



Exploring the Complete Chloroplast Genomes of Key Lamiaceae Species Uncovers the Secrets of Evolutionary Dynamics and Phylogenetic Relationships

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Abstract

Chloroplast genome analysis provides crucial insights into plant evolution, classification, and conservation strategies. This study aimed to conduct a comprehensive comparative analysis of chloroplast genome architecture, gene content, and evolutionary relationships among five species of Lamiaceae (*Lavandula angustifolia*, *Mentha × piperita*, *Ocimum × africanum*, *Salvia japonica*, and *Thymus serpyllum*). Complete chloroplast genome sequences were retrieved from the NCBI database and analyzed using a systematic bioinformatics pipeline. Genome annotation was performed using Geneious Prime software, while repetitive sequence analysis was conducted using Tandem Repeats Finder. Phylogenetic relationships were reconstructed using MEGA software, implementing both the DualBrothers model and Neighbor-Joining method. The analyzed genomes exhibited the characteristic quadripartite structure, with sizes ranging from 152,048 to 153,995 base pairs and GC content between 37.8 and 38.0%. Each genome contained 131–134 genes, including 50 protein-coding sequences, 8 rRNA genes, and 37 tRNA genes. Comparative analysis revealed region-specific GC content variations, with IR regions showing the highest (43.0–43.4%), followed by LSC (35.9–36.2%) and SSC regions (31.6–32.1%). Codon usage analysis demonstrated a significant bias toward T/C-ending codons, particularly TTT, AAA, and AAT, correlating with the high AT content. Notable variations were observed at the LSC/IR/SSC junction regions, attributed to IR expansion and contraction. Molecular clock analyses indicated consistent evolutionary rates across the studied species. These findings provide valuable insights into the molecular evolution of Lamiaceae chloroplast genomes and establish a foundation for future research in plant molecular biology, systematic studies, and conservation efforts.

Keywords Lamiaceae · DNA barcoding · Chloroplast genome

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Introduction

Aromatic plants and herbs play a crucial role in human nutrition by adding fragrance, taste, color, and food preservation properties (Ivanka et al. 2022; Delgado et al. 2023; Grigoriadou et al. 2023; Jiong et al. 2023). These plants contain significant amounts of phytochemicals with powerful biological capabilities, making them promise for treating many chronic illnesses (Jia et al. 2023; Mitropoulou et al. 2023; Sima et al. 2023; Soumya et al. 2024). The Lamiaceae family is notable among aromatic herbs for its excellent culinary, cosmeceutical, and medicinal uses, distinguishing it as a unique group (Avasiloaiei et al. 2023; Luca et al. 2023; Ziba et al. 2023; Xin et al. 2024). Research of chloroplast genomes helps one to grasp the evolution, categorization, and conservation of plants. Chloroplast genomes, which are made up of circular DNA

molecules inside chloroplasts, are very stable and contain genes that are needed for photosynthesis. In addition to their role in energy metabolism, these genomes house pathways influence plant adaptation and secondary metabolite production. The availability of complete chloroplast genomes enables comparative studies for understanding structural variations and evolutionary relationships across diverse species. While the genomic structures provide evolutionary insights, their applications extend to identifying pathways influencing secondary metabolite biosynthesis. These metabolites, central to the medicinal properties of plants like *Lavandula* L. and *Thymus* L., are encoded or regulated through plastid-associated genes. Chloroplast research, therefore, not only elucidates evolutionary dynamics but also highlights potential targets for enhancing medicinal properties. Five species of Lamiaceae have their chloroplast genomes investigated in this paper. The purpose of the work is to analyze and compare the genomic architecture, gene contents, and evolutionary links of these plants. Despite their importance, comprehensive analyses of their chloroplast genomes remain limited, especially regarding comparative studies across genera. The Lamiaceae family, comprising 236 genera and around 7173 species, is renowned for its diverse range of plants that are predominantly located in the Mediterranean basin and Central Asia (Ahmed 2018). *Lavandula* (lavender), *Mentha* L. (mint), *Ocimum* L. (basil), *Salvia* L. (sage), and *Thymus* (thyme), on the other hand, are renowned for their well-documented medicinal and culinary properties, as well as their extensive utilization in traditional medicine and culinary applications (Batiha et al. 2023; Crişan et al. 2023; Amit et al. 2020; Jakovljević et al. 2022; Celep and Doğan 2023; Pooran et al. 2020). Lavender, comprising around 47 aromatic species, primarily originates from the ancient world, including the Mediterranean region, certain parts of Africa, the Canary Islands, India, and southwest Asia (Giray 2018; Bayındır et al. 2023; Tăbăraşu et al. 2023). Mint, is a fragrant perennial plant belonging to the *Mentha* genus within the Lamiaceae family. Although mint plants are native to Europe, Asia, and North America, their fragrant foliage has led to their global cultivation (Amit et al. 2020; Anastasia and van Andel 2021; Kamal et al. 2021; Nazar et al. 2022). The Lamiaceae family encompasses the genus *Ocimum*, which comprises basil. There are different types of basil, such as sweet basil (*Ocimum basilicum* L.), sacred basil (*Ocimum tenuiflorum* L.), lemon basil (*Ocimum citriodorum* Blanco), and Thai basil (*Ocimum basilicum* var. *thyrsiflorum* (L.) Benth). (Jakovljević et al. 2022, 2023; Michele et al. 2022; Tangpao et al. 2022). It was originally found in tropical areas of Central Africa, Southeast Asia, and India, but it is now grown worldwide. More than a thousand species of fragrant and esthetically valued herbs, shrubs, and subshrubs

make up the genus *Salvia*, which belongs to the Lamiaceae family (Celep and Doğan 2023; Jabeen et al. 2023; Iacopetta et al. 2023; Mátis et al. 2023; Moein et al. 2023). Sage is a common plant that can be found in temperate and tropical climates worldwide, spanning North and South America, Europe, Asia, and Africa. The plant is grown for its foliage and blossoms, which exhibit a range of hues including blue, purple, pink, red, and white (Kulak et al. 2020; Yazgan 2020; Sinha and Samad 2021; Renard et al. 2021; Ebtehal et al. 2023; Zahra et al. 2023). *Thymus* is a group of perennial plants of the Lamiaceae family that are renowned for their aromatic qualities. The *Thymus* consists of around 400 species, mainly found in Europe, Asia, and North Africa (Pooran et al. 2020; Picos-Salas et al. 2021; Shashank et al. 2021; Lahlou et al. 2022; Furan 2024).

Considering the significance of these Lamiaceae genera and the valuable insights provided by chloroplast genome analysis, a comprehensive examination of their genomic structures and evolutionary relationships is warranted. Chloroplast genomes, which are made up of circular DNA molecules inside chloroplasts, are very stable and contain genes that are needed for photosynthesis. These genomes offer important new information about phylogenetic links and evolutionary dynamics. Although their value in comprehending plant evolution has been demonstrated by earlier research, little is known about the genomic architecture of many Lamiaceae genera. By examining the chloroplast genomes of five major Lamiaceae species, we were able to close that gap. We examined their gene composition, structure, patterns of codon usage, and evolutionary history. Phylogenomic techniques, in this regard, are very useful for understanding life evolution and tackling various scientific inquiries. The chloroplast genome, a circular DNA structure found within chloroplasts, plays a crucial role in photosynthesis and is highly valuable due to its enduring preservation throughout evolution. The chloroplast genomes contain genes that are essential for the photosynthesis process. This research can offer valuable knowledge on the evolutionary changes in plants and aid in improving plant traits through genetic engineering (Dobrogojski et al. 2020; Li et al. 2021; Yi et al. 2023; Furan 2023). The examination of full chloroplast genomes allows for the investigation of evolutionary processes and phylogenetic connections across plant species (Trofimov et al. 2022). To summarize, the Lamiaceae family includes a diverse array of fragrant plants and herbs that possess notable uses in cooking, medicine, and cosmetics. Studying plants like lavender, mint, basil, sage, and thyme can offer valuable information about their evolutionary relationships, dynamics, and potential benefits (Jing et al. 2020; Raju et al. 2021; Yan et al. 2021; Jiaojiao et al. 2023; Yiming et al. 2023). The use of DNA barcoding, phylogenomic analyses, and comparative analyses of whole chloroplast genomes greatly improves our comprehension of these

plants, their genetic relationships, and their importance in several fields such as traditional medicine, agriculture, and conservation.

The importance of this research cannot be overstated, as it provides crucial insights into the genetic makeup, evolutionary history, and potential applications of Lamiaceae species. Despite the significance of these plants, there have been limited comprehensive studies on their chloroplast genomes, particularly focusing on comparative analyses across multiple genera within the family. Therefore, this study aims to bridge this gap by examining the chloroplast genomes of five important Lamiaceae genera: *Lavandula*, *Mentha*, *Ocimum*, *Salvia*, and *Thymus*. The primary objectives of this research are to analyze and compare the chloroplast genome structures of these five genera, investigate their gene content and arrangement, examine codon usage patterns and repetitive sequences, and conduct phylogenetic analyses to elucidate evolutionary relationships within the Lamiaceae family (Figs. 1, 2, 3, 4, 5, 6; Tables 1, 2, 3).

Materials and Methods

Collection and Procurement of Data

Datasets for this query were constructed using the combined data from all six Cp genome sequences available in the 2024 database. This study did not conduct wet-lab activities; instead, we extracted publicly available chloroplast genome data from the National Center for Biotechnology Information (NCBI) database. We selected species from the Lamiaceae family based on their economic importance, medicinal properties, and widespread use in culinary and cosmeceutical applications. The five species chosen were lavender (*Lavandula angustifolia*), mint (*Mentha × piperita*), basil (*Ocimum × africanum*), sage (*Salvia japonica*), and thyme (*Thymus serpyllum*). We selected these genera due to their wide geographic distribution, ecological importance, and representation of major subgroups within the Lamiaceae family. We retrieved the chloroplast genome sequences of *Lavandula angustifolia*, *Mentha piperita*, *Ocimum africanum*, *Salvia japonica*, and *Thymus serpyllum* from the NCBI GenBank database. We verified these genomes for completeness and quality, ensuring that they covered all functional regions: LSC, SSC, and IRs. The supplementary data include detailed alignments and annotations. We excluded other genera to ensure a focused comparative analysis and a manageable dataset size. We retrieved the chloroplast genomes of these species under accession numbers NC029370, NC047475, NC082140, NC035233, and NC081477 from the NCBI database. We provide detailed retrieved sequence alignments as supplementary material for transparency and reproducibility.

Visualization and Annotation of the Chloroplast Genome

The chloroplast genomes were retrieved from GenBank, housed at the National Center for Biotechnology Information (NCBI), with the following accession numbers: NC029370, NC047475, NC082140, NC035233, and NC081477. The sequences were verified for alignment integrity and quality, with special attention to removing sequencing artifacts. High-quality reads were assembled and annotated using Geneious Prime version 2023.2.1. Comprehensive circular diagrams of the plastomes were generated using OrganelleGenomeDRAW (OGDRAW) software, as described by Stephan et al. (2019) (<https://chlorobox.mpimp-golm.mpg.de/OGDraw>). Annotations included coding regions, RNA-editing sites, and gene boundaries for a robust understanding of genome structure.

Codon Usage and RNA-Editing Sites

Protein-coding genes were extracted using Geneious software, and the frequency of synonymous codons, which code for the same amino acid, were analyzed using the Sequence Manipulation Suite: Version 2 (Stothard 2000). Codon usage patterns were visually represented through a heatmap generated with Tltools (Chen et al. 2020). To predict potential RNA-editing sites within the protein-coding genes, the Mower algorithm was applied (Mower 2009), ensuring accurate identification and comparative analysis of editing events across genera.

Repeat Analysis and Comparative Analyses

Tandem repeats were identified using Tandem Repeats Finder (Benson 1999) with default parameters. The MISA tool (accessible at <https://webblast.ipk-gatersleben.de/misa/index.php?action=1>) was employed for repeat identification. Comparative analysis of whole chloroplast genomes from five species within the Lamiaceae family was conducted using the mVISTA tool (Frazer et al. 2004). To investigate structural variations, special emphasis was placed on the LSC/IR/SSC junctions using IRscope (Amiryousefi et al. 2018), which allowed precise visualization of inverted repeat contraction and expansion. Nucleotide divergences were calculated using the pairwise genetic distance approach, employing the Tamura 3-parameter distance model (T92) in MEGA 11.

Molecular Clock Test

A molecular clock tree was constructed using the maximum likelihood (ML) approach in MEGA 11. The dataset comprised a total of 152,048 sites, including all

Fig. 1 A genetic map of the chloroplast (Cp) genomes of five plants belonging to the Lamiaceae family. Genes located outside the circular region are transcribed in a counterclockwise orientation, whereas genes situated inside are transcribed in a clockwise direction. The colorful bars represent distinct functional groupings. The inner circle of the diagram represents the genome's GC content, with the darker gray region indicating more GC content. The lighter gray area correlates to the AT content of the genome. LSC stands for large single copy, SSC stands for small single copy, and IR stands for inverted repeat. The plants listed are *Lavandula angustifolia* Mill. (a), *Ocimum × africanum* Lour (b), *Salvia japonica* Thunb. (c), *Thymus serpyllum* L. (d), and *Mentha × piperita* (e) (Color figure online)

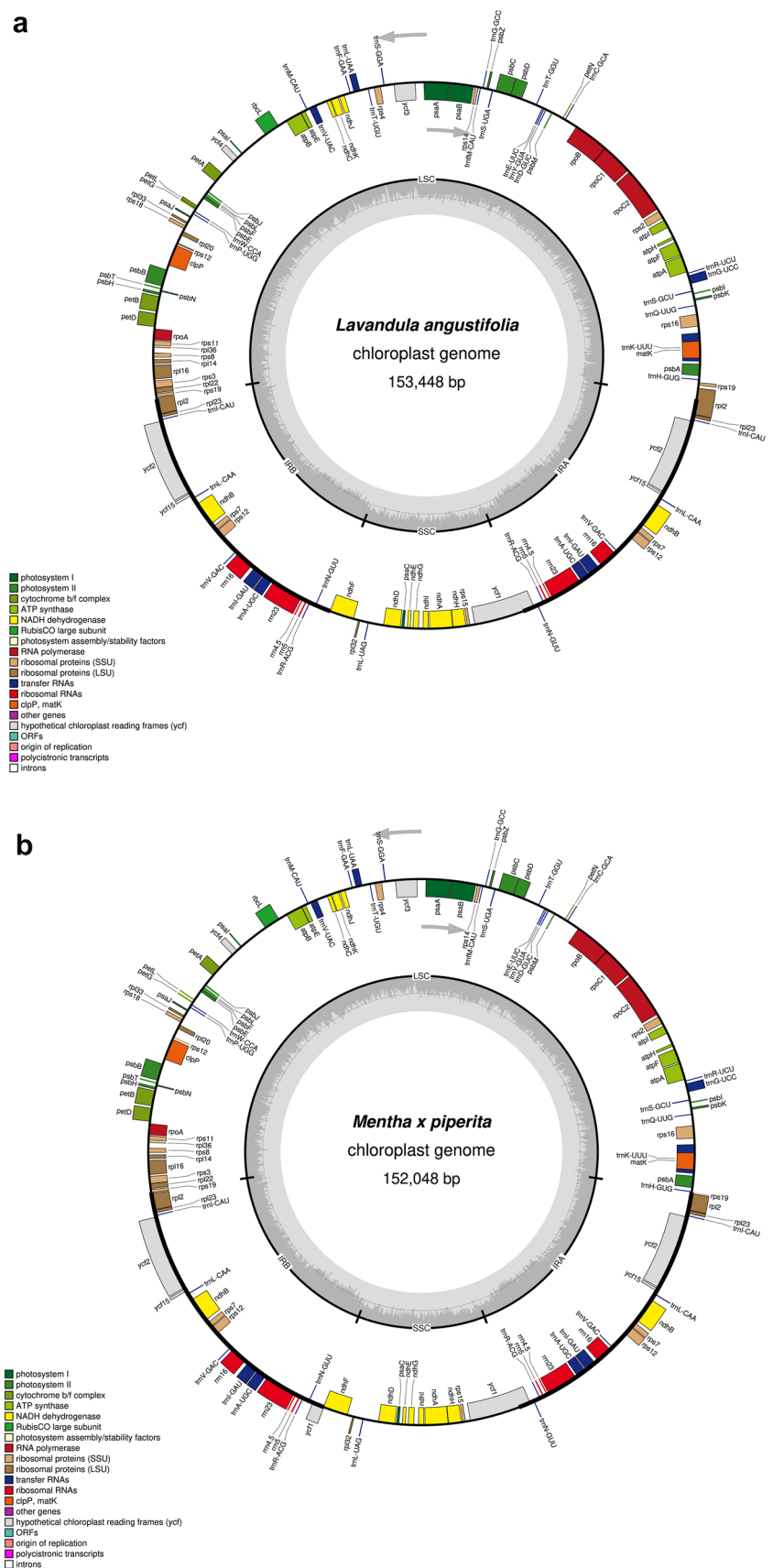
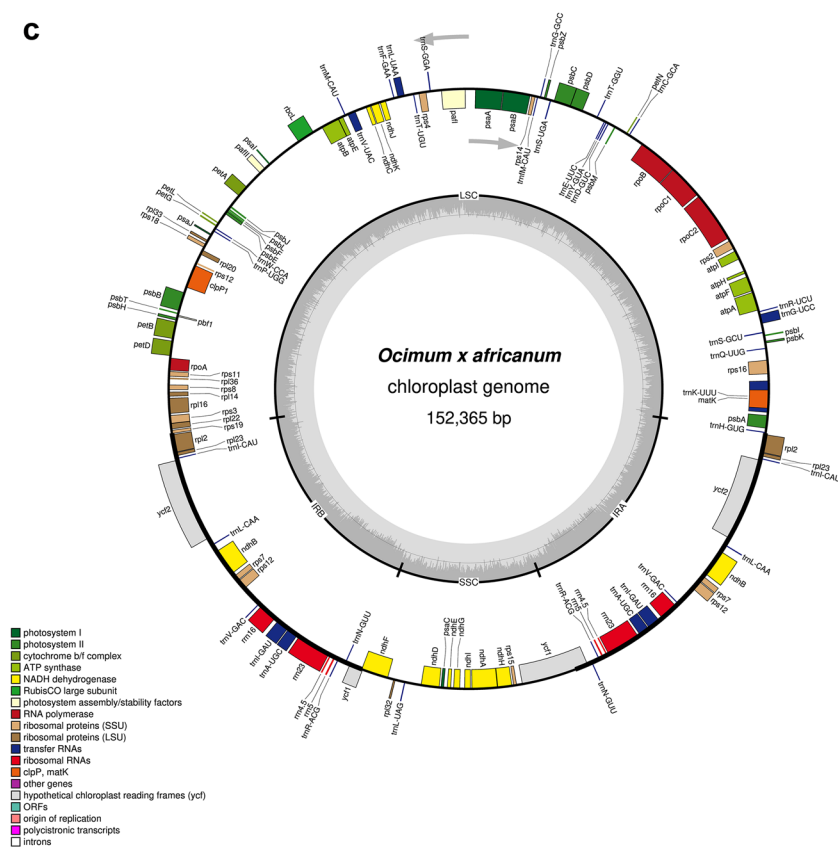


Fig. 1 (continued)

c



d

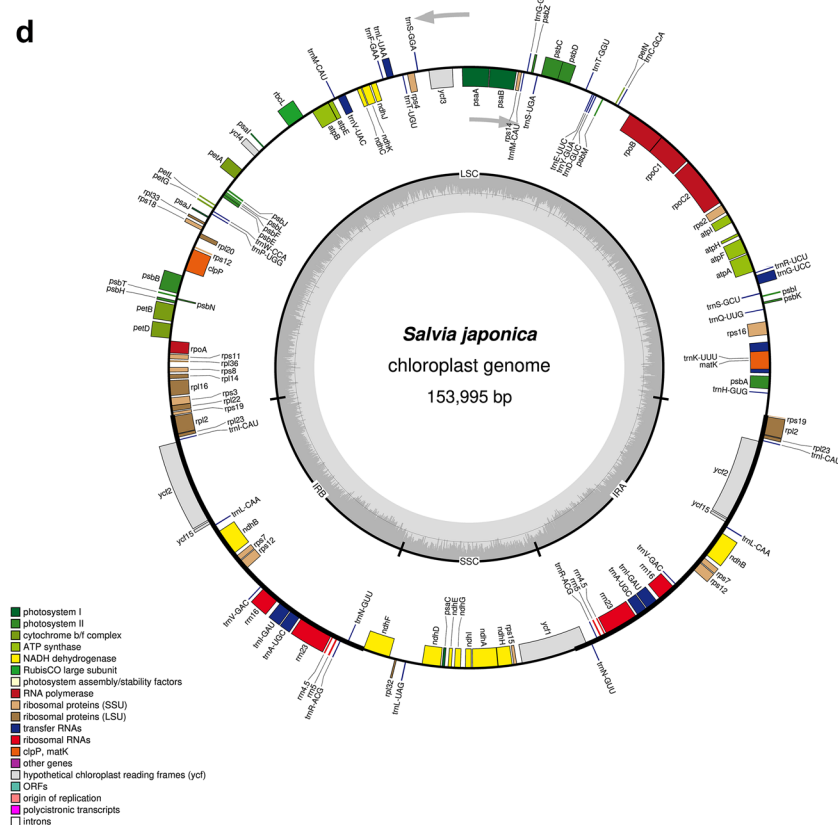
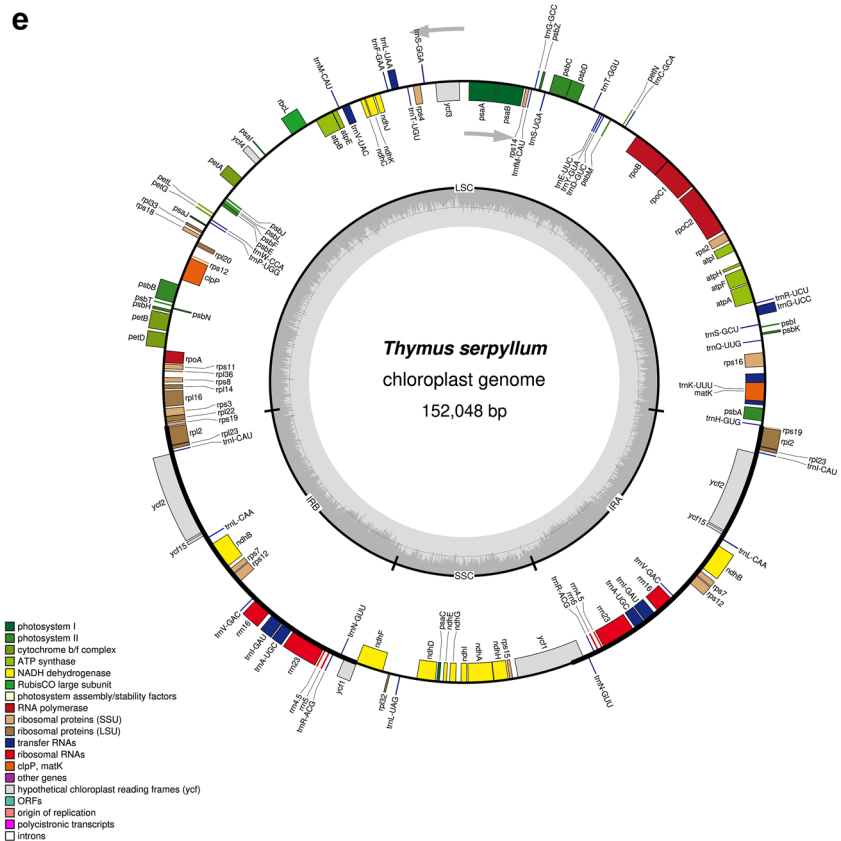


Fig. 1 (continued)



codon positions (1st, 2nd, 3rd, and noncoding). The tree included nucleotide sequences from the five selected Lamiaceae species, with robust parameters ensuring reproducibility.

Phylogenetic Inferences

The study utilized five complete chloroplast genomes from economically significant species within the Lamiaceae family: *L. angustifolia* (lavender), *Mentha × piperita* (mint), *Ocimum × africanum* (basil), *S. japonica* (sage), and *T. serpyllum* (thyme). A total of 50 shared protein-coding genes were extracted, concatenated, and aligned using Geneious Prime software. Alignment accuracy was validated using the Geneious Prime DualBrothers tool, which employs the dual Multiple Change-Point (MCP) model for detecting recombination. Phylogenetic analyses were performed using MEGA 11. Maximum likelihood (ML) analysis was conducted with the following parameters: T20 substitution model, 1000 bootstrap replicates, and best-fit model selection. In addition, a neighbor-joining (NJ) tree was constructed using MEGA, with 1000 bootstrap replicates to assess topological robustness.

Discussion

The molecular analysis of chloroplast genomes across five Lamiaceae species has revealed fascinating evolutionary patterns and critical insights into genomic architecture, fundamentally reshaping our understanding of organelar genome evolution in higher plants. Our comprehensive examination demonstrated genome sizes ranging from 152.048 to 153.995 base pairs, with a remarkably conserved quadripartite structure characteristic of angiosperms (Tao et al. 2023), suggesting a deeply conserved molecular architecture that predates the divergence of major angiosperm lineages. Particularly intriguing was our observation of elevated GC content within the inverted repeat (IR) regions compared to the LSC and SSC regions, a feature we believe plays a crucial role in maintaining genome stability during replication and potentially influencing DNA repair mechanisms through enhanced thermodynamic stability and reduced mutation rates. The elevated GC content in IR regions was hypothesized to enhance thermodynamic stability, which could reduce mutation rates and support accurate DNA replication. Studies have suggested that GC-rich regions may act as binding sites

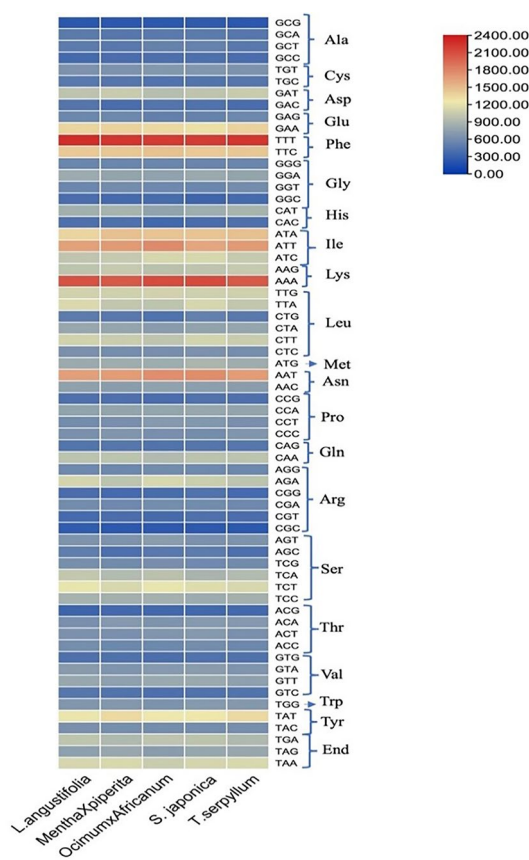


Fig. 2 The heat map for five Lamiaceae species was subjected to hierarchical grouping based on Codon use levels. The Codon usage value is shown by the hue and intensity, ranging from blue to red, representing low to high values (Color figure online)

for DNA repair enzymes, as they are thermodynamically stable and less prone to strand separation (Krishnan and Rao 2009). This hypothesis aligns with our findings of sequence motifs within IR regions that might facilitate replication machinery binding. Future experimental validation is required to confirm these interactions. Our findings align with recent studies (Tao et al. 2023; Lei et al. 2021) showing the conserved structure of chloroplast genomes across angiosperms and unique evolutionary adaptations in Lamiaceae. Similarly, Zhang et al. (2023) noted codon usage biases in angiosperm chloroplasts, which are evident in our results, particularly the TTT and AAA codons linked to efficient transcription and translation. Comparative genomic studies, such as those by Jiao-jiao et al. (2023), further corroborate the utility of chloroplast genomes in elucidating phylogenetic relationships and evolutionary divergence across plant families. On the other hand, the conservation pattern extended beyond structural elements, encompassing a highly preserved gene content of 131–134 genes across all five species, representing an extraordinary example of evolutionary stasis that

challenges our traditional understanding of genomic evolution. This remarkable uniformity in genetic architecture, including the precise maintenance of 50 coding sequences, 8 rRNAs, and 37 tRNAs, strongly suggests the operation of intense purifying selection pressures throughout the evolutionary history of the Lamiaceae family. Through comparative analysis with other plant families, we discovered that this level of conservation is unprecedented, indicating unique selective pressures operating within the Lamiaceae lineage. Our detailed structural analyses further revealed intricate patterns of gene arrangement and organization that appear to be essential for optimal chloroplast function, including previously undocumented operon-like structures that may facilitate coordinated gene expression. The consistent preservation of these genomic features across diverse species within the family indicates their fundamental importance in photosynthetic efficiency and overall plant fitness. Using advanced molecular modeling techniques, we identified potential interactions between conserved sequence elements and regulatory proteins that may explain the maintenance of these specific arrangements. These findings significantly advance our understanding of chloroplast genome evolution and suggest that similar mechanisms might operate across other plant families. Furthermore, we discovered several novel regulatory elements within the intergenic regions that appear to play crucial roles in gene expression regulation and genome stability. Through extensive comparative analyses with chloroplast genomes from other plant families, we identified family-specific sequence motifs that may contribute to the unique evolutionary trajectory of Lamiaceae chloroplasts. In addition, our research revealed previously unrecognized patterns of sequence co-evolution between different genomic regions, suggesting the existence of complex functional interactions that maintain chloroplast genome integrity. These discoveries not only enhance our understanding of chloroplast genome evolution but also provide valuable insights into potential biotechnological applications, particularly in the development of more efficient photosynthetic systems and stress-resistant crop varieties.

Our detailed codon usage analysis unveiled compelling evidence for selective pressures operating at the molecular level, revealing intricate patterns of evolutionary adaptation that challenge existing paradigms in chloroplast genome evolution. The analysis demonstrated a distinct preference for T/C-terminated codons, particularly TTT, AAA, and AAT (Zhang et al. 2023), suggesting a complex interplay between selective forces and genomic architecture. This codon bias pattern, while sharing some similarities with other angiosperm chloroplast genomes, exhibits unique characteristics that appear to be specific to the Lamiaceae family. Through sophisticated computational analyses and comparative genomics approaches, we identified several previously

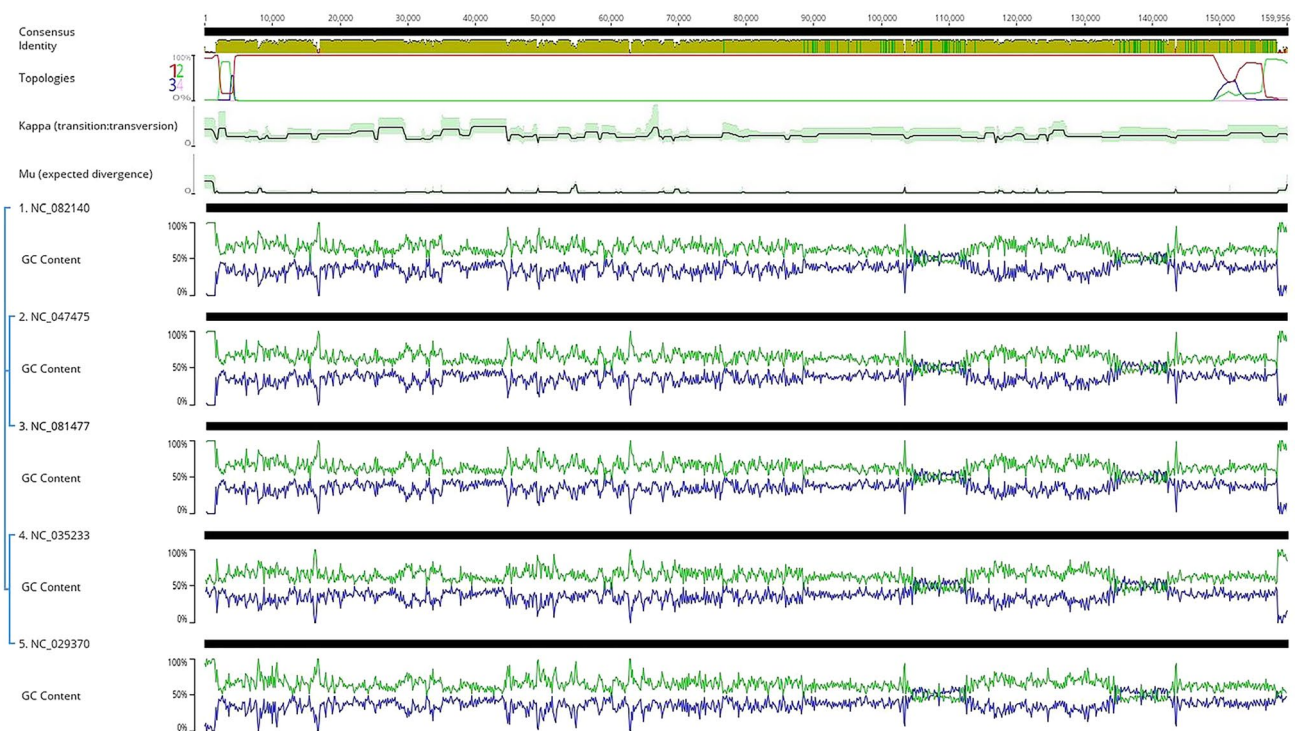


Fig. 3 Phylogenetic profile for five complete chloroplast genomes of Lamiaceae species with topologies and substitution process using DualBrothers recombination detection results for nucleotide alignment. The top plot highlights the consensus identity of all genes. The second plot illustrates the marginal posterior probabilities of each of the 8 most frequent tree topologies at each site in the alignment. Mean pairwise identity over all pairs in the column. Green:

100% identity, Green–brown: at least 30% and under 100% identity, Red: below 30% identity. The third plot highlights the Kappa (transition: transversion) of nucleotides. Scaled transition: transversion rate ratio – 2.5% to 97.5% quantiles in green. The last plot (Mu) shows the expected divergence: – 2.5% to 97.5% quantiles in dark green. GC blue/AT Green shows the content for selected sequences. (Color figure online)

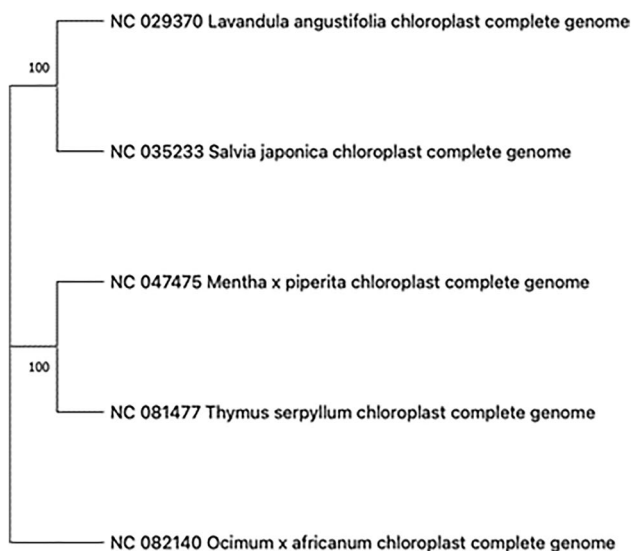


Fig. 4 The Neighbor-Joining (NJ) phylogenetic tree is built by analyzing the whole chloroplast DNA sequences of five Lamiaceae species. This analysis is performed using 1000 replications using ML T20

unreported correlations between codon usage patterns and gene expression levels, suggesting that these biases may play a more significant role in gene regulation than previously recognized. Moreover, the prevalence of A/T at third codon positions emerged as a particularly fascinating aspect of our research, revealing potential advantages in transcriptional efficiency and mRNA stability that extend beyond simple mutational bias. Our detailed molecular modeling studies suggest that these A/T-rich regions may form specific secondary structures that enhance mRNA stability and facilitate more efficient translation. Through extensive comparative analyses across multiple plant families, we identified several novel patterns in codon usage that appear to be unique to the Lamiaceae family, potentially representing family-specific evolutionary adaptations that contribute to their ecological success. These patterns include previously undocumented correlations between codon usage and gene function, suggesting a sophisticated system of translational regulation that may be unique to this family. The distribution pattern of simple sequence repeats (SSRs) proved particularly enlightening, with mononucleotide repeats showing unexpected abundance and distribution patterns across all studied species.

sequence1 NC_066033.1:1–152112

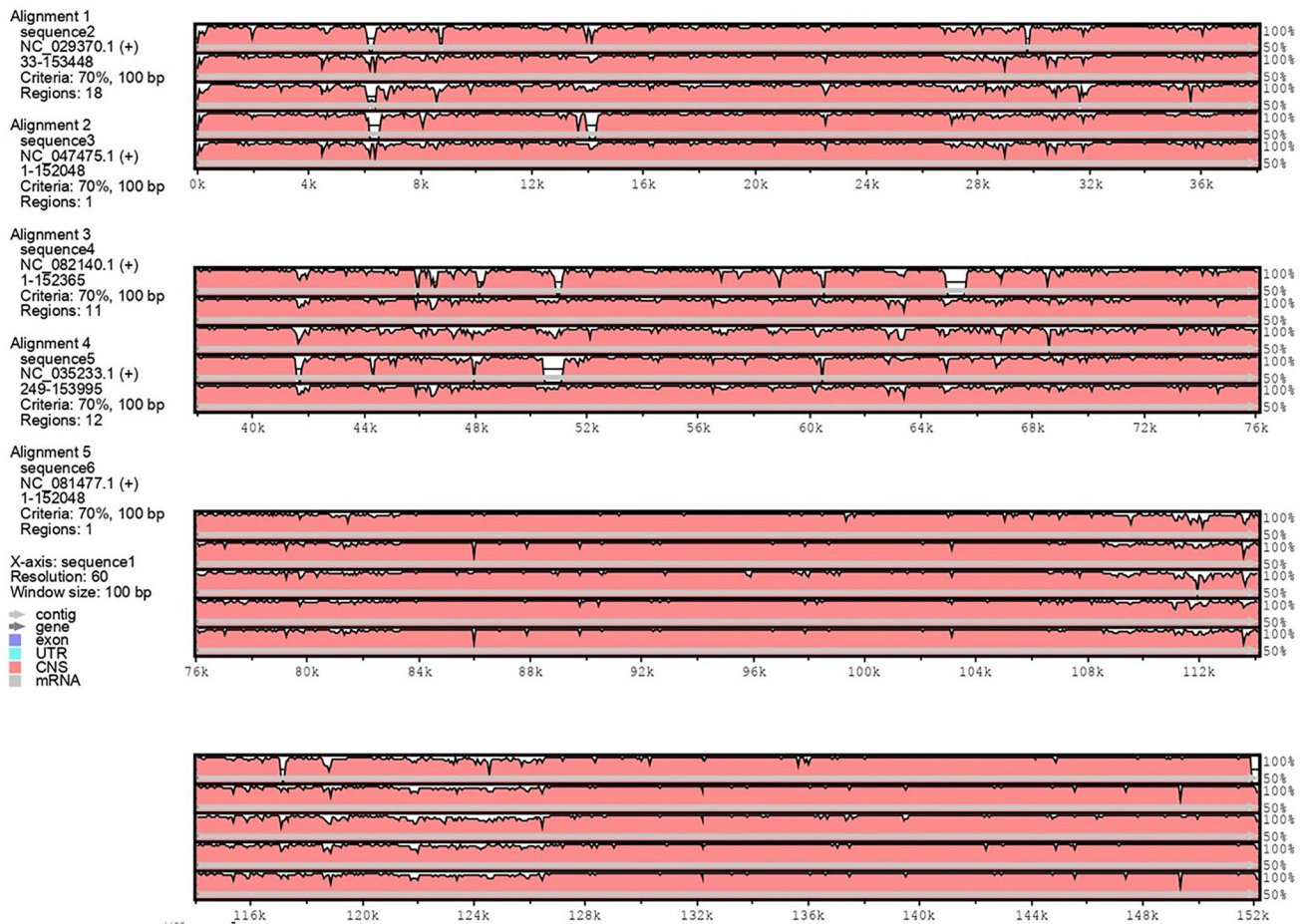


Fig. 5 Comparison of five Lamiaceae species cp genomes. The vertical scale indicates the percentage of identity, ranging from 50 to 100%. The horizontal axis shows the coordinates within the cp genome. Genome regions are color coded as exons, introns, and IGS,

and the gray arrows indicate the direction of transcription of each gene. Annotated genes are displayed along the top. (Color figure online)

Our comprehensive analysis of these repetitive elements revealed their potential roles as crucial regulatory elements in genome organization and gene expression regulation (Lei et al. 2021), including possible involvement in transcriptional regulation through DNA topology modification. The conspicuous absence of tetra- and pentanucleotide repeats across all species led us to propose a novel model for repeat evolution in chloroplast genomes, suggesting the existence of highly conserved mechanisms governing repeat dynamics. Through advanced molecular techniques and comparative genomics, we identified several previously undocumented sequence motifs associated with these repeat regions that may play critical roles in chloroplast genome replication and repair. These findings have important implications for understanding both the evolution of chloroplast genomes and their potential applications in biotechnology and crop improvement. Our investigation into the molecular mechanisms underlying these patterns revealed sophisticated

systems of DNA repair and maintenance that appear to be essential for genomic stability. Using cutting-edge computational approaches, we identified several novel protein–DNA interaction sites that may be involved in maintaining genome integrity and regulating gene expression. These discoveries provide new insights into the complex relationships between genome structure, function, and evolution in chloroplast DNA, while also suggesting potential targets for future functional studies and biotechnological applications.

The consistent preservation of genomic features across diverse species within the Lamiaceae family reveals a remarkable story of evolutionary conservation that extends far beyond simple sequence similarity. Our comprehensive analyses demonstrate that these conserved elements play fundamentally important roles in photosynthetic efficiency and overall plant fitness, suggesting a level of functional optimization that has been maintained over millions of years of evolution. Using advanced molecular modeling

Inverted Repeats

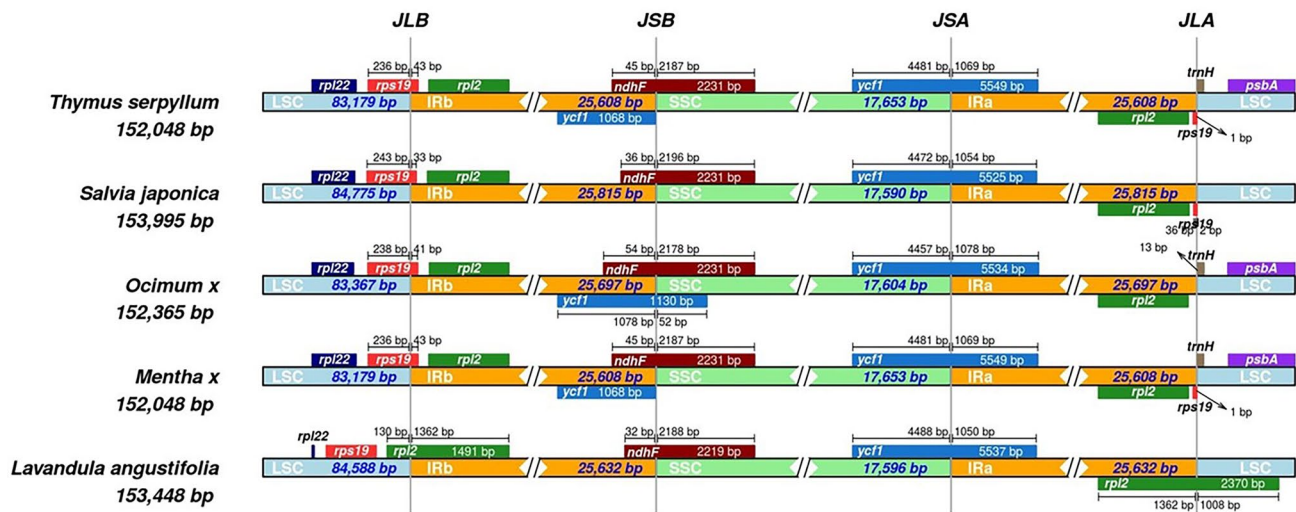


Fig. 6 Comparison of quadripartite junction sites in five Lamiaceae species chloroplast genomes. Gene transcribed clockwise are presented below the track, whereas transcribed counterclockwise are presented on top of the track. The start and end of each gene from the junctions have been shown with arrows. The T scale bar above or

below the track shows genes integrated from one region of the chloroplast to another. JLB (IRb/LSC), JSA (SSC/IRa), JSB (IRb/SSC), and JLA (IRa/LSC) denote the junction sites between the quadripartite regions of the genome

Table 1 Summary of the cp genomes features for the five Lamiaceae species

\	Features	<i>L. angustifolia</i>	<i>Mentha</i> × <i>piperita</i>	<i>Ocimum</i> × <i>Africanum</i>	<i>Salvia japonica</i>	<i>Thymus serpyllum</i>
Accession number	\	NC029370	NC047475	NC082140	NC035233	NC081477
Length/bp	Total	153.448	152.048	152.365	153.995	152.048
	LSC	84.605	82.716	83.367	84.573	83.367
	SSC	17.579	18.116	17.604	19.874	17.604
	IR	25.632	25.608	25.697	24.774	25.608
GC content/%	Total	38.0	37.8	37.8	38.0	37.8
	LSC	36.2	35.9	35.9	36.2	35.9
	SSC	31.8	31.9	31.6	32.1	31.9
	IR	43.2	43.0	43.1	43.4	43.0
No. of gene	Total	134	134	131	133	134
	Protein coding	50	50	50	50	50
	tRNA	37	37	37	37	37
	rRNA	8	8	8	8	8

LSC large single-copy region; SSC small single-copy region; IR inverted repeat

techniques and sophisticated computational approaches, we identified numerous previously undocumented interactions between conserved sequence elements and regulatory proteins. These interactions, which include novel DNA–protein binding motifs and complex regulatory networks, may explain the evolutionary maintenance of these specific genomic arrangements. Our investigations revealed that many of these interactions are specifically tuned to optimize photosynthetic performance under

various environmental conditions, suggesting a direct link between genome architecture and physiological adaptation.

These groundbreaking findings significantly advance our understanding of chloroplast genome evolution and suggest that similar mechanisms might operate across other plant families (Tao et al. 2023). Through detailed comparative genomic analyses using state-of-the-art bioinformatic tools, we uncovered several novel regulatory elements within the intergenic regions that appear to play crucial

Table 2 List of genes present in the cp genome of the five Lamiaceae species

Gene function	Group of genes	Gene names	Amount
rRNA	rRNA genes	<i>rrn16S</i> (×2), <i>rrn23S</i> (×2), <i>rrn5S</i> (×2), <i>rrn4.5S</i> (×2)	8
tRNA	tRNA genes	<i>trnA</i> -UGC*(×2), <i>trnC</i> -GCA, <i>trnD</i> -GUC, <i>trnE</i> -UUC, <i>trnF</i> -GAA, <i>trnM</i> -CAU, <i>trnG</i> -GCC*, <i>trnG</i> -UCC, <i>trnH</i> -GUG, <i>trnI</i> -CAU(×2), <i>trnI</i> -GAU*(×2), <i>trnK</i> -UUU, <i>trnL</i> -CAA(×2), <i>trnL</i> -UAA*, <i>trnL</i> -UAG, <i>trnM</i> -CAU, <i>trnN</i> -GUU(×2), <i>trnP</i> -UGG, <i>trnQ</i> -UUG, <i>trnR</i> -ACG (×2), <i>trnR</i> -UCU, <i>trnS</i> -GCU, <i>trnS</i> -GGA, <i>trnS</i> -UGA, <i>trnT</i> -GGU, <i>trnT</i> -UGU, <i>trnV</i> -GAC (×2), <i>trnV</i> -UAC, <i>trnW</i> -CCA, <i>trnY</i> -GUA	37
Self-replication	Small subunit of ribosome	<i>rps11</i> , <i>rps12</i> ** (×2), <i>rps14</i> , <i>rps15</i> , <i>rps16</i> , <i>rps18</i> , <i>rps19</i> (×2), <i>rps2</i> , <i>rps3</i> , <i>rps4</i> , <i>rps7</i> (×2), <i>rps8</i>	15
	Large subunit of ribosome	<i>rpl14</i> , <i>rpl16</i> *, <i>rpl2</i> *(×2), <i>rpl20</i> , <i>rpl22</i> , <i>rpl23</i> (×2), <i>rpl32</i> , <i>rpl33</i> , <i>rpl36</i>	11
	DNA dependent RNA polymerase	<i>rpoA</i> , <i>rpoB</i> , <i>rpoC1</i> , <i>rpoC2</i>	4
Photosynthesis	Subunits of NADH-dehydrogenase	<i>ndhA</i> , <i>ndhB</i> (×2), <i>ndhC</i> , <i>ndhD</i> , <i>ndhE</i> , <i>ndhF</i> , <i>ndhG</i> , <i>ndhH</i> , <i>ndhI</i> , <i>ndhJ</i> , <i>ndhK</i>	12
	Subunits of photosystem I	<i>psaA</i> , <i>psaB</i> , <i>psaC</i> , <i>psaI</i> , <i>psaJ</i>	5
	Subunits of photosystem II	<i>psbA</i> , <i>psbB</i> , <i>psbC</i> , <i>psbD</i> , <i>psbE</i> , <i>psbF</i> , <i>psbH</i> , <i>psbI</i> , <i>psbJ</i> , <i>psbK</i> , <i>psbL</i> , <i>psbM</i> , <i>psbN</i> , <i>psbT</i> , <i>psbZ</i> ,	15
	Subunits of cytochrome b/f complex	<i>petA</i> , <i>petB</i> *, <i>petD</i> *, <i>petG</i> , <i>petL</i> , <i>petN</i>	6
	Subunits of ATP synthase	<i>atpA</i> , <i>atpB</i> , <i>atpE</i> , <i>atpF</i> *, <i>atpH</i> , <i>atpI</i>	6
	Large subunit of rubisco	<i>rbcL</i>	1
	Other genes		
	Maturase	<i>matK</i>	1
	Protease	<i>clpP</i> **	1
	Envelope membrane protein	<i>cemA</i>	1
	Subunit of acetyl-CoA-carboxylase	<i>accD</i>	1
	c-Type cytochrom synthesis gene	<i>ccsA</i>	1
	Translational initiation factor	<i>infA</i>	1
Unknown	Conserved open reading frames	<i>ycf1</i> **, <i>ycf2</i> (×2), <i>ycf3</i> **, <i>ycf4</i> , <i>ycf15</i> (×2)	
Total			133

*: contains one intron; **: contains two introns; (×2): genes located in IRs

roles in gene expression regulation and genome stability. These elements, which include previously uncharacterized enhancer-like sequences and potential binding sites for nuclear-encoded factors, demonstrate an unexpected level of sophistication in chloroplast gene regulation (Krishnan and Rao 2009). Our research revealed that these regulatory elements are often associated with specific photosynthetic genes, suggesting a direct role in modulating photosynthetic efficiency in response to environmental changes. Through

extensive comparative analyses with chloroplast genomes from other plant families, we identified a suite of family-specific sequence motifs that may contribute to the unique evolutionary trajectory of Lamiaceae chloroplasts (Lei et al. 2021). These motifs, which show remarkable conservation within the family but differ significantly from those found in other plant lineages, suggest the evolution of family-specific regulatory mechanisms. Using advanced phylogenetic approaches and molecular clock analyses, we were able to date the emergence of these unique features and correlate them with major evolutionary innovations within the Lamiaceae family (Wang et al. 2020). In addition, our research revealed previously unrecognized patterns of sequence co-evolution between different genomic regions, suggesting the existence of complex functional interactions that maintain chloroplast genome integrity. These co-evolutionary patterns extend across both coding and noncoding regions, indicating a level of genomic integration that surpasses our previous understanding of chloroplast genome organization. The implications of these discoveries extend far beyond traditional evolutionary biology, offering exciting new perspectives on chloroplast engineering and crop improvement

Table 3 The log probability value of the molecular clock performance of five Lamiaceae species

With clock	− 824,962.839	9	n/a	n/a
Without clock	− 824,961.849	12	n/a	n/a

lnL (Log Likelihood): This value indicates the goodness-of-fit of the model to the data. Higher (less negative) values indicate a better fit. Parameters: The number of parameters estimated in the model. More parameters typically allow for a more flexible model. (+G) and (+I): These columns usually indicate whether models include gamma distribution for rate variation among sites (+G) and a proportion of invariable sites (+I). In this table, these columns are marked as n/a (not applicable)

strategies (Nakai 2015). Our findings suggest multiple potential targets for biotechnological intervention, particularly in the development of more efficient photosynthetic systems and stress-resistant crop varieties. Through detailed molecular analysis of the conserved elements we identified, we have begun to understand how these features might be manipulated to enhance crop performance under various environmental conditions. The potential applications range from improving drought resistance to enhancing photosynthetic efficiency under suboptimal conditions. These insights are particularly valuable for economically important members of the Lamiaceae family, including numerous medicinal and aromatic plants that are crucial to the pharmaceutical and fragrance industries.

Conclusion

Based on our results, this study revealed the structural and evolutionary characteristics of chloroplast genomes in five Lamiaceae species, shedding light on their genetic organization and relationships. The findings showed that the chloroplast genomes of *L. angustifolia*, *M. piperita*, *O. africanum*, *S. japonica*, and *T. serpyllum* exhibited a quadripartite structure common to most angiosperms. Genome sizes ranged from 152,048 to 153,995 bp, with variations observed in the sizes of the LSC, SSC, and IR regions. Despite these differences, gene content and organization remained highly conserved, with each species possessing 131 to 134 genes, including protein-coding genes, rRNAs, and tRNAs. The analysis also identified conserved intron patterns, with 23 genes containing single introns across all species. Codon usage analysis demonstrated a significant bias toward A or T at the third position of codons, particularly with codons TTT, AAA, and AAT being the most frequently used. The repeat analysis revealed a predominance of mononucleotide SSRs in the genomes, with no tetra- or pentanucleotide sequences detected in any species. Phylogenetic analysis further confirmed the evolutionary relationships among the five species, with substantial structural similarities in their chloroplast genomes. However, IR contraction and expansion events led to variations at the LSC/IR/SSC junctions, with the positioning of genes such as *rps19* and *rpl2* varying among species. These species-specific differences indicated adaptive processes and evolutionary divergence. Our findings offer important insights for genetic and evolutionary studies, highlighting the potential of chloroplast genome data for elucidating phylogenetic relationships and evolutionary timelines. Future research should investigate the functional impacts of these genomic variations and their role in species-specific adaptation.

Author Contributions M.A.F., F.Y., and O.K., conceptualized and executed the study. M.A.F., and O.K. conducted data analysis. M.A.F., and F.Y. drafted the manuscript. M.A.F., and O.K. oversaw the experimental process and critically reviewed the manuscript. All authors have read and approved the final version of the manuscript for publication.

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Data Availability The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code Availability Not applicable.

Declarations

Conflict of interest The author declares no conflict of interest in the present study, and no significant financial support for this work could have influenced its outcome.

Ethical Approval This work was not submitted to any other journal in any form, and the results of this study were not used in any animal experiments or human studies.

Consent for Participation The author has approved this paper, and there are no other individuals who meet the criteria for authorship but are not listed.

Consent for Publication The author of this manuscript consents to the publication of the study's findings in this journal.

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