COMPARATIVE CHLOROPLAST GENOME ANALYSIS AND PHYLOGENY OF THE GENUS *Rosa* (ROSACEAE)

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Abstract. The genus *Rosa* encompasses approximately 150–200 species distributed primarily across temperate and subtropical regions of the Northern Hemisphere, with Asia as a major center of diversity. Despite their ecological and economic importance, the phylogenetic relationships within *Rosa* remain incompletely resolved due to frequent hybridization, extensive polyploidy, and low sequence divergence. In this study, we sequenced and analyzed the complete chloroplast genomes of four wild *Rosa* species from Uzbekistan *R. ecae*, *R. fedtschenkoana*, *R. kokanica*, and *R. canina* and conducted comparative genomic analyses with a broader set of 71 *Rosa* plastomes. Our results revealed highly conserved plastome structure, gene content, and GC composition across species, with minor variations in IR boundary regions. Phylogenetic reconstruction based on whole plastome sequences delineated four major clades, highlighting clear evolutionary relationships and geographic patterns within the genus. However, pervasive interspecific hybridization and allopolyploidization complicate species delimitation and contribute to phylogenetic discordance between plastid and nuclear data. These findings emphasize the need for integrated nuclear and population genomic approaches to fully resolve *Rosa* evolutionary history. This study provides a refined plastome-based framework for *Rosa* systematics and offers molecular tools to support conservation and breeding efforts for wild and cultivated roses.

Key words: chloroplast genome; wild roses; Uzbekistan; comparative genomics; IR boundary variation; hybridization; polyploidy.

INTRODUCTION

The genus *Rosa* L., commonly known as roses, comprises approximately 150 to 200 species widely distributed across temperate and subtropical regions of the Northern Hemisphere, with Asia harboring approximately half of these species, making it a major center of diversity for the genus [5, 10, 26]. Roses have long been economically and culturally significant as ornamental plants, sources of essential oils, and traditional medicines, which has stimulated interest in their genetic diversity and evolutionary history [19, 20, 27, 28]. Despite this importance, the phylogenetic relationships within *Rosa* remain incompletely resolved due to several intrinsic challenges. These include frequent interspecific hybridization, extensive polyploidy, low sequence divergence in plastid and nuclear genomes, and the complex taxonomy resulting from morphological plasticity and historical hybridization events [5, 6, 13]. Consequently, traditional classifications based on morphology and chromosome numbers, such as Rehder's system [21] dividing *Rosa* into four subgenera and multiple sections, often do not correspond to phylogenetic lineages supported by molecular data [10, 25].

Chloroplast genome (plastome) analysis has emerged as a powerful tool for resolving phylogenies at different taxonomic levels due to the plastome's generally conserved structure, maternal inheritance, and moderate sequence variation [3, 8, 9, 13, 25]. Recent comparative plastid genome studies across *Rosa* species have identified mutation hotspots and provided insights into gene divergence and species relationships, although comprehensive sampling and analysis across wild taxa remain limited [11, 25]. Notably, plastid phylogenies frequently reveal deep splits corresponding to major subgenera and sections, but fine-scale resolution and disentangling of reticulate evolution require integration with nuclear data [6, 14]. Hybridization and polyploidization significantly shape the evolutionary history of *Rosa*, complicating phylogenetic reconstruction and species delimitation [5, 6, 27]. Studies utilizing nuclear markers alongside chloroplast data reveal frequent reticulate patterns and discordances between plastid and nuclear trees, indicative of historical and ongoing hybridization processes in the genus [14, 16].

These evolutionary processes have also contributed to the complex distribution patterns of species, with Asia playing a central role as a genetic reservoir and a probable source for subsequent dispersals to Europe and North America [6, 9, 10]. In the context of Uzbekistan and Central Asia, four species *Rosa ecae, R. fedtschenkoana, R. kokanica,* and *R. canina* represent valuable components of the regional wild rose flora but have not been extensively studied with modern plastome sequencing techniques (Fig. 1) [1, 7, 11, 25]. Their inclusion in comparative chloroplast genome studies offers an opportunity to elucidate phylogenetic placement, genetic divergence, and biogeographic relationships within the genus. Such research will contribute to resolving the phylogenetic framework of *Rosa*, improve taxonomic clarity, and facilitate conservation and breeding efforts informed by molecular evidence [6, 13].

This study aims to sequence and analyze the complete plastomes of these four *Rosa* species from Uzbekistan and perform comparative genomics with a broader set of *Rosa* plastomes available worldwide. We will investigate plastome structural features, mutation

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hotspots, and phylogenetic relationships, integrating findings with previous plastid data to better understand evolutionary dynamics within the genus.

MATERIALS AND METHODS

In June 2024, fresh leaf material from *Rosa ecae, R. fedtschenkoana, R. kokanica,* and *R. canina* was collected from natural populations growing in the wild in Uzbekistan. Species identification was confirmed by N. Beshko at the National Herbarium of Uzbekistan, and representative voucher specimens were deposited at the National Herbarium of Uzbekistan (TASH). Immediately after collection, the leaves were dried using silica gel and stored at ambient temperature until DNA extraction.

Genomic DNA was extracted from the dried leaf samples using a modified CTAB protocol [8], following the recommended procedure. Whole-genome sequencing was carried out on the Illumina NovaSeq 6000 platform (Illumina Inc, CA, USA), producing 150 bp paired-end reads. Quality control of the raw data, including the removal of low-quality reads and adapter sequences, was performed with Trimmomatic v0.39 [4]. Clean reads were assembled de novo using the GetOrganelle v1.7.5 pipeline [17]. Annotation of the assembled chloroplast genomes was completed using Geneious Prime v2025.1.2 (Biomatters Ltd., Auckland, New Zealand), referencing the *Rosa helenae* chloroplast genome (accession no. MZ261858). All annotations were manually reviewed for accuracy within Geneious Prime. The finalized genome maps were generated using the OGDRAW tool [12].

The boundaries between major regions of the plastomes—the large single-copy (LSC), small single-copy (SSC), and the two inverted repeats (IRs)—were identified and compared across the four *Rosa* species. Junctions between these regions (JLB: LSC/IRb, JSB: SSC/IRb, JSA: SSC/IRa, and JLA: IRa/LSC) were examined and visualized using IRscope [2] along with manual comparisons in Geneious Prime. To analyze genetic variability, complete chloroplast genome sequences were aligned using MAFFT v7.471 [18]. Nucleotide diversity (π) was calculated with DnaSP v6.12.03 [22], and a sliding window analysis (800 bp window with 200 bp step size) was applied to detect hypervariable regions, which may serve as informative molecular markers for species identification and phylogenetic analysis. Comparison of the plastid genomes among four *Rosa* plastomes was made using the progressive Mauve algorithm using the default settings from Mauve v2.4.0.

Phylogenetic reconstruction was based on full chloroplast genome sequences from *Rosa* and closely related genera such as *Potentilla* and *Rubus* (see Appendix). Sequence alignment was carried out using MAFFT v7.520, and phylogenetic trees were built using RAxML v8.2.12 [23] with the GTRGAMMA model and 1,000 bootstrap replicates to assess node support. Four species – *Rubus peltatus*, *Rubus tsangii*, *Potentilla parvifolia*, and *Potentilla lineata* were selected as outgroups.

RESULTS

The chloroplast genomes of 71 representative *Rosa* species shared a conserved quadripartite structure, consisting of a large single-copy (LSC) region, a small single-copy (SSC) region, and two inverted repeat (IR) regions. A schematic representation of the chloroplast genome of *R. kokanica*, used as a representative species, is displayed in Fig. 2. Although the overall

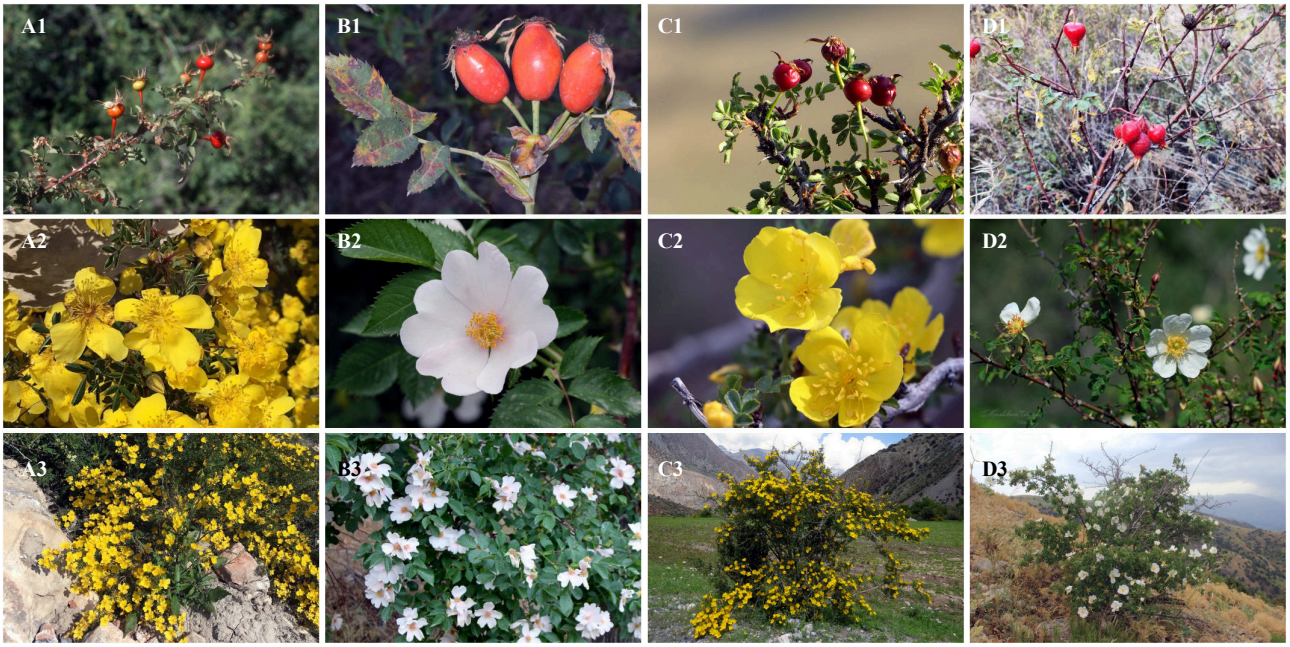

Figure. 1. Photographs of four species of the genus *Rosa* (1- the fruits of the plants, 2- the flowers of the plants, 3- entire plants). **A-** *R. kokanica*, **B-** *R. canina*, **C-** *R. ecae*, **D-** *R. fedtschenkoana*.

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structure was consistent, the total genome length and the sizes of individual regions showed minor variations among species. The chloroplast genome sizes ranged from 156,333 bp in *R. laevigata* to 157,396 bp in *R. minutifolia*. For the four newly sequenced species, the LSC region spanned between 85,640 bp (*R. canina*) and 86,300 bp (*R. fedtschenkoana*), while the SSC region ranges from 18,772 bp (*R. fedtschenkoana*) to 18,841 bp (*R. kokanica*). The size of the IR regions varied slightly, from 26,048 bp in *R. fedtschenkoana* to 26,068 bp in *R. canina*. The GC content remained highly consistent across the 71 species, with values between 37.2% and 37.3% (Table 1). Each *Rosa* plastome contained 114 unique genes, comprising 80 protein-coding genes, 30 transfer RNAs, and 4 ribosomal RNAs (Table 2). These findings are in agreement with previously reported gene content in the genus *Rosa*, reaffirming the conservation of chloroplast gene composition.

The gene order and junction regions in four *Rosa* species (*R. kokanica*, *R. fedtschenkoana*, *R. ecae*, and *R. canina*) appeared highly conserved with only minor differences in boundary lengths, suggesting evolutionary stability within these regions. Notably, genes such as *rpl22*, *rps19*, *rpl2*, and *psbA* were consistently positioned at the junctions of IR and single-copy regions with small variations in their precise locations or sequence lengths (Fig. 3). The sliding window analysis of nucleotide variability (π) across the chloroplast genomes of 71 *Rosa* species reveals regions of high and low sequence divergence. The first half of the genome exhibited higher nucleotide variability and the remaining showed indicative of conserved sequences. A sharp drop to near-zero π values was observed around the second half of the genome, corresponding to a highly conserved locus likely within the IRs, SSC regions, which typically shows reduced variability due to copy correction mechanisms. Higher variability regions appeared in the first half of the genome, potentially highlighting protein coding and non-coding regions there useful for phylogenetic markers (Fig. 4).

The phylogenetic analysis of *Rosa* species based on complete chloroplast genome sequences revealed four major clades (A, B, C, and D), clearly delineating evolutionary relationships within the genus (Fig. 5). Clade A comprised an early diverging species, *R. persica* (NC_045126), which was distinctly separated from all *Rosa* species. Clade B included species such as *R. xanthina, R. ecae, R. omeiensis,* and *R. mairei* supported by high bootstrap values indicating strong phylogenetic affinity. Clade C consisted of species such as *R. graciliflora*, *R. sinobiflora*, *R. glomerata*, and others, forming a well-supported group with internal subdivisions reflecting close genetic relationships. Clade D encompassed the largest and

Table 1. Genomic features of the complete chloroplast sequences from four *Rosa* species

Taxon	Total length (bp)	LSC (bp)	SSC (bp)	GC of LSC (%)	GC of SSC (%)	GC of IR (%)	Total number of genes	Total number of protein-coding genes	tRNA	rRNA
R. kokanica	157,231	86,260	18,841	35.2	31	42.7	132	87	37	8
R. fedtschenkoana	157,168	86,300	18,772	35.2	31	42.7	132	87	37	8
R. ecae	157,215	86,253	18,830	35.2	31	42.7	132	87	37	8
R. canina	156,613	85,640	18,837	35.2	31	42.7	132	87	37	8

Table 2. Genes identified in the chloroplast genomes of four *Rosa* species. [a] Genes containing introns. [b] Genes duplicated in the inverted repeat (IR) regions.

Category of genes	Name of genes
Genes for photosynthesis (PS)	
Subunits of ATP synthase (ATP)	*atpI, atpF, atpA, atpH, atpB, atpE*
Subunits of cytochrome b/f complex (PET)	*petL, petA, petD*[a]*, petN, petG, petB*[b]
Subunits of photosystem I (PSA)	*psaC, psaJ, psaA, psaI, psaB*
Subunits of photosystem II (PSB)	*psbE, psbM, psbN, psbT, psbF, psbK, psbZ, psbJ, ycf3*[a]*, psbD, psbL, psbA, psbI, psbC, psbB*
Subunits of NADH-dehydrogenase (NDH)	*ndhF, ndhC, ndhK, ndhB*[ab]*, ndhH, ndhE, ndhA*[a]*, ndhG, ndhD, ndhI, ndhJ*
Subunit of rubisco (RBC)	*rbcL*
Genes for self-replication (SR)	
Large subunit of ribosome (RPL)	*rpl36, rpl2*[ab]*, rpl22, rpl14, rpl33, rpl16*[a]*, rpl20, rpl32, rpl23*[b]
DNA-dependent RNA polymerase (RPO)	*rpoB, rpoC2, rpoA, rpoC1*[a]
Small subunit of ribosome (RPS)	*rps19, rps7*[b]*, rps3, rps15, rps4, rps14, rps2, rps11, rps16*[a]*, rps8, rps12*[ab]*, rps18*
Other genes (OG)	
Subunit of Acetyl-CoA-carboxylase (ACC)	*accD*
c-type cytochrome synthesis gene (CCS)	*ccsA*
Envelop membrane protein (CEM)	*cemA*
Protease (CLP)	*clpP*[a]
Maturase (MAT)	*matK*
Conserved open reading frames (ORFs)	*orf188, orf42b, ycf4, ycf2*[b]*, ycf1*
RNA genes	
Ribosomal RNA genes	*rrn4.5*[b]*, rrn5*[b]*, rrn16*[b]*, rrn23*[b]
Transfer RNA genes	*trnS-GCU, trnY-GUA, trnR-ACG*[b]*, trnD-GUC, trnL-CAA*[b]*, trnF-GAA, trnV-GAC*[b]*, trnP-UGG, trnL-UAG, trnG-UCC, trnI-GAU*[ab]*, trnT-UGU, trnQ-UUG, trnT-GGU*[b]*, trnL-UAA*[a]*, trnW-CCA, trnS-UGA, trnK-UUU*[a]*, trnE-UUC, trnM-CAU, trnI-CAU*[b]*, trnC-GCA, trnH-GUG, trnA-UGC*[ab]*, trnR-UCU, trnS-GGA, trnV-UAC*[a]*, trnfM-CAU, trnG-GCC, trnN-GUU*[b]

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most diverse group of species, including *R. persica*, *R. sericea*, *R. fedtschenkoana*, *R. chinensis*, *R. multiflora*, and *R. maximowiczii*, among others. This clade exhibited significant internal structure with several robustly supported subclades, highlighting detailed evolutionary divergences within the genus. The high bootstrap support values (mostly above 83%) across the majority of nodes indicate strong confidence in the inferred phylogenetic relationships. Overall, the phylogenetic tree confirmed the monophyly of *Rosa* and provided a refined framework for understanding the evolutionary history and species relationships within this important genus (Fig. 5).

DISCUSSION

The chloroplast genomes of *Rosa* species analyzed in this study demonstrate the conserved quadripartite structure typical of angiosperms, comprising the LSC, SSC, and two IR regions, consistent with previous reports across the genus and the broader Rosaceae family [11, 15, 25]. The conserved gene content, order, and GC content substantiate plastome structural stability in *Rosa* (Fig. 2), likely reflecting evolutionary constraints that preserve essential photosynthetic and housekeeping functions [24, 25]. Comparative analysis of IR/SC junctions among four *Rosa* species revealed minimal expansions and contractions, consistent with other Rosaceae plastomes, indicating that IR boundary shifts are subtle evolutionary mechanisms influencing plastome size variation without disrupting core gene architecture [11, 25]. Such stability supports the use of whole plastome sequences for robust phylogenetic inference, overcoming limitations posed by low variation in individual loci.

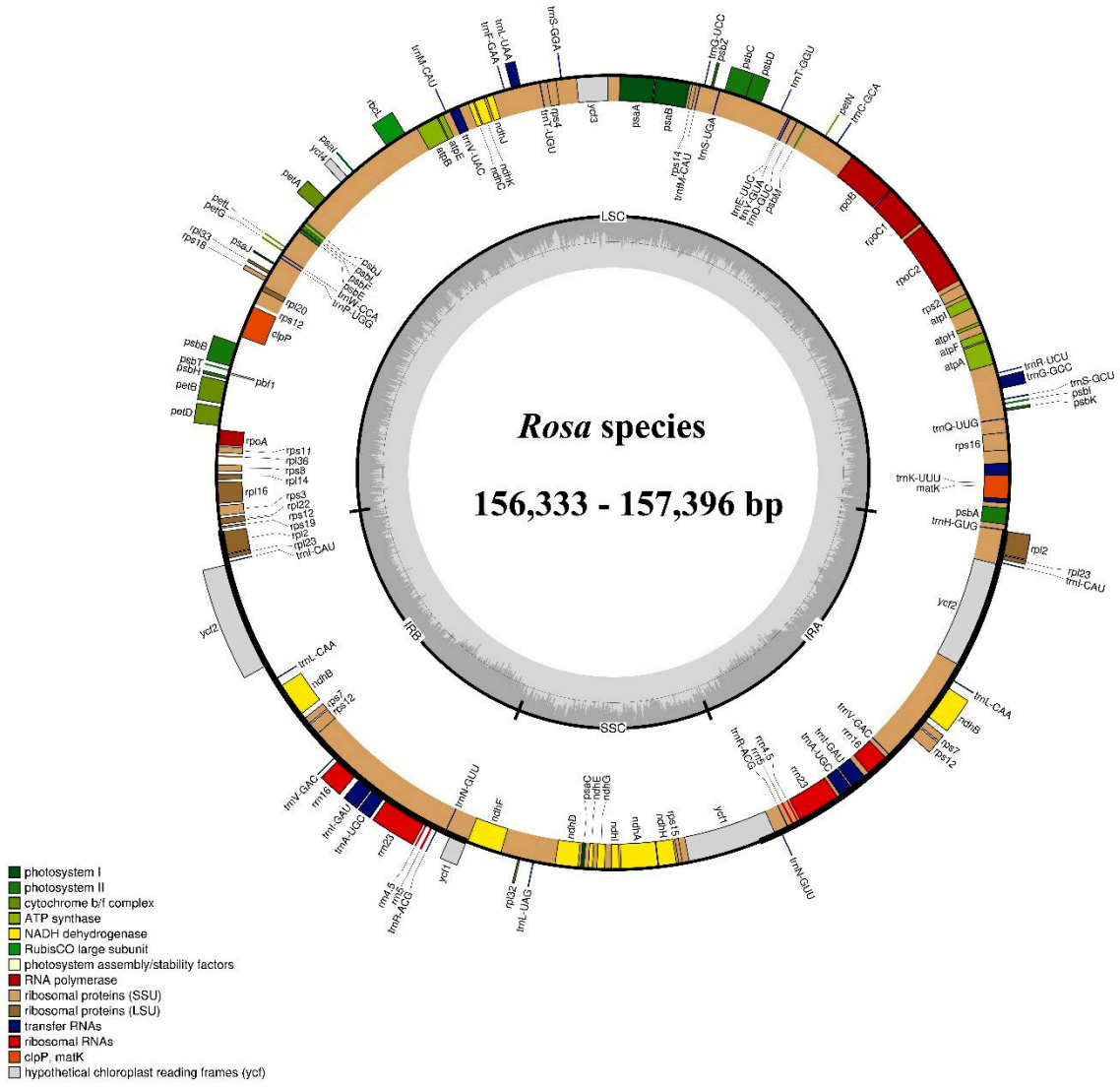

Figure 2. Gene map of the *Rosa* plastome. Genes located on the inside of the circular map are transcribed in the clockwise direction, while those on the outside are transcribed counterclockwise. Genes are color-coded based on their functional categories. The inner circle displays GC content in dark gray and AT content in light gray. Abbreviations: LSC – large single-copy region; SSC – small single-copy region; IRA/B – inverted repeat regions A and B.

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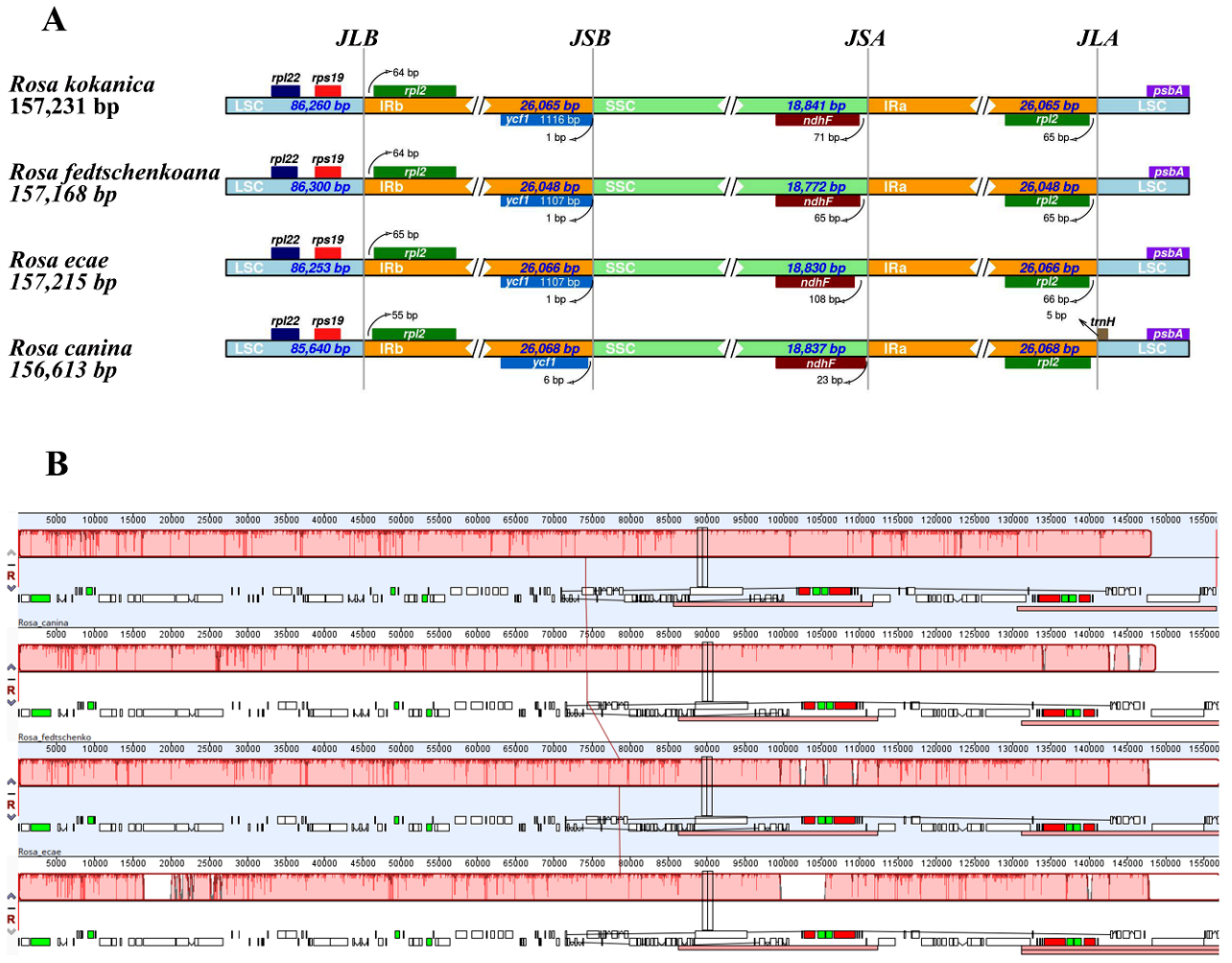

Figure 3. Comparative analysis of four *Rosa* chloroplast genomes. (a) Examination of the junctions between the large single-copy (LSC), inverted repeat (IR), and small single-copy (SSC) regions across four *Rosa* chloroplast genomes. Colored boxes represent the genes located at these border regions. (b) Collinearity analysis of the *Rosa* chloroplast genomes. Local collinear blocks (LCBs) are highlighted in different colors to represent conserved regions. The internal histograms within each block show the level of sequence similarity. The visualizations were generated using IRscope and Mauve.

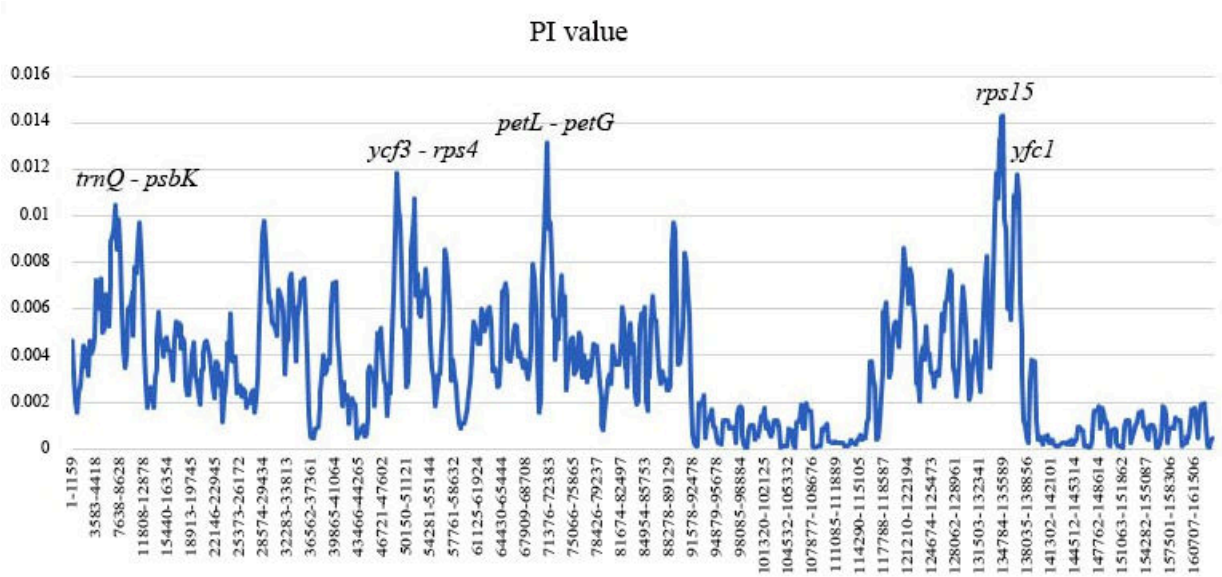

Figure 4. The nucleotide variability (Pi value) of the genomes the genus *Rosa* of the presented in a sliding window (window length: 800 bp; step size: 200 bp)

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Nucleotide variability profiling ighlights several highly polymorphic regions, notably intergenic spacers and coding regions in the LSC region, which correspond well with previously identified divergence hotspots in *Rosa* and related taxa [11, 25] (Fig. 4). These hotspots represent promising candidates for molecular marker development, critical for resolving the notoriously complex taxonomy and phylogeography of *Rosa* species complexes [15, 27].

The tree topology clearly separates the four major *Rosa* subgenera — *Hulthemia*, *Hesperrhodos*, *Platyrhodon*, and *Rosa* — in agreement with classical taxonomy (21; 5). The subgenus *Rosa* itself exhibits extensive diversification across sections such as *Synstylae, Chinenses, Cinnamomeae*, and *Pimpinelli foliae*, highlighting the complex reticulate evolution within the genus. As demonstrated in previous plastome and nuclear studies (28; 14; 15), these groups often fail to form clean, monophyletic units, and our tree corroborates this pattern: species of the sections *Synstylae* and *Cinnamomeae* are scattered across multiple clades, indicating para- or polyphyly. This pattern corroborates plastome-based studies showing that chloroplast genome variation often fails to fully capture hybridization events, leading to partial incongruence between plastid and nuclear phylogenies (28; 14; 15). It also contradicts earlier multilocus analyses, thereby validating subgenus *Hesperrhodos* as one of the earliest divergent lineages (6; 10; 22). In our analysis, the subgenus *Hulthemia* (*R. persica*

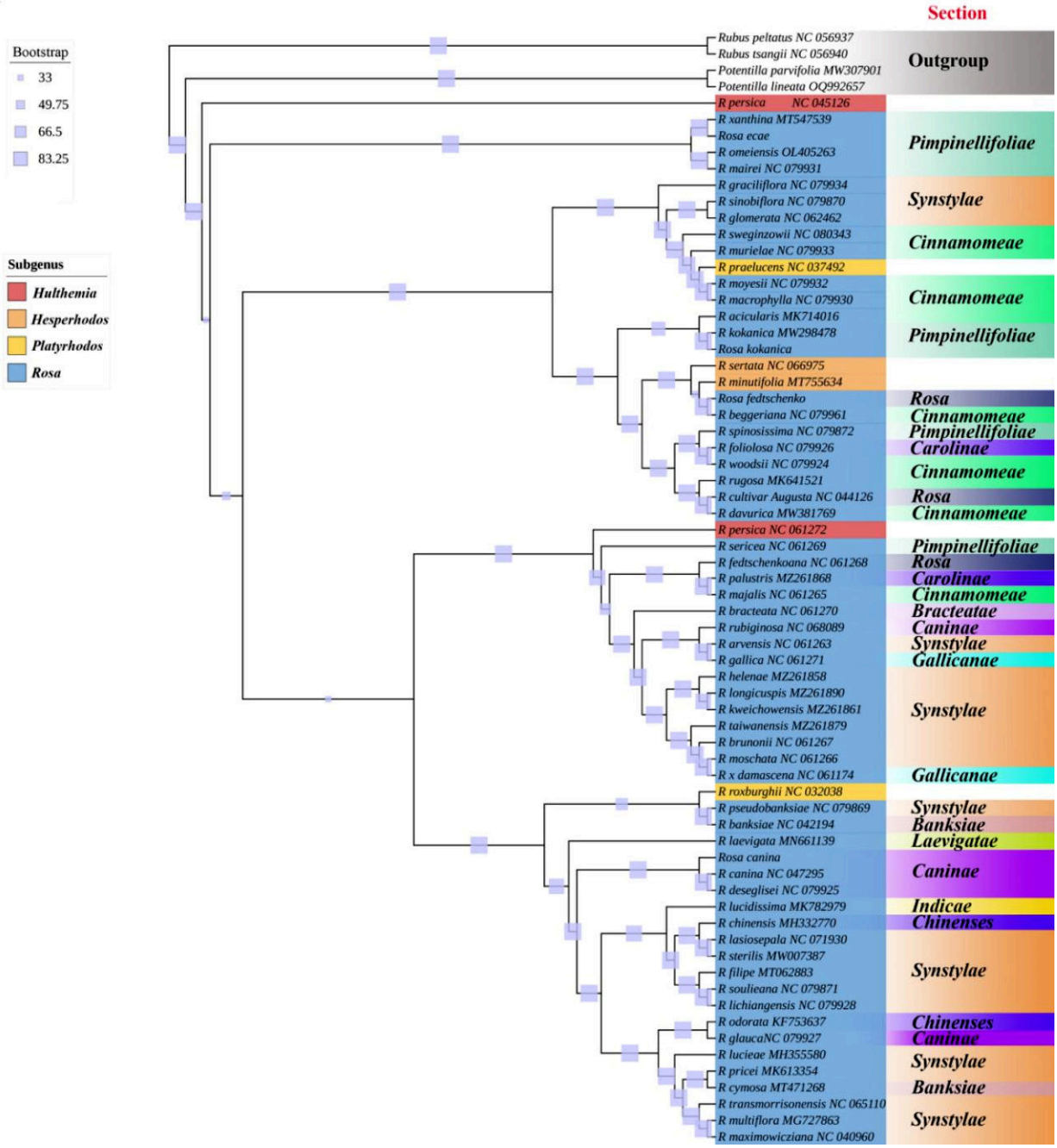

Figure 5. Phylogenetic tree of the species of the genus *Rosa* based on the whole chloroplast genome using maximum likelihood (ML). Maximum support values are indicated at the nodes. “label” on the left side above means bootstrap support.

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NC045126) occupies the basal position of the phylogenetic tree, followed by the subgenus *Rosa* (section *Pimpinellifoliae*). The two accessions of *Rosa persica* do not cluster together, indicating a likely issue with one of the samples. The sample with NC_045126 falls in the expected basal *Hulthemia* position, consistent with its well-established phylogenetic distinctiveness. In contrast, NC_061272 is placed deep within subgenus *Rosa*, a position incompatible with the morphology and known chloroplast lineage of *R. persica*. This incongruence suggests possible misidentification, plastome assembly error, or contamination in NC_061272. Therefore, NC_045126 should be considered the reliable accession, while NC_061272 requires independent verification.

Hybridization is a well-documented and significant evolutionary driver in *Rosa*, complicating taxonomy and species delimitation [6, 27]. The plastid genome, maternally inherited, offers a valuable but partial view of species histories; thus, integrating nuclear markers and genome-wide data is critical to accurately capture hybridization and polyploidy signals [6, 15]. The presence of reticulation demands careful interpretation of phylogenies and cautions against relying solely on plastome data for inferring species boundaries or evolutionary relationships.

Overall, the comparative plastome approach advances our understanding of *Rosa* evolution by providing high-resolution genomic data that support and refine previous taxonomic and phylogenetic frameworks [5, 11, 25]. The identification of mutation hotspots enhances marker development for conservation genetics and breeding applications, especially in economically important cultivated and wild roses [15, 27]. However, given the complex evolutionary history involving extensive hybridization and polyploidy, multilocus and population genomic studies integrating nuclear data (low-copy nuclear genes) remain essential for resolving outstanding phylogenetic uncertainties and informing taxonomy.

Future studies should prioritize expanded taxon sampling across the genus *Rosa* and the generation of genome-wide nuclear datasets, such as low-copy nuclear genes, RAD-seq, or whole-genome resequencing. Integrating these nuclear data with plastid genomes will allow robust phylogenetic reconstruction using coalescent-based species tree methods and admixture analyses, helping to disentangle the effects of hybridization, introgression, and polyploidy. Detailed population-level analyses will further clarify evolutionary relationships and genetic structure within and between species. Such integrative approaches will not only resolve outstanding phylogenetic uncertainties and improve taxonomic resolution but also support conservation strategies for endangered wild relatives and guide the genetic improvement of cultivated varieties.

Supplementary table 1. NCBI accession numbers of the species of the genus *Rosa* and outgroups.

No.	Species name	NCBI accession Number
1.	*Rosa acicularis*	MK714016
2.	*Rosa arvensis*	NC_061263
3.	*Rosa banksiae*	NC_042194
4.	*Rosa beggeriana*	NC_079961
5.	*Rosa berberifolia*	NC_045126
6.	*Rosa bracteata*	NC_061270
7.	*Rosa brunonii*	NC_061267
8.	*Rosa canina*	NC_047295
9.	*Rosa chinensis*	MH332770
10.	*Rosa cymosa*	MT471268
11.	*Rosa davurica*	MW381769
12.	*Rosa deseglisei*	NC_079925
13.	*Rosa fedtschenkoana*	NC_061268
14.	*Rosa filipe*	MT062883
15.	*Rosa foliolosa*	NC_079926
16.	*Rosa gallica*	NC_061271
17.	*Rosa glauca*	NC_079927
18.	*Rosa glomerata*	NC_062462
19.	*Rosa graciliflora*	NC_079934
20.	*Rosa helenae*	MZ261858
21.	*Rosa* 'Augusta'	NC_044126
22.	*Rosa kokanica*	MW298478
23.	*Rosa kokanica*	NC_060339
24.	*Rosa kweichowensis*	MZ261861
25.	*Rosa laevigata*	MN661139
26.	*Rosa lasiosepala*	NC_071930
27.	*Rosa lichiangensis*	NC_079928
28.	*Rosa longicuspis*	MZ261890
29.	*Rosa lucidissima*	MK782979
30.	*Rosa lucieae*	MH355580
31.	*Rosa macrophylla*	NC_079930
32.	*Rosa mairei*	NC_079931
33.	*Rosa majalis*	NC_061265
34.	*Rosa maximowicziana*	NC_040960
35.	*Rosa minutifolia*	MT755634
36.	*Rosa moschata*	NC_061266
37.	*Rosa moyesii*	NC_079932
38.	*Rosa multiflora*	MG727863
39.	*Rosa murielae*	NC_079933
40.	*Rosa omeiensis*	OL405263
41.	*Rosa palustris*	MZ261868
42.	*Rosa persica*	NC_061272
43.	*Rosa praelucens*	NC_037492
44.	*Rosa pricei*	MK613354
45.	*Rosa pseudobanksiae*	NC_079869
46.	*Rosa roxburghii*	NC_032038
47.	*Rosa rubiginosa*	NC_068089
48.	*Rosa rugosa*	MK641521
49.	*Rosa sericea*	NC_061269
50.	*Rosa sertata*	NC_066975
51.	*Rosa sinobiflora*	NC_079870
52.	*Rosa soulieana*	NC_079871
53.	*Rosa spinosissima*	NC_079872
54.	*Rosa sterilis*	MW007387
55.	*Rosa sweginzowii*	NC_080343
56.	*Rosa taiwanensis*	MZ261879
57.	*Rosa transmorrisonensis*	NC_065110
58.	*Rosa woodsii*	NC_079924
59.	*Rosa* × *damascena*	NC_061174
60.	*Rosa xanthina*	MT547539
61.	*Rosa ecae*	PV786059
62.	*Rosa fedtschenkoana*	PV786060
63.	*Rosa kokanica*	PV786061
64.	*Rosa canina*	PV786058
65.	*Rubus peltatus*	NC_056937
66.	*Rubus tsangii*	NC_056940
67.	*Potentilla parvifolia*	MW307901
68.	*Potentilla lineata*	OQ992657

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Conflict of interest. There is no actual or potential conflict of interest in relation to this article.

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