W. Sm.) Hand.-Mazz.) served as a reference. Geneious software was used for annotation, and the results were manually curated to confirm the correctness of start and stop codons and to accurately define the exon and intron regions of the protein-coding genes (Kearse et al., 2012). The final annotated genome sequences generated during this study are available in GenBank (https://www.ncbi.nlm.nih.gov).

Structural visualization and nucleotide diversity analysis

To visualize the architecture of the *Ziziphora* chloroplast genome, a circular map was created using OGDRAW v1.1 (Greiner et al., 2019). For the assessment of genetic variability, nucleotide diversity (Pi) was calculated using DnaSP v6.12.03 (Rozas et al., 2017), applying a sliding window approach. A window size of 600 base pairs and a 200-base pair step size were used to detect regions of higher genetic variation, which may indicate evolutionary or functional significance.

Moreover, the IR (inverted repeat) regions and other essential structural features of the genome were analyzed using the IRscope tool (Amiryousefi et al., 2018). This tool provides a graphical representation that helps evaluate the integrity and structural organization of the IR regions, aiding in the interpretation of genomic features.

Phylogenetic tree construction

To explore the evolutionary relationships, 49 complete chloroplast genomes were selected for phylogenetic analysis, including five *Ziziphora* species, as well as *Paulownia catalpifolia* T. Gong ex D.Y. Hong, *P. kawakamii* T. Itô, and *P. tomentosa* (Thunb.) Steud. (*Paulowniaceae*) as outgroup species. The genomes were aligned using the MAFFT alignment tool (Katoh, Standley, 2013), which is particularly effective for large-scale genomic datasets. The maximum likelihood ML analysis was implemented in RAxML GUI 2.0 (Edler et al., 2021) with the best-fit GTR + G model and 1000 bootstrap replicates.

To select the most appropriate nucleotide substitution model for the analysis, the Akaike Information Criterion (AIC) was applied using jModelTest v.2.1.4 (Darriba et al., 2012). Phylogenetic tree visualization was performed in FigTree v1.4.0 (Rambaut, 2012). This model selection ensures that the phylogenetic tree construction is based on the most suitable substitution model, thereby improving the accuracy and reliability of the results.

Results and Discussion

Chloroplast genomes in phylogenetic research

In recent years, chloroplast genomes have become increasingly significant in plant phylogenetic research, providing key insights into the evolutionary connections between species and genera. These genomes are crucial for understanding genetic diversity and improving the accuracy of systematic studies. In this research, we present the first in-depth analysis of the complete chloroplast genomes of *Ziziphora* species. The genomes examined range in size between 151,610 and 151,750 base pairs (bp) and follow the typical structure of plant chloroplast genomes, which includes both large and small single-copy regions (LSC and SSC), along with two inverted repeat regions (IRs).

Each of the five *Ziziphora* chloroplast genomes contains 131 genes, of which 86 are protein-coding. These genes are involved in fundamental processes, such as photosynthesis, respiration, and other key chloroplast functions. The remaining genes are responsible for encoding tRNAs and rRNAs, which are essential for the chloroplast's internal translation mechanisms. A prominent feature of these genomes is their circular shape, which is common in plant chloroplasts and supports the efficient replication and expression of genes (Fig. 2). The genome is divided into two inverted repeat regions, sharing the same sequence because of their important function in genome stability (Menéndez et al., 2023), as well as a large and a small single-copy region, each of which holds different classes of functional genes. Thus, previously researches reported, that the substitution rate in the IR regions of angiosperm plastomes is 3.7 times lower than those in SC regions, playing a critical role in genome stability (Zhu et al., 2016). These findings emphasize the evolutionary significance of IR dynamics in shaping plastid genome structure.

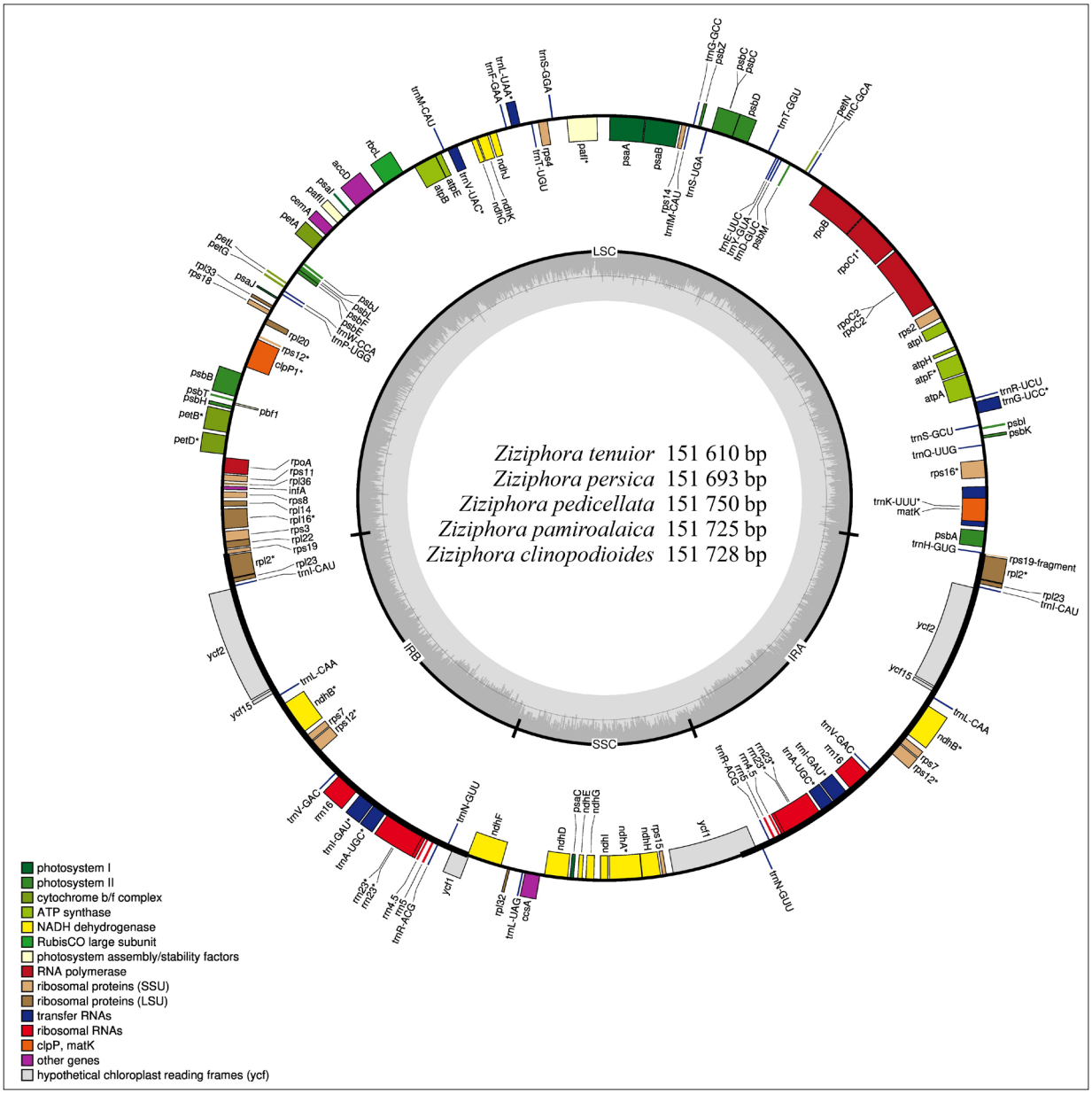

Fig. 2. Gene map of the chloroplast genome of the genus *Ziziphora*. Genes shown outside the outer circle are transcribed clockwise, and those inside are transcribed counterclockwise. Genes are color-coded according to different functional groups. Two copies of inverted repeats (IRA and IRB), a large single-copy (LSC) region, and a small single-copy (SSC) region

Gene duplications and intron-containing genes

Gene duplication is a characteristic feature in the *Ziziphora* chloroplast genomes, as reflected in the circular structure of the genomes. A total of 18 genes show duplication, including seven protein-coding genes (*ndhB*, *rpl2*, *rpl23*, *rps7*, *rps12*, *ycf2*, *ycf15*), four rRNA genes (*rrn16*, *rrn23*, *rrn4.5*, *rrn5*), and seven tRNA genes (*trnA-UGC*, *trnI-CAU*, *trnL-CAA*, *trnV-GAC*, *trnI-GAU*, *trnR-ACG*, *trnN-GUU*). These duplications ensure that the plant has sufficient quantities of essential chloroplast gene products, which are vital for energy production and metabolism (Table 2).

The GC content of the *Ziziphora* chloroplast genomes is relatively low, at 37.8%, a feature

Table 2. **Genes in the chloroplast genome of species of *Ziziphora***

Category	Group of genes	List of genes
Self-replication related genes	Large subunit of ribosome proteins	*rpl2**+, *rpl14*, *rpl16**, *rpl20*, *rpl22*, *rpl23*+, *rpl32*, *rpl33*, *rpl36*
	Small subunit of ribosomal proteins	*rps2*, *rps3*, *rps4*, *rps7*+, *rps8*, *rps11*, *rps12**+, *rps14*, *rps15*, *rps16**, *rps18*, *rps19*
	DNA-dependent RNA polymerase	*rpoA*, *rpoB*, *rpoC1**, *rpoC2*
	Ribosomal RNA	*rrn4.5*+, *rrn5*+, *rrn16*+, *rrn23*+
	Transfer RNA	*trnA-UGC**+, *trnC-GCA*, *trnD-GUC*, *trnE-UUC*, *trnF-GAA*, *trnfM-CAU*, *trnG-GCC*, *trnG-UCC**, *trnH-GUG*, *trnI-CAU*+, *trnI-GAU**+, *trnK-UUU**, *trnL-CAA*+, *trnL-UAA**, *trnL-UAG*, *trnM-CAU*, *trnN-GUU*+, *trnP-UGG*, *trnQ-UUG*, *trnR-ACG*+, *trnR-UCU*, *trnS-GCU*, *trnS-GGA*, *trnS-UGA*, *trnT-GGU*, *trnT-UGU*, *trnV-GAC*+, *trnV-UAC**, *trnW-CCA*, *trnY-GUA*
Photosynthesis related genes	Photosystem I	*psaA*, *psaB*, *psaC*, *psaI*, *psaJ*
	Photosystem I stability	*ycf3***, *ycf4*
	Photosystem II	*psbA*, *psbB*, *psbC*, *psbD*, *psbE*, *psbF*, *psbH*, *psbI*, *psbJ*, *psbK*, *psbL*, *psbM*, *psbN*, *psbT*, *psbZ*
	NADH oxidoreductase	*ndhA**, *ndhB**+, *ndhC*, *ndhD*, *ndhE*, *ndhF*, *ndhG*, *ndhH*, *ndhI*, *ndhJ*
	Cytochrome b6/f complex	*petA*, *petB**, *petD**, *petG*, *petL*, *petN*
	Cytochrome c synthesis	*ccsA*
	ATP synthase	*atpA*, *atpB*, *atpE*, *atpF**, *atpH*, *atpI*
	Rubisco	*rbcL*
Other genes	Maturase	*matK*
	Protease	*clpP***
	Envelope membrane protein	*cemA*
	Subunit acetyl-CoA-carboxylase	*accD*
	Translational initiation factor	*infA*
Unknown function genes	Conserved hypothetical chloroplast reading frames	*ycf1*, *ycf2*+, *ycf15*+
Total genes		131

* — Gene with one intron, ** — gene with two introns, + — duplicate gene.

commonly seen in chloroplast DNA. This low GC content reflects the unique functional role chloroplasts play in the plant. Furthermore, 21 intron-containing genes were identified, of which 19 genes possess a single intron. These include 13 protein-coding genes (*atpF*, *ndhA*, *petB*, *petD*, *rpl16*, *rpoC1*, *rps16*, and two copies of *ndhB*, *rpl2*, *rps12*) and six tRNA genes (*trnG-UCC*, *trnK-UUU*, *trnL-UAA*, *trnV-UAC*, and two copies each of *trnI-GAU*, *trnA-UGC*). Additionally, two genes — *clpP* and *ycf3* — contain two introns. These findings emphasize the complex structure of the *Ziziphora* chloroplast genome and the evolutionary importance of intron-containing genes.

Genetic diversity and variable regions

Nucleotide diversity (Pi) analysis revealed that the non-coding regions of the *Ziziphora* chloroplast genomes exhibit a significantly higher proportion of variable sites as compared to the coding regions (Fig. 3). Pi values in the coding regions ranged from 0 to 0.01333 (for the *trnH-GUG-psbA* region), with an average Pi value of 0.002712. Seven intergenic regions exhibited particularly high variability, with Pi values exceeding 0.01. These regions include *trnH-GUG-psbA*, *rps16-trnQ-UUG*, *rpoB-trnC-GCA*, *ndhC-trnV-UAC*, *rbcL-accD*, *psaI-ycf4*, and *ccsA-ndhD*. Furthermore, the ycf1 protein-coding gene also displayed significant variation, with a Pi value of 0.01233. These findings align with previous research (Niu et al., 2023), which highlighted the role of intergenic spacers as valuable phylogenetic markers. These variable regions are promising candidates for further phylogenetic studies, especially for exploring higher taxonomic levels within the genus *Ziziphora*.

Inverted repeat region expansion and contraction

The structural features of the inverted repeat (IR) regions in *Ziziphora* species were compared with closely related genera such as *Mentha* L., *Thymus* L., and *Nepeta* L. Overall, the IR regions exhibited a generally conserved structure, although there were some differences. In all *Ziziphora* species, the *rps19* gene is entirely located at the JLB junction (between the LSC and IRb regions), extending 43 base pairs into the IRb region, a feature also observed in *Thymus*, *Mentha*, and *Hyssopus* L. (Fig. 4).

The *ndh*F gene, which measures 2231 bp in most species (with slight variations in *Z. tenuior* and *Z. persica*), is consistently found at the JSB junction (between the small single-copy region SSC and IRb). This gene overlaps with the *ycf1* gene at the SSC/IRb boundary, a characteristic commonly observed in *Lamiaceae* (Niu et al., 2023). The overlap causes the creation of a pseudogene within the *ycf1* gene. The longest gene, *ycf1* (ranging from 5621 to 5624 bp), is located exclusively at the JSA junction (between the SSC and IRa) in all *Ziziphora* species. Moreover, the *rpl2* gene appears in both the IRa and IRb regions across all members of the subfamily *Nepetoideae*, and the *psbA* gene remains consistently located in the LSC region in all the studied species, highlighting shared structural features.

Phylogenetic analysis and taxonomic implications

Molecular taxonomic studies are essential for determining the evolutionary relationships and classification of the *Ziziphora* genus within the family *Lamiaceae*. Previous molecular studies based on ITS and *trnL-F* regions have confirmed that *Ziziphora* species form a monophyletic group (Dündar, Tümen, 2023). In this study, we constructed a detailed phylogenetic tree using the maximum likelihood (ML) method based on the complete chloroplast genomes of 46 species, representing 12 subfamilies within the family *Lamiaceae*, including *Ajugoideae*, *Callicarpoideae*, *Cymarioideae*, *Lamioideae*, *Nepetoideae*, and others. For the outgroup, species from the genus *Paulownia* (*Paulowniaceae*, also the order *Lamiales*) were chosen (Fig. 5).

Among the 49 chloroplast genomes analyzed, the total sequence length was 185,776 base pairs, which included 41,341 variable sites and 25,931 parsimony-informative sites. The phylogenetic analysis revealed the robust support for a classification of *Lamiaceae* into 12 rather distinct subfamilies, each forming a monophyletic group, with high bootstrap values confirming their evolutionary relationships (Zhao et al., 2021).

Within the subfamily *Nepetoideae*, the tribe *Mentheae,* which includes *Ziziphora* and its close relatives (*Hyssopus* L., *Mentha* L., *Nepeta* L., *Prunella* L., *Salvia* L., and *Thymus* L.), was identified as a major clade. The monophyly of the genus *Ziziphora* was confirmed, with all five species grouped together and showing close phylogenetic ties to other members of *Mentheae*, in agreement with prior studies (Bräuchler et al., 2010; Selvi et al., 2015; Nikitina et al., 2022). The phylogenetic tree produced strong support for the current taxonomic classification of *Ziziphora* species, with a maximum bootstrap value of 100%. Furthermore, the analysis indicated that the five species of *Ziziphora* (*Z. pamiroalaica*, *Z. pedicellata*, *Z. clinopodioides*, *Z. tenuior*, and *Z. persica*) share a common ancestor, emphasizing their shared evolutionary history.

Conclusion

This study represents the first comprehensive analysis of chloroplast genomes within the genus *Ziziphora*, providing in-depth insights into their structural features, comparative genomics, and phylogenetic relationships. By analyzing multiple

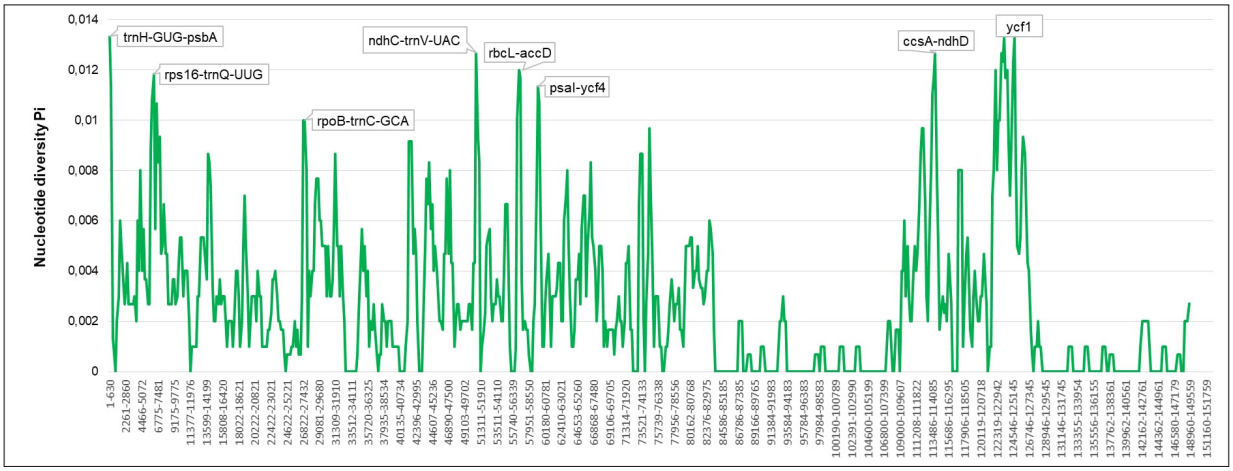

Fig. 3. Nucleotide diversity (Pi) values of the whole chloroplast genomes of five species of *Ziziphora* with a 600 bp and 200 bp sliding window. Genes with Pi values over 0.01 are annotated

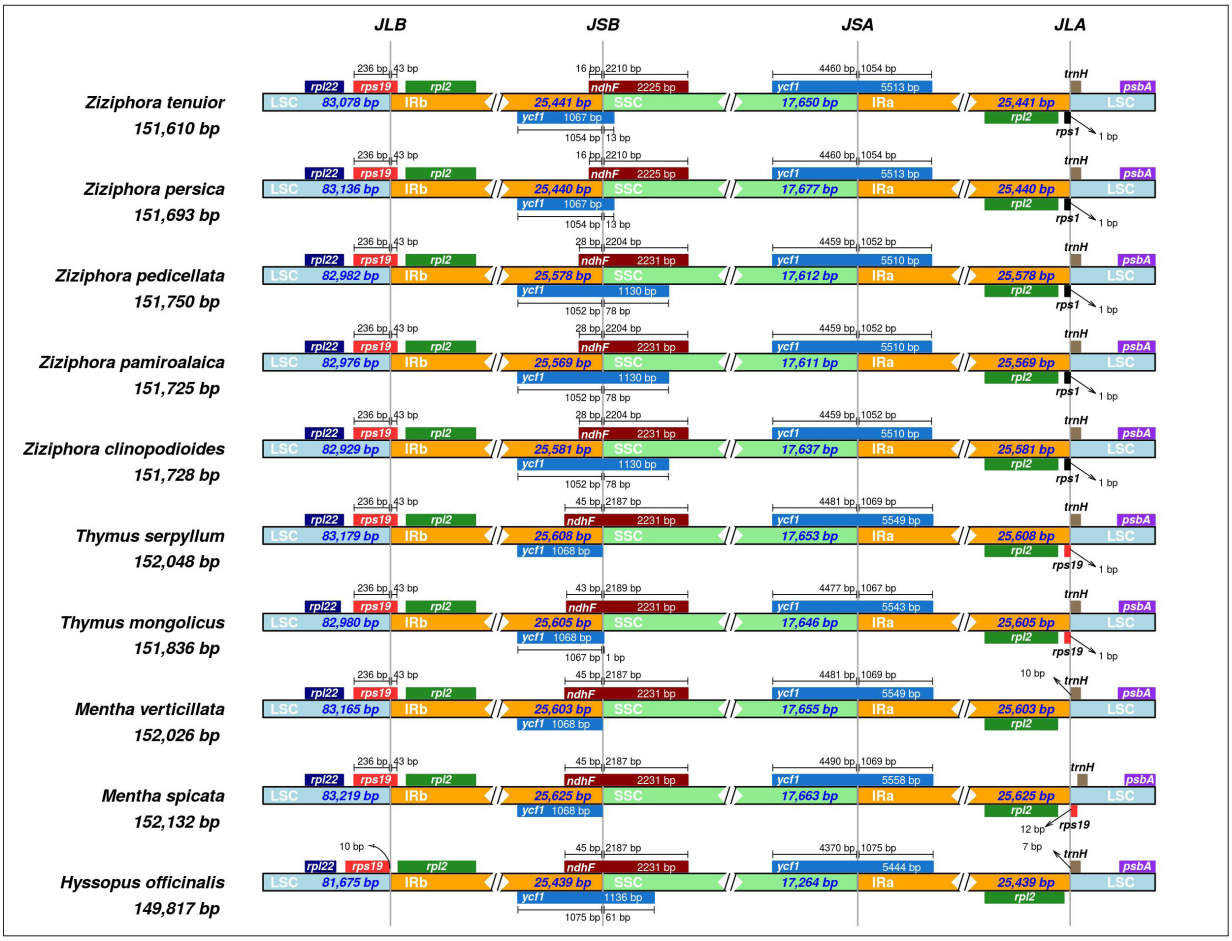

Fig. 4. Comparison of LSC, IR, and SSC junction positions among chloroplast genomes of five species of *Ziziphora* and five species of *Thymus*, *Mentha*, and *Hyssopus*. JLB represents LSC/IRb junction, JSB — SSC/IRb junction, JSA — SSC/IRa junction, and JLA — LSC/IRa junction

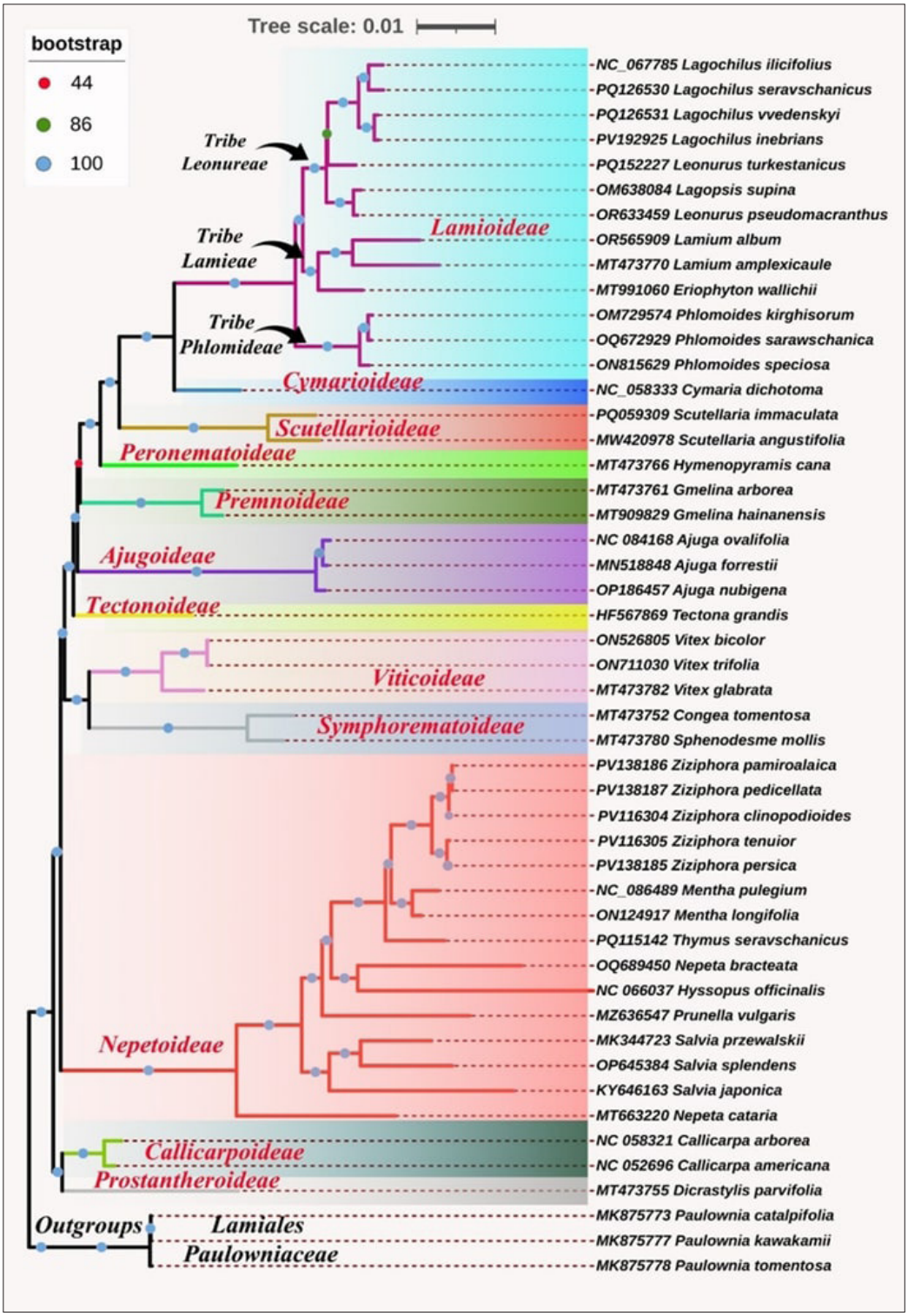

Fig. 5. Phylogenetic maximum likelihood (ML) cladogram of 46 species within *Lamiaceae* based on complete chloroplast genomes comparison. The bootstrap support values are shown on the branches

species of *Ziziphora*, we identified seven highly variable intergenic regions — *trnH-GUG–psbA*, *rps16–trnQ-UUG*, *rpoB–trnC-GCA*, *ndhC–trnV-UAC*, *rbcL–accD*, *psaI–ycf4*, and *ccsA–ndhD* — along with one protein-coding gene, *ycf1*, which exhibit substantial mutational hotspots. These highly variable regions offer promising potential as molecular markers for barcoding within the genus, facilitating more precise species identification and evolutionary studies.

In addition, a comprehensive chloroplast phylogenomic analysis of 46 species across *Lamiaceae* provided strong support for the monophyly of the major clades within the family, confirming the robustness of the current taxonomic framework based on the previous taxonomic research and recent molecular phylogenetic studies. The analysis strongly supports the classification of the five *Ziziphora* species studied as belonging to a single natural genus, forming a monophyletic group, and aligning with previous phylogenetic data.

Overall, we hope that this study significantly enhances our understanding of the genetic diversity and evolutionary relationships within *Ziziphora*, offering valuable molecular resources that will aid in future taxonomic revisions, phylogenetic analysis, and investigations into the evolutionary history of the genus. These findings contribute to a wider understanding of plant systematics within *Lamiaceae* and open up new avenues for research into the conservation and utilization of *Ziziphora* species in ecological and pharmaceutical applications.

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ETHICS DECLARATION

The authors declare no conflict of interest.

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Повний хлоропластний геном і філогенетичне положення видів роду *Ziziphora* (*Lamiaceae*) флори Узбекистану

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Реферат. Види роду *Ziziphora* (*Lamiaceae*) є цінними лікарськими та економічно важливими представниками флори Узбекистану, але ідентифікація цих видів через їхню морфологічну подібність є складною. Це дослідження є першим комплексним аналізом повних хлоропластних геномів видів роду *Ziziphora* природної флори Узбекистану. Порівняльний аналіз виявив варіабельність розміру генома, консервативні кільцеві структури та відмінності в нуклеотидному складі. Кожен геном містить 131 ген, 86 з яких є білок-кодуючими і переважно пов'язаними з фотосинтезом та функціонуванням пластид. Для хлоропластної ДНК характерний відносно низький вміст GC (~37,8%) порівняно з ядерними геномами видів роду *Ziziphora*. Філогенетичний аналіз на основі повних хлоропластних геномів та вибраних варіабельних маркерів показав, що види роду *Ziziphora* утворюють окрему монофілетичну лінію в межах триби *Mentheae* підродини *Nepetoideae*. Отримані результати підтверджують доцільність використання хлоропластної ДНК як надійного маркера в молекулярній філогенетичній систематиці та еволюційних дослідженнях. Це дослідження є вагомим внеском у розуміння генетичної структури, еволюційної історії та уточнення таксономічного положення таксонів роду *Ziziphora*, що є важливою основою для розробки стратегій їхнього збереження.

Ключові слова: *Lamiaceae*, *Ziziphora*, варіабельність розміру генома, генетична структура, молекулярна систематика, таксономічне положення, філогенетичний аналіз, хлоропластний геном